TREATISE ON
INVERTEBRATE PALEONTOLOGY

Part H
BRACHIOPODA
Revised

Volume 6:
Supplement

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, RÉMY 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, CARSTEN LÜTER,
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

PAUL A. SELDEN
Editor

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

THE GEOLOGICAL SOCIETY OF AMERICA, INC.
and
THE UNIVERSITY OF KANSAS
BOULDER, COLORADO, and LAWRENCE, KANSAS
2007

Library of Congress Catalogue Card Number 53-12913
ISBN 978-0-8137-3136-0

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

Citation information: Selden, P. A., ed. 2007. Treatise on Invertebrate Paleontology. Part H, Brachiopoda, Revised, vol. 6. Geological Society of America & Paleontological Institute. Boulder, Colorado, & Lawrence, Kansas. l + 906 p., 461 fig., 38 tables.

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

PART H, Revised

BRACHIOPODA

VOLUME 6:
Supplement

Alwyn Williams, C. H. C. Brunton, S. J. Carlson, Fernando Alvarez, P. G. Baker, M. G. Bassett, A. J. Boucot, J. L. Carter, L. R. M. Cocks, B. L. Cohen, G. B. Curry, Maggie Cusack, C. C. Emig, Rémy Gourvennec, D. A. T. Harper, L. E. Holmer, D. E. Lee, Alan Logan, Carsten Lüter, D. I. MacKinnon, M. O. Manceñido, Michal Mergl, L. E. Popov, P. R. Racheboeuf, Madis Rubel, N. M. Savage, T. N. Smirnova, Sun Dong-li, and A. D. Wright

CONTENTS

INFORMATION ON TREATISE VOLUMES

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

PUBLISHED VOLUMES

Part A. INTRODUCTION: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.

Part B. PROTOCTISTA 1 (Charophyta), xvi + 170 p., 79 fig., 9 tables, 2005.

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 (Demospongea, Hexactinellida, Heteractinida, Calcarea), xxxi + 872 p., 506 fig., 1 table, 2004.

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 I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 216 fig., 1960.

Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 361 fig., 1964.

Part L. MOLLUSCA 4 (Cephalopoda: Ammonoidea), xxii + 490 p., 558 fig., 1957.

Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 216 fig., 1996.

Part N. MOLLUSCA 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 613 fig., 1969; 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 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 H, Revised. BRACHIOPODA, Volume 6 (Supplement), l + 906 p., 461 fig., 38 tables, CD of compiled references from volumes 1–6, 2007.

VOLUMES IN PREPARATION

Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Diatomacea, etc.).

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 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).

Part V, Revised. GRAPTOLITHINA.

Part W, Revised. TRACE FOSSILS.

EDITORIAL PREFACE

PAUL A. SELDEN
[The University of Kansas]

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part H, Revised, Brachiopoda, Volume 6, has been prepared by such a team of specialists whose work prior to April 2004 was coordinated by Sir Alwyn Williams at The University of Glasgow. Subsequent coordination of this volume has been handled jointly by Dr. Howard Brunton (retired, formerly at the British Museum, Natural History) and Dr. Sandy Carlson at the University of California (Davis). Editorial matters specific to this volume are discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1999 in the *International Code of Zoological Nomenclature,* hereinafter referred to as the *Code,* provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code;* but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, revised the *Code* in 1999 to enhance further nomenclatorial stability, specifying that the revised *Code* should take effect at the start of 2000. Among other requirements, the revised *Code* is clear in Chapter 14 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 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 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 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 13.1), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code,* Article 13.2). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

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

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

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

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

GENUS-GROUP NAMES

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

As has been pointed out above, difficulty typically arises when one tries to decide whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has to be made often arbitrarily.

FAMILY-GROUP NAMES

Family-Group Names: Authorship and Date

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

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

Family-Group Names: Use of *nomen translatum*

The *Code* (Article 29.2) specifies the suffixes for tribe (-ini), subfamily (-inae), family (-idea) and superfamily (-oidea), the formerly widely used ending (-acea) for superfamily having been disallowed. All these family-group categories are defined as coordinate (*Code*, Article 36.1): "A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stemof 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 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 all family-group categories, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code,* Article 39), in which case ". . . it must be replaced either by the next oldest available name from among its synonyms [Art. 23.3.5], including the names of its subordinate family-group taxa, or, if there is no such synonym, by a new name based on the valid name . . . of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code,* however, specifies that for subsequent application of the rule of priority, the family-group name ". . . should be cited with its original author and date (see Recommendation 22A.2.2), followed by the date of its priority as determined by this Article; the date of priority should be enclosed in parentheses." Many family-group names that have been in use for a long time are *nomina nuda,* since they fail to satisfy criteria of availability (*Code,* Article 11.7). These demand replacement by valid names.

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

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

SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to kingdom) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on 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 -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 33.1 and Glossary) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *emend.* then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend.* with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered nomenclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the *Treatise* are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation *emend.* with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

Order ORTHIDA Schuchert & Cooper, 1932

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

Subfamily ROVEACRININAE Peck, 1943

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

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

In the *Treatise* the name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (*), with notation of the author, date, and page of original publication, except if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type. In this instance, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

Orionastraea Smith, 1917, p. 294 [**Sarcinula phillipsi* McCoy, 1849, p. 125; OD].

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

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

Actinocyathus d'Orbigny, 1849, p. 12 [**Cyathophyllum crenulate* Phillips, 1836, p. 202; M; =*Lonsdaleia floriformis* (Martin), 1809, pl. 43; validated by ICZN Opinion 419].

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

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

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication 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.

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

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

OTHER EDITORIAL MATTERS

BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as U.S.S.R., Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

Special considerations are necessary when referring to parts of the former Soviet Union. To some authors the term Central Asia, referring to Uzbekistan, Turkmenistan, Tadzhikistan, Kirgizistan, and sometimes all or part of Kazakhstan, has a distinct meaning from the less formal term central Asia, which is used more widely in the West. Accordingly, we have attempted to substitute the Russian term *Srednii Azii* to refer to Central Asia, as opposed to central Asia. Unfortunately, we are by no means certain that we have been fully consistent in this usage throughout the volume.

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

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a

Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, has been spelled more recently Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the roman spelling that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

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

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

MATTERS SPECIFIC TO THIS VOLUME

False cognates are the bane of inexperienced translators. The transliterated Russian term *gorizont*, usually translated *horizon*, is one such false cognate. The term horizon, of course, has no formal status in stratigraphic nomenclature and, in fact, should be used to refer to a surface and not to a thickness of strata. Thus, fossils cannot occur in a horizon, but their ranges may begin or end at a horizon. In some places we have translated *gorizont* as *beds*; in others, where *beds* is not an adequate usage, we have translated it as *stage*.

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 ranges of taxa have been compiled from the ranges of lower taxa. In all instances, we have used the *range-through* method of describing ranges. In instances, therefore, where the work of paleontology is not yet finished, some ranges of higher taxa will not show gaps between the ranges of their subtaxa and may seem to be more complete than the data warrant. Stratigraphic range charts typical of previous *Treatise* volumes will present a much more precise picture of the biostratigraphy of the brachiopods. The range chart for this revision on the Brachiopoda will be presented in the final volume of the series.

This volume breaks new ground for the *Treatise* series in that color is used for the first time. The stratigraphic charts (Curry, p. 2901–2965) would have been effectively unreadable without it. Also, this volume being the last in the part, we have taken the opportunity to present the reference list for all the Brachiopoda volumes in digital format on compact disk and hope that this will be useful to readers.

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Jill Hardesty, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task

of moving this volume through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team including Mike Cormack with his outstanding computer skills, Denise Mayse with her work on illustrations and general support, and Sounithta Vilayvanh with her work on illustrations. The editorial team would also like to extend special thanks to Dr. Albert J. Rowell for his support and help with various taxonomic and manuscript issues and to Dr. Stephen T. Hasiotis and Dr. Bruce S. Lieberman for their support and guidance.

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. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Finally, on behalf of the members of the staff of the Paleontological Institute, both past and present, it is my privilege to honor the memory of the late Sir Alwyn Williams by expressing gratitude for the unwavering scholarship, dedication to the task, and scrupulous attention to detail that marked his involvement with this project from the outset and, indeed, throughout his entire career as a specialist on the Brachiopoda.

REFERENCES

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature. London. 306 p.

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

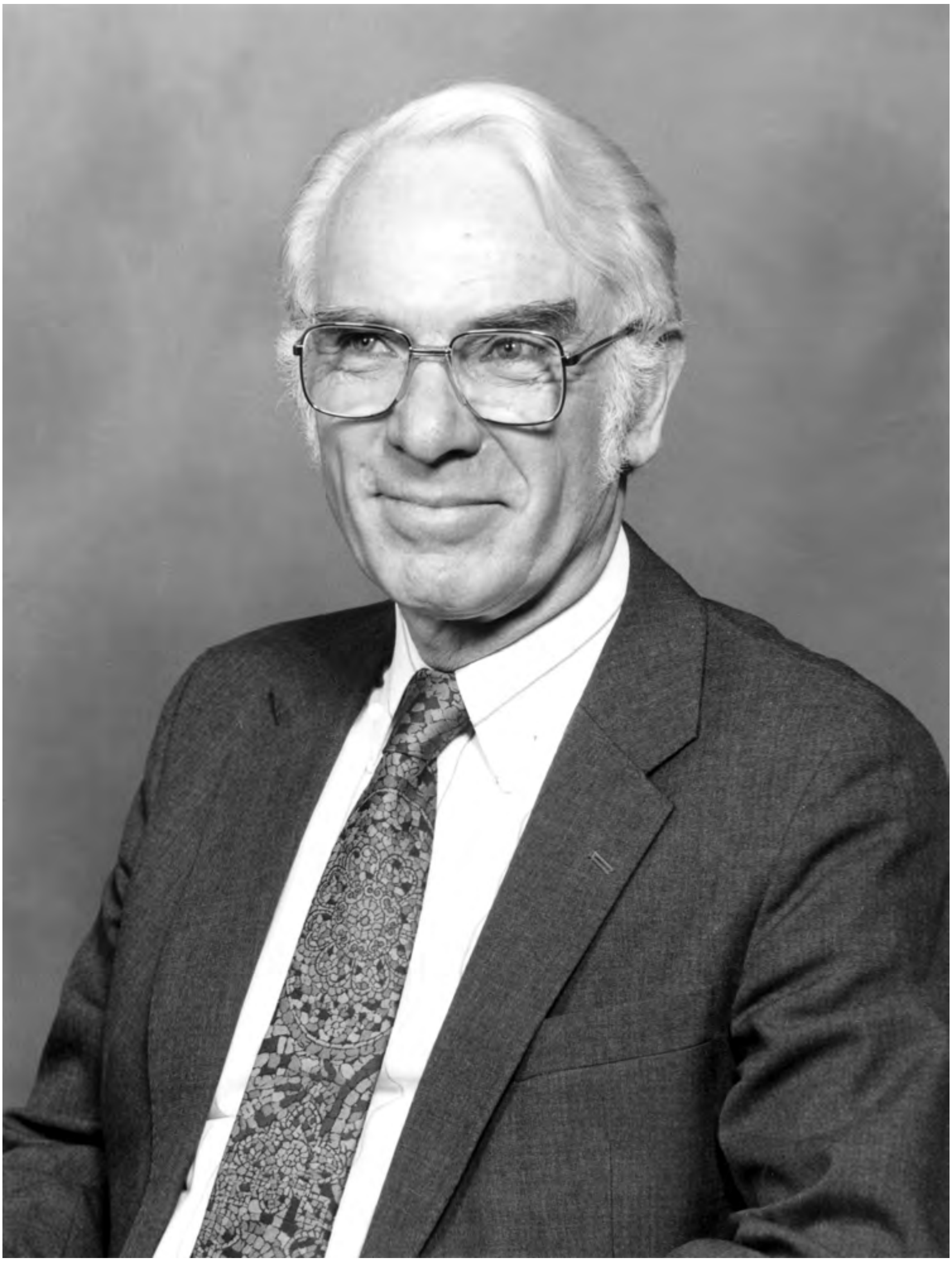
Robison, R. A., and C. Teichert. 1979. Treatise on Invertebrate Paleontology. Part A, Introduction. The Geological Society of America and The University of Kansas. Boulder & Lawrence. 569 p.

Paul A. Selden
Lawrence, Kansas
August 17, 2007

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (*e.g.,* subseries, stages, and substages) are more likely to be provincial in application. The stratigraphical units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to the 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. An updated time scale was published by the IUGS and UNESCO in 2000.

- **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)
    - Viséan Series
    - Tournaisian Series
- **Devonian System**
  - Upper Devonian Series
  - Middle Devonian Series
  - Lower Devonian Series
- **Silurian System**
  - Prídolí 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**
  - Upper Cambrian Series
  - Middle Cambrian Series
  - Lower Cambrian Series



Sir Alwyn Williams, 8 June 1921–4 April 2004. World renowned brachiopod specialist and coauthor for the two-volume brachiopod *Treatise*, 1965, and coordinating author for the revision volumes from 1988 until his death in 2004 (photo dated 1983, courtesy of Mrs. Joan Williams).

COORDINATING AUTHORS' PREFACE

C. Howard C. Brunton and Sandra J. Carlson

[retired, formerly of the Natural History Museum, London; and University of California, Davis]

[with contributions by A. J. (Bert) Rowell, Professor Emeritus, The University of Kansas, Lawrence]

This volume completes the revision of the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda.* It has developed from the concept of a simple supplement covering the latest taxa to a volume with much new information in its own right. The review chapters, forming the first part of the volume, bring up to date many topics concerning brachiopods. The first chapter by Lüter brings up to date recent work on the anatomy and particularly embryology of brachiopods. Studies of larval and early developmental stages in brachiopod ontogeny is leading to an improved understanding of phylogeny, general relationships, and the working brachiopod organism. Cohen provides an update of the research on the genome of brachiopods, which suggests that Phoronida may be nested within the Brachiopoda, rather than present as its sister group. The chapter by Williams and Carlson summarizes evolutionary trends in morphology and discusses the phylogenetic affinities of brachiopods among metazoans. Carlson's chapter, to be read in conjunction, provides a more recent update of these issues.

The shell chemicostructure chapter by Williams and Cusack discusses the unexpected and exciting discovery of siliceous tablets covering the surface of the first-formed organophosphatic shells of *Discinisca*. These tablets were predicted by Williams, Lüter, and Cusack (2001) a few years before Lüter (2004) demonstrated their existence through TEM and SEM studies. In addition a chapter by Cusack and Williams reviews biochemical diversity, and another short chapter by Parkinson and Cusack focuses on the interpretation and use of oxygen isotopes.

The chapter on the stratigraphical distribution of brachiopods through time, by Curry and Brunton, was introduced in the Preface to Volume 5 (Kaesler, 2006, p. xxix). Here the subject is developed further with a description of the technique used by Curry, brief discussions on the resulting distribution charts, and the publication of many of the charts derived from the *Treatise* data. Logan discusses, tabulates, and maps the distribution of extant articulated brachiopods in a separate chapter.

The second part of the volume is devoted to bringing up to date the record of newly described genera and other taxa described from the closing dates for each volume until September 2004. Those published since that date are listed here with author, date, and references, allowing readers to locate the newest descriptions of brachiopods. Thus the genera recorded herein amount to 380, making a total for the revised *Treatise* of 4322 genera described in the series, as compared to almost 1700 in the 1965 edition of the *Treatise.* All described genera, other than those with questionable age, locality, or classification, are included in the review chapter on stratigraphical distribution through time. We also include a list of errata found in previous volumes and submitted by our contributors and a comprehensive index from all six volumes.

Publication of this volume represents the final major achievement for Sir Alwyn Williams, who played a pivotal role as leading coordinator in the revision of these six *Treatise* volumes. He looked upon the *Treatise* revision as his most important job over the past 20 years, and he looked forward earnestly to seeing the job completed. Although he set completion well on its way, sadly he was denied the ultimate pleasure of seeing the full series published. His enormous contributions to international paleontology are partly reflected in his publication list. The breadth of subject material he covered and the novelty of approach he brought to bear on the study of brachiopods was both exceptional and unique. His remarkably broad experience with brachiopods, genial personality, and expert administrative abilities made him the ideal choice as coordinator for the first brachiopod *Treatise* (1965), and he rose to the occasion again 25 years later when asked to take on the full revision. Until his death in 2004, he shepherded the revision forward; by 2004 the path was well charted, and authors knew what was required to complete the remaining volumes.

The *Treatise* office, under the invaluable guidance of Roger L. Kaesler at the Paleontological Institute, University of Kansas, recognizes the enormous importance of Alwyn Williams in this revision. A. J. (Bert) Rowell, who assisted as a co-author of several chapters and wrote the systematic section on the Inarticulata in the first edition (1965), contributes the following acknowledgment to Alwyn's extraordinary efforts, with help from Jill Hardesty, Managing Editor at the Paleontological Institute.

Much has changed in the world in general and brachiopods in particular between the two editions of the *Treatise on Invertebrate Paleontology, Part H, Brachiopoda.* Some 19 authors were responsible for just under 1700 genera in the first edition, which was printed by linotype in two volumes in 1965. The six-volume revision has involved just over twice as many authors to cover nearly three times as many genera. Linotype is almost as extinct as the Productida and a few authors' names are common to both editions, but the most notable common factor other than topic and format is the hand of Alwyn Williams as overall coordinator of both editions.

At least from 1959, when Rowell joined the team of authors for the first edition, Williams coordinated the work with a very light rein. Subsequent to dividing the work into major chapters and assigning authors, coordination was more the product of cooperation between colleagues, many of whom were friends, rather than the result of a complex and ongoing planning process. When Williams and Rowell wrote the general chapters on brachiopod anatomy, morphology, evolution and phylogeny, and classification, they did so literally sitting side by side. They had both prepared draft text and draft illustrations of agreed-upon sections, Rowell working in Nottingham and Williams in Belfast. On two occasions between academic terms in 1961, Rowell, lacking administrative responsibilities, traveled to Belfast and lived in the Williams' household for several days. The authors spliced their contributions together, cutting and pasting sections, and where appropriate, writing and rewriting connective paragraphs and sentences. A day's work would be retyped the following day and commonly edited by the authors on the evening of the same day. Further polishing of text and refinement of figures was accomplished separately in Nottingham and Belfast before the final retyped version was mailed to Kansas. Individual systematic contributions were mailed directly to Kansas by the authors, who were asked to follow format instructions that were provided in a blue spiral-bound *Manual for Authors* by R. C. Moore himself! In the majority of cases, individual authors of systematic sections also provided photographs of specimens from which the final figures were assembled and labelled by illustrator Roger Williams in Kansas. Proof copy was available to contributors several months before the final version was printed and bound.

The need for a revision of the brachiopod *Treatise* was broached at the First Brachiopod Congress in Brest in 1985. The concept was accepted by the *Treatise* Advisory Board, and by late 1986, Editor Roger Kaesler had recruited Alwyn Williams to be coordinating author of the revision. Williams accepted the invitation on the understanding that he would be unable to commence work on the revision until October 1988, by which time he, Williams, would have stepped down from his position as Principal of the University of Glasgow and completed obligations as president of the Royal Society of Edinburgh. Kaesler and Williams met in Scotland in the summer of 1988, and by the end of the year, Williams had submitted a draft list of contents, provisional authors of the various chapters, and a very optimistic projection of publication in 1994.

What followed in the next few months revealed clearly the effects and experience of many years of senior-level management on Williams' administrative style. He recognized early that he was not immune to the passage of time and appointed Howard Brunton as his deputy coordinating author. This action was shortly followed by a list of 20 or so authors with suggested responsibilities, which Kaesler sent out to 4 experienced brachiopod workers for review. A few of the 20 potential authors had to decline because of prior long-term commitments or ill health, but by the middle of 1989, a group of authors, subsequently called senior authors with responsibility to produce copy for major sections of the text, had agreed to be involved in the revision and to provide an annual progress report.

At the turn of 1989, Williams and Brunton distributed a tentative glossary of morphological terms to all authors with the intention that it be discussed at the Second International Brachiopod Congress in Dunedin in February 1990. This glossary, accompanied by a circular letter, provided a brief synopsis of the state of progress of revised Part H and listed all authors and their assignments. The circular also introduced the possibility of senior authors co-opting junior contributors under appropriate circumstances and, furthermore, promised all contributors full minutes of the *Treatise* discussion session at Dunedin.

Such activity was typical of Williams' approach: he would expect much of those who worked with him but would do his utmost to ensure all were kept informed of overall progress and afford a platform for all voices to be heard. His subsequent guidance of the project was intense, and correspondence between Williams and the *Treatise* office in the intervening years now amounts to a 30-cm-tall stack!

Within a few days of completion of the Dunedin meeting, the fourth circular appeared and gave the first indication of the possibility of utilizing a cladistically based classification of major taxa in the revised Part H. Because of the possibility of using a cladistic approach to the classification, Sandy Carlson was invited to join the coordinating team in 1992. All senior authors were then asked to submit an exhaustive list of characters used in classifying taxa within their assignments. This request was repeated in the seventh circular letter of June 1990 together with a reminder of the need for authors to submit their annual report of progress. Circular letters and annual reports became a feature of Williams' style: he wrote 47 of the former and issued Annual Reports that covered the years from 1989–2003.

By mid-1992, Williams had appointed Carlson to handle the more derived brachiopod groups, pentamerides through terebratulides, and to help with the overall cladistic revision of the phylum. This self-inflicted task of producing a new higher-level classification of the Brachiopoda Williams regarded as the most important duty of his position as coordinating author. The plan he implemented with Brunton and Carlson was to develop a supraordinal classification, and he, as coordinating author of the revised Part H, would insert text received from senior authors, typically covering orders and subordinate taxa, into this new framework. Senior authors would have the opportunity to discuss this taxonomic placement in their own introductory sections.

The new classification appeared in 1996 (WILLIAMS & others, 1996), and reprints were made available to all senior authors. The classification has a strong cladistic flavor, although many higher taxa remain paraphyletic. The position of several inarticulated calcareous-shelled groups centering on the craniids is somewhat unstable. This latter group was treated as a third small subphylum, the Craniiformea, together with the well-defined phosphatic-shelled inarticulated subphylum, the Linguliformea, and the major group of largely articulated calcareous-shelled brachiopods constituting the subphylum Rhynchonelliformea. The classification, although something of a compromise, will likely be used well into this century.

The estimated number of volumes required to revise the brachiopods slowly increased over the years as the magnitude of the task became apparent. Twelve years ago, Williams was estimating that an introductory volume followed by the taxonomic sections in two volumes would suffice. The introductory volume dealing with general topics appeared in 1997, and even as late as that year Williams considered that a total of four volumes would complete the task. Time was to show otherwise. Volumes 2 and 3 were, "…numbered consecutively but issued simultaneously, like overweight twins after a long gestation, whose seniority is merely a matter of delivery" (WILLIAMS, 2000, p. xxvi). This allowed volume 4, published in late 2002, to commence with the pentamerides, the sister group of the remaining rhynchonelliformeans. Volume 5, published in early 2006, finished the systematic volumes of the series and covered the remaining groups of the Rhynchonelliformea.

Sadly, volume 4 was the last volume for which Williams would write the coordinating author's preface. Alwyn died on 4 April 2004. He would have smiled to realize that the numerical form of the date, 04/04/04, was unambiguous to both his Celtic ancestors and his American friends! He worked almost to the end. His last circular letter was dated 23 March 2004. He wrote separately to both Jill Hardesty and Bert Rowell 2 days before he died to discuss *Treatise* matters. We miss him terribly!

Alwyn Williams established a pattern and style of work ably continued by his deputy coordinating authors, and the completed revision of Part H is a fitting tribute to his influence on the study of brachiopods.

In total 48 people contributed scripts to the *Treatise* revision, without whom the project would not have been possible. But we are also particularly mindful of and grateful for the vast amount of work that has continued over the years in the Kansas *Treatise* office, particularly the meticulous editing of texts and reproduction to such high standards of the illustrations we nominated to illustrate our scripts.

At the start of the project Alwyn Williams set up a *Treatise* office at the University of Glasgow with a series of brilliant secretaries keeping the records, sending out mail, and communicating with Kansas. The last of these is Patricia Peters, who has eased our jobs considerably. The Glasgow office has been supported by the University of Glasgow and by the *Treatise* office at the University of Kansas. All these individuals and organizations deserve our appreciation, and as remaining coordinators, we want to thank you all for your support, and especially since 2004.

During the publication of volumes 1 to 5 (1997 to 2006) sadly we have had to record the deaths of five authors, Alan Ansell, Algirdas Dagys, Richard Grant, Jess Johnson, and Alwyn Williams. Since then Jin Yu-gan died in Nanjing in June 2006; he was a renowned paleontologist and stratigrapher specializing in the Permian system. This revised brachiopod *Treatise* provides clear evidence of their varied and eminent scholarship.

Finally, we deeply regret having to record the death of Roger Kaesler on 11th August 2007, just at a time when the final stages of editing and proof reading this volume were in progress. Roger had been the Editor for the *Treatise* series since 1987, during which time he had seen the publication of 13 volumes covering many phyla. However, brachiopods had always held a particular interest for him, and Roger followed the progress of this major brachiopod revision closely. Roger had a close and fruitful relationship with Alwyn Williams, so that as other *Treatise* commitments had to be dealt with, delays in this revision were minimized. Roger was always available to provide advice about any matter of concern to authors or coordinating authors, advice that was thoughtful and to the point. Besides being a powerful and productive figure in paleontology, Roger was a real gentleman, and it was a pleasure to be with him on such occasions as the 2000 International Brachiopod Congress held in London. The *Treatise* series owes him much, and he will be remembered for long through these volumes.

REPOSITORIES AND THEIR ABBREVIATIONS

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

AM: Australian Museum, Sydney, Australia
AMF: Australian Museum, Sydney, Australia
AMNH: American Museum of Natural History, New York, USA
ANU: Australian National University, Canberra, Australia
AU: Geology Department, Auckland University, Auckland, Australia
BAU: Buenos Aires University, Buenos Aires, Argentina
BGS, GSM, IGS: British Geological Survey (formerly Geological Survey Museum; Institute of Geological Sciences, London) Keyworth, Nottinghamshire, United Kingdom
BMNH: The Natural History Museum, London, United Kingdom [formerly British Museum (Natural History)]
BMR: see CPC
Br: see TAGI Br
BSM: Bavarian State Museum, Munich, Germany
BU: Department of Geology, Birmingham University, Birmingham, United Kingdom
BUM: Bristol University Museum, Bristol, United Kingdom
CAGS: Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China
CAS: California Academy of Sciences, Types Collections, San Francisco, California, USA
CB: Muséum d'Histoire Naturelle, Geneva, Switzerland
CEGH: see CORD-PZ
CFP UA: Compagnie Française Petroles, Paris, France
CGS: Czech Geological Survey, Prague, Czech Republic
CIGMR: Chengdu Institute of Geology and Mineral Resources, Chengdu, China
CMB: City Museum and Art Gallery, Bristol, UK
CMNH: Carnegie Museum, Pittsburgh, USA
CNIGR: Central Scientific Geological Exploration Museum (Tschernyshev Museum), St. Petersburg, Russia
CORD-PZ: Universidad Nacional de Córdoba, Argentina
CPC: Commonwealth Palaeontological Collections, Australian Geological Survey Organisation, Canberra, Australia
CRMGE: Central Research Museum of Geological Explorations, St. Petersburg, Russia
D, EM, ENSM, FSI, FSL, SSL, TA: Université Claude Bernard, Lyon I, Villeurbanne, France
DNGM: Servicio Nacional Minero Geológico, Buenos Aires, Argentina
DP, DPO: Departamento de Geología, Oviedo University, Oviedo, Spain
DPO: see DP
DPUCM: Departamento de Paleontologia, Universidad Complutense, Madrid, Spain
EM: see D
ENSM: see D
FD: Geological College of Eastern China, Fuzhou, China
FSI: see D
FSL: see D
GB: Xian Institute of Geology and Mineral Resources, Xian, China
GBA: Geologisches Bundesanstalt Museum, Vienna, Austria
GIB: Geological Institute, Bonn, Germany
GIBAS: Geological Institute, Bulgarian Academy of Sciences, Sofia, Bulgaria
GIN KAZ: Institute of Geology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan
GIN TAD: Institute of Geology, Dushanbe, Tadzhikistan
GIN UZ: Institute of Geology, Uzbek Academy of Sciences, Tashkent, Uzbekistan
GIUS: Department of Earth Sciences, Silesian University, Sosnowiec, Poland
GLAHM: Hunterian Museum, Glasgow University, Scotland, United Kingdom
GMC, IV: Geological Museum of China, Beijing, China
GMG: State Museum of Georgia (named after S. N. Djanashia), Academy of Sciences of the Georgian SSR, Tbilisi
GMUT: see TUG
GM YaRGTS: Geological Museum of the Regional Geological Centre, Yakutsk, Yakutia
GPIBo: Palaontological Institute, Bonn, Germany
GPIT: Geological and Palaeontological Institute, University of Tübingen, Germany (Geologisch-Paläontologisches Institut, Tübingen Universität)
GPZ: Department of Geology and Palaeontology, Zagreb, Croatia
GSC: Geological Survey of Canada, Ottawa, Ontario, Canada
GSE: see IGS GSE
GSI: Geological Survey of India, Calcutta, India
GSM: see BGS
GSQ: Geological Survey, Queensland, Australia
GSV: Geological Survey of Victoria, Australia
GSWA: Geological Survey of Western Australia, Perth, Australia
GS YA: see CGS
HB: Bureau of Geology and Mineral Resources of Hunan Province, Hunan, China
HGI: Hungarian Geological Institut, Budapest, Hungary
HIGS: Hangzhou Institute for Geological Science, Hangzhou, China
HM: see GLAHM

HNHMB: Hungarian Natural History Museum, Budapest, Hungary
HUB: see MB
I: New York State Geological Survey, Albany, New York, USA
ICPSB: Institute of Geology, University of Padua, Italy
IG: Palaeontological Collections of L'Institut Royal des Sciences Naturelles de Belgique, Brussels
IGAS: Institute of Geology, Chinese Academy of Sciences, Beijing, China
IGiG: Institute of Geology and Geophysics, Siberian Branch, Academy of Sciences, Akademgorodok, Russia
IGM: Instituto de Geología, Universidad Autónoma de México, Ciudad Univesitaria, México City, Mexico
IGN: Institute of Geological Sciences, Kiev, Ukraine
IGN SO RAN: Geological Museum of the Institute of Geological Sciences of Yakutia Sakha Scientific Centre, Siberian Division, Russian Academy of Sciences, Yakutsk, Yakutia
IGNA: Geological Museum of the Institute of Geological Sciences, Almaty, Kazakhstan
IGR: Institute of Geology, University of Rennes, Rennes, France
IGS GSE: Institute of Geological Sciences, Edinburgh, United Kingdom
IGS GSM: see BGS
IMGPT: Geological-Paleontological Institute and Museum of Tübingen University, Germany
Inst. Geol.: Geological Institute, Bishkek, Kyrgyzstan
IO: P. P. Shirshov Institute of Oceanology, Moscow, Russia
IV: see GMC
IPW: Institut für Paläontologie der Universität (Geozentrum), Vienna, Austria
IRScNB: Palaeontological Collections of L'Institut Royal des Sciences Naturelles de Belgique, Brussels
JCF: James Cook University, Townsville, Queensland, Australia
KAS, MANK: Geological Museum of Institute of Geological Sciences, Almaty, Kazakhstan
KHGU: Kharkov State University, Ukraine
KIGLGU: Geology Faculty of Leningrad State University, Paleontology-Stratigraphy Museum, St. Petersburg, Russia
L: National Museum, Prague, Czech Republic, Barrande specimens
LGE: St. Petersburg State University, St. Petersburg, Russia
LGI: Leningrad Geological Institute, Leningrad, Russia
LM: see LO
LMT: Loodus Museum, Tallinn, Estonia
LO (formerly LM): Lund University Museum, Sweden
LPB: Laboratoire de Paléontologie, Université de Bretagne Occidentale, Brest, France
LS: Linnean Society of London, United Kingdom
MANK: see KAS
MB (formerly HUB): Humboldt University, Berlin, Germany
M.Ch: Museum Chabarovsk, Verkhoyan, eastern Siberia, Russia
MBHR: Museum of Dr. B. Horák, Rokycany, Czech Republic
MCMB: Department of Geology, University of Beijing, Beijing, China
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MDSGF: Museo del Dipartimento di Scienze Geolgiche dell'Università di Ferrara, Ferrara, Italy
MDSGF: Museo del Dipartimento di Scienze Geolgiche dell'Università di Ferrara, Ferrara, Italy
MDTF: see MDSGF
MFLV: Museo dei Fossili della Lessinia, Verona, Italy
MFMGB: Museum of the Faculty of Mining and Geology, Belgrade University, Belgrade, Yugoslavia
MG: Institute of Geology, Ashkhabad, Turkmenistan
MGBW: Museum of the Geologische Bundesanstalt of Wien, Austria
MGRI: Moscow Geological Prospecting Institute, Moscow, Russia
MGSB: Museo Geológico del Seminario de Barcelona, Barcelona, Spain
MGU: Moscow State University, Russia
MGUH: Geological Museum, Copenhagen, Denmark
MGUP: Museum of Geology, University of Palermo, Sicily, Italy
MIP: see MLP
MLP: Invertebrate Paleontology Department, La Plata Natural Sciences Museum, La Plata, Argentina
MM: Geological Survey, Prague, Czech Republic
MM: Moravian Museum, Brno, Czech Republic
MMF: Geological and Mining Museum, Department of Mines, Sydney, Australia
MNB: see MB
MNHN: Muséum National d'Histoire Naturelle, Paris, France
MONZ: see NMNZ
MPL: see MLP
MPM: Milwaukee Public Museum, Milwaukee, Wisconsin, USA
MPUM: Museo di Paleontologia del Dipartimento di Scienze della Terra dell'Università degli Studi di Milano, Italy
MUGT: see GIN TAD
Muz IG: Geological Museum of the Geological Institute, Warsaw, Poland
MV: see NMVP
NHM: Natural History Museum, London, UK
NHMB: Natural History Museum, Basel, Switzerland (Naturhistorisches Museum Basel)
NHMW: Natural History Museum in Vienna, Naturhistorisches Museum, Wien, Austria
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NM: National Museum, Prague, Czech Republic
NMING: National Museum of Ireland, Dublin, Ireland
NMNZ: Te Papa, Museum of New Zealand, Wellington, New Zealand

NMVP: Victoria Museum, Melbourne, Victoria, Australia

NMW: National Museum of Wales, Cardiff, United Kingdom

NMV P: Department of Invertebrate Palaeontology, Museum of Victoria, Australia

NS: Northeastern Institute of Geology, Inner Mongolia

NUF: Department of Geology, University of Newcastle, New South Wales, Australia

NYSM: New York State Museum, Albany, USA

NZGS: New Zealand Geological Survey, Lower Hutt, New Zealand (presently called Institute of Geological and Nuclear Sciences)

NZOI: New Zealand Oceanographic Institute, National Institute of Water and Atmospheric Research, Wellington, New Zealand

OKGS: Oklahoma Geological Survey, Norman, Oklahoma, USA

OMR: District Museum, Rokycany, Czech Republic

OMR VH: see OMR

OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA

OU: University of Oklahoma, Norman, USA

OUM: Oxford University Museum, United Kingdom

OU NZ: Geology Department, Otago University, Dunedin, New Zealand

PAN: see PIN

PCZCU: Department of Biology, Západočeská univerzita, Plzeň, Czech Republic

PIN: Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia

PIN RAS: see PIN

PIW: Paleontological Institute, Würzburg University, Würzburg, Germany

PKUM: Geological Museum of Beijing University, China

PM (formerly PMU): Palaeontological Museum, Uppsala University, Uppsala, Sweden

PMNUF: Paleontological Museum, University of Naples 'Federico II', Naples, Italy

PMO: Paleontologisk Museum, University of Oslo, Norway

PMU: see PM

PRI: Paleontological Research Institute, Ithaca, New York, USA

PUM: Geology, Peking University, Beijing, China

QMF: Queensland Museum, South Brisbane, Australia

RCCBYU: Research Center for the Chengjiang Biota, Yunnan University, Yunnan, China

RGF VR: Institute of Regional Geology and Paleontology, Faculty of Mining and Geology, University of Belgrade, Belgrade, Serbia **RM, RMS:** Swedish Museum of Natural History, Stockholm, Sweden

ROM: Royal Ontario Museum, Toronto, Ontario, Canada

RX: Rowley Collection, University of Illinois, Urbana, Illinois, USA

SAM.P: South Australian Museum, Adelaide, South Australia

SBNML: National Museum, Prague, Czech Republic

SGU: Geological Survey of Sweden, Uppsala, Sweden

SIGM: Shenyang Institute of Geology and Mineral Resources, Shenyang, Liaoning, China

SM (formerly SMA): Sedgwick Museum, University of Cambridge, United Kingdom

SMF: Senckenbergische Museum, Frankfurt, Germany

SNM: Slovakian National Museum, Bratislava, Slovakia (Slovenské Narodné Múzeum, Bratislava)

SSL: see D

SUI: University of Iowa, Department of Geology, Iowa City, USA

SUP: Palaeontological collections, University of Sydney, New South Wales, Australia

T: Paleontological Museum, University of Naples, Naples, Italy

TA: see D

TAGI BR: Geological Museum, Institute of Geology, Tallinn Technical University, Tallinn, Estonia

TBR: see TF

TF: Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand

TsGM: see CNIGR

TsNIGRA: see CNIGR

TUBr: Paläontologische Sammlung, Institut für Geowissenschaften, Universität Tübingen, Germany

TUG: Museum of Geology, University of Tartu, Tartu, Estonia

UA: Geology Department, University of Alberta, Edmonton, Canada

UC: Field Museum of Natural History, Chicago, Illinois, USA

UCF: The University, Calgary, Canada

UCLA: University of California at Los Angeles, Los Angeles, California, USA

UCM: University of Canterbury, Christchurch, New Zealand

UCMP: University of California, Museum of Paleontology, USA

UD: University of Dijon, Dijon, France

UHR: Hokkaido University, Sapporo, Japan

UI: University of Illinois, Urbana, Illinois, USA

UL: Department of Geology and Palaeontology, University of Ljubljana, Slovenia

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

UMC (formerly UMO): University of Missouri, Columbia, Missouri, USA

UMMF: Department of Geology, University of Montpellier, Montpellier, France

UMUT: University Museum of the University of Tokyo, Tokyo, Japan

UND: University of Notre Dame, Indiana, USA

U.N.E: University of New England, Armidale, Australia

UPS: Université de Paris-Sud, France

UQF: University of Queensland, Department of Geology, Brisbane, Australia

USNM: United States National Museum, Washington, D.C., USA

UT: Department of Geology, University of Texas, Austin, Texas, USA
UTC: Department of Geology, University of Toronto, Toronto, Canada
UTGD: University of Tasmania Geology Department, Hobart, Tasmania, Australia
U.W.A.: University of Western Australia, Nedlands, Western Australia
VH: see OMR
VSEGEI: Russian Geology Institute, St. Petersburg, Russia
XAGM: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China
XB: Palaeontological Collections of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Xi'an, Shaanxi Province, China
XIGMR: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China
YaTGU: Geological Museum, Yakutsk, Yakutia
YIGM: Yichang Institute of Geology and Mineral Resources, Yichang, China
YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA
ZI: Zhejiang Institute of Geology and Mineralogy, Zhejiang, China
ZPAL Br: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland

OUTLINE OF SUPRAFAMILIAL CLASSIFICATION AND AUTHORSHIP

Alwyn Williams,[1] Sandra J. Carlson,[2] and C. Howard C. Brunton[3]
[[1]Deceased; formerly of The University of Glasgow; [2]The University of California, Davis; and [3]formerly of The Natural History Museum London]

The following outline of the classification of the Brachiopoda is an amended version of that published at the beginning of Volume 2 of the *Treatise on Invertebrate Paleontology, Part H (Revised), Brachiopoda,* edited by R. L. Kaesler (2000, p. 22–27). It lists all suprafamilial taxa recognized and described in the four systematic volumes (vols. 2–5) already published and those included in this last volume, volume 6. The main changes are the inclusion of suprafamilial taxa of uncertain order or class. The thirty-four contributors identified in the list were responsible for authorship of diagnoses for the listed taxa. In the case of orders, suborders, and superfamilies, the authors were also responsible for all lower-ranking taxa down to genera and subgenera. The systematic sections herein may include introductions in which alternative or slightly emended classifications to the section are discussed. The authors of these sections are responsible for their opinions on the classification of their particular taxonomic groups.

Linguliformea. Lower Cambrian–Holocene.
        Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
  Lingulata. Lower Cambrian–Holocene.
        L. E. Holmer & L. E. Popov
    Lingulida. Lower Cambrian–Holocene.
        L. E. Holmer & L. E. Popov
      Linguloidea. Lower Cambrian–Holocene.
        L. E. Holmer & L. E. Popov
      Discinoidea. Ordovician–Holocene.
        L. E. Holmer & L. E. Popov
      Acrotheloidea. Lower Cambrian–Lower Ordovician.
        L. E. Holmer & L. E. Popov
    Acrotretida. Lower Cambrian–Middle Devonian, ?Upper Devonian.
        L. E. Holmer & L. E. Popov
      Acrotretoidea. Lower Cambrian–Middle Devonian, ?Upper Devonian.
        L. E. Holmer & L. E. Popov
    Siphonotretida. Middle Cambrian–Ordovician.
        L. E. Holmer & L. E. Popov
      Siphonotretoidea. Middle Cambrian–Ordovician.
        L. E. Holmer & L. E. Popov
  Paterinata. Lower Cambrian–Upper Ordovician.
        J. R. Laurie
    Paterinida. Lower Cambrian–Upper Ordovician.
        J. R. Laurie
      Paterinoidea. Lower Cambrian–Upper Ordovician.
        J. R. Laurie
Craniiformea. ?Lower Cambrian, Middle Cambrian, Ordovician–Holocene.
        Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
  Craniata. ?Lower Cambrian, Middle Cambrian, Ordovician–Holocene.
        L. E. Popov, M. G. Bassett, & L. E. Holmer
    Craniopsida. ?Lower Cambrian, Middle Cambrian, Ordovician–Lower Carboniferous.
        L. E. Popov & L. E. Holmer
      Craniopsoidea. ?Lower Cambrian, Middle Cambrian, Ordovician–Lower Carboniferous.
        L. E. Popov & L. E. Holmer
    Craniida. Lower Ordovician–Holocene.
        M. G. Bassett
      Cranioidea. Ordovician–Holocene.
        M. G. Bassett

Trimerellida. Ordovician–Silurian.
L. E. Popov & L. E. Holmer
Trimerelloidea. Ordovician–Silurian.
L. E. Popov & L. E. Holmer
Rhynchonelliformea. Lower Cambrian–Holocene.
Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
Chileata. Lower Cambrian–Permian.
L. E. Popov & L. E. Holmer
Chileida. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Matutelloidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Dictyonellida. Upper Ordovician–Lower Permian.
L. E. Holmer
Eichwaldioidea. Upper Ordovician–Lower Permian.
L. E. Holmer
Obolellata. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Obolellida. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Obolelloidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Uncertain.
L. E. Popov & L. E. Holmer
Naukatida. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Naukatoidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Kutorginata. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Kutorginida. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Kutorginoidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Nisusioidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Strophomenata. Middle Cambrian–Upper Permian.
Alwyn Williams, C. H. C. Brunton, & L. R. M. Cocks
Strophomenida. Lower Ordovician–Carboniferous.
L. R. M. Cocks & Rong Jia-yu
Strophomenoidea. Ordovician–Carboniferous.
L. R. M. Cocks & Rong Jia-yu
Plectambonitoidea. Ordovician–Devonian.
L. R. M. Cocks & Rong Jia-yu
Uncertain.
Alwyn Williams & C. H. C. Brunton
Productida. Upper Ordovician–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
Chonetidina. Upper Ordovician–Permian, ?Lower Triassic.
P. R. Racheboeuf
Chonetoidea. Upper Ordovician–Permian, ?Lower Triassic.
P. R. Racheboeuf
Productidina. Lower Devonian–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Productoidea. Lower Devonian–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Echinoconchoidea. Middle Devonian–Upper Permian.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Linoproductoidea. Lower Devonian–Upper Permian.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Uncertain.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan

    - Strophalosiidina. Lower Devonian–Upper Permian.
      - C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Strophalosioidea. Lower Devonian–Upper Permian.
        - C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Aulostegoidea. Lower Carboniferous–Upper Permian.
        - C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
      - Richthofenioidea. Upper Carboniferous–Upper Permian.
        - B. R. Wardlaw, R. E. Grant, & C. H. C. Brunton
  - Lyttoniidina. ?Lower Carboniferous, Upper Carboniferous–Upper Permian.
    - Alwyn Williams, D. A. T. Harper, & R. E. Grant
    - Lyttonioidea. ?Lower Carboniferous, Upper Carboniferous–Upper Permian.
      - Alwyn Williams, D. A. T. Harper, & R. E. Grant
    - Permianelloidea. Permian.
      - Alwyn Williams, D. A. T. Harper, & R. E. Grant
  - Uncertain.
    - C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
- Orthotetida. Lower Ordovician–Upper Permian.
  - Alwyn Williams, C. H. C. Brunton, & A. D. Wright
  - Orthotetidina. Upper Ordovician–Upper Permian.
    - Alwyn Williams & C. H. C. Brunton
    - Orthotetoidea. Middle Devonian–Upper Permian.
      - Alwyn Williams & C. H. C. Brunton
    - Chilidiopsoidea. Upper Ordovician–Lower Carboniferous.
      - Alwyn Williams & C. H. C. Brunton
  - Triplesiidina. Lower Ordovician–upper Silurian.
    - A. D. Wright
    - Triplesioidea. Lower Ordovician–upper Silurian.
      - A. D. Wright
- Billingsellida. Middle Cambrian–Upper Ordovician.
  - Alwyn Williams & D. A. T. Harper
  - Billingsellidina. Middle Cambrian–Lower Ordovician.
    - Alwyn Williams & D. A. T. Harper
    - Billingselloidea. Middle Cambrian–Lower Ordovician.
      - Alwyn Williams & D. A. T. Harper
  - Clitambonitidina. Lower Ordovician–Upper Ordovician.
    - Madis Rubel & A. D. Wright
    - Clitambonitoidea. Ordovician.
      - Madis Rubel & A. D. Wright
    - Polytoechioidea. Ordovician.
      - Madis Rubel & A. D. Wright

- Rhynchonellata. Lower Cambrian–Holocene.
  - Alwyn Williams & S. J. Carlson
  - Protorthida. Lower Cambrian–Upper Devonian.
    - Alwyn Williams & D. A. T. Harper
    - Protorthoidea. Lower Cambrian–Middle Cambrian.
      - Alwyn Williams & D. A. T. Harper
    - Skenidioidea. Lower Ordovician–Upper Devonian.
      - Alwyn Williams & D. A. T. Harper
  - Orthida. Lower Cambrian–Upper Permian.
    - Alwyn Williams & D. A. T. Harper
    - Orthidina. Lower Cambrian–Lower Devonian.
      - Alwyn Williams & D. A. T. Harper
      - Orthoidea. Lower Cambrian–Lower Devonian.
        - Alwyn Williams & D. A. T. Harper
      - Plectorthoidea. Middle Cambrian–upper Silurian.
        - Alwyn Williams & D. A. T. Harper
    - Dalmanellidina. Lower Ordovician–Upper Permian.
      - D. A. T. Harper
      - Dalmanelloidea. Lower Ordovician–Upper Permian.
        - D. A. T. Harper
      - Enteletoidea. Lower Ordovician–Upper Permian.
        - D. A. T. Harper

- Uncertain.
  - Alwyn Williams & D. A. T. Harper
- Pentamerida. Lower Cambrian–Upper Devonian.
  - S. J. Carlson, A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
  - Syntrophiidina. Lower Cambrian–Lower Devonian.
    - S. J. Carlson
    - Porambonitoidea. Lower Cambrian–lower Silurian.
      - S. J. Carlson
    - Camerelloidea. Lower Ordovician–Lower Devonian.
      - S. J. Carlson
  - Pentameridina. Upper Ordovician–Upper Devonian.
    - A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
    - Pentameroidea. Upper Ordovician–Silurian.
      - A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
    - Stricklandioidea. Silurian.
      - A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
    - Gypiduloidea. Silurian–Upper Devonian.
      - R. B. Blodgett, A. J. Boucot, & Rong Jia-yu
    - Clorindoidea. lower Silurian–Middle Devonian.
      - R. B. Blodgett, A. J. Boucot, & Rong Jia-yu
- Rhynchonellida. Lower Ordovician–Holocene.
  - N. M. Savage, M. O. Manceñido, E. F. Owen, S. J. Carlson, R. E. Grant, A. S. Dagys, & Sun Dong-li
  - Ancistrorhynchoidea. Lower Ordovician–Lower Devonian.
    - N. M. Savage
  - Rhynchotrematoidea. Lower Ordovician–Lower Carboniferous.
    - N. M. Savage
  - Uncinuloidea. lower Silurian–Upper Devonian.
    - N. M. Savage
  - Camarotoechioidea. lower Silurian–Lower Carboniferous.
    - N. M. Savage
  - Pugnacoidea. Lower Devonian–Holocene.
    - N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
  - Stenoscismatoidea. Lower Devonian–Upper Permian.
    - S. J. Carlson & R. E. Grant
  - Lambdarinoidea. Upper Devonian–Upper Carboniferous.
    - N. M. Savage
  - Rhynchoporoidea. Upper Devonian–Upper Permian.
    - N. M. Savage
  - Dimerelloidea. Upper Devonian–Holocene.
    - M. O. Manceñido, E. F. Owen, N. M. Savage, & A. S. Dagys
  - Rhynchotetradoidea. Upper Devonian–Middle Jurassic.
    - N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
  - Wellerelloidea. Lower Carboniferous–Lower Jurassic.
    - N. M. Savage, M. O. Manceñido, E. F. Owen, A. S. Dagys, & Sun Dong-li
  - Rhynchonelloidea. Lower Triassic–Upper Cretaceous.
    - E. F. Owen & M. O. Manceñido
  - Norelloidea. Lower Triassic–Holocene.
    - M. O. Manceñido, E. F. Owen, A. S. Dagys, & Sun Dong-li
  - Hemithiridoidea. Middle Triassic–Holocene.
    - M. O. Manceñido, E. F. Owen, Sun Dong-li, & A. S. Dagys
  - Uncertain.
    - M. O. Manceñido, E. F. Owen, & Sun Dong-li
- Atrypida. Ordovician–Upper Devonian.
  - Paul Copper
  - Atrypidina. Ordovician–Upper Devonian.
    - Paul Copper
    - Atrypoidea. Ordovician–Upper Devonian.
      - Paul Copper
    - Punctatrypoidea. Silurian–Middle Devonian.
      - Paul Copper
  - Anazygidina. Ordovician–Silurian.
    - Paul Copper

Anazygoidea. Ordovician–Silurian.
Paul Copper
Davidsoniidina. Silurian–Middle Devonian.
Paul Copper
Davidsonioidea. Silurian–Middle Devonian.
Paul Copper
Palaferelloidea. Silurian–Middle Devonian.
Paul Copper
Lissatrypidina. Ordovician–Upper Devonian.
Paul Copper
Lissatrypoidea. Ordovician–Middle Devonian.
Paul Copper
Glassioidea. Silurian–Upper Devonian.
Paul Copper
Protozygoidea. Ordovician–Silurian.
Paul Copper
Athyridida. Upper Ordovician–Lower Jurassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Athyrididina. Upper Ordovician–Upper Triassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Athyridoidea. ?Upper Ordovician–Upper Triassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Meristelloidea. Upper Ordovician–Upper Carboniferous.
Fernando Alvarez & Rong Jia-yu
Nucleospiroidea. Silurian–Lower Permian.
Fernando Alvarez & Rong Jia-yu
Retzielloidea. Silurian–Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Uncertain.
Fernando Alvarez & Rong Jia-yu
Retziidina. Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Retzioidea. Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Mongolospiroidea. Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Rhynchospirinoidea. Silurian–Upper Devonian.
Fernando Alvarez & Rong Jia-yu
Koninckinidina. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Koninckinoidea. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Uncertain.
Fernando Alvarez & Paul Copper
Dayioidea. Silurian–Lower Devonian.
Fernando Alvarez & Paul Copper
Anoplothecoidea. Silurian–Middle Devonian.
Fernando Alvarez & Paul Copper
Uncitoidea. Middle Devonian.
Fernando Alvarez & Paul Copper
Uncertain.
Fernando Alvarez & Rong Jia-yu
Spiriferida. Upper Ordovician–Lower Triassic, ?Middle Triassic–?Upper Triassic.
J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-fei
Spiriferidina. Upper Ordovician, ?Middle Triassic–?Upper Triassic.
J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-fei
Cyrtioidea. Upper Ordovician–Lower Devonian.
J. G. Johnson & Hou Hong-fei
Adolfioidea. Silurian–Upper Devonian.
J. G. Johnson
Theodossioidea. Lower Devonian–Carboniferous.
J. G. Johnson, J. L. Carter, & Hou Hong-fei

Cyrtospiriferoidea. Lower Devonian–Upper Devonian.
J. G. Johnson
Ambocoelioidea. Silurian–Lower Triassic, ?Middle Triassic–?Upper Triassic.
J. G. Johnson, J. L. Carter, & Hou Hong-fei
Martinioidea. Silurian–Permian.
J. L. Carter & Rémy Gourvennec
Spiriferoidea. Upper Devonian–Permian.
J. L. Carter
Paeckelmannelloidea. Upper Devonian–Permian.
J. L. Carter
Brachythyridoidea. Upper Devonian–Permian.
J. L. Carter
Delthyridina. Silurian–Permian.
J. G. Johnson, Hou Hong-fei, J. L. Carter, & Rémy Gourvennec
Delthyridoidea. Silurian–Carboniferous.
J. G. Johnson & Hou Hong-fei
Reticularioidea. Silurian–Permian.
J. L. Carter & Rémy Gourvennec
Uncertain.
P. R. Racheboeuf
Spiriferinida. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinidina. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinoidea. Lower Devonian–Carboniferous.
J. G. Johnson
Suessioidea. Carboniferous–Lower Jurassic.
J. L. Carter
Spondylospiroidea. Middle Triassic–Upper Triassic.
J. L. Carter
Spiriferinidina. Upper Devonian–Lower Jurassic.
J. L. Carter
Syringothyridoidea. Upper Devonian–Permian.
J. L. Carter
Pennospiriferinoidea. Upper Devonian–Lower Jurassic.
J. L. Carter
Spiriferinoidea. Middle Triassic–Lower Jurassic.
J. L. Carter
Thecideida. Upper Triassic–Holocene.
P. G. Baker
Thecospiroidea. Upper Triassic.
P. G. Baker
Thecideoidea. Upper Triassic–Holocene.
P. G. Baker
Terebratulida. Lower Devonian–Holocene.
D. E. Lee, D. I. MacKinnon, T. N. Smirnova, P. G. Baker, Jin Yu-gan, & Sun Dong-li
Terebratulidina. Lower Devonian–Holocene.
D. E. Lee, A. S. Dagys, T. N. Smirnova, Sun Dong-li, & Jin Yu-gan
Stringocephaloidea. ?Silurian, Lower Devonian–Upper Devonian.
D. E. Lee
Cryptonelloidea. Lower Devonian–Upper Triassic.
Jin Yu-gan & D. E. Lee

Dielasmatoidea. Carboniferous–Lower Jurassic.
Jin Yu-gan, D. E. Lee, Sun Dong-li, T. N. Smirnova, A. S. Dagys, & M. R. Sandy
Terebratuloidea. ?Upper Jurassic, Lower Cretaceous–Holocene.
D. E. Lee & T. N. Smirnova
Loboidothyridoidea. Triassic–Lower Cretaceous.
D. E. Lee, T. N. Smirnova, & A. S. Dagys
Dyscolioidea. Lower Jurassic–Holocene.
D. E. Lee
Cancellothyridoidea. Lower Jurassic–Holocene.
D. E. Lee, T. N. Smirnova, & Sun Dong-li
Terebratellidina. Upper Triassic–Holocene.
D. I. MacKinnon, D. E. Lee, P. G. Baker, T. N. Smirnova, A. S. Dagys, & Sun Dong-li
Zeillerioidea. Lower Triassic–Holocene.
P. G. Baker
Kingenoidea. Middle Triassic–Holocene.
D. I. MacKinnon, T. N. Smirnova, & D. E. Lee
Laqueoidea. Upper Triassic–Holocene.
D. I. MacKinnon & D. E. Lee
Megathyridoidea. Lower Cretaceous–Holocene.
D. E. Lee, D. I. MacKinnon, & T. N. Smirnova
Bouchardioidea. Lower Cretaceous–Holocene.
D. I. MacKinnon & D. E. Lee
Platidioidea. Upper Cretaceous–Holocene.
D. I. MacKinnon & D. E. Lee
Terebratelloidea. Paleogene–Holocene.
D. I. MacKinnon & D. E. Lee
Kraussinoidea. Neogene–Holocene.
D. E. Lee & D. I. MacKinnon
Uncertain.
Gwynioidea. Middle Jurassic–Holocene.
D. I. MacKinnon
Uncertain. Middle Devonian.
Jin Yu-gan & D. E. Lee
Uncertain
P. G. Baker
Uncertain.
Jin Yu-gan
Uncertain
Cadomelloidea. Lower Jurassic.
D. I. MacKinnon
Uncertain
Jin Yu-gan & D. E. Lee
Uncertain
Alwyn Williams & C. H. C. Brunton
Uncertain
N. M. Savage
Uncertain
A. J. Boucot
Uncertain
D. A. T. Harper

ERRATA

Since publication of the first revised volume of the brachiopod *Treatise* in 1997, a few mistakes have been noted, largely by contributing authors. Simple and obvious spelling mistakes have not been included, unless they involve taxonomic names or make recognition or understanding difficult. Factual errors are included along with corrections to issues that may not have been clearly defined when written.

Volume 1

page 75, Caption for Figure 72: "*1–2*, recent rhynchonellids" should read "*1, 3,* recent rhynchonellides"; "*3*, terebratulide*"* should read "*2*, terebratulide."

page 164, Caption for Figure 164: 5 p.t. and 8 p.t. stages should be reversed.

page 334, right column, 7 lines from bottom: replace *Athyris* with *Hexarhytis* in the following sentence:

Regularly spaced lamellae of *Athyris* can extend forward as recurved microfrills more than 300 mm long (Fig. 296.1).

page 336, caption for Figure 296.1: Replace *Athyris campanesi* with *Hexarhytis campomanesi.*

page 397, "Morphology" chapter, 3rd line down, left column:

In some retzioids (e.g., *Nucleospira*), a juvenile median ridge grew ventroposteriorly into a hooklike structure extending into the ventral umbo (Fig. 363.1). This resembles a small version of the bilobed cardinal process of orthotetidine meekellids, but is built of medially united cardinal flanges. Unlike the bilobed cardinal process of strophomenates, which preserves growth traces of the myophores on the external (posterior) surfaces (Fig. 364), the retzioid structure is smooth as if secreted by conventional epithelium during growth.

The term "retzioid" should be replaced by "nucleospiroid."

page 398, last lines of left column:

The early terebratulides tend to display diductor attachment characters similar to those of athyridides with a dorsal foramen, and in stringocephaloid genera, with strongly developed ventral umbones, the cardinal process grew posteroventrally in an exaggerated fashion like those of some retzioids.

The term "retzioids" should be replaced by "nucleospiroids."

page 417, right column, 12th line: (Fig. 381.6) should read (Fig. 381.7).

In the chapter "Ecology of Articulated Brachiopods" (p. 441–462), references to *Magasella sanguinea* should read *Terebratella sanguinea.*

page 485, Figure 413, depth scale on left-hand side should read 200, 400, 600, 800, 1000, 1200 m.

Volume 2

page 30, diagnosis for Linguliformea: "tentacles in double row throughout ontogeny" should be changed to "ablabial tentacles added to adlabial tentacles in post-trocholophe stage of development."

page 30, diagnosis for Lingulata: "two rows of filaments during trocholophe stage" to "one row of filaments during trocholophe stage."

page 59, Figure 24: *Libyaeglossa* figures are views *2ab, Rafanoglossa* are views *4ab.*

page 106, Figure 53: view *4f* is *Linnarssonella*. See p. 114, Figure 58.

page 114, Figure 58: views 3d and 3f are *Apsotreta*. See p. 106, Figure 53.

page 398, genus *Aseptonetes* Isaacson, 1977, p. 177 [**A. boucoti;* M]: its type species was fixed by monotypy and is regarded as valid among Devonochonetinae; it should not be listed as an objective synonym of *Pleurochonetes* Isaacson, 1977, on page 402.

page 400, left column, lines 14–15 from bottom: *Strophonema* should read *Strophomena*.

page 402, genus *Pleurochonetes* Isaacson, 1977: synonym *Gamonetes* Isaacson, 1977, p. 168 [**G. anteloi;* M]: its type species was fixed by monotypy, and it is a subjective synonyn, NOT an objective synonym.

page 404, genus *Austronoplia,* within genus description, line 14, spelling should be *Austronoplia,* NOT *Austranoplia.*

Volume 3

page 518: Figure 357, 2d, ×l.5 should read ×1.

page 569, genus entry for *Licharewiella* Sokolskaya, 1960: delete reference to synonym *Magniderbyia* Ting, 1965, p. 265, which is regarded as an objective synonym of *Licharewiella* Ustritsky, 1960 *non* Sokolskaya, 1960 (family Strophalosiidae), as well as an objective synonym of *Licharewiella* Sokolskaya, 1960 *non* Ustritsky, 1960 (family Derbyidae, on p. 657, left column, near bottom).

page 804, genus *Heterorthina.* Stratigraphic and geographic range is Upper Ordovician (Caradoc–Ashgill): Europe and North America.

page 904, Index, spelling should be Austronoplia, NOT Austranoplia.

Volume 4

page 943: genus *Talovia* is from the Lower Ordovician (Caradoc), NOT lower Llanvirn, and the Bugrishikhinskii Gorizont, NOT Rudnikova Formation.

page 993, Figure 672,3 should read c–e, lateral, ventral, dorsal views, ×1; f–g, posterior, ventral interiors, ×2.

page 1196: genus *Sanjuania,* description for Figure 816,3a–b, should read ventral, dorsal.

page 1225–1227, Figures 834–836: captions should read Psilocamaridae, NOT Stenoscismatidae.

page 1325: Genus *Sphenarina,* description for Figure 898,*4f,* illustrated specimen number (USNM 549318a) should read (USNM 549381a).

page 1335: Genus *Pararhactorhynchia*, description for Figure 904,*3e–l* should read 904,4*e–l.*

page 1335: Genus *Yulongella*, description for Figure 904,*4e–k* should read 904,*3e–k*.

page 1462: Genus *Australina*, description for Figure 992,*1a–e,* enlargement (×2) should read ×3.

Volume 5

page xlv, page 2029, Superfamily Dielasmatoidea: stratigraphic range is Carboniferous (Mississippian)–Lower Jurassic, NOT Upper Devonian (Frasnian).

page 2188: Genus *Xenorina* Cooper, 1989, p. 115 [**X. ovata;* M] was fixed by monotypy.

page 2194: Stratigraphic range for subfamily Aulacothyropsinae should be Middle Triassic–Lower Cretaceous.

page 2197: Spelling for genus *Katchathyris* should be *Kachathyris.*

SUPPLEMENTAL GENERA LIST

The following genera have been published or found in the literature since September 2004, the cutoff date for inclusion of full generic descriptions for volume 6. This list represents a late-stage attempt at a complete generic record of the Brachiopoda. Generic names have been submitted by the contributing authors of previous sections of the brachiopod *Treatise*.

Order Productida, Suborder Productidina, Superfamily Productoidea, Family Productellidae

Dongpanoproductus He, Shen, Feng, & Gu, 2005, p. 931 [**D. elegans;* OD]. Type species, fig. 5.1–5.11, type specimen, holotype, DP730 (Micropalaeontology laboratory, Faculty of Earth Sciences, Wuhan, China); upper Changhsingian, Talung Formation, Dongpan Section, southern Guangxi, South China.

Weihong He, Shu-Zhong Shen, Qinglai Feng, & Songzhu Gu. 2005. A late Changhsingian (Late Permian) deepwater brachiopod fauna from the Talung Formation at the Dongpan section, southern Guangxi, South China. Journal of Paleontology 79(5):927–938.

Order Productida, Suborder Lyttoniidina, Superfamily Lyttonioidea, Family Lyttoniidae, Subfamily Linoldhamininae

Linoldhamina Xu, Shen, & Cheng, 2005, p. 1014 [**L. xainzaensis;* OD]. Holotype, NIGP137072, mid-Guadalupian, northern Tibet, China.

Han-Kui Xu, Shu-Zhong Shen, & Li-Ren Cheng. 2005. Linoldhamininae, a new subfamily of Lyttoniidae Waagen, 1883 (Brachiopoda) from the Guadalupian (middle Permian) Xiala Formation in the Xainza area, northern China. Journal of Paleontology 79(5):1012–1018.

Order Orthida?

Bethia Sutton, Briggs, Siveter, & Siveter, 2005, p. 1013 [**B. serraticulma*; OD]. Holotype, OUM C.29586, Wenlock, Silurian, Herefordshire.

Sutton, Mark D., Derek E. G. Briggs, David J. Siveter, & Derek J. Siveter. 2005. Silurian brachiopods with soft-tissue preservation. Nature 436/18:1013–1015.

Order Pentamerida, Suborder Syntrophiidina, Superfamily Porambonitoidea, Family Porambonitidae

Eoporambonites Popov, Egerquist, & Zuykov, 2005, p. 756 [**Porambonites latus* Pander, 1830, p. 98; OD]. Lower Arenig, Billingen Regional Stage, Maekula Member, St. Petersburg District, Russia, North Estonia.

Popov, L. E., Eva Egerquist, & M. A. Zuykov. 2005. Ordovician (Arenig-Caradoc) syntrophiidine brachiopods from the East Baltic region. Palaeontology 48(4):739–761, fig. 6A–I, K.

Order Rhynchonellida, Superfamily Rhynchotrematoidea, Family Leptocoeliidae

Antelocoelia Isaacson, 1977, p. 171 [**A. johnsoni;* M]. Lower Devonian–Middle Devonian. Bolivia.

Isaacson, P. E. 1977. Devonian stratigraphy and brachiopod paleontology of Bolivia. Part B, Spiriferida and Terebratulida. Palaeontographica (Abt. A) 156(4-6):168–217, pl. 1–9.

Order Rhynchonellida, Superfamily Pugnacoidea, Family Basiliolidae, Subfamily Pamirorhynchiinae

Jakubirhynchia Tomašových, 2006, p. 213 [**Rhynchonella latifrons* Geyer, 1889; OD]. Lower Jurassic (Hettangian–Sinemurian). West Carpathians–Eastern Alps (Slovakia, Austria).

Tomašových, Adam. 2006. A new Early Jurassic rhynchonellid brachiopod from the western Tethys and implications for systematics of rhynchonellids from the Triassic-Jurassic boundary. Journal of Paleontology 80(2):212–228.

Order Rhynchonellida, Superfamily Pugnacoidea, Family Basiliolidae

Mondegia Andrade, 2006, p. 59 [**M. limica;* OD]. Middle Jurassic (Bajocian). Portugal.

Andrade, Benito. 2006. Los braquiópodos del tránsito Jurásico Inferior-Jurásico Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56:5–194.

Order Spiriferida, Suborder Spiriferidina, Superfamily Cyrtospiriferoidea, Family Cyrtospiriferidae, Subfamily Cyrtiopsinae

Cratospirifer Tong, 1986, p. 682[684] [**C. biconvexus;* OD]. Lower Carboniferous. China (Sichuan).

Tong, Zheng-xiang. 1986. Early Early Carboniferous brachiopod fauna in northwest Sichuan. Acta Palaeontologica Sinica, 25(6):672–686, pl. 1–3.

In Chinese, with English summary.

Order Spiriferida, Suborder Spiriferidina, Superfamily Cyrtospiriferoidea, Family Cyrtospiriferidae, Subfamily Cyrtospiriferinae

Plicapustula Ma & Day, 2007, p. 298 [**Spirifer (Sinospirifer) gortanioides* Grabau, 1931; OD]. Upper Devonian (Famennian). Southern China, North America.

Ma Xueping, & Jed Day. 2007. Morphology and revision of Late Devonian (Early Famennian) Cyrtospirifer (Brachiopoda) and related genera from South China and North America. Journal of Paleontology 81(2):286–311.

Order Strophomenida, Superfamily Strophomenoidea, Family Douvillinidae, Subfamily Protodouvillininae

Undifossula Gratsianova & Yazikov, 1998, p. 65 [**Douvillina grandicula* Gratsianova, 1975; OD]. Lower Devonian (Givetian)–Middle Devonian (Emsian). Siberia. [Originally proposed as a subgenus of *Protodouvillina.*]

Gratsianova, R. T., & A. Yu. Yazikov. 1998. Rod *Protodouvillina* (Brakhiopody, Devon): reviziya sostava, novye taksony, filogeniya i filozony [=Genus *Protodouvillina* (Brachiopoda, Devonian): Revision, new taxa, phylogeny, phylozones]. Novosti Paleontologii i Stratigrafii, Vypusk 1 (supplement to Geologiya i Geofizika, 39): 57–79, pl. 1–3.
In Russian with English abstract.

Order Rhynchonellida, Superfamily ?Hemithiridoidea, Family Uncertain

Chathamirhynchia Lee & Motchurova-Dekova, 2007 [**C. kahuitara*; OD]. Upper Cretaceous (Campanian–Maastrichtian). New Zealand.

Lee, D. E., & Neva Motchurova-Dekova. 2007. *Chathamirhynchia kahuitara*, a new genus and species of Late Cretaceous rhynchonellide brachiopod from the Chatham Islands, New Zealand: Shell structure, paleoecology and biogeography. *In* Brachiopod Research into the Third Millennium, Transactions of the Royal Society of Edinburgh, Earth and Environmental Science, vol. 98(parts 3 and 4). Edinburgh.

Order Rhynchonellida, Superfamily Wellerelloidea, Family ?Allorhynchidae

Livarirhynchia V. Radulovič, 2007 [**L. rajkae*; OD]. Lower Jurassic (Pliensbachian). Montenegro and Italy.

Radulovič, Vladan. 2007 (in press). A new Pliensbachian rhynchonellide brachiopod from Livari (Rumija Mountain, Montenegro). Proceedings of the Fifth International Brachiopod Congress, Copenhagen 2005, Fossils and Strata 47.

Order Rhynchonellida, Superfamily Pugnacoidea, Family Basiliolidae

Basiliocostella Dulai, Bitner, & Müller, 2007 [**B. kambueheli;* OD].

Dulai, Alfréd, M. A. Bitner, & Pál Müller. 2007 (in press). A monospecific assemblage of a new rhynchonellide brachiopod from the Paleocene of Austria. Proceedings of the Fifth International Brachiopod Congress, Copenhagen 2005, Fossils and Strata 47.

Class Rhynchonellata, Order Uncertain, Family Apodosiidae

Apodosia Smirnova & MacKinnon, 1995, p. 686 [**Argyrotheca lorioli* Smirnova, 1972; OD]. Middle Jurassic (Bajocian), England; Lower Cretaceous (Berriasian), Ukraine (Crimea).

Smirnova, T. N., & D. I. MacKinnon. 1995. *Apodosia,* an enigmatic new genus of micromorphic brachiopod from the Cretaceous of Crimea, Ukraine, and the Jurassic of England. Journal of Paleontology 69(4):686–692.

Class Rhynchonellata, Order Uncertain

Arzonella Sulser, 2004, p. 423 [**A. exotica;* OD]. Lower Jurassic. Southern Alps.

Sulser, H. 2004. *Arzonella exotica* n. g. n. sp., a new brachiopod of indeterminate systematic position from the Lower Liassic (Broccatello) of Arzo (Southern Alps of Switzerland): A short note. Eclogae Geologica Helvetica 97(3):423–428.

Order Spiriferinida, Superfamily Spiriferinoidea, Family Spiriferinidae

Cisnerospira Manceñido, 2004, p. 272 [**Spiriferina adscendens* Deslongchamps, 1859; OD]. Lower Jurassic (Sinemurian–Pliensbachian). Mediterranean Europe.

Manceñido, M. O. 2004. Las "espiriferinas" del Jurásico Inferior: una mirada retrospectiva a los estudios de Daniel Jiménez de Cisneros. GeoTemas 7:269–272 + Errata: 1-2 (2005).

Order Athyridida, Suborder Athyrididina, Superfamily Athyridoidea, Family Comelicaniidae

Subfamily Araxathyriinae Shen, Grunt, & Jin, 2004, p. 888.

Order Athyridida, Suborder Athyrididina, Superfamily Athyridoidea, Family Comelicaniidae, Subfamily Sprigerellinae

Transcaucasathyris Shen, Grunt, & Jin, 2004, p. 893 [**Araxathyris araxensis* Grunt in Ruzhentsev & Sarytcheva, 1965, p. 247; OD].

Shen Shu-Zhong, T. A. Grunt, & Jin Yu-Gan. 2004. A comparative study of Comelicaniidae Merla, 1930 (Brachiopoda: Athyridida) from the Lopingian (Late Permian) of south China and Transcaucasia in Azerbaijan and Iran. Journal of Paleontology 78(5):884–899.

Order Athyridida, Suborder Athyrididina, Superfamily Athyridoidea, Family Athyrididae, Subfamily Cleiothyridininae

Baliqliqia Chen & Shi, 2006, p. 29 [**B. baliqliqensis;* OD].

Chen Z. Q., & Shi G. R. 2006. Artinskian-Kungurian (Early Permian) brachiopod faunas from the Tarim Basin, Northwest China. Part 2: Paleobiogeography, and systematics of Orthotetida, Orthida, Spiriferida, Spiriferinida, Rhynchonellida, Athyridida and Terebratulida. Palaeontographica (Abt. A) 275(1-3):1–53.

Order Athyridida, Suborder Athyrididina, Superfamily Athyridoidea, Family Athyrididae, Subfamily Spirigerellinae

Tarimathyris CHEN & SHI, 2006, p. 31 [**Athyris postambigua* USTRITSKY, 1960; OD].

Chen Z. Q., & Shi G. R. 2006. Artinskian-Kungurian (Early Permian) brachiopod faunas from the Tarim Basin, Northwest China. Part 2: Paleobiogeography, and systematics of Orthotetida, Orthida, Spiriferida, Spiriferinida, Rhynchonellida, Athyridida and Terebratulida. Palaeontographica (Abt. A) 275(1-3):1–53.

Order Terebratulida, Suborder Terebratulidina, Superfamily Cryptonelloidea, Family Cryptonellidae

Albelenina PEREZ-HUERTA, 2004, p. 1528 [**A. alvarezi* PEREZ-HUERTA, 2004, p. 1531; OD].

Pérez-Huerta, Alberto. 2004. New Carboniferous brachiopods from the eastern Great Basin, Nevada, USA: Implications for loop ontogeny and evolution in Late Paleozoic terebratuloids. Palaeontology 47(6):1519–1537.

Order Terebratulida, Suborder Terebratulidina, Superfamily Loboidothyridoidea, Family Muirwoodellidae

Lusothyris ANDRADE, 2006, p. 85 [**L. atlantica*; OD]. Middle Jurassic (Bajocian). Portugal.

Andrade, Benito. 2006. Los braquiópodos del tránsito Jurásico Inferior-Jurásico Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56:5–194.

Order Terebratulida, Suborder Terebratulidina, Superfamily Stringocephaloidea, Family Rhenorensselaeriidae

Crassirensselaeria SCHEMM-GREGORY & JANSEN, 2007, p. 415 [**Rensselaeria crassicosta* KOCH in KAYSER, 1881, p. 387; M]. Lower Devonian. Germany.

Kayser, E. 1881. Beitrag zur Kenntniss der Fauna des Taunusquarzits. Neues Jahrbuch fur Mineralogie, Geologie und Palaontologie 1881:386–387.

Schemm-Gergory, M., & U. Jansen. 2007. A new genus of terebratulid brachiopod from the Siegenian of the Rheinisches Scheifergebirge. Acta Palaeontologica Polonica 52(2): 413–422.

Order Terebratulida, Suborder Terebratellidina, Superfamily Zeillerioidea, Family Zeilleriidae

Neozeilleria ANDRADE, 2006, p. 119 [**Terebratula (Waldheimia) sharpei* CHOFFAT, 1947; OD]. Lower Jurassic (Toarcian)–Middle Jurassic (Bajocian). Portugal, Spain, England, France, Germany.

Andrade, Benito. 2006. Los braquiópodos del tránsito Jurásico Inferior-Jurásico Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56:5–194.

Order Terebratulida, Suborder Terebratellidina, Superfamily Laqueoidea, Family Laqueidae

Lusitanina ANDRADE, 2006, p. 143 [**L. bituminis;* OD]. Middle Jurassic (Bajocian). Portugal.

Andrade, Benito. 2006. Los braquiópodos del tránsito Jurásico Inferior-Jurásico Medio de la Cuenca Lusitánica (Portugal). Coloquios de Paleontología 56:5–194.

Order Terebratulida, Superfamily Compositelasmatoidea, Family Compositelasmatidae

Compositelasma SMIRNOVA, 2006.

Smirnova, T. N. 2006. New Upper Permian Superfamily Compositelasmatoidea (Brachiopoda, Terebratulida) from the East of the Russian Platform: The Specificity of Ontogenetic Transformations. Paleontological Journal 40(1):66–74.

Order Rhynchonellida, Superfamily Hemithiridoidea, Family Tetrarhynchiidae, Subfamily Viarhynchiinae

Antulanella B. RADULOVIČ in RADULOVIČ, MOTCHUROVA-DEKOVA, & RADULOVIČ, 2007 [**Rhynchonella Pancici* ANTULA, 1903; OD]

Radulovič, Barbara, Neda Motchurova-Dekova, & Vladan Radulovič. 2007. New Barremian rhynchonellide brachiopod from Serbia and the shell ultrastructure of Tetrarhynchiidae. Acta Palaeontologica Polonica, in press [cf. Abstracts, Fifth International Brachiopod Congress, Copenhagen 2005: 46–47].

Order Terebratulida, Suborder Terebratellidina, Superfamily ?Kingenoidea

Laurinia ZEZINA, 2005, p. 31 [**Fallax neocaledonensis* LAURIN, 1997, p. 444; OD]. Holocene. West Pacific (New Caledonia, Norfolk Ridge). [This genus is probably a synonym of *Fallax*.]

Zezina, O. N. 2005. On the systematic position of some recent brachiopod species from the Norfolk Ridge (West Pacific). Invertebrate Zoology, Moscow University 2(1):29–33.
In Russian.

ANATOMY

CARSTEN LÜTER

[Museum für Naturkunde der Humboldt-Universität zu Berlin]

INTRODUCTION

The following chapter contains new findings on brachiopod anatomy since the publication of volume 1 of the revised *Treatise* (WILLIAMS & others, 1997). The chapter's structure follows that of the anatomy section in volume 1. Where necessary, new subheadings were introduced. Some new results not only update the anatomy section but also contradict former interpretations given by WILLIAMS and others (1997). Whenever new results have led to new interpretations, the qualified section in volume 1 is cited. This gives the reader the opportunity for comparison and also provides a living picture of the progress being made in brachiopod research.

During the last decade brachiopod embryology and development have been studied in detail in order to understand the origin and formation of certain organ systems like metanephridia, nerve system or mesoderm, and coelom. The results of these investigations clearly show that brachiopod anatomy can hardly be understood without knowledge of the developmental processes leading to observations of adult morphology. Additionally, morphological characters of larval and juvenile brachiopods may provide a reliable set of hitherto unused soft tissue character sets, which are invaluable for future analyses of brachiopod phylogeny. Here, Fritz MÜLLER's drawing from 1859 may be reminiscent of the beginning of brachiopod developmental research (Fig. 1500).

MANTLES AND BODY WALLS

MARGINAL (LARVAL AND ADULT) SETAE

The ultrastructural reinvestigation of marginal setae in subadult *Lingula anatina* and the subsequent comparison with and new findings on setae growing from setal sacs in lecithotrophic larvae of rhynchonelliforms and early developmental stages of *Discinisca* sp. cf. *tenuis* showed differences not only in diameter of the setae of larvae and adults (see WILLIAMS & others, 1997, p. 52), but also in their composition and the secretory regime of the chaetoblast (LÜTER, 1998b, 2000b, 2001a). While *Lingula anatina*, when in its planktonic stage, does not possess any marginal setae, setal growth in the lecithotrophic larvae of, for example, the rhynchonelliform brachiopods *Notosaria nigricans* and *Calloria inconspicua* commences after mantle lobe formation during their early larval phase. As outlined by many authors, the setae of these larvae are arranged in four setal bundles (a dorsal pair and a dorsolateral pair).

In general, the overall architecture of brachiopod setae is the same in both larvae and adults, but the origin of the setal material and the composition of the epidermal invagination housing these setae is different. In postmetamorphic stages of brachiopods (juveniles to adults), each seta (called adult seta hereafter) is located in an epidermal or ectodermal invagination of cells, called the setal follicle (Fig. 1501). At the bottom of this follicle, the cup-shaped chaetoblast secretes setal material at the basis of its apical microvilli. These microvilli are of almost identical length and serve as a template for the future inner structure of the growing seta. Distally, the adult seta is accompanied by several follicle cells (the epidermal cellular lining of the follicle), which are also involved in setal construction. Comparable to the invaginated apical cell surface of the chaetoblast, each follicle cell bears an apical row of microvilli. These microvilli are connected to the setal surface by intermediate filaments (Fig. 1502a), which are cytokeratin components of the cytoskeleton (not chitinous fibers as assumed by WILLIAMS & others, 1997). These intermediate filaments run from cell-matrix contacts

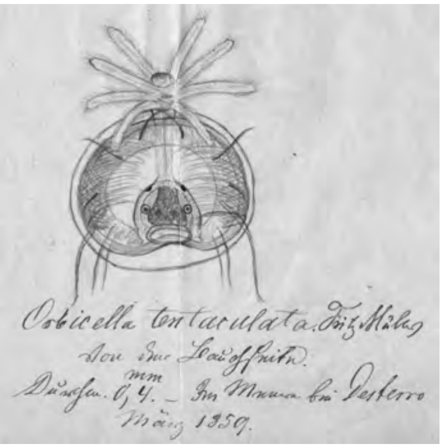


FIG. 1500. First picture of a brachiopod developmental stage, a pelagic juvenile of a discinid, drawn by Fritz Müller in a letter to his friend Max Schultze in March 1859; Müller wrote that the relationship to brachiopods is obvious, but he could not decide whether it was a larva of a brachiopod or not, mainly because he had not seen any adult brachiopods at the Desterro coast; provisionally, he named the new animal "*Orbicella tentaculata;*" in 1860 Müller described his new animal as the larva of a brachiopod, and his original lead pencil drawing was used as an illustration (Müller, 1860, taf. 1B,*2;* original letter courtesy of H. Lorenzen, Bovenden, Germany).

(hemidesmosomes) at each follicle cell's basal membrane through the cell body toward the tips of the microvilli, where they end in a hemidesmosome-like connective structure between the cell membrane and the extracellular setal material (Fig. 1502a). Due to their stiff texture, intermediate filaments provide a rather inelastic but strong connection between extracellular matrices and cells, so that the adult setae in *Lingula anatina* can be moved by contraction of well-developed muscle cells surrounding the setal follicle.

As stated correctly in volume 1 (WILLIAMS & others, 1997), the follicle cells are involved in the construction of each adult seta by secreting its outermost layer. In *Lingula anatina* this outermost layer consists of four sheets of setal material with differing electron density (Fig. 1502b; LÜTER, 2000b).

GUSTUS and CLONEY (1972) stated that the outermost setal layer, which they called enamel, is missing in brachiopod setae, but they were looking at lecithotrophic larvae of the rhynchonelliform brachiopod *Terebratalia transversa* and, similar to all other brachiopod larvae investigated so far, their larval setae indeed lack this outermost layer due to the differences in construction of brachiopod adult and larval setae (for definition of the term brachiopod larva, see Embryology and Development, p. 2339 herein).

With the exception of larvae of Thecideoidea and those of the terebratellides *Argyrotheca cistellula* (see GROBE & LÜTER, 1999) and *Macandrevia cranium* (see D'HONDT & FRANZEN, 2001) all brachiopod larval stages studied so far do have setae (called larval setae hereafter) of similar construction but differing arrangement. Early developmental stages of the linguliforms *Discinisca* sp. cf. *tenuis* from Namibia (LÜTER, 2001a) and *Discinisca strigata* from Panama (FREEMAN, 1999) have one pair of terminal bundles of larval setae, all rhynchonelliform brachiopod larvae (except those without setae) have two pairs of setal bundles (a dorsal and a dorsolateral pair), and those of the craniiform *Novocrania anomala* have three dorsal pairs of larval setae (NIELSEN, 1991).

Larval setae are exclusively produced by the chaetoblast. Several chaetoblasts are arranged in a cup-shaped invagination of the larval epidermis, the so-called setal sac. Either two (discinides), four (all rhynchonelliforms), or six (*Novocrania*) setal sacs can be found in the larvae. The process of production and release of setal material and the arrangement of the chaetoblast's apical microvilli forming a template for the inner setal structure are similar in both adults and larvae. The major difference is the lack of follicle cells in the larval epidermis. Larval setae in *Discinisca* sp. cf. *tenuis*, *Novocrania anomala*, *Notosaria nigricans,* and *Calloria inconspicua*, representing four Recent brachiopod superfamilies, have been observed to be accompanied only by a single epidermal cell (apart from the chaetoblast itself) before emerging from the larval body (Fig. 1503.1–1503.4; NIELSEN, 1991; LÜTER, 1998b, 2000b, 2001a; GROBE, 1999). This specialized epidermal cell looks like a thick-walled

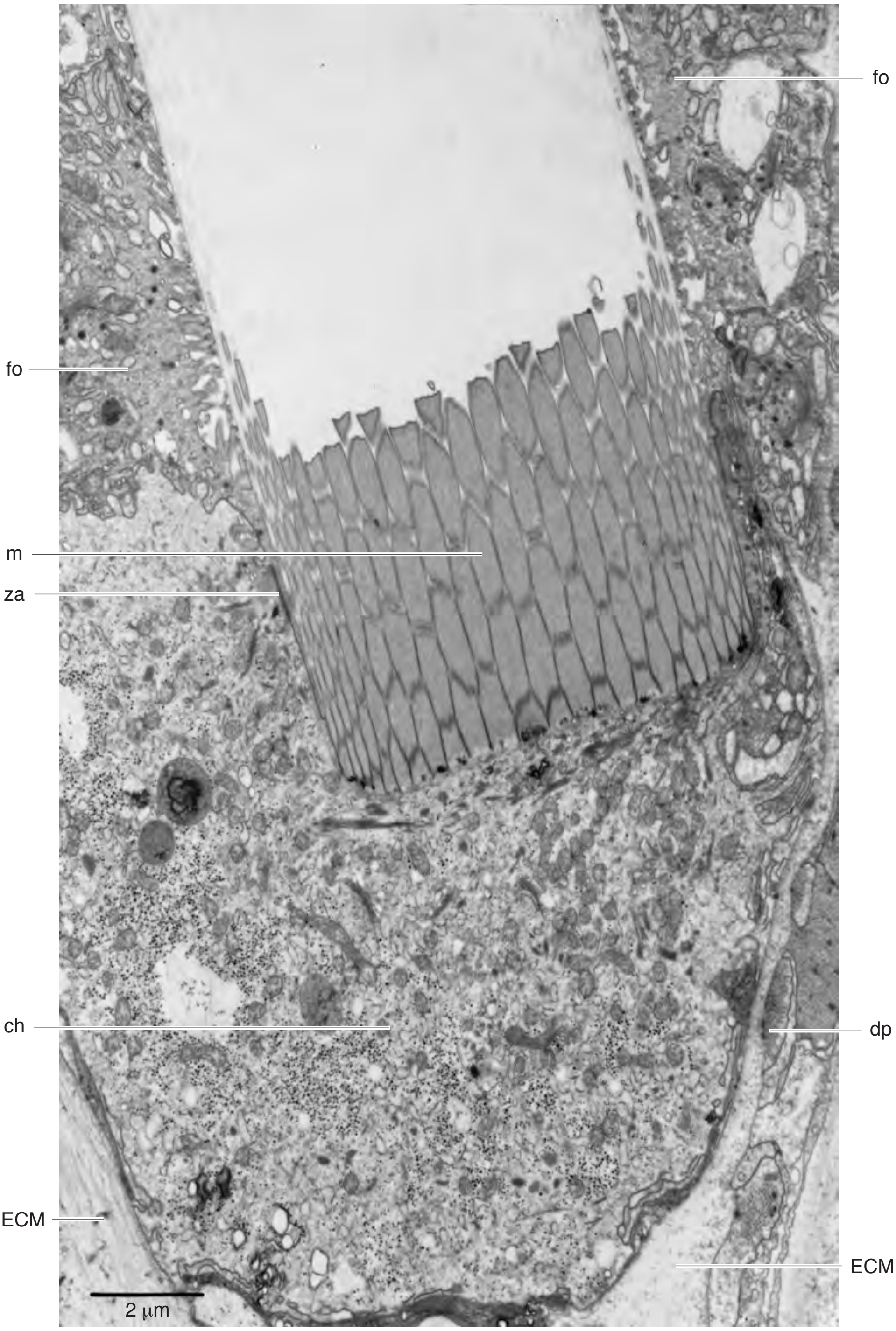


FIG. 1501. TEM micrograph of longitudinal section of setal follicle of *Lingula anatina*; chaetoblast (*ch*) is surrounded by collagenous extracellular matrix (*ECM*) and epithelial muscle cells connected to extracellular matrix by so-called dense plaques (*dp*); basal part of each setal canal filled with a microvillus (*m*). Adjacent to chaetoblast, follicle cells (*fo*) connect to setal surface through apical microvilli; *za*, zonula adhaerens (Lüter, 1998b).

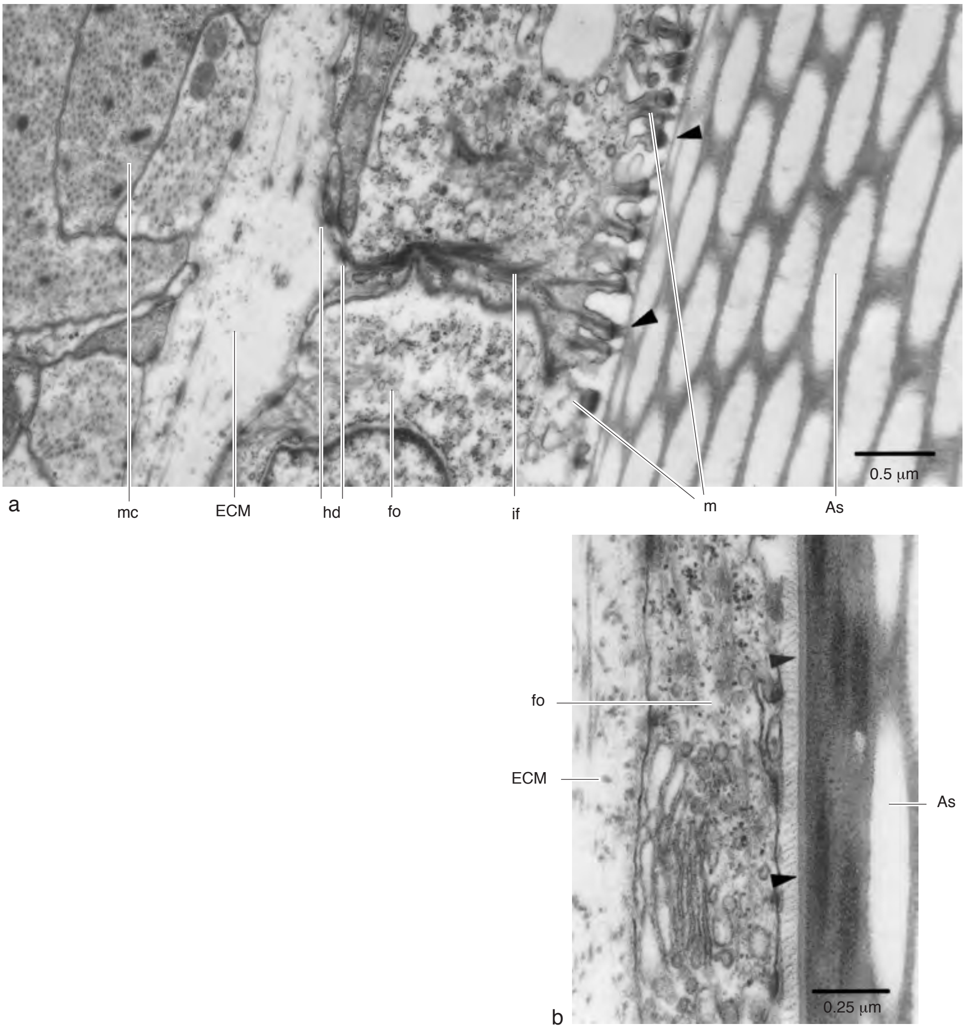


FIG. 1502. TEM micrographs of adult setae (*As*) of *Lingula anatina; a*, intermediate filaments (*if*) of follicle cells (*fo*) connect extracellular matrix and setal surface through basal hemidesmosomes (*hd*) and apical, hemidesmosomal-like contacts (*arrowheads*) at tips of follicle cell's microvilli (*m*); *b*, outer or enamel layer of adult seta consisting of four layers with differing electron density (*arrowheads*); *ECM*, extracellular matrix (Lüter, 2000b).

FIG. 1503. Reconstructions of brachiopod larval setae based on TEM cross sections; only two cells are involved, the chaetoblast and one specialized epidermal cell; *1*, larval seta (*ls*) of *Discinisca* sp. cf. *tenuis*; notice contact between specialized epidermal cell (*Epi*) and spine of larval seta (*arrow*) (Lüter, 2001a); *2*, larval seta of *Novocrania anomala*; the specialized epidermal cell (*Epi*) still produces a cilium (*Ci*), which runs parallel to larval seta through cell's tubelike canal; the microvilli of specialized epidermal cell do not contact larval setal surface (Grobe, 1999); *3*, larval seta (*Ls*) of *Notosaria nigricans;* setal spines (*sp*) of larval setae are made from setal material released by peripheral microvilli; *4*, larval seta (*Ls*) of *Calloria inconspicua*; next to specialized and invaginated epidermal cell (*inec*) a collar receptor cell (*co*) can be found; notice synaptic contact (*arrowhead*) of basal process of collar receptor cell to basiepidermal nerve cells (*nc*); *ch*, chaetoblast; *Coea*, cell of coelomic anlage; *ECM*, extracellular matrix; *mf*, myofilaments; *za*, zonula adhaerens (Lüter, 2000b).

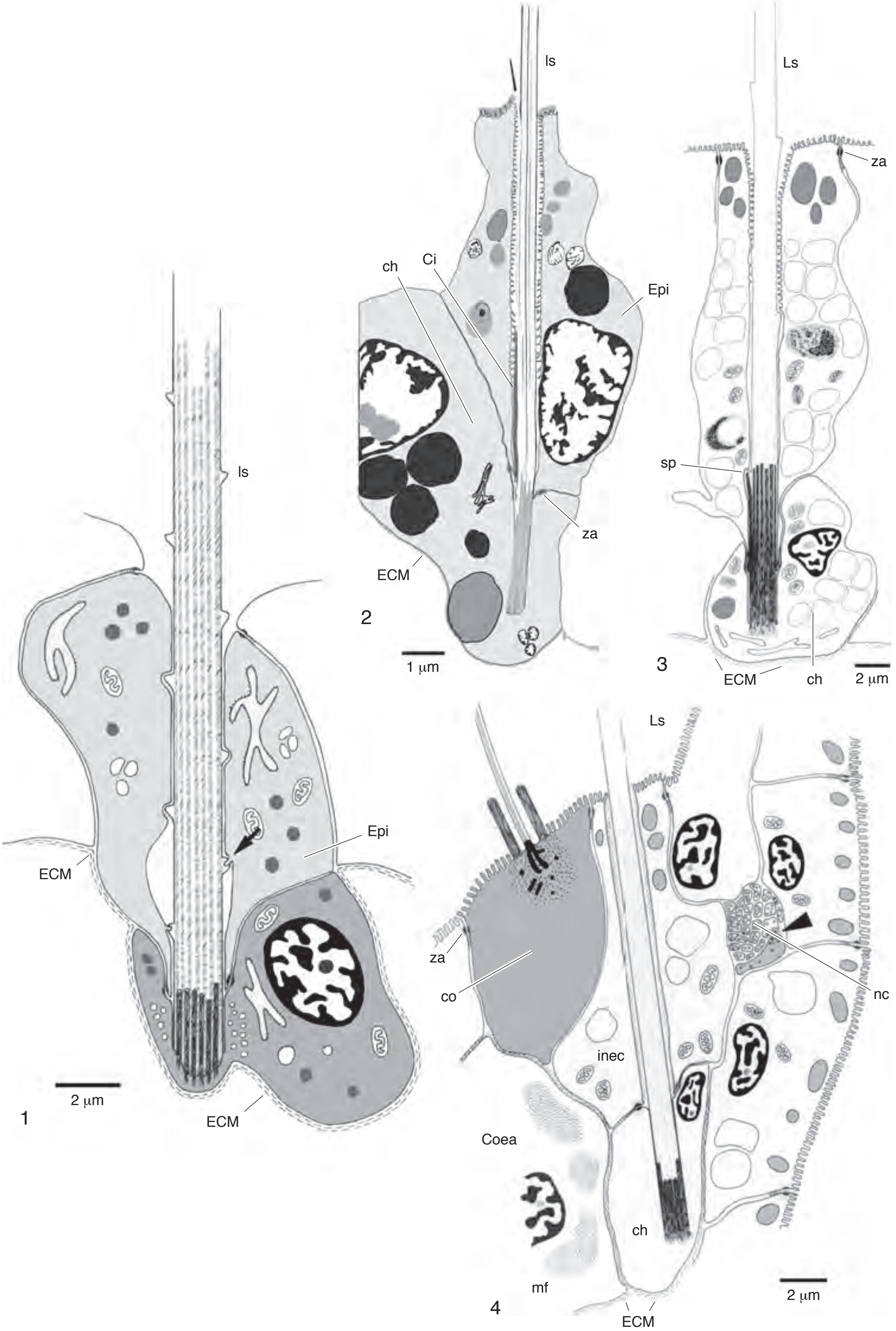


FIG. 1503. *For explanation, see facing page.*

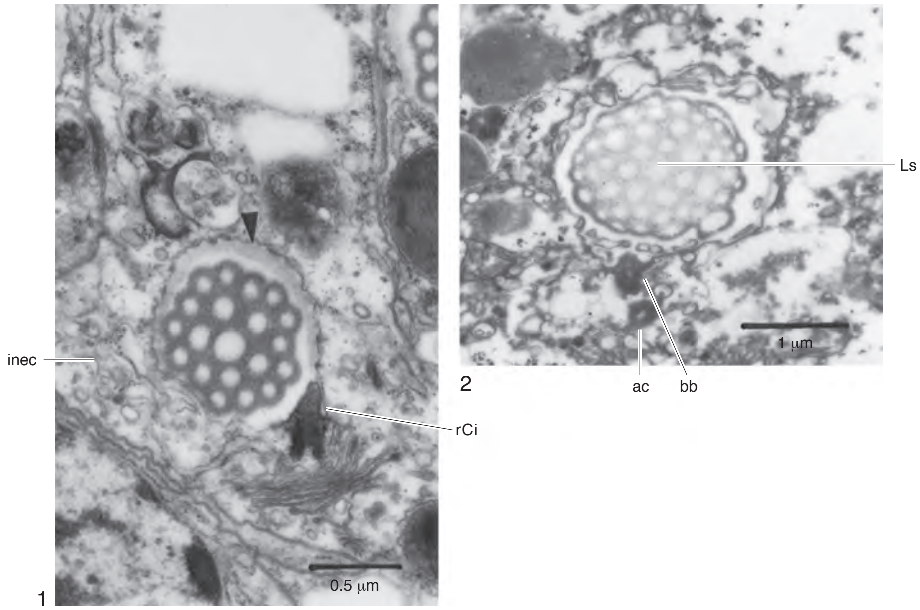


Fig. 1504. TEM micrographs of larval setae with accompanying rudimentary cilium; *1*, cross section of larval seta of *Calloria inconspicua*; specialized and invaginated epidermal cell (*inec*) bearing a rudimentary cilium (*rCi*); notice the glycocalyx (*arrowhead*) on cell surface; *2*, cross section of larval seta (*Ls*) of *Notosaria nigricans*; notice basal body (*bb*) and accessory centriole (*ac*) of rudimentary cilium (Lüter, 2000b).

tube, with its wall built by the cell soma. The longitudinal tubelike perforation enables the larval seta to pass through the cell toward the outside. In the tube the cell membrane of the specialized cell has no connection to the setal surface. Even if short microvilli are present, which in *Discinisca* sp. cf. *tenuis* can touch the setal surface, hemidesmosome-like connecting structures, as described for a setal follicle in adult brachiopods, cannot be observed. Additionally, each specialized cell surrounding a larval seta bears a rudimentary apical cilium, which projects into the tubelike perforation. Such a rudimentary cilium was already documented by Nielsen (1991, fig. 12A–C) for the larva of *Novocrania anomala,* and its presence was confirmed by Grobe (1999). Lüter (1998b, 2000b, 2001a) found this cilium also in the specialized cells of *Discinisca* sp. cf. *tenuis*, *Notosaria nigricans,* and *Calloria inconspicua* (Fig. 1504.1–1504.2).

Since follicle cells and their microvillous connection to the (adult) setal surface are responsible for production of the outermost setal layer, the latter is absent in brachiopod larval setae. In *Discinica* sp. cf. *tenuis* the specialized epidermal cell is folded around each larval seta so that a double cell membrane can be observed where the two sides of the cell are connected to each other. In rhynchonelliform brachiopod larvae and *Novocrania* (Lüter, 2000b; Grobe, 1999), each larval seta runs through the cell, with the tube forming during setal growth as a subsequent invagination (from inside to outside) of the epidermal cell's membrane. In contrast to adult setae, the larval equivalent is not connected to the accompanying cells (except the basal connection to the chaetoblast), and therefore active movement of setae by muscle contraction is impossible. Spreading of larval setae, observed in all larvae as possible defending behavior, is provided by complete contraction of the animal's longitudinal muscles. The resulting pressure within the body cavity forces the deeply invaginated setal sacs to shift toward the body surface. The epidermal layer is thereby stretched out like the rubber

FIG. 1505. TEM micrograph of intermediate filaments (*if*) connecting curved seta (cs) of pelagic juvenile of *Discinisca* sp. cf. *tenuis* with extracellular matrix (*ECM*) surrounding setal follicle; notice close contact of follicle cell's intermediate filaments (*if*) and epithelial muscle cells (*mc*) (new).

membrane of a squeezed balloon, leading to a passive process of setal spreading.

In contrast to the pelagic juveniles of linguloid brachiopods, the bivalved developmental stages of *Discinisca* sp. cf. *tenuis* develop five pairs of special marginal setae, which outreach the setae of the usual marginal setal fringe in both length and diameter. They were called curved setae by CHUANG (1977) or juvenile setae in WILLIAMS and others (1997). CHUANG separated them, together with what he called flexible setae of the mantle margin, from the larval setae of the unshelled earlier stages. These curved setae are clearly adult setae (see above). They are built within a setal follicle consisting of a basal chaetoblast and an adjacent row of follicle cells. The follicle cells are connected to the setal surface by intermediate filaments (Fig. 1505), and the ultrastructure of these setae is identical with the ultrastructure of marginal setae of already sessile linguloid brachiopods.

The most prominent pair of these curved setae appears at the caudal margin of the mantle. In dorsal view these setae are somewhat shaped like an inverted S. The tip of these setae has a prickly appearance in SEM pictures due to little spines covering the seta. These spines are products of peripheral microvilli of the chaetoblast, and they can also be found on larval setae of various groups and on the surface of adult setae of *Lingula anatina* for example. The growth process of adult setae is basically the same in all brachiopods: when the seta starts growing, the template for the first setal canals is built by only a few apical microvilli of the chaetoblast. Broadening the seta requires more microvilli in the periphery of the already-secreted setal material. In *Lingula anatina*, the chaetoblast's acquisition of peripheral microvilli is a highly coordinated process, which leads to a horsetail-like appearance of the setae, with peripheral setal canals ending up in a circle of spines (Fig. 1506; LÜTER, 1998b, 2000b). In the pelagic juvenile of *Discinisca* sp. cf. *tenuis,* every now and then a single peripheral microvillus is added to the chaetoblast's apical cell surface, having the effect that the spines on the curved setae are irregularly distributed over the setal surface. This has been shown for the adult marginal setae of *Discina striata* in WILLIAMS and others (1997, p. 53, fig. 47.2).

EXCRETORY SYSTEM

Brachiopods have one pair of metanephridia, except for rhynchonelloids, which have two pairs. In mature animals, the metanephridia additionally serve as gonoducts. Their excretory function can only be proven indirectly by ultrastructural details of the epithelial cells involved (LÜTER, 1995, 1998b). In principal, metanephridia are open canals connecting the secondary body cavity (coelom) and the outer medium. Such an open canal *per se* cannot work as an excretory organ. It directly depends on the process of ultrafiltration into the body cavity from an at least partly closed blood circulation system bounded by extracellular matrix (ECM). Blood pressure drives the filtration process by forcing low molecular waste molecules through the vessel-surrounding ECM. On the coelomic side, areas of filtration are characterized by a specialized coelomic epithelium with either gaps between single epithelial cells (fenestrated epithelium) or with podocytes. Both gaps and podocytes provide a direct neighborhood of blood vessels and the body cavity, separated only by a thin molecular sieve consisting of the fibrillar network of the ECM. So far, these filter structures have not been observed in brachiopods. It is therefore unclear whether metanephridia in brachiopods are functional excretory organs or not (LÜTER, 1995, 1998b).

On the other hand, the metanephridia show ultrastructural details typical for cells resorbing metabolites during excretion. Each metanephridium can be separated in two parts: a funnel-shaped nephrostome facing the body cavity and an outleading canal, open to the outer medium through a nephridiopore. In adult *Novocrania anomala* and *Terebratulina retusa*, one can observe a gradual change in the shape of the cells from the funnel toward the canal so that a distinction between funnel epithelium and canal epithelium is difficult (Fig. 1507; LÜTER, 1995). Pelagic juveniles of *Lingula anatina* (with six pairs of tentacles) already have fully developed metanephridia, and a distinction is possible. Five to seven cuboid nephrostome cells along the prospective funnel can be observed. In this early stage of development the funnel-like shape is not yet developed (Fig. 1508a). The prospective epithelial cells of the nephridial funnel can be distinguished from the coelomic epithelium by their lack of contractile filaments in the cytoplasm. In cross section, the prospective funnel is built by two nephrostome cells (Fig. 1508b). Additionally, the nephrostome cells have, if at all, very few, short microvilli extending into the lumen of the prospective funnel (Fig. 1508b). The cells of the canal epithelium look completely different. They are very large cells, with their cell apices extended into a dense row of very long microvilli (Fig. 1508c–1508d). At the base of these microvilli many coated pits and coated vesicles can be observed—a sign of active resorption from the lumen of the outleading

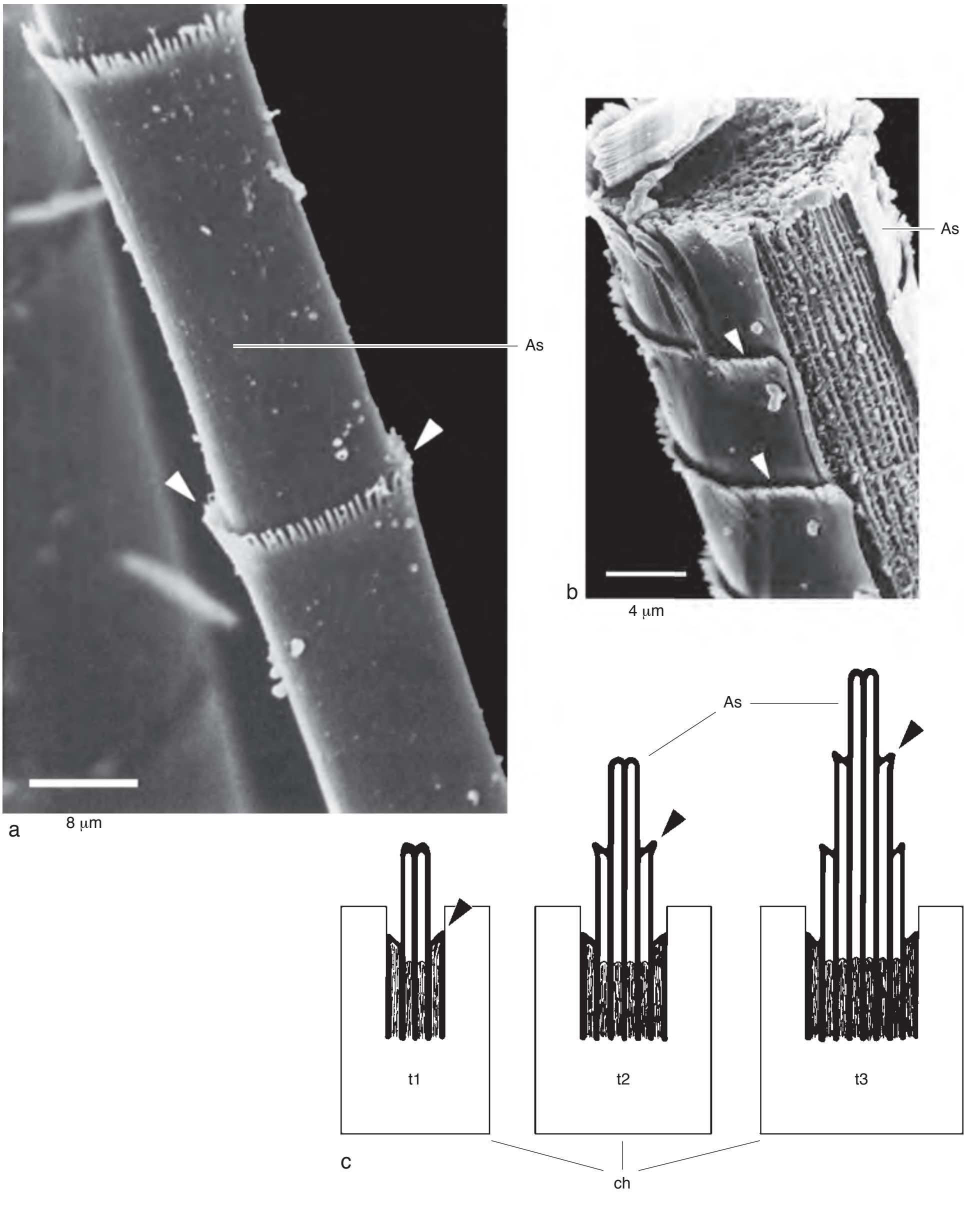


FIG. 1506. SEM micrographs and reconstruction of adult setae and their building process in *Lingula anatina*; *a*, detail of adult seta (*As*) showing its horsetail-like appearance due to regular circles of spines (*arrowheads*) produced by peripheral microvilli of the chaetoblast; *b,* fragment of an adult seta (*As*) illustrating architecture with each sheath of peripheral setal canals overlain by next younger layer (*arrowheads*); *c,* schematic reconstruction of growth process of adult seta (*As*) with chaetoblast (*ch*) shown at three different observation times (*t1*, *t2*, *t3*); simultaneously, new peripheral microvilli are built by chaetoblast, surrounding growing seta and secreting material for new peripheral layer of setal canals; *arrowheads* mark same setal canal at different times (Lüter, 2000b).

canal into the cells and a typical feature of a metanephridium at work (Fig. 1508c). According to these observations, brachiopod metanephridia are composed of two different cell types that may have originated from different epithelia. The nature of brachiopod metanephridia as heterogeneously assembled organs with a coelomic part (nephrostome)

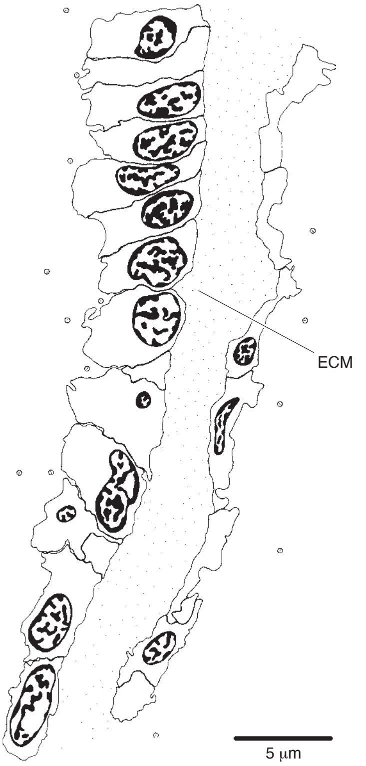


FIG. 1507. Reconstruction of gradually changing cells from funnel toward canal epithelium on left side of extracellular matrix (*ECM*) in metanephridium of *Terebratulina retusa*; a distinction between cells derived from either mesoderm or ectoderm is not possible (Lüter, 1995).

and an ectodermal part (canal) was anticipated very early (GOODRICH, 1945). This idea was corroborated by the results in *Lingula anatina* and could be demonstrated finally by studying the larval development of *Calloria inconspicua*.

The lecithotrophic larvae of *Calloria inconspicua* in their three-lobed stage have two symmetrically arranged canals leading from a pore in the outer epithelium toward the developing body cavity (Fig. 1509a–1509b). Both canals have blind ends (Fig. 1509b–1509c). A connection to the coelomic epithelium does not (yet) exist. The cells lining each canal are specialized epidermal cells that do not differ from typical cells lining a metanephridial canal in adult brachiopods. They already have the ability of metabolite resorption, clearly demonstrated by the presence of coated pits and coated vesicles (Fig. 1509d). Early postmetamorphic juveniles are different in having an open connection (a true metanephridium) from the body cavity to the outer medium. The invaginating cells of the metanephridial canal (Fig. 1510c–1510e), which had already been present in the pelagic larva, have broken through the ECM or basal lamina (Fig. 1510a–1510b) that separates ectoderm and mesoderm and made contact with the mesodermally derived future nephrostome cells (Fig. 1510a). This contradicts PERCIVAL's (1944) statements that in *Calloria inconspicua* the metanephridia are (1) coelomoducts, growing outwardly, and (2) that they are closed until sexual maturity. In contrast, metanephridia in *Calloria inconspicua* start growing during the pelagic larval phase and grow inwardly as an invaginating canal, which in a later stage connects to the coelomic epithelium, thereby forming a heterogeneously assembled organ, consisting of a nephrostome of mesodermal origin and an outleading canal of ectodermal origin. As long as ultrafiltration from the blood vessels into the body cavity is not confirmed in brachiopods, however, their metanephridia may primarily be regarded as gonoducts.

NERVOUS AND SENSORY SYSTEM

SETAE

Marginal setae in adult brachiopods as well as larval setae play an important role in protection and defence. Once the setae are mechanically stimulated, adult brachiopods close their shell with high speed. If a lecithotrophic brachiopod larva is disturbed mechanically or chemically, the animal contracts along its anterior-posterior axis, thereby spreading the larval setae beyond the outline of its body. This is interpreted as a behavior of defense, comparable to a curling hedgehog producing its spines in the presence of a potential predator. RUDWICK (1970)

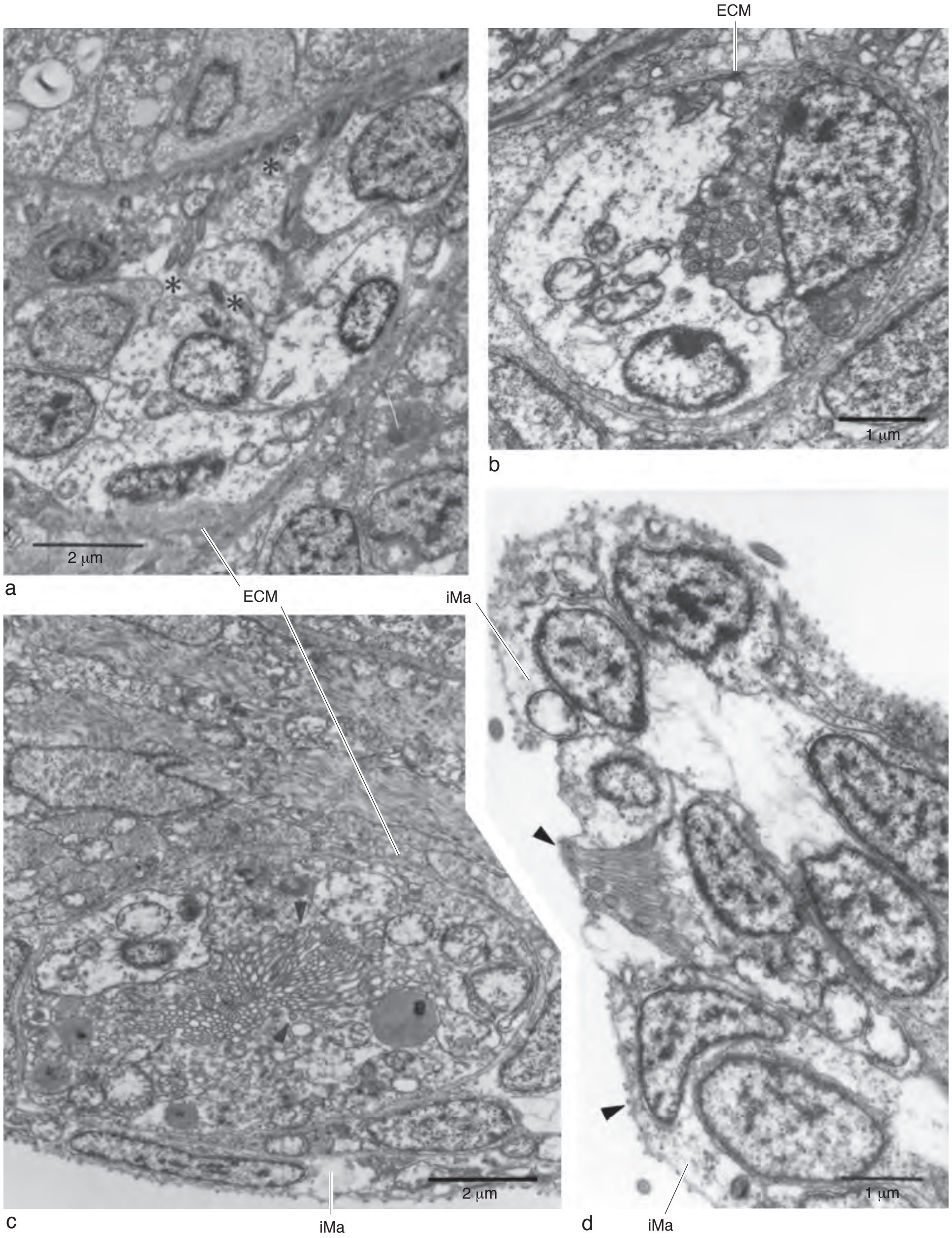


FIG. 1508. TEM micrographs of right metanephridium of pelagic juvenile (6 p.t. stage) of *Lingula anatina*; *a*, prospective nephrostome with first coelomic spaces (*asterisks*) between coelothelial cells; *b*, nephrostome further down metanephridium with only two nephrostome cells surrounding numerous cilia within prospective funnel lumen; *c*, cross section through metanephridial canal; notice long microvilli filling canal's lumen; presence of coated pits and coated vesicles (*arrowheads*) shows that canal cells are actively resorbing fluid from metanephridial lumen; *d*, nephridiopore with distalmost cell of metanephridial canal and surrounding cells of inner mantle epithelium (*iMa*). Notice length difference of microvilli of inner mantle epithelium and canal cells (*arrowheads*); *ECM*, extracellular matrix (Lüter, 1998b).

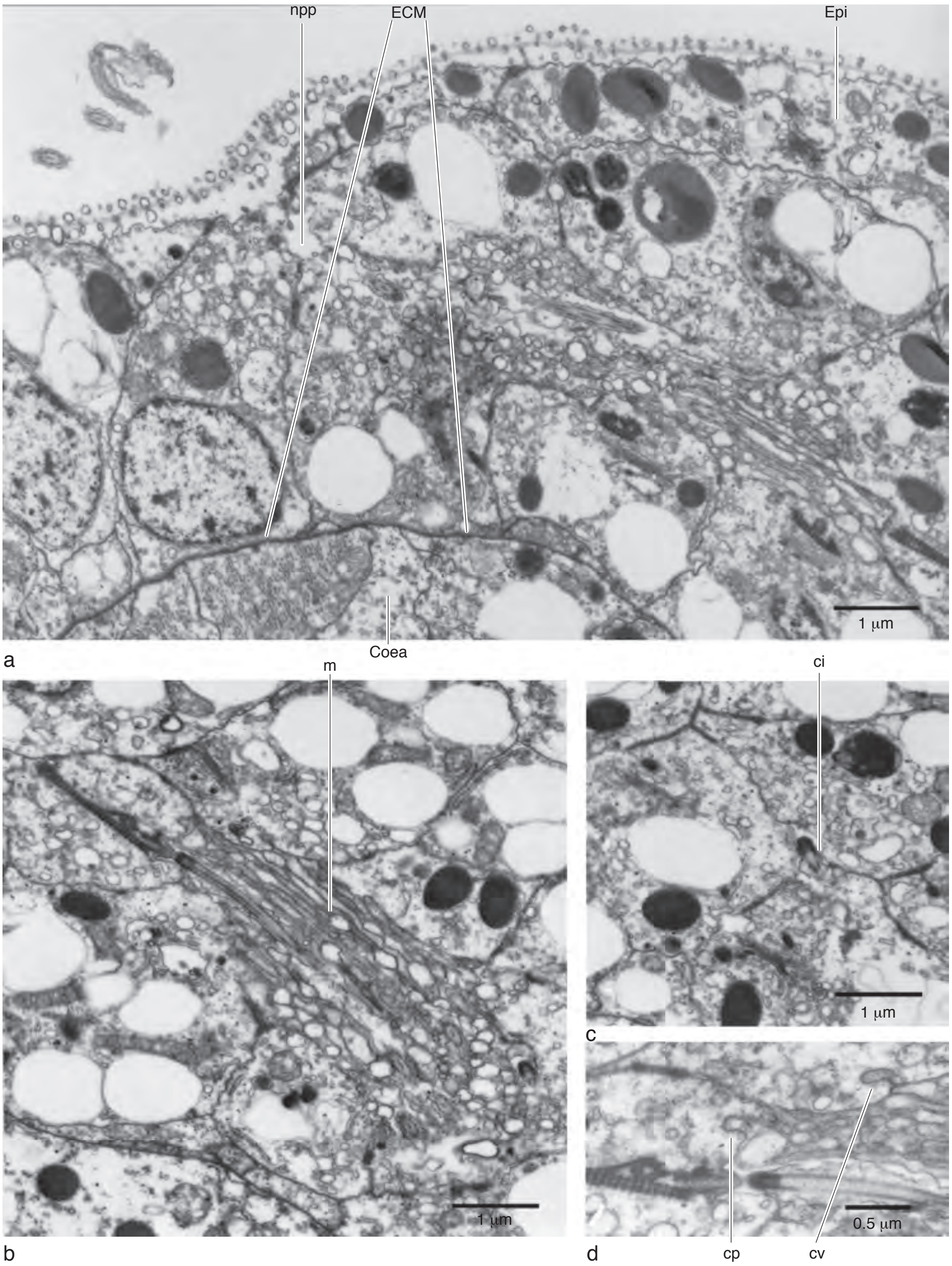


FIG. 1509. TEM micrographs of larval anlage of a metanephridium in a 3-lobed stage of *Calloria inconspicua*; *a*, nephridiopore (*npp*) opening to ventral side of larva; canal cells and epidermal cells (*Epi*) belong to same ectodermal epithelium, whereas coelomic anlage (*Coea*) is separated from ectoderm by extracellular matrix (*ECM*); *b*, lumen of metanephridial anlage with canal cells producing cilia (*ci*) and long microvilli (*m*); *c*, proximalmost canal cell of metanephridial anlage with cilium (*ci*); *d*, detail of two canal cells showing coated pits (*cp*) and coated vesicles (*cv*), indication of active resorption process (Lüter, 1998b).

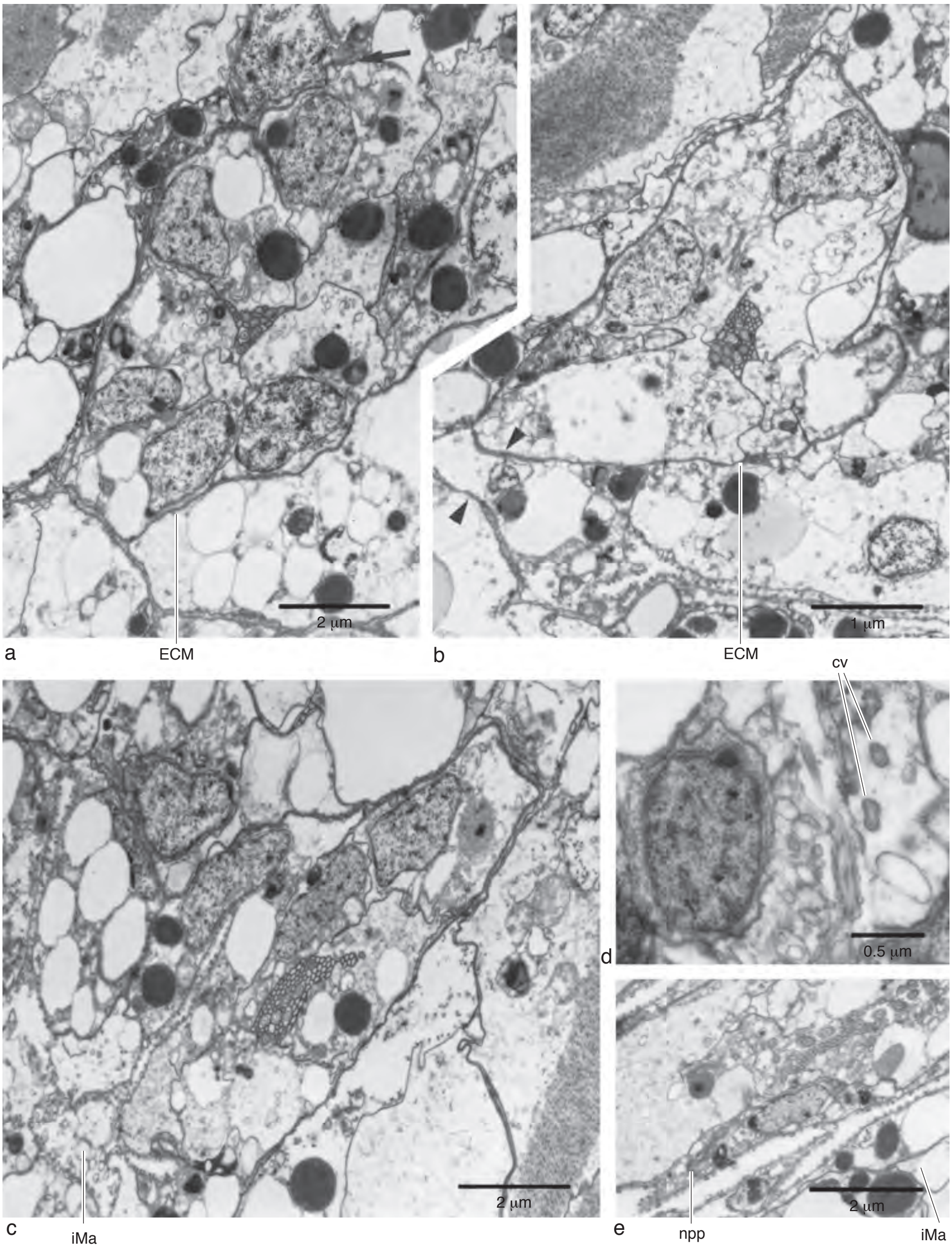


FIG. 1510. TEM micrographs of right metanephridium of postlarval *Calloria inconspicua* 9 days after metamorphosis; *a*, cross section through nephrostome with cilia filling lumen; where extracellular matrix (*ECM*) ends (*arrow*) nephrostome cells are in direct contact with myofilament-containing cells of coelomic lining; *b*, cross section of metanephridial canal showing prospective contact area (*top arrowhead*) of its surrounding extracellular matrix (*ECM*) with basal lamina (*bottom arrowhead*) of inner mantle epithelium; *c*, canal cells connect to inner mantle epithelium (*iMa*) a short distance from nephridiopore; *d*, coated vesicles (*cv*) in apical part of canal cells indicate activity of metanephridium; *e*, longitudinal section of distalmost part of metanephridial canal, showing nephridiopore (npp) in apical part of postlarval body; *iMa*, inner mantle epithelium (Lüter, 1998b).

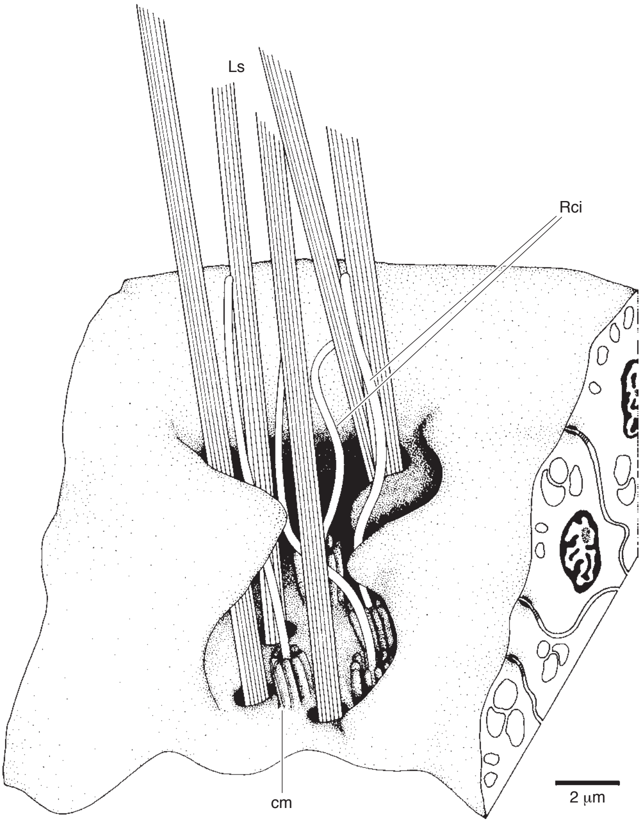


FIG. 1511. Reconstruction of sensory complex within left dorsolateral setal bundle, based on cross sections of three-lobed larva of *Calloria inconspicua* prior to metamorphosis, orientation upside down; notice receptive cilia (*Rci*) surrounded by circumciliary microvilli (*cm*) in direct neighborhood of larval setae (*Ls*) (Lüter, 2000b).

assumed a mechanical transmission of the setae's tactile properties to the mantle, since no direct connection of any seta and nerve cells had been observed and no specialized sense cells are known so far (JAMES & others, 1992). LÜTER (2000b) described a sensory complex of larval setae and collar receptor cells in the mantle anlage of three-lobed larvae of *Calloria inconspicua* (Fig. 1511; LÜTER, 2000b). As described above, larval setae of *Calloria inconspicua* are exclusively produced by a chaetoblast and accompanied by a single specialized epidermal cell, which itself has no direct connection to the setal surface. Within the setal sac of the primary receptor cells of full-grown *Calloria* larvae, so-called collar receptors can be observed in the direct neighborhood of the specialized epidermal cells. The receptor cell is monociliated, and the cilium is surrounded by a collar of nine thick and actin-filled microvilli (Fig. 1511, 1512a–1512b). The basal area of the receptor cell is filled with vesicles presumably containing a neurotransmitter, and here the collar receptor is separated from the neighboring nerve cell by a synaptic cleft (Fig. 1512c). Bending the larval setae obviously provides a mechanical stimulus transmitted onto the cilium of the receptor, and from there it travels to the nervous system, stimulating the larva to contract its longitudinal muscles. The sensory complex may also be present in *Terebratalia transversa*, as can be deduced from STRICKER and

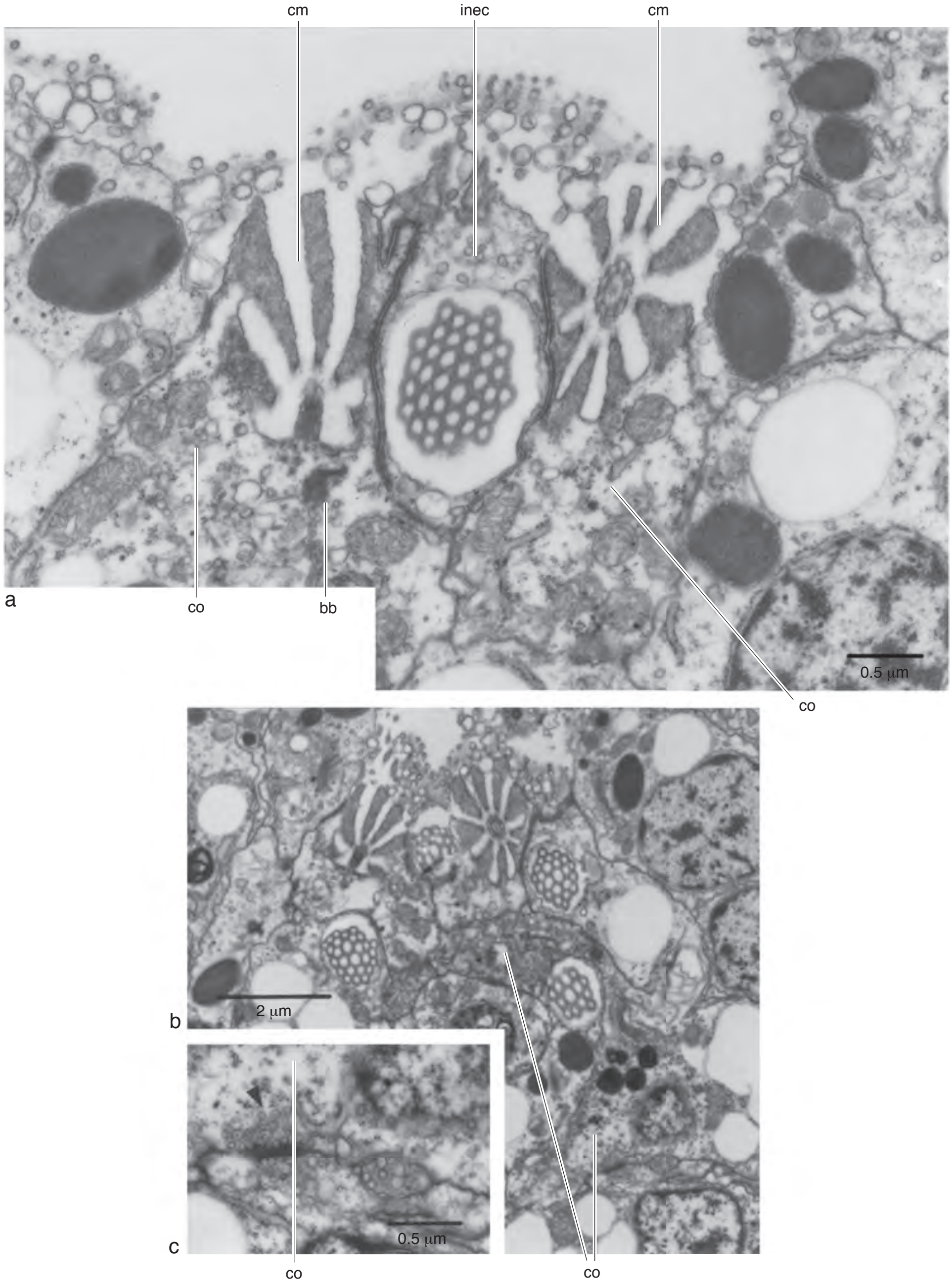


FIG. 1512. TEM micrographs of larval sensory complex in mantle lobe of three-lobed stages of *Calloria inconspicua*; *a*, alternating collar receptor cells (*co*) and specialized invaginated epidermal cells (*inec*); sensory cilium of receptor cell lacks ciliary rootlet and surrounded by a collar of 9 circumciliary microvilli (*cm*); *b*, collar receptor cells with a basal contact with nerve cells; *c*, detail of *b* showing a synaptic cleft between collar receptor (*co*) and nerve cell; notice transmitter vesicles (*arrowhead*) (Lüter 2000b).

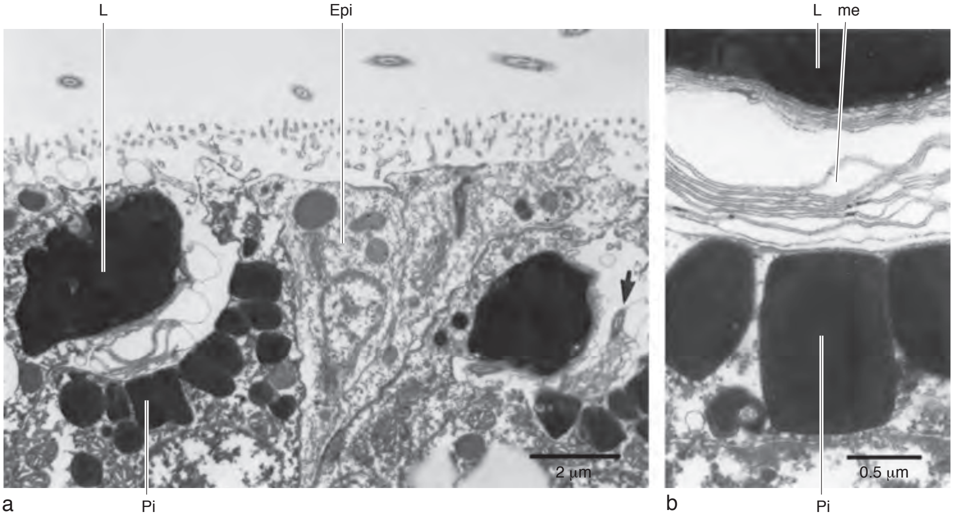


FIG. 1513. TEM micrographs of eyespots of three-lobed larval stages of *Terebratalia transversa*; *a*, eyespots embedded in epidermis (*Epi*) of apical lobe and consisting of pigment cell (*Pi*) and lens cell (*L*) with hollow space in between, filled by membrane staples from specialized cilium (*arrow*); *b*, details of pigment granules (*Pi*) in pigment cell, lens (*L*), and membrane (*me*) of cilium (Lüter, 1998b).

REED (1985a, fig. 6). This sensory complex consisting of larval setae and collar receptor cells may be an apomorphic character of terebratellid brachiopods.

EYESPOTS

Many authors report eyespots or pigment spots on apical lobes of lecithotrophic brachiopod larvae throughout the Recent superfamilies. In *Terebratalia transversa,* for example, 10 to 16 bilaterally arranged carmine-red eyespots are described. They form two rows that diverge in the anteroventral direction (LONG, 1964). Additionally, a defensive response to shading (retraction into the sediment) is reported for adult *Lingula anatina*. Their mantle margin shows numerous brownish spots that may serve as light-sensitive organs, but nothing is known about the ultrastructure of these spots.

Ultrastructural studies of larval eyespots in *Terebratalia transversa,* however, show that these eyespots are photosensitive organs composed of two specialized epidermal cells (Fig. 1513a). One sensory cell provides a cup-shaped arrangement of pigment granules (Fig. 1513a) and similarly acts as a receptor cell through a specialized, elongated cilium (Fig. 1513b) and a basal connection to the nervous system (not shown). The other cell has a bloblike apex containing a single large and electron-dark vesicle (Fig. 1513a). This cell presumably works as a lens (LÜTER, 1998b).

THE MEDIAN TENTACLE

Median tentacles only occur in lophophores of developmental stages of linguliform brachiopods (Fig. 1514a). Their occurence in lingulides and discinides has been observed many times. ROWELL (1960) and CHUANG (1974) also described a median tentacle in postsettlement stages of *Novocrania anomala*, but its occurrence in this species could not be confirmed by NIELSEN (1991). A sensory function of the median tentacle was assumed very early (YATSU, 1902; ASHWORTH, 1915; THOMSON, 1927) and was shown by LÜTER (1996) through ultrastructural studies of pelagic developmental stages of *Lingula anatina*.

The epidermal layer of the median tentacle in *Lingula anatina* contains numerous collar receptors (Fig. 1514b–1514d). They are primary receptor cells, divided in an apical cell body with a cilium surrounded by a

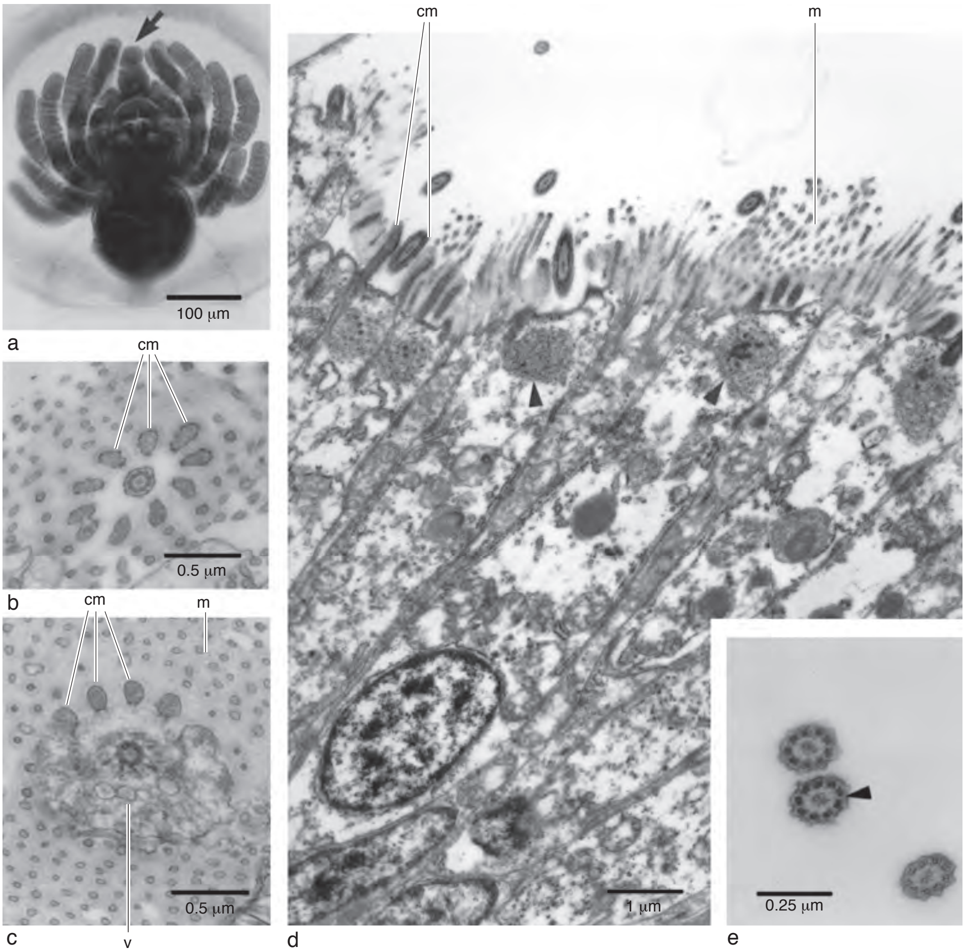


FIG. 1514. Light microscope and TEM micrographs of median tentacle of pelagic juveniles of *Lingula anatina*; *a*, light microscope micrograph of 7 p.t. stage with prominent median tentacle (*arrow*) in center of tentacle apparatus; *b–e,* TEM micrographs of 6 p.t. stage; *b*, collar of 10 circumciliary microvilli (*cm*) surrounding receptive cilium of collar receptor cells; *c*, basal body of cilium surrounded by electron vesicles (*v*); circumciliary microvilli (*cm*) conspicuously differ from normal microvilli (*m*); *d*, tip of median tentacle covered with collar receptor cells; their receptive cilia lack a ciliary rootlet, and their basal body is embedded in a ball-like structure of actin filaments (*arrowheads*); *e*, cilium of collar receptor cell with electron dark microtubuli (*arrowhead*) (Lüter, 1996, 1998b).

collar of 10 thick and actin-filled microvilli (Fig. 1514b–1514c, 1515a) and a basal axon (Fig. 1515b). The histology of these cells is unusual. The microtubules of the ciliary axoneme, apart from the central pair, are electron-dark in cross section (Fig. 1514e). This has also been observed in cilia of receptor cells in the tentacle epidermis of the Actinotroch-larva of *Phoronis muelleri*. Additionally, the sensory cilium has no rootlet. Its basal body is embedded in a ball-like structure of actin filaments (Fig. 1514d, 1515a). The basal axon is about one-tenth the diameter of the cell body and runs proximally toward the nervous system in the lophophore. The basalmost tip of the cell contains vesicles presumably filled with a neurotransmitter and is separated from the adjacent nerve cell by a synaptic cleft. Since the median tentacle is resorbed

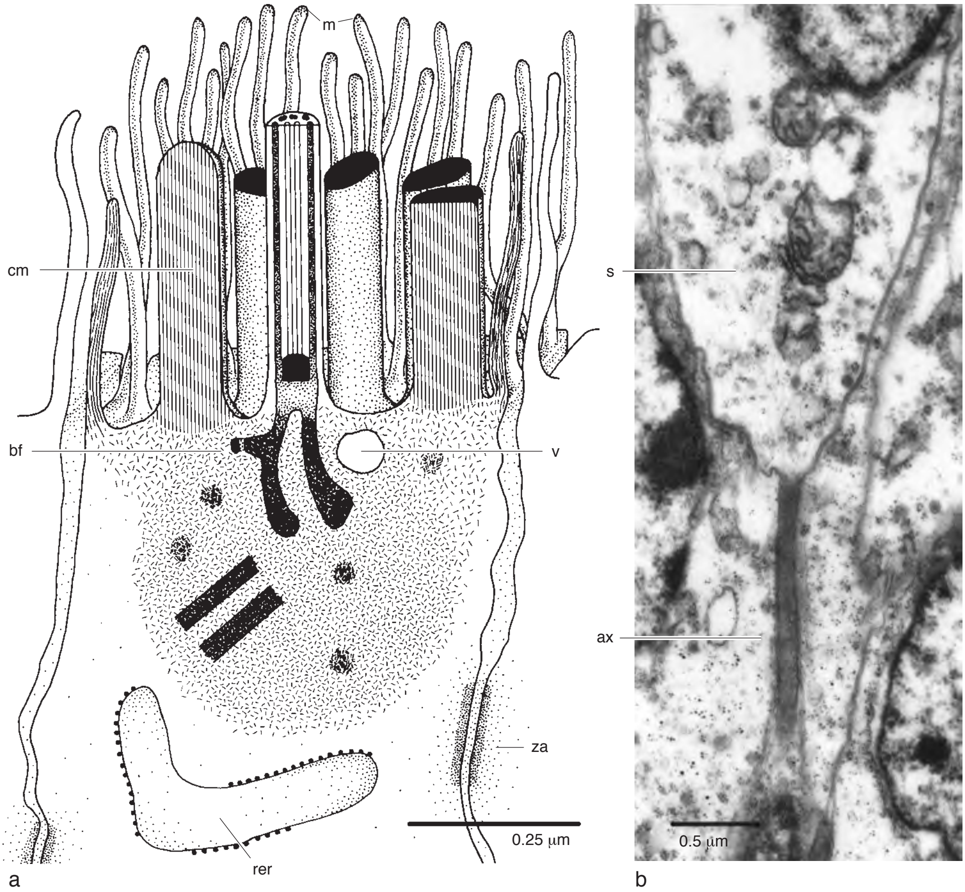


FIG. 1515. Reconstruction and TEM micrograph of receptor cell in median tentacle of 6 p.t. stage of *Lingula anatina*; *a*, reconstruction of apical part of receptor cell based on TEM cross sections; only half of cell shown; notice basal structure of receptive cilium; *b*, proximalmost part of collar receptor cell building an axon (*ax*), which connects receptor with basiepidermal nerve system; *bf*, basal foot; *cm*, circumciliary microvilli; *m*, microvilli; *rer*, rough endoplasmatic reticulum; *s*, cell soma; *v*, vesicle; *za*, zonula adhaerens (Lüter, 1996, 1998b).

in postsettlement stages of lingulides and discinides, its sensory function must be connected to the pelagic life habit of early free-swimming juveniles.

APICAL GANGLION

Studies of the development of the serotonergic system in pelagic developmental stages of *Glottidia* sp. have shown that brachiopods have an apical ganglion with numerous serotonergic neurons (HAY-SCHMIDT, 2000). The ganglion is located in the proximal half of the median tentacle and may, therefore, be a transitory morphological characteristic, since the median tentacle is resorbed during or after settlement of young linguloid brachiopods. Serotonergic cell bodies were absent along the ciliary band of the lophophore. Only two serotonergic tracts arise from the apical ganglion and project into the ciliary band. Since the concentration of serotonergic cell bodies in the apical ganglion seems to be a unique deuterostome character, HAY-SCHMIDT (2000) assumes that brachiopods (together with phoronids) are basal deuterostomes.

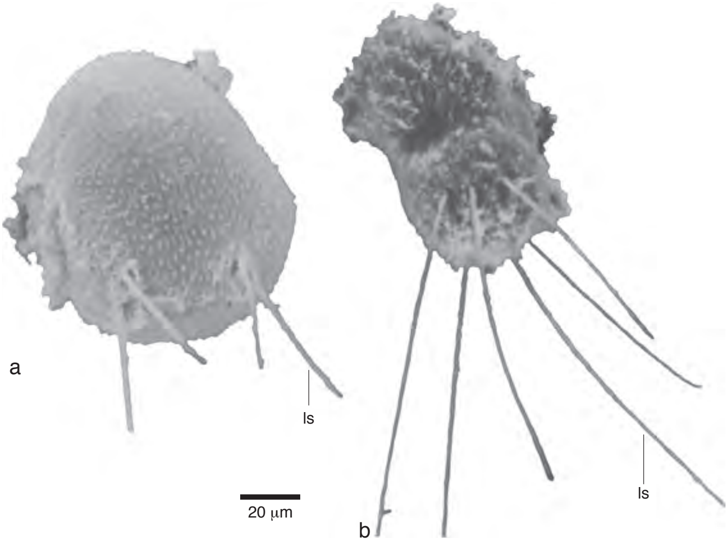


FIG. 1516. SEM micrographs of early developmental stages of *Discinisca* sp. cf. *tenuis*; *a*, embryo 20 h postinsemination, completely enclosed by vitelline membrane, with larval setae (*ls*) sticking out of egg shell; *b*, hatching stage ca. 27 h postinsemination resembling late wedge-shaped stage of rhynchonelliform brachiopods, with three larval setae (*ls*) on either side of larva (Lüter, 2001a).

EMBRYOLOGY AND DEVELOPMENT

GENERAL ASPECTS

WILLIAMS and others (1997, p. 153f.), in an attempt to standardize the terminology of brachiopod development and the corresponding developmental stages, mainly adopted the terminology of CHUANG (1990). According to CHUANG's account on brachiopod development and reproduction, all prehatching developmental stages when still surrounded by the vitelline membrane or egg shell should be named embryos. All posthatching stages, despite their obvious morphological differences in linguliform, craniiform, and rhynchonelliform brachiopods, are referred to as larvae. The postlarval or juvenile stage begins right after settlement; i.e., all juvenile stages are already immobilized through attachment on hard substrate. These definitions of developmental stages provided the basis for figure 158 in WILLIAMS and others (1997, p. 161). An extensive ultrastructural study of brachiopod development in *Lingula anatina*, *Discinisca* sp. cf. *tenuis*, *Notosaria nigricans,* and *Calloria inconspicua* (LÜTER, 1998a, 1998b, 2001a, unpublished data, 2001) led to a different conclusion. As already mentioned by LONG and STRICKER (1991), the bivalved, free-swimming stages of lingulid and discinid brachiopods resemble minute adults and therefore should be regarded as swimming juveniles rather than larvae. This is in accordance with LÜTER's results, the conclusion being that juveniles of *Lingula anatina* rather than larvae hatch from the egg shell. The stages corresponding to these free-swimming lingulid juveniles in rhynchonelliform brachiopods are their postsettlement stages. CHUANG's definition (1990) that all swimming stages are larvae and all sessile stages are juveniles or postlarvae puts too much weight on the ambient environment and the corresponding life habit of the developing brachiopods. Considering the morphology and especially the development of the excretory system (see below), CHUANG's definition does not apply. One possibility for measuring the stage of development is to count the number of pairs of lophophoral tentacles (LÜTER, 1998b). In rhynchonelliform brachiopods this is only possible in already settled postlarvae. A comparison of these postlarvae with free-swimming juveniles of lingulides or discinides shows similar progress in development: shell valves, coelomic cavities, tentacles, and coelomoducts (metanephridia) are present, and even the size of the animals is comparable.

In contrast, rhynchonelliform brachiopods hatch as ciliated gastrulae and subsequently develop such typical larval characters as an apical lobe with an apical tuft, larval setae, or a prototroch-like ring of prolonged cilia around the apical lobe for movement. All these features are missing from posthatching stages in lingulides but not in discinides. Already the prehatching stage of *Discinisca* sp. cf. *tenuis* develops a pair of setal bundles, with two larval setae each. They pierce the vitelline membrane at the caudal end of the embryo (Fig. 1516a). Finally, the hatching stage of *Discinisca* sp. cf. *tenuis* is a two-lobed larva, with long cilia on what can be identified as the apical lobe and two bundles of larval setae protruding from the future mantle (Fig. 1516b). Their overall similarity to two-lobed stages of rhynchonelliform brachiopods is striking. This provoked the following theory: Embryonic development in brachiopods takes place within the egg shell (vitelline membrane) up to a group-specific time of release (hatching): all brachiopods with true lecithotrophic development hatch as very young developmental stages, whereas discinides hatch as two-lobed larvae with (some) typical larval characters and lingulides hatch as feeding juveniles or postlarvae. In the latter two groups embryonic and larval development is either partly or fully restricted to the life phase within the egg shell (Fig. 1517; see also Table 21 for new findings on brachiopod reproductive cycles).

GAMETE MATURATION

In brachiopods, oocytes develop in close association with follicle cells, the latter building a protective sheath around each maturing egg. Prior to fertilization the oocyte has to shed the follicle cells, a process called ovulation (Fig. 1518), and in most cases the breakdown of the follicle is accompanied by a breakdown of the germinal vesicle (nucleus), with the oocyte reaching fertility through meiotic maturation. Stricker and Folsom (1997) have shown that in *Terebratalia transversa* the follicle has to be detached from the ovaries to stimulate ovulation and meiotic maturation. This is also the case in *Novocrania anomala* (Freeman, 2000). Additionally, if oocytes in *Terebratalia transversa* are mechanically stripped of their follicle cells too early after detachment of the follicle from the genital lamella, the nucleus fails to break down and meiotic maturation does not occur (Stricker & Folsom, 1997). Once the follicle is detached, the follicle cells themselves induce maturation by transferring a trigger-substance via junctional complexes connecting the follicle cells and the oolemma (Fig. 1519). Similar junctions have been observed in *Lingula* (Williams & others, 1997, fig. 150). In *Glottidia pyramidata* detachment of follicles by mechanically disrupting the ovaries fails to induce oocyte maturation, but leads to oocyte lysis (Freeman, 1994). The same is obviously true for *Lingula anatina*, since artificial insemination experiments following recipes given in Reed (1987) failed to produce embryos (C. Lüter, unpublished data, 1995). However, oocyte maturation can be induced in *Glottidia pyramidata* by incubation of ovaries with a lophophore extract. Obviously, the lophophore releases a trigger-substance, which itself stimulates the follicle cells to release their chemical signal for oocyte maturation (Freeman, 1994). Treatment of premature oocytes with cAMP has the same effect; i.e., follicle cells in *Glottidia pyramidata* seem to have a cAMP–signalling pathway (Freeman, 1994). If oocytes in *Glottidia* are mechanically denuded or stripped of their follicle cells, treatment with the lophophore extract fails to induce maturation.

EMBRYOLOGY

Our knowledge about the embryology of brachiopods has been significantly increased through the work of Freeman (1993b, 1995,

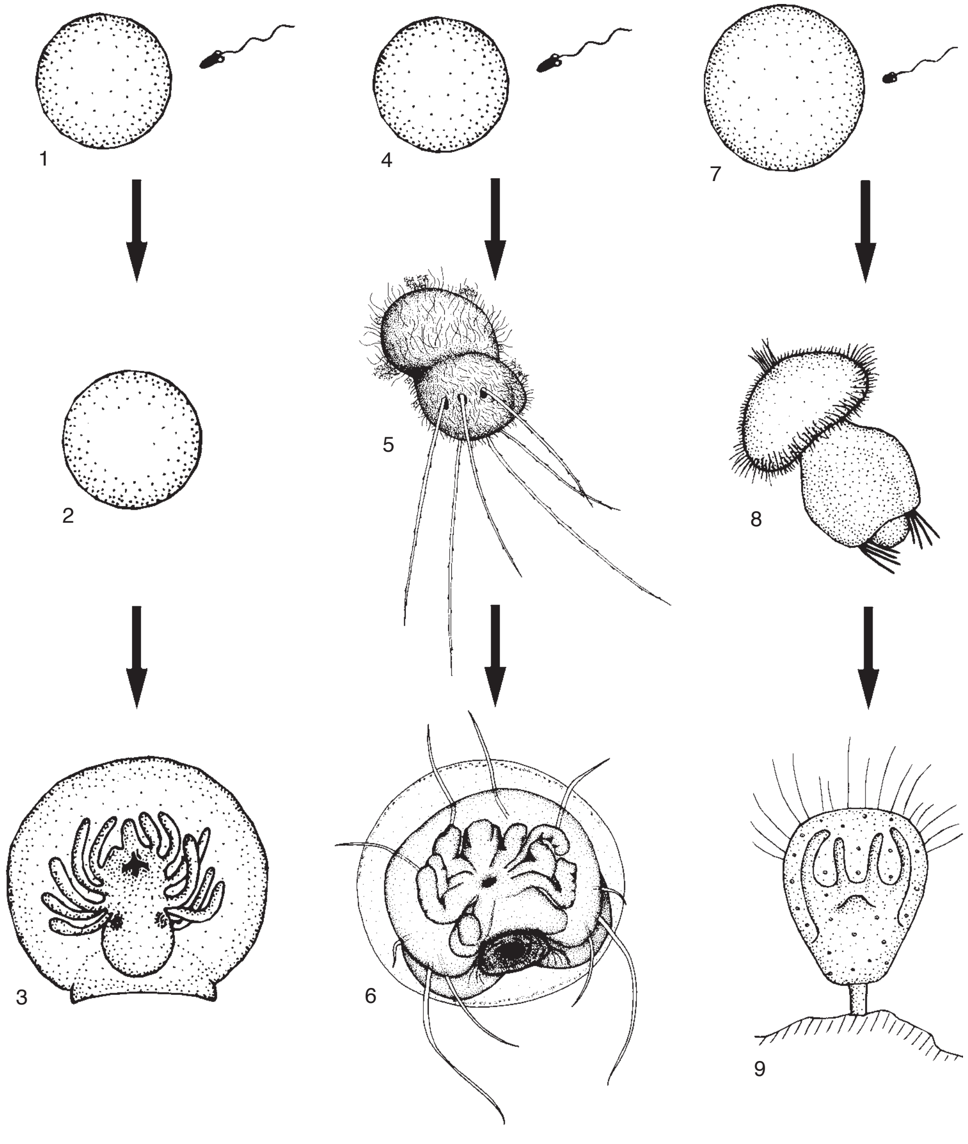


Fig. 1517. Comparison of developmental stages of lingulid (*1–3*), discinid (*4–5*) and rhynchonelliform (*6–9*) brachiopods. Comparable stages (semaphoronts, see definition in Hennig, 1966, p. 6) are shown on same level. Rhynchonelliforms and discinids share a hatching stage with larval setae (*5, 8*), whereas lingulids hatch as juveniles without any setae (*3*). Additionally, pelagic juveniles of discinids (*6*) have adult setae comparable to postmetamorphic stages of rhynchonelliforms (*9*). The overall similarity in structural development (e.g., presence of valves, certain number of tentacles, fully developed metanephridia) makes pelagic juveniles of linguliforms and postmetamorphic rhynchonelliforms (*3*, *6*, *9*) comparable semaphoronts *sensu* Hennig, 1966. This is in accordance with the free-swimming juvenile hypothesis of Long and Stricker, 1991. Drawing not to scale (new).

1999, 2000, 2001, 2003), who was able to construct fate maps for the development of *Glottidia pyramidata*, *Discinisca strigata*, *Novocrania anomala, Hemithiris psittacea*, *Terebratulina unguicula,* and *Terebratalia transversa*, thereby covering lingulides, discinides, craniides, and all rhynchonelliforms apart from thecideides. Experimental markings or destruction of blastomeres or parts of developing embryos led to

TABLE 21. Summary of brachiopod reproductive cycles. Table contains new findings that complement WILLIAMS and others (1997, p. 158, table 3); *RG,* ripe gonads; *SP,* spawning; *PH,* plankton hauls; *LR,* larval release; *BL,* brooded larvae (new).

Species	Author	Locality	Observation type	Month
Lingula anatina	Lüter, 1998b	Queensland, Australia	RG	Feb–Apr
Glottidia pyramidata	Freeman, 1995	Southern Florida	RG	May–June
Discinisca sp. cf. *tenuis*	Lüter, 2001a	Namibia	RG, PH	Feb–Apr
Discinisca strigata	Freeman, 1999	Panama, Pacific	RG	Dec–Feb
Notosaria nigricans	Lüter, 1998b	New Zealand	RG, SP	Apr–June
Tethyrhynchia mediterranea	Lüter, 2001b	Mediterranean Sea	BL	Jul[1]
Thecidellina blochmanni	Lüter, pers. obs., 2001	Christmas Island, Indian Ocean	BL	Feb
Kakanuiella chathamensis	Hoffmann, pers. obs., 2007	Chatham Rise, Southwestern Pacific	BL	Jan
Pajaudina atlantica	Hoffmann, pers. obs., 2007	La Palma, Canary Islands	BL	Jun
Ospreyella depressa	Lüter, pers. obs., 2000	Osprey Reef, Coral Sea, Australia	BL	Dec
Ospreyella maldiviana	Logan, 2005	South Male Atoll, Maldives	BL	Mar
Liothyrella neozelanica	Chuang, 1994	New Zealand	SP	Feb
Liothyrella uva	Peck & Holmes, 1989	Antarctica	SP, BL	Sept–Nov,[2] Jan–Feb
	Peck & Robinson, 1994	Antarctica	LR	Jan
	Peck, Meidlinger, & Tyler, 2001	Antarctica	LR	Dec–Feb
Macandrevia cranium	d'Hondt & Franzen, 2001	Western Sweden	SP	Nov
Calloria inconspicua	Chuang, 1996	New Zealand	SP	Feb–Apr
	Lüter, 1998a, 1998b	New Zealand	RG, SP	Apr–Jun
Argyrotheca cordata	Grobe & Lüter, 1999	Mediterranean Sea	RG, BL	all year
Argyrotheca cistellula	Grobe & Lüter, 1999	Mediterranean Sea	RG, BL	all year
Argyrotheca cuneata	Grobe & Lüter, 1999	Mediterranean Sea	RG, BL	all year[3]
Pumilus antiquatus	Lüter, pers. obs., 1996	New Zealand	RG	Apr–June

[1]almost constant environmental conditions possibly result in year-round reproduction; [2]indirect proof through tissue ash-free dry mass measurements; [3]uncertain due to small sample size.

differences in or failure of development of regions of embryos, having the effect that the responsibility of certain blastomeres for the construction of the epithelial layers like endoderm or mesoderm, for example, could be clarified. These experiments resulted in fate maps and developmental timetables (see Fig. 1520 and Table 22). Developmental timetables have been used by many authors (see JAMES & others, 1992; JAMES, 1997; WILLIAMS & others, 1997) to identify important steps in brachiopod development. However, larval development is temperature dependent and may also be influenced by the laboratory conditions under which all embryological investigations were conducted. The only direct comparison between two species from the same environment tested under similar conditions was documented by FREEMAN (2003). His results show that the terebratulid *Terebratulina unguicula* and the rhynchonellid *Hemithiris psittacea* differ significantly in their developmental times (see Table 22).

According to FREEMAN (2001) the assumption that embryogenesis takes place in a uniform manner in all brachiopods as implied by WILLIAMS and others (1997) is an oversimplification of the different developmental processes observed in the Recent brachiopod subphyla. Only the first two cleavages after oocyte fertilization are uniform in all brachiopods: The first cleavage occurs meridionally along the animal-vegetal axis of the egg, as does the second cleavage, but at 90 degrees from the plane of the first one. The third cleavage is equatorial in most cases, generating an embryo with four animal and four vegetal blastomeres. One can observe differences

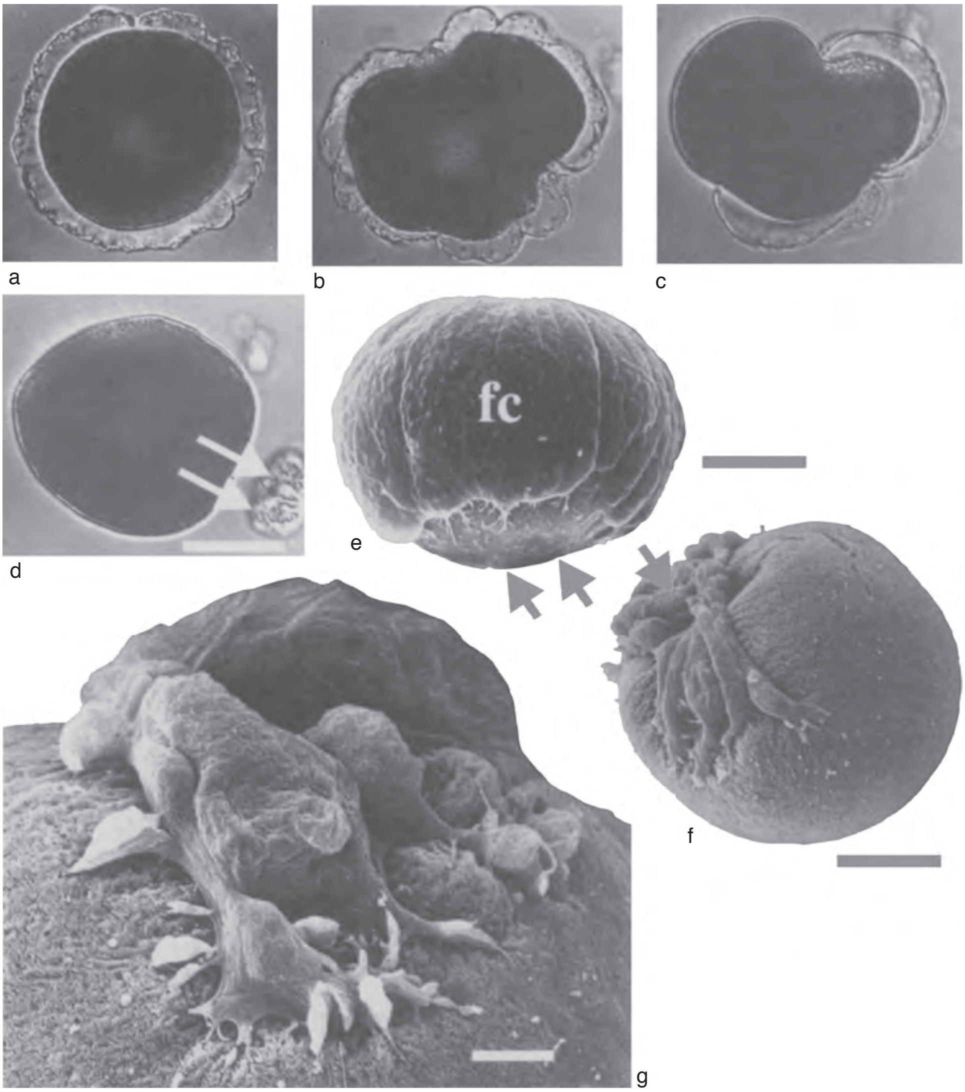


FIG. 1518. Ovulation of single oocyte of *Terebratalia transversa*; *a–d*, light microscope micrograph series of living oocyte, showing retraction of follicular sheath over about 90 min; follicular cells form cap of follicle cells (*arrows* in *d*), which eventually dislodges from oocyte; scale bar: 50 µm; *e–g,* SEM micrographs of oocytes retracting their follicular sheaths; *e*, oocyte 5 min after maceration of ovary with follicle cells (*fc*) covering most of oocyte except attachment site of oocyte to germinal epithelium (*arrows*), scale bar: 50 µm; *f,* oocyte 75 min after removal of ovary with nearly completed follicle cap (*arrow*), scale bar: 50 µm; *g*, detail of cap of follicle cells that form on one pole of oocyte during ovulation, scale bar: 10 µm (Stricker & Folsom, 1997).

between the brachiopod subgroups from the fourth cleavage on.

Lingulids and Discinids

The fourth cleavage occurs parallel to the plane of the first cleavage in the animal and vegetal blastomeres and generates a bricklike blastomere configuration that is four cells long (YATSU, 1902). Markings of the animal pole of the egg end up in the dorsal ectoderm of the embryo, whereas the apical part of the embryo originates largely from a lateral

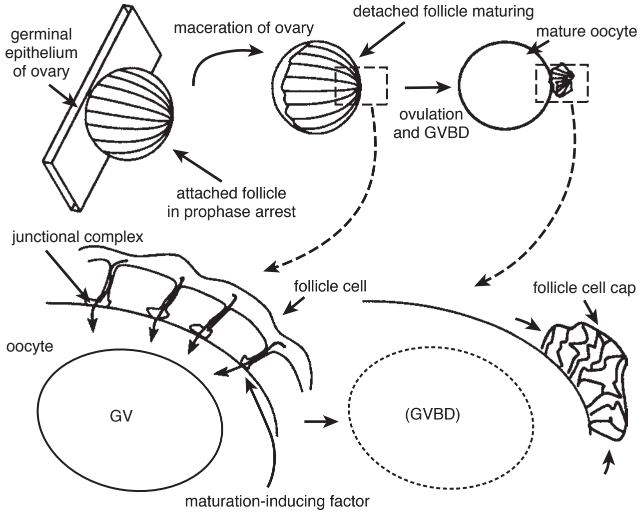


Fig. 1519. Diagram of key role that follicle cell-oocyte attachments are believed to play during oocyte maturation, based on video analyses and experiment manipulations; *GV*, germinal vesicle; *GVBD*, germinal versicle breakdown (Stricker & Folsom, 1997).

region of the egg. The vegetal part of the egg will in a later developmental stage represent the site of gastrulation. Although the anterior-posterior axis of the embryo can be detected very early, true bilateral symmetry becomes obvious through invagination of the archenteron. The plane of bilateral symmetry corresponds to the plane of the first cleavage, but it may already be fixed through anisotropy of the egg (Freeman, 1995, 1999, 2001).

Craniids and Rhynchonelliform Groups

Comparable to Linguliformea the fourth cleavage is meridional, but generates a morphologically different configuration of blastomeres, i.e., a double ring of cells enclosing a hollow space, referred to as a doughnut by Long and Stricker (1991). This was observed very early in rhynchonelliform brachiopod development (e.g., Conklin, 1902; Long, 1964) but comprehensively illustrated through SEM studies of the embryogenesis of *Terebratalia transversa* by Nislow (1994). By separating the blastomeres after the first cleavage, Nislow was able to show normal development of each blastomere into half-size larvae of *Terebratalia transversa*. He already assumed regulative development rather than mosaic development in rhynchonelliform brachiopods, which was corroborated by Freeman's results. In *Novocrania anomala* a mark of the animal pole of the egg will end up in the anterior region of the apical lobe, whereas a marked vegetal pole will end up at the site of gastrulation. In contrast to Linguliformea, there is no correspondence between the plane of the first cleavage and the future anterior-posterior axis of the embryo (Freeman, 2000, 2001).

Apart from shell formation, the most examined developmental process in brachiopods is the formation of the mesoderm and the subsequent development of the coelom. Many authors have tried to identify mesoderm cells in gastrulae, for example, and have followed their individual fate using light microscopy. This resulted in very different and sometimes contradictory hypotheses. Through the work of Freeman we now know that the origin of the mesoderm is already manifest in the early development of the embryo. In *Novocrania anomala* the vegetal half of the egg will form the mesoderm, which becomes evident once the embryo starts gastrulation. In contrast to Nielsen's (1991) observation that mesoderm cells are

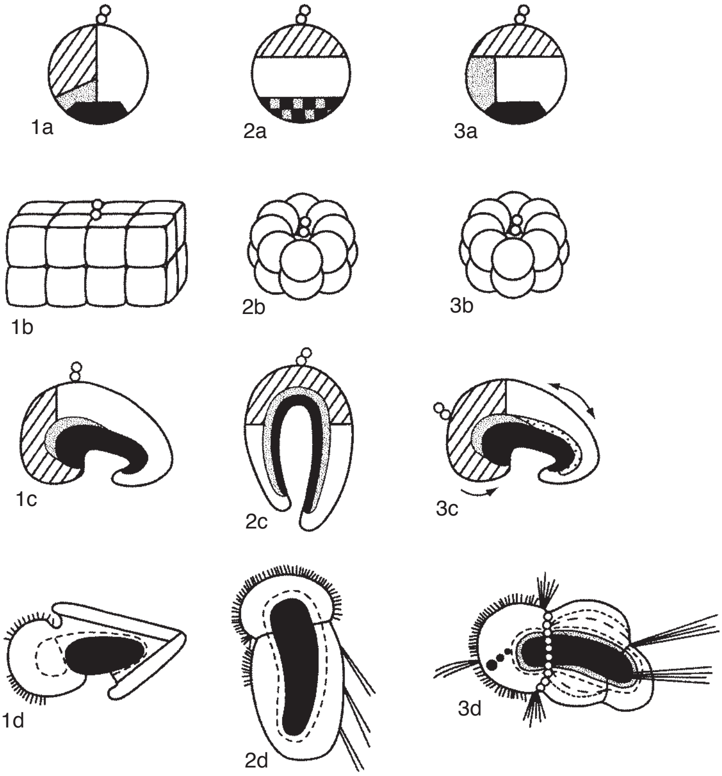


FIG. 1520. Fate maps of linguliform, craniiform, and rhynchonelliform brachiopods, showing different regions of uncleaved eggs (*1a*, *2a*, *3a*) and how they develop into endoderm, mesoderm, and anterior ectoderm, respectively, during ontogenesis; animal pole is marked by polar bodies, anterior is to left; *1b*, *2b*, *3b*, 16-cell embryos with anterior-posterior axis along plane of first cleavage in linguliforms (*1b*) and no relationship between plane of first cleavage and plane of bilateral symmetry in other two groups (*2b*, *3b*); *1c, 2c, 3c*, late gastrula stage, embryos oriented with blastopore (= vegetal pole) down; in linguliform brachiopods apical lobe on left (*1c–1d*) corresponding to placement of anterior ectoderm in fate map (*1a*). In craniiforms placement of anterior ectoderm is retained, whereas in rhynchonelliforms morphogenetic movements translocate apical lobe region (= anterior ectoderm) to left; *1d, 2d, 3d*, pre- (*1d*) and posthatching stages (*2d, 3d*) with orientation of apical lobe to left in linguliform and rhynchonelliform brachiopod developmental stages (Freeman, 2003).

built at the caudal part of the archenteron and subsequently grow forward by driving the endoderm and the ectoderm apart, FREEMAN (2000) postulated that the mesoderm in *Novocrania anomala* ingresses from multiple sites in the endodermal layer into the space between endoderm and ectoderm. Unfortunately, the youngest larval stage of *Novocrania anomala* so far investigated ultrastructurally is 64 hours old (GROBE, 1999). It has the full set of setae, and the blastopore is already closed. The archenteron is encircled by a mesodermal layer, the origin of which cannot be elucidated further at this stage. NIELSEN also described that by ingression of the three setal sacs on either side of the embryo, however, the coelomic anlage becomes divided in four parts: an unpaired anterior coelomic pouch and three paired posterior pouches. FREEMAN (2000) doubted the existence of the anterior coelomic pouch. The ultrastructural study of the larva of *Novocrania anomala* shows that neither of these pouches exists. Although the more-or-less compact mesodermal layer is to some extent compressed by the setal sacs, a continuous extracellular matrix surrounding the single pouches and separating them from other pouches does not exist. All mesodermal cells constitute a single coelomic

TABLE 22. Times of appearance of identifiable embryological features during development of brachiopods. Table contains new findings that complement WILLIAMS and others (1997, p. 180, table 5) (new).

Species	Egg diameter (µm)	Temperature (°C)	Time (h)	Developmental stage	Reference
Glottidia pyramidata	90	21–24	1	2-cell stage	Freeman, 1995
			2	8-cell stage	
			3	32-cell stage	
			6	blastula	
			10–12	gastrula	
			18	gut and valve formation	
			33	apical lobe and gut with cilia	
			48	hatching	
Discinisca sp. cf. *tenuis*	70	23–25	0.5–1	2-cell stage	Lüter, 2001a, unpub. data, 1998
			1	4-cell stage	
			18	gastrula	
			23	larval setae start growing	
			26	two-lobed stage, hatching	
			43	1 p.t. stage, median tentacle, functional gut	
			70	2 p.t. stage	
Discinisca strigata	65–70	29	1	2-cell stage	Freeman, 1999
			2	8-cell stage	
			3	32-cell stage	
			4	first cilia	
			5	blastula	
			9	early gastrula, invagination	
			11	apical tuft	
			18	setae, hatching	
			20	apical and mantle lobes	
			24	1 p.t. stage	
			26–27	2 p.t. stage	
			44	3 p.t. stage	
Novocrania anomala	130–135	11–14	2	2-cell stage	Freeman, 2000
			15–16	blastula, first cilia	
			27	gastrulation	
			36	embryo starts swimming	
			40	scattered mesodermal cells	
			55	constriction separates apical lobe from larval body	
			60–72	larval contraction (curling)	
			72	full-grown larva with 3 pairs of setal bundles	
Hemithiris psittacea	190–200	12–13	8	2-cell stage	Freeman, 2003
			47	ciliated blastula	
			57–72	gastrula	
			108[1]	3-lobed stage	
			150[1]	first setae	
Terebratulina unguicula	165–175	12–13	3, 5	2-cell stage	Freeman, 2003
			21	ciliated blastula	
			36–45	gastrula	
			70[1]	3-lobed stage	
			98[1]	first setae	

TABLE 22. *Continued.*

Species	Egg diameter (µm)	Temperature (°C)	Time (h)	Developmental stage	Reference
Liothyrella uva	–	0–2	24	gastrula	Peck & Robinson, 1994
			72	lobe formation starts	
			216	early 3-lobed stage	
			432	mantle lobe encircling pedicle lobe	
			936[2]	first larval setae	
			115–160 (days)[3]	settlement	
Terebratalia transversa	150	13	2	2-cell stage	Freeman, 1993b
			6–11	early blastula	
			11	first cilia	
			11–18	late blastula	
			18	invagination, beginning of gastrulation	
			25	apical tuft occurs	
			72	3-lobed stage, blastopore closed	
Terebratalia transversa	150	12	3	2-cell stage	Nislow, 1994
			4	4-cell stage	
			5	8-cell stage	
			7	16-cell stage	
			8–18	blastula	
			18	gastrulation	
			38	elongation of embryo	
			40–48	formation of larval mesoderm	
			48	mantle lobe formation	
			72–96	full-grown larva	
Laqueus californianus	130–140	10	3	2-cell stage	Pennington, Tamburri, & Barry, 1999
			4	4-cell stage	
			5	8-cell stage	
			6	16-cell stage	
			12–26	blastula	
			26–48	gastrula	
			48	wedge-shaped, elongation of blastopore, apical tuft	
			72	blastopore closed	
			80	mantle lobe formation, first setae	
			96	3-lobed stage	
			168	settlement	

[1] Time scale in Freeman (2003, fig. 4) slightly inconsistent. Between 84 and 108 hours of development, 12 h, 16 h, and 18 h intervals have the same scale.

[2] In experiments of Peck, Meidlinger, and Tyler (2001), larval setae occured only after 1200 h. [3] Estimated from spawning time in October. Peck, Meidlinger, and Tyler (2001, p. 82) give "more than 80 days" as the "longest times to reach the competent larval stage."

anlage without any separation of compartments throughout early larval development in *Novocrania anomala* (see GROBE, 1999). A separation of an anterior and a posterior compartment only happens shortly before settlement, but the two coelomic pouches stay in contact through a ventral bundle of longitudinal muscles responsible for the presettlement curling of the larva. NIELSEN based his interpretation of coelom development exclusively on light microscopy investigations and could not see the delicate extracellullar matrix and misinterpreted the very thin but still continuous mesodermal layer proximal to the setal sacs as true separations between coelomic pouches. These new findings are in accordance with embryological studies of rhynchonelliform brachiopod larvae. A single, undivided coelomic anlage has been described for *Terebratulina septentrionalis* (CONKLIN, 1902), *Terebratulina unguicula* and *Terebratalia transversa* (LONG, 1964), *Calloria inconspicua,* and *Notosaria nigricans* (LÜTER, 1998b, 2000a).

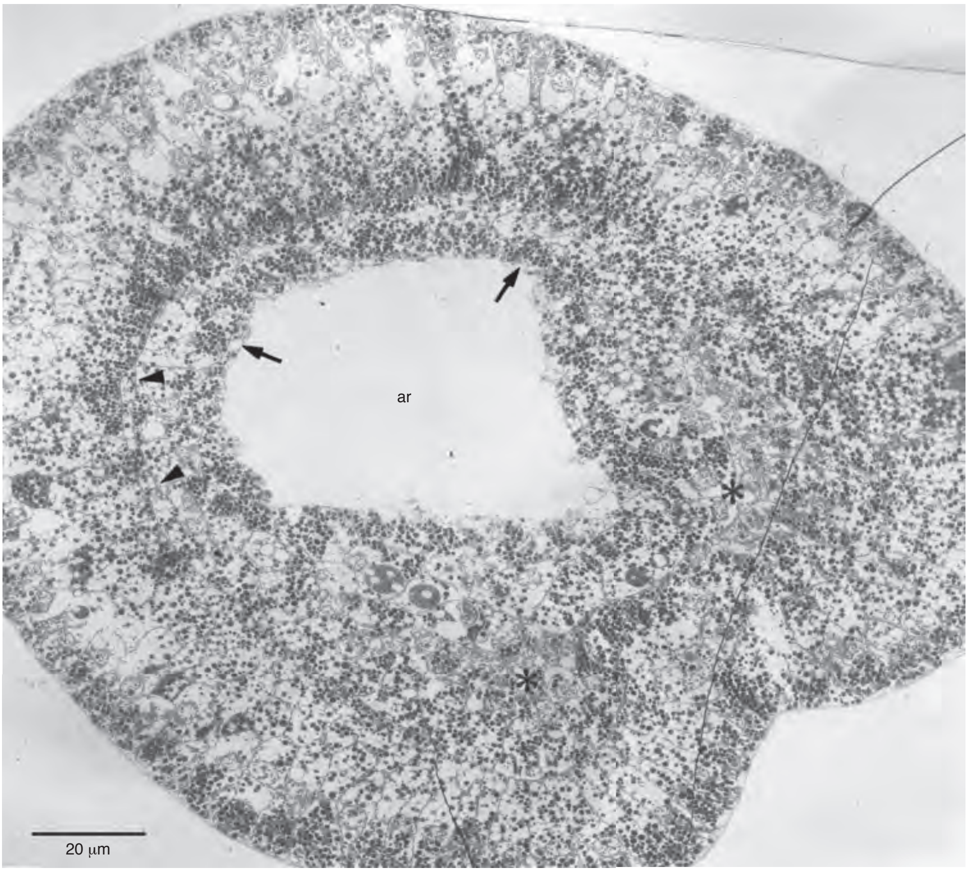


FIG. 1521. TEM micrograph of late wedge-shaped stage (~210 h postinsemination) of *Notosaria nigricans*; longitudinal section showing archenteron lined by a monolayered endoderm (*arrows*) and proliferating mesodermal cells (*asterisks*), which are beginning to be separated from endoderm through thin extracellular matrix (*arrowheads*) in frontal left area (right side of animal); *ar,* archenteron (Lüter, 2000a).

LARVAL DEVELOPMENT

Coelom formation

Secondary body cavities or coeloms in brachiopods are built by enterocoely, a process most extensively investigated and described in developing echinoderms. Echinoderm coelom formation is characterized by the formation of pouches of the archenteron in early larval stages. These pouches later become separated from the archenteron, thereby forming the tripartite arrangement of coelomic compartments. Each coelomic compartment consists of a membrane surrounding a monolayered coelomic epithelium (formerly archenteral epithelium), which itself encloses a fluid-filled chamber, the coelom (formerly archenteral lumen).

In brachiopods, coelom formation is basically the same. Invagination of the archenteron during gastrulation of the embryo displaces the blastocoel. In late wedge-shaped to early three-lobed larval stages of the rhynchonellid *Notosaria nigricans* and the terebratellid *Calloria inconspicua,* the prospective coelomic epithelium proliferates from the archenteral epithelium (Fig. 1521–1522). In *Notosaria nigricans* the cells proliferate from the caudolateral part of the archenteral wall, whereas in *Calloria inconspicua* it is the dorsolateral part of the archenteron (LÜTER, 1998b, 2000a). Growth of a so-called cellular curtain, as described

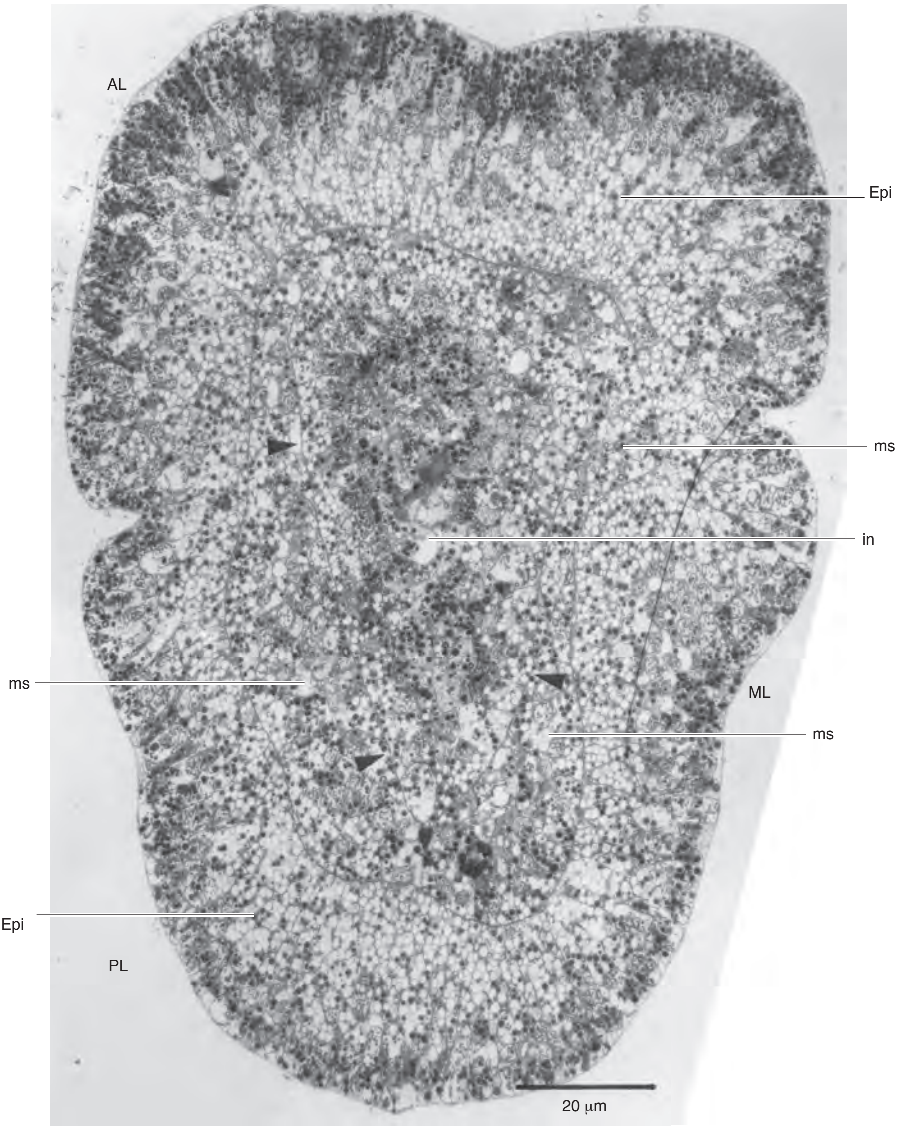


FIG. 1522. TEM micrograph of early three-lobed stage (~170 h postinsemination) of *Calloria inconspicua,* longitudinal section through midline of larva; mesodermal cells (*ms*) have proliferated from archenteral epithelium and are almost completely separated from future intestine (*in*) by extracellular matrix (*arrowheads*); *AL*, apical lobe; *Epi*, epidermis; *ML*, mantle lobe; *PL*, pedicle lobe (Lüter, 2000a).

for the mesoderm formation in *Terebratalia transversa* by LONG (1964, p. 59), could not be observed. In later stages, an extracellular matrix is secreted from the caudal end of the archenteron to the front, thereby separating the coelomic anlage from the archenteral epithelium.

The main difference from echinoderms is that in brachiopods the prospective coelomic epithelium proliferates as a compact cell mass. Initially, the prospective coelomic epithelium does not enclose a fluid-filled lumen. Throughout brachiopod larval life the coelomic anlage represents a solid mesodermal cell mass, and only during metamorphosis will the mesodermal cells diverge, thereby opening a lumen, the coelom. According to definitions of mechanisms of coelom formation given by LÜTER (2000a), the development of secondary body cavities in brachiopods can be identified as enterocoely, because the prospective coelomic epithelium originates from archenteral cells (for a critique of these definitions, see JENNER, 2004).

The Trimeric Organization

Recent results on coelom formation in different brachiopod species (see above) demonstrate that it is obvious that a tripartite body organization cannot be found in brachiopods. Many authors have claimed that brachiopods, similar to phoronids (which are not tripartite either) or echinoderms, have a trimeric body with a prosoma, a mesosoma, and a metasoma. Discrimination of three parts of the body only makes sense if this is reflected in the inner organization of the animal; but in brachiopods this is not the case. All brachiopods studied thus far start with having only one coelomic cavity (see above), which may (craniides) or may not (all other brachiopods) be completely divided into two coelomic compartments (mesocoel and metacoel, respectively) during their postsettlement life phase. A prosoma (with a protocoel) has been assumed to exist in different places of the anterior part of the brachiopod body. PROSS (1980) identified the large arm sinus together with the epistome in *Lingula anatina* as the prosoma with protocoel, which corresponds to the epistome of the phoronid actinotroch larva. HAY-SCHMIDT (1992) suggested that the median tentacle of juvenile lingulides is the prosoma and contains a protocoel. Both hypotheses were contradicted by ultrastructural studies of the lophophore of *Lingula anatina*, which showed that all mesodermal cells in the tentacle apparatus form a continuous coelomic epithelium without any connective tissue separating the lophophore coelom (mesocoel) from some anterior protocoel-like compartment (LÜTER, 1996, 1998b). This was already shown by earlier brachiopod researchers, for example in the line drawings of YATSU (1902) and ASHWORTH (1915). The most promising suspect for containing a protocoel, however, was the epistomal region or upper lip above the mouth opening (Fig. 1523a). As has been shown for juvenile *Lingula anatina* (LÜTER, 1998b), the epistome contains single muscle cells that are embedded in a rather strong connective tissue (Fig. 1523b–1523c). These muscle cells are connected to each other and form a continuous epithelium with the mesodermally derived coelomic epithelium of the lophophore. Thus, there is no epithelialized coelomic space to be found in the epistome, which is separated from other such coelomic compartments by extracellular matrix; i.e., the epistome cannot be regarded as a prosoma with a protocoel. As a consequence, brachiopods cannot be regarded as trimeric organisms. Their secondary body cavity is only divided in two compartments, and this truly applies only to craniides, where mesocoel and metacoel are fully separated in adults (BLOCHMANN, 1892), whereas according to HYMAN (1959) all other brachiopods have life-long connections between the two coelomic compartments.

Larval Behavior

In *Discinisca* sp. cf. *tenuis* the curved setae (see above) play an important role in the brachiopod's behavior during both the pelagic phase and the settlement process. The function of the curved setae is two-fold. The long and curved setae enhance buoyancy, helping the brachiopod to drift with the ambient water currents. The specific weight of pelagic juveniles of *Discinisca* sp. cf. *tenuis* is higher than that of the surrounding water, however. To stay in the water column, the brachiopod must extend its lophophore out of the shell using the movement of the tentacle cilia to propel itself forward, thereby avoiding sinking. This was documented in the first drawing of a brachiopod developmental stage ever published (see Fig. 1500). The curved setae assist in this process. Once the lophophore is protected between the

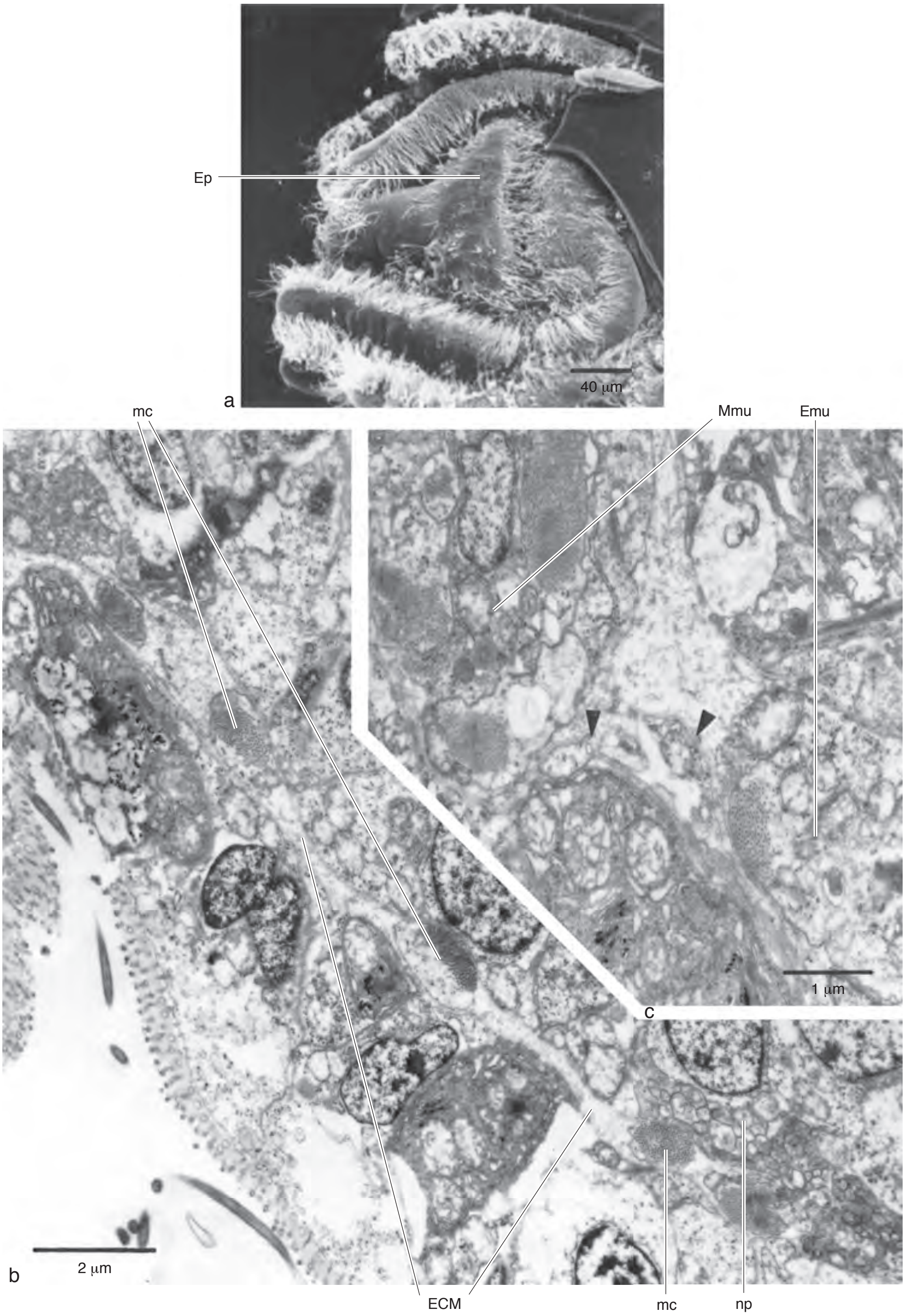


FIG. 1523. Epistome of pelagic juvenile of *Lingula anatina*; *a*, SEM of ventral side of epistome (*Ep*) or upper lip covering mouth opening of juvenile with 7 pairs of tentacles; *b*, TEM of longitudinal section through epistome of juvenile with 6 pairs of tentacles; muscle cells (*mc*) embedded in extracellular matrix (*ECM*) and in close contact to basiepidermal nerve cells (*np*); *c*, TEM micrograph of contact area (*arrowheads*) of epistomal muscle cells (*Emu*) and central musculature of median tentacle (*Mmu*) (Lüter, 1998b).

closed valves the young discinid immediately descends to the sea floor.

The second and more important function of the curved setae is to enable the juvenile discinid to move along the sea floor to search for a suitable attachment site. When the brachiopod leaves the plankton to start its benthic life phase, it sinks. Once it hits the sediment surface, the discinid performs a scissoring movement of the tiny valves. Adult linguloids use this type of valve movement in order to burrow into the soft sediment (EMIG, 1997b). Discinides live on hard substrates; i.e., the juvenile *Discinisca* has to find an attachment area, preferably on the upper valve of a conspecific specimen. The scissoring movement of the valves, together with the long and curved setae poking into the upper layer of the sediment allow the juvenile discinid to move in a walking-type motion. Functionally, the curved setae are stiff legs working against the scissoring movement of the valves (and the connected mantle). The discinides can thus walk to their final attachment site when they are ready to settle (Fig. 1524).

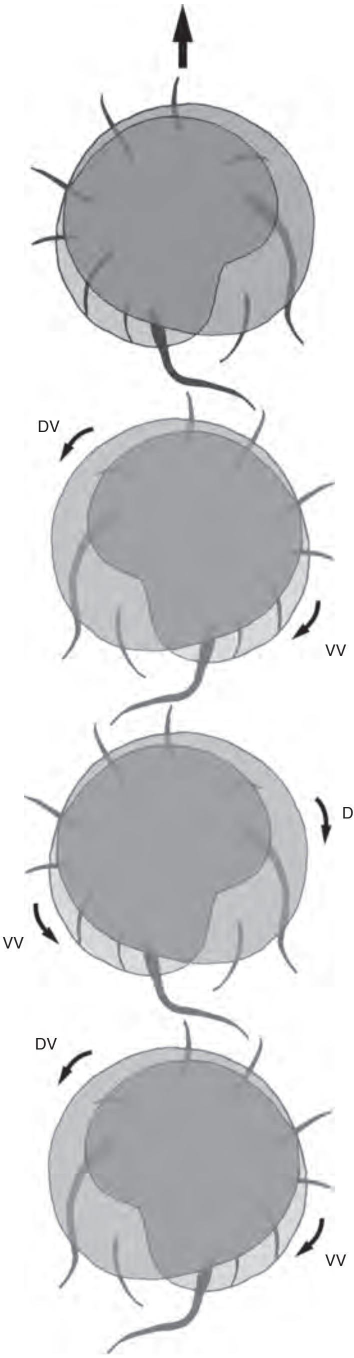


FIG. 1524. Schematic drawing of walking behavior of juvenile of *Discinisca* sp. cf. *tenuis* immediately prior to settlement; animal uses scissoring movements of dorsal (*DV*) and ventral valve (*VV*) against seafloor-touching curved setae to push itself forward in direction of *arrow* (new).

Larval Distribution and Survival

Lecithotrophic brachiopod larvae are characterized by a rather short pelagic phase. Accordingly, the dispersal ability of these larvae is said to be low. Brooded larvae are likely to settle in the vicinity of their parental stocks, since they leave the female's mantle cavity or brood pouch in an advanced developmental stage in which they may already have reached the competence to settle on hard substrates. In polar regions the speed of development is low due to ambient water temperatures. In the Antarctic species *Liothyrella uva,* development of brooded larvae is plastic, with larvae of different developmental stages present in brooding females and also differences among females in the same population (MEIDLINGER, TYLER, & PECK, 1998). Once the larvae are released they may take up to 160 days to develop into three-lobed stages competent to settle (see Table 22; PECK & ROBINSON, 1994). Obviously, these larvae are able to retard their development after reaching the three-lobed stage until a suitable attachment site is available (PECK, MEIDLINGER, & TYLER, 2001). A prerequisite for this development is water temperatures below 4.5° C. Higher temperatures are lethal for these cold-adapted larvae. Most larvae released in large populations of *Liothyrella uva* settle on conspecifics (PECK, MEIDLINGER, & TYLER, 2001). This has also been shown for the Pacific species *Laqueus californianus* (PENNINGTON, TAMBURRI, & BARRY, 1999). Survival of *Laqueus* larvae was also shown to be temperature dependent. They died after one day in 25° C, but reached settlement competence after 5 to 9 days in temperatures between 15° C and 5° C. Many larvae survived in temperatures between 10–15° C for more than 70 days (see Table 22). Survival for more than 70 days or even 160 days, as in *Liothyrella uva*, enables these larvae to drift in water currents over long distances. Using the circumpolar Antarctic current, *Liothyrella* larvae may travel some 3000 km before they reach appropriate settlement sites. Long-term survival during such a long drift phase would certainly be an advantage. Brooding is obviously not necessarily combined with short-term survival of their lecithotrophic larvae, and dispersal over long distances, at least in some rhynchonelliform species, is possible.

BROODING

Larval brooding occurs in several subgroups of rhynchonelliform brachiopods and extends from simple storage of developing larvae in the lophophore to development in brood pouches, which are invaginations of either the ventral or the dorsal mantle. The most elaborate brood protection is found in thecideide brachiopods. Because of their small shell size, thecideides have often escaped the attention of collectors, and therefore their larval development has been rather enigmatic so far. The only reliable account on the morphology of the larvae and the brood protection in a thecideide brachiopod dates back to the middle of the 19th century (LACAZE-DUTHIERS, 1861). Dealing exclusively with *Lacazella mediterranea*, LACAZE-DUTHIERS's work represents only one out of five Recent thecideide genera: *Lacazella*, *Pajaudina*, *Ospreyella*, *Kakanuiella*, and *Thecidellina*. These five genera fall into two groups: *Lacazella*, *Pajaudina*, *Ospreyella,* and *Kakanuiella* have only one brood pouch to rear their larvae (LOGAN, 1988b, 2004, 2005; LÜTER, WÖRHEIDE, & REITNER, 2003; LÜTER, 2005). This pouch is situated medially in the ventral mantle (Fig. 1525c). Additionally, species within these genera have specialized tentacles, as described for *Lacazella* in volume 1 of the revised *Treatise* (WILLIAMS & others, 1997), and a marsupial notch in the calcified bridge of their brachidium supporting the specialized tentacles involved in brooding. Specialized tentacles, median ventral brood pouch, and larvae have only recently been studied in (ultrastructural) detail in *Ospreyella maldiviana* from the Indian Ocean (Fig. 1525a–1525b; LOGAN, 2005). The marsupial notch is only present in females so that sexual dimorphism is recognizable even when the soft tissue is not preserved (Fig. 1526).

In contrast, *Thecidellina* has two brood pouches in the dorsal mantle on either side of the brachidium's median ridge (Fig. 1527). These brood pouches are only present in specimens that carry developing eggs or larvae so that sex discrimination may be possible as well, but only in reproducing specimens (Hoffmann, unpublished data, 2007). WILLIAMS and others (1997, p. 177) mentioned that, "*Thecidellina* [is] known to deliver [its] eggs into brood pouches," erroneously citing the Anatomy chapter in the first edition of the *Treatise* (WILLIAMS & ROWELL, 1965a), which lacks a description of the breeding behavior of *Thecidellina.* PAJAUD (1970) gave a detailed description of the morphology of *Thecidellina*'s brachidium, including what he calls the sac interbrachial on either side of the median ridge. Obviously PAJAUD never encountered larvae or developing eggs in these sacs, so he was not aware that these are indeed the two brood pouches present in all *Thecidellina* species. Developing embryos plus 15 to 25 eggs can

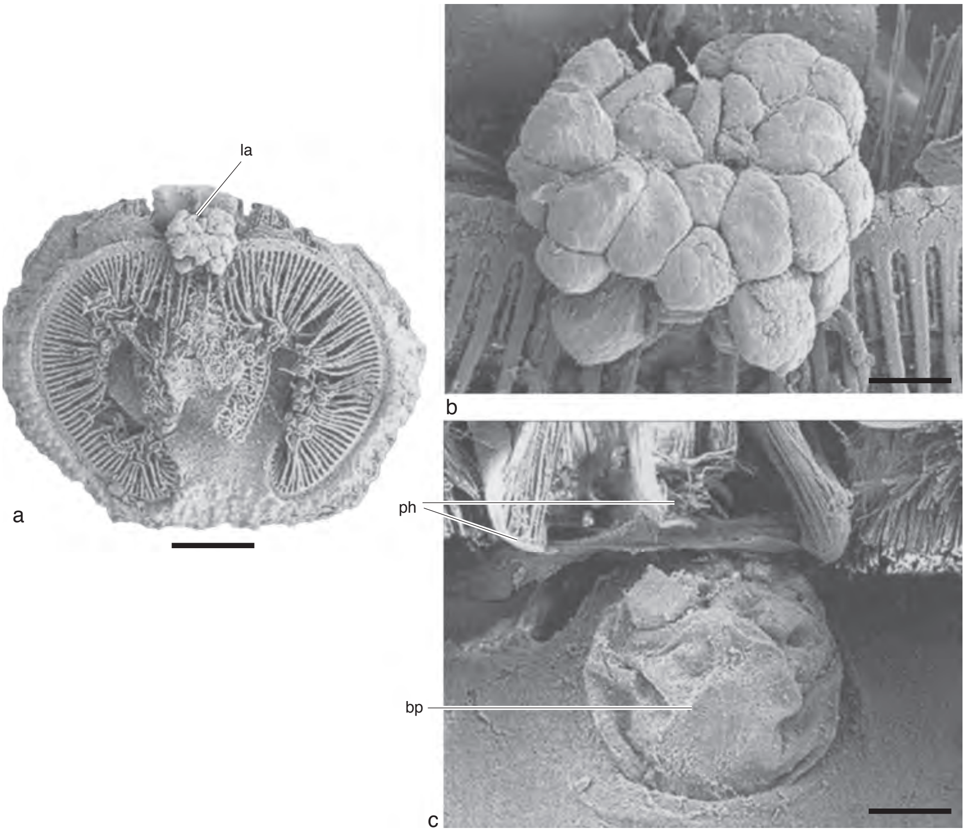


FIG. 1525. SEM micrographs of larvae of thecideide *Ospreyella maldiviana*; *a*, interior of dorsal valve with lophophore and several larvae (*la*) clinging to specialized pair of tentacles, scale bar: 1 mm; *b*, detail of *a* showing the larvae and parts of both specialized tentacles (*arrows*). In natural position tips of tentacles and larvae are situated in single brood pouch that is formed by ventral mantle; scale bar: 0.25 mm; *c*, empty brood pouch (*bp*) in ventral mantle of female below two prongs (*ph*) of hemispondylium; scale bar: 0.25 mm (Logan, 2005).

be found per brood pouch in large specimens of *Thecidellina blochmanni* from Christmas Island, Indian Ocean (C. LÜTER, personal observation, 2001), but the average number of embryos in brood pouches of *Thecidellina* spp. is much smaller (<10; Fig. 1527, indicating a yet undetermined *Thecidellina* sp. from Osprey Reef, Coral Sea, Australia). The brood pouches are invaginations of the dorsal mantle and can be covered by irregular calcitic spicules or tubercles. In some species the tubercles build an anastomosing network or even an almost solid calcitic plate. The morphology of this mantle calcification is highly variable on an individual level and cannot be used for species determination. The opening of each pouch is quite small and points backward toward the mouth opening. It is still unclear how the eggs enter the brood pouches, where they are fertilized, and how the fully grown larvae manage to escape from the pouch.

POSTLARVAL DEVELOPMENT

According to several authors (e.g., STRICKER & REED, 1985a), PERCIVAL (1944) mentioned shell secretion between the mantle lobes and the pedicle lobe in *Calloria inconspicua* during its late larval phase, but PERCIVAL's paper does not contain this statement. Instead he wrote that "during the later period of enclosure [of the apical lobe by the reversed mantle] … the outer surface of the mantle becomes glistening white and

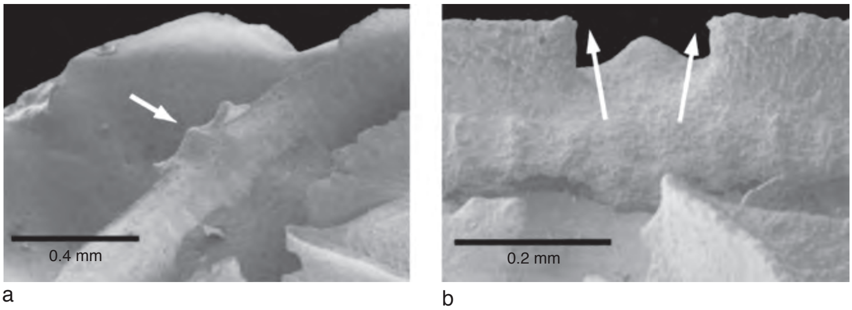


FIG. 1526. SEM micrographs of marsupial notch of thecideide *Ospreyella depressa*; *a*, ventral view of marsupial notch forming calcified plate (*arrow*) in center of posterior bridge; *b*, frontal view of marsupial notch with specialized tentacles (symbolized by *arrows*) reaching through central opening of bridge toward brood pouch in ventral mantle (Lüter, Wörheide, & Reitner, 2003).

smooth. The shape is no longer plastic and there is clear evidence of the formation of a hard shell" (PERCIVAL, 1944, p. 9–10). This happens only postsettlement, during or after metamorphosis and not while the animal is still in its pelagic, larval stage. The only material secreted between pedicle lobe and mantle lobe in rhynchonelliform brachiopod larvae is characterized as an amorphous substance (STRICKER & REED, 1985a, p. 248) followed by so-called multigranular bodies, observed in *Terebratalia transversa*. They may be precursors of the periostracum and were also found in premetamorphic stages of *Calloria inconspicua* (LÜTER, 1998b).

FREEMAN and LUNDELIUS (1999) suggested that fossil craniides had pelagic developmental stages comparable to discinides or lingulides. Examination of fossil craniid shells showed what FREEMAN and LUNDELIUS interpreted as larval shells, implying that through the Lower Jurassic all Craniidae possessed a larval mantle secreting a larval shell. According to the interpretation of lingulid and discinid bivalved developmental stages (see above; LONG & STRICKER, 1991) as pelagic juveniles, craniides would have also had a swimming planktotrophic juvenile (=postmetamorphic) stage. Within the craniides, several groups then may have evolved lecithotrophy during the Upper Jurassic, where "genera with a lecithotrophic larva that lacked a larval shell began to appear" (FREEMAN & LUNDELIUS, 1999, p. 197). The question remains whether these pelagic, shelled craniid developmental stages had a dorsal and a ventral valve. If this was the case, cementation of an already existing ventral valve on the substrate has to be explained. As far as is known from Recent craniides, the dorsal valve is always the first valve to appear. To provide suitable stability of attachment, it may be necessary for the postlarva to make sure that the developing ventral valve is in direct contact with the substrate from the very beginning of its appearance.

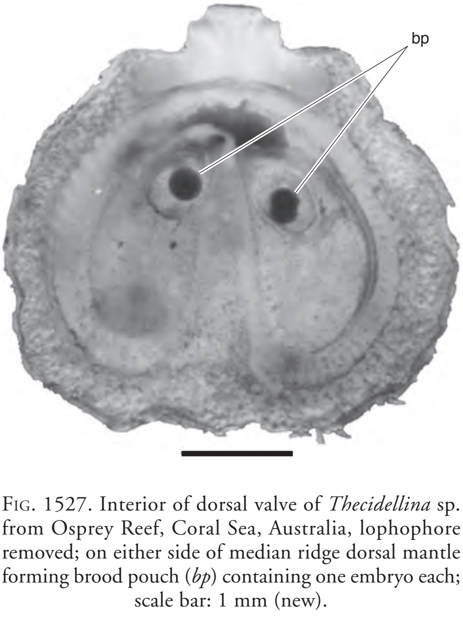


FIG. 1527. Interior of dorsal valve of *Thecidellina* sp. from Osprey Reef, Coral Sea, Australia, lophophore removed; on either side of median ridge dorsal mantle forming brood pouch (*bp*) containing one embryo each; scale bar: 1 mm (new).

THE BRACHIOPOD GENOME

BERNARD L. COHEN

[The University of Glasgow]

INTRODUCTION

The original chapter under this title was completed in August 1995. The most conspicuous advance since then, complete sequencing of nuclear genomes, has not involved brachiopods and is unlikely to do so unless a strong user community makes the case for it or data gathering becomes orders of magnitude less costly (as it shows signs of doing: BLAKESLEY & others, 2004). But smaller-scale progress can be reported, including the complete sequence of four mitochondrial genomes and a considerable quantity of taxonomically focused and phylogenetically valuable sequences derived from nuclear and mitochondrial genes.

The aim of the present chapter is to give an account of relevant work published since 1995 and to outline briefly what is known about work in progress or in press. It will start with an account of general progress and promise in phylogenetics. Then, relevant developments will be described under section headings derived from those used in the original chapter, following which additional new results will be described as far as possible in a descending systematic hierarchy, starting above the phylum level and following the general format of an earlier review (COHEN, 2001b). The reader is also referred to the molecular section of the Millennium Brachiopod Congress volume (BRUNTON, COCKS, & LONG, 2001, p. 119–159). Publications will be included only if they make a significant contribution to brachiopod (or phoronid) phylogeny; those that only incidentally include one or more of these organisms in a gene tree will be omitted, unless comment appears necessary.

General progress in phylogenetics is attributable first to the lower cost per nucleotide and increased throughput of automated DNA sequencing, second to the increased power of computers, and third to the development of new approaches and specialized software for phylogenetic analysis and hypothesis testing (see general accounts in PAGE & HOLMES, 1998; FELSENSTEIN, 2004). Large-scale comparative sequence analyses are in their infancy but have considerable promise and will grow rapidly in importance as more genome sequences are completed. One potential function of such genomic sequencing is to test the validity of phylogenetic inferences from individual or small numbers of genes (e.g., ROKAS & others, 2003; COPLEY & others, 2004; WOLF, ROGOZIN, & KOONIN, 2004). More surprisingly, even at this early stage, comparative genome analyses begin to allow the reconstruction of ancestral genomes (DANCHIN & PONTAROTTI, 2004). Smaller-scale analyses should be interpreted, as ever, with some caution, but large-scale analyses must also not be accepted uncritically, if only because most sequenced genes code for proteins that may be subject to divergent selection pressures in different lineages and at different times, while gene duplication and loss may result in unrecognized paralogy (TELFORD, 2002). There is some reason to expect that genes whose products are involved in complex intermolecular interactions (such as ribosomal RNAs and some proteins) may be among the more reliable indicators of phylogeny (e.g., ARIS-BROSOU, 2005).

STRUCTURE, COMPOSITION, AND ORGANIZATION OF THE NUCLEAR GENOME

COMPOSITION, SIZE, AND CHROMOSOME NUMBER

The only development under this heading has been the recent discovery of a thesis on the ontogeny of *Terebratalia transversa,* which contains good images of meiosis in a dividing oocyte (FLAMMER, 1963). Seven distinct, small chromosomes are visible, with a hint of a possible eighth (Fig. 1528). The potential importance of chromosome number and organization as markers of evolutionary history has been enhanced by the recent recognition that successive, whole-genome duplications have occurred in the evolutionary history of chordates (MULLEY & HOLLAND, 2004, and references therein). The fact that both *Lingula* (YATSU, 1902) and *Terebratalia* have similar numbers of small chromosomes may indicate that brachiopod chromosomes have undergone little major architectural change since the Cambrian; this seems unlikely, but important if true.

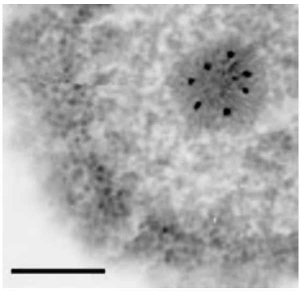


FIG. 1528. Chromosomes of *Terebratalia transversa*. Polar view of a meiotic second metaphase in an oocyte, showing seven clear chromosomes, with a suggestion of a possible eighth lying mostly out of the section plane. From a light-microscope histological study of embryology using stained, serial, 5 mm sections (Flammer, 1963). An inked label line on the left of the original illustration has been removed digitally, leaving a faint linear trace; scale bar, 10 mm (new).

STRUCTURE, COMPOSITION, AND ORGANIZATION OF MITOCHONDRIAL GENOME

In 1995, it was widely anticipated that complete mitochondrial genome sequences (mtDNAs) would prove to be a generally valuable source of phylogenetic information because in addition to straightforward evolution of maternally transmitted, homologous gene sequences, rare changes in gene order appeared to offer very strong phylogenetic characters (e.g., BOORE & others, 1995; BOORE, 1999). Broadly speaking, these hopes have been well satisfied within some groups (e.g., mammalian orders) from which a wide and representative selection of mtDNAs has been obtained, but results have not been so good where sampling has been narrower and at deep taxonomic levels. For example, gene order and sequence of mtDNAs only weakly resolves molluscan class-level relationships (ANDERSON, CORDOBA, & THOLLESON, 2004) and fails completely to resolve relationships between the major lophotrochozoan phyla. On the other hand, despite great morphological diversity, gene order appears to be relatively well conserved and informative among the major clades of annelids and in sipunculans (JENNINGS & HALANYCH, 2004). These and other examples show that the phylogenetic utility of complete mitochondrial sequences varies considerably; they are far from a panacea, and quite dense taxonomic sampling may be needed to obtain even modest resolution. Furthermore, accumulating evidence suggests that recombination of mitochondrial genomes of maternal and paternal origin may sometimes occur, though this should not affect phylogenetic inference above the population level (SLATE & GEMMELL, 2004). Despite these (and other) limitations, all published analyses of mitochondrial gene or genome sequences that include brachiopods and phoronids have strongly agreed that these taxa belong among the lophotrochozoan protostomes along with annelids and mollusks (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998; STECHMANN & SCHLEGEL, 1999; NOGUCHI & others, 2000; BOORE & STATON, 2002; TOMITA & others, 2002; BOORE, MEDINA, & ROSENBERG, 2004; HELFENBEIN & others, 2004; PAPILLON & others, 2004; RUIZ-TRILLO & others, 2004; WOLF, ROGOZIN, & KOONIN, 2004).

No concerted program to obtain complete mtDNA sequences of taxonomically representative brachiopods and phoronids has been funded, and the four brachiopods so far sequenced appear to have been those that could be most readily obtained by the workers concerned. Thus, complete mitochondrial genomes have been described from the cancellothyridid, *Terebratulina retusa* (Stechmann & Schlegel, 1999), the two terebratellids, *Laqueus rubellus* (Noguchi & others, 2000) and *Terebratalia transversa* (Helfenbein, Brown, & Boore, 2001), and from a lingulid, *Lingula anatina* (Endo & others, 2005), but no craniid, discinid, or rhynchonellide sequence has been seriously attempted. In addition, most of the mitochondrial genome of one phoronid has been reported (Helfenbein & Boore, 2004), and some work has been done on the mtDNA sequence of a second lingulid, *Glottidia* (K. Helfenbein and N. Tuross, personal communications, 2004). Not surprisingly, in view of the patchy taxonomic coverage, the resulting data have been relatively uninformative about brachiopod interrelationships, though they are of some molecular biological interest. Notable features of or inferences from the available brachiopod mtDNAs include the following.

The mitochondria of brachiopods use the same genetic code as most other protostomes (Saito, 1998; Stechmann & Schlegel, 1999; Saito, Kojima, & Endo, 2000).

Gene order in *Terebratulina* differs from that in a chiton (*Katharina*) by a single inversion. This was and probably still is the smallest difference between mitochondrial gene maps of any two metazoan phyla. The significance of this small difference remains uncertain, however (see below), as does the fact that in analyses of SSU rDNA sequences, a chiton was also found to be the closest outgroup to brachiopods and phoronids (Cohen & Gawthrop, 1996; Cohen, Gawthrop, & Cavalier-Smith, 1998). In *Terebratulina,* all the genes are transcribed from the same strand (Stechmann & Schlegel, 1999). This gene arrangement implies that transcription (i.e., synthesis of RNA complementary to DNA) is unidirectional, from a single origin. The significance of this is also uncertain (and see below), except that it may represent an evolutionary simplification.

The mitochondrial genome of *Laqueus* is small, with a compact organization in which overlaps of gene ends are prevalent. As in *Terebratulina*, all genes are coded in the same strand, but the overall gene arrangement differs from that of any other organism reported. Despite this, a number of short (2–3 gene) segments are arranged as in other mitochondrial genomes, including the chiton *Katharina* and the annelid *Lumbricus*, and hence may be interpreted as plesiomorphies (Noguchi & others, 2000).

The mitochondrial genome of *Terebratalia*, like that of *Laqueus*, is small for a metazoan (~1500 fewer nucleotides than *Terebratulina*), and again has all genes coded in the same strand, but with a radically different map order, though some gene junctions are shared with *Laqueus*. As expected from their consuperfamilial taxonomy, the *Laqueus* and *Terebratalia* genomes share features of base composition, codon usage pattern, and protein amino-acid composition, and differ from *Terebratulina* in these (related) properties. One laqueid noncoding (presumed replication start) region is the reverse complement of that in *Terebratulina*, suggesting that an inversion occurred in one lineage and that the origins of replication may be oppositely oriented. Comparison of gene junctions in all three brachiopod genomes and the chiton suggest that some are plesiomorphic and that the laqueid condition is derived (Helfenbein, Brown, & Boore, 2001), in keeping with other established gene sequence and morphological inferences. Although it is unfortunate that the brachiopod mitochondrial genome sample does not include all main lineages, the comparison of two laqueids with a cancellothyridid is useful.

For the phoronid, *Phoronis architecta*, the sequence of all but a small part of the mitochondrial genome has been reported. As in *Terebratulina*, there is remarkable similarity to the chiton, *Katharina*, with only 3 of 31 genes being differently arranged. Cladistic analysis of a gene adjacency matrix gives very strong support to the protostome, lophotrochozoan association of brachiopods and phoronids, and inversion of one particular gene junction suggests that lophotrochozoans are derived relative to deuterostomes. Again, however, there is insufficient information to resolve relationships between brachiopods and other lophotrochozoan phyla (HELFENBEIN & others, 2004).

The only mitochondrial complete sequence available from any inarticulated brachiopod, a specimen of *Lingula anatina*, is strikingly different in many respects from the metazoan norm, being unusually large (28.8 versus ~15 kb) with expanded genes that differ in nucleotide sequence from their homologues in other animals and also with much unassigned sequence and a highly divergent gene order (ENDO & others, 2005). This genome contains two major repeat regions and nested direct repeats of a complexity otherwise unparalleled in animal mtDNAs. Such a structure is not necessarily typical for lingulids, however, because unpublished data obtained by Southern blotting indicated that specimens of *Lingula* from other localities and of *Glottidia* appeared to have a more standard genome size (COHEN & GAWTHROP, cited in COHEN, 2001b). However, further examination of the blots has suggested that this conclusion may be unsafe (COHEN, unpublished observations, 2006).

The unusually large *Lingula* mtDNA could be explained by a model for mitochondrial gene rearrangement by duplication and nonrandom loss (LAVROV, BOORE, & BROWN, 2002), under which it might represent an intermediate evolutionary state between major duplication(s) and completed gene loss. This duplication or deletion model can also account for the (possibly independent) origin of mitochondrial lineages in which all genes are transcribed from the same strand, as in *Terebratulina*, *Laqueus,* and *Terebratalia* (LAVROV, BOORE, & BROWN, 2002).

Because the map order of most genes in the circular mitochondrial genome changes relatively slowly, high hopes have been entertained that map order comparisons would lead to strong phylogenetic inferences. This is a difficult problem when many maps are to be compared, made more difficult by ignorance of the full range of mechanisms by which these genomes become rearranged. A recent Bayesian analysis compared the full gene maps of 87 (and a limited set of 28) metazoan taxa (not including the incomplete phoronid sequence) using an admittedly oversimple evolutionary model in which inversion was the only allowed mechanism of change. Under this simplified model, and with the associated taxonomic priors, brachiopods, annelids, and mollusks group together with strong to moderate support, and brachiopods are a strongly supported sister group of annelids (LARGET & others, 2005). It is too early to know whether this result reflects the greater conservation of mitochondrial gene order in annelids than in mollusks or the relatively unrealistic evolutionary model used.

TOWARD A GENEALOGICAL CLASSIFICATION OF BRACHIOPODA

STUDIES ON PROTEIN AND NUCLEIC ACID SEQUENCES

The principles upon which molecular phylogenetic reconstructions proceed from protein (amino-acid) and nucleic acid (nucleotide base) sequences are generally well understood (e.g., PAGE & HOLMES, 1998; FELSENSTEIN, 2004), but until recently the accuracy of such reconstructions had been verified only indirectly. Strong, direct support has now been obtained in a biochemically defined, serial PCR (polymerase chain reaction) experiment (SANSON & others, 2002) in which all standard phylogenetic methods accurately reconstructed both known divergence times and ancestral sequences. This result strongly reinforces the general confidence already placed in the molecular approach to phylogeny reconstruction; although limited to crown taxa, it provides the best available independent test of phylogenetic inferences from morphology. Of course, morphology itself depends on genes, but those used in phylogenetics neither modulate morphology nor are closely linked to those that do and thus (are assumed to) evolve independently. Various other assumptions about gene evolution underlie our confidence in metazoan molecular systematics, especially that lateral gene transfer (LGT) between distantly related taxa will rarely confuse. A microbial example shows how LGT might operate to distort a phylogeny based on the SSU rRNA gene (Miller & others, 2005).

The principles that should be adopted when comparing phylogenetic inferences based on molecular sequence data with the existing systematics of an extensively studied group like the Brachiopoda have not been the subject of much overt discussion. Those that the author favors are as follows.

1. As direct representations of the primary vehicle of inheritance, gene sequences provide the inherently most reliable evidence of evolutionary history, though as potential palimpsests, their interpretation may be difficult.
2. Molecular results must be replicable and preferably replicated, if possible from a genetically independent source; e.g., nuclear and mitochondrial genomes or closely related taxa or from nuclear genes of different functional classes.
3. Obvious sources of error such as paralogy or amplification of pseudogenes must be excluded.
4. Confidence in the validity of molecular results is enhanced by a large measure of congruence between molecular and nonmolecular systematics.
5. If all sources of molecular error have been excluded, residual discordance points to probable errors in nonmolecular data or their interpretation, e.g., caused by unrecognized homoplasy.

Above the Phylum Level: Protostomes or Deuterostomes?

The majority of post-1995 analyses of metazoan nuclear gene sequences that include at least one brachiopod and phoronid have involved the SSU rDNA gene, and these have confirmed earlier reports (Halanych & others, 1995; Cohen & Gawthrop, 1996, 1997; Cohen, Gawthrop, & Cavalier-Smith, 1998; Cohen, 2001b) that these taxa belong among the lophotrochozoan protostomes, not among deuterostomes, and that a (brachiopod + phoronid) clade is generally recovered. Given the limited resolution available from the SSU rDNA gene, particular interest attaches to analyses that add data from a new gene, especially if it gives concordant overall interphylum relationships while increasing resolution. The most convincing such work (Mallatt & Winchell, 2002) belongs to a series that shows that the LSU rDNA gene has these properties, improving basal, phylum-level resolution (but not enough) and confirming the protostome and deuterostome relationships already inferred from SSU rDNA sequences. Because both SSU and LSU genes specify ribosomal components, they are not evolutionarily independent, but many of the rDNA results have been independently confirmed by analysis of the amino-acid sequence of a gene coding for a protein whose function is unrelated to that of the ribosome (Anderson, Cordoba, & Thollesson, 2004).

Other protein-coding genes may be more problematical, however. For example, in an analysis of flagellar creatine kinase paralogues (i.e., a multigene family that originated by gene duplication and in which descendants of different copies form clades), not only was phylogenetic resolution low, but protostome and deuterostome sequences appear intermingled within a clade (Suzuki & others, 2004). The brachiopod sequence was close to one from a polychaete, but adjacent polychaete and deuterostome (echinoid) sequences were paraphyletic. These extraordinary phylogenetic results probably reflect convergence of amino-acid sequences caused by natural selection acting via creatine kinase function. Problems also beset an analysis based on amino-acid sequences of a myosin subunit gene (Ruiz-Trillo & others, 2002), backed up by and combined with analyses of SSU rDNA sequences. The brachiopod myosin sequence came from a specimen of *Glottidia* sp. (identified by BLC from a specimen provided by I. Ruiz-Trillo, unpublished data, 2004), and it clustered well away from the phoronid, which appeared as the sister of a sipunculan, a relationship that has never emerged from SSU or LSU gene trees, in which available sipunculan sequences are divergent. The SSU analysis also widely separated the brachiopod (*Terebratalia*) and phoronid. Both unusual relationships probably result from inclusion in the alignment of highly divergent acoel sequences that necessitate the exclusion of many sites. Even in this analysis, however, the protostome affinities of brachiopods and phoronids were not in question.

Less comprehensive, but unambiguous reports of the protostome affinity of brachiopod genes, genome components, or gene products include the following: a brief account of 5S RNA (Küntzel, Piechulla, & Hahn, 1983) that escaped notice in our original chapter; an analysis of the phylogenetic distribution of structural forms of metazoan intermediate filament proteins that clearly distinguish protostomes from deuterostomes (Erber & others, 1998); a survey for the presence and phylogenetic relations of transposable elements (Arkhipova & Meselson, 2000); and a review that restated the already well-established protostome affinity based on *hox* and mitochondrial genes and genomes and went on strangely to discuss morphological and developmental characters based on information "mostly taken from classical zoological and developmental textbooks" (de Rosa, 2002, p. 855).

The number of independent lines of molecular evidence favoring a protostome affinity for brachiopods and phoronids is now too great for this to be discounted, which raises the matter of the current lack of congruence between inferences from molecules and from morphology. This is most strikingly demonstrated by a number of studies in which SSU rDNA alignments and morphological data have been combined in some sort of total evidence approach (e.g., Cavalier-Smith, 1998; Zrzavý & others, 1998; Peterson & Eernisse, 2001; Zrzavý, 2003; Glenner & others, 2004). In these analyses the molecular results on their own have given unqualified support to the position of brachiopods and phoronids within the lophotrochozoan protostomes, but the same cannot be said of the morphological results, in some of which, including one that explored differential morphological:molecular weighting (Zrzavý & others, 1998), the morphological characters clustered brachiopods and phoronids (and even ectoprocts) with deuterostomes. Traditional, noncladistic, morphological studies (e.g., Nielsen, 2002) also continue to favor a deuterostome affinity for brachiopods and phoronids, as do morphological cladistic analyses based on characters and codings that reflect similar assumptions (e.g., Nielsen, Scharff, & Eibye-Jacobsen, 1996; Sorensen & others, 2000).

It is at present unclear what features of the morphological characters or their analysis are responsible for the conflict. One possibility is that there may be too much morphological homoplasy for any analysis to retrieve a historically accurate evolutionary tree (Carlson, 1994), while weaknesses of character description and definition may also be involved (e.g., Jenner, 1999, 2000, 2001, 2002, 2004; Jenner & Schram, 1999), affecting both cladistic and traditional morphological studies. Evidence of the latter includes (1) an electron microscopical study that leads to revision of the traditional descriptions of a tripartite coelom in phoronids, suggesting that the light microscopy of stained tissue sections (the basis of most classical morphology) is not reliable for homology inference (Bartholomaeus, 2001); and (2) recent work on cell fate in a chiton, which sheds doubt on inferences based on the presence or absence of spiral cleavage (HENRY, OKUSO, & MARTINDALE, 2004). A potential weakness specific to combined analyses of molecular and morphological characters is that while each nucleotide sequence difference probably corresponds (at least for moderately close relatives) to a single, fixed, evolutionary event, we do not know how many such events (between one and thousands) underlie typical morphological differences. Thus, it is questionable to accord equal weight to molecular and morphological data-matrix elements, as is commonly done (but see SANDERSON & DONOGHUE, 1996), while the range of differential weighting so far explored may be inadequate. Thus, the supposed deuterostome affinity claimed by morphological analyses remains controversial, and it remains to be determined whether any characters that support it will survive critical reanalysis.

Monophyly of Lophophorates

Molecular evidence from the SSU rDNA gene has divided the four lophophorate phyla (pterobranchs, ectoproct bryozoans, phoronids, and brachiopods), putting pterobranchs into the deuterostome alliance alongside other hemichordates and the remainder among the lophotrochozoan protostomes (HALANYCH, 1995; HALANYCH & others, 1995). Until recently, only three ectoproct bryozoan SSU rDNA sequences were available, representing one gymnolaemate and two phylactolaemates, and in all analyses these fell among the lophotrochozoan protostomes but separate from brachiopods and phoronids (HALANYCH & others, 1995; COHEN & GAWTHROP, 1997; COHEN, GAWTHROP, & CAVALIER-SMITH, 1998; GIRIBET & others, 2000; PETERSON & EERNISSE, 2001). A further ten gymnolaemate and one stenolaemate sequence have since been deposited in GenBank (2006), so that all three ectoproct classes are now represented. When aligned with deuterostome and protostome sequences, the position remains as it was: ectoprocts are clearly lophotrochozoan protostomes, but there is no hint of support for a lophophorate or indeed an ectoproct clade (COHEN, unpublished data, 2005). A recent study of phylactolaemate interrelationships that involved a limited sample of other taxa arrived at similar conclusions (WOOD & LORE, 2005). Thus, when the body plans of phyla are compared, lophophores are either plesiomorphic or convergent; lophophorates are not monophyletic (as they were considered to be from morphology, e.g., HATSCHEK, 1888 in 1888–1891; EMIG, 1977).

Monophyly of Brachiopods, Position of Phoronids, and Relationships Between and Within Main Brachiopod Lineages

Whereas monophyly of brachiopods and phoronids has been supported by most SSU rDNA analyses that have included representatives of both taxa, their interrelationships have been less consistently reported, with an early SSU tree showing a (phoronid + articulated) but later ones a (phoronid + inarticulated) clade. This discrepancy was traced to the first phoronid sequence to be described (GenBank accession U12648, HALANYCH & others, 1995), which, by resequencing from the same nominate taxon, was inferred to be an artefactual chimaera, probably involving a phoronid and an articulated brachiopod (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998; COHEN, 2000). SSU analyses that exclude U12648 generally recover the (inarticulated + phoronid) clade, but depending on the alignment, phoronids may instead appear as the sister group of brachiopods (e.g., PETERSON & EERNISSE, 2001). Other analyses that have been misled by this sequence include ZRZAVÝ and others (1998) and WALLBERG and others (2004). The molecular monophyly of (brachiopods + phoronids) has led to three proposed reclassifications of brachiopods and phoronids: (1) as a new phylum, Phoronozoa (ZRZAVÝ & others, 1998, with second thoughts noted in proof), (2) as a new phylum Brachiozoa

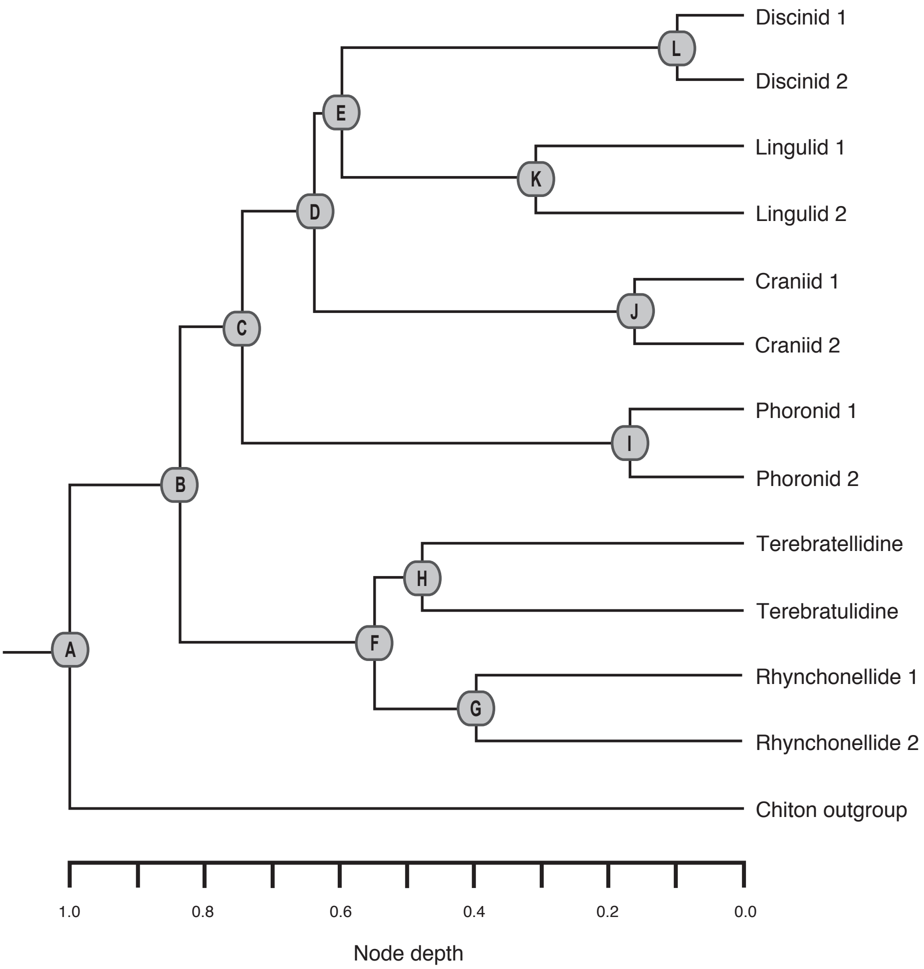


FIG. 1529. Phylogeny of brachiopods and phoronids. Nonparametric rate-smoothed maximum likelihood chronogram, with branch lengths proportionate to time depth. Node labels as in Cohen and Weydmann (2005) (new).

(CAVALIER-SMITH, 1998), or (3) phoronids as a subphylum Phoroniformea within a phylum Brachiopoda, redefined to include both shelled and tubiculous forms (COHEN, 2000). The last proposal was designed to fit into the supraordinal classification adopted in the present work (KAESLER, 1997, 2000, 2002, 2006; WILLIAMS & others, 1996), while avoiding the inconvenience of changing the name of a taxonomically rich phylum.

Following a demonstration that the LSU rDNA gene alone or in combination with SSU yields a well-resolved metazoan phylogeny congruent with other data (MALLATT & WINCHELL, 2002; WINCHELL & others, 2002), improved resolution of the (brachiopod + phoronid) clade and of the main brachiopod lineages has been sought by determining an informative portion of this gene in pairs of phoronids and of brachiopods from every main lineage except thecideidines. In the alignment analyzed, the SSU gene provided 170 and the LSU gene provided 377 variable sites, leading to greatly increased phylogenetic resolution (Fig. 1529). Analyses of these data, validated by recovery of both previously reported distant outgroup relationships and ingroup indicator clades, strongly placed phoronids within brachiopods, as sister to the three inarticulated lineages, craniids, discinids, and lingulids. In a Bayesian likelihood analysis the posterior probability of all clades was 0.90–1.00, and this strongly supported result was used to propose a further amended classification (Cohen & Weydmann, 2005) in which the phylum Brachiopoda was again retained, but with its definition amended (as in Cohen, 2000) to include the shell-less, tubiculous phoronids. The subphyla Linguliformea and Rhynchonelliformea were retained, the former being amended to include phoronids, which became a new class, Phoronata (as anticipated, Cohen, 2000). In addition (and see below) the subphylum Craniiformea was reduced to a class, Craniata, within Linguliformea. In this analysis, molecular evolutionary rates in brachiopods, phoronids, and the chiton and pectinid molluscan outgroups were not ideally clocklike. Nevertheless, after rate smoothing, the data could be calibrated against the fossil record and used to estimate that chitons diverged from (brachiopods + phoronids) in the late Proterozoic, supporting the idea that much paleontologically invisible metazoan diversity originated long before the Lower Cambrian (Cohen & Weydmann, 2005).

The position of phoronids as the sister group of the other extant inarticulated brachiopods could result from a artefact that has been termed short branch exclusion, i.e., these taxa might be incorrectly drawn together by plesiomorphic similarities that are present because all have experienced atypically little evolutionary change (Stiller & Harrell, 2005). If this were so, the position of phoronids should be sensitive to taxon composition, changing when faster-evolving, long-branched taxa are added or removed. However, no such changes were observed when the taxon set was enlarged to include distant and long-branched outgroups, nor when severely pruned (Cohen & Weydmann, 2005). Short branch exclusion could potentially account for the repeated observation (e.g., Cohen & Gawthrop, 1997; Cohen, Gawthrop, & Cavalier-Smith, 1998; Cohen & Weydmann, 2005) that a chiton is the closest sister-taxon of (brachiopods + phoronids), but this possibility is also not currently supported by any evidence. One notable feature of this SSU+LSU rDNA analysis (Fig. 1529) is the presence, for the first time, of the (discinid + lingulid) clade that is strongly predicted by morphology but which has never emerged from analyses of the SSU rDNA gene alone. This tree also confirms earlier molecular evidence that calcite mineralization in craniids and in rhynchonelliforms must have originated independently or is plesiomorphic (Carlson, 1994, 1995); craniids do belong among inarticulated, not among articulated brachiopods (*contra* Gorjansky & Popov, 1986; Popov & others, 1993; Williams & Holmer, 2002; Li & Xiao, 2004). Indeed, this tree suggests that the old classification, with subphyla Articulata and Inarticulata, had considerable merit.

As noted, not all molecular analyses unambiguously recover a (brachiopod + phoronid) clade. One that did not is based on analysis of a large subset (~300 taxa) of what is probably the most wide-ranging alignment of metazoan SSU rDNA sequences yet published (over 600 taxa, Peterson & Eernisse, 2001). Absence of the (brachiopod + phoronid) clade in this analysis can probably be attributed to the exclusion of many ambiguously aligned sites necessitated by the alignment of so many sequences. Another heavily pruned SSU rDNA analysis also failed to recover a (brachiopod + phoronid) clade (Ruiz-Trillo & others, 2002), but it is less understandable that the protein-coding gene included in that work also recovered unusual relationships, as discussed above.

Two wide-ranging collections of sequence data bear on the relationships of the main brachiopod lineages, but both are unfinished and neither has yet been published in full. In Glasgow, the author has continued to sequence SSU rDNA genes as and when new taxa arrive, and illustrative results from this data set are given in Figure 1530 (discussed below). Also, in view of the now-recognized limitations of SSU data, partial LSU sequences are being added as time and resources allow. In Japan, mitochondrial *cox1* sequences have been collected by Michiko SAITO, in some cases from the same individual DNAs used for rDNA gene amplification. The *cox1* data-set also includes closely related, especially laqueoid, species and genera that would not be appropriate candidates for rDNA sequencing, while the rDNA data set includes some taxa for which *cox1* sequences have not been obtained, either for want of opportunity and resources or because existing primers did not work well. Where they do overlap, there is a large measure of agreement between the two sources (COHEN, unpublished data, 2005, and see below). Separate and combined analyses of the SSU and *cox1* data will be presented elsewhere.

SSU rDNA Phylogeny of Brachiopods.—In general, the SSU rDNA gene clearly distinguishes animals from plants, and Radiata from Bilateria, and whether brachiopods belong in the protostome or deuterostome alliances, but it does not clearly resolve the interrelationships of the lophotrochozoan phyla nor the deepest (or shallowest) branchings of the extant brachiopod lineages. The failures probably reflect the duration and age of the cladogenetic events involved: a rapid sequence of divergence events will allow little phylogenetic signal to accumulate in such a slowly evolving gene, and the more ancient the divergence, the more likely the original signal will be overwritten (ADOUTTE & PHILIPPE, 1993). Moreover, resolution is further reduced because the most rapidly evolving gene regions are prone to length variation (necessitating the introduction of alignment gaps), and the wider the range of taxa involved the more must be excluded from analysis because gaps create alignment ambiguity. Figure 1530 is based on SSU rDNAs from 41 articulated brachiopods. The tree topology and clade support values were obtained by a Bayesian likelihood method, using a model of evolution and estimated parameters that best fitted the data, but without taking into account any differential rates applicable to base-paired and unpaired sites inferred from a secondary structure model. Note that Bayesian clade support values (posterior probabilities) are not directly comparable with bootstrap proportions (%).

The SSU rDNA results in Figure 1530 (which the reader might usefully compare with those in the original chapter, COHEN & GAWTHROP, 1997, fig. 180–188, p. 194, 196, 198, 200) illustrate the power and some pitfalls of molecular systematics. More detailed, but nonexhaustive discussion follows, group by group. The results shown generally satisfy the repeatability criteria noted above but reveal some disagreements with traditional, morphological systematics, of which some are dependent on the alignment and analysis method used, while others are taxon specific. The tree topology shown, while representative, is not definitive of the inferences available from the SSU rDNA gene and is deliberately incomplete; the craniid, discinid, and lingulid inarticulated lineages are omitted because this gene contains too few informative sites to reliably resolve their interrelationships (see Fig. 1529).

Molluscan Outgroups.—The chiton, *Acanthopleura*, was the designated outgroup (as discussed in COHEN, GAWTHROP, & CAVALIER-SMITH, 1998), and other short-branched mollusks were included to help indicate the reality of the (brachiopod + phoronid) clade.

Phoronids.—Resolution of the two phoronid genera is apparent, but otherwise the pattern of relationships resolved is unremarkable.

Rhynchonellides.—The five genera sequenced form two subclades, one containing members of the Basiliolidae (*Eohemithiris* and *Parasphenarina*), and one grouping together genera currently placed

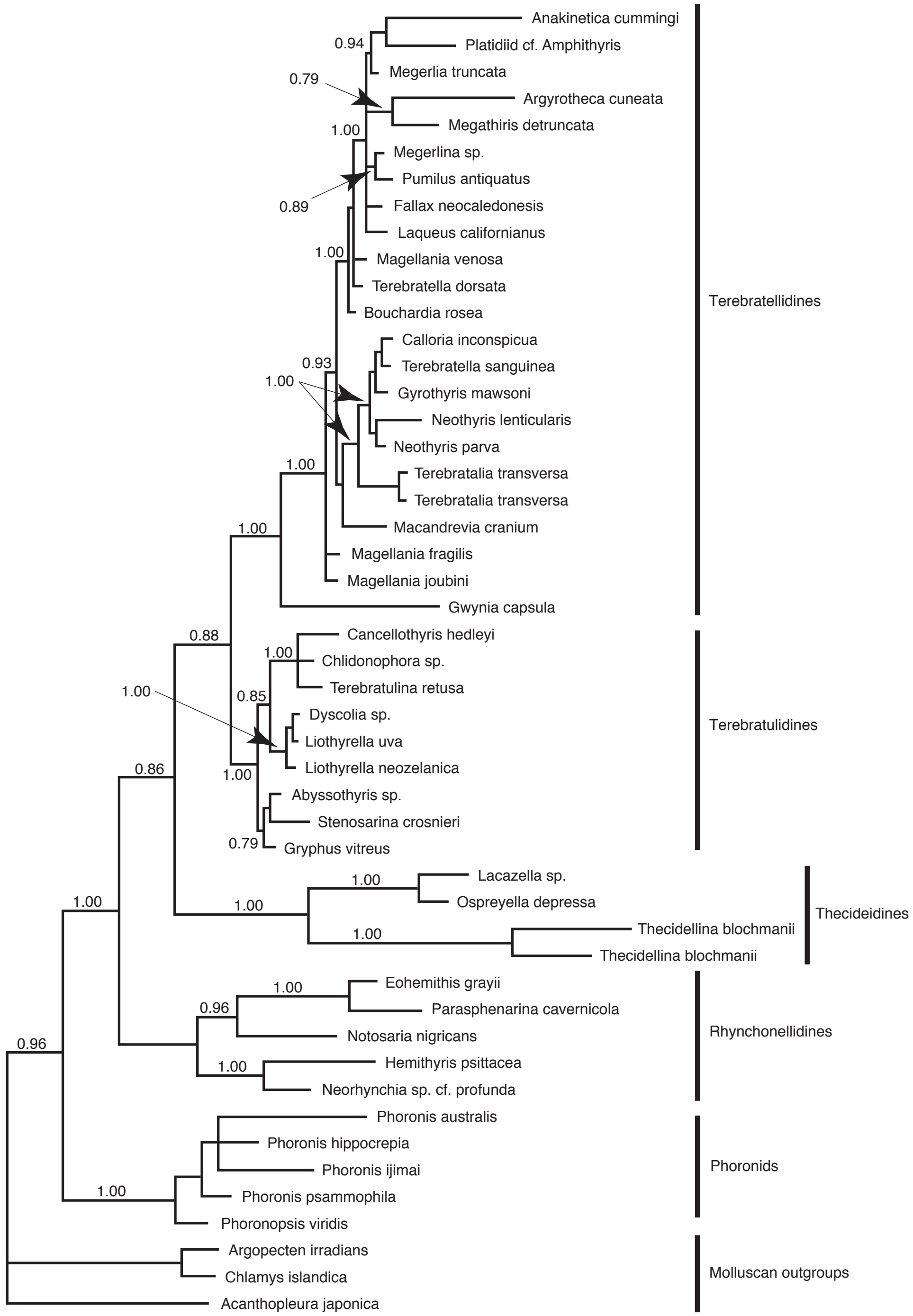


FIG. 1530. *For explanation, see facing page.*

in different superfamilies (*Hemithiris* and *Neorhynchia*). *Notosaria* is morphologically grouped with *Hemithiris*, but here joins the basiliolid clade with fairly strong support. These results both agree and disagree with the current classification (WILLIAMS, 2002). Rhynchonellides are undersampled and, as noted by WILLIAMS (2002), data from *Cryptopora* are awaited with interest. Unfortunately, first attempts to obtain SSU rDNA sequence from the only available specimen were not successful. A sample of the micromorph, *Tethyrhynchia* (LOGAN & ZIBROWIUS, 1994), also awaits analysis. The position of the rhynchonellides as the sister of loop-bearing extant rhynchonelliforms is compatible with the fossil record.

Thecideidines.—The phylogenetic position of thecideidines has long been enigmatic (e.g., BAKER, 1990; CARLSON, 1995; JAECKS & CARLSON, 2001, and references therein) and will evidently also be difficult for molecular data to resolve. When reliable sequence from *Lacazella* became available, our first sequence, supposedly from *Thecidellina* (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998), was recognized as a PCR artefact and withdrawn (COHEN, 2001a). The four genuine SSU rDNA sequences now available clearly belong to and distinguish lacazellid and thecidellinid subclades (the two specimens of *Thecidellina* are from widely separated Pacific Ocean localities) and thereby agree with morphology, but they are on long branches, and in other analyses the whole clade behaves as a sister group of rhynchonellides (not shown). Bayesian clade support for the position shown in Figure 1530 is not very high, and it will be necessary to collect more slow-evolving data before a reasonably reliable position for thecideidines is identified; unfortunately, first attempts to obtain LSU rDNA sequences were not successful (COHEN, unpublished data, 2005). Although the results do suggest that thecideidines belong within the Terebratulida and are not relics of an otherwise extinct lineage, long-branch attraction between thecideidines and rhynchonellides is a possibility that cannot yet be excluded.

Terebratulidines.—It has long been recognized that relatively few useful morphological

FIG. 1530. Phylogeny of articulated brachiopods. SSU rDNA sequences were aligned using Clustal-X v. 1.81 (THOMPSON & others, 1997) with gap opening or extension penalties 10/0.5 and with local realignment of highly variable regions, giving a total of 1816 aligned sites. Ambiguously aligned regions were then removed using Gblocks 1.91 (CASTRESANA, 2000), with default parameters (which vary according to the number of taxa and using the conserved block size recommended for rRNA sequence) leaving 1655 aligned sites (91% of 1816 sites), which were analyzed using MrBayes 3.0. The autocorrelated gamma maximum likelihood model was used because it gave a slightly higher likelihood than the AIC-optimal model (6st+invgamma) identified by MrModeltest 2.0 (NYLANDER, 2004). The Bayesian likelihood analyses were run more than once with default priors in 4 chains for 10^5 generations, sampled every 10^2 generations. All relevant parameters stabilized within 10^4 generations and the consensus tree shown was obtained from the last 5000 generations. Clade support values (posterior probabilities) are attached to selected, nonterminal nodes. Support for all terminal nodes was 0.93–1.00. Branch lengths are proportional to the number of inferred substitutions per site. In the following list accession numbers are provided for sequences obtained from GenBank, and unpublished sequences from the author's laboratory are identified by a D number: *Anakinetica cummingi* D1307, Platidiid cf. *Amphithyris* D1302, *Megerlia truncata* U08321, *Argyrotheca cuneata* AF119078, *Megathiris detruncata* D1292, *Megerlina* sp. AF025943, *Pumilus antiquatus* D1482, *Fallax neocaledonesis* AF025939, *Laqueus californianus* U08323, *Magellania venosa* D1390, *Terebratella dorsata* D1432, *Bouchardia rosea, Calloria inconspicua* AF025938, *Terebratella sanguinea* U08326, *Gyrothyris mawsoni* AF025941, *Neothyris lenticularis* DNZ361, *Neothyris parva* AF025944, *Terebratalia transversa* AF025945, *Terebratalia transversa* D1494, *Macandrevia cranium* AF025942, *Magellania fragilis* AF202112, *Magellania joubini* D1295, *Gwynia capsula* AF025940, *Cancellothyris hedleyi* AF025929, *Chlidonophora* sp. AF025930, *Terebratulina retusa* U08324, *Dyscolia* sp. AF025931, *Liothyrella uva* U08330, *Liothyrella neozelanica* U08332, *Abyssothyris* sp. AF025028, *Stenosarina crosnieri* AF025934, *Gryphus vitreus* AF025932, *Lacazella* sp. D1340, *Ospreyella depressa* D1414, *Thecidellina blochmanii* D1440, *Thecidellina blochmanii* D1339, *Eohemithis grayii* AF025936, *Parasphenarina cavernicola* D1422, *Notosaria nigricans* U08335, *Hemithyris psittacea* U08322, *Neorhynchia* sp. cf. *profunda* AF025937, *Phoronis australis* AF202111, *Phoronis hippocrepia* AF202112, *Phoronis ijimai* AF202113, *Phoronis psammophila* AF025946, *Phoronopsis viridis* AF123308, *Argopecten irradians* L11265, *Chlamys islandica* L11232, *Acanthopleura japonica* X70210. The sequence from *Bouchardia rosea* was provided by M. G. SIMÕES (new).

characters are available among terebratulidines, so that sequence analyses should be particularly valuable, and this was reinforced by an analysis that showed that nuclear and mitochondrial genes gave congruent trees for a few members of this group (COHEN & others, 1998). Cancellothyridids apart, few new, morphologically identifiable terebratulidine specimens have been received, however [no longer as true as it was, but it will take much time before the work is done], and this potential remains unexplored. Cancellothyridids (COOPER, 1973c) are the best-established morphological subgroup, and SSU rDNA agrees (Fig. 1530), yielding a well-supported clade, as well as two other clades not predicted from morphology. Interestingly, analyses with mtDNA sequences within cancellothyridids revealed paraphyly (LÜTER & COHEN, 2002): *Cancellothyris* and *Chlidonophora* nested within Terebratulina, suggesting that cancellothyridids have been oversplit through the use of unreliable morphological characters (COOPER, 1973c). In our analysis (LÜTER & COHEN, 2002) with rather divergent outgroup sequences (none others then being available), *T. unguicula* from Alaska appeared to be the sister-group of the other taxa, but the polarity of this clade is now suspect and requires reinvestigation with closer outgroups. In this study it was suggested that brachiopod populations may retain evidence of ancestral migration through Mesozoic Tethys. This suggestion was also made on the basis of mitochondrial sequence evidence for well-supported clades uniting *Dyscolia* (but not *Gryphus*) with *Liothyrella* and Pacific *Stenosarina* with *Abyssothyris* (Fig. 1530 and COHEN & others, 1998), and it was also raised in speculations on the origin of *Glottidia* (WILLIAMS & others, 2000). Similar evidence appears to be emerging from a study of craniid interrelationships (COHEN, LONG, & SAITO, 2007). With their cosmopolitan distribution, lecithotrophic larvae, and modest rate of sequence evolution, cancellothyridids have considerable potential as model organisms for the study of post-Mesozoic evolution in the deep sea, and many specimens from Pacific locations, including the Norfolk Ridge seamounts, await analysis.

Terebratellidines.—There is good support in the SSU tree for a terebratellidine clade (Fig. 1530), confirming the utility of loop ontogeny and morphology as diagnostic characters, but within this clade there is little strongly supported resolution, consistent with a relatively recent radiation. The New Zealand endemic genera form a strongly supported subclade, suggesting that they differentiated in isolation and that ~80 myr is enough to allow clear divergence to be recorded by this gene. The sister-group relationship of *Terebratalia* with the New Zealand endemics seen in these trees is contradicted by new LSU and *cox1* sequence analyses, which agree that *Magellania* spp. are the sister-group of the New Zealand endemics. Comparison of analyses of SSU, LSU, and mitochondrial *cox1* sequence within the *Magellania* clade reveal disagreements, however, probably caused by base composition differences (M. A. Bitner, personal communication, 2005).

In the remainder of the terebratellidine SSU rDNA subtree some unsurprising terminal nodes are well supported, coupling *Argyrotheca* with *Megathiris, Megerlina* with *Pumilus*, and *Megerlia* with *Anakinetica* and a platidiid, while the unexpectedly close relationship between *Terebratella dorsata* and *Magellania venosa* can be explained if, as now seems likely, the former were juveniles of the latter, misidentified by the author. They were collected in the same locality.

Gwynia (currently *incertae sedis*) is another potentially problematic taxon, appearing as the sister-group of all other terebratellidine taxa, separate from the megathyridids with which it has been associated morphologically (LOGAN, MACKINNON, & PHORSON, 1997).

This result is as yet unreplicated, however, and awaits confirmation.

Apart from the terebratellidine SSU results just described, valuable analyses based on the relatively slow-evolving mitochondrial gene *cox1* have focused on relationships among the Laqueoidea, leading to the suggestion that some traditionally important morphological character states (especially adult loop characters) are prone to homoplasy, but that a previously overlooked loop ontogeny character (MacKinnon, 1993; MacKinnon & Gaspard, 1995) may be more reliable (Saito, 1996, 1998; Saito, Kojima, & Endo, 2000; Saito & Endo, 2001; Saito, Endo, & Cohen, 2001). As noted above, *cox1* disagrees markedly in some respects with SSU rDNA. In particular, it gave good support to a sister-group relationship between Antarctic *Magellania* spp. and the New Zealand endemic genera, and it united two *Terebratalia* spp. with other laqueoids (Saito, Endo, & Cohen, 2001). Both of these results are more consistent with traditional systematics than the relationships proposed by the SSU rDNA analyses, which are based on weaker phylogenetic signals.

Calibrated Rates of Molecular Evolution and Dates of Major Divergences

In recent years, use of a molecular clock hypothesis to estimate the ages of past divergence events has undergone considerable development. Evidence has accumulated from detailed examination of the distribution of changes within genes that each nucleotide site or domain may have its own rate of change, while relative rate tests have shown that the clock may tick at different rates in different lineages. Moreover, at different past times, the rate of evolution at a site, domain, or in a lineage may have fluctuated, and inevitably, the longer the time involved, the more likely it is that such changes will have occurred and that fixed mutations will be overwritten, obscuring phylogenetic signals. The molecular clock rate is therefore only approximately constant, and a variety of methods have been developed in attempts to escape from or cope with the various complications. Cautious and critical interpretation remains necessary for divergence times estimated with a molecular clock hypothesis.

For brachiopods, the first molecular clock analysis was based on a simple, graphical method of rate estimation from an SSU rDNA gene tree (fig. 7 in Cohen, Gawthrop, & Cavalier-Smith, 1998), using data that (with the test then employed) showed no significant rate heterogeneity. This analysis gave a range of rates that placed in the late Proterozoic the extrapolated time of divergence between brachiopods and a chiton, consistent with some other molecular analyses of the metazoan radiation (e.g., Wray, Levinton, & Shapiro, 1996) that imply considerable divergence well before the Cambrian explosion. This result has been reinforced by a new study based on much more rDNA sequence data from fewer taxa, which, when analyzed with more sophisticated methods, gave a closely similar range of dates for the brachiopod:chiton divergence (Cohen & Weydmann, 2005). The discordance between the Cambrian explosion as seen in the fossil record and the much earlier timing of metazoan divergence often inferred from molecular data has been addressed in a recent experimental analysis of molecular evolution rates, which concluded that unless rates were greatly accelerated during the Cambrian, divergence started ~100 myr earlier (Levinton, Dubb, & Wray, 2004), consistent with the results described above for brachiopods. Timing metazoan divergence by the correlation of molecular and paleontological data may be controversial (e.g., Graur & Martin, 2004; Hedges & Kumar, 2004), but new ideas that take into account effects of body size, metabolic flux, and temperature (Gillooly & others, 2005) have the potential to solve some of the problems, and in doing so suggest that small brachiopods with low metabolic rates may be extremely suitable for the dating of ancient divergences.

A rate estimate has also been obtained for the SSU (12S) rDNA mitochondrial gene, calibrated by the likely time at which Antarctica and New Zealand *Liothyrella* sp. became isolated. This calibration gave a rate of mitochondrial sequence evolution (about 0.1% divergence per million years) several-fold slower than estimated for some other organisms. Since rate heterogeneity was absent, the *Liothyrella* rate was used to infer divergence times in *Terebratulina* sp., and it put the divergence between *T. unguicula* and the North Atlantic species *T. septentrionalis* and *T. retusa* at ~100 myr, and that between *T. septentrionalis* and *T. retusa* at ~60 myr. More recently, however, divergence between Antarctic and New Zealand craniids has been found to be greater than that between *Liothyrella* sp. (COHEN, unpublished data, 2005), which raises the possibility that effective separation of New Zealand and Antarctic *Liothyrella* populations may have been delayed by dispersal of long-lived larvae (PECK & ROBINSON, 1994). If so, and provided craniid and *Liothyrella* mitochondrial genes evolve at similar rates (unlikely!), the rate of evolution in *Liothyrella* may have been underestimated (by perhaps two-fold) and the divergence dates of *Terebratulina* sp. correspondingly overestimated. These questions are currently under review, and, in the light of the relationships shown in Figure 1530, it may also be necessary to reconsider the underlying assumption that isolation of the New Zealand brachiopod fauna dates from the time at which effective geographical isolation from Antarctica was established.

POPULATION DYNAMICS BELOW THE SPECIES LEVEL

In the only study under this heading since 1995, allozyme polymorphism was investigated in 10 population samples of *Terebratella sanguinea* in 5 New Zealand fjords (OSTROW & others, 2001). Most samples were in genetic equilibrium, but 2 from fjord-head sites were not. There was little evidence of large-scale genetic differentiation either within or between fjords, but some indications were obtained of small-scale differentiation between sample sites, with private alleles in single samples. Markers offering greater resolution than allozymes appear to be required for the resolution of brachiopod population structure and dynamics.

EVOLUTION AND DEVELOPMENT

Since 1995, the molecular analysis of animal development has greatly expanded, with further work on gene families such as *hox* (homeobox), *eng* (engrailed), and *wnt* (wingless) that encode signalling molecules with roles in the control of cell fate specification, proliferation, movement, and in segment polarity. The field has even acquired a nickname: EvoDevo (ARTHUR, 2002). A flavor of the complexity involved is given by the *wnt* gene family, of which one member has been isolated from a brachiopod (HOLLAND, WILLIAMS, & LANFEAR, 1991) but of which at least 9 (of 12 or more) subfamilies appear to have been present in the bilaterian common ancestor (PRUD'HOMME & others, 2002). Brachiopods and phoronids have been included in some genomic surveys for such genes (e.g., DE ROSA & others, 1999), but little or nothing has so far been published about their expression in development. Perhaps this is not such a major loss because co-option, co-evolution, and convergence are evidently implicated in the evolution of these genes (HOLLAND, 1990). For example, in some annelids, patterns of *eng* expression are unrelated to their clear segmentation (SEAVER & others, 2001, and references therein), and in echinoderms the roles of these genes evidently have been evolutionarily labile (LOWE & WRAY, 1997). Given such findings, it is perhaps not surprising that despite many detailed advances and many new hypotheses, no grand new understanding of the evolution of developmental systems and body plans has so far emerged. Indeed, the only conclusion so far of direct significance to brachiopod studies is that such relatively inaccessible, marine creatures are not likely to be favored as candidate model organisms for this sort of work (Tessmar-Raible & Arendt, 2003). Nevertheless, it is probably important to discover the expression patterns of developmentally important genes in brachiopods, even those potentially involved in segmentation. Even more than segmentation, left-right asymmetry is a developmental feature that has some potential to be discerned in fossils and, moreover, is ubiquitous in crown-group brachiopods. A small, core set of genes appears to be involved in the underlying symmetry-breaking process (Palmer, 2004), and perhaps these too would reward study.

Rather than attempt a comprehensive review of this field where so little is known that is directly relevant, the reader is referred to the discussion and bibliography in a recent, wide-ranging book (Valentine, 2004, especially chapter 3, p. 76–114).

ACHIEVEMENTS AND LIMITATIONS OF MOLECULAR SYSTEMATICS OF BRACHIOPODS

The main promise of molecular systematics, to provide a strong, independent test of morphological systematics, has been demonstrated and, in part, achieved. Monophyly of the Brachiopoda *s.s.* can no longer be in doubt, and accommodation of the Phoronida within Brachiopoda *s.l.,* though unanticipated, creates no known major conflict with morphotaxonomy. In addition, molecular data have revealed that brachiopods belong in the (morphologically unexpected) lophotrochozoan supraphylum alliance and have largely confirmed morphotaxonomic conclusions about the interrelationships of high-level brachiopod taxa, and confirmed the dual origins of calcitic mineralization. At lower levels and especially in phylogeography, insufficient work has been done to more than hint at gold waiting to be mined. Successes include the recognition of cancellothyridids as a clear clade and the distinction, in this family and in laqueoids, between some taxonomically reliable and unreliable morphological characters. For extant forms at least, the day of taxon-splitters is over, their bluff can be called.

The main limitations of molecular systematics reflect the cost, difficulty, and unpredictability of collecting, the cost of gene sequencing, the difficulty of distinguishing homoplasy from true evolutionary relationships, and the difficulty of knowing (when they disagree) which analytical method to trust. Because brachiopods are not perceived as model organisms and health-related connections are nonexistent, stable funding has been elusive and new workers scarce; except in paleontology, brachiopods do not appear to offer a safe basis on which to develop a research career. Thus, brachiopod molecular systematic and genomic analyses have not achieved a critical, self-sustaining mass and probably will not do so unless high-profile discoveries emerge, and because of the small size of the active, brachiopod-specific molecular research community these organisms are unlikely to win an early place in the comparative genomic sequencing roster. The case that needs to be made convincingly is that these creatures (especially craniids and discinids) may provide the clearest window into the state of the metazoan genome as it was in or before the Lower Cambrian, and they are therefore an essential component of comparative genomics.

GENE TREES AND IMMUNOTAXONOMY

Readers of the chapter on Shell Biochemistry: Immunology of Brachiopod Shell Macromolecules (Cusack, Walton, & Curry, 1997, p. 261–266) inexplicably were not alerted to discussions of the reliability of this approach and of its utility for the reconstruction of phylogeny (Cohen, 1992, 1994; Curry & others, 1993). The latest of these papers concluded that while the method "… has a potentially important role in the extension of genealogical classification to fossils and empty shells, … in its current state [it] departs in several important respects from immuno-taxonomic norms," (Cohen, 1994, p. 910). No more recent publication gives cause to revise this assessment, and comparison of the relationships shown in Cusack, Walton, and Curry (1997, fig. 219 and 220) reveals discordance with both morphology and with gene sequence-based trees (Cohen & Gawthrop, 1997, fig. 180–188) and Figure 1530 (herein).

ACKNOWLEDGMENTS

Larry Flammer kindly supplied scanned images of illustrations from his thesis. M. G. Simões (University Estadual Paulista, São Paulo, Brazil) kindly provided the SSU rDNA sequence of *Bouchardia rosea*. Financial support for work on thecideidines was received from the University of Kansas Paleontological Institute, through Alwyn Williams. The author is particularly grateful to brachiopods (*s.l.*) for providing a fresh and stimulating research interest, and to Gordon Curry (University of Glasgow), who opened the door to it.

BIOCHEMISTRY AND DIVERSITY OF BRACHIOPOD SHELLS

Maggie Cusack and Alwyn Williams

[University of Glasgow; and deceased, formerly of University of Glasgow]

INTRODUCTION

The Biochemistry section of Volume 1 (Cusack, Walton, & Curry, 1997, p. 243) introduced the complexity of the mineral-associated proteins of all three brachiopod subphyla. The mineral-associated proteins from modern brachiopods have been characterized in more detail (Williams & Cusack, 1999; Williams, Cusack, & Brown, 1999; Cusack & others, 2000; Cusack & Williams, 2001a, 2001b), and the complexity is now all the more apparent as is the rapid degradation of informative proteinaceous material (Williams & others, 1998). In the case of some modern brachiopods, the influence that these proteins have on crystallization *in vitro* has begun to be elucidated (Cusack & others, 2000; Lévêque & others, 2004). The catalysis of hydroxyapatite from amorphous calcium phosphate by proteins of *Lingula anatina* shells is unusual in that it is effected by proteins in solution (Lévêque & others, 2004). The discovery of siliceous tablets on the first-formed shell of discinids indicates major changes to biochemical regimes during ontogeny with a switch from the secretion of silica to that of apatite. The regularity of the shape and dimensions of the siliceous tablets suggests that they are produced intracellularly and secreted to the surface as intact, complete entities (Williams, Cusack, & Buckman, 1998) as confirmed by Lüter (2004; see section on discinoid juvenile shell in Chemicostructural Diversity Chapter, p. 2402 herein). The widely accepted description of rhynchonelliform brachiopod shell composition as low-Mg calcite is an oversimplification, since the concentration and distribution of magnesium varies considerably between species and even within species with a consistent species pattern in all cases. The magnesium content of the Craniiformea is uniformly high throughout the shell (England, Cusack, & Lee, 2007). The complexity of the magnesium distribution in brachiopod calcite must be understood fully in order for the Ca-Mg ratio to be exploited accurately as a paleothermometer (England, Cusack, & Lee, 2007).

ORGANOPHOSPHATIC SHELL CHEMISTRY

In the 1997 *Treatise* (Kaesler, 1997), the mineral component of the organophosphatic brachiopod shell was identified as a carbonate-containing fluorapatite (Watabe & Pan, 1984; LeGeros & others, 1985) with *Glottidia* containing higher concentrations of carbonate and thus having lower crystallinity than *Lingula*. Since then, there has been the discovery of intracellularly manufactured (Lüter, 2004) siliceous tablets on the larval surface of discinid valves (Williams & others, 1998; Williams & Cusack, 2001; see section on Lingulid Juvenile Shells in Chemicostructural Diversity, herein, p. 2409). The 1997 *Treatise* included details of proteins from valves of *Lingula anatina*, *Glottidia pyramidata,* and *Discinisca tenuis*, revealing different protein profiles in each case. More recent investigations of the organic components of organophosphatic shells have confirmed a wide diversity in the shell biochemistry of living lingulids. The ability of the proteins of *L. anatina* to catalyze the *in vitro* transformation from amorphous calcium phosphate to fluorapatite has been demonstrated (Lévêque & others, 2004). The rapid degradation of the organic components during fossilization has become apparent.

SHELL MINERALOGY

The basic apatitic unit of the discinid shell is a granule, 4–8 nm in diameter. The X-ray diffraction patterns of this biomineral in

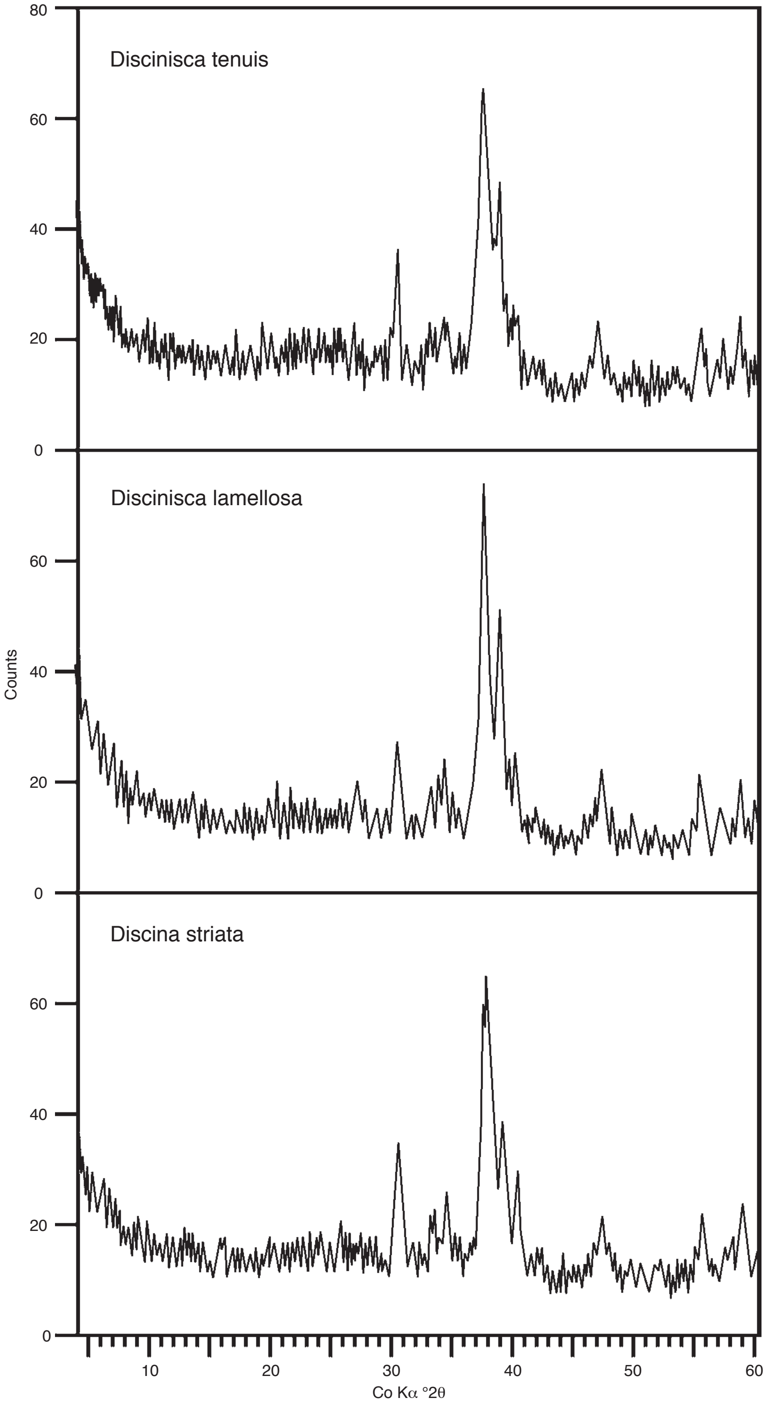


FIG. 1531. XRD line profiles of discinid shells. Shells powdered in acetone were poured over glass slides and XRD determinations made in a Philips PW 1050/35 XRD with a Co energy source (Williams, Cusack, & Buckman, 1998).

the shells of *D. tenuis*, *D. lamellosa,* and *D. striata* (Fig. 1531) are all comparable with those of *Glottidia pyramidata* and *Lingula anatina* obtained by LEGEROS and others (1985) who, using infrared (IR) absorption and fluorine analyses, described the mineral component of the two lingulids as "crystallo-chemically similar but not identical to marine phosphorite or mineral francolite, a carbonate-containing calcium fluorapatite" (LEGEROS & others, 1985, p. 99). PUURA and NEMLIHER (2001) examined the lattice parameters of Recent, subfossil, and fossil linguloid valves. They concluded that the lingulid shell mineral of ten specimens of *L. anatina* from the Philippines is a fluorine-containing carbonate-OH apatite, with lower OH and higher F content than in mammal teeth and bone. The range of lattice parameters within these ten specimens was a = 9.386–9.396Å and c = 6.859–6.864Å. In their study of ten subfossil valves of *Discinisca tenuis*, PUURA and NEMLIHER (2001) demonstrated that postmortem alteration processes partially replaced the *in vivo* shell apatite with apatite of lower OH content. In shells of fossil linguloids from the Upper Cambrian *Obolus* sandstone there was a mixture of diagenetically altered skeletal apatite and nonskeletal apatite that was precipitated during diagenesis. The range of lattice parameters of the fossil shells is a = 9.33–9.36Å and c = 6.87–6.89Å.

LIVING SHELL BIOCHEMISTRY

Shells of modern linguliform brachiopods, the lingulids and discinids, have a high organic and water content (Table 23). In *L. anatina* the organic components are concentrated in the shell anterior and lateral regions, while the posterior and median regions have a higher mineral content (CUSACK & WILLIAMS, 1996; LÉVÊQUE & others, 2004). *Lingula* and *Glottidia* shells have a higher organic and water content than discinid shells. The high level of organic material in lingulid shells relative to that of discinids (Table 23) is not reflected in the amino acid content, since the discinids have a higher concentration of amino acids than *Lingula* and *Glottidia* (Table 24). The high water content in *L. anatina* and *G. pyramidata* shells suggests a more hydrophilic organic component such as chitin or GAGs. Indeed, both glucosamine and galactosamine were detected after HCl dissolution of valves of *L. anatina* and *G. pyramidata* as well as *D. striata*. Failure to detect these amino sugars in *D. tenuis* and *D. lamellosa* is attributed to technical inadequacies, as amino sugars cannot be resolved from high levels of amino

TABLE 23. Water and organic content of three species of discinoid brachiopods as compared with linguloid brachiopods *Lingula anatina* and *Glottidia pyramidata*. Water content was determined at 30% relative humidity (new).

	Water	Organic (% wet weight)	Organic (% dry weight)
Discinisca tenuis	8.5	32.1	25.7
Discinisca lamellosa	6.8	31.5	26.5
Discina striata	6.1	41.1	37.3
Lingula anatina	9.7	42.2	35.9
Glottidia pyramidata	12.5	61.0	55.4

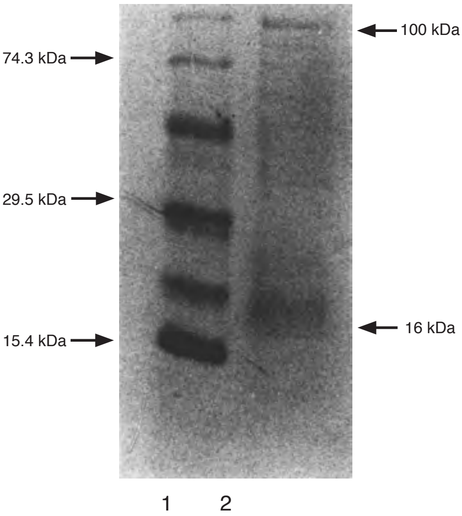


FIG. 1532. SDS PAGE of mineral-associated proteins of *D. tenuis* shells. EDTA-soluble proteins (equivalent to an extract from 1.1 g shell) were fractionated (*2*) in a 15% polyacrylamide gel alongside prestained proteins of known molecular weight (*1*). Proteins were revealed by staining with Coomassie Blue (Williams, Cusack, & Buckman, 1998).

TABLE 24. Amino acid content (pmoles/mg^{-1} shell) of three species of discinoid brachiopods as compared with linguloid brachiopods *Lingula anatina* and *Glottidia pyramidata* (new).

	Amino acid content
Discinisca tenuis	350 ± 48
Discinisca lamellosa	264 ± 35
Discina striata	257 ± 2
Lingula anatina	32 ± 4
Glottidia pyramidata	42 ± 8

acids. It is, therefore, likely that dilution of the amino acids from *D. tenuis* and *D. lamellosa* dilutes the amino sugars below the detection threshold (WILLIAMS, CUSACK, & BUCKMAN, 1998).

Proteins were extracted from shells of *D. tenuis* and *L. anatina* (WILLIAMS, CUSACK, & MACKAY, 1994) and fractionated on 15% polyacrylamide gels according to the method of SCHÄGGER and VON JAGOW (1987). Staining with Coomassie Blue reveals the most abundant proteins, while silver staining, which has much higher sensitivity, reveals those proteins present at lower concentrations. Protein glycosylation was determined by lectin binding using Concanavalin A-peroxidase (FAYE & CHRISPEELS, 1985). The EDTA-soluble mineral-associated proteins of *D. tenuis* are presented in Figure 1532, where Coomassie Blue staining reveals proteins in the molecular weight range of 16 to 100 kDa. Silver staining enlarges the lower range to 6.5 kDa (Fig. 1533). At least one of the proteins, molecular weight 13 kDa, is glycosylated (Fig. 1534). Coomassie Blue staining of proteins from *L. anatina* shells reveals relatively abundant proteins of molecular weight 21.5 and 24 kDa (Fig. 1535.2). Silver staining reveals the molecular weight range of 5 to 60 kDa (Fig. 1535.1). The two proteins of relatively high abundance and molecular weight 21.5 and 24 kDa are both glycosylated (Fig. 1535.3). The overall protein pattern is different for *D. tenuis* and *L. anatina* as is the pattern of glycosylation.

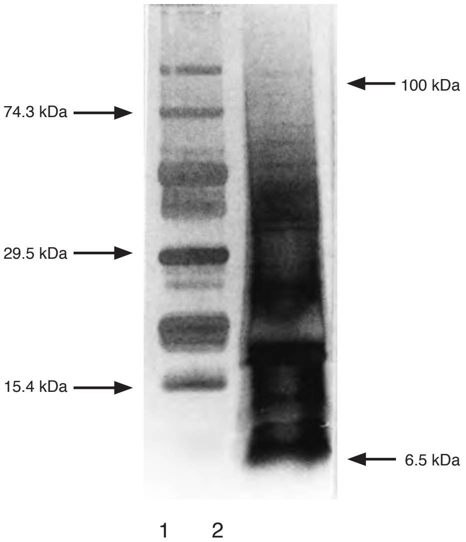


FIG. 1533. Silver staining of mineral-associated proteins of *D. tenuis* shells. EDTA-soluble proteins were fractionated by SDS PAGE and stained with silver (Morrisey, 1981) to reveal those proteins present at concentrations below the detection limit of Coomassie Blue; lanes (*1*) and (*2*) (Williams, Cusack, & Buckman, 1998).

The amino acid composition of the most abundant proteins extracted from *D. tenuis* and *L. anatina* is presented in Tables 25 and 26 respectively. Amino acid analysis does not distinguish between aspartic acid (D) and asparagine (N) nor glutamic acid (E) and glutamine (Q), and the total values for D+N and E+Q are here assumed to be acidic amino acids. In *D. tenuis*, the concentration of acidic residues is higher in the larger proteins, with mole% values of 26 for the proteins of molecular weight 100 kDa and 72 kDa. Although there is no information regarding the conformation of these proteins *in vivo*, comparison of the ratio of acidic to basic amino acid residues may indicate the overall charge of these proteins. The ratio of acidic (D, N, E, Q) to basic (H, R, K) residues is 4·2:1, 4·7:1, 2·6:1, 4·8:1, 3·1:1 and 4·4:1 for the 100, 72, 48, 34, 21, and 16 kDa proteins respectively. On this basis, the 34 kDa protein is the most acidic, and the 48 kDa protein the most basic.

The EDTA-soluble extract accounts for only a small proportion of the total shell

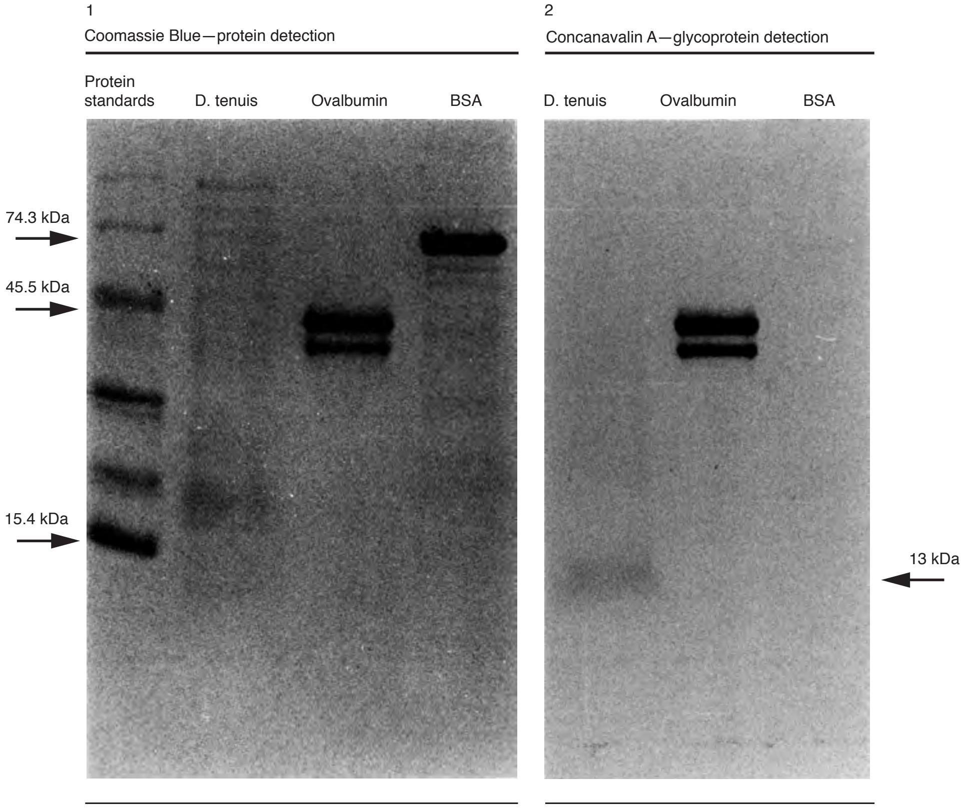


FIG. 1534. EDTA-soluble (glyco) proteins from *D. tenuis.* EDTA-soluble proteins of *D. tenuis* (equivalent to an extract from 1.1 g shell) were fractionated on SDS PAGE gels alongside proteins of known molecular weight and ovalbumin (3 µg), which is glycosylated, and bovine serum albumin (BSA; 5 µg), which is not. Duplicate samples were applied to the gel, and following electrophoresis, proteins were electroblotted onto ProBlott© membrane and the membrane halved; one portion (*1*) was stained with Coomassie Blue to reveal all proteins present; (*2*) the membrane was treated with the lectin, Concanavalin A to detect glycoproteins (Williams, Cusack, & Buckman, 1998).

protein (e.g., 0.016% of the total amino acid content of the shell of *D. tenuis*; WILLIAMS, CUSACK, & BUCKMAN, 1998), indicating that a large proportion of the shell protein is fibrous or at least insoluble to EDTA extraction. To extract information from the whole protein content, the total amino acid composition of the shells of four discinid species and those of *L. anatina* and *G. pyramidata* was determined by dissolving the shells with HCl (2N) and hydrolyzing all proteinaceous material released; the results are presented in Table 27.

As well as differences in the concentration of amino acids, which is higher in discinid than in lingulid shells (Table 24), some differences in amino acid composition between discinids and lingulids are also apparent. In the shells of living discinids, the average content of acidic amino acids (D/N and E/Q) is 14.5%, with *Pelagodiscus atlanticus* containing the highest concentration of acidic amino acids (16.9%) and *D. tenuis* the lowest (11.9%). For the basic amino acids (H, R, and K), the mean value is 13.2%, with *P. atlanticus* containing the highest concentration of basic amino acids (19.9%) and *D. tenuis* and *D. striata* the lowest, with 9.7% and 9.8% respectively. Glycine and alanine occur in large quantities. Glycine has an average value of 24.3%, with *D. tenuis* containing the highest concentration (31.6%) and *P. atlanticus* the lowest (8.8%). For alanine, the mean value is 22.7%, and in this case, *D. tenuis* contains the highest concentration (29.3%) and *D. lamellosa* the lowest (24%).

The shells of living lingulids contain higher concentrations of acidic amino acids than those of discinids, with an average value of 21.1%. The levels of basic amino acids (H, R, and K), with a mean of 9.1%, are lower than that of the discinids (13.2%). Glycine and alanine also occur at high concentrations in lingulids, averaging 19.6% and 22.95% respectively for *L. anatina* and *G. pyramidata*, although these are still lower than those in discinids.

These total amino acid compositions were compared, along with those of *L. reevii, L. parva,* and *G. palmeri*, by Principal Components Analysis, the results of which are presented in a 2-D scatterplot where the two eigenvectors account for 70% of the variation between samples (Fig. 1536). Glycine, histidine, and leucine constitute the major differences along the first eigenvector U1 with proline and valine also contributing. Along vector U2, arginine is the major contributor with threonine, methionine, and cysteine also contributing. The three species of *Lingula* cluster together with high values for vector U2. Three discinid species, *D. lamellosa*, *D. striata,* and *D. tenuis* cluster together, while *P. atlanticus* plots away from all other linguliform brachiopods analyzed. Taking the three species, *D. lamellosa*, *D. striata,* and *D. tenuis*, as the discinid cluster, *Lingula* plots further from the discinids than does *Glottidia*. Indeed *Glottidia* occupies an intermediate position between *Lingula* and the discinids. This intermediate position may relate to the occurrence of baculation within shells of *Discina* and *Discinisca,* but it does not account for the fact that *Pelagodiscus* occupies a position distant from the other organophosphatic brachiopods

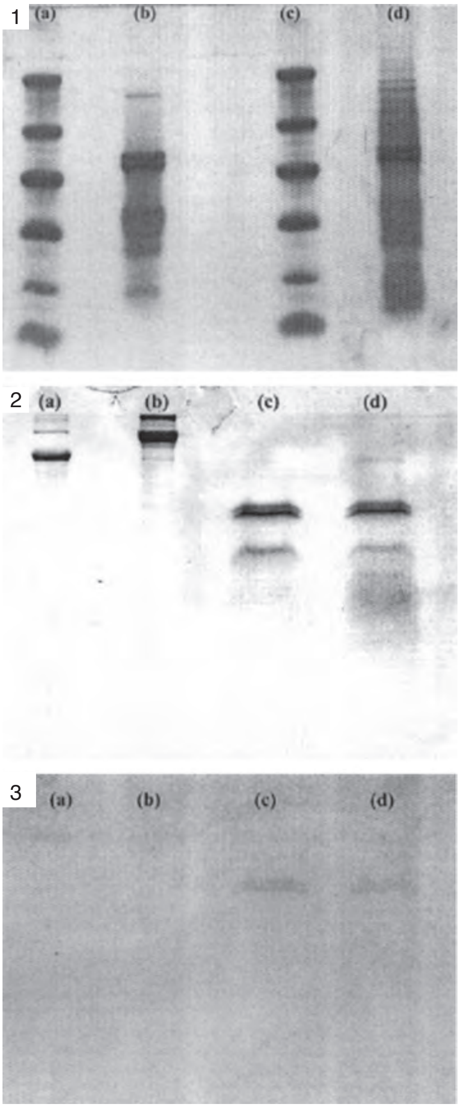


FIG. 1535. SDS PAGE gels and blot of protein extracts from *L. anatina* valves. *1,* SDS PAGE gels of (a and c) molecular weight markers corresponding to 44.7, 29.3, 20.2, 14.8, 5.7 and 2.9 kDa, (b) GnHCl-extracted proteins, and (d) EDTA-extracted proteins. Proteins were fractionated, fixed, and then silver stained; *2,* SDS PAGE gels of (a) ovalbumin (1 mg, 43 kDa), (b) bovine serum albumin (1 mg, 66 kDa), (c) GnHCl extract (3.9 mg protein), and (d) EDTA extract (3.9 mg protein); proteins were Coomassie stained; *3,* electroblot of duplicate gel as in *2,* probed for carbohydrate using Concanavalin-A (adapted from Lévêque & others, 2004).

TABLE 25. Amino acid composition (mole%), using one- letter code for amino acids, of EDTA-soluble mineral-associated proteins of *Discinisca tenuis* (new).

Amino acid	100 kDa	72 kDa	48 kDa	34 kDa	21 kDa	16 kDa
D/N	15.1	14.9	11.9	11.2	10.2	10.8
E/Q	11.4	11.7	8.5	10.8	10.5	10.6
S	11.4	9.7	5.8	7.5	6.1	8.1
G	14.6	14.9	18.9	11.6	12.7	8.5
H	-	-	3.9	-	1.7	1.6
R	4.7	4.8	3.0	3.3	2.9	0.1
T	8.8	6.0	6.5	6.2	6.1	5.9
A	9.9	13.3	13.5	15.6	12.9	7.2
P	3.6	4.0	8.0	6.4	6.9	6.0
Y	-	-	-	1.1	0.9	2.3
V	5.7	2.4	3.7	5.2	4.2	5.6
M	-	3.6	3.5	2.1	2.3	3.6
C	0.5	-	-	-	0.4	6.2
I	4.7	5.2	4.8	6.3	6.7	5.6
L	6.2	6.4	5.0	7.3	8.1	7.4
F	3.1	3.6	3.5	4.6	4.9	7.3
K	1.6	0.8	0.8	1.3	2.1	3.1

analyzed, since the shell of *Pelagodiscus* is also baculate.

The valves, setae, and pedicles of organophosphatic valves contain chitin as determined by pyrolysis GC-MS, which revealed the presence of acetamidofuran, 3-acetamido-5-methylfuran, and 3-acetamido-*n*-pyrone (WILLIAMS, LÜTER, & CUSACK, 2001), all three of which are unequivocal markers for chitin (STANKIEWICZ & others, 1996).

LINGULA ANATINA SHELL PROTEINS AND *IN VITRO* CRYSTALLIZATION

The protein mixture extracted from *Lingula anatina* valves (Fig. 1535) was added to buffered calcium phosphate/fluoride metastable solutions at constant temperature. The induction period for FAP crystallization was reduced by approximately 24% for a protein

TABLE 26. Amino acid composition (mole%), using one- letter code for amino acids, of EDTA-soluble mineral-associated proteins of *Lingula anatina* (new).

Amino acid	46kDa	36kDa	24kDa	21.5kDa	10kDa	6kDa
D/N	6.08	9.68	8.98	7.38	9.88	9.65
E/Q	8.45	20.93	11.72	14.52	22.73	17.2
S	12.14	7.74	7.23	8.63	6.16	6.6
G	24.53	4.5	9.68	11.03	9.17	6.14
H	1.35	0.83	0.89	0	2.08	2.2
R	2.44	4.61	3.04	2.81	2.83	2.3
T	5.69	5.61	5.42	4.16	3.89	7.36
A	10.53	13.06	12.51	15.86	9.82	9.64
P	5.21	2.27	5.26	3.63	4.19	6.29
Y	1.47	4.08	1.29	1.38	1.59	2.04
V	7.26	6.26	12.09	10.65	7.13	7.22
M	0	0.27	0	0	0	0
I	5.04	5.73	6.78	7.33	5.22	7.46
L	4.38	8.89	6.43	5.92	5.42	5.54
F	2.66	1.76	4.15	2.94	4.96	5.8
K	2.74	6.74	4.49	3.75	4.88	4.31

TABLE 27. Amino acid composition (mole%), using one-letter code for amino acids, in valves of six species of organophosphatic brachiopods (new).

Amino acid	*D. tenuis*	*D. lamellosa*	*D. striata*	*P. atlanticus*	*L. anatina*	*G. pyramidata*
D/N	5.4	9.0	10.5	13.1	16.8	15.9
E/Q	6.5	4.2	5.6	3.8	6.5	2.9
S	4.3	4.9	2.5	6.3	4.2	3.5
G	31.6	27.0	30.0	8.8	16.3	23.0
H	-	0.2	-	0.7	0.7	-
R	8.6	12.0	8.7	18.5	4.9	6.7
T	3.6	3.5	3.1	14.2	4.4	2.7
A	29.3	24.0	28.0	9.6	22.9	23.0
P	4.6	6.2	5.1	7.9	8.0	6.4
Y	0.3	0.2	0.5	0.8	0.5	1.1
V	1.4	2.3	1.8	6.1	5.2	4.2
M	0.1	0.2	-	0.4	-	-
C	-	-	-	0.7	-	-
I	1.0	1.7	1.2	1.9	1.7	1.3
L	1.1	2.0	1.6	4.3	3.5	3.3
F	0.7	0.7	0.4	1.8	2.1	2.0
K	1.1	1.4	0.9	1.4	2.3	2.9

concentration of 0.5 μg/ml, with the consequence that needlelike crystals, rather than ACP granules, were observed in samples removed after 30 minutes (Fig. 1537). This catalysis of the formation of crystalline fluorapatite from amorphous calcium phosphate *in vitro* suggests an important role in shell formation (LÉVÊQUE & others, 2004).

FOSSIL SHELL BIOCHEMISTRY

The rapid degradation of proteins during the fossilization of linguliform shells is

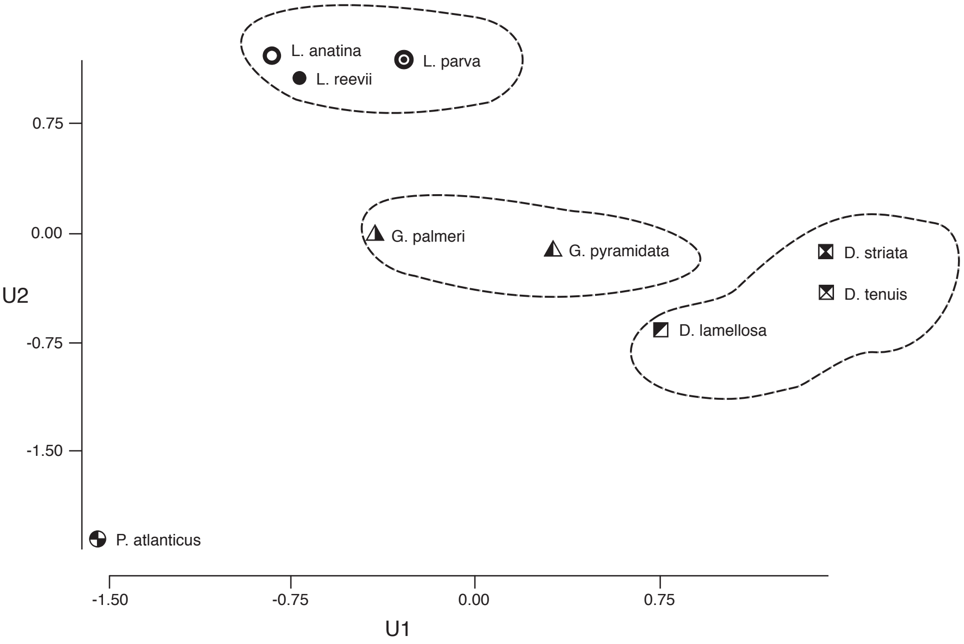


FIG. 1536. First two eigen vectors from principal component analysis of the amino acid content of valves of *L. anatina, L. reevii, L. parva, G. pyramidata, G. palmeri, D. striata, D. tenuis,* and *D. lamellosa* (data from Williams, Cusack, & Buckman, 1998 and Williams & others, 2000).

confirmed by comparing the amino acid suites of living *Discinisca* (Williams, Cusack, & Buckman, 1998, table 3) with that extracted from the Eocene *D. davisi* (Williams, Cusack, & Buckman, 1998, table 4). By the Carboniferous, amino acid suites surviving in lingulide shells are further reduced. Thus *Lingula squamiformis* retained low concentrations of some robust amino acids: aspartic acid/asparagine, glutamic acid/glutamine, glycine, alanine, tyrosine, and valine at total concentrations of 122 pmoles amino acid per mg of sample (Cusack & Williams, 1996). Moreover, shells of the contemporary discinid *Orbiculoidea nitida* retained the same suite of amino acids with the addition of alanine and threonine at a total concentration of 264 pmoles amino acid per mg of sample (Williams, Cusack, & Buckman, 1998). The residual amino acids extracted from the Ordovician shells of the discinoid *Schizotreta corrugata* and the linguloid *Pseudolingula*? spp. were essentially the same as those from the Carboniferous *O. nitida,* except for the absence of valine and the lower total concentration at 27 pmoles amino acid per mg sample (Williams, Cusack, & Buckman, 1998; Cusack, Williams, & Buckman, 1999). These examples serve to illustrate that degradation of proteins and polypeptides is thorough. In effect, fossilization results in the retention of only the most robust amino acids and the nullification of any taxonomic information that exists in amino acid suites of living lingulide shells. In modern *D. tenuis*, statistical analyses of amino acid shell extracts distinguish between the baculate ventral valve of *D. tenuis* and its nonbaculate dorsal counterpart (Cusack, Williams, & Buckman, 1999). Glutamic acid, glycine, alanine, arginine, and proline are associated with baculation and may be components of organic polymers involved in the formation of baculi. Such subtle differences, however, do not survive fossilization, so that amino acids retrieved from Paleozoic linguloid and discinoid shells are not statistically distinguishable (Cusack, Williams, & Buckman, 1999). Of course the shells of living linguloids and discinoids are chemicostructurally so close that some compositional convergence would have been inevitable among their Paleozoic ancestors, which would have distinguished them from contemporaneous linguliforms like paterinates and acrotretides. Amino acids survive in the earliest brachiopods, the paterinates with the suites extracted from the shells of the Cambrian *Askepasma* and *Micromitra,* and the Ordovician *Dictyonites* being the same as that recovered from the shell of the Carboniferous *L. squamiformis* except for the addition of serine and threonine (Williams, Popov, & others, 1998). The amino acid concentration in the *Dictyonites* shell was higher than those in the shells of Cambrian paterinates. The relative proportion of acidic amino acids, however, is much lower, which may be a consequence of the periodic reduction in the secretion of apatite that results in the perforations of the *Dictyonites* shell.

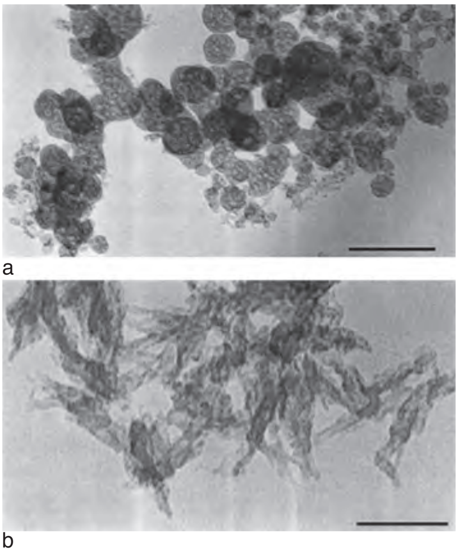


Fig. 1537. Catalysis of crystallization of fluorapatite by *L.anatina* shell proteins. TEM images of samples extracted after 30 min; *a,* control experiment showing spherical particles of hydrated ACP; *b,* fluorapatite crystals formed in the presence of *L. anatina* shell proteins at 0.5 µg/mL; scale bars, 100 nm (Lévêque & others, 2004).

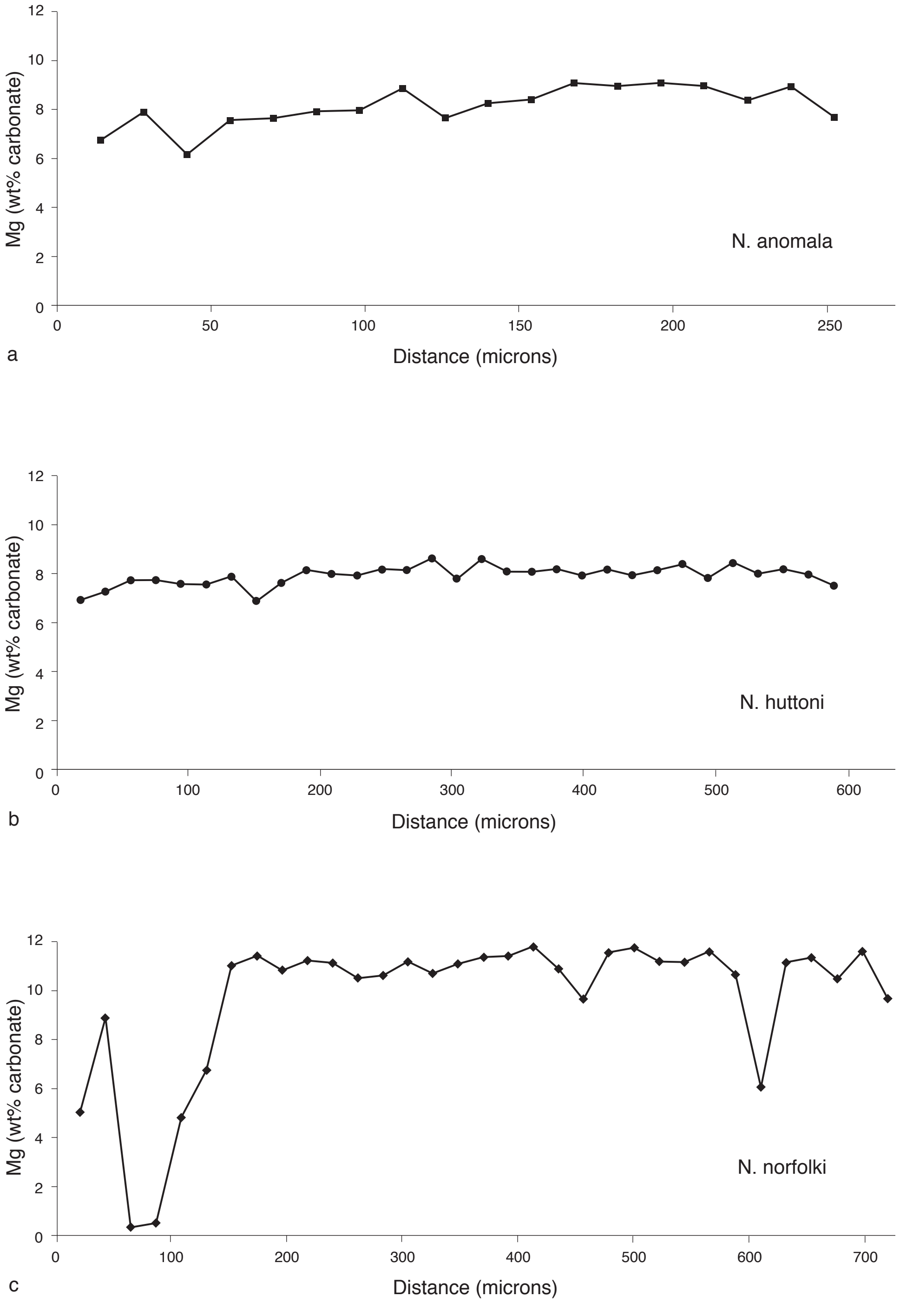


FIG. 1538. *For explanation, see facing page.*

SHELL CHEMISTRY OF CRANIIDS

The high concentration of magnesium in the calcite of craniid valves was noted in the 1997 *Treatise* (CUSACK, WALTON, & CURRY, 1997, p. 243). The distribution of magnesium in living craniid shells has now been determined, and the replacement of magnesium by calcium in fossil craniids has been demonstrated. The proteins of the *Novocrania anomala* shell as described in the 1997 *Treatise* have been further characterized. The principal calcifying proteins have been identified (CUSACK & others, 2000), and their location within the laminae of dorsal valves identified (BROWN, 1998; WILLIAMS, CUSACK, & BROWN, 1999).

SHELL MINERALOGY

The high magnesium concentration is constant throughout the primary and secondary layers of such modern craniid shells (Fig. 1538) as those of *Novocrania anomala* from Scotland, *Novocrania huttoni* from New Zealand, and *Neoancistrocrania norfolki* from the South Pacific. In *N. anomala* (Fig. 1538a) the average magnesium concentration is 8.07 wt%, in *N. huttoni,* 7.87 wt%, and in *N. norfolki,* 9.61 wt%. The apparently low values at some points in the *N. norfolki* valve occur because of the numerous cavities within the valve. Removing the cavities from the analyses would increase the average Mg content to around 11 wt%. XRD analysis confirms that, in each case, magnesium occurs in the calcite lattice since there is no separate mineral phase. The magnesium concentration of these living craniids is significantly higher than in the calcite of most rhynchonelliform brachiopods. The solubility of calcite increases as the concentration of Mg within the lattice increases (DAVIES, DOVE, & DE YOREO, 2000).

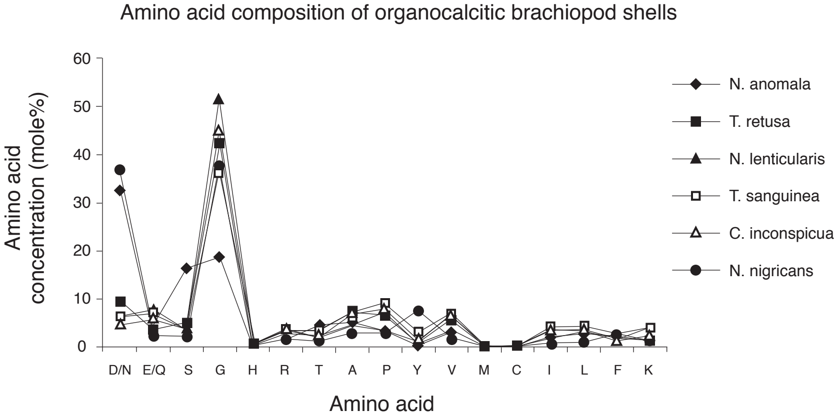
TABLE 28. Amino acid composition of the intracrystalline extracts from the dorsal and ventral valves of *N. anomala* (amino acids stated as residues per 100 amino acid residues) (new).

Amino acid	Dorsal	Ventral
D/N	32.6	18.9
E/Q	3.4	4.8
S	16.3	6.3
G	18.6	17.0
H	0.0	0.0
R	1.8	3.3
T	4.5	5.4
A	5.4	7.3
P	3.4	8.8
Y	0.4	0.7
V	3.2	6.4
M	0.0	0.0
C	0.0	0.1
I	1.5	3.9
L	2.9	5.9
F	1.1	3.0
K	3.5	8.1

LIVING SHELL BIOCHEMISTRY

Organic constituents account for 4.5% of the dry weight of *N. anomala* shells. The dorsal and ventral valves of *N. anomala* differ in their amino acid composition (Table 28), no less than their morphology and ultrastructure. The dorsal valves contain higher concentrations of aspartic acid/asparagine (D/N) and serine (S) and lower concentrations of all other amino acids except for glycine (G), hisidine (H), threonine (T), and

FIG. 1538. Magnesium concentration and distribution in calcite of craniiform shells. Shells of *a, N. anomala, b, N. huttoni,* and *c, N. norfolki* were sectioned from anterior to posterior, mounted in araldite blocks and carbon coated for electron microprobe analysis (EPMA). Electron microprobe spot analyses in a line perpendicular to the line of section (shell exterior to left) were determined for magnesium using a Cambax SX50 electron microprobe operating at 15KeV with a 10nA current and a 10 μm defocused electron beam for 30s counting time on each element. The instrument was calibrated for magnesium detection using a pure MgO standard. The totals for analysis varied between 98 wt% and 102 wt% and are within the acceptable error limit for carbonate analyses (Moberley, 1968). Since magnesium is substituting for calcium within the calcium carbonate and is not present as a separate phase, magnesium concentration is expressed as wt% carbonate throughout (new).



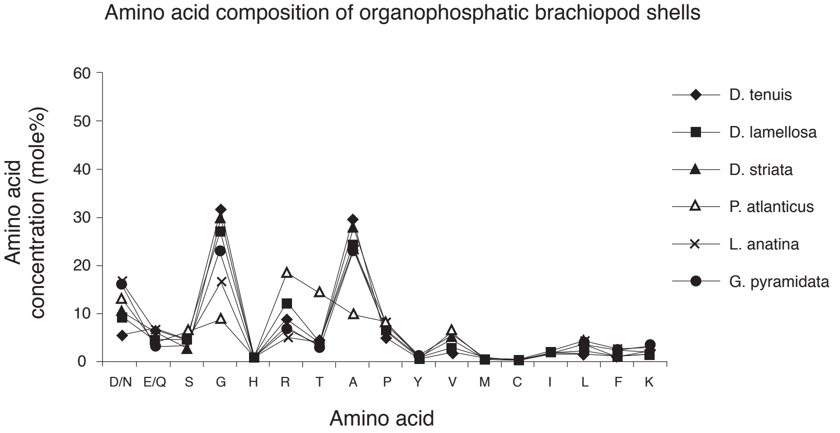


FIG. 1539. Amino acid composition of calcite and apatite brachiopod shells. Clean, powdered shells were dissolved in HCl (2N) at a ratio of 11 ml per mg shell. Following centrifugation, the amino acid composition of the supernatant was determined as follows. Supernatant samples were hydrolyzed by manual hydrolysis. Lyophilized samples in hydrolysis tubes were placed in hydrolysis vials containing 500 ml of HCl (6N). Vials were purged with argon at 2–3 psi for 30 sec, vials closed and heated at 165 °C for 1 hour for vapor-phase hydrolysis. Amino acid compositions were determined on a 420 amino acid analyzer from Perkin Elmer-Applied Biosystems (new).

methionine (M), which are within 80% of each other in both valves.

It is noteworthy that the amino acid composition of calcitic and apatitic shells of living craniiforms and linguliforms respectively is roughly similar (Fig. 1539). Apatitic valves contain 30% glycine and alanine, while calcitic valves contain higher concentrations of glycine (40%–50%) and much lower alanine concentrations (5%). The dorsal valve of *N. anomala*, however, contains a lower proportion of glycine (18%) than occurs in the calcitic shells of living rhynchonelliforms, which is closer to that of organophosphatic shells. The alanine content, in contrast, is like that of the shells of rhynchonelliforms.

Proteins, extracted from the dorsal valve of *N. anomala*, have been fractionated on 15% polyacrylamide gels according to the method of SCHÄGGER and VON JAGOW (1987). The EDTA-soluble extract from the dorsal valve of *N. anomala* contains two proteins of molecular weight 44 and 60 kDa

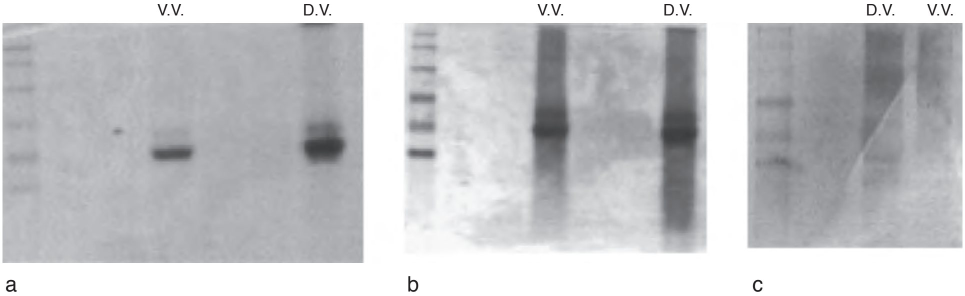


FIG. 1540. SDS PAGE gel and glyco-blot of protein extract from *N. anomala* valves. Digitized images of proteins extracted from the dorsal (*D.V.*) and ventral (*V.V.*) valves of *Neocrania anomala* and analyzed by SDS PAGE. Prestained proteins of apparent molecular weight 126, 102, 81, 53.5, 37, and 31 kDa were included in the left of each gel; *a,* proteins were fractionated by electrophoresis in a 15% polyacrylamide gel and then fixed and revealed using Coomassie-Blue; *b,* gel from *a* was then probed using silver staining; *c,* equivalent samples to those shown in *a* and *b* were electrophoresed on a 15% polyacrylamide gel and then electroblotted onto ProBlott membrane and probed with Concanavalin A to detect glycoproteins (Cusack & Williams, 2001a).

(Fig. 1540a). The 60 kDa protein is glycosylated (Fig. 1540c), as is a 30 kDa protein that is only evident using silver staining (Fig. 1540b) or by detection of the glycosylation (CUSACK & WILLIAMS, 2001a). The 44 kDa protein is present in both dorsal and ventral valves but is more abundant in dorsal valves. The 44 and 30 kDa proteins are present in both valves while only the 60 kDa protein is present in the dorsal valves. The amino acid composition of the most abundant protein, the 44 kDa protein, is presented in Table 29. The most striking features of this amino acid suite are the high proportion of acidic amino acids (aspartic acid and glutamic acid) and glycine and the low proportion of basic amino acids (histidine, arginine, and lysine).

This 44 kDa protein is the most abundant interlaminar polymer (BROWN, 1998). Induced degradation of laminae in craniid shells, including enzymic digestion, showed that calcite tablets were doped with proteins (WILLIAMS, CUSACK, & BROWN, 1999). Doping occurs by centripetal growth of the top granular layers of ramparts that trap the 44 kDa protein within tablets. The (0k.l) sites are doped mainly by the glycosylated 60 kDa protein (BROWN, 1998; WILLIAMS, CUSACK, & BROWN, 1999). The 44 and 60 kDa proteins react with Stains-All, indicating that these proteins are acidic (as confirmed by amino acid analysis) and suggesting that they are likely to be calcium binding (CUSACK & others, 2000).

NOVOCRANIA ANOMALA SHELL PROTEINS AND *IN VITRO* CRYSTALLIZATION

Synthetic calcite crystals were grown according to the method of ADDADI and WEINER (1985). The influence of *N. anomala* shell proteins on crystal growth was determined by introducing 10 µl of concentrated

TABLE 29. Amino acid composition (mole %), using the one letter code for amino acids, of the 44 kDa protein from *N. anomala* (new).

Amino acid	44 kDa
D/N	18.5
E/Q	13.9
S	7.6
G	9.1
H	6.0
R	3.9
T	4.5
A	3.4
P	4.9
Y	3.4
V	5.0
M	4.9
C	0.0
I	6.2
L	3.5
F	3.8
K	0.9

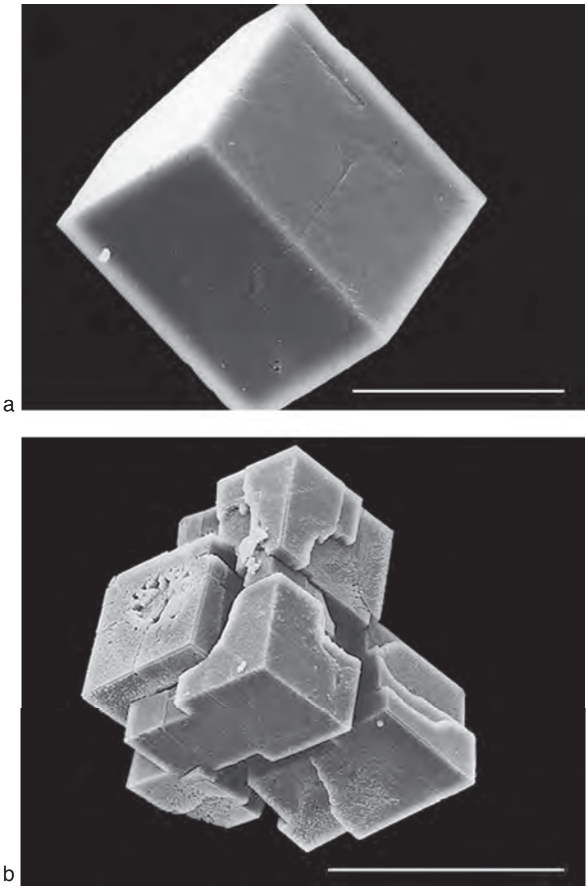


FIG. 1541. Influence of *N. anomala* shell proteins on calcite growth *in vitro*. Scanning electron micrographs of gold-coated calcite crystals grown *in vitro* according to the method of ADDADI and WEINER (1985) in the absence of any additives (*a*) and in the presence of 1.2 µg intracrystalline protein from *N. anomala* dorsal valves (*b*); scale bars: 20 µm and 50 µm (Cusack & others, 2000).

protein extract after 24 hours crystal growth. Controls were included in which only 18 MΩ water or nonmineral associated proteins such as serum albumin were added. Crystals grown in the absence of any protein had perfect rhombohedral morphology. The addition of intracrystalline proteins from *N. anomala* resulted in altered crystal morphology displaying intergrowth of crystals at final protein concentrations of 1.2 µg per ml (Fig. 1541). This effect is specific and is likely to result from the presence of the 44 and 60 kDa proteins, since at concentrations of 2 µg/ml, nonmineral associated proteins such as serum albumin had no effect on crystal morphology.

FOSSIL SHELL BIOCHEMISTRY

During fossilization, the magnesium in the calcite of the living craniid shell is replaced by calcium, and a high magnesium content is not diagnostic of fossil species (J. ENGLAND, personal communication, 2007). Magnesium distribution and concentration (Fig. 1542) was measured in the shells of the Ordovician *Petrocrania scabiosa*, the Carboniferous *Petrocrania modesta,* and the Cretaceous *Crania craniolaris*. None of the

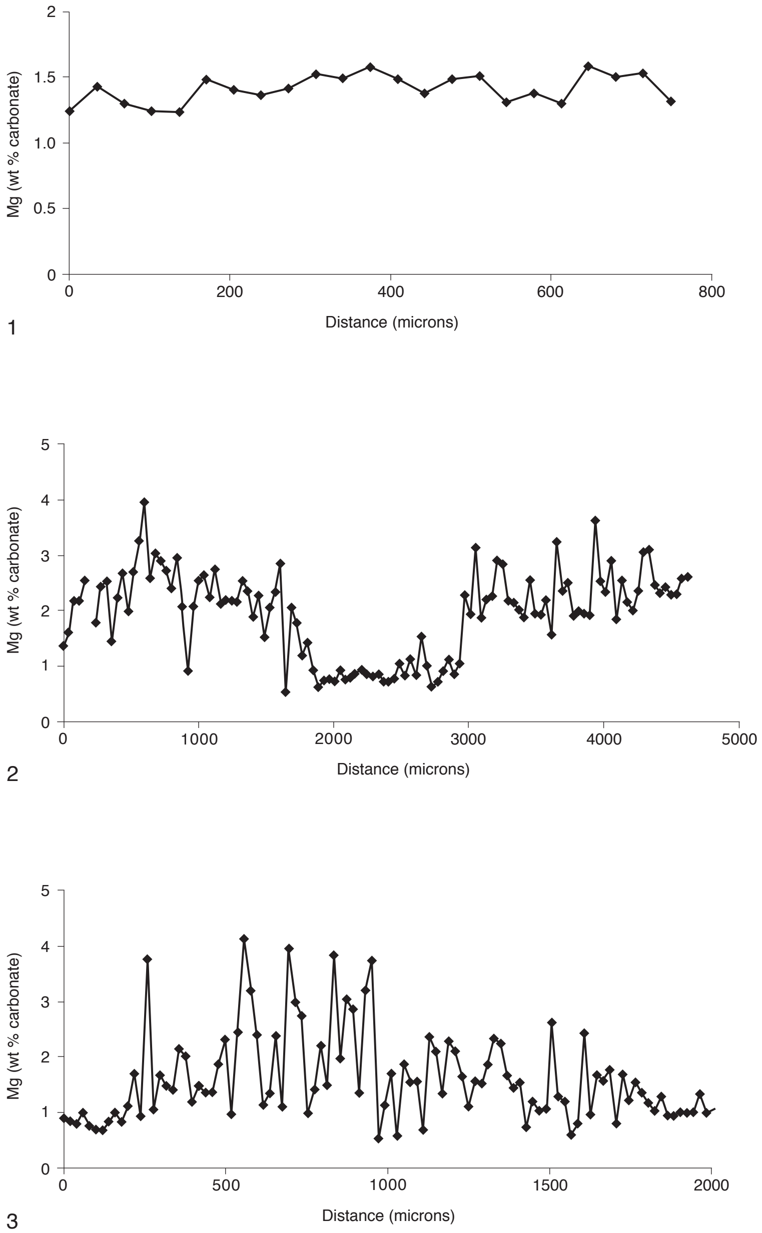


FIG. 1542. Magnesium concentration and distribution in calcite of fossil craniiform shells. Shells of *1, Crania craniolaris* (Cretaceous), *2, Petrocrania modesta* (Carboniferous), and *3, Petrocrania scabiosa* (Ordovician) were prepared and analyzed as described in Figure 1538 (new).

specimens had high magnesium concentrations.

In all fossil craniids examined by CUSACK and WILLIAMS (2001a), there is a reduction, with the increasing geological age of species, in the range and concentration of amino acids to a residue of acidic and aliphatic ones (Table 30). The acidic amino acids may be protected by interaction with calcite, while the other amino acids to survive are simple and robust like those preserved in other fossil brachiopods. Aspartic acid/asparagine,

TABLE 30. Amino acids extracted from shells of cranioid brachiopods; one-letter code for amino acids is used. Samples were dissolved in HCl. The values for modern valves are expressed as absolute quantities/mg shell and as mole% values; i.e., relative quantities if each valve contained 100 pmoles amino acid/mg shell. In all cases, values represent pmoles amino acid /mg sample (new).

Species	Age	Amino acids															
		D	E	S	G	H	R	T	A	P	Y	V	M	I	L	F	K	Total
Novocrania anomala (dorsal)	modern	32.6	3.4	16.3	18.6	0	1.8	4.5	5.4	3.4	0.4	3.2	0	1.5	2.9	1.1	3.5	100
Novocrania anomala (ventral)		18.9	4.8	6.3	17.0	0	3.3	5.4	7.3	8.8	0.7	6 .4	0	3.9	5.9	3.0	8.1	100

Species	Age	Amino acids								
		D	E	S	G	T	A	V	I	L	Total
Crania craniolaris (ventral)	Upper Cretaceous	4.2	5.1	4.4	15.1	2.0	11.3	4.5	4.1	2.7	53.4
Isocrania egnanbergensis (dorsal)	Upper Cretaceous	0.5	2.2	2.6	12.8	6.2	5.9	2.2	0	3.3	35.6
I. egnanbergensis (ventral)		0.3	2.1	2.2	11.6	6.4	5.8	2.3	1.5	2.7	34.8
Orthisocrania planissima (shell and matrix)	Upper Ordovician	7.8	2.2	1.0	5.3	0.8	1.1	0.5	0	1.0	19.7
O. planissima (shell)		0.6	1.6	3.0	8.5	1.2	2.5	1.2	0	0.8	19.4
matrix		0.5	0	0.6	3.3	0.6	0.9	0.4	0	0.7	7.0
Petrocrania scabiosa	Upper Ordovician	1.5	2.9	3.8	6.1	2.3	3.1	1.5	0	0.7	21.7
P. scabiosa Waynesville, Indiana		1.1	2.6	1.9	1.6	1.0	1.1	1.7	0	0.9	11.9
P. scabiosa Rafinesquina		0.9	1.8	3.8	12.4	2.8	3.1	3.5	0	1.0	29.3
P. scabiosa dalmanellid		1.0	0.7	1.3	5.3	0.5	1.1	0.5	0	1.3	11.8
Pseudocrania petropolitana (matrix)	Lower Ordovician	5.9	6.6	6.9	4.4	1.4	1.3	0.3	0	0.5	27.2
		0.4	0.3	1.5	3.2	1.3	1.7	0.9	0	0	9.3
Crania rhykholtiania (ventral, dorsal, and matrix)	Carboniferous	2.8	1.8	1.5	2.6	0	1.8	0	0	0	10.5
C. rhykholtiania (ventral and matrix)		2.2	0.9	0.8	3.9	0	2.3	0.8	0	0.8	11.7
matrix		3.3	1.6	1.5	3.4	0	1.7	0	0	0	11.5

serine, and glycine that occur in high concentrations in *Novocrania* shells survive in all fossil specimens from Upper Cretaceous and Carboniferous sediments. The ratio of D/N:S:G, however, bears no resemblance to that characterizing *Novocrania*. Basic amino acids (histidine, arginine, and lysine) and aromatic amino acids (tyrosine, proline, and phenylalanine) are not detected in the fossil samples.

ORGANOCARBONATE RHYNCHONELLIFORM SHELL CHEMISTRY

Since the 1997 *Treatise,* the distribution of magnesium in calcite of rhynchonelliform valves has been determined, and several of the proteins have been characterized further, identifying those that are glycosylated and those that have potential calcium-binding properties.

LIVING SHELL MINERALOGY

The mineral ultrastructure is consistent throughout the Rhynchonelliformea, with the primary layer of growth-banded calcite underlain by a secondary layer of calcite fibers as typified by living *Notosaria.* Most thecideidines vary from this theme with a shell comprised of primary layer throughout. The other variation occurs in *Liothyrella* where there is a tertiary layer of prismatic calcite (WILLIAMS, 1968a). Exceptions aside, the uniformity in ultrastructure is not registered in the concentration and distribution of magnesium in the calcite of rhynchonelliform shells.

In marine biogenic carbonates, the Mg:Ca ratio increases with increasing temperature, providing a means of determining the temperature at which the carbonate was precipitated. Mg:Ca ratio is a proxy that, unlike skeletal $\delta^{18}O$, is unaffected by seawater salinity (Klein, Lohmann, & Thayer, 1996). This relationship between Mg:Ca ratio and temperature has been demonstrated in several such marine carbonate systems as benthic foraminifera (Lear, Elderfield, & Wilson, 2000), planktonic foraminifera (Elderfield & Ganssen, 2000), and coccoliths (Stoll & others, 2001). In 1996, Rao demonstrated that Tasmanian brachiopods recorded accurately the temperature of calcite deposition as expected by slow-growing low magnesium calcite.

England, Cusack, and Lee (2007) reported differences between the magnesium content and distribution in shells of *Terebratulina retusa* and *Novocrania anomala* when the specimens were collected from the same site and the calcite had therefore been precipitated at the same temperature. While *N. anomala* has 2.55 wt% magnesium throughout the shell, *T. retusa* shells have a lower overall magnesium content. In *T. retusa*, however, the magnesium is not evenly distributed, with the highest concentration (3.5 wt%) being in the primary layer and a maximum concentration of 1.5 wt% in the secondary layer, with an average secondary layer concentration of 1 wt%. The contrast in magnesium distribution is not restricted to intersubphyla comparisons but is evident within the subphylum Rhynchonelliformea. Buening and Carlson (1992) noted changes in magnesium content associated with ontogeny in *Terebratulina unguicula* and *Terebratalia transversa,* where the magnesium concentration in the umbo is at least double that in the shell anterior. In 1961, Lowenstam suggested that magnesium and strontium varies with brachiopod taxonomy. Buening and Carlson (1992) demonstrated that, in addition to ontogenetic influences, taxonomic differences do occur with the demonstration that *Terebratulina unguicula* has a higher magnesium content than *Terebratalia transversa*. Buening (1998) expanded the analyses to include the elements copper, zinc, manganese, and iron in two species of rhynchonelliform brachiopods from New Zealand: *Calloria inconspicua* and *Notosaria nigricans*. In both species, the elements Cu, Mn, Fe, and Zn were concentrated in the primary layer of the shell.

The distribution of magnesium through the shell layers of several species of the class Rhynchonellata, including members of the three extant orders, Rhynchonellida, Thecideida, and Terebratulida, is presented in Figure 1543. The umbonal region was avoided, and analyses were carried out in the median area of the shell, avoiding any regions of specialization. In *Liothyrella uva*, the Mg concentration is on average 1.1 wt%, but Mg concentration in the inner, tertiary layer is much higher than in the outer two-thirds of shell. This is not the case in *Liothyrella neozelanica* where the Mg concentration is low and effectively constant (mean = 0.35 wt%) throughout the shell. *Neothyris lenticularis* valves contain similar Mg concentrations to *L. neozelanica* with an average Mg content of 0.34 wt% distributed evenly throughout the shell. *Laqueus rubellus* and *Terebratella sanguinea* also have similar Mg contents (0.46 wt% and 0.49 wt% respectively), and in both cases the innermost and outermost regions of the shell have slightly elevated Mg concentrations. In *Calloria inconspicua* the average Mg concentration is 0.45 wt%, with a lower Mg concentration in the inner third of the shell. *Lacazella mediterranea* has the lowest Mg content of the brachiopods surveyed, with a mean value 0.03 wt% throughout the shell. In contrast, *Thecidellina barretti* has an overall Mg content (10.15 wt%), similar to the craniiform valves. The distribution of Mg in *Terebratulina retusa* and *Notosaria nigricans* are similar, with elevated Mg concentration in the primary layer

FIG. 1543. Magnesium concentration and distribution in calcite of rhynchonelliform shells. Shells were prepared and analyzed as described in Figure 1538. Note different scales on graphs (new).

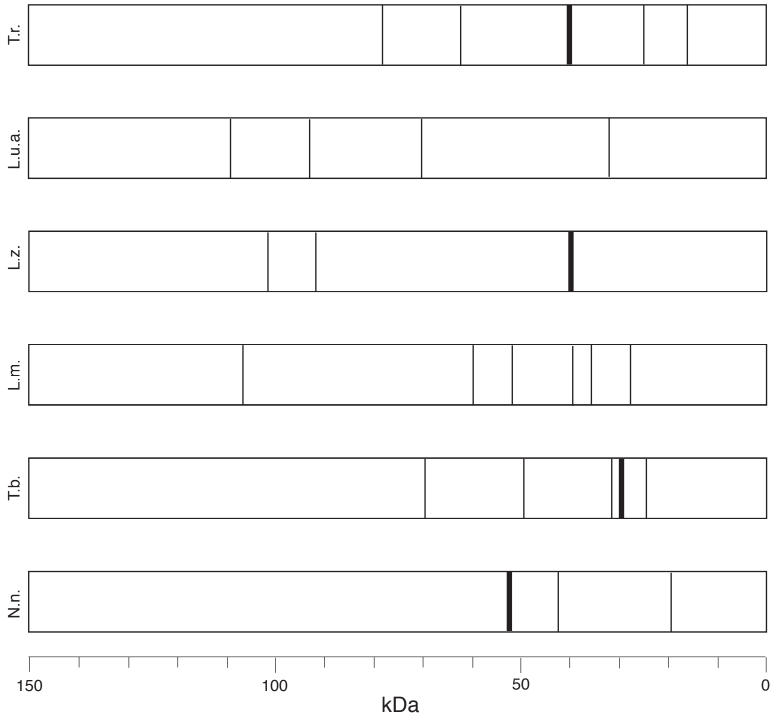


FIG. 1544. Diagrammatic representation of SDS PAGE analyses of proteins from rhynchonelliformean shells. Molecular weights (kDa) of the principal intracrystalline proteins, identified by SDS PAGE analysis in the shells of *Notosaria nigricans* (*N.n.*), *Thecidellina blochmanni* (*T.b.*), *Lacazella mediterranea* (*L.m.*), *Liothyrella neozelanica* (*L.z.*), *Liothyrella uva antarctica* (*L.u.a.*), and *Terebratulina retusa* (*T.r.*); thickened bars indicate proteins in comparatively high concentrations (Cusack & Williams, 2001b).

(1.2 wt% and 1.6 wt% respectively) and much lower and constant Mg concentrations throughout the rest of the shell (0.5 wt% and 0.3 wt% respectively). Overall, the Mg content of *T. retusa* is higher than that of *N. nigricans,* with mean values of 0.91 wt% and 0.66 wt% respectively.

LIVING SHELL BIOCHEMISTRY

Comparison of intracrystalline EDTA-soluble proteins from species of 3 ordinal groups revealed up to 21 proteins of molecular weight range 16 to 209 kDa (Fig 1544). None could be identified as specific to and therefore involved in the calcification of one or another of the layers of the rhynchonellate shell (CUSACK & WILLIAMS, 2001b). While the precise relationship between the organic and inorganic components is currently elusive, it is evident that not all of the proteins extracted need to play a calcifying role in the laminae. Indeed, some of these proteins could have arisen subsequent to the phylogenetic divergence of the terebratulides and thecideidines from their rhynchonellate sister group. Therefore, until those proteins involved in calcification are identified and their role understood, the protein chemistry of rhynchonellate shells is a less comprehensible guide than ultrastructure to ordinal genealogy (CUSACK & WILLIAMS, 2001b).

Organic content accounts for 3% of the dry weight of *T. retusa* shells. Proteins extracted and then fractionated using SDS PAGE had molecular weights of 16, 25,

FIG. 1545. SDS PAGE of proteins from shells of *T. retusa.* SDS PAGE gel of EDTA-soluble intracrystalline extract of *T. retusa and N. anomala. Lane 1.* Prestained proteins of apparent molecular weight 97.4, 68, 43, 29, and 18.4 and 14.3 kDa. *2.* Ovalbumin (5 µg). *3.* BSA (5 µg). *4.* Blank. *5. N. anomala* shell extract (1 µg protein). *6.* Blank. 7. *T. retusa* shell extract (1.05 µg protein). Proteins fixed and visualized with Coomassie Brilliant Blue (CBB) (Cusack & others, 2000).

TABLE 31. Amino acid composition of the 40 kDa intracrystalline protein from shells of *T. retusa* (amino acids stated as residues per 100 amino acid residues). Values are the average of three analyses (new).

Amino acid	40 kDa
D/N	11.3
E/Q	12.2
S	8.5
G	13.7
H	0.0
R	4.4
T	6.4
A	9.2
P	0.0
Y	1.2
V	8.4
M	1.8
C	0.0
I	8.9
L	9.7
F	4.0
K	0.0

40, 62, and 78 kDa (Fig. 1545). The 40 kDa protein is the most abundant protein present; its amino acid composition is given in Table 31. This protein contains a high proportion of acidic amino acids (aspartic acid and glutamic acid) and glycine and a smaller proportion of basic amino acids (histidine, arginine, and lysine). Both this 40 kDa and the 62 kDa protein are glycosylated (Fig. 1546).

TEREBRATULINA RETUSA SHELL PROTEINS AND *IN VITRO* CRYSTALLIZATION

Synthetic calcite crystals were grown using the methods described for *N. anomala.* The addition of intracrystalline proteins from *T. retusa* resulted in altered crystal morphology displaying intergrowth of crystals at protein concentrations of 0.04 µg per ml for *T. retusa* (Fig. 1547). At concentrations of 2

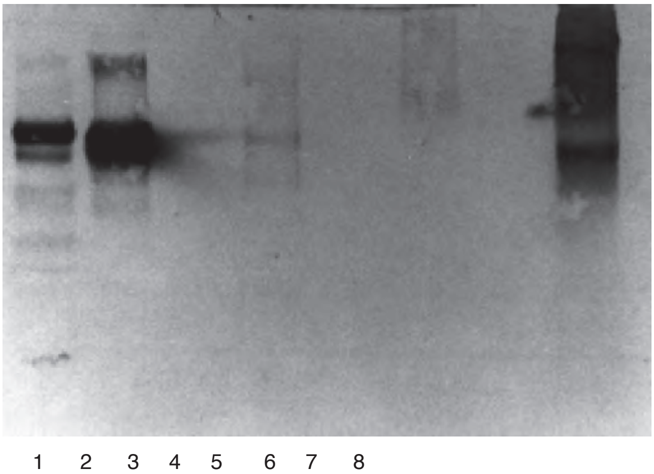


FIG. 1546. Electroblot of protein extract from *T. retusa* valves, reacted with Concanavalin-A to detect glycoproteins. Affinoblot of EDTA-soluble intracrystalline proteins from *T. retusa* and *N. anomala*, bovine serum albumin (BSA), and ovalbumin. Proteins fractionated by SDS PAGE, electrotransferred onto ProBlott membrane and reacted with Concanavalin A to detect glycoproteins (Faye & Chrispeels, 1985). *Lane 1.* Prestained proteins of apparent molecular weight 97.4, 68, 43, 29, 18.4, and 14.3 kDa. *2.* Ovalbumin (5 µg). *3.* BSA (5 µg). *4.* Osteonectin (0.6 µg). *5.* Blank. *6. N. anomala* shell extract (1 µg protein). *7.* Blank. *8. T. retusa* shell extract (1.05 µg protein) (Cusack & others, 2000).

µg/ml, nonmineral associated proteins such as serum albumin had no effect on crystal morphology. Crystal clustering occurs at much lower protein concentrations (0.04 µg/ml) with *T. retusa* shell proteins than with *N. anomala* proteins (1.2 µg/ml), suggesting that the *T. retusa* shell proteins or a component thereof is 30 times more potent than the *N. anomala* proteins.

FOSSIL SHELL BIOCHEMISTRY

Rapid and thorough degradation of proteins from Linguliformea and Craniformea shells strongly suggests that protein degradation would also be thorough in the Rhynchonelliformea, reducing the amino acids to a robust suite not representative of the diversity within the subphylum. One means of testing this assumption would be to carry out amino acid analyses from extracts of the same environment, perhaps using the well-preserved material of the Scottish Carboniferous.

CONCLUSIONS

Although rapid and almost complete protein degradation means that the rich source of information is lost in the fossil record, much information is to be gained regarding evolutionary relationships and biomineralization. In the three subphyla, the protein complement of the shells is complex and diverse. The characteristics of the proteins are specific to each subphylum. The role of these proteins in mineralization has been demonstrated for *L. anatina* and suggested for *N. anomala* and *T. retusa*. In order to progress these findings effectively, characterization of individual proteins and identification of their individual influence

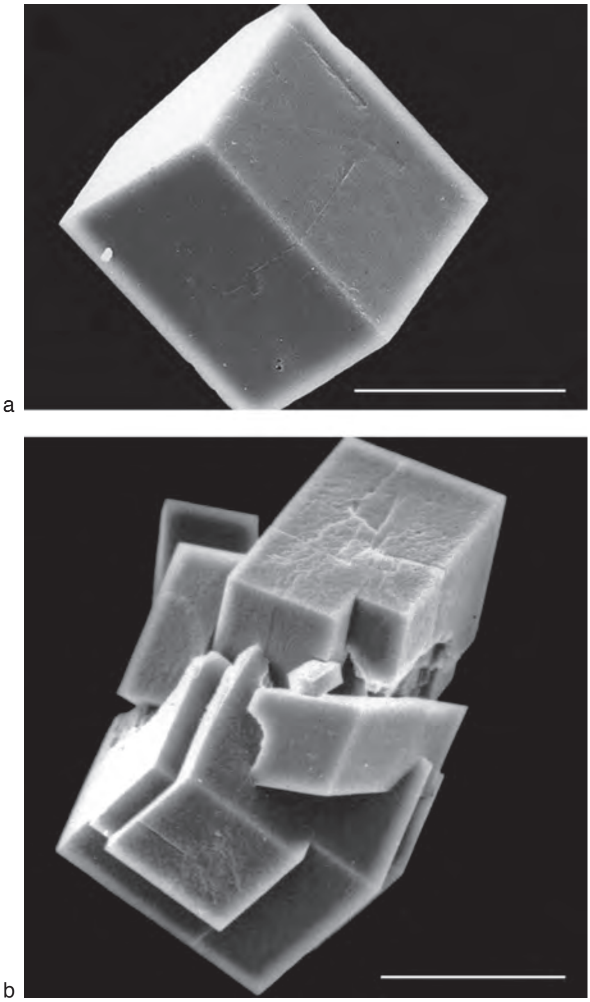


FIG. 1547. Influence of *T. retusa* shell proteins on calcite growth *in vitro*. Scanning electron micrographs of gold-coated calcite crystals grown *in vitro* according to the method of ADDADI and WEINER (1985) in the absence of any additives (*a*) and in the presence of 1.2 µg intracrystalline protein from *T. retusa* valves (*b*); scale bars: 20 µm (Cusack & others, 2000).

on mineral formation and thus their role in biomineralization would greatly advance our knowledge beyond the consideration of protein mixtures where there is always the possibility of the effect of one protein masking that of another. This approach of characterizing individual proteins has resulted in significant progress being made in other biominerals systems such as siliceous sponges (SHIMIZU & others, 1998) as well as other calcium carbonate marine invertebrates (MICHENFELDER & others, 2003; MARIN & others, 2005; KIM & others, 2006).

The observation that several of the brachiopod shell proteins are glycosylated should be pursued since the polysaccharide moieties of glycoproteins influence calcium carbonate growth *in vitro* (ALBECK, WEINER, & ADDADI, 1996). The presence of carbohydrates in brachiopod shells has been noted by several workers (JOPE, 1965; PAN & WATABE, 1988; 1989; COLLINS & others, 1991; CLEGG, 1993; CUSACK, WALTON, & CURRY, 1997). In addition, acidic sulphated sugars have been described in other marine invertebrate calcium carbonate biominerals including corals (CUIF & others, 2003) and bivalves (DAUPHIN & others, 2003, 2005). The widespread occurrence of these acidic polysaccharides suggests a fundamental role in biomineralisation that should be explored. The role of mucins in molluscan calcification (MARIN & others, 1996, 2000) suggests that this should also be investigated in brachiopods.

The assertion that the shells of the Rhynchonelliformea and Craniiformea are composed of low magnesium calcite is not true in all cases. Even in instances where it is true, magnesium distribution is not even. This has important implications for the use of brachiopod shells as paleothermometers since the magnesium content is influenced by temperature, but this may be via kinetic influence that could be exerted by other factors such as organic components. Ultimately, it is necessary to determine whether magnesium is a true lattice component, since this is the basis of the Mg:Ca ratio proxy for water temperature.

ACKNOWLEDGMENTS

I would like to acknowledge my huge appreciation of all that the late Sir Alwyn Williams taught me, mostly by example, over the course of our 14-year collaboration. A dear friend and colleague, his enthusiasm, drive, and scientific rigor have been inspirational.

Sincere thanks to all those institutions and individuals who provided material used in the work referred to in this chapter. Daphne Lee (University of Otago) is thanked for arranging provision of *N. huttoni* specimens from the National Museum of New Zealand and Bernie Cohen (University of Glasgow) for providing specimens of *N. norfolki*. Jenny England is thanked for her major contribution to the microprobe analyses of magnesium.

Financial assistance from the NERC (GR 3/09604 and GR 9/02038), the Royal Society (RSR A/C 027 and RSS QG 16604), and the EPSRC (GR/R23107/01) is gratefully acknowledged.

CHEMICOSTRUCTURAL DIVERSITY OF THE BRACHIOPOD SHELL

ALWYN WILLIAMS and MAGGIE CUSACK

[deceased, formerly of University of Glasgow; and University of Glasgow]

INTRODUCTION

Descriptions of the chemicostructure of the brachiopod shell published in Volume 1 of the revised *Treatise on Invertebrate Paleontology, Part H, Brachiopoda* (KAESLER, 1997), were submitted in 1995. They appeared in three chapters with little cross reference for a reason that was valid at the time. The structures of the periostracum and shell of living brachiopods were described in relation to the secreting outer epithelium of the mantle in the chapter on Anatomy (WILLIAMS & others, 1997, p. 9–41). The structures of periostracal casts and recrystallized shells of fossil brachiopods were described in another chapter on Shell Structure (WILLIAMS, 1997, p. 267–320). This segregation was imposed to distinguish paleontological inferences from neontological observations (WILLIAMS, 1997, p. 267). Six of the twelve or so distinctive structures characterizing the brachiopod shell are found in living species, especially the later rhynchonelliforms and craniiforms, and could be broadly identified in Paleozoic antecedents. Yet the shell structures of most extinct groups were evidently the product of secretory regimes that were then difficult to reconcile with living models. Shell biochemistry, which was described in a third chapter (CUSACK, WALTON, & CURRY, 1997, p. 243–264), was even more difficult to integrate into a chemicostructural phylogeny. In 1995, this kind of investigation had been sporadically pursued for only 30 years, and there had been little systematic sampling of the shell biochemistry of extant groups. More importantly, sophisticated techniques showed that the organic constituents of shells degraded rapidly during fossilization into residues that are no longer diagnostic of the original polymers.

Within the last decade, significant advances have been made in chemicostructural research on fossil as well as living shells. The full structural diversity of the mature shell is now better known, and feasible secretory regimes have been proposed to explain extinct fabrics. Ultrastructural and biochemical studies of the paracrystalline relationships between basic biomineral and polymeric units have revealed many processes of calcification, while mineral alignments in fossil shells have been used to identify their degraded, organic substrates and matrices. An unexpected discovery is that the mineral constituents of first-formed and juvenile shells can be different from those secreted during the mature phase of growth. Such profound changes in the ontogeny of secretory regimes were common in early lingulate brachiopods. The trace element and stable isotope contents of the brachiopod shell have also been studied and merit consideration, as do novel structures found in the exoskeletons of such early lingulates and Problematica as *Micrina*.

As a result of these advances, the processes of secretion responsible for the chemicostructural diversity of the living shell can be identified as homologous with regimes that secreted the various skeletal structures of extinct groups. Accordingly, changes in shell structures will be reviewed on assumptions that they reflect the evolution of a small number of secretory regimes that first differentiated in the early Paleozoic. Description of the phylogeny of skeletal chemicostructures, however, has to take into account regimes that were subject to ontogenetic changes. A hiatus in the secretion of juvenile and mature shells of lingulates can be traced throughout the geological record. It seems appropriate, therefore, to compare

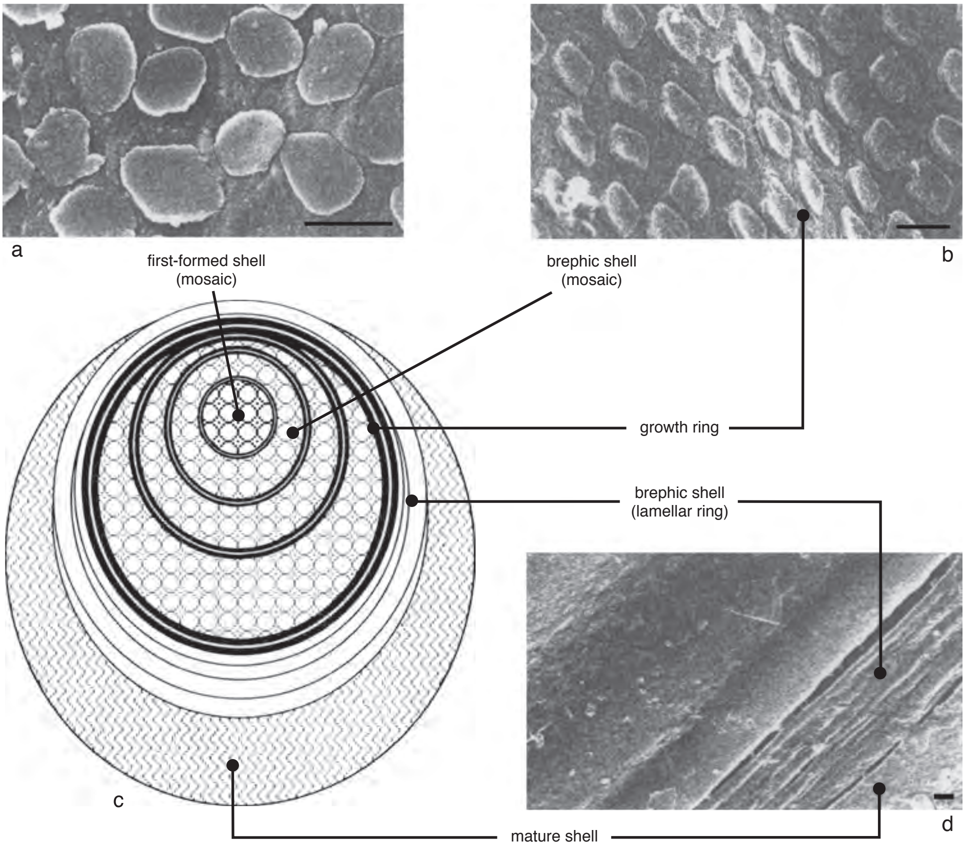


FIG. 1548. Illustration of terminology used to describe mosaic of siliceous tablets and its bounding lamellar ring in living *Discinisca* sp. cf. *tenuis* (SOWERBY). SEMs show disposition of tablets in first-formed and brephic shells and of lamellar ring relative to mosaic and mature shell; scale bars: 1 µm (Williams, 2003).

the chemicostructures of first-formed (and brephic) shells independent of the phylogeny of mature shells.

Finally, a terminology of the skeletal chemicostructures of brachiopods is now well established. A few new terms have been sparingly introduced during the last decade and are defined within the text. Two standardized terms, however, are required to describe the detailed as well as the general aspect of chemicostructures. In this chapter, the term fabric will be used to describe any particular chemicostructural feature as a whole; the term texture is used to describe the arrangement of the constituent parts of a fabric.

JUVENILE SHELL OF BRACHIOPODS

There is much confusion about what constitutes a first-formed, brephic, and juvenile shell (WILLIAMS, 2003). Their usage in this chapter is intended to describe phases in shell growth that are apposite for living and extinct species alike, as illustrated in Figure 1548. The so-called first-formed coat is simultaneously secreted by a collective of epithelial cells when they become differentiated from the ectoderm for such a role. The term is preferred to the embryonic shell of FREEMAN and LUNDELIUS (1999) because embryonic is also used for the vitelline

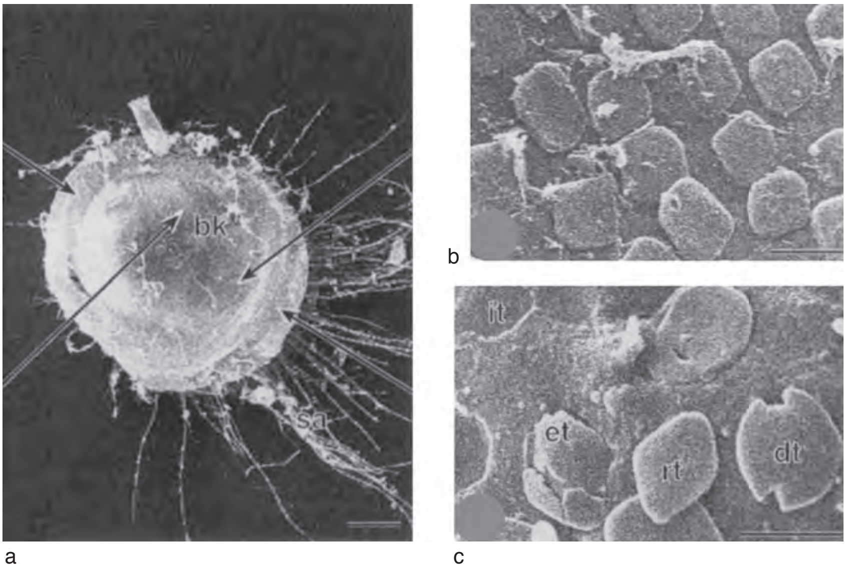


FIG. 1549. SEMs of gold-coated, dorsal surface of untreated, critical-point-dried, newly settled juvenile of *Discinisca* sp. cf. *tenuis; a*, general view showing sites of detailed studies relative to beak (*bk*) and setae (*sa*); scale bar: 100 µm; *b*, orderly, rhombically arranged tablets in midregion of mosaic; scale bar: 1 µm; *c*, mosaic at beak with deformed (*dt*) and rhombic (*rt*) tablets, latter dislodged, another escaping (*et*) from a ruptured, brittle vesicular cover and imprints (*it*); scale bar: 1 µm (Williams, Lüter, & Cusack, 2001).

(fertilization) membrane (WILLIAMS & others, 1997, p. 154). The coat may be an organic sheet as found in living lingulids (the protegulum of YATSU, 1902). It may be an organic sheet (periostracum), internally coated with mineral granules as in living rhynchonellates or craniids, or an organic sheet externally covered with a well-ordered array (mosaic) of mineralized tablets (WILLIAMS, CUSACK, & others, 1998). When mineralized, the coat or mosaic is referred to as the first-formed shell.

The brephic shell is the circular (or arcuate) zone enclosing the first-formed shell. It is secreted incrementally by a growing mantle lobe and may be bounded by a lamellar ring (the halo of CHUANG, 1977) composed of ripplelike folds or concentric lamellae. The mature shell surrounds the brephic shell and is characterized by the development of adult surface features including those that normally distinguish genera and species. In this context, the term juvenile can be used to identify the first-formed and brephic shells together.

The juvenile shells of the crown species of the three brachiopod subphyla differ not only from one another but also, with the possible exception of rhynchonelliforms, from those of their stem groups. The latter are more similar to the juvenile shells of contemporaneous, extinct groups, as will be shown in the text.

DISCINOID JUVENILE SHELLS

The juvenile shell of discinids is mineralized (WILLIAMS, CUSACK, & others, 1998). Thus, nearly all of the juvenile dorsal valve of *Discinisca* sp. cf. *tenuis*, approximately 0.5 mm in diameter, is covered by a single-layered mosaic of siliceous tablets typically arranged rhombically (Fig. 1549–1550). Tablets on the subconical, wrinkled first-formed shell are less well ordered and can vary in shape from rhombic to discoidal, with a mean length of 1 µm; but many are deformed, especially through the lack of secretion of their centers (Fig. 1551). Tablets of the brephic mosaic (Fig. 1552) are larger with a long diagonal averaging

1.54 µm and are overwhelmingly rhombic with rare deformities resulting mainly from conchoidal fracturing. They are well ordered but become more widely spaced and more closely crowded on the sides and in the troughs, respectively, of folds (growth rings). They may also be absent from patches of 50 µm^2 or more toward the margin.

The thickness of tablets is bimodally distributed at 30–90 nm and 120–210 nm. This distribution accords with tablets being unilamellar and bilamellar, predominantly so on the first-formed shell and toward the mosaic margin respectively. The lamellae are granular and, in bilamellar tablets, are separated by a slotlike cavity up to 70 nm deep. The edges of both lamellae commonly form an unbroken margin that confines the cavity within a tablet (Fig. 1552). Lamellae of degraded tablets have an exaggerated texture of granules that, under the TEM, are resolved as discrete rhombs, approximately 25 nm long diagonally and arranged in rhombic arrays (Fig. 1553a). Further degradation induced by reagents removes the polymeric glue binding the siliceous granules that then tend to aggregate along the frayed edges of tablets. In some parts of the mosaic, however, especially in the first-formed shell, an untreated substrate can also be coated with aggregates. These are likely to be siliceous spherules that had been secreted and dispersed before the formation of tablets.

Tablets are assembled intracellularly in the outer epithelial collective underlying the first-formed shell and in nascent vesicular cells being generated as the outer mantle lobe that secretes the growing margin of the brephic shell (Williams, Lüter, & Cusack, 2001, p. 33; Lüter, 2004). Each tablet grows within a vesicle (Fig. 1553b), initially by nucleation of siliceous rhombs and their organic coats on the inner surface of the vesicle. Traces of fibrils in the interstices between rhombs, as seen in TEM sections, suggest that the tablet matrix is a water-soluble polymer permeated by fibrous proteins. Further lateral accretion of rhombs complete a vesicular lining of granules that adopt the rhombohedral shape of silica, irrespective of organic constituents. When crystallization is complete, a cavity is normally created in the medial plane, as in an ellipsoidal geode, virtually dividing the tablet into a bilamellar structure. Unilamellar tablets are assumed to have crystallized in a flat vesicle that precludes the development of a medial cavity.

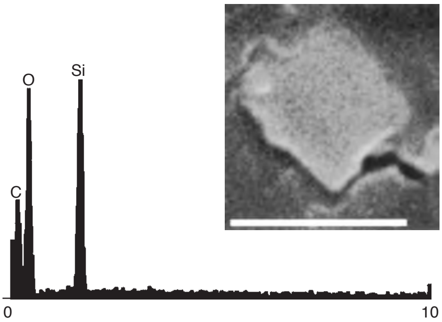


FIG. 1550. EDX spectrum (full scale 300 counts) of a carbon-coated tablet in acetate shown as a top-right inset; scale bar: 1 µm (Williams & others, 1998).

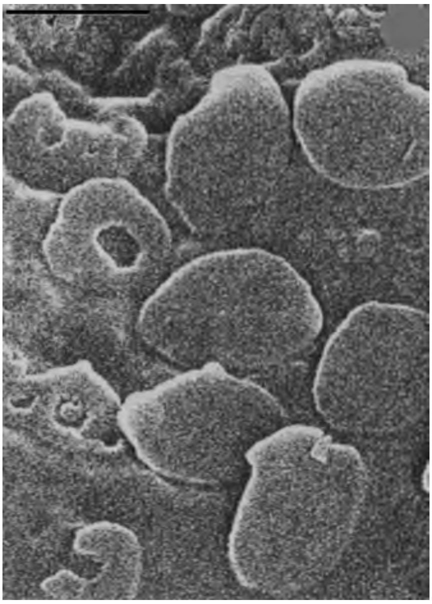


FIG. 1551. SEM of gold-coated, deformed and poorly ordered, overlapping tablets at beak of dorsal valve of settled juvenile *Discinisca* sp. cf. *tenuis* treated with bleach (0.7% by volume) for 18 h; scale bar: 1 µm (Williams, Lüter, & Cusack, 2001).

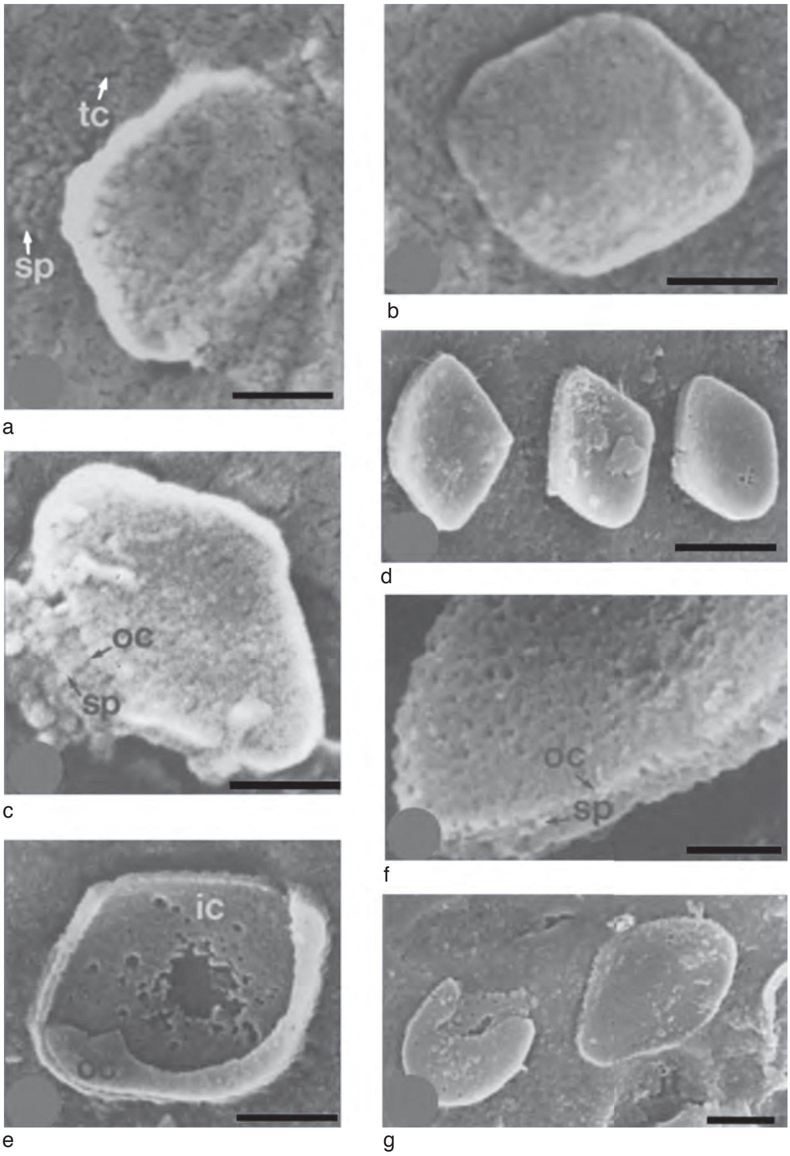


FIG. 1552. SEMs of larval shells of *Discinisca tenuis; a–b*, concave and convex tablets on dried dorsal valves, elevated above tension-cracked (*tc*), spherular (*sp*) primary layer, but also with tension-cracked, spherular coats (view *c*) with concave tablet on dried dorsal valve with coat split near outer edge (*oc*) to expose contents of spherular apatite (*sp*); scale bars: 0.5 µm; *d*, concave tablets on surface of dried dorsal valve displaying well-spaced nature; scale bar: 1 µm; *e–g,* tablets treated with 0.2% bleach, exposing spherular apatite (*sp*) between the outer (*oc*) and inner (*ic*) coats of partly digested tablets; scale bars: 0.5 µm, 200 nm, 0.5 µm (Williams, Cusack, & Buckman, 1998).

The exocytosis of tablets (enclosed in their vesicular coats) to form a monolayer under the external glycocalyx is followed by the secretion of a substrate of chitin and GAGs (glycosaminoglycans). The rheological condition of the substrate is confirmed by the way tablets tend to sink into it. Some tablets may be deeply embedded, while others may be so tilted as to leave lunate imprints on the substrate (Fig. 1549). Tablets are rarely

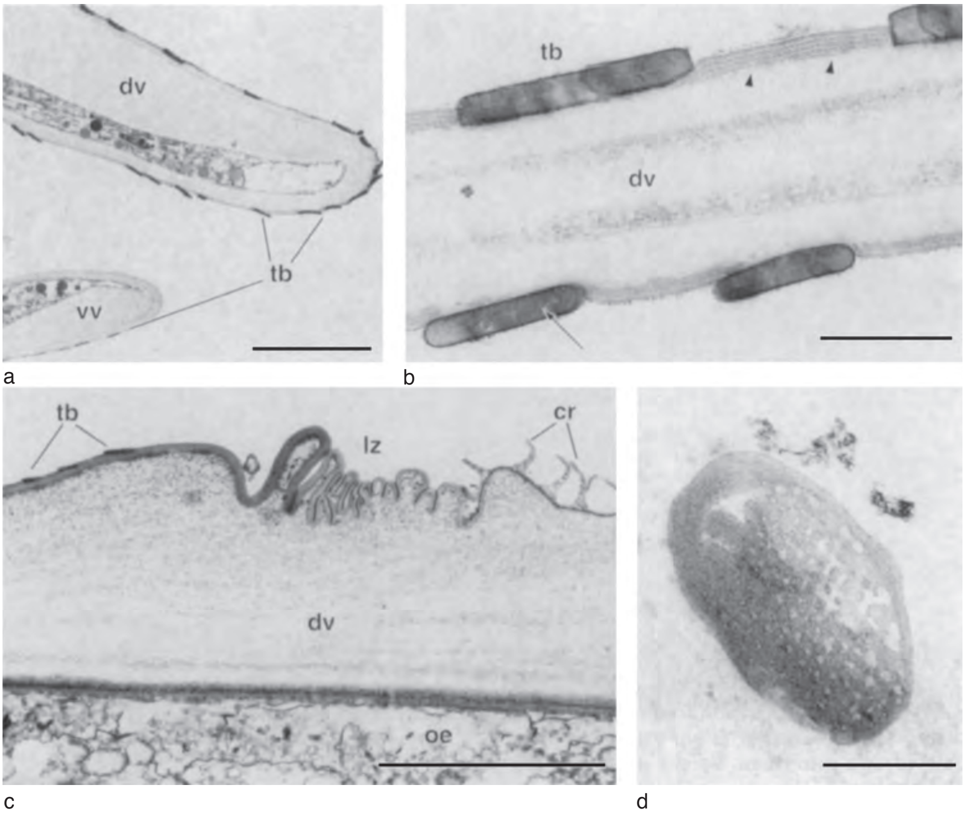


FIG. 1553. TEMs of pelagic and recently settled juveniles of *Discinisca* sp. cf. *tenuis; a–b, d,* free-swimming juvenile; *c,* recently settled juvenile. All specimens fixed and stained; *a,* margin of dorsal (*dv*) and ventral (*vv*) valve with tablets (*tb*) partly embedded in an outer layer correlating with periostracum; scale bar 5 µm; *b,* details of tablets (*tb*) with inner cavity (*arrow*) on dorsal valve (*dv*); note 5 electron-dense sheets of outer periostracal layer (*arrowheads*); scale bar 0.5 µm; *c,* lamellar ring (*lz*) separates mosaic with tablets (*tb*) and mature shell with superstructure of concentric ridges (*cr*); dorsal valve (*dv*) underlain by outer mantle epithelium (*oe*); scale bar: 5 µm; *d,* oblique section through tablet, showing rhombic arrangement of silica granules; scale bar: 0.25 µm (Williams, Lüter, & Cusack, 2001).

preserved on the juvenile surfaces of adult shells because they are dissolved or drift free of their substrate as the glycocalyx cover degrades. Their imprints on polymerized substrates betray their former presence, but even substrates can be abraded or stripped off the living shell by exfoliation, which accounts for the sporadic preservation of mosaic imprints in fossils.

The mosaic is bounded by a tablet-free ring of lamellae, separating it from the mature shell (Fig. 1554–1555). The junction between the lamellar ring and mosaic is sharp, with secretion of tablets ceasing within a zone approximately 5 µm wide, although cessation is not always simultaneous in the ventral and dorsal valves. The ring is composed of periostracum disposed as up to eight inwardly dipping lamellae that range from asymmetrical or isoclinal folds (Fig. 1554) to discrete sheets (Fig. 1555). The junction between the lamellar ring and the mature shell is also sharp, commonly with signs of rupture probably resulting from postmortem dehydration. The chitinous periostracum of the mature shell is also folded but is ornamented by its distinctive superstructure of concentric ridges composed of pellicular sheets of chitin (Fig. 1555).

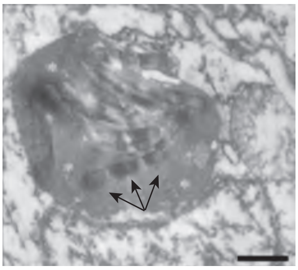


FIG. 1554. Cross section through a tablet-producing cell at hinge of periostracal slot of *Discinisca* sp. cf. *tenuis,* revealing a vesicle containing several siliceous tablets (*arrows*); scale bar: 0.5 µm (Lüter, 2004).

The folds and sheets of the lamellar ring are identical with disturbances affecting the periostracum and primary layer of brachiopods generally. They are caused by rapid retractions and advances of the outer mantle lobe (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 330). Their development in *Discinisca* coincides with the attachment of the juvenile to its benthic substrate. Yet it does not necessarily follow that these lamellae bordering the mosaic are so-called skeletonized shock waves registering the trauma of settlement, because traces of the lamellar ring have been found in one pelagic specimen but not in a few newly settled juveniles. The vacillations of the outer mantle lobe, as represented by the ring of lamellae, is more probably linked to genotypic as well as phenotypic factors, especially further differentiation of the periostracal slot and both inner and outer mantle lobes (WILLIAMS & others, 1997, p. 14).

The periostracum of the late brephic (lamellar ring) and mature shell is underlain by a layer of sulfated GAGs with some chitin. This succession correlates with the mosaic and its substrate. Both successions are secreted by cytologically similar outer epithelia with tubular microvilli. Despite this similarity, secretion of silica and apatite does not proceed simultaneously during shell growth. Ten young shells, 475–580 µm in diameter, were analyzed by EDX. The analysis of a pelagic juvenile showed that the inherent mineralizing element was Si with no trace of Ca or P (specimen 1 in Fig. 1556). This pelagic juvenile was within the size range for settlement, and tablet secretion

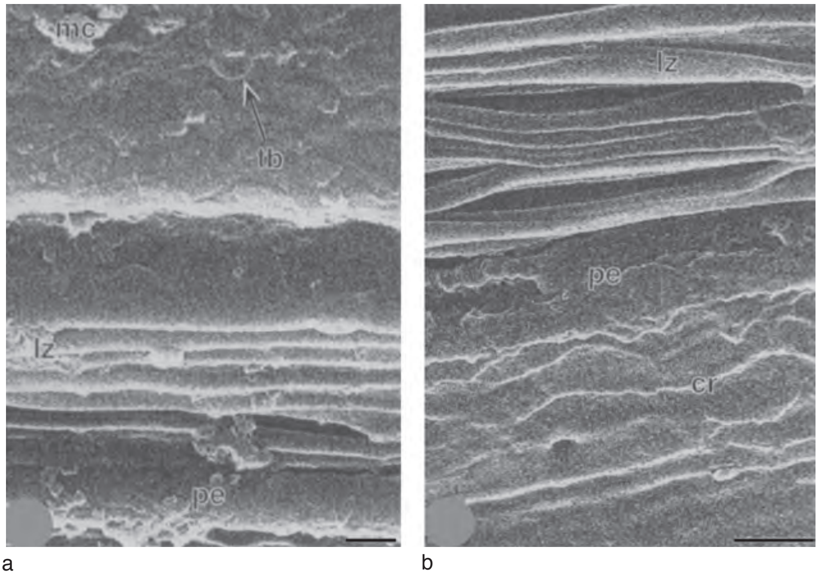


FIG. 1555. SEMs of gold-coated shells of recently settled juveniles of *Discinisca* sp. cf. *tenuis* sonicated for 15 min. in tap water; *a–b*, changes shown from mosaic (*mc*) with tablets (*tb*) outward to lamellar ring (*lz*) and periostracum (*pe*) of mature dorsal valve with its superstructure of concentric ridges (*cr*); scale bars: 1 µm (Williams, Lüter, & Cusack, 2001).

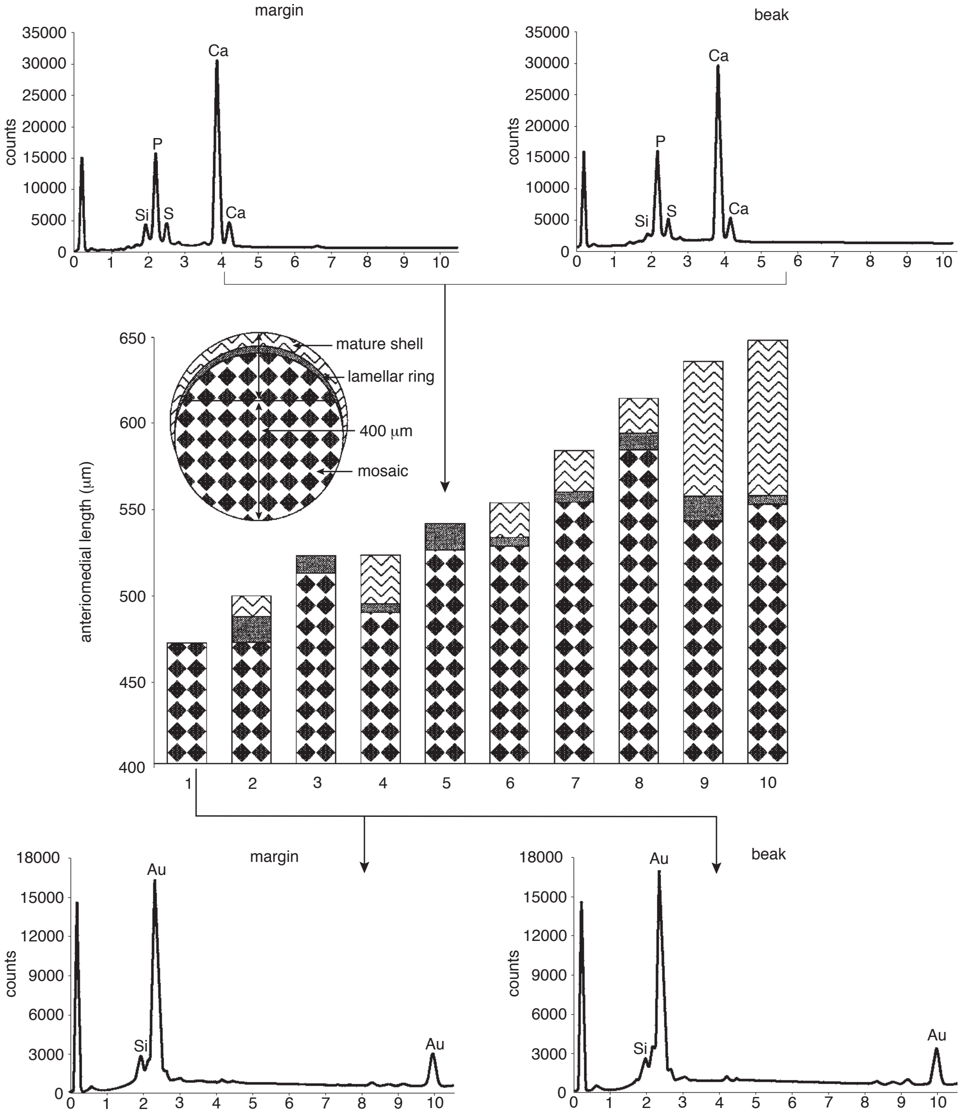


FIG. 1556. Graphical representation of variation in development and sagittal lengths of shell surfaces anteromedially of 400 µm of mosaic on ten smallest dorsal valves of *Discinisca* sp. cf. *tenuis* subjected to EDX analysis. Specimens 1 and 2 were gold coated, the remainder carbon coated; specimen 1, the only pelagic juvenile, was fixed in glutaraldehyde, specimen 2 in Bouin's, and remainder were dried, untreated valves. Spectra of valve margins and beaks of two specimens are shown for pelagic specimen 1 and the settled specimen 5, which was of intermediate length but without mature shell (Williams, Lüter, & Cusack, 2001).

may have ceased already on the concealed inner sides of the incipient outer mantle lobes. In contrast, in settled juveniles less than 50 µm longer (Fig. 1556), where cessation of silica secretion is confirmed by the presence of the lamellar ring, apatite could be traced everywhere from the first-formed shell to the margin. A subsidiary peak of S is also associated with the Ca and P peaks of apatite. It presumably signals the sulfated

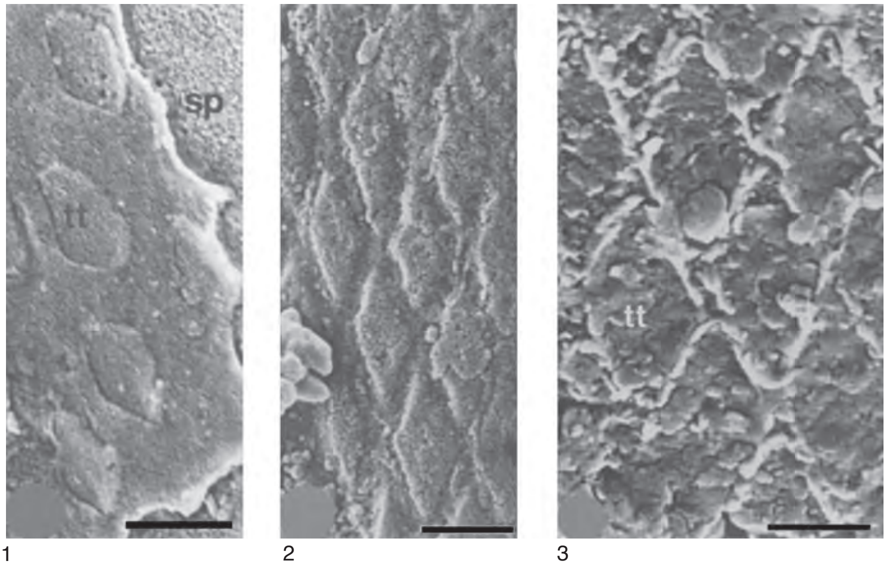


FIG. 1557. SEMs of exteriors of discinid larval shells; *1,* tension-cracked fragment of outermost coat of dried valve of *Discina striata*, bearing imprints of tablets (*tt*) and underlain by primary layer with spherular apatite (*sp*); scale bar: 1 µm; *2*, tablet imprints on tension-cracked, spherular external surface of primary layer of *Pelagodiscus atlanticus*, treated with subtilisin; scale bar: 1 µm; *3*, imprints of tablets (*tt*) on exterior of larval shell of Upper Jurassic *Discina*; scale bar: 1 µm (Williams, Cusack, & Buckman, 1998).

GAGs secreted as the matrix for the initial apatitic aggregates (WILLIAMS, CUSACK, & BUCKMAN, 1998, p. 2,008). Although apatitic secretion begins before the growth of the mature shell (specimen 5 in Fig. 1556), it appears to have a mutually exclusive relationship with the siliceous secretion of the mosaic. By the time an anteromedial arc of mature shell has appeared on the surface of a dorsal valve, even the apatite secreted under the mosaic of the first-formed shell is many times thicker than the overlying layer of siliceous tablets. In the absence of cytological differences, it is assumed that the epithelium generated outside the lamellar ring everywhere loses the capacity to secrete silica. In effect, there is a temporal and spatial hiatus in shell mineralization that precludes chemical interaction between the siliceous and phosphatic regimes. Both regimes operate consecutively within the outer epithelium underlying the mosaic. Yet the phosphatic regime of the mosaic area is not activated until apatite secretion begins under the lamellar ring (possibly some days after the deposition of the siliceous tablets) and is presumably triggered by a chemical signal from the ring region (WILLIAMS, LÜTER, & CUSACK, 2001, p. 34).

Imprints of mosaics occur on the juvenile shells of living *Discina* and *Pelagodiscus* (Fig. 1557; BALINSKI & HOLMER, 1999, fig. 3Q). *Discina* has been sporadically recorded in post-Paleozoic sediments but tablet imprints are rarely preserved (Fig. 1557) due to exfoliation or abrasion of the juvenile shells. Imprints of siliceous tablets have also been found on some juvenile shells of the Late Devonian *Schizobolus* (BALINSKI & HOLMER, 1999, fig. 3N) and the late Silurian *Opatrilkiella* (Fig. 1558). No mosaic imprints, however, have been found in the oldest discinoids, including the sister group of discinids (WILLIAMS, CUSACK, & others, 1998, p. 2096), the Ordovician orbiculoideids such as *Orbiculoidea* and *Schizotreta*. Species of the latter genera are common, and it can be confidently asserted

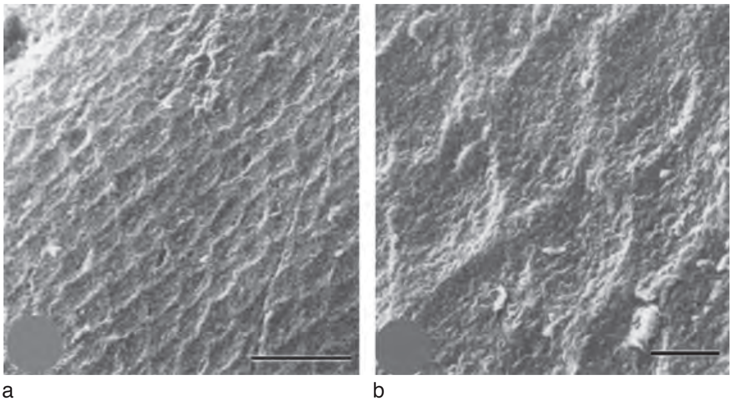


FIG. 1558. SEMs of gold-coated valve surfaces of lingulate shells dissolved out of rock; *Opatrilkiella minuta* MERGL, GLAHM 114648, upper Silurian, Czech Republic; *a*, dorsal valve of juvenile with *b,* details of rhombic imprints; scale bars: 1 µm (Williams, 2003).

that their juvenile shells, which are well delineated by lamellar rings, were devoid of imprints of any kind in contrast to their mature shells.

The development and mode of preservation of the discinoid juvenile shell have been described in detail because they serve as models to explain the origin of microornamentation of many early Paleozoic lingulates. Moreover, the physicochemical constraints imposed when shell secretion involves more than one mineral could have a bearing on how the organophosphatic and organocarbonate brachiopod shells were first differentiated.

ACROTRETIDE JUVENILE SHELL

Imprints made by structures associated with the periostracum or the first-formed cuticle occur on the shells of over 100 of the 250 or so genera assigned to the Lingulata. Only the Siphonotretida lack imprints that ornament the shells of about one-third of the Lingulida and are invariably present on the juvenile shells of the Acrotretida. The imprints of acrotretide mosaics were the first to be discovered and were described in Volume 1 as impressions of vesicular periostracum (WILLIAMS, 1997, p. 269–271). They will be discussed before those of lingulides (other than the discinids already described) because they are the best known and include all distinctive impressions characterizing the lingulates.

Only four distinctive kinds of imprints (Fig. 1559) are known (WILLIAMS, 2003). Imprints on a micrometric scale have either flat bases and vertical sides (discoidal or rhombic) or inwardly convex bases with sloping sides (hemispherical). Cylindroid pits on a nanometric scale can also occur in association with the flat-based or hemispherical imprints; they are small-scale versions of semiellipsoidal imprints found on lingulide shells. The subcircular areas bearing these imprints vary in diameter from approximately 150 µm (*Acrotretella*) to 220 µm (*Conotreta*) and occupy the beaks of shells. These areas are free of growth rings and are assumed to be the casts of first-formed shells. They are bounded by one or two growth rings that form a conspicuous, cylindroid ridge (roll) that is interpreted as the brephic shell.

Variations in the shapes and packing of flat-based imprints of acrotretides are exemplified by the mosaic casts of *Opsiconidion* and *Eoconulus*. The first-formed dorsal valve of *Opsiconidion* is wrinkled and raised as a pair of submedial ridges diverging anteriorly, but lacks growth bands (Fig. 1560). It is impressed by subcircular imprints that fade along an irregular boundary in the anteromedial sector of the roll. The imprints,

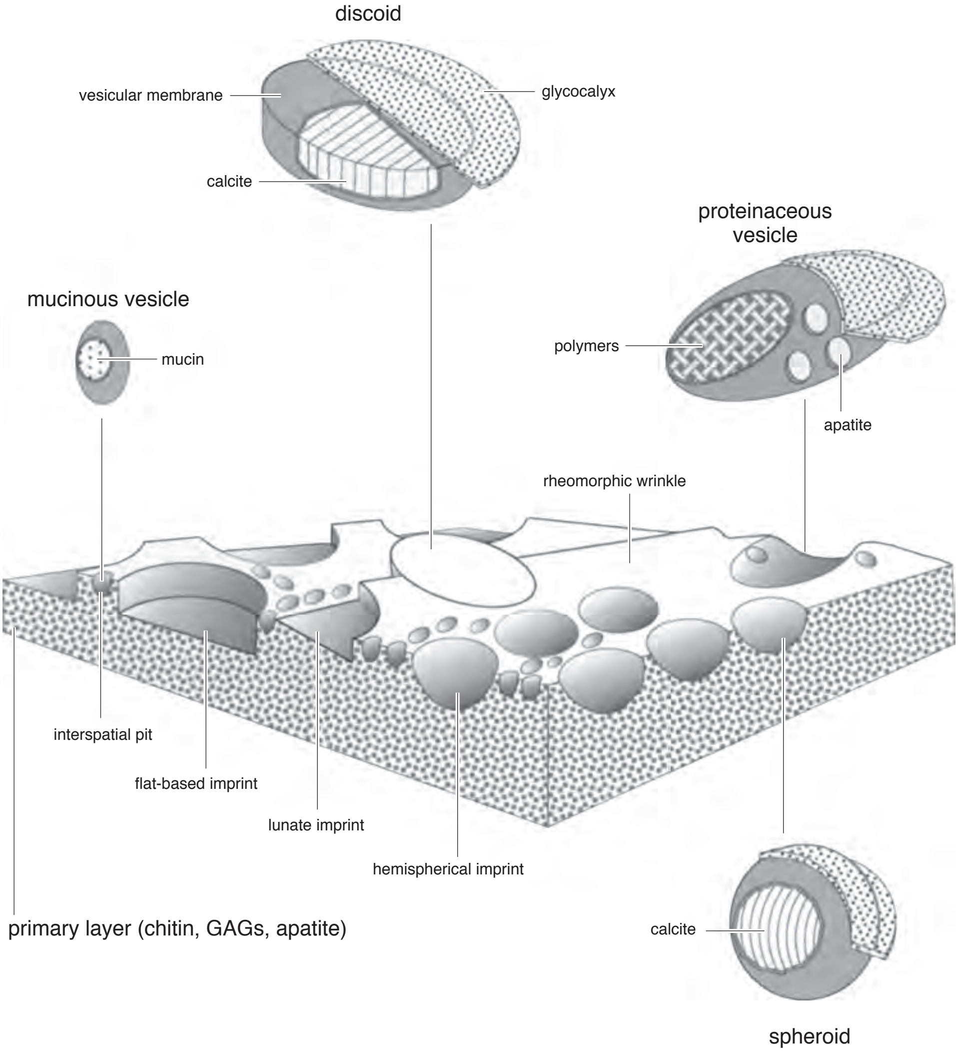


FIG. 1559. Graphical representation of a block section of juvenile acrotretide shell *in vivo* showing disposition of various imprints in primary layer (and first-formed lamina) and assumed chemicostructures of discoids, spheroids, and vesicles making imprints (Williams, 2003).

approximately 4.4 µm in diameter, are essentially arranged in hexagonal, close-packed arrays (Fig. 1560), but there is much overlap. Imprint surfaces are smooth or finely granular, and their vertical walls are up to 500 nm deep. The walls and interspaces between imprints are indented by cylindroid pits (Fig. 1560). In some *Opsiconidion* species, the first-formed shell consists of overlapping clusters of imprints, 2 µm to 7 µm in diameter. The imprints are usually arranged in successions up to five deep with the largest imprint being outermost and the smallest being innermost (Fig. 1560). The smoothly textured imprints may be flat or gently convex inwardly. They are so overcrowded that they amalgamate into chambers, reducing the substrate into flat-topped polygons. The imprints themselves may be pierced by cavities.

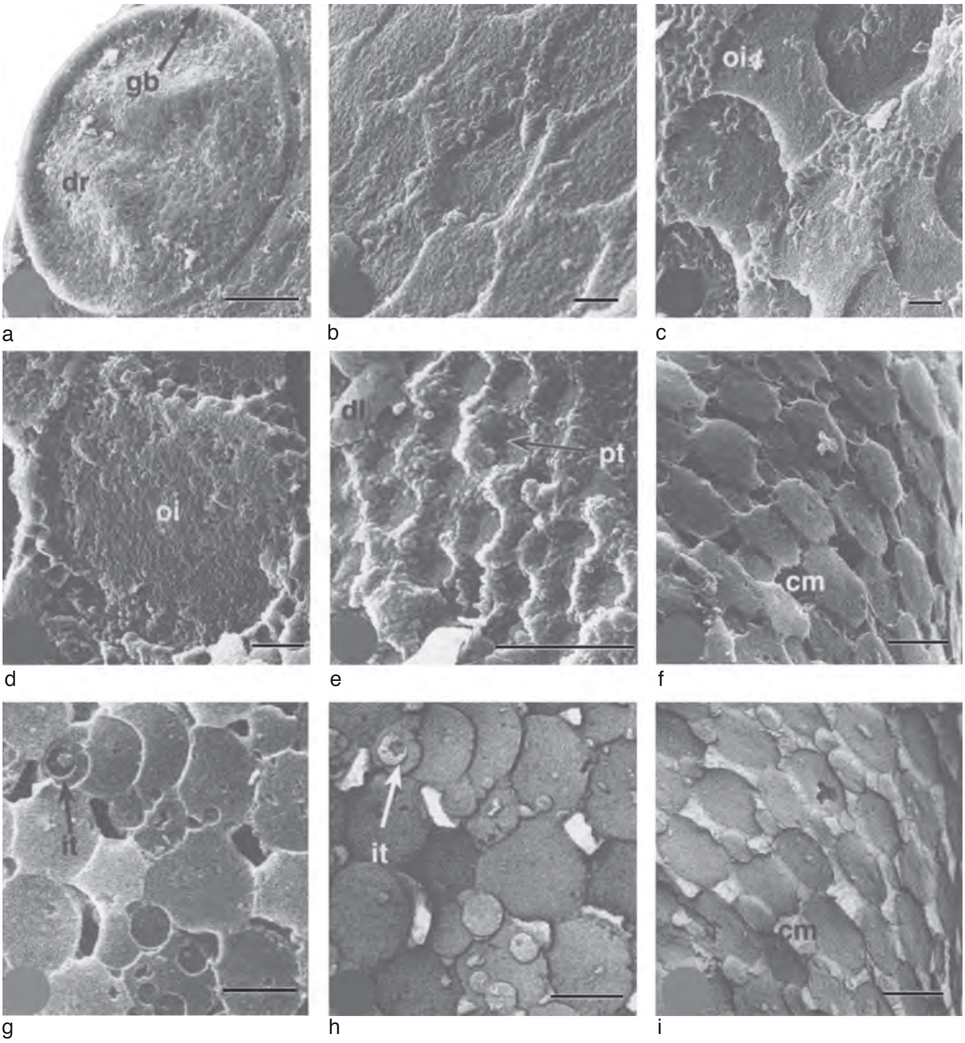


FIG. 1560. SEMs of gold-coated valve surfaces of acrotretide shells dissolved out of rock, various *Opsiconidion* species, upper Silurian, Czech Republic; *a, c–e, O. decessus* MERGL, GLAHM 114649; *b, O. ephemerus* MERGL, GLAHM 114650; *f–i, O. simplex* MERGL, GLAHM 114651; *a,* general view of first-formed dorsal valve bounded by growth band or roll (*gb*) with divergent ridges (*dr*); scale bar: 50 µm; *b,* flat-based elliptical imprints in hexagonal, close-packed array; scale bar: 5 µm; *c–e,* overlapping, flat-based imprints (*oi*) and details of pits (*pt*) in interspaces with dislodged panel (*dl*); scale bars: 1 µm; *f, i,* detail and inverted image of first-formed ventral valve with flat-based chambers (*cm*); scale bars: 5 µm; *g–h,* detail and inverted image of first-formed dorsal valve showing overlapping successions of flat-based circular imprints, some of which (*it*) had been incorporated within the primary layer; scale bars: 5 µm (Williams, 2003).

The flat-based imprints on the dorsal valve of *Eoconulus* (Fig. 1561) are approximately 8 µm in diameter medially, becoming smaller (approximately 6 µm) toward the roll. Their vertical sides may be more than 1 µm high and may be separated from the granular floor by a shallow gutter. The imprints are arranged in hexagonal arrays, and the walls and interspaces between them are flat topped and indented by close-packed, shallow to hemispherical pits, approximately 700 nm in diameter.

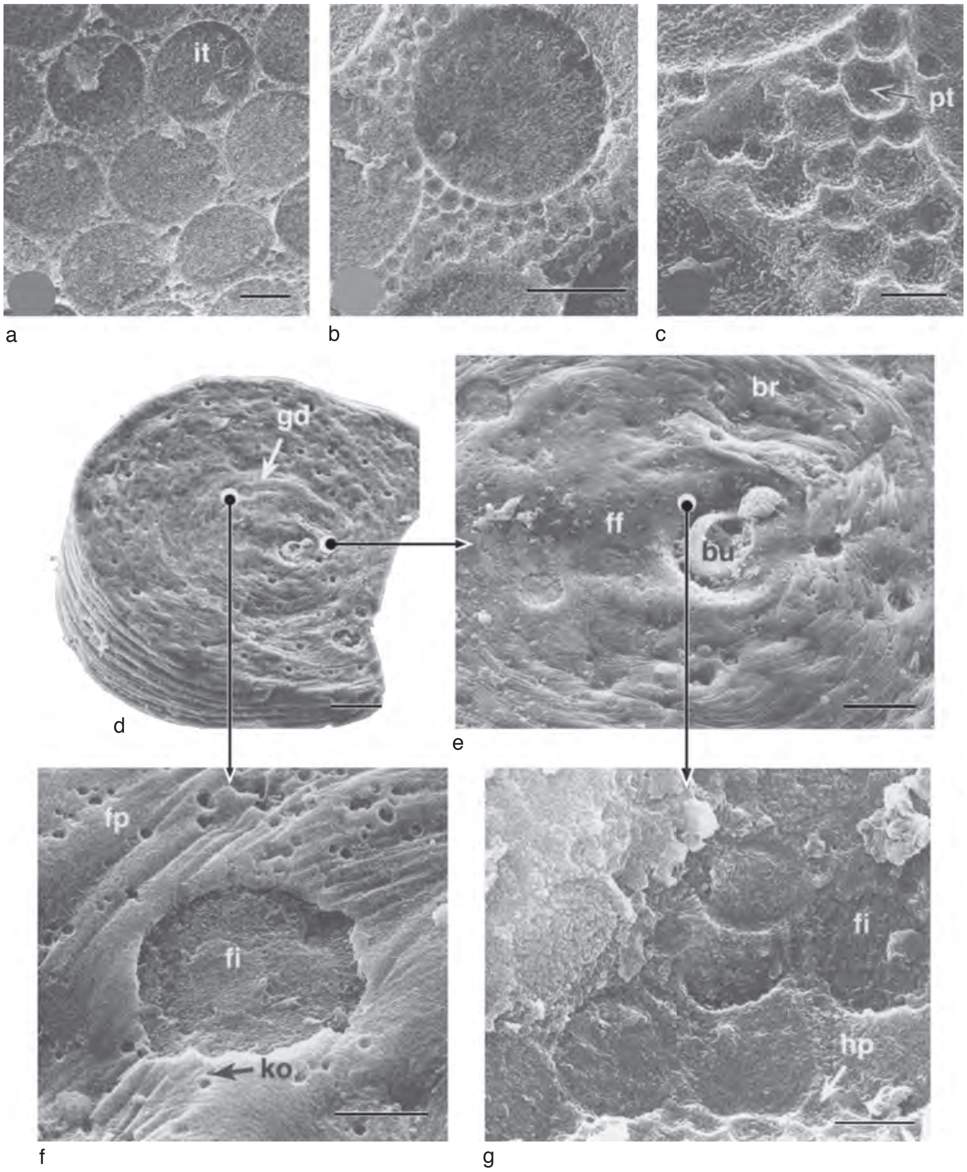


Fig. 1561. SEMs of gold-coated valve surfaces of acrotretide shells dissolved out of rock; *a–c*, *Eoconulus* sp. cf. *semiregularis* Biernat, GLAHM 114663, middle Ordovician, Sweden; general view and details of flat-based circular imprints (*it*) and interspaces with close-packed pits, some compound (*pt*); scale bars: 5, 5, and 1 µm respectively; *d–g*, SEMs of encrusting part of ventral valve of *Eoconulus* sp. cf. *semiregularis* Biernat, GLAHM 114652, middle Ordovician, Sweden, showing *d*, general disposition and *e*, details of surface features including bulla (*bu*) in first-formed shell (*ff*) with *g*, overlapping, flat-based imprints (*fi*) and small, hemispherical pits (*hp*), surrounded by eccentrically folded brephic zone (*br*) separated by growth disturbance (*gd*) from mature shell with tightly folded drapes (*fp*) perforated by sporadic, flat-based imprints (*fi*) and kiskinoids (*ko*) (view *f*); scale bars: 100, 25, 10, and 2.5 µm in *d–g* respectively (Williams, 2003).

Unlike other acrotretide shells, imprints on the encrusting surface of the ventral valve of *Eoconulus* differ from those of the dorsal valve (Fig. 1561). The juvenile shell, approximately 200 µm in diameter, consists of a vestigial holdfast approximately 25 µm in diameter within a first-formed valve delineated by a tightly folded brephic shell. The wrinkled first-formed shell is variably ornamented by poorly ordered flat-based imprints approximately 3.5 µm in diameter and close-packed hemispherical pits. The mature shell is also eccentrically folded and indented by widely scattered, flat-based circular imprints up to 25 µm in diameter. These imprints must have been made by bodies secreted on a folded periostracum, because they breach the surface without being affected by external folding. Sporadically occurring deep pits appear to have been mechanically excavated like koskinoids (Williams, 1997, p. 320).

Flat-based imprints are characteristic of the first-formed shells of the biernatiids, eoconulids, scaphelasmatids, torynelasmatids, and many acrotretid genera. Their mean diameters range from 1.4 µm to 4.8 µm, and their floors, which may be gently convex or concave (*Linnarssonella*), are commonly separated from their bounding walls by a gutter approximately 100 nm wide. The imprints of some species (*Conotreta*) are deep (700 nm) relative to their diameter (1.9 µm).

Hemispherical imprints are the most common impressions on lingulate shells. They ornament the first-formed shells of most acrotretids and torynelasmatids and all ephippelasmatids but with some variation. Thus, the hemispherical pits on the first-formed shell of *Numericoma* (Fig. 1562), which range in diameter from 0.7 to 2.7 µm, have smooth linings and are close packed with larger ones surrounded by clusters of smaller ones, giving a bubble-raft appearance (Biernat & Williams, 1970). The walls between contiguous imprints, however, may be as thin as 75 nm without being rheologically deformed, which precludes structural comparison with bubble rafts. The close-packed hemispherical to semiellipsoidal imprints on the first-formed shell of *Eurytreta* are smaller in mean diameter (1.5 µm) and mostly deep with rare, shallow impressions, possibly representing aborted secretion. The flat-topped walls and interspaces between imprints are indented by roughly bounded pits affected by cleavage. The mean diameters of hemispherical pits of other acrotretides vary from 1.1 µm (*Prototreta*) to 2.6 µm (*Apsotreta*). Pits indenting walls and interspaces are shallow (seldom more than 400 nm). The juvenile shell of *Ceratreta* is ill defined and unusual in two respects. It bears impersistent growth bands, and the small, hemispherical imprints (1.2 µm in diameter) are only sporadically preserved on surfaces apparently unaffected by exfoliation.

LINGULIDE JUVENILE SHELL

Unlike that of living discinids, the first-formed shell of living lingulids is a smooth organic sheet presumably chitinous, as are the discrete brephic valves. Balinski (1997), however, has shown that the first-formed shell of Devonian lingulids consists of two discrete, cuplike valves (approximately 90 µm in diameter) ornamented by radial ridges, tubercles, or hemispherical pits (1–3 µm in size). Some compound pits with rounded interspaces or bubble-raft casts characterize Early Devonian species. This evidence that the protegulum is a post-Devonian feature of the lingulid lineage accords with the fact that the first-formed shells of Paleozoic lingulides consist of discrete valves, although pitting is variably developed. There is also variation in the distribution of imprints on shell surfaces. In some groups, imprints are restricted to the juvenile shell; in others, imprints indent the entire shell or, more rarely, the mature shell only.

Lingulides with pitted juvenile shells include the linguloid paterulids and eoobolids and the acrotheloids. The first-formed

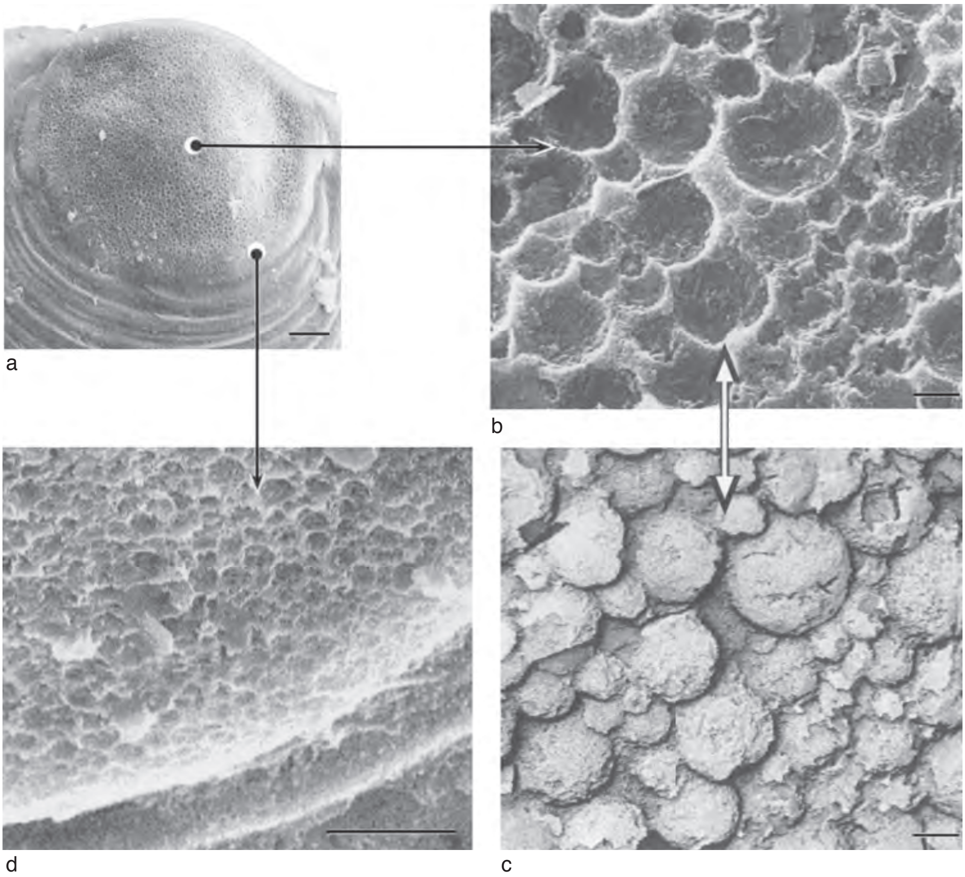


FIG. 1562. SEMs of a first-formed dorsal valve (*a*) and surface details (*b–c*) of *Numericoma perplexa* Holmer, GLAHM 114661, middle Ordovician, Sweden, showing clustering of smaller, hemispherical imprints around larger ones in cast and inverted image becoming shallower toward bounding roll (*d*); scale bars: 20, 1, 10, and 1 µm respectively (Williams, 2003).

shell of *Paterula*, approximately 60 µm in diameter, is impersistently and arcuately wrinkled, which affects the disposition and distribution of surface imprints (Fig. 1563). The circular, flat-based imprints (2.3 µm in mean diameter) are variably distributed. Groups of closely crowded, overlapping imprints, up to three deep, are scattered among more openly distributed clusters. Some overlapping imprints are presumably casts of bodies that accumulated on top of one another in the substrate. Others forming stacked, incomplete, lunate impressions could have been made by bodies that had been partly separated from the first-formed shell during its wrinkling (a common feature of the juvenile shells of living discinids). The first-formed shell is surrounded by a brephic zone of growth seldom more than 7 µm wide anteromedially. This zone is underlain by stratified laminae of the primary layer and with the bounding mature shell is gently folded into ripples, eccentric to the first-formed shell. The brephic shell surface is indented by close-packed elliptical imprints, although circular imprints also occur. The mature shell is characterized by highly ordered, rhombic impressions with long diameters aligned with the eccentric folding; despite their crystalline aspect, the impressions are surface ornament (Williams, 2003, p. 71).

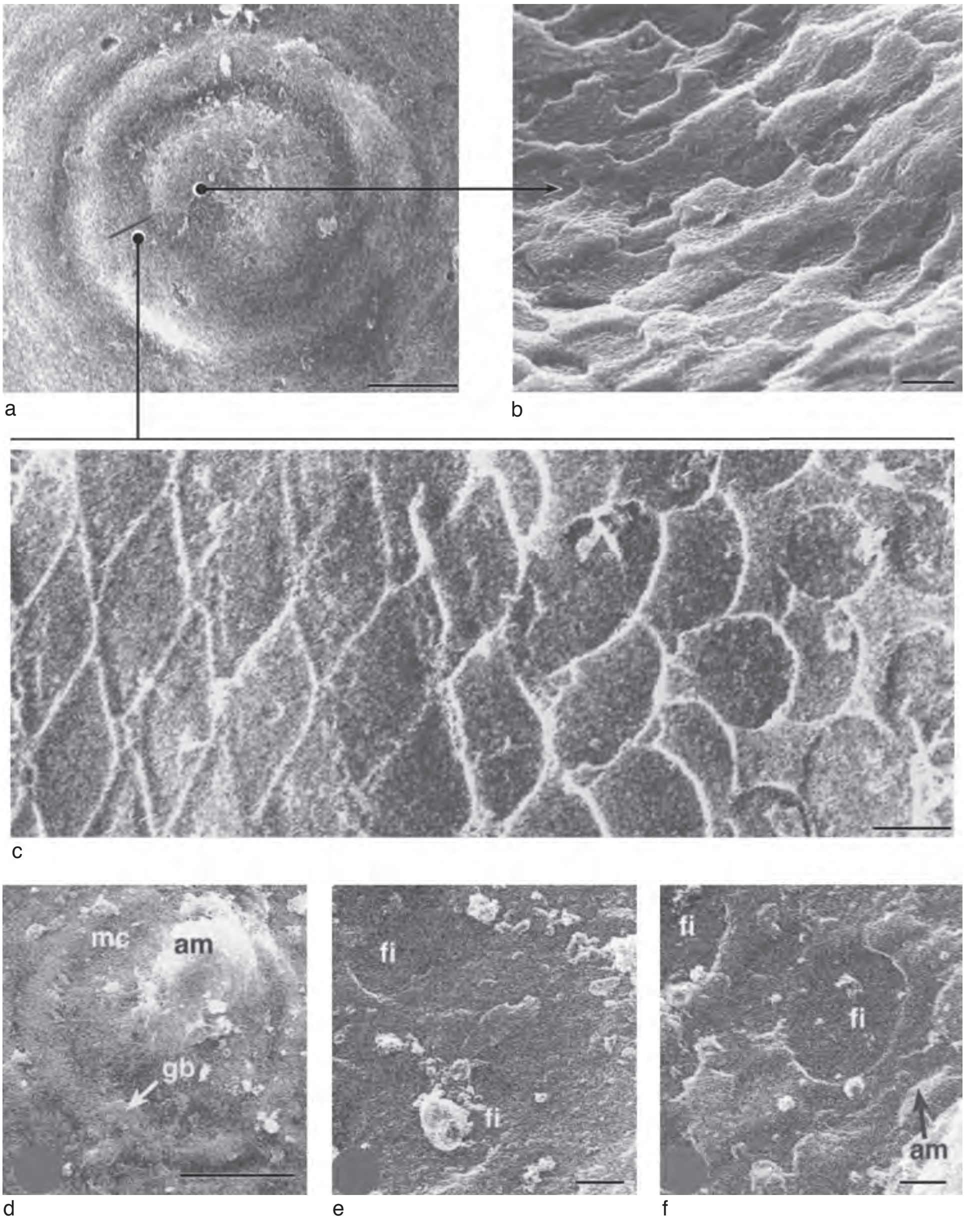


FIG. 1563. *a–c*, SEMs showing surfaces of juvenile and surrounding mature shell of dorsal valve of *Paterula* sp., GLAHM 114653, middle Ordovician, Sweden; scale bars: 25, 2, and 2 µm; *d–f*, *Paterula* sp., GLAHM 114656, middle Ordovician, Sweden; general view of untreated mudstone cast with adherent apatitic shell (*am*), identified by EDX, of dorsal, first-formed valve with bounding growth band (*gb*) and *e–f*, details of part of mudstone (*mc*), shown in *d*, bearing subcircular, shallow, flat-based imprints (*fi*); scale bars: 50, 1, and 1 µm respectively (Williams, 2003).

Nearly all chemicostructural studies of fossilized apatitic-shelled brachiopods have used specimens dissolved out of rock. This preparation could have affected imprints and any traces of the bodies making them. One sample giving evidence of the fossilized state of undissolved shells has been described (WILLIAMS, 2003, p. 82). In the dorsal valve

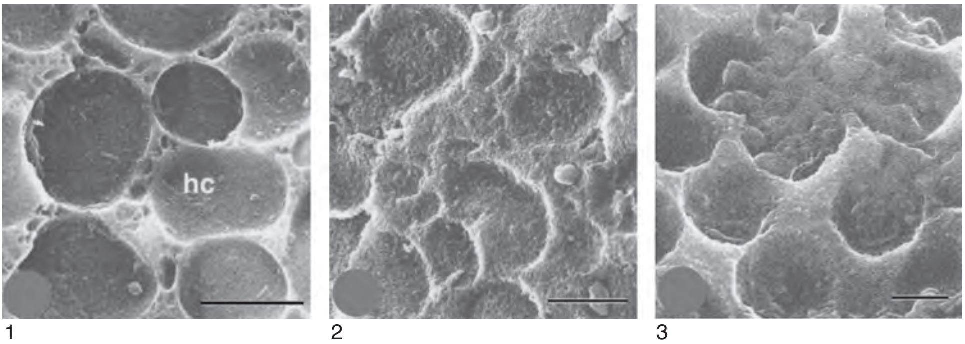


FIG. 1564. SEMs of gold-coated, first-formed dorsal valve surfaces of acrotretide shells dissolved out of rock; *1, Orbithele ceratopygorum* (BRÖGGER), GLAHM 101736, lower Ordovician, Sweden; view of flat-based, circular, and hemicylindroid (*hc*) imprints separated by pitted walls; scale bar: 5 µm; *2, Acrothele coriacea* LINNARSSON, GLAHM 101734, middle Ordovician, Sweden; flat-based hemispherical and deformed imprints with fracture section showing compact lamina of first-formed shell; scale bar: 5 µm; *3, Karathele napura* (KRUSE), GLAHM 101737, Lower Cambrian, Australia; view of hemispherical imprints; scale bar: 1 mm (Williams, 2003).

of *Paterula* embedded in mudstone, part of the first-formed shell had broken away to expose the interface between the valve exterior and mudstone (Fig. 1563). The mudstone is pitted with shallow, flat-based cavities that could only have been the external counterparts of imprints found on the first-formed shell. Unlike its apatitic primary layer, which was unaffected by diagenesis, the mosaic of the first-formed shell of *Paterula* must, therefore, have been composed of discoidal tablets that degraded mineralogically as well as organically during fossilization.

The juvenile shell of *Eoobolus* is well defined by a lamellar ring and is pitted by sharp-edged hemispherical imprints approximately 1 µm in diameter (HOLMER, POPOV, & WRONA, 1996).

The spinose juvenile shells of acrotheloids (Fig. 1564) are also well defined by a strong roll. Those of acrothelids (*Orbithele*) are ornamented by large (up to 9 µm in diameter), flat-based to convex (rarely concave)-based imprints. The imprints form hexagonal arrays with rare overlaps and deformed hemicylindroids. The gently rounded walls and interspaces are impressed by deformed hemispherical pits less than 1 µm in diameter. The juvenile shells of botsfordiids (*Karathele*) are indented by hemispherical pits approximately 1.5 µm in diameter and up to 1 µm deep. The pits are so closely packed as to be separated by knife-edge walls regularly culminating in interspaces indented by shallow depressions.

Apart from the paterulids and eoobolids, when pitting occurs on linguloid juvenile shells, it also indents mature shells as in all zhanatellids. The hemispherical imprints on the juvenile shell of *Rowellella* are alternately arranged in concentric rows. They are seldom more than 3 µm in diameter (compared with approximately 6 µm on the mature shell), and most have been made by spheroids that were rigid relative to a rheological substrate that is commonly deformed by radial drag into chevron folds around the pits (Fig. 1565). In contrast, the first-formed shell of the obolid *Obolus eichwaldii* are indented by large semiellipsoidal imprints arranged in radial rows and bounded by round-topped walls. In the brephic shell, three or so radial rows of concentrically disposed semicylindroids alternate with strips indented by lenticular slots oriented at all angles. The slots bear median ridges, indicating that they are casts of platy, bilamellar bodies. Small hemispheroidal pits sporadically indent the rounded borders separating the semicylindroids (Fig. 1565).

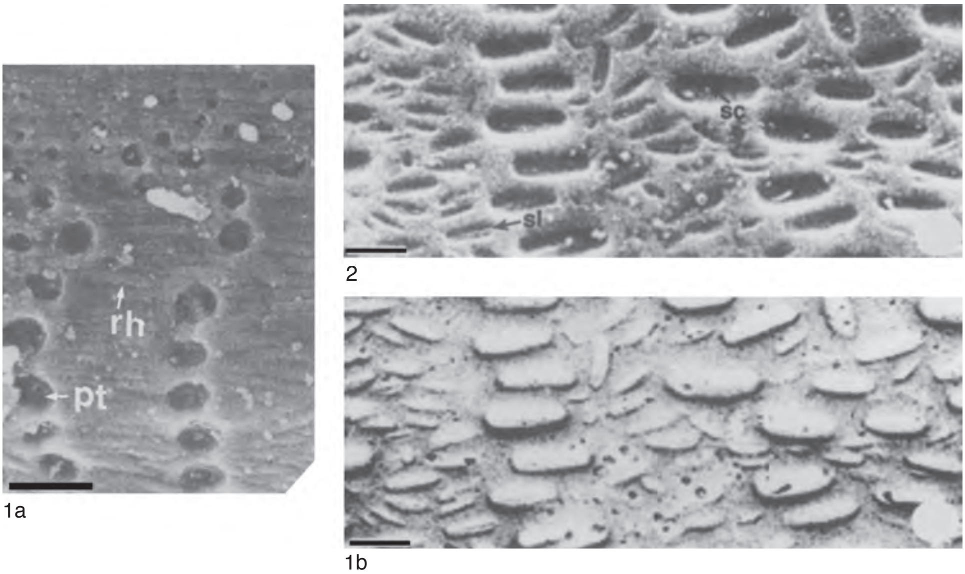


FIG. 1565. Shell exterior of *1, Rowellella rugosa* GORJANSKY, GLAHM 101723, Lower Ordovician; *1a,* initiation and development of radially disposed pits (*pt*) separated by rheomorphic folding (*rh*); scale bar: 10 µm; *1b,* general view; *2,* inverted image of pitted surface of mature shell of *Obolus eichwaldi* MICKWITZ, GLAHM 101451, Cambrian, Russia, showing orientation and inclination of semicylindroid pits (*sc*) and lenticular slots with median clefts (*sl*); scale bars: 5 µm (Cusack, Williams, & Buckman, 1999).

The most distinctive features, however, of linguloid pitted surfaces are the apatitic tablets and discoids still preserved in mature shells of the zhanatellid *Wahwahlingula antiquissima* (Fig. 1566). The borders and sides of the large, hemispherical imprints bear subcircular to prismatic, flat-bottomed imprints, 0.6–1.2 µm in maximum diameter. These imprints are not deformed but tilt into the sides of the larger pits as narrow slots. Some imprints contain closely fitting tablets of apatite, about 100 nm thick. This intimate association suggests that the prismatic to slotlike imprints are casts of apatitic tablets that occur in three or four horizons within the outermost zone of the primary layer (Fig. 1566).

At this juncture, it is relevant to note the nature of the imprints on discinoid orbiculoideids, even though they are restricted to the mature shell. The periodic disposition of the hemispherical imprints in discrete radial arrays on the *Orbiculoidea* shell has previously been interpreted as being determined by the distribution of setae at the mantle margin (WILLIAMS, 1997, p. 272). The pits, which are commonly deformed, average 2.5–3 µm in diameter and are graded in bands bounded by fila (WILLIAMS, CUSACK, & BUCKMAN, 1998, p. 2,022). On the outer side of a filum and extending outwardly for approximately 30 µm, the pits are hexagonally close packed before becoming aligned in radial arrays. The shell surface is seldom free of fine, rheomorphic folds that can occur in swarms in some interfilar surfaces. The pits are evidently hemispherical casts of presumed spheroidal bodies preserved in a rheological substrate. The bodies making the pits were not homogenous but composed of close-packed spheroids (Fig. 1567), which themselves appear to have been aggregates of small vesicles. The toughness of the coats of these composite spheroidal bodies is revealed by the way rheomorphic folds in the substrate can radiate from pits (Fig. 1567) that retained their shape (presumably during dehydration of exposed dead

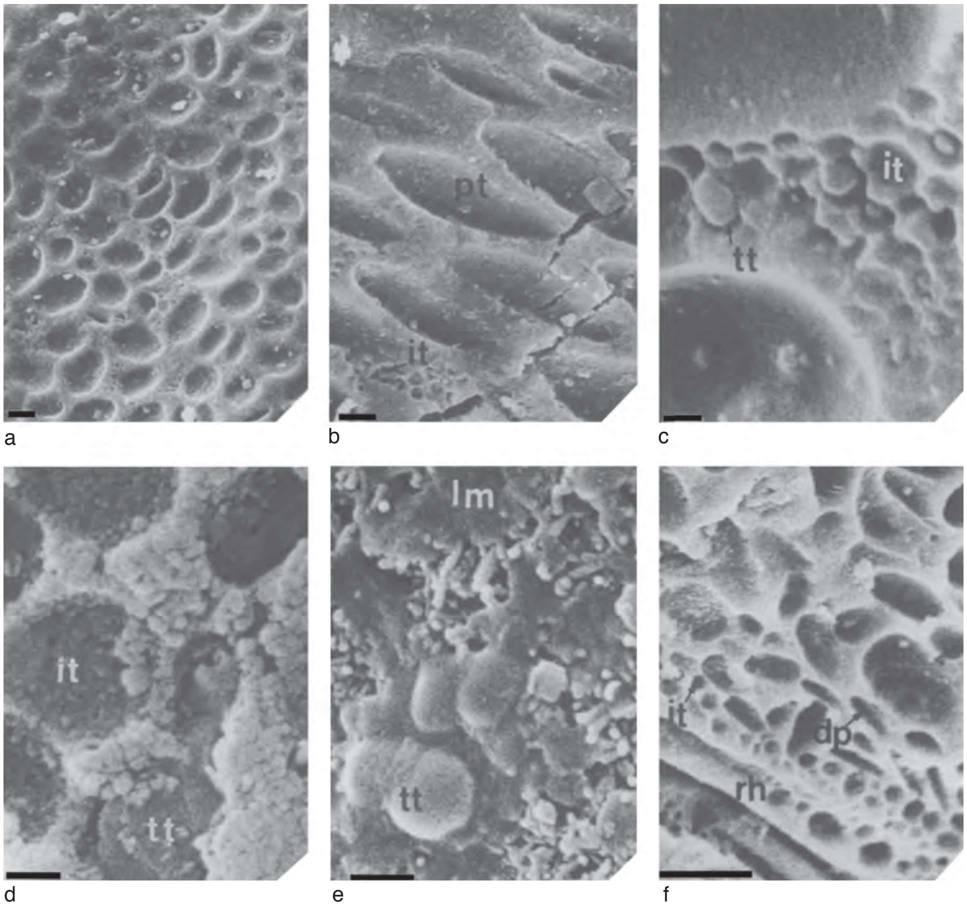


FIG. 1566. Shell exterior of *Lingulella* (?) *antiquissima* (JEREMEJEW), GLAHM 101691, Upper Cambrian, Russia; *a*, general view of pitted surface between two fila; scale bar: 5 µm; *b*, slotlike pits (*pt*) with long axes concentric with valve margin and casts of tablets (*it*) just beyond boundary of larval shell; scale bar: 2 µm; *c*, detail of borders between contiguous pits showing tablets (*tt*) and their casts (*it*); scale bar: 1 µm; *d*, flat-bottomed subcircular casts (*it*) of tablets (*tt*); scale bar: 500 nm; *e*, tablets (*tt*) within primary layer associated with lithified membranes (*lm*) and apatitic rods and spherules; scale bar: 1 µm; *f*, *in vivo* repair of damaged part of valve with radial, rheomorphic folding (*rh*) of primary layer with tablet casts (*it*) and deformed pits (*dp*) tracing zone of fusion of torn mantle edge; scale bar: 5 µm (Cusack, Williams, & Buckman, 1999).

shells prior to burial and fossilization). The pits on the mature shells of *Schizotreta*, the oldest orbiculoideid, are also in close-packed bands giving way to radial arrays but, despite being about three times as big as those of *Orbiculoidea*, were not similarly composed of casts of smaller spheroids.

PATERINATE JUVENILE SHELL

The paterinate juvenile shell is well defined by a raised border homologous with the lingulide lamellar ring (Fig. 1568). Its microtopography is variable, being mainly tuberculate (as in *Micromitra*) but is also indented with hemispherical imprints (*Askepasma*) or is featureless apart from wrinkling (*Dictyonites*).

The tubercles of *Micromitra* are arranged in open hexagonal arrays that become more sporadically distributed before dying out on the brephic growth band. They are hemispherical in the undeformed state, with diameters of 4.5–6 µm and have cores of apatitic spherules (Fig. 1568).

The hexagonally packed imprints of *Askepasma* indent the entire external surface, including the juvenile shell where they differ only in being less regularly distributed as a result of rheomorphic wrinkling (Fig. 1569). The imprints, approximately 7 µm in diameter, are bounded by rounded walls and are very rarely covered by gently convex, striated covers that are possibly phosphatized remnants of an original coat. Eight to thirteen apatitic domes, approximately 600 nm in diameter, are commonly found hexagonally arranged on the hemispherical floors. *In vivo*, the imprints and their substrate acted as an integrated rheological sheet so that the hexagonal arrangement of pits was deformed by changes in shell shape and became shallow or aborted on raised fila.

ORIGIN OF IMPRINTS ON LINGULIFORM JUVENILE SHELLS

Until the discovery of the flat-based impressions made by siliceous tablets on the juvenile shells of living discinids, all imprints on fossil linguliforms were interpreted as having been made by vesicles in the periostracal infrastructure (Williams, 1997, p. 269). A reappraisal of such imprints, however, suggests that they are the casts of four kinds of superficial, mineralized as well as organic, bodies (Williams, 2003).

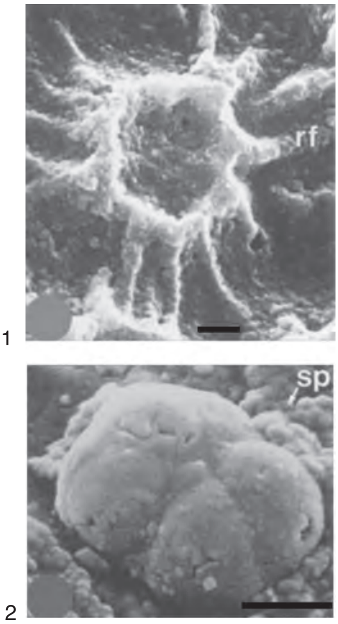


Fig. 1567. *1*, SEMs of pit on shell exterior of Lower Carboniferous *Orbiculoidea nitida,* England, showing composite nature of pit and raised substrate with radiating folds (*rf*); scale bar: 1 µm; *2*, internal view of imprint of composite vesicle in spherular (*sp*) primary layer of *Roemerella*; scale bar: 1 µm (Williams, Cusack, & Buckman, 1998).

Flat-based circular imprints indent the juvenile shells of many acrotretides and lingulide paterulids and acrotheloids. The diameter of imprints tended to vary only

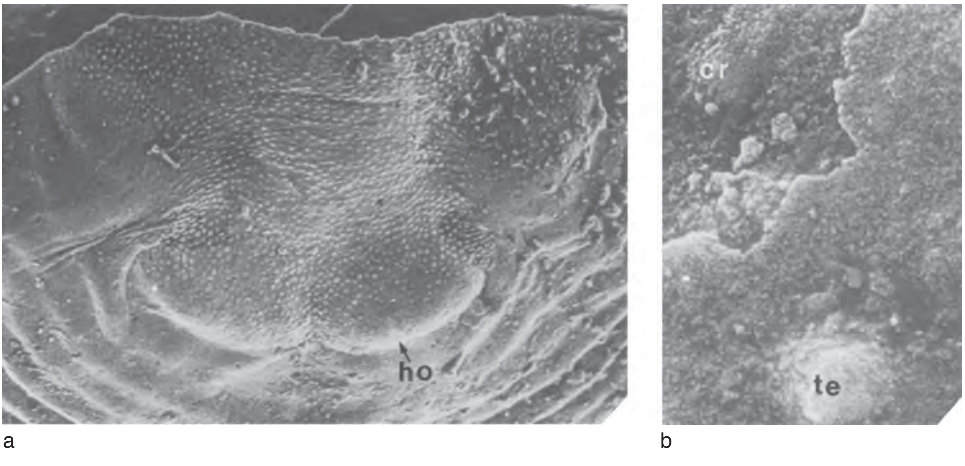


Fig. 1568. *Micromitra* sp. cf. *ornatella* (Linnarsson), Sosiuk Formation, Middle Cambrian, Turkey; *a,* tuberculate exterior of larval dorsal valve delineated by lobate halo (*ho*), ×180; *b*, detail of exfoliated tubercles (*te*) with solid cores (*cr*), ×4800 (Williams & others, 1998).

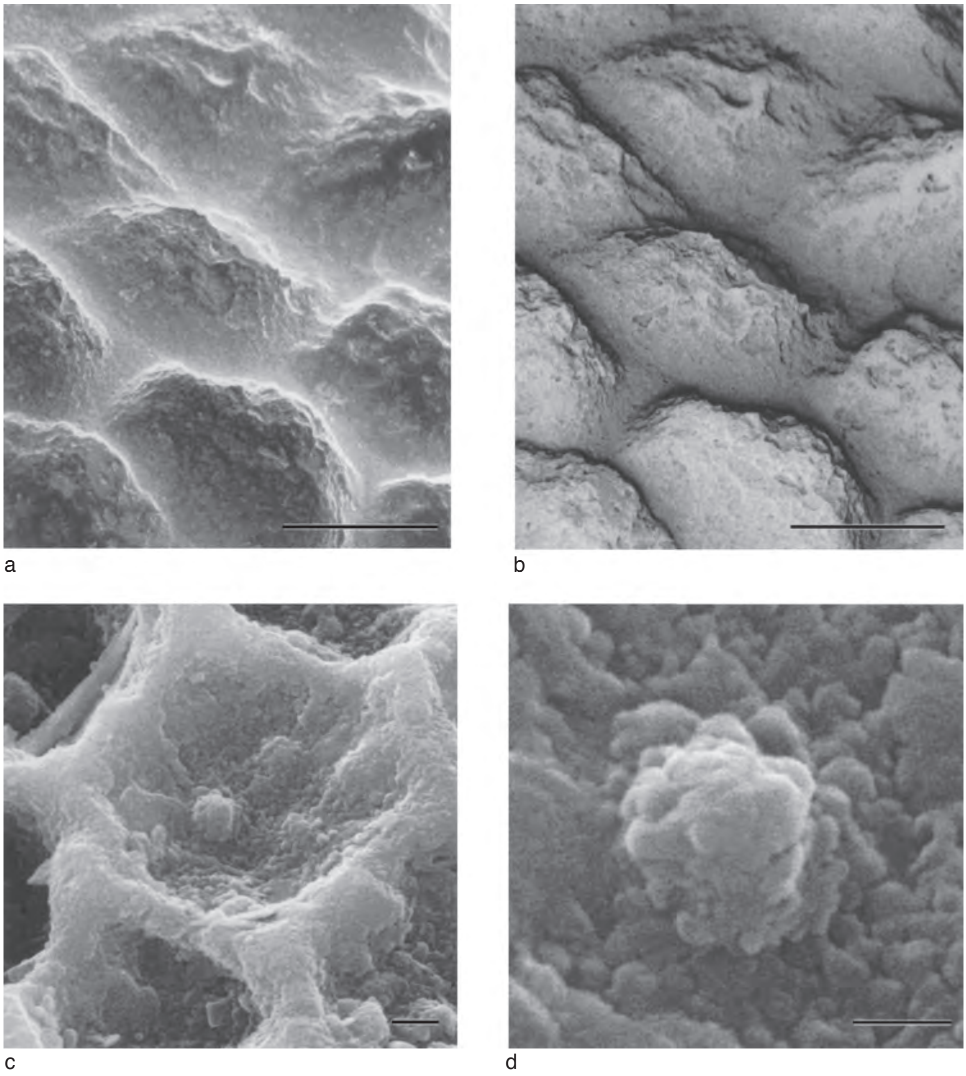


FIG. 1569. Hexagonally packed imprints on external surface of *Askepasma toddense* LAURIE, Todd River Dolomite, Australia, Lower Cambrian; *a–b*, general and inverted views; scale bars: 20 µm; *c–d,* view of single imprint with detail of dome composed of spherular apatite; scale bars: 1 µm and 0.5 µm respectively (new).

during shell growth in species but differ significantly among genera. The basic arrangement of imprints is a single-layered, close-packed hexagonal array, although some imprints are disordered as in *Opsiconidion* where they form clustered successions. Notwithstanding these differences in size and arrangement, evidence favors the imprints as casts of mineralized tablets. The finely textured surfaces of imprints and their constancy of shape suggest that they were membrane-bound discoidal tablets, assembled intracellularly. The chemicostructure of the tablets, as ordered mineral aggregates in an organic matrix, would account for the constant shape and thickness of imprints. The tablets would generally have been up to six times thicker than discinid siliceous rhombs, which would explain the better, more widespread preservation of their imprints.

No remnants of these postulated tablets have yet been found so that their composition is also a conjecture. In that respect, the fact that tablets have never been seen is the prime clue to their likely composition. Three factors militate against the survival of tablets on specimens prepared for ultrastructural studies. The glycocalyx covering mosaics and the membranes enclosing such tablets would have quickly degraded during the life of individuals (as in discinids) thereby facilitating the shedding of tablets during fossilization. Acrotretide and *Paterula* tablets, however, would have been virtually immersed in a rheological primary layer that, on phosphatization, frequently formed flaps over discoidal rims that should have been strong enough to trap some tablets. Of course, tablets would have been prone to degradation during fossilization but that would depend on their mineral composition. In the zhanatellid *Wahwahlingula*, for example, apatitic discoids are preserved within tightly folded imprints of the primary layer. Yet the mosaics of *Opsiconidion* that must have been sporadically stacked in clusters of five or so, deeply embedded in the primary layer of the shell, are now all represented by discoidal cavities beneath superficial imprints. This suggests that the mineral components of *Opsiconidion* tablets decomposed as completely as their organic matrix during fossilization.

Survival of tablets could also have been jeopardized by the way linguliform shells are dissolved out of rock for study. The structures exposed on rock matrix by the partial exfoliation of the first-formed shell of *Paterula* (Fig. 1563) were, therefore, noteworthy. The shallow, flat-based, circular cavities impressed on the mudstone could only have been the imprints of the external surfaces of discoidal tablets. Unlike its apatitic substrate, the primary layer, the mosaic of the first-formed shell of *Paterula* must have been composed of tablets that degraded mineralogically as well as organically during fossilization. The same assumptions can be made about the circular, flat-based cavities indenting the encrusting surface of *Eoconulus* (Fig. 1561). The adhesive periostracum of *Eoconulus* would have acted as a protective coat during fossilization, and the contents of the cavities could have been dissolved during the extraction of specimens of rock matrix.

The mineral components of living brachiopod skeletons consist almost exclusively of calcium fluorapatite (LEGEROS & others, 1985), calcium carbonate as calcite (JOPE, 1965, p. 158), and silica (WILLIAMS, CUSACK, & others, 1998, p. 2095). JOPE (1965) also reported traces of $FePO_4$, $MgCO_3$, and Fe_2O. If one of the three dominant minerals had been the sole inorganic constituent of the inferred tablets imprinted on the shells of acrotretides, acrotheloids, and paterulids, it is most likely to have been calcite (or aragonite; Fig. 1559), because apatitic tablets are still preserved and siliceous tablets still retained their rhombic shape in Paleozoic obolids and discinids respectively.

Apart from differing in shape, hemispherical imprints are also significantly smaller than discoidal ones. Structurally, however, they are similar in being unaffected by rheomorphic changes in the primary layer and were probably made by membrane-bound mineralized spheroids. Discoidal and hemispheroidal imprints are mutually exclusive in acrotretides but occur together in some acrotheloid shells, like that of *Acrothele* (which seems also to have been impressed by proteinaceous vesicles described below). Accordingly, the spheroids are assumed also to have been composed of calcitic granules in a proteinaceous matrix (Fig. 1559).

There are two other kinds of imprints that, being deformable to the same degree as their rheomorphic substrates, were probably made by organic bodies. The small, cylindroid to shallow, basinal depressions indenting the walls and interspaces of significantly larger imprints may coalesce into compound structures. Their lack of rigidity suggests they are casts of mucinous vesicles, secreted simultaneously with larger membrane-bound crystalline or organic structures.

The large (approximately 3–8 µm) pits, indenting the mature as well as the juvenile shell of many lingulides, are variably deformable in a manner suggesting that they are all casts of organic vesicles with differentially thickened bounding membranes. As they were probably an integral part of the periostracal infrastructure, they could have been analogous with the empty vesicles with glycoproteinaceous coats up to 250 nm thick found in the terebratulide periostracum (WILLIAMS & others, 1997, p. 15). The vesicles with thin membranes would have been deformed to the same extent as their rheological substrate (*Wahwahlingula*, *Obolus*), whereas those that retained their original shape (*Rowellella,* orbiculoideids) had thick coats. A repaired valve of *Wahwahlingula* confirmed that exocytosis of such vesicles was confined to the outer mantle lobe, whereas apatitic tablets were secreted immediately beneath the infrastructural boundary of the periostracum (CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 810).

The bodies that made the hemispherical imprints on the shells of such paterinates as *Askepasma* were also deformable and presumably organic in composition. They were, however, indented by pits represented by apatitic domelike casts, commonly arranged hexagonally on the floors and sides of imprints. The bodies are, therefore, unlikely to have been vesicles, but were possibly thornlike chitinous structures anchored within the imprints by fibrillar tissue occupying the pits.

CRANIIFORM JUVENILE SHELLS

Information about the chemicostructure of the juvenile shell of living craniiforms is meager and concerned exclusively with the dorsal valve of the lecithotrophic *Novocrania*. The first-formed dorsal valve is simultaneously secreted as a complete cover, approximately 100 µm in diameter, by an epithelial collective differentiated six days after fertilization (NIELSEN, 1991, p. 15; Fig. 1570). The rudimentary periostracum is little more than a cuticular film because a granular and platy calcitic coat is discernible below this substrate (NIELSEN, 1991, fig. 15B). By the eighth day after fertilization, when the dorsal valve is more than approximately 200 µm in diameter, a radially ribbed, brephic shell has been secreted holoperipherally around the first-formed shell (NIELSEN, 1991, fig. 15C). This differentiation of the juvenile dorsal valve of living *Novocrania* accords with that found on well-preserved beaks of more mature valves. The diameter of the juvenile valve is variable (up to 300 µm), and the first-formed and brephic parts are not always clearly distinguishable (Fig. 1571). The calcitic units secreted on the rudimentary periostracum of the first-formed valve are granular aggregates and rhombs 90–190 nm in size, while those of the brephic valve are finely laminar on a nanometric scale. Some of the radial ribbing figured by NIELSEN (Fig. 1570) represents the edges of laminae; others could be the beginning of slats found in the primary layer (CUSACK & WILLIAMS, 2001a, p. 882).

The several phases of recrystallization that affected most pre-Cenozoic craniids have obliterated the fine structure of juvenile shells preserved at the beaks of dorsal valves but not their micromorphology. Thus, FREEMAN and LUNDELIUS (1999) have argued

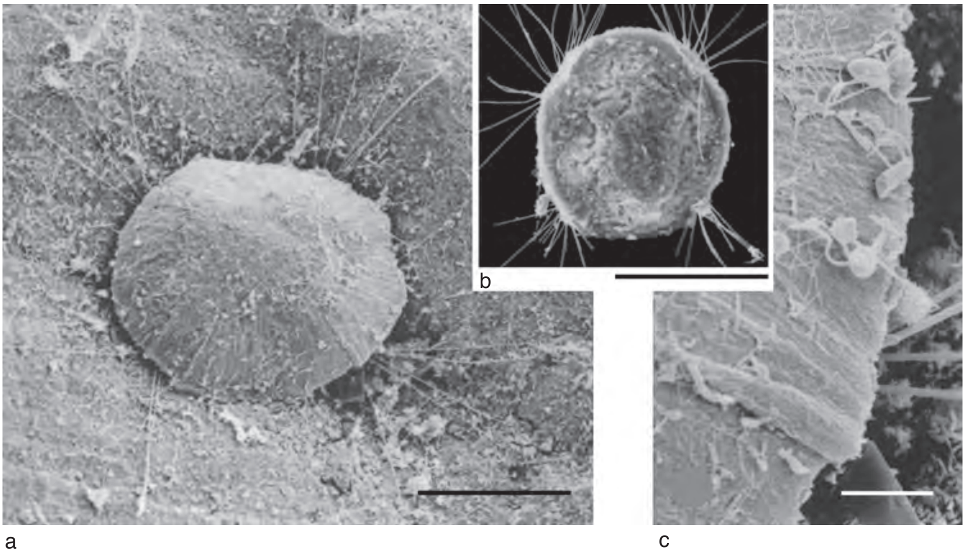


FIG. 1570. Metamorphosis of larva of *Crania*; *a*, brachial valve has reached periphery of body and pushed larval setae to sides; *b*, juvenile about three days after settling; *c*, detail of valve edge; scale bars 100 µm, 100 µm, and 10 µm respectively (Nielsen, 1991).

that the onset of growth banding (comparable with the lamellar ring) indicates that craniids were variably planktotrophic as late as the Tertiary. These aspects of fossilization characterize the juvenile shells of the Ordovician, free-lying *Orthisocrania,* which with *Pseudocrania* is assumed to represent the sister group of the contemporaneous attached craniid, *Petrocrania*. Both juvenile valves of *Orthisocrania* are delineated by growth banding as convex semiellipsoids up to 700 µm or so long (Fig. 1572). They are recrystallized but with hints of stratified lamination on their sides. The surface of one juvenile ventral valve is indented by a narrow imprint suggesting that the shell had been temporarily attached to a cylindroid substrate, presumably by cementation, as there are no traces of a pedicle opening. Otherwise, the juvenile shell of the earliest known craniids was similar to those of living species.

RHYNCHONELLIFORM JUVENILE SHELLS

Knowledge of the development of the first-formed shell of living rhynchonelliforms is limited to studies by STRICKER and REED (1985a, 1985b) of lecithotrophic juveniles of *Terebratalia*. The first-formed shell (the protegulum of STRICKER & REED) is secreted within the first day after metamorphosis. It consists of a nonhinged, bivalve structure with the ventral valve approximately 160 µm wide (STRICKER & REED, 1985b, p. 299). Each valve, which is wrinkled and lacks growth banding, is secreted simultaneously by the epithelial collective and consists

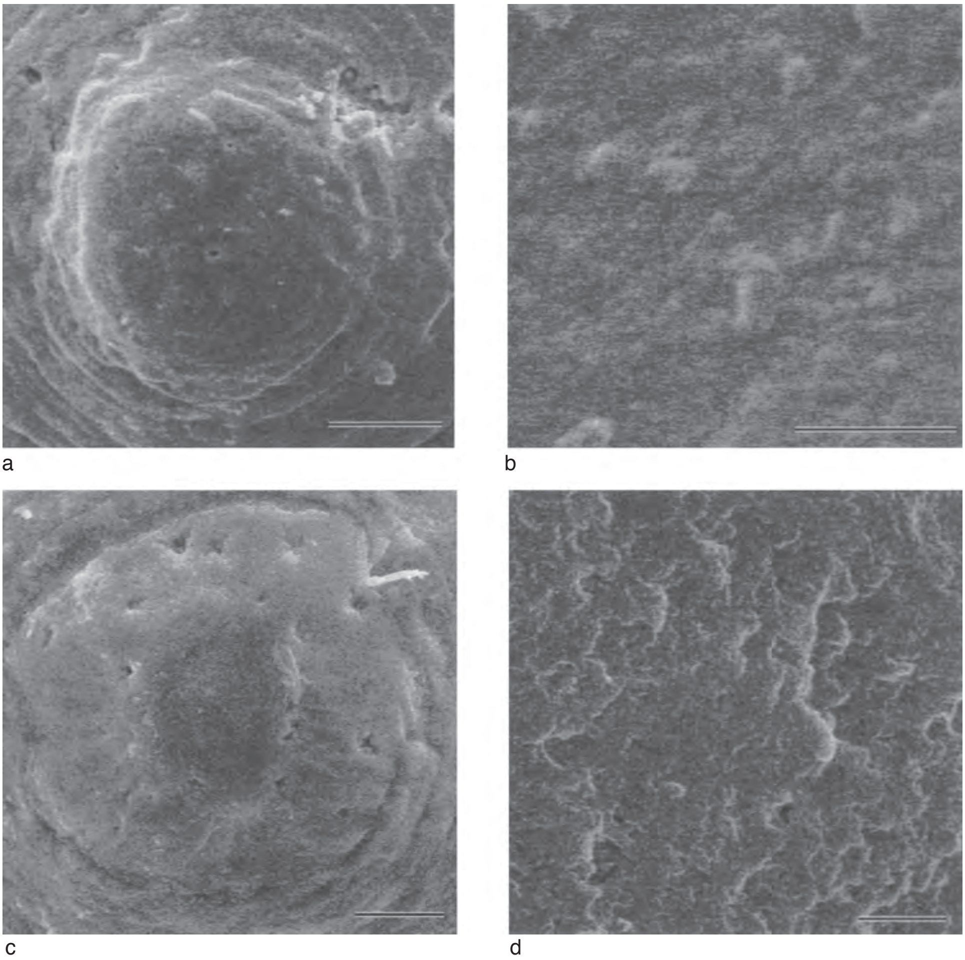


FIG. 1571. Two juvenile dorsal valves of Recent *Novocrania anomala* (MÜLLER), Oban, Scotland; *a–b,* poorly differentiated but well-preserved valve with textural detail of granular aggregates and rhombs of first-formed valve; scale bars: 100 µm and 0.5 µm respectively; *c–d,* well-differentiated first-formed and brephic shell with traces of radial ribbing and textural detail of finely laminar brephic shell; scale bars: 50 µm and 1 µm respectively (new).

of a rudimentary periostracum devoid of superstructures, which acts as a substrate for a coat of granules approximately 100 nm in size aggregating into monolayers of spherules and rhombs (Fig. 1573). The coat is calcitic (STRICKER & REED, 1985b; Fig. 1574). Valve surfaces are indented by close-packed, circular, shallow depressions approximately 1 µm in diameter (STRICKER & REED, 1985a, p. 266). Their origin is unknown as dimpling by dehydration on such a well-ordered scale is unlikely. They may be casts of mucinous droplets accumulating between a transient glycocalyx and the polymerizing periostracal rudiment.

An interesting aspect of the studies by STRICKER and REED (1985a, 1985b) is the abrupt change identified by them in the secretion of the brephic shell. On the fourth day after metamorphosis, secretion of the first-formed shell is followed abruptly by the deposition of the primary and secondary layers of the brephic shell, which "occurs more or less simultaneously throughout the

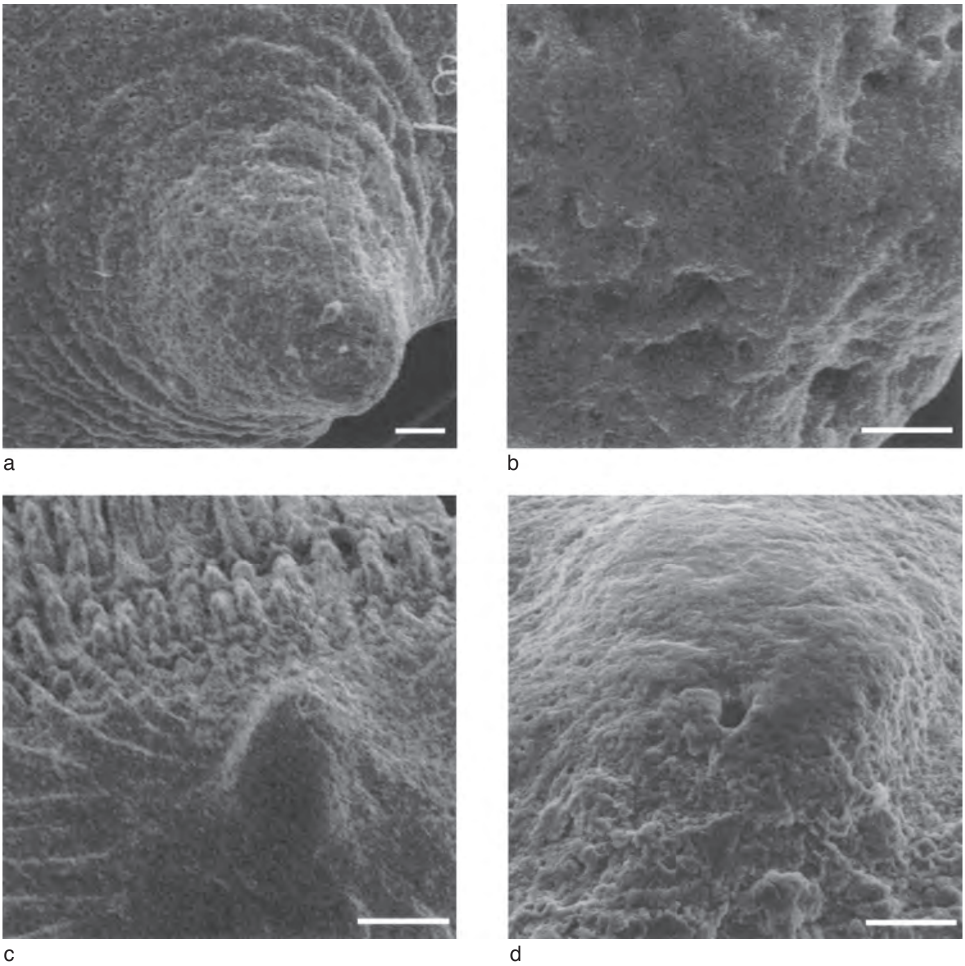


FIG. 1572. Juvenile shell of *Orthisocrania depressa* (VON EICHWALD), Ordovician, Grjazno Formation, St. Petersburg, Russia, lower Caradoc; *a–b*, juvenile ventral valve with surface detail of first-formed shell; scale bars: 100 µm and 25 µm respectively; *c–d,* juvenile dorsal valve with surface detail of first-formed shell; scale bars: 500 µm and 100 µm respectively (new).

epithelium" (STRICKER & REED, 1985a, p. 270) underlying the first-formed shell. Such a change is comparable with that affecting the secretory regime in the ontogeny of living discinids.

No microornament has been found on the first-formed shells of a sample of other living species, including another terebratulide (*Terebratulina*), a rhynchonellide (*Notosaria*), and a thecideide. Given the biological and ecological range of this sample, it is unlikely that the absence of pits is due to exfoliation or some such factor. Carbonate substrates do serve as casting materials, as is confirmed by the presence of sporadic, shallow depressions less than a micron in diameter preserved on the mature shells of the rhynchonellide *Frieleia* and presumably made by mucinous vesicles within the periostracal infrastructure. Accordingly, the pits on the first-formed shell of *Terebratalia* could be a generic feature.

The first-formed shells of extinct rhynchonelliforms are likely to have been secreted by planktootrophic larvae (FREEMAN & LUNDELIUS, 2005. Their surface features are poorly known but no microscopic imprints on them

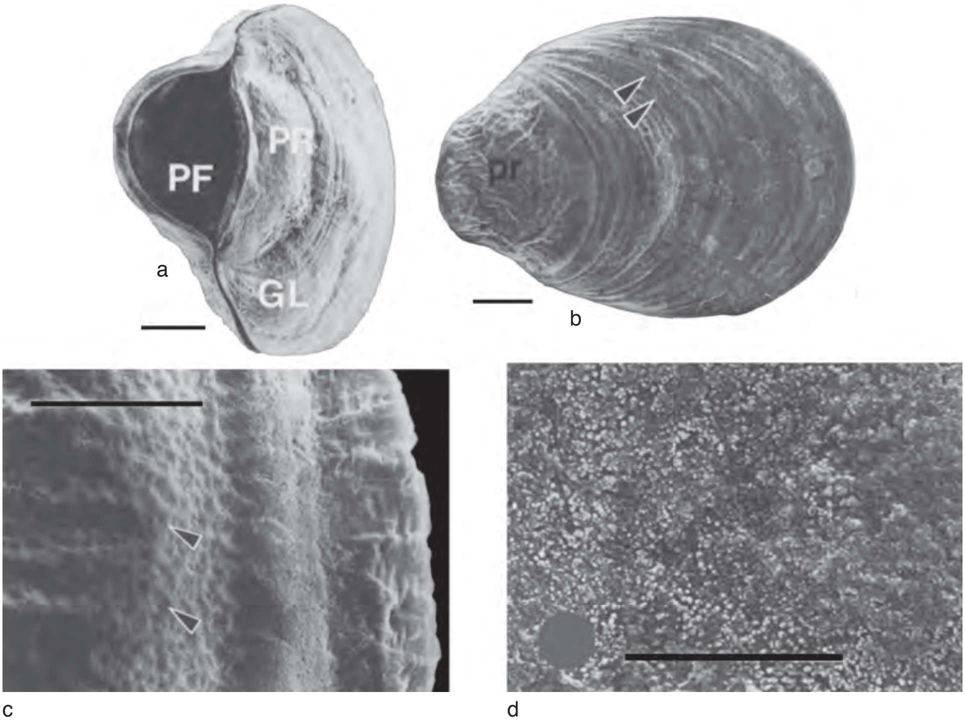


FIG. 1573. SEM of posterior end of juvenile *Terebratalia transversa* shell at *a,* 11 days postmetamorphosis; protegulum (*PR*) is visible at posterior end of shell, and concentrically arranged growth lines (*GL*) occur anterior to protegulum; posterior fenestration (*PF*) between two valves represents hole through which pedicle protrudes; scale bar: 50 µm (Stricker & Reed, 1985b); *b*, external surface of juvenile shell at 23 days postmetamorphosis; note protegulum at posterior end of shell; *double arrowheads* mark concentrically arranged growth lines resulting from periodic accretions of juvenile shell material; scale bar: 50 µm; *c*, outer surface of protegulum with numerous small indentations (*arrowheads*); scale bar: 10 µm; *d*, inner surface of protegulum at 1 day postmetamorphosis; scale bar: 5 µm (Stricker & Reed, 1985a).

have been reported, and it is unlikely that any inherent differences in their fabric would have survived fossilization.

DIVERSITY OF THE BRACHIOPOD JUVENILE SHELL

A comparative study of the juvenile shell throughout brachiopod phylogeny reveals a chemicostructural and micromorphological diversity that has always been greater in the organophosphatic linguliforms than in the organocarbonate craniiforms and rhynchonelliforms. In contrast, the progression of shell secretion during ontogeny seems to be the same, at least in living lingulates and rhynchonellates, with a discontinuity in the deposition of juvenile and mature skeletal successions. Several assumptions on the evolution of brachiopod secretory regimes can be drawn from these ontogenetic and phylogenetic differences. They are best presented by comparing skeletal successions with a standard secretory regime (Fig. 1575) with the rudimentary periostracum or cuticle as a reference layer separating superstructural and infrastructural features (WILLIAMS & others, 1997, p. 16).

Most of the diversity of the juvenile linguliform shell is related to the development of various superstructural features. The protegulum and siliceous tablets of living lingulids and discinids respectively are secreted with the glycocalyx serving as a substrate. The folded protegulum represents the first-formed lingulid shell. It follows therefore that the brephic shell is the pair of discrete

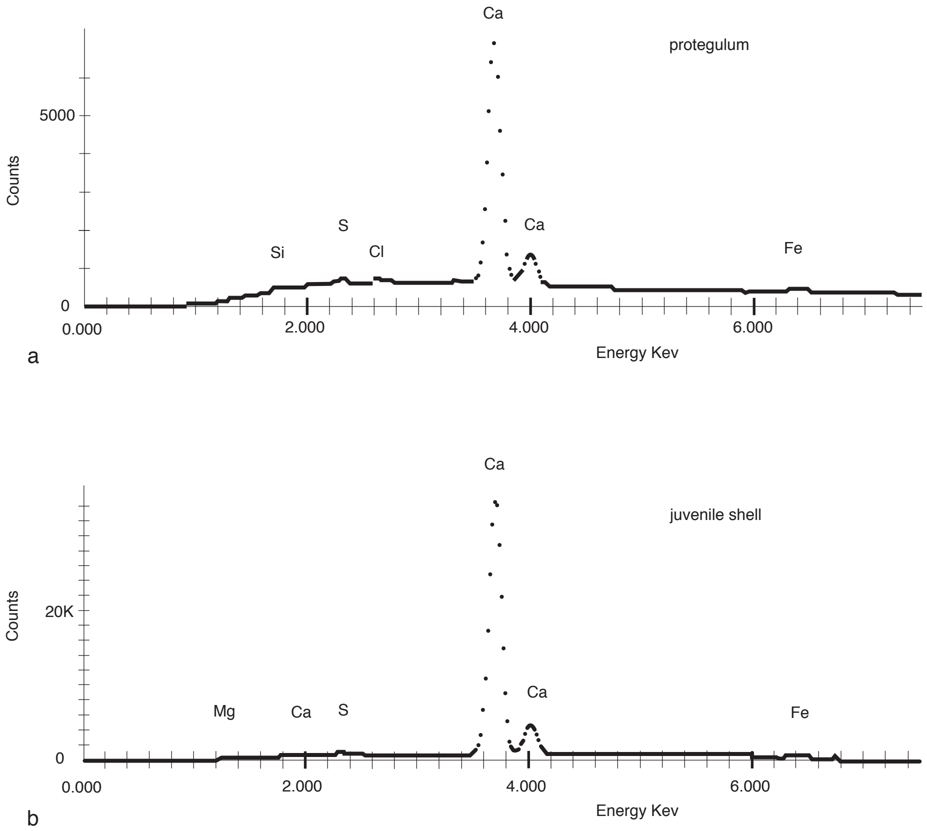


FIG. 1574. Qualitative electron microprobe analysis of elemental composition of protegulum (*a*) and a 23-day-old juvenile shell (*b*); *Ca,* calcium; *Cl,* chlorine; *Fe,* iron; *Mg,* magnesium; *Si,* silicon; *S,* sulfur; *Counts*, total counts detected during a 10 min. accumulation; *Energy Kev*, energy of X-ray (Stricker & Reed, 1985b).

valves secreted beneath and beyond the protegulum to the bounding lamellar ring. These valves appear to be composed largely, if not entirely, of a periostracal cuticle; but further study is needed to determine whether the onset of apatitic secretion coincides with the initial growth of the mature shell. If it does, the primary layer of the mature shell is the first mineralized lamination within the skeletal succession of living lingulids. This was not necessarily so in Paleozoic lingulids and many other extinct linguloids, which lacked protegula (BALINSKI, 1997) but had discrete, mineralized juvenile valves *ab initio*. It is therefore possible that these juvenile shells had an infrastructural apatitic layer that ceased being secreted in post-Paleozoic lingulids. The assumption is in accord with evidence that since the Carboniferous, the shell of *Lingula* (*s.l.*) has been undergoing a decalcification of its skeletal secretory regime (EMIG, 1990; CUSACK & WILLIAMS, 1996, p. 48). The juvenile parts of Paleozoic linguloid shells are rarely preserved, however, which suggests that they were not mineralized. In effect, linguloid juvenile shells have always been the same as those of living discinids except for the absence of superstructural mosaics in most species. This is the preferred assumption.

The development of mosaics in juvenile shells has an ambiguous role in postulating linguliform phylogeny based on shell structure. Mosaics have always consisted of a single layer of mineralized tablets (including spheroids) secreted on transient glycocalyces

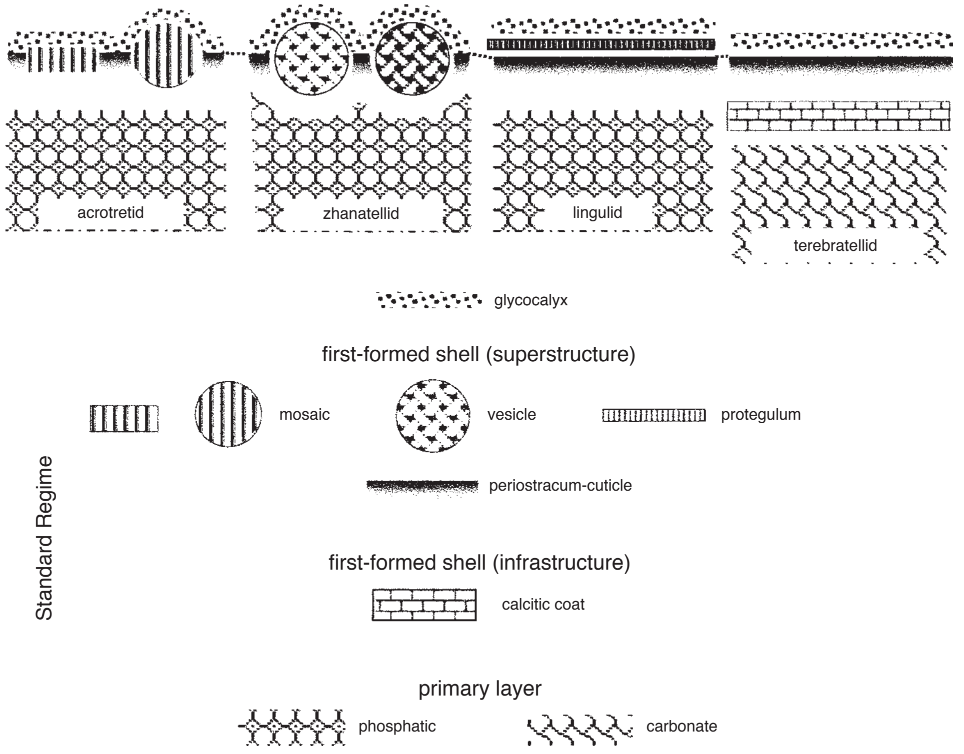


Fig. 1575. Graphical representation of full range of superstructures and infrastructures of brachiopod juvenile shell (standard secretory regime) as secreted relative to a correlated periostracal or cuticular base in four main types of successions (new).

and cemented together by penecontemporaneous exudations of a polymerizing periostracal cuticle as in living discinids. Yet there are two disconcerting aspects to such an extraordinary juvenile, superstructural, secretory regime. The tablets have varied in composition for they are demonstrably siliceous (discinids) and apatitic (arguably infrastructural in zhanatelids) but were inferentially calcitic in acrotretides and some lingulides. Morever, even if the mosaics of lingulide acrotheloids are plesiomorphously linked with those of acrotretides, the inferred calcitic mosaics of linguloid paterulids and siliceous mosaics of discinids were secreted by independently activated regimes.

Homoplasy also obscures relationships among lingulides with vesicular imprints. Apart from evidence that vesicles originally differed at least in the thickness and rigidity of their coats, their imprints on mature parts of shells indicate that they were constituents of fully developed periostraca and had been secreted by the vesicular cells of the outer mantle lobes (as in the zhanatellid, *Wahwahlingula*). According to this interpretation, the collective responsible for the secretion of a vesicular juvenile shell would have been cytologically homologous with those in the mature outer mantle lobe. It is, therefore, a moot point whether juvenile vesicles were secreted with the periostracum acting as a penecontemporaneous cement. We prefer this interpretation (Fig. 1572) and assume that such shells were nodular *in vivo*.

The deformable imprints of paterinates are unique among the Brachiopoda. They are unlikely to have been made by vesicles, but the conjecture (see p. 2418 herein) that they accommodated thornlike structures with basal pits occupied by fibrils is just one of several possible interpretations.

The infrastructural secretion of the first-formed shells of living craniids and terebratulides is not in phase with the superstructural secretion of lingulate mosaics (Fig. 1575). Secretion of mosaics continues during growth of the brephic shell of discinids until the planktotrophic larvae settle. Secretion of the infrastructural first-formed shell does not continue during the brephic shell growth of craniids and terebratulides but ceases as the lecithotrophic larvae settle. Accordingly it seems that the partition of shell secretion during ontogeny into two distinct regimes coincides with a change from a planktonic to a benthic mode of life. There then remains the possibility that chemicostructural differences between juvenile and mature shells reflect different functions of the respective mineralized covers during mobile and sedentary modes of life.

MATURE SHELL OF BRACHIOPODS

INTRODUCTION

The mature brachiopod shell is that part of the integument secreted by the mantle, a fold of epithelium that is first differentiated during brephic growth. The fold is marginally indented by a circumferential periostracal groove separating the outer, skeleton-secreting and inner, ciliated, epithelial sheets (WILLIAMS & others, 1997, p. 9). The outer epithelium secretes the periostracum, which is succeeded inwardly by the mineralized primary, secondary, and rare tertiary layers (WILLIAMS, 1997, p. 267). The diversity of mantle and shells has been extensively described in Volume 1. New data include: a more precise correlation of periostracal successions; a better understanding of the basic, mineral units of organophosphatic and organocarbonate shells, especially unit aggregation in relation to associated organic constituents; and a clearer picture of the origin and evolution of many shell textures. Apart from the ever-present periostracum and primary mineralized layer, there are three fabrics of the secondary mineralized shell to be considered: organophosphatic stratiform, organocarbonate tabular laminar, and organocarbonate fibrous. They will be reviewed in that order.

PERIOSTRACUM

The term periostracum has always been used for the outermost coat of the brachiopod shell, which can be up to 100 µm thick and is entirely organic in most species (WILLIAMS & others, 1997, p. 12). The organic constituents are varied and universally include polysaccharides and proteins according to standard staining techniques. β-chitin, however, has a restricted distribution. It is identifiable by Pyrolysis MS in the periostraca of living linguliforms, but there are no traces of it in the periostraca (or even the shells) of representative living craniiforms and rhynchonelliforms (WILLIAMS, LÜTER, & CUSACK, 2001).

The periostracum may also be multilayered, and confusion can arise when attempting to correlate different periostracal successions. Confusion is minimized by recognizing a bilamellar or electron-dense sheet separating superstructural and infrastructural features as a datum horizon (periostracal substratum). The substratum, up to 20 nm or so thick, is always present, being the first constituent of the periostracum to be secreted. It serves therefore as a substrate for both superstructural and infrastructural features. Recent studies of the tripartite periostracum of living lingulides have shown that it has a dual origin. The concentric, scalloped ridges forming the superstructure of the discinid periostracum (Fig. 1576f) consists of up to 100 or more, well-ordered fibrillar sheets disposed almost parallel with the periostracal substratum (WILLIAMS & others, 1997, p. 102; Fig. 1576a–c). The ridges, which are separated from one another by flat zones of several sheets, are commonly corrugated into dark and light strips approximately 80 nm wide and orthogonal to the substratum. The origin of this superstructure is revealed at and near the junction between the outer, nonciliated inner epithelium and the inner, vesicular epithelium of the inner and outer mantle lobes respectively (Fig. 1576a–b). Here fibrils, probably chitinous, are spun out from the inner epithelium and fabricated by microvilli into sheets that are constantly applied to the substratum, originating as a secretory product of the vesicular cells at the hinge (Fig. 1576b, 1576d–e). The sheets are fashioned into concentric ridges by rhythmic contractions of the microvilli. This dual system of secretion also accounts for the formation of the pellicle that is loosely connected to the substratum of lingulids. In *Glottidia*, for example, the pellicle is a compacted sheet of fibrils secreted by the microvilli of the inner epithelium and exceptionally bears imprints of the microvillous tips (Fig. 1577). In effect, the superstructures of mature periostraca of all brachiopods are secreted by nonciliated epithelium of the inner mantle lobe and the periostracal substratum and infrastructures by the lobate or vesicular cells of the outer mantle lobe. This dual system of secretion is at variance with the correlation of periostracal successions shown in figure 9 of Volume 1 (WILLIAMS & others, 1997, p. 16; an amended version is given herein (Fig. 1578).

Evidence for a dual secretion of the periostracum also helps to clarify the sources of imprints on both juvenile and mature shell surfaces of some lingulides (like zhanatellids) and paterinates (*Askepasma*). Assuming that the juvenile cuticle correlates with the periostracal substratum, the vesicles that made such imprints could not have been secreted by an inner epithelial collective overlying the juvenile shell and must have been infrastructural in origin.

ORGANOPHOSPHATIC SHELL

In Volume 1, the stratiform nature of the organophosphatic shell was described, as were its basic constituents, granular fluorapatite in diverse aggregations, and various intercrystalline and paracrystalline polymers, notably proteins, GAGs, and β-chitin. Emphasis was given to reconciling previous chemicostructural studies that had described and interpreted the stratiform, laminar successions in conflicting ways. The rheological properties of the primary layer were characterized. The rhythmic nature of most of the laminar sets of the secondary layer was clarified, and a standard terminology was proposed, based on the laminar successions of the living *Lingula* shell. Several fabrics were also described, including those of extinct groups. More recent investigations have afforded not only new information in all these different fields but also a feasible phylogeny for the more important fabrics. Such advances are described below, first with respect to the rheological properties of the primary layer and the canaliculate system characterizing most lingulates. This is followed by a review of new data on the fabrication of the basic constituents, especially in baculate, virgose, and columnar laminar sets, before dealing with the more problematic fabrics.

The primary layer is the initial coat of biominerals laid down on the periostracum as a foundation for the more elaborate fabrics of the secondary shell. Its rheological properties are such that the layer can be deformed by concentric folds (fila) and lamellose extensions without developing planes of disruption within the secondary layer. These surface ornamentations are common features of linguliforms, and their development

FIG. 1576. Secretion, structure, and morphology of mature periostracum of Recent *Discinisca* sp. cf. *tenuis* (SOWERBY), Swakopmund, Namibia; scalloped ridges (*sr*) constituting superstructure (view *f*) consist of fibrillar sheets (views *a–c*) secreted by microvilli (*ms*) of inner epithelium (*ie*) (views *a*, *d–e*) on periostracal substratum (*pe*) (view *c*) that originates as a secreted layer of vesicular cells (*vr*) at hinge of inner and outer mantle lobes (views *a–b*); scale bars: 300 nm, 200 nm, 100 nm, 200 nm, 100 nm, and 1 µm (new).

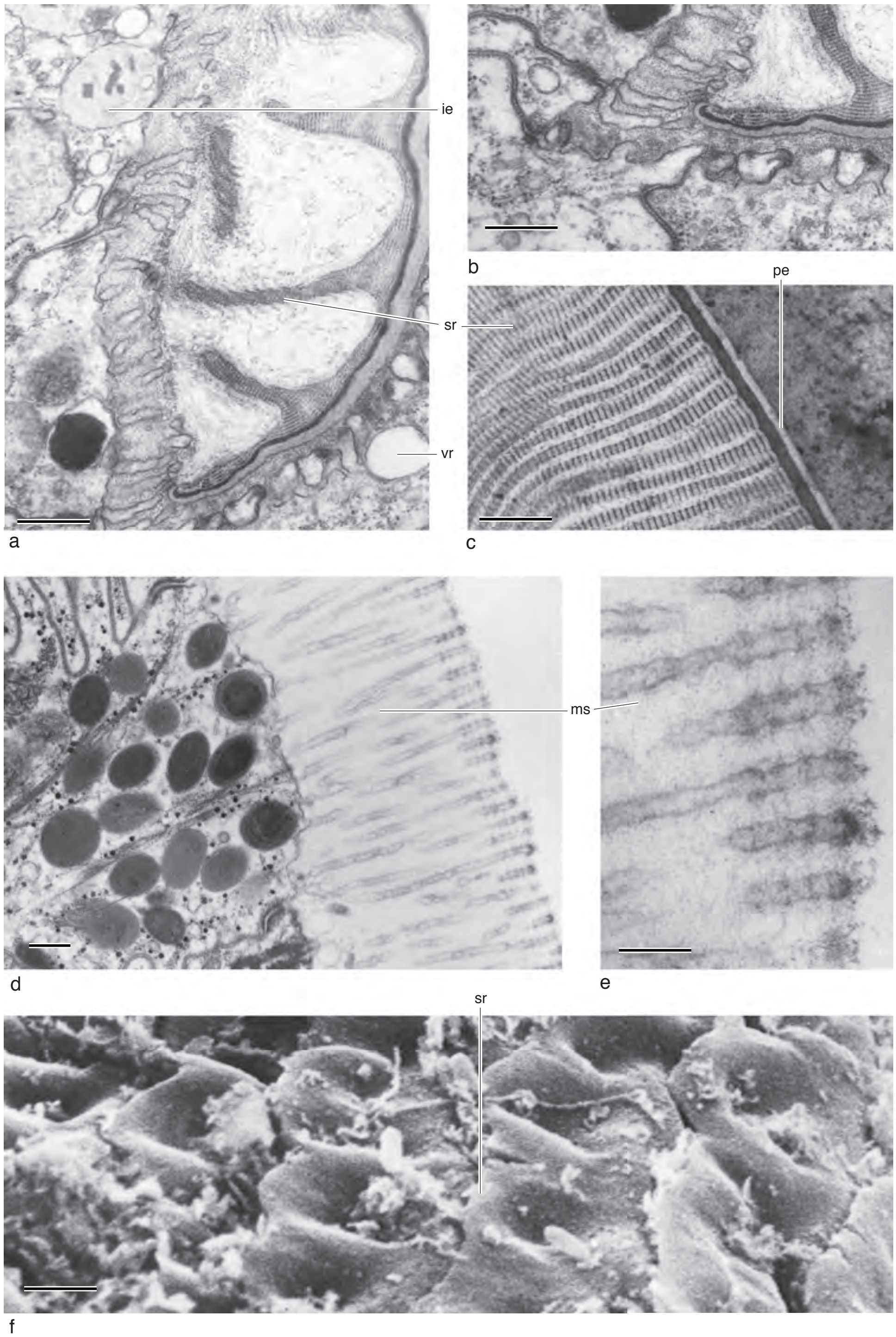


FIG. 1576. *For explanation, see facing page.*

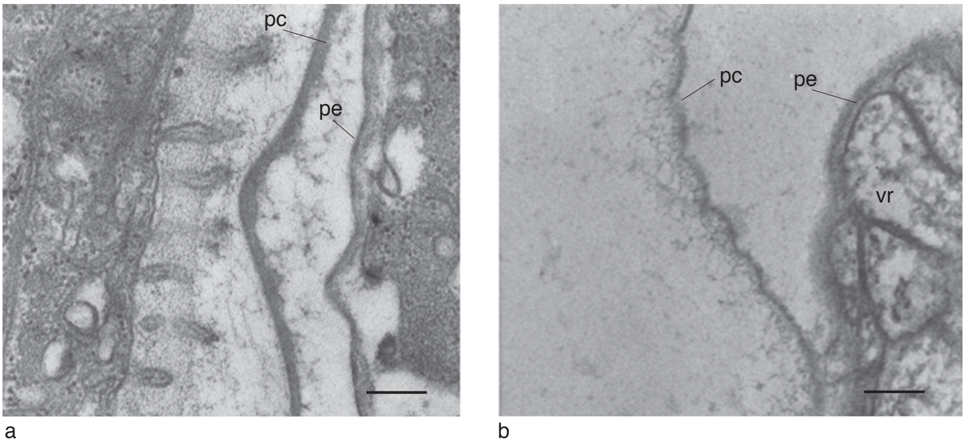


FIG. 1577. Two TEM sections of near proximal sectors of periostracal groove of *Glottidia pyramidata* (STIMPSON) (see fig. 7 in WILLIAMS & others, 1997) showing *a,* pellicle (*pc*), bearing imprints of secreting microvilli of inner epithelium (*pe*) in *b*, in relation to periostracal substratum (*pe*) secreted by vesicular cells (*vr*); scale bars: 100 nm (new).

has been studied in *Discinisca* (WILLIAMS, CUSACK, & BRUNTON, 1998, p. 2016).

Lamellae, which may extend for several millimeters beyond the curvature of a valve, are composed of periostracum and primary and outermost secondary layers. On the outer surface of a lamella, a periostracum and primary layer form folds induced by variations in the disposition of the outer mantle lobe and in the rate of shell secretion.

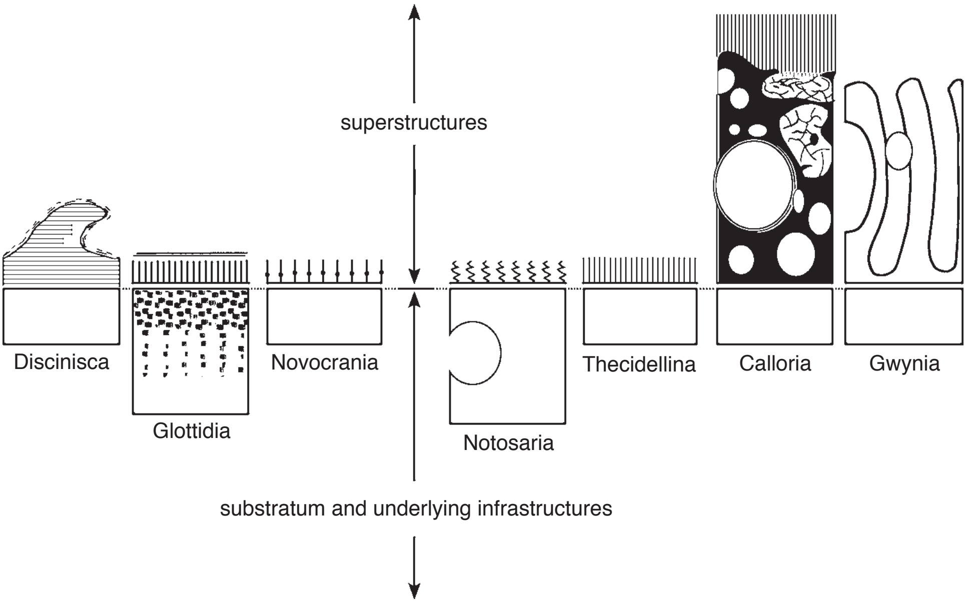


FIG. 1578. Amended version of figure 9 in WILLIAMS and others (1997) showing various stylized brachiopod periostracae correlated in relation to periostracal substrata (*thickened lines*) that serve as a substrate for organic structures secreted by inner epithelium (superstructures) and lobate and vesicular cells of outer mantle lobes (infrastructures) (adapted from Williams & others, 1997).

Immediately internal of a fold (Fig. 1579), a sequence of stratified laminae of the outermost secondary layer splits into two, which diverges within the core of the fold to form a wedge with the primary layer coating its outer face. The wedge is filled by an organic mesh with apatitic spherules deposited by an inframarginal band of the outer mantle lobe simultaneously with the secretion of periostracum and primary layer at the tip of the lobe. This same secretory regime gave rise to even the most conspicuous fila, such as those of *Schizotreta* (see Fig. 1596).

Several folds may develop before a lamellar extension is terminated. The termination is marked by a sudden retraction of the mantle so that no periostracum nor primary layer is deposited along the ledge or on the inner surface of a lamella; and their secretion begins again only when they form the outer coat of the next lamella (Fig. 1579). This process of accelerated forward growth terminated by sudden retraction of the outer mantle lobe is similar to that giving rise to lamellae in organocarbonate-shelled brachiopods (Williams, 1971, p. 61), although no proteinaceous coats covering the inner surfaces of the *Discinisca* lamellae have yet been found.

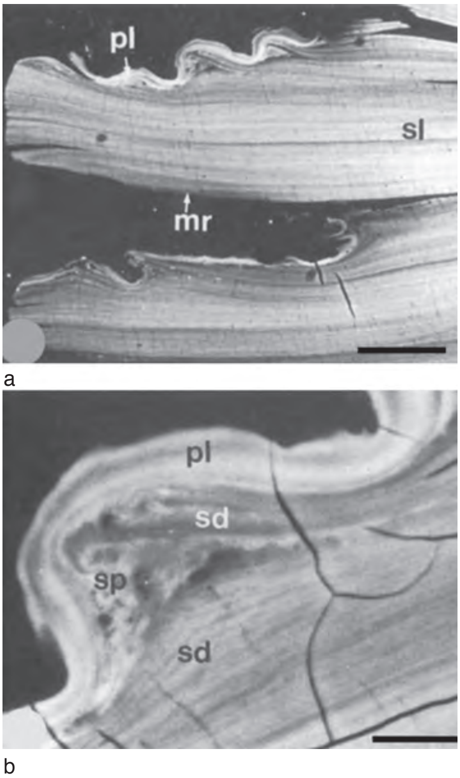


Fig. 1579. Back-scattered electron micrographs of polished vertical resin-impregnated section, treated with bleach, showing concentric lamellae on shell surface of *Discinisca lamellosa; a,* general view of two lamellae with rheomorphic folding of periostracum and primary layer (*pl*) relative to secondary layer (*sl*) and trace of mantle retraction (*mr*); scale bar: 50 µm; *b*, detail of rheomorphic fold showing continuity of periostracum and primary layer (*pl*), divergence of stratified laminae (*sd*) at steep outer face of fold and infill of spherular apatite in organic mesh (*sp*); scale bar: 10 µm (Williams, Cusack, & Buckman, 1998).

CANALS

Canals, originating within the primary layer or at its interface with the secondary layer (Williams, Brunton, & MacKinnon, 1997, p. 343) and orthogonally disposed to lamination, permeate the shells of living lingulids (Williams, Cusack, & Mackay, 1994, p. 251) and discinids (Williams, Cusack, & Brunton, 1998, p. 2013–2015). The two canal systems differ in detail but grow in the same way and are homologous so that the better known discinid canal system can be taken as typical, at least of the lingulides.

In *Discinisca* (Williams, Cusack, & Brunton, 1998), the canals, being approximately 350 nm in diameter, are densely distributed and frequently branch into parallel sets coalescing inwardly, with approximately 20 apertures per 100^2 µm of a dorsal interior. The canals are enmeshed in a chitinous and proteinaceous matrix. Galleries and chambers containing GAGs (Fig. 1580) with apatitic concretions are commonly enlarged around groups of canals. In *Discina* the wall and contents of a canal are secreted simultaneously with the laminar succession perforated by it. They are extruded from the same site on the apical plasmalemma and can usually be traced through several laminar sets in a vertical section (Fig. 1581).

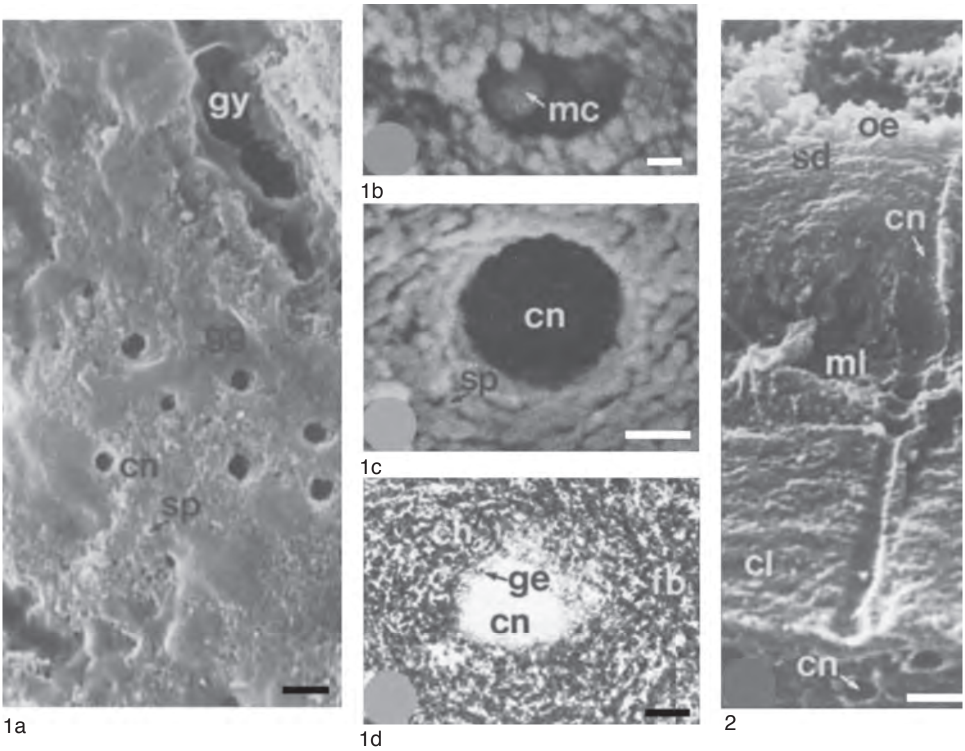


FIG. 1580. Scanning (*1a–c, 2*) and transmission (*1d*) electron micrographs of sections and interiors of *Discinisca tenuis* (*1a–d*) and *Discina striata* (*2*); *1a*, internal surface of spherular apatite (*sp*) and GAGs (*gg*) showing canal openings (*cn*) and galleries (*gy*), treated with buffer; scale bar: 1 µm; *1b*, detail of partly exposed chamber with mosaics (*mc*) in critical-point-dried vertical fracture section; scale bar: 200 nm; *1c–d,* cross sections of canals (*cn*) on internal surface treated with subtilisin and in demineralized rubbly lamina showing spherules (*sp*) and granules (*ge*) of apatite associated with electron-dense and electron-lucent fibrils that are assumed to be actin (*fb*) and chitin (*cn*) respectively; scale bars: 200 nm, 100 nm; *2*, critical-point-dried vertical fracture section of a succession of compact (*cl*), membranous (*ml*), and stratified (*sd*) laminae, secreted by outer epithelium (*oe*) and penetrated by a canal (*cn*); scale bar: 1 µm (Williams, Cusack, & Buckman, 1998).

The site of origin is marked by a lens of electron-dense fibrils and granules with a glycogen-rich cytosol immediately beneath the apical plasmalemma and its overlying recumbent tubular extensions that may be up to five deep. Tubules secreting the shell contain electron-lucent particles and fibrils. They show no signs of having been deflected by growing canal columns, suggesting that they are more or less permanently arranged into a flexible ring about the secretory site of a canal.

A typical canal has two structural aspects dependent on the composition of the surrounding laminae (Fig. 1580). In mineralized laminae, a canal is relatively narrow with a diameter of approximately 200 nm. Externally its membranous wall bears apatitic spherules and internally fibrils and rare spherules. The contents of a canal are also membrane bound and divided into unequal segments by perforated, transverse partitions (compare the partitions in *Lingula;* WILLIAMS & others, 1997, fig. 38, p. 44). In a predominately organic lamina, a canal rapidly widens in diameter to 750 nm or more (Fig. 1580). Its wall consists internally of hoops less than 100 nm wide and may bear rare apatitic spherules. The hoops comprise alternating bands of electron-lucent and darker, beaded lineations and are presumably chitinous. The external surface of the wall supports a dense mesh and more rare strands, presumably chitinous and proteinaceous, linking canals as in *Lingula* (WILLIAMS & others, 1997, fig. 21.1, p. 28).

The inferred function of the homologous canal systems permeating the shell of living lingulids and discinids has to be compatible with several aspects of their origin and growth. These include the following: the initiation of canals on the outer surface of the outer mantle lobe and their persistence throughout shell growth; the synthesis of annulated canal walls from persistent electron-dense, fibrous lenses just proximal of apical plasmalemmas of the outer epithelium; and the secretion of the canal system simultaneously with proteinaceous and chitinous networks of fibrils pervading the shell (Fig. 1582).

These criteria suggest that canals serve as vertical struts interconnecting with proteinaceous and chitinous nets to form an organic scaffolding in support of the stratiform successions of the shell. Indeed, laminar support seems to be the only feasible function. Unlike the large, papillose evaginations (caeca) of the mantle into the calcitic shells of punctate brachiopods, which serve as storage centers, no distinctively stored compounds have been found in canals. Only sporadic traces of shell constituents, degraded vesicular membranes, and myelin figures, periodically sealed by transverse membranes, have been identified. In structural terms, therefore, this canaliculate framework is to the organically rich lingulide shell what the cytoskeleton is to the cell.

In living lingulids, apatitic spherules seldom adhere to canal walls and do not aggregate into a mineralized coat (Fig. 1583). Consequently, traces of canals are rarely found in fossil lingulides except as perforations of compact laminae (Fig. 1584). The columnar fabric of some early linguloids and most acrotretides is possibly a mineralized canal system, but whether it is homologous with the canaliculate framework of lingulides will be considered later.

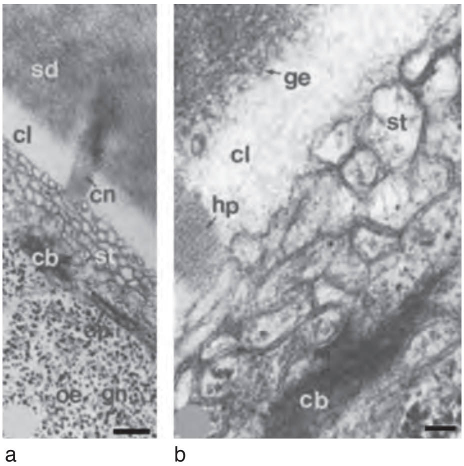


FIG. 1581. Transmission micrographs of canals in shells of *Discinisca tenuis; a*, demineralized section of integument showing relationship of a canal (*cn*) to a succession of stratified (*sd*) and compact (*cl*) laminae, secreting tubular extensions (*st*) of apical plasmalemma (*ap*) of outer epithelium (*oe*) rich in glycogen (*gn*) and electron-dense fibrillar source (*cb*) of canal; scale bar:1 µm; *b*, detail of a hooped lining (*hp*) of a canal in relationship to a compact lamina (*cl*) with proteinaceous coated granules (*ge*), a zone of tubular extensions of apical plasmalemma (*st*) and its source (*cb*); scale bar: 100 nm (Williams, Cusack, & Buckman, 1998).

BACULATE AND VIRGOSE SECONDARY LAYERS

The chemicostructure of living lingulid shells has been adopted as a standard for organophosphatic brachiopods because it includes two of the five main fabrics and most of the textures of the linguliforms as a whole. The textures and fabrics, identified in Figure 1585, are defined in Volume 1 (WILLIAMS & others, 1997, p. 24–32) but rhythmic sets (recurrent laminar sequences) as well as baculate and virgose fabrics require further consideration.

The laminar sets of the secondary shell of lingulids and discinids are rhythmically disposed (e.g., the four identified in Fig. 1585). Rhythms are frequently complicated by the repeated secretion of a lamina(e) or

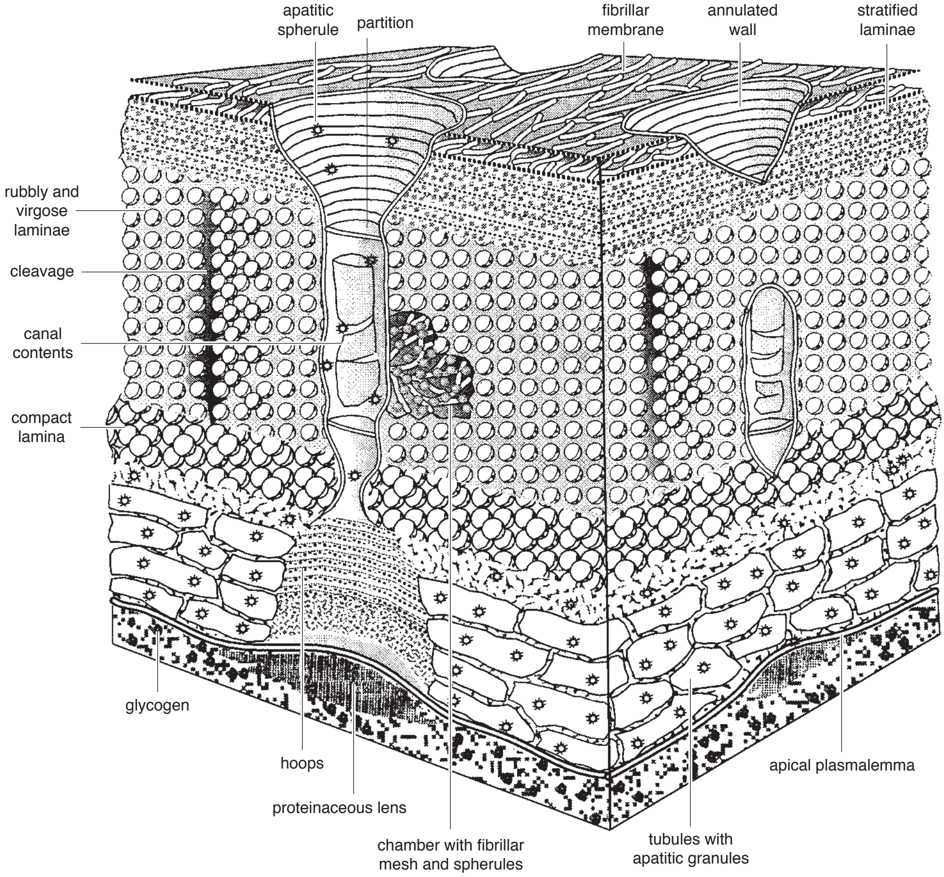


FIG. 1582. Stylized representation, at various magnifications, of secretion of discinid and lingulid canals and main structural changes affecting them in different kinds of lamination (Williams, Cusack, & Buckman, 1998).

by the omission of a lamina(e) characterizing the full cyclical suite. There is also ambiguity on how best to define a rhythm. The convention has been to identify the onset of a rhythm as the base of a graded sequence, which is in sharp contact with a different deposit, normally the same as the top of the graded sequence. In living lingulides, the sharpest interface is between a predominantly organic or membranous lamina and an apatitic, compact lamina. In *Lingula*, such a rhythmic sequence begins with a compact lamina grading inwardly into an increasing organic sequence containing botryoids and rods of apatite (virgose fabric), terminating in a membranous lamina that acts as the substrate for the succeeding rhythmic succession.

The rhythm of *Glottidia* is similar to that of *Lingula*, assuming that the baculate laminae of *Glottidia* are correlatives of the botryoidal, rubbly, and virgose laminae of *Lingula*. In the medial part of a valve, the typical rhythm begins with a compact lamina permeated by canals. The compact lamina grades inwardly into a baculate zone that may become gradually less biomineralized inwardly or more abruptly terminated by membranes serving as a substrate for the compact lamina of the succeeding rhythmic set. This rhythm is also characteristic of the highly inclined baculate sets toward the valve margin. The grading of baculate sets may be interrupted by sheets, presumably β-chitin, that are coated with granular apatite to form stratified lamination. The growth of baculi

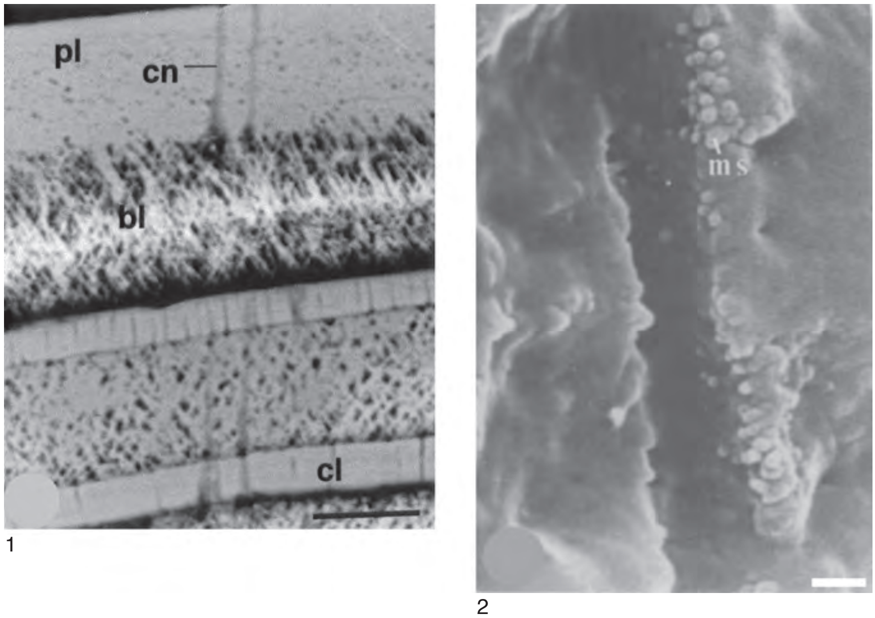


FIG. 1583. *1*, Back-scattered electron micrograph of polished transverse section of dorsal valve of Recent *Glottidia palmeri* DALL digested by subtilisin. Electron back-scatter image shows distribution of apatite (*white*) and organic (*grey* to *black*) constituents with primary layer (*pl*) to top and secondary graded baculate sets including compact (*cl*) and baculate (*bl*) laminae traversed by canals (*cn*); scale bar: 25 µm (Williams & Cusack, 1999); *2*, SEM of gold-coated vertical posteromedian section of valve of shell of *Lingula anatina*, digested with endoproteinase Glu-C, revealing canal wall studded with mosaics (*ms*) in botryoidal lamina; scale bar: 0.5 µm (Williams, Cusack, & Mackay, 1994).

can also be aborted into short rods similar to the virgose lamination of *Lingula,* and even reversals of the cycle can occur. Overall, however, the sets are asymmetrical for they almost invariably grade from biomineral-rich to organic-rich laminae (and only rarely vice versa).

In discinids, on the other hand, the dominant rhythm is the reverse with a wholly (or mainly) organic sequence grading inwardly through a baculate lamina into a compact lamina, abruptly succeeded by a membranous lamina marking the base of the succeeding rhythmic sequence.

Although laminar diversity has been described in Volume 1, two textural aspects of the secondary shell merit comment. Ellipsoids up to 1 µm long and 150 nm thick and disposed parallel with lamellar boundaries are confirmed as basic spherular aggregates of the secondary shell. They are mostly featureless, but degradation reveals outlines of apatitic spherules arranged linearly (Fig. 1586a). As these ellipsoids are scarcely digested by subtilisin, it is assumed that their coats (capsules) are not exclusively proteinaceous. Moreover, ellipsoidal capsules of other *Lingula* shells are degraded by bleach to reveal linear arrangements of apatitic spherules (Fig. 1586b). This differentially induced degradation suggests that capsules are composed predominantly of a polysaccharide like β-chitin or some other constituent of GAGs (WILLIAMS & others, 2000a, p. 1003). This texture is also found in discinids where spherules normally aggregate in hexagonal, close-packed arrangements (Fig. 1587). Aggregates, however, may also interlock like platy jigsaws or more rarely form ellipsoids with capsules (Fig. 1587; WILLIAMS, CUSACK, & BRUNTON, 1998, p. 2008).

The other textural detail especially relevant in assessing the effects of fossilization is cleavage, which is a common texture of shells of living species (WILLIAMS, CUSACK,

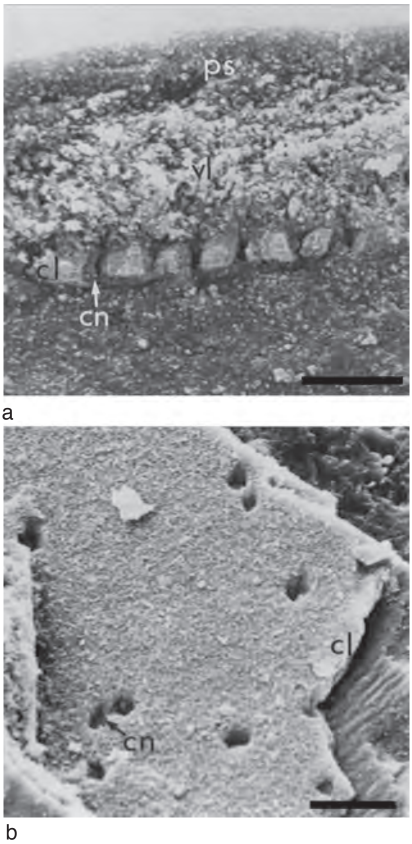


FIG. 1584. SEMs of gold-coated fracture sections of valves of *Lingula squamiformis,* Calderwood, Scotland; *a*, compact lamina (*cl*) perforated by canals (*cn*) and underlying standard outer succession of primary layer (*ps*) and virgose lamina (*vl*); scale bar: 5 µm; *b*, external surface of compact lamina (*cl*) perforated by canals (*cn*); scale bar: 10 µm (Cusack & Williams, 1996).

& BRUNTON, 1998, p. 2009). In fracture sections of discinids, for example, vertical cleavage can affect successions of compact and rubbly laminae (Fig. 1588). The cleavage appears to be related to the distribution of GAGs that are impersistent and sheetlike in the former and more pervasive and bulky in the latter laminae. The thicker compact lamina is more highly and obliquely cleaved, with successive sets of cleavage planes opening in opposite directions. In that part of the succession where the lamina becomes rubbly, a coarser, vertical cleavage predominates. Evidently dehydration of GAGs has an important role in inducing planes of weakness that probably influence the cleavage patterns of fossilized lingulides.

BACULATE LAMINATION

Baculate lamination is preeminently characteristic of lingulides, but the arrangement and structural constituents of baculi in the shells of living lingulids and discinids are different. In the lingulid *Glottidia pyramidata* the secondary shell contains lenses of baculate sets up to 25 µm or so thick. A lens is normally bounded by membranes of protein and β-chitin (Fig. 1589) and contains apatitic ovoids that tend to be linearly organized into baculi up to 750 nm in diameter but commonly more than 10 µm long. Pinacoidal plates orthogonally aligned by epitaxy or screw dislocation can also form baculi (Fig. 1589). The baculi are usually inclined at about 60° to the bounding surface but range in disposition from the vertical to the near horizontal. As aggregates of spherular apatite, the ovoids and ellipsoids are homologues of the spheroidal botryoids of *Lingula* (WILLIAMS & others, 1997), but in addition to their different shape, the *Glottidia* ellipsoids are normally indented at their poles by depressions approximately 30 nm in diameter that may represent traces of axial organic threads. The baculi as well as discrete apatitic spherules and ellipsoids are immersed in GAGs and enmeshed in organic strands that form an intricate web arising from the organic coats of canals and the bounding membranes of β-chitin (Fig. 1590). The fibrous web is structurally and functionally akin to the cytosol framework, and the polymer has been identified as an actinlike protein (CUSACK & WILLIAMS, 1996, p. 47). The web, however, resists digestion by proteinase-K and subtilisin, raising the possibility that it is mainly chitinous. The membranes may also serve as substrates for compact laminae composed of tightly packed, spherular aggregates up to several micrometers thick.

A transverse section of the midregion of a mature dorsal valve of *G. palmeri* shows

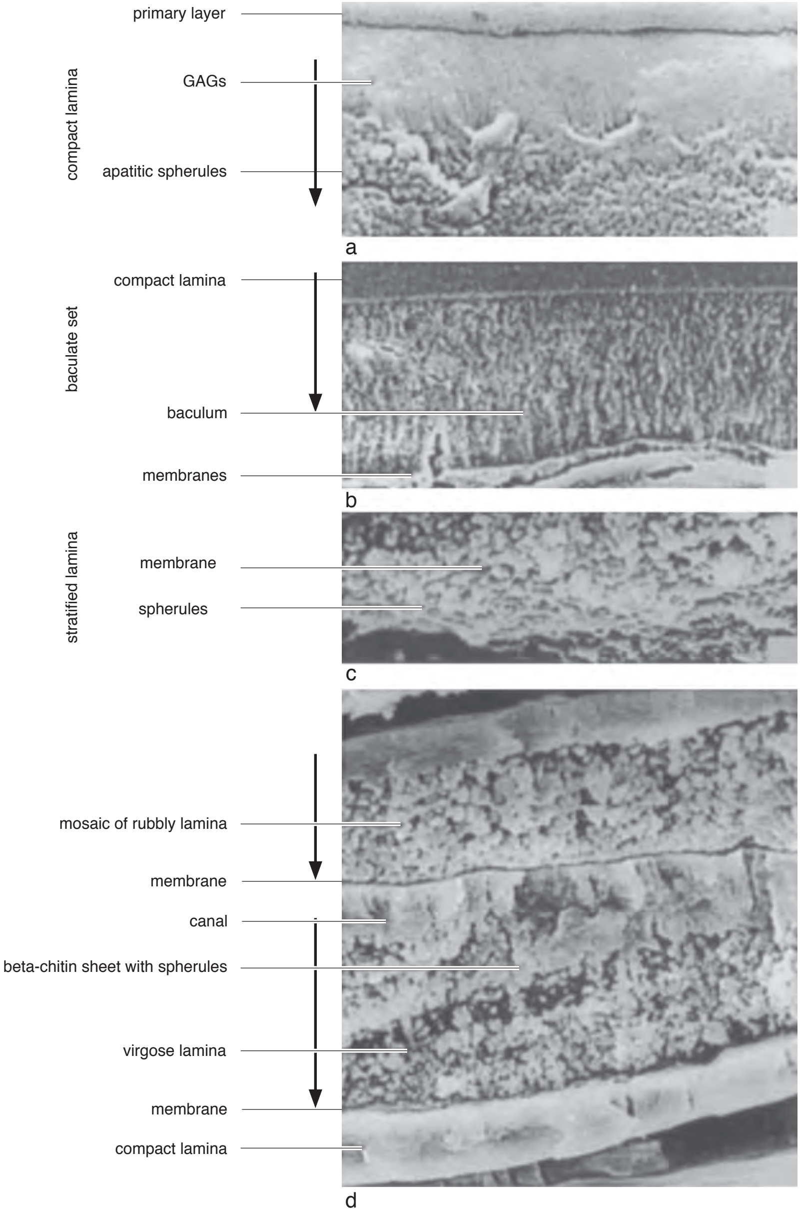


FIG. 1585. Montage of SEMs of shell of *Glottidia pyramidata* (STIMPSON) showing principal lingulide microfabrics; *a*, fracture section treated with phosphate buffer (100 mM, pH7), ×18,000; *b*, polished section of valve mounted in London resin, ×700; *c–d*, fracture sections digested in subtilisin (50 µM in phosphate buffer, 100 mM, pH7), ×3000, ×2000 respectively (Cusack, Williams, & Buckman, 1999).

the full differentiation of the *Glottidia* succession (Fig. 1591). The primary layer is underlain by approximately 20 µm of stratified laminae grading inwardly into a baculate zone. The first-formed baculate sets in the posteromedial region are like gently concave saucers with tapered rims. With further shell growth, outwardly successive baculate sets become more steeply inclined so that in the marginal transverse section

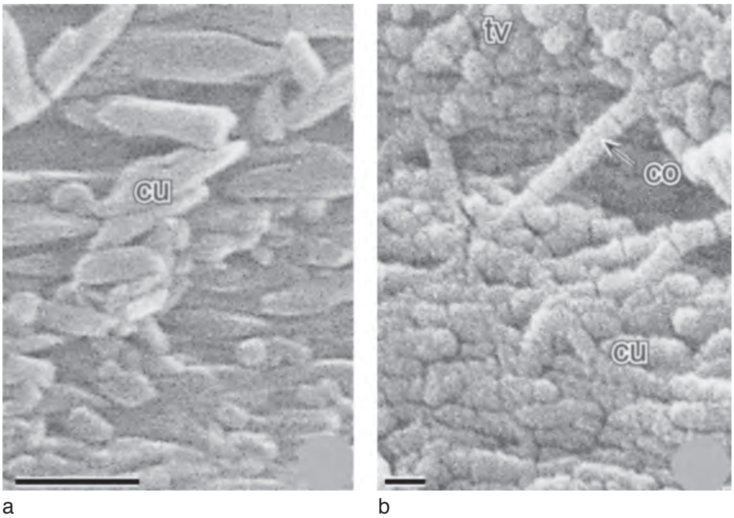


FIG. 1586. *a*, SEMs of scissor-cut, vertical sections of *Lingula parva* SMITH, West Africa, ZB 1533, digested in subtilisin. Detail of walled laminae showing capsules (*cu*) of apatitic spherules, dislodged by enzymic digestion; scale bar: 0.5 µm; *b*, SEM of vertical fracture section of *Lingula anatina* LAMARCK, Japan, digested in subtilisin. Detail of compact laminae showing linear arrangement of capsules (*cu*) composed of spherules with sporadically cross-striated collagen (*co*) and succeeding layer of capsules in transverse sections (*tv*); scale bar: 0.1 µm (Williams & others, 2000).

of a valve they appear as sigmoidal strips between the increasingly diverging zone of primary and stratified secondary shell and an internal zone of compact apatite. The internal zone is composed of apatite pervaded by canals orthogonal to the inner surface and is a condensed succession of compact laminae alternating with thin to

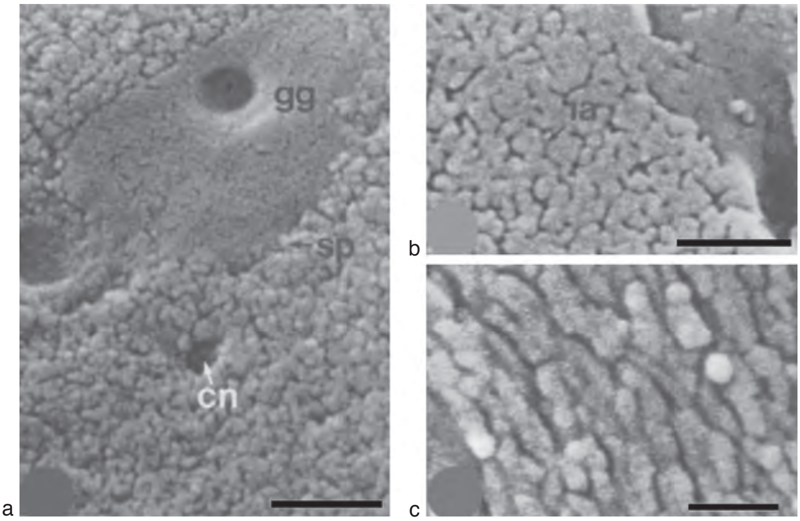


FIG. 1587. SEMs of structural components of shell of *Discinisca tenuis; a–b*, gold-coated internal surfaces treated with buffer, showing spherular (*sp*) and interlocking (*ia*) apatite, canals (*cn*), and GAGs (*gg*); scale bars: 0.5 µm; *c,* internal surface treated with proteinase-K showing rods of spherular apatite; scale bar: 250 nm (Williams, Cusack, & Buckman, 1998).

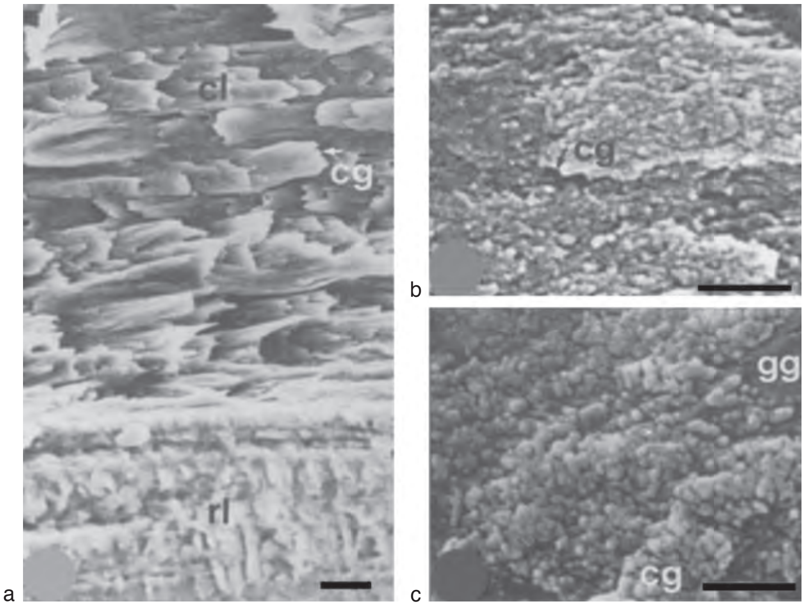


FIG. 1588. *a–c*, SEMs of secondary layer of shell of *Discinisca tenuis; a,* vertical fracture section treated with subtilisin and showing effects of distribution of GAGs on cleavage (*cg*) in compact laminae (*cl*); rubbly laminae (*rl*); *b–c,* enlarged; GAGs (*gg*); cleavage (*cg*) scale bars: 10 µm, 0.5 µm, 0.5 mm respectively (Williams, Cusack, & Buckman, 1998).

impersistently lenticular intercalations with a high organic content (Fig. 1591; CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 818). This zone has been identified as the inner zone in the shell of living discinids (IWATA, 1982, p. 960) and as a tertiary layer in fossil linguloids (HOLMER, 1989, p. 33). The intercalations within the internal zone, however, sporadically swell into baculate lenses. They and their bounding compact laminae are evidently the more medial correlatives of the overlying baculate sets. The internal zone is, therefore, as much a part of the secondary layer as the baculate sets and the stratified laminae underlying the primary layer.

Toward the valve margin the increasing inclination of baculate sets relative to the primary and outer secondary layers is an expression of allometric growth (Fig. 1591). At the margin of a mature valve, especially laterally where the vertical components of the growth vector become increasingly important, baculate sets may be inclined by as much as 60° to the external layer of primary and stratified secondary shell. The space within this outwardly facing baculate front and the inwardly curling marginal fold of periostracum and primary shell (Fig. 1591) contains the outer mantle lobe (and the periostracal lobe). The entire lobe, which is shaped rather like a rounded prism up to several hundred micrometers wide, contains the protractor muscle system responsible for the protrusion of setae. The lingulid outer lobe is unique among living brachiopods; and highly inclined secondary lamination at the shell margins of fossils is indicative of the *in vivo* presence of this kind of lobe.

The baculate shell structure of extinct linguloids is typified by that of the oldest known group, the obolids. A transverse section of the margin and midregion of a dorsal valve of *Obolus apollonis* showed a homogeneously, apatitic primary layer, underlain by a secondary layer composed of baculate sets (Fig. 1592). The sets were disposed as a succession of inwardly concave plates with swollen margins up to 80 µm thick. The plates were virtually separated from one another by gaps as wide

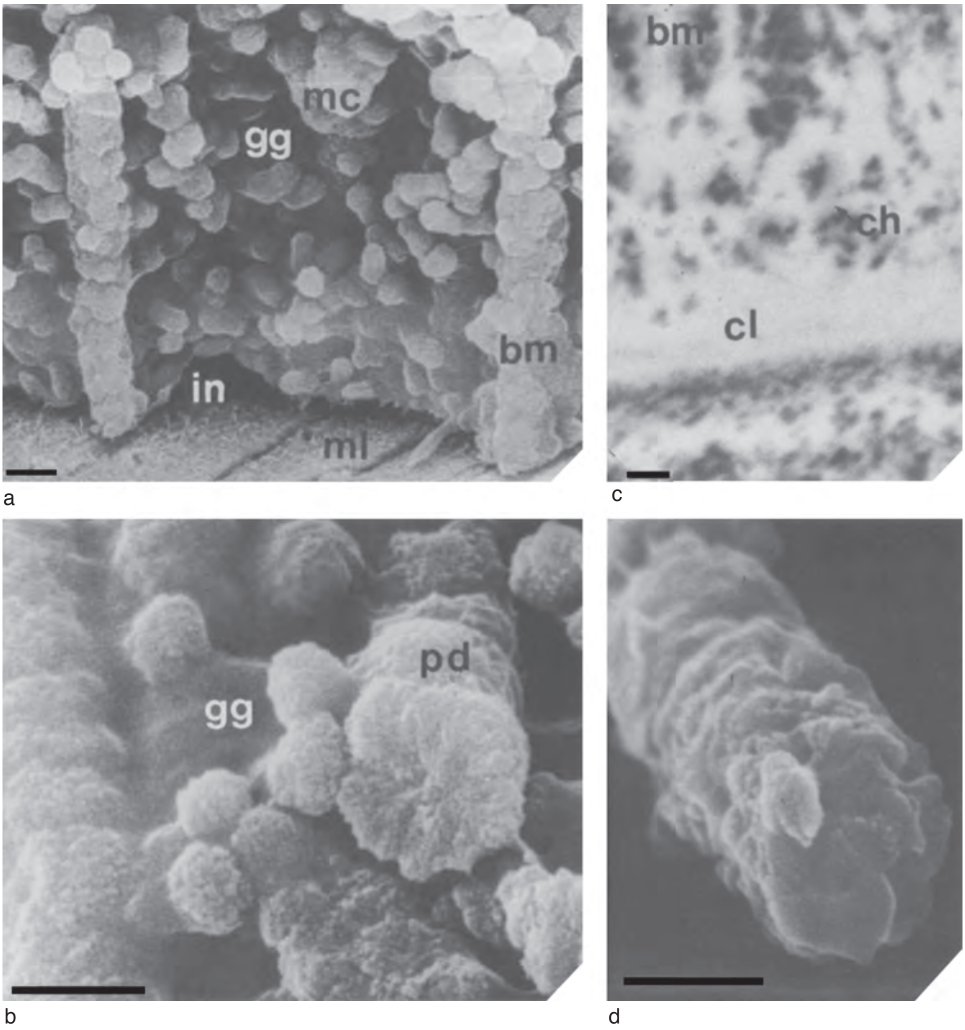


FIG. 1589. *a–b, Glottidia pyramidata*, Recent, Florida; views of baculate laminae exposed in fracture sections of body platforms of valves digested by subtilisin; *a*, baculi (*bm*) traversing mats of β-chitin coated with GAGs (*gg*) and apatitic mosaics (*mc*) at termination of a baculate set marked by interface (*in*) with a membranous lamina (*ml*) of β-chitin bearing proteinaceous strands; scale bar: 1 µm; *b*, detail of baculi showing pinacoidal epitaxis (*pd*) and mosaics associated with β-chitin mat with GAGs (*gg*); scale bar: 1 µm; *c*, detailed view in back-scattered electron micrograph of a carbon-coated, polished section of ventral valve of *Glottidia pyramidata* (STIMPSON), Recent, Florida, showing a succession of asymmetrical baculate sets underlying primary layer, with a compact lamina (*cl*) grading inwardly into trellised baculi (*bm*) transgressing apatitic-coated sheets of β-chitin (*ch*); scale bar: 5 µm; *d*, *Glottidia palmeri* (DALL), Recent, California; view of a fracture section of body platform of a dorsal valve digested in subtilisin showing detail of baculi with spirally stacked pinacoids; scale bar: 200 nm (Cusack, Williams, & Buckman, 1999).

as 500 nm, presumably the former sites of degraded membranous laminae. Eight such plates, varying in total thickness from 220 µm medially to 360 µm marginally, were composed of 27 baculate sets. The baculate sets were most fully developed marginally as inwardly tapering wedges, overlying one another en échelon and inclined at 10°–20° to the external surface. In this marginal zone, the sets were traversed by regularly disposed

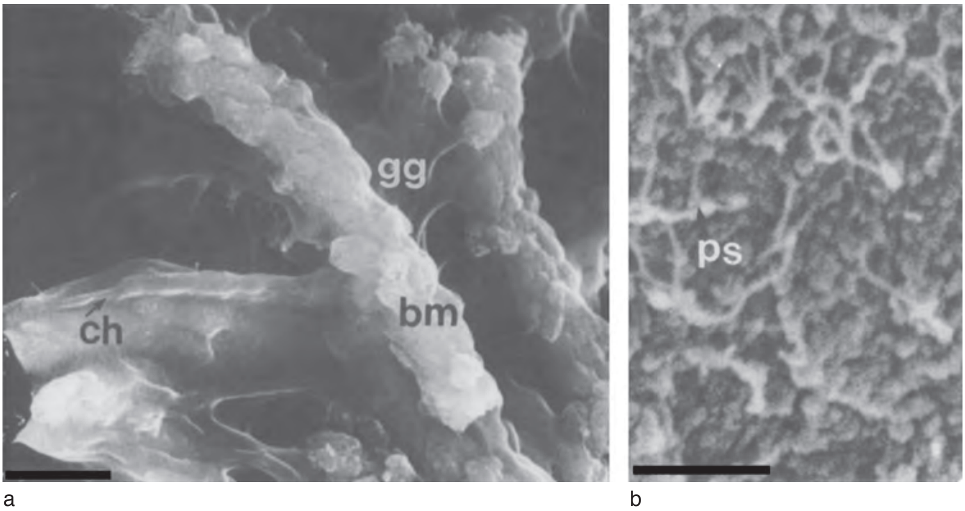


FIG. 1590. *Glottidia palmeri*, Recent, California; *a*, view of fracture section of body platform of dorsal valve digested in subtilisin with details of baculi (*bm*) transgressing β-chitin sheets (*ch*) and GAGs (*gg*); scale bar: 200 nm; *b,* anterior detail of internal surface of valve of *Glottidia pyramidata*, digested in proteinase-K, revealing proteinaceous network (*ps*) supporting apatitic spherules and mosaics; scale bar: 500 nm (Cusack, Williams, & Buckman, 1999).

trellises of baculi subtended between compact laminae (Fig. 1593). Contiguous pairs of compact laminae were separated by a break in continuity that probably represents a recrystallized, mainly organic sheet. The baculi had been recrystallized into aggregates of prismatic apatite (spherular mosaics are more prevalent in *O. transversa*). Medially, the gaps between the plates merged and the horizontally disposed sets became much thinner, mainly through the reduction of the baculate zones to a rubbly or virgose texture (Fig. 1592).

The biomineralized succession of the baculate sets of *Obolus* differs significantly from that of *Glottidia* and living discinids in being symmetrical about its medial plane with the rhythm of compact-baculate-compact laminae at the shell margins reducing to compact-virgose (or rubbly) compact laminae in midregion. The baculate sets of *Obolus* also differ in disposition from those of *Glottidia* in being uniformly gently inclined even at the shell margins. This attitude is not only an allometric consequence of the saucer shape of *Obolus* valves but also probably an indication that the marginal lobes of the obolid mantle were less intricate than those of living lingulids and more like those of discinids in lacking a periostracal lobe.

Recent chemicostructural studies of the shells of living and extinct discinoids (WILLIAMS, CUSACK, & BRUNTON, 1998; WILLIAMS, CUSACK, & others, 1998; WILLIAMS & others, 2000a) have enlarged and clarified the information on discinid baculation in Volume 1 (WILLIAMS & others, 1997, p. 26–27). The stratiform succession of the *Discinisca* shell serves as a living model, while that of the Ordovician *Schizotreta* is typical of the Paleozoic orbiculoideid sister group of the derived discinids.

In *Discinisca*, the dominant sequence in the secondary layer consists of alternations of compact and rubbly laminae with baculate lamination restricted to the outer secondary layer within the body platform (and septum) of mature ventral valves. Here, baculi occur in rhythmic sets and are typically subtended between rubbly or compact laminae (Fig. 1594). The inner boundary of such a set may be a succession of spherular-coated membranes or a compact

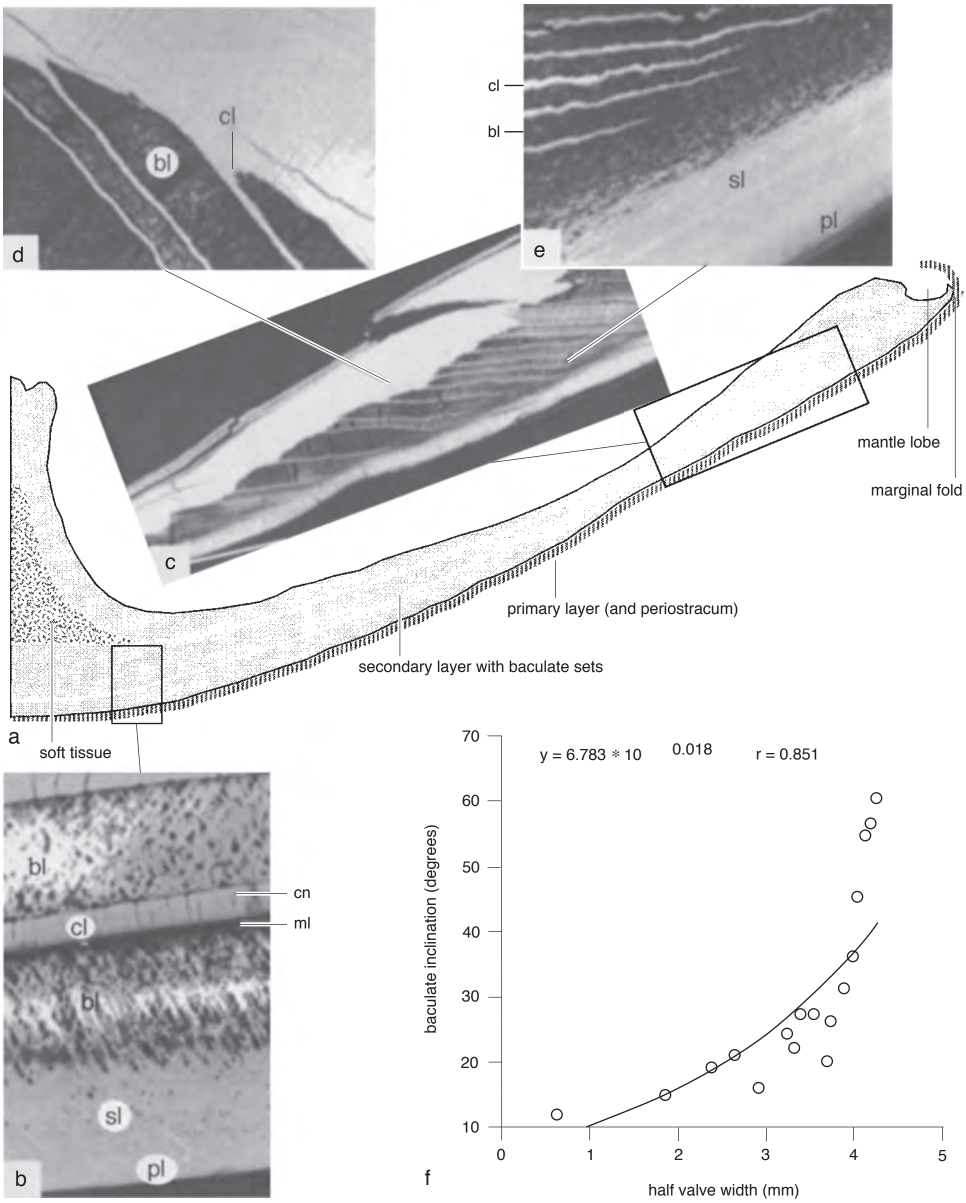


FIG. 1591. *a–f,* Montage of back-scattered electron micrographs of left half of polished posteriomedian transverse section (*a*) of dorsal valve of *Glottidia palmeri* DALL, Recent, California, showing distribution of apatitic (*white*) and organic (*black*) constituents in main stratiform features of shell; baculate laminae (*bl*), compact laminae (*cl*), canals (*cn*), primary layer (*pl*), membranous laminae (*ml*), and stratified laminae (*sl*); *b,* ×600, *c,* ×100, *d,* ×800, *e,* ×1700; *f,* graph in bottom righthand corner shows allometric increase in inclination of baculate laminae to shell surface from midregion to margin of valve (Cusack, Williams, & Buckman, 1999).

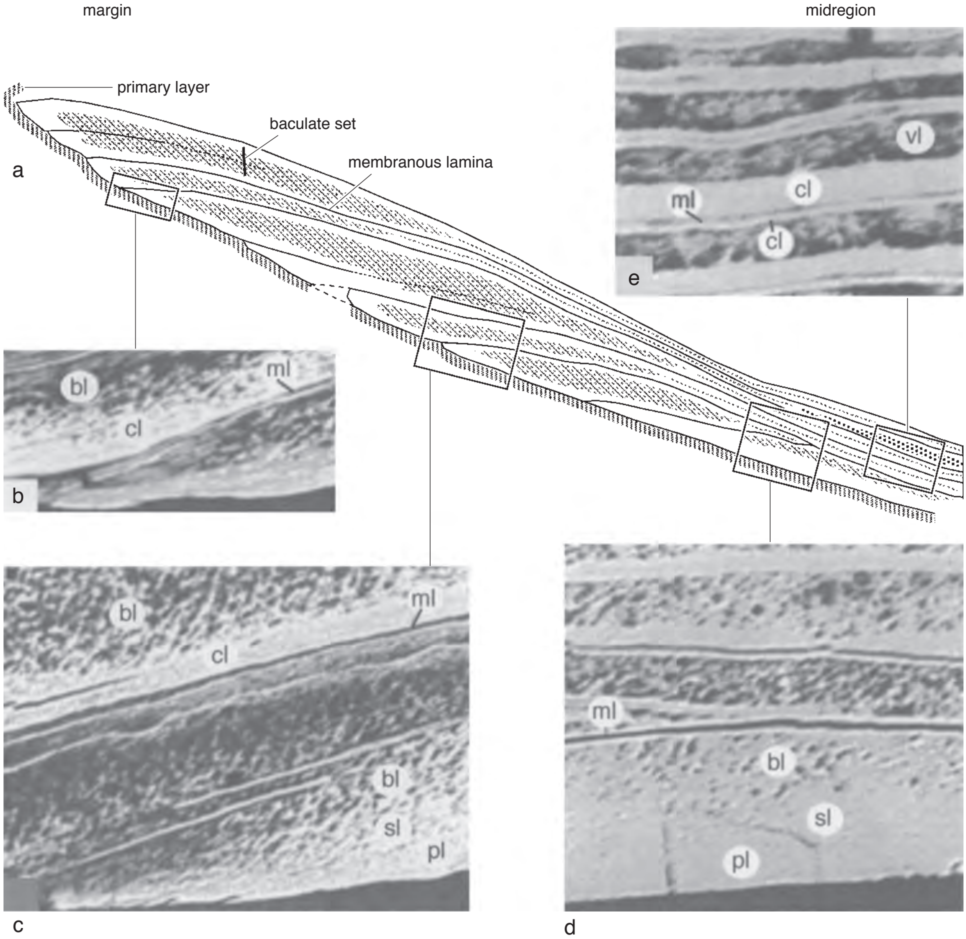


FIG. 1592. *a–e,* Montage of back-scattered electron micrographs of right side of polished posteromedian transverse section (*a*) of dorsal valve of *Obolus apollonis* EICHWALD, GLAHM 101670, Cambrian, Russia, showing distribution of apatitic (*white*) and organic (*black*) constituents in main stratiform features of shell; baculate laminae (*bl*), compact laminae (*cl*), membranous laminae (*ml*), primary layer (*pl*), stratified laminae (*sl*), and virgose laminae (*vl*); *b,* ×500, *c,* ×470, *d,* ×520, *e,* ×1800 (Cusack, Williams, & Buckman, 1999).

lamina with apatitic spherules aggregated into cylindroids at the interface. The outer boundary is commonly a less well defined transition with a high organic content. Individual baculi are 150–250 nm thick and may exceed 5 µm in length. They are unbranched and disposed vertically or at angles of approximately 60° to the substrates to form a three-dimensional trelliswork that, in the living shell, is supported by the all-pervasive GAGs. In dead shells the removal or shrinkage of GAGs by enzymic digestion or dehydration usually causes a partial collapse of the biomineralized framework and the fragmentation of baculi.

Baculate morphology is variable. The granular surfaces of most baculi, especially those held in place by radiating strands 90

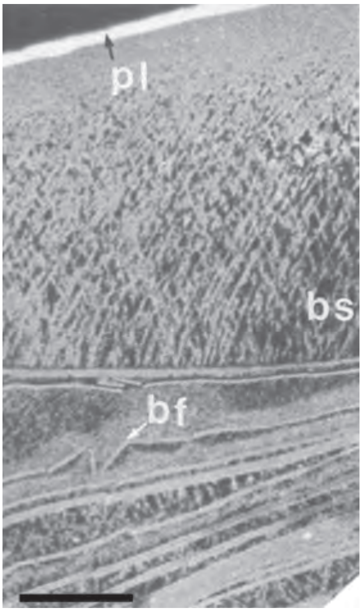


FIG. 1593. Back-scattered electron micrograph of carbon-coated, polished section of dorsal valve of *Obolus apollonis* EICHWALD, GLAHM 101667, Upper Cambrian, Russia, showing succession of baculate symmetrical sets (*bs*) succeeding primary layer (*pl*) with brittle fracture of compact laminae (*bf*); scale bar: 50 µm (Cusack, Williams, & Buckman, 1999).

nm or so thick, are studded with mosaics and cylindroids of spherular apatite (Fig. 1595). Some baculi, however, mainly consist of stacked pinacoids that grow in relation to fine horizontal meshes. Both strands and meshes are exposed when the GAGs matrix of baculate laminae is digested in proteinase-K or subtilisin. In contrast, transverse sections of broken baculi digested by these enzymes have hollow cores, about one-third the dimension of a rod or cores plugged by subcentral spherules. Transverse sections of broken baculi treated with buffered solutions, however, do not have hollow cores, only depressions within clusters of spherules. In both enzymically digested and buffered laminae, some baculi are closed by narrow rounded tips of spherules and are interpreted as having been terminated during laminar secretion. This differential digestion of the organic constituents of baculate laminae suggests that baculi have axial proteinaceous strands and that the protease-resistant strands and meshes are chitinous. Similar strands and meshes also support mosaics and short rods of spherular apatite in virgose laminae and are likewise assumed to be chitinous.

The baculate sets of fossil discinids and the Paleozoic *Orbiculoidea* are the same as those of living species. The baculate sets of *Schizotreta*, the earliest known orbiculoideid, the sister group of discinids, however, are similar to those of such early linguloids as *Obolus*, as are those of the discinoid trematids (WILLIAMS, CUSACK, & BRUNTON, 1998).

The secondary lamination of *Schizotreta* is dominated by baculate sets secreted at differing rates medially and marginally (Fig. 1596). *In vivo*, a set was composed of an outer membrane(s) succeeded inwardly by a compact lamina grading into a baculate zone capped by a second compact lamina. Although these laminae are now recrystallized, their original ultrastructure can be discerned. Thus, membranes are represented by a break in succession or a layer(s) of spherules; compact laminae by apatitic prisms and rare pinacoids with *c*-axes orthogonal to the set; and baculate laminae by spaces of variable thickness criss-crossed by trellised rods. In submedial successions, where they are well developed, baculi are approximately 500 nm thick. They consist of either irregularly stacked pinacoids or better-ordered prisms with *c*-axes parallel to baculum length. Both types have been found with central indentations suggestive of a nonmineralized core.

Medially, a baculate set is seldom more than a few microns thick, and the middle mineralized zones may be rubbly to virgose rather than baculate. The relatively slow secretion of the succession is confirmed by repeated imprints of hexagonally packed epithelial cells on the inner surfaces of compact laminae. Marginally toward the external shell surface where periodic development of concentric folds (fila) could only have been effected by accelerations in shell secretion, successions of enlarged baculate sets trace the advance of outer laminar lobes

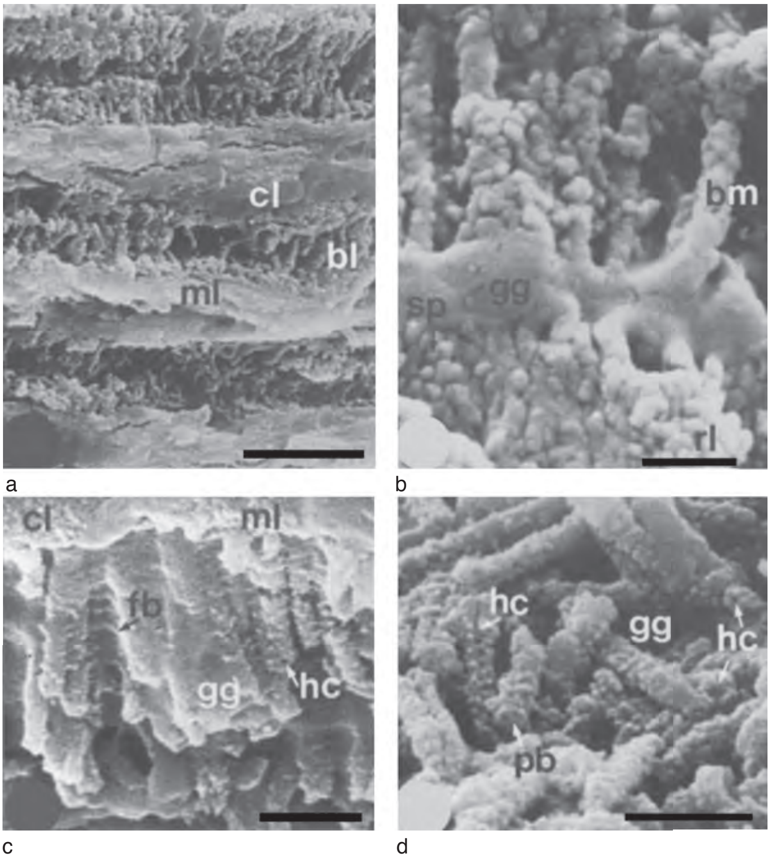


FIG. 1594. SEMs of baculate lamination in vertical fracture sections of secondary layer of *Discinisca lamellosa* (*a–c*) and *D. tenuis* (*d*); all sections treated with subtilisin; *a*, succession of baculate laminae (*bl*) in relation to compact (*cl*) and membranous (*ml*) laminae; scale bar: 5 µm; *b*, baculi (*bm*) some with hollow cores, spherules (*sp*) embedded in GAGs (*gg*) and interconnected by actin strands, succeeded by rubbly laminae (*rl*); scale bar: 0.5 µm; *c*, baculi with hollow cores (*hc*), embedded in GAGs (*gg*) and interconnected by actin strands (*fb*), succeeding compact (*cl*) and membranous (*ml*) laminae; scale bar 1 µm; *d*, broken baculi with some GAGs (*gg*) showing hollow cores (*hc*) and plugged baculi (*pb*); scale bar: 1 µm (Williams, Cusack, & Buckman, 1998).

relative to the main spread of the mantle. A filum would have been secreted by an outwardly deflected outer mantle lobe. The splayed membranes within the filum would have originated from an older membranous sequence secreted posteromedially of the filum. This inwardly located membranous sequence would have served as an axis about which the deflected outer mantle lobe rotated during secretion of the filum. The most striking aspect of a filum growing in this way is the five- or six-fold increase in the cumulative thickness of the baculate and rubbly laminae at its core. In life these wedgelike laminar sets would have consisted mainly of GAGs.

VIRGOSE LAMINATION

The shell structure of living *Lingula* is texturally similar to that of *Glottidia* except for the absence of baculate lamination, which is replaced by sets of a variety of apatitic structures suspended in GAGs. These sets were initially identified as rod and plate (WILLIAMS, CUSACK, & MACKAY, 1994, p. 246) in recognition of the apparent dominant habit of their apatitic aggregates. In the Carboniferous *Lingula squamiformis*,

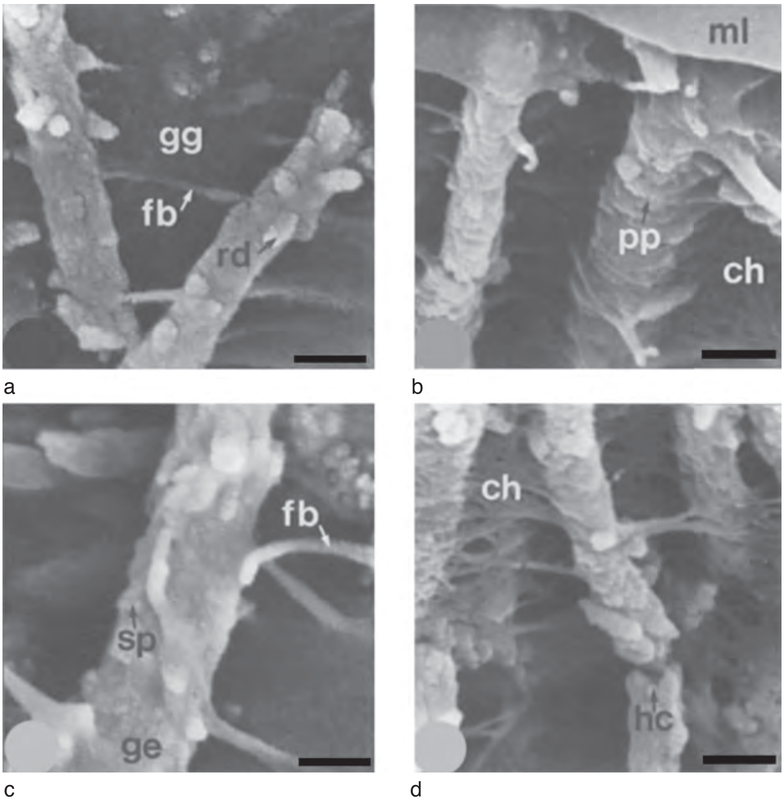


FIG. 1595. *a–d,* SEMs of membranes (*ml*) and baculi in vertical fracture sections of ventral valve of *Discinisca tenuis* treated with subtilisin. Baculi in GAGs (*gg*), composed of pinacoidal plates (*pp*) associated with nets of anastomosing fibrils identified as chitin (*ch*) or of granular (*ge*) spherules (*sp*) and rods simulating prisms (*rd*) associated with actin strands (*fb*) and some broken baculi with hollow cores (*hc*); *a, b,* and *d,* scale bars: 150 nm; *c,* scale bar: 100 nm (Williams, Cusack, & Buckman, 1998).

this fabric, which characterizes the stratiform succession (Fig. 1597), includes laths, plates, mosaics, botryoids, and especially cylindroids up to 1.7 µm long and approximately 250 nm thick (the virgose fabric of CUSACK & WILLIAMS, 1996, p. 40). The cylindroids are randomly stacked, but transverse fractures of some rods bear central depressions. The possibility that the rods had axial organic strands is strengthened by the fact that some may be sinuous, while others, rarely grouped in incipient trellises, are attached to bounding compact laminae (Fig. 1598). In effect, the virgose fabric of Carboniferous *Lingula* appears to represent a degenerate baculate fabric.

Recent comparative studies of the shell structure of living *Lingula* species (WILLIAMS & others, 2000a) have confirmed the prevalence of the virgose fabric and the invariable presence in it of bundles of equal-sized rods of apatitic spherules (fascicles) as displayed in the shell of *Lingula parva*.

A fascicle is an assemblage of several pods, each up to 500 nm long and 150 nm wide and containing three or four strings of beadlike, apatitic spherules that are exposed when the coats of pods are degraded by bleach. The pods are tightly adherent at one end of the aggregate (Fig. 1599), where they are normally attached to an organic strand(s) and splay outward at the other end, where

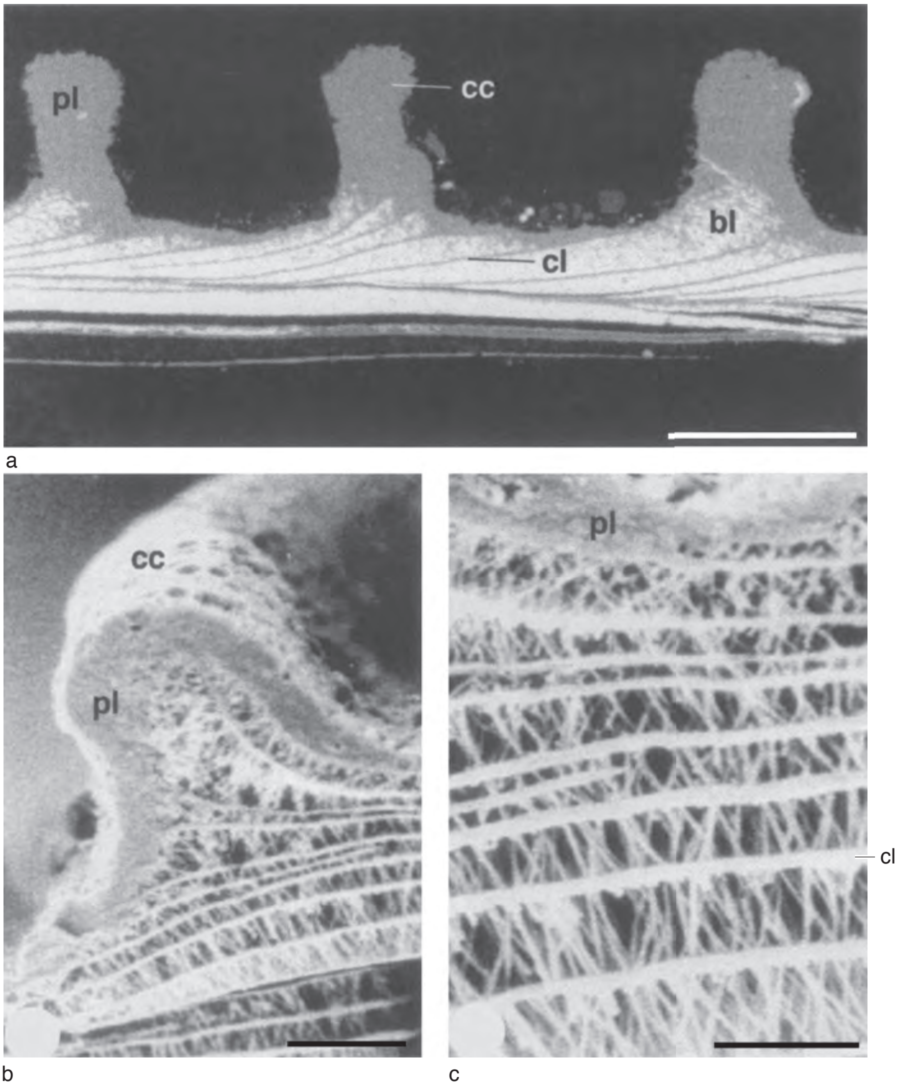


FIG. 1596. SEMs of vertical fracture sections of shell of *Schizotreta corrugata*; *a,* back-scattered SEM of polished vertical section showing distribution of baculate (*bl*) and compact (*cl*) laminae relative to variably thick primary layer (*pl*), forming concentric corrugations (*cc*) on valve surfaces; scale bar: 100 µm; *b–c,* view and detail of baculate sets of corrugations (*cl*) in relation to primary layer (*pl*); scale bars: 25 µm, 10 µm (Williams & Cusack, 1999).

their coats are more readily degradable. Fascicles may occur singly but are commonly attached at their adherent ends either in diametrically opposed pairs or in petaloid groups of four to six fascicles (Fig. 1600).

Toward the top of a fully developed virgose set in the shell of *L. parva*, single and compound fascicles, ellipsoids, and mosaics form discrete botryoidal masses, about one micrometer or so in size, suspended in GAGs (Fig. 1599). The botryoids, which are held in place by a framework of vertical and horizontal branching strands, are roughly aligned alternately. Spherulites are also suspended in GAGs and consist of closely packed pods that radiate from centers of attachment to vertical organic strands (Fig. 1599); the pods are organically coated strings of apatitic

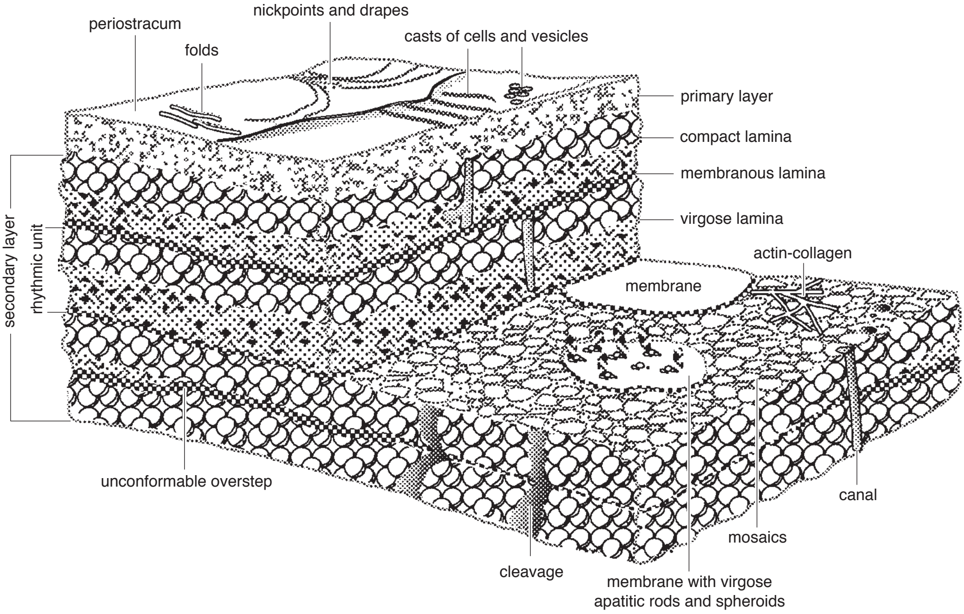


FIG. 1597. Diagrammatic reconstruction of laminar succession in midregion of mature, living valve of *Lingula squamiformis,* Lower Carboniferous, Scotland (Cusack & Williams, 1996).

spherules. Both botryoids and spherulites are not only held in place by the framework of strands but are also enmeshed in a finer organic network of threads (Fig. 1599). Both strands and threads have previously been identified based on their ultrastructural characteristics as collagen (WILLIAMS, CUSACK, & MACKAY, 1994, p. 240) and actin, respectively (CUSACK & WILLIAMS, 1996, p. 47). They have also been identified as β-chitin (WILLIAMS, CUSACK, & BRUNTON, 1998, p. 2011), but this glucosamine-rich constituent (IIJIMA & others, 1991), which imposes a linearity on the apatitic components of the shell, is more likely to be present as membranes and capsules.

Seven samples of the shell structure of other *Lingula* from the Pacific and Indian Oceans did not differ significantly from that of the Japanese *L. anatina,* which incidentally includes fascicles (see WILLIAMS, 1997, p. 279, fig. 237.2). A typical rhythmic unit of the secondary layer of these samples consisted of a compact (or stratified) lamina succeeded by botryoidal or walled laminae grading into a virgose lamina capped by a membrane(s). In contrast to their close packing in compact laminae, apatitic spherules were commonly encapsulated in succeeding laminae. The general parallelism of capsulated spherules, as seen in surface view and section, suggests some epitaxial control during the secretion of apatite and β-chitin. Virgose laminar sets were found in all samples, with ovoidal capsules and fascicles being especially prominent (Fig. 1600).

The geological range of lingulid shells with virgose lamination is poorly known. Fascicles are abundantly developed (Fig. 1601) in the virgose laminar sets of the Lower Cretaceous *Credolingula* (SMIRNOVA & USHATINSKAYA, 2001). A recrystallized bundle of rods has also been tentatively identified as a fascicle in the shell of the Carboniferous *L. squamiformis* (Fig. 1598); but even if the identification is correct, the structure must have been rarely developed in the shells of this species.

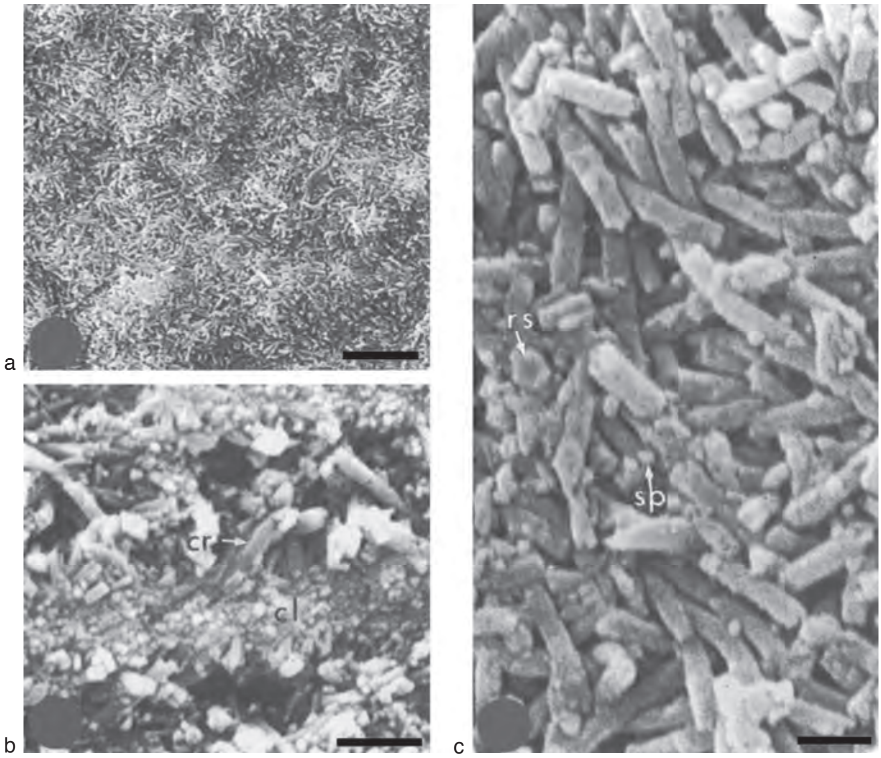


FIG. 1598. SEMs of various gold-coated surfaces of valves of *L. squamiformis,* Kinghorn; *a, c*, external view and detail of a virgose lamina with rods distributed as low mounds separated by shallow troughs reflecting microtopography of secreting plasmalemmas of outer epithelium; ringlike arrangement (*rs*) of spherules seen in transverse sections of some rods and scattered isolated spherules (*sp*); scale bars: 5 µm, 500 nm; *b*, vertical fracture section of compact lamina (*cl*) developed between two thin laminae of rods, some of which are curved (*cr*); scale bar: 1 µm (Cusack & Williams, 1999).

SECRETION OF BACULATE AND VIRGOSE LAMINAR SETS

The secretion of a baculate set has yet to be fully understood. There are at least two ways of secreting baculi to form a three-dimensional trellis. A baculate set is essentially a closed lenticular structure with a roof and floor of membranous or compact laminae enclosing a chamber containing a baculate trellis, secured by chitinous and proteinaceous strands within a GAGs matrix. Most baculi have organic cores; others are composed of pinacoidal stacks or ellipsoidal or linear aggregates of spherules. It is therefore possible that the contents of a chamber are initially secreted as an assortment of baculate components dispersed in GAGs. Differential polymerization within the GAGs chamber would then give rise to chitinous and proteinaceous strands. Some strands would serve as axes for the aggregation of apatitic spherular coats; others would become guy strands for wholly mineralized baculi growing by linear accretion.

This sequence of polymerization, aggregation, and accretion does not, however, account for the trellised arrangement of baculi. Such a well-ordered crystalline configuration appears to be controlled by the tubular apical plasmalemmas of the outer epithelium (WILLIAMS & others, 1997, p. 26–27). In this mode of secretion, the components of a baculate set would be assembled incrementally and extracellularly with continuously secreted GAGs acting as an extrapallial fluid during polymerization of fibrous strands and the aggregation of

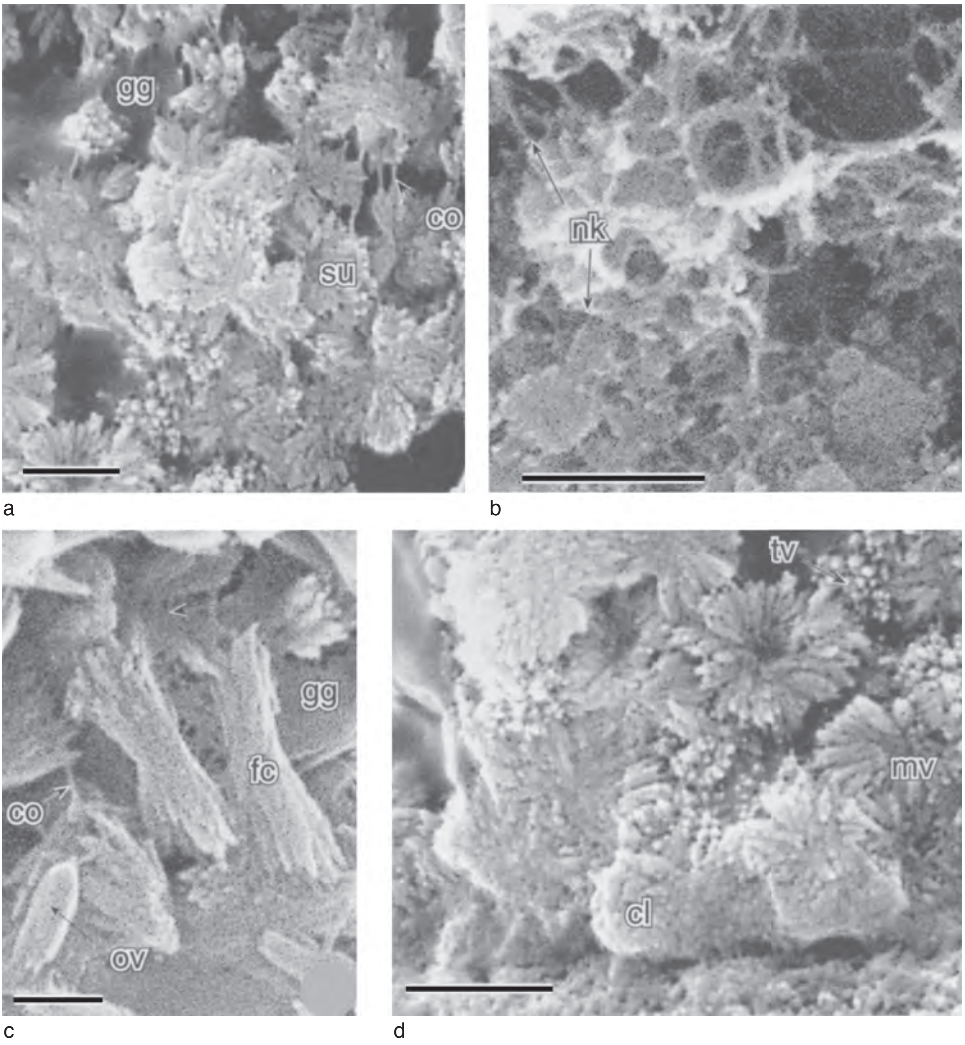


FIG. 1599. SEMs of scissor-cut, vertical sections of *Lingula parva* SMITH, West Africa, ZB 1533, digested in subtilisin; *a,* general view of spherulites (*su*) suspended in GAGs (*gg*) by a collagenous framework (*co*) with *d,* details of spherulites immediately succeeding a compact lamina (*cl*), and tangential (*tv*) and midsection (*mv*) views of spherulites with radiating rods; scale bars: 1 µm; *b,* detail of network of actin-related threads (*nk*) associated with botryoids; scale bar: 0.5 µm; *c*, detail of paired fascicles (*fc*) associated with ovoidal capsules (*ov*), GAGs (*gg*), and collagenous strands (*co*); scale bar: 0.5 µm (Williams & others, 2000).

apatitic granules. The flexibility of tubular plasmalemmas can form tilted surfaces on the tops and along the sides of tubes, with arrays of tops tending to secrete planar structures and the sides high-angled linear bodies (Fig. 1602). Once initiated, the pattern is envisaged as being repeated laterally with the linear bodies (baculi) lengthening inwardly by apical accretion within the thickening layer of GAGs. In effect, baculate trellises could owe their disposition to the flexibility of tubular plasmalemmas and their growth to the polymerization and accretion of organic and mineral constituents after those constituents had been exocytosed with GAGs.

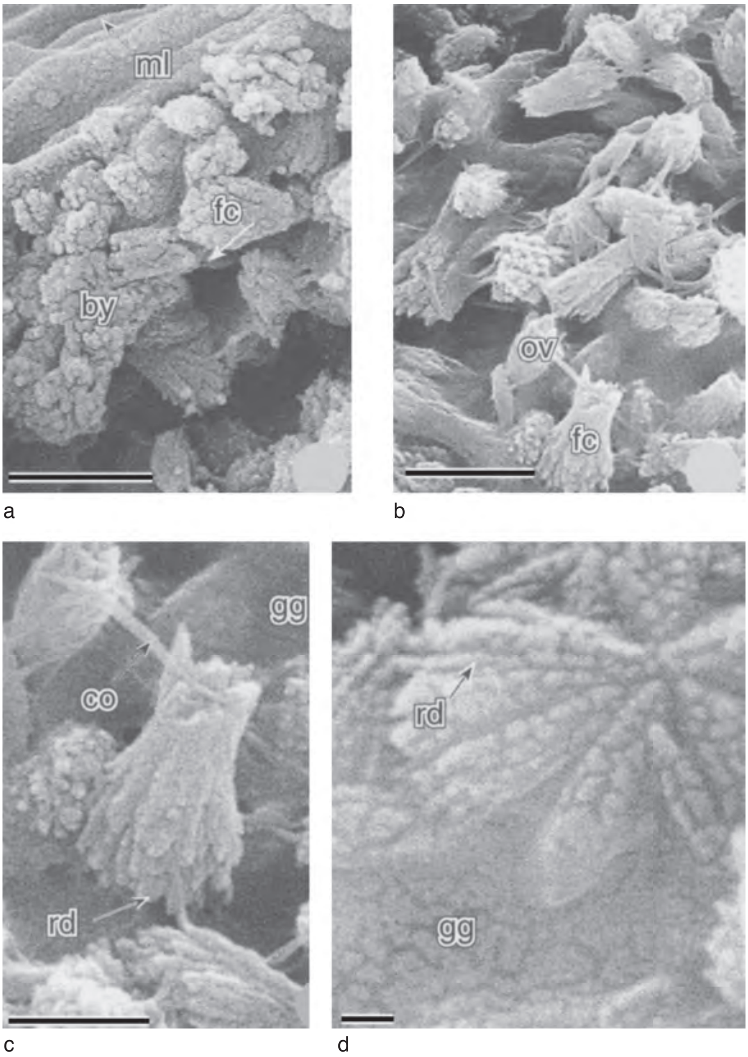


FIG. 1600. SEMs of scissor-cut, vertical sections of *Lingula*; sections treated with bleach; *a, Lingula* sp., Moluccas, NMWZ. 1999. 046.6; view of underside of membranes (*ml*) with GAGs speckled with apatitic spherules showing adherent botryoids (*by*) and fascicles (*fc*) of outer virgose lamina; scale bar: 1 µm; *b–c,* general view and detail of virgose lamina of *Lingula* sp., Western Australia, NMWZ. 1999. 046.8, showing fascicles (*fc*) composed of spherular rods (*rd*), suspended with ovoids (*ov*) in GAGs (*gg*) with connecting strands of collagen (*co*); scale bars: 1 and 0.5 µm respectively; *d, Lingula* sp., Yemen, NMWZ. 1999. 046.1-3; detail of flat-lying, petaloid group of fascicles that are part of an accretionary botryoid, showing disposition of apatitic spherules composing individual rods (*rd*) of fascicles embedded in tension-cracked GAGs (*gg*); scale bar: 0.1 µm (Williams & others, 2000).

A flexible tubular plasmalemma, however, cannot be solely responsible for the growth of baculate trellises. It is also characteristic of the integument of *Lingula*, which is chemicostructurally related to that of *Glottidia* except for the absence of baculate laminae. In a typical rhythmic sequence in the *Lingula* secondary shell, baculi are replaced by spheroidal, ellipsoidal, and fascicular bodies. No axial canals have been seen in these bodies, and it is assumed that a specific fibrous protein, absent from the *Lingula* shell, serves

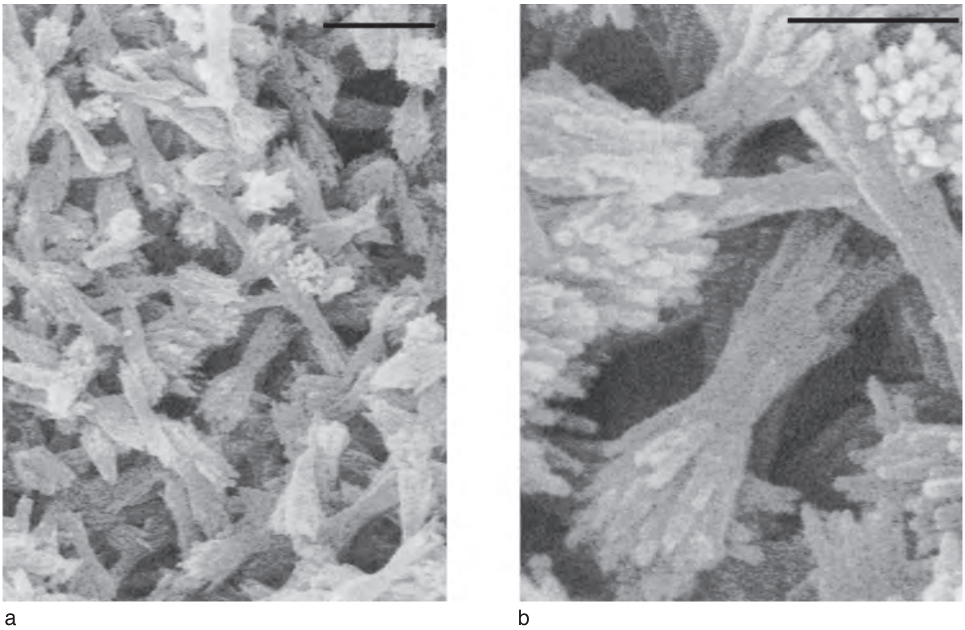


FIG. 1601. *a,* General view and *b,* detail of fracture section of virgose laminar set in shell of Lower Cretaceous *Credolingula olfevieri* SMIRNOVA, showing fascicles, principal components of virgose fabric; scale bars: 2 µm and 1 µm respectively (new).

as the axis of a baculum. The nature of virgose lamination in the Carboniferous *Lingula squamiformis* shells seems to support this interpretation with sporadic traces of aborted baculate growths on the compact laminae bounding virgose chambers.

The derivation of virgose lamination from baculate sets, however, involved more chemicostructural transformations than the loss of proteinaceous strands. The virgose lamination, possibly of *L. squamiformis* and certainly of *Credolingula* shells, is

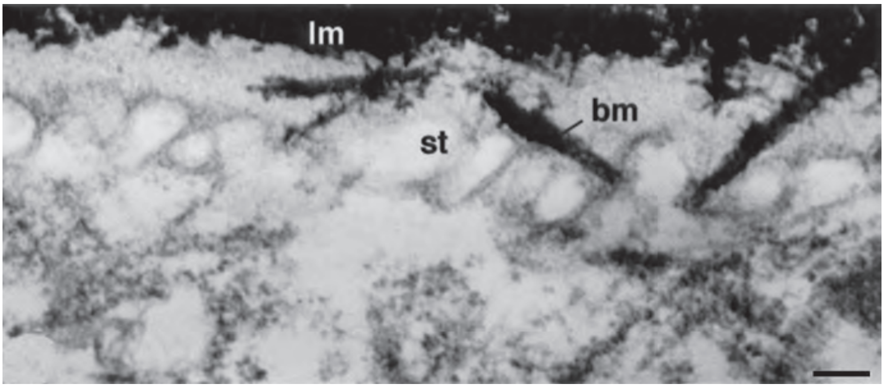


FIG. 1602. TEM of shell and associated outer epithelium of a dorsal valve of Recent *Discina striata*, stained with aqueous solution of lead citrate and uranyl acetate. Tubules (*st*) in relation to baculi (*bm*) accreting beneath a lamina (*lm*) with high organic content; scale bar: 100 nm (Williams & Cusack, 1999).

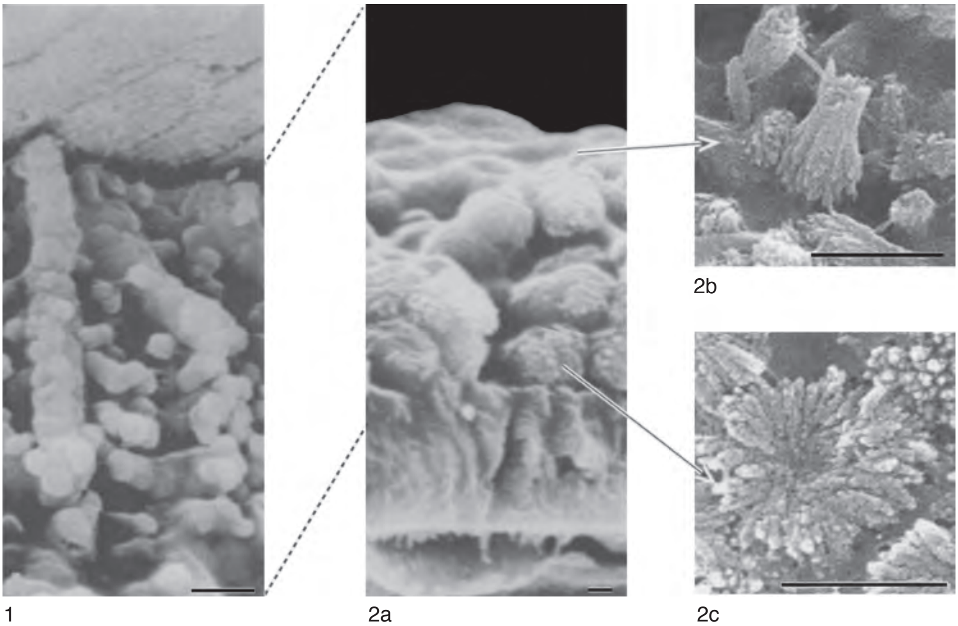


FIG. 1603. Laminar sets in shells of living lingulids: *1*, baculate set of *Glottidia* with baculi and ellipsoids in GAGs subtended between top of compact lamina (below) and membrane with actinlike threads underlying another compact lamina (above); *2a*, virgose set of *Lingula* with membrane (below) succeeded by compact lamina and botryoids in GAGs that have been completely removed toward top; *2b*, fascicles in a collagenous framework within GAGs zone in upper part of a set in *L.* sp. cf. *anatina*; *2c*, spherules in place of botryoids in *L. parva*; scale bars: 1 µm (Williams & others, 2000).

characterized by fascicles, a novel kind of aggregation. The invariable presence of fascicles in such fossil and all living species is noteworthy in two respects. Fascicles are virtually constant in shape with their constituent pods, approximately 500 nm long. They are also flat lying on open frameworks of collagenous strands and may occur at several horizons in a GAGs matrix. These characteristics suggest that fascicles are assembled intracellularly as bundles of linearly arranged apatitic spherules encapsulated in chitinoproteinaceous coats. They are probably secreted as diametrically opposed pairs that fracture easily in midregion during polymerization and dehydration of virgose sets. Spherulites, which so far have been found only in *L. parva*, are also probably assembled intracellularly. A correlation of the principal apatitic aggregates of baculate and virgose laminar sets is given in Figure 1603.

COLUMNAR AND CAMERATE SECONDARY LAYERS

The columnar and camerate fabric of acrotretide brachiopods has been extensively described (HOLMER, 1989; WILLIAMS & HOLMER, 1992), and its main features are summarized in Volume 1 (WILLIAMS, 1997, p. 281–282). Recent research on this fabric includes the discovery of homologous structures in the stem-group brachiopod *Mickwitzia* and in some Cambrian lingulides. The most relevant aspects of acrotretide shell structure leading to these discoveries merit a brief review.

The laminar sets of the acrotretide shell are distinctively stacked like shallow, asymmetric saucers with thickened margins that are wedgelike in section and up to five times thicker than the posteromedial centers of the sets. The relatively smooth columns pervading the secondary shell can be traced

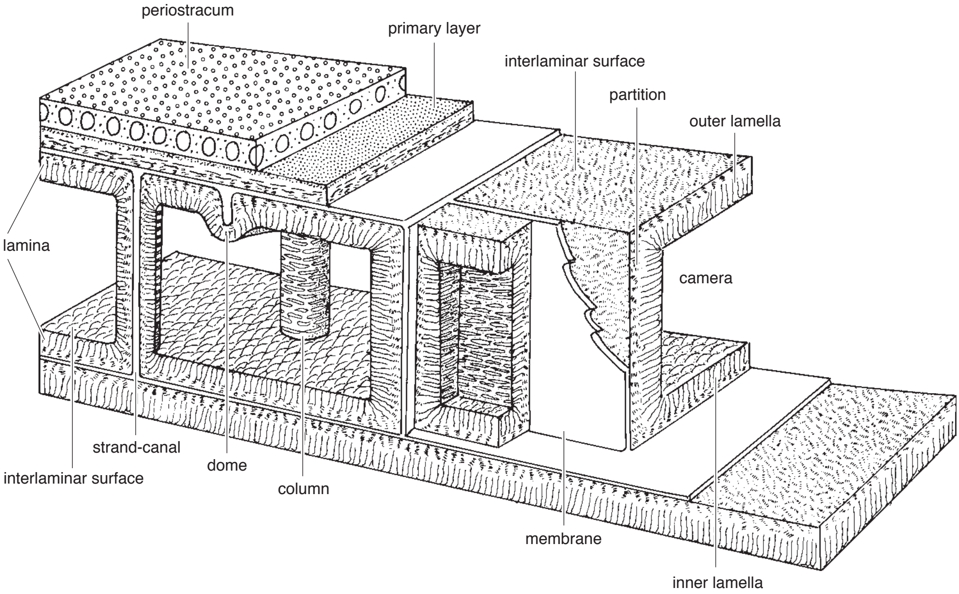


FIG. 1604. Composite diagram showing inferred relationships among various biomineral and morphological components of shell of living acrotretoids (Holmer & Williams, 1992).

through several sets for 30 µm or more; and although they range in diameter from 1.5 to 5 µm (average 2.3 µm), they are much less variable within a laminar set (Fig. 1604). The columns have axial canals, approximately 500 nm in diameter, which are commonly preserved as perforations in contiguous, interlaminar surfaces separating sets and occupied by membranes *in vivo* (WILLIAMS & HOLMER, 1992, pl. 4,*5*). Associated domes that are interpreted as aborted columns have a similar range of diameters and are composed of curved overlapping plates with sporadic central depressions (WILLIAMS & HOLMER, 1992, pl. 5,*5*). An interesting aspect of the acrotretide shell (Fig. 1604) is that although the structure in many species is columnar, in others it is camerate (*Scaphelasma*), while both fabrics characterize different laminar sets in some acrotretids (HOLMER, 1989, p. 54). This differential development of fabric suggests changes in the specificity of calcifying proteins as well as the secretion of interconnected organic partitions from intercellular pathways that replicate the boxlike shapes of outer epithelial cells (WILLIAMS & HOLMER, 1992, p. 684). As in living lingulides, the sets of compact laminae containing columns or partitions would initially have been filled with apatitic spherules dispersed in GAGs. As the GAGs degraded, the apatite would have aggregated on the membranous partitions or on orthogonal strands (or canal walls), dependent on the nature of the ambient calcifying protein.

Recent studies show that mineralized columns with axial canals also developed in *Mickwitzia*, the presumed stem-group brachiopod (HOLMER, SKOVSTED, & WILLIAMS, 2002), and in halkieriids like *Micrina*, the postulated sister group of the phylum (WILLIAMS & HOLMER, 2002). The laminar sets of *Mickwitzia* contain two kinds of columnar structures (HOLMER, SKOVSTED, & WILLIAMS, 2002, p. 878), as do those of acrotretides (Fig. 1605), differing only in their larger average diameter (5.5 µm). The one like the acrotretide column is composed of concentric layers that normally did not fill the core; the other kind, feasibly homologous with acrotretide domes composed of

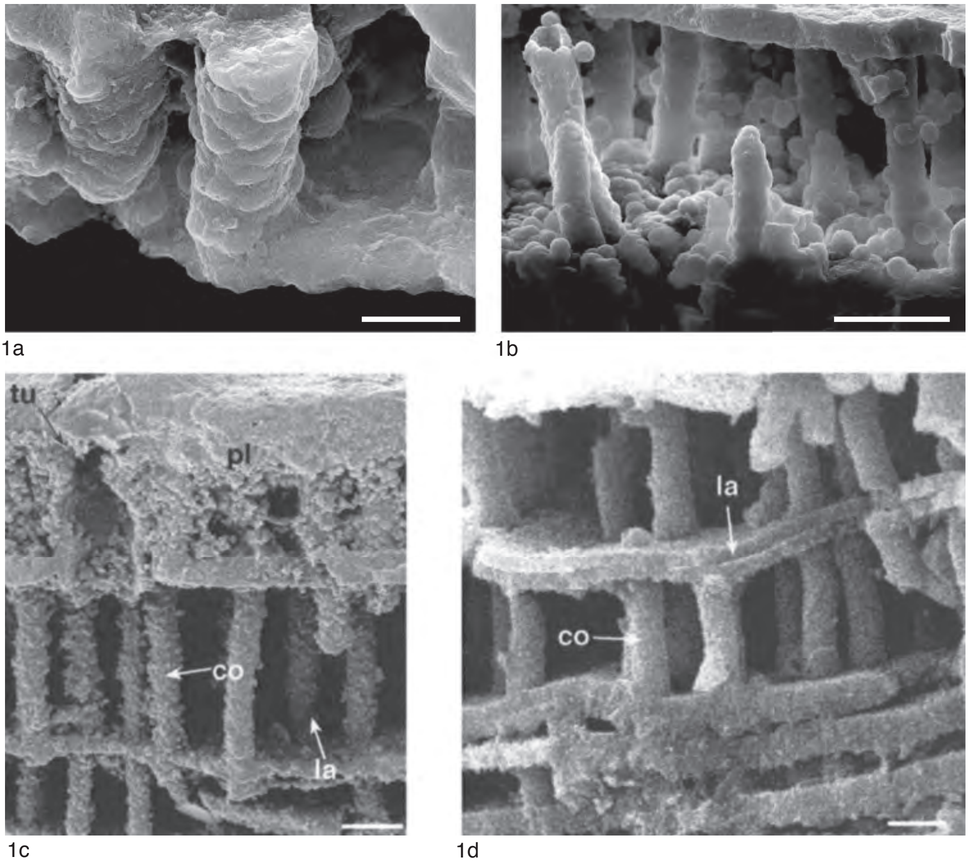


FIG. 1605. *a–b,* SEMs of gold-coated columnar structures of *Mickwitzia* sp. cf. *occidens* WALCOTT, Lower Cambrian; scale bars: 5 and 15 µm (new); *c–d*, SEMs of vertical fractures of shells for *Mickwitzia*, MGUH 26280 and *Prototreta*, GLAHM 14900, showing disposition of columns (*co*) relative to laminae (*la*) and primary layer (*pl*) and external surface in *Mickwitzia*, which is perforated by apertures of tubes (*tu*) with one longitudinal section; scale bars: 10 µm and 5 µm respectively (Holmer & others, 2002).

overlapping plates, consists of vertically stacked discoidal plates (Fig. 1605).

The presence of axial canals in columns and the relative smoothness and constant thickness of columnar walls in any one set have suggested two possible modes of growth. One assumes that mineralized columns were secreted within tubular organic coats by papillose extensions of outer epithelium that were continually entrapped axially by inwardly thickening apatitic walls (HOLMER, SKOVSTED, & WILLIAMS, 2002, p. 878). If that had been so, however, columns and not just canal perforations would have breached interlaminar spaces (compare WILLIAMS & HOLMER, 1992, pl. 4,*5*). The other assumption, which is preferred, is that the apatite of columns and domes aggregated on a chitinoproteinaceous framework morphologically like the lingulide canaliculate system but with a calcifying protein component(s) that promoted apatitic accretion (except in interlaminar spaces where membranes occurred *in vivo*). Certainly, the columnar and camerate fabrics must have owed their individuality to at least two mutually exclusive calcifying protein species that controlled the aggregation of apatite within the chambers of the GAGs of the acrotretide laminar sets. The columns and domes of the secondary shell of

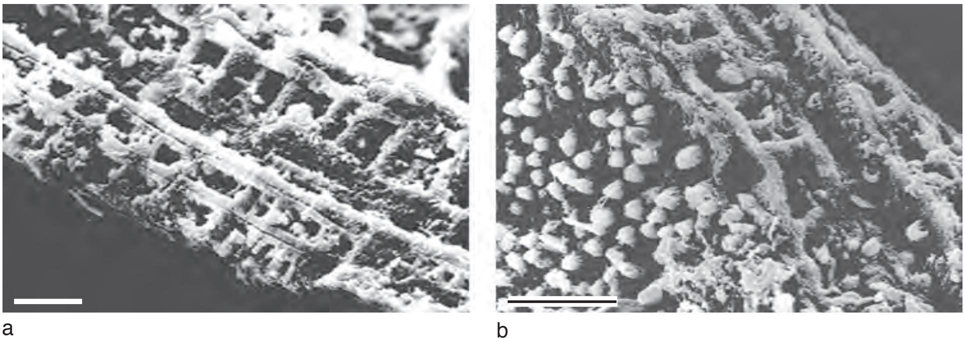


FIG. 1606. *a*, Fracture section of shell of Lower Cambrian *Lingulellotreta* sp., Kazakstan, showing *b,* columnar lamination with domes on an inner surface of a lamina; scale bars: 5 µm (new).

Lingulellotreta (Fig. 1606), with an average diameter of 2.6 µm, are homologous with those of the acrotretide columnar fabric (CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 830). The identification is significant in that the genus is among the oldest recorded lingulides (from the Botomian of the Lower Cambrian; other lingulellotretid genera are baculate; L. E. Popov, personal communication, June 2003). The laminar sets of the secondary shell of the Lower Cambrian halkieriid *Micrina* (WILLIAMS & HOLMER, 2002) are also perforated orthogonally by columns with axial canals (Fig. 1607), which appear to be homologous with the acrotretide columnar fabric. In contrast, the differentiation of cell imprints on the interiors of the obolid *Experilingula* into discrete, hexagonal to rectangular concave pieces (Fig. 1608) are unlikely to be homologues of the acrotretide camerate fabric. These pieces can occur on a sequence of at least three compact laminae; but they are not connected to one another by partitions, only by baculi (CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 826).

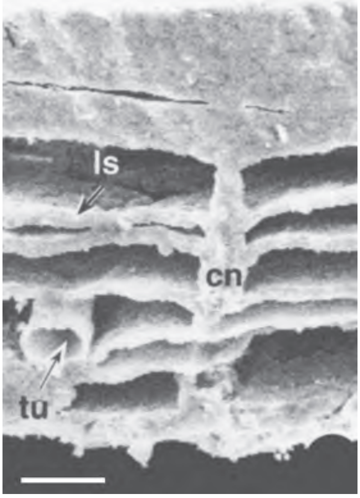


FIG. 1607. SEM of gold-coated fracture section of valve of *Micrina etheridgei,* GLAHM 114748; fracture section view of canals (*cn*) orthogonal to laminar successions (*ls*) relative to internal tube (*tu*) of tubular network; scale bar: 50 µm (Williams & Holmer, 2002).

OTHER LINGULIFORM SHELLS

The shells of the Lower Paleozoic lingulate siphonotretides, the paterinates, and the lingulide eoobolids are also stratiform. Their primary layers were orthodoxly rheological *in vivo,* albeit with bizarre rheomorphic features like the siphonotretide spines (WILLIAMS, HOLMER, & CUSACK, 2004), the paterinide asymmetric folds and basins (WILLIAMS, POPOV, & others, 1998), and the eoobolid asymmetric nodules (see Fig. 1615). Their secondary layers are basically laminar in fabric with little textural elaboration.

In Volume 1 (WILLIAMS, 1997, p. 279), the paterinate secondary shell was described as a laminar succession composed of close-packed hexagonal columns, approximately 8 µm in diameter, that had survived recrystallization only in *Cryptotreta* (Popov & Ushatinskaya, 1987). A more recent study has interpreted the *Cryptotreta* fabric as a succession of predominately organic, stratified laminae with a rhythmic unit of a few micrometers. Each unit bears the imprints of epithelial cells, which simulate hexagonal columns (Fig. 1609–1610). Rare lenticular chambers within the secondary layer contain walls and needles of apatite (with clays) that were presumably filled with GAGs and dispersed apatite in the living state (Williams, Popov, & others, 1998, p. 232).

The hexagonal imprint succession of the *Cryptotreta* secondary shell is not characteristic of other paterinates. It is not unique, however, being sporadically developed, for example, in contemporaneous *Lingulella* (Curry & Williams, 1983); and similar outer epithelial imprints occur on the internal surfaces of stratified laminae underlying posterolateral muscle scars of *Paterina* (Fig. 1611). The persistence of such imprints is attributed to the much higher membranous content of cryptotretid stratified lamination. Paterinid lamination is coarser, with the mineralized component tending to be compact to rubbly in texture (Fig. 1611).

Although the shell of the siphonotretides is stratiform with the usual rheomorphic primary layer and a simple laminar secondary layer, the basic apatitic constituents are different from other linguliforms. They are prismatic laths up to 60 nm or so long with some tablets and basal pinacoids. These components form monolayers stacked like stratified laminae. The laths may be well ordered, like cross-bladed arrays, but they are normally recrystallized to form a platy lamination (Fig. 1612). This platy lamination is randomly separated into nonlinear rhythmic sets by variably developed lenticular chambers up to 50 µm high (Fig. 1613). The chambers contain clusters of laths aggregating into ovoids, plates, and spherulites embedded in a mesh of nanometric-sized acicular apatite (Fig. 1613). A vertical view of the contents of a chamber shows laths arising from highly inclined apatitic plates delineating depressions that presumably accommodated extensions of the apical plasmalemma (Fig. 1614). The platy lamination characterizing the secondary shell of siphonotretides resembles the stratified lamination of other lingulates. The principal basic unit, however, is a lath, not a granular spherule. Moreover, although laths are stacked in monolayers, they may be well ordered but are differently oriented in successive laminae. These differences have chemicostructural implications including: a different calcifying protein that promoted prismatic rather than spherular accretion of apatite; polymeric substrates that facilitated prismatic growths; and a relatively loose attachment of the secreting epithelium to the thickening shell, unlike the close attachment that would have been effected in contemporaneous lingulates by canaliculate frames (lingulides) and apatitic columns (acrotretides). Lenticular cavities with apatitic deposits, sporadically distributed within the

Fig. 1608. View of internal surface of *Experilingula divulgata* Konreva & Popov, Upper Cambrian, Kazakhstan, showing discrete concave pieces of laminae, each secreted by outer epithelial cell and simulating camerate laminations; scale bar: 10 µm (new).

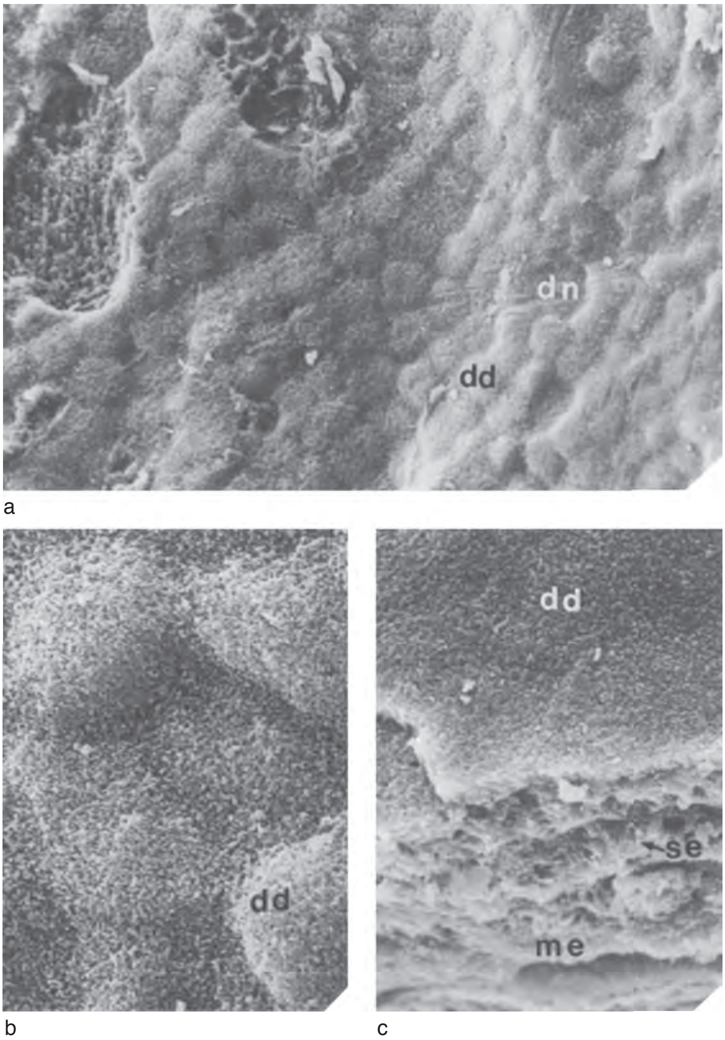


FIG. 1609. *a–b*. *Cryptotreta undosa* (LINNARSSON), Lower Cambrian, Kalmarsund Sandstone, Sweden; general and detailed views of external, subperiostracal surface of undulating lamina with low domes (*dd*) and few relatively depressed areas (*dn*), ×680, ×2800; *c*, *Cryptotreta undosa* (LINNARSSON), Lower Cambrian, Kalmarsund Sandstone; fracture section showing external surface with low domes (*dd*) underlain by stratified laminae of lithified membranes (*me*) and spherules (*se*), ×2000 (Williams, Popov, & others, 1998).

secondary layer, probably originated *in vivo* as localized exudations of excessive quantities of GAGs with dispersed apatitic granules. During fossilization the GAGs would have dehydrated and degraded to leave behind residual apatitic aggregates mainly as meshes of prismatic rods and laths.

The secondary fabric of *Eoobolus* has been described as virgose and precursory to baculation (CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 835). Well-preserved shells of *E. pristinus* from Greenland, however, reveal that the fabric of their stratiform successions is unlike those of other lingulides. The primary and secondary layers are separated by a break in succession about 1 µm thick (Fig. 1615b). The break is periodically sealed at inclined junctions marking the lamellose grooves on

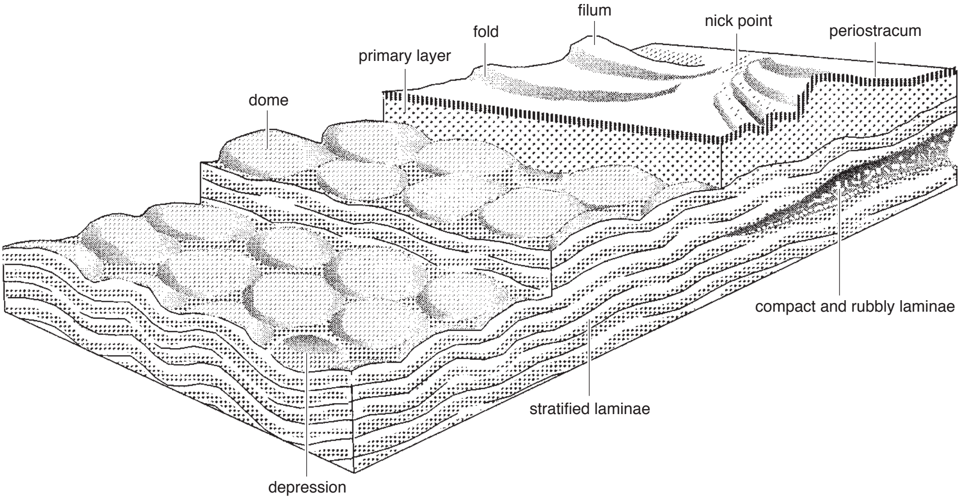


FIG. 1610. Diagrammatic representation of inferred shell structure of cryptotretid paterinates (Williams, Popov, & others, 1998).

the shell surface (Fig. 1615a). The stratified lamination of the secondary layer includes horizontal chambers with widely spaced laminar partitions (Fig. 1615b–c). The chambers are lined by unordered, low stacks and mounds of prismatic tablets of apatite up to 2 µm in size (Fig. 1615d). The fabric has been recrystallized but is neither virgose nor incipiently baculate. Presumably the tablets bear some resemblance to the microstructures that crystallized within the GAGs chambers of the eoobolid living shell.

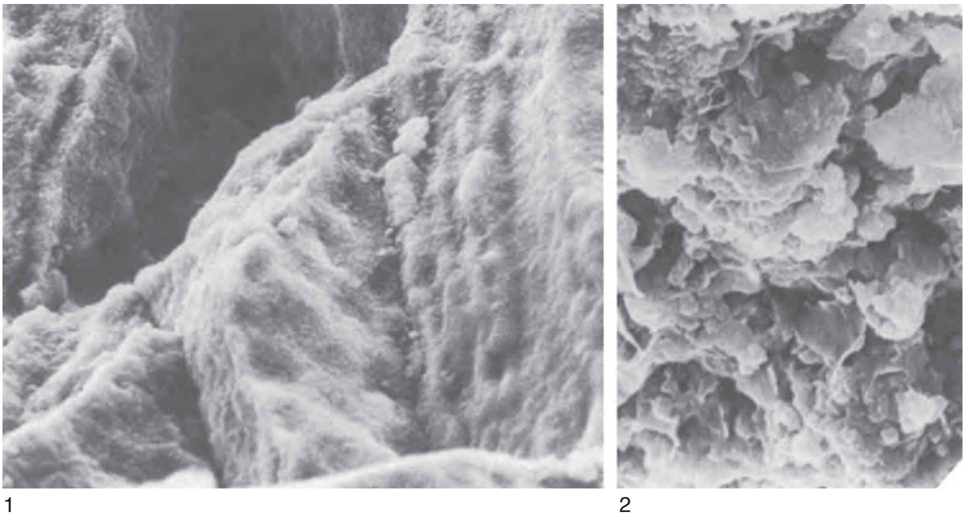


FIG. 1611. *Paterina*? sp., Lower Cambrian, Flinders Range, Australia; *1*, general view of succession of stratified laminae in posteromedian fracture section of mature dorsal valve with exposed internal surfaces bearing hexagonal, close-packed depressions, ×1050; *2*, *Dictyonites perforata* COOPER, Middle Ordovician, Pratt Ferry Formation, Alabama; fracture section of another bounding wall composed of stratified laminae, ×3000 (Williams, Popov, & others, 1998).

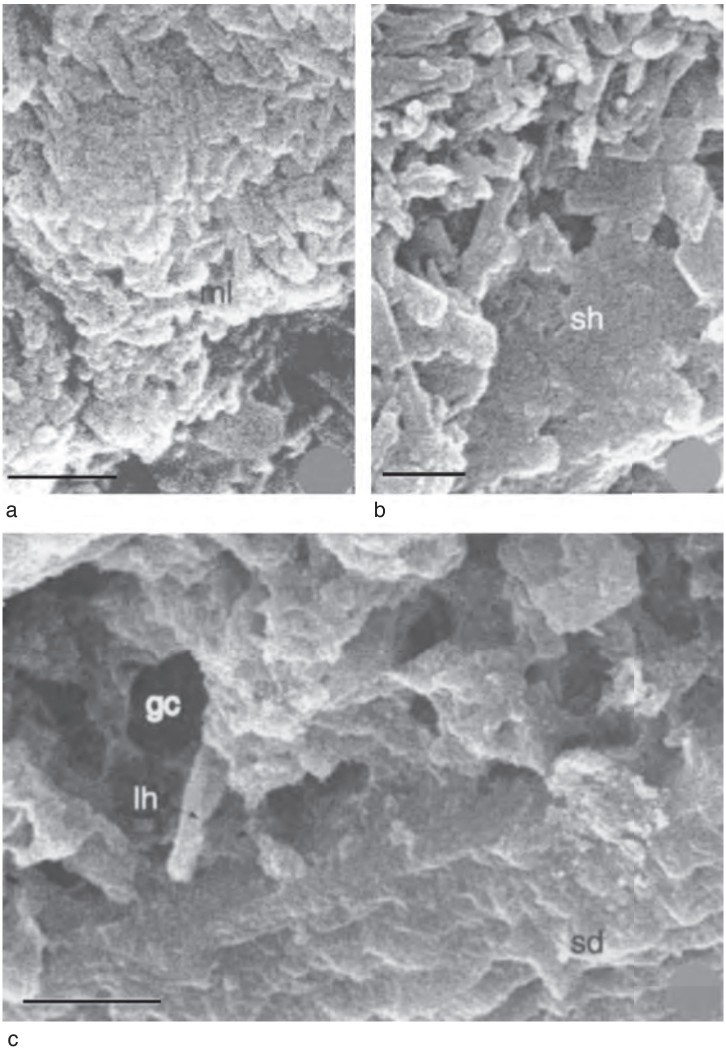


FIG. 1612. SEMs of gold-coated fracture sections of valves of *Siphonotreta unguiculata* (*a*, *c*, GLAHM 1147891; *b*, Br 135730); *a,* basic units of secondary layer, consisting of prismatic laths and minor pinacoidal plates, arranged in monolayers (*ml*) that usually recrystallized (view *b*) into platy laminae (*sh*), occasionally in a cross-bladed arrangement; scale bars: 0.5 µm; *c*, constituents of GAGs chambers (*gc*), floored by stratified laminae (*sd*), consisting of laths (*lh*); scale bar: 5 µm (Williams, Holmer, & Cusack, 2004).

The eoobolids are lingulide-like morphologically, including a pitted juvenile shell. Their relatively simple secondary shell succession is assumed to be a short-lived variant of the linguloid baculate fabric and not homologous with that of either the siphonotretides or the paterinates.

ORGANOPHOSPHATIC SHELL OF *MICRINA*

The problematic *Micrina* consists of a pair of bilaterally symmetrical (sellate and mitral) sclerites that have been interpreted as homologues (WILLIAMS & HOLMER, 2002) of the dorsal shells of *Halkieria* (CONWAY-MORRIS

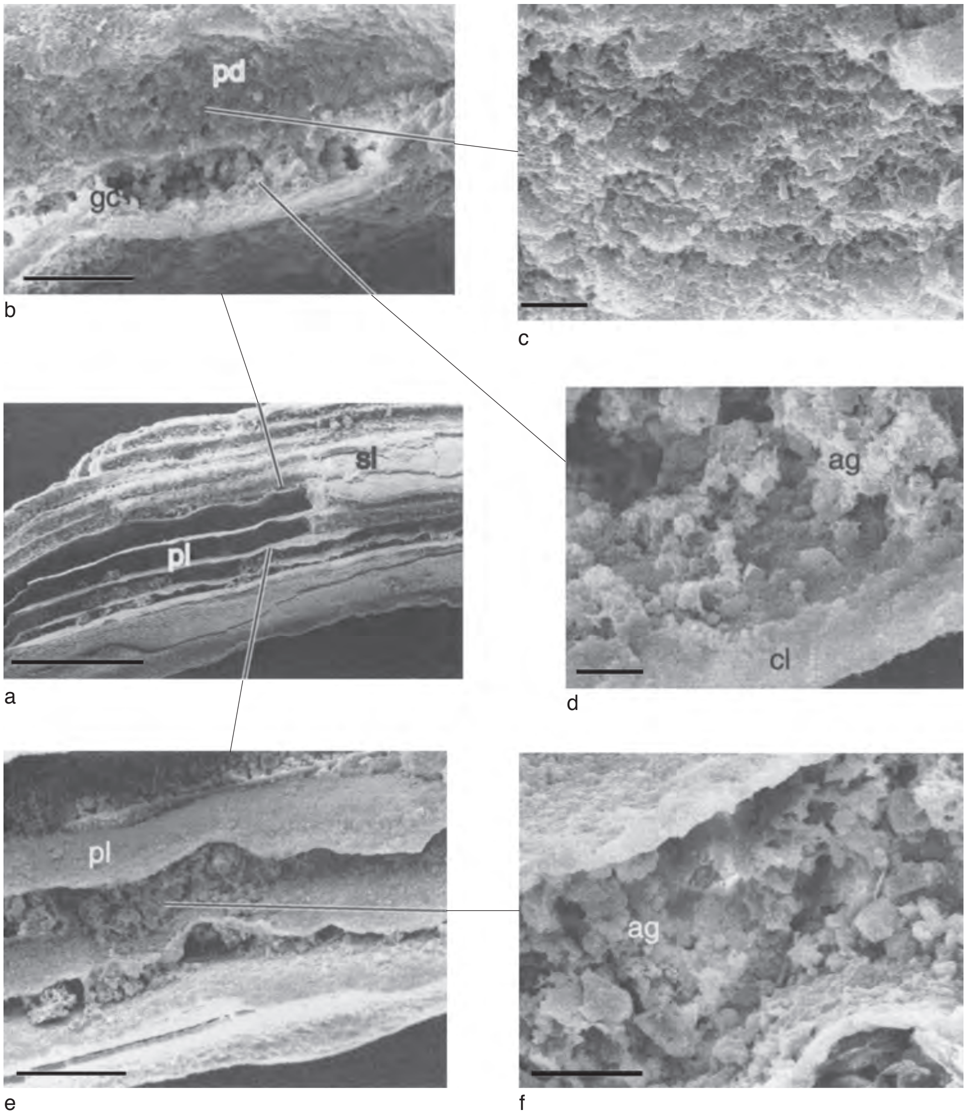


FIG. 1613. Internal view (*a*) and details of part of a mature margin of a dorsal valve (GLAHM 114792a) of *Siphonotreta unguiculata* with lamellae composed of primary shell (*pl*), secreted by a retractable outer mantle fold, interleaved with secondary shell (*sl*); *b*, presumed GAGs chamber (*gc*) within a stratiform succession (views *b–c*) of platy laminae (*pd*), partly compacted and cleaved (*cl*) as in *d* and containing apatitic aggregates (*ag;* view *d*); *e*, rheomorphically folded lamellae (*pl*) that enclosed GAGs chambers (view *f*) with apatitic aggregates (*ag*): scale bars: 1 mm, 50 µm, 5 µm, 5 µm, 200 µm, and 50 µm respectively (Williams, Holmer, & Cusack, 2004).

& PEEL, 1995). The stock has been identified as the sister group of the brachiopods mainly because the apatitic laminar shell of *Micrina* is virtually indistinguishable in structure from the organophosphatic stratiform shells of linguliform brachiopods (WILLIAMS & HOLMER, 2002). This skeletal homology has gained credence from the discovery that the shell structure of *Mickwitzia*, a stem-group brachiopod, is essentially an acrotretide columnar fabric perforated by the setigerous tubes of *Micrina* (HOLMER, SKOVSTED, &

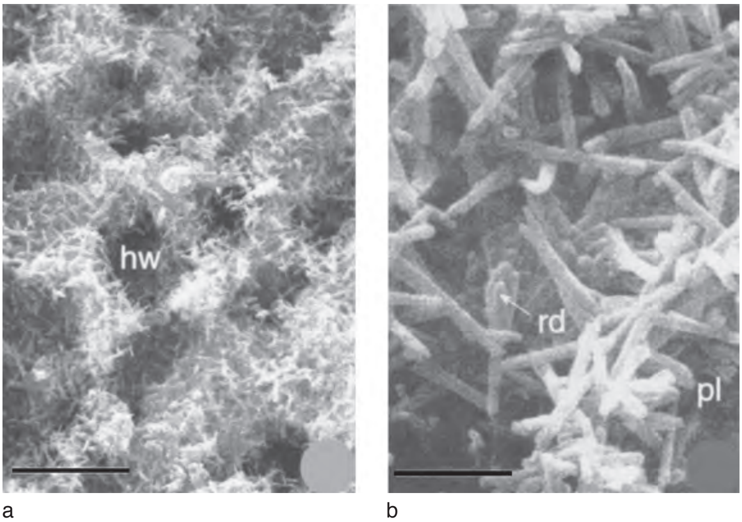


FIG. 1614. SEMs of gold-coated surfaces and fracture sections of *Siphonobolus uralensis*, GLAHM 114780; *a–b*, views of fractured edge and interior of GAGs chamber of mature valve showing mesh of rods (*rd*), laths, and plates (*pl*) indented by hollows (*hw*); scale bars: 5 µm and 1 µm respectively (Williams, Holmer, & Cusack, 2004).

WILLIAMS, 2002), which will be described later. The prospect that the fine structure of the *Micrina* sclerites could have been an ancestral brachiopod fabric has prompted this description, in linguliform terminology, of *Micrina* lamination.

The rheomorphic primary layer of *Micrina* sclerites typically consists of monolayers of platy apatite. The basic aggregates of the secondary layer are also monolayers that amalgamate into compacted, stratified laminae approximately 7 µm thick (Fig. 1616). Laminae delineate chambers that, when contiguous, are usually separated by empty slots or sutured interfaces. The chambers are the dominant structures of the *Micrina* secondary layer, but only their disposition in the mitral sclerite will be described (Fig. 1617). In the medial, abdeltoid zone of the sclerite, where the shell may be less than 100 µm thick, several discrete laminar successions are disposed more or less parallel to the external surface of the sclerite. Each discrete succession is divided medially by slots or impersistent sutures, presumably the sites of degraded membranes that served as substrates for oppositely thickening laminae. Each pair of laminae thicken toward each other to define the medial part of a chamber and are separated by a space diverging toward the sclerite margin. Here they unite into a lobe to enclose the marginal part of the chamber, which may be up to five times thicker than the medial space. In effect, a complete chamber is like an eccentric, thick-rimmed, shallow saucer enclosed by a pair of platy laminae continuous at the rim. The laminar sets enclosing chambers are arranged in a stack of increasingly larger saucers, a disposition that is virtually the same as that of columnar and baculate laminar sets in lingulate brachiopods. The chambers contain sporadically distributed clusters of crystalline bodies, mostly spherulites but also prisms and fascicles of lath or prisms of apatite (Fig. 1618). These clusters are common in the thickened margins of chambers where they are fused to the last-formed surfaces of the bounding laminae; they also aggregate around the tubes running through the chambers. As in lingulates, the chambers were probably filled with GAGs and dispersed apatitic granules *in vivo*. Indeed the main differences between the *Micrina* and lingulate shells are textural. In *Micrina*,

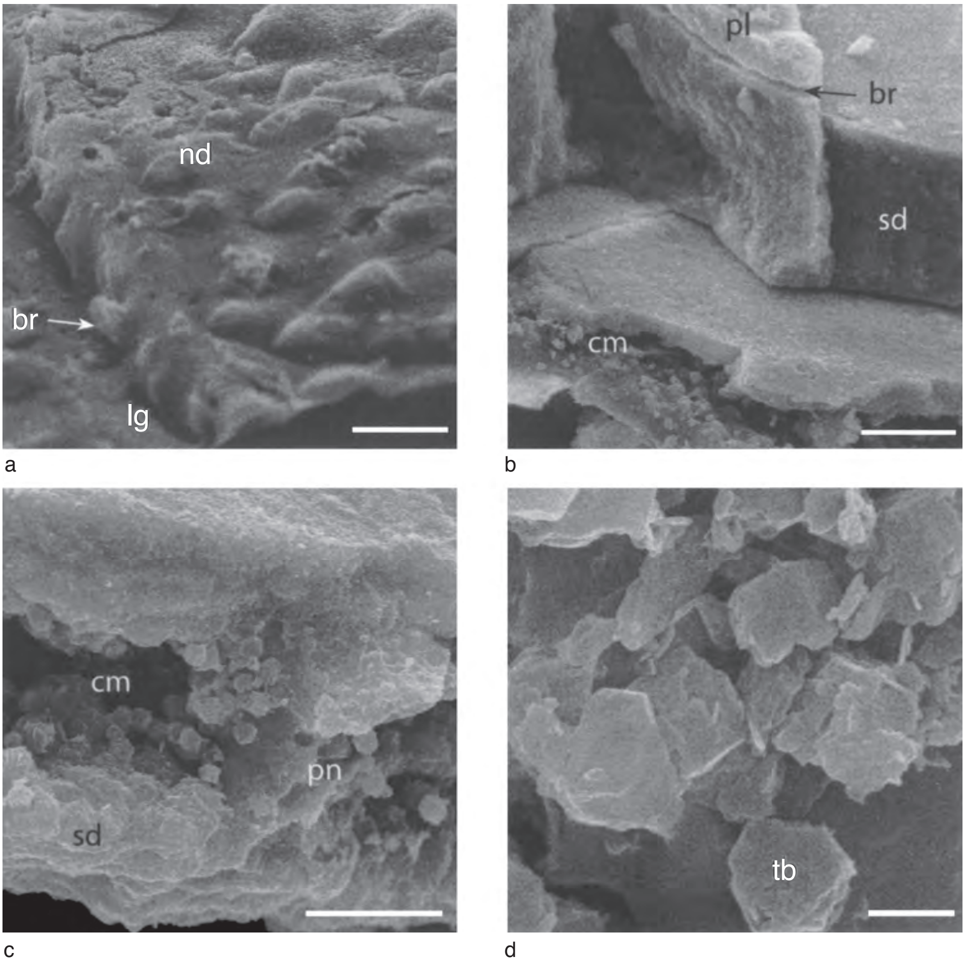


FIG. 1615. Surface ornamentation and shell structure of *Eoobolus pristinus* (POULSEN), Lower Cambrian, northeastern Greenland; *a*, oblique view of shell surface showing nodular ornamentation (*nd*) and a break (*br*) within a lamellar groove (*lg*); *b*, stratiform succession of shell with break (*br*) separating primary layer (*pl*) from secondary layer consisting of stratified laminae (*sd*) with chamber (*cm*); *c*, chamber (*cm*) within stratified laminar succession (*sd*) bounded by laminar partition (*pn*) with *d,* detail of apatitic prismatic tablets (*tb*) lining chamber; scale bars: 20 µm, 20 µm, 10 µm, and 1 µm respectively (new).

laminae are platy (not granular), and the apatitic aggregates in the chamber are spherulitic (not spherular). Such differences suggest that the calcifying proteins responsible for the mineralization of the *Micrina* sclerites were not the same as those controlling the development of the lingulate shell, despite the similarity of skeletal architecture.

ORGANOPHOSPHATIC TUBES

The shells of the lingulate siphonotretides and of *Micrina* and *Mickwitzia*, the postulated sister and stem groups respectively of the Brachiopoda, are pervaded by organophosphatic tubes that grew independently of lamination. The tubes are assumed to have given rise to mineralized surface features or

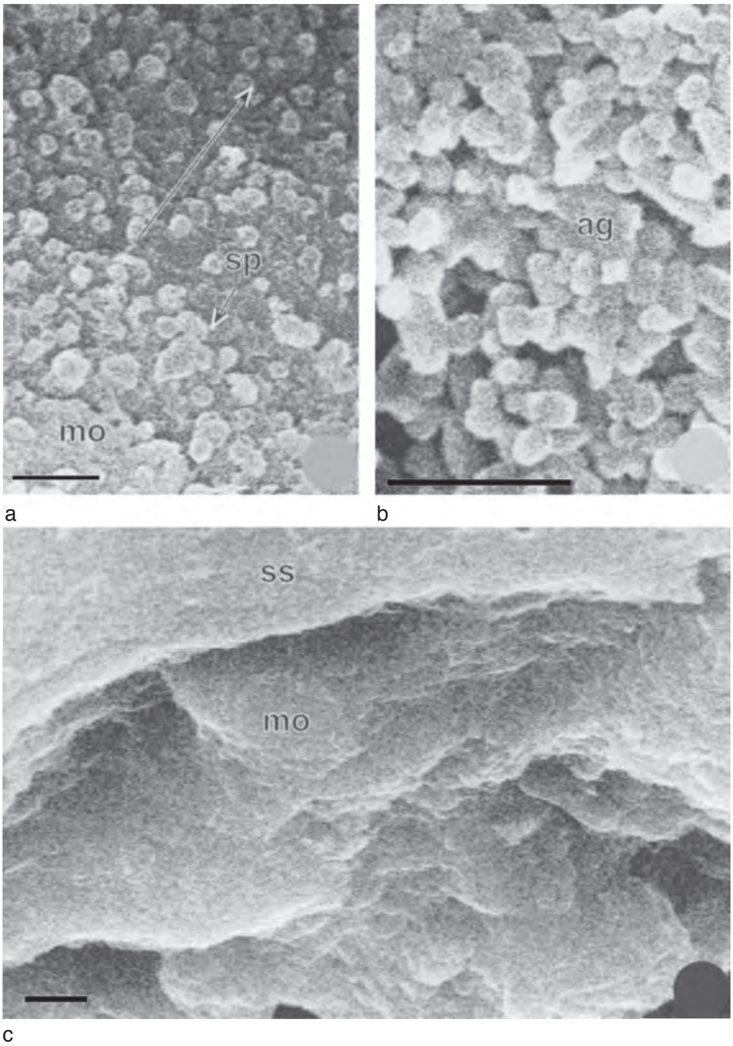


FIG. 1616. SEMs of gold-coated surfaces of mitral sclerites of *Micrina etheridgei*; *a*, GLAHM 114738, *b*, GLAHM 114744, *c*, GLAHM 114742; *a–b*, details of laminar surfaces showing pinacoids and prisms of apatite forming variably aggregated (*ag*) monolayers (*mo*) of tablets and discoids, facing directions of crystallographic steps (*sp*) indicated by *arrows*; scale bars: 1 and 0.5 mm respectively; *c*, platy monolayers (*mo*) of primary layer at margin of young sclerite as seen in oblique fracture, beneath external surface (*ss*); scale bar: 1 mm (Williams & Holmer, 2002).

to have contained setae; and a description of them is relevant to our understanding of brachiopod phylogeny as well as shell growth.

Except for *Schizambon*, the shells of all siphonotretides are perforated by unbranched canals, 20 to 80 or so µm in diameter, disposed orthogonally to lamination and leading to pits and spines ornamenting shell surfaces. Both pits and spines in similar offset patterns characterize postjuvenile shells. Pits are the sole ornamentation of a few siphonotretides, such as *Helmersenia*. On the more mature surface of most siphonotretides, however, pits are replaced by spines as in *Siphonotreta*.

The canals are differentiated at the shell margin as holes with sharp edges perforating

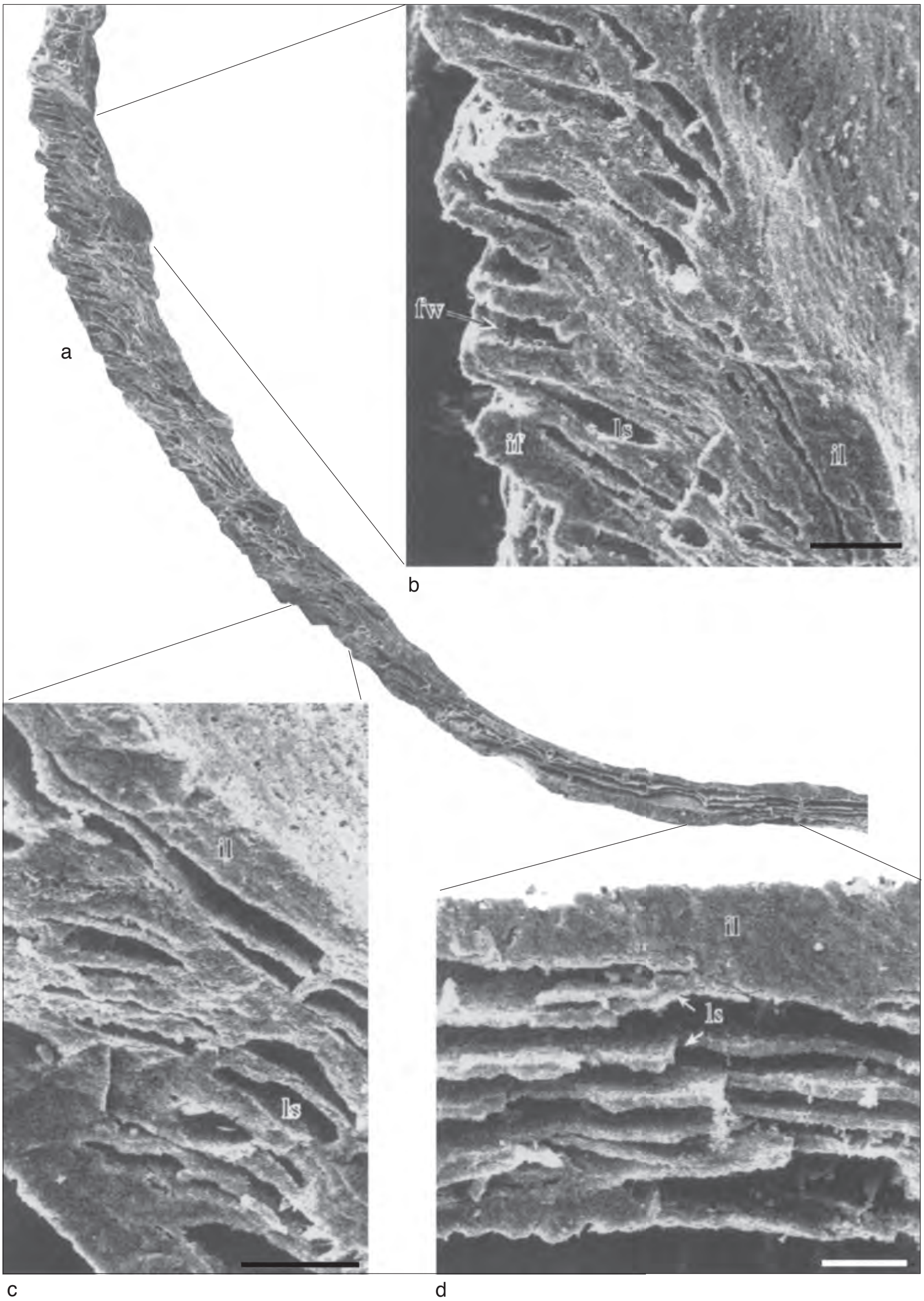


FIG. 1617. *a–d,* Half of transverse fracture section of mature mitral sclerite of *Micrina* (GLAHM 114738) showing progressive tilting of spherulitic laminar sets (*ls*) toward margin, relative to internal lamina (*il*) composed of bases of sets; furrows (*fw*); and chambers of sets with apatitic infills (*if*); scale bars: 100 µm (*b–c*) and 50 µm (*d*) (Williams & Holmer, 2002).

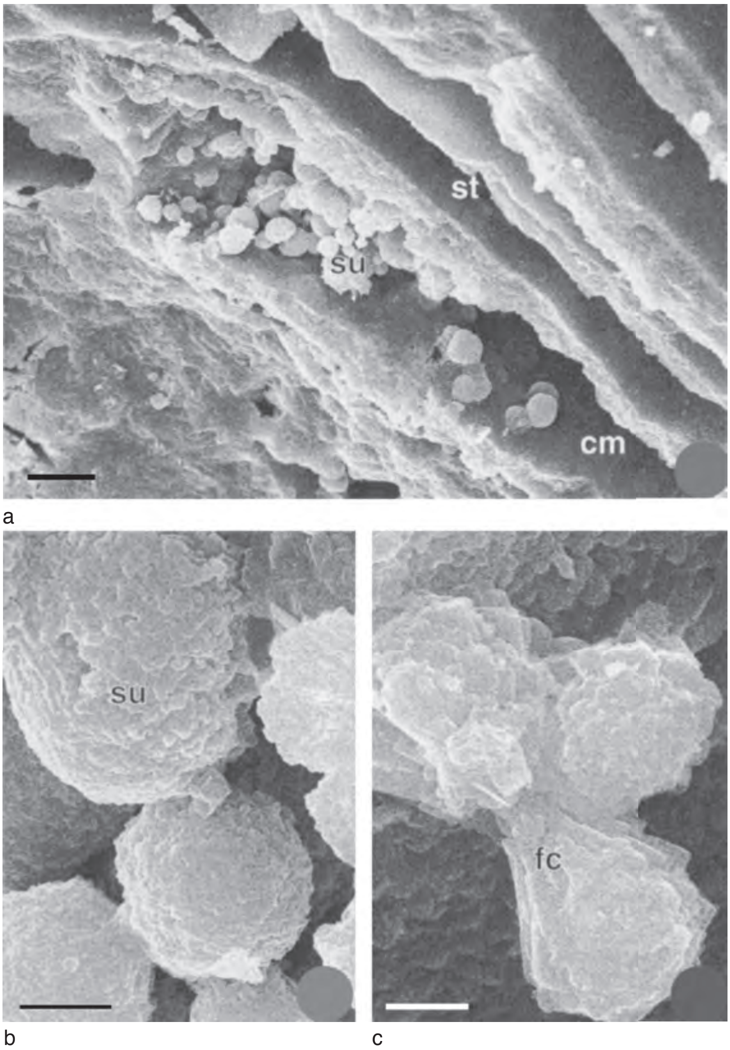


FIG. 1618. SEMs of gold-coated surfaces and fracture sections of mitral sclerites of *Micrina etheridgei*: *a–b*, GLAHM 114738; *c*, GLAHM 114746; *a*, transverse fracture section of laminar succession showing slots (*st*) between sets and spherulites (*su*) adhering to both walls of chamber (*cm*); scale bar: 20 µm; *b–c*, spatitic crystalline bodies in chambers of laminar sets, as platy spherulites (*su*) and prismatic fascicles (*fc*); scale bars: 2 and 1 µm respectively (Williams & Holmer, 2002).

the outer primary layer and are big enough to have been occupied by collectives of up to ten cells (Fig. 1619). Such collectives would have been generated as part of the outer mantle lobe but independently of surrounding vesicular cells. Each collective (acanthoblast of WILLIAMS, HOLMER, & CUSACK, 2004, p. 1333) would have been coated by a membrane that served as an organic coat ensheathing acanthoblasts in canals lacking mineralized walls as in *Helmersenia* (Fig. 1620) or as a substrate for apatitic canal walls like those penetrating the shell of *Siphonotreta* (Fig. 1621). The canal walls are best seen at the external surface where they emerge as spinal bases (Fig. 1622). The wall, being up to 10 µm thick, is normally recrystallized but traces of laminar stratification concentric to the axis can occur. The axial cavity, occupied

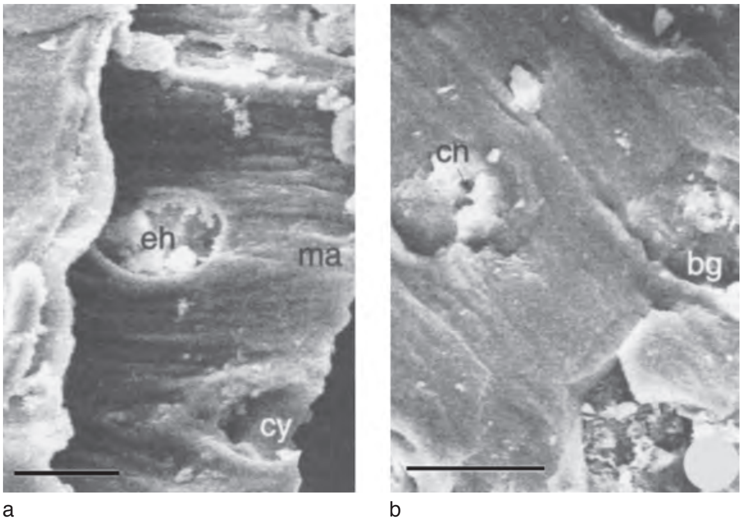


FIG. 1619. SEMs of gold-coated surfaces of valves of *Siphonotreta unguiculata*; *a,* internal view of margin (*ma*) of lamella showing elliptical holes (*eh*) with canopy (*cy*) within a slip stream of grooves orthogonal to margin; scale bar: 50 µm; *b*, internal laminar surface near margin of valve showing structural distinctiveness of penetrating spines with bounding walls (*bg*) and canals (*cn*); scale bar: 100 µm (Williams, Holmer, & Cusack, 2004).

by an acanthoblast in life, may be 30 µm in diameter but can be virtually closed by centripetally secreted apatite. The canal walls with their outer membranous coats retained their structural identity within the thickening shell as seen in fracture sections (Fig. 1621) and especially where they emerge as bosses and pillars within chambers that would have been filled with GAGs and apatitic aggregates *in vivo* (Fig. 1621). Both bosses and pillars normally have axial canals; coarse growth banding commonly gives pillars a crudely stacked appearance.

At the shell surface of *Helmersenia*, the canals are continuous with funnel-shaped antechambers with subcircular rims (Fig. 1620). The rim is broken anteroradially by a roughened, tongue-shaped depression. Within the rim, there is a ring composed of ledges of stratified laminae, some of which may extend centrally to form a concave sheet that may have been perforated in the living state. The morphology and textures of antechambers suggest that *in vivo* they contained degradable thornlike tubercles composed largely of chitin (Fig. 1620; WILLIAMS, HOLMER, & CUSACK, 2004, p. 1332).

The pits on the immature shell of *Siphonotreta* are not differentially structured like those of *Helmersenia* and were probably capped by simple, apatitic canopies or phosphatized membranes (compare those of *Acanthambonia,* Fig. 1623) that would have covered part of the acanthoblast occupying the membrane-lined pit. In later stages of shell growth this part of the acanthoblast would have started growing anteroradially and secreting apatitic laminae on its membranous coat to form a spine.

Spines vary in length and thickness (Fig. 1624). They may be several millimeters long but are seldom preserved intact, while their basal diameters average 80 µm. Although they originate in an offset pattern, they can be densely distributed, especially at the margins of mature shells (Fig. 1624). A typical spine has all the characteristics of a rheological body (Fig. 1622). Long creases deform the base while shorter, transverse ones indent the spinal surface away from the shell. Swellings also occur, as do growth bands and disruptions that dislodge segments. Spines are composed of at least one layer of apatite forming the bounding

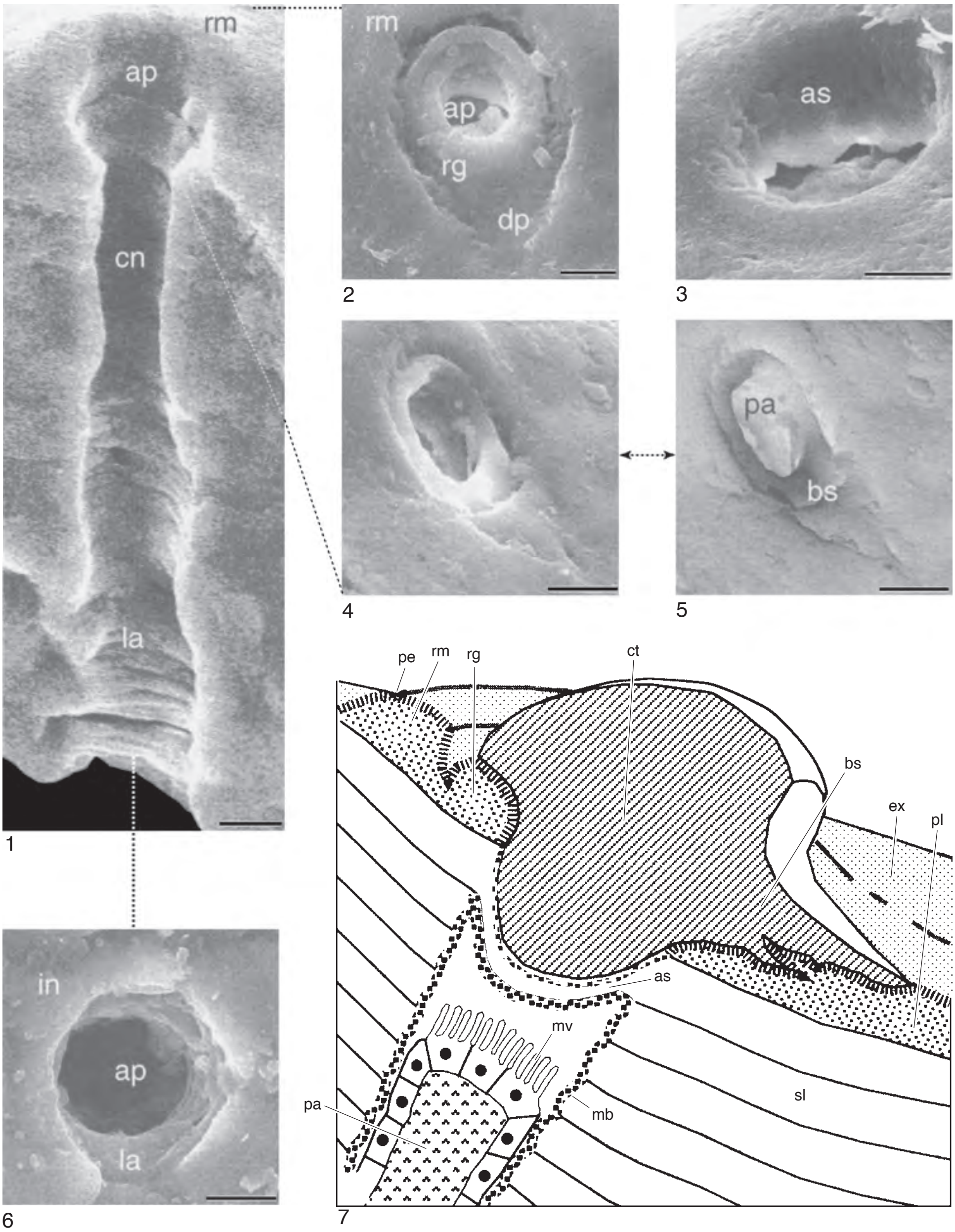


FIG. 1620. Various features of canals of *Helmersenia* (*1–6*) with diagrammatic reconstruction of distal parts of canal in living stage (*7*); *1,* vertical section through canal (*cn*) showing laminar ledges (*la*) forming wall with aperture (*ap*) and raised posterior rim (*rm*) at shell surface and internal (*in*) aperture (*6*) delineated by laminar ledges (*la*), GLAHM 114789; *2–3*, two external apertures (*ap*) in vertical and oblique views (GLAHM 114790, 114801) showing rims (*rm*), ring (*rg*), apatitic sheet (*as*), and anteroradial, tonguelike depression (*dp*); *4*, oblique view of external aperture, with inverted image (*5*) showing disposition of assumed papilla (*pa*) and basal chitinous sheets (*bs*) (GLAHM 114801); *7*, assumed components of canal in living shell with external (*ex*) periostracum (*pe*), rim (*rm*), and ring (*rg*) of primary layer (*pl*) with surface aperture, bounded by concave apatitic sheet (*as*), containing a chitinous (possibly with dispersed apatite) tubercle (*ct*) with basal sheets (*bs*) anteroradially and canal perforating secondary laminar layer (*sl*), lined with membrane (*mb*), and containing microvillous (*mv*) papilla (*pa*); scale bars: 10 µm (Williams, Holmer, & Cusack, 2004).

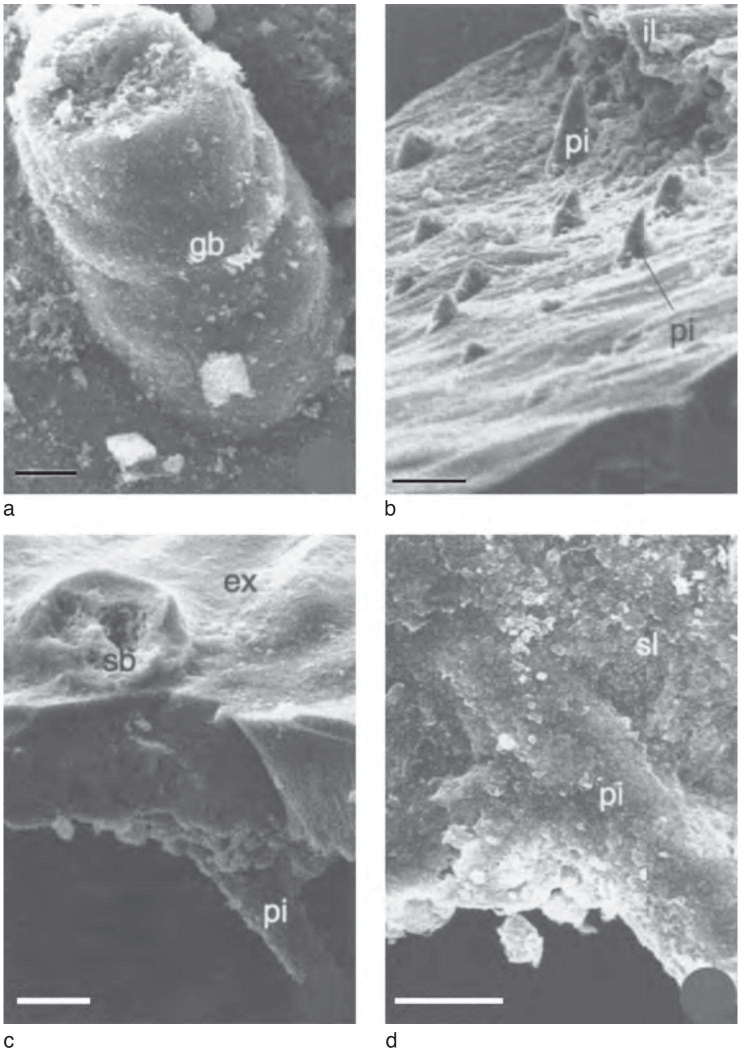


FIG. 1621. SEMs of gold-coated fracture sections and surfaces of *Siphonotreta unguiculata*; *a–b*, views of valve interiors showing bands of valve floors delineated by ridges (*il*) corresponding to external lamellae and containing arrays of pillars (*pi*) that may be growth-banded (*gb*) and terminated within a GAGs chamber; scale bars: 10 µm and 100 µm respectively; *c–d*, fracture sections showing penetration of recrystallized shells (*sl*) by pillars (*pi*) to connect with spinal base (*sb*) at valve exterior (*ex*); scale bars: 50 µm and 20 µm respectively (Williams, Holmer, & Cusack, 2004).

wall to an axial canal, which is variably constricted by an additional inner laminar layer(s).

The stresses set up by the differential growth of a spine and its supporting strip of shell, exceptionally delineated by grooves (Fig. 1622), gave rise to transverse folds around the spinal base at the surface and caused the forward bend of the spinal pillar within GAG chambers of the secondary layer. Such strains account for the boomerang shape of a spine, its canal wall, and internal pillar, all secreted by an acanthoblast (Fig. 1625).

The preeminent canal system of *Micrina* consists of a regular network of mineralized tubes that open at the external surfaces of both sclerites. On surfaces that grew radially

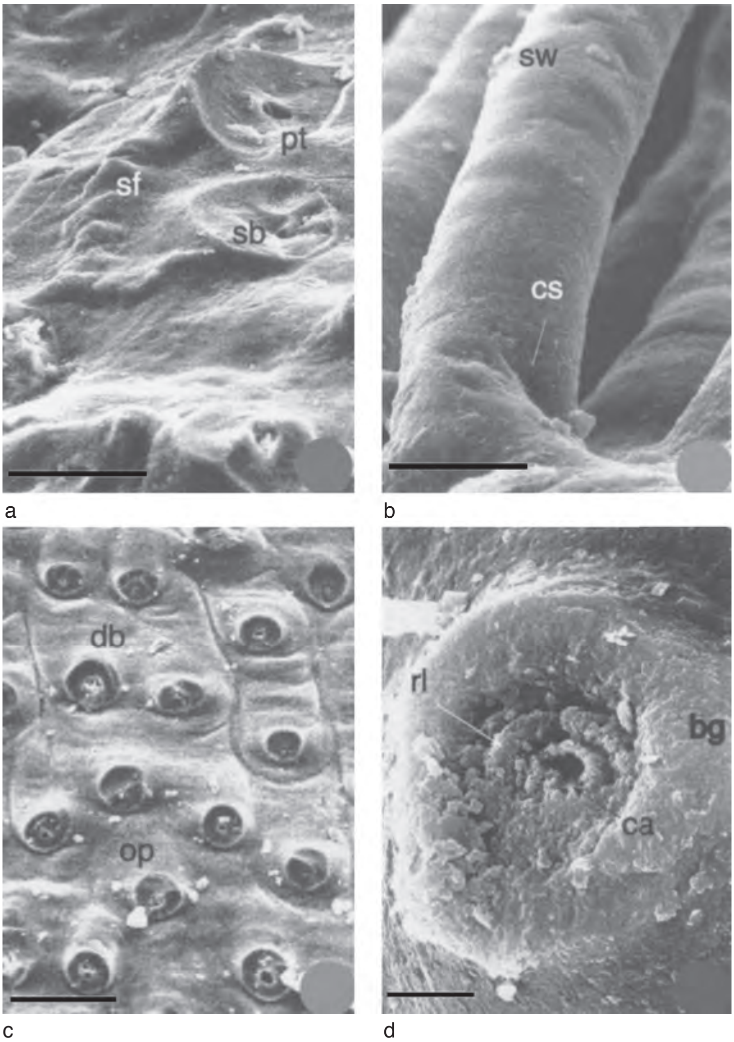


FIG. 1622. SEMs of gold-coated surfaces of valves of *Siphonotreta unguiculata*; *a–b*, conchoidally fractured spinal bases (*sb*) and pits (*pt*) with axial canals in relation to scalloped fila (*sf*) and views of creases (*cs*) at bases of spines with growth banding, sporadic swellings (*sw*); scale bars: 100 µm and 50 µm; *c*, spinal bases in offset (*op*) and dichotomous (*db*) arrangements, each delineated by a groove and contained between posterior transverse folds; scale bar: 200 µm; *d*, transverse section of large spine near its base, showing bounding wall (*bg*), a secondary layer of rubbly apatitic aggregates (*rl*), and tubular wall of compacted apatite (*ca*) delineating axial canal; scale bar: 10 µm (Williams, Holmer, & Cusack, 2004).

at a steady rate, the funnel-shaped openings are spaced concentrically, approximately 100 µm apart, and in alternating arcs (Fig. 1626). In zones where radial growth was slower, as at the sclerite margins, openings and tubes tend to crowd together (Fig. 1627). The tubes, circular to elliptical in cross section, extend throughout most, if not all, of the laminar secondary layer. They are disposed orthogonal to the external surface in the apical region (Fig. 1627) but become increasingly inclined marginally where they may lie virtually subparallel with laminar sets (Fig. 1627) and in line with hemicylindroid imprints extending beyond their funnels (Fig. 1625). The external surface

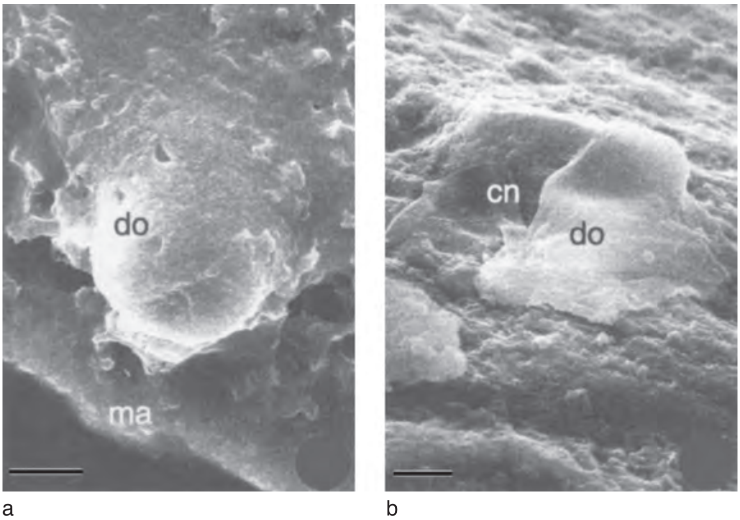


FIG. 1623. SEMs of gold-coated surfaces of *Acanthambonia delicatula* (GLAHM 114794, 114787). Surfaces of immature valves showing partial domes (*do*) that served as spinal joints at external surface, near valve margin (*ma*), and in oblique view with exposed canal opening (*cn*); scale bars: 10 µm and 25 µm respectively (Williams, Holmer, & Cusack, 2005).

of a tube is typically smooth with sporadic accretions of spherulites, laths, and prisms. The tube wall is approximately 4.5 µm thick and is composed of stratified laminae lying parallel with the surface. The tube interior is striated by alternating grooves and ridges parallel with the long axis. The ridges, up to 800 nm wide, are composed of flat-lying, well-ordered discoidal to subhexagonal tablets (Fig. 1628). Each tube consists of three elements: a superficial, funnel-shaped opening separated from the internal hollow, striated tube by an outwardly concave, perforated plate(s) (Fig. 1628). The funnel is typically approximately 10 µm deep with smooth, gently curved surfaces covering horizontally disposed stratified laminae of the primary layer. Its inner boundary is a sharply jagged rim separating it from an antechamber approximately 10 µm deep, with smooth, bulging walls. The inner boundary of the antechamber is a smooth ledge, below which is an outwardly concave apical plate (Fig. 1627) that, when complete, is indented by three oval imprints.

The structure and function of these mineralized tubes and their components in the living state have been interpreted as follows (Fig. 1629). The structures and impressions associated with funnels are consistent with their having contained organic rods that were disposed at high angles in the medial regions but tangentially toward the margins of mature sclerites. The cuticle of such a rod could have been continuous with the periostracum covering the sclerite along the jagged inner edge of the funnel. The base of the rod would have consisted of a disk occupying the antechamber, and, below the inner ledge, a hemisphere with three bosses that fitted into oval depressions or perforations in the outwardly concave plate that could have been little more than a phosphatized membrane. Because the apatitic tubes carrying the canals were secreted independently of laminar sets, they would have been deposited within a cylindroid organic coat that determined the diameter of the tube *ab initio*. The grooves striating the inner surface of the tube walls are consistent in size and disposition with there being casts of microvilli. This ensemble of external organic rods (interpreted as setae) occupying funnels and postulated microvillous cells occupying striated tubes suggests that the cell collectives were setoblasts. That being so, the setal rods and their bases

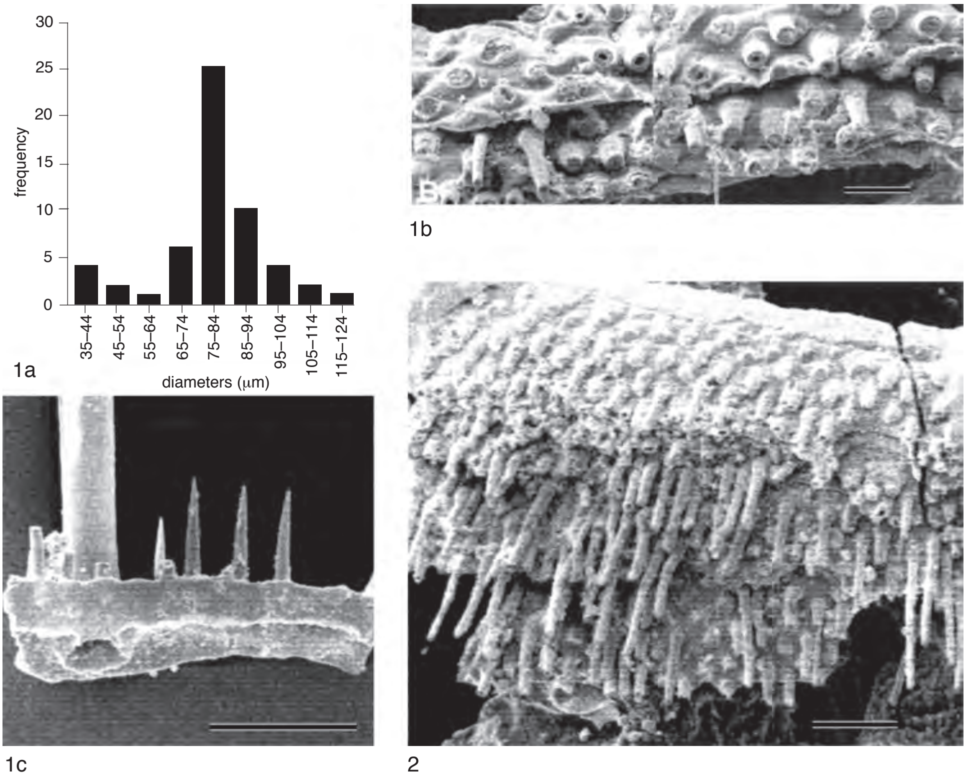


FIG. 1624. Variation in size and distribution of siphonotretide spines; *1a,* range of diameters of 55 spinal bases (mean 80.2 µm) on fragment (*1b*) of *Siphonotreta unguiculata* (GLAHM 114782a, b) bearing two lamellae; scale bar: 200 µm; *1c*, external view of a segment of mature shell of *S. unguiculata* (GLAHM 114781), showing crowded arrays of spines of varying diameter in contrast to differentiated large and small spines of *2, Eosiphonotreta verrucosa*, GLAHM 114798; scale bars: 0.5 mm (Williams, Holmer, & Cusack, 2005).

would have been chitinous and presumably mobile, possibly with fibrillar strands connecting the setal bosses to setoblasts that, however, would usually have been sealed off from the mantle during later sclerite growth (WILLIAMS & HOLMER, 2002).

The columnar shell of the stem-group brachiopod *Mickwitzia* (HOLMER, SKOVSTED, & WILLIAMS, 2002) is also pervaded by hollow tubes approximately 8 µm thick that grew independently of lamination. They are generally disposed orthogonal to the shell surface where they open as smooth rounded apertures. Some tubes are inclined, especially those perforating the ventral pseudointerarea, where they lie more or less in the plane of the pseudointerarea, the external surface of which is frequently indented by semicylindrical depressions immediately distal of the apertures. Striations parallel with their long axes have been found in some of these tubes (Fig. 1630), which are regarded as homologous with those of *Micrina*. The lack of elaborate devices such as antechambers beneath their surface apertures suggests that any setae occupying the apertures would not have been permanent features of the living shell.

EVOLUTION OF THE MATURE ORGANOPHOSPHATIC SHELL

The evolution of the mature linguliform shell is reflected mainly in the diverse fabrics of the secondary layer. The chemicostructure

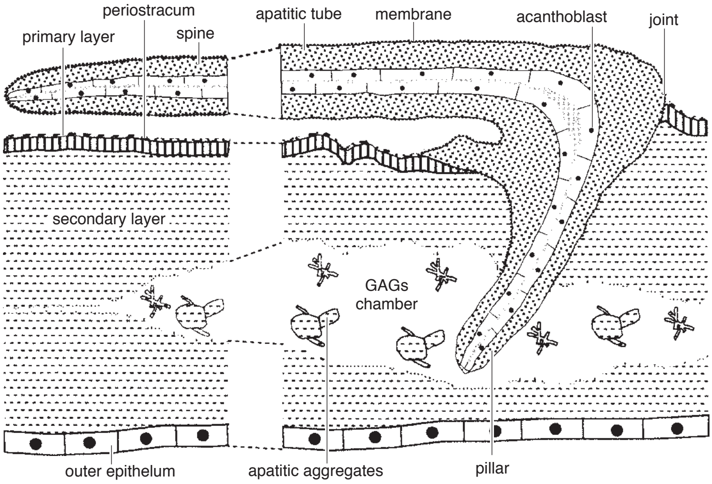


FIG. 1625. Diagrammatic section of *in vivo* siphonotretid integument showing relationship between membrane-bound spine secreted by inferred acanthoblast and stratiform shell secreted by outer epithelium. Reconstruction assumes acanthoblast has been sealed off from outer epithelium and its proximal apatitic tube (pillar) ends with GAGs chamber within secondary layer of shell; forward growth of membrane, showing as substrate for apatitic or GAGs secretion is assumed to have been by intussusception (Williams, Holmer, & Cusack, 2004).

of fossil as well as living shells indicates that the primary layer has always been a rheological coat composed of protein-coated apatite in GAGs; and only superficial rheomorphic and ornamental features survive fossilization. In contrast, six distinctive, long-lasting fabrics with significant textural variations characterize the linguliform secondary shell. Five of these fabrics were fully developed in Cambrian species. Their relationships have been phylogenetically analyzed (Fig. 1631; Table 32–33) on the assumption that all were derived from the secondary shell fabric of a stem-group brachiopod, like *Mickwitzia*, in phase with basic transformations of early brachiopod anatomy.

As shown in Figure 1631, both the columnar and baculate fabrics characterize the short-lived linguloid *Lingulellotreta* (L. E. Popov, personal communication, 2003). The older, columnar fabric is present in the shell of *Micrina*, the assumed sister group of the brachiopod phylum, and is as strongly developed in *Mickwitzia* as in acrotretides. There is no obvious chemicostructural relationship between the columnar and baculate fabrics. The apatite of columns probably aggregated on a chitinoproteinaceous frame disposed orthogonally to lamination, while baculi assembled in living lingulides as interconnected accretionary, apatitic rods with impersistent axial strands.

The columnar fabric, however, is feasibly a mineralized version of the lingulide canaliculate system, which is fabricated independently of baculi. The organic cores of columns would have been a framework similar to the caniculate system in dimensions and disposition. Admittedly, aggregates of apatitic spherules do occasionally adhere to the chitinoproteinaceous walls of canals in living *Lingula* (Fig. 1583), although the sporadic and differential nature of their accretion would preclude their accumulation as solid apatitic columns of uniform thickness. Canals that pass through the baculate fabric of *Glottidia* and living discinids, however, are free of the apatitic spherules that aggregate into baculi (Fig. 1583), as are the organic cores of columns in interlaminar spaces. If both organic frames are homologous, however, the lingulide canaliculate system could have been derived from the columnar fabric by the loss of the calcifying protein dedicated to effecting columnar accretion. In

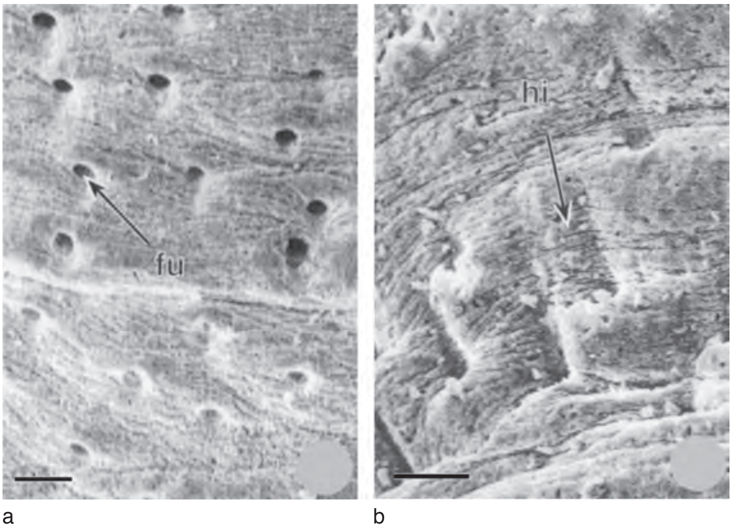


FIG. 1626. SEMs of gold-coated surfaces of mitral sclerites of *Micrina etheridgei; a,* GLAHM 114749; *b*, GLAHM 114741; surface views of funnels (*fu*) of tubular network disposed more or less orthogonally and alternately (*a*) and obliquely (*b*) where they are associated with hemicylindroid imprints (*hi*) indented on rheomorphic folds of external surfaces; scale bars: 100 µm (Williams & Holmer, 2002).

short, the substitution of a calcifying protein promoting baculation for one that effected columnar accretion would have transformed an ancient fabric into another that survives today.

The camerate texture of some acrotretides was also probably mediated by a novel calcifying protein that replaced, or was mutually exclusive with, the protein(s) responsible for the columnar fabric. The first sign of the

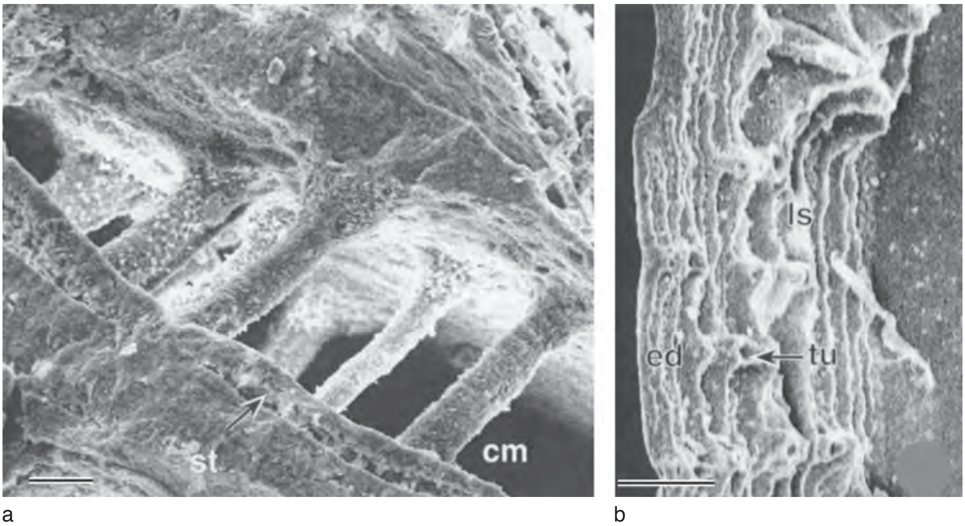


FIG. 1627. SEMs of gold-coated surfaces and fracture sections of sellate sclerites of *Micrina etheridgei*; *a,* tubes traversing a chamber (*cm*) of laminar set delineated by slots (*st*), with coatings of spherulitic apatite, GLAHM 114750; scale bar: 20 µm; *b*, exfoliated laminar sets (*ls*) at margin (*ed*) of mature sellate sclerite showing crowding together of near horizontal tubes (*tu*), GLAHM 114751; scale bar: 20 µm (Williams & Holmer, 2002).

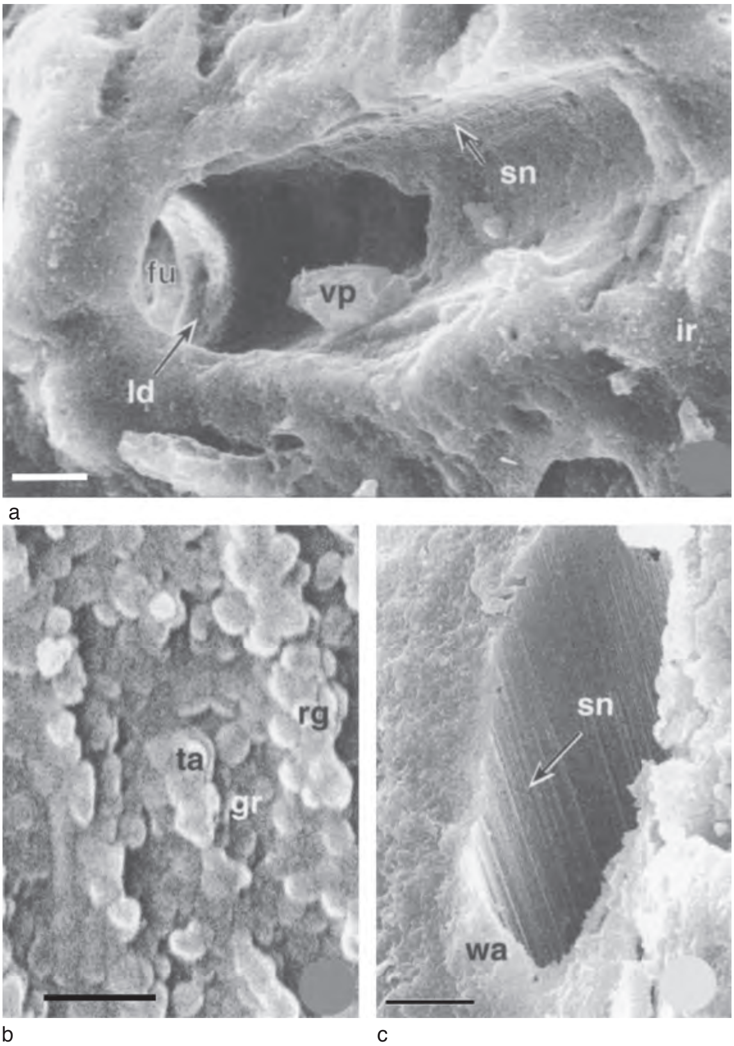


FIG. 1628. SEMs of gold-coated surfaces and fracture sections of mitral sclerites of *Micrina etheridgei*; *a,* general view of slightly inclined tube opening to interior (*ir*) and revealing striations (*sn*) on tube wall, remains of concave plate (*vp*), ledge (*ld*) leading to antechamber and funnel (*fu*); scale bar: 10 µm; *b*, details of tube consisting of grooves (*gr*) and ridges (*rg*) composed of tablets (*ta*), running parallel with tube axis; scale bar: 5 µm; *c,* rheomorphically deformed tube with wall (*wa*) bearing striations (*sn*); scale bar: 5 µm (Williams & Holmer, 2002).

linguloid virgose fabric, which was no later than the Carboniferous, is like a disordered baculation, especially in the way fascicles resemble crossed baculi. Fascicles of living *Lingula*, however, are probably assembled intracellularly and are likely to have originated as a chemicostructural novelty in place of baculate lamination.

In the phylogeny of Figure 1631, the paterinates and the siphonotretides are shown as the most derived linguliforms, but their relationships are open to question. Their defining synapomorphy, a stratiform shell with poorly defined GAGs chambers, confirms that the paterinate and siphonotretide shells are neither columnar nor

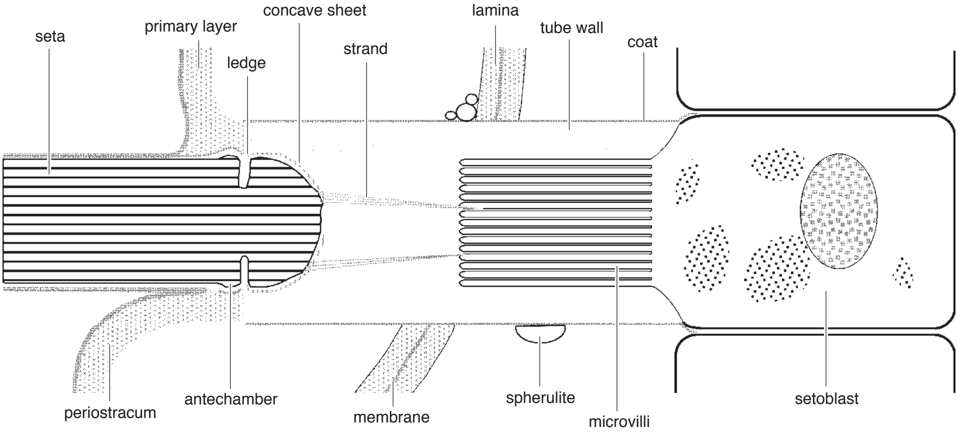


FIG. 1629. Graphical reconstruction of proximal part of seta and associated setoblast assumed to have occupied funnel-like opening leading into apatitic tube penetrating stratiform shell of *Micrina* sclerite (Williams & Holmer, 2002).

baculate and apparently lacked a canaliculate system. Even so, the difference between the acicular and granular nature of their basic apatitic constituents suggests that the similarity of their shell fabrics was due to convergence. The two groups certainly differ from one another as well as other linguliforms in other features. The acanthoblastic spines and tubes of siphonotretides are an apomorphy that developed independently of the setigerous tubes. The most striking differences, however, are those paterinate features that are shared with rhynchonelliforms, including the adductor-diductor muscle system, the development of mantle gonadal sacs, and the fused posterior mantle lobes (WILLIAMS, POPOV, & others, 1998).

ORGANOCARBONATE, TABULAR LAMINAR SHELL

The descriptions in Volume 1 (WILLIAMS & others, 1997, p. 22–23; WILLIAMS, 1997, p. 284–286) of the secretion and structure of organocarbonate, tabular laminar shells were based almost exclusively on investigations by SCHUMANN (1970) and WILLIAMS and WRIGHT (1970). These studies established that the secondary shell of living craniids, consisting of rhombs of calcite interleaved with glycoproteinaceous membranes, grows spirally with the membranes serving as substrates for calcitic tablets that enlarge and multiply by screw dislocation. The fabric of the secondary layer of extinct craniiforms was also shown to be laminar and different from that of the radially prismatic primary layer that characterizes living species (WILLIAMS & WRIGHT, 1970). Since 1997, research has concentrated on the organic constituents of the shell following the discovery that intracrystalline proteins with calcium-binding properties could be extracted from the shell of living *Novocrania* and that calcitic rhombohedra could be sectorally pitted by bleach (BROWN, 1998). By these procedures, the sites of proteins distinguished by their molecular weight have been identified on the secondary (WILLIAMS, CUSACK, & BROWN, 1999) and primary (CUSACK & WILLIAMS, 2001a) layers of the shell of living *Novocrania*. Moreover, by comparing organic residues from and the textures of craniid shells of different geological ages, it has been possible to estimate the extent of protein degradation and skeletal recrystallization during fossilization (CUSACK & WILLIAMS, 2001b).

CHEMICOSTRUCTURE OF THE *NOVOCRANIA* SHELL

The fabric of the dorsal valve of living *Novocrania* differs from that of the ventral valve, especially in the development of the

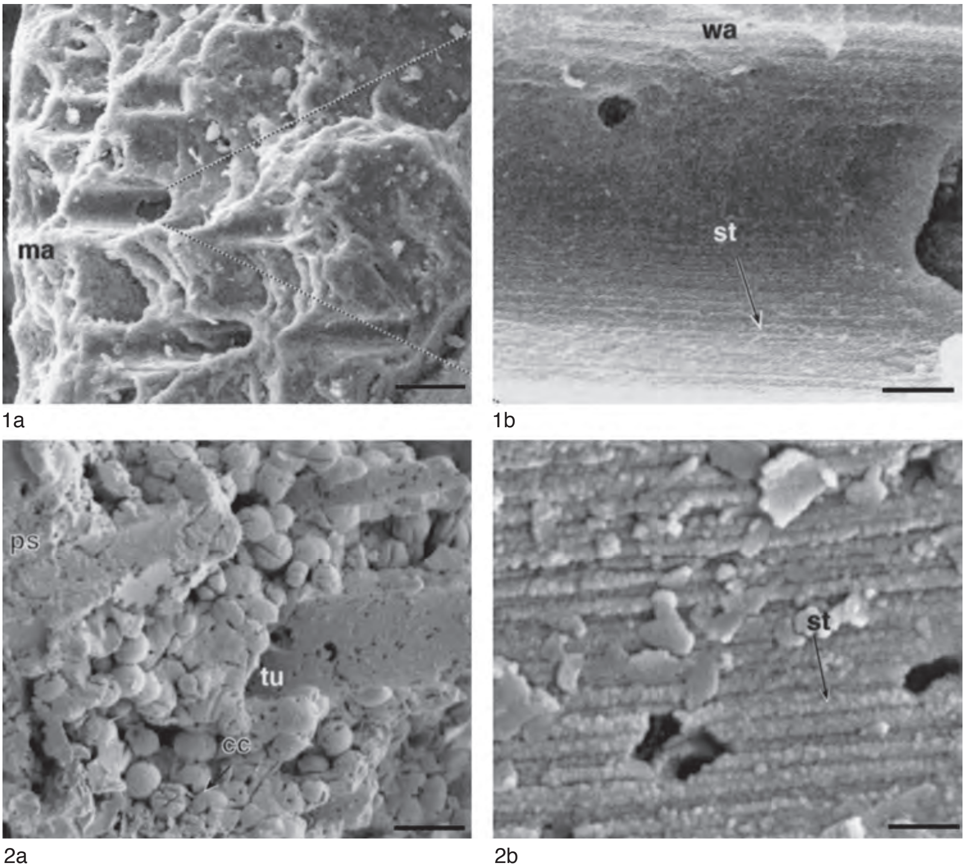


FIG. 1630. General views and details, under SEM, of setigerous tubes at margin (*ma*) of mitral sclerite of *1, Micrina* (GLAHM 114751) and on poorly preserved ventral pseudointeraea (*ps*) of *2, Mickwitzia* (MGUH 26279); tubes (*tu*) with laminar walls (*wa*), intact or fragmented with adhering phosphatized capsules of cocci (*cc*), are striated (*st*); scale bars from left to right: 10 µm and 5 µm in *Micrina*; 10 µm and 1 µm in *Mickwitzia* (Holmer, Skovsted, & Williams, 2002).

secondary layer. The chemicostructure of this layer will be described first because the spatial relationships of its organic and mineral components are the key to the growth of the shell as a whole. Irrespective of fabric differences, however, all mineralized structures are composed of spheroidal or rhombohedral granules of calcite approximately 30 nm in size, which are revealed by degrading the organic constituents and are assumed to be coated with a water-soluble protein (WILLIAMS, CUSACK, & BROWN, 1999). The organic constituents, on the other hand, vary in configuration as well as composition, as shown by plasma etching and bleach and enzymic treatment.

The secondary layer thickens and spreads by the spiral growth of calcitic laminae, through right- and left-handed screw dislocations of rhombohedra interleaving with glycoproteinaceous membranes that serve as substrates for the mineralized components of the secondary layer (WILLIAMS, 1970; WILLIAMS & WRIGHT, 1970).

The interlaminar membranes consist of an electron-dense mesh containing close-packed, electron light vesicles approximately 20 nm in diameter (Fig. 1632b). The membranes may terminate abruptly

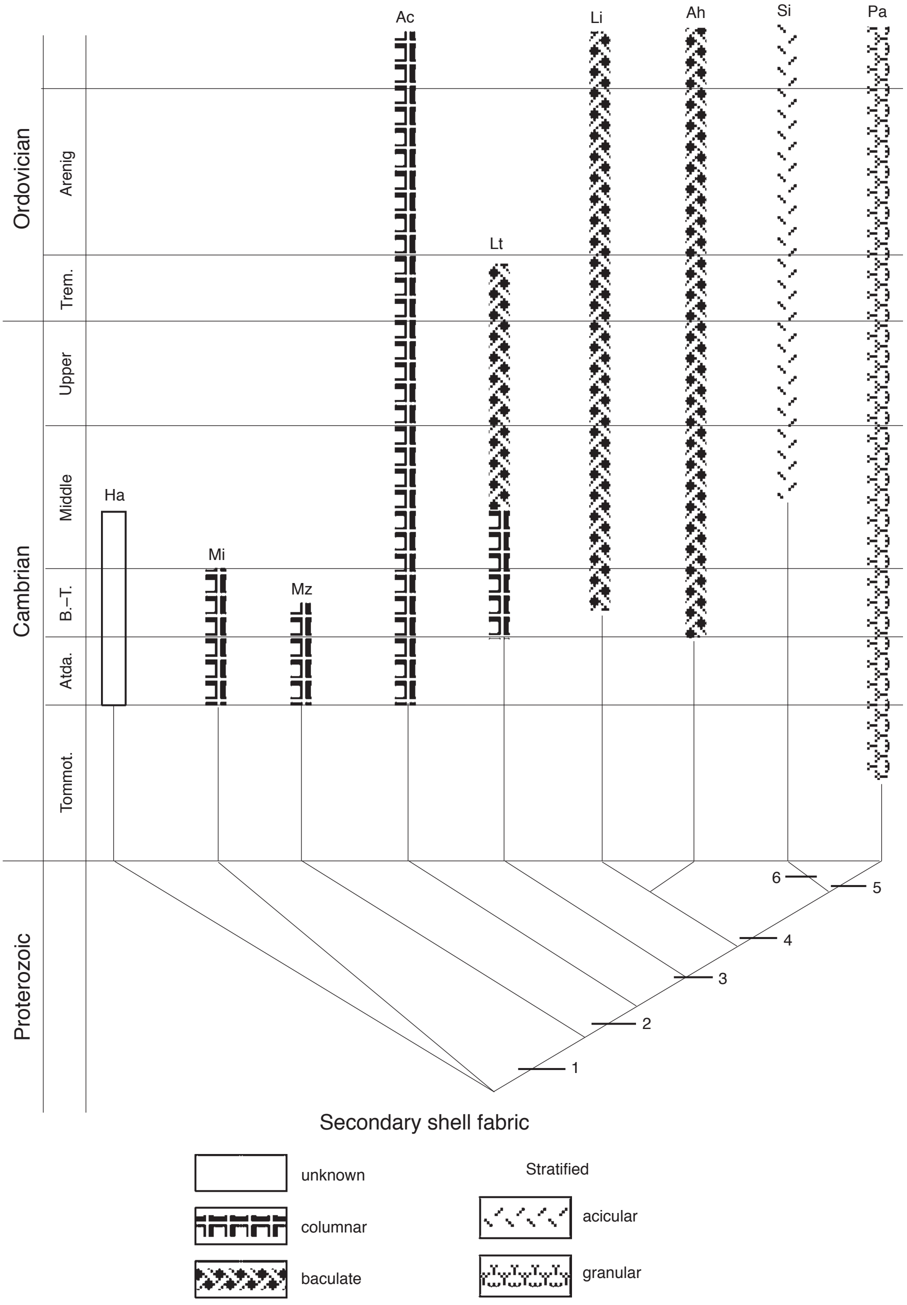


FIG. 1631. Chart showing evolution of main fabrics of secondary shells of Cambro-Ordovician linguliforms with *Halkieria* (*Ha*) and the presumed halkieriid *Micrina* (*Mi*) as sister groups. The linguliform groups are: stem-group *Mickwitzia* (*Mz*), acrotretides represented by *Prototreta* (*Ac*), linguloid *Lingulellotreta* (*Lt*), linguloid *Obolus* (*Li*), acrotheloid *Acrothele* (*Ah*), siphonotretide *Siphonotreta* (*Si*), and the paterinate *Paterina* (*Pa*). The cladogram, which is not to geological time scale, is a 50% majority-rule consensus of 6 trees generated by a PAUP heuristic search (10 stepwise additions) of 11 character states (Table 32) and matrix (Table 33) of 9 named taxa; numbered transformations are: *1,* development of brachipod body plan (characters 1–5 of Table 32); *2,* loss of setigerous tubes; *3,* change from columnar to baculate fabric; *4,* loss of baculi and well-defined GAGs chambers; *5,* development of adductor or diductor muscle systems (and other rhynchonelliform features); *6,* development of nonsetigerous tubes (new).

TABLE 32. List of 11 character states used in the cladogram of Figure 1631 to illustrate a possible origin of the diverse fabrics of the mature secondary shell of early linguliforms (new).

Body plan	
1. Bilaterally symmetrical body	segmented (0), unsegmented (1)
2. Disposition of body	straight (0), folded on transverse axis (1)
3. Valves (sclerites)	separated (0), conjoined (1)
4. Valve margins	not apposed (0), apposed (1)
5. Pedicle	absent (0), present (1)
Shell structure and morphology	
6. GAGs chambers	poorly defined (0), well developed marginally (1)
7. Columnar lamination	absent (0), present (1)
8. Baculate lamination	absent (0), present (1)
9. Setigerous tubes	absent (0), present (1), other tubes (2)
10. Pedicle opening	absent (0), at ventral beak (1), within ventral valve (2), between valves (3)
11. Muscles operating valves	unknown (0), obliques (1), diductors (2)

or branch at acute angles or in near-vertical steps (Fig. 1632a). Membranes immediately succeeding stepped zones are commonly fragmented. The membranes are differentially digested in enzymes but comprehensively degraded by plasma etching and bleach. All treatments permanently or transiently reveal fibrous networks that presumably support the vesicles (WILLIAMS, CUSACK, & BROWN, 1999). The most common interlaminar polymer extracted from the membranes is a calcium-binding 44 kDa protein with high levels of aspartic acid–asparagine, glutamic acid–glutamine, and serine (BROWN, 1998). The protein also occurs within calcitic laminae.

The basic structural unit of the mineralized secondary layer is a tabular rhombohedron, (10.4), that lies in the plane of the laminar succession and may exceed 5 µm diagonally. Faces sharing edges with the (10.4) face form steps that are seldom more than 300 nm high (Fig. 1633). Their indices can be used to distinguish edges shared with the (10.4) face. Up to four other minor steps are variably developed with edges parallel with the diagonals of the (10.4) face, and they too can be identified by general indices as shown in Figure 1633. The rhombohedra composing a lamina are separated from one another by sutures that sporadically enclose polygonal windows revealing inliers of older, outer laminae. Epitaxial alignment between and within laminae is localized but can extend through at least ten laminae. Rhombohedra enlarge by spiral or planar growth on interlaminar membranes and are found at all stages of accretion, virtually from nucleation on the internal surface of the valve. Despite their chemicocrystallographic homogeneity, rhombohedra are morphologically distinguishable as monolayered plates and multilayered tablets with different patterns of growth and macromolecular adsorption (Fig. 1634).

Plates occur discretely but more usually as foundations for tablet growth. They may be as small as approximately 150 nm in the long diagonal (Fig. 1635b–c) with (0k.1) steps, roughened by rhombohedral kinks generally developing in larger plates (Fig. 1635d). Plates are essentially flexible monolayers of spherular granules arranged in mosaics or

TABLE 33. Matrix of 11 characters described in Table 32 and 9 designated taxa (new).

	[11 12345678901]
Halkieria	00000?00?00
Micrina	00000110100
Obolus	11111101011
Prototreta	11111110011
Paterina	11111000032
Acrothele	11111101011
Siphonotreta	11111000221
Mickwitzia	1111111011?
Lingulellotreta	11111111011

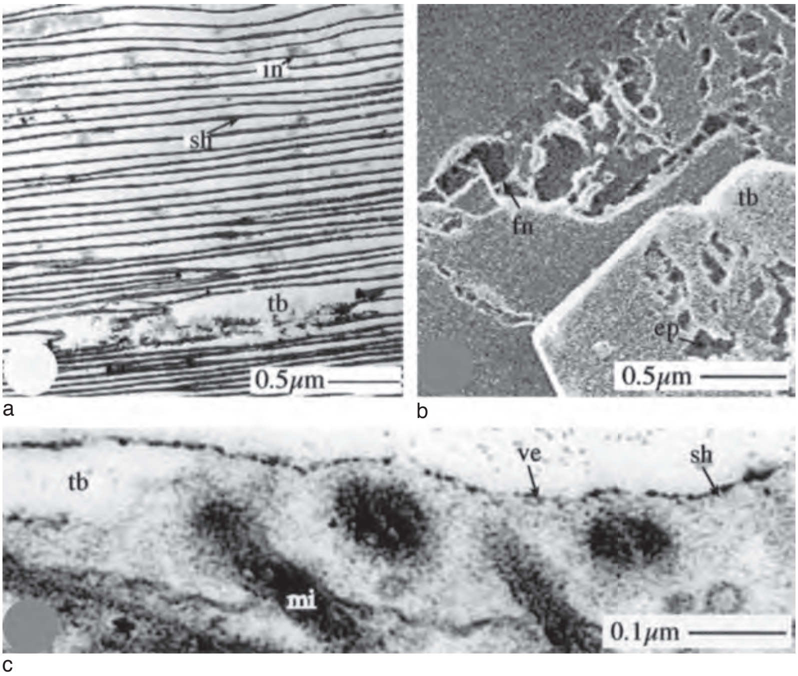


FIG. 1632. *Novocrania anomala; a,* integument*; b*, SEM of internal surface treated with 10% bleach for 1 h with etch pits (*ep*) in a tablet (*tb*) and revealing a fibrous network (*fn*) in substrate; *c,* TEM section of decalcified integument, stained with aqueous uranyl acetate and aqueous lead citrate showing electron-dense meshes with electron-light vesicles (*ve*) as sheets (*sh*) originating from microvilli (*mi*) of apical plasmalemma and disrupted above a tablet (*tb*), and as infills (*in*) between laminae in view *a* (Williams, Cusack, & Brown, 1999).

zoned in growth bands approximately 30 nm wide. Their surfaces are either flat or centrally depressed, where granules are more dispersed (Fig. 1635b–c).

Tablets consist of up to eight layers of granular mosaics that, like plates, accrete by planar or, more commonly, spiral growth (Fig. 1636a–b). Degraded surfaces are variably zoned parallel to the edges of tablet faces around flat granular or depressed proteinaceous centers (Fig. 1636a). Rough (0k.1) steps are usually well developed in larger tablets, and the triangular sectors of growth they subtend with the rhombohedral centers may be sharply delineated (Fig. 1636a). Rough (h^{-}0.1) steps, when developed, are short and remain so during growth, as is shown by their generation of banding in parallel strips (Fig. 1635d).

Just within the surface edge of a tablet, mosaics of granules may give way to bands of rhombohedra approximately 40 nm long (Fig. 1636c). The bands are the foundations of commonly occurring ramparts up to 600 nm high (Fig. 1636b). Ramparts are composed of rhombohedral aggregates or granules in bands parallel to the edges of tablets (Fig. 1636d). They accrete centripetally as well as vertically and may coalesce to cover organic infills of the central depression (Fig. 1636d).

Differential etching of the surfaces and steps of plates and tablets exposes the relief of the calcite and excavates sites of organic concentrations. The effects are generally more evident on underlying laminae exposed by degradation of organic substrates than on biomineralized surfaces being secreted at death (Fig. 1637d). This suggests that, in addition to some protein doping in the later stages of laminar formation, many organocalcitic microstructures are highly degradable in the living state and can even be destroyed by autolysis.

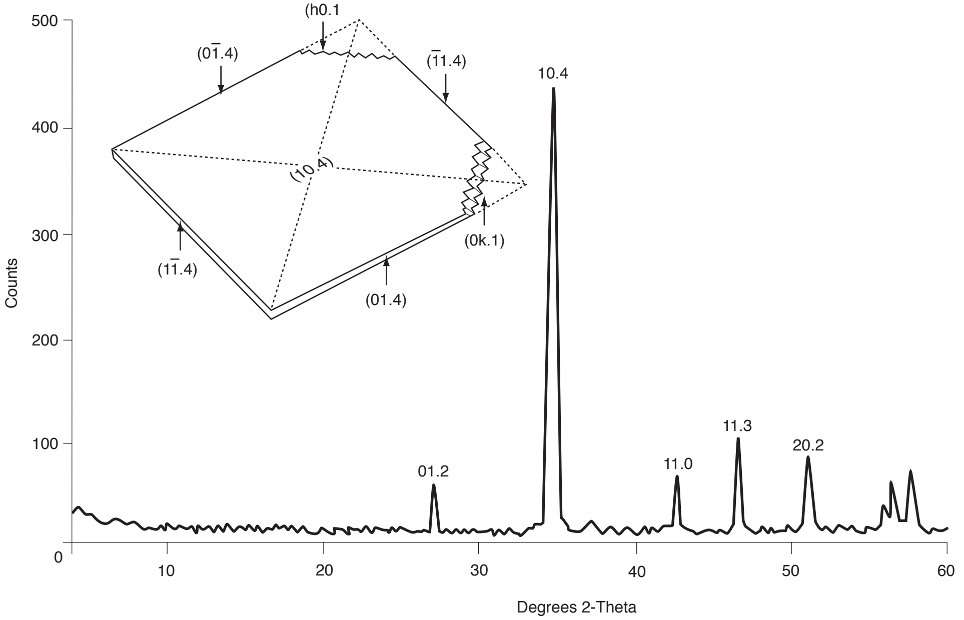


FIG. 1633. X-ray diffraction profile showing frequencies of principal crystal faces in calcite of dorsal valve of *Novocrania anomala* (MÜLLER); inset illustrates rhombohedral indices used in this chapter (Cusack & Williams, 2001).

The simplest etched features are slits or narrow clefts extending between the centers and the acute-angled corners of rhombohedral plates parallel to the long diagonal (Fig. 1638). Growth bands are not dislocated by the kinked sides of clefts that end centrally in a granular mosaic less than 500 nm in diameter. Opposite clefts in flat plates are aligned with each other and arise from a common center; but those in spirally growing plates are sinistrally and dextrally displaced, as are their separate centers in clockwise and anticlockwise spirals respectively (Fig. 1638b). These shifts are presumably a function of rhombohedral distortion by spiral growth. The removal of narrow strips of plates along their long diagonals by enzymes confirms that granules within these zones are invested in a protein that had been adsorbed at the junctions of the (01.4) ˆ(11.4) and (10.4)ˆ(01.4) steps, virtually from plate inception.

Surface etching of tablets by induced degradation is restricted to triangular zones (Fig. 1637a, 1638a) with bases at or just within the (0k.1) steps and apices, subtending angles up to 70° at central depressions. The sides of excavated (0k.1) sectors are more or less parallel with (10.4) edges but are commonly unequally developed, with one side forming a step and the other a break in slope; both are kinked by rhombohedral cleavage. Degraded sites vary from hillocks to labyrinthine walls or parallel ridges (Fig. 1637c). Deeply etched residues usually rest on basal plates and are aligned with rhombohedral cleavage. Ramparts can grow on the surfaces of tablets with etched (0k.1) sectors. Their subsequent centripetal growth can result in ledges coalescing inwardly to enclose organic infills in the central depressions of tablets (Fig. 1636d, 1637b). Such intralaminar deposits are really part of the organic interlaminar component of the secondary shell.

Degradation of laminae underlying the internal surface of a shell exposes plates and tablets coalesced within mosaics or concentric bands of granules with sutures sporadically enlarged by rhombohedral etch pits

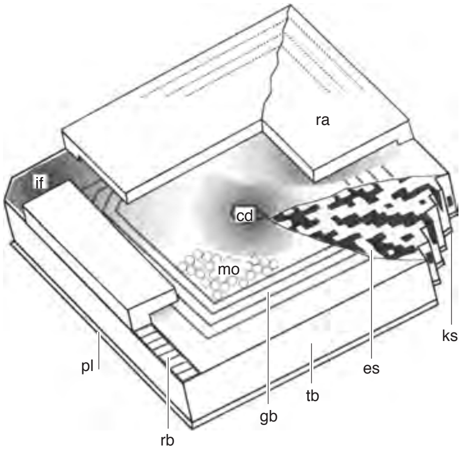


FIG. 1634. Crystallographic and chemicostructural terminology of secondary shell of *N. anomala*. Stylized etched tablet (*tb*) on plate (*pl*) with banded (*gb*), centrally depressed (*cd*), internal surface composed of granular mosaic (*mo*), coated with proteinaceous infill, 44 kDa (*if*) partly covered by ramparts (*ra*) accreting on foundation of banded rhombohedra (*rb*); etched (0k.l) sector (*es*) with ridges and hillocks delineating sites doped by 60 kDa protein along kinked steps (*ks*) (Williams, Cusack, & Brown, 1999).

(Fig. 1637c). Etched (0k.1) sectors in various stages of development and degradation occur together with rare rhombohedral and subtriangular faces that have been differentially etched into rhombohedral grilles or slats, parallel to a (10.4) edge (Fig. 1637d). These structures appear to result from adsorption of abnormal quantities of protein along the cleavage.

Induced degradation of laminae by enzymic digestion confirms that organic residues removed from excavated sites are predominantly proteinaceous. In addition to forming coats enclosing discrete calcitic granules, protein also occurs as infills along sutures and within rhombohedral tablets. These infills are the electron-dense structures subtended between membranes that are seen as particles in some sites of dissolved tablets (Fig. 1632a). This protein is assumed to be the electron-dense mesh of interlaminar organic sheets, secreted with vesicles by microvilli. It has been identified as the 44 kDa protein extracted from both laminae and membranous interleaves.

Tablets are doped with proteins in at least two ways. Centripetal growth of the top granular layers or ramparts can trap organic residues coating medial depressions of tablets. This is the main process for incorporating the 44 kDa protein within tablets. The other sites of doping are (0k.1) sectors. They vary from slits in plates representing kinks along the long diagonal to wide sectors in tablets characterized by strongly developed, kinked (0k.1) steps. Along slits, the protein is secreted as kinked strands at the lengthening junction between the growing $(1\bar{1}.4)$ and $(0\bar{1}.4)$ steps. In sectors, it forms strands aligned with cleavage with offsets enclosing granules so that degradation exposes calcitic ridges and hillocks and releases detached granular aggregates. Accretion of the protein can be periodic with repeated, sustained doping of the kinks in the (0k.1) steps to form more or less continuous organic bands many nanometers thick and parallel with the sector base. Secretion can be terminated within the base of a sector but such protein-free bands appear to be sites for rampart growth. The protein also forms sheets interleaved with granular monolayers; both constituents are restricted to (0k.1) sectors. The sectoral restriction in the secretion of this fibrous protein suggests that it is the exclusively intralaminar, glycosylated 60 kDa protein (BROWN, 1998). Sporadically preserved strands in etched sectors and sutures (Fig. 1632b) may be remnants of this proteinaceous network. The assumed distribution of the two dominant proteins doping calcitic tablets are shown diagrammatically in Figure 1634.

The primary, mineralized layer of the dorsal valve of *Novocrania* differs from the secondary layer in three respects. Although the mineralized components are also calcitic laminae, they expand peripherally, not by spiral growth, but along radial vectors. Moreover, these laminae are not interleaved with glycoproteinaceous membranes. Calcitic

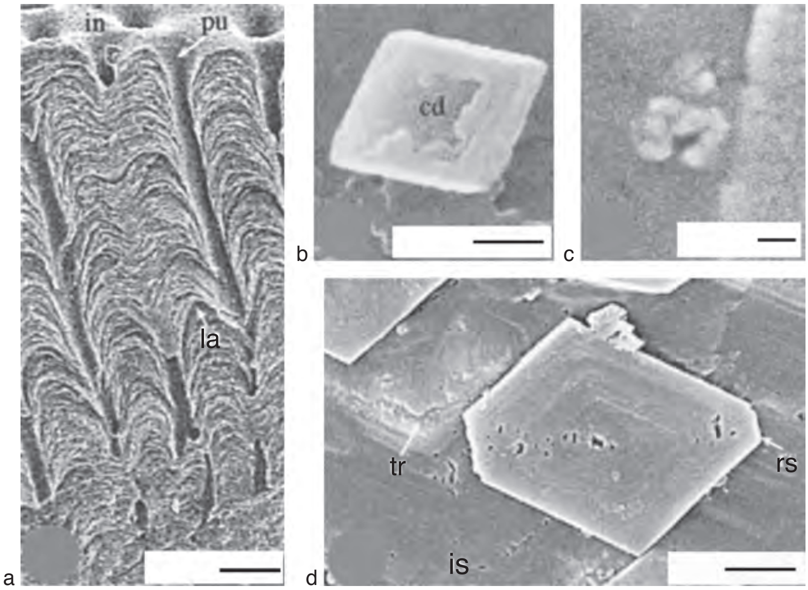


FIG. 1635. SEM views of internal surfaces and fracture sections of secondary shell of dorsal valves of *Novocrania anomala*; *a, c*, digested by proteinase-K in phosphate buffer; *b*, treated with 10% bleach by volume for 6 h; *d,* treated with Hepes buffer; *a,* fracture section showing disposition of laminae (*la*) relative to internal surface (*in*) and punctae (*pu*), *b–c*, immature and newly formed, granular rhombohedral plates with central depressions (*cd*); *d*, growth-banded plate with sparse etch pits along long diagonal between rough steps (0k.l) (*rs*) on interlaminar substrate (*is*) raised by tilted tablet (*tr*) (Williams, Cusack, & Brown, 1999).

structures are invested in, or associated with, an organic matrix that is not degraded by protease enzymes only by bleach and is presumably a polysaccharide. Finally, the pustules described below do not develop in the primary layer. The boundary between the primary and secondary layers is accordingly well defined in section and on the valve floor where the three-fold succession of the primary layer is exposed as three concentric zones (Fig. 1639).

At the margin of the mature valve, granular monolayers approximately 25 nm thick form a succession of 50 or more sheets in which the granules are generally arranged linearly parallel with the ($\bar{h}0.1$) planes (Fig. 1640a–b). This lineation is strongly developed in inwardly succeeding laminae that overlap one another like tiles (Fig. 1640c). Steps of (10.4) rhombohedra form growing edges of these laminae, which, in the degraded state, are divided into strips (slats). As this alignment is predominantly that of grills within the secondary layer, it is assumed that the primary laminae are also doped between slats by the fibrous 60 kDa protein. In the inwardly succeeding laminae, nearer the boundary with the secondary layer, hemicylindroid to flat-topped projections are commonly secreted as spines to virtually discrete laths of laminae (Fig. 1641a–b) with growing edges formed of (10.4) steps subtending rhombohedral angles. The spines are commonly banded at acute angles to their lath bases, indicating incremental forward growth by the secretion of monolayers of granular calcite. An amorphous organic residue persists in the spaces between spines when treated with proteinase-K, suggesting that such infills are polysaccharidal. Laminar successions, peripheral to the secondary layer, are normally composed of membranes interspersed with rhombohedral plates, fretted

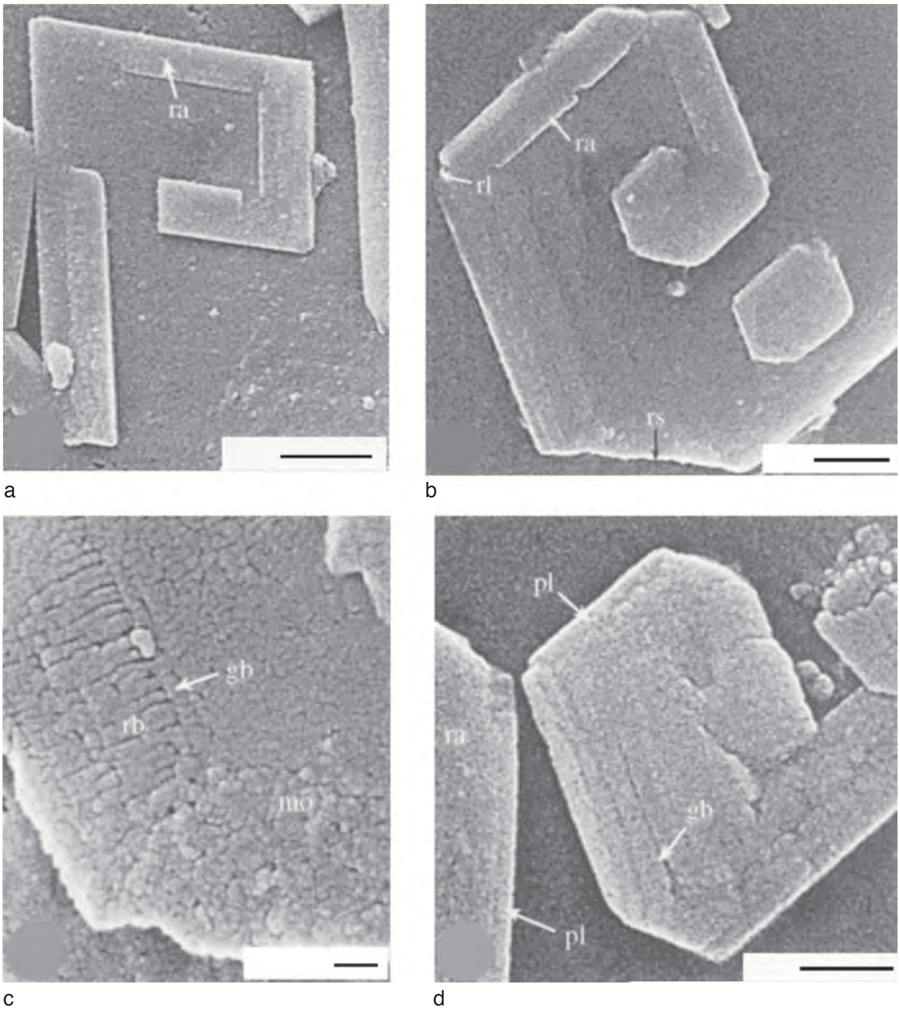


Fig. 1636. SEM views of internal surfaces and fracture sections of secondary shell of dorsal valves of *Novocrania anomala; a*, treated with 10% bleach for 6 h, *b, d*, digested by proteinase-K in phosphate buffer; *c*, treated with Hepes buffer; *a,* spiral tablet system with centripetally growing ramparts (*ra*) elevated above interlaminar substrate; *b*, clockwise spiral tablet system with centripetally growing rampart (*ra*) and (0k.l) and ($\bar{h}$0.l) rough steps (*rs*) and (*rl*) respectively; *c*, corner of tablet with growth banding (*gb*), bands of larger rhombohedra (*rh*) parallel with (01.4) step and granular mosaic (*mo*) within rough (0k.l) step; *d*, tablets on plates (*pl*) with growth-banded (*gb*) ramparts (*ra*) covering central depression (Williams, Cusack, & Brown, 1999).

or fragmented by bleach (Fig. 1642c–d) and also with some protein doping along the long diagonals revealed by digestion with proteinase-K. This succession is structurally preliminary to the spirally growing rhombohedra interleaved with glycoproteinaceous membranes of the secondary layer.

The weakly developed ventral valve of *Novocrania* is composed only of primary layer that occurs mainly as a thickened, finely nodular marginal ring (Cusack & Williams, 2001a, p. 886) with a coarsely tuberculate outer face. The peripheral periostracal strip is coated by a monolayer of calcitic gran-

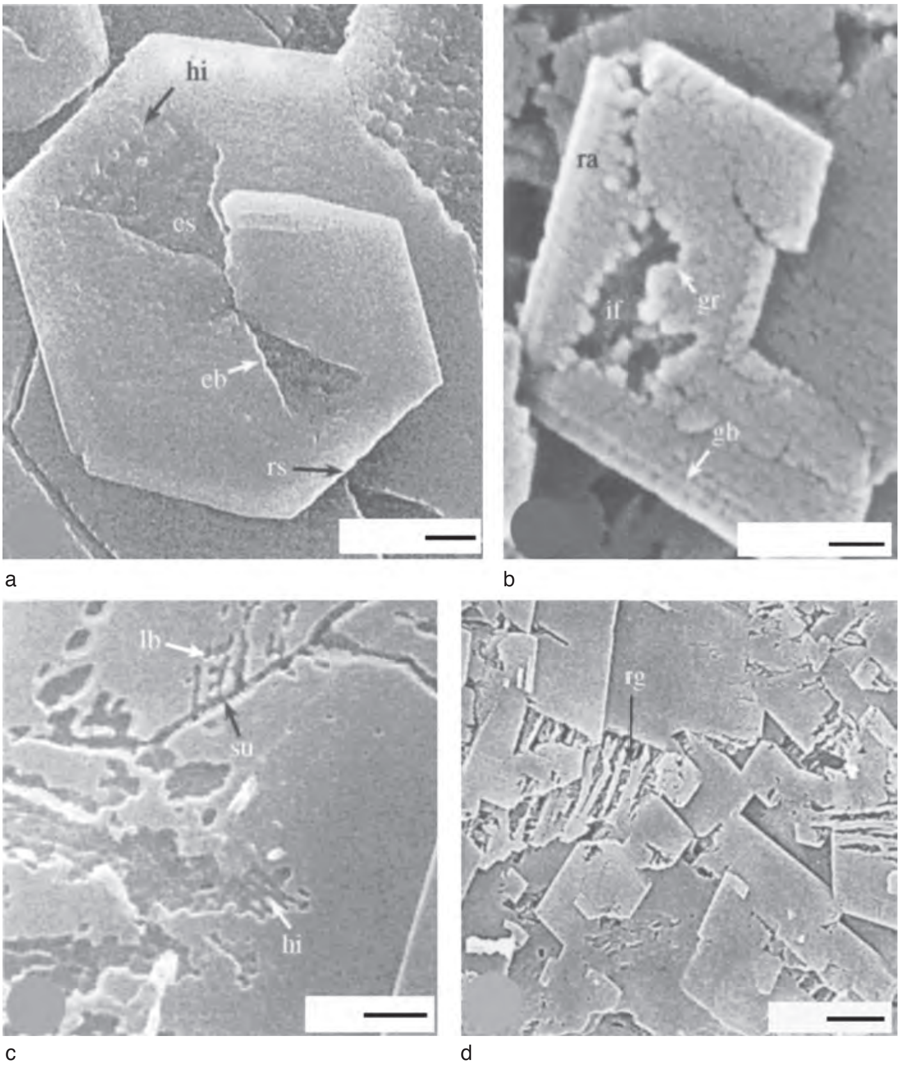


FIG. 1637. SEM views of internal surfaces of secondary shell of dorsal valves of *Novocrania anomala; a*, *c,* treated with bleach (10% and 20% v/v respectively) for 6 h; *b, d,* digested by proteinase-K buffered by Hepes; *a,* etched sectors (*es*) within, or delineating, rough (0k.l) edges (*rs*), bounded by etched, kinked steps (*eb*) parallel with $(1\bar{1}.4)$ and (01.4) edges and containing hillocks (*hi*) and granular sheets respectively; *b*, tablets, twinned on (0k.l) plane (?) with infill centers (*if*) revealed by degradation of centripetally grown, granular (*gr*) cover of banded (*gb*) ramparts (*ra*); *c*, laminar etching along sutures (*su*) with rhombohedral labyrinths (*lb*), ridges, and hillocks (*hi*); *d*, rhombohedral grilles (*rg*) in laminar substrates (Williams, Cusack, & Brown, 1999).

ules that form spherular and cylindroid aggregates (Fig. 1642a–c). The granules are coated with polysaccharide, traces of which survive degradation, while rare pinacoidal plates of calcite are presumably exocytosed in the completed state (Fig. 1642b–c). The boundary between the periostracal strip and the inner, nodular zone is relatively sharp, although nascent nodules can form on the periostracal calcitic coat. A nodule may be initiated as a cluster of discrete columns of rhombohedra that serve as the core of an

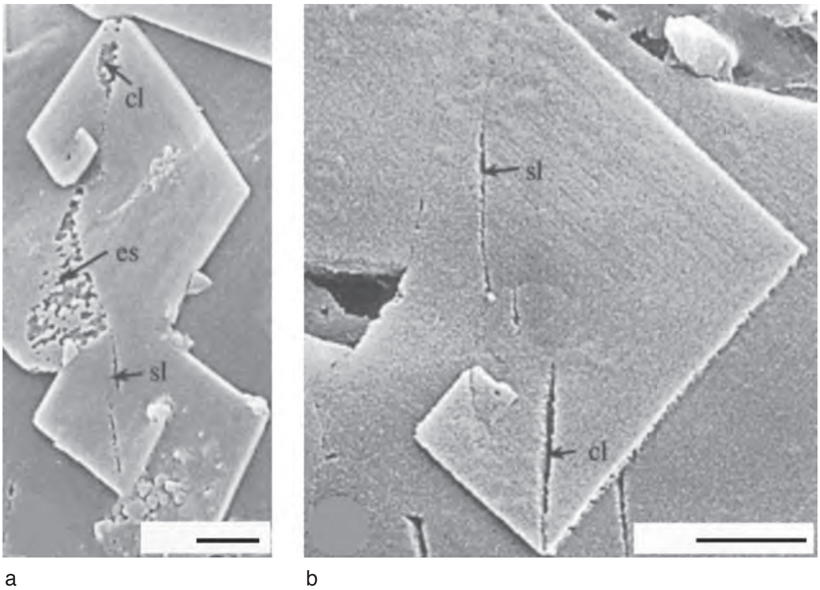


FIG. 1638. SEM views of internal surfaces of secondary shell of dorsal valves of *Novocrania anomala* digested by proteinase-K buffered by *a,* phosphate and *b,* Hepes, revealing slits (*sl*), clefts (*cl*), and etched (0k.l) sectors (*es*) in spirally growing plates and tablets (Williams, Cusack, & Brown, 1999).

assemblage of overlapping plates penetrated by cylindroid cavities approximately 100 nm in diameter. The full assemblage is a low semiellipsoid up to 10 µm in long diameter (Fig. 1642d–e). The nodules tend to be well ordered in close-packed rays or radial columns. When untreated the zone is coated with polysaccharide.

The tubercles on the outer face of the marginal ring form inwardly inclined projections approximately 150 µm long (Fig. 1642a), and their surfaces are nodular. Toward the crest of the marginal rim, the tips of the tubercles become flat topped and are composed of vestiges of nodules, broken granular plates and slats, spherules and GAGs, a fabric that is characteristic of resorption (Fig. 1643b). The superficial features of the shell underlying the mantle and body cavities are variable, for they include pustules, cleft cysts, and slats (CUSACK & WILLIAMS, 2001a, p. 888). The basic calcitic constituents of the succession, however, are rhombohedral plates with linearly arranged granules that also aggregate into spherules and tablets; laths, composed of such aggregates, commonly change directions through a laminar succession as in composite structures (Fig. 1644). Treatment with bleach or enzymes did not expose proteinaceous concentrations as slots or pitted sectors within the laminar successions.

The chemicostructural succession of the ventral valve suggests that the valve consists exclusively of a primary layer. The regular size and distribution of nodules are reminiscent of cellular imprints, suggesting that each nodule is secreted by an outer epithelial cell. This differential secretion is characteristic of the retractable outer lobe and adjacent mantle, which is probably attached to the flat-topped tubercles by myofibrillar bundles.

The recently studied pustules on the internal surface of the secondary layer of *Novocrania* (CUSACK & WILLIAMS, 2001a, p. 880–883) are noteworthy as similar features are the internal expressions of pseudopunctation that characterize many strophomenates (WILLIAMS, 1997, p. 305–312). The pustules, which are grouped approximately 30–50

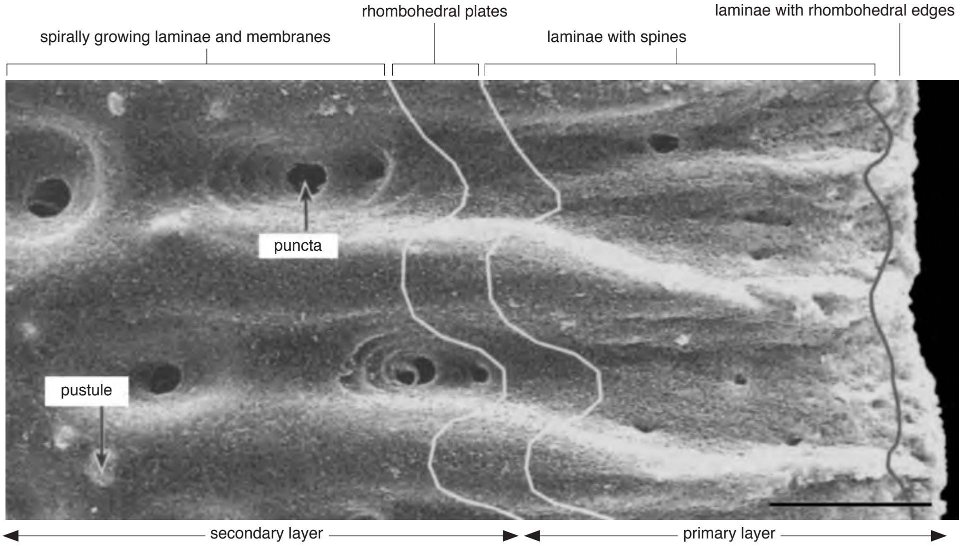


FIG. 1639. Various structural features characterizing surfaces of primary and secondary layers of dorsal valve of *Novocrania anomala* (MÜLLER); scale bar: 50 µm (Cusack & Williams, 2001).

µm apart around openings of punctae, are more or less hemispherical with bases 5–7 µm in diameter (Fig. 1645a–b). They are not superficial features because they can be traced within sections as cylindroid inward deflections of laminae (Fig. 1644a,c). These cylindroid cores may be impregnated with an amorphous tension-cracked, organic residue (Fig. 1644a–b) that is degraded by bleach but not by protease enzymes and is presumably a mucous polysaccharide secreted by specialized epithelial cells. The mucus is sporadically distributed as a plug along the core and invades deflected laminae bounding a pustule. The plugs contain laminar fragments as well as clusters or granules (Fig. 1644b). Their sites are bounded by walls of disrupted laminae, and they are separated from one another by outwardly arching laminar successions. This differentiation accords with surfaces of some pustules being completely coated by laminar sheets and plates (Fig. 1645b), while others are open to expose arcs of deflected laminae and disrupted cores (Fig. 1645c). The pattern suggests that each pustule is formed of intermittent discharges of mucus from a cell(s) that otherwise secretes secondary shell.

The pustules are comparable to pseudopunctae lacking taleolae, like those of orthotetidines and early strophomenoids (WILLIAMS, 1997, p. 306, fig. 266). Their ultrastructures are strikingly similar, including laminar fragments preserved in the cores of pseudopunctae that may also be capped by entire laminae. Pseudopunctae are assumed to have acted as holdfasts for mantle filaments (WILLIAMS, 1997, p. 311), but there is no morphological evidence of this function for craniid tubercles. The most striking feature of the tubercles is their regular distribution around punctal openings. The periodic secretion of mucus may therefore facilitate the growth of the glycoproteinaceous membranes that separate papillae of outer epithelium occupying punctae from the shell.

SHELL STRUCTURE OF FOSSIL CRANIIDS

The skeletal ultrastructure of craniids has not changed significantly since the earliest record of the group in the Ordovician (Arenig), although it has cumulatively undergone several phases of recrystallization.

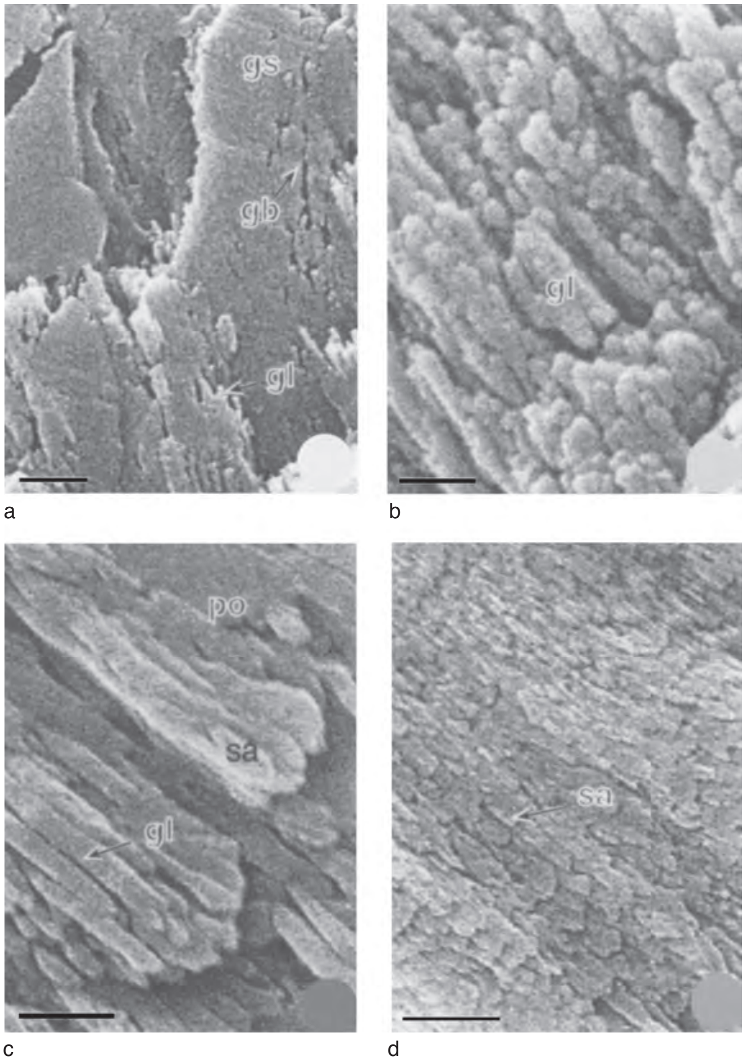


FIG. 1640. SEMs of internal surface of primary layer of dorsal valve of *Novocrania anomala* (MÜLLER), Oban, Scotland; surfaces shown in *a* and *b* immersed in phosphate buffer, those in *c* and *d* treated with bleach; *a–b*, general view and detail of granular plates (*gs*) at valve edge with rhombohedral growth banding (*gb*) and linear aggregates of granules (*gl*) aligned parallel with $(\bar{h}0.1)$ planes; scale bars: 500 nm, 200 nm; *c*, detail of slatlike rhombohedra (*sa*) composed of linear aggregates of granules (*gl*) with polysaccharide residues (*po*); scale bar: 1 µm; *d*, general view of slats with rhombohedral edges (*sa*); scale bars: 500 nm (Cusack & Williams, 2001).

The antiquity of the living shell structures is confirmed by comparisons of the fabrics of Upper Cretaceous *Crania* and *Isocrania*, the Lower Carboniferous *Crania*? *ryckholtiana* (DE KONINCK), and the upper Ordovician *Petrocrania* (CUSACK & WILLIAMS, 2001a). In all these extinct craniids, the primary layer was well developed as a succession of laminar sheets (Fig. 1646c). The laminae are normally degraded on the external surface into radially aligned laths up to 20 µm wide (Fig. 1647.1, 1647.3). In *Petrocrania* the laths usually coalesce distally to form solid lobate edges (Fig. 1647.4), possibly

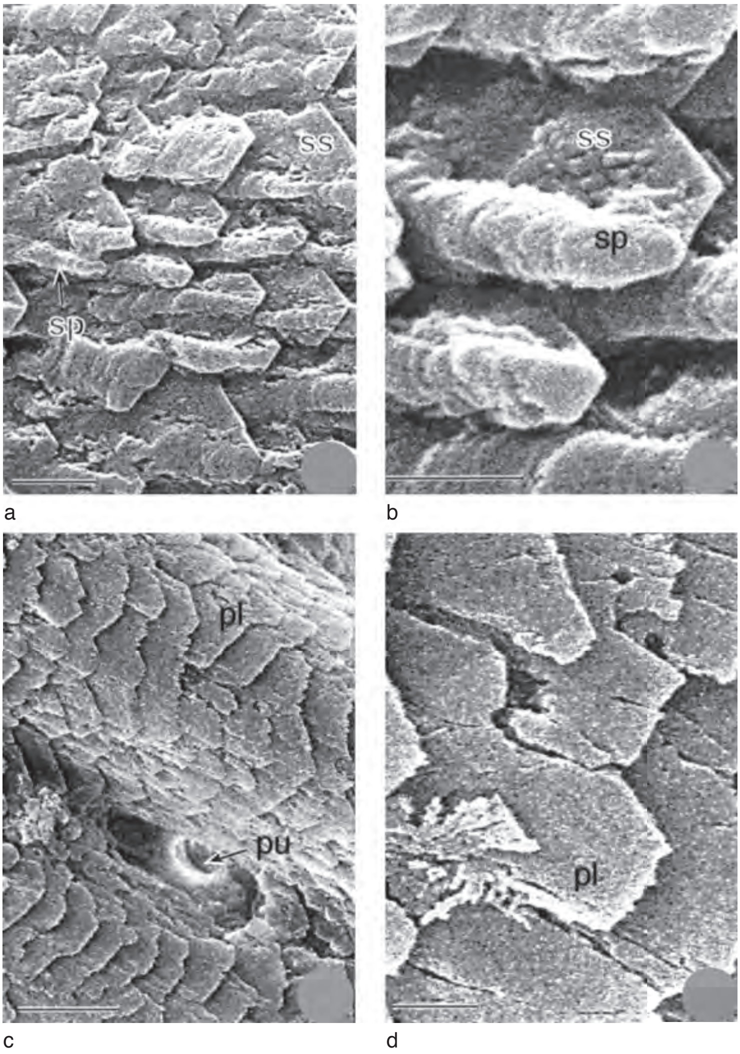


FIG. 1641. SEMs of internal surface of primary layer of dorsal valve of *Novocrania anomala* (MÜLLER), Oban, Scotland; surfaces shown in *a–b,* digested in proteinase-K; *c–d*, treated with bleach; *a–b*, general view and details of slats with rhombohedral edges (*ss*), bearing growth-banded spines (*sp*), one showing the granular texture of growth surface; scale bars: 1 µm and 500 nm; *c–d*, general view and detail of regularly overlapping rhombohedral plates (*pl*) with fretted edges and internal opening of puncta (*pu*); scale bars: 5 µm, 1 µm (Cusack & Williams, 2001).

as a result of recrystallization. Nodular tubercles characterize the internal margins of both valves in *Crania* and *Isocrania* (Fig. 1647.1). They are sporadically present in *Crania* but are a diagnostic feature of the craniid lineage, as they are well developed in the rims of the Ordovician *Orthisocrania* (CUSACK and WILLIAMS, 2001a, pl. 9,*3*) and consist of successions of laminar sheets as in living *Novocrania*.

The secondary layer of the dorsal valve is invariably developed, and, although internal surfaces are generally obscured by microspar, patches of recrystallized, screw-dislocated rhombohedra survive (Fig. 1646b). A secondary layer that grew spirally was also

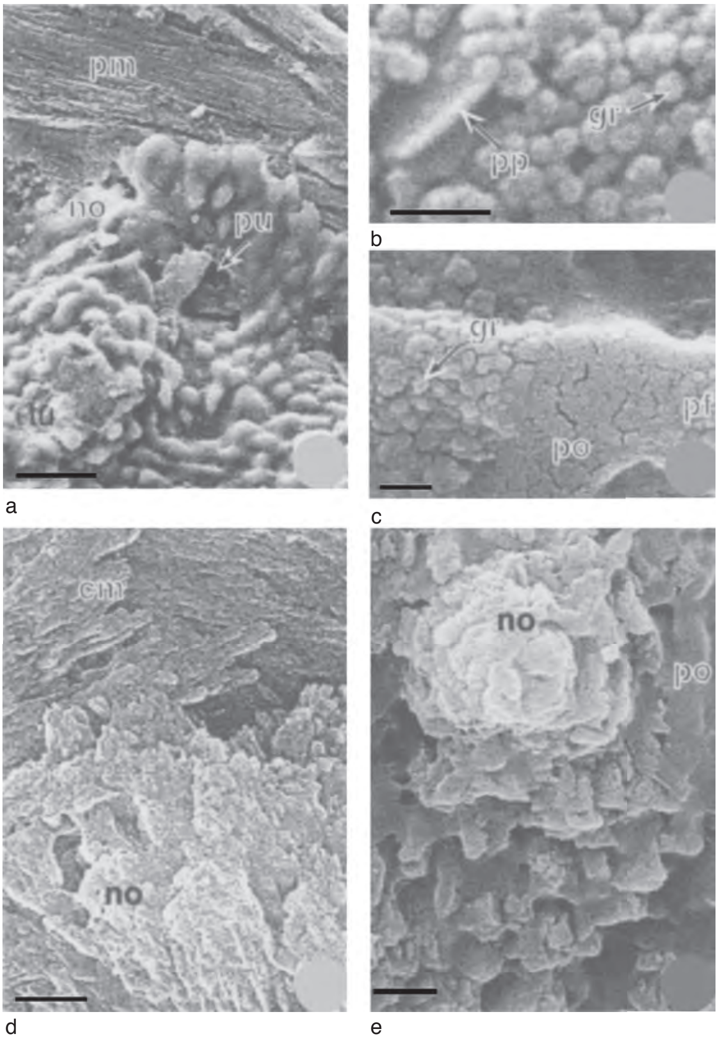


Fig. 1642. SEMs of internal surfaces of ventral valve of *Novocrania anomala* (Müller), Oban, Scotland; surfaces treated with 5% bleach for 6 h except view *c,* which was immersed in phosphate buffer; *a–c*, general view and details of periostracal strip (*pm*) bordering marginal rim, characterized by nodules (*no*), tubercles (*tu*), and punctae (*pu*) and consisting of impersistent concentric folds (*pf*) with coats of calcitic granules (*gr*), rare pinacoidal plates (*pp*), and polysaccharide (*po*); scale bars: 25 µm, 200 nm, 200 nm; *d*, newly formed nodule (*no*) composed of granular plates, secreted on calcitic monolayers (*cm*) of periostracal strip with cleavage lineation almost orthogonal to that of nodule; scale bar: 1 µm; *e*, view of nodule (*no*) showing they are composed of plates (inclined medially) arising from a similarly structured substrate of rhombohedral plates and polysaccharide (*po*); scale bar: 1 µm (Cusack & Williams, 2001).

secreted in the ventral valves of Cretaceous and Carboniferous species (Fig. 1646d, 1647.2). The ventral valve of *Petrocrania*, however, is nothing more than a thin calcitic film, a vestige of an incompletely developed first-formed shell (Cusack & Williams, 2001a). At its anterior margin, the shell consists of ill-fitting rhombohedra up to 20 µm long. Medioposteriorly, they are succeeded by calcitic blades disposed as impersistent concentric arcs; posterolaterally, presumably the sites of muscle attachments,

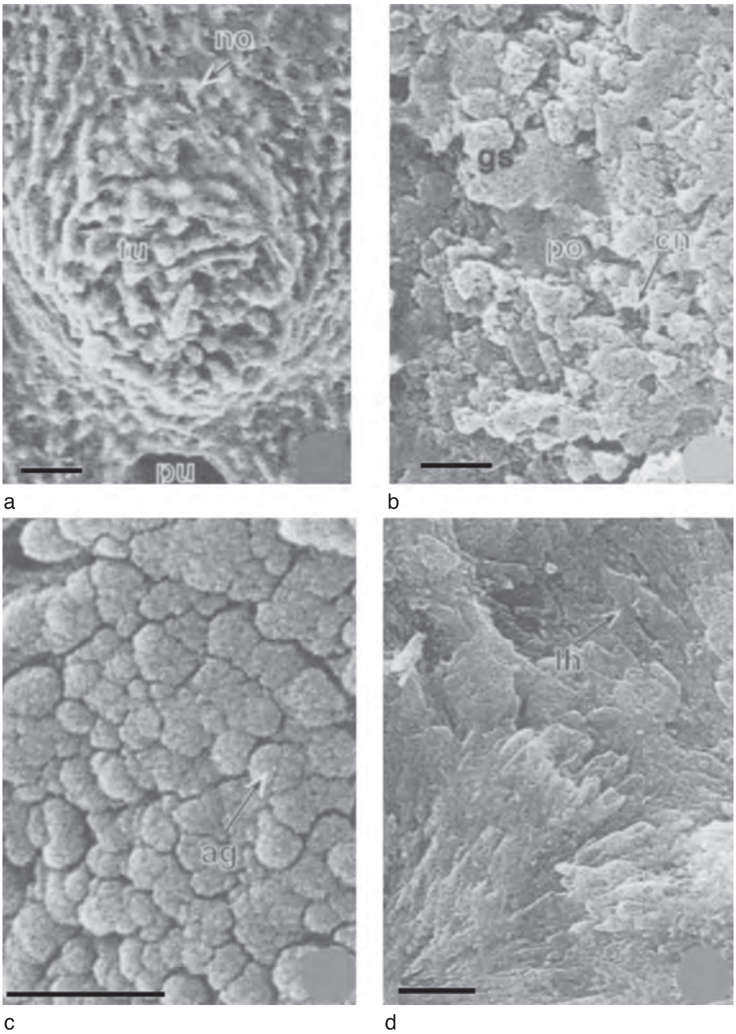


Fig. 1643. SEMs of internal surfaces of ventral valves of *Novocrania anomala* (Müller), Oban, Scotland; *a–b*, after incubation of fracture sections in phosphate buffer, general view of tubercle (*tu*) with a nodular (*no*) and punctate (*pu*) surface and detail of flat-topped surface of tubercle at crest of marginal rim, showing broken granular plates (*gs*), polysaccharides (*po*), and cylindroid cavities (*cn*); scale bars: 25 µm, 1 µm; *c*, coat of granular spherules of calcite (*ag*) on concentrically wrinkled membranous substrate and *d*, details of composite succession of calcitic laths (*lh*); scale bars: 20 and 10 µm respectively (Cusack & Williams, 2001).

the blades overlap like a composite fabric (Fig. 1648).

RECRYSTALLIZATION AND DEGRADATION OF FOSSIL CRANIIDS

Comparative chemicostructural studies of the shells of living *Novocrania* and late Cretaceous *Crania* and *Isocrania* (Fig. 1649) have established some of the diagnostic features distinguishing between phylogentic and diagenetic changes that affected fossil species (Cusack & Williams, 2001a). Apart from the development of a secondary layer in the ventral valves of the Cretaceous craniids, inherent chemicostructural differences are minor. Changes induced by diagenesis, however, are profound but are

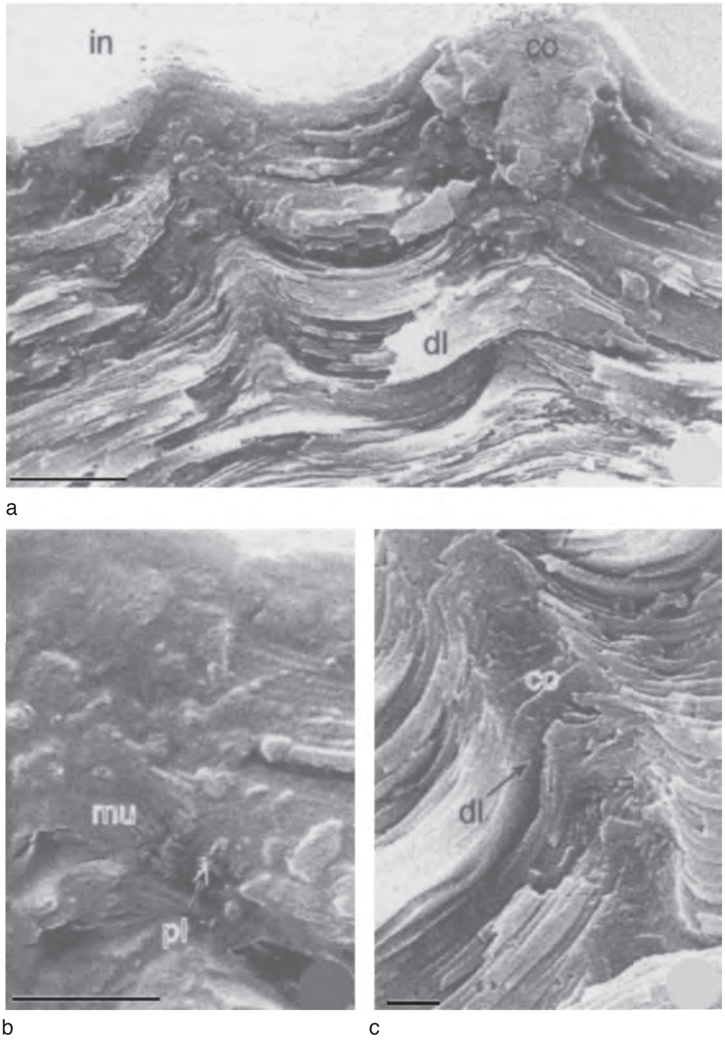


Fig. 1644. SEMs of pustules in dorsal valve of *Novocrania anomala* (Müller), Oban, Scotland, after treatment with proteinase-K; *a–c*, general view and details of two pustules exposed in a fracture section [interior (*in*) to the top] showing core (*co*), composed of fragments of laminae (*pl*) in a polysaccharide (*mu*), bounded by inwardly deflected laminae (*dl*); scale bars: 5 µm, 1 µm, and 1 µm respectively (Cusack & Williams, 2001).

structurally confusing as they commonly result in features similar to those produced by biogenic secretion and resorption. Cavities, intrinsic to internal laminae of the Cretaceous shells, are commonly bounded by mismatched crystal or curved faces and may penetrate several laminae. They are likely to have originated at junction windows and further modified during recrystallization (Fig. 1646b). This would account for the way cracks (originally junction sutures) radiate from many of them. In contrast tilted rhombohedral depressions (Fig. 1646d) are more likely to be true etch pits that originated with the degradation of the organic axial core of screw dislocations.

Treatment of the Cretaceous shells with bleach and HCl reveals that degradation of intracrystalline polymers took place before the recrystallization of laminae. Laminar

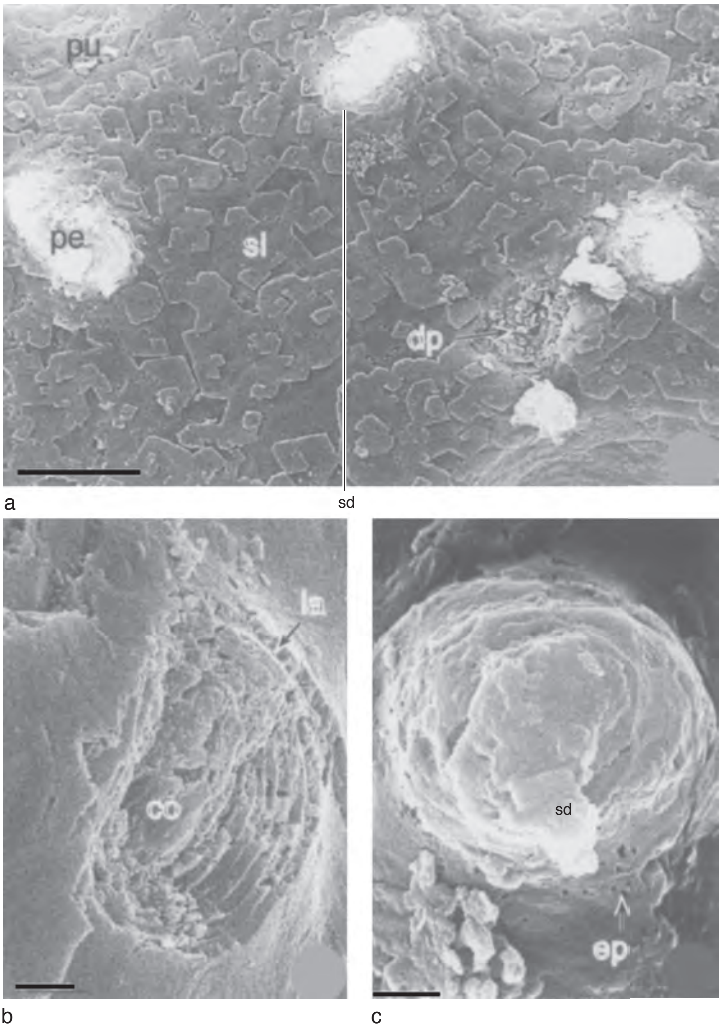


FIG. 1645. SEMs of pustules in dorsal valve of *Novocrania anomala* (MÜLLER), Oban, Scotland; *a* and *c* immersed in phosphate buffer and *b* digested in proteinase-K; *a,* general view and details of pustules (*pe*) on internal surface of punctate (*pu*), spirally growing laminar secondary layer (*sl*) with entire pustules covered with enzyme-pitted laminae (*ep*) and screw-dislocated plates (*sd*) in view *c* and degraded pustules (*dp*) in *a* and *b* showing polysaccharide-impregnated core (*co*) and successive inwardly deflected laminae (*la*); scale bars: 10 µm, 1 µm, and 1 µm respectively (Cusack & Williams, 2001).

surfaces are free of sectorally distributed cavities, like those induced by bleach in protein-doped rhombohedra of living shells. They become tension cracked and develop curved channels when treated with bleach, however. As these features are not induced by solution in HCl it seems that the volumetric changes that led to tension cracking resulted from the degradation of diffuse organic residues that had been produced and dispersed during the early stages of recrystallization (Fig. 1648).

The Paleozoic cranioids studied by CUSACK and WILLIAMS (2001a) were from nearshore calcareous siltstones and mudstones unaffected by significant geothermal changes or tectonic disturbances. Their shell ultrastructure confirmed that skeletal secretion was

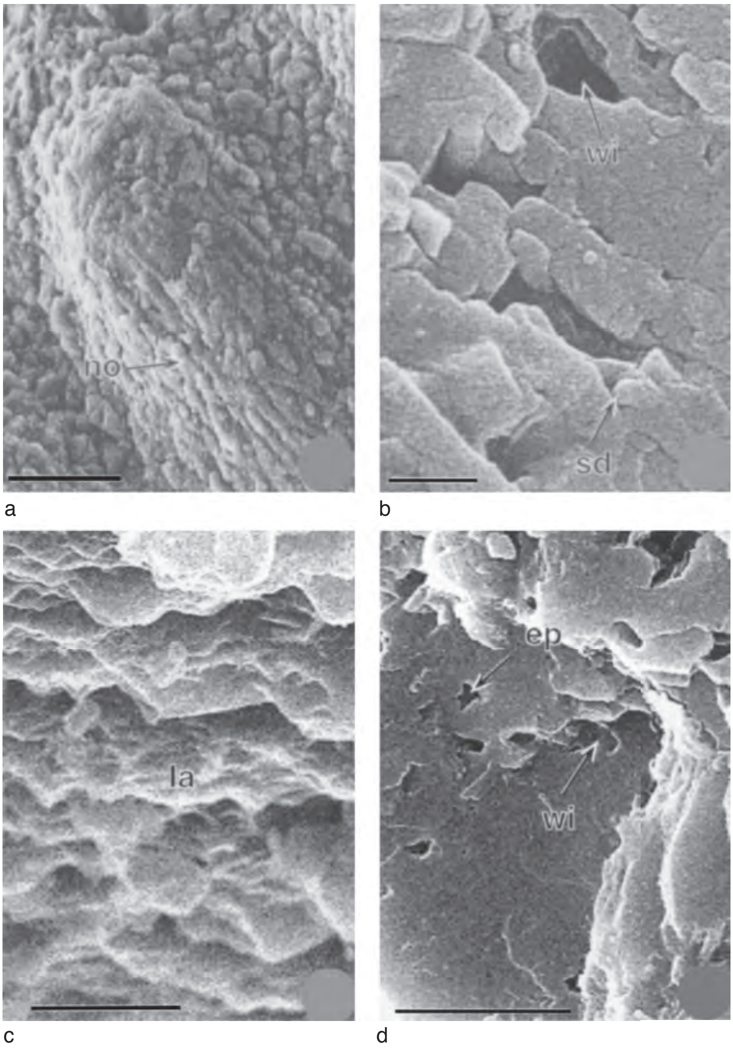


FIG. 1646. SEMs of *a,* internal margin of ventral valve of *Crania craniolaris* (LINNAEUS), Upper Cretaceous, Kristianstad, Sweden, and *b,* internal surface of dorsal valves after incubation with bleach (5% v/v) for 6 h; *c–d*, SEMs of fracture sections and internal surfaces within secondary layers of shell of *Isocrania egnabergensis* (RETZIUS), Upper Cretaceous, Egnaberg, Sweden; *a,* ellipsoidal nodules (*no*) aligned with long axis of tubercle at internal, ventral margin, GLAHM 114 279; scale bar: 50 µm; *b*, internal surfaces within successions of secondary layer (GLAHM 114 280) showing various features of laminae including etch pits, screw dislocated rhombohedra (*sd*), and junction windows (*wi*); scale bar: 1 µm; *c,* detail of fracture section of primary layer of dorsal valve showing sheetlike succession of laminae (*la*); scale bar: 5 µm; *d*, succession of laminar sheets in secondary layer of ventral valve (GLAHM 114 275) with etch pits (*ep*) and junction window (*wi*); scale bar: 10 µm (Cusack & Williams, 2001).

homologous with that of living *Novocrania*. The ultrastructure, however, had been partially obscured by repeated recrystallization that involved changes by pressure solution exploiting the original fabrics. Degradation of the organic components of the shells reached a steady state in Paleozoic craniids. The residual amino acids derived from the shells of all species are the same suite of the more robust molecules, although their

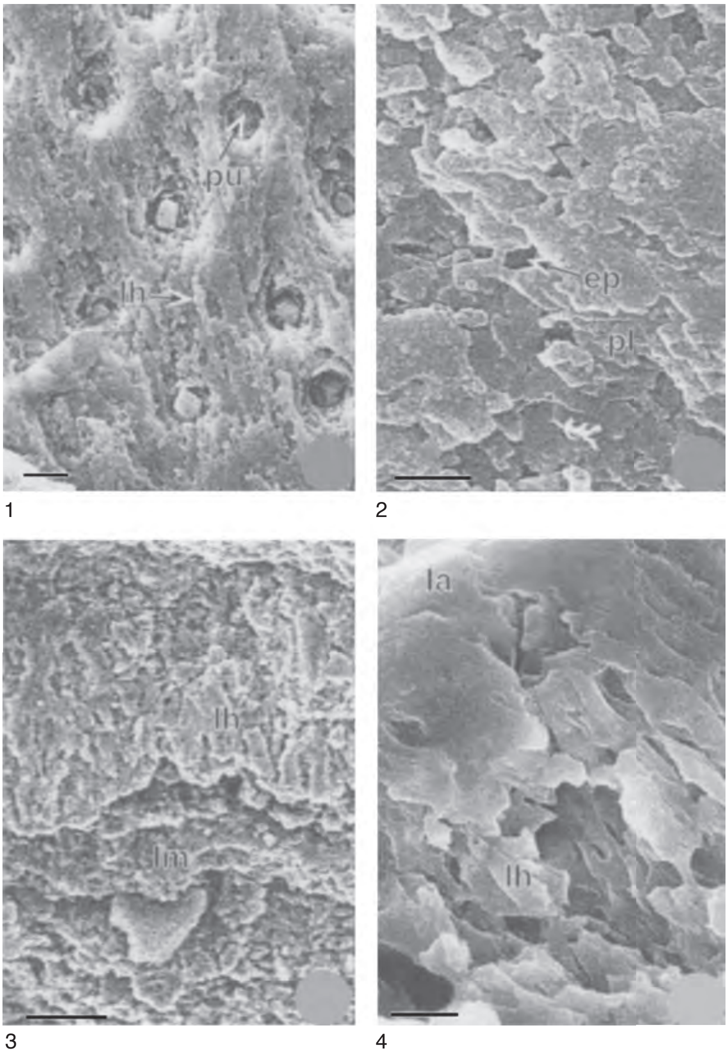


FIG. 1647. SEMs of surfaces and fracture sections of craniid shells; *a, Crania* ? *ryckholtiana* (DE KONINCK), Lower Carboniferous, Scotland; general view and detail of weathered exterior of dorsal valve (NMS 2346) showing punctae (*pu*) and laminae predominantly disposed as laths (*lh*); scale bar: 10 µm; *2*, vertical fracture section of *Rhipidomella* sp. showing etch pits (*ep*) and rhombohedral plates (*pl*) of secondary layer; scale bar: 1 µm; *3*, weathered external surface of dorsal valve of *Petrocrania scabiosa* (HALL), Upper Ordovician, Ohio, GLAHM 114 285, showing laths (*lh*) of lamellae (*lm*); scale bar: 100 µm; *4*, external surface of *Petrocrania scabiosa,* Upper Ordovician, Ohio, GLAHM 114 285, showing laths (*lh*) of primary layer coalescing distally to form a lobate lamella (*la*); scale bar: 5 µm (Cusack & Williams, 2001).

concentrations do not reduce in line with increasing geological age and were probably more closely related to the chemistry of invasive diagenetic fluids. Accordingly, it seems that most of the biochemical degradation of the craniid shell occurred within the last 80 myr, although repeated recrystallization replicated the original biomineral fabric long after it had lost its constraining organic membranes (Fig. 1650).

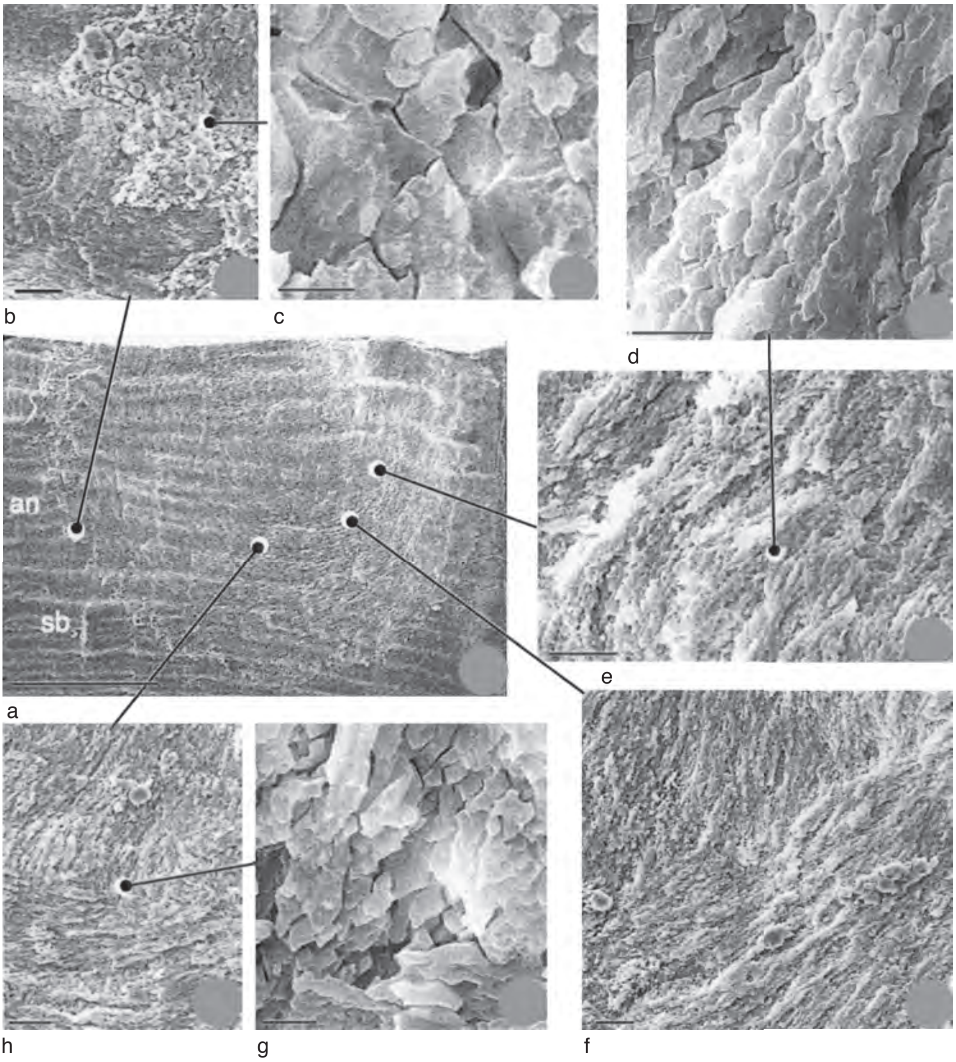


FIG. 1648. Ventral valve (GLAHM 114 284) of *Petrocrania scabiosa* (HALL); *a,* almost complete ventral valve, consisting of calcified film anteriorly (*an*) and thicker body platform posteriorly, cemented on substrate (*sb*) of a *Rafinesquina* shell; scale bar: 1 mm; *b–c*, general view and detail showing irregular boundary of film of overlapping rhombohedral plates at anterior margin; scale bars: 100 µm, 20 µm respectively; *d–e*, detail and general view of posteromedial interior showing overlapping concentric laths composed of rhombohedra, declined toward posterior margin; scale bars: 10 µm, 50 µm respectively; *f–h*, general views and detail showing composite disposition of calcitic laths in posterolateral successions of body platform; scale bars: 100 µm, 10 µm, 100 µm respectively (Cusack & Williams, 2001).

ORGANOCARBONATE FIBROUS SHELL

The fibrous fabric and its cross-bladed (composite) laminar and foliate variants characterize the organocarbonate shell of all rhynchonelliforms, the overwhelmingly dominant brachiopod group since the late Cambrian. The fibrous shell was the first major fabric to be comprehensively investigated (WILLIAMS, 1968a). Later studies have tended to be restricted to textural variation (BAKER, 1970; WRIGHT, 1970; GASPARD, 1974; SMIRNOVA, 1979) as outlined

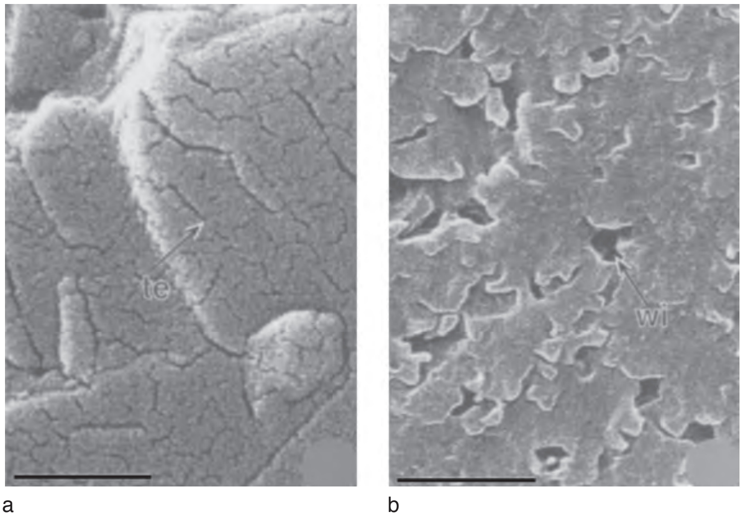


FIG. 1649. SEMs of fracture sections and internal surfaces within secondary layers of shell of *Isocrania egnabergensis* (RETZIUS), Upper Cretaceous, Egnaberg, Sweden; *a,* treated with bleach (5% v/v) for 15 h and *b,* dissolved in 0.5% HCl for 1 min; *a,* laminar successions of secondary layer of dorsal valves showing tension cracks (*te*) caused by bleaching, GLAHM 114 281; scale bar: 0.5 µm; *b,* laminae within secondary layer of dorsal valve (GLAHM 114 282) etched by HCl to show enlargement of junction windows (*wi*); scale bar: 1 µm (Cusack & Williams, 2001).

in Volume 1 (WILLIAMS, 1997, p. 280–295). More recently, investigations have concentrated on the chemicostructural accretion of living shells (CUSACK & WILLIAMS, 2001b). They show that, although the intracrystalline, calcifying proteins are more varied than was expected, biomineral accretion is virtually the same in species representing the three extant orders, the Rhynchonellida, Terebratulida, and Thecideida. A deeper understanding of rhynchonelliform secretory regimes has prompted this review of the relationship between the fabrics of living rhynchonellate shells and those that distinguish the shells of extinct groups like the strophomenates and obolellates.

CHEMICOSTRUCTURE OF LIVING RHYNCHONELLATE SHELLS

The rhynchonellide *Notosaria*, the terebratulide *Liothyrella,* and the thecideide *Thecidellina* not only typify the three extant rhynchonellate orders but also the full range of their shell fabric (WILLIAMS, 1997, p. 271–295). The shell of *Notosaria* with its undifferentiated primary and fibrous secondary layers serves as the standard rhynchonellate skeletal succession (WILLIAMS, 1968c, p. 269–270). In contrast, the secondary shell of *Thecidellina* (as in all living thecideides) is virtually suppressed, being restricted to patches on the cardinalia and the valve floors (WILLIAMS, 1973), while the dominant fabric of *Liothyrella* is a prismatic tertiary layer.

The identification of the organic components of the shell and their role in calcification involve some assumptions. In 1965, JOPE reported the presence of amino acids, lipids, and carbohydrates in living (and fossil) rhynchonellate shells. These organic residues, however, were mainly intercrystalline, notably the membranes ensheathing fibers, which had already been identified as glycoproteins by optical and electron microscopic staining techniques. Such membranes serve as substrates, and calcification of the fibers within them is effected by intracrystalline polymers incorporated within the fibers as they grow. These polymers account

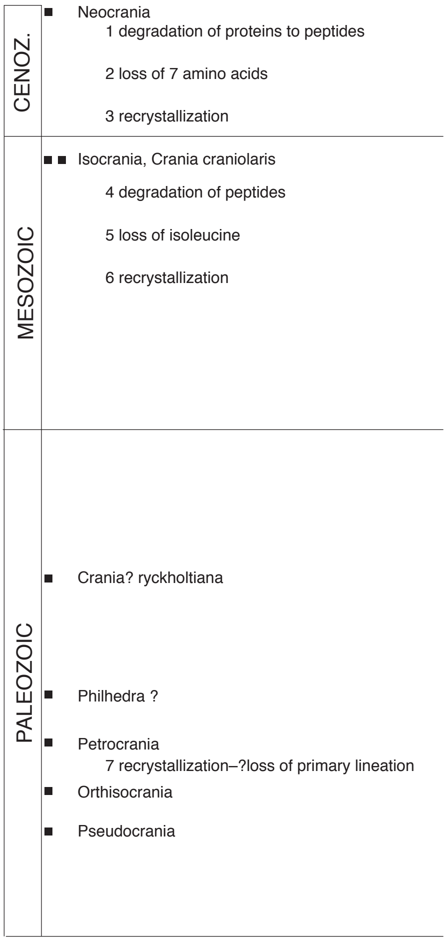


FIG. 1650. Inferred diagenetic changes in chemicostructure of shells of eight cranioid genera, arranged geochronologically and thereby showing relatively short time scale of principal phases of degradation and recrystallization (Cusack & Williams, 2001).

for only 0.3% of shell weight (COLLINS & others, 1991) and are evidently thinly and sporadically distributed. The differential treatment of rhynchonellate shells by degradants such as bleach and enzymes can, however, locate sites of polymer concentrations (doping) within calcitic successions and help to specify the organic components of the primary, secondary, and tertiary layers. The merits of this procedure rest on three assumptions: thecideide shells constitute samples of a universal rhynchonellate primary layer; any differences in the biochemistry of the rhynchonellide and thecideide shells are due to the presence of the secondary layer in rhynchonellides; and differences unique to the terebratulide *Liothyrella* can be attributed to the development of its tertiary layer.

Despite the distinctiveness of their fabrics, the basic biomineral unit of all three layers is structurally the same. It is an organically coated granule of calcite approximately 15–20 nm in diameter and commonly clustering into spherules approximately 50 nm in size. The granules are normally exocytosed to form monolayers that are commonly grouped into laminae (growth bands) up to but rarely exceeding 1 µm thick. Interfaces between laminae are exaggerated by degradants indicating the presence of organic films. As laminae accumulate orthogonal to the secreting plasmalemma, they are differently disposed relative to the isotopic boundaries of the three layers (WILLIAMS, 1997, p. 268). They are virtually flat lying in the primary and tertiary layers but variably inclined in the secondary layer to accord with the slope of the terminal faces of the fibers.

RHYNCHONELLATE PRIMARY LAYER

The rhynchonellate primary layer, as typified by *Notosaria*, can exceed 100 µm in thickness and is composed of granular monolayers aggregating as flat-lying laminae (Fig. 1651a–b). Rare organic inclusions consist of isolated strands approximately 30 nm thick (Fig. 1651a) and amorphous organic blobs within sporadically occurring arcuate grooves (Fig. 1651b). These grooves represent outlying sites of the aborted secretion of incipient membranes and secondary fibers; the blobs are therefore assumed to be glycoproteinaceous residues. The primary layer reacts differently to various degradants. Subtilisin excavates slots between granular laminae (Fig. 1651c–d), leaving amorphous blobs. Each slot evidently represents an organic substrate of a lamina, which

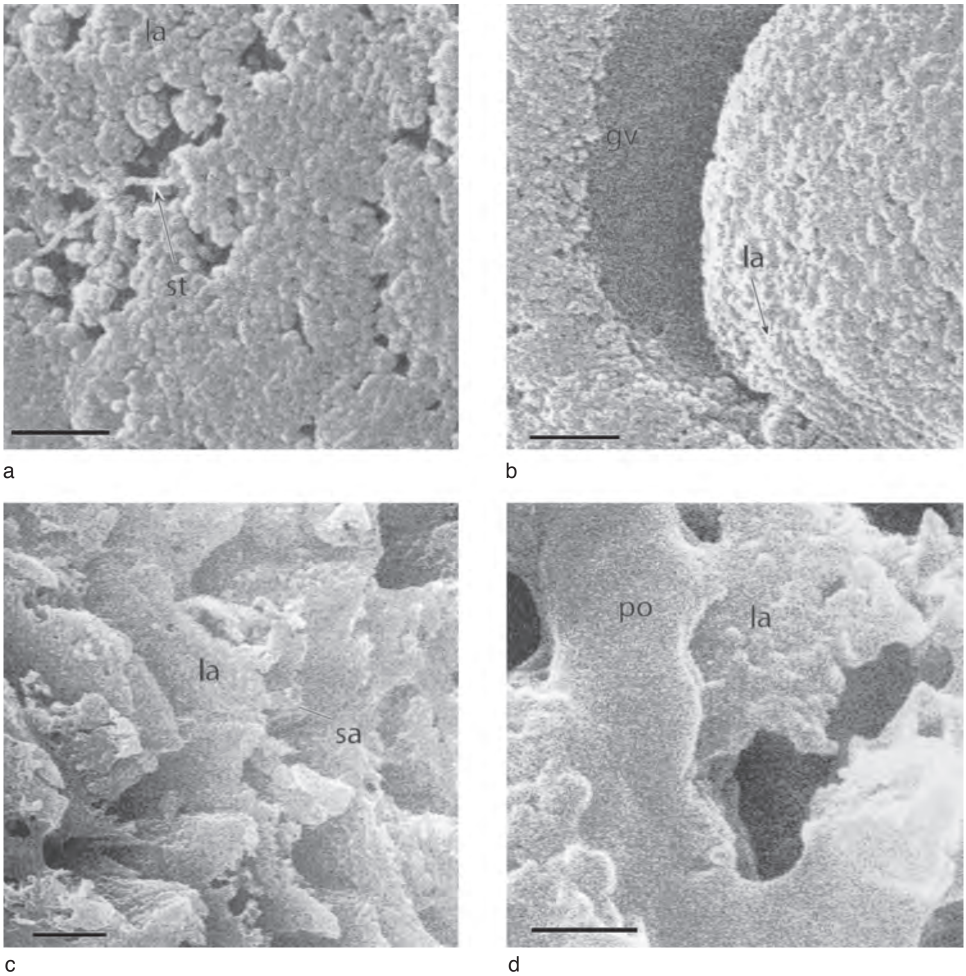


FIG. 1651. Structure of primary layer of *Notosaria nigricans* (SOWERBY), Holocene, New Zealand; *a,* features of near horizontal granular laminae (*la*) including ramifying strands (*st*); *b*, crystallographic continuity between primary and secondary laminae (*la*) present in early-forming fiber behind groove (*gv*) of undegraded glycoproteinaceous membrane; *c*, effects of subtilisin digestion with development of slots (*sa*) by removal of impersistent proteinaceous sheets and *d*, release of amorphous blobs (*po*) of a polysaccharide; *a* and *b* untreated, *c* and *d* digested in subtilisin; scale bars: 0.5, 1.0, 0.5, and 1.0 µm respectively (new).

is composed of protein and presumably an associated polysaccharide remaining as a blob. Both these organic components are degraded by bleach, which virtually destroys the primary layer peripheral to its junction with the secondary layer.

The shell of living thecideides consists almost exclusively of primary layer, because secondary fibers are restricted to isolated patches on the cardinalia and valve floors (WILLIAMS, 1973). The layer is texturally similar to that of *Notosaria,* for it is composed of granular laminae forming horizontal successions (Fig. 1652b), although blocky rhombohedra may also develop (Fig. 1652a). Rhombohedral cleavage, at 200–500 nm intervals, may extend through laminar successions for several micrometers (Fig. 1652c), indicating epitaxial continuity irrespective of the organic components.

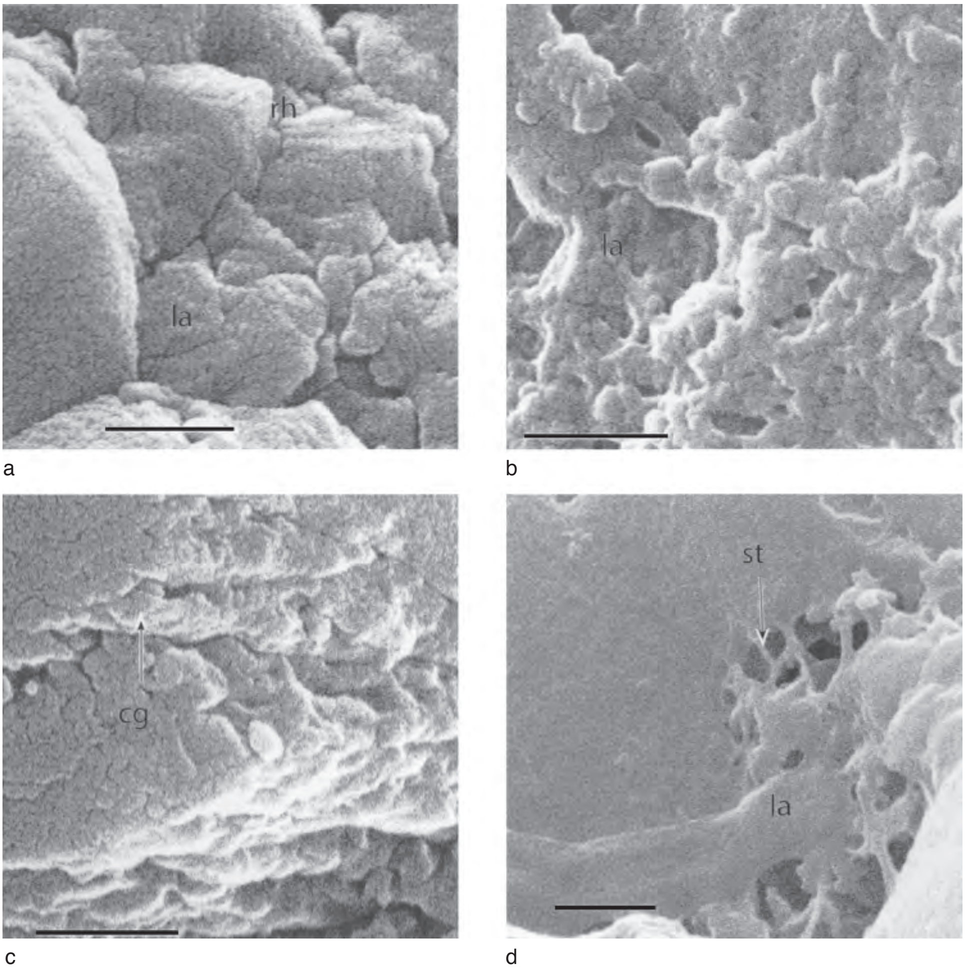


FIG. 1652. Structure of primary layer of *Thecidellina barretti* (DAVIDSON), Holocene, Bahamas; *a,* various features of granular laminae (*la*) including formation of blocky rhombohedra (*rh*); *b,* near horizontal disposition of laminar succession (*la*) in tubercles; *c,* detail of granular layer and cleavage (*cg*); *d,* laminar succession (*la*) with branching strands (*st*); *a* and *c* treated with bleach, *b* and *d* unbleached; scale bars: 0.5 µm (new).

Organic microstructures are rare but include branched strands up to 35 nm thick at laminar interfaces (Fig. 1652d).

RHYNCHONELLATE SECONDARY LAYER

The primary and secondary layers of rhynchonellate shells are structurally distinguishable solely on the interconnected growth of glycoproteinaceous membranes segregating the secondary layer into discrete fibers. Otherwise, the fibers are generally aligned crystallographically not only with one another (Fig. 1653a) but also with the mineral component of the primary layer (Fig. 1652b). The membranes, which act as substrates for a granular coat (Fig. 1653c–d) covering the stalks of forward-growing fibers, are synthesized at the distal and anterior margins of cells where they are exocytosed as a mass of fibrils serving as hemidesmosomes. The proximal and posterior margins of the exposed terminal faces of fibers subtend rhombohedral angles (Fig. 1654c). These

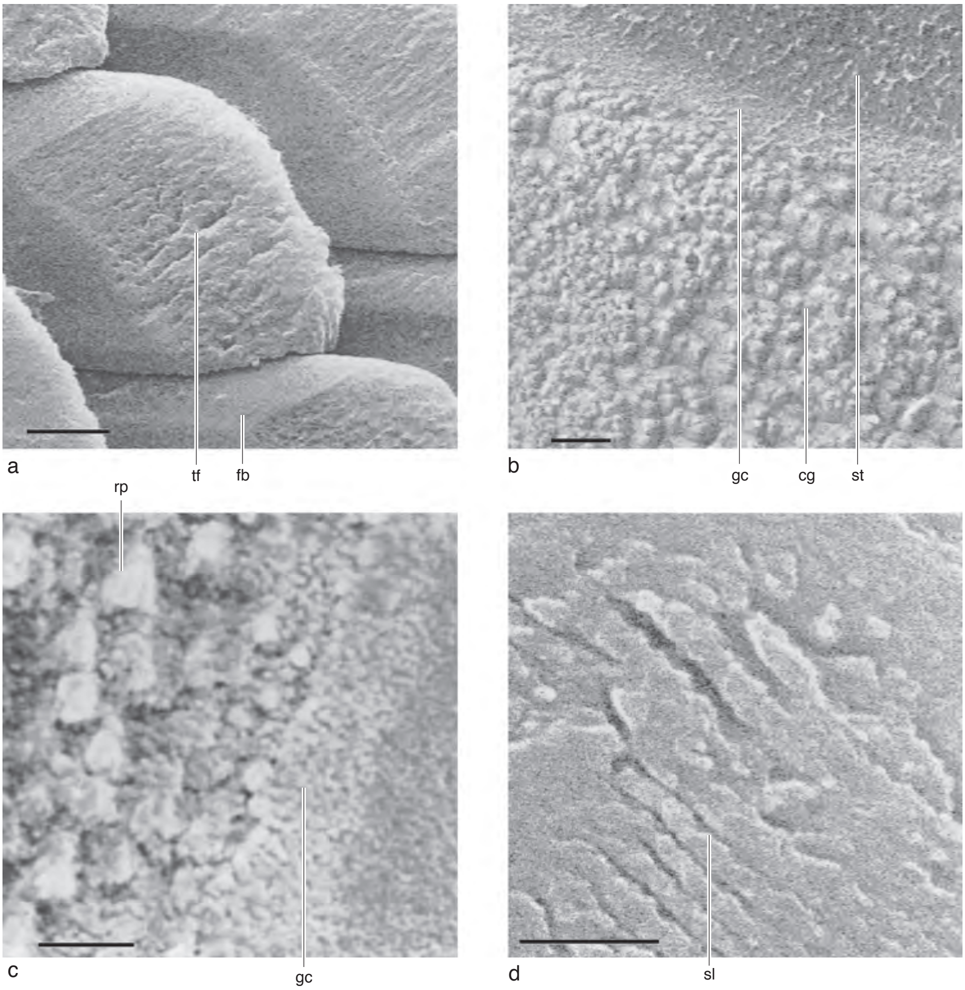


FIG. 1653. Structure of secondary layer of *Notosaria nigricans* (SOWERBY), Holocene, New Zealand; features of fibers (*fb*) and their terminal faces (*tf*) including *a,* crystallographic alignment of cleavage in contiguous fibers, remnants of strands (*st*) associated with an ensheathing membrane and *b–c,* its granular coat (*gc*) bounding cleaved (*cg*) rhombohedral granular plates (*rp*) of a fiber core and *d,* slats (*sl*) aligned with the short diagonal of a (10.4) face of a flat-lying fiber; *a, b, d* treated with bleach, *c* digested in subtilisin; scale bars: 2.5, 1.0, 0.5, and 0.5 µm respectively (new).

angles reveal the essential crystallography of terminal faces that, irrespective of their organic constituents, can be regarded as (10.4) rhombohedral plates constrained from full development by the arcuately disposed membranes being secreted distally. Narrow zones of pits sporadically develop along fiber axes parallel with the boundaries of the terminal faces. The pits mark changes in the rates of the forward growth of fibers and, as they are exposed after enzymic degradation of ensheathing membranes, they are probably sites of proteinaceous outgrowths (Fig. 1653b).

The cores of fibers, as exposed at their terminal faces, are composed of granular rhombohedral plates (Fig. 1653b–c) with edges (steps) more or less parallel with the

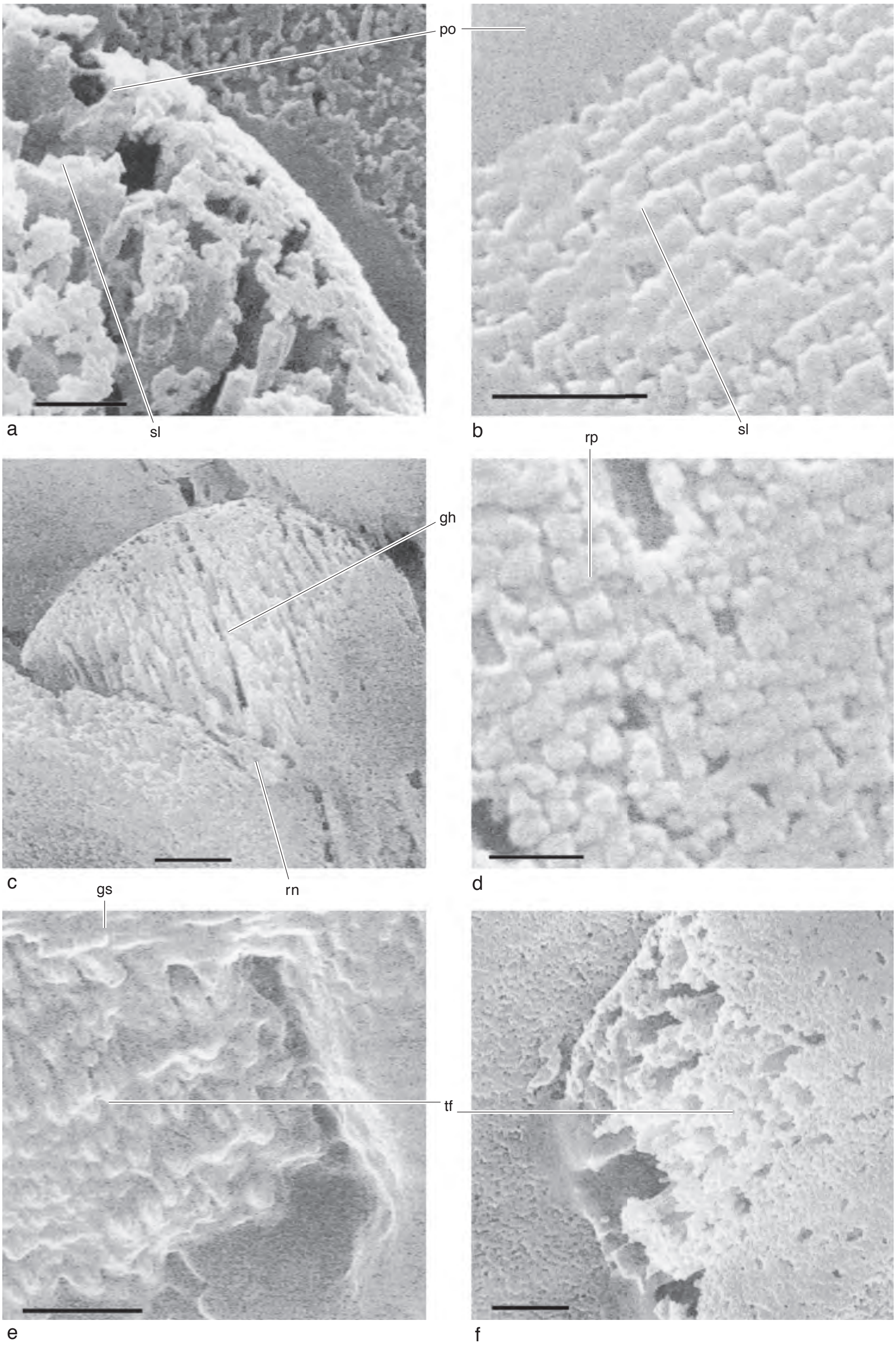


FIG. 1654. *For explanation, see facing page.*

proximal rhombohedral boundaries of the terminal faces. These plates are subparallel with the terminal faces of flat-lying fibers but dip more steeply in the faces of inclined fibers, where they commonly form arrays of rhombohedral tablets up to 2 µm in long diameter (Fig. 1653c). Cleavage develops parallel with both the (01.4) and $(1^{-}1.4)$ faces, although one is normally dominant. Degradants sporadically expose grooves delineating slats approximately 150 nm wide on terminal faces (Fig. 1653d).

A typical fiber of *Liothyrella* differs from that of *Notosaria* in being composed mainly of calcitic slats aligned with its long axis (stalk; Fig. 1654a). The slats are secreted as sequences of granular rhombohedral plates (Fig. 1654b, 1654d). They are segregated into bundles by proteinaceous sheets so that pits and gashes are left on the terminal faces and stalks of fibers when digested in enzymes (Fig. 1654c). Some organic residues, however, persist as amorphous blobs (Fig. 1654d) even after treatment with bleach and are identical with those left behind when glycoproteinaceous membranes are digested in enzymes.

RHYNCHONELLATE TERTIARY LAYER

In the transitional zone between the secondary and tertiary layers of *Liothyrella*, fibers become smaller within semiellipsoidal hollows coated with membranes (Fig. 1654f). The earliest secretion of the tertiary layer is marked by an encroachment of horizontally disposed granular sheets of calcite across fibers (Fig. 1654e). The sheets show strong cleavage and fragment as rhombohedral blocks.

The tertiary layer consists of polygonal prisms growing orthogonally to the terminal faces of secondary fibers. The prisms are not ensheathed in membranes but are separated from one another by irregularly developed organic partitions that are also probably glycoproteinaceous according to enzymic treatment. On untreated internal surfaces of the tertiary layer, the partitions are represented by a microstructural valley system delineating gently convex mounds 5–10 µm across (Fig. 1655a). The surface is pierced by micropunctae (Gaspard, 1990) and punctae.

Secretion of the prismatic layer is stratiform with laminae up to 500 nm thick and interleaved with organic substrates (Fig. 1655e). The early stages of laminar secretion are marked by rhombohedral aggregations of granules that may form slatlike arrays approximately 400 nm wide (Fig. 1655d). The slat boundaries tend to have a characteristic alignment for each mound, and sets of slats may form acute angles of 70° or so in contiguous features.

Untreated surfaces of dead shells are commonly indented by flat-bottom pits in a labyrinthine arrangement (Fig. 1655a) and are presumably sites of organic concentrates that have been etched out by postmortem degradation. Such pits in enzymically treated surfaces are greatly enlarged into cavities associated with strong grooves subtending rhombohedral angles with one another (Fig. 1655b–c). Enzymic digestion also exposes outcrops of laminae along the slopes of the mounds (Fig. 1655f). Slopes treated with subtilisin normally retain interleaves of amorphous polymers (Fig. 1655f).

ACCRETION OF LIVING RHYNCHONELLATE SHELLS

The shells of living rhynchonellates are structurally similar in two respects.

Fig. 1654. Structure of secondary layer of *Liothyrella neozelanica* (Thomson), Holocene, New Zealand; *a–b,* details of fibers including disposition of slats (*sl*) and polysaccharide blobs (*po*) in terminal faces, *c,* gashes (*gh*) representing doped sites on terminal faces of fiber with proximal boundary subtending rhombohedral angle (*rn*), *d,* rhombohedral tablets (*rp*) glued together by polysaccharide in a monolayer array and *e,* encroachment of granular sheets (*gs*) of tertiary layer across slats of terminal face (*tf*) of a fiber with *f,* another incipient fiber in transitional zone of tertiary layer; *b, d* digested in subtilisin, *a, c, f* digested in proteinase-K, *e* untreated; scale bars: 0.5, 0.5, 2.5, 0.2, 1, and 1 µm respectively (new).

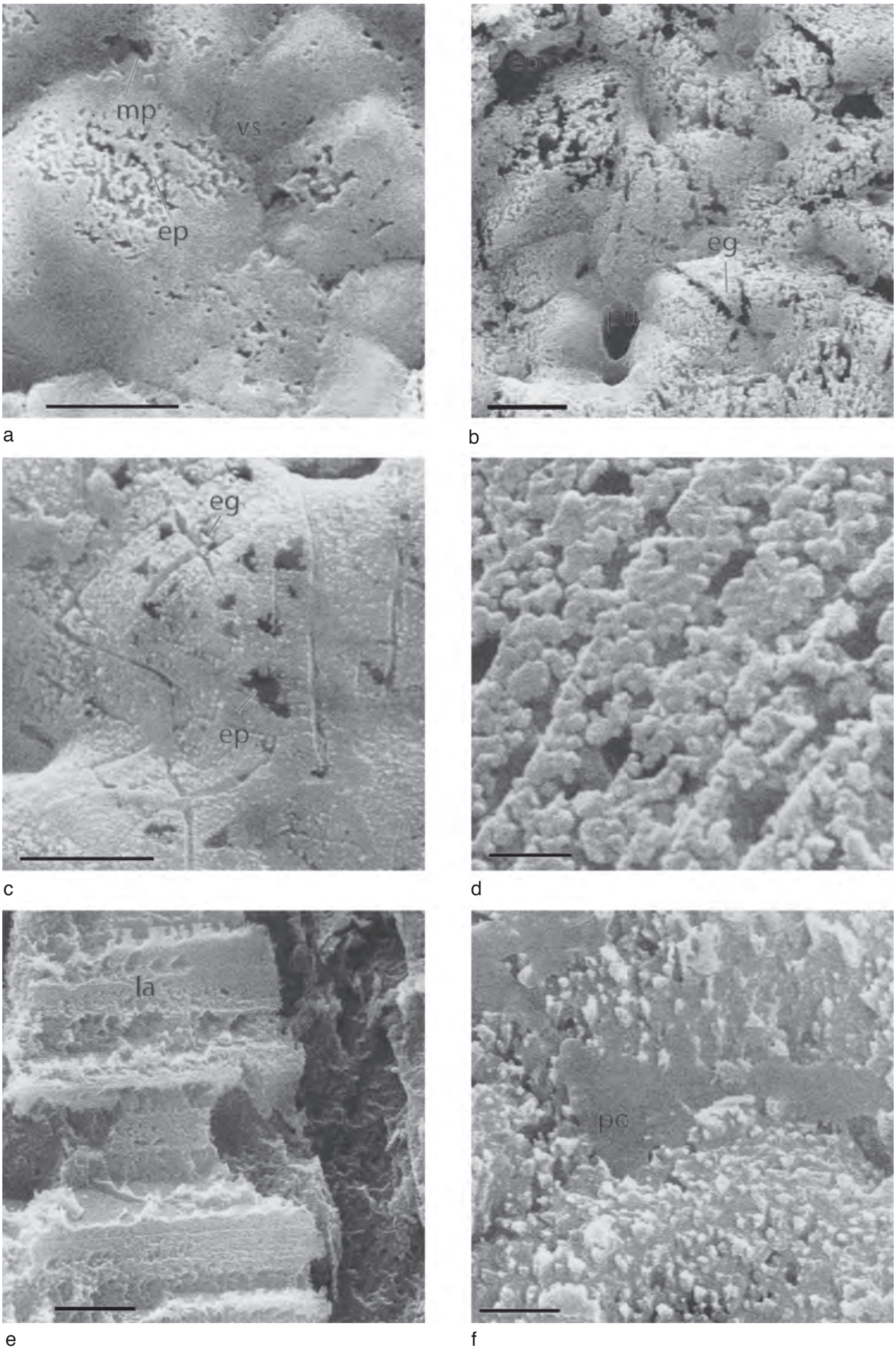


FIG. 1655. *For explanation, see facing page.*

They are composed of granules of calcite approximately 15 nm in size and normally assembled with a rhombohedral motif into monolayers. The monolayers aggregate into laminae of variable thickness that tend to have a crystallographic form that is more or less aligned throughout the shell, irrespective of organic inclusions. One manifestation of this continuity is the way the proximal boundaries of terminal faces of contiguous fibers are virtual sets of aligned (10.4) rhombohedral plates. As laminae grow by granular exocytosis orthogonal to the secreting plasmalemma, any crystallographic realignment is controlled by changing rates of sedimentation that cumulatively effect microtopographic changes in the internal surface of the shell and, therefore, the disposition of the epithelium. This is especially so in the growth of fibers, where the laminae of terminal faces are normally inclined in contrast to their near-horizontal disposition in primary and tertiary layers. In short, many skeletal structural differences characterizing thecideide, rhynchonellide, and terebratulide shells, layer for layer, are related to topographical variation in the internal surfaces of valves.

The precise relationship between the mineral and organic components of the rhynchonellate shell remains elusive. Organic constituents mediate shell growth with certain proteins effecting mineral precipitation and resorption in brachiopods (BROWN, 1998; CUSACK & WILLIAMS, 2001b), mollusks (FALINI & others, 1996), and so on. But the growth of a lamina (or monolayer) is a two-stage process that involves first the precipitation of calcitic units possibly aligned with the substrate fabric and then the binding together of the units into calcitic sheets. Newly formed primary layers at the margins of *Notosaria* and *Liothyrella* shells become slotted by enzymic digestion, presumably of impersistent proteinaceous membranes, but they are entirely destroyed by bleach. Amorphous organic blobs that appear during enzymic digestion of the glycoproteinaceous sheaths of fibers also occur in primary layers when they are similarly treated. These blobs are assumed to be residues of a polysaccharide that also acts as a glue binding together mineral units into laminae, not just in the primary layer but throughout the shell. Moreover, laminae in the inframarginal, older parts of the primary layer tend to interdigitate and are less prone to disintegration when treated with bleach. This increased durability could result from further polymerization of the polysaccharide matrix (CUSACK & WILLIAMS, 2001b).

In contrast to the ultrastructural conservatism of living rhynchonellate shells, the range of proteins, extracted from intracrystalline residues, is wide with no clear indication of specificity to any particular layer. As the primary, secondary, and tertiary layers are, presumably, structurally homologous throughout fossil and living rhynchonellate shells, it would have been reasonable to expect proteins specific to the primary and tertiary layers to be the dominant molecular weights determined for the thecideide and liothyrellid shells respectively, with proteins characteristic of the secondary layer restricted to *Liothyrella* and especially *Notosaria* where it should be prevalent. No such specificity occurs. Indeed as Figure 1544 suggests, a variety of intracrystalline proteins are likely to be involved in the calcification of each layer of the rhynchonellate shell. Not all of the 21 intracrystalline proteins,

FIG. 1655. Structure of tertiary layer of *Liothyrella neozelanica* (THOMSON), Holocene, New Zealand; *a–c,* internal surfaces of tertiary layer penetrated by micropunctae (*mp*) and punctae (*pu*) showing microtopography of mounds delineated by valley systems (*vs*) with etch pits (*ep*) and etch grooves (*eg*) revealed by *a,* natural degradation of organic constituents and *b–c,* exaggerated by enzymic digestion; scale bars: 10, 10, and 5 µm; *d–f,* details of effects of degradation on slats of fracture section of laminar succession (*la*) and of enzymic digestion on internal surface with laminae exposed in residual polysaccharide (*po*); scale bars: 0.5, 2.5, 1 µm; *a, d* untreated, *b, e* digested in proteinase-K, *c, f* digested in subtilisin (new).

however, necessarily have a calcifying role. One or more molecular weight estimates must represent actinlike strands, sporadically occurring within laminae, that are probably part of a paracrystalline framework strengthening successions. Pits and grooves in rhombohedral arrangements, like those exposed in treated *Liothyrella*, are likely to be sites doped with inclusions of intercrystalline substrates (compare Williams, Cusack, & Brown, 1999). Some intracrystalline proteins could even have arisen by molecular transformation subsequent to the phylogenetic divergence of the terebratulides and the thecideides from their rhynchonellide sister group. Should this be so, the protein chemistry of rhynchonellate shells is presently a less comprehensible guide than ultrastructure to ordinal genealogy.

CHEMICOSTRUCTURAL DIVERSITY OF EARLY RHYNCHONELLIFORM SHELLS

The extinct, organocarbonate-shelled chileate, obolellate, kutorginate, and strophomenate brachiopods are coeval with the early Cambrian rhynchonellates. The groups are morphologically related and probably a monophyly, but each is characterized by a distinctive secondary shell fabric. In attempting to derive these diverse fabrics from an ancestral node, two assumptions have to be made. First, the integument of the ancestral rhynchonelliform did not differ significantly in growth or in layering from that of living species. Secondly, variation in fabric reflects changes in the composition and sites of secretion of polymers acting as substrates for the accretion of relatively uniform, nanometrically sized granules or rhombs of calcite.

The primary layer also plays a crucial role in postulating changes in ancient secretory regimes that could have given rise to diverse secondary fabrics. As it is by definition the first mineralized layer to be secreted on the periostracum, it is invariably present and usually preserved, albeit in a recrystallized state. Indeed, the primary layer is a constant reminder that no mineral accretion can take place without a substrate; and the possible origin of its own substrate, the periostracum, is pertinent to an enquiry into the structural diversity of the rhynchonelliform shell. Presumably, a mucin-based glycocalyx was the precursor to the glycoproteinaceous periostracal substratum (Fig. 1575, 1578) that would have been the ancestral substrate for calcitic accretion in the earliest rhychonelliforms.

In living rhynchonellates, the onset of the fibrous secondary layer is signalled by the secretion of arcuate patches of a glycoproteinaceous membrane on the inner surface of the primary layer (Fig. 1651b). Each patch is secreted by a microvillous anterior arc of an outer epithelial cell (Williams & others, 1997, fig. 13, p. 20). As the secreting cell advances anteroradially, its patch is extended forward as a semicylindrical strip serving as a substrate for the outer edges of a stack of calcitic laminae (i.e., the fiber) being secreted by the rest of the plasmalemma behind the microvillous arc. This sequence of skeletal secretion by a cell is the same as shell deposition by the mantle where the periostracum is fabricated by the outer mantle lobe marginal to the outer advancing mineralized shell.

The plasmalemmas of outer epithelial cells are closely packed in alternating rows (Williams, 1997, p. 283). Consequently during continuing secretion by an array of cells, the membranes intermesh to ensheath fibers that are exposed only at their terminal faces. In effect, each cell fabricates a substrate for the granular calcite it secretes. The secretion of its own substrate and mineralized coat is a discrete, spatially ordered event, not a collective one involving an array of cells simultaneously secreting a layer of the same constituent, as when the primary layer is deposited on the periostracum. Not all linear calcitic structures, however, were secreted discretely with their substrates. Laths and blades, for example, the predominant calcitic structures of the strophomenate secondary shell, would have grown collectively by marginal accretion on an enlarging membranous sheet.

The singularity of the discrete secretory regime, giving rise to the fibrous secondary layer, militates against its having been an ancestral system of shell deposition. The collective secretory regime, on the other hand, is not only the mode of deposition of the primary layer but also of the stratiform shells of the linguliforms, the sister group of the rhynchonelliforms. It is, therefore, reasonable to assume that the fabric of the ancestral secondary shell was stratiform and probably structurally closer to that of an extinct rhynchonelliform group(s) than to the derived fibrous shell of living rhynchonellates. On this assumption, the secondary shell fabrics of the chileates, obolellates, kutorginates, and early strophomenates have been reviewed. As these fabrics are always recrystallized and seldom bear traces of their *in vivo* structure, new studies have been made to supplement published accounts.

The secondary shell fabric of the oldest known strophomenate, the Middle Cambrian *Billingsella*, is stratiform laminar (WILLIAMS, 1970). The basic laminar units are anastomosing calcitic sheets, each approximately 100 nm thick, that are commonly wrinkled into impersistent, radially disposed folds (Fig. 1656a–d). The sheets are interpreted as having originally been membranes coated with calcitic aggregates impregnated with polysaccharides that retained some of their rheological features on polymerization. Sets of sheets occur in close-packed successions, but they are more commonly thickened by the radial folds (8–10 µm wide) and discrete aggregates of radially aligned calcitic tablets or blocky calcite forming impersistent ridges (Fig. 1656e–f).

Although many morphological features distinguishing strophomenates from other rhychonelliforms are homoplastic, the group is probably monophyletic (WILLIAMS & others, 2000b, p. 215). The fabric of the strophomenate secondary shell (except for that of most plectambonitoids) is laminar as in the close-packed laminar sets of *Billingsella* (WILLIAMS, 1997, p. 287–293). The laminar texture, however, is cross bladed, which has an important bearing on changes in the relationship between shell and mantle during strophomenate evolution.

Strophomenate lamination is a collective fabric that was secreted by an array of outer epithelial cells as a recurring succession of a membranous substrate and a nanometrically thick, calcitic coat, sporadically interleaved with laminae thickened by various microstructures. In *Billingsella*, these include radially disposed folds of the calcified substrates and ridges, which would have been aligned more or less orthogonally to the growing margins of successive substrates. In other strophomenate shells, sets of close-packed laminae are also interleaved with thicker laminae mainly composed of tablets. These tablets are cross sections of thickened blades that commonly occur in localized parts of strophomenate shells (Fig. 1657; WILLIAMS, 1997, fig. 251, p. 291). The thickened blades look like the radial folds and ridges of *Billingsella* but are well ordered and differently oriented, being always aligned with the strophomenate cross-bladed fabric. Indeed, a typical section of the strophomenate secondary shell consists of alternating sets of arrays of tablets and laminae representing the transverse and longitudinal sections respectively of ordered successions of laths or blades (Fig. 1658), which is a composite fabric (NEVILLE, 1993).

In effect, cross-bladed lamination is a natural plywood, a helicoidal or pseudo-orthogonal composite, consisting of calcified substrates bearing closely spaced laths. The flat laths or blades, being not more

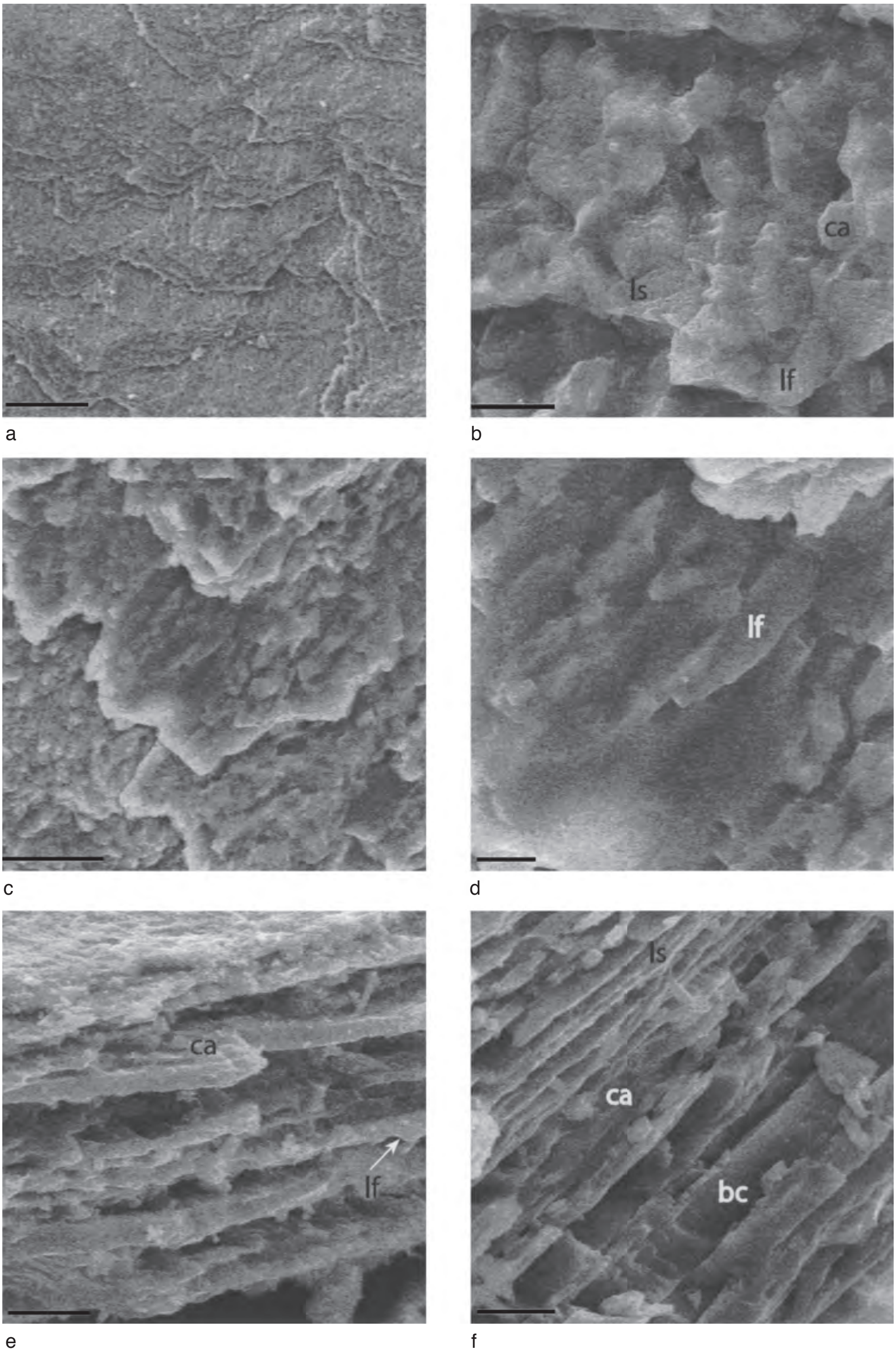


FIG. 1656. *For explanation, see facing page.*

than 6 µm wide, are generally discrete in older strophomenates (Fig. 1657, 1658.1a) and laterally fused into continuous sheets in younger species. They would not have conformed in size or shape to the secreting plasmalemmas of the strophomenate outer epithelium, assuming it to have been the same as in the mantle of living brachiopods. The incremental growth of laths is commonly recorded as transverse growth banding (Williams, 1997, fig. 250.3, p. 290), and the direction is indicated by the terminal, angular edges of laths (Fig. 1658.1a). Unlike the fibers of the rhynchonellate fabric, however, these growth vectors were only coincidentally orthogonal to the mantle edge of living strophomenates. As in all composite layers, they were determined by the polymeric configuration of the substratal membranes. In effect, the same array of outer epithelial cells secreted a succession of membranes that were so configured as to impose a helicoidal or pseudo-orthogonal lineation on their calcitic coats (Fig. 1658.2). The persistent association of the same array of cells with the laminar succession in the same part of the shell is consistent with the development of pseudopunctal ties between shell and mantle in most of the later strophomenates (Williams, 1997, p. 305–312).

The composition of the substratal membrane(s) that gave rise to strophomenate composite lamination must have differed from that of the substratal sheaths of rhynchonellate secondary fibers. The organic fibers that determine the fabric of a composite membrane are embedded in a polysaccharide or proteinaceous matrix and may be chitinous or proteinaceous (Neville, 1993, p. 85). There is some analogous support for the assumption that the membranous substrates, interleaved with strophomenate calcitic laminae, were chitinoproteinaceous, not glycoproteinaceous as in the rhynchonellate secondary layer. Thus, when glycoproteins form collective substrates for calcitic laminae, as in living craniid shells, the fabric is not composite (p. 2513, herein). Moreover, chitin is a common component of the shells of living lingulides and presumably of those linguliforms that were closely related to early rhynchonelliforms.

Attributing the structural difference between the fibrous and laminar secondary shells of rhynchonelliforms to glycoproteinaceous and chitinoproteinaceous membranes respectively, however, seems incompatible with the secondary shell fabric of the

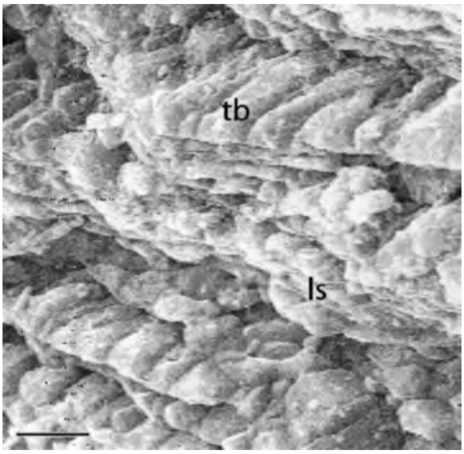


Fig. 1657. Fracture section of dorsal valve of early Ordovician (Arenig) strophomenide, *Hesperinia sinensis* Rong & others, showing thickened (*tb*) and normal sized (*ls*) blades of secondary shell laminae in transverse and longitudinal sections respectively; scale bar: 10 µm (new).

Fig. 1656. Secondary shell structure of *Billingsella lindstromi* (Linnarsson), Middle Cambrian, Sweden; *a–d*, internal views of fracture surfaces showing exfoliated sheets with anterior margin to bottom lefthand corner (*a–b*) and details of laminar sheets (*ls*) including laminar folds (*lf*) and calcitic aggregates (*ca*); scale bars: 220 µm, 10 µm, 50 µm, and 10 µm respectively; *e–f,* oblique fracture surfaces showing laminar successions with closely grouped laminar sets (*ls*) and thick laminae with laminar folds (*lf*), calcitic aggregates (*ca*), and blocky calcite (*bc*); scale bars: 25 µm and 10 µm respectively (new).

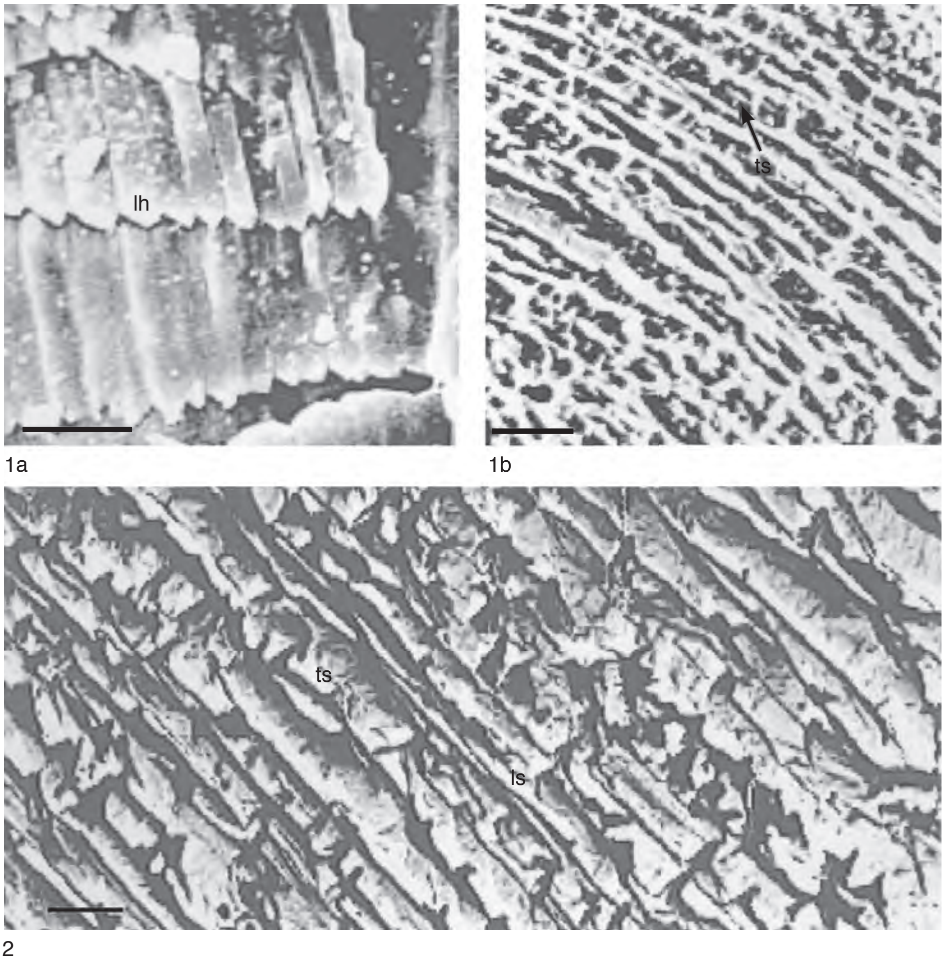


FIG. 1658. Strophomenate secondary shell structures; *1a–b,* exfoliated surface and resin-impregnated section of Upper Ordovician orthotetidine *Gacella insolita* WILLIAMS showing laminar laths in planar (*lh*) and transverse (*ts*) and longitudinal views, light bands and crossbars in *1b* represent resin infills and dark areas represent slightly etched laminae; scale bars: 5 µm; *2,* single stage negative replica of slightly etched polished vertical section of resin-impregnated shell of Middle Devonian *Pholidostrophia* sp. cf. *geniculata* IMBRIE showing plywood nature of laminar secondary shell with alternating sets of blades in longitudinal (*ls*) and transverse (*ts*) sections; scale bar: 5 µm (new).

strophomenide plectambonitoids, which are probably ancestral to the productide chonetidines. The plectambonitoid fabric is generally regarded as fibrous (WILLIAMS, 1997, fig. 252.3–252.4, p. 292), with the implication that the fibers are homologous with the orthodoxly stacked constituents of the rhynchonellate secondary layer (WILLIAMS, 1997, fig. 243, p. 284). In fact, as has been shown by BRUNTON (1972), the linear structures of the plectambonitoid secondary shell vary from flattened fibers without keels to blades with bevelled sides (Fig. 1659.1a–b). Moreover, the secondary shell structure of the earliest known chonetidines (the late Ordovician *Archaeochonetes*), which is accepted as a typical bladed lamination, is virtually indistinguishable from that of the plectambonitoid *Aegiromena* (BRUNTON, 1972; Fig. 1659.2–1659.3). Such

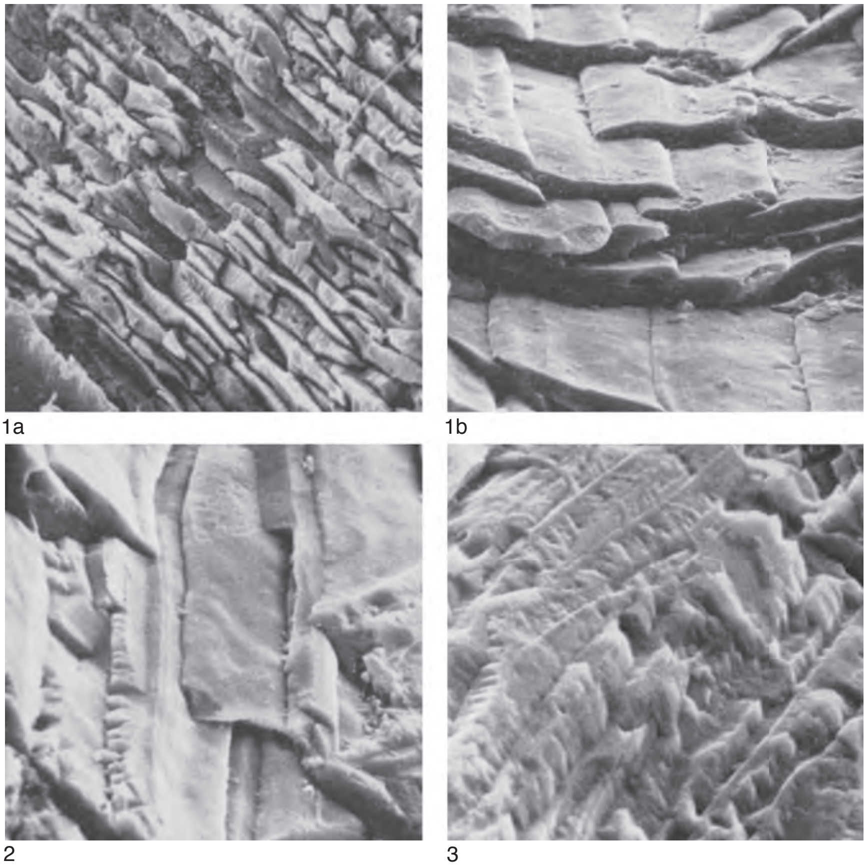


FIG. 1659. Strophomenate secondary shell structures; *1a–b,* lightly etched section and internal fracture surface of shell of Upper Ordovician plectambonitoid *Sowerbyella liliifera* (ÖPIK), showing stacked, flattened fibers, both ×1000; *2–3,* blades or fibers of Upper Ordovician plectambonitoid *Aegiromenia aquila* (BARRANDE) and Upper Ordovician chonetidines *Archaeochonetes primigenius* (TWENHOFEL) showing similarity in structure and stacking; ×1200, ×1000 respectively (Brunton, 1972).

a close relationship suggests that membranous substrates of the same composition were present in both secondary shells and are unlikely to have been chitin, which is absent from the shells of living rhynchonelliforms (and craniiforms). Whether these particular textural features indicate that the plectambonitoid fibrous fabric evolved independently of the rhynchonellate fabric will be considered later.

The composite fabric of the later strophomenides has evidently been derived from two sources. The basic constituent of the composite fabric of billingsellides (including orthotetidines and triplesiidines) and strophomenoids is a lath or blade that evolved from laminar folds as ridges as in those of the *Billingsella* shell. The basic constituent of the composite fabric of productides, on the other hand, was a flat, plectambonitoid fiber. The billingsellid ridge or blade had much in common with folii, and the plectambonitoid fiber had much in common with the rhynchonellate fibers. Both derived constituents grew on collective membranous substrates.

The presumed fabrics of the secondary shells of the three other early rhynchonelliform groups were first described more

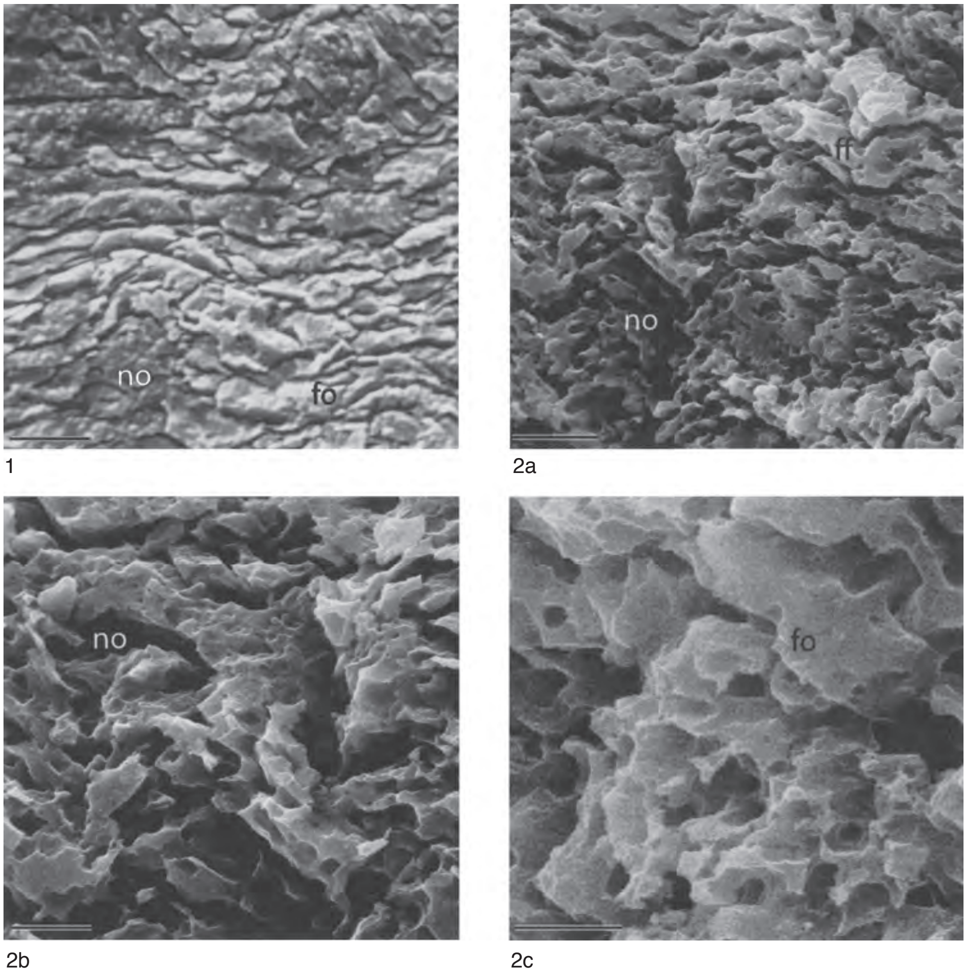


FIG. 1660. Secondary shell structure of *1, Trematobolus pristinus bicostatus* and *2a–c, Obolella* sp., Lower Cambrian, Rassokha River Basin, eastern Siberia; *1*, polished and slightly etched section showing folii (*fo*) disposed around nodules (*no*); scale bar: 25 µm; *2a–c*, fracture sections showing nodules (*no*) are composed largely of successive, hemispherical to semi-ellipsoidal layers of folded folii (*ff*) (*2a–b* with external shell surface to top of micrographs), and *2c,* detail of slightly etched, folded folii (*fo*); scale bars: 10 µm, 5 µm, and 5 µm respectively (new).

than thirty years ago, but they are rarely preserved and there has been some doubt about their textural authenticity. All three groups, the chileates, kutorginates, and obolellates, are restricted to the Lower and Middle Cambrian, although the chileates are tentatively regarded as being ancestral to the post-Cambrian dictyonellidines, whose secondary shells are disputably fibrous or aragonitic (HOLMER, 2000, p. 196). Recent work has clarified textural details of all three fabrics and has led to reinterpretations of their structures in the living state.

The obolellate secondary shell was first described as laminar and was homologized with the screw-dislocated lamination of living craniids (WILLIAMS & WRIGHT, 1970, p. 45). The relative coarseness of the laminae and their lenticularity in cross section, however, later prompted their redefinition as folii that had been sheathed by membranes in the living state, like rhynchonellate fibers

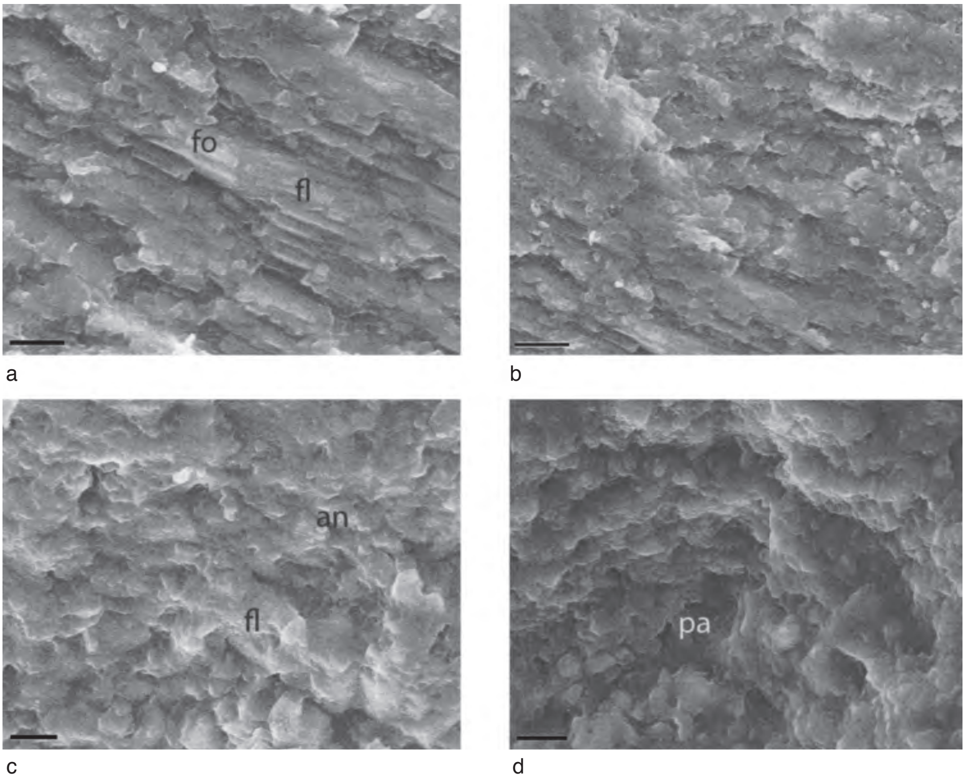


FIG. 1661. Secondary shell structure of chileate *Kotujella calva* ANDREEVA, Lower Cambrian, Rassokha River Basin, eastern Siberia; slightly etched fracture sections of ventral valve with external surface beyond top right corner of micrographs; *a–b,* succession of sets of folii (*fo*), some forming lenses (*fl*); scale bars: 20 µm; *c–d,* views of junction of anastomosing sets of folii (*an*) and puncta (*pa*) with frequent lenses of folii (*fl*); scale bars: 25 and 10 µm respectively (new).

(WILLIAMS, 1997, p. 286). The obolellide secondary shell fabric (Fig. 1660) is neither tabular in the manner of craniid laminae nor lenticular in cross section like rhynchonellate fibers. The fabric is laminar in the sense of having been secreted collectively, but the constituent plates are wrinkled into folds with wavelengths of approximately 5 µm. It seems appropriate therefore to recognize the distinctiveness of the obolellide fabric by continuing to describe it as foliate. The rheological state of *in vivo* folii is reflected in the way they form successive sheets composing the so-called nodules that occur in hexagonal-packed arrays throughout the shell and have been interpreted as hollows accommodating impersistent secretion bodies or as temporary sites of mantle muscle ties (WILLIAMS & WRIGHT, 1970, pl. 15,*4–6;* fig. 16).

The fabrics of the secondary shell of chileates and kutorginates were initially interpreted as having been fibrous in the living state with the chileate (*Kotujella*) shell also being punctate (WILLIAMS, 1968b, p. 487). Recent studies of *Kotujella*, however, indicate that its secondary shell (Fig. 1661) is composed of anastomosing sheets less than 300 nm thick, commonly occurring in sets approximately 25 µm thick, which may look like oblique sections of fibers but are structurally closer to foliate sets. The folii are not wrinkled but may be variably differentiated into lenticular tablets or occasional laths. The fabric of the kutorginate

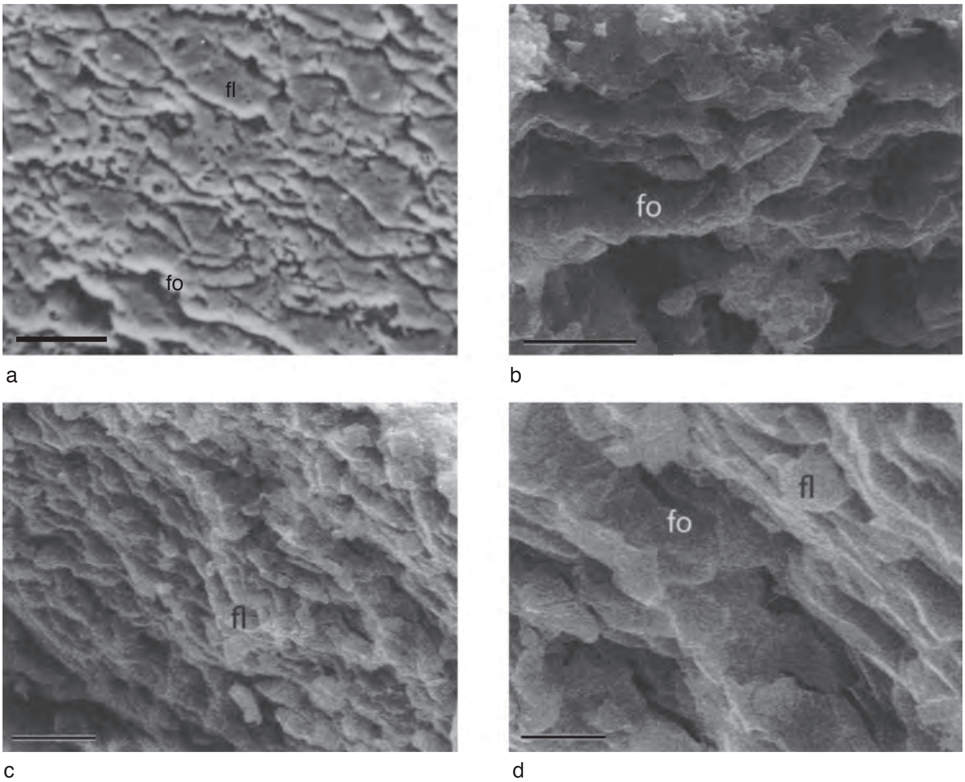


FIG. 1662. Secondary shell structure of kutorginate *Narynella ferganenis* (ANDREEVA), Lower Cambrian, Uzbekistan: *a*, polished and etched section showing succession of lenticular (*fl*) and laminar (*fo*) folii; scale bars: 10 µm; *b–d*, fracture sections showing foliate sets with slip planes developed on surfaces of folii that also enlarge into lenses (*fl*); scale bars: 20 µm, 25 µm, and 10 µm (new).

shell is also unlikely to have been fibrous in the living state. Sections of the nisusioid *Narynella* show horizons of ordered lenticles simulating fibers and interleaved with laminar sets (Fig. 1662). The lenticles are commonly composed of slip planes that are assumed to reflect recrystallized lamination in Mesozoic craniids (CUSACK & WILLIAMS, 2001a, p. 890). In short, the kutorginate secondary shell appears to be laminar, but with lenticles instead of laths and blades as in strophomenates. Both the wrinkled folii of chileates and lenticular folii of kutorginates could have been sheathed in membranes in the manner of a fiber. Both folii and their enclosing membranes, however, would still have been secreted collectively on membranous substrates as in laminar successions. In effect, the foliate fabric could have been transitional between the laminar and fibrous rhynchonelliform fabrics and ancestral to both or either. A relationship that presently best fits a phylogenetic model for the brachiopod phylum as a whole is considered in the Conclusions section, p. 2518 below (see also WILLIAMS & CARLSON, p. 2822, herein, and CARLSON, p. 2878, herein).

In attempting to ascertain the evolution of the rhynchonelliform secondary shell, the phylogeny of the brachiopod phylum as a whole has to be taken into account. Seven morphological and anatomical features, which have long been recognized in extinct as well as living groups as key aspects of the brachiopod body plan, have been used with five characteristics of the secondary shell (Tables 34–35) to construct a phylogenetic tree for the eight brachiopod classes. The choice of *Micrina* as an outgroup accords with the assumed derivation of brachiopods from halkieriids (Williams & Holmer, 2002). The resultant cladogram (Fig. 1663) is a feasible representation of brachiopod phylogeny. Among several novel features, it shows that the most dramatic transformations affecting the morphology of the brachiopod and the chemicostructure of its shell were out of phase and supports a rhynchonelliform ancestry for the craniates.

The morphological and anatomical evidence identifies lingulates as the sister group of all other brachiopods, including the paterinates that, with their strophic hinge lines, adductor and diductor musculature, and gonadal sacs in saccate mantle canal systems, are the stem group of rhynchonelliforms. Morphological evidence also identifies the three extinct rhynchonelliform classes, the chileates, kutorginates and obolellates, and the craniiforms as the most derived of the organocarbonate-shelled brachiopods. In passing, it is noteworthy that the three rhynchonelliform groups are characterized by apertures in their ventral valves that could have accommodated holdfasts as well as delthyrial openings for pedicles. A vestigial homologue of such a holdfast may initiate the cementation of the ventral valve of living craniids. This phylogenetic reconstruction also shows that the straight gut of craniates is a derived rather than an inherited ancestral state.

The most dramatic transformation in the chemicostructural differentiation of the brachiopod shell was the change from an organophosphatic to an organocarbonate composition (Fig. 1664 and Tables 36–37). The change included the replacement of apatite by calcite and the loss of GAGs and chitin from the greatly reduced organic content of carbonate shells. These changes distinguished the carbonate-shelled ancestor of the rhynchonelliforms (and craniiforms) from its paterinate sister group. The secondary layer of this ancestral calcitic shell was probably secreted collectively as a predominately foliate succession, but with glycoproteinaceous membranes serving as substrates for sporadically deposited laminae as well as the folii.

The transformation(s) leading to the secretion of the rhynchonellate fibrous secondary shell was little more than a switch from a collective epithelial secretion of folii and laminae on glycoproteinaceous sheets to a discrete cellular deposition of fibers on their glycoproteinaceous strips that intermeshed to form sheaths. The derivation of the secondary shell fabrics of strophomenates, the sister group of the rhynchonellates, was more complicated. The composite laminar fabric of later strophomenates convergently evolved from the coarse laminae of billingselloids (and strophomenoids) and the flat fibers of the plectambonitoids. As the strophomenates were probably monophyletic, the dual origin of the composite fabric needs clarification. Our assumptions are that the billingselloid lamination is closer to the fabric of the stem-group rhynchonelliforms, and that the plectambonitoid fibers developed later, independently of the fibrous secondary shell of rhynchonellates.

Tabular lamination is a fabric unique to craniate shells. In living craniids, it succeeds a primary layer that is also unique because it is inwardly differentiated into laths, laminae, and tablets with polysaccharide substrates. Now that the craniates can be feasibly derived from an early rhychonelliform, an alternative interpretation of their shell successions is tenable. The laths and laminae of the inner primary layer could really be vestiges of a foliate-derived secondary layer and the spirally growing tabular laminar succession, a novel tertiary layer (see also Carlson, p. 2878, herein, for a different perspective on brachiopod phylogeny).

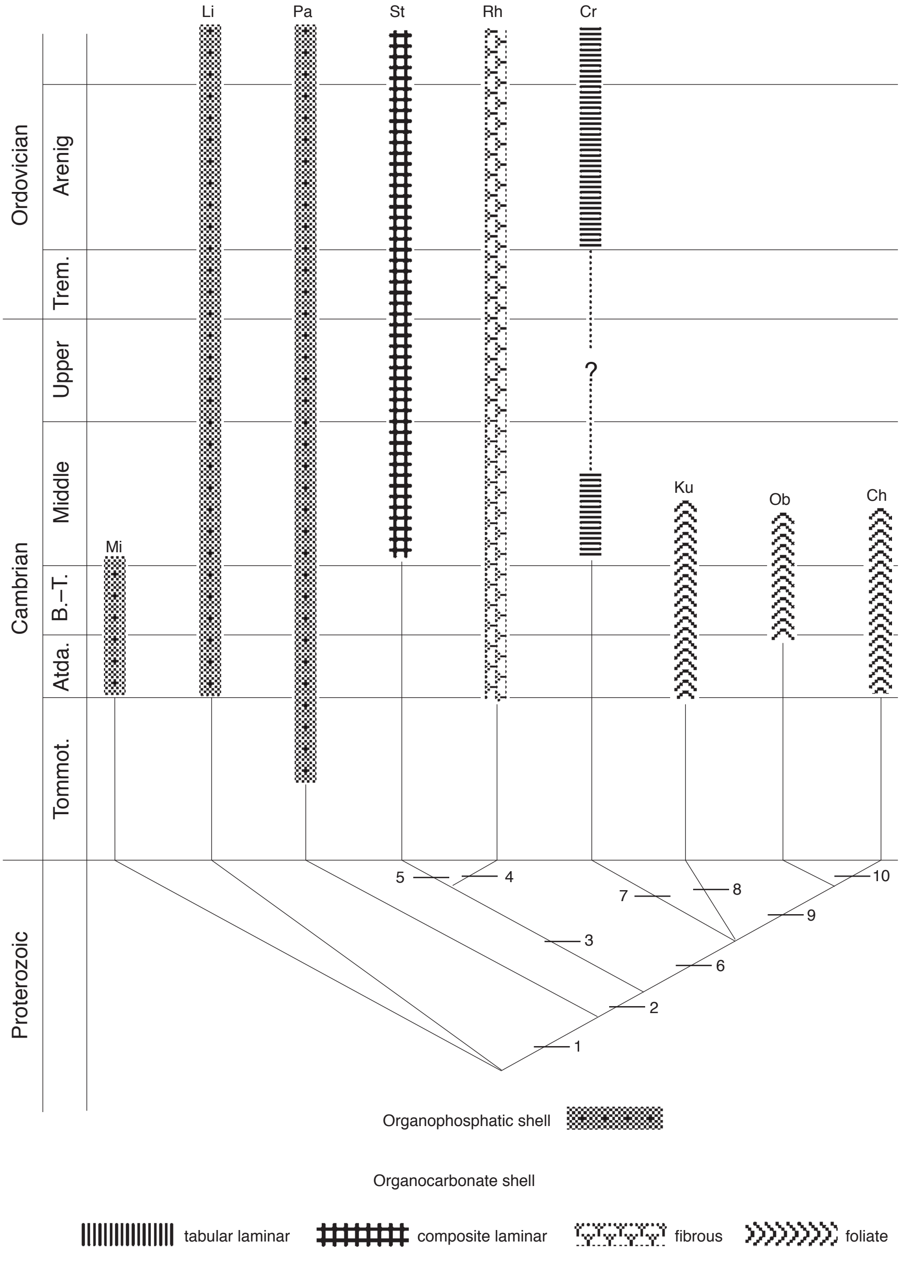


FIG. 1663. *For explanation, see facing page.*

TABLE 34. List of character states used in the cladogram of Figure 1663 to illustrate a possible origin of the diverse fabrics of the mature secondary shell of early rhynchonelliforms and craniiforms (new).

Morphology and anatomy	
1. Valve relationship	separated (0), conjoined (1), articulated (2), strophic (3), astrophic (4)
2. Dentition	no teeth (0), ventral denticles (1), by hinge margins (2), deltidiont (3), cyrtomatodont (4)
3. Gut disposition	straight (0), longitudinal U-bend (1), transverse U-bend (2)
4. Gonadal sacs	absent (0), present (1)
5. Principal muscle systems	unknown (0), obliques (1), dispersed adductors (and weak diductors) (2), adductors and diductors (3), quadripartite adductors (4)
6. Pedicle	absent (0), ventral body wall (1), holdfast (2), rudiment (3)
Shell chemicostructure	
7. Shell composition	organophosphatic (0), organocarbonate (1)
8. Secondary shell	stratiform (0), tabular laminar (1), composite laminar (2), foliate (3), fibrous (4)
9. Secretory regime	collective (0), discrete (1)
10. Chitin & GAGs	absent (0), present (1)
11. Canaliculate system	absent (0), present (1)

TABLE 35. Matrix of 11 characters described in Table 34 and 8 designated classes of Brachiopoda (new).

	[11
	12345678901]
Micrina	000?0000011
Lingulates	10101100011
Paterinates	10113100010
Craniates	10014(02)11000
Chileates	10112213000
Obolellates	(12)1102213(01)00
Kutorginates	22113213000
Strophomenates	3311311(24)(01)00
Rhynchonellates	(34)(34)(12)1(13)314100

FIG. 1663. Chart showing evolution of main fabrics of secondary shells of Cambro-Ordovician brachiopods with presumed halkieriide *Micrina* (*Mi*) as sister group; 8 brachiopod classes are lingulates (*Li*), paterinates (*Pa*), strophomenates (*St*), rhynchonellates (*Rh*), craniates (*Cr*), kutorginates (*Ku*), obolellates (*Ob*), and chileates (*Ch*). Cladogram (not to geological time scale) is a 50% majority-rule consensus of 4 trees generated by a PAUP heuristic search (10 stepwise additions) of 11 character states (Table 34) and matrix (Table 35). The numbered transformations are: *1,* loss of canaliculate system and acquisition of basic rhynchonelliform characters including development of diductor-adductor muscle system and gonadal sacs in mantles; *2,* loss of the organophosphatic, stratiform shell with GAGs and chitin and its replacement by an organocarbonate foliate shell; *3,* development of articulating shells with teeth and sockets and a fibrous fabric with a discrete secretory regime; *4,* differentiation of pedicles from apical rudiments; *5,* development of composite lamination; *6,* development of holdfasts, other than pedicles, breaching ventral valves; *7,* development of straight gut and tabular lamination and loss of diductor muscles; *8,* development of articulating hinge margins; *9,* comparatively weak differentiation of diductor-adductor muscle system; *10,* development of ventral denticles (new).

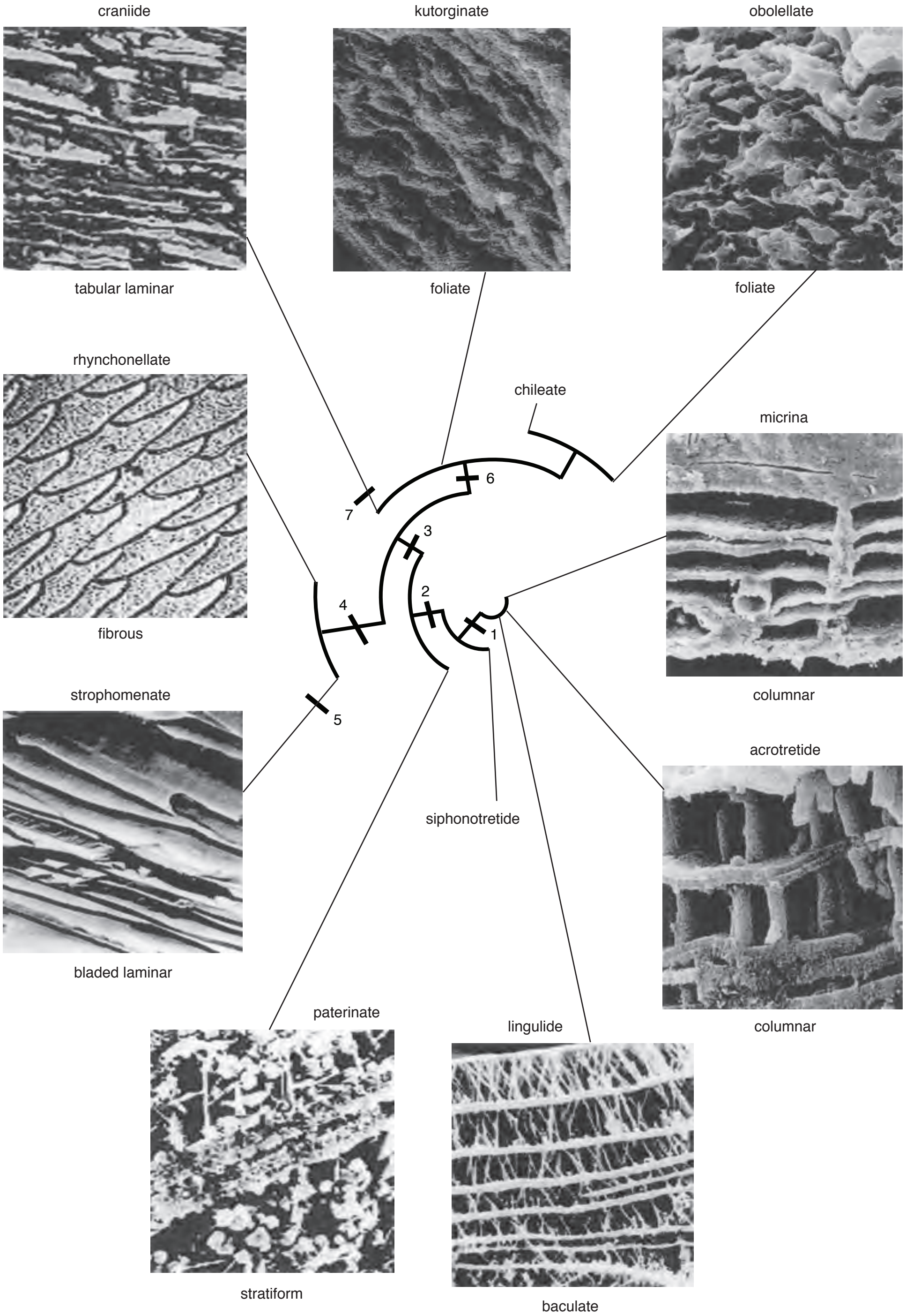


FIG. 1664. *For explanation, see facing page.*

TABLE 36. List of character states used in circle cladogram of Figure 1664 to illustrate a possible evolution of brachiopod secondary shell (new).

Body plan features	
1. Valve disposition	separated (0), conjoined (1), articulated (2), strophic (3), astrophic (4)
2. Dentition	no teeth (0), variable denticles (1), by hinge margins (2), deltidiont (3), cyrtomatodont (4)
3. Gut disposition	straight (0), longitudinal U-bend (1), transverse U-bend (2)
4. Gonadal mantle sacs	absent (0), present (1)
5. Principal muscle systems	unknown (0), obliques (1), dispersed adductors (and weak diductors) (2), adductors and diductors (3), quadripartite adductors (4)
6. Pedicle	absent (0), ventral body wall (1), holdfast (2), rudiment (3), within ventral valve (4)
Shell chemicostructure	
7. Shell composition	organophosphatic (0), organocarbonate (1)
8. Calcitic secondary shell	phosphatic (0), tabular laminar (1), composite laminar (2), foliate (3), fibrous (4)
9. Secretory regime	collective (0), discrete (1)
10. GAGs and chitin	absent (0), present (1)
11. Canaliculate system	absent (0), present (1)
12. Phosphatic secondary shell	calcitic (0), stratiform (1), columnar (2), baculate (3)
13. Setigerous tubes	absent (0), present (1), other (2)
14. GAGs chambers	absent (0), poorly developed (1), well developed (2)

TABLE 37. Matrix of 14 characters described in Table 36 and 11 listed taxa representing presumed halkieriide *Micrina* (as outgroup) and all 8 classes of Brachiopoda (new).

	[11111 12345678901234]
Micrina	000?0000011212
Lingulates	10101100011302
Paterinates	10113100010101
Craniates	10014(02)11000000
Chileates	10112213000000
Obolellates	(12)1102213(01)00000
Kutorginates	22113213000000
Strophomenates	3311311(24)(01)00000
Rhynchonellates	(34)(34)(12)1(13)314100000
Acrotretides	10101100011202
Siphonotretides	10101400010121

FIG. 1664. Circle cladogram representing 50% majority-rule consensus of 8 trees generated by PAUP heuristic search (10 stepwise additions) of character states (Table 36) and matrix (Table 37) that illustrates derivation of 7 main fabrics of secondary shells (in transverse sections) of halkieriide *Micrina* (columnar, with a column and setigerous tubes to left, ×130); acrotretide *Prototreta* (columnar sets, ×850); lingulide *Schizotreta* (baculate sets, ×800); the paterinates *Cryptotreta* (stratiform with poorly developed GAGs chambers, ×800); strophomenate *Strophomena* (cross-bladed laminar, ×1500); rhynchonellate terebratulide *Macandrevia* (fibrous, ×3800); craniide *Novocrania* (tabular laminar, ×7000); kutorginate *Narynella* (foliate, ×350); obolellate *Obolella* (foliate, ×100). The most important transformations that affected the brachiopod shell structure and body plan were *1,* loss of organic canaliculate framework and well-developed GAGs chambers with columns or baculi; *2,* development of rhynchonelliform body plan; *3,* replacement of organophosphatic, stratiform shell with GAGs and chitin by organocarbonate shell with foliate secondary layer; *4,* development of fibrous secondary shell; *5,* development of composite (cross-bladed) laminar secondary shell; *6,* development of holdfast; *7,* development of tabular laminar secondary shell (new).

CONCLUSIONS

Research since 1995 has overturned many of the long-held assumptions on the chemicostructure of the living and fossil brachiopod shell. The biochemistry of the living shell is more complex than pioneer investigations indicated. There is an unexpectedly wide range of polysaccharides and especially of proteins, which presently obscures identification of standard calcifying agents even within ordinal groups of brachiopods. Progress, however, has been made in determining the modes of association of intercrystalline as well as intracrystalline polymers within the mineral constituents, while analyses of the organic residues of fossilized shells have refined the geological time scale of polymeric degradation.

The mineralogy of the shell can no longer be regarded as exclusively apatitic or calcitic. The juvenile shell of organophosphatic discinids has been composed of siliceous tablets for over 400 myr, contrary to the belief that shell secretion within a life cycle has never involved more than one crystalline component. Indeed, there is evidence to suggest that many Paleozoic lingulates had calcitic juvenile and apatitic mature shells, which refutes the general opinion that these two mineral phases have always been mutually exclusive in the brachiopod secretory regime. The main fabrics of the mineral components of the shell are now known and have been traced throughout geological time. Their configuration in relation to the organic constituents of living shells is reasonably well understood, which has aided in the identification of extinct fabrics despite repeated recrystallization.

Any attempt at understanding the evolution of the brachiopod shell entails chemicostructural comparisons of living and fossilized exoskeletons. Changes in the organic and mineral components of the shell, however, begin in the postmortem stages of subfossilization and proceed at different rates and to different degrees of profundity. As has been shown, the disparities in these changes become so great in geologic time as to prompt their consideration separately. Even so, the nature of the more degradable organic contents can usually be inferred from the microstructures of the more enduring mineral components.

Brachiopod shells, like all other biominerals, are organic-inorganic composites. A range of organic components has been extracted from brachiopod shells, including amino acids (WALTON, CUSACK, & CURRY, 1993; CUSACK & others, 2000), proteins (CUSACK & others, 1992; CUSACK, 1996; WILLIAMS, CUSACK, & BUCKMAN, 1998; LÉVÊQUE & others, 2004), carbohydrates (COLLINS & others, 1991; BROWN, 1998), and lipids (CLEGG, 1993; MCCLINTOCK, SLATTERY, & THAYER, 1993; WILLIAMS, CUSACK, & BRUNTON, 1998; COBABE & PTAK, 1999). The high organic content determined by loss on ignition (LOI) experiments (e.g., 2.5 wt% and 5 wt% for the dorsal valves of *Terebratulina retusa* and *Novocrania anomala* respectively [ENGLAND, 2005]) and the relatively low protein concentrations of 0.8 µmoles intracrystalline EDTA-soluble amino acid/g shell of *T. retusa* and *N. anomala* respectively (CUSACK & others, 2000) suggest that, although soluble proteins are extremely important in biomineral formation (ADDADI & others, 1990; BELCHER & others, 1996; FALINI & others, 1996; CUSACK, WALTON, & CURRY, 1997; CUSACK & others, 2000), in brachiopods a large proportion of the organic components comprise fibrous proteins such as in *Discinisca tenuis* where the soluble protein fraction only accounts for about 0.016% of the total shell protein (WILLIAMS, CUSACK, & others, 1998). Other major organic components are lipids (CLEGG, 1993; MCCLINTOCK, SLATTERY, & THAYER, 1993) and carbohydrates (COLLINS & others, 1991). Indeed, many brachiopod shell proteins are glycosylated (WILLIAMS, CUSACK, & BRUNTON, 1998; LÉVÊQUE & others, 2004).

The organic components occupy various locations within the shell. Some of these organic polymers occur in intracrystalline positions, requiring complete dissolution of the mineral for their extraction. Others occur in membranes between laminae and in sheaths surrounding fibers (intercrystalline). Intercrystalline polymers trapped within the skeletal frame by crystal growth are termed paracrystalline, e.g., doped sites in craniiform laminae (WILLIAMS, CUSACK, & BROWN, 1999) or surrounding the apatite granules in spherules in *Lingula* (WILLIAMS, CUSACK, & MACKAY, 1994). Polymeric secretions also occur as large bodies within successions. Examples of these are the glycosaminoglycans (GAGs) chambers within linguliforms (CUSACK & WILLIAMS, 1996) and pustules that are vertical inclusions of mucins in craniiforms (CUSACK & WILLIAMS, 2001a). In rhynchonelliforms, polymeric secretions are likely to have occurred in the pseudopunctae evident in fossil strophomenides (WILLIAMS, HOLMER, & CUSACK, 2004).

In polymeric extractions, no distinction is made between primary and secondary shell except for thecideidides where only primary layer is present. Studies by the authors revealed about ten proteins in the molecular weight range of 6 kDa to 46 kDa in *Lingula anatina* (WILLIAMS, CUSACK, & MACKAY, 1994), two of which are glycosylated (LÉVÊQUE & others, 2004). In addition, GAGs were present throughout the shell of *L. anatina,* as a pervading isotropic gel and chitin was also evident, associated with proteins (WILLIAMS, CUSACK, & MACKAY, 1994). The discinoid succession is similar to that of lingulids with protein-coated francolite granules aggregated as spherules supported by proteinaceous and chitinous nets in GAGs (WILLIAMS, CUSACK, & BRUNTON, 1998). In *Discinisca tenuis*, proteins in the molecular weight range 6.5 to 100 kDa were extracted, one of which (13 kDa) is glycosylated (WILLIAMS, CUSACK, & BRUNTON, 1998). *Novocrania anomala* contains an intralaminar glycosylated 60kDa protein as well as a 44kDa protein that is incorporated into calcite tablets during growth by screw dislocation (WILLIAMS, CUSACK, & BROWN, 1999). In a small survey of intracrystalline shell proteins from species representing all extant rhynchonellate orders, 21 proteins of different molecular weight were identified from shells of six species that yielded sufficient protein extractions for reliable analyses (CUSACK & WILLIAMS, 2001b). Protein profiles range from three in *Notosaria nigricans* (20, 43, and 53 kDa) to six in *Liothyrella mediterranea* (28, 36, 40, 52, 60, and 107 kDa). Although five of these occur in the shells of more than one species, there is no evidence of proteins being specific to one layer. The chemicostructural differentiation of the rhynchonellate shell, as typified by living species of three ordinal groups, is less straightforward than their phylogenetic relationships and ultrastructures suggest.

Polysaccharides are present as intracrystalline cement of basic mineral units of craniiforms and rhynchonelliforms and possibly in coatings of granules in linguliforms. Polysaccharides occur as membranes of β-chitin in linguliforms, glycoproteinaceous sheets in craniiforms, and sheaths in rhynchonelliforms. In *Novocrania anomala*, the soluble extract has typically 0.75 µg carbohydrate per gram of shell (BROWN, 1998). Polysaccharides degrade during fossilization, possibly within Tertiary times. Although chitin is an extremely tough polysaccharide, even it is degraded in Cretaceous *Credolingula,* although ultrastructural casts of its fabric survive. Periostracum of late Cretaceous *Sellithyris* survives (GASPARD, 1982), most likely because it is a case of protein and carbohydrate sclerotization.

Methods employed for protein extraction from brachiopod shells preclude analyses of water-insoluble, intercrystalline, and paracrystalline proteins but include water-soluble proteins. This group of proteins exerts a very significant influence on the control of biomineral formation in other systems such as bivalve mollusks where soluble proteins control the polymorph of calcium carbonate produced (BELCHER & others, 1996; FALINI & others, 1996). The only work done on brachiopod insoluble proteins has been with traditional cytological staining or imaging using freeze-dried demineralized sections (James & others, 1992). Although investigation of intracrystalline proteins of rhynchonellate brachiopods revealed that it is difficult to generalize about protein profiles in brachiopods, in many species and indeed in all three subphyla, a protein of around 40kDa is often present. Further characterization of this protein is required to determine whether this is the same protein in all instances or a coincidence of molecular weight. There are broad distinctions in amino acid composition between the three subphyla. Organocalcitic brachiopod shells have very high concentrations of glycine, with the exception of craniids, as demonstrated by *Novocrania anomala,* which also has a higher aspartic acid and glutamic acid content, in common with *Notosaria nigricans* (Fig. 1539 herein; Walton, Cusack, & Curry, 1993). Organophosphatic brachiopod shells have lower glycine content and higher alanine content than the organocalcitic brachiopod shells. There are also differences in amino acid composition within the phyla. Williams, Cusack, and Brunton (1998) compared the amino acid content of two species of lingulid, *Lingula anatina* and *Glottidia pyramidata* with four species of discinids, *Discinisca tenuis*, *Discinisca lamellosa*, *Discina striata,* and *Pelagodiscus atlanticus*. Although lingulids have a higher organic content than discinids, discinids have greater amino acid content (Williams, Cusack, & Brunton, 1998). Differences in amino acid composition are also apparent with the shells of lingulids containing higher concentrations of acidic amino acids (glutamic acid and aspartic acid) than those of discinids, with an average of 21.1 mole% in lingulids compared to 14.5 mole% in discinids. The concentration of basic amino acids (lysine, histidine, and arginine) is lower in lingulids (mean 9.1 mole%) than in discinids (mean 13.2 mole%). Glycine occurs in high concentrations in lingulids and discinids, with average values of 19.6 mole% and 24.4 mole% respectively. Alanine occurs in similarly high concentrations (23 mole%) in lingulid and discinid shells (Williams, Cusack, & Brunton, 1998). The amino acid compositions of *L. anatina* and *G. pyramidata* are very similar (Cusack & Williams, 1996; Williams, Cusack, & Brunton, 1998), although comparisons of more species begin to differentiate *Lingula* from *Glottidia* (see Fig. 1536 herein). Within the discinids, the greatest difference in amino acid composition occurs in *P. atlanticus,* where glycine and alanine occur in much lower concentrations and arginine and threonine in much higher concentrations (Williams, Cusack, & Brunton, 1998; see also Fig. 1536 herein).

In fossil brachiopod shells, the remaining amino acid content in some cases appears to reflect some of the original composition; e.g., the high concentration of glutamic acid, glycine, and alanine in Carboniferous *Lingula squamiformis* shells; amino acids that are also present in high concentrations in living *Lingula anatina* shells (Cusack & Williams, 1996). However, expanding the survey of amino acids in fossil brachiopod shells reveals the tendency for the survival of similar suites of amino acids, the acidic amino acids possibly surviving by interaction with the carbonate or apatite matrix and the survival of the structurally simple, more robust amino acids. The fact that proteins are so information rich and relate directly to the DNA means that they are rich sources of information relating to evolutionary changes in living species genealogies. The low concentration of soluble proteins in brachiopod shells makes this difficult to achieve, however. The rapid diagenetic degradation of shell proteins rules out the use of proteins as a phylogenetic tool for fossil species genealogies.

STRUCTURAL EVOLUTION OF MATURE SHELLS

The structural differentiation of the juvenile shell of living and fossil brachiopods has already been described. As their secretion differs from that of mature shells and results in different structures, juvenile shells will not be further considered. Moreover, the primary and secondary (and the variant tertiary) layers of the mature shell have also been structurally distinct throughout the geological record. Indeed, the differences are so striking as to merit separate reviews of their fabrics.

Despite the invariable recrystallization of fossilized primary layers, it is safe to assume that their fabrics have never differed significantly from those characterizing living species of the three subphyla. The primary layers of the linguliforms (WILLIAMS, CUSACK, & MACKAY, 1994, p. 241; CUSACK, WILLIAMS, & BUCKMAN, 1999, p. 806) and rhynchonelliforms (CUSACK & WILLIAMS, 2001b, p. 19) have always been virtual pastes of apatitic granules in GAGs and calcitic granules in polysaccharides respectively, lining the periostracum and serving as a mineralized substrate for the succeeding secondary shell. Only the primary layer of living craniids (CUSACK & WILLIAMS, 2001a, p. 882), with its inner succession of calcitic granules and tablets aggregated into laminae of laths, differs from the fine undifferentiated lamination that commonly characterizes the linguliform and rhynchonelliform primary layer (as well as the outermost succession of the craniiforms).

In contrast to the limited structural variation of the primary layer, the fabrics of the secondary shell of living species are diverse, due to the development of intricate successions of anastomosing membranes that divide the mineralized part of the shell into distinctive units. Such mineralized structures also recrystallize during fossilization, but they are frequently converted into casts of the original structures even in nanometric detail. These mineralized records show that the fabric of the oldest known brachiopods was equally diverse with some surviving to the present day.

ACKNOWLEDGMENTS

This chapter summarizes much of the progress in the field of brachiopod chemicostructural diversity; a research field that Sir Alwyn Williams and I greatly enjoyed learning about and contributing to. The joy therein is contrasted with the difficulty of completing the chapter on Alwyn's behalf after his death. Here I would like to offer my heartfelt gratitude to Mrs. Patricia Peters, who helped me a great deal in the task of completing this chapter in such circumstances. We were both spurred on by thoughts of Alwyn's drive and enthusiasm and his sheer determination to ensure that the Brachiopoda volumes of the *Treatise* were completed.

Sincere thanks to all those institutions and individuals who provided material used in the work referred to in this chapter. Financial assistance from the NERC (GR 3/09604 and GR 9/02038), the Royal Society (RSR A/C 027 and RSS QG 16604), and the EPSRC (GR/R23107/01) is gratefully acknowledged.

STABLE OXYGEN AND CARBON ISOTOPES IN EXTANT BRACHIOPOD SHELLS: KEYS TO DECIPHERING ANCIENT OCEAN ENVIRONMENTS

DAVID PARKINSON and MAGGIE CUSACK

[University of Glasgow]

BACKGROUND

For over half a century the stable oxygen and carbon isotope ratios of fossilized shells of calcite brachiopods have been used to provide a record of environmental conditions in the ancient oceans in which they lived. The hypothesis that the abundance of the ^{18}O isotope in biogenic carbonates could be used as a proxy for the temperature of the seawater in which they were formed was first proposed by UREY (1947). The application of oxygen isotope paleothermometry became possible through the development of the stable isotope abundance mass spectrometer, pioneered by NIER (1940, 1947). Incorporating modifications by MCKINNEY and others (1950) and a reproducible method for producing carbon dioxide (CO_2) from carbonates by digestion in phosphoric acid (H_3PO_4) at a constant temperature, MCCREA (1950) significantly improved precision for measuring relative stable isotope abundances. Results of such analyses are reported by the standard delta (δ) notation in parts per thousand relative to the international standards Pee Dee Belemnite (PDB) and more recently Vienna PDB (VPDB) (for explanation see COPLEN, 1995; GONFIANTINI, STICHLER, & ROZANSKI, 1995; HOEFS, 1997; KOCH, 1998).

Construction of carbonate paleotemperature scales, which determined the relationship between temperature and oxygen isotope fractionation in carbonate water systems, has enabled $^{18}O/^{16}O$ ratio to be employed as a proxy indicator of fluctuations in the temperature of ancient oceans (M^c^CREA, 1950; EPSTEIN & others, 1951, 1953). The first practical paleotemperature equation was that of EPSTEIN and others (1953):

$$T\ (^{o}C) = 16.5\text{-}4.3(\delta^{18}O_{calcite}-\delta^{18}O_{seawater}) + 0.14(\delta^{18}O_{calcite} - \delta^{18}O_{seawater})^2$$

Palaeotemperatures, which are more correctly called isotopic temperatures (RYE & SOMMER, 1980), can be extrapolated from the $\delta^{18}O$ value of carbonate relative to the international standards PDB or VPDB when the $\delta^{18}O$ of ambient seawater (relative to the international standards SMOW or VSMOW) is also known (For explanation of international standards see GONFIANTINI, STICHLER, & ROZANSKI, 1995). Similarly, the expected range of oxygen isotope equilibrium can be calculated if the measured seawater temperature range of ambient seawater is available.

The equation of EPSTEIN and others (1953), based on biogenic calcium carbonate, agrees well with relations based on laboratory-synthesized calcite (e.g., O'NEIL, CLAYTON, & MAYEDA, 1969), suggesting that at least certain taxa (e.g., mollusks) precipitate shells in oxygen isotopic equilibrium with the water. Disequilibrium fractionation, termed vital effect (UREY & others, 1951), has been demonstrated in many taxa, however (COMPSTON, 1960; KEITH & WEBER, 1965; WEBER & RAUP, 1966; WEBER & WOODHEAD, 1970; EREZ, 1978; SWART, 1983; GONZALEZ & LOHMANN, 1985; ROSENBERG, HUGHES, & TKACHUCK, 1988; M^c^CONNAUGHEY, 1989a, 1989b; ORTIZ & others, 1996; BÖHM & others, 2000).

In a recent study ADKINS and others (2003) proposed an alternative mechanism to explain these observed variations. ADKINS and others (2003, p. 1130) proposed that vital effects observed in deep sea corals were the result of "a thermodynamic response to a biologically induced pH gradient in the calcifying region." Notwithstanding the mechanism, it is clear that stable isotope variation does occur in some biogenic carbonates. CARPENTER and LOHMANN (1995) maintained that if other calcareous marine organisms display vital effects, then there are too few data to confidently claim that brachiopods exhibit a unique characteristic. Thus, to ensure accurate determination of isotopic temperatures in fossil brachiopod specimens, isotopic studies are required on modern specimens.

Skeletal carbonates also record the carbon isotopic composition of dissolved inorganic carbon (DIC) in the ocean. This is a proxy for carbon cycling on local and global scales (VEIZER, FRITZ, & JONES, 1986; BRUCKSCHEN & VEIZER, 1997; VEIZER & others, 1999).

Brachiopods are considered to be exceptionally suitable for isotopic studies of ancient ocean temperatures and carbon cycling because the phylum is ubiquitous and continuous throughout the fossil record, spanning from Cambrian to Recent.In addition, most brachiopod species have shells composed of low-magnesium calcite (LMC). This is the most stable form of skeletal carbonate and the most resilient to diagenetic alteration (e.g., LOWENSTAM, 1961; AL-ASSAM & VEIZER, 1982; BRAND, 1989a).

BRACHIOPOD ISOTOPE RESEARCH

The first published research into the relative abundance of ^{18}O and ^{13}C stable isotopes in fossilized brachiopod shells was probably that of UREY and others (1951) in an investigation of paleotemperatures derived from fossil organisms extracted from Upper Cretaceous chalk of England, Denmark, and the southeastern United States. It was concluded that the temperature record within the shells of the brachiopods studied had been destroyed, possibly by diffusion of material into the open structure of the shell. A more detailed study using brachiopods and crinoids from the Devonian and Permian by COMPSTON (1960) also observed diagenetic alteration and only the Permian brachiopods retained the original $^{18}O/^{16}O$ composition. As with UREY and others (1951) it was concluded that alteration was due to impregnation of the shell structure by diagenetic calcite. This study also raised the possibility that brachiopods could exert some phylogenetic control over the carbon isotope fractionation, an issue that is commonly referred to as biological fractionation or vital effect.

LOWENSTAM (1961) was the first to test whether brachiopod shells were precipitated in oxygen isotope equilibrium with ambient seawater and thus were reliable materials for measuring isotopic temperatures. That influential study (LOWENSTAM, 1961) was based on the analyses of extant articulated brachiopod shells from a variety of different taxa collected from locations with different environmental conditions and latitudes around the world. The specimens came from the Marshall Islands in the Pacific, Bermuda, Barbados, California, New Zealand, the Mediterranean, and Alaska. Bottom water samples were collected from the sea at the same locations as the specimens and analyzed to determine the local ^{18}O content of the seawater. Temperatures derived from the equation of EPSTEIN and others (1953) agreed with measured seawater temperatures, leading LOWENSTAM (1961) to conclude that brachiopods precipitate their shell material in oxygen isotopic equilibrium with ambient seawater. Based on this foundation, LOWENSTAM (1961) compared data from modern brachiopod shells with fossil samples from the Pliocene, Cretaceous, Permian, and Carboniferous. Only samples that retained the original ultrastructure were used and comparisons made between the $^{18}O/^{16}O$ and $SrCO_3$ and $MgCO_3$ contents of the extant species. Where the relationship was compatible, it was concluded that the isotope signal remained intact.

The conclusion of LOWENSTAM (1961) that brachiopods precipitate skeletal calcite in equilibrium with ambient seawater was widely accepted. Workers studying paleoenvironments were confident that oxygen isotope analyses of fossil brachiopod shells provided an accurate record of ancient ocean temperatures, and any biological effects were minimal. It was also generally accepted that care must be taken when selecting fossil specimens for analysis, however, to make sure that the original calcite is unaltered by diagenetic processes. Trace element analysis and cathodoluminescence are commonly used to identify suitable samples. The theories and methods of these procedures have been discussed in detail (VEIZER, 1983a, 1983b; POPP, ANDERSON, & SANDBERG, 1986b; RUSH & CHAFETZ, 1990; MII & GROSSMAN, 1994; WENZEL & JOACHIMSKI, 1996; SAMTLEBEN & others, 2001).

Confidence in the analytical techniques, together with the abundance of brachiopod remains in the fossil record, has led to stable isotope analyses of fossil brachiopod shells being employed over the last 40 years in many extensive and detailed paleoenvironmental investigations covering periods ranging throughout the Phanerozoic. VEIZER, FRITZ, and JONES (1986) used trace element and isotope determinations from 319 brachiopod fossils spanning the Ordovician through to the Permian in order to establish evidence for change in the chemical composition of Paleozoic oceans. Similarly, POPP, ANDERSON, and SANDBERG (1986a, 1986b) analyzed brachiopods from Paleozoic limestones. Examples of other notable paleoenvironmental works involving isotopic analyses of brachiopods include: BRAND (1989a), Devonian–Carboniferous; BRAND (1989b), Carboniferous; MARSHALL and MIDDLETON (1990), Late Ordovician; GROSSMAN, MII, and YANCEY (1991, 1993), Carboniferous; QUING and VEIZER (1994) Ordovician; WENZEL and JOACHIMSKI (1996), Silurian; VEIZER and others (1999), Phanerozoic; WENZEL, LÉCUYER, and JOACHIMSKI (2000), Silurian; MII and GROSSMAN (1994), Carboniferous; and STANTON, JEFFERY, and AHR (2002), Carboniferous. Despite the widespread use of brachiopod shells in isotopic studies of Paleozoic and younger sedimentary rocks, uncertainties still exist in the factors controlling the oxygen and especially carbon isotopic compositions of brachiopod shells.

THE EQUILIBRIUM DEBATE

Underpinning the use of stable isotope determinations from brachiopod shells for environmental investigations is the conclusion of LOWENSTAM (1961) that brachiopod shells are secreted in oxygen isotopic equilibrium with ambient seawater. LEPZELTER, ANDERSON, and SANDBERG (1983) supported this supposition with a small study of $^{18}O/^{16}O$ ratios in several Recent species, which were considered representative of extant brachiopods. The study concurred with the finding of LOWENSTAM (1961) in that covariance between $\delta^{18}O$ and $\delta^{13}C$ was not observed, and the study concluded that brachiopod shells are precipitated in equilibrium with ambient seawater. The only detraction from this position noted by LEPZELTER, ANDERSON, and SANDBERG (1983) was in the case of specimens taken from cold-water habitats where isotopic disequilibrium was reported.

The first suggestion that variations in oxygen isotope ratios observed in disparate, but contemporary brachiopod genera collected from the same location could be due to biological rather than diagenetic effects was made by POPP, ANDERSON, and SANDBERG (1986a). The implication of this is that brachiopods could precipitate shell calcite out of isotopic equilibrium as a result of vital effects. Despite this possibility, however, little was done to test the reliability of stable isotopes in brachiopod shells as recorders of seawater temperature until CARPENTER and LOHMANN (1995).

Carpenter and Lohmann (1995) investigated $\delta^{18}O$ and $\delta^{13}C$ values in a range of extant brachiopods, using 44 specimens originating from a variety of environments and latitudes (Antarctica, United States, New Zealand, Japan and Palau in the Pacific; Norway, Canada, South Africa and Curacao, and Sicily). Their study examined intraspecimen, interspecimen, intraspecies, and interspecies isotopic variations using shell material extracted from a variety of areas differentiated by shell ultrastructure (e.g., external primary and internal secondary layers) and also from different morphological features of the secondary shell layer (i.e., hinge, foramen, brachidium, muscle scars). Direct measurements of seawater $\delta^{18}O$ ($\delta^{18}O_{water}$) were only available from one location. Therefore, it was necessary to calculate $\delta^{18}O_{water}$ from salinity information available from the National Oceanic and Atmospheric Administration (NOAA) and National Oceanographic Data Center (NODC) databases using the $\delta^{18}O_{water}$–salinity relationship described in Broecker (1989).

In all cases, the primary layer and areas of the secondary layer that form specialized morphological structures showed a high degree of covariance between $\delta^{18}O$ and $\delta^{13}C$. The reasons suggested are metabolic (vital effects) or kinetic effects, either during the hydroxylation of CO_2 or as a result of rapid calcite precipitation or possibly a combination of some or all of these factors. Carpenter and Lohmann (1995) advised against the use of these parts of the shell for investigations employing ancient brachiopods. The nonspecialized areas of the secondary layer close to the anterior margin, however, were less fractionated and therefore closer to equilibrium. There were two exceptions to this trend. 1) *Thecidellina* sp., which have no clearly defined secondary shell structure and are mainly comprised of primary layer calcite (Williams, 1973). Measurements from *Thecidellina* were frequently isotopically heavier than equilibrium. 2) As was the case with the cold-water brachiopods of lepzelter, Anderson, and Sandberg (1983), *Stethothyris* sp. from Antarctica, were considerably depleted relative to expected oxygen isotope equilibrium values.

The data of Carpenter and Lohmann (1995) show little evidence of carbon isotopic equilibrium as defined by Romanek, Grossman, and Morse (1992). Values of $\delta^{13}C$ were nearly always lower than the expected range.

Marshall and others (1996) studied the isotopic compositions of extant brachiopods from Antarctica. This study highlighted the uncertainties of determining meaningful oxygen isotope values from very low-temperature habitats to use as proxy indicators of seawater temperatures. The paleotemperature equations for biogenic carbonates (Epstein & others, 1953) is based on carbonates precipitated between 7 °C and 30 °C. In contrast, the inorganic calcite–water fractionation curve (O'Neil, Clayton, & Mayeda, 1969; Friedman & O'Neil, 1977) employed by Carpenter and Lohmann (1995) is based on equilibrium exchange experiments from 200–700 °C and precipitation experiments at 0 °C and 25 °C. Thus, the data represent a wider temperature range. Marshall and others (1996) further point out that, at very low temperatures, the lines for the two equations diverge, leaving no adequate method for determining oxygen isotope equilibrium at very low temperatures. Notwithstanding these difficulties, Marshall and others (1996) argue that the ~2‰ range of $\delta^{18}O$ values, which signifies a range of temperatures of around 8 °C, is difficult to justify given the very narrow seasonal variation in the Antarctic. This level of variation cannot be explained solely by problems with the paleotemperature scales.

Since Carpenter and Lohmann (1995) opened the equilibrium debate, four studies from temperate waters have considered the issue. Buening and Spero (1996) analyzed four specimens of the extant brachiopod *Laqueus californianus* collected near the

California coast. They were able to identify El Niño warming events and concluded that the ^{18}O content of the brachiopod shell is a useful recorder of environmental change in temperate waters.

Two other investigations were conducted with extant brachiopods collected from the Lacepede Shelf, southern Australia. Rahimpour-Bonab, Bone, and Moussavi-Harami (1997) investigated stable isotopes in the shells of extant gastropods, bivalves, and brachiopods. Ten brachiopod specimens were used, but the species were not specified. The results suggested that the gastropod and bivalve shells had δ^{18}O values in equilibrium with ambient seawater, whereas brachiopod shells were enriched in ^{18}O relative to equilibrium. Rahimpour-Bonab, Bone, and Moussavi-Harami (1997) also observed a high degree of carbon and oxygen isotopic covariance, which they suggest was indicative of vital effects, resulting in disequilibrium precipitation. Working with samples from the same location, James, Bone, and Kyser (1997) analyzed 48 extant brachiopods from 4 terebratulid species. The brachiopods were grab sampled, allowing differentiation between specimens from discrete parts of the shelf. Disregarding the recommendations of Carpenter and Lohmann (1995) on the grounds that primary layer calcite accounted for less than 6% of the bulk, James, Bone, and Kyser (1997) analyzed samples of whole shells. Their results distinguished between specimens collected in areas of the Lacepede Shelf influenced by seasonal upwelling of colder water and those not. The conclusion of the study was that the δ^{18}O content of the brachiopod shell did in general reflect equilibrium with ambient seawater.

Curry and Fallick (2002) added to the controversy when they reported different δ^{8}O values from the dorsal (1.06‰) and ventral (0.58‰) valves of the articulated brachiopod *Calloria inconspicua* from the Otago Shelf in New Zealand. This observation was corroborated in the same study using well-preserved fossil specimens of *C. inconspicua* extracted from upper Pleistocene deposits from the Wanganui Basin, North Island, New Zealand (Curry, 1999).

In a recent compilation, Brand and others (2003) combined extensive new and published data to assess δ^{18}O equilibrium in extant brachiopods. For equilibrium, the authors required that 75% of temperatures calculated from brachiopod shell carbonate fall within the measured seawater temperature range. Given this and the fact that, in many cases, measured seawater temperatures are wide ranging, there are still many analyses that fail their test and have ambiguous or disequilibrium results.

Clearly, there is still much controversy surrounding brachiopods and their ability to precipitate their shells in isotopic equilibrium with ambient seawater. It could be that the diversity of extant brachiopods with a variety of ecologies, environments, shell structures, and biomineralization regimes leads to many of the conflicting data. Understanding stable isotope distribution within living brachiopods is vital to deciphering the signal from fossil specimens and improving the resolution of paleoenvironmental investigations.

Parkinson and others (2005) sought to shed light on the situation in a large systematic study of extant brachiopods taken from a variety of environments and latitudes. In all cases, the brachiopods were collected alive. The specimens represented all extant groups of calcite-precipitating brachiopods, as defined by Williams and others (1996). The species analyzed in the Parkinson and others (2005) study are shown in Table 38. Parkinson and others (2005) examined the shell structures of each group to determine differences in ultrastructure. The inarticulated craniids had a thin acicular calcite primary (outer) layer overlying a secondary layer composed of laminar sheets of calcite (Williams & Wright, 1970; Williams, 1997). The articulated terebratulids and rhynchonellids also have acicular primary layers but fibrous secondary layers (Williams, 1968, 1997). The one exception was from the genus *Liothyrella*, a terebratulid whose

TABLE 38. Brachiopods included in isotope survey of PARKINSON and others (2005). Members of subphylum Craniiformea are inarticulated and those of subphylum Rhynchonelliformea are articulated (new).

Subphylum	Order	Suborder	Species	Location
Craniiformea	Craniida		*Novocrania anomala*	Scotland, UK
			Neoancistrocrania norfolki	South Pacific Ocean
Rhynchonelliformea	Rhynchonellida		*Notosaria nigricans*	New Zealand
	Terebratulida	Terebratulidina	*Terebratulina retusa*	Scotland, UK
			Laqueus rubellus	Japan
			Liothyrella neozelanica	New Zealand
			Liothyrella uva	Antarctica
			Calloria inconspicua	New Zealand
			Neothyris lenticularis	New Zealand
			Terebratella sanguinea	New Zealand
			Terebratalia transversa	Puget Sound, USA
	Thecideida		*Thecidellina barretti*	Jamaica

secondary layer is underlain by a tertiary succession of prismatic calcite (WILLIAMS, 1968, 1997). Thecideidine brachiopods are small articulated species that showed little secondary layer development and were composed of granular primary layer material (WILLIAMS, 1968, 1973, 1997).

PARKINSON and others (2005) used samples from the primary and secondary layers and in the case of *Liothyrella* the tertiary layer for stable oxygen and carbon analysis. The secondary and tertiary layer samples included material from nonspecialized as well as specialized areas that form readily identifiable morphological features (i.e. the cardinal process, loop, and muscle scars from the dorsal valves; pedicle foramen, teeth, and muscle scars from the ventral valves).

Carbon and oxygen isotopic compositions of the primary layer of terebratulids (e.g., Fig. 1665) showed a positive correlation, with a tendency for both isotopes to be depleted in the heavy isotope relative to the secondary layer. This was consistent with the findings of CARPENTER and LOHMANN (1995) and AUCLAIR, JOACHIMSKI, and LÉCUYER (2003) and is likely to result from kinetic fractionation, which can be the result of higher growth rates (M^CCONNAUGHEY, 1989a, 1989b; M^CCONNAUGHEY & others, 1997). In brachiopods, the primary layer is only precipitated from the edge of the mantle as the shell enlarges and is precipitated relatively faster than the secondary layer (RUDWICK, 1970). In all terebratulids other than *T. retusa,* δ^{18}O values for the primary layer fall outside the range expected for equilibrium with ambient seawater. These temperatures were calculated using measured seawater temperatures and δ^{18}O, with the paleotemperature equation recommended by ANDERSON and ARTHUR (1983), a modification of the original equation of EPSTEIN and others (1953). The rhynchonellid, *N. nigricans* in contrast showed no correlation between δ^{18}O and δ^{13}C, and the δ^{18}O values fell within the expected range for isotopic equilibrium with ambient seawater.

With the exception of *L. uva*, the fibrous secondary or prismatic tertiary material of the terebratulids and rhynchonellid did not display a correlation between δ^{18}O and δ^{13}C (PARKINSON & others, 2005). In *T. transversa,* samples from the teeth and pedicle foramen were not in δ^{18}O equilibrium with ambient seawater, but all other secondary-tertiary layer samples were, regardless of the specialization in the areas of the shell they were extracted. PARKINSON and others (2005) did not find any significant variation between the dorsal and ventral valves as reported by CURRY and FALLICK (2002). PARKINSON and others (2005) report the least variation in the nonspecialized material, however, which produced isotopic temperatures close to the mean measured

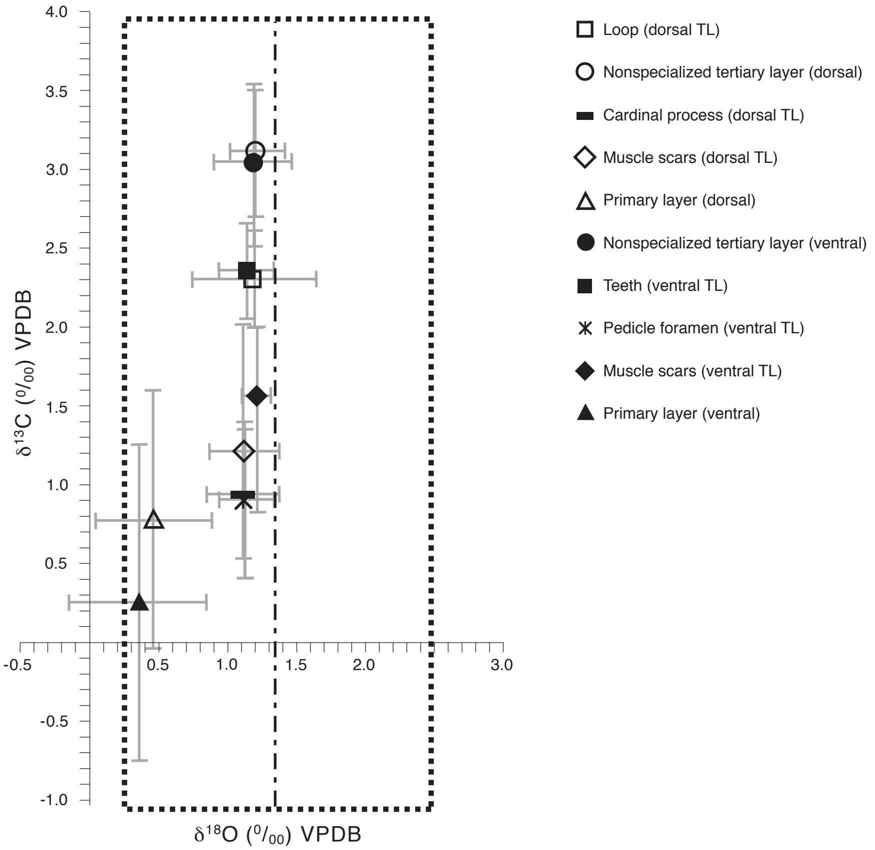


FIG. 1665. $\delta^{18}O$–$\delta^{13}C$ crossplot of *Liothyrella neozelanica* including all areas analyzed from both dorsal and ventral valves; *data points* represent mean values; *error bars* indicate 1σ; *dotted box* indicates oxygen isotope equilibrium parameters, with mean value indicated by *dashed line; TL,* tertiary layer (Parkinson & others, 2005).

annual temperatures for ambient seawater. *L. uva* specimens from Antarctica had a strong positive correlation between $\delta^{18}O$ and $\delta^{13}C$ in the tertiary layer, with many of the $\delta^{18}O$ values not in equilibrium with ambient seawater. This concurs with the observations of LEPZELTER, ANDERSON, and SANDBERG (1983), CARPENTER and LOHMANN (1995), and MARSHALL and others (1996) for brachiopods in very cold environments. Examination of the *L. uva* shells under a scanning electron microscope revealed that the tertiary succession in the shells of *Liothyrella* sp. (MACKINNON & WILLIAMS, 1974; WILLIAMS, 1997) was poorly formed, and fibrous secondary material dominated (PARKINSON & others, 2005). The implications are a possible link between abnormal shell growth and isotopic disequilibrium in brachiopod shells living in extreme environments. The thecideidine brachiopod *T. barretti* produced very consistent $\delta^{18}O$ and $\delta^{13}C$ values. It was not in isotopic equilibrium with ambient seawater, however, producing cooler isotopic temperatures than the measured range.

The $\delta^{13}C$ values from the secondary-tertiary layers of the articulated brachiopods (PARKINSON & others, 2005) were variable, although not correlated with $\delta^{18}O$ (Fig. 1665). They fall into palpable groups, however, dependent on the specialization of the area of the sample material (Fig. 1666–1667). The observed pattern, summa-

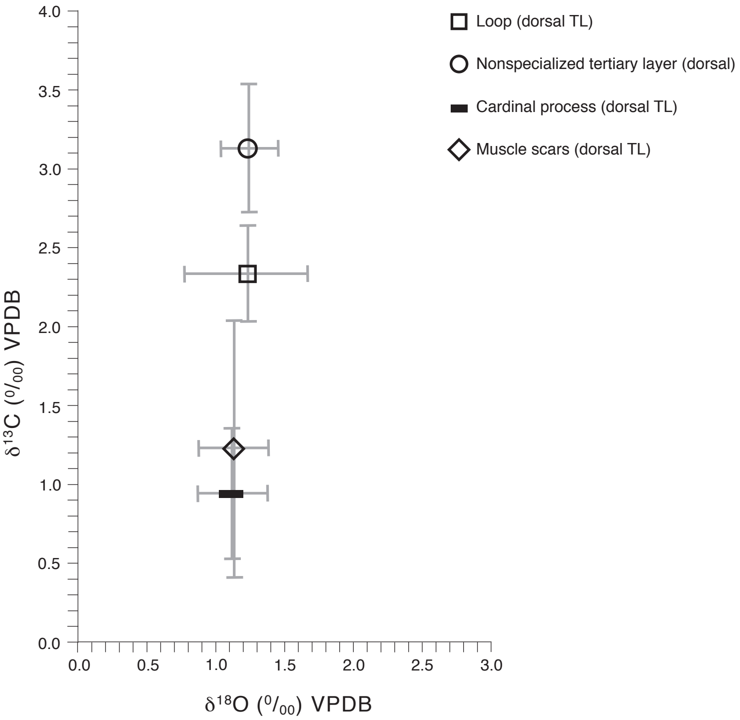


FIG. 1666. δ^{18}O–δ^{13}C crossplot of *Liothyrella neozelanica* dorsal valves; *data points* represent mean values; *error bars* indicate 1σ*; TL,* tertiary layer (new).

rized in Figure 1668, was independent of geographical location. The highest values were at the anterior of the valves, with the lowest values being recorded at the posterior. Although PARKINSON and others (2005) did not provide data for δ^{13}C equilibrium, it is inconceivable that all the areas of the secondary layer are in carbon isotopic equilibrium with the seawater. The conclusion was that the brachiopods may be controlling the incorporation of ^{13}C as a result of metabolic prioritization.

The inarticulated craniids displayed few discernable patterns. The primary layer of *N. anomala* was depleted in both isotopes and offset relative to the laminar secondary layer. Although some δ^{18}O values were in equilibrium, the distribution of both δ^{18}O and δ^{13}C was erratic, producing some extreme values. *N. norfolki* had no separation between different areas of the shell in terms of δ^{18}O and δ^{13}C. No δ^{18}O values were in isotopic equilibrium with ambient seawater.

While the majority of the paleothermometry studies on brachiopods have concentrated on calcite-shelled species, recent evidence indicates that while the phosphate in lingulid valves is not an accurate recorder of seawater oxygen isotope ratio, the carbonate component of the francolite may be used in paleothermometry (RODLAND & others, 2003).

IMPLICATIONS FOR USE IN PALEOENVIRONMENTAL INVESTIGATIONS

Stable isotope analyses of extant brachiopods are important because specimens can be collected from locations where the ambient environmental conditions can be

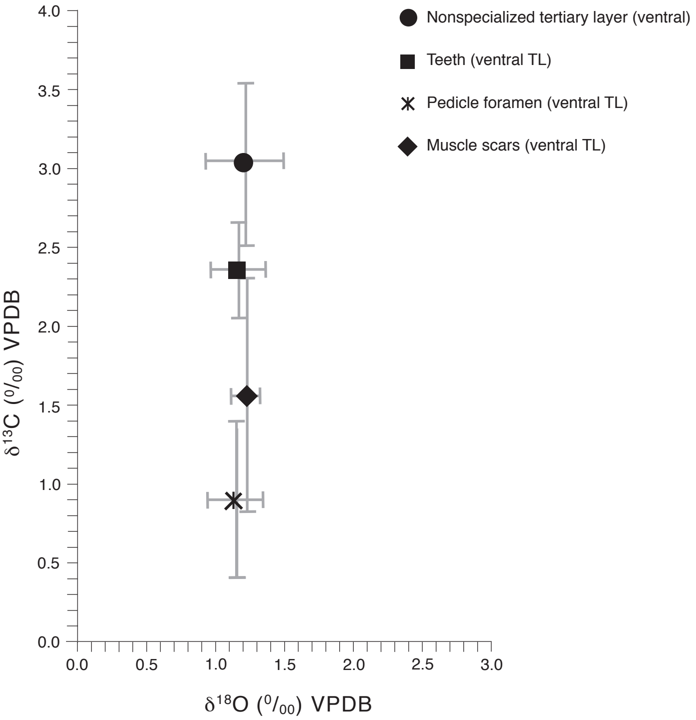
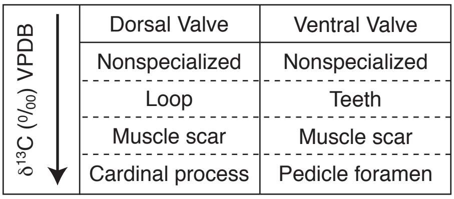


FIG. 1667. $\delta^{18}O$ – $\delta^{13}C$ crossplot of *Liothyrella neozelanica* ventral valves; *data points* represent mean values; *error bars* indicate 1σ*; TL,* tertiary layer (new).

measured. Studying the isotopic composition of extant brachiopod shells increases understanding of the limitations when using stable isotope determinations from fossil shells in paleoenvironmental investigations. Recent isotopic studies of extant brachiopods (e.g., CARPENTER & LOHMANN, 1995; AUCLAIR, JOACHIMSKI, & LÉCUYER, 2003; BRAND & others, 2003; PARKINSON & others, 2005) have shown that the oxygen isotope composition of brachiopods frequently records ambient seawater temperatures accurately. All the studies concur that the primary layer is usually in disequilibrium and should not be used. Notwithstanding the success reported by BUENING and SPERO (1996), seasonal profiling, which can only be effectively carried out on the outside of the shell where growth lines are visible, may be unreliable in modern brachiopod shells. This is not the case in all ancient brachiopods, however (MII & GROSSMAN, 1994). The



Dorsal Valve	Ventral Valve
Nonspecialized	Nonspecialized
Loop	Teeth
Muscle scar	Muscle scar
Cardinal process	Pedicle foramen

FIG. 1668. Trend of $\delta^{13}C$ within secondary shell layer of modern terebratulid and rhynchonellid brachiopods; general trend applies irrespective of geographical location (Parkinson & others, 2005).

secondary layer generally yields $\delta^{18}O$ values at or near equilibrium. Some precautions should be taken during sampling, however. Auclair, Joachimski, and Lécuyer (2003) observed that the upper portion of the secondary layer (i.e., immediately adjacent to the primary layer) is not in oxygen isotopic equilibrium, and only material close to the internal surface should be used. Carpenter and Lohmann (1995) and Parkinson and others (2005) reported that areas of the secondary layer, which form specialized morphological features, may be depleted in some species.

There are disequilibrium effects in the oxygen isotopic composition of some brachiopod groups. The Craniida show wide variation in $\delta^{18}O$ values (Carpenter & Lohmann, 1995; Brand & others, 2003; Parkinson & others, 2005). The craniids have a secondary layer composed of laminar sheets. It is possible that the biomineralization regime that produces this kind of ultrastructure could be related to the level of fluctuation in $\delta^{18}O$ values. Until there is a better understanding of the relationship between shell structure and oxygen isotope composition it is advisable to avoid fossil shells with this type of ultrastructure. The situation of the Thecideidina is uncertain, with oxygen isotope equilibrium noted by Brand and others (2003) and the contrary by Carpenter and Lohmann (1995) and Parkinson and others (2005).

Studies of extant brachiopods from cold-water environments have all found difficulty in producing meaningful environmental interpretations (e.g., Lepzelter, Anderson, & Sandberg, 1983; Carpenter & Lohmann, 1995; Marshall & others, 1996; Parkinson & others, 2005).

Incorporation of carbon isotopes into brachiopod shells is little understood and there is no consensus of opinion in the literature. There is evidence for metabolic effects (e.g., Buening & Spero, 1996; Auclair, Joachimski, & Lécuyer, 2003; Parkinson & others, 2005), but the mechanisms are unclear. If $\delta^{13}C$ values are to be useful proxies for environmental conditions, detailed physiological investigations are required.

Recent investigations of the stable isotope compositions of extant brachiopods have provided valuable insight into their usefulness as paleoenvironmental proxies. The potential resolution of future studies using fossil shells is therefore improved. Further research is required to increase the quality of understanding of the environmental information recorded in brachiopod shells.

ACKNOWLEDGMENTS

We are very grateful to The Scottish Association of Marine Science (SAMS) at Oban Scotland, especially Jim Watson and the Captain and crew of *RV Calanus*, for their considerable assistance with collection of samples in Firth of Lorne. We thank Terry Donnelly at Scottish Universities Environmental Research Centre for extensive technical assistance with the stable isotope analysis.

We also thank Professor Lloyd Peck (British Antarctic Survey); Dr. Kazuyoshi Endo (Institute of Geosciences, University of Tsukuba, Japan); Dr. Bernard L. Cohen (IBLS, Division of Molecular Genetics, University of Glasgow), and the late Sir Alwyn Williams for the supply of extant brachiopod specimens.

DP greatly acknowledges financial support of a Neilson Research Scholarship from the University of Glasgow.

This work is a contribution to the BioCalc Project of the EuroMinScI Programme ESF-EUROCORES, ERAS-CT-2003-980409) and Theme 3 (Atmosphere, Oceans and Climate) of SAGES (Scottish Alliance for Geoscience, Environment and Society).

SYSTEMATIC DESCRIPTIONS: BRACHIOPODA

UPDATES TO SYSTEMATIC VOLUMES 2–5

LINGULIFORMEA

L. E. HOLMER and L. E. POPOV

[University of Uppsala; National Museum of Wales, Cardiff]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

Subphylum LINGULIFORMEA Williams & others, 1996

Class LINGULATA Gorjansky & Popov, 1985

The phylogeny and classification of groups within the Lingulata are still most problematic, but the cladistic analyses by HOLMER and POPOV (1996, 2000) indicate that they can be divided into at least two monophyletic orders, the Siphonotretida and Acrotretida, as well as the Lingulida, which cannot be confirmed as a monophyletic group. As defined by HOLMER and POPOV (2000), the Lingulata comprises 22 extinct and only 2 extant families, the Lingulidae and Discinidae.

Recent chemicostructural studies of the shells of living and extinct linguliforms by WILLIAMS and others (1998), CUSACK, WILLIAMS, and BUCKMAN (1999), WILLIAMS and CUSACK (1999), WILLIAMS (2003), and WILLIAMS, HOLMER, and CUSACK (2004), have revealed the extraordinary complexities of organophosphatic skeletal systems. There is no doubt that basic characters of the shell structure are of primary importance for lingulate systematics; however, the significance of homoplasy in the evolution of organophosphatic brachiopod shell lamination, especially in the lingulides, is not yet completely clear. As a result, the published cladograms have so far been inconclusive with highly varying topology depending to a large degree on how characters were coded and which groups were included in the analysis. Thus, a complete phylogenetic revision of linguliform systematics has not been attempted at the present time.

Order LINGULIDA Waagen, 1885

HOLMER and POPOV (1996, 2000) expanded the concept of the order to include also the Discinoidea and Acrotheloidea, in view of their lingulid-like musculature and shell structure, but the detailed phylogenetic relationships between the Linguloidea and the discinoids and acrotheloids could not be determined. From the detailed structural shell studies and cladistic analyses of WILLIAMS, CUSACK, and BUCKMAN (1998), CUSACK, WILLIAMS, and BUCKMAN (1999), and WILLIAMS and CUSACK (1999), it is clear that the phylogeny and classification of the lingulides need to be revised considerably. These cladistic analyses (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999) of the lingulid superfamilies Linguloidea and Discinoidea indicate that they indeed form a monophyletic group within the Lingulida, defined mainly by the possession of a baculate shell structure (HOLMER, 1989), but excluding some groups that were assigned to the Linguloidea by HOLMER and POPOV (1996, 2000), most importantly the Lingulellotretidae. The latter group includes the earliest known Early Cambrian (Atdabanian) lingulid-like brachiopod with a long fleshy pedicle emerging through an enclosed pedicle foramen (see JIN, HOU, & WANG, 1993; HOLMER & others, 1997), but since it has an acrotretoid-like columnar shell structure (CUSACK, WILLIAMS, & BUCKMAN, 1999) it cannot be confirmed as a member of the linguloid-discinoid clade. In the same way, CUSACK, WILLIAMS, and BUCKMAN (1999) excluded the Paterulidae and Eoobolidae from the Linguloidea-Discinoidea, based on ultrastructural differences. The phylogenetic relationships and systematic composition of the families Zhanatellidae, Elkaniidae, and Dysoristidae also require revision following the work of CUSACK, WILLIAMS, and BUCKMAN (1999). In particular, the distributions of the various types of superficial pitted imprints need to be looked at in detail, since it is clear that they now can be divided into several distinct types (WILLIAMS, 2003).

In the cladistic analysis of HOLMER and POPOV (1996), the most derived families, the Pseudolingulidae, the Lingulasmatidae, and the Lingulidae, formed a monophyletic group, and this is supported in the cladogram of CUSACK, WILLIAMS, and BUCKMAN (1999). Within this clade, the Lingulidae is also monophyletic, first appearing at around the Late Devonian to Early Carboniferous; the separation between the two modern genera *Glottidia* and *Lingula* can be traced back to the Carboniferous, based on characteristics of their respective shell structure (WILLIAMS & others, 2000).

The new data on soft body anatomy of Early Cambrian lingulides from the Chengjiang Fauna published by ZHANG, HOU, and EMIG (2003) and ZHANG and others (2003) include important anatomical information including preservation of a pedicle, schizolophous lophophore, as well as a recurved, U-shaped digestive tract with a functional anus. This provides the first direct evidence that major features of soft body anatomy characteristic of Recent lingulates were already in place in Early Cambrian members. Considerable variation exists in pedicle morphology among the early lingulides. In particular, the acrotheloid *Diandongia pista* RONG had a long (up to 16 mm) and thin (less than 1 mm in diameter) pedicle lacking any annulations. Its distal part adhered to sand grains or was attached to bioclasts. It could not support the animal, however, to maintain a higher position in the water column or be used in active borrowing, as in Recent lingulides. New findings from the Chengjiang brachiopods also give additional insight into the paleoecology of Early Cambrian lingulids. For example, preservational aspects, the presence of a schizolophous lophophore, as well as pedicle morphology of *Lingulellotreta,* all suggest this lingulide was a high-level suspension feeder and was not adapted to an infaunal mode of life (ZHANG & others, 2004; see also HOLMER & others, 1997).

Superfamily LINGULOIDEA Menke, 1828

Family LINGULIDAE Gray, 1840

Credolingula SMIRNOVA in SMIRNOVA & USHATINSKAYA, 2001, p. 57 [**C. olferievi*; OD]. Shell slightly biconvex, equivalved, with poorly defined sulcus, bearing low indistinct median fold in both valves; pseudointerareas of both valves vestigial; ventral valve interior with asymmetrical paired umbonal muscle, bisected by pedicle nerve impression; dorsal interior with visceral area occupying about two-thirds of sagittal length; posterolateral muscle fields strongly asymmetrical; mantle canal system of both valves bifurcate. *Lower Cretaceous (Albian):* central European Russia.——FIG. 1669*a–h*. **C. olferievi*, lower Albian, Stoilo quarry near Staryi Oskol, central European Russia; *a*, holotype, ventral valve exterior, PIN4796/1, ×1.8; *b*, dorsal valve exterior, PIN4796/2, ×1.8; *c*, ventral valve exterior, PIN4796/5, ×7; *d*, ventral valve interior, PIN4796/6, ×6.5; *e*, dorsal valve interior, PIN4796/16, ×5; *f*, detail of ventral valve interior showing posterior part of visceral field, PIN4796/3, ×7; *g*, detail of dorsal valve interior showing anterior part of visceral field, PIN4796/17, ×7; *h*, detail of dorsal valve interior showing posterior part of visceral field, PIN4796/4, ×15 (Smirnova & Ushatinskaya, 2001).

Family PSEUDOLINGULIDAE Holmer, 1991

Meristopacha SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 57 [**Lingula granulata* PHILLIPS in PHILLIPS & SALTER, 1848, p. 370; OD]. Shell weakly biconvex, elongate subrectangular; dorsal valve with hemiperipheral growth; ventral interarea short to obsolescent; ornament of strong regular concentric rugae; ventral interior with low visceral platform raised anteriorly; dorsal interior with strong median ridge crossing visceral area and widely separated central and anterior lateral muscle scars; ventral mantle canals saccate baculate with straight,

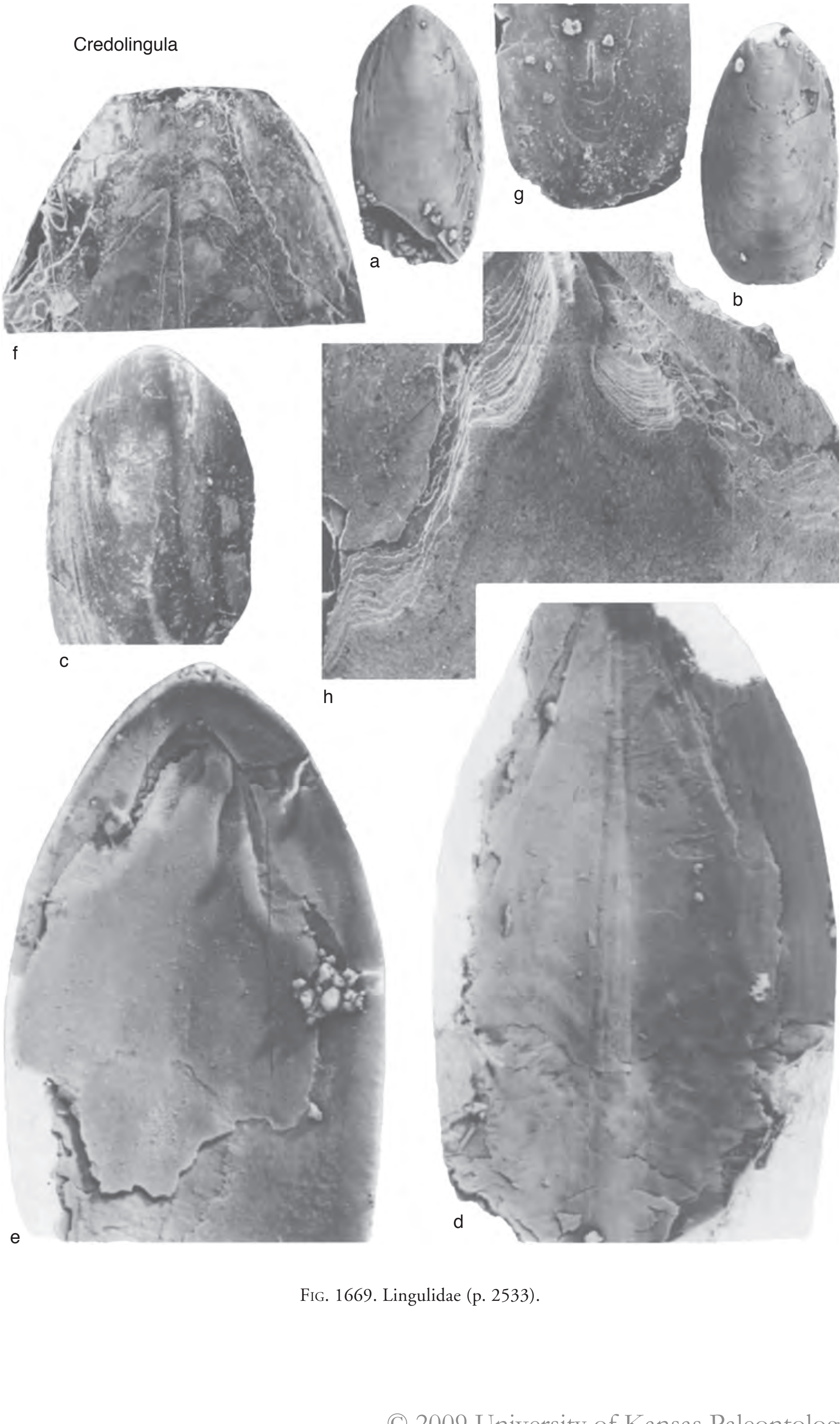


FIG. 1669. Lingulidae (p. 2533).

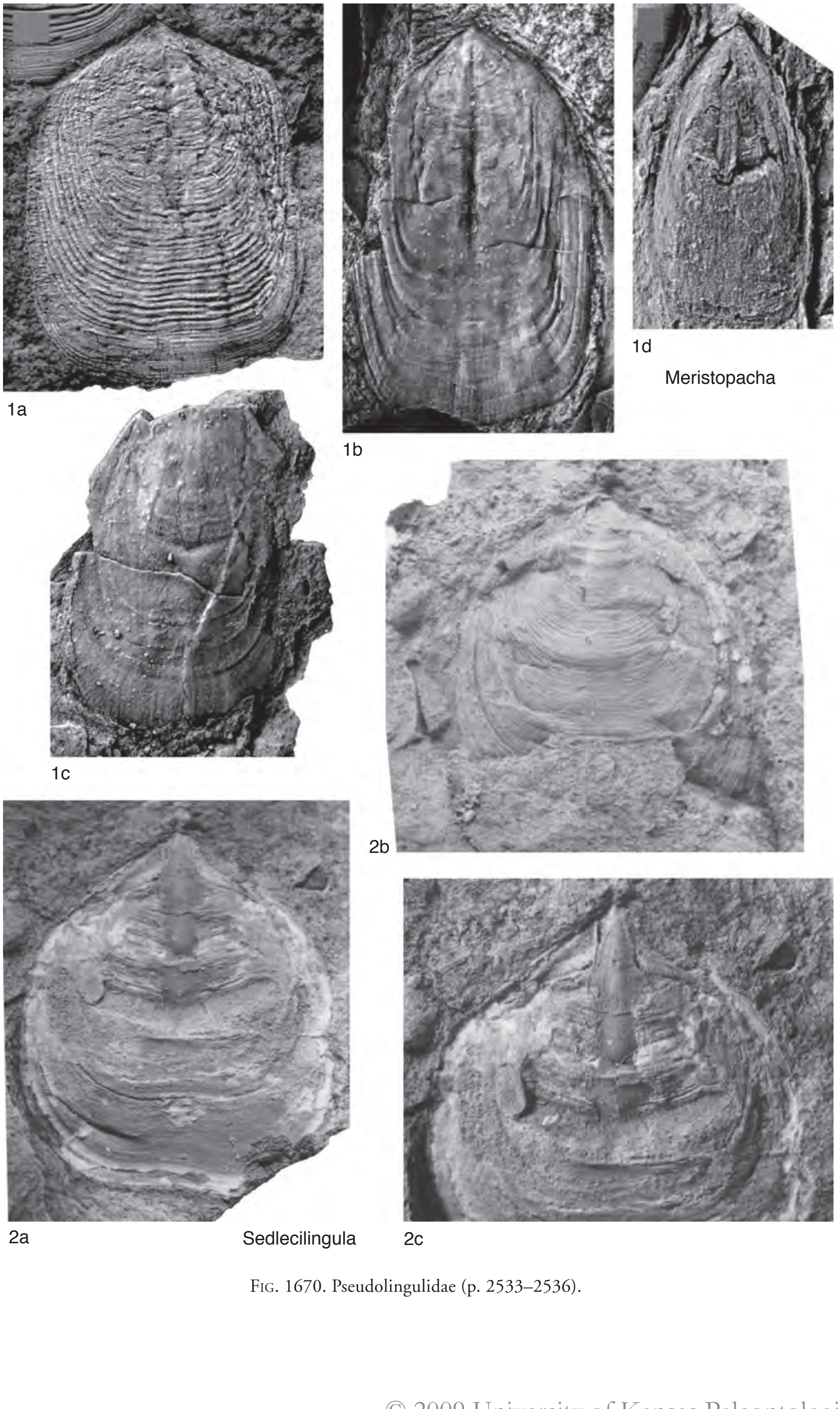


FIG. 1670. Pseudolingulidae (p. 2533–2536).

subparallel *vascula lateralia. Ordovician (Llanvirn–Llandeilo):* Great Britain.——FIG. 1670,*1a–d*. **M. granulata* (PHILLIPS), upper Llanvirn–Llandeilo; *a*, ventral valve exterior, SM A45419, ×2.5; *b*, dorsal internal mold, NHM BC51673, ×2.5; *c*, ventral internal mold, NHM BC51797, ×2.5; *d*, ventral internal mold, NMW 27.110G.437a, ×5 (Sutton, Bassett, & Cherns, 1999).

Sedlecilingula MERGL, 1997b, p. 98 [**S. sulcata*; OD]. Shell broadly elongate, both valves with sulcus, and weakly emarginated anterior margin; ornamentation with raised concentric fila; sulcus may bear faint radial plications; ventral pseudointerarea large, with well-defined propareas, separated by deep, moderately expanding pedicle groove; ventral interior with large raised muscle platform; posterior part of visceral area finely pitted; dorsal pseudointerarea well developed; dorsal interior lacking median ridge and paired umbonal scars. *Ordovician (Arenig):* Bohemia.——FIG. 1670,*2a–c*. **S. sulcata*, Klabava Formation, Sedlec; *a*, holotype, ventral internal mold, ×8; *b*, detail of visceral area and pseudointerarea, ×10; *c*, ventral valve exterior, latex cast, MBHR66837, ×8 (new). [Michal Mergl]

Family OBOLIDAE King, 1846

Subfamily OBOLINAE King, 1846

Atansoria POPOV, 2000a, p. 261 [**A. concava*; OD]. Shell concavoconvex, subcircular; dorsal valve mainly with hemiperipheral growth; dorsal pseudointerarea vestigial but undivided; dorsal interior with limbus; dorsal posterolateral muscle fields large and strongly impressed, outlined by muscle bounding ridges; dorsal central muscle scars strongly impressed, divided by median furrow, and partially enclosing small outside lateral muscle scars; dorsal mantle canal system baculate with arcuate, subperipheral *vascula lateralia* and short, divergent *vascula media*. *Ordovician (upper Caradoc–Ashgill):* Kazakhstan, Australia.——FIG. 1671,*2a–c*. **A. concava*, Mayatas Formation, upper Caradoc, northern coast of Atansor lake, Kazakhstan; holotype, dorsal valve interior, oblique lateral, and posterior views, NMW 98.65G.4, ×23 (Popov, 2000a).

Divobolus SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 36 [**Obolus quadratus* BULMAN in STUBBLEFIELD & BULMAN, 1927, p. 121; OD]. Shell weakly biconvex, slightly inequivalved, elongate oval to subcircular; ventral interarea low, apsacline, lacking flexure lines; pedicle groove shallow; dorsal pseudointerarea low, crescent shaped, not raised above valve floor; median groove shallow; visceral areas in both valves weakly impressed; dorsal interior with short median tongue, and closely placed central and outside lateral muscle scars; mantle canal system in both valves baculate; ventral *vascula lateralia* submarginal, widely divergent proximally; dorsal *vascula media* long, divergent. *Ordovician (Tremadoc)*: Great Britain.——FIG. 1672,*2a–d*. **D. quadratus* (BULMAN), Shineton Shale Formation, Shropshire, England; *a*, ventral internal mold, NHMBB73823, ×5; *b,* ventral external mold, ×5; *c,* detail of ornament, BGSRU8944A, ×10; *d*, holotype, dorsal internal mold, NHMB47342, ×5 (Sutton, Bassett, & Cherns, 1999).

Eodicellomus HOLMER & USHATINSKAYA in USHATINSKAYA & HOLMER, 2001, p. 125 [**E. elkaniiformis*; OD]. Shell close to equibiconvex; ornamentation of thin radial costellae; ventral pseudointerarea apsacline; pedicle groove deep, broadly triangular; propareas well developed, elevated; dorsal pseudointerarea anacline, with short median groove and flattened propareas; central and anterior parts of both valves strongly thickened, forming visceral platforms; vascular system of both valves well developed, with deep *vascula lateralia* and dorsal *vascula media. Lower Cambrian (Atdabanian–Botomian):* South Australia, Transantarctic Mountains.——FIG. 1673*a–k*. **E. elkaniiformis*, Parara Limestone, Botomian, Yorke Peninsula and Flinders Ranges; *a*, dorsal valve interior, PIN4664/6246, ×9; *b*, holotype, ventral valve interior, ×10; *c*, detail of visceral area, PIN4664/6172, ×18; *d*, oblique posterior view of dorsal umbo, PIN4664/6167, ×42; *e*, oblique posterolateral view of ventral umbo, ×24; *f*, detail of ornamentation, ×100; *g*, detail of ventral larval shell, PIN4664/6168, ×80; *h*, oblique lateral view of dorsal valve interior, PIN4664/6170, ×16; *i*, dorsal valve interior, ×11; *j*, detail of dorsal pseudointerarea, PIN4664/6173, ×22; *k*, oblique posterolateral view of ventral interior, PIN4664/6164, ×17 (Ushatinskaya & Holmer, 2001).

Josephobolus MERGL, 1997a, p. 137 [**J. regificus*; OD]. Shell broadly oval, subacuminate; ornamentation of oblique, parallel terrace lines on flanks; narrow posteromedian and anterolateral sectors with faint terrace lines crossing each other and forming a regular network of asymmetrical pits; ventral pseudointerarea large, with narrow propareas; pedicle groove deep, rapidly expanding anteriorly; dorsal pseudointerarea short; visceral areas of both valves weakly impressed; interior of shell densely covered by large pits. *Ordovician (Arenig):* Bohemia.——FIG. 1672,*1a–c*. **J. regificus*, Klabava Formation, Zbiroh; *a*, partial internal mold of ventral valve, MBHR 66781, ×5; *b*, ventral valve exterior, MBHR 66782, ×3.7; *c*, detail of ornamentation of fragmentary valve, MBHR 667893, ×8 (new). [Michal Mergl]

Kacakiella MERGL, 2001a, p. 13 [**K. bouceki*; OD]. Shell equibiconvex; ventral pseudointerarea with long pedicle groove; visceral area poorly impressed; exterior of larval shell smooth with several radial ribs, postlarval ornament of shallow pits in divaricate pattern; flanks with oblique terrace lines. *Silurian (Llandovery–Wenlock):* Bohemia.——FIG. 1674,*1a–d*. **K. bouceki*, Motol Formation,Wenlock, Loděnice, Svatý Jan pod Skalou; *a*, ventral valve interior, PCZCU503, ×8; *b*, detail of ornamentation, PCZCU466, ×45; *c*, ventral valve exterior

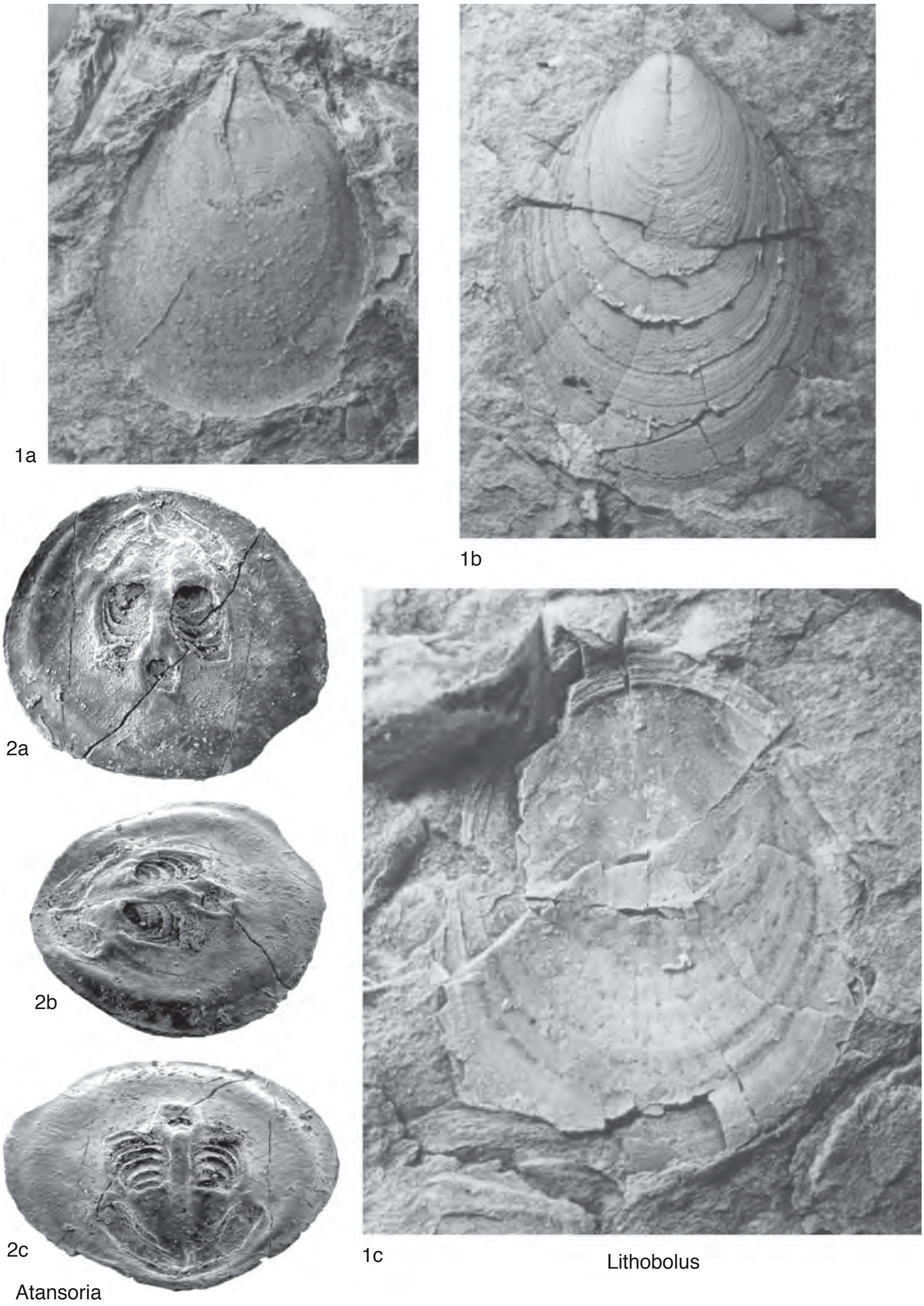


FIG. 1671. Obolidae (p. 2536–2542).

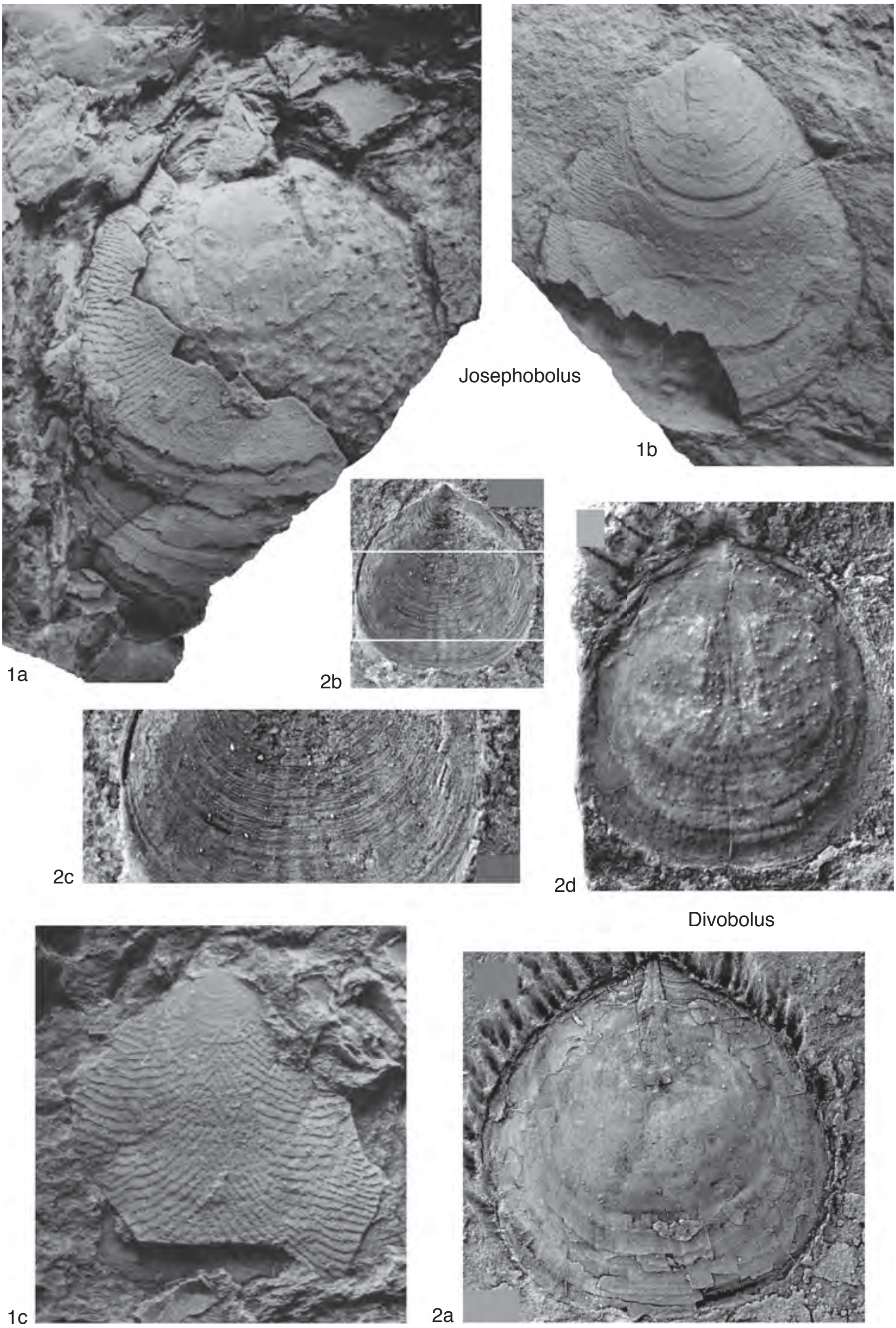


Fig. 1672. Obolidae (p. 2536).

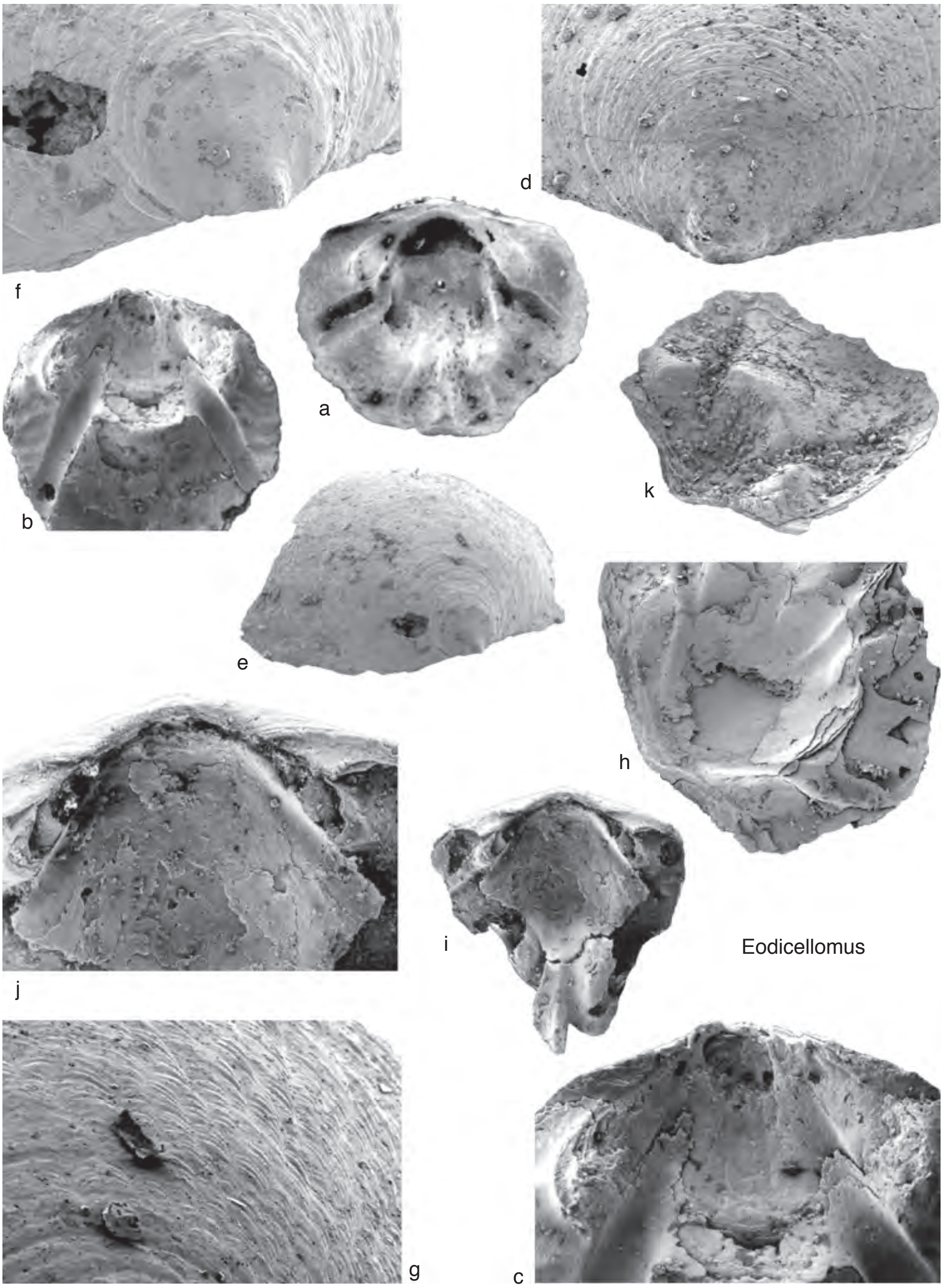


FIG. 1673. Obolidae (p. 2536).

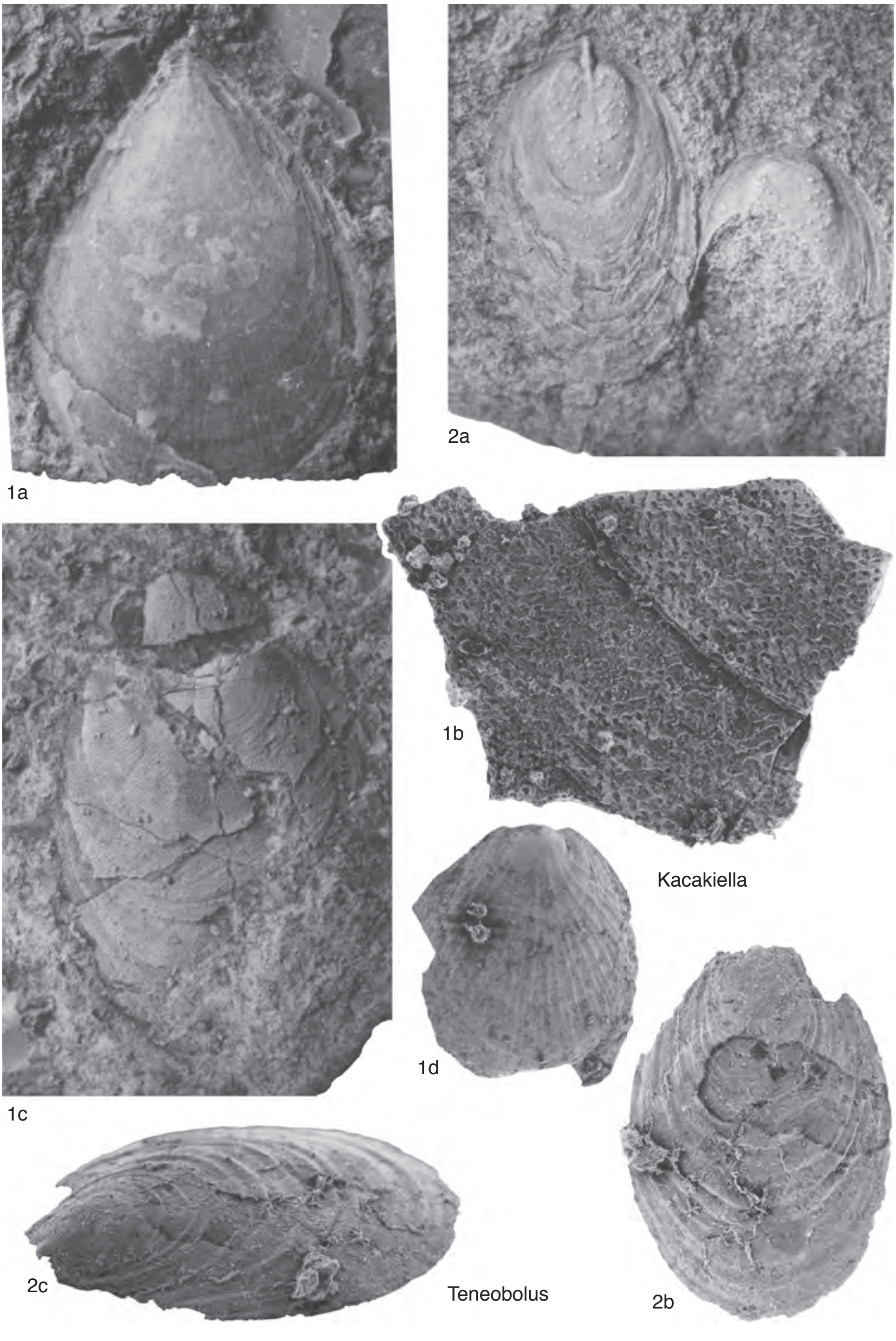


FIG. 1674. Obolidae (p. 2536–2542).

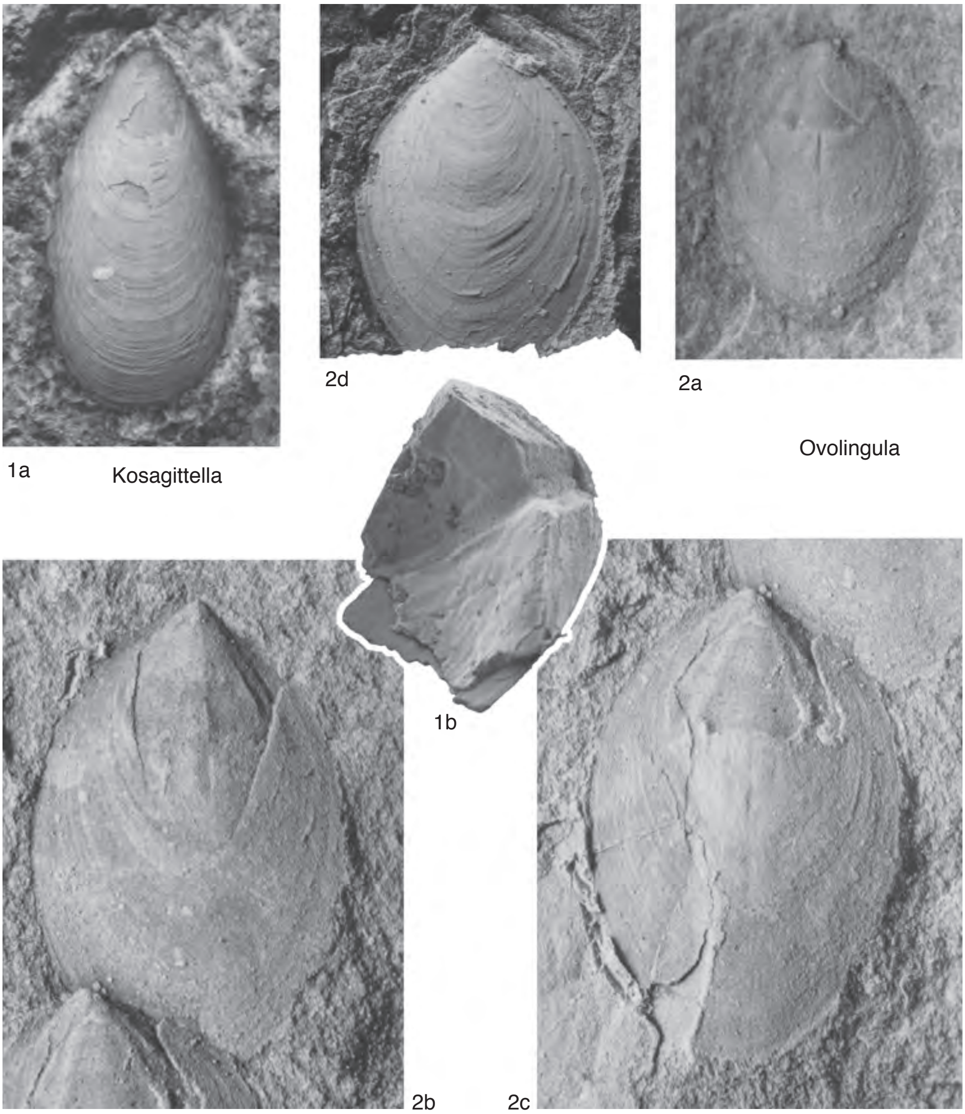


FIG. 1675. Obolidae (p. 2541–2542).

with divaricate ornamentation, PCZCU505, ×8; *d*, juvenile shell with radial ribs, PCZCU, ×40 (new). [Michal Mergl]

Kosagittella MERGL, 2001a, p. 11 [**K. clara*; OD]. Shell small, equibiconvex, elongate oval; ventral pseudointerarea small, orthocline; pedicle groove short, shallow; dorsal pseudointerarea short, with wide median groove and small propareas; dorsal *vascula media* subparallel, long, deeply impressed. *Silurian (Ludlow)–Devonian (Eifelian)*: Bohemia. ——FIG. 1675,*1a–b*. **K. clara*, Kopanina Formation, Ludlow, Králův Dvůr, Dlouhá hora; *a*, holotype, ventral valve exterior, NML34253, ×8; *b*, oblique lateral view of ventral pseudointerarea, PCZCU193, ×60 (new). [Michal Mergl]

Libecoviella MERGL, 1997a, p. 132 [**Lingula arachne* BARRANDE, 1879, pl. 111; OD]. Shell subacuminate, subtriangular to elongate oval, inequivalved; ornamentation of fine terrace lines, in posteromedian part arranged in divaricate pattern, anterolaterally and anteriorly with zigzag pattern; ventral pseudointerarea small, undercut, flexure lines poorly defined, pedicle groove parallel sided, deep, short; dorsal pseudointerarea short, with broad median groove; visceral field and muscle scars weakly impressed; ventral *vascula lateralia* broad, submarginal. Dorsal *vascula media* narrow, divergent. *Ordovician (Tremadoc):* Bohemia.——Fig. 1676,*1a–c*. **L. arachne* (Barrande), Třenice Formation, Libečov; *a*, dorsal valve exterior, latex cast, SBMNL32018, ×4; *b*, fragmentary ventral valve interior, SBNML32021, ×4; *c*, fragmentary dorsal valve interior, SBNML32020, ×4 (new). [Michal Mergl]

Lithobolus Mergl, 1996a, p. 45 [**L. plebeius*; OD]. Shell dorsibiconvex, elongate suboval; ventral pseudointerarea raised, lacking flexure lines; pedicle groove deep, broadly triangular; ventral visceral area poorly defined; dorsal pseudointerarea mainly occupied by median groove; interior of both valves with large pits. *Ordovician (Arenig)*: Bohemia.——Fig. 1671,*1a–c*. **L. plebeius*, Klabava Formation, Prague Basin, Ejpovice, Bukov; *a–b*, holotype, internal mold of ventral valve, latex cast of ventral valve external mold, MBHR66787, ×8; *c*, dorsal valve interior, MBHR66785, ×10 (new). [Michal Mergl]

Mytoella Mergl, 2002, p. 28 [**M. krafti*; OD]. Shell strongly biconvex for subfamily, small, thin shelled; ventral pseudointerarea low with distinct flexure lines; pedicle groove narrow and long; dorsal pseudointerarea short, with broad median groove; vascular markings obscure. *Ordovician (Llanvirn):* Bohemia.——Fig. 1677*a–e*. **M. krafti*, Šárka Formation, Osek, Mýto; *a*, holotype, internal mold of ventral valve, ×10; *b,* detail of ventral pseudointerarea, ×13; *c,* external mold of ventral valve, PCZCU557, ×10; *d*, dorsal valve exterior, PCZU556, ×4.8; *e*, internal mold of dorsal valve, PCZCU566, ×7.8 (new). [Michal Mergl]

Ovolingula Mergl, 1998, p. 225 [**Lingula ovum* Barrande, 1879, pl. 194; OD]. Shell elongate elliptical, biconvex; pseudointerareas of both valves minute; pedicle groove narrow and shallow; ventral visceral area with raised transverse platform; dorsal visceral area with large, triangular, raised platform, anteriorly supported by thin and long median septum. *Ordovician (Ashgill):* Bohemia, Ireland.——Fig. 1675,*2a–d*. **O. ovum* (Barrande), Králův Dvůr Formation, Bohemia; *a*, lectotype, internal mold of dorsal valve, SBNML25973, ×9; *b*, internal mold of ventral valve, MBHR1986, ×9; *c*, internal mold of dorsal valve, MBHR1986, ×9; *d*, ventral valve exterior, MBHR1989, ×9 (new). [Michal Mergl]

Pidiobolus Mergl, 1995, p. 103 [**P. minimus*; OD]. Shell thickened, strongly biconvex, minute, subcircular; exterior with fine pitting; ventral pseudointerarea undercut with deep and broad pedicle groove; dorsal pseudointerarea with broad median groove and minute propareas; dorsal central muscle scars large, spindle shaped. *Ordovician (Tremadoc–Arenig):* Bohemia.——Fig. 1678*a–g*. **P. minimus*, Klabava Formation, Arenig, Olešná Beds Member, Těně; *a*, ventral valve exterior, ×60; *b*, detail of pitted ornamentation, ×300; *c*, ventral valve interior, PCZCU607, ×60; *d*, detail of ventral pseudointerarea, ×160; *e*, oblique lateral view of ventral valve interior, PCZCU609, ×85; *f*, dorsal valve exterior, PCZCU608, ×60; *g*, oblique posterior view of dorsal valve exterior, PCZCU611, ×60 (new). [Michal Mergl]

Teneobolus Mergl, 1995, p. 104 [**T. gracilis*; OD]. Shell equally biconvex, elongate oval, smooth; ventral pseudointerarea with growth lines curved forward along narrow, deep, anteriorly projecting pedicle groove. *Ordovician (Arenig)*: Bohemia.——Fig. 1674,*2a–c*. **T. gracilis*, Klabava Formation, Olešná Beds Member, Těně; *a*, holotype, complete specimen with detached valves, internal mold of ventral (right) and dorsal (left) valves, MM512, ×10; *b*, juvenile dorsal valve exterior, ×55; *c*, oblique posterior view, PCZCU551, ×65 (new). [Michal Mergl]

Wadiglossella Havlíček, 1995, p. 55 [**W. odiosa*; OD; =*Lingula carens* Barrande, 1879, pl. 103] [=*Careniellus* Mergl, 2001a, p. 9 (type, *Lingula carens* Barrande, 1879, pl. 103; OD)]. Shell weakly equibiconvex, broadly oval; ornament of fine growth lines superposed on coarser fila; ventral pseudointerarea high and very short, with shallow pedicle groove; dorsal pseudointerarea short, undivided. *Silurian (Llandovery)–Devonian (Pragian):* Bohemia.——Fig. 1676,*2a–b*. **W. carens* (Barrande), Motol Formation, Wenlock, Loděnice, Černidla; *a*, lectotype, ventral valve interior, SBNML24458, ×8; *b*, dorsal valve exterior, SBNML24457, ×8 (new). [Michal Mergl]

Wosekella Mergl, 2002, p. 29 [**Lingula debilis* Barrande, 1879, pl. 102; OD]. Shell equibiconvex; ornamentation smooth medianly, with numerous radial plications and oblique wavy fila laterally; ventral pseudointerarea with flexure lines; pedicle groove long and deep; dorsal pseudointerarea with broad median groove; visceral area large but poorly defined. *Ordovician (Arenig–Llanvirn)*: Bohemia.——Fig. 1679*a–e*. **W. debilis* (Barrande), Šárka Formation, Llanvirn, Osek, Mýto, Bohemia; *a*, ventral external mold, latex cast, PCZCU573, ×7.8; *b*, external mold, latex cast showing ornamentation, PCZCU577, ×25; *c*, internal mold of ventral valve, PCZCU571, ×7.8; *d*, internal mold of dorsal valve, PCZCU572, ×7.8; *e*, internal mold of dorsal valve, PCZCU570, ×7.8 (new). [Michal Mergl]

Subfamily GLOSSELLINAE
Cooper, 1956

Barrandeoglossa Mergl, 2001a, p. 14 [**Lingula fissurata* Barrande, 1879, pl. 103; OD]. Shell equibiconvex; ornament of fine, elevated, sometimes wavy concentric fila; ventral pseudointerarea narrow, subtriangular, with deep, short pedicle groove; dorsal pseudointerarea absent; dorsal interior with median ridge. *Silurian (Ludlow)–Devonian*

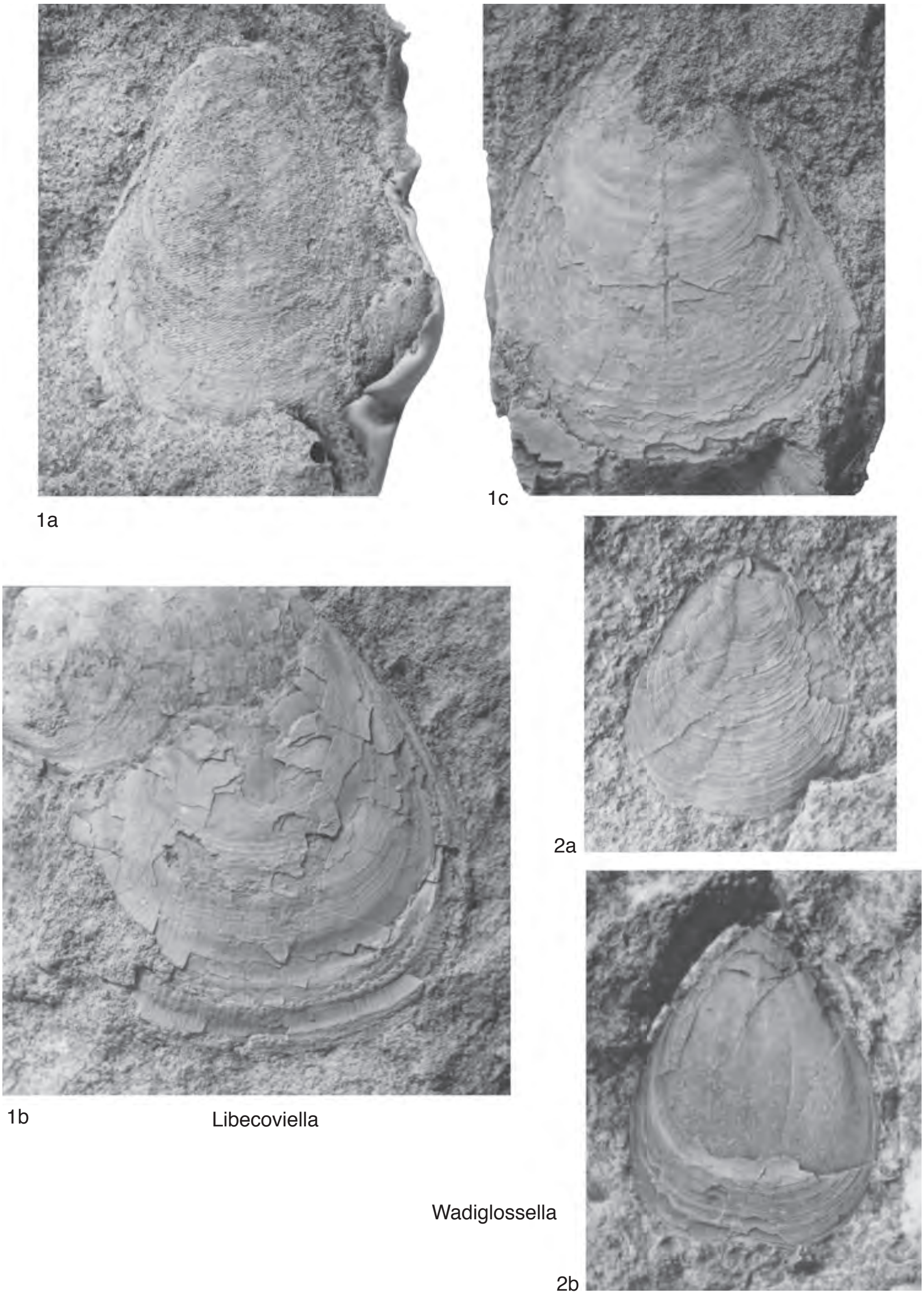


FIG. 1676. Obolidae (p. 2541–2542).

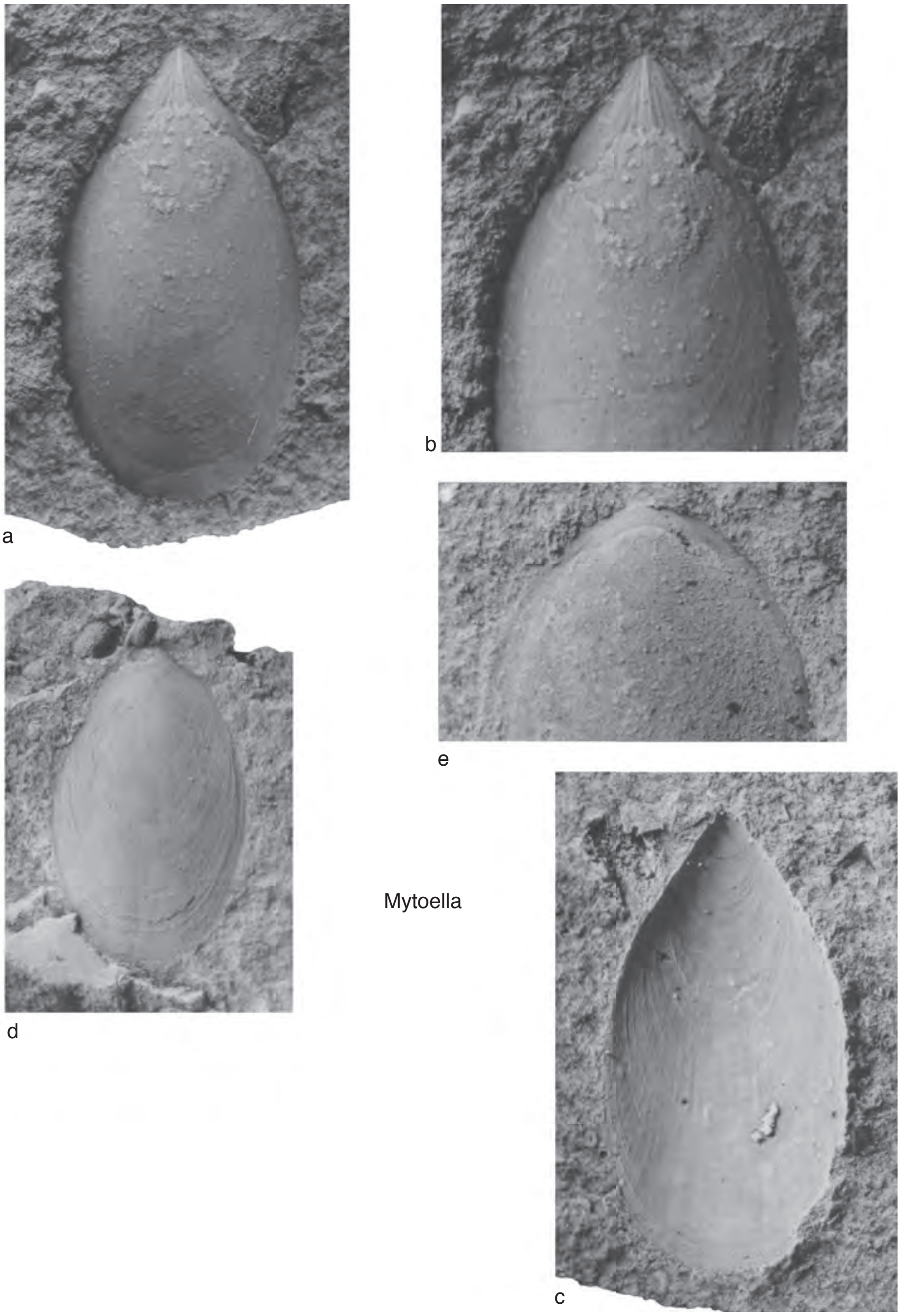


FIG. 1677. Obolidae (p. 2542).

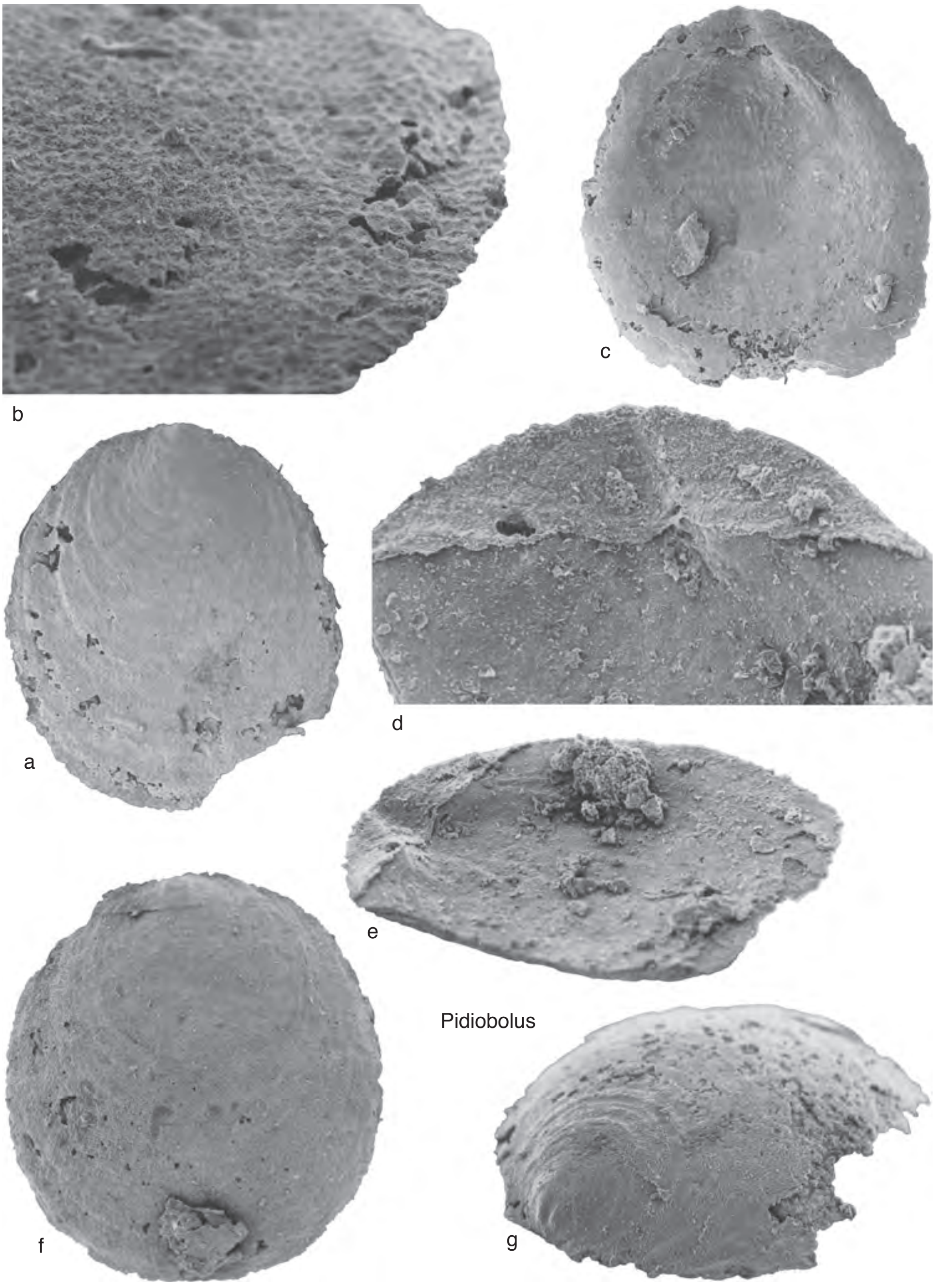


FIG. 1678. Obolidae (p. 2542).

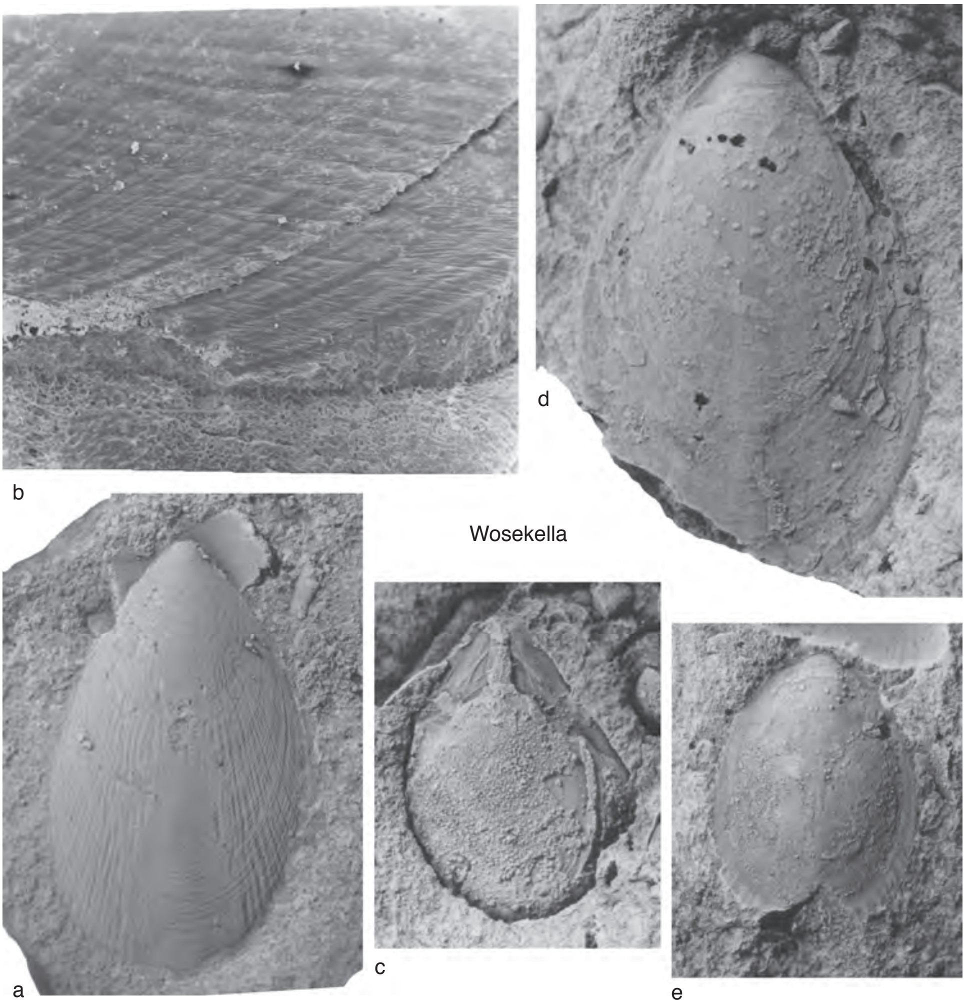


FIG. 1679. Obolidae (p. 2542).

(Lochkovian): Bohemia.——FIG. 1680*a–c*. **B. fissurata* (BARRANDE), Motol Formation, Wenlock, Beroun, Ratinka, and Svatý Jan pod Skalou; *a*, ventral valve interior, SBNML34251, ×5; *b*, dorsal valve interior, SBNML73198, ×5.5; *c*, detail of ornamentation, PCZCU206, ×30 (new). [Michal Mergl]

Prastavia MERGL, 2001a, p. 13 [**P. distincta*; OD]. Shell equibiconvex; ornament of discontinuous, elevated concentric fila; ventral pseudointerarea small, low, with shallow pedicle groove; dorsal pseudointerarea absent; visceral area of both valves prominent and thickened; ventral *vascula lateralia* with deeply impressed secondary branches. *Middle Devonian (Eifelian):* Bohemia.——FIG. 1681*a–f*. **P. distincta*, Choteč Formation, Praha–Holyně, Prastav; *a*, ventral valve interior, ×30; *b*, oblique lateral view, PCZCU238, ×38; *c*, holotype, ventral valve interior, ×30; *d*, oblique lateral view, PCZCU237, ×38; *e*, dorsal valve exterior, PCZCU197, ×30; *f*, oblique lateral view of dorsal valve interior, PCZCU235, ×45 (new). [Michal Mergl]

Subfamily ELLIPTOGLOSSINAE
Popov & Holmer, 1994

[incl. Litoperatidae SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 54]

Litoperata SUTTON in SUTTON, BASSETT, & CHERNS, 1999, p. 55 [**L. agolensis*; OD]. Shell weakly biconvex, elongate oval, with hemiperipheral growth; umbo of both valves marginal; ornament of strong, evenly spaced concentric rugellae; muscle

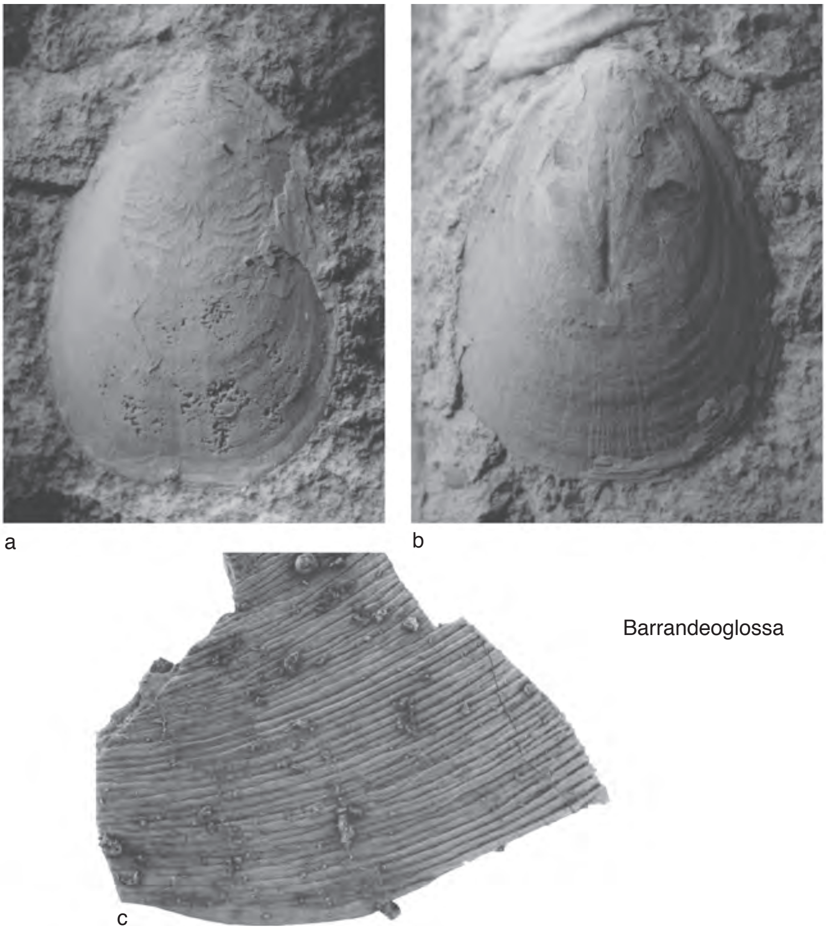


FIG. 1680. Obolidae (p. 2542–2546).

scars and mantle canals not impressed. *Ordovician (Llandeilo–Ashgill): Llandeilo,* Great Britain; *Ashgill,* Sweden.——FIG. 1682*a–d*. **L. agolensis*, Golden Groove Group, Llandeilo, Carmarthenshire, Great Britain; *a*, possible ventral valve exterior, NMW 96.8G.80, ×20; *b*, possible ventral valve interior, NMW 96.8G.803, ×20; *c*, possible dorsal valve exterior, NMW 96.8G.105, ×40; *d*, possible dorsal valve interior, ×40 (Sutton, Bassett, & Cherns, 1999).

Family ZHANATELLIDAE Koneva, 1986

Fagusella MERGL, 1996a, p. 46 [**F. indelibata*; OD]. Shell dorsibiconvex to convexoconcave; rugellose ornamentation; ventral pseudointerarea short, steeply apsacline, with broad and deep pedicle groove terminated posteriorly by large rounded subtriangular emarginature; dorsal pseudointerarea undivided, slightly raised above valve floor; ventral interior with large visceral area, broadly rhomboidal in outline, extended anterior to midvalve; ventral anterolateral muscle fields deeply impressed; dorsal visceral field bordered laterally by low rim, with anterior projection extending anteriorly beyond midvalve; dorsal median ridge long, bisecting visceral area; dorsal anterior lateral muscle scars small, situated close to large central scars. *Ordovician (Arenig):* Bohemia.——FIG. 1683,*1a–b*. **F. indelibata*, Klabava Formation, Prague Basin, Bukov; *a,* oblique lateral view of dorsal valve exterior, MBHR66798, ×35; *b,* holotype, ventral valve interior, MBHR66790a, ×10 (new).

Koneviella USHATINSKAYA, 1997, p. 495 [**K. menensis*; OD]. Shell weakly biconvex, subcircular; ornament of slightly irregular concentric rugellae; larval and postlarval shell finely pitted with hemispherical pits of varying sizes; ventral valve with emarginature; propareas raised, flattened and bisected by flexure

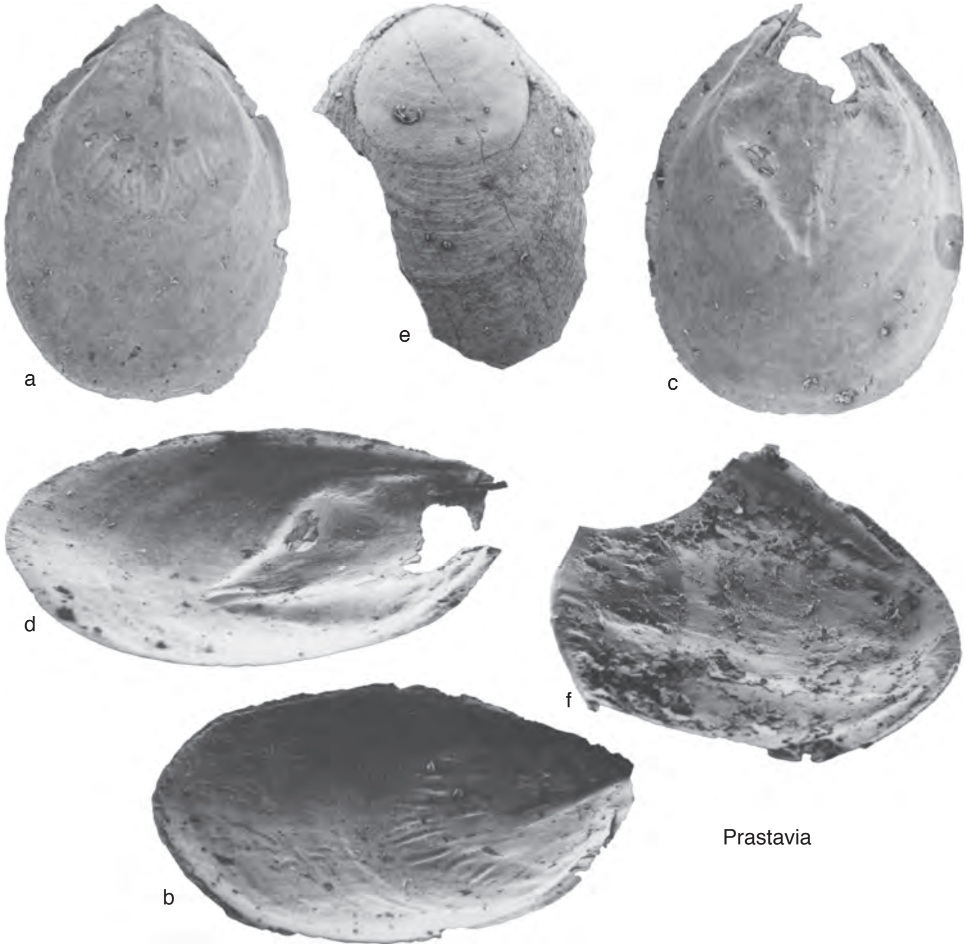


FIG. 1681. Obolidae (p. 2546).

lines, and with pitted ornamentation; pedicle groove deep; dorsal pseudointerarea low, occupied mainly by median groove; visceral areas and muscle scars of both valves weakly impressed; ventral mantle canals baculate with straight, divergent, subcentral *vascula lateralia*. *upper Middle Cambrian:* Russia (Siberia).——FIG. 1683,*2a–d*. **K. menensis*; Eirina Formation, *Glyptagnostus stolidotus* Biozone, Mene river, northcentral Siberia; *a*, holotype, ventral valve exterior, PIN4511/120, ×24; *b*, incomplete ventral valve interior, PIN4290/107, ×21; *c,* dorsal valve interior, ×30; *d,* pitted surface of dorsal propareas, PIN4511/122, ×700 (Ushatinskaya, 1997).

Wahwahlingula POPOV, HOLMER, & MILLER, 2002, p. 218 [**Lingula antiquissima* JEREMEJEW, 1856, p. 80; OD]. Shell slightly dorsibiconvex, elongate suboval to subtriangular; larval and postlarval shell with microornament of fine hemispherical pits; ventral pseudointerarea orthocline with narrow and shallow pedicle groove; propareas with flexure lines; dorsal pseudointerarea crescent shaped with rudimentary undivided propareas; ventral interior with weakly impressed visceral area bisected by pedicle nerve impression and baculate, submarginal *vascula lateralia*; dorsal interior with visceral area extending anterior to midvalve and bisected by fine median ridge; *vascular lateralia* marginal, arcuate; *vascular media* short, divergent. *Upper Cambrian–Ordovician (Tremadoc, ?Arenig):* northwestern Russia, western USA, ?Australia (Canning Basin).——FIG. 1683,*3a–e*. **W. antiquissima* (JEREMEJEW), Tosna Formation, Upper Cambrian, (*Cordylodus proavus* Biozone), Lava and Syas rivers, northwestern Russia; *a*, neotype, ventral valve exterior, CNIGR180/12348, ×3; *b*, ventral valve interior, CNIGR182/12348, ×11; *c*, dorsal valve interior, CNIGR12348, ×10; *d*, surface microornament, ×500; *e,* detail of pitted microornament, GLAHM 101691, ×800 (Popov, Holmer, & Miller, 2002).

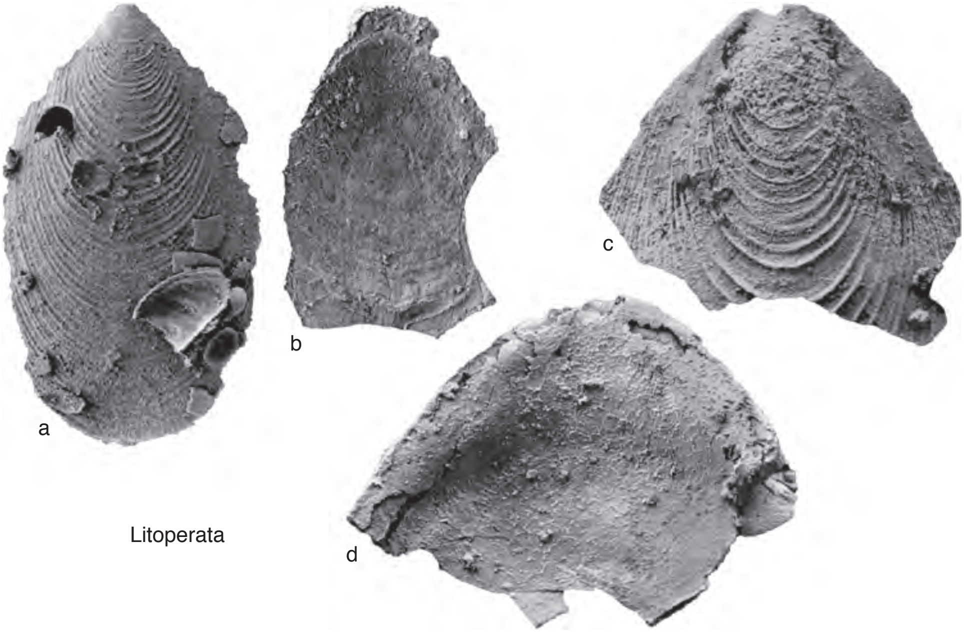


FIG. 1682. Obolidae (p. 2546–2547).

Family PATERULIDAE Cooper, 1956

Diencobolus HOLMER & others, 2001, p. 65 [**D. simplex*; OD]. Shell weakly biconvex, equivalved, elongate oval to subcircular; both valves with holoperipheral growth and eccentric to submarginal umbo; both valves lacking pseudointerareas and pedicle notch; larval and postlarval shell finely pitted with subcircular to subelliptical pits of varying sizes; ventral valve with weakly impressed visceral area, occupying median part of valve posterior to midlength; dorsal interior with a low median ridge widening anteriorly and bearing small, elongate suboval anterior lateral muscle scars at posterior end; central muscle scars large, suboval, at midvalve, lateral to median ridge. *Middle Cambrian–Lower Ordovician (Tremadoc–early Arenig)*: Kazakhstan (Malyi Karatau), Kyrgyzstan, Poland.——FIG. 1684,*2a–h*. **D. simplex*, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kyrshabakty, Kazakhstan; *a*, holotype, dorsal valve interior, IGNA427/87, ×13; *b–c*, dorsal valve exterior, oblique lateral view, ×43; *d,* detail of larval shell, ×140; *e,* microornament of larval shell, ×650; *f,* microornament of postlarval shell, NMW98.61G.55, ×1088; *g*, ventral valve interior, IGNA427/729, ×23; *h*, dorsal valve interior, IGNA427/730, ×32 (Holmer & others, 2001).

Eopaterula SUTTON in SUTTON, BASSETT, & CHERNS, 2000, p. 73 [**E. curtisi*; OD]. Shell subcircular to elongate suboval; ventral valve acuminate; true pseudointerareas lacking in both valves, but with thickened posterior margins, not differentiated from limbus; ventral thickened posterior margin, with narrow, subtriangular pedicle depression; dorsal thickened margin, with wide subtriangular to semicircular median depression. *Ordovician (Tremadoc):* England.——FIG. 1685*a–f.* **E. curtisi*, Micklewood Formation, Tortworth Inlier, Gloucestershire; *a*, holotype, internal mold of ventral valve, latex cast, CMBCc1679, ×15; *b*, internal mold of ventral valve, CMBCc1632a, ×15; *c*, exfoliated ventral valve, CMBCc1631b, ×10; *d*, exfoliated possible ventral valve, CMBCc1678a, ×15; *e*, internal mold of dorsal valve, CMBCc1661a, ×15; *f,* internal mold of dorsal valve, latex cast, CMBCc1654a, ×15 (Sutton, Bassett, & Cherns, 2000).

Tarphyteina SUTTON in SUTTON, BASSETT, & CHERNS, 2000, p. 74 [**T. taylorae*; OD]. Shell elongate suboval; true pseudointerareas lacking in both valves, but with thickened posterior margins; ventral thickened posterior margin elongate; dorsal thickened margin short, undivided. *Ordovician (Llandeilo):* Wales.——FIG. 1684,*1a–e*. **T. taylorae*, Golden Grove Group, upper Llandeilo, near Llandeilo, Carmarthenshire; *a*, holotype, ventral valve interior, NMW96.8G.109, ×40; *b*, ventral valve exterior, NMW96.8G.160, ×40; *c–d*, dorsal valve exterior, interior, NMW96.8G.108, ×40; *e*, detail of ornamentation, NMW96.8G.461, ×500 (Sutton, Bassett, & Cherns, 2000).

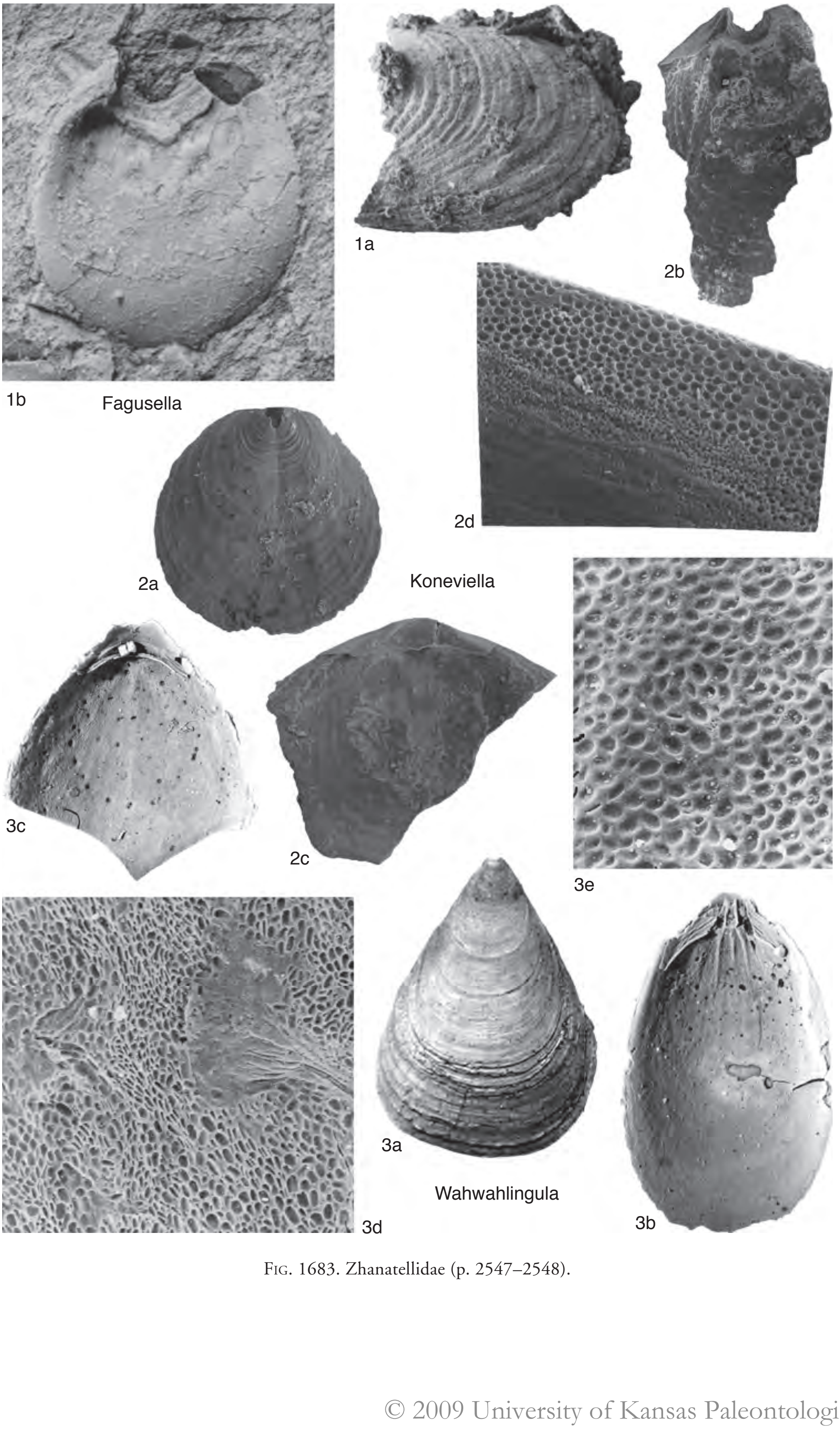


Fig. 1683. Zhanatellidae (p. 2547–2548).

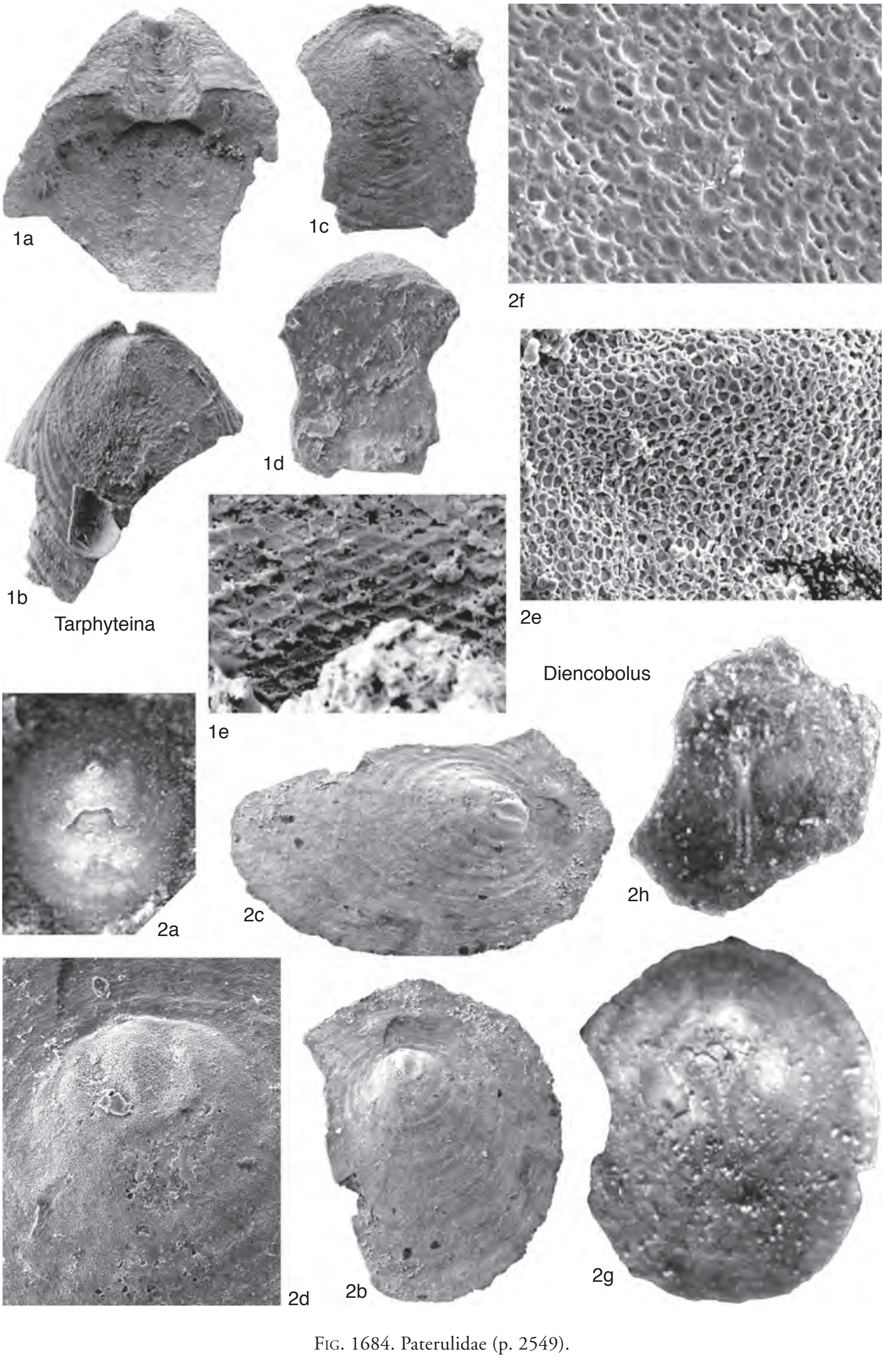


FIG. 1684. Paterulidae (p. 2549).

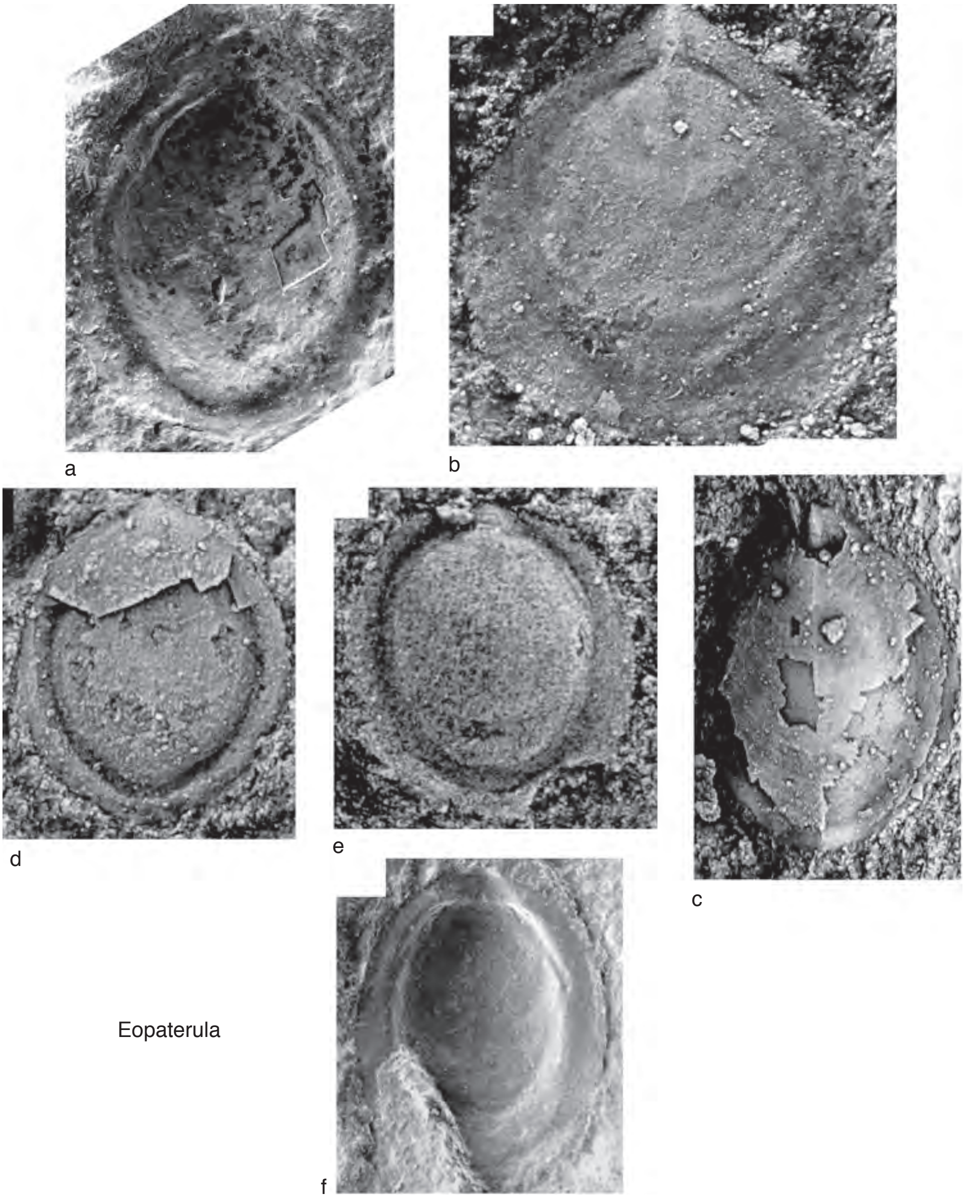


FIG. 1685. Paterulidae (p. 2549).

Superfamily DISCINOIDEA Gray, 1840

Family DISCINIDAE Gray, 1840

[incl. Ivanothelinae MERGL, 2001a, p. 25]

Chynithele HAVLÍČEK in HAVLÍČEK & VANĚK, 1996, pl. 101, case VIII, fig. 1 [**C. ventricona*; OD]. Ventral valve highly conical; dorsal valve flat; ornamentation with prominent rounded rugellae; external pedicle opening close to apex; listrium broad and short; muscle scars and mantle canals weakly impressed. *Lower Devonian (Emsian):* Bohemia.——FIG. 1686,*1a–e*. **C. ventricona*, Zlichov Formation, Chýnice Limestone, Bubovice, Čeřinka, Koněprusy, Zlatý Kůň, Voskop; *a*, ventral valve exterior, MBHR67654, ×10; *b*, internal mold of ventral valve, PCZCU516, ×10; *c*, ventral valve

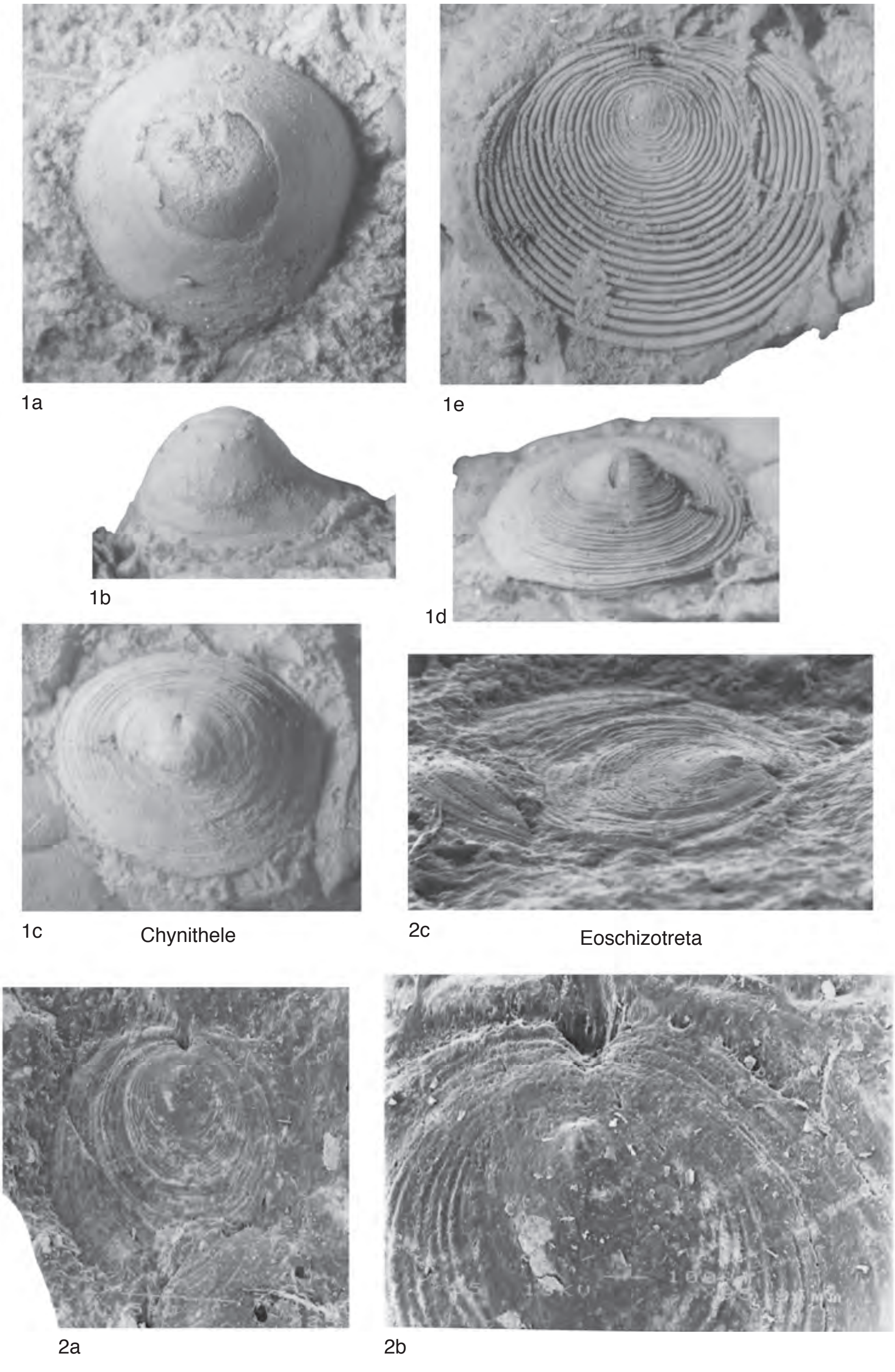


FIG. 1686. Discinidae (p. 2552–2555).

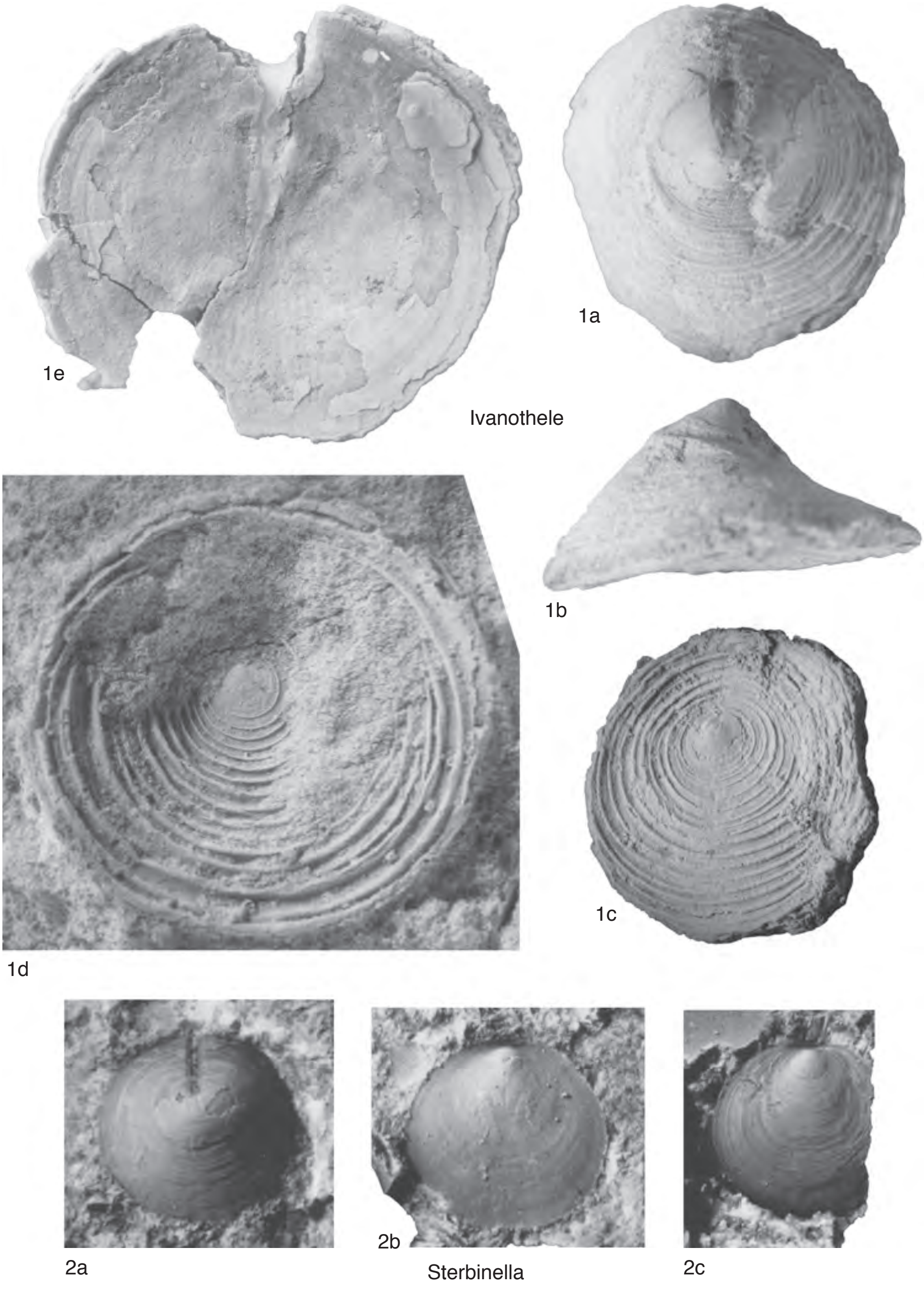


FIG. 1687. Discinidae (p. 2555–2556).

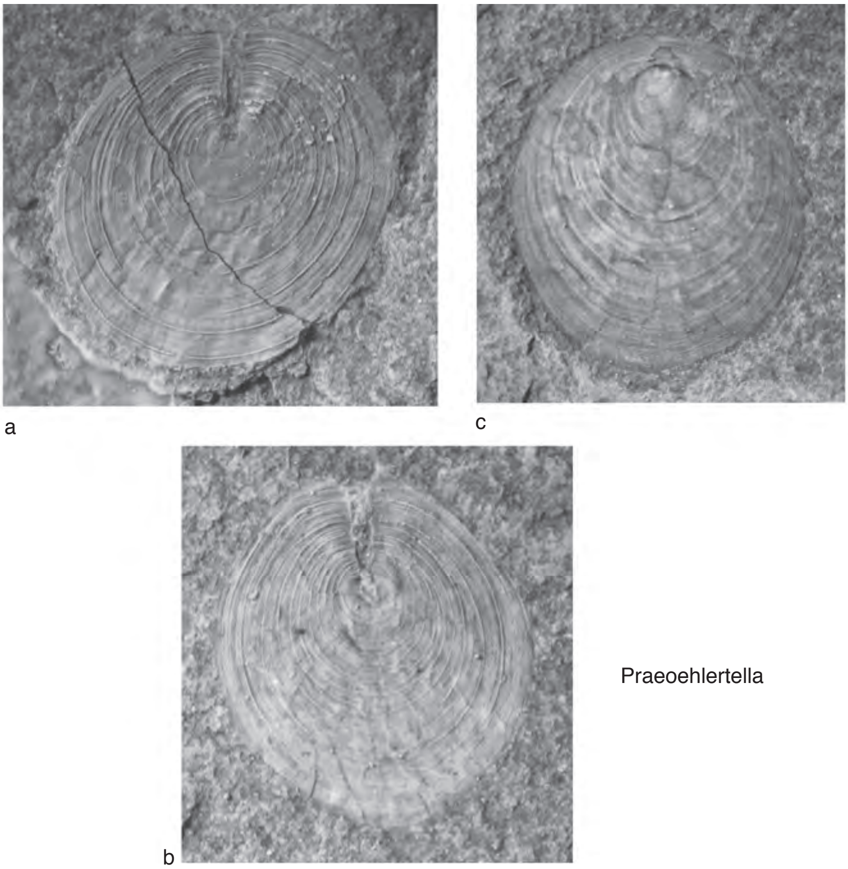


FIG. 1688. Discinidae (p. 2555–2556).

exterior, PCZCU518, ×10; *d*, oblique posterior view of ventral valve exterior, PCZCU518, ×10; *e*, dorsal valve exterior, PCZCU515, ×10 (new). [Michal Mergl]

Eoschizotreta MERGL, 2002, p. 46 [**E. veterna*; OD]. Shell with holoperipheral growth, weakly biconvex; pedicle notch short, broad, without distinct listrium; dorsal apex in posterior part of shell; ornament of fine concentric rugellae. *Ordovician (Arenig):* Bohemia.——FIG. 1686,*2a–c*. **E. veterna*, Klabava Formation, Hrádek; *a*, holotype, ventral valve exterior, latex cast, ×17; *b*, detail of umbo and pedicle notch, ×60; *c*, oblique lateral view, PCZCU629, ×23 (new). [Michal Mergl]

Ivanothele MERGL, 1996b, p. 123 [**I. mordor*, OD]. Shell planoconvex to concavoconvex, subcircular; exterior with coarse rugellae on both valves; ventral valve high, asymmetrically conical, with curved beak; pedicle track short, wide, mainly closed by listrium; internal tube thick walled, long and irregularly curved; dorsal valve with subcentral beak; dorsal visceral area large, at center of valve, with large anterior adductor muscle scars. *Silurian (Wenlock–Ludlow):* Bohemia.——FIG. 1687,*1a–e*. **I. mordor*, Kopanina Formation, Ludlow; *a–b*, holotype, ventral valve exterior, lateral view, ×5; *c*, dorsal valve exterior, MBHR19627, ×4; *d*, dorsal valve exterior, MM14a, ×5; *e*, dorsal valve interior, MM6a, ×5 (new). [Michal Mergl]

Praeoehlertella MERGL, 2001a, p. 28 [**P. umbrosa*; OD]. Shell elongate oval to subcircular, convexoplanar; ornamentation of fine, concentric, regularly spaced fila, passing into coarser, concentric rugellae; ventral valve with narrow pedicle track bordered

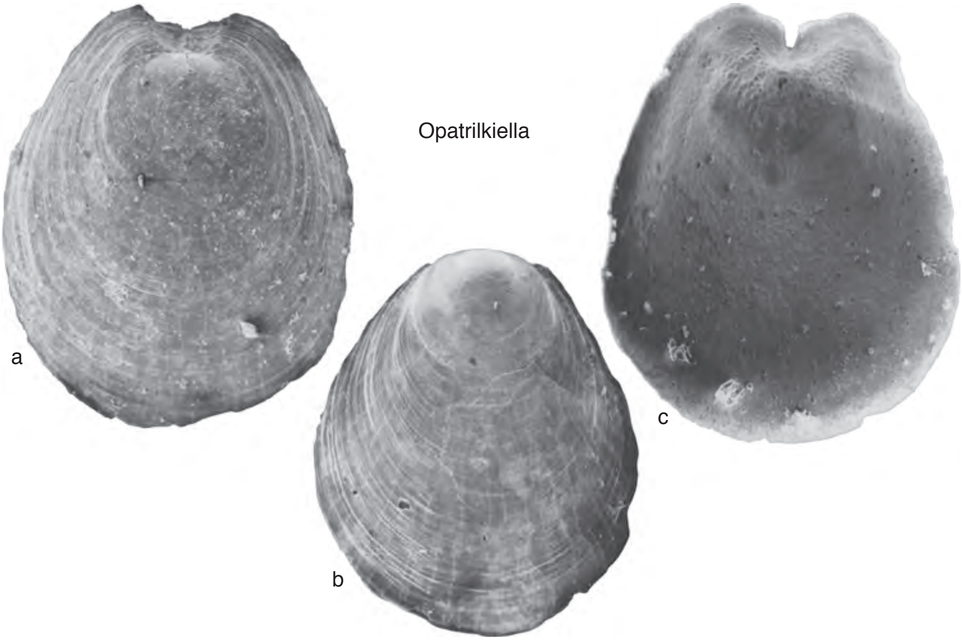


FIG. 1689. Trematidae (p. 2556).

by narrow bands; dorsal valve with submarginal apex. *Silurian (Llandovery)–Devonian (Pragian):* Bohemia.——FIG. 1688*a–c*. **P. umbrosa*, Praha Formation, Dvorce-Prokop Limestone, Pragian, Svatý Jan pod Skalou, Na stydlých vodách Quarry; *a*, holotype, ventral valve exterior, MBHR49779, ×9.5; *b*, ventral valve exterior, MBHR49775, ×9.5; *c*, dorsal valve exterior, MBHR49799, ×9.5 (new). [Michal Mergl]

Sterbinella MERGL, 2001a, p. 27 [**S. daphne*; OD]. Shell circular; ornamentation of fine concentric, slightly wavy fila; ventral valve depressed conical; dorsal valve flat with submarginal apex; pedicle track narrow, parallel sided, with narrow parallel slit. *Silurian (Přídoli)–Devonian (Famennian):* Bohemia, Poland.——FIG. 1687,*2a–c*. **S. daphne,* Požáry Formation, Přídoli, Králův Dvůr, Kosov Hill, Bohemia; *a*, ventral valve exterior, PCZCU525, ×13; *b*, dorsal valve exterior, PCZCU519, ×13; *c*, dorsal valve exterior, PCZCU522, ×13 (new). [Michal Mergl]

Family TREMATIDAE Schuchert, 1893

Opatrilkiella MERGL, 2001a, p. 29 [**O. minuta*; OD]. Shell elongate oval, equibiconvex; pitted postlarval microornamentation with wavy radial trails of minute pits superimposed on very finely pitted surface; ventral valve with submarginal apex; ventral pseudointerarea triangular, with narrow pedicle slit and broad propareas; dorsal valve with submarginal apex; dorsal pseudointerarea absent. *Silurian (Přídoli)–Devonian (Famennian):* Bohemia, Poland.——FIG. 1689*a–c*. **O. minuta*, Požáry Formation, Přídoli, Praha-Holyně, Opatřilka Quarry, Bohemia; *a*, ventral valve exterior, PCZCU472, ×55; *b*, holotype, ventral valve interior, PCZCU130, ×50; *c*, dorsal valve exterior, PCZCU124, ×60 (new). [Michal Mergl]

Family UNCERTAIN

Pyrodiscus LITTLE & others, 1999, p. 1056 [**P. lorrainae*; OD]. Genus poorly known; possible discinoid with suboval, uniplicate shell; both valves with mixoperipheral growth; narrow oval pedicle opening extending to posterior margin; listrium present. *?Silurian:* Russia (Orenburg district).

Superfamily ACROTHELOIDEA Walcott & Schuchert in Walcott, 1908

Family BOTSFORDIIDAE Schindewolf, 1955

Curdus HOLMER & USHATINSKAYA in USHATINSKAYA & HOLMER, 2001, p. 129 [**C. pararaensis*; OD].

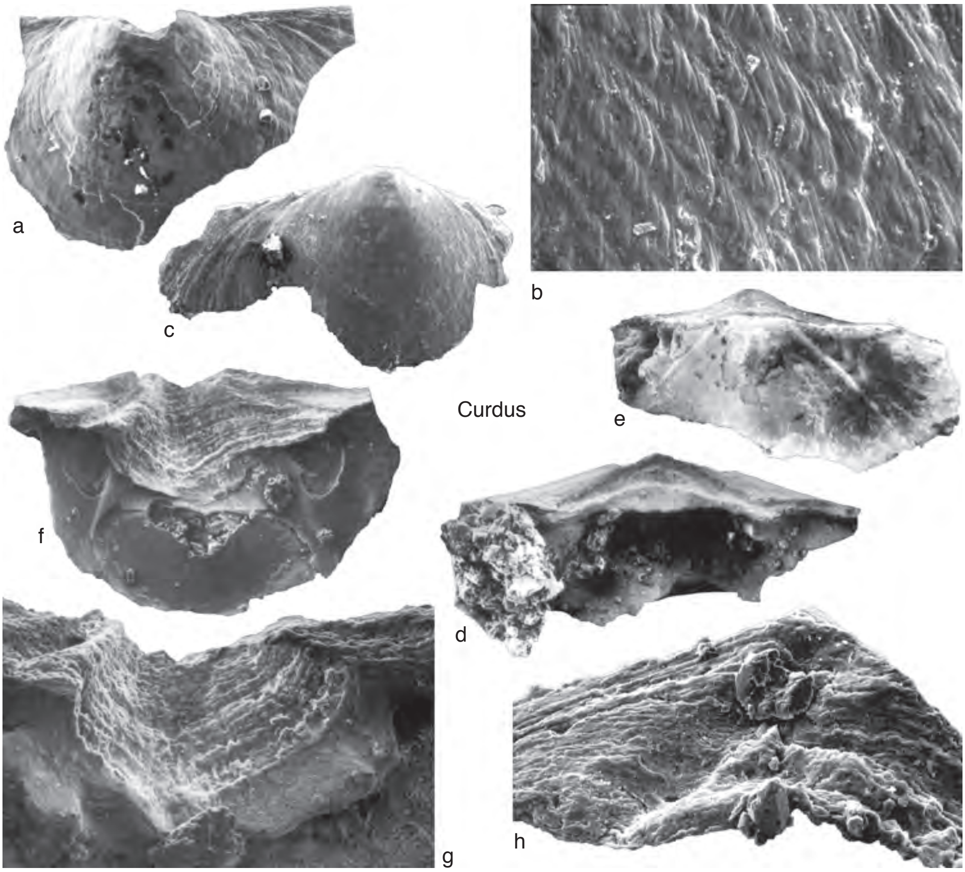


Fig. 1690. Botsfordiidae (p. 2556–2557).

Ventral valve with small umbonal notch; ventral pseudointerarea triangular, apsacline, divided by deep pedicle groove, forming triangular delthyrium; propareas long, with flexure lines; dorsal pseudointerarea anacline, with wide median groove; ornamentation of concentric growth lines, crossed by discontinuous wrinkles; ventral visceral field short, strongly thickened, with elevated posterolateral muscle scars; dorsal visceral field with low median ridge and pair of elongate posterolateral muscle scars; both valves with straight divergent *vascula lateralia*. *Lower Cambrian (Botomian):* South Australia.——Fig. 1690*a–h*. **C. pararaensis*, Koolywurtie Limestone, Yorke Peninsula; *a*, ventral valve exterior, ×24; *b*, detail of ornamentation, PIN4664/6207, ×160; *c*, dorsal valve exterior, PIN4664/6209, ×26; *d*, dorsal valve interior, PIN4664/6212, ×20; *e*, dorsal valve interior, PIN4664/6210, ×16; *f*, holotype, ventral valve interior, PIN4664/6211, ×24; *g*, detail of ventral pseudointerarea, PIN4664/6220, ×48; *h*, detail of dorsal pseudointerarea, PIN4664/6217, ×104 (Ushatinskaya & Holmer, 2001).

Minlatonia Holmer & Ushatinskaya in Ushatinskaya & Holmer, 2001, p. 130 [**M. tuckeri*; OD]. Ventral valve with pointed beak; ventral pseudointerarea apsacline, with triangular pedicle groove and long propareas; dorsal pseudointerarea anacline, flattened, with wide triangular median groove and low propareas; distinctive reticulate ornamentation, produced by intersecting radial and concentric striae; ventral visceral field thickened; dorsal visceral field slightly thickened, with long anterior projection, bisected by median ridge. *Lower*

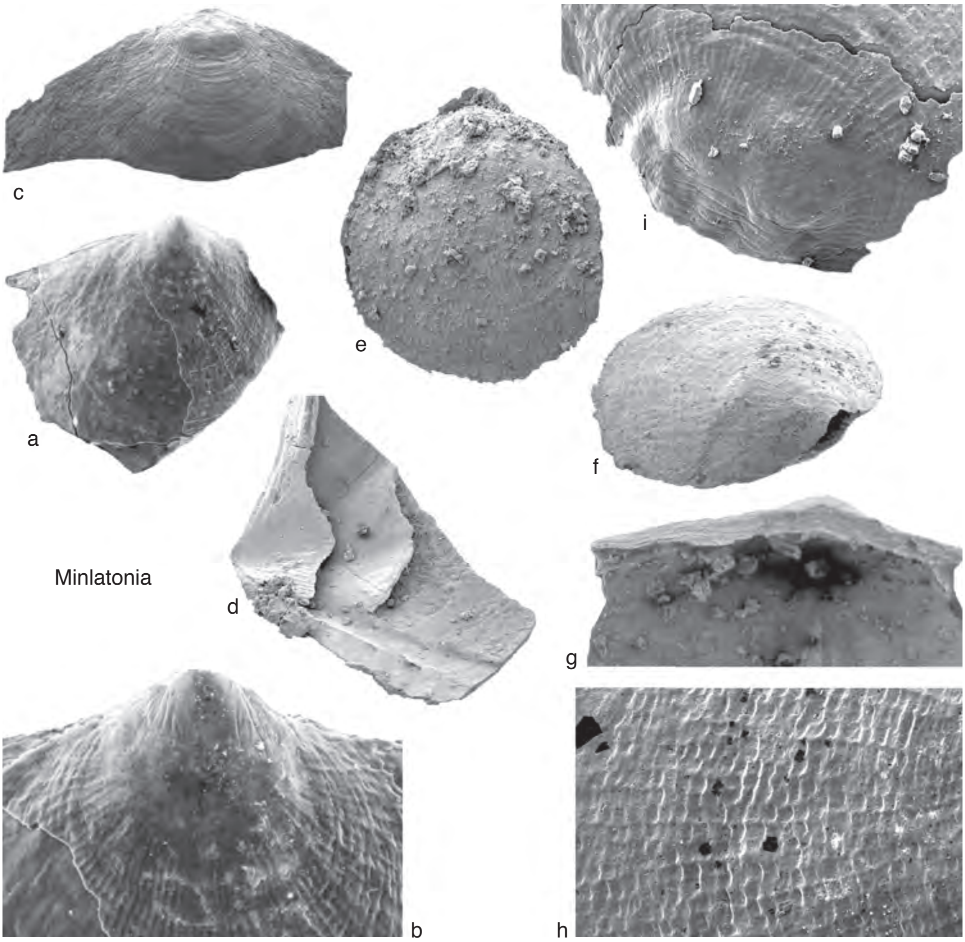


FIG. 1691. Botsfordiidae (p. 2557–2559).

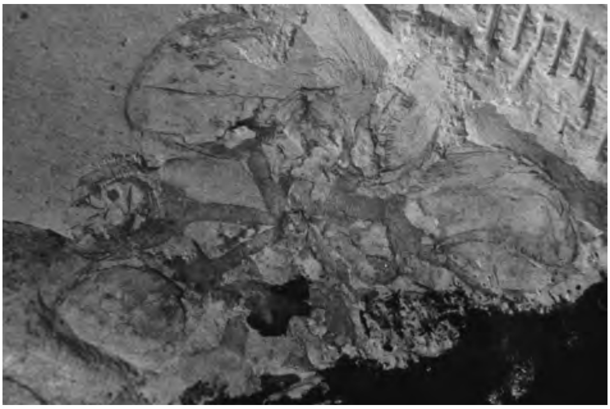


FIG. 1692. Uncertain (p. 2559).

Cambrian (Botomian): South Australia.——FIG. 1691*a–i*. **M. tuckeri*, Parara Limestone, Yorke Peninsula; *a*, ventral valve exterior, ×32; *b*, detail of umbo, PIN4664/6233, ×108; *c*, dorsal valve exterior, PIN4664/6221, ×32; *d*, oblique lateral view of ventral valve interior, PIN4664/6227, ×22; *e*, dorsal view of complete articulated shell, PIN4664/6230, ×30; *f*, oblique posterolateral view of complete articulated shell, PIN4664/6232, ×24; *g*, detail of dorsal pseudointerarea, PIN4664/6226, ×40; *h*, detail of reticulate ornamentation, PIN4664/6228, ×112; *i*, detail of dorsal umbo, PIN4664/6225, ×94 (Ushatinskaya & Holmer, 2001).

Superfamily and Family UNCERTAIN

Longtancunella HOU & others, 1999, p. 80 [**L. chengjiangensis*; OD]. Genus poorly known; thin, lingulid-like shell, slightly convex, subcircular; mostly occurring in clusters, individuals apparently joined by pedicles; internal characters unknown. *Lower Cambrian:* China (Yunnan Province).——FIG. 1692. **L. chengjiangensis*, Yu'anshan Formation, Qiongzhusian Stage; holotype, cluster of specimens with preserved pedicles, part, NIGPA1145a, ×2 (Hou & others, 2004).

ACROTRETIDA

LARS E. HOLMER and LEONID E. POPOV

[University of Uppsala; and National Museum of Wales]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

Order ACROTRETIDA Kuhn, 1949

The cladistic analyses by HOLMER and POPOV (1996, 2000) gave support for identifying the Acrotretida, and the Acrotretoidea, as a potential monophyletic group defined by numerous derived characters, including a columnar shell structure, a simplified linguliform muscle system, and development of an apical process; however, the interrelationships within the superfamily could not be resolved completely in any satisfactory way. It seems that the family Acrotretidae is a paraphyletic grouping, from which the other and potentially monophyletic families were derived (HOLMER & POPOV, 2000). This was also indicated in the cladistic analysis by STRENG (1999). The columnar shell structure of the acrotretoids has generally been assumed to be a derived unique feature within this group (HOLMER, 1989; WILLIAMS & HOLMER, 1992); however, as mentioned above (WILLIAMS & CUSACK, p. 2451, herein), this is now known to be a more widely distributed character that may prove to be a plesiomorphy (HOLMER, SKOVSTED, & WILLIAMS, 2002; SKOVSTED & HOLMER, 2003).

Superfamily ACROTRETOIDEA Schuchert, 1893

Family ACROTRETIDAE Schuchert, 1893

[incl. Neotretinae ROBSON, NOWLAN, & PRATT, 2003, p. 206]

Eohadrotreta LI & HOLMER, 2004, p. 204 [**E. zhenbaensis*; OD]. Shell subcircular to transversely oval, with rounded to straight posterior margin; ventral valve low conical to gently convex; ventral pseudointerarea gently procline, with shallow to vestigial intertrough; pedicle foramen not enclosed within larval shell, remaining as open notch through much of ontogeny; apical process and apical pits vestigial to absent; dorsal valve gently convex; dorsal pseudointerarea narrowly triangular, orthocline, with median groove; dorsal median buttress well developed; dorsal median septum well developed, extending anterior to midvalve. *Lower Cambrian:* China (Shaanxi Province).——FIG. 1693*a–h*. **E. zhenbaensis*, lower Shuijingtuo Formation, Qiongzhusian Stage, Xiaoyang section, Zhenba, South Shaanxi; *a*, dorsal valve exterior, NIGP135167, ×47; *b*, dorsal valve interior, ×50; *c*, oblique lateral view, NIGP135170, ×80; *d–e*, holotype, ventral valve exterior, oblique posterior view, NIGP135165, ×40; *f*, oblique posterior view of dorsal valve exterior, NIGP135176, ×93; *g*, posterior view of complete articulated juvenile shell, NIGP135175, ×100; *h*, oblique anterior view of ventral valve interior, ×80 (new).——FIG. 1694*a–c*. **E. zhenbaensis*, lower Shuijingtuo Formation, Qiongzhusian Stage, Xiaoyang section, Zhenba, South Shaanxi; *a*, oblique posterior view of unrestricted delthyrium, NIGP135174, ×400; *b*, ventral valve interior, NIGP135173, ×60; *c*, detail of larval shell and pedicle foramen, NIGP135166, ×200 (new).

Kostjubella POPOV, HOLMER, & GORJANSKY, 1996, p. 306 [**K. relaxata*, OD]. Shell ventribiconvex; ventral valve strongly convex in lateral profile with maximum height anterior to umbo; ventral pseudointerarea narrow, divided by deep intertrough; pedicle foramen small, elongate suboval, not enclosed within larval shell; dorsal valve gently convex with shallow sulcus; dorsal pseudointerarea low, with lenslike median groove; ventral interior with bosslike apical process, anterior to short internal pedicle tube; ventral mantle canals baculate; dorsal median ridge strong, subtriangular, buttressed posteriorly. *Middle Cambrian (Mayaian):* Kazakhstan (Tarbagatay Range).——FIG. 1695,*1a–f*. **K. relaxata*, Kostyube Mountain; *a*, ventral valve exterior, PMKz63, ×26; *b,* oblique lateral view, ×34; *c,* oblique posterior view, ×40; *d*, holotype, dorsal valve, interior, PMKz61, ×46.5; *e,* oblique lateral view, ×52.2; *f*, ventral valve interior, PMKz64, ×45 (Popov, Holmer, & Gorjansky, 1996).

Mixotreta USHATINSKAYA, 1998, p. 39 [**M. quasidentata*; OD]. Shell ventribiconvex; subcircular; ventral valve subconical; pseudointerarea procline to catacline, divided by narrow and shallow intertrough;

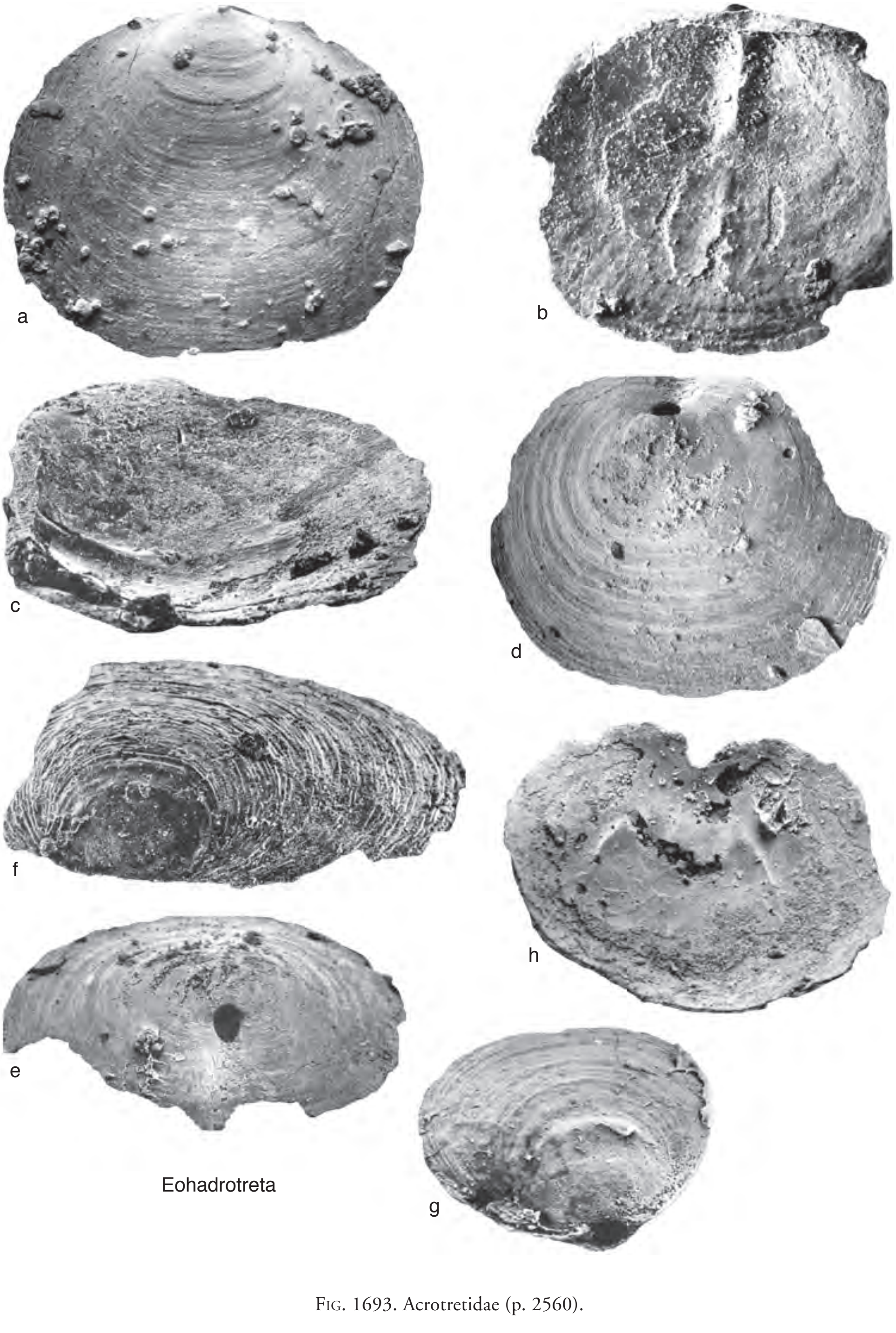


FIG. 1693. Acrotretidae (p. 2560).

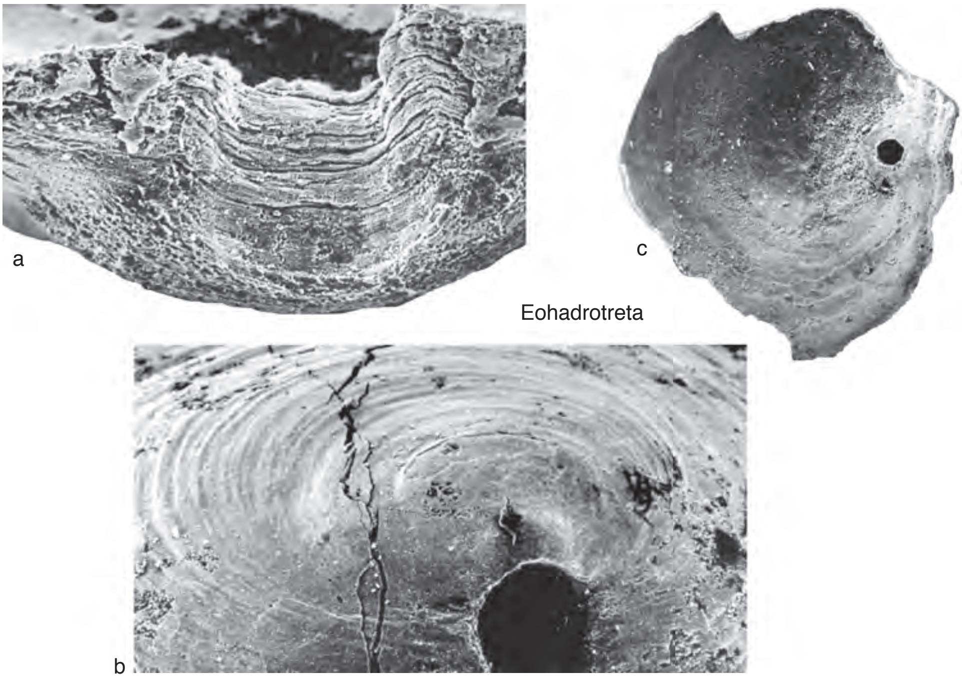


FIG. 1694. Acrotretidae (p. 2560).

pedicle foramen small, circular, within larval shell, at end of short recurved external tube; dorsal valve gently convex; pseudointerarea orthocline; median groove bisected by low ridge and bounded anteriorly by pair of toothlike projections; dorsal larval shell with median depression; apical process occluding umbonal part of valve and projecting anteriorly; internal pedicle tube perforating apical process, flanked by pair of apical pits; dorsal interior with large cardinal muscle fields separated by median buttress; central muscle scars well developed near midvalve; dorsal median ridge weakly developed or absent. *Middle Cambrian (Mayaian):* Russia (Siberia).——FIG. 1696,*1a–d*. **M. quasidentata*, *Corynexochus perforatus–Anopolenus henrici* biozones, Olenek river near mouth of Khorbusonka river, north-central Siberia; *a*, holotype, posterior view of conjoined valves, PIN 4290/301, ×50; *b*, ventral valve interior, PIN 4290/309, ×50; *c*, dorsal valve interior, ×30; *d,* pseudointerarea, PIN 4290/305, ×220 (Ushatinskaya, 1998).

Odontotreta USHATINSKAYA, 1998, p. 40 [**O. mirabilis*; OD; =*Stilpnotreta galinae* POPOV, HOLMER, & GORJANSKY, 1996, p. 310]. Shell ventribiconvex; ventral valve strongly convex to subconical; pseudointerarea apsacline, divided by intertrough, terminating with pair of toothlike projections; pedicle foramen within larval shell; dorsal valve convex; pseudointerarea subtriangular, orthocline, mainly occupied by median grove, which is divided medianly by strong ridge; ventral interior with elongate subtriangular apical process anterior to internal foramen; ventral mantle canals baculate; dorsal cardinal muscle large, fields extending anteriorly to midlength; median ridge low. *Middle Cambrian (Mayaian)*: Kazakhstan, Sweden, Denmark (Bornholm).——FIG. 1697,*1a–d*. **O. galinae* (POPOV, HOLMER, & GORJANSKY), Chingiz Formation, Chingiz Range, Central Kazakhstan; *a*, holotype, oblique posterior view of complete shell, PIN4672/1, ×65; *b*, oblique posterolateral view of ventral valve exterior, ×40; *c*, detail of ventral pseudointerarea with toothlike projections, PIN4672/2, ×130; *d*, dorsal valve interior, PIN4672/7, ×50 (Ushatinskaya, 1998).

Ombergia HOLMER, POPOV, & BASSETT, 2000, p. 374 [**O. mirabilis*; OD]. Shell subcircular; ventral valve highly conical with extremely long external pedicle tube; ventral pseudointerarea catacline to slightly procline, divided by weak intertrough; dorsal valve weakly convex, with subtriangular pseudointerarea, occupying about half of valve width, divided by broad median groove; ventral interior with thick apical process occluding umbo, buttressed dorsoanteriorly by septum; dorsal interior with thick, low, subtriangular median septum slightly buttressed posteriorly; dorsal cardinal muscle scars large, raised, extending anteriorly about half valve length. *Ordovician (upper Tremadoc–lower Arenig):* Baltoscandia, South Kyrgyzstan.——FIG. 1698*a–g*. **O. mirabilis*, Latorp Limestone, Hunneberg Regional Stage, Sweden; *a*, dorsal valve exterior,

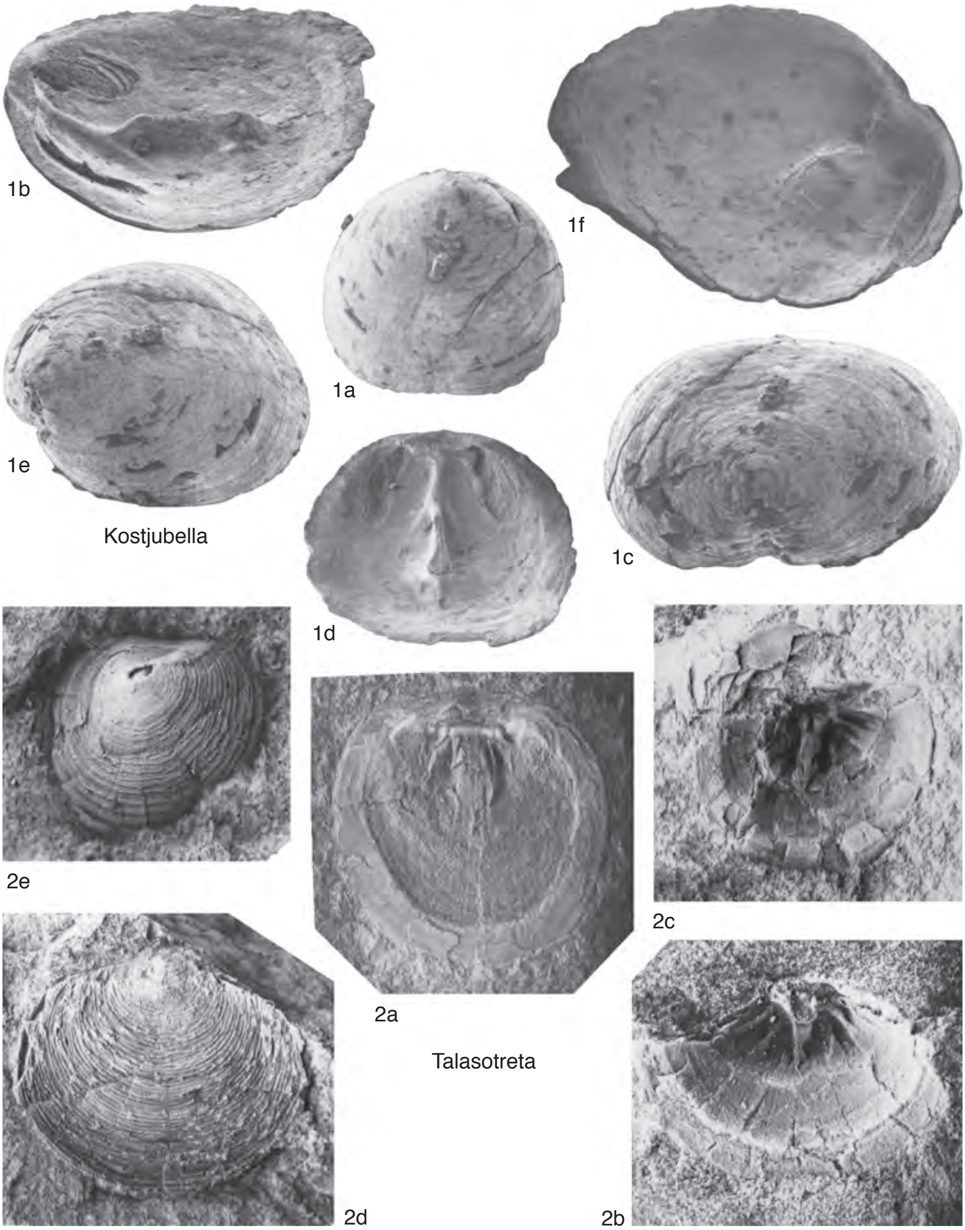


Fig. 1695. Acrotretidae (p. 2560–2566).

×32; *b*, detail of larval shell, ×110; *c*, detail of postlarval ornamentation, SGUType8511, ×235; *d*, dorsal valve interior, SGUType8512, ×40; *e*, holotype, ventral valve exterior, SGUType8508, ×25; *f*, oblique lateral view of ventral valve exterior, showing apical process buttressed by septum, SGUType8509, ×65; *g*, ventral valve interior, SGUType8510, ×75 (Holmer, Popov, & Bassett, 2000).

Talasotreta Holmer, Koneva, & Popov in Holmer & others, 1996, p. 484 [**T. apollonovi*; OD]. Shell ventribiconvex, ornamented by regularly spaced concentric rugellae, ventral valve broadly conical with procline to catacline pseudointerarea divided by intertrough; pedicle foramen enclosed within larval shell; dorsal valve gently convex with moderately high pseudointerarea divided by shallow broad subtriangular median grove;

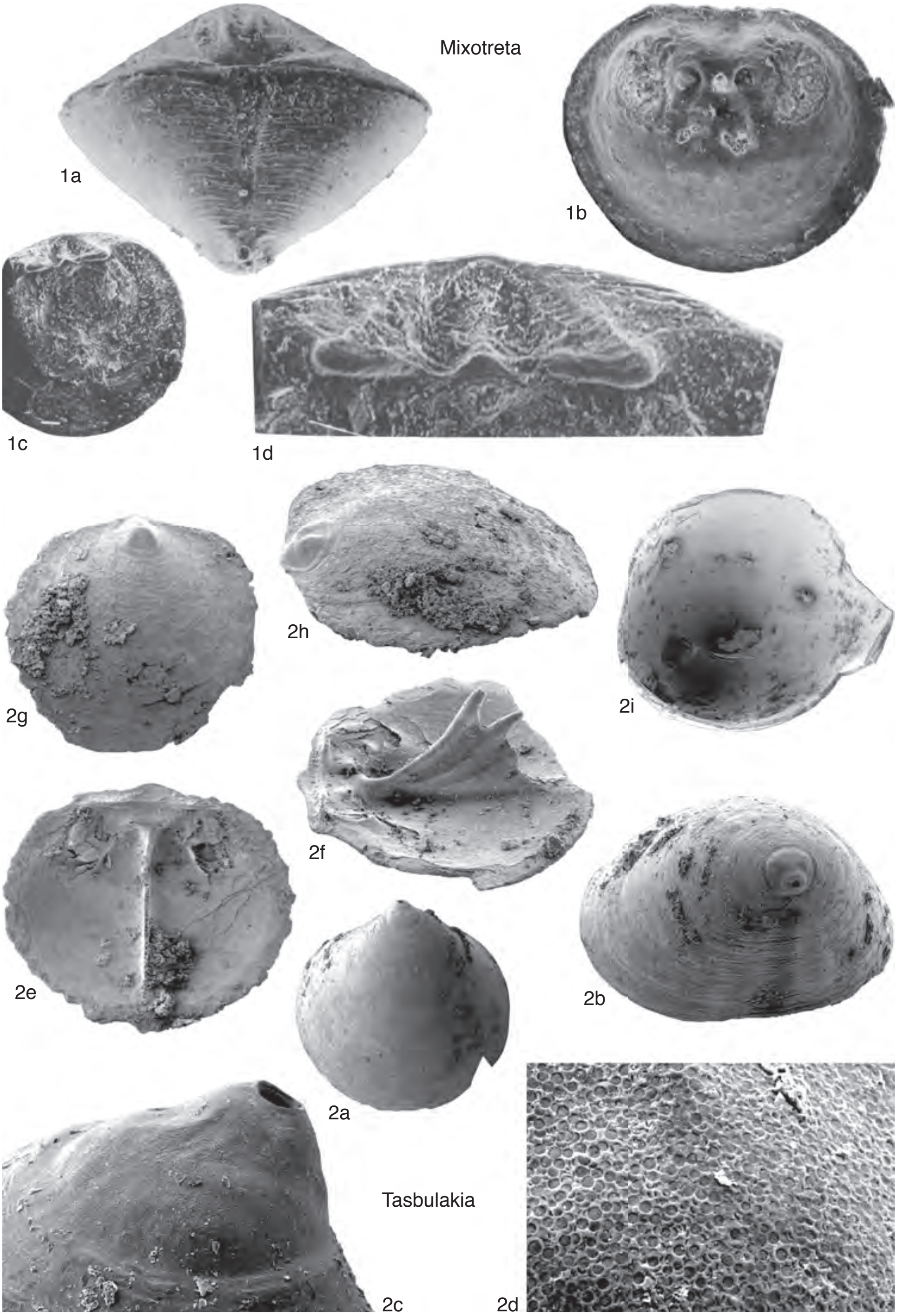


FIG. 1696. Acrotretidae (p. 2560–2566).

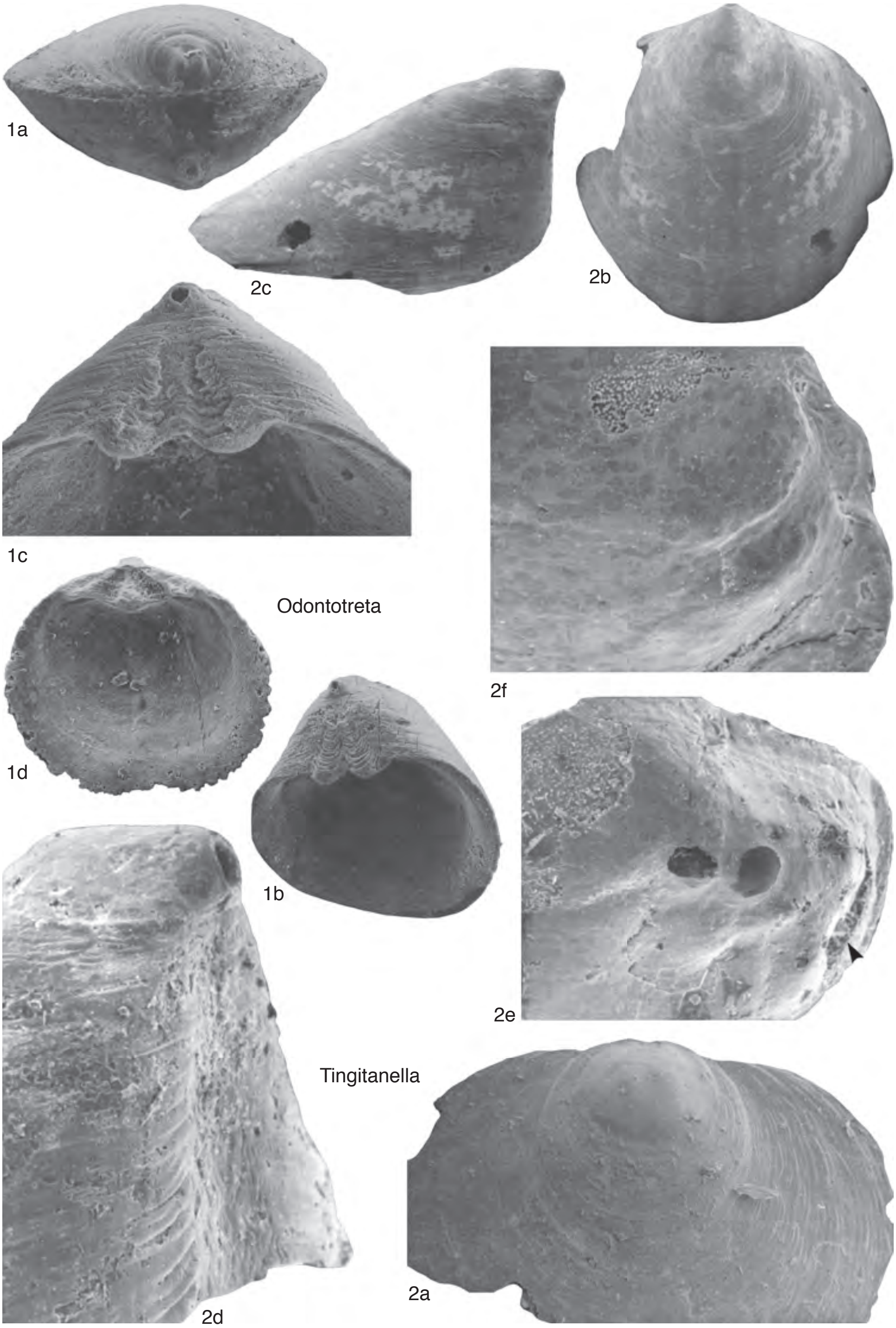


FIG. 1697. Acrotretidae (p. 2562–2566).

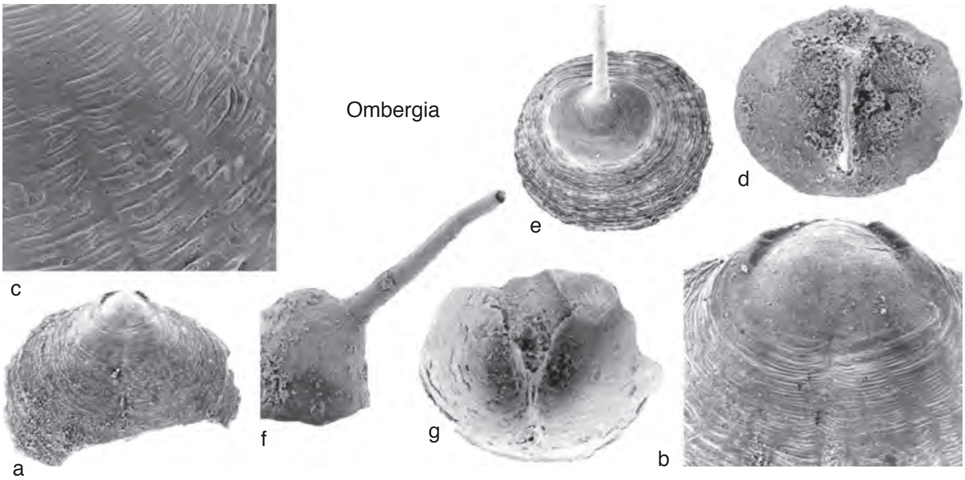


FIG. 1698. Acrotretidae (p. 2562–2563).

ventral interior with ridgelike apical process anterior to internal foramen, or occluding umbonal area in some species, ventral mantle canals pinnate; dorsal interior with low median ridge buttressed posteriorly. *Ordovician (upper Arenig–Llanvirn): Llanvirn,* Sweden, USA; *upper Arenig–Llanvirn,* Kazakhstan.——FIG. 1695,*2a–e.* **T. apollonovi*, Zyrykauz Formation, Llanvirn, Malyi Karatau Range; *a*, dorsal valve interior, IGCA 2943/28, ×4.5; *b*, ventral valve interior, IGCA 2943/31, ×5; *c*, ventral valve interior, IGCA 2943/32, ×5; *d*, dorsal valve exterior, IGCA 2943/33, ×5; *e*, ventral valve exterior, latex cast, IGCA, 2943/36, ×5 (Holmer & others, 1996).

Tasbulakia POPOV, 2000b, p. 425 [**T. tenuis*; OD]. Shell subcircular; ventral valve high, slightly apsaconical; ventral pseudointerarea poorly defined, divided by weak intertrough; pedicle foramen circular, facing posteriorly, within larval shell; dorsal pseudointerarea narrow, divided by deep median grove; internal pedicle tube supported anteriorly by ridgelike apical process; dorsal median septum high, triangular, bearing up to five septal rods, projecting anteriorly as long spines; dorsal cardinal muscle fields small, situated on raised platforms. *Upper Ordovician (lower Ashgill):* Kazakhstan.——FIG. 1696,*2a–i.* **T. tenuis*, Zharyk Beds, Zharyk; *a*, holotype, ventral valve exterior, ×20; *b,* oblique posterolateral view, ×29; *c,* detail of larval shell, ×174; *d,* detail of larval pitting, NMW98.65G.82, ×940; *e*, dorsal valve interior, NMW98.65G.89, ×25; *f,* oblique lateral view of ventral valve interior, NMW98.65G.86, ×46; *g*, dorsal valve exterior, ×26; *h,* oblique lateral view, NMW98.65G.93, ×35; *i*, ventral valve interior, NMW98.65G.91, ×38 (Popov, 2000b).

Tingitanella STRENG, 1999, p. 48 [**T. calamisca*; OD]. Shell subcircular to pentagonal in outline; posterior margin straight to gently convex; ventral valve apsaconical to cataconical; ventral pseudointerarea well defined, bisected by poorly defined intertrough; pedicle foramen circular, enclosed within larval shell, forming short external tube; dorsal valve gently convex; dorsal pseudointerarea with orthocline median groove and anacline propareas; apical process poorly developed, low, triangular; median buttress present; median septum or ridge absent. *lower Middle Cambrian:* Morocco.——FIG. 1697,*2a–f.* **T. calamisca*, Jbel Wawrmast Formation, *Hupeolenus*?, *Cephalopyge notabilis–Ornamentaspis frequens* biozones, Anti-Atlas; *a*, dorsal valve exterior, PIW96X134.2, ×70; *b*, holotype, ventral valve exterior, ×40; *c,* holotype, oblique lateral view, ×50; *d,* holotype, detail of pseudointerarea, PIW96X30.12, ×160; *e*, oblique anterolateral view of ventral valve interior, PIW96X30.11, ×100; *f,* oblique lateral view of dorsal valve interior, PIW96X30.14, ×160 (Streng, 1999).

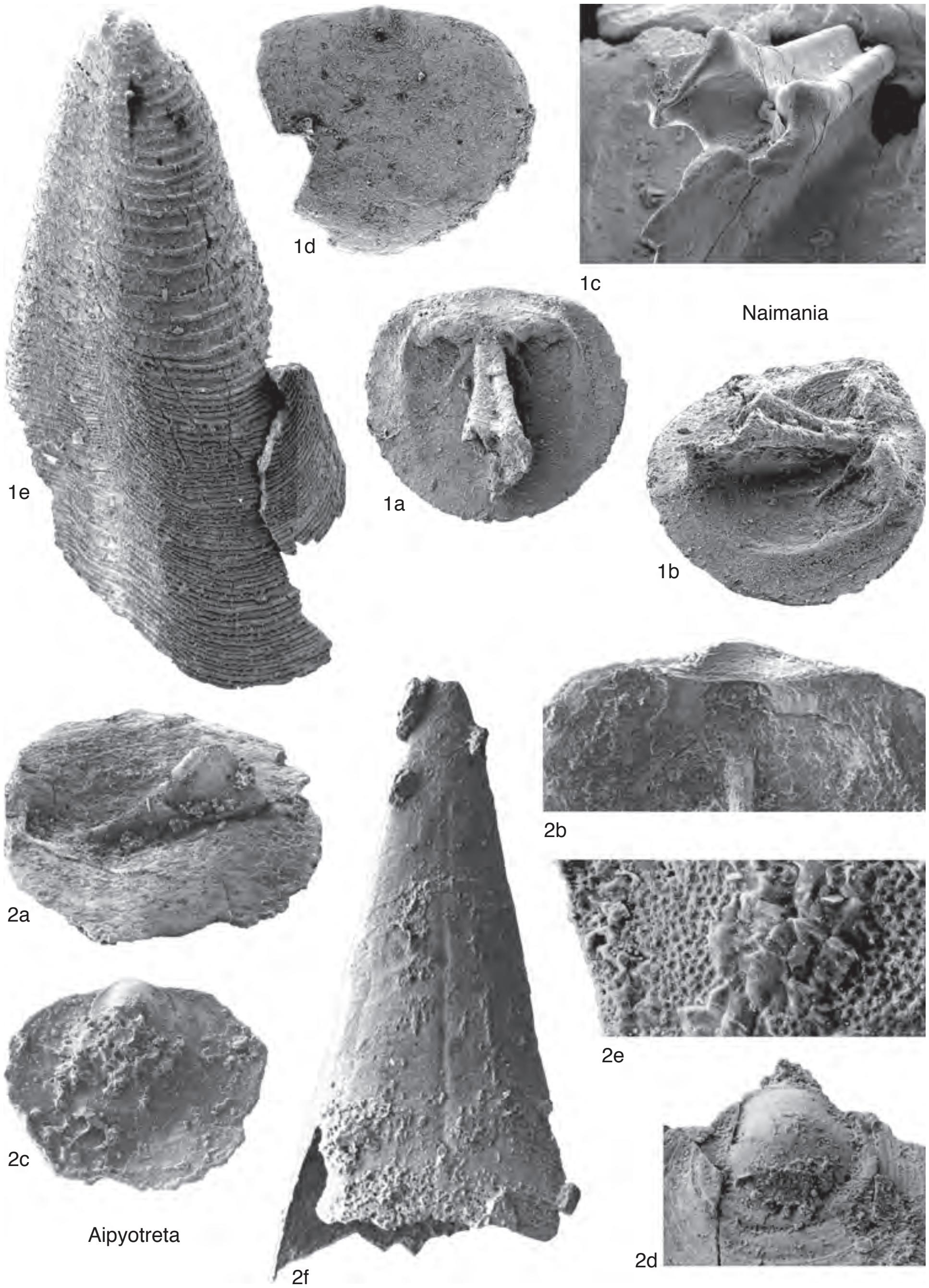


FIG. 1699. Torynelasmatidae and Ephippelasmatidae (p. 2568).

Family TORYNELASMATIDAE Cooper, 1956

Naimania Popov, 2000a, p. 271 [**Issedonia procera* Popov in Nazarov & Popov, 1980, p. 105; OD]. Shell subcircular in dorsal outline; ventral valve high, conical, nearly tubular; ventral pseudointerarea flat, catacline, with narrow intertrough; dorsal valve gently concave; dorsal pseudointerarea straight, anacline, divided by weak median groove; internal pedicle tube supported anteriorly by rudimentary ridgelike apical process; dorsal cardinal muscle scars large, strongly impressed; dorsal median septum high, triangular, with single rod and concave surmounting plate, bearing hemispherical cavity flanked by pair of rodlike processes. [No satisfactory illustrations of the holotype are available.] *Ordovician (upper Caradoc):* Kazakhstan.——Fig. 1699,*1a–e. A. concava*, Mayatas Formation, northern coast of Atansor lake; *a*, dorsal valve interior, ×28; *b,* oblique lateral view, NMW98.65.G.47, ×39; *c*, dorsal valve median septum and surmounting plate, NMW 98.65G.44, ×55; *d*, dorsal valve exterior, NMW98.65G.45, ×34; *e*, oblique posterolateral view of ventral valve exterior, NMW98.65G.43, ×67 (Popov, 2000a).

Family EPHIPPELASMATIDAE Rowell, 1965

Aipyotreta Sutton in Sutton, Bassett, & Cherns, 2000, p. 98 [**A. lockleyi*; OD]. Ventral valve highly conical; ventral pseudointerarea catacline to procline; ventral larval shell as conical as rest of valve; dorsal valve transversely oval; dorsal median septum consisting of simple vertical plate with surmounting rod. *Ordovician (Llandeilo):* Wales.——Fig. 1699,*2a–f.* **A. lockleyi*, Golden Grove Group, upper Llandeilo, Pen-yr-Allt, Carmarthenshire; *a*, holotype, oblique lateral view of dorsal interior, ×75; *b,* holotype, detail of dorsal pseudointerarea, ×100; *c,* holotype, dorsal valve exterior, NMW96.8G.775, ×50; *d*, detail of larval shell, NMW96.8G.770, ×100; *e*, detail of larval pitting, NMW96.8G.781, ×750; *f,* posterior view of ventral valve, NMW96.8G.766, ×50 (Sutton, Bassett, & Cherns, 2000).

Family BIERNATIDAE Holmer, 1989

Bathmoleca Sutton in Sutton, Bassett, & Cherns, 2000, p. 103 [**B. addisoni*; OD]. Ventral valve extremely conical, strongly apsacline; ventral larval shell less conical and apsacline; dorsal cardinal muscle scars on raised platform, undercut anteriorly; dorsal median septum with hollow surmounting rod on posterior slope of septum. *Ordovician (Llandeilo):* Wales.——Fig. 1700,*2a–f.* **B. addisoni*, Golden Grove Group, lower Llandeilo, near Llandeilo, Carmarthenshire; *a–b*, holotype, dorsal valve interior, oblique lateral view, NMW96.8G.181, ×60; *c–d*, dorsal valve exterior, interior, NMW96.8G.742, ×60; *e–f,* ventral valve lateral and top down views, NMW96.8G.203, ×60 (Sutton, Bassett, & Cherns, 2000).

Concaviseptum Brock, Engelbretsen, & Dean-Jones, 1995, p. 114 [**C. laurei*; OD]. Ventral interior with two parallel ridges extending along anterior internal surface; dorsal median septum high, deeply anteriorly excavated, with surmounting plate draping over to fuse dorsally with inner surface of valve; dorsal central muscle scars pyriform. *Lower Devonian (Pragian):* Australia (Victoria).——Fig. 1700,*1a–e*. **C. laurei*, Cooper Creek Limestone; *a,* dorsal valve exterior, AMF92867, ×44; *b*, dorsal valve interior, ×47; *c–d,* anterior and lateral view, AMF92865, ×60; *e*, ventral valve, oblique view of interior, AMF92869, ×83 (Brock, Engelbretsen, & Dean-Jones, 1995).

Havlicekion Mergl, 2001a, p. 35 [**H. splendidus*; OD]. Ventral valve highly conical; dorsal valve weakly sulcate, with deeply impressed muscle scars; dorsal median septum low, with robust, narrowly triangular to rodlike surmounting plate; postlarval shell with prominent, regular concentric rugellae. *Silurian (Wenlock)–Devonian (Pragian):* Bohemia, Australia.——Fig. 1701*a–d*. **H. splendidus*, Praha Formation, Dvorce-Prokop Limestone, Svatý Jan pod Skalou, Na Stydlých vodách Quarry, Bohemia; *a*, holotype, dorsal valve interior, ×60; *b*, oblique lateral view, PCZCU40, ×60; *c*, oblique lateral view of ventral valve exterior, ×60; *d*, oblique anterior view of ventral valve exterior, PCZCU36, ×60 (new). [Michal Mergl]

Family CERATRETIDAE Rowell, 1965

Acanthatreta Streng, 1999, p. 38 [**A. meiwirthae*; OD]. Shell ventribiconvex, transversely oval; ventral pseudointerarea poorly defined, steeply procline to catacline, bisected by intertrough; pedicle foramen circular to elongate oval, not enclosed within larval shell; dorsal pseudointerarea with deep, triangular median groove, with small propareas; apical process forming ridge connecting posterior and anterior valve slopes, and placed anterior to internal foramen, with filigree spine. *lower Middle Cambrian:* Morocco.——Fig. 1702*a–i*. **A. meiwirthae*, Jbel Wawrmast Formation, *Cephalopyge notabilis* Biozone, Tachguelt, High Atlas; *a*, dorsal valve exterior, PIW96X125.8, ×55; *b*, ventral valve exterior, PIW96X125.7, ×30; *c*, dorsal valve interior, PIW96X126.1, ×40; *d*, holotype, oblique anterolateral view of ventral valve interior, PIW96X25.15, ×35; *e*, detail of ventral pseudointerarea, PIW96X125.3, ×65; *f,* lateral view of ventral valve exterior, PIW96X25.9, ×50; *g,* oblique anterolateral view of dorsal valve interior, PIW96X25.14, ×50; *h*, detail of apical process, PIW96X30.1, ×95; *i*, detail of apical process, PIW96X25.11, ×150 (Streng, 1999).

Almohadella Streng, 1999, p. 43 [**A. braunae*; OD]. Shell ventribiconvex, transversely oval; ventral pseudointerarea steeply procline, bisected by broad intertrough, widening dorsally; pedicle foramen slitlike, not enclosed within larval shell; dorsal pseudointerarea with broad, triangular median

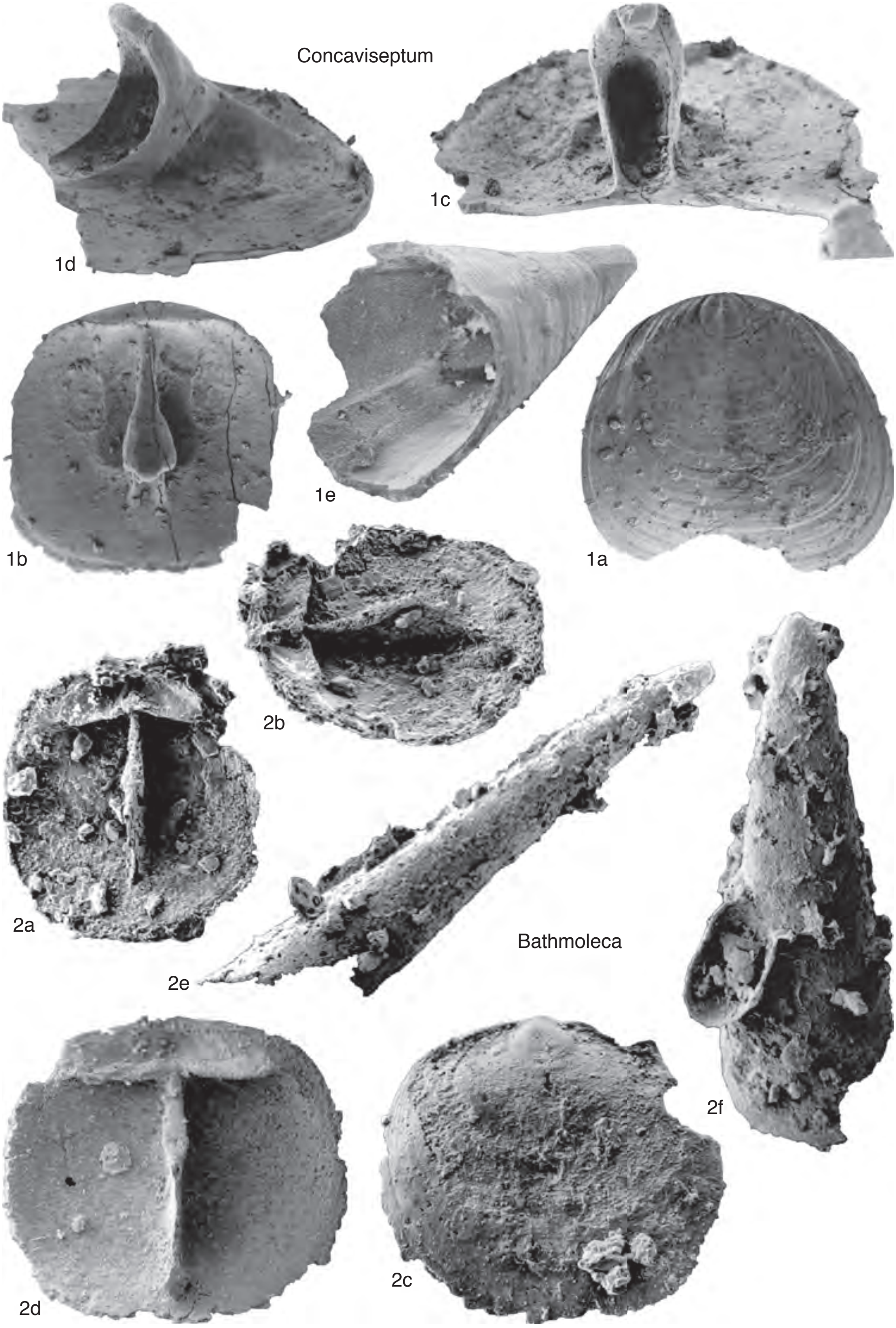


FIG. 1700. Biernatidae (p. 2568).

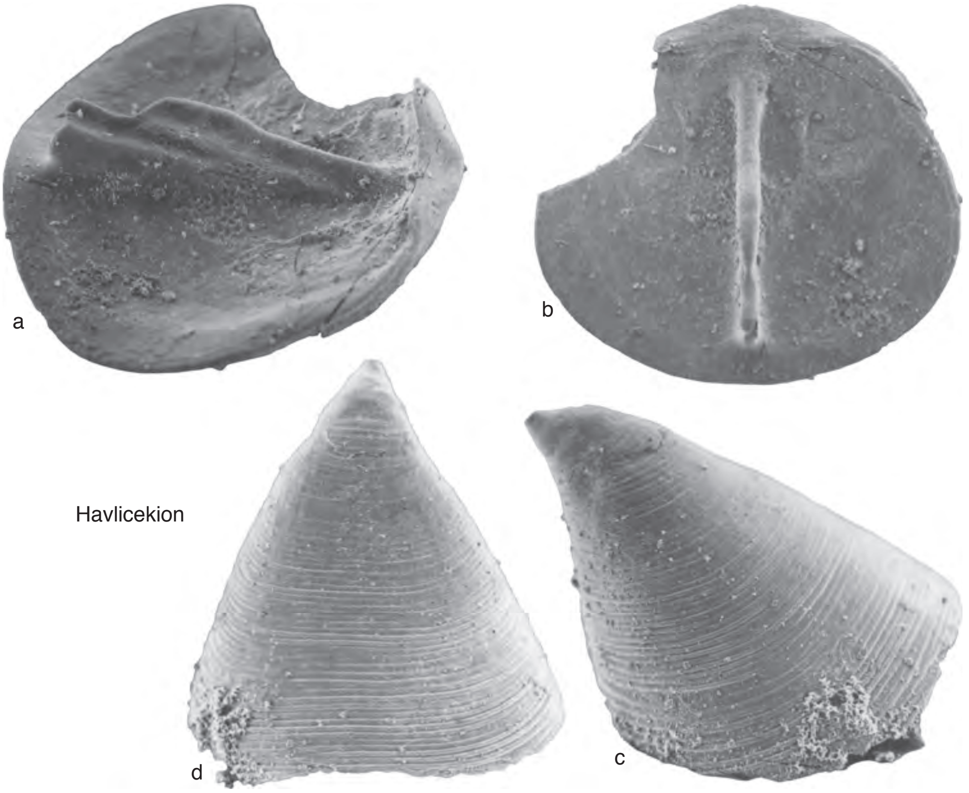


FIG. 1701. Biernatidae (p. 2568).

groove; propareas small; apical process forming robust ridge connecting posterior and anterior valve slopes; median buttress broad. *lower Middle Cambrian:* Morocco.——FIG. 1703*a–f*. **A. braunae*, Jbel Wawrmast Formation, *Cephalopyge notabilis–Ornamentaspis frequens* biozones, Lemdad Syncline, High Atlas; *a*, dorsal valve exterior, PIW96X21.3, ×35; *b*, dorsal valve interior, PIW96X22.6, ×40; *c*, detail of pedicle foramen, PIW96X18.6, ×160; *d*, oblique anterolateral view of dorsal valve interior, PIW96X22.9, ×40; *e*, holotype, ventral valve interior, ×25; *f*, holotype, detail of apical process, PIW96X3.14, ×85 (Streng, 1999).

Monophthalma STRENG, 1999, p. 32 [**Acrotreta eggegrundensis* WIMAN, 1903, p. 55; OD]. Ventral valve convex to low subconical; ventral pseudointerarea procline to slightly apsacline; pedicle foramen not enclosed within larval shell; dorsal pseudointerarea wide, with broad, subtriangular median groove; propareas small; ventral interior with collarlike thickening around apical process, with low ridge extending along anterior valve

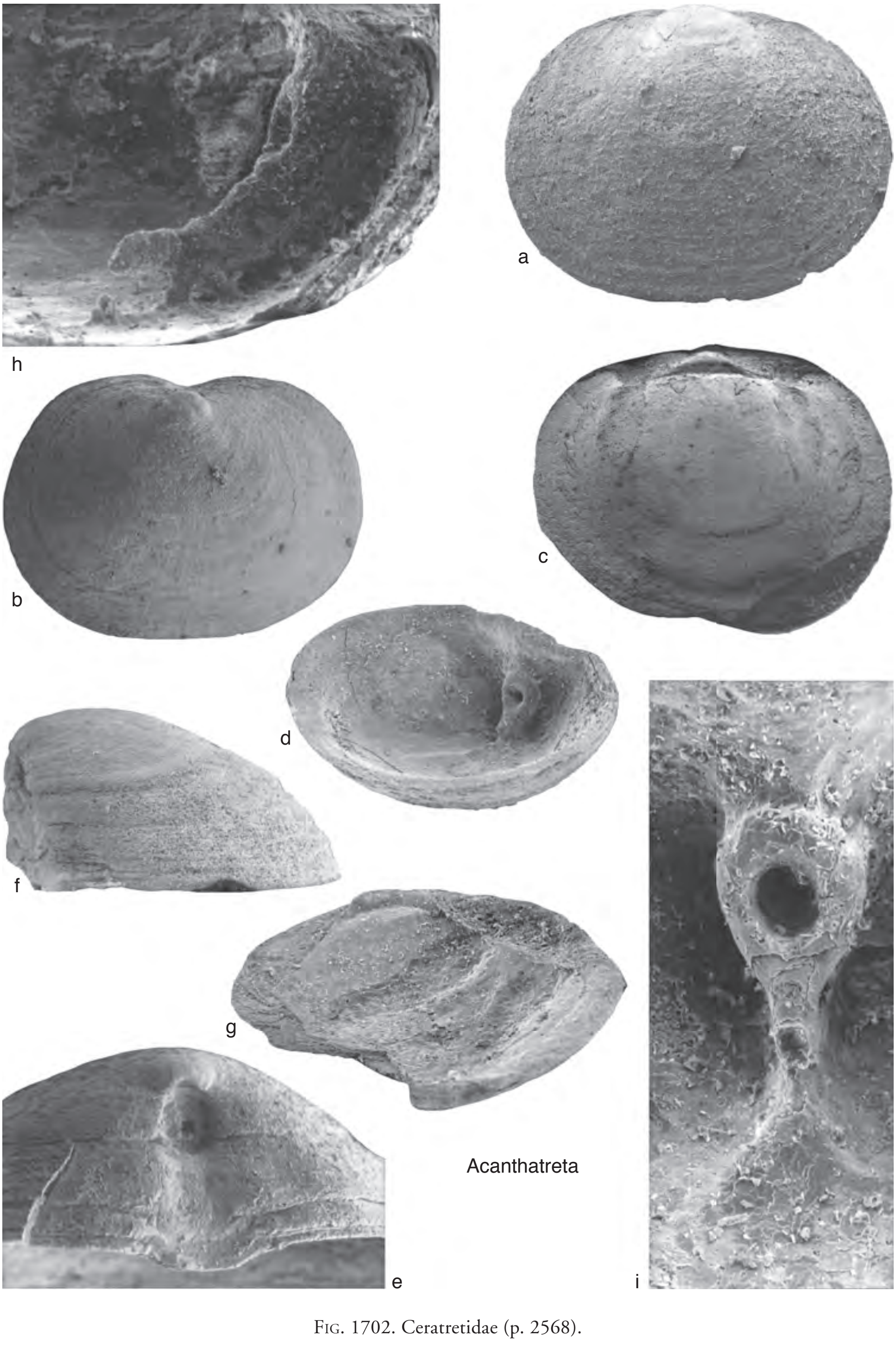


FIG. 1702. Ceratretidae (p. 2568).

FIG. 1703. Ceratretidae (p. 2568–2570).

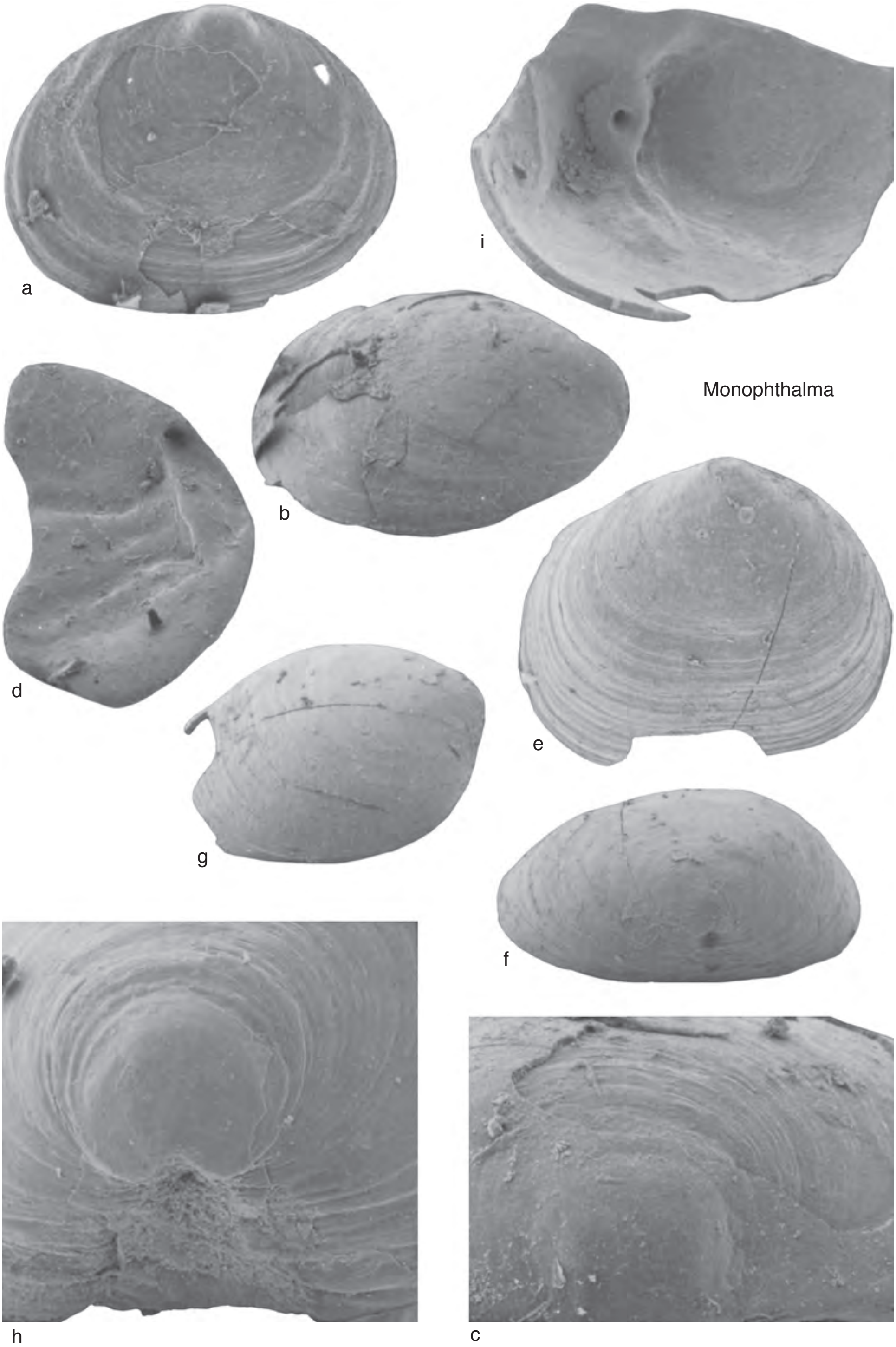


FIG. 1704. Ceratretidae (p. 2570–2574).

slope; dorsal median buttress and median ridge vestigial to absent; cardinal scars of both valves oval, widely separated. *Lower Cambrian (?Botomian), lower Middle Cambrian:* Sweden (South Bothnian Sea), Morocco.——FIG. 1704*a–i.* **M. eggegrundensis* (WIMAN), Cambrian glacial erratic boulder, ?Botomian, Eggegrund island, South Bothnian Sea, outside Gävle, Sweden; *a*, dorsal valve exterior, ×57; *b,* oblique lateral view, ×67; *c,* detail of larval shell, PMUB593, ×165; *d,* oblique lateral view of dorsal interior, PMUB594, ×49; *e*, ventral valve exterior, ×35; *f,* oblique posterior view, ×38; *g,* oblique lateral view, PMUB596, ×35; *h*, detail of ventral larval shell, PMUB598, ×135; *i*, ventral valve interior, PMUB597, ×45 (Holmer & Ushatinskaya, 1994).——FIG. 1705. **M. eggegrundensis* (WIMAN), Cambrian glacial erratic boulder, ?Botomian, Eggegrund island, South Bothnian Sea, outside Gävle, Sweden; oblique lateral view of dorsal pseudointerarea, PMUB595, ×180 (Holmer & Ushatinskaya, 1994).

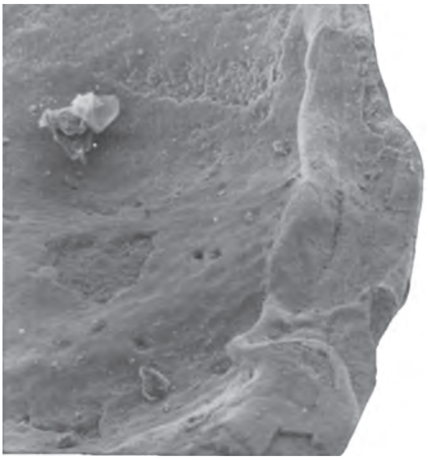


FIG. 1705. Ceratretidae (p. 2570–2574).

SIPHONOTRETIDA

Lars E. Holmer,[1] Leonid E. Popov,[2] and Michael G. Bassett[2]

[[1]University of Uppsala; and [2]National Museum of Wales]

[Bohemian materials prepared by Michal Mergl, Západočeská univerzita, Plzeň, Czech Republic]

Order SIPHONOTRETIDA Kuhn, 1949

Adult shell with hollow spines, in all but three genera, or completely lacking spines (*Schizambon* only) but with elongated pustules; adult shell of two genera (*Gorchakovia* and *Helmersenia*) perforated by canals with external depressions that probably contained chitinous tubercles in life; immature shell of most genera (except *Schizambon*) perforated by canals; shell usually ventribiconvex, inequivalved; shell structure with prismatic laminae with sporadically distributed cavities containing apatitic residues; larval and postlarval shell lacking pitted microornament; growth of ventral valve mixoperipheral or holoperipheral; pedicle foramen apical, circular, or extending anteriorly through resorption, producing elongate pedicle track; posterior part of pedicle track may be closed by plate, which may continue as internal pedicle tube; pseudointerareas of both valves poorly divided, lacking flexure lines; musculature not well known but apparently similar to that of lingulides; mantle canal system baculate with dorsal and ventral *vascula lateralia*; *vascula media* may be present. *upper Middle Cambrian (Mayaian)–Lower Devonian (Pragian, Emsian).*

The presence of hollow spines was regarded previously as the most important potential synapomorphic character of the order Siphonotretida (Holmer & Popov, 2000), but a recent study of the oldest siphonotretide, *Schizambon*, reveals that its shell is imperforated (Williams, Holmer, & Cusack, 2004). The surface ornamentation of *S. typicalis*, the type species of the genus, is covered by regular lamellae with upturned edges superimposed on sharp parvicostellae. The nodes formed at their intersection acquire the shape of elongate spinelike pustules (5–50 µm long), which were previously mistaken for bases of broken hollow spines (e.g., Popov, Holmer, & Miller, 2002). These spines, however, are solid, superficial structures, more likely to be homologous with the pustules of *Gorchakovia,* but not with the hollow spines of other siphonotretides (Williams, Holmer, & Cusack, 2004).

The shells of *Helmersenia* and *Gorchakovia* also lack spines, but they are perforated by canals with external depressions (antechambers) that possibly contained chitinous tubercles in life. Similar perforations can be observed also in the umbonal areas of both valves of *Siphonotreta* and most other siphonotretids. The mature part of their shells, however, bears recumbent, rheomorphic, hollow spines that grew forward out of pits (Williams, Holmer, & Cusack, 2004). It is possible that the canals with external depressions and their inferred external chitinous structures are homologous with the setigerous tubes found within the stem group of the Brachiopoda (see Organophosphatic Bivalved Stem-Group Brachiopods, p. 2580 herein), and represent a retained plesiomorphic character for the Siphonotretida. If this interpretation is correct, it would indicate that *Schizambon* is a derived member of the order that has

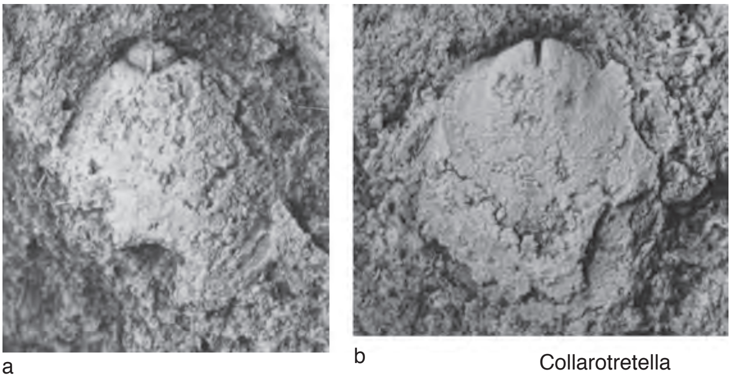


FIG. 1706. Siphonotretidae (p. 2576).

lost both the hollow spines and canals with external depressions.

The siphontretide pedicle foramen invariably is situated within and confined to the ventral valve. It is commonly enlarged anteriorly by shell resorption. This suggests that the pedicle of siphonotretides originated from within the epithelial tissue secreting the ventral valve. Thus, the siphonotretide foramen is here regarded provisionally as not being homologous with pedicle openings within the ventral valves of acrotretides or lingulides, such as the acrothelids and dysoristids, which represent postlarval enclosures of pedicles by the precocious differentiation of the posteromedial mantle lobe seen in immature *Discinisca*. The location of the siphonotretide pedicle wholly within the ventral valve may have been unique among linguliforms (WILLIAMS & CARLSON, p. 2843, herein).

Siphonotretides were long regarded as almost extinct by the end of the Ordovician. The recent discovery of *Orbaspina* by VALENTINE and BROCK (2003) expands the stratigraphic range of the group into the late Llandovery, however, and MERGL (2001a, 2001b) reported on the occurrence of the siphonotretide shell fragments in the lower Silurian to Lower Devonian of Bohemia. Unpublished occurrences from the Silurian of Canada, Great Britain, and the Island of Gotland also exist.

Order SIPHONOTRETIDA Kuhn, 1949

Superfamily SIPHONOTRETOIDEA Kutorga, 1848

Family SIPHONOTRETIDAE Kutorga, 1848

Collarotretella MERGL, 1997b, p. 102 [**C. septata*; OD]. Shell biconvex, broadly oval; exterior sparsely spinose, nearly smooth; foramen large, circular, directed posteroventrally, internally with thickened collar; ventral pseudointerarea low, small, undivided; dorsal pseudointerarea obscure; dorsal interior with short, distinct median septum. *Ordovician (Arenig):* Bohemia.——FIG. 1706*a–b*. **C. septata*, Klabava Formation, Hrádek; *a*, holotype, ventral valve internal mold, MBHR 66845, ×15; *b*, dorsal valve internal mold, MBHR 66847, ×15 (new). [Michal Mergl]

Orbaspina VALENTINE & BROCK, 2003, p. 237 [**O. gelasinus*; OD]. Pedicle foramen large, keyhole shaped, extending forward through resorption to form elongate, broadly triangular, pedicle track; pedicle track covered posteriorly by concave plate and anteriorly by short listrium-like plate; tubular hollow spines of uniform size; postlarval shell with numerous subcircular dimples, loosely arranged in concentric rows. *Silurian (Llandovery–Wenlock):* Australia (New South Wales).——FIG. 1707*a–g*. **O. gelasinus*, Boree Creek Formation, uppermost Llandovery, *amorphognathoides* Zone, to earliest Wenlock, *ranuliformis* Zone, central-western New South Wales; *a–b*, holotype, dorsal valve exterior, interior, ×17; *c*, detail of pseudointerarea, AMF120610, ×50; *d*, detail of postlarval dimpling, AMF122212, ×50; *e–f*, ventral valve exterior, interior, ×30; *g*, detail of spines, AMF120612, ×300 (new).

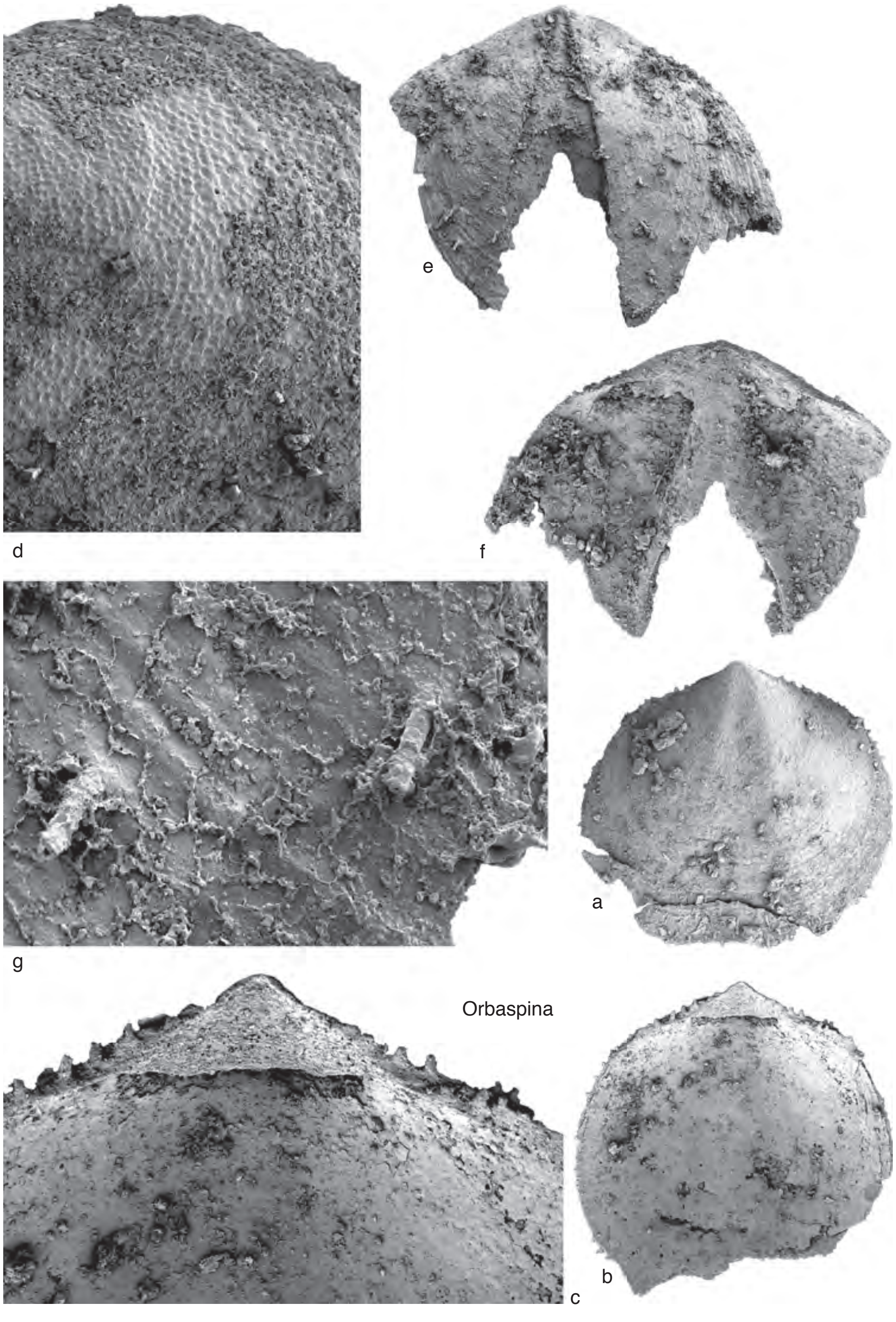


FIG. 1707. Siphonotretidae (p. 2576).

PATERINATA

LARS E. HOLMER and LEONID E. POPOV

[University of Uppsala; and National Museum of Wales]

[Bohemian materials prepared by MICHAL MERGL, Západočeská univerzita, Plzeň, Czech Republic]

Class PATERINATA Williams & others, 1996

The inclusion of the extinct class Paterinata within the Linguliformea is problematic, but is mainly due to the presence of an organophosphatic shell. [This small clade includes just 12 genera, divided into 2 families, the Cryptotretidae and Paterinidae (LAURIE, 2000). The paterinates have been difficult to classify since they were first discovered (WILLIAMS, POPOV, & others, 1998). The work by WILLIAMS, POPOV, and others (1998) indicates that they had fused mantle lobes in combination with an attachment to the substrate by means of a cuticular pad from the ventral mantle. The paterinates also differ from all other linguliforms in that they have true interareas with delthyria and notothyria and a musculature with diductor muscles, as well as rhynchonelliform mantle canal systems that may have contained gonads (LAURIE, 1987, 2000; WILLIAMS, POPOV, & others, 1998, fig. 3). WILLIAMS, POPOV, and others (1998) proposed that some of these features possibly represent plesiomorphic characters retained from the stem group. The paterinates also differ in shell structure from the linguliforms in that a canal system is lacking (e.g., WILLIAMS & CUSACK, 1999; WILLIAMS, POPOV, & others, 1998).]

Order PATERINIDA Rowell, 1965

Superfamily PATERINOIDEA Schuchert, 1893

Family PATERINIDAE Schuchert, 1893

Olenekina USHATINSKAYA, 1997, p. 55 [**O. olenekensis*; OD]. Shell ventribiconvex, transversely suboval; postlarval shell covered with slightly irregular concentric rugellae; larval shell finely granulated; ventral valve with open delthyrium and apsacline interarea; dorsal valve with open notothyrium underlined by median plate inside valve; interior characters weakly impressed with a pair of ridges parallel to hinge line in both valves. *upper Middle Cambrian:* north-central Siberia, Russia.——FIG. 1708,*2a–c*. **O. olenekensis*, Eirina Formation, *Glyptagnostus stolidotus* Biozone, Kotui river; *a*, holotype, dorsal valve exterior, PIN4510/141, ×25; *b*, ventral valve exterior, PIN4290/206, ×45; *c,* dorsal valve interior showing ridges along hinge line, PIN4510/146, ×70 (Ushatinskaya, 1997).

?Wynnia WALCOTT, 1908, p. 142 [**Orthis warthi* WAAGEN, 1891, p. 102; OD]. Genus inadequately known (previously questionably assigned to Orthida, but with organophosphatic shell); shell ventribiconvex, subcircular; ventral valve with open delthyrium and apsacline interarea; dorsal valve sulcate, with open notothyrium; ventral valve with elongate triangular muscle field, divided

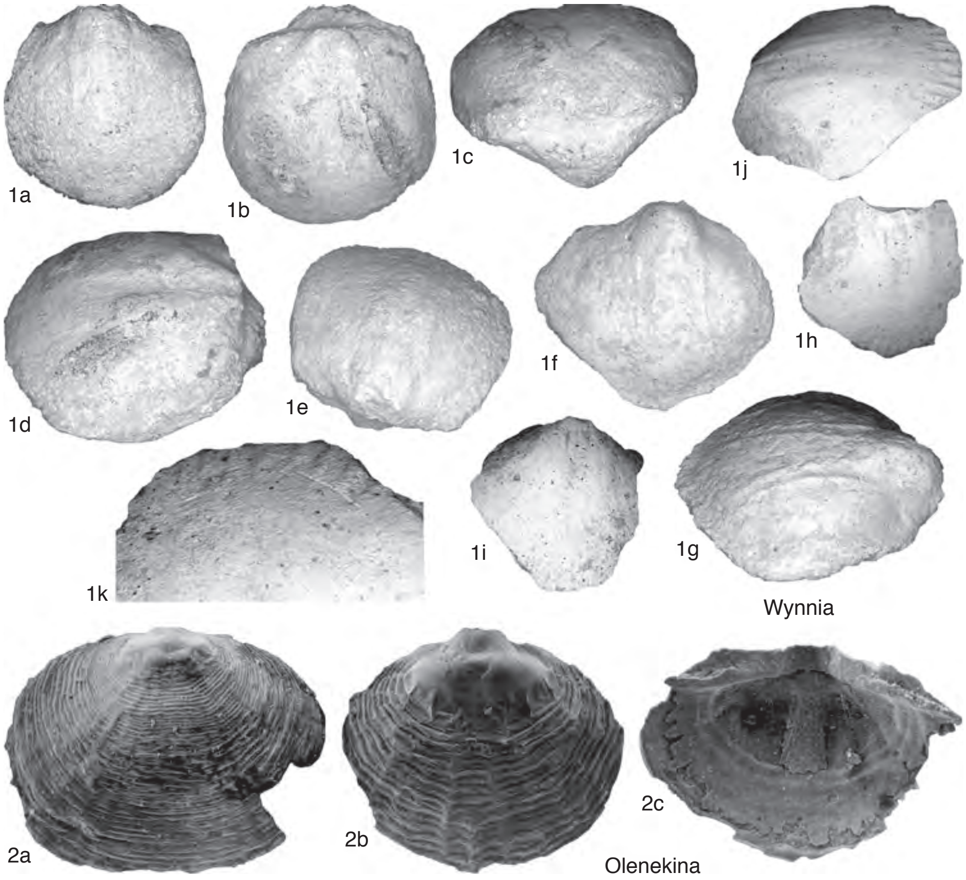


FIG. 1708. Paterinidae (p. 2578–2579).

by two subparallel *vascula media*; dorsal interior with poorly defined muscle fields separated by median ridge. *Lower Cambrian:* Pakistan.——FIG. 1708,*1a–k*. **W. warthi* (WAAGEN), *Neobolus* Beds, Tsanglangpuian, Kussak Fort Hill, Salt Range; *a–e*, internal mold of complete articulated shell, ventral view, dorsal view, oblique posterior dorsal view, oblique lateral dorsal view, oblique posterior ventral view, TUBr1080/110, ×4; *f–g*, internal mold of ventral valve, oblique lateral view, TUBr1080/109, ×4; *h–j*, exfoliated ventral valve (organophosphatic), oblique anterior view, oblique lateral view, ×6; *k,* detail of terminal vascular trunks, TUBr1080/111, ×15 (new).

INCERTAE SEDIS ORGANOPHOSPHATIC BIVALVED STEM-GROUP BRACHIOPODS

LARS E. HOLMER and LEONID E. POPOV
[University of Uppsala; and National Museum of Wales]

INTRODUCTION

With few exceptions, the stem and crown group concept (e.g., BUDD & JENSEN, 2000) has not been used generally for analyzing phylogenetic relationships within the Brachiopoda (CONWAY MORRIS, 1993, 1998; CONWAY MORRIS & PEEL, 1995; HOLMER, 2001). This situation is now changing rapidly, however, as a surprisingly rich record of Early Cambrian organophosphatic-shelled potential stem-group brachiopods is beginning to emerge (HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; SKOVSTED & HOLMER, 2003; BALTHASAR, 2004a; WILLIAMS & CARLSON, p. 2829, herein). These stem-group taxa fall outside any of the formal taxonomic units within the two currently recognized classes of the subphylum Linguliformea, the Lingulata and the Paterinata, discussed below; however, their organophosphatic shell, evidence of setae, and, in some exceptionally preserved forms, the presence of a lophophore (ZHANG, HOU, & EMIG, 2003), indicate clearly that they are linked phylogenetically with the linguliforms.

Proposed Early Cambrian stem-group brachiopods include the vermiform, organophosphatic, sclerite-bearing tannuolinids (WILLIAMS & HOLMER, 2002; LI & XIAO, 2004) and the more brachiopod-like *Mickwitzia* and *Heliomedusa* (HOLMER, SKOVSTED, & WILLIAMS, 2002; SKOVSTED & HOLMER, 2003; BALTHASAR, 2004a). But because the tannuolinids fall outside the clade defined by the presence of a bivalved body plan with lophophore (Fig. 1709), they are excluded here from further consideration.

The enigmatic bivalved organophosphatic-shelled *Mickwitzia* SCHMIDT is one of the largest known bivalved organisms from the Early Cambrian; the width of the shell can reach 60–72 mm. Although it has been referred commonly to the paterinid brachiopods (subphylum Linguliformea, class Paterinata; ROWELL, 1965), others questioned its brachiopod affinity. It was tentatively excluded from the Brachiopoda by LAURIE (2000, p. 156), in view of its enigmatic “punctate, three-layered phosphatic shell,” as well as the lack of any unequivocal brachiopod characters apart from the simple bivalved shell as apparent in all available material of the type species, *M. monilifera* (LINNARSSON), from the Early Cambrian of Baltoscandia. Better preserved material of *Mickwitzia* (referred to *M.* sp. cf. *occidens* WALCOTT, but probably a new species; see Fig. 1711–1712) described by SKOVSTED and HOLMER (2003) from the Early Cambrian of Greenland, demonstrates that the shell structure of *Mickwitzia*, on the contrary, is closely similar to the columnar shell of linguliform acrotretoid brachiopods as well as to the linguloid *Lingulellotreta,* in that it has slender columns in the laminar succession (CUSACK, WILLIAMS, & BUCKMAN, 1999). A columnar fabric is known also from the tannuolinid *Micrina*, thus indicating that this type of shell structure may be a plesiomorphic character (Fig. 1898, herein; WILLIAMS & HOLMER, 1992; CUSACK, WILLIAMS, & BUCKMAN, 1999; HOLMER, SKOVSTED, & WILLIAMS, 2002). The shell of *M.* sp. cf. *occidens* also has a very different kind of thicker cylindrical tubes, however, which were clearly open to the exterior surface and have a fine internal striation; this striation most probably represents imprints of microvilli, and the tubes can be inferred to have contained setal structures penetrating the shell (and causing external cylindrical imprints in the surrounding laminae; see

Fig. 1712c, 1713a; see also Balthasar, 2004a). This type of setae is not present in any known member of the crown group Brachiopoda, but identical structures have been described from tannuolinids (Conway Morris & Chen, 1990; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Li & Xiao, 2004). *M.* sp. cf. *occidens* also has evidence of a brachiopod-like soft anatomy, including a well-defined larval shell with preserved traces (so-called nick points) of setal follicles (Fig. 1712b), comparable with those described from other linguliform brachiopods by Williams and Holmer (1992), as well as a ventral pseudointerarea with a pedicle groove (Fig. 1712a).

M. occidens Walcott, from a new Lower Cambrian Lagerstätte in Nevada, confirms the setigerous nature of the thicker canals, since it has pyritized setae preserved extending from them (Fig. 1711d–f), and the interior surface of the parallel canals has striations that are identical with those from the other mickwitziids (Fig. 1711g–i).

The enigmatic *Heliomedusa* Sun and Hou, from the Early Cambrian Chengjiang Lagerstätte (Yu'anshan Formation), Yunnan, was most recently assigned provisionally to the craniopsid group of brachiopods (subphylum Craniiformea, class Craniata, order Craniopsida; Popov & Holmer, 2000a; Zhang, Hou, & Emig, 2003). New material demonstrates that the shell structure of *Heliomedusa* is identical with that of *Mickwitzia*, however, and has a punctate shell that was perforated by tubes, some of which contain chitinous setae at the surface (Fig. 1714–1716). The presence of these characters indicates instead that *Heliomedusa* belongs within the stem-group brachiopods together with *Mickwitzia* (but see Williams & Carlson, p. 2889 herein, and Chen, Huang, & Chuang, 2007, for an alternative point of view).

MICKWITZIIDS

[incl. Mickwitziidae Gorjansky, 1969, p. 104]

The family Mickwitziidae as used by Laurie (2000) and others (Skovsted & Holmer, 2003) is probably not a monophyletic group but seemingly represents a paraphyletic stem group, which now includes only two genera, *Mickwitzia* and *Heliomedusa*. At present it is preferred to include these taxa only within an informal grouping of mickwitziid-like stem-group brachiopods, pending further study. As noted by Balthasar (2004a), the great morphological variation between species presently placed within *Mickwitzia* (*sensu lato*) needs to be further investigated pending restudy of the type species. *Lower Cambrian (Atdabanian–Toyonian), ?Middle Cambrian.*

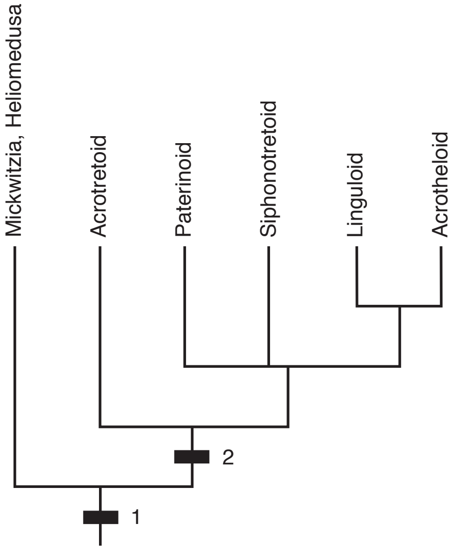


Fig. 1709. Cladogram of stem-group (*Heliomedusa* and *Mickwitzia*) and crown-group brachiopods (Acrotretoidea, Paterinoidea, Siphonotretoidea, Linguloidea, Acrotheloidea). The numbered transformations are *1,* bivalved body plan with lophophore, organophosphatic shell perforated by setigerous tubes, follicular mantle setae; *2,* loss of setigerous tubes (although highly modified tubes may be present in Siphonotretoidea), adult setae all follicular (topology adapted from Holmer, Skovsted, & Williams, 2002, fig. 4).

Mickwitzia Schmidt, 1888, p. 24 [*?*Lingula monilifera* Linnarsson, 1869, p. 344; OD] [=*Causea* Wiman, 1902, p. 53 (type, *C. formosa;* OD); ?*Microschedia* Geyer, 1994, p. 710 (type, *M. amphitrite,* OD)]. Shell ventribiconvex to planoconvex, inequivalved, ovate to subcircular; apex of both valves commonly submarginal and erect; ventral apex may be curved over posterior margin; lingulid-like larval shell may be present; mature shell pustulose, commonly with pustules arranged in radiating rows; pseudointerareas of both valves usually poorly defined in adults; ventral pseudointerarea rarely anacline (in early growth stages), more commonly apsacline to procline (in adults), and sometimes with narrow pedicle groove in juveniles; ventral pseudointerarea of some forms with minute arch-shaped posterior ridge (homeodeltidium) flanked by small procline to apsacline interareas in juveniles; interior of both valves inadequately known; shell organophosphatic, but may generally have been poorly mineralized; punctate shell structure; finely stratiform; may include slender acrotretoid-type columns (but not yet observed from type species) and thicker canals (=punctae) that are usually orthogonal, but also may be close to parallel with shell laminae; thicker canals open to external surface, internal striations (imprints of microvilli) may be present; shell layers most commonly bend inward at insertion of canals and form distinct inward-pointing cones with canals, forming a central tube; canals open to interior and exterior through shallow funnels that may be associated with cylindrical depressions; some forms also with internally striated thicker canals on ventral pseudointerarea; mantle canals poorly known. *Lower Cambrian (Atdabanian–Toyonian), ?Middle Cambrian*: USA (California, Nevada), Canada (Alberta, British Columbia, Nova Scotia), Greenland, Mexico, Sweden, Finland, Estonia, Lithuania, ?Morocco.——Fig. 1710*a–k*. **M. monilifera* (Linnarsson), File Haidar Formation (Mickwitzia beds), Atdabanian, Västergötland, Uppland (glacial erratics), Sweden; *a–c,* ventral valve exterior, oblique posterior, lateral view, PMB28, holotype of *C. formosa* Wiman, ×0.6; *d–f,* ventral valve exterior, exfoliated, posterior view, ×1, lateral view, SGUAa172, ×2; *g,* detail of lateral margin, showing more irregularly distributed parallel canals, ×24; *h,* juvenile ventral valve exterior, with pustulose ornamentation, RMBr1609, ×7; *i,* detail of pustulose ornamentation of juvenile dorsal valve, slightly exfoliated, RMBr1567, ×46; *j,* detail of margin of dorsal valve interior, exfoliated, showing possible terminal trunks of mantle canals, RMBr1593, ×3; *k,* detail of sectioned and polished section, etched with 3% HCl, showing thick, orthogonal canals, with shell layers bending inward to form distinct inward-pointing cones, with canals forming a central tube, RMBr133552, ×75 (new).——Fig. 1711*a–c.* **M. monilifera* (Linnarsson), File Haidar Formation (Mickwitzia beds), Atdabanian, Västergötland, Uppland (glacial erratics), Sweden; *a,* dorsal valve interior, exfoliated, ×2.5; *b,* detail of central median section, showing section through 13 regularly spaced thicker canals that are parallel with shell laminae, and numerous orthogonal canals, ×12; *c,* detail of parallel canal, RMBr1567, ×110 (new).——Fig. 1711*d–i. M. occidens* Walcott, Poleta Formation, upper Montezuman–lower Dyeran, Indian Springs Canyon, Esmeralda County, Nevada, USA; *d,* ventral valve exterior, exfoliated, with soft-bodied preservation of setae, ×3; *e,* detail of setae, backscatter image, ×40; *f,* detail of framboidal pyrite preservation of setae, USNM, ×160; *g,* detail of apex of ventral valve, smooth larval shell, and postlarval pustulose ornamentation, perforated by openings of thicker orthogonal canals, USNM, ×65; *h,* shell fragment with orthogonal and parallel canals, ×26; *i,* detail of striated interior of parallel canal, USNM, ×600 (new).——Fig. 1712*a–c. M.* sp. cf. *occidens* Walcott, Bastion and Ella Island Formations, Botomian, northeastern Greenland; *a,* ventral pseudointerarea of early mature valve with pedicle groove, MGUH26308, ×105; *b,* oblique posterior view of broken ventral apex, showing larval shell with nick points (disturbance by muscles of marginal setae), MGUH26300, ×95; *c,* ventral pseudointerarea, showing openings of setigerous thicker canals, causing cylindrical indentations in surrounding laminae, ×400 (new).——Fig. 1713*a–c. M.* sp. cf. *occidens* Walcott, Bastion and Ella Island Formations, Botomian, northeastern Greenland; *a,* detail of striated interior of two canals, MGUH26279, ×1900; *b,* fragmentary mature valve with pustulose ornamentation in radiating rows and openings of canals, MGUH26311, ×70; *c,* section through primary and secondary layer of mature shell, showing larger canals and columnar shell structure, MGUH26280, ×700 (new).

Heliomedusa Sun & Hou, 1987, p. 261[269] [**H. orienta;* OD]. Shell biconvex, inequivalved, subcircular; mixoperipheral growth in ventral valve, with beak marginal, and apsacline pseudointerarea; holoperipheral growth in dorsal valve, apex placed posterior to center; visceral area of both valves thickened slightly anteriorly, extending anterior to center; shell originally organophosphatic, but may generally have been poorly mineralized (invariably replaced by framboidal pyrite and clay minerals); punctate shell structure includes thick canals that are usually orthogonal, but also may be close to parallel with shell laminae; canals of both types can contain pyritized spinelike setae at surface; surface of both valves commonly also covered with impressions of numerous thinner, shorter spinelike possible setal structures; ontogeny includes differentiated juvenile shell, delineated by growth disturbance; both juvenile and mature shells with pustulose ornamentation, with pustules arranged in radiating rows. *Lower Cambrian (Atdabanian):* China (Yunnan).——Fig. 1714*a–f.* **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* ventral valve exterior, partly exfoliated, ×2; *b,* detail of posterior margin with preserved spinelike setae, ×15; *c,* exfoliated compressed ventral valve exterior covered by pyritized short spinelike structures, which may represent setal structures, ×15; *d,* detail of pyritized spinelike structures, NIGP12, ×100; *e,* thick spinelike pyritized setae at valve margin, NIGP34, ×15; *f,* exfoliated compressed ventral valve exterior covered by impressions of short spinelike structures, which may represent setal structures, NIGP14, ×30 (new).——Fig.

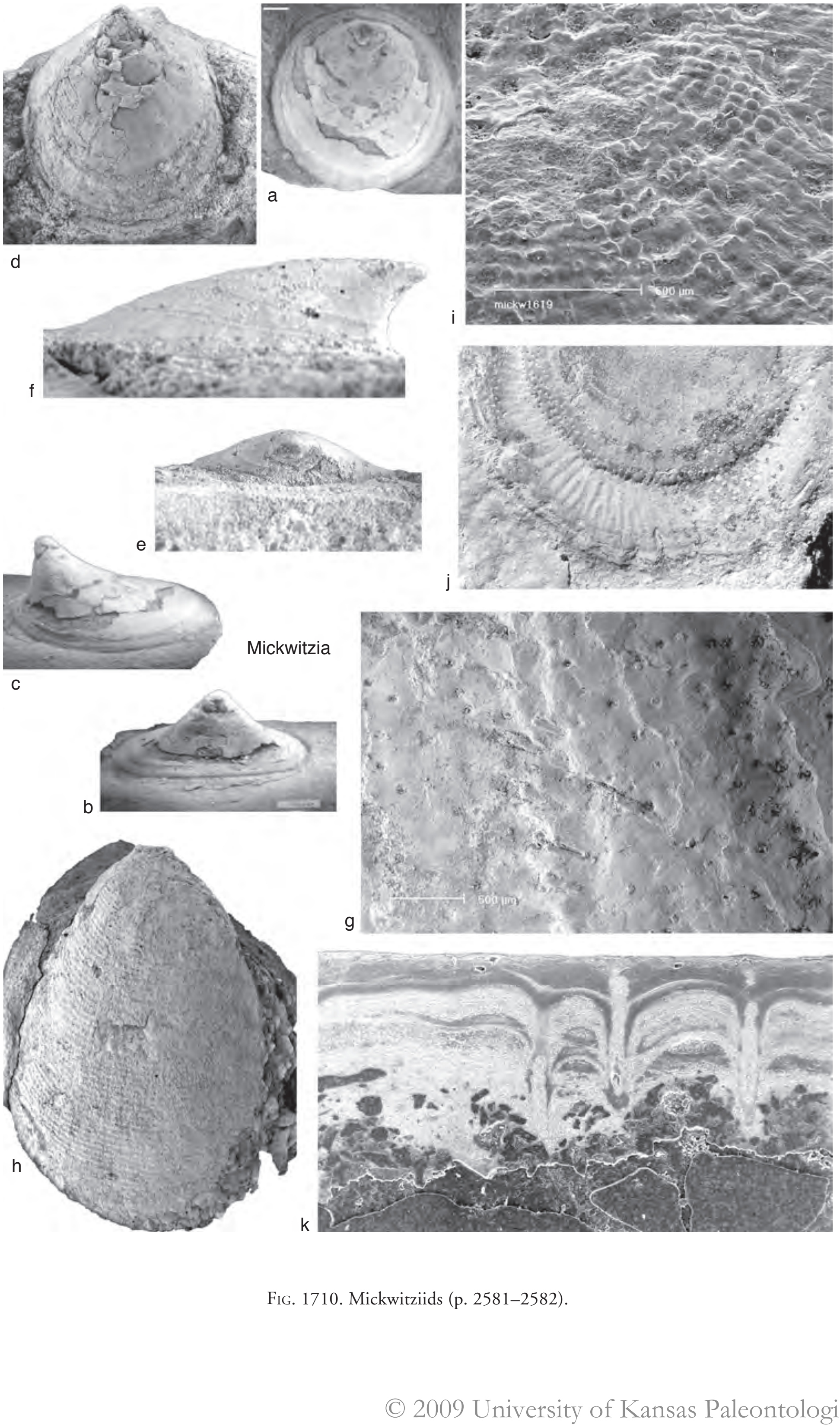


FIG. 1710. Mickwitziids (p. 2581–2582).

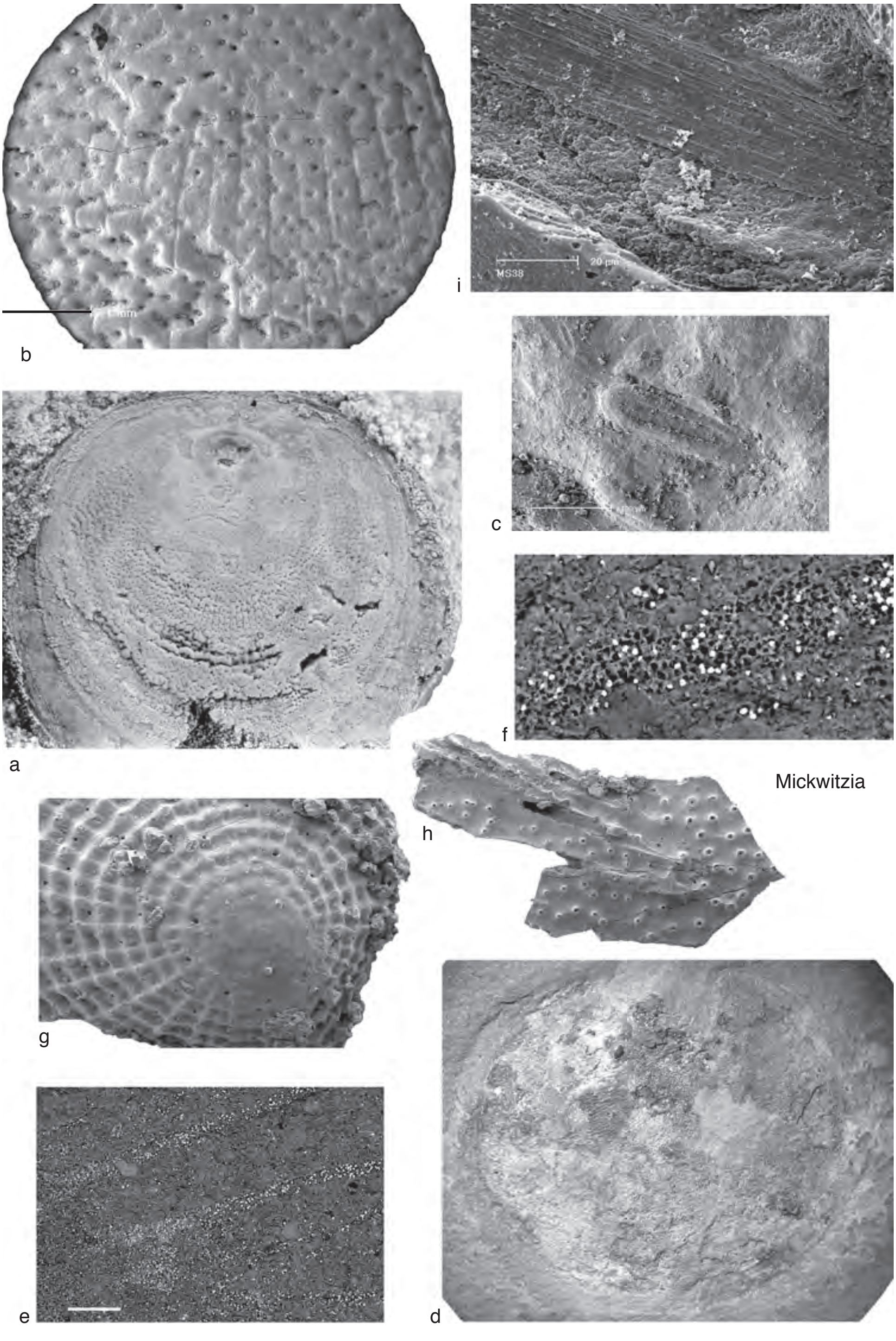


FIG. 1711. Mickwitziids (p. 2581–2582).

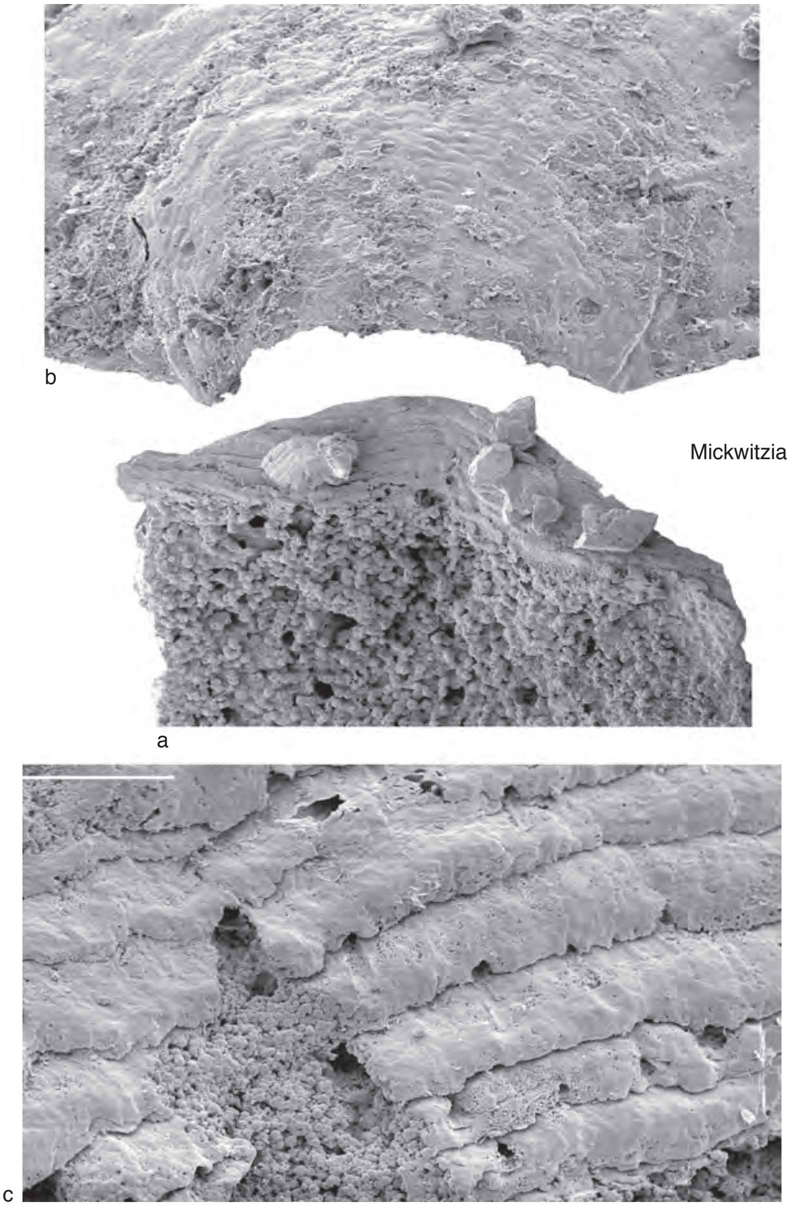


FIG. 1712. Mickwitziids (p. 2581–2582).

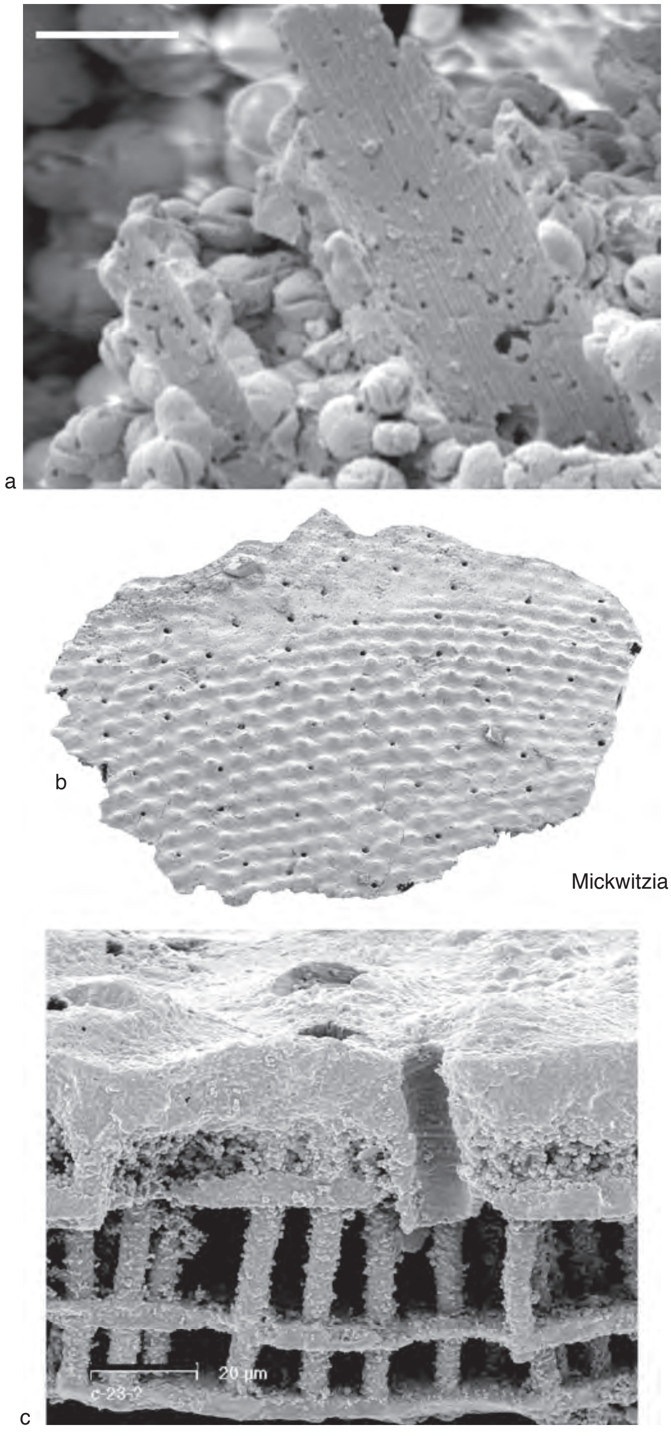


FIG. 1713. Mickwitziids (p. 2581–2582).

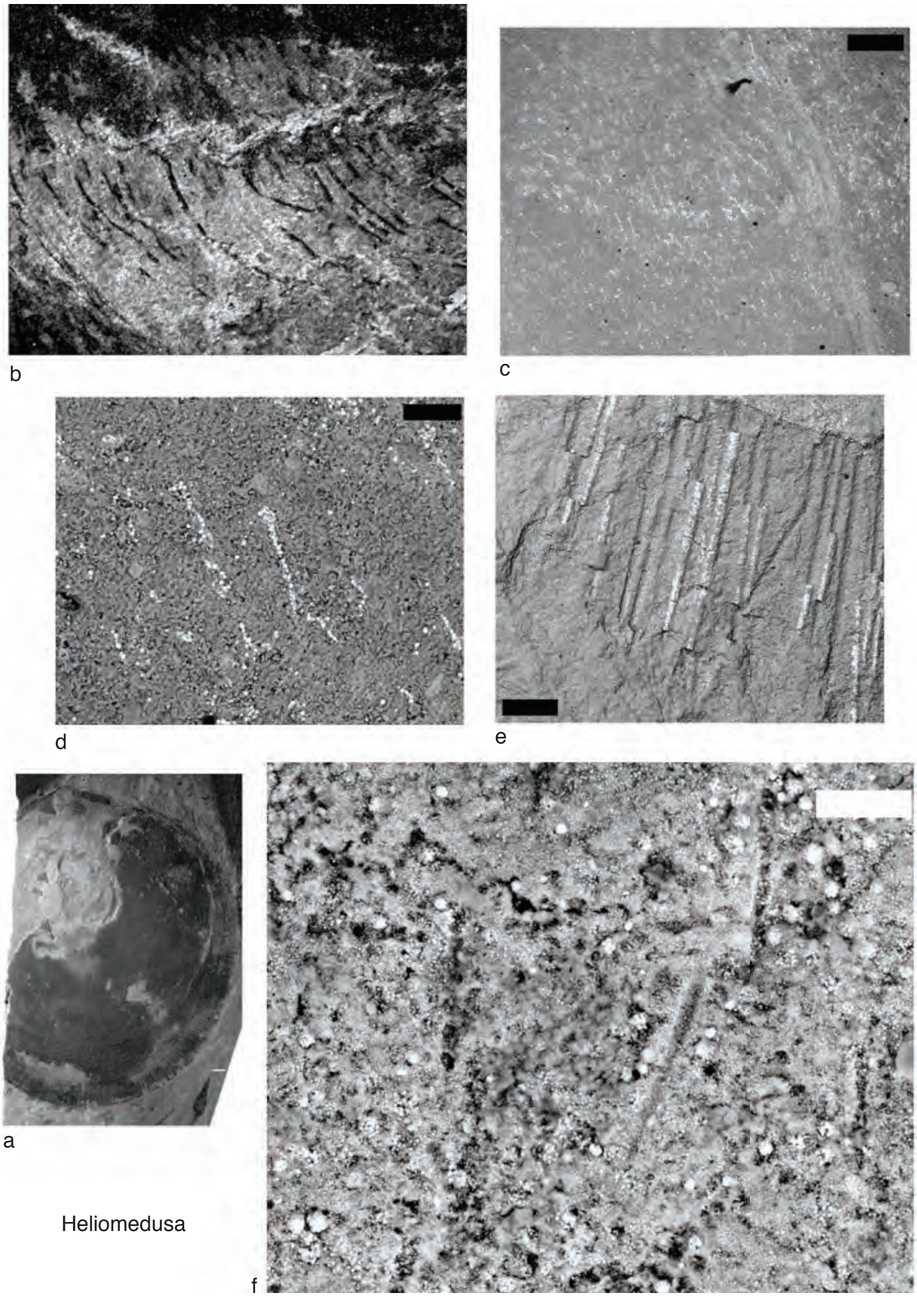


FIG. 1714. Mickwitziids (p. 2582–2590).

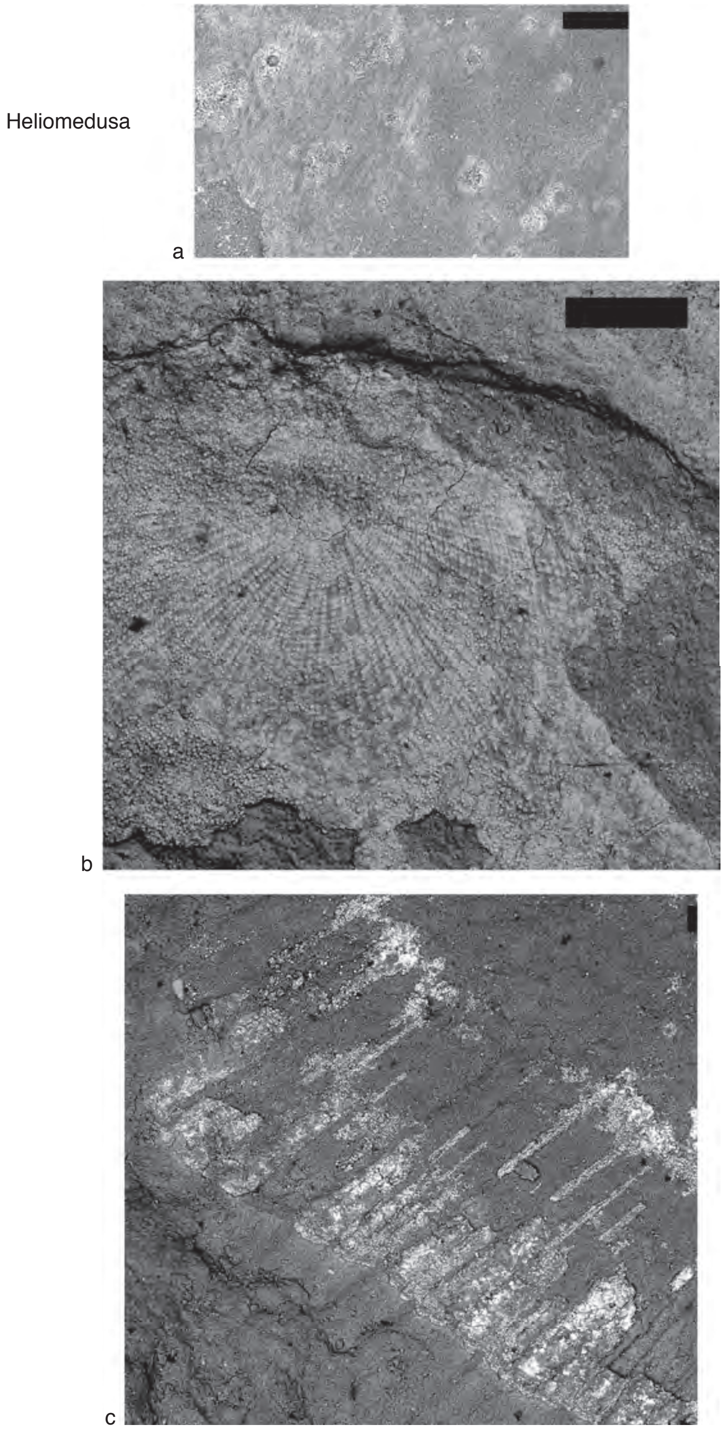


FIG. 1715. Mickwitziids (p. 2582–2590).

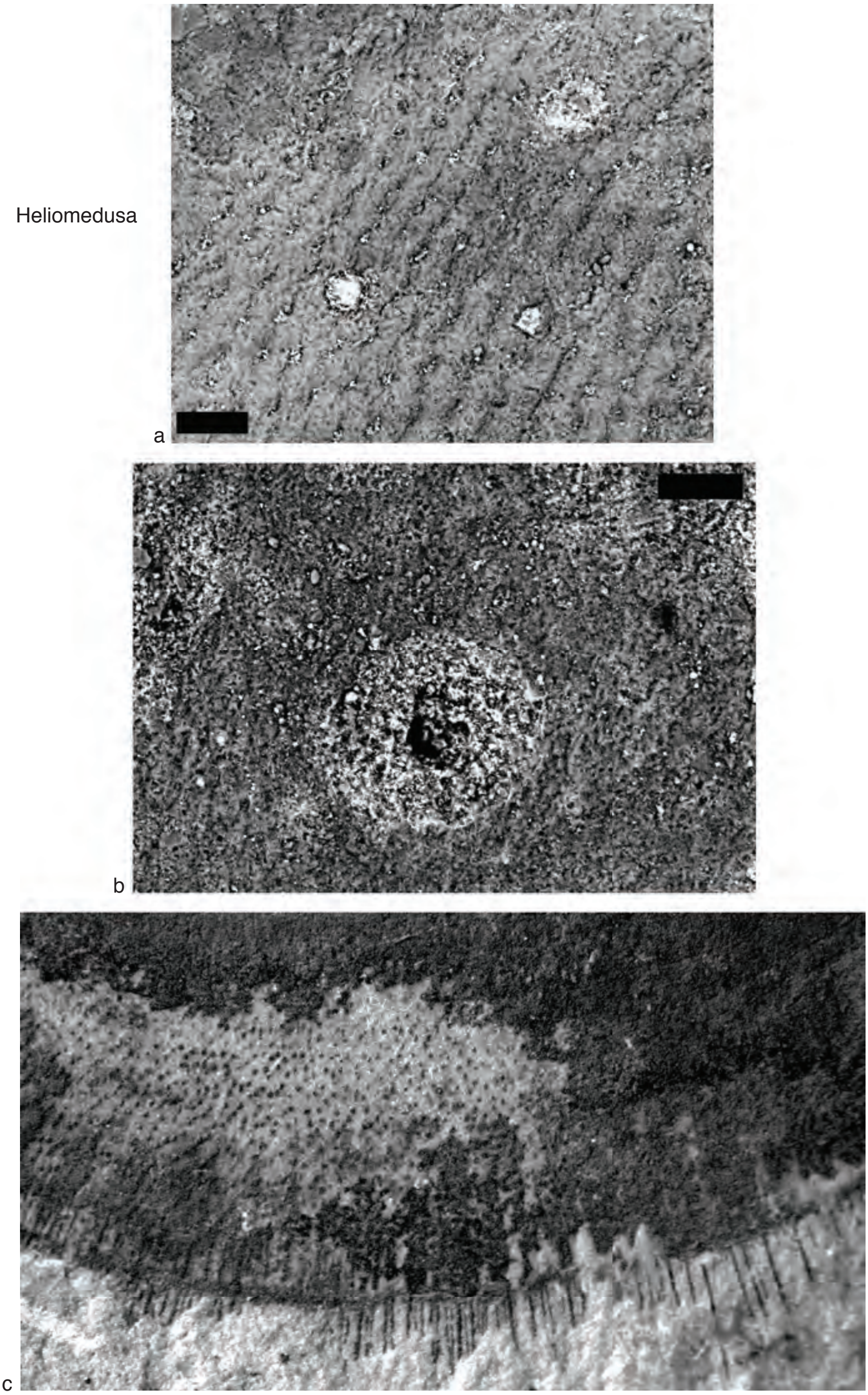


FIG. 1716. Mickwitziids (p. 2582–2590).

1715*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* apex of dorsal valve exterior, showing delineated juvenile shell, with rows of pustules, ×40; *b,* detail of anterolateral margin, showing parallel thick tubes, with pyritized spinelike setae, NIGP11, ×30; *c,* detail of punctate shell structure with thick orthogonal canals exposed on exfoliated surface of ventral valve exterior, ×40 (new).——FIG. 1716*a–c*. **H. orienta*, Chengjiang Lagerstätte, Yu'anshan Formation; *a,* detail of anterior margin showing punctate shell structure with openings of thick canals and preserved thick spinelike setae, as well as thinner (=possible marginal) setae, NIGP33, ×7; *b,* detail of one canal showing wall and central canal, width may have been enlarged during taphonomy, ×150; *c,* detail of pustulose ornamentation, with openings (and pyritized matter inside, which may represent setae) of orthogonal canals close to umbo, NIGP9, ×200 (new).

CRANIATA

LEONID E. POPOV,[1] MICHAEL G. BASSETT,[1] and LARS E. HOLMER[2]

[[1]National Museum of Wales; and [2]University of Uppsala]

Subphylum CRANIIFORMEA Popov & others, 1993

Class CRANIATA Williams & others, 1996

POPOV, BASSETT, and HOLMER (2000) reviewed the problems surrounding the classification of the groups included currently within the Craniata. In most previous phylogenetic models it was assumed that the three main groups of craniates, the Craniidae, Craniopsidae, and Trimerellidae, had originated from separate organophosphatic-shelled ancestors around the Ordovician, approximately (e.g., WILLIAMS & ROWELL, 1965c, fig. 141). The craniates form a monophyletic group in the analyses by HOLMER and others (1995), POPOV, HOLMER, and BASSETT (1996), and POPOV, HOLMER, and BASSETT (2000, fig. 1), whereas several cladograms in the studies by WILLIAMS and others (1996) and WILLIAMS, CARLSON, and BRUNTON (2000) were inconclusive, in particular regarding the phylogenetic position of the craniates relative to the class Chileata. This problem clearly needs further study, and the phylogenetic relationships between the three orders of craniates are still unresolved. The enigmatic *Heliomedusa* SUN & HOU from the Early Cambrian Chengjiang Lagerstätte (Yu'anshan Formation), Yunnan, was most recently assigned provisionally to the order Craniopsida within the Craniata (POPOV & HOLMER, 2000a; ZHANG, HOU, & EMIG, 2003). It can now be shown (reference to section above) to belong within the stem-group brachiopods, however, together with *Mickwitzia*. Thus, there is no longer any member of the class Craniata recorded from the Lower Cambrian, with only a potential Middle Cambrian representative (POPOV & HOLMER, 2000a), and the Cambrian origin of the craniiforms remains a problem.

Potential synapomorphies of the Craniata include possession of a nonfibrous carbonate shell and the lack of a pedicle. The mode of attachment of modern craniids may be important for understanding the origin and evolution of the brachiopod holdfast, however; WILLIAMS, BRUNTON, and MACKINNON (1997, p. 353) proposed that the attachment of modern *Novocrania* (NIELSEN, 1991), which consists of a thin patch of epithelium that is central to a shell secreted holoperipherally during postlarval growth, probably had as its plesiomorphy an atrophied holdfast acting as a pedicle. It is possible that this type of attachment may possibly be close to the primitive type of craniiform-rhynchonelliform pedicle. No craniate preserves any clear trace of a larval shell (CHUANG, 1977; but see FREEMAN & LUNDELIUS, 1999 for a contrasting view), indicating that their ontogeny was like that of Recent *Novocrania* (NIELSEN, 1991), where the first shell is secreted only after settlement. The mantle lobes remain separated throughout ontogeny (ROWELL, 1960), but NIELSEN (1991) showed that both valves are secreted initially within a single epithelial area on the dorsal side of the early postlarval stage. This may suggest that the adult separation of the mantle lobes represents a derived feature for the craniiforms, while fused mantle lobes may be the plesiomorphic state (and also in the paterinates and chileates). *?Middle Cambrian, Ordovician–Holocene.*

CRANIOPSIDA

LEONID E. POPOV and LARS E. HOLMER
[National Museum of Wales; and University of Uppsala]

Order CRANIOPSIDA Gorjansky & Popov, 1985

Only four genera can still be referred unquestionably to this group, all of which are Ordovician to Carboniferous in age. Craniopsides are characterized by extremely simple craniiform morphology and an impunctate calcareous shell; the cladistic analysis by POPOV, BASSETT, and HOLMER (2000) indicated that they might represent a paraphyletic stem group from which the Craniida and Trimerellida were derived. The only possible Cambrian craniopside is now the problematic Middle Cambrian *Discinopsis* (POPOV, HOLMER, & BASSETT, 1996; POPOV, BASSETT, & HOLMER, 2000). *?Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

CRANIIDA

MICHAEL G. BASSETT
[National Museum of Wales]

Since the earlier compilation of the craniide section in Volume 2 of the revised brachiopod *Treatise* (BASSETT, 2000), only two new craniid genera have been published, as detailed below. Molecular phylogenetic analyses (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998; COHEN, 2000) have confirmed the evolutionary stability of the group and its relationships with other brachiopod clades, including phoronids. Such stability is also reflected in the evolution of the chemicostructure and fabric of the craniid shell, which has been virtually unchanged since the first appearance of the stock in the Early Ordovician (Arenig) (CUSACK & WILLIAMS, 2001a; WILLIAMS, CUSACK, & BROWN, 1999; PEREZ-HUERTA, CUSACK, & ENGLAND, 2007); especially important in these studies has been a greater understanding of ventral valve structure, not least because this valve is generally weakly developed and differentially mineralized by comparison with the dorsal valve.

The order Craniida continues to consist of a single family (Craniidae) within a single superfamily (Cranioidea).

Order CRANIIDA Waagen, 1885

Superfamily CRANIOIDEA Menke, 1828

Family CRANIIDAE Menke, 1828

Celidocrania LIU, ZHU, & XUE, 1985, p. 9 [40] [**C. luohensis*; OD]. [This genus was earlier synonymized with *Acanthocrania* (see BASSETT, 2000, p. 171).

They are certainly very close in dorsal morphology, in particular with a common ornamentation of coarse spines and papillae and with distinctively large anterior adductor muscle scars divided by a weak myophragm, although in *Celidocrania* this latter feature becomes a distinct longitudinal ridge anteriorly. Closer comparison was originally not possible based only on the original illustrations of the Chinese material from Hinggan Ling in Heilongjiant Province. Recently, however, it has been possible to examine type specimens of *Celidocrania,* which confirms their general similarity to *Acanthocrania,* with the possible exception of the distinct anterior ridge.

One factor to bear in mind when comparing the two genera is their differences in age. Known specimens of *Acanthocrania* first appear in the lower Upper Ordovician (Caradoc, Sandbian). The type specimens of *Celidocrania* are from the Dazhi-Xiqiue lithological interval of somewhat earlier, mid-Ordovician age (upper Arenig–lower Llanvirn; Liu, Zhu, & Xue, 1985).]

Deliella HALAMSKI, 2004, p. 182 [**D. deliae*; OD]. Small, dorsal valve subconical, beak posteriorly subcentral, anterior face convex, posterior face subplanar; ornament of fine costae, branching costellae, and capillae; fine concentric growth lines forming a netlike granular pattern at intersection with radial ornament; encrusting; ventral valve not known. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Poland, Germany, Ukraine, North America.

Mesocrania SMIRNOVA, 1997, p. 998 [**Craniscus barskovi* SMIRNOVA, 1972, p. 20; OD]. Dorsal valve low and undulose or weakly subconical with subcentral to posterocentral beak; shell outline subsquare through subrectangular to slightly rounded; weakly preserved growth lines and occasional short, irregular riblets; dorsal posterior adductor scars large, separated, close under posterior margin; anterior adductors large, rounded to kidney shaped, raised on flaring platform and separated by a slender ridge; limbus–marginal rim slender; shell structure with some branching punctate canals; encrusting; ventral valve not known. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Berriasian)*: Ukraine.

Novocrania LEE & BRUNTON, 2001, p.5 [**Patella anomala* Müller, 1776, p. 237; OD]. [*Novocrania* is a *nomen novum* proposed as a replacement generic name for *Neocrania* LEE & BRUNTON, 1986, p. 150, which is preoccupied by an insect genus (Lepidoptera) published by DAVIS, 1978, p. 92 (type species, *Neocrania bifasciata*). Diagnostic characters, stratigraphic range, and geographic distribution of *Novocrania* are as set out by BASSETT, 2000, p. 180, fig. 100,*2a–h* (under *Neocrania*); one amendment is to note that in fact the thin, encrusting ventral valve of Recent species, including the type species, is not uncommonly weakly calcified, confirming the disposition of large, submarginal, rounded, and separated posterior muscle scars, with large, posterocentral, medially united anterior scars within a heart-shaped pit bounded by a strong rim; ventral limbus broad, pustulose; vascular system pinnate.]

TRIMERELLIDA

LEONID E. POPOV and LARS E. HOLMER

[National Museum of Wales; and University of Uppsala]

Order TRIMERELLIDA Gorjansky & Popov, 1985

The Trimerellida constitute a small but well-defined clade of quite large articulated organocarbonatic-shelled brachiopods. The analyses by POPOV, HOLMER, and BASSETT (1996) and POPOV, BASSETT, and HOLMER (2000) gave support for the view that they constitute a monophyletic group within the Craniata. The earliest known trimerellides, the Ussuniidae from the Llandeilo, show affinities with the craniopsides in their muscle system and other characters, as noted by GORJANSKY and POPOV (1986). *Ordovician (Llandeilo)–Silurian (Ludlow).*

Superfamily TRIMERELLOIDEA Davidson & King, 1872

Family TRIMERELLIDAE Davidson & King, 1872

[incl. Zhuzhaiidae XU & LI, 2002, p. 419]

Belubula PERCIVAL, 1995, p. 48 [**B. spectacula*; OD] [?=*Zhuzhaiia* XU & LI, 2002, p. 419 (type, *Z. transitense*)]. Shell large, globose, strongly biconvex; ventral valve with prominent, incurved beak; ventral interarea triangular, concave, divided by broad, concave homeodeltidium; ventral interior with deep umbonal cavities; muscle platform low, solid; cardinal buttress stout, wall-like; dorsal interior with low visceral platform, slightly vaulted anteriorly. *Ordovician (Caradoc, ?Ashgill):* Australia (New South Wales), ?China.——FIG. 1717,*4a–d*. **B. spectacula*, Belubula Limestone, Caradoc, New South Wales, Australia; *a*, dorsal valve interior, SUP73473, ×1.6;

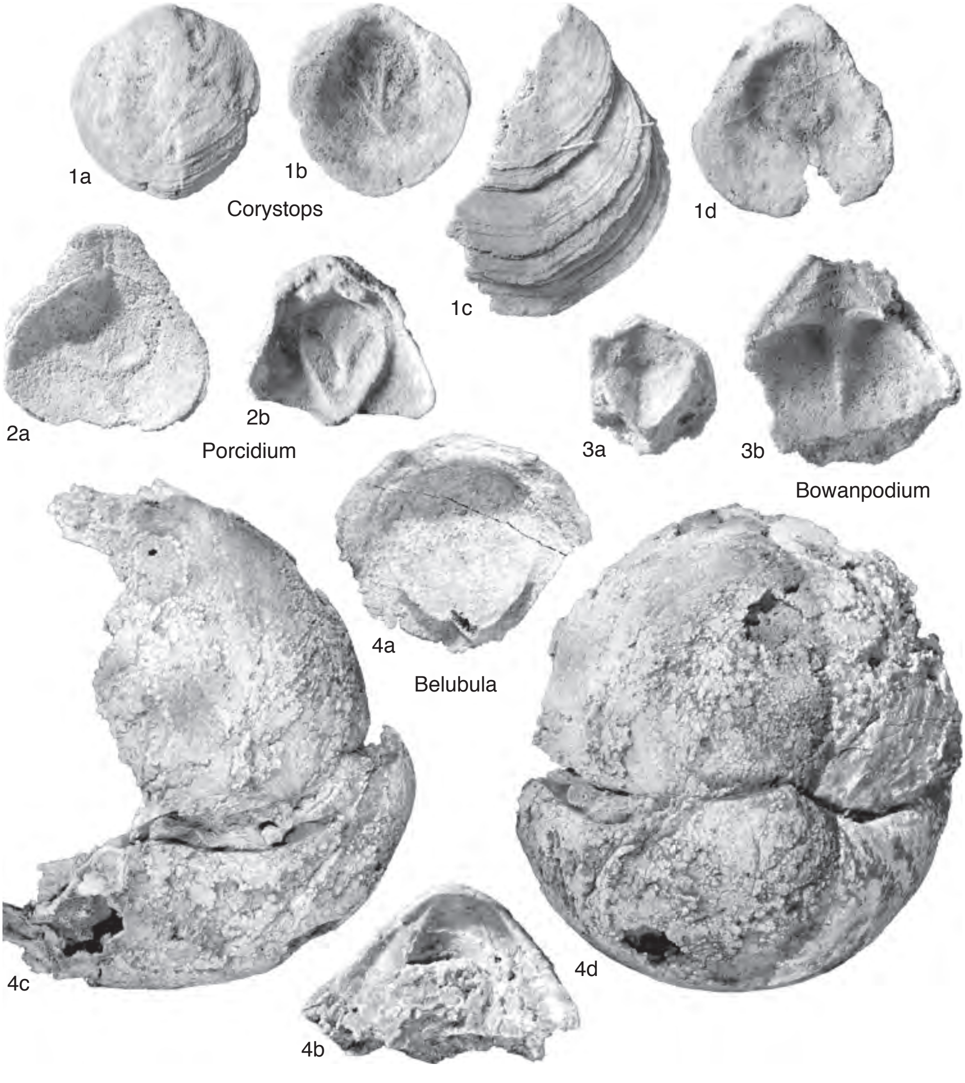


FIG. 1717. Trimerellidae (p. 2592–2594).

b, ventral valve, interarea, SUP73476, ×1; *c–d*, holotype, conjoined valves, lateral view, posterior view, SUP73470, ×1 (Percival, 1995).

Bowanpodium PERCIVAL, 1995, p. 55 [**B. solidum*; OD]. Shell biconvex; ventral valve with high interarea, divided by broad homeodeltidium; umbonal cavities vestigial, ventral muscle platform low, solid; cardinal buttress prominent, supported anteriorly by ridge; dorsal muscle platform solid, strongly thickened, elevated anteriorly and excavated anterolaterally, and with weak anterior median ridge. *Ordovician (Caradoc):* Australia (New South Wales).——FIG. 1717,*3a–b*. **B. solidum*, Quondong Limestone; *a*, holotype, dorsal valve interior, AMF60700, ×3; *b*, ventral valve interior, AMF60757, ×1.5 (Percival, 1995).

Corystops PERCIVAL, 1995, p. 55 [**C. lamellatus*; OD]. Shell dorsibiconvex to convexiplanar, lamellose; ventral interarea undivided, planar, and strongly apsacline; ventral interior with low, solid visceral platform; dorsal interior with low, solid visceral platform, divided anteriorly by median ridge. *Ordovician (Caradoc):* Australia (New South Wales).——FIG. 1717,*1a–d*. **C. lamellatus*, Quondong Limestone; *a–b*, holotype, dorsal valve exterior, interior of holotype, SUP63498, ×2; *c*, ventral valve exterior, SUP63502, ×2; *d*, ventral valve interior, SUP63503, ×2 (Percival, 1995).

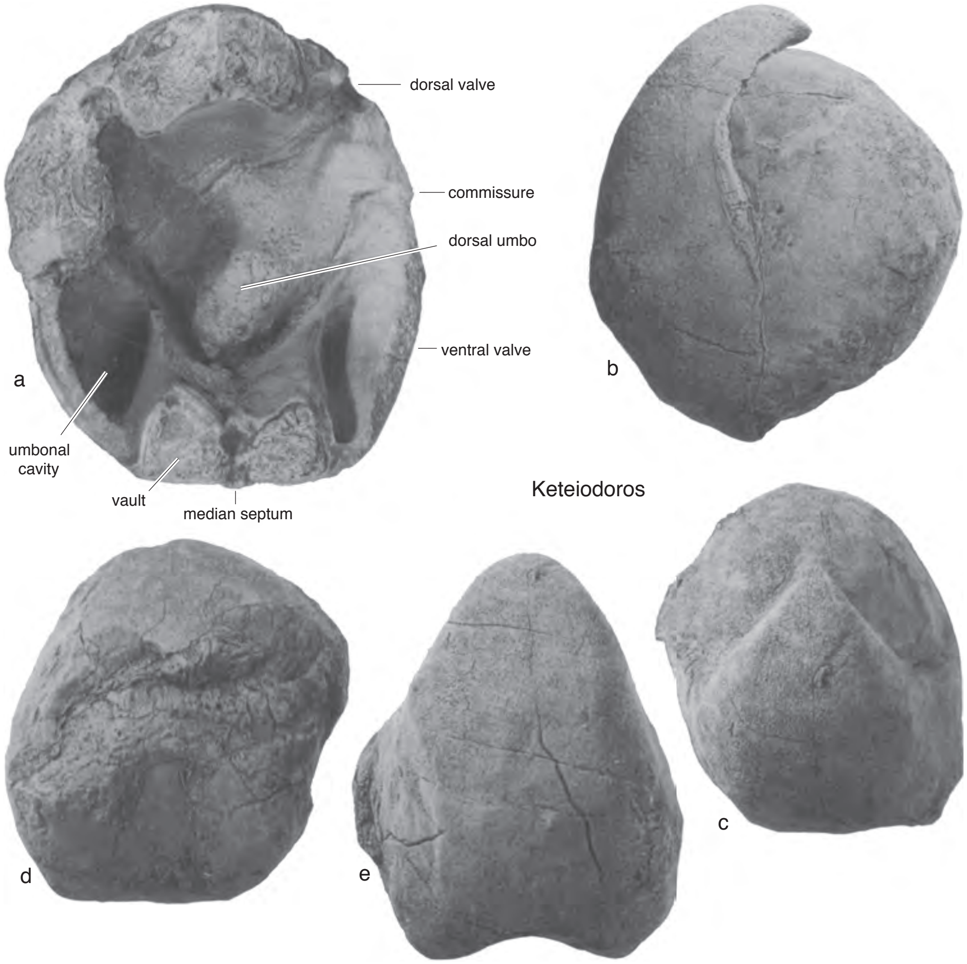


Fig. 1718. Trimerellidae (p. 2594).

Keteiodoros Strusz & others, 1998, p. 176 [**K. bellense*; OD]. Shell very large and strongly equibiconvex; ventral umbo long, incurved; dorsal umbo strongly incurved, bulbous, fitting against posterior end of ventral platform; long, thick longitudinally and transversely curved articulating plate, more or less concentric with umbo, extending from dorsal beak almost to surface of ventral platform; valve margins slightly overlapping dorsoventrally in front of flattened zones, serving as articulatory structure; both valves with deeply excavated, steep-sided platform supported by long median septum; ventral valve with deep umbonal cavities. *Silurian (Wenlock):* Australia (New South Wales).——Fig. 1718*a–e*. **K. bellense*, Dripstone Formation, southeast of Wellington, central New South Wales; *a*, holotype, anterior view of inside of complete articulated shell, AMF101116, ×0.4; *b–e*, lateral, posterior, anterior, and ventral views of complete articulated shell, AMF101117, ×0.4 (Strusz & others, 1998).

Porcidium Percival, 1995, p. 53 [**P. dorsilobum*; OD]. Shell dorsibiconvex; ventral interarea orthocline, planar to weakly concave, bisected by narrow ridgelike homeodeltidium, flanked by deep grooves; ventral interior with low, solid visceral platform, slightly elevated anteriorly; cardinal buttress rudimentary to absent; dorsal visceral platform low, solid, surrounded by raised peripheral rim, with anterior adductors bisected by low median ridge; hinge plate forming prominent curved transverse bar, with strongly impressed, paired internal oblique muscle scars. *Ordovician (Caradoc):* Australia (New South Wales).——Fig. 1717,*2a–b*. **P. dorsilobum*, Quondong Limestone; *a,* holotype, ventral valve interior, SUP63482, ×3; *b*, dorsal valve interior, SUP63493, ×3 (Percival, 1995).

CHILEATA

LEONID E. POPOV and LARS E. HOLMER

[National Museum of Wales; and University of Uppsala]

Subphylum RHYNCHONELLIFORMEA Williams & others, 1996
Class CHILEATA Williams & others, 1996

The chileates include the two orders Chileida and Dictyonellida. The systematic position of the latter group has long been problematic (ROWELL, 1965; WRIGHT, 1981). The chileides were first discovered by POPOV and TIKHONOV (1990) from the Botomian of Kyrgyzstan, and they became extinct by the Middle Cambrian (POPOV & HOLMER, 2000b). The chileides are the earliest known organocarbonatic-shelled brachiopod with a strophic hinge line; however, there are no articulatory structures associated with the posterior margin, and POPOV and TIKHONOV (1990; see also POPOV, 1992) proposed that fused mantle lobes fixed the axis of rotation. The cladistic analysis by POPOV, BASSETT, and HOLMER (2000) indicated that the Cambrian Chileida and the Ordovician-Permian Dictyonellida form a monophyletic group defined mainly by the development of a large umbonal perforation, which is enlarged by resorption and can be covered by a posterior plate, termed the colleplax (WRIGHT, 1981). WRIGHT (1981) proposed that this structure (in the dictyonellides) served as a holdfast by means of an organic pad, and this interpretation is also likely for the chileides. POPOV, HOLMER, and BASSETT (1996) suggested that many of the characters of the chileides might be primitive, and thus they were used to polarize the character transformation in the cladistic analysis of the organocarbonatic-shelled forms. *Lower Cambrian (Botomian)–Permian.*

Class OBOLELLATA Williams & others, 1996
Order NAUKATIDA Popov & Tikhonov, 1990
Superfamily NAUKATOIDEA Popov & Tikhonov, 1990
Family PELMANELLIDAE Popov & others, 1997

[Pelmanellidae POPOV & others, 1997, p. 343]

Shell with rudimentary dorsal interarea; notothytrial platform lacking; ventral interior lacking denticles on anteris; posterior adductor scars on separate paired cardinal muscle platforms in both valves. *Lower Cambrian (Botomian–Toyonian).*

Pelmanella POPOV & others, 1997, p. 343 [**P. borealis*; OD]. Shell ventribiconvex, elongate to subcircular, with straight anterior commissure; delthyrium open, narrow, triangular, with distal margins joined by anteris; ventral interior with central muscle platform separated from cardinal muscle platforms by deep oblique grooves; dorsal interior with medianly located anterior adductor scars divided by median ridge. *Lower Cambrian (Toyonian):* Greenland.——FIG. 1719*a–b*. **P. borealis*, Paralleldal Formation, Peary Land, central North Greenland; *a*, holotype, ventral valve interior, MGUH23743, ×5.4; *b*, dorsal valve interior, MGUH23747, ×5.4 (Popov & others, 1997).

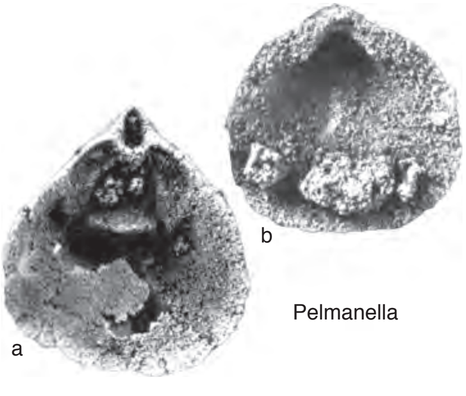


FIG. 1719. Pelmanellidae (p. 2595).

KUTORGINATA

LEONID E. POPOV and ALWYN WILLIAMS

[National Museum of Wales, Cardiff; deceased, formerly of the University of Glasgow]

Class KUTORGINATA Williams & others, 1996

The Cambrian genus *Anomalocalyx* cannot be assigned with confidence to any existing class or lower-ranked suprageneric taxon. The genus has a well-developed convex pseudodeltidium, broad open notothyrium, and possibly a perforated ventral umbo, which features are characteristic only of kutorginides among Early to Mid-Cambrian rhynchonelliform brachiopods. *Anomalocalyx* also possesses dorsal sockets and socket ridges, which are otherwise present in the Nisusioidea. The taxonomic position of the genus is therefore most likely to be within the Kutorginida. The presence of paired denticles along the posterior margin and a long tubelike structure, which according to BROCK (1999) shows remarkable similarity to the elongate, tapering, tube-shaped structure of the Permian richthofenioid *Cyndalia*, are anomalous. These features are otherwise unknown among Cambrian rhynchonelliforms.

Order KUTORGINIDA Kuhn, 1949

Superfamily and Family UNCERTAIN

Anomalocalyx BROCK, 1999, p. 182 [**A. cawoodi*; OD]. Shell with deeply coniform ventral valve; ventral interarea catacline to weakly procline with narrow delthyrium, covered completely by evenly convex pseudodeltidium; dorsal valve with incurved umbo, wide, poorly defined, open notothyrium and broad median sulcus; ornament of low, broad costellae becoming fluted at commissural margin and regular concentric growth lamellae; ventral interior with a pair of rounded, dorsally directed, nublike denticles situated on either side of delthyrium, and elongate, tapering, tubelike structure extending toward posterior shell margin directly under pseudodeltidium; dorsal interior with small, divergent socket ridges bordering anteriorly shallow sockets excavated into posterior valve wall. *Middle Cambrian (Floran–Undillan):* Australia (New South Wales).——FIG. 1720*a–g*. * *A. cawoodi*, Murrawong Creek Formation, Murrawong Creek; *a*, holotype, ventral valve oblique posterior, ×45; *b–c*, posterior and side views, AM F97383, ×43; *d–e*, oblique lateral views of incomplete ventral valve showing tubelike structure, AM F107867, ×35; *f*, dorsal valve interior showing socket ridges, AM F107869, ×51; *g*, dorsal valve exterior, AM F107870, ×38 (Brock, 1999).

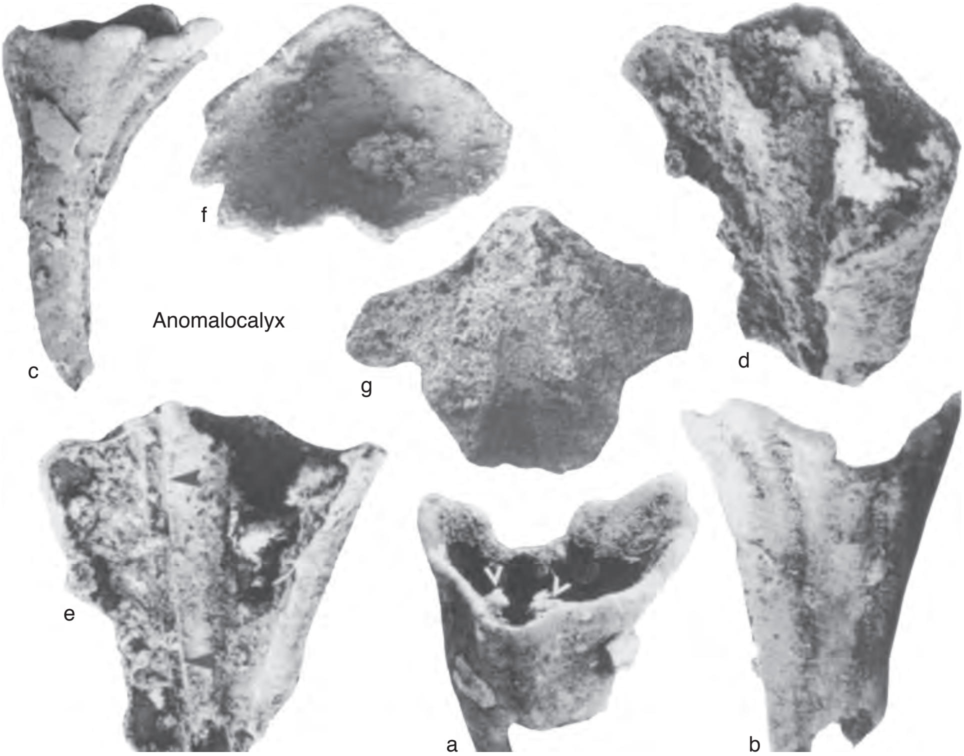


FIG. 1720. Uncertain (p. 2596).

STROPHOMENIDA

L. R. M. Cocks and Rong Jia-Yu

[The Natural History Museum, London; and Academia Sinica, Nanjing]

Class STROPHOMENATA Williams & others, 1996

Order STROPHOMENIDA Öpik, 1934

Since the publication of *Treatise Part H, revised,* volume 2 (Cocks & Rong, 2000, p. 216), an analysis of Ordovician brachiopods (Harper & others, 2004) has been published that includes not only the origins of the Strophomenoidea and Plectambonitoidea within the early Ordovician but also the differing distribution patterns within the two superfamilies (Fig. 1721), with the Plectambonitoidea peaking in the mid-Caradoc and the nondenticulate Strophomenoidea reaching their acme in the mid-Ashgill. The overall classification of the order remains unchanged from 2000.

Superfamily STROPHOMENOIDEA King, 1846

In the main treatment of the Strophomenoidea (Cocks & Rong, 2000, p. 217), the classification within the superfamily was based primarily on the different forms of the cardinal process, together with the presence or absence of denticles along the hinge line, which differentiated the various families following the analysis of Rong and Cocks (1994). This treatment has met with general acceptance and is unchanged here, apart from the addition of the subfamily Ungulomeninae within the Glyptomenidae.

Family STROPHOMENIDAE King, 1846

Subfamily STROPHOMENINAE King, 1846

Gunnarella Spjeldnæs, 1957, p. 149 [**Strophomena (G.) delta;* OD]. Outline semicircular; profile gently convex posteromedianly but anteriorly evenly resupinate, with concavity of up to 50°; distinctive ornament of costellae interrupting small rugellae over nearly all the valve surface; weak teeth but short dental plates extending anterolaterally to subparallel muscle-bounding ridges; ventral muscle field suboval and without bounding ridges anteromedianly; dorsal interior with short socket plates diverging at about 100°; dorsal side septa absent. [This genus is listed, and the type species figured, in Cocks & Rong, 2000, p. 302, fig. 194.*2a–b,* within Strophomenoidea family Uncertain. New understanding of the valve interiors (Cocks, 2005) enables firm positioning of the genus within the Strophomeninae.] *Ordovician (Caradoc–Ashgill):* Baltica and Avalonia.——Fig. 1722,*1a–c. G. magnifica* Cocks, Boda Limestone, middle Ashgill, Dalarna, Sweden; *a,* dorsal exterior, Kallholn Quarry, RMS Br 6988, ×2; *b,* holotype, dorsal exterior of conjoined valves showing interarea, Kallholn Quarry, RMS Br 6989, ×2.5; *c,* ventral interior, Osmundsberget Quarry, BMNH BC 58024, ×2 (Cocks, 2005).

Leigerina Rõõmusoks, 2004, p. 19 [**L. hiiuensis;* OD]. Semicircular outline; profile mainly gently biconvex, with dorsal valve slightly concave posteromedianly only. Ornament evenly parvicostellate; no rugae known. Relatively large apsacline ventral interarea with large pseudodeltidium; small anacline dorsal interarea with low chilidium. Ventral interior with relatively small flaring teeth merging anterolaterally with muscle-bounding ridges bordering subcircular muscle field; very thin and relatively inconspicuous ventral median septum. Dorsal interior with prominent erect cardinal process between prominent curved socket plates. Low myophragm and dorsal muscle field very weakly impressed. *Ordovician (Caradoc–Ashgill):* Baltica.——Fig. 1722,*2a–d. *L. hiiuensis,* Kõrgessare formation, Vormsi Stage, lower Ashgill, Estonia; *a,* holotype, dorsal exterior, Kõrgessare, TUG 1003-109, ×1.5; *b,* ventral interior, Kärdla, TUG 42-61, ×1.5; *c,* interarea of conjoined valves, Kõrgessare, TUG 50-30, ×2; *d,* dorsal interior, Kohila, TUG 106-20, ×1.5 (Rõõmusoks, 2004).

Nasutimena Jin & Zhan, 2001, p. 30 [**Strophomena fluctuosa* Billings, 1860, p. 57; OD]. Outline subtriangular to subpentagonal; smoothly geniculate profile; ornament unequally parvicostellate, with small concentric to crisscross rugae interrupted by the major costellae variably developed over all or part of shell. Ventral and dorsal interiors as in *Strophomena,* apart from shorter and weaker dorsal transmuscle septa. *Ordovician (Ashgill):* North America.——Fig. 1723*a–e. *N. fluctuosa; a–c,* holotype, dorsal, anterior, and ventral views of dorsal exterior, Vaureal Formation, middle Ashgill, Anticosti Island, Canada, GSC 2017, ×2; *d,* ventral

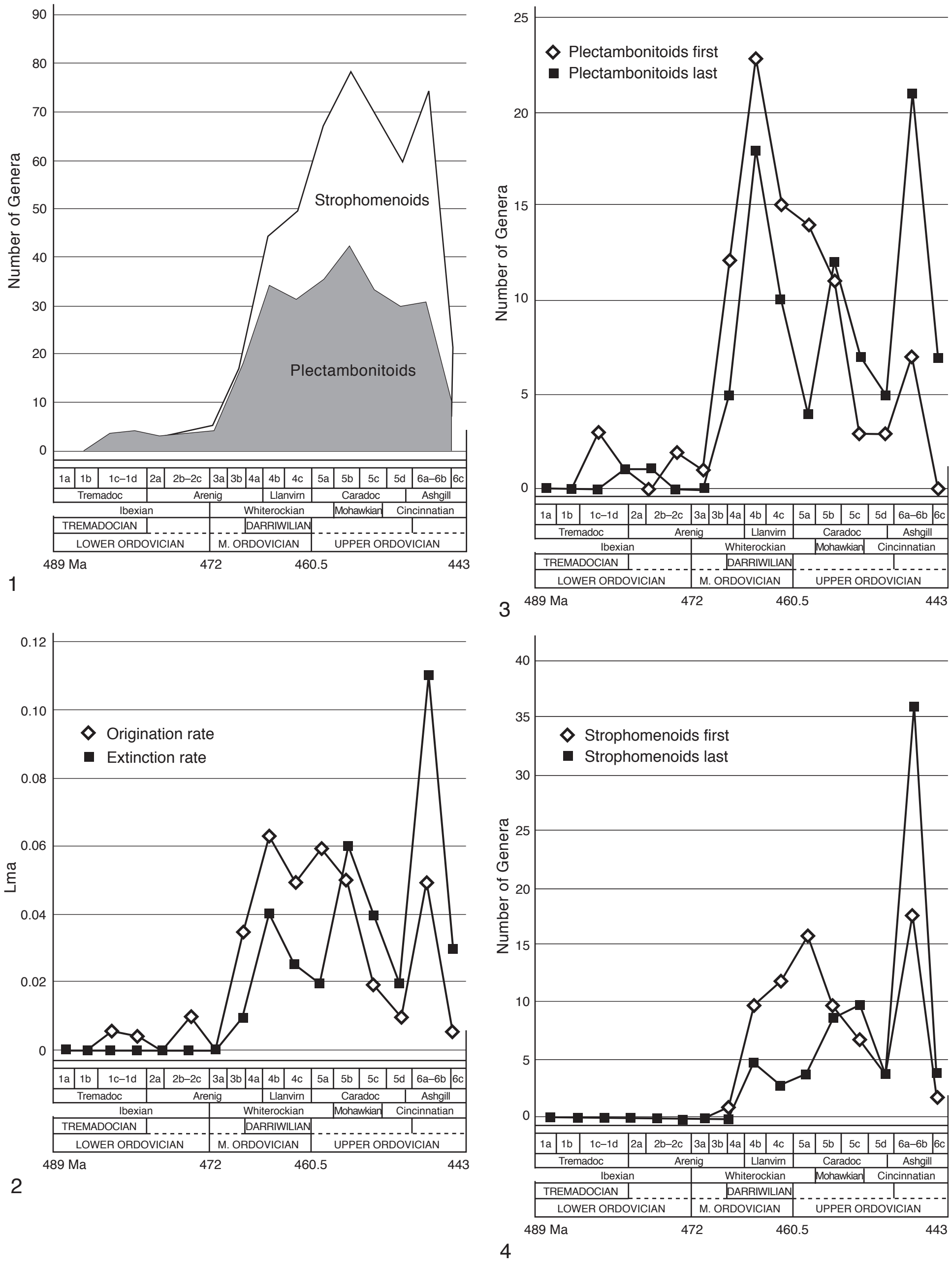


FIG. 1721. Strophomenide Ordovician diversity; *1,* absolute abundances of two superfamilies of strophomenide brachiopods; *2,* extinction and origination rates across strophomenoids; *3,* first and last appearances of plectambonitoideans; *4,* first and last appearances of strophomenoideans; *Lma,* lineage million years (adapted from Cocks in Harper & others, 2004).

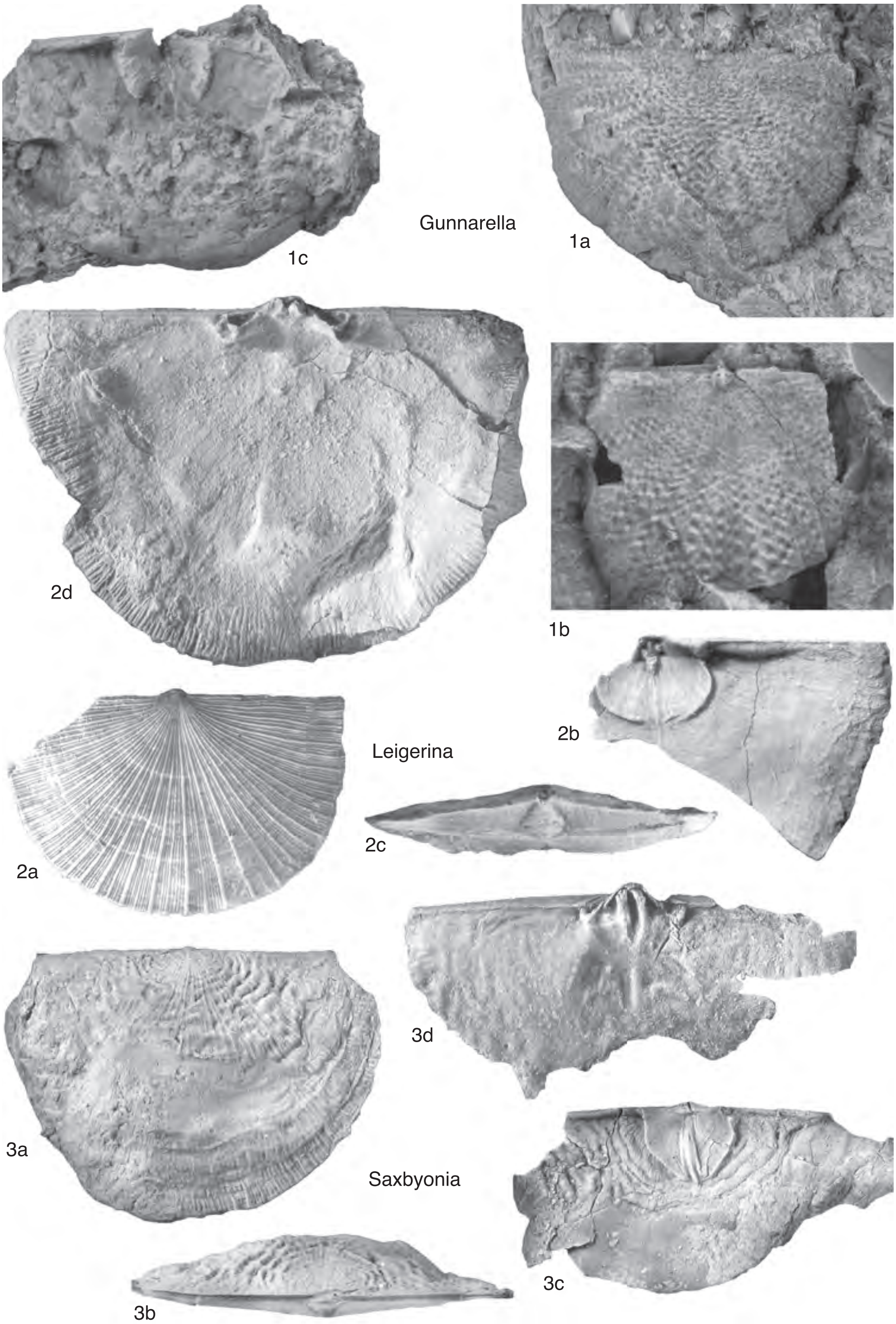


FIG. 1722. Strophomenidae (p. 2598–2602).

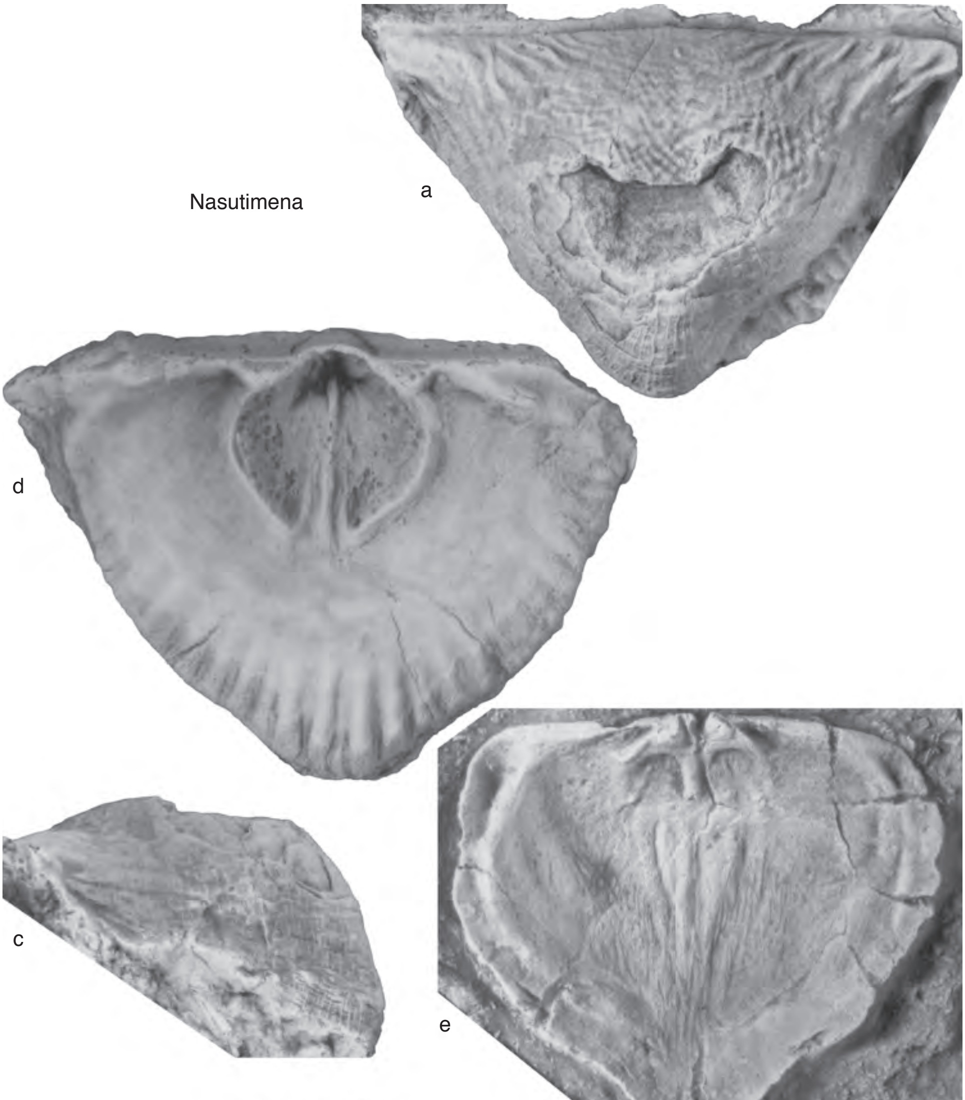


FIG. 1723. Strophomenidae (p. 2598–2602).

interior, Caution Creek Formation, middle Ashgill, Hudson Bay Lowlands, Canada, GSC 109020, ×2.5; *e,* dorsal interior, Stony Mountain Formation, Ashgill, southern Manitoba, Canada, GSC 109021, ×2.5 (new).

Pseudostrophomena Rõõmusoks, 1963, p. 237 [**P. reclinis;* OD]. [This genus has two entries: in Cocks & Rong, 2000, p. 224 within the Strophomenoidea, and in Williams and Brunton, 2000, p. 674 within the Chilidiopsoidea. Further work on and redescription of the type material from Estonia by Rõõmusoks (2004) has firmly established the presence of pseudopunctae and confirmed its position within the Strophomenoidea.] *Ordovician (Caradoc–Ashgill):* Baltic.

Saxbyonia Rõõmusoks, 2004, p. 20 [**S. fluctuosa;* OD]. Semicircular to trapezoidal outline. Profile initially biconvex; resupinate anteriorly. Ornament irregularly parvicostellate with distinctive small irregular rugae over much of the valve surface, particularly posteromedianly. Apsacline ventral interarea with pseudodeltidium; dorsal anacline interarea with chilidium of subequal size to pseudodeltidium, together filling delthyrium. Ventral interior with low teeth merging anterolaterally with subpentagonal muscle area, which is slightly raised and undercut. Dorsal interior with prominent cardinal process projecting posteriorly and extending for some distance anteriorly, uniting anteriorly onto low myophragm. Short but prominent curved socket plates. Dorsal muscle field poorly impressed. *Ordovician (Ashgill):* Baltica.——Fig. 1722,*3a–d.* **S. fluctuosa,* Kõrgessare Formation, Vormsi Stage, lower Ashgill, Estonia; *a–b,* holotype, dorsal and posterior views of conjoined valves, Vormsi Island, TUG 80-132, ×1; *c,* ventral interior, Kõrgessare, Hiiuma Island, TUG 50-24, ×1.5; *d,* dorsal interior, Kohila, GMUT Br 1546, ×1.5 (Rõõmusoks, 2004).

Subfamily FURCITELLINAE Williams, 1965

Bekkerina Rõõmusoks, 1993, p. 50 [**Rafinesquina dorsata* Bekker, 1921, p. 73; OD] [=*Haljalanites* Rõõmusoks, 2004, p. 29 (type, *Rafinesquina anijana* Öpik, 1930, p. 197, OD]. [*Haljalanites* is identical in all significant external and internal generic characters to *Bekkerina,* whose type species, *B. dorsata*, was illustrated by Cocks & Rong, 2000, fig. 138,*3a–d*, and the two nominal genera also overlap in distribution.] *Ordovician (Darriwilian–lower Caradoc):* Baltica.——Fig. 1724,*1a–c. B. assatkini* (Alichova), Kahula Formation, Hajala Stage, lower Caradoc, Aluvere Quarry, Estonia; *a,* ventral exterior, TUG 77-161, ×2; *b,* ventral interior, TUG 1003-41, ×2.5; *c,* dorsal interior, TUG 72-73, ×2.5 (Rõõmusoks, 2004).

?Djindella Menakova , 1991, p. 25 [**D. plana;* OD]. Semicircular to subquadrate outline; profile gently planoconvex to biconvex with low ventral fold and dorsal sulcus; low apsacline ventral interarea with pseudodeltidium covering delthyrium; strong teeth supported by dental plates extending anterolaterally into well-developed muscle-bounding ridges that converge anteriorly and form a high muscle platform supported by a median septum; dorsal interior with bifid cardinal process and notothyrial platform, otherwise poorly known. [This genus was originally described as an orthoidean; its dorsal interior is still poorly known, and it may be congeneric with *Dzhebaglina* (Cocks & Rong, 2000, p. 237).] *Ordovician (Ashgill):* central Asia. ——Fig. 1724,*2a–c.* **D. plana,* upper reaches of Dzhindy-Dariya River, Zerafshan Range, Tajikistan; holotype, dorsal, ventral, and lateral views of conjoined valves, Geological Museum of Tajikistan 1430/1, ×2 (Menakova, 1991).

Fenomena Zhan & Cocks, 1998, p. 45 [**F. distincta;* OD]. Profile planoconvex to slightly biconvex; rectangular to subsemicircular outline; large pseudodeltidium; small chilidium; dental plates short and weak with no ventral muscle-bounding ridges; strong bilobed cardinal process continuous with socket ridges laterally; short sockets with strong curved socket ridges; subperipheral rim in adults; elevated dissected dorsal muscle field; dorsal median septum. *Ordovician (Ashgill):* South China.——Fig. 1725,*2a–e.* **F. distincta*, Changwu Formation, middle Ashgill, Dianbian, Zhejiang Province; *a,* latex of dorsal exterior, NIGP 128077, ×4; *b–c,* internal mold and latex cast of ventral valve, NIGP 128073, ×2; *d–e,* internal mold and latex cast of dorsal valve, NIGP 128076, ×4 (Zhan & Cocks, 1998).

Karomena Popov, Nikitin, & Cocks, 2000, p. 855 [**K. squalida*; OD]. Profile dorsibiconvex to convexoplane, with slightly uniplicate anterior margin; ventral interarea planar, apsacline, with convex pseudodeltidium; dorsal interarea anacline, with entire convex chilidium; unequally parvicostellate ornament; ventral interior long, straight, divergent dental plates; poorly defined subrhomboidal muscle field with no bounding ridges; adductor scars completely separating diductor scars; dorsal interior with bilobed, posteriorly facing cardinal process on high notothyrial platform; strong socket ridges curved backward toward hinge line and fused with cardinal process; small adductor muscle field bisected by fine but prominent short median septum and two pairs of short, variable side septa, the subparallel inner pair being stronger. *Ordovician (Caradoc):* Kazakhstan.——Fig. 1724,*3a–e.* **K. squalida*, Otar Member, Dulankara Formation, upper Caradoc, Dulankara Mountain, Chu-Ili Range; *a–b,* ventral and lateral views of conjoined valves, CNIGR 63/12375, ×2; *c,* ventral internal mold, CNIGR 62/12375, ×2; *d–e,* dorsal internal mold, ×2, and latex cast, holotype, 61/12375, ×5 (Popov, Nikitin, & Cocks, 2000).

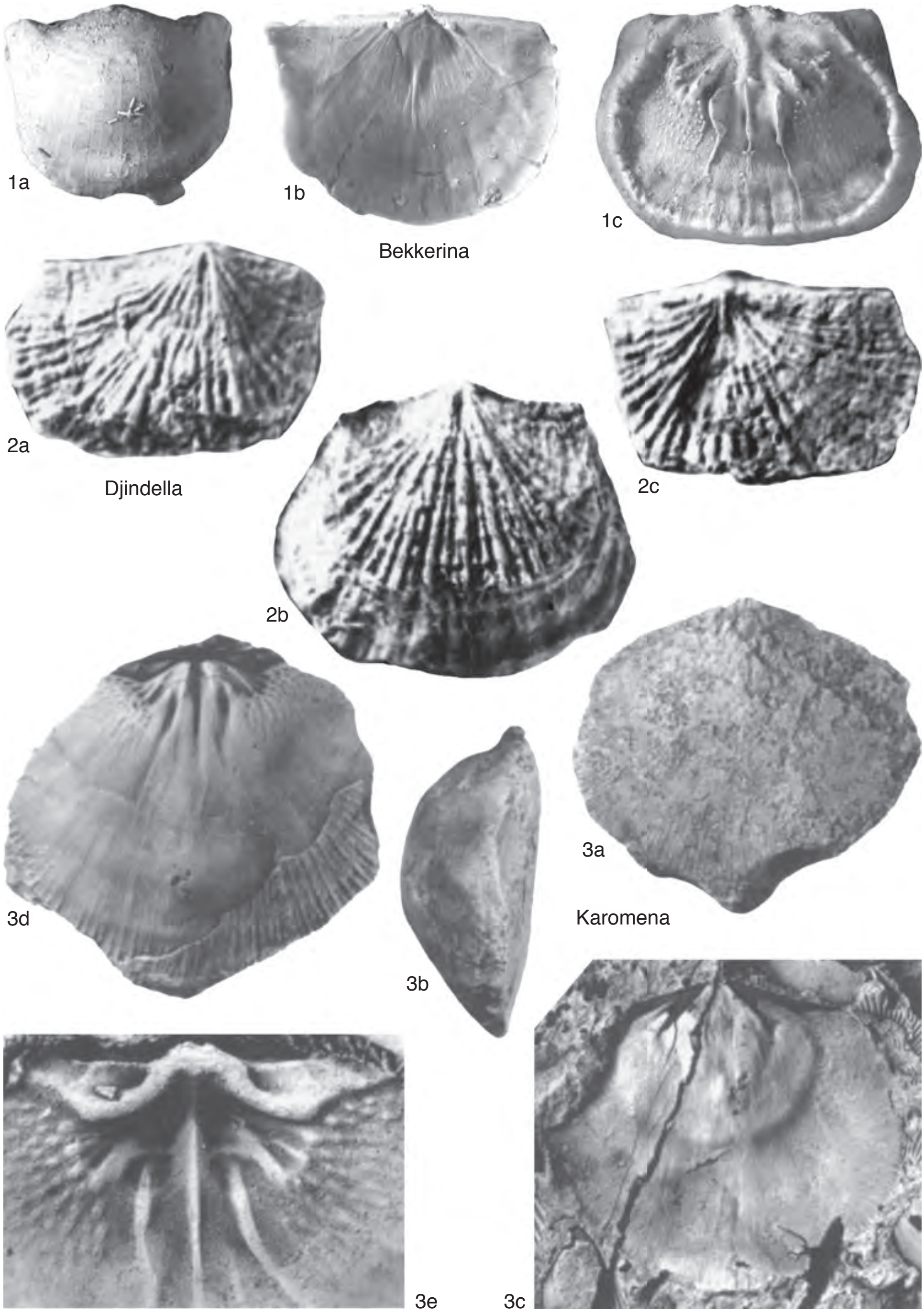


FIG. 1724. Strophomenidae (p. 2602).

Oepikoides Benedetto, 1995, p. 252 [**O. notus;* OD]. Dorsally gently geniculate profile; parvicostellate ornament; apsacline area with pseudodeltidium; suboval ventral muscle field without bounding ridges; similar to *Oepikina* in shape, but different internally in the lack of dorsal median septum, lateral septa, or subperipheral rim; internal papillae elongate, particularly posterolaterally; short flaring socket ridges; short erect cardinal process lobes directed posteriorly; mantle canals unknown. *Ordovician (Caradoc):* South America.——Fig. 1726,*1a–c.* **O. notus*, Las Plantas Formation, lower Caradoc, Gualcamayo, northern Precordillera, Argentina; *a,* ventral exterior, CEGH-UNC 13501, ×1.5; *b,* ventral interior, CEGH-UNC 13717, ×1.5; *c,* holotype, dorsal interior, CEGH-UNC 13716, ×2 (Benedetto, 1995).

Oxostrophomena Nikitina & others, 2006, p. 173 [**Strophomena dubia* Rukavishnikova, 1956, p. 143; OD]. Subquadrangular outline; profile strongly convexoconcave with very weak rounded geniculation. Ventral interarea apasacline with pseudodeltidium, dorsal interarea anacline to orthocline with discrete chilidial plates. Ornament parvicostellate with irregular small rugellae posterocentrally. Ventral interarea with large striated teeth supported by divergent dental plates extending anteriorly into muscle-bounding ridges at sides only of the suboval muscle field. Dorsal interior with cardinal process of narrow triangular notothyrial platform; short straight socket ridges striated posteriorly and divergent anteriorly; relatively small muscle field poorly developed; very short thin dorsal median septum in valve center only; mantle canals saccate. *Ordovician (Darriwilian):* Kazakhstan.——Fig. 1725,*3a–f.* **O. dubia*, Uzunbulak Formation, Kopalysai, Chu-Ili Range; *a–b,* dorsal and lateral views of dorsal exterior, USNM 485166, ×1.5; *c–d,* ventral interior mold and latex, USNM 485167, ×2; *e,* dorsal interior mold, ×2.2; *f,* latex mold, USNM 489169, ×3 (Nikitina & others, 2006).

Sakunites Rõõmusoks, 2004, p. 31 [**Leptaena luhi* Sokolskaya, 1954, p. 57; OD]. Outline semicircular with maximum width at hinge line or just anterior to it. Ventral valve profile gently convex, with minor and gradual geniculation near the anterolateral margins; dorsal valve relatively flat apart from gentle concavity at anterolateral margins. Umbo scarcely developed. Parvicostellate ornament with weak irregular rugae. Apsacline ventral interarea; smaller anacline dorsal interarea. Ventral interior with bilobed and slightly elevated muscle field surrounded by prominent muscle-bounding ridges. Dorsal interior with strong but short socket plates; narrow notothyrial platform; prominent muscle field with irregular margins that are elevated laterally. Short, fine dorsal median septum in valve center only. *Ordovician (Caradoc):* Baltica.——Fig. 1726,*2a–d. *S. luhi* (Sokolskaya), Vasalemma Formation, Oandu Stage, upper Caradoc, Estonia; *a,* ventral exterior, Tuula, TUG 72-237, ×2; *b*, ventral interior, Jõgisoo, TUG 72-175, ×1.5; *c–d,* exterior and interior of dorsal valve, Saku, TUG 72-173, ×2.7 (Rõõmusoks, 2004).

Tallinnites Rõõmusoks, 1993, p. 50 [**Oepikina? imbrexoidea* Sokolskaya, 1954, p. 51; OD] [=*Kukrusena* Rõõmusoks, 2004, p. 28 (type, *K. peetriensis,* OD)]. [See Cocks & Rong, 2000, p. 236. The nominal genus *Kukrusena* has all the generic characters of *Tallinnites,* whose type species, *T. imbrexoidea*, was illustrated by Cocks & Rong, 2000, fig. 144,*3a–c*.] *Ordovician (Darriwilian–lower Caradoc):* Baltica.——Fig. 1725,*1a–d. T. peetriensis* (Rõõmusoks), Viivikonna Formation, Kukruse Stage, lower Caradoc, Estonia; *a–b,* holotype, ventral and lateral views of ventral exterior, Peetri, TUG 1054-181, ×2; *c,* ventral interior, Peetri, TUG 72-201, ×1.8; *d,* dorsal interior, Humala, TUG 1003-345, ×2 (Rõõmusoks, 2004).

Trigrammaria Wilson, 1945, p. 140 [**T. trigonalis;* OD] [=*Microtrypa* Wilson, 1945, p. 144 (type, *M. altilis,* OD); *Crassoseptaria* Rõõmusoks, 2004, p. 37 (type, *Trigrammaria virve* Rõõmusoks, 1985, p. 134, OD)]. [The nominal genus *Crassoseptaria* has all the generic characters of *Trigrammaria,* whose type species, *T. trigonalis*, was illustrated by Cocks & Rong, 2000, fig. 145,*2a–c,* into which its type species was originally placed. See Cocks & Rong, 2000, p. 237.] *Ordovician (Darriwilian–Caradoc):* Laurentia, Baltica.——Fig. 1726,*3a–c. T. virve* Rõõmusoks, Paekna Formation, Nabala Stage, upper Caradoc, Estonia; *a*, holotype, conjoined valves, Laitse, TUG Br 1190, ×1.5; *b*, ventral interior, Nõmmeküla, TUG Br 1194, ×1.4; *c,* dorsal interior, Nõmmeküla, TUG Br 1193, ×4 (Rõõmusoks, 2004).

Family RAFINESQUINIDAE
Schuchert, 1893
Subfamily RAFINESQUININAE
Schuchert, 1893

Dirafinesquina Cocks & Zhan, 1998, p. 125 [**D. globosa*; OD]. Strongly convex ventral profile, gently concave and geniculate dorsal profile; semicircular outline; ventral bounding ridges surrounding a suboval and bilobed muscle field; cardinal process lobes variably developed from ponderous to weak but erect rather than anteriorly directed; low, short, straight, but variably thick socket ridges flaring laterally and separate from cardinal process; circular dorsal muscle field; low wide myophragm starting from notothyrial platform and narrowing anteriorly; mantle canals unknown. *Ordovician (Darriwilian–Caradoc):* Southeast Asia.——Fig. 1727,*3a–d.* **D globosa*; Naungkangyi Group, lower Caradoc, Linwe, Shan States, Myamnar, Burma; *a,* lateral view of ventral internal mold, BMNH BB37607, ×1.5; *b–c,* dorsal and posterior views of ventral internal mold, BMNH BB37619, ×2; *d,* holotype, latex cast of dorsal interior, BMNH BB37593, ×5 (Cocks & Zhan, 1998).

Hedstroemina Bancroft, 1929, p. 58 [**H. fragilis;* OD] [=*Virunites* Rõõmusoks, 2004, p. 41 (type, *Rafinesquina orvikui* Oraspõld, 1956, p. 49, OD)]. [*Virunites* has the same generic external and internal characters as *Hedstroemina,* whose

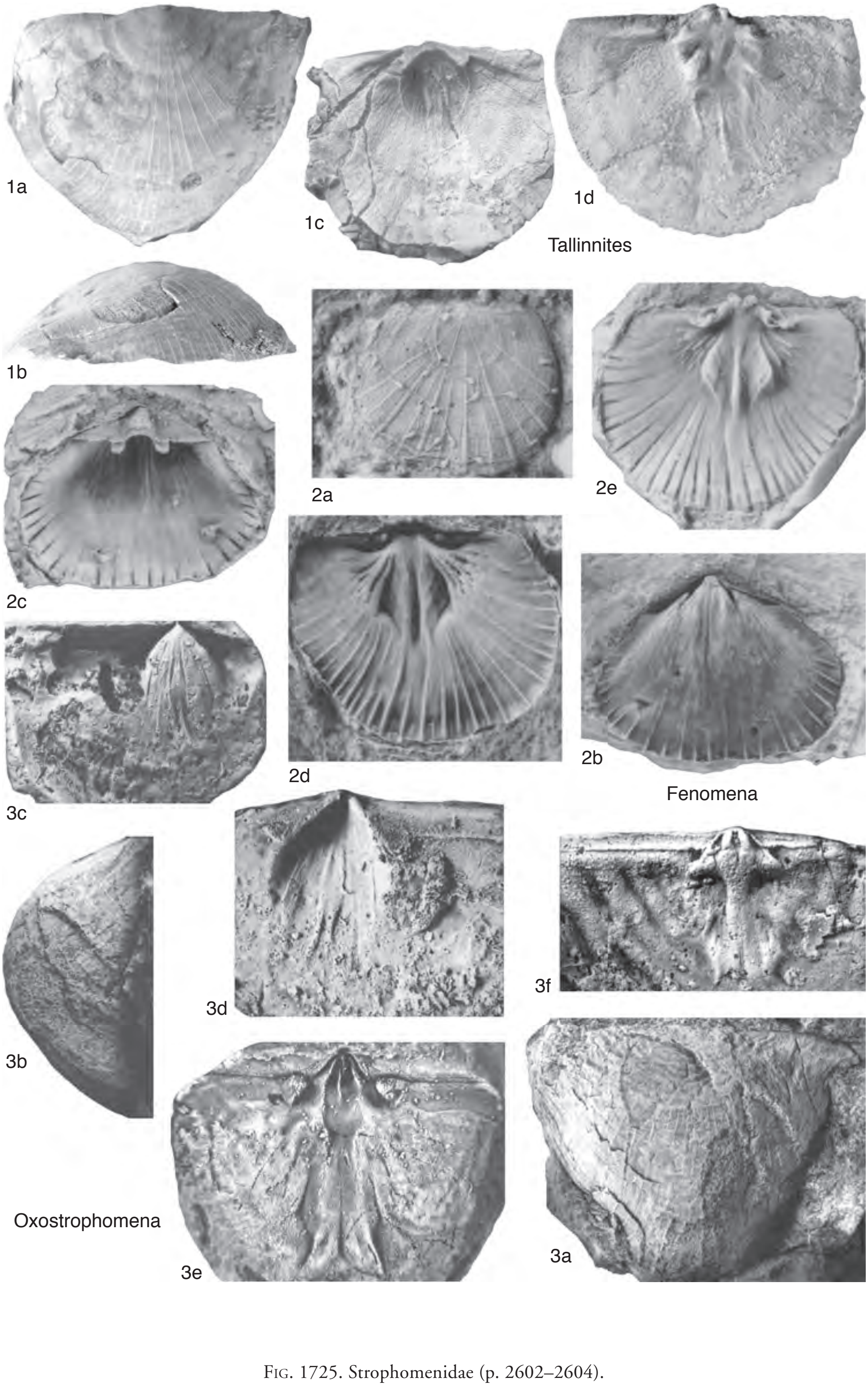


FIG. 1725. Strophomenidae (p. 2602–2604).

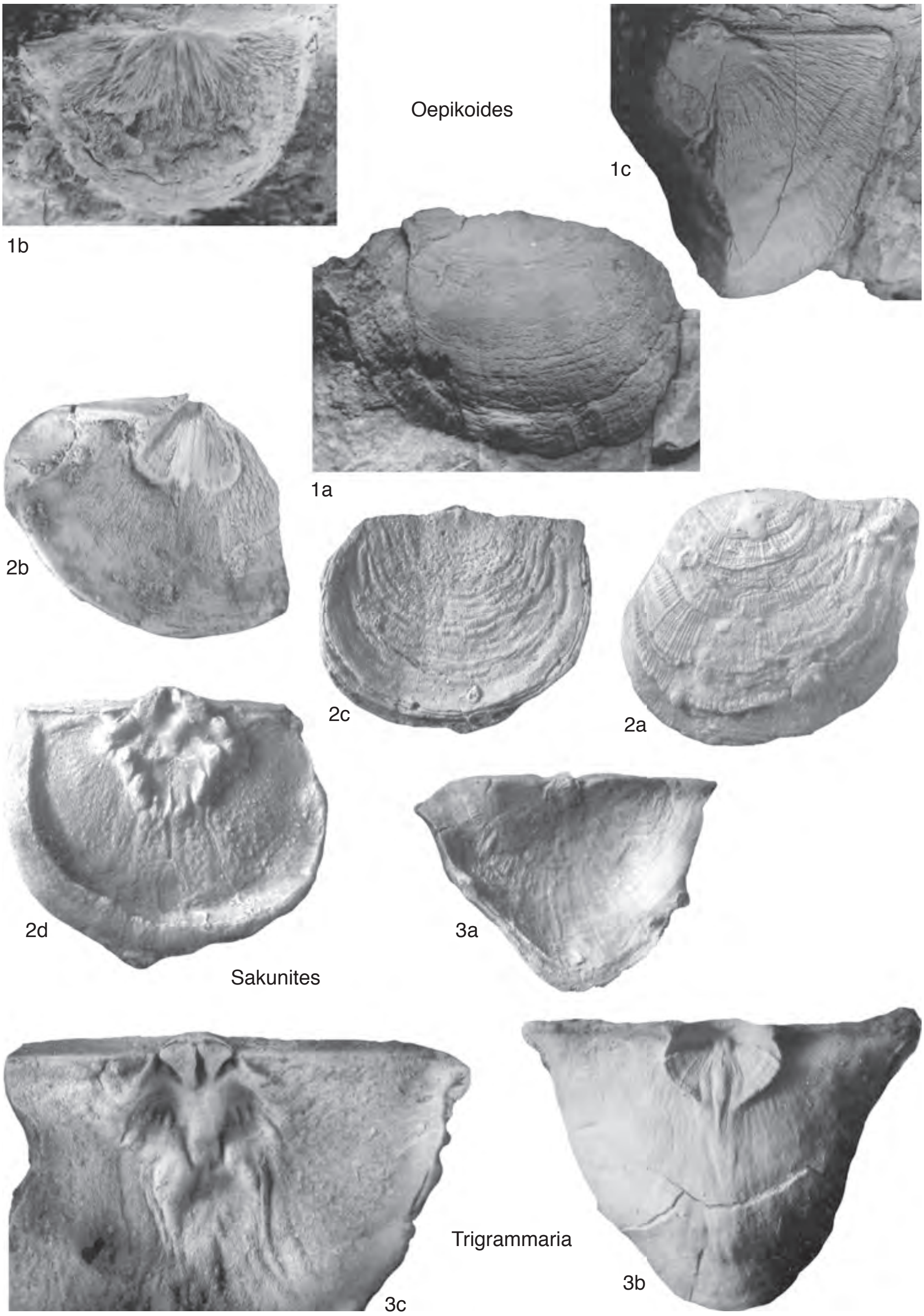


FIG. 1726. Strophomenidae (p. 2604).

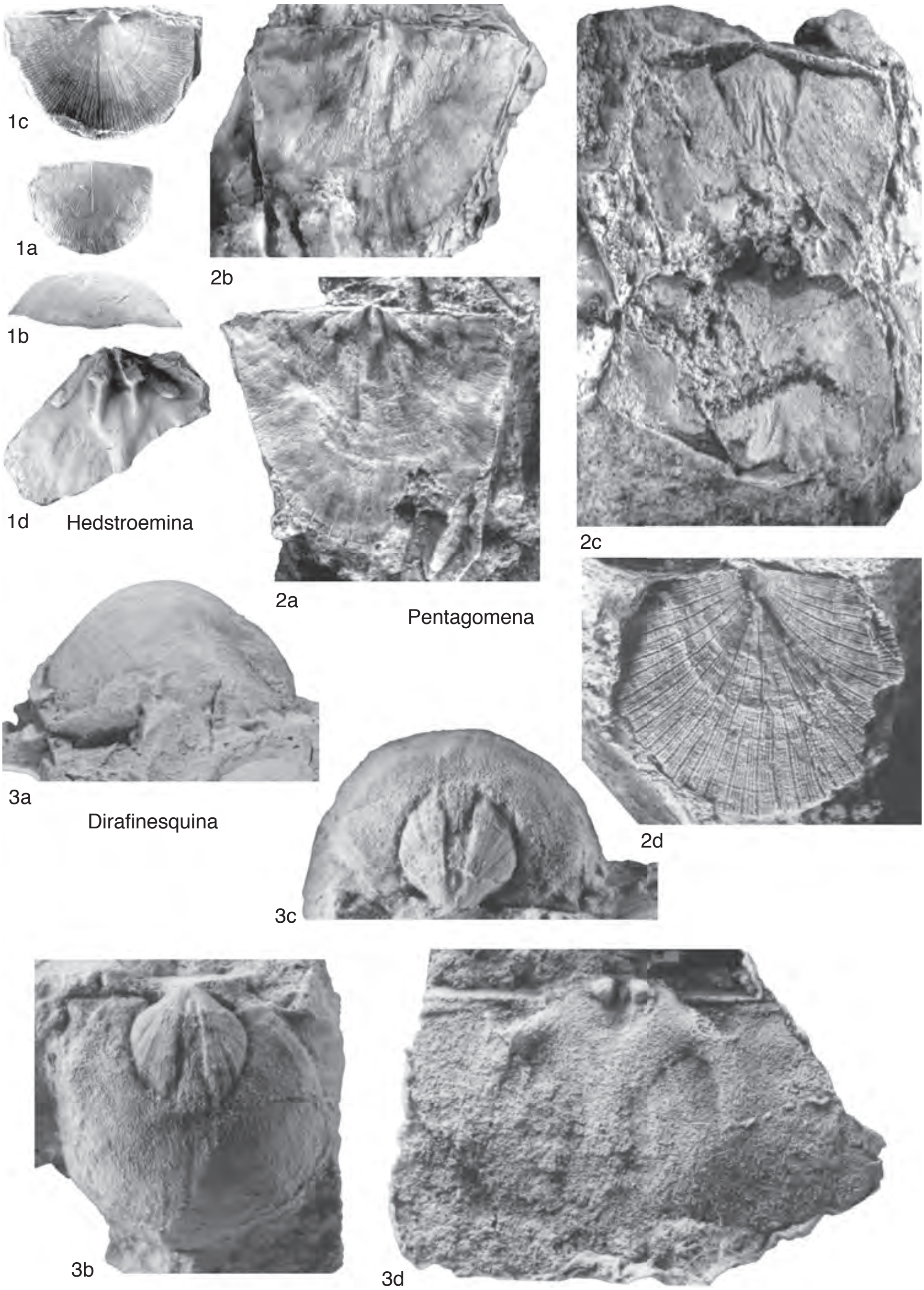


FIG. 1727. Rafinesquinidae (p. 2604–2608).

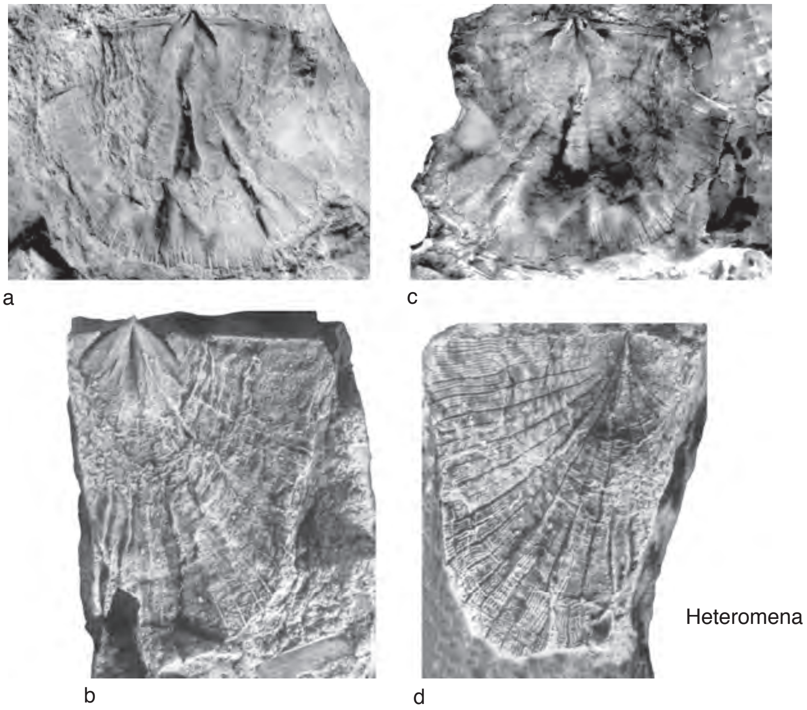


FIG. 1728. Rafinesquinidae (p. 2608).

type species, *H. fragilis*, was illustrated by Cocks & Rong, 2000, fig. 148,*2a–c*.] *Ordovician (Caradoc):* Avalonia, Baltica.——FIG. 1727,*1a–d. H. orvikui* (Oraspõld), Hirmuse Formation, Oandu Stage, middle Caradoc, Estonia; *a–b,* holotype, ventral and lateral views of ventral exterior, Oandu, TUG 1009-1, ×1; *c,* ventral interior, Tõrremägi, TUG 102-14, ×1.5; *d,* dorsal interior, Tõrremägi, TUG 102-13, ×3 (Rõõmusoks, 2004).

Heteromena Zhan & Jin, 2005, p. 42 [**H. dorsiconversa;* OD]. Profile weakly concavoconvex. Ornament regular parvicostellae with irregular rugae in posteromedian area only. Small pseudodeltidium and chilidium. Ventral interior with short dental plates, diverging anteriorly; ventral muscle field subcircular in outline, with weak muscle-bounding ridges. Dorsal interior with cardinal process lobes strong but thin, platelike, with much of cardinal process posterior to hinge line; myophragm also thin but well developed; strong but short socket ridges diverging at about 120°; notothyrial platform absent; weakly impressed dorsal muscle field with no transmuscle septa. *Ordovician (Arenig–Llanvirn):* South China.——FIG. 1728*a–d.* **H. dorsiconversa,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan Province, southwestern China; *a–b,* internal and external molds of ventral valve, NIGP 134442, ×2; *c–d,* holotype, mold and latex cast of dorsal interior, NIGP 134441, ×2 (Zhan & Jin, 2005).

Pentagomena Zhan & Jin, 2005, p. 40 [**P. parvicostellata;* OD]. Profile gently concavoconvex to weakly biconvex; vestigial pseudodeltidium; small chilidium; ornament of regular parvicostellae, rugae absent. Ventral interior with thin, widely diverging dental plates; ventral muscle field elongately subpentagonal with variably developed muscle-bounding ridges; thin notothyrial platform. Dorsal interior with cardinal process mostly anterior to hinge line; socket ridges relatively weak; subpentagonal dorsal muscle field weakly impressed; transmuscle septa weakly developed. *Ordovican (Arenig–Llanvirn):* South China.——FIG. 1727,*2a–d.* **P. parvicostellata,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan Province, southwestern China; *a,* mold of ventral exterior, NIGP 134437, ×2; *b,* ventral interior mold, NIGP 134435, ×2; *c–d,* holotype, dorsal internal mold and latex cast, NIGP 134421, ×2 (Zhan & Jin, 2005).

Subfamily LEPTAENINAE
Hall & Clarke, 1895

Leptaena Dalman, 1828, p. 94 [**L. rugosa;* SD King, 1846, p. 28]. [See Cocks & Rong, 2000, p. 241, in which, in addition to *Leptaena (Leptaena),* there are also a large number of generic synonyms and the subgenus *Leptaena (Septomena)*. The distinctive ornament of *Leptaena (Ygdrasilomena)* is quite

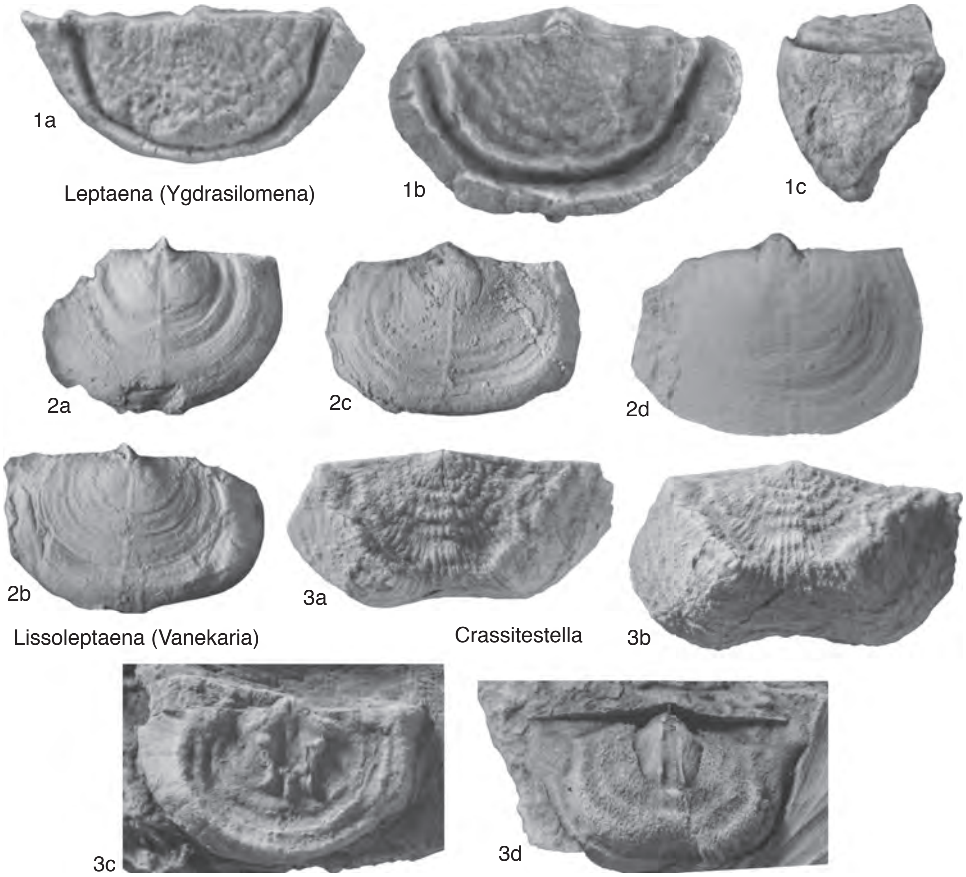


FIG. 1729. Rafinesquinidae (p. 2609–2610).

different from the regular rugae of the other two subgenera recognized within *Leptaena*.] *Ordovician (Llanvirn)–Devonian (Pragian, ?Emsian):* cosmopolitan.

Leptaena (Ygdrasilomena) COCKS, 2005, p. 260 [**L. (Y.) roomusoksi;* OD]. Profile, outline, and interior similar to *L. (Leptaena)* but with distinctive ornament of diagonal rugae forming an interference pattern on disc, in contrast to simple pattern of laterally extensive rugae in *L. (Leptaena)*. *Ordovician (Ashgill):* Sweden, Iran.——FIG. 1729,*1a–c*. **L. (Y.) roomusoksi,* Boda Limestone, middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; holotype, ventral, dorsal, and lateral views of conjoined valves, RMS Br 102778a, ×4 (Cocks, 2005).

Crassitestella BAARLI, 1995, p. 39 [**Leptaena reedi* COCKS, 1968, p. 310; OD]. Ventral profile convex to rounded and geniculate, sharply geniculate dorsal profile; outline relatively transverse for family; parvicostellate ornament with continuous rugae except on trail; gently concave and apsacline ventral interarea with wide delthyrium; dorsal interarea short and anacline with small, convex chilidial plates extending laterally across hinge line as raised plates with flanking grooves; blunt teeth; dental plates short and stout, continuing as strong, curved muscle-bounding ridges not meeting anteriorly; strong cardinal process; sockets deep, subparallel to hinge line, sometimes crenulated; notothyrial platform high; strong socket ridges; short median ridge variably developed and may be grooved to form a double ridge; paired outwardly concave transmuscle septa strongest at midvalve length; occasional extra septa developed laterally; saccate mantle canal system. *Silurian (Llandovery):* Europe.——FIG. 1729,*3a–d*. **C. reedi* (COCKS), Woodland Formation, Rhuddanian, Woodland Point, Girvan, Scotland; *a–b,* ventral exterior, BMNH B73341, ×3; *c,* ventral internal mold, BMNH BB31458, ×3; *d,* dorsal interior, BMNH B73342, ×3 (Cocks, 1968).

Lissoleptaena HAVLÍČEK, 1992, p. 171 [**L. lissodermis;* OD]. See COCKS and RONG, 2000, p. 250. *Lower Devonian*: Europe.

L. (Lissoleptaena). Similar to *Leptaena* but with no radial ornament laterally, although present near median plane; rugae faint. *Devonian (Lochkovian)*: Europe.

?L. (Vanekaria) Havlíček in Havlíček & Vaněk, 1998, p. 60 [**Lissoleptaena vicaria* Havlíček, 1992, p. 173; OD]. [This was designated as a separate genus even though its type species was orginally assigned to *Lissoleptaena*. There is a single prominent median costellae as the only radial ornament. The dental plates are shorter than *Lissoleptaena,* but the specimens are small. Although the ventral muscle field is stated to be subcircular and nonbilobate, their diagram and plate clearly shows a bilobate field as in *Lissoleptaena*. No dorsal interiors are known, but the name is provisionally retained here as a possible subgenus of *Lissoleptaena*.] *Lower Devonian*: Czech Republic.——Fig. 1729,*2a–d.* **L? (V.) vicaria,* Pragian, Bohemia; *a,* holotype, ventral valve, Slivenec Limestone, Srbsko, VH 5194, ×4.3; *b,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 5196, ×4; *c,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 8212, ×3.8; *d,* ventral valve, Dvorce-Prokop Limestone, Konváčka, Smíchov, VH 100902a, ×6 (Havlíček & Vaněk, 1998).

Family GLYPTOMENIDAE
Williams, 1965

[*nom. transl.* Rong & Cocks, 1994, p. 664, *ex* Glyptomeninae Williams, 1965c, p. 388] [=Yushanomenidae Zeng & Hu, 1997, p. 8]

Cocks (2005) reviewed the appropriate subfamilial classification within the Glyptomenidae and concluded that the family is best divided into three subfamilies. The unifying familial character is the distinctive Type C cardinal process of Rong and Cocks (1994). In addition, to differentiate between the subfamilies, the nominal subfamily, the Glyptomeninae, has no side septa or dorsal median septum, the Teratelasminae has both side septa and a dorsal median septum, and the Ungulomeninae differs from the other two in the possession of a prominent dorsal diaphragm. A separate family, the Yushanomenidae, was erected by Zeng and Hu (1997), but this is placed in synonymy with the Teratelasminae (see below).

Subfamily GLYPTOMENINAE
Williams, 1965

Glyptomenoides Popov & Cocks, 2006, p. 259 [**Rafinesquina girvanensis* Salmon, 1942, p. 571; OD]. Outline semicircular to subrectangular with maximum width at hinge line; profile with pedicle valve convex and gently geniculate, and dorsal valve relatively flat with dorsal geniculation; ventral interarea apsacline with small deltidial plates; dorsal interarea narrower, anacline with chilidium. Ornament unequally parvicostellate and irregularly rugate. Ventral interior with short stout teeth and short dental plates; muscle field bilobed, flabellate anteriorly and with short curved muscle-bounding ridges developed laterally only. Dorsal interior with small divided cardinal process lobes fused with prominent strong socket plates; short stout myophragm with bilobed muscle scars; pair of very small septa inside muscle area and a larger pair anterior to it and curved toward valve center; subperipheral diaphragm variably developed at geniculation point. Similar to *Glyptomena* but geniculate and rugate. *Ordovician (Caradoc):* Laurentia, ?Kazakhstan.——Fig. 1730,*1a–d*. **G. girvanensis* (Salmon), Balclatchie Formation, lower Caradoc, Girvan, Scotland; *a,* ventral internal mold, BMNH B 73288, ×2; *b–c,* mold and latex cast of dorsal interior, BMNH B 73290, ×3; *d,* latex cast of dorsal interior, BMNH B15213, ×4 (new).

Paromalomena Rong, 1984, p. 150 [**Platymena polonica* Temple, 1965, p. 407; OD]. See Cocks and Rong, 2000, p. 254. *Ordovician (Ashgill):* cosmopolitan.

P. (Paromalomena). Similar to *P. (Shanomena)* but with incipient anterior fold and corresponding sulcus and ornamentation of irregular and sporadic rugae and costellae of variable strength; ventral muscle field flabellate anteriorly; dorsal transmuscle septa absent. *Ordovician (Ashgill):* cosmopolitan.

P. (Shanomena) Cocks & Fortey, 2002, p. 68 [**Stropheodonta mcmahoni* Reed, 1915, p. 76; OD]. Similar to *P. (Paromalomena)* but with no anterior fold or sulcus; ornamentation of small irregular rugae, more pronounced anteriorly; fine subequal parvicostellae; ventral muscle field bilobed; weekly developed dorsal transmuscle septa. *Ordovician (Ashgill):* Burma (Myanmawr).——Fig. 1730,*2a–e*. **P. (S.) mcmahoni* (Reed), Panghsa-pye Formation, Hirnantian, Panghsa-pye, Northern Shan States; *a–b,* ventral internal mold and latex cast, BMNH BC 56785, ×2; *c–d,* lectotype, dorsal internal mold and latex cast, GSI 11611 (BMNH BC 56789), ×2; *e,* latex cast of dorsal valve, BMNH BC 56786, ×2 (Cocks & Fortey, 2002).

Subfamily TERATELASMINAE
Pope, 1976

Tashanomena Zhan & Rong, 1994, p. 418 [**T. variabilis*; OD] [=*Yushanomena* Zeng & Hu, 1997, p. 9 (type, *Y. elegans,* OD)]. [*Yushanomena,* from the early Llandovery, Wangjiaba, Yushan county, Jiangxi Province, China, has all the generic characters of *Tashanomena* (Cocks & Rong, 2000, p. 256), but extends its stratigraphic range.] *Ordovician (Ashgill)–Silurian (Llandovery):* southeastern Asia.

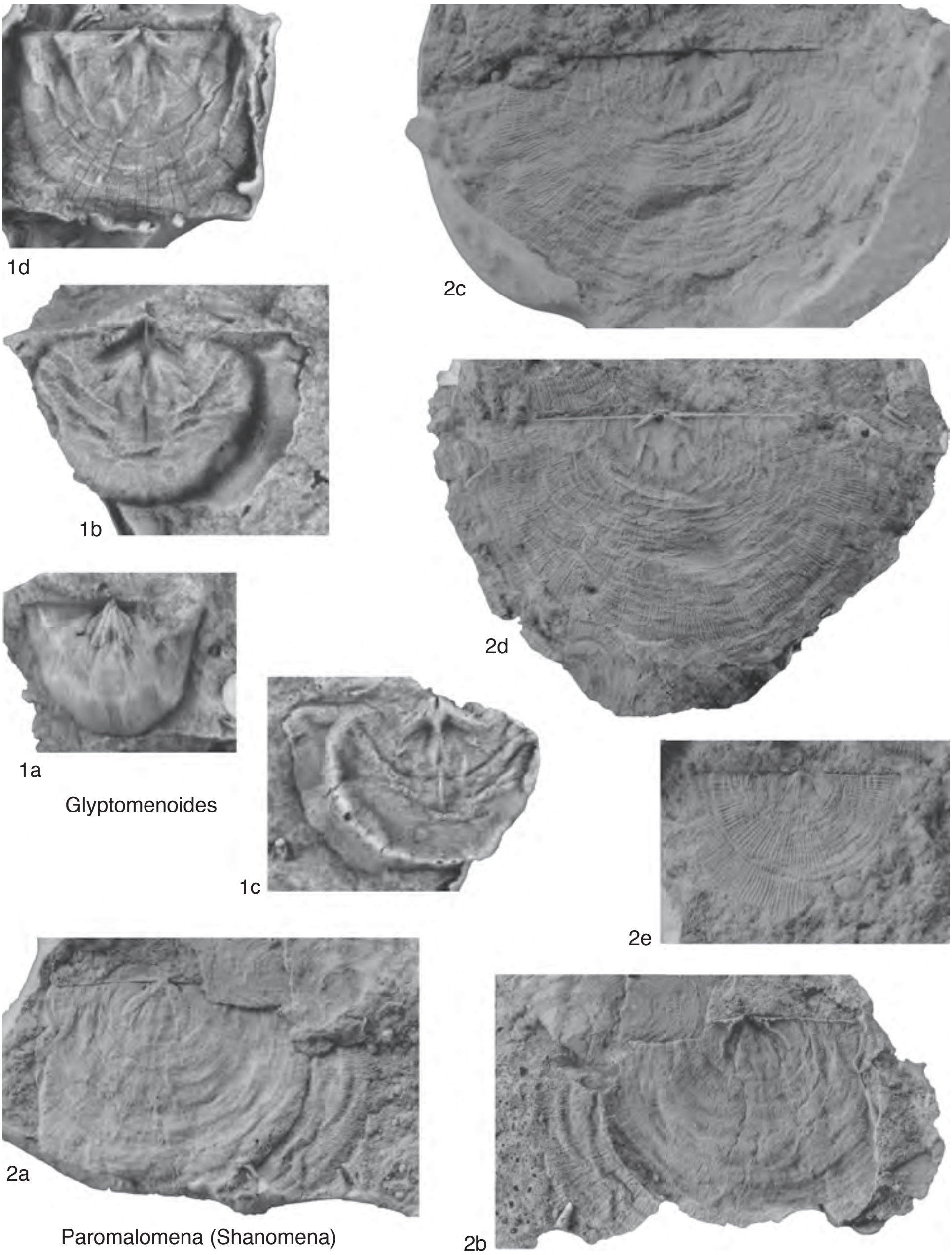


FIG. 1730. Glyptomenidae (p. 2610).

Trondomena COCKS, 2005, p. 264 [**T. bella;* OD]. Glyptomenid with gentle but normal convexity and elongately semicircular outline; robust flaring teeth; flaring crenulated dorsal socket plates, initially straight, but curving round anterolaterally, and supported by short dental plates; prominent dorsal socket plates curved and extending laterally up to half hinge width; weak subparallel dorsal side septa; dorsal median septum absent. *Ordovician (Ashgill):* Baltica.——FIG. 1731*a–e.* **T. bella*, Boda Limestone, middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; *a–b,* ventral and lateral views

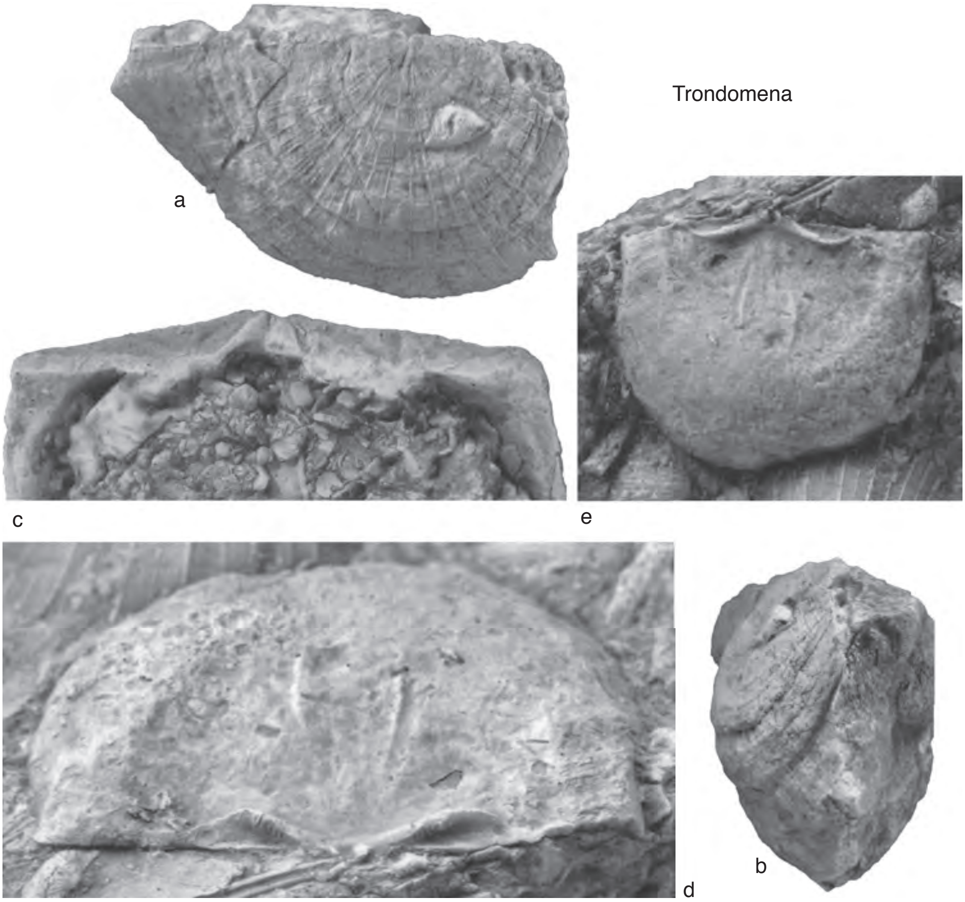


FIG. 1731. Glyptomenidae (p. 2611–2612).

of ventral valve, LO 9582, ×2; *c*, ventral interior showing interarea and teeth, BMNH BC 58018, ×1.5; *d–e,* holotype, posterior, ×3, and dorsal, ×1.5, views of dorsal interior, RMS Br 138091 (Cocks, 2005).

Subfamily UNGULOMENINAE Cocks, 2005

[Ungulomeninae COCKS, 2005, p. 265]

Glyptomenids with side septa, small dorsal median septum and substantial diaphragm. *Ordovician (Ashgill).*

Ungulomena COCKS, 2005, p. 265 [**U. lindstroemi;* OD]. Subquadrangular transverse outline; gently convex ventral valve with marked but evenly rounded geniculation at about two-thirds valve length; flat dorsal valve until geniculation, which matches ventral valve. Central ventral sulcus and dorsal fold on trail. Large apsacline interarea with large pseudodeltidium; smaller anacline dorsal interarea with chilidium smaller than pseudodeltidium. Ventral interior with large triangular teeth that flare sharply but diminish quickly laterally; dental plates initially diverging at about 90°. Dorsal interior with upright cardinal process; well-developed socket plates flaring laterally and curving posteriorly; weak myophragm extending anteriorly to a short weak median septum at about two-thirds disc length; pair of slightly curved to straight dorsal side septa only in disc center; variable but usually prominent dorsal diaphragm corresponding to the crest of geniculation, diaphragm undercut by up to 2 mm. *Ordovician (Ashgill):* Baltica.——FIG. 1732*a–g.* **U. lindstroemi,* Boda Limestone, Middle Ashgill, Osmundsberget Quarry, Dalarna, Sweden; *a–c,* ventral, dorsal, and lateral views of conjoined valves, ×2.5; *d,* posterior view of interarea of conjoined valves, LO 9583, ×3; *e*, ventral interior mold, BMNH BC 58233, ×2.5; *f–g,* dorsal view, ×2.5, and posterior view of dorsal valve, holotype, BMNH BC 57970, ×5 (Cocks, 2005).

FIG. 1732. Glyptomenidae (p. 2612).

Family AMPHISTROPHIIDAE Harper, 1973

Subfamily AMPHISTROPHIINAE Harper, 1973

Amphistrophia HALL & CLARKE, 1892, p. 292.

Amphistrophia (Amphistrophia) HALL & CLARKE, 1892, p. 292 [**Strophomena striata* HALL, 1843, p. 104; OD]. See COCKS and RONG, 2000, p. 260.

Amphistrophia (Sulcatastrophiella) BOUCOT & BLODGETT in BOUCOT, BLODGETT, & STEWART, 1997, p. 282 [**Amphistrophiella (Sulcatastrophia) stinnesbecki;* OD]. Similar to *A. (Amphistrophia)* but with relatively narrow but pronounced dorsal valve sulcus and corresponding ventral valve fold. *Silurian (Wenlock–Ludlow):* North and South America.——FIG. 1733,*2a–c*. **A. (S.) stinnesbecki*, Canon de Caballeros Formation, Wenlock, Ciudad Victoria, northeastern Mexico; *a–b,* holotype, exterior and interior molds of ventral valve, USNM 220896, ×2; *c,* interior mold of ventral valve, IGM 6894a, ×2 (Boucot, Blodgett, & Stewart, 1997).

Family DOUVILLINIDAE Caster, 1939

Subfamily PROTODOUVILLININAE Harper & Boucot, 1978

Arcticastrophia LI & JONES, 2002, p. 653 [**A. costellata*; OD]. Similar to *Borealistrophia* LI & JONES, but with gently convex ventral valve lacking sulcus and ventral muscle-bounding ridges high and prominent, in order to support elevated muscle field in ventral valve. *Devonian (Eifelian):* North America.——FIG. 1733,*4a–d*. **A. costellata*, Baad Fiord Member of Bird Fiord Formation, Ensorcellement River, Grinnell Peninsula, Devon Island, Arctic Canada; *a–b,* holotype, dorsal view and dorsal interior, UA12086, ×2.3; *c,* paratype, ventral interior, UA12082, ×2.7; *d,* paratype, dorsal view, UA12081, ×2.5 (Li & Jones, 2002).

Borealistrophia Li & Jones, 2002, p. 650 [**B. rongi*; OD]. Similar to *Nadiastrophia*, but with much shorter, cordate ventral muscle scars, more prominent and thicker socket plates, and much shorter side septa in dorsal valve. *Lower Devonian (uppermost Emsian)–Middle Devonian (Eifelian):* North America.——Fig. 1733,*1a–c*. **B. rongi*, Baad Fiord, Blubber Point, and Norwegian Bay members of Bird Fiord Formation, Eifelian, southwestern Ellesmere Island, North Kent Island, Devonian Island, Grinnell Peninsula and Bathurst Island, Arctic Canada; *a–b,* holotype, dorsal exterior and interior, UA12075, ×3.7; *c,* paratype, ventral interior, UA12078, ×3 (Li & Jones, 2002).

Cymostrophia Caster, 1939, p. 39 [**Leptaena stephani* Barrande, 1848, p. 230; OD]. See Cocks and Rong, 2000, p. 268. *Silurian (Ludlow)–Devonian (Givetian):* cosmopolitan.

C. (Cymostrophia). Transverse outline; strongly convex profile; ornament of very pronounced rugae interrupted by radial costellae. *Devonian (Lochkovian–Givetian):* cosmopolitan.

C. (Cymostrophiella) Havlíček in Havlíček & Vaněk, 1998, p. 63 [**Leptaena convoluta* Barrande, 1848, pl. 20,*8;* OD]. Although erected as an independent genus, differs from *Cymostrophia* only in ornament and is thus relegated to a subgenus here. Radial costellae absent on dorsal valve, where they are replaced by grooves; concentric rugellae absent or confined to ventral umbonal region to form very weak undulations. *Devonian (Pragian):* Czech Republic.——Fig. 1733,*3a–c*. **C. (C.) convoluta* (Barrande); *a,* ventral exterior, Vinařice Limestone, west of Měňany, Bohemia, VH 10693g, ×1.5; *b,* dorsal exterior, Vinařice Limestone, west of Měňany, Bohemia, VH 10695i, ×2; *c,* ventral interior, Koněprusy Limestone, Koněprusy, Bohemia, VH 9491c, ×2 (Havlíček & Vaněk, 1998).

C. (Protocymostrophia) Harper & Boucot, 1978, p. 127 [**Strophomena ivanensis* Barrande, 1879, pl. 52,*IV 1-4, 9-12;* OD]. Similar to *C. (Cymostrophia),* but with suboval rather than transverse outline; gently concavoconvex profile; less pronounced interrupted rugae in ornament. *Silurian (Ludlow)–Devonian (Eifelian):* cosmopolitan.

Family LEPTOSTROPHIIDAE
Caster, 1939

Eocymostrophia Baarli, 1995, p. 48 [**E. balderi*; OD]. Profile gently concavoconvex; outline transverse to semicircular; ornament regular but very fine parvicostellae with fine rugae broken by parvicostellae. Denticles on short denticular plates; dental plates absent; triangular ventral muscle field well impressed posterolaterally with short straight muscle-bounding ridges posterolaterally only; variable cardinal process lobes, but usually erect and ponderous; deep alveolar pit; very thin, poorly developed dorsal median septum and thin, straight, subparallel to slightly divergent dorsal transmuscle ridges. *Silurian (Llandovery):* Baltic.——Fig. 1734,*1a–c. *E. balderi,* Vik Formation, Telychian, Sandvika, Norway; *a,* dorsal external mold, PMO 135.935, ×2; *b,* ventral internal mold, PMO 135.945, ×1.5; *c,* holotype, dorsal internal mold, PMO 135.968, ×1.5 (Baarli, 1995).

Mesoleptostrophia Harper & Boucot, 1978, p. 68 [**M. kartalensis;* OD]. [See Cocks & Rong, 2000, p. 286. There are already two subgenera, *Mesoleptostrophia* and *Paraleptostrophia,* within *Mesoleptostrophia.* It is uncertain whether or not *Rhytirugea* should be included within the genus, and, if so, what its relationships with the other subgenera are. It was erected as a subgenus of *Leptostrophiella*, which was synonymized within *Mesoleptostrophia* in Cocks & Rong, 2000, p. 286; however, it may be a synonym of *Paraleptostrophia*, but the characteristic cardinal process lobes of that subgenus are not described for *Rhytirugea.* The type species was previously assigned to *Rhytistrophia* by Havlíček, 1967.] *Silurian (Telychian)–Devonian (Eifelian):* cosmopolitan.

Mesoleptostrophia (Rhytirugea) Havlíček & Vaněk, 1998, p. 61 [**Leptaena sowerbyi* Barrande, 1848, p. 239; OD]. Outline semicircular and alate; shell thin; profile biconvex posteriorly but ventral valve subplanar anteriorly; ventral interarea low, apsacline, with small pseudodeltidium; dorsal interarea small and thin. Ornament costellate and often slightly undulose, with some intervening parvicostellae; irregular rugae variably developed over entire valve. Ventral interior with small ventral process; triangular muscle field, flabellate and weakly impressed anteriorly; small, lanceolate adductor scars. Dorsal interior with denticulate hinge line to over half valve width; massive cardinal process lobes; muscle field bounded posterolaterally by short substantial ridges. Mantle canals not impressed. *Devonian (Pragian):* Czech Republic. ——Fig. 1734,*2a–d. *M? (R.) sowerbyi* (Barrande); *a,* ventral exterior, Koněprusy Limestone, Koněprusy, NM L6673, ×1.5; *b–c,* holotype, dorsal view of conjoined valves, Koněprusy Limestone, Koněprusy, NM L6457, ×1.5 and ×3; *d,* dorsal internal mold, Zlíchov Limestone, Hlubočepy, VH 438, ×4 (Havlíček & Vaněk, 1998).

Nervostrophia Caster, 1939, p. 79 [**Strophomena nervosa* Hall, 1843, p. 266; OD]. See Cocks and Rong, 2000, p. 286. *Devonian (?Givetian, Frasnian):* cosmopolitan.

Nervostrophia (Nervostrophia). Description as for genus. *Devonian (?Givetian, Frasnian):* cosmopolitan.

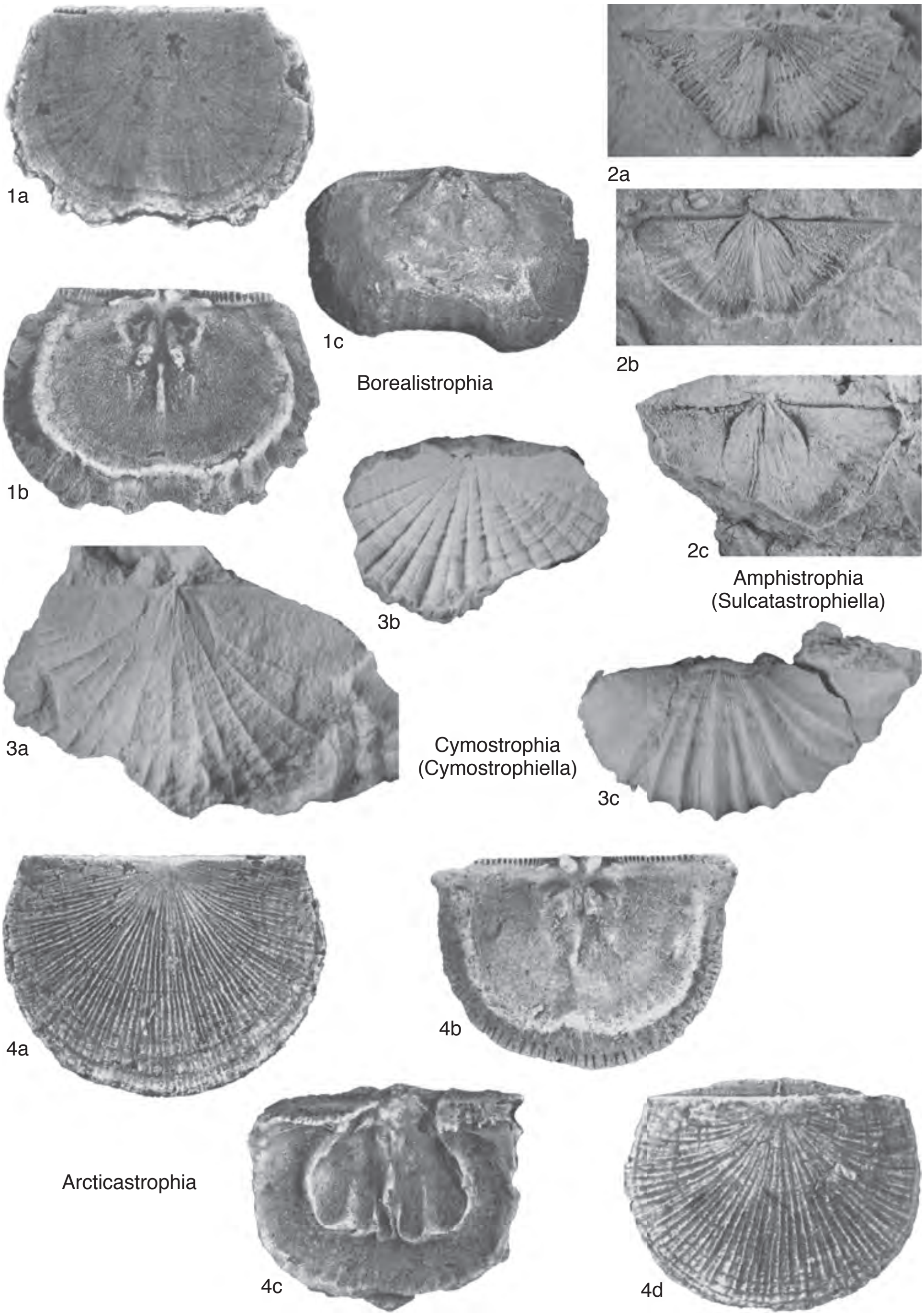


FIG. 1733. Amphistrophiidae and Douvillinidae (p. 2613–2614).

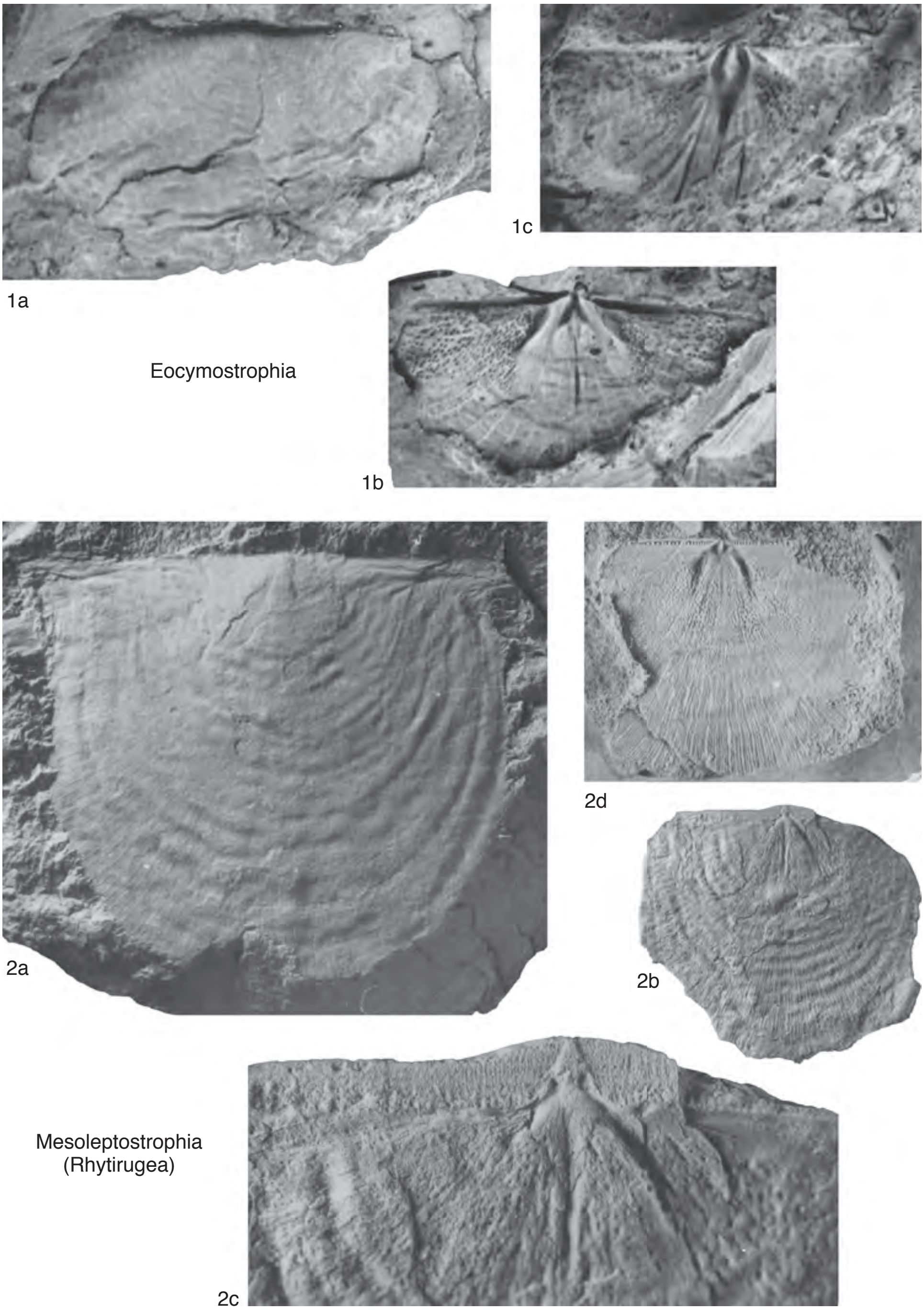


FIG. 1734. Leptostrophiidae (p. 2614).

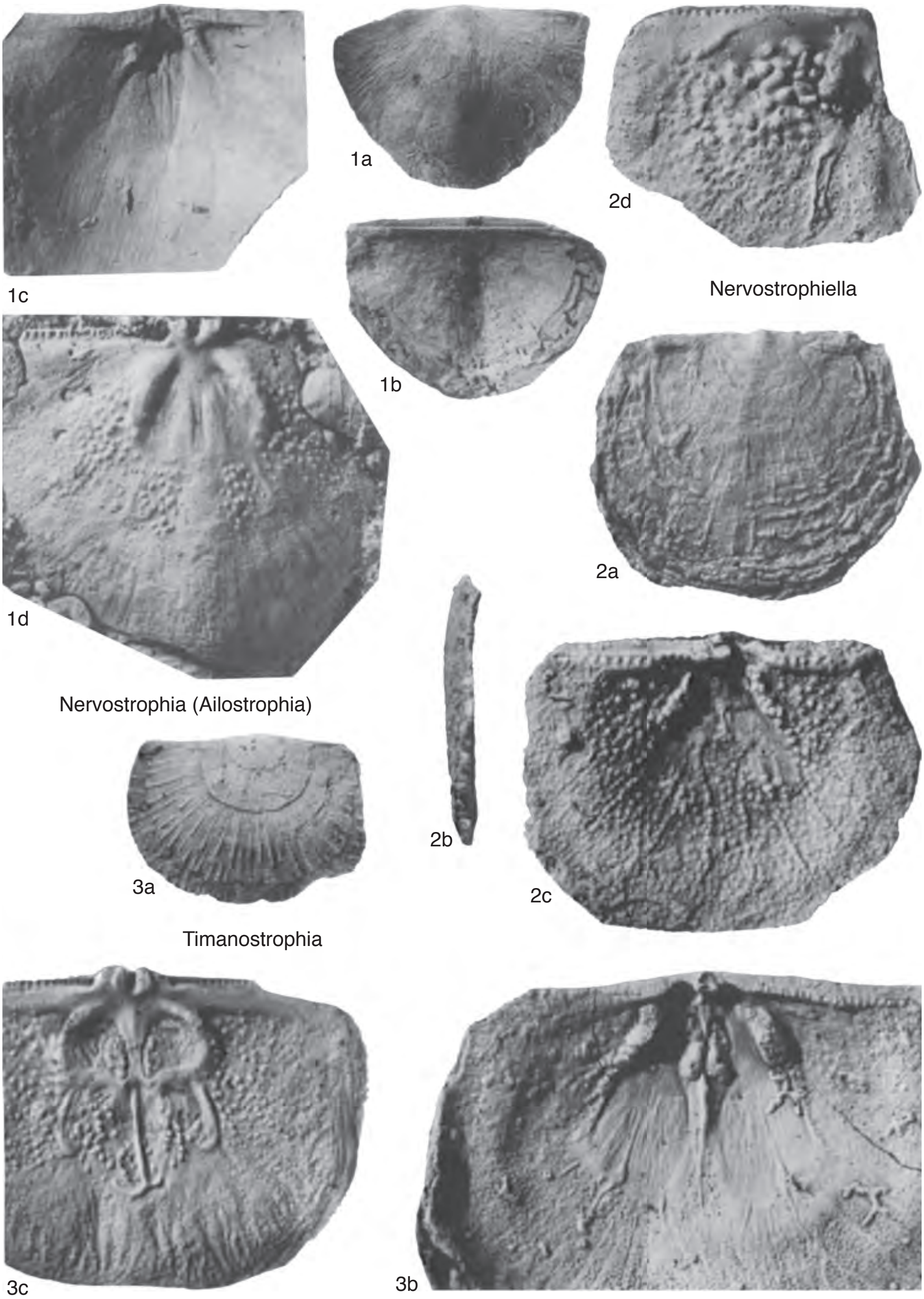


FIG. 1735. Leptostrophiidae (p. 2618).

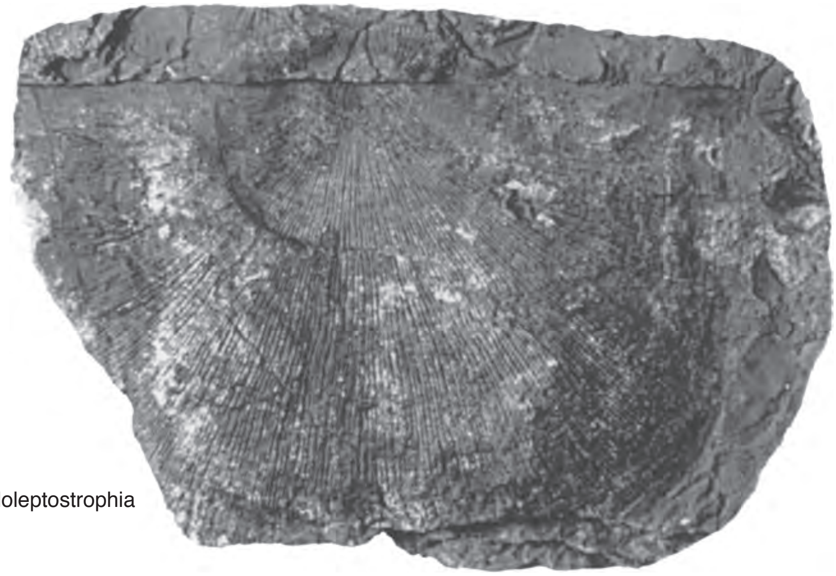


FIG. 1736. Leptostrophiidae (p. 2618).

Nervostrophia (Ailostrophia) ALEKSEEVA, 2003, p. 25 [**Leptaena asella* DE VERNEUIL, 1845, p. 224]. [Although erected as a separate genus, this subgenus is very similar to *Nervostrophia,* in particular with the very distinctive ornament, in which the primary costellae are differentially and irregularly enhanced along their lengths. *Ailostrophia* only differs from *Nervostrophia* in having a carinate ventral valve that is more strongly convex than that of *Nervostrophia.*] *Devonian (Frasnian):* Russian Platform.——FIG. 1735,*1a–d.* **N. (A.) asella* (VERNEUIL), Semilukskii Horizon, right bank of Don River, Pentino, central part of Russian Platform; *a–b,* ventral and dorsal views of conjoined shell, VNIGNI 141, ×3; *c,* ventral interior, VNIGNI 5367, ×3; *d,* dorsal interior, VNIGNI 5365, ×3 (Alekseeva, 2003).

Nervostrophiella ALEKSEEVA, 2003, p. 31 [**N. plana*; OD]. Similar to *Nervostrophia* in shape, outline, and interior features but with much smaller shell size, very fine and weak costellae sporadically enhanced near valve margin, and flat pseudodeltidium and chilidium. *Devonian (Frasnian):* Russia (southern Timan).——FIG. 1735,*2a–d.* **N. plana*, Lyaiolskaya Formation, right bank of Lyaiol River; *a–b,* holotype, ventral and dorsal views of conjoined valves, VNIGNI 5495, ×4; *c,* ventral interior, VNIGNI 5496, ×4; *d,* dorsal interior, VNIGNI 5497, ×4 (Alekseeva, 2003).

Pseudoleptostrophia GAD, 1997, p. 192 [**Leptostrophia dahmeri* RÖSLER, 1954, p. 36; OD]. Outline semicircular; profile gently resupinate; ventral interarea apsacline and entire; dorsal interarea unknown. Ornament of fine multicostellae. Ventral interior similar to *Leptostrophia*, with prominent myophragm posteriorly, but with muscle-bounding ridges variable from straight to slightly incurved anteriorly. Dorsal interior with denticulate hinge line to over three-quarters of valve width; robust, erect cardinal process lobes, posterolaterally and parallel to which run very short socket plates no longer than cardinal process lobes. Short myophram within muscle field extending anteriorly into a very weak median septum up to one-third valve length. Mantle canals not impressed. *Devonian (Emsian):* Germany.——FIG. 1736. **P. dahmeri* (RÖSLER), Dillenberger Formation, lower Emsian, Dörsbachtal; mold of ventral exterior, GLR-P 5611/5, ×1.5 (new).——FIG. 1737*a–c.* **P. dahmeri* (RÖSLER), Dillenberger Formation, lower Emsian, Dörsbachtal; *a,* lectotype, mold of ventral interior, GLR-P Mbg 2031, ×1.5; *b,* mold of ventral interior, GLR-P 5611/6, ×1.5; *c,* mold of dorsal interior, GLR-P Sch 194/18, ×1.5 (new).

Timanostrophia ALEKSEEVA, 2003, p. 29 [**T. ukhtensis*; OD]. Similar to *Nervostrophia* in shape, outline, and distinctive ornament but with thick and strong brachial ridges and brevisepta in dorsal valve. *Devonian (Frasnian):* Russia (Timan).——FIG. 1735,*3a–c.* **T. ukhtensis*, Sirachoiskii Horizon, right bank of Ukhty River, Sirachoi, southern Timan; *a,* holotype, ventral and dorsal views of a conjoined shell, VNIGNI 5385, ×2; *b,* ventral interior, VNIGNI 5391, ×3; *c,* dorsal interior, VNIGNI 5394, ×3 (Alekseeva, 2003).

FIG. 1737. Leptostrophiidae (p. 2618).

Superfamily PLECTAMBONITOIDEA Jones, 1928

The familial and subfamilial taxonomy of the Plectambonitoidea has remained unchanged since the treatment in COCKS and RONG (2000, p. 304). More has been published on the Plectambonitoidean mode of life, however, which we did not discuss earlier. For example, DATTILO (2004) has described many specimens of the abundant *Sowerbyella rugosa*, from the Late Ordovician of Kentucky, United States. In these the brachiopods are in apparent life positions in which the shells have their hinge lines facing downward into the sediment and where sedimentary structures surrounding the individuals suggest that they may have been partially immersed in the sediment through burrowing. Whether these burrows were merely escape structures or whether *Sowerbyella* occupied them for longer periods is unclear. DATTILO (2004) surmised that the valves flapped both to escape from predators or other threats and also to burrow. COCKS (1970) had also envisaged that the valves flapped, certainly so that the plectambonitoids could return to an upright position if they had been overturned and possibly also so that water could be pumped between the valves to enhance the brachiopods' feeding, which would explain the substantial septa and bema in the dorsal valve. HURST (1976), however, while endorsing the concept of valve flapping for valve position recovery, presented a convincing reconstruction of the ontogeny of both soft and hard parts within the dorsal valve of the sowerbyellid *Eoplectodonta.* This showed the lophophore developing from a juvenile trocholophe into an adult schizolophe that would have enabled feeding through the ciliary action common to all living brachiopods and did not need to invoke any flapping to enhance food capture by the lophophore.

Family PLECTAMBONITIDAE Jones, 1928

Subfamily TAPHRODONTINAE Cooper, 1956

Bandaleta NIKITIN & POPOV, 1996, p. 5 [**B. plana*; OD]. Profile planoconvex to slightly concavoconvex; transverse outline; parvicostellate ornament; ventral pseudointerarea apsacline with pseudodeltidium; dorsal bilobed ventral muscle field with long divergent diductor scars; strong teeth; dental plates vestigial to absent; simple, small, knoblike cardinal process; high dorsal double septum continuing to subperipheral rim; subrectangular dorsal muscle field with bounding ridges; ventral mantle canals saccate and dorsal mantle canals lemniscate. *Ordovician (Darriwilian–Caradoc):* Kazakhstan.——FIG. 1738,*4a–d*. **B. plana,* Dulankara Regional Stage, upper Caradoc, Betpak-Dala Desert; *a,* exterior of conjoined valves, CNIGR 3/12877, ×3; *b,* ventral internal mold, CNIGR 4/12877, ×3; *c–d,* latex cast and internal mold of dorsal valve, CNIGR 5/12877, ×2 (Nikitin & Popov, 1996).

Uzunbulakia NIKITINA & others, 2006, p. 178 [**U. rugosa;* OD]. Transverse outline; concavoconvex profile; small interarea with ventral pseudodeltidium; ornament finely multicostellate with rugellae posteriorly. Ventral interior with widely divergent short teeth; no dental plates; small bilobed muscle field; prominent subperipheral rim. Dorsal interior with small, simple, bulbous cardinal process; median ridge low and broad, proceeding from low notothyrial platform that becomes double-crested anteriorly and does not extend anteriorly beyond entire diaphragm. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1738,*1a–d*. **U. rugosa,* Uzunbulak Formation, Uzunbulak, Chu-Ili Range; *a,* dorsal exterior, USNM 485144, ×3; *b,* holotype, ventral interior, USNM 485142, ×3; *c–d,* internal mold and latex cast of dorsal interior, USNM 485143, ×3 (Nikitina & others, 2006).

Family TAFFIIDAE Schuchert & Cooper, 1931

Subfamily TAFFIINAE Schuchert & Cooper, 1931

Tinopena LAURIE, 1997b, p. 712 [**T. shergoldi;* OD]. Profile concavoconvex; outline subcircular to transversely ovate; parvicostellate ornament; ventral interarea orthocline to apsacline; dorsal interarea catacline; chilidium completely covering notothyrium; subcordate ventral muscle field; teeth with shelflike fossettes; small dental plates; subperipheral rim in both valves; bladelike to subcircular cardinal process; short socket ridges; ovate posterior dorsal adductor muscle scars larger than subcircular

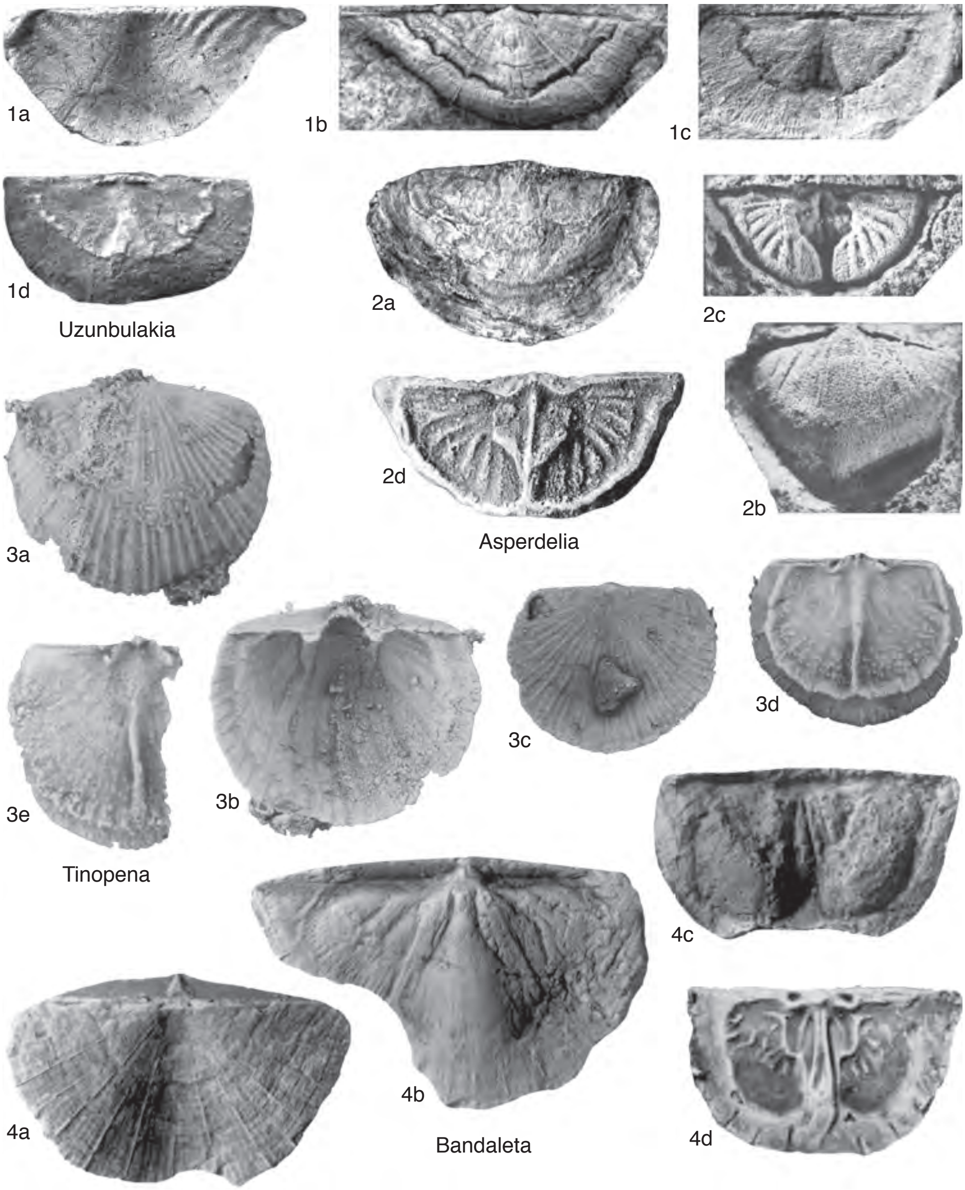


FIG. 1738. Plectambonitidae, Taffiidae, and Bimuriidae (p. 2620–2622).

anterior pair; narrow dorsal median septum to subperipheral rim; similar to *Spanodonta* but with dorsal median septum. *Ordovician (Darriwilian):* Australia.——FIG. 1738,*3a–e.* **T. shergoldi,* Gap Creek Formation, Kunian Gap, Emanuel Range, Western Australia; *a–b,* exterior and interior views of ventral valve, CPC 33269, ×4; *c–d,* exterior and interior views of dorsal valve, CPC 33270, ×4; *e,* holotype, dorsal interior, CPC 33273, ×4 (Laurie, 1997b).

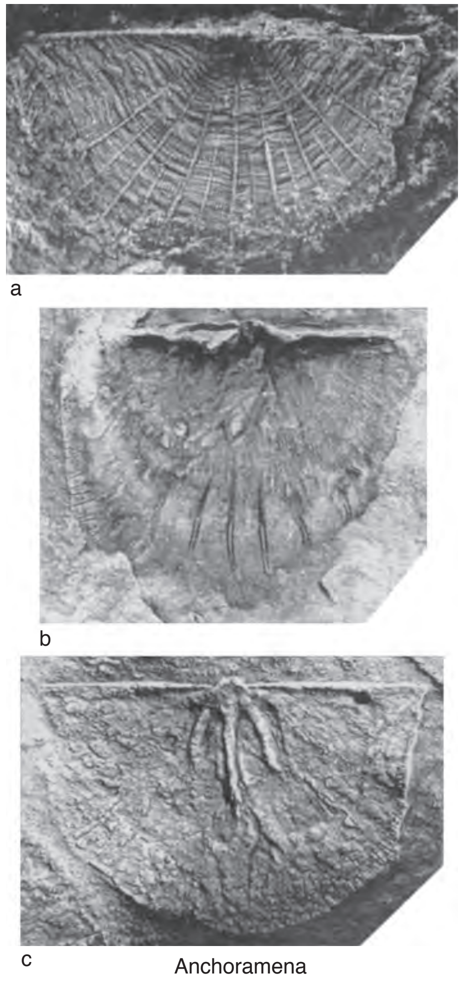


Fig. 1739. Leptellinidae (p. 2622).

Family BIMURIIDAE Cooper, 1956

Asperdelia Nikitina & others, 2006, p. 176 [**A. villosa;* OD]. Outline transverse with alate cardinal extremities; profile concavoconvex with gently sulcate anterior commissure and short trail anterolaterally; ventral interarea apsacline; dorsal interarea ancline with prominent chilidium. Fine parvicostellate ornament; comae common. Ventral interior with short divergent teeth; muscle field weakly impressed. Dorsal interior with simple undercut cardinal process fused with socket plates; dorsal median septum present, crossing spearhead-shaped bema and extending anteriorly to strong subperipheral rim. Mantle canals saccate and strongly impressed in dorsal valve. *Ordovician (Darriwilian):* Kazakhstan.——Fig. 1738,*2a–d.* **A. villosa,* Uzunbulak Formation, Kurzhaksai, Chu-Ili Range; *a*, ventral exterior, USNM 485161, ×2; *b,* ventral interior, USNM 485159, ×2.5; *c–d,* mold and latex of dorsal interior, USNM 489158, ×3 (Nikitina & others, 2006).

Family LEPTELLINIDAE
Ulrich & Cooper, 1936
Subfamily
PALAEOSTROPHOMENINAE
Cocks & Rong, 1989

Anchoramena Benedetto, 1995, p. 251 [**A. cristata;* OD]. Outline semicircular to transverse; profile resupinate; unequally parvicostellate ornament with small posterolateral rugae; ventral interarea apsacline; vestigial pseudodeltidium; dorsal interarea anacline; no chilidium known; dental plates absent; differs from *Palaeostrophomena* in lacking bounding ridges to weakly developed ventral muscle field; relatively small trifid cardinal process; small socket plates flaring anterolaterally; dorsal median septum originating from anterior end of small notothyrial platform; well-impressed dorsal muscle field bounded posteriorly and laterally with prominent bounding ridges; well-impressed saccate mantle canals. *Ordovician (Caradoc):* South America.——Fig. 1739*a–c.* **A. cristata*, Las Plantas Formation, lower Caradoc, River Gualcamayo, northern Precordilleras, Argentina; *a,* dorsal exterior, CEGH-UNC 13695, ×4; *b,* ventral interior, CEGH-UNC 13686b, ×2; *c,* holotype, dorsal interior, CEGH-UNC 13686a, ×2.5 (Benedetto, 1995).

Leptastichidia Zhan & Jin, 2005, p. 34 [**L. catatonosis;* OD]. Convexoconcave, dorsal geniculation short; pseudodeltidium small. Ornament of unequal parvicostellae with accentuated major costellae; posterolateral rugae common. Ventral interior lacking dental plates; ventral muscle field small, trilobed, with straight anterior margin. Dorsal interior with ridgelike or sometimes bulbous cardinal process; socket ridges thin, high, raised laterally from valve floor; myophragm large, merging anteriorly with weak dorsal median septum; platform absent in both valves. *Ordovician (Arenig–Llanvirn):* South China.——Fig. 1740,*3a–d.* **L. catatonosis,* Dashaba Formation, upper Arenig–Llanvirn, Shuanghe, Changning County, Sichuan province, southwestern China; *a–b,* ventral internal mold and latex cast, NIGP 134409, ×3; *c–d,* holotype, dorsal internal mold and latex cast, NIGP 134411, ×4 (Zhan & Jin, 2005).

Nikitinamena Popov & Cocks, 2006, p. 266 [**N. bicostata;* OD]. Outline rhomboidal; profile concavoconvex; evenly geniculate; anterior commisure weakly uniplicate; ventral valve with widely diverging pair of low angular plications enclosing very shallow sulcus; ventral interarea apsacline with small apical pseudodeltidium; dorsal interarea hypercline with small separate chilidial plates. Ornament of fine unequal parvicostellae. Ventral interior with small teeth and small bilobed muscle

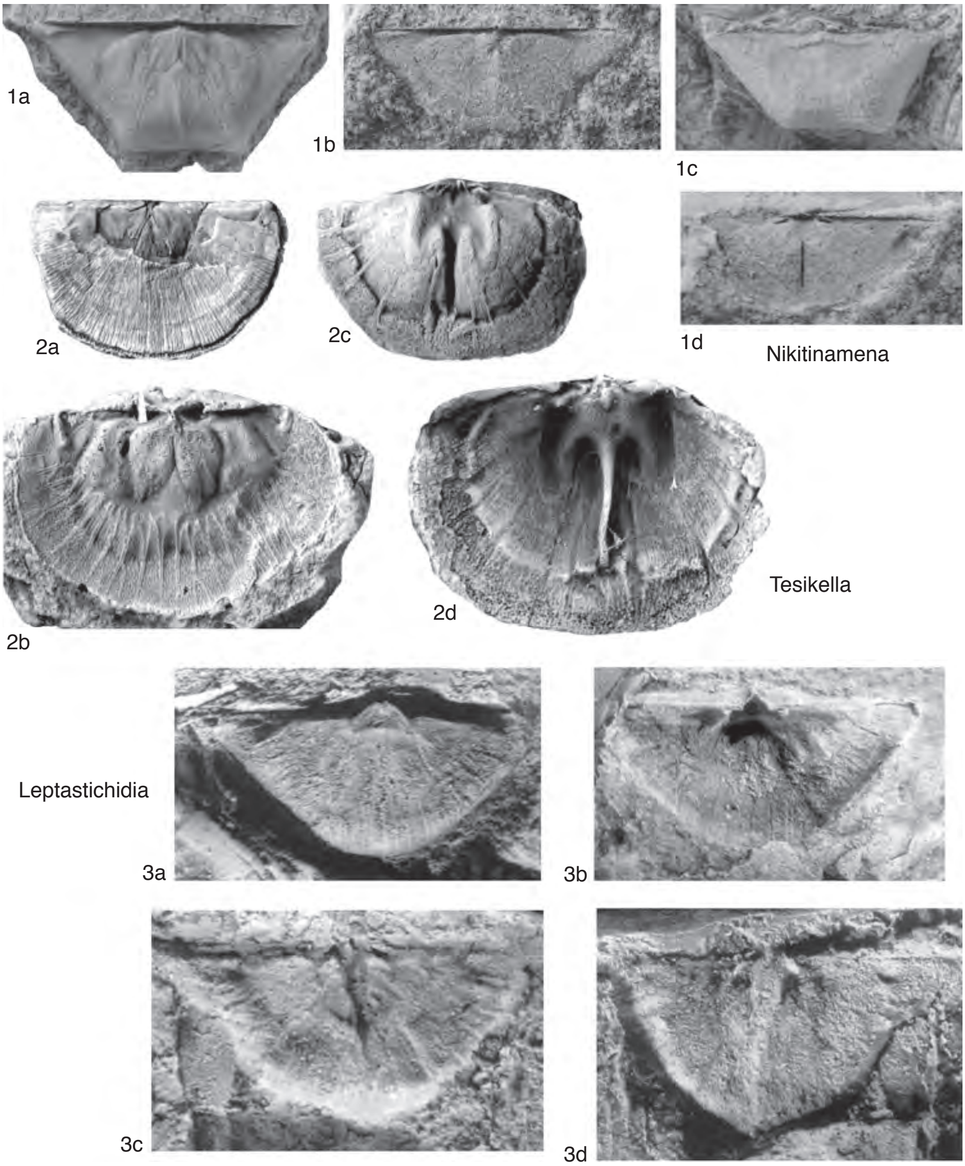


FIG. 1740. Leptellinidae (p. 2622–2624).

field with short adductor scars separating larger diductor scars; ventral mantle canals saccate with short, diverging vascular media. Dorsal interior with simple, bulbous cardinal process on low notothyrial platform; small, curved socket plates; fine median septum extending to midlength. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1740,*1a–d*. **N. bicostata,* Degeres Member, Dulankara Formation, upper Caradoc, Dulankara Mountains, Chu-Ili Range; *a,* holotype, ventral internal mold, BMNH BC 57716, ×4; *b*, internal mold of juvenile ventral valve, BMNH BC 57718, ×4; *c,* dorsal interior, BMNH BC 57717, ×3; *d,* dorsal internal mold, BMNH BC 57720, ×4 (Popov & Cocks, 2006).

Tesikella POPOV, COCKS, & NIKITIN, 2002, p. 44 [**Palaeostrophomena necopina* POPOV, 1980, p. 145; OD]. Outline semicircular to transversely subrectangular, maximum width just anterior to hinge line; profile gently resupinate; ventral interarea low, catacline with strong but narrow pseudodeltidium; dorsal interarea low, anacline, with separate chilidial plates. Ornament parvicostellate. Ventral interior with double teeth; no dental plates; bilobed muscle field with low but entire muscle-bounding ridges; subperipheral rim variably developed. Dorsal interior with trifid cardinal process on low notothyrial platfom; low, widely divergent socket ridges. Strong narrow median septum over three-quarters of valve length joined anteriorly to subperipheral diaphragm. Mantle canals well impressed and saccate. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1740,*2a–d.* **P. necopina* (POPOV), Anderken Formation, lower to middle Caradoc, Anderkenyn-Akchoku, Chu-Ili Range; *a,* ventral exterior, BMNH BC 57434, ×2; *b,* mold of ventral interior, BMNH BC 57432, ×2; *c–d,* mold, ×2, and latex cast, ×3, of dorsal interior, BMNH BC 57604 (Popov, Cocks, & Nikitin, 2002).

Family LEPTESTIIDAE
Öpik, 1933

Bekella NIKITINA & others, 2006, p. 185 [**B. paula;* OD]. Outline semicircular; profile concavoconvex; ventral interarea apsacline. Ornament finely parvicostellate. Ventral interior with small teeth; dental plates absent; small, poorly defined muscle field, anterolaterally to which are a pair of subquadrangular structures rising from valve floor. Dorsal interior with trifid cardinal process; small but distinctive bema bisected by a median septum that forks for a short distance anteriorly; small rod-shaped process rising from valve floor anterolateral to muscle field. Strong subperipheral diaphragm developed. Similar to *Leangella* except distinctive rodlike structures in interiors of both valves. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1741,*2a–e.* **B. paula,* Uzunbulak Formation, Kurzhaksai, Chu-Ili Range; *a,* ventral exterior, USNM 485150, ×9; *b,d,* internal mold, ×5, and latex cast, ×8.5, USNM 485148: *c,e,* latex cast of dorsal interior oblique, ×10, and straight views, ×12, holotype, USNM 485155 (Nikitina & others, 2006).

Sortanella NIKITIN & POPOV, 1996, p. 9 [**S. quinquecostata;* OD]. Profile weakly resupinate with anterior margin sulcate in juveniles and uniplicate in adults; transverse outline; pseudodeltidium and chilidium well developed, unequal parvicostellate ornament; simple teeth; dental plates absent; cordate ventral muscle field with weak median ridge; two distinctive peripheral rims, the inner merging with hinge line at midwidth; trifid not undercut cardinal process; broad, short, strongly elevated dorsal median septum uniting anteriorly with diaphragm bounding small bema; dorsal subperipheral rim. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1741,*3a–c.* **S. quinquecostata,* Dulankara Regional Stage, upper Caradoc, Sortan-Manai Salt Marsh, Betpak-Dala Desert; *a,* ventral view of conjoined valves, CNIGR 11/12877, ×3; *b,* ventral internal mold, CNIGR 14/12877, ×3; *c,* dorsal internal mold, CNIGR 13/12877, ×3 (Nikitin & Popov, 1996).

Family XENAMBONITIDAE
Cooper, 1956
Subfamily AEGIROMENINAE
Havlíček, 1961

Cathrynia CANDELA, 1999, p. 91 [**C. puteus*; OD]. Outline semicircular to subrectangular; maximum width at hinge line; profile planoconvex; ventral interarea narrow, apsacline; dorsal interarea narrower and hypercline. Ornament finely parvicostellate with concentric filae. Ventral interior with short flaring teeth; small bilobed muscle field; very short median septum in posterior only; radial rows of papillae near anterolateral margins; weak peripheral rim often developed. Dorsal interior with simple undercut cardinal process fused with widely flaring, straight to slightly curved socket ridges; prominent median septum less than half valve length ending anteriorly and fused with pair of lateral septules; irregular bilobed bema bordered by coarse papillae. Mantle canals not impressed. *Ordovician (Caradoc):* Ireland.——FIG. 1742,*1a–d.* **C. puteus,* Bardahessiagh Formation, middle Caradoc, Pomeroy, County Tyrone, Northern Ireland; *a,* latex cast of ventral exterior, K27230, ×10.5; *b,* ventral internal mold, K27340(7), ×10.5; *c–d,* holotype, mold and latex cast of dorsal interior, K27239, ×10.5 (Candela, 1999).

Tenuimena NIKITINA & others, 2006, p. 188 [**T. planissima;* OD]. Outline semicircular, maximum width just anterior to hinge line; profile planoconvex to weakly resupinate; small interarea with pseudodeltidium and chilidium. Ornament finely parvicostellate. Ventral interior with small flaring teeth; dental plates absent; suboval muscle field flanked posterolaterally by short, relatively straight muscle-bounding ridges. Dorsal interior with simple undercut cardinal process; short, flaring socket plates; fine median septum to half valve length. Mantle canals not impressed. Differs from other Aegiromeninae in lacking papillae and from *Chonetoidea* in lacking obvious bema and dental plates. *Ordovician (Darriwilian):* Kazakhstan.——FIG. 1742,*3a–c.* **T. planissima,* Uzunbulak Formation, Kurzhakai, Chu-Ili Range; *a,* latex of ventral exterior, USNM 485108, ×2; *b,* ventral internal mold, USNM 485105, ×5; *c,* holotype, latex of dorsal interior, USNM 485105a, ×5 (Nikitina & others, 2006).

Family HESPEROMENIDAE
Cooper, 1956

Rongambonites ZHAN & COCKS, 1998, p. 33 [**R. bella;* OD]. Outline semielliptical to semicircular;

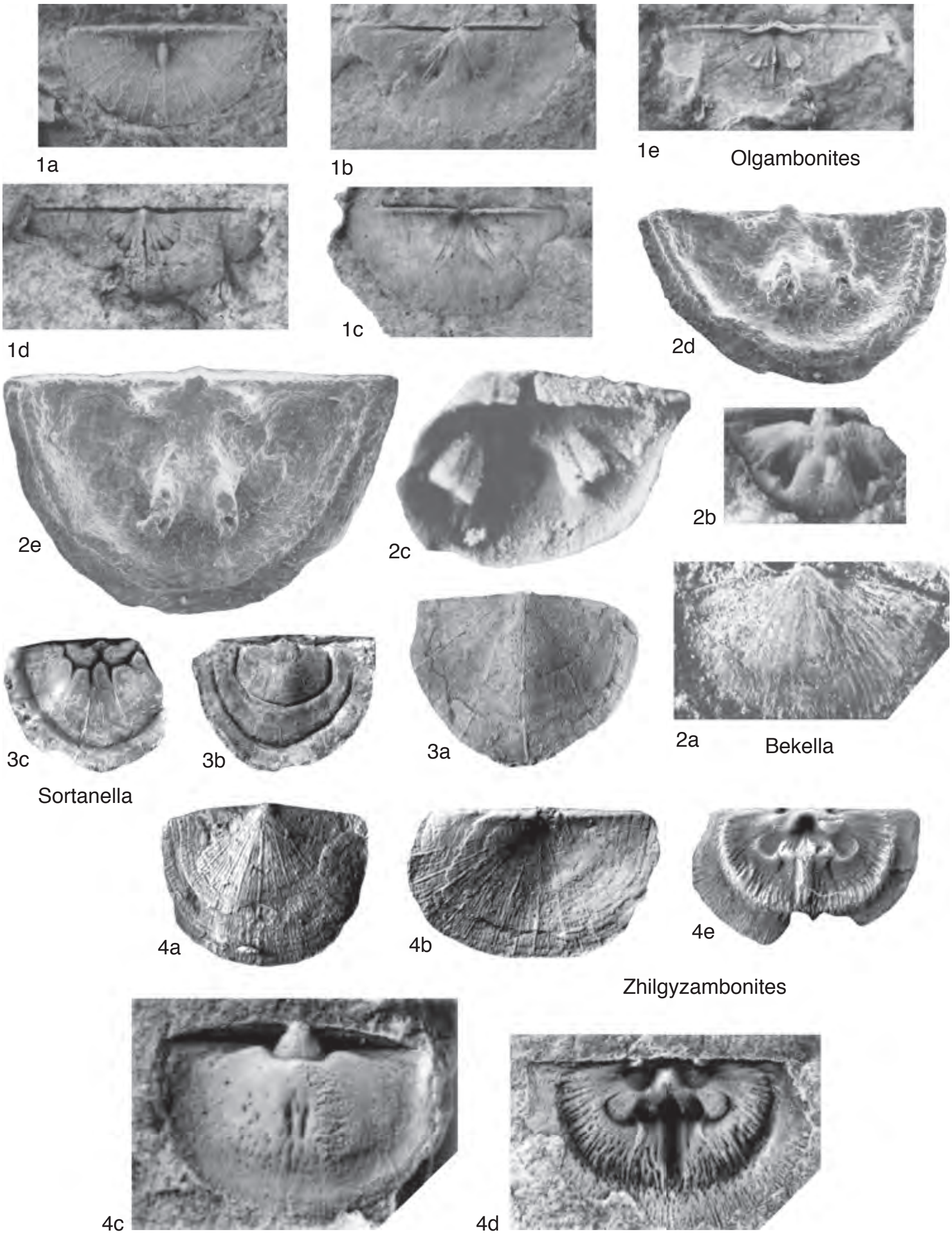


FIG. 1741. Leptestiidae and Sowerbyellidae (p. 2624–2627).

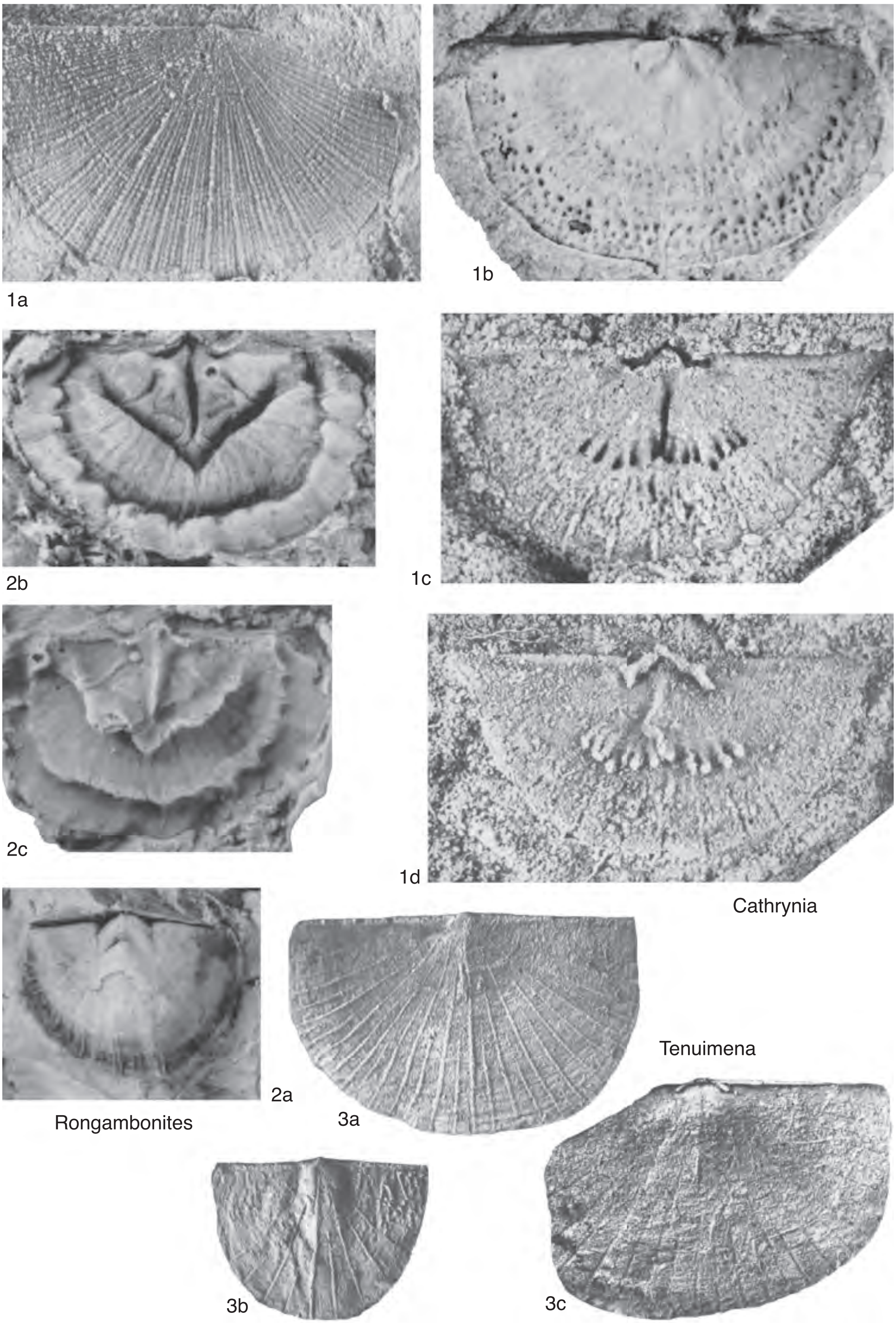


FIG. 1742. Xenambonitidae and Hesperomenidae (p. 2624–2627).

profile concavoconvex with strongly convex ventral valve and dorsal concavity variable; parvicostellate ornament; ventral interarea apsacline; dorsal interarea anacline; strong teeth; variable dental plates fusing anterolaterally with bounding ridges of relatively small bilobed ventral muscle field; undercut cardinal process strongly striated posteriorly and connecting laterally with curved socket plates; triangular platform with strong, straight, anterolateral bounding ridges joined anteriorly by a curved and raised section; high dorsal median septum not reaching platform anteriorly; muscle field variably impressed with weak, anterolaterally directed side septa. *Ordovician (Ashgill):* South China.——FIG. 1742,*2a–c.* **R. bella,* Changwu Formation, middle Ashgill, Dianbian of Daqiao, Zhejiang Province; *a,* ventral internal mold, NIGP 128051, ×3; *b–c,* dorsal internal mold and latex cast, NIGP 128053, ×3 (Zhan & Cocks, 1998).

Family SOWERBYELLIDAE Jones, 1928

Subfamily SOWERBYELLINAE Jones, 1928

Olgambonites POPOV, COCKS, & NIKITIN, 2002, p. 50 [**O. insolita;* OD]. Outline transverse; profile gently resupinate; ventral interarea procline to slightly apsacline with apical pseudodeltidium; dorsal interarea anacline with separate chilidial plates. Ornament unequally parvicostellate. Ventral interior with small teeth; dental plates absent; small bilobed muscle field with short adductor scars completely separating larger diductor scars; ventral mantle canals lemniscate. Dorsal interior with simple undercut cardinal process fused with narrow socket ridges; fine median septum and bilobed bema bordered by rim and bearing up to 8 small side septa. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1741,*1a–e.* **O. insolita,* Anderken Formation, lower to middle Caradoc, Anderkenyn-Akchoku, Chu-Ili Range; *a,* latex cast of ventral exterior, BMNH BC 57592, ×4; *b–c,* mold and latex cast of ventral interior, BMNH BC 56664, ×4; *d–e,* holotype, mold and latex cast of dorsal interior, BMNH BC 56663, ×4 (Popov, Cocks, & Nikitin, 2002).

Zhilgyzambonites POPOV, COCKS, & NIKITIN, 2002, p. 52 [**Z. extenuata;* OD]. Outline rectimarginate; profile concavoconvex; ventral interarea apsacline with delthyrium completely covered by pseudodeltidium; dorsal interarea anacline with chilidium. Ornament of fine unequal parvicostellae. Ventral interior with small teeth; dental plates absent; muscle field small but raised high anteriorly; variably developed broad subperipheral rim. Dorsal interior with undercut cardinal process fused with flaring, curved socket ridges; deep alveolus and strongly elevated entire bema; prominent median septum originating anterior to bema and not extending anteriorly of prominent subperipheral rim. *Ordovician (Caradoc):* Kazakhstan.——FIG. 1741,*4a–e.* **Z. extenuata,* Anderken Formation, lower to middle Caradoc, Anderken-Akchoku, Chu-Ili Range; *a,* latex cast of ventral exterior, BMNH BC 57490, ×6; *b,* latex cast of dorsal exterior, BMNH BC 57491, ×6; *c,* ventral internal mold, BMNH BC 57493, ×6; *d–e,* internal mold and latex cast of dorsal interior, BMNH BC 57492, ×5 (Popov, Cocks, & Nikitin, 2002).

CHONETIDINA

PATRICK R. RACHEBOEUF

[Université de Bretagne Occidentale]

INTRODUCTION

Since the publication of *Treatise, Part H, Brachiopoda (revised),* volume 2 (KAESLER, 2000), 28 new names have been published for brachiopods belonging to the suborder Chonetidina: 1 subfamily in the Rugosochonetidae (Riosanetinae), 23 genera (5 strophochonetids; 2 chonostrophiids; 8 anopliids, and 8 rugosochonetids), and 4 subgenera of *Neochonetes*. Stratigraphically speaking, these 27 generic and subgeneric names are distributed as follows: Silurian (2), Devonian (7), Carboniferous (7), and Permian (11). A twenty-fourth generic name, the Silurian genus *Zephyronetes* HAVLÍČEK, 1995, was unfortunately forgotten during the preparation of volume 2 and is included here.

Such a complementary list of recently described new taxa calls for some comments. When reading diagnoses and discussions (and comparisons between closely allied genera and type species) of several of the new taxa, it becomes clear that variations in the relative development of both external and internal morphological characters, which were recently considered to be of intrageneric value, are now used to distinguish new genera, while species-level characters are used to define subgenera. Such a splitting tendency inevitably leads to new genera (and subgenera) being defined upon increasingly discrete characters. Ultimately this leads to the monotypy of most genera (while subgenera will be elevated to the genus rank), followed by subfamilies and families. The Permian genus *Neochonetes,* which now includes six subgenera, is undoubtedly in need of further investigation. The same is true for the subfamily Anopliinae and the family Anopliidae in general.

The illustration of decalcified specimens, where only external and internal molds are preserved, provides inadequate information for the detailed comparisons required today if rubber positives (casts) are not also illustrated. This is especially important in the description of new taxa and their comparison with existing genera and species, so as far as is possible, both natural molds and replica figures are provided here.

Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959

Suborder CHONETIDINA Muir-Wood, 1955

Superfamily CHONETOIDEA Bronn, 1862

Family STROPHOCHONETIDAE Muir-Wood 1962

Subfamily STROPHOCHONETINAE Muir-Wood 1962

Bacbonetes RACHEBOEUF & TONG-DZUY, 2000, p. 1052 [**B. janvieri*; OD]. Shell medium, transversely subrectangular, with faintly differentiated median enlarged costa in ventral valve; spines cyrtomorph extraverse, with two proximal spines lacking on left side; distal spines implantation alternating on both sides; dorsal interior with weakly elevated cardinal process; inner socket ridges poorly developed, low and short. *Lower Devonian:* Vietnam.——FIG. 1743,*2a–d*. **B. janvieri*; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Cyrtochonetes RACHEBOEUF & TONG-DZUY, 2000, p. 1059 [**Chonetes indosinensis* MANSUY, 1916, p. 47; OD]. Shell medium, transversely subrectangular, with cyrtomorph intraverse, symmetrically arranged spines; weak ventral median enlarged costa in juveniles, becoming obscure with growth; dorsal interior with internally subglobose, deeply bilobed cardinal process. *Lower Devonian*: Vietnam. ——FIG. 1743,*3a–c*. **C. indosinensis* (MANSUY); ventral exteriors, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Leptochonetina HAVLÍČEK, 1998, p. 117 [**L. vulgaris;* OD]. Shell small, thin, semicircular in outline with markedly convex ventral valve and moderately concave dorsal valve; surface smooth, rarely with median costa; orthomorph oblique spines, asymmetrically arranged, spines on right side appearing before left ones; cardinal process small, U-shaped; cardinal process pit elongate, extending anteriorly

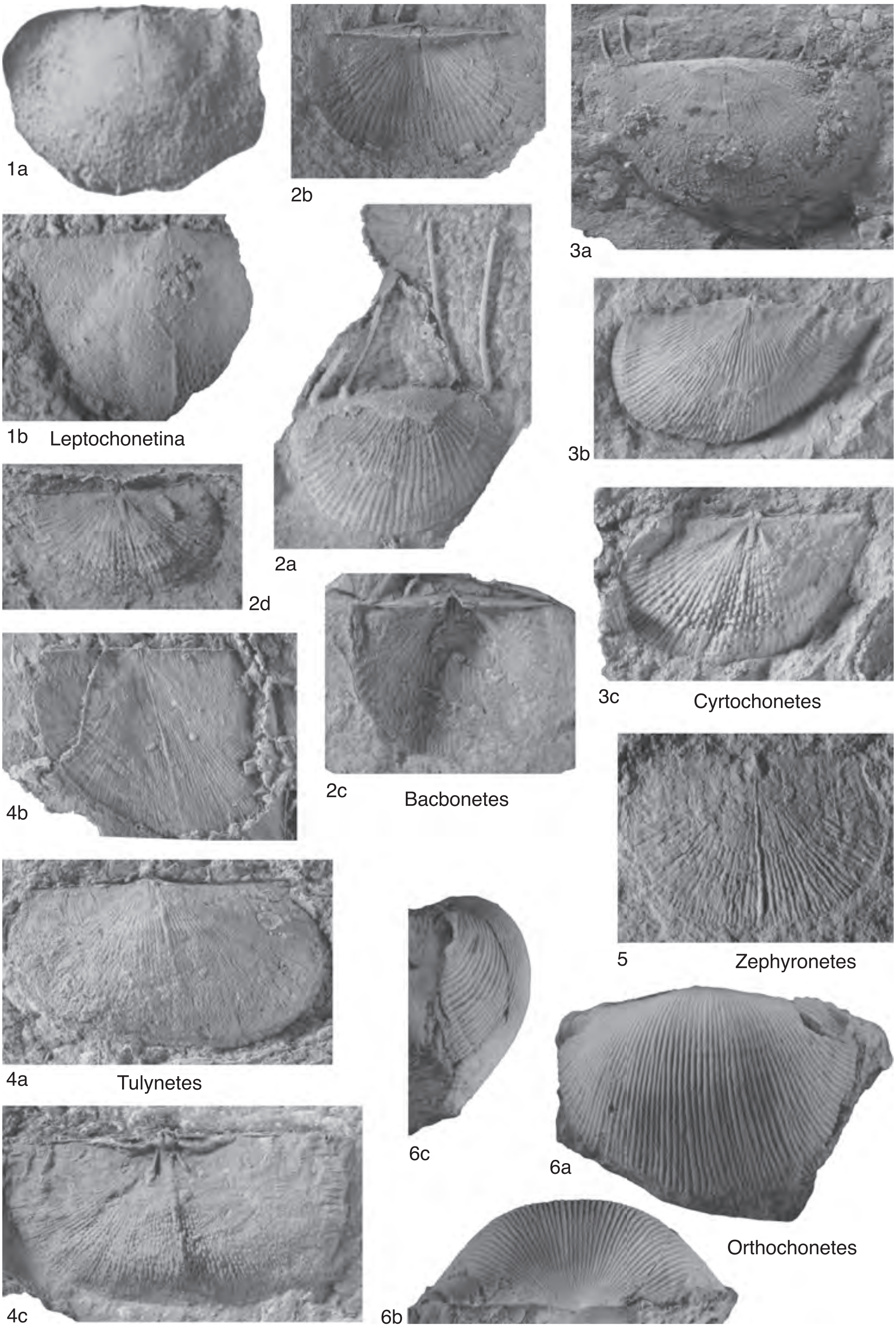


FIG. 1743. Strophochonetidae (p. 2628–2630).

to about one-quarter valve length; inner socket ridges long, straight, rather strong, widely divergent, almost parallel to hinge line; anderidia absent; low and short, breviseptum-like ridge, flanked by pair of weak lateral septa, may be developed. *Lower Devonian (Zlichovian):* Czech Republic (Bohemia).——FIG. 1743,*1a–b*. **L. vulgaris; a,* ventral valve internal mold, ×3.4; *b,* ventral internal mold with enlaged median costa, ×5.5 (Havlíček, 1998).

Tulynetes RACHEBOEUF & TONG-DZUY, 2000, p. 1048 [**Chonetes hoabinhensis* MANSUY, 1914, p. 58; OD]. Shell medium, costellate with median enlarged costa variably developed, in ventral valve only or in both valves; spines orthomorph perpendicular, with two proximal spines lacking on left side; ventral interior with relatively short, laterally elongated, subrectangular hinge teeth; dorsal interior with strongly bilobed and dorsally geniculated cardinal process, elevated above valve floor; breviseptum-like, often spinose median ridge, and medially well-developed endospines; long, narrow, posteriorly bent inner socket ridges. *Lower Devonian:* Vietnam.——FIG. 1743,*4a–c*. **T. hoabinhensis* (MANSUY); ventral exterior, dorsal exterior, dorsal interior, ×3 (Racheboeuf & Tong-Dzuy, 2000).

Zephyronetes HAVLÍČEK, 1995, p. 56 [**Chonetes zephyrus* BARRANDE, 1879, pl. 46, IV, 1–3; OD; =*Strophochonetes (Zephyronetes)* HAVLÍČEK, 1995, p. 56]. Shell small and thin walled, almost biplanar in lateral profile; spines symmetrically arranged, orthomorph perpendicular to intraverse; dorsal interior with slender and long socket ridges; anderidia extremely reduced to undiscernible. *Silurian (Wenlock):* Czech Republic (Bohemia).——FIG. 1743,*5*. **Z. zephyrus* (BARRANDE); ventral exterior, ×5 (Havlíček, 1995).

Subfamily PARACHONETINAE Johnson, 1970

Orthochonetes RACHEBOEUF & TONG-DZUY, 2000, p. 1065 [**Chonetes verneuili* BARRANDE, 1848, p. 248; OD]. Parachonetinae with transverse, markedly arched shell; spines numerous, orthomorph perpendicular, and symmetrically displayed; radial costellae relatively narrow, elevated, with vertical flanks. *Lower Devonian (Pragian):* Czech Republic (Bohemia).——FIG. 1743,*6a–c*. **O. verneuili* (BARRANDE); ventral valve, ventral, posterior, and lateral views, ×1.2 (Racheboeuf & Tong-Dzuy, 2000).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

Balikunochonetes CHEN & ARCHBOLD, 2002, p. 235 [**B. liaoi*; OD]. Shell medium, semicircular in outline; shell costellate; ventral valve exterior rugose forward; spines orthomorph, high angled, at 75° to 90°; myophragm long and elevated, extending anteriorly beyond midlength; dorsal median septum thin, extending to midlength; pentalobed myophore; anderidia at about 80°; accessory septa broad, thick, extending anteriorly almost to anterior margin, anteriorly divergent at 15° to 35°, with two pairs of subparallel, adventitious septa. [It appears that in the original diagnoses and descriptions, anderidia, accessory septa, and even socket ridges have been misinterpretated.] *Upper Devonian (Famennian):* northwestern China (Xinjiang).——FIG. 1744,*1a–b*. **B. liaoi; a,* ventral interior, ×2; *b,* dorsal interior, ×4 (Chen & Archbold, 2002).

Santanghuia CHEN & ARCHBOLD, 2002, p. 233 [**S. santanghuensis*; OD]. Shell medium, semicircular in outline, with catacline interarea; shell finely costellate; spines orthomorph oblique, low angled, less than 45°; myophragm thick, high, extending anteriorly to midlength; strong cardinal process with pentalobed myophore; no dorsal median septum; anderidia faintly developed; accessory septa thick, broad, long, reaching anterior margin, anteriorly divergent at 10° to 20°. [The same misinterpretations for *Balikunochonetes* apply to this genus.] *Upper Devonian (Famennian):* northwestern China (Xinjiang).——FIG. 1744,*2a–c*. **S. santanghuensis;* ventral interior, dorsal interiors, ×4 (Chen & Archbold, 2002).

Family ANOPLIIDAE Muir-Wood, 1962

Subfamily ANOPLIINAE Muir-Wood, 1962

Adatsagochonetes AFANASJEVA, 2004b, p. 164 [**A. mongolicus*; OD]. Shell medium, semicircular in outline; longitudinal profile concavoconvex, moderately arched; five pairs of oblique orthomorph spines at about 50°; ventral interior with myophragm extending anteriorly to midlength; dorsal interior with elevated cardinal process anteriorly bounded by cardinal process pit; no median septum or radial ridges; numerous irregularly displayed endospines on dorsal valve interior. [According to the author, *Adatsagochonetes* is similar to *Kaninochonetes,* from which it differs in the elevated cardinal process (instead of flattened) and by the absence of radially arranged endospines in the dorsal interior only. These variations in characters can be considered to be of intrageneric value.] *Lower Permian (Artinskian):* central Mongolia.——FIG. 1745,*1a–b*. **A. mongolicus;* ventral internal mold, dorsal internal mold, ×3 (Afanasjeva, 2004b).

Kaninochonetes AFANASJEVA, 2004a, p. 35 [**K. kaninensis*; OD]. Shell medium, semicircular in outline, weakly concavoconvex; four or five pairs of oblique orthomorph spines at about 50°–60°; ventral interior with myophragm extending anteriorly to midlength; dorsal interior with flattened cardinal process anteriorly bounded by cardinal process pit; no median septum nor radial ridges; small endospines arranged in numerous radial rows.

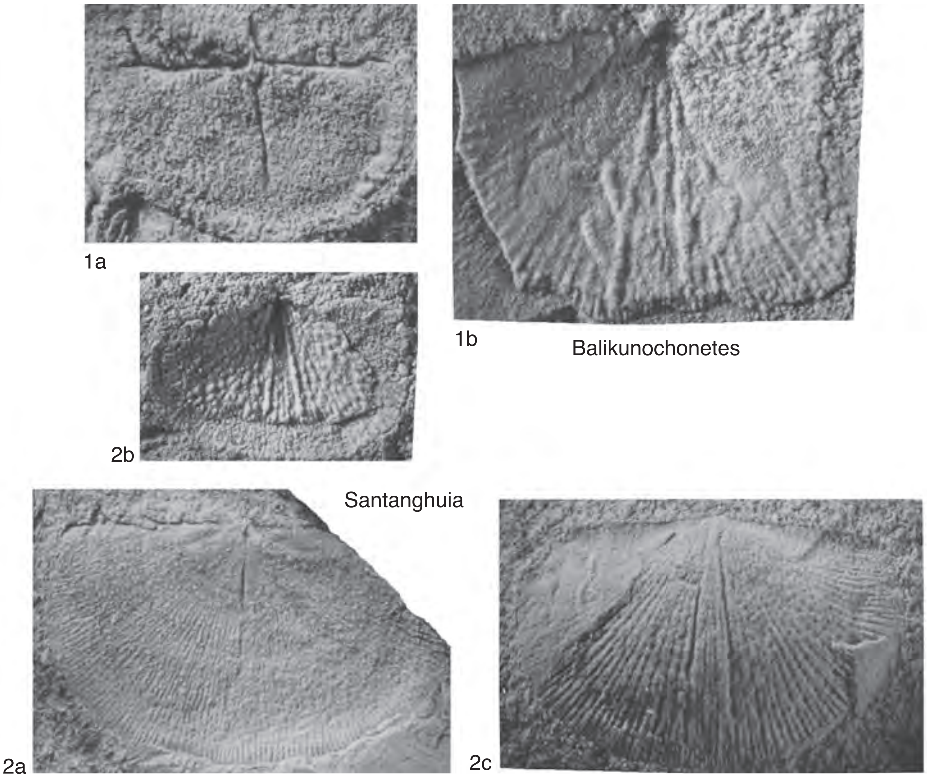


FIG. 1744. Chonostrophiidae (p. 2630).

Middle Permian (lower Guadalupian, Ufimian): northern part of Russian Platform.——FIG 1745,*2a–c*. **K. kaninensis*, Kanin Peninsula; ventral exterior, ventral interior, dorsal interior, ×3 (Afanasjeva, 2004a).

Palaeoanopliopsis AFANASJEVA, 2002, p. 627 [**P. glabra;* OD] [Junior subjective synonym of *Anopliopsis* GIRTY, 1938, p. 281; see RACHEBOEUF, 2000, p. 382]. [According to the author, *Palaeoanopliopsis* differs from *Anopliopsis* in its lack of flattened ears and by a longer dorsal median septum only. Variations in these characters are of intrageneric value; *Anopliopsis* is North American and Viséan to Namurian in age; *Palaeoanopliopsis* is from the Tournaisian, *Gattendorfia* Zone, of Germany.] (Afanasjeva, 2002).

Subfamily CAENANOPLIINAE Archbold, 1980

Chilenochonetes ISAACSON & DUTRO, 1999, p. 627 [**C. anna*; OD]. Shell medium, markedly concavoconvex, with maximum width anterior to hinge line; shell surface capillate with interspaces twice their width; ventral interior with short myophragm; hinge teeth small, laterally elongate; dorsal interior with large cardinal process pit, short median septum, not extending anteriorly beyond midline, with a pair of long and narrow accessory septa, short anderidia, and short, prominent, socket ridges. *Carboniferous (lower Tournaisian):* northern Chile.——FIG. 1746,*1a–d*. **C. anna; a,* ventral interior, ×2; *b,* dorsal interior, latex, ×2.5; *c–d,* ventral exterior and dorsal interior, latex, ×2 (Isaacson & Dutro, 1999).

Gibberochonetes AFANASJEVA, 2002, p. 59 [**G. gibber;* OD]. Shell small, semicircular; ventral sulcus distinct in largest shells; no dorsal fold; spines almost vertical or weakly cyrtomorph intraverse; ornament of rounded, thin, radial costae anteriorly bifurcating, crossed by very fine concentric growth lines; myophragm about one-fourth valve length; dorsal interior with low, knoblike cardinal process with cardinal process pit; no median septum or brachial ridges; strong endospines forming two weakly divergent radial rows near midline. [This genus was originally described within the subfamily Anopliinae, but according to its radial ornament, it is better placed within the subfamily Caenanopliinae, together with the genus *Caenanoplia,* from

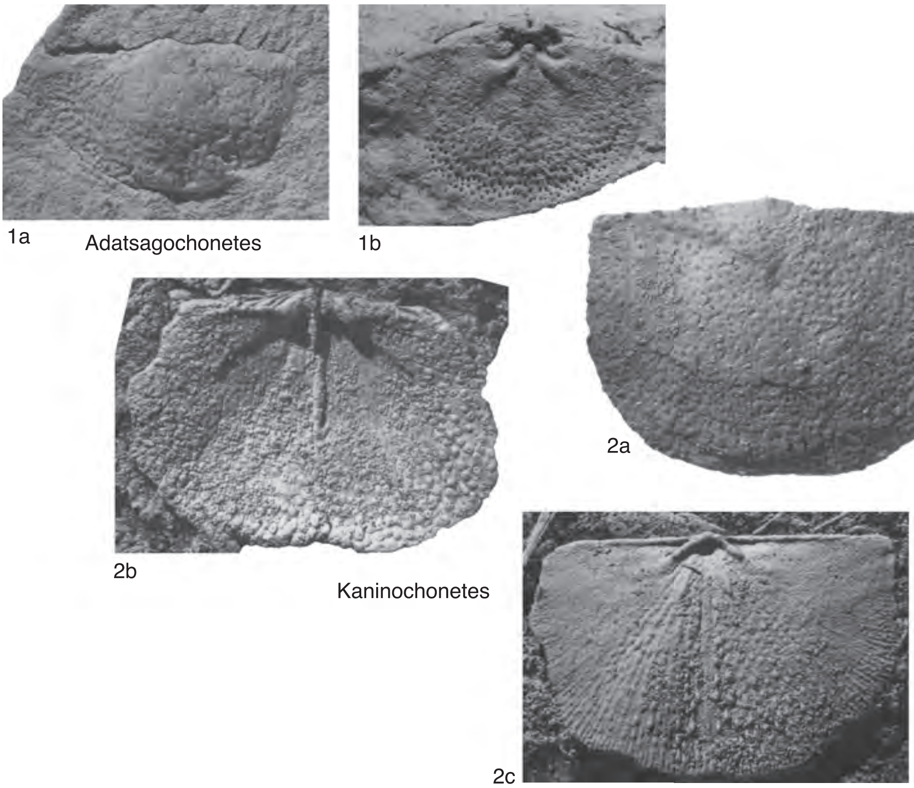


FIG. 1745. Anopliidae (p. 2630–2631).

which it differs in the development of a weak ventral sulcus and stronger radial external ornament. No suitable illustrations are available.] *Upper Devonian* (*Famennian*).

Gonzalezius TABOADA, 2004, p. 413 [**G. naranjoensis*; OD]. Shell weakly concavoconvex, subcircular in outline; shell surface capillate, with well-marked concentric growth lines; spines orthomorph oblique and symmetrically arranged; ventral interior with long and narrow myophragm and parallel hinge teeth; dorsal interior with cardinal process pit and two or more thin, weakly divergent accessory septa; short and narrow breviseptum; anderidia very thin, long, bladelike. *Carboniferous (Namurian):* Argentina.——FIG. 1746,*3a–c*. **G. naranjoensis,* San Juan Province; ventral external mold, ventral internal mold, dorsal internal mold, ×4 (Taboada, 2004)

Ogorella RACHEBOEUF, 2001, p. 579 [**O. janickae*; OD]. Shell small, with orthomorph oblique, symmetrical spines; radial ornamentation of costae originating anterior of beaks, widening up to commissures; ventral and dorsal interareas flat, lying in same plane; large pseudodeltidium and chilidium; stout, laterally elongated and horizontal hinge teeth; short myophragm dividing relatively small muscle field; dorsal interior with short septum supporting cardinal process, with low and wide myophore; anderidia long and narrow, strongly divergent; accessory septa markedly divergent, narrow, and spinose; periphery of both valves smooth, flat. *Middle Devonian (Givetian):* western Europe.——FIG. 1746,*4a–d*. **O. janickae*, Massif Armoricain; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×4 (Racheboeuf, 2001).

Pinegochonetes AFANASJEVA, 2000, p. 287 [**Chonetes pinegensis* KULIKOV, 1974, p. 144; OD]. Shell medium sized, semicircular in outline, concavoconvex to almost planoconvex, with distinct sulcus and fold; radial ornament of bifurcating and intercalating costae and costellae; spines oblique orthomorph at about 35°–40°, symmetrically arranged; ventral interior with stout myophragm extending about two-thirds valve length; dorsal interior with cardinal process elevated above valve floor, anteriorly bounded by cardinal process pit; inner socket ridges parallel to hinge line; no median septum or brachial ridges; inner surface covered with radially displayed endospines; two rows of

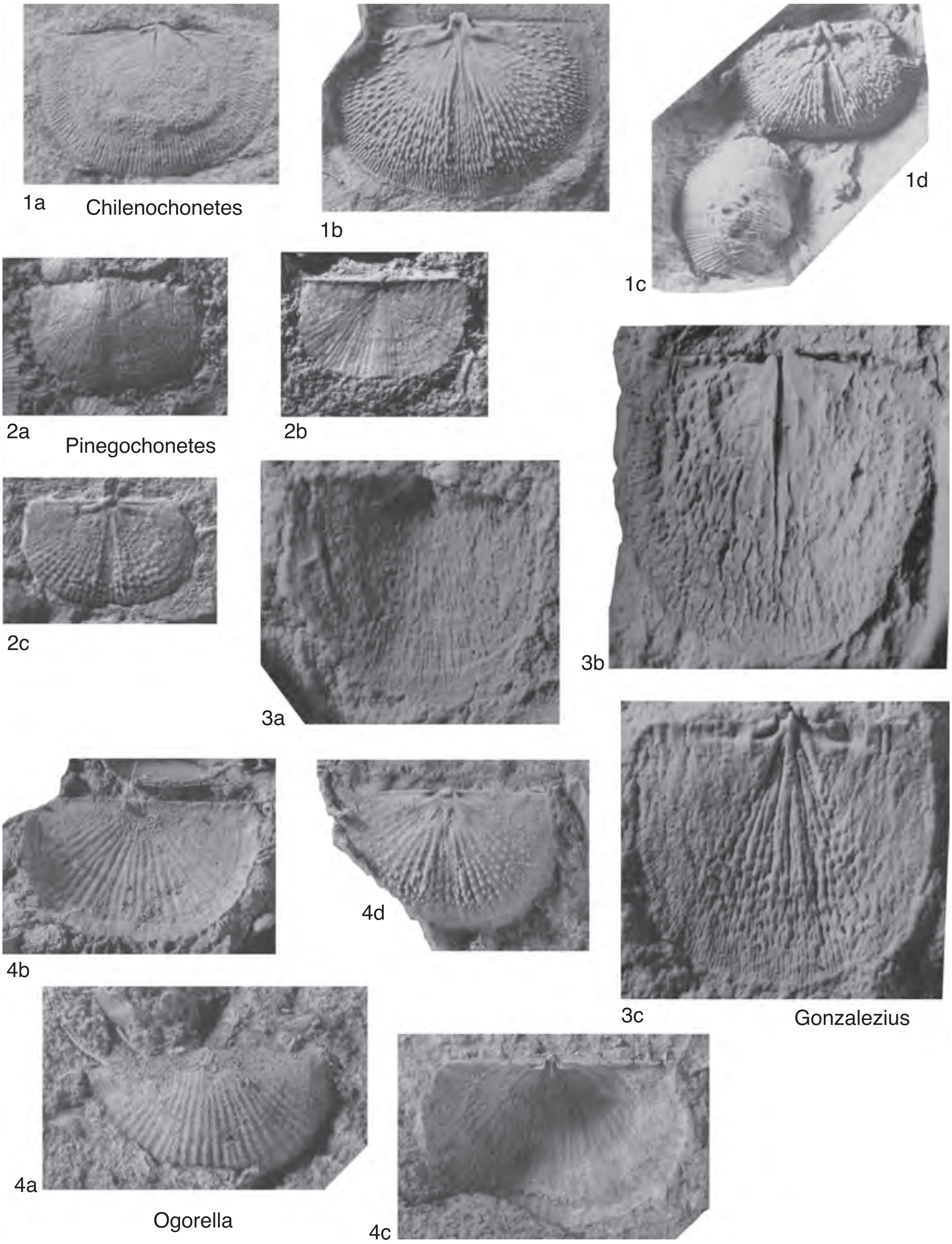


FIG. 1746. Anopliidae (p. 2631–2633).

stronger endospines forming accessory septa similar to feature near midline. [This genus was originally described within the subfamily Anopliinae, but according to its radial ornament, it is better placed within the subfamily Caenanopliinae.] *Upper Permian (lower Kazanian):* north of Russian Platform (Arkhangelsk Region).——FIG. 1746,*2a–c*. **P. pinegensis* (KULIKOV), Pinega River; ventral exterior, dorsal exterior, dorsal interior, ×1.5 (Afanasjeva, 2000).

Family RUGOSOCHONETIDAE Muir-Wood, 1962

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

Neochonetes Muir-Wood, 1962, p. 87.

Neochonetes (Huangichonetes) Shen & Archbold, 2002, p. 335 [**Chonetes substrophomenoides* Huang, 1932, p. 3; OD]. Small, reverse, trapezoidal *Neochonetes* shell with small but prominent and acute ears, and conspicuous and moderately wide sulcus; strongly convex visceral disc; hinge spines projecting posterolaterally at 30°–40° to hinge line; radial costellae fine, numbering 30–50 near margin; ventral interior with very short myophragm. *Upper Permian (Lopingian):* South China.——Fig. 1747,*1a–d.* **N. (H.) substrophomenoides* (Huang); ventral internal mold, dorsal external mold, juvenile dorsal interior, adult dorsal interior, ×3 (Shuzhong Shen & Archbold, 2002).

Neochonetes (Nongtaia) Archbold, 1999, p. 75 [**N. (N.) taoni*; OD]. Similar to *Neochonetes (Neochonetes),* but shell small, subquadrate, with relatively narrow, distinct sulcus, distinct dorsal fold, distinct ornament of coarse capillae increasing in number by bifurcation. *middle Permian (lower Guadalupian (Ufimian = Roadian):* southeastern Asia.——Fig. 1748,*2a–d.* **N. (N.) taoni,* Ufimian, Thailand; ventral exterior, dorsal exterior, ventral interior, dorsal interior, ×4.5 (Archbold, 1999).

Neochonetes (Zechiella) Archbold, 1999, p. 78 [**Chonetes davidsoni* von Schauroth, 1856, p. 222; OD]. Small, thin-shelled *Neochonetes* with obsolescent radial capillae, sulcus absent, internal structures poorly developed. *middle Permian (lower Guadalupian (Ufimian = Roadian):* southeastern Asia, Germany, England.——Fig. 1748,*1a–b.* **N. (Z.) davidsoni* (von Schauroth), Germany; ventral valve with spines, dorsal side of articulated shell, ×4 (Archbold, 1999).

Neochonetes (Zhongyingia) Shen & Archbold, 2002, p. 333 [**Neochonetes zhongyingensis* Liao, 1980, p. 257; OD]. Reverse, trapezoidal outline with acute ears, greatest width at hinge line, with cardinal extremities extended; spines less than 45°; ventral valve slightly convex with shallow and broad sulcus; shell surface finely costellate; dorsal interior with long lateral ridges parallel to hinge line. *Upper Permian (Lopingian):* South China.——Fig. 1747,*2a–f.* **N. (Z.) zhongyingensis* (Liao); ventral and dorsal exteriors, latex, ventral internal mold and latex, dorsal interior, latex and internal mold, ×3 (Shen & Archbold, 2002).

Robertsella Chen & Shi, 2003, p. 135 [**Rugosochonetes macgregori* Roberts, 1971, p. 62; OD]. Shell medium, subrectangular in outline; valve exteriors densely costate and irregularly lamellose; cardinal extremities angular to subrounded; hinge spines orthomorph oblique; ventral interior with short myophragm; dorsal interior with high and thick inner socket ridges, bilobed cardinal process, large and deep cardinal process pit; short median septum not extending anteriorly beyond midlength, slightly elevated anteriorly. [There are no suitable illustrations available of the type species.] *Lower Carboniferous (Viséan):* northwestern China, Australia (New South Wales).——Fig. 1749,*2a–c. R. tarimensis* Chen & Shi, northwestern China; ventral exterior, ventral internal mold, dorsal interior, ×2 (Chen & Shi, 2003).

Tethyochonetes Chen & others, 2000, p. 5 [**Waagenites soochowensis quadrata* Zhan, 1979, p. 70; OD]. Shell small, transversely rectangular, strongly concavoconvex; cardinal extremities varying from acute to slightly semielliptical; ears smooth, broad, flattened, or slightly swollen; sulcus varying from deep, broad, and distinct to shallow, narrow, and indistinct; sulcal bounding flanks distinct to depressed; fold slightly raised to flattened; external ornament with robust and rounded costae, sometimes bifurcating; ventral myophragm thin and high, extending anteriorly to half valve length; cardinal process rounded and blunt, bilobed internally, trilobed externally; dorsal median septum stout, raised at its middle to anterior part, originating anterior to cardinal process pit, continuing forward for half valve length; lateral septa stout, short, and distinct; brachial scars strongly swollen and semicircular in outline. *Upper Permian (Wuchiapingian–uppermost Changhsingian):* eastern and southwestern China.——Fig. 1749,*1a–b.* **T. quadrata* (Zhan), uppermost Changhsingian; ventral valve, dorsal interior, ×3 (Chen & others, 2000).

Thuringochonetes Afanasjeva, 2002, p. 630 [**T. thuringicus;* OD]. Shell small, semicircular in outline, without sulcus and fold, and weakly concavoconvex; external ornament with very thin radial costellae, sometimes bifurcating, and alternating with some stronger radial costae; spines symmetrically arranged, oblique orthomorph to weakly cyrtomorph, low angled, becoming almost parallel toward cardinal angles; ventral myophragm restricted to umbonal region, dividing a markedly bilobate diductor muscle field; adductor scars adjacent, smooth, and semiellipical in outline; cardinal process knob shaped, anteriorly bounded by large cardinal process pit; dorsal median septum low and narrow, not extending beyond midlength of valve; anderidia relatively long. [The genus was originally placed within the family Strophochonetidae owing to the presence of enlarged capillae and to the strongly bilobed nature of the ventral muscle field. These characters do not support such a family assignment in comparison with features such as spines and the morphology of the dorsal interior.] *Lower Carboniferous (Tournaisian):* Thuringia and Rhenish Slate Mountains (Germany).

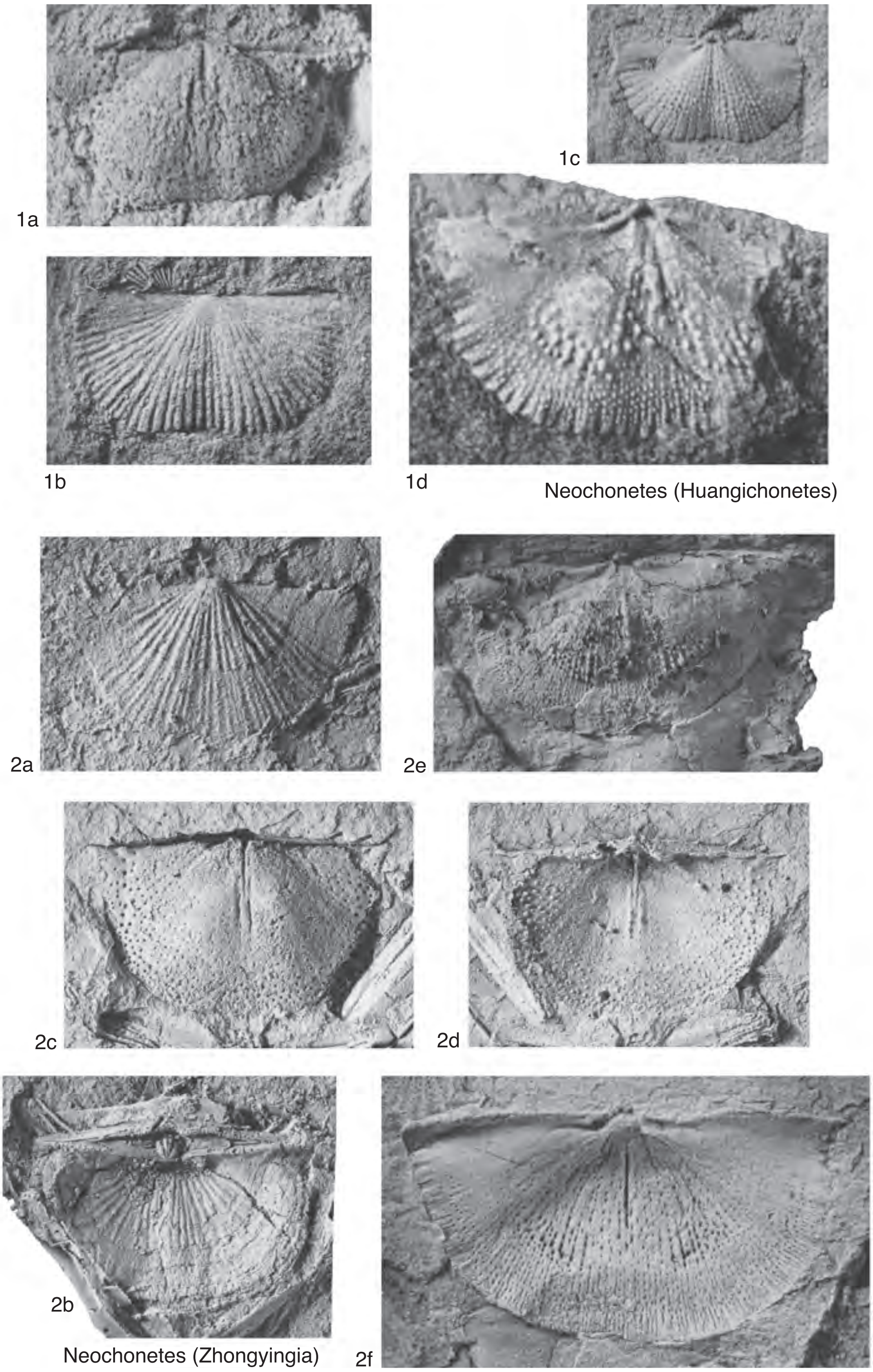


FIG. 1747. Rugosochonetidae (p. 2634).

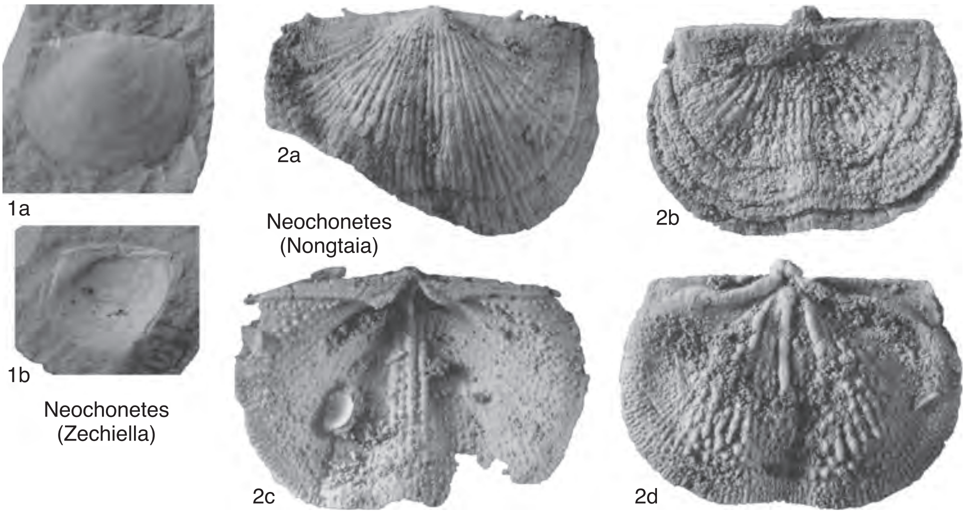


Fig. 1748. Rugosochonetidae (p. 2634).

——Fig. 1749,*3a–e.* **T. thuringicus;* ventral exterior, damaged ventral valve with spines, dorsal exterior, dorsal interior, ventral internal mold, ×4 (Afanasjeva, 2002).

Subfamily PLICOCHONETINAE Sokolskaya, 1960

Nisalarinia Waterhouse, 2004, p. 58 [**Rugaria nisalensis* Waterhouse, 1978, p. 60; OD] [Junior subjective synonym of *Rugaria* Cooper & Grant, 1969; see Racheboeuf, 2000, p. 411]. [As stated by its author, the new genus mainly differs from *Rugaria* by longer anderidia, finer radial ribbing, smooth ears and posteriorly thicker myophragm (=ventral septum). These characters are considered to be within the limits of intrageneric variation.] (Waterhouse, 2004).

Subfamily RIOSANETINAE Martínez Chacón & Winkler Prins, 2000

[Riosanetinae Martínez Chacón & Winkler Prins, 2000, p. 226] [Type genus, *Riosanetes* Martínez Chacón & Winkler Prins, 2000, p. 226]

Small to medium rugosochonetids with costellate ornamentation; oblique orthomorph spines. Dorsal interior without median septum. *Lower Carboniferous (Tournaisian).*

Riosanetes Martínez Chacón & Winkler Prins, 2000, p. 226 [**R. fernandezi*; OD]. Shell small with thin valves, planoconvex to slightly concavoconvex, subrectangular; cardinal extremities rounded; costellate ornamentation with fine costae and costellae, apart from smooth ears; external ornamentation especially prominent internally, indicating very thin valves; ventral interior with short myophragm, posteriorly elevated; without vascular ridges; dorsal interior with very thin anderidia, high and strong inner socket ridges, without median septum; tubercles placed in rows along the intercostal sulci, occasionally tubercles of central rows are more marked but never form septa; brachial ridges not developed. *Lower Carboniferous (lower Tournaisian).* northern Spain (Cantabrian Mountains).——Fig. 1750,*2a–c.* **R. fernandezi;* ventral internal mold, dorsal external mold, dorsal internal mold, ×5 (Martínez Chacón & Winkler Prins, 2000).

Aitegounetes Chen & Shi, 2003, p. 138 [**A. aitegouensis*; OD] [=*Aitegouchonetes* Chen & Shi, 2003, p. 138, lines 8 and 14, *nom. null.*; *Aitegouensis* Chen & Shi, 2003, p. 138, line 17, *nom. null.*]. Shell small to medium, markedly concavoconvex, and subrectangular; cardinal extremities angular

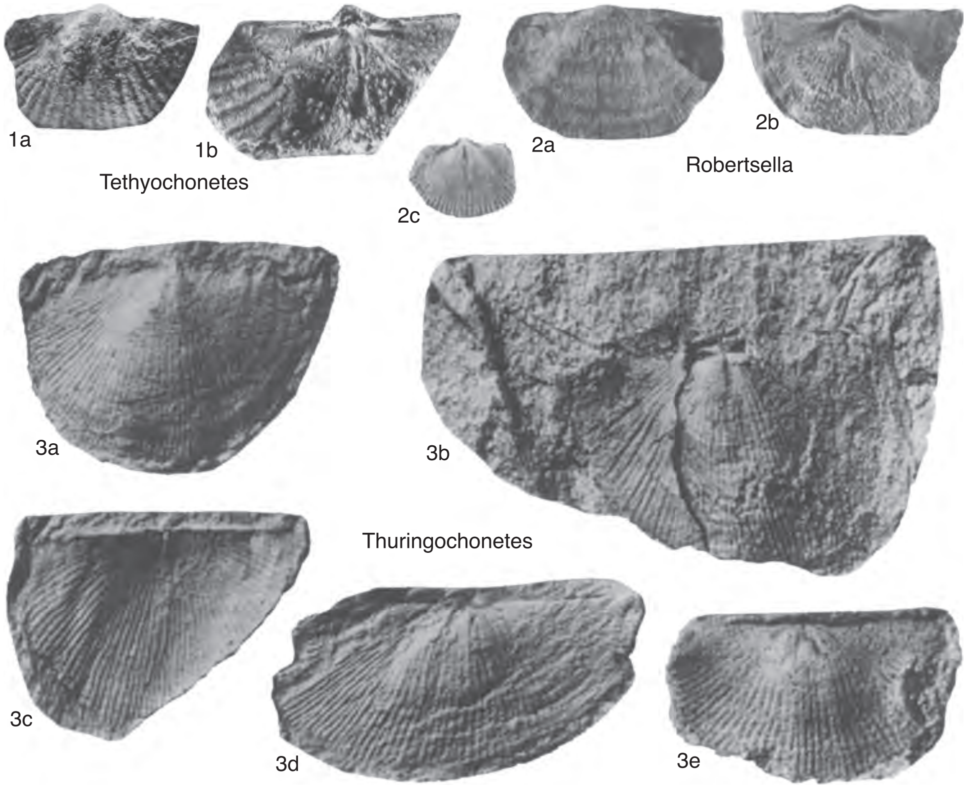


Fig. 1749. Rugosochonetidae (p. 2634).

to subrounded; valve exteriors strongly costellate except for weakly ribbed ears; oblique orthomorph, low-angled spines; ventral interior with thin myophragm about half valve length; dorsal interior with pair of short, thin anderidia, stout inner socket ridges, but without median septum; valve covered with radial rows of endospines, never fused; no brachial ridges. *Lower Carboniferous* (*Viséan*): northwestern China.——Fig. 1750,*3a–c*. **A. aitegouensis;* ventral exterior, dorsal exterior, dorsal interior, ×3 (Chen & Shi, 2003).

Linshuichonetes Campi & Shi, 2002, p. 110 [**L. elfinis*; OD]. Small, subquadrate to semicircular rugosochonetid, characterized externally by fine capillation, a weak or absent median sulcus and fold, internally by a lack of median, lateral, and accessory septa in dorsal interior; absence of vascular mantle canals in ventral interior and presence of distinct radiating rows of papillae in interiors of both valves, except on either side of midline in posterior part of dorsal valve, where only raised clusters of papillae occur. *Lower Permian (upper Artinskian)–middle Permian (Wordian):* southwestern China (Sichuan), Thailand.——Fig. 1750,*1a–c*. **L. elfinis*, Wordian, Sichuan, southwestern China; *a,* ventral exterior, ×7; *b–c,* dorsal exteriors, ×12, ×10 (Campi & Shi, 2002).

Subfamily STRIOCHONETINAE
Waterhouse & Piyasin, 1970

Binderochonetes Afanasjeva, 2004b, p. 162 [**B. manankovi*; OD] [Junior subjective synonym of *Striochonetes* Waterhouse & Piyasin, 1970; see

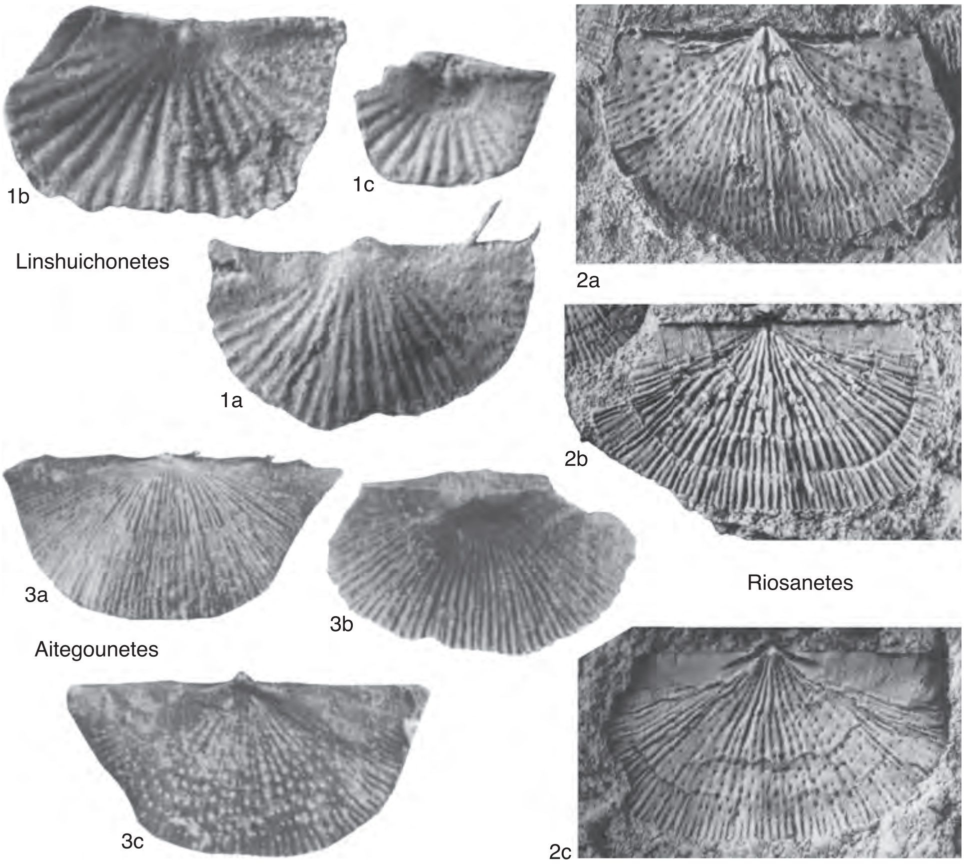


FIG. 1750. Rugosochonetidae (p. 2634–2636).

RACHEBOEUF, 2000, p. 415]. [The distinguishing characters given by the author in the diagnosis of the new genus, as well as in the comparison between the two type species (p. 164), are considered to be no more than intrageneric variations possibly resulting from evolutionary changes. Both type species are Upper Permian, that of *Striochonetes* (southern Thailand) being Kazanian in age, while that of *Binderochonetes* (northeastern Mongolia) is Tatarian in age.] (AFANASJEVA, 2004b).

PRODUCTIDINA

C. H. C. Brunton

[retired from The Natural History Museum, London]

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTOIDEA Gray, 1840

Family PRODUCTELLIDAE Schuchert, 1929

Subfamily PRODUCTININAE Muir-Wood & Cooper, 1960

Tribe PRODUCTININI Muir-Wood & Cooper, 1960

Caruthia Lazarev & Carter, 2000, p. 12 [**C. borealis*; OD]. Small, outline subrounded with well-differentiated, subtriangular ears; lateral profile almost semicircular; corpus shallow; ribbing weak on both valves, originating on corpus; rugae weak dorsally; spines rare, scattered on venter and rows separating ears from flanks; lateral ridges in both valves, dorsally extending as weak marginal ridges. *Upper Carboniferous (upper Bashkirian–lower Moscovian):* USA (southeastern Alaska).——Fig. 1751,*1a–f.* **C. borealis*, Prince of Wales Island; *a–d,* holotype, ventral, anterior, posterior, and lateral views, USNM 498809, ×2; *e–f,* dorsal valve interior, ventral and posterior views, ×2 (Lazarev & Carter, 2000).

Tribe PARAMARGINIFERINI Lazarev, 1990

Tethysiella Kotlyar, Zakharov, & Polubotko, 2004, p. 521 [**Productus* (*Productus*) *urushtensis* Licharew, 1936, p. 36; OD]. Small, transverse shells with prominent ears and well-developed trails that may be nasute, separated from the corpus by a cincture; ribbing is strong and rugae confined posterolaterally; spines appear to be in rows between ears and flanks plus some anterolaterally on ventral valve close to cincture. [A reason given for creating this genus was the near absence of spines, but the published photographs do not seem to support this. The genus was assigned to the Marginiferidae by its Russian authors (Kotlyar, Zakharov, & Polubotko, 2004), but here it is thought to resemble *Rugivestis* (see Brunton & others, 2000, p. 431) belonging to the Paramarginiferini.] *Upper Permian (Changhsingian)*: Russia (northwestern Caucasus mountains).——Fig. 1751,*2a–e.* **T. urushtensis* (Licharew), Urushten Formation; *a,* ventral valve exterior, ventral view, ×2; *b,* anterior view, ×1; *c,* incomplete ventral valve exterior, anterolateral view, ×2; *d,* ventral valve lateral view, ×2; *e,* dorsal valve exterior, ×2 (Kotlyar, Zakharov, & Polubotko, 2004).

Subfamily OVERTONIINAE Muir-Wood & Cooper, 1960

Tribe AVONIINI Sarytcheva, 1960

Lazarevonia Waterhouse, 2001, p. 22 [**Krotovia arcuata* Waterhouse, 1978, p. 52; OD]. Small, somewhat resembling *Quasiavonia* in shape, having a moderately inflated umbo, but differing in its elongate and more frequent spine bases ventrally and small rounded bases with fine spines dorsally; weakly lamellose growth lines; lateral ridges may extend around visceral disc as slight shell thickening. *Upper Permian (upper Capitanian–Changhsingian):* Himalaya (western Nepal, Tibet).——Fig. 1752,*3a–f.* **L. arcuata* (Waterhouse), West Dolpo, western Nepal; *a,* holotype, partially exfoliated ventral valve exterior, UQF 68815, ×2; *b,* partially exfoliated ventral valve exterior, ×2; *c,* mold of dorsal valve exterior, ×2; *d,* largely exfoliated dorsal valve exterior with remaining shell in areas of shell thickening, ×2 (Waterhouse, 1978); *e,* rubber replica of dorsal valve interior, ×2; *f,* internal mold of ventral valve, ×2 (Waterhouse, 2001).

Tribe COSTISPINIFERINI Muir-Wood & Cooper, 1960

Callyconcha Waterhouse, 2001, p. 23 [**Comuquia australis* Archbold, 1984, p. 86; OD]. Resembles *Comuquia* in shape, but differs in having few strong ventral spines, mostly limited to flanks, and apparently no dorsal spines; lamellose growth lines present ventrally. *Lower Permian (upper Sakmarian):* Western Australia (Carnarvon Basin), ?southern Himalayas.——Fig. 1752,*1a–d.* **C. australis* (Archbold), Callytharra Springs, Carnarvon Basin; *a–c,* holotype, ventral, dorsal, and posterior views, GSWA F11050, ×3.5; *d,* ventral valve exterior, ×3.2 (Archbold, 1984).

Dalinuria Li & Gu, 1976, p. 245. Spelling correction for that listed in Brunton and others (2000, p. 434–435).

Tribe KROTOVIINI Brunton, Lazarev, & Grant, 1995

Krotovia Fredericks, 1928, p. 779 [**Productus spinosus* J. Sowerby, 1814 in 1812–1815, p. 155; OD] [=*Guangia* Waterhouse, 2002b, p. 46 (type, *Krotovia inflata* Shen & others, 2000, p. 739, OD)] [Although it is tempting to reduce the stratigraphical range of *Krotovia* by the introduction of *Guangia* in the Upper Permian, justification based on morphological reasons has yet to be made. The original diagnosis of *Guangia* reads as

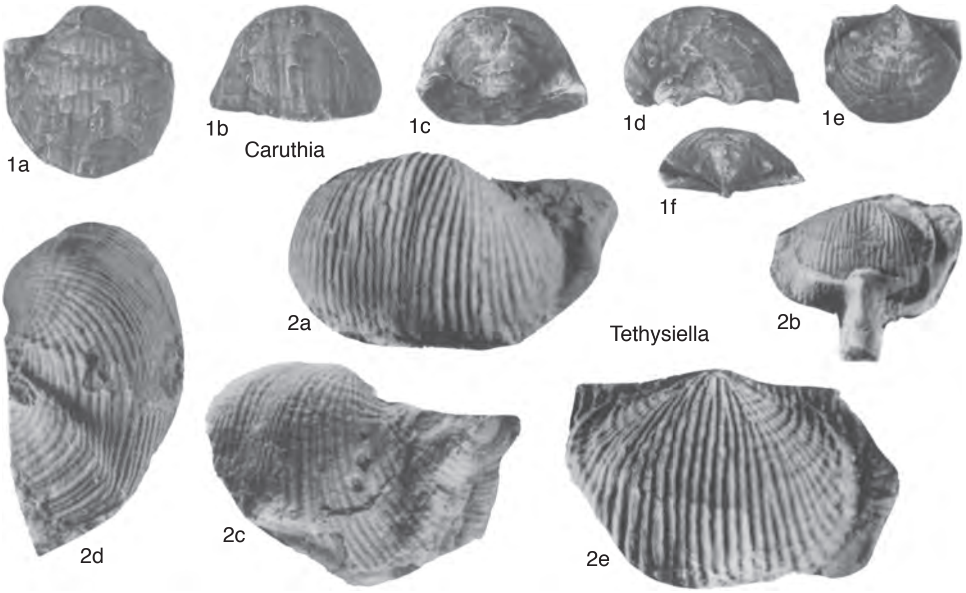


FIG. 1751. Productellidae (p. 2639).

if for the type species of *Krotovia*, but for "dorsal spines few." (Waterhouse, 2002b, p. 46). Shen and others (2000, p. 739) describe their *K. inflata* as having numerous small dorsal spines, however, and their illustration supports this. The degree to which spine bases are swollen may increase in Permian species, but this small difference does not warrant a new genus. *Guangia* is a junior subjective synonym of *Krotovia* with description as in Brunton and others, 2000, p. 438.] *Lower Carboniferous–Upper Permian:* Eurasia, northern Africa.——FIG. 1752,*2a–b*. *K. inflata* (Shen & others), Lopingian, southern Tibet; *a,* holotype, incomplete ventral valve exterior, NMVP148883, ×1.5; *b,* dorsal valve external mold, ×1.5 (Shen & others, 2000).

Tribe LETHAMIINI Waterhouse, 2001

[Lethamiini Waterhouse, 2001, p. 17] [type genus, *Lethamia* Waterhouse, 1973, p. 38]

Overtoniinae with shallow corpus cavity, fine dorsal and ventral spines, and weak concentric ornamentation. *Upper Carboniferous (Kasimovian)–Lower Permian (Artinskian), ?Upper Permian (Changhsingian).*

Lethamia Waterhouse, 1973, p. 38 [**L. ligurritus*; OD]. Resembles *Stictozoster* but larger with less distinctive spine bands; dorsal adult internal morphology more clearly defined, with median septum more prominent anteriorly and well-differentiated ears. [Waterhouse (2001) erected the tribe Lethamiini for this genus, which was not illustrated in Brunton and others (2000, p. 436). Other genera probably within this tribe would be *Amosia*, *Archboldina, Dyschrestia, Stictozoster*, *Tuberculatella, Tubersulculus,* and *Wooramella*. *Rugoclostus*, mentioned by Waterhouse (2001) as possibly related, is felt to be distinctive because of its rugae, corpus depth, and strong hinge spines.] *Lower Permian (Sakmarian)–Upper Permian (Changhsingian):* New Zealand, eastern and Western Australia.——FIG. 1753,*1a–e*. **L. ligurritus*, holotype, Roadian, mid-Permian, South Island, New Zealand, BR 957; *a,* internal mold, dorsal view; *b,* external mold of dorsal valve and ventral umbo; *c,* rubber replica of *b; d,* rubber replica of ventral valve exterior, ×1.5; *e,* rubber replica of posteromedian part of dorsal interior, ×1.5 (Waterhouse, 1982).

Amosia Simanauskas, 1996, p. 378 [**A. sueroi*; OD; =*Productella* aff. *bifaria* (Stainbrock in Amos, 1961, p. 91; 1979, p. 75)]. Small- to medium-sized concavoconvex shells with shallow corpus cavity, outline semicircular, and somewhat resembling *Dyschrestia*; ornament weakly lamellose, no ribbing; spines fine, but more robust at ears, close to hinge line, and anteriorly, dorsal spines sparse and fine; cardinal process sessile, quadrifid to trifid, not supported by short, narrow median septum, lateral ridges short; interiors endospinose. [Simanauskas (1996) placed his genus in the Overtoniidae and Overtoniinae of Muir-Wood and Cooper, 1960. The family Overtoniidae was not used in Brunton and others (2000), and the genus is here placed in the tribe Lethamiini.] *Lower Permian (Sakmarian):* Argentina (Tepuel-Genoa Basin, Chubut Province).——FIG. 1753,*2a–f*. **A. sueroi*, Chubut Province; *a,* ventral valve, anteroventral view, ×2; *b,* ventral valve viewed laterally, ×2; *c,*

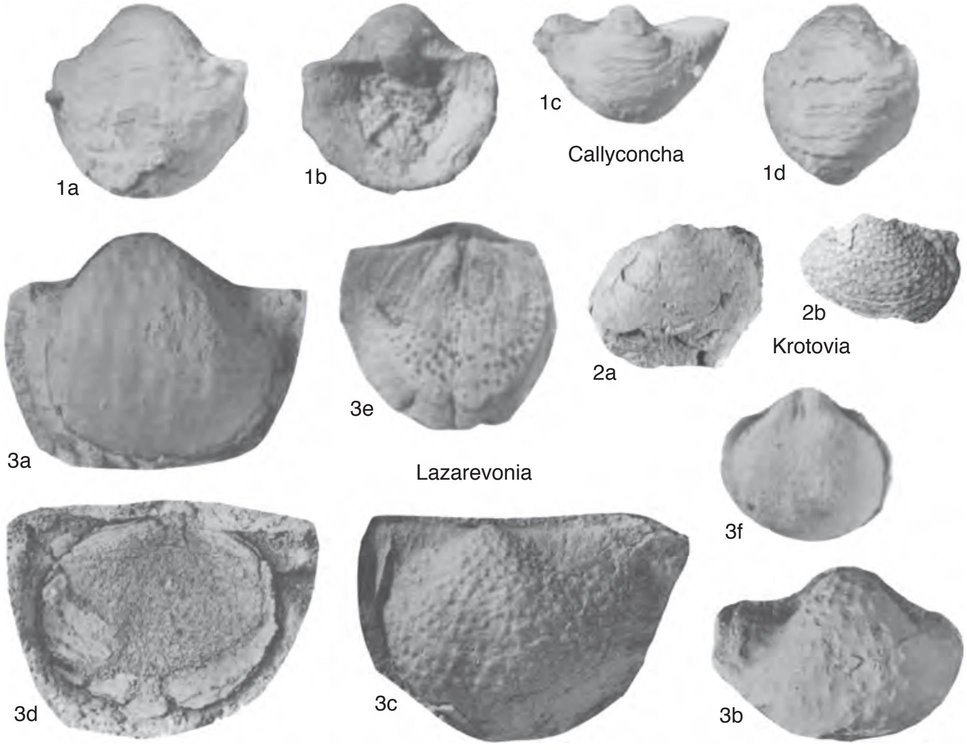


FIG. 1752. Productellidae (p. 2639–2640).

incomplete ventral valve viewed obliquely showing spines, ×2; *d,* holotype, replica of incomplete dorsal valve interior, MLP 26003a, ×3; *e,* shell, dorsal view, ×2; *f,* replica from internal mold showing ventral interior, ×2 (Simanauskas, 1996).

Archboldina WATERHOUSE, 2001, p. 22 [**Pustula micracantha* HOSKING, 1933, p. 49; OD]. Small, evenly spinose, concavoconvex shells resembling *Wooramella*, but with weakly rugose ears that lack spines, more strongly defined concentric ornament dorsally and somewhat swollen spine bases ventrally; dorsal interiors with anteriorly weak subperipheral rim and anteriorly elevated adductor muscle scars. [WATERHOUSE's (2001) suggestion that this genus might belong in his new tribe Lethamiini, is accepted here]. *Lower Permian (upper Sakmarian):* Western Australia.——FIG. 1754,*1a–f.* **A. micracantha* (HOSKING), Callytharra Formation, Carnarvon Basin; *a–b,* lectotype, crushed dorsal valve, dorsal and ventral views, GSWA 1/4970b, ×2; *c,* crushed ventral valve exterior, ×1.8; *d,* dorsal valve exterior, ×1.6; *e,* interior showing subperipheral rim, prominent muscle scars, and brachial impressions, ×1.8; *f,* posterodorsal view showing cardinal process and high lateral ridges, ×2.2 (Archbold, 1984).

Tuberculatella WATERHOUSE, 1982, p. 42 [**T. tubertella*; OD]. Similar to *Lethamia*, but with pustulose ventral spine bases, a weak ventral median sulcus, and narrow dorsal medium septum. [This genus was inadvertently omitted from BRUNTON and others (2000). The holotype is housed at Geological Survey of Thailand, Bangkok.] *Upper Carboniferous (Kasimovian–Gzhelian):* eastern Europe, Asia. ——FIG. 1754,*3a–e.* **T. tubertella,* Huai Bun Nak, Thailand; *a–b,* holotype, internal mold viewed ventrally and dorsally, TBR 579, ×2; *c,* dorsal valve external mold, ×2; *d,* latex replica of ventral valve exterior with swollen spine bases, ×2; *e,* ventral valve internal mold, posterior view showing muscle fields and median sulcus, ×2 (Waterhouse, 1982).

Wooramella ARCHBOLD in HOGEBOOM & ARCHBOLD, 1999, p. 260 [**Pustula senticosta* HOSKING, 1933, p. 47; OD]. Medium sized, outline subrounded, concavoconvex profile, and shallow corpus cavity; spines on both valves arranged in concentric bands but absent from hinge lines; internal features poorly known, but cardinal process said to be bilobed and low, with short thin medium septum. [ARCHBOLD (in HOGEBOOM & ARCHBOLD, 1999) placed this genus in the Tubersulculinae BAMBER & WATERHOUSE, 1971, but BRUNTON and others (2000, p. 434) placed it into the tribe Costispiniferini MUIR-WOOD & COOPER, 1960. If genera with relatively shallow corpus cavities were removed from the costispiniferins then *Wooramella* joins similar genera, such as *Archboldina, Dyschrestia, Lethamia,*

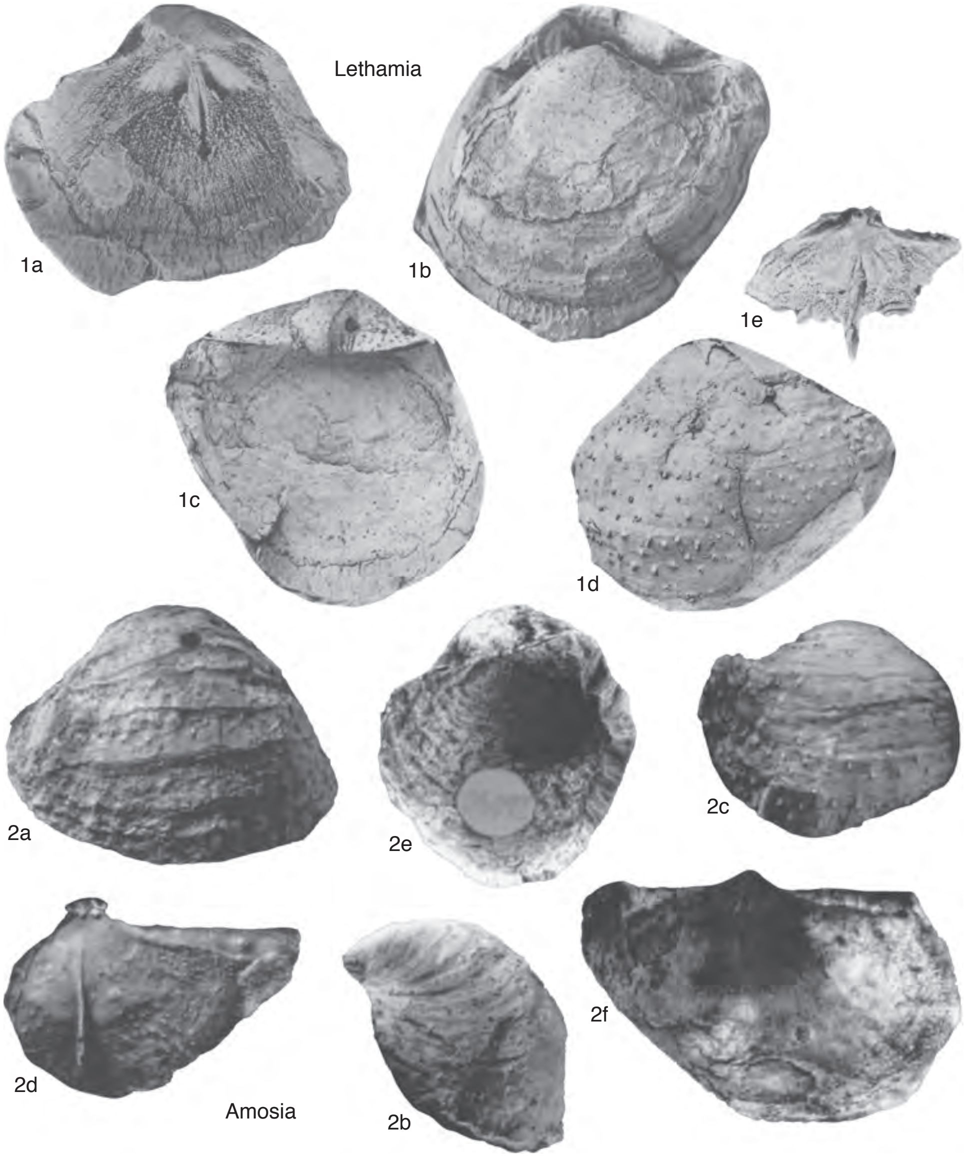


Fig. 1753. Productellidae (p. 2640–2641).

and *Stictozoster,* in the Lethamiini.] *Lower Permian (upper Sakmarian):* Western Australia.——Fig. 1754,*2a–g.* **W. senticosa* (Hosking), Callytharra Formation, Carnarvon Basin; *a–c,* lectotype, ventral, dorsal, and posterior views, GSWAFI/4970a1, ×1.8; *d,* crushed shell with ventral valve umbo missing and showing the dorsal cardinal process and medium septum, ×2 (Archbold, 1984); *e–g,* partially crushed shell, dorsal, ventral, and anterior views, ×1.5 (Archbold, 1999).

Subfamily MARGINIFERINAE Stehli, 1954

Tribe PAUCISPINIFERINI Muir-Wood & Cooper, 1960

Jinomarginifera Shen, Shi, & Archbold, 2003b, p. 231 [**J. lhazeensis*; OD]. Medium-sized marginiferine with deep corpus cavity, resembling *Rectimarginifera*, but with less coarse costae, weaker

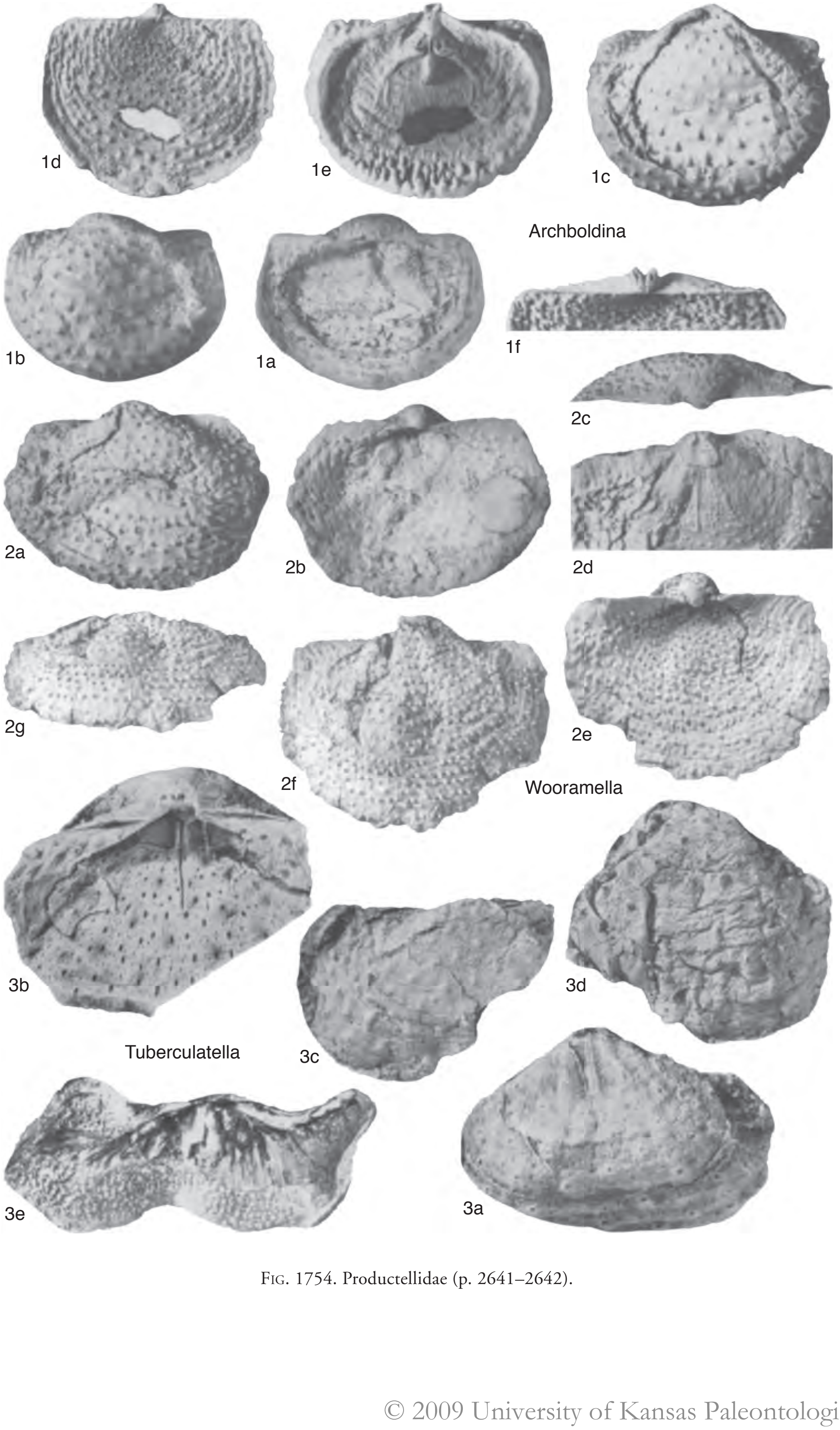


FIG. 1754. Productellidae (p. 2641–2642).

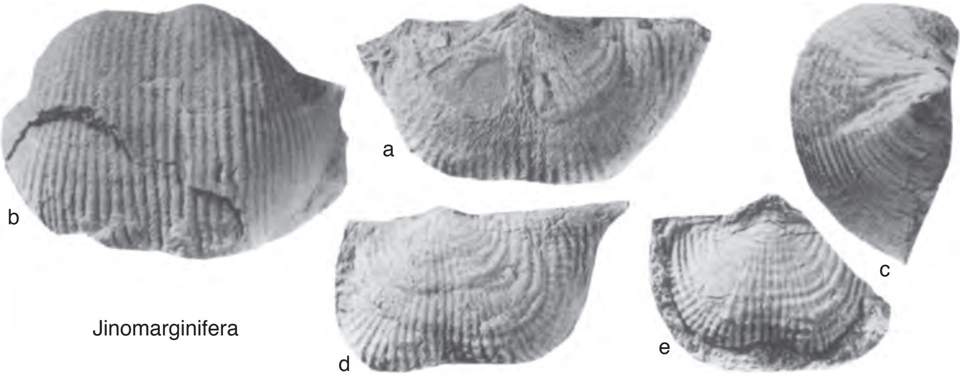


FIG. 1755. Productellidae (p. 2642–2644).

median reticulation, and thin ventral spines on flanks, disc, and ears, lacking six major halteroid spines and with no dorsal internal anterior subperipheral ridge. *upper Upper Permian (upper Capitanian):* southern and western China, including southern Tibet.——FIG. 1755*a–e.* **J. lhazeensis; a–c,* holotype, posteroventrally exfoliated shell, ventral, anteroventral, and lateral views, NMV P308105, ×1.5; *d,* ventral valve exterior, ventral view, ×1.5; *e,* external mold of dorsal valve with fragment of ventral umbo in place, ×1.5 (Shen, Shi, & Archbold, 2003b).

Subfamily PLICATIFERINAE Muir-Wood & Cooper, 1960
Tribe PLICATIFERINI Muir-Wood & Cooper, 1960

Labaella KOTLYAR, ZAKHAROV, & POLUBOTKO, 2004, p. 517 [**Productus* (*Productus*) *bajarunassi* LICHAREW, 1937, p. 47 [111]; OD]. Medium to large Plicatiferini with widely extended ears; fine ribbing and delicate rugation forming reticulation over corpus with ribbing continued on trails; spine row at low angle from hinge line and grouped on anteroventral ear surface, rare elsewhere; dorsal interior resembles that of *Plicatifera.* [This genus somewhat resembles *Lazarevia* CARTER & POLETAEV, 1998, from the early Upper Carboniferous but differs in being smaller, with more prominent ears, and it has a clear median ventral sulcation. The authors placed the new genus in a new family, but this is unnecessary.] *Upper Permian (upper Changhsingian):* Russia (northwestern Caucasus mountains).——FIG. 1756*a–f.* **L. bajarunassi* (LICHAREW), Nikitin Formation, Nikitin Ravine; *a–c,* anterior view, ventral view, and with corpus removed showing exfoliated dorsal valve exterior (the broken anterior edge shows as a crack line on *a*), ×1; *d,* internal mold of dorsal valve, ×1; *e–f,* shell viewed ventrally showing spine bases close to hinge line and on ears and anteriorly with anterior part of corpus and ventral trail missing, ×1 (Kotlyar, Zakharev, & Polubotko, 2004).

Lazarevia CARTER & POLETAEV, 1998, p. 125 [**L. stepanowensis;* OD]. Resembling *Plicatifera* in shape, but with more numerous, weaker, and less regular rugae on corpus; ribbing covering corpus and trails; spines fine, scattered sparsely over ventral valve, plus some near hinge line and row separating ears from flanks; corpus cavity shallow; ventral interior with variably developed submarginal rim. *lower Upper Carboniferous (upper Bashkirian–lower Moscovian):* Canadian Archipelago (Ellesmere Island).——FIG. 1757*a–f.* **L. stepanowensis,* Hare Fiord Formation; *a–e,* holotype, ventral, dorsal, anterior, posterior, and lateral views, GSC 115552, ×1; *f,* natural mold of ventral valve interior, ×1 (Carter & Poletaev, 1998).

Family PRODUCTIDAE Gray, 1840
Subfamily PRODUCTINAE Gray, 1840
Tribe RETARIINI Muir-Wood & Cooper, 1960

Pitakpaivania WATERHOUSE, 2004, p. 69 [**Kutorginella aprica* GRANT, 1976, p. 143; OD]. Retariin lacking strong ventral sulcus, with weak reticulation on corpus only, but ribs becoming strong on trail; spines fine at hinge and on both corpus surfaces, strong halteroid on flanks and trail medianly, plus a pair anterodorsally; ventral interior with weak lateral ridges continuing across ears; dorsal interior with trifid cardinal process and lateral ridges continuing as weak submarginal ridges laterally. [Differentiation of this genus is not entirely clear, and in several characters it resembles *Retaria* MUIR-WOOD & COOPER, 1960 more closely than *Kutorginella* IVANOVA, 1951. The former typically comes from late Lower to early Upper Permian, while the latter is of late Upper Carboniferous age. GRANT (1976) commented on the similarity of his species to *Retaria* from Texas and further study may indicate that *Retaria* and *Kutorginella* are valid genera, with

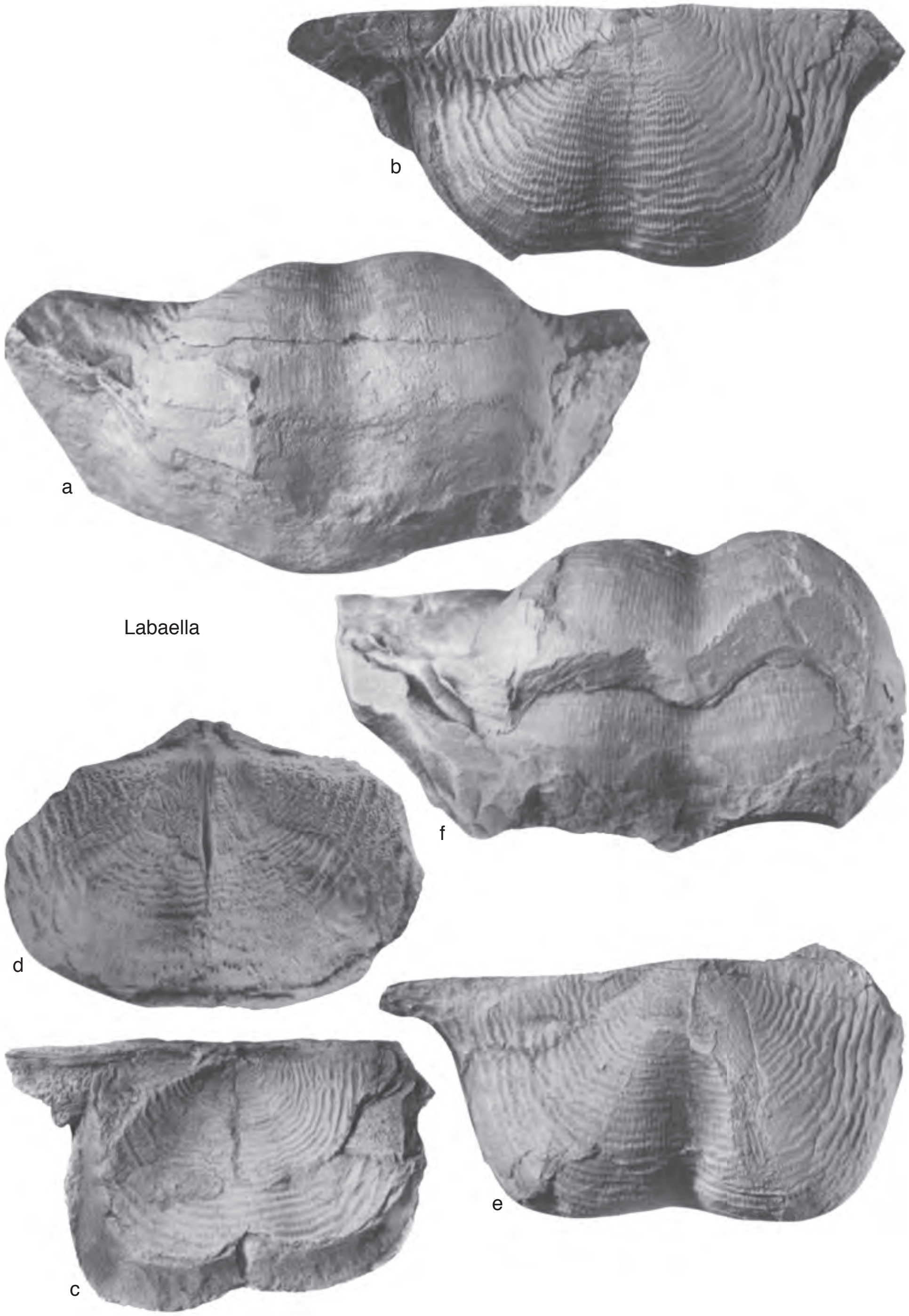


FIG. 1756. Productellidae (p. 2644).

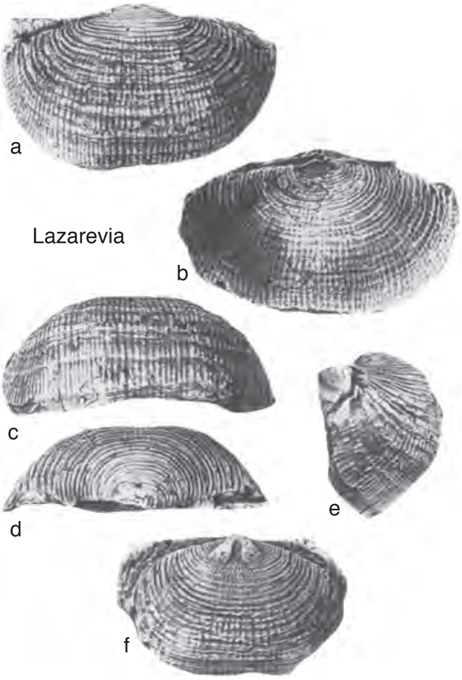


Fig. 1757. Productellidae (p. 2644).

Pitakpaivania being closely related to *Retaria*, or its junior synonym.] *Upper Permian (Guadalupian):* southern Thailand (Rat Buri Formation).——Fig. 1758,*1a–g*. **P. aprica* (Grant), Ko Muk, Thailand peninsula; *a–d,* holotype, dorsal view of incomplete shell, lateral view, ventral view, and anterior view, USNM 212481, ×1.5; *e,* oblique dorsolateral view of shell showing a moderately deep corpus cavity, ×1; *f,* lateral view showing thick spines on flank and trail, ×1.5; *g,* incomplete ventral valve interior, ×1.5 (Grant, 1976).

Subfamily DICTYOCLOSTINAE Stehli, 1954

Tribe DICTYOCLOSTINI Stehli, 1954

[*nom. transl.* Brunton, herein, *ex* Dictyoclostinae Stehli, 1954, p. 316] [type genus, *Dictyoclostus* Muir-Wood, 1930, p. 103]

Medium to large; trails long, simple; ribbing complete with reticulation posteriorly; ventral spines commonly stout halteroid, dorsal spines absent; dorsal adductor scars positioned close to hinge line; marginal structures absent or weak. [The genera in this tribe are as in the Dictyoclostinae (Brunton & others, 2000, p. 488–496) other than for those in the Liraplectini, e.g., *Liraplecta* and *Tarimoplecta.*] *Lower Carboniferous (Viséan)–Upper Permian (Tatarian).*

Callytharrella Archbold, 1985, p. 19 [**Dictyoclostus callytharrensis* Prendergast, 1943, p. 13; OD]. [Since the publication of Brunton and others (2000, p. 489), Archbold has described (in Hogeboom & Archbold, 1999) new topotypic material in which he demonstrated the presence of a curved row of spines on each flank, just anteroventral to the large reflexed ears, in addition to the large spines that grew near the posterior margins of the weakly rugose ears (Brunton & others, 2000, fig. 333,*2a*).] *Lower Permian (Sakmarian):* Western Australia, Himalayas.——Fig. 1758,*3*. **C. callytharrensis* (Prendergast), Callytharra Formation, Carnarvon Basin, Western Australia; detail of ear and flank showing positions of spines on and close to ear, ×2 (Hogeboom & Archbold, 1999).

Tribe LIRAPLECTINI Chen & Shi, 2000

[Liraplectini Chen & Shi, 2000, p. 329] [type genus, *Liraplecta* Jin & Sun, 1981, p. 137]

Dictyoclostinae with ribbed plus finely capillate dorsal valves. [The new tribe includes *Liraplecta* Jin & Sun, 1981, and *Tarimoplecta* Chen & Shi, 2000; see below]. *Lower Permian (Sakmarian–Kungurian).*

Tarimoplecta Chen & Shi, 2000, p. 336 [**T. tarimensis*; OD]. Medium-sized Liraplectini with planoconvex deep corpus cavity and long trail; ventral ribbing increasingly coarse anteriorly; rugae not extending onto venter; spines strong on ears and trail, sparse and finer on ventral corpus; cardinal process weakly trifid, supported by strong but short lateral ridges, and narrow median septum reaching anterior border of corpus. *Lower Permian (Artinskian):* northwestern China (Tarim Basin).——Fig. 1758,*2a–d*. **T. tarimensis*, Keziliqiman Formation, southern Xinjiang; *a,* holotype, ventral valve in anteroventral view, NMV P303392, ×1; *b,* ventral valve viewed ventrolaterally with dorsal valve internal mold viewed anteriorly to left, ×1; *c,* dorsal valve interior, ×1; *d,* incomplete ventral valve internal mold, ×1 (Chen & Shi, 2000).

Subfamily YAKOVLEVIINAE Waterhouse, 1975

[Yakovleviinae Waterhouse, 1975, p. 11]

Productidae commonly with external reticulation on discs; spines widely scattered on ventral valve only; corpus cavity moderate

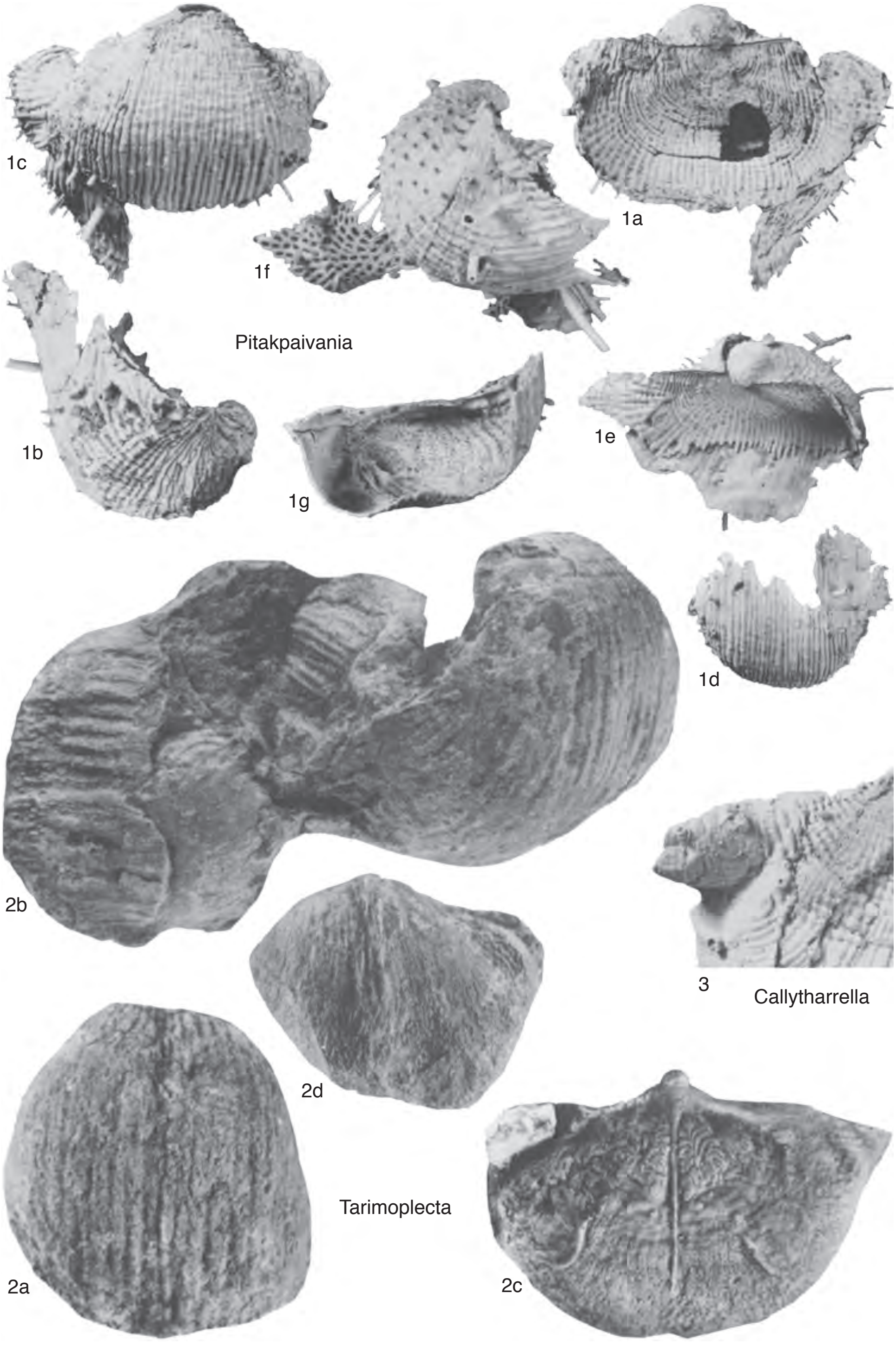


FIG. 1758. Productidae (p. 2644–2646).

to deep; lacking shagreen centrally in ventral umbo; commonly lacking dorsal internal marginal structures. [Following the joint revision of the Productellinae with BRUNTON in 1997 (in BRUNTON & LAZAREV, 1997), LAZAREV has continued his revision of parts of the Productidae. Within this family LAZAREV (2000a and 2000b) has elevated the tribe Yakovleviini of BRUNTON and others (2000, p. 464) to a subfamily, removing it from the Productellidae where its position was somewhat insecure. The new subfamily contains four tribes, Yakovleviini WATERHOUSE, 1975, Latispiniferini LAZAREV, 2000b, Reticulatiini LAZAREV, 2000a, and Rigrantiini LAZAREV, 2000b. In addition, within these tribes, LAZAREV (2000b) described four new genera, which are presented below. LAZAREV based his revision largely on the distribution of a texture on the internal surfaces of the valves, especially in the ventral umbonal region; a texture of fine tubercles and pits that he called shagreen and interpreted as representing areas of mantle cavity.

The descriptions below are based on those by LAZAREV (2000a, 2000b, and 2000c) in translated versions of the Paleontological Journal, volume 34, numbers 4–6. Pages in square brackets indicate translations.] *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).*

Tribe YAKOVLEVIINI Waterhouse, 1975

Ventral disc flattened and reticulate ornament commonly weak; spines few, thick, and placed symmetrically; corpus cavity may be only moderately deep. *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).*

Tribe LATISPINIFERINI Lazarev, 2000

[Latispiniferini LAZAREV, 2000b, p. 26 [496]] [type genus, *Latispinifera* LAZAREV, 2000b, p. 27 [496]]

Discs strongly reticulate; spines in row around base of flanks, not arising from a ridge, becoming strong anterolaterally and of similar size to those anteriorly on ventral trail; dorsal disc with dimples representing positions of ventral spine bases. *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).*

In addition to the type genus, LAZAREV assigned *Sterochia* GRANT, 1976, and *Callytharrell*a ARCHBOLD, 1985 (Dictyoclostinae of BRUNTON & others, 2000, p. 496 and p. 489 respectively) and *Costiferin*a MUIR-WOOD & COOPER, 1960 (Paucispiniferini of the Productellidae of BRUNTON & others, 2000, p. 444) to the Latispiniferini. *Callytharrella* is here retained in the Dictyoclostinae.

Latispinifera LAZAREV, 2000b, p. 27 [496] [**L. chaykensis*; OD; =*Reticulatia huecoensis* SARYTCHEVA, 1977, p. 94, *non* KING, 1931, p. 68]. Valves thin shelled; in profile, border between corpus and trails indistinct; ribs on trail not coarse, six or more in 10 mm width; spines with thickest rows on flanks. *Carboniferous (Viséan–Moscovian):* Russia (Cape Chayka), northwestern Spain.——FIG. 1759*a–e*. **L. chaykensis*; *a–b,* holotype, ventral valve, anterior and posterior views, Moscovian, Cape Chayka, PIN 2833/26, ×1; *c,* ventral valve exterior, ventral view, ×1; *d,* dorsal exterior, ×1; *e,* internal mold of dorsal valve, ×1 (Sarycheva, 1977).

Tribe RETICULATIINI Lazarev, 2000

[Reticulatiini LAZAREV, 2000a, p. 40 [400]] [type genus, *Reticulatia* MUIR-WOOD & COOPER, 1960, p. 284]

Yakovleviinae of medium to large size and deep corpus cavity; both discs reticulate; ventral spines thick, halteroid, and numerous. [LAZAREV erected this tribe based on *Reticulatia* MUIR-WOOD & COOPER, 1960, which was assigned to the Dictyoclostinae of BRUNTON & others (2000, p. 496). LAZAREV's (2000a) action restricts *Reticulatia* to the Lower Permian of North America, while other Carboniferous species are assigned by LAZAREV (2000b) to his new genus *Admoskovia*.] *Upper Carboniferous (Bashkirian)–Lower Permian (Artinskian).*

Admoskovia LAZAREV, 2000b, p. 28 [499] [**Dictyoclostus inflatiformis* IVANOV, 1935, p. 64 [110]; OD]. Ears strongly defined, forming widest part of shell; reticulation on discs relatively weak; ribbing entire and may form weak plications on trail; spines on ears strongly developed, smaller spines in rows on flanks and scattered on venter; cardinal process

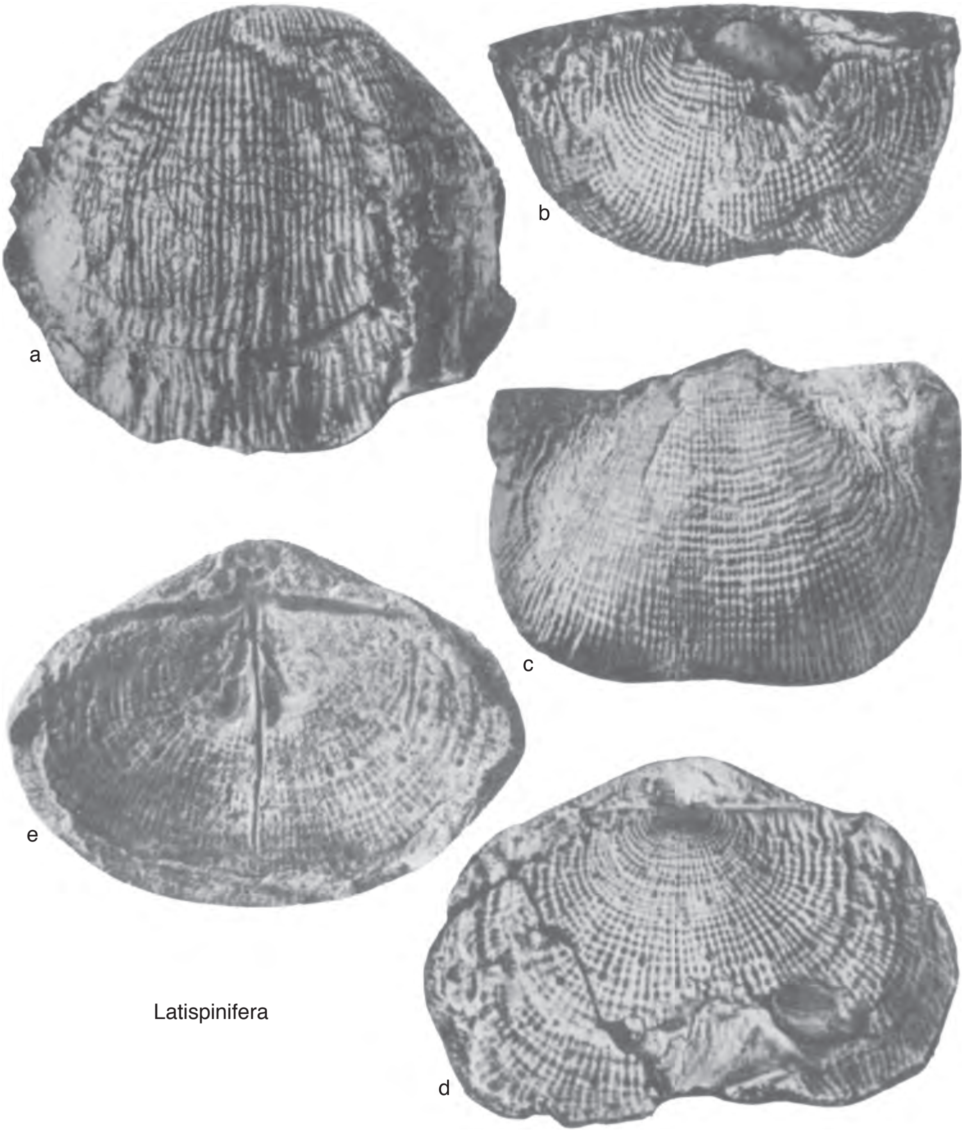


FIG. 1759. Productidae (p. 2648).

low, supported by strong lateral ridges extending to border of corpus posteriorly; median septum short. *Upper Carboniferous (Bashkirian–Kasimovian):* Eurasia and mid-Asia.——FIG. 1760*a–c*. **A. inflatiformis* (IVANOV), Kasimovian, River Medvedka of the Moscow river, Neverov Formation; *a,* ventral valve exterior showing ear spines, ×1; *b,* somewhat crushed ventral valve exterior showing hinge, ear, and flank spines, ×1; *c,* shell viewed ventrally with part of ventral valve missing to show dorsal interior, ×1 (Lazarev, 2000c).——FIG. 1760*d. A. ivanovorum* LAZAREV; incomplete dorsal valve interior, ×1 (Lazarev, 2000c).——FIG. 1760*e. A.* sp.; incomplete ventral valve interior, ×3 (new).

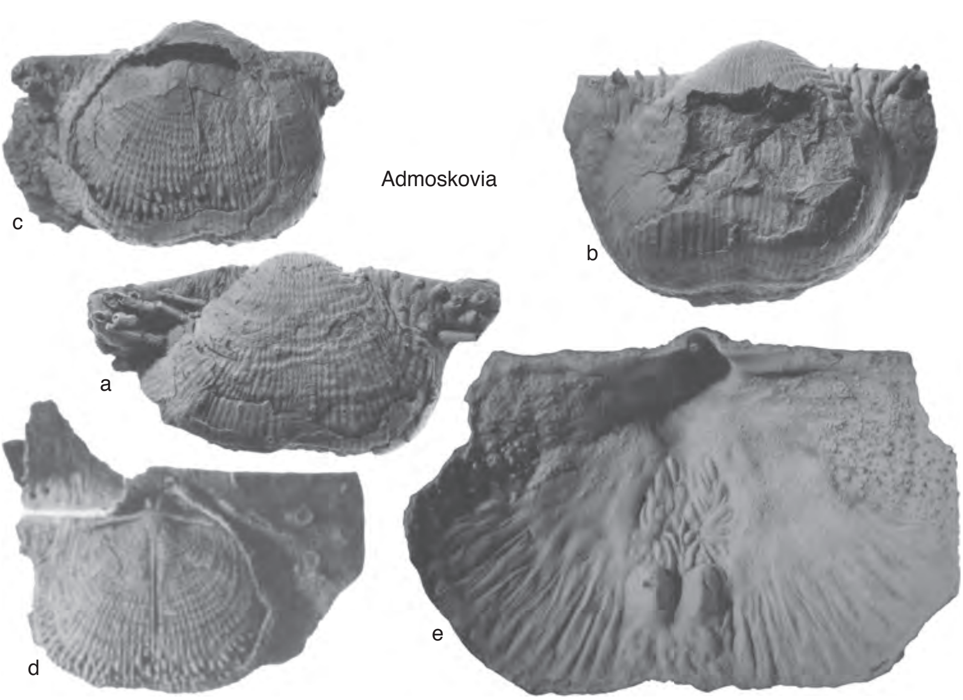


FIG. 1760. Productidae (p. 2648–2649).

Tribe RIGRANTIINI Lazarev, 2000

[Rigrantiini LAZAREV, 2000b, p. 28 [497]] [type genus, *Rigrantia* LAZAREV, 2000b, p. 28 [499]]

Reticulate ornament variably developed; spines at base of flanks thick and arising from prominent ridge; dorsal disc commonly dimpled; dorsal interior with narrow ridges separating ears. *?uppermost Lower Carboniferous, Upper Carboniferous (Serpukhovian)–Lower Permian (Artinskian).*

Rigrantia LAZAREV, 2000b, p. 28 [499] [**Antiquatonia planumbona* STEHLI, 1954, p. 316; OD]. Spines at hinge well developed and of similar size to those on flanks; reticulate ornament fine, regular, and covering entire disc; ears distinct and internally may be separated from corpus by ear baffles. *Lower Permian (Artinskian):* USA (Texas).——FIG. 1761,*1a–f. *R. planumbona* (STEHLI), Bone Spring Formation, western Texas; *a–c,* lectotype, posterior, anteroventral, and lateral views, AMNH 27299/2:1, ×1; *d,* shell viewed dorsally, ×1; *e–f,* dorsal valve viewed internally and externally, ×1 (Cooper & Grant, 1975).

Bicarteria LAZAREV, 2000b, p. 28 [497] [**Productus semireticulatus* var. *hermosanus* GIRTY, 1903, p. 359; OD]. Spines at hinge thinner than larger (youngest) spines in rows at flanks; reticulate ornament commonly irregular and may not reach margin of venter; cardinal ridge weak, may diverge from hinge slightly. *Upper Carboniferous (Serpukhovian–Kasimovian):* North America, ?southeastern Urals.——FIG. 1761,*2a–f. *B. hermosana* (GIRTY), Bashkirian, Colorado, USA; *a–c,* ventral valve, ventral, anterior, and posterior views, ×1; *d–e,* ventral valve, ventral and lateral views, ×1; *f,* dorsal valve, lateral view, ×1 (Girty, 1903).

Superfamily ECHINOCONCHOIDEA Stehli, 1954

Family ECHINOCONCHIDAE Stehli, 1954

Subfamily JURESANIINAE Muir-Wood & Cooper, 1960

Tribe WAAGENOCONCHINI Muir-Wood & Cooper, 1960

Contraspina WATERHOUSE, 2002b, p. 46 [**Productus purdoni* DAVIDSON, 1862, p. 31; OD]. Resembling *Waagenoconcha (Gruntoconcha)* but having more elongate outline and spine bases closely

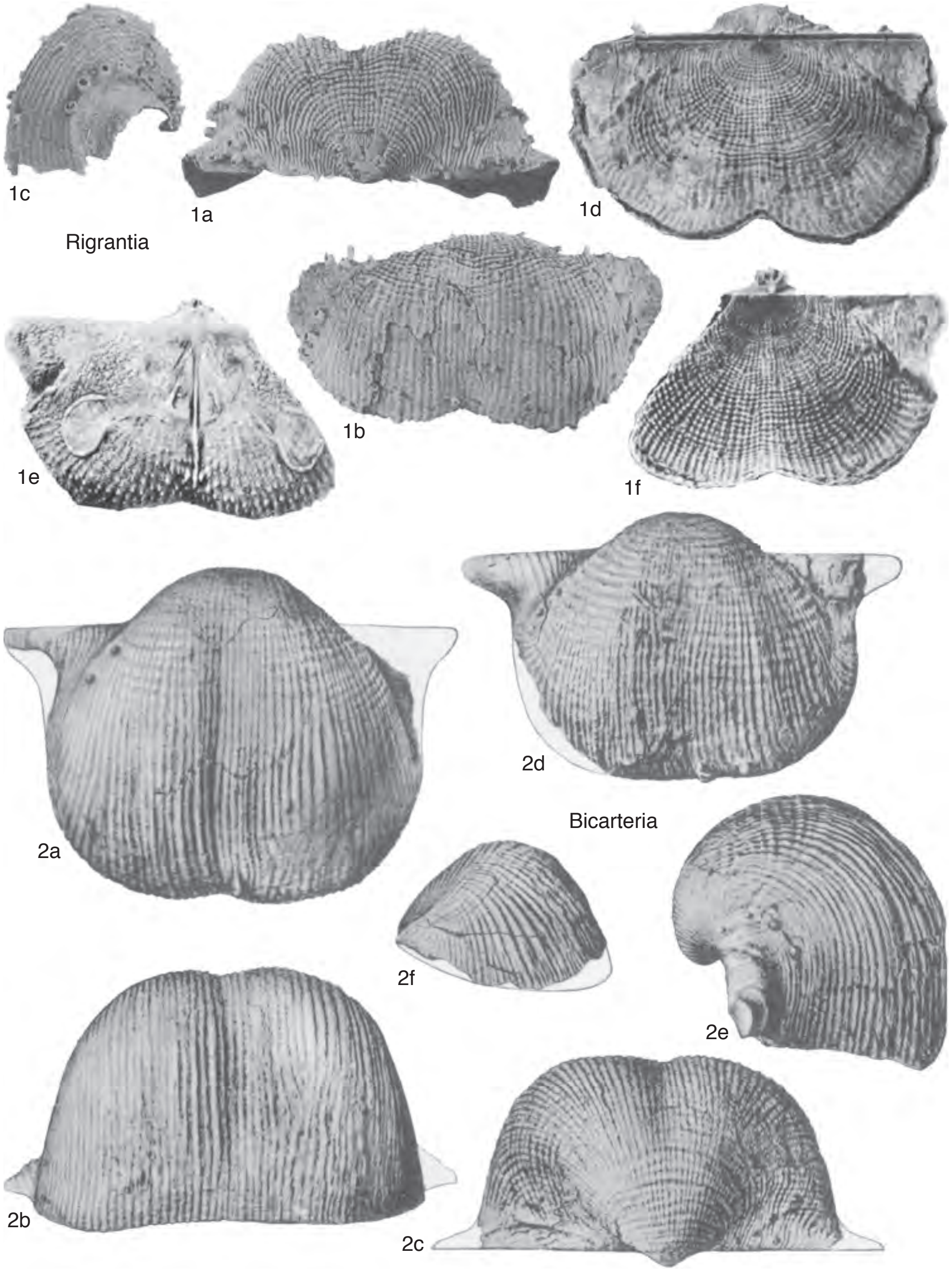


FIG. 1761. Productidae (p. 2650).

spaced and fine posteriorly, becoming somewhat coarser anteriorly; well-developed median fold and sulcus from umbo to anterior margins; interiors unknown. *Upper Permian (Capitanian):* Pakistan (Salt Range).——FIG. 1762,*2a–f.* **C. purdoni* (DAVIDSON); *a–c,* holotype, ventral, lateral, and dorsal views, BMNH B82367, ×1; *d–f,* juvenile specimen, ventral, lateral, and dorsal views, ×1 (new).

Fostericoncha WATERHOUSE, 2002b, p. 48 [**Waagenoconcha? gigantea* WATERHOUSE, 1983, p. 125; OD]. Large to gigantic transverse waagenoconchin with wide ears; ventral umbo low; sulcus and dorsal fold originating near umbos; spines fine on both valves, but thicker and lacking fine elongate bases toward ventral hinge and ears, dorsal spines from rounded pustules. [Preservation and quantity of available specimens are poor, so aspects of morphology remain unknown. In 1983 WATERHOUSE appeared to think his new species, ?*W. gigantea*, belonged to his new genus *Wimanoconcha*, placed in BRUNTON and others (2000, p. 516) within *Waagenoconcha*.] *Upper Permian (upper Capitanian):* Nepal.——FIG. 1762,*1a–c.* **F. gigantea* (WATERHOUSE), Pija Member, Manang; *a–b,* holotype, part of ventral valve external mold and its rubber replica, UQF73619, ×1; *c,* part of ventral valve internal mold, and at the margin, external mold, ×1 (Waterhouse, 1983).

Superfamily LINOPRODUCTOIDEA

Stehli, 1954

Family LINOPRODUCTIDAE

Stehli, 1954

Subfamily LINOPRODUCTINAE

Stehli, 1954

Aurilinoproductus SHEN, SHI, & ARCHBOLD, 2003a, p. 79 [**A. alatus*; OD]. Median to large Linoproductinae with large triangular alae extending up to 20 mm beyond corpus width; spines not observed at hinge line, but on ears and common on venter with elongate spine bases. *Upper Permian (Changhsingian)*: China (southern Tibet).——FIG. 1763,*2a–e.* **A. alatus*, Qubuerga Formation; *a–d,* holotype, viewed anteriorly, posteriorly, laterally, and ventrally, NMV P305973, ×1; *e,* incomplete ventral valve exterior, ×1 (Shen, Shi, & Archbold, 2003a).

Cimmeriella ARCHBOLD & HOGEBOOM, 2000, p. 101 [**Productus foordi* ETHERIDGE, 1903, p. 19; OD]. Small to medium Linoproductinae with globose corpus shape and long trails; ventral profile strongly convex with weakly concave, geniculate dorsal valve; ribbing well defined, entire; rugae weak, on flanks only; spines confined to single rows close to hinge line, enlarging laterally; low cardinal process supported by short, wide medium septum and paired ridges partially enclosing adductor scars posteriorly. *Lower Permian (upper Sakmarian):* Western Australia, Timor, Malaysia, Yunnan, Tibet, and Karakorum.——FIG. 1763,*1a–f.* **C. foordi* (ETHERIDGE), Callytharra Formation, Carnarvon Basin; *a–b,* ventral valve in ventral and posterior views, ×1; *c,* almost complete ventral valve in lateral view, ×1; *d,* ventral valve interior, ×1; *e–f,* incomplete dorsal valve viewed externally and internally, ×1.2 (Archbold, 1983).

Subfamily ANIDANTHINAE

Waterhouse, 1968

Anidanthus HILL, 1950, p. 9 [**Linoproductus springsurensis* BOOKER, 1932, p. 67; OD] [=*Anidanthus* WHITEHOUSE, 1928, p. 282, *nom. nud.*; ?*Pseudomarginifera* STEPANOV, 1934, p. 56 (type, *Productus ussuricus* FREDERICKS, 1924b, p. 8); *Protoanidanthus* WATERHOUSE, 1986, p. 60 (type, *P. compactus*; OD)]. [*Protoanidanthus* should have been included as a junior synonym of *Anidanthus* HILL, 1950 in the revised *Treatise* (BRUNTON & others, 2000, p. 531). WATERHOUSE (1986) diagnosed his genus as having smaller ears than *Anidanthus*. We believe this to be an intrageneric character. *Protoanidanthus* was described from the Lower Permian (Artinskian) of Australia (Queensland). The description of the genus *Anidanthus* in BRUNTON and others (2000, p. 531) remains unchanged, as do the entries for stratigraphy, distribution, and illustrations. This is only a note of emendation correcting an omission from the 2000 description of the genus *Anidanthus*.]

Subfamily PAUCISPINAURIINAE

Waterhouse, 1986

[Paucispinauriinae WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 2]

Linoproductids with varied fine or strong spines commonly on both valves; those ventrally may have elongate spine bases. Lacking marginal structures or trails.

The subfamily name Grandaurispininae LAZAREV, 1986, used in the *Treatise* (BRUNTON & others, 2000, p. 533) has proved a junior synonym for Paucispinauriinae WATERHOUSE in WATERHOUSE & BRIGGS, 1986. Some genera within the Grandaurispininae (BRUNTON & others, 2000) such as *Lyonia* have shallow corpus cavities and belong within the Auriculispininae below. *?Lower Permian, Upper Permian.*

Pinegeria WATERHOUSE, 2001, p. 49 [**Terrakea? pinegensis* GRIGORIEVA in SARYTCHEVA, 1977, p. 144; OD]. Subcircular outline with relatively narrow hinge line and virtually no ears; semioval lateral profile with geniculate dorsal valve; prominent costellation and weak rugae dorsally; ventral

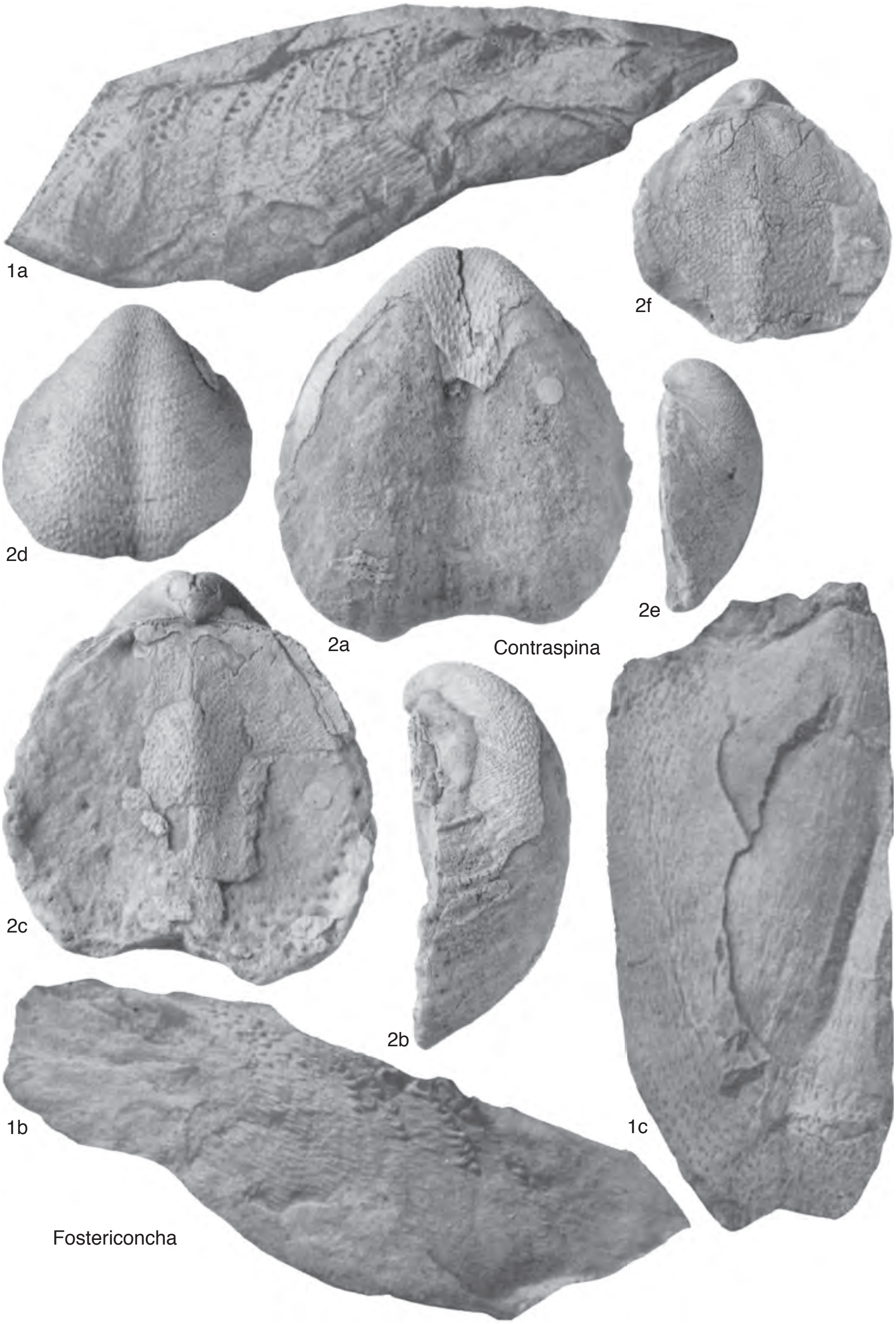


FIG. 1762. Echinoconchidae (p. 2650–2652).

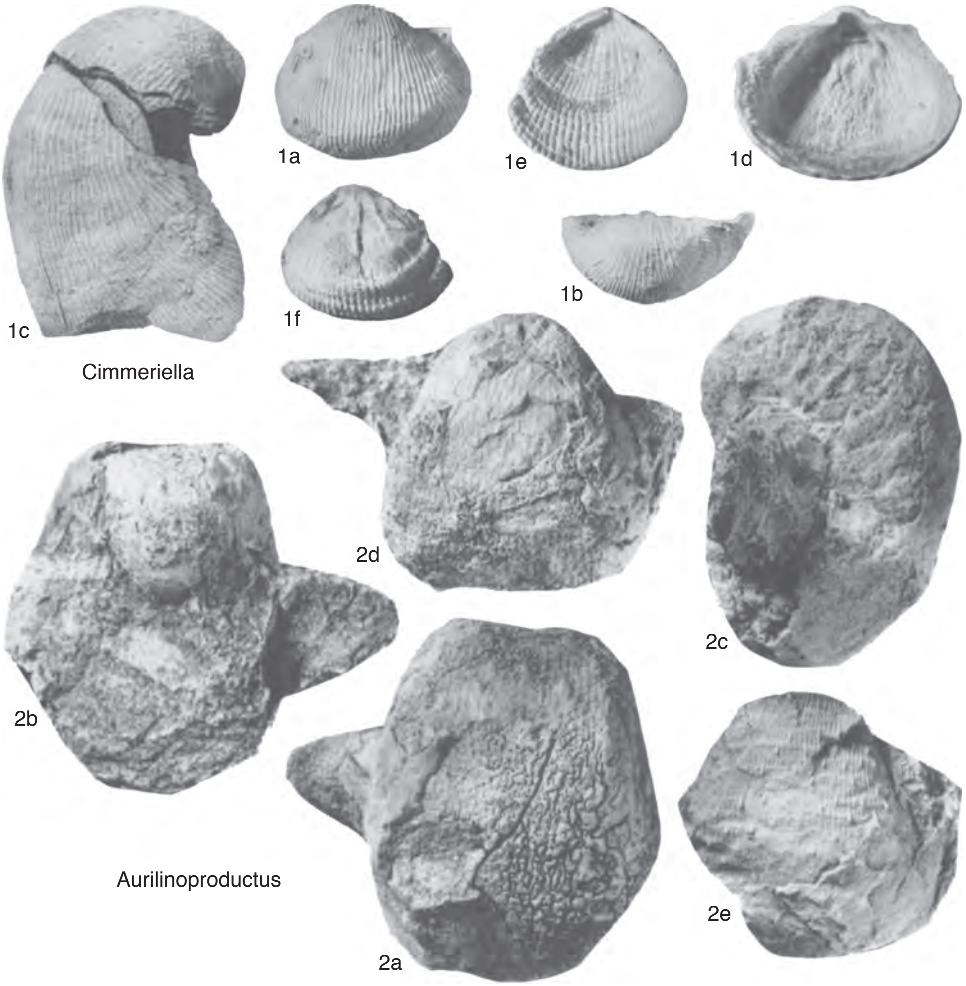


Fig. 1763. Linoproductidae (p. 2652).

spines fine posteriorly, larger posterolaterally, laterally, and on trail, fine and erect on dorsal valve; cardinal process squat, trifid to quadrifid. [This species is readily distinguishable from the others described by Grigorieva in 1977 as being a possible Russian *Terrakea* species.] *Upper Permian (Kazanian):* northern and western Russia.——Fig. 1764,*2a–e*. **P. pinegensis* (Grigorieva); *a–c,* holotype, shell viewed ventrally, dorsally, and laterally, PIN 1120/771, ×1; *d,* detail of cardinal process viewed posteriorly, ×6; *e,* dorsal valve interior, ×1 (Sarytcheva, 1977).

Spargospinosa Waterhouse, 2001, p. 41 [**Terrakea belokhini* Ganelin in Sarytcheva, 1977, p. 141; OD]. Resembles *Terrakea* but said to be less strongly spinose at ventral hinge line; corpus quite deep and trail present; ventral spines erect, sparse at hinge and ears, scattered over corpus and trail, some may have swollen spine bases; ventral interior resembling *Terrakea*. [It appears that species attributed to *Terrakea* in the past and now divided into separate genera, whether from Australia or Russia, display continuous variation in their morphology (Briggs, 1998). A meaningful differentiation of nominal genera in this group is questionable, other than for the new genus *Pinegeria*.] *Upper Permian (Wordian–Capitanian):* Russian arctic (Siberia).——Fig. 1764,*1a–f*. **S. belokhini* (Ganelin); *a–c,* holotype, viewed anteroventrally with part of ventral trail missing, laterally and posteriorly showing part of ventral valve internal mold, PIN 28834/349, ×1; *d,* another posterior view of partially exposed ventral internal mold and part of spinose hinge line on right, ×1; *e–f,* ventral valve exterior viewed ventrally and anteriorly, showing larger spine bases on trail, ×1 (Sarytcheva, 1977).

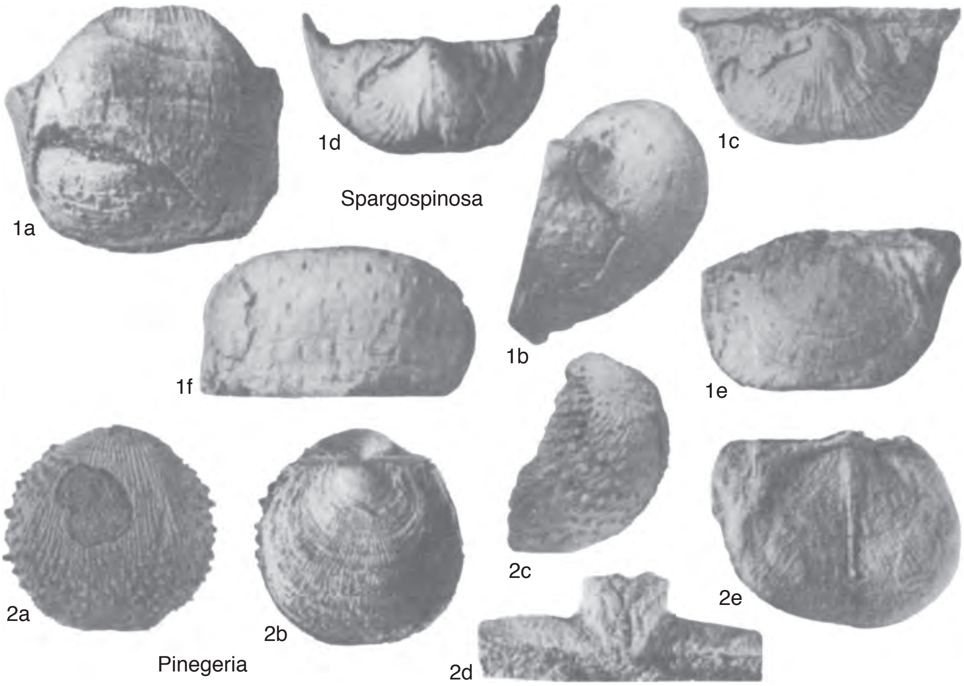


Fig. 1764. Linoproductidae (p. 2652–2654).

Family MONTICULIFERIDAE Muir-Wood & Cooper, 1960

Subfamily AURICULISPININAE Waterhouse, 1986

Small- to medium-sized monticuliferids with transverse to elongate outlines, spines on ventral valve, but lacking or rare on dorsal valves; spine bases ventrally commonly elongate. *Lower Carboniferous (Tournaisian)–Upper Permian (Changhsingian).*

Tribe AURICULISPININI Waterhouse, 1986

[*nom. transl.* Waterhouse, 2001, p. 30, *ex* Auriculispininae Waterhouse in Waterhouse & Briggs, 1986, p. 57]

Auriculispinines with transverse outline viewed ventrally, but those with long trails became elongate in outline; spines may form clusters posteriorly and on ears. [Acceptance of the Lyoniini necessitates the use of the Auriculispinini for other genera in the subfamily. This is not the place to research the full redistribution of genera in this and other subfamilies, as does Waterhouse (2002b) with his five new tribes in this subfamily.] *Lower Carboniferous (upper Tournaisian)–Upper Permian (Capitanian).*

Bocharella Ganelin & Lazarev, 2000, p. 39 [41] [**B. zyrjankensis*; OD]. Small to medium sized with weakly concavoconvex corpus and geniculated trails of similar length; spines absent on ears, but short single rows at anterior margins of ears, elongate spine bases rare and mainly on trail; lateral ridges in both valves; cardinal process wide with paired supporting ridges from anterior ends of which a medium septum extends to three-quarters disc length. *lower Upper Permian (Kazanian):* northeastern Asia.——Fig. 1765,*2a–d*. **B. zyrjankensis*, Ufimian, lower Kazanian, Verkhnii Koargychan River; *a,* holotype, ventral valve viewed ventrally, PIN 2834/1562, ×1; *b,* ventral valve viewed anteroventrally, ×1; *c,* ventral valve viewed laterally, ×1; *d,* dorsal valve external mold showing lines of dimples representing spine positions on ventral valve, ×1 (Ganelin & Lazarev, 2000).

Costatamulus Waterhouse in Waterhouse & Briggs, 1986, p. 58 [**Auriculispina tumidus* Waterhouse, Briggs, & Parfrey, 1983, p. 133; OD] [=*Auritusinia* Waterhouse, 2002b, p. 52 (type, *Costatamulus tazawai* Shen & others, 2000, p. 743)]. [The only points of differentiation given by Waterhouse (2002b) for separating *C. tazawai* from *Costatamulus* are more strongly developed rugae and more strongly developed ears on the new genus. Comparisons of the original descriptions and illustrations by WATERHOUSE (1986) and SHEN and others (2000) show similar ears and only some difference in the development of rugae, which tends to be a variable character. The type species of *Costatamulus* is Lower Permian in age, and that of *Auritusinia* is upper Upper Permian. The type species, *C. tumidus*, was illustrated in the genus entry of the *Treatise* (BRUNTON & others, 2000, p. 538). Here a second species from younger strata is illustrated.] *Lower Permian (Artinskian)–Upper Permian (Changshingian):* Australia, Tibet, central Himalayas.——FIG. 1765,*1a–c. C. tazawai* SHEN & others, Lopingian, southern Tibet; *a,* holotype, ventral valve exterior, NMV P148917, ×1.5; *b,* ventral valve exterior with elongate spine bases, ×1.5; *c,* external mold of a dorsal valve showing one ear, ×1.5 (Shen & others, 2000).

Kolymaella GANELIN & LAZAREV, 2000, p. 40 [43] [**Cancrinella ogonerensis* ZAVODOWSKY, 1960, p. 65; OD]. Medium-sized, very weakly concavoconvex shells with geniculations and short trails; spines in single rows crossing each ear, with elongate spine bases on venter and tending to become arranged concentrically on trail; dorsal lateral ridges diverging from hinge line (40° to 45°); paired supporting ridges extending anteriorly from cardinal process base, no medium septum. *lower Upper Permian (lower Kazanian):* northeastern and Central Asia.——FIG. 1765,*4a–e.* **K. ogonerensis* (ZAVODOWSKY), Ufimian, Munugudzhak River; *a,* group of ventral valve exteriors, ×1; *b,* ventral valve exterior showing fine ribbing and swollen spine bases, ×1; *c,* dorsal valve interior, ×1; *d,* incomplete dorsal valve interior showing paired supporting ridges, ×1; *e,* dorsal valve external mold with cardinal process remaining, ×1 (Ganelin & Lazarev, 2000).

Striapustula GANELIN & LAZAREV, 1999, p. 33 [246] [**Productus koninckianus* KEYSERLING, 1846, p. 203; OD]. Small, thin-shelled, concavoconvex specimens with long trails; ribbing fine on both valves, spines only ventrally, at hinge line and ears, scattered with swollen elongate bases on corpus and trail; rugae only posterolaterally; cardinal process bilobed, sessile, with shallow cardinal pit between paired weak ridges, cardinal ridges diverging slightly from hinge line toward ears, do not reach lateral margin, median septum reaches 0.8 disc length. *Lower Permian (Artinskian–Kungurian):* northeastern Asia (Verkhoyansk region, Pechora Basin), Spitsbergen.——FIG. 1765,*3a–d.* **S. koninckianus* (KEYSERLING); *a,* ventral valve exterior, ×1; *b,* ventral valve anterior view, ×1; *c,* lateral view of shell, ×1; *d,* partially exfoliated dorsal valve interior, ×2 (Ganelin & Lazarev, 1999).——FIG. 1765,*3e. S. pectiniformis* GANELIN & LAZAREV, Vokuta river; cast of natural external mold of ventral valve, ×2 (Ganelin & Lazarev, 1999).——FIG. 1765,*3f. S. spitsbergiana* (GOBBETT), Spitsbergen; ventral valve viewed laterally, ×1 (Ganelin & Lazarev, 1999).

Tribe LYONIINI Waterhouse, 2001

[Lyoniini WATERHOUSE, 2001, p. 32] [type genus, *Lyonia* ARCHBOLD, 1983, p. 244]

Auriculispinines with wide hinges and one or two rows of ventral hinge spines; ribbing weakly developed and body spines with elongate bases; cardinal process sessile with low myophores. [This tribe contains a recognizable group of genera including *Lyonia* and *Bandoproductus*, now known to have shallow corpus cavities, and they should be removed from the Lindproductidae (BRUNTON & others, 2000, p. 529 and p. 533) and included in this tribe in the Monticuliferidae. Other genera assigned here are *Nambdoania, Nambucculinus,* and probably *Nisalaria* (described below). WATERHOUSE (2001) is probably correct in also assigning *Cancrinelloides* to this tribe.] *Upper Carboniferous (upper Gzhelian)–Upper Permian (Changhsingian).*

Nambuccalinus WATERHOUSE, 2001, p. 33 [**Lyonia bourkei* BRIGGS, 1998, p. 147; OD]. Medium sized, somewhat transverse outline and with shallow corpus cavity; similar to *Lyonia;* spines on both valves, ventrally scattered, subprostrate from short spine bases plus two or three rows of larger spines along hinge margins, dorsally finer spines cover all but ears; rugae weak; dorsal cardinal ridges weak and median septum narrow, short. [WATERHOUSE (2001) placed this genus in his new tribe Lyoniini for its wide costellate shells with a shallow corpus and one or two rows of erect ventral hinge spines. The distinction, however, between the new genus and *Lyonia* can be made by the single row of hinge spines, perhaps fewer dorsal spines, and presence of dorsal dimples in the latter. The evidence from BRIGGS (1998) suggests that the dorsal interior of *N. bourkei* is closely similar to that of *Lyonia*, so the validity of *Nambuccalinus* remains questionable.] *Upper Carboniferous (?upper Gzhelian), Lower Permian (Asselian):* eastern Australia.——FIG. 1766,*1a–d.* **N. bourkei* (BRIGGS), Giro Group, Asselian, Sydney-Bowen Basin; *a,* holotype, dorsal external mold of complete shell, UQF75314, ×2; *b,* rubber replica of posterior region of ventral valve exterior, ×2; *c,* external mold of dorsal valve showing on valve exterior that dimples represented ventral hinge spine positions, ×2; *d,* rubber replica of dorsal valve interior, ×2 (Briggs, 1998).

Nambdoania WATERHOUSE, 2002b, p. 52 [**Cancrinella papilionata* WATERHOUSE, 1978, p. 109; OD]. Resembles *Lyonia*, but lacks dorsal spines, and single rows of ventral hinge spines are less prominent; cardinal process less flattened than in *Lyonia* and supported by a short median septum and

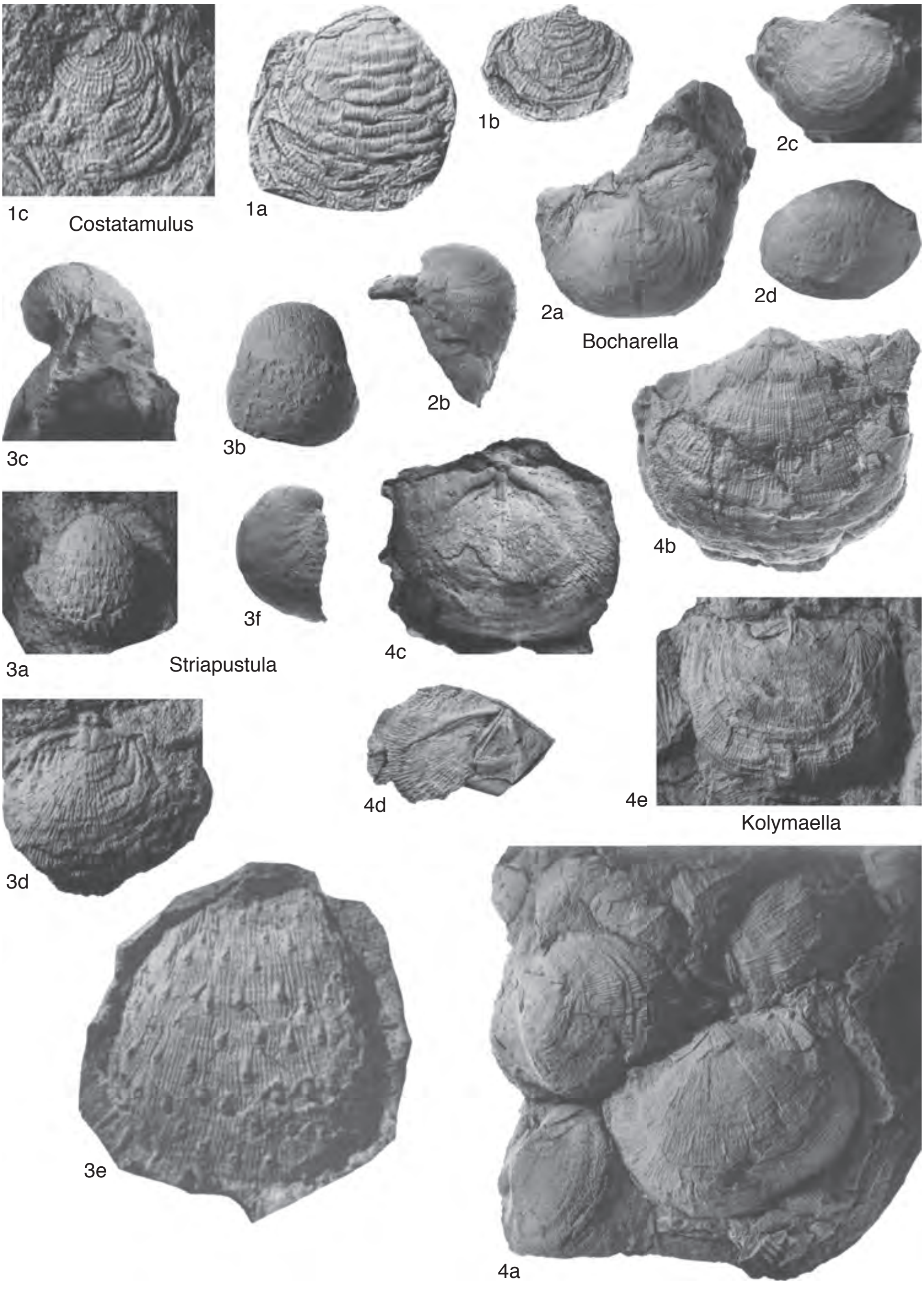


FIG. 1765. Monticuliferidae (p. 2655–2656).

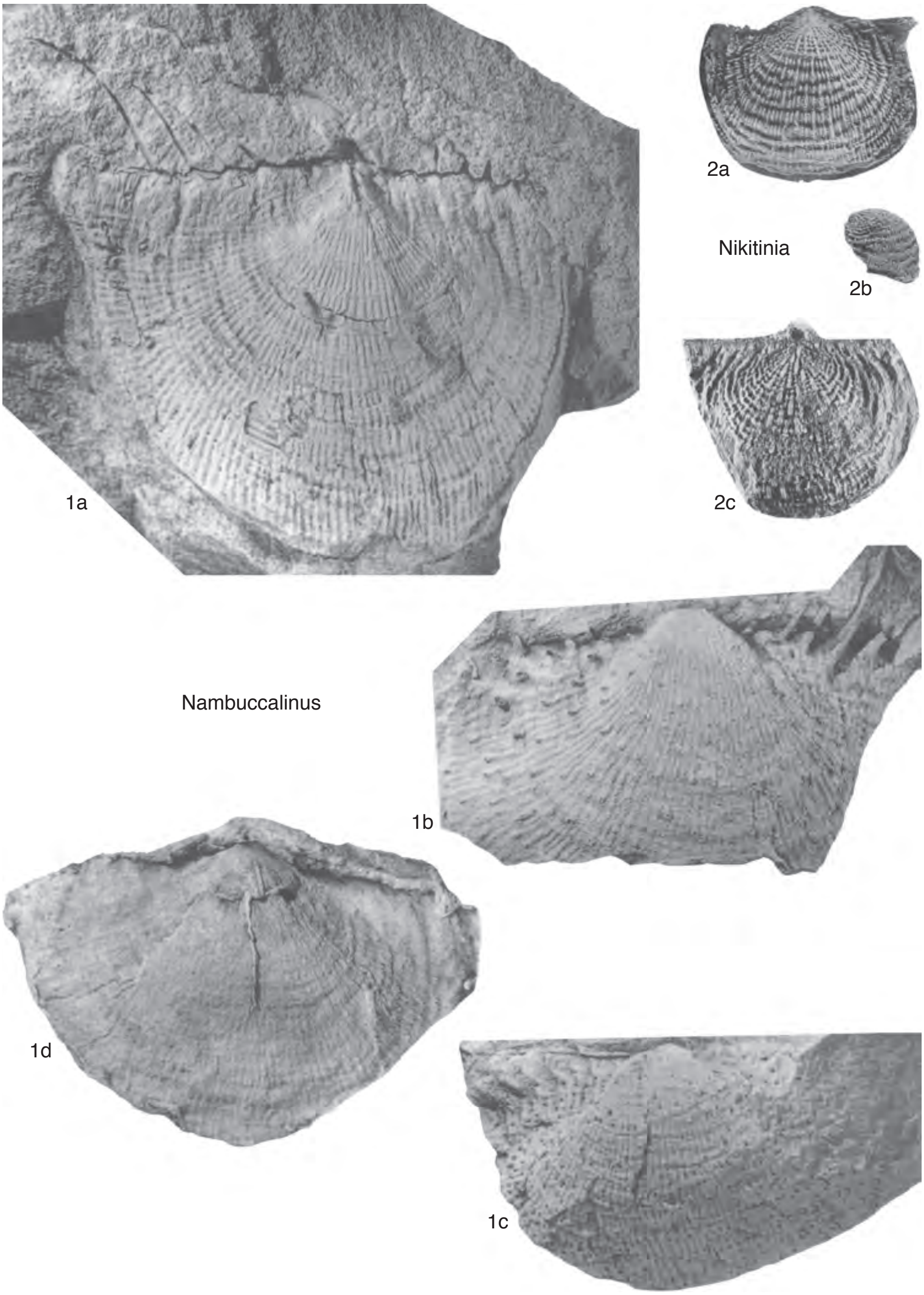


FIG. 1766. Monticuliferidae (p. 2656–2659).

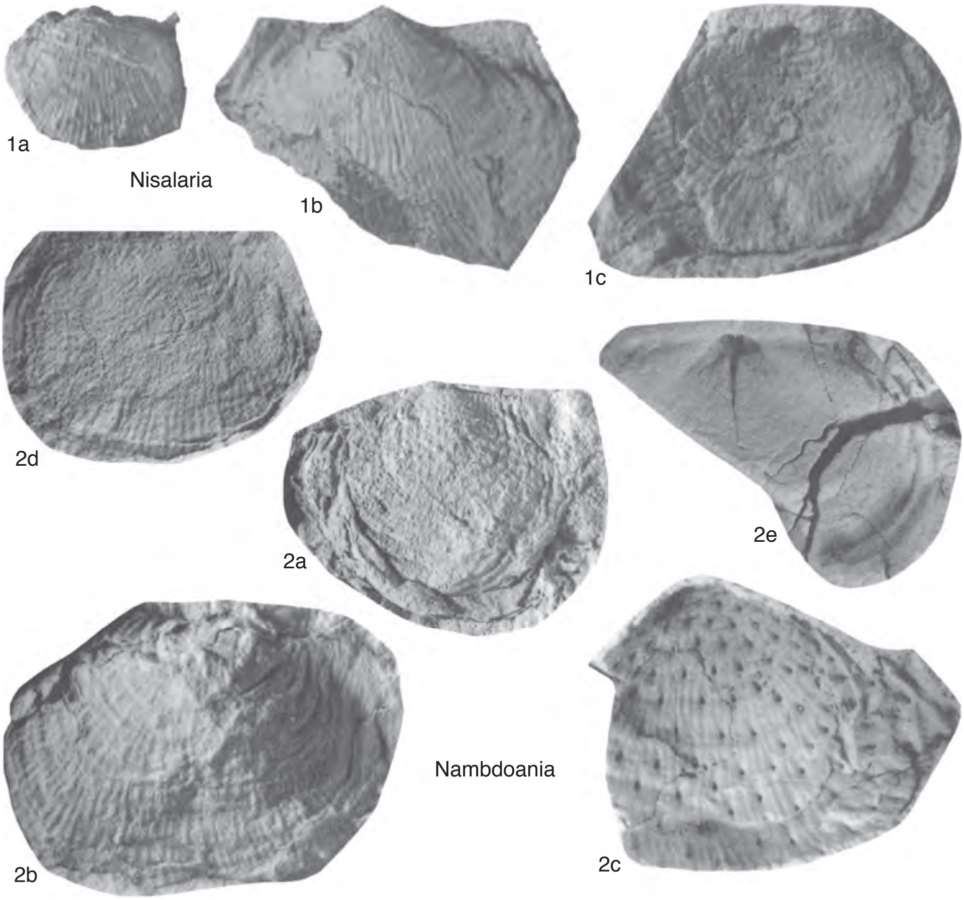


Fig. 1767. Monticuliferidae (p. 2656–2660).

weak cardinal ridges. *Upper Permian (Changhsingian):* Nepal.——Fig. 1767,*2a–e.* **N. papilionata* (Waterhouse), Nambdo Member, Dolpo, western Nepal; *a,* holotype, dorsal valve external mold, UQF 69029, ×1; *b,* ventral valve exterior, ×2; *c,* ventral valve external mold, ×2; *d,* dorsal valve external mold, ×1.5; *e,* dorsal valve interior, ×1.5 (Waterhouse, 1978).

Nikitinia Kotlyar, Zakharev, & Polubotko, 2004, p. 521 [**N. licharewi;* OD; =*Productus* (*Productus*) *cancriniformis* Licharew, 1937, p. 38 [105], *non* Chernyschew, 1889]. Small with subcircular outline, small ears; concavoconvex profile and shallow corpus cavity; rugae dominate fine ribbing, especially ventrally over corpus; elongate spine bases accentuate ribs from which they arose, spine row close to ventral hinge extending to ears. [The authors only describe spines as being near the hinge and on the ears, but their illustrations and those of Licharew (1937) appear to show well-developed spine bases on the ventral corpus, similar to those of several linoproductoids. Their assignment to the Linoproductidae is not in accord with the current *Treatise* classification (Brunton & others, 2000, p. 526) largely because of the shallow corpus cavity.] *Upper Permian (Changhsingian):* Russia (northwestern Caucasus mountains).——Fig. 1766,*2a–c.* **N. licharewi*, Lower Urushten Formation, Urushten River; *a,* holotype, ventral view, CRMGE 268/2139, ×2; *b,* lateral view, ×1; *c,* partial internal mold of dorsal valve showing impressions from ventral valve spine row near hinge, ×2 (Kotlyar, Zakharev, & Polubotko, 2004).

Nisalaria Waterhouse, 2002b, p. 51 [**Cancrinelloides (Bandoproductus) inflata* Waterhouse, 1983, p. 130; OD] [=*Cancrinella* sp. Waterhouse, 1978, p. 76]. Weakly concavoconvex with low ventral umbo; spines in single row at hinge, on umbo, and scattered on venter, arising anteriorly from elongate spine ridges more prominent than costellation; no dorsal spines. [The three descriptions of the type species by Waterhouse (1978, 1983, and 2002b) differ slightly in terms of profile and umbonal inflation, so the above is based, to some extent, on the cited figures of 1978. Waterhouse (2002b) placed his genus in the Auriculispinini, but a lack of spine clustering at the hinge or ears seems more appropriate to the Lyoniini. The reference to *Cancrinella* sp. WATERHOUSE, 1978, was to his use of the name (no species mentioned) in 1978 for some specimens from the same locality as the type of *Nisalaria* and which would seem to be conspecific, although not named in 1978. It is not considered to belong to *Cancrinella* as now defined.] *Upper Permian (Changhsingian):* Nepal.——FIG. 1767,*1a–c.* **C. inflata* (WATERHOUSE), Nisal member, Dolpo, western Nepal; *a,* holotype, ventral valve exterior, UQF 68909, ×1; *b,* ventral valve exterior, ×2; *c,* incomplete dorsal valve exterior plus part of ventral trail external mold, ×2 (Waterhouse, 1978).

Subfamily COMPRESSOPRODUCTINAE Jin & Hu, 1978

Regrantia WATERHOUSE, 2001, p. 28 [**Striatifera linoproductiformis* COOPER & GRANT, 1975, p. 1210; OD]. Moderately sized compressoproductines with variably narrow hinge resulting from attachment to hard substrates; lateral profile modest at ventral umbo, relatively flat corpus with weakly geniculate trail, dorsal valve concave and shallow corpus cavity; rugae irregular; posterolateral rhizoid spines with few scattered spines on ventral corpus; cardinal process weakly bilobed, from just posterior of hinge line, extending anteroventrally so as to lie ventrally on long narrow median septum. [The complete reclassification of the Linoproductoidea presented by WATERHOUSE (2001, p. 24) is based on keeping the superfamily "as a well-defined group, and separate from its ancestors," with the result that it differs from that adopted by BRUNTON and others (2000). WATERHOUSE placed his genus *Regrantia* in his tribe Compressoproductini, which was said to have a moderately high body corpus, and he described *Regrantia* as having a deep body corpus. However, inspection of the lavish original illustrations and full description (with measurements) of the type species by COOPER and GRANT (1975) shows it to have a shallow corpus depth, enabling it to fit well into the BRUNTON & others (2000) classification.] *Lower Permian (Asselian):* USA (Texas).——FIG. 1768,*1a–g.* **R. linoproductiformis* (COOPER & GRANT), Neal Ranch Formation, Glass Mountains; *a–c,* holotype, viewed laterally, ventrally, and dorsally, USNM 153972b, ×1; *d,* posteroventral view of attached specimen showing rhizoid spines, ×2; *e,* posterior end of shell in dorsal view, ×3; *f–g,* dorsal valve interior and in lateral view showing disposition of cardinal process, ×2 (Cooper & Grant, 1975).

Subfamily STRIATIFERINAE Muir-Wood & Cooper, 1960

[Striatiferinae MUIR-WOOD & COOPER, 1960, p. 328]

Shell large to medium; outline elongate or with tubiform trail, hinge narrow; spines commonly on ventral valve only.

Tribe STRIATIFERINI Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 930, *ex* Striatiferinae MUIR-WOOD & COOPER, 1960, p. 328]

Large, with very shallow corpus; trails simple; spines fine, rarely also on dorsal valve; cardinal process of single ridge continuous with median septum.

Striatiferella LEGRAND-BLAIN in LEGRAND-BLAIN, DELVOLVÉ, & HANSOTTE, 1996, p. 195 [**S. arizensis;* OD]. Medium-sized, weakly concavoconvex shells with hinge line up to one-third maximum width and resembling *Striatifera* other than in its fine dorsal spines at ears and trail. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* France (Pyrenees).——FIG. 1768,*2a–e.* **S. arizensis; a–c,* holotype, dorsal valve external mold, internal replica, MH5a1, ×1, and detail of external ornament at margin showing molds of spine bases, ×2; *d–e,* ventral valve external replica and internal mold, ×1 (Legrand-Blain, Delvolvé, & Hansotte, 1996).

Subfamily SCHRENKIELLINAE Lazarev, 1990

[Schrenkiellinae LAZAREV, 1990, p. 122]

LAZAREV (2004) argues for the elevation of this subfamily to full family status containing the Schrenkiellinae and his new subfamily the Coopericinae. Thus the Schrenkiellidae comes alongside the Linoproductidae and Monticuliferidae. An appraisal of this new classification is beyond the scope herein so the three new genera are here simply included within the Schrenkiellinae.

Coopericus LAZAREV, 2004, p. 161 [**Linoproductus angustus* KING, 1931, p. 67; OD]. Schrenkiellin spine pattern of single hinge row of strong clasping spines with few or no other spines, together with an elongate outline; corpus convex, but with umbo and trails weakly convex in lateral profile; rugae prominent on ears and close to hinge line; cardinal process extending slightly posteriorly into small ventral umbo. [LAZAREV (2004) placed this genus in his new subfamily, the Coopericinae, separated from other schrenkiellids by its shell shape and stratigraphy.] *Upper Carboniferous (Moscovian)–Lower Permian:* Bone Spring Formation, North America (Texas), Russia (Moscow Basin).——FIG. 1769,*1a–h.* **L. angustus* (KING), Skinner Ranch and Bone Spring Formations, Lower Permian, Glass Mountains, Texas; *a–c,* lectotype, ventral valve, ventral, lateral, and posterior views, YPM 11519a, ×1; *d–e,* ventral valve, lateral and posterior views, ×1; *f–g,* dorsal valve, external and internal views, ×1; *h,* posterior region of ventral valve with complete row of clasping spines viewed internally, ×1 (Cooper & Grant, 1975).

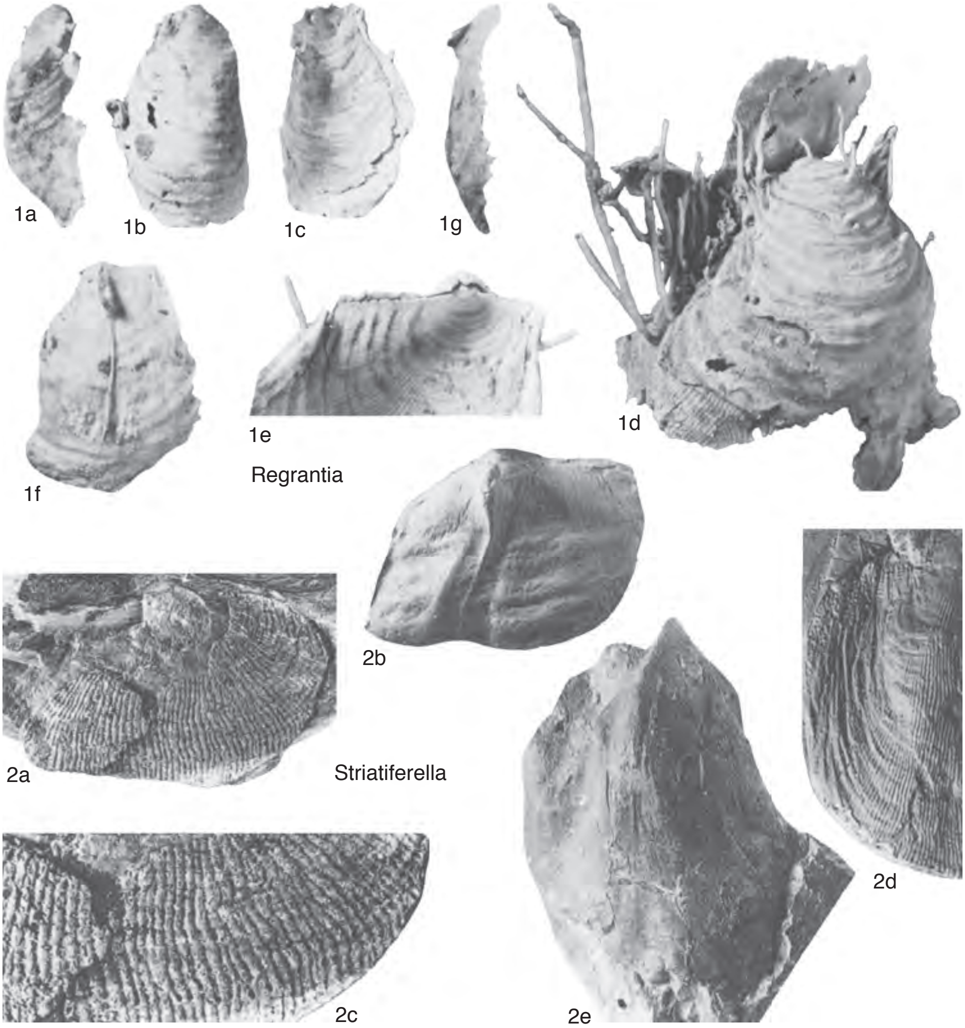


FIG. 1768. Monticuliferidae (p. 2660).

Elalia LAZAREV, 2004, p. 159 [**E. aljutovensis*; OD]. Size medium to large; ribs and interspaces approximately equal in width; rugae irregular, extending onto trail; spines in single row at hinge, relatively thick, with few or no other spines; cardinal process lobes medianly fused, and cardinal ridges weak. *Upper Carboniferous (Bashkirian–Gzhelian):* Russia, North America.——FIG. 1769,*2a–c*. **E. aljutovensis*, early Moscovian, Moscow Basin, Russia; *a,* holotype, ventral valve viewed ventrally, PIN 3452/3161, ×1; *b,* dorsal valve exterior, ×1; *c,* dorsal valve interior, ×1 (Lazarev, 2004).——FIG. 1769,*2d*. *Elalia* sp.; ventral valve exterior, ×1 (Lazarev, 2004).

Krekarpius LAZAREV, 2004, p. 159 [**Productus praelaevicostus* KRESTOVNIKOV & KARPYSHEV, 1948, p. 45; OD]. Medium sized with strongly convex ventral corpus profile, trail less convex; umbo projecting only weakly posterior to hinge line; rugae weakly developed, only at flanks; spines thin, most prominently in row close to hinge line, with thinner ones scattered on venter and flanks. *Upper Devonian (upper Famennian)–Lower Carboniferous:* Russia (southern Urals).——FIG. 1769,*3a–d*. **K. praelaevicostus* (KRESTOVNIKOV & KARPYSHEV); *a–b,* ventral valve, ventral and posterior views, upper Famennian, southern Ural Mountains, ×1; *c,* ventral valve lateral view, upper Famennian, southern Ural Mountains, ×1 (Krestovnikov & Karpyshev, 1948); *d,* incomplete dorsal valve interior, Zelenetskii horizon, uppermost Famennian, Mid-Pechora region, Russia, ×1 (Lazarev, 2004).

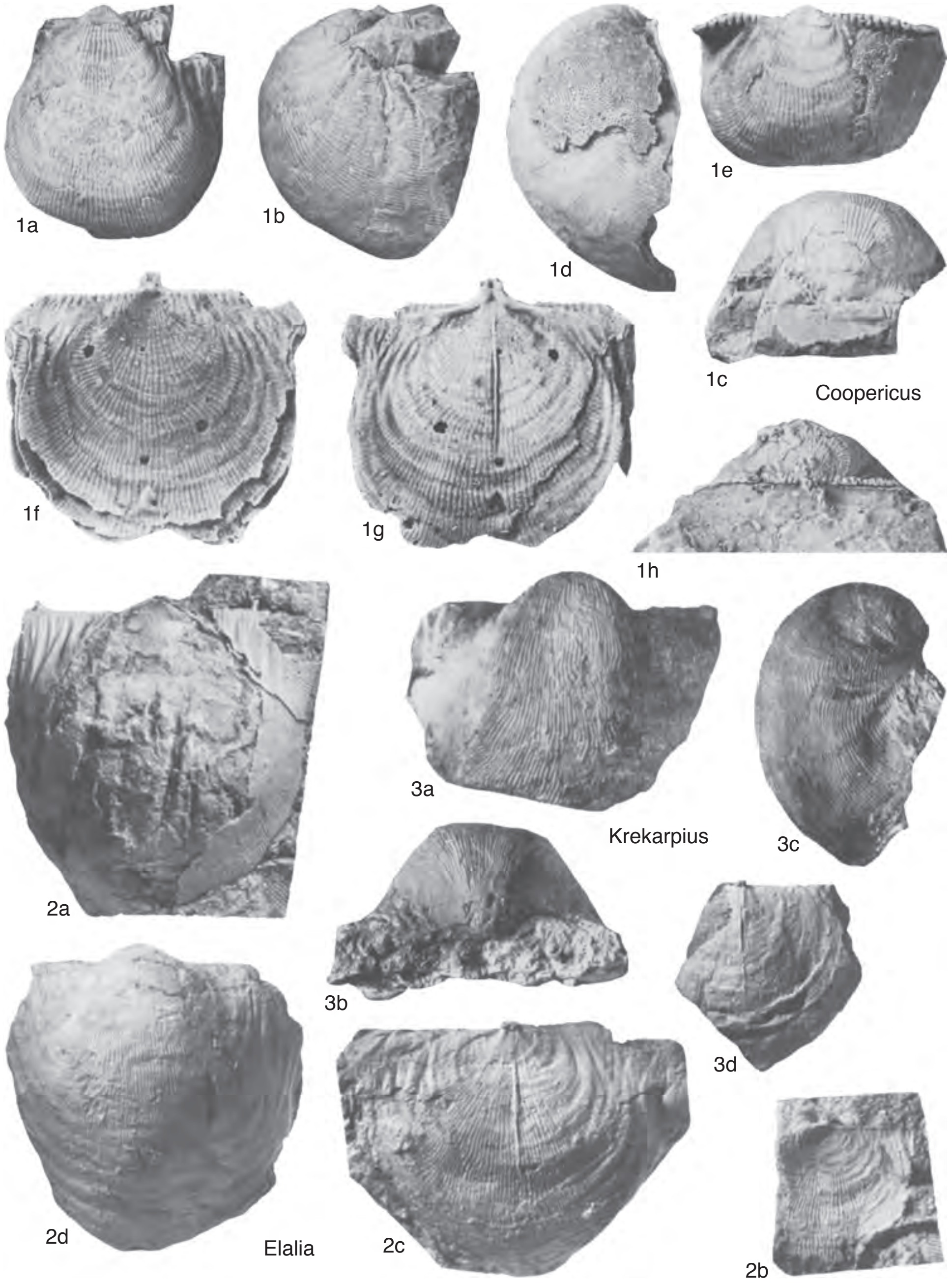


FIG. 1769. Monticuliferidae (p. 2660–2661).

Suborder STROPHALOSIIDINA Schuchert, 1913

Superfamily STROPHALOSIOIDEA Schuchert, 1913

Family STROPHALOSIIDAE Schuchert, 1913

Subfamily STROPHALOSIINAE Schuchert, 1913

Biplatyconcha WATERHOUSE, 1983, p. 125, *nom. nov. pro Platyconcha* WATERHOUSE, 1975, p. 8, *non* LONGSTAFF, 1933, p. 41 (type, *Platyconcha grandis* WATERHOUSE, 1975, p. 8, OD)] [=*Megalosia* WATERHOUSE, 1988, p. 44 (type, *M. chuluensis,* OD)]. Resembling *Marginalosia*, but large size and with no dorsal spines; narrow, but well-differentiated ventral interarea and strong teeth; dorsal valve thin shelled and elongate dimples representing ventral valve elongate spine bases; dorsal lateral ridges continue as subperipheral rim. [This genus was originally assigned to the Waagenoconchidae and in BRUNTON and others (2000, p. 516) to the Waagenoconchini. BRIGGS (1998) demonstrated that it is a strophalosiid, figuring the ventral interarea and teeth. It was BRIGGS who suggested that *Megalosia* was an objective synonym, and WATERHOUSE (2002b) acknowledges this. The same position was taken by SHEN, SHI, and ARCHBOLD (2003a), who figured examples of the type species from southern Tibet.] *Upper Permian (Changhsingian):* northwestern Nepal, southern Tibet.——FIG. 1770*a–e.* **B. grandi*s (WATERHOUSE), Qubuerga Formation, north of Mount Qomolangma, Everest, southern Tibet; *a,* ventral valve exterior, ×1; *b,* dorsal valve exterior, ×1; *c,* ventral valve internal mold, ×1; *d,* dorsal valve internal mold, ×1 (Shen, Shi, & Archbold, 2003a); *e,* rubber cast of part of ventral valve showing teeth and interarea, ×2 (Briggs, 1998).

Kufria WATERHOUSE, 2002b, p. 53 [**Strophalosia blanfordi* REED, 1944, p. 104; OD]. Medium sized, transversely subelliptical outline and low, convex ventral profile; dorsal disc flat with short trails; elongate ventral spine bases do not form strong ribs as in *Licharewiella* but are variable in length and strength, bearing fine spines anteriorly; interareas appear to be minute, but REED (1944) recorded an umbonal cicatrix. [Differentiation of this genus rests on its unusual external ornamentation of long, riblike spine bases, but REED's (1944) description and figures are of one specimen only. In 1944 REED attributed his previously described variety *Productus (Waagenoconcha) abichi* WAAGEN var. *consors* to his new species, but also, incorrectly, *Strophalosia gerardi* KING (1850, pl. 19,*6–7*), which illustrate the type specimen for the type species of *Strophalosia,* according to the ICZN (1962)]. *Upper Permian (upper Capitanian):* Pakistan (Salt Range).——FIG. 1771,*1a–b.* **K. blanfordi* (REED), Chhidru Formation; holotype, by monotypy, ventral and posterior views showing broken ventral umbo, GSI 16884, ×1.5 (Reed, 1944).——FIG. 1771,*1c–d. K.* (*Waagenoconcha) abichi* WAAGEN, var. *consors* (REED); internal cast of shell, ventral and posterior views with broken umbo exposing mold of cardinal process, ×1 (Reed, 1931).

Tupelosia ARCHBOLD & SIMANAUSKAS, 2001, p. 222 [**T. paganzoensis*; OD]. Circular to slightly elongate small shells with coarse, recumbent ventral spines, including a row close to hinge; cicatrix minute; teeth small; cardinal process squat, separated from short median septum by posteroventrally facing impressed adductor scars; shell substance thick. *Lower Permian (Asselian):* Argentina (Paganzo Basin).——FIG. 1771,*2a–e.* **T. paganzoensis*, Tupe Formation, upper Asselian; *a–b,* holotype, external and internal views of dorsal valve, DCG-MLP356f, ×3; *c–e,* ventral valve posterior, ventral, and internal views, ×3 (Archbold & Simanauskas, 2001).

Subfamily DASYALOSIINAE Brunton, 1966

Dasyalosia MUIR-WOOD & COOPER, 1960, p. 76 [**Spondylus goldfussi* VON MÜNSTER, 1839, p. 44; OD] [=*Bruntonaria* WATERHOUSE, 2001, p. 85 (type, *Dasyalosia panicula* BRUNTON, 1966, p. 191, OD)]. Description as in BRUNTON and others, 2000, p. 569, including distributions. [WATERHOUSE (2001) diagnosed his genus as being small with moderately to well-developed lamellae, and long, densely disposed ventral and dorsal spines of two series. This is acceptable. He described the ventral spines as mostly subprostrate, however, which is not true for either *Dasyalosia goldfussi* (see MUIR-WOOD & COOPER, 1960, p. 76) or for the two Irish species he assigned to his new genus (see BRUNTON, 1966, p. 191, pl. 2,*9*) in which there is a predominance of erect spines. In addition, WATERHOUSE (2001, p. 85) helped to differentiate his new genus from *Dasyalosia* by writing that the cardinal process of the latter is low when in fact the illustrations in MUIR-WOOD and COOPER (1960, pl. 6) are of a valve with a broken cardinal process (see BRUNTON, 1966, p. 190–191). Complete cardinal processes extend well posterior of the hinge line. As yet, insufficient clear distinction has been made to separate *D. panicula* BRUNTON from *Dasyalosia*, despite the stratigraphical interval, so *Bruntonaria* is placed into junior synonymy with *Dasyalosia*. The assertion that the Irish species of *Dasyalosia* are more similar to *Acanthalosia* than to *Dasyalosia* (WATERHOUSE, 2001, p. 85) is here rejected.] *upper Lower Carboniferous–lower Upper Permian:* Western Europe.——FIG. 1772,*3a–b.* **D. goldfussi* (VON MÜNSTER), lower Upper Permian, Gara, Germany; dorsal valve interior and posterior showing disposition of cardinal process, but with abraded terminal myophores, ×3 (new).

Guadalupelosia ARCHBOLD & SIMANAUSKAS, 2001, p. 223 [**Strophalosia inexpectans* COOPER & GRANT, 1975, p. 795; OD] [=*Muirwoodicia* WATERHOUSE, 2002b, p. 54, obj.]. Medium-sized, weakly

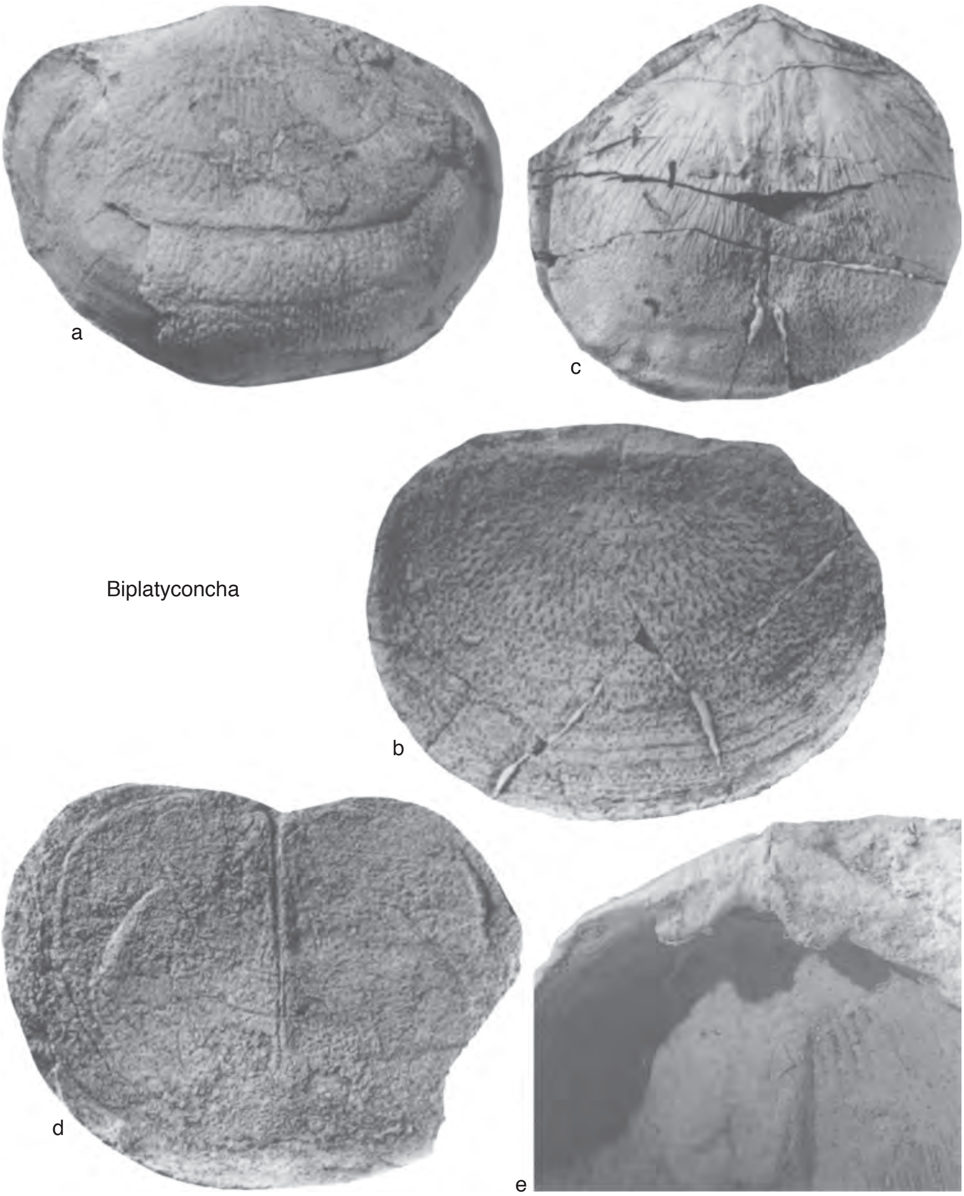


FIG. 1770. Strophalosiidae (p. 2663).

concavoconvex shells with short trails; hinge line about two-thirds maximum width, with low interareas and weakly convex narrow pseudodeltidium; cicatrix minute; delicate, fine recumbent spines on both valves; teeth small, but well formed; ventral adductor scars rounded with raised rims; inner socket ridges extending as cardinal then lateral ridges and continuing as subperipheral rim defining corpus area, which is fully bisected by narrow median septum. *Upper Permian (Wordian):* USA (western Texas).——FIG. 1772,*2a–i*. **G. inexpectans* (COOPER & GRANT), Cherry Canyon Formation; *a–e,* holotype, ventral valve anterior, posterior, lateral, ventral, and internal views, USNM 151229b, ×1; *f,* posterodorsal view showing interarea and teeth, ×3; *g,* dorsal valve exterior, ×1; *h–i,* interior and posteriorly, ×3 (Cooper & Grant, 1975).

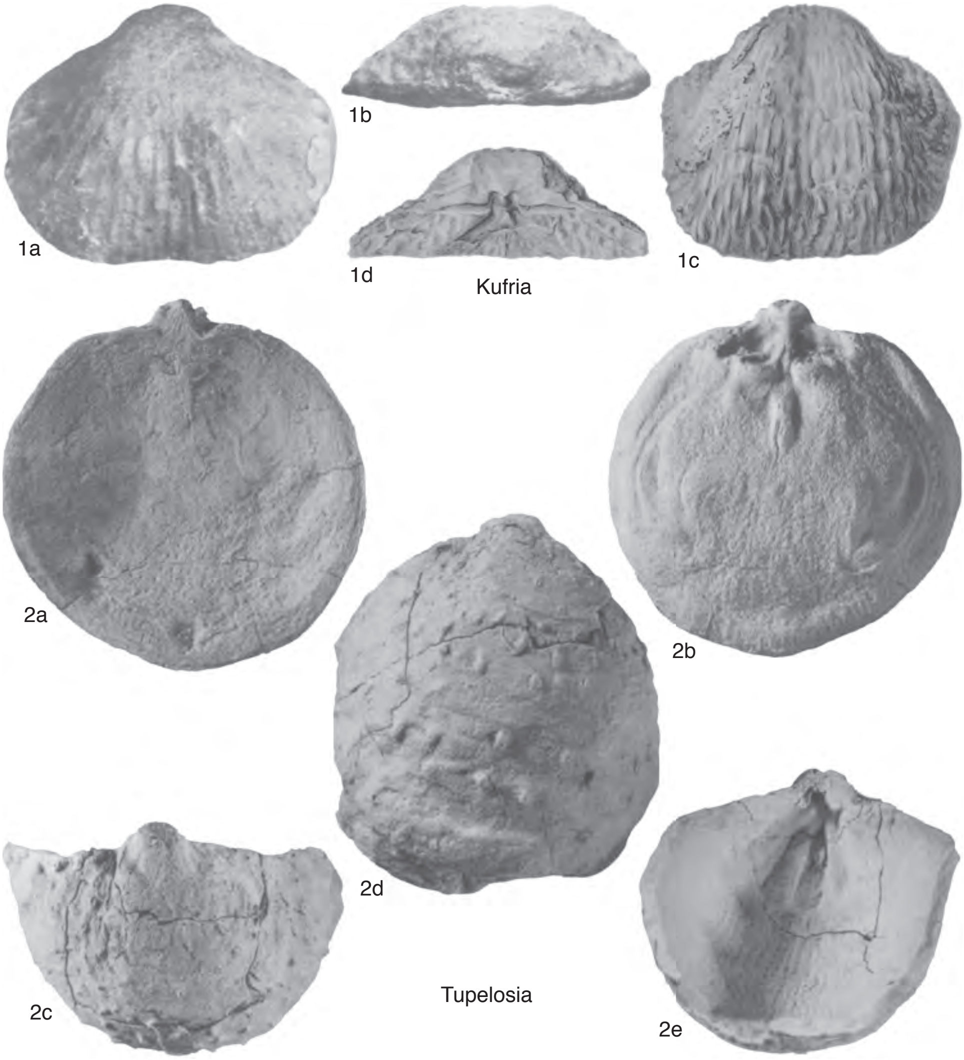


FIG. 1771. Strophalosiidae (p. 2663).

Subfamily ECHINALOSIINAE Waterhouse, 2001

[Echinalosiinae WATERHOUSE, 2001, p. 57] [type genus, *Echinalosia* WATERHOUSE, 1967, p. 167]

[This subfamily, based on *Echinalosia* WATERHOUSE, 1967, separates those strophalosiids in BRUNTON and others (2000), mainly assigned to the Dasyalosiinae, but differentiated by having dorsal spines that are all erect. WATERHOUSE (2001) also included genera with lamellose or a fine radial ornamentation. The dorsal valve of *Echinalosia* is concave over the corpus, curving into a short trail, while those of *Dasyalosia* and *Crossalosia*, representing the remaining Dasyalosiinae, are flat over the corpus, and this feature should perhaps also be included in any discussion separating these strophalosiids.] *upper Lower Permian (Artinskian)–Upper Permian (Changhsingian).*

Capillaria WATERHOUSE, 2001, p. 67 [**Strophalosia preovalis* var. *warwicki* MAXWELL, 1954, p.

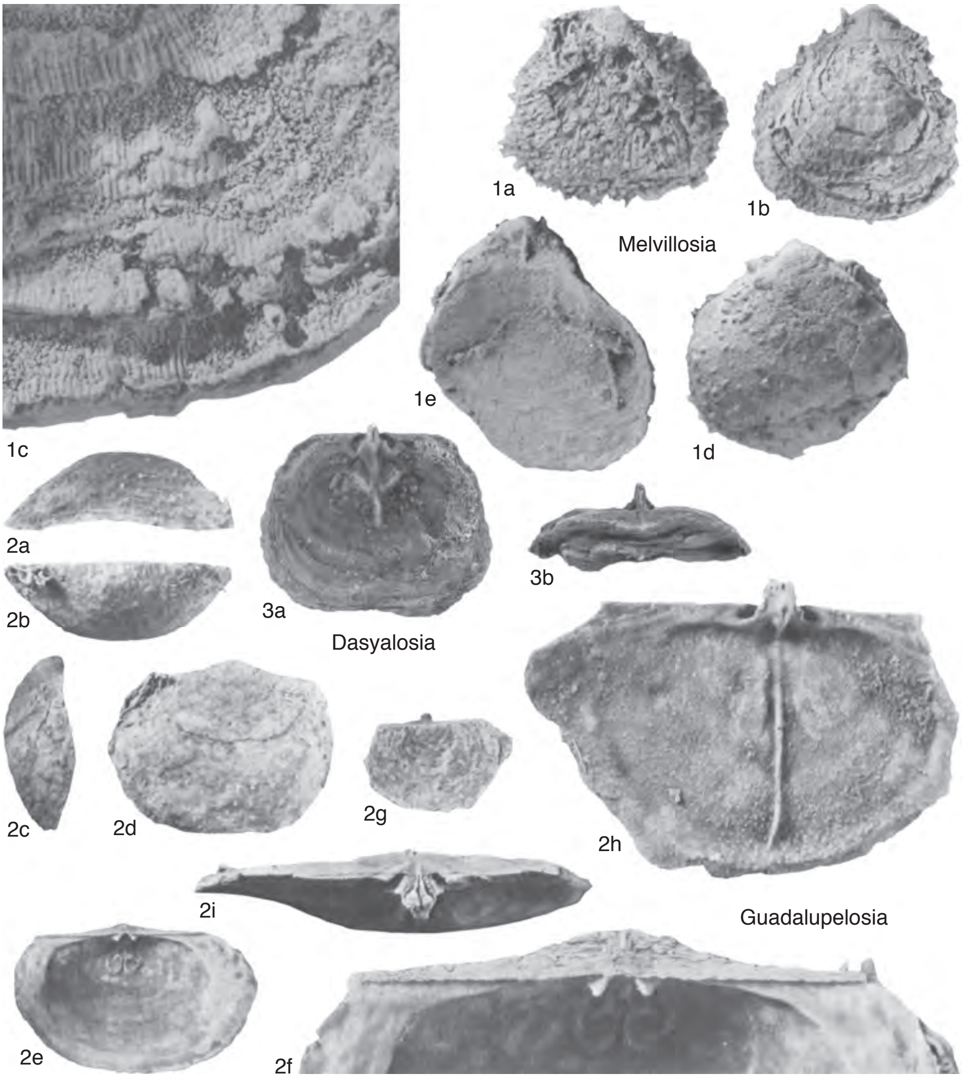


FIG. 1772. Strophalosiidae (p. 2663–2667).

543; OD]. Small or medium-sized rounded shells resembling *Echinalosia*, but with fine capillae and few spines dorsally; ventral spines in two series, small unbonally and increasing in size to posterolateral margins and anteriorly. *Lower Permian (Sakmarian)–Upper Permian (Capitanian):* Eastern Australia and Tasmania.——FIG. 1773*a–e*. **C. warwicki* (MAXWELL); *a,* holotype, ventral valve internal mold, UQF15626, ×2; *b,* cast of posterolateral region of ventral valve exterior, ×2; *c,* cast of shell exterior viewed posterodorsally, ×2; *d,* dorsal valve external mold showing fine capillae, ×3; *e,* cast of incomplete dorsal valve interior, ×2 (Briggs, 1998).

Pseudostrophalosia CLARKE, 1970, p. 987 [**Strophalosia brittoni* MAXWELL, 1954, p. 543, partim.; OD]. Medium-sized ovate shells with geniculate dorsal valves and short trails; ventral spines semirecumbent, fine to coarse toward anterior and coarse at ears; dorsal spines fine, numerous and between weakly lamellose rugae; dorsal lateral ridges impersistent, but may continue as ear baffles and subperipheral rim. [BRIGGS (1998) published his study of the Strophalosiidina and Productidina of eastern Australia, which included the reinvestigation of this genus in which he recorded convincing evidence for its separation from *Wyndhamia*, where it was included in BRUNTON and others (2000, p.

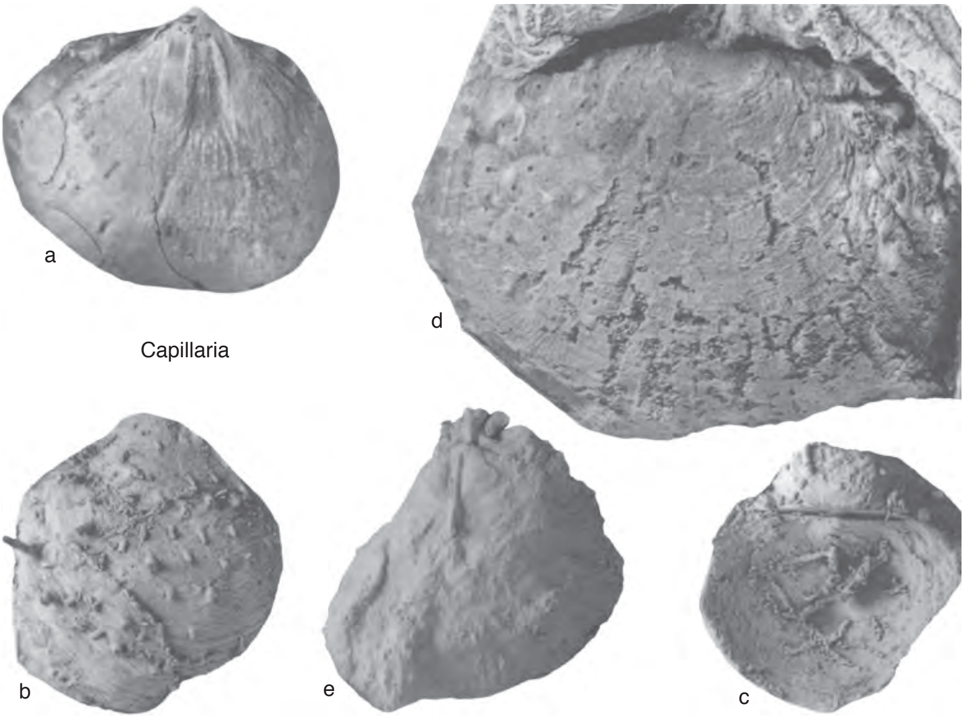


FIG. 1773. Strophalosiidae (p. 2665–2666).

574).] *Lower Permian (Artinskian)–Upper Permian (Kazanian):* East Australia.——FIG. 1774*a–e.* **P. brittoni* (MAXWELL); *a,* replica of ventral valve exterior, ×2; *b,* mold of dorsal valve exterior, ×2; *c–d,* internal mold of ventral valve and replica of posterior region showing teeth, interarea, and muscle field, ×2; *e,* replica of dorsal valve interior, ×2 (Briggs, 1998).

Subfamily MINGENEWIINAE Archbold, 1980

Melvillosia WATERHOUSE, 2001, p. 56 [**M. canadensis;* OD; *nom. nov. pro Craspedalosia pulchella* WATERHOUSE, 1969, *non* DUNBAR, 1955, p. 81]. Small to medium size with oval to subtriangular outline; cicatrix minute to absent; interareas narrow but prominent ventrally; spines on ventral valve in two series, strong erect and fine semirecumbent with slightly swollen bases, dorsal valve with rare suberect spines; weakly to strongly lamellose with fine capillae, especially dorsally; interiors not known. [WATERHOUSE (2001) placed *Melvillosia* in the subfamily, altering its definition to include genera with capillate ornament, but he did not consider the presence of dorsal spines on his genus as significant. In view of MUIR-WOOD and COOPER's (1960) mention of rare capillae on dorsal valves of *Craspedalosia,* the distinction between it and *Melvillosia* is not entirely secure. If dorsal spines are considered important, then *Orthothrix* with its similar outline and lamellose plus spinose dorsal valve has to be compared.] *Upper Permian (Wordian, ?Capitanian):* Canadian Arctic.——FIG. 1772,*1a–e.* **M. canadensis,* Melville Island; *a–b,* holotype, viewed ventrally and dorsally, GSC 23828, ×1; *c,* detail of dorsal valve margin showing capillate lamellae and spine bases, ×4; *d–e,* specimen stripped of spines, ventral and dorsal views, ×1 (Waterhouse, 1969).

Family CHONOPECTIDAE Muir-Wood & Cooper, 1960

Eileenella RACHEBOEUF in WONGWANICH & others, 2004, p. 1081 [**E. elegans;* OD]. Small leptaenid-like geniculate chonopectid shells with weak concentric, sublamellose growth lines, especially on short trail; ventral and dorsal valves almost flat; hinge spines not extending to ears; rounded peripheral ventral ridge bearing row of stubby, flattened spiny tubercles projecting anteriorly and anterolaterally; ventral valve interior with well-developed diductor muscle field divided by thin myophragm; dorsal interior with short and wide cardinal process supported by short inner socket ridges and median septum; thin, broadly lobate peripheral ridges bordering disc. *Upper Carboniferous (Namurian, Bashkirian):* southern

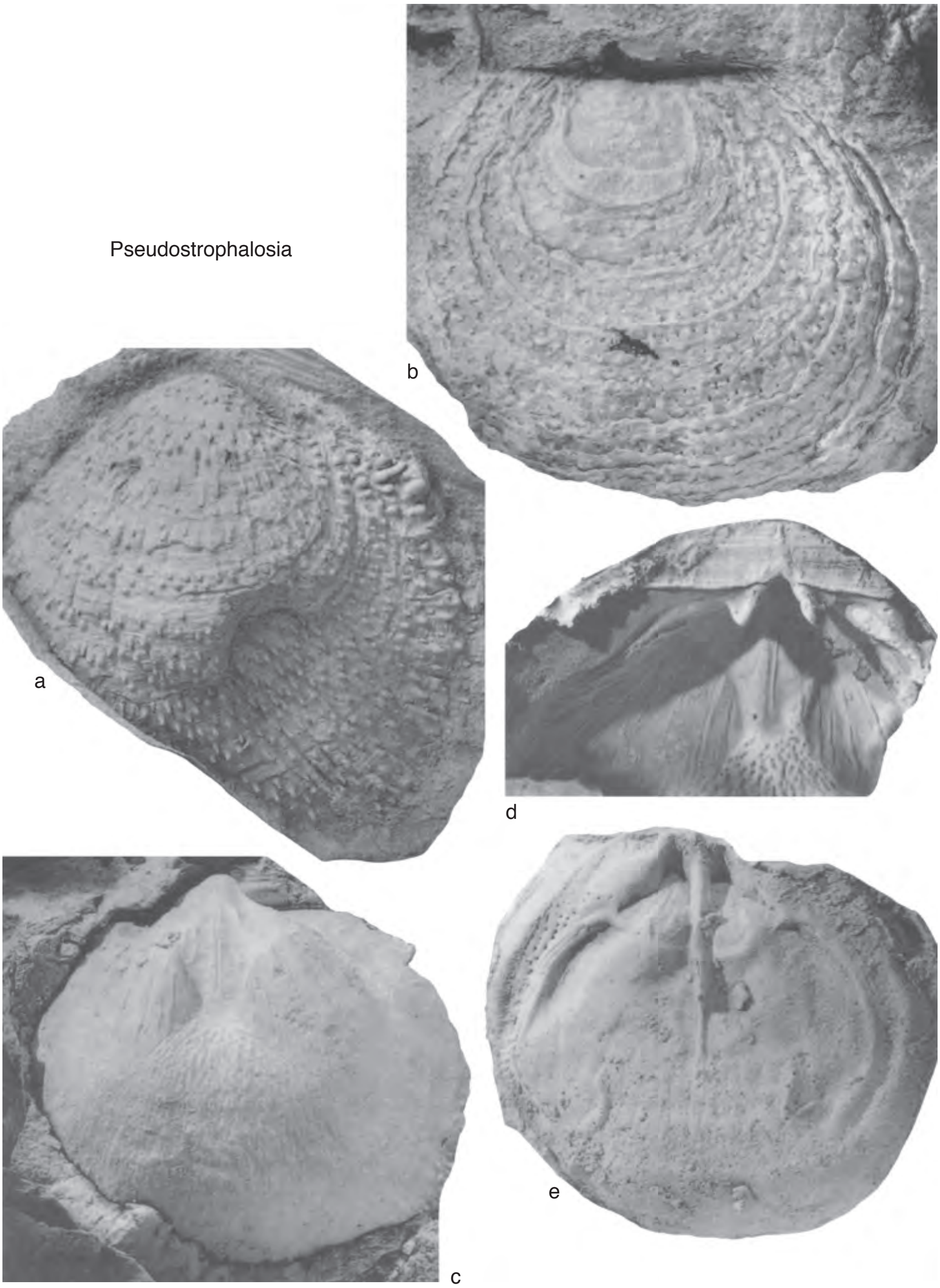


FIG. 1774. Strophalosiidae (p. 2666–2667).

Thailand.——FIG. 1775,*1a–f*. **E. elegans*; *a,* holotype, rubber replica of ventral valve exterior showing anterior spinose tubercles, BMNH BD12524, ×5; *b–c,* rubber replica showing spine bases at hinge line and ventral valve internal mold, ×5; *d,* rubber replica of dorsal valve interior, ×5; *e,* rubber replica of incomplete dorsal valve interior, ×5; *f,* reconstruction drawing of articulated shell viewed laterally, ×5 (Wongwanich & others, 2004).

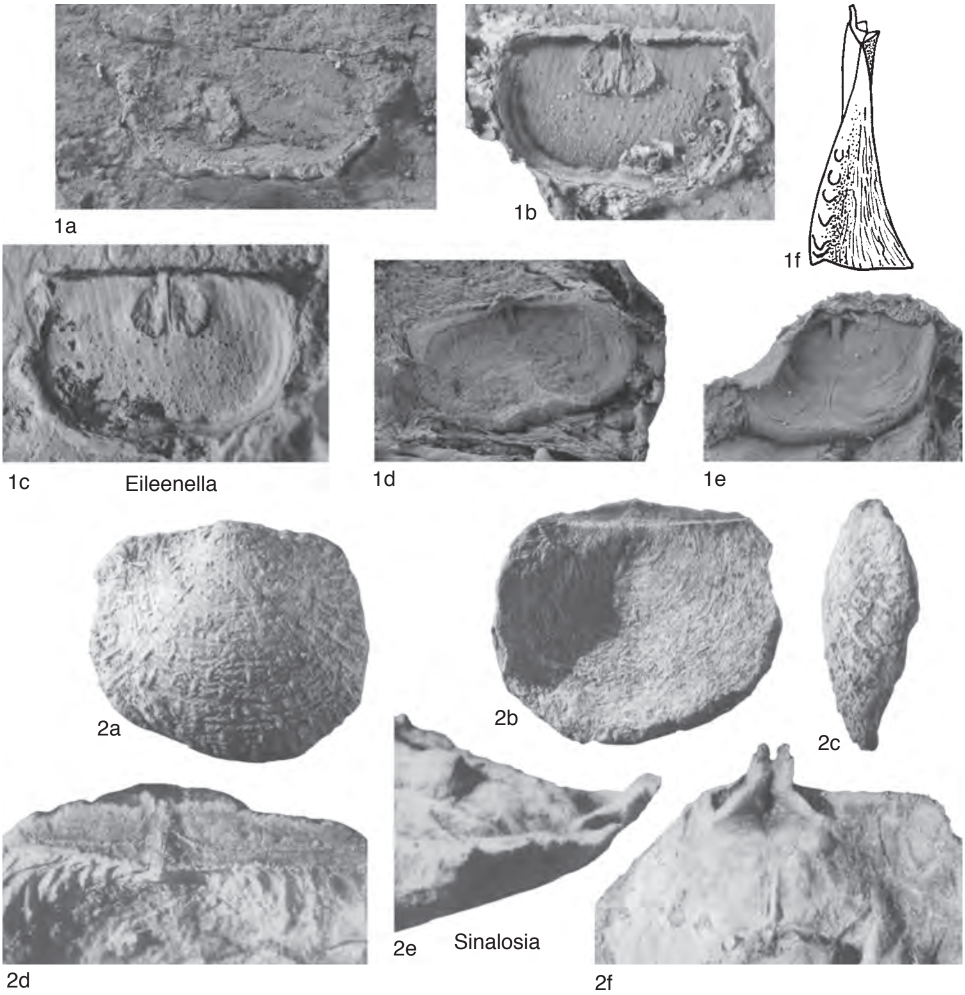


FIG. 1775. Chonopectidae and Araksalosiidae (p. 2667–2669).

Family ARAKSALOSIIDAE
Lazarev, 1989
Subfamily RHYTIALOSIINAE
Lazarev, 1989

Sinalosia MA & SUN in MA & others, 2002, p. 386 [**S. rugosa;* OD]. Small to medium weakly concavo-convex araksalosiids with short, wide interareas; cicatrix weak to absent; rugae fine and undulose, less prominent dorsally; spines thin, recumbent over ventral valve and rare erect thicker hinge spines; inner socket ridges short, well developed, median septum weak, reaching about midcorpus length. *Upper Devonian (upper Frasnian):* southern China (central Hunan).——FIG. 1775,*2a–f*. **S. rugosa; a–c,* holotype, ventral, dorsal, and lateral views, PUM 00017, ×2; *d,* posterodorsal view of shell showing interareas, pseudodeltidium, and chilidium, ×6; *e–f,* dorsal valve cardinalia, lateral and dorsal views, ×6 (Ma & others, 2002).

Superfamily AULOSTEGOIDEA
Muir-Wood & Cooper, 1960
Family AULOSTEGIDAE
Muir-Wood & Cooper, 1960
Subfamily AULOSTEGINAE
Muir-Wood & Cooper, 1960

Carilya ARCHBOLD in BRUNTON, COCKS, & LONG, 2001, p. 369 [**Taeniothaerus miniliensis* COLEMAN, 1957, p. 96; OD] [=*Miniliconcha* WATERHOUSE, 2004, p. 71, obj.]. Large subquadrate shell with weak ventral median sulcus, differing from *Taeniothaerus* in having finer and more densely arranged spines arising ventrally from small spine ridges, coarser clusters of spines directed posterolaterally from small ears and posterolateral margins; dorsal valve with dimples and fine spines; dorsal adductor scars enclosed posterolaterally by thickened shell. [The description of *Carilya*, based on species previously described as *Taeniothaerus* from Western Australia, narrows the definition of *Taeniothaerus* to species found in Tasmania and eastern Australia. WATERHOUSE's junior objective synonym is based entirely on the specimens and holotype of COLEMAN, 1957.] *Lower Permian (upper Artinskian–lower Kungurian):* Western Australia.——FIG. 1776*a–h*. **C. miniliensis* (COLEMAN), Wandagee Formation, lower Kungurian, Minilya River, Carnarvon Basin; *a–b,* holotype, viewed posteriorly and laterally, UWA 34445, ×1 (Coleman, 1957); *c–d,* lateral and part dorsal views (Muir-Wood & Cooper, 1960); *e,* dorsal valve interior, ×1 (Coleman, 1957); *f–h,* incomplete dorsal valve interior, exterior, and lateral view showing posteroventrally directed cardinal process, adductor scars, and incomplete long median septum, ×1 (Muir-Wood & Cooper, 1960).

Saeptathaerus WATERHOUSE, 2002a, p. 230 [**Aulosteges fairbridgei* COLEMAN, 1957, p. 40; OD]. Medium to large aulostegine resembling *Megasteges* in shape and with bands of stronger, more erect spines on ventral trail, other ventral and thinner dorsal spines arising from anterior ends of spine ridges; ridges diverging narrowly from cardinal process base, enclosing dorsal adductor scars posterolaterally and almost equalling length of median septum. *Upper Permian (Tatarian):* Western Australia, Himalayas.——FIG. 1777*a–f*. **S. fairbridgei* (COLEMAN), Herdman Formation, lower Tatarian, western Kimberly; *a–d,* holotype, internal cast of shell with little remaining shell material, posterior, dorsal (umbonal area), lateral, and ventral views, UWA 29438f, ×1; *e–f,* smaller internal cast, dorsal and ventral views, ×1 (Coleman, 1957).

Taeniothaerus WHITEHOUSE, 1928, p. 281 [**P. subquadratus* MORRIS in STREZELECKI, 1845, p. 284; OD]. Large, relatively thick-shelled, sulcate ventral valve with irregular concentric bands of coarse, elongate spine bases and relatively thick spines interspersed with fewer finer spines anteriorly, plus stronger posterolateral spines; dorsal valve with concentric coarse dimples and few spines; dorsal adductor scars posteriorly bordered by ridges extending from cardinal process shaft. [The erection of *Carilya* results in the need for a redefinition of this genus.] *Lower Permian (Artinskian):* eastern Australia.——FIG. 1778*a–d*. **T. subquadratus* (MORRIS); *a–b,* lectotype, partly exfoliated ventral valve exterior viewed ventrally and laterally, near Hobart, Tasmania, BMNH B91171, ×1 (new); *c,* dorsal valve interior with exposed external mold anteriorly showing positions of spine bases, Berriedale Limestone, near Granton, Tasmania, ×0.8; *d,* incomplete dorsal valve interior, Counsel Creek Formation, Maria Island, Tasmania, ×1 (Parfrey, 1983).——FIG. 1779*a–b*. **T. subquadratus* (MORRIS); *a,* ventral valve exterior showing finer spines anteriorly, Enstone Park Limestone, Elephant Pass, Tasmania, ×0.6 (Parfrey, 1983); *b,* replica of ventral valve exterior, Tiverton Formation, ×1 (Waterhouse, Briggs, & Parfrey, 1983).

Subfamily INSTITELLINAE Muir-Wood & Cooper, 1960

Licharewiconcha KOTLYAR, ZAKHAREV, & POLUBOTKO, 2004, p. 517 [**Productus* (*Sinuatella*) *subsinuatus* LICHAREW, 1936, p. 116; OD]. Medium sized, subquadrate to transverse outline, strong triangular ears, probably with shallow corpus cavity and with well-differentiated trails; interarea wide, but short; ribbing well defined, but lacking on ears; rugae slightly more prominent than ribbing posteromedianly, not on anterior corpus, ears, or trails; median sulcus and dorsal fold start close to umbones; spines large (?), clasping clumps on lateral hinge line and ears, possibly finer spines on ventral corpus. [This genus was described in its own new family, but it fits well within the Institellinae. The genus authors do not mention a type specimen, but their figures 8.6–9 appear to match closely those of the named holotype by LICHAREW (1936) and figured by him as pl. 1,*7a–c*.] *Upper Permian (upper Changhsingian):* Russia (northwestern Caucasus mountains). ——FIG. 1780,*2a–f*. **L. subsinuatus* (LICHAREW), Urushten Formation, near Kutan; *a–d,* possible holotype, almost complete shell, ventral, anterior, lateral, and dorsal views showing short interarea and impressions of ventral spine bases in a row between ears and flanks, CRMGE 890/2139, Severnaya Ravine, ×1; *e,* dorsal view of shell showing some ventral hinge spines projecting posteriorly, ×1; *f,* incomplete ventral valve exterior showing spine cluster at one ear and possible smaller spine bases on corpus, ×2 (Kotlyar, Zakharev, & Polubotko, 2004).

Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

Colemanosteges WATERHOUSE, 2002b, p. 49 [**Taeniothaerus(?) fletcheri* COLEMAN, 1957, p. 91; OD]. Small to medium-sized rhamnariine with a planoconvex profile and short trails; hinge line about one-half to three-quarters maximum width with narrow, short ventral interarea with open delthyrium; ventral spines coarse, recumbent with elongate bases and interspersed fine spines toward anterior margin, clusters on ears; spines fine dorsally; cardinal process buttress plates slightly divergent to posterior ends of weakly raised adductor scars. [The above follows COLEMAN's description and illustrations (1957).] *Upper Permian (lower Tatarian):* Western Australia, ?southern Tibet.——FIG. 1780,*1a–e*. **C. fletcheri* (COLEMAN), Liveringa

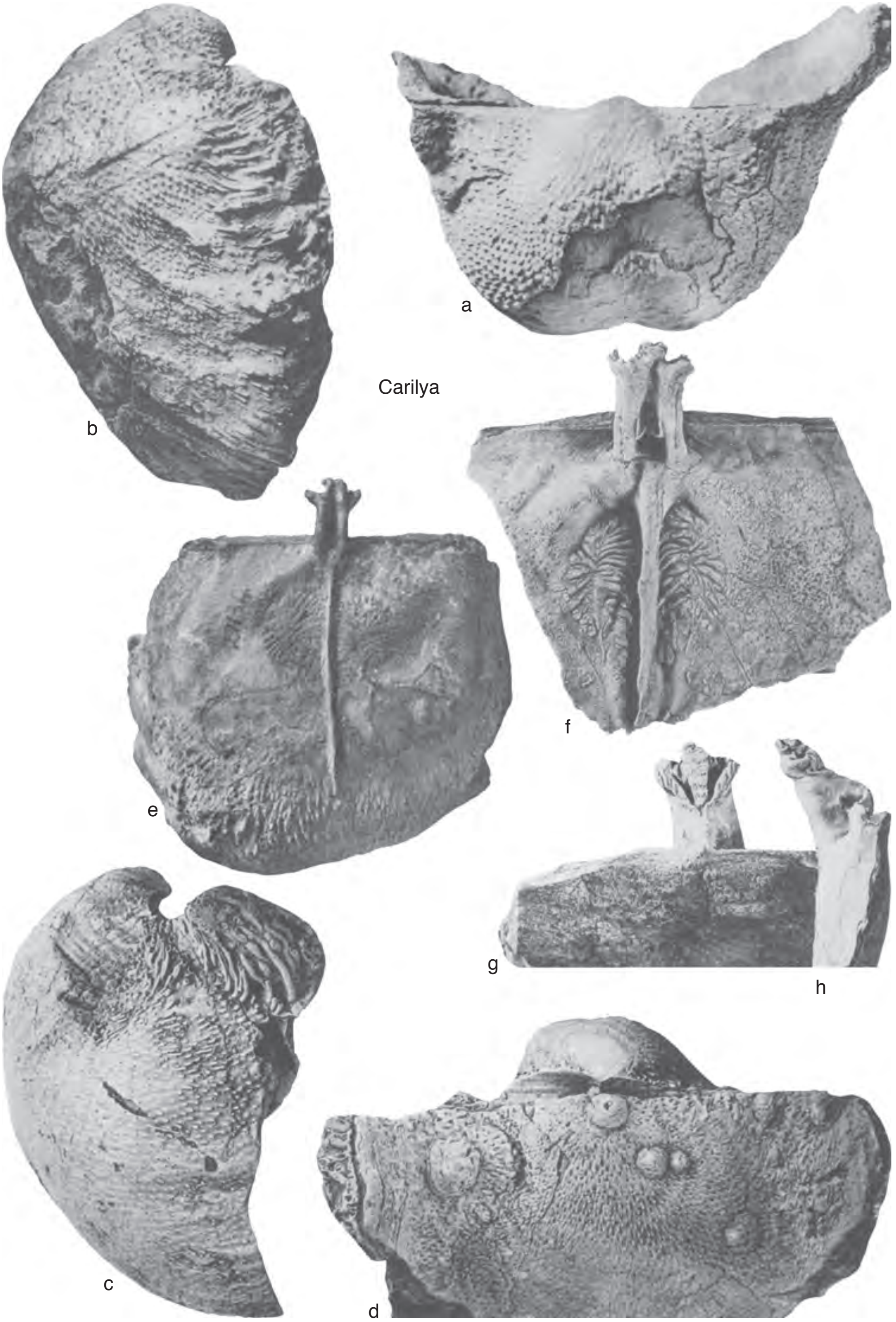


FIG. 1776. Aulostegidae (p. 2669–2670).

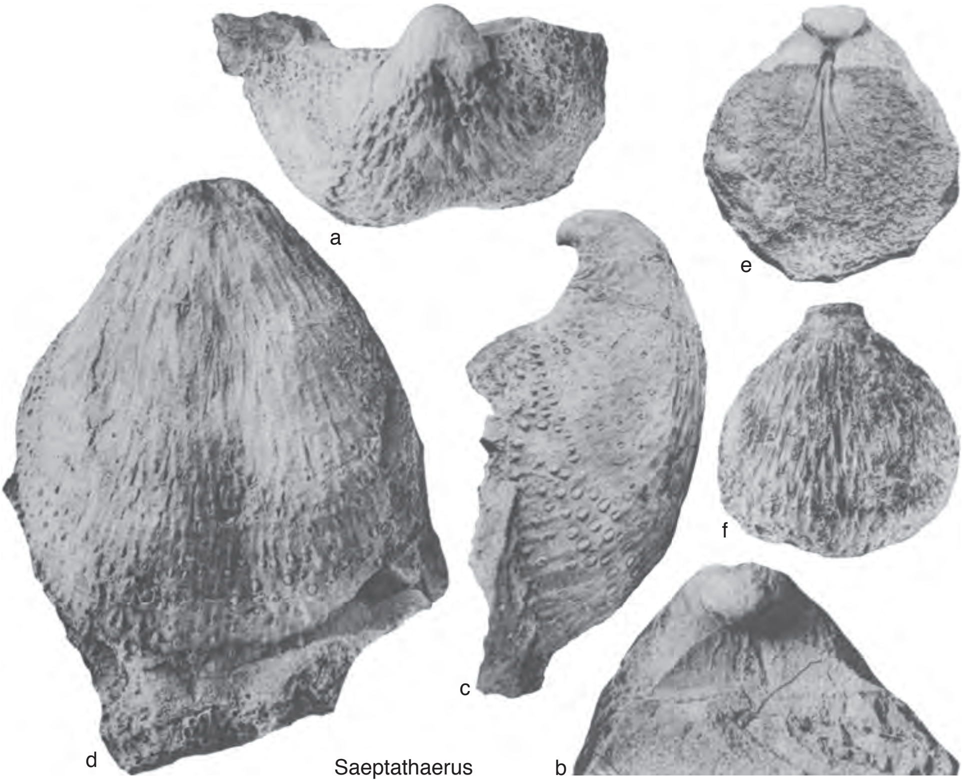


FIG. 1777. Aulostegidae (p. 2670).

Formation, western Kimberly, Australia; *a–b,* holotype, ventral valve, ventral and dorsal views, CPC 1950, ×0.67; *c,* holotype, ventral valve viewed laterally, CPC 1950, ×1; *d,* dorsal view of specimen with cluster of posteroventral spines, ×1; *e,* incomplete dorsal valve interior, ×1 (Coleman, 1957).

Family TSCHERNYSCHEWIIDAE Muir-Wood & Copper, 1960

[*nom. transl.* BRUNTON, herein, *ex* Tschernyschewiinae MUIR-WOOD & COOPER, 1960, p. 126]

Description as in subfamily Tschernyschewiinae in BRUNTON and others (2000, p. 608).

Reedosepta WATERHOUSE, 2002b, p. 50 [**Productus (Tschernyschewia) parilis* REED, 1944, p. 86; OD]. Similar in size and shape to *Tschernyschewia*, but differing in its ventral ornamentation of pustulose spine bases of differing sizes, somewhat resembling the ornament of *Juresania*, clusters of erect spines lacking swollen bases on small ears and posterior flanks; dorsal spines with fewer and smaller spine bases. *Upper Permian (upper Capitanian):* Pakistan (Salt Range).——FIG. 1781,*1a–f.* **R. parilis* (REED), Middle *Productus* Limestone, Wargal Formation; *a–e,* lectotype, ventral, lateral, dorsal, and posterior views, GSI 16856 (selected by WATERHOUSE, 2002b), ×1.5, and detail of ventral valve spine base ornament, ×2; *f,* posterior view of broken ventral valve showing high median septum, ×1.5 (Reed, 1944).

Trigonoproductus WATERHOUSE, 2002b, p. 51 [**Tschernyschewia inexpectans* COOPER & GRANT, 1975, p. 915; OD]. Similar in size and outline to *Tschernyschewi*a, but with well-formed ears, double row of strong rhizoid spines at ventral hinge line, and dorsal valve with well-developed anterior fold; dorsal valve median septum starting between adductor scars and reaching anterior border of disc. *Lower Permian (Sakmarian):* USA (western Texas).——FIG. 1781,*2a–f.* **T. inexpectans* (COOPER & GRANT), Hess Formation, Glass Mountains; *a–d,* holotype, incomplete shell, dorsal, posterior, lateral, and anterolateral views showing part of shell interior, USNM 152681, ×1; *e,* ventral valve exterior in

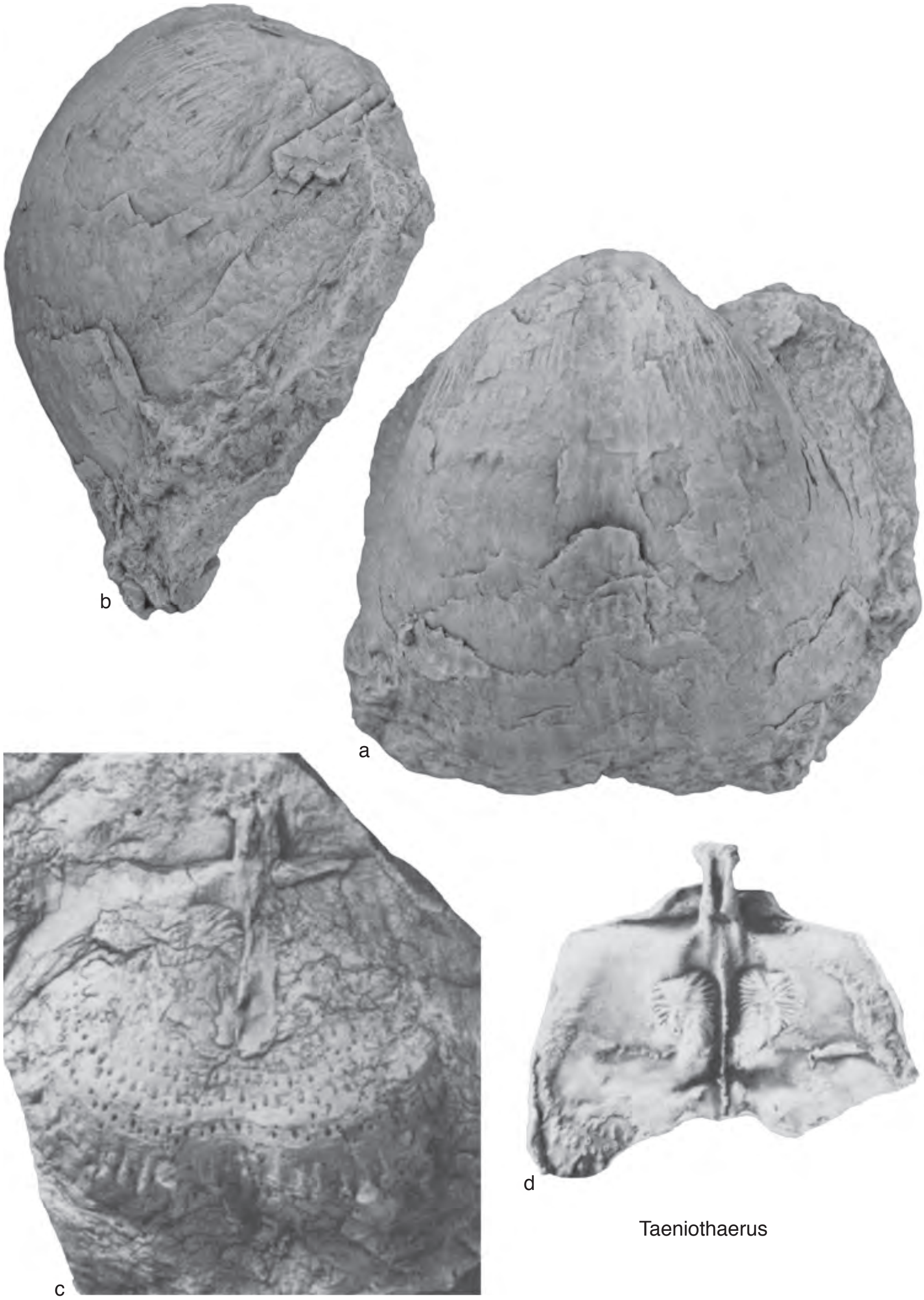


FIG. 1778. Aulostegidae (p. 2670).

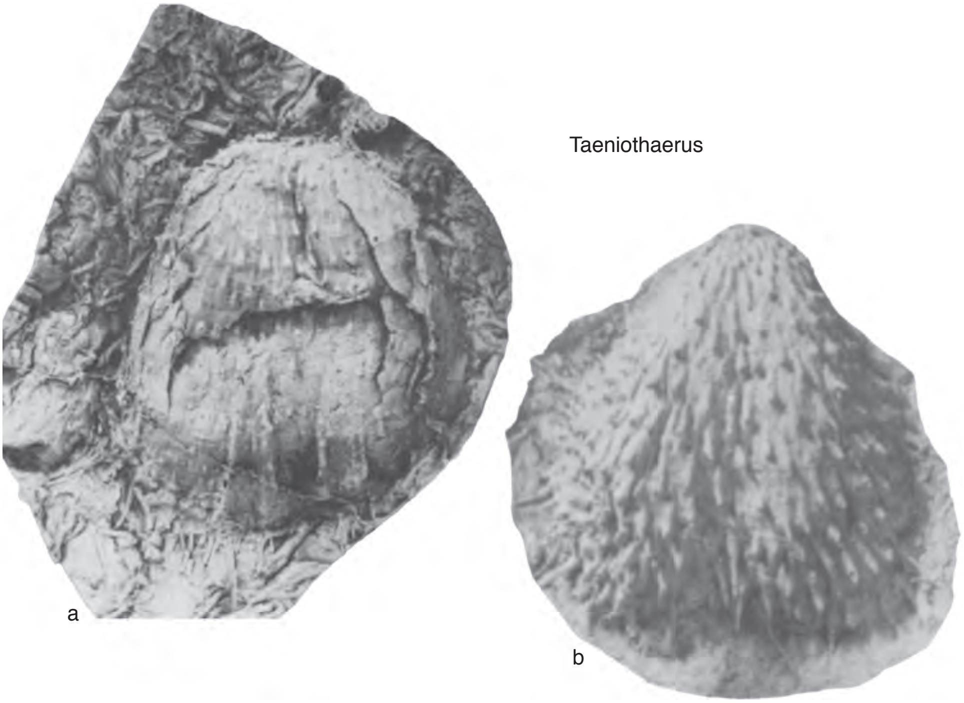


FIG. 1779. Aulostegidae (p. 2670).

anteroventral view, ×1; *f,* dorsal cardinalia, internal view, ×2 (Cooper & Grant, 1975).

Order ORTHOTETIDA
Waagen, 1884
Superfamily ORTHOTETOIDEA
Waagen, 1884
Family SCHUCHERTELLIDAE
Williams, 1953

Ventral valve variable in size and shape, deformed by attachment but normally with high ventral interarea; shell usually finely costellate rarely with secondary costation; discrete dental plates; cardinal process lobes low, discrete, becoming long and fused proximally into single shaft; socket ridges recurved to divergent, becoming fused with cardinal process base, brachiophore bases developing later, normally prolonged as brachiophores; shell extropunctate with oldest representatives retaining pseudopunctation. *Middle Devonian–Permian.*

Subfamily SCHUCHERTELLINAE
Williams, 1953

Schuchertellopsis MAILLIEUX, 1939, p. 5 [**S. durbutensis*; OD]. Small (10 to 12 mm wide), irregularly shaped shells with ventral valve cemented almost completely to substrate; hinge line approximately widest part of shell, ventral profile irregular, dorsal profile plane to weakly convex; ventral interarea with arched pseudodeltidium, dorsal interarea weak; irregularly costellate; dental ridges unsupported; dorsal valve poorly known. [In WILLIAMS & BRUNTON (2000, p. 667), MAILLIEUX's genus was questionably assigned to the Schuchertellinae of the Orthotetidina. In 1978 STRUVE divided the genus into two subgenera by the description of *Schuchertellopsis (Krejcigrafella)*. *Schuchertellopsis s.s.* comes from the upper Frasnian of Belgium and *Krejcigrafella* from the lower Eifelian of Germany.

These subgenera are both closely and almost completely attached by their ventral valves, and at the time of preparation for the orthotetidines for the revised *Treatise* (Vol. 3, WILLIAMS & BRUNTON, 2000) it was not entirely clear as to whether they would best be classified with the orthotetidines or attached davidsonioids. The main feature differentiating these two taxa is shell structure; the former having laminar shell and the latter fibrous shell. Study of MAILLIEUX'S original collection shows the

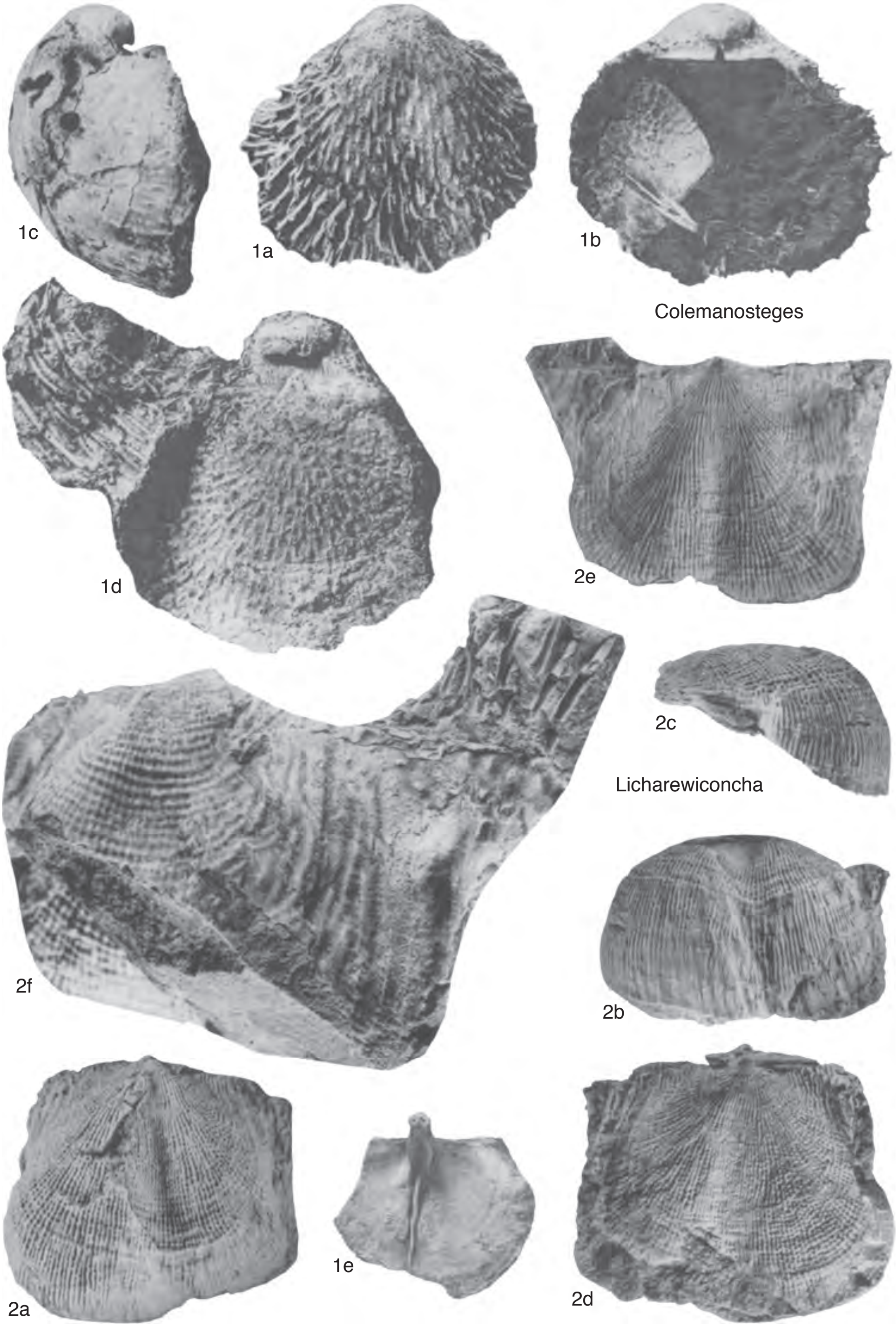


FIG. 1780. Aulostegidae (p. 2670–2672).

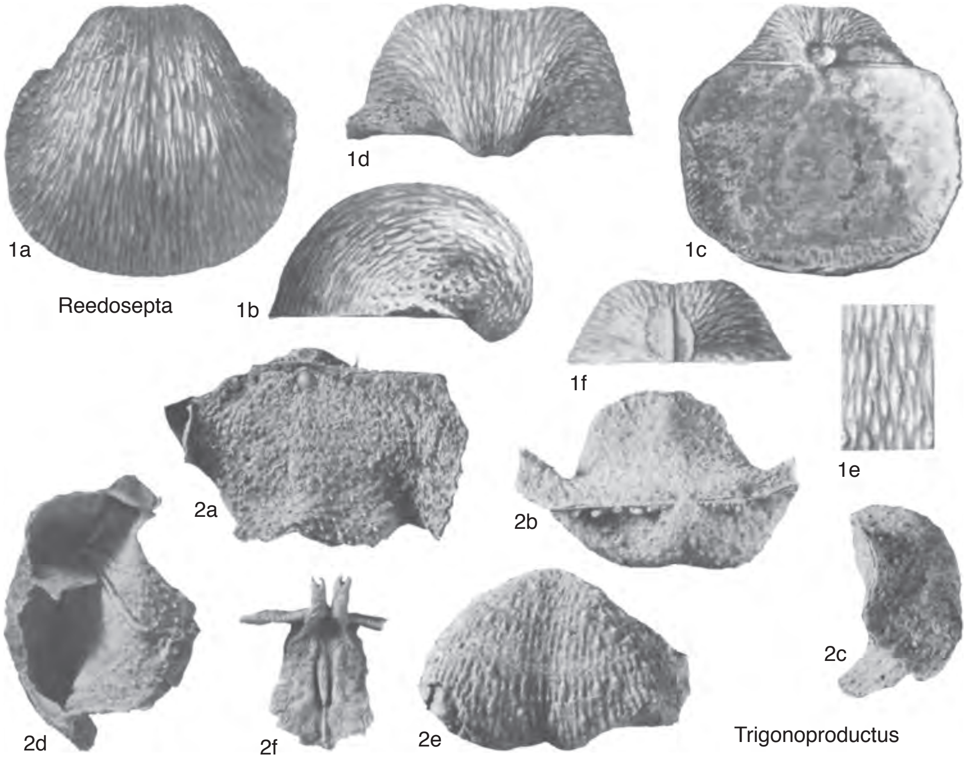


FIG. 1781. Tschernyschewiidae (p. 2672–2674).

following orthotetidine features, not seen in davidsonioids: (1) wide ventral interarea with delthyrium covered completely by an arched pseudodeltidium, and (2) shell fabric laminar with pseudupunctae forming pustulose internal surfaces, and sparse extropunctae forming small depressions internally (Fig. 1782).

WILLIAMS and BRUNTON (2000) characterized the Schuchertellidae by, among other features, their unsupported teeth and extropunctate shell, the only family known to have such microstructures in the shell. The finding of extropunctae in *Schuchertellopsis*, together with its schuchertellid morphology, confirms its position in the Schuchertellidae, and its morphology is similar to the Schuchertellinae. The genus is, however, unique as yet in having both pseudopunctae and extropunctae; it is also the oldest known member of the family. We conclude, therefore, that the pseudopunctation is a holdover from ancestral stock that was pseudopunctate.

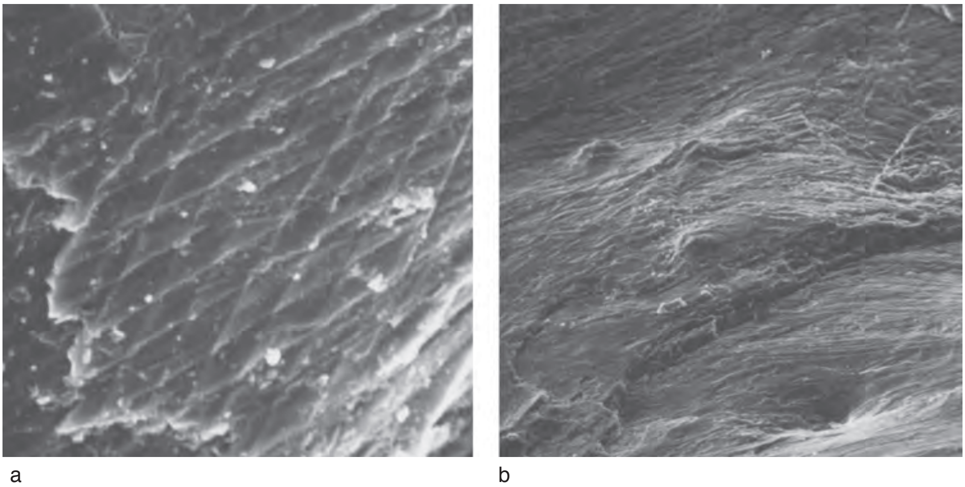


FIG. 1782. Schuchertellidae (p. 2677).

The extropunctation seen in *Schuchertellopsis* is less developed than in Carboniferous and Permian genera and would appear to be a new structure introduced to the family at about mid-Devonian time.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* western Europe, ?southern North America.

S. (Schuchertellopsis). Lacking ventral median septum; inner socket ridges extending at shallow angle from hinge, muscle fields indistinct; shell extropunctate and pseudopunctate. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* western Europe.——FIG. 1782*a–b*. **S. (S.) durbutensis,* Mailleux collection, Institut Royal des Sciences Naturelles de Belgique, Brussels; *a,* SEM of exfoliated internal surface of ventral valve showing cross-bladed laminae, ×3000; *b,* SEM of exfoliated ventral valve interior showing extropunctae, represented by pits, and pseudopunctae represented by tubercles, ×300 (new).

S. (Krejcigrafella) STRUVE, 1978.

ORTHOTETIDA

David A. T. Harper

[University of Copenhagen]

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily CHILIDIOPSOIDEA Boucot, 1959
Family EOCRAMATIIDAE Williams, 1974

[Eocramatiidae Williams, 1974, p. 127; *emend.*, Harper, herein]

Subquadrate, costellate; apsacline ventral interarea with submesothyrid foramen and convex pseudodeltidium; narrow, hypercline dorsal interarea with small convex chilidium; teeth largely unsupported, ventral muscle scar more or less limited to delthyrial cavity; chilidial plates ankylosed to socket ridges or plates that are divergent or parallel with hinge line; dorsal adductor scars quadripartite about low myophragm; dorsal platforms variably developed; shell impunctate. [Identification of laminar secondary shell in the genus *Neocramatia* suggests assignment of this family to the Orthotetidina rather than the Plectambonitoidea. Moreover, cladistic analysis indicates a position for the family within the Chilidiopsoidea. This new assignment and the addition of *Neocramatia* to the family require some modification of the respective diagnoses for both the genera and the family]. *Ordovician (Llanvirn–Ashgill).*

Eocramatia Williams, 1974, p. 128 [**E. dissimulata*; OD]. Planoconvex, gently uniplicate, finely costellate by branching and intercalation; socket ridges widely divergent, near parallel to hinge line. *Ordovician (Llanvirn):* England.——Fig. 1783,*1a–d*. **E. dissimulata*, Hope Shale Formation, Brithdir Farm, Shropshire; *a–b*, rubber replicas of dorsal exterior and interior, BMNH BB35489a,b, ×5.8; *c–d*, internal mold and rubber replica of ventral valve, BMNH BB35488a, ×3.5 (Williams, 1974).

Neocramatia Harper, 1989, p. 102 [**N. diffidentia*; OD]. Concavoconvex, costellate with branching and intercalated ribs; socket ridges divergent; bilobed dorsal platform present together with arcs of pustules in both ventral and dorsal valves near anterior margin. *Ordovician (Caradoc):* Scotland.——Fig. 1783,*2a–f*. **N. diffidentia,* Myoch Formation, Girvan, southwestern Scotland; *a–b*, internal mold of ventral valve and rubber replica, HML 12412, ×6; *c–d*, internal mold of dorsal valve and rubber replica, HML 8910, ×9; *e*, rubber replica of dorsal exterior, HML 12148b, ×5; *f*, rubber replica of ventral exterior, HML 12148a, ×6.5 (Harper, 1989).

TRIPLESIOIDEA

A. D. Wright

[The University of Leicester]

Suborder TRIPLESIIDINA Moore, 1952
Superfamily TRIPLESIOIDEA Schuchert, 1913
Family TRIPLESIIDAE Schuchert, 1913

Acaretyrricula Jin & Chatterton, 1997, p. 23 [**A. tenuiguttae;* OD]. Small, triradiate shell, waisted in front of narrow hinge line; both beaks elongate, ventral extremely so; pseudodeltidium monticulate; surface smooth apart from growth lines, anterior emargination formed by abrupt median deflection, giving tongue to dorsal valve, with corresponding ventral reflection of ventral valve; dental plates long, subparallel, cardinal process proximally grooved, distally unknown. *Silurian* (*Llandovery*): Canada (Northwest Territories).——Fig. 1783,*3a–c*. **A. tenuiguttae*, Telychian; *a,* holotype, view of ventral valve interior and interarea, ×15; *b,* ventral valve exterior, ×15; *c,* dorsal valve interior, ×20 (Jin & Chatterton, 1997).

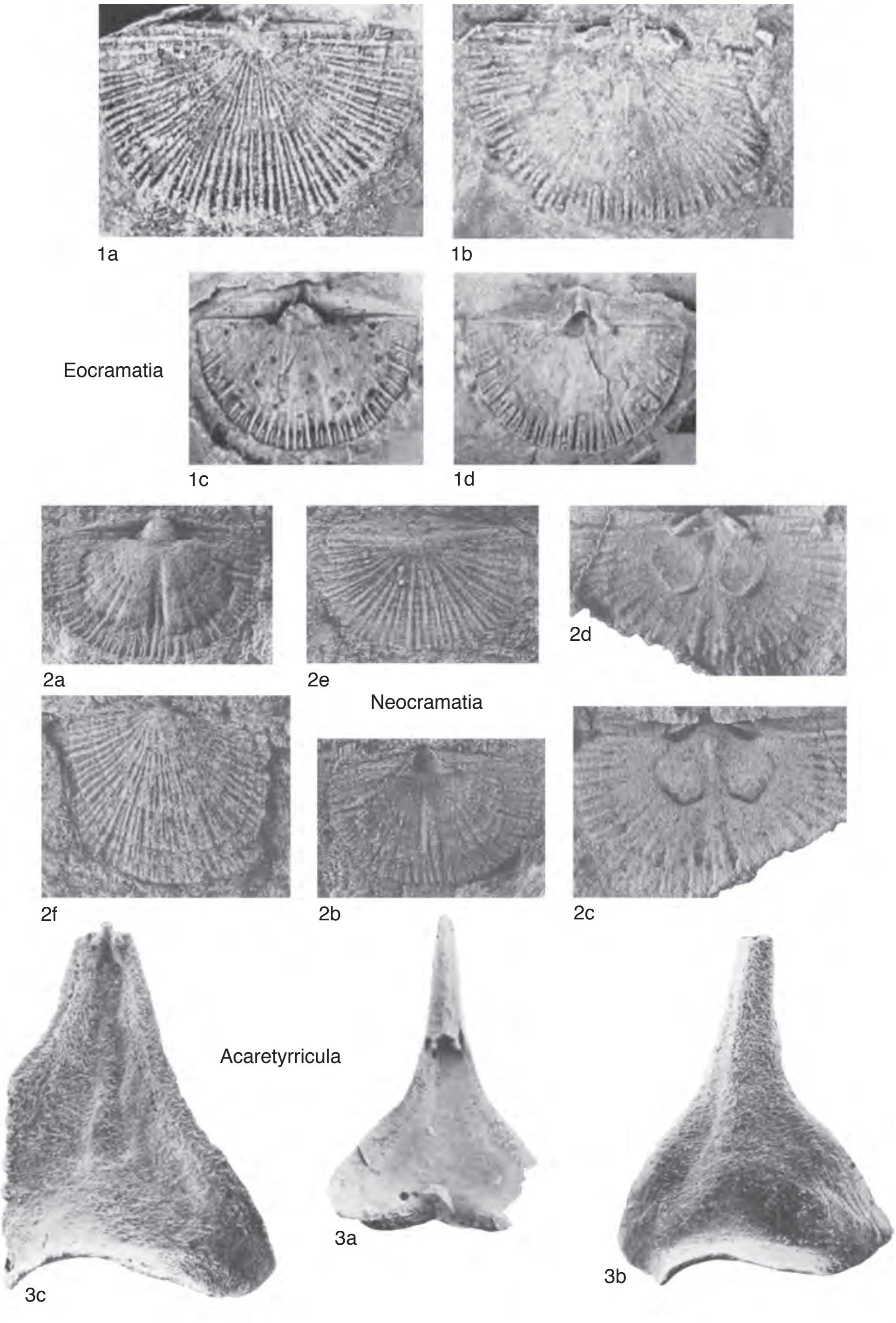


FIG. 1783. Eocramatiidae and Triplesiidae (p. 2678).

CLITAMBONITIDINA

MADIS RUBEL

[University of Tartu]

Suborder CLITAMBONITIDINA Öpik, 1934

Superfamily CLITAMBONITOIDEA Schuchert & Cooper, 1931

Family ARCTOHEDRIDAE Williams & Harper, 2000

[Arctohedridae WILLIAMS & HARPER, 2000, p. 710; *emend.,* RUBEL, herein]

Costellate, unisulcate clitambonitoids with subpyramidal ventral valve; teeth simple, spondylium free; well-developed notothyrial platform with simple cardinal process; divergent rodlike brachiophores joined to hinge line by concave fulcral plates defining sockets and subtending narrow notothyrial plate flanking median elevation that extends anteriorly and divides subequally quadripartite adductor scars; ventral mantle canal system probably saccate with divergent *vascula media. Middle Cambrian.*

Arctohedra COOPER, 1936, p. 210 [**A. minima;* OD]. Transversely semioval with acute cardinal extremities, ventribiconvex to planoconvex, coarsely costellate to ramicostellate; well-developed notothyrial platform, simple cardinal process, and straight, divergent brachiophores. [The type species is illustrated in WILLIAMS and HARPER, 2000, p. 712, fig. 514,*1a–d.* Description and illustration of silicified material from northeastern New South Wales (BROCK, 1998) has confirmed the presence of a cardinal process in this important genus; the diagnosis is emended accordingly and new illustrations provided. The new and more informative material from Australia provides more details of the cardinalia. *Arctohedra* is now regarded as more closely related to the clitambonitidines than the protorthides where it was provisionally placed, in the newly created Arctohedridae, by WILLIAMS and HARPER (2000, p. 710). That provisional assignment was based on the assumption that the free spondylium of *Arctohedra*, a basic protorthide character, is systematically more important than the cardinalia, both of which were considered to

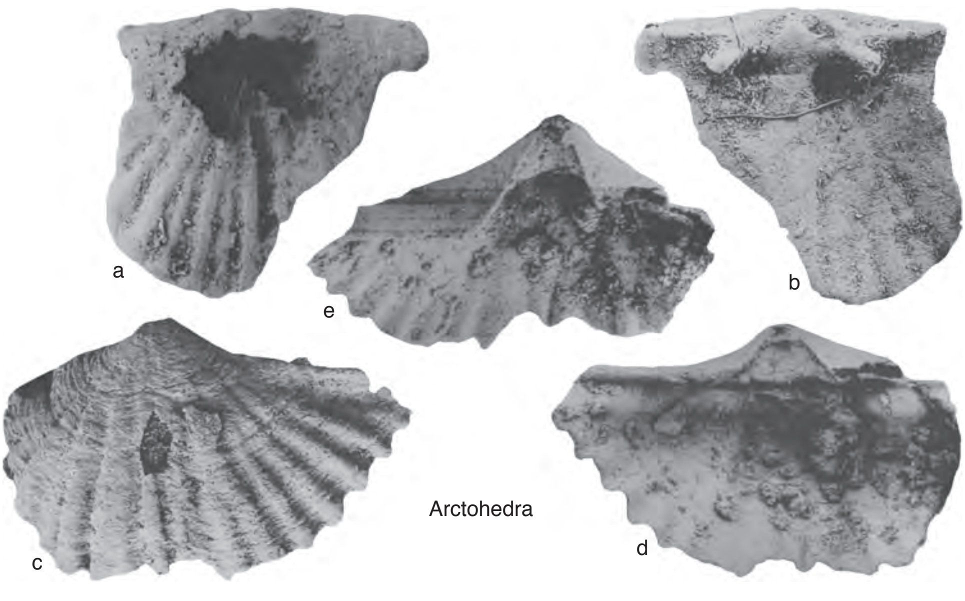


FIG. 1784. Arctohedridae (p. 2680–2681).

be orthide (Williams & Harper, 2000, p. 710). A free spondylium, however, is now known to be characteristic of clitambonitidine juvenile shells (Popov, Vinn, & Nikitina, 2001, p. 155). This discovery facilitates the transfer of the Arctohedridae (with *Arctohedra* but not *Loperia* Walcott; see p. 2682 herein) to the Clitambonitidina. The transfer greatly extends the stratigraphic range of the suborder.] *Middle Cambrian:* North America (Alaska), Australia (New South Wales), Central Asia (Turkestan, Tian Shan).——Fig. 1784*a–e*. *A. austrina* Brock, Murrawong Creek Formation, northeastern New South Wales, Australia; *a–b*, external and internal views of dorsal valve, AMF97369, ×40; *c–e*, external, internal, and internal oblique views of ventral valve, AMF97373, ×21 (Brock, 1998).

Superfamily POLYTOECHIOIDEA Öpik, 1934

Family POLYTOECHIIDAE Öpik, 1934

Tritoechia Ulrich & Cooper, 1936b, p. 624 [**Deltatreta typica* Schuchert & Cooper, 1932, p. 206; OD] [=*Pinatotoechia* Benedetto, 2001, p. 140 (type, *P. acantha,* OD)]. The so-called tubular spines that are diagnostic of *Pinatotoechia* (Benedetto, 2001, fig. 3B) are identical with the aditicules characterizing the type species of *Tritoechia*.

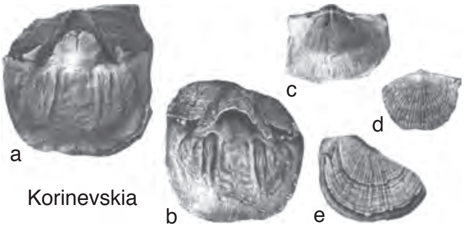


Fig. 1785. Polytoechiidae (p. 2681).

Korinevskia Popov, Vinn, & Nikitina, 2001, p. 149 [**Billingsella akbulakensis* Andreeva, 1960, p. 291; OD]. Similar to *Protambonites*, but complete chilidium, large ventral adductor scars, short dental plates; ventral mantle canal system saccate. *Ordovician (upper Tremadoc–lower Arenig):* southern Urals.——Fig. 1785*a–e*. **K. akbulakensis* (Andreeva); *a–b,* mold of ventral interior and rubber replica, ×2; *c,* rubber replica of dorsal interior, ×2; *d,* rubber replica of juvenile ventral exterior, ×2; *e,* rubber replica of incomplete ventral exterior, ×2 (Popov, Vinn, & Nikitina, 2001).

PROTORTHIDA

David A. T. Harper

[University of Copenhagen]

Class RHYNCHONELLATA Williams & others, 1996

Order PROTORTHIDA Schuchert & Cooper, 1931

Superfamily PROTORTHOIDEA Schuchert & Cooper, 1931

Family PROTORTHIDAE Schuchert & Cooper, 1931

Loperia Walcott, 1905, p. 287 [**Protorthis (Loperia) dougaldensis;* OD]. The genus *Loperia* Walcott is poorly known and is provisionally transferred from the Arctohedridae to the Protorthidae, where it was originally assigned in the first edition of the *Treatise* (Moore, 1965). It does, however, possess distinctive cardinalia and resupination that may form the basis for an alternative taxonomic placement when the genus is revised in modern terms. *Middle Cambrian:* eastern Canada.

Saesorthis Geyer & Mergl, 1997, p. 796 [**Israelaria simplicissima* Mergl, 1983, p. 339; OD]. Medium sized, subequally biconvex, subrectangular, uniplicate, finely ramicostellate; apical plate small; brachiophore nubs small. *Middle Cambrian:* Morocco. ——Fig. 1786*a–e*. **S. simplicissima* (Mergl), Jbel Wawrmast Formation, lower Middle Cambrian; *a*, rubber replica of ventral interior, PIW 92IV137a, ×7; *b*, mold of dorsal interior, PIW 92IV118a, ×4; *c*, dorsal interior, PIW 92IV121, ×7; *d*, partially exfoliated dorsal valve, MM 189a, ×4; *e*, detail of ornament on dorsal valve, MM 189c, ×7 (Geyer & Mergl, 1997).

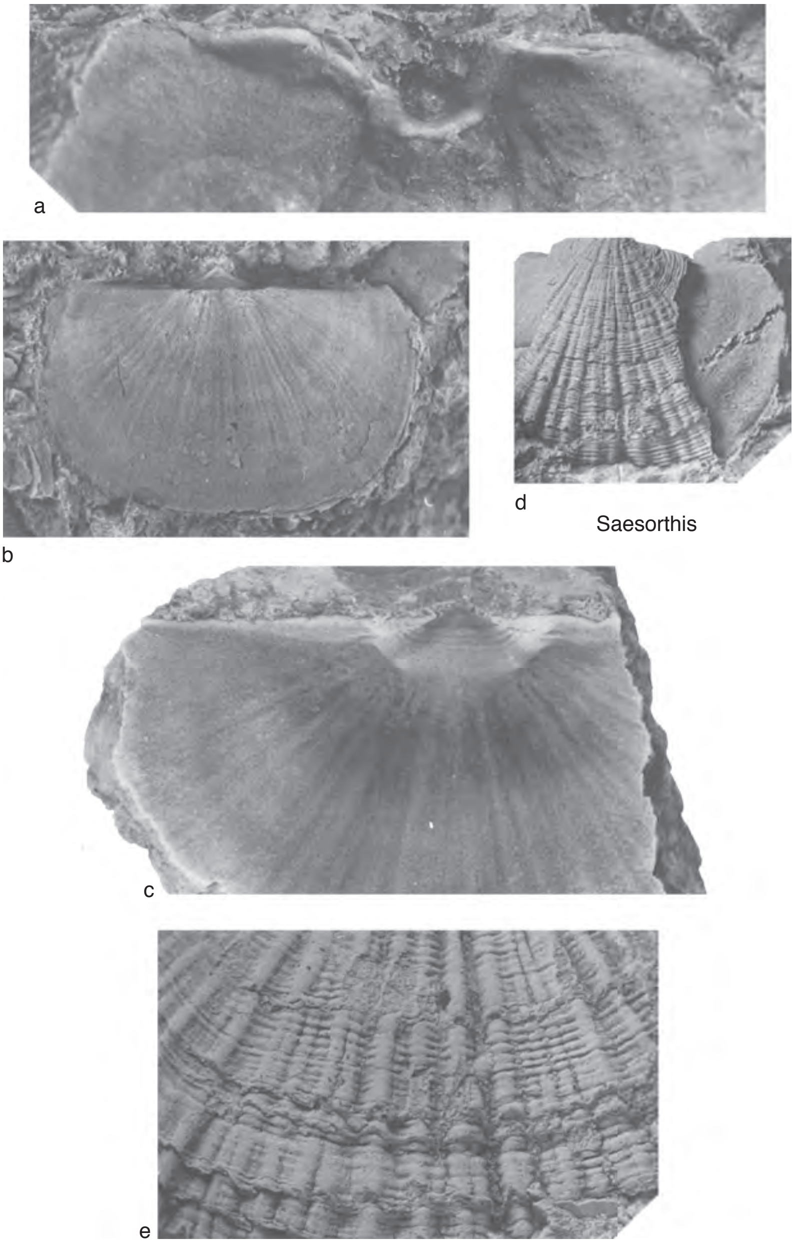


FIG. 1786. Protorthidae (p. 2682).

ORTHIDA

DAVID A. T. HARPER

[University of Copenhagen]

[with family descriptions composed jointly with Alwyn Williams, deceased, formerly of The University of Glasgow]

Order ORTHIDA Schuchert & Cooper, 1932

Suborder ORTHIDINA Schuchert & Cooper, 1932

Superfamily ORTHOIDEA Woodward, 1852

Family ORTHIDAE Woodward, 1852

Celsiorthis PATERSON & BROCK, 2003, p. 223 [**C. bulancis*; OD]. Medium sized, ventribiconvex, rectimarginate, ramicostellate; ventral interarea high, steeply apsacline to catacline; ventral muscle scar bilobed, dental plates large; brachiophores tusklike with thick bases; dental sockets wide and deep. *Lower Ordovician (Arenig):* Australia.——FIG. 1787,*2a–e*. **C. bulancis*, Tabita Formation, northwestern New South Wales; *a*, mold of ventral interior, AM F120716, ×4; *b*, rubber replica of ventral interior, AM F120714, ×7.5; *c*, rubber replica of ventral exterior, AM F120717, ×6; *d–e*, anterior and dorsal views of interior, AM F120710, ×7.5 (Paterson & Brock, 2003).

Leoniorthis EGERQUIST, 2003, p. 35 [**L. robusta*; OD]. Small, ventribiconvex, shallow sulcus, coarsely costellate; ventral muscle scar suboval; cardinal process forming high ridge. *Lower Ordovician (Arenig):* Estonia, western Russia.——FIG. 1787,*1a–c*. **L. robusta*, Volkhov Formation, Putilova, western Russia; *a*, ventral interior, PMU In 144, ×4; *b*, ventral exterior, PMU In 125, ×6; *c*, dorsal interior, PMU In 120, ×5 (Egerquist, 2003).

Suriorthis BENEDETTO, 2003, p. 225 [**S. depressus*; OD]. Small, dorsibiconvex, alate, sharply sulcate, costate or sparsely costellate; ventral muscle scar, short and triangular, *vascula media* strongly divergent; simple, bladelike cardinal process situated on small triangular notothyrial platform, continuous anteriorly with thick median ridge. *Lower Ordovician (Arenig):* Argentina.——FIG. 1788*a–f*. **S. depressus*, Suri Formation, northwestern Argentina; *a–b*, mold of ventral interior and rubber replica, CEGH-UNC 19801, ×5; *c–d*, mold of dorsal interior and rubber replica, CEGH-UNC 15762, ×5; *e*, rubber replica of ventral exterior, CEGH-UNC 15758, ×4; *f*, rubber replica of dorsal interior, CEGH-UNC 15920, ×5 (Benedetto, 2003).

Family ARCHAEORTHIDAE new family

[Archaeorthidae WILLIAMS & HARPER, herein, *nom. nov. pro* Nanorthidae HAVLÍČEK, 1977, p. 59] [type genus, *Archaeorthis* SCHUCHERT & COOPER, 1931, p. 243]

[ALWYN WILLIAMS and DAVID A. T. HARPER]

Generally small, ventribiconvex, costellate, commonly capillate orthoids with very short, curved interarea; teeth usually supported by short, recessive dental plates, suboval ventral muscle scar normally impressed on valve floor without median ridge; adductor track undifferentiated and relatively wide, normally not shorter than flanking diductor scars; pedicle callist well developed in some species; notothyrial platform normally present with variably developed, simple cardinal process; short, bladelike brachiophores variably disposed on either side of median ridge with posteromedian parts of anterior adductor scars inserted between posterior pair; ventral mantle canal system saccate with divergent *vascula media*, dorsal system more rarely impressed, digitate to pinnate. *Lower Ordovician (Tremadoc)–Upper Ordovician (Ashgill)*.

In 1931, SCHUCHERT and COOPER (p. 243) erected the subfamily Orthinae (within the Orthidae WOODWARD) for orthids with short, curved ventral interareas. In due course, the genera *Nanorthis* ULRICH and COOPER

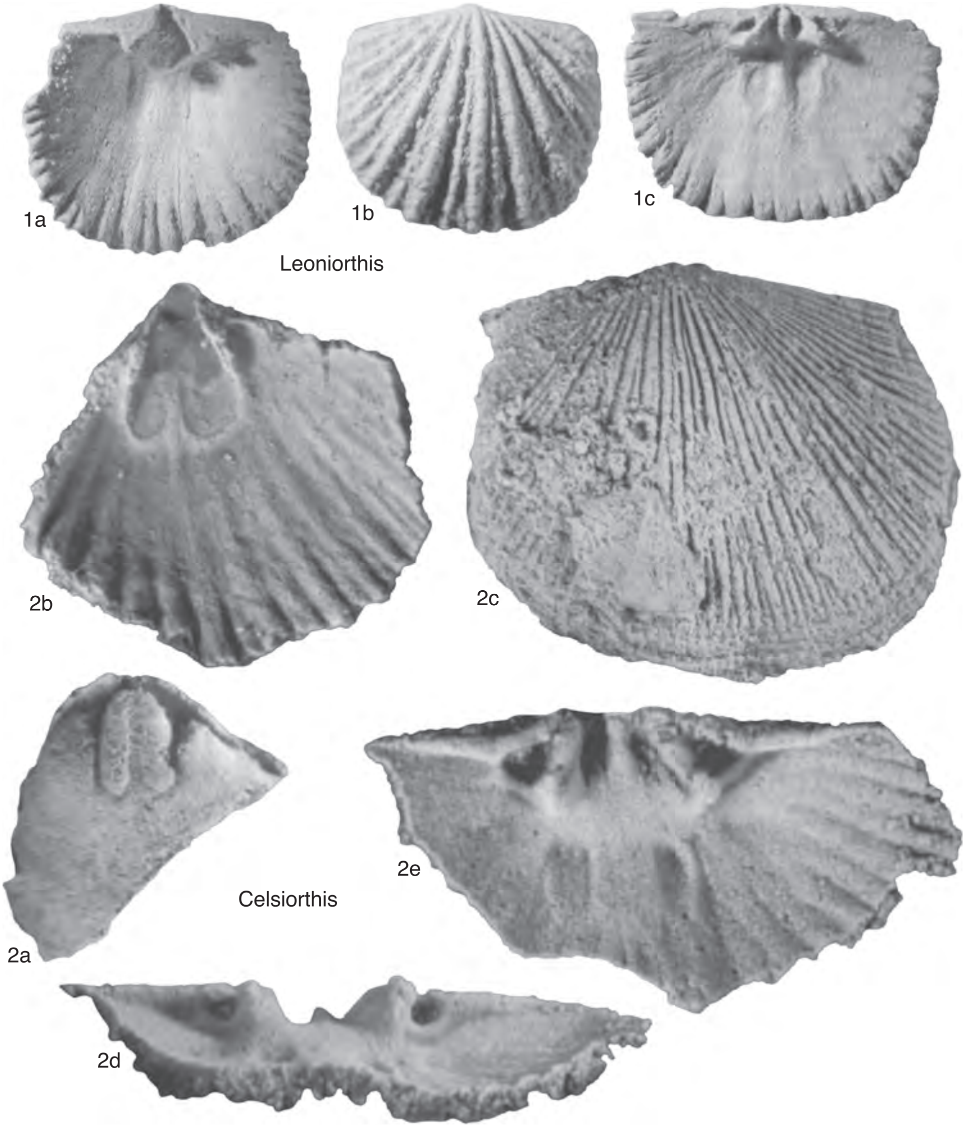
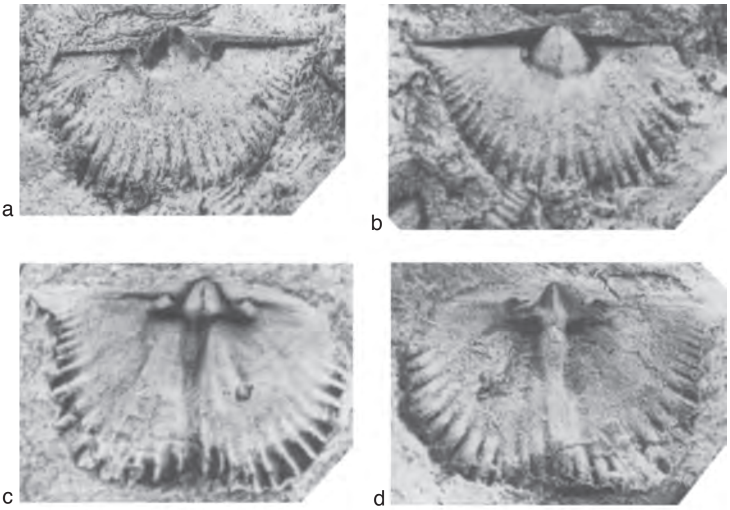


FIG. 1787. Orthidae (p. 2684).



Suriorthis

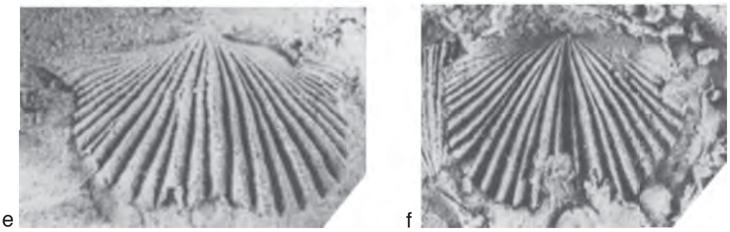


FIG. 1788. Orthidae (p. 2684).

(1936, p. 621) and *Nothorthis* ULRICH and COOPER (1938, p. 106) were assigned to the subfamily, a taxonomic practice continued by COOPER (1956a, p. 293) and adopted by WILLIAMS and WRIGHT (1965, p. 313).

In 1977, HAVLÍČEK proposed an extensive revision of the classification of the Orthida. It included the erection of the Nanorthidae (HAVLÍČEK, 1977, p. 59) for small orthids with a dalmanelloid appearance that are similar to the Ranorthidae but differ in their orthoid "dorsal muscle field, absence of fulcral plates and a fairly narrow notothyrial chamber." The new family embraced *Archaeorthis* SCHUCHERT and COOPER and *Trondorthis* NEUMAN [now reassigned to the Orthidae by WILLIAMS and HARPER (2000, p. 728)]. *Nothorthis* was reallocated to the Ranorthidae on the grounds that, contrary to previous opinion, it has fulcral plates (HAVLÍČEK, 1977a, p. 54).

WILLIAMS and HARPER (2000, p. 742–745) incorporated the Nanorthidae into their classification and assigned to the family eight more genera, including *Nothorthis*. Further phylogenetic analyses that credited *Nothorthis* with fulcral plates, as identified by HAVLÍČEK in illustrations of the type dorsal valve, supported its inclusion in the plectorthoid Ranorthidae (WILLIAMS & HARPER, 2000, p. 777). The assignments of *Nothorthis* to both the Nanorthidae and Ranorthidae were inadvertently published in WILLIAMS and HARPER (2000, p. 778), although the inclusion of *Nothorthis* within the Ranorthidae was expressedly preferred.

This confusing outcome prompted a reinvestigation of the cardinalia of *Nanorthis* and *Nothorthis*, in the hope of determining their microstructures by SEM studies. Topotypes of the type species of both genera were obtained from the U.S. National Museum Collections, through the courtesy of Dr. J. Thomas Dutro. Unfortunately, the specimens, like the types themselves, are silicified. Even so, the valves had been finely enough replaced by silica to reveal features that were incompatible with any of the current taxonomic options. The brachiophores of *Nanorthis* are buttressed by supporting plates and subtend concave fulcral plates with the hinge line (see Fig. 1791,*2g–h*), while the brachiophores of *Nothorthis* are embedded in secondary shell that is built up as walls across the lateral margins of the sockets in simulation of fulcral plates (see Fig. 1789,*2g–h*). More surprisingly, the sharply crested ramicostellae of *Nanorthis* appear to have been indented by aditicules in the style of many plectorthoids (Fig. 1791,*2e–f*); and the more rounded costellae of *Nothorthis* bear silicified remnants of capillae (Fig. 1789,*2e–f*) that characterize the typical orthid.

These newly discovered features significantly change the position of the two genera within the orthide taxonomic hierarchy. The presence of supporting and fulcral plates in the cardinalia and probably of aditicules on the shell surface place *Nanorthis* within the Plectorthidae (SCHUCHERT & LEVENE, 1929) where it compares quite closely with *Desmorthis* ULRICH and COOPER. The assignment leads to the suppression of the Nanorthidae in favor of the earlier-founded Plectorthidae. This suppression deprives a group of dalmanellid-like orthoids of familial status. A new family has therefore been erected for them: the Archaeorthidae (based on their longest established genus), which can also accommodate *Nothorthis* with its simple cardinalia and capillate costellae.

The revision entails amended descriptions of both *Nanorthis* and *Nothorthis* as well as a diagnosis for the Archaeorthidae, which is little changed from that defining the suppressed Nanorthidae. The diagnoses of other archaeorthid genera are the same as those given by WILLIAMS and HARPER (2000, p. 742–745). Accordingly, this revision only lists such genera.

Alocorthis PATERSON & BROCK, 2003, p. 227 [**A. psygmatelos*; OD]. Medium sized, transverse, weakly ventribiconvex, rectimarginate, ramicostellate; ventral muscle scar subtriangular, slightly raised on secondary shell; cardinal process absent; brachiophores short and widely divergent, marked by furrows on dorsal surfaces and fanlike terminations. *Lower Ordovician (Arenig):* Australia.——FIG. 1789,*1a–c*. **A. psygmatelos*, Tabita Formation, northwestern New South Wales; *a–b*, rubber replica and internal mold of ventral valve, AM F120723, ×10; *c*, rubber replica of dorsal interior, AM F120719, ×16 (Paterson & Brock, 2003).

Archaeorthis SCHUCHERT & COOPER, 1931, p. 243 [**Orthis electra* BILLINGS, 1865–1865, p. 79; OD]. Described in WILLIAMS and HARPER (2000, p. 743).

Cyrtonotella SCHUCHERT & COOPER, 1931, p. 243 [**Orthis semicircularis* VON EICHWALD, 1829, p. 276; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Diplonorthis MITCHELL, 1977, p. 30 [**D. portlocki*; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Nicoloidea ZENG, 1987, p. 215 [**N. mina*; OD]. Described in WILLIAMS and HARPER (2000, p. 744).

Nothorthis ULRICH & COOPER, 1938, p. 106 [**N. delicatula*; OD]. Subquadrate with obtuse cardinal extremities, rounded, capillate ramicostellae; teeth deltidiodont (crural fossettes not recorded), suboval ventral muscle scar impressed on callosity; short, divergent brachiophores with secondary shell deposits forming lateral boundaries to sockets. *Lower Ordovician (Tremadoc–Llanvirn):* eastern North America, Baltic, Siberia, Scotland, Bohemia, China, Ireland, Central Asia (Altai Mountains).——FIG. 1789,*2a–d*. **N. delicatula*, Tremadoc, eastern North America; *a*, ventral exterior, ×3; *b*, dorsal exterior, ×3; *c*, ventral interior, ×4; *d*, dorsal interior, ×4 (Ulrich & Cooper, 1938).——FIG. 1789,*2e–h*. **N. delicatula*, Tremadoc, eastern North America, topotypes; *e–f*, ventral exterior and detail showing silicified capillae on costellae, ×7, ×95; *g–h*, ventral and tilted views of cardinalia, ×33 (new).

Pleurorthis COOPER, 1956a, p. 329 [**P. fascicostellata*; OD] [=*Ambardella* ANDREEVA, 1987, p. 37 (type, *A. anabarensis,* OD)]. Described in WILLIAMS and HARPER (2000, p. 744).

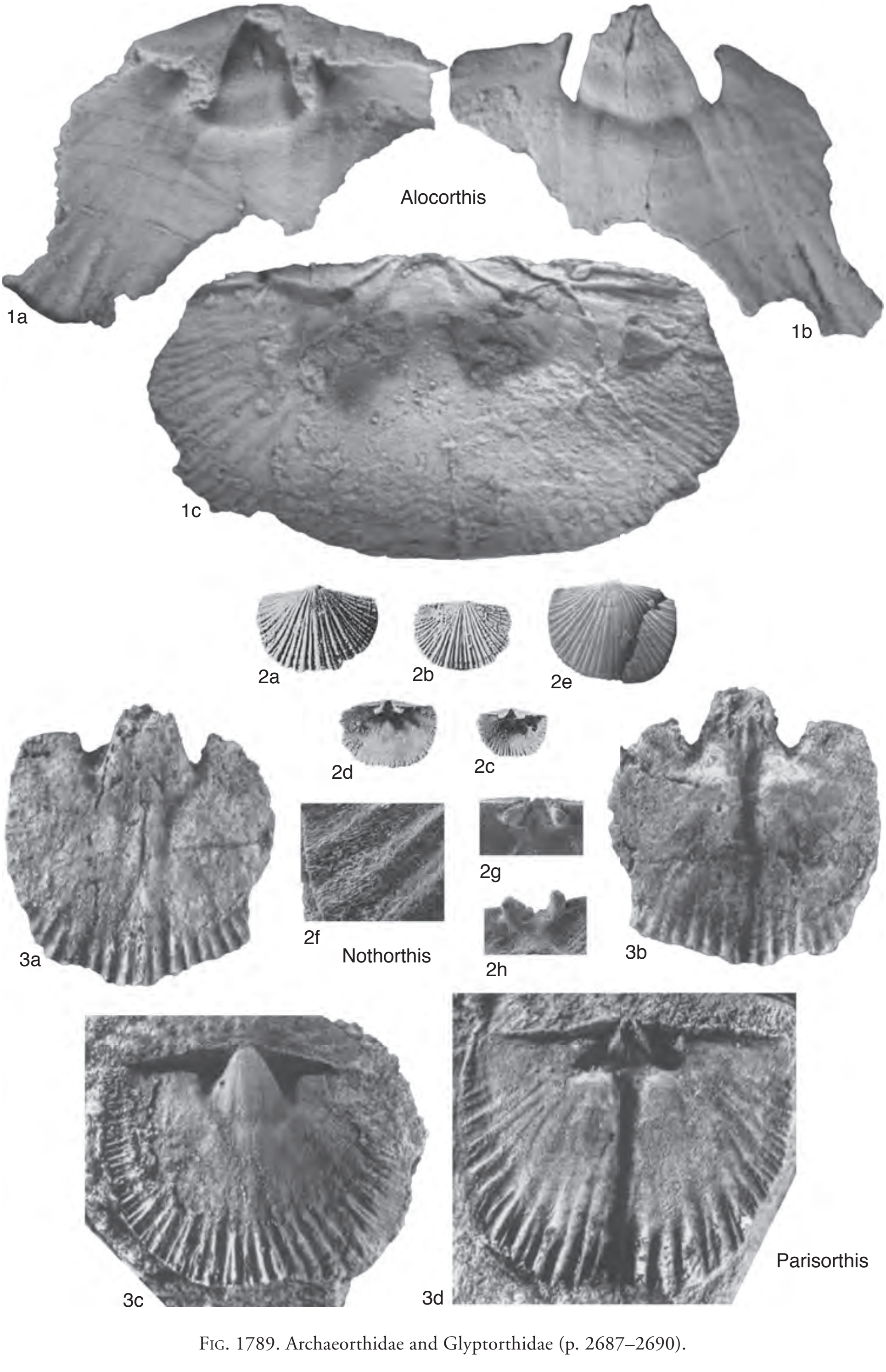


FIG. 1789. Archaeorthidae and Glyptorthidae (p. 2687–2690).

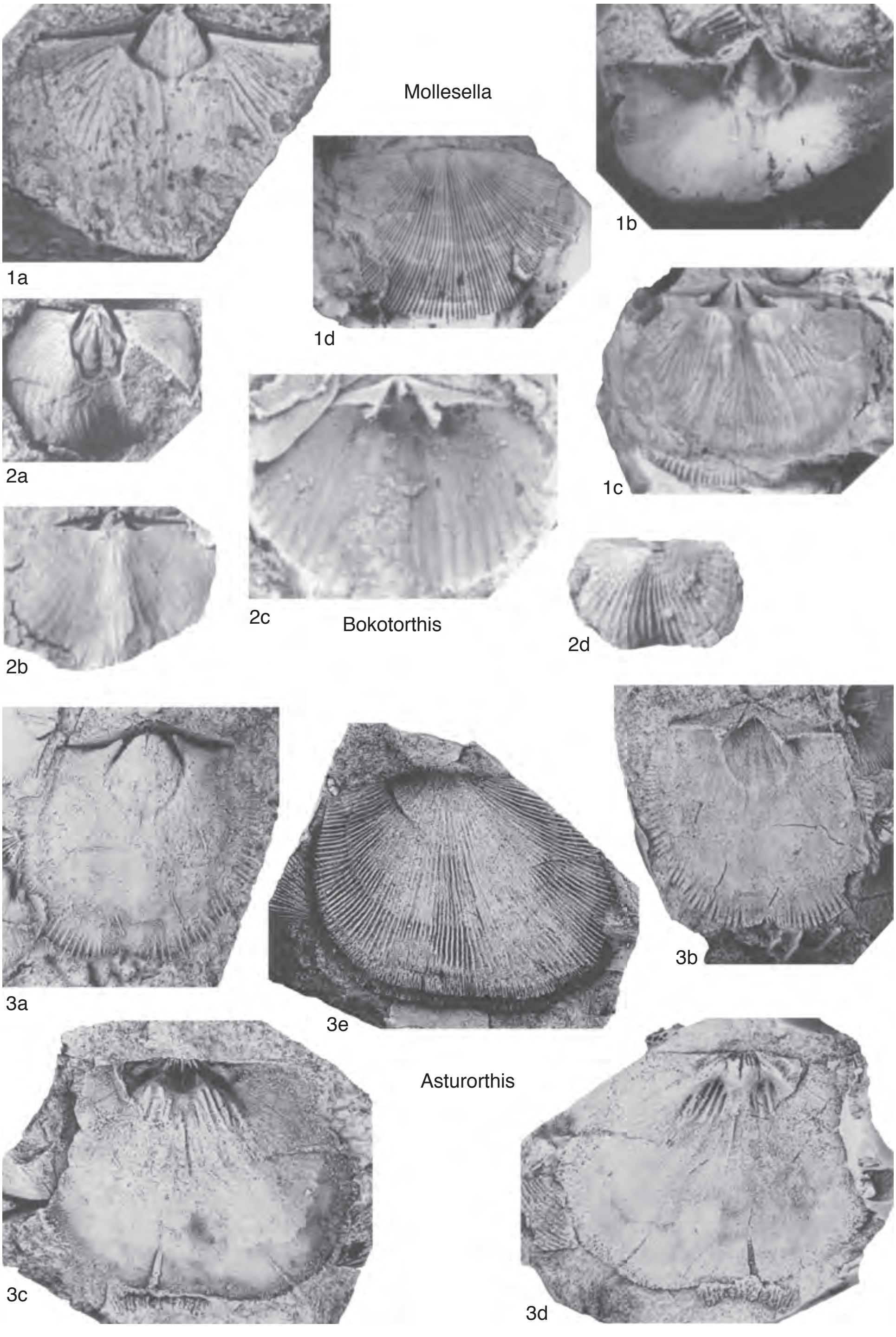


FIG. 1790. Hesperonomiidae, Hesperorthidae, and Plaesiomyiidae (p. 2690).

Riograndella Kobayashi, 1937, p. 422 [**R. subcircus*; OD]. Described in Williams and Harper (2000, p. 745).

Shoshonorthis Jaanusson & Bassett, 1993, p. 51 [**Orthis michaelis* Clark, 1935, p. 242; OD]. Described in Williams and Harper (2000, p. 745).

Xinanorthis Xu, Rong, & Liu, 1974, p. 145 [**X. striata*; OD]. Described in Williams and Harper (2000, p. 745).

Family GLYPTORTHIDAE
Schuchert & Cooper, 1931

Parisorthis Zhan & Jin, 2005, p. 16 [**P. dischidanteris*; OD]. Medium sized, ventribiconvex, sulcate; shell surface multicostellate, imbricate, tuberculate; dental plates parallel, short; cardinal process with thick shaft and bilobed myophore on elevated notothyrial platform. *Middle Ordovician (Llanvirn):* China.——Fig. 1789,*3a–d*. **P. dischidanteris*, Dashaba Formation, Sichuan Province, southern China; *a–b,* ventral and dorsal interiors of conjoined valves, NIGP 134340, ×3; *c*, internal mold of ventral valve, NIGP 134345, ×2.5; *d*, internal mold of dorsal valve, NIGP 134347, ×4 (Zhan & Jin, 2005).

Family HESPERONOMIIDAE
Ulrich & Cooper, 1936

Mollesella Benedetto, 2003, p. 231 [**M. planiventralis*; OD]. Large, convexiplane, semielliptical, sulcate, finely multicostellate; ventral muscle scar triangular; notothyrial platform raised with thickened, usually bulbous, cardinal process. *Lower Ordovician (Arenig):* Argentina.——Fig. 1790,*1a–d*. **M. planiventralis*, Molles Formation, northwestern Argentina; *a,* internal mold of ventral valve, CEGH-UNC 19649, ×1.5; *b,* rubber replica of ventral interior, CEGH-UNC 19673, ×1.5; *c*, internal mold of dorsal valve, CEGH-UNC 15895c, ×5; *d,* rubber replica of dorsal exterior, CEGH-UNC 19654, ×1.2 (Benedetto, 2003).

Family HESPERORTHIDAE
Schuchert & Cooper, 1931

Asturorthis Villas & Cocks, 1996, p. 573 [**A. sarreoensis*; OD]. Large, dorsibiconvex, subquadrate, ramicostellate; delthyrium with apical plate; cardinal process bilobed with crenulated posterior surfaces. *lower Silurian (Llandovery):* Spain.——Fig. 1790,*3a–e*. **A. sarreoensis*, El Castro Formation, northern Spain; *a–b*, internal mold and rubber replica of ventral valve, DPO 29464, ×1.5; *c–e*, internal mold and rubber replicas of dorsal valve, interior and exterior, DPO 29467, ×1.5 (Villas & Cocks, 1996).

Family PLAESIOMYIIDAE
Schuchert, 1913

Bokotorthis Popov, Nikitin, & Cocks, 2000, p. 848 [**Schizophorella kasachstanica* Rukavishnikova, 1956, p. 118; OD]. Medium sized, biconvex, uniplicate, coarsely costate. *Upper Ordovician (Caradoc):* Kazakhstan.——Fig. 1790,*2a–d*. **B. kasachstanica* (Rukavishnikova), Dulankara Formation, Chu-Ili Range; *a*, internal mold of ventral valve, CNIGR 38/12375, ×2; *b*, internal mold of dorsal valve, CNIGR 39/12375, ×3; *c*, rubber replica of dorsal interior, CNIGR 34/12375, ×4; *d*, rubber replica of ventral exterior, CNIGR 36/12375, ×2 (Popov, Nikitin, & Cocks, 2000).

Superfamily
PLECTORTHOIDEA
Schuchert & LeVene, 1929
Family PLECTORTHIDAE
Schuchert & LeVene, 1929

[Alwyn Williams and David A. T. Harper]

Nanorthis Ulrich & Cooper, 1936, p. 621 [**Orthis hamburgensis* Walcott, 1884, p. 73; OD] [=*Evenkinorthis* Yadrenkina, 1977, p. 27 (type, *E. dualis,* OD)]. Subcircular with obtuse cardinal extremities, ramicostellae with sharp crests, apparently indented by aditicules; short, bladelike brachiophores with convergent supporting plates and fulcral plates, notothyrial platform rudimentary, lacking cardinal process. [*Evenkinorthis* has been erected for inadequately described and illustrated specimens from the Lower Ordovician of Siberia. With regard to such features as are unambiguously determinable, the genus is indistinguishable from *Nanorthis*. The reasons for amending the diagnosis of *Nanorthis* and transferring the genus from the Orthoidea (see Williams & Harper, 2000, p. 742) to the Plectorthoidea are given herein, p. 2684–2687.] *Lower Ordovician (Tremadoc):* cosmopolitan.——Fig. 1791,*2a–h*. **N. hamburgensis* (Walcott), western USA; *a*, dorsal exterior, ×4.5; *b*, ventral exterior, ×4.5; *c,* dorsal interior, ×6; *d*, ventral interior, ×6 (Ulrich & Cooper, 1938); *e–f,* topotypes, ventral exterior with detail showing siliceous nodules on costellae, interpreted as aditicules, ×12, ×35; *g–h*, topotypes, ventral and tilted views of dorsal cardinalia, ×27, ×24 (new).

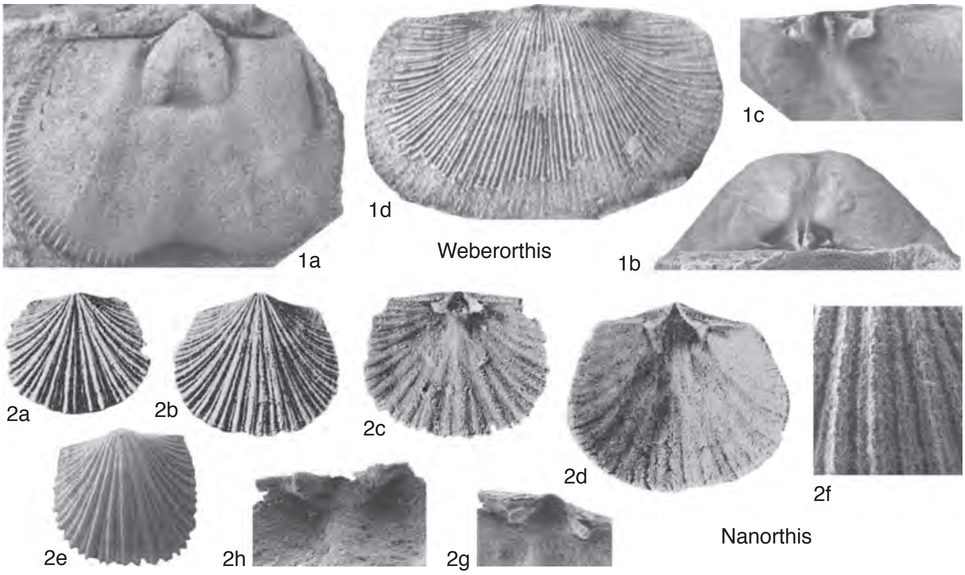


FIG. 1791. Plectorthidae (p. 2690–2691).

Weberorthis POPOV & COCKS, 2006, p. 277 [**Mimella brevis* RUKAVISHNIKOVA, 1956, p. 116; OD]. Medium sized, dorsibiconvex, subquadrate, uniplicate, finely multicostellate; short dental plates continuous anteriorly with muscle-bounding ridges completely confining ventral muscle field; high, narrow notothyrial platform with expanded, bulbous, cardinal process; ventrolaterally directed brachiophores with bases convergent onto median ridge. *Upper Ordovician (Caradoc):* Kazakhstan.——FIG. 1791,*1a–d*. **W. brevis* (RUKAVISHNIKOVA), Dulankara Formation, Chu-Ili Range; *a,* internal mold of ventral valve, BMNH BC 57749, ×2.5; *b–c*, posterior view of internal mold of dorsal valve and rubber replica of cardinalia, BMNH BC 57751, ×2, ×3; *d*, rubber replica of dorsal exterior, BMNM BC 57613, ×3 (Popov & Cocks, 2006).

Family EOORTHIDAE Walcott, 1908

Roanella BROCK & TALENT, 1999, p. 111 [**Orthis (Plectorthis) platystrophoides* CHAPMAN, 1911, p. 311; OD]. Small, semicircular to subquadrate, ventribiconvex, unequally costellate; deltidial plates fused to form symphytium; anterior margin of ventral muscle scar marked by raised median boss. [Although this genus has strong similarities with a number of billingselloids, its features, particularly those of the dorsal valve, are more typically orthoid; it is transferred pending data on shell structure.] *Upper Cambrian:* Australia.——FIG. 1792*a–i*. **R. platystrophoides* (CHAPMAN), Garvey Gully Formation, East Central Victoria; *a–e,* dorsal, ventral, anterior, lateral, and posterior views of conjoined valves, NMV P148697, ×3.5; *f–g*, external and internal views of ventral valve, NMV P148703, ×3.5; *h–i*, external and internal views of dorsal valve, NMV P148705, ×3.5 (Brock & Talent, 1999).

Family GIRALDIELLIDAE
Williams & Harper, 2000

Kvania HAVLÍČEK, 1994, p. 298 [**Nothorthis kvanica* MERGL, 1984, p. 17; OD]. Small, ventribiconvex, subcircular, sulcate, fascicostellate; ventral muscle scar subpentagonal; notothyrial platform small, lacking cardinal process. *Lower Ordovician (Tremadoc):* Bohemia, Germany, Argentina.——FIG. 1793,*1a–c*. **K. kvanica* (MERGL), Milina Formation, Bohemia; *a*, internal mold of ventral valve, MM 076, ×14.5; *b,* internal mold of dorsal valve, MM 075, ×6.6; *c*, internal mold of dorsal valve, MM 074, ×8.8 (Mergl, 1984).

Family PLATYSTROPHIIDAE Schuchert & LeVene, 1929

Gnamptorhynchos JIN, 1989, p. 75 [**P. regularis globata* TWENHOFEL, 1928, p. 177; OD]. Large, dorsibiconvex, globose, uniplicate, strong angular to subangular costae; well-developed dental plates; bladelike cardinal process, uni- or trilobate; elevated notothyrial platform supported by one or two ridges. [JIN & ZHAN (2000) transferred JIN's aberrant genus from the rhynchonellids to the platystrophiids on the basis of its orthide ventral muscle field and dental plates.] *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* North America.——FIG. 1793,*2a–e*. **G. globatum* (TWENHOFEL), Ellis Bay Formation, Ashgill, Anticosti Island, Canada; dorsal, ventral, lateral, posterior, and anterior views of conjoined valves, YPM10420, ×2 (Jin & Zhan, 2000).

Siljanostrophia ZUYKOV & EGERQUIST, 2005, p. 2 [**S. jaanussoni*; OD]. Medium sized, biconvex, uniplicate, costate with shell surface additionally ornamented by thin hollow spines; ventral interior with pseudospondylium; cardinal process simple; elevated notothyrial platform supported by two ridges. *Upper Ordovician (Ashgill):* Sweden.——FIG. 1793,*3a–f*. **S. jaanussoni*, Boda Limestone, Dalarne; *a–d*, posterior, dorsal, ventral, and lateral views of conjoined valves, RM Br135287, ×3; *e*, ventral interior, RM Br 99630, ×4.5; *f*, dorsal interior, CNIGR 2/13121, ×3 (Zuykov & Egerquist, 2005).

Suborder DALMANELLIDINA Moore, 1952

Superfamily DALMANELLOIDEA Schuchert, 1913

Family DALMANELLIDAE Schuchert, 1913

Subfamily DALMANELLINAE Schuchert, 1913

Christiferina COOPER, 1956a, p. 961 [**C. cristata*; OD]. Small, ventribiconvex, subcircular, multicostellate; cordate ventral muscle scar; cardinal process with grooved shaft and expanded myophore capped by sharp crest; high median ridge bisecting dorsal muscle scar. *Middle Ordovician (Caradoc)*: Scotland, USA.——FIG. 1794,*1a–e*. **C. cristata,* Virginia; *a–c*, lateral, anterior, and dorsal views of conjoined valves, Edinburg Formation, Strasburg, USNM 117353, ×2; *d,* ventral interior, Chatham Hill Formation, Sharon Springs, USNM 111794c, ×2; *e,* dorsal interior, Chatham Hill Formation, Sharon Springs, USNM 111794d, ×2 (Cooper, 1956a).

?Minororthis IVANOV in IVANOV & MIAGKOVA, 1950, p. 23 [**M. nalivkini;* OD]. Small, subquadrate with obtuse cardinal extremities, ventribiconvex, multicostellate; dorsal valve sulcate, ventral valve subcarinate; cardinal process flanked by high, divergent brachiophores. [The figured material is poorly preserved, lacks institution accession numbers, and is not well illustrated. The overall features suggest placement within the Dalmanellidae, possibly even the Dalmanellinae, but in the absence of critical information such as the nature of the shell substance, this assignment is tentative.] *Middle Ordovician (Caradoc):* Russia (central Ural Mountains).——FIG. 1794,*2a–d*. **M. nalivkini*; *a,* dorsal exterior, ×2; *b,* ventral valve, ×2; *c,* dorsal interior, ×2; *d,* internal mold of ventral valve, ×2 (Ivanov & Miagkova, 1955).

Subfamily ISORTHINAE Schuchert & Cooper, 1931

Pelecymya MAWSON & TALENT, 1999, p. 151 [**P. caperata*; OD]. Medium sized, biconvex to planoconvex, slightly sulcate, multicostellate; ventral muscle scar cordate to subpentagonal; dorsal adductor scars separated by strip of thickened shell bearing low, thin median septum. *Lower Devonian (Lochovian):* Australia.——FIG. 1794,*3a–d*. **P. caperata*, Windellama Limestone, southeastern Australia; *a–b*, ventral exterior and interior, AM F105137, ×5; *c–d*, dorsal exterior and interior, AM F105133, ×5 (Mawson & Talent, 1999).

Family HARKNESSELLIDAE Bancroft, 1928

Haymina BOGOYAVLENSKAYA, 1991, p. 84 [**H. carinata*; OD]. Medium sized, subrectangular, dorsibiconvex, with ventral carina and narrow dorsal sulcus; ventral muscle field cordate, teeth small; notothyrium platform absent; cardinal process simple and bladelike; brachiophores short. *Middle Ordovician (Llanvirn):* Russia (Northern Urals).——FIG. 1795,*1a–c*. **H. carinata*, Khaiminskaya Formation; *a*, internal mold of ventral valve, 138/2087, ×1; *b*, internal mold of dorsal valve, 140/2087, ×1; *c*, detail of ornament, 136/2087, ×6 (Bogoyavlenskaya, 1991).

Family HETERORTHIDAE Schuchert & Cooper, 1931

Fehamaya MERGL, 1983, p. 340 [**F. circula*; OD]. Large, markedly ventribiconvex, rectimarginate

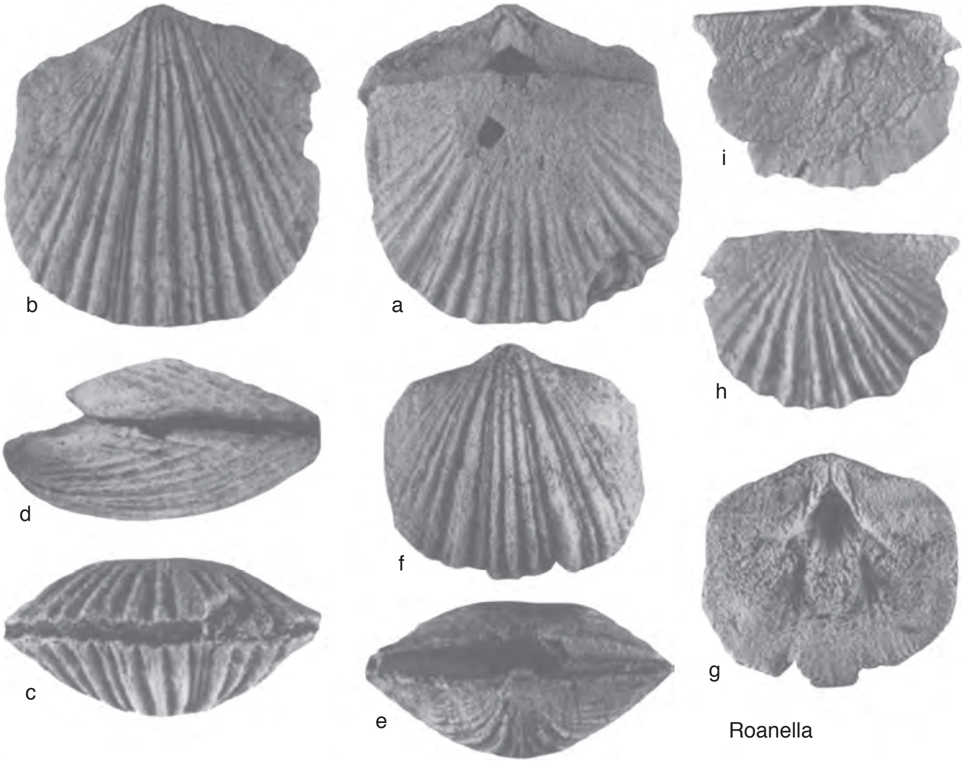


FIG. 1792. Eoorthidae (p. 2691).

valves, finely multicostellate; ventral muscle scar large and flabellate with diductors enclosing adductor scars; cardinal process large, posterior part of myophore bilobate; brachiophores short and divergent. *Upper Ordovician (Ashgill):* North Africa.——FIG. 1795,*2a–c*. **F. circula*, Hirnantian, upper Ashgill rocks, Foum el Fehamaya, Morocco; *a–b,* internal and external molds of ventral valve, VH 4015a,b, ×1.7; *c,* internal mold of dorsal valve, VH 4015d, ×1.3 (Mergl, 1983).

Family PAURORTHIDAE Öpik, 1933

Tenuiseptorthis MÉLOU in MÉLOU, OULEBSIR, & PARIS, 1999, p. 830 [**T. niliensis*; OD]. Small, planoconvex, rectimarginate, fascicostellate; widely divergent brachiophores, almost parallel to hinge line; ventral muscle scar short and wide; notothyrial platform reduced or absent, with small cardinal process and thin median septum. *Middle Ordovician (Llanvirn):* Algeria.——FIG. 1795,*3a–e*. **T. niliensis*, Argiles dOued Saret, Borj Nili; *a–b*, internal mold of ventral valve and rubber replica, LPB 17301, ×10; *c–d*, internal mold of dorsal valve and rubber replica, LPB 17302, ×10; *e*, rubber replica of ventral exterior, LPB 17306, ×2 (Mélou, Oulebsir, & Paris, 1999).

Superfamily ENTELETOIDEA Waagen, 1884

Family DRABOVIIDAE Havlíček, 1950

Draborthis MAREK & HAVLÍČEK, 1967, p. 280 [**D. caelebs*; OD]. Small, planoconvex, sulcate, multicostellate; ventral muscle scar large, oval; dorsal interior

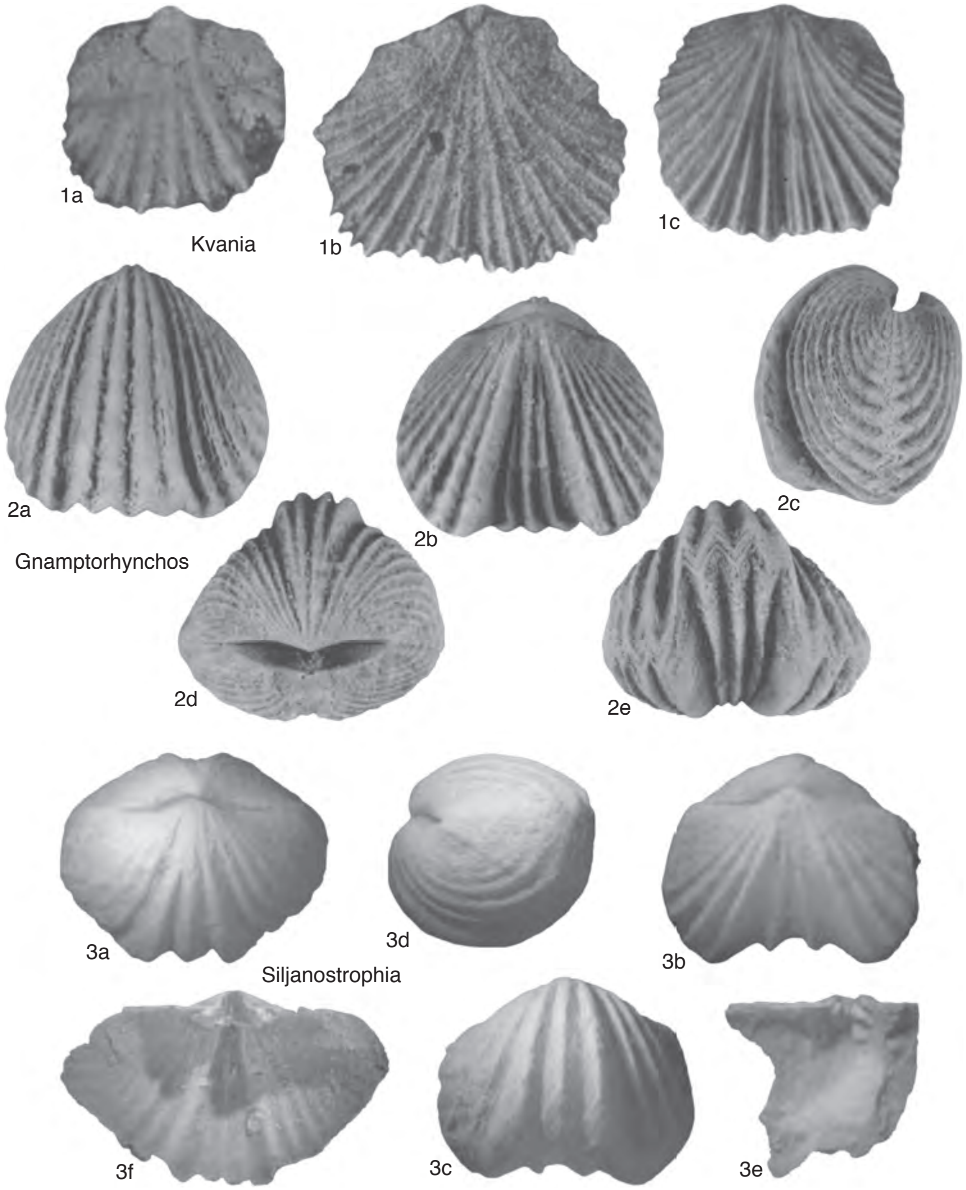


FIG. 1793. Giraldiellidae and Platystrophiidae (p. 2691–2692).

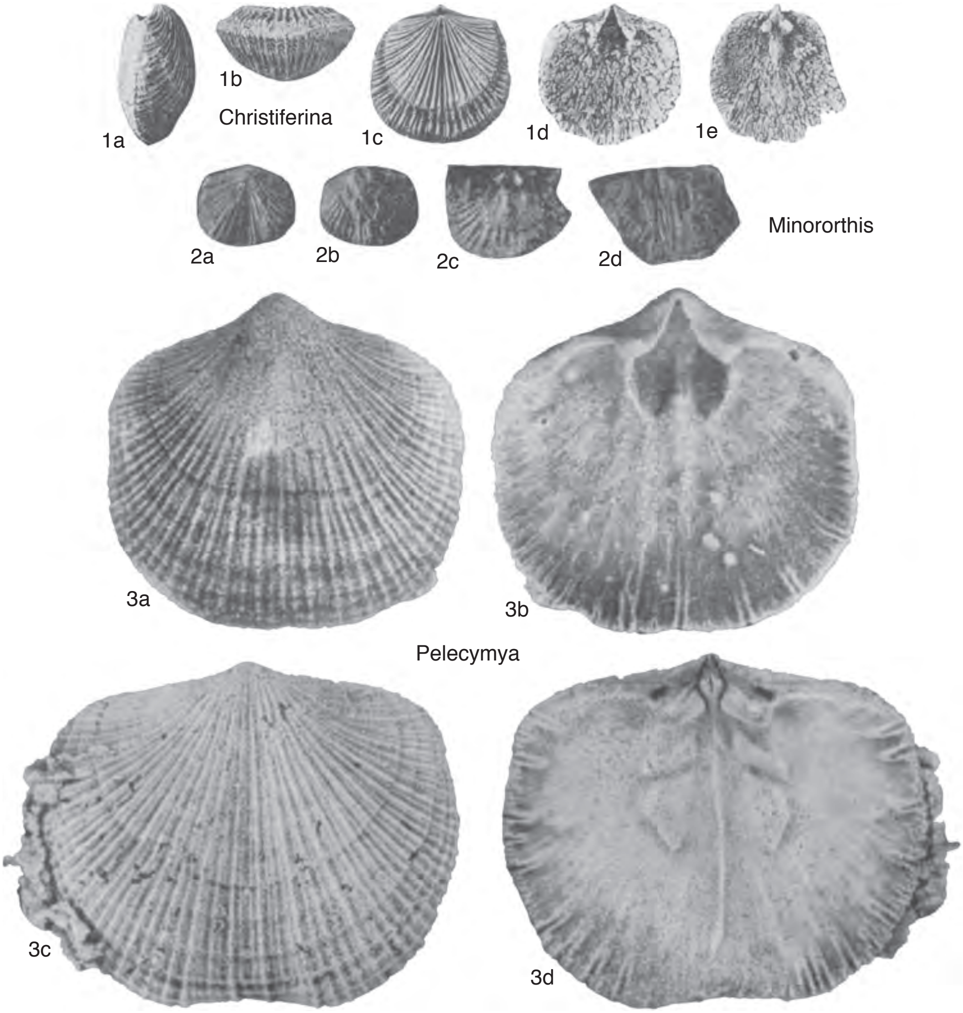


FIG. 1794. Dalmanellidae (p. 2692).

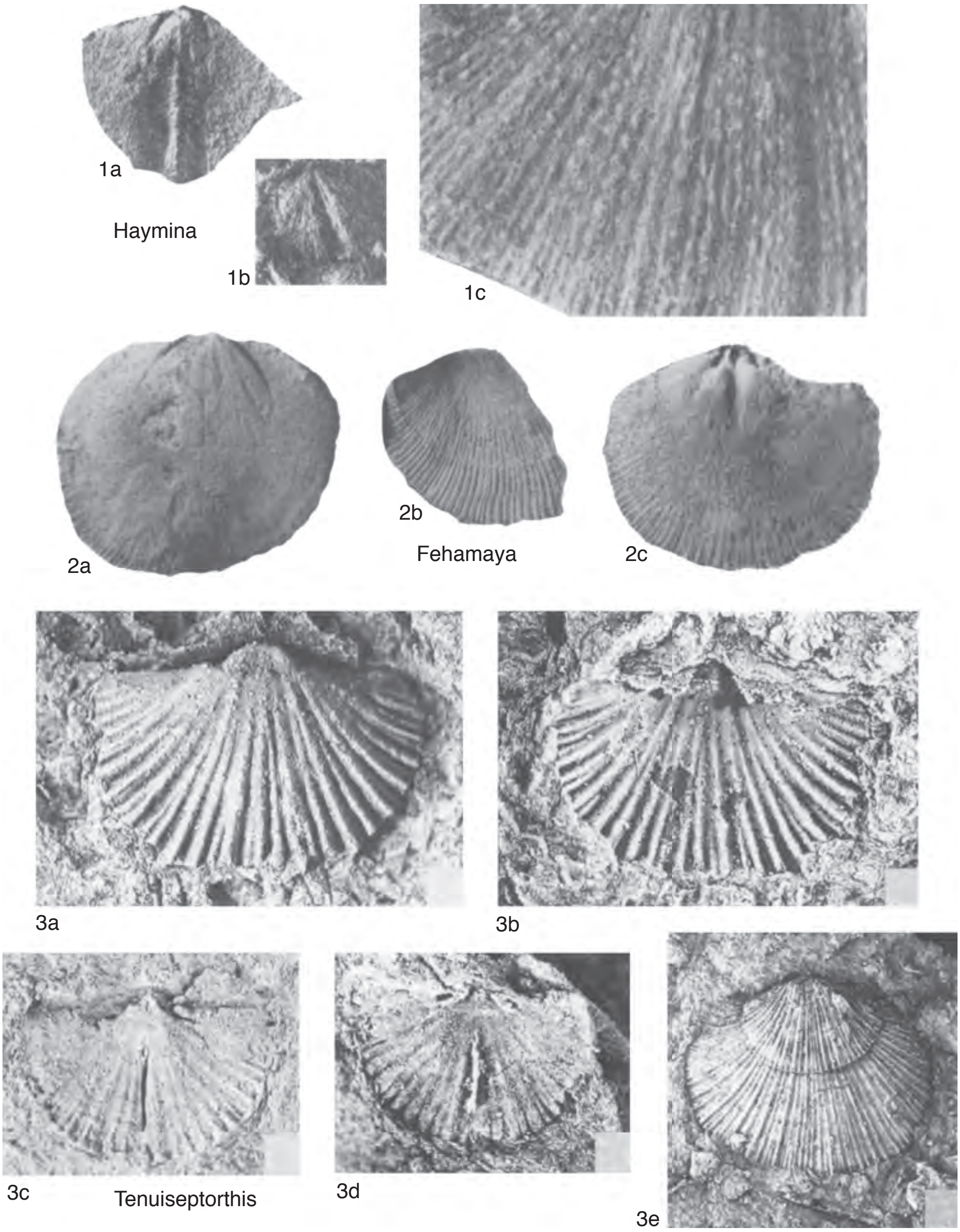


FIG. 1795. Harknessellidae, Heterorthidae, and Paurorthidae (p. 2692–2693).

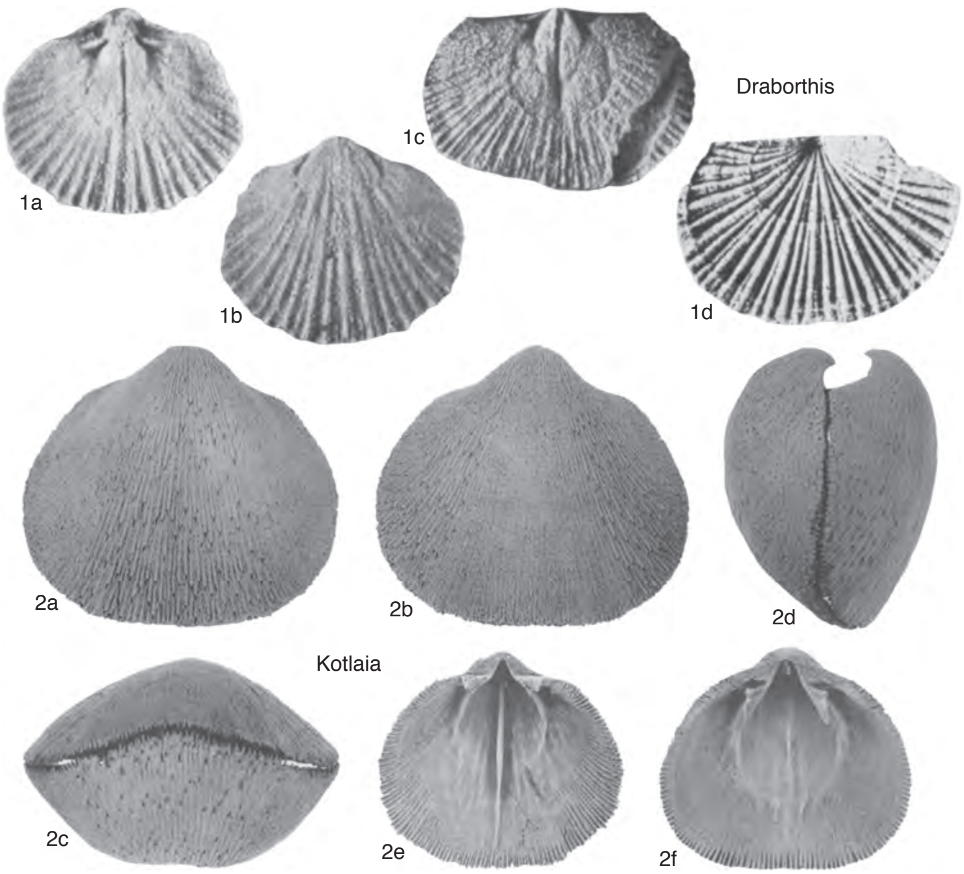


FIG. 1796. Draboviidae and Schizophoridae (p. 2693–2697).

with low septum and divergent brachiophore bases. *Upper Ordovician:* widespread.——FIG. 1796,*1a–d*. **D. caelebs,* Kosov Formation, Ashgill, Bohemia; *a–b*, dorsal and ventral views of conjoined internal molds, VH 1470, ×5; *c*, internal mold of dorsal valve, VH 1464a, ×5; *d*, external mold of dorsal valve, VH 531a, ×5 (Havlíček, 1977).

Family LINOPORELLIDAE
Schuchert & Cooper, 1931

Lipanorthis BENEDETTO in BENEDETTO & CARRASCO, 2002, p. 656 [**L. andinus*; OD]. Medium sized, ventribiconvex, sulcate; ventral interarea curved, steeply apsacline to catacline; ventral muscle scar bilobed to cordate; cardinalia short with ridgelike cardinal process on low septalium. [Identification of endopunctae indicates this is a dalmanellidine (HARPER & others, 2004), and the genus is accordingly placed here rather than within the plectorthoids. The mold material illustrated here demonstrates clearly the presence of endopunctae, not immediately identifiable on the type species.] *Lower Ordovician:* Argentina.——FIG. 1797*a–d*. *L. santalaurae* BENEDETTO, Coquena Formation, Tremadoc; *a,* internal mold of ventral valve, CORD-PZ 30401-1, ×2.5; *b–c*, internal mold and rubber replica of dorsal interior, CORD-PZ 30434-1, ×5; *d*, rubber replica of dorsal exterior, CORD-PZ 30435.b-4, ×2.5 (Harper & others, 2004).

Family SCHIZOPHORIIDAE
Schuchert & LeVene, 1929

Kotlaia GRANT, 1993, p. 4 [**K. capillosa*; OD]. Medium sized, subcircular, weakly sulcate, costellae fine and tubular; ventral interior with long, low median septum and short, divergent dental plates; brachiophores long and laterally compressed. *middle Permian–Upper Permian:* Greece, Pakistan.——FIG. 1796,*2a–f*. **K. capillosa*, Chhidru Formation, Upper Permian, Pakistan; *a–d*, ventral, dorsal, anterior, and lateral views of conjoined valves, USNM 402084, ×2; *e–f*, ventral and dorsal interiors, USNM 402085, ×2 (Grant, 1993).

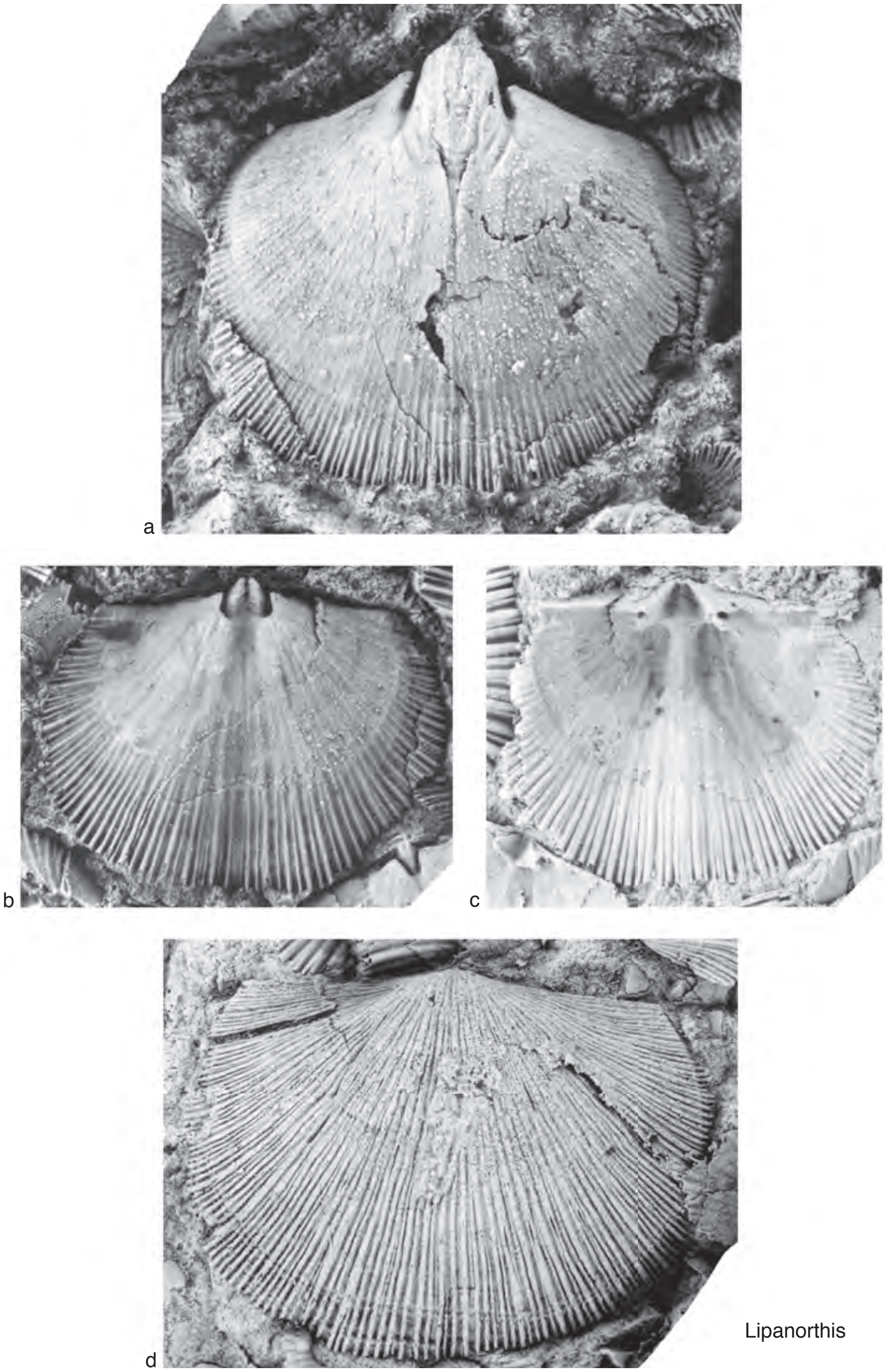


FIG. 1797. Linoporellidae (p. 2697).

PENTAMERIDA

Sandra J. Carlson

[University of California, Davis]

Order PENTAMERIDA Schuchert & Cooper, 1931

Suborder SYNTROPHIIDINA Ulrich & Cooper, 1936

Superfamily PORAMBONITOIDEA Davidson, 1853

Family HUENELLIDAE Schuchert & Cooper, 1931

Subfamily MESONOMIINAE Ulrich & Cooper, 1936

Radkeina Laurie, 1997a, p. 185 [**R. taylori*; OD]. Small, strongly biconvex, fascicostellate shells; dental plates converging to form sessile spondylium supported anteriorly only by fairly high, wide median ridge, accessory septa present rarely; short, shallow recumbent socket plates; fulcral plates well developed, thick. Similar to *Glyptotrophia* with wide hinge line and distinct cardinal process, but biconvexity stronger, and dorsal adductor muscle field elevated on callosities. *Upper Cambrian (?Trempealeauan):* Australia (Queensland).——Fig. 1798,*1a–h*. **R. taylori*, Chatsworth Limestone, Georgina Basin; *a,* ventral valve exterior, ×4; *b,* ventral valve, lateral view, ×4; *c,* dorsal valve exterior, ×4; *d,* dorsal valve, posterior view, ×4; *e,* ventral valve interior, ×4; *f,* ventral valve interior, ×4; *g,* dorsal valve interior, ×4; *h,* dorsal valve interior, ×4 (Laurie, 1997a).

Subfamily RECTOTROPHIINAE Bates, 1968

Trigonostrophia Benedetto, 2003, p. 237 [**T. reversa*; OD]. Small to medium-sized triangular shells; exterior smooth with very fine radial striations; commissure gently lobate to parasulcate, with shallow sulcus in each valve, anterior margin of ventral valve strongly deflected dorsally; hinge line narrow with low, narrow interareas; teeth thin, short; parallel dental plates extending anteriorly and converging to form long, narrow pseudospondylium, extending to 40 percent of valve length, slightly raised above valve floor, supported anteriorly in some specimens by very low, short median septum; notothyrial platform short, slightly elevated anteriorly; cardinal process absent; dorsal mantle canal system digitate, with two pairs of straight trunks and several shorter, closely spaced minor trunks. Similar to *Rectotrophia*, but cardinal process absent, pseudospondylium longer and narrower. [Benedetto (2003) makes a case for separating *Rectotrophia* and *Trigonostrophia* from the huenellids and placing them into a revised family Rectotrophiidae Bates, 1968. The smooth exterior and narrower hinge line are the main characters upon which this reassignment is based; both of these characters can and do vary considerably among confamilial genera, even congeneric species. The presence of a pseudospondylium in *Rectotrophia*, *Trigonostrophia,* and the huenellids is considered here to represent a feature shared due to common ancestry. If Rectotrophiidae is recognized as a distinct family or as a distinct subfamily Rectotrophiinae within Huenellidae, it most likely shared more recent common ancestry with Huenellidae than any other family of syntrophiidines.] *Lower Ordovician (Arenig):* northwestern Argentina.——Fig. 1798,*2a–f*. **T. reversa*, Suri Formation, Famatina Range; *a,* ventral valve exterior, ×2.5; *b,* dorsal valve exterior, ×2; *c,* ventral valve interior mold, ×2.5; *d,* cast of ventral valve interior mold, ×2; *e,* posterior oblique view of dorsal valve interior mold, ×2; *f,* dorsal valve interior mold, ×2.5 (Benedetto, 2003).

Family CLARKELLIDAE Schuchert & Cooper, 1931

Parallelostrophia Benedetto, Cech, & Esbry, 2003, p. 526 [**P. septata*; OD]. Medium-sized smooth shells; commissure apparently rectimarginate, lacking fold and sulcus; wide hinge line with well-developed ventral interareas; spondylium simplex supported by long, high median septum and two strong accessory septa; long, initially convergent, then subparallel socket plates, accessory septa may be present; adductor muscle field not discernible. Similar to *Calliglypha*, but lacking ornament, with rectimarginate commissure, strong ventral accessory septa and longer socket plates; similar to *Yangtzeella*, but rectimarginate and lacking septalium. *Lower Ordovician (lower Arenig):* Argentina (Precordilleran basin).——Fig. 1799,*1a–e*. **P. septata*, San Juan Formation, Cerro San Roque section; *a,* ventral valve exterior, ×2; *b,* ventral valve interior, ×2; *c,* ventral valve interior, anterior oblique view, ×2; *d,* dorsal valve interior, ×2; *e,* dorsal valve interior, ×2 (Benedetto, Cech, & Esbry, 2003).

Punastrophia Benedetto, 2001, p. 141 [**P. multiseptata*; OD]. Small- to medium-sized, smooth, subelliptical shells; hinge line narrow, with narrow interareas in each valve; spatulate spondylium simplex supported by a robust median septum extending anterior to spondylium, 3 or more pairs of thin, short accessory septa present; ventral mantle canals digitate; slightly elevated, concave,

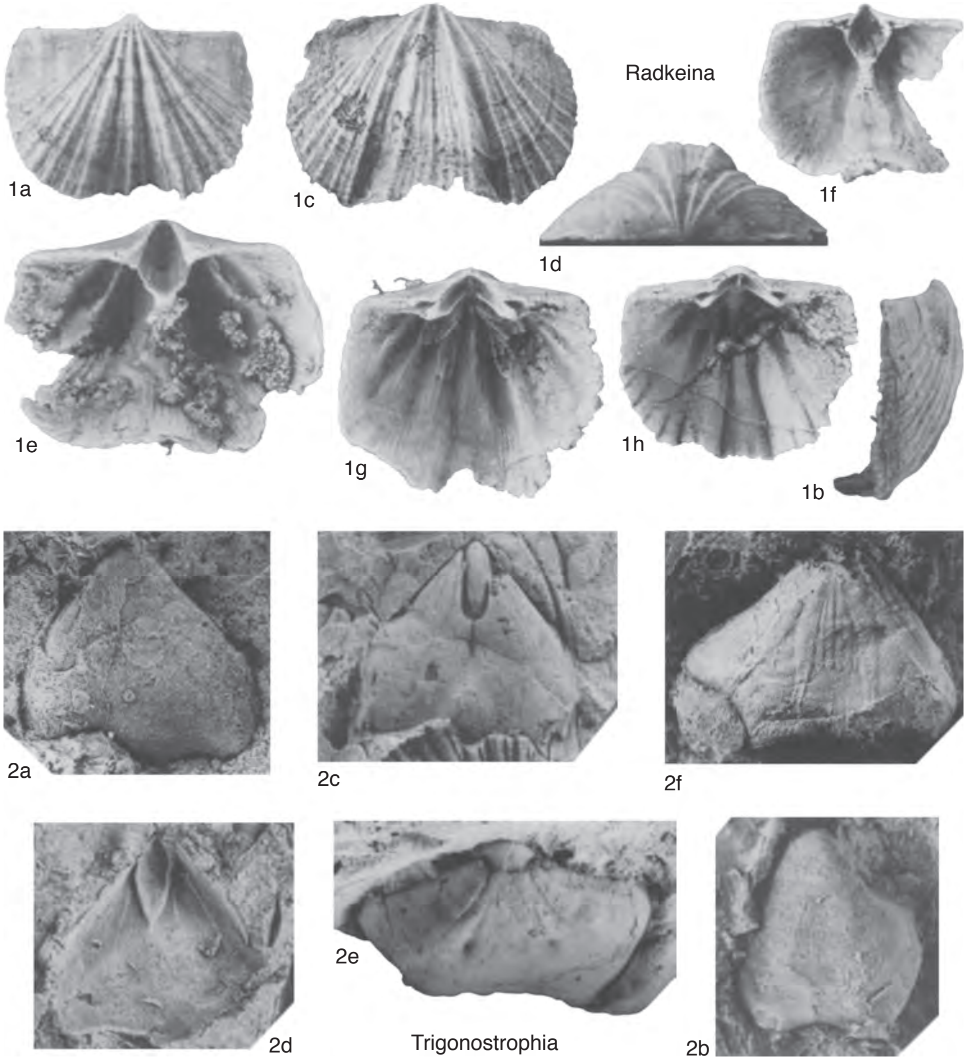


FIG. 1798. Huenellidae (p. 2699).

and somewhat triangular notothyrial platform present, cardinal process unknown; sockets delimited by distinct fulcral plates, socket plates with up to 3 pairs of long, shallow accessory septa; 2 or 3 distinct, shallow dorsal median septa present; dorsal mantle canal system digitate. Very similar to *Clarkella*, but *Punastrophia* has 2 or 3 shallow median dorsal septa and more pairs of accessory septae supporting ventral spondylium and dorsal socket plates. [The precise nature of the number and variation of the number of septa in each valve is somewhat unclear at this time; given the variation observed thus far, distinguishing a new genus apart from *Clarkella* appears warranted.] *Lower Ordovician (Arenig):* northwestern Argentina.——FIG. 1799,*2a–e*. **P. multiseptata*, Vega Pinato, Puna region; *a,* ventral valve exterior mold, ×3; *b,* ventral valve interior mold, ×3; *c,* cast of ventral valve interior mold, ×4; *d,* dorsal valve interior mold, ×3; *e,* cast of dorsal valve interior mold, ×3 (Benedetto, 2001).

Superfamily CAMERELLOIDEA Hall & Clarke, 1895

Family PARASTROPHINIDAE Schuchert & LeVene, 1929

Eosotrophina ZHAN & RONG, 1995, p. 568 [**Camerella uniplicata* LIANG in LIU, XU, & LIANG, 1983,

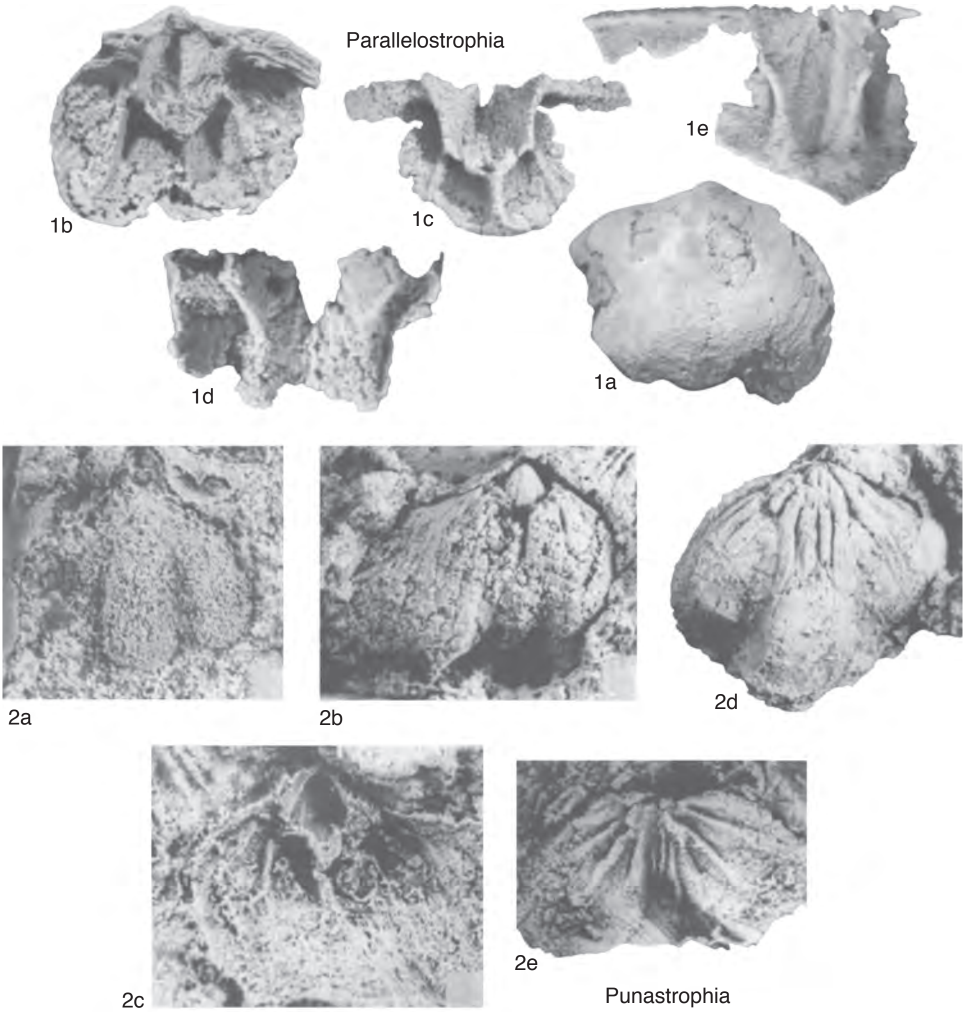


FIG. 1799. Clarkellidae (p. 2699–2700).

p. 282; OD]. Small- to medium-sized, smooth shells; outline rhombic to pentameral, wider than long; strongly uniplicate; teeth strong; spondylium duplex supported for entire length by low median septum extending anterior to spondylium; outer hinge plates well developed, widely divergent; long inner hinge plates that converge and unite with long median septum to form long septalium duplex, median septum increasing in height anteriorly; alate plates poorly developed, fine and very short. Similar to *Liostrophia* but smaller, with well-developed outer hinge plates and poorly developed alate plates. *Upper Ordovician (middle Ashgill):* East China (southwestern Zhejiang).——FIG. 1800,*1a–g*. **E. uniplicata* (LIANG), Xiazhen Formation, Dianbian-Shiyang, Jiangshan County; *a,* ventral valve exterior, ×2; *b,* articulated valves, posterior view, ventral below, ×2; *c,* articulated valves, anterior view, ventral below, ×2; *d,* dorsal valve exterior, ×2; *e,* articulated valves, lateral view, ventral on right, ×2; *f–g,* serial sections 1.6 and 2.6 mm from posterior end of specimen, ventral valve above, magnification not given (Zhan & Rong, 1995).

Ilistrophina POPOV, COCKS, & NIKITIN, 2002, p. 69 [**I. tesikensis;* OD]. Small, smooth shells; outline rounded pentameral, varies from wider than long to longer than wide; strongly uniplicate, fold and sulcus varies from rounded to broad and flat, originating anterior to midvalve; teeth small, strong; spondylium sessile posteriorly, raised and supported anteriorly by low median septum extending anterior

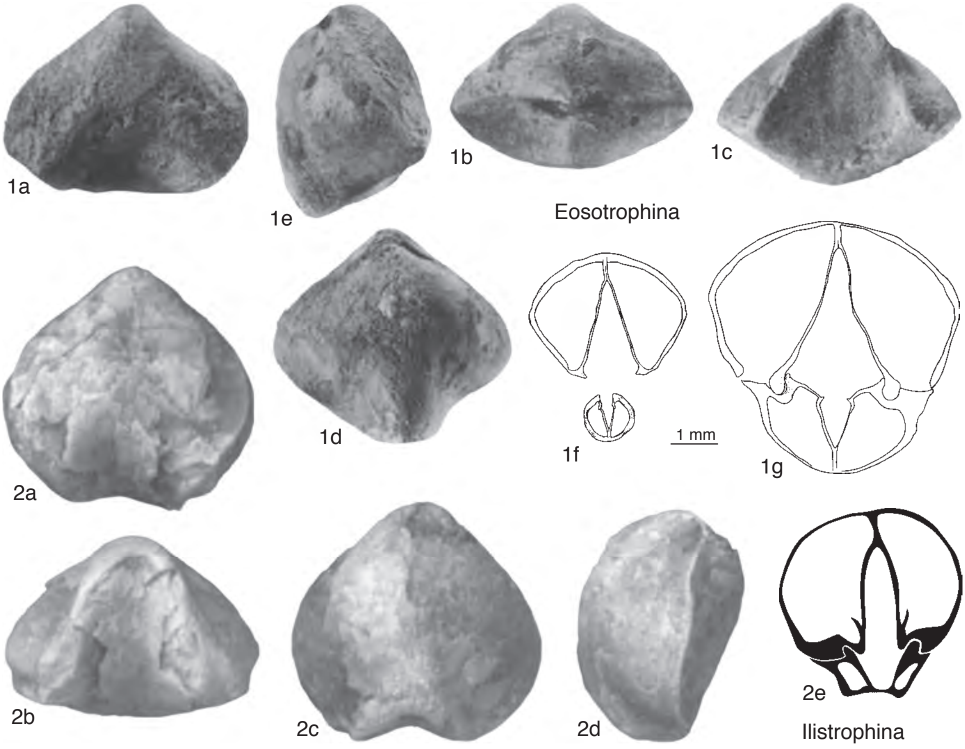


FIG. 1800. Parastrophinidae (p. 2700–2702).

to spondylium; outer hinge plates short, subparallel to convergent; inner hinge plates long, converging and uniting with long, high median septum to form long, deep septalium duplex; crura long; alate plates well developed. Similar to *Eosotrophina* but smaller and with sessile spondylium. *Upper Ordovician (lower Caradoc–middle Caradoc):* southeastern Kazakhstan (Chu-Ili Range).——FIG. 1800,*2a–e.* **I. tesikensis,* Anderken Formation, Tesik River; *a,* ventral valve exterior, ×4; *b,* articulated valves, anterior view, ventral below, ×4; *c,* dorsal valve exterior, ×4; *d,* articulated valves, lateral view, ventral on right, ×4; *e,* serial section 0.9 mm from posterior end of specimen, dorsal valve above, ×7 (Popov, Cocks, & Nikitin, 2002).

RHYNCHONELLIDA (part)

Norman Savage

[University of Oregon]

Order RHYNCHONELLIDA Kuhn, 1949

Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913

Family TRIGONIRHYNCHIIDAE Schmidt, 1965

Subfamily TRIGONIRHYNCHIINAE Schmidt, 1965

Tectogonotoechia García-Alcalde, 1998, p. 769 [**T. tectogonia*; OD]. Small with slightly elongate subpentagonal outline and dorsibiconvex profile. Beak suberect to erect; delthyrium with conjunct deltidial plates. Fold and sulcus narrow, arising at one-third shell length; anterior commissure uniplicate, rounded, dentate. Costae strong, angular, numerous, simple, extending from beaks. Dental plates short, thin, vertical; teeth short. Dorsal median septum low, short; septalium with cover plate; cardinal process lacking; crura unknown. *Lower Devonian (Lochkovian):* Spain.——Fig. 1801*a–l*. **T. tectogonia*, Felmin Formation, 1.3 km north of Barrios de Luna, Cantabrian Mountains, Dominio Palentino, northern Spain; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l*, hypotype, serial sections 0.25, 0.35, 0.85, 1.1, 1.35, 1.5, 1.55, 1.6 mm from posterior, ×5 (García-Alcalde, 1998).

Subfamily RIPIDIORHYNCHINAE Savage, 1996

Hunanotoechia Ma, 1993, p. 717 [**H. tieni*; OD]. Small; subcircular to subpentagonal outline; dorsibiconvex profile. Beak erect; small deltidial plates disjunct; foramen ovate, laterally flattened. Fold and sulcus arising at about midlength; anterior commissure uniplicate; tongue high, rounded, serrate. Costae numerous, angular with rounded tops, simple, from beaks, well developed over whole shell. Dental plates short, vertical or slightly divergent ventrally; teeth stout. Hinge plates short, horizontal, united at small septalium; dorsal median septum low, extending about one-third valve length; crural bases triangular in section; crura slender, laterally flattened distally. *Upper Devonian (upper Frasnian):* China.——Fig. 1802,*1a–j*. **H. tieni*, lower part of Changlungchieh Shale, Xikuangshan, central Hunan; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3; *f–j*, serial sections 0.4, 0.8, 1.0, 1.4, 1.8 mm from posterior, ×6 (Ma, 1993).

Orophomesorhynchus Sartenaer, 2001, p. 203 [**Terebratula huotina* de Verneuil, 1845, p. 81; OD]. Medium size; subpentagonal outline; strongly dorsibiconvex profile. Ventral beak erect, projecting. Strong fold and sulcus arising at umbones; anterior commissure uniplicate; tongue high, trapezoid with rounded top, dentate. Costae strong, simple, regular, angular with rounded crests; starting near beaks; some parietal costae; lateral costae numerous,

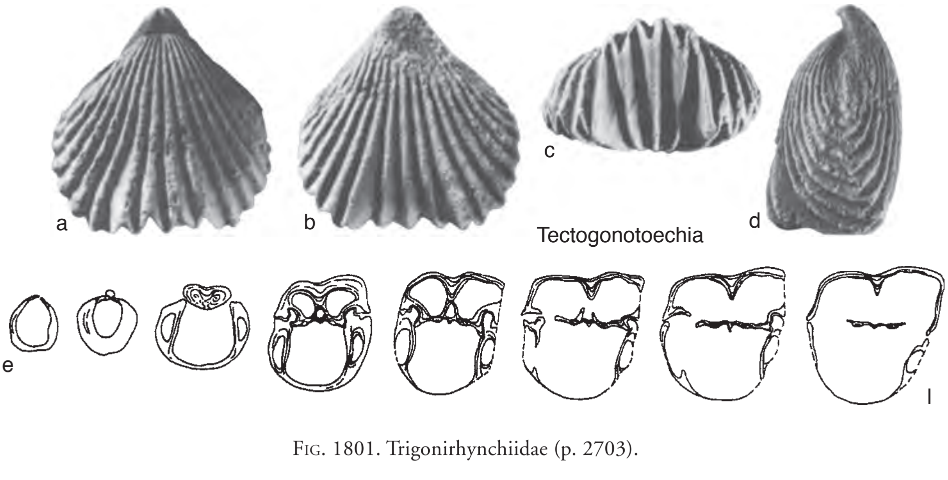


Fig. 1801. Trigonirhynchiidae (p. 2703).

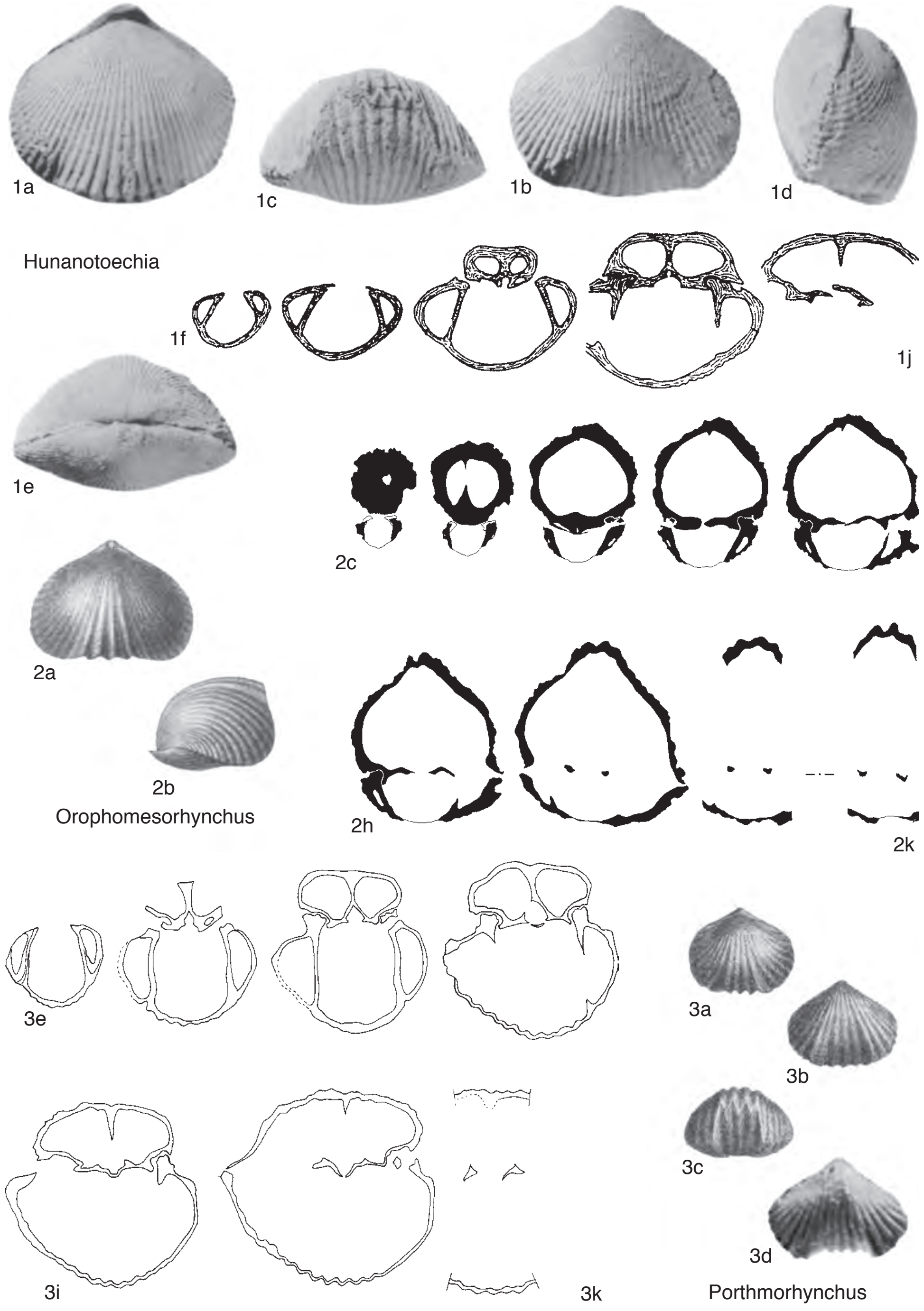


FIG. 1802. Trigonirhynchiidae (p. 2703–2705).

narrow, angular. Dental plates short, convergent ventrally; umbonal cavities narrow; teeth short, stout. Septalium and dorsal median septum lacking; hinge plates thick posteriorly, becoming thinner and almost meeting anteriorly; crural bases subtriangular in section; crura subtriangular in section proximally, becoming crescentic distally with convex surface dorsal. *Upper Devonian (lower Famennian):* European Russia.——FIG. 1802,*2a–k*. **O. huotinus* (DE VERNEUIL), Zadonsk beds, Horizon, Middle and Late *Palmatolepis triangularis* and *crepida* Zones, town of Zadonsk, left bank of River Don, Central Devonian Field; *a–b*, dorsal and lateral views, ×1 (de Verneuil, 1845); *c–k*, topotype, serial sections 1.15, 1.5, 2.2, 2.6, 3.1, 3.4, 4.05, 4.4, 5.25 mm from posterior, ×1.6 (Sartenaer, 2001).

Paropamisorhynchus SARTENAER, 2001, p. 201 [**Ripidiorhynchus* (?) *kotalensis* BRICE, 1971, p. 38; OD]. Medium to large size; subcircular to subpentagonal outline; strongly dorsibiconvex profile. Ventral beak slightly incurved. Strong fold and sulcus arising close to beaks; anterior commissure uniplicate; tongue high, rounded, dentate. Costae strong, simple, angular with rounded crests, arising at beaks, some parietal costae present. Dental plates strong, convergent ventrally; teeth stout. Dorsal median septum high, extending well past hinge area; septalium short, with cover plate anteriorly; hinge plates united; crura subtriangular in section proximally, convex ventrolaterally in section distally. *Upper Devonian (middle Frasnian, ?lower Famennian):* Afghanistan.——FIG. 1803,*1a–p*. **P. kotalensis* (BRICE), Ghouk, bed 1 in BRICE, 1971, west-central Afghanistan; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–n*, topotype, serial sections 0.25, 0.65, 0.8, 0.9, 1.15, 1.4, 1.5, 1.75, 2.4 mm from posterior, ×3; *o–p*, paratype, serial sections 5.0, 6.1 mm from posterior, scale not given, copied at ×0.5 (Brice, 1971).

Piridiorhynchus SARTENAER, 2001, p. 192 [**P. confinium*; OD]. Medium size; subpentagonal outline; strongly biconvex to inflated profile. Beak erect to incurved; deltidial plates observed in sections. Fold and sulcus strong, narrow, extending from umbones; anterior commissure uniplicate; tongue high, rounded. Costae medium, angular with rounded top, simple, from beaks; parietal costae commonly present. Dental plates short, slightly convergent ventrally; teeth short, stout. Hinge plates short, divided, horizontally flattened; septalium small; dorsal median septum slender, high posteriorly, extending one-third valve length; crura rodlike proximally, convex ventrolaterally in section, slightly curved toward ventral valve distally. *Upper Devonian (lowermost Famennian):* Belgium, Russia.——FIG. 1803,*4a–o*. **P. confinium*, Early *Palmatolepis triangularis* Zone, Sinsin, near Aye, Belgium; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o*, paratype, serial sections 1.05, 1.4, 1.7, 2.0, 2.45, 2.55, 2.85, 4.4, 4.8, 5.2 mm from posterior, ×1.6 (Sartenaer, 2001).

Poleomesorhynchus SARTENAER, 2001, p. 206 [**Camarotoechia gregeri* BRANSON, 1923, p. 91; OD]. Small to medium size with subtriangular to subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, rounded, dentate. Costae distinct, simple, arising at beaks, angular with rounded crests; parietal costae present. Dental plates vertical, extending to hinge area; umbonal cavities large; teeth stout. Dorsal median septum low and thick, extending well past hinge area; hinge plates undivided; septalium deep, short, with cover plate; crura suboval proximally, convex ventrolaterally in section distally. *Upper Devonian (lower Frasnian)*: North America.——FIG. 1803,*3a–o*. **P. gregeri* (BRANSON), Snyder Creek Shale, Cow Creek, Calloway County, central Missouri; *a–b*, topotype, dorsal and lateral views, ×1.1; *c,* second topotype, ventral view, ×1.1; *d–e*, third topotype, dorsal and lateral views, ×1.1 (Branson, 1923); *f–o*, topotype, serial sections 1.5, 1.75, 2.0, 2.25, 2.35, 2.55, 2.75, 2.9, 3.15, 3.3 mm from posterior, ×3.25 (Sartenaer, 2001).

Porthmorhynchus SARTENAER, 2001, p. 200 [**Rhynchonella ferquensis* GOSSELET, 1887, p. 199; OD] [=*Hypselororhynchus* SARTENAER, 2001, p. 199 (type, *Ripidiorhynchus farsani* BRICE in BRICE & FARSAN, 1977, p. 227, OD)]. Small to medium size with subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, extending from near beaks; anterior commissure uniplicate; tongue high, trapezoidal, dentate. Costae strong, simple, angular with rounded crests, arising at beaks; parietal costae rarely present. Dental plates vertical, subparallel, short; umbonal cavities distinct; teeth stout. Dorsal median septum short, low; hinge plates separated by short, moderately deep septalium; cover plate present anteriorly; crura triangular in cross section proximally. *Upper Devonian (middle Frasnian–upper Frasnian):* Europe, Iran, Afghanistan.——FIG. 1802,*3a–k*. **P. ferquensis* (GOSSELET), middle Frasnian, Boulonnais, northern France; *a–c,* hypotype, dorsal, ventral, and anterior views, Massif d'Hestrud, Hestrud, ×1 (Gosselet, 1887); *d,* lectotype, ventral view, Calcaire de Ferques, Ferques, ×1; *e–k,* paratype, serial sections 0.65, 1.15, 1.4, 1.55, 1.75, 1.9, 2.1 mm from posterior, Calcaire de Ferques, Ferques, ×3 (Brice & Meats, 1972).

Saxulirostrum SARTENAER, 2001, p. 203 [**Rhynchonella (Stenocisma) contracta* var. *saxatilis* HALL, 1867, pl. 54A,*44–48;* OD] [=*Kedridorhynchus* SARTENAER, 2001, p. 199 (type, *Camarotoechia cedarensis* STAINBROOK, 1942, p. 611, OD)]. Small with subpentagonal outline and dorsibiconvex profile. Ventral beak suberect to erect. Fold and sulcus strong, wide, arising at umbones; anterior commissure uniplicate, tongue high, dentate.

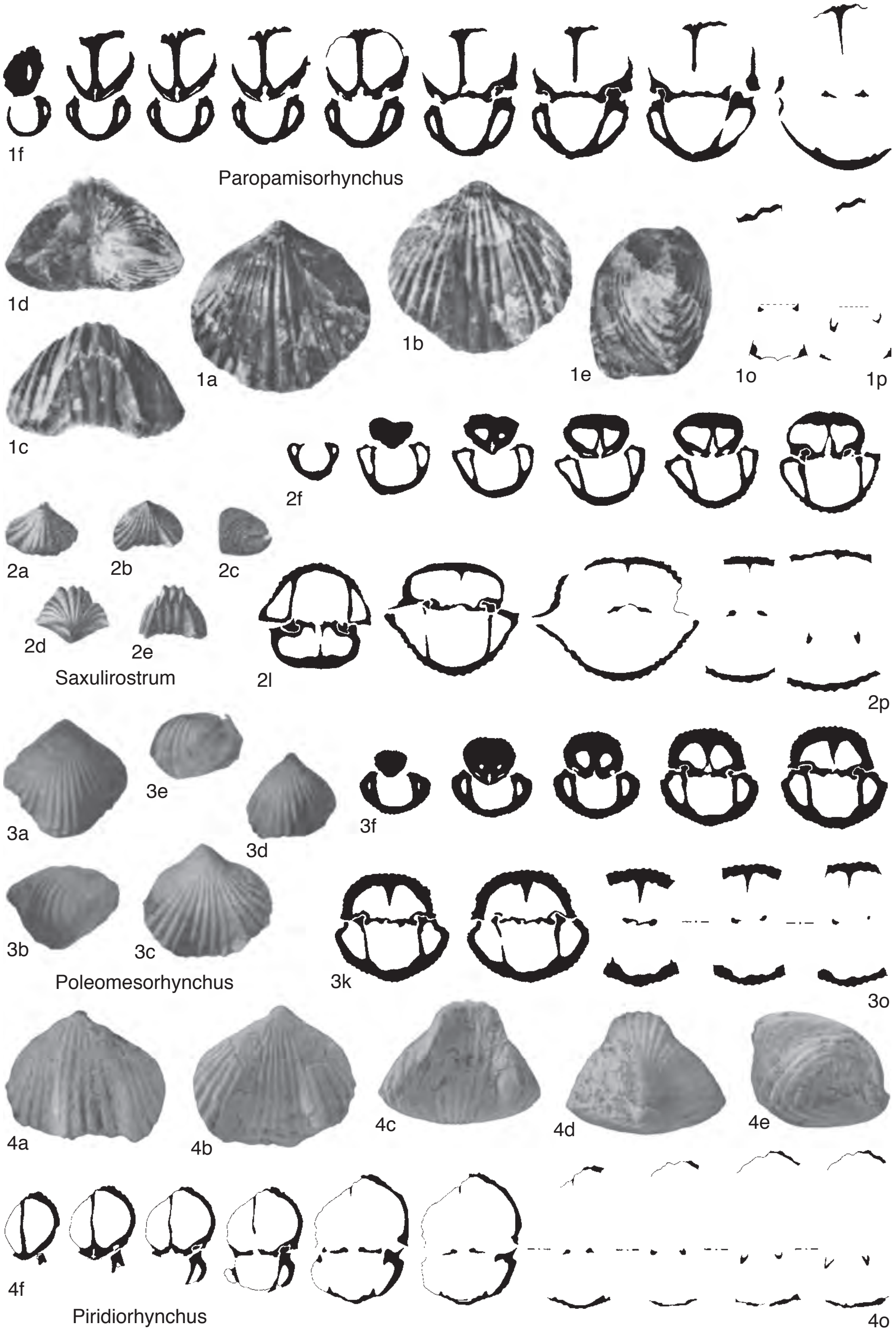


FIG. 1803. Trigonirhynchiidae (p. 2705–2707).

Costae strong, few, arising at beaks, angular with rounded crests, present on fold, sulcus, and flanks. Dental plates well developed, extend past hinge area, subvertical to slightly convergent ventrally; umbonal cavities large; teeth stout. Dorsal median septum short, low; septalium deep; hinge plates undivided; crura rodlike proximally in section, then V-shaped, then crescentic distally. *Upper Devonian (upper Frasnian)*: North America.——FIG. 1803,*2a–p*. **S. saxatile* (HALL), Lime Creek Formation, Cerro Gordo Member, Rockford, Floyd County, Iowa; *a–e*, lectotype, dorsal, ventral, lateral, posterior, and anterior views, ×1 (Hall, 1867); *f–p*, topotype, serial sections 0.55, 1.0, 1.05, 1.15, 1.2, 1.4, 1.55, 1.75, 1.95, 2.0, 2.6 mm from posterior, ×4.4 (Sartenaer, 2001).

Superfamily UNCINULOIDEA Rzhonsnitskaia, 1956

Family HEBETOECHIIDAE Havlíček, 1960

Subfamily HEBETOECHIINAE Havlíček, 1960

Cerveratoechia GARCÍA-ALCALDE, 1998, p. 774 [**Hebetoechia cantabrica* BINNEKAMP, 1965, p. 25; OD]. Medium size; subpentagonal to subcircular outline with length slightly greater than width; equibiconvex to subglobular. Beak erect; foramen with disjunct deltidial plates. Dorsal fold and ventral sulcus arising at about one-third valve length; umbones smooth; tongue strong, rectangular; costae broad, angular, but with rounded crests, 3 or 4 on fold, 2 or 3 in sulcus, 4 or 5 on flanks; anterior commissure dentate with short marginal spines; squamae and glottae well developed. Dental plates short, slightly convergent ventrally; teeth small. Dorsal median septum high, septalium small, with short cover plate; calluslike cardinal process developed in more mature specimens; crural bases triangular in section; crura closely set, laterally flattened. Muscle fields well impressed. *Lower Devonian:* Spain, ?North Africa.——FIG. 1804,*2a–l*. **C. cantabrica* (BINNEKAMP), Lochkovian, Lebanza Formation, Cantabrian Mountains, Dominio Palentino, northern Spain; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l*, serial sections 0.5, 1.1, 1.45, 2.1, 2.45, 3.85, 4.1, 4.4 mm from posterior of young specimen, ×1.5 (García-Alcalde, 1998).

Lebanzuella GARCÍA–ALCALDE, 1999, p. 250 [**Uncinulus lebanzus* BINNEKAMP, 1965, p. 24; OD]. Medium size; subpentagonal outline; equibiconvex to subglobular; beak suberect; foramen with deltidial plates; dorsal fold and ventral sulcus arising at about one-third valve length; umbones smooth; tongue strong, rectangular; costae broad, angular but with rounded crests, 3 to 5 on fold, 2 to 4 in sulcus, 7 to 8 on flanks; anterior commissure dentate with short marginal spines; squamae and glottae well developed. Dental plates short, slightly convergent ventrally; teeth stout. Dorsal median septum moderately high, septalium small; multilobed cardinal process with about 6 thin lobes separated medially by groove; crural bases triangular in section; crura closely set, horizontally flattened proximally, laterally flattened distally. Muscle fields well impressed with low median myophragm in each valve. *Lower Devonian (Pragian):* Spain.——FIG. 1804,*1a–l*. **L. lebanza* (BINNEKAMP), Lebanza Formation, Cantabrian Mountains, northern Spain; *a–d*, holotype, dorsal, ventral, lateral, and anterior views, top, Member E, of Lebanza Formation, Lebanza village, ×1 (Binnekamp, 1965); *e–l*, serial sections 0.9, 1.75, 2.05, 2.6, 2.95, 3.15, 4.1, 5.5 mm from posterior of hypotype from Member E of Lebanza Formation, Lebanza village; *e–h,* ×6, *i–l,* ×3 (García-Alcalde, 1999).

Family INNAECHIIDAE Baranov, 1980

[Innaechiidae BARANOV, 1980, p. 78; *emend.,* SAVAGE, herein]

Uncinuloidea lacking cardinal process, septalium absent or very small. *upper Silurian (Ludlow)–Middle Devonian (Eifelian).*

Subfamily INNAECHIINAE Baranov, 1980

[*nom. transl.* SAVAGE, 1996, p. 253, *ex* Innaechiidae BARANOV, 1980, p. 78]

Innaechiidae with median septum; dental plates very short. *Lower Devonian (Lochkovian–Pragian).*

Dubovikovia BARANOV in ALEKSEEVA & others, 1996, p. 82 [**Hebetoechia settedabanica* RZHONSNITSKAIA in ALEKSEEVA, 1967, p. 48; OD]. Small with transversely subpentagonal outline; dorsibiconvex profile, anteriorly inflated. Beak erect. Fold and sulcus developed anteriorly; tongue high, rectangular. Costae simple, developed from about midlength, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short, slightly convergent ventrally; teeth very short. Dorsal median septum high, thin, extending about one-quarter valve length; hinge plates divided anterior of very short septalium; crural bases inclined mediodorsally; crura rodlike proximally, laterally flattened distally. *Lower Devonian (Lochkovian–Pragian):* eastern Siberia.——FIG. 1805,*1a–i*. **D. settedabanica* (RZHONSNITSKAIA), Lochkovian, lower part of Settedaban Formation, Sette-Daban Range, Tikhiy Creek; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i*, serial sections, intervals and distance from posterior not given, reoriented, ×3 (Alekseeva, 1967).

Family HYPOTHYRIDINIDAE Rzhonsnitskaia, 1956

Tullypothyridina SARTENAER, 2003, p. 31 [**Rhynchonella venustula* HALL, 1867, p. 346; OD]. Medium

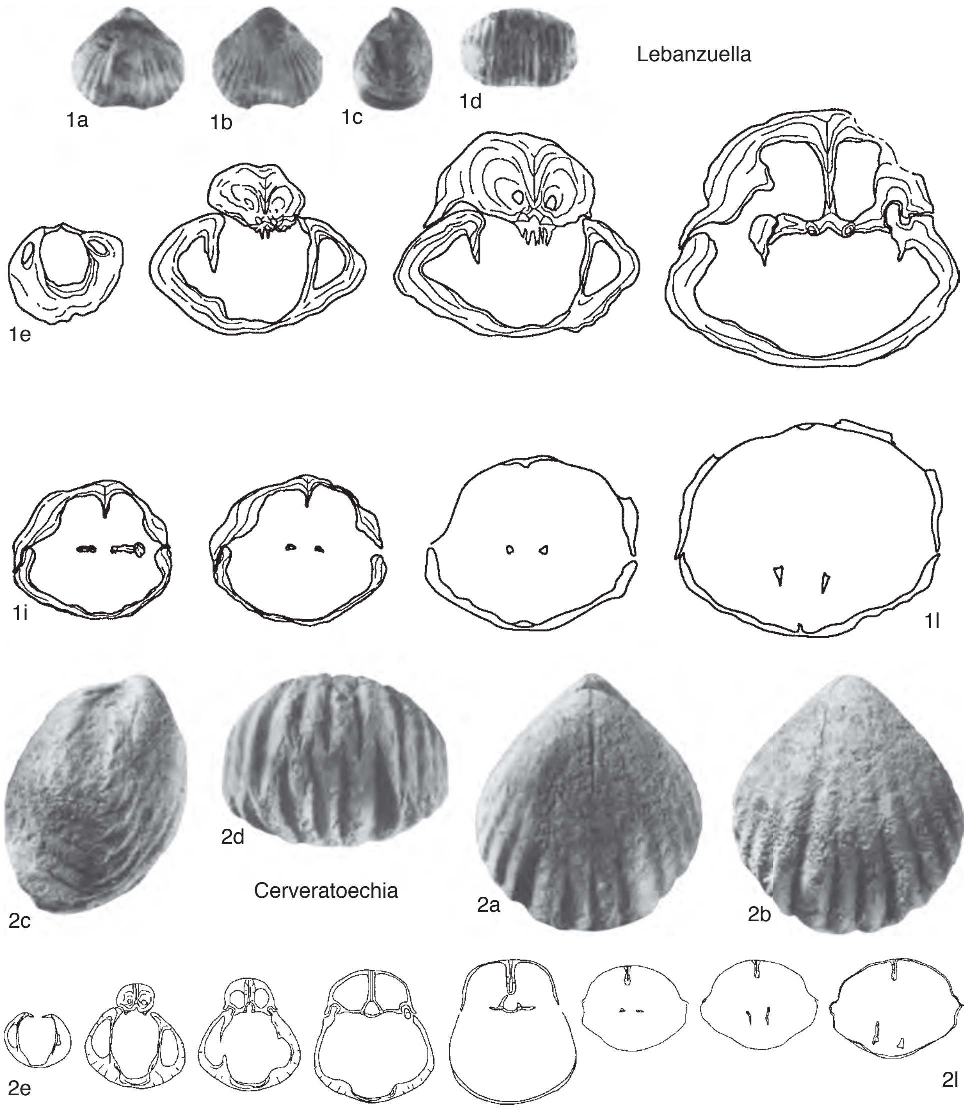


FIG. 1804. Hebetoechiidae (p. 2707).

to large; subcuboidal with subcircular outline and strongly dorsibiconvex profile; lateral and anterior margins steep to vertical. Ventral beak erect to incurved. Fold and sulcus weak, becoming most evident anteriorly; tongue very high, rectangular to rounded. Costae numerous, simple or rarely divided, arising at beaks, flattened and bearing median grooves from about midlength and especially on tongue; marginal spines developed. Dental plates short, slender, ventrally convergent; teeth small, short. Dorsal median septum and septalium absent; hinge plates divided, horizontal; cardinal process comprising distinct central ridge and several thin flanking growths; crura closely set, flattened horizontally, short, delicate. *Middle Devonian (upper Givetian)*: North America.——FIG. 1805,*2a–p*. **T. venustula* (HALL), Tully Limestone, Apulia Member, June's quarry, central New York; *a*, lectotype, anterior view, ×1 (Hall, 1867); *b–f*, topotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *g–p*, topotype, serial sections 0.95, 1.25, 1.325, 1.4, 1.55, 1.75, 1.95, 2.1, 2.25, 2.5 mm from posterior, ×2.3 but with enlargements (×4.6) of the cardinal process shown within sections *h–j* (Sartenaer, 2003).

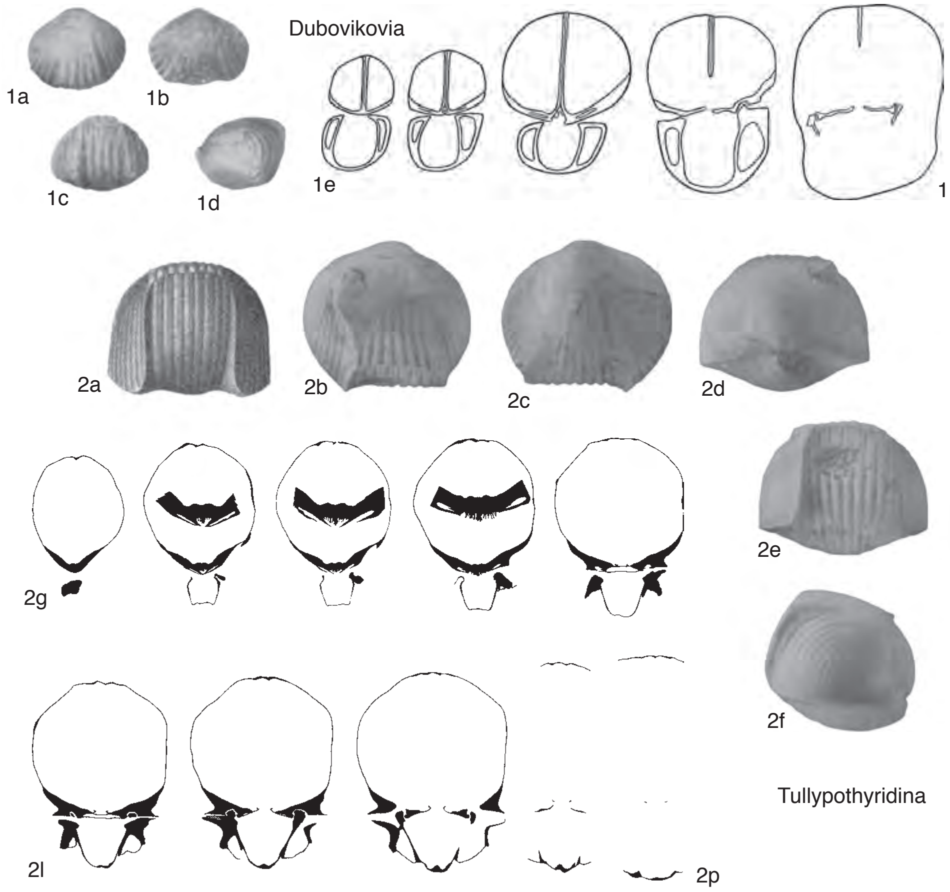


FIG. 1805. Innaechiidae and Hypothyridinidae (p. 2707–2708).

Superfamily CAMAROTOECHIOIDEA Schuchert, 1929

Family LEIORHYNCHIDAE Stainbrook, 1945

Subfamily LEIORHYNCHINAE Stainbrook, 1945

Azurduya CISTERNA & ISAACSON, 2003, p. 65 [**Camarotoechia chavelensis* AMOS, 1958, p. 839; OD]. Medium size, subtriangular to subpentagonal outline with width and length about equal; dorsibiconvex profile; lateral and anterior slopes gentle. Beak suberect. Dorsal fold and ventral sulcus developed only anteriorly. Simple subangular costae arising at umbones, 7–8 on fold and sulcus, up to 8 on flanks. Anterior commissure uniplicate. Dental plates anteriorly divergent, reaching up to one-fifth of valve length; teeth small, smooth, rounded. Dorsal median septum long, reaching one-third to half valve length; short septalium uniting hinge plates; dorsal muscle scars subrhomboidal in outline; crura unknown. *Lower Carboniferous (Tournaisian):* Argentina.——FIG. 1806,*1a–g*. **A. chavelensis* (AMOS), lower part of Malimán Formation, Cortaderas Creek, about 5 km northeast of Malimán, San Juan province; *a–e*, neotype, dorsal, ventral, lateral, posterior, and anterior views, ×2; *f–g*, topotypes, internal mold of ventral valve, and dorsal view of internal mold of articulated specimen, ×2 (Cisterna & Isaacson, 2003).

Sphaeridiorhynchus SARTENAER, PUSHKIN, & KOTLYAR, 1997, p. 39 [**S. kuzmichiensis*; OD]. Small to medium size; globular; subcircular outline and inflated, dorsibiconvex profile. Beak wide, slightly incurved, with small foramen; deltidial plates evident in sections. Fold and sulcus low, only visible anteriorly; anterior commissure uniplicate; tongue low. Median costae very weak; lateral costae absent. Dental plates lacking; teeth simple, short. Hinge plates short, divided; median septum and septalium absent; long crura closely set, oval to

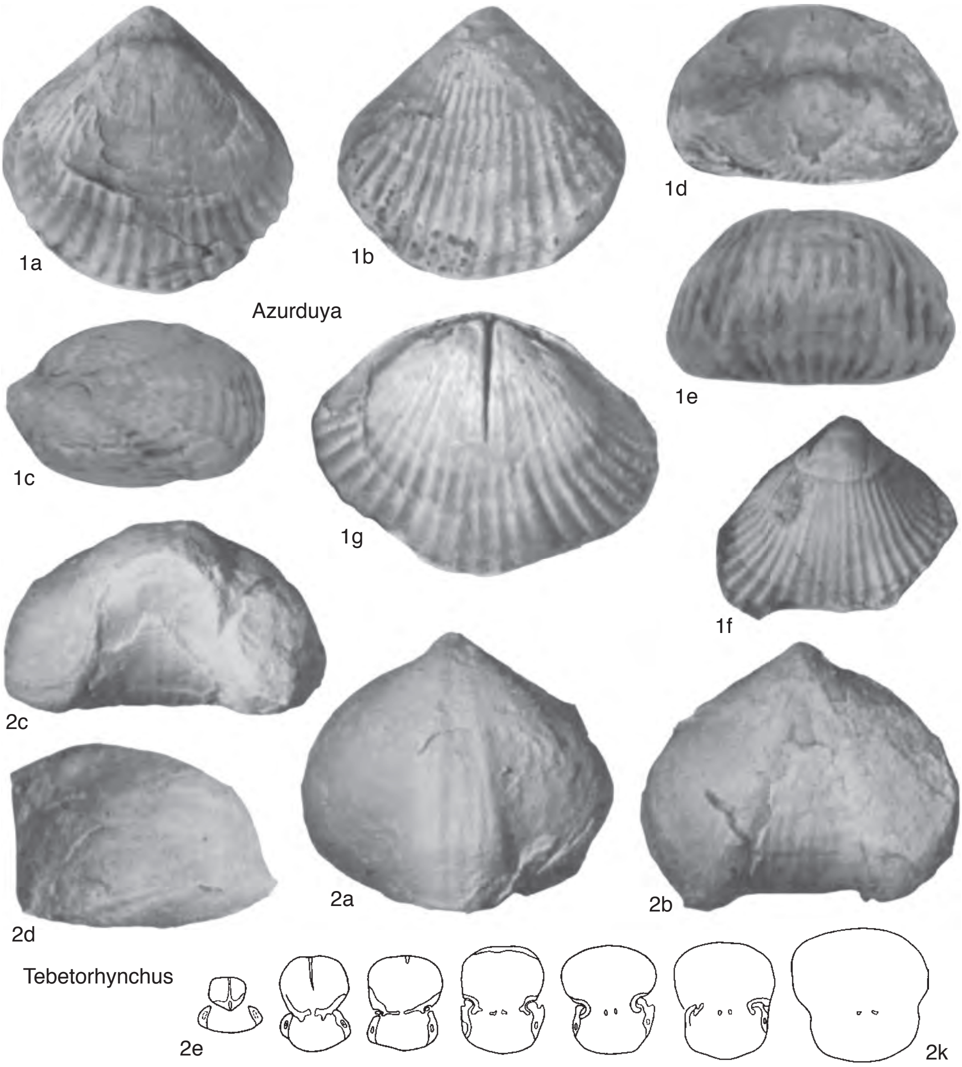


Fig. 1806. Leiorhynchidae (p. 2709–2710).

rounded in cross section. *Upper Devonian (lower Famennian):* Belarus, Ukraine.——Fig. 1807*a–n.* **S. kuzmichiensis*, Kuz'michi 1 borehole, Kuz'michi village, Pripyat Depression, near Minsk, Belarus; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–n,* paratype, serial sections 1.15, 1.25, 1.45, 1.7, 1.9, 2.3, 2.5, 2.85, 4.3 mm from posterior, ×2.15 (Sartenaer, Pushkin, & Kotlyar, 1997).

Tebetorhynchus Baranov in Alekseeva & others, 1996, p. 74 [**T. abramovi*; OD]. Large; subcircular to transversely ovate outline; dorsibiconvex profile. Beak suberect. Fold and sulcus arising at umbones; anterior commissure uniplicate with high, rounded tongue. Costae very weak, restricted to fold and sulcus. Dental plates short; close to valve walls. Dorsal median septum short, low; septalium very short to absent; hinge plates divided; crura closely set, rodlike proximally, unknown distally. *Lower Devonian (Emsian):* northeastern Russia.——Fig. 1806,*2a–k.* **T. abramovi*, Khobochalinska Formation, *Ivdelinia ivdelensis* Zone, lower Emsian, right bank lower reaches of Tebeti River, Tas-Khayakhtakh; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k*, paratype, serial sections 0.5, 1.9, 2.9, 3.8, 4.1, 4.6, 5.7 mm from posterior, scale not given (Alekseeva & others, 1996).

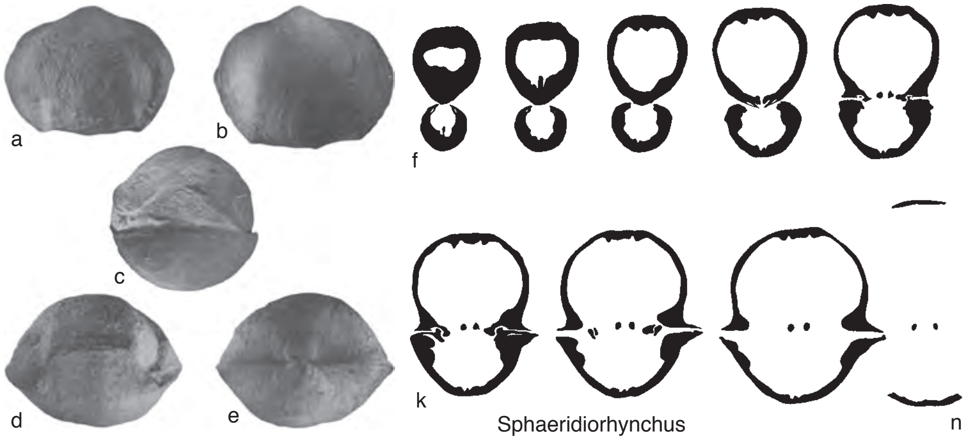


FIG. 1807. Leiorhynchidae (p. 2709–2710).

Subfamily CALVINARIINAE
Sartenaer, 1994

Tchernarhynchia TCHERKESOVA, 1998, p. 44 [**T. dichotoma*; OD]. Medium to large size, with transversely ovate to subpentagonal outline and dorsibiconvex profile, anteriorly swollen; gentle lateral slopes. Ventral beak incurved, dorsal beak erect. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, rounded, serrate. Costae fine, numerous, angular to rounded, arising at beaks, dichotomizing, strongly developed over whole shell surface. Dental plates short; teeth large. Dorsal median septum high, thin; septalium short, distinct; hinge plates divide just anterior of septalium; crura unknown. *Upper Devonian (middle Frasnian):* Russia.——FIG. 1808,*2a–k*. **T. dichotoma*, upper Zhandr Horizon, Lichutin, Gorbov Islands, Novaya Zemlya; *a–e*, holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f–k*, paratype, serial sections, intervals and scale not given (Tcherkesova, 1998).

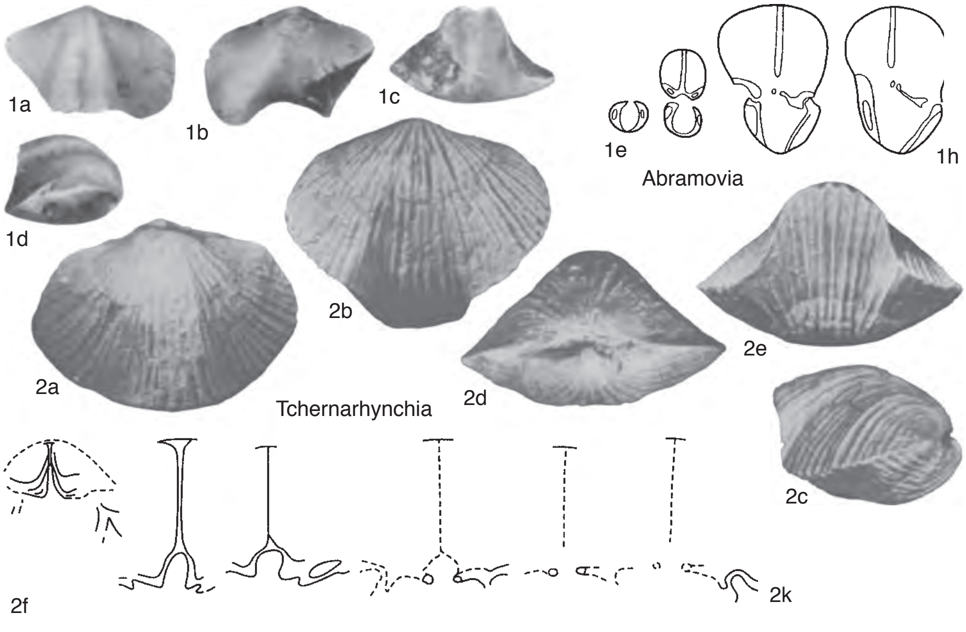


FIG. 1808. Leiorhynchidae (p. 2711–2712).

Subfamily BASILICORHYNCHINAE Savage, 1996

Leiorhynchidae with subcircular outline; high tongue; strong costae. Dental plates and dorsal median septum distinct. [Stratigraphic range emended herein.] *Lower Devonian–Upper Devonian.*

Abramovia Baranov in Alekseeva & others, 1996, p. 76 [**A. pteroidea*; OD]. Medium size; strongly transversely ovate outline with emarginate anterior margin; dorsibiconvex profile modified anteriorly by high fold. Ventral beak erect to incurved. Fold and sulcus arising at umbones and becoming strong anteriorly; fold with median broad groove, and sulcus with median rounded ridge; anterior commissure uniplicate to sulciplicate. Dental plates short, ventrally convergent. Dorsal median septum high, long; septalium short; hinge plates divided anterior of septalium; crura not described. *Devonian (Emsian–Famennian)*: Russia, Alaska.——Fig. 1808,*1a–h*. **A. pteroidea*, Emsian, lower part of Krivoy Ruchey Formation, Selennyakh Ridge, right bank of Talyndzha River, upper reaches of Krivoy stream, northeastern Russia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h*, paratype, serial sections, intervals not given, ×3.5 (Alekseeva & others, 1996).

Superfamily PUGNACOIDEA Rzhonsnitskaia, 1956

Family ROZMANARIIDAE Havlíček, 1982

[*nom. transl.* Havlíček, 1990, p. 214, *ex* Rozmanariinae Havlíček, 1982, p. 112; *emend.,* Savage, 1996]

Pugnacoidea with transversely ovate to subcircular outline; fold and sulcus sometimes low, generally fold in dorsal valve but may be in ventral valve; costae weak to absent; foramen with conjunct deltidial plates anteriorly. Dental plates short to absent. Dorsal median septum low or lacking; hinge plates divided; cardinal process absent. *Lower Devonian (Pragian)–Upper Devonian (Famennian).*

Iphinerrhynx Havlíček & Vaněk, 1998, p. 72 [**I. iphinoe*; OD]. Small; subpentagonal to rounded outline; ventribiconvex profile. Beak incurved; ventral fold and dorsal sulcus wide, poorly differentiated; anterior commissure unisulcate; both valves smooth or with barely visible undulations. Dental plates short, thin, almost vertical or slightly divergent toward valve floor. Hinge plates divided; dorsal median septum lacking; crural bases and crura not recorded. *Lower Devonian (Pragian):* Czech Republic.——Fig. 1809,*1a–e*. **I. iphinoe*, Slivenec Limestone, Kacak valley south of Hostim, Prague Basin, Bohemia; *a–c*, holotype, dorsal, ventral, and anterior views, ×5; *d–e*, serial sections 6.5, 6.0 mm from anterior, ×8 (Havlíček & Vaněk, 1998).

Leptoterorhynchus Sartenaer, 1998, p. 121 [**Rozmanaria magna* Biernat & Racki, 1986, p. 90; OD]. Transversely ovate outline and equibiconvex, lenticular profile. Beak wide, suberect to erect; may be resorbed by small foramen. Low ventral fold and shallow dorsal sulcus; anterior commissure unisulcate. Costae lacking. Dental plates short, rudimentary; teeth short and stout; ventral muscle field with distinct diductor scars enclosing elongate adductor scars. Hinge plates short, divided; septalium and dorsal median septum absent; crura laterally compressed with distal ends curved ventrally. *Upper Devonian (Famennian):* Poland, Germany.——Fig. 1809,*2a–l*. **L. magnus* (Biernat & Racki), middle Famennian, Wola Quarry, Kowala, Holy Cross Mountains, Poland; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×2 (Biernat, 1988); *e–l*, topotype, serial sections 0.4, 0.7, 0.9, 1.15, 1.25, 1.45, 1.8, 2.6 mm from posterior, ×2.2 (Sartenaer, 1998).

Novaplatirostrum Sartenaer, 1997, p. 27 [**N. sauerlandense*; OD]. Medium size shell. Subcircular outline and flattened, equibiconvex, lenticular profile. Beak erect to slightly incurved, in contact with dorsal posterior; foramen or delthyrium unknown. Low, wide dorsal fold and shallow ventral sulcus arising at about three-quarters shell length; anterior commissure uniplicate, undulate. Costae low, angular with rounded top, most evident anteriorly on fold and in sulcus; most of shell surface smooth. Dental plates rarely visible in thick shell walls; teeth small, wide, strong. Hinge plates divided, flat; dorsal median septum and septalium absent; crural bases stout, subtriangular in section; crura short, convex ventrolaterally, hooked distally. Muscle fields well impressed. *Upper Devonian (Famennian):* Germany.——Fig. 1810,*1a–o*. **N. sauerlandense*, upper Famennian, Wocklum Limestone, Hasselbachtal, northwestern Saurerland; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1 (Sartenaer, 1997); *f–o*, paratype, serial sections 1.0, 1.2, 1.4, 1.6, 1.7, 1.8, 2.25, 2.5, 2.8, 3.0 mm from posterior, ×2.2 (Sartenaer, 1997).

Phacoiderhynchus Sartenaer, 2000, p. 75 [**P. antiatlasicus*; OD]. Large; transversely elliptical outline; equibiconvex, lenticular profile. Beak erect to incurved. Low, wide, dorsal fold and shallow ventral sulcus arising at about two-thirds valve length; anterior commissure uniplicate, undulate. Costae low, angular, arising at about two-thirds shell length, well developed on fold, in sulcus, and also on flanks anterolaterally. Dental plates strong, convergent; teeth short, stout. Divided hinge plates wide, flattened; crural bases subtriangular in section; crura convex ventrolaterally in section, slightly curved distally toward ventral valve. Very short, delicate cardinal process. Dorsal median

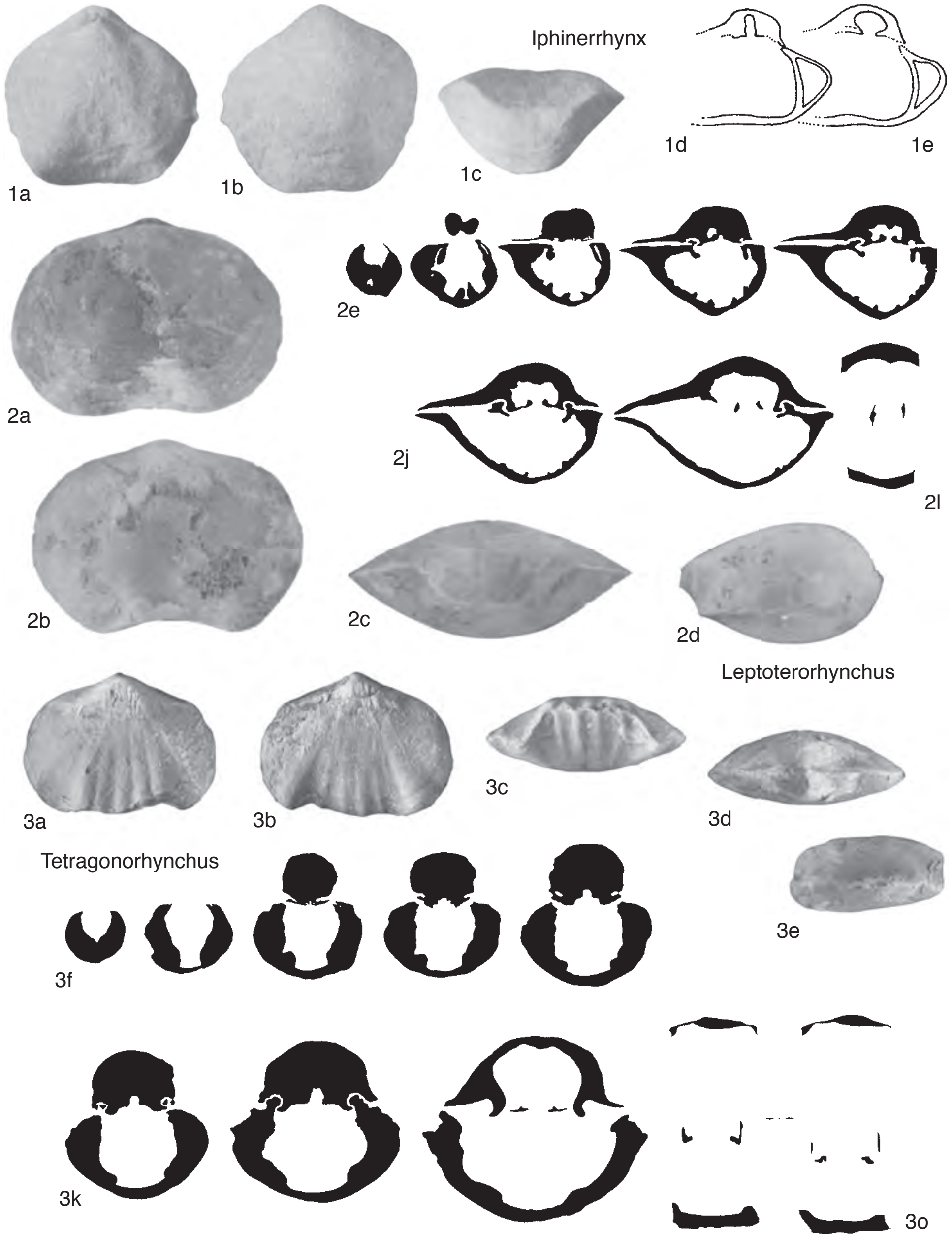


FIG. 1809. Rozmanariidae (p. 2712–2714).

septum absent. Muscle fields well impressed. *Upper Devonian (Famennian):* Morocco.——FIG. 1810,*2a–q*. **P. antiatlasicus*, middle Famennian, Maïder, southern Morocco; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–k*, paratype, serial sections 0.75, 0.85, 0.925, 1.05, 1.25, 1.4 mm from posterior, ×2.4; *l–q*, paratype, serial sections 0.8, 1.0, 1.15, 1.55, 2.1, 3.1 mm from posterior, ×2.4 (Sartenaer, 2000).

Tetragonorhynchus SARTENAER, 1999a, p. 67 [**T. mrakibensis*; OD]. Medium size shell; subquadrangular to transversely ovate in outline with an

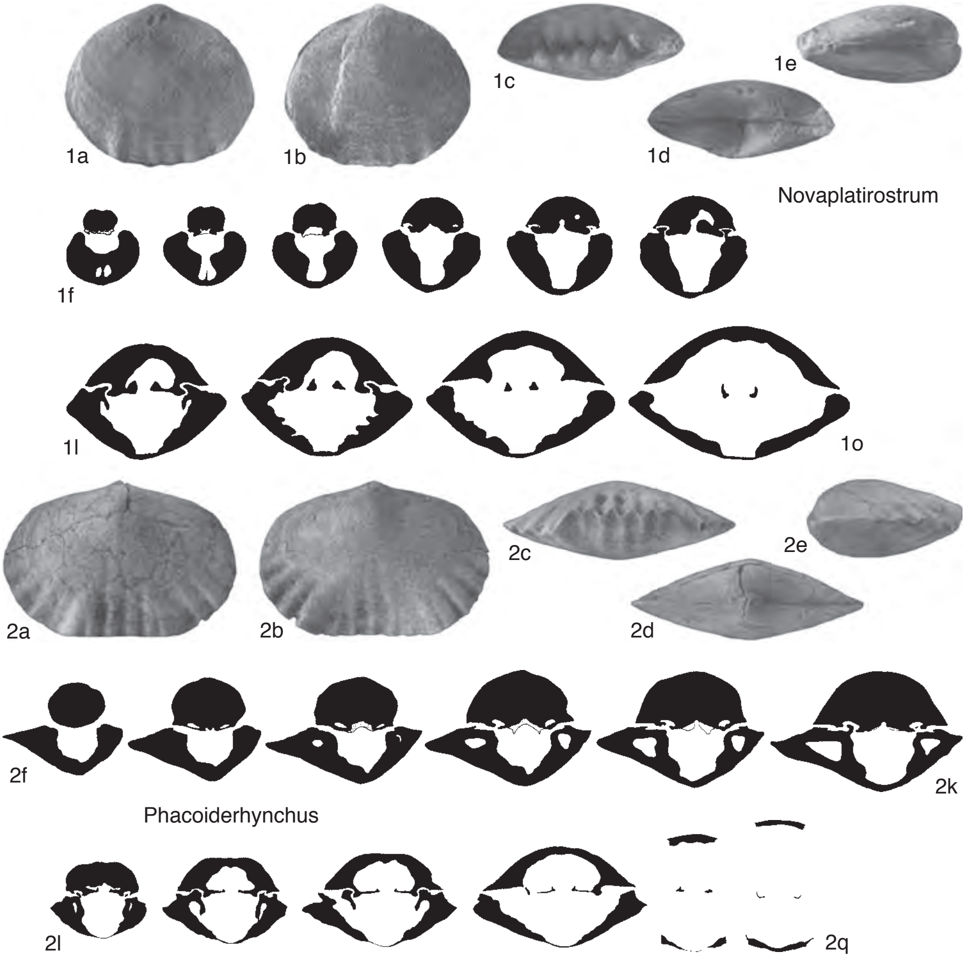


FIG. 1810. Rozmanariidae (p. 2712–2713).

equibiconvex, lenticular profile. Beak erect to incurved and resorbed by circular foramen. Low, wide dorsal fold and shallow ventral sulcus arising at about one-third valve length; faint median depression on fold and corresponding rise in sulcus; anterior commissure uniplicate, undulate. Costae low, rounded, from about midlength; most evident on fold and in sulcus, barely developed on flanks. Dental plates not visible in thick shell wall; teeth short. Divided hinge plates passing into short, flattened crural bases; crura short, ventrally curved at distal ends. Very short, delicate cardinal process visible in serial sections. Dorsal median septum absent. Muscle fields well impressed. *Upper Devonian (Famennian):* Morocco.——FIG. 1809,*3a–o.* **T. mrakibensis*, upper Famennian, upper Ibaoune Formation, Maïder, southern Morocco; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o,* paratype, serial sections 0.7, 1.05, 1.15, 1.31, 1.49, 1.55, 1.85, 2.45, 3.4, 3.9 mm from posterior, ×3.25 (Sartenaer, 1999a).

Family ASEPTIRHYNCHIIDAE Savage, 1996

Polyptychorhynchus SARTENAER, 1999b, p. 79 [**P. cavernosus*; OD]. Very large with transversely elliptical outline and biconvex profile. Ventral beak small, incurved; delthyrium with deltidial plates. Fold and sulcus wide, well marked, fold gently convex, sulcus strong anteriorly; anterior commissure uniplicate, tongue pronounced, trapezoidal. Flanks of both valves convex. Costae strong on fold and in sulcus, simple, arising at umbones, with rounded tops; costae on flanks arising at about midlength, wide, rounded. Shell thick, especially posteriorly. Dental plates short and mostly buried in shell wall; teeth stout, short,

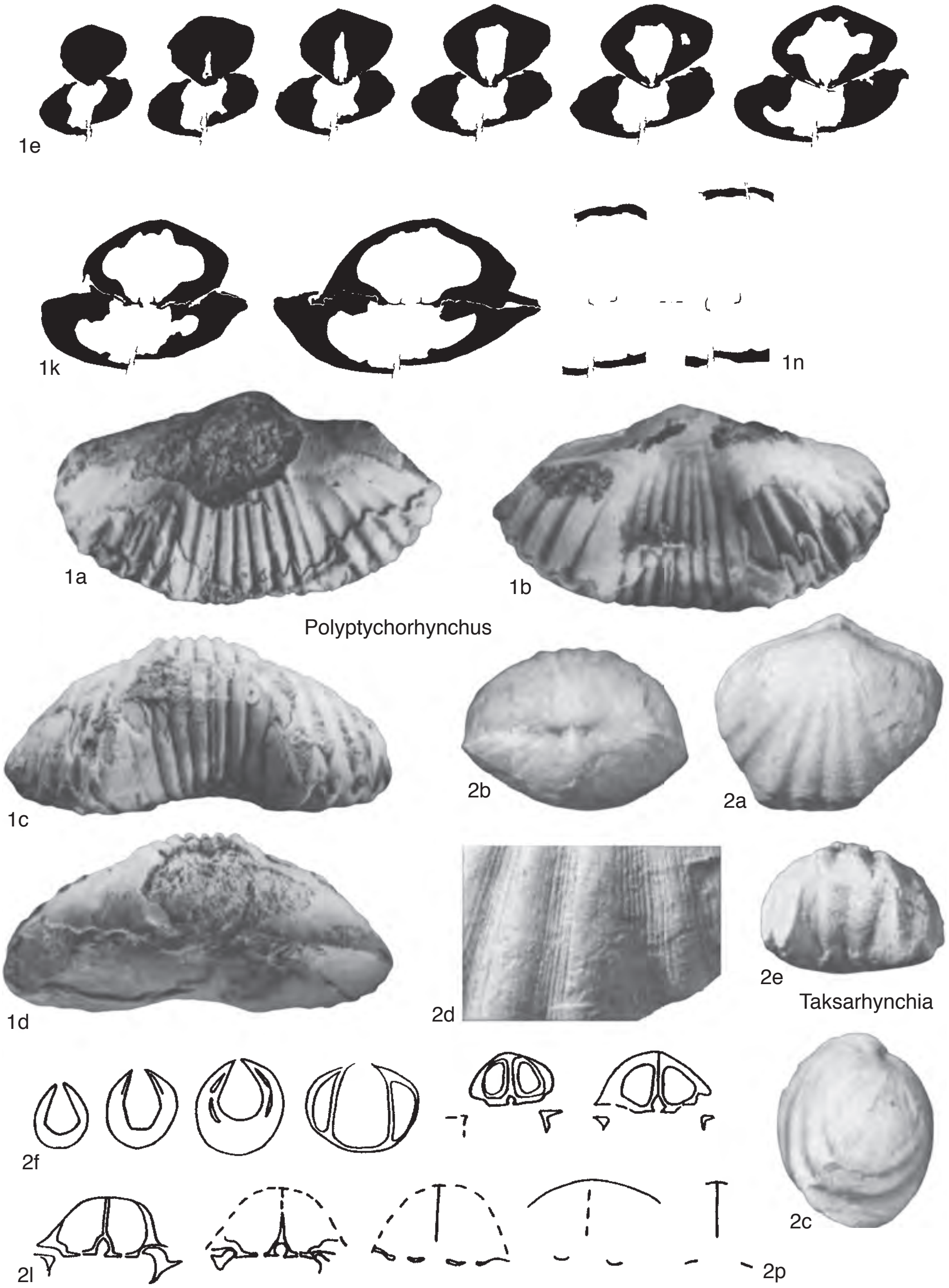


FIG. 1811. Aseptirhynchiidae and Yunnanellidae (p. 2714–2716).

wide; ventral muscle field well impressed. Dorsal median septum absent; hinge plates divided, subhorizontal, with short, wide sockets and low inner socket ridges; crural bases horizontal; crura subtriangular in cross section, distal parts curving ventrally, inner surfaces concave. *Upper Devonian (Famennian):* northwestern Australia.——FIG. 1811,*1a–n*. **P. cavernosus*, middle Famennian, Middle to Late *Marginifera* Zones, near Casey Falls, Virgin Hills Formation, Emanual Range, Canning Basin, Western Australia; *a–d,* paratype, dorsal, ventral, anterior, and posterior views, ×1; *e–n,* serial sections 1.9, 2.2, 2.4, 2.7, 2.8, 3.0, 3.3, 3.9, 5.1, 6.4 mm from posterior, ×2 (Sartenaer, 1999b).

Family YUNNANELLIDAE Rzhonsnitskaia, 1959

Taksarhynchia TCHERKESOVA, 1997, p. 48 [**T. sobolevi*; OD]. Medium to large; subpentagonal outline with greatest width near hinge line; dorsibiconvex profile. Ventral beak incurved. Fold and sulcus strong, arising at umbones. Anterior commissure uniplicate, tongue high, typically tridentate. Costae coarse, angular with rounded crests, arising at umbones. Whole shell surface bearing fine radial striae. Dental plates short, subvertical. Dorsal median septum high, thin, extending anterior of hinge area. Septalium short; hinge plates horizontal, divided anterior of septalium; crural bases horizontal; crura horizontal proximally, unknown distally. *Upper Devonian (upper Famennian):* Russia.——FIG. 1811,*2a–p.* **T. sobolevi*, Taksagerbei unit, Yurtaraga River, Taksa Range, central Taimyr, Russia; *a–c*, holotype, dorsal, posterior, and lateral views, ×1; *d*, holotype, striae, ×3; *e,* paratype, anterior view; *f–p*, same paratype, serial sections, intervals and distances from posterior and scale not given (Tcherkesova, 1997).

STENOSCISMATOIDEA

SANDRA J. CARLSON

[University of California, Davis]

Superfamily STENOSCISMATOIDEA Oehlert, 1887 (1883)

Family PSILOCAMARIDAE Grant, 1965

Subfamily PSILOCAMARINAE Grant, 1965

Bicamella WATERHOUSE, 2004, p. 88 [**Camarophoria timorensis* HAYASAKA & GAN, 1940, p. 129; OD]. Medium-sized shells, typically wider than long; outline subtriangular; weakly to strongly uniplicate; rounded to sharp costae, variable in number and intercalation style, commonly absent on valve flanks and near umbos, may be present on entire valve; beak prominent, incurved over delthyrium; delthyrium apparently open but constricted by dorsal valve; valve edges nonoverlapping; stolidium present; spondylium duplex supported by high median septum; hinge plate divided, very short but broad posteriorly, extending anterolaterally on each side of small, narrow, steep-sided camarophorium; intercamarophorial plate absent; cardinal process small; crura unknown. Similar to *Stenoscisma* externally and *Camarophorinella* internally but with stolidium. *Permian (?Artinskian):* Timor.——FIG. 1812,*1a–d.* **B. timorensis* (HAYASAKA & GAN), Besleo Beds; *a,* ventral valve exterior, ×1; *b,* articulated valves, lateral view, ventral on left, ×1; *c,* dorsal valve exterior, ×1 (Hayasaka & Gan, 1940); *d,* section near posterior end of specimen, ventral valve below, ×1 (Broili, 1916).

Neopsilocamara SHEN & others, 2000, p. 747 [**N. laevis*; OD]. Medium-sized, smooth, thick shells; weakly to moderately dorsibiconvex; outline subcircular; commissure rectimarginate; beak prominent, incurved over delthyrium; delthyrium apparently open but constricted by dorsal valve; valve edges nonoverlapping; stolidium unknown; well-developed spondylium duplex supported by low median septum extending anterior to spondylium; intercamarophorial plate absent; cardinal process unknown; crura unknown. Similar to *Camarophorinella* but lacking costae and fold and sulcus; similar to *Psilocamara* but not uniplicate and not strongly dorsibiconvex. *Upper Permian (Wuchiapingian [lower Tatarian]):* China (Tibet).——FIG. 1812,*2a–e.* **N. laevis*, Selong Group, Selong Xishan section; *a,* ventral valve exterior, ×1.5; *b,* posterior view, dorsal valve above, ×1.5; *c–e,* serial sections 0.54, 1.80, 2.29 mm from posterior end of specimen, dorsal valve above, ×2.5 (Shen & others, 2000).

Subfamily CYROLEXINAE Carlson, 2002

Careoseptum CARTER & POLETAEV, 1998, p. 139 [**C. septentrionalis*; OD]. Valves small, rounded pentameral in outline, strongly dorsibiconvex, smooth, strongly uniplicate, rarely weakly sulciplicate; valve edges nonoverlapping; beak short, erect to incurved; stolidium not apparent; delthyrium apparently open but constricted by dorsal valve; spondylium sessile posteriorly, elevated on low septum or more commonly free anteriorly; camarophorium supported by median septum only in extreme posterior, otherwise free; intercamarophorial plate absent; cardinal process unknown; crura unknown. *Upper Carboniferous (lower Moscovian):* Arctic Canada (northern Ellesmere Island).——FIG. 1812,*3a–k.* **C. septentrionalis*, Hare Fiord Formation, Hare Fiord; *a,* ventral valve exterior, ×2; *b,* articulated valves, anterior view, ventral below, ×2; *c,* articulated valves, lateral view, ventral on right, ×2; *d,* dorsal valve exterior, ×2; *e–k,* serial sections 1.4, 1.7, 1.8, 2.0, 2.4, 2.6, 3.0 mm from posterior end of specimen, ventral valve above, ×4 (Carter & Poletaev, 1998).

Family STENOSCISMATIDAE Oehlert, 1887 (1883)

Subfamily STENOSCISMATINAE Oehlert, 1887 (1883)

Liufaia WATERHOUSE, 2004, p. 84 [**Stenoscisma tetricum* GRANT, 1976, p. 185; OD]. Medium-sized shells; elongated, narrow triangular outline, maximum shell width near anterior margin; numerous, subequal costae may be absent from umbo or straight lateral flanks or present on entire valve, commonly bifurcating or intercalating, may be simple; commissure rather weakly uniplicate; valve edges between beak and stolidium smooth, flattened, with dorsal valve strongly overlapping ventral; stolidium present on both valves but discontinuous between fold and flanks; nature of delthyrium unclear; deep spondylium sessile, supported anteriorly only by very low median septum; intercamarophorial plate extending beyond anterior edge of hinge plate, may be buried in gerontic shell material; hinge plate flat, broad, narrowing distally; crura present, similar to *Stenoscisma*; cardinal process wedge shaped, with apex pointing posteriorly. Similar to *Stenoscisma* overall, but with triangular valve outline, costae that branch and intercalate, and weak uniplication. *Lower Permian (upper Artinskian):* Thai-

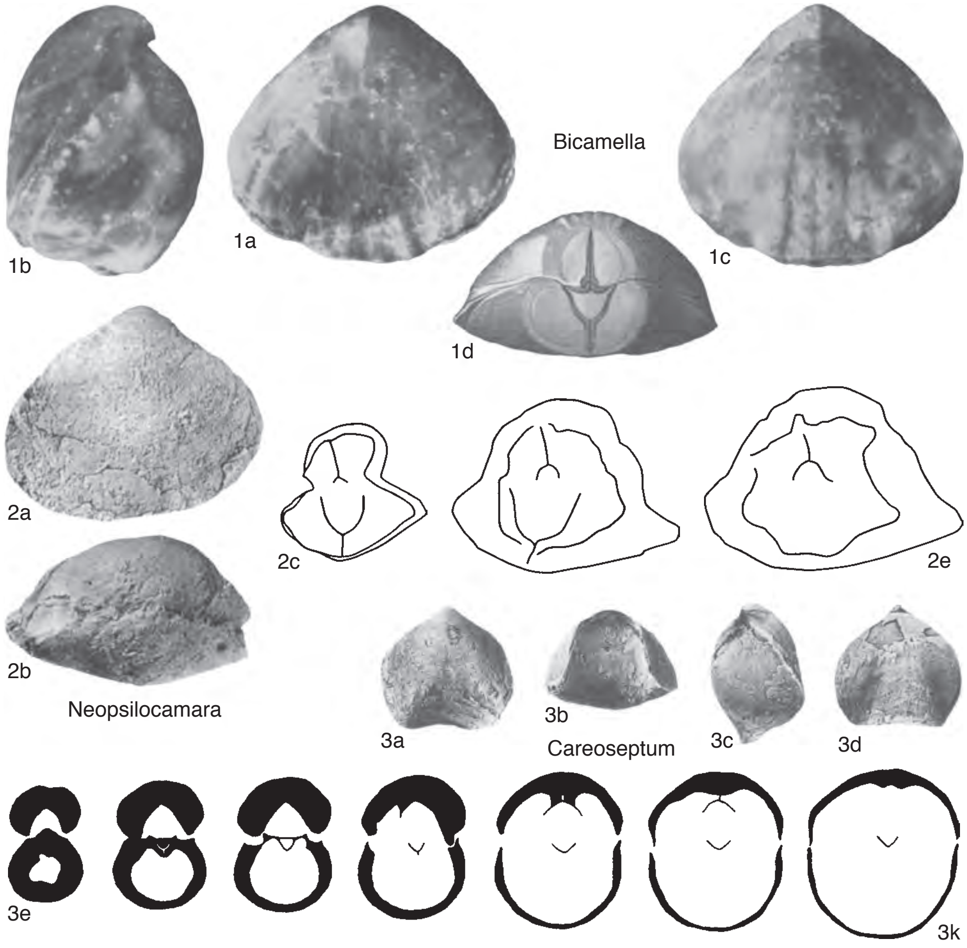


FIG. 1812. Psilocamaridae (p. 2717).

land, South Primoyre, Ussuriland, Japan, Inner Mongolia, northeastern China.——FIG. 1813,*1a–g*. **L. tetricum* (GRANT), Rat Buri Limestone, Ko Muk locality, southern Thailand; *a,* ventral valve exterior, ×1; *b,* articulated valves, lateral view, ventral on left, camarophorium and spondylium visible through broken exterior, ×1; *c,* articulated valves, anterior view, ventral below, stolidium visible, ×1; *d,* dorsal valve exterior, ×1; *e,* ventral valve interior, ×2; *f,* dorsal valve interior, ×1; *g,* detached camarophorium with crura and part of septum below, ×2 (Grant, 1976).

Sedecularia WATERHOUSE, 2004, p. 82 [**Stenoscisma glabra* WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 67; OD]. Small- to medium-sized smooth shells; outline oval to subrounded; valves only weakly dorsibiconvex; commissure weakly uniplicate to rectimarginate; extent of valve edge overlap

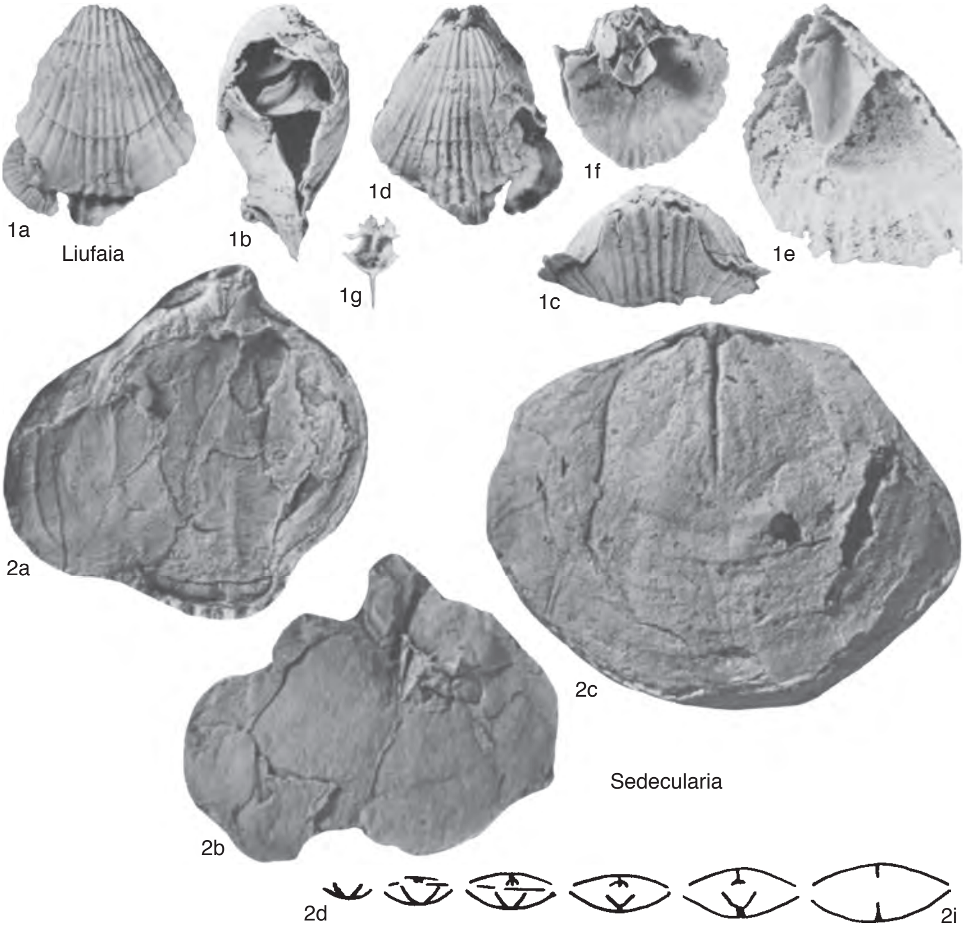


FIG. 1813. Stenoscismatidae (p. 2717–2719).

unknown; stolidium not apparent; beak straight; nature of delthyrium unclear; spondylium sessile, but supported anteriorly only by very low median septum extending a short distance anterior to spondylium; intercamarophorial plate high, short; cardinal process laminated; crura unknown. Similar to *Stenoscisma* but smooth, with subrounded and weakly dorsibiconvex valves. *Permian (Sakmarian–Kazanian):* Australia (Queensland).——FIG. 1813,*2a–i*. **S. glabra* (WATERHOUSE), Brae Formation, Bowen Basin; *a,* dorsal valve external mold with portion of ventral interior attached, ×3.2; *b,* ventral valve interior, partially crushed, ×2; *c,* dorsal valve internal mold, ×2; *d–i,* serial sections at 1 mm intervals from specimen posterior, ventral valve below, ×1 (Waterhouse, 2004).

DIMERELLOIDEA

Norman Savage

[University of Oregon]

Superfamily DIMERELLOIDEA Buckman, 1918

Family PEREGRINELLIDAE Ager, 1965

Subfamily DZIEDUSZYCKIINAE Savage, 1996

[Dzieduszykckiinae Savage, 1996, p. 257; *emend.,* Savage, herein]

Large, transversly ovate Peregrinellidae with strong, simple, full costae; bisulcate or with dorsal sulcus and weak ventral fold; dental plates short, vertical; dorsal median septum short; crura long, thin, closely set. *Upper Devonian–Lower Carboniferous*.

Ibergirhynchia Gischler, Sandy, & Peckmann, 2003, p. 293 [**Terebratula contraria* Roemer, 1850, p. 31; OD]. Medium to large with transversely ovate to subpentagonal shell and biconvex profile. Biconvex profile with greater convexity in ventral valve; weakly sulcate dorsal valve with corresponding fold in ventral valve; fold may be flat topped. Anterior commissure weakly sulcate. Costae numerous, arising at beaks. Dental plates short, convex toward valve walls, convergent ventrally; teeth small; ventral muscle field weakly impressed. Dorsal median ridge short, low; wide, flat hinge plates; crura thin, rodlike. *Lower Carboniferous (upper Viséan):* Germany.——Fig. 1814,*2a–k*. **I. contraria* (Roemer), Iberg Reef, Harz Mountains; *a–d,* neotype, dorsal, ventral, anterior, and posterior views, ×2.4; *e–k,* topotype, serial sections 0.3, 0.5, 0.9, 1.1, 1.2, 1.4, 1.5 mm from posterior, ×7 (Gischler, Sandy, & Peckmann, 2003).

Superfamily WELLERELLOIDEA Licharew, 1956

Family WELLERELLIDAE Licharew, 1956

Subfamily EXLAMINELLINAE new subfamily

[Exlaminellinae Savage, herein] [type genus, *Exlaminella* Carter & Poletaev, 1998, p. 142]

Wellerellidae with strong plicae in anterior part of shell. Dental plates and dorsal median septum absent. Hinge plates divided. *Upper Carboniferous (upper or lower Moscovian)*.

Exlaminella Carter & Poletaev, 1998, p. 142 [**E. insolita*; OD]. Small; subtriangular to subpentagonal outline with dorsibiconvex profile, strongly inflated anteriorly. Ventral beak small, slightly incurved; foramen and delthyrium not observed. Fold and sulcus starting at midlength; anterior commissure uniplicate; tongue high, wide, typically tridentate. Plicae strong, simple, angular, arising at midlength. Dental plates and dorsal median septum absent. Hinge plates divided; crura falciform. Dorsal and ventral muscle scars well impressed. *Upper Carboniferous (upper Bashkirian or lower Moscovian):* Arctic Canada.——Fig. 1814,*1a–l*. **E. insolita*, lower Hare Fiord Formation, Ellesmere Island; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l,* paratype, serial sections 0.6, 0.9, 1.0, 1.2, 1.5, 1.8, 2.2, 2.4 mm from posterior, ×4 (Carter & Poletaev, 1998).

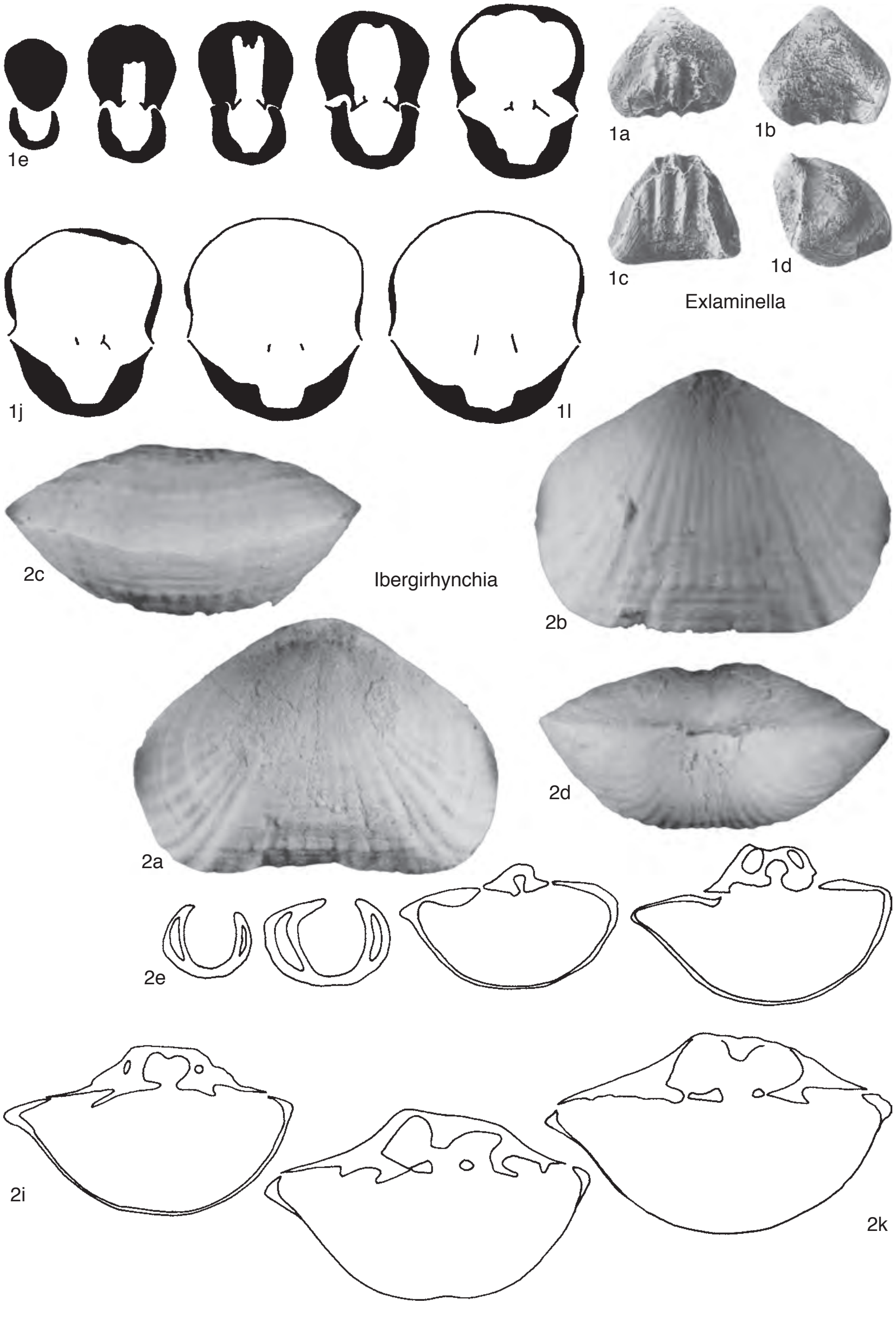


FIG. 1814. Peregrinellidae and Wellerellidae (p. 2720).

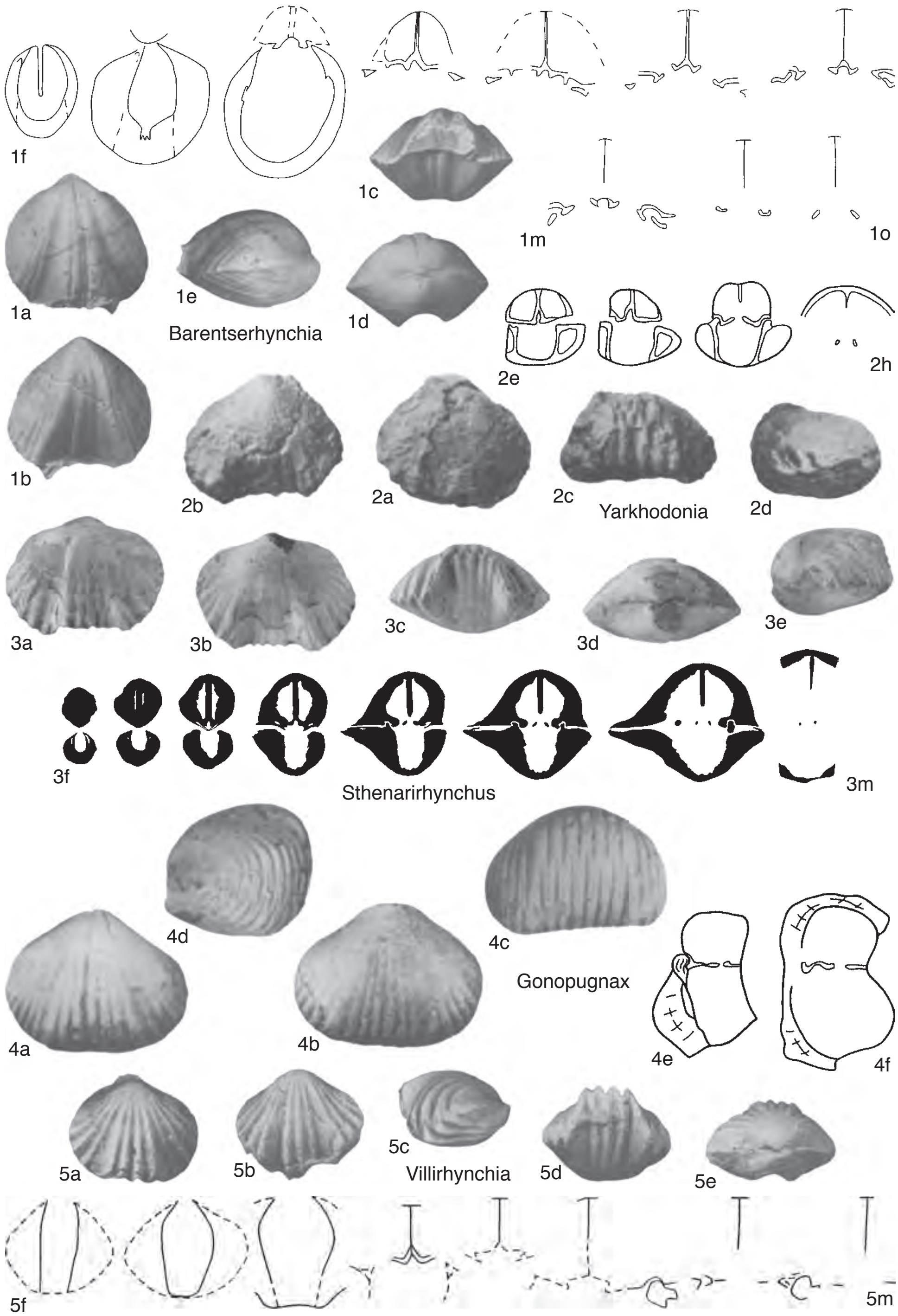


FIG. 1815. Synonyms (p. 2723).

SYNONYMS

Junior synonym of **Orbiculatisinurostrum** Sartenaer, 1984, p. 2. See also Savage in Savage & others, 2002, p. 1142.

Barentserhynchia Tcherkesova, 1999, p. 39 [**B. gorbovensis*; OD]. Medium size, subcircular to subpentagonal outline; biconvex profile; lateral and anterior slopes gentle. Beak erect to incurved. Fold and sulcus extending from umbones, progressively widening anteriorly; fold with medium groove that divides anteriorly, sulcus with low median ridge that divides anteriorly; anterior commissure uniplicate to sulciplicate. Costae low, weak, arising at umbones, increasing by bifurcation. Dental plates very short. Dorsal median septum thin, high, extending over one-fifth valve length; septalium short; hinge plates short, divided; crura closely set, slightly flattened rods, curving into ventral valve distally. *Upper Devonian (Frasnian):* Russia.——Fig. 1815,*1a–o*. **B. gorbovensis*, Voroninskaya Formation, lower part of Menshikov Horizon, southwestern William Island, northwestern Novaya Zemlya, northern Russia; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o*, topotype, serial sections 0.2, 0.3, 0.4, 0.7, 0.8, 0.9, 1.0, 1.1, 1.3, 1.7 mm from posterior, scale not given (Tcherkesova, 1999).

Junior synonym of **Plionoptycherhynchus** Sartenaer, 1979, p. 537. See also Savage in Savage & others, 2002, p. 1151.

Sthenarirhynchus Sartenaer, 1999c, p. 275 [**S. dionanti*; OD]. Medium to large, with transversely ovate outline and dorsibiconvex profile; gentle lateral slopes. Beak erect to incurved; foramen obscured by dorsal umbo. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, trapezoid, serrate. Costae distinct, subangular, simple, extending from umbones, present on fold, sulcus, and flanks. Dental plates barely visible in serial sections at extreme posterior; ventral muscle field narrow, deeply impressed in thick shell material. Dorsal median septum long, high, thick; septalium short; hinge plates dividing immediately anterior of septalium; crura closely placed, fine, rodlike, straight. *Upper Devonian (middle Frasnian):* Belgium.——Fig. 1815,*3a–m*. **S. dionanti*, *Palmatolepis punctata* Zone, Marloie railway station, west of Dinant, southern Belgium; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–m*, serial sections 0.65, 0.8, 1.15, 1.45, 1.65, 1.9, 2.2, 3.5 mm from posterior, ×3.25 (Sartenaer, 1999c).

Junior synonym of **Plionoptycherhynchus** Sartenaer, 1979, p. 537. See also Savage in Savage & others, 2002, p. 1151.

Villirhynchia Tcherkesova, 1999, p. 41 [**V. villiamensis*; OD]. Medium size; transversely ovate to subpentagonal outline and biconvex profile; gentle lateral slopes. Ventral beak erect to incurved. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, extending from umbones; approximately 4 on fold, 3 in sulcus, several on flanks. Dental plates short, slightly convergent ventrally. Dorsal median septum long, high, thin; septalium short; hinge plates horizontal, divided anterior of septalium; crura closely set. *Upper Devonian (Frasnian):* Russia.——Fig. 1815,*5a–m*. **V. villiamensis*, Voroninskaya Formation, lower part of Menshikov Horizon, southeastern coast of William Island, northwestern Novaya Zemlya, northern Russia; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–m*, topotype, serial sections 0.2, 0.4, 0.6, 0.8, 0.9, 1.0, 1.1, 1.3 mm from posterior, scale not given (Tcherkesova, 1999).

Junior synonym of **Basilicorhynchus** Crickmay, 1952, p. 1. See also Savage in Savage & others, 2002, p. 1156.

Yarkhodonia Baranov in Alekseeva & others, 1996, p. 78 [**Y. recta;* OD]. Subcircular outline with dorsibiconvex profile. Beak erect to incurved. Fold and sulcus arising at about midlength. Anterior commissure uniplicate; tongue serrate. Costae few, coarse, subangular, restricted to anterior. Dental plates short, slightly convergent ventrally. Dorsal median septum short, low; septalium small, V-shaped; hinge plates divided anterior of septalium; crura closely set proximally, unknown distally. *Upper Devonian (lower Frasnian)*: northeastern Russia.——Fig. 1815,*2a–h*. **Y. recta*, Yarkhodonskaya Formation, *Mucrospirifer novosibiricus* Zone, upper reaches of Malii Yarkhodon River, Sredne Prikolimbyi, northeastern Asiatic Russia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h*, paratype, serial sections 1.5, 1.7, 2.0, 2.7 mm from posterior, ×5 (Alekseeva & others, 1996).

Junior synonym of **Dogdoa** Baranov, 1982, p. 42. See also Savage in Savage & others, 2002, p. 1120.

Gonopugnax Baranov in Alekseeva & others, 1996, p. 94 [**G. galkini*; OD]. Medium size; transversely subpentagonal outline; dorsibiconvex profile. Beak erect. Fold and sulcus arising at umbones; strong anteriorly; anterior commissure uniplicate, tongue distinct, wide, rounded to trapezoid. Costae medium, simple, rounded, arising at umbones, flattened and grooved on *paries genicularis*; marginal spines present. Dental plates absent or mostly buried in callus. Hinge plates divided, horizontal; septalium, dorsal septum, and crura unknown. *Lower Devonian (lower Lochkovian):* eastern Siberia.——Fig. 1815,*4a–f*. **G. galkini*, Sagyr Formation, Selennyakh ridge; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, right bank of Talyndzha River, Krivoy stream, ×1.1; *e–f*, paratype, two serial sections, intervals and distances from posterior, right bank of Talyndzha River, Gon stream, scale not given (Alekseeva & others, 1996).

Synonym of **Tchernarhynchia** Tcherkesova, 1998, p. 44, chosen herein by first revising author. See also Savage, herein, p. 2711.

Kumzharhynchia Tcherkesova, 1998, p. 41 [**K. bondarevi*; OD]. Shell large, transversely ovate

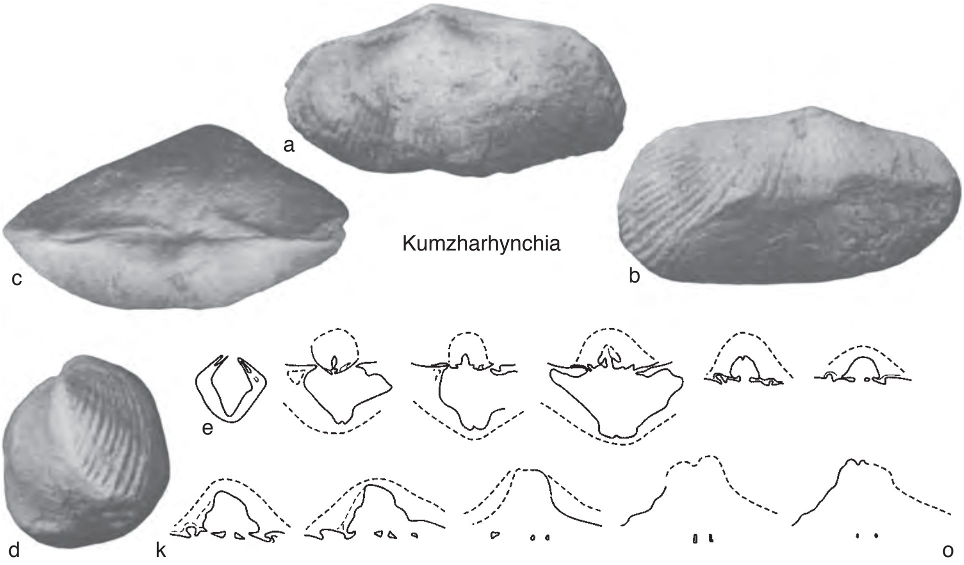


FIG. 1816. Synonyms (p. 2723–2724).

(holotype probably transversely deformed); dorsibiconvex profile, expanded anteriorly by fold. Ventral beak incurved. Fold and sulcus wide, arising at about one-third shell length; anterior commissure uniplicate. Costae fine, numerous, dichotomizing, developed over whole shell surface. Dental plates short; teeth poorly known. Dorsal median septum poorly known; septalium short, poorly known; hinge plates divided; crural bases triangular in section; crura rodlike, thin, closely set. *Upper Devonian (middle Frasnian):* Russia.——FIG. 1816*a–o.* **K. bondarevi*, upper Zhandr Horizon, upper reaches of Kumzha River, South Island of Novaya Zemlya; *a–d*, holotype, dorsal, ventral, posterior, and lateral views, ×1; *e–o*, paratype, serial sections, intervals and scale not given (Tcherkesova, 1998).

NOMINA DUBIA

The following genera are considered *nomina dubia,* in most instances because the type material is insufficiently well preserved or insufficiently well described to warrant generic status at this time.

Altaethyrella SEVERGINA, 1978, p. 38 [**A. megala*; OD]. Shell subpentagonal; fold and sulcus from umbones; anterior commissure uniplicate, tongue moderately high. Costae arising at beaks. Short dental plates. Short, ridgelike cardinal process; lacking septalium and dorsal median septum. [The figures of holotype mold specimen are poor, and the internal features are unclear. This genus is best considered as a *nomen dubium* until better topotype material is available. KULKOV and SEVERGINA (1989, p. 160–161) decided to make *Otarorhyncha* a junior subjective synonym of *Altaethyrella* and assign it to the Ancistorhynchoidea, a decision followed by POPOV, NIKITIN, and COCKS (2000), who assigned their subtriangular, more elongate material to *Otarorhyncha otarica* (RUKAVISHNIKOVA), the type species of *Otarorhyncha*. The type material of *Otarorhyncha* has a short median septum, however, and appears to belong to the Rhynchotrematoidea. The photographs of the calcareous topotype specimen provided for the revised *Treatise* (SAVAGE in SAVAGE & others, 2002, p. 1048, Fig. 707,*3a–d*) by NIKIFOROVA show a transversly subpentagonal specimen with distinctive ribbing different from that of the mold material of POPOV, NIKITIN, and COCKS (2000), which clearly lacks a median septum. Thus, assigning the material of POPOV, NIKITIN, and COCKS to *O. otarica* is unsound and does not help clarify the features of *Altaethyrella.*] *Upper Ordovician (Ashgill):* Altai, Siberia.——FIG. 1817,*4a–d.* **A. megala*, northwestern Altai, Kolmogorovo area, locality 12 of Severgina, Ordovsky suite; holotype, dorsal, ventral, anterior, and posterior views of internal mold, ×2 (Severgina, 1978).

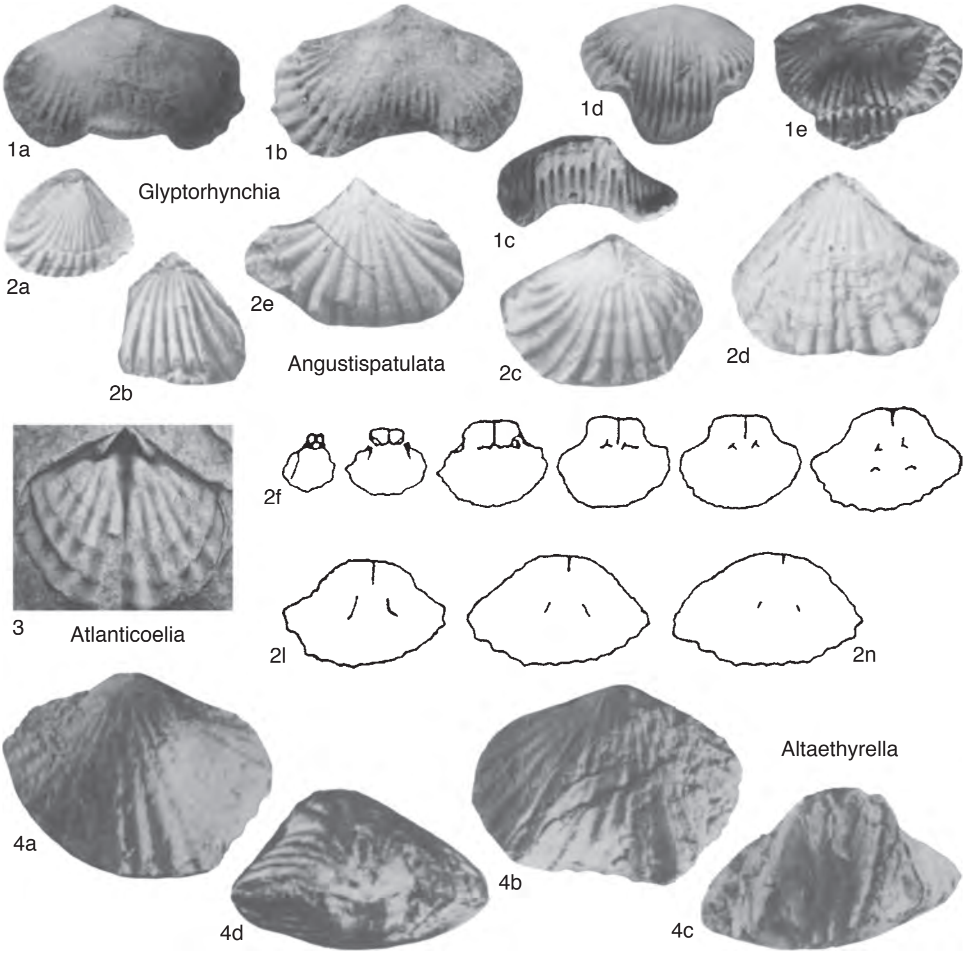


Fig. 1817. Nomina Dubia (p. 2724–2726).

Angustispatulata Qian & Roberts, 1995, p. 265 [**A. campbelli*; OD]. Small with subpentagonal outline and biconvex profile; foramen small, deltidial plates conjunct. Fold and sulcus arising at umbones; anterior commissure uniplicate, tongue high, serrated; costae strong, simple, angular; arising at beaks, covering whole of shell. Dental plates short. Dorsal median septum long, slender; septalium short, without cover plate; hinge plates dividing immediately anterior of septalium; crura highly curved ventrally, laterally flattened. [Holotype (internal mold) is poorly illustrated, and features are uncertain. Other photographs of molds are inadequate. Serial sections are of specimen from a locality and formation different from that of the holotype. This genus should be considered a *nomen dubium* until it is reillustrated using better topotype specimens.] *Lower Carboniferous (upper Tournaisian)*: eastern Australia.——Fig. 1817,*2a–n*. **A. campbelli*, *Schellwienella burlingtonensis* brachiopod Zone, New England area of New South Wales; *a–b*, holotype, Ararat Formation, two views of internal mold, ×2; *c*, hypotype, mold of dorsal valve interior, ×2; *d*, mold of ventral valve exterior, ×2; *e*, mold of ventral valve interior, ×2; *f–n*, hypotype, serial sections, Namoi Formation, intervals not given, ×1.5 (Qian & Roberts, 1995).

Atlanticoelia KOCH, 1996, p. 1088 [**Atrypa acutiplicata* CONRAD, 1841, p. 54; OD]. Small to medium, subcircular to subpentagonal outline, planoconvex to biconvex lateral profile; costae simple, strong, rounded crests, extending from beaks; broad dorsal sulcus. Interior poorly known. [This genus is best considered a *nomen dubium* until the type species is fully described and a lectotype designated. CONRAD, 1841, p. 54, gave a brief description of material from the Onondaga Limestone near Waterville, New York, but without illustrations. HALL, 1867, pl. 57,*30–39,* and HALL & CLARKE, 1895, pl. 53,*32–35,* described and illustrated the exterior of a specimen assigned to the species but from Jamesville, New York, 40 miles from Waterville, along with illustrations of interiors from Waterloo, New York, 50 miles west of Jamesville. KINDLE, 1912, p. 84, described the species but used interiors from Pennsylvania, Virginia, and Maryland. KOCH (1996, p. 1088, fig. 1), in proposing the new genus, illustrated a single dorsal internal mold from Rosendale, New York, many miles from all the above localities, and gave emphasis to the presence of a large, knoblike cardinal process, not noted by CONRAD, HALL, or KINDLE.] *Lower Devonian:* USA (New York).——FIG. 1817,*3*. **A. acutiplicata* (CONRAD); dorsal internal mold, ×1 (Koch, 1996).

Glyptorhynchia SHEN & HE, 1994, p. 449 [**G. lens*; OD]. Shell small, transversely ovate. Fold and sulcus from about midlength; anterior commissure uniplicate, tongue high. Costae numerous, simple, arising at umbones. Dental plates short. Hinge plates reported to be divided. [The interior of the genus is uncertain, therefore it is difficult to assign to a family or a genus. This genus is best considered as a *nomen dubium.*] *Upper Permian (Changhsingian)*: China.——FIG. 1817,*1a–e*. **G. lens*, Changhsing Formation, Guiding, Guizhou; *a–b*, holotype, dorsal and ventral views; *c–e*, paratype, anterior, ventral, and dorsal views, ×2 (Shen & He, 1994).

POST-PALEOZOIC RHYNCHONELLIDA

MIGUEL O. MANCEÑIDO,[1] E. F. OWEN,[2] and D.-L. SUN[3]

[[1]La Plata Natural Sciences Museum, Argentina; [2]retired from The Natural History Museum, London; and [3]Nanjing Institute of Geology and Palaeontology]

Since the manuscript for *Treatise* Part H, volume 4 (KAESLER, 2002) was submitted, not only were about a dozen new genera proposed, but a number of contributions addressing matters relevant for a better understanding of the order have appeared, some of which are summarized below.

The importance of crural types for classification and for unravelling major evolutionary lineages, when used in conjunction with other anatomical features, has been confirmed in an overview of the systematic relationships among the seven superfamilies presently recognized (MANCEÑIDO & OWEN, 2001). Individual crural types discussed and figured by SAVAGE and others (2002, p. 1036–1040, fig. 700–702) may be assembled according to structural and cross-sectional variation into four fundamental groups, as follows.

Arcual group, including arcuiform, spinuliform, plus distally expanded (=luniform) and spiculated variants, and possibly also clivuliform types.

Septifal group, comprising falciform, subfalciform, hamiform (=ex prefalciform), and septiform types, and certain structural or distal end modifications.

Raducal group, including raduliform, calcariform, and canaliform types (plus variations of their cross section and of their distal ends).

Ensimergal group, comprising mergiform, submergiform (=ex terebratuliform), ensiform, maniculiform, and perhaps also ciliform types (cf. MANCEÑIDO, 1998, 2000).

Certain features of the shell structure may prove helpful for the broad classification of basic stocks, although further work is needed, as noted by LEIDHOLD (1921) and AGER (1957, 1965), who called the attention to the potential value of the so-called shell mosaic (*Schalenmosaik* or *Schuppenpanzerstruktur*), occasionally observable on the inner surface of either valve and on internal molds of exceptionally well-preserved material. The mosaic results from regular stacking of calcitic fibers of the secondary layer of the shell wall, is very stable, and yields a characteristic geometrical pattern on the inside valve floor (WILLIAMS, 1997, Fig. 242.1, 242.3). Transverse sections of the valves may also show a characteristic fabric, particularly under SEM (WILLIAMS, 1997, Fig. 242.2, 242.4). Recent additional studies on Mesozoic and extant rhynchonellides (MOTCHUROVA-DEKOVA & TADDEI-RUGGIERO, 2000; MOTCHUROVA-DEKOVA, 2001; MOTCHUROVA-DEKOVA, SAITO, & ENDO, 2002) expanded earlier work (e.g., KAMYSHAN, 1977; SMIRNOVA, 1984) and report at least two distinct microstructural patterns. These are respectively made up of finer, isometric fibers, and less uniform, coarser, rhombic fibers, and have been claimed to have suprageneric significance. In fact, thus far the former, leptinoid type (fiber average size 5–30 µm) has been recorded in hemithiridoids and rhynchonelloids (Fig. 1818.1–1818.5), whereas the second, eurinoid type (fiber size range 40–140 µm wide) has been reported widely among pugnacoids and norelloids, seemingly even in a rhynchotetradoid (Fig. 1818.6–1818.12). Although little is known at present about the possible influence of ontogenetic stage and environmental factors upon mosaic coarseness and morphology, this is a line of research worth pursuing further.

Similarly, patterns of the mantle canal system represent fairly stable characters, yet apparently exhibit interesting variations between major stocks. Although illustrations of vascular markings in older literature often do not match the detail recorded in modern studies, certain broad indications

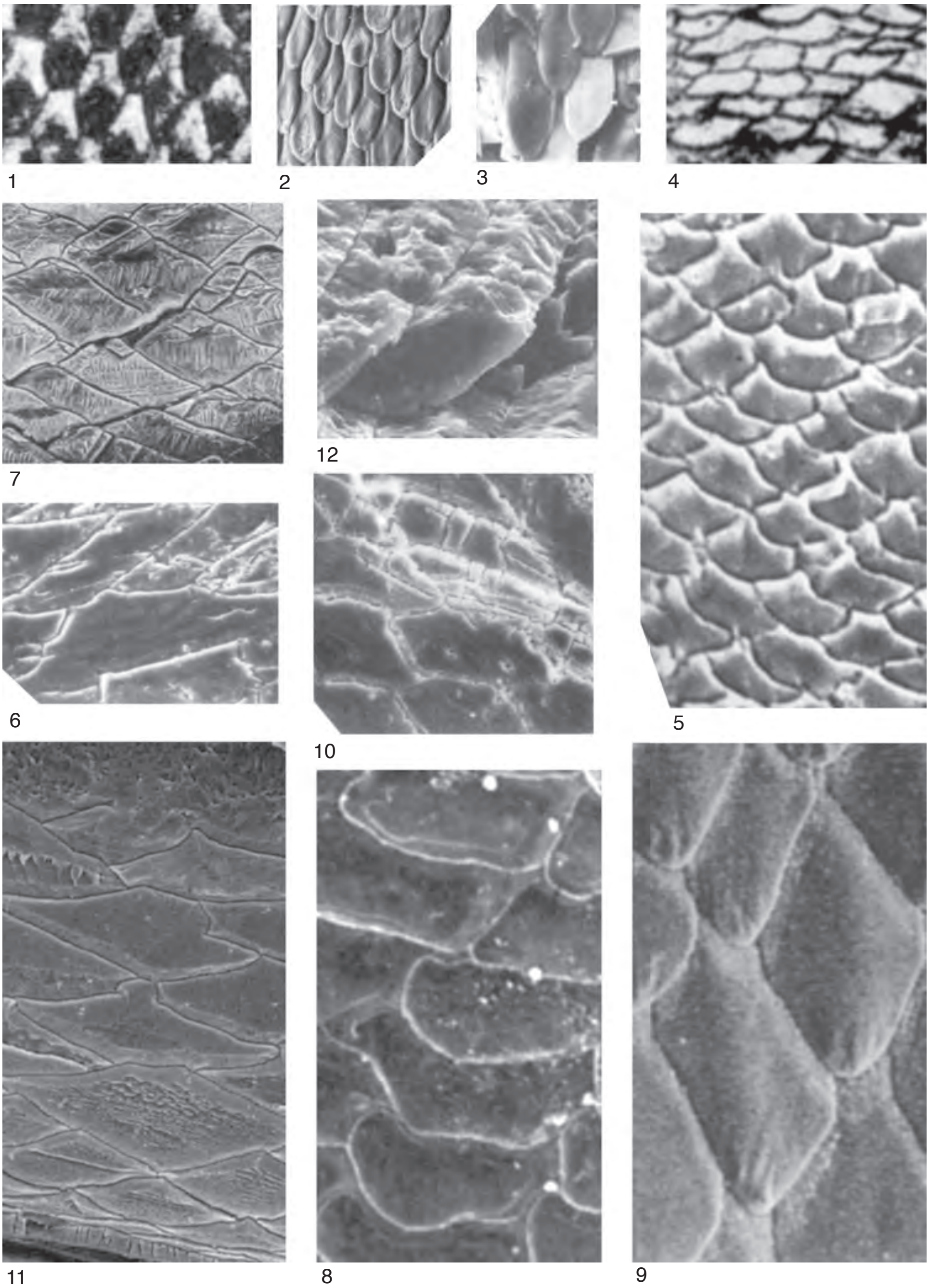


FIG. 1818. *For explanation, see facing page.*

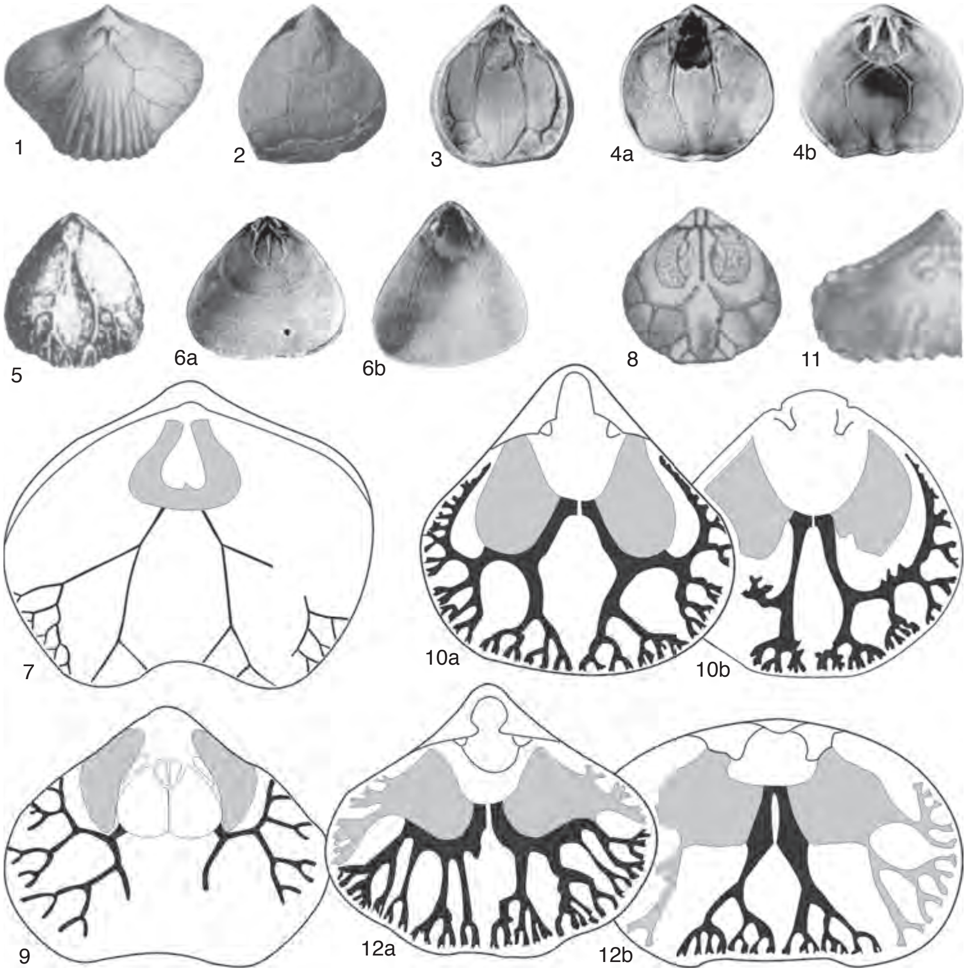


FIG. 1819. Mantle canal patterns, selected examples, both fossil (1, 2, 5, 7, 8, 9, 11) and extant (3, 4, 6, 10, 12); *1–4*, pugnacoids; *5–6*, norelloids; *7–8*, rhynchonelloids; *9–12*, hemithiridoids; *1*, Upper Jurassic *Lacunosella,* ×0.68 (Quenstedt, 1871 in 1868–1871); *2*, upper Oligocene *Aetheia*, ×1.26 (Cooper, 1959); *3*, Recent *Basiliola*, ×1.32 (Cooper, 1959); *4*, Recent *Rhytirhynchia,* ×1.32 (Cooper, 1959); *5*, Mid-Triassic *Norella,* ×1.2 (Bittner, 1890); *6*, Recent *Hispanirhynchia,* ×1.1 (Cooper, 1959); *7*, Upper Triassic *Superbirhyncha,* ×2 (Siblík, 2002); *8*, Lower Jurassic *Cuneirhynchia,* ×2 (Quenstedt, 1871 in 1868–1871); *9*, Upper Cretaceous *Bohemirhynchia,* approximately ×2.5 (Nekvasilová, 1973); *10*, Recent *Hemithiris,* approximately ×1.2 (Williams & Rowell, 1965b); *11*, Upper Jurassic *Torquirhynchia,* approximately ×0.5 (Quenstedt, 1871 in 1868–1871); *12*, Recent *Notosaria,* approximately ×1.5 (Williams & Rowell, 1965b).

FIG. 1818. Shell mosaic and secondary layer cross-sectional patterns, selected examples, both fossil (1, 3, 4, 5, 6, 7, 10, 12) and extant (2, 8, 9, 11) (all approximately ×500); *1*, rhynchonelloid; *2–5*, hemithiridoids; *6–7*, pugnacoids; *8–11*, norelloids; *12*, rhynchotetradoid; *1*, mosaic of Upper Jurassic *Rhynchonella* (Ager, 1957); *2*, mosaic of Recent *Notosaria* (Williams, 1990); *3*, mosaic of upper Aptian *Cyclothyris* (Smirnova, 1984); *4*, cross section of Upper Triassic *Fissirhynchia* (Radulović, Urošević, & Banjac, 1992); *5*, cross section of Mid-Jurassic *Isjuminella* (Taddei-Ruggiero & Ungaro, 1984); *6*, cross section of Lower Cretaceous *Lacunosella* (Smirnova, 1984); *7*, cross section of Upper Cretaceous *Costerymnaria* (Motchurova-Dekova & Taddei-Ruggiero, 2000); *8*, mosaic of Recent *Tethyrhynchia* (Logan & Zibrowius, 1994); *9*, mosaic of Recent *Frieleia* (Motchurova-Dekova, Saito, & Endo, 2002); *10*, cross section of Lower Cretaceous *Monticlarella* (Smirnova, 1984); *11*, cross section of Recent *Parasphenarina* (Motchurova-Dekova, Saito, & Endo, 2002); *12*, cross section of Upper Triassic *Austrirhynchia* (Michalík, 1993).

of kinship may be recognizable. Thus, a simplified, widely dichotomous, sparsely distributed pattern seems prevalent among Mesozoic and Recent pugnacoids (basilioline, acanthobasilioline, lacunoselline, and aetheine basiliolids; Fig. 1819.1–1819.4) and is similar to what is known in a few fossil and extant norelloids (norellid and frieleiid; Fig. 1819.5–1819.6). On the other hand, among Recent and fossil hemithiridoids, peripherally more densely branched patterns are known, sometimes inequidistributed saccate (e.g., hemithiridids and tetrarhynchiids) and sometimes apocopate lemniscate (notosariids and cyclothyridids; Fig. 1819.9–1819.12). The pattern in rhynchonelloids (Fig. 1819.7–1819.8) looks similar to that shown in hemithiridids and perhaps is somewhat intermediate between it and the pattern in basiliolids.

As pointed out by Manceñido and Owen (2001), these interim results suggest a promising future and may stimulate the necessary additional research. It may be significant that molecular phylogenetic studies on living species result in hierarchical taxonomic relationships consistent with those achieved by morphological comparative studies, providing an assurance that classical paleontological methods remain a useful approach (see Williams, 2002, p. xxviii).

Superfamily PUGNACOIDEA Rzhonsnitskaia, 1959

Family BASILIOLIDAE Cooper, 1959

Subfamily PAMIRORHYNCHIINAE Ovcharenko, 1983

Orbirhynchopsis Sun & Zhang, 1998, p. 227 [278] [**O. tianshuihaiensis*; OD]. Small, gently biconvex, roundly oval in outline; beak short, nearly straight; beak ridges angular; foramen circular, permesothyrid; deltidial plates triangular, barely touching; fold and sulcus scarcely developed; commissure rectimarginate to slightly and broadly uniplicate; ornamented with numerous low, round costae, occasionally bifurcating; umbonal region with fine costae or smooth. Dental plates conspicuous and slightly divergent ventrally; umbonal chambers narrow; hinge plates divided; crura falciform; pedicle collar present. [This genus is readily referable to Pamirorhynchiinae, being very similar to *Orbirhynchia* Pettit and *Rahouiarhynchia* Tchoumatchenko. Thus, in the previous entry for the latter (Savage & others, 2002, p. 1208), the queried record from China may be deleted.] *Middle Jurassic (Callovian):* China (northern Karakorum, Tibet).——Fig. 1820,*1a–l*. **O. tianshuihaiensis*, Longshan Formation, Tianwendian and Tianshuihai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP121059, ×1.5; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.4, 1.0, 1.5, 1.8, 2.0, 2.3, 2.5, 2.9, NIGP 121060, approximately ×4 (Sun & Zhang, 1998).

Family ERYMNARIIDAE Cooper, 1959

Subfamily ERYMNARIINAE Cooper, 1959

Costerymnaria Motchurova-Dekova & Taddei-Ruggiero, 2000, p. 182 [**C. italica*; OD]. Erymnariinae with numerous, well-developed costae, beginning from the umbonal region; shell elongate-subtriangular to subcircular, strongly subequibiconvex; anterior commissure asymmetrically twisted. Internal characters as in *Erymnaria*; dental plates convex in cross section; septiform crura, sometimes lyre shaped distally. *Upper Cretaceous (Cenomanian–upper Campanian):* Italy.——Fig. 1820,*2a–l*. **C. italica*, Cenomanian, Matese Group, Molise; *a–d,* holotype, dorsal, lateral, anterior, ventral views, PMNUF 6/M 16999, ×2; *e–l,* transverse serial sections, distances in mm from ventral umbo, 2.1, 2.8, 3.2, 3.8, 4.3, 4.7, 5.2, 5.4, PMNUF 7/M 16998-2, ×2.5 (Motchurova-Dekova & Taddei-Ruggiero, 2000).

Superfamily WELLERELLOIDEA Licharew, 1956

Family PONTISIIDAE Cooper & Grant, 1976

Subfamily PONTISIINAE Cooper & Grant, 1976

Saubachia Siblík, 2000, p. 421 [**S. inflata;* OD]. Small, equibiconvex shells, globose, subtrigonal in outline; pronounced smooth stage, initial ribbing or a few rounded costae anteriorly; strong uniplication, fold slightly elevated; beak strong and low, suberect. Delthyrial cavity quadrate in cross section between thin, subparallel dental plates, lateral umbonal cavities semicircular; pedicle collar not observed; hinge teeth strongly crenulated, laterally expanded,

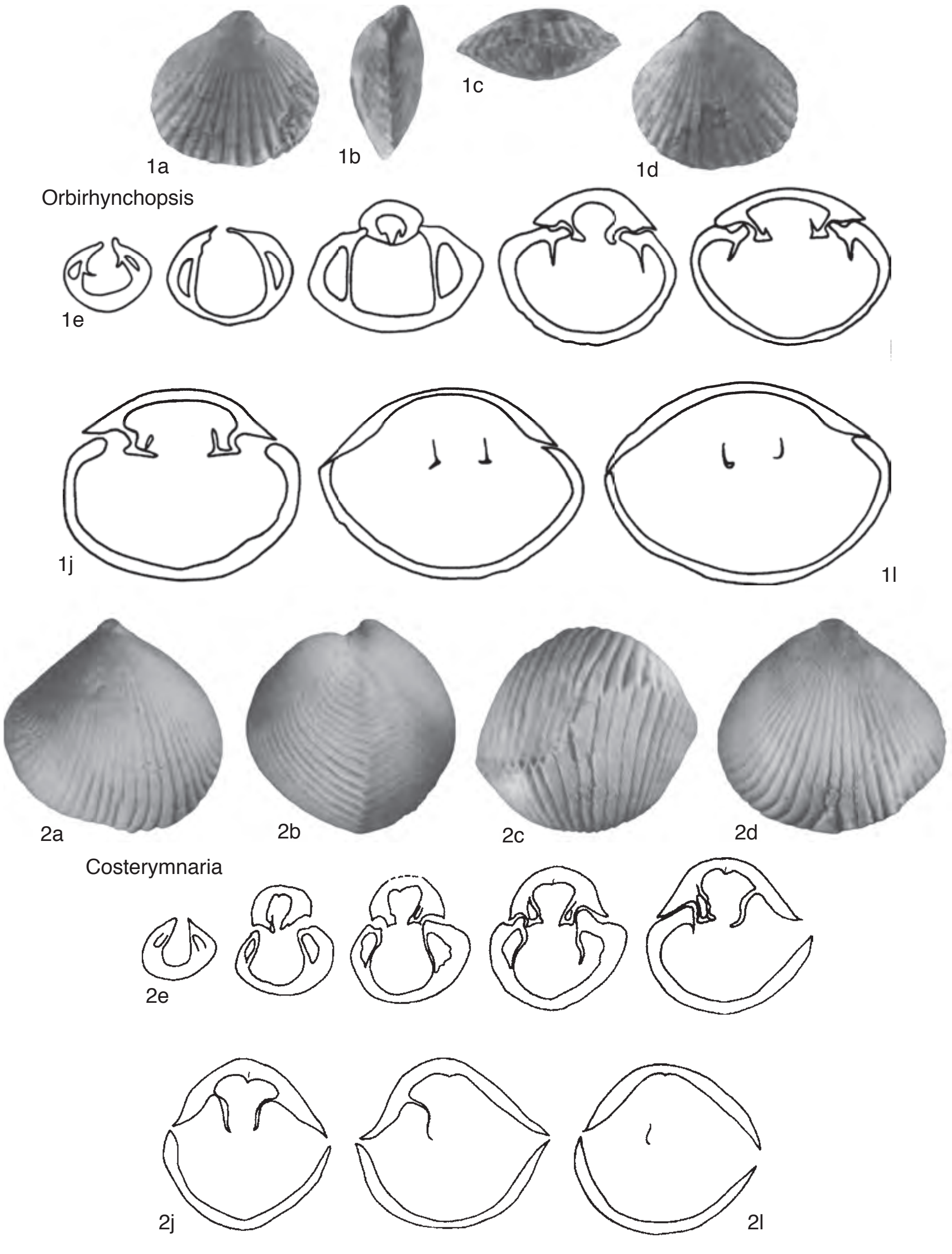


FIG. 1820. Basiliolidae and Erymnariidae (p. 2730).

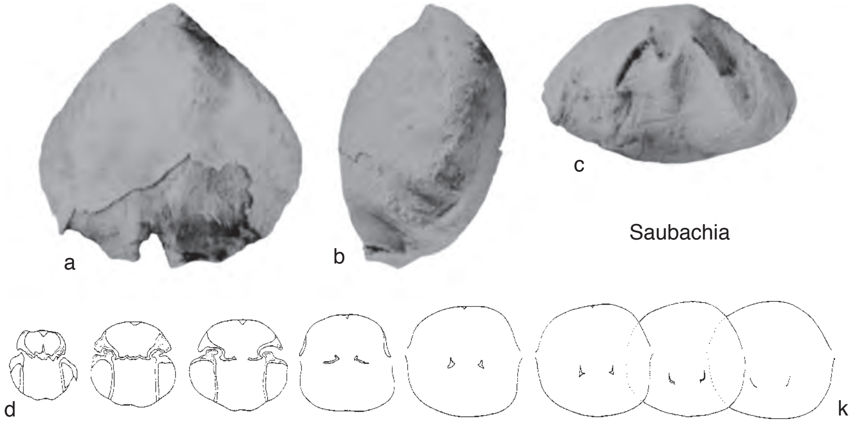


FIG. 1821. Pontisiidae (p. 2730–2732).

with hollows for reception of outer and inner socket ridges; septalium absent; hinge plates fused, their inner and outer parts characteristically delimited; dorsal median septum confined posteriorly only and reduced anteriorly to a low ridge; alleged raduliform crura, convex outward in cross section, fitting better into hamiform type. [This monotypic new genus was originally referred to Wellerellidae, which is consistent with hamiform (rather than raduliform) crura seen in sections, yet, it may likewise belong in Pontisiidae, as suggested by entire hinge plates and strong overall similarity to *Bodrakella* MOISEEV (it is probably ancestral to, if not synonymous with, the latter).] *Lower Jurassic (Hettangian):* Alps (Austria, Germany).—— FIG. 1821*a–k*. **S. inflata*, Kendlbach Beds, Saubachgraben, near Salzburg; *a–c,* holotype, dorsal, lateral, anterior views, coll. IPW, ×3; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.8, 1.1, 1.5, 1.7, 2.1, 2.25, ×2 (Siblík, 2000).

Superfamily RHYNCHONELLOIDEA d'Orbigny, 1847

Family RHYNCHONELLIDAE d'Orbigny, 1847

Subfamily RHYNCHONELLINAE d'Orbigny, 1847

Choffatirhynchia GARCÍA JORAL & GOY, 2004, p. 242 [**Rhynchonella Vasconcellosi* CHOFFAT in DUBAR, 1931, p. 122; OD]. Medium-sized, dorsibiconvex shells, subtetrahedral to globose, usually wider than long; well-marked subrectangular uniplication in anterior commissure, but rather ill-defined trilobation; with numerous, dense, simple, subangular costae (5 to 8 on fold) that extend full length (somewhat effaced near umbos, at most); suberect, narrow, prominent beak; foramen relatively large, cardinal area ill developed. Narrow, shallow septalium; dental plates thin, subparallel or slightly convergent ventrally, in section; crura raduliform. [Although this new genus was originally placed among Rhynchonellinae, certain affinities with Ivanoviellines may not be disregarded.] *Lower Jurassic (Toarcian):* Spain, Portugal, France, northern Africa.——FIG. 1822*a–k*. **C. vasconcellosi* (CHOFFAT), lower Toarcian, Turmiel Formation, Ariño, Teruel, Spain; *a–c,* dorsal, lateral, anterior views, DPUCM Ar.11.402, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.9, 2.1, 2.5, 3.3, 4.0, 4.7, 5.0, DPUCM Ar.11.501, ×2.6 (García Joral & Goy, 2004).

Grestenella SIBLÍK, 2000, p. 435 [**Rhynchonella austriaca* SUESS, 1854, p. 53; OD]. Medium-sized shells, subtrigonal to subcircular in outline, dorsibiconvex; with strong uniplication in anterior commissure, and high fold well developed in anterior half of shell; multicostate, sharp, angular costae, rarely short, smooth area around umbones; beak usually high and strong, but shorter, slightly incurved in some globular specimens; beak ridges delimiting small impressed planareas. Delthyrial cavity subquadrate in cross section, lateral umbonal cavities subtrigonal; dental plates subparallel or slightly divergent ventrally; sometimes with pedicle collar and double deltidial plates; hinge teeth strong, straight, and crenulated; conspicuous, deep, v-shaped septalium between subhorizontal hinge plates; raduliform crura distally curving toward ventral valve, with strongly expanded ventral parts. [This monotypic new genus is referred to Rhynchonellidae, established mainly for subcynocephalous shells with unusual development of crural terminations; seems most closely related to *Rhynchonelloidea* BUCKMAN.] *Lower Jurassic:* Austria (Alps, pre-Alps).——FIG. 1823*a–m*. **G. austriaca* (SUESS), Sinemurian–Pliensbachian, Gresten Limestone, Pechgraben, near Weyer; *a–c,* lectotype, dorsal, lateral, anterior views, GBA 1854/6/13, ×1.5 (new,

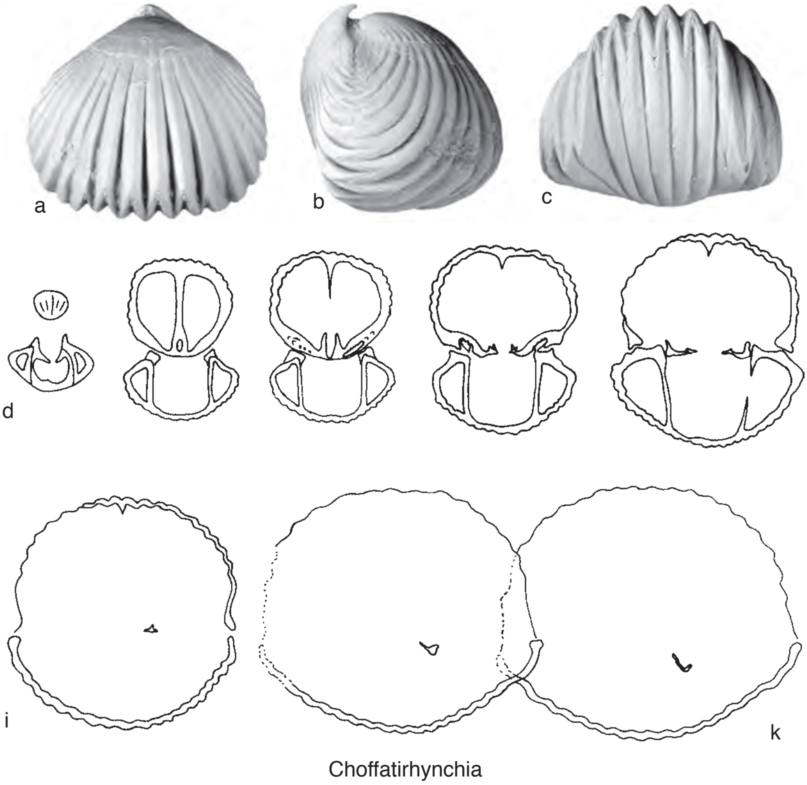


FIG. 1822. Rhynchonellidae (p. 2732).

courtesy of M. Siblík); *d–m,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.0, 2.0, 2.4, 2.6, 3.1, 3.7, 4.6, 5.2, 5.4, 5.6, coll GBA, ×1.5 (Siblík, 2000).

Subfamily URALORHYNCHIINAE Manceñido & Owen, 2002

Superbirhyncha SIBLÍK, 2002, p. 101 [**Rhynchonella superba* BITTNER, 1890, p. 228; OD]. Medium to large, subtrigonal to rounded pentagonal in outline, width exceeding length in most cases; strongly dorsibiconvex in profile, ventral valve almost flat sometimes; fold and sulcus well developed anteriorly, but poorly detached from lateral slopes; anterior commissure with broad, strong uniplication; few, low, blunt costae on fold and sulcus, prominent anteriorly, but indistinct toward umbos; lateral and posterior parts nearly smooth or with poorly developed ribbing; slight posterior dorsal sulcation present; growth lines conspicuous along margins; ventral beak erect and slightly swollen, foramen small, submesothyrid. Shell walls very thick; lateral umbonal chambers filled largely with secondary callus, almost completely obscuring dorsally divergent dental plates; teeth strong, crenulated, inserted into large sockets; septalium short, narrow, but relatively deep and thickened; dorsal median septum strong, short, reduced to a ridge; inner socket ridges continuous with thick hinge plates; crura raduliform, proximally close to median septum; muscle scars usually strongly impressed. [This monotypic new genus was initially referred to Tetrarhynchiinae but in view of noticeable lack of squama and glotta, it may be better allocated among Rhynchonellidae, with affinities to Uralorhynchiinae most likely, on the basis of evident similarities to other Late Triassic genera such as *Sulcorhynchia* DAGYS and *Omolonella* MOISEEV (whereas resemblance to *Moisseievia* DAGYS seems superficial only). The species has been recorded from China, too, but such extension of the new genus range would require further substantiation.] *Upper Triassic (Norian):* Northern Alps (Austria).——FIG. 1824*a–o.* **S. superba* (BITTNER), Hallstatt Limestone, Hütteneckalpe; *a–c,* dorsal, anterior, lateral views, NHMW, ×1.5; *d–o,* transverse serial sections, distances in mm from ventral

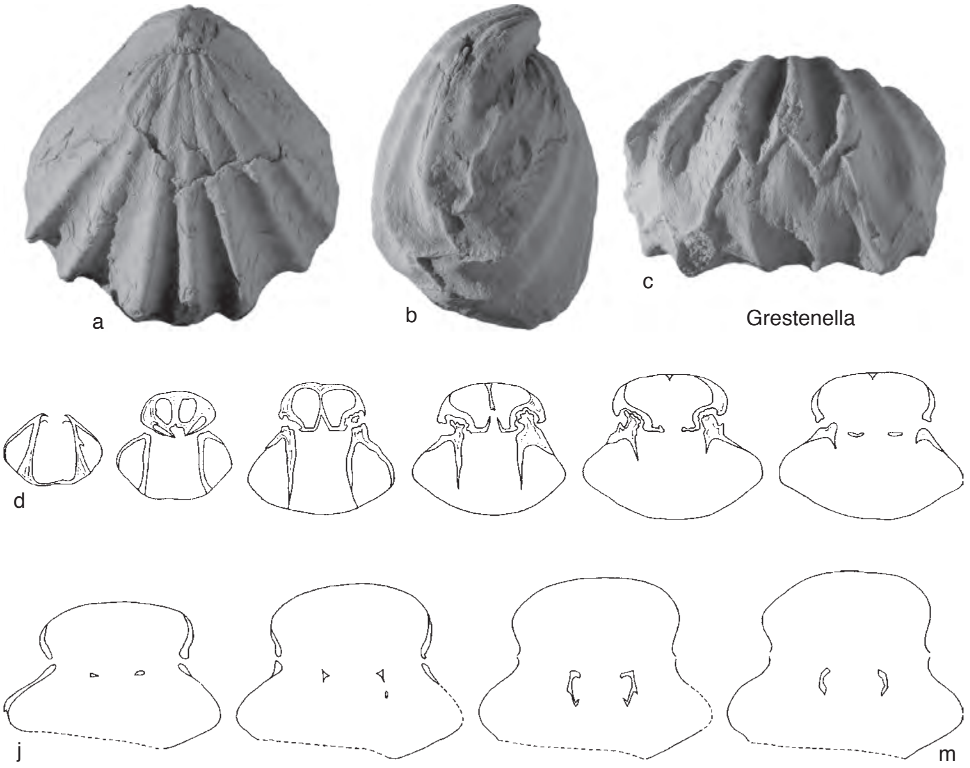


FIG. 1823. Rhynchonellidae (p. 2732–2733).

umbo, 0.7, 0.9, 1.3, 1.7, 2.3, 2.7, 3.4, 3.7, 3.9, 4.4, 4.6, 5.7, ×1.5 (Siblík, 2002).

Superfamily NORELLOIDEA Ager, 1959

Family NORELLIDAE Ager, 1959

Subfamily PARANORELLININAE Xu, 1990

Laevorhynchia Shen & He, 1994, p. 449 [453] [**L. tenuis*; OD]. Shell very small, ventribiconvex, transversely elliptical in outline; beak indistinct; dorsal valve nearly flat with anterior part slightly concave, forming wide and shallow sulcus; anterior commissure sulcate; surface smooth. Ventral interior with short dental plates; dorsal interior with an undivided hinge plate, but with shallow notch at anterior edge; crura "extending anteriorly" (Shen & He, 1994, p. 453; =possibly spinuliform). [This is an overlooked genus with evident affinities to Paranorellininae, yet discrimination from *Meishanorhynchia* Chen & Shi in Chen, Shi, & Kaiho, 2002, and *Paranorellina* Dagys, 1974, not adequately solved, in part because serial sections (implicit in description of internal characters) were not published in original paper, and no comparisons with material from around Meishan-Changxing (Zhejiang) were given.] *Lower Triassic (lowest Scythian):* China (Guizhou).——Fig. 1825,*2a–d.* **L. tenuis*, lower Induan, Feihsienkuan Formation, Guiding; holotype, ventral, dorsal, lateral, anterior views, GD-8190, ×2 (Shen & He, 1994).

Meishanorhynchia Chen & Shi in Chen, Shi, & Kaiho, 2002, p. 154 [**M. meishanensis*; OD; =*Paranorellina*? *changxingensis* Liao, 1984, p. 283, subj.]. Small and smooth shells with reversed fold and sulcus; subpentagonal to subcircular in outline; subequi- to dorsibiconvex in profile; anterior commissure rectimarginate to broadly sulcate; ventral median fold visible on umbonal region; shallow dorsal median sulcus beginning anterior to midlength; external surface with concentric growth lines and microscopic radial striae; few, short, round plicae, limited to anterior margins; lateral slopes smooth; beak and foramen small but distinct. Ventral valve with short, indistinct teeth; dental plates thin, short, fused to shell walls in early stage, then separate but laterally placed; dorsal inner hinge plate united posteriorly and divided

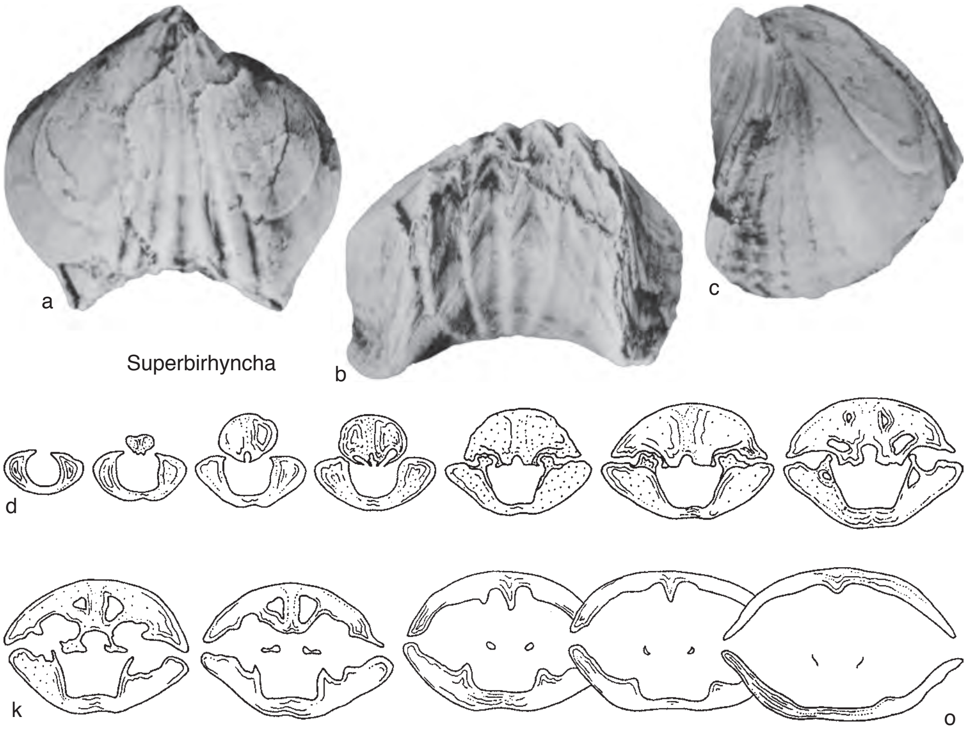


FIG. 1824. Rhynchonellidae (p. 2733–2734).

anteriorly; myophragm low, short; crura apparently spinuliform. [The claim that LIAO's species (which holds priority as a subjective synonym) is a *nomen nudum* is wrong; examination of well-preserved specimens held at Nanjing support a valid species with plainly smooth surface, thus alleged radial striae seem to be due to decortication of primary layer. In addition, spinuliform crura and overall shape are norellid features and may even be included within the scope of the genus *Paranorellina* DAGYS (like the previous genus).] *Lower Triassic (lowest Scythian=Griesbachian):* China (Zhejiang).——FIG. 1825,*1a–l*. **M. changxingensis* (LIAO), Griesbachian, Induan, upper Yinkeng Formation, Meishan; *a–d,* holotype, dorsal, anterior, ventral, posterior views, NMV P1456852, ×6; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.7, 1.0, 1.2, 1.3, 1.5, 1.9, NMV P1456856, ×4 (Chen, Shi, & Kaiho, 2002).

Family FRIELEIIDAE Cooper, 1959

Parasphenarina MOTCHUROVA-DEKOVA, SAITO, & ENDO, 2002, p. 301 [**P. cavernicola*; OD]. Micromorphic, teardrop-shaped, subcircular to suboval in outline, subequibiconvex in profile; shell thin, translucent to transparent, mostly smooth, but may bear radial striae on protegular nodes; anterior commissure rectimarginate; beak pointed, suberect; foramen hypothyrid, deltidial plates disjunct, auriculate. Dorsal valve lacking median ridge, but a shallow groove between two paired low ridges is often present instead. Crura spinuliform; cardinal process and septalium absent; hinge plates and inner socket ridges discrete posteriorly. [Living species are bathyal or from submarine caves. This further requires deletion of the Holocene record from Flores Sea in the previous entry for *Sphenarina* (MANCEÑIDO & others, 2002, p. 1325). In addition, the validity of distinguishing Frieleiinae from Hispanorhynchiinae on the basis of presence or absence of septalium has been questioned by MOTCHUROVA-DEKOVA, SAITO, & ENDO (2002).] *Holocene:* Japan and Flores Sea (off Bali).——FIG. 1826*a–l*. **P. cavernicola*, Miyako Island, Okinawa, Japan; *a–c,* holotype, dorsal, lateral, anterior views, UMUT RB 28220-MN01-a, ×15; *d,* detail of protegular nodes, UMUT RB 28220-R1-7; *e,* detail of ventral beak, UMUT RB 28219-R4-1; *f,* juvenile ventral interior, UMUT RB 28220-R5-11; *g–l,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.7, 0.8, 0.95, 1.05, 1.2, UMUT RB 28220-MN01-c, ×18 (Motchurova-Dekova, Saito, & Endo, 2002).——FIG. 1827*a–f*. **P. cavernicola*, Miyako Island, Okinawa, Japan; *a,* ventral interior, UMUT RB 28220-R2-9; *b,* dorsal

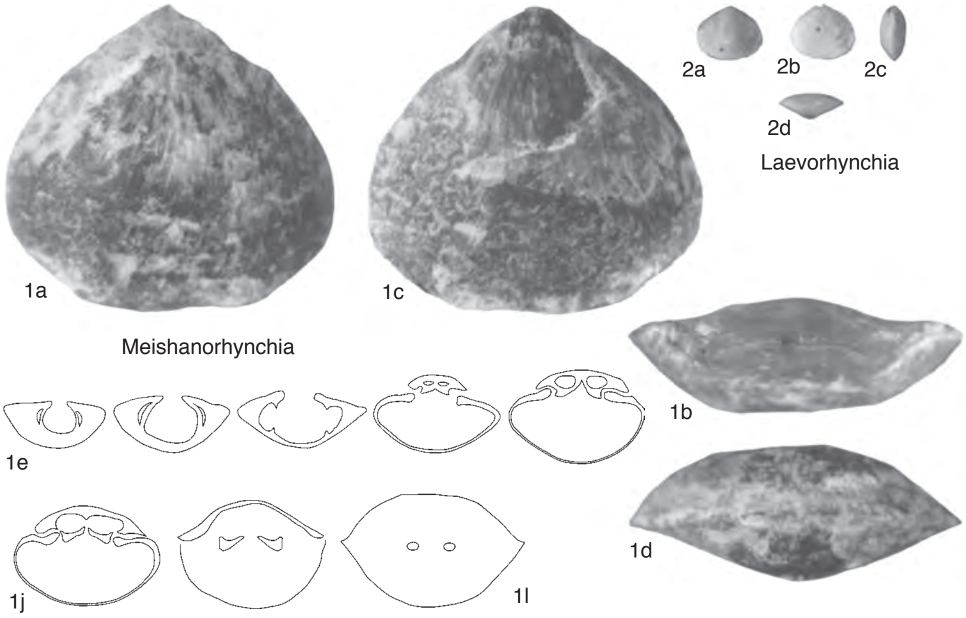


Fig. 1825. Norellidae (p. 2734–2735).

interior oblique view, UMUT RB 28220-R1-12; *c,* cardinalia, UMUT RB 28220-R1-3; *d,* detail of juvenile crus, UMUT RB 28220-R5-4; *e,* detail of crura, UMUT RB 28220-R1-10; *f,* schizolophe inside juvenile, UMUT RB 28214-MD03-a, ×32 (Motchurova-Dekova, Saito, & Endo, 2002).

Superfamily
HEMITHIRIDOIDEA
Rzhonsnitskaia, 1956
Family CYCLOTHYRIDIDAE
Makridin, 1955
Subfamily CYCLOTHYRIDINAE
Makridin, 1955

Woodwardirhynchia Simon & Owen, 2001, p. 57 [**Cretirhynchia cuneiformis* Pettitt, 1950, p. 6; OD]. Costate dorsibiconvex shells, slightly wider than long; costae dense, becoming subangular toward margins, with narrow intervening sulci; beak short and curved; beak ridges distinct, flanking conspicuous palintrope; hypothyridid, auriculate foramen. Pedicle collar well developed; dental plates divergent ventrally in their early stages and subparallel to slightly convergent anteriorly; forked hinge plates, generally short, triangular in outline with a ventral concave surface; crura diverging laterally, inwardly concave, and becoming straight in transverse section near distal end; thin median septum persistent on dorsal valve floor. [This genus was segregated from *Cretirhynchia* Pettitt and assigned to Cyclothyridinae.] *Upper Cretaceous (Turonian–Maastrichtian):* England, France, Belgium, ?Poland, ?India.——Fig. 1828*a–m.* **W. cuneiformis* (Pettitt), upper Turonian, Bardouville near Rouen, Seine Maritime, France; *a–e,* ventral, dorsal, lateral, anterior, posterior views, IRScNB IST 10832, ×1.74; *f–m,* transverse serial sections, distances in mm from ventral umbo, 2.35, 2.65, 3.15, 3.75, 4.2, 4.55, 4.8, 5.05, IRScNB IST 10832, approximately ×1.65 (Simon & Owen, 2001).

Family TETRARHYNCHIIDAE
Ager, 1965
Subfamily CRETIRHYNCHIINAE
Kats, 1974

?Harmignirhynchia Simon & Owen, 2001, p. 85 [**Cretirhynchia intermedia* Pettitt, 1950, p. 14; OD]. Multicostate, slightly biconvex, symmetrical shells, transversely oval in outline, always wider than long; lenticular in anterior view and lateral profile; numerous faint costae, sometimes reduced in number near commissure. Dental

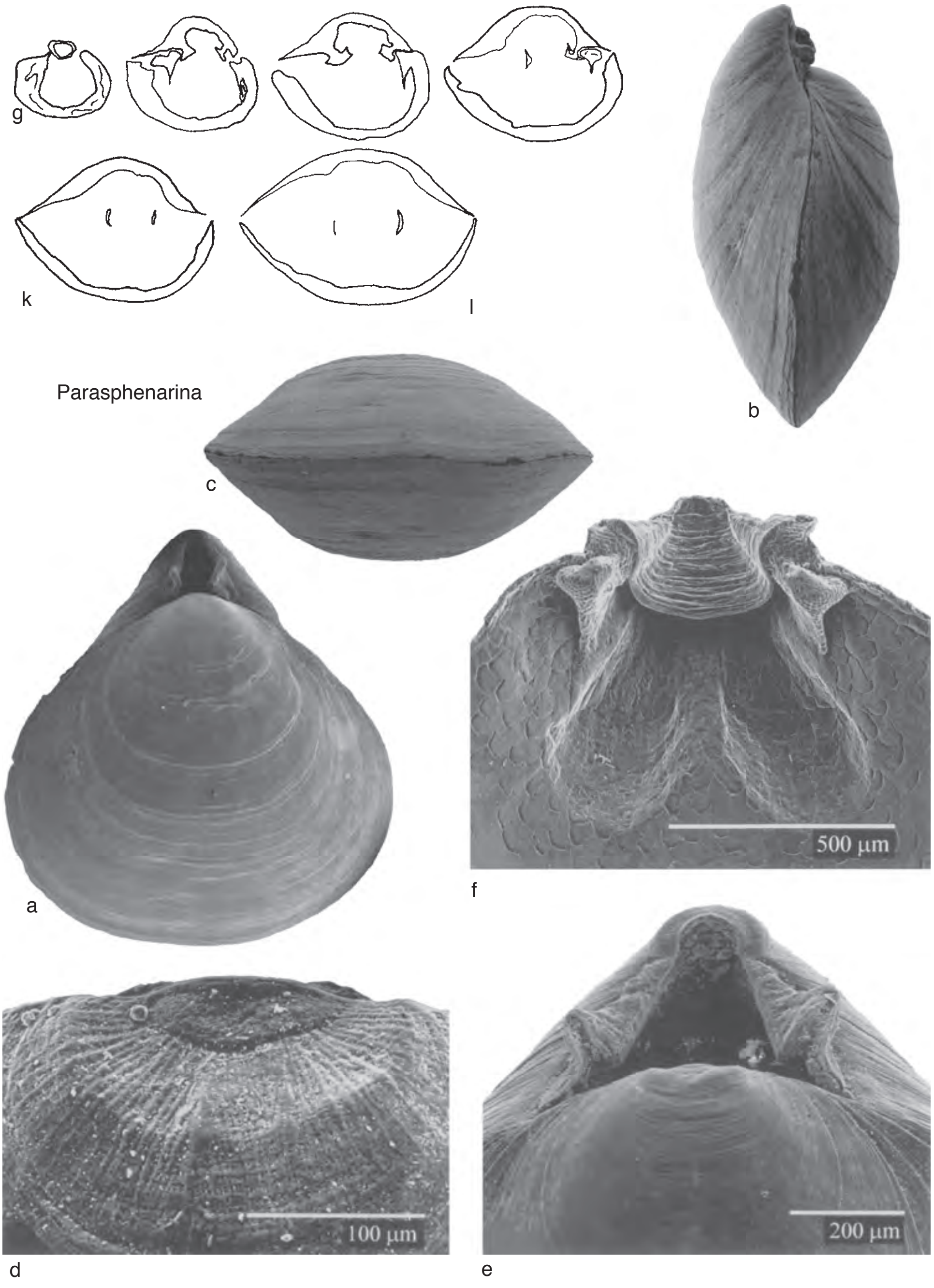


FIG. 1826. Frieleiidae (p. 2735–2736).

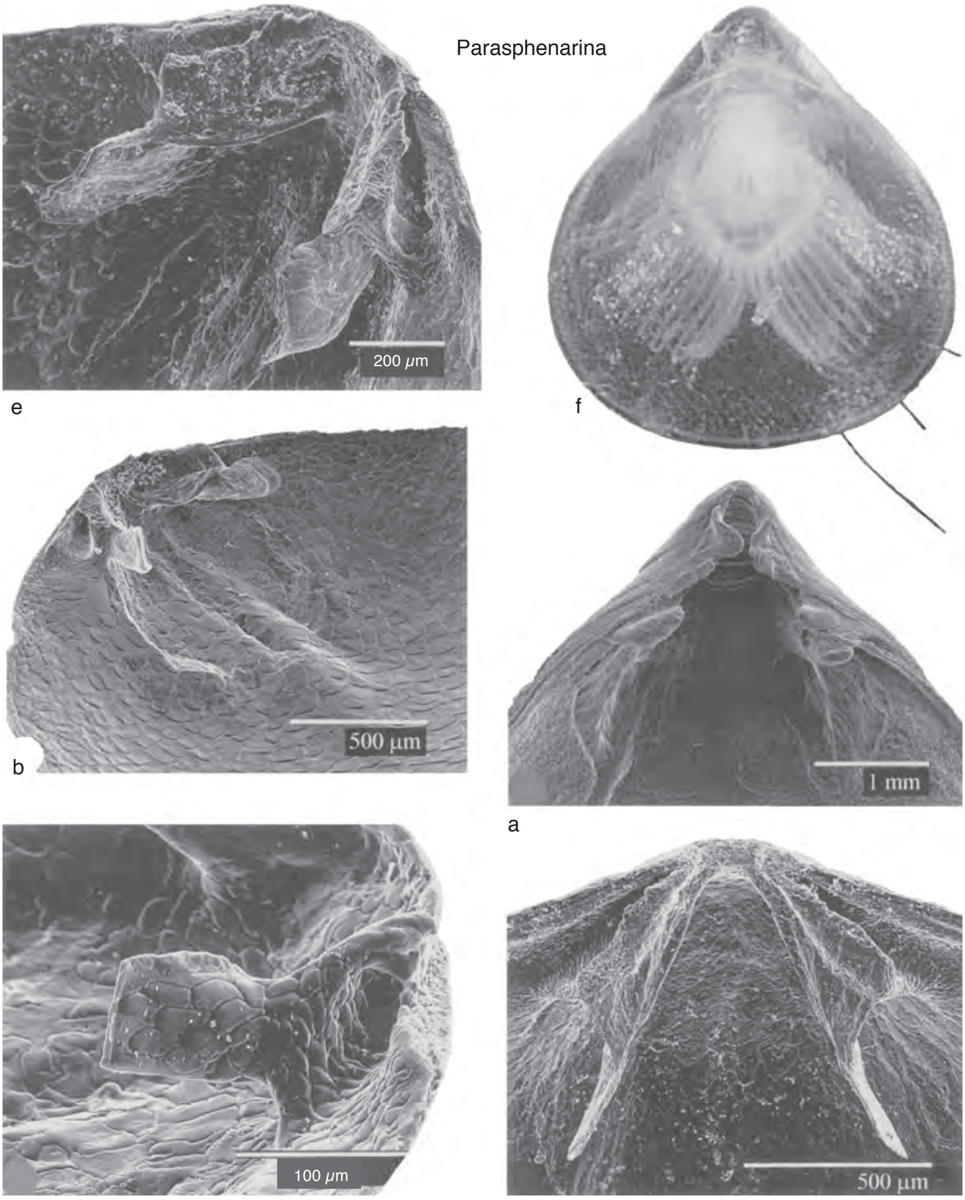


FIG. 1827. Frieleiidae (p. 2735–2736).

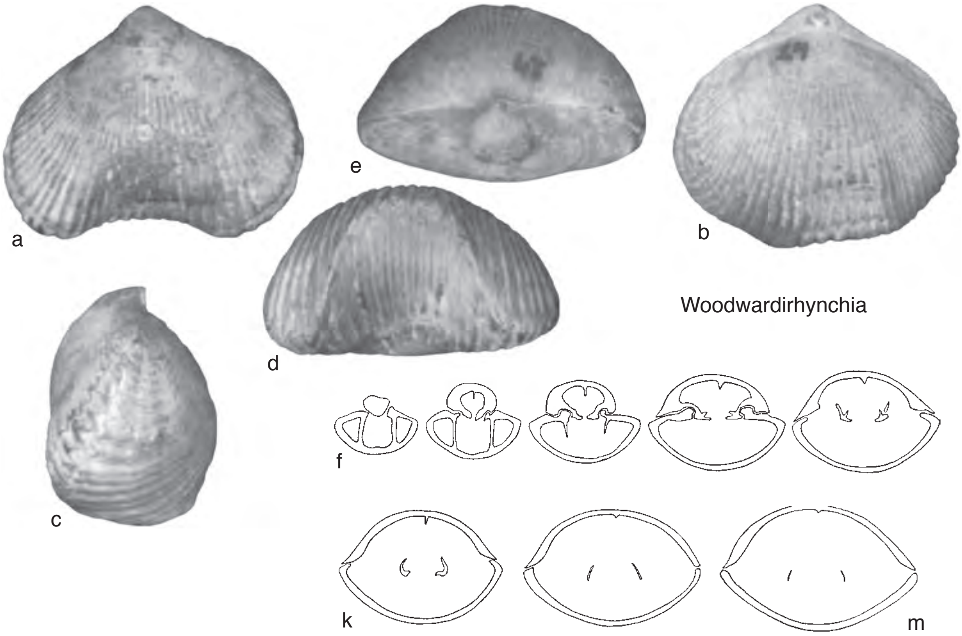


FIG. 1828. Cyclothyrididae (p. 2736).

plates convergent ventrally; dorsal myophragm low, short; hinge plates relatively wide and crural bases subquadrate but often inwardly concave; posterior part of crura strongly concave; crura steep, deflected ventrally, remaining close together or slightly diverging laterally; angle formed by distal parts of crura widely obtuse in transverse section. [Originally proposed as a subgenus of *Cretirhynchia* PETTITT, this genus is admittedly a close ally to *Homaletarhynchia* SIMON & OWEN; yet, both may be treated independently for having also such affinities to aphelesiines as inwardly concave crura, resembling subfalciform-hamiform in scope.] *Upper Cretaceous (lower Campanian–upper Campanian):* United Kingdom, Belgium.——FIG. 1829,*1a–m.* **H. intermedia* (PETTITT), lower Campanian, East Harnham, Wiltshire, England; *a–e,* topotype, ventral, dorsal, lateral, anterior, posterior views, BMNH B.92742-5, ×2.4; *f–m,* transverse serial sections, distances in mm from ventral umbo, 2.3, 3.0, 3.8, 4.15, 4.65, 4.85, 5.15, 5.55, BMNH B.92742-5, approximately ×1.46 (Simon & Owen, 2001).

?Homaletarhynchia SIMON & OWEN, 2001, p. 91 [**Terebratulites limbatus* VON SCHLOTHEIM, 1813, p. 113; OD]. Medium-sized, symmetrical, biconvex shells; ornamentation generally smooth or with very faint radial grooves; development of costae limited to anterolateral commissure; beak small, pointed, and generally curved; beak ridges well developed; hypothyridid foramen with conjunct, protruding deltidial plates. Dental plates ventrally convergent; pedicle collar rarely developed; dorsal myophragm stout, long; very strong hinge structure, with ventrally expanded inner socket ridges; crural bases subquadrate, crura slightly concave in their posterior part, remaining close together. [Originally proposed as a subgenus of *Cretirhynchia* PETTITT, this may be regarded as a full genus, perhaps ancestral to *Aphelesia* COOPER, due to inwardly concave crura, resembling hamiform-subfalciform in scope. Additional evidence in support of sound family reallocation is forthcoming from current detailed SEM studies of excavated crura and shell microstructure by MOTCHUROVA-DEKOVA and SIMON (2007).] *Upper Cretaceous (Santonian–*

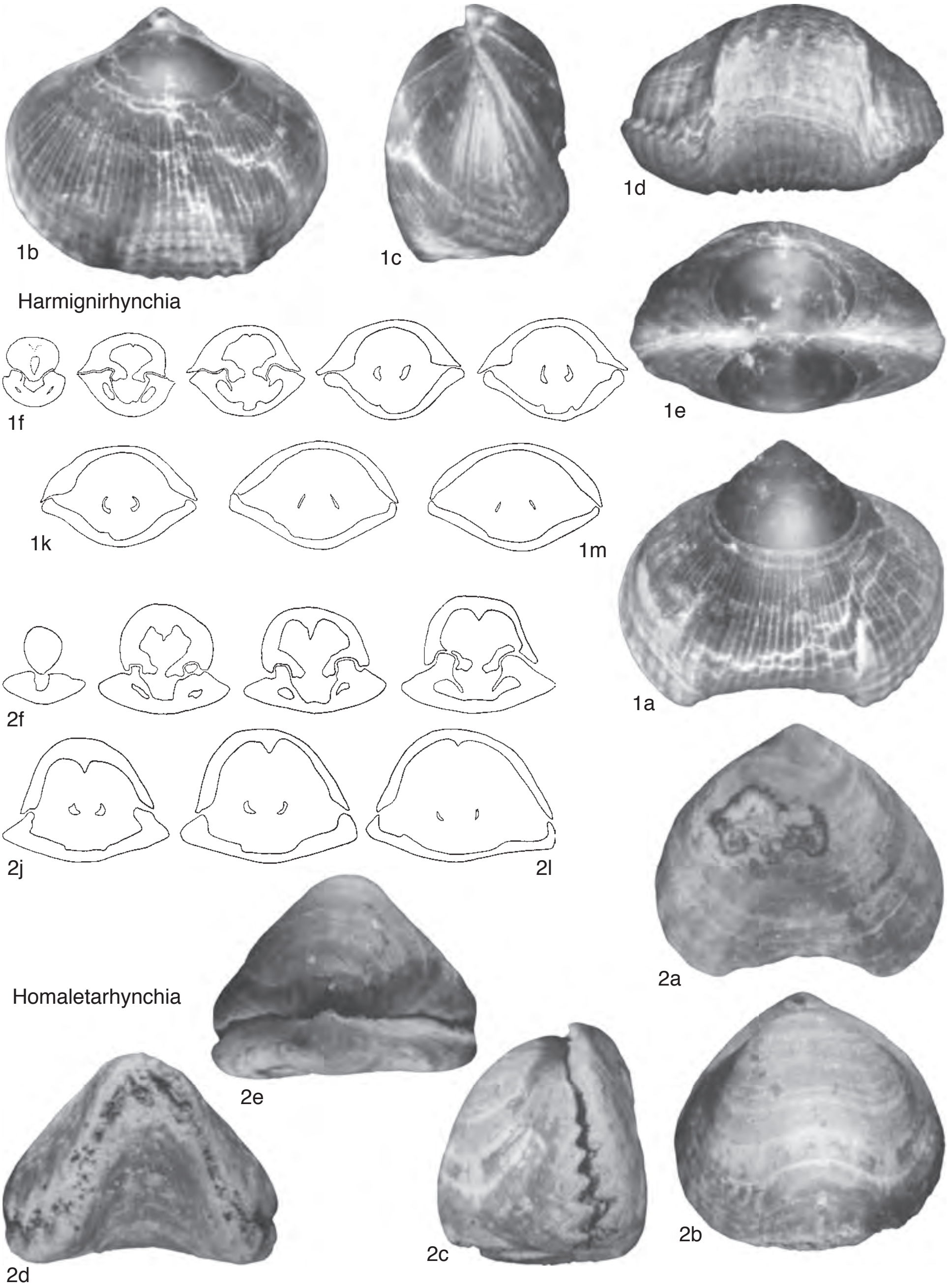


FIG. 1829. Tetrarhynchiidae (p. 2736–2741).

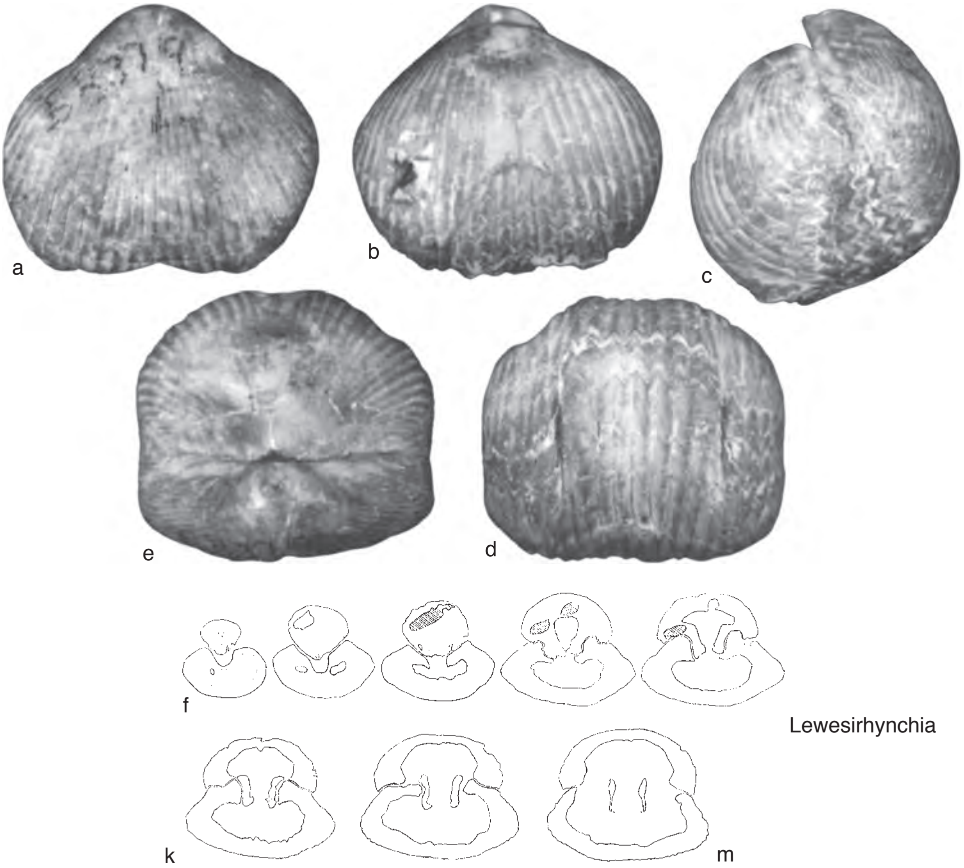


FIG. 1830. Tetrarhynchiidae (p. 2741).

Maastrichtian): England, Ireland, France, Belgium, Germany, Poland.—— FIG. 1829,*2a–l.* **H. limbata* (von Schlotheim), upper Maastrichtian, Jandrain, Brabant, Belgium; *a–e,* hypotype, ventral, dorsal, lateral, anterior, posterior views, IRScNB IST 10838, ×1.87; *f–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.6, 2.0, 2.3, 2.55, 2.9, 3.2, IRScNB IST 10838, approximately ×1.65 (Simon & Owen, 2001).

Lewesirhynchia Simon & Owen, 2001, p. 77 [**Terebratula octoplicata* J. Sowerby, 1816, in 1815–1818, p. 37; OD]. Multicostate, biconvex, symmetrical shells, with numerous costae generally faint near umbo, becoming elevated toward margins; near commissure, costae sometimes reduced in number, but incipient splitting of them is observed occasionally. Thick shelled, umbo filled with callus; pedicle collar absent; thick dental plates, convergent ventrally; dorsal myophragm variably developed; inner socket ridges extending anteriorly; hinge plates very small, triangular, becoming anteriorly indistinct; crural base inwardly concave, developing with hinge plate and anterior part of inner socket ridge, original hook structure visible in transverse section; crura raduliform, slightly diverging. [This genus was originally proposed as a subgenus of *Cretirhynchia* Pettitt, but both genera may be treated independently, pending further revision.] *Upper Cretaceous (Coniacian–lower Campanian, ?lower Maastrichtian):* United Kingdom, ?India. ——FIG. 1830*a–m.* **L. octoplicata* (Sowerby), Coniacian, Chalk, Lewes, Sussex, England; *a–e,* topotype, ventral, dorsal, lateral, anterior, posterior views, BMNH B.8379-1, ×1.77; *f–m,* transverse serial sections, distances in mm from ventral umbo, 3.5, 4.35, 4.75, 5.65, 6.1, 6.65, 7.3, 8.05, BMNH B.8379-1, approximately ×1 (Simon & Owen, 2001).

ATHYRIDIDA

Fernando Alvarez

[University of Oviedo, Spain]

Order ATHYRIDIDA Boucot, Johnson, & Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson, & Staton, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family ATHYRIDIDAE Davidson, 1881
Subfamily ATHYRIDINAE Davidson, 1881

Ceresathyris Havlíček in Havlíček & Vaněk, 1998, p. 89 [**Terebratula ceres* Barrande, 1847, p. 395; OD]. Small to medium, dorsibiconvex shells of subpentagonal to elongated elliptical outline; maximum width at midvalve; with numerous (up to 40 in a specimen 15 mm long), evenly spaced, short growth lamellae; with shallow ventral sulcus and low dorsal fold with or without shallow median groove; anterior commissure weakly uniplicate; ventral beak moderately to strongly incurved, with small, circular foramen in permesothyridid position; delthyrium open, obscured by dorsal beak; shell thick in umbonal region; dental plates obscured by callus, free only anteriorly, subparallel to slightly convergent ventrally; lateral apical cavities very short; ventral muscle field weakly impressed; cardinalia thick posteriorly, dental sockets poorly developed anteriorly, cardinal flanges absent, hinge plate short, apically perforated by large foramen, slightly convex ventrally; without dorsal septum or myophragm; spiral cones laterally directed, jugum unknown. [This genus resembles *Athyris* M'Coy externally, but the umbonal region is thick shelled in both valves, dental plates are subparallel to slightly convex ventrally, obscured by callus, free only anteriorly, and reportedly without ventral foramen, but it seems to be present in some of Havlíček's illustrations (e.g., Havlíček in Havlíček & Vaněk, 1998, pl. 8,*12a*). It differs from *Leptathyris* Siehl in its hinge plate being slightly convex ventrally as in some *Pachyplax* Alvarez & Brunton, from which *Ceresathyris* differs in growth lamellae morphology and ventral interior. The lack of information on the brachiojugal system makes impossible its comparison with those developed by other athryridid genera. May be synonymous with *Athyris*.] *Lower Devonian (Pragian):* Europe (Bohemia).——Fig. 1831,*2a–l*. **C. ceres* (Barrande), Koněprusy Limestone, Koněprusy, Prague Basin; *a–c,* dorsal, ventral, and anterior views, Havlíček collection, VH 12123a, ×2 (Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček); *d–l,* transverse serial sections 13.7, 13.5, 13.0, 12.7, 12.6, 11.1, 11.6, 11.8, 12.2 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998).

Drovithyris Jafarian [1973, unpublished manuscript deposited in the Université Claude Bernard, Lyon, France (M. A. Jafarian, personal communication, 7 May, 2002)]. This genus was described as a subgenus of *Athyris* by Jafarian, 1973, and listed but not described or diagnosed, as both subgenus and genus by Jafarian, 2000, p. 223, tables 3–4 respectively. Only one species, *Athyris (Drovithyris) genus nov.* and *sp. nov.* [sic] was included in the genus-subgenus by Jafarian (2000, p. 229, pl. 3,*10a–b, 11a–b*). [This genus is in need of proper validation.] *Upper Devonian (?middle Frasnian, upper Famennian):* southeastern Anarak, north of Esfahan, Chah-Riceh, Iran.

Grinnellathyris Li & Jones, 2002, p. 656 [**G. alvarezis*; M]. Small, commonly elongate, subelliptical, rarely circular or slightly transverse, equally biconvex to slightly ventribiconvex shells; maximum width near midvalve; surface with numerous (up to 16 in a specimen 12 mm long) short growth lamellae; ventral beak prominent, recurved, foramen large, rounded, permesothyrid, delthyrium open; shallow sulcus originating at about midlength; anterior commissure weakly uniplicate to slightly parasulcate; dental plates short, dorsally convergent, lateral apical cavities narrow, teeth small; cardinal plate imperforate, subtriangular, flat to slightly concave ventrally, cardinal flanges absent, socket ridges low; no dorsal septum or myophragm; laterally directed spiralia of fewer than about 10 whorls; U-shaped jugum, lateral branches of jugum almost vertical, starting midway along length of dorsal valve; jugal saddle moderately developed, jugal stem and accessory lamellae absent. [This genus differs from externally similar *Athyris* M'Coy and *Protathyris* Kozlowsky mainly in its imperforate cardinal plate, which is not trilobed anteriorly (*Protathyris*), jugum without stem and accessory jugal lamellae, and jugal saddle only moderately developed; differs from *Buchanathyris* Talent in shorter dental plates, not being concave medially, jugum with jugal saddle moderately developed and without short, posteriorly directed, stemlike process. Although similar in shell size and internal structures, *Johnsonathyris* Savage, Eberlein, & Churkin differs in shell being strongly biconvex, subglobular, ventral foramen minute, commissure strongly uniplicate anteriorly, shell exterior with fine growth lamellae crossed by regularly developed fine costellae, cardinal plate medially crested, and jugum placed anterior of midlength, without any saddle. When erected, *Grinnellathyris* was tentatively included in the Athyridinae, although the

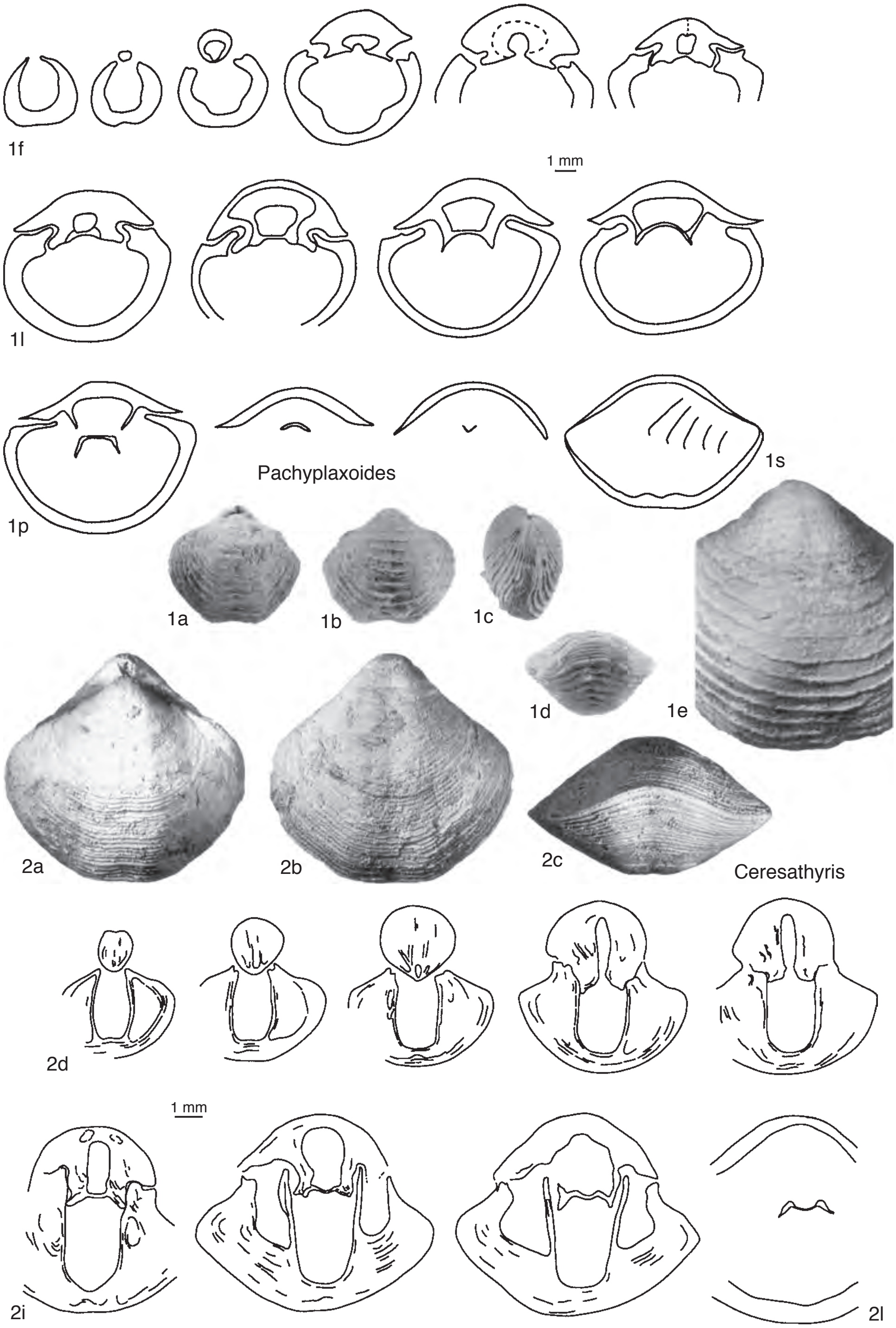


FIG. 1831. Athyrididae (p. 2742–2744).

authors considered it advisable to establish a new subfamily, Johnsonathyridinae, for athyridines, as *Johnsonathyris* and *Grinnellathyris*, with imperforate cardinal plate. In the athyridids, the dorsal foramen is generally small or even very small, and easy to be overlooked when dorsal interiors are studied from serial sections of few specimens that are commonly adults. This feature is not evident if only adult or gerontic specimens are studied as it may become partially or completely infilled by secondary shell thickening during ontogeny. *Grinnellathyris* is therefore kept here also within the Athyridinae.] *Middle Devonian (Eifelian):* Bathurtst Insland, Grinnell Peninsula, North Kent Island, Arctic Canada.——FIG. 1832*a–s*. **G. alvarezis*, Bird Fiord Formation, Grinnell Peninsula, Devon Insland, Arctic Canada; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, UA 12090, ×5.5; *f,* ventral view showing growth lamellae, UA 12091, ×3 (Li & Jones, 2002); *g–s,* transverse serial sections 0.7, 1.3, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 3.1, 4.5, 6.85, 7.1, 7.5 mm from ventral umbo (adapted from Li & Jones, 2002).

Pachyplaxoides GRUNT in GRUNT & RACKI, 1998, p. 369 [**P. postgyralea*; M]. Small to medium, ventribiconvex to nearly equally biconvex shells of subpentagonal to subcircular outline; equidimensional to slightly wider than long, commonly widest near midlength, with maximum thickness at posterior third of shell; with numerous (up to 20 in a specimen 27 mm long), variably developed growth lamellae; shallow ventral sulcus and flat, or slightly depressed medianly, dorsal fold beginning in posterior third of shell; anterior commissure weakly uniplicate; ventral beak short, incurved, truncated by small, permesothyridid foramen; delthyrium open, obscured by dorsal beak; internally without dental plates; no dorsal septum or myophragm; cardinal flanges absent, cardinal plate thin, subtrapezoidal, apically perforated, ventrally concave anteriorly, crural bases poorly developed; spires seem to be present but their number, disposition, and jugum unknown. [This genus differs from closely related athyridids such as *Protathyris* KOZLOWSKI and *Alvarezites* STRUVE, with similar, delicate, and not very long growth lamellae, in its general morphology and internal characters. It differs from *Lamellosathyris* JIN & FANG and *Pachyplax* ALVAREZ & BRUNTON in its external ornamentation, type of cardinalia, and lack of dental plates. *Lamellosathyris* has long, radially corrugated shell flanges extending from rugae of both valves. In *Pachyplax*, the growth lamellae are thick and overlap strongly so that the combination of lamellae and the entrapped sediment between them gives a rough, rugose external appearance to the shells, which are rather different than those of *Pachyplaxoides*. Internally, in *Pachyplax* as in many other Devonian related genera, more or less developed cardinal flanges are confined posteriorly on the hinge plate, a myophragm divides the dorsal muscle scars, and more or less clear dental plates support the hinge teeth; all these structures are absent in *Pachyplaxoides*. In *Lamellosathyris* the cardinal flanges project posteroventrally and the diductor myophores spread over most of ventral surface of the reduced but heavily thickened cardinal plate. The genus differs externally from *Planalvus* CARTER and *Densalvus* CARTER, also without dental plates; *Planalvus* is slightly uniplicate, dorsibiconvex with an almost flat ventral valve; while *Densalvus* is rectimarginate, with strongly inflated ventral valve and weakly convex dorsal valve. The lamellae of *Pachyplaxoides* are not finely striated and fringed with minute solid spines (*Planalvus*) or weakly and finely capillate (*Densalvus*). Lack of information on the brachiojugal system makes impossible its comparison with those developed by other athryridid genera.] *Upper Devonian (upper Frasnian):* central Poland (Holy Cross Mountains), Germany (Eifel).——FIG. 1831,*1a–s*. **P. postgyralea*; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, Quarry Reichle, Prümer Mulde, Eifel, Germany, SFM 59509, ×1.2; *e,* enlargement of ornament of ventral valve, Łgawa Hill, Bolechowice, Holy Cross Mountains, central Poland, GIUS 4-1477/GL-102, ×7.5 (Grunt & Racki, 1998); *f–s,* transverse serial sections 1.4, 1.6, 1.7, 2.0, 2.2, 2.4, 2.7, 2.8, 2.9, 2.95, 3.0, 3.3, 3.7, 4.0 mm from ventral umbo, Łgawa Hill, Bolechowice, Holy Cross Mountains, central Poland, GIUS 4-1477/GL-140, (adapted from Grunt & Racki, 1998).

Subfamily ATHYRISININAE Grabau, 1931

[Athyrisininae GRABAU, 1931a, p. 509; *emend.*, RONG & others, 2004, p. 824]

Shell small to large, moderately rostrate, commonly with very strong ventral umbo curvature; growth lamellae generally well developed, may be squamose; fold and sulcus well developed; dental plates commonly short (long in *Bruntosina*), converging dorsally, may become subparallel anteriorly; dorsal myophragm absent; cardinal plate and jugum essentially as in *Athyris*, but without cardinal flanges. [Recently, RONG and others (2004), in their revision of this subfamily, excluded from the Athyrisininae the following genera: *Pseudohomeospira* NIKIFOROVA, *Ikella* TYAZHEVA, *Squamathyris* MODZALEVSKAYA, and *Homeathyris* MODZALEVSKAYA. They placed them in a new athyridid subfamily, Homeathyridinae (see below). In addition to the type genus, *Athyrisina* HAYASAKA (in YABE & HAYASAKA), RONG and others (2004) included in the subfamily Athyrisininae the following genera: *Parathyrisina* WANG in WANG, YU, & WU, *Athyrisinoidea* CHEN & WAN in WAN,

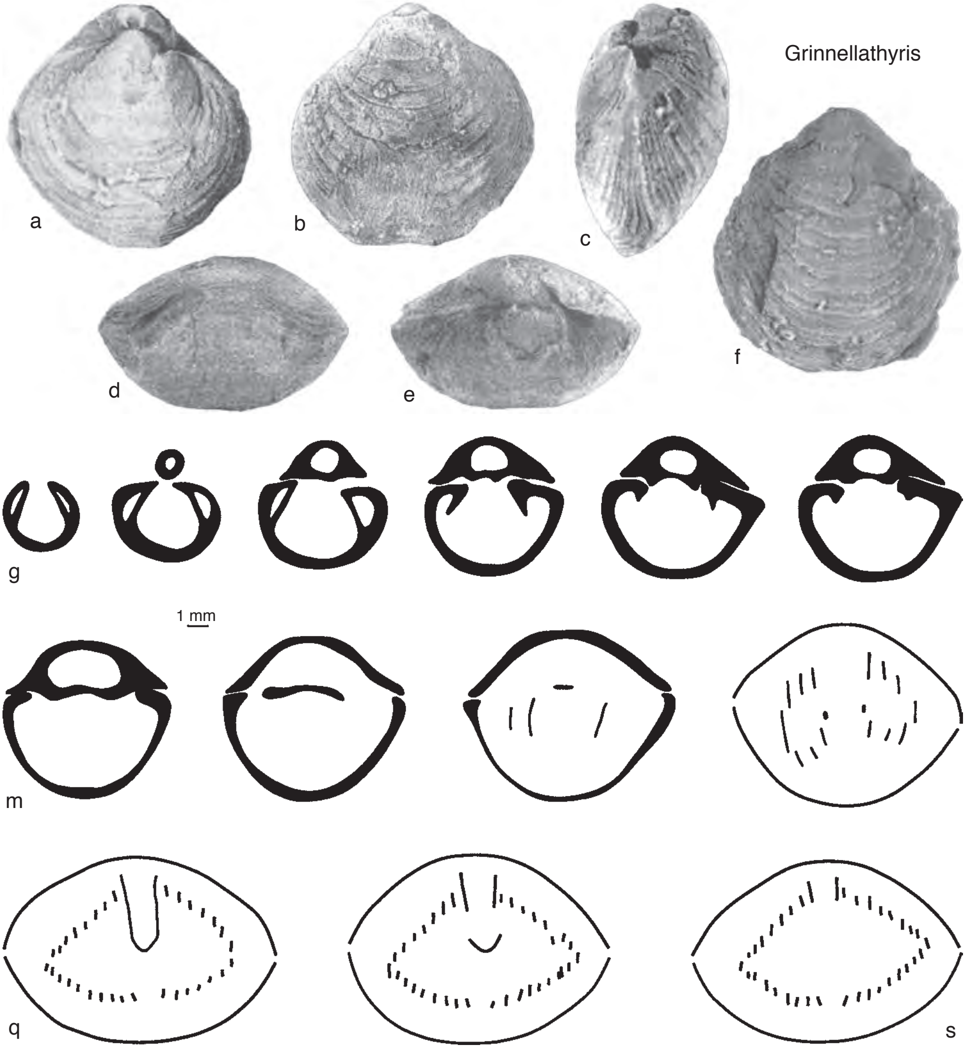


FIG. 1832. Athyrididae (p. 2742–2744).

Neoathyrisina CHEN, and *Bruntosina* RONG & others from South China (plus western Sichuan and Qinling regions) and northern Vietnam.] *Lower Devonian (Pragian)–Middle Devonian (Givetian).*

Athyrisina HAYASAKA in YABE & HAYASAKA, 1920, p. 176; *emend.*, RONG & others, 2004, p. 827 [**A. squamosa;* OD] [=*Kwangsia* GRABAU, 1931a, p. 204 (type, *K. yohi,* OD); *Plectospirifer* GRABAU, 1931a, p. 379 (type, *P. heimi,* OD); *Kwangsiella* GRABAU, 1932, p. 82 (type, *K. yohi,* OD); *Pseudoathyrisina* CHEN, 1979, p. 17 (type, *P. fasciata,* OD); *Athyrisinopsis* ZHANG, 1983, p. 354 (type, *A. uniplicata,* OD)]. Small to large shells with rounded subpentagonal to transversely elliptical dorsal outline, with short to relatively long hinge line, ventribiconvex lateral profile; ventral sulcus and dorsal fold usually well developed; pauciplicate to costellate, radial elements may bifurcate; growth lamellae numerous, commonly well developed and regularly spaced; dental plates thin, short, lateral apical cavities very narrow; cardinal plate perforated apically by minute foramen, spiralia with 10 to 18 whorls. [Distinguished from other Athyrisininae by having 3 or more ribs in the sulcus, of the same width as those on the flanks. Radial elements are more numerous in *Athyrisina* than in *Bruntosina* RONG & others and *Parathyrisina* WANG, and the

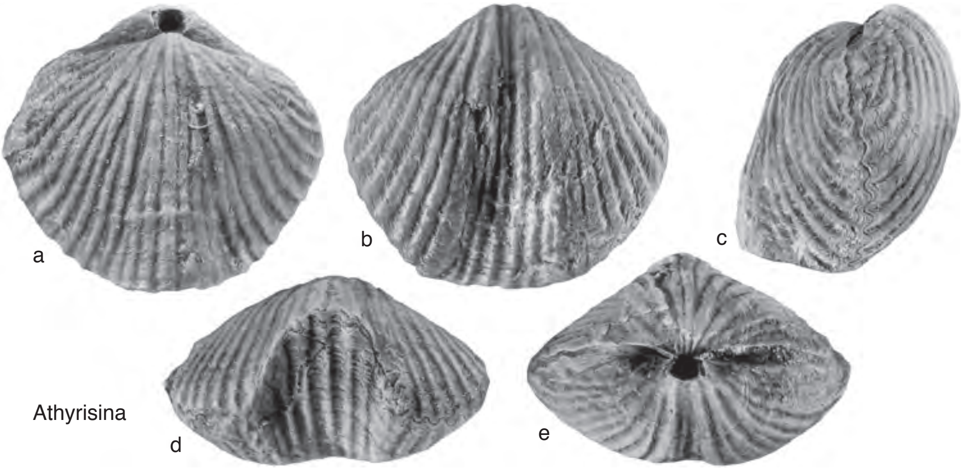


FIG. 1833. Athyrididae (p. 2745–2746).

ribs bounding the sulcus are similar to those on the flanks and sulcus.] *Lower Devonian (upper Pragian)–Middle Devonian (Givetian):* southern China (northern Sichuan, southeastern Guizhou, eastern Yunnan, Guangxi), Qinling region (western and eastern Shaanxi, southeastern Gansu, northernmost Sichuan), western Sichuan (Ganzi Block), northern Vietnam.——FIG. 1833*a–e*. **A. squamosa;* neotype, dorsal, ventral, lateral, anterior, and posterior views, Yangmaba Formation, upper Emsian, Heitupo, Wenchuan County, northern Sichuan Province, NIGP 134224, ×1.5 (Rong & others, 2004).

Bruntosina RONG & others, 2004, p. 837 [**Athyrisinopsis gansuensis* ZHANG in ZHANG & FU, 1983, p. 355; OD; =*Athyrisinopsis trapeziformis* ZHANG, 1987, p. 126]. Medium to large, elongate oval, subcircular to transversely oval and nearly equally biconvex shells; ventral sulcus and dorsal fold well developed; pauciplicate on flanks, without bifurcation or intercalation, a single costa characteristically present in middle of sulcus, and shallow furrow on middle of fold; variably spaced growth lamellae, on any of which there are up to 80 growth lines; dental plates thin, long, and parallel, lateral apical cavities wider than for subfamily; cardinalia, spiralium and jugum essentially as in *Athyrisina*. [*Bruntosina* has a more restricted distribution than the other athyrisinins: it is only known from upper Emsian and Eifelian of the West Qinling Mountains. It resembles *Athyrisina* HAYASAKA, type genus of Athyrisininae, but has fewer plications (generally 2) on flanks, and ribs bounding the sulcus are stronger. Radial elements are more numerous in *Athyrisina,* being simple costae or less frequently costae and costellae. *Bruntosina* characteristically has a single, narrow costa in the middle of the sulcus, whereas *Athyrisina* has three or more ribs (of the same width as those on the flanks) in the sulcus, and *Parathyrisina* WANG has no radial elements on the sulcus or fold. Growth lamellae are numerous and regularly spaced in *Athyrisina*, but in *Bruntosina* they are variably spaced (up to 5 on adult valves), with up to 80 fine growth lines on each lamellae. Internally, dental plates are long and parallel in *Bruntosina*, but very short, with very narrow lateral apical cavities in *Athyrisina* and *Parathyrisina*.] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* China (western and eastern Qinling, southeastern Gansu).——FIG. 1834*a–j*. **B. gansuensis* (ZHANG), Dangduo Formation, upper Emsian–lower Eifelian; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, Pulaigou, Tewo County, southeastern Gansu, XB 239, ×1.5; *f–h*, dorsal, ventral, and anterior views, Xiawunagou, Tewo County, southeastern Gansu, XB 231, ×1.5; *i–j,* ventral view and enlargement showing characteristic single costa in middle of sulcus and concentric ornamentation, Dangduobeigou, Tewo County, southeastern Gansu, XB 230, ×1.5, ×8.5 (Rong & others, 2004).——FIG. 1835*a–u*. **B. gansuensis* (ZHANG), Dangduo Formation, upper Emsian–lower Eifelian; transverse serial sections 1.2, 1.9, 2.6, 3.0, 4.0, 4.6, 5.0, 5.5, 5.9, 6.1, 6.7, 8.6, 9.7, 10.3, 10.6, 10.8, 11.4, 12.2, 12.5, 14.9, 15.2 mm from ventral umbo, distance from ventral umbo to first section approximate, Pulaigou, Tewo County, southeastern Gansu, ×1.5 (Rong & others, 2004).

Parathyrisina WANG in WANG, YU, & WU, 1974, p. 41; *emend.*, RONG & others, 2004, p. 832 [**P. bella;* OD; =*Athyrisina tangnae* HOU, 1963, p. 416] [=*Athyrisinoides* CHEN & WAN in XU, WAN, & CHEN, 1978, p. 351 (type, *A. typica,* OD); *Athyrisinoidea* CHEN & WAN in WAN, 1980, p. 105 (type, *A. typica,* OD), *nom nov. pro Athyrisinoides* CHEN & WAN in XU, WAN, & CHEN, 1978, p. 351; *Neoathyrisina* CHEN, 1988, p. 36, obj.]. Commonly small to medium, rarely large, transverse subelliptical to subcircular outline, equally to subequally biconvex shells; pedicle opening large, palintrope reduced;

ventral sulcus and dorsal fold rounded, commonly well developed, without radial elements; lateral slopes bearing 3 or more costae, growth lamellae well developed; interior and jugum essentially as in *Athyrisina.* [This genus is distinguished from other Athyrisininae in lacking radial elements on sulcus and fold; internally, the dental plates are long and parallel in *Bruntosina* but very short with very narrow lateral apical cavities, in both *Athyrisina* and *Parathyrisina*. For illustrations see ALVAREZ & RONG, 2002, fig. 1022*a–x* and revision in RONG & others, 2004.] *Lower Devonian (upper Pragian–upper Emsian):* southern China (Guangxi, Sichuan), southeastern Gansu, northwestern Sichuan, western Qinling.

Subfamily CLEIOTHYRIDININAE
Alvarez, Rong, & Boucot, 1998

Bruntonathyris CHEN, SHI, & ZHAN, 2003, p. 853 [**B. amunikeensis*; OD]. External shape, folding, and concentric ornamentation resembling those of transverse *Actinoconchus* M'COY; exfoliated surfaces displaying a delicate radial pattern. Interior similar to that of some cleiothyridinins; cardinalia with poorly developed cardinal flanges. Spiralium and jugum unknown. [This genus was assigned by its authors to the Cleiothyridininae notwithstanding the absence of flat, solid spinelike projections from growth lamellae, anteriorly and anterolaterally directed, which are diagnostic of that subfamily. In fact, these shells could be either athyridinins or cleiothyridinins dependent on their ornamentation, which is not well preserved in the material studied; internal structure of brachidia unknown.] *Lower Carboniferous (upper Tournaisian–Viséan):* northwestern China (Qaidam Basin), *upper Tournaisian–Viséan*; southern China, Japan (Akiyoshi), Russia (Urals, Moscow Basin, Donetsk Basin), England, *Viséan*.——FIG. 1836*a–p*. **B. amunikeensis,* Tournaisian, Chuanshangou section, Qaidam Basin, northwestern China; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, NMV P309563, ×1.5; *f–h,* dorsal and ventral views, and detail of ventral umbonal region, exfoliated, showing radial striae, NMV P309561, ×1.5, ×3; *i–o,* transverse serial sections 0.5, 1.5, 2.0, 2.5, 3.2, 3.7, 4.0 mm from ventral umbo, NMV P309564; *p,* dorsal interior reconstructed from serial sections, NMV P309564 (Chen, Shi, & Zhan, 2003).

Subfamily DIDYMOTHYRIDINAE
Modzalevskaya, 1979

Fastigata BARANOV & AL'KHOVIK, 2001, p. 41 [**F. longa*; M]. Small-sized, elongate subelliptical to subpentagonal, subequally biconvex, rectimarginate to slightly uniplicate shells; widest and thickest near midlength; ventral beak slightly curved, delthyrium reportedly covered by deltidial plates; valve surface with spaced growth lamellae and fine tubular ribs similar to that of some atrypids; dental plates short, thin to more or less thick, converging slightly dorsally; cardinal plate apically perforated, slightly ventrally concave posteriorly to slightly ventrally convex anteriorly; cardinal flanges absent; low and short dorsal myphragm may be present; spiralia with up to six laterally directed whorls, jugum with relatively short saddle and stem, accessory jugal lamellae very short or absent. [*Fastigata* is similar to *Pseudoprotathyris* in shape, but differs in its ornamentation, cardinalia, and jugum. It differs from *Atrythyris* in its hinge plate not being depressed medially, poorly developed cardinal flanges, and much shorter accessory jugal lamellae; it differs from *Bruntonathyris* by inner hinge plates situated in similar plane to the outer hinge plates. Exfoliated surfaces in *Bruntonathyris* display a delicate radial pattern; in *Fastigata,* although material is too poorly preserved, fine tubular ribs seem to be interrupted by regular growth lamellae.] *Lower Devonian (lower Lochkovian):* Tas-Khayakhtakh Ridge and southern Verkhoyansk region, eastern Yakutia.——FIG. 1837,*2a–t*. **F. longa*; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia, IGN SO RAN 171/1, ×3; *e–f,* partly exfoliated ventral valve showing tubular ribs, basal Datna Formation, Tas-Khayakhtakh Ridge, IGN SO RAN 171/7, ×3, ×10 (Baranov & Al'khovik, 2001); *g–s,* transverse serial sections 0.5, 0.7, 0.8, 1.1, 1.85, 2.6, 2.7, 3.4, 3.6, 3.9, 4.1, 4.5, 4.6 mm from ventral umbo, distance from ventral umbo to first section approximate, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia IGN SO RAN 171/8; *t,* transverse serial section at approximately 2.0 mm from ventral umbo, lower Sette-Daban Formation, Sette-Daban Ridge, southern Verkhoyansk region, eastern Yakutia, IGN SO RAN 171/9 (adapted from Baranov & Al'khovik, 2001).

Mica BARANOV & AL'KHOVIK, 2001, p. 44 [**M. borea*; M] [=*Micathyris* BARANOV & AL'KHOVIK, 2001, p. 42, fig. 2, incorrect subsequent spelling]. Very small, subequally biconvex shells with outline elongate subelliptical; dorsal fold and ventral sulcus absent or poorly developed anteriorly; growth lines weak; ventral beak high, slightly curved, delthyrium reportedly covered by deltidial plates; dental plates thin, high, short, subparallel, teeth small; hinge plate ventrally concave, apically perforated, septum or dorsal myophragm absent; spiralia with up to four laterally directed whorls, jugum poorly preserved, seemingly without saddle, stem, or accessory jugal lamellae. [*Mica* resembles *Fastigata, Glassina, Dogdathyiris,* or *Svetlania* in outline and lateral profile, but differs internally by nature of cardinalia and brachidium; this genus requires revision.] *Lower Devonian (Emsian):* Ulakhan-Sis Ridge, eastern Yakutia.——FIG. 1837,*1a–l*. **M. borea*; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, Krivoi Ruchei Formation, Ulakhan-Sis Ridge, eastern Yakutia, IGN SO RAN 171/16, ×3 (Baranov & Al'khovik, 2001); *e–l,* transverse serial sections 1.3, 1.5, 1.8, 2.2, 2.4, 2.7, 3.0, 3.3

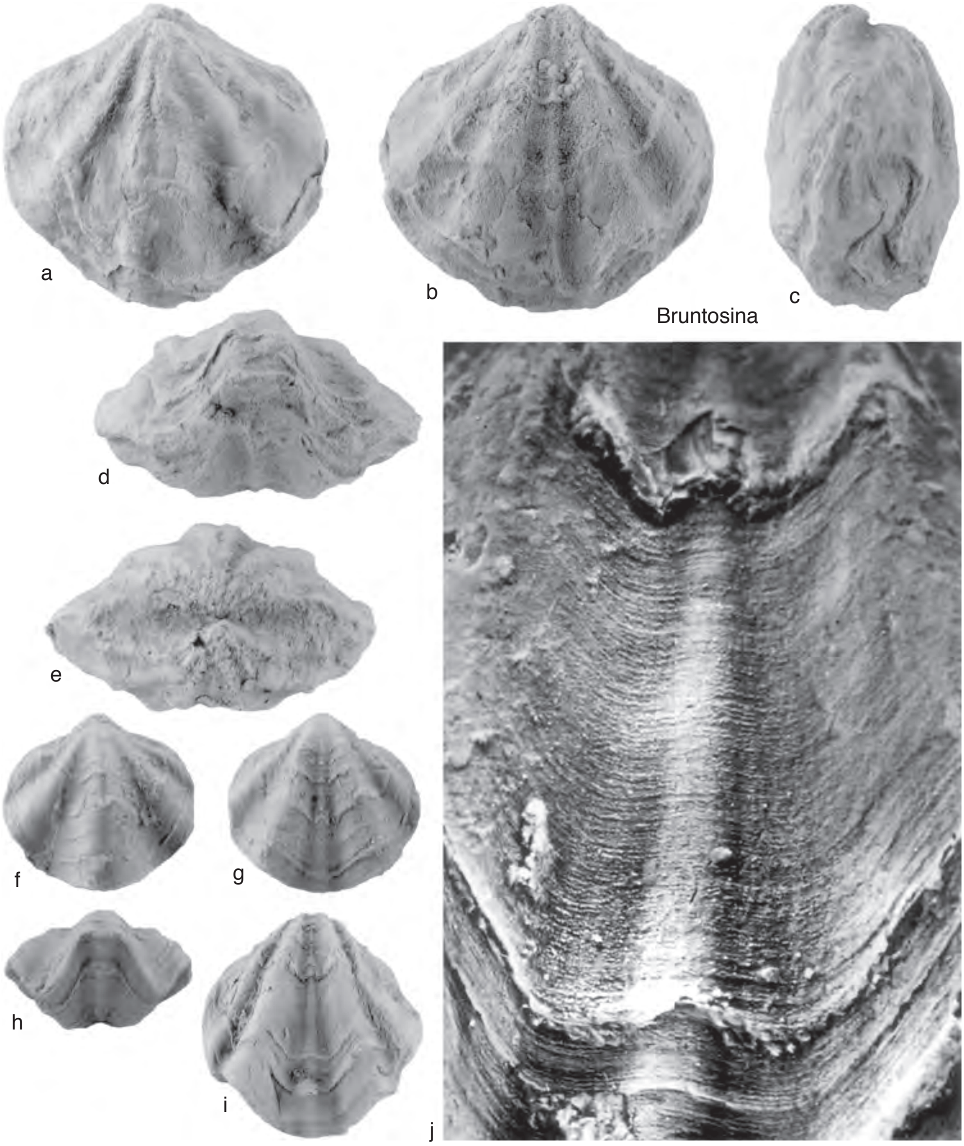


FIG. 1834. Athyrididae (p. 2746).

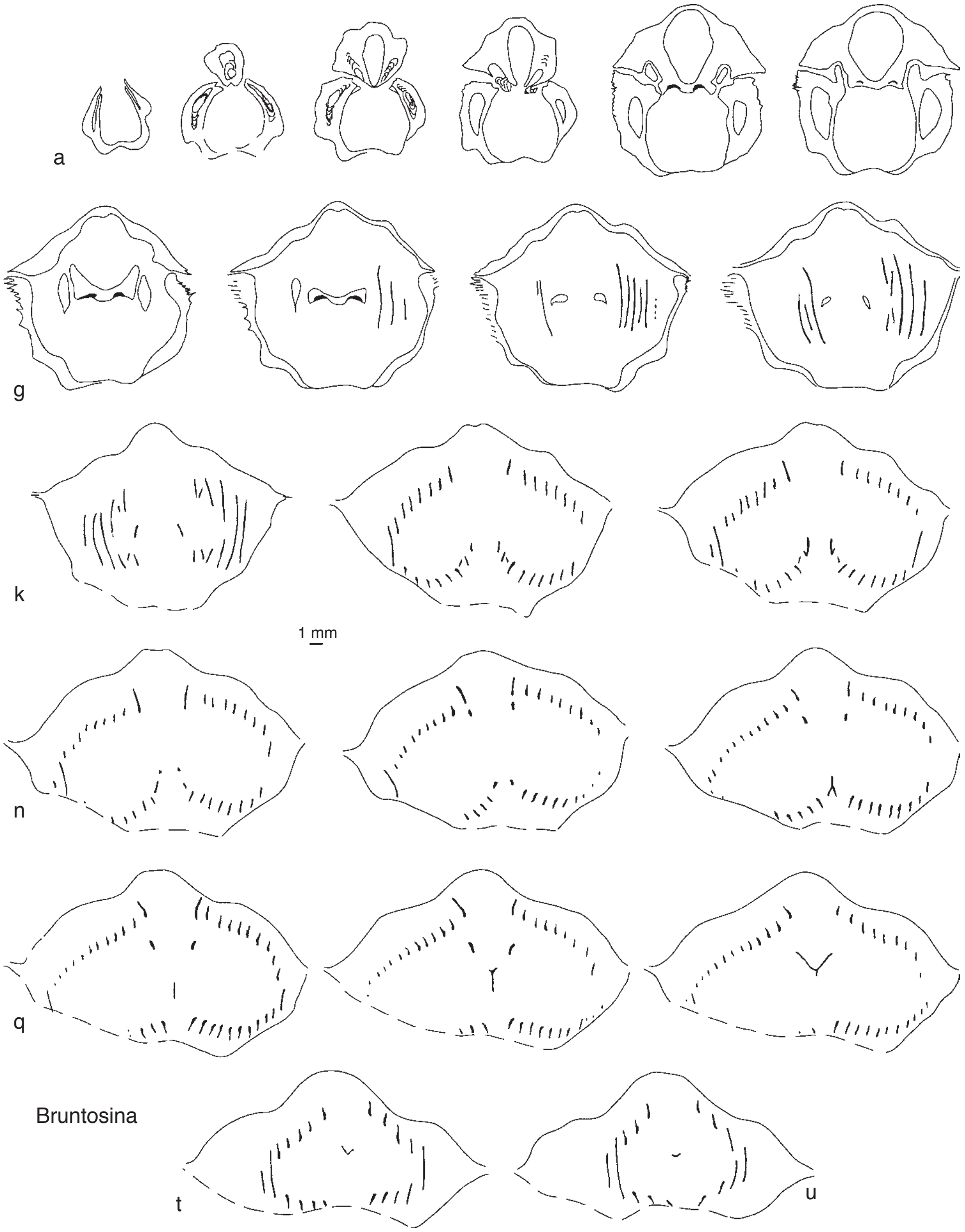


FIG. 1835. Athyrididae (p. 2746).

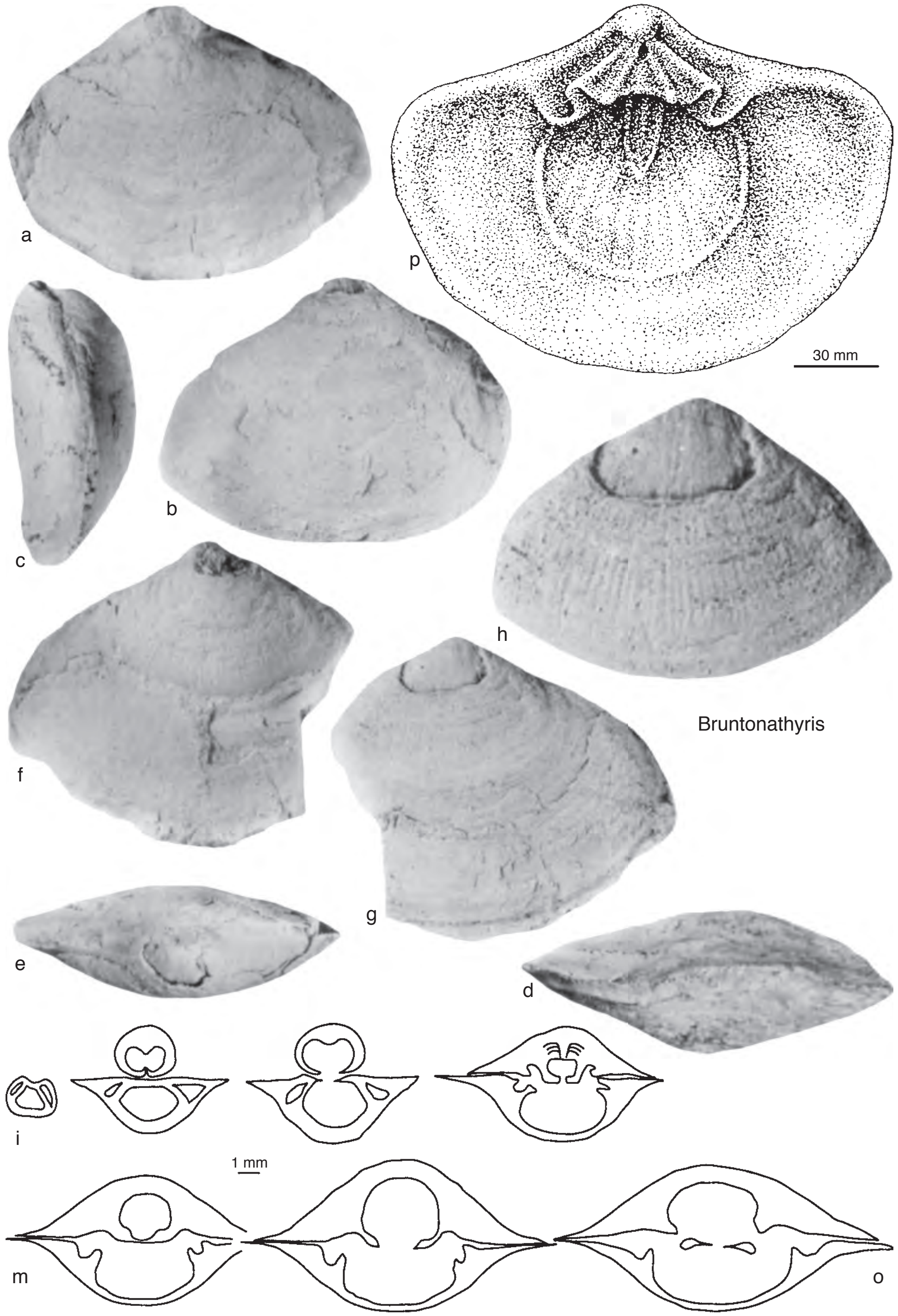


FIG. 1836. Athyrididae (p. 2747).

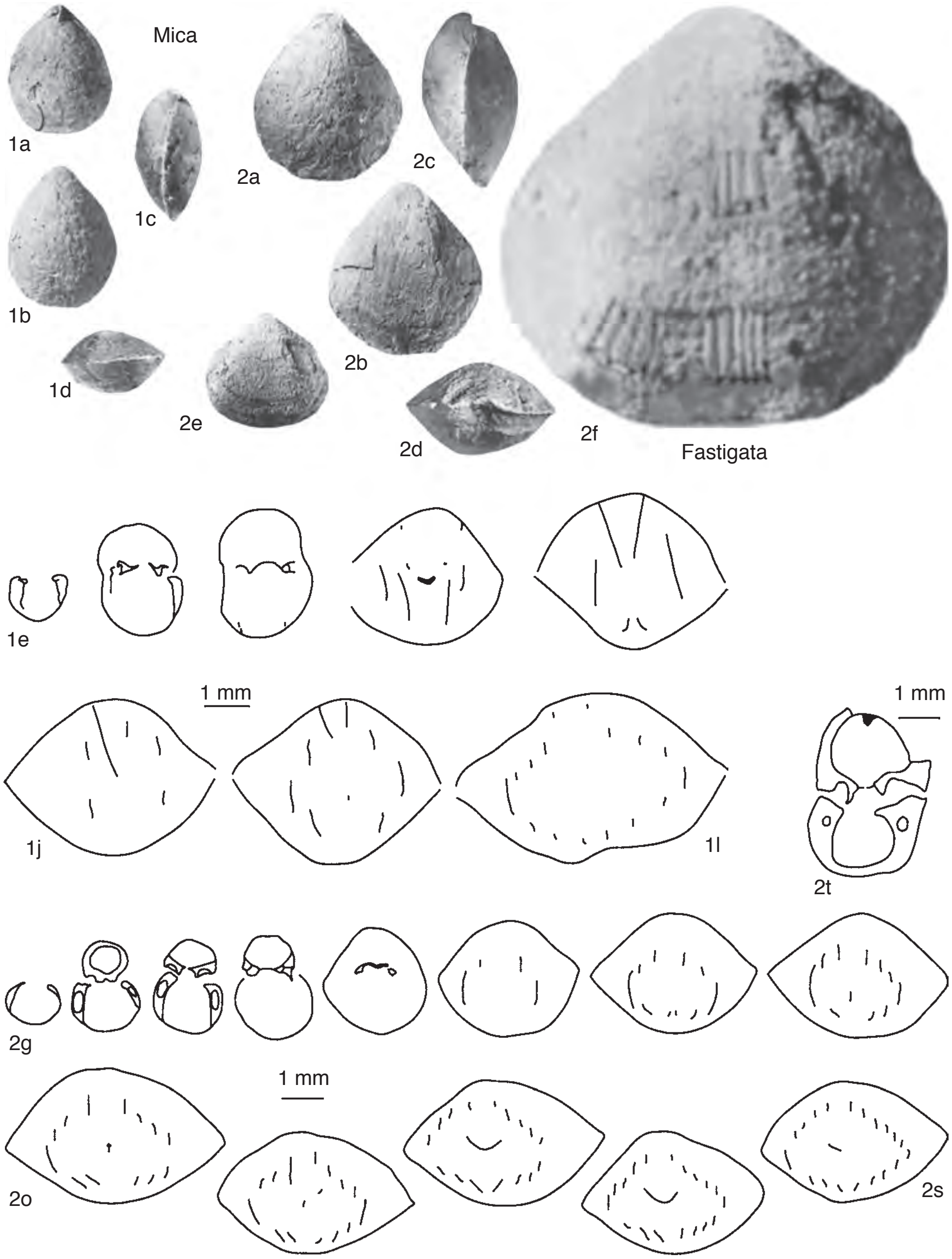


Fig. 1837. Athyrididae (p. 2747–2752).

mm from ventral umbo, distance from ventral umbo to first section approximate, Krivoi Ruchei Formation, Ulakhan-Sis Ridge, eastern Yakutia, IGN SO RAN 171/22 (adapted from Baranov & Al'khovik, 2001).

Pygmis BALIŃSKI, 2002, p. 299 [**Nucleospira jablonensis* BIERNAT, 1983, p. 142; M]. Small, smooth, slightly rostrate, ventribiconvex to nearly equally biconvex, weakly uniplicate; delthyrium open; subcircular to subpentagonal, commonly widest near midlength; internally with short, subparallel dental plates; cardinal plate apically perforated; spiralia with up to 5 laterally directed whorls and complete jugal arch. [This genus differs from externally similar Helenathyridinae in lacking a double spiralium with the accessory jugal lamellae intercalating with spiralial loops to apex; differs from *Leptathyris* in weakly uniplicate, not faintly bisulcate, anterior commissure and cardinal plate without a medial depression. *Pygmis* differs from *Nucleospira*, where the type species was placed originally, in having dental plates, very different cardinalia, and neither low median ridge on both valves nor the typical external ornamentation of fine, solid spines covering entire shell and projecting radially at different angles from valve surface of well-preserved *Nucleospira*. Most features are typically didymothyridine, but shell interiors are affected by recrystallization, and consequently the details of the cardinalia, spiralium, and jugum were missed on serial sections; better, nonrecrystallized specimens are needed to check its taxonomic position within the Athyrididae and its possible phylogenetic relationship with the Helenathyridinae.] *Upper Devonian (Famennian):* southern and central Poland (Kraków area, Holy Cross Mountains), ?Turkestan.——FIG. 1838*a–y*. **P. jablonensis* (BIERNAT); *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, Jabłonna, Holy Cross Mountains, central Poland, ×3 (new; photographs courtesy of A. Baliński); *f–h,* ventral, lateral, and anterior views, Dębnik, Kraków area, southern Poland ZPAL Bp 46/57b, ×1.5 (Baliński, 2002; photographs courtesy of A. Baliński); *i–p,* transverse serial sections 0.4, 0.6, 0.65, 0.7, 0.75, 0.9, 1.2, 1.3 mm from ventral umbo, ZPAL Bp 46/57e; *q–v,* transverse serial sections 0.6, 0.7, 2.2, 2.5, 2.6, 2.8 mm from ventral umbo, ZPAL Bp 46/58; *w–y,* transverse serial sections 3.25, 3.4, 3.7 mm from ventral umbo, ZPAL Bp 46/57f (adapted from Baliński, 2002).

Subfamily HOMEATHYRIDINAE Rong & others, 2004

[Homeathyridinae RONG & others, 2004, p. 842] [Type genus, *Homeathyris* MODZALEVSKAYA, 1997a, p. 7]

Shell small to medium, biconvex, moderately to strongly rostrate, costate, or costellate; growth lamellae commonly poorly developed, but may be squamose (*Squamathyris*); fold and sulcus variably developed, variably developed furrow, commonly shallow, may divide medially the dorsal fold (*Homeathyris*); hypothyridid pedicle opening commonly partially closed by deltidial plates; dental plates commonly short, converging dorsally, may become subparallel anteriorly; large delthyrial chamber with pedicle support consisting of pedicle collar (*Pseudohomeospira*) or two variably developed curved plates, formed of secondary layer, medially and apically situated between dental plates and joined with them at their posterodorsal end (*Homeathyris* and *Squamathyris*); cardinal plate apically perforated posteriorly; hinge plate ventrally concave in early forms, flat in latest species; spiralium and jugum resembling that of typical athyridines but with very short accessory lamellae. *Silurian (Ludlow-Přídolí).*

Genera assigned. In addition to the type genus, *Pseudohomeospira* NIKIFOROVA and *Squamathyris* MODZALEVSKAYA were placed in this subfamily. [These three genera were removed by RONG and others (2004) from the Athyrisininae, where they were commonly placed (e.g., NIKIFOROVA, 1970; MODZALEVSKAYA, 1981, 1994, 1997a, 1997b; GRUNT, 1984, 1986; ALVAREZ, RONG, & BOUCOT, 1998; ALVAREZ & RONG, 2002). See RONG and others (2004) for comparison with other subfamilies of the Athyrididae.]

Homeathyris MODZALEVSKAYA, 1997a, p. 7; *emend.,* RONG & others, 2004, p. 824 [**H. insularis;* OD] [=*Homeathyris* MODZALEVSKAYA in MODZALEVSKAYA & others, 1994, p. 66, *nom. nud.; Homeathyris* MODZALEVSKAYA, 1994, p. 147, *nom. nud.*]. Small to medium, subequally to ventribiconvex shells of subpentagonal to longitudinally oval outline; hypothyridid pedicle opening partially covered by deltidial plates; variably developed furrow dividing the dorsal fold medially; ornament of costae or low plications, bifurcated costellae developed in sulcus and median furrow, growth lamellae poorly developed, commonly absent; dental plates short, lateral cavities narrow, delthyrial chamber with two variably developed curved plates medially, apically situated between dental plates, and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with 7–10 whorls. [This genus differs externally from *Pseudohomeospira* NIKIFOROVA and *Squamathyris* MODZALEVSKAYA in having a variably developed

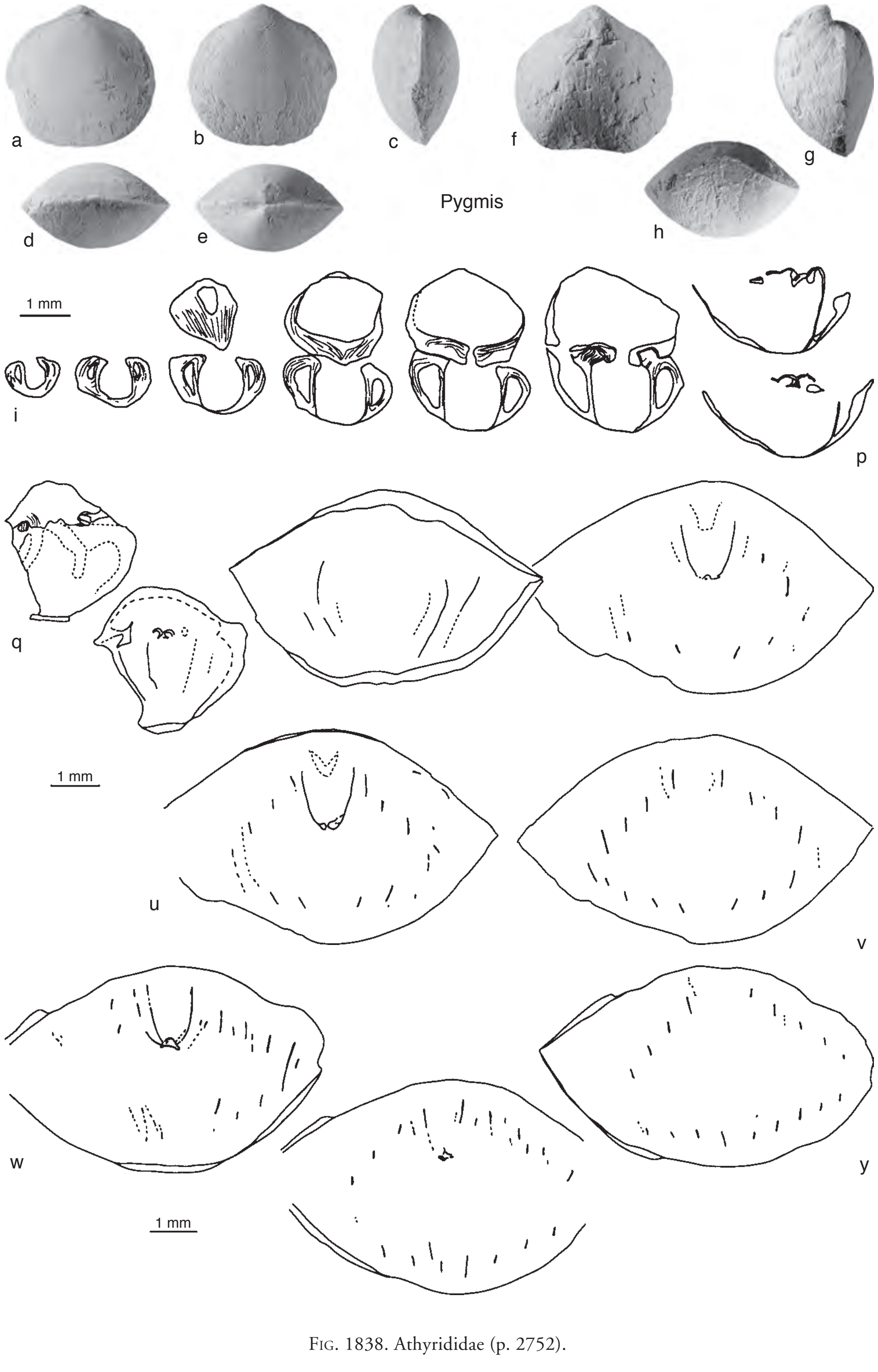


FIG. 1838. Athyrididae (p. 2752).

furrow dividing the dorsal fold medially. Growth lamellae are poorly developed in *Homeathyris* and *Pseudohomeospira*, but well developed (being *squamosus*) in *Squamathyris*. Internally, *Homeathyris* and *Squamathyris* have a subtriangular and ventrally concave hinge plate, while this is almost flat in *Pseudohomeospira*. *Homeathyris* and *Squamathyris* also differ from *Pseudohomeospira* in having medially and apically situated plates between the dental plates and joined with them at their posterodorsal ends, while *Pseudohomeospira* has a pedicle collar. These pedicle supports are commonly longer, in relation to the total length of the ventral valve, in *Homeathyris* than in the other two genera.] *upper Silurian (Ludfordian):* Russia (Arctic Russia, southern island of Novaya Zemlya, Dolgii Island, western slope of the Central Urals).——FIG. 1839*a–s*. *H. plicatella* (MODZALEVSKAYA), Zelenets Formation, Dolgii Island; *a–k,* transverse serial sections 10.7, 10.0, 9.9, 9.0, 8.3, 8.2, 7.4, 7.1, 6.8, 6.7, 6.6 mm from anterior margin of the shell, CNIGR N2/13099; *l–s,* tangential serial sections, parallel to commissural plane, 4.3, 4.2, 4.0, 3.7, 3.3, 2.8, 2.7, 1.9 mm from dorsal valve, CNIGR N3/13099 (Rong & others, 2004). [See also FIG. 1021,*2a–b* in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]

Pseudohomeospira NIKIFOROVA, 1970, p. 139; *emend.,* RONG & others, 2004, p. 846 [**P. polaris;* OD]. Small, biconvex, elongate oval, costate shells; ventral sulcus and dorsal fold weakly developed anteriorly; costae subangular or rounded, each valve with 12–16 costae, bifurcating in fold and sulcus; hypothyridid pedicle opening may be partially closed by deltidial plates; pedicle collar present; short ventral ridge may be present apically; dental plates thin, of moderate length, dorsally convergent apically, with very narrow lateral apical cavities, subparallel posteriorly; minute dorsal foramen, very low dorsal myophragm may be present apically; spiralia directed laterally, jugum unknown. [*Pseudohomeospira* is more elongate than *Homeathyris* and *Squamathyris,* which are commonly almost equidimensional. *Pseudohomeospira* characteristically has a weakly developed dorsal fold and ventral sulcus displayed only anteriorly. Ventral beak relatively high, slightly curved, with a hypothyridid pedicle opening partially closed by deltidial plates and pedicle support resembling internal characteristics of didymothyridin *Collarothyris* MODZALEVSKAYA, 1970, from beds of Ludlow age in western Russia and adjacent areas. Better, nonrecrystallized specimens are needed, which will allow the study of jugal structures.] *upper Silurian (Přídolí):* Russia (Arctic Russia, southern island of Novaya Zemlya, Vaigach Island, western slope of Polar and Central Urals).——FIG. 1840,*1a–g*. **P. polaris*, Tselebej Formation, western slope of Polar Urals; transverse serial sections 10.0, 9.4, 9.3, 8.5, 8.3, 7.9, 7.6 mm from anterior margin of shell, CNIGR N86/10629 (Rong & others, 2004). [See also FIG. 1021,*1a–b* in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]

Squamathyris MODZALEVSKAYA, 1981, p. 153; *emend.*, RONG & others, 2004, p. 848 [**S. glacialis;* OD]. Shell of medium size, biconvex, moderately to strongly rostrate, subpentagonal outline, with strong costae and numerous and squamose growth lamellae; ventral sulcus and dorsal fold moderately developed; hypothyridid pedicle opening restricted laterally by deltidial plates; dental plates short, delthyrial chamber with two variably developed curved plates medially and apically situated between dental plates and joined with them at their posterodorsal end; hinge plate subtriangular, ventrally concave; spiralia with up to ten whorls, jugum unknown. [This genus differs from *Homeathyris* and *Pseudohomeospira* in having stronger costae and numerous and squamose growth lamellae. Internally, the hinge plate is ventrally concave in *Squamathyris* but almost flat in *Pseudohomeospira*. *Squamathyris* also differs from *Pseudohomeospira* in having medially and apically situated plates between the dental plates and joined with them at their posterodorsal ends as in *Didymothyris*, while *Pseudohomeospira* has a pedicle collar; the internal jugal structure is unknown.] *upper Silurian (Ludfordian):* Russia (Arctic Russia, southern island of Novaya Zemlya, Vaigach and Dolgii islands). ——FIG. 1840,*2a–n.* **S. glacialis*, Zapadno-Khatanzeya Formation, southern island of Novaya Zemlya; transverse serial sections 16.0, 15.6, 15.5, 14.5, 13.6, 13.2, 13.05, 13.0, 12.5, 12.4, 12.2, 12.0, 11.95, 11.9 mm from anterior margin of the shell, CNIGR N5/13099 (Rong & others, 2004). [See also fig. 1021,*3a–d* in ALVAREZ & RONG, 2002; and revision in RONG & others, 2004.]

Subfamily JANICEPSINAE Posenato, 2001

[Janicepsinae POSENATO, 2001, p. 204] [Type genus, *Janiceps* FRECH, 1901, p. 551]

Commonly small to medium size, rarely larger, subtrigonal to transversely subrectangular, astrophic to almost strophic shells, moderately to strongly biconvex, with ventral sulcus and dorsal sulcate fold; lateral plications may be developed; smooth, with fine growth lines; ventral beak short, incurved, truncated by small, permesothyridid foramen; delthyrium open, obscured by dorsal beak; pedicle support absent; dental plates thin, relatively short, may be close to valve walls or obscured by callus but distinct in specimens sectioned, low dental flanges may support teeth anteriorly; cardinal plate subquadrangular and thick, serrated cardinal flanges moderately to strongly developed posteroventrally, carrying the myophores deeply into the ventral umbo; inner socket

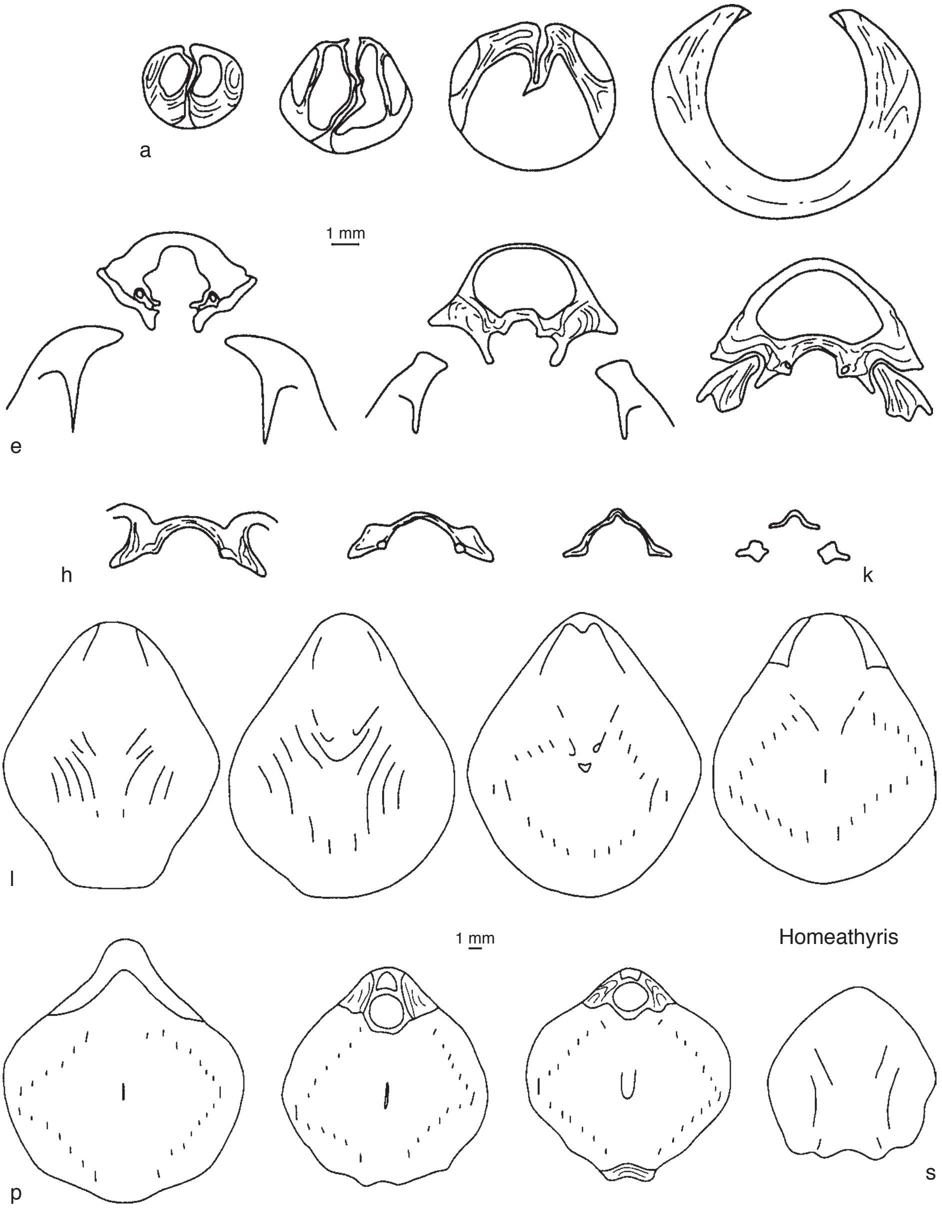


Fig. 1839. Athyrididae (p. 2752–2754).

ridges high; dorsal foramen infilled; dorsal myophragm or septum absent; jugum as in *Athyris* with short accessory jugal lamellae. [There is a great external and internal morphologic variation within the species and genera traditionally included within the Spirigerellinae (e.g., Grunt, 1986; Alvarez, Rong & Boucot, 1998; Posenato, 1998, 2001; Alvarez & Rong, 2002). The variability displayed by the Comelicaniinae from the Southern Alps was studied in detail by Posenato (1998) who recently suggested (Posenato, 2001) that some Permian shells, included until now within the subfamily

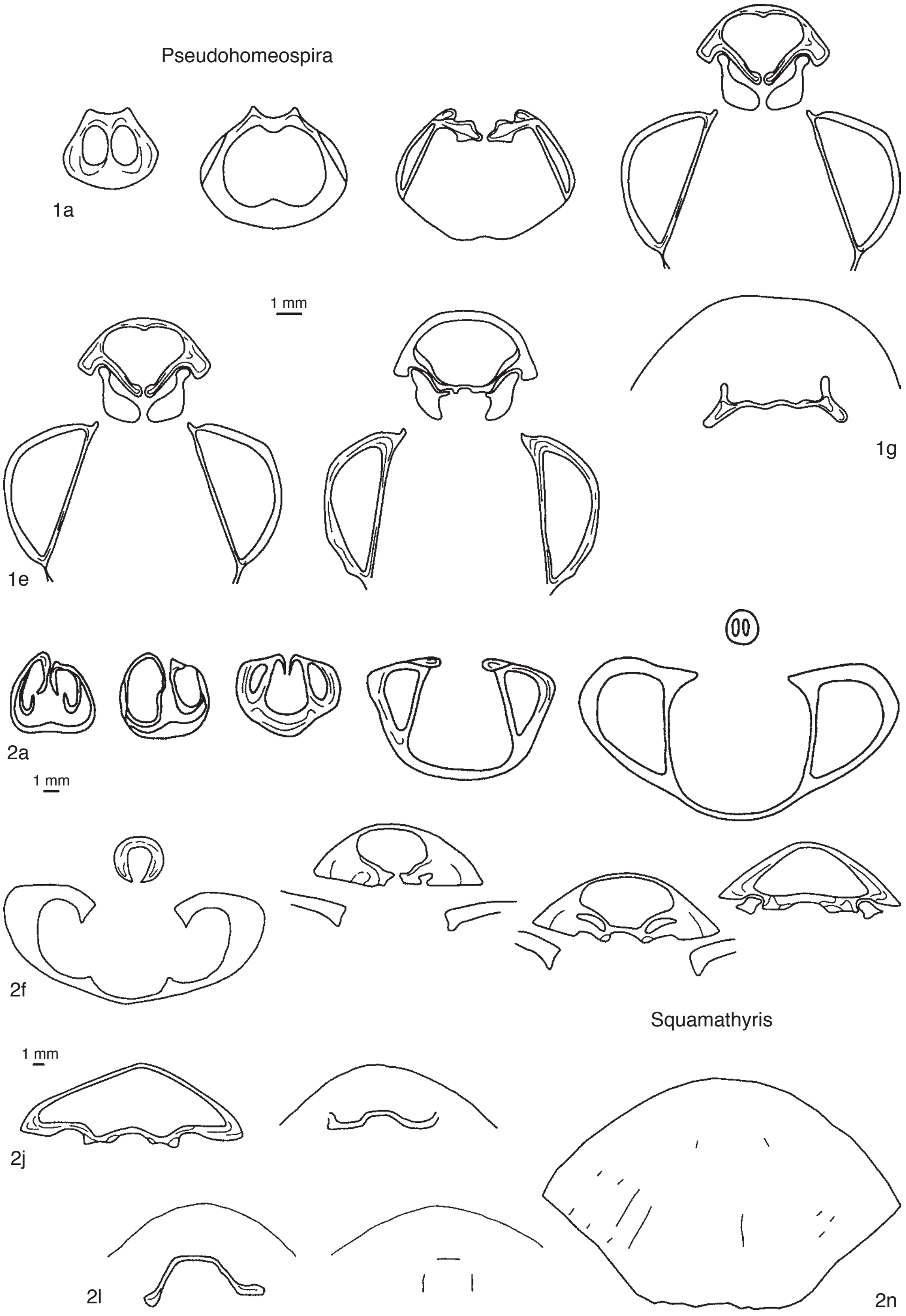


FIG. 1840. Athyrididae (p. 2754).

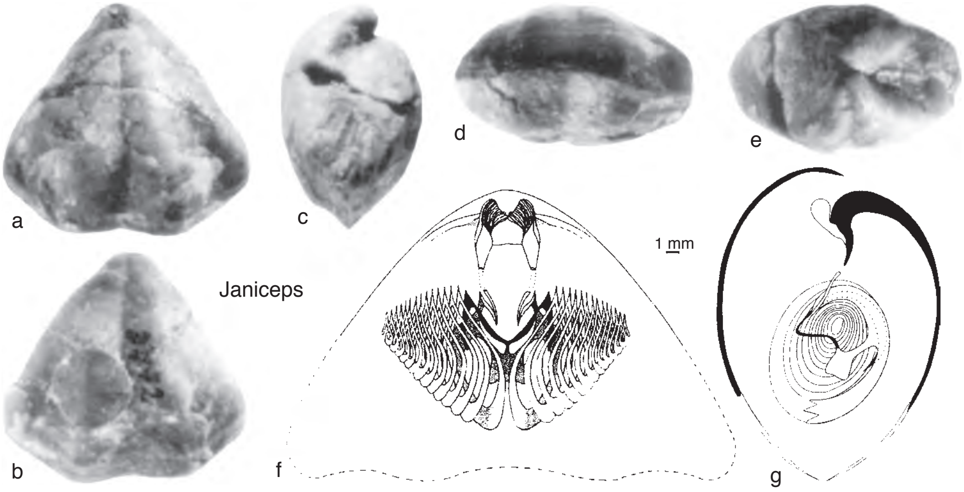


FIG. 1841. Athyrididae (p. 2757–2758).

Spirigerellinae, are paedomorphic derivatives of the Comelicaniinae. To avoid a polyphyletic origin to the spirigerellins, POSENATO (2001) erected the Janicepsinae for *Janiceps* and *Comelicothyris*. The shells of the Comelicaniinae are large to extremely large, while the Janicepsinae shells are small to moderately so, and it is likely that the failure to develop in the Janicepsinae some characters of the immediate ancestors was probably achieved by early sexual maturity, progenesis, than by delayed somatic development of certain parts, neoteny. As possibly paedomorphism was involved more frequently than described, a complete and detailed revision of the species included in the Spirigerellinae, and related groups, is needed to better understand their phylogenetic affinities.] *Upper Permian (Changhsingian).*

Genera assigned. When the subfamily was erected, two genera were included: *Janiceps* FRECH, 1901 and *Comelicothyris* POSENATO, 2001. According to Article 16.2 of the 4th edition of the *Code* (1999), any new family-group name published after 1999 must satisfy the provisions of Articles 13–15 and must be accompanied by citation of the name of the type genus (the name from which the family-group name is formed). Although POSENATO did not expressly cite *Janiceps* as the type genus for the subfamily, it is clear throughout the paper that the subfamily-group name was formed from that genus. Authorship, date, and bibliographic reference of the work in which *Janiceps* was established was provided by the author, thereby avoiding possible ambiguities.

Janiceps FRECH, 1901, p. 551; *emend.,* POSENATO, 2001, p. 205 [**Spirigera peracuta* STACHE, 1878, p. 152; SD SCHUCHERT & LEVENE, 1929, p. 70]. Small to medium sized, subtrigonal, biconvex, and astrophic shells with ventral sulcus and dorsal sulcate fold, lateral grooves may be developed; anterolateral extremities pointed or rounded; ventral umbo small, recurved, and pointed; only very fine growth lines; pedicle support absent; dental plates thin and short, mostly buried in secondary shell material; cardinal plate subquadrangular and thick; inner socket ridges high; dorsal foramen absent; cardinal flanges variably developed; dorsal myophragm or septum absent; jugum as in *Athyris* with short accessory jugal lamellae. *Upper Permian (Changhsingian):* Italy (southern Alps). [Extralpine, older occurrences from Transcaucasia (upper Djulfian to lower Dorashamian) and China (Wuchiapingian and Changhsingian) need revision (POSENATO, 2001).]——FIG. 1841*a–g*. **J. peracuta* (STACHE), upper Changhsingian, southern Alps; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, Monte Croce di Comelico, Stache collection, MGBW 1878/1/47a, ×1.5 (Posenato, 2001; photographs courtesy of R. Posenato); *f–g,* reconstruction of internal characters of dorsal valve viewed ventrally and laterally, Val Brutta, MDTF 6 (Posenato, 2001). [See also Fig. 1045,*3a–t* in ALVAREZ & RONG, 2002; and revision in POSENATO, 2001.]

Comelicothyris POSENATO, 2001, p. 217 [**Athyris protea* var. *recticardinis* MERLA, 1930, p. 67; OD]. Shell medium sized, strongly biconvex, rounded triangular to subpentagonal or transverse subrectangular, almost strophic; maximum width near midvalve; ventral sinus relatively deep and dorsal sulcus on slightly raised fold; dental plates very thin and short, not fused to thick lateral walls; cardinalia as in *Comelicania*, with well-developed cardinal flanges and myophores facing sagittal plane; spiralia and jugum poorly known. [The outline of *Comelicothyris* juveniles is rounded-subtriangular and *Janiceps*-like, while the outline of adults resembles that of late *Comelicania* species. This genus differs from *Comelicania* in its smaller size, maximum width near midvalve, not at hinge margin, lack of small winglike extensions at cardinal extremities, dental plates thin, short, and not fused to lateral walls. Juveniles and adult *Janiceps* have an astrophic, subtriangular to rhomboidal shell with maximum width at anterior third of shell, close to front. In *Janiceps* the thin and short dental plates may be buried in secondary shell material that is strongly developed in umbonal cavities, and low dental flanges may support teeth anteriorly (see POSENATO, 1998, 2001). *Araxathyris* differs from *Comelicothyris* in its parasulcate to bisulcate anterior commissure; growth laminae widely and irregularly spaced; medially concave dental plates forming narrow sessile spondylium; cardinal plate thinner, triangular, apically perforated, with lower cardinal flanges; short and low myophragm, tertiary layer present (e.g., GRUNT, 1965, 1986).] *Upper Permian (upper Changhsingian):* eastern southern Alps.——FIG. 1842*a–p*. **C. recticardinis* (MERLA); *a,* lectotype, ventral view, Monte Croce di Comelico, Merla collection, MDGP 24840, ×1; *b*, ventral view, Monte Croce di Comelico, Merla collection, MDGP 24834, ×1 (Posenato, 2001; photographs courtesy of R. Posenato); *c–p,* transverse serial sections 0.45, 1.5, 2.55, 2.7, 3.2, 4.05, 4.15, 4.3, 4.5, 4.85, 5.35, 6.15, 6.85, 7.1 mm from ventral umbo, Val Brutta, MDTF 15 (Posenato, 2001).——FIG. 1842*q–t*. *C. laterosulcata* POSENATO; holotype, dorsal, ventral, lateral, and posterior views, Sass de Putia, Bolzano, MDTF 54, ×0.8 (Posenato, 2001; photographs courtesy of R. Posenato).

Subfamily PLICATHYRIDINAE Alvarez, 1990

Anathyris VON PEETZ, 1901, p. 134 [**Spirifera phalaena* PHILLIPS, 1841, p. 71; SD SCHUCHERT & LEVENE, 1929a, p. 29]. Small to very large transverse shells commonly with overall winged outline; almost opposite to more or less well-developed mixed folding; pedicle foramen in permesothyridid position; delthyrium wide, triangular, open or partially restricted laterally by narrow deltidial plates; internally similar to *Plicathyris*. *Lower Devonian (Emsian)–Upper Devonian (Frasnian), ?Lower Carboniferous:* northwestern Spain, France, Bohemia, Czech Republic, northern Africa, Saudi Arabia, *Emsian;* England, Timan, Kuznetsk Basin, North America, *Middle Devonian;* Timan, Urals, Kuznetsk basin, Afghanistan, *Frasnian;* ?Hunan, *?Lower Carboniferous.*

A. (Anathyris). Medium to very large transverse *Anathyris* with overall winged outline; hinge line almost straight, equal to or slightly shorter than maximum width; folding almost opposite and anterior commissure straight in juveniles, passing during ontogeny to develop a clearer mixed folding; ventral cardinal area well defined, rather high, subtrapezoidal, concave, ranging from apsacline to almost catacline in lateral regions to strongly curved anacline centrally; area covered by numerous, close and horizontal, well-marked growth lines; internally teeth and dental plates thicker than in *Plicathyris*; in late growth stages of some specimens dorsal foramen filled. [For discussion of its type species and other species included, see ALVAREZ, 1990, p. 206–207. The inclusion of *A. rhomboidalis* from the Lower Carboniferous of Hunan, China, may extend the range from the Upper Devonian, Frasnian, but its assignment is uncertain.] *Lower Devonian (Emsian)–Upper Devonian (Frasnian), ?Lower Carboniferous:* northwestern Spain, France, northern Africa, Saudi Arabia, *Emsian;* England, Timan, Kuznetsk Basin, North America, *Middle Devonian;* Timan, Urals, Kuznetsk basin, Afghanistan, *Frasnian;* ?Hunan, *?Lower Carboniferous.* [For illustrations, see ALVAREZ & RONG, 2002, fig. 1039.]

A. (Ranathyris) HAVLÍČEK, 1998, p. 120 [**Anathyris inconsueta* HAVLÍČEK, 1956, p. 620; M]. Small to medium, rounded subpentagonal *Anathyris* with strongly biconvex lateral profile; maximum width anterior to midlength, close to anterior margin; ventral beak thick, incurved, with large pedicle foramen; poorly developed mixed folding, folds round, poorly developed, or absent in ventral valve, ventral median sulcus shallow to moderately deep and subangular; dorsal valve with narrow median depression bounded by two rounded submedian folds; lateral folds gentle and rounded in both valves; teeth small, supported by short, thin, nearly parallel dental plates; spiralia and jugum unknown. [HAVLÍČEK (1998) established a new subgenus for this widespread and relatively common mid-Paleozoic genus; *Ranathyris* is based only on *A. inconsueta* HAVLÍČEK. As many of the diagnostic features of this subgenus are manifest in the main *Anathyris* line, their use is restricted.] *Lower Devonian (lowest Emsian):* Prague Basin (Bohemia).——FIG. 1843,*1a–g*. **A. (R.) inconsueta* (HAVLÍČEK), Zlíchov Formation; *a,* holotype, ventral view, Havlíček collection, VH13268b, ×1 (Havlíček, 1956); *b–c,*

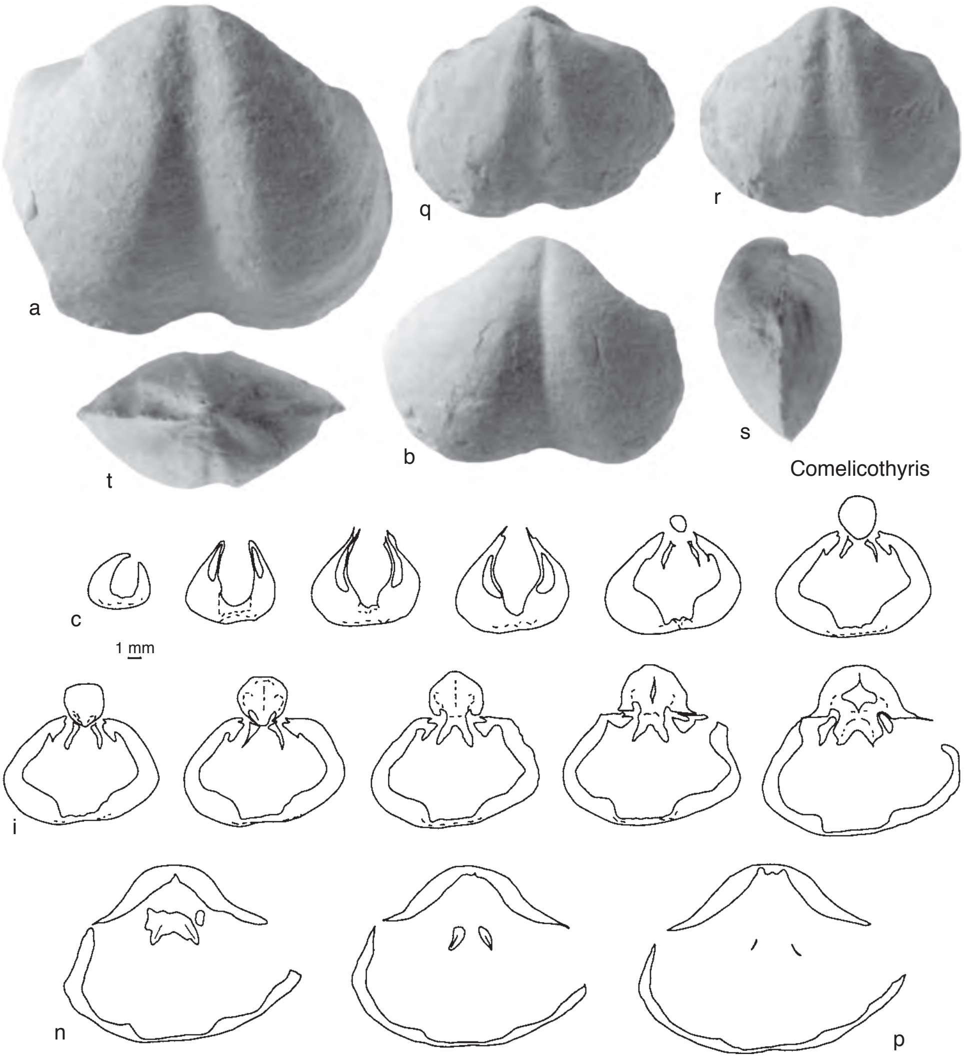


FIG. 1842. Athyrididae (p. 2758).

dorsal and ventral views, VH13268a, ×1; *d–e,* ventral and anterior views, Havlíček collection, VH13190a, ×1.4; *f,* dorsal interior, Havlíček collection, VH13274c, ×2.7; *g,* drawing of ventral valve interior, Havlíček collection, VH13270a (Havlíček, 1998).

Subfamily SPIRIGERELLINAE Grunt, 1965

Gruntea SHI, SHEN, & ARCHBOLD, 1999, p. 347 [**Posicomta grunti* SHI & SHEN, 1997, p. 46; M]. Small to medium, moderately subequally biconvex shells, subpentagonal or rounded subtriangular to subcircular, equidimensional to wider than long, commonly widest slightly anterior to midlength, with broadly spaced growth lamellae; ventral sulcus narrow, originating from beak as a prominent groove, slightly widening and deepening anteriorly; anterior commissure uniplicate; ventral beak strongly incurved, often closely appressed to dorsal umbo, foramen very small or absent, delthyrium completely filled by dorsal umbo without deltidial plates; dental plates thin, fused to thick shell walls or obscured by callus; cardinalia typically spirigerellin; spiralia and jugum unknown. [*Gruntea* is possibly synonymous with *Posicomta* GRUNT, but with a slightly more subtriangular

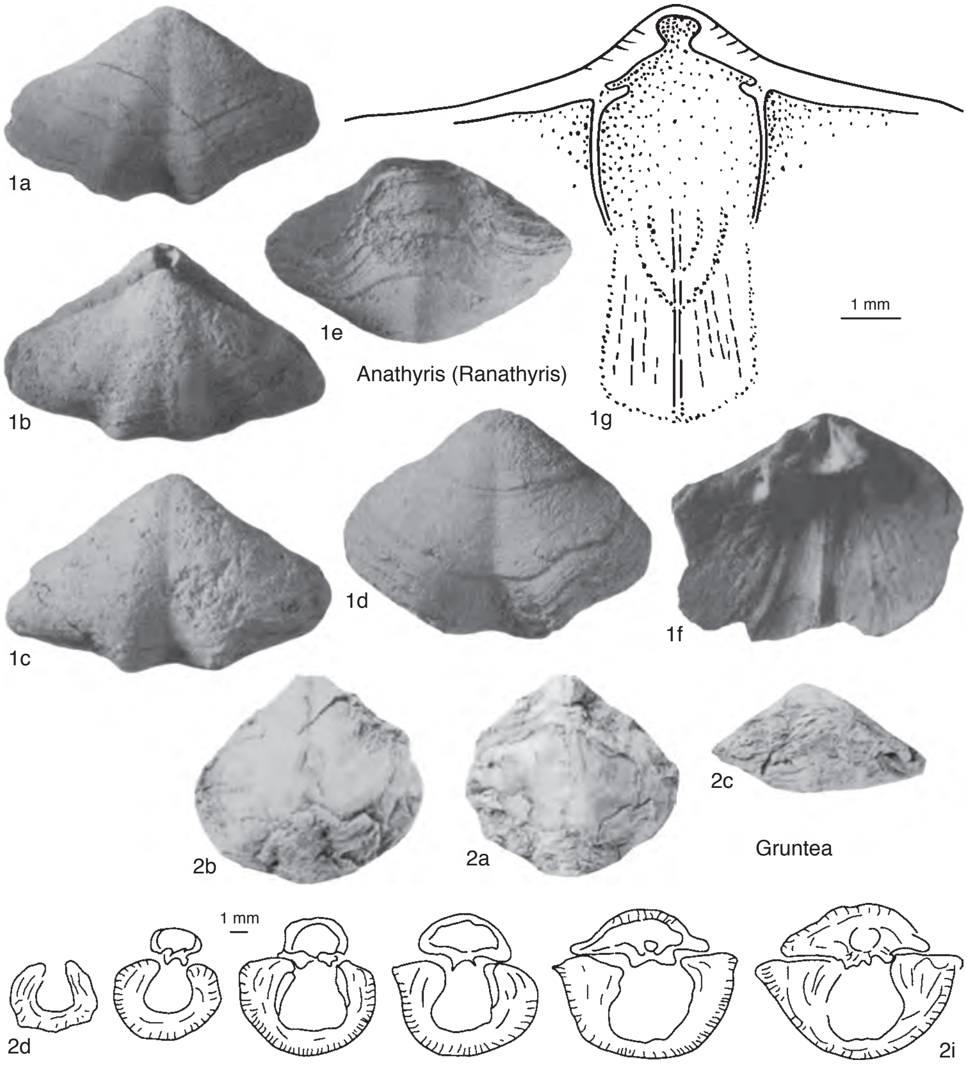


FIG. 1843. Athyrididae (p. 2758–2760).

outline, dental plates being fused to thick shell walls, and having a deeper impressed ventral muscle field; internal structure of brachidia unknown.] *Upper Permian:* China (Xizang, southern Tibet), ?northwestern India.——FIG. 1843,*2a–i.* **G. grunti* (SHI & SHEN), ?Kazanian, Tatarian, Selong Group, Selong Xishan section, southen Tibet, China; *a–c,* holotype, dorsal, ventral, and anterior views, NMV P145689, ×2.8 (Shi & Shen, 1997); *d–i,* transverse serial sections 0.8, 1.2, 2.5, 3.0, 4.0, 7.0 mm from ventral umbo (adapted from Shi & Shen, 1997).

Superfamily MERISTELLOIDEA Waagen, 1883

Family MERISTIDAE Hall & Clarke, 1895

Subfamily MERISTINAE Hall & Clarke, 1895

Cammerista HAVLÍČEK in HAVLÍČEK & VANĚK, 1998, p. 85 [**Terebratula calypso* BARRANDE, 1847, pl. 16,*10;* OD]. Small to medium size; elongate oval

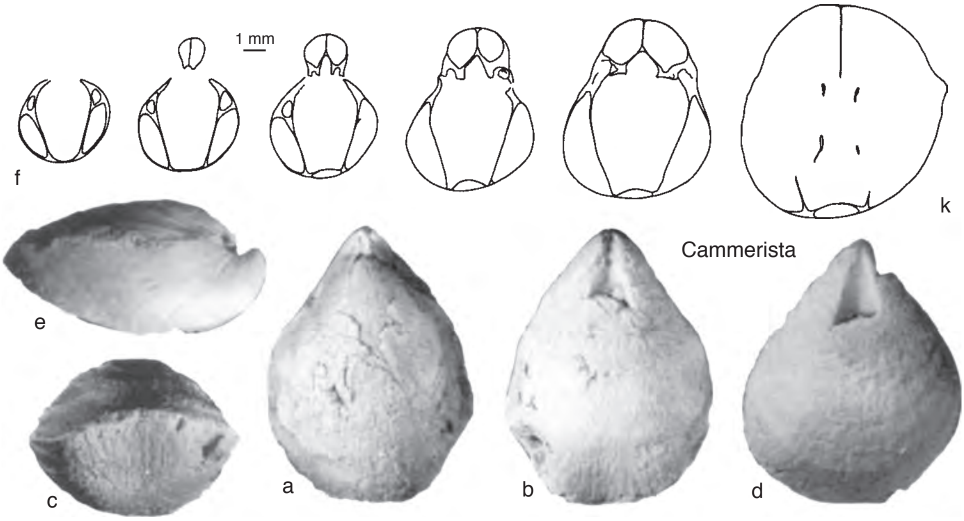


FIG. 1844. Meristidae (p. 2760–2761).

in outline, longer than wide; subequally biconvex; smooth but for few growth lines and low, rounded costellae, present only on anterior half; rectimarginate to slightly uniplicate anterior commissure; ventral beak moderately incurved, pierced by minute foramen; small, conjunct deltidial plates reportedly present; dental plates high, long, converging ventrally, reinforced by mystrochial plates; thin, gently convex shoelifter developing between dental plates, starting anterior of plates; septalium supported by high and thin median septum; spiralium and jugum unknown. [*Cammerista* is similar to *Dicamara* but with mystrochial plates and lacking dorsal shoelifter. It differs from *Dicamaropsis* in its ventral shoelifter being relatively narrow, placed between ventrally converging dental plates, deeper septalium without middle knob, and lack of dorsal shoelifter. In *Dicamaropsis* the shoelifter supports ventrally parallel dental plates. Lack of information on the brachiojugal system makes impossible its comparison with those developed by other meristelloid genera.] *Silurian (?Llandovery, ?Ludlow), Lower Devonian (Pragian):* ?North America (Oklahoma), *Ludlow*; ?Russia (Gorny Altai), *Llandovery*; Europe (Bohemia), *Pragian*.——FIG. 1844*a–k*. **C. calypso* (BARRANDE), Pragian, Koněprusy Limestone, Koněprusy, Prague Basin, Bohemia; *a–c,* holotype, dorsal, ventral, and anterior views, L 23898, ×3.4; *d–e,* ventral, and lateral views, Havlíček collection, VH 10798a, ×2.2 (Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček); *f–k,* transverse serial sections 12.8, 12.4, 12.0, 11.9, 11.4, 10.3 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998).

Subfamily UNCERTAIN

Muhuathyris SUN & others, 2004, p. 240 [**M. circularis*; M]. Medium-sized meristids with subcircular to subpentagonal outline; dorsal fold and ventral sulcus commonly weak; well-developed dental plates, laterally buttressed by mystrochial plates, converging to form a spondylium sitting on long, low median septum; septalium rhombic, relatively broad, supported by low median septum and by a pair of plates laterally; spiralium and jugum unknown. [Articulated shells were not found; the diagnosis is presently based on isolated valves, 13 dorsal and 11 ventral, found in the same beds. Assigned by its authors to the Rowleyellinae, these medium-sized meristid shells resemble *Camarophorella* HALL & CLARKE externally and in their ventral interior, but clearly differ in the dorsal interior; in *Muhuathyris* the septalium is typically meristelloid but a pair of plates support laterally the septalium; *Muhuathyris* also lacks the dorsal shoe-lifter characteristic of Meristidae subfamilies and the long cruralium characteristic of Rowleyellinae, so its subfamily affinity is uncertain.] *Lower Carboniferous (Tournaisian):* southwestern China (Guizhou).——FIG. 1845*a–s*. **M. circularis,* Muhua III section, Changshun County; *a–d,* holotype, dorsal, ventral, lateral, and posterior views of dorsal valve, PKUM02 0012, ×1.3; *e,* cardinalia viewed anteroventrally, PKUM02 0012, ×7.7; *f,* cardinalia viewed anteriorly, PKUM02 0014, ×8; *g,* paratype, dorsal interior viewed anterolaterally, PKUM02 0015, ×10.2; *h–j,* paratype, external, internal, and posterior views of ventral valve, PKUM02 0004, ×1.5; *k,* paratype, anterior

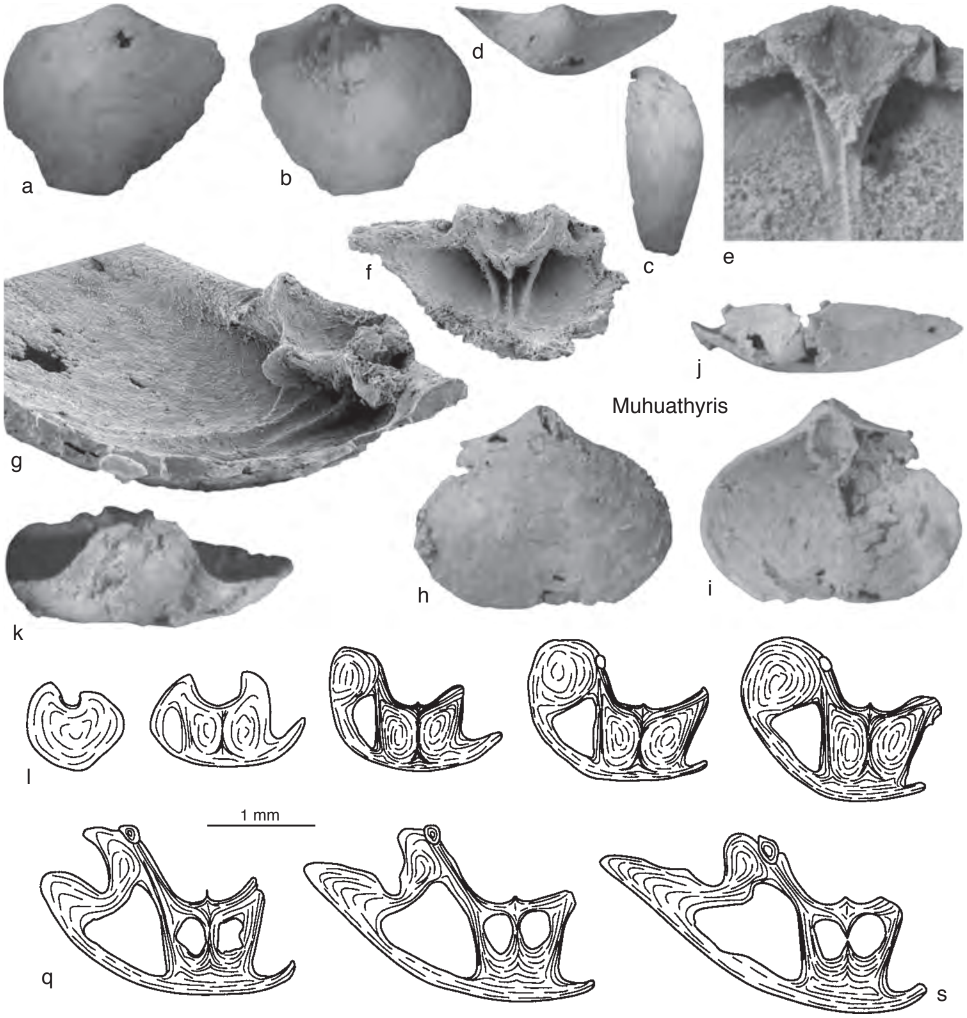


FIG. 1845. Meristidae (p. 2761–2762).

view of ventral valve, PKUM02 0005, ×1.8; *l–s,* transverse serial sections of broken dorsal valve, 0.16, 0.25, 0.34, 0.50, 0.65, 0.82, 0.91, 1.00 mm from dorsal umbo (Sun & others, 2004; photographs courtesy of Yualin Sun).

Family UNCERTAIN

Bimeristina GARCÍA-ALCALDE, 2003, p. 107 [**B. binnekampi*; M]. Small to medium, elongate to equidimensional, rounded-subpentagonal, moderately biconvex, faint sulcus on both valves, anterior commissure rectimarginate or almost rectimarginate; dorsal septum long; jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae that reunite with stem; a second pair of accessory jugal lamellae joining laterally the jugal arch with second whorl of each spiralial cone. [This genus resembles externally the subfamily Whitfieldellinae; septalium and dental plates are as in Triathyridinae; the jugum is similar to that of *Meristella* HALL except that in *Bimeristina,* the jugum projects also laterally into two apophyses that connect the jugal arch with secondary lamellae of spiralium; this unusual jugal system was reconstructed from serial sections made parallel to commissural plane from one specimen; sections of more specimens, especially those perpendicular to the plane of symmetry, are important to confirm the morphology of this complex jugum. At present, although all other features are typically meristellide, the development of laterally directed apophyses on the jugal arch makes the family assignment uncertain.] *Lower Devonian (Pragian):*

Spain (Palencia, Aragón, Guadalajara), ?Czech Republic.——FIG. 1846,*1a–p*. **B. binnekampi,* Lebanza Formation, Lebanza, Palencia, northern Spain; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, DPO 30895, ×1; *e–i,* transverse serial sections 2.0, 2.5, 2.95, 3.5, 4.7 mm from ventral umbo, DPO 38570; *j–o,* tangential serial sections, parallel to commissural plane, 3.2, 3.7, 4.65, 5.1, 5.55, 5.7 mm to ventral valve, DPO 38572; *p*, ventral view of reconstructed jugum, ×3 (adapted from García-Alcalde, 2003).

Fayettella WATKINS, 1999, p. 16 [**F. peninsulensis*; M]. Small, thin, smooth, with few growth lines, subtrigonal to elongate oval in outline, greatest width anterior to midvalve, dorsi- to almost equibiconvex; rectimarginate; ventral beak prominent, narrow, slightly to moderately curved, delthyrium high, open, anteriorly obscured by strongly incurved dorsal beak, foramen small, permesothyrid; long, cyrtomatodont hinge teeth supported by short dental plates; dorsal interior without septum and septalium but with spoon-shaped cardinal plate supported by two crural plates connected to valve floor; median ridge or myophragm dividing long, elongate, but poorly impressed muscle scars; spiralium and jugum unknown. [When erected, this genus was included in the superfamily Meristelloidea, but no family assignment was attempted. Externally, this genus resembles young *Whitfieldella*, but its unusual cardinalia makes the assignment uncertain. Lack of information on the brachiojugal system makes impossible its comparison with those of other meristelloid genera.] *lower Silurian (Aeronian):* USA (Burnt Bluff Group, Great Lakes Region, Wisconsin, Michigan).——FIG. 1847*a–i*. **F. peninsulensis,* Hendricks Formation, Fayette, Michigan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, MPM28522, ×12.6, ×13, ×6.25, ×11.7, ×6.5; *f,* ventral interior, MPM28525, ×4.5; *g–h,* dorsal interior viewed ventrally and anteroventrally, MPM28523, ×5; *i,* drawing of dorsal interior viewed anteroventrally (Watkins, 1999; drawing and photographs courtesy of R. Watkins & P. Mayer).

Iuxtathyris HAVLÍČEK in HAVLÍČEK & VANĚK, 1998, p. 90 [**Terebratula vultur* BARRANDE, 1847, p. 385, pl. 14,*4;* M]. Small to medium, equibiconvex, smooth shells with subquadrate to transversely elliptical outline, maximum width at midvalve; ventral beak short, incurved, closely appressed on dorsal umbo; weak dorsal fold and ventral sulcus starting near umbo, less commonly developed only anteriorly; anterior commissure weakly uniplicate; tongue low, wide, trapezoidal; dental plates short, medially concave; dorsal valve with short, shallow septalium supported by high, long, blade-like septum; spiralia with up to 5 laterally directed whorls and reportedly with angular jugal saddle, with a sharp crest anteroventrally, without jugal stem. [This rare genus has an unusual combination of dorsal internal characters including dorsal septalium, typically meristelloid; and jugum with jugal saddle, typically athyridoid. Jugal system known from few serial sections taken in only one specimen; jugal morphology requires further investigation. Presence of supported septalium suggests affinity with Meristelloidea.] *Lower Devonian (Pragian):* Europe (Bohemia).——FIG. 1848*a–l*. **I. vultur* (BARRANDE), Koněprusy Limestone, Koněprusy, Prague Basin; *a–c,* dorsal, ventral, and anterior views, Havlíček collection, VH 12777a, ×2.3; *d–l,* transverse serial sections 13.9, 13.0, 12.0, 11.1, 10.6, 10.4, 10.1, 9.8, 9.7 mm from anterior margin of shell (adapted from Havlíček & Vaněk, 1998; photographs courtesy of the late V. Havlíček).

Kellerella NIKITIN & POPOV in NIKITIN, POPOV, & HOLMER, 1996, p. 93 [**K. ditissima*; M]. Smooth, ventribiconvex, elongate subtriangular to subpentagonal outline; anterior commissure more or less parasulcate; sulcus very shallow, occasionally with low median plication, fold very low, both originating in anterior third of shell, often near anterior margin, bounded laterally by two plications; ventral valve often subcarinate posteriorly; small, strongly curved beak, delthyrium narrow, deltidial plates absent; interior with small, delicate teeth supported by small dental plates, close to posterolateral valve margins; cardinalia small, without inner hinge plates, median septum or myophragm absent; spiralia with up to 4 laterally directed whorls and very short, discrete, posteroventrally directed jugal processes. [This genus is differentiated from Ordovician smooth Lissatrypidae in having the spiralial whorls laterally directed and short, disjunct jugal processes posteroventrally directed. It resembles *Nikolaispira,* from which it mainly differs in the type of cardinalia. For overall affinity, see comments in square brackets in *Nikolaispira*.] *Upper Ordovician (lower Caradoc–lower Ashgill):* southeastern Kazakhstan (Chu Ili Range), *lower Caradoc–middle Caradoc;* central Kazakhstan (Dulankara Regional Stage, northern Betpak-Dala Desert), *upper Caradoc–lower Ashgill.*——FIG. 1849*a–q*. **K. ditissima*; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 39/12888, ×3 (Nikitin, Popov, & Holmer, 1996; photographs courtesy of L. E. Popov); *f–o,* transverse serial sections 0.7, 1.2, 1.6, 2.6, 3.0, 3.2, 3.5, 3.9, 4.3, 6.0 mm from ventral umbo, distance approximate from ventral umbo to first section, and between sections (Nikitin, Popov, & Holmer, 1996); *p–q,* ventral and lateral views showing reconstructed spiralium and jugal processes (Popov, Nikitin, & Sokiran, 1999).——FIG. 1849*r–dd. K. misiusi* POPOV, NIKITIN, & SOKIRAN, Anderken Formation, lower Caradoc–middle Caradoc, eastern Kazakhstan; *r–bb,* transverse serial sections 0.1, 0.9, 1.2, 1.3, 1.8, 2.8, 3.8, 4.8, 5.8, 7.5, 8.8 mm from ventral umbo; *cc–dd,* ventral and lateral views showing reconstructed spiralium, short jugal processes, and approximate position of serial sections (adapted from Popov, Nikitin, & Sokiran, 1999).

Nikolaispira NIKITIN & POPOV in NIKITIN, POPOV, & HOLMER, 1996, p. 95 [**N. rasilis*; M]. Smooth,

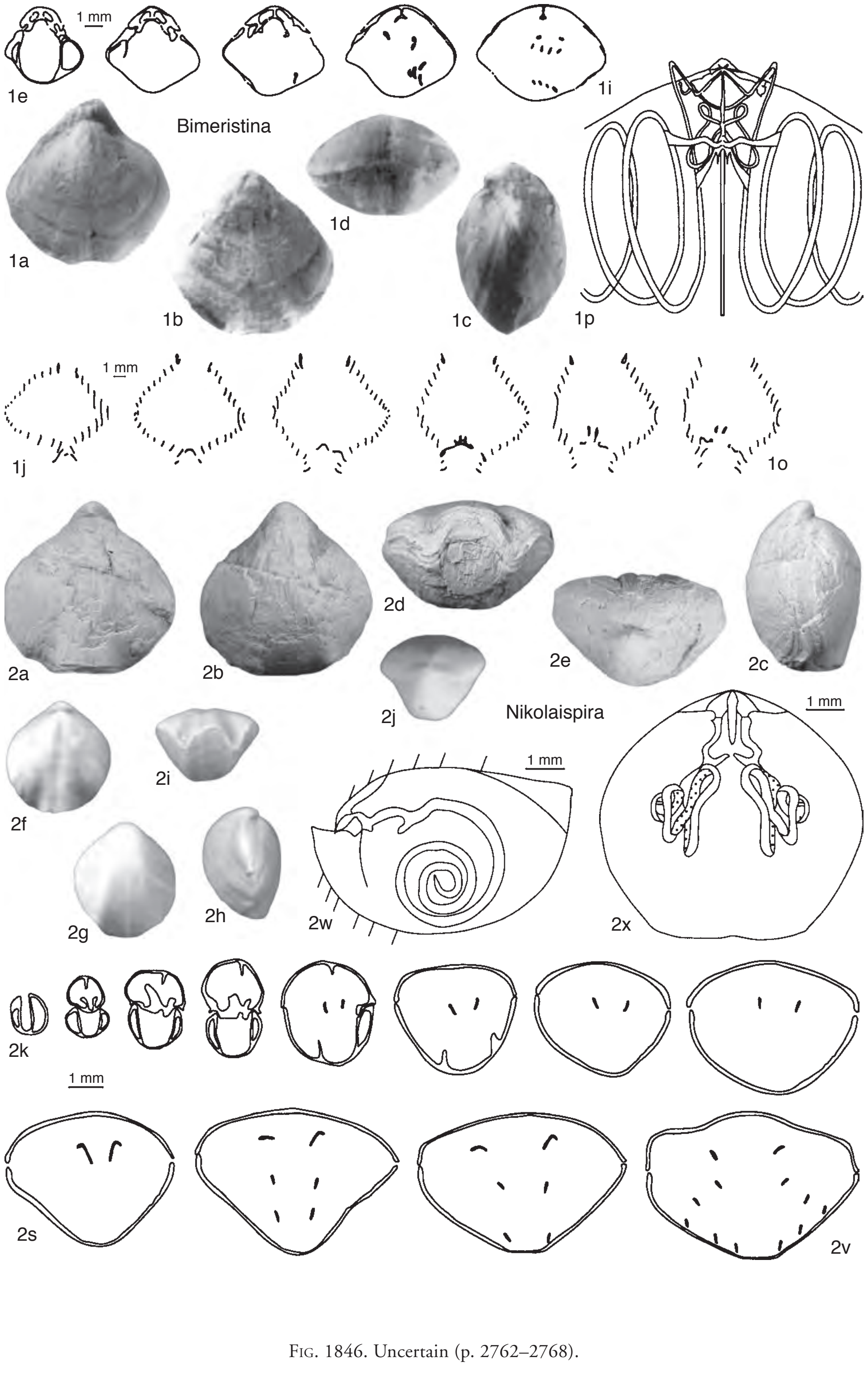


FIG. 1846. Uncertain (p. 2762–2768).

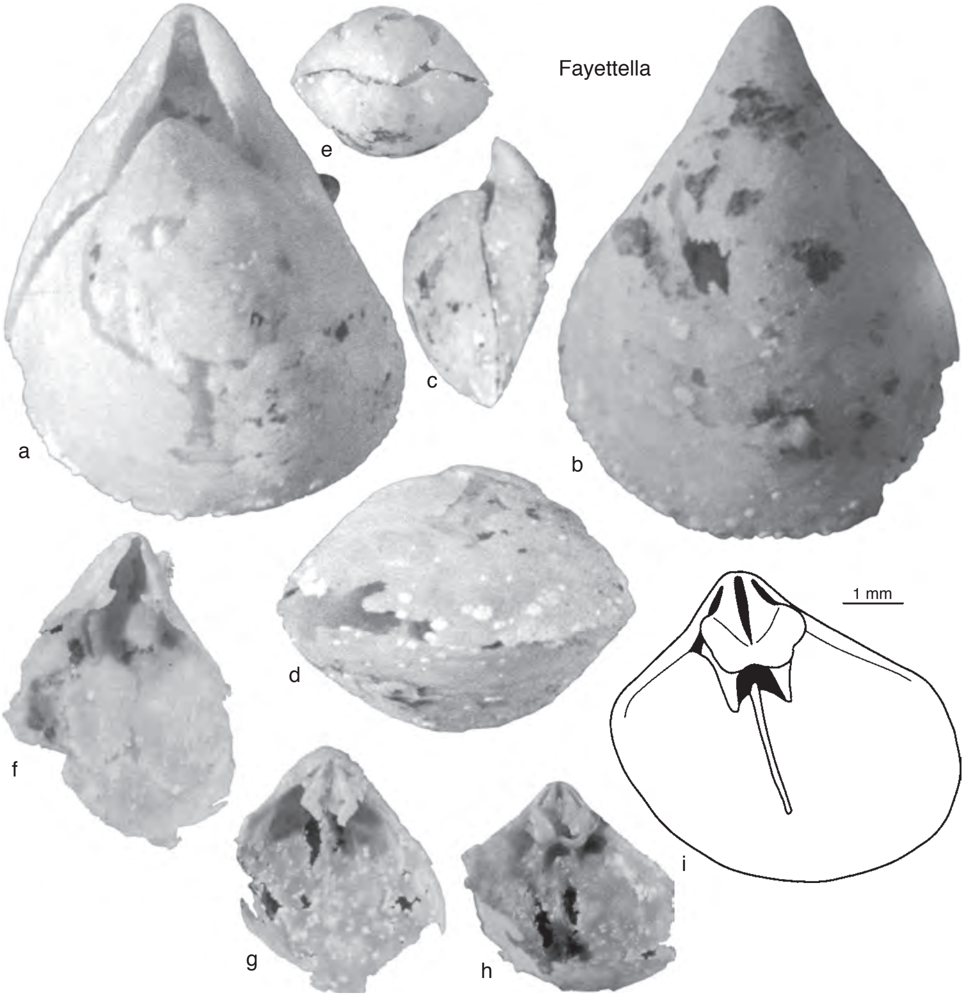


FIG. 1847. Uncertain (p. 2763).

ventribiconvex, elongate subpentagonal; parasulcate; shallow ventral sulcus and low dorsal fold originating anterior to midvalve, bounded laterally by two plications; small, incurved beak, delthyrium open; interior with small teeth supported by short, thin, laterally placed dental plates; deep, narrow septalium, also reported as cruralium, supported by low, thin median septum reportedly present; spiralia with up to 4 laterally directed whorls and small, discrete, posteroventrally directed jugal processes. [This genus is similar to such coeval smooth atrypids as *Cyclospira* or *Rozmanospira,* from which it differs in having more than one laterally directed spiral whorl. It has a less corrugated adult commissure than *Manespira*. It resembles the Silurian *Dayia,* from which it differs in having small, discrete jugal processes instead of the simple and medially to anteriorly located, jugum of *Dayia*. *Nikolaispira* is possibly synonymous with *Kellerella*, but with different cardinalia. When erected, *Nikolaispira* and *Kellerella* were included in the Athyridoidea, Meristellidae, and considered as the earliest athyridides. The cardinalia of these two genera are distinctly different from those developed by early Athyridida as *Hindella* (=*Cryptothyrella*) or *Whitfieldella*. Only some Upper Ordovician (?Caradoc, Ashgill), strongly convex and rostrate Hyattidinidae developed a cardinalia with thin, flat, triangular, inner hinge plates separated by a narrow fissure, which could resemble the small cardinalia, without inner hinge plates, of *Kellerella*. *Weibeia* and *Apheathyris*, both from the lower Caradoc of northern China, are too poorly known to allow comparison. *Nikolaispira* and *Kellerella* have small, discrete, jugal processes (as *Manespira* and derived Atrypida) but lack the complete jugum

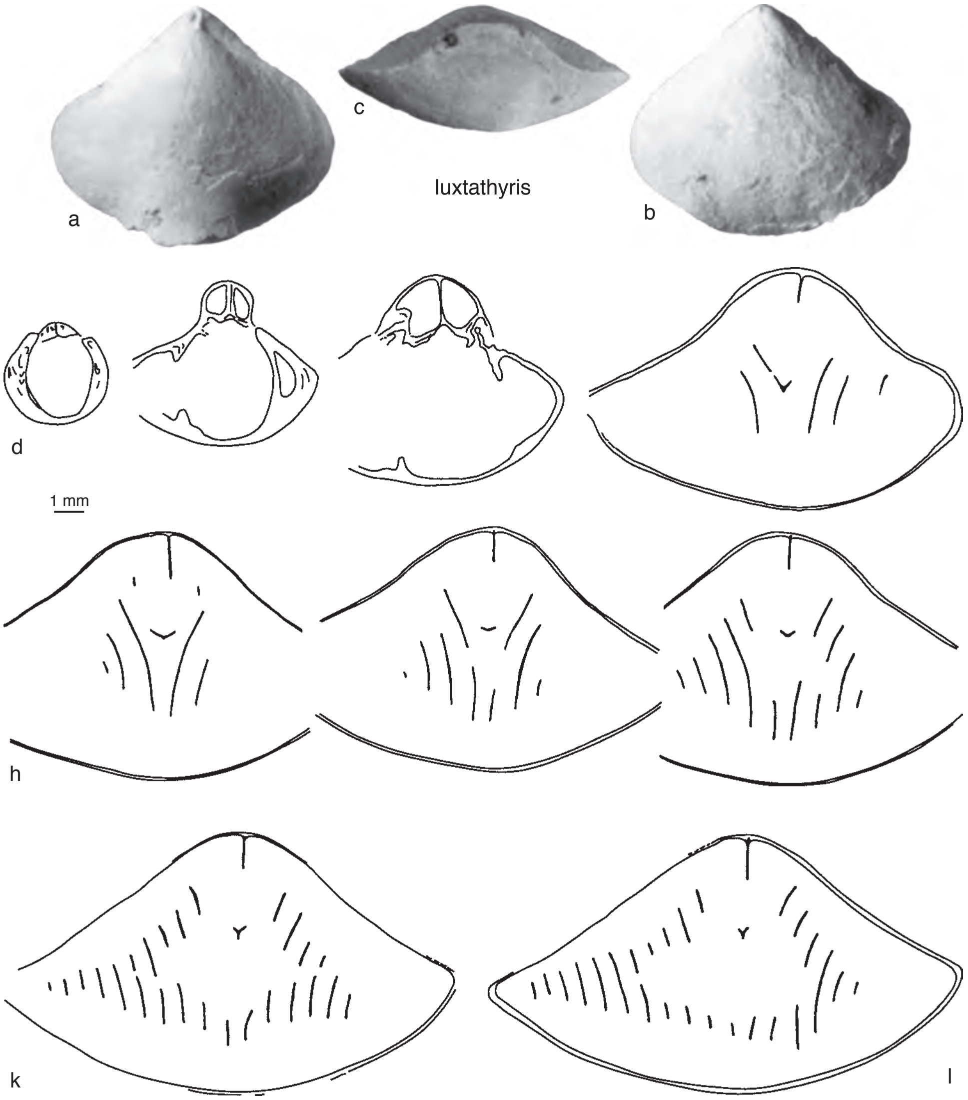


FIG. 1848. Uncertain (p. 2763).

of most primitive Atrypida and all Athyrididina and Retziidina. In both genera, the spiral whorls are, as in most primitive Atrypida and homeomorphic Dayioidea, placed ventrally, with the jugal processes dorsally or posterodorsally located. In the Athyridida, however, the spiral whorls tend to occupy the complete volume available in the shell interior, and the jugum is typically placed between the spiral cones, not below them (near the dorsal interior). This genus is assigned to Athyridida because it has more than one spiral whorl that is laterally directed, but its overall affinity is uncertain. To better evaluate affinities between closely related early spire bearers and envisage phyletic lineages, new discoveries of internally well-preserved Ordovician brachiopods are needed. *Nikolaespira* is an incorrect subsequent spelling of *Nikolaispira.*] *Upper Ordovician (lower Caradoc–lower Ashgill):* southeastern Kazakhstan (Chu Ili Range), *lower Caradoc–middle Caradoc;* central Kazakhstan (Dulankara Regional Stage, northern Betpak-Dala Desert), *upper Caradoc–lower Ashgill.*——FIG. 1846,*2a–x.* **N. rasilis*; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 44/12888, ×3; *f–j,* paratype, dorsal, ventral, lateral, anterior, and posterior views, CNIGR 45/12888, ×3 (Nikitin, Popov, & Holmer, 1996; photographs courtesy of L. E. Popov); *k–v,* transverse serial

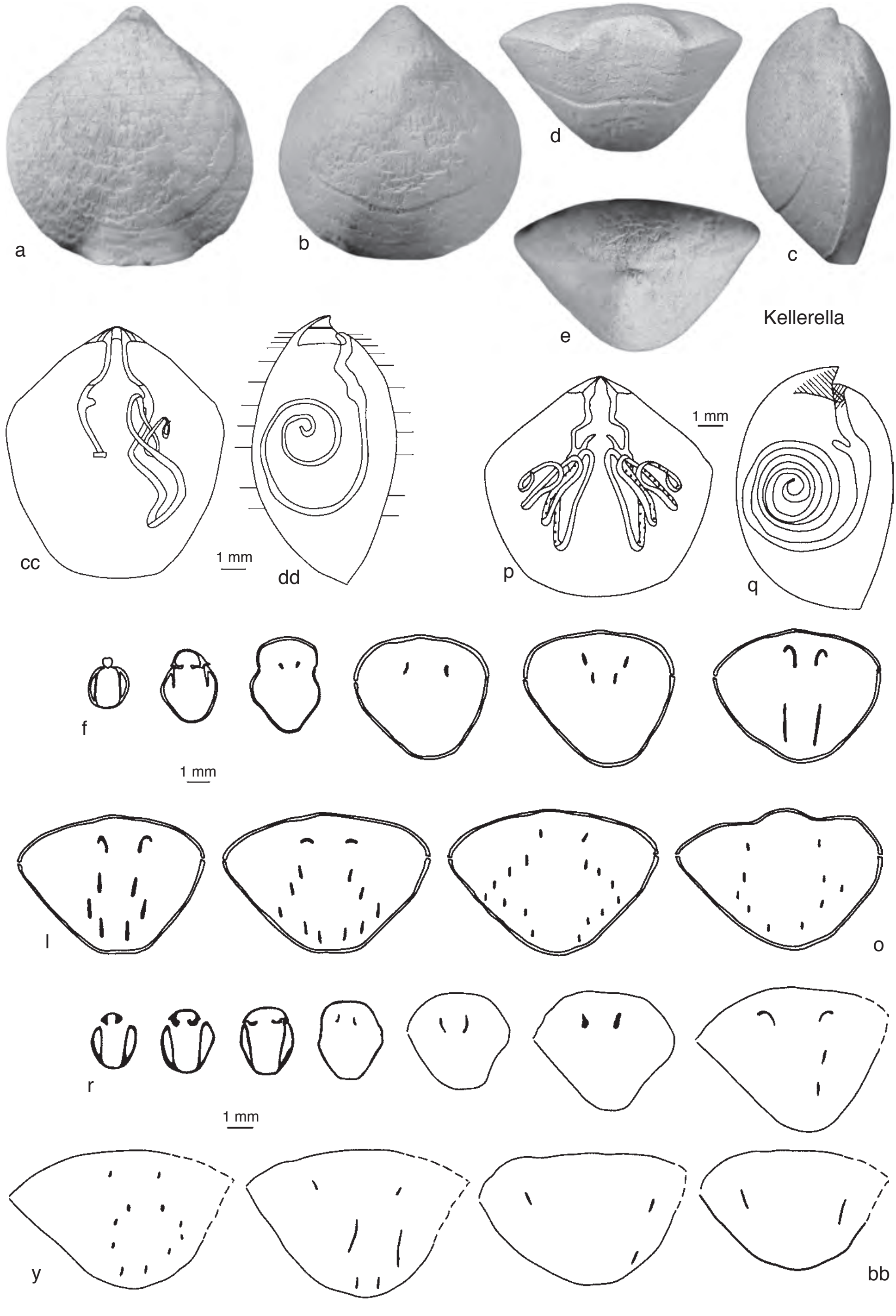


FIG. 1849. Uncertain (p. 2763).

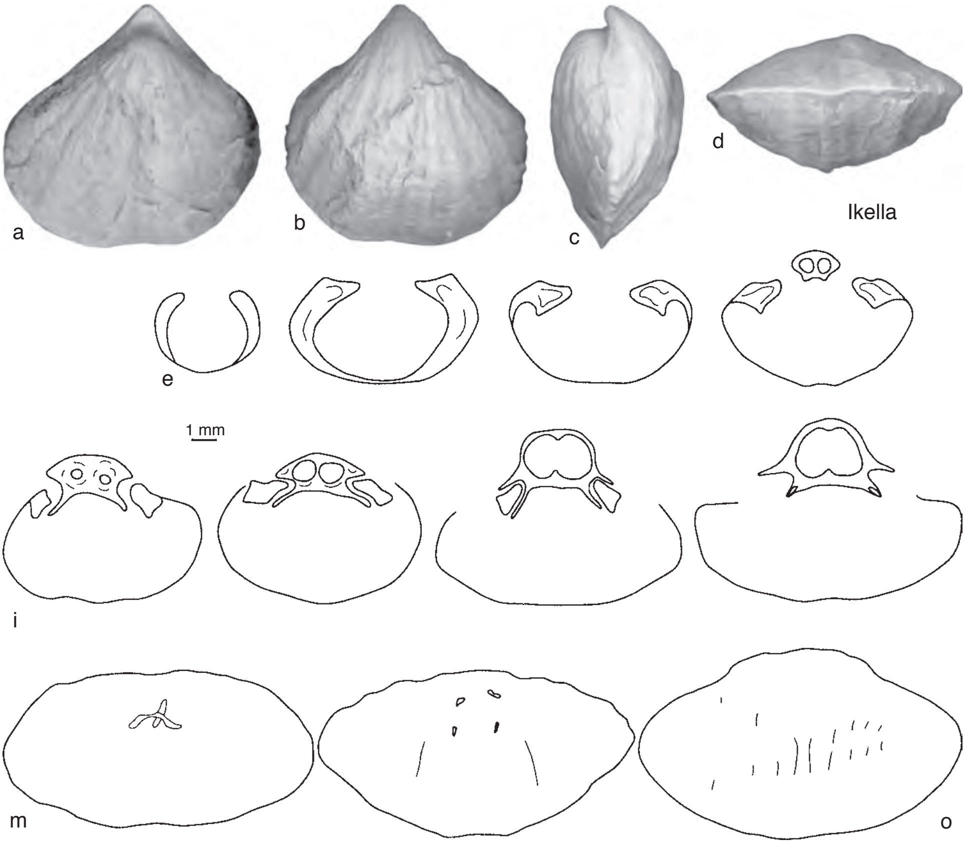


Fig. 1850. Retziellidae (p. 2768–2769).

sections; *w,* lateral view of sectioned specimen showing approximate position of serial sections (adapted from Nikitin, Popov, & Holmer, 1996); *x,* ventral view showing reconstructed spiralium and jugal processes (adapted from Popov, Nikitin, & Sokiran, 1999).

Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974

Family RETZIELLIDAE Rzhonsnitskaya, 1974

Ikella Tyazheva, 1972, p. 205; *emend.*, Rong & others, 2004, p. 849 [**I. numerosa;* OD]. Small, subequally to ventribiconvex shells of rounded subpentagonal to elongate subelliptical outline; costae rounded, faint, bifurcating or not, in corresponding position on each valve, growth lines faint, not lamellose; dorsal fold and ventral sulcus poorly developed anteriorly, commonly absent; delthyrium may be restricted laterally by narrow deltidial plates; dental plates and pedicle support absent; cardinal plate wide, flat, not perforated apically and supported posteriorly by very short ridge; dental sockets deep, bordered by ventrolaterally directed prominent inner socket ridges, overhanging socket; spiralia with 7–12 whorls, apices laterally directed, jugum unknown. [The cardinalia of *Ikella,* as described by Modzalevskaya in Rong & others, 2004, clearly differ from the hinge plates present in the athyrisinids and homeathyridins. It resembles the cardinalia of some retzielloids, although typically retzielloids have variably developed outer hinge plates, and the inner hinge plates are absent or form a short, shallow septalium partially covered by long, platelike crural bases, supported by a moderately high median septum (e.g., *Retziella, Metathyrisina*). The highly crystalline nature of the matrix has made examination of the internal structure very difficult, so the spiralium remains poorly known and the jugal structures are unknown; therefore, the superfamilial and familial assignments of this genus should be regarded as provisional.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Russia (Bashkorkostan, western slope of Southern Urals).——Fig. 1850*a–o.* **I. numerosa,* below mouth of Karagailka River, Malyi

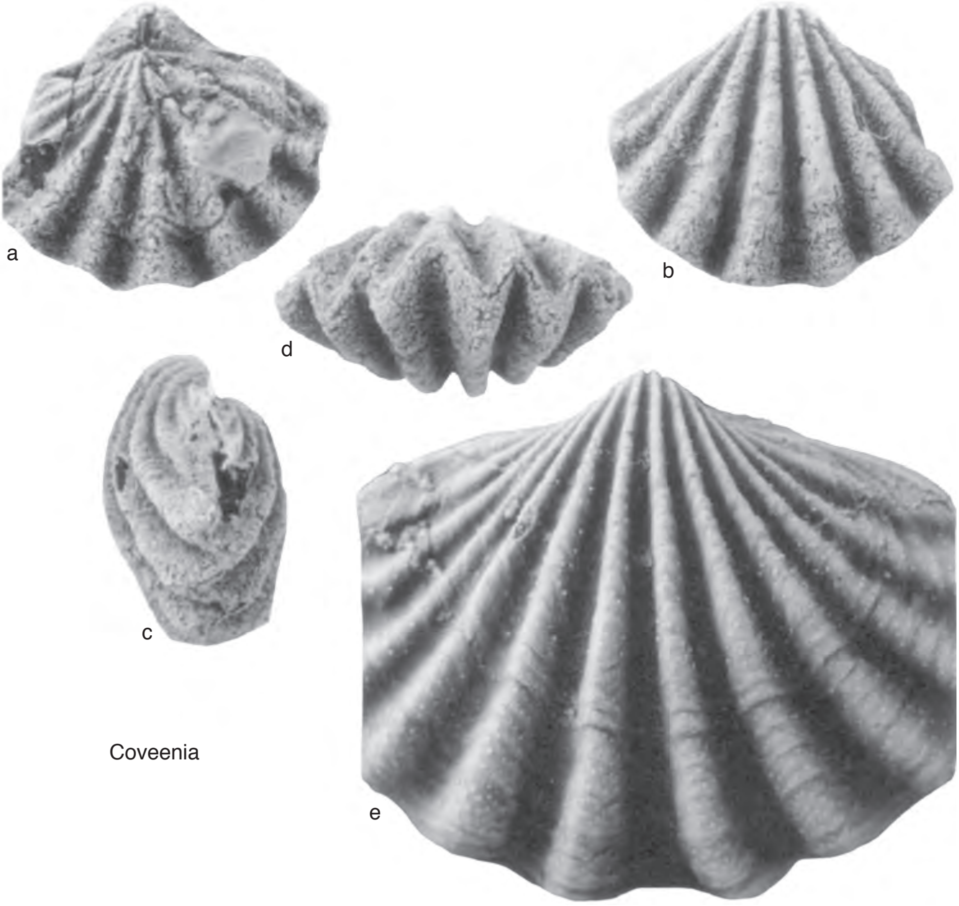


FIG. 1851. Neoretziidae (p. 2769–2771).

Ik River, western slope of Southern Urals; *a–d,* dorsal, ventral, lateral, and anterior views, Zhavoronkova collection, CNIGR N6/13099, ×1.4; *e–o,* transverse serial sections 9.0, 7.5, 7.2, 7.0, 6.8, 6.7, 6.6, 6.5, 6.3, 6.2, 5.7 mm from anterior margin of shell, Zhavoronkova collection, CNIGR N8/13099 (Rong & others, 2004).

Suborder RETZIIDINA Boucot, Johnson, & Staton, 1964

Superfamily RETZIOIDEA Waagen, 1883

Family NEORETZIIDAE Dagys, 1972

Subfamily HUSTEDIINAE Grunt, 1986

Coveenia ALVAREZ & BRUNTON, 2000, p. 821 [**Retzia ulothrix* DE KONINCK, 1843 in 1841–1844, p. 292; OD]. Medium-sized shells with subcircular to transversely oval outline and biconvex to dorsibiconvex profile, 7 to 11 strong costae on ventral valves and a median dorsal costa, forming a highly zigzag anterior commissure; fine pustulose to spinose microornament, frequently present; internally dorsal median septum and pedicle collar weak to absent; cardinalia lacking ligulate process, jugum without spines, jugal stem poorly developed or absent. *Lower Carboniferous (Tournaisian–Viséan):* western Europe (including British Isles).——FIG. 1851*a–e.* **C. ulothrix* (DE KONINCK), Ivorian, Tournaisian, Tournai, Belgium; *a–d,* neotype, dorsal, ventral, lateral, and anterior views, de Koninck collection, IRScNB a5507, ×3; *e,* ventral view showing rounded costae and typical microornament, de Koninck collection, IG4789(1), ×5 (Alvarez & Brunton, 2000).——FIG. 1852*a–i.* **C. ulothrix* (DE KONINCK), Ivorian, Tournaisian, Tournai, Belgium; transverse serial sections 1.4, 3.1, 3.7, 3.9, 5.1, 6.4, 6.7, 6.8, 7.7 mm from ventral

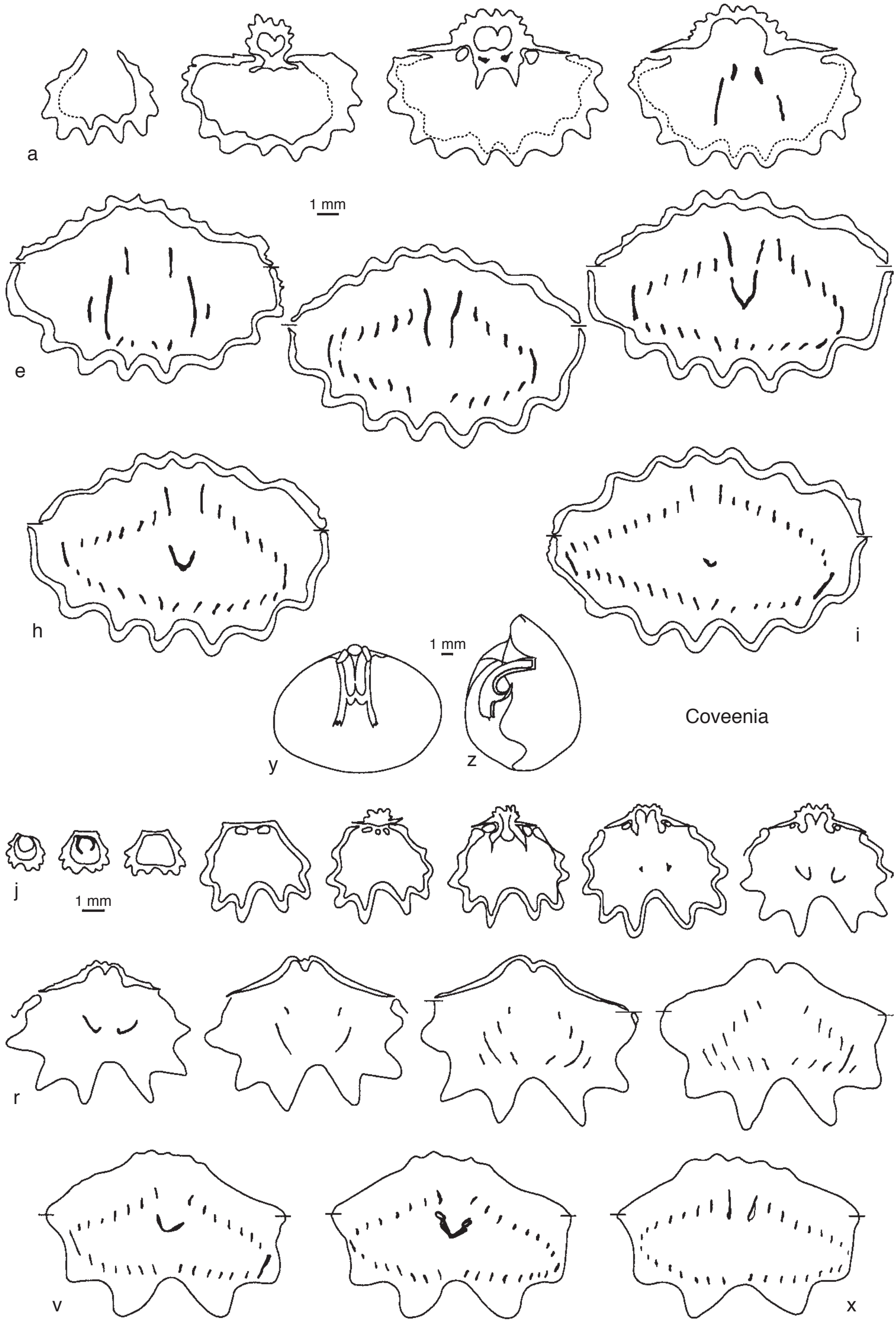


FIG. 1852. Neoretziidae (p. 2769–2771).

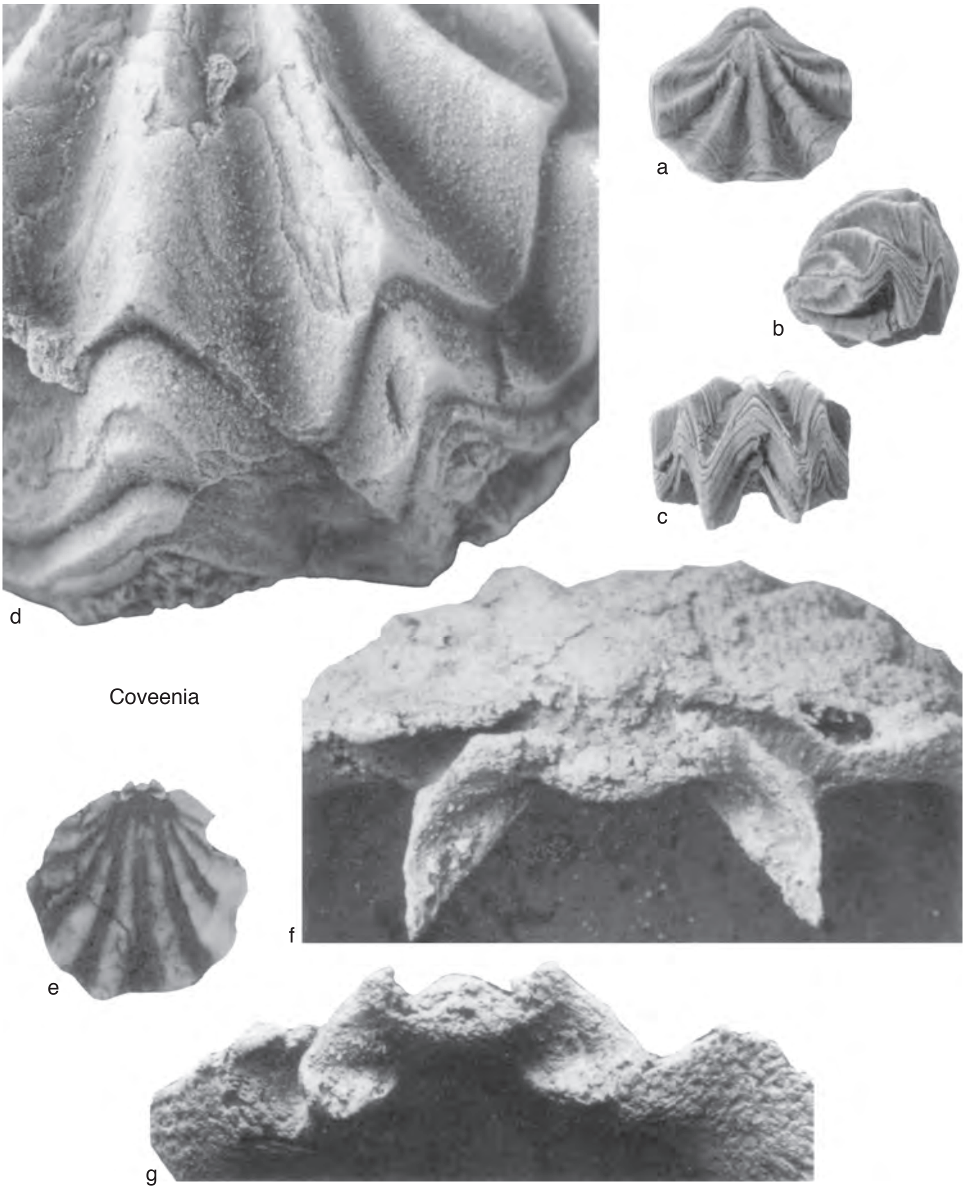


FIG. 1853. Neoretziidae (p. 2769–2771).

umbo, BMNH B20147 (Alvarez & Brunton, 2000).——FIG. 1852*j–z. C. tilsleia* ALVAREZ & BRUNTON; *j–x,* transverse serial sections 0.2, 0.7, 0.8, 2.2, 2.5, 2.9, 3.4, 3.5, 3.8, 4.3, 4.7, 5.2, 6.2, 6.4, 6.9 mm from ventral umbo, Asbian, Viséan, Treak Cliff, Derbyshire, England, BD 10479; *y–z,* ventral and lateral reconstruction of jugum (Alvarez & Brunton, 2000).——FIG. 1853*a–g. C. tilsleia* ALVAREZ & BRUNTON; *a–c,* holotype, dorsal, lateral, and anterior views, Asbian, Viséan, Treak Cliff, Derbyshire, England, Tilsley collection, BD9701, ×2.2; *d,* detail of external microornamentation, Asbian, Viséan, Alstonfield, Staffordshire, England, Davidson collection, B5388, ×10; *e,* interior of dorsal valve, Asbian, Viséan, Carrich Lough, County Fermanagh, Ireland, BB63417, ×5; *f–g,* cardinalia on posteroventral and anteroventral views, Asbian, Viséan, Carrich Lough, County Fermanagh, Ireland, BB63417, ×43.5, ×37.6 (Alvarez & Brunton, 2000).

SPIRIFERIDA AND SPIRIFERINIDA

Rémy Gourvennec and John L. Carter

[Université de Bretagne Occidentale; retired from Carnegie Museum of Natural History]

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily ADOLFIOIDEA Sartenaer, 1966

Family ADOLFIIDAE Sartenaer, 1966

Subfamily ADOLFIINAE Sartenaer, 1966

Brevispinifera García-Alcalde, 2005, p. 81 [**Spirifer Cabanillas* de Verneuil & d'Archiac, 1845, p. 475; OD]. Capillate with pustulose spine bases normal to surface; long dental plates and occasional delthyrial plate; short crural plates and ctenophoridium present; otherwise similar to *Brevispirifer*. *Lower Devonian (upper Emsian):* northern Spain.——Fig. 1854,*3a–e*. **B. cabanillas* (de Verneuil & d'Archiac); *a–d,* ventral, dorsal, lateral, and anterior views, ×1; *e,* enlarged view of ventral valve showing spinose ornament, ×5 (García-Alcalde, 2005). [Rémy Gourvennec]

Ferronia García-Alcalde, 2005, p. 75 [**Spirifer subspeciosus* de Verneuil, 1850, p. 179; OD]. Small, transverse; curved apsacline ventral interarea with open delthyrium; fold and sulcus smooth, somewhat flattened anteriorly; flanks plicate; surface capillate with marginal spines; long dental plates; delthyrial plate lacking; short crural plates; ctenophoridium present on secondary shell elevation. *Lower Devonian (upper Emsian):* northern Spain. ——Fig. 1854,*2a–d*. **F. subspeciosa* (de Verneuil); *a–c,* holotype, ventral, dorsal, and lateral views, ×1 (Comte, 1938); *d,* dorsal interior, ×1 (García-Alcalde, 2005). [Rémy Gourvennec]

Paillettia García-Alcalde, 2005, p. 83 [**Spirifer Paillettii* de Verneuil, 1850, p. 177; OD]. Small, transverse, with acute cardinal angles; ventral interarea high, slightly curved with open delthyrium; fold and strong median sulcus rib developing a typical long anterior protrusion of shell; flanks costate; surface capillate with marginal spines; dental plates thin and short; short crural plates and ctenophoridium present on a thick secondary shell platform. [The species name (a dedication to A. Paillette) was incorrectly spelled *paillettii* by de Verneuil in place of *paillettei*. The latter, correct spelling was used by subsequent authors and is accepted here.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* northern Spain, Algeria.——Fig. 1854,*5a–e*. **P. paillettei* (de Verneuil), upper Emsian, northern Spain; ventral, dorsal, lateral, anterior, and posterior views, ×2 (García-Alcalde, 2005).——Fig. 1854,*5f*. *P.* sp. cf. *cancellata* García-Alcalde, upper Emsian, northern Spain; enlargement of ventral valve showing ornament, ×5 (García-Alcalde, 2005). [Rémy Gourvennec]

Subfamily PINGUISPIRIFERINAE Havlíček, 1971

Microttia García-Alcalde, 2005, p. 90 [**M. collensis;* OD]. Small, slightly transverse; ventral interarea apsacline to catacline, with narrow deltidium; fold and sulcus smooth, narrow, somewhat flattened; flanks with few strong costae; surface with capillae and microfila; long dental plates; crural plates lacking. *Lower Devonian (upper Emsian):* northern Spain.——Fig. 1854,*1a–e*. **M. collensis;* holotype, ventral, dorsal, lateral, anterior, and posterior views, ×3 (García-Alcalde, 2005). [Rémy Gourvennec]

Superfamily CYRTOSPIRIFEROIDEA Termier & Termier, 1949

Family CYRTOSPIRIFERIDAE Termier & Termier, 1949

Subfamily CYRTOSPIRIFERINAE Termier & Termier, 1949

Nikospirifer Gretchishnikova, 1996, p. 34 [**N. praebisinus*; OD]. Medium size; transverse with acute cardinal extremities; ventral interarea high, curved, apsacline to catacline; fold and sulcus well delimited, costate; flanks with numerous simple costae; surface with tubercles; dental plates thin, long, subparallel; delthyrial plate present; dorsal interior unknown. *Middle Devonian (Givetian):* Transcaucasus.——Fig. 1855,*1a–g*. **N. praebisinus*; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* microornament, ×4; *g,* transverse section, ×2 (Gretchishnikova, 1996). [Rémy Gourvennec]

Pripyatispirifer Pushkin, 1996, p. 43 [**Cyrtospirifer belorussicus* Liashenko, 1959, p. 207; OD]. Small to medium size; cardinal angles acute to slightly mucronate; ventral interarea low, curved, apsacline; delthyrium narrow, almost entirely covered by deltidium (or possibly stegidium) with central foramen; fold and sulcus well defined, costate; surface with fila and capillae; dental plates short; subparallel, thick crural bases without crural plates; multilobed cardinal process possibly lacking cteno-

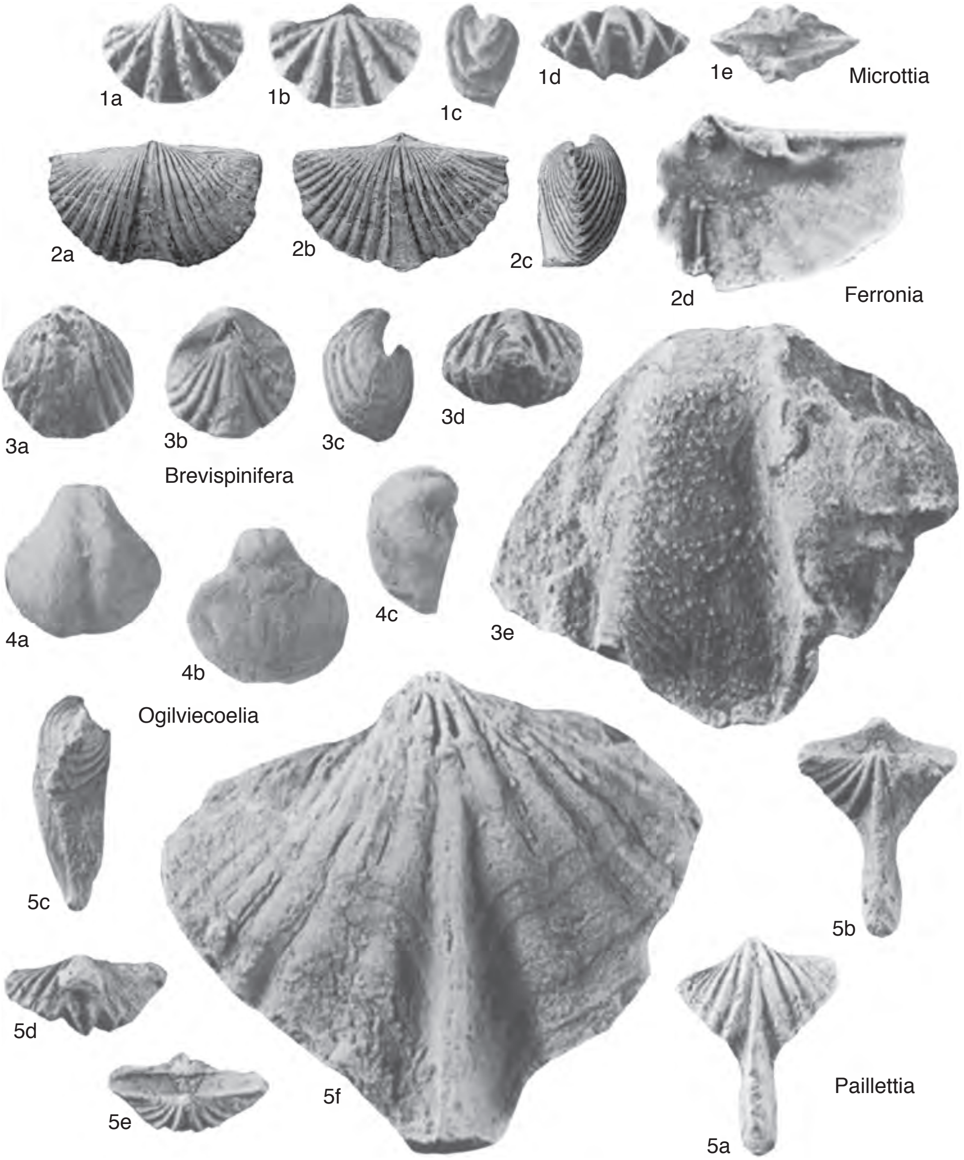


Fig. 1854. Adolfiidae and Ambocoeliidae (p. 2772–2776).

phoridium. *Upper Devonian (lower Famennian):* Belarus.——Fig. 1855,*2a–g*. **P. belorussicus* (Liashenko), Pripyat, Lyakhovichi 54 borehole; *a–e*, dorsal, ventral, anterior, posterior, and lateral views, ×1.5; *f–g*, dorsal and ventral interiors, ×5 (Pushkin, 1996). [Rémy Gourvennec]

Subfamily CYRTIOPSINAE
Ivanova, 1972

Pseudocyrtiopsis Ma & Day, 1999, p. 618 [**Cyrtiopsis spiriferoides* Grabau, 1931b, p. 486; OD]. Small to medium size; cardinal angles generally

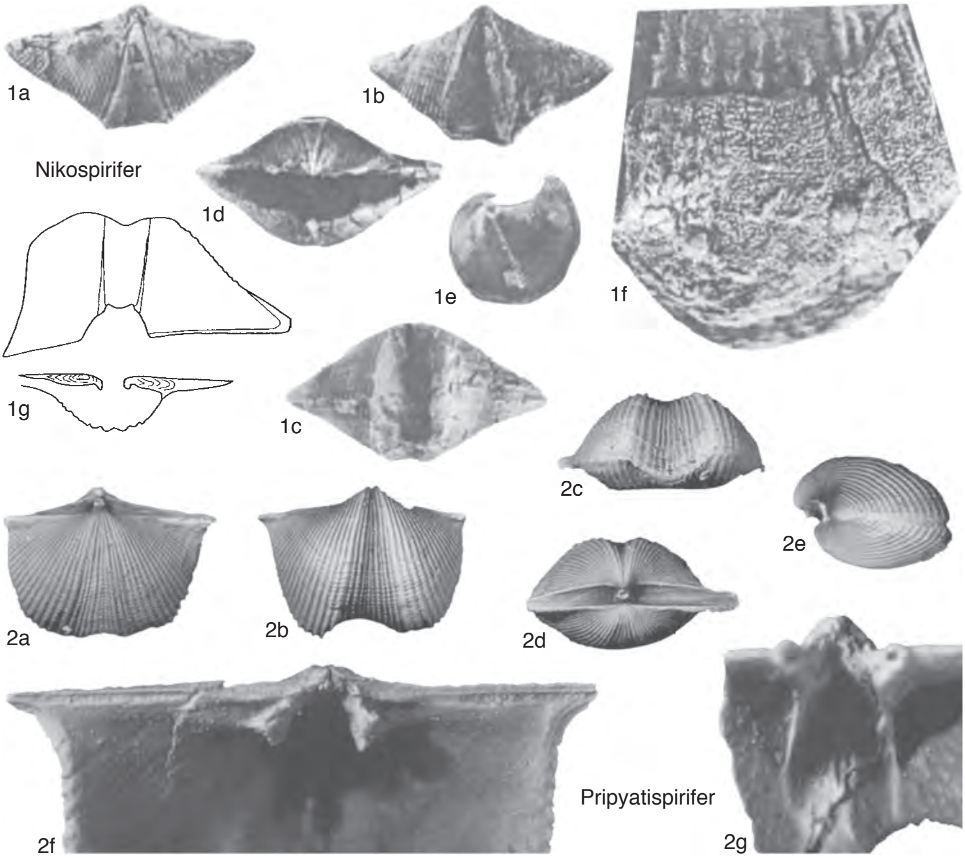


FIG. 1855. Cyrtospiriferidae (p. 2772–2773).

mucronate; high, slightly curved, apsacline ventral interarea; delthyrium covered by pseudodeltidium apically pierced by foramen; fold and sulcus well delimited, costate; flanks costate; microornament capillate, becoming pustulate on adult stage; dental plates and delthyrial plate present; bilobed ctenophoridium located on cardinal platform. *Upper Devonian (lower Famennian):* southern and northwestern China, ?Belgium.——FIG. 1856,*1a–g*. **P. spiriferoides* (GRABAU), central Hunan, southern China; *a–e*, dorsal, ventral, anterior, posterior, and lateral views, ×1.5; *f*, transverse section of dorsal valve, ×5; *g*, transverse section of ventral valve, ×2.5 (Ma & Day, 1999). [Rémy Gourvennec]

Tiocyrspis SARTENAER, 1994b, p. 32 [**Spirifer (Cyrtiopsis) klähni* PAECKELMANN, 1942, p. 163; OD]. Medium size; generally ventribiconvex with obtuse and blunt cardinal extremities; ventral interarea apsacline; delthyrium entirely covered by pseudodeltidium (stegidium); fold and sulcus costate, well delimited; median costae generally narrower and divided; flanks with numerous, flat-rounded, simple plications; surface with radial or subradial capillae and spines; dental plates thick, long, intrasinal; no delthyrial plate; crural bases and ctenophoridium present. *Upper Devonian (upper Frasnian):* Germany, Belgium.——FIG. 1856,*2a–g*. **T. klaehni* (PAECKELMANN), Germany; *a–e*, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f*, microornament, ×7; *g*, transverse section, ×1.5 (Sartenaer, 1994b). [Rémy Gourvennec]

Family CONISPIRIFERIDAE
Ma & Day, 2000

[Conispiriferidae MA & DAY, 2000, p. 456] [type genus, *Conispirifer* LIASHENKO, 1985, p. 16]

Entire shell plicate; fold and sulcus weak to obsolescent; delthyrial plate very short. *Upper Devonian (middle Frasnian–upper Frasnian).* [Rémy Gourvennec]

Conispirifer LIASHENKO, 1985, p. 16 [**C. rotundus;* OD]. Subrectangular cardinal extremities; fold and sulcus weak, obsolescent, variably developed anteriorly; delthyrial plate short; budlike ctenophoridium; otherwise similar to *Pyramidaspirifer*.

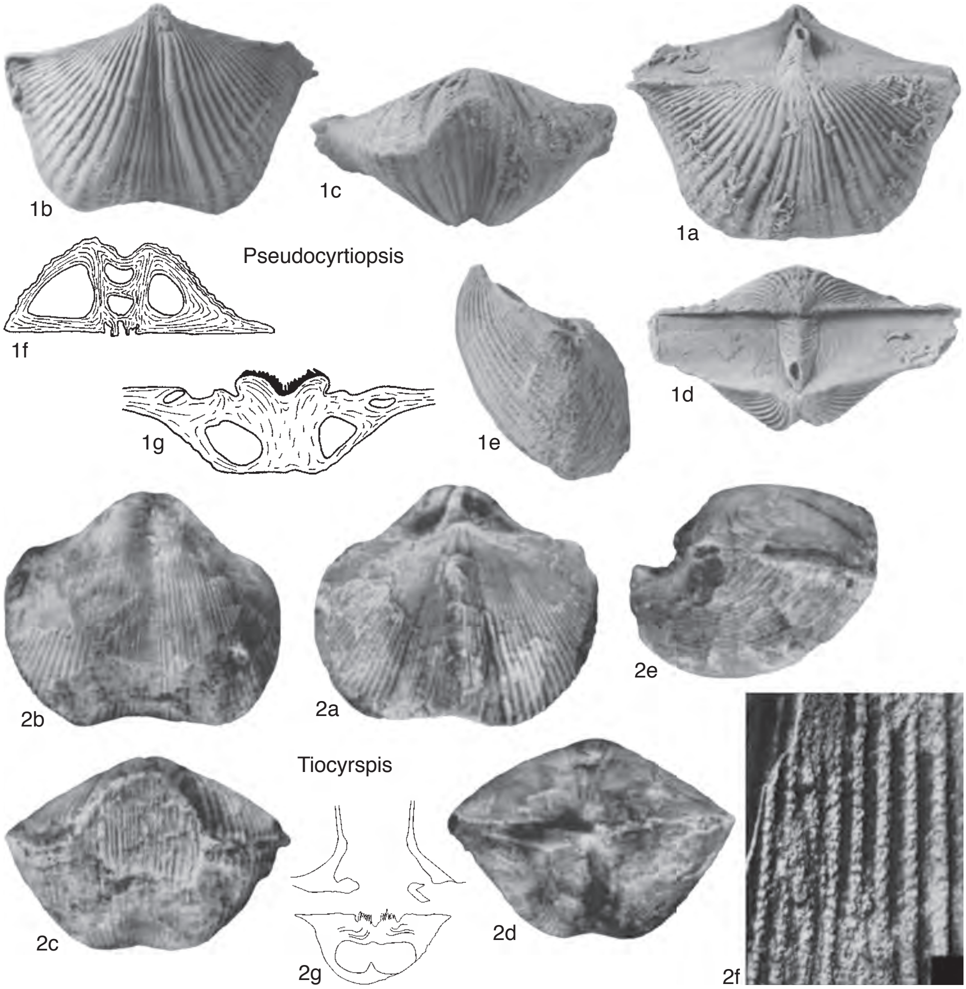


FIG. 1856. Cyrtospiriferidae (p. 2773–2774).

Upper Devonian (middle Frasnian–upper Frasnian): central and western North America, Germany, central Russian Platform.——FIG. 1857,*1a–e.* **C. rotundus*, Timan; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, approximately ×1 (Liashenko, 1985). [Rémy Gourvennec]

Pyramidaspirifer MA & DAY, 2000, p. 459 [**Platyrachella alta* FENTON & FENTON, 1924, p. 165; OD]. Small to medium size with wide hinge line and extended cardinal extremities; ventral interarea high, flat, catacline to slightly procline; narrow delthyrium with small apical pseudodeltidium; fold and sulcus costate, poorly defined, originating close to apex; flanks plicate; surface with fila and pustulose capillae; short, widely spaced dental plates and delthyrial plate present; ctenophoridium on septalium-like cardinal platform. *Upper Devonian (upper Frasnian):* North America.——FIG. 1857,*2a–f.* **P. alta* (FENTON & FENTON), Iowa, USA; *a–e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f*, transverse section of dorsal valve, ×4 (Ma & Day, 2000). [Rémy Gourvennec]

Superfamily AMBOCOELIOIDEA

George, 1931

Family AMBOCOELIIDAE

George, 1931

Subfamily AMBOCOELIINAE

George, 1931

Ogilviecoelia SHI & WATERHOUSE, 1996, p. 119 [**O. inflata;* OD]. Very small, subrounded, length and

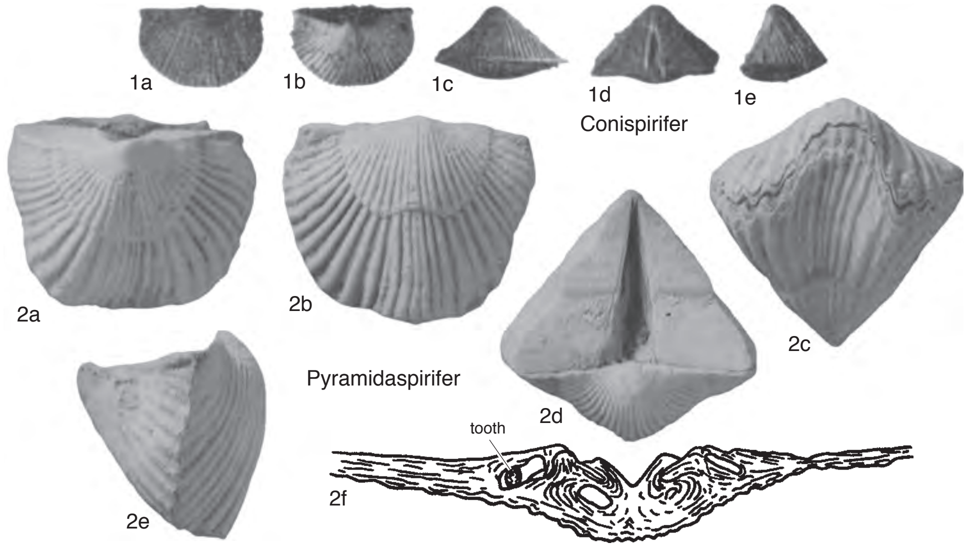


Fig. 1857. Conispiriferidae (p. 2774–2775).

width subequal; ventribiconvex but dorsal valve anteriorly flattened or slightly concave; sulcus narrow, deep; microornament of few short elongate grooves, spines absent; ventral muscle field large, elongate-oval, well differentiated; crural plates sessile. *Permian (upper Sakmarian):* Canada (Yukon Territory).——Fig. 1854,*4a–c.* **O. inflata*; holotype, ventral, dorsal, and lateral views, ×2 (Shi & Waterhouse, 1996).

Superfamily MARTINIOIDEA Waagen, 1883

Family ELYTHYNIDAE Gourvennec in Carter & others, 1994

Planispirifer Breivel & Breivel, 1999, p. 91 [**P. apertus;* OD]. Large, slightly transverse; cardinal extremities angular to rounded; ventral interarea moderately high, curved, apsacline, with open delthyrium; fold and sulcus well delimited, wide anteriorly, smooth or with incipient ridge in sulcus anteriorly; surface with densely crowded elongate tubercles radially distributed in quincunx; dental plates present; well-developed crural bases not meeting valve floor; ctenophoridium present. [This genus was originally assigned to the Eospiriferinae, but its ornament is not compatible with such an assignment, the Elythynidae being a better placement.] *Lower Devonian (Pragian):* northeastern Urals.——Fig. 1858,*5a–f.* **P. apertus; a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×0.7; *e,* ornament, ×3; *f,* apical section of dorsal valve, ×3 (Breivel & Breivel, 1999). [Rémy Gourvennec]

Family MARTINIIDAE Waagen, 1883

Subfamily MARTINIINAE Waagen, 1883

Chapursania Angiolini, 1995, p. 210 [**C. tatianae;* OD]. With coarse sinuous vascular impressions connected by transverse channels; otherwise similar to *Tiramnia* Grunt, 1977. *Permian (Guadalupian):* northern Pakistan.——Fig. 1858,*4a–b.* **C. tatianae*; *a,* holotype, mold of ventral interior, ×1; *b,* diagram of ventral vascular system, ×1.5 (Angiolini, 1995). [John Carter]

Ladoplica Xu & Grant, 1996, p. 310 [**L. zigzagiformis*; OD]. Medium size, moderately to strongly inflated, subequally biconvex; outline subpentagonal; beak strongly incurved; small interareas on both valves; sulcus shallow, flattened, producing large tongue anteriorly in type species. *Permian (Changhsingian*): China.——Fig. 1858,*1a–d.* **L. zigzagiformis;* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Xu & Grant, 1996). [John Carter]

Subfamily ELIVELLINAE Carter, 1994

Chuiella Chen & Shi, 1999, p. 266 [**Martiniella chinglungensis* Chu, 1933, p. 48; OD]. Medium size, ventribiconvex, outline subovate to transversely subquadrate; ventral interarea well developed, delthyrium wide and open; sulcus variably developed; microornament of capillae and growth lines; interior with dental adminicula and short crural plates. [This genus is proposed as a replacement name for all the previously described species ascribed to the genus *Martiniella* Grabau & Tien, 1931. The authors restrict *Martiniella* to

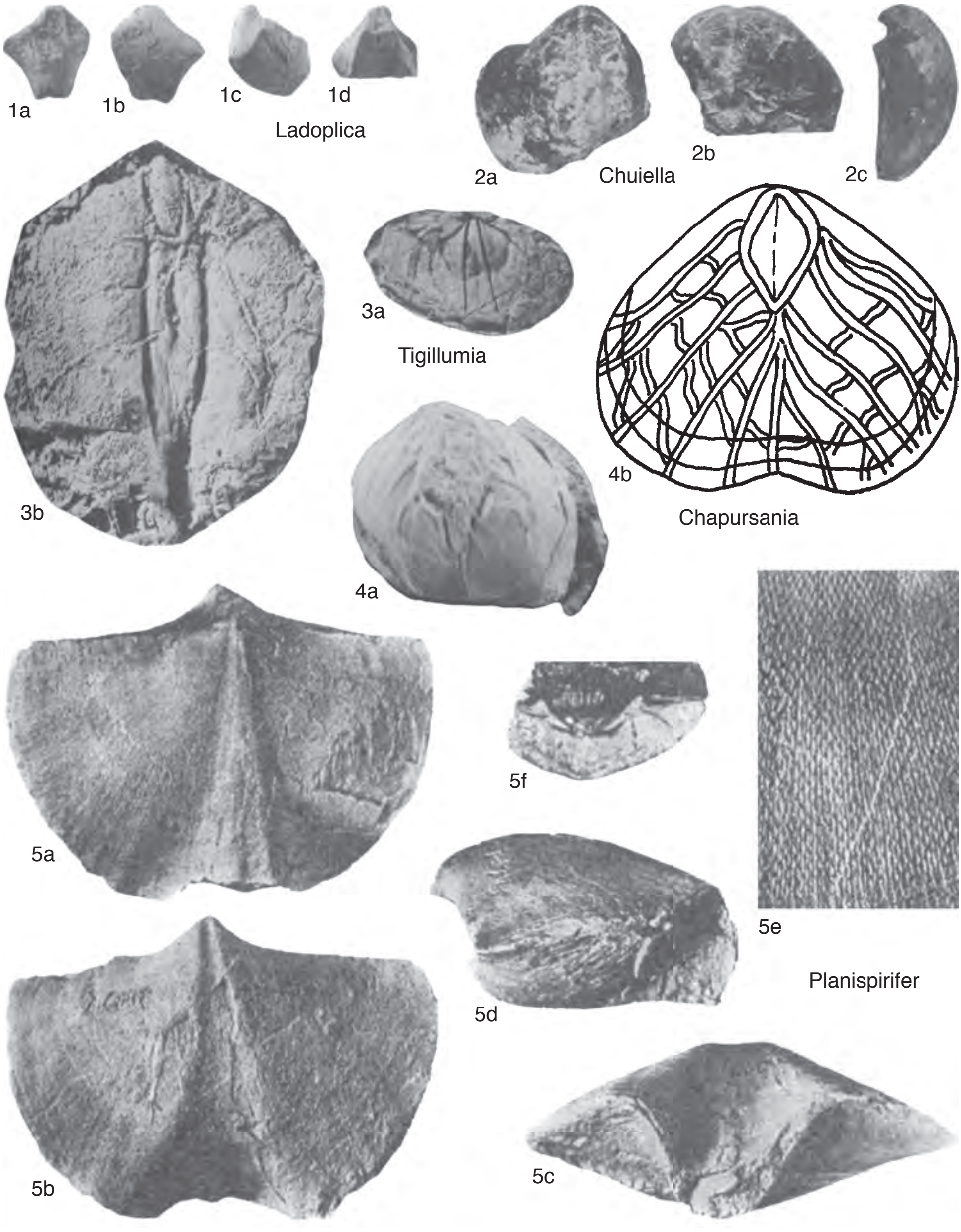


Fig. 1858. Elythynidae, Martiniidae, and Ingelarellidae (p. 2776–2779).

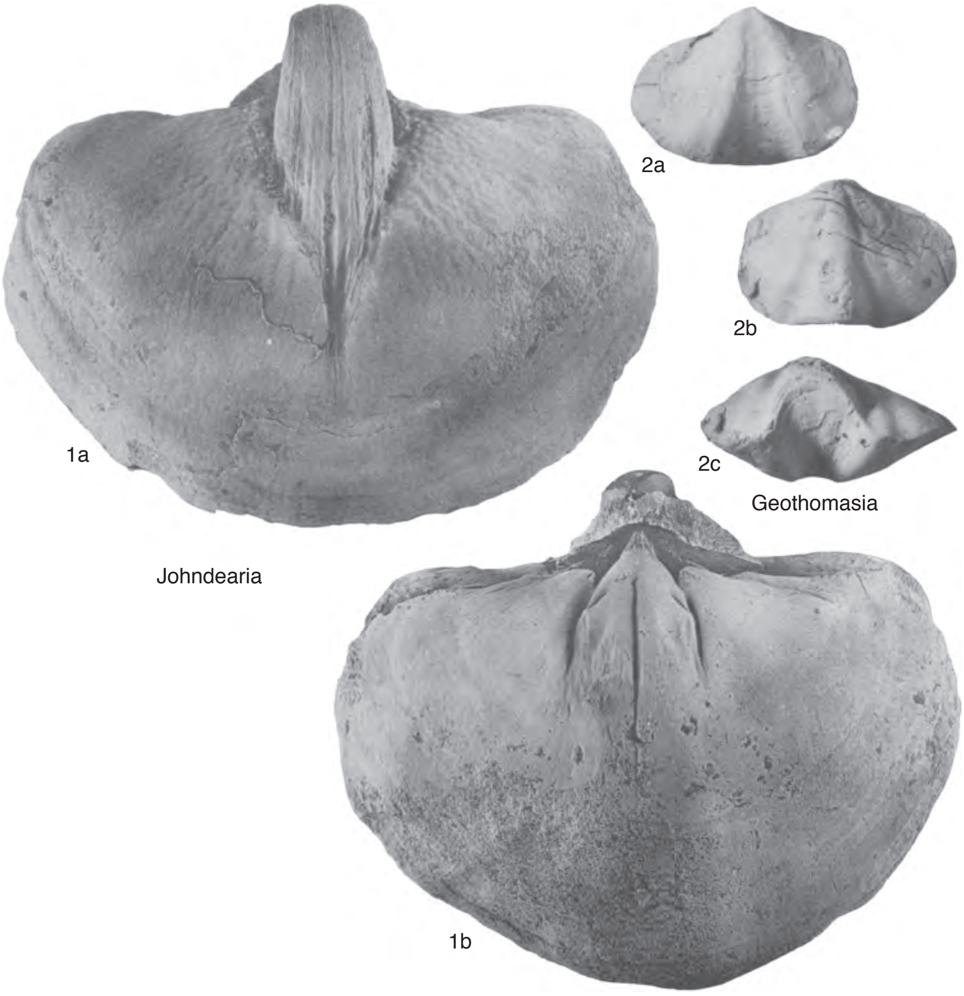


FIG. 1859. Ingelarellidae (p. 2778–2779).

its type species, *M. nasuta* Grabau & Tien, 1931, a *nomen nudum*.] *Lower Carboniferous (Tournaisian):* China.——Fig. 1858,*2a–c*. **C. chinglungensis* (Chu); syntype, ventral, posterior, and lateral views of ventral valve, ×1 (Chu, 1933). [John Carter]

Family INGELARELLIDAE
Campbell, 1959
Subfamily INGELARELLINAE
Campbell, 1959

Geothomasia Waterhouse, 1998, p. 23 [**Tomiopsis teicherti* Archbold & Thomas, 1986b, p. 593; OD]. Medium size, outline transversely subovate; fold and sulcus well developed; flanks with low plicae; shell substance thin; ventral adminicula thin, often subparallel, extending forward to near midlength; dorsal adminicula short to moderate in length, often widely diverging. [This taxon was originally proposed as a subgenus of *Tomiopsis* Benediktova, 1956.] *Permian (Cisuralian–Guadalupian):* Australia.——Fig. 1859,*2a–c*. **G. teicherti* (Archbold & Thomas), Artinskian; holotype, ventral, dorsal, and anterior views, ×1 (Archbold & Thomas, 1986b). [John Carter]

Johndearia Waterhouse, 1998, p. 18 [**Ingelarella isbelli* Campbell, 1961, p. 181; OD]. Large, with thickened valves; flanks smooth or weakly plicate; fold and sulcus weak; ventral and dorsal adminicula short, often buried in callus; ventral median ridge anterior to muscle field; otherwise similar to *Ingelarella*. [This taxon was originally proposed as a subgenus of the genus *Tomiopsis* Benediktova, 1956.] *Permian (Cisuralian–Lopingian):* Australia, New Zealand.——Fig. 1859,*1a–b*. **J.*

isbelli (Campbell), Australia; holotype, ventral and dorsal internal molds, ×1 (Campbell, 1961). [John Carter]

Tigillumia Waterhouse, 1998, p. 26 [**Martiniopsis biparallela* Waterhouse, 1987, p. 25; OD]. Flanks lacking plicae, sulcus absent or weak, fold generally lacking; ventral adminicula long, closely set, enclosing narrow muscle field bounded laterally by ridges that coalesce anteriorly; dorsal adminicula of moderate length; otherwise similar to *Martiniopsis*. *Permian (Cisuralian–Guadalupian)*: Australia, New Zealand.——Fig. 1858,*3a–b*. **T. biparallela* (Waterhouse), Artinskian, Australia; *a,* holotype, ventral internal mold, ×1; *b,* ventral internal mold, ×2 (Waterhouse, 1987). [John Carter]

Subfamily GLENDONIINAE
Clarke, 1992

Mesopunctia Waterhouse, 1998, p. 41 [**Notospirifer macropustulosus* Waterhouse, 1968, p. 76; OD]. Small, slightly transverse; fold and sulcus smooth, rounded; flanks with few rounded plicae; microornament of fine elongate grooves with small thick pustules posteriorly and short mesopunctae anteriorly. *Permian (Cisuralian–Guadalupian)*: New Zealand, Australia.——Fig. 1860,*3a–b*. **M. macropustulosus* (Waterhouse), Cisuralian, New Zealand; *a,* holotype, mold of ventral interior, ×3; *b,* mold of dorsal interior, ×3 (Waterhouse, 1968). [John Carter]

Monklandia Waterhouse, 1998, p. 37 [**M. gympiensis*; OD]. Large, slightly transverse, strongly plicate; sulcus wide, shallow, with two weak plicae; fold low, flattened, with median groove; microornament of C-spines with fine anterior grooves; ventral adminicula long; dorsal adminicula short but long for family. *Permian* (*Cisuralian*): Australia.——Fig. 1860,*4a–b*. **M. gympiensis*; *a,* holotype, mold of dorsal interior; *b,* internal mold of ventral valve, ×1 (McClung, 1978). [John Carter]

Wairakispirifer Waterhouse, 1998, p. 40 [**Notospirifer microstriatus* Waterhouse, 1964, p. 170; OD]. Small, transverse, weakly inflated; sulcus well developed, smooth; fold low, wide; flanks with well-developed plicae; ventral adminicula well developed; dorsal adminicula lacking; microornament of quincuntially arranged fine grooves with punctae anteriorly penetrating secondary layer. *Permian (Cisuralian)*: New Zealand, Australia. ——Fig. 1860,*2a–b*. **W. microstriatus* (Waterhouse), New Zealand, holotype; *a,* ventral valve mold, ×2; *b,* latex cast showing exterior ornament, ×4 (Waterhouse, 1964). [John Carter]

Subfamily NOTOSPIRIFERINAE
Archbold & Thomas, 1986

Papulinella Waterhouse, 1998, p. 34 [**Notospirifer hillae* Campbell, 1961, p. 185; OD]. Medium to large, transversely subovate outline; fold and sulcus moderately well developed; sulcus smooth, fold rarely with median groove; flanks with few broad low plicae; microornament of quincuntially and densely arranged spinules with narrow anterior grooves passing into globose cavities within primary layer; otherwise similar to *Notospirifer*. *Carboniferous (?Kasimovian), Permian (Cisuralian):* Australia, New Zealand.——Fig. 1860,*1a–c*. **P. hillae* (Campbell), Cisuralian, Australia; *a–b,* holotype, ventral valve mold and latex cast, ×1; *c,* enlarged latex cast of dorsal valve exterior, ×2 (Campbell, 1961). [John Carter]

Superfamily SPIRIFEROIDEA
King, 1846

Recently Waterhouse (2004) proposed a complete revision of the classification of the Spiriferoidea with the erection of several new subfamilies and genera while other suprageneric taxa were drastically redistributed. Mostly based on the external morphology of ribbing, of fold-sulcus, and, to a lesser extent, on aspects of the cardinal extremities, this classification leads to a mixture of morphologically different genera in inconsistent (sub)families that are not retained here. Taking into account both internal and external features, most of the subfamilies erected by Waterhouse (2004) should be assigned elsewhere. For example, there are strong affinities between Neospiriferinae, Gypospiriferinae, and Kaninospiriferinae, and there is no reason for placing them in different families. The family Choristitidae (*sensu* Carter & others, 1994) is a consistent entity, and we do not consider it necessary to remove the Angiospiriferinae and Tangshanellinae and replace them with the Prospirinae and Purdonellinae; the resulting family Choristitidae (*sensu* Waterhouse, 2004) is much less homogeneous (e.g., including genera with or without delthyrial plate).

Focusing on the lack of ventral adminicula and the presence of dorsal adminicula in *Alphaneospirifer* Gatinaud, 1949, Waterhouse (2004) erected the family Alphaneospiriferidae that was assigned to *Incertae Sedis.* Nevertheless, the presence of well-developed crural plates is not incompatible with an assignment of the genus to the Tangshanellinae: although the occurrence of crural plates is rare in the Spiriferoidea,

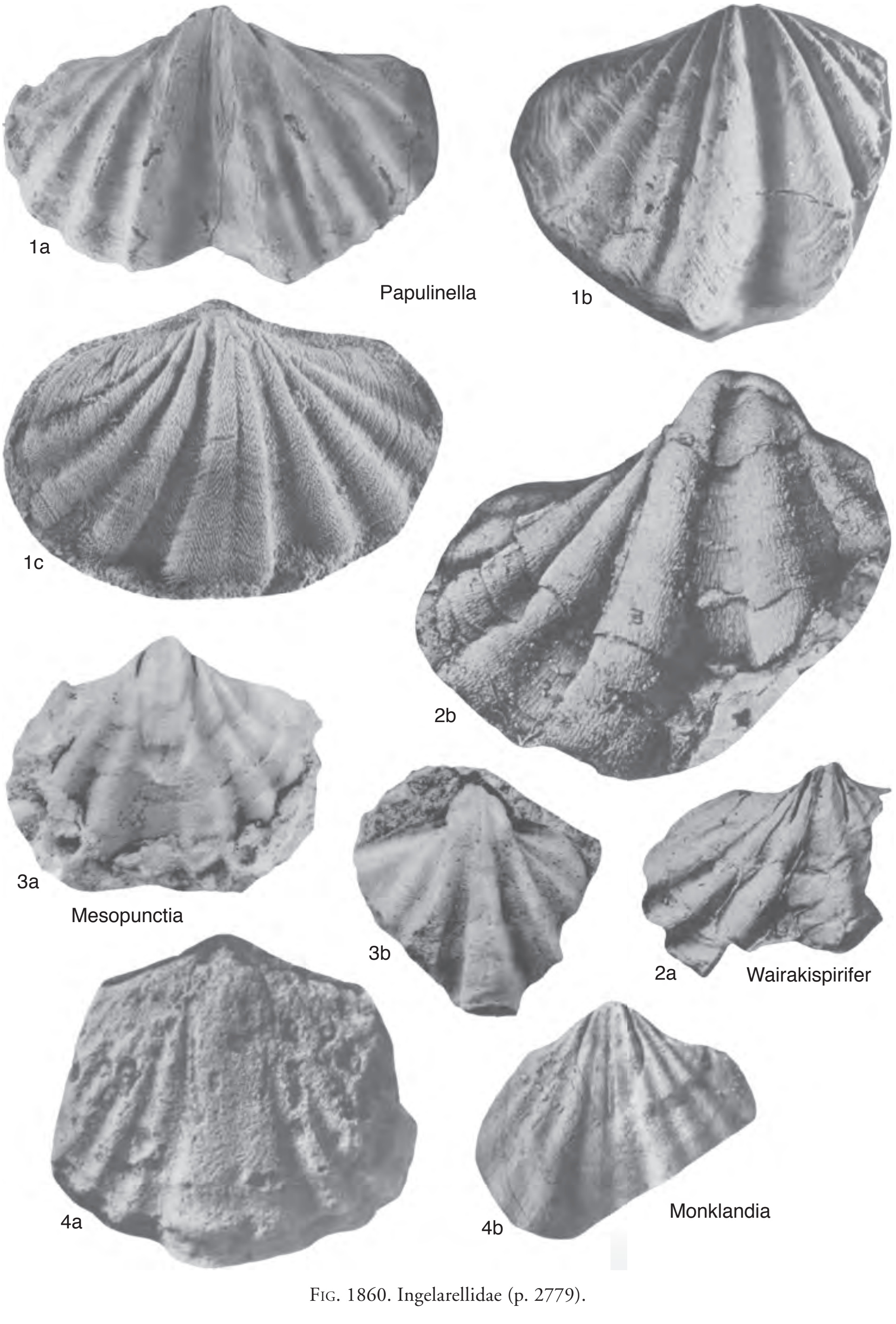


FIG. 1860. Ingelarellidae (p. 2779).

some exceptions are known in different families, and the erection of a new family is not regarded here as necessary.

Concerning the 16 new genera erected by WATERHOUSE (2004), their descriptions and figures are not sufficiently developed to allow a clear opinion about their status. Further work beyond the scope of this contribution is needed to test the classification by WATERHOUSE (2004), and the new genera are tentatively assigned to existing families.

[The author (RG) is most grateful to Dr. Lucia Angiolini (Università degli Studi di Milano) for her helpful comments on Permian spiriferids.]

Family SPIRIFERIDAE King, 1846

Subfamily PROSPIRINAE Carter, 1974

Atylephorus SARTENAER & PLODOWSKI, 1996, p. 57 [**Spirifer tornacensis* DE KONINCK, 1883, p. 373; OD]. Large, transverse, ventribiconvex, mucronate; ventral interarea apsacline, weakly concave, with subparallel borders; sulcus narrow, shallow, costate, poorly defined; fold narrow, low, costate, rising above flanks only near anterior margin, well delimited by fold bounding grooves; flanks with numerous, slightly flattened costae with narrow interspaces; costae near fold and sulcus freely bifurcating; ventral interior with stout divergent adminicula and short delthyrial plate buried in callus. *Carboniferous (Tournaisian)*: Belgium.——FIG. 1861,*2a–e*. **A. tornacensis* (DE KONINCK); neotype, dorsal, ventral, anterior, posterior, and lateral views, ×1 (Sartenaer & Plodowski, 1996). [John Carter]

Donispirifer POLETAEV, 2000, p. 279 [**Spirifer (Neospirifer?) baschkovensis* ROTAI, 1951, p. 34; OD]. Medium size, subsemicircular to subquadrate in outline; moderately subequally biconvex; maximum width at hinge line, ears slightly mucronate; fold and sulcus moderately narrow, well defined; sulcus rounded to subangular; fold low, sharply delimited by deep bounding interspaces; ventral interarea low, sharply defined, almost parallel sided, truncated laterally; flanks with moderately numerous, simple, bifurcating, or more rarely, trifurcating costae near fold-sulcus; ventral interior with short divergent dental adminicula. *Carboniferous (Bashkirian–Moscovian)*: Ukraine, Urals, USA (?New Mexico).——FIG. 1861,*1a–d*. **D. baschkovensis* (ROTAI), Moscovian, Ukraine; holotype, ventral, dorsal, lateral, and posterior views, ×1 (Rotai, 1951). [John Carter]

Subfamily SERGOSPIRIFERINAE Carter in Carter & others, 1994

Eobrachythyris BRICE, 1971, p. 182; *emend.,* BRICE, 1997, p. 72; BRICE in BRICE & NICOLLIN, 2000, p. 57 [**E. proovalis;* OD]. Small to medium size; length and width nearly equal; outline subovate to rounded subquadrate; fold and sulcus weakly developed but well differentiated; lateral slopes with few simple costae or divided costae near sulcus-fold in younger forms; sulcus smooth or with median costa and 1 or 2 obsolete lateral costae; delthyrial plate lacking or rudimentary, buried in apical callosity. *Upper Devonian (Famenian)–Lower Carboniferous (Tournaisian):* Afghanistan, Iran, Morocco. [See CARTER, 2006, p. 1779, fig. 1173.] [Rémy Gourvennec]

Family CHORISTITIDAE Waterhouse, 1968

Subfamily ANGIOSPIRIFERINAE Legrand-Blain, 1985

Unicostatina WATERHOUSE, 2004, p. 184 [**Sulciplica subglobosa* CLARKE, 1990, p. 64; OD]. Medium size, with obtuse to rounded cardinal angles; delthyrium open; sulcus with single median costa; dental plates present; otherwise similar to *Sulciplica*. [This genus, as other genera in the subfamily Angiospiriferinae, was assigned to the Trigonotretidae by WATERHOUSE (2004) but is maintained here in the Choristitidae.] *Permian (Asselian):* Tasmania.——FIG. 1861,*3a-c*. **U. subglobosa* (CLARKE), Tasmania; *a*, ventral view, ×1; *b*, holotype, posterior view, ×1; *c*, ventral interior, ×1 (Clarke, 1990). [Rémy Gourvennec]

Family TRIGONOTRETIDAE Schuchert, 1893

Subfamily NEOSPIRIFERINAE Waterhouse, 1968

Cracowspira WATERHOUSE, 2004, p. 151 [**Fusispirifer laminatus* WATERHOUSE, 1987, p. 23; OD]. [Junior subjective synonym of *Fusispirifer* WATERHOUSE, 1966 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]

Fasciculatia WATERHOUSE, 2004, p. 95 [**F. greenlandicus;* OD]. [Junior subjective synonym of *Kaninospirifer* KULIKOV & STEPANOV in STEPANOV, KULIKOV, & SULTANAEV, 1975 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]

Georginakingia WATERHOUSE, 2004, p. 184 [**Spirifera avicula* MORRIS, 1845, p. 282, *non* SOWERBY, 1844, p. 160; OD]. [Junior subjective synonym of *Fusispirifer* WATERHOUSE, 1966 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]

Gobettifera WATERHOUSE, 2004, p. 100 [**G. angulata;* OD]. [Junior subjective synonym of *Septospirifer*

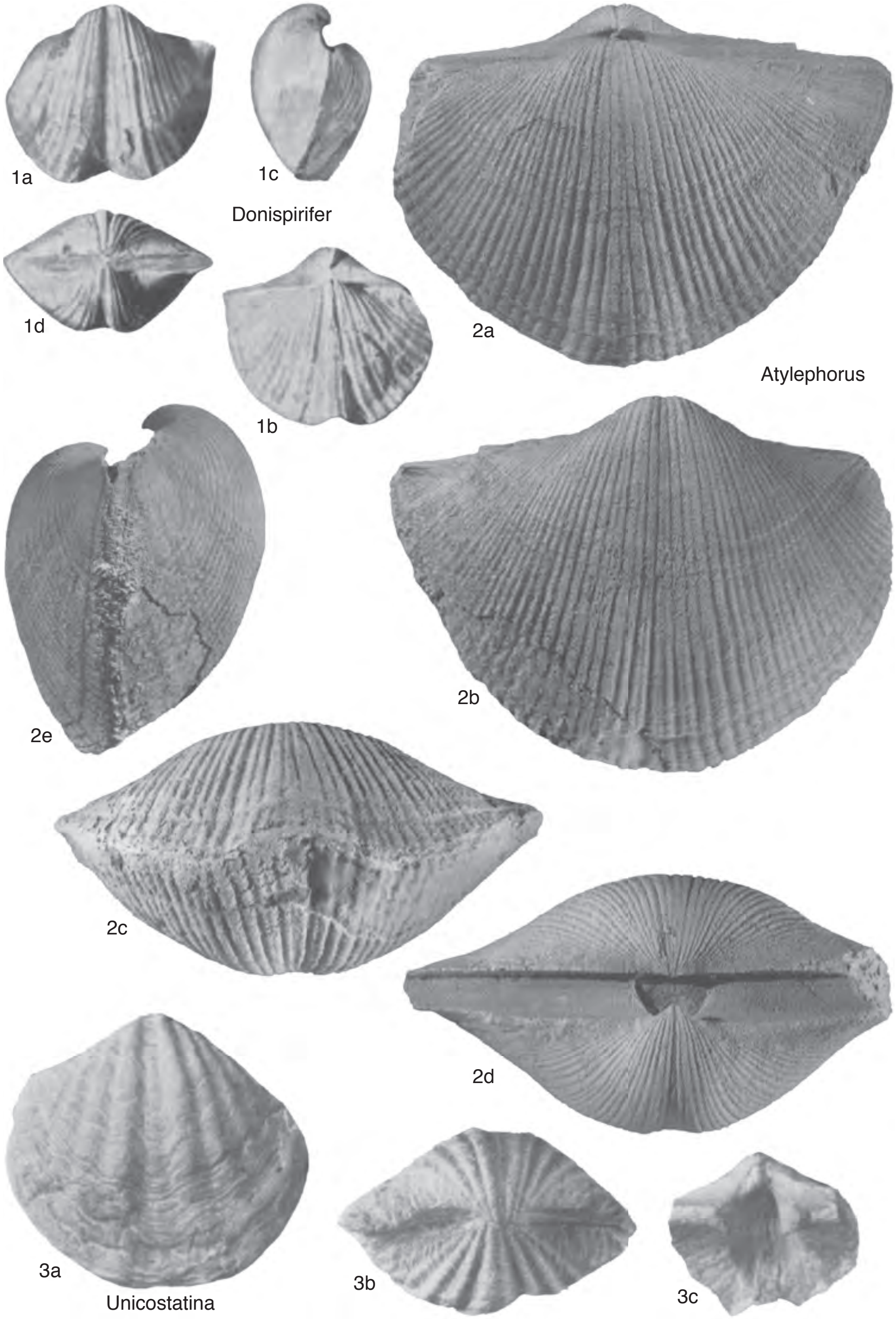


FIG. 1861. Spiriferidae and Choristitidae (p. 2781).

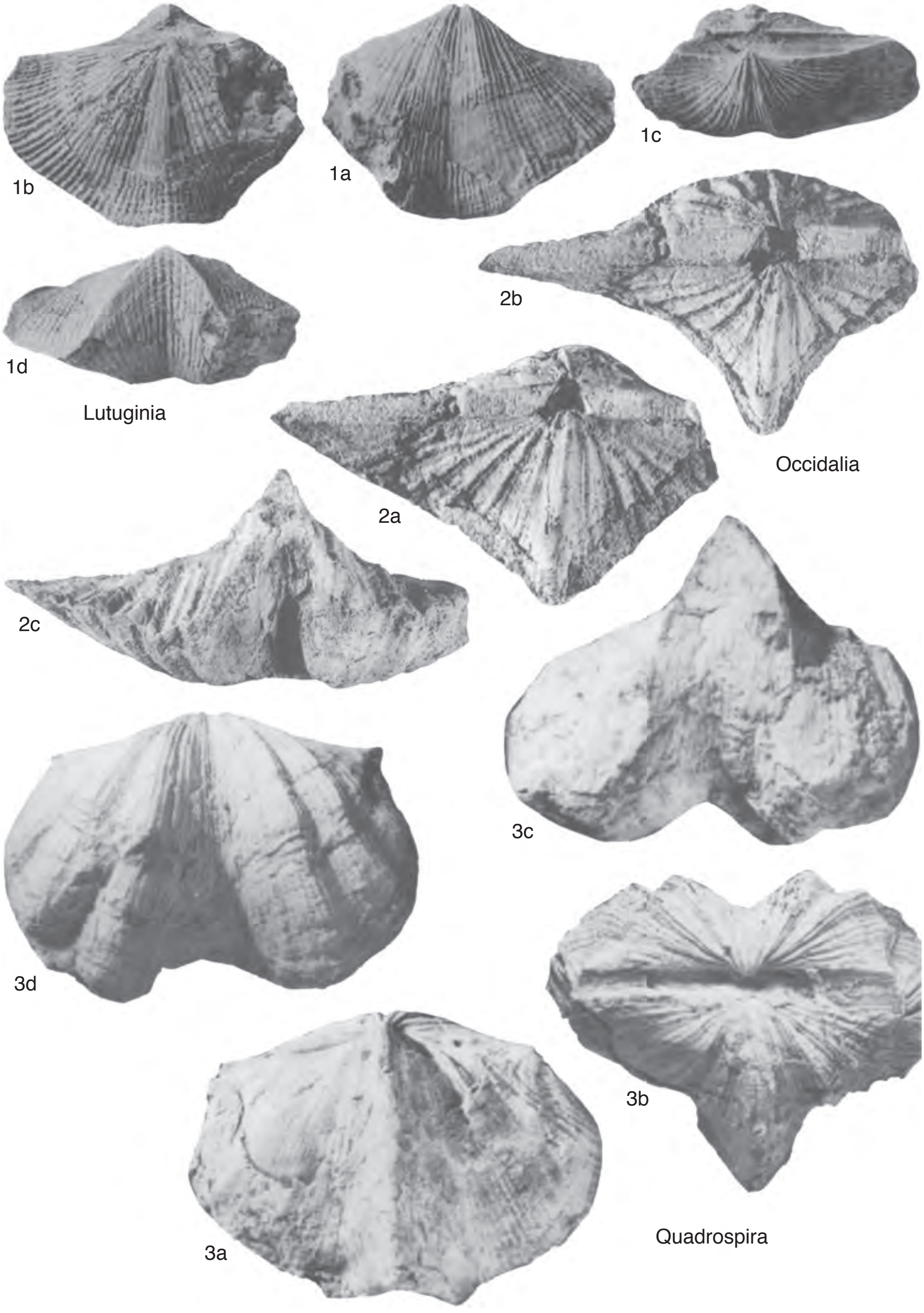


FIG. 1862. Trigonotretidae (p. 2784).

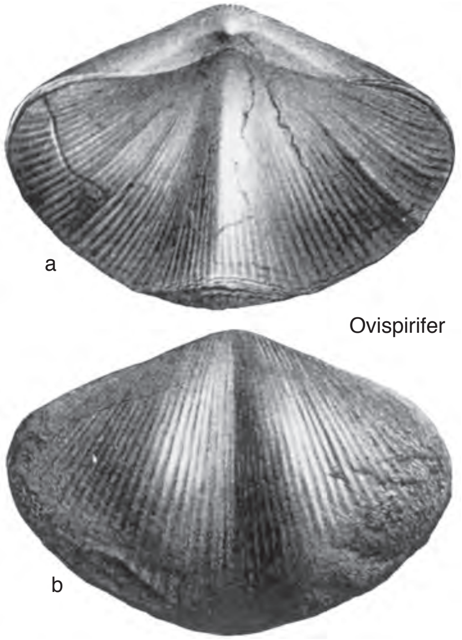


FIG. 1863. Trigonotretidae (p. 2784).

WATERHOUSE in BAMBER & WATERHOUSE, 1971 (see CARTER, 2006, p. 1799).] [Rémy Gourvennec]

Lutuginia POLETAEV, 1997, p. 309 [**Spirifer lutugini* ROTAI, 1931, p. 73; OD]. Medium size, outline transversely subovate; cardinal extremities rounded, hinge line shorter than maximum width in adults; fold and sulcus well developed, almost V-shaped; sulcus flaring anteriorly, incorporating additional costae; fold rising moderately, almost carinate; ventral interarea low, acutely triangular; costae numerous, bifurcating 2 or 3 times to form distinct fascicles on lateral slopes, each fascicle composed of 3 to 6 costae; entire surface regularly imbricate; ventral interior with short, thin delthyrial plate and short, thin, subparallel adminicula; shell substance thin. *Carboniferous (upper Viséan–lower Bashkirian):* Ukraine, Russia, Kazakhstan.——FIG. 1862,*1a–d.* **L. lutugini* (ROTAI), upper Serpukhovian, Ukraine; holotype, ventral, dorsal, posterior, and anterior views, ×1 (Rotai, 1931). [John Carter]

Occidalia ARCHBOLD, 1997, p. 216 [**O. shahi*; OD]. Strongly transverse with alate cardinal extremities; lateral slopes with several moderate to strong plicae covered with fasciculate costae; fold and sulcus narrow, crudely V-shaped; sulcus anteriorly deflected to form tongue nearly perpendicular to lateral commissure; microornament of tegulate growth lamellae and weak capillae. *Permian (Cisuralian–Arkinskian):* Western Australia, India. ——FIG. 1862,*2a–c.* **O. shahi*, Artinskian, Western Australia; holotype, dorsal, posterior, and anterior views of latex cast, ×1 (Archbold, 1997). [John Carter]

Ovispirifer WATERHOUSE, 2004, p. 99 [**Spirifer oldhamianus* WAAGEN, 1883, p. 518; OD]. Hinge line short; widely rounded cardinal angles; plicae few with simple bifurcating costae; otherwise similar to *Gypospirifer*. *Middle Permian (lower Guadalupian):* Pakistan.——FIG. 1863*a–b.* **O. oldhamianus* (WAAGEN), Salt Range; dorsal, ventral views, ×1 (Waagen, 1883). [Rémy Gourvennec]

Quadrospira ARCHBOLD, 1997, p. 214 [**Neospirifer plicatus* ARCHBOLD & THOMAS, 1986a, p. 133; OD]. Large, outline subquadrate in type species; fold and sulcus well developed; flanks with few medium to strong plicae with fasciculate costae; ventral interarea wide, truncated by small mucronations; microornament tegulate and capillate. [This genus was proposed as a subgenus of *Neospirifer*. The latter cannot be firmly diagnosed until its microornament is elucidated, however. It seems prudent to consider *Quadrospira* a separate genus for the time being.] *Permian (Cisuralian)*: Australia, Timor, and southeastern Asia.——FIG. 1862,*3a–d.* **Q. plicata* (ARCHBOLD & THOMAS), Artinskian, Western Australia; holotype, dorsal, posterior, anterior, and ventral views, ×1 (Archbold & Thomas, 1986a). [John Carter]

Wadispirifer WATERHOUSE, 2004, p. 138 [**Neospirifer grandis* ARCHBOLD & THOMAS, 1986a, p. 143; OD]. [Junior subjective synonym of *Betaneopirifer* GATINAUD, 1949 (see CARTER, 2006, p. 1789).] [Rémy Gourvennec]

Subfamily TRIGONOTRETINAE Schuchert, 1893

Costuloplica WATERHOUSE, 2004, p. 188 [**Neospirifer campbelli senilis* MAXWELL, 1964, p. 31; OD]. Small to large, transverse; 6–9 pairs of ribs separated by narrow interspaces; dental adminicula short; dental plates low; umbonal callosity present; crural plates low and strong; low to absent dorsal median septum. [This genus was originally assigned to the subfamily Costuloplicinae, which is not recognized here.] *Carboniferous (Serpukhovian–Moscovian):* Australia, Russia (Baikal region), Kazakhstan, Argentina.——FIG. 1864,*2a–d.* **C. senilis* (MAXWELL), Australia; *a–b*, dorsal, ventral views, ×1; *c*, internal mold of dorsal valve, ×1; *d*, holotype, interior of ventral valve, ×1 (Maxwell, 1964). [Rémy Gourvennec]

Koenigoria WATERHOUSE, 2004, p. 173 [**Trigonotreta neoaustralis* ARCHBOLD & THOMAS, 1986a, p. 152; OD]. [Junior subjective synonym of *Trigonotreta* KOENIG, 1825 (see CARTER, 2006, p. 1801).] [Rémy Gourvennec]

?Maxwellispirifer WATERHOUSE, 2004, p. 127 [**Neospirifer campbelli exora* MCKELLAR, 1965, p. 10; OD]. Small, transverse, with rounded cardinal angles; delthyrium open; costae coarse; dental plates and short adminicula present; delthyrial plate lacking; moderate apical shell thickening; cteno-

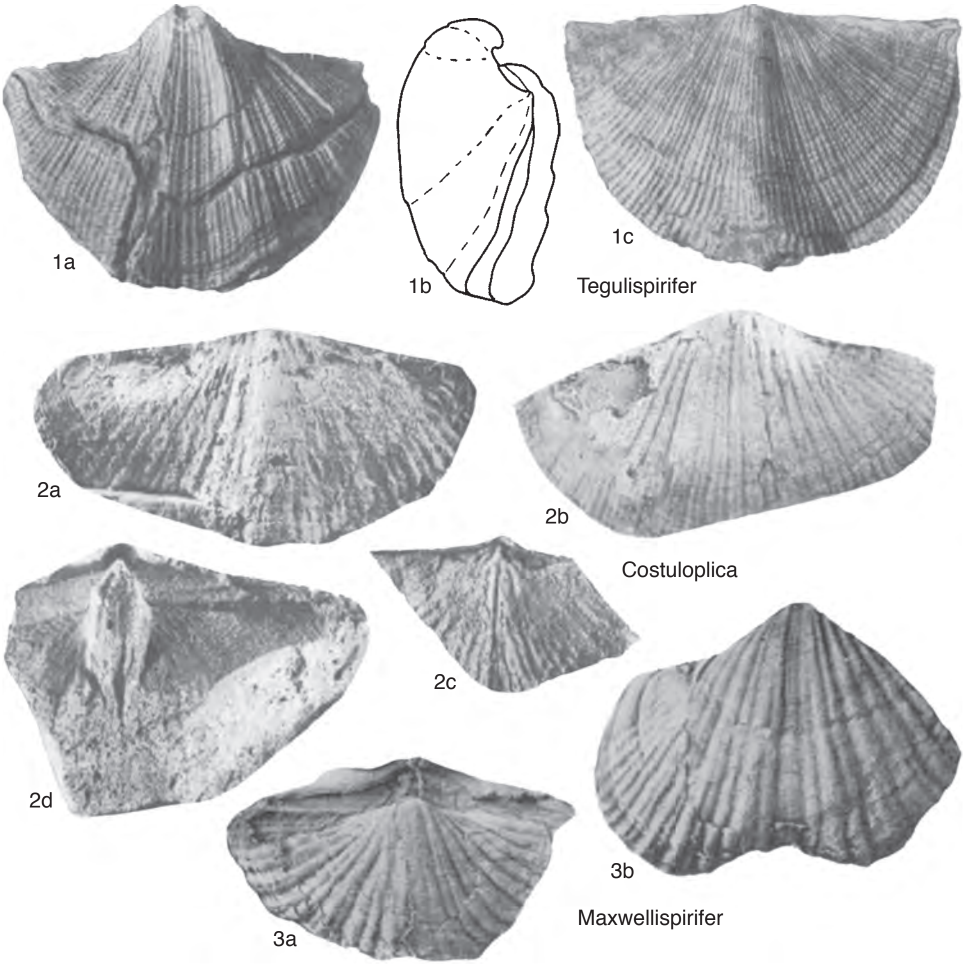


Fig. 1864. Trigonotretidae (p. 2784–2785).

phoridium, thick crural plates, and low median septum (possible myophragm) present. [This is a poorly defined genus, possibly a synonym of some neospiriferin.] *Lower Carboniferous (Serpukhovian):* Australia.——Fig. 1864,*3a–b.* **M. campbelli exora* (McKellar); *a*, dorsal view, ×1.5; *b*, holotype; ventral view, ×1.5 (McKellar, 1965). [Rémy Gourvennec]

Tegulispirifer Poletaev, 2000, p. 282 [**Spirifer tegulatus* Trautschold, 1876, p. 354; OD]. Medium to large; outline subrhomboidal in juveniles to transversely subovate in adults; maximum width attained at hinge line; cardinal extremities mucronate in juveniles, often subangular in adults; fold and sulcus well developed and defined, rounded to subangular; ventral interarea acutely triangular in juveniles, truncated in adults; delthyrium closed by stegidial plates fused with apical callosity; flanks with numerous freely bifurcating costae, forming fascicles of 7 to 9 ribs at anterior commissure; fascicles usually forming 1 or 2 weak plicae on each flank; microornament regularly imbricate; ventral interior obscured by callus. *Carboniferous (upper Serpukhovian–Kasimovian)*: Ukraine, Russia, Spain.——Fig. 1864,*1a–c.* **T. tegulatus* (Trautschold), Moscovian–Kasimovian, Moscow Basin; *a–b,* holotype, ventral and lateral views, ×1; *c,* dorsal valve, ×1 (Ivanov & Ivanova, 1937). [John Carter]

Family SPIRIFERELLIDAE Waterhouse, 1968

Aequalicosta Waterhouse, 2004, p. 193 [**Eliva inflata* Cooper & Grant, 1976a, p. 2239; OD] [Junior subjective synonym of *Elivina* Frederiks, 1924 (see Carter, 2006, p. 1805).] [Rémy Gourvennec]

Bamberina Waterhouse, 2004, p. 218 [**Elivina*? *annectens* Cooper & Grant, 1976a, p. 2242; OD]. Small, hinge line short; sulcus shallow with median trough; flanks with broad, low, rarely bifurcate costae; microornament pustulose; short dental plates and adminicula; small, thick crural plates, ctenophoridium and low median septum (possible myophragm) present. *Permian (Guadalupian–Lopingian):* USA (Texas), Canada, Himalaya, Verkhoiansk Range, Western Timor.——Fig. 1865,*1a–g*. **B. annectens* (Cooper & Grant), Lopingian, Texas, USA; *a–e*, holotype, dorsal, ventral, anterior, posterior, lateral views, ×1; *f*, ventral interior, ×2; *g*, dorsal interior, ×2 (Cooper & Grant, 1976a). [Rémy Gourvennec]

Canalisella Waterhouse, 2004, p. 217 [**Spiriferella leviplica* Waterhouse & Waddington, 1982, p. 26; OD]. [Junior subjective synonym of *Spiriferella* Chernyshev, 1902 (see Carter, 2006, p. 1805).] [Rémy Gourvennec]

Darbandia Angiolini, 2001b, p. 336 [**D. vagabunda*; OD]. Medium to large, with extended ventral umbo and very high, weakly apsacline to nearly orthocline, ventral interarea; hinge line moderately narrow; flanks with bifurcating costae that produce poorly defined fascicles; microornament absent; ventral interior with apical callosity and divergent dental adminicula. *Permian (Guadalupian–Wordian):* Pakistan.——Fig. 1865,*4a–c*. **D. vagabunda*, Wordian; holotype, ventral, dorsal, and lateral views, ×1 (Angiolini, 2001b). [John Carter]

Dissimiliplica Waterhouse, 2004, p. 226 [**Spirifer mexicanus* var. *compactus* Girty, 1909, p. 361; OD]. [Junior subjective synonym of *Elivina* Frederiks, 1924 (see Carter, 2006, p. 1805).] [Rémy Gourvennec]

Hunzina Angiolini, 1995, p. 186 [**H. electa*; OD]. Medium size, outline subovate to subtriangular; hinge line narrow, apsacline; delthyrium open; fold and sulcus moderately developed, slightly narrow; surface costate with bifurcations near fold-sulcus and sometimes forming few fascicles; ventral valve with thick callus obscuring adminicula; microornament of pustules and capillae. *Permian (Cisuralian):* Pakistan, China.——Fig. 1865,*2a–c*. **H. electa*, Sakmarian, Pakistan; *a–b,* holotype, lateral and ventral views, ×1; *c,* dorsal valve, ×1 (Angiolini, 1995). [John Carter]

Quispira Waterhouse, 2004, p. 225 [**Elivina detecta* Cooper & Grant, 1976a, p. 2244; OD]. [Junior subjective synonym of *Elivina* Frederiks, 1924 (see Carter, 2006, p. 1805).] [Rémy Gourvennec]

Tintoriella Angiolini, 1996, p. 195 [**Spirifera rajah* Salter in Salter & Blandford, 1865, p. 59; OD]. Large, strongly plicate; hinge line less than maximum width; delthyrium open; fold and sulcus narrow; flanks with strong fascicles of 3 to 6 costae; dental adminicula long and high; otherwise similar to *Spiriferella*. *Permian (Lopingian):* Himalayan Region.——Fig. 1865,*3a–b*. **T. rajah* (Salter), Wuchiapingian, Kashmir; holotype, dorsal and ventral views, ×1 (Davidson, 1866). [John Carter]

Superfamily PAECKELMANNELLOIDEA Ivanova, 1972

[*nom. correct.* Waterhouse, 2004, p. 227, *pro* Paeckelmanelloidea Carter in Carter & others, 1994, p. 347, *nom. correct. pro* Paeckelmanellacea Ivanova, 1981, p. 22, *nom. transl. ex* Paeckelmanellidae Ivanova, 1972, p. 40]

Waterhouse (2004), as suggested by Reed (1944), proposed an emendation of the name *Paeckelmanella* Likharev, 1934 to *Paeckelmannella*, since the intention of Likharev was clearly a dedication of the genus to W. Paeckelmann. The spelling of Likharev's genus by subsequent authors shows no consistency. Such an emendation seems acceptable according to the *Code* (1999, Art. 33), and the names of suprageneric taxa are consequently corrected. [Rémy Gourvennec]

Family STROPHOPLEURIDAE Carter, 1974

Subfamily STROPHOPLEURINAE Carter, 1974

Triangularia Poletaev, 2001, p. 492 [**T. tumida*; OD]. Small to medium, subtriangular to subquadrate in outline; maximum width at hinge line; ears subangular to mucronate; sulcus narrow, with single subangular rib; fold moderately to well developed, with carinate median crest, forming anterior prolongation with ventral median rib; ventral interarea moderately high, concave, variable in inclination; delthyrium narrow; flanks with few rounded plications separated by interspaces of equal width; microornament of regularly spaced growth lamellae and fine capillae; ventral interior lacking septa or plates. *Carboniferous (upper Serpukhovian)*: Ukraine.——Fig. 1866,*2a–c*. **T. tumida*; holotype, ventral, lateral, and dorsal views, ×2 (Poletaev, 2001). [John Carter]

Subfamily BASHKIRIINAE Nalivkin, 1979

?Varuna Waterhouse, 2004, p. 186 [**Spirifer varuna* Diener, 1915, p. 43; OD]. Small, transverse; dental plates and short crural plates present; otherwise similar to *Adminiculoria.* [The genus was originally assigned to the Angiospiriferinae, but it is similar to *Adminiculoria* and is tentatively placed in the Strophopleuridae.] *Carboniferous (Serpukhovian–Bashkirian):* India.——Fig. 1866,*1a–b*. **V. varuna* (Diener); *a*, lectotype, dorsal view, ×1; *b*, ventral interior, ×1 (Waterhouse, 2004). [Rémy Gourvennec]

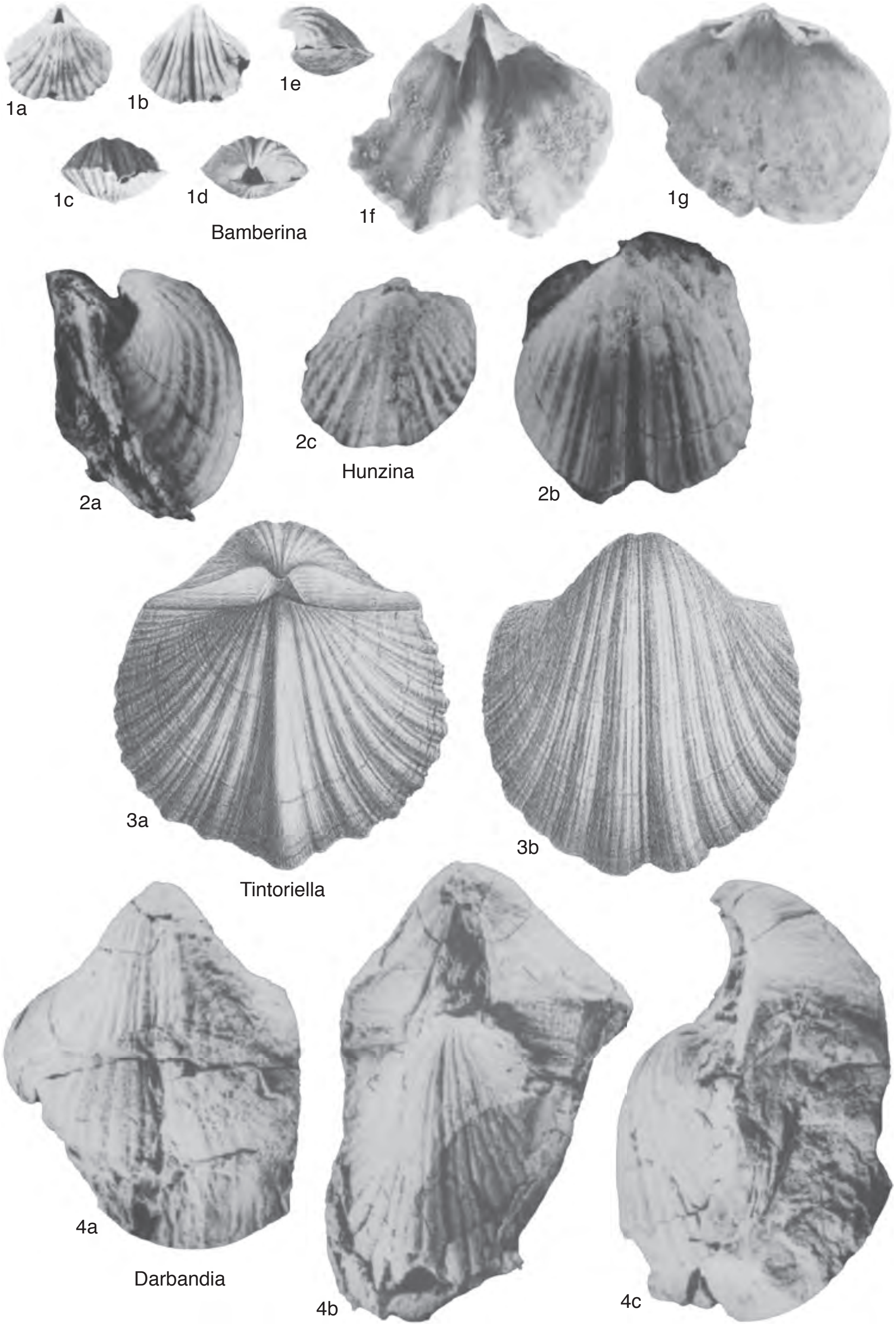


FIG. 1865. Spiriferellidae (p. 2786).

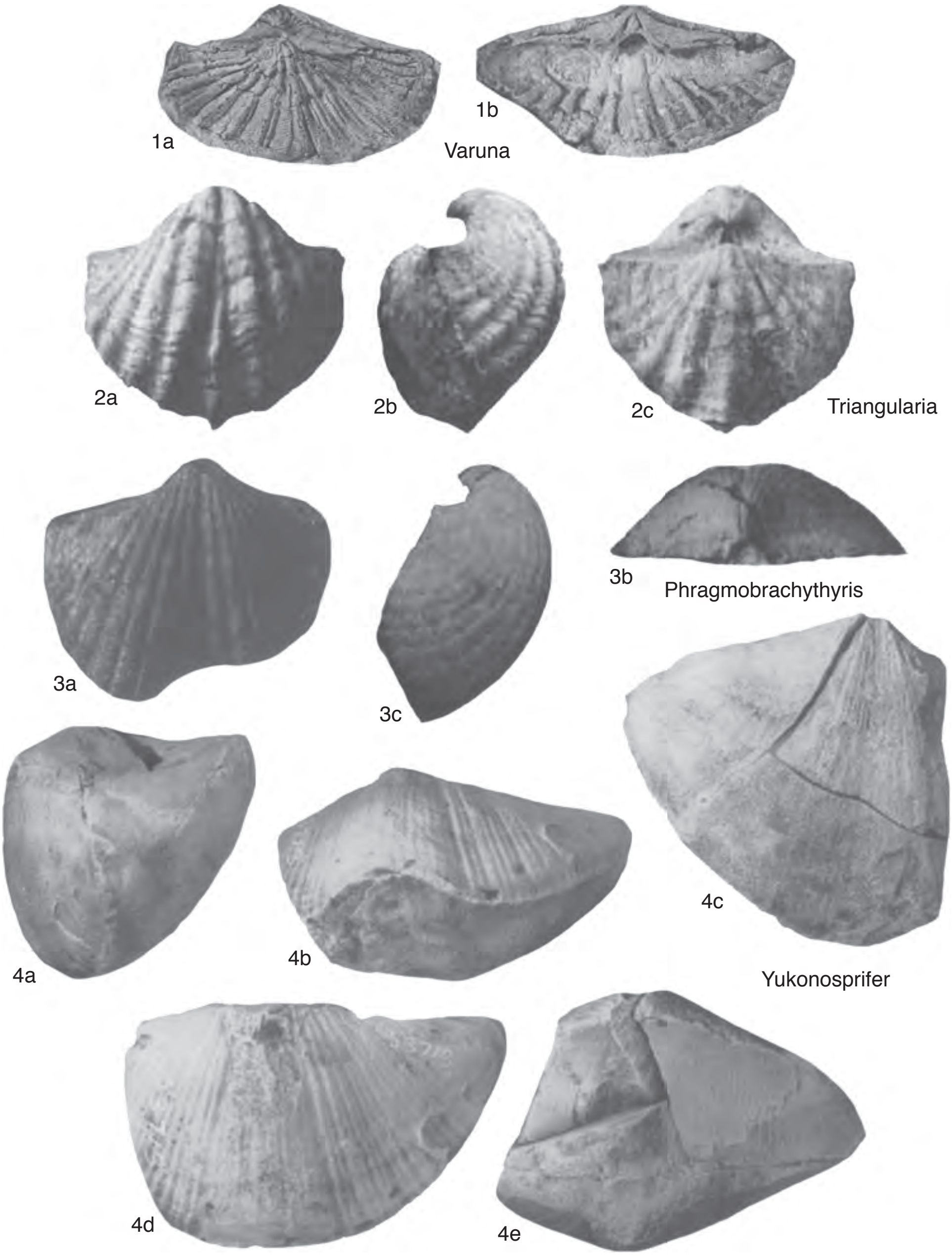


FIG. 1866. Strophopleuridae and Brachythyrididae (p. 2786–2789).

Subfamily PTEROSPIRIFERINAE Waterhouse, 1975

Johncarteria WATERHOUSE, 2004, p. 230 [**Spiriferinaella scalpata* COOPER & GRANT, 1976a, p. 2217, *non Spirifernaella scalpata*, *lapsus calami*; OD]. [Junior subjective synonym of *Pteroplecta* WATERHOUSE, 1978 (see CARTER, 2006, p. 1818).] [Rémy Gourvennec]

Yukonospirifer SHI & WATERHOUSE, 1996, p. 122 [**Y. yukonensis*; OD]. Medium to large, transversely subtrigonal in outline, subpyramidal in profile; ventral umbo poorly produced; fold and sulcus rounded, not well defined; ventral interarea high, flattened, almost catacline, vertically grooved; hinge line denticulate; flanks and fold-sulcus covered with numerous, freely bifurcating, subfasciculate costae; ventral interior with delthyrial plate and high, long adminicula; dorsal interior and microornament unknown. *Permian* (*Cisuralian–Sakmarian*): Canada (Yukon Territory).——FIG. 1866,*4a–e*. **Y. yukonensis*; holotype, lateral, anterior, ventral, dorsal, and posterior views, ×1 (Shi & Waterhouse, 1996). [John Carter]

Superfamily BRACHYTHYRIDOIDEA Fredericks, 1924

Remark: As in the superfamily Spiriferoidea (see above), WATERHOUSE (2004) proposed a revision of the superfamily Brachythyridoidea, in which he emphasized the absence of ventral adminicula and moved subfamilies from the Spiriferoidea to the Brachythyridoidea. WATERHOUSE (2004) also erected the family Brachythyrinidae (not the Brachythyridinidae as spelled on p. 236) and the subfamily Pustuloplicinae, which again leads to a mixture of taxa with different morphologies (e.g., delthyrial morphology, deltidial cover, ornament), and his classification is not followed here. [Rémy Gourvennec]

Family BRACHYTHYRIDIDAE Frederiks, 1924

Subfamily SKELIDORYGMIDAE Carter in Carter & others, 1994

Phragmobrachythyris POLETAEV, 1999, p. 260 [**P. stylaensis*; OD]. Medium to large, outline transversely subquadrate, moderately to strongly inflated; hinge line narrow, cardinal extremities rounded; delthyrium covered by deltidium; fold and sulcus moderately developed, rounded, ribbed; lateral slopes costate; median sulcal costa weaker than lateral sulcal costae; costae on flanks broad, flattened, those nearest fold-sulcus may bifurcate at umbo; ventral interior with short distinct myophragm; otherwise similar to *Skelidorygma*. *Carboniferous (Tournaisian–Viséan)*: Ukraine, Russia, Mongolia, Australia, Britain, USA.——FIG. 1866,*3a–c*. **P. stylaensis,* Viséan, Donetz Basin; holotype, ventral, posterior, and lateral views of ventral valve, ×1 (Poletaev, 1999). [John Carter]

Suborder DELTHYRIDINA Ivanova, 1972

Superfamily DELTHYRIDOIDEA Phillips, 1841

Family HYSTEROLITIDAE Termier & Termier, 1949

Subfamily HYSTEROLITINAE Termier & Termier, 1949

Gaspespirifer BIZZARRO & LESPÉRANCE, 1999, p. 1065 [**Spirifer gaspensis* BILLINGS, 1874, p. 44; OD]. Medium to large, transverse; cardinal extremities acute to mucronate; ventral interarea curved, apsacline; fold and sulcus smooth with subtrapezoidal section anteriorly; flanks with simple plications; surface with growth lamellae and marginal spines; curved dental plates present; ventral muscle field variably impressed; short crural plates and ctenophoridium present. *Lower Devonian (Pragian–Emsian):* North and South America, France.——FIG. 1867,*1a–c*. **G. gaspensis* (BILLINGS), Emsian, Gaspé Peninsula; *a*, lectotype, posterior view, ×1.1; *b–c*, dorsal and ventral views of internal mold, ×1.2 and ×0.9 respectively (Bizzarro & Lespérance, 1999). [Rémy Gourvennec]

Subfamily FIMBRISPIRIFERINAE Pitrat, 1965

Bultynckia GARCÍA-ALCALDE, 2004, p. 22 [**Spirifer Rojasi* DE VERNEUIL, 1850, p. 178; OD]. Medium to large, brachythyrid, entirely ribbed; ventral interarea curved, apsacline with deltidial plates joining apically in a short deltidial cover; ribs generally simple or 1 to 3 internal pairs bifurcating anteriorly; microornament capillate with marginal spines; long dental plates and short crural plates present. *Lower Devonian (Pragian–Emsian):* Spain, western France.——FIG. 1867,*2a–f*. **B. rojasi* (DE VERNEUIL); *a–e,* dorsal, anterior, posterior, ventral, and lateral views, ×1; *f,* transverse section, ×7 (García-Alcalde, 2004). [Rémy Gourvennec]

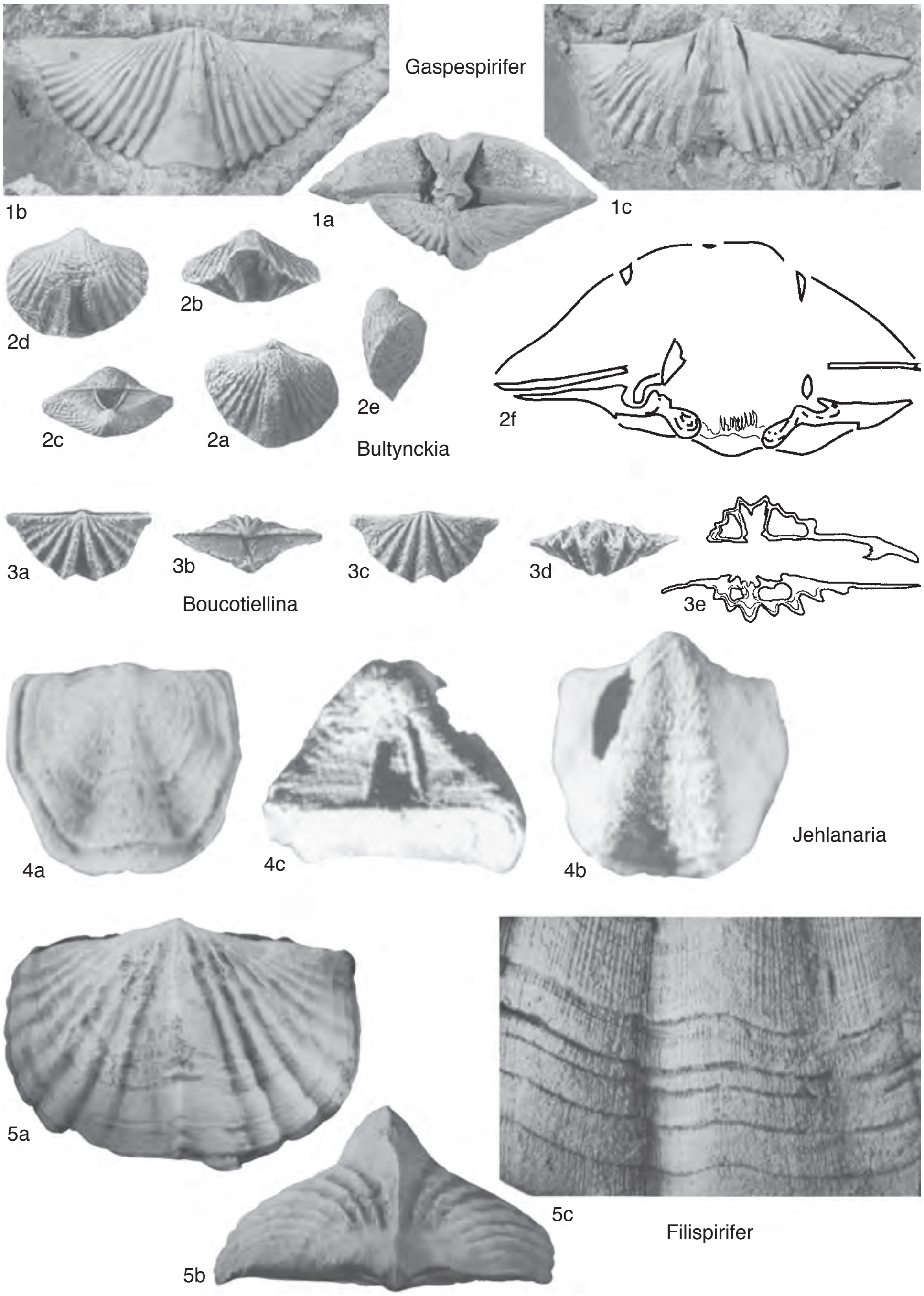


Fig. 1867. Hysterolitidae, Acrospiriferidae, and Cyrtinopsidae (p. 2789–2791).

Family ACROSPIRIFERIDAE Termier & Termier, 1949

[*nom. transl.* Johnson & Hou in Carter & others, 1994, p. 351, *ex* Acrospiriferinae Termier & Termier, 1949, p. 96] [type genus, *Acrospirifer* Helmbrecht & Wedekind, 1923, p. 952]

Medium to large size, transverse, generally capillate with fila, occasionally with a tendency to develop marginal spines; crural plates variably present. [Jansen (2001a) illustrated spines on some well-preserved specimens attributed to *Acrospirifer primaevus* from the *regio typica* (but not from the type locality). We cannot be sure that these specimens are conspecific with the type specimens of the genus *Acrospirifer,* which when illustrated by Jahnke (1971) show no spines. If we retain the possibility of a spinose *Acrospirifer,* the genus may become restricted to its type species only. The genus *Filispirifer* erected by Jansen (2001b) in order to gather most of the capillate species previously assigned to *Acrospirifer* also shows a slight tendency to develop rudimentary marginal spines, indicating that the two genera are very closely related.] *Lower Devonian (upper Lochkovian)–Middle Devonian (Eifelian).* [Rémy Gourvennec]

Filispirifer Jansen, 2001b, p. 269 [**F. merzakhsaiensis;* OD]. 5 to 15 ribs on each flank, those bordering sulcus often deflated; ornament capillate (with a low tendency to develop marginal spines); notothyrial platform poorly expressed; otherwise similar to *Acrospirifer. Lower Devonian (upper lower Pragian–lower lower Emsian):* Europe, northern Africa, Turkey.——Fig. 1867,*5a–c.* **F. merzakhsaiensis*, Dra-Ebene, Morocco, holotype; *a–b*, dorsal, posterior views, ×0.7; *c*, ornament, ×4.9 (Jansen, 2001b). [Rémy Gourvennec]

Family CYRTINOPSIDAE Wedekind, 1926

Subfamily CYRTINOPSINAE Wedekind, 1926

Jehlanaria Havlíček in Havlíček & Vaněk, 1998, p. 94 [**Cyrtina vlasta* Havlíček, 1956, p. 607; OD]. Small, cyrtiniform, with high catacline to procline ventral interarea; narrow deltidial plates fused apically; fold and sulcus well delimited, smooth; flanks with one obsolete plication; dental plates united to median septum to form narrow spondylium. *Lower Devonian (Pragian):* Czech Republic (Prague Basin).——Fig. 1867,*4a–c.* **J. vlasta* (Havlíček), dorsal, ventral, and posterior views, ×7.1 (Havlíček & Vaněk, 1998). [Rémy Gourvennec]

Subfamily ARASPIRIFERINAE Johnson in Carter & others, 1994

Boucotiellina García-Alcalde, 2004, p. 27 [**Spirifer Ezquerra* de Verneuil, 1850, p. 178; OD]. Small, transverse to slightly mucronate; high, apsacline ventral interarea with open delthyrium; fold and sulcus smooth; lateral plications strong, angular; microornament capillate and spinose; dental plates and low, short, poorly developed median septum; short crural plates and small, rudimentary ctenophoridium [The genus is assigned to the Araspiriferinae due to the presence of short crural plates. A median septum is a characteristic of the Cyrtinopsinae, but it is poorly developed here, and moreover the Cyrtinopsinae lack crural plates.] *Lower Devonian (upper Emsian):* northern Spain, northern China (?Nei Mongol).——Fig. 1867,*3a–e.* **B. ezquerrai* (de Verneuil); *a–d*, ventral, posterior, dorsal, and anterior views, ×2; *e*, transverse section, ×3 (García-Alcalde, 2004). [Rémy Gourvennec]

Superfamily RETICULARIOIDEA Waagen, 1883

Family RETICULARIIDAE Waagen, 1883

Subfamily RHENOTHYRIDINAE Gourvennec in Carter & others, 1994

Lubricospirifer Chen & Yao, 1999, p. 238 [**L. gumoensis;* OD]. Medium size; rounded or slightly elongate with high, apsacline, curved ventral interarea; delthyrium open; fold and sulcus well defined; flanks smooth or with 1–2 weak plicae; surface with growth lamellae and marginal spines; dental plates thin, subparallel; faint delthyrial ridges; crural plates united in trough or septalium; ctenophoridium present. *Lower Devonian (upper Emsian):* southern China.——Fig. 1868*a–f.* **L. gumoensis*, central Guangxi; *a–c*, lectotype, dorsal, ventral, and anterior views, ×1.5; *d*, lateral view, ×1; *e*, microornament, ×10; *f*, transverse section, ×2 (Chen & Yao, 1999). [Rémy Gourvennec]

Plicambocoelia Boucot & Brunton in Wongwanich & others, 2004, p. 1081 [**P. tansathieni;* OD]. [Junior subjective synonym of *Echinocoeliopsis* Hamada, 1968 (see Carter & Gourvennec, 2006, p. 1857).] [Rémy Gourvennec]

Quasiprosserella Boucot & Cocks in Boucot, Cocks, & Racheboeuf, 1999, p. 855 [**Q. samedensis*; OD]. [Junior subjective synonym of *Prosserella* Grabau in Grabau & Sherzer, 1910 (see Carter & Gourvennec, 2006, p. 1852).] [Rémy Gourvennec]

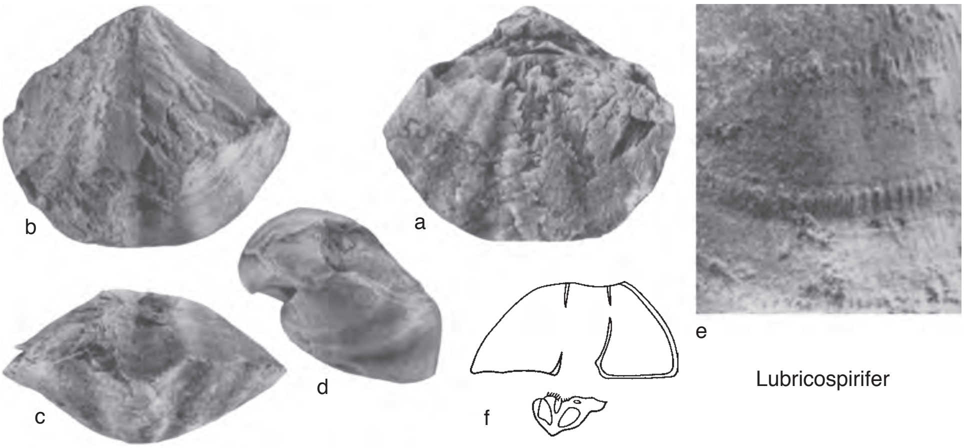


FIG. 1868. Reticulariidae (p. 2791).

Order SPIRIFERINIDA Ivanova, 1972

Suborder CYRTINIDINA Carter & Johnson in Carter & others, 1994

Superfamily CYRTINOIDEA Frederiks, 1911

Family CYRTINIDAE Frederiks, 1911

Cyrtina DAVIDSON, 1859 in 1858–1863, p. 66.

Cyrtina (Hystricocyrtina) HAVLÍČEK in HAVLÍČEK & VANĚK, 1998, p. 100 [**Cyrtina kazi kazi* HAVLÍČEK, 1956, p. 606; OD]. Pseudodeltidium pierced by large foramen; ornament of relatively strong, erect, randomly distributed spines; otherwise similar to *Cyrtina (Cyrtina).* [*Hystricocyrtina* was erected as a new genus by HAVLÍČEK (1998), but it is so close to *Cyrtina*, except for its ornament, that we retain it here only at the subgeneric rank. Thus the genus *Cyrtina* now includes two subgenera: *C. (Cyrtina),* the diagnosis of which corresponds to that given in JOHNSON, 2006, p. 1881, and *C. (Hystricocyrtina)* here described.] *Lower Devonian (Pragian):* Czech Republic (Prague Basin).——FIG. 1869,*1a–d.* **C. (H.) kazi* (HAVLÍČEK); *a–c*, dorsal, ventral, and posterior views, ×6.5; *d*, dorsal interior, ×9.2 (Havlíček & Vaněk, 1998). [Rémy Gourvennec]

Moniellocyrtina GARCÍA-ALCALDE, 2001, p. 126 [**M. orthoclina*; OD]. Large with orthocline to slightly anacline, strongly curved, high ventral interarea; otherwise similar to *Cyrtina. Lower Devonian (upper Emsian):* northern Spain.——FIG. 1869,*2a–d.* **M. orthoclina;* ventral, dorsal, lateral, and anterior views, ×3 (García-Alcalde, 2001). [Rémy Gourvennec]

Suborder SPIRIFERINIDINA Ivanova, 1972

Superfamily SYRINGOTHYRIDOIDEA Frederiks, 1926

Family SYRINGOTHYRIDIDAE Frederiks, 1926

Subfamily PERMASYRINXINAE Waterhouse, 1986

Remark: The assignment of the following genera to the family Syringothyrididae, subfamily Permasyrinxinae remains provisional until the presence of perideltidial areas or syrinx is elucidated.

Cundaria ARCHBOLD, 1996, p. 28 [**C. aquilaformis*; OD]. Outline transversely and acutely triangular with wide alate cardinal extremities; costae on ears may bifurcate; fold with shallow median groove; sulcus with pair of weak costae on sides; fold well delineated; delthyrium very wide; microornament of grooves with posterior papillae and anterior pits. *Permian (Cisuralian–Artinskian)*: Western Australia.——FIG. 1870,*1a–e.* **C. aquilaformis*;

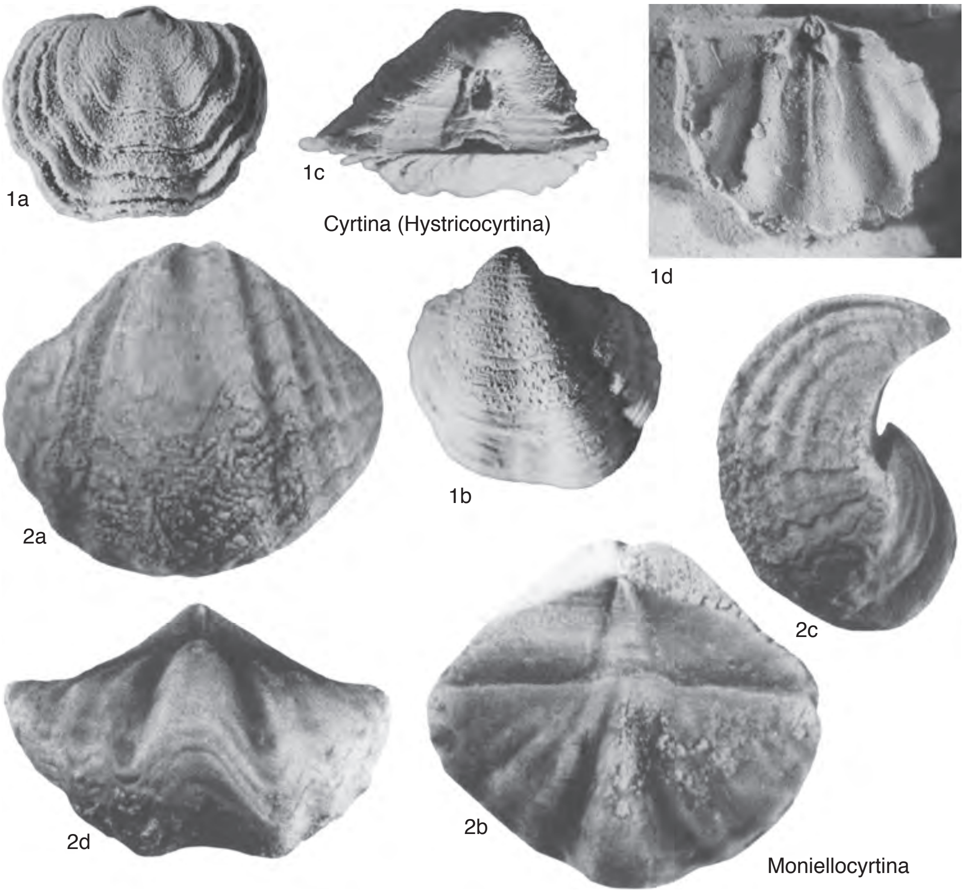


FIG. 1869. Cyrtinidae (p. 2792).

holotype, internal mold in dorsal, ventral, and posterior views and incomplete latex cast of dorsal and posterior exteriors, ×1 (Archbold, 1996). [John Carter]

?Kyutepia KLETS, 1998, p. 95 [**K. alata*; OD]. Presence of perideltidial areas unknown; otherwise similar to *Myodelthyrium.* [If *Kyutepia alata* KLETS, 1998, lacks perideltidial areas then the genus is valid and should be assigned to the Licharewiidae.] *Permian (Cisuralian)*: northeastern Siberia.——FIG. 1870,*2a–c.* **K. alata*; *a,* holotype, partial internal mold of ventral interarea, ×1.5; *b,* internal mold of ventral interarea showing muscle impressions and median ridge on delthyrial plate, ×1; *c,* mold of dorsal valve interior, ×1 (Klets, 1998). [John Carter]

Pachycyrtella ANGIOLINI, 2001a, p. 126 [**P. omanensis*; OD]. Large, outline subtrigonal; ventral interarea high, concave, apsacline to orthocline; sulcus narrow, shallow, smooth; fold well delineated, low, with deep mesial furrow; flanks with moderately coarse costae; ventral interior with long thick delthyrial plate and long adminicula that surround much of muscle field; shell substance very thick; otherwise similar to *Cyrtella. Permian (Cisuralian–Sakmarian)*: Oman, Afghanistan, India, ?Australia.——FIG. 1871,*2a–b.* **P. omanensis*, Sakmarian, Oman; holotype, dorsal and ventral views, ×1 (Angiolini, 2001a). [John Carter]

?Syrella ARCHBOLD, 1996, p. 32 [**S. occidenta*; OD]. Small to medium, transversely subovate in outline, ventribiconvex; flanks with up to 12

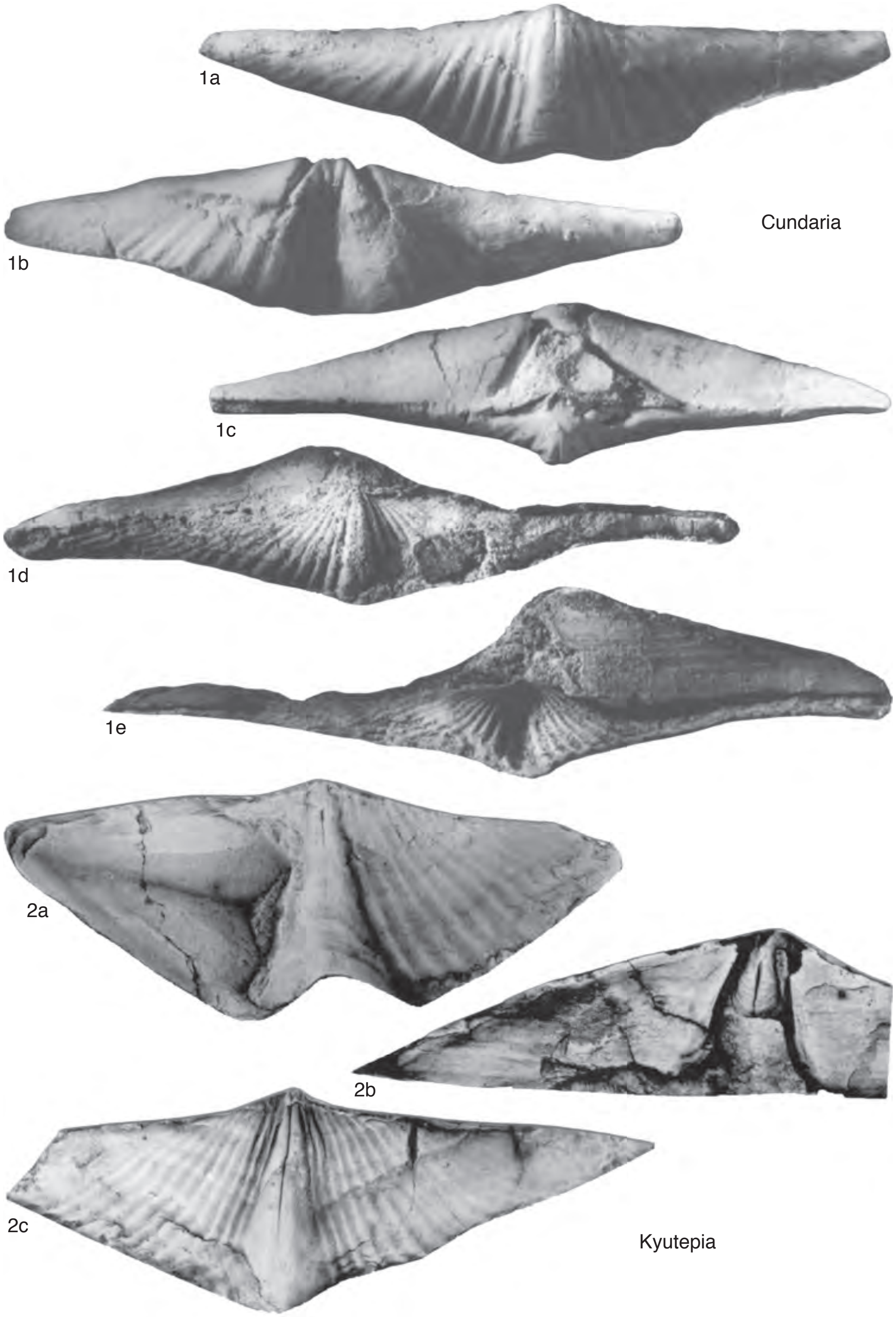


FIG. 1870. Syringothyrididae (p. 2792–2793).

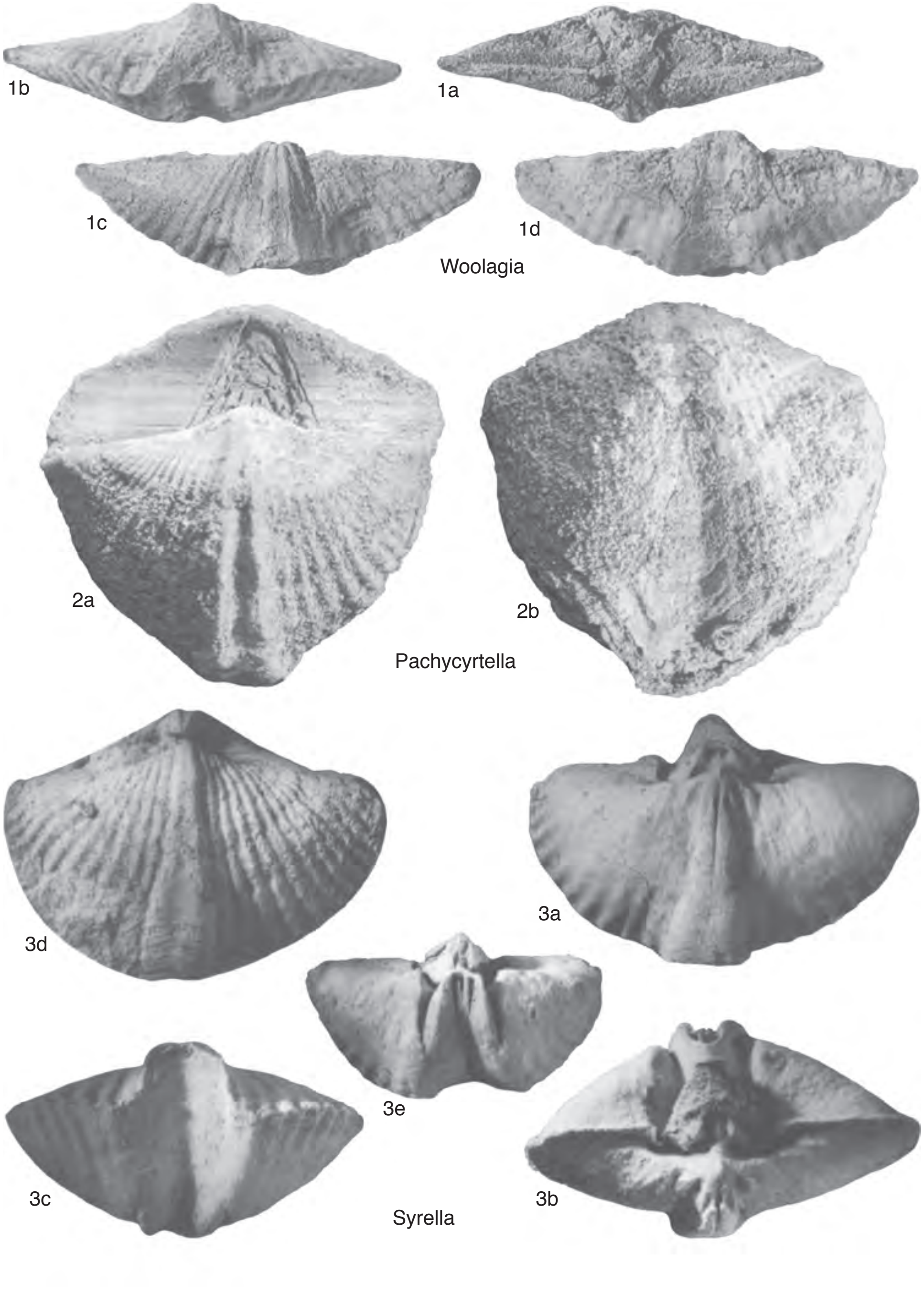


FIG. 1871. Syringothyrididae (p. 2793–2796).

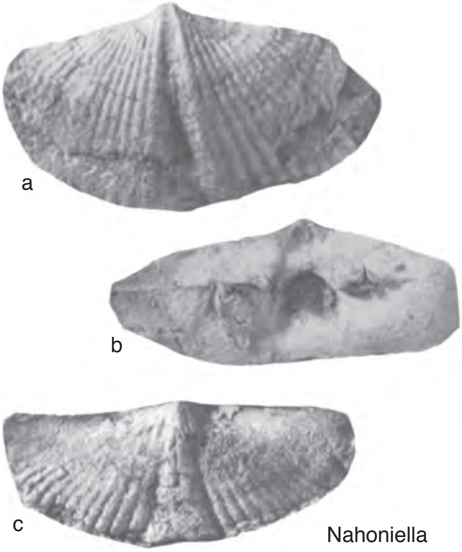


FIG. 1872. Licharewiidae (p. 2796).

pairs of rounded simple costae; ventral interarea of moderate height, concave, apsacline; fold and sulcus well delineated; fold with shallow depression or groove for entire length; ventral adminicula extending forward about one-third valve length; ventral muscle field with several myophragms that become stronger with age. [Assignment of this genus to the Permasyrinxinae is uncertain because perideltidial areas are unknown. It could well belong in the Licharewiidae.] *Permian (Cisuralian–Artinskian):* Western Australia.——FIG. 1871,*3a–e.* **S. occidenta*; *a–d,* holotype, internal mold in dorsal, posterior, and anterior views, latex cast of dorsal valve, ×1.25; *e,* ventral view showing muscle field, ×1 (Archbold, 1996). [John Carter]

Woolagia ARCHBOLD, 1997, p. 218 [**W. playfordi*; OD]. Medium size, strongly transverse, with acutely subtrigonal outline; fold with broad mesial furrow and pair of low lateral costae; sulcus smooth or with weak pair of lateral costae; flanks with moderately numerous, simple, rounded costae; ventral interarea moderately low, concave, apsacline; ventral interior with short, thick dental adminicula and short, thick delthyrial plate; microornament of delicate radial grooves only. *Permian (Cisuralian–Artinskian)*: Western Australia.——FIG. 1871,*1a–d.* **W. playfordi*; holotype, posterior, anterior, dorsal, and ventral views of internal mold, ×1 (Archbold, 1997). [John Carter]

Family LICHAREWIIDAE
Sliusareva, 1958

Nahoniella SHI, 1998, p. 935, *nom. nov. pro Yukonella* SHI & WATERHOUSE, 1996, p. 127, *non Yukonella* SENOWBARI-DARYAN & REID, 1986, p. 900 [**Yukonella plana*; OD]. Delthyrial plate large, covering half or more of delthyrium; ovarian impressions poorly developed; otherwise similar to *Permospirifer*. *Permian (Cisuralian–Artinskian)*: Canada (Yukon Territory).——FIG. 1872*a–c.* **N. plana* (SHI & WATERHOUSE); *a,* holotype, ventral valve, ×1; *b,* ventral interior, latex cast, ×1; *c,* dorsal exterior, ×1 (Shi & Waterhouse, 1996). [John Carter]

Superfamily
PENNOSPIRIFERINOIDEA
Dagys, 1972
Family SPIROPUNCTIFERIDAE
Carter in Carter & others, 1994

Spiropunctifera IVANOVA, 1971, p. 120.

S. (Larbontella) LEGRAND-BLAIN, 1996, p. 201 [**Spiropunctifera (Larbontella) dubari;* OD]. Costae freely bifurcating on flanks and fold-sulcus; dorsal adminicula moderately long; otherwise similar to *S. (Spiropunctifera)*. *Carboniferous (upper Viséan or lower Serpukhovian)*: French Pyrenees.——FIG. 1873*a–c.* **S. (L.) dubari;* holotype, exterior, interior, and posterior mold, ventral valve, ×1.5 (Legrand-Blain, 1996). [John Carter]

FIG. 1873. Spiropunctiferidae (p. 2796).

THECIDEIDA

Peter G. Baker

[University of Derby]

Order THECIDEIDA Elliott, 1958

Superfamily THECIDEOIDEA Gray 1840

Family THECIDELLINIDAE Elliott, 1958

Subfamily THECIDELLININAE Elliott, 1953

Kakanuiella Lee & Robinson, 2003, p. 344 [**Thecidellina hedleyi* Thomson, 1915, p. 463; OD]. Small, subtriangular, hinge line relatively short, ventral interarea flat with no trace of pseudodeltidium or delthyrial notch; ventral valve with sessile hemispondylium bounded laterally by slightly concave vertical plates, teeth subtriangular, relatively widely spaced, floor of valve ornamented by tiny, acicular crystallite calcite spines on either side of high bladelike median septum extending almost to anterior border; dorsal valve variable but usually subquadrate, relatively flattened away from convex umbonal region, cardinal process broad rectangular in outline, border narrow, outer surface of subperipheral rim ornamental by low ribs, brachial bridge with ventral groove (marsupial notch) and small, posteriorly directed spur, median septum typically tapering posteriorly, extending to edge of body cavity, ventral edge flanked by anteriorly divergent, serrated ridges to create appearance of small central depression, brachial lobes auriform with serrated margins but without intrabrachial depressions, probably not canopied; fibrous secondary shell completely suppressed, shell composed of acicular crystallite calcite intermixed with patches of interlocking granules of calcite, especially in teeth; groove and spur structure on brachial bridge possibly indicative of sexual dimorphism. [Lüter (2005, p. 105) regarded the marsupial notch as a diagnostic lacazellin character and placed *Kakanuiella* in subfamily Uncertain. Because it is only present in females, however, and the presence or absence of a marsupial notch cannot be established in the majority of fossil thecideides, *Kakanuiella* currently remains assigned to the Thecidellininae.] *Paleogene–Holocene:* New Zealand (Oamaru District), *lower Eocene (Ypresian)–lower Oligocene (Rupelian)*; New Zealand (Chatham Rise), *Holocene*.——Fig. 1874*a–e*. **K. hedleyi* (Thomson); *a*, ventral valve interior, Priabonian, Cape Wanbrow, ×14; *b*, acicular crystallites on valve floor, Priabonian, Cape Wanbrow, University of Otago, OU43125a, ×1400; *c,* dorsal valve interior, Priabonian, Cape Wanbrow, OU43127, ×16; *d*, dorsal valve interior, Rupelian, Kakanui, ×18; *e*, dorsal valve marginal ornament, Rupelian, Kakanui, OU43122, ×75 (Lee & Robinson, 2003).

Family THECIDEIDAE Gray, 1840

Subfamily LACAZELLINAE Backhaus, 1959

Ospreyella Lüter & Wörheide in Lüter, Wörheide, & Reitner, 2003, p. 1425 [**O. depressa* Lüter in Lüter, Wörheide, & Reitner, 2003, p. 1425; OD]. Medium size, pyriform, unequally biconvex, dorsal valve almost lidlike, with low anterior uniplication, ventral valve cup-shaped with small cicatrix, ventral interarea flat, clearly developed with convex pseudodeltidium; ventral valve interior papillose with papillae more prominent near edge, hemispondylium projecting anteriorly with upraised edges and prominent median myophragm; outer rim of dorsal valve strongly papillose, cardinal process incipiently trilobed with bulbous median ridge, median septum with sinus replaced anteriorly by shallow sulcus breaching subperipheral rim to reach anterior margin, posteriorly median ridge upraised, free-standing, and folded backward with edges convoluted to form up to four short ramuli and terminating as a median concave channel (median ramus) connected to jugum, brachial lobes long, narrow, crescentic with serrated edges and small perforate reticulum connecting with jugum and posterior extensions interdigitating with ramuli; endopunctate; mantle spiculate; sexually dimorphic, brachial bridge of females with marsupial notch. [The organization of the brachial skeletal elements is reminiscent of the arrangement in *Vermiculothecidea.*] *Holocene*: Western Pacific (Coral Sea).——Fig. 1875*a–g*. **O. depressa*, Coral Sea, Osprey Reef, off Cooktown, Australia; *a*, holotype, female ventral valve interior, QM G318534, ×5; *b*, paratype, female dorsal valve interior, ZMB 2000, ×7; *c*, three-quarters profile view showing marsupial notch, ×30; *d*, paratype, male dorsal valve anterior view showing sulcus, ZMB 2005, ×7; *e*, enlargement of ventral valve interior showing hemispondylium, ×27; *f*, paratype, male ventral valve showing jugum (*arrow*) and bridge (*arrowhead*), ZMB 2004, ×15, *g*, juvenile dorsal valve interior, ZMB 2001, ×30 (Lüter, Wörheide, & Reitner, 2003).

Protolacazella Baker, 2005, p. 1311 [**P. scripta* Baker, 2005, p. 1312; OD]. Small, outline rounded to rounded and transversely oblong, large attachment scar and high free ventral wall usually with shallow anterior sulcus, hinge line only slightly less than maximum width of shell, ventral interarea

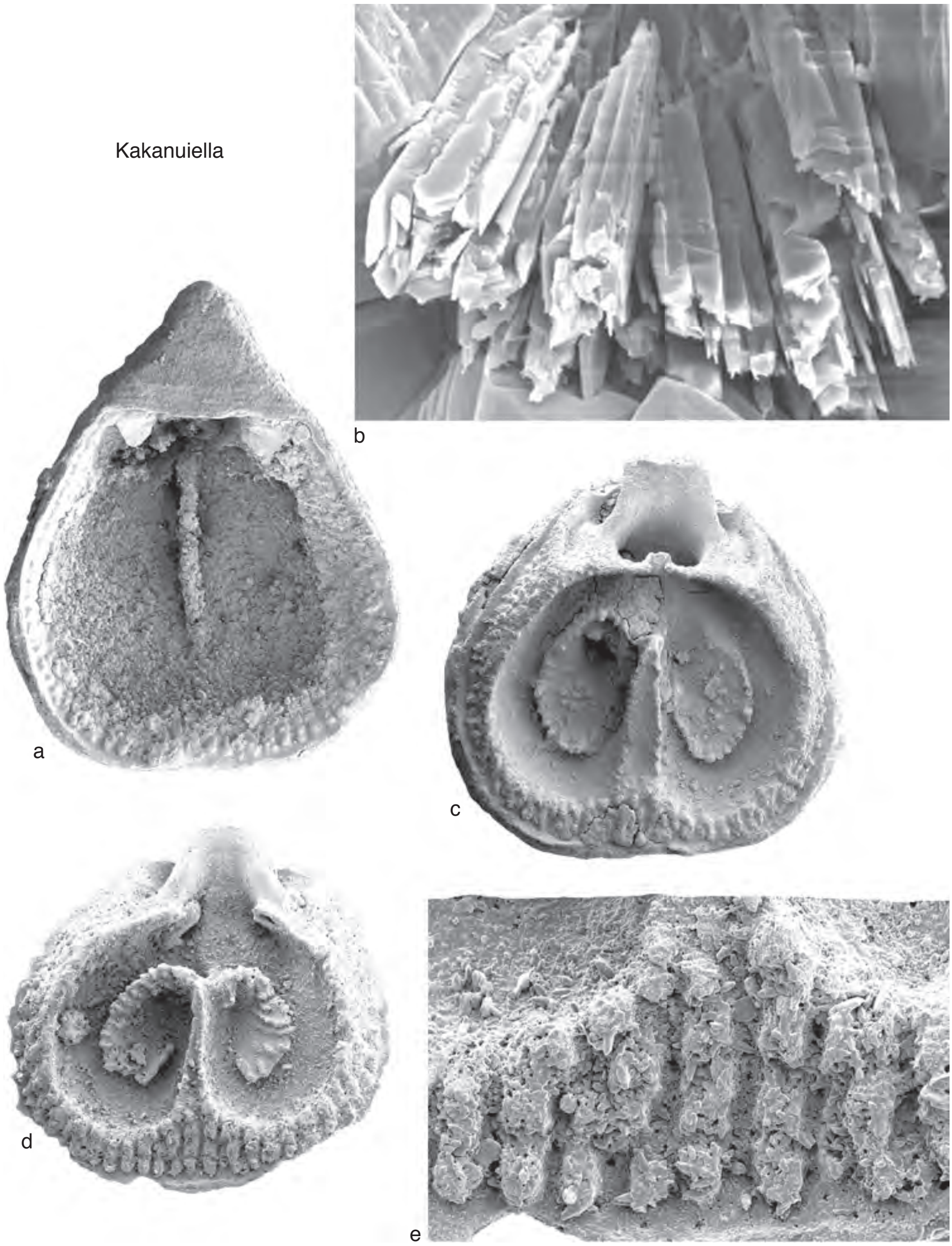


FIG. 1874. Thecidellinidae (p. 2797).

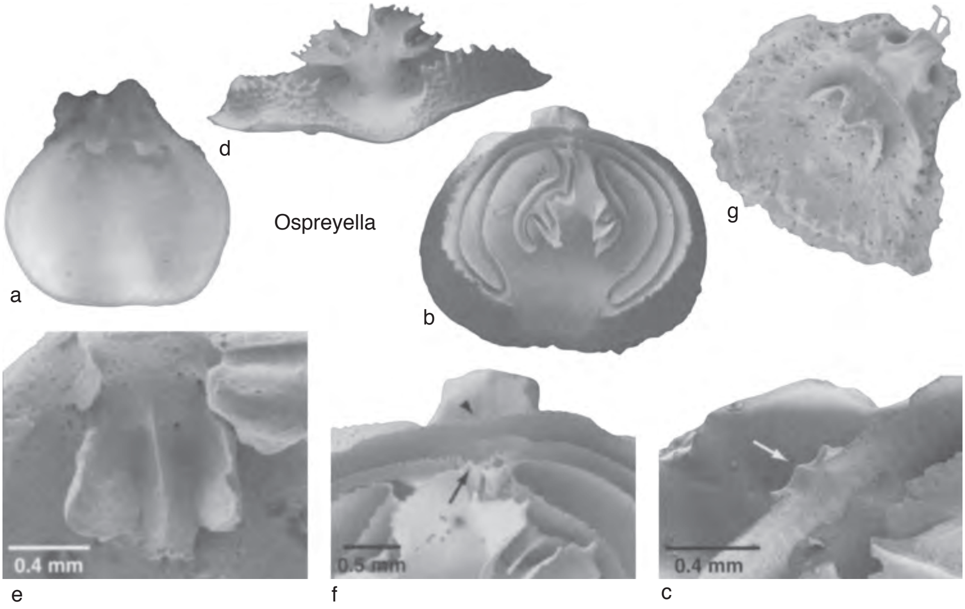


Fig. 1875. Thecideidae (p. 2797).

narrow, laterally attenuated with small, indistinct, shallowly convex pseudodeltidium; ventral valve with large sessile hemispondylium with characteristic W outline, inner surface of free ventral wall ornamented by low tubercles; dorsal valve with high subperipheral rim with outer surface ornamented by elongate tubercles, median septum with well-developed sinus and short ramuli, brachial cavities occupied typically by two brachial tubercles supporting perforate brachial lobes, posteriorly arching toward midline to form a reticulum united with jugal pillar; impunctate; probably possessed marsupium indicative of sexual dimorphism. The unobtrusive ventral interarea together with an angle of intersection between commissural plane and plane containing attachment scar typically about 60°, giving shell a characteristically triangular lateral profile. *Middle Jurassic (upper Aalenian)*: England (Cotswolds).——Fig. 1876*a–z*. **P. scripta; a–c,* sectioned paratype, dorsal, lateral, anterior views, BMNH BD9381, ×20; *d*, paratype, ventral valve interior, BMNH BD9380, ×20; *e–f,* holotype, dorsal valve interior, anterior view, BMNH BD9379, ×20; *g*, paratype, typically preserved dorsal valve interior, BMNH BD9382, ×20; *h*, early juvenile dorsal valve interior, BMNH BD9383, ×35; *i–z,* paratype, serial horizontal sections, ventral valve stippled, BMNH BD9381, ×10 (Baker, 2005).

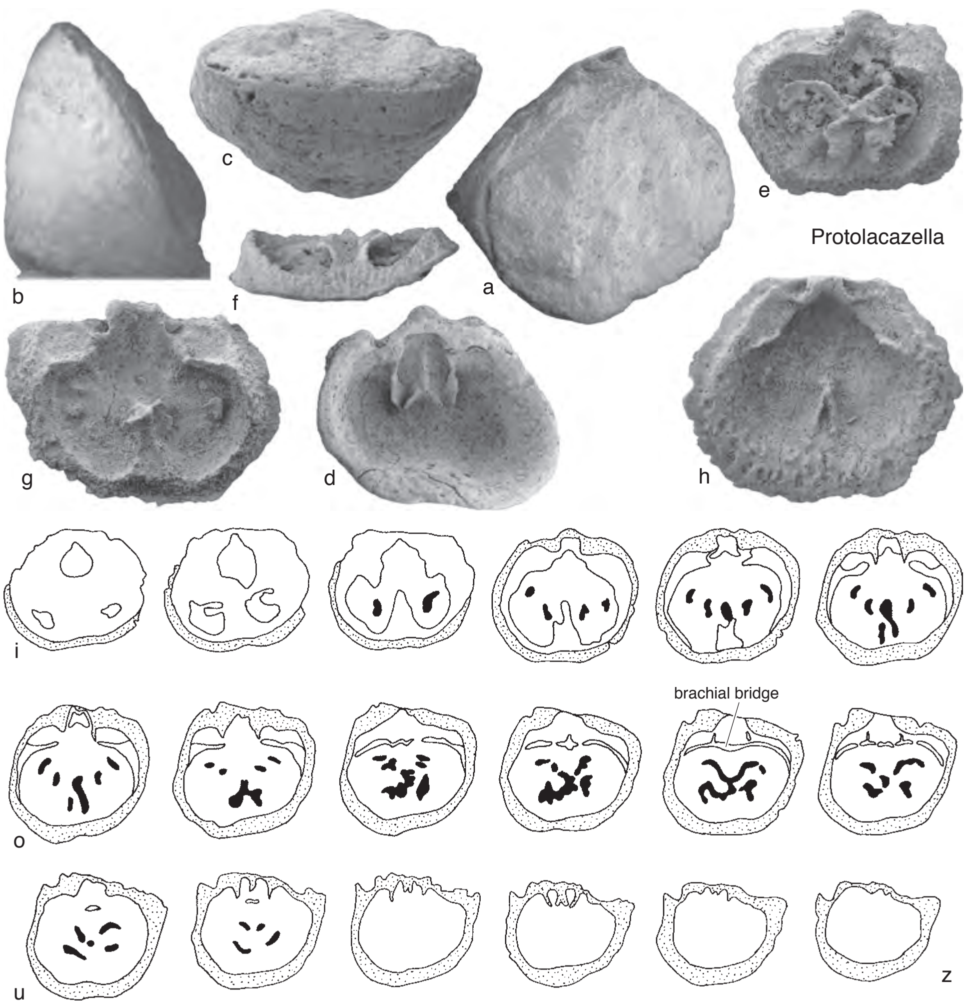


FIG. 1876. Thecideidae (p. 2797–2799).

TEREBRATULIDINA

D. E. Lee,[1] D. I. MacKinnon,[2] and T. N. Smirnova[3]

[[1]University of Otago; [2]University of Canterbury; and [3]University of Moscow]

Order TEREBRATULIDA Waagen, 1883

Suborder TEREBRATULIDINA Waagen, 1883

Superfamily DIELASMATOIDEA Schuchert, 1913

Family DIELASMATIDAE Schuchert, 1913

Campbellelasma Smirnova, 2004b, p. 24 [**C. variiforme*; OD]. Small to medium, smooth, biconvex, subpentagonal, may have slight sulcus in ventral valve; beak incurved, foramen labiate. Pedicle collar present; dental plates short, septalium resting on septum of variable height; outer hinge plates concave, crural processes wide, loop narrow. *Permian (Kazanian):* Russia (eastern Russian Platform).——Fig. 1877,*4a–j*. **C. variiforme; a–c,* holotype, dorsal, lateral, and anterior views, PIN 4898/1710, *a,* ×2, *b–c,* ×1; *d–j,* serial transverse sections 1.0, 2.0, 3.0, 3.3, 3.65, 4.05, 5.05 mm from first section, ×1 (Smirnova, 2004b).

Grigorjevaelasma Smirnova in Smirnova, Madison, & Esaulova, 2004, p. 40 [**G. rossica*; OD]. Small, smooth, ventribiconvex, elongate oval to subpentagonal. Pedicle collar present; dental plates long, inner hinge plates V-shaped, may be supported by septum, outer hinge plates slightly concave; crura long; crural bases oblique, loop 0.4 dorsal valve length, transverse band broadly arched. *Permian (Kazanian):* Russia (eastern Russian Platform).——Fig. 1877,*1a–e*. **G. rossica; a–c,* holotype, dorsal, lateral, and anterior views, PIN 4898/45, ×1; *d–e*, reconstructions of loop, ×1 (Smirnova, Madison, & Esaulova, 2004).

Gruntelasma Smirnova in Smirnova, Madison, & Esaulova, 2004, p. 50 [**G. bajtuganensis*; OD]. Small, smooth, ventribiconvex, elongate to subtrigonal, anterior commissure rectimarginate to uniplicate. Pedicle collar present; dental plates short, inner hinge plates widely arched, outer hinge plates and crural bases horizontal, crura long, loop 0.3 dorsal valve length, transverse band strongly arched. *Permian (Kazanian):* Russia (eastern Russian Platform).——Fig. 1877,*2a–e*. **G. bajtuganensis; a–c,* holotype, dorsal, lateral, and anterior views, PIN 4898/1, ×1; *d–e*, reconstructions of loop, ×1 (Smirnova, Madison, & Esaulova, 2004).

Family BEECHERIIDAE Smirnova, 2004

Sokelasma Smirnova, 2004a, p. 166 [**S. guttiformis*; OD]. Small, smooth, biconvex, rounded, anterior commissure slightly uniplicate. Dental plates variable, narrow outer hinge plates discernible in apical region of beak; septalium supported by crural plates and distinct septum; crural plates attached to valve floor, close to or separated from inner socket ridges; loop narrow, 0.4 dorsal valve length, transverse band broadly arched. Differs from *Beecheria* in biconvex valves, distinct septum, narrow outer hinge plates and position of crural plates. *Permian (Kazanian):* Russia (eastern Russian Platform).——Fig. 1877,*3a–k*. **S. guttiformis; a–c,* holotype, dorsal, lateral, and anterior views, PIN 4898/75, ×1; *d–k,* serial transverse sections 1.0, 1.4, 1.95, 2.2, 2.3, 2.9, 3.5, 3.9 mm from first section, ×1 (Smirnova, 2004a).

Family UNCERTAIN

Adygellopsis Sun & Shi in Jin & others, 1985, p. 228 [**A. pentagonalis*; OD]. Small, roundly pentagonal, biconvex, anterior commissure rectimarginate; beak massive, slightly incurved, beak ridges angular; foramen subcircular, mesothyrid to permesothyrid; deltidial plates covering delthyrium. Pedicle collar absent; dental plates inclined toward lateral wall; teeth thin, long; cardinal process obscure; hinge plates narrow; septalium shallow, small; inner socket ridges strongly developed; septum high, stout, extending to midvalve; crural process low, loop deltiform, more than 0.5 dorsal valve length, with low-arched transverse band. Differs from *Adygella* in lacking a septalium and in loop. *Upper Triassic:* China (Yunnan).——Fig. 1878,*1a–i*. **A. pentagonalis*; *a–b*, dorsal and lateral views, ×1; *c–i,* serial transverse sections 0.2, 3.9, 4.3, 4.5, 4.8, 6.9 mm from first section, ×1 (Jin & others, 1985).

?Athyrorhynchia Xu & Liu, 1983, p. 91 [**A. athyroformis*; OD]. Small to medium, smooth or with fine costellae; subpentagonal, biconvex, ventral sulcus wide, shallow; anterior commissure uniplicate; beak short, strongly incurved, concealing delthyrium. Dental plates nearly parallel; hinge plates discrete, fused with socket ridges; no median septum; loop unknown. [The status of this genus is uncertain as the loop is unknown.] *Middle Triassic:* China (Qinghai).——Fig. 1878,*2a–h*. **A. athyroformis*; *a–c*, dorsal, lateral, and anterior views, ×1; *d–h*, incomplete serial transverse sections 1.2, 1.6, 2.4, 3.1, 3.6 mm from ventral umbo, ×1 (Xu & Liu, 1983).

?Paradygella Liao & Sun, 1974, p. 352 [**P. magna*; OD]. Large, smooth, oval, biconvex; anterior commissure uniplicate; beak large, foramen large, permesothyrid. Pedicle collar thick, long; dental plates extending to valve floor; no cardinal process; hinge plates divided, septalium with median ridge;

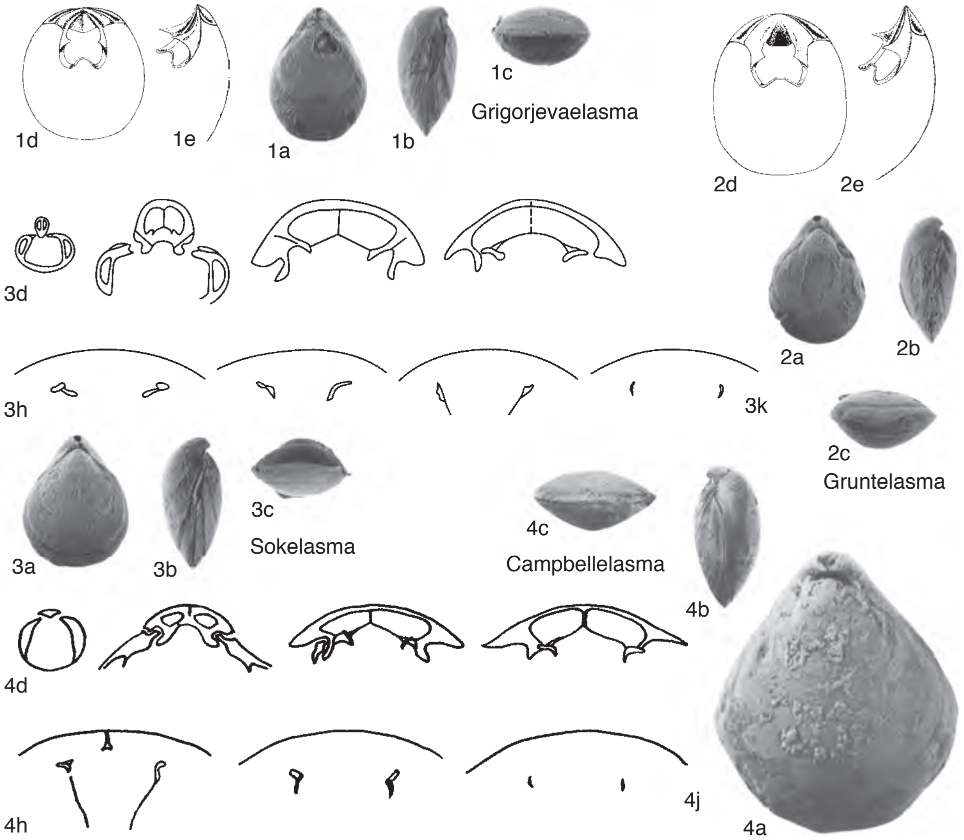


FIG. 1877. Dielasmatidae and Beecheriidae (p. 2801).

median septum long and high, loop short, deltiform. [The status of this genus is uncertain as no serial sections are available for this species.] *Middle Triassic:* China (Sichuan).——FIG. 1878,*6a–c*. **P. magna;* dorsal, lateral, and anterior views, ×1 (Liao & Sun, 1974).

?Proanadyrella XU & LIU, 1983, p. 106 [**P. circularia*; OD]. Small to medium, subcircular to oval, smooth, ventribiconvex, anterior commissure sulciplicate; beak small, incurved. Pedicle collar present; dental plates divergent, reaching lateral walls; cardinal process bilobate, hinge plates discrete, inner socket ridges well developed, crural plates attached to floor of dorsal valve; median septum present, loop long, possibly lacking ascending branches (loop may be broken). Differs from *Antezeilleria* in having median septum and sulciplicate commissure. [The status of this genus is uncertain because loop of type specimen may be broken.] *Lower Triassic:* China (Qinghai).——FIG. 1878,*3a–h*. **P. circularia*; *a–c*, dorsal, lateral, and anterior views, ×2; *d–h*, serial transverse sections 0.9, 1.8, 2.5, 3.3, 4.6 mm from ventral umbo, ×2 (Xu & Liu, 1983).

?Pseudopygoides XU, 1978, p. 303 [**P. jueyongensis*; OD]. Medium, subpentagonal, ventribiconvex; shell margin geniculate; anterior commissure rectimarginate, may have resorbed so-called keyhole; beak low, erect; foramen circular, mesothyrid; beak ridges obtusely rounded. No pedicle collar or dental plates; cardinal process may be present; dorsal septum low, short; septalium V-shaped, wide, deep; loop moderately long, deltiform. [The status of this genus is uncertain because the internal structures are not fully known.] *Upper Triassic:* Tibet.——FIG. 1878,*5a–h*. **P. jueyongensis*; *a–c*, dorsal, lateral, and anterior views, ×1; *d–h,* incomplete serial transverse sections, no distances given, ×1 (Xu, 1978).

?Thyratryaria XU & LIU, 1983, p. 92 [**T. pinguis*; OD]. Small to medium, elongate oval to pear shaped, rarely circular, strongly biconvex, smooth, inner layer of shell ornamented with irregular radial costellae, anterior commissure uniplicate or slightly sulciplicate; beak low, incurved, foramen large, incurved. Dental plates present; hinge plates narrow, divided; crural plates reaching floor of dorsal valve; loop short, not fully known. [The status of this genus is uncertain because the internal

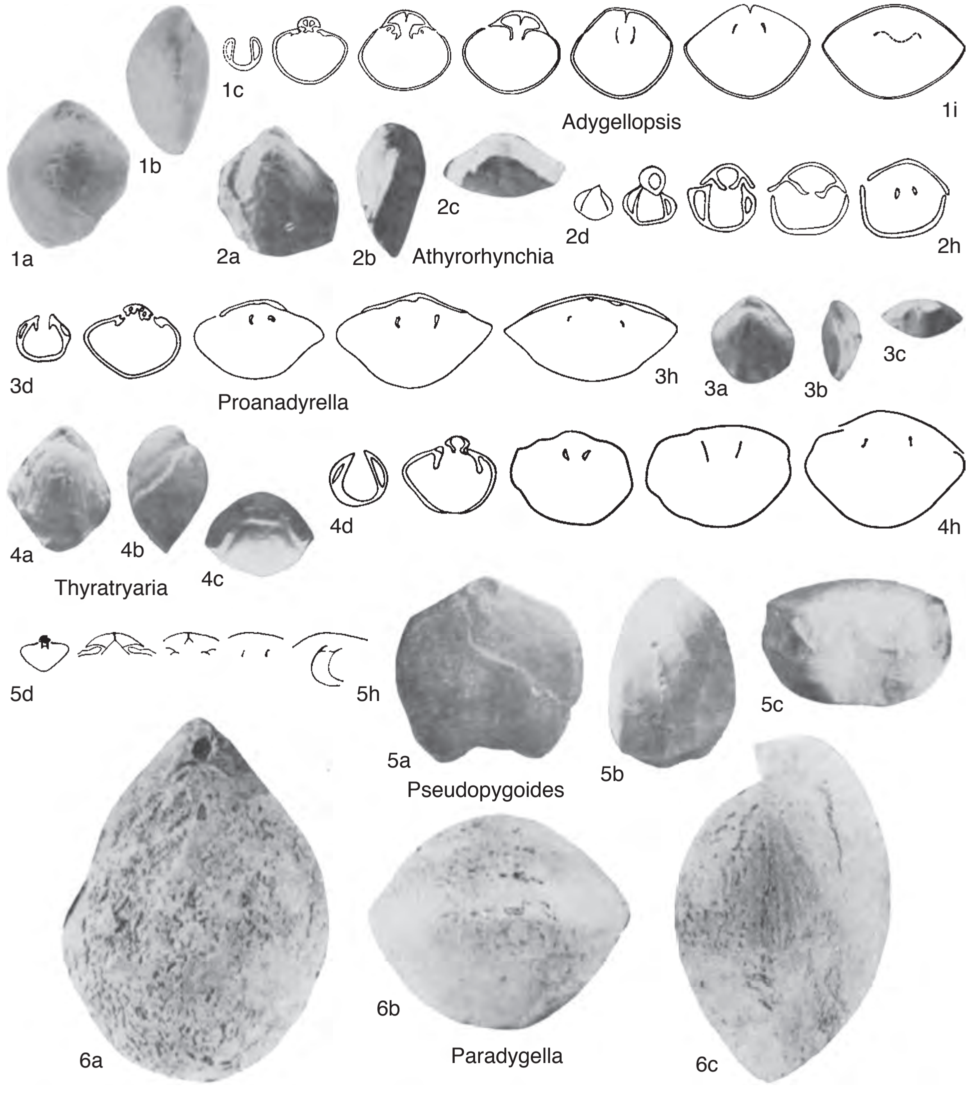


FIG. 1878. Uncertain (p. 2801–2803).

structures are not fully known]. *Middle Triassic:* China (Qinghai).——FIG. 1878,*4a–h.* * *T. pinguis*; *a–c*, dorsal, lateral, and anterior views, ×2; *d–h,* serial transverse sections 0.9, 2.0, 3.1, 4.4, 5.1 mm from ventral umbo, ×2 (Xu & Liu, 1983).

Superfamily
TEREBRATULOIDEA
Gray, 1840
Family UNCERTAIN

Almiralthyris CALZADA BADIA, 1994, p. 42 [**Terebratula sampelayoi* BATALLER, 1943, p. 33; OD]. Very large, smooth, ventribiconvex, oval to subpentagonal in outline, strongly biplicate; foramen small, permesothyrid, loop narrow, short, triangular, without crural points. *Eocene (Bartonian)*: Spain. ——FIG. 1879,*5a–d.* **A. sampelayoi* (BATALLER); *a–c,* holotype, dorsal, lateral, and anterior views, MGSB 2704, ×0.6; *d,* reconstruction of loop, ×1 (Calzada Badia, 1994).

Eichwaldithyris SMIRNOVA, 2001, p. 602 [**R. rasilis*; OD]. Medium, oval to pear shaped, anterior commissure uniplicate or biplicate; plications in anterior third; beak high, curved, foramen submesothyrid. Pedicle collar present; cardinal process low; hinge plates wide, concave; crural

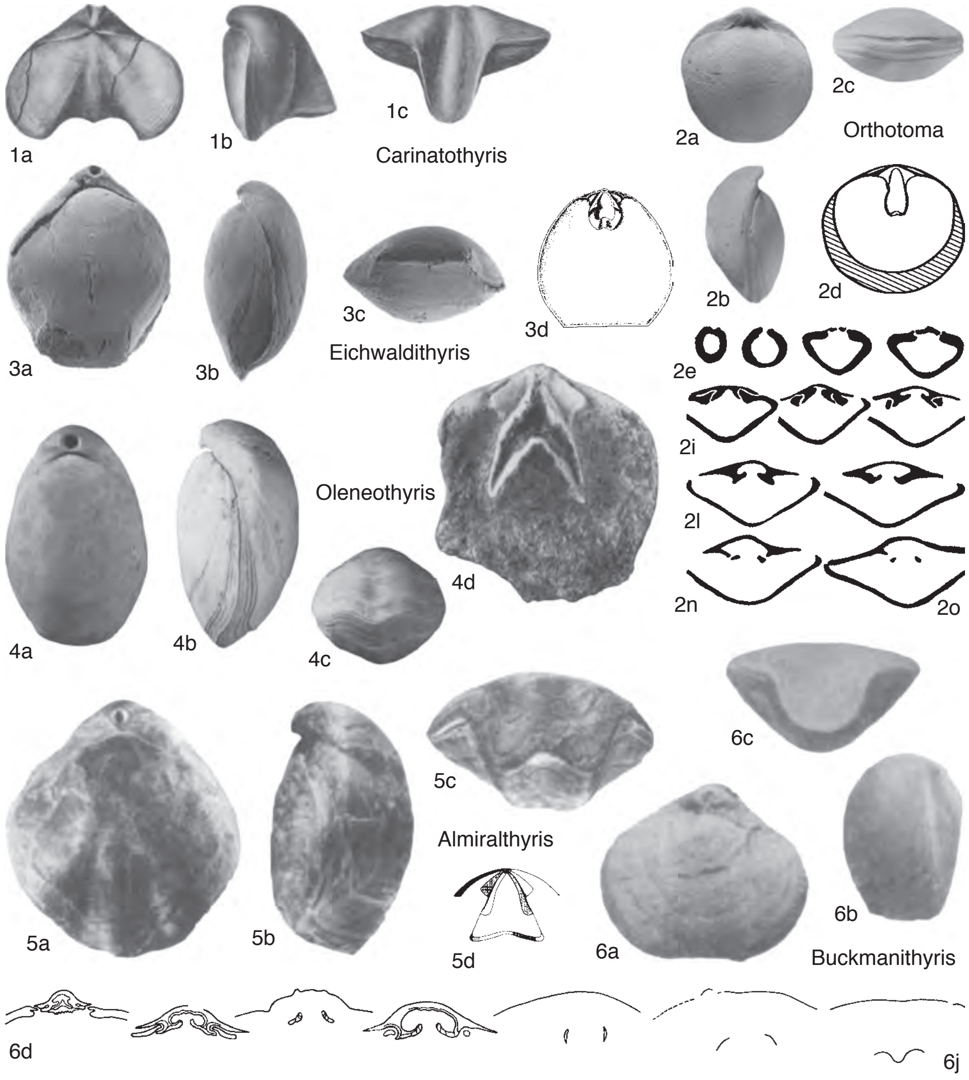


FIG. 1879. Uncertain and Orthotomidae (p. 2803–2807).

bases high, ventrally sharp and dorsally keeled; crural processes wide; loop slender, 0.25 dorsal valve length; descending branches short, transverse band arched. *Lower Cretaceous:* Crimea, Ukraine. ——FIG. 1879,*3a–d*. **R. rasilis*; *a–c,* holotype, dorsal, lateral, and anterior views, MGSB, ×1; *d,* reconstruction of loop, ×2 (Smirnova, 2001).

Oleneothyris COOPER, 1942, p. 233 [**Terebratula harlani* MORTON, 1828, p. 73; OD]. Large, smooth, elongate oval, ventribiconvex; anterior commissure uniplicate to sulciplicate; foramen large, submesothyrid, symphytium mostly concealed. Ventral valve thickened posteriorly; pedicle collar long, tubular; cardinal process large, semielliptical; crural processes large, triangular; crural bases forming ridge along inner edge of narrow, concave outer hinge plates; loop variable, 0.3 dorsal valve length, triangular, with strongly arched transverse band; some loops with long terminal points resembling those of some Jurassic loboidothyridoids. *Paleocene:* USA (New Jersey, North Carolina).——FIG. 1879,*4a–d*. **O. harlani* (MORTON), New Jersey; *a–c*, dorsal, lateral, and anterior views, ×0.5; *d,* interior of dorsal valve, ×1 (Cooper, 1983).

Superfamily LOBOIDOTHYRIDOIDEA
Makridin, 1964
Family UNCERTAIN

Aschuthyris Ovtsharenko, 1993, p. 17 [**A. aschuensis*; OD]. Medium, biconvex, anterior lateral commissures rectimarginate. Outer hinge plates slender, fused with inner socket ridges; crura wide, directed ventrally; loop approximately 0.5 dorsal valve length, flanges slender, subparallel, transverse band strongly arched with median fold. *Upper Jurassic:* southwestern Pamirs.——Fig. 1880,*2a–c*. **A. aschuensis*; dorsal, lateral, and anterior views, ×1 (Ovtsharenko, 1993).

Dhosathyris Ovtsharenko, 1993, p. 16 [**Terebratula dhosaensis* Kitchin, 1900, p. 15; OD]. Medium size, biplicate, biconvex. Cardinal process well defined; outer hinge plates horizontal with subperpendicular crural bases; crura wide, directed ventrally; loop broad, less than 0.5 dorsal valve length, transverse band thin, flanges subparallel. *Upper Jurassic:* Pamirs, India.——Fig. 1880,*3a–d*. *D. dhosaensis* (Kitchin); *a–c,* dorsal, lateral, and anterior views, ×1; *d,* reconstructions of loop, ×1 (Ovtsharenko, 1993).

Neaguithyris Georgescu, 1991, p. 242 [**N. neagui*; OD]. Medium, smooth, ventribiconvex, subpentagonal; anterior commissure sulciplicate. Cardinal process bilobate; hinge plates very thin; loop short (0.25 dorsal valve length); transverse band strongly bilobate. *Middle Jurassic (upper Bajocian–lower Bathonian):* Romania (eastern Carpathians).——Fig. 1880,*4a–i*. **N. neagui; a–c, holotype,* dorsal, lateral, and anterior views, LPB IIIb0196, ×1; *d–i,* serial transverse sections 1.2, 3.5, 5.0, 5.8, 7.5, 9.2 mm from ventral umbo, ×1 (Georgescu, 1991).

Peristerothyris Manceñido, 1983, p. 349 [**P. columbiniformis*; OD]. Very large, smooth, subcircular to subpentagonal, biconvex, anterior commissure biplicate; beak massive, incurved; foramen large, permesothyrid. Cardinal process broad, flat, crenulated; hinge plates not keeled, with a distally cuneate, virgate core and a distally clubbed, concave sheath. *Lower Jurassic (?Sinemurian, Pliensbachian):* Argentina, USA (?California).——Fig. 1880,*5a–h*. **P. columbiniformis*, Argentina; *a–c,* dorsal, lateral, and anterior views, ×0.5; *d–h,* serial transverse sections 5.9, 8.3, 9.8, 12.2, 12.7 mm from ventral umbo, ×1 (Manceñido, 1983).

Sogxianthyris Sun, 1981, p. 235 [**S. pentagonalis*; OD]. Medium, subpentagonal, unequally biconvex to nearly planoconvex; anterior commissure sulciplicate; smooth or weakly capillate; beak large, protuberant, foramen large, epithyrid. Pedicle collar ringlike; no dental plates, cardinal process low, bilobate; hinge plates divided and slightly concave; crural bases attached to outer hinge plates ventrally; loop trigonal, 0.5 dorsal valve length; terminal points long. *Middle Jurassic:* Tibet.——Fig. 1880,*6a–j*. **S. pentagonalis; a–c,* dorsal, lateral, and anterior views, ×1; *d–j,* serial transverse sections 4.9, 6.8, 8.1, 9.1, 11.8, 14.4, 16.7 mm from ventral umbo, ×1 (Sun, 1981).

Thadiqithyris Alméras, 1987, p. 189 [**T. thadiqiensis*; OD]. Medium size, biconvex, rectimarginate; lateral and anterior commissure finely multiplicate; foramen large, labiate, epithyrid; symphytium narrow; loop 0.5 dorsal valve length. *Middle Jurassic (Callovian):* Saudi Arabia, Syria.——Fig. 1880,*1a–c*. **T. thadiqiensis*, Syria; dorsal, lateral, and anterior views, ×1 (Alméras, 1987).

Superfamily DYSCOLIOIDEA
Fischer & Oehlert, 1891
Family UNCERTAIN

Buckmanithyris Tchorszhewsky, 1990, p. 33 [**B. dziruliensis*; OD]. Medium size, subpentagonal, smooth, strongly unisulcate; cardinal process small, loop very short. *Lower Jurassic*: Carpathians, Caucasus.——Fig. 1879,*6a–j*. **B. dziruliensis,* ?Carpathians; *a–c,* dorsal, lateral, and anterior views, ×1; *d–j,* serial transverse sections 1.3, 1.6, 1.85, 2.0, 2.3, 4.0, 4.8 mm from ventral umbo, ×1.5 (Tchorszhewsky, 1990).

Carinatothyris Tchorszhewsky, 1990, p. 33 [**Terebratula (Pygope) aspasia* Meneghini [Mgh], var. *carinata* Haas, 1912, p. 258; OD]. Small, smooth, subtriangular to rhomboidal; median ridge in dorsal valve, anterior commissure strongly unisulcate; loop short, rounded. *Lower Jurassic:* Italy.——Fig. 1879,*1a–c*. **C. carinata* (Haas); dorsal, lateral, and anterior views, ×1 (Tchorszhewsky, 1990).

Superfamily UNCERTAIN
Family ORTHOTOMIDAE
Muir-Wood, 1936

[Orthotomidae Muir-Wood, 1936, p. 224]

Small, smooth or rarely capillate, adult shells hypothyrid, with triangular delthyrium bordered by jugate deltidial plates below tapering, acute beak; no dental plates; loop short, deltiform. *Lower Jurassic*.

Orthotoma Quenstedt, 1869 in 1868–1871, p. 315 [**Terebratula heyseana* Quenstedt, 1869, p. 315, *non* Dunker, 1847; =*Orthotoma spinati* Rau, 1905, p. 54; SD Buckman, 1918, p. 96] [=*Orthoidea* Friren, 1876, p. 1 (type, *O. liasina,* OD)]. Ventribiconvex, becoming sulcoconvex, anterior commissure rectimarginate to unisulcate, beak ridges angular. Cardinal process minute, projecting vertically as two small ears; hinge plates in transverse section ventrally convex, dorsally inclined, tapering, not differentiated from inner socket ridges; loop short (0.3 dorsal valve length) with low arched transverse band. *Lower Jurassic:* Europe, China, ?Saudi Arabia.——Fig. 1879,*2a–d*.

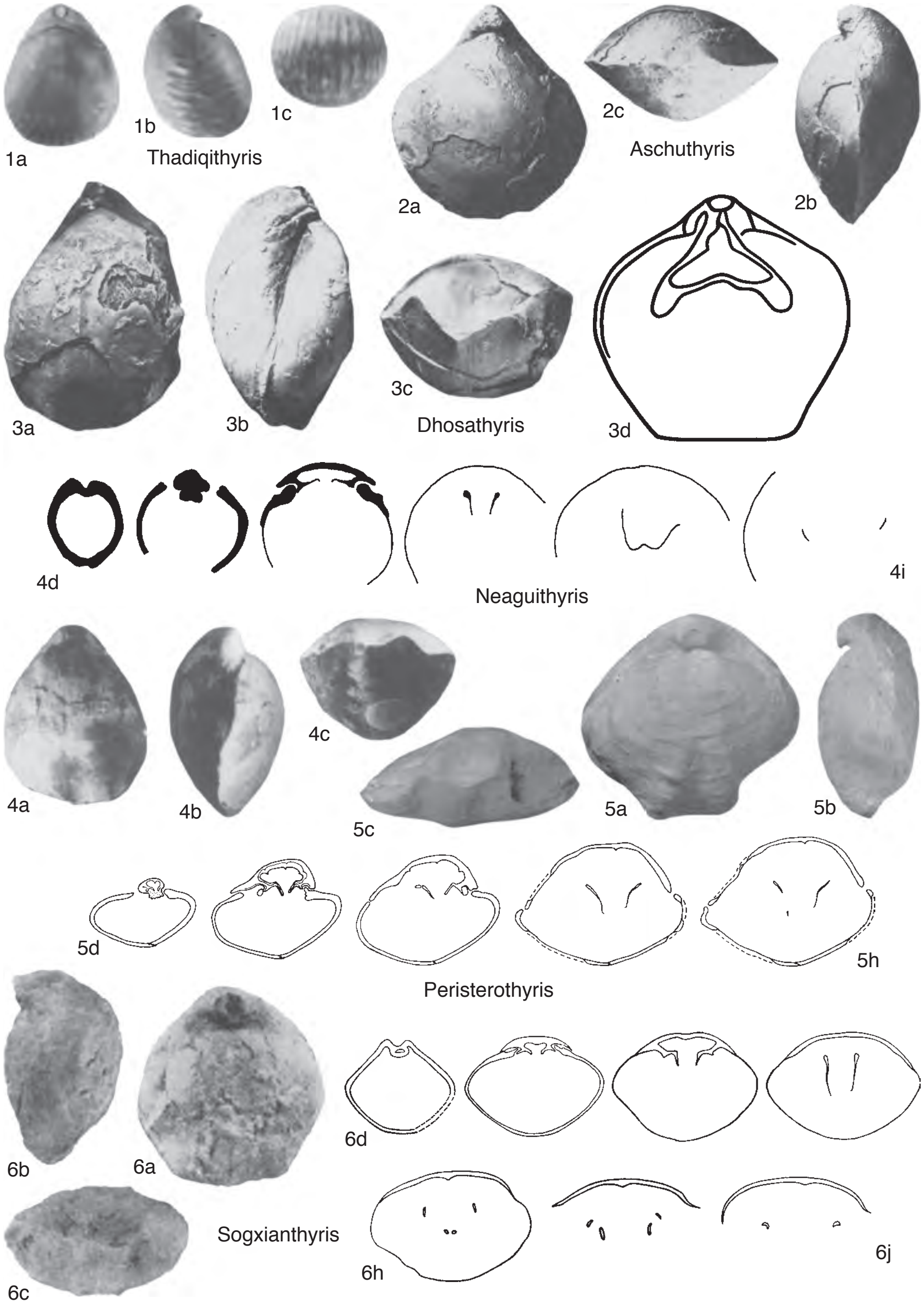


FIG. 1880. Uncertain (p. 2805).

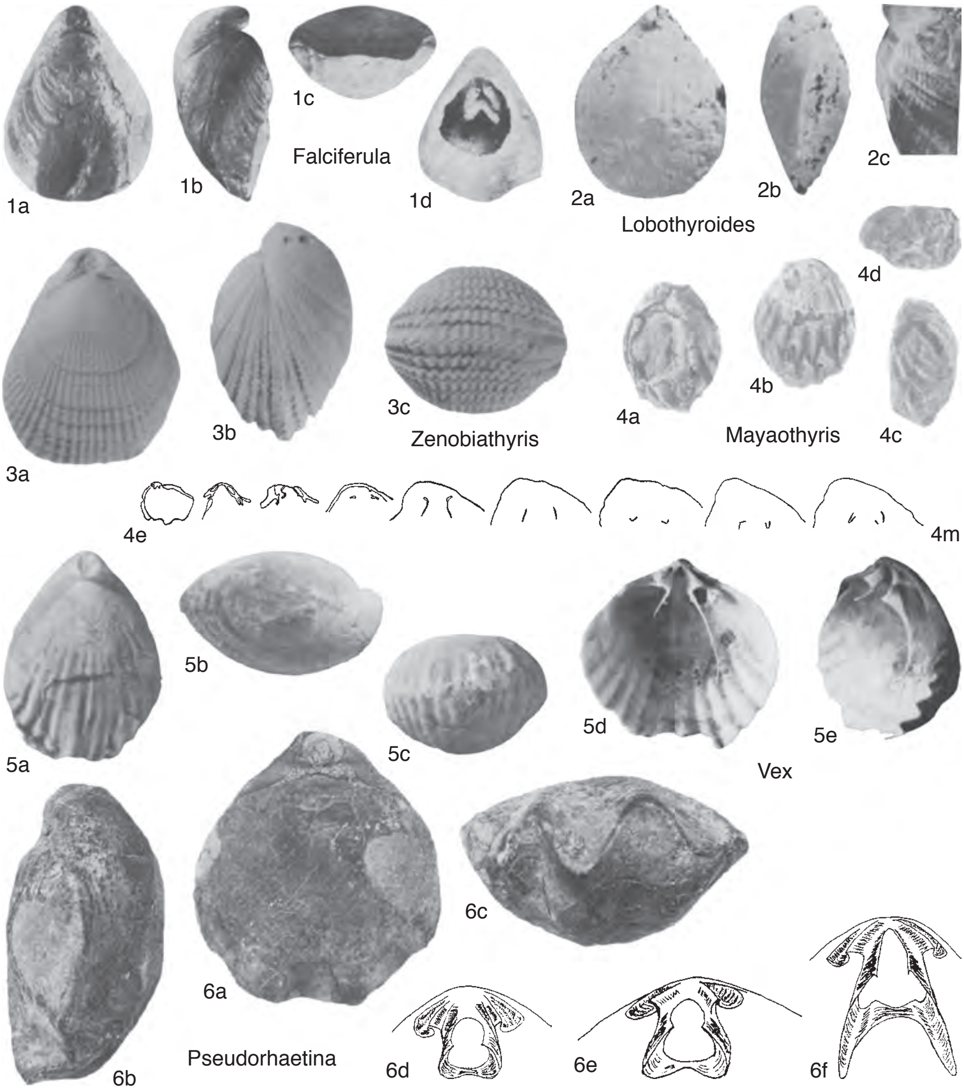


FIG. 1881. Uncertain (p. 2807–2808).

**O. spinati* (RAU), Germany; *a–c*, dorsal, lateral, and anterior views, ×2; *d*, reconstruction of loop, ×2 (Muir-Wood, 1965).——FIG. 1879,*2e–o. O. quenstedti*, Germany, serial transverse sections at 0.1 to 0.3 mm intervals, ×3 (Muir-Wood, 1965).

Superfamily UNCERTAIN
Family UNCERTAIN

Falciferula TCHOUMATCHENCO, 1987, p. 56 [**F. stoytchevi*; OD]. Medium, subtriangular, biconvex, anterior commissure broadly unisulcate or sulciplicate; foramen large. Crural bases thin, falcifer; loop narrow, 0.3 dorsal valve length, may be spinose; transverse band strongly arched. *Jurassic:* Algeria. ——FIG. 1881,*1a–d*. **F. stoytchevi; a–c,* dorsal, lateral, and anterior views, ×1; *d,* ventral view of loop, ×1 (Tchoumatchenco, 1987).

Lobothyroides XU, 1978, p. 307 [**L. striata*; OD]. Large, oval, ventribiconvex, smooth or with obscure striae laterally and anteriorly, beak short; foramen large, mesothyrid, anterior commissure rectimarginate. Pedicle collar present; dental plates absent; cardinal process small; outer hinge plates narrow, tapering; loop narrow, short (less than 0.3 dorsal valve length), transverse band strongly arched. *Upper Triassic:* southwestern China (Sichuan).——FIG. 1881,*2a–c*. **L. striata*; *a–b*, dorsal and lateral views, ×1; *c*, close up of ornament, ×2 (Xu, 1978).

Mayaothyris SUN, 1987, p. 74 [**M. typica*; OD]. Small to medium, oval, biconvex; shell ornamented with broad, sharply angular costae from umbo; foramen permesothyrid; delthyrium covered by symphytium, anterior commissure rectimarginate; no dental plates, cardinal process low; hinge plates separate, merged with inner socket ridges; crural plates united with floor of dorsal valve, slightly inclined toward midline; crural bases arising from ventral side of hinge plates; crura of *Dielasma* type; loop possibly short; other loop details unknown. [Description is based on one incomplete, now sectioned, individual.] *Lower Cretaceous (Aptian):* northern Tibet.——FIG. 1881,*4a–m*. **M. typica; a–d,* dorsal, ventral, lateral, and anterior views, ×1; *e–m*, serial transverse sections of incomplete damaged specimen 1.6, 2.9, 3.6, 4.8, 5.5, 6.4, 6.9, 7.2, 7.4 mm from ventral umbo, ×1 (Sun, 1987).

Pseudorhaetina SANDY in STANLEY & others, 1994, p. 19 [**P. antimoniensis*; OD]. Medium to large, subpentagonal, biconvex, foramen permesothyrid, anterior commissure biplicate. Hinge plates narrow, crural bases well developed; crural processes high; no median septum; juvenile loop simple deltiform; adult loop 0.5 dorsal valve length, long flanged; transverse band high arched. [The loop develops in characteristic terebratuloid fashion from simple extensions of the crura, but the adult loop resembles that of loboidothyridoids.] *Upper Triassic (Norian):* Mexico.——FIG. 1881,*6a–f*. **P. antimoniensis*; *a–c*, dorsal, lateral, and anterior views, ×2; *d–e*, reconstruction showing loop development, ×5; *f*, reconstruction showing loop development, ×2 (Sandy, 1998).

Vex HOOVER, 1979, p. 9 [**Terebratula semisimplex* WHITE, 1879, p. 108; OD]. Small to medium, subtriangular to subpentagonal, ventribiconvex, smooth posteriorly, variably multicostate anteriorly; anterior commissure rectimarginate to slightly uniplicate, beak erect to incurved, foramen small, deltidial plates disjunct. Distinct pedicle collar; no dental plates; cardinal process well developed, bilobate; outer hinge plates broad, planar; no inner hinge plates; no median septum; loop delicate, with large crural processes; descending lamellae slender; loop not fully known. *Lower Triassic:* USA (Idaho).——FIG. 1881,*5a–e*. **V. semisimplex* (WHITE); *a–c*, lectotype, dorsal, lateral, and anterior views, USNM 8190a, ×2 (Hoover, 1979); *d–e*, ventral and lateral views of cardinalia and broken loop, ×2 (Cooper, 1983).

Zenobiathyris CRAIG, 1999, p. 427 [**Z. mutabilis*; OD]. Small to medium, subpentagonal, biconvex, capillate, rugose, anterior commissure rectimarginate to uniplicate; foramen large, mesothyrid, deltidial plates conjunct. Pedicle collar narrow, sessile; cardinal process delicate; no median septum; crural base fused to inner socket ridge, no hinge plates discernible; loop short, thin; transverse band short, wide, with median fold. No illustration of loop available. *Upper Cretaceous (Santonian–Maastrichtian):* Western Australia (Perth Basin, Carnarvon Basin).——FIG. 1881,*3a–c*. **Z. mutabilis;* holotype, dorsal, lateral, and anterior views, WAM83.3148a, ×2 (Craig, 1999).

Suborder TEREBRATELLIDINA Muir-Wood, 1955

Superfamily ZEILLERIOIDEA Allan, 1940

Family ZEILLERIIDAE Allan, 1940

Subfamily ZEILLERIINAE Allan, 1940

Paraulacothyris SUN & ZHANG, 1998, p. 267 [**P. qipuqiapuensis*]. Small, smooth, globose, rounded subpentagonal, smooth, strongly sulcate; beak low, erect, beak ridges rounded, palintrope small, foramen small, circular and permesothyrid; delthyrium covered by symphytium. Dental plates parallel; pedicle collar short. Hinge plates thick, septalium narrow and shallow, supported by stout and high median septum that extends almost to anterior margin; crural bases attaching to dorsal side of hinge plates; crura hamiform; crural processes not developed; cardinal process poorly developed; loop teloform, extending about 0.75 valve length, with narrow descending lamellae, broad ascending lamellae, and wide, saddle-shaped transverse band. [SUN & ZHANG (1998) assigned *Paraulacothyris* to the family Laqueidae, subfamily Aulacothyropsinae; however, similarities with *Bakonyithyris* VOROS, 1983, and *Aulacothyris* DOUVILLÉ, 1879, particularly in sulcation and teloform loop, suggest assignment to the subfamily Zeilleriinae is more appropriate.] *Lower Jurassic:* China (Karakorum region).——FIG. 1882,*3a–n*. **P. qipuqiapuensis*; *a–c*, dorsal, lateral, and anterior views, ×1; *d–n,* serial transverse sections 1.0, 1.7, 2.7, 4.0, 4.4, 5.1, 5.7, 6.1, 8.0, 8.5, 9.0 mm from ventral umbo, ×1 (Sun & Zhang, 1998).

Pictetella RADULOVIĆ, RADULOVIĆ, & RABRENOVIĆ 2002, p. 790 [**P. serbica;* OD]. Small, 7 to 8 strong costae, moderately biconvex, elongate oval to subcircular, anterior commissure multiplicate. Beak suberect to erect, beak ridges sharp and short, defining narrow palintrope; foramen large, mesothyrid. Dental plates lamellar and gently curved. Cardinal process not developed; septalium well developed, concave posteriorly, broadening and shallowing anteriorly, supported by high median septum; outer hinge plates buttressing inner socket ridges, inner hinge plates thin and anteriorly subhorizontal. Loop teloform, thin and very long with narrow descending and wide ascending branches. [RADULOVIĆ, RADULOVIĆ, & RABRENOVIĆ (2002) assigned *Pictetella* to family Dallinidae, subfamily Gemmarculinae; on the basis of the revised diagnoses of both family Dallinidae and

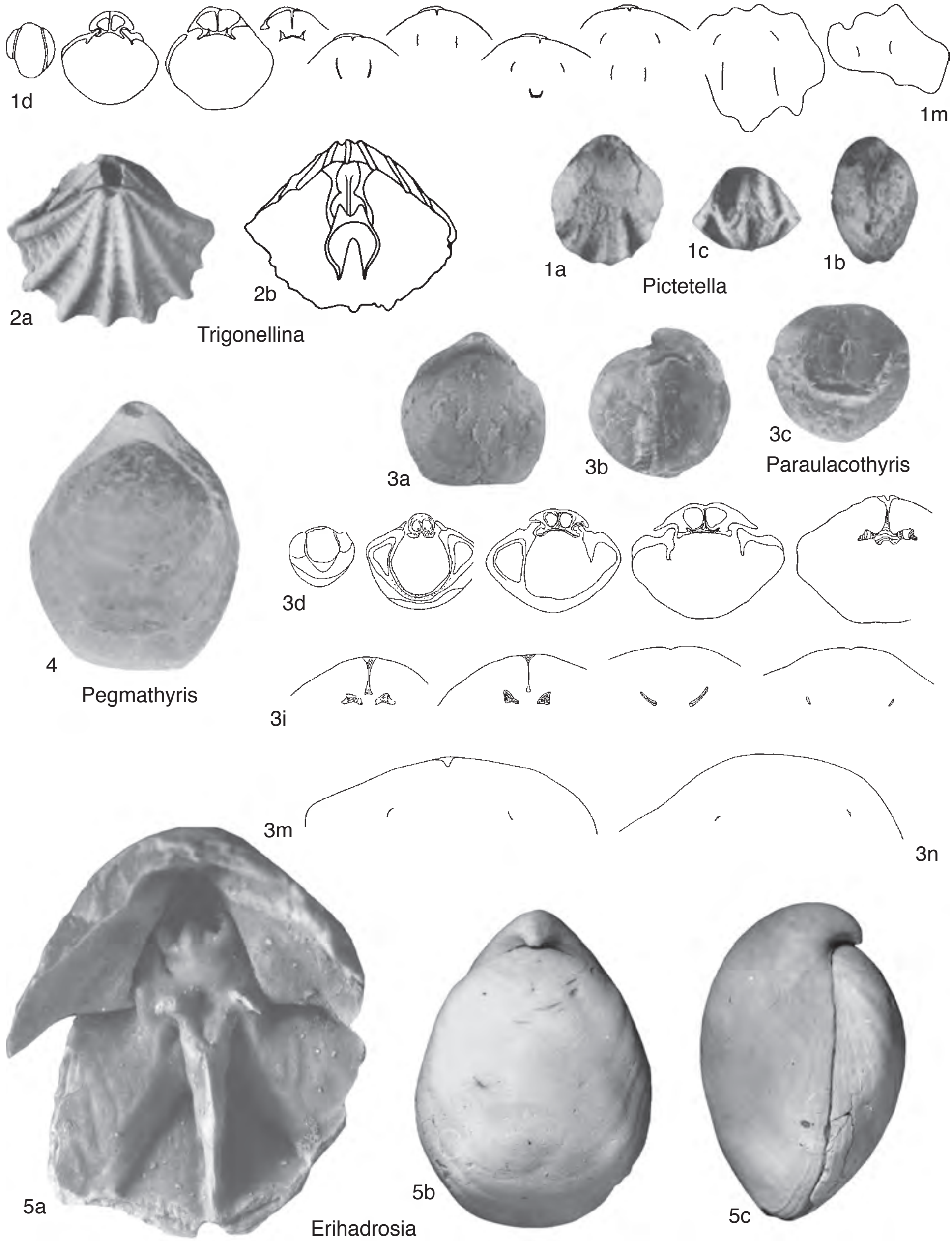


Fig. 1882. Zeilleriidae, Uncertain, Terebratellidae, and Dallinidae (p. 2808–2810).

subfamily Gemmarculinae (MacKinnon & Lee, 2006), *Pictetella* is now reassigned to the family Zeilleriidae.] *Lower Cretaceous (Barremian, ?Valanginian):* Serbia, ?Switzerland.——Fig. 1882,*1a–m*. *P. serbica; Barremian, eastern Serbia; *a–c*, dorsal, lateral, and anterior views, Museum d'Histoire Naturelle, Geneva, VR76/1, ×1; *d–m*, serial transverse sections 0.4, 1.7, 2.2, 2.5, 3.2, 3.6, 4.5, 5.0, 7.0, 9.0 mm from ventral umbo, ×2 (Radulović, Radulović, & Rabrenović, 2002).

Superfamily KINGENOIDEA Elliott, 1948

Family UNCERTAIN

Trigonellina Buckman, 1907, p. 342 [**Terebratulites pectunculus* von Schlotheim, 1820, p. 272; OD]. Small, transverse, shell thick, scaly, ornamented by several well-spaced, rounded, opposite carinae, foramen with conjunct deltidial plates; hinge line nearly strophic; small median septum in ventral umbo. Cardinalia with inner socket ridges prominent, cardinal process small, small cardinal platform buttressed by median septum extending to midvalve, loop small, diploform. *Upper Jurassic:* Europe.——Fig. 1882,*2a–b*. **T. pectunculus* (von Schlotheim), Germany; *a,* dorsal view; *b,* drawing of dorsal valve interior, ×4 (adapted from von Zittel, 1870).

Superfamily TEREBRATELLOIDEA King, 1850

Family TEREBRATELLIDAE King, 1850

Subfamily UNCERTAIN

Erihadrosia Hiller & MacKinnon, 2000, p. 76 [**Stethothyris epsilon* Allan, 1940, p. 287; OD]. Very large, smooth, elongate oval; ventribiconvex, anterior commissure rectimarginate to slightly unisulcate; beak slender, strongly incurved; foramen small, mesothyrid; cardinal area wide, low to hidden, convex to concave; shell strongly thickened posteriorly, but thin anteriorly. Cardinal process very large, cuplike; socket ridges, crural bases, and hinge plates becoming fused to restrict hinge trough; median septum high, bifurcating posteriorly to join with cardinalia posterior of crura, becoming thicker. *Neogene (lower Miocene–middle Miocene):* New Zealand.——Fig. 1882,*5a–c*. **E. epsilon* (Allan); *a–b,* dorsal and lateral views, ×0.5; *c,* interior view of broken conjoined valves, ×0.5 (Hiller & MacKinnon, 2000).

Family DALLINIDAE Beecher, 1893

Subfamily DALLININAE Beecher, 1893

Pegmathyris Hatai, 1938, p. 225 [**Dallina miyatokoensis* Hatai, 1936b, p. 315; OD]. Similar to *Dallina* but differing in thicker shell, rectimarginate folding, high symphytium, straighter and stronger beak, strong cardinal process, stronger median septum, inner hinge plate horizontal instead of inclined. *Miocene:* Japan.——Fig. 1882,*4*. **P. miyatokoensis* (Hatai); dorsal view, ×1 (Elliott & Hatai, 1965).

Superfamily UNCERTAIN

Family UNCERTAIN

Antigoniarcula Elliott, 1959, p. 146 [**Argiope perrieri* Eudes-Deslongchamps, 1853, p. 5; OD]. Small, transverse, alate, hinge line strophic; test costate and scaly; foramen large; deltidial plates narrow. Pedicle collar present; cardinal process small, hinge plates small, delimited by inner socket ridges, supported anteriorly by very short, thin median septum, crura thin and delicate, loop angular, apparently teloform, anteriorly produced into sharp points [The loop reconstruction is uncertain in this genus.] *Lower Jurassic:* Western Europe.——Fig. 1883,*1a–c*. **A. perrieri* (Eudes-Deslongchamps), France; *a–b*, dorsal and ventral valve views, ×2; *c*, dorsal valve interior showing loop, reconstructed, ×2 (Elliott, 1965).

Eogryphus Hertlein & Grant, 1944, p. 88 [**E. tolmani*; OD]. Medium, smooth, subcircular to ovate, ventribiconvex; dorsal valve with shallow median sulcus, anterior commissure rectimarginate to unisulcate; beak short, slightly incurved, foramen very small, permesothyrid; deltidial plates conjunct; thick dorsal median septum present; other internal characters unknown. *Eocene:* USA (California).——Fig. 1883,*5*. **E. tolmani*; holotype, dorsal view, UCLA 6203, ×1 (Hertlein & Grant, 1944).

Gwyniella Johansen, 1987, p. 26 [**G. persica*; OD]. Minute, smooth, subcircular to subpentagonal in outline, resupinate to biconvex; beak very low, recessed; foramen hypothyrid. Hinge weak, brachidium poorly developed, consisting of short, delicate crura and short, high, pointed septal pillar; lophophore probably schizolophous. *Paleocene (lower Danian):* Denmark.——Fig. 1883,*3a–c*. **G. persica; a*, holotype, dorsal view, MGUH 16953, ×10; *b*, interior of ventral valve, ×10, *c*, interior of dorsal valve, ×10 (Johansen, 1987).

Hercothyris Cooper, 1979, p. 25 [**H. borroi*; OD]. Medium, pentagonal to oval, ventribiconvex, smooth to faintly costellate in posterolateral regions, uniplicate; foramen large, mesothyrid, deltidial plates conjunct. No dental plates; ventral interior with strong median septum extending to midvalve. Cardinalia consisting of strong socket ridges fused to crural bases; no outer hinge plates; cardinal process small and transverse; dorsal median septum long, bladelike, triangular; loop probably long, possibly teloform. *Eocene:* Cuba.——Fig. 1883,*2a–f*. **H. borroi; a–c*, holotype, dorsal, lateral, and anterior views, USNM 549396a, ×1; *d*, dorsal interior, ×1; *e*, transverse section showing dorsal median septum extending to ventral valve, ×2; *f*, transverse section 10 mm anterior to beak, showing dorsal septum tapering anteriorly, ×2 (Cooper, 1979).

Holobrachia Zezina, 2001b, p. 66 [**H. vietnamica*; OD]. Medium, biconvex, smooth, subcircular to subpentagonal, anterior commisure unisulcate, deltidial plates conjunct; foramen small, submesothyrid, beak short, erect. Dental plates curved and partially obscured by shell thickening in gerontic specimens; cardinalia prominent, with small cardinal process located posteromedianly between stout inner hinge plates; cardinalia uniting anteriorly with median septum that extends for 0.33 valve length. Adult loop modified trabecular,

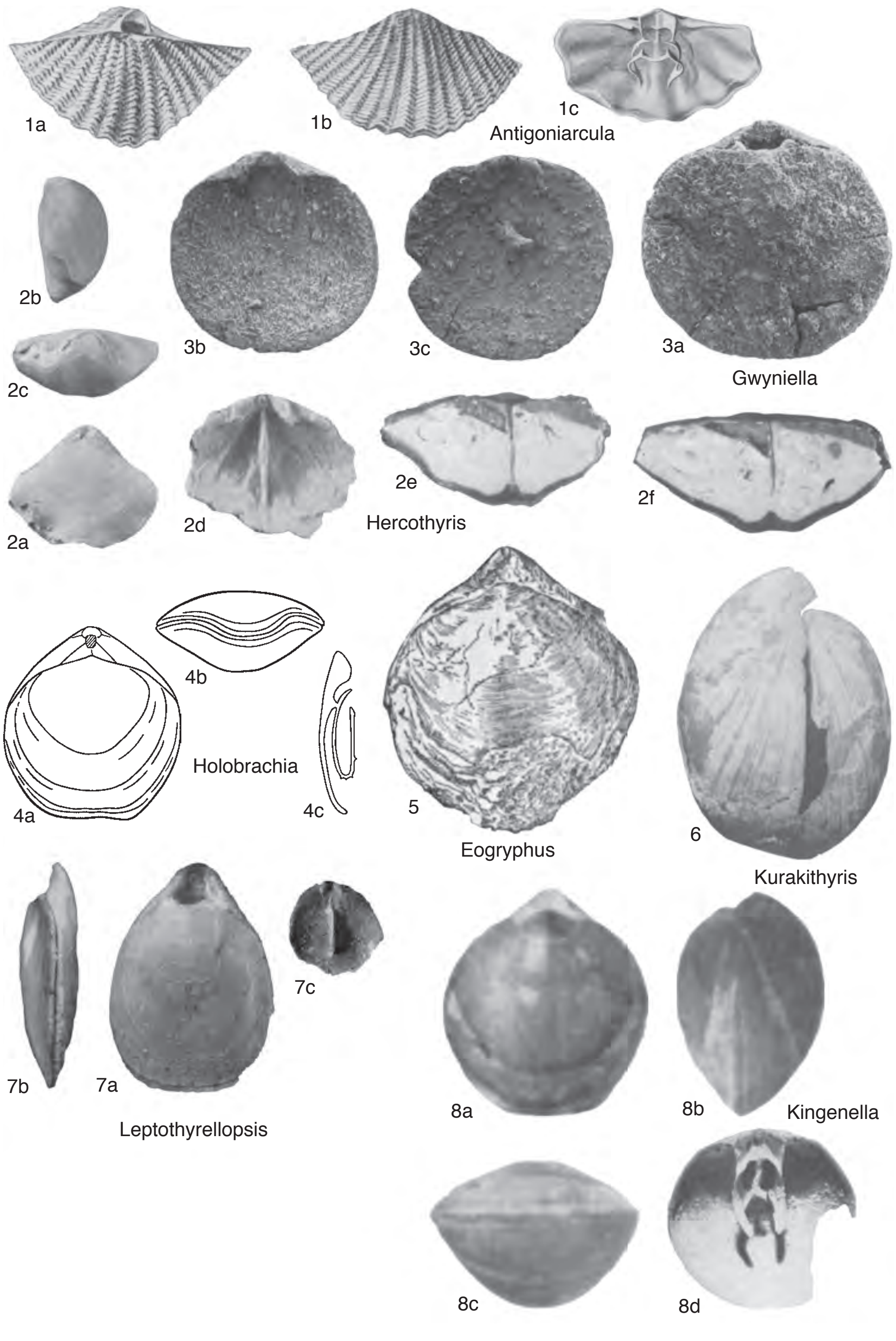


FIG. 1883. Uncertain (p. 2810–2812).

lacking crura. *Holocene:* off Vietnam.——FIG. 1883,*4a–c*. **H. vietnamica*; *a–b,* holotype, dorsal and anterior views, IO N XI-52-13/1, ×2; *c*, drawing of loop, ×2 (Zezina, 2001b).

Kingenella POPIEL-BARCZYK, 1968, p. 72 [**K. kongieli*; OD]. Small to medium, subcircular to oval in outline, smooth or slightly capillate, strongly biconvex, rectimarginate; beak ridges weak, beak obtuse, generally truncated but may be recurved; deltidial plates disjunct, foramen hypothyrid. Ventral valve with short pedicle collar, hinge teeth small, thick; no dental plates; cardinal process vestigial, outer and inner hinge plates fused to produce a flat platform attached to very long median septum; crura short, loop trabecular, strongly spiculate. *Upper Cretaceous*: Poland, Belgium, Ukraine. ——FIG. 1883,*8a–d. *K. kongieli,* Maastrichtian, Poland; *a–c*, holotype, dorsal, lateral, and anterior views, MZ VIII Bra. 411/7, ×2; *d*, dorsal valve interior, ×2 (Popiel-Barczyk, 1968).

Kurakithyris HATAI, 1946, p. 98 [**K. quantoensis*; OD]. Biconvex, rectimarginate to unisulcate, foramen possibly permesothyrid, deltidial plates conjunct, median ridge low; hinge teeth weak, with ventrally recessive dental plates, no median ridge in ventral valve; pedicle collar indistinct. Cardinalia weak, divided into inner and outer hinge plates by swollen bases of crural processes, inner hinge plate troughlike, supported by median septum, excavated beneath; descending branches attached to median septum by short connecting bands in young but becoming free in adult. [The status of this genus is doubtful. It is based on a single specimen that was said to have no loop preserved (HATAI, 1948).] *Pliocene:* Japan——FIG. 1883,*6*. **K. quantoensis*; lateral view, ×1 (Hatai, 1965c).

Leptothyrellopsis BITNER & PISERA, 1979, p. 82 [**L. polonicus*; OD]. Minute, shell smooth, elongate oval, flatly biconvex, anterior commissure rectimarginate, beak erect, foramen large, subtriangular, hypothyrid, deltidial plates narrow. No pedicle collar; inner socket ridges high; high, platelike septal pillar in dorsal valve. *Upper Cretaceous:* Poland, Denmark.——FIG. 1883,*7a–c*. **L. polonicus*, Poland; *a–b*, holotype, dorsal and lateral views, ×10; *c*, dorsal valve interior, ×10 (Bitner & Pisera, 1979).

Luppovithyris LOBATSCHEVA, 1990, p. 100 [**L. ovalis*; OD]. Medium, biconvex, elongate-oval or rounded-pentagonal, prominently costate around commissure, rectimarginate to commonly uniplicate with weakly developed fold and sulcus; beak short, erect, beak ridges rounded, foramen small, mesothyrid. Dental plates short, ventrally divergent; pedicle collar present. Inner socket ridges fused to massive hinge plates, inner hinge plates long, well developed; septalium broad, buttressed by high, wedgelike septum extending for about 0.33 length of dorsal valve; cardinal process present; crural bases prominent dorsally; loop teloform. [For discussion of problems associated with this genus, see LEE & SMIRNOVA, 2006, *Glosseudesia,* p. 2062.] *Lower Cretaceous (Neocomian)*: Turkmenistan.——FIG. 1884,*4a–n*. **L. ovalis*; *a–c,* holotype, dorsal, lateral, and ventral views, ×1; *d–n,* serial transverse sections 0.6, 1.4, 2.0, 3.1, 3.9, 4.3, 4.6, 5.3, 6.15, 7.3, 11.7 mm from ventral umbo, ×1 (Lobatscheva, 1990).

Lutetiarcula ELLIOTT, 1954, p. 727 [**L. perplexa*; OD]. Small, biconvex, solid, strong brachial cardinalia, cardinal process low, median septum well developed, extending nearly to anterior margin; curved lateral brachial ridges on valve floor. *Eocene:* France.——FIG. 1884,*2a–b*. **L. perplexa; a,* dorsal valve interior, ×5; *b*, posterior view of dorsal valve interior, ×5 (Elliott, 1954).

Magas J. SOWERBY, 1816 in 1815–1818, p. 39 [**M. pumilus* (illustrated in FAUJAS, 1798, pl. 26,*6*); OD; =*Terebratulites chitoniformis* VON SCHLOTHEIM, 1813, p. 113 (see WIND, 1954, p. 79)]. Small, smooth, planoconvex, unisulcate, beak strongly incurved, deltidial plates narrow, triangular, beak ridges sharp. Ventral interior with constricted beak area, hinge teeth with swollen bases, short, low median ridge tapering anteriorly and posteriorly with deep muscle scars. Cardinalia wide, inner socket ridges thick, sunken median cardinal platform with small cardinal process raised on this; septalium but tressing cardinalia and rising very high as anteriorly directed pillar, crura short, descending branches narrow, straight, broadly attached to septum beneath two posteriorly directed curved lamellae, loop annular; spiculate. *Upper Cretaceous:* Europe.——FIG. 1884,*1a–e*. **M. chitoniformis* (VON SCHLOTHEIM); *a–b,* dorsal and lateral views, ×2; *c–d,* interior views of ventral and dorsal valve with reconstructed loop, ×4.2; *e,* lateral view of reconstructed loop, ×2 (Elliott & Hatai, 1965).

Miogryphus HERTLEIN & GRANT, 1944, p. 95 [**M. willetti*; OD]. Medium, smooth or with few anterior radial plications; subpentagonal to ovate, biconvex with low dorsal median fold, anterior commissure rectimarginate to unisulcate; foramen large, possibly mesothyrid; symphytium present; dorsal median septum present; other internal characters unknown. *Miocene:* USA (California).——FIG. 1885,*3a–c*. **M. willetti*; holotype, dorsal, ventral, and anterior views, CAS 7361, ×1 (Hertlein & Grant, 1944).

Praeneothyris KATZ, 1962, p. 143 [**P. darvaensis*; OD]. Large, subcircular, smooth, rectimarginate, beak erect, strongly incurved, foramen minute, mesothyrid. Hinge teeth large, cardinal process and dorsal median septum thickened; ventral septum may be present; loop teloform. *Upper Cretaceous:* Tadzhikistan, Caucasus, Bulgaria, India, Madagascar.——FIG. 1885,*4a–d*. **P. darvaensis,* Tadzhikistan; *a–c*, dorsal, lateral, and anterior views, ×1; *d*, reconstruction of loop, ×1 (Katz, 1962).

Rhynchora DALMAN, 1828, p. 135 [**Terebratula costata* NILSSON, 1827, p. 37; OD; =*Anomites costatus* WAHLENBERG, 1821, p. 62; *Anomia pectinata* LINNAEUS, 1758, p. 701]. Large, thick shelled,

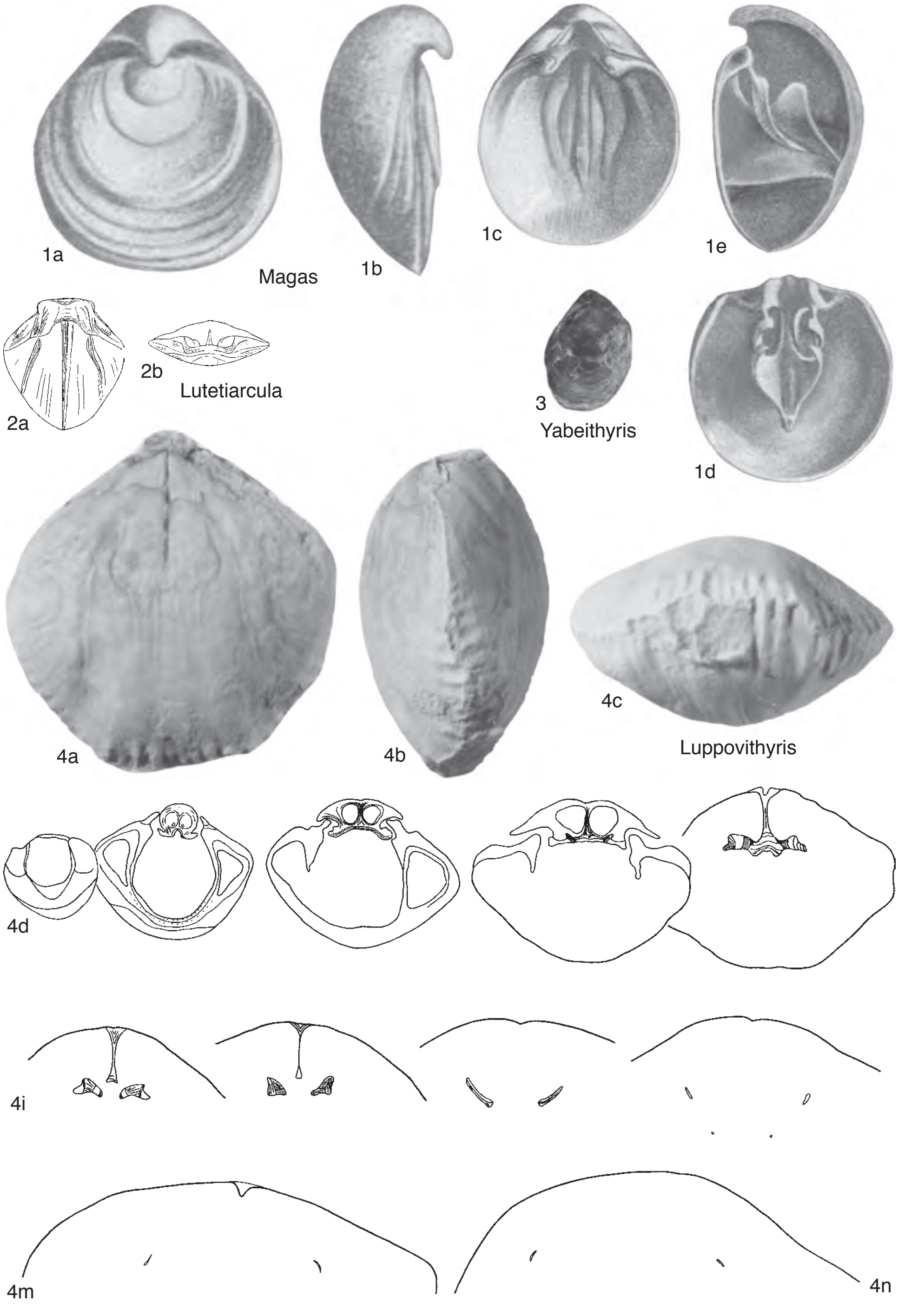


FIG. 1884. Uncertain (p. 2812–2816).

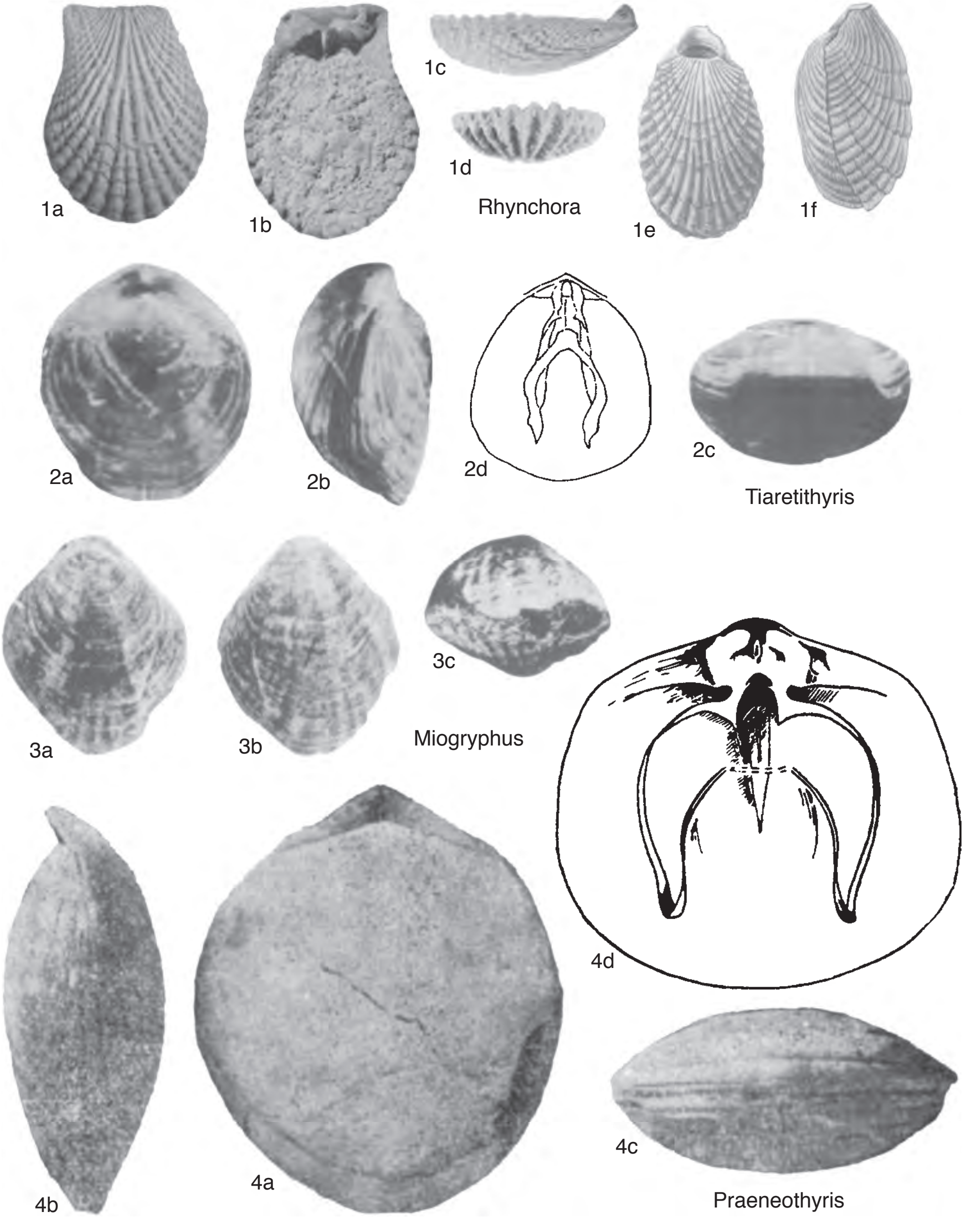


FIG. 1885. Uncertain (p. 2812–2816).

ventribiconvex, coarsely costate, unisulcate; foramen very large, small deltidial plates; hinge teeth large, widely separated, short, low median ridge; cardinalia thick, rounded, socket ridges thick and fused with cardinal platform; cardinal process a large, slightly raised median surface area on platform, hollows under cardinal platform beneath crural processes, median septum thin, supporting cardinalia, high posteriorly and extending to midvalve; loop unknown. *Upper Cretaceous:* northwestern Europe.——FIG. 1885,*1a–f.* **R. pectinata* (LINNAEUS), Sweden; *a–d*, lectotype, exterior, interior, lateral, and anterior views of dorsal valve, Linnean Collection, Linnean Society of London, ×1 (Brunton, Cocks, & Dance, 1967); *e–f,* dorsal and lateral views, ×1 (Elliott & Hatai, 1965).

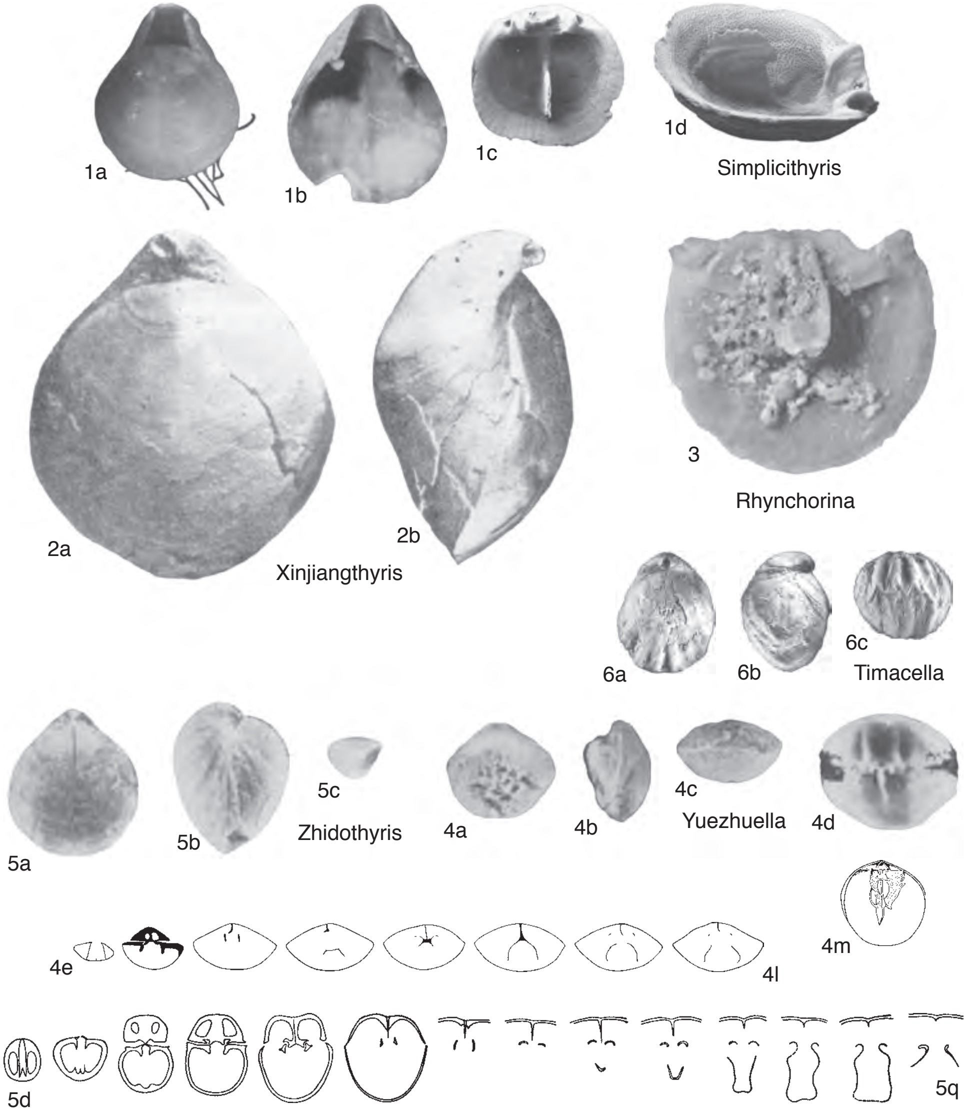


FIG. 1886. Uncertain (p. 2815–2816).

Rhynchorina OEHLERT, 1887, p. 1326 [**Anomites spathulatus* WAHLENBERG, 1821, p. 62; OD]. Similar to *Rhynchorina*, but differing in smooth exterior, cardinalia with very wide concave outer hinge plates, marked crural bases with convex inner hinge plates arching over septum and meeting in median ridge, which runs back to cardinal process, loop similar to that of *Magas*. *Upper Cretaceous:* northwestern Europe.——FIG. 1886,*3*. **R. spathulata* (WAHLENBERG); interior of dorsal valve, ×5 (Elliott & Hatai, 1965).

Simplicithyris ZEZINA, 1976b, p. 101 [**S. kurilensis*; OD]. Small, smooth, slightly biconvex, rectimarginate to slightly unisulcate; foramen permesothyrid, deltidial plates narrow; pedicle collar broad, dental plates strong; median septum subrectangular; no cardinal process, crura, brachial loop, or spicules. Differs from *Amphithyris* in possession of dental plates and permesothyrid foramen and from *Pumilus* in possession of dental plates, smooth inner surface, and lack of spicules. *Holocene:* northwestern Pacific (Kurile-Kamchatka region).——FIG. 1886,*1a–d*. **S. kurilensis*; *a,* holotype, dorsal view, IO XI-52-1, ×4; *b*, interior of ventral valve, ×4; *c–d*, interior of dorsal valve, ×4 (Zezina, 1976b).

Tiaretithyris TCHOUMATCHENCO, 1986, p. 113 [**T. tiaretensis*; OD]. Small to medium, smooth, subcircular to subpentagonal, ventribiconvex, commissure broadly uniplicate; foramen small, circular, mesothyrid. Dental plates well developed; cardinal process present or absent; septum long, crural bases short, adult loop teloform. Differs from *Kachathyris* in lacking capillae. *Upper Jurassic:* Algeria.——FIG. 1885,*2a–d*. **T. tiaretensis*; *a–c*, holotype, dorsal, lateral, and anterior views, ×1; *d*, reconstruction of loop, ×1 (Tchoumatchenco, 1986).

Timacella RADULOVIĆ & RADULOVIĆ, 2002, p. 405 [**Waldheimia (Zeilleria) timacensis* ANTHULA, 1903, p. 50; OD]. Medium size, biconvex, semi-ribbed, outline elongate oval to rarely subcircular; beak small, erect with mesothyrid circular foramen; fold and sulcus not developed; anterior commissure rectimarginate, crenulate; internal characters as in *Psilothyris*. *Cretaceous (upper Barremian):* Carpatho-Balkanides, eastern Serbia.——FIG. 1886,*6a–c*. **T. timacensis* (ANTHULA); neotype, dorsal, lateral, and anterior views, RGF VR 25/15, ×1 (Radulović & Radulović, 2002).

Xinjiangthyris SUN & WANG, 1984, p. 95 [**X. ovalis*; OD]. Large, transversely oval, rectimarginate, smooth, planoconvex to biconvex; beak slightly incurved, foramen mesothyrid, delthyrium covered with henidium; beak ridges angular. Teeth large, with swollen bases; no dental plates; cardinalia strong, massive; cardinal process high, bulbous, with bilobate myophore; hinge plates thick, united with and supported by stout septum; septalium short; loop teloform. *Upper Cretaceous:* China (Xinjiang).——FIG. 1886,*2a–b*. **X. ovalis;* holotype, dorsal and lateral views, ×1 (Sun & Wang, 1984).

Yabeithyris HATAI, 1948, p. 498 [**Y. notoensis*; OD]. Smooth, anterior commissure rectimarginate, symphytium short, with median ridge; pedicle collar indistinct. Dental plates ventrally recessive, cardinalia with deep divergent trough posteriorly, crural bases divergent, median septum well developed. *Miocene:* Japan.——FIG. 1884,*3*. **Y. notoensis;* dorsal valve exterior, ×1 (Hatai, 1948).

Yuezhuella JIN & YE in YE & YANG, 1979, p. 69 [**Y. minor;* OD]. Small, roundly pentagonal, biconvex, smooth; anterior commissure rectimarginate to weakly uniplicate; foramen submesothyrid. Dental plates short, slightly divergent; hinge plates fused with inner socket ridges; septalium wide, shallow, supported by long, high septum; crura short; loop long (about 0.5 dorsal valve length); descending branches uniting with septum anteriorly. *Lower Cretaceous–Upper Cretaceous:* Tibet. ——FIG. 1886,*4a–m*. **Y. minor; a–c*, dorsal, lateral, and anterior views, ×2; *d,* anterior view of interior, ×2; *e–l*, serial transverse sections 0.12, 1.0, 1.5, 1.9, 2.1, 2.6, 3.0, 3.3 mm from ventral umbo, ×2; *m,* loop reconstruction, ×2 (Ye & Yang, 1979).

Zhidothyris JIN, SUN, & YE in JIN & others, 1979, p. 216 [**Z. carinata*; OD]. Small to medium, elliptical, ventribiconvex, smooth; anterior commissure unisulcate; dorsal valve with wide, deep sulcus, ventral valve carinate posteriorly; beak strongly incurved, foramen small, mesothyrid; symphytium arched. Dental plates short, parallel; hinge plates narrow, separate; crural plates erect and attached to floor of valve; septum long, high; loop long. *Upper Triassic:* China.——FIG. 1886,*5a–c*. **Z. carinata*; dorsal, lateral, and anterior views, ×1 (Jin & others, 1979).——FIG. 1886,*5d–q*. *Z. yulongensis* SUN; serial transverse sections 1.7, 2.6, 2.8, 3.3, 3.7, 4.1, 5.0, 6.4, 6.8, 7.0, 7.2, 7.5, 7.9, 9.7 mm from ventral umbo, ×1 (Sun, 1981).

UNCERTAIN

A. J. BOUCOT

[Oregon State University, Corvallis]

Order and Superfamily UNCERTAIN

Family UNCERTAIN

Microbilobata JIN & CHATTERTON, 1996, p. 47 [**M. avalanchensis;* OD]. Very small, subpentagonal outline, smooth, dorsal sulcus, with low, rounded, medial costa, and corresponding ventral sulcus and medial costa, moderately biconvex, emarginated anterior commissure, no evident deltidial plates. Ventral internal features obscured, dorsal loop narrow, anteriorly pointed, relatively long. Punctae possibly present. [This enigmatic shell may represent an early centronelliform loop-bearer reminiscent of the terebratuloids; if so it is the earliest member of the taxon or a convergent development that possibly simulates that taxon. Alternatively, it may be a late representative of those Ordovician atrypaceans bearing a loop that is basically a jugum without accompanying spiralia. The questionable presence of punctae in *Microbilobata* is unhelpful in making any decision. The earliest Pridolian terebratuloids as well as subsequent earlier Devonian taxa in that group have an external form very different from *Microbilobata*. See also JIN & LEE, 2006, p. 2252.] *Silurian (upper Wenlock):* northwestern Canada.——FIG. 1887*a–g.* **M. avalanchensis; a–c,* dorsal, lateral, and anterior views, ×42; *d–e,* ventral and side views, ×32; *f,* dorsal view, ×30; *g,* silicified shell with ventral valve removed to show acuminate loop, ×40 (Jin & Chatterton, 1996).

Subfamily MUTATIONELLINAE Cloud, 1942

Aqqikkolia SUN & CHEN, 1998, p. 198 [**A. kalachukaensis;* OD]. Small, ventribiconvex, coarsely costate, subcircular, triangular delthyrium. Strong hinge teeth, short dental lamellae. Cardinal plate unsupported by crural plates. Loop unknown. Punctae unrecognized. [The absence of fold or sulcus removes this taxon from placement in the Brachzyginae or Adreninae of the Meganteridae, but makes placement in the Mutationellinae reasonable. However, the nonrecognition of either a loop or punctae makes assignment to the terebratuloids somewhat uncertain.] *Devonian (Emsian):* China (Kunlun region, Xinjiang).——FIG. 1888*a–w.* **A. kalachukaensis; a–d,* dorsal, ventral, lateral, and anterior views, ×5; *e–w,* serial transverse sections 0.2, 0.5, 1.0, 1.3, 1.5, 1.7, 1.9, 2.0, 2.1, 2.3, 2.6, 2.7, 2.8, 2.9, 3.1, 3.2, 3.3, 3.4, 3.5 mm from ventral umbo (Sun & Chen, 1998).

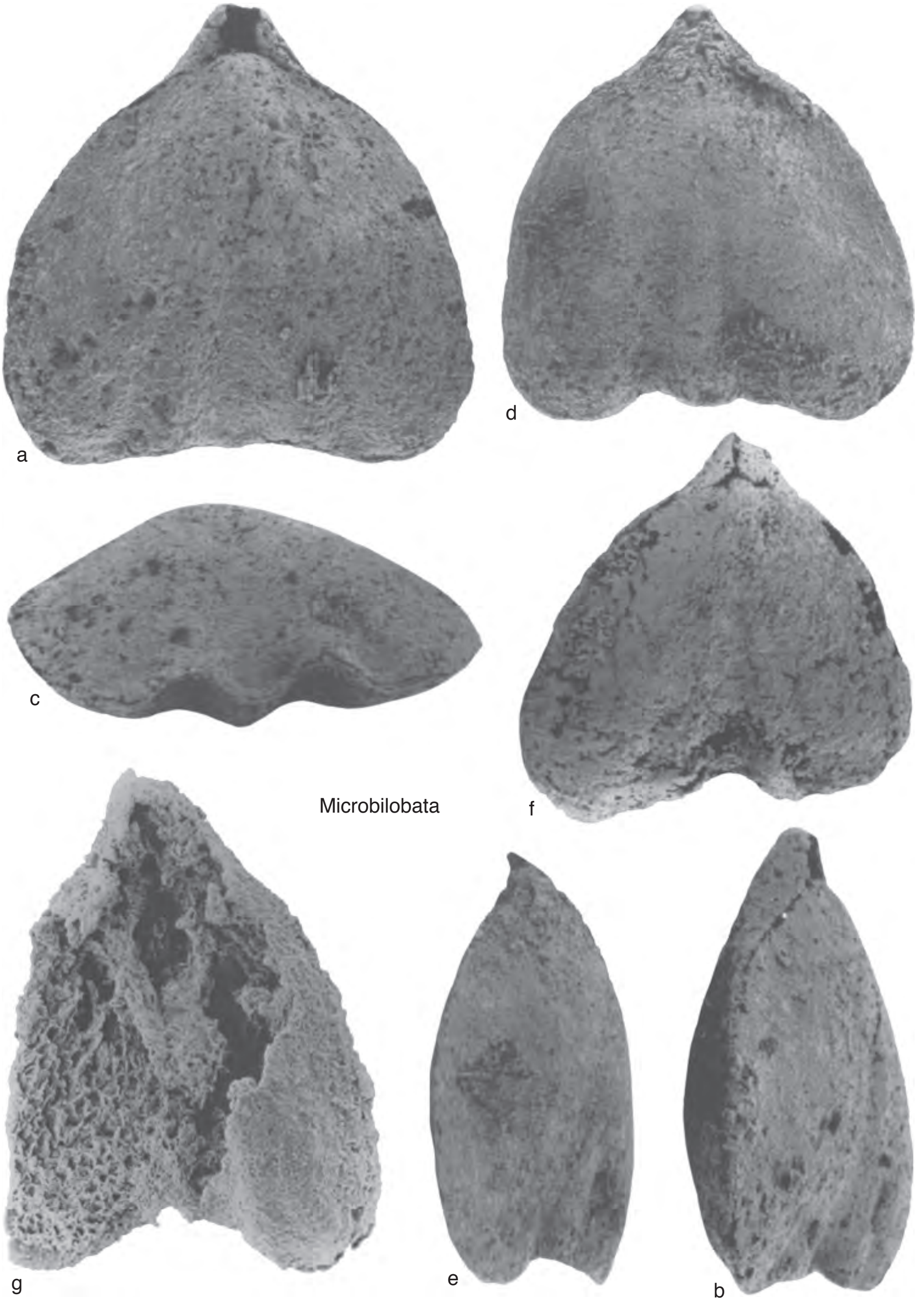


FIG. 1887. Uncertain (p. 2817).

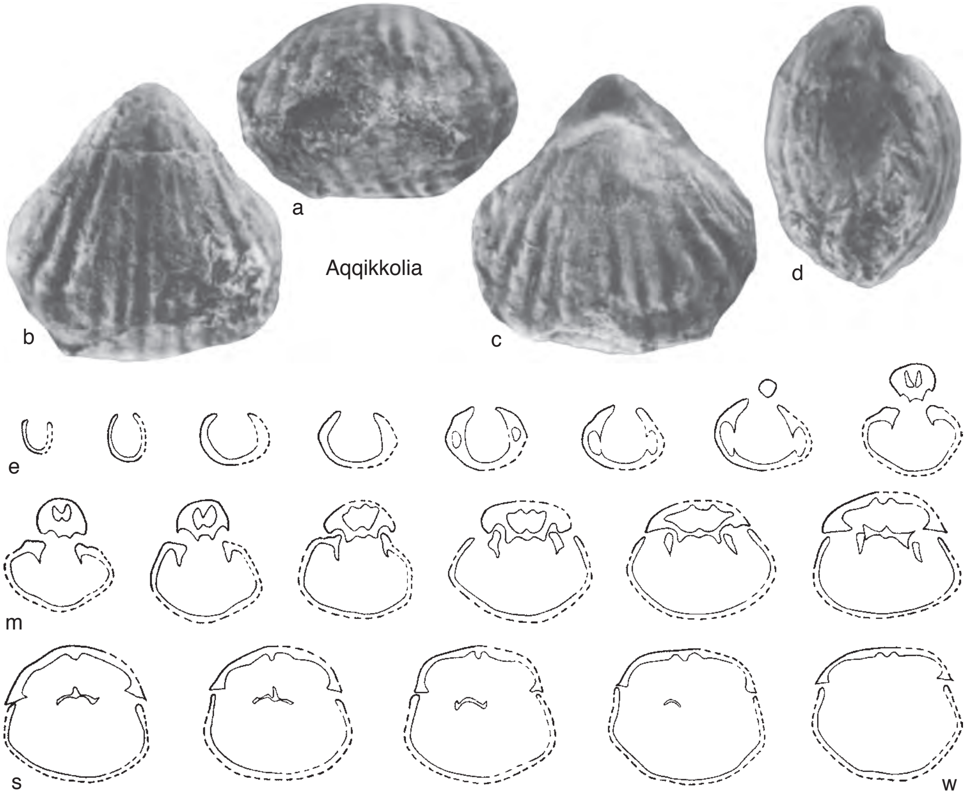


FIG. 1888. Uncertain (p. 2817).

UNCERTAIN

Norman Savage

[University of Oregon]

Order UNCERTAIN
Family CARDIARINIDAE Cooper, 1956

[Cardiarinidae Cooper, 1956b, p. 527]

Very small, cordiform, emarginated, biconvex brachiopods with beak straight, projecting; foramen round, apical; symphytium flat elongate. Surface smooth, impunctate. Dorsal parathyridia. Dental plates supporting narrow, elongate teeth. Hinge plates undivided; crura possibly supporting loop. *Upper Carboniferous:* USA, Europe.

Although assigned to the Rhynchonellida by Cooper (1956b), he considered the ordinal affinities of *Cardiarina* to be uncertain. Richard Hoare (personal communication, 1995) examined Dickerson Shale brachiopods (Pennsylvanian, Desmoinesian, Texas) that included specimens he assigned to *Cardiarina.* He observed a partial loop during serial sectioning and concluded *Cardiarina* was possibly a terebratulid. Hoare and Mapes (1997) described the Texas material as ?*Cardiarina cordata* and illustrated sections and a reconstructed dorsal valve interior based on the sections. During preparation of the Rhynchonellida for Volume 4 of the revised *Treatise* (Kaesler, 2002), it was decided to transfer *Cardiarina* to the Terebratulida, although it was included in the Rhynchonellida in the 1965 *Treatise* (Moore, 1965). The family Cardiarinidae is not in volumes 4 or 5 of the revised *Treatise;* to avoid the omission of this well-known genus from the *Treatise* it now seems appropriate to include *Cardinarina* in the *Treatise* Supplement herein under order Uncertain.

Cardiarina Cooper, 1956b, p. 527 [**C. cordata*; OD]. Very small with cordiform, emarginated outline and biconvex profile. Beak straight, projecting; foramen round, apical; symphytium flat elongate. Bisulcate with strong dorsal sulcus and weak ventral sulcus; anterior commissure rectimarginate to sulcate. Surface smooth, impunctate. Dorsal parathyridia deep. Dental plates extending from foramen along margins of symphytium to support teeth and then laterally to valve margin; teeth narrow, elongate, with medially directed tips. Hinge plates undivided; notothyrial platform thick; sockets elongate, curved; outer socket ridges thin; inner socket ridges thick, high; crura possibly supporting loop; muscle fields poorly known. *Upper Carboniferous (upper Pennsylvanian):* USA, Europe.——Fig. 1889,*1a–h.* **C. cordata*, upper Magdalena Formation, Sacramento Mountains, Grapevine Canyon, New Mexico, USA; *a–b*, dorsal and oblique dorsolateral views of holotype; *c*, ventral valve interior; *d*, dorsal valve interior, ×20; *e–f*, drawings of interior and lateral views of ventral valve showing symphytium, teeth, and long dental plates, ×20; *g–h*, interior and lateral views of dorsal valve showing parathyridium and cardinalia, ×20 (Cooper, 1956b).

UNCERTAIN

David A. T. Harper

[University of Copenhagen]

Order UNCERTAIN
Superfamily UNCERTAIN
Family TROPIDOLEPTIDAE
Schuchert, 1896

[*nom. transl.* Schuchert & Cooper, 1932, p. 152, *ex* Tropidoleptinae Schuchert, 1896, p. 330]

Transverse, subquadrate, concavoconvex to planoconvex, costellate valves; massive cyrtomatodont teeth supported by strong dental plates; ventral muscle scar large and flabellate with large diductors flanking narrow adductors; high, complex cardinal process on thick notothyrial platform; pair of long crurae with apophyses; hinge plates subdued; thick median septum bisecting elongate diductor scars, expanded distally;

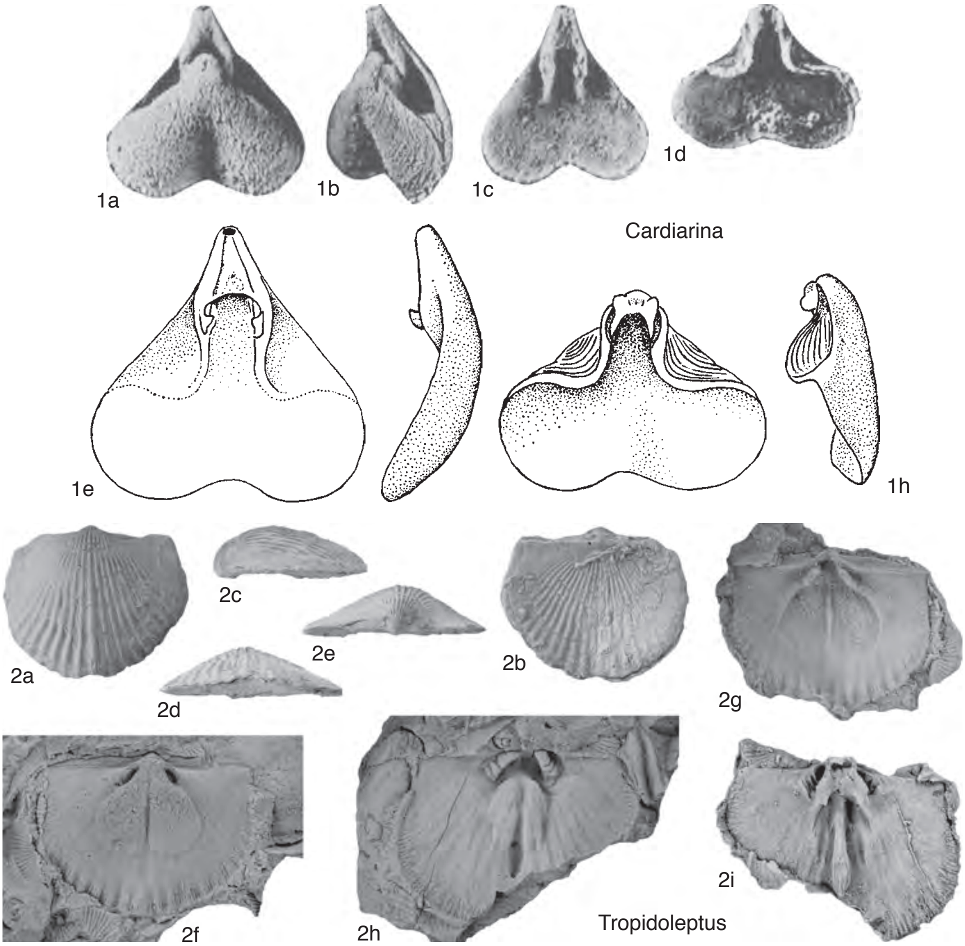


FIG. 1889. Cardiarinidae and Tropidoleptidae (p. 2820–2821).

shell endopunctate. [Placement of this common and distinctive group of brachiopods has proved difficult. *Tropidoleptus* has, for example, been related to orthides, strophomenides, and terebratulides. In the first edition of the *Treatise,* the genus was assigned to the Enteletoidea (WRIGHT, 1965, p. 328), largely on the basis of its general shape and the presence of punctation. The cyrtomatodont dentition, however, and complex cardinalia with crurae, apophyses, and a median septum are more typical of some of the more unusual rhynchonellides, for example, the Uncinuloidea, and more specifically the Eatoniidae. A punctate shell condition, nonetheless, has not been reported for that group.] *Devonian.*

Tropidoleptus HALL, 1857, p. 151 [**Strophomena carinata* CONRAD, 1839, p. 64; OD]. Concavo-convex, subquadrate with narrow ventral fold and dorsal sulcus, broad, rounded costae and costellae. *Devonian:* cosmopolitan.——FIG. 1889,*2a–i.* **T. carinatus* (CONRAD); *a–e,* ventral, dorsal, lateral, anterior, and posterior views of conjoined valves, Hamilton Group, New York State, BMNH B 75889, ×1; *f–g,* internal mold and rubber replica of ventral valve, Hamilton Group, New York State, BMNH B 10549, ×1; *h–i,* internal mold and latex replica of dorsal interior, Stadtfeld Beds, Humerich, Oberstadtfeld, Germany, BMNH B 94629, ×1 (new).

AFFINITIES OF BRACHIOPODS AND TRENDS IN THEIR EVOLUTION

Alwyn Williams and Sandra J. Carlson

[Deceased, formerly of the University of Glasgow; and The University of California, Davis][1]

INTRODUCTION

[Alwyn Williams]

Among living, skeletonized metazoans, brachiopods probably have the longest and most complete geological record. Linguliform (paterinate) shells occur in the earliest Cambrian (Tommotian) fossil assemblages; and species of three of the eight Cambro-Ordovician classes that constitute the phylum ubiquitously inhabit modern seas. This wealth of data has sustained two centuries of anatomical, embryological, morphological, and, now, molecular enquiries into the sister group and ancestry of brachiopods. Morphological studies are especially important in postulating ancestral features, not just because of the richness of the fossil record. Brachiopod valves are bilaterally symmetrical with the plane of shell opening (commissural plane) transverse to the bilateralian body. This unusual body plan is a simple but potentially important clue when researching assemblages of earliest Cambrian problematic sclerites for possible sister groups of ancient brachiopods. Such use of fossil data has its place alongside molecular and biological evidence, which is considered in the section on brachiopod affinities (p. 2383 herein).

Despite the distinctiveness of their body plan, brachiopods have often been grouped with other phyla, especially the phoronids. The body plan itself has been regarded as diphyletic in one molecular study, and although this conclusion proved untenable (and is based on artifacts), relationships among brachiopod classes are not always clear. A discussion of brachiopod monophyly and intraphylum relationships is included herein (p. 2830).

The course of brachiopod evolution is documented, albeit incompletely, in the 4800 or so genera described in this revision of *Treatise Part H* (Kaesler, 1997, 2000, 2002, 2006, and herein); but the use of such a formidable quantity of data has been subjective as well as selective. If the hierarchy used to identify the described brachiopods had been wholly phylogenetic and not Linnaean, this chapter would have been a description of those clades that, in our opinion, best exemplify brachiopod evolution. The classification, however, is not yet fully consistent phylogenetically in the way genera have been assembled hierarchically. Some have been assembled cladistically, which has at least the merit of exposing homoplasy. Other parts of the hierarchy have been built up by systematic, mostly morphological, comparison. The data used to establish the hierarchy are also variable in quality and inclusiveness. Ninety-five percent of the classified genera are extinct; and the data distinguishing them are limited to the chemical composition, microstructure, and morphology of their shells, although this can include mantle imprints and skeletal devices for the accommodation and support of various organs. The preponderance of

---

[1] Alwyn Williams prepared the initial outline and framework for the components contained within this chapter, derived from a remarkably rich and productive lifetime devoted to the study of brachiopods, their morphology, and evolution. Alwyn and I each wrote separate accounts of our interpretations of brachiopod affinities and trends, with the intention of combining and coordinating our different points of view in the final draft. Sadly, Alwyn passed away before completion of the final draft of this chapter, making such a coordinated effort impossible. Alwyn worked steadily on various drafts up until a week before his death, in keeping with his indefatigable spirit and determination to complete the *Treatise* revision. After his death, numerous studies appeared in the literature that affect some interpretations presented in his drafts. As such, Alwyn's section on affinities in this first chapter is focused more on establishing elements of brachiopod evolution as we understood them just prior to his death. Bracketed notes highlighting recent research were added after his death, and authorship is clearly noted for each section. My section forms a separate, subsequent chapter focused more on raising questions about issues that are not yet understood in light of these more recent studies, with the hope that this approach will encourage others to pursue answers to these questions in the coming years. SJC.

data on brachiopod evolution and trends in morphological evolution is, therefore, weighted in favor of skeletal differentiation, as is evident in the section on brachiopod evolution (herein, p. 2833).

One aspect of brachiopod evolution that has to be taken into account is that material evidence of it is scattered throughout 550 million years of rock successions. This stratigraphic evidence can, on occasion, conflict with phylogenetic relationships inferred from biological and morphological studies and with molecular estimates of time derived from genealogies. These issues are considered in various sections below and in CARLSON, herein, p. 2878.

BRACHIOPOD AFFINITIES

[Alwyn Williams]

Even before the Darwinian theory of evolution and the Haekelian concept of phylogeny had taken root, opinions on the metazoan affinities of the Brachiopoda were being obliquely expressed by classificatory practices. At the beginning of the 19th century, brachiopods were commonly classified as mollusks (LAMARCK, 1801) or molluscoides. The latter name was used by HUXLEY (1869) to accommodate his view (shared with HANCOCK, 1859) that brachiopods and polyzoans (bryozoans or ectoprocts) are related. MORSE (1902), on the other hand, concluded that the brachiopods are more closely related to the annelids and cited the possession of setae as part of the evidence of common ancestry.

CLASSICAL (EMBRYOLOGICAL, ANATOMICAL, AND MORPHOLOGICAL) STUDIES

The formal recognition that brachiopods are bilaterian animals came with HATSCHEK's use of the body plan (1888–1891) as a tool in uncovering metazoan affinities. In particular, the comparative studies of anatomy and larval development of brachiopods and *Phoronis* (CALDWELL, 1882) led HATSCHEK (1888–1891, p. 40) to propose a new phylum for brachiopods, bryozoans, and phoronids: the Tentaculata (later more appropriately renamed Lophophorata [HYMAN, 1959, p. 229]).

Further refinement of metazoan phylogeny, distinguishing the Protostomia from the Deuterostomia, has caused dissension over the precise rooting of brachiopods within the Bilateria. Initially the lophophorates were regarded as protostomes. Reservations on how to interpret the development of the brachiopod gut and coelom prompted HYMAN (1959, p. 230) to suggest that the lophophorates "form some sort of link between the Protostomia and the Deuterostomia." In effect, the lophophorates could be the sister group of either clade; and there is currently some (albeit controversial) support for describing brachiopods as deuterostomes as well as protostomes.

A deuterostomous origin of all lophophorates has attracted support especially among biologists interpreting classical embryological, anatomical, and morphological data. It has been the prevalent opinion among such zoologists as BRUSCA and BRUSCA (1990), SCHRAM (1991), MEGLITSCH and SCHRAM (1991), and EERNISSE, ALBERT, and ANDERSON (1992). A more recent study by LÜTER (2000a) of the development of the mesoderm in brachiopod (rhynchonelliform) larvae suggested that the coelom may be enterocoelic. He concluded that the Brachiopoda and the Deuterostomia are sister groups and rejected a brachiopod sister-group relationship with *Phoronis* so that, in his opinion, the lophophorates are paraphyletic. NIELSEN (1995, p. 6) also regarded the lophophorates as paraphyletic but as a result of different groupings. On the basis of further studies and reinterpretations of lophophorate larval development, NIELSEN assigned the bryozoans to the protostomes and the brachiopods and phoronids to the deuterostomes (Fig. 1890), as sister groups (NIELSEN, 2001). In his view, several features upholding lophophorate monophyly, like the lophophore itself, are not synapomorphies but homoplasies. NIELSEN's conclusions are supported by the immunohistochemical

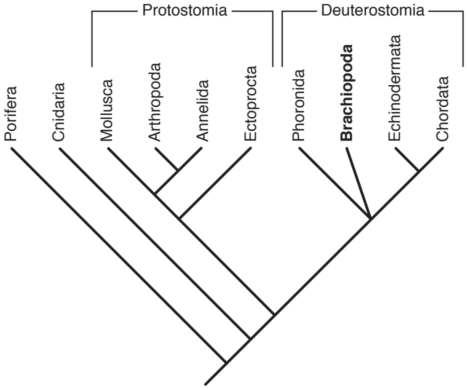


FIG. 1890. Cladogram of major animal groups, showing brachiopods nested among the deuterostomes (adapted from Nielsen, 1995).

study by HAY-SCHMIDT (2000) of the serotonergic larval nervous systems of species representing a number of deuterostomes and protostomes. The brachiopods (*Glottidia*) and phoronids group with the deuterostomes; bryozoans with the protostomes.

MOLECULAR STUDIES

In contrast to the weight of classical data favoring brachiopods as deuterostomes (or a sister group thereof), molecular studies have consistently placed the phylum among the protostomes. These studies have been based on the following: partial and complete sequences of nuclear-encoded, small (18S) and large (28S) subunit ribosomal RNA genes by FIELD and others (1988), LAKE (1990), HALANYCH and others (1995), COHEN and GAWTHROP (1997), COHEN, GAWTHROP, and CAVALIER-SMITH (1998), and COHEN and WEYDMANN (2005); partial and complete sequences of mitochondrial DNA (mtDNA) by COHEN and others (1998) and STECHMANN and SCHLEGEL (1999); and Hox genes, involved in the directional development of bilaterians, by DE ROSA and others (1999). In all but the earliest, pioneering studies, two branches of the Protostomia are recognized: the Lophotrochozoa (HALANYCH & others, 1995) consisting of the lophophorates, mollusks, annelids, and selected other phyla; and the Ecdysozoa.

There was, however, no agreement on the sister group to the brachiopods being within the lophotrochozoans. HALANYCH and others (1995) concluded that brachiopods are not monophyletic because phoronids, not the linguliforms (represented by *Glottidia*), are the sister group of the rhynchonelliforms (represented by *Terebratalia*). The results, which led to the recognition of a new infrakingdom, the Lophotrochozoa, were regarded as premature by CONWAY MORRIS and others (1996), especially on the grounds that these early lophophorate sequences were unreliable.

In their study, which was primarily concerned with the genealogy of 37 brachiopod species representing all extant orders of the phylum, COHEN, GAWTHROP, and CAVALIER-SMITH (1998, p. 2056) found evidence for including the phoronids in a lingulide-craniide clade (the outgroup used for the tree was a chiton). Further study of relevant 18S rDNA gene sequences convinced COHEN (2000) that the phoronids nest within the brachiopod clade (Fig. 1891) with weak support for craniides as a sister group, which, in turn, cluster with lingulides as a sister group to the discinoids (COHEN, 2000, p. 228). COHEN, therefore, reclassified the phoronids as a subphylum (Phoroniformea) of the Brachiopoda. Neither the mtDNA nor the relevant Hox gene sequences of *Phoronis* were used in the analyses of STECHMANN and SCHLEGEL (1999) and of DE ROSA and others (1999). Moreover, their comparative analyses were restricted to *Terebratulina* and *Lingula* respectively so far as the brachiopod genomes were concerned. Interestingly, however, STECHMANN and SCHLEGEL, like COHEN and GAWTHROP (1997) and COHEN and others (1998), found a close affinity between *Terebratulina* and a polyplacophoran mollusk (chiton).

RECONCILIATION OF CLASSICAL AND MOLECULAR STUDIES

Unsurprisingly, several reviews have challenged the reliability of classical or molecular data or have attempted to reconcile the conclusions drawn from them. Different methods have been used to assess the relative merits of classical and molecular evidence. The comprehensiveness of several reviews has inevitably been affected by the pace of later research, especially in the molecular field. Comparisons of some of the more recent reviews, however, are informative in revealing conflicting interpretations of biological and molecular evidence. Thus, attempts by biologists (LÜTER & BARTOLOMAEUS, 1997) to reconcile both kinds of data involved the reassessment of seven morphological and embryological complexes that, overall, relate brachiopods to the deuterostomes. They concluded that all but the presence of setae confirmed this relationship. Conversely, strategic insertions of brachiopods or phoronids as a sister group to selected phyla in a spiralian tree required too many convergences to become congruent, in their opinion. In contrast, the protostomous affinity of brachiopods was reaffirmed by DE ROSA (2001) in his review of molecular and biological evidence. Six morphological and embryological complexes, largely overlapping those reviewed by LÜTER and BARTOLOMAEUS (1997), were assessed as being unreliable evidence for the deuterostomous grouping of brachiopods.

A more comprehensive review by PETERSON and EERNISSE (2001) involving phylogenetic analyses of classical and molecular (18S rDNA) data, separately and together, appears to resolve several issues of conflict (Fig. 1892). In both separate analyses, brachiopods and phoronids group within the protostomes, although their molecular data do not support brachiopod monophyly. In the combined analyses, however, the Brachiopoda are monophyletic with *Phoronis* as a sister group. The evidence amassed by PETERSON and EERNISSE (2001, p. 188) appears to be sufficient to "challenge the formal inclusion of phoronids with the brachiopods," as had been proposed by COHEN (2000) and adopted by GenBank (2006) [see COHEN & WEYDMANN, 2005 for a more recent investigation].

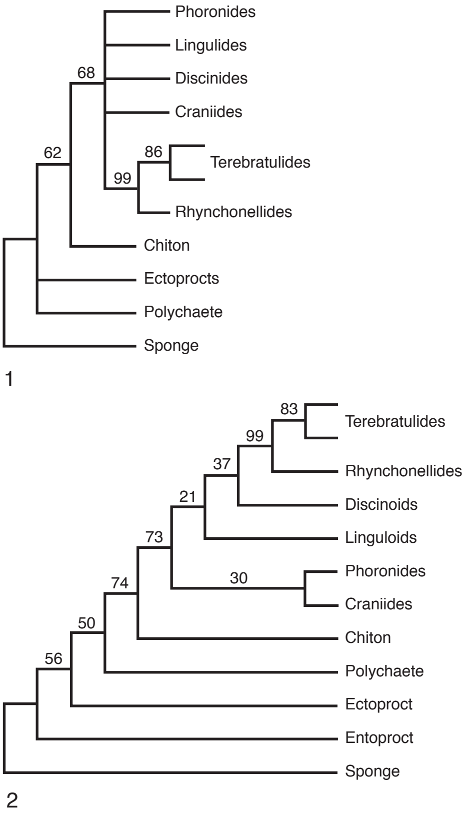


FIG. 1891. Results of phylogenetic analyses of 18S rDNA sequences of representative extant brachiopod species, showing nesting of phoronids among brachiopods. *1,* Maximum parsimony bootstrap 50% majority rule consensus cladogram (nodes with less than 50% support collapsed); *2,* same as in 1, but nodes with less than 50% support not collapsed (adapted from Cohen, 2000).

Reviews of the animal kingdom by CAVALIER-SMITH (1998) and ZRZAVY and others (1998) are both phylogenetic in method and comprehensive in their use of data but are classificatory in aim and are consequently characterized by a plethora of new and amended taxonomic names. CAVALIER-SMITH (1998, p. 235) recognized the brachiopods and phoronids as sister groups forming a new phylum Brachiozoa which, in turn, is classified as a sister group of the Mollusca within a new protostomous superphylum, Conchozoa, diagnosed as: "vascular system; ancestrally with a calcareous shell,

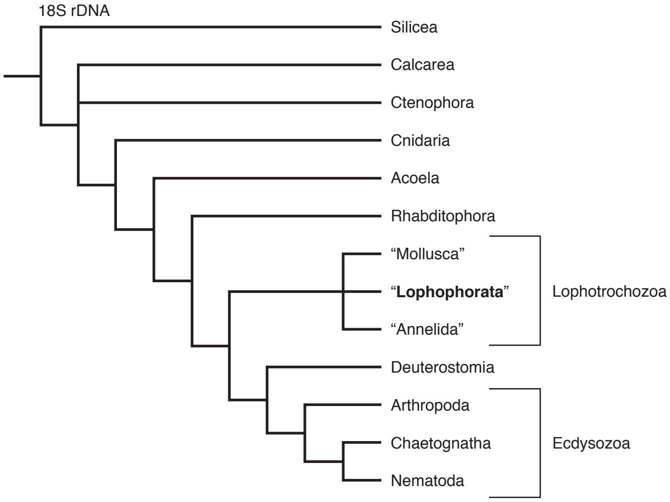


FIG. 1892. Summary of phylogenetic analyses of 18S rDNA sequences of representative extant metazoans with brachiopods in the Lophophorata within the Lophotrochozoa; *quotation marks* indicate possible paraphyly of the taxon named (adapted from Peterson & Eernisse, 2001).

primitively bivalved and unhinged." CAVALIER-SMITH justified the taxonomic demotion of the brachiopods and phoronids (1998, p. 241) on the grounds that they "share a basically similar body plan," contrary to the findings of NIELSEN (1991, p. 25). Likewise, his assertion that the common ancestor of his superphyla Polyzoa and Conchozoa had a bivalved larva (CAVALIER-SMITH, 1998, p. 242) disregarded the disposition of shells relative to the body axes in stocks assigned to these groups.

The unstable nature of the metazoan phylogeny proposed by ZRZAVY and others (1998) is suggested by radical changes to the taxonomic status of the brachiopods and phoronids, proposed by these authors in a postscript. The preferred phylogeny (ZRZAVY & others, 1998, p. 250), which is based on analyses of combined classical and 18S rDNA data, favored the Phoronozoa (a new phylum composed of phoronids and brachiopods) as a sister group of the deuterostomes, although their discussion of this relationship covers all options (ZRZAVY & others, 1998, p. 268). A footnote added in proof (ZRZAVY & others, 1998, p. 271) took into account the newly accessible studies of COHEN, GAWTHROP, and CAVALIER-SMITH (1998) and COHEN and others (1998) and concluded that the Phoronozoa should be reclassified into two phyla, Phoronida and Brachiopoda, the latter with four subphyla: Linguliformea, Disciniformea, Craniiformea, and Rhynchonelliformea. Although the authors equivocated on whether these taxa are deuterostomes or protostomes, the bulk of the defensible evidence now appears to point to a protostome affinity for brachiopods.

FOSSIL EVIDENCE

Several contradictions are exposed in attempts to identify the sister group of the brachiopods by comparing classical and molecular versions of metazoan phylogeny. Both versions recognize the deep divisions within the Bilateria between the deuterostomes and the protostomous lophotrochozoans and ecdysozoans. They do, however, place a minority of phyla, including the brachiopods, within different infrakingdoms; and there is not much satisfactory evidence of reconciliation in reviews using both kinds of data to produce a hybrid metazoan phylogeny.

These two different approaches do have one thing in common: their data are drawn exclusively from living species without regard for fossil evidence. The omission is, of course, inevitable in molecular studies but is a practice of obdurate tradition among biologists that has been defended (PATTERSON, 1981, p. 218) on the grounds that fossil evidence rarely challenges theories of relationships based on living data. This is an indefensible presumption especially when dealing with phyla of controversial affinities, like the brachiopods, that have long geological records incorporating many extinct groups. Twenty-six brachiopod orders are currently recognized, each distinguished by a substantial assemblage of transformations (WILLIAMS & others, 1996). Ten orders are recorded in the Lower Cambrian but only one of these (Lingulida) is represented among the five orders with living species.

This preponderance of extinct groups has determined the kind of characters used to trace early brachiopod evolution. They are overwhelmingly related to the composition and morphology of the shell. Such features may seem superficial but they are biomineralized (and cuticular) manifestations of the mantle (and pedicle) epidermis. Accordingly, morphological analyses, based on the exoskeleton, should enjoy as much credence as molecular analyses (see GEE, 1995; CONWAY MORRIS, 1995), especially in sorting out brachiopod stem groups and identifying feasible sister groups among contemporaneous skeletonized stocks of the Early Cambrian when diversification of metazoan body plans was under way (VALENTINE, JABLONSKI, & ERWIN, 1999; BROMHAM & HENDY, 2000).

The best prospect for identifying the extinct sister group of brachiopods lies among Early Cambrian Problematica, assemblages of sclerites of uncertain taxonomic affiliation. On the basis of bilateral symmetry and devices suggesting articulation, CONWAY MORRIS and BENGTSON (in BENGTSON & others, 1990) described two seemingly calcareous bivalves, *Apisthoconcha* and *Aroonia* as of "possible brachiopod affinity" (1990, p. 164). We concur, however, with their concession that these stocks could also be "products of convergent evolution from other soft-bodied ancestors" (1990, p. 186).

A potentially more promising source of brachiopod ancestry lies in the group of sclerites, sometimes referred to as tommotiids, which were identified as the sister group of brachiopods by CONWAY MORRIS (1993, p. 223). He later homologized the shells on the dorsum of *Halkieria* with brachiopod valves (CONWAY MORRIS & PEEL, 1995; CONWAY MORRIS, 1998) and concluded that brachiopods might have been derived by the folding of the halkieriid bilaterian body across a transverse plane as postulated by NIELSEN (1991) to explain the U-shaped gut of linguliforms (see also COHEN, HOLMER, & LÜTER, 2003).

The tommotiid sclerites, *Tannuolina* and *Micrina,* are perforated by tubes (FONIN & SMIRNOVA, 1967; LAURIE, 1986; QIAN & BENGTSON, 1989; CONWAY MORRIS & CHEN, 1990). More detailed studies of the *Micrina* sclerites by WILLIAMS and HOLMER (2002) showed that they consist of a stratiform succession of laminar sets that might be homologous with those of lingulate shells, complete with internal impressions of muscle bases and gonads; and that the pervading tubes could have contained setae. WILLIAMS and HOLMER (2002, p. 868) further identified *Micrina* sclerites as halkieriid shells (as did USHATINSKAYA, 2002) and postulated a series of transformations that could have changed the sclerites into a linguliform shell (Fig. 1893). Concurrently, the enigmatic, bilaterally symmetrical, apatitic bivalve, *Mickwitzia*, was shown to have a shell structure apparently homologous with the columnar lamination of lingulates and to be pervaded by tubes that, on the ventral pseudointerarea at least, appear to be identical with those of *Micrina* (HOLMER, SKOVSTED, & WILLIAMS, 2002). Shell structure and body plan, therefore, suggest that *Micrina*, a presumed halkieriid, might be

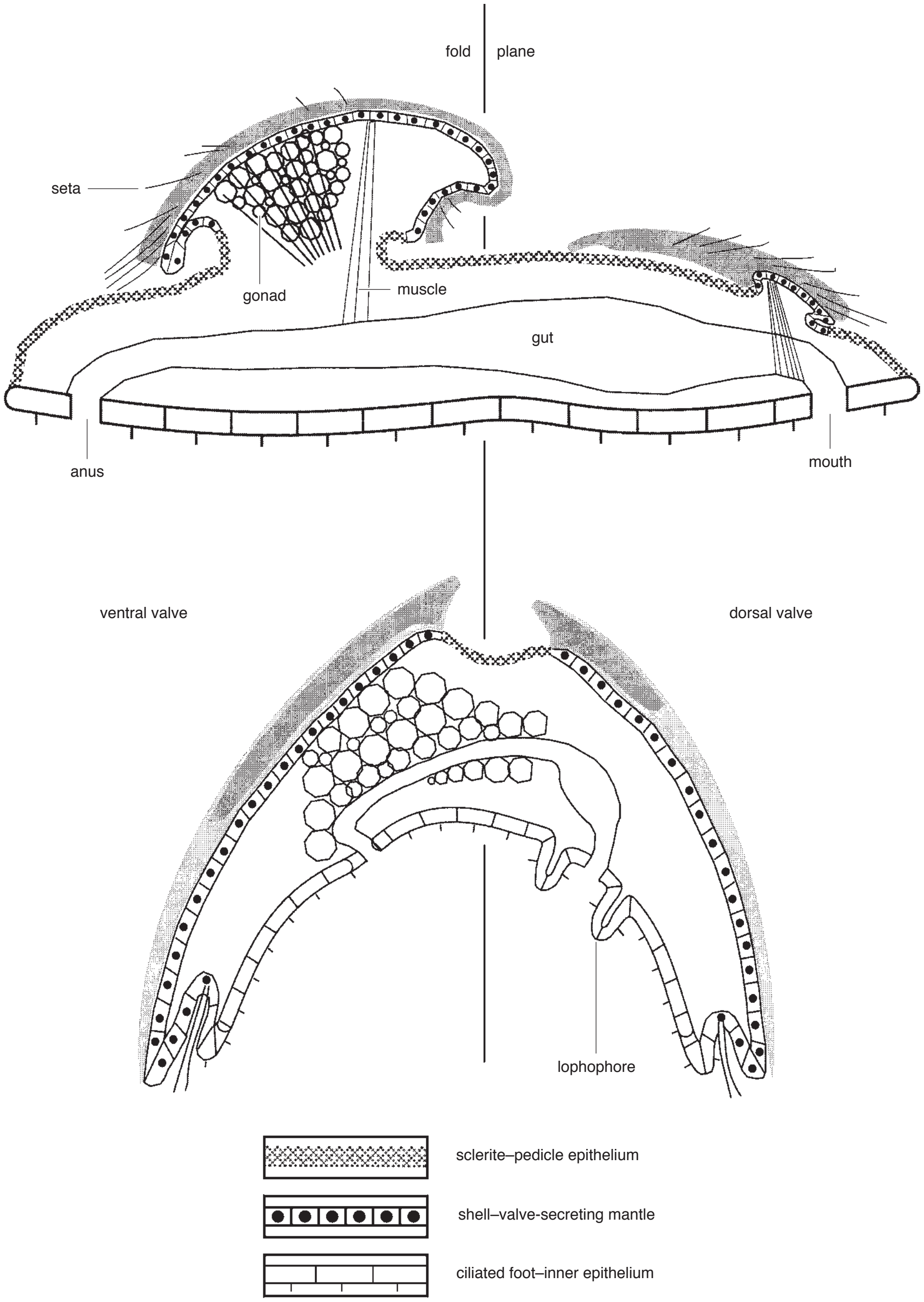


Fig. 1893. Graphical representation of possible evolution of an ancestral brachiopod from a presumed halkieriid, *Micrina* (Williams & Holmer, 2002).

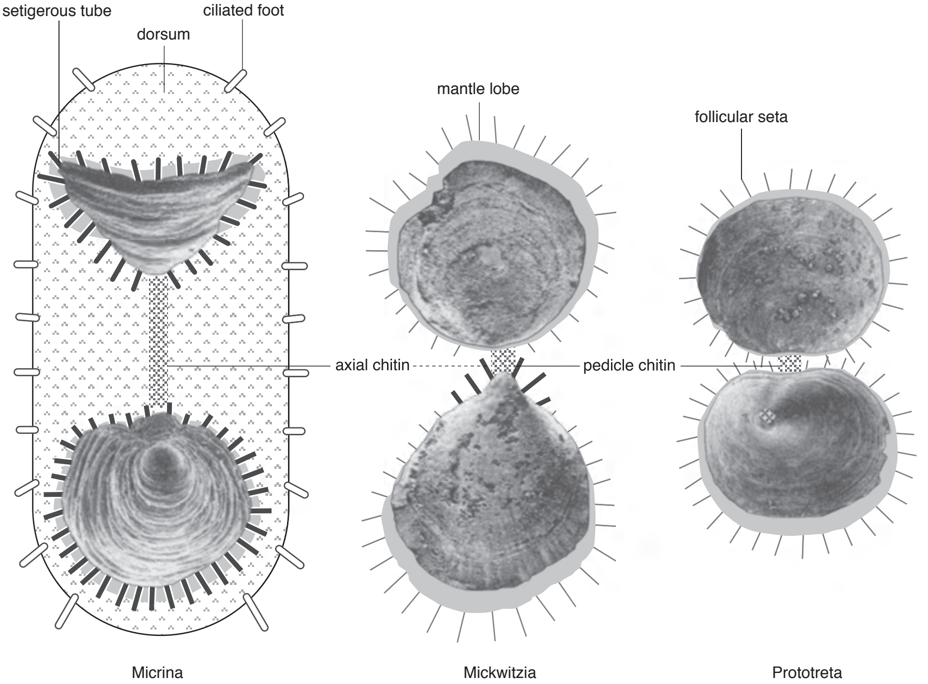


FIG. 1894. Generalized reconstruction of living parts of *Micrina*, *Mickwitzia*, and *Prototreta*, showing *Mickwitzia* as a possible stem-group brachiopod (adapted from Holmer, Skovsted, & Williams, 2002).

the sister group of the Brachiopoda with *Mickwitzia* as a stem-group brachiopod (Fig. 1894).

This version of brachiopod ancestry has been challenged in two ways. LI and XIAO (2002) described the scleritome of *Tannuolina* as consisting of juxtaposed dextral and sinistral mitral sclerites and imbricated sellate sclerites. They concluded that the morphologically similar sclerites of *Micrina* are not homologous with the shells of *Halkieria*, *Mickwitzia*, or brachiopods. They further attributed the similar shell structures of *Micrina*, *Mickwitzia*, and lingulate brachiopods to convergence. WILLIAMS and HOLMER (2002, p. 868) pointed out that the dextral and sinistral mitrals of *Tannuolina* are only homologous with the bilaterally symmetrical mitral sclerite of *Micrina* if they are capped with metameric, juvenile shells. They do not appear to be; only a fused complementary pair of mitral sclerites straddling the bilateral axis of *Tannuolina* could be homologous with the mitral sclerite of *Micrina*. Moreover, it seems improbable that the fine structure of sclerites and shells is homoplastic, while the extremely variable morphology of these skeletal pieces is homologous.

RUNNEGAR (2000), in proposing that the halkieriids were ancestral to chitons, precluded any affinity with organophosphatic brachiopods on the grounds that the scleritome of *Halkieria* was likely to be calcareous. *Micrina,* and possibly *Halkieria,* sclerites are apatitic, as evidenced by their rheomorphically deformed shells (WILLIAMS & HOLMER, 2002, p. 868–869). It is also remotely possible that the embryonic and larval shells of many Early Paleozoic lingulates were calcitic as well as apatitic and siliceous (WILLIAMS, 2003); we cannot yet reject the hypothesis that multimineralic mineralization may have been possible early in shell development.

It is noteworthy that a chiton has emerged as the most proximal outgroup in comprehensive studies of the molecular phylogeny of brachiopods (COHEN, GAWTHROP, & CAVALIER-SMITH, 1998, p. 2040). Such a sister-group relationship is at least consistent with the derivation of polyplacophorans as well as brachiopods from a halkieriid-like ancestor.

MONOPHYLY AND INTRAPHYLUM GROUPINGS OF THE BRACHIOPODA

[Alwyn Williams]

The long-held view that lophophore-bearing animals form a closely related phylogenetic unit of brachiopods, phoronids, and bryozoans (see EMIG, 1977, 1984) has recently been convincingly challenged (NIELSEN, 1995; HALANYCH, 1995). There has never been much doubt, however, of the close relationship between brachiopods and phoronids despite their morphological dissimilarity. This affinity has been recognized taxonomically by classifying them together as a phylum (EMIG, 1997a; CAVALIER-SMITH, 1998; ZRZAVY & others, 1998) with the phoronids as a sister group of the brachiopods, a relationship also upheld when they are both recognized as phyla (PETERSON & EERNISSE, 2001).

There is no indisputable fossil evidence of the first appearance of phoronids notwithstanding the phoronid-style of U-shaped borings (*Diorygma*) in the Devonian (MACKINNON & BIERNAT, 1970). Apart from lacking a shell, *Phoronis* has a U-shaped gut, the outer side of which is ventral and not dorsal as in brachiopods (NIELSEN, 1991, p. 26). Such an orientation suggests that *Phoronis* could not have evolved directly from a halkieriid-like ancestor by an orthodox folding of the body axis (Fig. 1895). The presence of sulphated glycosaminoglycans (GAGs) in the chitinous cuticle of *Phoronis* (HERRMANN, 1997, p. 215) would suggest a link [and quite possibly a plesiomorphic link; COHEN & WEYDMANN, 2005] with linguliforms, as GAGs are unknown in rhynchonelliform shells (Fig. 1891, 1896).

If phoronids are excluded from the brachiopod phylum, three subphyla are presently recognized (WILLIAMS & others, 1996): laminar organophosphatic-shelled linguliforms attached to, or within, the substrate by a pedicle developing as an extension of the posterior body wall; fibrous organocarbonate-shelled rhynchonelliforms attached by a pedicle developing from a larval lobe; and laminar organocarbonate-shelled craniiforms attached by an adhesive ventral valve in place of a pedicle.

Living species of these three subphyla have differently disposed and developed guts (Fig. 1895). The linguliform gut is U-shaped with both mouth (originating near the blastopore) and anus opening into the mantle cavity (NIELSEN, 1991). The rhynchonelliform gut is folded more or less normal to the dorsal valve and lacks an anus, but the mouth, opening into the mantle cavity, also originates near the blastopore (NIELSEN, 1995, p. 318; WILLIAMS & others, 1997, p. 163). Morphological evidence (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 387) suggested that the distinctive pedicle and gut of living rhynchonelliforms are synapomorphies of all rhynchonellate ordinal taxa originating after the Cambrian. The pedicle of older, extinct rhynchonelliforms, like the protorthides, orthides, and pentamerides, which first occur in the Lower Cambrian, is likely to have been accommodated also in the notch (delthyrium) that indented their ventral valves. We assume that their gut was disposed like that of the crown rhynchonelliforms but possibly with an anus entering the mantle cavity as in linguliforms.

The affinities of the paterinates are ambiguous in that their shells are phosphatic like

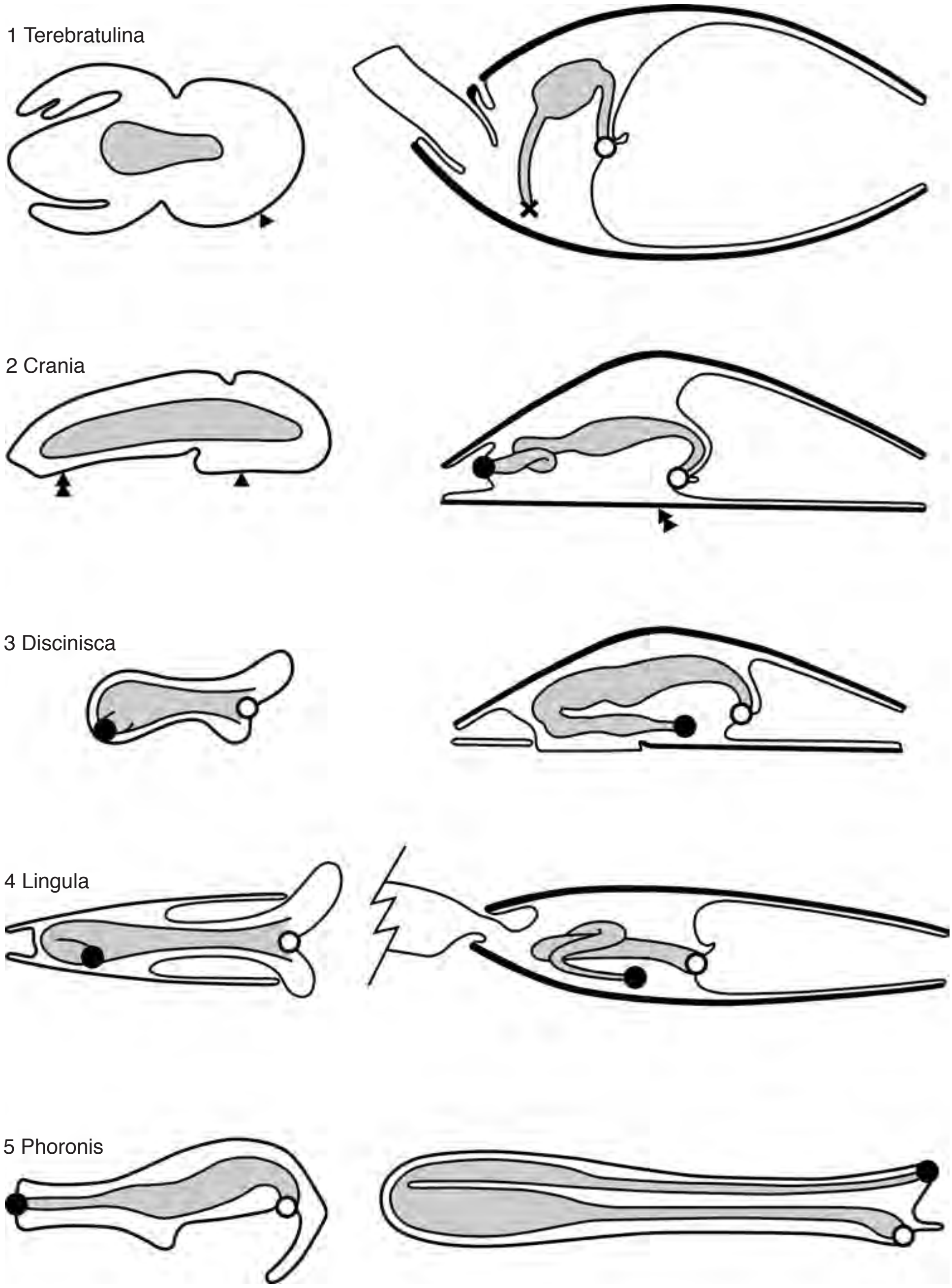


FIG. 1895. Comparison between main body axes and gut orientation of larvae (*left column;* almost to scale) and adults (*right column;* not to scale) of 4 brachiopod genera and *Phoronis* (adapted from Nielsen, 1991); mouth is indicated by *open circle,* the anus by *black dot* (blind intestine marked by *X*), position of closed blastopore by *double arrowhead,* and position of future mouth by *single arrowhead;* anterior part of gut is horizontal in all.

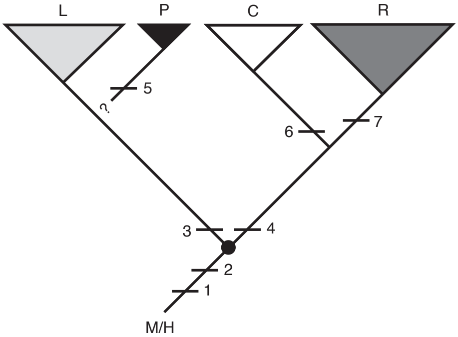


FIG. 1896. Proposed relationships among crown groups of brachiopods Linguliformea (*L*), Phoroniformea (*P*), Craniiformea (*C*), and Rhynchonelliformea (*R*), if they are derived from a halkieriid stem group (*M/H, Micrina-Halkieria*); *numbered dashes* indicate one hypothesis of character evolution: *1,* folded body axis; *2,* pedicle from ventral body wall; *3,* apatitic shell; *4,* calcitic shell; *5,* reoriented body axis, no pedicle, loss of shell; *6,* reoriented body axis, no pedicle; *7,* pedicle from larval lobe (adapted from Williams & Holmer, 2002).

those of other linguliforms, but their body plan is rhynchonelliform (WILLIAMS, POPOV, & HOLMER, 1998, p. 259). Either way, an anus, if developed, would have opened into the mantle cavity. There is, therefore, no need to postulate the existence of a posterior body wall (WILLIAMS, POPOV, & HOLMER, 1998, p. 242) to carry the anus as in craniiforms.

The development and organization of living craniiforms are different. No pedicle develops, and attachment is effected by posteroventral epidermal cells secreting an adhesive ventral valve. The blastopore becomes the site of the future anus on the posterior body wall, and the future mouth breaks through anteriorly into the future mantle cavity (NIELSEN, 1991; FREEMAN, 2000, 2003). The absence of possible pedicle openings from the shells of all groups assigned to the Craniiformea suggests that their body plan has changed very little since the Cambrian. In effect, the anus could always have breached the posterior body wall and never have opened into the mantle cavity with an attendant U-shaped bend in the gut as in linguliforms (Fig. 1895).

There are some early rhynchonelliforms (Chileata, Obolellata, and Kutorginata), in which the anus may have breached a posterior body wall, as has been inferred for the kutorginate *Nisusia* (ROWELL & CARUSO, 1985). Such an intestinal disposition would have accorded with that of the craniiform crown group, as a possible symplesiomorphy.

Despite the divisions between the linguliforms and rhynchonelliforms, their close phylogenetic relationship is confirmed by recent molecular and biological studies. The oldest known rhynchonelliform, a Lower Cambrian (Atdabanian), foliated, carbonate-shelled obolellate, is contemporaneous with the oldest phosphatic-shelled lingulate; both are only slightly younger (<5 million years) than the earliest known brachiopod (a Tommotian phosphatic-shelled paterinate). The apatitic or calcitic composition of brachiopod shells, therefore, seems to have been mutually exclusive *ab initio*.

An interchangeability of these two biomineralizing regimes, however, becomes a possibility if halkieriids were ancestral to brachiopods. The shells of *Micrina* are phosphatic. Those of *Halkieria* are inferred to have been calcareous as were the sclerites coating the dorsum (CONWAY MORRIS & PEEL, 1995, p. 305). The *Halkieria* shells, however, are thought to have been highly rheological in the living state in the manner of linguliform valves (WILLIAMS & HOLMER, 1992). Degradable organophosphatic-shells as part of the *Halkieria* scleritome, which is otherwise chitinocarbonate, cannot, therefore, be ruled out [see VINTHER & NIELSEN, 2005, for an alternative point of view]. In all, the composition of halkieriid scleritomes could have been quite variable. A differentiated secretory system could have given rise to calci-apatitic as well as calcareous or phosphatic scleritomes. *Micrina* could even have been a halkieriid with organophosphatic shells but with the rest of the dorsum covered with discrete, chitinous setae instead of other biomineralized or polymeric sclerites. Such a differentiation would be in keeping with compositional changes apparent in some lingulate shells. It is conceivable that Early Paleozoic lingulates, all with organophosphatic adult shells, may have had apatitic, calcitic, or siliceous juvenile shells (mosaics; WILLIAMS, 2003), but the evidence upon which this is based is highly speculative. An ontogenetic change in biomineral secretion has been documented for living discinids, with their juvenile siliceous mosaics and apatitic adult shells (WILLIAMS & others, 1998; WILLIAMS, LÜTER, & CUSACK, 2001).

The difficulties in relating craniiforms to other brachiopod crown groups, had they evolved from a halkieriid stem group, echoes the contradictions posed by molecular, embryological, and classical phylogenetic studies. Analyses based on 18S rDNA gene sequences place the craniids within living linguliforms (COHEN, 2000) or more recently as their sister group (COHEN & WEYDMANN, 2005; see CARLSON, herein, p. 2883). Some embryological studies suggest a close relationship with the rhynchonelliforms (NIELSEN, 1991), others support a close relationship with the linguliforms (FREEMAN, 2003; see CARLSON, herein, p. 2883), while classical interpretations found their affinities so equivocal as to prompt their provisional classification as a separate subphylum (WILLIAMS & others, 1996, fig. 1). Among the many curious features of craniiforms, the anterior-posterior alignment of the gut is incompatible with a hypothesized transverse folding of the body axis in the midregion. Nor can the craniiform body plan, with the anus at virtually the same site as the linguliform pedicle, be easily interpreted as precursory to folding as inferred in NIELSEN's review (1991, p. 25) of brachiopod evolution. It has, therefore, been claimed (WILLIAMS & HOLMER, 2002) that the Craniiformea is the most derived brachiopod group although so transformed as to defy an unequivocal identification of its sister group (Fig. 1896). The craniiform laminar shell structure is also unique but is, at least, carbonate and, on balance, it has been concluded that the group may have diverged from one of the early rhynchonelliform stocks (WILLIAMS & HOLMER, 2002) [for an alternative point of view, see CARLSON, herein, p. 2883, as well as FREEMAN, 2003].

TRENDS IN BRACHIOPOD EVOLUTION

[Alwyn Williams and Sandra J. Carlson]

As already noted, 95 percent of all brachiopod generic stocks are extinct, so that most of the evidence for the phylogenetic diversity of the phylum is drawn from fossilizable parts of the animal, principally the shell (and endoskeletal spicules). Yet fossilized shells, even from the Lower Cambrian, are a rich source of phylogenetic data on a surprisingly large number of organs. The shape of the shell (itself an intimate record of the integument) and the impressions and apophyses it bears provide evidence of the Phanerozoic evolution of embryological and larval development; the pedicle; shell articulation and its attendant muscle systems; the mantle canal system and gonadal disposition; and the lophophore. Comparative studies of these data in living and fossil brachiopods reveal the chronology of the main transformations that led to many of the basic differences among living species.

The origin of other anatomical differences without a fossil record, like the number of metanephridia, can also be dated in relation to the phylogenetic tree as a whole, as has been shown in conjectures regarding the disposition of the brachiopod gut. Trends in the evolution of these features are outlined below.

EVOLUTION OF EMBRYONIC AND LARVAL MANTLE AND SHELLS

[Alwyn Williams and Sandra J. Carlson]

During ontogeny, three stages in the growth of the brachiopod mantle and shell may be distinguishable: embryonic, larval, and juvenile (postmetamorphic). They can signal not only phases in the development of the animal but also changes in its mode of life. The stages can last for varying amounts of time from species to species: the pelagic larval stage is quite long (weeks to months) in planktotrophic linguliforms and much shorter (days) in lecithotrophic craniiforms and rhynchonelliforms. The terminology used to identify these ontogenetic stages, however, is confused because it has been applied differently by paleontologists and morphologists (WILLIAMS & BRUNTON, 1997; WILLIAMS, LÜTER, & CUSACK, 2001; WILLIAMS, 2003) and neontologists and embryologists (FREEMAN, 1999, 2000, 2001, 2003; FREEMAN & LUNDELIUS, 1999, 2005; G. FREEMAN, personal communication, 2005). In some cases, the same terms (e.g., brephic) have been used to refer to different entities. In order to make the existing literature in each of these two fields more easily accessible to all, both terminologies are discussed below, beginning with the neontological (see also LÜTER, herein, p. 2321). Understanding the processes by which these features of mantle and shell are formed can imbue them with different meanings than can a static view of morphology alone.

Mantle formation and shell deposition are different processes that can occur at different times in brachiopod development. Mantle can form for the first time at different stages of development; it does not form at the same stage of development in all living (or apparently all fossil) brachiopods. Mantle can begin to form during embryogenesis (as in *Lingula*), but not all brachiopods do this. Mantle that forms during embryogenesis is small, roughly the diameter of the egg. Mantle forms more commonly during the larval period (as in *Discinisca*), although mantle lobes are present in the embryos and larvae of both craniiforms and rhynchonelliforms. The mantle reverses during metamorphosis in rhynchonelliforms but does not reverse in craniiforms.

Mantle always forms prior to shell formation, but shells may form on those mantles quite some time following the formation of the mantles; shell can form on mantle that was formed at different developmental stages. Mineralized shell always forms at or immediately after metamorphosis and only very rarely before; this is true for extant representatives of all three subphyla (with shells). Only two exceptions are known: in *Terebratalia* larvae that have been prevented from metamorphosing (FREEMAN, 1993a), and in the siliceous mosaics formed by *Discinisca* swimming larvae (WILLIAMS, CUSACK, & others, 1998), which may or may not be considered the same as more typical shell formation occurring at metamorphosis. Mosaics of mineralized tablets may form during either embryonic or larval periods (*Discinisca*); WILLIAMS, CUSACK, and others (1998), and WILLIAMS (2003) referred to both as the first-formed coat.

Neontological terminology refers to the protegulum as the shell formed on mantle formed during the embryonic or larval stages, before metamorphosis. Brephic shell is the first-formed shell after metamorphosis, laid down on new mantle formed after metamorphosis, during the juvenile stage. WILLIAMS, CUSACK, and others (1998) and WILLIAMS (2003) referred to brephic shell as shell that forms on mantle formed during the larval period, so differs from the neontological definition of the word. Neanic shell refers to shell formed on mantle formed during the adult stage of development.

Traces of the earliest growth stages of the shell can be preserved on mature brachiopod shells irrespective of their geological age or of the composition of the juvenile integument. Because development cannot be observed directly in fossils, a discussion of the terminology of WILLIAMS (2003) is retained here (below) in order to clarify the definitive body of literature by WILLIAMS (1955, 1956, 1970a, 1973, 1997, 2003) on brachiopod shell formation, which dominates the paleontological literature. In WILLIAMS's terminology, embryonic, larval, and juvenile shell refers to shell that has formed on embryonic, larval, or juvenile (postmetamorphic) mantle. Thus, the first-formed coat is that cover secreted by the newly differentiated collective of mantle epithelial cells (the embryonic mantle of FREEMAN & LUNDELIUS [1999, p. 199], which is roughly the "diameter of the egg"). The first-formed shell may be enclosed by mature shell secreted by an incipient mantle lobe developing around the collective. This arrangement signifies that the embryo had settled on the substrate before further growth took place (lecithotrophic larvae). On the other hand, the first-formed shell may be enclosed by the brephic shell (larval in WILLIAMS's terminology; juvenile [from larval mantle] in FREEMAN's), which is separated from the encircling mature shell by a growth disturbance, the lamellar ring of WILLIAMS, LÜTER, and CUSACK (2001). The ring more or less coincides with the settlement of the animal on a substrate and indicates that postembryonic growth (of mantle) took place before settlement (of planktotrophic larvae).

Three styles of development characterize the shell ontogenies of living brachiopods (Fig. 1897). In planktotrophic living lingulids, the first-formed shell (the protegulum of YATSU, 1902) is a single organic sheet that ruptures transversely to the body axis, and the outwardly succeeding brephic shell (formed on larval mantle) consists of separate valves, each delineated by a lamellar ring. In planktotrophic living discinids, the first-formed shell (on embryonic mantle) consists of two separate, opposing valves, each covered externally by a mosaic of siliceous tablets that also ornaments the surface of the brephic shell up to its bounding lamellar ring (WILLIAMS, LÜTER, & CUSACK, 2001). The larvae of living craniiforms (NIELSEN, 1991) and rhynchonelliforms (STRICKER & REED, 1985a, 1985b) are lecithotrophic, and their first-formed coats are two separate valves internally coated with calcitic granules.

The distinctive features of the early ontogeny of living lingulids are unlikely to be older than the Late Paleozoic (Fig. 1897). BALINSKI (1997a) has shown that the first-formed shell of Devonian lingulids are a pair of cup-shaped structures ornamented by pits, tubercles, and radiating setigerous ribs, which must have been secreted by two separate epithelial collectives. Identical structures have been found in a Silurian zhanatellid (L. E. HOLMER, personal communication, 02 September 2002). Traces of the first-formed shells in Lower Paleozoic linguloids are rare, but there is no evidence to contradict BALINSKI's assumption (1997a; see also FREEMAN & LUNDELIUS, 1999). HOLMER (1989, p. 52–67) identified the lamellar rings bounding subcircular to oval juvenile valves in many Cambro-Ordovician linguloids but not a first-formed valve, except in the acrotretide *Eoconulus* where it is an irregularly circular structure that must have been secreted by an independent collective. The entire shells of some linguloids, like those of zhanatellids, are pitted, presumably by the imprints of polymeric vesicles secreted beneath the juvenile cuticle and the mature periostracum.

The prospect that the first-formed shell of Early Cambrian linguloids consisted of independently secreted valves accords with the evidence of embryonic shell secretion in other linguliforms. The siliceous mosaics and bounding lamellar rings of the independently secreted juvenile valves of living discinids also characterize the late Silurian *Opatrilkiella*, the oldest known discinid (WILLIAMS, 2003; but see also CHEN, HUANG, & CHUANG, 2007), although the well-defined larval shells (shell formed on larval mantle) of older discinoids, ranging back to the Ordovician, lack tablet imprints. Yet the juvenile shells of acrotretides, one of the earliest known linguliform groups, are also pitted but with imprints of tablets that, on the basis of their preservation, are less likely to have been siliceous and may even have been calcitic (WILLIAMS, 2003; although the evidence is questionable (CARLSON, herein, p. 2891). The genealogical significance of the possibly different mineralogies of discinoid and acrotretide shell mosaics has yet to be resolved. Was the exocytosis of mosaics, albeit of different composition, a synapomorphy of both groups; or were the possibly differently composed tablets secreted by

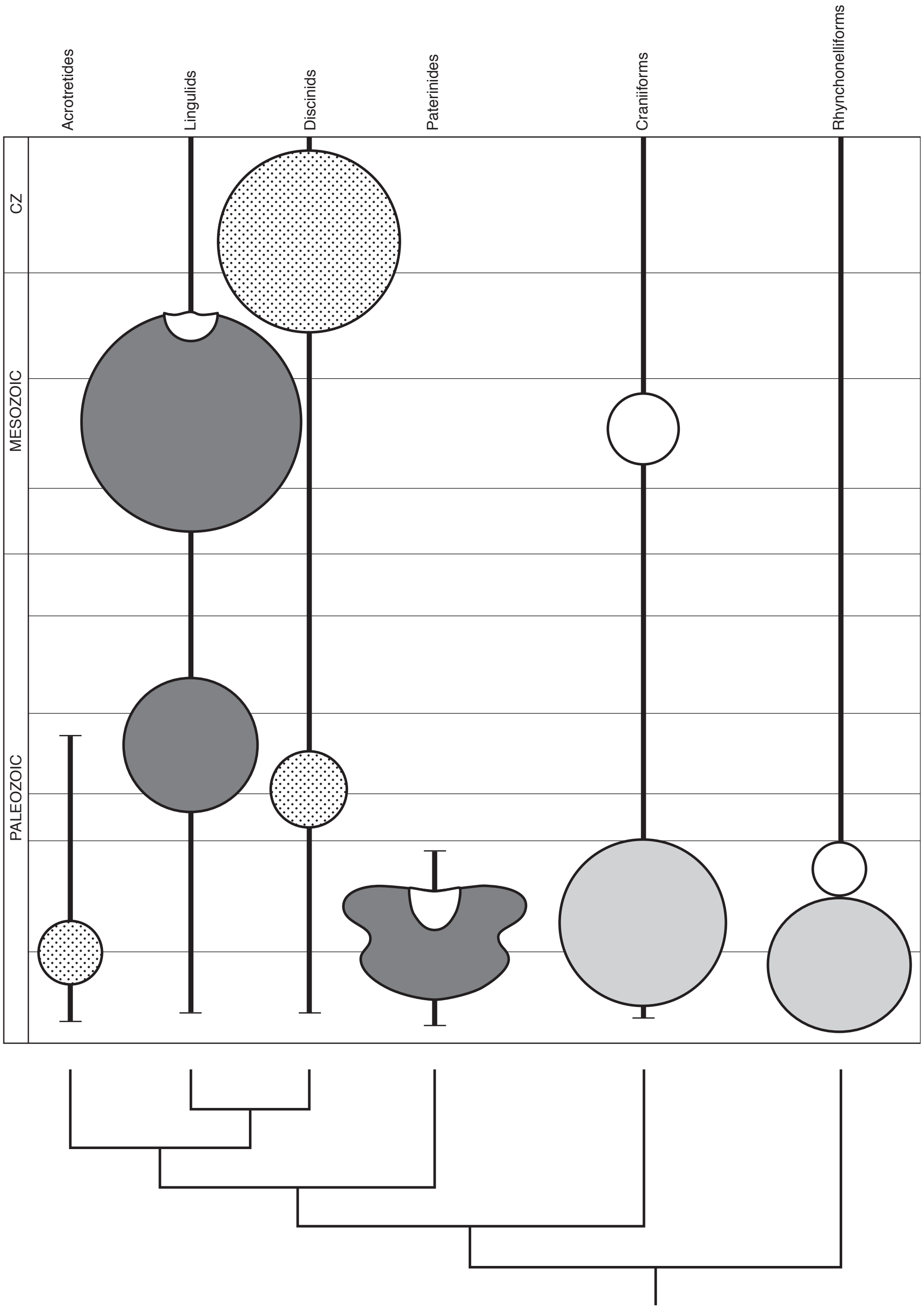


FIG. 1897. Phylogenetic distribution of clearly identified embryonic, larval, or undifferentiated juvenile shells of rhynchonelliforms, craniiforms, and most linguliform groups plotted near their first appearance in the stratigraphic record. Diameter of schematic shells scaled to actual size (5 mm = 50 µm); *open circles* indicate embryonic mantle and shell; *shaded circles* indicate larval mantle and shell; *light shading,* organocalcitic; *dark shading,* organophosphatic; *stippled pattern,* a mineralized mosaic (adapted from Freeman & Lundelius, 1999, 2005; Williams, 2003).

independently developing regimes? Either way, the regime(s) constitutes evidence that at least one group of protostomes secreted a mineralized cover of discrete units before developing a continuous shell. Such mosaics possibly functioned as ultraviolet reflectors during the planktotrophic stage of growth (WILLIAMS, 2003), or possibly as a less dense, lighter weight, and more flexible type of protection from predation prior to settlement [see also herein, p. 2891]. Shells mineralized on larval mantle of the remaining lingulates, the siphonotretides (WILLIAMS, HOLMER, & CUSACK, 2004), are also well defined by lamellar rings, confirming planktotrophic phases in their early ontogeny. An interesting feature of Early Paleozoic lingulate larval shells is that they appear to have been significantly smaller than those of their living descendants. Acrotretide larval shells, for example, are well within the upper limit (225 µm) given by FREEMAN and LUNDELIUS (1999, p. 211) for the diameter of lecithotrophic shells (but see also FREEMAN & LUNDELIUS, 2005). Acrotretides are micromorphs and many species could have been epiplanktonic in adult life, but the larval shells of other contemporaneous lingulates are also small (Fig. 1897).

The embryonic and larval shells of the paterinate linguliforms, the oldest known brachiopod stock, are especially interesting. They may be ornamented by pustules (*Micromitra*) or by pits that cover the entire shell (*Askepasma*) and probably represent imprints of vesicles on a cuticular-periostracal coat. Features of the *Micromitra* juvenile shell are also significant. The first-formed shells of both valves are creased by transverse furrows (possibly metameric traces), while the dorsal valve is quadrilobate and has been interpreted [perhaps incorrectly; see CARLSON, herein, p. 2834] as having accommodated two pairs of larval setae in the manner of lecithotrophic rhynchonelliform larvae (WILLIAMS, POPOV, & HOLMER, 1998).

The modes of life of the lecithotrophic larvae of living craniiforms and rhynchonelliforms and the planktotrophic larvae of living linguliforms are different, but this seems not always to have been so. FREEMAN and LUNDELIUS (1999, p. 211) identified larval shells (shells mineralized on larval mantles), indicative of planktotrophy in all Paleozoic craniiforms, by the presence of lamellar rings (or other morphological changes) with diameters of more than 400 µm. They found that the first signs of lecithotrophy did not appear until the Late Jurassic (in *Craniscus*) and became evident independently and at different times in the genera *Isocrania* and *Crania* during the Tertiary.

Evidence for planktotrophy in the evolution of the rhynchonelliforms is no longer ambiguous (FREEMAN & LUNDELIUS, 2005). Clear evidence for planktotrophy in earlier rhynchonellates appears to be present in shells of Obolellata, Strophomenata, Protorthida, and Orthida. In many strophomenates, early growth stages are morphologically distinguishable from the rest of the shell (KEMEZYS, 1965). The protegular structures of incipient ribs and nodes occupy surfaces approximately 1 mm in diameter that may or may not be part of the mature shell. This interpretation would accord with that of P. RACHEBOEUF's (personal communication, 03 September 2002) interpretation of the early growth stages of chonetidines, where the presumed larval shell, approximately 1.5 mm long, is not delineated by growth disturbances but only by the appearance of costellae flanking a medial juvenile costa. BRUNTON (1966) observed growth banding in productides (ventral grooves, dorsal ridges) delineating umbonal shells, approximately 200 µm in diameter, which is within the size range of overlap indicating either lecithotrophic or planktotrophic larvae.

In general, traces of larval valves on the carbonate shells of early rhynchonelliforms may be less likely to have survived diagenetic crystallization (including silicification) than those on the phosphatic shells of linguliforms, and potentially less reliable evidence has to be used. Thus, the distribution of Early Cambrian *Kutorgina*, which is as widespread as contemporaneous linguliforms that had undoubted planktotrophic larvae, has prompted speculation that kutorginid larvae were also planktotrophic (POPOV & others, 1997). No known kutorginids, however, bear growth disturbances that support this assumption (L. E. POPOV, personal communication, 04 September 2002). Syntrophiidines, the probable sister group of the rhynchonellides (CARLSON, 1996), are among the oldest rhynchonelliforms known, and some, but not all, genera appear to bear umbonal features identifiable as juvenile valves (FREEMAN & LUNDELIUS, 2005).

Planktotrophy thus appears to be the ancestral condition for brachiopods as a whole, with lecithotrophy evolving independently in craniiforms and rhynchonelliforms, marking a significant feature of brachiopod evolution. The onset of lecithotrophy is first detected in the Pentamerida in the Late Cambrian or Early Ordovician, and in the Rhynchonellida, Atrypida, and Athyridida near the Ordovician-Silurian boundary. The onset of lecithotrophy in the Rhynchonelliformea has been associated with the developmental innovation of mantle reversal (FREEMAN & LUNDELIUS, 2005), a feature that distinguishes this clade from the Craniiformea and Linguliformea. Why lecithotrophy is not associated with mantle reversal in the Craniiformea is not known at present.

EVOLUTION OF THE INTEGUMENT (MANTLE EPITHELIUM)

[Alwyn Williams]

The brachiopod skeleton affords a comprehensive record of the evolution of the integument even though the mineral components are usually the only recognizable constituents of fossils. Shell surfaces may bear imprints of the periostracum and the secreting outer epithelium. Shell fabrics and textures reveal the nature of the organic substrates on which the mineral constituents were secreted, while cylindroid extensions of the plasmalemma and outer epithelium penetrate the shell through canals and punctae. As for the shell itself, three distinctive compositional and structural types have persisted throughout the geological record: the organophosphatic stratiform successions of linguliforms from the Early Cambrian (Tommotian); the organocarbonate laminar successions of indisputable craniiforms from the Early Ordovician (Arenig); and the organocarbonate fibrous successions of rhynchonelliforms from the Early Cambrian (Atdabanian). There are no known gradations between these types, and each has undergone fabric transformations. Such biomineral and structural differentiation inevitably prompts questions as to how three different secretory systems originated within the monophyletic brachiopods (see discussion herein, p. 2889).

The most profound differentiation of the brachiopod shell is compositional. The mutually exclusive organophosphatic or organocarbonate compositions of adult brachiopod shells throughout the geological record suggest an inability of the mantle to switch from one mineral-secreting regime to another after the initial divergence had taken place. This is not so in living discinids with shells composed of larval siliceous mosaics and adult phosphatic laminae (see also LÜTER, 2004). Umbonally, these successions are consecutively secreted by the same epithelial collective but with the secretion of the larval shell ceasing everywhere before the deposition of the adult shell. This hiatus in secretion is presumably brought to an end by a biochemical signal released with the first apatitic exudation initiating the growth of the adult shell (WILLIAMS, LÜTER, & CUSACK, 2001, p. 34). A more relevant switch in composition is that assumed to have characterized the secretion of the acrotretide shell with its inferred (and highly speculative; see Carlson, herein, p. 2891) juvenile calcitic mosaic succeeded by an adult apatitic sequence (WILLIAMS, 2003). If it existed, in such a bimineral-secreting regime a neotenous retention of the organic substrates and calcifying proteins ensuring the continuing deposition of an organocarbonate succession could have initiated the development of adult calcareous shells. Suppression of the secretion of a different mineral in larval stages of growth, on the other hand, would have given rise to a monomineral shell that is characteristic of the overwhelming majority of brachiopods. It is important to point out again, however, that the transition from carbonate to phosphate mineralization and respective organic substrates is not known to exist in any extant brachiopod, and the evidence for such a transition in fossil brachiopods is extremely slim and based on the lack of preservation of the purported carbonate larval precursor (see herein, p. 2891). The additional requirement of a heterochronic transition over evolutionary time puts a high burden on this hypothetical scenario.

The larval shell of a stem-group brachiopod, the organophosphatic-shelled *Mickwitzia*, is unknown (WILLIAMS & HOLMER, 2002). *Mickwitzia*, however, appears to be a sister group of organophosphatic-shelled lingulates, including acrotretides with larval mosaics that were possibly calcitic (WILLIAMS, 2003). It may also be chemicostructurally related to the presumed halkieriid *Micrina* with purportedly organophosphatic larval and adult shells and, more remotely, to other halkieriides with shells that were possibly calcareous (and chitinous) as well as phosphatic. In short, the exoskeletons of the presumed brachiopod ancestors must have been diverse in their chemicostructure and flexible in their secretory regimes in order to have been the source of apatitic-shelled and calcitic-shelled stocks, derived independently or one from another [see also discussion herein, p. 2889]. Present understanding of the chemicostructural evolution of the shell in relation to basic features of the body plan (WILLIAMS, HOLMER, & CUSACK, 2004) appears to favor the derivation of the organocarbonate-shelled brachiopods from the paterinates, the sister group of the lingulates (Fig. 1898), unless both mineralogical types evolved from nonmineralized ancestors. The paterinate body plan is essentially rhynchonelliform. The earliest rhynchonelliforms could, therefore, have been derived from a paterinate ancestor by the replacement of an organophosphatic, stratiform shell with GAGs and chitin by an organocarbonate foliate shell. Unless paterinates are actually more closely related to rhynchonelliforms than lingulates and evolved an organophosphatic shell completely independently of the lingulates, this phylogenetic scenario appears no more likely than any other (see CARLSON, herein, Fig. 1908). The conflict between mineralogy and morphology in the paterinates is a continuing puzzle in working out relationships among these early brachiopod groups, which remain unresolved (WILLIAMS, POPOV, & HOLMER, 1998).

The structural transformations of the brachiopod shell are less dramatic than the compositional changes, but they are more helpful in understanding the evolution of the phylum as a whole. The primary layer of all brachiopod shells has always been a uniform mineralized layer secreted on the periostracal substrate. In linguliform shells it is composed principally of GAGs with dispersed apatitic granules; in craniiform and rhynchonelliform shells it is composed mainly of calcite with some glycoprotein. The secondary layer, on the other hand, varies greatly in fabric. The plesiomorphy of the secondary layer of linguliforms is a stratified succession of apatitic laminae alternating with proteinaceous and chitinous substrates (WILLIAMS, 1997). The evolution of this layer involved the periodic secretion of lenses of GAGs with apatite, which, as revealed by postmortem dessication and fossilization, form chambers within the stratiform succession. The chambers may be sporadically distributed with aggregates of residual apatite as in paterinates (WILLIAMS, POPOV, & HOLMER, 1998) and siphonotretides (WILLIAMS, HOLMER, & CUSACK, 2004). More commonly, however, the chambers are arranged in rhythmic laminar sets with well-ordered apatitic structures. The most common fabrics are pillars orthogonal to lamination (columnar) and rods arranged like trellises (baculate). Although both fabrics characterize the earliest lingulates, the columnar sets are probably the

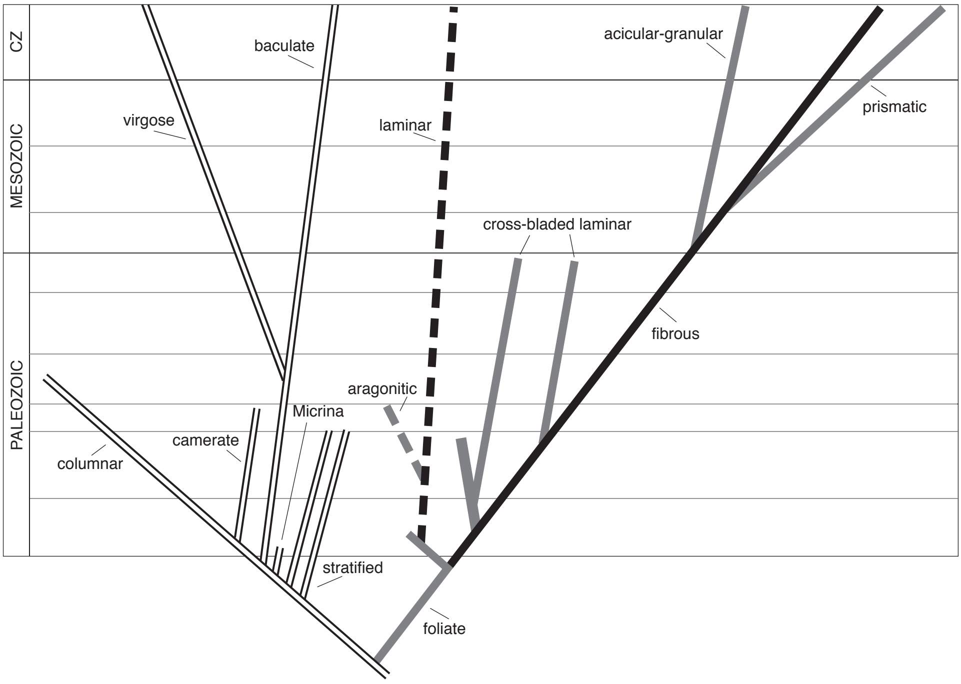


FIG. 1898. Highly schematic stratigraphic and phylogenetic pattern of main microtextures characterizing organophosphatic (linguliform, *open lines*) and organocarbonate (craniiform, *dashed lines;* rhynchonelliform, *shaded lines*) brachiopods (new).

older. Apatitic columns with axial canals are found in *Mickwitzia* (HOLMER, SKOVSTED, & WILLIAMS, 2002), acrotretides (HOLMER, 1989), and lingulide lingulellotretids (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999), which also include genera with baculi that had been secreted as linear aggregates of apatite (L. E. POPOV, personal communication, June 2003). Columnar lamination did not survive beyond the Devonian, and in some acrotretide stocks the columns were replaced by mineralized walls (camerate; HOLMER, 1989), presumably by a change in the specificity of the calcifying proteins. Baculate lamination, on the other hand, survives to the present day, as does a transformation whereby baculi are replaced by spheroidal aggregates and fascicles of apatite (virgose). Both fabrics are associated with a canaliculate system of organic strands free of apatitic columns (CUSACK, WILLIAMS, & BUCKMAN, 1999; WILLIAMS & CUSACK, 1999).

In summary, the chemicostructural evolution of the lingulate shell seems to have involved the phosphatization of an organic scaffold of chitinoproteinaceous laminae and their interconnecting canaliculate strands. The baculate lamination was apparently derived from the columnar lamination with each later giving rise respectively to virgose and camerate successions.

Despite the distinctiveness of these fabrics, some have arisen homoplastically. Partitions simulating camerae, for example, were developed in the baculate obolid *Experilingula* (CUSACK, WILLIAMS, & BUCKMAN, 1999). Siphonotretides, which lack a canaliculate system, were the most derived linguliform descendants of the hypothesized stem-group brachiopod (Fig. 1898). Paterinates, which also lack a canaliculated system, are more like rhynchonelliforms in body plan, while the canals associated with siphonotretide spines may be homologues of the setigerous tubes found in *Mickwitzia* (WILLIAMS, HOLMER, & CUSACK, 2004).

The preeminent secondary shell fabric of the rhynchonelliforms is fibrous. It is a common fabric of the Early Cambrian organocarbonate-shelled brachiopods and overwhelmingly so in living descendants. The fibers, each secreted discretely on a membranous sheath by an epithelial cell, are essentially the same throughout the geological record, differing only in their micromorphology. In contrast, the organic constituents of fibers and the primary and tertiary layers of living species are surprisingly wide ranging in molecular weight. This variability must reflect not only some selective doping with intercrystalline substrates but also molecular transformations of the calcifying proteins (CUSACK & WILLIAMS, 2001a), which apparently did not greatly affect fiber shape and stacking.

Changes of varying significance, however, did take place. The secondary shells of the Early Cambrian chileates, kutorginates, and obolellates are foliate with irregular laminae of tablets, probably secreted by epithelial collectives on membranous sheets (WILLIAMS, HOLMER, & CUSACK, 2004). This arrangement is possibly ancestral to the orthodox stacking of fibers in rhynchonellates (Fig. 1898 and see CARLSON, herein, Fig. 1908).

A more significant change was the transformation of flat fibers into sheets composed of laths. The laths were no longer secreted in glycoproteinaceous sheaths but on organic sheets as laminar aggregates (WILLIAMS, 1970a) that became cross-bladed (composite). This composite fabric evolved twice within a group (strophomenates) that was apparently monophyletic in other respects (although see CARLSON & LEIGHTON, 2001). Thus, many strophomenates with cross-bladed laminar shells evolved from the laminar-shelled billingsellides, but the productides were derived through the chonetidines from fibrous-shelled plectambonitoids (Fig. 1898; BRUNTON, 1972) that evolved independently of the rhynchonellate fibrous shells.

More recent transformations effected changes in the standard rhynchonelliform succession (Fig. 1898). In thecideides the fibrous secondary layer became reduced so that the shells of living species are composed mostly or entirely of primary shell (with a granular and acicular texture; WILLIAMS, 1973). Prismatic calcite as a tertiary layer (MACKINNON & WILLIAMS, 1974) or as lenses among secondary fibers is a homoplastic feature of the shells of the older pentamerides, athyridides, and spiriferides, as well as the terebratulides.

The chemicostructure of the craniiform shell is no more helpful than body plan features in determining the sister group of this subphylum. The inner layer of spirally growing calcitic laminae interleaved with their glycoproteinaceous substrates (CUSACK & WILLIAMS, 2001a) characterized the craniides from their first occurrence in the Lower Ordovician. The laminar-shelled craniopsides are now accepted as having first been recorded without question in the Ordovician (Llanvirn; L. E. HOLMER, personal communication, May 2003), although more questionable occurences extend the range into the Middle Cambrian; they were probably derived from the craniides. The foliate secondary shell of early rhynchonelliforms is, however, structurally comparable with the laths and laminae forming the inner succession of the primary layer of living craniides (CUSACK & WILLIAMS, 2001a). If the craniide shell succession, currently described as the primary layer, is a homologue of the foliate fabric, it is possible that it shares this feature (primitively) with one of the early rhynchonelliforms, like the chileates.

Rhynchonelliform and craniiform shells are commonly pierced by canals (punctae) or calcitic rods (pseudopunctae) that, contrary to previous widely held views, appear to have limited phylogenetic significance in defining major clades within the phylum. Various papillose outgrowths of the mantle have effected a punctate condition in craniids and most rhynchonelliforms (Williams, 1997). Only the endopunctae of terebratulides and thecideides, however, with their perforated canopies, can confidently be homologized and possibly derived from a Paleozoic spire bearer (possibly retziidines). In contrast, pseudopunctation, which was long regarded as an important synapomorphy of the strophomenates, involves two different structures that arose independently in four different stocks (Williams & Brunton, 1993).

In review, the chemicostructural evolution of the brachiopod integument broadly accords with the phylogenies of other features of the phylum. The dichotomy between the organophosphatic-shelled and the organocarbonate-shelled brachiopods is out of phase with the most important changes between the lingulate's linguliform and paterinate's rhynchonelliform body plans, however. The origin of the craniiform integument also remains in doubt. Not only is the tabular laminar shell unique (and possibly a novel tertiary layer), but the absence of the inner mantle lobe and lobate cells that develop in all other extant brachiopods is unique as well (Williams & Mackay, 1979). This latter difference might reflect the loss of marginal setae during adult growth.

Marginal setae are present in larvae of all extant brachiopods (one pair in linguliforms and two pair in rhynchonelliforms; see Lüter, herein, p. 2321), except for thecideoids and the terebratellids *Argyrotheca* and *Macandrevia.* They were apparently present in extinct brachiopods as well. They have been documented to occur in juvenile *Novocrania* (three pairs; Nielsen, 1991) but are absent in adult craniates as well as adult thecideidines and megathyrid terebratulides (Williams, 1997), both of which are very small bodied as adults. Adult setae, where they occur, are not retained from the larvae but are shed and then redeveloped. Setae appear to have been absent in paterinates, but this is difficult to confirm. *Heliomedusa* exhibits setae, and if classified as a discinid rather than a craniopsid (Chen, Huang, & Chuang, 2007), it indicates that setae were present primitively in at least some of the stratigraphically earliest brachiopods (also *Mickwitzia*, Holmer, Skovsted, & Williams, 2002; Balthasar, 2004a; herein, p. 2888). The presence of setae in linguliforms and rhynchonelliforms could be a derived condition, having evolved twice from nonsetigerous ancestors, or may possibly represent the basal condition, having been lost in the phoronids, paterinates, and adult craniates. Gustus and Cloney (1972) claimed that brachiopod setae are indistinguishable from chaetae in annelids and pogonophorans. Even though they may be very similar structurally, the homology of these structures among phyla is not yet clear (see also Lüter, 2000a, 2001b), but it is possible that they may be shared more broadly among lophotrochozoans (see Balthasar, 2004a).

EVOLUTION OF THE PEDICLE

[Alwyn Williams]

The pedicle is one of the most distinctive features of most Brachiopoda. It is basically an epidermal extension that secretes an adhesive polysaccharide, attaching the animal to the substrate. It is, however, a versatile organ of varying complexity, functioning not only as a holdfast but also as a burrowing device in *Lingula* (Emig, 1997b, p. 474) or an adjustable tether in the terebratulide *Parakinetica* (Richardson, 1997a, p. 441) and apparently in many strophomenates as well. It may atrophy as in the terebratulide *Neothyris* (Richardson, 1997a, p. 445) or not develop at all, as in craniides and thecideides. In extinct groups, the posterior part of the shell usually serves as a kind of natural cast, recording the morphology of the pedicle as well as its disposition relative to the valves. By this means, it is evident that the diversity in structure and function of the pedicle in living brachiopods has characterized the phylum throughout its geological record. The different modes of attachment can be traced throughout each of the three subphyla, and the evolutionary changes they underwent will be considered within this phylogenetic framework (see also CARLSON, herein, Fig. 1908).

The phylogenetic distribution of pedicles inferred to be present in early brachiopods, however, is far from resolved. It is widely held that true relationships are obscured by the use of the pedicle to identify all organs serving as brachiopods anchors (ROWELL & CARUSO, 1985, p. 1231). There are certainly gross anatomical differences between the coelomic cores of living lingulides and the cartilaginous cores of living terebratulide pedicles. Yet, their basic function of attaching linguliforms and rhynchonelliforms to a substrate is effected in all living species by a distal tip of pedicle epithelium, hypothesized to be homologous in all brachiopods possessing a pedicle that is capable of secreting adhesive mucin and etchants capable of dissolving hard substrates (WILLIAMS & others, 1997, p. 64). Moreover, this distinctive collective is surrounded by a variably developed chitinous cuticle, even in rhynchonellate brachiopods that otherwise lack chitin (WILLIAMS & HOLMER, 2002, p. 870; see also CARLSON, 1995). Accordingly, in this review, the term pedicle is used with the distal homologues of pedicle epithelium (and associated cuticle) in mind; the analogous, proximal parts of the organs will be further distinguished as coelomic or cartilaginous.

These terms, however, are inappropriate for living species of craniiforms, because their cementation is effected by an attachment area that is unlikely to be pedicle epithelium; this attachment area will hereafter be referred to as a holdfast. The developing larva bends or curls ventrally so that the posterior part of the body becomes located ventrally (C. NIELSEN, personal communication, 2005; LÜTER, herein, p. 2321). No pedicle structure develops, and the periostracum of the holoperipherally growing ventral valve also adheres to the substrate.

The site of the pedicle in the ventral valves of lingulides is posterior or posterodorsal to the juvenile part of the valve. It can vary from a groove in a posteromedial, dorsally inclined pseudointerarea to a foramen piercing the valve subcentrally (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 347–353). These extreme dispositions can be reconciled by taking into account the differential growth of the pedicles and ventral valves of living *Lingula* and *Discinisca* (Fig. 1899). In *Lingula*, the muscle-lined pedicle with its proximal chitinous cuticle and distal adhesive bulb is a cylindroid extension of the ventral body wall and coelom. In *Discinisca*, the muscle-filled pedicle is also an outgrowth of the ventral body wall but rotated ventrally into the plane of the valve so that it and its cuticular border are subtended within a posteromedial notch in the mineralized part of the ventral valve, with the apex of the notch indenting the posterior border of the juvenile valve. With further growth, the mantle lobe, secreting the mineralized valve at the corners of the notch, encroaches posteromedially to fuse into a continuous arc enclosing the pedicle sector (WILLIAMS, HOLMER, & CUSACK, 2004). In Paleozoic adult discinids, like *Orbiculoidea*, the fused lobes secreted an arc of shell that restricted the pedicle to a foramen.

These differences in the accommodation of the pedicles of linguloids and discinoids persisted throughout their geological records but with some variation, such as the lack of mineralization in the posteromedial pedicle sector of the discinoid *Trematis* and the development in the linguloid *Lingulellotreta* of a pedicle foramen within the pseudointerarea by fusion of the trough walls. An interesting deviation was the development of the enclosed pedicle foramen in the ventral valve of the linguloid *Dysoristus.* During adult growth, the pedicle foramen migrated anteromedially from the umbonal area by resorption along the anterior arc and the secretion of a plate along the posterior arc. Such a migration also characterized the siphonotretides (see below), but in *Dysoristus* the young pedicle must have emerged in a trough prior to the growth of an undivided pseudointerarea because all traces of the

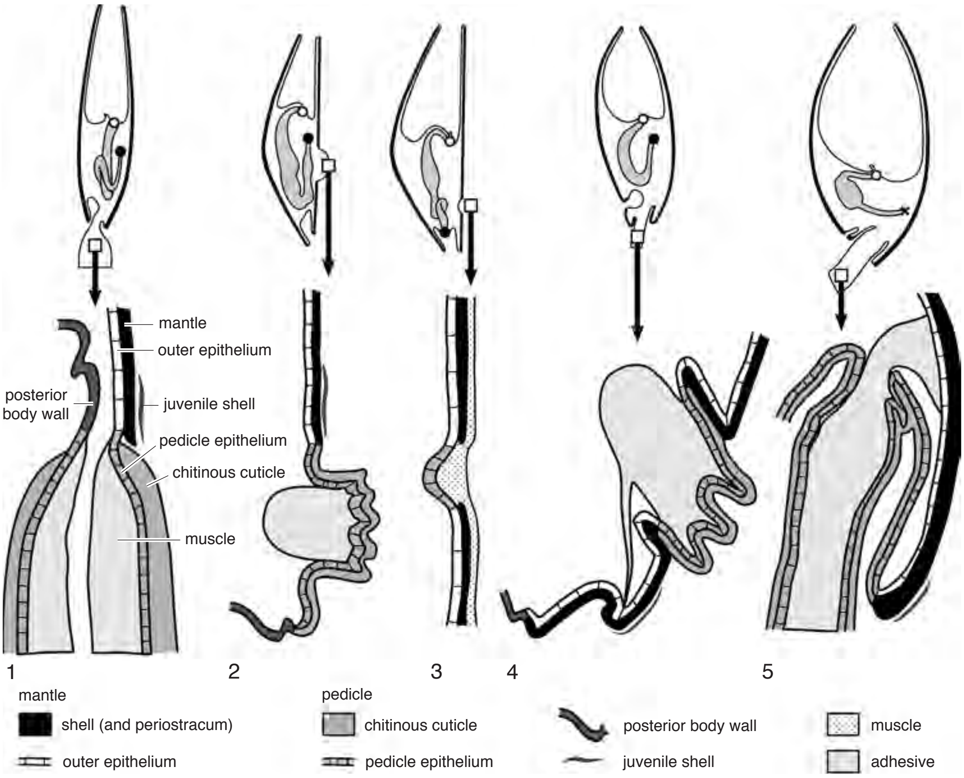


FIG. 1899. Different types of pedicle in relation to ventral valves and body plans as represented by disposition of gut (*open circle,* mouth; *filled circle,* anus; *x,* blind intestine) of *1, Lingula*; *2, Discinisca*; *3, Novocrania*; *4,* a kutorginate (hypothetical); *5, Terebratulina; 1–2,* linguliform type of pedicle growth; *3,* craniiform type; *4,* hypothetical early variant of rhynchonelliform type; *5,* rhynchonelliform type (new).

juvenile ventral valve have been destroyed by resorption.

The pedicle openings in acrotretide ventral valves vary in position from a slitlike foramen in the pseudointerarea of *Keyserlingina* posterodorsal of the apical juvenile ventral valve, to a rounded foramen enclosed within the juvenile valve as in *Ephippelasma*. HOLMER (1989, p. 63) traced the ontogeny of the pedicle opening in the acrotretide *Scaphelasma* from a notch indenting the ventral valve margin just posteromedially of its juvenile pitted mosaic to an oval foramen encroaching anteriorly by resorption into the mosaic and becoming closed posteriorly by the converging edges of the growing pseudointerarea. This growth, in relation to the secretion of the ventral valve, is virtually the same as that of *Discinisca*, and the shifts in the foramen sites can be attributed to the differential rates of growth of pedicle and valve. When the pedicle developed precociously in the juvenile phase of growth, its foramen would have been enclosed by pitted shell. Later development, however, would have resulted in the foramen lying partly, or even entirely, within the adult shell of the pseudointerarea. This is contrary to the views of WILLIAMS, BRUNTON, and MACKINNON (1997, p. 352), who concluded that the pedicle opening initially developed within the juvenile shell and subsequently shifted by resorption to a posterior position during adult growth in some acrotretides.

The pedicle openings of the remaining linguliform brachiopods, the lingulate siphonotretides and the paterinates, cannot be explained in terms of the differential growth of pedicle and shell of living lingulides. In siphonotretides, the pedicle opening originated forward of the posterior margin of the juvenile valve (Fig. 1899). It never indented the ventral pseudointerarea, which is invariably undivided and normally overhung by a beak bearing traces of the juvenile valve. During growth, the enlarging openings migrated anteromedially by the process of anterior resorption and posterior secretion. When surface migration of the foramen ceased, an internal apatitic tube usually developed (presumably secreted by outer epithelium). Pedicle tubes are repeatedly developed in lingulates but no others originated in the same way, although they all must have accommodated the same kind of muscular pedicle. Accordingly, it is assumed that the siphonotretide pedicle differentiated from within the epithelial attachment area that secreted the juvenile ventral valve, and that the pedicle stem cells migrated to that site as a detachment of the posterior body wall attachment area during larval growth (Williams, Holmer, & Cusack, 2004).

Impressions of the paterinate *Dictyonina* attached to the sponge *Choia* are preserved in the Middle Cambrian Burgess Shale (Whittington, 1980). They show a fringe of setae around the shell except for the wide, straight posterior margin, possibly with a short holdfast. This setal arrangement is consistent with the hypothesis that the paterinate posterior margin is homologous with the strophic posterior margin of rhynchonelliforms (Williams, Popov, & Holmer, 1998). In this context, the paterinate ventral valve has a well-developed orthocline to apsacline interarea that may be divided by a wide delthyrium commonly with a convex mineralized cover (homeodeltidium, structurally indistinguishable from a pseudodeltidium). The shell is not articulated by mineralized devices, but the edge of the ventral interarea of *Askepasma* has been interpreted as bearing traces of an outer or pedicle epithelial junction and the interareas of both valves as having been juxtaposed as in early strophic rhynchonelliforms (Williams, Popov, & Holmer, 1998, p. 242). The presence of a homeodeltidium in some paterinates (and presumably a cuticular arch in others) has prompted the assumption that a posteromedial muscle system, like diductors, passed between the valves beneath a shallow-based pedicle (Williams, Popov, & Holmer, 1998, p. 246). Should this have been so, the paterinate pedicle may have had an axial coelom, but this is highly speculative.

The living craniiforms differ from all other extant brachiopods in their cemented ventral valve without a pedicle and in the orientation of their straight body axis relative to a larval attachment area that is located ventrally but represents the posterior part of the larval body that has bent ventrally (Nielsen, 1991, fig. 8; C. Nielsen, personal communication, 2005). The ventral valve grows holoperipherally around this initial holdfast in a plane that is more or less congruent with the straight long axis of the gut lying between the mantle cavity and the posterior body wall (Fig. 1899.4 and 1900). This relationship must have characterized the earliest craniides and the Cambrian craniopsides for even the shells of free-living species bear no openings that could have contained pedicles, only apical cicatrices (L. E. Popov, personal communication, 2002), indicating that attachment has always been restricted to early stages of growth.

The ontogeny of the pedicle of living rhynchonelliforms has been broadly known for well over a century. But electron microscopic studies of the larval and juvenile pedicle of terebratulides, notably by Stricker and Reed (1985a, 1985b), have revealed further details that also confirm past interpretations of the impressions of pedicle bases in extinct rhynchonelliforms.

In the larval stage, a pedicle lobe is differentiated posterior to a ringlike mantle lobe that, after inversion, develops into the dorsal and ventral valves. In effect, the pedicle arises between the valves despite the fact that during further growth, it is normally confined to the delthyrium of the ventral valve and may become completely

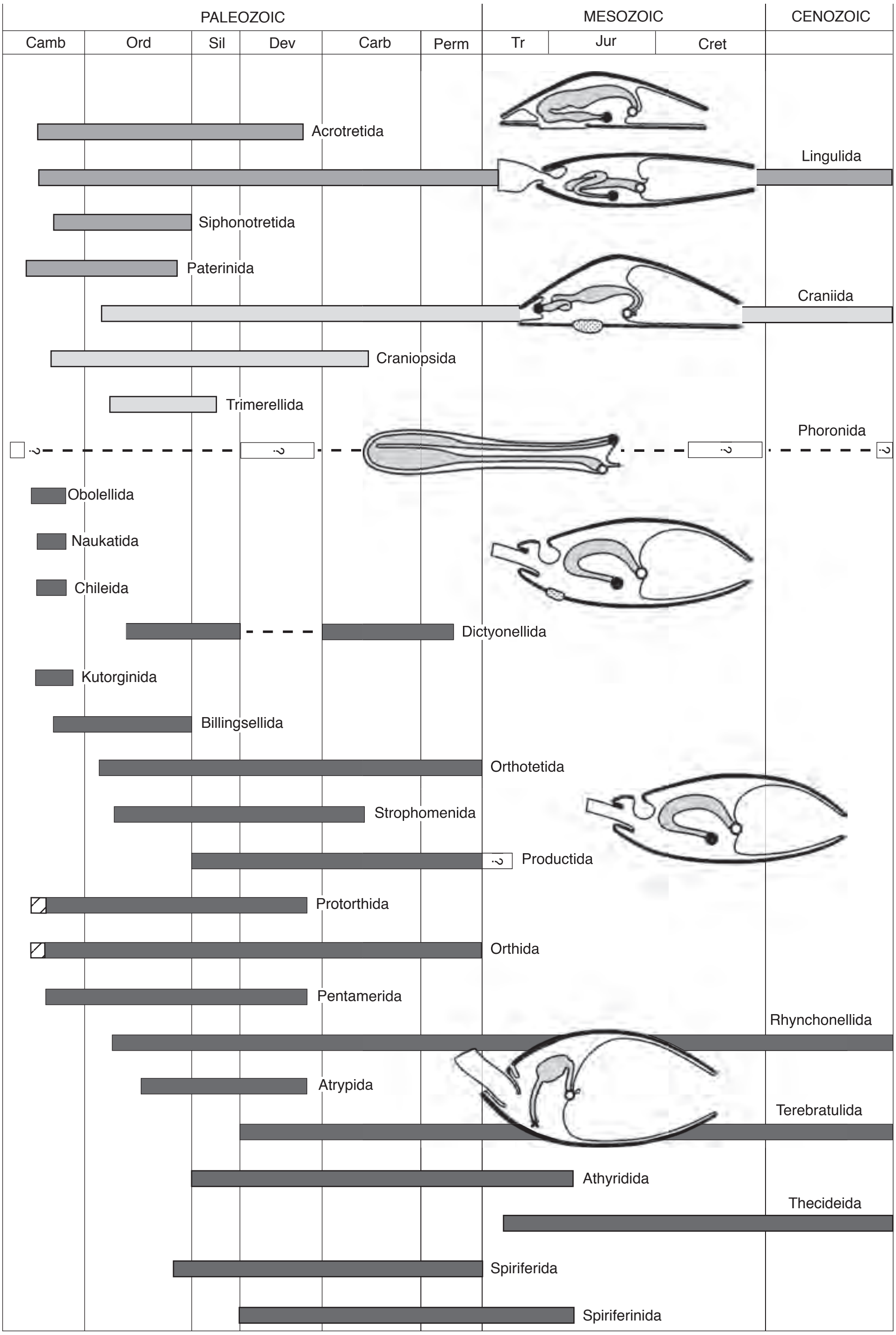


FIG. 1900. Known and inferred structures and dispositions of pedicles, holdfasts, and guts characterizing major groups of brachiopods: discinids and lingulids; craniids; phoronids; hypothetical chileid; hypothetical kutorginate; rhynchonellates (new).

enclosed there by a symphytium (Williams & Hewitt, 1977). The pedicle also differs from its lingulate analogue in its proximal differentiation into a capsule of connective tissue (Stricker & Reed, 1985b, p. 254), forming a deep-seated pedicle base that fills the umbonal chamber of adult ventral valves (Fig. 1899). Muscles attached to the capsule adjust both pedicle and shell to each other. They may be restricted to one median pedicle muscle attached to the ventral valve forward of the umbonal chamber but more usually consist of two pairs of ventral and dorsal adjustors (Williams & others, 1997, p. 67).

The development of a pedicle capsule is accompanied by a forward (anterior) shift of muscle systems controlling valve movement with a concomitant displacement of the ventral muscle scars outside the umbonal chambers (Williams, Brunton, & MacKinnon, 1997, p. 387). [Alternatively, the development of a pedicle capsule in derived rhynchonelliforms can be considered as a posterior shift in the umbonal chamber, relative to the valve commissural plane and muscular system; see Carlson herein, p. 2850.] Such displacements are normally recorded in fossilized adult shells. The geological record confirms that the development of a pedicle from a posterior larval lobe is a synapomorphy of all later rhynchonellates: the rhynchonellides, spire-bearers (*s.l.*), and terebratulides. Pedicle lobes also appear to be present in the larvae of cemented thecideides (Lacaze-Duthiers, 1861).

In older rhynchonelliforms, the ventral muscle system occupied the umbonal chamber, which suggests that the pedicle capsule was not developed. In orthides and the pentameride syntrophiidines (hypothesized to be the sister group of the later rhynchonellate clade; Carlson, 1996), the umbonal chamber contained adjustor scars as well as an apical pedicle callist that probably represents the ventral attachment zone of a shallow-based pedicle (Williams & others, 1996, p. 1179). A shallow-based pedicle must also have characterized protorthides and early strophomenates, although adjustors were not developed or too weakly so to have left identifiable scars (Williams & others, 1996, p. 1179). The strophomenate pedicle also underwent transformations that resulted in a relocation of the pedicle and its postlarval loss in most lineages. The pedicles of the oldest strophomenates (billingsellides, early strophomenides, and orthotetides) were evidently fully functional albeit restricted to the delthyrial apex by an undivided deltidium or pseudodeltidium. In younger strophomenates, including later strophomenides, the pseudodeltidium is entire, with the pedicle foramen shifted to a supra-apical position. The juvenile pedicle was commonly enclosed in an erect, mineralized tube (pedicle sheath) but was lost in adults that became free-lying or cemented to the substrate by umbonally secreted polysaccharide (orthotetidines) or spines (productides; Williams, Brunton, & MacKinnon, 1997, p. 357–359). It is noteworthy that, in early strophomenates, a medial gap existed between the edges of the pseudodeltidium and a complementary dorsal cover (chilidium). As the gap could not have accommodated the pedicle, it must have been closed by inner epithelium presumably homologous with a posterior body wall (Williams, Brunton, & MacKinnon, 1997, p. 358), as can be postulated for a similar gap in the kutorginate shell described below. This epithelial strip would have covered the diductor muscles passing between the valves and probably would not have been breached by an anus. The shift of the pedicle from an apical to a supra-apical site during strophomenate evolution could have been a manifestation of the migration of pedicle stem cells from a posterior body wall collective as in the lingulate siphonotretides. The transformations effecting these shifts, however, would have occurred convergently and at different phylogenetic rates.

The rhynchonelliforms still to be considered, the chileates, obolellates, and kutorginates, are among the earliest known brachiopods and did not survive beyond the Middle Cambrian, except for the later Paleozoic dictyonellidines, which seem to have an affinity with the chileides (see CARLSON, herein, Fig. 1908). The three groups are morphologically disparate as befits their taxonomic status, but they have two features in common [whether shared due to common ancestry or not is not yet clear; see CARLSON, herein, p. 2878]. First, their body plan, as mirrored by their shells, was essentially that of a strophic rhynchonelliform with devices effecting a crude articulation of the valves that could have been juxtaposed about a transverse plane of folding of the gut. Secondly, there are openings at or forward of the apices of their ventral valves that could feasibly be interpreted as the passageways of holdfasts, like pedicles. The prospect that the groups had folded guts and pedicles emerging from their ventral valves is challenged by the discovery of a complete silicified shell of the kutorginide *Nisusia* with a supra-apical opening in the ventral valve and a cylindroid protrusion, approximately 2 mm in length and in proximal diameter, emerging between the pseudodeltidium and the dorsal interarea (ROWELL & CARUSO, 1985).

If the protrusion between the valves is silicified feces, as suggested by ROWELL and CARUSO (1985), the supra-apical foramen could have accommodated a pedicle (POPOV & WILLIAMS, 2000, p. 210), and the gut would have been aligned like that of craniiforms, not rhynchonelliforms [possibly as a shared primitive feature among early brachiopods; see CARLSON, herein, p. 2883]. ROWELL and CARUSO (1985) gave a detailed account of why they rejected the possibilities that the cylindroids were silicified pedicles or foreign objects in favor of their being coprolites, notwithstanding that feces of living brachiopods are ejected as mucin-bound pellets, 5–10 μm in size, every 15 minutes or so (RUDWICK, 1970, p. 123; JAMES & others, 1992, p. 294).

It is unlikely, but not impossible, that a wholly organic feature like a pedicle could have been silicified. If, however, the protrusion is a silicified pedicle cast composed of sediment, as the morphology of the cylindroids suggests (with ringed furrows replicating the wrinkled state of such pedicles), the kutorginide body plan could have been like that of the later rhynchonelliforms, but this would leave the supra-apical foramen without an orthodox function. In the belief that the protrusion was a fossilized pedicle cast, POPOV (1992, p. 406) advanced the possibility that the supra-apical foramen of *Nisusia* was a "rudiment of a hydrodynamic shell-opening mechanism," like the device he had proposed as occupying the large colleplax-backed opening in the chileate ventral valve. The anatomical topography of such a device, however, which would necessarily have been lined with ciliated epithelium, is too contrived to be feasible. More recently, POPOV (personal communication, 2002) suggested that the supra-apical foramen is a trace of an ancestral larval pedicle and that the cartilaginous pedicle is a later larval development in the kutorginates and such contemporaneous rhynchonellates as the orthides. It is also possible that the cylindroid was not part of the living kutorginates, which may have had a supra-apical pedicle and a body plan similar to that of later rhynchonellates, except possibly for the presence of an anus opening into the mantle cavity.

These conflicting interpretations of the extraordinary features of the *Nisusia* sample have been given in full because they present fundamentally different body plans for early rhynchonelliforms. If the *Nisusia* cylindroids are coprolites, the early rhynchonelliform body plan was similar to that of living craniides, and the holdfast, occupying the supra-apical or ventral apertures, may have been homologous with the craniide attachment area. If, on the other hand, the *Nisusia* cylindroids are pedicle casts, the early rhynchonelliform body plan would have been similar to that of later rhynchonellates (although possibly with an anus opening into the mantle cavity), while the supra-apical foramen is indeed a trace of transient larval attachment.

Both interpretations can be challenged. Most *Nisusia* occur as disarticulated valves, but cylindroids have been found in 15 of the 18 complete shells recovered from numerous thin, resistant beds throughout 12 m of strata (ROWELL & CARUSO, 1985). It is unlikely that excreta could have retained a constant shape in such a high proportion of shells collected (ROWELL & CARUSO, 1985, p. 1227). Yet the other interpretation, that the supra-apical foramen contained a transient larval holdfast prior to the growth of a posteromedial pedicle, also has its weaknesses. It is based on the assumption that two areas of adhesive epithelium differentiated independently in different sites during larval growth. Moreover, even if these areas were cytologically distinct, they could have remained fully functional in some mature kutorginates, like *Trematosia*.

In deciding which of these interpretations is more feasible, account has to be taken of the gross morphology and inferred anatomy of early rhynchonelliforms. All three classes, the chileates, obolellates, and kutorginates, are typified by strophic shells in the rhynchonellate style but with perforated ventral valves and a posteromedial gap subtended by a delthyrium with an apical pseudodeltidium. In some obolellides, the ventral perforation may extend anteriorly by resorption as a slitlike, superficial extension (*Trematobolus*) or may perforate the concave pseudodeltidium (*Naukat*). In chileides and dictyonellides, the opening is greatly enlarged by resorption and is commonly underlain posteriorly by a colleplax, and an open delthyrium may be present. The opening has been interpreted as a means of facilitating the hydraulic opening of the shell (POPOV, 1992), which seems increasingly unlikely. The preferred interpretation is that the subtriangular opening accommodated a cuticular holdfast (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 360). In the absence of data on the ontogeny of these openings, it is assumed that initially they were underlain by a group of mucus-secreting cells located within the juvenile mantle, as in siphonotretides rather than strophomenates.

It is also feasible to consider the possibility that these three groups had a potentially dual system of attachment, capable of activation at different times in ontogeny and probably involving stem cell collectives with different modes of secretion and organ growth at different phases of phylogenetic differentiation. Thus, in chileates, ventral valve attachment was paramount, presumably by a mucinous pad (compare WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 321). In most kutorginates, on the other hand, attachment was dominantly by a (possibly) coelomic pedicle, like the silicified cylindroid of *Nisusia*, while the supra-apical foramen apparently accommodated nothing more than a transient, larval mucinous pad. In effect, a craniiform-style holdfast may have been as much a feature of the three oldest classes of rhynchonelliforms as a coelomic pedicle but was eliminated with the emergence and evolution of the rhynchonellates.

In review, it seems that brachiopods have attached to the substrate by one of three kinds of holdfast (Fig. 1899–1900): first, a pedicle, developed from the posterior body wall and coelom, tethering a shell with a gut folded parallel with the commissural plane (lingulate type); second, a pedicle developed from a larval pedicle lobe (with or without a capsule), anchoring a shell with a bent gut ending blindly, but possibly evolving from an open gut folded parallel with the commissural plane (rhynchonellate type); and third, an adhesive holdfast within the ventral valve of a shell enclosing the gut lying parallel to the commissural plane (craniate type).

Many transformations affected these attachments during brachiopod evolution. The pedicles of the lingulate siphonotretides and the later strophomenates were accommodated in the ventral valve apparently after having migrated there as epithelial attachment areas. Cementation, with a concomitant loss of pedicle, occurred in the lingulates and especially the strophomenates and rhynchonellates. In craniates, cementation was effected by mucinous holdfasts. Craniate-type holdfasts may also have been present, at least during larval growth, in early rhynchonelliforms, which were additionally equipped with coelomic pedicles. This interpretation necessarily concedes that mucinous holdfasts may have been associated with different developments of the rectum. In living (and presumably stem-group) craniiforms, migration of the holdfast *cum* ventral mantle fold attachment area to the posteroventral side of the larva is followed by the formation of an anus breaching the posterior body wall connecting the two valves. In early rhynchonelliforms, however, an attachment area giving rise to a coelomic pedicle was differentiated early within the posterior body wall, and the rectal region of a bent gut either terminated blindly or breached the anterior body wall in the early phases of rhynchonelliform evolution.

EVOLUTION OF MUSCLE SYSTEMS

[Sandra J. Carlson]

The presence of two mineralized valves is characteristic of all brachiopods (except for phoronids, if they are considered as nesting within Brachiopoda). The muscle systems in extant brachiopods, and those reconstructed from the scars on the interior of fossil brachiopod valves, serve largely to connect the two valves to one another and move them relative to one another (Williams & others, 1997). Some extant brachiopods (e.g., craniids and discinids) possess muscles that move the lophophore slightly relative to the valves (brachial elevators and protractors); others (e.g., rhynchonellides and terebratulides) have adjustor muscles that move the valves relative to the pedicle. The principal muscles, however, extend between dorsal and ventral valves (originate on the dorsal valve and insert on the ventral valve) and effect movement between them.

Comparing musculature among the major groups of extant brachiopods, it is clear that the brachiopods lacking valve articulation have more muscles overall, particularly more transverse, lateral, and oblique muscles, enabling various types of sliding and twisting movements of the two valves relative to one another. Brachiopods articulating by means of teeth and sockets are limited functionally to the rotation of one valve relative to the other in a plane parallel to the sagittal plane; transverse, lateral, and oblique muscles are not functionally required or present.

Extant brachiopods possess either columnar or tendonous muscles. Extant inarticulated (and thecideide) brachiopods have columnar muscles (Hyman, 1959; Williams & Rowell, 1965d; Rudwick, 1970). Columnar muscle fibers extend from their origin on one valve to their insertion on the other, are often perpendicular to the valves, and are thus relatively short, like the adductor (central and umbonal) muscles in inarticulated brachiopods. The cross-sectional area of columnar muscles relates to the power they can generate in contraction—the larger the area, the stronger the force the muscle can generate (Alexander, 1968). In contrast, muscle length relates to the total amount of contraction possible (effecting the degree of gape angle)—the longer the muscle, in general, the greater the amount of contraction possible. The various oblique, lateral, and transverse or transmedian muscles typically originate and insert at lower angles (<90 degrees) to the valves and are commonly longer than the adductors.

Extant articulated brachiopods (with the exception of thecideides) have tendonous muscles (Hyman, 1959; Williams & Rowell, 1965d; Rudwick, 1970), where the contractile muscle fibers extend only a short distance from their origin or insertion on the valves and are united by a tendon spanning the mantle cavity. Tendon is almost inextensible, compared to the muscle fibers themselves, and the power and degree of muscle contraction in articulated brachiopods is dictated by the length and area of the muscle fibers only, not the tendon.

Tracing particular muscles in living organisms from their origin on one valve to their insertion on the other is the most direct way to determine the correspondence of muscle scars among dorsal and ventral valves. In extinct forms only, the scars remain, distinguished by differences in shell fabric and occasionally low ridges or platforms; direct tracing of muscles is not possible. For this reason, multiple interpretations of corresponding muscle origin and insertion scars in extinct brachiopods are to be expected (e.g., WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 385, fig. 346; HOLMER & POPOV, 2000, fig. 75; BASSETT, POPOV, & HOLMER, 2001). Thus, when considering the function and evolution of muscle systems, it is all the more important to be able to construct defensible hypotheses of muscle homology among extinct and extant brachiopods (WILLIAMS & others, 1997; HOLMER & POPOV, 2000; POPOV & HOLMER, 2000a, 2000b, 2000c; BASSETT, POPOV, & HOLMER, 2001). Determining the relative positional relationships of muscle scars to one another is necessary to establish a framework for interpreting the evolution of muscle systems in all brachiopods.

Linguliformea

Musculature is quite variable among linguliform brachiopods, inferred on the basis of muscle scars preserved on the interior of the valves (compare WILLIAMS & others, 1997, p. 83, fig. 82; HOLMER & POPOV, 2000, fig. 7, 39, 44, 51, 75; WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 386, fig. 346). One of the difficulties in reconstructing musculature and determining muscle homologies in all linguliforms is that all are extinct except for a few representatives of the discinids and lingulids. The living lingulids are atypical compared to other inarticulated brachiopods, as a result of their burrowing behavior and infaunal life style, thus rendering them less than ideal to serve as representatives for the entire subphylum. Discinids, therefore, will be referred to as the most plausible example of the primitive type of linguliform musculature.

Discinisca, an extant discinid brachiopod, has paired posterior and anterior adductor muscles that dominate the valve interiors in terms of muscle scar area (WILLIAMS & others, 1997, p. 84, fig. 83). Paired posterior, internal, and lateral oblique muscles are also present, as well as small paired brachial retractor muscles. *Schizotreta* (WILLIAMS & others, 1997, p. 45, fig. 39), an Ordovician-Silurian discinoid, has smaller anterior adductor scars, and the valve musculature appears to occupy a smaller area located more posteriorly in the valves than in *Discinisca* and suggests that closing the valves with the anterior adductors has evolved as the dominant function of the muscular system in living *Discinisca*.

Lower Cambrian (Atdabanian) *Heliomedusa* has recently been assigned to the discinids (CHEN, HUANG, & CHUANG, 2007) and removed from the craniopsoids (JIN & WANG, 1992; HOU & others, 2004) on the basis of characteristic discinid features (e.g., primarily the presence of a ventral pedicle foramen and median ridge) preserved on a larger sample of well-preserved specimens collected from the Chengjiang fauna. The identity of numerous internal features characterized by JIN and WANG (1992) are reinterpreted by CHEN, HUANG, and CHUANG (2007) as entirely different features, including the identity of the dorsal and ventral valves, and underscores the difficulty of attributions of soft anatomy even in abundant, well-preserved, ancient fossils. Muscle scars are not especially well preserved in these fossils, but *Heliomedusa* appears to have elongate, platformlike muscle attachments. A small, pear-shaped central muscle scar is present in the ventral valve (as interpreted by CHEN, HUANG, & CHUANG, 2007, *contra* JIN & WANG [1992] who identify this as the dorsal valve), as is a tear-drop–shaped anterior muscle scar (JIN & WANG, 1992). On either side of the central muscle is a

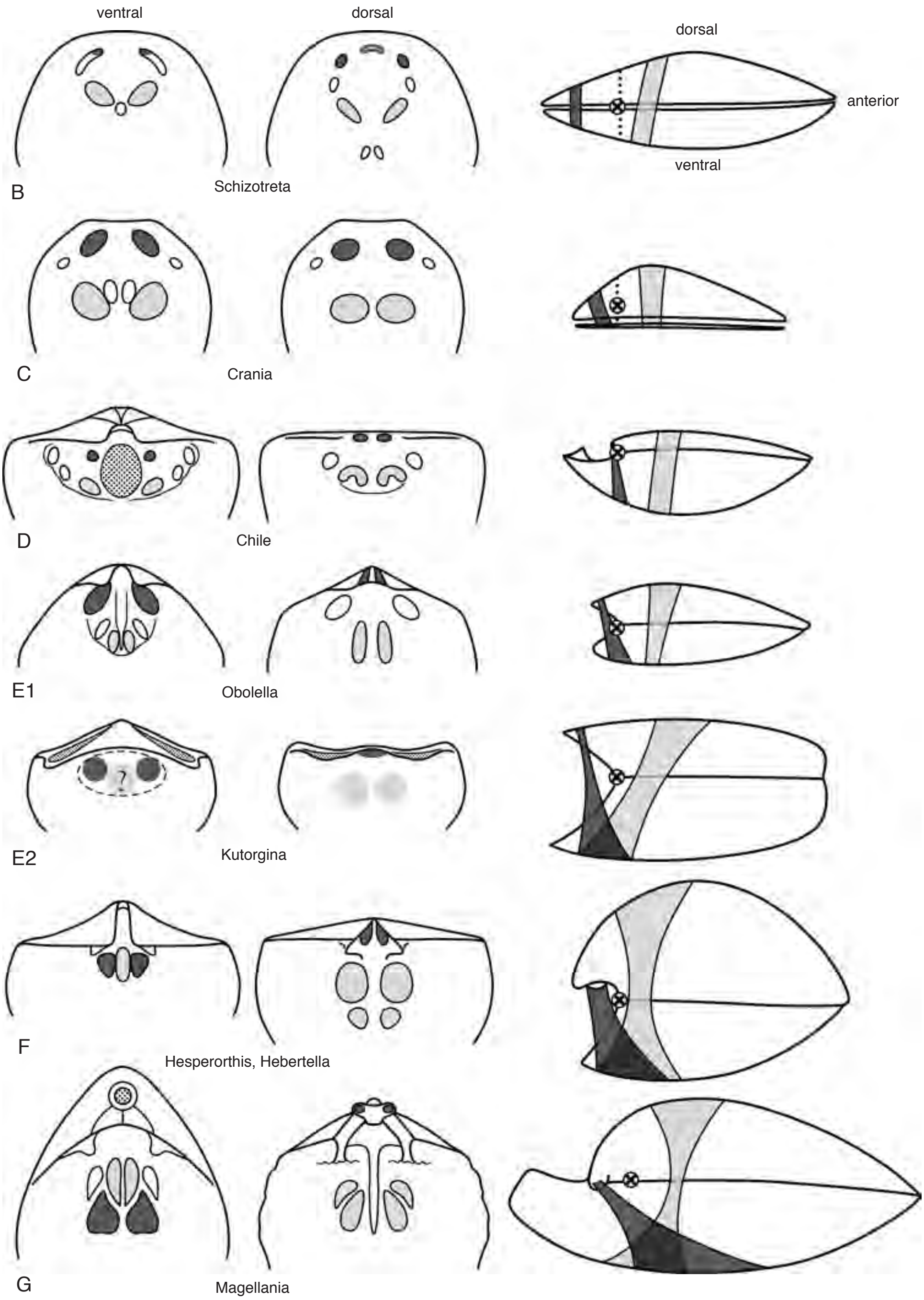


FIG. 1901. *For explanation, see facing page.*

single kidney-shaped anterolateral scar and two slender, elongate posterolateral muscle scars. Homologies with muscles in living discinids are not clear.

Living lingulids have more pairs of muscles than do other lingulides and other inarticulated brachiopods, and more of them extend from one side of one valve to the opposite side of the other valve. *Lingula* possesses a single or paired umbonal muscle, three to four pairs of oblique muscles (transmedian; outside, anterior, and middle laterals), and a central muscle (WILLIAMS & others, 1997, p. 83, fig. 82). The complexity in lingulid musculature is almost certainly related to the scissorlike, sliding, or twisting motions of the valves relative to one another, effected by the contraction of the various oblique muscles when burrowing into soft substrates. This is most likely to represent a derived morphology and behavior, despite the early appearance of the group in the fossil record (see CARLSON, herein, Fig. 1908). Lingulid umbonal and central muscles may well be homologous with posterior and anterior adductors of discinoids and craniides, based largely on patterns of innervation (BLOCHMANN, 1892, 1900; WILLIAMS & others, 1997).

Muscles in Siphonotretida (extinct) appear to be generally comparable to those in early discinids (Fig. 1901 and Table 39), although differences of opinion exist about the correspondence of dorsal and ventral scars and the identity of the particular muscles associated with the scars (HOLMER & POPOV, 2000, fig. 75). Among acrotretides, the muscles appear to be somewhat similar to, but less numerous than in lingulides. The highly conical ventral valve in many

TABLE 39. List of different types of valve interactions described in text and reconstructed schematically in Figure 1901 (new).

A. Multi-element, not articulated
Halkieriids
Micrina
Tannuolina

B. Bivalved with hinge axis, but no hinge line
Linguloids
Discinoids
Acrotheloids
Craniopsides
Most siphonotretides
Some acrotretides

C. Strophic posterior valve edges, no articulatory structures
Craniides
Some acrotretides

D. Hinge axis coincident with strophic hinge line, no articulatory structures
Paterinates
Chileates

Valves secondarily lost or primitively absent
Phoronids

E. Articulatory structures rudimentary and diverse
Kutorginates
Most trimerellides
Most obolellates

F. Deltidiodont articulatory structures
Protorthides
Orthides
Most strophomenates
Most pentamerides
Possibly spiriferides and spiriferinides

Articulatory structures lost
Some strophomenates (productides)

G. Cyrtomatodont articulatory structures
Rhynchonellides
Terebratulides
Thecideides
Atrypides
Athyridides
Possibly spiriferides and spiriferinides
Some pentamerides

FIG. 1901. Schematic reconstructions of relative positions of muscle origins and insertions on interior of ventral valve (left column) and dorsal valve (center column), and in lateral view, with valves in life position or articulated (right column); *open circle with X* marks position of hinge axis; *dark shading* indicates muscles functioning to open valves relative to one another (posterior adductors or diductors); *open ellipses* indicate oblique lateral or oblique internal muscles; *light shading* indicates anterior adductors that function to close valves; *letters* correspond to different types of valve interaction, whether inarticulated or articulated, as discussed in the text and listed in Table 39. Ventral and dorsal valve interiors redrawn from *B,* Holmer and Popov (2000); *C,* Bulman (1939); *D,* Popov and Holmer (2000a); *E1,* Popov and Holmer (2000b); *E2,* Popov and Williams (2000); *F,* Rudwick (1970); *G,* Clarkson (1979) (new).

acrotretides makes homologies with lingulides uncertain (WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 385, fig. 346). Dorsal valve originations are most similar in relative position to lingulides and craniides, but the insertions on the ventral valve are quite different. The central muscle is absent in most but may be homologous with the acrotretide anterior lateral muscle; extended discussion of acrotretide muscle systems can be found in HOLMER and POPOV (2000, p. 99–103, fig. 51). These authors suggested that the muscles in the highly conical acrotretides might have been tendonous, not columnar, consistent with the apparent evolution of tendonous muscles in rhynchonellate brachiopods as the valves increased in convexity and globosity (RUDWICK, 1970). A saddle-shaped plate extending from the dorsal valve interior of some acrotretides (e.g., *Ephippelasma*) has been interpreted as a muscle platform (RUDWICK, 1970) or as a lophophore support structure (WILLIAMS & ROWELL, 1965d; WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 384).

Paterinata is now affiliated with Lingulata, in Linguliformea (POPOV & others, 1993; HOLMER & others, 1995; HOLMER & POPOV, 2000), on the basis of shell mineralogy and microstructure, despite considerable differences in musculature and mantle canal systems. The relationship of the paterinates to the lingulates does not appear to be supported strongly (LAURIE, 2000), however, and paterinate monophyly is in question as well (WILLIAMS, POPOV, & HOLMER, 1998; LAURIE, 2000). Paterinates are the first brachiopods to appear in the stratigraphic record (Tommotian), and their muscle scars bear a close correspondence to those in orthide brachiopods (RUDWICK, 1970) and other rhynchonellates with deltidiodont dentitions; their muscle scars are remarkably similar to articulated brachiopods in aspect. In their reconstruction of paterinate muscles, WILLIAMS, POPOV, and HOLMER (1998, fig. 6) recognize separate muscle fields on the dorsal valve for the diductor muscles and the posterior adductor muscles. This reconstruction is contrary to the view of RUDWICK (1970, p. 72; a view shared by SC [Carlson, 2005, personal observation]) that the posterior adductor muscles in inarticulated brachiopods (including paterinates) are likely to be homologous with the diductor muscles in articulated brachiopods. Despite their phosphatic valve mineralogy and lack of articulatory structures, it is at least possible that paterinates may share closer common ancestry with the early rhynchonelliforms than with the linguliforms, or it is perhaps more likely that paterinates share with rhynchonelliforms this more general (primitive, ancestral) pattern of musculature, regardless of valve mineralogy and articulation, which may have evolved multiple times (see CARLSON, herein, p. 2891).

Craniiformea

Craniiform muscle systems are quite similar to discinoids: at least some of the muscles can be identified in corresponding positions on the valves in each group (compare fig. 83–84, p. 84–85, in WILLIAMS & others, 1997) and are assumed to be homologues. The basic pattern of musculature in craniides and craniopsides consists of paired adductor muscles, posterior and anterior, passing more or less directly between the valves, which are considered to be homologous with the paired umbonal and central muscles of lingulids; this may well represent the most primitive condition for brachiopods (WILLIAMS & others, 1997), consistent with the tentative consensus phylogeny in CARLSON (herein, Fig. 1908). An unpaired median muscle is also present near the valve posterior, as are longer, paired internal and lateral oblique muscles. Small, paired brachial elevator and protractor muscles originate on the dorsal valve and insert on the lophophore, allowing some movement of the lophophore relative to the valve.

Trimerelloids have muscle platforms in one or both valves to accommodate (primarily) the origin and insertion of the anterior adductor muscles. Trimerelloid muscle scars are generally similar to craniides in their relative positions on the valves, but appear to be even more similar to those in the chileides (Fig. 1901D). Positional relationships among the muscles scars of trimerelloids and other brachiopods suggest that the posteriormost muscle scars in each valve correspond to the posterior adductors, while the anterior adductor muscles originate at the larger pair of scars in the dorsal valve and insert on the anteromedial scars in the ventral valve. Some trimerelloids exhibit a kind of rudimentary articulation, in that a dorsal hinge plate fits tightly into a cardinal socket in the ventral valve, defining a hinge line about which the valves rotate (Fig. 1901E).

Rhynchonelliformea

Among the rhynchonelliforms, extant rhynchonellides and terebratulides have very similar patterns of musculature, with diductor muscles originating at the posterior of the dorsal valve, often on a cardinal process, and inserting approximately midvalve on the ventral valve (Fig. 1901). Paired anterior and posterior adductor muscles originate approximately midvalve in the dorsal valve and insert slightly posteromedial to the diductor muscles on the ventral valve. Pedicle adjustor muscles may also be present, leaving scars on either dorsal or ventral valve interiors. This general pattern of musculature is characteristic of most rhynchonellate brachiopods, commonly with cyrtomatodont (interlocking) dentitions.

Diductor muscle scars in orthides are typically located on a dorsal cardinal process and on either side of the medial adductor muscle scars in the ventral valve. Two pairs of adductor muscle scars are located midvalve in the dorsal valve. Although a pedicle also emerged from the open (or covered) delthyrial opening, its primary function seems to have enabled the diductor muscles to gain leverage in opening the valves. This general pattern of musculature is characteristic of most strophomenate brachiopods as well. Because of the large number of strophomenates with broad, but rather flat mantle cavities (e.g., *Strophonelloides, Stropheodonta, Chonetes*), ventral muscle scars in particular tend to be quite large and may splay out anteriorly; the muscles intersect the valve interior at a very low angle and thus occupy a relatively larger area on the valve floor, even though their cross-sectional area is not very much larger. Greatly elongated cardinal processes, some bifurcate or trifurcate, evolve within the strophomenates, possibly several times independently. These elongate cardinal processes can function both to increase the mechanical advantage of the valve opening system (CARLSON, 1989) and also effect a type of single tooth valve articulation, helping to reduce torsion or slip between the valves (C. H. C. BRUNTON, personal communication, 2004).

Muscle platforms are often developed in one or both valves of some protorthides (e.g., *Skenidium*), billingsellides (e.g., *Estlandia*), and pentamerides (e.g., *Camerella*) and are thought to have evolved more than once independently. They most likely functioned to reduce the distance between muscle origin and insertion in columnar muscles, as valve globosity increased and before tendonous muscles evolved, possibly as rhynchonellides evolved from pentamerides (RUDWICK, 1970).

Muscle scars are inadequately known for most fossil rhynchonellides (SAVAGE & others, 2002), but we assume they are similar to extant rhynchonellides. Pentameride muscle scars, when visible, are initially orthoidlike (Fig. 1901F) and evolve to more rhynchonellide-like (similar to Fig. 1901G) positions in the valves. Within the evolution of the rhynchonellates, therefore, the ventral insertion of the diductor muscles migrates anteriorly later in time (WILLIAMS & ROWELL, 1965d; CARLSON & others, 2002), which typically improves the mechanical advantage of the valve opening system (CARLSON, 1989). Atrypides (COPPER, 2002), athyridides (ALVAREZ & RONG, 2002), and spiriferides and spiriferinides (CARTER & others, 2006) share the same basic pattern of musculature, although differences in detail obviously exist; muscle scars are commonly impressed clearly on the valve interiors of these taxa. In athyridides, it has been suggested that the single (or fused, paired) juvenile dorsal median attachment of the diductor muscles migrated laterally onto the paired outer hinge plates (cardinal flanges) during ontogeny (ALVAREZ & BRUNTON, 1990; BRUNTON, ALVAREZ, & MACKINNON, 1996).

Obolellate musculature appears to be similar to lingulates, with oblique muscle scars still present, as well as other early rhynchonelliforms, with diductor muscle scars in the extreme posterior of the dorsal valve (Fig. 1901C; see also BASSETT, POPOV, & HOLMER, 2001). Chileates also exhibit somewhat similar muscle patterns (Fig. 1901E). The diductor muscles in these taxa are more likely to be homologous with the posterior adductor muscles rather than with the internal oblique muscles in discinids and craniids because of their position in the valves relative to the other muscle scars. Some naukatides have rudimentary ventral denticles fitting into dorsal sockets (e.g., *Oina*). As articulatory structures evolve in brachiopods, the oblique muscle scars move further laterally on the valves, and the muscles are eventually lost entirely.

In Kutorginata, muscle scars are visible but are not impressed strongly on valve interiors. They appear to be similar to most deltidiodont strophomenates and rhynchonellates, with diductor and adductor impressions in similar positions (POPOV & WILLIAMS, 2000, fig. 127; see also Fig. 1901E). The muscles were located fairly far to the posterior in both valves, as is common in Early Paleozoic brachiopods. The very wide, open notothyrium and delthyrium functioned primarily as a broad notch to allow the muscles to pass from their origin in the extreme posterior of the dorsal valve to their insertion in the ventral valve (RUDWICK, 1970; GUTMANN, VOGEL, & ZORN, 1978; BASSETT, POPOV, & HOLMER, 2001).

Evolutionary Patterns in Musculature Morphology and Function

If halkieriids are provisionally accepted as the brachiopod sister group, it is possible to construct a scenario of the evolution of the muscle system and articulation from their common ancestor. WILLIAMS and HOLMER (2002) outlined a ten-step process by which brachiopods could transform from *Micrina*, which they interpret as a halkieriid (but see also LI & XIAO, 2004) (Fig. 1896). Brachiopods do not necessarily have to be derived from halkieriids directly, only that the two may have shared a common ancestor, perhaps quite distantly (see VINTHER & NIELSEN, 2005). The two shells of halkieriids appear to be located dorsally, one posterior and one anterior, on the organism (CONWAY MORRIS & PEEL, 1995). The posterior shell bears a strong resemblance to certain brachiopod ventral valves (some acrotretides), with a straight (strophic) edge anteriorly and what looks much like a pseudointerarea. The anterior shell is similar to some brachiopod dorsal valves (not acrotretides, interestingly, but more like some craniopsoids or siphonotretoids) with a triangular shape and no strophic posterior edge. The anterior shell retains this basic triangular shape throughout ontogeny; the posterior shell exhibits more pronounced allometric changes as it grows from a similar triangular-shaped shell early in ontogeny. If we hypothesize the halkieriid valves as homologues of brachiopod valves, the halkieriid body plan must be folded transversely in order to place the two shells opposite one another, in an opposing bivalved configuration (see WILLIAMS & HOLMER, 2002; COHEN, HOLMER, & LÜTER, 2003). Alternatively, the common ancestor of both halkieriids and brachiopods could have had a body form (not preserved or not recognized in the fossil record thus far) dissimilar to either of its descendants.

Musculature in halkieriid shells is unknown (even if one accepts *Micrina* as a halkieriid; WILLIAMS & HOLMER, 2002). It is unlikely that the two halkieriid shells interacted directly with one another on an individual organism (CONWAY MORRIS & PEEL, 1995), therefore any musculature they might have possessed is not likely to be homologous with brachiopod musculature. Additional study on a larger sample of halkieriid shells may reveal more useful evidence of soft tissue attachment.

The evolution of musculature in brachiopods closely accompanies the evolution of the two valves. Although not all muscles are associated with the valves, the majority of them are, and it becomes necessary to consider the evolution of muscle systems with respect to the functional morphology of relative valve motion, as well as articulation between the valves. As with articulation, the patterns of musculature preserved on the interior of brachiopods shells as old as the Tommotian demonstrate that a diversity of types of musculature are in place and fully functional in the Early Cambrian.

It is time to reevaluate long-entrenched scenarios of evolutionary polarity in which lingulids figure prominently as the most primitive brachiopods and thus provide a comparison for all other brachiopods, extant and extinct. While they do appear early in the fossil record (mid-Atdabanian; HOLMER, 2001) and have survived as living fossils ever since, many other valve morphologies (those in acrotretides, trematobolids, and kutorginoids; HOLMER, 2001) appear at this early time as well; some (those in paterinates and obolellates) appear even earlier (early Atdabanian; HOLMER, 2001). Among extant brachiopods, discinid and craniid musculature are more similar to one another and are likely to represent a more primitive (phylogenetically; see CARLSON, herein, Fig. 1908) pattern of musculature than what we see in lingulids, because of secondary modifications due to lingulid burrowing behavior and infaunal life mode. This is particularly true now that *Heliomedusa* (Atdabanian) has been reinterpreted as a discinid and not a craniopsid (CHEN, HUANG, & CHUANG, 2007), and the obolid *Xianshanella* (Atdabanian) appears to have been attached to the shells of other organisms by means of a long pedicle (ZHANG & others, 2006).

Major muscle systems in all brachiopods lie primarily (linguloids, trimerelloids, craniopsides, acrotretides) or exclusively (in other inarticulated and articulated brachiopods) in the posterior half of the valves. This nearly universal configuration of musculature, lying with the viscera mostly posterior to the midline, and the lophophore and mantle cavity lying mostly anterior to the midline, ensures that contraction of the posteriormost muscles will result in at least some rotation of the valves, assuming the more anteriorly located muscles (or any muscles anterior to the hinge axis) are capable of some extension and do not contract at the same time as do the more posterior muscles (Fig. 1901). The fulcrum (hinge axis) about which the valves may rotate with respect to one another remains between the posteriormost and the more anterior muscles, regardless of what names they have each been given in different groups of brachiopods. It is quite possible, therefore, that the posterior adductor muscles in inarticulated brachiopods are homologous with the diductor muscles in articulated brachiopods (RUDWICK, 1970). This interpretation is contrary to that outlined in GUTMANN, VOGEL, and ZORN (1978), which appears to oversimplify and thus misinterpret the functional musculature of inarticulated brachiopods. Adductor muscles, which bring the valves together (typically in closure), can effect a separation of the valves at one end (anteriorly) if they are positioned at the other end of the two valves, as is the case for the posterior adductor (umbonal) muscles (RUDWICK, 1970). The axis of rotation remains between these two sets of muscles; the viscera act as a fulcrum about which rotation occurs.

As ventral valves (particularly) evolved from relatively flat (craniids, discinids, lingulids) to more biconvex-cap shapes (acrotretides, kutorginides, orthides), the posterior edges of the valves had to separate in some way in order to accommodate the muscles (GUTMANN, VOGEL, & ZORN, 1978) extending from one valve to the other. This separation took the form of the large, broad delthyrial openings in kutorginides and the open delthyrium in obolellides and other early rhynchonelliforms to allow the muscles to span the distance between the two valves without disruption (RUDWICK, 1970). GUTMANN, VOGEL, and ZORN (1978, fig. 3)

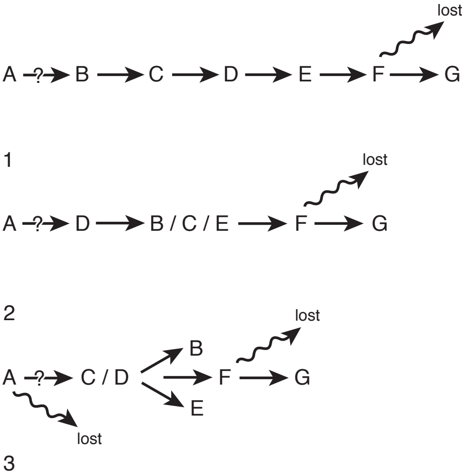


FIG. 1902. Hypothetical scenarios of evolution of valve-to-valve interactions and valve articulation; *letters* refer to types of valve interaction described in text and figured in Figure 1901 and Table 39; *arrows* indicate evolutionary transitions; *1,* a somewhat conventional evolutionary functional scenario; *2,* based on relative stratigraphic position; *3,* following topology in Figure 1908 (new).

assumed erroneously that the anterior edge of the interareas corresponded to the hinge axis; it does not (Fig. 1901). Determining the precise axis of rotation of the valves as they open and close is a critical piece of information; the ability of the muscles to open or close the valves by contraction is specified by the position of the hinge axis relative to the muscles. The position of the umbonal muscles does not shift relative to the hinge axis during this functional-evolutionary transition (*contra* GUTMANN, VOGEL, & ZORN, 1978), because the hinge axis is not colinear with a hinge line located on the valves (i.e., the edge of the interareas) in brachiopods with musculature similar to that described and illustrated in Figure 1901. The hinge axis always lies between the posterior adductors and the anterior adductors in this functional transition, regardless of which evolutionary pathway is followed (Fig. 1902).

All brachiopods must be able to separate or rotate their valves relative to one another to allow the cilia on the lophophore to establish an incurrent and excurrent water flow through the mantle cavity (LABARBERA, 1977, 1981), enabling the organism to obtain oxygen and food as well as release wastes and gametes. In addition, lingulids alone must be able to open their valves for a very different purpose: to assist the pedicle in penetrating the sediment substrate during burrowing and to help maintain the organism in a vertical position in its burrow (RUDWICK, 1970; THAYER & STEELE-PETROVIC, 1975; EMIG, 1981; TRUEMAN & WONG, 1987; SAVAZZI, 1991; RICHARDSON, 1997a). TRUEMAN and WONG (1987) documented increases in pressure in the perivisceral coelom during the valve-opening phases associated with burrowing. The pressure increases were attributed to contraction of the circumferential muscles in the body wall of the lingulid. These experimental observations led them to conclude that (pedicle and perivisceral) coelomic fluid functions as a hydrostatic skeleton with respect to valve movements—contraction of the circumferential muscles applies pressure to the coelom and pushes the viscera posteriorly, thus forcing the valves open hydrostatically.

If contraction of the thin, sheetlike muscles in the body wall are capable of effecting an increase in pressure in the coelom to the extent that the valves can be opened relative to one another, then it is highly likely that the contraction of the umbonal muscle, which has a much larger cross-sectional area than the myoepithelium of the body wall, could effect a slight opening of the valves as well. If the umbonal (posteriormost) muscle contracts while the central muscle remains relaxed and uncontracted (this can and should be verified experimentally), then both the contraction of the muscles in the body wall and the contraction of the umbonal muscle could effect valve opening in the lingulids. The precise pattern of muscle firing in contraction has not yet been verified throughout the burrowing sequence in lingulids, to our knowledge. A valve-opening scenario in lingulids involving both hydrostatic and muscular forces has broader potential applicability to muscle systems in all brachiopods, not merely in lingulids with their unusual lifestyle. Posterior adductor or umbonal muscles could effect slight (six degrees in *Lingula*) opening of the valves anteriorly if contracted (and not opposed by contraction of the anterior adductors), because the viscera in between the two sets of muscles (in inarticulated brachiopods) acts as a fulcrum (RUDWICK, 1970). The two sets of adductors could contract and relax alternately in time, in a see-saw–like fashion, effecting either opening or closing of the valves anteriorly.

EMIG (1997a, p. 480) stated that "shells of discinids and craniids gape quite widely [presumably more than six degrees] at the anterior edge and more narrowly at the posterior margin," consistent with a scenario involving contraction of the posterior adductor, while the anterior adductor muscles remain relaxed and are allowed to extend. RUDWICK (1970, p. 72) claimed that "the way in which the valves [of living inarticulates] are observed to open by rotation does not support the suggestion that the coelom is used as a hydrostatic chamber." It is difficult to justify a wide gape by contraction of the body wall myoepithelium alone, particularly since *Novocrania* at least does not have a well-developed musculature in the body wall, as *Lingula* does (WILLIAMS & others, 1997). This hypothesis could be tested using electromyography to document the relative timing of muscle contraction. A strophic valve edge immediately posterior to the posterior muscle (as in *Novocrania* or *Cyrtonotreta*) could potentially allow even greater anterior gapes, because the strophic posterior shell edge would not interfere with greater valve rotation as much as a rounded posterior edge.

A comparison of discinids and craniids, assuming them to represent the evolutionarily basal type of musculature among brachiopods, reveals that two pairs of muscles dominate in effecting the opening and closing of the valves. Contraction of the posterior adductors causes the valves to gape somewhat (ATKINS & RUDWICK, 1962; RUDWICK, 1970), and contraction of the anterior adductors closes the gape. The various transmedian and oblique muscles present in discinids, craniids, and lingulids function only in brachiopods that lack both a hinge line and articulatory structures on the valves. As valve rotation about a hinge axis coincident with a hinge line located on the valves (such as seen in paterinates, chileates, and kutorginates, as well as some obolellates and trimerelloids) evolves, the transmedian and oblique muscles are lost evolutionarily. If we compare the position of the discinoid and cranioid posterior adductor muscles across a broader range of brachiopods, assuming them to perform the same function in each (that of effecting a gape angle), these muscles are likely to be homologous with what have been referred as umbonal muscles in lingulids, acrotheloids, acrotretoids, and siphonotretoids (BLOCHMANN, 1892, 1900; WILLIAMS & others, 1997; HOLMER & POPOV, 2000); internal oblique muscles in obolellates (POPOV & HOLMER, 2000c; BASSETT, POPOV, & HOLMER, 2001), trimerelloids (POPOV & HOLMER, 2000a), and chileates (POPOV & HOLMER, 2000b); diductor muscles in paterinates (LAURIE, 1987, 2000; WILLIAMS, POPOV, & HOLMER, 1998) and kutorginates (POPOV & WILLIAMS, 2000; BASSETT, POPOV, & HOLMER, 2001) as well as strophomenates and rhynchonellates (Fig. 1901). Muscles that have been labeled as internal obliques or oblique internals in lingulates and cranioids (where their origin and insertion can be verified directly in extant forms) are not positionally homologous with muscle scars given the same names (oblique internals) in obolellates, trimerelloids, and chileates. Because obolellates, trimerelloids, and chileates are all extinct, it is not possible to test this hypothesis of homology directly, but arguments based on relative muscle position and postulated function in other brachiopods support this hypothesis, which merits further testing.

Assuming that the discinid and craniid type of musculature is primitive for brachiopods, an assumption supported by the stratigraphic record (Atdabanian *Heliomedusa*) as well as molecular systematic data (craniids as primitive among living brachiopods; Cohen & Weydmann, 2005; see Carlson, herein, Fig. 1907–1908; see also Williams & Holmer, 2002), it is possible to hypothesize an evolutionary transition from this basal inarticulated pattern of musculature to a more derived, articulated type of musculature (Fig. 1901–1902). In this scenario, the origin of the paired posterior adductor muscles on the dorsal valve, which could rotate the valves open slightly anteriorly as they contract, migrates posteriorly to occupy a posteriormost position, eventually occupying a cardinal process or homologous structure on the dorsal valve. In some taxa, the muscle origin migrated well beyond the posterior edge of the dorsal valve (e.g., *Triplesia*, at the end of a long, hook-shaped cardinal process). It is noteworthy that in such situations the dorsal myophores are positioned anteriorly or even posterodorsally, allowing muscle contraction to effect the maximum rotation of the cardinal process, the dorsal valve, and consequently, the anterior gape (C. H. C. Brunton, personal communication, 2004). The insertion of the paired posterior adductor muscles on the ventral valve migrated anteriorly to a position lateral to (in Paleozoic orthides, Williams & Harper, 2000, p. 717, fig. 518) and eventually (in extant terebratulides) anterolateral to the anterior adductor muscles (Fig. 1901G), which results in greater mechanical advantage of the diductors in opening the valves. In this evolutionary transition, oblique and transverse muscles of inarticulated brachiopods are lost, the dorsal origin of the posterior adductor (functional diductor) muscle decreases in area, and the ventral insertion of the posterior adductor (diductor) muscle increases in area, due in part to the lower angle at which it intersects the ventral valve interior in articulated brachiopods, and due in part to their tendonous structure. Tendonous muscles cannot generate as great a degree of valve opening as columnar muscles might be able to because of their shorter muscle fiber length, but with large cross-sectional area they could still generate considerable power.

Evolutionary changes in the brachiopod muscle system, as outlined in Figures 1901–1902, can be understood functionally as increasing the mechanical advantage of the posteriormost muscles in opening the valves (Carlson, 1989). Accompanying these changes in musculature are increases in the convexity of the valves, which have been attributed to selection for increased mantle cavity volume, allowing greater three-dimensional complexity in lophophore geometry and function (McGhee, 1980). Apart from the evolutionary migrations of the origin and insertion of the posterior adductor muscles (and their homologues) and the loss of numerous transverse and oblique muscles as valve articulation and articulatory structures evolve, the fundamental arrangement of the major muscles relative to one another and relative to the axis of valve rotation has not changed significantly throughout brachiopod evolution (*contra* Gutmann, Vogel, & Zorn, 1978). The size, shape, and geometry of the valves themselves changed in the evolutionary transition from more primitive to more derived brachiopods, from the Tommotian to today, but the relative arrangement of the muscles and hinge axis have not changed significantly, from a functional perspective.

EVOLUTION OF ARTICULATION

[Sandra J. Carlson]

Mapping out the details of the pattern of evolution of valve articulation is one of the great unsolved mysteries of brachiopod evolution. Many of the major changes in the classification of Brachiopoda since the 1965 *Treatise* (Moore, 1965)—abandoning Inarticulata and Articulata is one prominent example—relate to continuing evolution in our thinking about articulation over the past several decades. Several aspects of the evolution of articulation are clear: the type of tooth and socket structures (and corresponding functions) we associate with extant articulated brachiopods are evolutionarily derived within Brachiopoda and a variety of types of rudimentary articulation, including rotation of the valves about a hinge axis not located on the valves themselves and producing an anterior gape can be found in stratigraphically lower and phylogenetically more basal brachiopods. Are these different types of articulation homologous? How can we test this possibility, and explain the greater variety of valve-to-valve associations that existed early in the history of the phylum?

Any discussion of the evolution of articulation is necessarily related to the evolution of mantle mineralization, which results in two mineralized valves in brachiopods, one dorsal and one ventral (apparently; see also Cohen, Holmer, & Lüter, 2003). It is intriguing to note that brachiopods, as a clade excluding phoronids, are defined by a number of morphological synapomorphies (e.g., including a double row of lophophore filaments on only one side of the adult lophophore arms, two coelomic spaces per lophophore arm, and a subenteric primary nervous ganglion) that do not require the possession of two valves (Carlson, 1995). This suggests that the presence of two valves, whether articulated or not, is not required for membership in the clade Brachiopoda. Thus, it is possible that mineralized valves arose more than once independently within a monophyletic Brachiopoda defined on the basis of other characters unrelated to valves (Wright, 1979); given the major functional advantages to having mineralized valves, it is not unreasonable to consider their multiple independent origins (see also Runnegar, 1982; Bengtson, 2004). The most parsimonious interpretation involves a single origin of valve mineralization, coincident with the origin of the Brachiopoda (secondarily lost in phoronids if they nest within Brachiopoda), but there is no evidence at present that would allow us to reject definitively several parallel origins of mineralized shells early in brachiopod evolutionary history.

Whether they evolved once or more than once in the Brachiopoda, the two valves can interact with one another in one of several different ways: (1) rotate minimally in a dorsoventral direction about a hinge axis (or hinge plane) that is not located on the valves themselves (Fig. 1901B); (2) slide or twist relative to one another (lingulids only); (3) rotate about a hinge axis not located on the valves, as in #1 (Fig. 1901B and Table 39), but with strophic posterior valve edges, allowing moderate valve rotation to occur (Fig. 1901C); (4) rotate about a hinge axis coincident with a strophic hinge line located on the valves, but lacking articulatory structures (Fig. 1901D); (5) rotate about a hinge line distinguished by the presence of articulatory structures, either rudimentary or well developed (Fig. 1901E–1901G). Each of these combinations of characters, which may characterize either a grade of organization or possibly a clade, is discussed further below, exemplified by the taxa that exhibit them.

Type A: Multi-Element Mineralized Skeleton, Not Articulated

Halkieria possesses three distinct types of sclerites in addition to two dorsal shells, one anterior and one posterior, that are considered to be potentially homologous with the brachiopod dorsal and ventral valves (Conway Morris & Peel, 1995). The two shells are not in articulation, and do not even touch one another. If brachiopods share common ancestry with the halkieriids (Conway Morris & Peel, 1995; or the tannuolinids, Williams & Holmer, 2002), several functional and morphological transformations must have occurred in this evolutionary transition. Williams and Holmer (2002) outlined an evolutionary scenario by which brachiopods might have evolved from halkieriids (Fig. 1894), which involves the loss of sclerites and transverse folding of the body axis (Cohen, Holmer, & Lüter, 2003), as well as regrouping of the muscles and internal organs, eventually resulting in two shells juxtaposed as in extant brachiopods. The difficult behavioral and

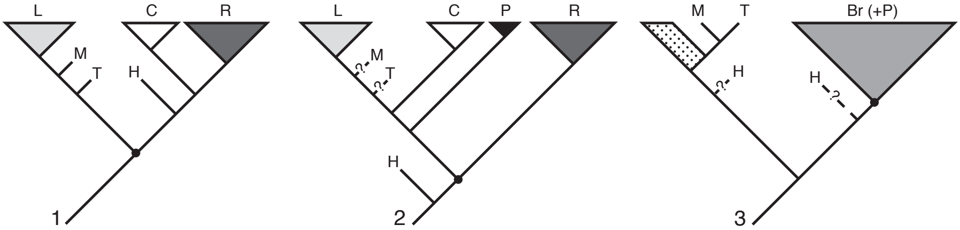


FIG. 1903. Hypothesized phylogenetic relationships among Linguliformea (*L*), Brachiopoda (*Br*), Craniiformea (*C*), Rhynchonelliformea (*R*), Phoroniformea (*P*), *Micrina* (*M*), *Tannuolina* (*T*), and *Halkieria* (*H*). *1,* constructed from discussion in Li and Xiao (2004) following topology in Williams and Holmer (2002); *2,* constructed following topology in Cohen and Weydmann (2005); *3,* constructed from discussion in Li and Xiao (2004) following Bengtson and others (1990); tannuolinids and tommotiids in *stippled box* (new).

whole-organism functional rearrangements that must have accompanied this morphological transition have not yet been thoroughly considered, however (C. NIELSEN, personal communication, 2005).

Phylogenetic relationships among these various scleritic Lower Cambrian fossils (*Halkieria, Tannuolina, Micrina*) are not at all widely agreed upon, much less their relationship to brachiopods (Fig. 1896, 1903). WILLIAMS and HOLMER (2002) considered *Micrina* to be a halkieriid, with the halkieriids (thus defined more broadly) as the phosphatic ancestral stock from which brachiopods evolved (Fig. 1896). This scenario is consistent with the diphyletic origin of brachiopods proposed by GORJANSKY and POPOV (1986), in which calcareous brachiopods evolved two shells independently from phosphatic brachiopods (see also discussion in POPOV, 1992). LI and XIAO (2004) suggested a somewhat different scenario, in which halkieriids (which they consider to be most likely calcareous) might be most closely related to the calcareous brachiopods, while phosphatic *Mickwitzia* (and *Micrina* and *Tannuolina*) might be most closely related to the phosphatic brachiopods (Fig. 1903.1). Unless one considers all these taxa to be included within the clade Brachiopoda, this scenario also renders brachiopods diphyletic, again consistent with GORJANSKY and POPOV (1986). Both of these scenarios are inconsistent, however, with a growing body of data from molecular systematic analyses of extant taxa (COHEN, 2000; PETERSON & EERNISSE, 2001; COHEN & WEYDMANN, 2005) that places the calcareous inarticulated brachiopods more closely related to the phosphatic inarticulated brachiopods than to the calcareous articulated brachiopods (see also CARLSON, 1995). This suggests that a calcareous shell might be basal for brachiopods, or at least that a phosphatic shell is less likely to be basal, or that valve mineralogy is largely homoplastic (and phylogenetically unreliable) among these early taxa. Consistent with this overall pattern of relationships, it is conceivable that *Micrina* and *Tannuolina* are most closely related to the phosphatic lingulates, while halkieriids share common ancestry with all brachiopods (Fig. 1903.2).

More traditional views (BENGTSON, 1970; LANDING, 1984; LAURIE, 1986; also LI & XIAO, 2004) of the relationships of these Tommotian fossils considered *Micrina* and *Tannuolina* to be closely related to one another on the basis of sclerite morphology and microstructure, and both closely related to other tommotiids, while more distantly related to all brachiopods (Fig. 1903.3). Halkieriids could still be hypothesized as the sister group to the phoronids and brachiopods but would then be considered more distantly related to the other tommotiids like *Micrina*. At this time, none of these hypotheses can be rejected definitively, but evidence is mounting against the hypothesis illustrated in Figures 1896 and 1903.1. Depending on which pattern of relationships one supports, it is clear that different scenarios of the evolution of articulation result.

Micrina (but not *Tannuolina*) mitral sclerites have paired apophyses, or toothlike structures present just below the deltoid area, suggesting their positional homology to ventral teeth in brachiopods. WILLIAMS and HOLMER (2002, p. 846) claimed, however, that there is no structural evidence that they were used as articulatory devices. It is not clear what the structural evidence would consist of and raises the possibility that the apophyses served as a kind of preadaptation, or functional precursor, for teeth. If *Micrina* apophyses were not teeth used in valve-to-valve articulation, then it is at least possible that the rudimentary teeth (denticles, hinge ridges) in kutorginates, some obolellates, and trimerellates (Fig. 1901E) may also have lacked any valve articulatory function. Very few components of these many linked assertions regarding function and ancestry are known with great certainty.

Mineralized Elements Lost?

If the relationships illustrated in CARLSON (herein, Fig. 1907) (COHEN & WEYDMANN, 2005; see also ZRZAVY & others, 1998) are accurate, phoronids are phylogenetically nested within brachiopods, as the sister group to the linguliform + craniiform clade (Fig. 1903.2). This pattern of relationships suggests that mineralized valves have become secondarily lost in the evolution from a mineralized common ancestor, or possibly that a primitive nonmineralized condition was retained in the phoronids only. If some halkieriid group shares common ancestry with all brachiopods, including phoronids, the most parsimonious scenario posits the loss of a mineralized skeleton in the phoronids, from that common ancestor. If some unmineralized group of organisms, for which we have no fossil record yet, shares common ancestry with brachiopods (and phoronids) instead, then it is possible that phoronids retained their nonmineralized condition, and valves evolved twice independently within brachiopods (Fig. 1903.2).

Phoronids nested within brachiopods remains a somewhat contentious pattern of relationships, however. It is problematic that a fundamental feature like gut orientation would be opposite in two groups thought to be so closely related to one another (Fig. 1895, 1899; C. NIELSEN, personal communication, 2005). Several studies of morphological and molecular data conclude that phoronids lie outside the articulated + inarticulated brachiopod clade, as their sister group (GIRIBET & others, 2000; PETERSON & EERNISSE, 2001; MALLATT & WINCHELL, 2002; see also WILLIAMS & HOLMER, 2002). Using mitochondrial gene arrangements, LARGET, KADANE, and SIMON (2005) suggested (albeit with substantial qualification) that annelids are the sister group to brachiopods. If so, it is possible that the absence of mineralization is basal, with mineralization evolving (twice independently) in brachiopods after divergence from a common ancestor with annelids. The current data are sufficiently conflicted that it is premature to make a definitive statement about the relationship among brachiopods, phoronids, and other protostomes.

Type B: Bivalved Shells Rotate About a Hinge Axis; Hinge Line Absent

Many of the taxa formerly included in Inarticulata can be described by this type of valve-to-valve interaction: linguloids, discinoids (*Schizotreta*), acrotheloids, craniopsides, most siphonotretoids (*Siphonotreta*), and some acrotretoids (*Conotreta*). Valve-to-valve contact during muscle contraction is minimal to nonexistent. The hinge axis about which minimal dorsoventral valve rotation occurs exists between the valves and might be described more accurately as a dorsoventral hinge plane, perpendicular to both the sagittal and commissural planes, passing through the viscera between the posterior (umbonal) and anterior (central) adductor muscles (Fig. 1901). Lingulids represent a special case of this type of valve-to-valve interaction, in which sliding and transverse, twisting motions occur between valves, as well as minimal dorsoventral rotation (see discussion in Evolution of Muscle Systems, herein, p. 2850). Posterior dorsal valve edges are either rounded (*Discina*), or acute (*Glossella*), but almost never strophic. No articulatory structures are present on the valves. Pseudointerareas commonly, but not invariably, exist, but the anterior edge of the pseudointerarea does not serve as a hinge axis (*contra* GUTMANN, VOGEL, & ZORN, 1978).

Type C: Posterior Valve Edges Strophic; Articulatory Structures Absent

Most craniides (*Ancistrocrania*) and some siphonotretoids (*Cyrbasiotreta*) and acrotretoids (*Treptotreta*) have two valves that appear to contact one another posteriorly in an approximately straight (strophic) line (Fig. 1901C) when the posteriormost muscles are contracted. No articulatory structures are present on the valves. The valves can rotate until the straight posterior edges come into contact with one another at the maximum extent of muscle contraction, as in some Recent craniides. This strophic valve edge at least allows the possibility that gapes in taxa with this type of articulation could be wider than in lingulids, which is consistent with RICHARDSON's (1997a) observations on living craniids. ATKINS and RUDWICK (1962, p. 474; and see also C. NIELSEN, personal communication, 2005) stated that "When the shell [of *Crania*] opens, it does so by a rotation of the dorsal valve about an axis corresponding to the posterior side of the shell, where the valve edges remain in contact." Other behavioral observations suggest that no such rotation of the dorsal valve need occur (C. H. C. BRUNTON, personal communication, 2004), even if it is possible to do so. A strophic valve edge also makes it more likely that valve-to-valve contact will occur along a line, in the process of valve rotation, unlike the slight opening effected in lingulids and discinids where no such valve-to-valve contact need occur at all.

Many acrotretoids have ventral valves that are nearly conical in shape (*Ceratreta*, *Ephippelasma*); hypotheses of muscle homology and the nature of valve-to-valve contact in acrotretoids relative to other brachiopods are thus more difficult to reconcile. Nevertheless, many acrotretoids have strophic posterior valve edges, and it is relatively easy to envision a functional scenario in which a lidlike dorsal valve can be rotated open relative to a conical ventral valve about a hinge axis, possibly one coincident with the strophic valve edge, in a manner similar to craniides.

Type D: Hinge Axis Coincident with Strophic Hinge Line; Articulatory Structures Absent

Paterinates, chileates, and some trimerellides have distinct strophic hinge lines and muscle scars arranged in a manner more (*Paterina*) or less (*Chile*) similar to those in strophic articulated brachiopods, leading to the interpretation (POPOV & TIKHONOV, 1990; POPOV, 1992; BASSETT, POPOV, & HOLMER, 2001; WILLIAMS, 2003) that the axis of valve rotation is coincident with the strophic hinge line, with the two valves in contact throughout the process of valve rotation (Fig. 1901D). Yet, all taxa with this type of valve-to-valve contact lack distinct articulatory structures, and all are extinct; the axis of rotation may have been fixed entirely by fused mantle lobes (POPOV & TIKHONOV, 1990; POPOV & HOLMER, 2000a), but this possibility is very difficult to test.

Type E: Articulatory Structures Rudimentary and Diverse

Some trimerelloids (*Eodinobolus*) have what might be called an astrophic hinge line, where the valves contact one another primarily at two points rather than along a straight line (Fig. 1901E). The ventral valve is larger than the dorsal, with a large ventral pseudointerarea present. A dorsal hinge plate fits tightly into a so-called cardinal socket in the ventral valve and appears to have fixed the axis of rotation in a manner similar to that of articulated brachiopods (POPOV & HOLMER, 2000c). This type of valve-to-valve contact has been referred to as a rudimentary form of valve articulation, but one that is lacking in paired teeth and sockets.

In kutorginates (*Kutorgina* and *Nisusia*), which also have a kind of astrophic hinge line, the lateral margins of the pseudodeltidium fit into sockets at the end of furrows or grooves in the dorsal valve located between narrow, elongate socket plates and the so-called interarea (Fig. 1901E); this has been described as a rudimentary articulatory system (POPOV & WILLIAMS, 2000; BASSETT, POPOV, & HOLMER, 2001) and is quite different from the morphology in trimerelloids. Paired teeth and sockets are lacking, but there are clearly structures of positive relief that fit into structures of negative relief, which could serve to define a hinge axis about which valve rotation could occur.

Most obolellates—naukatides (*Oina*) and obolellides (*Trematobolus*)—possess articulatory structures in the form of paired ventral denticles and dorsal sockets. They are similar to a primitive type of deltidiodont structure, but the homology of obolellate denticles and deltidiodont teeth is not clear. Structures referred to as interareas are present (*Trematobolus* and *Oina)*; the anterior edge of the interareas, where the paired denticles are located, may serve as a hinge axis in these taxa, consistent with GUTMANN, VOGEL, and ZORN (1978). The muscle serving to rotate the valves open inserts on the posterior side of the hinge axis on the dorsal valve, however, and inserts on the anterior side of the hinge axis on the ventral valve. Rather than requiring a hydraulic opening mechanism, therefore, a standard lever system can effect valve rotation in obolellates, as is apparently also true for kutorginates and trimerelloids (see BASSETT, POPOV, & HOLMER, 2001).

Type F: Deltidiodont Articulatory Structures

Protorthides, orthides, most strophomenates, most pentamerides, and possibly some spiriferides and spiriferinides are characterized by deltidiodont articulatory structures. Minor variations exist among deltidiodont dentitions, but the basic pattern of valve articulation remains more or less the same in each (JAANUSSON, 1971; CARLSON, 1989). Two ventral teeth sit in two dorsal sockets; the dorsal and ventral valves may be separated from one another easily because the teeth do not interlock with the sockets. Valve rotation is effected by contraction of the diductor muscles to open the valves anteriorly and adductor muscles to close the valves.

Post-Devonian productidines and some pre-Devonian strophomenides have lost the deltidiodont tooth and socket articulation; the lack of articulatory structures is clearly secondary and derived. Despite selection pressures causing the loss of a pair of ventral teeth fitting into dorsal sockets, the functional need for valve-to-valve stability allowed a different but apparently effective type of articulation to evolve. These shells articulated effectively by means of a somewhat peglike cardinal process that extends into the ventral umbonal cavity. On either side of the base of the cardinal process are the median ends of cardinal or lateral ridges that provide articulation surfaces with the edges of the ventral umbo. As these shells are almost universally deeply concavoconvex, commonly with long trails and wide hinge lines coincident with the axis of rotation, the dorsal valve opened within the convexity of the ventral valve and these prevented any differential movement away from the simple rotation about the hinge axis (C. H. C. BRUNTON, personal communication, 2004). This functional articulation involves a single dorsal tooth (cardinal process) fitting into a ventral socket (umbonal cavity). Multiple denticulations have evolved along the hinge line more than once among strophomenates (e.g., *Strophodonta*, *Leptostrophia*; RONG & COCKS, 1994; COCKS & RONG, 2000) and served largely to prevent torsion of one valve relative to the other.

In general, brachiopods with deltidiodont dentition also have strophic (straight) hinge lines. Thecideides, brachiopods with strophic hinge lines and cyrtomatodont dentitions, present the most unambiguous contradiction to this generalization. JAANUSSON (1971, 1981) argued that all strophic spire-bearers have cyrtomatodont articulation. Examination of a wide variety of strophic spire-bearers (CARLSON, personal observation, 1989) suggests that some are very likely to be deltidiodont, not cyrtomatodont. The detailed nature of hinge structures in the strophic spire-bearers is not entirely clear, however, and merits further, comprehensive investigation.

The rudimentary types of articulation present in many obolellates could be considered deltidiodont, in that articulatory structures are present but do not interlock with one another. Interestingly, these early forms of articulation tend to be associated with astrophic, or curved, hinge lines, rather than strophic, or straight, hinge lines. A number of early brachiopods with strophic hinge lines (paterinates, chileates, some acrotretides) lack any vestige of articulatory structures.

Type G: Cyrtomatodont Articulatory Structures

Rhynchonellides, terebratulides, thecideides, atrypides, athyridides, some pentamerides, and possibly most spiriferides and spiriferinides comprising the rhynchonellate crown group (see CARLSON, herein, Fig. 1908) have cyrtomatodont dentitions. All extant articulated brachiopods have interlocking teeth and sockets that generally prevent easy separation of the valves from one another. The nature of the fit of the teeth in the sockets can limit the degree of valve rotation possible about the hinge axis, which is coincident with an astrophic hinge line in most cyrtomatodont brachiopods. It is possible that cyrtomatodont dentitions have evolved more than once independently (possibly in *Porambonites*, for example), but this does not detract from the hypothesis of synapomorphy for cyrtomatodont dentitions among the derived rhynchonellate brachiopods (see CARLSON, herein, Fig. 1908).

The central role of shell resorption in crafting cyrtomatodont dentitions is undeniable. Interlocking teeth and sockets cannot form and grow through ontogeny without continual resorption and mineralization. It doesn't necessarily follow, however, that taxa with deltidiodont dentitions were not capable of shell resorption. If one looks carefully at the strophomenates (e.g., *Edriosteges, Bathymyonia, Triplesia*), it is possible (but not necessarily required; C. H. C. BRUNTON, personal communication, 2004) that elongated, hook-shaped cardinal processes also involved shell resorption and mineralization in order to form and grow through ontogeny (CARLSON, 1989).

Evolutionary Patterns in Valve Articulation

To move beyond a simple categorization of types of articulation, it is necessary to place these functional groups in some kind of order, ideally an order representing the evolution of the articulatory system. The order in which these various types are listed, from A to G, characterizes a more conventional functional scenario (Fig. 1902.1) in order of increasing complexity in valve-to-valve interaction: hinge axis, but no hinge line (Fig. 1901B); hinge line, but no articulation (Fig. 1901D); articulatory structures primitive, then more derived (Fig. 1901E–1901G).

Stratigraphic polarity alone imposes a structure on these functional groups, but it is a structure dependent on the vagaries of preservation and taphonomic control. The halkieriid sister-group relationship to brachiopods has not yet been tested rigorously, so does not yet impose a clear polarity on these transitions in articulation. Based strictly on relative stratigraphic position, the following order can be deduced (Fig. 1902B): (1) multielement halkieriids appear first in the Nemakit-Daldynian; (2) paterinates, with strophic hinge lines but lacking articulation appear next in the Tommotian; (3) discinoids (*Heliomedusa*) that lack valve-to-valve contact appear in the lower Atdabanian, as do obolelloids with strophic hinge lines bearing small, rudimentary ventral denticles and dorsal sockets (*Trematobolus*) and other obolelloids (*Obolella*) with strophic hinge lines but no articulatory structures; (4) protorthides, orthides, and pentamerides, with deltidiodont articulation of noninterlocking ventral teeth fitting into dorsal sockets, appear in the Toyonian; (5) rhynchonellides with interlocking cyrtomatodont dentition appear in the Llanvirn. This pattern, if truly representative of the order of the evolution of these features, reveals that a strophic hinge line lacking articulatory structures, about which the valves rotate, is the most primitive type of articulation, followed closely in time by three different and coeval functional types of articulation. Stratigraphic polarity cannot yet provide insight into which of these three may be more basal than the others. More typical deltidiodont articulation appears later, and interlocking cyrtomatodont appears later still.

Outgroup polarity may have the power to resolve further the pattern of evolution of articulation (Fig. 1902.3). Among extant brachiopods only, both molecular (Cohen & Gawthrop, 1997; Cohen & Weydmann, 2005) and some (but not all, see Holmer & others, 1995) morphological analyses (Carlson, 1995) support the hypothesis that craniids share most recent common ancestry with discinids and lingulids (see Carlson, herein, Fig. 1907–1908). If so, the nature of valve-to-valve interaction in lingulid and discinid brachiopods (type B) would represent a more derived condition than what exists in craniids (type C). If the various rudimentary articulatory structures seen in kutorginates and some obolellates and trimerelloids (type E) are truly homologous with deltidiodont and cyrtomatodont dentitions (this has certainly not been tested in any rigorous fashion and may well be false), it is reasonable to hypothesize that types B and C, lacking articulatory structures, are more primitive than those with rudimentary structures (type E). Types B, C, D, and E are all more primitive than is F, and it is difficult to say with certainty which of these four types is truly the most basal. When these various articulatory functional groups are mapped onto the pattern of relationships illustrated in Carlson (herein, Fig. 1908), all four types appear near the base of the cladogram.

Consistent with the evolutionary transformation discussed previously for muscle systems, I suggest the following evolutionary transformation in valve articulation, outlined in Figure 1902.3. These morphological transformations can be polarized by stratigraphic or outgroup criteria; both criteria together seem to provide the greatest resolution (Fig. 1902.3; and see Carlson, herein, Fig. 1908), but even that resolution is not particularly clear. It is entirely possible that each of the articulatory types described here represents a grade of functional organization, rather than synapomorphies defining clades (Bassett, Popov, & Holmer, 2001); this would seem to be most plausible for types C, D, and E. With the information that can be gleaned from specimens currently in hand, it is difficult to test these competing hypotheses.

Bassett, Popov, and Holmer (2001) argued that the diverse types of articulation observed among the early rhynchonelliforms are so different that they could not have shared common ancestry and must have evolved independently. Specifically, they argued that the primitive, rudimentary types of articulation seen in obolellates, chileates, and kutorginates evolved independently of one another and that deltidiodont articulation evolved independently in protorthides and orthides. Given the relatively small numbers of specimens collected from these early groups and their variable states of preservation, particularly of anatomical features, it is essentially impossible to reject any hypothesis of relationship of articulatory styles among the Early Cambrian brachiopods at this time.

The lesson of *Heliomedusa* is an important one to remember: numerous conclusions (Jin & Wang, 1992) reached about the identity and position of anatomical features after examination of 185 well-preserved specimens collected by 1992 were rejected upon examination of 1150 specimens collected by 2004 (Chen, Huang, & Chuang, 2007). It is not possible at this time to reject the hypothesis of multiple convergent or parallel evolution of different styles of articulation suggested by Bassett, Popov, and Holmer (2001), but it is not necessarily the most parsimonious interpretation of the evidence currently in hand (Fig. 1902). It is not clear, for example, why articulation in protorthides and orthides is said to have evolved convergently, when these two taxa appear to share the most recent common ancestry (see Carlson, herein, Fig. 1908; see also Carlson & Leighton, 2001). Mapping the pattern of articulatory types onto the cladogram illustrated in Carlson (herein, Fig. 1908), one can construct numerous functional and phylogenetic scenarios to explain the origin and evolution of the pattern. Depending on how one resolves the polytomies or how unwilling one is to accept the pattern of relationships presented here, almost any hypothesis imaginable can be proposed; testing the hypotheses with evidence is the truly challenging aspect of the analysis of the evolution of articulation.

EVOLUTION OF LOPHOPHORE AND SUPPORT STRUCTURES

[Sandra J. Carlson]

Given our current understanding of metazoan phylogeny (Zrzavy & others, 1998; Giribet & others, 2000; Nielsen, 2001; Peterson & Eernisse, 2001; Valentine, 2004; Larget, Kadane, & Simon, 2005; Passamaneck & Halanych, 2006), it is likely that the extant sister group to brachiopods does not possess a lophophore. Of the other two lophophorate phyla, phoronids may well cluster within the brachiopod clade (Cohen, 2000; Cohen & Weydmann, 2005; see also Freeman & Lundelius, 2005), rather than as the brachiopod sister group, but this hypothesized relationship remains controversial (see herein, p. 2880). Bryozoans are now thought to be rather distantly related to brachiopods, and their lophophores not homologous (Nielsen, 1985; Valentine, 2004); pterobranchs have been described as possessing a lophophore-like tentacular crown containing coelomic extensions (Brusca & Brusca, 2003), even though the mouth lies outside the ring of tentacles, and they are clearly more closely related to the deuterostome taxa. This suggests that the two-armed brachiopod lophophore was a novel feature and evolved from an ancestor lacking a lophophore.

In all brachiopods except thecideides (and phoronids), the lophophore tentacles are paired and located on either one or both sides of the arm axis (Emig, 1976; Williams & others, 1997). Given the phylogenetic hypothesis illustrated in Carlson (herein, Fig. 1908), it is possible to argue either that unpaired tentacles evolved twice independently in phoronids and thecideides (with adlabial tentacles only) or that thecideides alone among brachiopods reversed to a primitive state shared by phoronids. The loss of the ablabial tentacles might be related to their truncation in development, as a result of the small adult size of thecideides (Carlson, 1995), or might possibly relate to reproduction by brooding rather than dispersal (C. H. C. Brunton, personal communication, 2004); both might relate to each other.

Lophophore Ontogeny

The ontogenetic pathways in lophophore geometry observed among extant brachiopods have been amply characterized (Atkins, 1959a, 1960a, 1961c; Rudwick, 1962a, 1970; Baker, 1990, 1991, 2006, Emig, 1992; Williams & others, 1997, p. 112, fig. 111). Not surprisingly, geometric complexity of the lophophore increases as body size increases during ontogeny, as more tentacles are required to support the physiological needs of larger individuals. A simple, ring-shaped trocholophe is the first functional lophophore configuration to develop, formed by paired semicircular brachial axes (from which the lophophoral tentacles emerge), one on either side of the mouth.

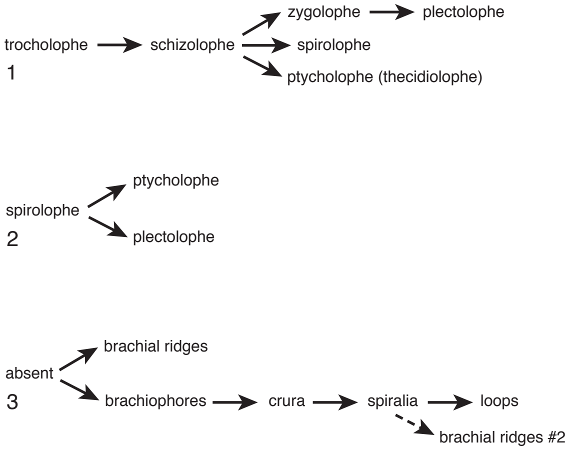


FIG. 1904. Lophophore ontogeny and evolution; *1,* lophophore ontogeny, following RUDWICK, (1970); *2,* lophophore evolution, following topology in Figure 1908; *3,* hypothetical brachidial evolution, following topology in Figure 1908 (new).

The lophophore apices are located anteriorly, opposite the mouth, located posteriorly. The trocholophe stage is followed by a schizolophe or split bilobed configuration (Fig. 1904.1), in which the apices of the lophophore (brachial axis) migrate posteriorly toward the mouth. The brachial axis lies within a plane parallel to the commissural plane in both stages. This initial developmental pattern appears to be shared universally by all extant brachiopods.

Following the schizolophe stage, however, three distinctly different developmental pathways may be pursued, producing either a spirolophe, plectolophe, or ptycholophe lophophore. The ptycholophe is characteristic of thecideide brachiopods today, particularly thecidellinids, and involves additional infolding of the brachial axis in the same plane as the schizolophe. In extant spirolophes, the brachial axis may migrate helically in either a dorsal (craniids, rhynchonellides) or ventral (discinids) direction, or it may rotate 90 degrees to migrate medially, as in lingulids. The plectolophe is characteristic of terebratulide brachiopods and is typically preceded ontogenetically by a zygolophe stage, in which the brachial axis migrates first ventrally and then posteriorly. Eventually the apices of the brachial axis migrate medially, forming an inner planispiral spirolophe (median coil) not unlike that seen in lingulids.

Ontogenetic changes in the calcareous lophophore supports among extant brachiopods include elongation of the crura in rhynchonellides (SAVAGE & others, 2002 and references therein) and increased infolding and lobation in the brachial ridges of thecideides (for example, BAKER, 1969, 1970, 2006). As BAKER (1989) pointed out, our knowledge of ontogenetic changes in the morphology of lophophore support structures is poor for many groups of fossil and Recent brachiopods. Studies by MACKINNON and coworkers (MACKINNON, 1993; MACKINNON & SMIRNOVA, 1995), however, have greatly improved our knowledge of loop ontogeny in terebratellidine brachiopods. Among long-looped terebratulides, teloform (adult) loops can develop in at least two different ways. In most terebratellidines, most elements of the loop develop from a septal pillar arising from the center of the dorsal valve; some of the posterior section of the descending lamellae derive from the cardinalia as well (LEE & others, 2006). Paleozoic terebratulidine teloform loops, almost indistinguishable morphologically from terebratellidine teloform loops, develop in some taxa from the cardinalia (crura) alone (MacKinnon, 1993; Lee & others, 2006; see also Baker, 1972; Richardson, 1975). Among short-looped terebratulidine brachiopods, the loop develops entirely from the cardinalia; no septal pillar exists.

Lacking Recent articulated brachiopods with mineralized spiral brachidia, our knowledge of the details of spiralium development is quite poor (but see Copper, 2002; Alvarez & Rong, 2002). It appears that spiralia developed exclusively from the dorsal cardinalia, largely from the crura.

Lophophore Evolution

What relationship, if any, exists between these ontogenetic pathways and patterns of evolution in lophophore morphology? Among extant brachiopods, a spirolophe lophophore is the most evolutionarily primitive adult form (see Carlson, herein, Fig. 1908), based on either stratigraphic (Williams & others, 1996; Williams, Carlson, & Brunton, 2000) or outgroup (Carlson, 1995) polarity criteria. Emig (1992) stated that the spirolophe has evolved as least twice independently, possibly referring to the fact that the lophophore configuration in many Paleozoic rhynchonelliforms is not known with complete certainty. Spirolophes occur in all inarticulated brachiopods, in phoronids, and in rhynchonellides. Brachiopods with ptycholophe lophophores (thecideides and rare terebratulides, e.g., *Megathiris*) and plectolophe lophophores (most terebratulides) both evolved from ancestors with spirolophe lophophores. Some taxa with small body sizes as adults have retained the primitive juvenile type of trocholophe, zygolophe, or schizolophe lophophore (e.g., *Pumilus*, Williams & others, 1997, fig. 112). Lower Cambrian *Heliomedusa* (Chen, Huang, & Chuang, 2007) appears to possess a distinctive type of spirolophe lophophore, adding further fossil support to the idea that a spirolophe is the basal lophophore state among brachiopods.

Mineralized lophophore support structures are absent in all the more basal brachiopods, as well as phoronids (see Carlson, herein, Fig. 1908). This is thought to result from their absence in the living organisms, rather than nonpreservation in the fossil record. Structures interpreted to have provided support for the lophophore first appear as brachial ridges in most strophomenates and as extensions of the inner socket ridges referred to as brachiophores in early rhynchonellates and in some orthotetidines (Fig. 1904). Brachiophores became elongated and elaborated as crura in derived pentamerides and in rhynchonellides, which became further elaborated as spiralia in the spire-bearing brachiopods and then transformed to loops in terebratulides. If some strophic spire-bearers share closer common ancestry with the impunctate orthoids (Wright, 1979; Gourvennec in Copper & Gourvennec, 1996; Gourvennec, 2000), then spiralia evolved at least twice independently among rhynchonellates, as also did laterally directed spiralia. If thecideides share closer common ancestry with the spiriferides (Baker, 1984, 1990), then brachial ridges have evolved at least twice independently. *Thecospira*, the most basal thecideide (Jaecks & Carlson, 2001), possesses spiralia, supporting this latter possibility.

Brachiophores are considered to be the homologues of crural plates in rhynchonellides (Brunton, Alvarez, & MacKinnon, 1996; Williams, Brunton, & MacKinnon, 1997, p. 369, fig. 329) and socket plates in porambonitoids (Carlson, 2002). It is possible that they may have provided some posterior support to the lophophore in some orthoids, protorthoids (*Enteletes, Skenidioides*), and orthotetidines. Brachiophores are not developed or are very rare in most protorthides, strophomenoids, and clitambonitoids.

Short rodlike or bladelike crura evolved in the clade that includes rhynchonellides and camerelloids as sister taxa (Carlson, 2002). Porambonitoids do not have elongated crura or brachiophores, but very short and morphologically simple socket plates that are unlikely to have provided much lophophoral support. Crura continue to elongate and become more morphologically complex in later rhynchonellides. Diversity in known crural morphology is great, and this diversity provides structure for much of the classification of the superfamilies of rhynchonellides (SAVAGE & others, 2002). Evolutionary relationships among these many, distinct crural types have not yet been determined in detail. Because of their long and delicate structure, crura break easily after death and are thus rather poorly known in a great many rhynchonellides, particularly in the Paleozoic (SAVAGE & others, 2002), complicating the task of determining their phylogenetic relationships.

Because of their considerable morphological complexity and the absence of spire-bearing brachiopods in the Recent fauna, the evolution of spiralia continues to be a contentious topic (RUDWICK, 1970; WRIGHT, 1979; GRUNT, 1982; COPPER & GOURVENNEC, 1996; GOURVENNEC, 2000). The apices of the spiralia point in different directions in different spire-bearing brachiopods: in atrypides they point medially or dorsomedially; in athyridides they point laterally or lateroventrally (ventrally in koninckinoids); in spiriferides and spiriferinides they point laterally or posterolaterally. Several evolutionary hypotheses have been proposed (Fig. 1905) that afford different degrees of importance to the direction in which the spires point, the relative order of appearance of certain features in the stratigraphic record, the significance of a strophic or astrophic hinge line in conjunction with a spiralium, and finally the presence or absence of a complete jugum or medial band connecting the two lamellae of the spiralia.

Monophyly of the spire-bearing brachiopods is supported by COPPER in COPPER and GOURVENNEC (1996; see also DAVIDSON, 1882; WAAGEN, 1883). In this hypothesis, spiralia evolved once, and all spire-bearers (Atrypida, Athyridida, Spiriferida, Spiriferinida) are thus closely related and evolved in relative stratigraphic order from Rhynchonellida (Fig. 1905.1). This hypothesis emphasizes the evolutionary importance of the presence of spiralia and the stratigraphic order of appearance of the different groups characterized by the orientation of the spires.

The diphyletic origin of spiralia was proposed by RUDWICK (1970) and expanded upon by subsequent authors (WRIGHT, 1979; GRUNT, 1982; GOURVENNEC in COPPER and GOURVENNEC, 1996; GOURVENNEC, 2000) proposing several different hypotheses. Strophic spire-bearers (spiriferides and spiriferinides) shared ancestry with strophic orthides, while the astrophic spire-bearers (atrypides and athyridides) shared ancestry with the astrophic rhynchonellides (Fig. 1905.2; RUDWICK, 1970; WRIGHT, 1979). Spiralia evolved twice independently, as also did laterally directed spiralia. Uncertainty about deltidiodont or cyrtomatodont hinge structures contributes to this debate; strophic spire-bearers seem to be deltidiodont (CARLSON & LEIGHTON, 2001, but see also JAANUSSON, 1971), while astrophic are cyrtomatodont. A variant of this hypothesis is discussed by COPPER (in COPPER & GOURVENNEC, 1996), in which both athyridides and spiriferides, the two groups with laterally directed spiralia, evolve from the orthides, while the atrypides with dorsomedially directed spiralia evolve from the rhynchonellides, with dorsally directed lophophore spires (Fig. 1905.3). In this hypothesis, the direction of the spires is granted greater evolutionary importance than the nature of the hinge line. A third diphyletic hypothesis was proposed by GRUNT (1982) in which the atrypides and athyridides each evolved spiralia independently from the rhynchonellides, with the spiriferides (and spiriferinides) evolving subsequently from the athyridides (Fig. 1905.4).

Various aspects of the evolution of the jugum, a calcareous band that connects the two halves of the spiralia in some taxa (athyridides in particular) were discussed in WILLIAMS, BRUNTON, and MACKINNON (1997, p. 374+) and will not be repeated

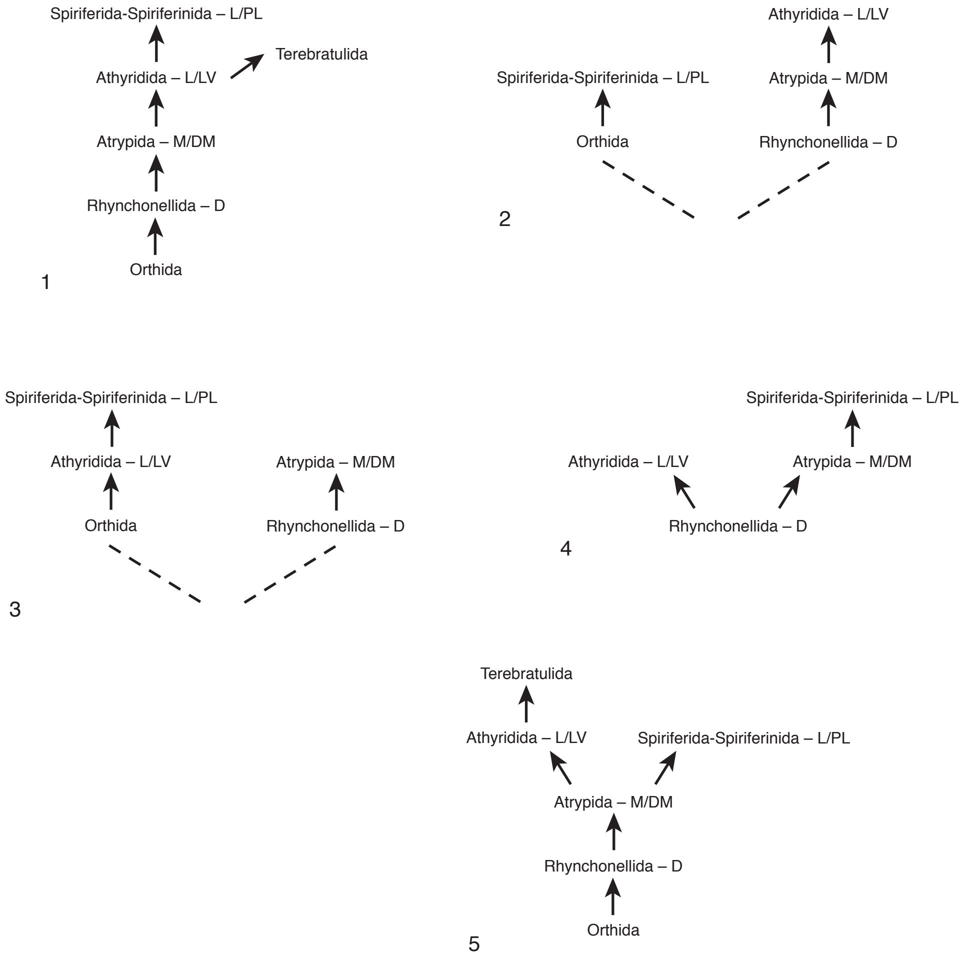


FIG. 1905. Hypotheses of evolution of spiralia among spire-bearing brachiopods; *1,* following Copper in Copper and Gourvennec (1996); *2,* following Rudwick (1970) and Wright (1979); *3,* discussed in Copper and Gourvennec (1996); *4,* following Grunt (1982); *5,* following Rong and Zhan (1996); *L/PL* indicates lateral-posterolateral orientation of spiralia; *L/LV,* lateral-lateroventral; *M/DM,* medial-dorsomedial; *D,* dorsal (new).

here. The presence or absence of a jugum is considered to play an important role in these competing evolutionary hypotheses, however. COPPER predicts that finding a complete jugum in the earliest spiriferides (e.g., *Eospirifer*) would support the evolution of the spiriferides from the athyridides (most of which have a complete jugum) and thus the monophyletic origin of spiralia (COPPER & GOURVENNEC, 1996). This scenario would also support the hypotheses illustrated in Figure 1905.3 or 1905.4, however, and does not appear to be as definitive a piece of evidence as COPPER asserts. The discovery of additional specimens of *Eospirifer* and *Striispirifer* (RONG & ZHAN, 1996) that possess a small jugal process but lack a complete jugum is not consistent with COPPER's prediction, which GOURVENNEC (2000) suggested should lead to a reexamination of the monophyly hypothesis. RONG and ZHAN (1996) proposed that the spiriferides and atrypides share closer common ancestry, based on the absence of a complete jugum (Fig. 1905.5). Clearly, some of the characters evaluated in these hypotheses of relationships are homoplastic, not homologous; just which ones they are, however, has yet to be determined.

The presence of a loop in all but the medial (spiral) coil of the plectolophe lophophore is a synapomorphy (shared derived character) of the Terebratulida. As discussed earlier with respect to loop ontogeny, the morphologically simpler of the two loop types (so-called short-looped forms, in Terebratulidina) first appears in the Early Devonian; the loop develops from the crura only. The more derived, long-looped forms in Terebratellidina first appear much later in the Early Triassic; the loop develops from both the crura and the septal pillar (MacKinnon, 1993; Lee & others, 2006). A loop has originated independently of the terebratulides in *Tropidoleptus* (possibly an orthide; Williams & Wright, 1961) and *Enantiosphen* (possibly a pentameride; Boucot, Rong, & Blodgett, 2002). Although their developmental and evolutionary origin is somewhat perplexing, these few instances of homoplasy (possibly due to paedomorphosis) are not sufficient to cause us to reject the hypothesis of the homology of the loop within the terebratulide clade. The occurrence of loops in species outside terebratulides demonstrates that at least a certain amount of developmental flexibility in lophophore mineralization and configuration exists and makes it more difficult to reject the diphyly hypotheses of spiralia evolution.

Brachial ridges are present on the dorsal valve interior in some strophomenides, productides, and thecideides. Their shapes suggest support for schizolophe (*Christiania*, *Reticulatia*, *Anidanthus*, *Urushtenia*), planispiral spirolophe (*Leptaenisca*), or ptycholophe lophophores (most thecideides). Stratigraphy, shell structural changes, and other morphological changes support the evolutionary changes seen in the lophophore supports in plectambonitoids, through Chonetidina to the Productidina and Strophalosiidina (Brunton, 1972). In the very shallow-bodied aegiromenine plectambonitoids, the more usual strophomenate brachiophores are lost, and small anderidia are found in a few genera. These paired ridges on the dorsal interior extend forward from the adductor scars, becoming raised and pointed anteriorly where they are interpreted as supporting the body wall in positions where the lophophore was attached. These structures are found virtually throughout the chonetidines, which do not have well-developed brachial ridges. Anderidia are found also in the three earliest known genera of the productidines and strophalosiidines, but by the Eifelian they are lost, and brachial ridges become increasingly prominent. These features mark the positions on the dorsal valve where the mantle epithelium supported the lophophore, which curved ventrally onto the body wall in which the mouth was placed, and thence anteroventrally on the body wall covering the ventral attachments of the diductor muscles and probably diverticula around the stomach.

The platform of some plectambonitoids (Cocks & Rong, 2000, p. 306) is similar to the tuberculate and ridged borders of dorsal valves in some chonetidines such as *Dyoros (Tetragonetes)* and probably indicates the outline of the lophophore, but the lophophore always remained unsupported by any internal skeletal structures. For this reason, it depended on epithelial attachment that, when intimately associated with the valve interior, caused the growth of shelly brachial ridges.

Brachial ridges are well formed in many productidines and strophalosiidines but are unknown in other groups apart from exaggerated brachial structures in the lyttoniidines and thecideides. In the Productida they probably increased in size and development as these shells grew in size during their range to the Late Permian, with increased demands upon their roles in respiration, collection of food, and clearing of waste products and gametes. The lyttoniidines, a highly derived group of productides, possess a curious, highly lobate internal plate that has a generally ptycholophous shape (Williams, Carlson, & Brunton, 2000).

The most complicated calcified brachidium of Grant (1972) is found in the Permian strophalosiidine *Falafer* (Brunton, Lazarev, & Grant, 2000, p. 355). Thecidiolophe (Pajaud, 1970; Baker, 1990) supports have evolved in some thecideides (lacazelloids), in which the ptycholophe emerges from the floor of the valve and folds in a ventral and posterior direction, not unlike the folded ptycholophe of *Falafer*. These are exaggerated shelly forms of folded brachial ridges, possibly resulting from the wide gape of these small dorsal valves so that the lophophore became more fully exposed to the surrounding sea (C. H. C. Brunton, personal communication, 2005).

Evolution of Coelom, Mantle Canal Systems, and Gonadal Repositories

[Alwyn Williams]

The shape and distribution of the coelom and its contents differ among living representatives of all three brachiopod subphyla. The coelom itself varies in the development of sinuses within the mantle; and, because such patterns are impressed by differential shell secretion on valve interiors, changes in the branching and functions of sinuses have been traced throughout the geological record. Muscles and gonads, being directly attached to the shell, have also left imprints on the interiors of fossil brachiopods. The main evolutionary changes affecting muscle systems have already been discussed in the context of valve movement and articulation. The implications of changes in gonadal imprints are considered here in relation to the development of coelomic sinus systems (mantle canals). Changes in the anatomy and disposition of the gut and the nervous and excretory systems, on the other hand, almost never leave any trace on the fossilized integument. Gut morphology can, to some extent, be inferred from the disposition of the valves relative to one another and to the pedicle. It has been considered in this context elsewhere in the chapter (see Fig. 1899–1900). No such inferences can be made about past nervous and excretory systems. Each, however, has undergone significant changes at the subphylum level, as reflected in living species, and will be briefly addressed here.

Distributional changes in the mantle canals and gonadal repositories in extinct and living brachiopods reflect the evolution of the body cavity relative to muscle and gonadal attachments and the folded epithelial mantles of both valves (Fig. 1906). Sinuses and canals (in up to four orders of branching) invade the connective tissue of the mantle of both brachiopod valves. The sinuses accommodate gonads while each canal branch is divided into two channels by a median ridge of ciliated epithelium, which circulates coelomic fluid in opposite directions throughout the mantles and their marginal setal follicles. Distributional changes in these canals and sinuses are complex in detail in extinct and living species. On the broad scale, however, they reflect the evolution of the body cavity and its mantle extensions relative to the disposition of muscle bases and gonads. Such changes are noteworthy as they suggest that a divergence in body cavity size occurred among stem-group brachiopods and has persisted, with thematic variation, to the present day.

The basic lingulate pattern (Fig. 1906), as impressed on the shells of earliest Cambrian lingulides and acrotretides, is typified by that of living discinoids. Within their relatively large body cavities, gonadal lamellae are attached to gastroparietal and ileoparietal bands or exceptionally lie free. Two primary mantle canals (*vascula lateralia*), controlled by muscular valves and emerging from submedial muscle fields, divide into arcuate, posterior, and anterior trunks. In the dorsal valve, an additional pair of canals emerges anteromedially from the muscle field (*vascula media*). This baculate canal system is more variable in acrotretides, with a stronger development of *vascula media* in Early Cambrian botsfordiids and repeated first-order branching of the *vascula lateralia* of both valves of later acrotretides (pinnate condition). The most dramatic change, however, was the suppression of the *vascula* *media* in the lingulids and their presumed sister group, the pseudolingulids (bifurcate condition).

The distribution and function of mantle canals in living craniids differ from the lingulate system in several respects (Fig. 1906). Adult craniids are without setae (a feature shared with the thecideides, the shells of which are also cemented). Accordingly, mantle distributaries do not exceed third-order branching and end well within the valve margins. Pairs of pinnate *vascula lateralia* and *vascula media* are the only canals developed in the ventral and dorsal valves respectively. There are six gonads: two in the main body cavity and one in each of the principal canals, which are not closed by muscular valves (Williams & others, 1997, p. 130). The gonads within the canals are supported on genital lamellae developing from the inner epithelium of the mantle.

The earliest (Lower Ordovician) craniides are the cemented *Petrocrania* and the free-lying *Pseudocrania*. The canal systems of the former are convergent with those of lingulids (bifurcate) in that both valves are characterized only by *vascula lateralia*. The key to the vagaries of the craniid canal systems, however, appears to be the pattern characteristic of *Pseudocrania*. In juvenile stages of growth, *Pseudocrania* (with *Orthisocrania*, the presumed sister group of cemented craniids) was attached to the substrate by a transient holdfast in a calcareous sheath. Its canal system was not only baculate but also extended to the shell margins, suggesting that setal follicles were present (see Bassett, 2000, p. 169, fig. 93). The ensemble may be reminiscent of early lingulid patterns, but the pinnate divisions of the primary canals suggest that the canals contained palmate gonads as in living craniids.

Of the two other orders assigned to the craniiforms, the mantle canal systems of craniopsides are poorly known, while those of the trimerellides are quite variable with *vascula media* being more fully developed in the ventral mantle in some stocks and with bifurcate as well as baculate patterns characterizing others.

All crown-group rhynchonelliforms belong to the Rhynchonellata, with orthides, protorthides, and syntrophiidines well represented in the Cambrian (Fig. 1906). The development of a mantle system to operate articulating valves and the grouping of gonads within mantle sinuses resulted in a significant reduction of the body cavity and a complementary increase in the feeding region, the mantle cavity. This radical anatomical change is reflected in the mantle canal systems that, in the earliest stem-group species, typically consist of a pair of *vascula media* enclosing a pair of gonadal pouches in the ventral valve (saccate condition); and two pairs of primary canals, the *vascula media* and the *vascula myaria* (issuing from the posteromedian adductor field), and a pair of digitating gonads connecting with the posterolateral setal follicles of the dorsal valve (digitate condition). In penecontemporaneous syntrophiidines, the sister group of modern rhynchonellates (Carlson & others, 2002, p. 922), the gonadal sacs within the ventral mantle were also digitate and the peripheral arcs of the *vascula media* proportionately reduced.

Variations of these basic canal systems characterize descendant rhynchonellates. The most divergent involved the transformation of digitate gonads into repositories of radiating canals that served all but the anteromedial arc of the valve margin (pinnate condition) or a pair of greatly enlarged gonadal sacs dominating a reticulate network of canals (lemniscate condition). The extent to which these patterns repeatedly developed, even within rhynchonellate families, is shown by the variation found in living rhynchonellides and terebratulides (see Carlson, herein, Fig. 1907). The patterns in both valves of the rhynchonellides *Hemithiris* and *Notosaria* are respectively saccate and lemniscate (Williams & others, 1997, p. 75).

The saccate-digitate mantle canal systems of the apparent stem-group strophomenates, the Cambro-Ordovician billingsellides, are homologous with those of stem-group rhynchonelliforms (Fig. 1906). Moreover,

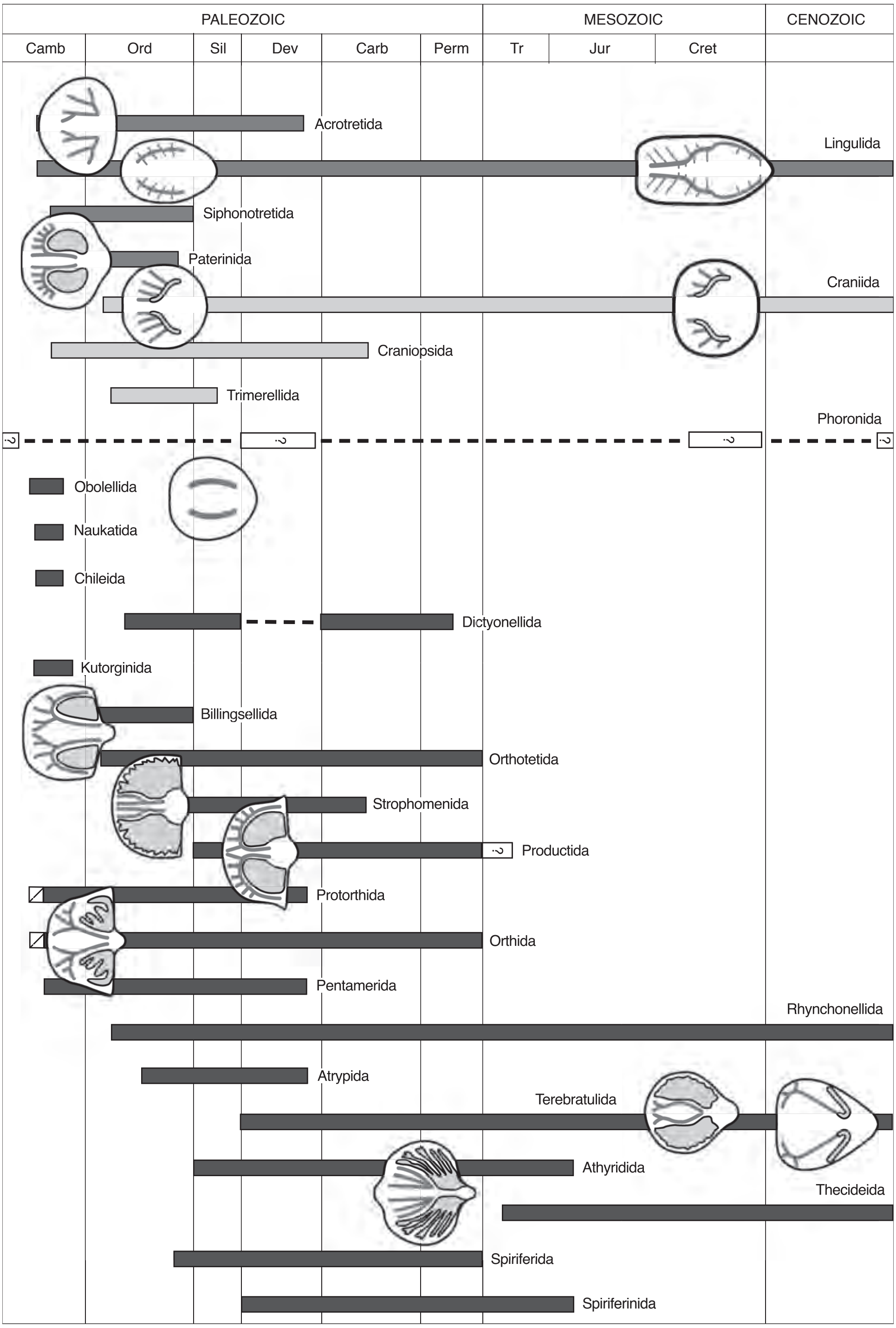


FIG. 1906. Ventral mantle canal and gonadal repository patterns characterizing selected ordinal groups of brachiopods throughout their evolution (new).

during strophomenate evolution, not only is the billingsellide pattern retained (*Leptaena*) but also homoplastic versions of lemniscate (*Strophomena*) and incipient pinnate (*Palaeostrophomena*) patterns developed in many lineages.

The most surprising apparent homology, however, involves the paterinates, which have a saccate canal system at least in the ventral valve (Fig. 1906) and probably in the dorsal valve as well (Williams, Popov, & Holmer, 1998, p. 258; Laurie, 2000, p. 149). In effect, the anatomy of the paterinates is rhynchonelliform despite their linguliform organophosphatic shell.

The mantle canal systems of the remaining rhynchonelliform classes (Fig. 1906) are more like those of derived lingulates than stem-group rhynchonellates or strophomenates. The mantle canal systems of obolellates are baculate, while the absence of gonadal imprints is consistent with the forward disposition of the muscle bases. The canal imprints of chileates are pinnate, but there is no evidence that the canals contained gonads, which is unlikely as the muscle fields of both valves would have to have been housed in a large body cavity. The kutorginate mantle canal system is also pinnate, but unlike the chileates, clearly defined muscle scars have yet to be described and the absence of gonadal extensions into canals is less certain.

EVOLUTION OF EXCRETORY (AND GONODUCT) AND NERVOUS SYSTEMS

[Alwyn Williams]

Apart from very rare nerve imprints on shell interiors, no decipherable traces of the excretory or nervous systems have yet been found in fossil brachiopods. They are briefly considered here, however, because their differentiation in living species has a bearing on brachiopod phylogeny.

All living brachiopods, except for most rhynchonellides, have one pair of metanephridia. In the rhynchonellide *Notosaria*, a second, smaller pair does not develop until the animal is at least 2.5 mm long (Percival, 1960, p. 453). In the micromorphic cryptoporids, however, with adult shells of all three assigned genera varying from 2.4 mm to 4.6 mm in length (Manceñido & others, 2002, p. 1243–1245), only the larger pair develops (Helmcke, 1940; confirmed by C. Lüter, personal communication, 2002; Lüter, herein, p. 2321). The cryptoporids are doubtfully included in the Dimerelloidea ranging back to the Upper Devonian. Living pugnacoids (in the family Basiliolidae) have two pairs of metanephridia; the superfamily extends back to the Lower Devonian.

The presence of a single pair of metanephridia in linguiforms, craniiforms, and most rhynchonelliforms is most likely a shared and primitive condition for all brachiopods, with two pairs of metanephridia evolving only within the rhynchonellides, for an as yet unknown reason. The absence of the second pair of metanephridia in cryptoporids could reflect a paedomorphic loss or some other kind of later, heterochronic transformation (C. Lüter, personal communication, 2002).

Nerve distributaries can vary greatly in detail; the prime zones of sensitivity in the brachiopod include the mantle margins, muscle fields, and pedicle. The only imprints to have been unequivocally identified in fossils, however, are those of the paired pedicle nerves found in the ventral valves of acrotretides as well as lingulides. The main concentration of nerve tissue occurs around the esophagus of all living species studied, where a relatively large subenteric ganglion is responsible especially for the innervation of the mantles, adductor muscles, and pedicles. In rhynchonelliforms, a supraenteric ganglion is also developed and is the principal source of lophophore innervation. In linguliforms and craniiforms, the supraenteric ganglion is absent, being functionally replaced by a circumenteric ring; the craniiform ganglion is divided into two masses. These differences appear not to have been accompanied by any significant changes in the patterns or sources of innervation.

RECENT RESEARCH ON BRACHIOPOD EVOLUTION

SANDRA J. CARLSON

[The University of California, Davis]

INTRODUCTION

Several issues in brachiopod evolutionary history have become the focus of rather intense scrutiny in the past few years. These issues appear to have become more complicated and more interesting with the discovery of many new fossils and the generation of new data from extant brachiopods. I discuss below five different phylogenetic issues relevant to brachiopod origins and evolution, the evidence presented to support them, and the different perspectives on each that have been raised: (1) relationship of brachiopods and phoronids; (2) relationship of craniiform brachiopods to other brachiopods; (3) relationship of thecideide brachiopods to other brachiopods; (4) relationship of brachiopods to the Tommotian fauna; and (5) relationships among all brachiopods. Against the backdrop of these various evolutionary perspectives, character homology and polarity for each of the character complexes can be evaluated.

All interpretations of the evolution of character complexes and evolutionary trends among brachiopods depend fundamentally on our current understanding of phylogenetic relationships among brachiopod taxa (CARLSON, 1995; HOLMER & others, 1995; HOLMER & POPOV, 1996; WILLIAMS & others, 1996; COHEN & GAWTHROP, 1997; COHEN, 2000; CARLSON & LEIGHTON, 2001; HOLMER, 2001; HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; COHEN & WEYDMANN, 2005). In very few cases are these various phylogenetic hypotheses, in part or in whole, fully corroborated and unanimously agreed upon, so differences of opinion necessarily exist. In an attempt to provide a balanced and comprehensive account of character evolution in the brachiopods, I present alternative interpretations that are consistent with existing phylogenetic hypotheses, fully realizing that these interpretations will themselves evolve as new evidence from fossil and Recent brachiopods comes to light.

In order to discuss the evolution of character complexes, hypotheses of character polarity (determining which character states came first and which came later in evolution) must be developed, and some criteria for determining polarity adopted (see also CARLSON, 1999). Issues of polarity determination play a particularly fundamental role in shaping our understanding of brachiopod evolution. Character transformation can be polarized by several different methods, none of which is without problems. Outgroup criteria has become the most common method used in most cladistic analyses and relies upon a comparison of the ingroup (in this case, brachiopods) with character states present in the closest relative (sister group); those characters shared between the ingroup and outgroup are more general and thus considered to be shared due to common ancestry (i.e., primitive in the ingroup). The problem with this approach in the study of brachiopod phylogeny is the uncertainty that persists with regard to the identity of the brachiopod sister group. Much anatomical data suggests that other lophophorates, or possibly some deuterostome taxa, are likely sister groups (EMIG, 1984; CARLSON, 1995; NIELSEN, SCHARFF, & EIBYE-JACOBSEN, 1996; LÜTER & BARTOLOMAEUS, 1997; LÜTER, 2000a; SORENSON & others, 2000; NIELSEN, 2001). The preponderance of molecular systematic data now argues strongly in favor of protostomes, namely mollusks (Fig. 1907; COHEN & GAWTHROP, 1997; COHEN, 2000; COHEN & WEYDMANN, 2005) or other Eutrochozoa (VALENTINE, 2004) as the brachiopod sister group. Too few comprehensive morphological studies have been completed at this date to be able to evaluate

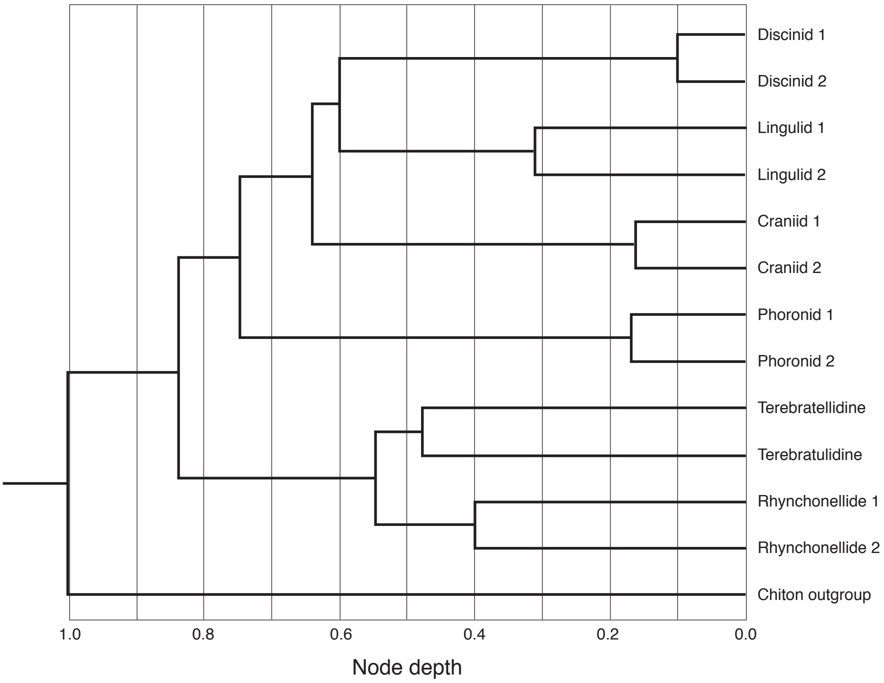


FIG. 1907. Phoronid and brachiopod phylogeny, generated from maximum likelihood (*ML*) heuristic search and bootstrap analysis of 3275 sites of concatenated SSU + LSU alignment. Nonparametric rate smoothing method used to rate-smooth ML chronogram shown; branch lengths proportional to node depth (adapted from Cohen & Weydmann, 2005).

morphological character transformation in brachiopods in detail, with respect to chitons (see VINTHER & NIELSEN, 2005) and other mollusks, rather than other lophophorates and deuterostomes. Because these molecular data have forced a rather fundamental shift in our perspective on brachiopod evolution, this is an exciting, if somewhat unsettled, time to be studying brachiopod evolution.

Apart from outgroup methods, another criterion for polarity determination available to paleontology is relative stratigraphic position (the traditional paleontological approach). Rather than comparing presumed closest relatives, comparisons can be made between the relative appearance of characters in the stratigraphic column; those features appearing earlier (lower) in the fossil record are more likely to be primitive, or general, than those appearing later (higher). As more brachiopod fossils are collected lower in the stratigraphic record, distinctions in relative stratigraphic order that have been made previously on the basis of smaller samples become less distinct, and one could argue that relative stratigraphic position is becoming less and less useful as a polarity criterion for evolutionary events in the critically important Early Cambrian. So much mineralogical and morphological diversity appears within Lower Cambrian strata, a period of perhaps 25 million years only, occurring over 500 million years ago, that it has become increasingly difficult to use relative stratigraphic position as a criterion for polarity determination of features among all brachiopods. Within Brachiopoda, however, stratigraphic data can play an increasingly significant role, in addition to morphological and molecular data, in evaluating hypotheses of phylogenetic relationships (CARLSON & LEIGHTON, 2001).

Ontogenetic transformations (FREEMAN & LUNDELIUS, 1999, 2005; FREEMAN, 2000, 2001), based on our current understanding of the living forms, can also provide an axis for determining polarity of character transformation. Features appearing earlier in ontogeny are considered more general (primitive) and those appearing later more specific (derived) (following NELSON, 1978). Because fewer than 5% of brachiopods are extant, ontogeny cannot provide a detailed determination of polarity for all taxa, but it does appear that early embryogenesis is quite different in living linguliforms, craniiforms, and rhynchonelliforms (NIELSEN, 1991; FREEMAN & LUNDELIUS, 1999, 2005; FREEMAN, 2000, 2001; see FREEMAN, 2003, for a more complete discussion of features in early development), providing additional support for the existence of three separate clades designated as the three brachiopod subphyla. Without an independent criterion of polarity, however, it is difficult to determine whether the characters that appear to be shared (homologous) by any two of these groups are shared and apomorphic (derived; see POPOV & others, 1993; WILLIAMS, CARLSON, & BRUNTON, 2000), shared and plesiomorphic (basal or primitive; CARLSON, 1995; COHEN, 2000; COHEN & WEYDMANN, 2005), or nonhomologous similarities, having arisen independently in different groups (FREEMAN, 2001; FREEMAN & LUNDELIUS, 2005). Fortunately, an approach combining both stratigraphic and ontogenetic polarity criteria is revealing, for example, the independent origination of lecithotrophic larvae among brachiopods and provides strong support for the rejection of lecithotrophy as a shared derived (or shared primitive) character uniting craniiforms and rhynchonelliforms (FREEMAN & LUNDELIUS, 2005).

Finally, the use of parsimony as a criterion for choosing among multiple hypotheses of phylogenetic relationship has come under increasing scrutiny recently (see FELSENSTEIN, 2004). Likelihood methods hold greater promise in their potential to provide a statistical assessment of the likelihood of particular topologies rather than merely choosing the shortest topology given the data in hand. Unfortunately, likelihood methods developed thus far lend themselves much more easily to molecular sequence data than to morphological data (although see WAGNER, 1998; LEWIS, 2001). Results obtained using parsimony analyses should therefore be considered, as always, as testable hypotheses that must be tested empirically, rather than as statements of fact about phylogenetic relationships.

RELATIONSHIP OF PHORONIDS AND BRACHIOPODS

The traditional view of brachiopod relationships has considered phoronids as the most likely sister group to brachiopods (EMIG, 1977, 1984; BRUSCA & BRUSCA, 1990, 2003; WILLMER, 1990; CARLSON, 1995; WILLIAMS & others, 1996; WILLIAMS, CARLSON, & BRUNTON, 2000; NIELSEN, 2001). Phoronids clearly share many developmental and anatomical features with brachiopods, with the major difference between them being the presence of two mineralized valves in brachiopods, which are commonly assumed to have evolved after divergence from a common shell-less ancestor with phoronids. Another significant difference is in the configuration of the gut in adults, which curves ventrally in brachiopods and dorsally in phoronids (NIELSEN, 1991).

Compelling evidence in the form of DNA sequence data is mounting (COHEN, 2000; COHEN & WEYDMANN, 2005) that suggests that phoronids are nested within brachiopods (Fig. 1907–1908), as a derived shell-less clade, rather than being the likely brachiopod sister group (WILLIAMS & others, 1996; WILLIAMS, CARLSON, & BRUNTON, 2000). If phoronids are actually shell-less brachiopods, rather than the brachiopod sister group, our understanding of brachiopod character evolution, as well as monophyly, will require adjustment. It is possible that differences in curvature of the gut in the two groups would preclude the derivation of one from the other (C. NIELSEN, personal communication, 2005). Several scenarios consistent with the topology in Figure 1907 appear equally likely at this time. Mineralized valves might have been lost secondarily in phoronids relative to a shelled common ancestor shared with brachiopods, thus brachiopods retained shells primitively. If the common ancestor was shell-less, then shells originated in brachiopods secondarily, and the absence of a mineralized shell in phoronids could be a primitive condition retained from the common ancestor. Also, brachiopods may have acquired shells twice (once in linguliforms and craniiforms as a clade, and once in rhynchonelliforms as a clade) from a shell-less common ancestor. If the topology illustrated in Figure 1907 cannot be rejected as additional evidence is gathered, the most parsimonious interpretation suggests that a calcareous mineralized skeleton is primitive, shared with the chiton (molluscan) sister group, with shell loss occurring in phoronids, and evolutionary mineralogical transformation (or loss and then gain) of a phosphatic shell occurring in the linguliform brachiopods.

Recent molecular results (Fig. 1907; COHEN & WEYDMANN, 2005) unambiguously place phoronids as a sister group to the craniiform + linguliform clade. If phoronids are simply pruned from this cladogram, brachiopod relationships have the same topology as earlier results using morphological characters to investigate relationships among the major groups of extant brachiopods (CARLSON, 1995). If phoronids are not the sister group to brachiopods, other candidates must be sought; continuing uncertainty in identifying the brachiopod sister group makes it difficult to determine the polarity of character transformation of shells and shell features in brachiopods and remains a necessary and intriguing field of inquiry. COHEN and WEYDMANN (2005) presented molecular evidence that argues in favor of chitons and against annelids as the extant sister group to brachiopods, as CONWAY MORRIS and PEEL (1995) suggest. CONWAY MORRIS and PEEL (1995) rejected a close relationship of halkieriids to chitons, but this position should certainly be reexamined in light of the new molecular evidence (COHEN & WEYDMANN, 2005) and morphological analyses of halkieriids (VINTHER & NIELSEN, 2005).

Similarities in the fate maps and mode of gastrulation between extant phoronids and rhynchonelliforms (G. FREEMAN, personal communication, 2004) provide embryological support (as shared primitive features) for the topology in Figure 1907, in which phoronids are the most basal of the three nonrhynchonelliform groups. Phoronids possess planktotrophic (feeding) larvae, a characteristic they share with linguliforms, basal (but not Recent) craniiforms (see section below; FREEMAN & LUNDELIUS, 1999), and basal (but not Recent) rhynchonelliforms (Fig. 1908; FREEMAN & LUNDELIUS, 2005). Similarities in the relative position of the mouth (anterior) and anus (posterior) in the larvae of brachiopods and phoronids suggest a common larval body plan (see WILLIAMS and CARLSON, herein, Fig. 1895) but do not speak directly to the relative position of phoronids as a brachiopod sister group or as part of the brachiopod ingroup clade. Differences in gut curvature are significant, however, and suggest that two different developmental pathways have been chosen by phoronids and brachiopods (C. NIELSEN, personal communication, 2005).

Lacking a mineralized skeleton, the assignment of fossils to the phoronids is necessarily quite tentative. Phoronid fossils may first appear as early as the Early Cambrian (Atdabanian, lowermost Botomian) in the Chengjiang fauna as *Iotuba* (CHEN & ZHOU, 1997; HOU & others, 2004). It is less than clear that this fossil is actually a phoronid (see COHEN & WEYDMANN, 2005, table 2). The next possible fossil occurrences are vertical burrows (*Skolithos*) in the Devonian (FENTON & FENTON, 1924; MACKINNON & BIERNAT, 1970) attributed to phoronids, but this assignment is extremely tentative, as is

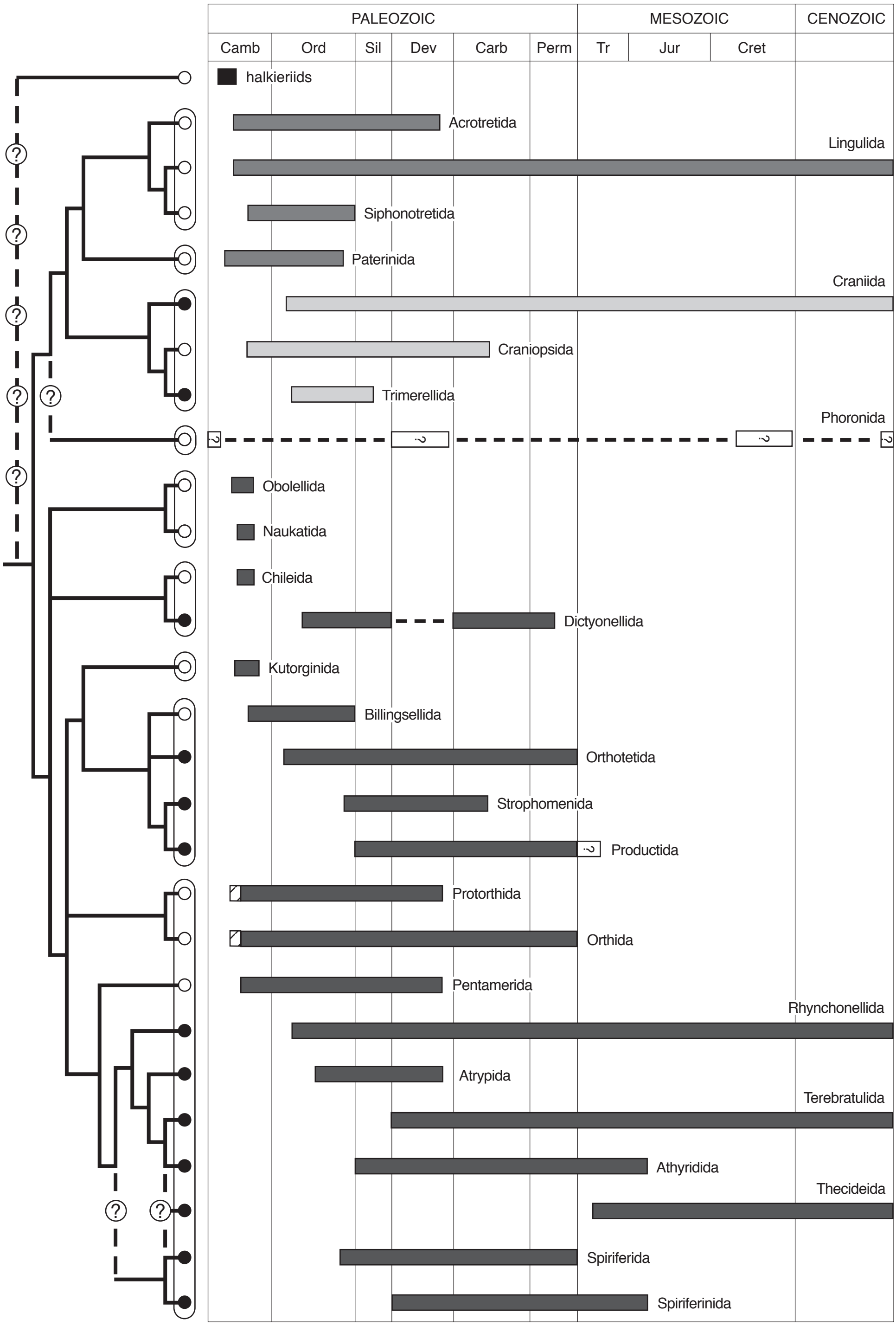


FIG. 1908. *For explanation, see facing page.*

a Cretaceous boring attributed to phoronids (JOYSEY, 1959).

RELATIONSHIP OF CRANIIFORMEA TO OTHER BRACHIOPODS

As reflected in the 1965 *Treatise* classification of brachiopods (WILLIAMS & ROWELL, 1965d; also ROWELL, 1981a, 1981b, 1982), craniides have traditionally been considered to be more closely related to the other inarticulated brachiopods than to the articulated brachiopods, largely on the basis of a lack of valve-to-valve articulation, although many other characters, both morphological (CARLSON, 1995) and molecular (COHEN, 2000; COHEN & WEYDMANN, 2005), support the hypothesis as well. Following this phylogenetic hypothesis (Fig. 1907–1908), Recent craniiform characters shared with Recent rhynchonelliforms may be either homologous and plesiomorphic (for example, CARLSON, 1995; LÜTER, 2001b) or nonhomologous (or example, FREEMAN & LUNDELIUS, 1999, 2005).

Challenges have been raised against the hypothesis that craniiforms are more closely related to linguliforms than to rhynchonelliforms (GORJANSKY & POPOV, 1985; HOLMER, 1991; NIELSEN, 1991; POPOV, 1992; POPOV & others, 1993; LÜTER, 2001b; WILLIAMS & HOLMER, 2002). Craniides have been proposed as the sister group to rhynchonelliforms, and characters they share with rhynchonelliforms are considered to be synapomorphies. Lack of articulation has been argued to be a primitive character (HOLMER, 1991; POPOV & others, 1993) and therefore cannot be used to diagnose the inarticulates as a clade.

Extant craniiform and rhynchonelliform brachiopods both have lecithotrophic (nonfeeding) larvae that remain in the plankton only a short while before settlement (NIELSEN, 1991; LÜTER, 2001b). Partly on this basis, NIELSEN (1991) suggested that craniides and articulates are likely to be sister taxa. LÜTER (2001b) argued, also on this basis, that lecithotrophy is more likely to be a shared and primitive condition for all brachiopods. FREEMAN and LUNDELIUS (1999), however, argued persuasively that Paleozoic craniiforms possessed planktotrophic larvae. Examining hundreds of fossil brachiopods, they measured the width of the protegulum, mineralized during the embryonic or larval stages of growth; larger valve size is indicative of a planktotrophic larval life history. Lower Paleozoic craniopsides possess a larval shell most likely mineralized during a longer-term planktotrophic larval stage. In a later study, FREEMAN and LUNDELIUS (2005) argued that Paleozoic rhynchonelliforms also possessed planktotrophic larvae. These studies provide strong support for the hypothesis that planktotrophy (present today in extant linguliforms and phoronids) represents the evolutionarily primitive condition for the brachiopods. Lecithotrophy in extant craniiforms and rhynchonelliforms has evolved independently twice from planktotrophic ancestors. Therefore, lecithotrophy is not an evolutionarily shared (homologous)

FIG. 1908. Stratigraphic ranges and consensus cladogram illustrating one hypothesis of phylogenetic relationship among the 26 orders of brachiopods currently recognized, and phoronids, constructed from data derived primarily from analyses of COHEN and WEYDMANN (2005) and COHEN (herein, p. 2356) using molecular sequence data from living brachiopods and phoronids; WILLIAMS, CARLSON, and BRUNTON (2000), HOLMER and POPOV (2000), and POPOV, BASSETT, and HOLMER (2000) using morphological data from mostly Cambrian and Ordovician taxa; CARLSON (1995) using morphological data from Recent brachiopods; and CARLSON and LEIGHTON (2001) using morphological and stratigraphic data together for all rhynchonelliform suborders. *Dark shading* of stratigraphic ranges indicates rhynchonelliforms, *medium shading* linguliforms, and *lightest shading* craniiforms; *open circles* immediately below stratigraphic ranges indicate those orders first appearing in the Cambrian, *closed circles* those first appearing in the post-Cambrian; *elongated ellipses* surrounding circles identify the 8 classes and phoronides; *encircled question marks* indicate uncertainties in topology discussed in text (new).

character and cannot be used to argue for a sister-group relationship between craniides and rhynchonelliforms.

The presence of a calcareous shell is likely to be homologous in craniiforms and rhynchonelliforms but could be either symplesiomorphic (shared and primitive) or synapomorphic (shared and derived). The assumption of synapomorphy led WILLIAMS and HOLMER (2002) to conclude that the craniiforms "diverged from one of the early rhynchonelliform stocks" (p. 871) as a sister clade to Linguliformea + Phoroniformea (see WILLIAMS and CARLSON, herein, Fig. 1896). They suggested that the craniiform "body plan has not changed much since the early Cambrian" (p. 870), yet they somewhat paradoxically claimed that the "craniiforms are the most derived brachiopod group" (p. 871) on the basis of their calcitic shell and differences apparent in development and organization relative to other extant brachiopods. Adult *Novocrania* have a body plan that is quite similar to the larval body plan of linguliforms and phoroniforms (see WILLIAMS and CARLSON, herein, Fig. 1895; NIELSEN, 1991), having a posterior anus and anterior mouth, suggesting that these similarities are more likely to be shared and primitive rather than uniquely derived.

The relative position of the mouth and anus in the larvae of brachiopods and phoronids is similar: posterior anus and anterior mouth (originating from the blastopore in phoronids and linguliforms and from the site of the blastopore in rhynchonelliforms, but only after the blastopore closes completely; LONG, 1964; NIELSEN, 1991) (see WILLIAMS and CARLSON, herein, Fig. 1895). In adults of these taxa, however, differences emerge (NIELSEN, 1991, see also COHEN, HOLMER, & LÜTER, 2003). In craniiforms, the gut does not curve or fold, and the anus remains medioposterior and mouth anterior in both larvae and adult; this straight gut has been considered to be the more primitive condition among metazoans (HYMAN, 1959; CARLSON, 1995). In phoronids, the gut curves into a U-shape and the anus becomes anterodorsal. In linguliforms, the gut curves into a U-shape and the anus becomes right lateral or ventrolateral. In rhynchonelliforms, the gut curves somewhat into a C-shape and the (blind) anus becomes posteroventral in position.

NIELSEN (1991) proposed an intriguing hypothesis regarding body plan evolution in brachiopods (Fig. 1909), which has since come to be known as the brachiopod fold hypothesis (HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; COHEN, HOLMER, & LÜTER, 2003). CONWAY MORRIS and PEEL (1995) adopted this perspective in suggesting the evolution of brachiopods from halkieriids. The fold hypothesis proposes that the anterior-posterior body axis is folded transversely during ontogeny, so that valves now considered to be dorsal and ventral should more accurately be described as dorsal anterior and dorsal posterior. This folding better explains the bilateral symmetry of each of the two valves in brachiopods (COHEN, HOLMER, & LÜTER, 2003) and is consistent with the observation of YATSU (1902) that a single circular embryonic shell in *Lingula* later divides to form a dorsal and ventral valve. Craniiform brachiopods appear to conflict with this hypothesis, however, in that their bodies do not fold during ontogeny (FREEMAN, 2001). According to NIELSEN (1991, fig. 3), *Crania (Novocrania)* larvae develop four coelomic sacs (C1, C2, C3, C4), arranged anteroposteriorly (Fig. 1909). At a later stage in development, coelomic sacs C1 and C4 "curled up ventrally" (NIELSEN, 1991, fig. 3 caption) and came to occupy a position below C2 and C3, respectively. One valve mineralized on the dorsal side of C2 and C3, after C1 and C4 migrated ventrally; this valve is currently considered to be the dorsal valve. At a later time, C1 and C4 can no longer be recognized in older larvae, and a second valve is mineralized topologically ventral to C2 and C3, but on the larval dorsal surface of these coelomic sacs. If this accurately represents the temporal series of events in *Novocrania* ontogeny, then the two valves currently considered to be dorsal and ventral in orientation appear to be topologically dorsal and ventral, yet developmentally dorsal anterior and dorsal posterior. Interestingly, however, the timing of formation of the valves is not coordinated—the dorsal valve forms first. It has been suggested that the dorsal and ventral mantles in strophomenates may also have developed at separate times, but that the ventral mantle (and thus valve) formed first; in rhynchonellates, dorsal and ventral mantle formation appears to be coordinated (Freeman & Lundelius, 2005). Depending on the phylogenetic position of craniiforms and the phylogenetic interpretation of body orientation, the never-folded craniiform body plan could represent either the primitive condition for brachiopods (Carlson, 1995) or a uniquely derived condition within brachiopods (Williams & Holmer, 2002).

Craniiforms lack a pedicle throughout ontogeny, which may represent the primitive condition for brachiopods, a condition shared with phoronids. If so, the pedicles of linguliforms (which are coelomate, muscular, and develop from the inner epithelium as an evagination of the ventral body wall) and rhynchonelliforms (which are not coelomate, not muscular, and develop from the larval pedicle lobe, not from the ventral body wall) are clearly not homologous (Carlson, 1995). The absence of a pedicle in thecideides certainly represents a secondary loss, relative to the ancestral pediculate condition.

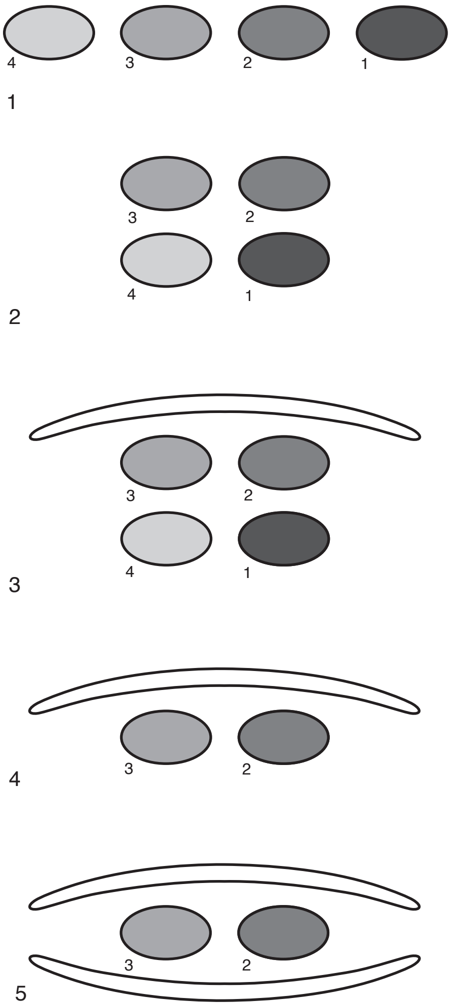


Fig. 1909. Reconstructions of developmental stages of *Novocrania* (adapted from Nielsen, 1991). *Shaded ellipses* represent paired coelomic sacs, numbered from anterior to posterior: *1,* arranged linearly; *2,* later ventral migration of first and fourth pairs of coelomic sacs; *3,* dorsal valve forms; *4,* first and fourth pairs of coelomic sacs can no longer be recognized; *5,* ventral valve forms, after dorsal valve (new).

RELATIONSHIP OF THECIDEIDA TO OTHER BRACHIOPODS

The relationship of thecideides to all other brachiopods has been fraught with controversy for decades; the first *Treatise* named them as a suborder in order Uncertain (Elliott, 1965). Thecideides have very small body sizes as adults, lack pedicles and live cemented to a hard substrate, possess brachial ridges on the dorsal valve interior to support the ptycholophous lophophore, have a strophic hinge line and cyrtomatodont dentition, columnar muscles, and a punctate shell with reduced secondary layer in many species.

Earlier claims (Elliott, 1948) of strophomenide ancestry were abandoned when it was determined (Elliott, 1953; Williams, 1955) that the shell structure of thecideides was punctate, not pseudopunctate. Williams (1973) suggested that thecideides might be paedomorphic descendants of the terebratulides (also punctate); preliminary molecular systematic studies appeared to support this hypothesis (Cohen & Gawthrop, 1997; Cohen & others, 1998) but have since been rejected (Cohen, 2001a). The extensive and meticulous studies of thecideide shell structure and morphology by Baker (1983, 1984, 1990, 1991) argued convincingly instead for descent from impunctate spiriferides on the basis of a hypothesis of homology of thecideide tubercles with spiriferide denticles; endopunctae thus appear to be homoplastic in these taxa. More recently, however, it has been suggested (Baker, 2006) that the cytological similarities in the endopunctae of thecideides, terebratulides, and some spire-bearers are too great to be attributed to homoplasy (supported, albeit ambiguously, by the analyses of Carlson & Leighton, 2001; see also Fig. 1908, 1911).

Spire-bearing *Thecospira* is considered to be the most primitive thecideide (Baker, 1990; Jaecks & Carlson, 2001), lending additional support to the hypothesis of spire-bearing ancestry and suggesting that brachial ridges evolved twice independently in strophomenates and more derived thecideides. But which spire-bearers are the thecideide sister group? Brunton (1972) and Brunton and MacKinnon (1972) argued for a close phylogenetic relationship between *Thecospira* and the koninckinoids (now a suborder in Athyridida; Alvarez & Rong, 2002; MacKinnon, 2002), suggesting that thecideides and athyridides may be more closely related than thecideides and spiriferides, a hypothesis supported by analyses of morphology and relative stratigraphic position by Carlson and Leighton (2001).

In a phylogenetic analysis of morphology, Jaecks (2001) demonstrated that the differences in topology of thecideide relationships polarized by strophomenate and spiriferide outgroups were surprisingly minor, underscoring the combination of strophomenate and spiriferide characters possessed by thecideides. Distinguishing homoplastic from homologous characters, and determining their polarity, will eventually help resolve the question of thecideide ancestry, as will obtaining robust molecular sequence data and reconstructing ontogenetic patterns of shell morphology and shell structure in a broader range of thecideides and other derived rhynchonellate brachiopods.

Molecular sequence data have not yet been as helpful as might be desired in locating the thecideides among the other extant brachiopods. Thecideides are not present in the topology illustrated in Figure 1907 (Cohen & Weydmann, 2005). Cohen (herein, p. 2356) considered thecideides as the sister group to the terebratulides, with rhynchonellides a sister group to both thecideides and terebratulides together. If koninckinides are the sister group to thecideides (Brunton, 1972; Brunton & MacKinnon, 1972) and koninckinides are athyridides (MacKinnon, 2002), this topology is consistent with morphological data from these extinct taxa. The branches connecting thecideides to the terebratulides (Cohen, herein, p. 2356) are very long, however, raising suspicions about the topology (see Felsenstein, 2004); further analyses (molecular, embryological, and developmental, in particular) of more taxa must be completed in order to test this hypothesis of relationships. Abundant morphological data supports thecideides as the sister group to terebratulides + rhynchonellides (Carlson, 1995), which is at least consistent with thecideides being more closely related to the extinct strophic spire-bearers (spiriferides; Baker, 1990, 1991, 2006). The trustworthiness of characters supporting this topology is not entirely clear, however; juvenilized thecideide characters might obscure the true pattern of relationships, forcing them down artificially into the most basal position in the topology of all extant brachiopods.

RELATIONSHIP OF BRACHIOPODS TO THE TOMMOTIAN (AND ATDABANIAN) FAUNA

The earliest brachiopods to appear in the Lower Cambrian are diverse mineralogically and morphologically, yet they can be easily recognized as brachiopods. This suggests that the common ancestor of brachiopods may have evolved earlier than the Early Cambrian, leaving no obvious Precambrian fossil record, which is not surprising. This possibility has led to a search for a brachiopod sister group among Lower Cambrian fossils that are less obviously brachiopod-like in their overall morphology but may share certain morphological characters with them because of descent from a common ancestor. A potentially rich source of characters is revealed in the diverse small shelly fossils of the Tommotian and raises numerous issues of character homology and polarity. Some of these are discussed below with reference to particular taxa and particular character complexes.

SIGNIFICANT FOSSIL GROUPS

Halkieriids

Conway Morris and Peel (1995) were the first to discuss in any detail the possibility that brachiopods evolved from one group of the (broadly paraphyletic) halkieriids (see also Conway Morris & Peel, 1990; Yochelson, 1993; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Cohen, Holmer, & Lüter, 2003). Halkieriids are a curious group of fossils, known from the Nemakit-Daldynian to Atdabanian, with a stratigraphic range extending into Middle Cambrian sedimentary rocks (Porter, 2004). Discovery of articulated specimens of Atdabanian halkieriids from Greenland (Conway Morris & Peel, 1995) establish the spatial relationships of the skeletal elements to one another on the body of *Halkieria evangelista*. Four different elements are known per organism: two shells (one anterior and one posterior) and three different types of sclerities (siculates, cultrates, palmates), each with many elements. The anterior and posterior shells of halkieriids were proposed as homologues of the dorsal and ventral shells, respectively, of brachiopods (Conway Morris & Peel, 1995); an evolutionary transformation involving the juxtaposition of the two shells along their median edges and folding of the body axis along this line (see also Nielsen, 1991; Cohen, Holmer, & Lüter, 2003) has been proposed to account for the evolution of brachiopods from halkieriids (see Fig. 1908; see also Williams and Carlson, herein, Fig. 1903).

A recent paper by Vinther and Nielsen (2005, p. 86–87) asserted that "a comparison of the morphological characters of *Halkieria*, molluscs, brachiopods, and annelids unequivocally supports the interpretation of *Halkieria* as a crown group mollusc" (p. 86) and that "no characters indicate a sister-group relationship" (p. 87) with brachiopods (Williams & Holmer, 2002) or annelids (Endo, 2001). Their argument is based on characters that "are compatible with characters in living molluscs" (p. 81), although no rigorous analysis of the homology or polarity of these characters is presented. Vinther and Nielsen argued that halkieriids are likely to be calcareous (following Bengtson & Missarzhevsky, 1981; Bengtson & Conway Morris, 1984; Bengtson & others, 1990) on the basis of their mode of preservation in the Sirius Passet fauna. In other fossil deposits, mollusks and other calcareous organisms are often preserved as steinkerns of secondary phosphates, while inarticulated brachiopods and tommotiids are preserved with primary mineralogy and ultrastructure. It is not clear, however, that originally mineralized organisms exist as fossils in the Sirius Passet fauna (which includes arthropods, sponges, a palaeoscolecidan, polychaete annelids, and halkieriids: Conway Morris & Peel, 1995); certainly none that are unequivocally phosphatic have been found.

Micrina

Micrina and *Tannuolina* together make up the Tannuolinidae, one of four families in the order Tommotiida (Missarzhevsky, 1970 as emended by Landing, 1984) or one of two families in the order Mitrosagophora (Bengtson, 1970). They are found in the Tommotian and Atdabanian, possibly extend into the early Botomian, and consist of two phosphatic elements or sclerites (Laurie, 1986; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Cohen, Holmer, & Lüter, 2003; Li & Xiao, 2004) that look superficially similar to brachiopod valves. It is not clear if an individual organism consists of only one of each of these two elements or if other elements or multiples of each element also occur. No articulated *Micrina* individuals have been found, only partially articulated individuals of *Tannuolina* that have been argued to be closely related to *Micrina* (Li & Xiao, 2002, 2004). Are *Micrina* sclerites homologous with brachiopod valves or not?

Controversy exists regarding the status of *Micrina* (and *Tannuolina*) as halkieriids, and their status as possible close relatives to brachiopods. One possibility is that *Micrina* is a halkieriid (based on the similarity in shape of *Micrina* sclerites and halkieriid shells and on their bilateral symmetry), that both *Micrina* and halkieriids were originally phosphatic (based on the nature of the rheomorphic deformation of the exterior surfaces of the sclerites), and that halkieriids (including *Micrina*) give rise to *Mickwitzia* (both sharing the same type of setigerous tubes in the microstructure of the sclerites), which then give rise to other brachiopods in a direct evolutionary sequence (see Williams and Carlson, herein, Fig. 1893; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002).

Li and Xiao (2004) presented a counterargument that, while *Micrina* and *Tannuolina* are likely to be closely related to one another on the basis of shared characters such as spaced growth lamellae and presence of canals (referred to as setigerous tubes by Williams & Holmer, 2002) in the sclerites that open to pores on the exterior surface, the homology of the sclerites in these two taxa is not clear, particularly for the mitral sclerites. They argued that even if *Micrina* and *Tannuolina* are closely related, both are likely to be only distantly related to halkieriids on the basis of the differences in sclerite morphology and body orientation in the articulated specimens of *Tannuolina* (Li & Xiao, 2004) and *Halkieria* (Conway Morris & Peel, 1995). *Tannuolina* sclerites are oriented with their axis of bilateral symmetry perpendicular to the long axis of the individual organism, with sellate sclerites apparently imbricated in anterior-posterior rows, while *Halkieria* shells are oriented with their axis of bilateral symmetry parallel to the long axis of the individual organism, with no imbrication of multiple shells apparent. Similarities in sclerite microstructure are thus thought to be convergent rather than homologous (see Williams & Carlson, herein, Fig. 1903).

Mickwitzia

Mickwitzia possesses an unusual combination of characters, leading to considerable uncertainly regarding its phylogenetic affinities (Laurie, 2000; Skovsted & Holmer, 2000, 2003, 2005; Holmer, Skovsted, & Williams, 2002; Williams & Holmer, 2002; Balthasar, 2004a). It first appears (questionably) in the Tommotian, and extends to the Botomian. Rowell (1965) placed it, with reservation, in the Paterinida; Laurie (2000) removed it to a more uncertain position as a so-called brachiopod-like fossil. Skovsted and Holmer (2000) claimed *Mickwitzia,* originally phosphatic in composition, is a linguliform brachiopod with shells composed of columnar laminae, a feature it appears to share with acrotretide brachiopods (by virtue of common ancestry according to Holmer, Skovsted, & Williams, 2002); it is referred to simply as a stem-group brachiopod by Skovsted and Holmer (2005). *Mickwitzia* also has striated, apatitic tubes indistinguishable from those in *Micrina* (Williams & Holmer, 2002), which are claimed to have held setae in the living animals. Balthasar (2004a, p. 381) argued that the setal tubes in *Mickwitzia* are "distinct from that previously recognized of *Micrina,*" although he acknowledges that *Mickwitzia*-type setae may be homologous to adult setae of extant brachiopods, while *Micrina*-type setae may be homologous to juvenile setae of extant brachiopods. On this basis, Balthasar (2004a) claimed that *Mickwitzia* is closely related to paterinide brachiopods, either as a derived, peramorphic paterinide or as a possible sister group to paterinides.

Heliomedusa

Heliomedusa, from the Chengjiang fauna of the Lower Cambrian (Atdabanian to lowermost Botomian) of southwestern China, was originally classified as a jellyfish (Sun & Hou, 1987) but has since been reassigned among several groups of brachiopods: as an unspecified inarticulated brachiopod (Conway Morris & Robison, 1988); an obolellid (Chen, Hou, & Erdtmann, 1989); and a craniopside (Jin & Wang, 1992; Zhang, Hou, & Emig, 2003; Hou & others, 2004). No original shell material is still preserved associated with these fossils, but it was assumed to have been originally calcareous, not phosphatic, and later replaced diagenetically by iron-rich clays (see also Balthasar, 2004a). Chen, Huang, and Chuang (2007) removed *Heliomedusa* from the Craniopsoidea (Jin & Wang, 1992) and placed it in Discinoidea on the basis of several synapomorphies seen in the soft tissues preserved as impressions in a larger collection of better-preserved individuals: a longitudinally oval pedicle foramen is present in the anterior region of the posterior sector of the ventral valve (which Jin & Wang, 1992, identified apparently erroneously as the dorsal valve) as in discinids; a short, straight pedicle is present, indicating that *Heliomedusa* is not cemented or free-living; elongate scars of paired anterior and posterior adductor muscles are also present; and the lophophore itself is preserved in association with the dorsal valve. These strong similarities to discinoids in soft-part anatomy imply that the *Heliomedusa* shell was chitinous or chitinophosphatic, not calcareous.

MORPHOLOGICAL COMPLEXES AND CHARACTER DISTRIBUTIONS

Mineralized or Not

The hypothesis that mineralized bivalved brachiopod shells evolved multiple times from various unmineralized ancestors has been proposed (Valentine, 1975, 2004; Wright, 1979; Gorjansky & Popov, 1985, 1986; Willmer, 1990), suggesting that brachiopods as a group are polyphyletic (or diphyletic). Among fossil brachiopods, all characters uniting them are related to the two mineralized valves, and it has been difficult to consider what a brachiopod without two valves would look like and how we would recognize it as a brachiopod even if we had collected it as a fossil. And yet, all living brachiopods share certain soft-part anatomical (Rowell, 1981a, 1981b, 1982; Carlson, 1995) and genetic characters (Cohen, 2000) that have little to do with the presence of two valves and provide strong evidence in favor of the monophyly of the group apart from the possession of two valves. If halkieriids prove to be the brachiopod sister group and the two valves of brachiopods can be demonstrated to be homologous with the two shells of halkieriids, then two valves in brachiopods may be most parsimoniously interpreted as a plesiomorphic character, retained from their common ancestor.

Even with brachiopod monophyly supported with confidence on the basis of nonmineralized features, it is quite possible that two valves evolved multiple times within the clade Brachiopoda. Unfortunately, it is not possible to test this latter hypothesis rigorously at this time, because the nonmineralized Proterozoic fossil record of metazoans is sparse and discontinuous in time, space, and morphology. Parsimony encourages us to favor the simplest explanation for a body of data currently in hand, which suggests that two valves evolved once in the evolution of brachiopods and serve as a synapomorphy for the group. It would be foolish, however, not to at least consider that methodological parsimony may be of little relevance to processes of biomineralization early in the Cambrian. Our understanding of processes and constraints in mineralization is so limited for this critically important time in metazoan evolution that we can reject relatively few hypotheses with substantial evidence (B. Runnegar, personal communication, 2004).

Number of Mineralized Elements

Is a multielement mineralized fossil organism the sister group to the brachiopods, rather than a two-element or unmineralized organism? There seems to be no strong evidence in favor of a bivalved sister group to brachiopods, among either the extant or extinct fauna. Halkieriids clearly have multielement skeletons. Although sellate and mitral sclerites of *Micrina* are each bilaterally symmetrical and have been argued to be homologous with the anterior and posterior shells of *Halkieria* (and possibly the dorsal and ventral shells of brachiopods; Williams & Holmer, 2002; see Williams and Carlson, herein, Fig. 1903), the *Micrina* scleritome is generally thought to have been more consistent with a multielement model than a two-shell model (Li & Xiao, 2004). In addition to bearing setae (setigerous), *Micrina* sellate sclerites (located anteriorly) possess internal markings suggesting a pair of muscles, thought to support the mouth, and *Micrina* mitral sclerites (located posteriorly) possess features interpreted as gonadal sacs (similar to saccate mantle canals in brachiopods). But mitral and sellate sclerites are not complementary bivalves (Williams & Holmer, 2002) in the same configuration as brachiopod bivalves, and it seems at least equally plausible that the apparent similarities between the two are homoplastic (convergent) rather than homologous.

Li and Xiao (2004), attempting to accommodate the Williams and Holmer (2002) argument about the homology of shell mineralogy and structure in tannuolinids and brachiopods, presented the independent origin of two shells from a multielement ancestor as a possible scenario for brachiopod origins (see Williams and Carlson, herein, Fig. 1903.1). This scenario implies either that monophyletic brachiopods are primitively multielement and that both tannuolinids and halkieriids can be considered brachiopods or that diphyletic brachiopods evolved independently twice from a multielement ancestor.

The use of a chiton as the outgroup taxon for molecular systematic analyses of brachiopods (e.g., Cohen & Gawthrop, 1997; Cohen & Weydmann, 2005; see also Vinther & Nielsen, 2005) raises the possibility for interesting speculation on morphology and evolution. Chitons have multielement skeletons, today composed of eight separate dorsal plates (called valves) underlain by a thick mantle (girdle) that often has calcareous or chitinous spines. Early chitons may have had more than eight valves (see Vendrasco, Wood, & Runnegar, 2004). This skeletal arrangement is at least reminiscent of the two dorsal shells and multiple small sclerites in halkieriids. The individual plates are imbricated, one behind (posterior to) and under the one in front, with the axis of symmetry of each plate parallel to the long axis of the organism; this is not consistent with the arrangement of sclerites in *Tannuolina* (Li & Xiao, 2004). Chiton plates also possess aesthetes, or sensory structures that sit in canals that penetrate the valves; they bear a certain similarity to endopunctae (containing caecae) in some near-basal brachiopods (e.g., craniids; see Baxter, Sturrock, & Jones, 1990). This similarity has long been thought to indicate no more than convergent similarity, but may now bear closer scrutiny with increased confidence in recent molecular results using chitons as the brachiopod outgroup (Cohen & Weydmann, 2005).

Mineralogy

Both phosphatic and calcitic shells appear very early in the fossil record, at almost indistinguishably different times. Phosphatic shells appear slightly earlier (Williams, Carlson, & Brunton, 2000; Holmer, 2001), supporting the long-held view among brachiopod paleontologists that phosphatic mineralogy is plesiomorphic (primitive) for brachiopods. This runs counter to outgroup analyses suggesting that phosphatic shells are almost certainly derived relative to calcitic shells (within the Eutrochozoa; Valentine, 2004; see also Carlson, 1995; Cohen & Weydmann, 2005).

Is it possible that these evolutionarily early shells were bimineralic or even multimineralic? The unexpected discovery of siliceous tablets in the first-formed shells of discinid brachiopods, which mineralize chitinophosphatic shells for the remainder of their ontogeny (Williams & others, 1998; Williams, Lüter, & Cusack, 2001; see also Williams & Holmer, 2002; Williams, 2003) opens up the hitherto unexplored possibility of bimineralic shells. Secondary diagenetic alteration of primary mineralogy is not at all uncommon in fossil brachiopods, however, and it can be difficult to distinguish primary mineralogy from secondary replacement. For example, the multimineralic state of *Mickwitzia* fossils appears to be diagenetic rather than primary (Balthasar, 2004a).

Apparently building on his discovery of bimineralic discinids, Williams (2003) described microscopic imprints on juvenile shells of Paleozoic linguliform brachiopods and argues that these imprints were likely to have been formed by calcareous discoids and spheroids, rather than phosphatic elements as in the later-formed shell, on the basis of their apparently greater solubility than the phosphatic shell material. No original calcareous shell material remains, however, and it is not clear that relative solubility can be predicted with much certainty in the absence of information about the chemical conditions of diagenesis. Although there is now evidence for the mineralization of siliceous tablets early in the ontogeny of shell secretion in discinids, no extant brachiopod is known to mineralize both calcareous and phosphatic shells over the course of their ontogeny. It is not clear what constraints, if any, might operate to prevent this combination of mineralogies, but no direct evidence yet exists demonstrating calcareous and phosphatic mineralization in the same shell. Opaline silica has a lower specific gravity (2.0–2.5) than either calcite (2.7) or apatite (3.1–3.2); first-formed tablets of less-dense silica would confer lower weight than apatite, an advantage for larval energy expenditure, since in *Discinisca* the tablets begin to be mineralized while the planktotrophic larvae are still in the water column (see also discussion in Freeman & Lundelius, 2005). Interestingly, given our current knowledge of brachiopod biomineralization, a bimineralic shell demonstrating an ontogenetic transformation in mineralogy (siliceous to phosphatic, as in discinids, or calcareous to phosphatic, as hypothesized by Williams, 2003) would suggest that phosphatic shells are derived, using the ontogenetic polarity criterion, which is consistent with the polarity of evolutionary mineralogical transformation suggested by outgroup analyses.

Micrina and *Mickwitzia* were both originally phosphatic (Laurie, 1986; Skovsted & Holmer, 2000; Williams & Holmer, 2002; Balthasar, 2004a), a conclusion based convincingly on details of fossil shell fabric and the fabric of living *Discina*. *Heliomedusa* was originally thought to be calcareous (Jin & Wang, 1992) but is now thought to have been phosphatic (Chen, Huang, & Chuang, 2007). The original mineralogy of halkieriid shells is not clear; no original shell material exists. Halkieriid sclerites were found to be aragonitic (Bengtson & Conway Morris, 1984; Bengtson & others, 1990; Porter, 2004) on the basis of the preservation of needlelike fibers similar to those seen in originally aragonitic skeletons and the similar preservation of other elements of the fauna (Porter, 2004) known to be aragonitic. A calcareous mineralogy for the shells is inferred on the basis of the preservation (decalcified) of associated metazoans (trilobites, hyoliths) known to have had originally calcareous skeletons and the brittle deformation of the anterior shell of *Halkieria* in compaction (Conway Morris & Peel, 1995). No *Halkieria* shells are present in the Monastery Creek Formation (Porter, 2004), even though sclerites (originally aragonitic) are abundant, suggesting a different mineralogy of the shells and the sclerites in the same individuals. This type of simultaneous bimineralic composition of different elements at the same ontogenetic stage is not known in extant brachiopods, even though ontogenetic transformations in mineralogy are known, as discussed above (Williams & others, 1998). Williams and Holmer (2002) argued that halkieriid shells were originally phosphatic, based on the rheomorphic (plastic) deformation of surfaces and the nature of the draping of the shell fabric in shell formation and development similar to the type of deformation seen in fossil brachiopods known to have been phosphatic (acrotretides). They describe a ten-step hypothetical evolutionary transformation from halkieriids (as including *Micrina*) to *Mickwitzia* to brachiopods that relies on the consistency in phosphatic mineralogy, as they interpret it, among all these groups. Given the diversity of opinion cited above, it is clear that the mineralogy of halkieriid shells is currently not universally agreed upon.

Shell Structure

Shell microstructure has long been considered to be a critical source of reliable, if contentious, information on phylogenetic relationships among brachiopods (e.g., Williams, 1956; Williams & others, 1996). For example, Williams (2003; Fig. 1910.4) derived acrotretides from within the linguloids almost exclusively on the basis of shell structural similarities, *contra* Holmer and Popov (2000; Fig. 1910.3), who placed acrotretides as the sister group to the linguloids and all other phosphatic brachiopods except paterinides, and Holmer, Skovsted, and Williams (2002), who placed acrotretoids as basal to all brachiopods, including paterinides (Fig. 1910.5). The microstructures of the various mineralized elements present in Lower Cambrian fossils share similar elements, as well as distinct differences, and currently leave open the question of whether the similarities are homologous or homoplastic.

Determining the level of homology of microstructural features almost certainly plays a major role in deciphering their evolution. Three major types of shell perforations are recognized among brachiopods: canals (extremely fine), punctae (large, lacking distal brushes), and endopunctae (large, with distal brushes). Just as bird, bat, and pterosaur wings are homologous as forearms, but not as wings, these three types of structures may be homologous as shell perforations, but not as punctae. All brachiopods with a canalicular shell structure may be homologous, but they may not be homologous with terebratulide endopunctae, or more generally with chiton aesthetes. More broadly among metazoans, various biomineralized structural features can be notoriously homoplastic (e.g., echinoderm stereom and vertebrate trabecular bone).

The nature of shell lamination and tubes or canals penetrating the shell fabric are the two microstructural features that have figured most prominently in discussions of phylogenetic affinity among the taxa considered here. Acrotretide brachiopods, *Tannuolina*, and *Mickwitzia* are characterized by columnar lamination. *Micrina* sclerites (mitral and sellate) are characterized by stratiform lamination, and these stratified laminar sets are claimed to be indistinguishable from

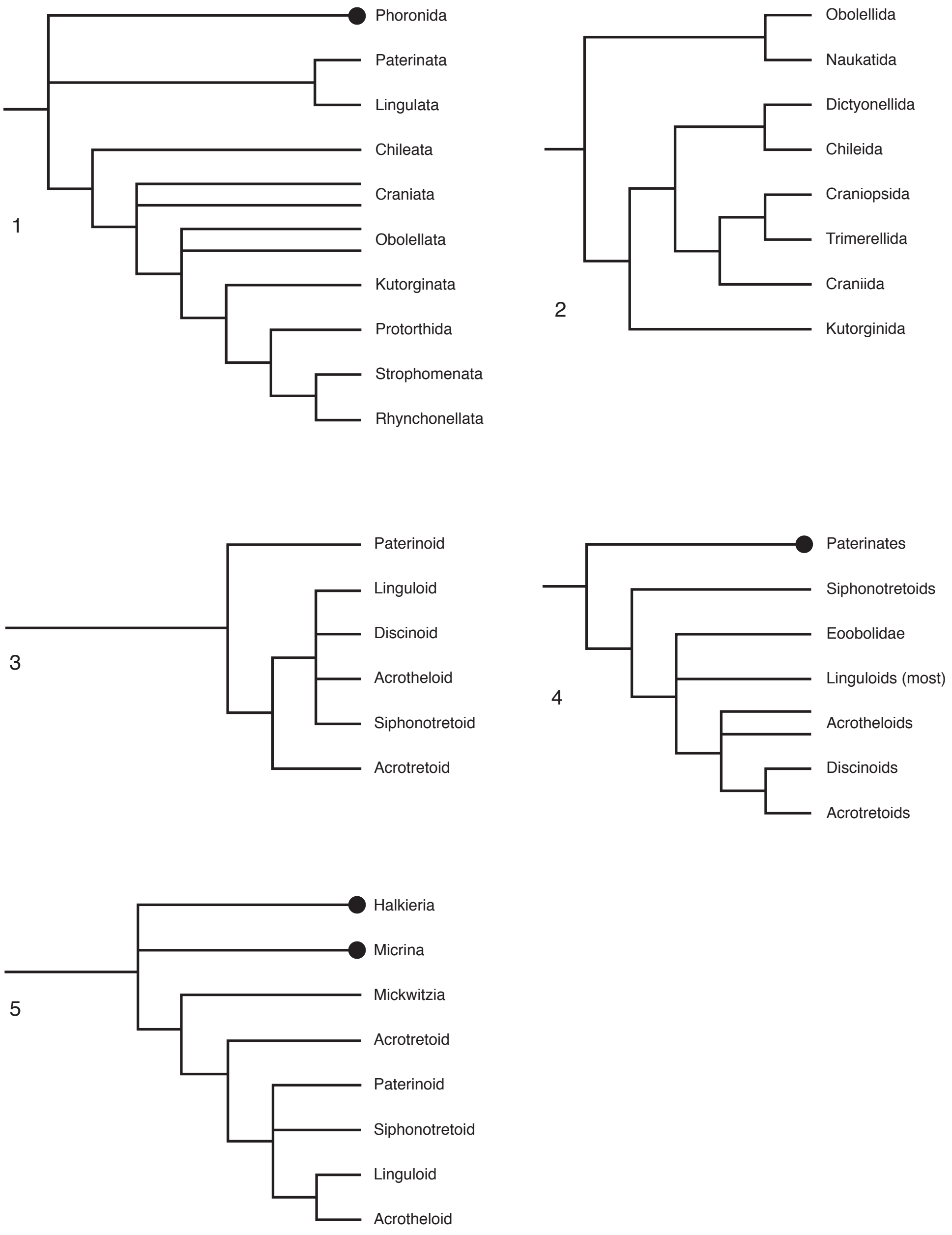


Fig. 1910. Hypothesized phylogenetic relationships among various brachiopod taxa, adapted from sources indicated; *black dots* identify outgroup taxa; *1,* eight brachiopod classes plus phoronides and protorthides (Williams & others, 2000; Bassett, Popov, & Holmer, 2001); *2,* major groups of early calcareous brachiopods (Popov & others, 2000); 3, major groups of phosphatic brachiopods (Holmer & Popov, 2000); *4,* a different view of relationships among major groups of phosphatic brachiopods (Williams, 2003); *5,* major groups of phosphatic brachiopods plus *Micrina*, *Mickwitzia*, and *Halkieria* (Holmer, Skovsted, & Williams, 2002).

those in lingulide brachiopods (Williams & Holmer, 2002). Lingulides do not have striated tubes throughout their shell fabric, however; their canalicular structures are not striated and apparently not homologous to striated tubes in *Micrina*. Li and Xiao (2004) characterized the laminar features in *Micrina* simply as basal internal growth lamellae. Nothing is known of halkieriid shell structure, as noted above.

Micrina and *Mickwitzia* possess striated (apparently setigerous) tubes running perpendicularly through the shell fabric (Williams & Holmer, 2002; Balthasar, 2004a) and secreted independently of the laminar fabric of the shell. A canal system of very small (10–20 µm) striated tubes (spaced concentrically according to Williams & Holmer, 2002, but unevenly distributed according to Li & Xiao, 2004) permeate entire sclerites of *Micrina*, but extant brachiopod setae (in follicles, not striated tubes) are restricted to a band in the groove between outer and inner mantle lobes and are never incorporated into the shell (see Lüter, 2000a), not even (apparently) in Cambrian forms. Micropunctae (canals in linguliforms) are typically around 180–850 µm in diameter, an order of magnitude larger than setigerous canals in *Micrina*. Baculi (apatitic rods) are present in linguloids and acrotheloids and are not homologous with striated tubes in *Micrina*. Spherulitic apatitic aggregates in *Micrina* were apparently formed from a different set of calcifying proteins (Williams & Holmer, 2002) than apatitic aggregates in linguloid and acrotretoid brachiopods.

It is possible that the shell structural similarities between *Micrina* and linguliform brachiopods result from shared properties of organic-rich, chitinophosphatic shells, rather than common ancestry—providing some kind of constructional constraint rather than a phylogenetic constraint. If phosphatic biominerals, as well as secondary phosphatic preservation, were more common in the Early Cambrian than today, one could argue on the basis of ocean chemistry that Cambrian phosphatic biominerals and the shell structures that they necessarily form are more likely to be convergent than homologous. This is consistent with the more traditional interpretation of tommotiid relationships (Bengtson 1970; Bengtson & others, 1990; Conway Morris & Peel, 1995), which posits some halkieriids (as a broadly paraphyletic grouping) sharing common ancestry with brachiopods (and other halkieriids sharing closer common ancestry with annelids) and the phosphatic tommotiids (e.g., *Micrina*) separate from the *Halkieria* + brachiopod clade (see Williams and Carlson, herein, Fig. 1903.3). Also, if linguliforms are derived within brachiopods (Carlson, 1995; Cohen, 2000; Cohen & Weydmann, 2005; Fig. 1908; and see Williams and Carlson, herein, Fig. 1903.3) rather than basal, then the argument that the similarity of *Micrina* and linguliforms is due to close common ancestry is considerably weakened.

Body Orientation or Plan

Are the two brachiopod valves now referred to as dorsal and ventral actually dorsal and ventral relative to their embryological orientation? It has been claimed that the two valves are more accurately characterized as anterodorsal and posterodorsal (Nielsen, 1991; Cohen, Holmer, & Lüter, 2003; Vinther & Nielsen, 2005), having both formed from the originally dorsal surface of the developing embryo (in *Crania* [*Novocrania]*). Recall that Yatsu (1902) also observed the formation of a single, nearly circular shell that grows, folds transversely, and divides to form two valves. As discussed earlier, however, it may be that the dorsal valve forms first on the dorsal surface of the embryo, while the ventral valve forms later, on the topologically ventral surface of the embryo (Fig. 1909). Further investigation of the timing of embryological events is necessary to resolve this issue more fully (C. Nielsen, personal communication, 2005).

There is also little agreement on the arrangement of sclerites in the scleritome of mitrosagophorans. Li and Xiao (2004) discovered partially articulated specimens of *Tannuolina* (thought to be closely related to *Micrina*, implying that these two taxa share the same body plan inherited from a common ancestor) that reveal pairs of articulated (left-right) mitral sclerites oriented with the sagittal plane of the sclerites perpendicular, rather than parallel, to the long axis of the body. This suggests a different body orientation, by 90 degrees, than in the WILLIAMS and HOLMER (2002) reconstruction. Also, the hypothesized body plan of tannuolinids (LI & XIAO, 2004), with symmetrical rows of imbricated sellate sclerites flanking symmetrical pairs of mitral sclerites, appears to be fundamentally different from the body plan of brachiopods with two valves, apparently dorsal and ventral. This argument is based entirely on the assumption of a close phylogenetic relationship between *Tannuolina* and *Micrina*, since the preservational evidence is based entirely on *Tannuolina* specimens. Body orientation of sclerites on *Micrina* individuals is not clear. LAURIE (1986) described the sclerites as anterior (sellate) and posterior (mitral), but it is not yet known whether the sclerite arrangement is comparable to that in *Halkieria*, as USHATINSKAYA (2001, 2002) suggested. Mitral and sellate sclerites of *Micrina* are each bilaterally symmetrical and do not occur in left and right forms.

Metamerism

Were these Early Cambrian forms metameric? If so, what does this imply about possible brachiopod metamerism? *Micrina* is claimed to be initially (ontogenetically) segmented, based on transverse furrows in juvenile mitral sclerites (WILLIAMS & HOLMER, 2002), but this constitutes rather weak supporting evidence for metamerism. Metamerism is consistent with the reconstruction of *Tannuolina* presented in LI and XIAO (2004); if determined to be closely related to *Micrina*, this interpretation could apply also to *Micrina*. *Halkieria* clearly exhibits the serial repetition of sclerites (CONWAY MORRIS & PEEL, 1995), but great caution is urged in interpreting serial repetition as evidence of actual metamerism. Nevertheless, *Halkieria* has been claimed to have a segmented body form (as coded in the data matrix in HOLMER, SKOVSTED, & WILLIAMS, 2002); the data supporting this assertion are not clear. *Eoobolus*, a linguloid brachiopod, has also recently been claimed to be segmented (BALTHASAR, 2004b). If verified with additional evidence, this would suggest that brachiopods might have evolved from a metameric ancestral body form.

EVOLUTIONARY INTERPRETATIONS

Considering the foregoing discussion of these early fossils and the characters they exhibit, three different perspectives on their evolutionary significance emerge.

Homologous and Derived

Morphological and mineralogical similarities among brachiopods and these Tommotian fossils are synapomorphies, or features shared due to common ancestry and derived relative to the ancestral state present among more distant relatives. Supporting this point of view is a phosphatic mineralogy, present in *Mickwitzia* and linguliforms (and inferred to be phosphatic or bimineralic [calcareous and phosphatic] in *Micrina* and halkieriids), the presence of striated, apatitic tubes in *Micrina* and *Mickwitzia* (inferred to have been setigerous), and the columnar lamination of the shell in *Mickwitzia* and acrotretides (Fig. 1910; and see WILLIAMS and CARLSON, herein, Fig. 1896; HOLMER, SKOVSTED, & WILLIAMS, 2002; WILLIAMS & HOLMER, 2002; WILLIAMS, 2003). A modified version of this argument is discussed in LI and XIAO (2004; see WILLIAMS and CARLSON, herein, Fig. 1903.1). If halkieriids were calcareous, as LI and XIAO inferred, they could be the sister group to the craniiforms + rhynchonelliforms, with *Micrina* being the sister group to the linguliforms; this scenario is not consistent with the molecular systematic data (COHEN & WEYDMANN, 2005). This implies that the bivalved body form in brachiopods evolved twice independently from multielement ancestors and that *Micrina, Tannuolina* (if it is closely related to *Micrina*), and halkieriids are nested within the brachiopod crown group, at its base (see Williams and Carlson, herein, Fig. 1903.1).

Homologous and Basal (Primitive)

Morphological and mineralogical similarities among brachiopods and Tommotian fossils might be homologous (if halkieriids are calcareous), but plesiomorphic (primitive), not apomorphic. It is possible that *Micrina* shares common ancestry with the linguliforms, via *Mickwitzia*, with halkieriids as a sister group to all brachiopods (see Williams and Carlson, herein, Fig. 1903.2), or perhaps even more broadly to a more inclusive group of lophotrochozoans. If the molecular sequence data (Cohen & Weydmann, 2005) suggest a more accurate pattern of relationship, then this scenario is much less likely, complicated by the phylogenetic position of the craniides. This scenario (see Williams and Carlson, herein, Fig. 1903.2) would require that *Micrina* (and other tannuolinids) retain the primitive multielement body plan after phoronids and craniiforms had diverged from the brachiopod common ancestor. It is much more likely that the similarities *Micrina* appears to share with phosphatic brachiopods are convergent (see Williams and Carlson, herein, Fig. 1903.3), as discussed below.

It is also possible that halkieriids are not the sister group to brachiopods at all or may be only much more distantly related, leaving us again with a question mark about the identity of the (extant or extinct) brachiopod sister group. The evidence presented in support of brachiopod ancestry (Conway Morris & Peel, 1995; Williams & Holmer, 2002) from halkieriids is not particularly robust; the evidence presented in support of molluscan ancestry (with halkieriids within the crown group) is also not especially strong (Vinther & Nielsen, 2005). It may be that the existing data are simply not yet sufficient to allow us to reject either hypothesis at this time. Yet another possibility, consistent with both hypotheses, is that halkieriids are part of the stem group of Lophotrochozoa (see Williams and Carlson, herein, Fig. 1892; also Valentine, 2004) and are distantly related to both mollusks and brachiopods.

Not Homologous

Morphological and mineralogical similarities among brachiopods and the Tommotian fossils are convergent or homoplastic. In other words, they are not homologous, and thus not derived, but result from independent evolutionary events (Bengtson, 1970; Laurie, 1986; Li & Xiao, 2004). In this scenario (see Williams and Carlson, herein, Fig. 1903.3), halkieriids, if calcareous, might be the sister group to a monophyletic Brachiopoda (Conway Morris & Peel, 1995), but *Micrina* and the other tannuolinids and tommotiids are only rather distantly related to the halkieriid + brachiopod clade (see Williams and Carlson, herein, Fig. 1903.3). Phosphatic shell mineralogy and associated shell structural similarities are likely to have evolved independently in linguliforms and tannuolinids.

RELATIONSHIPS AMONG ALL BRACHIOPODS

Most brachiopod workers agree that all available data should be brought to bear on the question of determining phylogenetic relationships among all extant and extinct brachiopods. In this spirit, a consensus cladogram was constructed (Fig. 1908), by eye or hand, with data derived primarily from analyses of Cohen and Weydmann (2005) and Cohen (herein, p. 2356) using molecular sequence data from living brachiopods and phoronids (Fig. 1907); Holmer and Popov (2000), Popov, Bassett, and Holmer (2000), and Williams, Carlson, and Brunton (2000) using morphological data from mostly Cambrian and Ordovician taxa (Fig. 1910); Carlson (1995) using morphological data from Recent brachio-

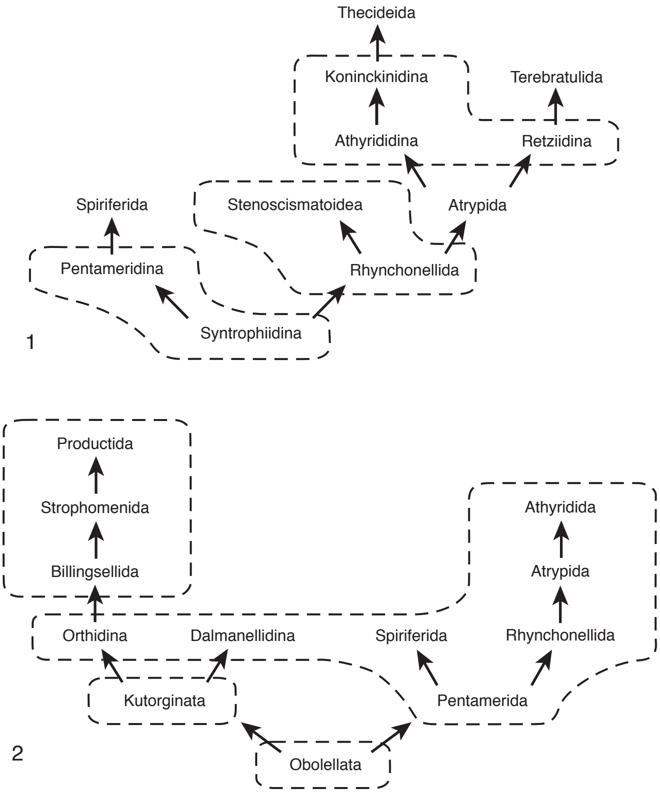


Fig. 1911. Results of two different ANOP (All Nodes Occupied Phylogeny) analyses among selected groups of rhynchonelliform brachiopods, utilizing morphological and stratigraphical data together; *1,* selected derived rhynchonellates, *dashed lines* unite suborders in Pentamerida, Rhynchonellida, and Athyridida; *2,* including more basal rhynchonelliforms as well, *dashed lines* unite suborders in classes Obolellata, Kutorginata, Rhynchonellata, and Strophomenata (adapted from Carlson & Leighton, 2001).

pods; and Carlson and Leighton (2001) using morphological and stratigraphic data together for all rhynchonelliform suborders (Fig. 1911). All branches of the cladogram should be interpreted as testable hypotheses that may well change over time, but this topology represents the consensus that seems to most accurately and honestly combine the results of the analyses listed above and to concur with our present state of understanding about brachiopod phylogenetic relationships.

Rhynchonelliformea (articulates) is the sister group to a clade that includes Linguliformea, Craniiformea (the inarticulates), and Phoronida; together they comprise the two major clades within Brachiopoda, generally consistent with the old class-level terminology (Williams & Rowell, 1965d). Now, however, the inarticulates include phoronids, according to SSU (18S) rDNA evidence (Cohen & Weydmann, 2005). Cohen and Weydmann (2005) have further suggested modifying the current classification so that Lingulata, Craniata, and Phoronata (each named after the most ancient extant subclade [order]) are recognized as classes within Linguliformea, with Phoronata at the base of this clade. Further study of *Iotuba*, from the Chengjiang fauna, and the complete fossil record of phoronids would be valuable in testing this phylogenetic hypothesis (Fig. 1908). Rhynchonelliforms have a large and diverse (12 orders) stem group; the crown group (7 orders) is long lived, first appearing in the Lower Ordovician.

Relationships among the obolellates and chileates and other early rhynchonelliforms are becoming clearer but are not yet rigorously supported (Popov & others, 1996; Holmer & Popov, 2000; Bassett, Popov, & Holmer, 2001; Holmer, 2001). Rhynchonelliforms are united by the presence of the fibrous secondary layer of an organocarbonate shell, a pedicle, and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas (Williams, Carlson, & Brunton, 2000), discussed in greater detail in the section on articulation below (p. 2899). Each new fossil discovered from the Lower Cambrian has the potential to provide a critical test of the hypotheses of relationships among the early rhynchonelliforms proposed thus far.

The position of orthides and protorthides is not universally agreed upon. They may share most recent common ancestry with the other rhynchonellates, as the revised *Treatise* classification implies (Williams, Carlson, & Brunton, 2000, fig. 6). The evidence supporting this hypothesis is the following: development of a pedicle rudiment (inferred); loss of posterior body wall (which presumably persisted in Strophomenata); loss of the anus; and the appearance of projecting brachiophores in the cardinalia. Alternatively, they may share most recent common ancestry with the kutorginate + strophomenate clade (Carlson & Leighton, 2001, fig. 26.1) or more likely perhaps with the strophomenates, both having evolved from the kutorginates (Fig. 1911.2; Carlson & Leighton, 2001). Given the continuing uncertainty in the patterns of relationship among these early rhynchonelliforms, they are represented in an as yet unresolved tritomy with the kutorginate + strophomenate clade and the other rhynchonellates (Fig. 1908).

It is not clear if the strophic spire-bearers are all nested within the crown-group rhynchonellates (Williams, Carlson, & Brunton, 2000) or if they represent an older, deeper divergence from the pentamerides (Carlson & Leighton, 2001; Fig. 1911). Confusion about the homology and polarity of the calcareous lophophore supports continues to plague this issue, which is discussed in greater detail in the section on the lophophore below (p. 2899). Ideally, resolving relationships among thecideides and the other extant brachiopods (discussed in an earlier section, herein, p. 2885) could clarify the relationships among all spire-bearers to one another.

CONCLUDING SYNTHESIS

EVOLUTION OF MAJOR CHARACTER COMPLEXES

Juvenile Mantles and Shells

Planktotrophy is the primitive state for brachiopods, including phoroniforms (Carlson, 1995; Freeman & Lundelius, 2005). Valves are mineralized at or immediately following metamorphosis in all brachiopods except phoronids. Mineralization on embryonic mantle has evolved several times independently within the linguliforms, which are generally characterized by a long stage of (planktotrophic larval) swimming juvenile growth. Lecithotrophy evolved twice independently: once in the Craniiformea (Craniida) sometime in the mid-Jurassic (Freeman & Lundelius, 1999) and once in the crown-group Rhynchonelliformea sometime in the evolution of rhynchonellides from pentamerides (?Lower Ordovician) (Freeman & Lundelius, 2005). In the Craniiformea, no mantle reversal accompanied the transformation to lecithotrophy, while in the Rhynchonelliformea, mantle reversal did accompany the transformation (Nielsen, 1991; Freeman & Lundelius, 1999, 2005).

Integument and Shell Structure

The presence of mineralized valves appears to be primitive for brachiopods (shared with chitons and other lophotrochozoans, possibly including halkieriids); the absence of shells in phoronids (if they are brachiopods), appears to be derived, but this is far from certain. Two valves appear to be derived for brachiopods (from more than two in chitons and halkieriids), but this is also far from certain. If chitons and halkieriids are only very distantly related to brachiopods, the sister group–ancestor may have been lacking shells altogether, and shells themselves may have evolved more than once. Calcareous laminar shells appear to be primitive for brachiopods; fibrous shell structure is derived within rhynchonelliforms. Phosphatic stratiform shells are derived in the Linguliformea (the most parsimonious interpretation of the distribution of shell mineralogy; other interpretations are possible, but less parsimonious—see discussion in Recent Research section, herein, p. 2891). Punctae have clearly evolved several times independently from the primitive impunctate condition. Pseudopunctae appear to be shared and derived for the Strophomenata, excluding Billingsellida (CARLSON & LEIGHTON, 2001). Various shell fabrics have been identified and named (see WILLIAMS and CARLSON, herein, Fig. 1898) and are almost certainly homoplastic within brachiopods, having evolved several times independently.

Pedicle

Pedicles appear to have evolved twice independently, once in linguliforms and once in rhynchonelliforms (Fig. 1908; see WILLIAMS and CARLSON, herein, Fig. 1899–1900), with different morphology, anatomy, and development. The nature of the attachment of valves to a substrate in several of the early rhynchonelliform groups is not universally agreed upon but may have involved an adhesive holdfast in the form of a mucinous pad. The absence of a pedicle in craniiforms and phoronids appears to represent the primitive state among brachiopods, but this conclusion requires additional investigation of both fossil and living brachiopods.

Muscle Systems

Muscle systems have evolved in concert with changes in articulation. Not surprisingly, the muscles that close the shell are always located anterior to the hinge axis, and the muscles that open the shell are always located posterior to the hinge axis. The insertion of the opening (posterior adductor or diductor) muscles on the ventral valve has migrated anteriorly from a position clearly posterior to the adductors (in linguliforms and craniiforms as well as early rhynchonelliforms; see WILLIAMS and CARLSON, herein, Fig. 1901B, 1901D, 1901E) to a position collinear with or anterior to the adductors (see WILLIAMS and CARLSON, herein, Fig. 1901E–1901G). The origin of the opening muscles on the dorsal valve has migrated posteriorly from a posterior position (see WILLIAMS and CARLSON, herein, Fig. 1901B) to a posteriormost position (see WILLIAMS and CARLSON, herein, Fig. 1901G). This evolutionary transition results in greater mechanical advantage to the valve opening system.

Articulation

The evolution of articulation is complex, with many components in the transition from no articulation to articulation (see WILLIAMS and CARLSON, herein, Fig. 1901B; Table 39). Phoronids have no valves and thus no articulation; craniiforms and linguliforms have no articulatory structures; early rhynchonelliforms have rudimentary articulation. More derived rhynchonelliforms have deltidiodont (noninterlocking) articulation, and cyrtomatodont (interlocking) articulation evolved within the derived rhynchonellates. The complex distribution of different articulatory structures defies, as yet, a simple but more detailed explanation of character evolution across the phylum.

Lophophore

The spirolophe lophophore is primitive; plectolophe and ptycholophe lophophores are both derived from the spirolophe condition. All linguliforms, craniiforms, and early rhynchonelliforms lack mineralized lophophore supports. Brachial ridges evolved within the strophomenates and again a second time in thecideides (from the spire-bearers). Spiralia and then loops, three-dimensional structures supported only at their base by crura, appear to have evolved once in the crown-group rhynchonellates (with unusual genera like *Enantiosphen* and *Tropidoleptus* representing rare, independent originations of mineralized lophophore supports).

Summary

In conclusion, all sources of data, if sufficiently robust and well corroborated, are best analyzed together—morphological, molecular, developmental, and stratigraphic, with additional insights gained from paleobiogeographic and functional analyses. Separate analysis of each alone is essential, and comparative analysis of all together provides the most comprehensive basis for interpreting the evolution of a group like the brachiopods, with a long and rich fossil record and a relatively diminished extant diversity (see also CARLSON, 2001). The evolution of each of the morphological complexes discussed here has been evaluated with respect to hypotheses of phylogenetic relationships structured in part according to several criteria of polarity (outgroup, stratigraphic, and ontogenetic), each of which has strengths and weaknesses, as discussed in WILLIAMS and CARLSON, herein, p. 2833.

Our understanding of brachiopod evolution has increased greatly since the last *Treatise* volumes were published (MOORE, 1965), thanks to greater numbers of fossil specimens collected, improved understanding of living brachiopods, and improved methods for analyzing and comparing these various data. Many questions remain unanswered, however. The phylogenetic hypothesis presented in Figure 1908 must be tested in detail, and the polytomies resolved. Are the thecideides more closely related to the athyridide or spiriferinide spire-bearers? Have mineralized valves, spiralia, and articulation evolved more than once among brachiopods? How are other metazoans and halkieriids and other Early Cambrian fossils related to brachiopods? The evolutionary questions that remain keep the study of brachiopods interesting and compel us to continue searching for evidence that will allow us to reject some of the many alternatives discussed in this chapter.

STRATIGRAPHIC DISTRIBUTION OF BRACHIOPODS

GORDON B. CURRY and C. HOWARD C. BRUNTON

[University of Glasgow; retired, formerly of the Natural History Museum, London]

INTRODUCTION

The compilation of the revised brachiopod *Treatise* presented an outstanding opportunity for a detailed investigation of the stratigraphic distribution of the phylum. This comprehensive taxonomic census has produced a prodigious amount of information on the occurrences of brachiopod genera, on all continents and all Phanerozoic stratigraphic horizons, with a precision that has never before been achieved. The records available are not perfect, but they are as close to perfect as can be achieved given the vagaries of preservation in the geologic record and the many other complications that affect the reliability of stratigraphic data.

This chapter presents a brief synthesis of the accumulated data on the stratigraphic distribution of the entire phylum, covering the stratigraphic distributions of a total of over 4200 genera. The data are presented by system and are summarized by order, and hence this chapter only skims the surface of the available information that covers all constituent taxonomic levels from genera upward, and at a resolution of individual stages. This chapter describes the distribution of orders and makes brief reference to the wider biological and geologic implications of major features of these distributions, but space precludes detailed discussion. The analysis presented here includes the most up-to-date stratigraphic information available, including the stratigraphic distributions of recently described genera (herein, p. 2532–2821), as well as any new updated stratigraphic information on genera published in earlier volumes (in effect all available, valid, stratigraphic information on brachiopods up to mid-September 2006).

STRATIGRAPHIC NOMENCLATURE

The aim of this chapter is to analyze the distribution of brachiopods in terms of standardized stratigraphic units. All the data used here comes directly from the generic records in the *Treatise* volumes 2 to 6 (2000–2007). Of overriding importance for the stratigraphic analyses presented here was the decision taken at the outset of the project to adopt a single stratigraphic scale for all *Treatise* descriptions. Such a decision was agreed by all authors, at the instigation of Coordinating Author Alwyn Williams, and thereby provided a standardized stratigraphic classification for all taxonomic descriptions. Our knowledge of global stratigraphy is changing fast, and over the last 16 years as this *Treatise* revision was being prepared, there have been major emendations to the naming, correlation, and absolute dating of stratigraphic units. While such changes are valuable in advancing the resolution and accuracy of stratigraphic analysis, they are problematic for a *Treatise* compilation. To have attempted to keep in step with such changes over a 16-year period would have created a totally confusing situation in which it was impossible to know how to compare stratigraphic data compiled by different researchers.

In addition, books such as this have a long shelf life, almost 40 years in the case of the original brachiopod *Treatise* (MOORE, 1965), and hence the data presented must be standardized throughout the entire series of volumes to avoid present and future confusion, as far as is possible. For this reason, all authors for the revisions of the brachiopod *Treatise* agreed to use the stratigraphic chart published by the International Union of Geological Sciences (IUGS) in 1989 (Cowie & Bassett, 1989). An abbreviated version of the standard stratigraphic scale has been included in the preface of every volume of the revised brachiopod *Treatise* (e.g., p. xx in Vol. 1 [Kaesler, 1998], or herein, p. xxix) listing a total of 38 series assigned to 12 different systems. Many taxonomic descriptions in the *Treatise* do indeed cite stratigraphic ranges down to stage level. It was also invaluable to have a comprehensive taxonomic framework for the entire phylum established in advance of starting the compilation of the stratigraphic data in the form of a supraordinal classification (Williams & others, 1996).

It is important to clarify some aspects of the complex and potentially confusing protocols of stratigraphic nomenclature. Historically, subdivisions of the stratigraphic scale, such as stage, were defined by stratotypes, based on a combination of localized lithologic units and major evolutionary events, such as extinctions or radiations. These stages were readily applicable within a restricted geographic area but were much more problematic in attempts to apply them globally because of correlation complications and the existence of many discontinuities in the geologic record. As a result, discrete geographic regions and countries often adopted quite different stratigraphic classifications, based on different and nonoverlapping nomenclatures. Thus, the 1982 compilation of *A Geologic Time Scale* (Harland & others, 1982) had to correlate a number of quite different regional stratigraphic classifications in an attempt to establish a globally applicable scheme. For example, the Cretaceous chart had to reconcile a total of seven entirely different stage nomenclatures, from France, England, the USSR, Japan, New Zealand, Canada, and the United States (Harland & others, 1982).

Stratigraphic procedures are further complicated by the understandable interest in the integration of absolute time determinations (such as are available from radiometric dating of rocks) into the stratigraphic framework. This led to a modification of the concepts of stratigraphic classification, with terms such as system, series, and stage being considered as chronostratigraphic (or time-rock) units, each consisting of all the rocks formed globally during a specified time interval (Gradstein, Ogg, & Smith, 2004). However, the establishment of a fully functional geologic time scale requires that the chronostratigraphic scale be calibrated using a chronometric scale of absolute dates (Gradstein, Ogg, & Smith, 2004). Merging of the two scales was complicated by the fact that the physical geologic record is punctuated by gaps, in contrast to abstract geologic time, which is continuous (Gradstein, Ogg, & Smith, 2004). The disparity between these two scales became so acute as the precision and scope of absolute dating increased that it was necessary to develop a distinct but parallel chronometric nomenclature to distinguish between absolute time on one hand and chronostratigraphic units on the other. In the chronometric scale, terms such as period, epoch, and age were the direct equivalent of system, series, and stage as used in chronostratigraphy. Strictly speaking, therefore, the term Permian Period refers to a range of absolute time expressed in millions of years, while the term Permian System refers to all the rock that accumulated during that particular time.

In practice, however, the terms system and period are often used interchangeably. This dual nomenclature is clearly less than ideal, and recent efforts have concentrated on defining Global Stratotype Sections and Points (GSSPs) that mark the beginning of chronostratigraphic units with precisely defined, globally applicable, isochronous horizons, in many respects rendering the dual system obsolete and unnecessary (Walsh, 2001, 2003; Remane, 2003). GSSPs are not yet available for all subdivisions of geologic time, however. Accordingly chronostratigraphic units, as portrayed in the 1989 IUGS Chart and used throughout the *Treatise* revision, will also be used in this chapter. In any meaningful sense, terms such as system and stage are directly equivalent to period and age respectively in the geochronologic scale. Most diagrams plotted here use the chronostratigraphic units as the horizontal ordinate, with each stage equally spaced, and hence make no attempt to account for differences in absolute time duration of individual stages.

STRATIGRAPHIC SUBDIVISIONS

The major increase in resolution of the resulting stratigraphic analysis reported herein, as compared with the previous *Treatise*, is readily apparent. In 1965, the entire geologic history of the brachiopods was summarized in graphs with a maximum of 28 census points, mostly corresponding to lower, middle, and upper divisions of individual systems (e.g., Lower Ordovician, Upper Permian). By contrast, the analyses presented here divide the geologic history of the brachiopods into 113 census points, overwhelmingly corresponding to named stages in the 1989 IUGS chart.

Arriving at these 113 units was not just a matter of extracting the appropriate names from the IUGS chart, however. In 1989, as with all compilations of stratigraphic units, there were some systems that were clearly subdivided with names that were universally or widely accepted, while there were others for which contrasting nomenclatures were in usage, often varying in different countries with no international agreements or correlations. Such complexities will probably always bedevil stratigraphic analysis and reanalysis, but for this compilation the 113-point census scale was developed before any of the taxonomic descriptions became available, and having been agreed in advance by the *Treatise* authors, it is therefore consistent for all taxa analyzed in this chapter (Table 40, and see discussion below).

Even with this prior agreement, plotting cited stratigraphic distributions is not always straightforward. An encouraging number of stratigraphic distributions in this *Treatise* were cited using the stages defined in the 1989 IUGS compilation, implying a high degree of resolution of our existing knowledge of the taxon's geologic history. For others, the citation of a stratigraphic range in terms of an entire system or systems is open to numerous interpretations and at least implies lower stratigraphic resolution. Thus, the citation of Ordovician could indicate the taxon is known to be present in all stages of the Ordovician (and hence its range is known very accurately), or at the other extreme its range could be poorly known although definitely recorded from some subdivision or subdivisions of the Ordovician. Or it could indicate that it is found in rocks that are definitely known to be Ordovician, but its precise range cannot be more accurately determined from the original published descriptions. Such a citation could also mean that the genus is poorly constrained in terms of its stratigraphic range but is assumed, suspected, or inferred by the compiling author to be present in Ordovician rocks.

All that can be done in these cases is to adopt a standard protocol, and in keeping with the practice adopted in the previous brachiopod *Treatise* (Williams, 1965b), citations of a system has been interpreted as being present in all stages of that system (the so-called range-through assumption). Undoubtedly this will overestimate the stratigraphic range of some taxa, but as long as that is clearly realized by all users of the *Treatise* as being the inevitable consequences of how stratigraphic data are recorded, there will be no significant problems.

Furthermore, for some systems, such as the Permian and Carboniferous, there were several different stratigraphic schemes in common use during the compilation of the *Treatise* data, and these were used by *Treatise* authors who often had no alternative but to cite records using the scheme prevalent in the geographic area from where the fossils were collected and described. Similar and inevitable problems occur when the only stratigraphic information available to the

TABLE 40. Overview of stratigraphic zonation scheme used for all analyses in this chapter, based largely on 1989 IUGS chart (Cowie & Bassett, 1989). Conventions used to interpret cited ranges from *Treatise* descriptions that are not present in IUGS chart are also included (i.e., use of Lopingian for Upper Permian). Names enclosed in "…" are not formal stratigraphic names but are used throughout as convenient, widely recognized labels (for example, for stages that have not been formally defined and named). Some of the names included under the series heading (column 2) are similarly not formalized, and many include part stages but are again included as commonly used terms in stratigraphic determinations. Individual stage names are listed as are the standardized three letter codes for each stage (e.g., TOM for Tommotian). Columns 5, 6, and 7 list absolute age determinations for midstage, base, and duration in millions of years of each stage. Graphs in this chapter plotted using absolute age ordinates use midstage age. Absolute age data are cited in millions of years before present (i.e., Ma) for base and midpoint of each stage; they are an amalgamation of dates from 1989 IUGS chart and widely accepted absolute dating modifications current during 1999. Dates presented in this table therefore correspond to no single compilation of the Geological Time Scale (Gradstein, Ogg, & Smith, 2004) (new).

System	Series	Stage	Code	Midstage Age	Base (Ma)	Duration (myr)	Stage No.
"Quaternary"	"Holocene"	"Holocene"	HOL	0.0	0.0		1
	"Pleistocene"	"Pleistocene"	PLE	0.8	1.6	1.6	2
Neogene	Pliocene	Piacenzian	PIA	2.5	3.3	1.7	3
		Zanclean	ZAN	4.2	5.1	1.8	4
	Miocene	Messinian	MES	5.8	6.5	1.4	5
		Tortonian	TOR	8.9	11.3	4.8	6
		Serravallian	SRV	13.2	15.0	3.7	7
		Langhian	LAN	15.6	16.2	1.2	8
		Burdigalian	BUR	17.6	19.0	2.8	9
		Aquitanian	AQT	21.0	23.0	4.0	10
Paleogene	Oligocene	Chattian	CHT	25.0	27.0	4.0	11
		Rupelian	RUP	28.8	30.5	3.5	12
	Eocene	Priabonian	PRB	32.3	34.0	3.5	13
		Bartonian	BRT	36.5	39.0	5.0	14
		Lutetian	LUT	42.0	45.0	6.0	15
		Ypresian	YPR	49.0	53.0	8.0	16
	Paleocene	Thanetian	THA	56.0	59.0	6.0	17
		Danian	DAN	61.7	64.4	5.4	18
Cretaceous	Upper Cretaceous	Maastrichtian	MAA	64.5	64.6	0.2	19
		Campanian	CMP	73.8	83.0	18.4	20
		Santonian	SAN	84.5	86.0	3.0	21
		Coniacian	CON	87.0	88.0	2.0	22
		Turonian	TUR	89.5	91.0	3.0	23
		Cenomanian	CEN	93.0	95.0	4.0	24
	Lower Cretaceous	Albian	ALB	101.0	107.0	12.0	25
		Aptian	APT	110.5	114.0	7.0	26
		Barremian	BRM	115.0	116.0	2.0	27
		Hauterivian	HAU	118.0	120.0	4.0	28
		Valanginian	VLG	124.0	128.0	8.0	29
		Berriasian	BER	131.5	135.0	7.0	30
Jurassic	Upper Jurassic	Tithonian	TTH	137.0	139.0	4.0	31
		Kimmeridgian	KIM	141.5	144.0	5.0	32
		Oxfordian	OXF	148.0	152.0	8.0	33
	Middle Jurassic	Callovian	CLV	155.5	159.0	7.0	34
		Bathonian	BTH	164.5	170.0	11.0	35
		Bajocian	BAJ	173.0	176.0	6.0	36
		Aalenian	AAL	178.0	180.0	4.0	37
	Lower Jurassic	Toarcian	TOA	184.0	188.0	8.0	38

TABLE 40. *Continued.*

		Pliensbachian	PLB	191.5	195.0	7.0	39
		Sinemurian	SIN	198.0	201.0	6.0	40
		Hettangian	HET	203.0	205.0	4.0	41
Triassic	Upper Triassic	Rhaetian	RHT	207.5	210.0	5.0	42
		Norian	NOR	215.0	220.0	10.0	43
		Carnian	CRN	225.0	230.0	10.0	44
	Middle Triassic	Ladinian	LAD	232.5	235.0	5.0	45
		Anisian	ANS	237.5	240.0	5.0	46
	Lower Triassic	Scythian	SCY	245.0	250.0	10.0	47
Permian	Upper Permian	Changhsingian	CHA	252.5	255.0	5.0	48
		Capitanian	CAP	256.3	257.5	2.5	49
		Wordian	WOR	258.8	260.0	2.5	50
	Lower Permian	Roadian	ROA	265.0	270.0	10.0	51
		Artinskian	ART	272.5	275.0	5.0	52
		Sakmarian	SAK	277.5	280.0	5.0	53
		Asselian	ASS	285.0	290.0	10.0	54
Carboniferous	"Upper Gzhelian"	"Upper Gzhelian"	GZE	291.7	293.3	3.3	55
	Kasimovian	Barruelian	BAR	295.0	296.7	3.4	56
		Cantabrian	CAN	298.4	300.0	3.3	57
	"Westphalian D"	"Westphalian D"	WES	301.3	302.5	2.5	58
	Moscovian	Bolsovian	BOL	303.8	305.0	2.5	59
		Duckmantian	DUC	306.3	307.5	2.5	60
	Bashkirian	Langsettian	LAN	308.8	310.0	2.5	61
		Yeadonian	YEA	311.1	312.1	2.1	62
		Marsdenian	MAR	313.2	314.3	2.1	63
		Kinderscoutian	KIN	315.3	316.4	2.1	64
	Serpukhovian	Alportian	ALP	317.4	318.5	2.1	65
		Chokierian	CHO	319.6	320.6	2.1	66
		Arnsbergian	ARN	321.7	322.8	2.1	67
		Pendleian	PEN	323.9	325.0	2.3	68
	Viséan	Brigantian	BRI	327.1	329.3	4.3	69
		Asbian	ASB	331.4	333.6	4.3	70
		Holkerian	HOL	335.7	337.9	4.3	71
		Arundian	SPK	340.0	342.1	4.3	72
		Chadian	VIS	344.3	346.4	4.3	73
	Tournaisian	Ivorian	IVO	348.6	350.7	4.3	74
		Hastarian	HAS	352.9	355.0	4.3	75
Devonian	Upper Devonian	Famennian	FAM	360.0	365.0	10.0	76
		Frasnian	FRS	370.0	375.0	10.0	77
	Middle Devonian	Givetian	GIV	377.5	380.0	5.0	78
		Eifelian	EIF	382.5	385.0	5.0	79
	Lower Devonian	Emsian	EMS	387.5	390.0	5.0	80
		Pragian	PRA	395.0	400.0	10.0	81
		Lochkovian	LOC	405.0	410.0	10.0	82
Silurian	"Přídolí"	"Přídolí"	PRD	412.3	414.7	4.7	83
	Ludlow	Ludfordian	LUD	417.0	419.3	4.7	84
		Gorstian	GOR	421.7	424.0	4.7	85
	Wenlock	Homerian	HOM	425.0	426.0	2.0	86
		Sheinwoodian	SHE	427.0	428.0	2.0	87
	Llandovery	Telychian	TEL	429.7	431.3	3.3	88
		Aeronian	AER	433.0	434.7	3.3	89
		Rhuddanian	RHU	436.3	438.0	3.3	90
Ordovician	Cincinnatian	Hirnantian	HIR	439.0	440.0	2.0	91
		Rawtheyan	RAW	441.0	442.0	2.0	92
		Cautleyan	CAU	443.0	444.0	2.0	93
		Pusgillian	PUS	445.0	446.0	2.0	94
		Onnian	ONN	446.6	447.3	1.3	95
		Actonian	ACT	447.9	448.6	1.3	96

TABLE 40. *Continued.*

	Champlainian	Marshbrookian	MAR	449.2	449.9	1.3	97
		Longvillian	LON	450.5	451.1	1.3	98
		Soudleyan	SOU	451.8	452.4	1.3	99
		Harnagian	HAR	453.1	453.7	1.3	100
		Costonian	COS	454.4	455.0	1.3	101
		"Llandeilo-Llanvirn"	LLL	462.5	470.0	15.0	102
		"Arenig"	ARG	476.5	483.0	13.0	103
	Canadian (incl. lower Arenig)	"Tremadoc"	TRE	486.5	490.0	7.0	104
Cambrian	Upper Cambrian	Trempealeauan	TRM	491.7	493.3	3.3	105
		Franconian	FRA	495.0	496.7	3.3	106
		Dresbachian	DRE	498.3	500.0	3.3	107
	Middle Cambrian	Mayaian	MAY	502.3	504.5	4.5	108
		Amgaian	AMG	506.8	509.0	4.5	109
	Lower Cambrian	Toyonian	TOY	514.3	519.5	10.5	110
		Botomian	BOT	524.8	530.0	10.5	111
		Atdabanian	ATD	532.5	535.0	5.0	112
		Tommotian	TOM	537.5	540.0	5.0	113

Treatise researchers were published records from the past, which used outdated stratigraphic nomenclature. Again, standard protocols have been adopted for dealing with all such cases; not everyone will necessarily agree with such conventions, but they are at least applied consistently throughout this chapter.

Another important convention adopted throughout this stratigraphic analysis was the method of handling question marks (?) to indicate either doubtful taxa or doubtful stratigraphic ranges. Before starting this analysis, the authors of this chapter (including the late Alwyn Williams) agreed that all records marked with a question mark were to be excluded, because such records indicated that the compiling authors had significant reservations about the validity of these records. Furthermore, any component of the cited stratigraphic record of a genus that included a question mark was also excluded. Thus, in a record that read "Antarctica, ?Upper Cretaceous, Paleogene–Holocene," the taxon would only be recorded as being present from the Paleogene to the Holocene and not in the Cretaceous. Again there was considerable value in applying this convention consistently to all the stratigraphic ranges cited in the new *Treatise*, as it will widen the application and maximize the shelf life of this volume. As the main focus of this chapter is to analyze the stratigraphic distribution of brachiopod orders, valid genera listed within the *Treatise* that were not assigned to one of the 26 established orders (i.e., listed as order Uncertain) were also excluded from this stratigraphic analysis. As the number of genera in this category was very small, the effect of such a procedure on the overall distribution of the brachiopods is insignificant.

ABSOLUTE GEOLOGIC TIME

As discussed above, it is desirable to assign absolute ages to stratigraphic units, and thereby present the data using a time rather than a stratigraphic scale. The absolute dating of stratigraphic units has also changed markedly over recent years, however, arguably more radically than the stratigraphic units themselves. The most recent version of *A Geologic Time Scale 2004* (GRADSTEIN, OGG, & SMITH, 2004) used figures to display just how profoundly the absolute time scale had changed over the last 50 years or so (GRADSTEIN, OGG, & SMITH, 2004, fig. 1.5–1.6). These graphs compared the geologic time scales as presented by Arthur HOLMES in 1937, with the latest version compiled by GRADSTEIN, OGG, and SMITH (2004). In the modern synthesis, the Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, and Jurassic are assigned ages that are entirely different and nonoverlapping with those cited by HOLMES, while there are significant areas of nonoverlap in ages assigned to the Cambrian and Cretaceous. In effect, therefore, the absolute geologic time scale has changed completely over the last 67 years, and there is every likelihood that it will continue to evolve incrementally over the coming decades. This results from different absolute ages for the starts and ends of geologic systems, as well as significant changes in the duration of some individual systems and stages.

Indeed, by the time work started on this chapter in 1999, there were already some significant absolute age changes that had become widely accepted from the dates presented in the IUGS 1989 stratigraphic chart (COWIE & BASSETT, 1989). For example, the base of the Cambrian System, cited at around 570 Ma (with alternative sources giving 540) in the 1989 IUGS Chart was, by 1999, widely recognized as much more accurately considered as 540 Ma (and 542 Ma in GRADSTEIN, OGG, & SMITH, 2004). Similar adjustments were required to the absolute ages assigned to the base of the Ordovician System, from 510 Ma cited in the 1989 IUGS Chart to 490 Ma in more recent compilations. In view of the long shelf life of the *Treatise*, it was clearly inappropriate to use an absolute time scale when presenting the stratigraphic data, as the raw data had not been compiled as absolute ages and as it is very likely that the absolute time scale will continue to evolve. So using absolute age dates throughout would give primacy to what is essentially secondary information derived from the stratigraphic information, as opposed to data collected in terms of a standardized scheme of chronostratigraphic units. As Alwyn Williams, one of the original authors of this chapter, wrote in 1999:

"We are constrained by two considerations:

* The chapter is about the 'stratigraphic distribution' of brachiopods;

* The decision taken in 1990 to standardize all our stratigraphic terminology in line with that of the IUGS chart.

These constraints immediately relegate absolute time ordinates to derived text figures. In the first instance, all our processed data should be presented according to the chronostratigraphic units set out in the IUGS chart."

Absolute time plots, however, do have some significant advantages over stratigraphic plots, most notably in providing a more realistic portrayal of the rate of changes. In this chapter a few graphs using absolute age ordinates are presented where such a procedure contributes significantly to the discussion. Wherever this has been done, a different, simplified, graphical format has been adopted to emphasize the derived nature of the graph. Such an approach, for example, has been used to demonstrate the major biodiversification event at the beginning of the Ordovician (see Fig. 1914 and 1919). When plotted using chronostratigraphic ordinates, this appears to be a very rapid event, but plotted using time ordinates it becomes a much more gradual event (for example, see the comparison between Fig. 1912 and 1914 below).

Because of the evolving establishment of a chronometric scale for Earth history since 1989 it is important for us to be explicit in stating the absolute ages used in any analysis presented here. Thus, Table 40 represents a composite of the dates given in the 1989 IUGS chart, together with the widely accepted modifications up to 1999 (when the stratigraphic analysis of brachiopod taxa began). Absolute age determinations, in millions of years, were assigned to each of the 113 subdivisions of the Phanerozoic (predominantly corresponding to stages) used in the analysis (Table 40). Major boundaries, such as those between systems, were generally well constrained in absolute terms, but ages for some stages had to be extrapolated using the nearest dated horizons. These absolute dates were then frozen at their 1999 state, again to avoid future confusion. If major changes to absolute age determinations have appeared in more recent work (for example, GRADSTEIN, OGG, &

Smith, 2004), these are discussed in the text, but have not been included in Table 40. The absolute ages from the most recent compilation of the geologic time scale (Gradstein, Ogg, & Smith, 2004), however, have been cited at the beginning of each section dealing with the stratigraphic distribution of brachiopods within a system. Although potentially confusing, this practice simply recognizes the dynamic nature of stratigraphic procedures and dating; as the source of the differing dates are fully acknowledged in each case, this chapter reflects the significant changes that have taken place in the absolute dating of systems from the 1989 IUGS chart to the 2004 geologic time scale compilation (Gradstein, Ogg, & Smith, 2004).

The absolute dates used result in a mean duration for each stage of 4.8 million years (standard deviation = 3.3 million years). The stages range in duration from 18.4 million years to 0.2 million years (excluding the Holocene, which is essentially used to describe Recent, or living taxa, but has a nominal duration of 10,000 years). There are notable variations in the durations of stages within different systems, which clearly have an influence on the distributional patterns. For example, the Carboniferous System is divided into a large number of stages that are of relatively similar duration (21 stages, with a mean duration of 3.1 million years (standard deviation = 0.9 million years). By comparison, the mean duration of Ordovician stages is very similar (3.7 million years), but the standard deviation is much higher (4.6 million years). This discrepancy is a reflection of much greater variation in the duration of the individual stages, with the Lower Ordovician stages being of much longer duration (Tremadoc: 7.0 million years; Arenig: 13.0 million years; Llandeilo-Llanvirn: 15.0 million years). The mean duration of Upper Ordovician stages is much less (at 1.5 ± 0.4 million years). Similar heterogeneities are apparent at other parts of the stratigraphic column. The stage with the longest duration is the Campanian of the Upper Cretaceous, while the average duration of the Lower Cretaceous is similarly distorted by the abnormally long Albian Stage (12 million years). In the Upper Cretaceous the longest stage (Campanian) is immediately followed by the shortest (Maastrichtian). Such inconsistencies are being addressed in the latest version of the geologic time scales but are not yet fully in place (for example, the Ordovician includes 7 (rather than 14) stages of more homogeneous duration, but 4 of them are as yet unnamed; Gradstein, Ogg, & Smith, 2004). A more refined subdivision of the Ordovician into 19 time slices was described by Webby, Cooper, and others (2004) and used as the basis for stratigraphic analysis conducted on the Great Ordovician Biodiversification Event (Webby, Paris, & others, 2004).

METHODOLOGY

In this chapter the emphasis is very much on the generic abundances of brachiopods that, with the provisos noted above, can be reliably and accurately extracted from the taxonomic descriptions provided in this series of *Treatise* volumes. Indeed, the high degree of standardization of the format of the *Treatise* has allowed automated computer extraction of all the data, including stratigraphic ranges, contained in the taxonomic descriptions (Curry, Connor, & Simeoni, 2001; Curry & Connor, 2007). This is a result of adopting a standard method of citing stratigraphic ranges, which first lists the overall range in systems and stages, and then cites precise ranges in different geographic areas. Italicizing these data, enclosing stage names in parentheses, and separating them with a colon from the geographic range not only provides a very brief but informative overview for the readers (e.g., *Lower Devonian (Emsian)–Middle Devonian (upper Givetian):* Europe, Central Asia, China, USA (Nevada) (Kaesler, 2002, p. 1444), but also allows the development of computerized techniques to find and extract this information automatically from raw data with such a high degree of internal structure (Curry, Connor, & Simeoni, 2001; Curry & Connor, 2007).

The nature of the raw data available for analysis varied during the course of the study. For some genera, the stratigraphic data were extracted from the full taxonomic description provided in Microsoft Word™ files provided by the *Treatise* editorial office. For other genera, we were provided with text files by Jill Hardesty, assistant editor for the *Treatise,* which included just the taxon name and the cited stratigraphic range. Stratigraphic information was also available for recently described, amended, or corrected, generic data in volume 6 of this *Treatise* (herein, p. 2532–2821), and these data have been included in the analyses presented in this chapter. A complete listing of the stratigraphic range of each taxon is included elsewhere in this *Treatise* (herein, p. 2966–3081). Whatever the source and the extent of initial processing, all the stratigraphic data were formatted in an identical fashion by the contributing authors and editors and were transferred by us into Microsoft Excel™ spreadsheets for analysis and preparation of graphs. These software packages have the advantage of being very commonly used and allowing all necessary graphical interpretations of the compiled stratigraphic data for the purpose of this chapter.

Table 40 provides a summary of the conventions used to analyze all of the stratigraphic data included in the taxonomic descriptions of brachiopod genera, including the ages assigned to each stage (in this chapter a few diagrams plotted using absolute time ordinates use the inferred midpoint ages listed in Table 40). Such a diagram will be important when using stratigraphic data from this *Treatise*, as it provides a snapshot of the prevailing stratigraphic zonation when some systems had already been subdivided into well-established stages, while others were yet to achieve formalized chronostratigraphic unit boundaries. In addition, it has already become quite difficult to obtain copies of the 1989 IUGS chart, so incorporating information on the precise stratigraphic units used in compiling this chapter is essential for future work. For the most part, the units of analysis are formally identified stages, based on internationally agreed subdivisions of the geologic record. Since the compilation and publication of the previous *Treatise* in 1965 (Moore, 1965), there has been a considerable advance in the standardization of the stratigraphic units, notably in the replacement of regional schemes (e.g., European, North American, Russian, Chinese) by a single, well-defined, chronostratigraphic scale that is applicable globally.

Even this approach is not without its complications. There are systems in which the formal stages presented in the 1989 IUGS chart were not universally agreed or recognizable, as is inevitable in a constantly evolving field of research. This was most apparent for the Ordovician and Silurian Systems during the current analysis. For example, many descriptions of Ordovician brachiopods utilized series names (such as Tremadoc, Arenig, Llandeilo-Llanvirn, Caradoc, Ashgill), but for this analysis such citations had to be plotted onto the appropriate stage or stages. Taxa therefore cited as being present in the Caradoc Series were, in practice, entered in the database as being present in the 7 stages within the Caradoc in the 1989 chart (Costonian, Harnagian, Soudleyan, Longvillian, Marshbrookian, Actonian, Onnian). Such a process probably explains why some major features of brachiopod diversity over time occur over several time intervals and are not constrained to a single stage.

Furthermore, in 1989 there were some series without defined stages, for example the Tremadoc and Llarnvirn-Llandeilo, and in these cases the series names were used. Similarly, the widely utilized name Arenig has been used despite the fact that Fennian–Moridunian and Yapeenian–Bendigonian were local names assigned to this interval (neither of which appeared in the brachiopod taxonomic descriptions). Most of the series and stage names for the Ordovician used here have disappeared from *A Geologic Time Scale 2004,* and indeed there are several unnamed stratigraphic units awaiting formal naming by the International Commission on Stratigraphy (Gradstein, Ogg, & Smith, 2004). The nomenclature used here is still common in the literature, is widely used and understood, and hence should be readily transferred onto any future classification. Using such procedures and adopting the conventions shown in Table 40 to plot unconventional stratigraphic data onto the standardized 1989 stratigraphic column resulted in a matrix of the number of genera present in each stage, and this was used to prepare the diagrams presented in this chapter.

ESTIMATES OF BIODIVERSITY?

Although the graphs presented here have been generated from stratigraphic range data, there is a strong inclination to analyze the resulting graphs as indicators of the biologic diversity of brachiopods through time. In reality, there are considerable difficulties in using stratigraphic ranges as measures of taxonomic diversity. The brachiopod community has long discussed the techniques used to analyze stratigraphic data (Cooper & Williams, 1952; Williams, 1965b; Ager, 1988). Extensive literature on the topic has addressed the problem and suggests a range of different metrics to generate more accurate estimates of biodiversity from the raw stratigraphic data. These include mathematic procedures such as normalizing the data to account for the fact that results are biased because taxa are rarely present throughout the entire stratigraphic unit in which they appear and disappear (Sepkoski, 1975). A recent test of some of these techniques (Cooper, 2004) using a model dataset indicated that total diversity (counts of the total number of taxa present in each stratigraphic unit) tended to consistently overestimate actual diversity (i.e., in the model test set of stratigraphic ranges). This phenomenon declined in significance, however, when higher taxonomic units (e.g., genera) and shorter time periods were used (decreasing the number of taxa that are present in only part of a time period; Cooper, 2004).

The procedures adopted in this chapter will no doubt overestimate the actual biodiversity but probably not to a significant extent. In any event, the major interest in the data presented here lies more in trends and patterns than in absolute diversities or inferences about the rates of evolutionary change. Using the total number of genera recorded in each stage will, on the available evidence, most likely enhance trends and patterns without distorting them significantly. This approach has the added value of ensuring that future investigators are completely clear about the methodology used, without the complication of data processing procedures that may well evolve with time.

Simple counts of numbers will not take into account the relative abundance of taxa, so although the first and last appearance of a genus that dominates a fauna is of far greater biological significance than that of a genus with very few fossilized individuals, both will carry a similar weighting in the analyses. Furthermore, it is entirely possible to overlook turnover events in geologic history, because the replacement of established taxa by an equal or very similar number of newly evolved stocks will not show up as a biotic turnover event but will instead look like stasis. Other factors having a major influence on the interpretation of stratigraphic distribution curves, in terms of real biological or environmental events, are the degree to which rocks of a particular geologic system have been exposed at the Earth's surface over the last 200 years or so and the extent to which brachiopods are preserved in the rocks that have been available for study over that period. The early onset of silicification, for example, has clearly had a significant effect on stratigraphic abundances of brachiopods (e.g., the enormously diverse North American Glass Mountain faunas in the Permian; Cooper & Grant, 1969, 1974, 1975, 1976a, 1976b). Similarly it has been suggested that major events such as extinctions in the fossil record are primarily the result of intervals in which widespread marine transgressions have preserved marine strata that are often destroyed during low-stand periods. In effect therefore, these events may be artefacts of the fossil record due to unequal exposure and preservation, various other biases resulting from geologic processes, and as a result of preferential collection or monographic treatment (Cooper & Williams, 1952; Sheehan, 1977; Grant, 1980; Smith, 2001; Smith, Gale, & Monks, 2001; Benton, 2004).

Such complications, however, are primarily relevant for interpretations of biodiversity through geologic time. In this chapter, great care has been taken to distinguish between cited stratigraphic distribution, which at the time of the *Treatise* census is as accurate and standardized as any such data can be, as compared with the much more speculative interpretations and discussions. The former will stand the test of time, while the latter are likely to change to a greater or lesser extent in future years, with improvements in our understanding of the effects of taxonomic procedures and geologic processes on the completeness of the fossil record. Interpretations that correlate patterns of abundance to biological or environmental causes should be considered as speculative and possibly, at best, coarse-scale interpretations applicable only to major events. An alternative approach, taking the data presented here and studying the life-style and morphological characteristics of the taxa concerned and the exposure and preservation of the host stages and systems, may prove a much more productive line of enquiry into the validity and causes in brachiopod diversity over time. Throughout this chapter, the use of the term diversity should be interpreted as referring to the stratigraphic diversity of taxa rather than genuine biological diversity, unless explicitly stated otherwise.

Environmental Proxies

Since the publication of the first brachiopod *Treatise* in 1965 (Moore, 1965) the use of geochemical and isotopic measurements from rocks and fossils has increased dramatically. New techniques are constantly adding to the spectrum of proxies that can be measured to reveal information about environmental conditions far back in geologic time, for which direct evidence is lacking or extremely rare. Refinements and greatly extended usage of isotopic data (such as stable oxygen and carbon isotopic ratios that are expressed as $\delta^{18}O$ and $\delta^{13}C$) has provided important new data on major changes in environmental conditions over geologic time and of the consequences of such changes on life in the past. Such paleoenvironmental reconstructions are all the more valuable when the correlation between the isotopic compositions of the biominerals in a shell has been comprehensively investigated to confirm that it accurately reflects the isotopic composition of the surrounding seawater. The shells of a number of organisms investigated in this way have proved not to be in equilibrium with the surrounding seawater, and such complications, known as vital effects, will distort any paleoenvironmental reconstruction. The low-magnesium shells of calcareous brachiopods have been subjected to extensive isotopic investigation in Recent seas, however, and large parts of their skeletal ultrastructure have proved to be in equilibrium with the surrounding seawater, hence justifying the widespread use of brachiopod shell isotopic compositions as paleoenvironmental indicators in the geologic record (e.g., Veizer & others, 1999; Parkinson & others, 2005; Parkinson & Cusack, herein, p. 2522–2531). Undoubtedly, however, the validity of such determinations becomes progressively more uncertain in specimens of increasing age. There are many different types of geochemical and isotopic proxies, and some of them, such as determinations of strontium isotope ratios, have not only provided a valuable new tool for global stratigraphic correlation but have also generated new insights on the major trends in planetary dynamics (Veizer, 1989).

This chapter briefly discusses the extent to which the apparent changes in brachiopod diversity over time can be correlated to Earth history events that are either well documented or inferred from proxy data. Comprehensive coverage of what is now an enormous area of research cannot be included here, but clearly it is of great interest to at least note the degree to which investigations of ancient environmental conditions provide possible explanations for the observed distribution of brachiopods through time. For example, intervals where brachiopod diversity changed significantly in apparent synchroneity with major climatic events, as they are presently understood, could plausibly be interpreted as being more reliable records of genuine biological responses to environmental stimuli than those that are not obviously correlated with such events. Conversely, climatic and paleo-oceanographic interpretations will undoubtedly be refined and changed in future years, and it will be intriguing to investigate to what extent the data presented here is consistent with or contradictory to any future developments.

OVERALL DISTRIBUTION

Figure 1912 shows the overall distribution of all brachiopod genera as compiled from the taxonomic descriptions included in the revised *Treatise*, volumes 2 to 6. For comparison, Figure 1913 shows a reconstruction of the hand-drawn stratigraphic distribution chart published in the 1965 brachiopod *Treatise* (Williams, 1965b, fig. 149). For the most part, the available data in the 1965 chart were collated in terms of lower, middle, and upper subdivisions of each system, and for this study the number of genera in each subdivision was extracted from the 1965 diagram (Williams, 1965b, fig. 149) and the resulting data used to prepare Figure 1913.

The most recent compilation of brachiopod genera presented in this revised *Treatise* includes records for a total of 4218 genera that are valid for analysis using the stratigraphic and taxonomic criteria discussed above (i.e., ignoring uncertain taxa or distributions). This compares with around 1650 genera recorded in the 1965 *Treatise*, representing an increase of over 2500 genera, or 155%, over the last 41 years. The number of genera in the revised *Treatise* represents an even more dramatic rise, as this analysis excludes all genera with questionable validity and stratigraphic information, and in reality the number of brachiopod genera has probably tripled between the 1965 *Treatise* and this revision. Using the 113-point scale, the 4218 genera analyzed herein generated a total of 17,107 records (i.e., 1 record corresponds to 1 genus present in 1 stage). The 1965 *Treatise* generated about 3000 records, although the use of only 28 census points makes it impossible to directly compare the

Fig. 1912. Cumulative abundance of all brachiopod genera described in the revised brachiopod *Treatise*. The horizontal axis is divided into 113 stages are listed in Table 40 (starting from Tommotian on left through to Holocene on right), and systems are divided by vertical lines (Pleistocene and Holocene stages are unlabelled on the extreme right-hand side of diagram). The term Quaternary is no longer applicable as a convenient grouping, as INQUA has proposed that the Quaternary be formally defined to include the Pleistocene, the Holocene, and the upper part of the Neogene (Gradstein, Ogg, & Smith, 2004). The 113 stages (census points) are equally spaced irrespective of absolute ages assigned to each stage (i.e., they are chronostratigraphic ordinates, and no attempt has been made to incorporate absolute time estimates). Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Note that the method employed here of displaying the data graphically as an area curve will cause apparent leakage of taxa into later stages as an inevitable result of the curve returning to zero in the stage immediately after the one in which that group of brachiopods was last recorded. The diagram represents an update of that produced for the introduction to volume 5 (Kaesler, 2006, fig. 1101) and includes several thousand more stratigraphic records following the stratigraphic information available on recently described genera and the amended stratigraphic information on previously described genera (as published herein, p. 2532–2821) (new).

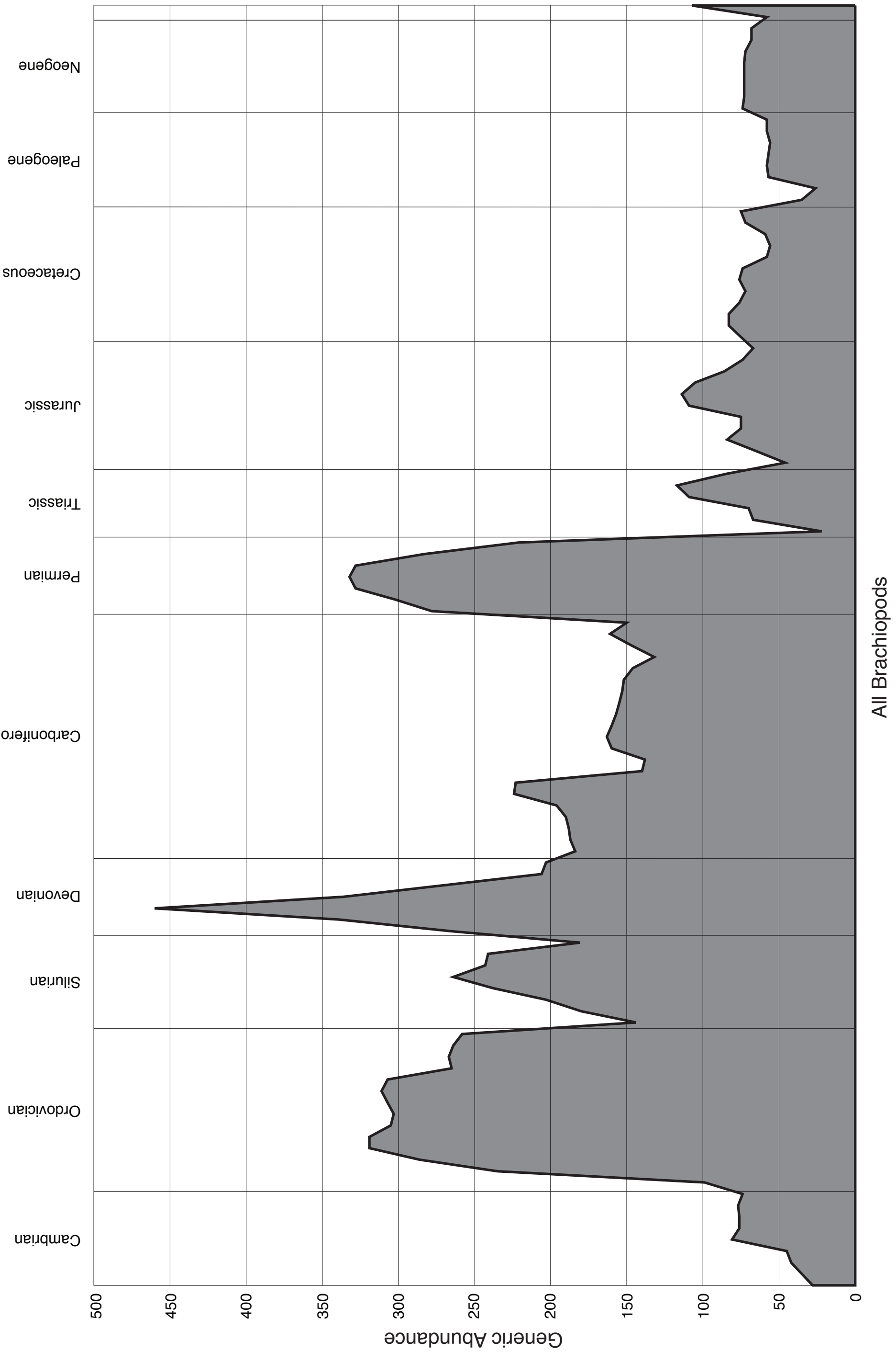


FIG. 1912. *For explanation, see facing page.*

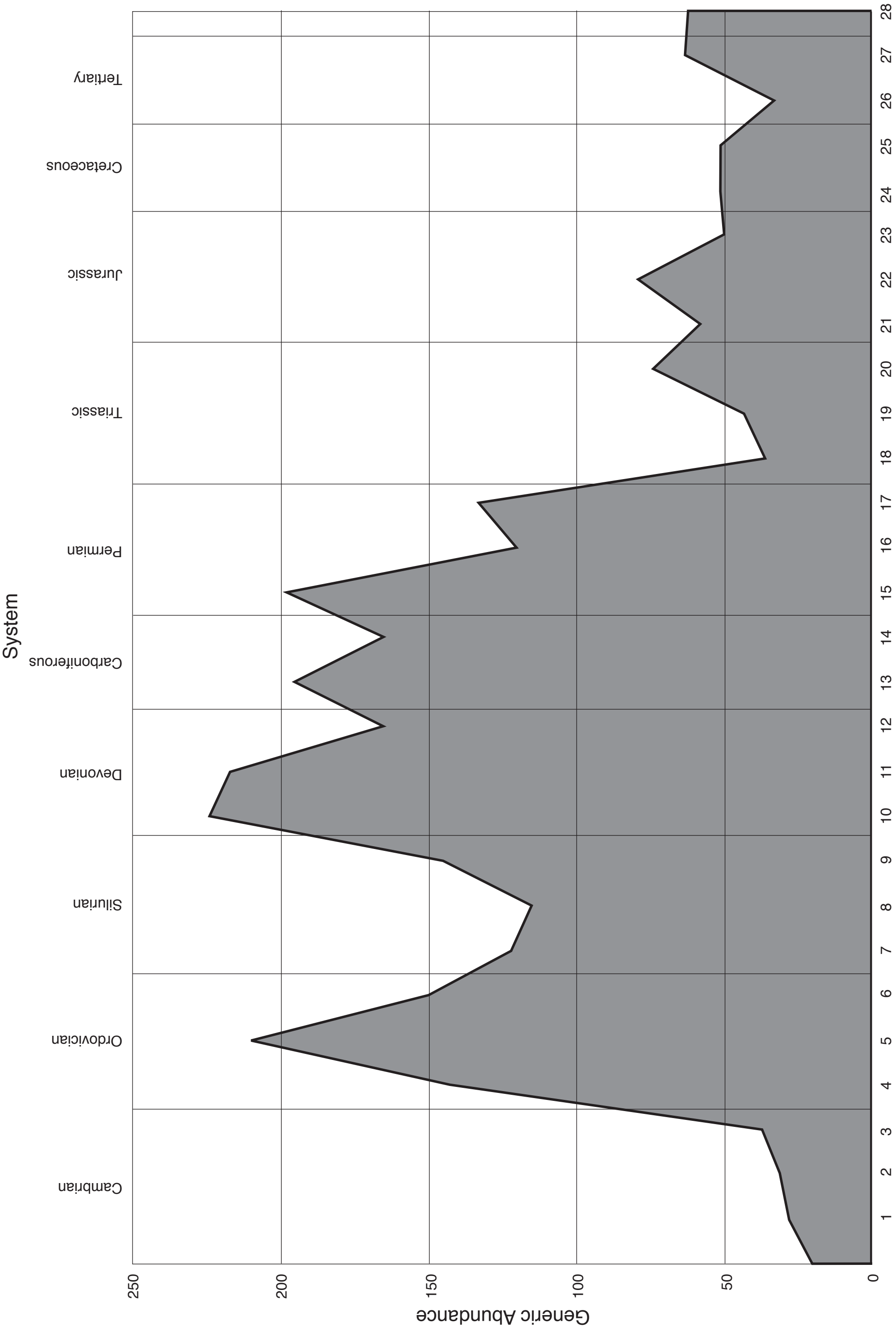


FIG. 1913. *For explanation, see facing page.*

two data sets (for example, an extreme case would be when a single record in the 1965 *Treatise* [Upper Ordovician] is now represented by 11 records [each corresponding to a single stage] in the current analysis).

The overall distribution pattern is similar in both graphs: a slow increase during the Cambrian followed by a rapid increase in generic numbers during the Lower Ordovician, maintaining a comparatively high level of diversity throughout the Silurian, Devonian, Carboniferous, and Permian, with a number of intervals when diversity decreased sharply and then recovered. The greatest decrease in numbers occurred at the end of the Permian, after which the generic diversities of brachiopods never approached the levels of diversity seen throughout the Paleozoic. The Mesozoic and Cenozoic stages, while still showing significant fluctuations, are characterized by diversity of the order of 50–100 genera, as compared with peaks of diversity ranging from 250 to over 450 genera in the Paleozoic. The major changes, such as in the number of ordinates in each system (from 2 to 21 census points in the Carboniferous in the most extreme case), have not seriously distorted the overall pattern of diversity (i.e., higher generic numbers are present in the Lower Carboniferous compared to Upper Carboniferous in the original and the revision of the *Treatise*). Whatever they indicate, it is encouraging that the overall pattern of brachiopod diversity throughout the Phanerozoic has proved to be robust, despite the big increase in the number of genera, the modifications that have occurred in stratigraphic nomenclature, and many other changes that have occurred over the last 40 years.

A comparison of the two graphs clearly reveals the impact of much greater stratigraphic resolution adopted for the current *Treatise*. The peak of brachiopod diversity falls within the Lower Devonian in both graphs, but the greater resolution in Figure 1912 reveals that, while brachiopod diversity was increasing throughout the earliest Devonian (i.e., the Lochkovian and Pragian Stages), the peak of diversity actually occurred within the Emsian Stage (Fig. 1912). The new data present in this chapter reveal that this peak in the Emsian dominates the distribution to a much greater extent than in the 1965 *Treatise,* and the number of genera have more than doubled, from a maximum of 224 for the Lower Devonian in 1965 to 460 for the Emsian Stage in the revised *Treatise*. The rapid Emsian increase in generic numbers was followed by a progressive and equally rapid decline of taxa during the Middle and Late Devonian (Eifelian, Givetian, and Frasnian Stages). The number of brachiopod genera becomes much more stable in the latest Devonian stage (the Famennian) and then increases at a much more modest rate during the Lower Carboniferous. A plot of this data using absolute age ordinates (Fig. 1914) yields a very similar overall curve, with the most obvious difference being the much more gradual slope for the Lower Ordovician increase in the number of brachiopod genera (because of the long duration of the Lower Ordovician stages, as discussed above and in the following sections).

Direct comparisons between the 1965 and 2007 totals are not entirely meaningful, as the former represents the total number of genera in the Lower Devonian (i.e., a

---

FIG. 1913. Cumulative abundances of brachiopod genera recorded in the first brachiopod *Treatise*, reconstructed by measuring and extrapolation from figure 149 in WILLIAMS (1965b); raw data used to construct the original 1965 graph is not available. The census points along horizontal axis are, in sequence from left-hand side of diagram: (1) Lower Cambrian, (2) Middle Cambrian, (3) Upper Cambrian, (4) Lower Ordovician, (5) Middle Ordovician, (6) Upper Ordovician, (7) Lower Silurian, (8) Middle Silurian, (9) Upper Silurian, (10) Lower Devonian, (11) Middle Devonian, (12) Upper Devonian, (13) Lower Carboniferous, (14) Upper Carboniferous, (15) Lower Permian, (16) Middle Permian, (17) Upper Permian, (18) Lower Triassic, (19) Middle Triassic, (20) Upper Triassic, (21) Lower Jurassic, (22) Middle Jurassic, (23) Upper Jurassic, (24) Lower Cretaceous, (25) Upper Cretaceous, (26) Lower Tertiary, (27) Upper Tertiary, (28) Quaternary (unlabelled section on the extreme right-hand side of diagram) (new).

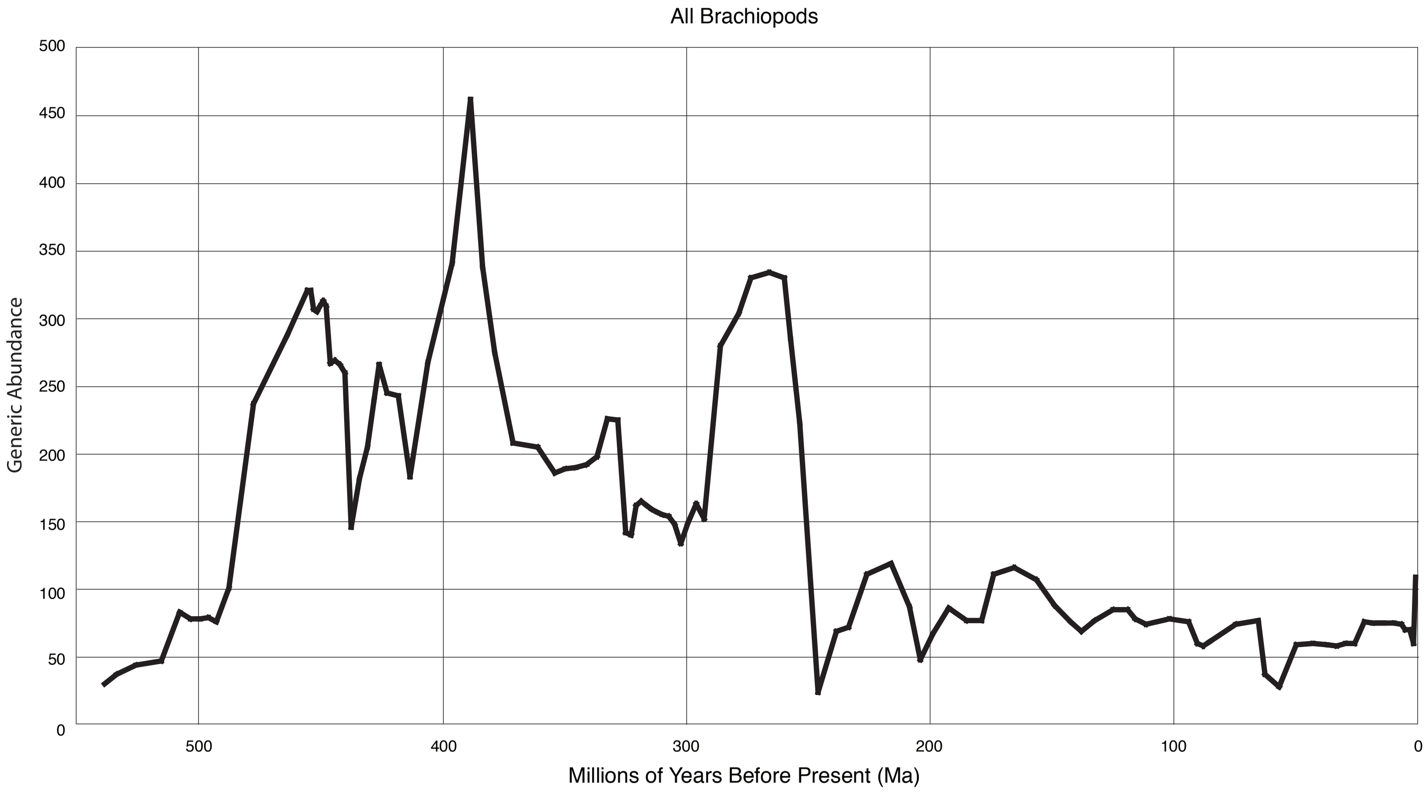


FIG. 1914. Cumulative plot of generic abundances of brachiopods in 113 stages, plotted according to absolute age determinations for the midpoint of each stage. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. This graph plots same data as used in Figure 1912 but uses absolute age ordinates on horizontal axis rather than equally spaced stages (new).

total of 3 stages), while the latter represents the total number of genera recorded in a single stage. In reality, therefore, the increase in brachiopod genera in the Lower Devonian over the last 40 years is even more dramatic, as the total number of distinct genera recorded from the three stages of the Lower Devonian in the revised *Treatise* would be even greater than 460.

Figure 1912 demonstrates that the Roadian Stage of the Permian System has the second greatest diversity of brachiopod genera and that the Costonian Stage of the Ordovician System has the third greatest diversity. Again, this is similar to the pattern seen in the 1965 *Treatise*, but the maximum number of genera has increased by about a third in both cases (again with the proviso that the 1965 figures represent the diversity of the Lower Permian and Lower Ordovician respectively rather than the Roadian and Costonian Stages). In 1965 the Ordovician had the second greatest diversity of any system, but in 2007 the Permian System has slightly more brachiopod genera than the Ordovician System (332 genera as compared with 319).

One striking feature of the stratigraphic data presented here is the extent to which many of the systems begin and end with significant decreases in the numbers of brachiopod genera (Fig. 1912). Such a phenomenon is at least partly a legacy of the historical use of major biological turnover events in the geologic record to define major stratotype boundaries. Note that the method employed here of displaying the data graphically as an area curve will cause apparent leakage of taxa into later stages as an inevitable result of the curve returning to zero in the stage immediately after the one in which that group of brachiopods was last recorded. In Figure 1912 the lines separating systems have been drawn midway between the last stage of one system and the first of the succeeding system. Other differences between the 1965 and 2007 *Treatise* data, such as the dramatic increase in generic diversity during the Permian System and the equally dramatic decline into the Triassic, will be discussed in the appropriate section below.

EXTINCTIONS AND RADIATIONS

Throughout the stratigraphic column, as it was defined in 1989 (Table 40), there are 18 stages (out of a total of 113) in which more than 10% of the genera in the previous stage disappeared from the geologic record. A further 29 stages saw the number of genera increase by over 10% compared to the preceding stage. Brachiopod stratigraphic history is therefore characterized by extensive change. In a total of 47 stages out of a total of 113 (i.e., 42%), brachiopod diversity increased or decreased by 10% or more as compared with the previous stage. Throughout their geologic history, the number of brachiopod genera changed by an average of 6.3% from one stage to another. What is unknown, of course, is the extent to which artefacts, both geologic and human, have contributed to this pattern of apparent extinctions and radiations; and several authors have debated the issue (Ager, 1988; Smith, 2001; Smith, Gale, & Monks, 2001).

What is clear from the analyses presented here is that, in absolute terms, there are 14 stages where 20 genera or more disappear, and 22 stages in which 20 genera or more are added to global diversity of the phylum. Again, the pattern is for the number of brachiopod genera to be noticeably changeable throughout the Phanerozoic, with 32% of stages recording either an increase or a decrease of 20 or more genera.

The most significant extinction event in brachiopod history was at the Permian-Triassic boundary. Over 90% of the genera present in the Changhsingian disappeared at the end of stage, and this event was also the largest in brachiopod history in absolute terms (199 genera disappear). The end-Emsian (Devonian) was the second largest extinction event in brachiopod history in absolute terms (124 genera disappeared), but it was much less significant (27%) in percentage terms. The end-Hirnantian (Ordovician) decline (114 genera) was the third greatest in brachiopod history, and also the third most significant in percentage terms (44%). The end-Cretaceous was the second largest apparent extinction in brachiopod history in terms of percentages (53%) but involved the disappearance of only 40 genera, so was low in terms of absolute numbers of genera disappearing. In addition to the end-Permian, end-Emsian, and end-Hirnantian events, there are a further five stages that witnessed more absolute generic reductions than the end-Cretaceous event: end-Capitanian: 62 genera; end-Wordian: 45 genera; end-Brigantian: 83 genera; end-Givetian: 67 genera; end-Onnian: 42 genera. Major radiation and extinction events are discussed in more detail in the sections that follow; there is also extensive literature on the subject (e.g., AGER, 1987; BOUCOT, 1996; MACLEOD & KELLER, 1996; SHEN & SHI, 1996; BASSETT, POPOV, & HOLMER, 1999; DULAI, 2001; CHEN, SHI, & KAIHO, 2002; MACLEOD, 2003; MILLER, 2004; ALVAREZ, 2006; HARPER, 2006).

CAMBRIAN SYSTEM

The Cambrian System (542 ± 1.0 Ma to 488.3 ± 1.7 Ma; GRADSTEIN, OGG, & SMITH, 2004) is subdivided into nine stages (Table 40), and the numbers of brachiopod genera increase progressively but slowly from the Lower Cambrian Tommotian Stage (a total of 28 genera recorded) through to 45 genera in the uppermost Lower Cambrian Toyonian Stage (Fig. 1915). The Amgaian Stage is characterized by a significant increase in brachiopod genera, with 81 genera recorded. With minor fluctuations, the number of brachiopod genera found in the subsequent stages of the upper Middle and Upper Cambrian stages remains relatively constant at around 75 genera.

The brachiopod faunas in the Cambrian are taxonomically diverse. Overall the system contains representatives assigned to no less than 12 different orders out of a total of 26 orders described for the entire phylum. For the entire Cambrian System, brachiopods assigned to the Lingulida and Acrotretida are dominant, together representing over half the total diversity (Fig. 1916).

Four out of a total of 26 brachiopod orders are restricted to the Cambrian System (the Kutorginida, Naukatida, Obolellida, and Chileida), and all disappeared by the end of the Middle Cambrian. The Chileida and the Naukatida last appear in the lowermost Amgaian Stage of the Middle Cambrian, while the Kutorginida and the Obolellida make their last appearance in the uppermost Mayaian Stage of the Middle Cambrian. None of these orders are represented by large numbers of taxa, with a maximum, in any one stage, of 8 Obolellida genera, 8 Kutorginida genera, 3 Chileida genera, and 2 Naukatida genera (Fig. 1916). These orders were a significant, but short-lived, component of the Cambrian explosion and the Paleozoic fauna (SEPKOSKI, 1975). Although relatively trivial in number, these genera are important for what they tell us about the tremendous burst of evolutionary innovation and diversification in the Lower Cambrian.

While some of the orders that appeared in the Lower Cambrian had a short geologic history, others were represented by increased numbers of genera in the Upper Cambrian stages (Fig. 1916). The Lingulida and the Acrotretida in particular radiated markedly during the Upper Cambrian, and although the diversity of both declined sharply at the end of the Cambrian, both orders subsequently recovered during the Lower Ordovician. Together with the two other orders that constitute the Linguliformea (the Paterinida and the Siphonotretida), the subphylum achieved its maximum diversity during the Lower Ordovician.

Examining the taxonomic diversity of brachiopods present in different stages of the Cambrian demonstrates considerable variability. The Lower Cambrian Tommotian

Stage is dominated by Lingulida (21%) and Obolellida taxa (21%), while the Paterinida (14%), the Kutorginida (14%), and the Protorthida (14%) also represent significant contributions to the overall brachiopod generic abundances that include representatives of a total of 8 orders (Fig. 1916). The Naukatida first appeared in the Botomian Stage, and so by the uppermost Toyonian stage of the Lower Cambrian a total of 9 orders were represented by the 45 genera recorded, and the Lingulida had become the dominant order (33%), followed by the Kutorginida (16%) and the Obolellida (11%).

The comparatively large increase in the number of brachiopod genera recorded in the Amgaian Stage (lowermost Middle Cambrian) reflected not only the appearance of two new orders (the Pentamerida and the Billingsellida, bringing the total number of orders to 11) and the continuing dominance of the Lingulida, but most significantly, great increases in the numbers of Acrotretida (from 11% in the Toyonian to 27% in the Amgaian) and the Orthida (2% in the Toyonian to 16% in the Amgaian). The remainder of the Cambrian was characterized by a very similar number of genera but a decrease in overall diversity, down to 7 orders by the end of the Cambrian. Indeed, the Middle Cambrian witnessed the last occurrences of no less than 4 orders. The Chileida and Naukatida made their last appearance in the Amgaian Stage, and the Obolellida and the Kurtorginida in the Mayaian Stage. The only example of taxonomic diversification during the Middle Cambrian was the first appearance of the Siphonotretida in the Mayaian. By the uppermost Cambrian the Lingulida and the Acrotretida had become even more dominant constituents of brachiopod faunas (collectively representing 69% of recorded taxa). The Protorthida are absent from the Upper Cambrian but appear again in the Lower Ordovician.

The absolute age range of the Cambrian System has changed significantly since 1989, when the cited duration was from 570 Ma (or 540 Ma, as a result of complications with the correlation of the base of the Tommotian and the Proterozoic–Lower Cambrian boundary) to 510 Ma (a total duration ranging from 60 to 30 million years). The composite time scale adopted here (in which all the stratigraphic units below the Atdabanian were labelled as Tommotian for simplicity; Table 40) has a time span of 540–490 Ma, a total range of 50 million years, which is very similar to that given in the latest compilation of *A Geologic Time Scale 2004* (452 ± 1.0 Ma to 488.3 ± 1.7 Ma = 53.7 million years; Gradstein, Ogg, & Smith, 2004). The Cambrian stages have undergone extensive modification since 1989, however, and there are now a total of 6, although only one of these stages has been formally named (Gradstein, Ogg, & Smith, 2004).

Whatever the complexities of stratigraphic nomenclature, it is clear that brachiopods were taxonomically very diverse at the base of the Cambrian and hence must have an extensive but so far unrecorded or unrecognized Precambrian presence as organisms without a mineralized skeleton. The available data indicates that the diversity and abundance of brachiopods remained virtually unchanged throughout the Lower Cambrian (approximately 30 million years from the base of the Cambrian, using the absolute dates shown in Table 40).

The major change in the number of genera within the Cambrian occurred in the lower Middle Cambrian Amgaian Stage when generic abundances increased by 80% compared to the preceding uppermost Lower Cambrian Toyonian Stage, while overall taxonomic diversity only increased slightly (to 11 orders as compared with 10 in the Lower Cambrian). A sharp excursion in carbon isotope ratio at the Lower to Middle Cambrian boundary has been thought to correlate with a trilobite mass extinction event (Montañez & others, 2000). Brachiopods may therefore have radiated in the aftermath of such an event. The stocks that underwent the greatest increase in

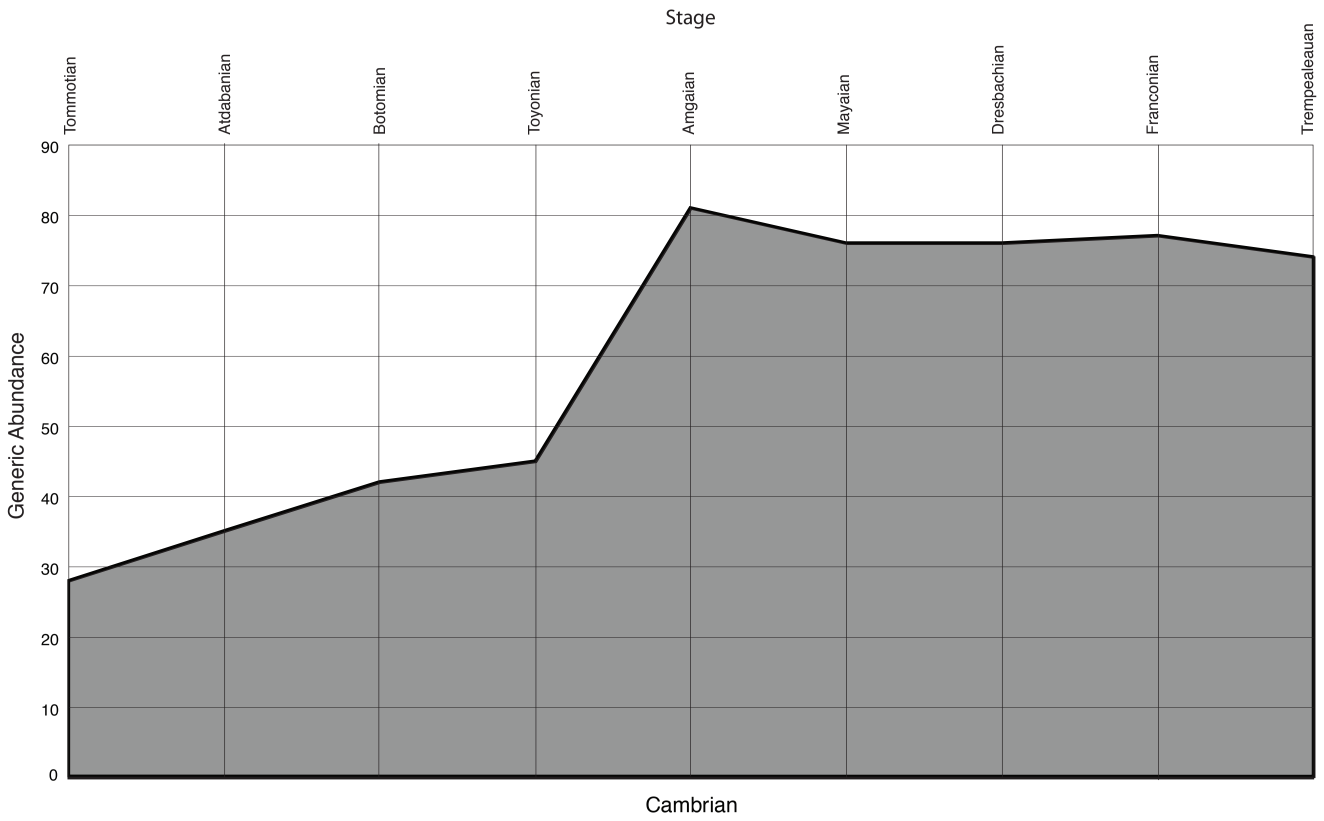


FIG. 1915. Abundance of brachiopods in each of the 9 stages (horizontal axis) assigned to Cambrian System, with lowermost stage (Tommotian) on left-hand side of horizontal axis and uppermost Trempealeauan Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

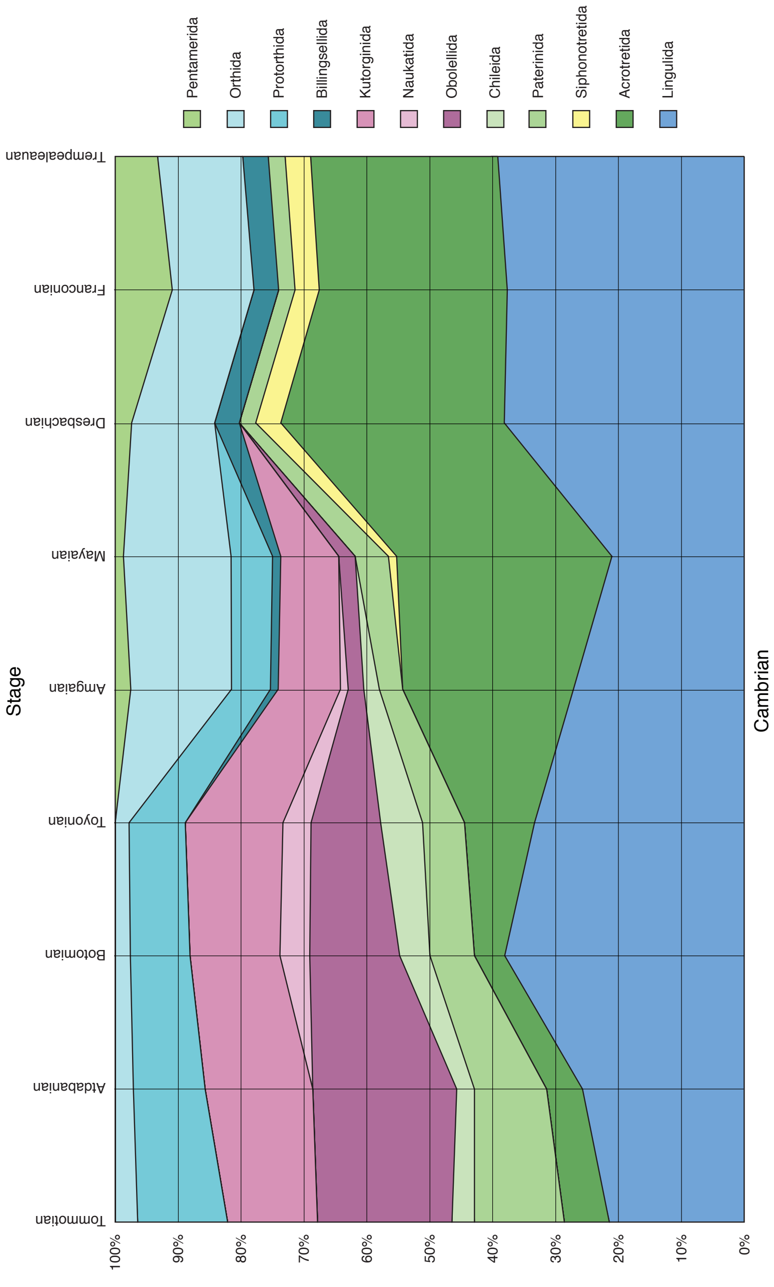


Fig. 1916. Relative proportions of different orders of brachiopods recorded from each of 9 stages of Cambrian System, with lowermost stage (Tommotian) on left-hand side of horizontal axis and uppermost Trempealeauan Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Key on right indicates different brachiopod orders present (new).

the Middle Cambrian were the Lingulida and the Acrotretida. The increase in the number of the Acrotretida was the most dramatic, from 5 in the Toyonian to 22 in the Amgaian, and the order maintained a level of at least 22 genera throughout the remainder of the Cambrian and reached a maximum diversity of 27 genera in the Dresbachian Stage.

The overall generic abundances of brachiopods are lower in the Cambrian than in virtually any other system throughout the Phanerozoic (with the exception of parts of the Cretaceous, Paleogene, and Neogene; Fig. 1912). In addition, the antiquity, relatively poor preservation, and limited exposure of Cambrian rocks makes it difficult to interpret the Cambrian stocks of brachiopods in anything other than very general terms. Brachiopods are undoubtedly significant and diverse components of the explosion of metazoans that acquired mineralized skeletons in the Lower Cambrian, and the earliest representatives of the subphylum Linguiformea represent some of the oldest known benthic organisms with a mineralized skeleton (Bassett, Popov, & Holmer, 1999). The number of brachiopod genera recorded increased markedly at the beginning of the Middle Cambrian and thereafter remained relatively stable for the remainder of the Cambrian despite the fact that taxonomic diversity declined markedly in the Upper Cambrian. Bassett, Popov, and Holmer (1999) noted that the two most diverse orders of organophosphatic-shelled brachiopods (i.e., the Lingulida and the Acrotretida) were major constituents of the initial Cambrian radiation and, by the end of the Cambrian, had colonized all types of marine depositional environments. Furthermore, during the Cambrian, the Lingulida had spread progressively from predominantly shallow-water habitats to deep-water environments and had become dominant constituents of the faunas in areas of high-energy sand deposition (Bassett, Popov & Holmer, 1999). Indeed, brachiopods were, after trilobites, the second most important constituents of benthic communities in shelf and platform environments during the Cambrian.

Information on the climates and environments in the Cambrian System are sparse; there are, for example, limited isotopic data that could be used as a proxy for environmental change. What is known about the conditions on Earth suggests comparatively warm climates prevailed globally (Montañez & others, 2000), implying that there were no significant glacioeustatic changes in sea level that might have had a discernible effect on brachiopod diversity. There is clear faunal provinciality in the Cambrian and tectonic events such as the opening of the Iapetus Ocean and progressive drift of continents toward the equator. It would seem doubtful that global tectonism had a significant effect on brachiopod diversity at the level of resolution of the stratigraphic data presented here. The comparative success of the Acrotretida and Lingulida may have owed more to their morphological adaptability and environmental tolerance of the Cambrian oceans, where conditions would have been very different from those in present-day oceans. It has been suggested that the success of the subphylum Linguliformea in the Cambrian and early Ordovician might be related to their low energy requirement and their tolerance of significant daily fluctuations in the oxygen content of seawater; such attributes therefore allow them to colonize marginal habitats (Bassett, Popov, & Holmer, 1999). Whatever the reason, it is clear that the Cambrian is a system in which there was considerable evolutionary experimentation with several distinct groups arising and dying out relatively quickly.

ORDOVICIAN SYSTEM

Although the Ordovician (488.3 ± 1.7 Ma to 443.7 ± 1.5 Ma; Gradstein, Ogg, & Smith, 2004) saw one of the most significant radiations in the number of brachiopod genera throughout their entire geologic history (increasing to 19 orders, as compared with a total of 12 recorded in the Cambrian), the system started on a subdued note with the Lower Ordovician Tremadoc Stage registering only a slight increase in the total number of genera compared to the Upper Cambrian (Fig. 1917). A total of 99 genera have been recorded from the Tremadoc Stage, as compared with 74 for the uppermost Cambrian Toyonian Stage. The seven orders present in the Tremadoc are the same ones present in the uppermost Cambrian Trempealeauan Stage, although there are some changes in the relative proportions of genera assigned to these orders between the Trempealeauan and the Tremadoc Stage. The most notable changes are in the diversity of the Lingulida and the Acrotretida, which had been dominant in the Upper Cambrian and which would diversify further in subsequent Ordovician stages, but suffered significant decreases in the numbers of genera in the Tremadoc Stage. Much of the increase in the overall number of genera can be attributed to a significant radiation in taxa assigned to the Orthida from the uppermost Cambrian Toyonian Stage (10 genera as compared with 35 genera in the Tremadoc Stage) and the Pentamerida (5 genera as compared with 14 genera in the Tremadoc Stage).

Although the details are intensively debated, there is no doubt that the Ordovician Period was characterized by major fluctuations in both climate and sea level (NIELSEN, 1992). Tremadoc Stage brachiopod distributions may reflect the effects of such changes, as the evidence suggests that there was a major increase in sea level in the lower Tremadoc (a transgression) and an abrupt and pronounced decrease in sea level (a regression) in the middle to upper Tremadoc (NIELSEN, 1992). Oxygen isotope determinations remain essentially level throughout the stage (VEIZER & others, 1999; GRADSTEIN, OGG, & SMITH, 2004), which implies that there were no major global temperature fluctuations, although the sampling interval may have been too large to pick up short-term events that may have influenced brachiopod diversity. If eustatic changes did have an impact on Tremadoc brachiopod faunas, then it is clear that the Lingulida and Acrotretida were disadvantaged, while the Orthida and Pentamerida flourished.

The succeeding Arenig Stage is thought to have started and ended with comparatively low sea levels, but for the majority of its 13 million years, Earth is thought to have experienced high sea levels. Indeed, overall the Ordovician is characterized by comparatively high sea levels, perhaps the highest in the Phanerozoic (FRAKES, FRANCIS, & SYKES, 1992; HALLAM, 1992). Such conditions may well have contributed to the success of the brachiopods during the Arenig, when the diversity more than doubled (to 235 genera) compared with the Tremadoc, and a total of 10 orders were present, when the Craniida and the Strophomenida appeared for the first time (Fig. 1918). The latter order was particularly successful, with 33 Strophomenida genera recorded during the Arenig, while the diversity of the organophosphatic-shelled brachiopods increased significantly during the late Tremadoc and early Arenig Stages (BASSETT, POPOV, & HOLMER, 1999).

It would be too simplistic to regard increasing brachiopod diversity as a reflection of persistent warm climates and high sea levels, because there is considerable geochemical evidence of major environmental perturbations within the Arenig. For example the ^{87}Strontium/^{86}Strontium ratio increased throughout the Ordovician, but at a higher rate in the Arenig than in any other Phanerozoic stage (QING & others, 1998). The steepness of the change, along with coeval variations of a similar nature in the oxygen and carbon isotope signal, have been interpreted as evidence of global oceanic and terrestrial changes (SHIELDS, CARDEN, & VEIZER, 2003). Attempts to correlate periods of significant environmental perturbation with brachiopod diversity are obviously complicated by the long duration of the Arenig.

The Llandeilo-Llanvirn Stage saw continued diversification, with 286 genera representing a total of 15 orders (Fig. 1918).

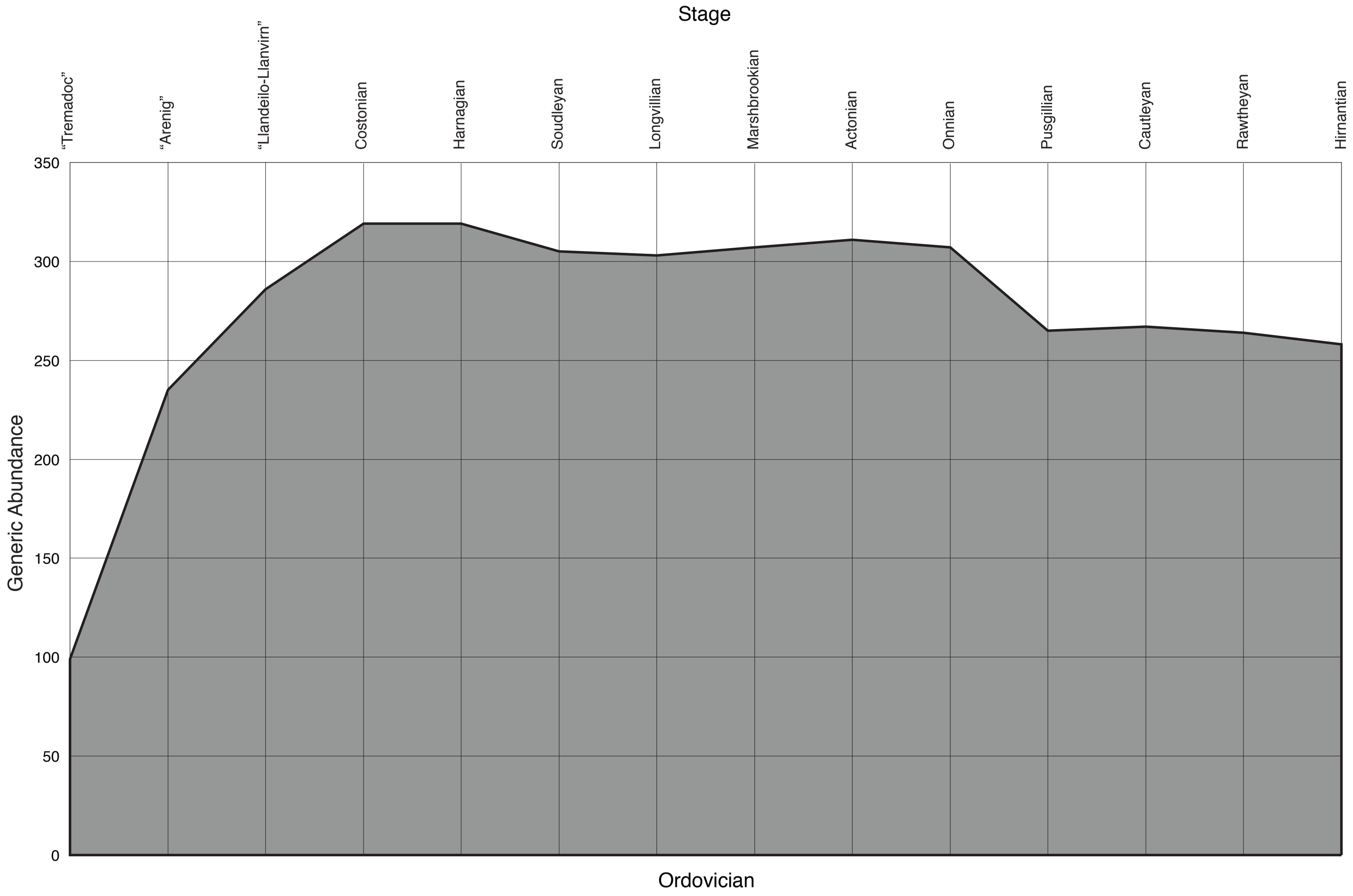


FIG. 1917. Abundance of brachiopods in each of 14 stages (horizontal axis) assigned to Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. See Table 40 for stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) (new).

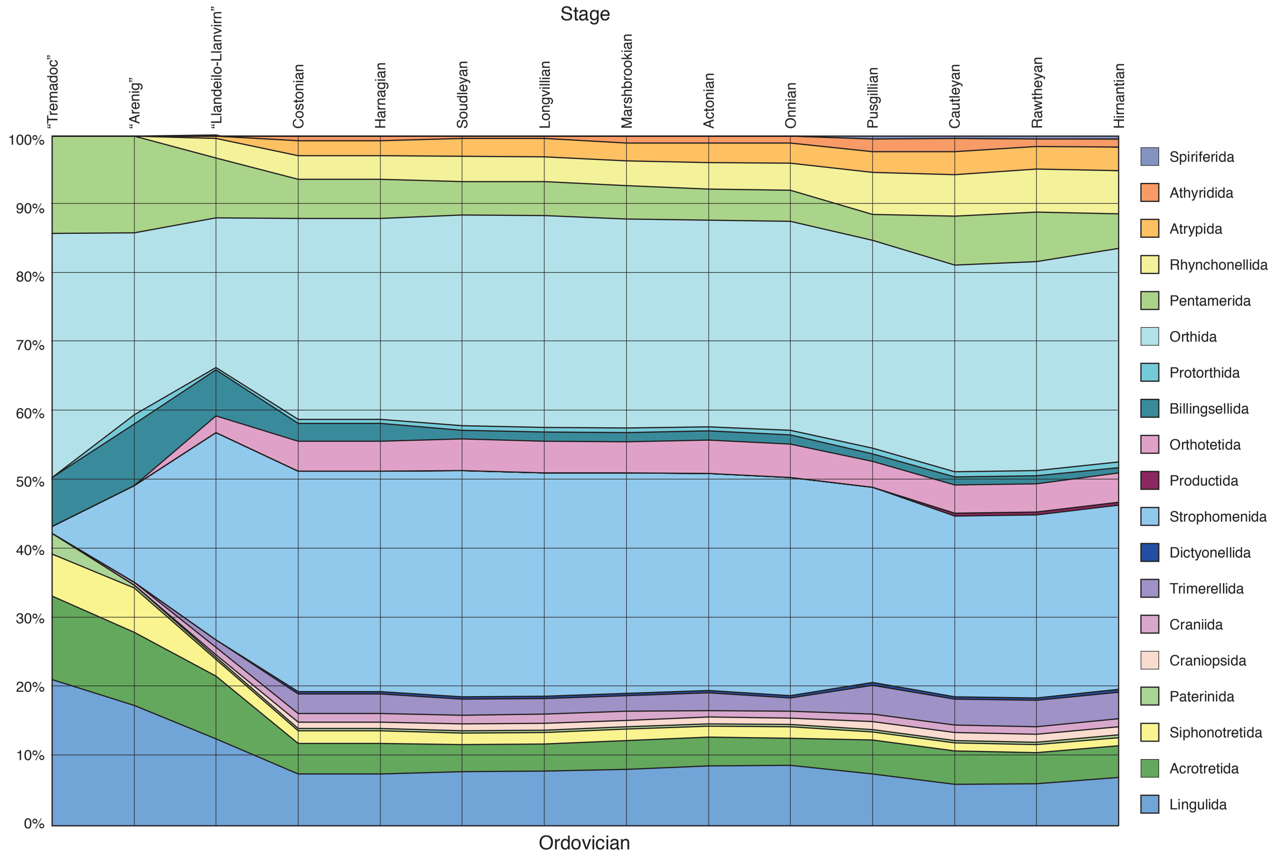


FIG. 1918. Relative proportions of different orders of brachiopods recorded from each of 14 stages of Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. Some orders are recorded in such low numbers that they are hard to distinguish (for example, Spiriferida and Dictyonellida) but are included in diagram to ensure completeness; see Table 40 for meaning of quotation marks (new).

The Craniopsida, Trimerellida, Orthotetida, Rhynchonellida, and Atrypida all appeared for the first time, although in relatively small numbers. By far the largest change in brachiopod diversity during the Llandeilo-Llanvirn Stage was the continuing dramatic increase in numbers of Strophomenida first apparent in the Arenig; generic numbers increased to 86 (up from 33 in the Arenig). Between 50% and 60% of the organophosphatic brachiopods disappeared during the Llandeilo-Llanvirn, however, and it was particularly noticeable that communities from nearshore and inner-shelf habitats where lingulide brachiopods commonly had an epibenthic life-style were replaced during the Llandeilo-Llanvirn by brachiopod-mollusk assemblages in which the predominant brachiopods were burrowing lingulides (Bassett, Popov, & Holmer, 1999).

The overall trend of increasing generic numbers continued into the succeeding Costonian Stage, reaching a total of 319 genera, the highest of any Ordovician stage. Taxonomic diversity also increased to 17 orders, with the first appearance, in low numbers, of the Athyridida and Dictyonellida. The number of Strophomenida genera continued to increase but more slowly (to 102 genera from 86 in the Llandeilo-Llanvirn), but the most dramatic increase was in Orthida genera (to 93 from 62 in the Llandeilo-Llanvirn). As a result, over 30% of Costonian genera were Orthida. The decline of the Pentamerida, from 33 genera in the Arenig to 25 in the Llandeilo-Llanvirn, continued into the Costonian, and only 18 genera are recorded from this stage. The number of Pentamerida genera fluctuated slightly during the remainder of the system, but there were always fewer than 20 genera in any subsequent Ordovician stage.

The divergence between chronostratigraphic and absolute time ordinates has a particularly strong effect on the perception of the brachiopod's role in the Great Ordovician Biodiversification Event. The use of chronostratigraphic ordinates gives the impression of a very rapid increase in brachiopod generic numbers (e.g., Fig. 1912, 1917). The use of absolute time ordinates, which take into account the much greater duration of Lower and Middle Ordovician stages, demonstrates a much more gently sloping curve (Fig. 1919), testimony to a diversification that remains dramatic but is much more sustained than abrupt. Most of the reorganized Ordovician stages remain unnamed (Gradstein, Ogg, & Smith, 2004), but Ordovician workers have divided the system into a total of 19 time slices that are of much more equable duration (Webby, Cooper, & others, 2004). The use of such time slices as ordinates for stratigraphic charts would certainly refine our understanding of brachiopod history (Harper & others, 2004), but such resolution was not attainable from the data present in the revised *Treatise*. Applying different methods of estimating diversity to alternative data sets produced distributions that differed in small detail but were very similar in overall appearance (Harper & others, 2004).

A variety of environmental factors are thought to have been significant in influencing brachiopod diversity during the Ordovician. Apart from sea level and climate mentioned above, there is evidence that some groups migrated into deeper water (Harper, Rong, & Zhan, 1999), while others radiated into a number of shallow-water carbonate environments (Harper & others, 2004). Some stocks are thought to have first appeared in equatorial regions characterized by a range of separate tectonic plates and numerous volcanic arcs (Popov & others, 1997). The habitats occupied by brachiopods also diversified during the Ordovician (Harper & others, 2004), and the existence of calcitic seas during the period may also have been significant for the diversification of calcareous-shelled brachiopods (Stanley & Hardie, 1999). It does seem as if the reasons for the Ordovician diversification of brachiopods are complex and not yet fully resolved, although clearly worthy of further research. There are extensive publications on this

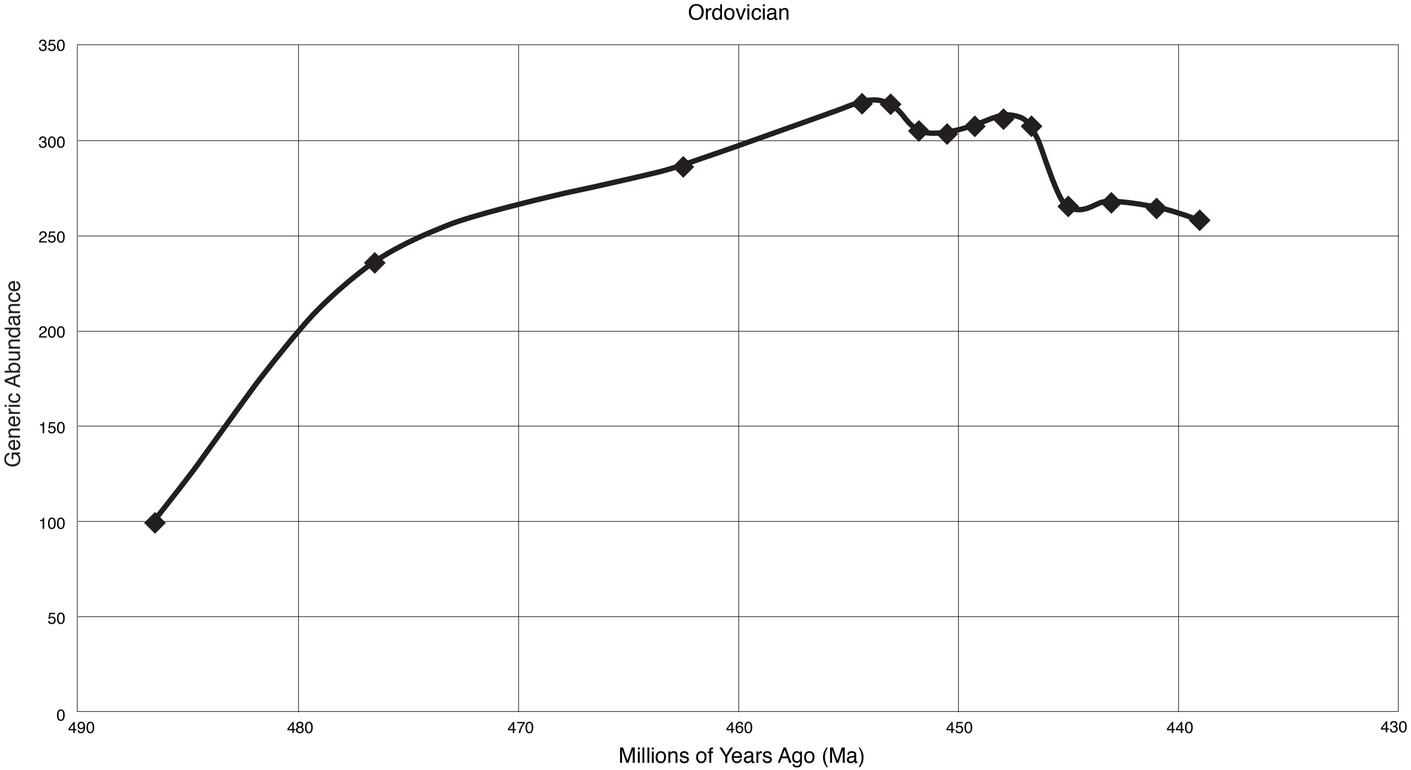


Fig. 1919. Plot of generic abundances of brachiopods in each of 14 stages (horizontal axis) assigned to Ordovician System, with lowermost stage (Tremadoc) on left-hand side of horizontal axis and uppermost Hirnantian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Graph plots same data as used in Figure 1917, but used absolute age ordinates on horizontal axis rather than equally spaced stages. Diagram demonstrates the much more gradual nature of Ordovician Biodiversification Event than is apparent from plotting data using equally spaced stage ordinates on horizontal axis (i.e., Fig. 1917) (new).

intriguing topic, including the role played by brachiopods and other phyla in the Great Ordovician Biodiversification Event (Webby, Paris, & others, 2004). Among the topics discussed as being of possible significance for the radiation of the brachiopods have been food resources, increases in absolute sizes of individuals, morphological innovation, and exploitation of the phylum of far-reaching changes in the marine communities of the time (Harper & others, 2004). It is also possible that the diversification involved more than one event (Harper, 2006).

After the extensive taxonomic turnover witnessed in the Cambrian and the Lower and Middle Ordovician, the Upper Ordovician was a time of continuity, with little taxonomic change and comparatively constant generic numbers (Fig. 1918). Two new major taxa appeared (the suborder Chonetidina within the Productida in the Cautleyan and the Spiriferida in the Pusgillian), although they are represented by very few genera. By the end Ordovician Hirnantian Stage, a total of 19 orders were represented, although a progressive decline in the number of Strophomenida (down to 69 genera in the Hirnantian from a peak of 102 genera in the Costonian and Harnagian) was the principle reason for a decrease in the overall number of genera to 258 in the Hirnantian Stage (Fig. 1917).

The Hirnantian Stage experienced the culmination of a global cooling event that resulted in high-latitude glaciations (Brenchley, 2004) and a dramatic global extinction event (Sepkoski, 1995) estimated to have seen the demise of over 20% of all families, 60% of all genera, and over 80% of species (Jablonski, 1991; Sepkoski, 1995; Brenchley, 2004). The extinction event occurred in two phases: first, in the lower Hirnantian and second, in the middle and upper Hirnantian (Sheehan, 2001). The sharp decline in numbers of Strophomenida genera in the Hirnantian probably reflects major environmental changes resulting from glaciation. Most of the impact of the event will not show up within the Hirnantian data, as most genera that became extinct during the stage will be recorded as present, even if this was just for a small part of the stage. The Hirnantian ice age is clearly demonstrated in oxygen isotope determinations and confirmed by extensive sedimentary and faunal evidence (Brenchley, 2004).

Other factors that may have had an influence on perceived brachiopod diversity in the Ordovician include the availability of extensive silicified faunas, which almost certainly facilitates the recovery of a much greater proportion of the fauna than is the case with nonsilicified specimens. The role played by silicification is considered in more detail in the section dealing with Carboniferous brachiopod faunas.

SILURIAN SYSTEM

Brachiopod diversities in the initial Rhuddanian Stage of the Silurian (443.7 ± 1.5 Ma to 416.0 ± 2.8 Ma; Gradstein, Ogg, & Smith, 2004) demonstrate the dramatic effect of the Hirnantian glaciation (Fig. 1920). The 144 genera recorded in the Rhuddanian represent a decline of 44% from that recorded in the uppermost Ordovician Hirnantian Stage. Subsequently, the number of genera increased steadily in succeeding stages, almost doubling by the Homerian Stage (to 264 genera), and thereafter declining again to 181 in the Přídolí Stage (Fig. 1920). Three orders present in the uppermost Ordovician Hirnantian Stage (the Siphonotretida, Paterinida, and Billingsellida) did not survive into the lowermost Silurian Rhuddanian Stage, although all three orders were represented by relatively few genera in the Ordovician.

The taxonomic diversity of the brachiopods was high during the Silurian, with representatives of 16 out of a total of 26 brachiopod orders. In the Silurian, the Pentamerida displayed their maximum generic diversity with 52 genera recorded from the Gorstian Stage. There is a relatively small increase in numbers of chonetidine Productida during the Silurian, after having evolved in the Upper Ordovician. No other productides appeared until the lower Devonian. Similarly, the Spiriferinida and Terebratulida did not appear until the Lower Devonian.

A striking feature of the Silurian brachiopod faunas is their taxonomic homogeneity over a period of approximately 28 million years. In all but the last stage there are 16 orders represented (genera assigned to the Trimerellida appear for the last time in the penultimate Ludfordian Stage of the Silurian). The Orthida, Rhynchonellida, Strophomenida, Pentamerida, and Atrypida are dominant in the Rhuddanian Stage and indeed throughout most of the Silurian Period (Fig. 1921). The Spiriferida undergo the most dramatic radiation during the Silurian, increasing from 2 genera in the basal Rhuddanian Stage (1% of the total number of brachiopods in that stage) to 28 genera in the uppermost Přídolí Stage (15% of the total number of genera; Fig. 1921). Indeed, by the Přídolí Stage, the Spiriferida had become the most abundant order (Fig. 1921).

While the number of Spiriferida increased progressively throughout the Silurian, it was the Pentamerida that displayed the greatest variability in numbers, ranging from 16 genera in the Rhuddanian (11% of the total number of brachiopod genera recorded from that stage) to around 50 genera in the Homerian, Gorstian, and Ludfordian (ranging from 19% to 21% of the total) and then declining to 19 genera (11%) in the uppermost Silurian Přídolí Stage.

Thus, the peak of absolute diversity in the Homerian largely reflects the radiation of the Pentamerida and the continued success of the Orthida (to 42 genera [16%] from 36 in the Rhuddanian [25% of the lower absolute number of brachiopods recorded from that stage]). As occurred with the Pentamerida, the Orthida diversities declined markedly again in the Přídolí (to 20 genera [11%]). Throughout the Silurian the diversity of the Athyridida remained fairly constant (Fig. 1921).

Reconstructions of Silurian climates indicate that the system was characterized by a gradual warming following the Hirnantian ice age, punctuated by short periods during which continental ice sheets returned (Frakes, Francis, & Sykes, 1992; Grahn & Caputo, 1992). Such an interpretation is consistent with measured $\delta^{18}O$ ratios that show an overall trend toward lower values (implying warming or less glaciation) interspersed with shorter periods of more pronounced oxygen isotope variation (Azmy & others, 1999; Veizer & others, 1999). Strontium isotope ratios also increased gradually throughout the Silurian, and again, this is thought to be a reflection of increasing input of terrestrial sediments as erosion rates and subsequent river transportation of sediments increased as the climate warmed. There are a number of short duration excursions in the $\delta^{18}O$ record, some of which have been interpreted as the result of the periodic development of continental ice sheets during the Silurian (Caputo, 1998), although some other $\delta^{18}O$ excursions (such as determined from the late Homerian and Ludfordian) are not accompanied by any evidence of ice growth and have been attributed to other types of climatic shifts (such as from humid to more arid; Samtleben & others, 1996; Samtleben, Munnecke, & Bickert, 2000). Whatever the nature and duration of these climatic changes, they did not have major effects on overall brachiopod diversity, although factors related to changing climates such as facies changes may well have had an influence on the changing relative dominance of different brachiopod orders during the Silurian.

At the resolution of the stratigraphic data presented here, the Orthida were the dominant order in the aftermath of the major environmental perturbations caused by the Hirnantian glaciation. Although their numbers declined by more than half across the Ordovician Silurian boundary,

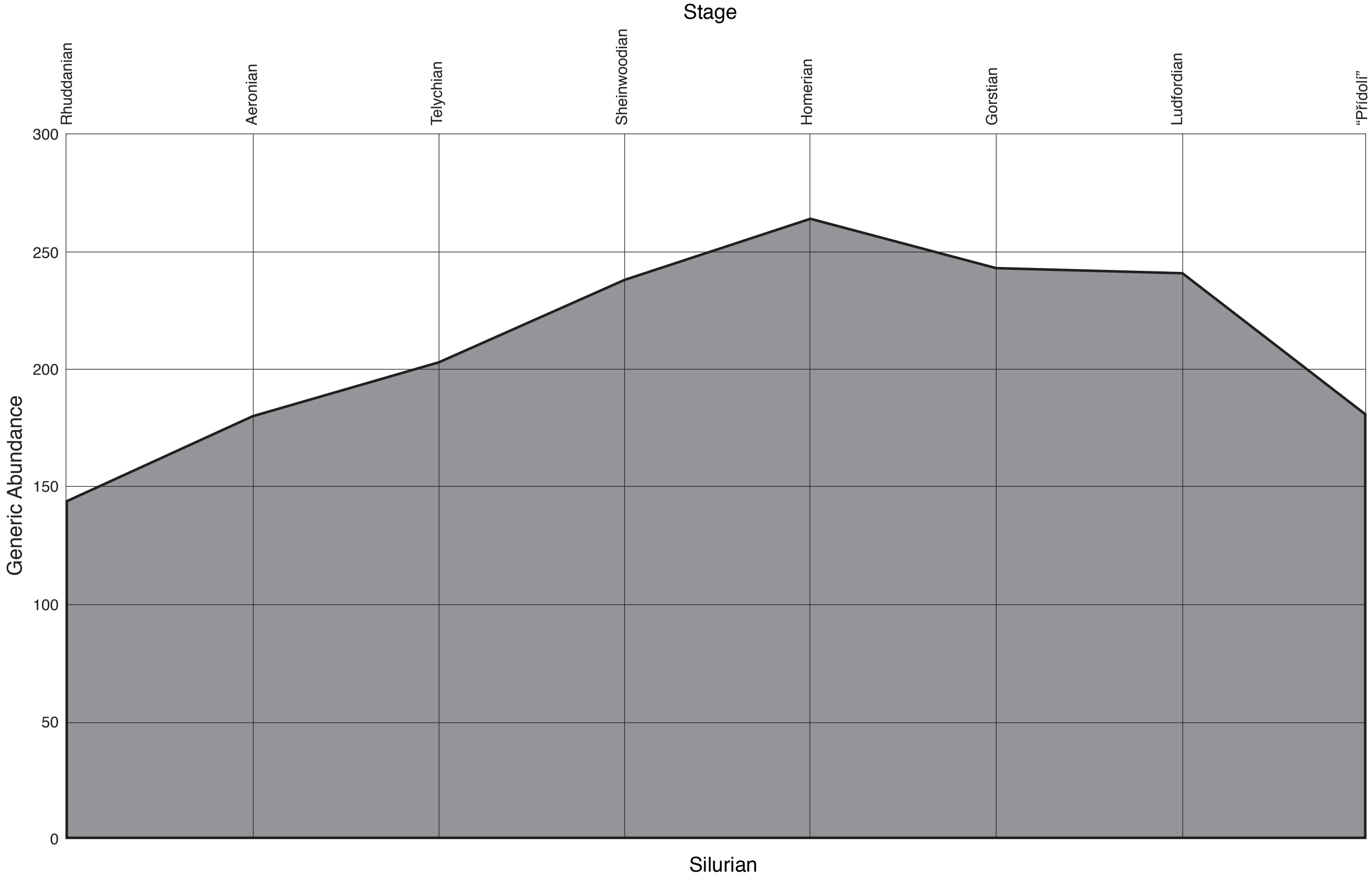


FIG. 1920. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to the Silurian System, with lowermost stage (Rhuddanian) on left-hand side of horizontal axis and uppermost Přídolí Stage on right-hand side. See Table 40 for stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) (new).

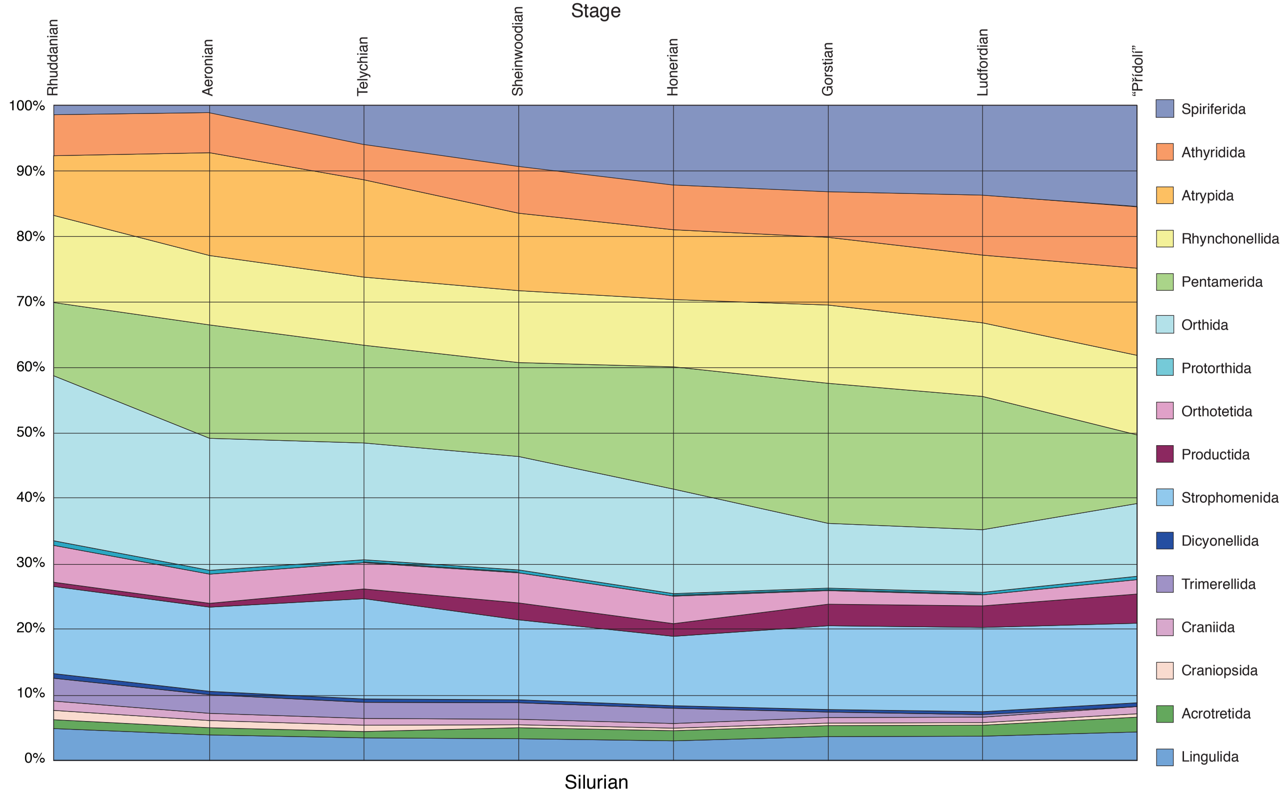


FIG. 1921. Relative proportions of different orders of brachiopod recorded from each of 8 stages of the Silurian System, with lowermost stage (Rhuddanian) on left-hand side of horizontal axis and uppermost stage (Přídolí) on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

they remained the dominant order in the Rhuddanian, but this dominance subsequently declined as the Pentamerida and the Spiriferida became proportionately more significant constituents of the Homerian, Gorstian, and Ludfordian faunas (Fig. 1921). The observed pattern of brachiopod diversity may well be influenced by the evolution of novel and advantageous morphological characters, allowing brachiopods to exploit a wider range of habitats, a phenomenon that will be explored in more detail in the section below dealing with Carboniferous brachiopod diversity.

DEVONIAN SYSTEM

The Devonian System (416.0 ± 2.8 Ma to 359.2 ± 2.5 Ma; Gradstein, Ogg, & Smith, 2004) witnessed two of the most dramatic diversity changes in brachiopod history. Indeed, the most distinctive feature of the system is the fact that not only did the phylum achieve its greatest diversity during the Devonian, but within the system it also suffered one of its greatest declines, second only to that experienced during the mass extinction at the end of the Permian System. These events during the Devonian are unique in brachiopod history, not just in terms of their magnitude, but also because of their stratigraphic and temporal proximity.

Brachiopod diversity increased dramatically during the Lower Devonian, with 266 genera recorded from the Lochkovian Stage, 339 genera from the Pragian Stage, and 460 genera from the Emsian Stage. The latter uppermost Lower Devonian stage records a higher number of brachiopod genera in a single stage than occurs at any other interval of their entire geologic history. In the Middle Devonian the number of brachiopod genera declined significantly and progressively (to 336 genera in the Eifelian and 273 genera in the Givetian), and this trend was continued in the Upper Devonian System, with 206 genera being recorded in the Frasnian and 203 genera in the uppermost Upper Devonian Famennian Stage. Thus, the Devonian System witnessed the greatest recorded diversity of brachiopods, and yet there were fewer brachiopods present at the end of the system than had been present at its beginning (Fig. 1922).

It is also remarkable that the taxonomic diversity of brachiopods, at least at the level of order, changed very little during the expansion and decline of brachiopod diversity during the Devonian. A total of 17 orders are recorded from the entire Devonian System (Fig. 1923), and all 17 of these are present throughout the Lochkovian Stage, the Pragian Stage, and the Emsian Stage. Moreover, they are present in much the same proportions, so the dramatic rise in brachiopod diversity reflects the relative success of a range of orders. Particularly successful, and at least doubling their diversities, were the Strophomenida (increasing from 29 genera in the Lochkovian Stage to 37 in the Pragian Stage and 60 in the Emsian Stage), the Productida (14 genera in the Lochkovian Stage, 31 in the Pragian Stage, 43 in the Emsian Stage), the Spiriferida (40 in the Lochkovian Stage, 70 in the Pragian Stage, 102 in the Emsian Stage), and the Terebratulida (11 in the Lochkovian Stage, 12 in the Pragian Stage, 27 in the Emsian Stage). The Rhynchonellida recorded more modest but still significant proportional increases during the same stages (46 in the Lochkovian, 55 in the Pragian, and 67 in the Emsian). Rhynchonellida genera display an interesting distribution, with a pronounced double peak, each of which involves over 60 genera (a greater number of Rhynchonellida than is present during the Jurassic (a system in which the order achieved a maximum diversity, in any one stage, of 48 genera). Among major groups of brachiopods, only the Orthida failed to capitalize on the rapid expansion of the brachiopods in the Lower Devonian System, and their generic diversities (29 genera in the Lochkovian Stage, 32 in the Pragian Stage, 28 in the Emsian Stage) remained essentially constant during the dramatic rise in the number of genera that culminated during the Emsian Stage.

Thus, the proportions of brachiopod orders remained relatively constant during the Lower Devonian (Fig. 1923). Even in the Middle Devonian, as generic numbers declined, the proportions of the various orders remained fairly constant, marked only by the slight decline of the Pentamerida and Orthida in the Givetian Stage (Fig. 1923) and the increasing proportion of Terebratulida. The Upper Devonian witnessed much greater taxonomic change, with the continuing decline and eventual disappearance of the Pentamerida by the Famennian Stage. The Atrypida, a significant component of brachiopod faunas throughout much of the Devonian System, similarly disappeared at the end of the Frasnian Stage, while the relative contribution of the Strophomenida was greatly reduced during this stage. Several orders that had been present in small numbers also disappeared (the Acrotretida and Protorthida), while the Dictyonellida are only recorded in the Lower Devonian and are not recorded in the Middle or Upper Devonian (although representatives are present in the Lower Carboniferous).

During the Famennian Stage, the relative proportion of nonchonetidine Productida and Spiriferida increased dramatically (Fig. 1923). Despite the fact that the overall number of brachiopod genera decreased significantly, the Productida actually achieved their greatest Devonian diversity during the Famennian Stage (47 genera as compared to 43 during the Emsian Stage), as did the Rhynchonellida with 71 genera from the order being recorded during the Famennian Stage, compared with 67 genera in the Emsian Stage. By contrast, the number of genera of the other major groups of brachiopods present in the Famennian Stage, the Spiriferida had been greatly reduced from their Emsian maximum (42 genera, as compared to 102 genera during the Emsian Stage). The pattern of Terebratulida diversity is also of interest. Having achieved a total of 27 genera in the Emsian Stage, the order achieved a peak of Devonian diversity in the Givetian Stage (33 genera, representing 13% of brachiopods recorded from this stage) before declining drastically to 7 and 3 genera in the Frasnian and Famennian Stages respectively (Fig. 1923).

The Upper Devonian in particular witnessed therefore not only a major reduction of brachiopod genera but also major changes in the relative proportion of different brachiopod groups. Brachiopod faunas at the end of the Devonian were dominated by the Rhynchonellida (35% of the total brachiopod diversity), the Spiriferida (24% of the total), and the Productida (23% of the total, including the Chonetidina as an important suborder at this time). By the end of the system, the number of orders had been reduced to 12.

The Strophomenida is represented in the Devonian Period by both constituent superfamilies, but the Plectambonitoidea died out in the Eifelian, and the Strophomenoidea suffered a major drop in numbers toward the end of the Devonian. The Lower Devonian saw the introduction of two suborders, the Productidina and the Strophalosiidina, which increased in diversity throughout the Devonian System, while the suborder Chonetidina achieved its greatest diversity in terms of the number of genera recorded (39 in the Emsian Stage). In the Famennian, the Protorthida, Pentamerida, and Atrypida died out. The Spiriferinida first appeared near the base of the system, while the Silurian distribution of the Spiriferida reveals a major peak of diversity of 102 genera. The Athyridida continued to increase in numbers from their Silurian high of 22 genera to reach 46 genera by the Emsian Stage, although they declined slightly by the Upper Devonian (Fig. 1921). The Middle Devonian Emsian and Eifelian strata in many places yield well-preserved and readily extractable fossils, so there are well-documented brachiopod faunas from these times when brachiopods were clearly abundant.

The overall pattern of brachiopod diversity during the Devonian has several intriguing aspects. The more rapid diversity

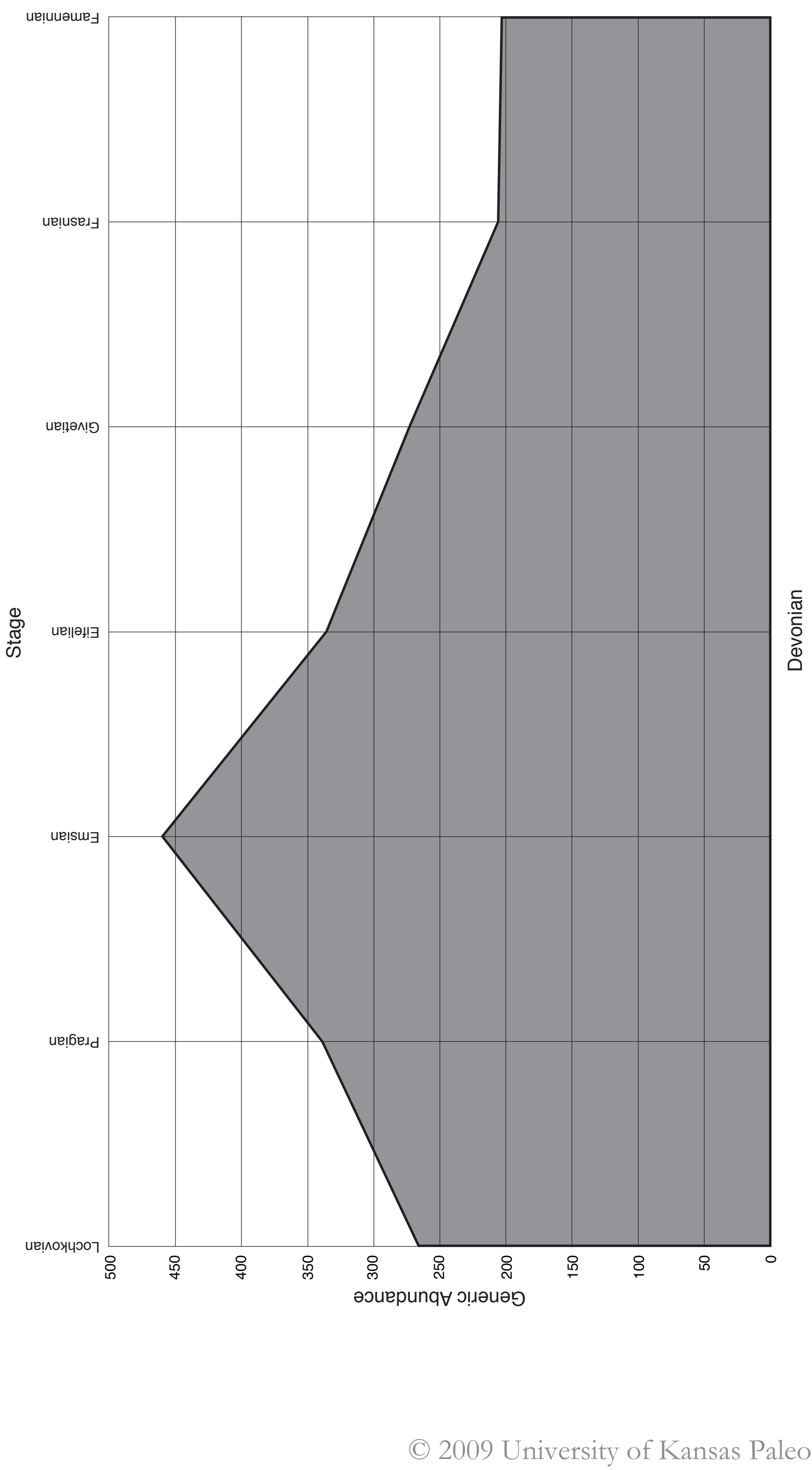


FIG. 1922. Abundance of brachiopods in each of 7 stages (horizontal axis) assigned to the Devonian System, with lowermost stage (Lochkovian) on left-hand side of horizontal axis and uppermost Famennian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

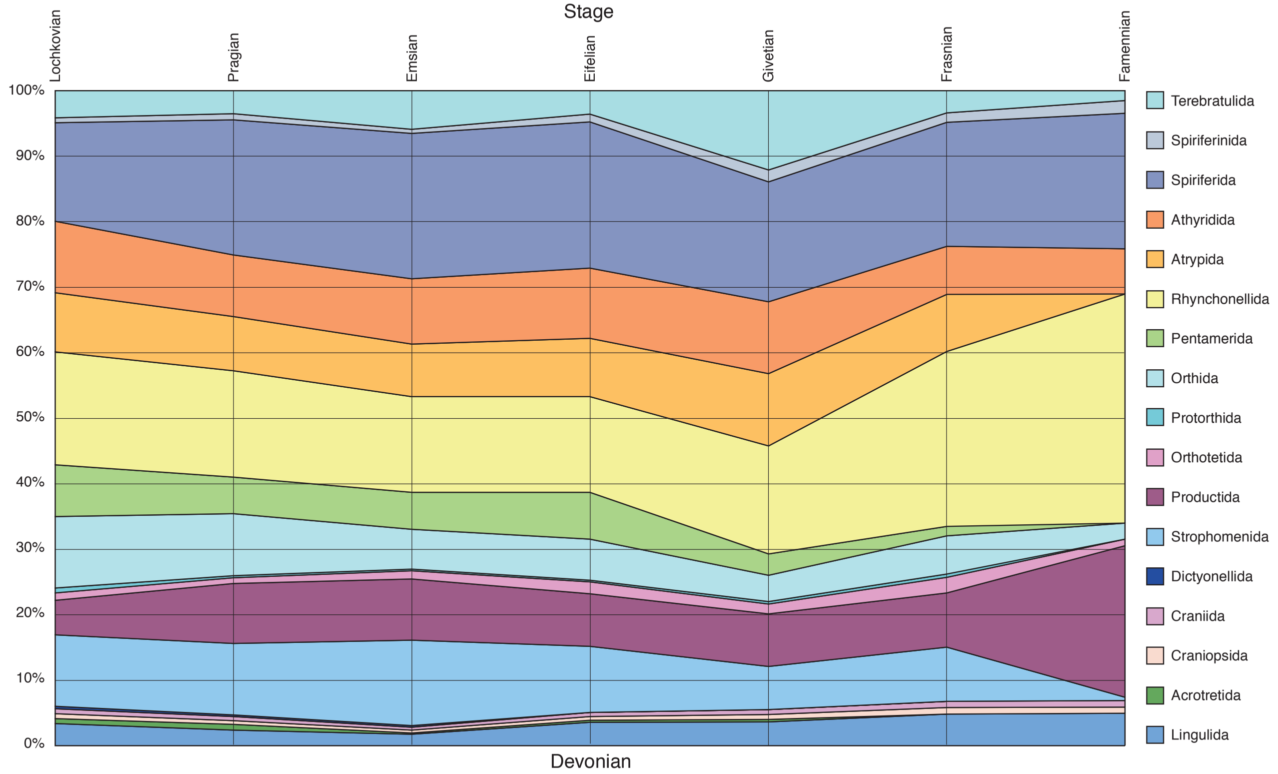


FIG. 1923. Relative proportions of different orders of brachiopods recorded from each of 8 stages of the Devonian System, with lowermost stage (Lochkovian) on left-hand side of horizontal axis and uppermost Famennian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. Some orders recorded in such low numbers that they are difficult to distinguish in diagram (for example, Protorthida, Dictyonellida, Craniida, Craniopsida, and Acrotretida) but are included in diagram to ensure completeness (new).

increase in brachiopod history was due to increasing numbers of the great majority of dominant groups present at the beginning of the system. This diversification event occurred during a period in the history of the Earth that was marked by a series of marine transgressions and regressions. The indications are that brachiopods flourished in the shallow marine habitats that were created during intervals dominated by marine transgressions and that diversities were not noticeably affected, in this analysis, during periods of regression. Of the major brachiopod groups at the time, only the orthids failed to flourish during the Lower Devonian, perhaps indicating that other stocks possessed some competitive edges in terms of ecological adaptation or habitat colonization.

The decline in brachiopod diversity in the Middle and Upper Devonian is equally intriguing. The Devonian did experience fluctuations in the carbon, oxygen, and strontium isotope curves (HAYES, STRAUSS, & KAUFMAN, 1999; VEIZER & others, 1999). These geochemical indicators of significant environmental perturbation do not, however, appear to provide a ready explanation for the decrease in brachiopod diversity. If the oxygen isotope measurements are considered purely as a valid temperature proxy, then oceanic temperatures were somewhat lower during the Middle Devonian than in the Lower Devonian, but they then suggest that global oceanic temperatures warmed again in the Upper Devonian and were similar to those of the Lower Devonian. There were, however, a number of glaciation events during the Upper Devonian.

The Upper Devonian Frasnian to Famennian event has been considered to be the fifth largest extinction event during the Phanerozoic, although a recent reappraisal has suggested that the Givetian Stage, the Frasnian Stage, and the Famennian Stage all had elevated rates of extinction (HOUSE, 2002). If the patterns observed in the brachiopod stratigraphic charts are real, then it does seem that many representatives of the phylum were initially able to exploit favorable conditions in the Lower Devonian but were then drastically reduced in diversity during the Middle and Upper Devonian. HOUSE (2002) noted that there are numerous extinction events during the Devonian and that many of those in the Middle and Upper Devonian in particular are short-term, clearly defined events related to transgressive-regressive cycles, which are marked by the development of anoxic sediments. The timing of such events (in some cases several occur within a single stage) may be related to Milankovitch cyclicity, in the absence of evidence for volcanic or tectonic influences (HOUSE, 2002).

It may also be that the dramatic patterns of brachiopod diversity in the Devonian reflect the existence of good exposures of particularly richly fossiliferous Devonian strata or the culminations of many years of concentrated activity by brachiopodologists on this system. Alternatively, evolutionary innovation at a level below the orders discussed here might help explain the observed patterns: morphological features that may initially have allowed brachiopods to exploit the Devonian seas but were then too specialized to survive the numerous environmental perturbations (such as the development of anoxic events). HOUSE (2002) stressed that the various Devonian extinction events are related to different phases of transgression-regression cycles and probably have multiple causes. Whatever the cause, it is clear that the Devonian System warrants detailed investigation.

CARBONIFEROUS SYSTEM

At the start of the Carboniferous System (359.2 ± 2.5 Ma to 299.0 ± 0.8 Ma; GRADSTEIN, OGG, & SMITH, 2004), there were 13 orders of Brachiopoda, the 12 present in the uppermost Upper Devonian and the Dictyonellida, a few representatives of which had reappeared after the order was absent from the Middle and Upper Devonian (Fig. 1924). The system was dominated by two of the three orders that had been the major

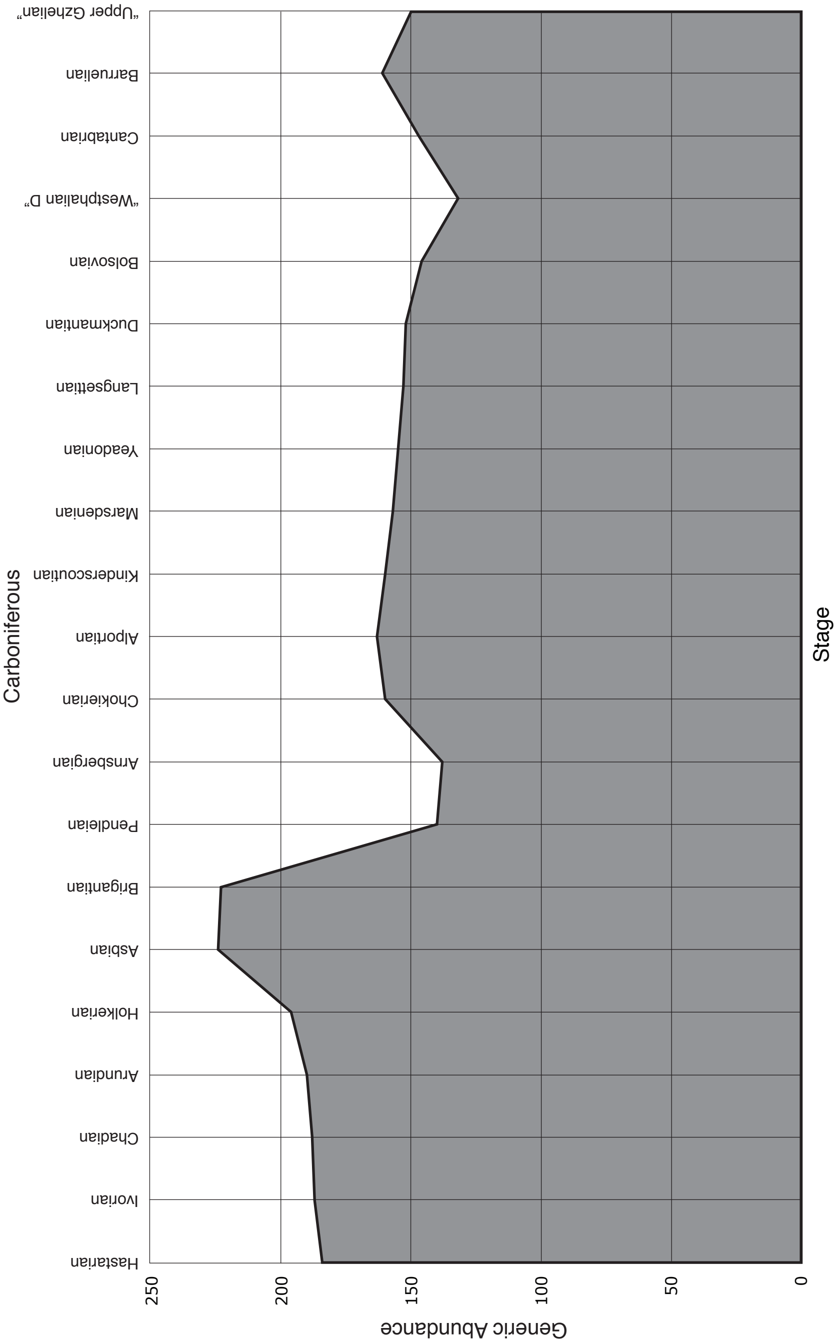


Fig. 1924. Abundance of brachiopods in each of 21 stages (horizontal axis) assigned to Carboniferous System, with lowermost stage (Hastarian) on left-hand side of horizontal axis and uppermost upper Gzhelian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

contributors to brachiopod faunas in the Upper Devonian, namely the Productida (34% of the total number of genera recorded from the entire system) and the Spiriferida (22% of the total number of genera recorded from the Carboniferous). The dominance of the Productida contained representatives of all three constituent suborders (the Productidina, Strophalosiidina, and Chonetidina). All three of these productid suborders waned during the Upper Carboniferous but then increased in generic diversity again during the Gzhelian Stage.

The other dominant order in the Upper Devonian, the Rhynchonellida, declined in numbers drastically at the beginning of the Carboniferous (to represent 16% of the brachiopod fauna in the Hastarian Stage) and declined even further subsequently in the Carboniferous (see Fig. 1926).

The Lingulida and Craniopsida (which died out early in the Carboniferous System), Craniida (with a break in its occurrences in the Upper Carboniferous), and Dictyonellida make up only about 5% of the total brachiopod generic diversity throughout the system (Fig. 1926). In this analysis, the Craniida display the most patchy distribution of any brachiopod order, not only being absent in the great majority of stages in the Upper Carboniferous System (only recorded in the Alportian Stage out of the 12 stages in the Upper Carboniferous), but also lacking any representatives in the Upper Permian System, the entire Triassic System, and being absent from the Lower and Middle Jurassic System (Fig. 1925). Throughout its geologic history the number of Craniida genera has remained very low, reaching a maximum of 5 genera in the uppermost Maastrichtian Stage of the Cretaceous. Taken together, the Terebratulida, Orthida, Spiriferinida, Athyridida, Orthotetida, and Rhynchonellida make up about 39% of the total brachiopods recorded from the Carboniferous System.

During the Carboniferous System the Strophomenida was represented by only a single genus, and the order died out by the Duckmantian Stage. The number of Orthida genera remained almost constant throughout the Carboniferous System, while the Rhynchonellida display a rapid drop from their high in the Devonian and thereafter stabilized in terms of diversity at a plateau of 13 to 16 genera, including 4 endopunctate genera that survived from the Upper Devonian right through to the Upper Permian. The Athyridida show a slow decline throughout the Carboniferous System, with 21 genera in the lowermost Hastarian Stage and only 7 genera by the uppermost upper Gzhelian Stage (Fig. 1926).

In terms of absolute abundances, the generic abundances for the Carboniferous were much lower and much more constant (Fig. 1924) than those for the Devonian, possibly influenced by the fact that the system had been closely subdivided into 21 stages. The overall data show a gradual increase from 184 genera in the lowermost Hastarian Stage of the Carboniferous to a peak of 224 and 223 in the Asbian Stage and the Brigantian Stage respectively (Fig. 1924). This was followed by a sharp decline to 140 and 138 genera, respectively, in the Pendleian Stage and the Arnsbergian Stage, before increasing again, modestly, to remain at 150 to 160 genera for the remainder of the Carboniferous (although the Westphalian D, an unnamed stage in the 1989 IUGS Chart, has only yielded a total of 132 genera).

The initial increase in brachiopod diversity in the Lower Carboniferous can largely be attributed to the success of the Productida, in which the suborder Chonetidina became less abundant, leaving the morphologically diverse true productids to flourish in various environments (Fig. 1926). By the peak of Carboniferous brachiopod diversity, during the Asbian and Brigantian Stages (Fig. 1924, 1926), the Productida had diversified to such an extent that they constituted about half the total brachiopod fauna (in total recording 97 genera out of 224 in the Asbian Stage or 223 in the Brigantian Stage, i.e., 43%). Conversely, by the Chokierian Stage and the Alportian Stage (Fig. 1926), the Productida were still dominant in a fauna that was

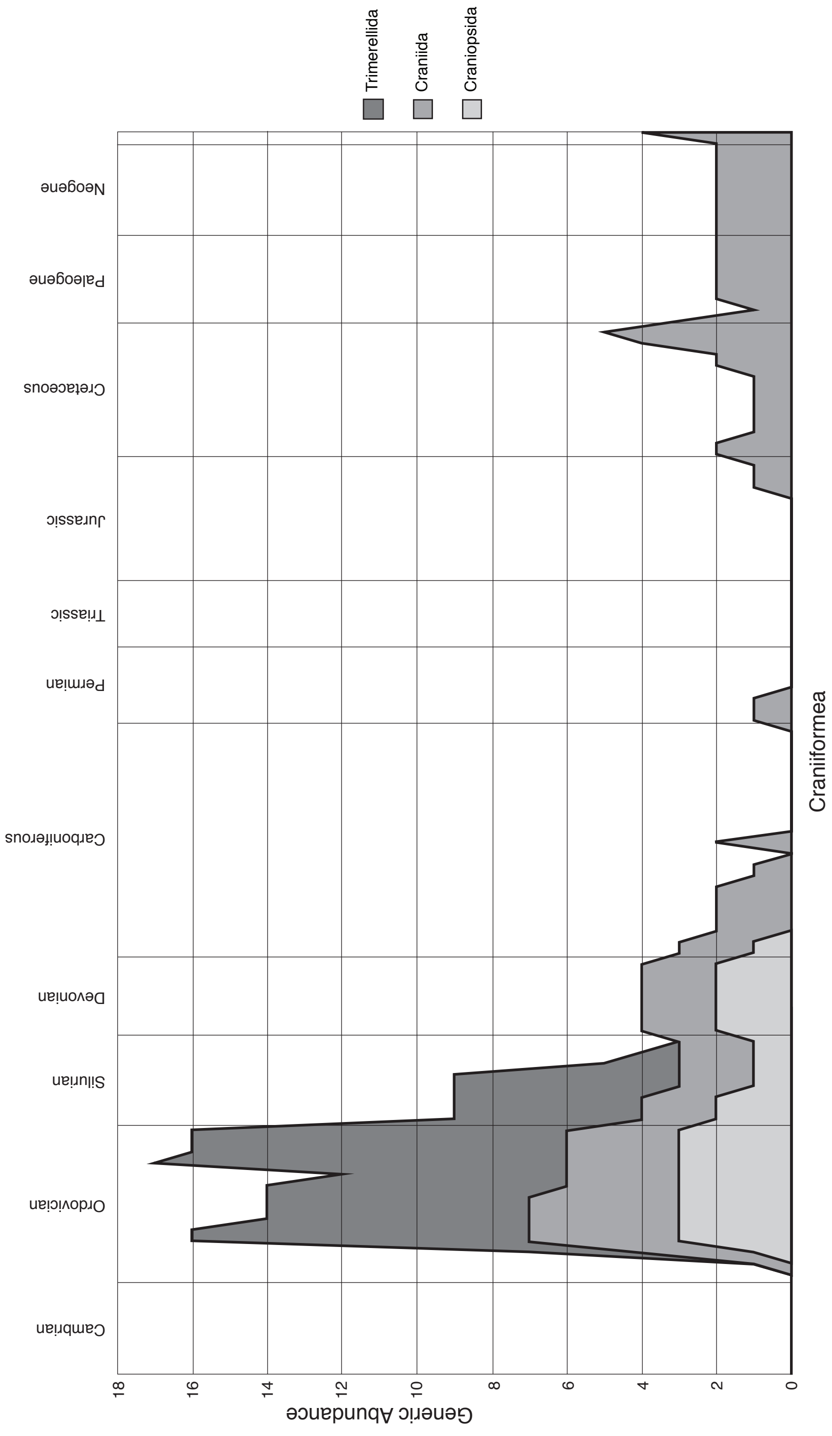


FIG. 1925. Stratigraphic distribution of three orders that comprise subphylum Craniiformea (Trimerellida, Craniida, and Craniopsida). Major gaps are evident in the stratigraphic record of Craniida. Far right, unlabelled segment of diagram portrays distribution in Pleistocene and Holocene stages (new).

considerably reduced in total genera, but the Spiriferida had increased significantly in terms of percentage representation. The total number of Spiriferida genera was virtually identical in the Asbian, Brigantian, Chokierian, and Alportian Stages, but had declined by about a third in the intervening Arnsbergian and Pendleian Stages. This decline is probably linked to the increasingly nonmarine cyclical sedimentation in many areas, leading ultimately to the development of the extensive coal measures that are common throughout the Langsettian Stage to the Westphalian D Stage and obviously led to the disappearance of brachiopods, at least locally.

The differences in diversity and relative proportions may reflect to a certain extent changing sedimentary environments; in Europe at least there is a noticeable change from richly fossiliferous reefal habitats in the Asbian Stage and the Brigantian Stage to more impoverished offshore clastic-dominated environments in the Chokierian and Alportian Stages. From the Chadian Stage to the late Brigantian Stage, warm marine conditions were widespread, with the development of sheet and knoll-like reefs bordering several tectonically controlled blocks. These reefs provided a rich variety of habitats, many of which were exploited by productidines and strophalosiidines, leading to a great variety of morphologies (and taxa) to allow attachment to the varied substrates. Faunas were commonly accessible, readily collected, and, in a few localities, delicately silicified so that paleontologists were able to describe their fossils in detail and great numbers.

The modest peak of 224 genera in the Lower Carboniferous Asbian Stage is surprising in view of the diversity of environments present and the length of time these well-represented rocks have been studied. It seems likely that modern reappraisal of some of these faunas might recognize many more genera than currently listed.

Climate change and associated environmental stress may also have been a factor. The lowermost Lower Carboniferous appears to have been largely ice-free, while subsequently the Carboniferous is characterized by widespread and persistent glaciation, particularly in the southern hemisphere (Mii & others, 2001), during the intervals of Earth history when brachiopod diversity remained low. Rapid shifts in oxygen isotope ratios, including from brachiopod shells (Veizer & others, 1999; Mii & others, 2001) testify to major climatic fluctuations that could well have had a significant influence on brachiopod diversity. Lithologic evidence suggests that glacial and periglacial conditions fluctuated throughout the Early Permian, although there is not universal agreement on this (Dickins, 1996, 2001).

By the end of the Carboniferous System, in the upper Gzhelian Stage, there were 10 orders of extant Brachiopoda. During the Carboniferous the Strophomenida had made their last appearance in the Langsettian Stage, while the Craniopsida barely survived into the Carboniferous and were last recorded in the early Lower Carboniferous Ivorian Stage. As mentioned above, the Craniida have the most disjointed stratigraphic distribution of any brachiopod order (Fig. 1925) and are absent throughout all Upper Carboniferous stages, although they reappear subsequently, and indeed representatives survive to the present day.

PERMIAN SYSTEM

The Permian (299.0 ± 0.8 Ma to 251.0 ± 0.4 Ma; Gradstein, Ogg, & Smith, 2004) is a system of extremes: from ice house to greenhouse, from humid to arid, and from rapid expansion in diversity to one of the largest extinctions recorded in the geologic record. Major excursions in the oxygen, strontium, and carbon isotopic record testify to major environmental perturbations during the Permian (Hayes, Strauss, & Kaufman, 1999; Veizer & others, 1999), yet for much of the system the conditions were conducive for marine life, and brachiopods certainly thrived. Permian reefal facies are present in many parts of the world and appear to

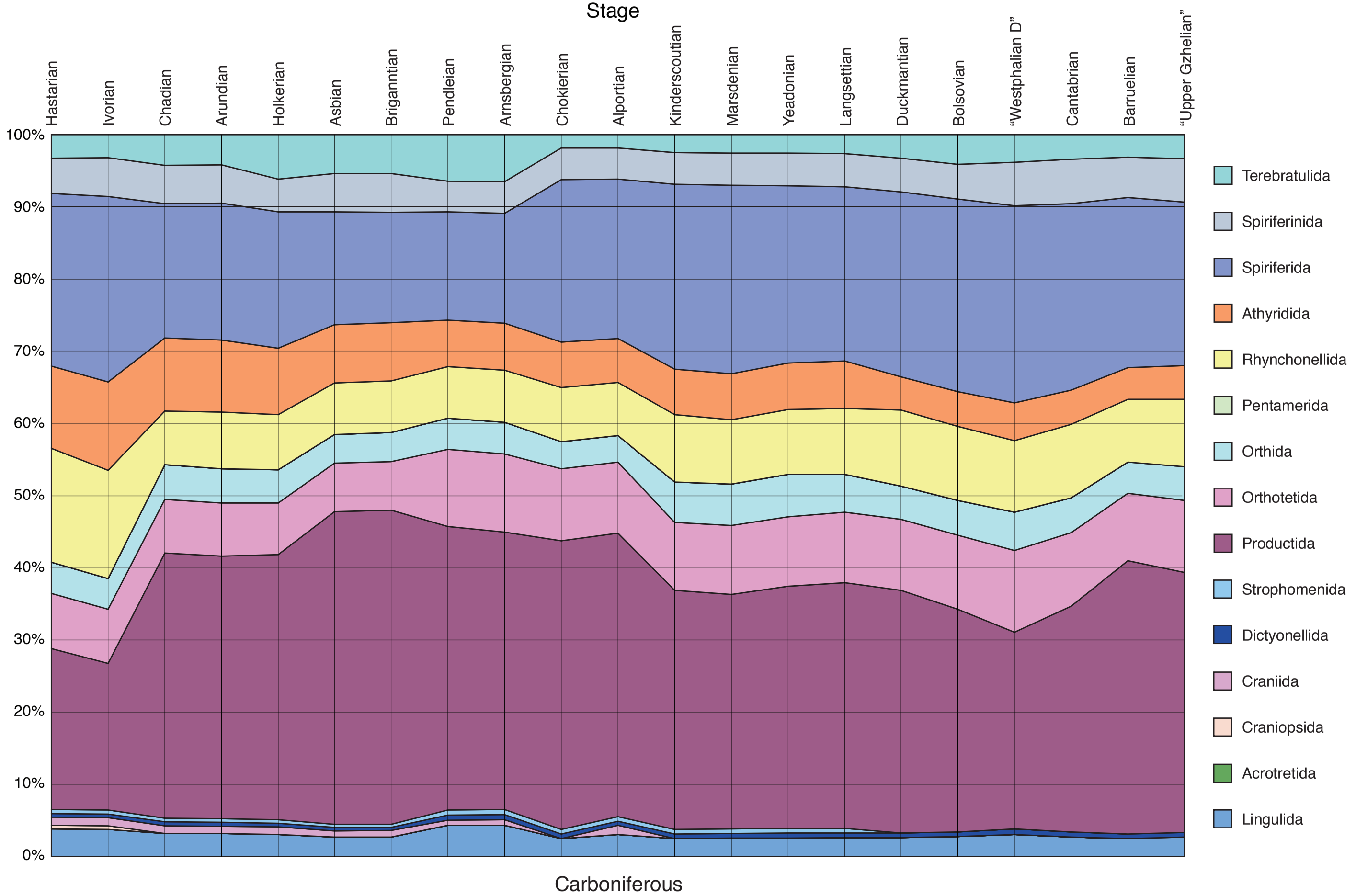


FIG. 1926. Relative proportions of different orders of brachiopod recorded from each of 21 stages of Carboniferous System, with lowermost stage (Hastarian) on left-hand side of horizontal axis and uppermost upper Gzhelian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

have supported diverse brachiopod faunas. Some of the Permian brachiopod fossils are silicified and thus readily extracted almost complete and in large numbers.

Thus, during the Lower Permian, brachiopod diversity climbed steadily to 332 genera in the Roadian Stage, the second highest diversity of brachiopods during their geologic history and more than double the number of genera present throughout most of the Carboniferous Stages. Yet by the end of the Permian System the number of brachiopods was over 100 genera lower than that recorded in the Roadian Stage, the culmination of a decline that started with a very small reduction in the Wordian Stage (to 328 genera), had gathered much greater momentum with the disappearance of 45 genera in the Capitanian Stage (down to 283 genera), and an even more dramatic decline in the Changhsingian Stage (with the disappearance of a further 62 genera to leave a total of 221 genera; Fig. 1927). This was only a precursor to the greatest extinction to affect brachiopods, or indeed many other phyla, as reflected in the number of genera recorded in the succeeding Triassic System (see below).

Representatives of 11 orders are present in the lowermost Asselian Stage of the Permian System, although one of these is the Craniida, which appears impersistently throughout the stratigraphic record and is here only present in the three lowest stages of the Lower Permian. The remaining 10 orders persist throughout the Permian (Fig. 1928). Two of these orders, the Lingulida and the Dictyonellida, are long-ranging groups represented by relatively few genera. The majority of the remaining orders constitute relatively similar proportions of the brachiopod faunas in all seven stages of the Permian, although the Terebratulida increase dramatically in the Upper Permian, contributing a much greater percentage (13%) of the genera in the uppermost Changhsingian Stage of the Upper Permian (up from 5% in the lowermost Asselian Stage of the Permian; Fig. 1928).

The most dramatic feature in the Permian is the major expansion in the numbers of Productida, including the relatively small chonetidine suborder (Fig. 1928). Representatives of the order continue the dominance of brachiopod faunas seen in the Carboniferous, expanding even further during the Permian. 106 genera of Productida were recorded in the lowermost Asselian Stage of the Permian (38% of a total brachiopod fauna of 278 genera; Fig. 1928). By the Roadian Stage of the uppermost Lower Permian, Productida generic numbers had increased to 171 and accounted for 48% of the total brachiopod fauna recovered from this stage (Fig. 1928). Such overwhelming dominance of the faunas continues into the lowermost Upper Permian Wordian Stage (155 genera, equivalent to 50% of a total of 328 genera in this stage). In subsequent stages the number of Productida recorded declines (to 127 genera in the Capitanian Stage and 80 genera in the Changhsingian Stage). Despite this decline in absolute numbers, the Productida remained the dominant order of brachiopods throughout the Permian. In the Changhsingian Stage, for example, the Productida contribute 36% of brachiopod genera, more than double the representation of the two other high-abundance orders (the Spiriferida at 16% and the Terebratulida at 13%; Fig. 1928).

A dramatic change in the taxonomic components of brachiopod faunas occurred between the Roadian and the Changhsingian Stages (Fig. 1928). The reduction in Productida (in both absolute number of genera and percentage of the total number of brachiopods) may reflect a life-style of strong substrate attachment that was more successful in the carbonate-dominated Roadian Stage than in the Changhsingian Stage when clastic deposition was more widespread. Such a phenomenon could also help explain the doubling of the number of Terebratulida genera (to 29 genera [13%] in the Changhsingian Stage from 15 in the Roadian Stage [5%] during a period in which the overall number of brachiopods dropped by a third. The pedunculate lifestyle of the Terebratulida may well be more suitable for clastic-dominated environments, compared to the free-living or closely attached Productida life habit that proved so successful during the Roadian Stage with its firm reefal substrates. SHEN and SHI (1996) discussed the diversification and extinction patterns of Permian brachiopods from southern China.

During the Lower Permian the global climates gradually warmed from the glacial conditions that prevailed during the Upper Carboniferous. It was during these favourable conditions that the Permian expansion in brachiopod diversity occurred. It has been suggested that the peak of brachiopod diversity in the Middle Permian was related to the closing ocean between the converging Indian and Eurasian tectonic plates. As conditions warmed after a colder interval in Earth history, the development of abundant islands and small terranes would have provided numerous ideal environments for brachiopods to proliferate. The absolute peak in brachiopod diversity in the Roadian Stage actually occurred during an interval of Earth history when the global climates were showing signs of cooling again (i.e., the global oxygen isotope curve; VEIZER & others, 1999), and indeed there is localized evidence of further and very significant cooling after the Roadian Stage (GRADSTEIN, OGG, & SMITH, 2004).

Although there are good grounds for accepting the validity of the Permian for demonstrating the greatest ever brachiopod diversity, there are also indications that this is perhaps the best example of the significant effect that excellent preservation and human effort can have on the recorded stratigraphic distribution of the brachiopods. The rich brachiopod faunas of the reefal lithologies in the Glass Mountains, Texas, United States, have been preserved in superb detail by silicification, which allows them to be extracted from carbonate rocks by dissolution of the matrix using dilute acid. Such preservation should allow a much greater proportion of the fauna to be recovered than is the case with clastic sediments. The descriptions of the Glass Mountain faunas mainly cover the Artinskian to the Wordian Stages, with a peak in the Roadian Stage (and hence closely follows the overall pattern of brachiopod diversity during the Permian System). Here, as in the Lower Carboniferous, the reefal environments supported large proportions of productidines and strophalosiidines, together with richthofeniids and lyttoniids, all of which display an array of morphological adaptations fitting them to their particular habitats. The numbers of genera described by COOPER and GRANT from the Glass Mountains (COOPER & GRANT, 1969, 1974, 1975, 1976a, 1976b) were prodigious. Other Permian brachiopod specialists have contributed many generic names from other geographic areas, adding to the scale of the mid-Permian peak. The question is whether these high diversity numbers are biologically realistic in areas of high productivity, or whether they present a more or less artificial picture of diversity due to the acutely tuned differentiation of morphological features resulting from excellent preservation and intense research work by numerous experts?

PERMO-TRIASSIC EXTINCTION EVENT

The most dramatic event in brachiopod history occurred at the Permian-Triassic boundary. In a global event affecting many other phyla, brachiopod diversity was decimated, literally, by the greatest mass extinction during the Phanerozoic. Only 22 genera are recorded in the lowermost Scythian Stage of the Triassic (Fig. 1929), compared with 221 genera in the uppermost Changhsingian Stage of the Permian System. The situation may be even more dramatic as only 4 of the 22 genera recorded from the Scythian Stage range through from older stages. The remainder presumably evolved during the Scythian (although such a small number may reflect human bias in that investigators may well expect to encounter new genera

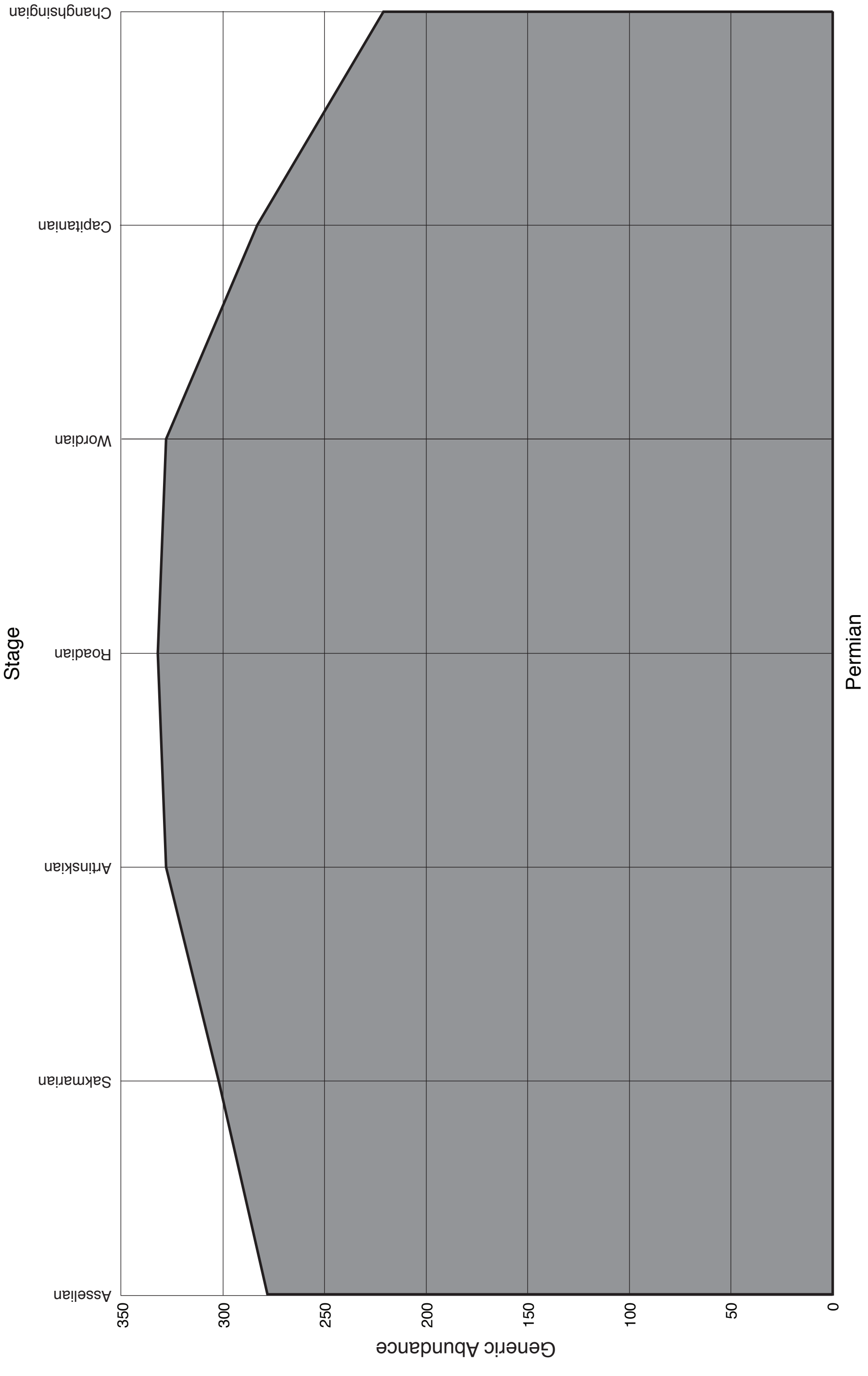


FIG. 1927. Abundance of brachiopods in each of seven stages (horizontal axis) assigned to Permian System, with lowermost stage (Asselian) on left-hand side of horizontal axis and uppermost Changhsingian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

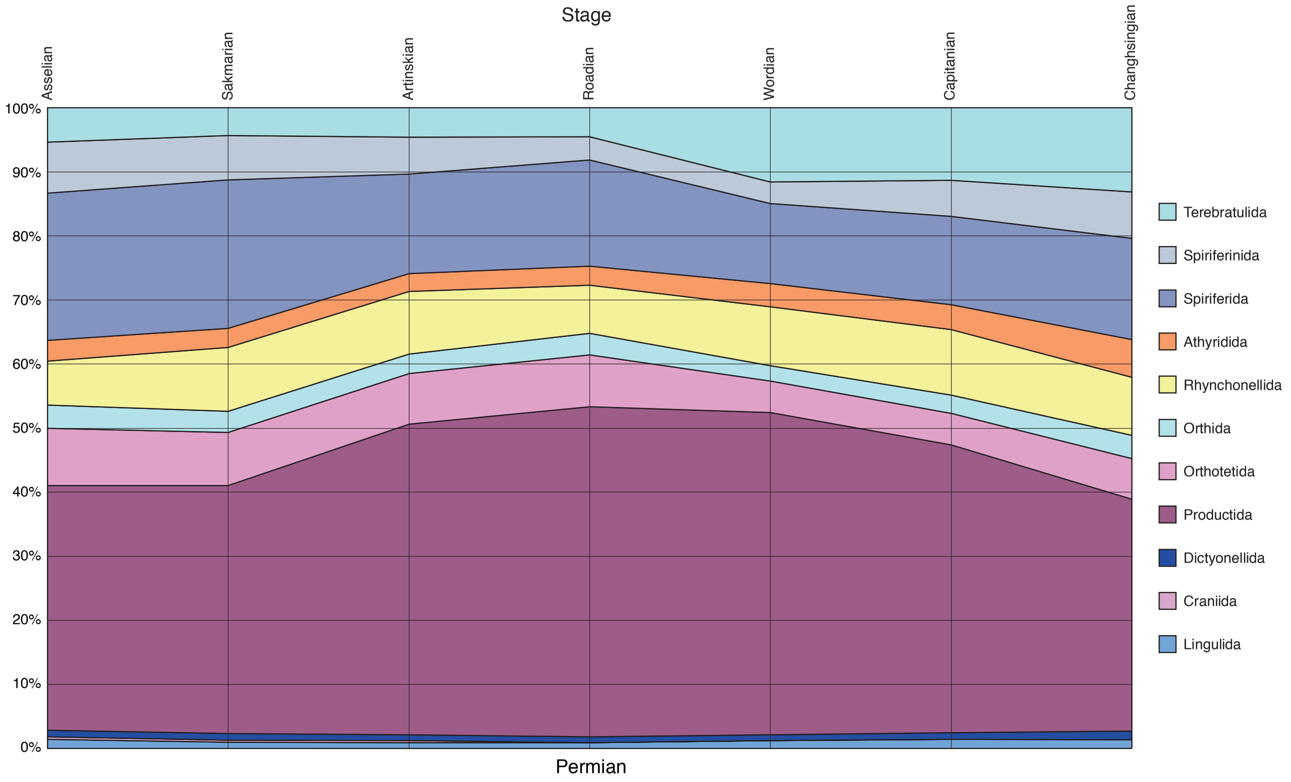


FIG. 1928. Relative proportions of different orders of brachiopod recorded from each of 7 stages of Permian System, with lowermost stage (Asselian) on left-hand side of horizontal axis and uppermost Changhsingian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present. One order (Craniida) is recorded in such low numbers that it is difficult to distinguish but is included in the diagram to ensure completeness (new).

immediately following such a major extinction). Furthermore, 4 genera are only listed as being present in the Triassic and hence may or may not be present in the Scythian Stage. Indeed, recent evidence from Shen and others (2006) indicates that among the brachiopods only lingulids may have crossed the actual boundary, as it is exposed in northern Italy and southern China. Therefore, during the Scythian Stage there may have been as few as 18 brachiopod genera on Earth, and some of these may have evolved during the 10-million-year extent of the stage as it was defined in the 1989 IUGS Chart (although in the most recent review, the stage had been subdivided into two stages, the Induan Stage and the Olenekian Stage, and the absolute age range of the pre-Anisian Stage Triassic successions has been reduced to approximately 6 million years; Gradstein, Ogg, & Smith, 2004).

If extraordinarily low numbers of brachiopods did survive the transition from the Permian to the Triassic, then the pace of generic reintroduction after the mass extinction must have been rapid. The data presented here suggests that a number of brachiopod orders display continuity through the Permian-Triassic crisis (such as the Athyridida). Furthermore, the Spiriferida increased its generic diversity from the Carboniferous into the Permian and did not die out until the end of the lower Triassic.

The causes of the Permian-Triassic extinction event have been much debated and appear complex (Wignall, 2001; Erwin, Bowring, & Jin, 2002; Shen & others, 2006). Current explanations suggest that rapid warming during the Late Permian (possibly associated with the formation of the supercontinent Pangea), interspersed with short intervals of pronounced cooling (due to the eruption of extensive basalts in what is now Siberia), were major controlling factors in the mass extinction. The effects of poorly oxygenated waters spreading over areas of shallow seas, of the type inhabited by brachiopods, has also been implicated (Wignall & Hallam, 1992). Whatever the causes, there is extensive evidence of major environmental change and faunal turnover at the Permian-Triassic boundary, although geochemical evidence suggests that this was only the culmination of severe climatic and biological perturbations that are evident in the Late Permian. There is a major carbon isotope excursion in the Changhsingian Stage, for example, testifying to major changes in the biogeochemical cycling of carbon, which is almost certainly related to the extinction.

Taking the reduction of brachiopod generic abundances at face value may be an oversimplification, however. A high proportion of taxa (up to 50%) that apparently become extinct at the Permian-Triassic boundary reappear later in the stratigraphic record (so-called Lazarus taxa; Erwin, Bowring, & Jin, 2002), demonstrating the imperfection of the fossil record and the effects of exposure and taxonomic practice. Certainly, brachiopod diversity does increase subsequently, to 117 genera in the middle Upper Triassic Norian Stage.

Whatever the cause and the true extent of brachiopod mass extinction at the generic level, there is no doubt that the phylum underwent a major decline, one from which it never recovered. Certainly, the brachiopods were never again to dominate global benthic marine communities to the extent that was evident during the Paleozoic. The number of genera recorded in the Scythian Stage is the lowest of any stage in their entire geologic history, and if the *Treatise* data are representative, then there are more than five times the number of genera present in today's oceans, where the phylum has a very low profile. Once again, however, the apparent significant rise in brachiopod generic diversity from the Pleistocene to the present day (Fig. 1912, and discussed below) is almost certainly a clear demonstration of the imperfection of the fossil record, and the concentration of human interest, rather that an indication of a revival of fortune for the phylum.

TRIASSIC SYSTEM

In the Triassic System (251.0 ± 0.4 Ma to 199.6 ± 0.6 Ma; Gradstein, Ogg, & Smith, 2004), four of the ten orders recorded from the uppermost Changhsingian Stage of the Permian System had disappeared, and the Craniida, which have a particularly patchy stratigraphic record (Fig. 1925), were also absent. The four orders that had disappeared were the Orthida, Orthotetida, Dictyonellida, and Productida (although some workers argue that there was a small holdover from the Permian by the Productida [Shen & others, 2006], but evidence is scant and much appears to depend upon the exact timing of the main extinction episodes as compared to the end of the Permian). These orders represented, respectively, 4%, 6%, 1%, and 36% of the Upper Permian Changhsingian Stage brachiopod faunas. There is a record of 8 productid species surviving into the Triassic, at least in China (Shen & Shi, 1996), but these records are not present in the *Treatise* data summarized here.

The *Treatise* data indicate that a total of six brachiopod orders are unequivocally represented in the lowermost Scythian Stage of the Triassic System (Fig. 1930), and major taxonomic components of all Mesozoic and subsequent brachiopod faunas have become established. By the beginning of the Triassic System all the major Paleozoic brachiopod orders had disappeared. Although not as numerically significant as the Productida, Orthida, Spiriferida, or Pentamerida, the Rhynchonellida did survive and continue to the present day.

The genera that survived the mass extinction are predominantly the Terebratulida and Rhynchonellida, two orders that, along with the long-lived Lingulida and the inconsistently recorded Craniida, survive to the present day. By the Upper Triassic Carnian Stage, the Thecideida, an order that also survives to the present day in small numbers, had appeared. A further two orders that have no living relatives survived the mass extinction, namely the Spiriferinida and the Athyridida. The Spiriferinida in particular thrived in all post-Scythian Stages of the Triassic System (Fig. 1930). The nonpunctate Athyrididina and the endopunctate Retziidina within the Athyridida died out by the end of the Triassic (in the upper Norian Stage). Only the distinctive koninckinidines have been definitely recorded in the Lower Jurassic. Another order, the Craniida, has been recorded in systems before and after, but not in, the Triassic System (Fig. 1925).

In terms of absolute generic numbers, brachiopods actually staged a modest but sustained recovery during the Triassic, to such an extent that 117 genera were present during the penultimate Norian Stage of the Upper Triassic (Fig. 1929–1930). The faunas of the Norian were dominated by the Rhynchonellida (30 genera: 26% of the total fauna) and the Terebratulida (36 genera: 31%), and these two orders remained dominant throughout the Mesozoic and up to the present day. The Spiriferinida also remained a major contributor to Triassic faunas, accounting for 25% of the genera recorded (29 out of a total of 117 genera recorded from the Norian Stage). The Athyridida were also well represented, with 16 genera in the Norian Stage representing 14% of the fauna. Indeed, combining all stages of the Triassic, the Spiriferinida were the most abundant order (29% of the total fauna), followed in descending order (based on percentage contribution to the total Triassic fauna), by the Terebratulida (25%), Rhynchonellida (24%), and Athyridida (16%; Fig. 1930).

The uppermost Rhaetian Stage of the Triassic witnessed a significant drop in brachiopod diversity, with the total number of genera dropping by 32 (to 85) as

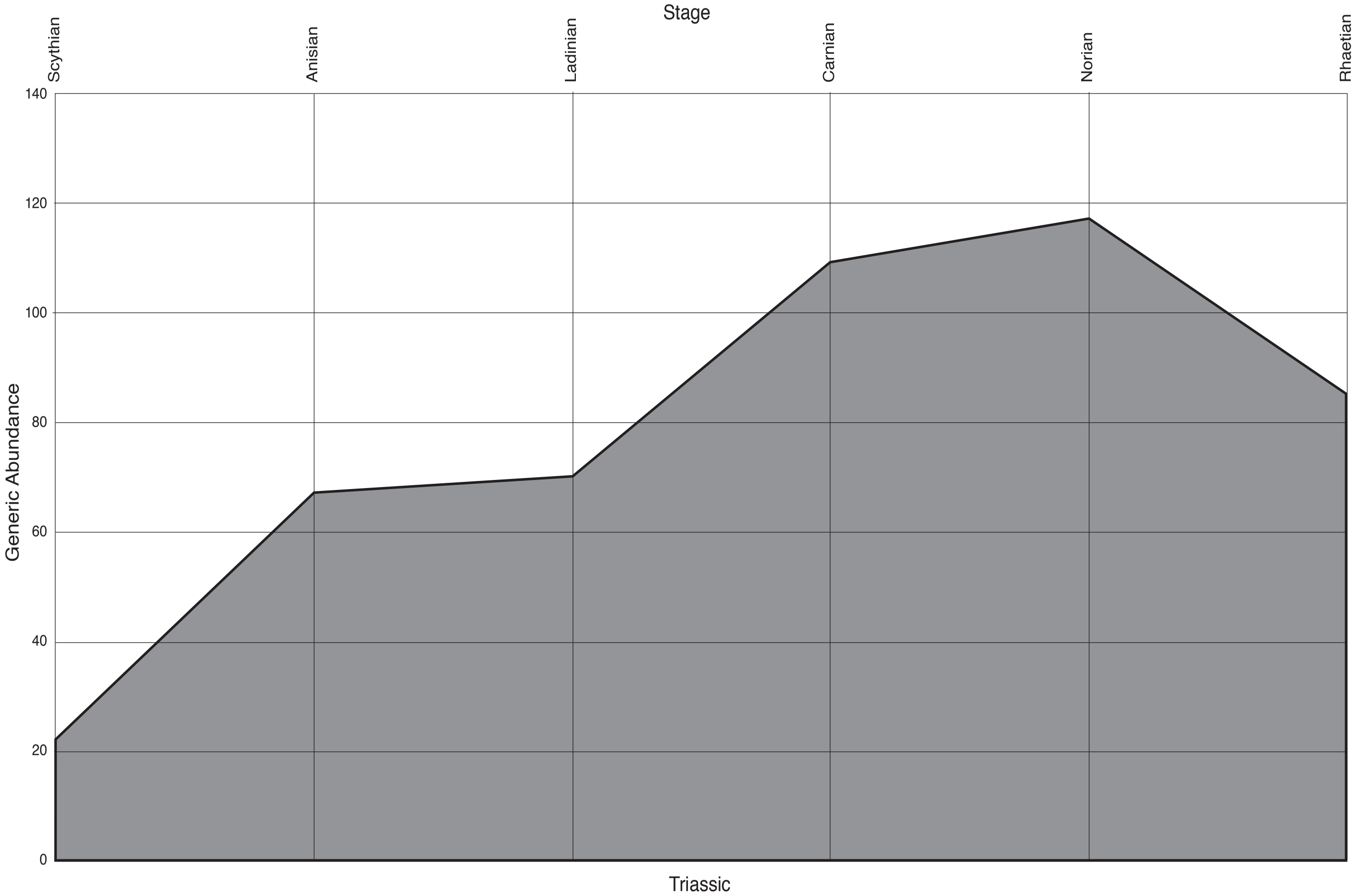


Fig. 1929. Abundance of brachiopods in each of 6 stages (horizontal axis) assigned to Triassic System, with lowermost stage (Scythian) on left-hand side of horizontal axis and uppermost Rhaetian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

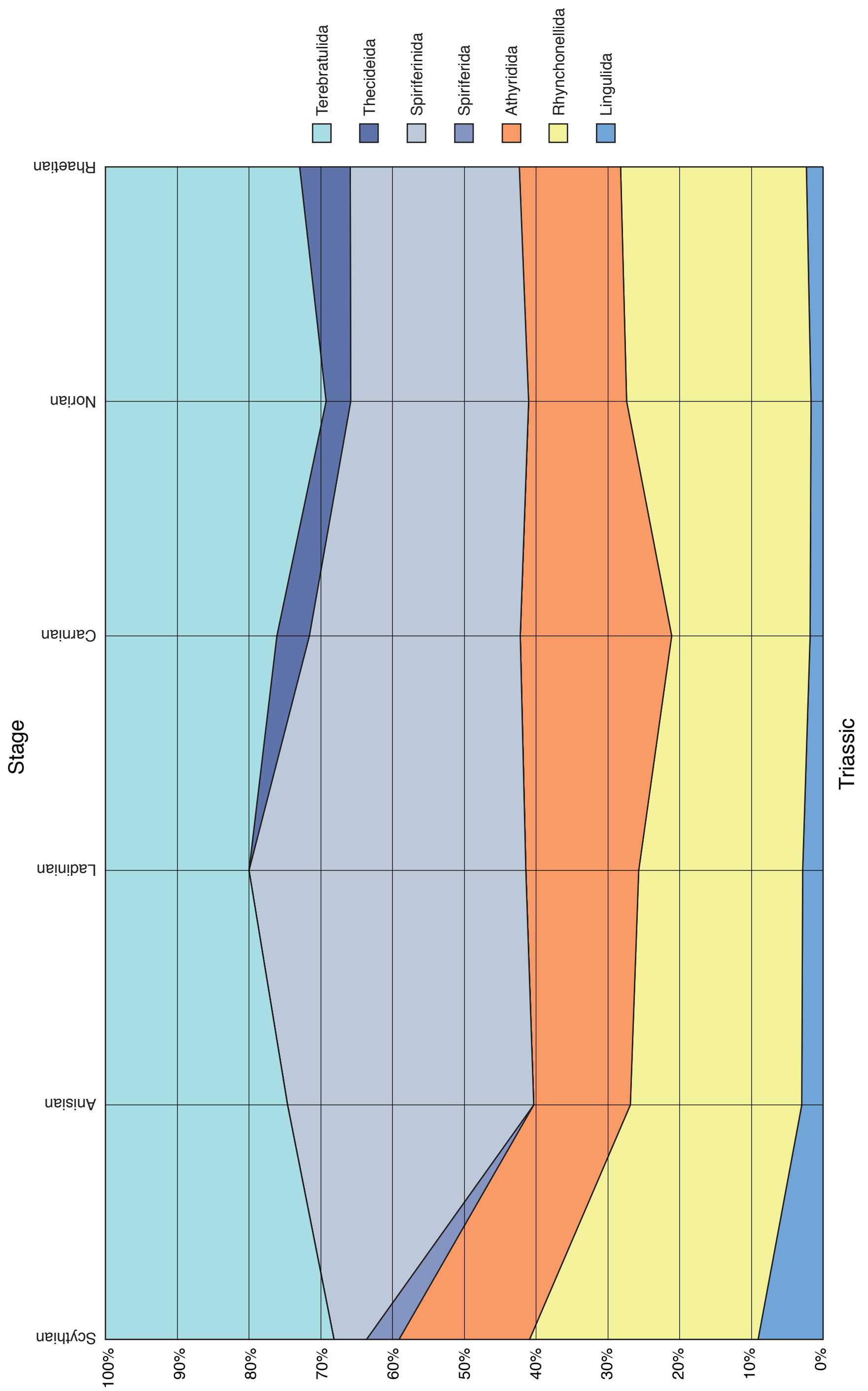


Fig. 1930. Relative proportions of different orders of brachiopods recorded from each of 6 stages of Triassic System, with lowermost stage (Scythian) on left-hand side of horizontal axis and uppermost Rhaetian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

compared with the preceding Norian Stage. This reduction affected all major groups of Triassic Brachiopoda: the Terebratulida (down to 23 in the Rhaetian Stage from 36 in the Norian Stage), Rhynchonellida (down to 22 in the Rhaetian Stage from 30 in the Norian Stage), Spiriferinida (down to 20 in the Rhaetian Stage from 29 in the Norian Stage), and Athyridida (down to 12 in the Rhaetian Stage from 16 in the Norian Stage). By contrast, the recently evolved Thecideida showed an increase from 4 genera in the Norian Stage to 6 in the Rhaetian Stage. The Lingulida are represented by two genera in all Triassic stages. In terms of percentages, most groups of brachiopods were affected equally by the decline in the Rhaetian Stage, with perhaps the Terebratulida being the most strongly affected (down to 27% of the fauna in the Rhaetian Stage from 31% of the fauna in the Norian Stage).

This apparent decline is not accompanied by any known geochemical perturbation that might indicate some environmental shift that could have had a negative impact on brachiopod diversities in the Rhaetian Stage. Indeed, this apparent decline could well demonstrate an artefact of the stratigraphic process. In the 1989 stratigraphic chart, the Rhaetian Stage was considered to have an absolute age range from around 210 to 205 Ma, in effect lasting for 5 million years, while the Norian Stage represented 10 million years of geologic history (220 to 210 Ma). This discrepancy is even greater in the most recent revision of the geologic time scale (GRADSTEIN, OGG, & SMITH, 2004), in which the absolute range of the Norian Stage is extended to 13 million years (from 216.5 Ma to 203.5 Ma), while that of the Rhaetian Stage has been reduced to approximately 4 million years (203.5 to 199.6 Ma). The Norian Stage has a duration that is comparable to that of all other Triassic stages, suggesting that the steady increase in brachiopod generic abundance up to the Norian Stage probably does reflect a genuine progressive recovery of the phylum from the Permo-Triassic mass extinction. The abnormally short duration of the Rhaetian Stage, however, may be a contributing factor in the apparent decline in generic diversity recorded in this stage. The succeeding Hettangian Stage of the Jurassic, in common with many Jurassic stages, also has a relatively short absolute time range (Table 40). A total of 26 genera recorded from the Hettangian Stage appear for the first time in this basal Jurassic stage, compared with only 14 that range through from the uppermost Triassic Rhaetian Stage. Therefore, if the two stages were combined into a single stratigraphic entity, approximately comparable in duration to the preceding Triassic stages (9 million years as compared with 10 million years for the Norian and Carnian Stages), then the total number of genera recorded would be 111 (as compared with 112 in the Norian Stage and 106 in the Carnian Stage). There is nevertheless a sustained decline in brachiopod diversity in post-Hettangian Stages during the Lower Jurassic, and it was not until the Middle Jurassic that the total number of genera achieved levels comparable to those that prevailed during most of the Upper Triassic (see below).

JURASSIC SYSTEM

In the Jurassic System (199.6 ± 0.6 Ma to 145.5 ± 4.0 Ma; GRADSTEIN, OGG, & SMITH, 2004), the four stages of the lower series saw brachiopod diversities reach a maximum of 84 genera in the Pliensbachian Stage, having increased from 46 genera in the Hettangian Stage, and 65 genera in the Sinemurian Stage. During the uppermost Toarcian Stage of the Lower Jurassic, the number of genera declined slightly to 75 genera (Fig. 1931). This level of diversity was sustained in the lowermost Aalenian Stage of the Middle Jurassic (with 75 genera), increased to 109 genera in the Bajocian, and reached a maximum, for the Jurassic, of 114 genera in the Bathonian Stage. The succeeding Callovian Stage, the uppermost Middle Jurassic stage, recorded 105 brachiopod genera. Never again in any younger stage during their subsequent geologic history would there be more than 100 brachiopod genera (with the exception of the Holocene stage, which is anomalous for a paleontological analysis, in that it includes all the taxa described in the present oceans; see below). The three stages of the Upper Jurassic witnessed the onset of the decline, with a steady decrease in brachiopod diversity from 86 genera in the Oxfordian Stage, to 74 genera in the Kimmeridgian Stage, and finally to 67 genera in the Tithonian Stage (the uppermost stage of the Jurassic System; Fig. 1931).

In brachiopod terms, the Jurassic is the age of the Terebratulida and the Rhynchonellida (Fig. 1932). The proportion of Jurassic faunas represented by the Terebratulida increases steadily, from 43% in the lowermost Hettangian Stage of the Jurassic to 67% in the uppermost Tithonian Stage of the Jurassic. The predominance of the Rhynchonellida fluctuates much more, from a low of 25% in the uppermost Upper Jurassic Tithonian Stage and 26% in the lowermost Lower Jurassic Hettangian Stage to a high of 42% of the brachiopod fauna in the Bathonian Stage and 43% in the Aalenian Stage (Fig. 1932). In the Sinemurian Stage, the Rhynchonellida actually contributed a greater percentage of the fauna (26 genera representing 40% of the fauna) than the Terebratulida (25 genera representing 38% of the fauna). By the three stages of the Upper Jurassic however, the Rhynchonellida contribution to the fauna had declined to between 28% and 27% of the brachiopod faunas, with a total of 23 genera in the Oxfordian Stage, 19 genera in the Kimmeridgian, and 17 genera in the uppermost Upper Jurassic Tithonian Stage (Fig. 1932).

The same 6 orders that were present in the Upper Triassic were present throughout the Lower Jurassic (Fig. 1932). The ever-present Lingulida are represented by their customary small number of genera, while the Thecideida, which first evolved in the Triassic System, maintained a consistent presence in all Jurassic stages, although represented by only a few genera (ranging from a maximum of 5 in the Toarcian, Aalenian, and Bajocian Stages to a minimum of 2 in the Kimmeridgian and Tithonian Stages).

The Spiriferinida survived as significant constituents of brachiopod faunas throughout the Lower Jurassic (6 genera in all three stages), but disappear from the geologic record by the lowermost mid-Jurassic Aalenian Stage (Fig. 1932). The Athyridida have a similar history, although represented by only three genera throughout the Lower Jurassic (all included in the suborder Koninckinidina). The last appearance of both orders in the uppermost Lower Jurassic Toarcian Stage therefore coincides with the trough in the distribution curve in the succeeding Aalenian stage (Fig. 1931). The predominance of Terebratulida and Rhynchonellida was therefore well established by the beginning of the Middle Jurassic (Fig. 1932). The increase in the absolute abundance of brachiopods recorded in the Bajocian and Bathonian Stages is almost entirely due to the success of the Terebratulida, which almost doubled in diversity between the Aalenian and the Bajocian Stages (from 35 to 60 genera). Rhynchonellida generic abundances increased only slightly in these stages (32 genera in the Aalenian Stage and 39 in the Bajocian Stage). The impersistent Craniida reappeared in the Upper Jurassic Oxfordian Stage (Fig. 1925) but are represented by only 1 genus throughout the last three stages of the Upper Jurassic. Accordingly, by the end of the Jurassic there were 5 orders present, although the Terebratulida and Rhynchonellida so dominated faunas that together they contributed 92% of the genera recorded from the uppermost Tithonian Stage. These five orders all survive to the present day, in much the same proportions as were evident during the Middle and Upper Jurassic, a period of around 175 million years (GRADSTEIN, OGG, & SMITH, 2004).

For brachiopods, the most dramatic phenomena during the Jurassic were the events during the Toarcian Stage that may

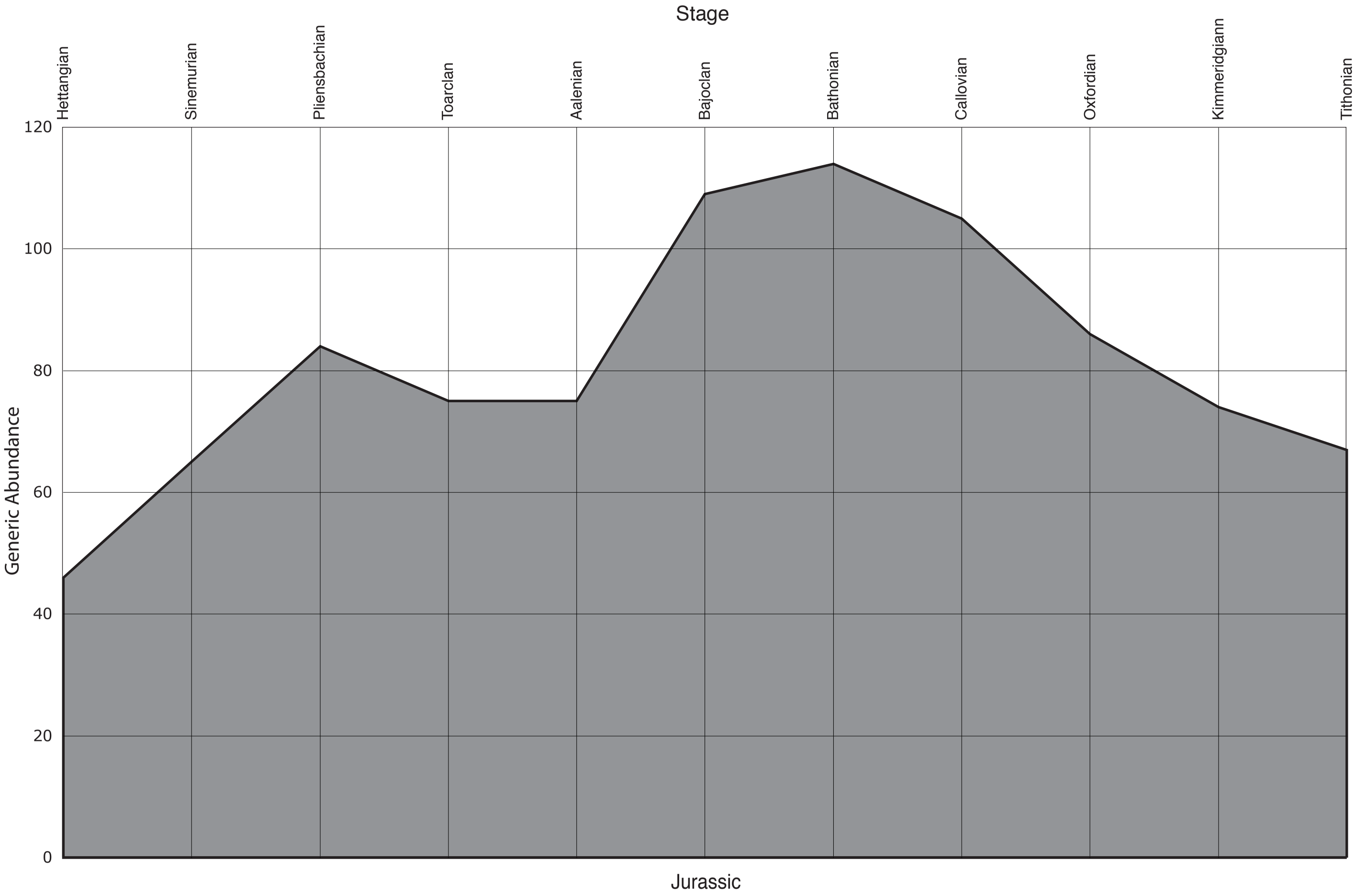


FIG. 1931. Abundance of brachiopods in each of 11 stages (horizontal axis) assigned to Jurassic System, with lowermost stage (Hettangian) on left-hand side of horizontal axis and uppermost Tithonian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

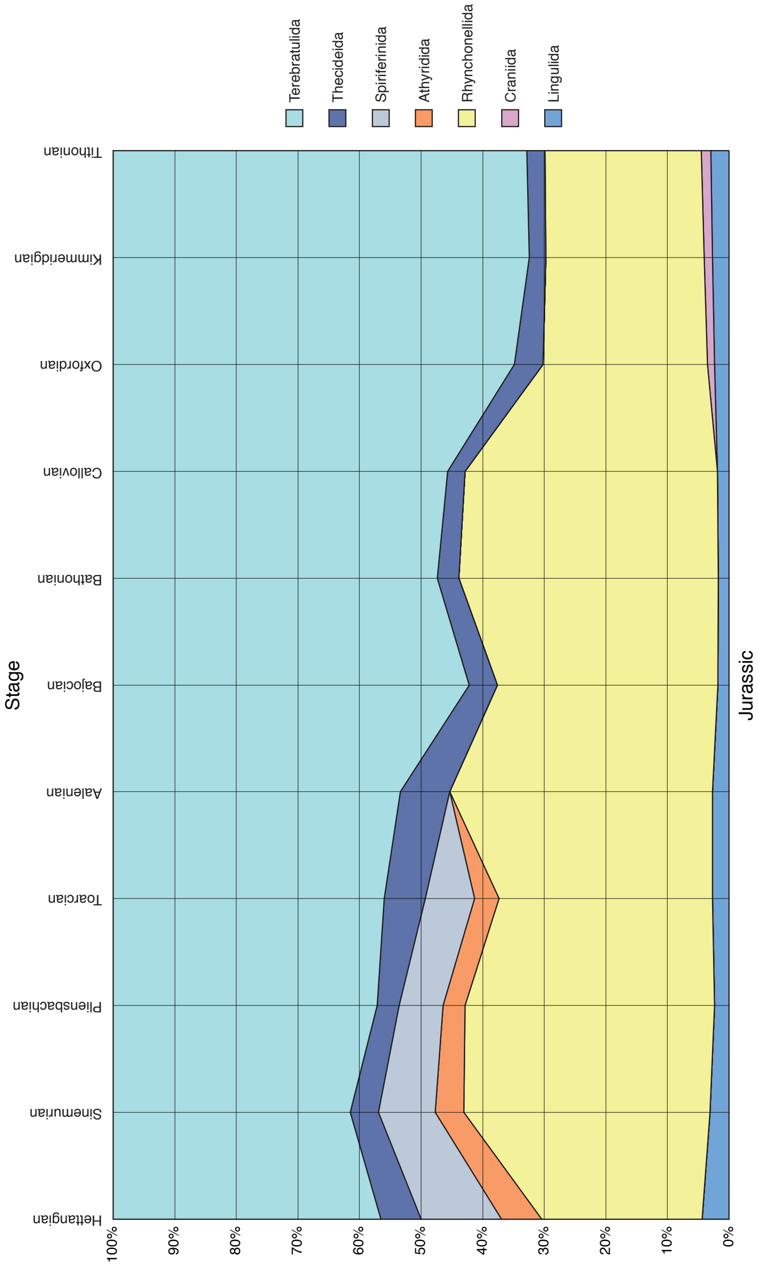


FIG. 1932. Relative proportions of different orders of brachiopods recorded from each of 11 stages of the Jurassic System, with lowermost stage (Hettangian) on left-hand side of horizontal axis, and uppermost Tithonian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

have influenced the disappearance of the Spiriferinida and the Athyridida (ALVAREZ, 2006) and the post-Aalenian Stage conditions that might have contributed to the radiation of the Terebratulida. From isotopic evidence it appears that global climates did fluctuate during the Jurassic but with a much less wide range than in other parts of the geologic record (see compilation in GRADSTEIN, OGG, & SMITH, 2004). There were, however, several pronounced negative excursions in the carbon isotope record during the Jurassic (JENKYNS & others, 2002). The most dramatic of these and, indeed, one of the largest carbon isotope excursions recorded throughout the Phanerozoic (HESSELBO, GROCKE, & JENKYNS, 2000), occurred during the early Toarcian Stage (MCARTHUR & others, 2000). This event, which coincided with the deposition of extensive organic-rich sediments such as the Jet Rock in England, is believed to represent a major oceanic anoxic event, although this and many other similar events may also have represented the culmination in periods of enhanced oceanic productivity that increased the rate of organic carbon burial (see discussion in Cretaceous section below). Although lasting for only 0.5 million years and composed of several pulses (MCARTHUR & others, 2000), this event seems to have had a dramatic impact on brachiopod diversity and probably contributed to the extinction of two orders (the Athyridida and Spiriferinida) that were long lived (from the Upper Ordovician [Costonian] and Lower Devonian), and which had been present, albeit in small numbers of genera, throughout the Lower Jurassic (Fig. 1932).

If the global spread of anoxic conditions or enhanced organic carbon deposition did indeed contribute to the extinction of the Athyridida and the Spiriferinida, then it may also have had a discernible effect on the Rhynchonellida, which declined from 34 genera in the Pliensbachian Stage to 26 genera in the Toarcian Stage, before their diversity increased to 32 genera in the Aalenian Stage and 39 in the Bathonian Stage. Simple diversity counts will not take into account evolutionary innovations among constituents of the lineages, but the raw abundance data suggests that Terebratulida were much less affected by events during the Toarcian Stage. Terebratulida generic abundances were 36 in the Pliensbachian Stage and 33 in the overlying Toarcian Stage, before increasing again to 35 genera in the lowermost Middle Jurassic Aalenian Stage and climbing to 63 genera in the overlying Bajocian Stage. By the Bathonian Stage a total of 60 genera of Terebratulida are recorded, as compared with 57 genera in the uppermost Middle Jurassic Callovian Stage. The implication is that Terebratulida were able to survive, or recover from, a global reduction in the oxygenation levels of the ocean better than any other brachiopod stock. The data also suggest that they were better equipped to exploit the post-Toarcian Stage recovery to more normal oxygen conditions; although Terebratulida recovery initially appears to be slower than that of the Rhynchonellida, in the long run it was more sustained.

Even though Terebratulida became by far the dominant component of brachiopod faunas in the Upper Jurassic, the absolute numbers of Terebratulida genera declined, however, from a high of 63 genera in the Middle Jurassic Bajocian Stage to a low of 45 genera in the uppermost Tithonian Stage of the Upper Jurassic. There was another major negative carbon oxygen excursion in the Upper Jurassic Oxfordian Stage (PADDEN, WEISSERT, & DE RAFELIS, 2001), again thought to indicate the spread of anoxic or low-oxygen conditions in the oceans following the release of methane into the atmosphere from gas hydrates. This event was marked by the deposition of sediments with high organic contents (e.g., black shales), due to the decay of enhanced quantities of organic material that brought about a reduction in oxygen levels. Along with a series of smaller events during the Jurassic, such environmental stresses may have influenced the diversity of Terebratulida subsequent to their peak in the Bathonian

Stage. There was, however, a major, positive excursion in carbon isotope ratios in the Bajocian Stage (see composite curve in Gradstein, Ogg, & Smith, 2004), and brachiopods achieved their greatest Jurassic diversity in that stage and in the overlying Bathonian Stage. These two stages are also characterized by the highest ever diversity of Terebratulida in any one stage (with the exception of the Holocene, which is anomalous in containing extant genera). It may also be that the subsequent progressive decline in brachiopod diversity in the Upper Jurassic is due to other factors, such as changes in the sedimentary environments, especially if they were particularly pronounced in shallow marine areas from which the majority of brachiopods recorded in these stages have been described. The low overall number of brachiopods may also make them much more vulnerable to exposure issues. It has been estimated that the exposure of Jurassic rocks (in terms of km^2 per year) is much lower than for the preceding Permian and Triassic Systems (Raup, 1976).

CRETACEOUS SYSTEM

In the Cretaceous System (145.5 ± 4.0 Ma to 65.5 ± 0.3 Ma; Gradstein, Ogg, & Smith, 2004), brachiopod diversity remained fairly constant at around 70 to 85 genera during the Lower Cretaceous Berriasian to Albian Stages (Fig. 1933). The lowermost Cenomanian Stage of the Upper Cretaceous had a very similar number of genera (74), but brachiopod diversity declined noticeably in the Turonian Stage (to 58 genera), and similarly low diversities were maintained in the overlying Coniacian and Santonian Stages (56 and 59 genera respectively; Fig. 1933). The number of genera increased again in the Campanian (72 genera) and in the succeeding Maastrichtian Stage (75 genera), the uppermost stage of the Upper Cretaceous. The same five orders present at the end of the Jurassic persisted throughout the Cretaceous System, but their relative proportions varied (Fig. 1934). The Terebratulida are the dominant stock in all Cretaceous stages but range from a high of 81% of the total brachiopod fauna in the Lower Cretaceous Aptian Stage to a low of 58% in the Upper Cretaceous Campanian Stage. The overall trend, especially in the Upper Cretaceous, is for the proportion of the total fauna represented by the Terebratulida to decline (Fig. 1934). The Rhynchonellida represent only 10% of the total fauna during the Aptian stage, but contribute between 19% and 24% of the total fauna throughout all stages of the Upper Cretaceous. The Thecideida, and to a lesser extent, the Craniida, contribute an increasing proportion of the fauna in the uppermost Campanian (11% and 6% respectively) and Maastrichtian Stages (12% and 7% respectively) of the Cretaceous System.

The total number of brachiopod orders recorded during the Cretaceous drops to 5 out of the total of 26, the lowest of any system since the beginning of the Cambrian System. This low taxonomic diversity follows the disappearance of the Athyridida and the Spiriferinida in the Jurassic. Throughout the Cretaceous, representatives of the Terebratulida are dominant, and in the 6 stages of the Lower Cretaceous their generic diversity is very consistent, varying between 55 and 58 genera. Terebratulida diversity in the lowermost Upper Cretaceous Cenomanian Stage was at 52 genera but thereafter dropped to 38, 35, and 36 genera respectively in the Turonian, Santonian, and Coniacian Stages of the middle Upper Cretaceous. The uppermost two stages of the Upper Cretaceous witnessed a slight recovery in Terebratulida diversity, up to 42 genera in the Campanian Stage and 44 genera in the Maastrichtian Stage.

The Rhynchonellida are the second most abundant component of Cretaceous brachiopod faunas, reaching a maximum diversity of 19 genera in the middle Lower Cretaceous Hauterivian Stage and then declining to only 7 genera in the upper Lower Cretaceous Aptian Stage. Throughout their geologic history the Rhynchonellida do appear to be particularly prone to fluctuating diversity

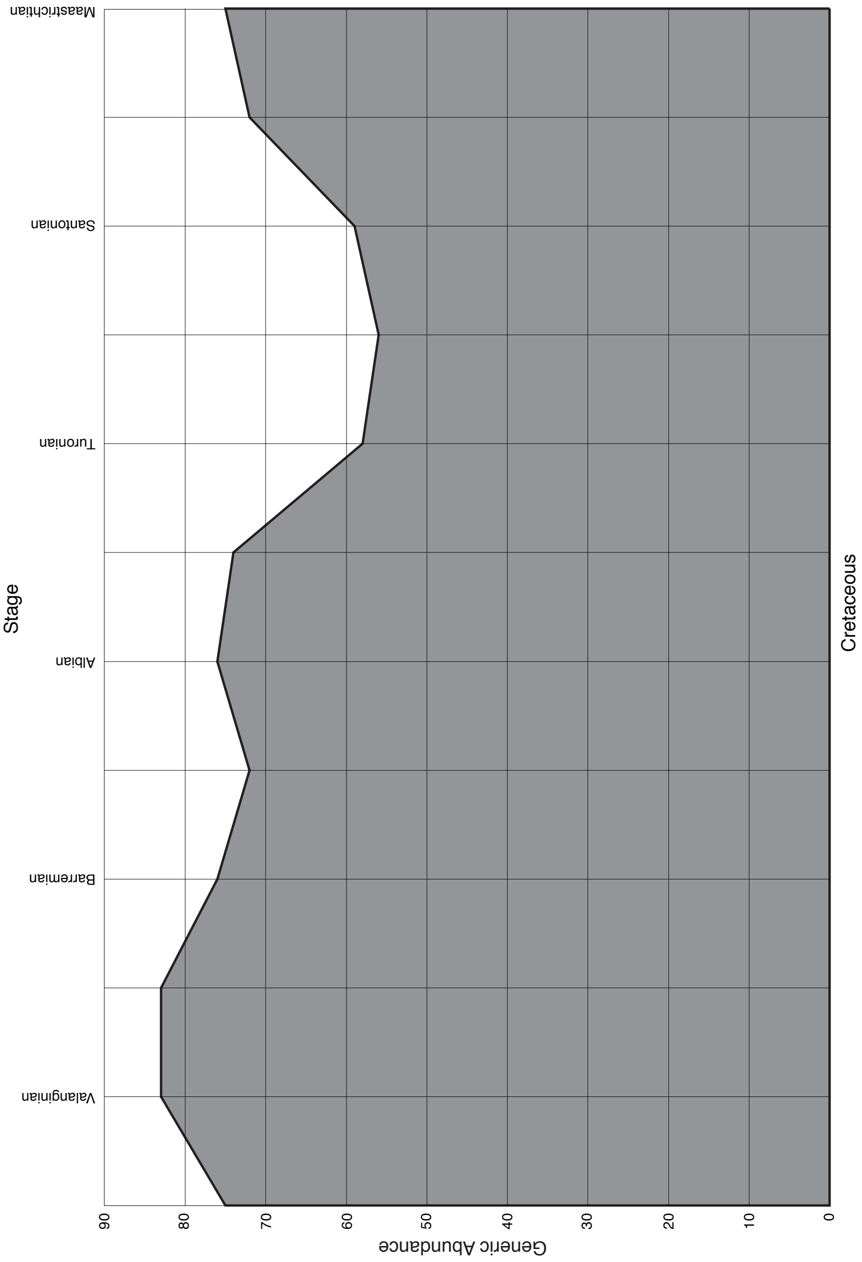


FIG. 1933. Abundance of brachiopods in each of 12 stages (horizontal axis) assigned to Cretaceous System, with lowermost stage (Berriasian) on left-hand side of horizontal axis and uppermost Maastrichtian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

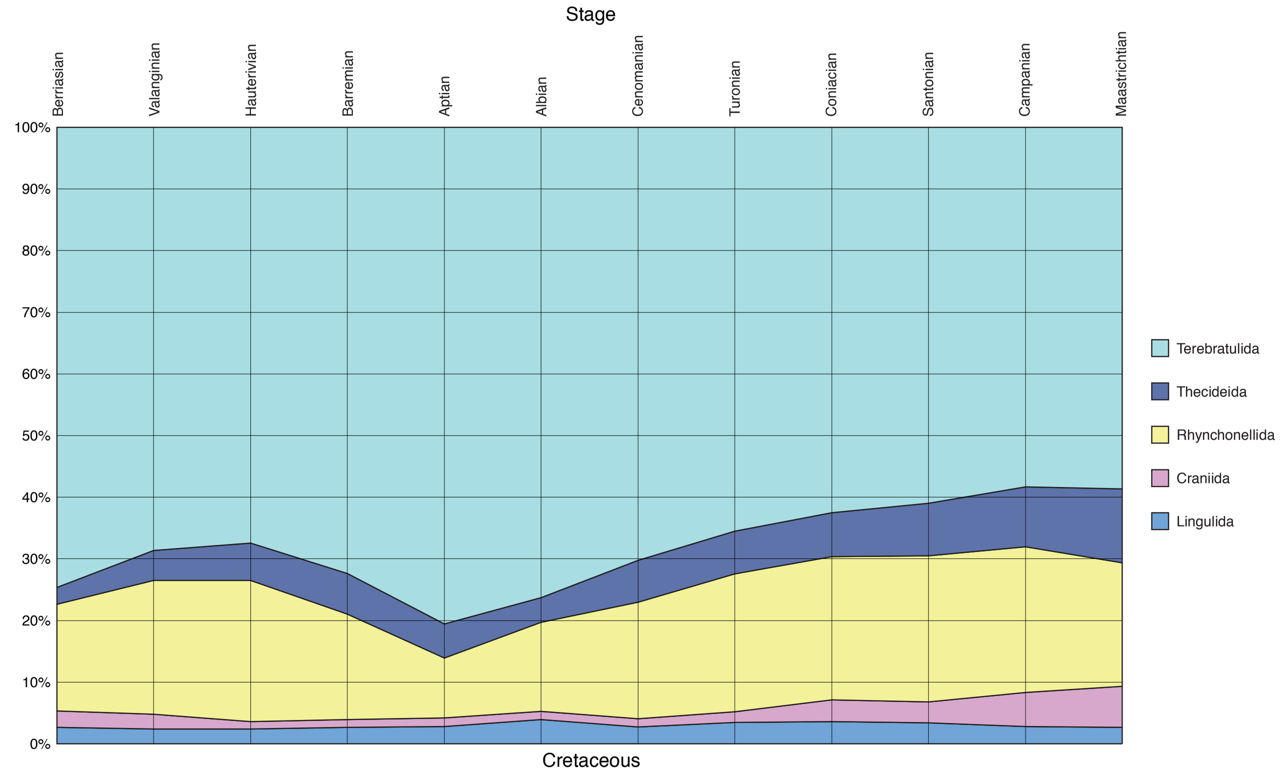


FIG. 1934. Relative proportions of different orders of brachiopods recorded from each of 12 stages of Cretaceous System, with lowermost stage (Berriasian) on left-hand side of horizontal axis and uppermost Maastrichtian Stage on right-hand side. Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present (new).

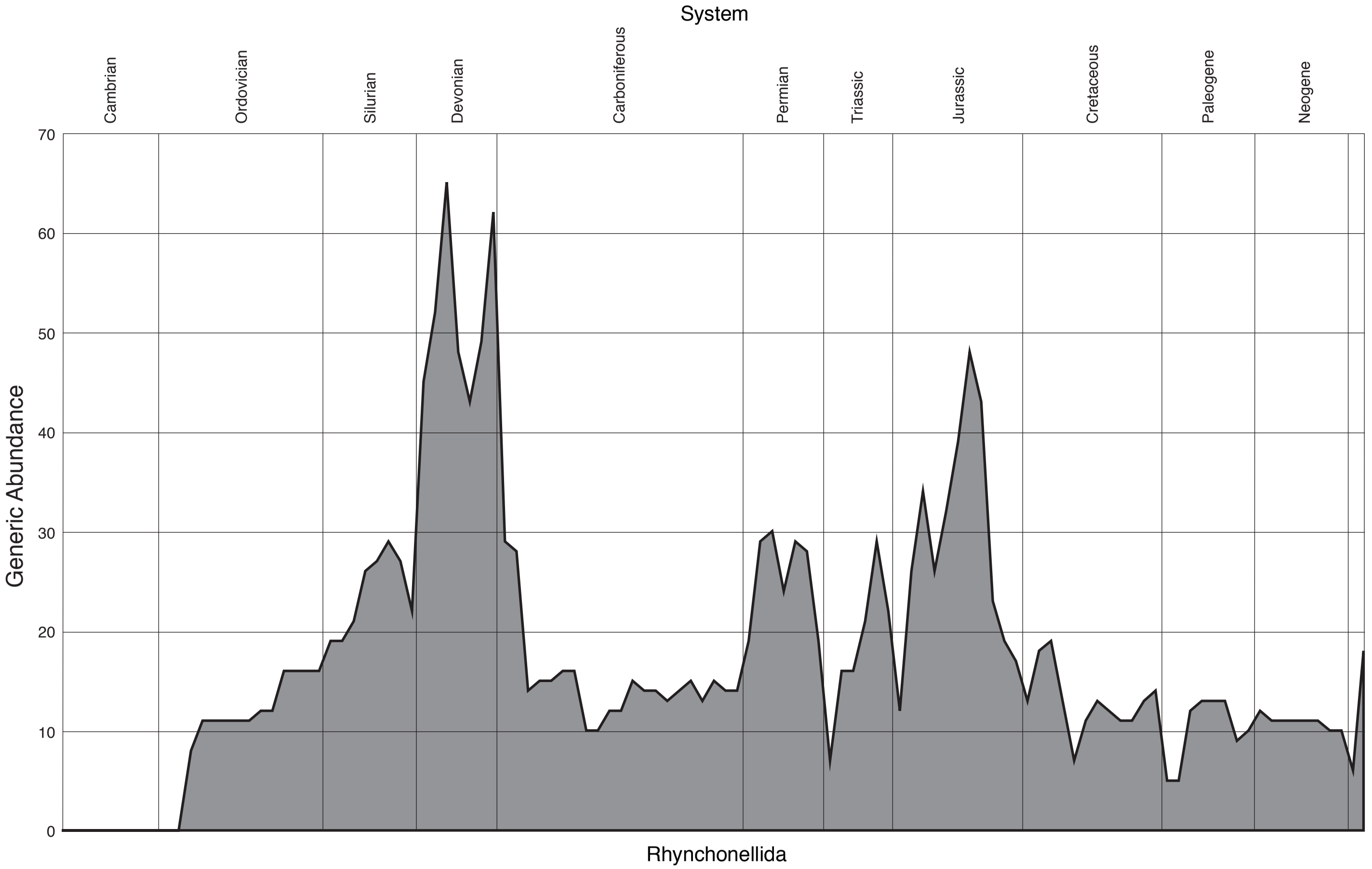


FIG. 1935. Stratigraphic distribution of order Rhynchonellida, demonstrating great longevity and considerable fluctuations in diversity. Three systems display 2 well-defined peaks of Rhynchonellida diversity (Devonian, Permian, and Jurassic). Far right, unlabelled segment of diagram portrays Rhynchonellida distribution in Pleistocene and Holocene stages (new).

(Fig. 1935), although to some extent this may be due to artefacts associated with the taxonomic procedures applied to Rhynchonellida (such as the practice of treating Paleozoic and Mesozoic genera separately). Rhynchonellida generic numbers recovered to 11 in the uppermost Lower Cretaceous Albian Stage and remain comparatively high, at 13 to 17 genera, throughout all stages of the Upper Cretaceous. The Thecideida reached a maximum diversity in the Late Cretaceous of 9 genera; for the earlier part of the system there are only 3 to 5 genera present. For most of the Cretaceous the only surviving linguliforms are the Lingulida and Craniida, and these two orders are represented by a combined total of only 3 or 4 genera; in the Upper Cretaceous Campanian and Maastrichtian Stages, however, the number of Craniida genera increases to 4 and 5 respectively.

Overall, the Cretaceous witnessed relatively low numbers of brachiopod genera. During the Jurassic the total numbers of genera peaked at 114 (in the Bathonian Stage), but the maximum number of genera recorded in any Cretaceous stage was 83 genera (in the Valanginian and Hauterivian Stages) and the mean number of genera in the six stages of the Upper Cretaceous was 66.

The most distinctive feature of brachiopod stratigraphic distribution in the Cretaceous is the decline in absolute numbers of genera in the Turonian stage, a decline that persisted into the overlying Coniacian and Santonian Stages. Brachiopod diversity again seems to have been adversely affected by global events at the Cenomanian-Turonian boundary, the physical evidence of which is a significant horizon of organic-rich sediments that has been recorded globally. This event, known as the Oceanic Anoxic Event 2, or the Bonarelli Event, is also marked by a pronounced carbon isotope excursion (Jenkyns, Gale, & Corfield, 1994). While establishing direct links between such events and brachiopod diversity seems likely, such suggestions must be treated with caution given the provisos mentioned at the beginning of this chapter. It is plausible, however, to envisage a situation in which the widespread accumulation of organic-rich sediments created problems for brachiopods that had previously colonized areas of quite different sedimentation. The evidence from the global survey of brachiopod diversity presented in the *Treatise* seems to imply that low-oxygen conditions may have had a profound effect on the phylum and at least contributed to a 22% reduction of the number of brachiopod genera between the Cenomanian and Turonian Stages.

PALEOGENE, NEOGENE, PLEISTOCENE, AND HOLOCENE

Although representing the last 65.5 million years of geologic history, the 18 stages from the beginning of the Paleogene (65.5 ± 0.3 Ma to 23.04 ± 0 Ma; Gradstein, Ogg, & Smith, 2004) to the present day will be discussed together, as brachiopod diversities were low throughout, and the phylum represents minor constituents of marine faunas. That is not to imply that the stratigraphic distribution of brachiopods over the last 65.5 million years is without interest. The lowermost Danian Stage of the Paleogene includes a total brachiopod fauna of 35 genera, the third lowest in their geologic record (Fig. 1936) and one of the largest percentage declines in their history, in which there was a 53% reduction in the number of the brachiopod genera compared to the preceding uppermost Cretaceous Maastrichtian Stage. The succeeding Thanetian Stage witnessed a further reduction, down to a total of 26 genera, the second lowest diversity of any stage in the Phanerozoic and again one of the most significant percentage declines in their geologic history (representing a reduction of 26% in the total number of brachiopod genera compared to the Danian Stage). Over a period of 11.4 million years from the end of the Cretaceous, therefore (i.e., the duration

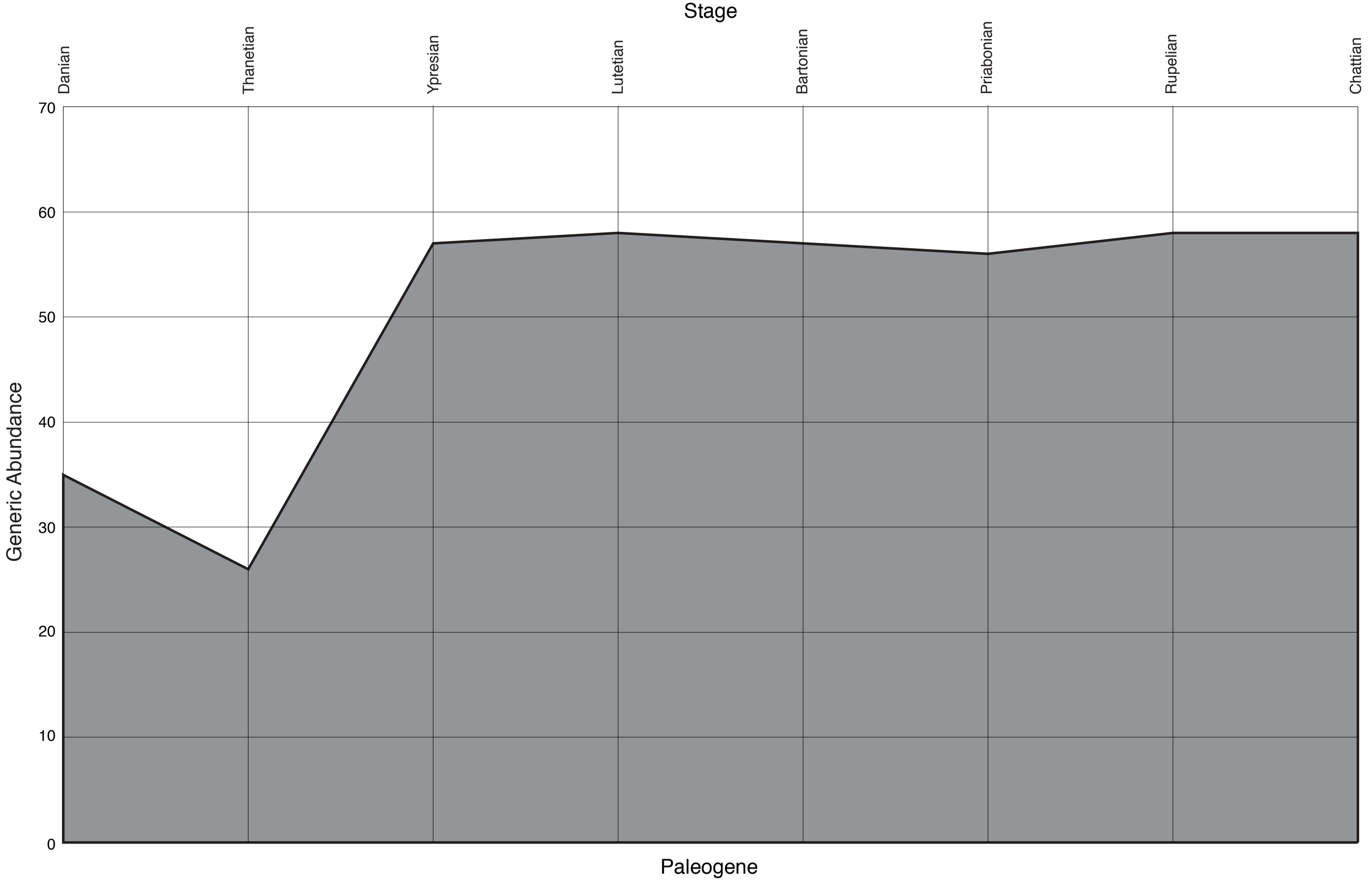


FIG. 1936. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to Paleogene System, with lowermost stage (Danian) on left-hand side of horizontal axis and uppermost Chattian Stage on right-hand side. Stage nomenclature, common abbreviation, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

of the Danian and Thanetian Stages, which together comprise the Paleocene Series), brachiopod diversities declined dramatically. In Gradstein, Ogg, and Smith (2004) the duration of the Paleocene has been reduced to a still significant 10.3 million years (and a new stage, the Selandian, has been established between the Danian and Thanetian Stages).

The event that precipitated such a long-lived decline in brachiopod diversities was of course the end-Cretaceous extinction, by far the most studied event of its type (MacLeod & Keller, 1996). For some years extensive evidence has been presented that seemed to indicate that the extinction event was primarily related to the impact of an extraterrestrial body, in particular an asteroid that left a crater at Chicxulub, off the Yucatan Peninsula (Alvarez & others, 1980). This assertion has recently been challenged, however, by the suggestion that the Chicxulub impact crater actually occurred around 300,000 years before the Cretaceous-Paleogene boundary (Keller & others, 2003; Keller, Adatte, & Stinnesbeck, 2003). An alternative, or complementary, explanation is that the end-Cretaceous extinction event was caused by severe environmental change brought about by much greater than normal levels of volcanic activity at the time (i.e., the formation of the Deccan Traps in Asia and the volcanism associated with the opening of the Atlantic Ocean). In this scenario (McLean, 1985), the Earth's atmosphere, climate, and oceans were subjected to major perturbation (e.g., sulphur dioxide aerosols from volcanic eruptions in the stratosphere inducing cooling and enhanced concentrations of toxic trace elements).

Isotopic evidence from marine microorganisms suggests that ocean temperatures during the Mid-Cretaceous were very high (more than 10 °C higher than today; Huber, Norris, & MacLeod, 2002) but had declined progressively from a maximum in the Turonian. Some groups of organisms appear to have been unaffected by the end-Cretaceous event (MacLeod & others, 1997), however, including representatives of phyla that would be expected to be particularly vulnerable to such radical environmental disturbances. Certainly some brachiopod workers have drawn attention to the fact that the phylum was relatively unaffected by this extinction event (Ager, 1988). It may well be, therefore, that the notoriety of the end-Cretaceous extinction may well have increased the proportion of pseudoextinctions (as taxonomists expect to find different taxa on either side of the stratigraphic boundary). Certainly taxonomic procedures are thought to have a significant effect on ancient biodiversity studies (Sheehan, 1977).

Whatever the cause, or causes, of the extinction, just over half the brachiopod genera recorded in the uppermost Maastrichtian Stage of the Cretaceous became extinct by the lowermost Danian Stage of the Paleogene (Fig. 1936). In percentage terms this sustained decline is exceeded in brachiopod history only by that recorded at the Permian-Triassic boundary. The much lower number of brachiopod genera in the Late Cretaceous and Paleocene suggests that any conclusions must be treated with great caution, however, as artefacts of preservation, exposure, and taxonomic practice will be proportionately much more significant at this extinction event.

Post-Thanetian Stage, the number of brachiopod genera recovered to a total of between 56 and 58 genera throughout the 6 stages that make up the Eocene and the Oligocene Series of the Paleogene System. Brachiopod generic numbers increased again during the 6 stages of the Miocene Series (the lower part of the Neogene System; 23.04 ± 0 Ma to 1.81 ± 0 Ma; Gradstein, Ogg, & Smith, 2004) at a very consistent level of 72 to 74 genera. In the two stages of the Pliocene Series (the upper part of the Neogene System) brachiopod generic abundances remained very similar at 68 genera in both the Zanclean and the Piacenzian Stages (Fig. 1937). The apparent slight decline in brachiopod diversity in the

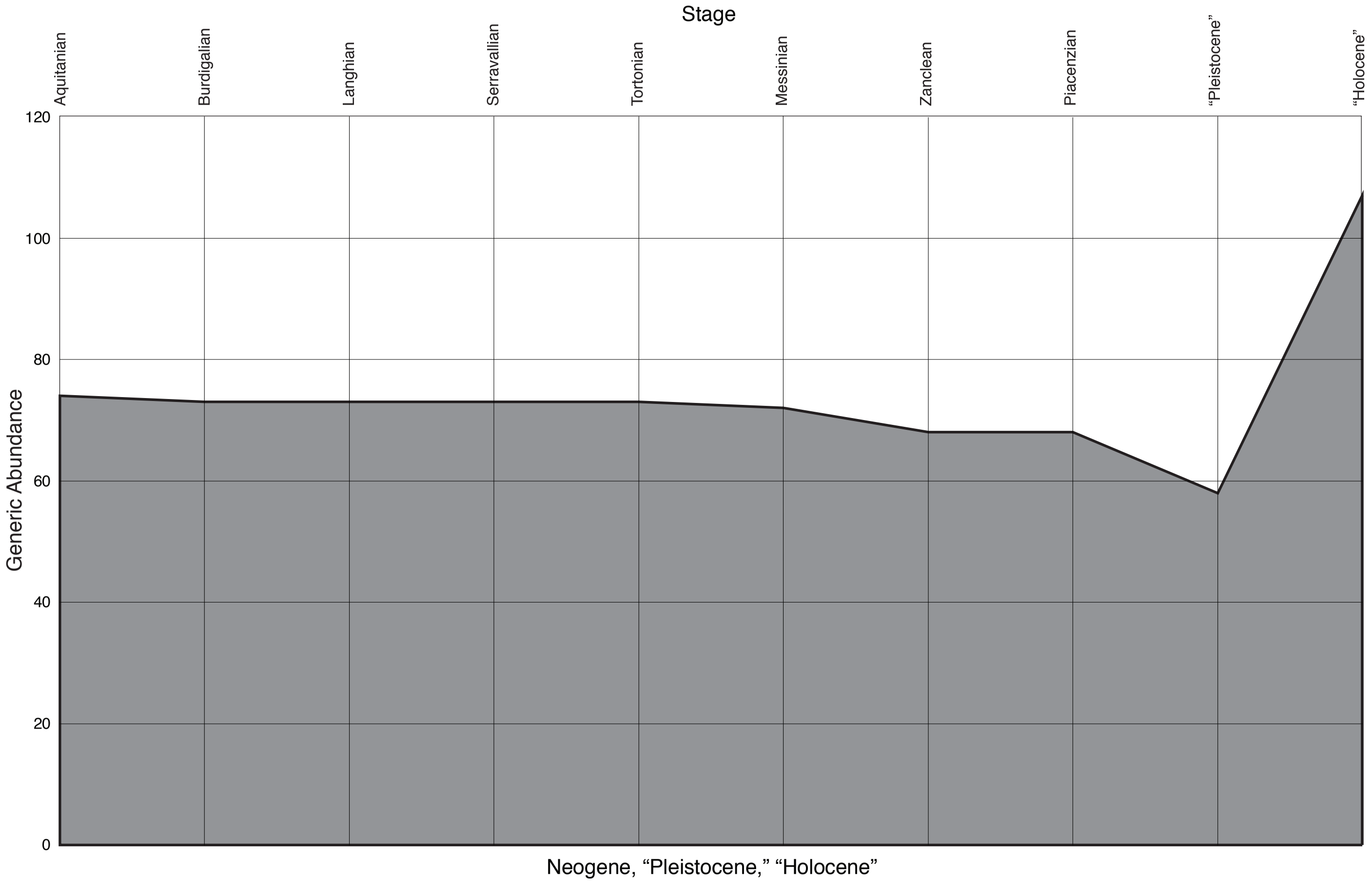


FIG. 1937. Abundance of brachiopods in each of 8 stages (horizontal axis) assigned to Neogene System (from lowermost Aquitanian Stage on left-hand side of diagram to uppermost Piacenzian Stage), along with Pleistocene and Holocene stages (latter including Recent genera). Stage nomenclature, common abbreviations, meaning of quotation marks, and absolute ages (midpoint, base, and duration) listed in Table 40 (new).

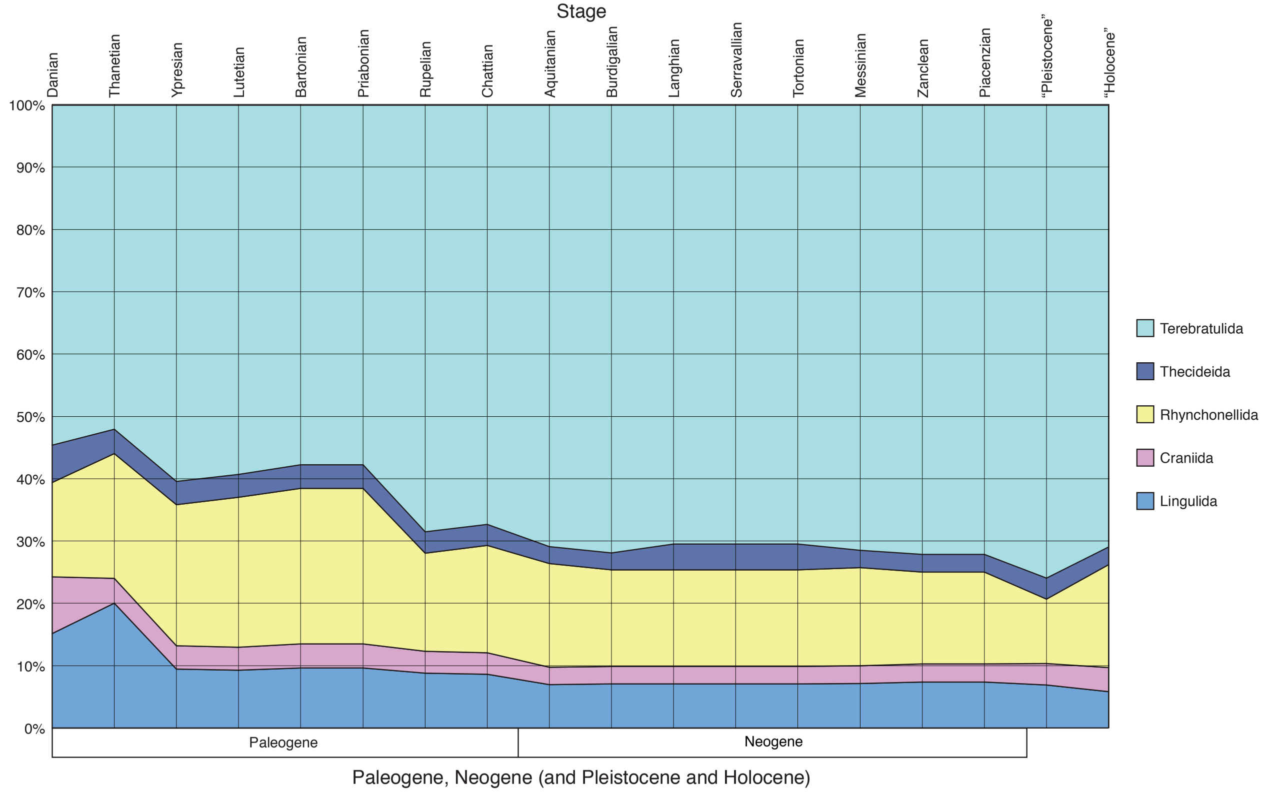


FIG. 1938. Relative proportions of different orders of brachiopods recorded from each of 8 stages of Paleogene System (Danian to Chattian), 8 stages of overlying Neogene System (Aquitanian to Piacenzian), and Pleistocene and Holocene stages (latter including Recent genera). Vertical axis displays percentage of total brachiopods recorded from a particular stage assigned to each order. Key on right indicates different brachiopod orders present; see Table 40 for meaning of quotation marks (new).

Pleistocene (to below 60 genera; 1.81 ± 0 Ma to 0.01 ± 0 Ma; Gradstein, Ogg, & Smith, 2004) and the subsequent dramatic increase to 107 genera in the Holocene (including Recent genera; 0.01 ± 0 Ma to present day; Gradstein, Ogg, & Smith, 2004) are almost certainly artefacts of the fossil record. Many Pleistocene deposits are unconsolidated (hence prone to erosion and poor exposure), and marine successions of this stage are often inaccessible (in sediment accumulations on the seabed). The 84% increase in brachiopod genera recorded in the present day perhaps provides a crude estimate of the incompleteness of the fossil record, because there are no indications of major evolutionary innovation among extant stocks and the expansion is most likely due to the better preservation and information content of Recent, as compared to fossil, specimens.

Little has changed taxonomically over the last 65 million years (Fig. 1938). The same five orders that were present during the Cretaceous occur throughout these intervals of Earth history. The dominance of the Terebratulida continued and indeed increased through this period of Earth history, to such an extent that over 70% of brachiopod genera were Terebratulida in all stages from the base of the Neogene System. In Recent seas, not only is the generic diversity of Terebratulida comparatively high (75 genera representing 70% of the total fauna), but they also tend to occur in relatively high numbers. The diversity of Terebratulida rose consistently from about 20 genera at the start of the Paleogene System (i.e., the Danian Stage of the Paleocene Series) to 39 by the end of the system (i.e., in the two stages [Rupelian and Chattian] that make up the Oligocene Series). In all 6 stages assigned to the Miocene, Terebratulida diversities are very consistent at 52 or 53 genera. Such consistency is probably again influenced by the large numbers of Holocene Terebratulida genera that have been described due to their better accessibility. A total of 75 Holocene Terebratulida genera have been described, the highest number of representatives of this order recorded in any stage throughout their geologic history. Many of these genera have extensive geologic records that will range through stages in which brachiopods are poorly known due to exposure gaps. By comparison, the 1965 *Treatise* (Moore, 1965) recorded about 45 Holocene terebratulide genera. The Rhynchonellida, continuing to display the fluctuations in diversity that are evident throughout their geologic history, increased from about 5 genera at the start of the Paleocene to 13 in three stages in the middle of the system, reduced slightly in numbers to range from 10 to 12 throughout the 8 stages that make up the Neogene System (i.e., the Miocene and Pliocene), and then increased to 18 genera at the present day (i.e., the Holocene stage).

During these intervals of Earth history the number of Lingulida genera increased to 5, while Craniida diversity mostly remained at 2 genera, although it has increased to 4 genera in recent times. Representatives of the other extant order, the Thecideida, declined somewhat to between 2 and 3 genera over this time span, but 3 genera from this order are still living today.

ACKNOWLEDGMENTS

Many individuals have contributed greatly to the compilation of this chapter; among those who deserve particular mention are Patricia Peters, whose help over several years to update the stratigraphic data following the various and often extensive updates and revisions has been invaluable. A number of colleagues have read and reviewed drafts of this chapter, and we are particularly grateful for the comments of Fernando Alvarez, Miguel Manceñido, Sandy Carlson, Bert Rowell, Lars Holmer, Tatiana Smirnova, and Alberto Perez-Huerta. Many others, too numerous to mention individually, have provided expert advice and information over the more than 10 years during which the stratigraphic data presented in this chapter was compiled and analyzed.

All such comments are gratefully acknowledged, as are the outstanding efforts of the entire brachiopod community; without the hard work of so many individuals an overall synthesis of brachiopod stratigraphic distributions would not have been possible. We have not always been able to incorporate all suggestions raised, due to the colossal amount of stratigraphic data generated during this project, but this chapter has undoubtedly benefited from the views of so many brachiopod experts.

We have also received considerable help over the last 10 years from the *Treatise* Office in the Paleontological Institute at the University of Kansas, and would like to thank Roger Kaesler and Jill Hardesty for all their encouragement, help, and consideration. The Department of Geographical and Earth Sciences at the University of Glasgow provided facilities and office space to allow the *Treatise* work to be completed, and this is also gratefully acknowledged. The task of completing the compilation and analysis of the stratigraphic data on the brachiopods would not have been possible without such assistance.

Finally we must acknowledge the overwhelming contribution of the late Alywn Williams. His foresight in persuading authors to adhere, as far as possible, to a single stratigraphic chart throughout the preparation of the *Treatise* taxonomic data was of fundamental importance in allowing this stratigraphic chapter to be prepared. We believe that the information summarized in this chapter and published in taxonomic descriptions throughout the six volumes of the revised brachiopod *Treatise* are the highest quality stratigraphic data achieved, or achievable, for any phylum, and therefore represents one of the many important legacies of Alywn Williams for future generations of researchers. Alwyn Williams was heavily involved in the preparation of this chapter until his death, and the layout, content, and style of the chapter was greatly influenced by our discussions with him and by various forms of correspondence with him. We have incorporated many of his ideas and suggestions, and it is our profound hope that the entire contents come close to the standards he would have set had he been an author, as was always intended.

RANGES OF TAXA

The stratigraphic distribution of the Brachiopoda recognized in Part H, Revised, volumes 2–6 is shown graphically in the range chart (Table 41).

Because of the very long stratigraphic ranges of many higher taxa of Brachiopoda, ranges in the chart are rather broad in order to ensure that all periods are included. For more detailed stratigraphic information, refer to the systematic sections of volumes 2–6, p. 28–2330 and p. 2532–2821.

The following chart was compiled using software developed for the Paleontological Institute by Kenneth C. Hood and David W. Foster.

It must be emphasized that the order of taxa in this chart is governed entirely by their stratigraphic range and, within that, by alphabetical order, and differs in some cases from the taxonomic order in the systematic parts of the volumes. No taxonomic conclusions should be drawn from the position of taxa in this chart.

Explanation for Table 41	
PHYLUM SUBPHYLUM	█████
CLASS	█████
ORDER SUBORDER	▬▬▬▬▬
SUPERFAMILY FAMILY SUBFAMILY TRIBE	━━━━━
Genus	─────
Occurrence questionable	????
Occurrence inferred	▬ ▬ ▬

TABLE 41. Stratigraphic Distribution of the Brachiopoda.

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
BRACHIOPODA	▬	▬	▬	▬	▬	▬	▬	▬	▬	▬	▬	▬
CRANIIFORMEA	▬	▬	▬	▬	▬	▬	–	▬	▬	▬	▬	▬
CRANIATA	▬	▬	▬	▬	▬	▬	–	▬	▬	▬	▬	▬
CRANIOPSIDA	▬	▬	▬	▬	▬							
CRANIOPSOIDEA	▬	▬	▬	▬	▬							
CRANIOPSIDAE	▬	▬	▬	▬	▬							
?Discinopsis	▬											
?Heliomedusa	?											
Pseudopholidops		▬										
Paracraniops		▬	▬									
Craniops		▬	▬	▬	▬							
Lingulapholis				▬								
TRIMERELLIDA		▬	▬									
TRIMERELLOIDEA		▬	▬									
ADENSUIDAE		▬										
Adensu		▬										
USSUNIIDAE		▬										
Ussunia		▬										
TRIMERELLIDAE		▬	▬									
Belubula		▬										
Bowanpodium		▬										
Corystops		▬										
Costitrimerella		▬										
Eodinobolus		▬										
Fengzuella		▬										
?Gyroselenella		▬										
Ovidiella		▬										
Palaeotrimerella		▬										
Paradinobolus		▬										
Peritrimerella		▬										
Porcidium		▬										
Sinotrimerella		▬										
Gasconsia		▬	▬									
Monomerella		▬	▬									
Trimerella		▬	▬									
Dinobolus			▬									
Keteiodoros			▬									
Rhynobolus			▬									
Yidurella			▬									
CRANIIDA		▬	▬	▬	▬	▬	–	▬	▬	▬	▬	▬
CRANIOIDEA		▬	▬	▬	▬	▬	–	▬	▬	▬	▬	▬
CRANIIDAE		▬	▬	▬	▬	▬	–	▬	▬	▬	▬	▬
Celidocrania		▬										
Orthisocrania		▬										
Philhedra		▬										
Pseudocrania		▬										
Acanthocrania		▬	▬	▬	▬							
Petrocrania		▬	▬	▬	▬							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Deliella				—								
Lepidocrania						—						
Nematocrania						—						
Mesocrania								—	—			
Craniscus								—	—	—	—	—
Conocrania									—			
Crania									—			
Ancistrocrania									—	—		
Danocrania									—	—		
Isocrania									—	—		
Novocrania										—	—	—
Neoancistrocrania												—
Valdiviathyris												—
LINGULIFORMEA	━	━	━	━	━	━	━	━	━	━	━	━
PATERINATA	━	━										
PATERINIDA	━	━										
PATERINOIDEA	━	━										
CRYPTOTRETIDAE	━											
Aldanotreta	—											
Askepasma	—											
Cryptotreta	—											
Dzunarzina	—											
Salanygolina	—											
PATERINIDAE	━	━										
Dictyonina	—											
Micromitra	—											
Olenekina	—											
Paterina	—											
?Wynnia	—											
Dictyonites		—										
Kolihium		—										
Lacunites		—										
UNCERTAIN	━											
MICKWITZIIDAE	━											
Mickwitzia	—											
TIANZHUSHANELLIDAE	━											
Apistoconcha	—											
Aroonia	—											
Tianzhushanella	—											
LINGULATA	━	━	━	━	━	━	━	━	━	━	━	━
SIPHONOTRETIDA	━	━	━									
SIPHONOTRETOIDEA	━	━	━									
SIPHONOTRETIDAE	━	━	━									
Gorchakovia	—											
Helmersenia	—	—										
Schizambon	—	—										
Acanthambonia		—										
Alichovia		—										

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Celdobolus		■										
Collarotretella		■										
Cyrbasiotreta		■										
Eosiphonotreta		■										
Karnotreta		■										
Mesotreta		■										
Multispinula		■										
Nushbiella		■										
?Quasithambonia		■										
Siphonobolus		■										
Siphonotreta		■										
Siphonotretella		■										
Orbaspina			■									
ACROTRETIDA	■	■	■	■								
ACROTRETOIDEA	■	■	■	■								
CERATRETIDAE	■											
Acanthatreta	■											
Almohadella	■											
Bozshakolia	■											
Ceratreta	■											
Erbotreta	■											
Keyserlingia	■											
Kleithriatreta	■											
Monophthalma	■											
CURTICIIDAE	■											
Curticia	■											
UNCERTAIN	■	■										
Craniotreta	■											
Dzhagdicus	■											
Schizotretoides		■										
EPHIPPELASMATIDAE	■	■										
Akmolina	■	■										
Pomeraniotreta	■	■										
Aipyotreta		■										
Ephippelasma		■										
Lurgiticoma		■										
Mamatia		■										
Myotreta		■										
Numericoma		■										
Rhinotreta		■										
Veliseptum		■										
SCAPHELASMATIDAE	■	■	■									
Batenevotreta	■											
Eoscaphelasma	■											
?Tobejalotreta	■											
Rhysotreta		■										
Scaphelasma		■										
Artiotreta			■									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
ACROTRETIDAE	—	—	—									
Acrothyra	—											
Amictocracens	—											
Anabolotreta	—											
Anelotreta	—											
Angulotreta	—											
Aphelotreta	—											
Apsotreta	—											
Araktina	—											
Canthylotreta	—											
Dicondylotreta	—											
Eohadrotreta	—											
Galinella	—											
Hadrotreta	—											
Kostjubella	—											
Kotylotreta	—											
Linnarssonella	—											
Linnarssonia	—											
Mixotreta	—											
Neotreta	—											
Odontotreta	—											
Olentotreta	—											
Opisthotreta	—											
Picnotreta	—											
Prototreta	—											
Quadrisonia	—											
Rhondellina	—											
Satpakella	—											
Stilpnotreta	—											
Tingitanella	—											
Treptotreta	—											
Vandalotreta	—											
Physotreta	—	?										
Dactylotreta	—	—										
Eurytreta	—	—										
Longipegma	—	—										
Semitreta	—	—										
Acrotreta		—										
Aktassia		—										
Conotreta		—										
Cyrtonotreta		—										
Ditreta		—										
Fascicoma		—										
Hansotreta		—										
Hisingerella		—										
Ombergia		—										
Ottenbyella		—										
Spondylotreta		—										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Talasotreta		—										
Tasbulakia		—										
Eschatelasma			—									
EOCONULIDAE		━										
Eoconulus		—										
Otariconulus		—										
Undiferina		—										
TORYNELASMATIDAE		━	━									
Cristicoma		—										
Issedonia		—										
Mylloconotreta		—										
Naimania		—										
?Paratreta		—										
Polylasma		—										
Sasyksoria		—										
Torynelasma		—										
Acrotretella		—	—									
BIERNATIDAE		━	━	━								
Bathmoleca		—										
Biernatia		—										
Opsiconidion		—	—	—								
Havlicekion			—	—								
Concaviseptum				—								
LINGULIDA	━	━	━	━	━	━	━	━	━	━	━	━
ACROTHELOIDEA	━	━										
BOTSFORDIIDAE	━											
?Bomina	—											
Botsfordia	—											
Curdus	—											
Diandongia	—											
Edreja	—											
Glyptias	—											
Karathele	—											
Minlatonia	—											
Neobolus	—											
ACROTHELIDAE	━	━										
CONODISCINAE	━	━										
Conodiscus	—	?										
?Discotreta		—										
ACROTHELINAE	━	━										
Acrothele	—											
Eothele	—											
Schizopholis	—											
Spinulothele	—											
Orbithele	—	—										
LINGULOIDEA	━	━	━	━	━	━	━	━	━	━	━	━
EOOBOLIDAE	━											
Eoobolus	—											

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Vassilkovia	—											
DYSORISTIDAE	━	━										
Dysoristus	—											
Ferrobolus	—	—										
ELKANIIDAE	━	━										
?Pseudodicellomus	—											
Broeggeria	—	—										
Elkania	—	—										
Elkanisca		—										
Keskentassia		—										
Lamanskya		—										
Monobolina		—										
Tilasia		—										
Volborthia		—										
LINGULELLOTRETIDAE	━	━										
Aboriginella	—											
Lingulellotreta	—											
Vaculina	—											
Mirilingula	—	—										
ZHANATELLIDAE	━	━	?									
?Canalilatus	—											
Fossuliella	—											
Koneviella	—											
Tropidoglossa	—											
Zhanatella	—											
Wahwahlingula	—	—										
Paldiskia	?	—										
Fagusella		—										
Hyperobolus		—										
Rosobolus		—										
Thysanotos		—										
Rowellella		—	?									
PATERULIDAE	━	━	━	?								
Diencobolus	—	—										
Eopaterula		—										
Tarphyteina		—										
Paterula		—	—	?								
OBOLIDAE	━	━	━	━	━							
OBOLINAE	━	━	━	━	━							
Aksarinaia	—											
Chakassilingula	—											
Dicellomus	—											
Eodicellomus	—											
Euobolus	—											
Experilingula	—											
Fordinia	—											
Kyrshabaktella	—											
Lindinella	—											

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Notiobolus	—											
Oepikites	—											
Palaeobolus	—											
Palaeoschmidtites	—											
Rebrovia	—											
Schmidtites	—											
?Sinoglossa	—											
Ungula	—											
Westonia	—											
Lingulepis	—	?										
Ralfia	—	?										
Lingulella	—	—										
Obolus	—	—										
Agalatassia		—										
Anomaloglossa		—										
Apatobolus		—										
Atansoria		—										
Barbatulella		—										
Divobolus		—										
Expellobolus		—										
Foveola		—										
?Gorjanskya		—										
Josephobolus		—										
Leontiella		—										
Leptembolon		—										
Libecoviella		—										
Lingulobolus		—										
Lithobolus		—										
Mytoella		—										
Ovolingula		—										
Palaeoglossa		—										
Pidiobolus		—										
Pseudobolus		—										
Spinilingula		—										
?Squamilingulella		—										
Teneobolus		—										
?Westonisca		—										
Wosekella		—										
Kacakiella			—									
Kosagittella			—	—								
Wadiglossella			—	—								
Trigonoglossa			?	—	—							
ELLIPTOGLOSSINAE		—	—									
Elliptoglossa		—										
Litoperata		—										
Lingulops		—	—									
GLOSSELLINAE		—	—	—	?							
?Anx		—										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Casquella		—										
?Ectenoglossa		—										
Fezzanoglossa		—										
Glossella		—										
Glyptoglossella		—										
Leptobolus		—										
?Libyaeglossa		—										
Pachyglossella		—										
Plectoglossa		—										
Rafanoglossa		—										
?Spondyglossella		—										
?Tunisiglossa		—										
Barrandeoglossa			—	—								
Prastavia				—								
?Lachrymula					?							
AULONOTRETIDAE		—										
Aulonotreta		—										
LINGULASMATIDAE		—										
Lingulasma		—										
PSEUDOLINGULIDAE		—	-	—	—							
Meristopacha		—										
Pseudolingula		—										
Sedlecilingula		—										
?Tarutiglossa				—								
Bicarinatina				—	—							
?Wadiglossa				—	—							
UNCERTAIN		—	-	—	—	—						
Oxlosia		—										
Tomasina		—										
Bistramia		?										
Dignomia				—								
Laima				—								
Timalina				—								
Lingulipora				—	—							
Lunoglossa						—						
LINGULIDAE				?	—	—	—	—	—	—	—	—
?Apsilingula				?								
?Barroisella				?	—							
?Langella					—	—						
Lingularia					—	—	—	—	—	?	?	
Semilingula						—						
Credolingula									—			
Glottidia									?	—	—	—
Lingula									?	—	—	—
DISCINOIDEA		—	—	—	—	—	?	—	—	—	—	—
TREMATIDAE		—	—	—								
Drabodiscina		—										
Tethyrete		—										

TABLE 41. *(Continued).*

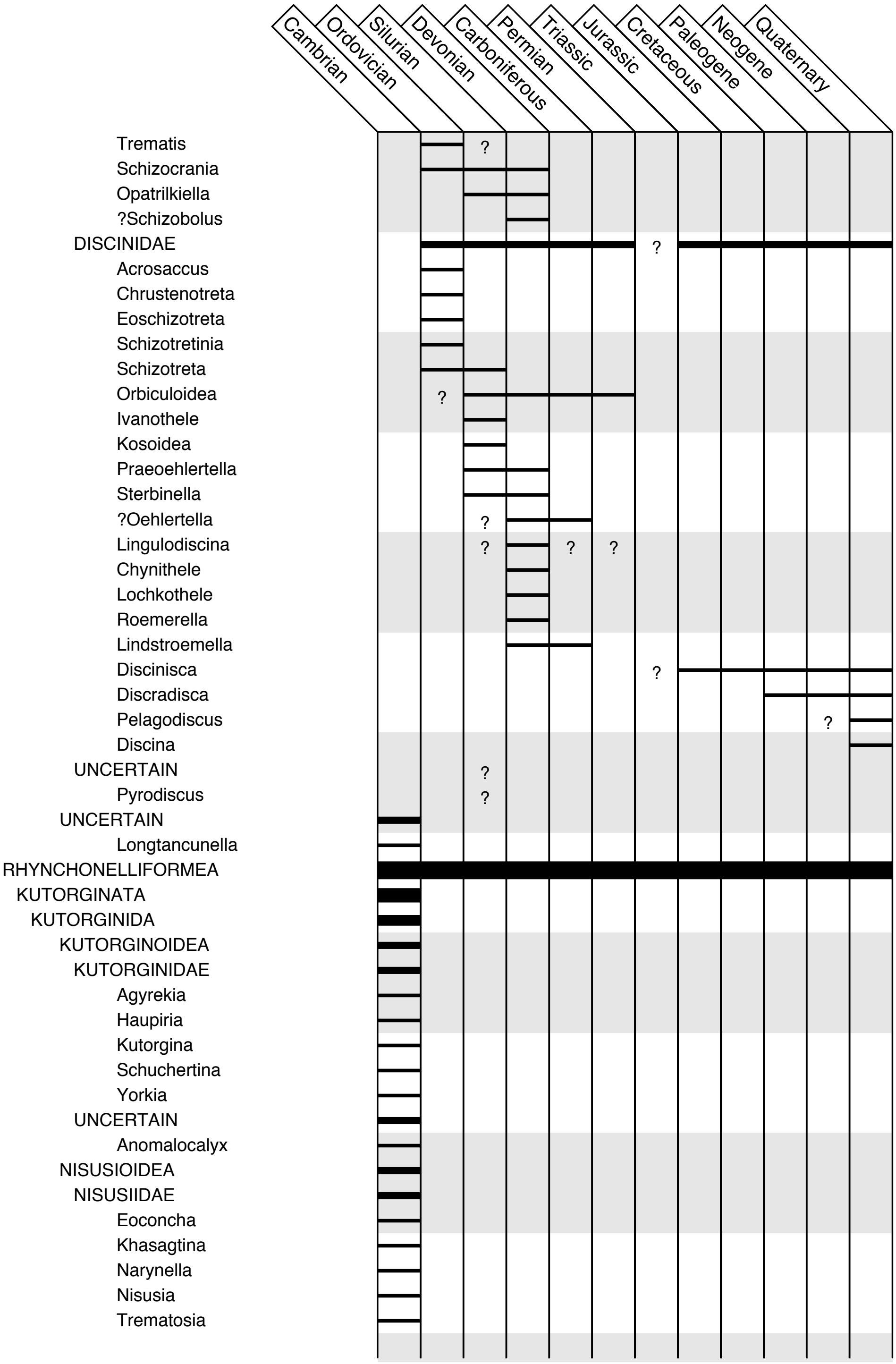


TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
OBOLELLATA	●											
NAUKATIDA	●											
NAUKATOIDEA	●											
NAUKATIDAE	●											
Bojarinovia	●											
Bynguanoia	●											
Naukat	●											
Oina	●											
?Swantonia	●											
PELMANELLIDAE	●											
Pelmanella	●											
OBOLELLIDA	●											
OBOLELLOIDEA	●											
OBOLELLIDAE	●											
Bicia	●											
Brevipelta	●											
Ivshinella	●											
Magnicanalis	●											
Obolella	●											
TREMATOBOLIDAE	●											
Alisina	●											
Sibiria	●											
Trematobolus	●											
UNCERTAIN	●											
Monoconvexa	●											
Nochoroiella	●											
CHILEATA	●	●	●	●	●	●						
CHILEIDA	●											
MATUTELLOIDEA	●											
CHILEIDAE	●											
Acareorthis	●											
Chile	●											
MATUTELLIDAE	●											
Kotujella	●											
Matutella	●											
DICTYONELLIDA		●	●	●	●	●						
EICHWALDIOIDEA		●	●	●	●	●						
EICHWALDIIDAE		●	●	●								
Eichwaldia		●										
Eodictyonella		●	●	●								
ISOGRAMMIDAE					●	●						
Isogramma					●							
Megapleuronia						●						
Schizopleuronia						●						
STROPHOMENATA	●	●	●	●	●	●	?					
BILLINGSELLIDA	●	●										
CLITAMBONITIDINA	●	●										
CLITAMBONITOIDEA	●	●										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
ARCTOHEDRIDAE	■											
Arctohedra	—											
CLITAMBONITIDAE		■										
Apomatella		—										
Atelelasma		—										
Clinambon		—										
Clitambonites		—										
Fistulogonites		—										
Hemipronites		—										
Ilmarinia		—										
Iru		—										
Lacunarites		—										
Neumania		—										
Pahlenella		—										
Vellamo		—										
GONAMBONITIDAE		■										
Anchigonites		—										
Antigonambonites		—										
Atelelasmoidea		—										
Estlandia		—										
Gonambonites		—										
Jaanussonites		—										
Kullervo		—										
Oslogonites		—										
Raunites		—										
POLYTOECHIOIDEA		■										
POLYTOECHIIDAE		■										
Acanthotoechia		—										
Admixtella		—										
Asymphylotoechia		—										
Eremotoechia		—										
Korinevskia		—										
Martellia		—										
Peritritoechia		—										
Platytoechia		—										
Polytoechia		—										
Pomatotrema		—										
Protambonites		—										
Tritoechia		—										
BILLINGSELLIDINA	■	■										
BILLINGSELLOIDEA	■	■										
BILLINGSELLIDAE	■	■										
Saccogonum	—											
Billingsella	—	—										
Xenorthis	—	—										
Cymbithyris		—										
Eosotrematorthis		—										
Kozhuchinella		—										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
STROPHOMENIDA		■	■	■	■							
PLECTAMBONITOIDEA		■	■	■								
BIMURIIDAE		■										
Asperdelia		■										
Bimuria		■										
Craspedelia		■										
GRORUDIIDAE		■										
Calyptolepta		■										
Diambonioidea		■										
Grorudia		■										
Railtonella		■										
Tetraodontella		■										
HESPEROMENIDAE		■										
Anoptambonites		■										
Aulie		■										
Chaganella		■										
Hesperomena		■										
Kassinella		■										
Rongambonites		■										
PLECTAMBONITIDAE		■										
PLECTAMBONITINAE		■										
?Akelina		■										
Ingria		■										
Plectambonites		■										
Plectella		■										
TAPHRODONTINAE		■										
Bandaleta		■										
Isophragma		■										
Taphrodonta		■										
Uzunbulakia		■										
SYNDIELASMATIDAE		■										
Sowerbyites		■										
Syndielasma		■										
TAFFIIDAE		■										
AHTIELLINAE		■										
Ahtiella		■										
Borua		■										
Guttasella		■										
Inversella		■										
?Rutrumella		■										
Sanjuanella		■										
Schedophyla		■										
LEPTELLINAE		■										
Leptella		■										
Vehnia		■										
PELONOMIINAE		■										
Pelonomia		■										
TAFFIINAE		■										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Aporthophyla		─										
Aporthophylina		─										
Spanodonta		─										
Taffia		─										
Tinopena		─										
Tourmakeadia		─										
LEPTELLINIDAE		━	━									
PALAEOSTROPHOMENINAE		━										
Anchoramena		─										
Apatomorpha		─										
Glyptambonites		─										
?Goniotrema		─										
Ishimia		─										
Lepidomena		─										
Leptastichidia		─										
Nikitinamena		─										
Onegia		─										
Palaeostrophomena		─										
Tesikella		─										
Titanambonites		─										
Toquimia		─										
Ujukites		─										
LEPTELLININAE		━	━									
Acculina		─										
Bekkerella		─										
Benignites		─										
Dulankarella		─										
Kajnaria		─										
Leptelloidea		─										
Mabella		─										
Reversella		─										
Shlyginia		─										
Leptellina		─	─									
LEPTESTIIDAE		━	━									
Bekella		─										
Bilobia		─										
Leptestia		─										
Rurambonites		─										
Sampo		─										
Sortanella		─										
Leangella		─	─									
XENAMBONITIDAE		━	━	━								
XENAMBONITINAE		━										
Metambonites		─										
Synambonites		─										
Xenambonites		─										
AEGIROMENINAE		━	━	━								
Aegiromena		─										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Cathrynia		—										
Chonetoidea		—										
Multiridgia		—										
Tenuimena		—										
Aegiria		—	—									
Jonesea		—	—									
Epelidoaegiria			—									
Mezounia			—									
Nabiaoia				—								
SOWERBYELLIDAE		━	━	━								
PTYCHOGLYPTINAE		━										
Ptychoglyptus		—										
SOWERBYELLINAE		━	━	━								
Eochonetes		—										
Gunningblandella		—										
Olgambonites		—										
Sowerbyella		—										
Zhilgyzambonites		—										
Anisopleurella		—	—									
Eoplectodonta		—	—									
Dubioleptina			—									
Plectodonta			—	—								
UNCERTAIN		━										
Leptoptilum		—										
Paucicostella		—										
Ukoa		—										
STROPHOMENOIDEA		━	━	━	━							
CHRISTIANIIDAE		━										
Christiania		—										
Nubialba		—										
FOLIOMENIDAE		━										
Foliomena		—										
EOPHOLIDOSTROPHIIDAE		━	━									
Origostrophia		—										
Eopholidostrophia		—	—									
Mesopholidostrophia			—									
Mongolostrophia			—									
GLYPTOMENIDAE		━	━									
UNGULOMENINAE		━										
Ungulomena		—										
GLYPTOMENINAE		━	━									
Bystromena		—										
Glyptomena		—										
Glyptomenoides		—										
?Hesperinia		—										
?Mjoesina		—										
Paromalomena		—										
?Pionomena		—										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Platymena		■										
Pomeromena		■										
?Proboscisambon		■										
Rhactomena		■										
Linostrophomena			■									
Qianomena			■									
TERATELASMINAE		■	■									
Teratelasma		■										
Trondomena		■										
Tashanomena		■	■									
STROPHOMENIDAE		■	■									
STROPHOMENINAE		■										
Actinomena		■										
Drummuckina		■										
Esilia		■										
Gunnarella		■										
Holtedahlina		■										
Infurca		■										
Leigerina		■										
Longvillia		■										
Nasutimena		■										
Pseudostrophomena		■										
Saxbyonia		■										
Strophomena		■										
Trotlandella		■										
FURCITELLINAE		■	■									
?Bajanhongorella		■										
Bekkerina		■										
Biparetis		■										
Dactylogonia		■										
?Djindella		■										
?Dzhebaglina		■										
Fenomena		■										
Furcitella		■										
Geniculina		■										
Iberomena		■										
Karomena		■										
Kirkina		■										
Luhaia		■										
Maakina		■										
?Mansina		■										
Molongcola		■										
Murinella		■										
Oepikina		■										
Oepikoides		■										
?Oslomena		■										
Oxostrophomena		■										
Panderites		■										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Quondongia		—										
Sakunites		—										
Tallinnites		—										
Teratelasmella		—										
?Titanomena		—										
Trigrammaria		—										
Bellimurina		—	—									
Katastrophomena		—	—									
?Hostimena			—									
Laevicyphomena			—									
Pentlandina			—									
UNCERTAIN		▬	▬	▬								
Playfairia		—										
Idioglyptus			—									
Douvinella				—								
Rhenostrophia				—								
Syntrophodonta				—								
LEPTOSTROPHIIDAE		▬	▬	▬								
Eostropheodonta		—	—									
Brachyprion			—									
Castellaroina			—									
Eocymostrophia			—									
Eomegastrophia			—									
Erinostrophia			—									
Palaeoleptostrophia			—									
?Tudiaophomena			—									
Tuvaechonetes			—									
Tuvaestrophia			—									
Viodostrophia			—									
Mesoleptostrophia			—	—								
Protomegastrophia			—	—								
?Barbaestrophia				—								
Chynistrophia				—								
Gamphalosia				—								
Gibberostrophia				—								
Leptostrophia				—								
Nervostrophia				—								
Nervostrophiella				—								
Protoleptostrophia				—								
Pseudoleptostrophia				—								
Rotundostrophia				—								
Timanostrophia				—								
?Tubulostrophia				—								
Velostrophia				—								
RAFINESQUINIDAE		▬	▬	▬	▬							
RAFINESQUININAE		▬	▬									
Colaptomena		—										
Dirafinesquina		—										

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Hedstroemina		—										
Heteromena		—										
?Hibernodonta		—										
Kjaerina		—										
Kjerulfina		—										
Megamyonia		—										
Odoratus		—										
Pentagomena		—										
Rafinesquina		—										
Rhipidomena		—										
Kosomena			—									
LEPTAENINAE		━	━	━	━							
Harjumena		—										
Hingganoleptaena		—										
Kiaeromena		—										
Limbimurina		—										
Leptaena		—	—	—								
?Bracteoleptaena			—									
Crassitestella			—									
?Lioleptanea			—									
Mackerrovia			—									
Scamnomena			—									
?Tchadania			—									
Glossoleptaena			—	—								
Lepidoleptaena			—	—								
Hollardina				—								
Leptaenopyxis				—								
Lissoleptaena				—								
Rugoleptaena				—								
Notoleptaena				?								
Leptagonia				—	—							
LEPTAENOIDEIDAE			━	━								
Leptaenoidea			—									
Liljevallia			—									
Leptaenisca				—								
Leptaenomendax				—								
?Taleoleptaena				—								
AMPHISTROPHIIDAE			━	━								
AMPHISTROPHIINAE			━	━								
Eoamphistrophia			—									
Amphistrophia			—	—								
Devonamphistrophia				—								
MESODOUVILLININAE			━	━								
Desistrophia			—									
Eomaoristrophia			—									
Gladiostrophia			—	—								
Mclearnites			—	—								
Mesodouvillina			—	—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Jakutostrophia				■								
Maoristrophia				■								
Sinostrophia				■								
DOUVILLINIDAE			■	■								
PROTODOUVILLININAE			■	■								
Cymostrophia			■	■								
Protodouvillina			■	■								
Arcticastrophia				■								
Bojodouvillina				■								
Borealistrophia				■								
?Contradouvillina				■								
Douvillinella				■								
Hercostrophia				■								
Malurostrophia				■								
Megastrophiella				■								
?Moravostrophia				■								
Nadiastrophia				■								
Paucistrophia				■								
Phragmostrophia				■								
Radiomena				■								
Taemostrophia				■								
Teichostrophia				■								
Telaeoshaleria				■								
Tsaganella				■								
DICOELOSTROPHIINAE				■								
Dicoelostrophia				■								
DOUVILLININAE				■								
Douvillina				■								
Douvillinaria				■								
Douvillinoides				■								
LEPTODONTELLINAE				■								
Leptodontella				■								
Parastrophonella				■								
?Spinostrophia				■								
Sulcatostrophia				■								
Zophostrophia				■								
SHALERIIDAE			■	■								
Shaleriella			■									
Shaleria			■	■								
STROPHODONTIDAE			■	■								
Lissostrophia			■									
?Neumanella			■									
Strophodonta			■	■								
Arbizustrophia				■								
Boucotstrophia				■								
Dictyostrophia				■								
Fascistropheodonta				■								
Galateastrophia				■								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Gorgostrophia				—								
Khangaestrophia				—								
?Leptodonta				—								
Megastrophia				—								
Minutostropheodonta				—								
Papillostrophia				—								
Parapholidostrophia				—								
Pholidostrophia				—								
Pterostrophia				—								
Strophonelloides				—								
?Trilobostrophia				—								
STROPHONELLIDAE			━	━								
Eostrophonella			—									
Strophonella			—	—								
UNCERTAIN		━										
EOCRAMATIIDAE		━										
Eocramatia		—										
ORTHOTETIDA		━	━	━	━	━						
TRIPLESIIDINA		━	━									
TRIPLESIOIDEA		━	━									
TRIPLESIIDAE		━	━									
Amphiplecia		—										
Bicuspina		—										
Caeroplecia		—										
Craigella		—										
Grammoplecia		—										
Ogmoplecia		—										
Onychoplecia		—										
Oxoplecia		—	?									
Cliftonia		—	—									
Paraonychoplecia		—	—									
Streptis		—	—									
Triplesia		—	—									
Acaretyrricula			—									
Brachymimulus			—									
Onychotreta			—									
Placocliftonia			—									
Placotriplesia			—									
Plectotreta			—									
ORTHOTETIDINA		━	━	━	━	━						
CHILIDIOPSOIDEA		━	━	━	━							
EOCRAMATIIDAE		━										
Eocramatia		—										
Neocramatia		—										
CHILIDIOPSIDAE		━	━	━								
GACELLINAE		━										
Gacella		—										
CHILIDIOPSINAE		━	━	━								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Fardenia		—	—									
Iridistrophia		—	—	—								
Coolinia			—									
Morinorhynchus			—									
Valdaria			—									
Hipparionix				—								
Xystostrophia				—								
AREOSTROPHIIDAE			━	━	━							
AREOSTROPHIINAE			━	━								
Aesopomum			—	—								
Areostrophia			—	—								
Carinastrophia				—								
ADECTORHYNCHINAE			━	━	━							
Terazkia			—									
Drahanostrophia				—								
Eoschuchertella				—								
Floweria				—								
Guistrophia				—								
Orthopleura				—								
Adectorhynchus					—							
ORTHOTETOIDEA				━	━	━						
PULSIIDAE				━	━							
Schellwienella				—	—							
Pulsia					—							
SCHUCHERTELLIDAE				━	━	━						
SCHUCHERTELLINAE				━	━	━						
Schuchertellopsis				—								
Schuchertella				—	—	—						
Serratocrista					—							
Goniarina						—						
STREPTORHYNCHINAE					━	━						
Drahanorhynchus					—							
Kiangsiella					—	—						
Streptorhynchus					—	—						
Arctitreta						—						
Bothrostegium						—						
Chelononia						—						
Notostrophia						—						
Taimyropsis						—						
Tropidelasma						—						
DERBYIIDAE					━	━						
Dorsoscyphus					—							
Streptopomum					—							
Derbyia					—	—						
Diplanus						—						
Nothopindax						—						
MEEKELLIDAE					━	━						
MEEKELLINAE					━	━						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Asiomeekella					—	—						
Geyerella					—	—						
Meekella					—	—						
Orthothetina					—	—						
Alatorthotetina						—						
Niviconia						—						
Paraorthotetina						—						
Perigeyerella						—						
Sicelia						—						
OMBONIINAE						—						
Ombonia						—						
ORTHOTETIDAE					—	—						
Apsocalymma					—							
Brochocarina					—							
Derbyoides					—	—						
Orthotetes					—	—						
Tapajotia					—	—						
Tethorotes					—	—						
Werriea					—	—						
Liberella						—						
ORTHOTETELLIDAE						—						
Hypopsia						—						
Orthotetella						—						
PRODUCTIDA		—	—	—	—	—	?					
CHONETIDINA		—	—	—	—	—	?					
CHONETOIDEA		—	—	—	—	—	?					
STROPHOCHONETIDAE		—	—	—								
STROPHOCHONETINAE		—	—	—								
Archeochonetes		—	—									
Spinochonetes			—									
Strophochonetes			—									
Zephyronetes			—									
Amosina			—	—								
Dawsonelloides			—	—								
Sanjuanetes			—	—								
Andalucinetes				—								
Asymmetrochonetes				—								
Australostrophia				—								
Babinia				—								
Bacbonetes				—								
Borealinetes				—								
Chlupacina				—								
Ctenochonetes				—								
Cyrtochonetes				—								
Johnsonetes				—								
Kentronetes				—								
Leptochonetes				—								
Leptochonetina				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Novellinetes				—								
Perichonetes				—								
Pseudostrophochonetes				—								
Tulynetes				—								
PARACHONETINAE			■	■								
Eccentricosta			—									
Orthochonetes				—								
Parachonetes				—								
Pseudochonetes				—								
Squamatina				—								
PROTOCHONETINAE			■	■								
Eoplicanoplia			—									
Hypselonetes			—									
Protochonetes			—									
Shagamella			—									
Nabarredia			—	—								
Quadrikentron				—								
CHONETIDAE				■								
CHONETINAE				■								
Boicinetes				—								
Chonetes				—								
Plebejochonetes				—								
DAGNACHONETINAE				■								
Dagnachonetes				—								
Frankiella				—								
Luanquella				—								
Mamutinetes				—								
Nurochonetes				—								
Pradochonetes				—								
Rhyssochonetes				—								
Sinochonetes				—								
DEVONOCHONETINAE				■								
Aseptonetes				—								
Devonochonetes				—								
Hallinetes				—								
Huananochonetes				—								
Longispina				—								
Montsenetes				—								
Striatochonetes				—								
Xinjiangochonetes				—								
NOTIOCHONETINAE				■								
Allanetes				—								
Notiochonetes				—								
Pleurochonetes				—								
Prachetes				—								
RETICHONETINAE				■								
Austronoplia				—								
Retichonetes				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
EODEVONARIIDAE				—								
Davoustia				—								
Eodevonaria				—								
Lomaella				—								
Loreleiella				—								
Renaudia				—								
CHONOSTROPHIIDAE				—	—							
Balikunochonetes				—								
Chonostrophia				—								
Chonostrophiella				—								
Santanghuia				—								
Tulcumbella					—							
ANOPLIIDAE				—	—	—						
HOLYNETINAE				—	—							
Herrerella				—								
Holynetes				—								
Malayanoplia				—								
Septachonetes				?								
Saharonetes					—							
Trichochonetes					—							
ANOPLIINAE				—	—	—						
Anoplia				—								
Anopliella				—								
Tornquistia				—	—	—						
Anopliopsis					—							
Yagonia					—							
Chonetina					—	—						
Adatsagochonetes						—						
Demonedys						—						
Gatia						—						
Glabrichonetina						—						
Kaninochonetes						—						
CAENANOPLIINAE				—	—	—						
Arcuaminetes				—								
Caplinoplia				—								
Celtanoplia				—								
Corbicularia				—								
Devonaria				—								
Gibberochonetes				—								
Klocinetes				—								
Ogorella				—								
Plicanoplia				—								
Semicaplinoplia				—								
Globosochonetes				—	—							
Caenanoplia					—							
Chilenochonetes					—							
Gonzalezius					—							
Subglobosochonetes					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Costachonetes					■	■						
Costachonetina						■						
Permochonetes						■						
Pinegochonetes						■						
Pygmochonetes						■						
Songzichonetes						■						
AIRTONIINAE					■							
Airtonia					■							
DAVIESIELLIDAE					■							
Daviesiella					■							
RUGOSOCHONETIDAE					■	■	?					
DELEPINEINAE					■	■						
Delepinea					■							
Gibbochonetes					■							
Megachonetes					■							
Petalochonetes					■							
Mongolochonetes						■						
PLICOCHONETINAE					■	■						
Plicochonetes					■							
Prorugaria					■							
Hemichonetes						■						
Rugaria						■						
Sulcirugaria						■						
RIOSANETINAE					■	■						
Aitegounetes					■							
Riosanetes					■							
Linshuichonetes						■						
CAPILLOMESOLOBINAE					■	■						
Mesolobus					■							
Capillomesolobus					■	■						
Tenuichonetes						■						
SVALBARDIINAE					■	■						
Eolissochonetes					■							
Leiochonetes					■							
Lissochonetes					■	■						
Quadrochonetes					■	■						
Capillonia						■						
Chonetinetes						■						
Dyoros						■						
Leurosina						■						
Sulcataria						■						
Svalbardia						■						
Tivertonia						■						
Zhexichonetes						■						
RUGOSOCHONETINAE					■	■	?					
Isochonetes					■							
Jakutochonetes					■							
Paramesolobus					■							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Robertsella					—							
Rugosochonetes					—							
Schistochonetes					—							
Sokolskya					—							
Thuringochonetes					—							
Chonetinella					—	—						
Neochonetes					—	—						
Alatochonetes						—						
Arctochonetes						—						
Fanichonetes						—						
Komukia						—						
Tethyochonetes						—						
Waagenites						—						
Waterhouseiella						—						
Fusichonetes						—	?					
LAMELLOSIINAE						—						
Lamellosia						—						
Parademonedys						—						
QUINQUENELLINAE						—						
Quinquenella						—						
Sandrella						—						
STRIOCHONETINAE						—						
Striochonetes						—						
UNDULELLINAE						—						
Micraphelia						—						
Undulella						—						
STROPHALOSIIDINA				—	—	—						
STROPHALOSIOIDEA				—	—	—						
ARAKSALOSIIDAE				—	—							
RHYTIALOSIINAE				—								
Agramatia				—								
Rhytialosia				—								
Sinalosia				—								
Steinhagella				—								
Veeversalosia				—								
DONALOSIINAE				—	?							
?Auchmerella				—								
Australosia				—								
Devonalosia				—								
Dichacaenia				—								
Donalosia				—								
Dotswoodia				—								
Eostrophalosia				—								
?Irboskites				—								
Morganella				—								
Oligorhachis				—								
Ralia				—								
Truncalosia				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Enigmalosia					?							
ARAKSALOSIINAE				━	━							
Araksalosia				—								
Hamlingella				—								
Kahlella				—								
Acanthatia				—	—							
Whidbornella				—	—							
Ruthiphiala					—							
QUADRATIINAE					━							
Chonetipustula					—							
Cyphotalosia					—							
Plicaea					—							
Plicatiferina					—							
Quadratia					—							
CHONOPECTIDAE				━	━							
Chonopectus				—	—							
Dengalosia					—							
Eileenella					—							
Parmephrix					—							
Semenewia					—							
STROPHALOSIIDAE					━	━						
DASYALOSIINAE					━	━						
Crossalosia					—							
Hontorialosia					—							
Dasyalosia					—	—						
Acanthalosia						—						
Arcticalosia						—						
?Costalosiella						—						
Echinalosia						—						
Guadalupelosia						—						
Marginalosia						—						
Notolosia						—						
Orthothrix						—						
Wyndhamia						—						
STROPHALOSIINAE					━	━						
Leptalosia					—							
Heteralosia					—	—						
Biplatyconcha						—						
Coronalosia						—						
Craspedalosia						—						
Etherilosia						—						
Kufria						—						
Lialosia						—						
Licharewiella						—						
Liveringia						—						
Megalosia						—						
Sphenalosia						—						
Strophalosia						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Subtaeniothaerus						—						
Taeniothaerus						—						
Tupelosia						—						
ECHINALOSIINAE						━						
Capillaria						—						
Pseudostrophalosia						—						
MINGENEWIINAE						━						
Melvillosia						—						
Mingenewia						—						
AULOSTEGOIDEA					━	━						
AULOSTEGIDAE					━	━						
GONDOLININAE					━							
Gondolina					—							
AGELESIINAE					━	━						
Stipulina					—							
Agelesia						—						
?Rhytibulbus						—						
INSTITELLINAE					━	━						
Institina					—							
Retroplexus					—							
Rugicostella					—							
Sinuatella					—							
Costellarina						—						
Craspedona						—						
Glyptosteges						—						
Institella						—						
Licharewiconcha						—						
Polymorpharia						—						
ECHINOSTEGINAE					━	━						
Archaiosteges					—							
Limbella					—	—						
Baissalosteges						—						
Echinosteges						—						
Edriosteges						—						
Girlasia						—						
Howseia						—						
Sphenosteges						—						
?Strophalosiella						—						
Strophalosiina						—						
Xenosteges						—						
?Spiriosium						?						
AULOSTEGINAE						━						
Aulosteges						—						
Carilya						—						
Lipanteris						—						
Megasteges						—						
Reedoconcha						—						
Saeptathaerus						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Taeniothaerus						—						
Wyatkina						—						
CHONOSTEGINAE						━						
Chonosteges						—						
Chonostegoides						—						
Costisteges						—						
Urushtenia						—						
Urushtenoidea						—						
CTENALOSIINAE						━						
Ctenalosia						—						
Mongolosia						—						
RHAMNARIINAE						━						
Cactosteges						—						
Colemanosteges						—						
Ramavectus						—						
Ramovsina						—						
Rhamnaria						—						
Spuriosia						—						
COOPERINIDAE						━						
COOPERININAE						━						
Ansehia						—						
Atelestegastus						—						
Cooperina						—						
Falafer						—						
EPICELIINAE						━						
Ceocypea						—						
Epicelia						—						
SCACCHINELLIDAE						━						
SCACCHINELLINAE						━						
Derbyella						—						
Scacchinella						—						
TSCHERNYSCHEWIIDAE						━						
Megatschernyschewia						—						
Reedosepta						—						
Trigonoproductus						—						
Tschernyschewia						—						
RICHTHOFENIOIDEA					━	━						
CYCLACANTHARIIDAE					━	━						
ZALVERINAE					━							
Zalvera					—							
TEGULIFERININAE					━	━						
Ardmosteges					—							
Planispina					—	—						
Proteguliferina					—	—						
Teguliferina					—	—						
Acritosia						—						
CYCLACANTHARIINAE						━						
Collumatus						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Cyclacantharia						■						
Sestropoma						■						
Taphrosestria						■						
GEMMELLAROIIDAE						■						
Cyndalia						■						
Gemmellaroia						■						
Tectarea						■						
HERCOSIIDAE						■						
Hercosestria						■						
Hercosia						■						
Neorichthofenia						■						
Sicularia						■						
Strophorichthofenia						■						
RICHTHOFENIIDAE						■						
Coscinarina						■						
Globosobucina						■						
Richthofenia						■						
Seseloidia						■						
Striirichthofenia						■						
PRODUCTIDINA				■	■	■	?					
ECHINOCONCHOIDEA				■	■	■						
SENTOSIIDAE				■	■	■						
CAUCASIPRODUCTINAE				■								
Caucasiproductus				■								
Praewaagenoconcha				■								
Strophoproductus				■								
SENTOSIINAE				■	■	■						
SENTOSIINI				■	■	■						
Laminatia				■								
Malloproductus				■								
Productellana				■								
Sentosia				■								
Sentosioides				■								
Jakutella					■							
Stegacanthia					■							
Markamia					■	■						
Alatoproductus						■						
BAGRASIINI					■							
Ericiatia					■							
ECHINOCONCHIDAE					■	■						
PUSTULINAE					■							
?Etheridgina					■							
Pustula					■							
Scutepustula					■							
?Septarinia					■							
ECHINOCONCHINAE					■	■						
CALLIPROTONINI					■	■						
Calliprotonia					■	■						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
ECHINOCONCHINI					━	━						
Echinoconchus					—							
Echinaria					—	—						
Stepanoconchus					—	—						
KARAVANKININI					━	━						
Echinoconchella					—							
Karavankina					—	—						
JURESANIINAE					━	━						
JURESANIINI					━	━						
Buntoxia					—							
Cubacula					—							
Densepustula					—							
Pulchratia					—							
Juresania					—	—						
Parajuresania					—	—						
Ametoria						—						
Bathymyonia						—						
Bilotina						—						
Vediproductus						—						
WAAGENOCONCHINI					━	━						
Balkhasheconcha					—							
Buxtoniella					—							
Spinauris					—							
Waagenoconcha					—	—						
Contraspina						—						
Fostericoncha						—						
UNCERTAIN						━						
Septiconcha						—						
LINOPRODUCTOIDEA				━	━	━						
MONTICULIFERIDAE				━	━	━						
DEVONOPRODUCTINAE				━								
Chonopectoides				—								
Devonoproductus				—								
Poloniproductus				—								
EOPRODUCTELLINAE				━								
Eoproductella				—								
Plicoproductus				—								
Striatoproductella				—								
SCHRENKIELLINAE				━	━	━						
Krekarpius				—	—							
Elalia					—							
Coopericus					—	—						
Dictyoclostoidea						—						
Permundaria						—						
Schrenkiella						—						
Striatospica						—						
GIGANTOPRODUCTINAE					━							
GIGANTOPRODUCTINI					━							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Beleutella					—							
Datangia					—							
Gigantoproductus					—							
Globosoproductus					—							
Kansuella					—							
Kueichowella					—							
Serbarinia					—							
Titanaria					—							
Xinjiangiproductus					—							
SEMIPLANINI					▬							
Latiproductus					—							
Semiplanella					—							
Semiplanus					—							
Talasoproductus					—							
STRIATIFERINAE					▬							
PROBOSCIDELLINI					▬							
Proboscidella					—							
STRIATIFERINI					▬							
Striatifera					—							
Striatiferella					—							
AURICULISPININAE					▬	▬						
AURICULISPININI					▬	▬						
Linoprotonia					—							
Ovatia					—							
Papiliolinus					—							
Undaria					—							
?Vitiliproductus					—							
Asperlinus						—						
Auriculispina						—						
Bocharella						—						
Cancrinelloides						—						
Chianella						—						
Costatumulus						—						
Filiconcha						—						
Globiella						—						
Kolymaella						—						
Liraria						—						
Magniplicatina						—						
Pseudohaydenella						—						
Spitzbergenia						—						
Striapustula						—						
Teleoproductus						—						
Undellaria						—						
Magadania						?						
LYONIINI					?	▬						
Nambuccalinus					?	—						
Nambdoania						—						
Nikitinia						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Nisalaria						—						
COMPRESSOPRODUCTINAE						▬						
Compressoproductus						—						
Fallaxoproductus						—						
Regrantia						—						
Sarytchevinella						—						
MONTICULIFERINAE						▬						
Chilianshania						—						
Monticulifera						—						
?Paramonticulifera						—						
Zhenania						—						
LINOPRODUCTIDAE					▬	▬						
ANIDANTHINAE					▬	▬						
Zia					—	—						
Akatchania						—						
Anidanthus						—						
Fusiproductus						—						
Kuvelousia						—						
Megousia						—						
Protanidanthus						—						
GRANDAURISPININAE					▬	▬						
Cancrinella					—	—						
Grandaurispina						—						
Holotricharina						—						
Lyonia						—						
Paucispinauria						—						
Stepanoviella						—						
Terrakea						—						
LINOPRODUCTINAE					▬	▬						
Balakhonia					—							
Fluctuaria					—							
Marginovatia					—							
Bandoproductus					—	—						
Linoproductus					—	—						
Aurilinoproductus						—						
Cimmeriella						—						
Coolkilella						—						
Kasetia						—						
?Mistproductus						—						
PAUCISPINAURIINAE						▬						
Pinegeria						—						
Spargospinosa						—						
SIPHONOSIINAE						▬						
Siphonosia						—						
UNCERTAIN						▬						
Selloproductus						—						
PRODUCTOIDEA				▬	▬	▬	?					
PRODUCTIDAE				▬	▬	▬						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
LEIOPRODUCTINAE				━	━	━						
LEIOPRODUCTINI				━	━							
Ardiviscus				—								
Bispinoproductus				—								
Galeatella				—								
Grandiproductella				—								
Leioproductus				—								
Mesoplica				—								
Productelloides				—								
Kavesia				?	—							
?Hunanoproductus					—							
Magnumbonella					—							
SEMIPRODUCTINI				━	━							
Acanthoproductus				—								
Margaritiproductus				—								
Nigerinoplica				—								
Semiproductus				—	—							
Lomatiphora					—							
Seminucella					—							
Spinocarinifera					—							
Yanguania					—							
HORRIDONIINI					━	━						
Praehorridonia					—							
?Rugoclostus					—							
Bailliena					—	—						
Burovia						—						
Horridonia						—						
Tityrophoria						—						
TYLOPLECTINI						━						
Araxilevis						—						
Pseudoantiquatonia						—						
Tyloplecta						—						
BUXTONIINAE					━	━						
BUXTONIINI					━	━						
Buxtonia					—							
Buxtonioides					—							
Flexaria					—							
Labriproductus					—							
Marginicinctus					—							
Setigerites					—							
?Bellaclathrus						—						
Kochiproductus						—						
TOLMATCHOFFIINI					━	━						
Acanthocosta					—							
Brasilioproductus					—							
Libys					—							
Marginatia					—							
Piloricilla					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Scissicosta					—							
Tolmatchoffia					—							
Tomilia					—							
Tomiproductus					—							
Umboanctus					—							
Xinshaoproductus					—							
Peniculauris						—						
Spinifrons						—						
Squamaria						—						
YAKOVLEVIINAE					━	━						
LATISPINIFERINI					━							
Latispinifera					—							
RETICULATIINI					━							
Admoskovia					—							
RIGRANTIINI					━	━						
Bicarteria					—							
Rigrantia						—						
DICTYOCLOSTINAE					━	━						
DICTYOCLOSTINI					━	━						
Auloprotonia					—							
Dictyoclostus					—							
Ozora					—							
Pugilis					—							
Reticulatia					—	—						
Callytharrella						—						
Chaoiella						—						
Dasysaria						—						
Kunlunia						—						
Liraplecta						—						
?Niutoushania						—						
Rugatia						—						
Stereochia						—						
LIRAPLECTINI						━						
Tarimoplecta						—						
PRODUCTINAE					━	━						
PRODUCTINI					━							
Carlinia					—							
Companteris					—							
Diaphragmus					—							
Dowhatania					—							
Lopasnia					—							
?Marginirugus					—							
Productus					—							
SPYRIDIOPHORINI					━	━						
Alexenia					—							
Spyridiophora						—						
KOZLOWSKIINI					━	━						
Eomarginifera					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Minispina					—							
Kozlowskia					—	—						
RETARIINI					━	━						
Antiquatonia					—							
Kelamelia					—							
Keokukia					—							
Marginoproductus					—							
Promarginifera					—							
Tesuquea					—							
Kutorginella					—	—						
Tubaria					—	—						
Thamnosia					?	—						
Pitakpaivania						—						
Svalbardoproductus						—						
PRODUCTELLIDAE				━	━	━	?					
PRODUCTELLINAE				━								
Chattertonia				—								
Helaspis				—								
Productella				—								
Sinoproductella				—								
Spinulicosta				—								
Stelckia				—								
PLICATIFERINAE				━	━	━						
RUGAURINI				━	━							
Iniproductus				—								
Planoproductus				—								
Orbinaria				—	?							
Carringtonia					—							
Rugauris					—							
LEVITUSIINI					━							
Acanthoplecta					—							
Admodorugosus					—							
Geniculifera					—							
Kadraliproductus					—							
Levitusia					—							
Spinorugifera					—							
LEVIPUSTULINI					━	━						
Bulahdelia					—							
Impiacus					—							
Lanipustula					—							
Levipustula					—							
Onopordumaria					—							
Verchojania					—							
Jakutoproductus						—						
Piatnitzkya						—						
PLICATIFERINI					━	━						
Absenticosta					—							
Aseptella					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Crossacanthia					—							
Ferganoproductus					—							
Lazarevia					—							
Platyselma					—							
Plicatifera					—							
?Rugoconcha					—							
Labaella						—						
SEMICOSTELLINI					━	━						
Cinctifera					—							
Limbifera					—							
Maemia					—							
Pharcidodiscus					—							
Rhytiophora					—							
Semicostella					—							
Overtoniina						—						
Spinosteges						—						
YAKOVLEVIINI					━	━						
Duartea					—							
Inflatia					—							
Sajakella					—							
Tenaspinus					—							
Yakovlevia						—						
OVERTONIINAE				━	━	━						
AVONIINI				━	━	━						
Barunkhuraya				—								
Avonia					—							
Onavia					—							
Quasiavonia					—							
Lazarevonia						—						
INSTITIFERINI					━							
Institifera					—							
?Thomasella					—							
LETHAMIINI					━	━						
Tuberculatella					—							
Amosia						—						
Archboldina						—						
Lethamia						—						
Wooramella						—						
COSTISPINIFERINI					━	━						
Tubersulculus					—	—						
Callyconcha						—						
Comuquia						—						
Costispinifera						—						
Dalinuria						—						
Dorashamia						—						
Dyschrestia						—						
Echinauriella						—						
Echinauris						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Lethamia						—						
Neoplicatifera						—						
Paraplicatifera						—						
Pseudoavonia						—						
Stictozoster						—						
Zhuaconcha						—						
KROTOVIINI					━	━						
Scoloconcha					—							
Krotovia					—	—						
OVERTONIINI					━	━						
Overtonia					—							
Fimbrinia					—	—						
PRODUCTININAE				━	━	━	?					
PRODUCTININI				━	━							
Dorsirugatia				—								
Productellina				—	—							
Productina				—	—							
Argentiproductus					—							
Caruthia					—							
PARAMARGINIFERINI					━	━	?					
Alitaria					—							
Eomarginiferina					—							
?Protoniella					—							
Bibatiola						—						
Bothrionia						—						
Cymoproductus						—						
Huatangia						—						
Paramarginifera						—						
Rugivestis						—						
Tethysiella						—						
Cathaysia						—	?					
?Paryphella						—	?					
CHONETELLINI						━						
Celebetes						—						
Chonetella						—						
Haydenella						—						
Ogbinia						—						
?Parachonetella						—						
Planihaydenella						?						
MARGINIFERINAE					━	━						
BREILEENIINI					━							
Breileenia					—							
Desmoinesia					—							
Sandia					—							
PAUCISPINIFERINI					━	━						
Jiguliconcha					—							
Hystriculina					—	—						
Shanxiproductus					—	—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Anemonaria						—						
Azygidium						—						
Caricula						—						
Caucasoproductus						—						
Costiferina						—						
Elliottella						—						
Jinomarginifera						—						
Lamnimargus						—						
Lampangella						—						
Liosotella						—						
Nudauris						—						
Oncosarina						—						
Paucispinifera						—						
Retimarginifera						—						
Spinarella						—						
Transennatia						—						
Xestosia						—						
INCISIINI						▬						
Cyrtalosia						—						
Incisius						—						
Rhytisia						—						
Scapharina						—						
Simplicarina						—						
MARGINIFERINI						▬						
Entacanthadus						—						
?Jipuproductus						—						
Marginifera						—						
Otariella						—						
Probolionia						—						
Spinomarginifera						—						
UNCERTAIN						▬						
Liolimbella						—						
UNCERTAIN						▬						
Lercarella						—						
Zhejiangoproductus						—						
UNCERTAIN							?					
Gosaukammerella							?					
LYTTONIIDINA					▬	▬						
LYTTONIOIDEA					▬	▬						
LYTTONIIDAE					▬	▬						
LYTTONIINAE					▬	▬						
Eolyttonia					—	—						
Keyserlingina					—	—						
Cardinocrania						—						
Collemataria						—						
Coscinophora						—						
Leptodus						—						
Loxophragmus						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Matanoleptodus						■						
Oldhamina						■						
Oldhaminella						■						
Petasmaia						■						
Pirgulia						■						
POIKILOSAKINAE					■	■						
Poikilosakos					■	■						
Adriana						■						
Choanodus						■						
Pseudoleptodus						■						
Sceletonia						■						
RIGBYELLIDAE						■						
Paralyttonia						■						
Rigbyella						■						
PERMIANELLOIDEA						■						
PERMIANELLIDAE						■						
Dicystoconcha						■						
Laterispina						■						
Permianella						■						
Tenerella						■						
UNCERTAIN						■						
LOCZYELLINAE						■						
Caninella						■						
Litocothia						■						
Loczyella						■						
UNCERTAIN						■						
?Chonopectella						■						
Ploughsharella						■						
?Punctoproductus						■						
UNCERTAIN						■						
LIOSOMENIDAE						■						
Liosomena						■						
RHYNCHONELLATA	■	■	■	■	■	■	■	■	■	■	■	■
PROTORTHIDA	■	■	■	■								
PROTORTHOIDEA	■											
LEIORIIDAE	■											
Leioria	■											
PROTORTHIDAE	■											
Glyptoria	■											
Israelaria	■											
Jamesella	■											
Loperia	■											
Protorthis	■											
Psiloria	■											
Saesorthis	■											
SKENIDIOIDEA		■	■	■								
SKENIDIIDAE		■	■	■								
Crossiskenidium		■										

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Protoskenidioides		─										
Replicoskenidioides		─										
Tropidothyris		─										
Skenidioides		─	─	─								
Skenidium				─								
PENTAMERIDA	━	━	━	━								
SYNTROPHIIDINA	━	━	━	━								
PORAMBONITOIDEA	━	━	━									
EOSTROPHIIDAE	━											
Cambrotrophia	─											
Syntrophioides	─											
HUENELLIDAE	━	━										
HUENELLINAE	━	━										
Huenellina	─											
Huenella	─	─										
Bondarevia		─										
Eosyntrophopsis		─										
Rectotrophia		─										
Rhabdostrophia		─										
MESONOMIINAE	━	━										
Mogoktella	─											
Radkeina	?											
Glyptotrophia	─	─										
Mesonomia	─	─										
RECTOTROPHIINAE		━										
Trigonstrophia		─										
TETRALOBULIDAE	━	━										
SYNTROPHOPSINAE	━	━										
Bobinella	─											
Plectotrophia	─											
?Tcharella	─											
Palaeostrophia	─	─										
Altunella		─										
Hesperotrophia		─										
Rhysostrophia		─										
Syntrophopsis		─										
PUNCTOLIRINAE		━										
Cuparius		─										
Pseudoporambonites		─										
Punctolira		─										
Rugostrophia		─										
Talovia		─										
TETRALOBULINAE		━										
Disepta		─										
Doloresella		─										
Imbricatia		─										
Tetralobula		─										
CLARKELLIDAE		━										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Acanthoglypha		—										
Calliglypha		—										
Clarkella		—										
Diaphelasma		—										
Fenxiangella		—										
Parallelostrophia		—										
Punastrophia		—										
Stichotrophia		—										
Syntrophina		—										
Syntrophinella		—										
Yangtzeella		—										
SYNTROPHIIDAE		━										
SYNTROPHIINAE		━										
Syntrophia		—										
XENELASMATINAE		━										
Rhyselasma		—										
Rosella		—										
Xenelasma		—										
Xenelasmella		—										
Xenelasmopsis		—										
PORAMBONITIDAE		━	━									
Porambonites		—	—									
CAMERELLOIDEA		━	━	━								
PARALLELELASMATIDAE		━										
Didymelasma		—										
Limstrophina		—										
Metacamarella		—										
Salonia		—										
Schizostrophina		—										
Vaga		—										
CAMERELLIDAE		━	━	━								
STENOCAMARINAE		━										
Boreadocamara		—										
Stenocamara		—										
CAMERELLINAE		━	━	━								
?Branconia		—										
Brevicamera		—										
Idiostrophia		—										
Karakulina		—										
Kokomerena		—										
Liricamera		—										
Neostrophia		—										
Perimecocoelia		—										
Plectosyntrophia		—										
Psilocamerella		—										
Tuloja		—										
Xizangostrophia		—										
Plectocamara		—	?									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Camerella		—	—									
Bleshidium			—									
Llanoella				—								
PARASTROPHINIDAE		▬	▬	▬								
Eoanastrophia		—										
Eosotrophina		—										
Ilistrophina		—										
Liostrophia		—										
Maydenella		—										
Parastrophina		—										
Parastrophinella		—	—									
Jolkinia			—									
Anastrophia			—	—								
PENTAMERIDINA		▬	▬	▬								
PENTAMEROIDEA		▬	▬									
VIRGIANIDAE		▬	▬									
MARIANNAELLINAE		▬	▬									
Eoconchidium		—										
Galeatellina		—										
Brevilamnulella		—	—									
Disulcatella			—									
Mariannaella			—									
VIRGIANINAE		▬	▬									
Proconchidium		—										
Prostricklandia		—										
Tcherskidium		—										
Holorhynchus		—	—									
Borealis			—									
Pseudoconchidium			—									
Virgiana			—									
Virgianella			—									
PLEURODIINAE			▬									
Pleurodium			—									
Plicidium			—									
PENTAMERIDAE			▬									
Bisulcata			—									
Brooksina			—									
Capelliniella			—									
Eokirkidium			—									
Harpidium			—									
Jolvia			—									
Kirkidium			—									
Lissocoelina			—									
Nanukidium			—									
Pentamerifera			—									
Pentameroides			—									
Pentamerus			—									
Rhipidium			—									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Stenopentamerus			—									
Twenhofelia			—									
SUBRIANIDAE			━									
CONCHIDIINAE			━									
Aliconchidium			—									
Conchidium			—									
Cymbidium			—									
Lamelliconchidium			—									
Lissidium			—									
?Plicocoelina			—									
Raridium			—									
Severella			—									
Spondylopyxis			—									
Vosmiverstum			—									
SUBRIANINAE			━									
Subriana			—									
Vagranella			—									
STRICKLANDIOIDEA			━									
AENIGMASTROPHIIDAE			━									
Aenigmastrophia			—									
Rugolepyros			—									
Vadimia			—									
STRICKLANDIIDAE			━									
KULUMBELLINAE			━									
Chiastodoca			—									
Kulumbella			—									
Microcardinalia			—									
Plicostricklandia			—									
Stricklandiella			—									
STRICKLANDIINAE			━									
?Aenigmastricklandia			—									
Costistricklandia			—									
Ehlersella			—									
Stricklandia			—									
?STRICKLANDISTROPHIIDAE			━									
Spondylostrophia			—									
Stricklandistrophia			—									
CLORINDOIDEA			━	━								
CLORINDIDAE			━	━								
PENTAMERELLINAE			━	━								
Clorindella			—									
Clorindina				—								
Clorindinella				—								
Pentamerella				—								
CLORINDINAE			━	━								
Barrandina			—									
Boucotides			—									
Indaclor			—									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Antirhynchonella			—	—								
Clorinda			—	—								
GYPIDULOIDEA			━	━								
GYPIDULIDAE			━	━								
DEVONOGYPINAE			━	━								
?Wyella			—	—								
Devonogypa				—								
Gypidulella				—								
Pseudosieberella				—								
GYPIDULINAE			━	━								
Amsdenina			—									
Ascanigypa			—									
Breviseptum			—									
Caryogyps			—									
Cadudium			—	—								
Galeatagypa			—	—								
Gashaomiaoia			—	—								
Gypidula			—	—								
Carinagypa				—								
Gypidulina				—								
Gypiduloides				—								
Levigypa				—								
Lysigypa				—								
Multicosta				—								
Novozemelia				—								
Physemella				—								
Plicogypa				—								
Sieberella				—								
Sieberelloides				—								
LEVIGATELLINAE			━	━								
Levigatella			—	—								
CONCHIDIELLINAE				━								
Biseptum				—								
?Glyptogypa				—								
Leviconchidiella				—								
Zdimir				—								
?Zdimirella				—								
GENICULIGYPINAE				━								
Geniculigypa				—								
IVDELINIINAE				━								
Ivdelinia				—								
Ivdeliniella				—								
ENANTIOSPHENIDAE				━								
Enantiosphen				—								
Enantiosphenella				—								
ORTHIDA	━	━	━	━	━	━						
ORTHIDINA	━	━	━	━								
PLECTORTHOIDEA	━	━	━									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
EOORTHIDAE	■	■										
Austrohedra	■											
Brahimorthis	■											
Glaphyrorthis	■											
Otusia	■											
Pompeckium	■											
Roanella	■											
Apheoorthis	■	■										
Eoorthis	■	■										
Ocnerorthis	■	■										
Apheoorthina		■										
Jivinella		■										
Robertorthis		■										
FINKELNBURGIIDAE	■	■										
Finkelnburgia	■	■										
Orusia	■	■										
Diparelasma		■										
Fasciculina		■										
Notoscaphidia		■										
CREMNORTHIDAE		■										
Brandysia		■										
Cremnorthis		■										
Septorthis		■										
CYCLOCOELIIDAE		■										
Cyclocoelia		■										
Rhynchorthis		■										
EUORTHISINIDAE		■										
Euorthisina		■										
Notorthisina		■										
PHRAGMORTHIDAE		■										
Phragmorthis		■										
PLECTORTHIDAE		■										
Apollonorthis		■										
Atlantida		■										
Corineorthis		■										
Desmorthis		■										
Doleroides		■										
Hebertella		■										
Irhirea		■										
Mimella		■										
Nanorthis		■										
Oligorthis		■										
Paterorthis		■										
Plectorthis		■										
Pseudomimella		■										
Schizophorella		■										
Severginella		■										
Weberorthis		■										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
RANORTHIDAE		▬										
Eodalmanella		—										
Ranorthis		—										
RHACTORTHIDAE		▬										
Aberia		—										
Eripnifera		—										
Rhactorthis		—										
TASMANORTHIDAE		▬										
Tasmanorthis		—										
WANGYUIIDAE		▬	▬									
Bowanorthis		—										
Sigmelasma		—										
Toxorthis		—										
Wangyuia			—									
GIRALDIELLIDAE		▬	▬									
Comatopoma		—										
Famatinorthis		—										
Gelidorthis		—										
Kvania		—										
Phaceloorthis		—										
Scaphorthis		—										
Tazzarinia		—										
Giraldibella		—	—									
Giraldiella		—	—									
Gelidorthina			—									
Proteorthis			—									
PLATYSTROPHIIDAE		▬	▬									
Acanthorthis		—										
Ffynnonia		—										
Mcewanella		—										
Salacorthis		—										
Siljanostrophia		—										
Gnamptorhynchos		—	—									
Platystrophia		—	—									
ORTHOIDEA	▬	▬	▬	▬								
BOHEMIELLIDAE	▬											
Bohemiella	—											
Chilidorthis	—											
Cymbricia	—											
Diraphora	—											
Murrinyinella	—											
Oligomys	—											
Wimanella	—											
ANOMALORTHIDAE	▬	▬										
Mogoktella	—											
Alimbella		—										
Anomalorthis		—										
Astraborthis		—										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Medessia		—										
HESPERONOMIIDAE	━	━										
Hesperonomiella	—	—										
Hesperonomia		—										
Mollesella		—										
Monorthis		—										
Murjukiana		—										
Protohesperonomia		—										
Treioria		—										
ARCHAEORTHIDAE		━										
Alocorthis		—										
Archaeorthis		—										
Cyrtonotella		—										
Diplonorthis		—										
Nicoloidea		—										
Nothorthis		—										
Pleurorthis		—										
Riograndella		—										
Shoshonorthis		—										
Xinanorthis		—										
LYCOPHORIIDAE		━										
Lycophoria		—										
ORTHIDIELLIDAE		━										
Eostrophomena		—										
Orthidiella		—										
Orthidium		—										
Trematorthis		—										
Tuvinia		—										
PLAESIOMYIDAE		━										
EVENKININAE		━										
Evenkina		—										
METORTHINAE		━										
Metorthis		—										
PLAESIOMYINAE		━										
Austinella		—										
Bokotorthis		—										
Campylorthis		—										
Chaulistomella		—										
Dinorthis		—										
Multicostella		—										
Pionorthis		—										
Plaesiomys		—										
Retrorsirostra		—										
Valcourea		—										
PORAMBORTHIDAE		━										
Poramborthis		—										
PRODUCTORTHIDAE		━										
GLOSSORTHINAE		━										

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Glossorthis		—										
Krattorthis		—										
Nicolorthis		—										
Prantlina		—										
PRODUCTORTHINAE		━										
Ferrax		—										
Nicolella		—										
Panderina		—										
Productorthis		—										
Saucrorthis		—										
Styxorthis		—										
WHITTARDIIDAE		━										
Marginorthis		—										
Whittardia		—										
GLYPTORTHIDAE		━	━									
Lepidorthis		—										
Lomatorthis		—										
Parisorthis		—										
Schalidomorthis		—										
Spinorthis		—										
Eridorthis		—	—									
Glyptorthis		—	—									
Cinerorthis			—									
ORTHIDAE		━	━	━								
Celsiorthis		—										
Diochthofera		—										
Leoniorthis		—										
Orthambonites		—										
Orthis		—										
Paralenorthis		—										
Sinorthis		—										
Sivorthis		—										
Sulcatorthis		—										
Sulevorthis		—										
Suriorthis		—										
Taphrorthis		—										
Trondorthis		—										
Orthokopis			—									
Orthostrophella			—	—								
Orthostrophia			—	—								
HESPERORTHIDAE		━	━	━								
Barbarorthis		—										
Boreadorthis		—										
Lordorthis		—										
Paradolerorthis		—										
Hesperorthis		—	—									
Dolerorthis		—	—	—								
Ptychopleurella		—	—	—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Asturorthis			—									
Flabellitesia			—									
Schizonema			—									
DALMANELLIDINA		—	—	—	—	—						
DALMANELLOIDEA		—	—	—	—	—						
ANGUSTICARDINIIDAE		—										
Angusticardinia		—										
Apatorthis		—										
PAURORTHIDAE		—										
Cyclomyonia		—										
Nereidella		—										
Paurorthis		—										
Tenuiseptorthis		—										
PORTRANELLIDAE		—										
Portranella		—										
HARKNESSELLIDAE		—	—									
Harknessella		—										
Haymina		—										
Horderleyella		—										
Reuschella		—										
Smeathenella		—										
Wulongella		—										
Kampella			—									
HETERORTHIDAE		—	—									
Arenorthis		—										
Cacemia		—										
Cilinella		—										
Fehamaya		—										
Heterorthina		—										
Heterorthis		—										
Incorthis		—										
Marionites		—										
Svobodaina		—										
Tafilaltia		—										
Tarfaya		—										
Tissintia		—										
Heterorthella			—									
TYRONELLIDAE		—	-	—								
Tyronella		—										
Didymoparcium				—								
PLATYORTHIDAE		—	—	—								
Crozonorthis		—										
Diceromyonia		—										
Elsaella		—										
Eorhipidomella		—										
Marklandella			—									
Platyorthis			—	—								
DALMANELLIDAE		—	—	—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
DALMANELLINAE		━	━									
Bancroftina		—										
Christiferina		—										
Cryptothyris		—										
Eremotrema		—										
Howellites		—										
?Minorothis		—										
Mirorthis		—										
Onnizetina		—										
Paucicrura		—										
Trucizetina		—										
Wysogorskiella		—										
Dalmanella		—	—									
Onniella		—	—									
Ravozetina		—	—									
TEMPLEELLINAE		━	━									
Templeella		—	—									
RESSERELLINAE		━	━	━								
Dedzetina		—										
Karlicium		—										
Visbyella			—									
Molongella			—	—								
Parmorthina			—	—								
Resserella			—	—								
Fascicostella				—								
Fascizetina				—								
Zlichopyramis				—								
ISORTHINAE			━	━								
Isorthis			—	—								
Levenea			—	—								
Protocortezorthis			—	—								
Tyersella			—	—								
Costisorthis				—								
Pelecymya				—								
Peleicostella				—								
CORTEZORTHINAE				━								
Cariniferella				—								
Cortezorthis				—								
Reeftonia				—								
PROKOPIINAE				━								
Eosophragmophora				—								
Miniprokopia				—								
Phragmophora				—								
Prokopia				—								
Protophragmapora				—								
DICOELOSIIDAE		━	━	━								
Epitomyonia		—	—									
Dicoelosia		—	—	—								

TABLE 41. *(Continued).*

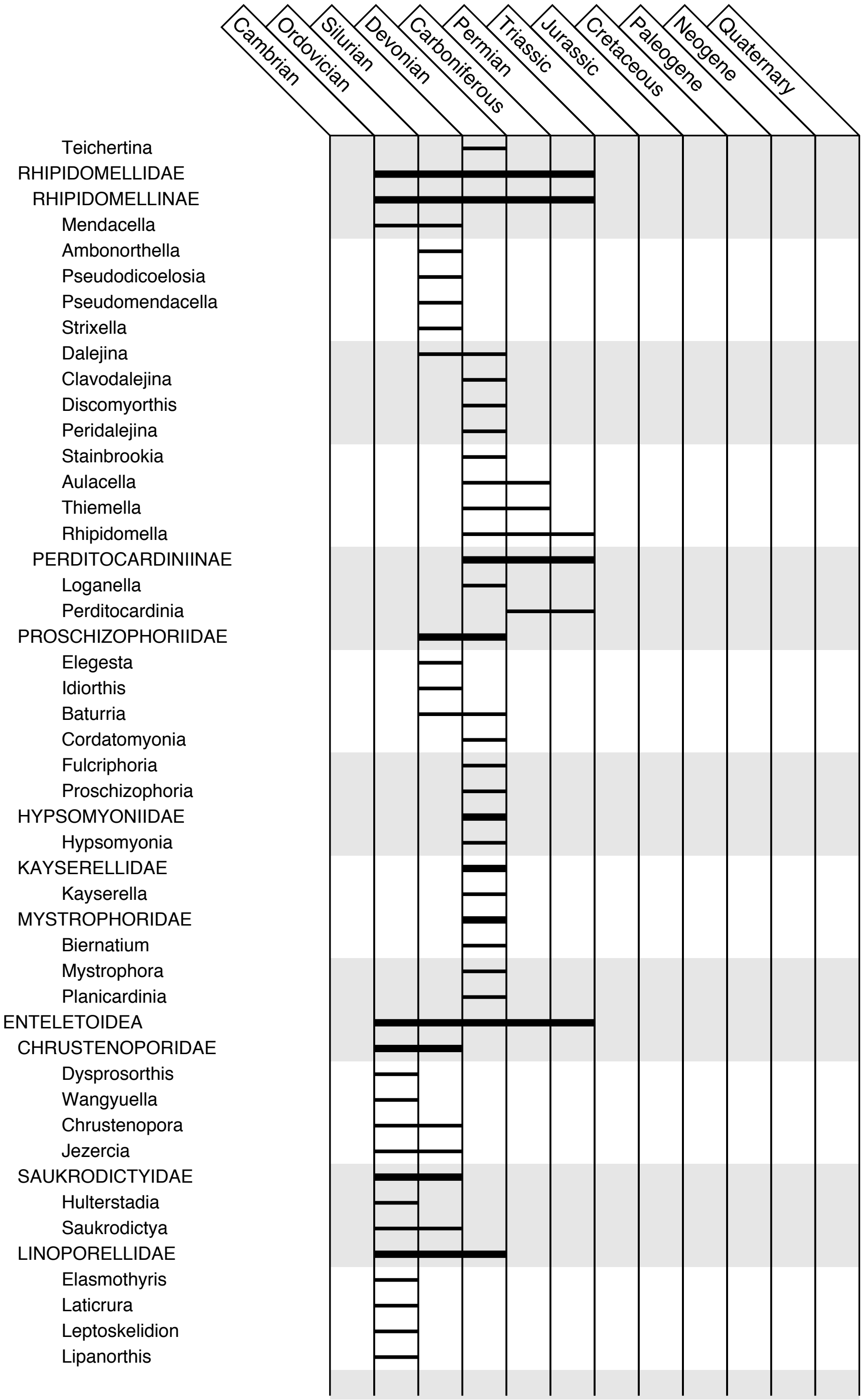


TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Salopia		—										
Linoporella			—									
Orthotropia			—									
Cycladigera				—								
DRABOVIIDAE		━	━	━								
DRABOVIINAE		━	━	━								
Boticium		—										
Destombesium		—										
Diorthelasma		—										
Draborthis		—										
Drabovia		—										
Drabovinella		—										
Eodiorthelasma		—										
Nocturnellia		—										
Oanduporella		—										
Pionodema		—										
Protomendacella		—										
Fascifera		—	—									
Hirnantia		—	—									
Kinnella		—	—									
Salopina		—	—	—								
Talentella			—	—								
Dalmanellopsis				—								
Megasalopina				—								
Orthiella				—								
Sphenophragmus				—								
MONELASMINIINAE				━								
Monelasmina				—								
Muriferella				—								
Vallomyonia				—								
SCHIZOPHORIIDAE			━	━	━	━						
Palaeoschizophoria			—									
Eoschizophoria			—	—								
Schizophoria				—	—							
Aulacophoria					—							
Enteletoides					—							
Neoschizophoria					—							
Acosarina					—	—						
Orthotichia					—	—						
Kotlaia						—						
Sunacosarina						—						
ENTELETIDAE					━	━						
Enteletes					—	—						
Parenteletes					—	—						
Enteletella						—						
Enteletina						—						
Mapingtichia						—						
Peltichia						—						

TABLE 41. *(Continued).*

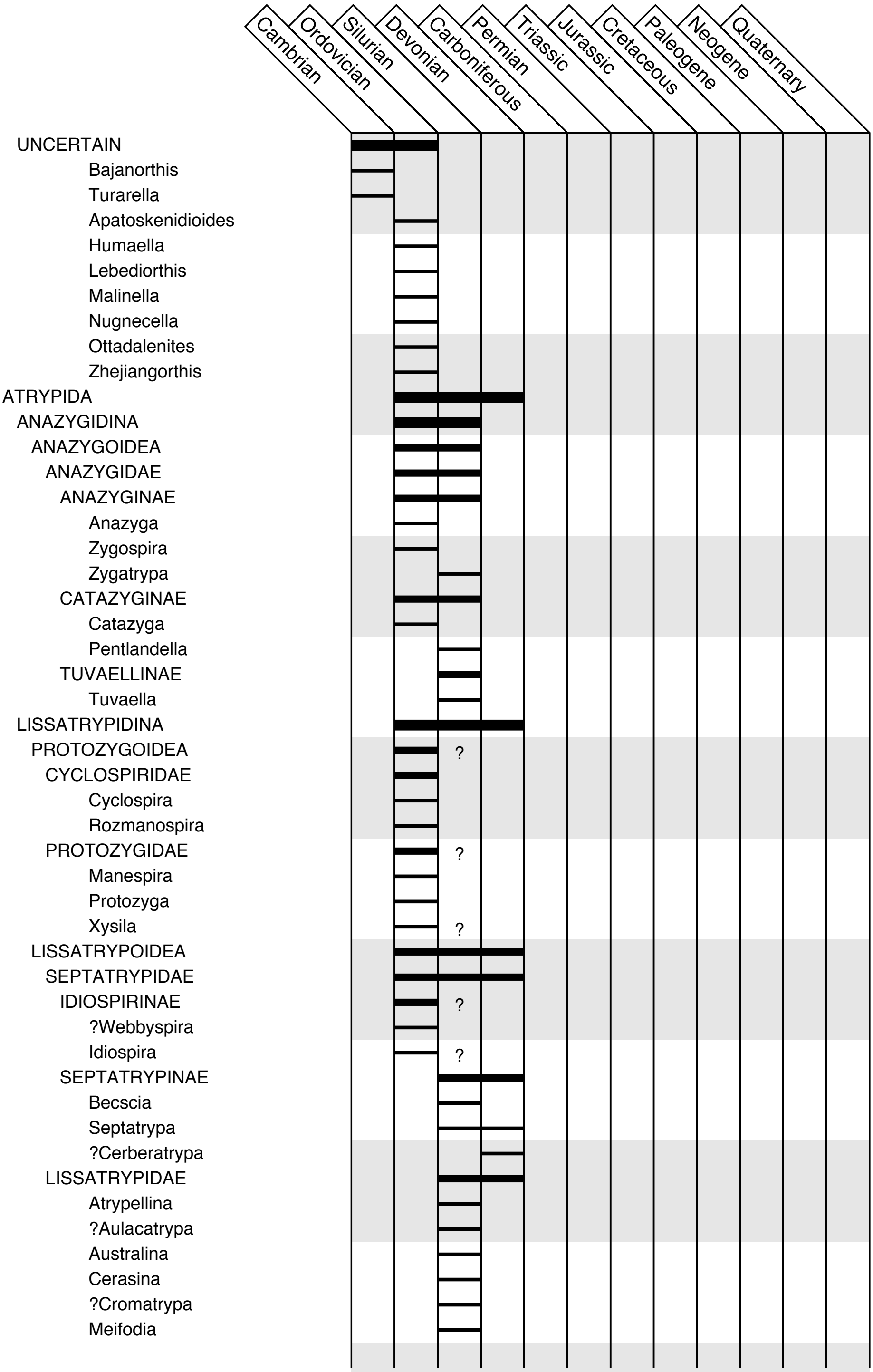


TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Parmula			—									
?Shrockia			—									
?Tectatrypa			—									
Atrypoidea			—	?								
Lissatrypa			—	—								
?Holynatrypa				—								
Levispira				—								
?Radimatrypa				—								
GLASSIOIDEA			━	━								
GLASSIIDAE			━	━								
Glassia			—									
?Nanatrypa			—									
Karbous				—								
Peratos				—								
?Trigonatrypa				—								
ATRYPIDINA		━	━	━								
ATRYPOIDEA		━	━	━								
ATRYPINIDAE		━	━	━								
PLECTATRYPINAE		?	━									
Sypharatrypa		?	—									
Plectatrypa			—									
Xanthea			—									
ATRYPININAE		━	━	━								
Atrypina		—	—	—								
Gracianella			—	—								
SPIRIGERININAE		━	━	━								
?Australispira		—										
Pectenospira		—										
Sulcatospira		—										
Schachriomonia		—	?									
Eospirigerina		—	—									
?Otarella		—	—									
Qilianotryma		—	—									
Spirigerina			—	—								
Neospirigerina				—								
?Ogilviella				—								
CLINTONELLINAE			━	━								
Alispira			—									
Anabaria			—									
Athyrisinoides			—									
Beitaia			—									
Clintonella			—									
Nalivkinia			—									
?Uncitispira			—									
Tibetatrypa				—								
ATRYPIDAE			━	━								
ATRYPINAE			━	━								
Dihelictera			—									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Endrea			—									
Gotatrypa			—									
Joviatrypa			—									
Oglupes			—									
?Omnutakhella			—									
Procarinatina			—									
Protatrypa			—									
Zygospiraella			—									
Atrypa			—	—								
Rugosatrypa			?	—								
Atryparia				—								
Kyrtatrypa				—								
?Togatrypa				—								
SPINATRYPINAE			━	━								
Eospinatrypa			—									
Spinatrypina			—	—								
?Catatypa				—								
?Gibberosatrypa				—								
Invertrypa				—								
Isospinatrypa				—								
?Oglu				—								
?Punctspinatrypa				—								
Spinatrypa				—								
?Tuberculatospira				—								
Waiotrypa				—								
INVERTININAE				━								
?Falsatrypa				—								
Invertina				—								
Kerpina				—								
PSEUDOGRUENEWALDTIINAE				━								
Iowatrypa				—								
Pseudogruenewaldtia				—								
VARIATRYPINAE				━								
Anatrypa				—								
Desquamatia				—								
Devonatrypa				—								
Heckerella				—								
Pseudoatrypa				—								
Radiatrypa				—								
Uralospira				—								
Variatrypa				—								
PUNCTATRYPOIDEA			━	━								
PUNCTATRYPIDAE			━	━								
ATRYPINELLINAE			━	━								
?Istokina			—									
Limbatrypa			—									
Atrypinella			—	—								
Reticulatrypa			?	—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
PUNCTATRYPINAE				■								
Crassipunctatrypa				■								
Fossatrypa				■								
Punctatrypa				■								
Sinopunctatrypa				■								
Undatrypa				■								
DAVIDSONIIDINA			■	■								
DAVIDSONIOIDEA			■	■								
CARINATINIDAE			■	■								
?Plesicarinatina			■	■								
Biconostrophia				■								
Carinatina				■								
Carinatrypa				■								
Eifelatrypa				■								
?Mangkeluia				■								
Mogoliella				■								
DAVIDSONIIDAE			■	■								
Zeravshania			■	■								
Davidsonia				■								
Prodavidsonia				■								
Rugodavidsonia				■								
PALAFERELLOIDEA			■	■								
SYMMATRYPIDAE			■									
Symmatrypa			■									
KARPINSKIIDAE			■	■								
KARPINSKIINAE			■	■								
Crassatrypa			■									
Eokarpinskia			■	■								
Karpinskia				■								
Mimatrypa				■								
Neokarpinskia				■								
VAGRANIINAE				■								
Desatrypa				■								
Vagrania				■								
?Weizhouella				■								
PALAFERELLIDAE				■								
Gruenewaldtia				■								
SPIRIFERIDA		■	■	■	■	■	■					
SPIRIFERIDINA		■	■	■	■	■	■					
CYRTIOIDEA		■	■	■								
CYRTIIDAE		■	■	■								
EOSPIRIFERINAE		■	■	■								
Eospirifer		■	■	■								
Endospirifer			■									
Espella			■									
Mictospirifer			■									
Nurataella			■									
Striispirifer			■									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Xinanospirifer			—									
Yingwuspirifer			—									
Havlicekia			—	—								
Hedeina			—	—								
Janius			—	—								
Macropleura			—	—								
Myriospirifer			—	—								
Badainjarania				—								
Lobvia				—								
CYRTIINAE			▬									
Cyrtia			—									
Dongbeiispirifer			—									
Plicocyrtia			—									
HEDEINOPSIDAE			▬									
HEDEINOPSINAE			▬									
Hedeinopsis			—									
Tannuspirifer			—									
ADOLFIOIDEA			▬	▬								
ADOLFIIDAE			▬	▬								
PINGUISPIRIFERINAE			▬	▬								
Nikiforovaena			—	—								
Spurispirifer			—	—								
Amoenospirifer				—								
Brevispirifer				—								
Ljudmilispirifer				—								
Microttia				—								
Pinguispirifer				—								
ADOLFIINAE				▬								
Acutatheca				—								
Adolfia				—								
Allanella				—								
Brevispinifera				—								
Chimaerothyris				—								
Eospiriferina				—								
Ferronia				—								
Fidespirifer				—								
Guicyrtia				—								
Paillettia				—								
Spinella				—								
Volgospirifer				—								
CALLISPIRIFERINAE				▬								
Callispirifer				—								
Rochtex				—								
EUREKASPIRIFERINAE				▬								
Eurekaspirifer				—								
ECHINOSPIRIFERIDAE				▬								
Adolfispirifer				—								
Arctospirifer				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Echinospirifer				—								
Enchondrospirifer				—								
Hispidaria				—								
Howittia				—								
Indospirifer				—								
Rigauxia				—								
Sergunkovia				—								
MARTINIOIDEA			—	—	—	—						
TENELLODERMIDAE			—	—								
Tenellodermis			—	—								
Cingulodermis				—								
ELYTHYNIDAE				—								
Elythyna				—								
Najadospirifer				—								
Planispirifer				—								
Tatjanaspirifer				—								
GERKISPIRIDAE				—	—							
Acanthospirina				—								
Oiosia				—								
Spinospirifer				—								
Gerkispira					—							
Punctothyris					—							
MARTINIIDAE				—	—	—						
ELIVELLINAE				—	—	—						
Ushkolia				—								
Chuiella					—							
?Martiniella					—							
Elivella						—						
Moumina						—						
EOMARTINIOPSINAE				?	—	—						
Eomartiniopsis				?	—							
Globispirifer					—							
Kisilia					—							
Merospirifer					—							
Heteraria						—						
Rallacosta						—						
MARTINIINAE					—	—						
Beschevella					—							
Implexina					—							
Jilinmartinia					—							
Weiningia					—							
Martinia					—	—						
Tiramnia					—	—						
Chapursania						—						
Ladoplica						—						
Postamartinia						—						
Spinomartinia						—						
PERISSOTHYRIDIDAE					—							

Table 41. *(Continued).*

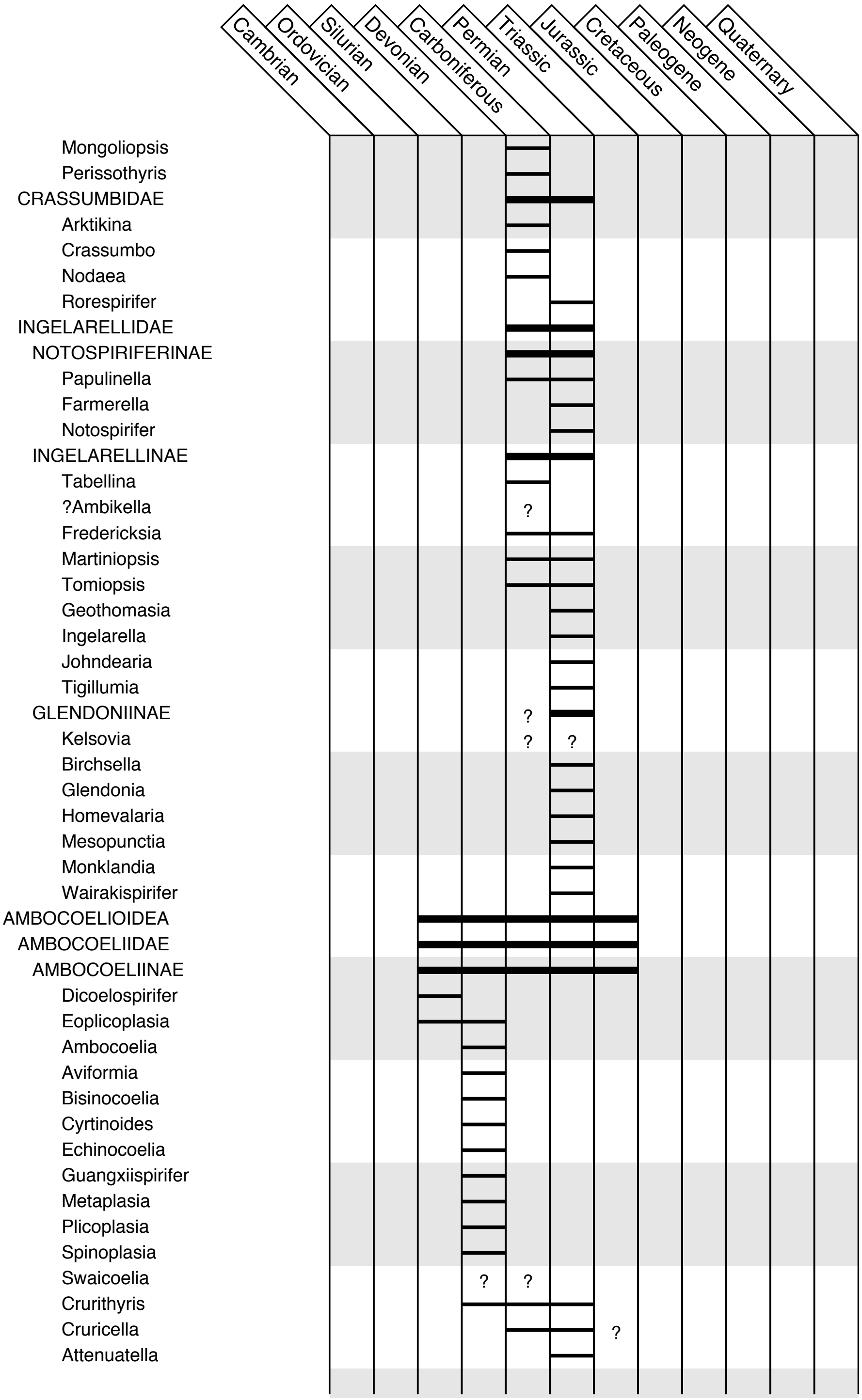


TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Biconvexiella						—						
Ogilvicoelia						—						
Orbicoelia						—						
Paracrurithyris						—	—					
RHYNCHOSPIRIFERINAE				━								
Amboglossa				—								
Ambothyris				—								
Changtangella				—								
Choperella				—								
Crurispina				—								
Diazoma				—								
Emanuella				—								
Ilmenia				—								
Ilmeniopsis				—								
Ilmenispina				—								
Ilmospirifer				—								
Kosirium				—								
Ladjia				—								
Levibiseptum				—								
Moravilla				—								
Rhynchospirifer				—								
Zhonghuacoelia				—								
LAZUTKINIIDAE				━								
Lazutkinia				—								
Prolazutkinia				—								
VERNEUILIIDAE				━	━							
Nuguschella				—								
Verneuilia				—	—							
Minythyra					—							
EUDOXINIDAE				━	━	━						
Paulonia				—	—							
Eudoxina					—							
Costicrura						—						
Wilberrya						—						
CYRTOSPIRIFEROIDEA				━								
CONISPIRIFERIDAE				━								
Conispirifer				—								
Pyramidaspirifer				—								
CYRTOSPIRIFERIDAE				━								
CYRTIOPSINAE				━								
Acutella				—								
Cyrtiopsis				—								
Dichospirifer				—								
Dmitria				—								
Eodmitria				—								
Mennespirifer				—								
Platyspirifer				—								
Pseudocyrtiopsis				—								

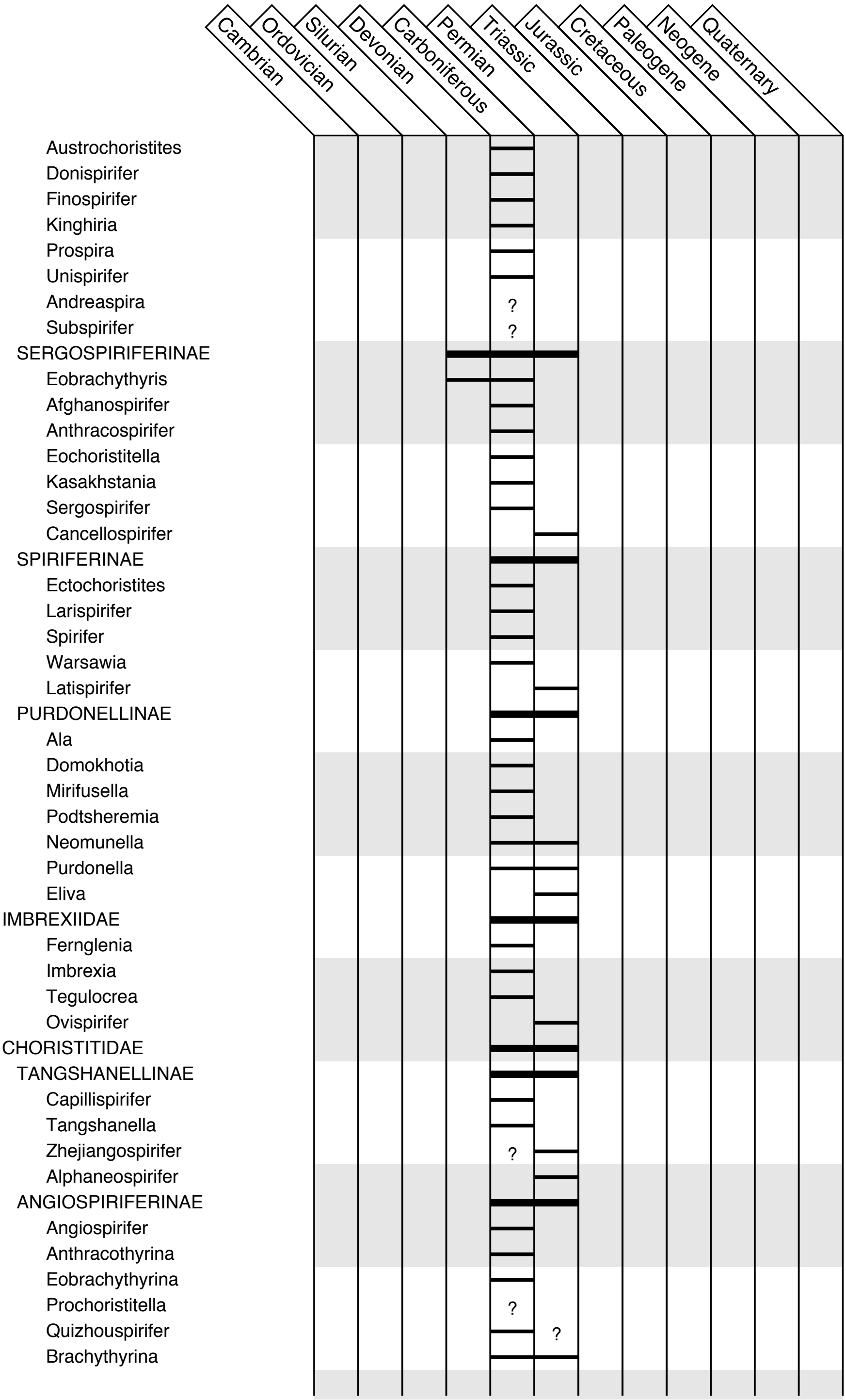
TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Tiocyrspis				■								
Uchtospirifer				■								
CYRTOSPIRIFERINAE				■								
Austrospirifer				■								
Cyrtospirifer				■								
Geminisulcispirifer				■								
Liraspirifer				■								
Nikospirifer				■								
Petshorospirifer				■								
Pripyatispirifer				■								
Regelia				■								
Sinospirifer				■								
Sphenospira				■								
Syringospira				■								
Tarandrospirifer				■								
Tenticospirifer				■								
SPINOCYRTIIDAE				■								
Acutoria				■								
Alatiformia				■								
Carpinaria				■								
Duryeella				■								
Eosyringothyris				■								
Mediospirifer				■								
Orthospirifer				■								
Platyrachella				■								
Spinocyrtia				■								
Subcuspidella				■								
THEODOSSIOIDEA				■	■							
THEODOSSIIDAE				■								
BRANIKIINAE				■								
Branikia				■								
Jilinospirifer				■								
Lenzia				■								
THEODOSSIINAE				■								
Paralazutkinia				■								
Theodossia				■								
Urella				■								
ULBOSPIRIFERIDAE				■								
PALAEOSPIRIFERINAE				■								
Palaeospirifer				■								
ULBOSPIRIFERINAE				■								
Cyrtiorina				■								
Tenisia				■								
Ulbospirifer				■								
PALAEOCHORISTITIDAE				■	■							
Eochoristites				■	■							
Palaeochoristites					■							
BRACHYTHYRIDOIDEA				■	■	■						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
SKELIDORYGMIDAE				■	■							
Litothyris				■								
Phragmobrachythyris					■							
Skelidorygma					■							
BRACHYTHYRIDIDAE				■	■	■						
Brachythyris				■	■							
Meristorygma					■	■						
Cathayspirina						■						
Dalaia						■						
Ella						■						
Pustuloplica						■						
PAECKELMANNELLOIDEA				■	■	■						
STROPHOPLEURIDAE				■	■	■						
STROPHOPLEURINAE				■	■							
Strophopleura				■								
?Iwaispirifer				■	■							
Acuminothyris					■							
Avisyrinx					■							
Calvustrigis					■							
Cantabriella					■							
Triangularia					■							
Voiseyella					■							
BASHKIRIINAE					■							
Bashkiria					■							
Celsifornix					■							
Fusella					■							
Varuna					■							
Adminiculoria					?							
PTEROSPIRIFERINAE					■	■						
Alispirifer					■							
Spiriferinaella					■	■						
Haplospirifer						■						
Pteroplecta						■						
Pterospirifer						■						
Xizispirifer						■						
Yukonosprifer						■						
PAECKELMANELLIDAE						■						
PAECKELMANELLINAE						■						
Darvasia						■						
Odontospirifer						■						
Paeckelmanella						■						
SCENESIINAE						■						
Scenesia						■						
SPIRIFEROIDEA				■	■	■						
SPIRIFERIDAE				■	■	■						
PROSPIRINAE				■	■							
Parallelora				■	■							
Atylephorus					■							

TABLE 41. *(Continued).*



	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Austrochoristites					—							
Donispirifer					—							
Finospirifer					—							
Kinghiria					—							
Prospira					—							
Unispirifer					—							
Andreaspira					?							
Subspirifer					?							
SERGOSPIRIFERINAE				━	━	━						
Eobrachythyris				—	—							
Afghanospirifer					—							
Anthracospirifer					—							
Eochoristitella					—							
Kasakhstania					—							
Sergospirifer					—							
Cancellospirifer						—						
SPIRIFERINAE					━	━						
Ectochoristites					—							
Larispirifer					—							
Spirifer					—							
Warsawia					—							
Latispirifer						—						
PURDONELLINAE					━	━						
Ala					—							
Domokhotia					—							
Mirifusella					—							
Podtsheremia					—							
Neomunella					—	—						
Purdonella					—	—						
Eliva						—						
IMBREXIIDAE					━	━						
Fernglenia					—							
Imbrexia					—							
Tegulocrea					—							
Ovispirifer						—						
CHORISTITIDAE					━	━						
TANGSHANELLINAE					━	━						
Capillispirifer					—							
Tangshanella					—							
Zhejiangospirifer					?	—						
Alphaneospirifer						—						
ANGIOSPIRIFERINAE					━	━						
Angiospirifer					—							
Anthracothyrina					—							
Eobrachythyrina					—							
Prochoristitella					?							
Quizhouspirifer					—	?						
Brachythyrina					—	—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Elinoria					—	—						
Unicostatina						—						
CHORISTITINAE					━	━						
Alphachoristites					—							
Choristitella					—							
Settedabania					—							
Choristites					—	?						
Parachoristites					—	—						
SPIRIFERELLIDAE					━	━						
Plicatospiriferella					—							
Eridmatus					—	—						
Spiriferella					—	—						
Alispiriferella						—						
Arcullina						—						
Bamberina						—						
Darbandia						—						
Elivina						—						
Hunzina						—						
Rhombospirifer						—						
?Spiriferelloides						—						
Timaniella						—						
Tintoriella						—						
Tipispirifer						—						
TRIGONOTRETIDAE					━	━						
TRIGONOTRETINAE					━	━						
Costuliplica					—							
Frechella					—							
?Maxwellispirifer					—							
Tegulispirifer					—							
Aperispirifer						—						
Brachythyrinella						—						
Sulciplica						—						
Trigonotreta						?						
NEOSPIRIFERINAE					━	━						
Gibbospirifer					—							
Lutuginia					—							
?Betaneospirifer					—	—						
Gypospirifer					—	—						
Tibetospirifer					—	—						
Blasispirifer						—						
Cartorhium						—						
Costatispirifer						—						
Crassispirifer						—						
Cratispirifer						—						
Fusispirifer						—						
Imperiospira						—						
Kaninospirifer						—						
Lepidospirifer						—						

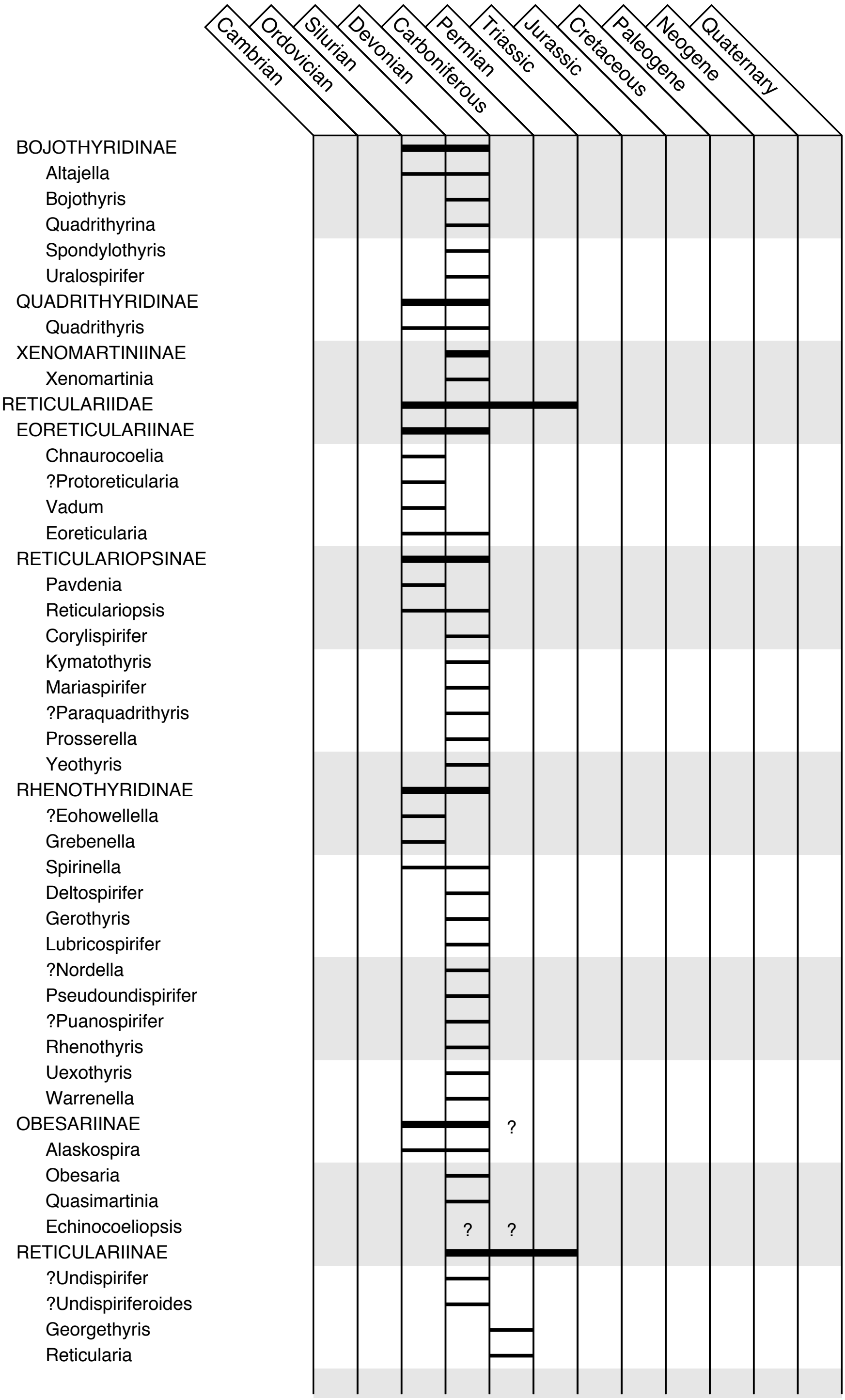
TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Neospirifer						—						
Occidalia						—						
Pondospirifer						—						
Quadrospira						—						
Septospirifer						—						
UNCERTAIN			━	━								
Notanoplia			—	—								
Notoparmella			—	—								
Boucotia				—								
Callicalyptella				—								
Costanoplia				—								
Guixiella				—								
Hollardiella				—								
Jacetanella				—								
Luofuia				—								
Paracostanoplia				—								
Paraplicanoplia				—								
Plicanoplites				—								
Septaparmella				—								
Serrulatrypa				—								
Tangxiangia				—								
DELTHYRIDINA			━	━	━	━						
DELTHYRIDOIDEA			━	━	━							
CYRTINOPSIDAE			━	━								
ARASPIRIFERINAE			━									
Araspirifer			—									
Boucotinskia			—									
CYRTINOPSINAE			━	━								
Kozlowskiellina			—									
Cyrtinopsis				—								
Jehlanaria				—								
Megakozlowskiella				—								
Plicocyrtina				—								
DELTHYRIDIDAE			━	━								
DELTHYRIDINAE			━	━								
Delthyris			—	—								
Ivanothyris				—								
HOWELLELLINAE			━	━								
Rufispirifer			—									
Acanthospirifer			—	—								
Aldanispirifer			—	—								
Howellella			—	—								
Howelloidea				—								
Orientospirifer				—								
Pseudokymatothyris				—								
Qiansispirifer				—								
Quiringites				—								
Xenospirifer				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
ACROSPIRIFERIDAE				━								
ACROSPIRIFERINAE				━								
Acrospirifer				—								
Filispirifer				—								
Mauispirifer				—								
Xerospirifer				—								
COSTISPIRIFERINAE				━								
Costispirifer				—								
Cumberlandina				—								
ELYMOSPIRIFERINAE				━								
Borealispirifer				—								
Elymospirifer				—								
Multispirifer				—								
Perryspirifer				—								
HYSTEROLITIDAE				━								
FIMBRISPIRIFERINAE				━								
Bultynckia				—								
Fimbrispirifer				—								
Struveina				—								
Vandercammenina				—								
HYSTEROLITINAE				━								
Antispirifer				—								
Arduspirifer				—								
Australospirifer				—								
Brachyspirifer				—								
Costellispirifer				—								
Dixonella				—								
Dyticospirifer				—								
Euryspirifer				—								
Gaspespirifer				—								
Hysterolites				—								
Otospirifer				—								
Paraspirifer				—								
Patriaspirifer				—								
Rostrospirifer				—								
Trigonospirifer				—								
Xinjiangospirifer				—								
MUCROSPIRIFERIDAE				━	━							
MUCROSPIRIFERINAE				━								
Apousiella				—								
Eleutherokomma				—								
Mucrospirifer				—								
Sulcatospirifer				—								
TYLOTHYRIDINAE				━	━							
Tylothyris				—	—							
Texathyris					—							
RETICULARIOIDEA			━	━	━	━						
XENOMARTINIIDAE			━	━								

TABLE 41. *(Continued).*



	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
BOJOTHYRIDINAE			—	—								
Altajella			—	—								
Bojothyris				—								
Quadrithyrina				—								
Spondylothyris				—								
Uralospirifer				—								
QUADRITHYRIDINAE			—	—								
Quadrithyris			—	—								
XENOMARTINIINAE				—								
Xenomartinia				—								
RETICULARIIDAE			—	—	—	—						
EORETICULARIINAE			—	—								
Chnaurocoelia			—									
?Protoreticularia			—									
Vadum			—									
Eoreticularia			—	—								
RETICULARIOPSINAE			—	—								
Pavdenia			—									
Reticulariopsis			—	—								
Corylispirifer				—								
Kymatothyris				—								
Mariaspirifer				—								
?Paraquadrithyris				—								
Prosserella				—								
Yeothyris				—								
RHENOTHYRIDINAE			—	—								
?Eohowellella			—									
Grebenella			—									
Spirinella			—	—								
Deltospirifer				—								
Gerothyris				—								
Lubricospirifer				—								
?Nordella				—								
Pseudoundispirifer				—								
?Puanospirifer				—								
Rhenothyris				—								
Uexothyris				—								
Warrenella				—								
OBESARIINAE			—	—	?							
Alaskospira			—	—								
Obesaria				—								
Quasimartinia				—								
Echinocoeliopsis				?	?							
RETICULARIINAE				—	—	—						
?Undispirifer				—								
?Undispiriferoides				—								
Georgethyris					—							
Reticularia					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Parareticularia						—						
Squamularia						—						
THOMASARIIDAE				━								
Thomasaria				—								
ELYTHIDAE				━	━	━						
ELYTHINAE				━	━							
Elita				—								
Kitakamithyris					—							
MARTINOTHYRIDINAE					━	━						
Martinothyris					—							
Orenburgella					—							
Latiplecus						—						
TORYNIFERINAE					━	━						
Plicotorynifer					—							
Torynifer					—							
Toryniferella					—							
Spirelytha						—						
Stepanoviina						—						
Taimyrella						—						
PHRICODOTHYRIDINAE					━	━						
Nebenothyris					—	—						
Phricodothyris					—	—						
Astegosia						—						
Bajkuria						—						
Bullarina						—						
Permophricodothyris						—						
ANOMALORIINAE						━						
Anomaloria						—						
Zhinania						—						
ATHYRIDIDA		━	━	━	━	━	━	━				
ATHYRIDIDINA		━	━	━	━	━	━	?				
MERISTELLOIDEA		━	━	━	━							
MERISTELLIDAE		━	━	━								
WHITFIELDELLINAE		━	━	?								
Whitfieldella		—	—	?								
Koigia			—									
Kozlenia			—									
Tschatkalia			—									
MERISTELLINAE		━	━	━								
Hindella		—	—									
Arctomeristina			—									
?Pseudomeristina			—									
Meristina			—	—								
Meristella			?	—								
Charionella				—								
Charionoides				—								
?Imdentistella				—								
?Meristelloides				—								

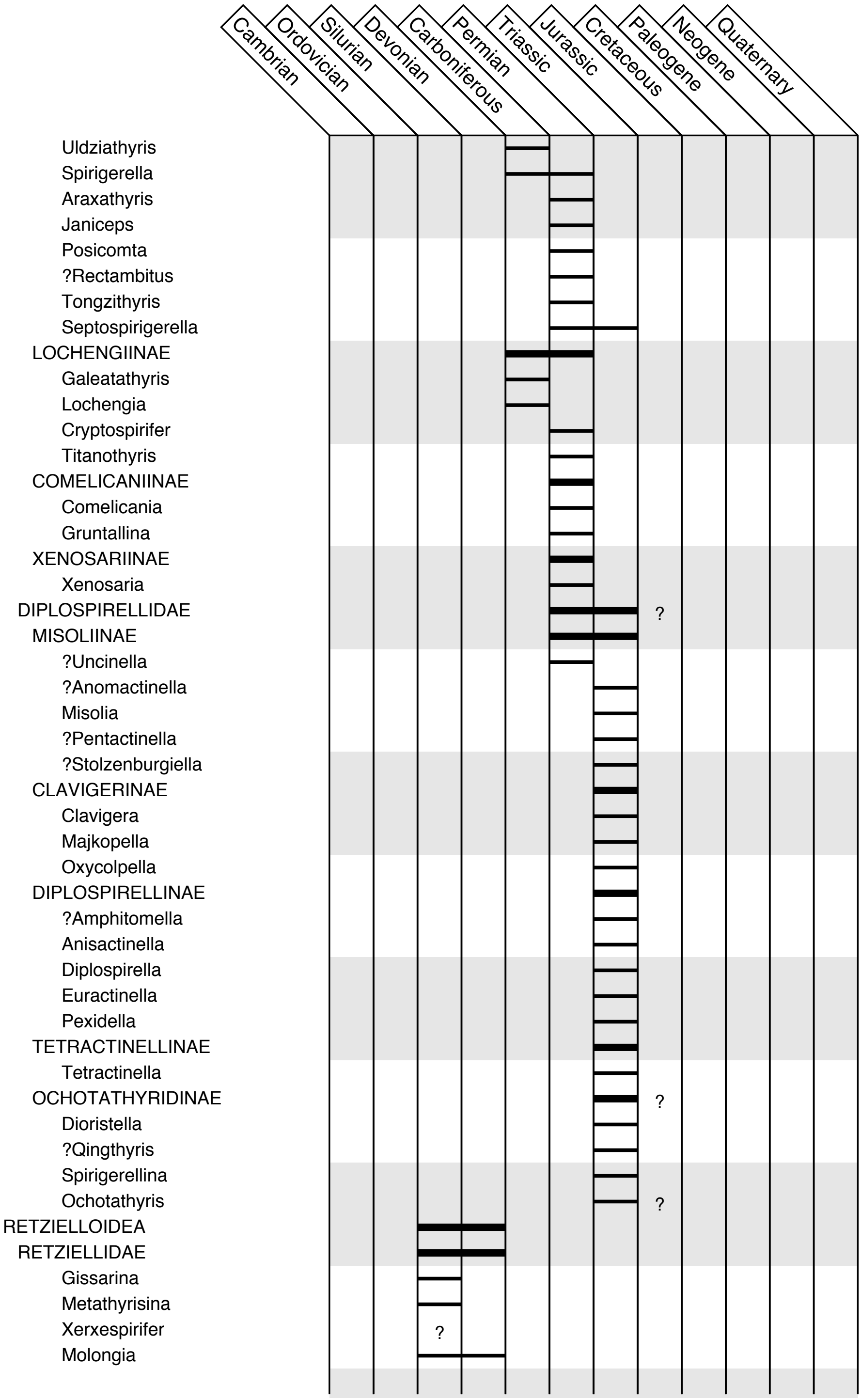
TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Pentagonia				■								
?Plancella				■								
MERISTIDAE		■	■	■	■							
MERISTINAE		■	■	■	■							
Aulidospira		■										
Amerista			■									
Dicamaropsis			■									
Merista			■	■								
Dicamara				■								
Tyrganiella				■								
Camarium				■	■							
CAMAROPHORELLINAE			■	■	■							
?Liocoelia			■									
Camarospira				■								
Camarophorella				■	■							
ROWLEYELLINAE					■							
Rowleyella					■							
TRIATHYRIDIDAE				■								
SEPTATHYRIDINAE				■								
Septathyris				■								
TRIATHYRIDINAE				■								
Triathyris				■								
ATHYRIDOIDEA		■	■	■	■	■	■	?				
HYATTIDINIDAE		■	■									
Hyattidina		■	■									
?Argella			■									
ATHYRIDIDAE			■	■	■	■	■					
ATHYRISININAE			■	■								
Homeathyris			■									
Pseudohomeospira			■									
Squamathyris			■									
Athyrisina				■								
?Ikella				■								
Parathyrisina				■								
DIDYMOTHYRIDINAE			■	■								
Collarothyris			■									
Didymothyris			■									
Glassina			■									
Greenfieldia			■									
?Jarovathyris			■	■								
Pseudoprotathyris			■	■								
Buchanathyris				■								
Dogdathyris				■								
Leptathyris				■								
Svetlania				■								
ATHYRIDINAE			■	■	■	?						
Protathyris			■	■								
Alvarezites				■								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Atrythyris				—								
Brimethyris				—								
Bruntonites				—								
Eifyris				—								
?Gonathyris				—								
Imacanthyris				—								
Johnsonathyris				—								
?Meristospira				—								
Pachyplax				—								
Zonathyris				—								
Athyris				—	?							
Lamellosathyris				—	—							
Actinoconchus				—	—	?						
HELENATHYRIDINAE				—								
Biernatella				—								
Eobiernatella				—								
Helenathyris				—								
Sphaerathyris				—								
PRADOIINAE				—								
?Dichozygopleura				—								
Guaxa				—								
Pradoia				—								
Quadriloba				—								
PLICATHYRIDINAE				—	?							
Anathyrella				—								
Hexarhytis				—								
Plicathyris				—								
Sulcathyris				—								
Anathyris				—	?							
CLEIOTHYRIDININAE				—	—	—						
Cleiothyridina				—	—	—						
Crinisarina				—	—	—						
Carteridina					—							
?Deltachania					—							
Leiothycridina					—							
?Rawdonia					—							
Bajtugania						—						
?Himathyris						—						
Pinegathyris						—						
SPIRIGERELLINAE				—	—	—	—					
Planalvus				—	—							
Composita				—	—	—						
Cardiothyris					—							
Densalvus					—							
Iniathyris					—							
Nordathyris					—							
Pseudopentagonia					—							
Tulathyris					—							

TABLE 41. *(Continued).*



	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Uldziathyris					—							
Spirigerella					—	—						
Araxathyris						—						
Janiceps						—						
Posicomta						—						
?Rectambitus						—						
Tongzithyris						—						
Septospirigerella						—	—					
LOCHENGIINAE					—	—						
Galeatathyris					—							
Lochengia					—							
Cryptospirifer						—						
Titanothyris						—						
COMELICANIINAE						—						
Comelicania						—						
Gruntallina						—						
XENOSARIINAE						—						
Xenosaria						—						
DIPLOSPIRELLIDAE						—	—	?				
MISOLIINAE						—	—					
?Uncinella						—						
?Anomactinella							—					
Misolia							—					
?Pentactinella							—					
?Stolzenburgiella							—					
CLAVIGERINAE							—					
Clavigera							—					
Majkopella							—					
Oxycolpella							—					
DIPLOSPIRELLINAE							—					
?Amphitomella							—					
Anisactinella							—					
Diplospirella							—					
Euractinella							—					
Pexidella							—					
TETRACTINELLINAE							—					
Tetractinella							—					
OCHOTATHYRIDINAE							—	?				
Dioristella							—					
?Qingthyris							—					
Spirigerellina							—					
Ochotathyris							—	?				
RETZIELLOIDEA			—	—								
RETZIELLIDAE			—	—								
Gissarina			—									
Metathyrisina			—									
Xerxespirifer			?									
Molongia			—	—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Retziella			─	─								
?Argorhynx				─								
Qinlingia				─								
?Ufonicoelia				─								
NUCLEOSPIROIDEA			━	━	━	━						
NUCLEOSPIRIDAE			━	━	━	━						
Nucleospira			─	─	─	─						
UNCERTAIN		━										
Apheathyris		─										
RETZIIDINA			━	━	━	━	━					
RHYNCHOSPIRINOIDEA			━	━								
RHYNCHOSPIRINIDAE			━	━								
Homoeospirella			─	?								
Homoeospira			─	─								
Rhynchospirina			─	─								
Leptospira				─								
Pseudoparazyga				─								
Trematospira				─								
PARAZYGIDAE				━								
Parazyga				─								
RETZIOIDEA			━	━	━	━	━					
RETZIIDAE			?	━	━	━						
Retzia			?	─	─							
Acambona					─							
Eumetria					─	─						
NEORETZIIDAE			━	━	━	━	━					
PLECTOSPIRINAE			━	━	?							
Plectospira			─	─	?							
Cooperispira				─								
HUSTEDIINAE					━	━	━					
Hustedia					─	─						
Thedusia					─	─						
Hustedtiella							─					
Schwagerispira							─					
HUNGARISPIRINAE							━					
Hungarispira							─					
NEORETZIINAE							━					
Cassianospira							─					
Neoretzia							─					
MONGOLOSPIROIDEA				━								
MONGOLOSPIRIDAE				━								
Mongolospira				─								
KONINCKINIDINA							━	━				
KONINCKINOIDEA							━	━				
KONINCKINIDAE							━	━				
Amphiclina							─					
Carinokoninckina							─					
Koninckina							─					

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Lamellokoninckina							—					
Septamphiclina							—					
Amphiclinodonta							—	—				
Koninckella							—	—				
Koninckodonta								—				
UNCERTAIN			▬	▬								
DAYIOIDEA			▬	?								
DAYIIDAE			▬	?								
Protozeuga			—									
Dayia			—	?								
ANOPLOTHECOIDEA			▬	▬								
ANOPLOTHECIDAE			▬	▬								
ANOPLOTHECINAE			▬	▬								
?Dnestrina			—									
Anoplotheca				—								
Bifida				—								
?Butkovia				—								
COELOSPIRINAE			▬	▬								
?Coelospirella			—	—								
Navispira			—	—								
Coelospira				—								
Coelospirina				—								
KAYSERIIDAE				▬								
Kayseria				—								
UNCERTAIN				▬								
?Neocoelia				—								
UNCITOIDEA				▬								
UNCITIDAE				▬								
Uncites				—								
RHYNCHONELLIDA		▬	▬	▬	▬	▬	▬	▬	▬	▬	▬	▬
ANCISTRORHYNCHOIDEA		▬	▬	▬								
OLIGORHYNCHIIDAE		▬										
Oligorhynchia		—										
Paraoligorhyncha		—										
Tonsella		—										
SPHENOTRETIDAE		▬										
Dorytreta		—										
Sphenotreta		—										
ANCISTRORHYNCHIDAE		▬	▬	▬								
Ancistrorhyncha		—										
Drepanorhyncha		—										
Nikolaevirhynchus			—									
Tyryrhynchus			—									
Kholbotchonia				—								
Obscurella				—								
NIORHYNICIDAE			▬									
Leptolepyron			—									
Niorhynx			—									

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
RHYNCHOTREMATOIDEA		■	■	■	■							
ORTHORHYNCHULIDAE		■	■									
Orthorhynchuloides		■										
Orthorhynchyllion		■										
Tasmanella		■										
Orthorhynchula		■	■									
Tuvaerhynchus			■									
RHYNCHOTREMATIDAE		■	■									
LEPIDOCYCLINAE		■	■									
Hypsiptycha		■										
Lepidocyclus		■										
Rhytidorhachis			■									
RHYNCHOTREMATINAE		■	■									
Hiscobeccus		■										
Otarorhyncha		■										
Rhynchotrema		■	■									
Pleurocornu			■									
Stegerhynchus			■									
Stegocornu			■									
TRIGONIRHYNCHIIDAE		■	■	■	■							
ROSTRICELLULINAE		■	■									
Azamella		■										
Evenkorhynchia		■										
Lepidocycloides		■										
Plectothyrella		■										
Rostricellula		■	■									
VIRGINIATINAE		■	■									
Thebesia		■	■									
Hostimex			■									
Rhynchotreta			■									
Virginiata			■									
HEMITOECHIINAE		■	■	■	■							
Lenatoechia		■	■									
Luterella			■									
Hemitoechia			■	■								
Nymphorhynchia			■	■								
Alorostrum				■								
Bathyrhyncha				■								
Browneella				■								
Centrorhynchus				■								
Dalerhynchus				■								
Dushanirhynchia				■								
Libyaerhynchus				■								
Losvia				■								
Pampoecilorhynchus				■								
Paurogastroderhynchus				■								
Tabarhynchus				■								
Yanetechia				■								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Ptychomaletoechia				—	—							
TRIGONIRHYNCHIINAE			—	—	—							
Aratoechia			—									
Myrmirhynx			—									
Oxypleurorhynchia			—									
Sufetirhyncha			—									
Agarhyncha			—	—								
Ancillotoechia			—	—								
Hercotrema			—	—								
Microsphaeridiorhynchus			—	—								
Stenorhynchia			—	—								
Trigonirhynchia			—	—								
Astua				—								
Bortegitoechia				—								
Cupularostrum				—								
Iberirhynchia				—								
Lissopleura				—								
Morphorhynchus				—								
Nasonirhynchia				—								
Oligoptycherhynchus				—								
Sinotectirostrum				—								
Tectogonotoechia				—								
Tetratomia				—								
Wilsoniella				—								
Nekhoroshevia				—	—							
Macropotamorhynchus					—							
Moorefieldella					—							
RIPIDIORHYNCHINAE				—	—							
Cyphoterorhynchus				—								
Hunanotoechia				—								
Orophomesorhynchus				—								
Parapamisorhynchus				—								
Piridiorhynchus				—								
Poleomesorhynchus				—								
Porthmorhynchus				—								
Pseudosinotectirostrum				—								
Ripidiorhynchus				—								
Saxulirostrum				—								
Hemiplethorhynchus					—							
LEPTOCOELIIDAE			—	—								
Anabaia			—									
Eocoelia			—									
Platytrochalos			—									
Australocoelia				—								
Leptocoelia				—								
Leptocoelina				—								
Pacificocoelia				—								
MACHAERARIIDAE				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Australirhynchia				■								
Callipleura				■								
Cherubicornea				■								
Ferganella				■								
Latonotoechia				■								
Machaeraria				■								
Machaeratoechia				■								
Sicorhyncha				■								
Thliborhynchia				■								
Yukiangides				■								
Zeravshanotoechia				■								
Zlichorhynchus				■								
PHOENICITOECHIIDAE				■								
Kotysex				■								
Phoenicitoechia				■								
Praegnantenia				■								
UNCINULOIDEA			■	■								
EATONIIDAE			■	■								
Aratanea			■									
Boucotella			■									
Clarkeia			■									
Diabolirhynchia			■									
Eatonioides			■									
Plagiorhyncha			■									
Sulcatina			■									
Costellirostra				■								
Eatonia				■								
Pegmarhynchia				■								
Pleiopleurina				■								
OBTURAMENTELLIDAE			■	■								
Pectorhyncha			■									
Obturamentella				■								
GLOSSINOTOECHIIDAE			■	■								
Eoglossinotoechia			■	■								
Chlupacitoechia				■								
Glossinotoechia				■								
Glossinulus				■								
HEBETOECHIIDAE			■	■								
HEBETOECHIINAE			■	■								
Hebetoechia			■	■								
Lanceomyonia			■	■								
Cerveratoechia				■								
Gerrhynx				■								
Lapradella				■								
Lebanzuella				■								
Mongolorhynx				■								
Voskopitoechia				■								
SPHAERIRHYNCHIINAE			■	■								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Estonirhynchia			—									
Notoconchidium			—									
Tadschikia			—									
Sphaerirhynchia			—	—								
AMSDENELLINAE				━								
Amsdenella				—								
BECKMANNIINAE				━								
Beckmannia				—								
Cassidirostrum				—								
Homeocardiorhynchus				—								
BETTERBERGIINAE				━								
Betterbergia				—								
Kransia				—								
Nalivkinaria				—								
Primipilaria				—								
GLOSSINULININAE				━								
Glossinulina				—								
Glossinulinirhynchia				—								
Nordotoechia				—								
Pseudoglossinotoechia				—								
INNAECHIIDAE			━	━								
CORVINOPUGNACINAE			━	━								
Xeniopugnax			—									
Decoropugnax			—	—								
Aseptalium				—								
Corvinopugnax				—								
DOGDOINAE				━								
Dogdoa				—								
Lezhoeviella				—								
Sibirirhynchia				—								
INNAECHIINAE				━								
Dubovikovia				—								
Innaechia				—								
VLADIMIRIRHYNCHINAE				━								
Alekseevaella				—								
Selennjachia				—								
Sulcicostula				—								
Tatjania				—								
Vladimirirhynchus				—								
Yakutijaella				—								
HADRORHYNCHIIDAE				━								
Droharhynchia				—								
Hadrorhynchia				—								
HYPOTHYRIDINIDAE				━								
Glosshypothyridina				—								
Hypothyridina				—								
Lorangerella				—								
Pseudouncinulus				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Tullypothyridina				—								
Uchtella				—								
Xiaobangdaia				—								
UNCINULIDAE				━								
Bulgania				—								
Eucharitina				—								
Fitzroyella				—								
Flabellulirostrum				—								
Markitoechia				—								
Paraglossinulus				—								
Plethorhyncha				—								
Remnevitoechia				—								
Taimyrrhynx				—								
Uncinulus				—								
CAMAROTOECHIOIDEA			━	━	━							
CAMAROTOECHIIDAE			━	━								
LINGUOPUGNOIDINAE			━	━								
Linguopugnoides			—	—								
Astutorhyncha				—								
CAMAROTOECHIINAE				━								
Camarotoechia				—								
Ellesmerhynchia				—								
LEIORHYNCHIDAE			━	━	━							
FENESTRIROSTRINAE			━	━								
Fenestrirostra			—									
Felinotoechia			—	—								
Pachancorhynchia				—								
BASILICORHYNCHINAE				━								
Abramovia				—								
Basilicorhynchus				—								
Gastrodetoechia				—								
Minirostrella				—								
Rugaltarostrum				—								
CALVINARIINAE				━								
Calvinaria				—								
Canavirilia				—								
Lateralatirostrum				—								
Navalicria				—								
Plionoptycherhynchus				—								
Tchernarhynchia				—								
Tomestenoporhynchus				—								
Vincalaria				—								
GIGANTORHYNCHINAE				━								
Gigantorhynchus				—								
Momarhynchus				—								
INNUITELLINAE				━								
Innuitella				—								
PLATYTERORHYNCHINAE				━								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Insignitisinurostrum				—								
Platyterorhynchus				—								
Stenaulacorhynchus				—								
STENOMETOPORHYNCHINAE				━								
Stenometoporhynchus				—								
LEIORHYNCHINAE				━	━							
Caryorhynchus				—								
Eliorhynchus				—								
Eoparaphorhynchus				—								
Eumetabolotoechia				—								
Evanescirostrum				—								
Hadrotatorhynchus				—								
Havlicekella				—								
Hyborhynchella				—								
Iloerhynchus				—								
Ilopsyrhynchus				—								
Katuniella				—								
Leiorhynchus				—								
Leptocaryorhynchus				—								
Mononusphaericorhynchus				—								
Orbiculatisinurostrum				—								
Parvulaltarostrum				—								
Paurorhyncha				—								
Properotundirostrum				—								
Ryocarhynchus				—								
Sphaeridiorhynchus				—								
Stenoglossariorhynchus				—								
Striatorhynchus				—								
Tebetorhynchus				—								
Tenuisinurostrum				—								
Werneckeella				—								
Yocrarhynchus				—								
Ypsilorhynchus				—								
Azurduya					—							
Rossirhynchus					—							
SEPTALARIIDAE				━								
Amissopecten				—								
Athyrhynchus				—								
Bergalaria				—								
Monadotoechia				—								
Nemesa				—								
Onugorhynchia				—								
Phlogoiderhynchus				—								
Pseudocamarophoria				—								
Rzonsnickiana				—								
Sagueresia				—								
Septalaria				—								
Septalariopsis				—								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
LAMBDARINOIDEA				▬	▬							
LAMBDARINIDAE				▬	▬							
LOBORININAE				▬								
Loborina				—								
LAMBDARININAE					▬							
Hampsia					—							
Lambdarina					—							
MINYSPHENIINAE					▬							
Minysphenia					—							
RHYNCHOPOROIDEA				▬	▬	▬						
RHYNCHOPORIDAE				▬	▬	▬						
GREIRINAE				▬								
Greira				—								
ARARATELLINAE				▬	▬							
Araratella				—	—							
TRETORHYNCHINAE					▬							
Tretorhynchia					—							
RHYNCHOPORINAE					▬	▬						
Rhynchopora					—	—						
STENOSCISMATOIDEA				▬	▬	▬						
STENOSCISMATIDAE				▬	▬	▬						
PROATRIBONIINAE				▬								
?Beichuanella				—								
Paratribonium				—								
Proatribonium				—								
STENOSCISMATINAE				▬	▬	▬						
Atribonium				—	—							
Coledium				—	—	—						
Sedenticellula					—							
Camerisma					—	—						
Stenoscisma					—	—						
Liufaia						—						
Sedecularia						—						
Torynechus						—						
PSILOCAMARIDAE					▬	▬						
CYROLEXINAE					▬	▬						
Careoseptum					—							
Callaiapsida					—	—						
Cyrolexis					—	—						
Septacamarella						—						
Ussuricamara						—						
PSILOCAMARINAE					▬	▬						
Psilocamara					—	—						
Camarophorina						—						
Camarophorinella						—						
Goleomixa						—						
Hybostenoscisma						—						
Neopsilocamara						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Zhejiangella						—						
Zhejiangellina						—						
Bicamella						?						
RHYNCHOTETRADOIDEA				━	━	-	━	━				
RHYNCHOTETRADIDAE				━	━							
AXIODEANEIINAE				━	━							
Paraphorhynchus				—	—							
Axiodeaneia					—							
RHYNCHOTETRADINAE					━							
Goniophoria					—							
Nepasitoechia					—							
Rhynchotetra					—							
Trasgu					—							
TETRACAMERIDAE					━							
Rotaia					—							
Tetracamera					—							
Yanishewskiella					—							
AUSTRIRHYNCHIIDAE							━					
Austrirhynchia							—					
Decurtella							—					
Excavatorhynchia							—					
?Trigonirhynchella							—					
PRIONORHYNCHIIDAE							━	━				
Amoenirhynchia							—					
Lokutella								—				
Prionorhynchia								—				
?Sphenorhynchia								—				
DIMERELLOIDEA				━	━	-	━	━	━	━	━	━
PEREGRINELLIDAE				━	━	-	━	━	━			
DZIEDUSZYCKIINAE				━	━							
Dzieduszyckia				—								
Ibergirhynchia					—							
PEREGRINELLINAE							━	━	━			
?Carapezzia							—	—				
Peregrinella									—			
PEREGRINELLOIDEINAE								━				
Anarhynchia								—				
Peregrinelloidea								—				
HALORELLIDAE							━					
Halorella							—					
Halorelloidea							—					
DIMERELLIDAE							━	━				
DIMERELLINAE							━					
Dimerella							—					
RHYNCHONELLININAE							━	━				
Rhynchonellina							—	—				
Sulcirostra							—	—				
Cooperrhynchia								—				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
CRYPTOPORIDAE									━	━	━	━
?Cryptoporella									─			
Cryptopora										─	─	─
Aulites										─	─	─
PUGNACOIDEA				━	━	━	━	━	━	━	━	━
ASEPTIRHYNCHIIDAE				━								
Aseptirhynchia				─								
Brunnirhyncha				─								
Carolirhynchia				─								
Chalimia				─								
Isopoma				─								
Polyptychorhynchus				─								
Westbroekina				─								
CAMEROPHORINIDAE				━								
Camerophorina				─								
LADOGIIDAE				━								
Camarothyridina				─								
Comiotoechia				─								
Gracilotoechia				─								
Ladogia				─								
Ladogifornix				─								
Ladogilina				─								
Semiotoechia				─								
Xinshaoella				─								
PLECTORHYNCHELLIDAE				━								
PLECTORHYNCHELLINAE				━								
Ipherron				─								
Kindleina				─								
Nyege				─								
Plectorhynchella				─								
Pseudoyunnanella				─								
PYGMAELLINAE				━								
Pygmaella				─								
Sibiritoechia				─								
ROZMANARIIDAE				━								
Errhynx				─								
Hadyrhyncha				─								
Iphinerrhynx				─								
Leptoterorhynchus				─								
Levipugnax				─								
Novaplatirostrum				─								
Phacoiderhynchus				─								
Planovatirostrum				─								
Pugnaria				─								
Rackirhynchia				─								
Rozmanaria				─								
Tetragonorhynchus				─								
YUNNANELLIDAE				━								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Ladogioides				—								
Nayunnella				—								
Schnurella				—								
Taksarhynchia				—								
Yunnanella				—								
PETASMARIIDAE				**—**	**—**	**—**						
Athabaschia				—								
Eurycolporhynchus				—								
Megalopterorhynchus				—								
Mirantesia				—								
Parvaltissimarostrum				—								
Petasmaria				—								
Porostictia				—								
Ovlatchania					—							
Pugnoides					—							
Shumardella					—							
Leiorhynchoidea					—	—						
Bryorhynchus						—						
PUGNACIDAE				**—**	**—**	**—**						
Aikarhyncha				—								
Allorhynchoides				—								
Cavatisinurostrum				—								
Chapinella				—								
Coeloterorhynchus				—								
Colophragma				—								
Dimensionaequalirostrum				—								
Eopugnax				—								
Evanidisinurostrum				—								
Filigreenia				—								
Globulirhynchia				—								
Hypseloterorhynchus				—								
Kwangsirhynchus				—								
Longdongshuia				—								
Pammegetherhynchus				—								
Parapugnax				—								
Paromoeopygma				—								
Perrarisinurostrum				—								
Solidipontirostrum				—								
Trifidorostellum				—								
Ujandinella				—								
Zilimia				—								
Pugnax				—	—	—						
Ningbingella					—							
Pleuropugnoides					—							
Propriopugnus					—							
PARANORELLIDAE					**—**	**—**						
IOWARHYNCHINAE					**—**							
Iowarhynchus					—							

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
PARANORELLINAE					—	—						
Sanjuania					—							
Boloria						—						
Paranorella						—						
ERYMNARIIDAE							—	—	—	—		
CRYPTORHYNCHIINAE							—	—				
Crurirhynchia							—					
Dierisma							—					
Aethirhynchia								—				
Cryptorhynchia								—				
CALVIRHYNCHIINAE								—				
Calvirhynchia								—				
SEPTOCRURELLINAE								—				
Caucasella								—				
Septocrurella								—				
ERYMNARIINAE									—	—		
Erymnaria									—	—		
BASILIOLIDAE							—	—	—	—	—	—
PAMIRORHYNCHIINAE							—	—	—	—		
Veghirhynchia							—					
Pamirorhynchia								—				
Pseudogibbirhynchia								—				
Rahouiarhynchia								—				
Gagriella								—	—			
?Kvesanirhynchia									—			
Orbirhynchia									—			
?Parthirhynchia									—			
?Riorhynchia										—		
LACUNOSELLINAE								—	—			
Stolmorhynchia								—				
Lacunosella								—	—			
BASILIOLINAE								—	—	—	—	—
?Almorhynchia								—				
Apringia								—				
?Soaresirhynchia								—				
Fortunella								—	—			
Rionirhynchia									—			
Probolarina									—	—		
Basiliola									—	—	—	—
Eohemithiris										—	—	
Streptaria										—	—	
Rhytirhynchia											—	—
Basiliolella												—
UNCERTAIN									—	- -	- -	—
?Dagysorhynchia									—			
?Striarina												—
AETHEIINAE										—	—	
Aetheia										—	—	

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
APHELESIINAE										━	━	
Aphelesia										—	—	
Phapsirhynchia											—	
ACANTHOBASILIOLINAE											━	━
Acanthobasiliola											—	—
WELLERELLOIDEA					━	━	━	━				
ALLORHYNCHIDAE					━	━	━					
Grammorhynchus					—							
Allorhynchus					—	—						
Terebratuloidea					—	—						
Aldina						—						
Deltarina						—						
Fascicosta						—						
Gerassimovia						—						
Hemileurus						—						
Pseudowellerella						—						
Ptilotorhynchus						—						
Caucasorhynchia							—					
Hagabirhynchia							—					
?Maorirhynchia							—					
Neofascicosta							—					
Septaliphorioidea							—					
WELLERELLIDAE					━	━	━	━				
EXLAMINELLINAE					━							
Exlaminella					—							
WELLERELLINAE					━	━						
Lissella					—							
Plekonella					—	—						
Wellerella					—	—						
Cenorhynchia						—						
Myopugnax						—						
Phrenophoria						—						
Tautosia						—						
MADAROSIINAE						━						
Madarosia						—						
NIPPONIRHYNCHIINAE						━						
Nipponirhynchia						—						
STRIGIRHYNCHIINAE						━						
Chaeniorhynchus						—						
Holosia						—						
Strigirhynchia						—						
TRICORIINAE						━						
Tricoria						—						
TROPHISININAE						━						
Trophisina						—						
UNCINUNELLININAE						━						
Uncinunellina						—						
CIRPINAE							━	━				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Apertirhynchella							─					
Euxinella							─					
Moisseievia							─					
?Robinsonella							─					
Calcirhynchia							─	─				
?Vincentirhynchia							─	─				
Cirpa								─				
?Salgirella								─				
PONTISIIDAE					━	━	━	━				
PONTISIINAE					━	━	━	━				
Pontisia					─	─						
Anteridocus						─						
Antronaria						─						
Divaricosta						─						
Lirellaria						─						
Prelissorhynchia						─	─					
Lissorhynchia							─					
?Bodrakella								─				
ACOLOSIINAE						━						
Acolosia						─						
Aphaurosia						─						
AMPHIPELLIDAE						━						
Amphipella						─						
PETASMATHERIDAE						━						
Elassonia						─						
Iotina						─						
Petasmatherus						─						
Ptygmactrum						─						
SINORHYNCHIIDAE							━					
Sinorhynchia							─					
?Volirhynchia							─					
RHYNCHONELLOIDEA							━	━	━			
RHYNCHONELLIDAE							━	━	━			
BILAMINELLINAE							━	━				
Saccorhynchia							─					
Bilaminella								─				
NUCLEUSORHYNCHIINAE							━	━				
Nucleusorhynchia							─					
Uniplicatorhynchia							─					
?Murihikurhynchia							─	─				
DAVANIRHYNCHIINAE							━	━	━			
Rimirhynchopsis							─					
Cubanirhynchia								─				
Davanirhynchia								─				
Furcirhynchia								─				
Rimirhynchia								─				
Akopovorhynchia									─			
IVANOVIELLINAE							━	━	━			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Himalairhynchia							—					
Bihendulirhynchia								—				
?Bradfordirhynchia								—				
Ivanoviella								—				
Lotharingella								—				
?Microrhynchia								—				
Minutulirhynchia								—				
Ptyctorhynchia								—				
Rhynchonelloidella								—				
Sharpirhynchia								—				
Thurmannella								—				
?Waikatorhynchia								—				
Grasirhynchia									—			
Malwirhynchia									—			
Rochatorhynchia									—			
?Urbanirhynchia									—			
URALORHYNCHIINAE							━	━	━			
Omolonella							—					
Sulcorhynchia							—					
Uralorhynchia								—	—			
PIARORHYNCHIINAE							━	━	━			
Abrekia							—					
Aorhynchia							—					
Paranudirostralina							—					
Sinuplicorhynchia							—					
Piarorhynchia							—	—				
Sakawairhynchia							—	—				
Caledorhynchia								—				
Cuneirhynchia								—				
Rutorhynchia								—				
?Tainuirhynchia								—				
Ptilorhynchia								—	—			
Talovkorhynchia									—			
RHYNCHONELLINAE							━	━	━			
?Lunarhynchia							—					
?Nudirostralina							—					
?Herangirhynchia							—	—				
Homoeorhynchia							—	—				
?Planirhynchia							—	—				
Rhynchonelloidea							?	—				
?Curtirhynchia								—				
Laevigaterhynchia								—				
?Fusirhynchia								—	—			
Rhynchonella								—	—			
Kabanoviella									—			
STRIIRHYNCHIINAE								━				
Capillirhynchia								—				
?Lirellarina								—				

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Neocirpa								▬				
Striirhynchia								▬				
?Trichorhynchia								▬				
ACANTHOTHIRIDIDAE								▬	▬			
ACANTHOTHIRIDINAE								▬				
Acanthothiris								▬				
Kawhiarhynchia								▬				
?Paraacanthothyris								▬				
ACANTHORHYNCHIINAE								▬	▬			
?Acanthothyropsis								▬				
Acanthorhynchia								▬	▬			
Echinirhynchia								▬	▬			
NORELLOIDEA							▬	▬	▬	▬	▬	▬
NORELLIDAE							▬	▬	▬			
HOLCORHYNCHELLINAE							▬					
Holcorhynchella							▬					
Piarorhynchella							▬					
PARANORELLININAE							▬					
Costinorella							▬					
Paranorellina							▬					
?Qilianoconcha							▬					
DIHOLKORHYNCHIINAE							▬	▬				
Diholkorhynchia							▬					
Maxillirhynchia							▬	▬				
Gnathorhynchia								▬				
Holcorhynchia								▬				
LAEVIRHYNCHIINAE							▬	▬				
Laevirhynchia							▬					
Nannirhynchia								▬				
NORELLINAE							▬	▬				
Norella							▬					
?Austriellula							▬	?				
?Kericserella								▬				
Pisirhynchia								▬				
Rectirhynchia								▬				
PRAEMONTICLARELLINAE							▬	▬				
?Aparimarhynchia							▬					
Pseudohalorella							▬					
?Wairakirhynchia							▬					
Praemonticlarella								▬				
Pseudomonticlarella								▬				
Scalpellirhynchia								▬				
MONTICLARELLINAE							▬	▬	▬			
Batangorhynchia							▬					
?Osmarella							▬	▬				
Capillirostra								▬				
Homaliarhynchia								▬				
Monticlarella								▬	▬			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
?Oriensellina									—			
Suiaella									—			
?OCHOTORHYNCHIIDAE								━	━			
Ochotorhynchia								—				
?Tonasirhynchia									—			
FRIELEIIDAE										━	━	━
HISPANIRHYNCHIINAE										━	━	━
Hispanirhynchia										—	–	—
Sphenarina											—	—
Abyssorhynchia												—
?Manithyris												—
FRIELEIINAE										?	━	━
Frieleia										?	—	—
Compsothyris												—
Grammetaria												—
NEORHYNCHIINAE												━
Neorhynchia												—
TETHYRHYNCHIIDAE												━
Tethyrhynchia												—
HEMITHIRIDOIDEA							━	━	━	━	━	━
?TRIASORHYNCHIIDAE							━					
Multicorhynchia							—					
Triasorhynchia							—					
TETRARHYNCHIIDAE							━	━	━			
TETRARHYNCHIINAE							━	━	━			
Eoseptaliphoria							—					
Baeorhynchia								—				
Cymatorhynchia								—				
Daghanirhynchia								—				
Deltarhynchia								—				
Druganirhynchia								—				
Echyrosia								—				
Goniorhynchia								—				
Grandirhynchia								—				
Orlovirhynchia								—				
Pontaltorhynchia								—				
Pycnoria								—				
Quadratirhynchia								—				
Robustirhynchia								—				
Somalirhynchia								—				
Tetrarhynchia								—				
?Belbekella									—			
Korjakirhynchia									—			
GIBBIRHYNCHIINAE								━				
Amydroptychus								—				
Burmirhynchia								—				
?Colpotoria								—				
Conarosia								—				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Gibbirhynchia								—				
Nastosia								—				
?Schizoria								—				
ISJUMINELLINAE								━				
Costirhynchia								—				
Isjuminella								—				
Mosquella								—				
Russirhynchia								—				
KALLIRHYNCHIINAE								━				
Kallirhynchia								—				
Kutchirhynchia								—				
Obsoletirhynchia								—				
Rhactorhynchia								—				
CRETIRHYNCHIINAE									━			
Begiarslania									—			
Bohemirhynchia									—			
Burrirhynchia									—			
Cretirhynchia									—			
VIARHYNCHIINAE									━			
Hemithyropsis									—			
Septatoechia									—			
Viarhynchia									—			
CYCLOTHYRIDIDAE							━	━	━			
CYCLOTHYRIDINAE							━	━	━			
Costirhynchopsis							—					
?Halorellina							—					
Septocyclothyris							—					
Timorhynchia							—					
Yidunella							—					
?Yulongella							—					
Fissirhynchia							—	—				
Aucklandirhynchia								—				
Bicepsirhynchia								—				
Globirhynchia								—				
Granulirhynchia								—				
Lacunaerhynchia								—				
Pararhactorhynchia								—				
?Rudirhynchia								—				
?Squamirhynchia								—				
Septaliphoria								—	—			
Torquirhynchia								—	—			
Almerarhynchia									—			
Cyclothyris									—			
Hesperorhynchia									—			
Lamellaerhynchia									—			
Lepidorhynchia									—			
Owenirhynchia									—			
Plicarostrum									—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Proteorhynchia									—			
Sulcirhynchia									—			
CARDINIRHYNCHIINAE								━				
Cardinirhynchia								—				
Eurysites								—				
Flabellirhynchia								—				
Parvirhynchia								—				
INDORHYNCHIINAE								━				
Indorhynchia								—				
Moquellina								—				
Strongyloria								—				
Tanggularella								—				
?SEPTIRHYNCHIIDAE								━				
Heteromychus								—				
Lessinirhynchia								—				
Septirhynchia								—				
NOTOSARIIDAE									━	━	━	━
?Protegulorhynchia									—			
?Paraplicirhynchia										—		
Plicirhynchia										—		
Tegulorhynchia										—	—	
Notosaria										—	—	—
HEMITHIRIDIDAE										━	━	━
?Patagorhynchia										—		
Hemithiris										—	—	—
Pemphixina												—
UNCERTAIN							━	━	━			
Sacothyropsis							—					
Barzellinia							?	?				
Isjuminelina								—				
Yunshannella									—			
TEREBRATULIDA			━	━	━	━	━	━	━	━	━	━
UNCERTAIN			━	━	━	–	━	━	━	━	━	━
CADOMELLOIDEA								━				
Cadomella								—				
GWYNIOIDEA								━	–	–	━	━
Zellania								—				
Gwynia											—	—
UNCERTAIN			━	━	━	–	━	━	━	━	━	━
UNCERTAIN			━	━	–	–	━	━	━	━	━	━
Microbilobata			—									
Rugosothyris				—								
Parasulcatinella							—					
Triseptothyris							—					
Zhidothyris							—					
Antigoniarcula								—				
Tiaretithyris								—				
Kingenella									—			

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Leptothyrellopsis									—			
Luppovithyris									—			
Magas									—			
Praeneothyris									—			
Rhynchora									—			
Rhynchorina									—			
Timacella									—			
Xinjiangthyris									—			
Yuezhuella									—			
Eogryphus										—		
Gwyniella										—		
Hercothyris										—		
Lutetiarcula										—		
Kurakithyris											—	
Miogryphus											—	
Yabeithyris											—	
Holobrachia												—
Simplicithyris												—
MUTATIONELLINAE				━								
Aqqikkolia				—								
MONGOLELLIDAE				━								
Mongolella				—								
OBOLORUGIDAE				━								
Obolorugia				—								
TROPIDOLEPTIDAE				━								
Tropidoleptus				—								
CARDIARINIDAE					━							
Cardiarina					—							
TEREBRATULIDINA			?	━	━	━	━	━	━	━	━	━
STRINGOCEPHALOIDEA			?	━								
MEGANTERIDIDAE			?	━								
BRACHYZYGINAE			?	━								
Brachyzyga			?	—								
ADRENINAE				━								
Adrenia				—								
Barbarothyris				—								
Cydimia				—								
Lingshanella				—								
Micidus				—								
Sturtella				—								
ANTISTRIXINAE				━								
Antistrix				—								
MEGANTERIDINAE				━								
Meganterella				—								
Meganteris				—								
Reeftonella				—								
MUTATIONELLINAE				━								
Cloudella				—								

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Derbyina				─								
Mendathyris				─								
Mutationella				─								
Paulinella				─								
Pleurothyrella				─								
Podolella				─								
Prorensselaria				─								
Scaphiocoelia				─								
Xana				─								
CENTRONELLIDAE				━								
AMPHIGENIINAE				━								
Amphigenia				─								
CENTRONELLINAE				━								
Centronella				─								
Oriskania				─								
Proboscidina				─								
EURYTHYRIDINAE				━								
Beachia				─								
Cloudothyris				─								
Eurythyris				─								
Prionothyris				─								
RENSSELAERIINAE				━								
Etymothyris				─								
Nanothyris				─								
Rensselaeria				─								
Rensselaerina				─								
RHIPIDOTHYRIDIDAE				━								
GLOBITHYRIDINAE				━								
Globithyris				─								
RHENORENSSELAERINAE				━								
Lievinella				─								
Rhenorensselaeria				─								
RHIPIDOTHYRIDINAE				━								
Neoglobithyris				─								
Rhipidothyris				─								
Septothyris				─								
STRINGOCEPHALIDAE				━								
BORNHARDTININAE				━								
Bornhardtina				─								
Hessenhausia				─								
Pseudobornhardtina				─								
GERANOCEPHALINAE				━								
Geranocephalus				─								
Paracrothyris				─								
Stringomimus				─								
Xiangzhounia				─								
KAPLEXINAE				━								
Erectocephalus				─								

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Kaplex				■								
LEIOSEPTATHYRIDINAE				■								
Leioseptathyris				■								
OMOLONINAE				■								
Hemistringocephalus				■								
Kumbella				■								
Omolonia				■								
RENSSELANDIINAE				■								
Chascothyris				■								
Ectorensselandia				■								
Elmaria				■								
Newberria				■								
Rensselandioidea				■								
Subrensselandia				■								
STRINGOCEPHALINAE				■								
Parastringocephalus				■								
Stringocephalus				■								
Stringodiscus				■								
UNCERTAIN				■								
?Guangshunia				■								
CRYPTONELLOIDEA				■	■	■	■					
CIMICINELLIDAE				■								
Cimicinella				■								
?Cimicinoides				■								
UNCERTAIN				■	■							
?Zhongpingia				■								
Romingerina					■							
CRANAENIDAE				■	■	■						
AFILASMATINAE				■								
Afilasma				■								
CRANAENINAE				■	■	■						
Asiacranaena				■								
Costacranaena				■								
Maclarenella				■								
Cranaena				■	■							
Hamburgia				■	■							
Pelaiella					■							
Anomalesia						■						
Planothyris						■						
Pontielasma						■						
GIRTYELLINAE					■	■						
Girtyella					■							
Harttella					■							
Eremithyris						■						
CRYPTONELLIDAE				■	■	■	■					
CRYPTONELLINAE				■	■	■						
Cryptonella				■								
Dielasmella					■							

TABLE 41. *(Continued).*

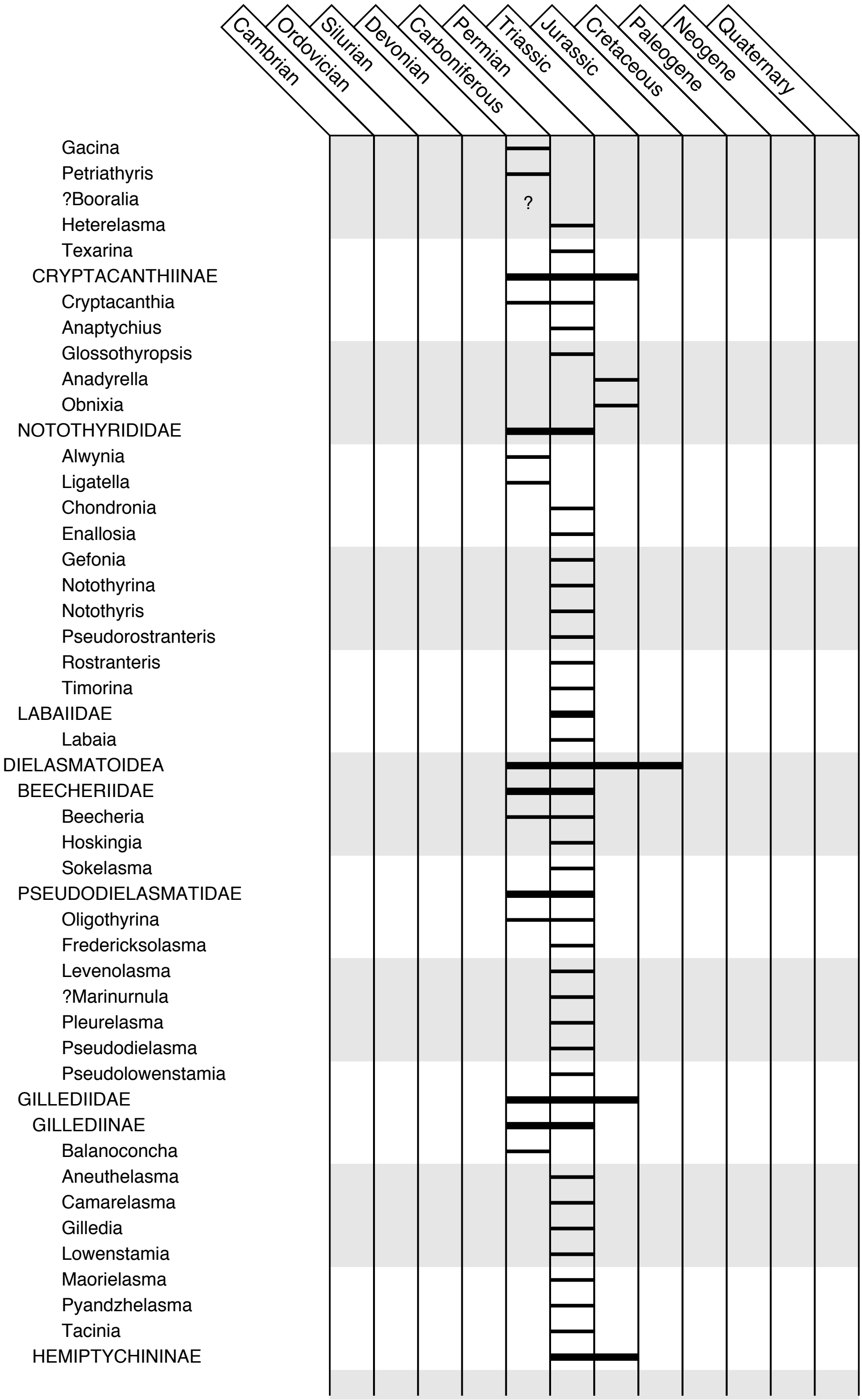


TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Hemiptychina						—						
Latiflexa						—						
Mongolina						—						
Pseudojisuina						—						
Sichuanothyris						—						
Costoconcha							—					
Parahemiptychina							—					
DIELASMATIDAE					━	━	━	?				
CENTRONELLOIDEINAE					━							
Centronelloidea					—							
DIELASMATINAE					━	━	━					
Dongbaella					—							
Dielasma					—	—						
Amygdalocosta						—						
Campbellelasma						—						
Dielasmina						—						
Ectoposia						—						
Elasmata						—						
Fletcherithyris						—						
Grigorjevaelasma						—						
Gruntelasma						—						
Plectelasma						—						
Whitspakia						—						
Yochelsonia						—						
Adygella							—					
Aspidothyris							—					
Coenothyris							—					
Cruratula							—					
Dareithyris							—					
?Paradygella							—					
Pirithyris							—					
Sulcatinella							—					
Tibetothyris							—					
Tosuhuthyris							—					
Tunethyris							—					
NUCLEATULINAE							━	?				
Arctothyris							—					
Dinarella							—					
Nucleatula							—					
Sulcatothyris							—					
Propygope							—	?				
HETERELASMINIDAE						━						
Amurothyris						—						
Gundarolasmina						—						
Heterelasmina						—						
Mimaria						—						
Permicola						—						
Pseudolabaia						—						

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Qinglongia						—						
ANGUSTOTHYRIDIDAE						━	━	?				
Praeangustothyris						—						
Angustothyris							—					
Caucasothyris							—					
Cubanothyris							—					
Cystothyris							—					
Paradoxothyris							—					
Praecubanothyris							—					
Rhaetina							—	?				
ANTEZEILLERIDAE							━					
Antezeilleria							—					
Emeithyris							—					
?Epithyroides							—					
ZUGMAYERIIDAE							━					
Adygelloides							—					
Portneufia							—					
Zugmayeria							—					
JUVAVELLIDAE							━	━				
Juvavella							—					
Wittenburgella							—					
Slavinithyris								—				
UNCERTAIN						━	━					
Pseudoharttina						—						
Adygellopsis							—					
?Athyrorhynchia							—					
?Paradygella							—					
?Proanadyrella							—					
?Pseudopygoides							—					
?Thyratryaria							—					
LOBOIDOTHYRIDOIDEA							━	━	━			
PLECTOCONCHIDAE							━	━				
Plectoconcha							—					
Merophricus								—				
TRIADITHYRIDIDAE							━	━				
Laevithyris							—					
Triadithyris							—					
Inversithyris								—				
Lenothyris								—				
Viligothyris								—				
UNCERTAIN							━	━				
UNCERTAIN							━	━				
?Lobothyroides							—					
Pamirothyris							—					
Aschuthyris								—				
Dhosathyris								—				
Gibbithyrella								—				
Jaisalmeria								—				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Kendzhilgithyris									—			
?Magharithyris									—			
Naradanithyris									—			
Neaguithyris									—			
Neumayrithyris									—			
Peristerothyris									—			
Rarithyris									—			
Rugithyris									—			
Sogxianthyris									—			
Taurothyris									—			
Thadiqithyris									—			
Trichothyris									—			
Tshemsarythyris									—			
Viallithyris									—			
Weldonithyris									—			
GONIOTHYRIDINAE									━			
Goniothyris									—			
HETEROBROCHINAE									━			
Heterobrochus									—			
PSEBAJITHYRIDINAE									━			
Placothyris									—			
Psebajithyris									—			
Unkurithyris									—			
CHEIROTHYROPSIDAE									━			
Cheirothyropsis									—			
CHENIOTHYRIDIDAE									━			
Cheniothyris									—			
DIENOPIDAE									━			
Dienope									—			
HESPERITHYRIDIDAE									━			
Hesperithyris									—			
LISSAJOUSITHYRIDIDAE									━			
LISSAJOUSITHYRIDINAE									━			
Apatecosia									—			
Arcelinithyris									—			
Dorsoplicathyris									—			
Eristenosia									—			
Lissajousithyris									—			
Monsardithyris									—			
Rouillieria									—			
Strongylobrochus									—			
Stroudithyris									—			
Uralella									—			
Vladimirella									—			
MORRISITHYRIDINAE									━			
Morrisithyris									—			
LOBOTHYRIDIDAE									━			
LOBOTHYRIDINAE									━			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Cuersithyris									—			
Exceptothyris									—			
Inaequalis									—			
Lobothyris									—			
Notosia									—			
Rhapidothyris									—			
Telothyris									—			
LOPHROTHYRIDINAE									━			
Argovithyris									—			
Aromasithyris									—			
Lophrothyris									—			
Odarovithyris									—			
Tubithyris									—			
TCHEGEMITHYRIDIDAE									━			
TCHEGEMITHYRIDINAE									━			
Tchegemithyris									—			
TURKMENITHYRIDINAE									━			
Turkmenithyris									—			
TEGULITHYRIDIDAE									━			
Prototegulithyris									—			
Tegulithyris									—			
TRIGONITHYRIDIDAE									━			
Lazithyris									—			
Trigonithyris									—			
POSTEPITHYRIDIDAE									━	━		
Arceythyris									—			
Caryona									—			
Conarothyris									—			
Epithyris									—			
Euidothyris									—			
Ferrythyris									—			
Galliennithyris									—			
Gigantothyris									—			
Glyphisaria									—			
Habrobrochus									—			
Heimia									—			
Holcothyris									—			
Juralina									—			
Karakulithyris									—			
Kutchithyris									—			
Millythyris									—			
Moeschia									—			
Moisseevia									—			
Perrierithyris									—			
Petalothyris									—			
Plectoidothyris									—			
Postepithyris									—			
Somalithyris									—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Xestosina								▬				
Maritimithyris									▬			
Peculneithyris									▬			
Pseudoaulacothyris									▬			
BOREIOTHYRIDIDAE								■	■			
Boreiothyris								▬				
Omolonithyris								▬				
Pamirothyropsis								▬				
Taimyrothyris								▬	▬			
Siberiothyris									▬			
DICTYOTHYRIDIDAE								■	■			
Dictyothyris								▬	▬			
LOBOIDOTHYRIDIDAE								■	■			
BOTHROTHYRIDINAE								■				
Bothrothyris								▬				
CERERITHYRIDINAE								■				
Animonithyris								▬				
Cererithyris								▬				
Mexicaria								▬				
Plectothyris								▬				
Rocheithyris								▬				
LOBOIDOTHYRIDINAE								■	■			
Arabatia								▬				
Avonothyris								▬				
Bihenithyris								▬				
Charltonithyris								▬				
Colosia								▬				
Dolichobrochus								▬				
Ectyophoria								▬				
Loboidothyris								▬				
Pseudoglossothyris								▬				
Ptyctothyris								▬				
Sphaeroidothyris								▬				
Stiphrothyris								▬				
Striithyris								▬				
Wattonithyris								▬				
Pinaxiothyris								▬	▬			
MUIRWOODELLIDAE								■	■			
KARADAGITHYRIDINAE								■				
Karadagella								▬				
Karadagithyris								▬				
MUIRWOODELLINAE								■				
Goniothyropsis								▬				
Muirwoodella								▬				
UNCERTAIN								■	■			
Dzharithyris								▬				
Negramithyris								▬				
?Praegoniothyris								▬				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Svaljavithyris								—	—			
ALABUSHEVOTHYRIDIDAE									━			
Alabushevothyris									—			
CLATHRITHYRIDIDAE									━			
Clathrithyris									—			
HARPOTOTHYRIDIDAE									━			
Atelithyris									—			
Convexothyris									—			
Harpotothyris									—			
Lissothyris									—			
Okathyris									—			
MAMETOTHYRIDIDAE									━			
Mametothyris									—			
Penzhinothyris									—			
SPASSKOTHYRIDIDAE									━			
Spasskothyris									—			
Volgathyris									—			
DYSCOLIOIDEA								━	━	━	━	━
NUCLEATIDAE								━	━			
Kubanithyris								—				
Linguithyris								—				
Phymatothyris								—				
Nucleata								—	—			
PYGOPIDAE								━	━			
PYGOPINAE								━	━			
Pygites								—	—			
Pygope								—	—			
TRIANGOPINAE								━	━			
Securithyris								—				
Triangope								—	—			
DYSCOLIIDAE									━	━	━	━
EURYSORIINAE									━			
Eurysoria									—			
DYSCOLIINAE									━	-	━	━
Moraviaturia									—			
Waisiuthyrina											—	
Dyscolia											—	—
Goniobrochus												—
AENIGMATHYRIDINAE										━	━	━
Aenigmathyris										—		
Faksethyris										—		
Ceramisia											—	
Abyssothyris											—	—
Acrobelesia												—
Xenobrochus												—
UNCERTAIN								━				
Buckmanithyris								—				
Papodina								—				

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
CANCELLOTHYRIDOIDEA								━	━	━	━	━
UNCERTAIN								━				
Pseudokingena								—				
CHLIDONOPHORIDAE								━	━	━	━	━
CHLIDONOPHORINAE								━	━	━	-	━
Deslongchampsithyris								—				
Disculina								—				
Prochlidonophora									—			
Rugia									—			
Meonia									—	?		
Gisilina									—	—		
Chlidonophora									?	-	-	—
DRACIINAE									━			
Dracius									—			
ORTHOTHYRIDINAE									━			
Orthothyris									—			
EUCALATHINAE										━	━	━
Eucalathis										—	—	—
Bathynanus												—
Nanacalathis												—
Notozyga												—
AGULHASIINAE											━	━
Agulhasia											—	—
CANCELLOTHYRIDIDAE								━	━	━	━	━
UNCERTAIN								━				
Cooperithyris								—				
CRICOSIINAE								━	━	━		
Symphythyris								—	—			
Cricosia									—			
Cruralina									—			
Gyrosoria									—			
Bisulcina									—	—		
CANCELLOTHYRIDINAE								━	━	━	━	━
Terebratulina								—	—	—	—	—
Ortholina									—			
Trochifera									—			
Rhynchonellopsis										—		
Murravia										—	—	—
Sendaithyris											—	
Cancellothyris											—	—
?Surugathyris												—
ALITHYRIDINAE									━			
Alithyris									—			
INOPINATARCULIDAE									━			
Inopinatarcula									—			
CNISMATOCENTRIDAE									━	-	-	━
ARCUATOTHYRIDINAE									━			
Arcuatothyris									—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Nucleatina									—			
CNISMATOCENTRINAE												━
Cnismatocentrum												—
TEREBRATULOIDEA								━	━	━	━	━
WEBERITHYRIDIDAE								━	━			
Weberithyris								—	—			
SELLITHYRIDIDAE								?	━	━		
RECTITHYRIDINAE								?	━			
Tropeothyris								?	—			
Collinithyris									—			
Cyrtothyris									—			
Moutonithyris									—			
Neoliothyrina									—			
Praelongithyris									—			
Rectithyris									—			
Rhombothyris									—			
SELLITHYRIDINAE									━			
Boubeithyris									—			
Glosseudesia									—			
Loriolithyris									—			
Musculina									—			
Ovatathyris									—			
Paraboubeithyris									—			
Phaseolina									—			
Sellithyris									—			
?Walkerithyris									—			
NERTHEBROCHINAE									━	━		
Dilophosina									—			
Hadrosia									—			
Harmatosia									—			
Nerthebrochus									—			
Leymerithyris										—		
CAPILLITHYRIDIDAE									━			
ANIABROCHINAE									━			
Aniabrochus									—			
Bolgarithyris									—			
Dyscritothyris									—			
Iberithyris									—			
Lunpolaia									—			
Middlemissithyris									—			
Paraplatythyris									—			
Sardope									—			
CAPILLITHYRIDINAE									━			
Capillithyris									—			
Liramia									—			
?Paracapillithyris									—			
UNCERTAIN									━	━		
Eichwaldithyris									—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Heligothyris									—			
?Longithyris									—			
Najdinothyris									—			
Almiralthyris										—		
Ilyinella										—		
Oleneothyris										—		
GIBBITHYRIDIDAE									━	━		
RHOMBARIINAE									━			
Rhombaria									—			
CARNEITHYRIDINAE									━	━		
Carneithyris									—	—		
Giraliathyris										—		
GIBBITHYRIDINAE									━	━		
Concinnithyris									—			
Gibbithyris									—			
Hesperosia									—			
Ornatothyris									—			
Praegibbithyris									—			
Pseudogibbithyris									—			
Sahnithyris									—			
Orientothyris									—	—		
TEREBRATULIDAE										━	━	━
PLICATORIINAE										━		
Plicatoria										—		
Tanyoscapha										—		
SEYMOURELLINAE										━		
Seymourella										—		
GRYPHINAE										━	━	━
Gryphus										—	—	—
TEREBRATULINAE										━	━	━
Pycnobrochus										—		
Rhytisoria										—		
Pliothyrina										—	—	
Acrobrochus										—	—	—
Liothyrella										—	—	—
Maltaia											—	
Terebratula											—	
TICHOSININAE										━	━	━
Tichosina										—	—	—
Dolichozygus											—	—
Arctosia												—
Dysedrosia												—
Erymnia												—
Zygonaria												—
DALLITHYRIDINAE										?	━	━
Dallithyris										?	—	—
Stenosarina											—	—
Kanakythyris												—

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
UNCERTAIN							—	—	—			
UNCERTAIN							—	—	—			
Lobothyroides							—					
Pseudorhaetina							—					
Vex							—					
Falciferula								—				
Goliathyris								—				
Mayaothyris									—			
Zenobiathyris									—			
ORTHOTOMIDAE								—				
Orthotoma								—				
TEREBRATELLIDINA							—	—	—	—	—	—
ZEILLERIOIDEA							—	—	—	—	—	—
GUSARELLIDAE							—	—				
Protogusarella							—					
Gusarella								—				
Paragusarella								—				
ZEILLERIIDAE							—	—	—	—	—	—
VECTELLINAE							—	—	—			
Aulacothyroides							—					
Fletcherithyroides							—					
Gemerithyris							—					
Parantiptychia							—					
Tauromenia							?	—				
Carpatothyris								—				
Cheirothyris								—				
Delmontanella								—				
Epicyrta								—				
Karpatiella								—				
Zeillerina								—				
Ornithella								—	?			
Advenina									—			
Enodithyris									—			
Kedrovothyris									—			
Modestella									—			
Tetjuchithyris									—			
Vectella									—			
ZEILLERIINAE							—	—	—			
Eoantiptychia							—					
Kolymithyris							—					
Periallus							—					
Sacothyris							—					
Silesiathyris							—					
Worobievella							—					
Aulacothyris							?	—				
Zeilleria							?	—				
Ajukuzella								—				
Antiptychina								—				

Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Bakonyithyris								—				
Bazardarella								—				
Cincta								—				
Digonella								—				
Fimbriothyris								—				
Irenothyris								—				
Keratothyris								—				
Kuntella								—				
Lazella								—				
Mycerosia								—				
Obovothyris								—				
Parathyridina								—				
Paraulacothyris								—				
Pirotella								—				
Plesiothyris								—				
Securina								—				
Tubegatanella								—				
Uniptychina								—				
Calpella								?				
Somalitela								?				
Rugitela								—	?			
Pictetella									—			
UNCERTAIN								━				
Polyplectella								—				
MACANDREVIINAE										━	━	━
Macandrevia										—	—	—
EUDESIIDAE								━				
Apothyris								—				
Eudesia								—				
Flabellothyris								—				
Praeudesia								—				
Sphriganaria								—				
Xenorina								—				
KINGENOIDEA							━	━	━	━	━	━
AULACOTHYROPSIDAE							━	━	━	- -	- -	━
AULACOTHYROPSINAE							━	━	━			
Aulacothyropsis							—					
Camerothyris							—					
Ornatothyrella							—					
Pseudorugitela							—					
Coriothyris								—				
Oppeliella								—				
Smirnovina									—			
BABUKELLINAE							━	━	━	- -	- -	━
Babukella							—					
Hynniphoria								—				
Vandobiella								—				
Makridinithyris								—	—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Kachathyris									—			
Fallax												—
Septicollarina												—
KINGENIDAE								━	━	━	━	━
KINGENINAE								━	━	━	━	
Dictyothyropsis								—				
Zeuschneria								—				
Zittelina								—	?			
Kingena									—			
Tulipina									—			
Aldingia										—		
Laquethiris										—		
Paraldingia										—	—	
ECNOMIOSINAE									━	- -	- -	━
Belothyris									—			
Dzirulina									—			
Vaniella									—			
Ecnomiosa												—
UNCERTAIN								━				
Trigonellina								—				
LAQUEOIDEA							━	━	━	━	━	━
LAQUEIDAE							━	━	━	- -	━	━
TEREBRATALIOPSINAE							━	━	━			
Eodallina							—					
Hamptonina								—				
Terebrataliopsis								—	—			
Kafirnigania									—			
Psilothyris									—			
DALLIGADINAE									━			
Dalligas									—			
PARAKINGENINAE									━			
Colinella									—			
Langshanthyris									—			
Parakingena									—			
Rossithyris									—			
Waconella									—			
LAQUEINAE											━	━
Laqueus											—	—
GLACIARCULINAE												━
Glaciarcula												—
TEREBRATALIIDAE								━	━	━	━	━
GEMMARCULINAE								━	━			
Ismenia								—	—			
Arenaciarcula									—			
Choristothyris									—			
Gemmarcula									—			
Helvetella									—			
Oblongarcula									—			

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Ruegenella									—			
TRIGONOSEMINAE									━			
Dereta									—			
Terebrirostra									—			
Trigonosemus									—			
TEREBRATALIINAE									━	━	━	━
Xenothyris									—			
Terebratalia										—	—	—
Coptothyris											—	—
Dallinella											—	—
Diestothyris											—	—
Tythothyris												—
FRENULINIDAE											━	━
FRENULININAE											━	━
Frenulina											—	—
Jolonica											—	—
PICTOTHYRIDINAE											━	━
Kikaithyris											—	—
Pictothyris											—	—
SHIMODAIINAE												━
Shimodaia												—
BOUCHARDIOIDEA									━	━	━	━
BOUCHARDIIDAE									━	━	━	━
Australiarcula									—			
Bouchardiella									—	—		
Bouchardia									?	—	—	—
Malleia										—	—	
Neobouchardia										—	—	
MEGATHYRIDOIDEA									━	━	━	━
PRAEARGYROTHECIDAE									━			
Evargyrotheca									—			
Krimargyrotheca									—			
Praeargyrotheca									—			
MEGATHYRIDIDAE									━	━	━	━
Bronnothyris									—	—		
Argyrotheca									—	—	—	—
Megathiris									—	—	—	—
Phragmothyris										—		
THAUMATOSIIDAE												━
Thaumatosia												—
PLATIDIOIDEA									━	━	━	━
PLATIDIIDAE									━	━	━	━
PLATIDIINAE									━	━	━	━
Scumulus									—			
Aemula									—	—		
Platidia										—	—	—
Annuloplatidia											—	—
Amphithyris												—

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
PHANEROPORINAE												—
Leptothyrella												—
Phaneropora												—
TEREBRATELLOIDEA										—	—	—
DALLINIDAE										—	—	—
NIPPONITHYRIDINAE										—	—	—
Landonella										—		
Campages											—	—
Nipponithyris											—	—
Jaffaia												—
DALLININAE											—	—
Pegmathyris											—	
Dallina											—	—
TEREBRATELLIDAE										—	—	—
ADNATIDINAE										—		
Adnatida										—		
STETHOTHYRIDINAE										—	—	
Aliquantula										—		
Pilkena										—		
Stethothyris										—		
Tiorirothyris										—		
Austrothyris										—	—	
Epacrothyris										—	—	
Rhizothyris										—	—	
Cudmorella											—	
Elderra											—	
MAGELLANIINAE										—	—	—
Diedrothyris										—	—	
Victorithyris										—	—	
Magellania											?	—
ANAKINETICINAE										—	—	—
Anakinetica										—	—	—
Parakinetica												—
TEREBRATELLINAE										—	—	—
Magella										—		
Praemagadina										—		
Gmelinmagas										—	—	
Magadina										—	—	
Pachymagas										—	—	
Waiparia										—	—	
Terebratella										—	—	—
Iheringithyris											—	
Calloria											—	—
Neothyris											—	—
Aerothyris												—
Aneboconcha												—
Dyscritosia												—
Fosteria												—

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Gyrothyris												—
Syntomaria												—
UNCERTAIN										—	—	—
Chathamithyris										—		
Magadinella										—	—	—
Erihadrosia											—	
Tanakura											—	
Pirothyris												—
KRAUSSINOIDEA											—	—
KRAUSSINIDAE											—	—
Kraussina											—	—
Megerlia											—	—
Megerlina											—	—
Pumilus												—
SPIRIFERINIDA				—	—	—	—	—				
CYRTINIDINA				—	—	—	—	—				
CYRTINOIDEA				—	—							
KOMIELLIDAE				—								
Komiella				—								
CYRTINIDAE				—	—							
Cyrtinaella				—								
Moniellocyrtina				—								
Squamulariina				—								
Tecnocyrtina				—								
Cyrtina				—	—							
SUESSIOIDEA					—	—	—	—				
DAVIDSONINIDAE					—							
Carbocyrtina					—							
Davidsonina					—							
LABALLIDAE						—	—					
LABALLINAE						—	—					
Eolaballa						—						
Laballa							—					
Pseudolaballa							—					
PARALEPISMATININAE							—					
Paralepismatina							—					
SPINOLEPISMATININAE							—					
Klipsteinella							—					
Klipsteinelloidea							—					
Spinolepismatina							—					
BITTNERULIDAE							—					
BITTNERULINAE							—					
Bittnerula							—					
Leiolepismatina							—					
Thecocyrtella							—					
Thecocyrtelloidea							—					
HIRSUTELLINAE							—					
Flabellocyrtia							—					

TABLE 41. *(Continued).*

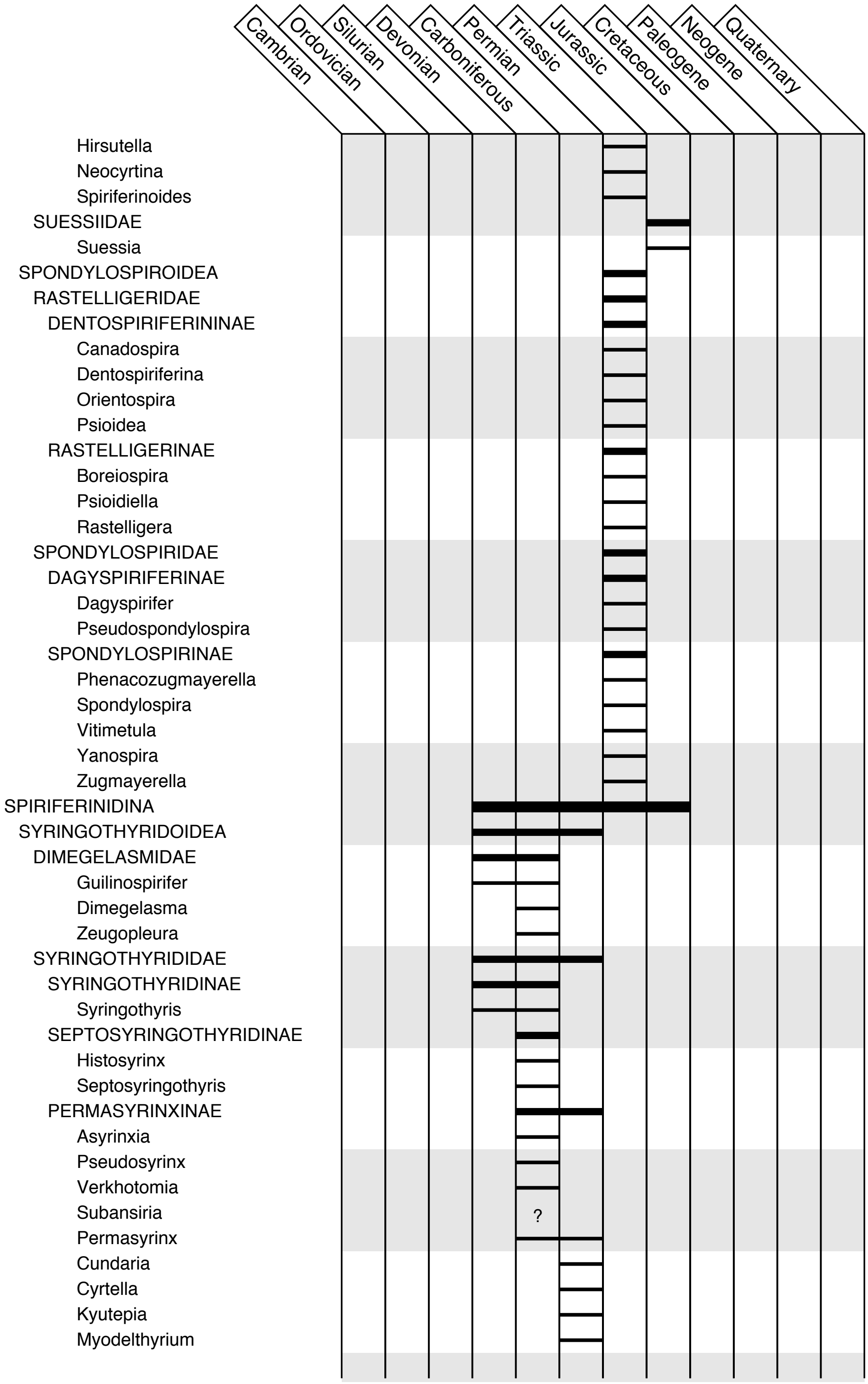


Table 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
Pachycyrtella						—						
Primorewia						—						
Pseudosyringothyris						—						
Sulcicosta						—						
Syrella						—						
Woolagia						—						
LICHAREWIIDAE					━	━						
Orulgania					—							
Licharewia						—						
Nahoniella						—						
Olgerdia						—						
Penzhinella						—						
Permospirifer						—						
Pyramidathyris						—						
Tumarinia						—						
Tuotalania						—						
PENNOSPIRIFERINOIDEA				━	━	━	━	━				
PUNCTOSPIRIFERIDAE				━	━	━	━					
Ziganella				—								
Punctospirifer				?	—							
Liriplica					?							
Lamnaespina						—						
Pustulospiriferina						—						
Alipunctifera							—					
Yangkongia							—					
SPIROPUNCTIFERIDAE					━	━						
Spiropunctifera					—							
Genuspirifer						—						
RETICULARIINIDAE					━	━						
Gjelispinifera					—							
Spinuliplica					?							
Reticulariina					—	—						
Altiplecus						—						
PARASPIRIFERINIDAE					?	━						
Polystylus					?							
Zaissania					?	—						
Callispirina						—						
Lamniplica						—						
Paraspiriferina						—						
Yaonoiella						—						
SPIRIFERELLINIDAE					━	━	━					
Crenispirifer					—	—						
Spiriferellina					—	—						
Metriolepis						—						
Sulcispiriferina						—						
Lancangjiangia							—					
Pseudospiriferina							—					
Tulungospirifer							—					

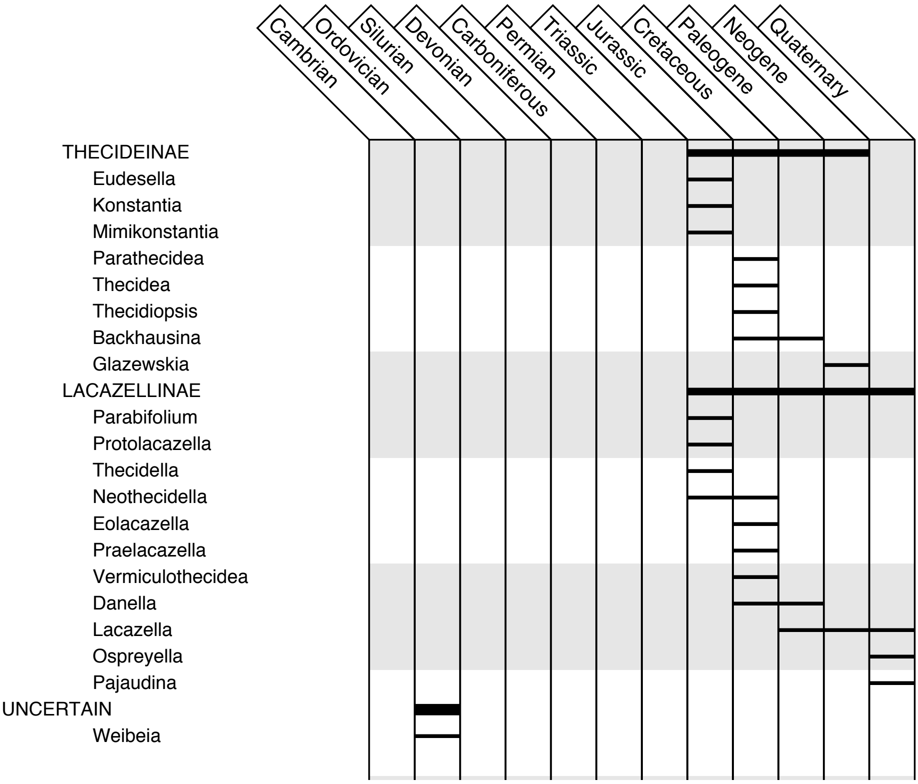
TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
PENNOSPIRIFERINIDAE					—	—	—	—				
PUNCTOSPIRELLINAE					—	—	—					
Laioporella					—							
Xestotrema					—	—						
Arionthia						—						
Punctospirella							—					
PENNOSPIRIFERININAE							—	—				
Pennospiriferina							—					
Callospiriferina								—				
SARGANOSTEGIDAE						—						
Sarganostega						—						
BALATONOSPIRIDAE							—					
BALATONOSPIRINAE							—					
Balatonospira							—					
Dinarispira							—					
Koeveskallina							—					
Nudispiriferina							—					
Tylospiriferina							—					
YALONGIINAE							—					
Sinucostella							—					
Yalongia							—					
Aequspiriferina							?					
LEPISMATINIDAE							—	—				
LEPISMATININAE							—					
Altoplicatella							—					
Lepismatina							—					
Pseudolepismatina							—					
PSEUDOCYRTININAE							—					
Bolilaspirifer							—					
Pseudocyrtina							—					
DISPIRIFERININAE							—	—				
Qingyenia							—					
Dispiriferina								—				
SPIRIFERINOIDEA							—	—				
SINUCOSTIDAE							—	?				
JIANGDASPIRIFERINAE							—					
Jiangdaspirifer							—					
SINUCOSTINAE							—	?				
Mentzeliopsis							—					
Qispiriferina							—					
Sinucosta							—	?				
SPIRIFERINIDAE							—	—				
MENTZELIINAE							—					
Madoia							—					
Mentzelia							—					
Paramentzelia							—					
PARALABALLINAE							—					
Paralaballa							—					

TABLE 41. *(Continued).*

	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
TETHYSPIRINAE							▬					
Spondylospiriferina							—					
Tethyspira							—					
SPIRIFERININAE							▬	▬				
Mentzelioides							—					
Qinghaispiriferina							—					
Triadispira							—					
Viligella							—					
Calyptoria								—				
Liospiriferina								—				
Spiriferina								—				
THECIDEIDA							▬	▬	▬	▬	▬	▬
THECOSPIROIDEA							▬					
HUNGARITHECIDAE							▬					
HUNGARITHECINAE							▬					
Hungaritheca							—					
PAMIROTHECINAE							▬					
Pamirotheca							—					
THECOSPIRELLIDAE							▬					
Bittnerella							—					
Thecospirella							—					
THECOSPIRIDAE							▬					
Thecospira							—					
THECIDEOIDEA							▬	▬	▬	▬	▬	▬
BACTRYNIIDAE							▬	▬				
BACTRYNIINAE							▬					
Bactrynium							—					
DAVIDSONELLINAE							▬	▬				
Davidsonella							—	—				
Agerinella								—				
THECIDELLINIDAE							▬	▬	▬	▬	▬	▬
MOORELLININAE							▬	▬	▬			
Moorellina							—	—				
Pachymoorellina								—				
Bosquetella									—			
THECIDELLININAE								▬	▬	▬	▬	▬
Rioultina								—				
Stentorina								—				
Bifolium									—			
Eothecidellina									—			
Mesoseptina									—			
Kakanuiella										—	—	—
Thecidellina										—	—	—
ENALLOTHECIDEIDAE								▬				
Enallothecidea								—				
THECIDEIDAE								▬	▬	▬	▬	▬
ANCORELLININAE								▬				
Ancorellina								—				

TABLE 41. *(Continued).*



	Cambrian	Ordovician	Silurian	Devonian	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Paleogene	Neogene	Quaternary
THECIDEINAE								■	■	■	■	
Eudesella								■				
Konstantia								■				
Mimikonstantia								■				
Parathecidea									■			
Thecidea									■			
Thecidiopsis									■			
Backhausina									■	■		
Glazewskia											■	
LACAZELLINAE								■	■	■	■	■
Parabifolium								■				
Protolacazella								■				
Thecidella								■				
Neothecidella								■	■			
Eolacazella									■			
Praelacazella									■			
Vermiculothecidea									■			
Danella									■	■		
Lacazella										■	■	■
Ospreyella												■
Pajaudina												■
UNCERTAIN		■										
Weibeia		■										

GEOGRAPHIC DISTRIBUTION OF EXTANT ARTICULATED BRACHIOPODS

ALAN LOGAN

[University of New Brunswick, Canada]

INTRODUCTION

Brachiopods were important members of the benthos of ancient seas, with over 5000 fossil genera known (WILLIAMS, 1996). They reached their acme of evolutionary development in the Paleozoic, but their importance, as measured by diversity, diminished drastically at the beginning of the Mesozoic, following the end-Permian extinction event that affected them greatly. Since then their numbers have stabilized, but today they remain a minor phylum, reduced to 336 extant species belonging to 100 genera. Nevertheless, they are widely distributed geographically, range greatly in depth, and are sometimes the dominant benthos in areas where competition for resources with other benthos may be reduced. Recent discoveries of new taxa have come from areas where accessibility and sampling is difficult (e.g., submarine caves, abyssal substrates), or where exploration and collecting has been limited. In this respect, little has yet been obtained from the Red Sea–Gulf of Aden (but see LOGAN & others, 2007) and Persian Gulf–Gulf of Oman areas or the shallow waters around northern Europe and Scandinavia, particularly the North Sea and Baltic Sea, although some of these areas are floored mainly by sediments, an environment generally inimical to articulated brachiopods.

Although many early taxonomic studies on articulated brachiopods (e.g., DAVIDSON, 1886–1888; FISCHER & OEHLERT, 1891; DALL, 1920) mentioned aspects of biogeography, the first work devoted to the subject was by SCHUCHERT (1911). This was followed by ELLIOTT's (1951) study on the geographical distribution of the then superfamily Terebratellacea, in which he recognized three distributional classes: a worldwide group, a northern hemisphere group, and a southern hemisphere group. Surprisingly, there was little mention of biogeography in the first edition of Part H (Brachiopoda) of the *Treatise on Invertebrate Paleontology* (MOORE, 1965). The biogeography of extant articulated brachiopods was subsequently treated in detail by ZEZINA (1976a,1985, 2001a) and RICHARDSON (1997b), with particular regard to physical and biological factors governing their distribution as well as their family origins and dispersal paths, topics that need not be repeated here. RICHARDSON (1997b) followed ELLIOTT (1951) in recognizing similar general distributional patterns for extant articulated brachiopods at the family level, noting that terebratellids occur exclusively in the southern hemisphere, laqueids are predominantly northern Pacific, and all other families are worldwide in distribution. Examples of other publications that have touched upon articulated brachiopod biogeography, either by genus, group, or region, include MUIR-WOOD (1959: Indian Ocean), FOSTER (1969: Antarctic–New Zealand), LOGAN (1979; LOGAN & others, 2004: Mediterranean Sea), BRUNTON & CURRY (1979: Britain), DAWSON (1991: New Zealand), LEE (1991: New Zealand), RICHARDSON (1994: Terebratellinae), ZEZINA (1997a: bathyal zone; 1997b: Arctic seas), BITNER and CAHUZAC (2004: *Cryptopora*), and ALVAREZ and EMIG (2005: Iberia and the Balearic Islands).

The present work updates that of ZEZINA (1985) and supplements that of RICHARDSON (1997b) by documenting the geographic distribution, depth ranges, and selected primary references (see References, p. 3116) for 336 extant articulated brachiopod species belonging to 100 genera (Tables 44–58), including those belonging to the superfamilies Pugnacoidea, Dimerelloidea, Norelloidea, Hemithiridoidea, Terebratuloidea,

TABLE 42. Depth ranges of species within superfamilies of extant articulated brachiopods (new).

Superfamily	# of species	0–500 neritic only	0–2000 neritic-upper bathyal	0–4000 neritic-lower bathyal	0–4000+ neritic-abyssal	500–4000 bathyal only	500–4000+ bathyal-abyssal	4000+ abyssal only	No depth data
Pugnacoidea	11	4	6	1	0	0	0	0	
Dimerelloidea	7	3	2	1	1	0	0	0	
Norelloidea	14	4	2	3	0	3	1	1	
Hemithiridoidea	7	2	2	1	0	0	0	0	2
Thecideoidea	13	11	1	0	0	0	0	0	1
Terebratuloidea	55	20	22	3	0	10	0	0	
Dyscolioidea	15	2	7	1	0	4	1	0	
Cancellothyridoidea	51	14	16	4	1	12	1	1	2
Zeillerioidea	10	0	1	2	1	5	1	0	
Kingenoidea	7	2	3	0	0	2	0	0	
Laqueoidea	37	27	9	1	0	0	0	0	
Megathyridoidea	25	18	7	0	0	0	0	0	
Bouchardioidea	1	1	0	0	0	0	0	0	
Platidioidea	16	6	3	2	2	3	0	0	
Terebratelloidea	48	28	15	1	0	1	0	0	3
Kraussinoidea	17	13	4	0	0	0	0	0	
Gwynioidea	2	0	2	0	0	0	0	0	
Totals	336	155	102	20	5	40	4	2	8
Percentage		46.1	30.4	6.0	1.5	11.9	1.2	0.6	2.4

Dyscolioidea, and Cancellothyridoidea, which were not included in RICHARDSON (1997b). The classification scheme of WILLIAMS, CARLSON, and BRUNTON (2002) adopted by SAVAGE and others (2002) for the Rhynchonellida and LEE and others (2006) for the Terebratulida is followed. The geographic distribution of each genus has also been plotted on world maps (Fig. 1939–1960) to accompany the tables.

The latitudinal distribution of the articulated brachiopods was discussed by RUDWICK (1977), who showed that they are most abundant in temperate latitudes in both hemispheres. Bathymetric ranges of Recent brachiopods have been discussed by ZEZINA (1970, 1976a), COOPER (1977), EMIG (1988), and RICHARDSON (1997b), most of whom have concluded that they make poor analogs for paleobathymetric reconstructions because of their great depth ranges. The depth ranges for individual species of articulated brachiopods are shown in Tables 44–58, and those for the extant articulated brachiopods as a whole are shown in Table 42. For the purpose of describing the depth range of species, the neritic zone is here recognized as extending from low tide to 500 m, the bathyal zone from 500–4000 m (with the upper bathyal zone from 500–2000 m and the lower bathyal zone from 2000–4000 m), and the abyssal zone from 4000 m to the greatest depths recorded in the oceans. ZEZINA (1970) maintained that the majority of brachiopods (including the inarticulated forms) occur within the neritic zone, and this is supported by an analysis of the depth data for the articulated brachiopods here (Table 42), with 46% of species found only in this zone and a further 30% found in the neritic zone but not restricted to it, ranging down into the upper bathyal zone. A further 6% range from 500–2000 m, bringing the total for species found in the neritic and upper bathyal zones to over 80%. The rest are found either in the lower bathyal zone or the abyssal zone. Only the Terebratuloidea, Cancellothyridoidea, and Zeillerioidea have significant numbers of deep-water species. For articulated species as a whole, only 9

TABLE 43. List of superfamilies and extant genera of articulated brachiopods documented in this chapter (new).

Superfamily (Number of genera)	Genera
Pugnacoidea (5)	*Basiliola, Basiliolella, Rhytirhynchia, Acanthobasiliola, Striarina*
Dimerelloidea (2)	*Cryptopora, Aulites*
Norelloidea (9)	*Frieleia, Compsothyris, Grammetaria, Hispanirhynchia, Abyssorhynchia, Manithyris, Parasphenarina, Neorhynchia, Tethyrhynchia*
Hemithiridoidea (3)	*Hemithiris, Pemphyxina, Notosaria*
Thecideoidea (5)	*Lacazella, Pajaudina, Ospreyella, Thecidellina, Kakanuiella*
Terebratuloidea (12)	*Acrobrochus, Liothyrella, Gryphus, Tichosina, Arctosia, Dolichozygus, Dysedrosia, Erymnia, Zygonaria, Dallithyris, Kanakythyris, Stenosarina*
Dyscolioidea (5)	*Dyscolia, Goniobrochus, Abyssothyris, Acrobelesia, Xenobrochus*
Cancellothyridoidea (10)	*Cancellothyris, Murravia, Terebratulina, Chlidonophora, Eucalathis, Bathynanus, Nanacalathis, Notozyga, Agulhasia, Cnismatocentrum*
Zeillerioidea (1)	*Macandrevia*
Kingenoidea (3)	*Ecnomiosa, Fallax, Septicollarina*
Laqueoidea (12)	*Laqueus, Glaciarcula, Frenulina, Jolonica, Pictothyris, Shimodaia, Terebratalia, Coptothyris, Dallinella, Diestothyris, Simplicithyris, Tythothyris*
Megathyridoidea (3)	*Megathiris, Argyrotheca, Thaumatosia*
Bouchardioidea (1)	*Bouchardia*
Platidioidea (5)	*Platidia, Amphithyris, Annuloplatidia, Leptothyrella, Neoaemula*
Terebratelloidea (19)	*Terebratella, Aerothyris, Aneboconcha, Calloria, Dyscritosia, Fosteria, Gyrothyris, Neothyris, Syntomaria, Anakinetica, Parakinetica, Magellania, Holobrachia, Magadinella, Pirothyris, Dallina, Nipponithyris, Campages, Jaffaia*
Kraussinoidea (4)	*Kraussina, Megerlia, Megerlina, Pumilus*
Gwynioidea (1)	*Gwynia*

species belonging to 9 genera are known to extend below 4000 m into the abyssal zone. These are: *Cryptopora gnomon, Abyssorhynchia craneana, Neorhynchia strebeli, Abyssothyris wyvillei, Terebratulina kiiensis, Chlidonophora incerta, Bathynanus inversus, Annuloplatidia indopacifica,* and *Leptothyrella incerta. N. strebeli* is the only species so far found only in the abyssal zone. The greatest known depth for living shells is 5800 m for *Annuloplatidia indopacifica,* and the greatest recorded depth range is 370–5800 m for the same species (ZEZINA, 1985).

ORDER RHYNCHONELLIDA

The superfamilies and their genera documented here are listed in Table 43. The order Rhynchonellida contains 4 superfamilies with extant genera (SAVAGE & others, 2002). These superfamilies are the Pugnacoidea, Dimerelloidea, Norelloidea, and Hemithiridoidea. While rhynchonellide species are relatively uncommon in modern seas, 39 Recent species belonging to 18 genera have so far been described (Tables 44–47; Fig. 1939–1942). The geological ranges of all extant rhynchonellide genera may be found in SAVAGE and others (2002).

PUGNACOIDEA

The superfamily Pugnacoidea contains 11 extant species belonging to 5 genera (Table 44, Fig. 1939). All species have a relatively restricted depth range within the neritic and upper bathyal zones, with the exception of *Basiliola pompholyx*, which has been found below 2000 m. Geographically, living pugnacoids are Indo-Pacific in distribution, with particular concentration in the western Pacific; they are not represented in the Atlantic or from polar latitudes. *Basiliolella* is found in an arc from eastern Australia to the Loyalty Islands and New Caledonia. Three of the genera are monotypical, with *Rhytirhynchia* and *Striarina* found only in the central Indian Ocean, while *Acanthobasiliola* occurs from Japan to the Banda Sea.

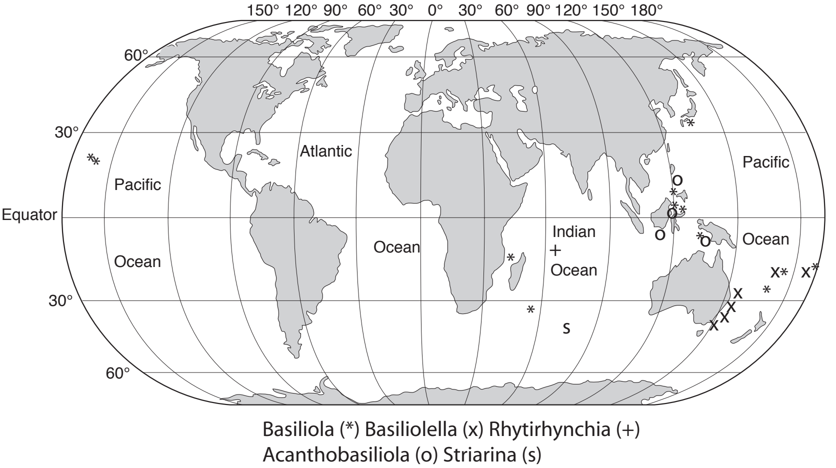


FIG. 1939. Geographic distribution of extant articulated brachiopod genera in superfamily Pugnacoidea (new).

TABLE 44. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Pugnacoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Basiliola Dall, 1908	5	250–380	*B. arnaudi* Cooper, 1981a: Indian Ocean: N. Moçambique Channel; Samper Bank, SE of Madagascar (Cooper, 1981a; Zezina, 1987)
		260–735	*B. beecheri* (Dall, 1895): Pacific Ocean: Hawaiian Is., New Caledonia and Loyalty Is., Fiji; Norfolk Ridge (Dall, 1895, 1920; Cooper, 1959; Zezina, 1981b, 2005; Laurin,1997; Bitner, 2006)
		44–981	*B. elongata* Cooper, 1959: Pacific Ocean: S. Philippines, Celebes, ?Kei Is. (Dall, 1920; Cooper, 1959)
		80–520	*B. lucida* (Gould, 1862): Pacific Ocean: Japan; New Caledonia and Loyalty Is. (Davidson, 1887 in 1886–1888; Dall, 1920; Hatai, 1936a, 1940; Cooper, 1959; Laurin, 1997)
		275–2009	*B. pompholyx* Dall, 1920: Pacific Ocean: Philippines, Borneo, Kei Is. (Dall, 1920; Jackson & Stiasny, 1937; Cooper, 1959; Zezina, 1981a)
Basiliolella d'Hondt, 1987	3	181–300	*B. colurnus* (Hedley, 1905): Pacific Ocean: Australia, eastern coast from 28° S to eastern Bass Strait at 40° S (Dall, 1920; Zezina, 1981a, 1985)
		210–250	*B. ferox* d'Hondt, 1987: Pacific Ocean: New Caledonia and Loyalty Is. (d'Hondt, 1987)
		160–600	*B. grayi* (Woodward, 1855): Pacific Ocean: Fiji, New Caledonia, Loyalty Is. (Woodward, 1855; Laurin, 1997)
Rhytirhynchia Cooper, 1957	1	223–278	*R. sladeni* (Dall, 1910): Indian Ocean: S. of Saya de Malha Bank (Dall, 1910, 1920; Cooper, 1959)
Acanthobasiliola Zezina, 1981a	1	240–635	*A. doederleini* (Davidson, 1886 in 1886–1888): Pacific Ocean: Japan, Philippines, Celebes Sea, Banda Sea, Java Sea (Davidson, 1887 in 1886–1888; Dall, 1920; Jackson & Stiasny, 1937; Cooper, 1959; Zezina, 1981a)
Striarina Cooper, 1973	1	672	*S. valdiviae* (Helmcke, 1940): Indian Ocean: east of St. Paul Is. (Helmcke, 1940; Zezina, 1985)

DIMERELLOIDEA

The superfamily Dimerelloidea contains seven extant species belonging to two genera (Table 45, Fig. 1940). *Cryptopora* contains six extant species and is represented in all the oceans of the world and at virtually all latitudes. The biogeography and geological history of Recent and fossil species of this genus has been discussed by Bitner & Cahuzac (2004). Although widely distributed, *C. gnomon* is particularly well represented in the North Atlantic. Notwithstanding the wide depth range of both this species and its congener *C. boettgeri* from the Indo-Pacific, both are regarded as typically deep-water forms, with *C. gnomon* ranging down into the abyssal zone (Cooper, 1973d; Curry, 1983). *Cryptopora curiosa*, on the other hand, is a distinctive shallow-water species present in the Red Sea–Gulf of Aden area and northwestern Indian Ocean (Cooper, 1973b; Logan & others, 2007). The three remaining species are all neritic and upper bathyal zone dwellers. The genus *Aulites* is monotypical, with *A. brazieri* being restricted to the neritic zone of the eastern, southern, and western coasts of Australia (Richardson, 1987).

NORELLOIDEA

The superfamily Norelloidea contains 14 extant species belonging to 9 genera (Table 46, Fig. 1940–1941). *Parasphenarina* from the Indo–West Pacific and the monotypical *Tethyrhynchia* from the Mediterranean are both micromorphic forms that typically inhabit shallow-water caves (Logan & Zibrowius, 1994; Motchurova-Dekova &

Table 45. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Dimerelloidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Cryptopora Jeffreys, 1869	6	250–3045	*C. boettgeri* Helmcke, 1940: Atlantic Ocean–Indian Ocean: off Dar-es-Salaam, Tanzania; S. Africa; Pacific Ocean: New Caledonia; S. Australia (Helmcke, 1940; Foster, 1969; Cooper, 1973b, 1973d; d'Hondt, 1987; Hiller, 1991, 1994)
		50–1537	*C. curiosa* Cooper, 1973b: Indian Ocean: Andaman Is.; Mozambique; S. Africa; NE end of Somalia; Red Sea–Gulf of Aden (Cooper, 1973b; Hiller, 1994; Logan & others, 2007)
		300–4060 (5950?)	*C. gnomon* Jeffreys, 1869: Atlantic Ocean: Franz Josef Land; Barents Sea; Iceland; Norway; British Isles; G. of Gascogne; N. Spain; Morocco; Azores; Canary Is.; W. Greenland; Davis Strait; Labrador; Newfoundland; eastern Canada and USA to Florida; G. of Mexico; Caribbean: Bermuda, Panama; NE of Falkland Is.; Pacific: New Zealand, Macquarie Is. (Fischer & Oehlert, 1891; Dall, 1920; Massy, 1925; Wesenberg-Lund, 1938, 1939, 1940b, 1941; Cooper, 1954a, 1959, 1973d, 1981b; Zezina, 1975a, 1975b, 1981, 1997b, 2000, 2001a; Dawson, 1991; Bitner & Cahuzac, 2004; Alvarez & Emig, 2005)
		170	*C. hesperis* Cooper, 1982: Pacific Ocean: southern Oregon (Cooper, 1982)
		927	*C. maldiviensis* Muir-Wood, 1959: Indian Ocean: Maldive Is., (Muir-Wood, 1959)
		136–850	*C. rectimarginata* Cooper, 1959: Caribbean Sea: G. of Mexico; Florida Keys; Bahamas; Saba Bank; Barbados (Cooper, 1959, 1977; Asgaard & Stentoft, 1984; Logan, 1990)
Aulites Richardson, 1987	1	34–228	A. *brazieri* (Crane, 1886): Pacific Ocean: eastern, southeren, and western coasts of Australia between 23°–39° S and 113°–154° E (Hedley, 1906; Dall, 1920; Foster, 1969; Richardson, 1987)

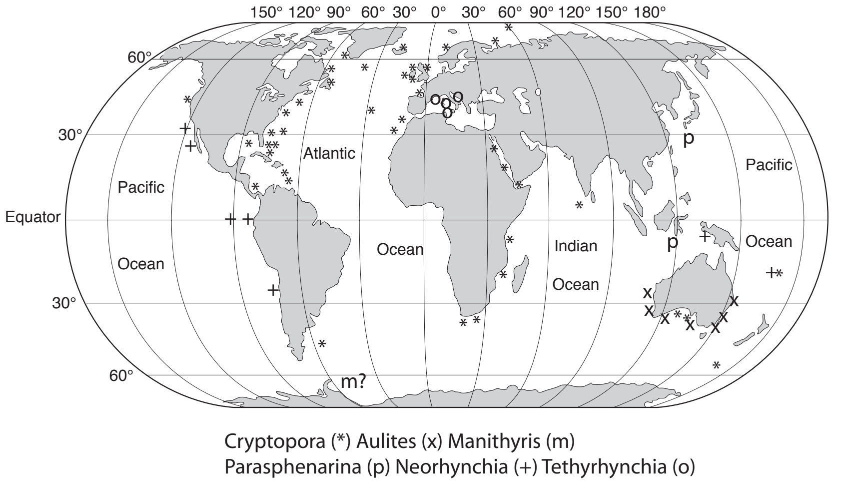


FIG. 1940. Geographic distribution of extant articulated brachiopod genera in superfamilies Dimerelloidea and Norelloidea (part) (new).

others, 2002). Both species of *Grammetaria* are also relatively shallow, but all other norelloid genera show most of their species ranging down into the bathyal, and, in the case of *Abyssorhynchia* and *Neorhynchia*, the abyssal zone. Geographically the group is widespread. *Manithyris* and *Compsothyris* are typically deep-water forms off Antarctica, while *Frieleia* occurs north of 30° N on both sides of the Pacific Ocean. *Grammetaria* is more widespread longitudinally than latitudinally, its geographic range stretching from Cape of Good Hope to Indonesia and as far east as the Loyalty Islands and New Caledonia. In contrast, *Hispanirhynchia cornea* is common only off the eastern Atlantic coasts and northwestern Africa. *Abyssorhynchia* is a central and eastern Pacific form, while *Neorhynchia* occurs in the western Pacific around New Guinea and New Caledonia and along the eastern Pacific seaboard for over 60° of latitude.

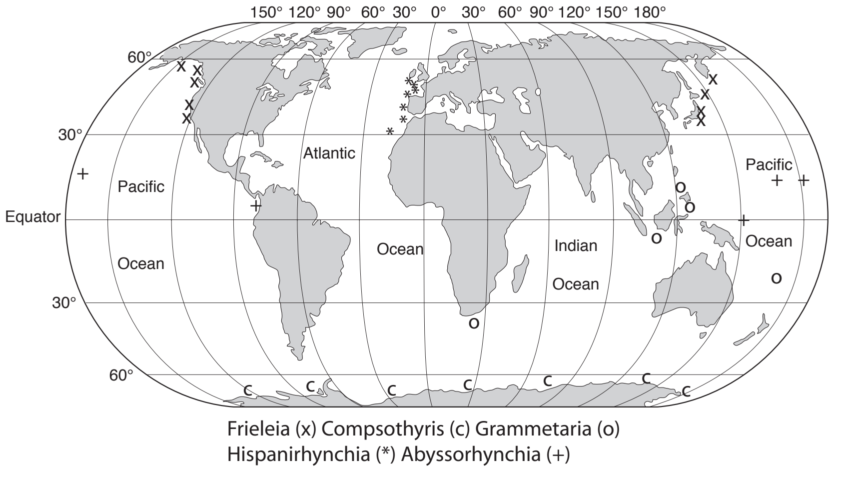


FIG. 1941. Geographic distribution of extant articulated brachiopod genera in superfamily Norelloidea (part) (new).

TABLE 46. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Norelloidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Frieleia Dall, 1895	2	38–2393	*F. halli* Dall, 1895: Pacific Ocean: Japan, Honshu; Bering Sea; Kuril Is.; Kamchatka Penin.; Alaska; British Columbia; Washington; Oregon; California (Dall, 1895, 1920; Hatai, 1936a, 1940; Cooper, 1959; Bernard, 1972; Zezina, 1997b)
		311	*F. pellucida* (Yabe & Hatai, 1934): Pacific Ocean: Japan, eastern coast of Shikoku (Hatai, 1936a, 1940; Cooper, 1959)
Compsothyris Jackson, 1918	2	2507–2525	*C. ballenyi* Foster, 1974: Antarctica: Balleny Is. (Foster, 1974)
		329–2580	*C. racovitzae* (Joubin, 1901): Antarctica: circumpolar (Cooper, 1959; Foster, 1974)
Grammetaria Cooper, 1959	2	292–780	*G. bartschi* (Dall, 1920): Pacific Ocean: Philippines, Moluccas, Indian Ocean: south of Bali (Dall, 1920; Cooper, 1959; Zezina, 1981b)
		240–700	*G. africa* Hiller, 1986: Indian Ocean: S. Africa; W. Pacific Ocean: New Caledonia, Loyalty Is. (Hiller, 1986, 1991, 1994; Laurin, 1997)
Hispanirhynchia Thomson, 1927	1	105–2388	*H. cornea* (Fischer, 1887): Atlantic Ocean: British Isles; G. of Gascogne; N. Spain; Portugal; Morocco; Canary Is. (Davidson, 1887 in 1886–1888; Fischer & Oehlert, 1891; Cooper, 1959; d'Hondt, 1976; Brunton & Curry, 1979; Cooper, 1981b; Logan, 1988a; Anadón, 1994; Alvarez & Emig, 2005)
Abyssorhynchia Zezina, 1980	1	1409–4600	*A. craneana* (Dall, 1895): Pacific Ocean: G. of Panama; Marcus-Necker seamounts; Kipingamarangi Rise (Dall, 1920; Zezina, 1981b)
Manithyris Foster, 1974	1	2897–2904	*M. rossi* Foster, 1974: Antarctica: northern part of Ross Sea (Foster, 1974)
Parasphenarina Motchurova-Dekova, Saito, & Endo, 2002	2	0–40	*P. cavernicola* Motchurova-Dekova, Saito, & Endo, 2002: Pacific Ocean: Japan, Okinawa (Motchurova-Dekova, Saito, & Endo, 2002)
		240	*P. ezogremena* Zezina, 1981a: Indian Ocean: Flores Sea, north of Bali (Zezina, 1981a; Motchurova-Dekova, Saito, & Endo, 2002)
Neorhynchia Thomson, 1915	2	4124–4513	*N. strebeli* (Dall, 1908): Pacific Ocean: Galapagos Is., Peru; Chile; New Guinea; New Caledonia (Dall, 1920; Cooper, 1959, 1972, 1973b; Muir-Wood, 1960; McCammon & Buchsbaum, 1968; Foster, 1974; Laurin, 1997)
		3039–3916	*N. profunda* Cooper, 1972: Pacific Ocean: California; Baja California, Mexico (Cooper, 1972; Brand & others, 2003)
Tethyrhynchia Logan, 1994	1	3–60	*T. mediterranea* Logan, 1994: Mediterranean Sea: S. France; Tunisia; Croatia; Italy, Sicily, Ustica Is. (Logan & Zibrowius, 1994; La Perna, 1998; Simon & Willems, 1999; Di Geronimo & others, 2001; Logan & others, 2004)

TABLE 47. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Hemithiridoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Hemithiris d'Orbigny, 1847	4	0–2078	*H. psittacea* (Gmelin, 1790): Arctic Ocean: circumpolar: Chukchi Sea; E. Siberia Sea; Laptev Sea; Kara Sea; Barents Sea; Atlantic Ocean: Greenland; Faroes; Baffin Bay; E. Canada to G. of St. Lawrence and Newfoundland; Iceland; Norway; N. British Isles; Scandinavia; Pacific Ocean: N. Japan (Hokkaido); Kuril Is.; Kamchatka Penin.; Sea of Okhotsk; Bering Sea; Alaska; British Columbia to S. Oregon (Jeffreys, 1878; Davidson, 1887 in 1886–1888; Dall, 1920; Hatai, 1940; Wesenberg-Lund, 1938, 1939, 1940a, 1940b, 1941; Cooper, 1959, 1973d; Bousfield, 1960; Bernard, 1972; Brunton & Curry, 1979; Zezina, 1997b; Saito & Tazawa, 2002)
		20–166	*H. woodwardi* (Adams, 1863): Pacific Ocean: Japan, Hokkaido; (Cooper, 1959; Saito & Tazawa, 2002)
		?	*H. braunsi* Hayasaka, 1928: Pacific Ocean: Japan (Cooper, 1959)
		?	*H. peculiaris* Nomura & Hatai, 1936: Pacific Ocean: Japan (Cooper, 1959)
Pemphyxina Cooper, 1981a	1	90–315	*P. pyxidata* (Davidson, 1880): Indian Ocean: Kergeulen Is; Amsterdam, Heard Is. (Davidson, 1880; Stüder, 1889; d'Hondt, 1976; Cooper, 1981a)
Notosaria Cooper, 1959	2	0–800	*N. nigricans* (Sowerby, 1846): Pacific Ocean: New Zealand, Kermadec Is., Chatham Is. (Cooper, 1959; Bowen, 1968; Foster, 1974; Lee, 1978; Lee & Wilson, 1979; Richardson, 1981)
		805	*N. reinga* Lee & Wilson, 1979: Pacific Ocean: New Zealand, Three Kings Is., N. Island, Kermadec Is. (Lee & Wilson, 1979; Dawson, 1991)

HEMITHIRIDOIDEA

The superfamily Hemithiridoidea has 7 extant species belonging to 3 genera (Table 47, Fig. 1942). *Hemithiris* has 4 species but little is known about *H. braunsi* and *H. peculiaris,* emphasizing the need for a restudy of these (and other) Japanese species. *Hemithiris psittacea* is a common boreal species of wide longitudinal and great bathymetric range, always occurring above 30° N, and succeeded southward in the northeastern Atlantic by *Hispanirhynchia cornea*, or elsewhere in the Atlantic, by terebratuloids. *Pemphyxina* contains one species, found in shallow water only in the vicinity of the Kerguelen Islands, southern Indian Ocean. *Notosaria* is represented by 2 species from the neritic and upper bathyal zones around New Zealand and the Kermadec Islands to the east.

ORDER THECIDEIDA

THECIDEOIDEA

The order Thecideida contains only the superfamily Thecideoidea (BAKER, 2006) with 13 extant species belonging to 5 genera (Table 48, Fig. 1943). The lacazelline subfamily is represented by *Lacazella, Pajaudina,* and *Ospreyella*, the thecidellinine subfamily by *Thecidellina* and *Kakanuiella*. *Lacazella* occurs in the Mediterranean Sea, Caribbean Sea, and the Indian Ocean, although there is an undescribed form from Okinawa, Japan (M. SAITO, personal communication, 25 September 2003). *Pajaudina* is monotypic and known only

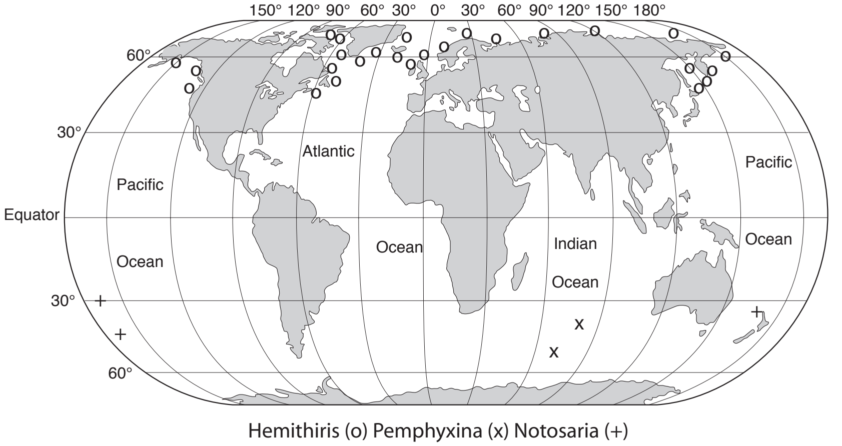


FIG. 1942. Geographic distribution of extant articulated brachiopod genera in superfamily Hemithiridoidea (new).

from the Canary Islands and *Ospreyella* from the Great Barrier Reef, the Maldive Islands, and the northwestern Pacific (LOGAN, 2005; personal observation, 2007). *Thecidellina* is recorded from Cape Verde, the Caribbean Sea, Red Sea, and Indo-Pacific region. LEE and ROBINSON (2003), LÜTER and others (2003), and LOGAN (2005) have reviewed the status, ecology, and biogeography of Recent lacazelline and thecidellinine species. All are small cementing forms, variable in shape, and typically occur in shallow but poorly accessible cryptic habitats, hence the occasional discovery of new taxa by divers. Living thecideoids are typically low latitude, neritic zone dwellers, but their latitudinal and bathymetric range has been extended by the recent discovery by LÜTER (2005) of a new extant species of the thecidellinine genus *Kakanuiella* from the bathyal zone south of New Zealand at a latitude of 44° S.

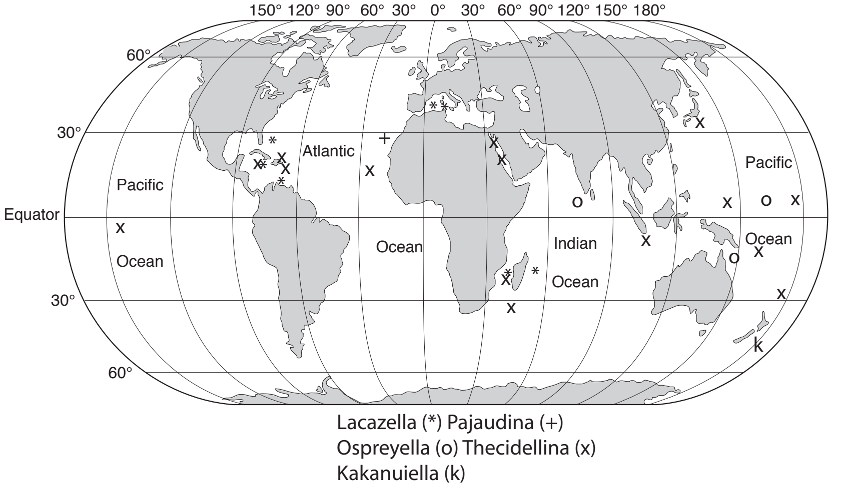


FIG. 1943. Geographic distribution of extant articulated brachiopod genera in superfamily Thecideoidea (new).

TABLE 48. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Thecideoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Lacazella Munier-Chalmas, 1881	3	25–60	*L. caribbeanensis* Cooper, 1977: Caribbean Sea: Bahamas, Jamaica, Curaçao (Meile & Pajaud, 1971; Pajaud, 1974; Cooper, 1977; Logan, 2004)
		?	*L. mauritiana* Dall, 1920: Indian Ocean: Mauritius, ?Europa Is. (Dall, 1920; Cooper, 1973b; Zezina, 1987)
		1–110	*L. mediterranea* (Risso, 1826): Mediterranean Sea: Tunisia, Algeria (Pajaud, 1970; Logan, 1979, 2004; Logan & others, 2004)
Pajaudina Logan, 1988	1	10–50 (1000?)	*P. atlantica* Logan, 1988: Atlantic Ocean: Canary Is. (Logan, 1988a, 1988b, 2004; Alvarez & Emig, 2005)
Ospreyella Lüter, Worheide, & Reitner, 2003	2	15–20	*O. depressa* Lüter, 2003: Pacific Ocean: NE Australia, Coral Sea (Lüter, Worheide, & Reitner, 2003)
		24–39	O. *maldiviana* Logan, 2005: Indian Ocean: Maldive Is. (Logan, 2005)
Thecidellina Thomson, 1915	6	3–130 (850?)	*T. barretti* (Davidson, 1864): Caribbean Sea: Jamaica, Cayman Is., Puerto Rico; Dominican Republic, Guadeloupe, Saba; Atlantic Ocean: Cape Verde (Davidson, 1887 in 1886–1888; Cooper, 1934; Pajaud, 1970; Jackson, Goreau, & Hartman, 1971; Cooper 1977; Logan, 1977, 1988a, 1990; Lee & Robinson, 2003)
		55–84 (1463?)	*T. blochmanni* Dall, 1920: Indian Ocean: Europa Is., Christmas Is., Réunion (Pajaud, 1970; d'Hondt, 1987; Lee & Robinson, 2003)
		0–436	*T. congregata* Cooper, 1954b: Pacific Ocean: Marshall Is., Guam, Saipan, Palau (Cooper, 1954b; Pajaud, 1970; Jackson, Goreau, & Hartman, 1971; Grant, 1987; Thayer & Allmon, 1991; Lee & Robinson, 2003)
		150–183	*T. japonica* (Hayasaka, 1938): Pacific Ocean: Japan (Hatai, 1940; Pajaud, 1970; Lee & Robinson, 2003)
		47–146	*T. maxilla* (Hedley, 1899): Pacific Ocean: Kermadec Is., Tuvalu, New Hebrides Is., Marshall Is., Taumotu Is; Indian Ocean: Réunion (Cooper, 1954b, 1964; d'Hondt, 1987; Lee & Robinson, 2003)
		380	*T. minuta* Cooper, 1981a: Indian Ocean: south of Madagascar (Cooper, 1981a; Lee & Robinson, 2003)
Kakanuiella Lee & Robinson, 2003	1	405–1024	*K. chathamensis* Lüter, 2005: Pacific Ocean: east of Chatham Island and on Chatham Rise, New Zealand (Lüter, 2005)

TABLE 49. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Terebratuloidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Acrobrochus Cooper, 1983	3	1058–2342	*A. blochmanni* (Jackson, 1912): Antarctica: Ross and Weddell Seas (Jackson, 1912; Foster, 1974; Cooper, 1983)
		415–612	*A. hendleri* (Cooper, 1982): Atlantic Ocean: off S. Sandwich Is. (Cooper, 1982, 1983)
		732–1919?	*A. vema* (Cooper, 1973d): Atlantic Ocean: S. America: Burdwood Bank, off southeastern tip of Argentina; S. Georgia Is. (Cooper, 1973d, 1982, 1983)
Liothyrella Thomson, 1916	9	7–2273	*L. antarctica* (Blochmann, 1906): Antarctica: circumpolar; S. Georgia Is.; Falkland Is.; S. Orkney Is. (Blochmann, 1906; Foster, 1974; Zezina, 1985)
		760–1208?	*L. delsolari* Cooper, 1982: Pacific Ocean: Peru; Cape Horn (Cooper, 1982; Foster, 1989)
		110–384	*L. moseleyi* (Davidson, 1878): Indian Ocean: Crozet and Kerguelen Is. (Davidson, 1886 in 1886–1888; Dall, 1920; Foster, 1974; Cooper, 1981a)
		1058–2342	*L. multiporosa* Foster, 1974: Antarctica: Ross Sea (Foster, 1974)
		6–805	*L. neozelanica* Thomson, 1918: Pacific Ocean: S. Island, New Zealand; Chatham Rise (Bowen, 1968; Dawson, 1971, 1991; Foster, 1974, 1989; Richardson, 1981; Campbell & Fleming, 1981; Cooper, 1983; Lüter, 2007)
		75–198	*L. oblonga* Cooper, 1973d: Atlantic Ocean: southern tip of S. America: Tierra del Fuego, Burdwood Bank, south of Falkland Is. (Cooper, 1973d)
		516–1244	*L. scotti* Foster, 1974: Antarctica: Scott Island (Foster, 1974)
		7–974	*L. uva* (Broderip, 1833): Pacific Ocean: Mexico, Panama, Ecuador, Chile; S. Atlantic O. and Antarctica: Strait of Magellan, S. Argentina, Falkland Is., S. Georgia Is., S. Orkney Is., S. Sandwich Is. (Davidson, 1886 in 1886–1888; Dall, 1920; Cooper, 1973d, 1982, 1983; Foster, 1974, 1989; Peck, Brockington, & Brey, 1997)
		672–680	*L. winteri* (Blochmann, 1906): Indian Ocean: St. Paul Is.; Kerguelen Is. (Blochmann, 1906; Helmcke, 1940; Foster, 1974; d'Hondt, 1977)
Gryphus Megerle von Mühlfeldt	5	125–915	*G. bartlettii* Dall, 1882: Caribbean Sea: G. of Mexico; Cuba; Lesser Antilles (Virgin Is., Martinique, Montserrat, Grenada, St. Kitts, Barbados) (Davidson, 1886 in 1886–1888; Dall, 1920; Cooper, 1934, 1954a, 1977; Logan, 1977; Asgaard & Stentoft, 1984)
		50–240	*G. capensis* Jackson, 1952: Indian Ocean: S. coast of S. Africa (Jackson, 1952; Hiller, 1991; 1994)
		2136–3700	*G. clarkeana* Dall, 1920: Pacific Ocean: SW of Galapagos Is.; G. of Panama (Dall, 1895, 1920)
		120–549	*G. tokionis* Dall, 1920: Pacific Ocean: Japan; Honshu (Dall, 1920; Hatai, 1936a, 1940)
		73–2663	*G. vitreus* (Born, 1778): Atlantic Ocean: Mediterranean Sea; G. of Gascogne; Portugal; N. Spain; NW Africa; Cape Verde? (Forbes, 1844; Davidson, 1886 in 1886–1888; Fischer & Oehlert, 1891; Dall, 1920; d'Hondt, 1976; Logan, 1979; Brunton & Curry, 1979; Cooper, 1981b, 1983; Emig, 1985, 1987; Brunton, 1988; Aliani, 1994; Logan & others, 2004; Alvarez & Emig, 2005)
Tichosina Cooper, 1977	20	165–229	*T. abrupta* Cooper, 1977: Caribbean Sea: SW coast of Florida (Cooper, 1977)
		512–686	*T. bahamiensis* Cooper, 1977: Caribbean Sea: Grand Bahama Is., Bahamas (Cooper, 1977)
		164–909	*T. bartschi* (Cooper, 1934): Caribbean Sea: north coast of Virgin I.; Puerto Rico; G. of Mexico (Cooper, 1934, 1977)
		201–289	*T. bullisi* Cooper, 1977: Caribbean Sea: Nicaragua (Cooper, 1977, 1983)
		146–963	*T. cubensis* (Pourtalès, 1867): Caribbean Sea: Florida; Bahamas; Greater and Lesser Antilles (Dall, 1871, 1920; Cooper, 1954a, 1977)
		123–458	*T. dubia* Cooper, 1977: Caribbean Sea: Lesser Antilles; Guyana (Cooper, 1977, 1983)
		120–732	*T. elongata* Cooper, 1977: Caribbean Sea: Cuba; Guyana (Cooper, 1977; Logan, 1990)
		494–695	*T. erecta* Cooper, 1977: Caribbean Sea: Florida; Bahamas; Cuba (Cooper, 1977)
		348–549	*T. expansa* Cooper, 1977: Caribbean Sea: southernmost Bahamas; Yucatan Channel, Mexico (Cooper, 1977)
		119–218	*T. floridensis* Cooper, 1977: Caribbean Sea: G. of Mexico; W. Florida; Dry Tortugas; Cuba (Cooper, 1977)

Table 49. *Continued.*

		231–258	*T. labiata* Cooper, 1977: Caribbean Sea: east side of St. Vincent (Cooper, 1977)
		309	*T. martinicensis* (Dall, 1920): Caribbean Sea: west side of Martinique (Cooper, 1977, 1983)
		60–641	*T. obesa* Cooper, 1977: Caribbean Sea: G. of Mexico, Strait of Yucatan; Venezuela; French Guiana (Cooper, 1977, 1983)
		366	*T. ovata* Cooper, 1977: Caribbean Sea: G. of Mexico, south of New Orleans, Louisiana (Cooper, 1977, 1983)
		130–165	*T. pillsburyae* Cooper, 1977: Caribbean Sea: Dominican Republic (Cooper, 1977)
		93–115	*T. plicata* Cooper, 1977: Caribbean Sea: Venezuela; Trinidad (Cooper, 1977, 1983)
		201–534	*T. rotundovata* Cooper, 1977: Caribbean Sea: east coast of Florida; Strait of Florida; Bahamas; Yucatan Channel, Mexico (Cooper, 1977)
		210–302	*T. solida* Cooper, 1977: Caribbean Sea: G. of Mexico, south of New Orleans, Louisiana; Strait of Florida (Cooper, 1977, 1983)
		403–708	*T. subtriangulata* Cooper, 1977: Caribbean Sea: Cuba; Puerto Rico (Cooper, 1977)
		284–650	*T. truncata* Cooper, 1977: Caribbean Sea: Bahamas; Strait of Yucatan, Mexico (Cooper, 1977)
Arctosia Cooper, 1983	1	136–1500	*A. arctica* Friele, 1877: Atlantic Ocean: E. Greenland; Iceland; Jan Mayen Is.; Barents Sea? (Davidson, 1886 in 1886–1888; Dall, 1920; Wesenberg-Lund, 1938, 1941; Cooper, 1983; Zezina, 1997b)
Dolichozygus Cooper, 1983	1	101–219	*D. stearnsi* Dall & Pilsbry, 1891: Pacific Ocean: Japan; Strait of Korea; Banda Sea (Kei Is.) (Hatai, 1936a, 1940; Cooper, 1983; Zezina, 1987)
Dysedrosia Cooper, 1983	1	240–930	*D. borneoensis* (Dall, 1920): Pacific Ocean: Indonesia; Borneo (Sibuko Bay); Kei Is. (Dall, 1920; Jackson & Stiasny, 1937; Zezina, 1981a; Cooper, 1983)
Erymnia Cooper, 1977	1	275–575	*E. muralifera* Cooper, 1977: Caribbean Sea: Bahamas; Virgin Is. (Cooper, 1977, 1983)
Zygonaria Cooper, 1983	2	101–780	*Z. davidsoni* (Adams, 1867): Pacific Ocean: S. Japan; Strait of Korea; Indian Ocean: south of Bali (Dall, 1920; Hatai, 1940; Zezina, 1981a; Cooper, 1983)
		190–578	*Z. joloensis* (Dall, 1920): Pacific Ocean: Philippines (Dall, 1920; Cooper, 1983)
Dallithyris Muir-Wood, 1959	3	165–275	*D. fulva* Blochmann, 1906: Pacific Ocean: S. Australia; Tasmania (Blochmann, 1906; Cooper, 1983)
		240–970	*D. murrayi* Muir-Wood, 1959: Indian Ocean: Maldive Is., Saya de Malha Bank; Pacific Ocean: Nazca Ridge (Muir-Wood, 1959; Cooper, 1983; Zezina, 1985, 1990)
		640–753	*D. pacifica* Bitner, 2006b: Pacific Ocean: Fiji (Bitner, 2006b)
Kanakythyris Laurin, 1997	1	245–470	*K. pachyrhynchos* Laurin, 1997: Pacific Ocean: New Caledonia; Loyalty Is. (Laurin, 1997)
Stenosarina Cooper, 1977	8	183–375	*S. angustata* Cooper, 1977: Caribbean Sea: Bahamas; Gulf of Mexico, Campeche Shelf north of Yucatan Peninsula (Cooper, 1977, 1983)
		275–1140	*S. crosnieri* (Cooper, 1983): Indian Ocean: NW side of Madagascar; W. Pacific Ocean: Norfolk Ridge; New Caledonia; Loyalty Is. (Cooper, 1983; Laurin, 1997; Zezina, 2005)
		255–2220	*S. davidsoni* Logan, 1998: Atlantic Ocean: N. Spain; Portugal; G. of Gascogne; Azores; Ascension Is.; Canary Is.; Cape Verde; seamounts off Iberian Peninsula and Morocco; ?Caribbean Sea: Florida; Cuba; Barbados (Davidson, 1886 in 1886–1888; Fischer & Oehlert, 1891; Dall, 1920; Muir-Wood, 1959; Cooper, 1981b, 1983; Logan, 1988a, 1998; Gaspard, 2003b; Alvarez & Emig, 2005)
		280–520	*S. globosa* Laurin, 1997: Pacific Ocean: New Caledonia; Loyalty Is. (Laurin, 1997)
		850–965	*S. lata* Laurin, 1997: Pacific Ocean: New Caledonia (Laurin, 1997)
		549–608	*S. nitens* Cooper, 1977: Atlantic Ocean: NW side of Dominica; eastern end of Dominican Republic (Cooper, 1977, 1983)
		384	*S. oregonae* Cooper, 1977: Atlantic Ocean: G. of Mexico, Campeche Bank; off W. Cuba (Cooper, 1977)
		439–549	*S. parva* Cooper, 1977: Atlantic Ocean: between Puerto Rico and Dominican Republic (Cooper, 1977, 1983)

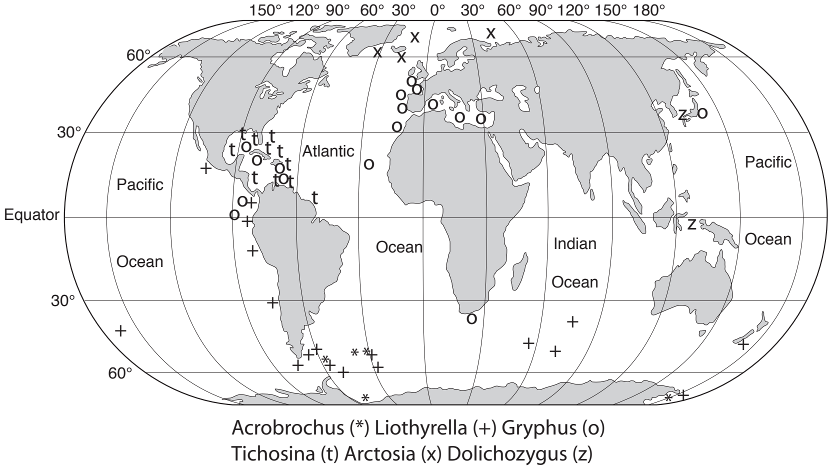


FIG. 1944. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratuloidea (new).

ORDER TEREBRATULIDA

The order Terebratulida contains 12 superfamilies (listed below) with extant genera. Their geological ranges may be found in LEE and others (2006).

TEREBRATULOIDEA

The superfamily Terebratuloidea includes 55 extant species belonging to 12 genera (Table 49, Fig. 1944–1945). Five genera are monotypical: *Arctosia* is a neritic–upper bathyal form from boreal latitudes in the Atlantic, *Dolichozygus* (neritic) and *Dysedrosia* (neritic–upper bathyal) are found in the western Pacific from Japan and Indonesia, while *Erymnia* from the Caribbean and *Kanakythyris* from the southwestern Pacific occur in the upper bathyal zone. *Zygonaria* with 2 species has a similar geographic distribution and depth range as *Dysedrosia*. The 3 species of *Acrobrochus*

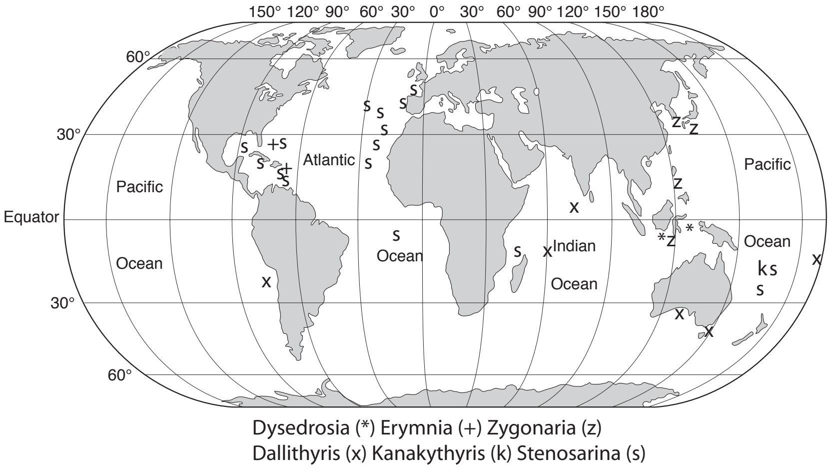


FIG. 1945. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratuloidea (new).

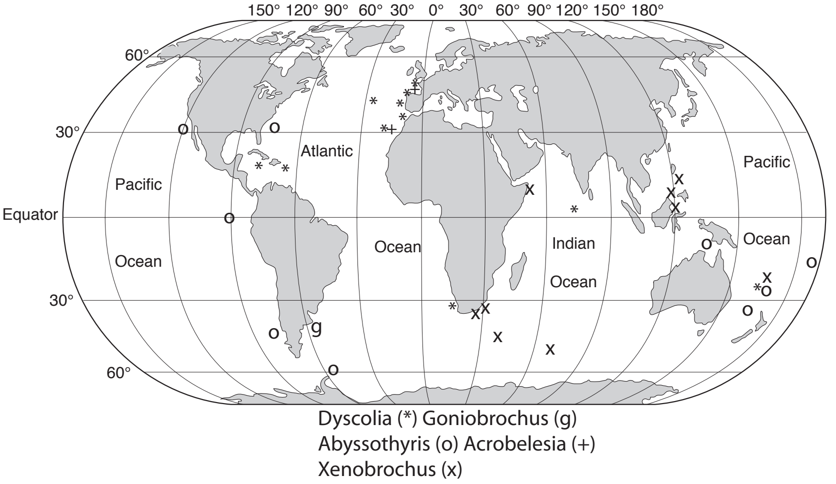


FIG. 1946. Geographic distribution of extant articulated brachiopod genera in superfamily Dyscolioidea (new).

all occur in the bathyal zone at high latitudes in the South Atlantic and Antarctica. *Dallithyris* has 3 species, one of which is from the central Indian Ocean, another from southern Australia, and a third from the eastern Pacific. The most common species of *Gryphus* is *G. vitreus* from the eastern Atlantic and the Mediterranean, where in the latter region it is particularly abundant on gravels at the heads of submarine canyons in the neritic–uppermost bathyal transitional zone (LOGAN, 1979; EMIG, 1985, 1987). Other species of *Gryphus* are known from the Caribbean, eastern Pacific, Japan, and off the southern tip of South Africa. *Tichosina* has 20 described species, all from the neritic and upper bathyal zones of the Caribbean region (COOPER, 1977) and needs to be restudied from larger populations than previously. Of the 9 species of *Liothyrella*, 8 are found in the neritic and bathyal zones of the southern hemisphere from the South Atlantic and Antarctica through the southern Indian Ocean to the southwestern Pacific Ocean, with only *L. uva* extending its range north into Central America. *Stenosarina* has 8 species, 4 of which are known only from the Caribbean area. *S. davidsoni* is typically found around the coasts, offshore islands, and seamounts of the eastern North Atlantic from the Gulf of Gascogne to Cape Verde, at depths ranging from 255–2220 m (LOGAN, 1998; GASPARD, 2003b).

DYSCOLIOIDEA

The superfamily Dyscolioidea includes 15 extant species belonging to 5 genera (Table 50, Fig. 1946). *Acrobelesia* and *Goniobrochus* are monotypical genera from the upper bathyal zone of the northeastern and southwestern Atlantic, respectively. *Dyscolia* and *Abyssothyris* each contain 3 species and are widely distributed geographically. *Dyscolia* is known from the bathyal zone of all three major oceans, with only the Atlantic-Caribbean species *D. wyvillei* extending up into the neritic zone. Similarly, all three species of *Abyssothyris* are predominantly deep-water forms, with *A. wyvillei* reaching one of the greatest depths (5631 m) of any modern brachiopod (FOSTER, 1989). *Abyssothyris* is widely distributed in all oceans except the Indian Ocean (COOPER, 1983). *Xenobrochus*, which is restricted to the Indian Ocean and western Pacific region, contains 7 species, most of which are neritic and upper bathyal zone dwellers.

CANCELLOTHYRIDOIDEA

The superfamily Cancellothyridoidea contains 51 extant species belonging to 10

TABLE 50. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Dyscolioidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Dyscolia Fischer & Oehlert, 1890	3	735–1463	*D. johannisdavisi* (Alcock, 1894): Indian Ocean: Maldive Is.; east coast of S. Africa. Pacific Ocean: New Caledonia, Chesterfield Is. (Alcock, 1894; Helmcke, 1940; Muir-Wood, 1959; Cooper, 1983; Hiller, 1986, 1991, 1994; Laurin, 1997)
		550–1098	*D. subquadrata* (Jeffreys, 1878): Atlantic Ocean: Portugal; G. of Gascogne; Canary Is. (Jeffreys, 1878; Davidson, 1886 in 1886–1888; Cooper, 1983; Logan, 1983)
		73–1557	*D. wyvillei* (Davidson, 1878): Atlantic Ocean: Azores; coast of NW Africa and offshore seamounts; N. Spain; Caribbean Sea: St. Thomas; Jamaica (Davidson, 1886; Fischer & Oehlert, 1891; d'Hondt, 1976; Cooper, 1977, 1983; Logan, 1998; Alvarez & Emig, 2005)
Goniobrochus Cooper, 1983	1	595–642	*G. ewingi* (Cooper, 1973d): Atlantic Ocean: SE of Mar del Plata, Argentina (Cooper,1973d, 1983)
Abyssothyris Thomson, 1927	3	420–2590	*A. atlantica* Cooper, 1977: Atlantic Ocean: Cape Fear, S. Carolina; seamounts off NW Africa (Cooper, 1977; 1983; Logan, 1998; Alvarez & Emig, 2005)
		3601–3687	*A. elongata* Cooper, 1972: Pacific Ocean: off Baja California, Mexico (vicinity of 31°N, 119°W); S. Atlantic Ocean: S. Shetland Is. (Cooper, 1972, 1982, 1983)
		400–5631	*A. wyvillei* (Davidson, 1878): Pacific Ocean: Galapagos Is.; S. Australia; south of New Guinea; NW of New Zealand; New Caledonia and Loyalty Is.; Fiji; Chile; Antarctica; S. Atlantic Ocean: S. Shetland Is. (Davidson, 1886 in 1886–1888; Muir-Wood, 1960; Cooper, 1975, 1982, 1983; Foster, 1989; Dawson, 1991; Laurin, 1997; Bitner, 2006b)
Acrobelesia Cooper, 1983	1	330–1000	*A. cooperi* (d'Hondt, 1976): Atlantic Ocean: Gulf of Gascogne; Canary Is. (d'Hondt, 1976; Cooper, 1981b, 1983; Logan, 1983)
Xenobrochus Cooper, 1981a	7	240–675	*X. africanus* (Cooper, 1973b): Indian Ocean: S. Africa; Pacific Ocean: New Caledonia, Loyalty Is. (Cooper, 1973b, 1981a, 1983; Hiller, 1986, 1991, 1994; Laurin, 1997)
		155–620	*X. agulhasensis* (Helmcke, 1939): Indian Ocean: S. Africa, west, south, and east of Cape of Good Hope (Helmcke, 1939; Foster, 1974; Hiller, 1986, 1991, 1994)
		204–460	*X. anomalus* Cooper, 1981a: Indian Ocean: SE of Marion Is. at 46°57'S, 37°59'E (Cooper, 1981a)
		790	*X. australis* Cooper, 1981a: Indian Ocean: W. of Heard Is. at 53°20'S, 72°29'E (Cooper, 1981a)
		65–300	*X. indianensis* (Cooper, 1973b): Indian Ocean: Somalia; S. Africa; Pacific Ocean: Matthew Is., Loyalty Is. (Cooper, 1973b; Hiller, 1991, 1994; Laurin, 1997)
		70–780	*X. naudei* Hiller, 1994: Indian Ocean: east coast of S. Africa (Hiller, 1986, 1991, 1994)
		89–1272	*X. translucidus* (Dall, 1920): Pacific Ocean: Philippines; Indonesia; Borneo; Celebes Is. (Dall, 1920; Jackson & Stiasny, 1937; Cooper, 1983)

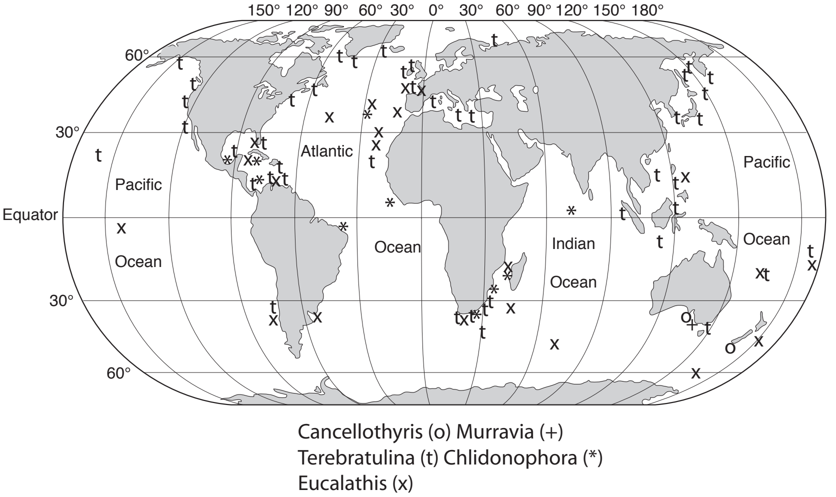


FIG. 1947. Geographic distribution of extant articulated brachiopod genera in superfamily Cancellothyridoidea (new).

genera (Table 51, Fig. 1947–1948). Three genera are monotypical: *Cancellothyris* is restricted to the neritic and upper bathyal zones around Australia and New Zealand, *Murravia* to South Australia, and *Agulhasia* to the southern tip of South Africa. The superfamily is dominated by two genera, *Terebratulina* and *Eucalathis*, which together account for 37 of the 50 extant species. *Terebratulina* is well represented in the North Atlantic and the adjacent seas of the Caribbean and Mediterranean but is absent from the South Atlantic. Ten species have been described from Japan and adjacent waters, which suggests that a reappraisal might be in order. While most species are neritic and upper bathyal zone dwellers, *T. septentrionalis* and *T. kiiensis* have great depth ranges. The 14 species of *Eucalathis* are also widely distributed, except for the northwestern Pacific area. Best known are the North Atlantic species *E. ergastica* and *E. tuberata,* both of which range greatly in depth. However, the 3 species of *Bathynanus* from the Indo-Pacific all appear to be predominantly deep water forms, with *B. inversus* reaching a depth of 5160 m. In contrast, both extant species of *Cnismatocentrum* from the northwestern Pacific have so far been obtained only from the neritic zone.

ZEILLERIOIDEA

The superfamily Zeillerioidea comprises 10 extant species belonging to a single genus, *Macandrevia* (Table 52, Fig. 1949). The genus occurs from pole to pole but is absent from the Indian Ocean and the western and central Pacific Ocean. The most common species is *M. cranium*, found throughout the North Atlantic from the equator to 77° N. Of the 10 species of *Macandrevia* that are known, 4 range down to the base of the bathyal zone, with *M. diamantina* extending into the abyssal zone, while only 3 are found in the neritic zone, indicating that this is a predominantly deep-water genus characteristic of the bathyal zone (COOPER, 1975; RICHARDSON, 1997b).

Table 51. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Cancellothyridoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Cancellothyris Thomson, 1926	1	6–366	*C. hedleyi* (Finlay, 1927): Pacific Ocean: Australia: S. Australia, Tasmania; New Zealand (Davidson, 1880, 1886 in 1886–1888; Blochmann, 1910; Dall, 1920; Foster, 1989; Dawson, 1991; Lüter & Cohen, 2002; Brand & others, 2003)
Murravia Thomson, 1916	1	73–273	*M. exarata* (Verco, 1910): Pacific Ocean: S. Australia (Blochmann, 1910; Thomson, 1927)
Terebratulina d'Orbigny, 1847	23	0–450	*T. abyssicola* Adams & Reeve, 1850: Indian Ocean: S and SE coasts of S. Africa, Moçambique (Dall, 1920; Jackson, 1952; Cooper, 1973b, 1973d; Hiller, 1991, 1994)
		400–410	*T. australis* Bitner, 2006b: Pacific Ocean: Fiji (Bitner, 2006b)
		18–700	*T. austroamericana* Zezina, 1980: Pacific Ocean: S. America: Chile (Zezina, 1985)
		32–1163	*T. cailleti* Crosse, 1865: Caribbean Sea: G. of Mexico; Florida to Barbados; northern coast of S. America (Dall, 1920; Cooper, 1954a, 1973d, 1977; Logan, 1977, 1990; Asgaard & Stentoft, 1984; Zezina, 2000)
		160–631	*T. callinome* Dall, 1920: Pacific Ocean: Japan; Philippines; Indonesia; Borneo (Dall, 1920; Hatai, 1936a; Jackson & Stiasny, 1937; Cooper, 1973c; Zezina, 1981a)
		236–545	*T. cavata* Verco, 1910: Pacific Ocean: S. Australia (Blochmann, 1910; Dall, 1920)
		485	*T. compressa* Cooper, 1973c: Pacific Ocean: Japan (Cooper, 1973c)
		113–858	*T. crossei* Davidson, 1882: Pacific Ocean: Japan; Sea of Okhotsk; Sakhalin Is.; Kuril Is.; Kamchatka Penin.; British Columbia; California (Davidson, 1886 in 1886–1888; Dall, 1920; Hatai, 1940; Bernard, 1972; Zezina 1997b)
		146	*T. hataiana* Cooper, 1973c: Pacific Ocean: Philippines (Cooper, 1973c)
		?	*T. hawaiiensis* Dall, 1920: Pacific Ocean: Hawaiian Is. (Dall, 1920; Cooper, 1973c)
		15–767	*T. japonica* (Sowerby, 1846): Pacific Ocean: Japan; Korea Strait; Fiji (Davidson, 1886 in 1886–1888; Dall, 1920; Cooper, 1957; Endo & Curry, 1991; Bitner, 2006b)
		18–4640	*T. kiiensis* Dall & Pilsbry, 1891: Pacific Ocean: Japan; Kuril Is. and Trench; Alaska; Washington; California; Chile (Dall, 1895; Zezina, 1970, 1997b; Cooper, 1982; Foster, 1989)
		?	*T. kitakamiensis* Hayasaka, 1938: Pacific Ocean: Japan: Honshu (Hatai, 1940)
		514	*T. kyusyuensis* Yabe & Hatai, 1934: Pacific Ocean: Japan: Kyushu (Hatai, 1936a)
		50–340	*T. meridionalis* Jackson, 1952: Atlantic–Indian Ocean: Cape of Good Hope; Moçambique Channel; Marion Is. (Davidson, 1880; Jackson, 1952; Cooper, 1973b; Hiller, 1991, 1994)
		102–550	*T. pacifica* Yabe & Hatai, 1934: Pacific Ocean: Japan; Loyalty Is. (Hatai, 1940; Zezina, 1981a; Laurin, 1997)
		119–981	*T. photina* Dall, 1920: Pacific Ocean: Japan; Philippines; Celebes Is.; Borneo; S. China Sea (Dall, 1920; Hatai, 1936a, 1940; Jackson & Stiasny, 1937; Cooper, 1973c; Zezina, 2001b)
		182	*T. radula* Hedley, 1904: Pacific Ocean: E. Australia (Dall, 1920)
		18–963	*T. reevei* Dall, 1920: Pacific Ocean: Philippines; Celebes Is.; Borneo; Loyalty Is.: Fiji; Norfolk Ridge (Dall, 1920; Cooper, 1973c; Laurin, 1997; Zezina, 2005; Bitner, 2006b)
		18–2157	*T. retusa* (Linnaeus, 1758): Atlantic Ocean: Barents Sea; Greenland; Iceland; Faroes; Norway; Sweden; Cape Verde; Mediterranean Sea (Fischer & Oehlert, 1891; Dall, 1920; Wesenberg-Lund, 1938, 1939, 1940a, 1941; Logan, 1979, 1983, 1988a; Brunton & Curry, 1979; Cooper, 1981b; Curry, 1982; Cohen & others, 1991, 1993; Zezina, 1997b, 2001b; Lüter & Cohen, 2002; Alvarez & Emig, 2005)
		0–3592	*T. septentrionalis* (Couthouy, 1838): Atlantic Ocean: western Greenland; Iceland; Faroes; Davis Strait; Labrador; Newfoundland; Nova Scotia to New York (Davidson, 1886 in 1886–1888; Dall, 1920; Wesenberg-Lund, 1938, 1940a, 1941; Logan & Noble, 1971; Witman & Cooper, 1983; Cohen & others, 1991; Lüter & Cohen, 2002)
		11–1247	*T. unguicula* (Carpenter, 1864): Pacific Ocean: Sea of Okhotsk; Kuril Is.; Kamchatka Penin.; Alaska; British Columbia; Washington; California (Dall, 1920; Cooper, 1973c; Thayer, 1975; Tunnicliffe & Wilson, 1988; Zezina, 1997b)
		73–1750	*T. valdiviae* Blochmann, 1908: Pacific Ocean: Japan; Philippines; Celebes Sea; Indian Ocean: SW of Sumatra (Blochmann, 1908; Dall, 1920; Jackson & Stiasny, 1937; Helmcke, 1940)
Chlidonophora Dall, 1903	2	630–2745	*C. chuni* Blochmann, 1906: Indian Ocean: Maldive Is.; Moçambique; Madagascar; South Africa (Blochmann, 1906; Helmcke, 1940; Muir-Wood, 1959; Cooper, 1973b; Hiller, 1986, 1991, 1994; Zezina, 1987)
		534–5310	*C. incerta* (Davidson, 1878): Caribbean Sea: G. of Mexico; Cuba, Jamaica, Haiti, Curaçao, Bonaire, Colombia; Atlantic Ocean: Azores; NE Brazil; off Sierra Leone (Dall, 1920; Cooper, 1954a, 1973d, 1977; Zezina, 1975a, 2000)
Eucalathis Fischer & Oehlert, 1890	14	380–635	*E. costellata* Cooper, 1981a: Indian Ocean: Moçambique Channel; banks south of Madagascar (Cooper, 1981a; Zezina, 1987)
		320–2005	*E. cubensis* Cooper, 1977: Caribbean Sea: Cuba, Bonaire, Curaçao, Saba Bank (Cooper, 1977; Logan, 1990; Zezina, 2000)
		280–2736	*E. ergastica* Fischer & Oehlert, 1890: Atlantic Ocean: N. Spain; Azores; Canary Is.; NW Africa and offshore seamounts; G. of Gascogne (Fischer & Oehlert, 1891; Cooper, 1981b; Logan, 1983, 1998; Anadón, 1994; Zezina, 2000; Gaspard, 2003b; Alvarez & Emig, 2005)

TABLE 51. *Continued.*

		915–1280	*E. fasciculata* Cooper, 1973b: Indian Ocean: Moçambique Channel; banks south of Madagascar; S. Africa (Cooper, 1973b; Hiller, 1986, 1991, 1994; d'Hondt, 1987)
		366	*E. floridensis* Cooper, 1977: Caribbean Sea: Florida (Cooper, 1977)
		595–642	*E. inflata* Cooper, 1973d: Atlantic Ocean: Argentina (Cooper, 1973d)
		2710–3870	*E. macroctena* Zezina, 1981: Pacific Ocean: Chile (Zezina, 1985)
		326–1153	*E. macrorhynchus* Foster, 1974: Pacific Ocean: Pacific-Antarctic Ridge (Foster, 1974, 1989)
		790	*E. magna* Cooper, 1981a: Indian Ocean: Heard Is; Kerguelen Is. (Cooper, 1981a)
		1098–2342	*E. murrayi* (Davidson, 1878): Indian Ocean: Kerguelen Is., Moçambique Channel; Pacific Ocean: Marquesas Is., Fiji, New Zealand (Kermadec Is.) (Davidson, 1880; Dawson, 1971, 1991; Foster, 1974; Zezina, 1987; Bitner, 2006a)
		185–360	*E. rotundata* Cooper, 1981a: Indian Ocean: S. of Madagascar (Cooper, 1981a; d'Hondt, 1987)
		192–1140	*E. rugosa* Cooper, 1973c: Indian Ocean: Moçambique Channel, Pacific Ocean: Philippines; Loyalty Is. (Cooper, 1973c; Zezina, 1981b, 1987; Laurin, 1997)
		909–1834	*E. trigona* (Jeffreys, 1878): Atlantic Ocean: Portugal; G. of Gascogne (Jeffreys, 1878; Dall, 1920; Saiz Salinas, 1989)
		549–2995	*E. tuberata* (Jeffreys, 1878): Atlantic Ocean: W of Gibraltar; G. of Gascogne; Canary Is.; N of Azores; seamounts off NW Africa (Jeffreys, 1878; Fischer & Oehlert, 1891; Dall, 1920; Brunton & Curry, 1979; Cooper, 1981b; Logan, 1983, 1988a; Zezina, 2000; Gaspard, 2003b; Logan & others, 2004; Alvarez & Emig, 2005)
Bathynanus Foster, 1974	3	4600–5160	*B. inversus* Zezina, 1981c: Indian Ocean: E and W of Ninety East Ridge (Zezina, 1981c, 1985)
		2520–3490	*B. rhizopodus* Zezina, 1981c: Indian Ocean: west of Maldive Is., (Zezina, 1981c, 1985)
		3843	*B. tenuicostatus* Foster, 1974: Pacific Ocean: (40ºS, 119º36'W) (Foster, 1974; Zezina, 1985)
Nanacalathis Zezina, 1981c	2	3340–3731	*N. atlantica* Zezina, 1991: Atlantic Ocean: 25-29ºN, 28-77ºW (Cooper, 1973d; Zezina, 1991, 2000)
		289	*N. minuta* Zezina, 1981: Indian Ocean: Nazareth Bank; Mascarene Plat. (16ºS, 61ºE) (Zezina, 1981c, 1985)
Notozyga Cooper, 1977	2	740–800	*N. gracilis* Hiller, 1986: Indian Ocean: S. Africa (Hiller, 1986, 1990, 1994)
		320–732	*N. lowenstami* Cooper, 1977: Atlantic, off Bermuda; Caribbean Sea: Bonaire, Curaçao (Cooper, 1977; Logan, 1990)
Agulhasia King, 1871	1	50–800	*A. davidsoni* King, 1871: Indian Ocean: S. Africa: Cape Town, Agulhas Bank, Durban (Helmcke, 1940; Jackson, 1952; Cooper, 1973b, 1973d; Hiller, 1986, 1991, 1994)
Cnismatocentrum Dall, 1920	2	110–375	*C. sakhalinensis* (Dall, 1908): Pacific Ocean: Sea of Okhotsk; Sakhalin Is.; Alaska (Dall, 1920; Hatai, 1940; Zezina, 1997b)
		34–121	*C. parvum* Zezina, 1970: Pacific Ocean: Sea of Okhotsk; Kamchatka Penin.; Kuril Is.; Commander Is. (Zezina, 1997b)

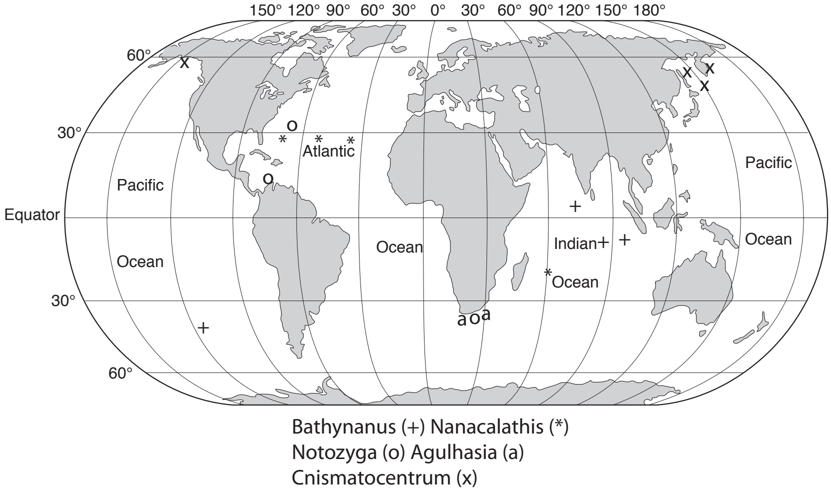


FIG. 1948. Geographic distribution of extant articulated brachiopod genera in superfamily Cancellothyridoidea (new).

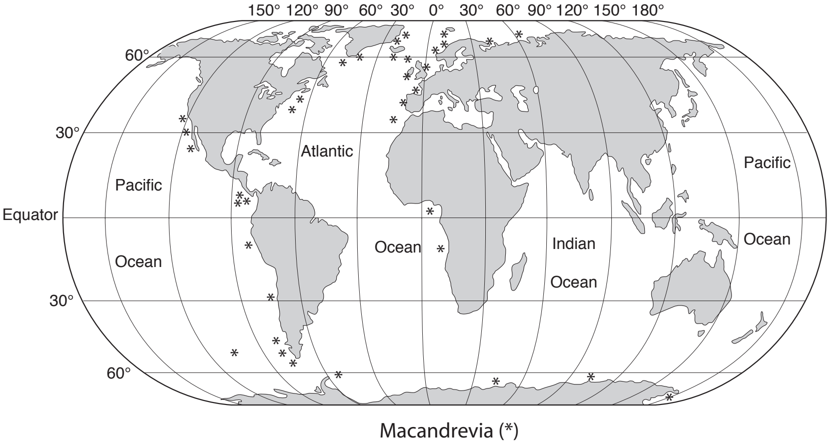


Fig. 1949. Geographic distribution of extant articulated brachiopod genera in superfamily Zeillerioidea (new).

Table 52. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Zeillerioidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Macandrevia King, 1859	10	3601–3972	*M. abyssa* Cooper, 1972: Pacific Ocean: California; Baja California; S. Pacific at 56°17'S, 156°13'W (Cooper, 1972, 1975)
		2332–3797	*M. africana* Cooper, 1975: Atlantic Ocean: G. of Guinea; Angola (Cooper, 1975; Laurin & Gaspard, 1987; Gaspard, 2003a)
		112–4066	*M. americana* Dall, 1895: Pacific Ocean: California; Panama; Chile; Atlantic Ocean: G. of Guinea; Angola; S. Sandwich Is.; S. Shetland Is.; Antarctica (Dall, 1920; Cooper, 1973d, 1982; Foster, 1974, 1989; d'Hondt, 1976)
		2268–3340	*M. bayeri* Cooper, 1975: Atlantic Ocean: SE of Benin at 4°58'N, 3°48-52'E; G. of Guinea; and near Azores (Cooper, 1975; Zezina, 1985, 2000; Laurin & Gaspard, 1987)
		2150	*M. craniella* Dall, 1895: Pacific Ocean: G. of Panama (Dall, 1920; Cooper, 1975)
		50–2951	*M. cranium* (Müller, 1776): Atlantic-Arctic Ocean: Norway; Svalbard; Novaya Zemlya; Barents Sea; Greenland; Iceland; Faroes; Canary Is.; G. of Gascogne; Morocco; N. Spain; Portugal; E. Atlantic seamounts; British Isles (Davidson, 1886 in 1886–1888; Fischer & Oehlert, 1891; Dall, 1920; Massy, 1925; Wesenberg-Lund, 1938, 1939, 1940a, 1940b, 1941; Atkins, 1959c; d'Hondt, 1973, 1976; Cooper, 1973d, 1975, 1981b; Brunton & Curry, 1979; Logan, 1983; Anadón, 1994; Zezina, 1997c, 2000; Gaspard, 2003a, 2003b; Logan & others, 2004)
		2140–4600	*M. diamantina* Dall, 1895: Pacific Ocean: G. of Panama; Peru; Antarctica (Dall, 1920; Cooper, 1972, 1975; Foster, 1974, 1989)
		1837–2338	*M. novangliae* Cooper, 1977 (not Dall, 1920): Atlantic Ocean: eastern USA; G. of Gascogne; N. Spain (Dall, 1920; Cooper, 1975, 1977, 1981b; Saiz Salinas, 1989)
		207–2654	*M. tenera* (Jeffreys, 1876): Atlantic Ocean: entrance to Davis Strait and east of Cape Farewell, Greenland, Labrador (Jeffreys, 1878; Davidson, 1886 in 1886–1888; Cooper, 1973d, 1975)
		119–930	*M. vanhoeffeni* Blochmann, 1906: Antarctica: circumpolar (Blochmann, 1906; Foster, 1974; Cooper, 1975)

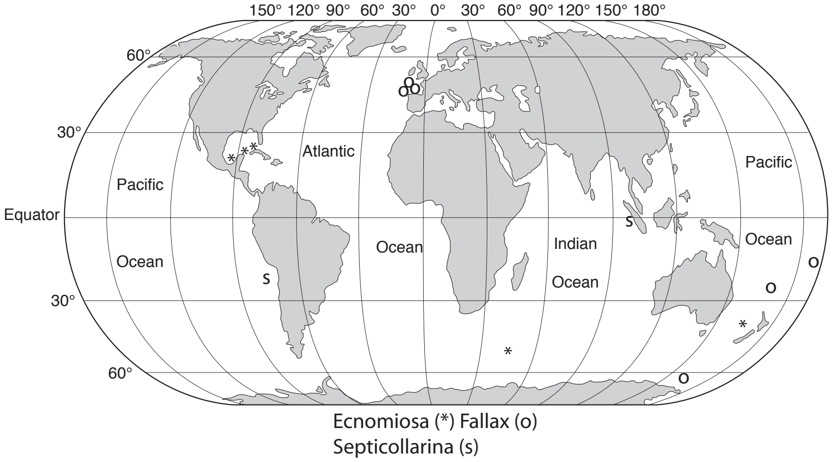


FIG. 1950. Geographic distribution of extant articulated brachiopod genera in superfamily Kingenoidea (new).

TABLE 53. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Kingenoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Ecnomiosa Cooper, 1977	2	723–915	*E. gerda* Cooper, 1977: Caribbean Sea: G. of Mexico; west of Cuba; Campeche shelf, S. Mexico; SW of Dry Tortugas, Florida (Cooper, 1977)
		884–1500	*E. inexpectata* Cooper, 1981a: Indian Ocean: Crozet Is. at 46°18'S, 51°14'E; Pacific Ocean: seamount west of Cook Strait, New Zealand (Cooper, 1981a; Lüter, 2007)
Fallax Atkins, 1960a	3	2285–2342	*F. antarcticus* Foster, 1974: Antarctica: at 62°47-50'S, 158°12-21'E (Foster, 1974; Zezina, 1985)
		219–1421	*F. dalliniformis* Atkins, 1960a: Atlantic Ocean: western English Channel; G. of Gascogne; N. Spain (Atkins, 1960a; Brunton & Curry, 1979; Cooper 1981b; Anadon, 1994)
		33–1620	*F. neocaledonensis* Laurin, 1997: Pacific Ocean: Loyalty Is. (Laurin, 1997; Bitner, 2006b). Zezina (2005) designated this as *Laurinia neocaledonesis*
Septicollarina Zezina, 1981	2	240	*S. hemiechinata* Zezina, 1981a: Indian Ocean: near Java at 07°29'S, 114°49' E (Zezina, 1981a, 1997a)
		270–485	*S. oceanica* Zezina, 1990: Pacific Ocean: Nazca Ridge (Zezina, 1990, 1997a)

TABLE 54. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Laqueoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Laqueus Dall, 1870	13	104–1839	*L. blanfordi* (Dunker, 1882): Pacific Ocean: Japan; Kamchatka Penin.; Bering Sea (Dall, 1920; Hatai, 1936a; Zezina, 1997b)
		338	*L. concentricus* Yabe & Hatai, 1936: Pacific Ocean: Japan, at 36°16'N, 139°29'E (Hatai, 1940)
		58–1565	*L. erythraeus* Dall, 1920: Pacific Ocean: Catalina Is., California; Alaska; Bering Sea; Sea of Okhotsk; Sikhote Alin (Dall, 1920; Hertlein & Grant, 1944; Zezina, 1997b; MacKinnon & Long, 2000)
		104–454	*L. japonicus* Yabe & Hatai, 1934: Pacific Ocean: Japan (Hatai, 1936a, 1940)
		222	*L. morsei* Dall, 1908: Pacific Ocean: Sea of Japan (Dall, 1920)
		115–604	*L. orbicularis* Yabe & Hatai, 1934: Pacific Ocean: Sea of Japan (Hatai, 1936a)
		23–205	*L. pacificus* Hatai, 1936a: Pacific Ocean: Japan (Hatai, 1936a, 1940)
		41–100	*L. pictus* (Chemnitz, 1839): Pacific Ocean: Japan; Strait of Korea (Davidson, 1887)
		150–194	*L. proprius* Yabe & Hatai, 1934: Pacific Ocean: Japan (Hatai, 1936a, 1940; Zezina, 1985)
		86–307	*L. quadratus* Yabe & Hatai, 1934: Pacific Ocean: Japan; Taiwan (Hatai, 1936a, 1940)
		80–907	*L. rubellus* (Sowerby, 1846): Pacific Ocean: Japan; Hawaiian Is. (Davidson, 1887; Dall, 1920; Hatai, 1936a, 1940; Zezina, 1981a; Saito, 1996)
		115–243	*L. suffusus* (Dall, 1870): Pacific Ocean: Japan; Strait of Korea (Dall, 1920; Hatai, 1940)
		2–494	*L. vancouverensis* Davidson, 1887: Pacific Ocean: western coast of Canada; USA (not California) (Davidson, 1887; Bernard, 1972; Thayer, 1975; Tunnicliffe & Wilson, 1988; MacKinnon & Long, 2000)
Glaciarcula Elliott, 1956	1	50–2700	*G. spitzbergensis* (Davidson, 1852d): Arctic Ocean–Atlantic Ocean: circumpolar: Greenland; Iceland; Norway; Faroes; Svalbard; Russian shorelines of Kara, Laptev, and Chukchi seas; Bering Sea (Kamchatka Penin.); Sea of Okhotsk (Kuril Is.), E. Canada; Portugal (above 40°N) (Davidson, 1887; Dall, 1920, Wesenberg-Lund, 1938, 1939, 1940a, 1940b, 1941; Brunton & Curry, 1979; Zezina, 1985, 1997b, 2001)
Frenulina Dall, 1895	3	59–110	*F. cruenta* Cooper, 1973b: Indian Ocean: Somalia; Moçambique Channel; S. Africa (Cooper, 1973b; Zezina, 1985; Hiller, 1994)
		260–458	*F. mauiensis* Dall, 1920: Pacific Ocean: Hawaiian Is. (Dall, 1920)
		5–541	*F. sanguinolenta* Gmelin, 1790: Pacific Ocean: Indonesia; Japan; Philippines; Marshall Is.; Loyalty Is.; Hawaiian Is.; Marquesas Is., Fiji; Tahiti; Tonga; E. Australia (Dall, 1920; Hatai, 1936a, 1940; Jackson & Stiasny, 1937; Cooper, 1957; Richardson, 1973; d'Hondt, 1987; Grant, 1987; Saito, 1996; Laurin, 1997; Bitner, 2006a, 2006b)
Jolonica Dall, 1920	4	187	*J. alcocki* (Joubin, 1906): Indian Ocean: southwest of southern point of India (8°23'N, 76°28'E) (Dall, 1920; Cooper, 1973b)
		0–200	*J. suffusa* (Cooper, 1973b): Indian Ocean: SE Africa, Moçambique; S. Africa (Cooper, 1973b; Hiller, 1991, 1994)
		262–579	*J. hedleyi* Dall, 1920: Pacific Ocean: Japan; China; Philippines; Celebes Is. Indian Ocean: Malay Archipelago; Bali (Dall, 1920; Jackson & Staisny, 1937; Cooper, 1957; Zezina, 1981a)
		91–106	*J. nipponica* Yabe & Hatai, 1934: Pacific Ocean: Shikoku Is., Izu Is., Japan (Hatai, 1936a, 1940; Saito, 1996)
Pictothyris Thomson, 1927	3	75	*P. elegans* Yabe & Hatai, 1936: Pacific Ocean: Oki Is., Sea of Japan (Hatai, 1940)
		119	*P. laqueformis* Yabe & Hatai, 1936: Pacific Ocean: W. Kyushu, E. China Sea (Hatai, 1940)
		28–205	*P. picta* (Dillwyn, 1817): Pacific Ocean: Sea of Japan; Honshu; Philippine Sea (Hatai, 1936a, 1940; Saito, 1996)
Shimodaia MacKinnon, Saito, & Endo, 1997	2	37–98	*S. pterygiota* MacKinnon, Saito, & Endo, 1997: Pacific Ocean: Japan, Honshu; S. China Sea (MacKinnon, Saito, & Endo, 1997)
		?	*S.* sp. nov. MacKinnon & Long (2007): Pacific Ocean: S. China Sea (MacKinnon & Long, 2007)

TABLE 54. *Continued.*

Terebratalia Beecher, 1893	5	13–287	*T. coreanica* (Adams & Reeve, 1850): Pacific Ocean: Japan, S. Hokkaido; China; Korea; Russia, Sikhote Alin (Davidson, 1887; Dall, 1920; Hatai, 1936a, 1940; Saito, 1996; Zezina, 1997b)
		307–1112	*T. gouldii* (Dall, 1891): Pacific Ocean: Japan (Dall, 1920; Hatai, 1940)
		31–467	*T. tisimana* (Nomura & Hatai, 1936): Pacific Ocean: Russia, Kuril Is.; Sea of Okhotsk; Kamchatka Pen.; Aleutian Is. (Hatai, 1940; Zezina, 1985, 1997b)
		0–1700	*T. transversa* (Sowerby, 1846): Pacific Ocean: Alaska; Aleutian Is.; British Columbia; Washington; California; Mexico (Davidson, 1887; Dall, 1920; Bernard, 1972)
		117–156	*T. xanthica* Dall, 1920: Pacific Ocean: Russia, Sakhalin Is.; Japan (Dall, 1920; Hatai, 1936a, 1940)
Coptothyris Jackson, 1918	1	115–353	*C. grayi* (Davidson, 1852d): Pacific Ocean: Japan; Strait of Korea (Davidson, 1886 in 1886–1888; Hatai, 1940; Saito, 1996)
Dallinella Thomson, 1915	1	91–205	*D. obsoleta* (Beecher, 1893): Pacific Ocean: California (Dall, 1920)
Diestothyris Thomson, 1916	1	0–435	*D. frontalis* (Middendorf, 1849): Pacific Ocean: Russia; Aleutian Is.; Sea of Okhotsk; Sikhote Alin; Kuril Is.; Kamchatka Penin.; Japan, Hokkaido; Alaska; British Columbia (Davidson, 1887; Dall, 1920; Hatai, 1936a, 1940; Bernard, 1972; Zezina, 1997b)
Simplicithyris Zezina, 1976b	2	5–580	*S. kurilensis* Zezina, 1976b: Pacific Ocean: Kamchatka, Kuril Is. (Zezina, 1976b, 1985, 1997b)
		118	*S. japonica* Dall, 1920: Pacific Ocean: Japan (off Hondo, Yokohama) (Dall, 1920; Hatai, 1936a, 1940; Zezina, 1985)
Tythothyris Zezina, 1979	1	5–400	*T. rosimarginata* Zezina, 1979: Pacific Ocean: Sea of Okhotsk; Kuril Is.; Commander Is.; Kamchatka Penin.; Sakhalin Is. (Zezina, 1997b)

KINGENOIDEA

The superfamily Kingenoidea includes 7 extant species belonging to 3 genera, *Ecnomiosa*, *Fallax,* and *Septicollarina* (Table 53, Fig. 1950). There are 2 species of *Ecnomiosa* known: *E. gerda* from the Caribbean Sea and *E. inexpectata* from the southern Indian Ocean, although this latter species has recently been identified from a seamount just west of Cook Strait, New Zealand at a depth of 957–1055 m by LÜTER (2007). While both species of *Ecnomiosa* are absent from the neritic zone, 2 of the 3 species of *Fallax* have been recorded from shallow water, although they range down into the bathyal zone. *Fallax neocaledonensis* and *F. antarcticus* occur in the western Pacific, north and south of New Zealand, respectively; the third species, *F. dalliniformis,* is typically a neritic and upper bathyal zone species known only from the eastern Atlantic, where, as the name implies, it is easily misidentified as *Dallina septigera* (ATKINS, 1960b). *Septicollarina* has 2 species from shallow water, one from the Indian Ocean around Java and the other from the Nazca Ridge area of the eastern Pacific**.**

LAQUEOIDEA

The superfamily Laqueoidea includes 37 extant species belonging to 12 genera (Table 54, Fig. 1951–1953). This is predominantly a shallow-water group, with over 70% of the species restricted to the neritic zone and 97% to the neritic to upper bathyal zone. Nine genera are restricted to the northern hemisphere, with only *Frenulina* and *Jolonica* represented south of the equator. *Glaciarcula*, with the Arctic species *G. spitzbergensis* as sole representative, is circumpolar in distribution and ranges greatly in depth. *Shimodaia* is a northeastern Pacific genus with 2 species so far obtained only from the neritic zone; *Coptothyris* and *Tythothyris* have similar geographic distributions to *Shimodaia* but extend into the uppermost bathyal zone, while *Diestothyris* is known from the northern Pacific region as far east as British

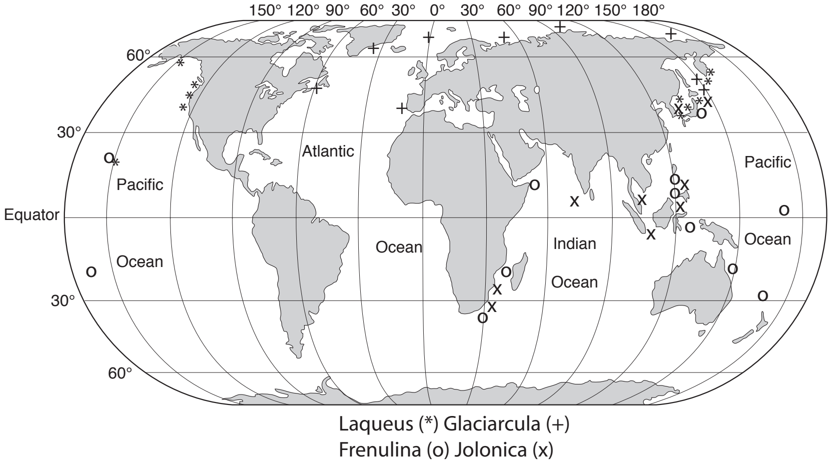


FIG. 1951. Geographic distribution of extant articulated brachiopod genera in superfamily Laqueoidea (new).

Columbia, where it is succeeded in California by the neritic zone genus *Dallinella*. The genus *Simplicithyris*, which has 2 extant species from the northwestern Pacific, is retained in the Laqueoidea following RICHARDSON (1997b). Of the remaining genera, *Laqueus* has 13 species, of which 11 are recorded from the neritic and upper bathyal zones around Japan. The Indo-Pacific genus *Frenulina* has 3 species, all living more or less in the neritic zone, with the Pacific species *F. sanguinolenta* being the most distinctive, although none are exclusive to shallow reefal substrates, as suggested by RICHARDSON (1997b). Three of the 4 species of the Indo-Pacific genus *Jolonica* are known only from the neritic zone, while the 3 shallow-water species of *Pictothyris* have all been described from the area around Japan. Of the 5 species of *Terebratalia* known, all are from the northern Pacific, *T. transversa* from the western coast of North America being the best known.

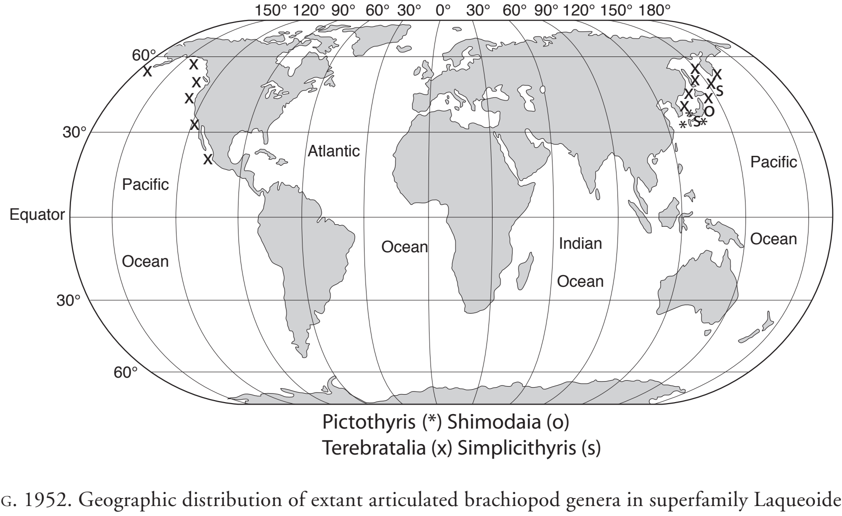


FIG. 1952. Geographic distribution of extant articulated brachiopod genera in superfamily Laqueoidea (new).

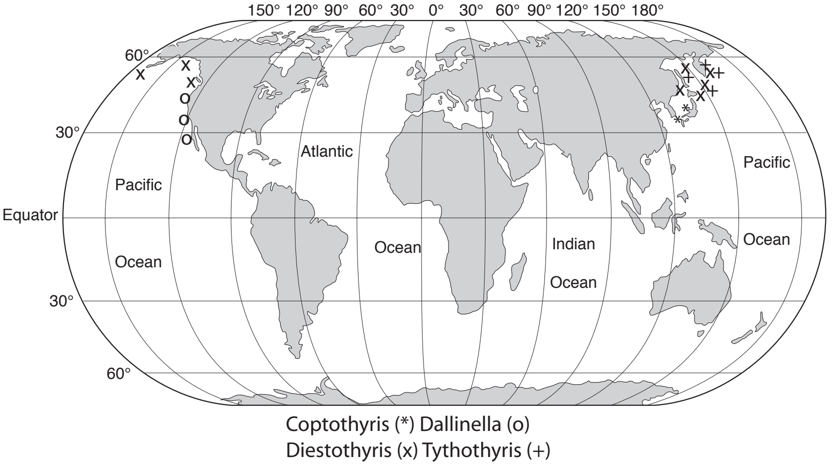


Fig. 1953. Geographic distribution of extant articulated brachiopod genera in superfamily Laqueoidea (new).

MEGATHYRIDOIDEA

The superfamily Megathyridoidea includes 25 extant species belonging to 3 genera (Table 55, Fig. 1954). All species occur in the neritic to upper bathyal zones. *Thaumatosia* is monotypical, with *T. anomala* recorded only from the neritic zone of the Andaman Sea. *Megathiris* comprises 2 species, with *M. capensis* being restricted to the neritic zone off the western coast of South Africa, while *M. detruncata* is a common and distinctive species in the Mediterranean and eastern North Atlantic (although a record from Guadeloupe in the Caribbean Sea should be questioned; Dall, 1920; Cooper, 1977). The diminutive genus *Argyrotheca* is one of the most common and diverse in the neritic and upper bathyal zones of all the oceans of the world, although most of the 22 named Caribbean species need to be restudied from larger collections to assess their range of variation. Many of these micromorphs take refuge on the undersides of coral colonies within coral reefs (Logan, 1975, 1977). The Caribbean, eastern North Atlantic, and Mediterranean are the areas where species of *Argyrotheca* are most prevalent, although they are also known from the Indo-Pacific region. One species, *A. jacksoni*, was described by Cooper (1973b) from shallow-water reef caves in the northern Red Sea and it has since been found in other parts of the Red Sea (Logan & others, 2007).

BOUCHARDIOIDEA

The superfamily Bouchardioidea includes 1 extant species belonging to the genus *Bouchardia* (Table 55, Fig. 1954). This species is *Bouchardia rosea,* which is present in high densities on the outer part of the shelf off the coast of Brazil. It is endemic to this region, where it occurs preferentially on carbonate substrates where shelf-break upwelling occurs (Kowalewski & others, 2002).

PLATIDIOIDEA

The superfamily Platidioidea includes 16 extant species belonging to 5 genera (Table 56, Fig. 1955). The genus *Platidia,* which comprises 5 extant species, is widely distributed in all the major oceans, ranging in depth from the shallow neritic to the upper bathyal zones. *P. anomioides* and *P. davidsoni* are the most common species in the Atlantic and Mediterranean and difficult to tell apart. The 4 species of *Amphithyris* are all relatively shallow-water forms. Three are found around New Zealand and the fourth (*A. hallettensis*) is known from Antarctica. *Annuloplatidia*

TABLE 55. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamilies Megathyridoidea, Gwynioidea, and Bouchardioidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
MEGATHYRIDOIDEA			
Megathiris d'Orbigny, 1847	2	50–100	*M. capensis* Jackson, 1952: Atlantic Ocean: west coast of S. Africa (Saldanha Bay) (Jackson, 1952; Hiller, 1991, 1994)
		5–896	*M. detruncata* (Gmelin, 1790): Atlantic Ocean: British Isles; Portugal; Morocco; Canary Islands; Cape Verde; Madeira; seamounts off NW Africa; Mediterranean Sea; ?Caribbean Sea (Guadeloupe) (Davidson, 1887; Fischer & Oehlert, 1891; Dall, 1920; Atkins, 1960c; Cooper, 1977; Brunton & Curry, 1979; Logan, 1979, 1983, 1988a, 2003; Logan & others, 2002, 2004; Gaspard, 2003b; Alvarez & Emig, 2005)
Argyrotheca Dall, 1900	22	460–500	*A. angulata* Zezina, 1987: Indian Ocean: Glorieuse Is.; Moçambique Channel, 11°30'S, 47°20'E (Zezina, 1987)
		14–120+	*A. arguta* Grant, 1983: Pacific Ocean: Marshall Is: Eniwetak, Bikini atolls (Cooper, 1954b; Grant, 1983, 1987)
		36–550	*A. australis* (Blochmann, 1910): Pacific Ocean: S. Australia, Indian Ocean: Glorieuse Is.; Moçambique Channel, 11°30'S, 47°20'E (Blochmann, 1910; Zezina, 1987)
		34–1473	*A. barrettiana* (Davidson, 1866): Caribbean Sea: Gulf of Mexico; Jamaica; Florida; Bahamas; Honduras; Cuba; Panama; Barbados (Davidson, 1887; Dall, 1920; Cooper, 1954a, 1977; Asgaard & Stentoft, 1984)
		1–46	*A. bermudana* Dall, 1911: Atlantic Ocean: Bermuda, Caribbean Sea: Barbados; Grenada (Logan, 1975; Cooper, 1977; Asgaard & Stentoft, 1984)
		5–236 (?2324)	*A. cistellula* (Searles-Wood, 1841): Atlantic Ocean: British Isles; N. France; Channel Is.; Portugal; Canary Is.; Azores; seamounts off NW Africa; N. Spain; Norway; Mediterranean Sea; Adriatic Sea: Croatia (Fischer & Oehlert, 1891; Dall, 1920; Massy, 1925; Rioult, 1971; Logan, 1979, 2003; Brunton & Curry, 1979; Besteiro & Urgorri, 1984; Logan, MacKinnon, & Phorson, 1997; Simon & Willems, 1999; Di Geronimo & others, 2001; Gaspard, 2003b; Alvarez & Emig, 2005)
		3–600	*A. cordata* (Risso, 1826): Atlantic Ocean: British Isles; Canary Is.; Mediterranean Sea; Adriatic Sea: Croatia; Red Sea (Davidson, 1887; Dall, 1920; Atkins, 1960c; Logan, 1979, 1983, 1988a, 2003; Logan & Noble, 1983; Brunton, 1988; Simon & Willems, 1999; Alvarez & Emig, 2005; Logan & others, 2007)
		5–645	*A. cuneata* (Risso, 1826): Atlantic Ocean; British Isles; Madeira; Canary Is.; Cape Verde; seamounts off NW Africa; Mediterranean Sea; Adriatic Sea: Croatia (Davidson, 1887; Dall, 1920; Atkins, 1960c; Logan, 1979, 1983, 1988a, 2003; Brunton, 1988; Simon & Willems, 1999; Gaspard, 2003b; Alvarez & Emig, 2005)
		37–285	*A. crassa* Cooper, 1977: Caribbean Sea: Barbados, Grenada (Dall, 1920; Cooper, 1977; Asgaard & Stentoft, 1984)
		330–785	*A. grandicostata* Logan, 1983: Atlantic Ocean: Canary Is. (Logan, 1983, 1988a)
		95–120	*A. hewatti* Cooper, 1977: Caribbean Sea: Gulf of Mexico, off Texas; Guyana (Cooper, 1977; Logan, 1990)
		<10–90	*A. jacksoni* Cooper, 1973b: Red Sea (Jackson, Goreau, & Hartman, 1971; Cooper, 1973b; Logan & others, 2007)
		10–50	*A. johnsoni* Cooper, 1934: Caribbean Sea: Bahamas; Jamaica; Puerto Rico (Cooper, 1934, 1977; Jackson & others, 1971)
		37	*A. lowei* Hertlein & Grant, 1944: Pacific Ocean: Gulf of California (Hertlein & Grant, 1944)
		54–150	*A. lutea* (Dall, 1871): Caribbean Sea: Gulf of Mexico; Cuba; Barbados (Cooper, 1977; Logan, 1977)
		145	*A. mayi* Blochmann, 1914: Pacific Ocean: Australia, E. Tasmania (Blochmann, 1914)
		26–55	*A. rubrocostata* Cooper, 1977: Caribbean Sea: Panama; Honduras; Belize (Cooper, 1977)

TABLE 55. *Continued.*

		55–140	*A. rubrotincta* (Dall, 1871): Caribbean Sea: Florida; Guyana; Curaçao; Bonaire; Barbados (Dall, 1871; Cooper 1977; Asgaard & Stentoft, 1984; Logan, 1990)
		6–981	*A. schrammi* (Crosse & Fischer, 1866): Caribbean Sea: Yucatan; Guadeloupe; Barbados (Davidson, 1887; Dall, 1920; Cooper, 1954a, 1977; Logan, 1975, 1977; Asgaard & Stentoft, 1984)
		59–80	*A. somaliensis* Cooper, 1973b: Indian Ocean: NE Somalia (Cooper, 1973b)
		84–137	*A. thurmanni* Cooper, 1973d: Atlantic Ocean: Brazil (Cooper, 1973d)
		2–110	*A. woodwardiana* (Davidson, 1866): Caribbean Sea: Jamaica; Cayman Is. (Davidson, 1887; Cooper, 1977; Logan, 1977,1981)
Thaumatosia Cooper, 1973b	1	40–77	*T. anomala* Cooper, 1973b: Indian Ocean: Andaman Sea, off Thailand; Andaman Islands (Cooper, 1973b)
GWYNIOIDEA			
Gwynia King, 1859	2	3–800 (?4060)	*G. capsula* (Jeffreys, 1859): Atlantic Ocean: British Isles; Channel Is.; N. France; N. Spain; Azores; E. Atlantic seamounts; Mediterranean Sea; Adriatic Sea: Croatia; Caribbean Sea: Windward Is., Lesser Antilles (Fischer & Oehlert, 1891; Dall, 1920; Massy, 1925; Rioult, 1971; Zezina, 1975a; Brunton & Curry, 1979; Besteiro & Urgorri, 1984; Harper & others, 1996; Logan, MacKinnon, & Phorson, 1997; Simon & Willems, 1999; Gaspard, 2003b; Alvarez & Emig, 2005)
		1605–1865	*G. macrodentata* Lüter, 2007: Pacific Ocean: Moore Seamount, east of New Zealand (Lüter, 2007)
BOUCHARDIOIDEA			
Bouchardia Davidson, 1850	1	10–108 (?200)	*B. rosea* (Mawe, 1823): Atlantic Ocean: S. America: Brazil: Uruguay (Davidson, 1887; Dall, 1920; Tommasi, 1970; Manceñido & Griffin, 1988; Brunton, 1996; Kowalewski & others, 2002)

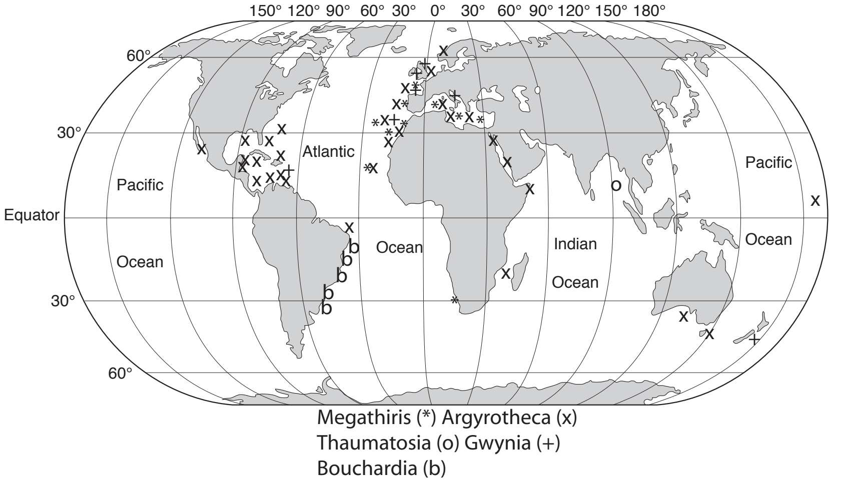


FIG. 1954. Geographic distribution of extant articulated brachiopod genera in superfamilies Megathyridoidea, Gwynioidea, and Bouchardioidea (new).

TABLE 56. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Platidioidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Platidia Costa, 1852	5	8–2190	*P. anomioides* (Scacchi & Philippi, 1844): Atlantic Ocean: Portugal; offshore seamounts; British Isles; Mediterranean Sea; Caribbean Sea: Barbados; Florida; Cuba; Grenada; Cayman Is.; Brazil; Pacific Ocean: Nazca and Juan de Fuca ridges; Red Sea; Antarctica (Jeffreys, 1878; Davidson, 1887; Fischer & Oehlert, 1891; Massy, 1925; Atkins, 1959a; Cooper, 1977, 1981b; Logan, 1979, 1981, 1983, 1998; Brunton & Curry, 1979; Asgaard & Stentoft, 1984; Zezina, 1987, 1990, 2000; Foster, 1974, 1989; Dawson, 1991; Hiller, 1991, 1994; Laurin, 1997; Kowalewski & others, 2002; Gaspard, 2003b; Logan & others, 2007)
		73–325	*P. clepsydra* Cooper, 1973a: Caribbean Sea: G. of Mexico; Florida; Barbados (Cooper, 1973a, 1977; Asgaard & Stentoft, 1984)
		595–1590	*P. concentrica* Zezina, 1980: Atlantic Ocean: Argentina; S. Shetland Is.; S. Orkney Is.; Pacific Ocean: Nazca and Juan de Fuca ridges (Zezina, 1985, 1990)
		82–897	*P. davidsoni* (Eudes-Deslongchamps, 1855): Atlantic Ocean: British Isles; NW Africa; Canary Is.; Mediterranean Sea; Caribbean Sea: Gulf of Mexico; Bahamas; Cuba; Argentina, Pacific Ocean: N. Caledonia (Davidson, 1887; Fischer & Oehlert, 1891; Atkins, 1959a; Cooper, 1973d, 1977; Logan, 1979; Brunton & Curry, 1979; Saiz Salinas, 1989; Laurin, 1997)
		105–1440	*P. marionensis* Cooper, 1981a: Indian Ocean: Marion Is.; Kerguelen Is. (Cooper, 1981a)
Amphithyris Thomson, 1918	4	91–1865	*A. buckmani* Thomson, 1918: Pacific Ocean: New Zealand, Cook Strait, South Island fiords; Chatham Rise; Fiji (Thomson, 1927; Bowen, 1968; Dawson, 1971, 1991; Richardson, 1981; Bitner, 2006b; Lüter, 2007)
		346–641	*A. hallettensis*, Foster, 1974: Antarctica: Ross Sea, off Cape Hallett; S. Orkney Is. (Foster, 1974)
		74–385	*A. richardsonae* Campbell & Fleming, 1981: Pacific Ocean: New Zealand, fiords of S. Island; Indian Ocean: S. Africa (west coast) (Campbell & Fleming, 1981; Hiller, 1994)
		366	*A. parva* MacKinnon& others, 2007. Pacific Ocean: Cook Strait, New Zealand (MacKinnon & others, 2007)
Annuloplatidia Zezina, 1981b	3	1298–2419	*A. annulata* (Atkins, 1959b): Atlantic Ocean: western entrance to English Channel, E. Pacific Ocean: Cocos Ridge (Atkins, 1959b; Brunton & Curry, 1979; Lüter, pers. comm., 2004)
		45–370	*A. horni* (Gabb, 1861): Pacific Ocean: British Columbia; Central California; Mexico (Bernard, 1972)
		370–5800	*A. indopacifica* Zezina, 1981b: Pacific Ocean: E. Indian Ocean: (Zezina, 1981b, 1985)
Leptothyrella Muir-Wood, 1965	3	335–5300	*L. incerta* (Davidson, 1880): Atlantic Ocean: Azores; Madeira; Canary Is.; Cape Verde; NW Africa; Atlantis Seamount; Caribbean Sea: St. Thomas (Davidson, 1880; 1887, Fischer & Oehlert, 1891; Zezina, 1981a, 2000; Logan, 1983, 1988a, 1998)
		225–3493	*L. galatheae* Zezina, 1981a: Atlantic Ocean: offshore seamounts, W. Pacific Ocean: Arafura Sea, New Guinea; Australia, Gt. Australian Bight, Tasmania; New Caledonia; New Zealand; Indian Ocean: Moçambique Channel; Antarctica: 120–180°, from south of N. Guinea to Antarctica (Zezina, 1981a, 1987; Foster, 1989; Laurin, 1997; Gaspard, 2003b)
		1987–2881	*L. ignota* (Muir-Wood, 1959): Indian Ocean: G. of Aden; Zanzibar; S. Africa (Muir-Wood, 1959; Zezina, 1981a; Hiller, 1986, 1994)
Neoaemula MacKinnon & others, 2007	1	20–30	*N. vector* MacKinnon & others, 2007: Fiordland, New Zealand (MacKinnon & others, 2007)

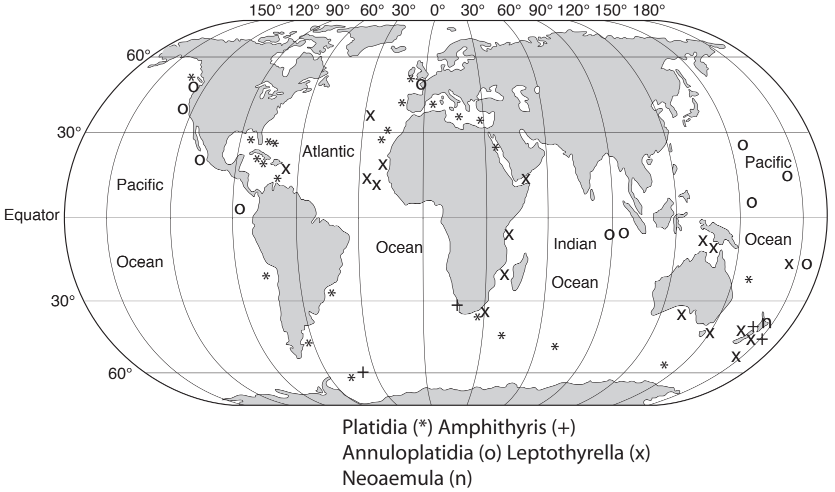


FIG. 1955. Geographic distribution of extant articulated brachiopod genera in superfamily Platidioidea (new).

is widely distributed, occurring in all three major oceans, and has 3 species, one of which (*A. indopacifica*) has a remarkable depth range of 370–5240 m in the west and central Pacific and descends to 5800 m in the region of the Kokosov Ridge west of Sumatra in the Indian Ocean (ZEZINA, 1981b, 1985). *Leptothyrella* (formerly *Phaneropora*) is also widely distributed geographically; of its 3 species, 2 are markedly eurybathic: *L. incerta*, a common North Atlantic form with a depth range of 335–5300 m, and *L. galatheae* from the Indo–West Pacific with a range of 225–3493 m. The third, *L. ignota*, occurs in the Red Sea–Gulf of Aden area, along with *Platidia anomioides* (MUIR-WOOD, 1959; LOGAN & others, 2007). A fifth genus, *Neoaemula*, with similarities to

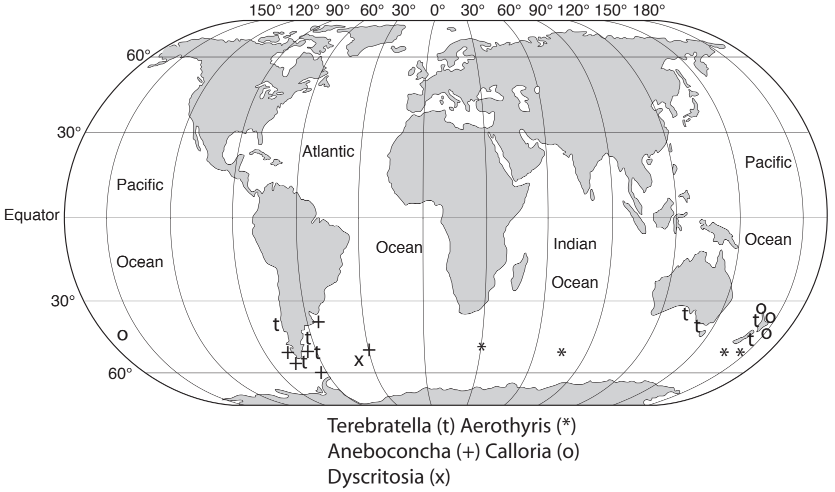


FIG. 1956. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratelloidea (new).

TABLE 57. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Terebratelloidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Terebratella d'Orbigny, 1847	5	9–500	*T. dorsata* (Gmelin, 1790): Pacific–Atlantic Ocean: Chile; Strait of Magellan; Argentina; Falkland Is. (Davidson, 1880, 1887; Fischer & Oehlert, 1892; McCammon & Buchsbaum, 1968; Cooper, 1973d, 1982; Foster, 1974, 1989; Richardson, 1994)
		36–146	*T. haurakiensis* Allan, 1931: Pacific Ocean: N. Island, New Zealand (Bowen, 1968; Dawson, 1971, 1991; Foster, 1974, 1989; Richardson, 1994)
		36–180	*T. mayi* Blochmann, 1914: Pacific Ocean: Australia, Tasmania (Blochmann, 1914; Zezina, 1985)
		?	*T. rubicunda* Sowerby, 1846: Pacific Ocean: New Zealand (Davidson, 1887; Jackson, 1918; Brand & others, 2003)
		9–139 (236)	*T. sanguinea* (Leach, 1814): Pacific Ocean: S. Island, New Zealand (Foster, 1974, 1989; Richardson, 1981, 1994; Cooper & Lee, 1993; Ostrow & others, 2001)
Aerothyris Allan, 1939	2	6–930	*A. kerguelensis* (Davidson, 1878): Indian Ocean: Crozet Is.; Kerguelen Is. (Davidson, 1880, 1886 in 1886–1888; Dall, 1920; d'Hondt, 1977; Cooper, 1981a; Richardson, 1994)
		72–181	*A. macquariensis* (Thomson, 1918): Pacific Ocean: Macquarie and Antipodes Is., S. of New Zealand (Bowen, 1968; Foster, 1969, 1974; Dawson, 1971, 1991; Richardson, 1994)
Aneboconcha Cooper, 1973d	1	129–726	*A. obscura* Cooper, 1973d: Atlantic Ocean: southernmost S. America, Argentina; Tierro del Fuego; S. Shetland Is.; Burdwood Bank (Cooper, 1973d; Richardson, 1994)
Calloria Cooper & Lee, 1993	2	0–92 (184)	*C. inconspicua* (Sowerby, 1846): Pacific Ocean: New Zealand, Chatham Is. (Dall, 1920; Bowen, 1968; Foster, 1974; Doherty, 1979; Cooper & Lee, 1993; Richardson, 1981, 1994)
		10–30	*C. variegata* Cooper & Doherty, 1993: Pacific Ocean: N. Island, New Zealand (Cooper & Doherty, 1993; Richardson, 1994)
Dyscritosia Cooper, 1982	1	66–872	*D. secreta* (Cooper, 1982): Atlantic Ocean: east of Cape Horn, north of S. Georgia Is. (Cooper, 1982; Richardson, 1994)
Fosteria Zezina, 1980	1	311–1226	*F. spinosa* Zezina, 1980: Antarctica: Ross Sea, Weddell Sea (Foster, 1974; Zezina, 1980; Richardson, 1994)
Gyrothyris Thomson, 1918	1	79–563	*G. mawsoni* Thomson, 1918: Pacific Ocean: S. and E. of New Zealand, Antipodes Is., Macquarie Is. (Foster, 1974, 1989; Richardson, 1994; Lüter, 2007)
Neothyris Douvillé, 1879	6	36–236	*N. compressa* Neall, 1972: Pacific Ocean: New Zealand, Cook Strait (Richardson, 1981, 1994; Chapman & Richardson, 1981; Foster, 1989)
		203–274	*N. dawsoni* Neall, 1972: Pacific Ocean: New Zealand, Chatham Rise (Neall, 1972; Chapman & Richardson, 1981; Richardson, 1994)
		0–500	*N. lenticularis* (Deshayes, 1839): Pacific Ocean: New Zealand, S. Island; Chatham Rise; Lord Howe Rise (Dall, 1920; Rudwick, 1962b; Bowen, 1968; Neall, 1970, 1972; Dawson, 1971; Richardson, 1981, 1994; Zezina, 1980; Chapman & Richardson, 1981; Foster, 1989; Lüter, 2007)
		?	*N. ovalis* (Hutton, 1886): Pacific Ocean: New Zealand (Dawson, 1971, 1991)
		?	*N. parva* Cooper, 1982: Pacific Ocean: S. Island, New Zealand (Cooper, 1982)
		410–460	*N. westpacifica* Zezina, 2001b: Pacific Ocean: S. China Sea (Zezina, 2001b)
Syntomaria Cooper, 1982	1	181–486	*S. curiosa* Cooper, 1982: Atlantic Ocean: S. Sandwich Is. (Cooper, 1982; Richardson, 1994)
Anakinetica Richardson, 1987	1	31–222	*A. cumingii* (Davidson, 1852): Pacific Ocean: Australia, New South Wales, Bass Strait (Richardson, 1987; Brand & others, 2003)
Parakinetica Richardson, 1987	1	82	*P. stewarti* Richardson, 1987: Pacific Ocean: Australia, Bass Strait (Richardson, 1987)
Magellania Bayle, 1880	5	11–182	*M. flavescens* (Lamarck, 1819): Pacific Ocean: Australia, W. Australia: Queensland, Tasmania (Davidson, 1886; Blochmann, 1910; Dall, 1920; Foster, 1974; Richardson, 1994)
		75–1254	*M. fragilis* Smith, 1907: Antarctica: circumpolar (Jackson, 1918; Foster, 1974, 1989; Richardson, 1994)
		80–1894	*M. joubini* Blochmann, 1906: Antarctica: circumpolar (Blochmann, 1906; Jackson, 1918; Foster, 1974, 1989; Richardson, 1994)
		2–1362	*M. venosa* (Solander, 1789): Pacific–Atlantic Ocean: southernmost S. America: Chile–Uruguay, Strait of Magellan, Falklands Is. (Davidson, 1886 in 1886–1888; Fischer & Oehlert, 1892; Dall, 1920; McCammon, 1973; Cooper, 1973d; Foster, 1974, 1989; Richardson, 1994)
		284–494	*M. wyvillei* (Davidson, 1878): Pacific Ocean: Chile, southernmost S. America (Davidson, 1880, 1886 in 1886–1888; Hertlein & Grant, 1944; Foster, 1974)

TABLE 57. *Continued.*

Holobrachia Zezina, 2001b	1	410–460	*H. vietnamica* Zezina, 2001b: Pacific Ocean: S. China Sea (Zezina, 2001b)
Magadinella Thomson, 1915	1	67–281	*M. mineuri* Richardson, 1987: Pacific Ocean: Australia, Bass Strait (Richardson, 1987; Brand & others, 2003)
Pirothyris Thomson, 1927	1	29–363	*P. vercoi* (Blochmann, 1910): Pacific Ocean: S. Australia, Bass Strait (Blochmann, 1910; Dall, 1920; Richardson, 1987)
Dallina Beecher, 1893	8	123–567	*D. elongata* Hatai, 1940: Pacific Ocean: Japan, Kermadec Is. (Hatai, 1940; Foster, 1989; Dawson, 1991)
		339–1208	*D. eltanini* Foster, 1974: Pacific–Atlantic Ocean: Pacific-Antarctic Ridge and Drake Passage, southernmost S. America (Foster, 1974, 1989)
		64–724	*D. floridana* (Pourtalès, 1868): Caribbean Sea: Florida; Cuba; Puerto Rico; G. of Mexico (Dall, 1871; Davidson, 1886 in 1886–1888; Dall, 1920; Cooper, 1977)
		117	*D. obessa* Yabe & Hatai, 1934: Pacific Ocean: Sea of Japan (Hatai, 1936a, 1940)
		860–910	*D. parva* Cooper, 1981b: Atlantic Ocean: G. of Gascogne (Cooper, 1981b)
		81–563	*D. raphaelis* Dall, 1870: Pacific Ocean: Japan; New Zealand, Chatham Is. (Davidson, 1886 in 1886–1888; Dall, 1920; Hatai, 1936a, 1940; Lüter, 2007)
		37–2338	*D. septigera* (Lovén, 1846): Atlantic Ocean: North Sea; Barents Sea; Norway; Iceland; Faroes; British Isles; G. of Gascogne; N. Spain; Portugal; Canary Is.; offshore seamounts (Davidson, 1886 in 1886–1888: Fischer & Oehlert, 1891; Dall, 1920; Massy, 1925; Wesenberg-Lund, 1938, 1939, 1940a, 1941; Atkins, 1960b; d'Hondt, 1973, 1976; Brunton & Curry, 1979; Cooper, 1981b; Logan, 1983, 1988a, 1998; Anadón, 1994; Zezina, 1997b, 2000, 2001; Gaspard, 2003b; Logan & others, 2004)
		402	*D. triangularis* Yabe & Hatai, 1934: Pacific Ocean: Japan, Kyushu (Hatai, 1936a, 1940)
Nipponithyris Yabe & Hatai, 1934	2	690–1170	*N. afra* Cooper, 1973b; Indian Ocean: Moçambique; S. Africa; Pacific Ocean: Loyalty Is. (Cooper, 1973b; Hiller, 1994; Laurin, 1997)
		86–454	*N. nipponensis* (Yabe & Hatai, 1935): Pacific Ocean: Japan, Sea of Japan; Kyushu (Hatai, 1936a, 1940; Cooper, 1973b; Zezina 1985)
Campages Hedley, 1905	7	204–631	*C. asthenia* Dall, 1920: Pacific Ocean: Philippines; Borneo; Celebes Is.; Kei Is.; Japan (Dall, 1920; Jackson & Stiasny, 1937)
		23–1272	*C. basilanica* Dall, 1920: Pacific Ocean: Japan; Philippines; S. China Sea; Kei Is.; Celebes Is. (Dall, 1920; Hatai, 1936a, 1940; Jackson & Stiasny, 1937)
		110–123	*C. dubius* (Hatai, 1940): Pacific Ocean: Japan (Hatai, 1940)
		208–500	*C. furcifera* Hedley, 1905: Pacific Ocean: eastern coast of Australia; Loyalty Is.; Indian Ocean: S. of Bali (Dall, 1920; Zezina, 1981a; d'Hondt, 1987)
		38–108	*C. mariae* (Adams, 1860): Pacific Ocean: Japan; Kei Is. (Hatai, 1936a, 1940)
		91–102	*C. nipponensis* Yabe & Hatai, 1935: Pacific Ocean: Japan, Kyushu (Hatai, 1936a, 1940)
		208–402	*C. pacifica* Hatai, 1940: Pacific Ocean: Japan, Kyushu (Hatai, 1940)
Jaffaia Thomson, 1927	1	78–549	*J. jaffaensis* (Blochmann, 1910): Pacific Ocean: S. coast of Australia; Perth-Sydney (Blochmann, 1910; Zezina, 1981a, 1985; Richardson, 1994)

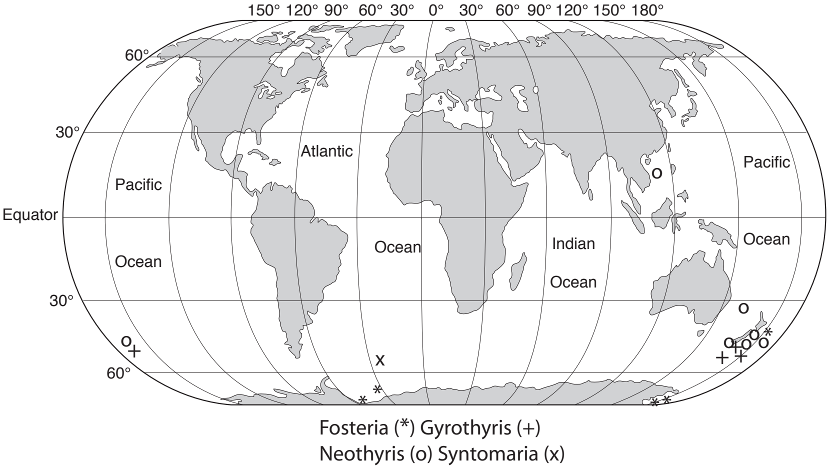


FIG. 1957. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratelloidea (new).

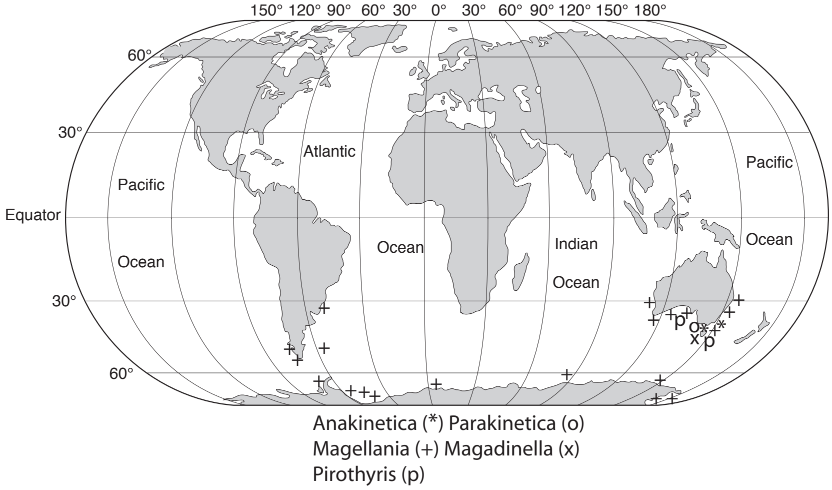


FIG. 1958. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratelloidea (new).

the Cretaceous genus *Aemula,* has recently been described from New Zealand by MACKINNON and others (2007).

TEREBRATELLOIDEA

The superfamily Terebratelloidea includes 48 extant species belonging to 19 genera (Table 57, Fig. 1956–1959). The life habits and biogeography of one subfamily, the Terebratellinae, were discussed in detail by RICHARDSON (1997b), to which the reader is referred. All members of this subfamily were formerly restricted in distribution to the southern hemisphere, but the discovery of a new species of *Neothyris* in the South China Sea by ZEZINA (2001b) has expanded its range northward. Nevertheless, 15 genera in the superfamily have species that are found

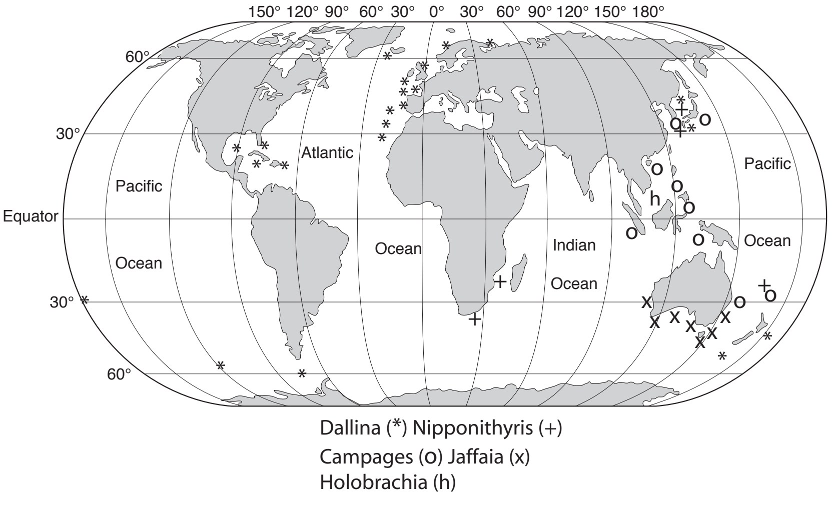


FIG. 1959. Geographic distribution of extant articulated brachiopod genera in superfamily Terebratelloidea (new).

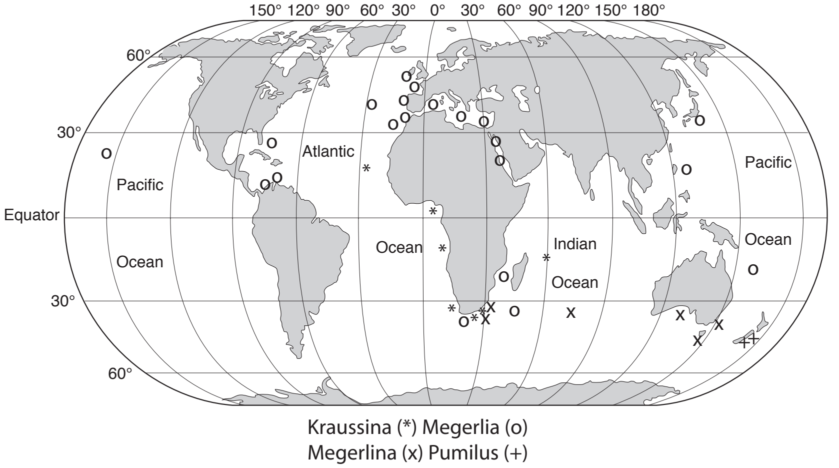


FIG. 1960. Geographic distribution of extant articulated brachiopod genera in superfamily Kraussinoidea (new).

almost entirely in latitudes higher than 30° S, either around Australia (*Terebratella, Jaffaia, Magellania, Magadinella, Pirothyris, Anakinetica, Parakinetica*), New Zealand (*Terebratella, Calloria, Aerothyris, Gyrothyris, Neothyris*), the southern Indian Ocean (*Aerothyris*), the South Atlantic (*Syntomaria, Aneboconcha, Dyscritosia, Magellania*), or Antarctica (*Fosteria, Magellania*).

The genera *Aneboconcha, Dyscritosia, Holobrachia, Magadinella, Pirothyris, Jaffaia, Fosteria, Gyrothyris, Syntomaria, Anakinetica*, and *Parakinetica* are all monotypical. Most terebratelloid genera (almost 90%) have species with a depth range exclusively in the neritic zone (*Calloria, Anakinetica, Parakinetica*) or from the neritic to upper bathyal zones. *Dallina*, with 8 extant species, is the most widely distributed, with most species being found on the shelf and upper slope—only the well-known North Atlantic species *Dallina septigera* descends to over 2000 m.

KRAUSSINOIDEA

The superfamily Kraussinoidea includes 17 extant species belonging to 4 genera (Table 58, Fig. 1960). All species are found at depths of less than 2000 m, with 13 of the 17 known species restricted to the neritic zone. *Pumilus* is monotypical, with *P. antiquatus* being restricted to intertidal areas around South Island, New Zealand. There are 7 species of *Megerlina*, all confined to localities in the southern hemisphere above 30° S (southern Australia, southern Indian Ocean), and all found in the neritic zone. *Kraussina* is found mainly in the southern Indian Ocean at relatively shallow depths, especially off the southern coast of South Africa, and is also present along the eastern South Atlantic as far north as Cape Verde. *Megerlia* is perhaps the best known kraussinoid genus, with *M. truncata* common in the neritic and upper bathyal zones in the Mediterranean Sea and eastern North Atlantic. The closely related *M. echinata* is also present in the eastern Atlantic but additionally has been recorded from the Caribbean Sea, Indian Ocean, and Pacific. Although normally a bathyal species (Table 58), it has been found with *Argyrotheca jacksoni* in shallow reef caves at 10 m depth in the northern Red Sea (COOPER, 1973b), probably another example of a bathyal island occurrence similar to those seen for *M. truncata* in shallow caves from France, Spain, and Croatia in the Mediterranean area (LOGAN, 2003).

GWYNIOIDEA

The superfamily Gwynioidea includes 2 extant species belonging to the single

Table 58. Depth range and geographic distribution of extant species of articulated brachiopods belonging to superfamily Kraussinoidea (new).

Genus	N	Depth or range (m)	Species, geographic distribution, and selected references
Kraussina Davidson, 1859	5	0–50	*K. cognata* (Sowerby, 1847): Atlantic-Indian Ocean: South Africa (Jackson, 1952; Hiller, 1991, 1994)
		42–82	*K. crassicostata* Jackson, 1952: Atlantic-Indian Ocean: South Africa (Jackson, 1952; Cooper, 1973d; Hiller, 1991, 1994)
		223–278	*K. gardineri* Dall, 1910: Indian Ocean: south of Saya de Malha Banks (Dall, 1910; Cooper, 1973b)
		9–930	*K. mercatori* Helmcke, 1939: Atlantic Ocean: Cape Verde; G. of Guinea (Anobon Is., Sao Tome Is.); Angola coast (Helmcke, 1939; Cooper, 1975; Logan, 1988a, 1993)
		40–165	*K. rubra* (Pallas, 1776): Atlantic-Indian Ocean: southern coast of Africa (Namibia to Moçambique) (Jackson, 1952; Cooper, 1973d; Hiller, 1986, 1991, 1994)
Megerlia King, 1850	4	50–290	*M. acrura* Hiller, 1986: Atlantic-Indian Ocean: South Africa; Moçambique (Hiller, 1986, 1991, 1994)
		10–1970	*M. echinata* (Fischer & Oehlert, 1890): Atlantic Ocean: NW Africa and seamounts; SW Ireland, SW England; Caribbean Sea: Florida; ?Barbados; Venezuela; Indian Ocean: coast of South Africa; Red Sea; Pacific Ocean: New Caledonia (Fischer & Oehlert, 1891; Massy, 1925; Atkins, 1961a, 1961b; Cooper, 1973b, 1977; Hiller, 1991; Laurin 1997; Gaspard, 2003b; Logan & others, 2007)
		185–600	*M. gigantea* (Deshayes, 1863) Indian Ocean: Moçambique Channel; S. of Madagascar (Walters Bank, Samper Bank) (Cooper, 1981a; d'Hondt, 1987; Zezina, 1987)
		8–1086	*M. truncata* (Linnaeus, 1767): Atlantic Ocean: Canary Is.; Madeira; Portugal; G. of Gascogne; Morocco; Mediterranean Sea; Adriatic Sea; Red Sea; ?Pacific Ocean: Philippines; Hawaiian Is.; Japan (Davidson, 1887; Atkins, 1961b; Brunton & Curry, 1979; Logan, 1979, 1983, 1988a, 2003, 2004; Cooper, 1981b; Brunton, 1988; Logan & others, 2007) (*M. truncata* includes citations of var. *monstruosa* by many authors)
Megerlina Eudes-Deslongchamps, 1884	7	18	*M. atkinsoni* (Tenison-Woods, 1878): Pacific Ocean: Australia, southern Tasmania (Davidson, 1887; Blochmann, 1910)
		50–420	*M. capensis* (Adams & Reeve, 1850): Atlantic-Indian Ocean: South Africa to Moçambique (Jackson, 1952; Hiller 1991, 1994)
		3–30	*M. davidsoni* (Vélain, 1877): Indian Ocean: St. Paul Is. (38°43'S, 77°32'E) (Davidson, 1887; Cooper, 1981a)
		36–200	*M. lamarckiana*: (Davidson, 1852): Pacific Ocean: Australia, N.S.W., S. Australia, Tasmania (Davidson, 1880, 1887; Blochmann, 1910; Dall, 1920)
		100–150	*M. natalensis* (Krauss, 1844): Atlantic-Indian Ocean: South Africa to Moçambique (Cooper, 1973d; Hiller 1991, 1994)
		0–272	*M. pisum* (Lamarck, 1819): Atlantic-Indian Ocean: South Africa to Moçambique; Moçambique Channel (Davidson, 1880, 1887; Jackson, 1952; Savage, 1972; Zezina, 1987; Hiller, 1986, 1991, 1994)
		32–450	*M. striata* Jackson, 1952: Atlantic–Indian Ocean: South Africa to Moçambique (Davidson, 1880, 1887; Jackson, 1952; Cooper, 1973d; Hiller, 1991, 1994)
Pumilus Atkins, 1958	1	intertidal	*P. antiquatus* Atkins, 1958: Pacific Ocean: New Zealand, S. Island (Atkins, 1958; Rudwick, 1962b; Bowen, 1968)

genus *Gwynia* (Table 55, Fig. 1954). The most common modern representative is the micromorphic species *Gwynia capsula,* from the eastern North Atlantic and the Adriatic Sea. LOGAN and others (1997) provided strong evidence in support of this form as a distinct species in its own right and listed collecting localities from the coasts of Britain, Ireland, France, and Spain. It is most commonly found in the neritic zone but may range down into the upper bathyal zone. There is a questionable record of a specimen dredged by *Talisman* in 1883 from 4060 m north of the Azores by FISCHER and OEHLERT (1891). Recently LÜTER (2007) has described a second species from the upper bathyal zone east of New Zealand. This specimen has similarities to the Jurassic form *Zellania* but is so far only represented by a single juvenile with a trocholophous lophophore.

CONCLUSIONS

In summary, the extant articulated brachiopods, although much less diverse than their fossil counterparts, are represented in the benthos of all the oceans of the world and in all depth zones. While most species occur in the neritic zone, many range down into the bathyal zone and a few into the abyssal zone. It is expected that further discoveries will be made in the future as exploration and sampling of the benthos of geographically remote areas and the deeper parts of the ocean continues.

REFERENCES

Adams, A. 1860. On some new genera and species of Mollusca from Japan. Annals and Magazine of Natural History (series 3) 5:405–422.

Adams, A. 1863. On the genera and species of Recent Brachiopoda found in the seas of Japan. Annals and Magazine of Natural History 11:98–101.

Adams, A. 1867. Description of new shells from Japan. Proceedings of the Zoological Society of London 1867:309–315.

Adams, A., and A. L. Reeve. 1850. Mollusca. Part 1, Zoology of the Voyage of H.M.S. Samarang. London. p. 72, pl. 21, fig. 5.

Addadi, L., A. Berman, J. Moradian-Oldak, and S. Weiner. 1990. Turning of crystal nucleation and growth by proteins: Molecular interactions at solid-liquid interfaces in biomineralization. Croatia Chemica Acta 63(3):539–544.

Addadi, L., & S. Weiner. 1985. Interactions between acidic proteins and crystals: Stereochemical requirements in biomineralization. Proceedings of the National Academy of Sciences 82:4110–4114.

Adkins, J. F., E. A. Boyle, W. B. Curry, & Audrey Lutringer. 2003. Stable isotopes in deep-sea corals and a new mechanism for "vital effects." Geochimica et Cosmochimica Acta 67:1129–1143.

Adoutte, André, & Hervé Philippe. 1993. The major lines of metazoan evolution: Summary of traditional evidence and lessons from ribosomal RNA sequence analysis. *In* Y. Pichon, ed., Comparative Molecular Neurobiology. Birkhauser. Basel. p. 1–30.

Afanasjeva, G. A. 2000. *Pinegochonetes*—novye rod Khonetid (Brakhiopody) iz Kazakhskogo yarussa severa Russkoy platformy [A new genus *Pinegochonetes* (Brachiopoda, Chonetida) from the Kazanian of the Russian Platform]. Paleontologicheskii Zhurnal 3:58–61.

English translation in Paleontological Journal 34(3):287–289.

Afanasjeva, G. A. 2002. Brakhiopody otryda Chonetida iz basseynovskikh fa pogranitchnikh otlodjeniie Devona i Karbona Tchuringskikh i Reniskikh slan gor (Germania) [Brachiopods of the order Chonetida from the Basin Facies of the Devonian-Carboniferous Transitional Strata of the Thuringian and Rhenish Slate mountains (Germany)]. Paleontologicheskii Zhurnal 6:57–62.

English translation in Paleontological Journal 36(6):626–631.

Afanasjeva, G. A. 2004a. Novye khonetidy (Brakhiopody) iz Ufimskogo iarusa verkhnei Permi poluosstrova Kanin [New chonetids (Brachiopods) from the Upper Permian Ufimian Stage of the Kanin Peninsula]. Paleontologicheskii Zhurnal 1:34–36.

English translation in Paleontological Journal 38(1):35–38.

Afanasjeva, G. A. 2004b. Novye permckie khonetidy (Brakhiopody) Mongolii [New Permian chonetids (Brachiopods) from Mongolia]. Paleontologicheskii Zhurnal 2:47–49.

English translation in Paleontological Journal 38(2):162–165.

Ager, D. V. 1957. The true *Rhynchonella.* Palaeontology 1(1):1–15, pl. 1–2.

Ager, D. V. 1959. The classification of the Mesozoic Rhynchonelloidea. Journal of Paleontology 33(2):324–332, pl. 49.

Ager, D. V. 1965. Mesozoic and Cenozoic Rhynchonellacea. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 597–625.

Ager, D. V. 1987. Why the rhynchonellid brachiopods survived and the spiriferids did not: A suggestion. Palaeontology 30(4):853–857.

Ager, D. V. 1988. Extinctions and survivals in the Brachiopoda and the dangers of data bases. *In* G. P. Larwood, ed., Extinction and Survival in the Fossil Record. Clarendon Press. Oxford. p. 89–97.

Al-Assam, I., & J. Veizer. 1982. Chemical stabilisation of low-Mg calcite: An example of brachiopods. Journal of Sedimentary Petrology 52:1101–1109.

Albeck, S., S. Weiner, & Addadi, L. 1996. Polysaccharides of intracrystalline glycoproteins modulate calcite crystal growth *in vitro*. Chemistry A European Journal 2:278–284.

Alcock, A. 1894. A new brachiopod. Natural History notes from the Royal Indian Marine Survey steamer "Investigator," Commander C. F. Oldham, R.N., commanding. Journal of the Asiatic Society of Bengal 63 (series II, no. 13):139–140, pl. 8.

Alekseeva, R. E. 1967. Brakhiopody i stratigrafiia nizhnego Devona Severo-Vostoka [The Lower Devonian Brachiopoda and stratigraphy of the northeast of the USSR]. Nauka. Moscow. 144 p., 16 pl.

Alekseeva, R. E. 2003. Devonian Nervostrophiinae from the Russian Platform (Strophomenida, Brachiopoda). Palaeontologicheskii Zhurnal 2003(2):21–32, pl. 3–4.

In Russian.

Alekseeva, R. E., A. I. Sidjachenko, I. N. Manankov, G. A. Afanasjeva, S. S. Lazarev, V. V. Baranov, V. N. Komarov, & T. A. Grunt. 1996. Atlas of Devonian brachiopods of north-east Russia (East Yakutia and Magadan District). Trudy Palaeontologicheskogo Instituta 266:227 p.

Alexander, R. M. 1968. Animal Mechanics. Sedgwick and Jackson. London. 346 p.

Aliani, Stefano. 1994. I fondi a *Gryphus vitreus* (Brachiopoda) dell'arcipelago Toscano (Mediterraneo occidentale). Atti del 10° Congresso della Associazione Italiana di Oceanologia e Limnologia, Alassio, 4–6 November, 1992. Genova. p. 209–220, 4 fig.

Alichova, T. N. 1951. Brachiopods of the middle and upper parts of the lower Silurian of the Leningrad region and their stratigraphical significance. VSEGEI. Moscow. 81 p., 4 pl.

In Russian.

Allan, R. S. 1931. On a new Recent *Terebratella* from northern New Zealand. New Zealand Journal of Science and Technology 12(6):385–387, 4 fig.

Allan, R. S. 1939. Studies on the Recent and Tertiary Brachiopoda of Australia and New Zealand. Part I. Canterbury Museum, Records 4(5):231–248, 3 pl.

Allan, R. S. 1940. A revision of the classification of the terebratelloid Brachiopoda. Canterbury Museum, Records 4(6):267–275.

Alméras, Yves. 1987. Les Brachiopodes du Lias-Dogger: Paléontologie et Biostratigraphie. *In* R. Enay, Le Jurassique d'Arabie Saoudite Centrale. Geobios, Mémoire Spécial 9:161–219, 11 pl.

Alméras, Yves, & Mikhail Mouty. 2001. Les Brachiopodes du Jurassique de Syrie. Revue de Paléobiologie 20(1):9–17.

Alvarez, Fernando. 1990. Devonian athyrid brachiopods from the Cantabrian Zone (NW Spain). Biostratigraphie du Paléozoïque 11:1–311.

Alvarez, Fernando. 2006. Forty years since Boucot, Johnson and Staton's seminal paper "On some atrypoid, retzioid and athyridoid Brachiopoda." Palaeoworld 15:135–149.

Alvarez, Fernando, & C. H. C. Brunton. 1990. The shell structure, growth and functional morphology of some Lower Devonian athyrids from Northwest Spain. Lethaia 23(2):117–131.

Alvarez, Fernando, & C. H. C. Brunton. 2000. A review of two de Koninck retzioid brachiopod species, and description of a new genus from the Carboniferous of Europe. Palaeontology 43:817–832.

Alvarez, Fernando, & C. C. Emig. 2005. Brachiopoda. *In* F. Alvarez, C.C. Emig, C. Roldan, & J. M. Vieitez, Lophophorata, Phoronida, Brachiopoda, *in* A. Ramos and others, eds., Fauna Ibérica. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Cientificas. Madrid. p. 57–177.

Alvarez, Fernando, & Rong Jia-yu. 2002. Athyridida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H. Brachiopoda (Revised), vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1475–1601, fig. 1001–1092.

Alvarez, Fernando, Rong Jia-yu, & A. J. Boucot. 1998. The classification of athyridid brachiopods. Journal of Paleontology 72:827–855.

Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel. 1980. Extraterrestrial cause for the Cretaceous-Tertiary extinction. Science 208:1095–1108.

Amos, A. J. 1958. Some Lower Carboniferous brachiopods from the Volcan Formation, San Juan, Argentina. Journal of Paleontology 32(5):838–845, 2 pl.

Amos, A. 1961. Algunos Chonetacea y Productacea del Carbonífero inferior y superior del Sistema de Tepuel, Provincia de Chabut. Revista de la Asociación Geológica Argentina 15(1-2):81–107.

Amos, A. J. 1979. Guía Paleontológica Argentina. Parte I: Paleozoico. Sección V–Faunas Carbónicas, Sección VI—Faunas Pérmicas. Consejo Nacional de Investigaciones Científicas y Técnicas. Buenos Aires. 158 p.

Anadón, Nuria. 1994. Braquiópodos actuales de la plataforma y talud continental de la costa central de Asturias (norte de España). Boletín de la Real Sociedad Española de Historia Natural, Sección Biológica 91(1-4):65–77, 1 fig., 3 pl.

Anderson, F. E., A. J. Cordoba, & M. Tholleson. 2004. Bilaterian phylogeny based on analyses of a region of the sodium-potassium ATPase alpha-subunit gene. Journal of Molecular Evolution 58:252–268.

Anderson, T. F., & M. A. Arthur. 1983. Stable isotopes of oxygen and carbon and their application to sedimentologic and paleoenvironmental problems. *In* M. Arthur, T. F. Anderson, I. R. Kaplan, J. Veizer, and L. S. Land, eds., Stable Isotopes in Sedimentary Geology, SEPM Short Course Notes No. 10. Society of Economic Paleontologists and Mineralologists. Tulsa, Oklahoma. p. 1–151.

Andreeva, Olga N. 1960. Novye vidy ordovikskikh brakhiopod Urala i Mugodzhar [New species of Ordovician brachiopods of the Urals and Mugodzar], part 1. Novye vidy drevnikh rastenii i bezpozvonochnykh SSSR. VSEGEI. Moscow. p. 286–298.

Andreeva, O. N. 1987. Kembriiskie zamkovye brakhiopody [Cambrian articulate brachiopods]. Paleontologicheskii Zhurnal 1987(4):31–40, 2 pl.

Angiolini, Lucia. 1995. Permian brachiopods from Karakorum (Pakistan). Pt. 1 (with appendix). Rivista Italiana di Paleontologia e Stratigrafia 101(2):165–214.

Angiolini, Lucia. 1996. Genus *Tintoriella. In* Garzanti, E., L. Angiolini, and D. Sciunnach. 1996. The Permian Kuling Group (Spiti, Lahaul and Zanskar; NW Himalaya): Sedimentary evolution during rift/drift transition and initial opening of Neo-Tethys. Rivista Italiana di Palaeontologia e Stratigrafia 102(2):175–200.

Angiolini, Lucia. 2001a. New syringothyridid genus (Spiriferinida, Brachiopoda) from the Early Permian of interior Oman. Rivista Italiana di Paleontologia e Stratigrafia 107(1):125–130.

Angiolini, Lucia. 2001b. Permian brachiopods from Karakorum (Pakistan) Pt. 3. Rivista Italiana di Paleontologia e Stratigrafia 107(3):307–344.

Anthula, D. J. 1903. Sredni Neokom Kod Tsralevitse [Middle Neocomian at Crnoljevica]. Annales geologiques de la Peninsule Balkanique (Belgrade), 6(1):6–73.
In Serbian.

Archbold, N. W. 1980. *Mingenewia* n. gen. (Strophalosiidina, Brachiopoda) from the western Australian Permian. Journal of Paleontology 54:253–258.

Archbold, N. W. 1983. Studies on Western Australian Permian brachipods. 3. The family Linoproductidae Stehli 1954. Proceedings of the Royal Society of Victoria 95(3–4):237–254, 5 fig.

Archbold, N. W. 1984. Studies on Western Australian Permian brachiopods. 4. Productellidae Schuchert & LeVene 1929 and Overtoniidae Muir-Wood & Cooper 1960. Proceedings of the Royal Society of Victoria 96(2):83–92.

Archbold, N. W. 1985. Studies on Western Australian Permian brachiopods. 5. The family Dictyoclostidae Stehli 1954. Proceedings of the Royal Society of Victoria 97(1):19–30.

Archbold, N. W. 1996. Studies on Western Australian Permian brachiopods. 13. The fauna of the Artinskian Mingenew Formation, Perth Basin. Proceedings of the Royal Society of Victoria 108(1):17–42.

Archbold, N. W. 1997. Studies on Western Australian Permian brachiopods. 14. The fauna of the Artinskian High Cliff Sandstone, Perth Basin. Proceedings of the Royal Society of Victoria 109(2):199–231.

Archbold, N. W. 1999. Additional records of Permian brachiopods from near Rat Buri, Thailand. Proceedings of the Royal Society of Victoria 111(1):71–86.

Archbold, N. W., & T. Hogeboom. 2000. Subsurface brachiopoda from borehole cores through the early Permian sequence of the Carnarvon Basin, Western Australia: Correlations with palynological biostratigraphy. Proceedings of the Royal Society of Victoria 112(1):93–109.

Archbold, N.W., & T. Simanauskas. 2001. New Strophalosiidae (Brachiopoda) from the early Pemian of Argentina. Proceedings of the Royal Society of Victoria 113(2):217–227.

Archbold, N. W., & G. A. Thomas. 1986a. *Neospirifer* and *Trigonotreta* (Spiriferida, Brachiopoda) from the Permian of Western Australia. Alcheringa 10(2):125–161, 19 fig.

Archbold, N. W., & G. A. Thomas. 1986b. Permian Ingelarellidae (Brachiopoda) from Western Australia and Argentina. Journal of Paleontology 60(3):581–605.

Aris-Brosou, S. 2005. Determinants of adaptive evolution at the molecular level: The extended complexity hypothesis. Molecular Biology and Evolution 22:200–209.

Arkhipova, I., & M. Meselson. 2000. Transposable elements in sexual and ancient asexual taxa. Proceedings of the National Academy of Sciences 97:14,473–14,477.

Arthur, Wallace. 2002. The emerging conceptual framework of evolutionary developmental biology. Nature 415:757–764.

Asgaard, Ulla, & Niels Stentoft. 1984. Recent micromorph brachiopods from Barbados: Palaeoecological and evolutionary implications. Geobios (mémoire special) 8:29–33, 2 pl.

Ashworth, J. H. 1915. On larvae of *Lingula* and *Pelagodiscus* (Discinisca). Transactions of the Royal Society of Edinburgh 51:45–69.

Atkins, Daphne. 1958. A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. Proceedings of the Zoological Society of London 131(4):559–581, 14 fig., 1 pl.

Atkins, Daphne. 1959a. The growth stages of the lophophore of the brachiopods *Platidia davidsoni* (Eudes Deslongchamps) and *P. anomioides* (Philippi), with notes on the feeding mechanism. Journal of the Marine Biological Association of the United Kingdom 38:103–132, 23 fig.

Atkins, Daphne. 1959b. A new species of *Platidia* (Brachiopoda) from the La Chapelle Bank region. Journal of the Marine Biological Association of the United Kingdom 38:133–142, 8 fig.

Atkins, D. 1959c. The early growth stages and adult structure of the lophophore of *Macandrevia cranium* (Müller)(Brachiopoda, Dallinidae). Journal of the Marine Biological Association of the United Kingdom 38:335–350, 11 fig.

Atkins, Daphne. 1960a. A new species and genus of Brachiopoda from the Western Approaches, and the growth stages of the lophophore. Journal of the Marine Biological Association of the United Kingdom 39:71–89, 14 fig., 1 pl.

Atkins, Daphne. 1960b. A note on *Dallina septigera* (Lovén), (Brachiopoda, Dallinidae). Journal of the Marine Biological Association of the United Kingdom 39:91–99, 3 fig., 1 pl.

Atkins, Daphne. 1960c. The ciliary feeding mechanism of the Megathyridae (Brachiopoda), and the growth stages of the lophophore. Journal of the Marine Biological Association of the United Kingdom 39:459–479, 10 fig.

Atkins, Daphne. 1961a. The generic position of the brachiopod *Megerlia echinata* (Fischer & Oehlert). Journal of the Marine Biological Association of the United Kingdom 41:89–94, 4 fig.

Atkins, Daphne. 1961b. The growth stages and adult structure of the lophophore of the brachiopods *Megerlia truncata* (L.) and *M. echinata* (Fischer & Oehlert). Journal of the Marine Biological Association of the United Kingdom 41:95–111, 16 fig.

Atkins, Daphne. 1961c. A note on the growth stages and structures of the adult lophophore of the brachiopod *Terebratella (Waltonia) inconspicua* (G. B. Sowerby). Proceedings of the Zoological Society of London 136:255–271.

Atkins, Daphne, & M. J. S. Rudwick. 1962. The lophophore and ciliary feeding mechanism of the brachiopod *Crania anomala* (*Muller*). Journal of the Marine Biological Association of the United Kingdom 42:469–480.

Auclair, A.-C., M. M. Joachimski, & C. Lécuyer. 2003. Deciphering kinetic, metabolic and environmental controls on stable isotope fractionations between seawater and the shell of *Terebratalia transversa* (Brachiopoda). Chemical Geology 202:59–78.

Azmy, K., J. Veizer, B. Wenzal, Mike Bassett, & P. Copper. 1999. Silurian strontium isotope stratigraphy. Geological Society of America Bulletin 111:475–483.

Baarli, B. G. 1995. Orthacean and strophomenid brachiopods from the Lower Silurian of the central Oslo Region. Fossils and Strata 39:1–93, 19 pl.

Backhaus, Egon. 1959. Monographie der cretacischen Thecideidae (Brach.). Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg 28:5–90, fig. 1–14, pl. 1–7.

Baker, P. G. 1969. The ontogeny of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. Palaeontology 12:388–399.

Baker, P. G. 1970. The growth and shell microstructure of the thecideacean brachiopod *Moorellina granulosa* (Moore) from the Middle Jurassic of England. Palaeontology 13:76–99.

Baker, P. G. 1972. The development of the loop in the Jurassic brachiopod *Zeilleria leckenbyi*. Palaeontology 15:450–472.

Baker, P. G. 1983. The diminutive thecideidine brachiopod *Enallothecidea pygmaea* (Moore) from the Middle Jurassic of England. Palaeontology 26:663–669.

Baker, P. G. 1984. New evidence of a spiriferide ancestor for the Thecideidina (Brachiopoda). Palaeontology 27:857–866.

Baker, P. G. 1989. Location and interpretation of ontogenetic relics in the shell of adult brachiopods. Lethaia 22:241–245.

Baker, P. G. 1990. The classification, origin and phylogeny of thecideidine brachiopods. Palaeontology 33:175–191.

Baker, P. G. 1991. Morphology and shell microstructure of Cretaceous thecideidine brachiopods and their bearing on thecideidine phylogeny. Palaeontology 34:815–836.

Baker, P. G. 2005. A new lacazellin thecideoid brachiopod from the Middle Jurassic of the Cotswolds, England. Palaeontology 48:1311–1319, fig. 1–2, pl. 1–2.

Baker, P. G. 2006. Thecideida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, Revised, vol. 5. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1938–1964.

Baliński, Andrzej. 1997a. Evolution of the embryonic development in lingulid brachiopods. Acta Palaeontologica Polonica 42(1):45–56.

Baliński, Andrzej. 1997b. A new atrypid genus (Brachiopoda) from the Frasnian of Poland. Acta Paleontologica Polonica 42(3):427–435.

Baliński, Andrzej. 2002. Frasnian-Famennian brachiopod extinction and recovery in southern Poland. Acta Palaeontologica Polonica 47(2):289–305.

Baliński, Andrzej, & Lars E. Holmer. 1999. The Late Devonian trematid lingulate brachiopod *Schizobolus* from Poland. Acta Paleontologica Polonica 44(3):335–346.

Balthasar, Uwe. 2004a. Shell structure, ontogeny and affinities of the Lower Cambrian bivalved problematic fossil *Mickwitzia muralensis* Walcott, 1913. Lethaia 37(4):381–400.

Balthasar, Uwe. 2004b. A metameric brachiopod from the Lower Cambrian. Geological Society of America Abstracts with Programs 36(5):522.

Bamber, E. W., & J. B. Waterhouse. 1971. Carboniferous and Permian stratigraphy and paleontology, northern Yukon Territory, Canada. Bulletin of Canadian Petroleum Geology 19:29–250, 27 pl.

Bancroft, B. B. 1928. The Harknesellinae. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 72:173–196, 3 pl.

Bancroft, B. B. 1929. Some new genera and species of Strophomenacea from the Upper Ordovician of Shropshire. Memoirs and Proceedings of the Manchester Literary and Philosophical Society 73:33–65, pl. 1–2.

Baranov, V. V. 1980. Morfologiia crur i novye taksony rinkhonellid [Morphology of crura and new rhynchonellid taxa]. Paleontologicheskii Zhurnal 1980(4):75–90, 1 pl.

Baranov, V. V. 1982. Novye Devonskie rinkhonellidy i Atiridídy Vostochnoi Iakutii [New Devonian rhynchonellids and athyridids from eastern Jakutia]. Paleontologicheskii Zhurnal 1982(2):41–51, 1 pl.

Baranov, V. V., and T. S. Al'khovik. 2001. Novye atiridídy iz nizhnego devona vostochnoi iakutii [New athyridids (Brachiopoda) from the Lower Devonian of Eastern Yakutia]. Paleontologicheskii Zhurnal 3:41–45.

Barrande, Joachim. 1847. Über die Brachiopoden der silurischen Schichten von Böhmen. Naturwissenschaftlichen Abhandlungen. I Band. W. Haidinger. Wien. p. 357–475, pl. 14–22.

Barrande, Joachim. 1848. Über die brachiopoden der silurischen Schichten von Böhmen. Naturwissenschaftliche Abhandlungen, II Band:155–256, pl. 15–23.

Barrande, Joachim. 1879. Système Silurien du centre de la Bohême. 1ère partie. Recherches paléontologiques, vol. 5. Classe des Mollusques. Ordre des Brachiopodes. Published by the author. Prague & Paris. 226 p., 153 pl.

Bartholomaeus, Thomas. 2001. Ultrastructure and formation of the body cavity lining in *Phoronis muelleri* (Phoronida, Lophophorata). Zoomorphology 130:135–148.

Bassett, M. G. 2000. Craniida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 169–183.

Bassett, M. G., L. E. Popov, & L. E. Holmer. 1999. Organophosphatic brachiopods: Patterns of biodiversification and extinction in the early Palaeozoic. Geobios 32:145–163.

Bassett, M. G., L. Ye. Popov, & L. E. Holmer. 2001. Functional morphology of articulatory structures and implications for patterns of musculature in Cambrian rhynchonelliform brachiopods. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Proceedings of the Millennium Brachiopod Congress, 2000. The Systematics Association Special Volume Series 63. Taylor and Francis, London. p. 163–176.

Bataller, J. R. 1943. Una nueva 'Terebratula' del Eoceno catalán. Instituto Geológico y Minero de España, Notas y Comunicaciones 11:33–36.

Bates, D. E. B. 1968. The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. British Museum (Natural History), Bulletin (Geology) 16(4):125–199, pl. 1–14.

Baxter, J. M., M. G. Sturrock, & A. M. Jones. 1990. The structure of the intrapigmented aesthetes and the properiostracum layer in *Callochiton achatinus* (Mollusca, Polyplacophora). Journal of Zoology 220:447–468.

Bayle, C. E. 1880. Liste rectificative de quelques noms de genres et d'espèces. Journal de Conchyliologie (series 2) 28(3):240–251.

Beecher, C. E. 1893. Revision of the families of loop-bearing Brachiopoda. The development of *Terebratalia obsoleta* Dall. Connecticut Academy of Arts and Sciences, Transactions 9(2):376–399, 3 pl.

Bekker, Hendrik. 1921. The Kuckers Stage of the Ordovician rocks of north-east Estonia. Acta et

Commentationes Universitatis Tartuensis (Dorpatensis) A2:1–92, 15 fig., 12 pl.

Belcher, A.M., Wu X. H., R. J. Christensen, P. K. Hansma, G. D. Stucky, & D. E. Morse. 1996. Control of crystal phase switching and orientation by soluble mollusc-shell proteins. Nature 381:56–58.

Benedetto, J. L. 1995. La fauna de braquiópodos de la Formación Las Plantas (Ordovícico tardío, Caradoc), Precordillera Argentina. Revista Española de Paleontología 10:239–258, 5 pl.

Benedetto, Juan L. 2001. Una fauna de braquiópodos arenigianos (Ordovícico temprano) en rocas volcanoclásticas de la Puna occidental de Argentina: Implicaciones paleoclimáticas y paleogeográficas. Ameghiniana 38(2):131–146.

Benedetto, J. L. 2003. Early Ordovician (Arenig) brachiopods from volcaniclastic rocks of the Famatina Range, Northwest Argentina. Journal of Paleontology 77:212–242.

Benedetto, J. L., & P. A. Carrasco. 2002. Tremadoc (earliest Ordovician) brachiopods from Purnamarca and the Sierra de Mojotoro, Cordillera Oriental of northwestern Argentina. Geobios 35:647–661.

Benedetto, J. L., N. Cech, and C. Esbry. 2003. New late Tremadoc–early Arenig silicified brachiopods from the lower part of the San Juan Formation, Argentine Precordillera. Ameghiniana 40(4):513–530.

Benediktova, R. N. 1956. Spiriferidy ostrogskoi svity Kuzbassa [Spiriferids of the Ostrogsk Formation of the Kuzbass]. Voprosy Geologii Kuzbassa 1:169–182.

Bengtson, Stefan. 1970. The Lower Cambrian fossil *Tommotia*. Lethaia 3:363–392.

Bengtson, Stefan. 2004. Early skeletal fossils. *In* J. H. Lipps & B. M. Waggoner, eds., Neoproterozoic–Cambrian Biological Revolutions. The Paleontological Society Papers 10:67–78.

Bengtson, Stefan, & Simon Conway Morris. 1984. A comparative study of Lower Cambrian *Halkieria* and Middle Cambrian *Wiwaxia*. Lethaia 17:307–329.

Bengtson, Stefan, Simon Conway Morris, B. J. Cooper, P. A. Jell, & B. N. Runnegar. 1990. Early Cambrian fossils from South Australia. Memoirs of the Association of Australasian Paleontologists 9:1–364.

Bengtson, Stefan, & V. V. Missarzhevsky. 1981. Coeloscleritophora, a major group of enigmatic Cambrian metazoans. *In* M. E. Taylor, ed., Short Papers for the Second International Symposium on the Cambrian System. U. S. Geological Survey Open-File Report 810743:19–21.

Benigni, Chiara, & Cesare Corselli. 1981. Chiave ai generi attuali mediterranei del phylum Brachiopoda e loro ecologia. Bolletino Malacoligico Milano 17(3-4):51–54, 4 fig.

Benson, D. A., I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, & D. J. Wheeler. 2005. GenBank. Nucleic Acids Research 33:D34–D38.

Benton, M. J. 2004. The quality of the fossil record. *In* P. C. J. Donoghue and M. P. Smith, eds., Telling the Evolutionary Time: Molecular Clocks and the Fossil Record: Systematics Association Special Volume Series 66. Taylor and Francis. London. p. 66–90.

Bernard, F. R. 1972. The living Brachiopoda of British Columbia. Syesis 5:73–82, 15 fig.

Besteiro, C., & V. Urgorri. 1984. Sobre la presencia de *Argyrotheca cistellula* (Searles-Wood, 1841), *Gwynia capsula* (Jeffreys, 1859) (Brachiopoda, Terebratulida) y *Leptosynapta minuta* (Becher, 1906) (Holothuroidea, Apoda) en las costas gallegas. *In* V. M. Marques, ed., Actas do IV° Simpósio ibérico de estudos do benthos marinho, vol. 3, 2–25 May, 1984. Lisboa. p. 219–226, 2 fig.

Biernat, Gertruda. 1983. Ramienionogi z utworów famenu Jabłonnej, Góry Świętokrzyskie [On the Famennian Brachiopods from Jablonna, Góry Swietokrzyskie Mts., Poland]. Biuletyn Instytutu Geologicznego 345:135–154, 47(2): 289–305.

Biernat, Gertruda. 1988. Famennian brachiopods of the Holy Cross Mountains, Poland. *In* N. J. McMillan, A. F. Embry, & D. J. Glass, eds., Devonian of the World, Proceedings of the Second International Symposium on the Devonian System, Calgary, Canada, III: Paleontology, Paleoecology and Biostratigraphy. Memoirs of the Canadian Society of Petroleum Geologists 14:327–335.

Biernat, Gertruda, & Grzegorz Racki. 1986. A rhynchonellid-dominated late Famennian brachiopod assemblage from the Holy Cross Mountains (Poland). Acta Palaeontologica Polonica 31(1–2):85–109, pl. 35–46.

Biernat, Gertruda, & Alwyn Williams. 1970. Ultrastructure of the protegulum of some acrotretide brachiopods. Palaeontology 13:491–502.

Billings, Elkanah. 1860. Description of some new species of fossils from the lower and middle Silurian rocks of Canada. The Canadian Naturalist and Geologist 5:49–69.

Billings, Elkanah. 1874. Palaeozoic fossils, vol. 2, part 1. Geological Survey of Canada. Montréal. 144 p.

Binnekamp, J. G. 1965. Lower Devonian brachiopods and stratigraphy of North Palencia (Cantabrian Mountains, Spain). Leidse Geologische Mededelingen 33:1–62.

Bitner, M. A. 2006a. First record of brachiopods from the Marquesas Islands, French Polynesia, south central Pacific. Pacific Science 60: 417–424, 3 fig.

Bitner, M. A. 2006b. Recent Brachiopoda from the Fiji and Wallis and Futuna Islands, south-west Pacific. *In* B. Richer de Forges & J.-L. Justine, eds., Tropical Deep-Sea Benthos, vol. 24. Mémoires du Muséum national d'Histoire naturelle 193:15–32, 6 fig.

Bitner, M. A., & Bruno Cahuzac. 2004. The genus *Cryptopora* (Brachiopoda) from the Miocene of France and its history and biogeography. Geobios 37:1–12, 6 fig.

Bitner, M. A., & A. Pisera. 1979. Brachiopods from the Upper Cretaceous Chalk of Mielnik (Eastern Poland). Acta Geologica Polonica 29(1):67–88, 7 pl.

Bittner, Alexander. 1890. Brachiopoden der Alpinen Trias. Abhandlungen der Geologischen Reichsanstalt 14:1–325, pl. 1–41.

Bizzarro, Martin, & Pierre Lespérance. 1999. Systematics of some Lower and Middle Devonian spiriferid brachiopods from Gaspé with a revision of the superfamily Delthyridoidea. Journal of Paleontology 73(6):1056–1077.

Blakesley, R. W., N. F. Hansen, J. C. Mullikin, P. J. Thomas, J. C. McDowell, B. Maskeri, A. C. Young, B. Benjamin, S. Y. Brooks, B. I. Coleman, J. Gupta, S. L. Ho, E. M. Karlins, Q. L. Maduro, S. Stantripop, C. Tsurgeon, J. L. Vogt, M. A. Walker, C. A. Masiello, X. Guan, G. G. Bouffard, & E. D. Green. 2004. An intermediate grade of finished genomic sequence suitable for comparative analyses. Genome Research 14:2235–2244.

Blochmann, Friedrich. 1892. Untersuchungen über den Bau der Brachiopoden I: Die Anatomie von *Crania anomala* O.F.M. Gustav Fischer Verlag. Jena. p. 1–68.

Blochmann, Friedrich. 1900. Untersuchungen uber den Bau der Brachiopoden. II. Die Anatomie von *Discinisca lamellosa* (Broderip) und *Lingula anatina* (Bruguiere). Jena. Gustav Fischer. p. 69–124.

Blochmann, F. 1906. Neue Brachiopoden der Valdivia- und Gaussexpeditionen. Zoologischer Anzeiger 30(21-23):690–702, 3 fig.

Blochmann, F. 1908. Zur Systematik und geographischen Verbreitung der Brachiopoden. Zeitschrift für wissenschaftliche Zoologie 90:596–644, 6 fig., 5 pl.

Blochmann, F. 1910. New brachiopods from South Australia. Transactions of the Royal Society of South Australia 34:90–99, 2 pl.

Blochmann, F. 1914. Some Australian brachiopods. Papers and Proceedings of the Royal Society of Tasmania for 1913:112–115, 3 pl.

Bogoyavlenskaya, V. M. 1991. Brachiopods. *In* V. N. Puchkov, ed., [Ordovician of the Polar Urals. Palaeontology]. Uralskoye Otdeleniye Akademii Nauk SSSR, Sverdlovsk, p. 74–105.
In Russian.

Böhm, F., M. M. Joachimski, W.-C. Dullo, A. Eisenhauer, H. Lehnert, J. Reitner, & G. Wörheide. 2000. Oxygen isotope fractionation in marine aragonite of coralline sponges. Geochimica et Cosmochimica Acta 64:1695–1703.

Booker, F. W. 1932. A new species of *Productus* from the Lower Bowen series—Queensland. Proceedings of the Royal Society of Queensland 43:66–72.

Boore, J. L. 1999. Animal mitochondrial genomes. Nucleic Acids Research 27:1767–1780.

Boore, J. L., T. M. Collins, D. Stanton, L. I. Daehler, & W. M. Brown. 1995. Deducing the pattern of arthropod phylogeny from mitochondrial DNA rearrangements. Nature 376:163–165.

Boore, J. L., M. Medina, & L. A. Rosenberg. 2004. Complete sequences of the highly rearranged molluscan mitochondrial genomes of the scaphopod *Graptacme eborea* and the bivalve *Mytilus edulis.* Molecular Biology and Evolution 21:1492–1503.

Boore, J. L., & J. L. Staton. 2002. The mitochondrial genome of the sipunculid *Phascolopsis gouldii* supports an association with Annelida rather than Mollusca. Molecular Biology and Evolution 19:127–137.

von Born, I. 1778. Index rerum naturalium Musaei Caeserei Vindobonensis. Pt. I. Testacea. Verzeichnis der natürlichen Seltenheiten des K.K. Naturalien Cabinets zu Wien, 1 Schaltiere. Vindobonae. 458 p., 1 pl.

Boucot, A. J. 1959. A new family and genus of Silurian orthotetacid brachiopods. Journal of Paleontology 33(1):25–28, fig. 1–2, pl. 3.

Boucot, A. J. 1996. Epilogue. *In* L. C. S. Ivany & K.M. Schopf eds., New perspectives on faunal stability in the fossil record. Palaeogeography, Palaeoclimatology, Palaeoecology 127(1-4):339–359.

Boucot, A. J., R. B. Blodgett, & J. H. Stewart. 1997. European Province late Silurian brachiopods from the Ciudad Victoria area, Tamaulipas, northeastern Mexico. Geological Society of America Special Paper 321:273–293, 10 fig.

Boucot, A. J., L. R. M. Cocks, & P. R. Racheboeuf. 1999. Early Devonian brachiopods from Satun Province, Southern Thailand. Journal of Paleontology 73(5):850–859.

Boucot, A. J., J. G. Johnson, & R. D. Staton. 1964. On some atrypoid, retzioid, and athyridoid Brachiopoda. Journal of Paleontology 38:805–822, fig. 1–6, pl. 125–128.

Boucot, A. J., Rong Jia-yu, & R. B. Blodgett. 2002. Pentameridina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 960–1026.

Bousfield, E. L. 1960. Canadian Atlantic Sea Shells. National Museum of Canada. Ottawa. 72 p., 13 pl.

Bowen, Z. P. 1968. A guide to New Zealand Recent brachiopods. Tuatara 16(2):127–150, 11 fig.

Brand, U. 1989a. Biogeochemistry of Late Paleozoic North American brachiopods and secular variation of seawater composition. Biogeochemistry 7:159–193.

Brand, U. 1989b. Global climatic changes during the Devonian-Mississippian: Stable isotope biogeochemistry of brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 75:175–191.

Brand, Uwe, Alan Logan, Norton Hiller, & J. R. Richardson. 2003. Geochemistry of modern brachiopods: Applications and implications for oceanography and paleoceanography. Chemical Geology 198:305–334, 10 fig.

Branson, E. B. 1923. The Devonian of Missouri. Missouri Bureau of Geology and Mines, Second Series, 17(1922):1–129, 276–279.

Breivel, M. G., & I. A. Breivel. 1999. Novye Spiriferidy iz nijne-srednedevonskikh boksitonosnykh otlojenii vostochnogo sklona severnogo Urala [New spiriferids from the lower-middle Devonian bauxite-bearing deposits of the eastern slope of the northern Urals]. *In* K. K. Zoloeva & N. Ia. Antsigina, eds., Problemy stratigrafii i paleontologii Urala [Problems of stratigraphy and palaeontology in Urals]. Sbornyk nautchnikh trudov. Ekaterinburg. p. 88–95, 2 fig., 5 pl.

Brenchley, P. J. 2004. End Ordovician Glaciation. *In* B. D. Webby, F. Paris, M. L. Droser, and I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 81–83.

Brice, Denise. 1971. Étude paléontologique et stratigraphique du Dévonien de l'Afghanistan. Contribution à la connaissance des brachiopodes et des polypiers rugueux. Notes et Mémoires sur le Moyen-Orient 11:1–364, 59 fig., 20 pl.

Brice, Denise. 1997. Clarification sur la position systématique de *Spirifer strunianus* Gosselet, 1879, brachiopode du Famennien supérieur de l'Avesnois (N. France). Emendation du genre *Eobrachythyris* Brice, 1971. Geobios (mémoire special) 20:67–73.

Brice, Denise, & M. Farsan. 1977 [1976]. Brachiopods from the Upper Devonian of Robat-e-Paï (Afghanistan). Société Géologique du Nord, Annales 96(3):225–232.

Brice, Denise, & P. Meats. 1972 [1971]. Le genre *Ripidiorhynchus* Sartenaer, 1966 (Rhynchonellida-Brachiopodes) dans le Dévonien de Ferques (Boulonnais, France). Société Géologique du Nord, Annales 91(4):215–228.

Brice, Denise, & J.-P. Nicollin. 2000. *Eobrachythyris* Brice, 1971, an index genus (spiriferid brachiopod) for the Late Devonian and Early Carboniferous in Southern Anti Atlas (N. Africa) North Gondwana. Travaux de l'Institut des Sciences de Rabat, Série Géologie & Géographie Physique 20:57–68, 7 fig., 1 pl.

Briggs, D. J. C. 1998. Permian Productidina and Strophalosiidina from the Sydney-Bowen Basin and New England Orogen. Association of Australasian Palaeontologists, Memoir 19:258 p.

Broderip, W. J. 1833a. Descriptions of some new species of Cuvier's family of Brachiopoda. Zoological Society of London, Proceedings 1:124–125, pl. 22–23.

Broderip, W. J. 1833b. Description of some species of Cuvier's Family of Brachiopoda. Zoological Society of London, Proceedings 1:141–144, pl. 23.

Brock, G. A. 1998. Middle Cambrian brachiopods from the Southern New England Fold Belt, Northeastern N.S.W., Australia. Journal of Paleontology 72:604–619.

Brock, G. A. 1999. An unusual micromorphic brachiopod from the Middle Cambrian of north-eastern New South Wales, Australia. Records of the Australian Museum 51:179–186.

Brock, G. A., M. J. Engelbretsen, & G. Dean-Jones. 1995. Acrotretid brachiopods from the Devonian of Victoria and New South Wales. Memoir of the Association of Australasian Palaeontologists 18:105–120, 9 fig.

Brock, G. A., and J. A. Talent. 1999. *Roanella*, a new ?billingselloid brachiopod from the Late Cambrian Dolodrook Limestones, east-central Victoria. Proceedings of the Royal Society of Victoria 111:107–120.

Broecker, W. S. 1989. The salinity contrast between the Atlantic and Pacific Oceans during glacial time. Paleoceanography 4:207–212.

Broili, Ferdinand. 1916. Die permischen Brachiopoden von Timor. *In* J. Wanner, ed., Palaeontologie von Timor, no. 7, pt. 12. E. Schweizerbartchen Verlag-Buch-handlung. Stuttgart. 104 p.

Bromham, L. D., & M. D. Hendy. 2000. Can fast early rates reconcile molecular dates with the Cambrian explosion? Proceedings of the Royal Society of London (Series B, Biological Sciences) 267(1447):1041–1047.

Bronn, H. G. 1862. Die Klassen und Ordnungen der Weichthiere (Malacozoa), vol. 3(1). C. F. Winter'sche Verlagshandlung. Leipzig & Heidelberg. 518 p., 44 pl.

Brown, Karen. 1998. Biomineralisation of the calciticshelled inarticulate brachiopod, *Neocrania anomala*. Unpublished PhD thesis. University of Glasgow. Glasgow. 125 p.

Bruckschen, Peter, & Ján Veizer. 1997. Oxygen and carbon isotopic composition of Dinantian brachiopods: Paleoenvironmental implications for the lower Carboniferous of western Europe. Palaeogeography, Palaeoclimatology, Palaeoecology 132:243–264.

Brunton, C. H. C. 1966. Silicified productoids from the Viséan of County Fermanagh. Bulletin of the British Museum (Natural History), Geology 12:175–243.

Brunton, C. H. C. 1972. The shell structure of chonetacean brachiopods and their ancestors. British Museum (Natural History), Bulletin (Geology) 21:1–26, 9 pl.

Brunton, C. H. C. 1988. Some brachiopods from the eastern Mediterranean Sea. Israel Journal of Zoology 35:151–169, 28 fig.

Brunton, C. H. C. 1996. The functional morphology of the Recent brachiopod *Bouchardia rosea*. Acta Zoologica 77:233–240, 12 fig.

Brunton, C. H. C., Fernando Alvarez, & D. I. MacKinnon. 1996. Morphological terms used to describe the cardinalia of articulate brachiopods: Homologies and recommendations. Historical Biology 11:9–41.

Brunton, C. H. C., L. R. M. Cocks, & S. P. Dance. 1967. Brachiopods in the Linnaean Collection. Linnean Society of London, Proceedings 178(2):161–181, 4 pl.

Brunton, C.H.C., L. R. M. Cocks, & S. L. Long, eds. 2001. Brachiopods Past and Present. The Systematics Association Special Series 63. Taylor & Francis, London and New York. 441 p.

Brunton, C. H. C., and G. B. Curry. 1979. British Brachiopods. *In* D. M. Kermack & R. S. K. Barnes, eds., Synopses of the British Fauna (new series) 17:64 p., 30 fig.

Brunton. C. H. C., and S. S. Lazarev. 1997. Evolution and classification of the Productellidae (Productida), Upper Paleozoic brachiopods. Journal of Paleontology 71(3):381–394.

Brunton, C. H. C., S. S. Lazarev, & R. E. Grant. 1995. A review and new classification of the brachiopod order Productida. Palaeontology 38(4):915–936, fig. 1–4.

Brunton, C. H. C., S. S. Lazarev, & R. E. Grant. 2000. Productida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 350–362.

Brunton, C. Howard C., S. S. Lazarev, R. E. Grant, and Jin Yu-gan. 2000. Productidina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised), vol. 3. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 424–609.

Brunton, C. H. C., & D. I. MacKinnon. 1972. The systematic position of the Jurassic brachiopod *Ca-*

domella. Palaeontology 15(3):405–411, 1 fig., pl. 76–78.

Brusca, R. C., & G. J. Brusca. 1990. Invertebrates. Sinauer. Sunderland, Massachusetts. 936 p.

Brusca, R. C., & G. J. Brusca. 2003. Invertebrates, 2nd ed. Sinauer. Sunderland, Massachusetts. 880 p., 615 fig.

Buckman, S. S. 1907. Brachiopod Morphology: *Cincta, Eudesia,* and the development of ribs. Geological Society of London, Quarterly Journal 62:338–343.

Buckman, S. S. 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. Memoirs of the Geological Survey of India, Palaeontologia Indica (new series) 3(2):1–299, pl. 1–21.
Published for 1917.

Budd, G. E., & Soren Jensen. 2000. A critical reappraisal of the fossil record of the bilaterian phyla. Biological Reviews 75:253–295.

Buening, Nancy. 1998. Synchotron x-ray fluorescence analyses of elemental concentrations in selected brachiopod shells: A sensitive tool to detect diagenesis. Geological Society of America, 1998 Annual Meeting, Abstracts with Programs 30:384.

Buening, Nancy, & S. J. Carlson. 1992. Geochemical investigation of growth in selected Recent articulate brachiopods. Lethaia 25:331–345.

Buening, Nancy, & H. J. Spero. 1996. Oxygen- and carbon-isotope analyses of the articulate brachiopod *Laqueus californianus*: A recorder of environmental changes in the subeuphotic zone. Marine Biology 127:105–114.

Bulman, O. M. B. 1939. Muscle systems of some inarticulate brachipoods. Geological Magazine 76:434–444.

Caldwell, W. 1882. Preliminary notes on the structure, development, and affinities of *Phoronis*. Proceedings of the Royal Society of London 34:371–383.

Calzada Badia, S. 1994. Revision de *Terebratula sampelayoi,* braquiópodo del Eoceno catalán. Batalleria 4:41–44.

Campbell, J. D., and C. A. Fleming. 1981. Brachiopoda from Fiordland, New Zealand, collected during the *Golden Hind* Expedition, 1946. New Zealand Journal of Zoology 8:145–155, 36 fig.

Campbell, K. S. W. 1959. The *Martinioposis*-like spiriferids of the Queensland Permian. Palaeontology 1:333–350, pl. 56–57.

Campbell, K.S.W. 1961. New species of the Permian spiriferoids *Ingelarella* and *Notospirifer* from Queensland and their stratigraphic implications. Palaeontographica (Abt. A) 117(5–6):159–192.

Campi, M. J., & Shi G. R. 2002. *Linshuichonetes* gen. nov., a new rugosochonetid (Brachiopoda) genus from the Liangshan Formation (Early Permian) in Sichuan, China, and its ecology. Acta Palaeontologica Sinica 41(1):105–118.

Candela, Y. 1999. A new genus of xenambonitid brachiopod from the Caradoc of Pomeroy, Co. Tyrone, Northern Ireland. Irish Journal of Earth Sciences 17:91–101, 5 fig.

Caputo, M. V. 1998. Ordovician-Silurian glaciations and global sea-level changes. *In* E. Landing and M. E. Johnson, eds., Silurian Cycles: Linkage of Dynamic Stratigraphy with Atmospheric, Oceanic and Tectonic Changes. New York State Museum Bulletin 491:15–25.

Carlson, S. J. 1989. The articulate brachiopod hinge mechanism: Morphological and functional variation. Paleobiology 15:364–386.

Carlson, S. J. 1994. Investigating brachiopod phylogeny and classification—A response to Popov et al. 1993. Lethaia 26:383–384.

Carlson, S. J. 1995. Phylogenetic relationships among extant brachiopods. Cladistics 11:131–197.

Carlson, S. J. 1996. Revision and review of the order Pentamerida. *In* P. Copper and Jisuo Jin, eds. Brachiopods. Proceedings of the Third International Brachiopod Congress, 1995. A. A. Balkema. Rotterdam. p. 53–58.

Carlson, S. J. 1999. Phylogenetic systematics and palaeontology. *In* D. A. T. Harper, ed., Numerical Palaeobiology. John Wiley & Sons. London. p. 41–91.

Carlson, S. J. 2001. Ghosts of the past, present, and future in brachiopod systematics. Journal of Paleontology 75(6):1109–1118.

Carlson, S. J. 2002. Suborder Syntrophiidina (order Pentamerida). *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 929–960.

Carlson, S. J., A. J. Boucot, Rong Jia-Yu, & R. B. Blodgett. 2002. Introduction: Order Pentamerida. *In* R. L. Kaesler, ed. Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 921–928.

Carlson, S. J., & L. R. Leighton. 2001. Incorporating stratigraphic data in the phylogenetic analysis of the Rhynchonelliformea. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Procedings of the Millennium Brachiopod Congress, 2000. The Systematics Association Special Volume Series 63. Taylor and Francis. London. p. 248–258.

Carpenter, S. J., & K. C. Lohmann. 1995. $\delta^{18}O$ and $\delta^{13}C$ values of modern brachiopod shells. Geochimica et Cosmochimica Acta 59:3749–3764.

Carter, J. L. 1974. New genera of spiriferid and brachythyridid brachiopods. Journal of Paleontology 48:674–696, 4 fig., 4 pl.

Carter, J. L. 2006. Spiriferoidea, Packelmanelloidea. *In* R. L. Kaesler, Treatise on Invertebrate Paleontology. Part H, Brachiopoda, revised, vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1769–1824.

Carter, J. L., & R. Gourvennec. 2006. Martinioidea, Reticularoidoidea. *In* R. L. Kaesler, Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado, and Lawrence, Kansas. p. 1747–1768, 1848–1870.

Carter, J. L., J. G. Johnson, Rémy Gourvennec, & Hou Hong-fei. 1994. A revised classification of the spiriferid brachiopods. Annals of Carnegie Museum 63:327–374.

Carter, J. L., J. G. Johnson, Rémy Gourvennec, & Hou Hong-fei. 2006. Spiriferida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 5. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1689–1887.

Carter, J. L., & V. I. Poletaev. 1998. Atokan (late Bashkirian or early Moscovian) brachiopods from the Hare Fiord Formation of Ellesmere Island, Canadian Arctic Archipelago. Annals of Carnegie Museum 67(2):105–180.

Caster, K. E. 1939. A Devonian fauna from Colombia. Bulletin of American Paleontology 24:1–218, pl. 1–14.

Castresana, J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Molecular Biology and Evolution 17:540–552.

Cavalier-Smith, Tom. 1998. A revised six-kingdom system of life. Biological Reviews 73:203–266.

Chapman, B. E., & J. R. Richardson. 1981. Recent species of *Neothyris* (Brachiopoda: Terebratellinae). New Zealand Journal of Zoology 8:157–161, 2 fig.

Chapman, F. 1911. On a trilobite fauna of Upper Cambrian age (Olenus Series) in N.E. Gippsland, Victoria. New or little known Victoria fossils in the National Museum, Part 12. Proceedings of the Royal Society of Victoria 23:305–323, pl. 59–61.

Chen Jun-Yuan, Hou Xianguang, & B. D. Erdtmann. 1989. New soft-bodied fossil fauna near the base of the Cambrian System at Chengjiang, Eastern Yunnan, China. *In* Chinese Academy of Sciences, Developments in Geoscience. Science Press. Beijing. p. 265–278.

Chen Jun-Yuan, Huang Di-Ying, & Chuang Shou-Hwa. 2007. Reinterpretation of the Lower Cambrian brachiopod *Heliomedusa orienta* Sun & Hou, 1987a as a discinid. Journal of Paleontology 81:38–47.

Chen J. Y., & Zhou G. Q. 1997. Biology of the Chengjiang fauna. Bulletin of the National Musem of Natural Science 5:1–93.

Chen X.-q., & Yao Z.-g. 1999. Early Devonian (late Emsian) brachiopods from Zhongping, Xiangzhou, central Guangxi, China. Senckenbergiana lethaea 79(1):223–265, 13 fig., 12 pl., 1 table.

Chen Yuan-ren. 1979. [The fossil brachiopods from the Tudiling Member of the Early Devonian (Bailiuping Formation) in the Longmenshan area, northwestern Sichuan, and their stratigraphic significance]. Journal of the Chengdu College of Geology 1978:1–49, 11 pl.
In Chinese, with English abstract.

Chen Yuan-ren. 1988. The succession of *Orientospirifer-Neoathyrisina* community from the early Lower Devonian of Longmenshan area Sichuan. Journal of Chengdu College of Geology 15(1):36–49.
In Chinese, with English abstract.

Chen Zhong-qiang, & N. W. Archbold. 2002. New chonostrophiid brachiopods from the Famennian (Late Devonian) of the Santanghu Basin, Xinjiang, Northwest China. Journal of Paleontology 76(2):229–238.

Chen Zhong-qiang, and Shi G. R. 1999. *Chuiella* gen. nov. (Brachiopoda) and palaeoecology from the Lower Carboniferous of the Kunlun Mountains, NW China. Alcheringa 23:259–275.

Chen Zhong-qiang, & Shi G. R. 2000. A tribe of dictyoclostid brachiopods from the Lower Permian of the Tarim Basin, northwest China. Palaeontology 43:325–342.

Chen Zhong-qiang, & Shi G. R. 2003. Early Carboniferous brachiopod faunas and their biogeographical affinities from the western Kunlun Mountains, North-west China. Palaeontographica (Abt. A) 268:103–187.

Chen Zhong-Qiang, Shi G. R., & Kaiho Kunio. 2002. A new genus of rhynchonellid brachiopod from the Lower Triassic of South China and implications for timing the recovery of Brachiopoda after the end-Permian mass extinction. Palaeontology 45(1):149–164, pl. 1.

Chen Zhong-qiang, Shi G. R., Shen Shu-zhong, & N. W. Archbold. 2000. *Tethyochonetes* gen. nov. (Chonetida, Brachiopoda) from the Lopingian (Late Permian) of China. Proceedings of the Royal Society of Victoria 112(1):1–15.

Chen Zhong-qiang, Shi G. R., & Zhan Li-pei. 2003. Early Carboniferous athyridid brachiopods from the Qaidam Basin, northwest China. Journal of Paleontology 77:844–862.

Chernyshev, T. N. 1902. Die obercarbonischen Brachiopoden des Ural und des Timan. Comité Géologique, Mémoires 16(2):1–749, 63 pl.

Chu S. 1933. Corals and Brachiopoda of the Kinling Limestone. Monograph of the National Research Institute of Geology (series A) 2:1–73.

Chuang S. H. 1974. Observations on the ciliary feeeding mechanism of the brachiopod *Crania anomala*. Journal of Zoology, London 173:441–449.

Chuang S. H. 1977. Larval development in *Discinisca* (inarticulate brachiopod). American Zoologist 17:39–53.

Chuang S. H. 1990. Brachiopoda. *In* K. G. Adiyodi & R. G. Adiyodi, eds., Reproductive biology of invertebrates IV (B): Fertilization, development and parental care. Oxford & IBH Publishing. New Delhi. p. 211–254.

Chuang S. H. 1994. Observations on the reproduction and development of *Liothyrella neozelanica* Thomson 1918 (Terebratulacea, Articulata, Brachiopoda). Journal of the Royal Society of New Zealand 24:209–218.

Chuang S. H. 1996. The embryonic, larval and early postlarval development of the terebratellid brachiopod *Calloria inconspicua* (Sowerby). Journal of the Royal Society of New Zealand 26:119–137.

Cisterna, G. A., & P. E. Isaacson. 2003. A new Carboniferous brachiopod genus from South America. Alcheringa 27:63–73.

Clark, T. H. 1935. A new Ordovician graptolite locality in Utah. Journal of Paleontology 9:239–246, pl. 24.

Clarke, M. J. 1970. New Permian strophalosiid genus from eastern Australia. Journal of Paleontology 44:986–987.

Clarke, M. J. 1990. Late Palaeozoic (Tamarian: Late Carboniferous–Early Permian) cold-water brachiopods from Tasmania. Alcheringa 14(1):53–76, 8 fig.

Clarke, M. J. 1992. A new notospiriferine genus (Spiriferida: Brachiopoda) from the Permian of Tasmania. Papers and Proceedings of the Royal Society of Tasmania 126:73–76, 1 pl.

Clarkson, E. N. K. 1979. Invertebrate Paleontology and Evolution. George Allen & Unwin. London, Boston, & Sydney. 323 p.

Clegg, H. 1993. Biomolecules in Recent and fossil articulate brachiopods. Unpublished PhD thesis, University of Newcastle. Newcastle upon Tyne. 246 p.

Cloud, P. E., Jr. 1942. Terebratuloid Brachiopoda of the Silurian and Devonian. Geological Society of America, Special Papers 38:1–182, pl. 1–26.

Cobabe, E. A., & A. J. Ptak. 1999. Comparison of in situ mineral-associated lipid compositions in modern invertebrate skeletons: Preliminary evidence of dietary and environmental influence. Paleobiology 25(2):201–211.

Cocks, L. R. M. 1968. Some strophomenacean brachiopods from the British Lower Silurian. Bulletin of the British Museum (Natural History), Geology 15:285–324, pl. 1–14.

Cocks, L. R. M. 1970. Silurian brachiopods of the superfamily Plectambonitacea. Bulletin of the British Museum (Natural History), Geology 19:139–203, pl. 1–17.

Cocks, L. R. M. 2005. Strophomenate brachiopods from the Late Ordovician Boda Limestone of Sweden: Their systematics and implications for palaeogeography. Journal of Systematic Palaeontology 3:243–282, pl. 1–12.

Cocks, L. R. M., & R. A. Fortey. 2002. The palaeogeographical significance of the latest Ordovician fauna from the Panghsa-Pye Formation of Burma. Special Papers in Palaeontology 67:57–76.

Cocks, L. R. M., & Rong Jia-yu. 1989. Classification and review of the brachiopod superfamily Plectambonitacea. British Museum (Natural History), Bulletin (Geology) 45:77–163, 24 pl.

Cocks, L. R. M., & Rong Jia-yu. 2000. Order Strophomenida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 216–348.

Cocks, L. R. M., & Zhan Ren-bin. 1998. Caradoc brachiopods from the Shan States, Burma (Myanmar). Bulletin of the Natural History Museum, London (Geology) 54:109–130, 5 pl.

Cohen, B. L. 1992. Utility of molecular phylogenetic methods: A critique of immuno-taxonomy. Lethaia 24:441–442.

Cohen, B. L. 1994. Immuno-taxonomy and the reconstruction of brachiopod phylogeny. Palaeontology 37:907–911.

Cohen, B. L. 2000. Monophyly of brachiopods and phoronids: Reconciliation of molecular evidence with Linnaean classification (the subphylum Phoroniformea nov.). Proceedings of the Royal Society, London (series B) 267:225–231.

Cohen, B. L. 2001a. Brachiopod molecular phylogeny advances. *In* C. H. C. Brunton, L. R. M. Cocks, & S. Long, eds., Brachiopods Past and Present. Proceedings of the Millennium Brachiopod Congress, 2000. The Systematics Association Special Volume Series 63. Taylor & Francis. London. p. 121–128.

Cohen, B. L. 2001b. Genetics and molecular systematics of brachiopods. *In* S. J. Carlson & M. R. Sandy, eds., Brachiopods Ancient and Modern. A Tribute to G. Arthur Cooper, vol. 7. The Paleontological Society. Pittsburgh. p. 53–67.

Cohen, B. L., Peter Balfe, Moyra Cohen, & G. B. Curry. 1991. Genetic divergence within and between populations of the North Atlantic morphospecies *Terebratulina retusa* and *T. septentrionalis*. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5-9 February, 1990. Balkema. Rotterdam. p. 109–115, 3 fig.

Cohen, B. L., Peter Balfe, Moyra Cohen, & G. B. Curry. 1993. Molecular and morphometric variation in European populations of the articulate brachiopod *Terebratulina retusa*. Marine Biology 115:105–111, 2 fig.

Cohen, B. L., & A. B. Gawthrop. 1996. Brachiopod molecular phylogeny. *In* P. Copper & J. Jin, eds., Brachiopods: Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario. 1995. Balkema. Rotterdam. p. 73–80.

Cohen, B. L., & A. B. Gawthrop. 1997. The brachiopod genome. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 189–211.

Cohen, B. L., A. B. Gawthrop, & Tom Cavalier-Smith. 1998. Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. Philosophical Transactions of the Royal Society (series B) 353:2039–2061.

Cohen, B. L., L. E. Holmer, & Carsten Lüter. 2003. The brachiopod fold: A neglected body plan hypothesis. Palaeontology 46:59–65.

Cohen, B. L., S. L. Long, & Michiko Saito. 2007. Living craniids: Preliminary molecular evidence of their inter-relationships. *In* D. A. T. Harper, S. L. Long, & C. Nielsen, eds., Proceedings of the 5th International Brachiopod Congress, Copenhagen, July 4–8, 2005. Blackwell. London. Fossils and Strata 54.

Cohen, B. L., Susan Stark, A. B. Gawthrop, M. E. Burke, & C. W. Thayer. 1998. Comparison of articulate brachiopod nuclear and mitochondrial gene trees leads to a clade-based redefinition of protostomes (Protostomozoa) and deuterostomes (Deuterostomozoa). Proceedings of the Royal Society, London (series B) 265:475–482.

Cohen, B. L., & Agata Weydmann. 2005. Molecular evidence that phoronids are a subtaxon of brachiopods (Brachiopoda: Phoronata) and that genetic divergence of metazoan phyla began long before the Early Cambrian. Organisms, Diversity & Evolution 5(4):253–273.

Coleman, P. J. 1957. Permian Productacea of Western Australia. Bulletin of the Bureau of Mineral Resources, Geology & Geophysics 40:189 p.

Collins, M., G. Muyzer, G. B. Curry, P. Sandberg, & P. Westbroek. 1991. Macromolecules in brachiopod shells—Characterization and diagenesis. Lethaia 24(4):387–397.

Compston, W. 1960. The carbon isotopic compositions of certain marine invertebrates and coals from the Australian Permian. Geochimica et Cosmochimica Acta 18:1–22.

Comte, Pierre. 1938. Brachiopodes dévoniens des gisements de Ferroñes (Asturies) et de Sabero (León). Annales de Paléontologie 27:41–88, pl. 5–8.

Conklin, E. G. 1902. The embryology of a brachiopod, *Terebratulina septentrionalis* Couthouy. Proceedings of the American Philosophical Society 168:41–76.

Conrad, T. A. 1839. Second annual report on the paleontological department of the survey. New York Geological Survey, Annual Report 3:57–66.

Conrad, T. A. 1841. Fifth annual report on the paleontology of the state of New York. New York Geological Survey Annual Report 5:25–57, 1 pl.

Conway Morris, Simon. 1993. The fossil record and the early evolution of the Metazoa. Nature 361:219–225.

Conway Morris, Simon. 1995. Nailing the lophophorates. Nature 375:365–366.

Conway Morris, Simon. 1998. The Crucible of Creation. Oxford University Press. Oxford. 242 p.

Conway Morris, Simon, & Chen Menge. 1990. Tommotiids from the Lower Cambrian of South China. Journal of Paleontology 64(1):169–184.

Conway Morris, Simon, B. L. Cohen, A. B. Gawthrop, T. Cavalier-Smith, & B. Winnepenninckx. 1996. Lophophorate phylogeny. Science 272:282.

Conway Morris, Simon, & J. S. Peel. 1990. Articulated halkieriids from the Lower Cambrian of north Greenland. Nature 345:802–805.

Conway Morris, Simon, & J. S. Peel. 1995. Articulated halkeriids from the Lower Cambrian of North Greenland and their role in early protostome evolution. Philosophical Transactions of the Royal Society of London (series B) 347:305–358.

Conway Morris, Simon, & R. A. Robison. 1988. More soft-bodied animals and algae from the Middle Cambrian of Utah and British Columbia. Paleontological Contributions, University of Kansas, Papers 122:1–48.

Cooper, G. A. 1934. New brachiopods. Reports on the collections obtained by the first Johnson-Smithsonian deep-sea expedition to the Puerto Rican Deep. Smithsonian Miscellaneous Collections 91(10):5 p., 2 pl.

Cooper, G. A. 1936. New Cambrian brachiopods from Alaska. Journal of Paleontology 10:210–214, pl. 26.

Cooper, G. A. 1942. New genera of North American brachiopods. Washington Academy of Sciences, Journal 32(8):228–235.

Cooper, G. A. 1954a. Brachiopoda occurring in the Gulf of Mexico. Fishery Bulletin of the Fish and Wildlife Service 55:363–365.

Cooper, G. A. 1954b. Recent Brachiopods. Bikini and nearby atolls, Marshall Islands. Geological Survey Professional Paper 260-G:315–318, 2 pl.

Cooper, G. A. 1956a. Chazyan and related brachiopods. Smithsonian Miscellaneous collections 127:1–1024.

Cooper, G. A. 1956b. New Pennsylvanian brachiopods. Journal of Paleontology 30(3):521–530.

Cooper, G. A. 1957. Tertiary and Pleistocene brachiopods of Okinawa, Ryukyu Islands. United States Geological Survey Professional Paper 314-A:20 p., 5 pl.

Cooper, G. A. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. Smithsonian Miscellaneous Collections 139(5):1–90, pl. 1–22.

Cooper, G. A. 1964. Brachiopods from Eniwetok and Bikini drill holes. Bikini and nearby atolls, Marshall Islands. United States Geological Survey Professional Paper 260-FF:1117–1120.

Cooper, G. A. 1972. Homeomorphy in Recent deep-sea brachiopods. Smithsonian Contributions to Paleobiology 11:25 p., 5 fig., 4 pl.

Cooper, G. A. 1973a. Brachiopods (Recent). Memoirs of the Hourglass Cruises 3(3):17 p., 6 fig., 1 pl.

Cooper, G. A. 1973b. New Brachiopoda from the Indian Ocean. Smithsonian Contributions to Paleobiology 16:43 p., 1 fig., 8 pl.

Cooper, G. A. 1973c. Fossil and Recent Cancellothyridacea (Brachiopoda). Science Reports of the Tohoku University, Sendai, Japan, Second Series (Geology), Special Volume 6 (Hatai Memorial Volume):371–390, 2 fig., 5 pl.

Cooper, G. A. 1973d. *Vema*'s Brachiopoda (Recent). Smithsonian Contributions to Paleobiology 17:51 p., 5 fig., 9 pl.

Cooper, G. A. 1975. Brachiopods from West African waters with examples of collateral evolution. Journal of Paleontology 49(5):911–927, 7 fig., 4 pl.

Cooper, G. A. 1977. Brachiopods from the Caribbean Sea and adjacent waters. Studies in Tropical Oceanography no. 14. Rosenstiel School of Marine and Atmospheric Science, University of Miami. Miami. 212 p., 8 fig., 35 pl.

Cooper, G. A. 1979. Tertiary and Cretaceous brachiopods from Cuba and the Caribbean. Smithsonian Contributions to Paleobiology 37:1–45, 2 pl.

Cooper, G. A. 1981a. Brachiopoda from the southern Indian Ocean (Recent). Smithsonian Contributions to Paleobiology 43:93 p., 30 fig., 14 pl.

Cooper, G. A. 1981b. Brachiopoda from the Gulf of Gascogne, France (Recent). Smithsonian Contributions to Paleobiology 44:35 p., 5 fig., 3 pl.

Cooper, G. A. 1982. New brachiopods from the Southern Hemisphere and *Cryptopora* from Oregon (Recent). Smithsonian Contributions to Paleobiology 41:43 p., 4 fig., 7 pl.

Cooper, G. A. 1983. The Terebratulacea (Brachiopoda), Triassic to Recent: A study of the brachidia (loops). Smithsonian Contributions to Paleobiology 50:445 p., 17 fig., 77 pl.

Cooper, G. A., & P. J. Doherty. 1993. *Calloria variegata*, a new Recent species of brachiopod (Articulata: Terebratulida) from northern New Zealand. Journal of the Royal Society of New Zealand 23(3):271–281, 7 fig.

Cooper, G. A., & R. E. Grant. 1969. New Permian brachiopods from west Texas I. Smithsonian Contributions to Paleobiology 1:1–20, 5 pl.

Cooper, G. A., & R. E. Grant. 1974. Permian brachiopods of west Texas, II. Smithsonian Contributions to Paleobiology 15:233–793, fig. 40, pl. 24–191.

Cooper, G. A., & R. E. Grant. 1975. Permian brachiopods of west Texas, III. Smithsonian Contributions to Paleobiology 19:795–1298 (part 1, text); p. 1299–1921, pl. 192–502 (part 2, plates).

Cooper, G. A., & R. E. Grant. 1976a. Permian brachiopods of west Texas, IV. Smithsonian Contributions to Paleobiology 21:1923–2607, pl. 503–662.

Cooper, G. A., & R. E. Grant. 1976b. Permian brachiopods of west Texas, V. Smithsonian Contributions to Paleobiology 24:2609–3159, pl. 663–780.

Cooper, G. A., & D. E. Lee. 1993. *Calloria*, a replacement name for the Recent brachiopod genus *Waltonia* from New Zealand. Journal of the Royal Society of New Zealand 23(3):257–270, 3 fig.

Cooper, G. A., & A. Williams. 1952. Significance of the stratigraphic distribution of brachiopods. Journal of Paleontology 26(3):326–337.

Cooper, R. A., 2004. Measures of Diversity. *In* B. D. Webby, F. Paris, M. L. Droser, and I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 52–57.

Coplen, T. B. 1995. New manuscript guidelines for the reporting of stable hydrogen, carbon and oxygen isotope-ratio data. Geothermics 24:707–712.

Copley, R. R., P. Aloy, R. B. Russell, & M. J. Telford. 2004. Systematic searches for molecular synapomorphies in model metazoan genomes give some support for Ecdysozoa after accounting for the idiosyncrasies of *Caenorhabditis elegans.* Evolution and Development 6:164–169.

Copper, Paul. 2002. Atrypida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1377–1474.

Copper, Paul, & Rémy Gourvennec. 1996. Evolution of the spire-bearing brachiopods (Ordovician–Jurassic). *In* Paul Copper & J. Jin, eds., Brachiopods: Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2–5 September 1995. A. A. Balkema. Rotterdam. p. 81–88.

Costa, O. G. 1852. Class V, Brachiopodi. Fauna del Regno di Napoli 10:1–60, 9 pl.

Couthouy, P. 1838. Description of new species of Mollusca and shells, and remarks on several polypi, found in Massachusetts Bay. Boston Journal of Natural History 2:53–111, 3 pl.

Cowie, J. W., and M. G. Bassett. 1989. International Union of Geological Sciences 1989 global stratigraphic chart with geochronometric and magnetostratigraphic calibration, Supplement. Episodes 12:1 sheet.

Craig, R. S. 1999. Late Cretaceous brachiopods of the Perth and Carnarvon basins, Western Australia. Records of the Western Australian Museum 19:413–442.

Crane, Agnes. 1886. On a brachiopod of the genus *Atretia* named in MS. by the late Dr. T. Davidson. Proceedings of the Scientific Meetings of the Zoological Society of London [April 6], p. 181–184.

Crickmay, C. H. 1952. Nomenclature of certain Devonian brachiopods. Published by the author. Calgary. 2 p.

Crosse, H. 1865. Description d'espèces nouvelles de la Guadeloupe. Journal de Conchyliologie 3:27–38, 1 pl.

Crosse, H., and P. Fischer, 1866. Journal de Conchyliologie 14:269.

Cuif, J. P., Y. Dauphin., J. Doucet., M. Salome., & J. Susini. 2003. XANES mapping of organic sulfate in three scleractinian coral skeletons. Geochimica Cosmochimica Acta 67: 75–83.

Curry, G. B. 1982. Ecology and population structure of the Recent brachiopod *Terebratulina* from Scotland. Palaeontology 25(2):227–246, 8 fig.

Curry, G. B. 1983. Ecology of the Recent deep-water rhynchonellid brachiopod *Cryptopora* from the Rockall Trough. Palaeogeography, Palaeoclimatology, Palaeoecology 44:93–102.

Curry, G. B. 1999. Original shell colouration in Late Pleistocene terebratulid brachiopods from New Zealand. Palaeontologica Electronica 2:32 p.

Curry, G. B., & R. J. Connor. 2007. Automated extraction of biodiversity data from taxonomic descriptions. *In* G. B. Curry and C. J. Humphries, eds., Biodiversity Databases: Techniques, Politics, and Applications. Systematics Association Special Volume 73. CRC Press. Boca Raton, Florida. p. 63–81.

Curry, G. B., R. Connor, & F. Simeoni. 2001. Stratigraphic distribution of brachiopods—A new method of storing and querying loosely structured biodiversity information. *In* C. H. C. Brunton, L. R. M. Cocks, and S. Long, eds., Brachiopods: Past and Present. Systematics Association Special Volume Series, vol. 63. Taylor and Francis. London and New York. p. 424–433.

Curry, G. B., & A. E. Fallick. 2002. Use of stable oxygen isotope determinations from brachiopods in palaeoenvironmental reconstruction. Palaeogeography, Palaeoclimatology, Palaeoecology 182:133–143.

Curry, G. B., R. Quinn, M. J. Collins, K. Endo, S. Ewing, G. Muyzer, & P. Westbroek. 1993. Molecules and morphology—The practical approach. Lethaia 26:5–6.

Curry, G. B., & Alwyn Williams. 1983. Epithelial moulds on the shells of the early Palaeozoic brachiopod *Lingulella*. Lethaia 16:111–118.

Cusack, Maggie. 1996. The mineral-associated proteins of *Lingula anatina.* Bulletin de l'Institut Océanographique 14:271–275.

Cusack, Maggie, G. B. Curry, H. Clegg, & G. Abbott. 1992. An intracrystalline chromoprotein from red brachiopod shells: Implications for the process of biomineralization. Comparative Biochemistry and Physiology 102B:93–95.

Cusack, Maggie, J. H. Laing, K. Brown, & D. Walton. 2000. Amino acids and proteins of calcitic brachiopod shells. Trends in Comparative Biochemistry and Physiology 6:47–56.

Cusack, M., D. Walton, & G. B. Curry. 1997. Shell Biochemistry. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 243–266.

Cusack, Maggie, & Alwyn Williams. 1996. Chemico-structural degradation of Carboniferous lingulid shells. Philosophical Transactions of the Royal Society of London (series B) 351(1335):33–49.

Cusack, Maggie, & A. Williams. 2001a. Evolutionary and diagenetic changes in the chemico-structure of the shell of the cranioid brachiopods. Palaeontology 44:875–903.

Cusack, Maggie, & A. Williams. 2001b. Chemico-structural differentiation of the organocalcitic shells of rhynchonellate brachiopods. *In* C. H. C. Brunton, L. R. M. Cocks, and S. L. Long, eds., Brachiopods Past and Present. The Systematics Association Special Volume Series 63. Taylor & Francis. London. p. 17–27.

Cusack, Maggie, Alwyn Williams, & James O. Buckman. 1999. Chemico-structural evolution of linguloid brachiopod shells. Palaeontology 42(5):799–840.

Dagys, A. S. 1972. Morfologiia i Systematika Mezozoiskikh Retsiodnykh Brakhiopod [Morphology and systematics of Mesozoic retzioid brachiopods]. Morfologicheskie i Filogeneticheskie Voprosy Paleontologii [Morphological and phylogenetic questions of Palaeontology]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy 112:94–105.

Dagys, A. S. 1974. Triasovye brakhiopody (Morfologiia, sistema, filogeniia, stratigraficheskoe znachenie i biogeografiia) [Triassic brachiopods (Morphology, classification, phylogeny, stratigraphical significance and biogeography)], vol. 214. Sibirskoe Otdelenie Izdatel'stvo "Nauka." Novosibirsk. p. 1–387, fig. 1–171, pl. 1–49.

Dall, W. H. 1870. A revision of the Terebratulidae and Lingulidae, with remarks on and descriptions of some Recent forms. American Journal of Conchology 6(2):88–168, pl. 6–8.

Dall, W. H. 1871. Report on the Brachiopoda obtained by the United States Coast Survey Expedition, in charge of L.F. de Pourtalès, with a revision of the Craniidae and Discinidae. Bulletin of the Museum of Comparative Zoology, Harvard University 3(1):1–45, 2 pl.

Dall, W. H. 1895. Report on Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian Islands, with illustrations of hitherto unfigured species from northwest America. Scientific results of explorations by the U.S. Fish Commission Steamer *Albatross*. Proceedings of the United States National Museum 17:675–733, 1 fig., pl. 23–32.

Dall, W. H. 1900. Some names which must be discarded. Nautilus 14:44–45.

Dall, W. H. 1903. Contributions to the Tertiary fauna of Florida. Wagner Free Institute of Science of Philadelphia, Bulletin 3(6):1219–1620, pl. 48–60.

Dall, W. H. 1908. The Mollusca and the Brachiopoda. *In* Reports on the dredging operations off the west coast of America to the Galapagos. Harvard University, Museum of Comparative Zoology, Bulletin 43:205–487, 22 pl.

Dall, W. H. 1910. Report on the Brachiopoda obtained from the Indian Ocean by the *Skylark* Expedition, 1905. The Transactions of the Linnean Society of London 13(3):439–441, 1 pl.

Dall, W. H. 1920. Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms. Proceedings of the United States National Museum 57(2314):261–377.

Dall, W. H., & H. A. Pilsbry. 1891. On some Recent Japanese Brachiopoda, with a description of a species believed to be new. Academy of Natural Sciences of Philadelphia, Proceedings (series 3) 43:165–171, pl. 4.

Dalman, J. W. 1828. Upställning och Beskrifning af de i sverige funne Terebratuliter. Kongliga Svenska Vetenskaps-akademian Handlingar för År 1827:85–155, pl. 1–6.

Danchin, E. G. J., & P. Pontarotti. 2004. Towards the reconstruction of thebilaterian ancestral pre-MHC region. Trends in Genetics 20:587–591.

Datillo, B. F. 2004. A new angle on strophomenid paleoecology: Trace-fossil evidence of an escape response for the plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the Upper Ordovician Kope Formation (Edenian) of northern Kentucky. PALAIOS 19:332–348.

Dauphin, Y., J.-P. Cuif, J. Doucet, M. Salome., J. Susini, & C. T. Williams. 2003. *In situ* mapping of growth lines in the calcite prismatic layers of mollusc shells using X-ray absorbtion near-edge structure (XANES) spectroscopy at the sulphur K-edge. Marine Biology 142:299-304.

Dauphin, Y., J.-P. Cuif, M. Salome, & J. Susini. 2005. Speciation and distribution of sulfur in a mollusk shell as revealed by in situ maps using X-ray absorption near-edge structure (XANES) spectroscopy at the S *K*-edge. American Mineralogist 90:1748-1758.

Davidson, Thomas. 1850a. Sur quelques brachiopodes nouveaux ou peu connus. Société Géologique de France, Bulletin (series 2) 8:62–74, 1 pl.

Davidson, Thomas. 1850b. Notes on an examination of Lamarck's species of fossil Terebratulae. Annals and Magazine of Natural History (series 2) 5:433–449, 3 pl.

Davidson, Thomas. 1850c. On the internal structure of *Terebratula pectunculoides* Schl., *Terebratula pulchella* Nils., and *Terebratula deslongchampsi* Nob. Annals and Magazine of Natural History (series 2) 5:449–450, pl. 15.

Davidson, Thomas. 1850d. On the genus *Waltonia.* Annals and Magazine of Natural History (series 2) 5:474–476.

Davidson, Thomas. 1852a. A Monograph of the British Fossil Brachiopoda (Vol.1, Part 2: The Cretaceous Brachiopoda). Palaeontographical Society Monograph 6:1–54, pl. 1–5.

Davidson, Thomas. 1852b. Notes and descriptions of a few Brachiopoda; including a monograph of the French Liassic spirifers. Annals and Magazine of Natural History (series 2) 9:249–267, pl. 13–15.

Davidson, Thomas. 1852c. Descriptions of a few new Recent species of Brachiopoda. Zoological Society of London, Proceedings 20:75–83, 1 pl.

Davidson, Thomas. 1852d. Sketch of a classification of Recent Brachiopoda; based upon internal organization. Annals and Magazine of Natural History (series 2) 9:361–377.

Davidson, Thomas. 1853. British fossil Brachiopoda, vol. I. Introduction. Palaeontographical Society Monograph. London. 136 p., pl. 9.

Davidson, Thomas. 1859. British Fossil Brachiopoda, vol. 2. Permian and Carboniferous species, part 5, no. 2. Palaeontographical Society Monograph. London. p. 49–80, pl. 9–16.

Davidson, T. 1862. On some Carboniferous Brachiopoda, collected in India by A. Fleming, M.D., and W. Purdon, Esq., F.G.S. Geological Society of London Quarterly Journal 18:25–35.

Davidson, T. 1866. Notes on the Carboniferous Brachiopoda collected by Captain Godwin-Austen in the Valley of Kashmir. The Quarterly Journal of the Geological Society of London 22:39–45.

Davidson, Thomas. 1878. A monograph of the British fossil Brachiopoda, vol. 4. Tertiary, Cretaceous, Jurassic, Permian, and Carboniferous supplements; and Devonian and Silurian Brachiopoda that occur in the Triassic Pebble Bed of Budleigh Salterton in Devonshire, part 3. Palaeontographical Society Monograph. London. p. 145–242, pl. 27–29.

Davidson, Thomas. 1880. Report on the Brachiopoda dredged by H.M.S. *Challenger* during the years 1873-76. *In* Report of the Scientific Results of the Voyage of H.M.S. *Challenger* during the years 1873–1876. Zoology 1:67 p., 4 pl.

Davidson, Thomas. 1881. On genera and species of spiral-bearing Brachiopoda from specimens developed by Rev. Norman Glass: With notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire. Geological Magazine (new series, decade II) 8(1):1–13.

Davidson, Thomas. 1882. A monograph of the British fossil Brachiopoda, Devonian and Silurian supplements. Palaeontographical Society, Monograph 5(1):1–134.

Davidson, Thomas. 1858–1863. A monograph of the British fossil Brachiopoda, Carboniferous, vol. 2, part 5. Palaeontographical Society Monograph. London. p. 1–280, pl. 1–55.

Davidson, Thomas. 1864. On the Recent and Tertiary species of the genus *Thecidium.* Geological Magazine 1:12–22, pl. 1–2.

Davidson, Thomas. 1886–1888. A monograph of Recent Brachiopoda. The Transactions of the Linnean Society of London. Second Series, Volume IV, Zoology. Part I, 1886:1–74, 13 pl., Part II, 1887:75–182, 12 pl., Part III, 1888:183–248, 5 pl.

Davidson, Thomas, & W. King. 1872. Remarks on the genera *Trimerella, Dinobolus* and *Monomerella.* Geological Magazine 9:442–445.

Davies, K. J., P. M. Dove, & J. J. De Yoreo. 2000. The role of Mg^{2+} as an impurity in calcite growth. Science 290:1134–1137.

Davis, D.R. 1978. A revision of the North American moths of the superfamily Eriocranioidea with the proposal of a new family, Acanthopteroctetidae (Lepidoptera). Smithsonian Contributions to Zoology 251: 1–131.

Dawson, E. W. 1971. A reference list and bibliography of the Recent Brachiopoda of New Zealand. Journal of the Royal Society of New Zealand 1(2):159–174.

Dawson, E. W. 1991. The systematics and biogeography of the living Brachiopoda of New Zealand. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February, 1990. Balkema. Rotterdam. p. 431–437.

Deshayes, G. P. 1839. Térébratules de la Nouvelle Zelande. Revue Zoologique, par la Société Cuvierienne 2:359.

Deshayes, G. P. 1863. Catague des Mollusques de l'île de la Réunion (Bourbon). Paris. 14 pl.

De Strezelecki, P. E. 1845. Physical description of New South Wales and Van Diemans' Land. Longman, Brown & Co. London. 462 p, 19 pl.

Dickins, M. J. 1996. Problems of late Palaeozoic glaciation in Australia and subsequent climate in the Permian. Palaeogeography, Palaeoclimatology, Palaeoecology 125:185–197.

Dickins, M. J. 2001. Tethys and the relationship of southeastern Asia and Gondwanaland in the Permian. *In* R. H. Weiss, ed., Contributions to Geology and Paleontology of Gondwana—In honour of Helmut Wopfner. Geologisches Institut, Universität zu Köln. Koln. p. 127–135.

Diener, Carl. 1915. The Anthracolithic faunas of Kashmir, Kanaur and Spiti. Geological Survey of India, Memoirs, Palaeontologia Indica 5(2):1–135, 11 pl.

Di Geronimo, I., R. La Perna, A. Rosso, R. Sanfilippo, & E. Taddei Ruggieri. 2001. Associazioni bentoniche da sedimenti di grotto carsiche in Sicilia. Atti del 1° Seminario di Studi sul il Carsismo negli Iblei e nell'area sud Mediterranea, Ragusa, 9–11 aprile, 1999. Speleologia Iblea 8:97–102, 1 fig., 1 pl.

Dillwyn, L. W. 1817. A Descriptive Catalogue of Recent Shells, arranged according to the Linnean Method with Particular Attention to the Synonymy, 2 vol. London. 1092 p.
Brachiopods, p. 285–298.

Doherty, P. J. 1979. A demographic study of a subtidal population of the New Zealand articulate brachiopod *Terebratella inconspicua*. Marine Biology 52:331–342, 12 fig.

Douvillé, Henri. 1879. Note sur quelques genres de brachiopodes (Terebratulidae et Waldheimiidae).

Société géologique de France, Bulletin (series 3) 7:251–277, fig. 1–19.

Dubar, G. 1931. Brachiopodes liasiques de Catalogne et des régions voisines. Butlletí de la Institució Catalana de Historia Natural 31(4):103–180, pl. 1–5.

Dulai, A. 2001. Diversification of Mediterranean Early Jurassic brachiopods after the end-Triassic mass extinction—New results from Hungary. *In* C. H. C. Brunton, L. R. M. Cocks, & S. Long, eds., Brachiopods Past and Present. The Systematics Association Special Volume Series 63. Taylor & Francis. London. p. 411–423.

Eernisse, D. J., J. S. Albert, & F. E. Anderson. 1992. Annelida and Arthropoda are not sister taxa: A phylogenetic analysis of spiralian metazoan morphology. Systematic Biology 41:305–330.

Egerquist, Eva. 2003. New brachiopods from the Lower–Middle Ordovician (Billingen-Volkhov stages) of the East Baltic. Acta Palaeontologica Polonica 48:31–38.

von Eichwald, C. E. 1829. Zoologia Specialis, quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vilnensi habendarum, vol. 1. Josephi Zawadzki. Vilnae. 314 p., 5 pl.

Elderfield, H., & G. Ganssen. 2000. Past temperature and δ^{18}O of surface ocean waters inferred from foraminiferal Mg/Ca ratios. Nature 405:442–445.

Elliott, G. F. 1948. Palingenesis in *Thecidea* (Brachiopoda). Annals and Magazine of Natural History (series 12) 1:1–30.

Elliott, G. F. 1951. On the geographical distribution of terebratelloid brachiopods. Annals and Magazine of Natural History (series 12) 4(no. 40, article 33):305–334, 5 fig.

Elliott, G. F. 1953. The classification of the thecidean brachiopods. Annals and Magazine of Natural History (series 12) 6:693–701, pl. 18.

Elliott, G. F. 1954. New Brachiopoda from the Eocene of England, France and Africa. Annals and Magazine of Natural History (series 12) 7:721–728, pl. 15.

Elliott, G. F. 1956. On Tertiary Transarctic brachiopod migration. Annals and Magazine of Natural History (series 12) 9(100):280–286.

Elliott, G. F. 1958. Classification of thecidean brachiopods. Journal of Paleontology 32:373.

Elliott, G. F. 1959. Six new genera of Mesozoic Brachiopoda. Geological Magazine 96:146–148.

Elliott, G. F. 1965. Order Uncertain—Thecideidina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 2. The Geological Society of America and University of Kansas Press. New York and Lawrence, Kansas. p. 857–862.

Elliott, G. F., & K. Hatai. 1965. Family Dallinidae and Family Terebratellidae. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 2. Geological Society of America & University of Kansas Press. New York & Lawrence, Kansas. p. 835–845, 847–855.

Emig, C. C. 1976. Le lophophore-structure significative des Lophophorates (Brachiopoda, Bryozoa, Phoronida). Zoologica Scripta 5:133–137.

Emig, C. C. 1977. Un nouvel embranchement: Les Lophophorates. Bulletin de la Société Zoologique de France 102:341–344.

Emig, C. C. 1981. Observations sur l'écologie de *Lingula reevii* Davidson (Brachiopoda: Inarticulata). Journal of Experimental Marine Biology and Ecology 52(1):47–61.

Emig, C. C. 1984. On the origin of the Lophophorata. Zeitschrift für Zoologische Systematik und Evolutionforschung 22:91–94.

Emig, C. C. 1985. Distribution et synécologie des fonds à *Gryphus vitreus* (Brachiopoda) en Corse. Marine Biology 90:139–146, 2 fig.

Emig, C. C. 1987. Offshore brachiopods investigated by submersible. Journal of Experimental Marine Biology and Ecology 108:261–273, 9 fig.

Emig, C. C. 1988. Les Brachiopodes actuels sont-ils des indicateurs (paléo) bathymétriques? Géologie Méditerranéenne 15(1):65–71, 3 fig.

Emig, C. C. 1990. Examples of post-mortality alteration in Recent brachipod shells and (paleo) ecological consequences. Marine Biology 104:233–238.

Emig, C. C. 1992. Functional disposition of the lophophore in living Brachiopoda. Lethaia 25:291–302.

Emig, C. C. 1997a. Les Lophophorates constituent-ils un embranchement? Bulletin de la Société Zoologique de France 122:279–288.

Emig, C. C. 1997b. Ecology of inarticulated brachiopods. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 473–495.

Endo, Kazuyoshi. 2001. The phylogenetic position of brachiopods inferred from mitochondrial gene orders. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Proceedings of the Millennium Brachiopod Congress, 2000. The Systematics Association Special Volume Series 63. Taylor and Francis. London. p. 142–149.

Endo, Kazuyoshi, & G. B. Curry. 1991. Molecular and morphological taxonomy of a Recent brachiopod genus *Terebratulina*. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February, 1990. Balkema. Rotterdam. p. 101–108, 4 fig.

Endo, Y., Y. Noguchi, R. Ueshima, & H. J. Jacobs. 2005. Novel repetitive structures in the mitochondrial genome of the brachiopod *Lingula anatina.* Journal of Molecular Evolution 61:36–53.

England, Jennifer K. 2005. Calcium carbonate biomineralisation in disparate systems—Common mechanisms? Unpublished PhD thesis. University of Glasgow. p. 157.

England, Jennifer K., Maggie Cusack, and M. Lee. 2007. Magnesium and sulfur in the calcite shells of two brachiopods. Lethaia 40:2–10.

Epstein, S., R. Buchsbaum, H. A. Lowenstam, & H. C. Urey. 1951. Carbonate-water isotopic temperature scale. Bulletin of the Geological Society of America 62:417–426.

Epstein, S., R. Buchsbaum, H. A. Lowenstam, & H. C. Urey. 1953. Revised carbonate-water isotopic temperature scale. Bulletin of the Geological Society of America 64:1315–1326.

Erber, A., D. Riemer, M. Bovenschulte, & K. Weber. 1998. Molecular phylogeny of metazoan intermediate filament proteins. Journal of Molecular Evolution 47:751–762.

Erez, J. 1978. Vital effect on stable isotope compositions seen in foraminifera and coral skeletons. Nature 273:199–202.

Erwin, D. H., S. A. Bowring, & Jin Yugan. 2002. End-Permian mass extinctions: A review. *In* C. Koeberl and K. G. MacLeod, eds., Catastrophic Events and Mass Extinctions: Impacts and Beyond. Geological Society of America Special Paper 356:363–383.

Etheridge, R., Jr. 1903. Descriptions of Carboniferous fossils from the Gascoyne District, Western Australia. Bulletin of the Geological Survey of Western Australia 10:1–41.

Eudes-Deslongchamps, Eugène. 1853. Notes sur quelques brachiopods nouveaux du Lias. Annuaire de l'Institut des Provinces (Caen) 1853:3–7.

Eudes-Deslongchamps, Eugène. 1855 [1854]. Notice sur un genre nouveau de brachiopodes. Avec la description de quelques espèces nouvelles de la Grande Oolithe et du Lias de Normandie. Annuaire de l'Institut des Provinces et des Congrès Scientifiques 1855:529–553, 1 pl.

Eudes-Deslongchamps, Eugène. 1884. Études critiques sur des brachiopodes nouveaux ou peu connus. Bullétin de la Société Linnéenne de Normandie (3)8:161-350.

Falini, G., S. Albeck, S. Weiner, & L. Addadi. 1996. Control of aragonite or calcite polymorphisms by mollusk shell macromolecules. Science 271:67–96.

Faujas de Saint-Fond, B. 1798. Histoire naturelle de la Montagne Saint-Pierre de Maestricht. Paris.

Faye, L., & M. J. Chrispeels. 1985. Characterization of N-linked oligosaccharides by affinoblotting with concanavalin A-peroxidase and treatment of the blots with glycosidases. Analytical Biochemistry 149:218–224.

Felsenstein, Joseph. 2004. Inferring Phylogenies. Sinauer Associates, Inc. Sunderland, Massachusetts. 664 p.

Fenton, C. L., & M. A. Fenton. 1924. The stratigraphy and fauna of the Hackberry stage of the Upper Devonian. The University of Michigan Museum of Paleontology, Contributions 1:1–260, 45 pl.

Field, K. G., G. J. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace, & R. A. Raff. 1988. Molecular phylogeny of the animal kingdom. Science (Washington, D.C.) 239:748–753.

Finlay, H. J. 1927. New specific names for austral Mollusca. New Zealand Institute, Transactions and Proceedings 57:488–533.

Fischer, Paul, & D.-P. Oehlert. 1890. Diagnoses de nouveaux brachiopodes. Journal de Conchyliologie (series 2) 38(1):70–74.

Fischer, P., & D.-P. Oehlert. 1891. Brachiopodes. Expéditions scientifiques du *Travailleur* et du *Talisman* pendant les années 1880, 1881, 1882, 1883. Masson. Paris. 139 p., 15 fig., 8 pl.

Fischer, P., & D.-P. Oehlert. 1892. Brachiopodes. Mission scientifique du Cap Horn (1882–1883), Bulletin de la Société d'Histoire Naturelle d'Autun 5:82 p., 7 fig., 5 pl.

Flammer, L. I. 1963. Embryology of the brachiopod *Terebratalia transversa.* Master of Science thesis. University of Washington. Seattle. p. 1–42.

Fonin, V. D., & T. N. Smirnova. 1967. A new group of problematic Early Cambrian organisms and some methods of preparing them. Paleontologicheskii Zhurnal 2:15–27.
In Russian.

Forbes, Edward. 1844. Report on the Mollusca and Radiata of the Aegean Sea, and on their distribution, considered as bearing on geology. Report of the British Association for the Advancement of Science, 1843, Palliobranchiata. London. p. 130–147.

Foster, M. W. 1969. Distribution of selected groups of marine invertebrates in waters South of 35°S Latitude. Brachiopoda. Folio 11, Antarctic Map Folio Series, American Geographical Society. p. 21–22, 1 pl.

Foster, M. W. 1974. Recent Antarctic and Subantarctic brachiopods. American Geophysical Union, Antarctic Research Series 21:189 p., 39 fig., 25 pl.

Foster, M. W. 1989. Brachiopods from the extreme South Pacific and adjacent waters. Journal of Paleontology 63(3):268–301, 17 fig.

Frakes, L. A., J. E. Francis, & J. I. Sykes. 1992. Climate Models of the Phanerozoic. Cambridge University Press. Cambridge. 274 p.

Frech, Fritz. 1901. I Theil, Lethaea palaeozoica, Band 2, Lieferung 3, Die Dyas. *In* C. F. von Roemer, Lethaea geognostica, oder Beschreibung und Abbildung der für die Gebirgs-Formationen bezeichnendsten Versteinerungen. E. Schweizerbart'sche Verlagshandlung (E. Nägelei). Stuttgart. p. 435–578.

Fredericks, G. 1928 [1927]. Materialy dlya klassifiatsii roda *Productus* Sow [Contribution to the classification of the genus *Productus* Sow]. Izvestiia Geologicheskogo Komiteta Leningrad 46(7):773–792.

Frederiks, G. N. 1911. Zametka o nekotorykh verkhnepaleozoiskikh okamenelostyakh iz okrectnostei gor. Krasnoufimska [Bemerkung über einige oberpalaeozoische Fossilien von Krasnoufimsk]. Prilozhenie k' protokolan Zastdanii Obshchestva Estestvoisnytatelei pri Imperatorskom Kazanskom' Universitete (Kazan) 42(269):1–12, 1 pl.

Frederiks, G. N. 1924a [1919]. Paleontologicheskye stiudy. 2. O Verkhne-Kamennougol'nykh spiriferdakh Urala [Paleontological studies. 2. On Upper Carboniferous spiriferids from Urals]. Geologicheskogo Komiteta, Izvestiya 38(3):295–324, 7 fig.

Frederiks, G. N. 1924b. Ussuriiskii verkhnii paleozoi. I. Brachiopoda [Upper Paleozoic of the Ussuriland, I: Brachiopoda]. Materialy po Geologii i Poleznym Iskopaemym Dal'nego Vostoka 28:1–53, 1 pl.

Frederiks, G. N. 1926. Tablitsa dlya opredeleniia rodov semeistva Spiriferidae King [Classification table of the genera of the family Spiriferidae King]. Akademia Nauk SSSR, Izvestiya [Academy of Sciences U.R.S.S., Bulletin] (series 6) 20(5/6):393–423.

Freeman, Gary. 1993a. Metamorphosis in the brachiopod *Terebratalia*—Evidence for a role of calcium-channel function and the dissociation of shell formation from settlement. Biological Bulletin 184(1):15–24.

Freeman, G. 1993b. Regional specification during embryogenesis in the articulate brachiopod *Terebratalia*. Developmental Biology 160:196–213.

Freeman, G. 1994. The endocrine pathway responsible for oocyte maturation in the inarticulate brachiopod *Glottidia*. Biological Bulletin 186:263–270.

Freeman, G. 1995. Regional specification during embryogenesis in the inarticulate brachiopod *Glottidia*. Developmental Biology 172:15–36.

Freeman, G. 1999. Regional specification during embryogenesis in the inarticulate brachiopod *Discinisca*. Developmental Biology 209:321–339.

Freeman, G. 2000. Regional specification during embryogenesis in the craniiform brachiopod *Crania anomala*. Developmental Biology 227:219–238.

Freeman, Gary. 2001. The developmental biology of brachiopods. *In* S. J. Carlson & M. R. Sandy, eds., Brachiopods Ancient and Modern: A Tribute to G. Arthur Cooper. The Paleontological Society Papers 7:69–88.

Freeman, G. 2003. Regional specification during embryogenesis in rhynchonelliform brachiopods. Developmental Biology 261:268–287.

Freeman, Gary, & J. W. Lundelius. 1999. Changes in the timing of mantle formation and larval life history traits in linguliform and craniiform brachiopods. Lethaia 32:197–217.

Freeman, Gary, & J. W. Lundelius. 2005. The transition from planktotrophy to lecithotrophy in larvae of Lower Paleozoic rhynchonelliform brachiopods. Lethaia 38:219–254.

Friedman, I., & J. R. O'Neil. 1977. Compilation of stable isotope fractionation factors of geochemical interest. *In* M. Fleisher, ed., Data of Geochemistry, Chapter KK, 6th ed. United States Geological Survey Professional Paper 440-K.

Friele, H. 1877. The development of the skeleton in the genus *Waldheimia*. Archiv for Mathematik og Naturvidenskab 2(4):380–386, 6 pl.

Friren, A. 1876. Mélanges Paléontologiques. Art. 1. *Orthoidea, Straparolus, Ammonites Aulacoceras*, et *Tisoa siphonalis* du Lias moyen. Société d'Histoire Naturelle de Metz, Bulletin (series 2) 2:1–22, pl. 1–2.

Gad, J. 1997. Eine neue Brachiopodengattung *Pseudoleptostrophia* aus dem Unterdevon des Rheinischen Schiefergebirges und erganzende morphologische Daten über die Typusart *Pseudoleptostrophia dahmeri*. Mainzer Geowissenschaftliche Mitteilungen 26:191–200.

Ganelin, V. G., & S. S. Lazarev. 1999. Revision of the Permian Thin-Ribbed Linoproductoids: 1. Linoproductoids of the "*Cancrinella*" *koninckiana* (Keyserling, 1846) group. Paleontological Journal 33 (3):243–253.
Translation from Paleontologicheskii Zhurnal 1999(3):30–40.

Ganelin, V. G., & S. S. Lazarev. 2000. Revision of the Permian thin-ribbed linoproductoids. Article 2. The "*Cancrinella*" *ogonerensis* Zavodowsky group, 1960. Paleontological Journal 34:40–46.
Translated from Paleontological Zhurnal 2000(1):38–44.

García-Alcalde, J. L. 1998. Braquiópodos rinconélidos del Lochkoviense (Devónico Inferior) de la Cordillera Cantábrica (Norte de España). Geobios 31:767–789.

García-Alcalde, J. L. 1999. Nuevo género de braquiópodos rinconélidos del Praguiense (Devónico Inferior) de la region Cántabro-Celtibérica (España). Revista Española de Paleontología 14:247–255.

García-Alcalde, Jenaro L. 2001. Paleobiogeographical relationships between North Gondwana and South Baltica: The *Ivanothyris havliceki* fauna (Cantabrian Zone, latest Emsian). Journal of the Czech Geological Society 46(3-4):121–130, 5 fig., 2 pl.

García-Alcalde, J. L. 2003. *Bimeristina binnekampi* n.g., n.sp., meristeloideo (braquiópodo) del Devónico Inferior (Praguiense) de España. Revista Española de Paleontología 18:103–112.

García-Alcalde, Jenaro L. 2004. Lower Devonian Delthyridoidea (Brachiopoda, Delthyridina) of the Cantabrian Mountains (N Spain). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre (supplement) 74:9–38, 15 fig., 4 pl.

García-Alcalde, Jenaro L. 2005. Upper Emsian Spinelloidea and Cyrtospiriferoidea (Brachiopoda, Spiriferidina) of the Cantabrian Mountains (N Spain). Geobios 38(1):69–97, 10 fig.

García Joral, Fernando, & Antonio Goy. 2004. Caracterización de *Choffatirhynchia* nov. gen. (Brachiopoda, Rhynchonellida) en el Toarciense (Jurásico) de la Cordillera Ibérica (España). Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica) 99(1–4):237–250.

Gaspard, Danièle. 1974. Aspects microstructuraux de la coquille de quelques térébratules biplissés au Crétacé. Bulletin de la Société Géologique de France 16:91–97.

Gaspard, Danièle. 1982. Microstructure de *Térébratulés biplissées* (Brachiopodes) du Cénomanien de la Sarthe (France). Affinités d'une des formes avec le genre *Sellithyris* Midd. Annales de Paléontologie, Invertébrés (Paris) 68(1):1–14, 3 pl.

Gaspard, Danièle. 1990. Diagenetic evolution of shell microstructure in the Terebratulida (Brachiopoda, Articulata) II. *In* J. G. Carter, ed., Skeletal biomineralization: Patterns, Processes and Evolutionary Trends, vol. 1. Van Nostrand Reinhold. New York. p. 53–56.

Gaspard, Danièle. 2003a. Some Cretaceous long-looped terebratulide brachiopods analysed in the light of the diversity observed in the ontogeny of Recent representatives. Bulletin Société géologique de France 174(3):261–269, 2 fig.

Gaspard, Danièle. 2003b. Recent brachiopods collected during the SEAMOUNT 1 Cruise off Portugal and the Ibero-Moroccan Gulf (northeastern Atlantic) in 1987. Geobios 36(3):285–304, 6 fig.

Gatinaud, G. 1949. Contributions à l'étude des Brachiopodes Spiriferidae. 1. Exposé d'une nouvelle méthode d'étude de la morphologie externe des Spiriferidae à sinus plissé: Muséum d'Histoire Naturelle, Bulletin (Series 2) 21(1):153–159; 21(2):300–307; 21(3):408–413; 21(4):487–492.

Gee, Henry. 1995. Lophophorates prove likewise variable. Nature 374:493.

GenBank. 2006. NIH genetic sequence database, annotated collection of all publicly available DNA sequences. Nucleic Acids Research (Jan 1) 34(Database issue):D16–20.

George, T. N. 1931. *Ambocoelia* Hall and certain similar British Spiriferidae. Geological Society of London, Quarterly Journal 87:30–61, 3 fig., pl. 3–5.

Georgescu, M.-D. 1991. A new Middle Jurassic brachiopod from the Bucegi Mts. (Eastern Carpathians, Romania). Geologica Carpathica 42(4):241–245, 1 pl.

Geyer, G. 1994. An enigmatic bilateral fossil from the Lower Cambrian of Morocco. Journal of Paleontology 68(4):710–716.

Geyer, Gerd, & Michal Mergl. 1997. Protorthacean brachiopods from the Middle Cambrian of Morocco. Journal of Paleontology 71:791–812.

Gillooly, J. F., A. P. Allen, G. B. West, & J. H. Brown. 2005. The rate of DNA evolution: Effects of body size and temperature on the molecular clock. Proceedings of the National Academy of Sciences 102:doi/10.1073/pnas.0407735101.

Giribet, Gonzalo, D. L. Distel, Martin Polz, Wolfgang Sterrer, & W. C. Wheeler. 2000. Triploblastic relationships with emphasis on the acoelomates, and the position of Gnathostomulida, Cycliophora, Platyhelminthes and Chaetognatha: A combined approach of 18S rDNA sequences and morphology. Systematic Biology 49:539–562.

Girty, G. H. 1903. The Carboniferous Formations and Faunas of Colorado. USGS Professional Papers 16:546 p.

Girty, G. H. 1909. The Guadalupian fauna. U.S. Geological Survey, Professional Papers 58:651 p., 31 pl.

Girty, G. H. 1938. Descriptions of a new genus and a new species of Carboniferous brachiopod. Journal of the Washington Academy of Sciences 28:278–284, fig. 1–5.

Gischler E., M. R. Sandy, & J. Peckmann. 2003. *Ibergirhynchia contraria* (F. A. Roemer, 1850), an Early Carboniferous seep-related rhynchonellide brachiopod from the Harz Mountains, Germany—A possible successor to *Dzieduszyckia*. Journal of Paleontology 77:293–303.

Glenner, H., A. J. Hansen, M. V. Sorensen, F. Ronquiat, J. P. Huelsenbeck, & E. Willerslev. 2004. Bayesian inference of the metazoan phylogeny: combined molecular and morphological approach. Current Biology 14:1644–1649.

Gmelin, J. F. 1790. Systema Naturae, editio decima tertia aucta. Reformata I. Ps. VI. Vermes. Lipsiae. p. 3021–4120.

Gonfiantini, R., W. Stichler, & K. Rozanski. 1995. Standards and intercomparison materials distributed by the International Atomic Energy Agency for stable isotope measurements, Reference and intercomparison materials for stable isotopes of light elements. International Atomic Energy Agency, TECDOC-825:13–29.

Gonzalez, L. A., & K. C. Lohmann. 1985. Carbon and oxygen isotopic composition of Holocene reefal carbonates. Geology 13:811–814.

Goodrich, E. S. 1945. The study of nephridia and genital ducts since 1895. Quarterly Journal of Microscopical Science 86:113–395.

Gorjansky, V. Iu. 1969. Bezamkovye brakhiopody kembriiskikh i ordovikskikh otlozhenii severo-zapada Russkoi platformy [Inarticulate brachiopods of the Cambrian and Ordovician of the northwest Russian Platform]. Materialy po Geologii i Poleznym Iskopaemym Severo-Zapada RSFSR 6:173 p., 21 pl. In Russian.

Gorjansky, V. Y., & L. Ye. Popov. 1985. Morfologiya, sistematicheskoe polozhenie i proiskhozhdenia bezzamkovykh brakhiopod s karbonatnoj rakovinoj [The morphology, systematic position, and origin of inarticulate brachiopods with carbonate shells]. Paleontologicheskii Zhurnal 1985:3–13.

Gorjansky, V. Y., & L. Ye. Popov. 1986. On the origin and systematic position of the calcareous-shelled inarticulate brachiopods. Lethaia 19:233–240.

Gosselet, J. 1887. Note sur quelques rhynchonelles du terrain Devonique supérieur. Société Géologique du Nord, Annales 14:188–221, 3 pl.

Gould, A. A. 1862. Descriptions of shells and molluscs from 1839–1862. *Ostia conchologia. Boston.* 256 p.

Gourvennec, Rémy. 2000. The evolution, radiation and biogeography of early spiriferid brachiopods. Records of the Western Australian Museum Supplement 58:335–347.

Grabau, A. W. 1931a. The Permian of Mongolia. American Museum of Natural History, Natural History of Central Asia 4:665 p., 35 pl.

Grabau, A. W. 1931b. Devonian Brachiopoda of China-I: Devonian Brachiopoda from Yunnan and other districts in South China. Paleontologia Sinica (series B) 3(3):1–545, 54 pl.

Grabau, A. W. 1932. The Brachiopoda, Part 3. Studies for students, I. Palaeontology. Science Quarterly of the National University of Peking 3(2):75–112.

Grabau, A. W., & W. H. Sherzer. 1910. The Monroe Formation of southern Michigan and adjoining regions. Michigan Geological and Biological Survey (Geology series 1) 2:1–248, 32 pl.

Grabau, A. W., & Tien Q. X. 1931. Fengninian (Lower Carboniferous) Brachiopoda of China. Geological Survey of China, Palaeontologica Sinica (series B) 3(3):421.

Gradstein, F., J. Ogg, & A. Smith. 2004. A Geologic Time Scale 2004. Cambridge University Press. Cambridge. 589 p.

Grahn, Y. G., & M. V. Caputo. 1992. Early Silurian glaciation in Brazil. Palaeogeography, Palaeoclimatology, Palaeoecology 99:9–15.

Grant, R. E. 1965. The brachiopod superfamily Stenoscismatacea. Smithsonian Miscellaneous Collections 148(20):1–192, 24 pl.

Grant, R. E. 1972. The lophophore and feeding mechanism of the Productidina (Brachiopoda). Journal of Paleontology 46:213–248.

Grant, R. E. 1976. Permian brachiopods from southern Thailand. Journal of Paleontology (The Paleontological Society Memoir 9) 50(supplement to 3):1–269.

Grant, R. E. 1980. The human face of the brachiopod. Journal of Paleontology 54(3):499–507.

Grant, R. E. 1993. Permian brachiopods from Khios Island, Greece. Paleontological Society Memoir 33:1–21.

Grant, R. R. 1983. *Argyrotheca arguta*, a new species of brachiopod from the Marshall Islands, western Pacific. Proceedings of the Biological Society of Washington 96(1):178–180, 1 fig.

Grant, R. R. 1987. Brachiopods of Enewetak Atoll. *In* D. M. Devaney, E. S. Reese, B. L. Burch, & P. Helfrich, eds., The Natural History of Enewetak Atoll, vol. 2. Biogeography and Systematics. Office of Scientific and Technical Information, U.S. Department of Energy. Oak Ridge, Tennessee. p. 77–84, 9 fig.

Graur, D., & W. Martin. 2004. Reading the entrails of chickens: Molecular timescales of evolution and the illusion of precision. Trends in Genetics 20:80–86.

Gray, J. E. 1840. Synopsis of the contents of the British Museum, 42nd edition. British Museum. London. 370 p.

Gretchishnikova, I. A. 1996. Novye Givetskie Spiriferidy (Brachiopoda) Zakavskazia [New Givetian Spiriferids (Brachiopoda) of Transcaucasus]. Paleontologicheskii Zhurnal 4:34–37, 2 fig., 1 pl.

Grobe, P. 1999. Zur Entwicklung und Ultrastruktur der Larvae von *Neocrania anomala* (Müller, 1776). Diplom-Thesis, University of Göttingen. Göttingen. 37 p.

Grobe, P., & C. Lüter. 1999. Reproductive cycles and larval morphology of three Recent species of *Argyrotheca* (Terebratellacea: Brachiopoda) from Mediterranean submarine caves. Marine Biology 134:595–600.

Grossman, E. L., Mii H.-S., & T. E. Yancey. 1993. Stable isotopes in Late Pennsylvanian brachiopods from the United States: Implications for Carboniferous paleoceanography. Geological Society of America Bulletin 105:1284–1296.

Grossman, E. L., C. Zhang, & T. E. Yancey. 1991. Stable-isotope stratigraphy of brachiopods from Pennsylvanian shales in Texas. Geological Society of America Bulletin 103:953–965.

Grunt, T. A. 1965. Nadsemeistvo Athyridasea [Superfamily Athyridacea]. *In* V. E. Ruzhencev & T. G. Sarycheva, eds., Razvitie i smena morskikh organizmov na rubezhe paleozoia i mesozoia [Evolution and change of marine organisms at the Paleozoic-Mesozoic boundary]. Akademiia Nauk SSSR, Trudy Paleontologicheskogo Instituta 108:237–253.

Grunt, T. A. 1977. Kamennougol'nye spiriferidy semeistva Martiniidae Sibiri i Arktiki [Carboniferous spiriferids of the family Martiniidae of Siberia and the Arctic]. *In* T. G. Sarycheva, ed., Brakhiopody verkhnego paleozoiia Sibiri i Arktiki [Brachiopods of the Upper Paleozoic of Siberia and Arctic], Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 162:63–71, fig. 12–15, pl. 11–12. In Russian.

Grunt, T. A. 1982. Mikrostructura rakoviny brakhiopod otriada Athyridida [Shell structure in brachiopods, order Athyridida]. Paleontologicheskii Zhurnal 4:21–35.

Grunt, T. A. 1984. Morfogenez, sistema, osnovnye napravleviia evoliutsii brakhiopod otriada Athyridida [Morphogenesis, classification and main evolutionary trends of brachiopods in the order Athyrididae]. *In* E. A. Ivanova & G. A. Afanas'eva, eds., Voprosy evolutsionnoi morfologii brakhiopod. Akademiia Nauk SSSR, Trudy Paleontologicheskogo Instituta 199:63– 80.

Grunt, T. A. 1986. Sistema brakhiopod otriada atiridida [Classification of brachiopods of the order Athyridida]. Akademiia Nauk SSSR, Trudy Paleontologicheskogo Instituta 215:200 p., 80 fig., 32 pl.

Grunt, T. A., & Grzegorz Racki. 1998. Late Frasnian Athyridida (Brachiopoda) from Poland and the Late Devonian biotic turnover. Acta Palaeontologica Polonica 43(2):361–378.

Gustus, R. M., & R. A. Cloney. 1972. Ultrastructural similarities between setae of brachiopods and polychaetes. Acta Zoologica 53:229–233.

Gutmann, W. F., K. Vogel, & H. Zorn. 1978. Brachiopods: Biomechanical interdependencies governing their origin and phylogeny. Science 199:890–893.

Haas, O. 1912. Die Fauna des mittleren Lias von Ballino in Südtirol, I: Brachiopoden, Lamellibrachiaten und Gastropoden. Beiträge zur Palaeontologie und Geologie Österreich-Ungarns und des Orients 25(4):223–285, pl. 19–20.

Halamski, A.T. 2004. *Deliella,* a new Devonian craniid brachiopod. Neus Jahrbuch für Geologie und Paläontologie Monatshefte 2004(3):181–192, 3 fig.

Halanych, K. M. 1995. The phylogenetic position of the pterobranch hemichordates based on 18S rDNA sequence data. Molecular Phylogenetics and Evolution 4:72–76.

Halanych, K. M., J. D. Bacheller, A. M. A. Aguinaldo, S. M. Liva, D. M. Hillis, & J. A. Lake. 1995. Evidence from 18S ribosomal DNA that the lophophorates are protostome animals. Science 267:1641–1643.

Hall, James. 1843. Survey of the Fourth Geological District. Natural History of New York, Geology, vol. 4. Carrol & Cook. Albany. ix + 525 p., pl. 1–19.

Hall, James. 1857. Descriptions of new species of Palaeozoic Fossils, from the Lower Helderberg, Oriskany Sandstone, Upper Helderberg, Hamilton and Chemung Groups. New York State Cabinet of Natural History 10th Annual Report, Part C. Albany. Appendix. p. 41–186.

Hall, James. 1867. Descriptions and figures of the fossil Brachiopoda of the Upper Helderberg, Hamilton, Portage and Chemung Groups. Palaeontology of New York 4(1):1–428, 63 pl.

Hall, James, & J. M. Clarke. 1892. An introduction to the study of the genera of Palaeozoic Brachiopoda. Natural History of New York, Palaeontology, vol.

8, part 1. New York Geological Survey, Charles van Benthuysen & Sons. Albany. 367 p., 20 pl.

Hall, James, & J. M. Clarke. 1895[1894]. An introduction to the study of the genera of Palaeozoic Brachiopoda, Natural History of New York, Palaeontology, vol. 8, part 2. New York Geological Survey. Charles van Benthuysen & Sons. Albany. xvi + 394 p., pl. 21–84.
Pages 1–317 were previously published in 1893 (see Hall & Clarke, 1893). Pages 318–394 and the plates were published for the first time in 1895. The date on the title page is 1894 but the book was not released until early 1895.

Hallam, A. 1992. Phanerozoic Sea-Level Changes. Columbia University Press. New York. 266 p.

Hamada, Takashi. 1968. Ambocoeliids from Red Beds in the Malayan Peninsula. *In* T. Kobayashi & R. Toriyama, eds., Geology and Palaeontology of Southeast Asia, vol. 5. University of Tokyo Press. Tokyo. p. 13–25.

Hancock, A. 1859. On the organisation of the Brachiopoda. Philosophical Transactions of the Royal Society 148:791–869.

Harland, W. B., A. V. Cox, P. G. Llewellyn, C. A. G. Pickton, A. B. Smith, & R. Walters. 1982. A Geologic Time Scale. Cambridge University Press. Cambridge. 131 p.

Harper, C. W. Jr. 1973. Brachiopods of the Arisaig Group (Silurian–Lower Devonian) of Nova Scotia. Geological Survey of Canada Bulletin 215:1–163, pl. 1–28.

Harper, C. W. Jr., & A. J. Boucot. 1978. The Stropheodontacea, parts I–III. Palaeontographica (Abt. A) 161:55–175, pl. 1–35; 162:1–80, pl. 36–50.

Harper, D. A. T. 1989. Brachiopods from the Upper Ardmillan succession (Ordovician) of the Girvan district, Scotland. Palaeontographical Society Monograph 579(2):78–128, pl. 12–22.

Harper, D. A. T. 2000. Dallmanellidina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised), vol. 3. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 782–844.

Harper, D. A. T. 2006. The Ordovician biodiversification: Setting an agenda for marine life. Palaeogeography, Palaeoclimatology, Palaeoecology 232:148–166.

Harper, D. A. T., L. R. M. Cocks, L. Popov, P. M. Sheehan, M. G. Bassett, P. Copper, L. E. Holmer, Jin Jisuo, & Rong Jia-yu. 2004. Brachiopods. *In* B. D. Webby, F. Paris, M. L. Droser, and I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 157–178.

Harper, D. A. T., S. K. Donovan, & C. J. Veltkamp. 1996. The micromorphic articulate brachiopod *Gwynia* from the Western Approaches, U.K. Journal of Paleontology 70(2):331–333, 1 fig.

Harper, D. A. T., Rong J.-Y., & Zhan R.-B. 1999. Late Ordovician development of deep-water brachiopod faunas: *Quo Vadis* Ordovician? Short papers of the 8th International Symposium on the Ordovician System, Acta Universitas Carolinae, Geologica 43(1-2):351–353.

Harper, D. A. T., Enrique Villas, & Gladys Ortega. 2004. *Lipanorthis* Benedetto from the Tremadocian of NW Argentina reidentified as a dalmanellidine: Significance for origin and early radiation of the punctate orthide brachiopods. Lethaia 37:271–279.

Hatai, K. M. 1936a. The geographic distribution of Brachiopoda. Part 1. Recent Brachiopoda of Japan. Bulletin of the Biogeographical Society of Japan 6(8):64–70.

Hatai, K. M. 1936b. Neogene Brachiopoda from Japan. Japanese Journal of Geology and Geography 13(3-4):283–324, pl. 34–35.

Hatai, K. M. 1938. The Tertiary and Recent Brachiopoda of Northeast Honsyu, Japan. Saito Ho-on Kai Museum Research Bulletin 16: 89–246, pl. 16–20.

Hatai, K. M. 1940. The Cenozoic Brachiopoda of Japan. Science Reports of the Tohuku Imperial University, Sendai, Japan (second series, Geology) 20:413 p., 26 fig.,12 pl.

Hatai, K. M. 1946. *Kurakithyris*, Tertiary brachiopod genus from Central Honsyu, Japan. Proceedings of the Japan Academy 22(4):98–101.

Hatai, K. M. 1948. New Tertiary Brachiopoda from Japan. Journal of Paleontology 22(4):494–499, pl. 78.

Hatai, K. M. 1965. Family Laqueidae. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence, Kansas. p. 845–847.

Hatschek, B. 1888–1891. Lehrbuch der Zoologie. Fischer. Jena. 144 p.

Havlíček, Vladimír. 1950. Ramenonozci Ceského Ordoviku [The Ordovician Brachiopoda from Bohemia]. Rozpravy Ústředního ústavu geologického 13:1–72, 17 fig., 13 pl.
English translation on p. 75–135.

Havlíček, Vladimír. 1956. Ramenonožci vápenců branickýh a hlubočepskýh z nejbližšiho prazského okolí [The brachiopods of the Braník and Hlubocepy Limestones in the immediate vicinity of Prague]. Sborník Ústředního ústavu geologického 22:535–665, 12 pl.
English version, vol. 22, p. 1–13, pl. 1–11.

Havlíček, Vladimír. 1960. Bericht über die Ergebnisse der Revision der Böhmischen Altpäozoischen Rhynchonelloidea. Věstník Ústředního ústavu geologického 35(3):241– 244.

Havlíček, Vladimír. 1961. Plectambonitacea im böhmischen Palaözoikum (Brachiopoda). Věstník Ústředního ústavu geologického 36(6):447–451.

Havlíček, Vladimír. 1967. Brachiopods of the suborder Strophomenidina in Czechoslovakia. Rozpravy Ústředního ústavu geologického 33:1–235, pl. 1–52.

Havlíček, Vladímir. 1971. Non-costate and weakly costate Spiriferidina (Brachiopoda) in the Silurian and Lower Devonian of Bohemia. Sborník Geologickych Věd (Paleontologie) 14:7–34, 8 pl.

Havlíček, Vladímir. 1977. Brachiopods of the order Orthida in Czechoslovakia. Rozpravy Ústředního Ústavu Geologického 44:327 p., 56 pl.

Havlíček, Vladimír. 1982. New Pugnacidae and Plectorhynchellidae (Brachiopoda) in the Silurian and Devonian Rocks of Bohemia. Věstník Ústředního Ústavu geologického 57(2):111–114.

Havlíček, Vladimír. 1990. New Lower Devonian (Pragian) rhynchonellid brachiopods in the Koněprusy Area (Czechoslovakia). Věstník Ústředního Ústavu geologického 65(4):211–221, 2 pl.

Havlíček, Vladimír. 1992. New Silurian and Devonian Strophomenidina (Brachiopoda) in Bohemia. Věstník Českého geologického ústavu 67:169–178, 2 pl.

Havlíček, Vladimír. 1994. *Kvania* n.g. and *Petrocrania* Raymond (Brachiopoda, Ordovician) in the Prague Basin. Journal of the Czech Geological Society (Prague) 39:297–300, pl. 1–2.

Havlíček, Vladimír. 1995. New data on the distribution of brachiopods in the Motol and lowermost Kopanina Formations (Wenlock, lower Ludlow, Prague Basin, Bohemia). Věstník Českého Geologického ústavu 70(4):47–63, 5 fig., 3 pl.

Havlíček, Vladimír. 1998. Review of brachiopods in the Chapel Coral Horizon (Zlichov Formation, lower Emsian, Lower Devonian, Prague Basin). Věstník Českého Geologického Ústavu 73:113–132.

Havlíček, Vladimír, & Jiří Vaněk. 1996. Brachiopods and trilobites in the Chýnice Limestone (Emsian) at Bubovice (Cerinka hillside; Prague Basin). Palaeontologia Bohemiae 1996:1–16, 3 fig., 4 pl.

Havlíček, Vladimír, & Jiří Vaněk. 1998. Pragian brachiopods, trilobites, and principal biofacies in the Prague Basin (Lower Devonian, Bohemia). Sborník geologickŷch věd, Paleontologie 34:27–109, 36 fig., 16 pl., 10 tables.

Hayasaka, Ichiro. 1938. A new neotreme genus of Brachiopoda from Japan. Venus 8(1):9–13, fig. 1–2.

Hayasaka, Ichiro, & Soha Gan. 1940. A note on *Camarophoria* "*purdoni*" from the Permian of Timor. Journal of the Geological Society of Japan 47:127–132.

Hayes, J. M., H. Strauss, & A. J. Kaufman. 1999. The abundance of 13C in marine organic matter and isotope fractionation in the global biogeochemical cycle of carbon during the past 800 Ma. Chemical Geology 161:103–125.

Hay-Schmidt, A. 1992. Ultrastructure and immunocytochemistry of the nervous system of the larvae of *Lingula anatina* and *Glottidia* sp. (Brachiopoda). Zoomorphology 112:189–205.

Hay-Schmidt, A. 2000. The evolution of the serotonergic nervous system. Proceedings of the Royal Society, London (series B) 267:1071–1079.

Hedges, S. B., & S. Kumar. 2004. Precision of molecular time estimates. Trends in Genetics 20:242–247.

Hedley, C. 1899. The Mollusca. Part 2. Pelecypoda and Brachiopoda. The atoll of Funafuti, Ellice Group: Its zoology, botany, ethnology, and general structure based on collections made by Mr. Charles Hedley of the Australian Museum. Part 8. Australian Museum, Memoir 3:491–510.

Hedley, C. 1904. Studies on Australian Mollusca. Part VIII. Proceedings of the Linnaean Society of New South Wales 28:182–211.

Hedley, C. 1905. Mollusca (and Brachiopoda) from One Hundred and Eleven Fathoms, East of Cape Byron, New South Wales. Australian Museum, Records 6(2):41–54.

Hedley, C. 1906. The Mollusca of Mast Head Reef, Capricorn Group, Queensland. Proceedings of the Linnean Society of New South Wales 31:453–467, 1 pl.

Helfenbein, K. G., & J. L. Boore. 2004. The mitochondrial genome of *Phoronis architecta*–comparisons demonstrate that phoronids are lophotrochozoan protostomes. Molecular Biology and Evolution 21:153–157.

Helfenbein, K. G., W. M. Brown, & J. L. Boore. 2001. The complete mitochondrial genome of the articulate brachiopod *Terebratalia transversa.* Molecular Biology and Evolution 18:1734–1744.

Helfenbein, K. G., H. M. Fourcade, R. G. Vanjani, & J. L. Boore. 2004. The mitochondrial genome of *Paraspadella gotoi* is highly reduced and reveals chaetognaths are a sister group to protostomes. Proceedings of the National Academy of Science 101:10,639–10,643.

Helmbrecht, W., & R. Wedekind. 1923. Versuch einer biostratigraphischen Gliederung der Siegener Schichten auf Grund von Rensselaerien und Spiriferen. Glückauf, Berg- und Hüttenmännische Zeitschrift 59(41):949–953.

Helmcke, J. G. 1939. *Kraussina mercatori* n. sp. und die Verbreitung der Gattung *Kraussina*. Résultats scientifiques des croisières du Navire-École Belge "Mercator," vol. 2. Mémoires Museum Royal d'Histoire naturelle de Belgique (series 2, fasc. 15) 11(10):135–139, 1 pl.

Helmcke, J. G. 1940. Die Brachiopoden der deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899, vol. 24, no. 3. G. Fischer Verlag. 1932–1940. Jena. p. 217–316, 40 fig.

Hennig, W. 1966. Phylogenetic Systematics. University of Illinois Press. Urbana and Chicago. xiii + 263 p., fig. 1–69.

Henry, J. Q., A. Okuso, & M. Q. Martindale. 2004. The cell lineage of the polyplacophoran, *Chaetopleura apiculata:* Variation in the spiralian program and implications for molluscan evolution. Developmental Biology 272:145–160.

Herrmann, K. 1997. Phoronida. *In* F. W. Harrison & R. M. Woollacott, eds., Microscopic Anatomy of Invertebrates, 13: Lophophorates, Entoprocta, and Cycliophora. Wiley-Liss. New York. p. 207–236.

Hertlein, L. G., & U. S. Grant IV. 1944. The Cenozoic Brachiopoda of western North America. Publications of the University of California at Los Angeles in Mathematical and Physical Sciences 3:236 p., 21 pl.

Hesselbo, S. P., D. R. Grocke, & H. C. Jenkyns. 2000. Massive dissociation of gas hydrate during a Jurassic oceanic anoxic event. Nature 406:392–395.

Hill, Dorothy. 1950. The Productinae of the Artinskian Cracow fauna of Queensland. University of Queensland, Department of Geology, Papers 3:1–36, 9 pl.

Hiller, Norton. 1986. The South African Museum's *Meiring Naude* cruises, Part 16. Brachiopoda from the 1975–1979 cruises. Annals of the South African Museum 97:97–140, 19 fig.

Hiller, Norton. 1991. The southern African Recent brachiopod fauna. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February, 1990. Balkema. Rotterdam. p. 439–445, 9 fig.

Hiller, Norton. 1994. The environment, biogeography, and origin of the southern African Recent brachiopod fauna. Journal of Paleontology 68(4):776–786, 12 fig.

Hiller, N., & D. I. MacKinnon. 2000. A reappraisal of the systematics of the *Stethothyris* group of brachiopods from the Cenozoic of New Zealand and Australia. New Zealand Journal of Geology and Geophysics 43:59–81.

Hoare, R. D., & R. H. Mapes. 1997. *Cardiarina cordata* Cooper, 1956 (Brachiopoda), terebratuloid or rhynchonelloid? Journal of Paleontology 71:32–34.

Hoefs, J. 1997. Stable Isotope Geochemistry. Springer. Berlin. 244 p., 78 fig.

Hogeboom, T., & N. W. Archbold. 1999. Additional specimens of early Permian brachiopods from the Callytharra Formation, Carnarvon Basin, Western Australia: New morphological data. Proceedings of the Royal Society of Victoria 111(2):255–269.

Holland, P. W. H. 1990. Homeobox genes and segmentation: co-option, co-evolution and convergence. Developmental Biology 1:135–145.

Holland, P. W. H., N. A. Williams, & J. Lanfear. 1991. Cloning of segment polarity gene homologues from the unsegmented brachiopod *Terebratulina retusa* (Linnaeus). Febs Letters 291:211–213.

Holmer, L. E. 1989. Middle Ordovician phosphatic inarticulate brachiopods from Västergötland and Dalarna, Sweden. Fossils and Strata 26:1–172, 118 fig.

Holmer, L. E. 1991. Phyletic relationships within the Brachiopoda. Geologiska Foreningens i Stockholm Forhandlingar 113:84–86.

Holmer, L. E. 2000. Dictyonellida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 196–200.

Holmer, L. E. 2001. Phylogeny and classification: Linguliformea and Craniiformea. *In* S. J. Carlson & M. R. Sandy, eds., Brachiopods ancient and modern—A tribute to G. A. Cooper. The Paleontological Society Papers 7:11–26.

Holmer, L.E., S. P. Koneva, L. E. Popov, & A. M. Zhylkaidarov. 1996. Middle Ordovician (Llanvirn) lingulate brachiopods and conodonts from the Malyi Karatau Range, Kazakhstan. Paläontologisches Zeitschrift 70(3–4):481–495, 7 fig.

Holmer, L. E., & L. E. Popov. 1996. Early Paleozoic radiation and classification of organo-phosphatic brachiopods. *In* P. Copper and J. Jin, eds., Brachiopods: Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, 1995. Balkema. Rotterdam. p. 117–121.

Holmer, L. E., & L. Ye. Popov. 2000. Lingulata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 30–146.

Holmer, L. E., L. E. Popov, & M. G. Bassett. 2000. Early Ordovician organophosphatic brachiopods with Baltoscandian affinities from the Alay Range, southern Kirgizia. GFF 123:367–375, 5 fig.

Holmer, L. E., L. Ye. Popov, M. G. Bassett, & J. R. Laurie. 1995. Phylogenetic analysis and classification of the Brachiopoda. Palaeontology 38:713–741.

Holmer, L. E., L. E. Popov, S. P. Koneva, & M. G. Bassett. 2001. Cambrian–Early Ordovician brachiopods from Malyi Karatau, the western Balkhash Region, and northern Tien Shan, Central Asia. Special Papers in Palaeontology 65:180 p., 18 fig., 51 pl.

Holmer, L.E., L. E. Popov, S. P. Koneva, & Rong J. 1997. Early Cambrian *Lingulellotreta* (Lingulata, Brachiopoda) from South Kazakhstan (Malyj Karatau Range) and South China (Yunnan). Journal of Paleontology 71:577–583.

Holmer, Lars E., Leonid E. Popov, & Ryszard Wrona. 1996. Early Cambrian lingulate brachiopods from glacial erratics of King George Island (South Shetland Islands), Antarctica. Palaeontologia Polonica 55:37–50.

Holmer, Lars E., Christian B. Skovsted, & Alwyn Williams. 2002. A stem group brachiopod from the Lower Cambrian: Support for a *Micrina* (halkieriid) ancestry. Palaeontology 45(5):875–882.

Holmer, L. E., & G. T. Ushatinskaya. 1994. Ceratretide brachiopods from the Early and Middle Cambrian of Sweden, Kazakhstan, and Siberia. GFF 116:203–210.

Holmes, A. 1937. The Age of the Earth. Thomas Nelson. London. 285 p.

d'Hondt, Jean-Loup. 1973. Bryozoaires et Brachiopodes de la Campagne Noratlante. Bulletin du Muséum national d'Histoire naturelle (series 3, no. 179) Zoologie 118:1209–1223, 5 fig.

d'Hondt, Jean-Loup. 1976. Sur quelques Brachiopodes actuels (océan Atlantique, Mediterranée, Kerguelen). Bulletin du Muséum national d'Histoire naturelle (series 3, no. 350) Zoologie 243:1–13, 4 fig.

d'Hondt, Jean-Loup. 1977. Brachiopodes. Résultats scientifiques de la campagne MDO4/Benthos du "Marion-Dufresne." Comité national français des recherches antarctiques 42:65–69.

d'Hondt, Jean-Loup. 1987. Observations sur les Brachiopodes actuels de Nouvelle-Calédonie et d'autres localités de l'Indo-Pacifique. Bulletin du Muséum national d'Histoire naturelle (series 4) 9(section A, no. 1):33–46, 4 pl.

d'Hondt, J.-L., & Å. Franzen. 2001. Observations on embryological and larval strages of *Macandrevia cranium* (Müller, 1776) (Brachiopoda, Articulata). Invertebrate Reproduction and Development 40:153–161.

Hoover, P. R. 1979. Early Triassic terebratulid brachiopods from the Western Interior of the United States. United States Geological Survey Professional Paper 1057:1–21, 4 pl.

Hosking, L. F. V. 1933. Fossils from the Wooramel District. Series 2. Journal of the Royal Society of Western Australia 19:43–66.

Hou Hong-fei. 1963. Some new Middle Devonian brachiopods from the provinces of Guangxi and Yunnan. New genera and species of Middle Devonian brachiopods. Acta Palaeontologica Sinica 11(3):412–432. In Chinese, with Russian abstract.

Hou Xian-guang, R. J. Aldridge, J. Bergström, D. J. Siveter, & Feng Xian-hong. 2004. The Cambrian Fossils of Chengjiang, China. The Flowering of Early Animal Life. Blackwell Science Ltd. Malden. 233 p.

Hou Xian-guang, J. Bergström, Wang Hai-feng, Feng Xiang-hong, & Chen Ai-lin. 1999. The Chengjiang Fauna. Exceptionally well-preserved animals from 530 million years ago. Yunnan Science and Technology Press. Kunming, Yunnan Province, China. 170 p. In Chinese.

House, M. R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology 181:2–25.

Huang T. K. 1932. Late Permian brachiopods of southwestern China. Part 1. Palaeontologia Sinica (series B) 9(1):1–138, pl. 1–9.

Huber, B. T., R. D. Norris, and K. G. MacLeod. 2002. Deep Sea paleotemperature record of extreme warmth during the Cretaceous. Geology 30:123–126.

Hurst, J. M. 1976. The function of the brachial valve septa in plectambonitacean brachiopods. Lethaia 8:63–67.

Huxley, T. H. 1869. An Introduction to the Classification of Animals. John Churchill & Sons. London. 147 p.

Hyman, L. H. 1959. The Invertebrates: Smaller Coelomate Groups, Vol. 5. McGraw-Hill. New York. 783 p., fig. 1–240.

Iijima, M., T. Hiroko, M. Yutaka, & K. Yoshinori. 1991. Difference of the organic component between the mineralized and the non-mineralized layers of Lingula shell. Comparative Biochemistry and Physiology 98A:379–382.

Isaacson, P. E., & J. T. Dutro. 1999. Lower Carboniferous brachiopods from Sierra de Almeida, Northern Chile. Journal of Paleontology 73(4):625–633.

Ivanov, A. P. 1935. Fauna brakhiopod srednego i verkhnego karbona podmoskovnogo basseina. Chast 1. Productidae Gray [Brachiopods of the Middle and Upper Carboniferous of the Moscow basin, part 1: Productidae Gray]. Moskovskyi Geologicheskii Tresta, Trudy 8:163 p., 15 pl.

Ivanov, A. P., & E. A. Ivanova. 1937. Brachiopoda of the Middle and Upper Carboniferous of the Moscow Basin (*Neospirifer, Choristites*). Akademiia Nauk SSSR i Bsesoiuznii Institut Mineral'nogo Ser'ia NKTN, Moscow, Leningrad, Paleozoologicheskogo Institut, Trudy 6(2):1–213.

Ivanov, A. N., & E. I. Miagkova. 1950. Opredelitel' fauny ordovika zapadnogo sklona Srednego Urala. Akademiia Nauk SSSR, Ural'skii Filial, Gorno-Geologicheskii Intitut, Trudy 18:1–32, 19 pl. In Russian.

Ivanov, A. N., & E. I. Miagkova. 1955. Fauny ordovika zapadnogo sklona Srednego Urala. Akademiia Nauk SSSR, Ural'skii Filial, Gorno-Geologicheskii Intitut, Trudy 23:9–68. In Russian.

Ivanova, E. A. 1951. Novye danne po sisteme Producktid (rod *Kutorginella*) [New data on Productid systematics (genus *Kutorginella*)]. Comptes Rendus de l'Académie des Sciences URSS 77(2):329–331.

Ivanova, E. A. 1971. [On a new spiriferinid genus]. Paleontologicheskii Zhurnal 1971(1):120–123, 1 fig. In Russian.

Ivanova, E. A. 1972. Osnovnyye zakonomernosti evolyutsii spiriferid (Brachiopoda). [Main features of spiriferid evolution (Brachiopoda)]. Paleontologicheskii Zhurnal 1972(3):28–42, 5 fig. In Russian.

Ivanova, E. A. 1981. Morfologiia i razvitie brakhiopod (Nadcemeistvo Paeckelmanellacea) [Morphology and evolution of the brachiopods (superfamily Paeckelmanellacea)]. Akademiia Nauk SSSR, Paleontologicheskogo Instituta, Trudy 195:1–54, 14 fig., 8 pl. In Russian.

Iwata, K. 1982. Ultrastructure and calcification of the shells in inarticulate brachiopods. Part 2. Ultrastructure of the shells of *Glottidia* and *Discinisca*. Journal of the Geological Society of Japan 88:957–966.

Jaanusson, Valdar. 1971. Evolution of the brachiopod hinge. *In* J. T. Dutro, ed., Paleozoic Perspectives: A Paleontological Tribute to G. Arthur Cooper. Smithsonian Contributions to Paleobiology 3:33–46, 6 fig., pl. 1–2.

Jaanusson, Valdar. 1981. Functional thresholds in evolutionary progress. Lethaia 14(3):251–260.

Jaanusson, Valdar, & M. G. Bassett. 1993. *Orthambonites* and related Ordovician brachiopod genera. Palaeontology 36:21–63, 9 pl.

Jablonski, D. 1991. Extinctions: A paleontological perspective: Science 253:754–757.

Jackson, J. B. C., T. F. Goreau, & W. D. Hartman. 1971. Recent brachiopod-coralline sponge communities and their paleoecological significance. Science 173:623–625, 2 fig.

Jackson, J. W. 1912. The Brachiopoda of the Scottish National Antarctic Expedition. Transactions of the Royal Society of Edinburgh 48(2):367–390.

Jackson, J. W. 1918. Brachiopoda. British Antactic ("Terra Nova") Expedition 1910. British Museum of Natural History, Reports in Zoology 2(8):177–202, 1 pl.

Jackson, J. W. 1952. A revision of some South African Brachiopoda; with descriptions of new species. Annals of the South African Museum 41(1):40 p., 3 pl.

Jackson, J. W., & G. Stiasny. 1937. The Brachiopoda of the Siboga Expedition. *In* M. C. W. Weber, ed., Siboga Expedité (Leiden) 27:20 p., 2 pl.

Jaecks, G. S. 2001. Thecideide phylogeny, heterochrony, and the gradual acquisition of characters. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Procedings of the Millennium Brachiopod Congress, 2000. The

Systematics Association Special Volume Series 63. Taylor and Francis, London. p. 240–247.

Jaecks, G. S., & S. J. Carlson. 2001. How phylogenetic inference can shape our view of heterochrony: Examples from thecideide brachiopods. Paleobiology 27(2):205–225.

Jafarian, M. A. 2000. Late Devonian Index Brachiopoda of North-East Esfahan in correlation with other regions. Journal of Sciences Islamic Republic of Iran, 11(3):221–232.

Jahnke, Hans. 1971. Fauna und Alter der Erbslochgrauwacke (Brachiopoden und Trilobiten, Unter-Devon, Rheinisches Schiefergebirge und Harz). Göttinger Arbeiten zur Geologie und Paläontologie 9:1–105, 50 fig., 11 pl.

James, M. A. 1997. Brachiopoda: Internal anatomy, embryology, and development. *In* F. W. Harrison & R. M. Woollacott, eds., Microscopic Anatomy of Invertebrates, vol. 13: Lophophorata, Entoprocta, and Cycliophora. Wiley-Liss. New York. p. 297–407.

James, M. A., A. D. Ansell, M. J. Collins, G. B. Curry, L. S. Peck, & M. C. Rhodes. 1992. Biology of living brachiopods. Advances in Marine Biology 28:175–387.

James, N. P., Y. Bone, & T. K. Kyser. 1997. Brachiopod $\delta^{18}O$ values do reflect ambient oceanography: Lacepede Shelf, southern Australia. Geology 25:551–554.

Jansen, Ulrich. 2001a. On the genus *Acrospirifer* Helmbrecht et Wedekind, 1923 (Brachiopoda, Lower Devonian) (Contributions to Lower Devonian brachiopods from the Rheinisches Schiefergebirge and adjacent areas, 1). Journal of the Czech Geological Society, Havlíček Volume 46(3-4):131–144, 3 pl.

Jansen, Ulrich. 2001b. Morphologie, Taxonomie und Phylogenie unter-devonischer Brachiopoden aus der Dra-Ebene (Marokko, Prä-Sahara) und dem Rheinischen Schiefergebirge (Deutschland). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 554:1–389, 34 fig., 34 pl., 25 tables.

Jeffreys, J. G. 1859. Gleanings in British conchology. Annals and Magazine of Natural History (series 3) 3:30–43, 106–120, pl. 2.

Jeffreys, J. G. 1869. The deep-sea dredging expedition in H.M.S. "Porcupine." Nature 1(5):135–137.

Jeffreys, J. G. 1876. On some new and remarkable North-Atlantic Brachiopoda. Annals & Magazine of Natural History (series 4) 18:250–253.

Jeffreys, J. G. 1878. On the Mollusca procured during the "Lightning" and "Porcupine" Expeditions, 1868–70. (Part I), Volume for 1878. Proceedings of the Zoological Society of London. p. 393–416, 2 pl.

Jenkyns, H. C., A. S. Gale, & R. M. Corfield. 1994. Carbon- and oxygen-isotope stratigraphy of the English Chalk and the Italian Scaglia and its palaeoclimatic significance. Geological Magazine 131:1–34.

Jenkyns, H. C., C. E. Jones, D. R. Gröcke, S. P. Hesselbo, & D. N. Parkinson. 2002. Chemostratigraphy of the Jurassic System: Applications, limitations and implications for palaeoceanography. Journal of the Geological Society of London 159:351–78.

Jenner, R. A. 1999. Metazoan phylogeny as a tool in evolutionary biology: Current problems and discrepancies in application. Belgian Journal of Zoology 129:245–262.

Jenner, R. A. 2000. Evolution of animal body plans: The role of metazoan phylogeny at the interface between pattern and process. Evolution and Development 2:208–221.

Jenner, R. A. 2001. Bilaterian phylogeny and uncritical recycling of morphological data sets. Systematic Biology 50:730–742.

Jenner, R. A. 2002. Boolean logic and character-state identity: Pitfalls of character coding in metazoan cladistics. Contributions to Zoology 71:67–91.

Jenner, R. A. 2004. Towards a phylogeny of the metazoa: evaluating alternative phylogenetic positions of Platyhelminthes, Nemertea, and Gnathostomulida, with a critical reappraisal of cladistic characters. Contributions to Zoology 73:3–163.

Jenner, R. A., & F. R. Schram. 1999. The grand game of metazoan phylogeny: Rules and strategies. Biological Reviews 74:121–142.

Jennings, R. M., & K. M. Halanych. 2004. Mitochondrial genomes of *Clymenella torquata* (Maldanidae) and *Riftia pachyptila* (Siboglinidae): Evidence for conserved gene order in Annelida. Molecular Biology and Evolution 22:210–222.

Jeremejew, P. 1856. Geognostische Beobachtungen an den Ufern des Wolchow. Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen 10:63–84.

Jin Jisuo. 1989. Late Ordovician–Early Silurian rhynchonellid brachiopods from Anticosti Island, Québec. Biostratigraphie du Paléozoique 10:127 p., 30 pl.

Jin J., & B. D. E. Chatterton. 1996. *Microbilobata,* a new genus of earliest terebratuloid brachiopod from the Lower Silurian of northwestern Canada: Implications for the origin of higher taxa. Historical Biology 11:43–56.

Jin Jisuo, & B. D. E. Chatterton. 1997. Latest Ordovician–Silurian articulate brachiopods and biostratigraphy of the Avalanche Lake area, southwestern District of Mackenzie, Canada. Palaeontographica Canadiana 13:167 p.

Jin Jisuo, & Zhan Renbin. 2000. Evolution of the Late Ordovician orthid brachiopod *Gnamptorhynchos* Jin, 1989 from *Platystrophia* King, 1850, in North America. Journal of Paleontology 74:983–991.

Jin Jisuo, & Zhan Ren-bin. 2001. Late Ordovician articulate brachiopods from the Red River and Stony Mountain Formations, southern Manitoba. National Research Council of Canada Press. Ottawa. 117 p., 23 pl.

Jin Yugan, Hou Xianguang, & Wang Huayu. 1993. Lower Cambrian pediculate lingulids from Yunnan, China. Journal of Paleontology 67:788–798.

Jin Yu-gan, & Hu Shi-zhong. 1978. Brachiopods of the Kuhfeng Formation in south Anhui and Nanking Hills. Acta Palaeontologica Sinica 17(2):101–127, 4 pl.
English abstract, p. 124–127.

Jin Yu-gan, & D. E. Lee. 2006. Uncertain. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H (Revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 2252.

Jin Yu-gan, & Sun Dong-li. 1981. Palaeozoic brachiopods from Xizang. *In* Palaeontology of Xizang, Book III (The Series of the Scientific Expedition to the Qinghai-Xizang Plateau). Science Press. Beijing. p. 127–176, fig. 1–13, pl. 1–12.

Jin Yu-gan, & Wang Hua-Yu. 1992. Revision of the Lower Cambrian brachiopod *Heliomedusa* Sun & Hou, 1987. Lethaia 25(1):35–49, fig. 1–14.

Jin Yu-Gan, Wang Yue, Sun Dong-Li, & Shi Quan. 1985. [Late Paleozoic and Triassic Brachiopods from the East of the Qinghai-Xizang Plateau]. *In* [Stratigraphy and Palaeontology in W. Sichuan and E. Xizang, China, Part 3]. Chengdu: Sichuan Science and Technology Publishing House. p. 182–249, 20 pl.

Jin Yu-Gan, Ye Song-Ling, Xu Han-Kui, & Sun Dong-Li. 1979. [Brachiopoda]. *In* [Paleontological Atlas of Northwestern China, Qinghai Province, vol. 1, Lower Paleozoic-Cenozoic]. Geological Press. Beijing. p. 60–225, pl. 18–57.

Johansen, M. B. 1987. Brachiopods from the Maastrichtian-Danian Boundary Sequence at Nye Klov, Jylland, Denmark. Fossils and Strata 20:1–57, 20 pl.

Johnson, J. G. 1970. Great Basin Lower Devonian Brachiopoda. Geological Society of America Memoir 121:1–421, 74 pl.

Johnson, J. G. 2006. Cyrtinoidea. *In* R. L. Kaesler, Treatise on Invertebrate Paleontology. Part H, Brachiopoda, revised, vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado, and Lawrence, Kansas. p. 1,881–1,883.

Jones, O. T. 1928. *Plectambonites* and some allied genera. Memoirs of the Geological Survey of Great Britain, Palaeontology, London 1:367–527, pl. 21–25.

Jope, H. M. 1965. Composition of brachiopod shell. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 156–164.

Joubin, Louis. 1901. Brachiopodes. Résultats du voyage du S.Y. Belgica, 1897-1898-1899, sous le commandement de A. de Gerlache de Gomery. Rapports Scientifiques publiés aux frais du Gouvernement Belge sous la direction de la Commission de la Belgica–Zoologie, vol. 7–9. J.-E. Buschmann. Anvers. p. 1–12, pl. 1–2.

Joubin, M. L. 1906. Note sur un brachiopode nouveau de l'Océan Indien, *Kingena alcocki*. Bulletin du Muséum d'Histoire Naturelle 12: 529–532, 2 pl.

Joysey, K. A. 1959. Probable cirripede, phoronoid, and echiuroid burrows within a Cretaceous echinoid test. Palaeontology 1:397–400.

Kaesler, R. L., ed. 1997. Treatise on Invertebrate Paleontology. Part H (Revised), vol. 1. Geological Society of America & University of Kansas Press. Boulder, Colorado & Lawrence, Kansas. xx + 539 p., 417 fig., 40 tables.

Kaesler, R. L. ed. 2000. Treatise on Invertebrate Paleontology. Part H (Revised), vol. 2–3. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. xxx + 919 p., 616 fig., 17 tables.

Kaesler, R. L. ed. 2002. Treatise on Invertebrate Paleontology. Part H (Revised), vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. xxxix + 768 p., 484 fig., 3 tables.

Kaesler, R. L. ed. 2006. Treatise on Invertebrate Paleontology. Part H (Revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. xlvi + 631 p., 398 fig.

Kamyshan, V. P. 1977. Urovni organizatsii rakovinnogo veshchestva, struktury i tekstury rakovin mezozoiskikh i kainozoiskikh rinkhonellid [Levels of organization of the shell substance, structure and texture of Mesozoic and Cainozoic rhynchonellide shells]. III-ia Vsesoyuznaia Konferentsiia po Mezozoiskim i Kainozoiskim Brakhiopodam [Third All-Union Conference on Mesozoic and Cainozoic Brachiopods] Tezisy Dokladov [Theses Reports]. Kharkov University. Khar'kov. p. 21–24.
In Russian.

Kats, Iu. I. 1974. Tip Brachiopoda. *In* G. Ia. Krymgol'ts, ed., Atlas verkhnemelovoi fauny Donbassa [Atlas of the Upper Cretaceous Fauna of the Don Basin]. Izdatel'stvo “Nedra.” Moskva. p. 240–275, pl. 82–87.

Katz, Y. I. 1962. Novye rody pozdnemelovykh zamkovykh brakhiopod Tadzhikskoi depressii i prilezhashchikh k nei regionov [New genera of Late Cretaceous articulate brachiopods from the Tadjik Depression and the adjoining regions]. Zapiski Geologicheskogo Otdeleniia Kharkovskogo Gosudarstvennogo Universiteta 15:132–154, 2 pl.

Keith, M. L., & J. N. Weber. 1965. Systematic relationships between carbon and oxygen isotopes in carbonates deposited by modern corals and algae. Science 150:498–501.

Keller, G., T. Adatte, & W. Stinnesbeck. 2003. The non-smoking gun. Geoscientist 13:8–11.

Keller, G., W. Stinnesbeck, T. Adatte, & D. Stueben. 2003. Multiple impacts across the Cretaceous-Tertiary boundary. Earth Science Reviews 62:327–363.

Kemezys, K. J. 1965. Significance of punctae and pustules in brachiopods. Geological Magazine 102:315–324.

Keyserling, Alexander. 1846. Geognostische Beobachtungen. *In* P. von Krusenstern & Alexander Keyserling, eds., Wissenshaftlic Beobachtungen auf einer Reise in das Petschora-Land im Jahre 1843. I. Paleontologische Bemerkungen. II. Geognostische Reise St. Petersburg. Carl Kray. St. Petersburg. p. 151–406.

Kim, I. W., S. Collino, D. E. Morse, & J. S. Evans. 2006. A crystal modulating protein from molluscan nacre that limits the growth of calcite in vitro. Crystal Growth & Design 6:1078–1082.

Kindle, E. M. 1912. The Onondaga fauna of the Allegheny region. United States Geological Survey Bulletin 508:144 p.

King, R. E. 1931 [1930]. The Geology of the Glass Mountains, Texas, part II: Faunal summary and correlation of the Permian formations with description of Brachiopoda. University of Texas Bulletin 3042:1–245, pl. 1–44.

King, William. 1846. Remarks on certain genera belonging to the class Palliobranchiata. Annals and Magazine of Natural History, London 18:26–42.

King, William. 1850. A Monograph of the Permian Fossils of England. Palaeontographical Society Monograph 3:xxxvii + 258 p., 29 pl.

King, William. 1859. On *Gwynia, Dielasma,* and *Macandrevia,* three new genera of Palliobranchiata Mollusca, one of which has been dredged in the Strangford Lough. Dublin University Zoological and Botanical Association, Proceedings 1(3):256–262. Also published in Natural History Review 6:516–520.

King, William. 1871. On *Agulhasia davidsonii,* a new palliobranchiate genus and species. Annals and Magazine of Natural History (series 4) 7:109–112, pl. 11.

Kitchin, F. L. 1900. Jurassic Fauna of Cutch. Part 1. The Brachiopoda. Geological Survey of India, Memoirs, Palaeontologia Indica (series 9) 3(1):1–87, 15 pl.

Klein, R. T., K. C. Lohmann, & C. W. Thayer. 1996. Bivalve skeletons record sea-surface temperature and $\delta^{18}O$ via Mg/Ca and $^{18}O/^{16}O$ ratios. Geology 24:415–418.

Klets, A. G. 1998. Novie stratigraficheski znachimie brakhiopodi iz verkhnego paleozoia iugo-zapadnogo verkhoian'ia. Novosti paleontologii i stratigrafii. 1998. Prilozhenie k Zhurnalu "Geologiia i Geophizika" 39(1):91–101.

Kobayashi, Teiichi. 1937. The Cambro-Ordovician shelly faunas of South America. Journal of the Faculty of Science, Imperial University of Tokyo, Section II (Geology, Mineralogy, Geography, Seismology) 4(4):369–522, pl. 1–8.

Koch, P. L. 1998. Isotopic reconstruction of past continental environments. Annual Review of Earth and Planetary Sciences 26:573–613.

Koch, W. F. 1996. *Altantocoelia*, new leptocoeliid (Brachiopoda) genus from the Devonian of eastern North America. Journal of Paleontology 70(6):1088–1090.

Koenig, Carl. 1825. Icones Fossilium Sectiles. British Museum. London. 4 p., 8 pl.

Koneva, S. P. 1986. Novoe semeistvo kembriiskikh bezzamkovykh brakhiopod [A new family of the Cambrian inarticulate brachiopods]. Paleontologicheskii Zhurnal 1986(1):49–55, 1 pl.

de Koninck, L. G. 1841–1844. Description des animaux fossiles qui se trouvent dans le terrain Carbonifère de la Belgique, 2 vol. H. Dessain. Liège. 650 p., 55 pl.

de Koninck, L. G. 1876–1877. Recherches sur les fossiles paléozoïques de la Nouvelles Galles de Sud (Australie). Mémoire Société Scientifique, Liège, 2, 6, 7:1–373.

de Koninck, L. G. 1883. Sur le *Spirifer Mosquensis* et sur ses affinités avec quelques autres espèces du même genre. Bulletin du Musée royal d'Histoire naturelle de Belgique 2:371–395.

Kotlyar, G. V., Y. D. Zakharov, & I. V. Polubotko. 2004. Late Changhsingian fauna of the northwestern Caucasus mountains, Russia. Journal of Paleontology 78(3):513–527.

Kowalewski, Michel, M. G. Simões, Monica Carroll, & D. L. Rodland. 2002. Abundant brachiopods on a tropical upwelling-influenced shelf (Southeast Brazilian Bight, South Atlantic). PALAIOS 17:277–286, 9 fig.

Krauss, F. von. 1844. Brachiopoda, vol. 7. *In* H. C. Küster, Conchylin-Cabinet von Martini und Chemnitz. plates (1844), text (1848).

Krestovnikov, V. N., & V. S. Karpyshev. 1948. Fauna and stratigraphy of the Etroeungian beds of the Zigan river (southern Ural mountains). Trudy Geologicheskii Institut Akademii Nauk SSSR (Geologii) 66(21):29–66.
In Russian.

Kuhn, Oskar. 1949. Lehrbuch der Paläozoologie. E. Schweizerbart'sche Verlagsbuchhandlung. Stuttgart. 326 p.

Kulikov, M. V. 1974. Brakhiopody kungurskogo iarusa Urala [Brachiopods from the Kungurian stage of the Urals.] *In* G. N. Panalov and B. I. Chubashov, eds., Vodorosli, brakhiopody i miospory iz Permskikh otlozhenii Zapadnogo Urala [Algae, brachiopods and miospores from Permian strata of the western Urals]. Akademia Nauk SSSR, Uralskii Nauchnyi Tsentr, Trudy Instituta Geologii i Geokhimi, Bulletin 109:138–153, 8 pl.

Kulkov, N. P., & L. G. Severgina. 1989. Stratigrafiia i brakhiopody Ordovika i Nizhnego Silura Gornogo Altaia [Stratigraphy and brachiopods of the Ordovician and Lower Silurian of the Gorny Altai]. Akademia Nauk SSSR Sibirskoe Otdelenie Institut Geologii i Geofiziki (IGIG), Trudy (Novosibirsk) 717:221 p., 32 pl.

Küntzel, H., B. Piechulla, & U. Hahn. 1983. Consensus structure and evolution of 5S rRNA. Nucleic Acids Research 11:893–900.

Kutorga, S. S. 1848. Ueber die Brachiopoden-Familie der Siphonotretaceae. Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersbourg, Verhandlungen 1847:250–286, pl. 6–7.

LaBarbera, Michael. 1977. Brachiopod orientation to water movement. I. Theory, laboratory behavior and field observation. Paleobiology 3:270–287.

LaBarbera, Michael. 1981. Water flow patterns in and around three species of articulate brachiopods. Journal of Experimental Marine Biology and Ecology 55:185–206.

Lacaze-Duthiers, F. J. H. de. 1861. Histoire naturelle des brachiopodes vivants de la Mediterranée. I. Histoire naturelle de la Thecidie (*Thecidium mediterraneum*). Annales des sciences naturelles Zoologie (serie 4) 15:259–330.

Lake, J. A. 1990. Origin of the Metazoa. Proceedings of the National Academy of Sciences, U.S.A. 87:763–766.

Lamarck, J. B. P. A. de M. de. 1801. Système des Animaux sans Vertèbres. Deterville. Paris. 432 p.

Lamarck, J. B. P. 1819. Histoire Naturelle des Animaux sans Vertèbres, 1st. ed., vol. 6, no. 1. Paris. p. 1–343.

Landing, Ed. 1984. Skeleton of lapworthwellids and the suprageneric classification of tommotiids (Early and Middle Cambrian phosphatic Problematica). Journal of Paleontology 62:788–798.

La Perna, R. 1998. A new Mediterranean *Skenoides* (Gastropoda: Skeneidae) from a shallow-water cave. Journal of Conchology 36(4):21–27, 13 fig.

Larget, B., J. B. Kadane, & D. L. Simon. 2005. A Bayesian approach to the estimation of genome arrangements. Molecular Phylogenetics and Evolution 36(2):214–223.

Larget, B., D. L. Simon, J. B. Kadane, & D. Sweet. 2005. A Bayesian analysis of metazoan mitochondrial genome rearrangements. Molecular Biology and Evolution 22:486–495.

Laurie, J. R. 1986. Phosphatic fauna of the Early Cambrian Todd River Dolomite, Amadeus Basin, central Australia. Alcheringa 10:431–454.

Laurie, J. R. 1987. The musculature and vascular system of two species of Cambrian Paterinida (Brachiopoda). Bureau of Mineral Resources Journal of Australian Geology and Geophysics 10:261–265.

Laurie, J. R. 1997a. Silicified Late Cambrian brachiopods from the Georgina Basin, western Queensland. Alcheringa 21:179–189.

Laurie, J. R. 1997b. Early Ordovician fauna of the Gap Creek Formation, Canning Basin, Western Australia. Journal of Australian Geology and Geophysics 16:701–716, 11 fig.

Laurie, J. R. 2000. Class Paterinata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (revised), vol. 2. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 147–157.

Laurin, Bernard. 1997. Brachiopodes récoltés dans les eaux de la Nouvelle-Calédonie et des îles Loyauté, Matthew et Chesterfield. *In* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, vol. 18. Mémoires du Muséum national d'Histoire naturelle 176:411–471, 47 fig.

Laurin, Bernard, & Danièle Gaspard. 1987. Variations morphologiques et croissance du brachiopode abyssal *Macandrevia africana* Cooper. Oceanologica Acta 10(4):445–454, 8 fig., 2 pl.

Lavrov, D. V., J. L. Boore, & W. M. Brown. 2002. Complete mtDNA sequences of two millipedes suggest a new model for mitochondrial gene rearrangements: Duplication and nonrandom loss. Molecular Biology and Evolution 19:163–169.

Lazarev, S. S. 1986. Osnovnye napravleniia evoliutsii i sistema brakhiopod podotriada Productidina [The main directions of evolution and systematics of the brachiopod suborder Productidina]. Avtoreferat dissertatsii na soiskanie ushenoi stepeni doktora biologicheskikh Nauk. Akademiia Nauk SSSR, Paleontologicheskii Institut. Moscow. p. 1–41.

Lazarev, S. S. 1989. Sistema Devonskikh brakhiopod podotriada Strophalosiidina [Systematics of Devonian brachiopods of suborder Strophalosiidina]. Paleontologicheskii Zhurnal 1989(2):27–39, pl. 3.

Lazarev, S. S. 1990. Evoliutsiia i sistema produktid [Evolution and systematics of productids]. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 242:171 p., 40 pl.

Lazarev, S. S. 2000a. Brachiopods of the new tribe Reticulatiini from the Moscow region, 1 Meronomic basis for phylogeny and taxonomy. Paleontological Journal. 43(4):400–410.
Translated from Paleontologicheskii Zhurnal 4:40–49.

Lazarev, S. S. 2000b. Brachiopods of the tribe Reticulatiini from the Carboniferous of the Moscow region: Part 2. On the systematic position of Reticulatiini, with proposed sister-tribes and description of a new genus, *Admoskovia*. Paleontological Journal 34(5):495–503.
Translated from Paleontologicheskii Zhurnal 5:25–33.

Lazarev, S. S. 2000c. Brachiopods of the tribe Reticulariini from the Carboniferous of the Moscow Basin. 3. Descriptions of the Myachkovian and Upper Carboniferous species. Paleontological Journal 34(6):613–621.
Translated from Paleontologicheskii Zhurnal, No. 6, 2000, p. 32–39.

Lazarev, S. S. 2004. Revision of the brachiopod family Schrenkiellidae Lazarev, 1990. Paleontological Journal 38(2):154–161.
Translated from Paleontologicheskii Zhurnal 2004(2):40–46.

Lazarev, S. S., & J. L. Carter. 2000. New Atokan productoid brachiopods from the Upper Carboniferous of Ladrones Limestone of southeastern Alaska, with a preliminary note of the phylogeny and classification of the tribe Retariini. Annals of Carnegie Museum 69(1):11–21.

Leach, W. E. 1814. Zoological miscellania, being descriptions of new or interesting animals, vol. 1.144 p. 60 pl.

Lear, C.H., H. Elderfield, & P. A. Wilson. 2000. Cenozoic Deep-Sea Temperatures and Global Ice Volumes from Mg/Ca in Benthic Foraminiferal Calcite. Science 287:269–272.

Lee, D. E. 1978. Aspects of the ecology and paleoecology of the brachiopod *Notosaria nigricans* (Sowerby). Journal of the Royal Society of New Zealand 8(4):395–417, 8 fig.

Lee, D. E. 1991. Aspects of the ecology and distribution of the living Brachiopoda of New Zealand. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February, 1990. Balkema. Rotterdam. p. 273–279, 1 fig.

Lee, D. E., & C. H. C. Brunton. 1986. *Neocrania* n. gen., and a revision of Cretaceous-Recent brachiopod genera in the family Craniidae. Bulletin of the British Museum (Natural History), Geology 40(4): 141–160, fig. 1-49.

Lee, D. E., & C. H. C. Brunton. 2001. *Novocrania,* a new name for the genus *Neocrania* Lee & Brunton, 1986 (Brachiopoda, Craniida), preoccupied by *Neocrania* Davis, 1978 (Insecta, *Lepidoptera*). Bulletin of The Natural History Museum London (Geology) 57:1–5, fig. 1–2.

Lee, D. E, D. I. MacKinnon, T. N. Smirnova, P. G. Baker, Jin Yu-Gan, & Sun Dong-Li. 2006. Terebratulida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1965–1993.

Lee, D. E., & J. H. Robinson. 2003. *Kakanuiella* (gen. nov.) and *Thecidellina*: Cenozoic and Recent thecideide brachiopods from New Zealand. Journal of the Royal Society of New Zealand 33(1):341–361, fig. 1–38.

Lee, D. E., & T. N. Smirnova. 2006. Terebratuloidea. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 2054–2081.

Lee, D. E., & J. B. Wilson. 1979. Cenozoic and Recent rhynchonellide brachiopods of New Zealand: Systematics and variation in the genus *Notosaria*. Journal of the Royal Society of New Zealand 9(4):437–463, 16 fig.

LeGeros, R.Z., C. M. Pan, S. Suga, & N. Watabe. 1985. Crystallo-chemical properties of apatite in atremate brachiopod shells. Calcified Tissue International 37(1):98–100.

Legrand-Blain, Marie. 1985. A new genus of Carboniferous spiriferid brachiopod from Scotland. Palaeontology 28(3):567–576.

Legrand-Blain, M. 1996. Subgenus *Larbontella. In* Marie Legrand-Blain, J.-J. Devolvé, and Michel Hansotte, Carboniferous brachiopods from the Arize Massif (Ariège), French Pyrénées. Géobios 29(2):177–207.

Legrand-Blain, M., J.-J. Delvolvé, & M. Hansotte. 1996. Carboniferous brachiopods from the Arize Massif (Ariège), French Pyrénées. Geobios 29:177–207.

Leidhold, Claus. 1921. Beitrag zur genaueren Kenntnis und Systematik einiger Rhynchonelliden des reichsländischen Jura. Neues Jahrbuch für Mineralogie, Geologie und Paläontoloie (Beilage Band) 44(2):343–368, pl. 4–6.
Published for 1920.

Lepzelter, C. G., T. F. Anderson, & P. A. Sandberg. 1983. Stable isotope variations in modern articulate brachiopods. American Association of Petroleum Geologists Bulletin 67:500–501.

Lévêque, L., Maggie Cusack, S. A. Davis, & Stephen Mann. 2004. Promotion of fluorapatite crystallization by soluble matrix proteins from *Lingula anatina* shells. Angewandte Chemie 43:885–888.

Levinton, J., L. Dubb, & G. A. Wray. 2004. Simulations of evolutionary radiations and their application to understanding the probablility of a Cambrian explosion. Journal of Paleontology 78:31–38.

Lewis, P. O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. Systematic Biology 50(6):913–925.

Li G., & L. E. Holmer. 2004. Early Cambrian lingulate brachiopods from the Shaanxi Province, China. GFF 126(2):193–211.

Li Guoxiang, & Shuhai Xiao. 2002. *Micrina* and *Tannuolina* from the Lower Cambrian of eastern Yunnan, South China. Geological Society of America, Abstracts with Programs 34:80–81.

Li Guoxiang, & Xiao Shuhai. 2004. *Tannuolina* and *Micrina* (Tannoulinidae) from the Lower Cambrian of Eastern Yunnan, South China, and their scleritome reconstruction. Journal of Paleontology 78(5):900–913.

Li Li, & Gu Feng. 1976. Brachiopoda (Carboniferous–Permian). *In* Paleontological Atlas of North China—Inner Mongolia, vol. 1. Geological Publishing House. Beijing. p. 228–306, pl. 131–184.
In Chinese.

Li Rong-yu, & Brian Jones. 2002. New brachiopod genera from Bird Fiord Formation (Devonian), Arctic Canada. Journal of Paleontology 76:648–658.

Liao Zhuo-ting. 1980. Upper Permian brachiopods from western Guizhou. *In* Stratigraphy and Paleontology of Upper Permian Coal-Bearing Formations in West Guizhou and East Yunnan. Scientific Press. Beijing. p. 241–277, 9 pl.
In Chinese.

Liao Zhuo-ting. 1984. New genus and species of late Permian and earliest Triassic brachiopods from Jiangsu, Zhejiang and Anhui provinces. Acta Palaeontologica Sinica 23(3): 276–285, pl. 1–2.
In Chinese, with English abstract.

Liao Zhuo-Ting, & Sun Dong-Li. 1974. [Brachiopoda—Triassic]. *In* [A Handbook of the Stratigraphy and Palaeontology in southwest China]. Science Press. Beijing. p. 351–353.

Liashenko, A. I. 1959. Atlas brakhiopod i stratigrafiya devonskikh otlojenii centraliikh oblasti russkoy platformi [Atlas of Brachiopods and Devonian stratigraphy of the Devonian deposits of the Central Russian platform]. Vsesoyoznii Nautcho-issledovateliskii geologorazvedochnii nephtianoi Institut (VNIGNI). Moscow. 451 p., 87 pl.

Liashenko, A. I. 1985. Novye verkhnedevonskie brakhiopody iuzhnogo Timana [New Upper Devonian brachiopods from southern Timan]. *In* V. D. Il'ina & V. V. Lipatova, eds., Stratigraficheskye Issledovaniia Prirodnykh Rezervuarov Nefti i Gaza [Stratigraphic investigations of natural reservoirs of oil and gas]. Sbornyk nauchnykh Trudov. Moscow. p. 9–18, pl. 1–2.

Licharew, B. K. 1936. Permian Brachiopoda of the Northern Caucasus. Families Chonetidae Hall and Clarke, and Productidae Gray. Monograph on Paleontology of the USSR (Leningrad-Moscow) 39(1):1–151.
In Russian.
See also Likharev, B. K.

Licharew, B. K. 1937. Permskie brakhiopody Severnogo Kavkaza. Semeistva Chonetidae Hall et Clarke i Productidae Gray [Brachiopoda of the Permian System of USSR, Fascicule I. Permian Brachiopoda of North Caucasus: Families: Chonetidae Hall & Clarke and Productidae Gray]. Monografii po Paleontologii SSSR 39(1):152 p., 13 pl.
See also Likharev, B. K.

Licharew, B. K. 1956. *In* M. A. Rzonsnitskaia, Systematization of Rhynchonellida. International Geological Congress, Mexico, Report 20:125–126.
See also Likharev, B. K.

Likharev, B. K. 1934. On some new genera of upper Paleozoic Brachiopoda. Académie des Sciences de l'URSS, Comptes Rendus (new series) 1(4):210–213.
See also Licharew, B. K.

Linnaeus [Linné], C. 1758. Systema Naturae, sive Regna tria Naturae systematicae proposita per Classes, Ordines, Genera et Species, 10th ed., vol. 1. Holmiae. Stockholm. 823 p.

Linnaeus [Linné], C. 1767. Systema Naturae, sive Regna tria Naturae systematicae proposita per Classes, Ordines, Genera et Species, 12th ed., vol. 1, no. 2. Holmiae. p. 533–1327.

Linnarsson, J. G. O. 1869. Om några försteningar från Vestergötlands sandstenslager [On some fossils found in the Eophyton Sandstone at Lugnas, in Sweden]. Kongliga Svenska Vetenskaps-Akademiens, Förhandlingar 3:337–357, pl. 7–9.
Also published in 1870 in Geological Magazine (Dec. 1) 6:393–406.

Little, C. T. S., V. V. Maslennikov, N. J. Morris, & A. P. Gubanov. 1999. Two Palaeozoic hydrothermal vent communities from the southern Ural Mountains, Russia. Palaeontology 42(6):1043–1078.

Liu Di-yong, Xu Han-kui, and Liang Wen-ping, eds. 1983. Brachiopoda. Nanjing Institute of Geology and Mineral Resources, Paleontological Atlas of East China (1), Volume of Early Palaeozoic. Geological Publishing House. Beijing. p. 254–286.
In Chinese.

Liu Di-yong, Zhu Ci-Ying, & Xue Chun-Ting. 1985. Ordovician brachiopods from northwestern Xiao Hinggan Ling, northeast China. Bulletin of the Shenyang Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences 11:1–46, pl. 1–12.
In Chinese with English abstract.

Lobatscheva, S. V. 1990. O gomeomorfii nekotorykh rebristykh terebratulid (Brakhiopody) [On homeomorphy of some ribbed terebratulids (Brachiopoda)]. Ezhegodnik Vsesoiuznogo Paleontologicheskogo Obshchestva 33:94–103, 1 pl.

Logan, Alan. 1975. Ecological observations on the Recent articulate brachiopod *Argyrotheca bermudana* Dall from the Bermuda Platform. Bulletin of Marine Science 25:186–204, 6 fig.

Logan, Alan. 1977. Reef-dwelling articulate brachiopods from Grand Cayman, B.W.I. Proceedings of the Third International Coral Reef Symposium, Miami, vol. 1. Biology. p. 87–93, 2 fig.

Logan, Alan. 1979. The Recent Brachiopoda of the Mediterranean Sea. Bulletin de l'Institut Océanographique, Monaco 72(1,434):112 p., 22 fig., 10 pl.

Logan, Alan. 1981. Sessile invertebrate coelobite communities from shallow reef tunnels, Grand Cayman, B.W.I. Proceedings of the Fourth International Coral Reef Symposium, Manila 2:735–744, 5 fig.

Logan, Alan. 1983. Brachiopoda collected by CANCAP I-III expeditions to the south-east North Atlantic, 1976–1978. Zoologische Mededelingen 57(18):165–189, 3 fig., 1 pl.

Logan, Alan. 1988a. Brachiopoda collected by CANCAP IV and VI expeditions to the south-east North Atlantic. 1980–1982. Zoologische Mededelingen 62(5):59–74, 2 fig.

Logan, Alan. 1988b. A new thecideid genus and species (Brachiopoda, Recent) from the southeast North Atlantic. Journal of Paleontology 62(4):546–551, 18 fig.

Logan, Alan. 1990. Recent Brachiopoda from the *Snellius* and *Luymes* expeditions to the Surinam-Guyana Shelf, Bonaire-Curacao, and Saba Bank, Caribbean Sea, 1966 and 1969–72. Zoologische Mededelingen 63(11):123–136, 1 fig.

Logan, Alan. 1993. Recent brachiopods from the Canarian-Cape Verdean region: Diversity, biogeographic affinities, bathymetric range and life habits. Courier Forschungs-Institut Senckenberg, 159:229–233.

Logan, Alan. 1998. Recent Brachiopoda from the oceanographic expedition SEAMOUNT 2 to the north-eastern Atlantic in 1993. Zoosystema 20(4):549–562, 4 fig.

Logan, Alan. 2003. Marine fauna of the Mljet National Park (Adriatic Sea, Croatia). 3. Brachiopoda. Natura Croatica 12(4):233–243, 3 fig.

Logan, Alan. 2004. Ecological, reproductive and ontogenetic features in *Pajaudina atlantica* Logan (Thecideidae, Brachiopoda, Recent) from the Canary Islands. P.S.Z.N.: Marine Ecology 25(3):207–215, 4 fig.

Logan, Alan. 2005. A new lacazelline species (Brachiopoda, Recent) from the Maldive Islands, Indian Ocean. Systematics and Biodiversity 3(1):97–104, 4 fig.

Logan, Alan, C. K. Bianchi, Carla Morri, & Helmut Zibrowius. 2004. The present-day Mediterranean brachiopod fauna: Diversity, life habits, biogeography and paleobiogeography. *In* J. D. Ros, T. T. Packard, J. M. Gili, J. L. Pretus, & D. Blasco, eds., Biological Oceanography at the turn of the Millennium. Scientia Marina 68(supplement 1):163–170.

Logan, Alan, C. K. Bianchi, Carla Morri, Helmut Zibrowius, & Ghazi Bitar. 2002. New records of Recent brachiopods from the eastern Mediterranean Sea. Annali del Museo Civico di Storia Naturale "G. Doria," Genova 94:407–418, 1 fig.

Logan, Alan, D. I. MacKinnon, & J. E. Phorson. 1997. Morphology, distribution, life habits and phylogenetic affinities of the Recent brachiopod *Gwynia capsula* (Jeffreys). P.S.Z.N.: Marine Ecology 18(3):239–252, 4 fig.

Logan, Alan, & J. P. A. Noble. 1971. A Recent shallow-water brachiopod community from the Bay of Fundy. Maritime Sediments 7(2):85–91, 5 fig.

Logan, Alan, & J. P. A. Noble. 1983. Recent brachiopods from Malta. Central Mediterranean Naturalist 1:34–42, 2 pl.

Logan, Alan, Adam Tomasovych, Martin Zuschin, & Bettina Grill. 2007. Recent brachiopods from the

Red Sea and Gulf of Aden. *In* D. A. T. Harper, S. L. Long, & C. Nielsen, eds., Proceedings of the 5th International Brachiopod Congress, Copenhagen, July 4–8, 2005. Blackwell. London. Fossils and Strata 54.

Logan, Alan, & Helmut Zibrowius. 1994. A new genus and species of rhynchonellid (Brachiopoda, Recent) from submarine caves in the Mediterranean Sea. P.S.Z.N.: Marine Ecology 15 (1):77–88, 2 fig., 2 pl.

Long, J. A. 1964. The embryology of three species representing three superfamilies of articulate Brachiopoda. Ph.D. thesis. University of Washington. Seattle. 185 p.

Long, J. A., & S. A. Stricker. 1991. Brachiopoda. *In* A. C. Giese, J. S. Pearse, & V. B. Pearse, eds., Reproduction of marine invertebrates, Vol. VI: Echinoderms and Lophophorates. The Boxwood Press. Pacific Grove. p. 46–79.

Lovén, S. 1846. Index Molluscorum litora Scandinaviae occidentalia habitantium. Stockholm. 50 p.

Lowe, C. J., & G. A. Wray. 1997. Radical alterations in the roles of homeobox genes during echinoderm evolution. Nature 389:718–721 and see p. 679.

Lowenstam, H. A. 1961. Mineralogy, $^{18}O/^{16}O$ ratios and strontium and magnesium contents of Recent and fossil brachiopods and their bearing on the history of the oceans. Journal of Geology 69:241–260.

Lüter, Carsten. 1995. Ultrastructure of the metanephridia of *Terebratulina retusa* and *Crania anomala* (Brachiopoda). Zoomorphology 115:99–107.

Lüter, Carsten. 1996. The median tentacle of the larva of *Lingula anatina* (Brachiopoda) from Queensland, Australia. Australian Journal of Zoology 44:355–366.

Lüter, Carsten. 1998a. Note: Embryonic and larval development of *Calloria inconspicua* (Brachiopoda, Terebratellidae). Journal of the Royal Society of New Zealand 28:165–167.

Lüter, Carsten. 1998b. Zur Ultrastruktur, Ontogenese und Phylogenie der Brachiopoda. Cuvillier Verlag. Göttingen. v + 184 p., fig. 1–56.

Lüter, Carsten. 2000a. The origin of the coelom in Brachiopoda and its phylogenetic significance. Zoomorphology 120:15–28.

Lüter, Carsten. 2000b. Ultrastructure of larval and adult setae of Brachiopoda. Zoologischer Anzeiger 239:75–90.

Lüter, Carsten. 2001. Brachiopod larval setae—A key to the phylum's ancestral life cycle? *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Procedings of the Millennium Brachiopod Congress, 2000. The Systematics Association Special Volume Series 63. Taylor and Francis, London. p. 46–55.

Lüter, Carsten. 2001b. Larval brooding and development of the micromorph rhynchonellid Tethyrhynchia mediterranea (Brachiopoda, Recent). Journal of the Marine Biological Association of the United Kingdom 81:939–942.

Lüter, Carsten. 2004. How brachiopods get covered with nanometric silicon chips. Proceedings of the Royal Society London (series B, Supplement) Biology Letters 271:S465–S467.

Lüter, Carsten. 2005. The first Recent species of the unusual brachiopod *Kakanuiella* (Thecideidae) from New Zealand deep waters. Systematics and Biodiversity 3(1):105–111, 3 fig.

Lüter, Carsten. 2007. Recent brachiopods collected during the deep-sea cruise SO 168 ZEALANDIA with the research vessel FS Sonne between Mt. Spong (Tasman Sea) and the Chatham Islands (Pacific) in 2002–2003. *In* D. A. T. Harper, S. L. Long, & C. Nielsen, eds., Proceedings of the 5th International Brachiopod Congress, Copenhagen, July 4–8, 2005. Blackwell. London. Fossils and Strata 54.

Lüter, Carsten, & T. Bartolomaeus. 1997. The phylogenetic position of Brachiopoda—A comparison of morphological and molecular data. Zoologica Scripta 26(3):245–253.

Lüter, Carsten, & B. L. Cohen. 2002. DNA sequence evidence for speciation, paraphyly and a Mesozoic dispersal of cancellothyrid articulate brachiopods. Marine Biology 141:65–74, 1 fig.

Lüter, Carsten, Gert Wörheide, & Joachim Reitner. 2003. A new thecideid genus and species (Brachiopoda, Recent) from submarine caves of Osprey Reef (Queensland Plateau, Coral Sea, Australia). Journal of Natural History 37:1423–1432, 3 fig.

Ma Xue-ping. 1993. *Hunanotoechia*: A new Late Devonian rhynchonellid brachiopod from Xikuangshan, Hunan, China. Acta Palaeontologica Sinica 32(6):716–724.
In Chinese with English summary.

Ma Xueping, & Jed Day. 1999. The late Devonian brachiopod *Cyrtiopsis davidsoni* Grabau, 1923, and related forms from central Hunan of South China. Journal of Paleontology 73(4):608–624.

Ma Xueping, & Jed Day. 2000. Revision of *Tenticospirifer* Tien, 1938, and similar spiriferid brachiopod genera from the Late Devonian (Frasnian) of Eurasia, North America, and Australia. Journal of Paleontology 74(3):444–463.

Ma Xue-ping, Sun Yuan-lin, Hao Wei-cheng, & Liao Wei-hua. 2002. Rugose corals and brachiopods across the Frasnian-Famennian boundary in central Hunan, South China. Acta Palaeontologica Polonica 47(2):373–396.

MacKinnon, D. I. 1993. Loop ontogeny and ultrastructure in brachiopods of the Family Terebratellidae. *In* I. Kobayashi, H. Mutvei, & A. Sahni, eds., Structure, Formation, and Evolution of Fossil Hard Tissues. Tokai University Press, Tokyo. p. 313–340.

MacKinnon, D. I. 2002. Koninckinidina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1601–1604.

MacKinnon, D. I., & Gertruda Biernat. 1970. The probable affinities of the trace fossil *Diorygma atrypophilia*. Lethaia 3:163–172.

MacKinnon, D. I., & D. Gaspard. 1995. Similarity of early loop ontogeny in the Recent brachiopods *Macandrevia* King and *Ecnomiosa* Cooper: Taxonomic and phylogenetic implications. *In* P. Copper & J. Jin, eds., Third International Brachiopod Congress, Abstracts. Laurentian University. Sudbury, Ontario. p. 49.

MacKinnon, D. L., Norton Hiller, S. L. Long, & B. A. Marshall. 2007. *Neoaemula*, a new genus of platidiid brachiopod, with new observations on species referred to the Recent platidiid brachiopod *Amphithyris* Thomson. *In* D. A. T. Harper, S. L. Long, & C. Nielsen, eds., Proceedings of the 5th International Brachiopod Congress, Copenhagen, July 4–8, 2005. Blackwell. London. Fossils and Strata 54.

MacKinnon, D. I., & D. E. Lee. 2006. Terebratelloidea. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (revised), vol. 5. Geological Society of America & Paleontological Institute. Boulder, Colorado, and Lawrence, Kansas. p. 2227–2244.

MacKinnon, D. L., & S. L. Long. 2000. *Terebratula californiana* Küster, 1844, and reappraisal of west coast North American brachiopod species referred to the genus *Laqueus* Dall, 1870. Bulletin of the Natural History Museum of London (Geology) 56(2):85–90, 19 fig.

MacKinnon, D. L., & S. L. Long. 2007. A new species of the Recent brachiopod genus *Shimodaia* (Laqueoidea, Terebratulida) from the South China Sea. Paleontological Research.

MacKinnon, D. I., Michiko Saito, & Kazuyoshi Endo. 1997. Morphology and systematics of the Recent Japanese brachiopod *Shimodaia pterygiota* gen. et sp. nov. (Laqueidae: Terebratulida). Paleontological Research 1(3):225–233, 7 fig.

MacKinnon, D. I., & T. N. Smirnova. 1995. Scanning electron microscopy study of Cretaceous brachiopods of the new Family Praeargyrothecidae: Implications for megathyroid systematics and terebratulide phylogeny. Journal of Paleontology 69:670–685.

MacKinnon, D. I., & Alwyn Williams. 1974. Shell structure of terebratulid brachiopods. Palaeontology 17(1):179–202, fig. 1–3, pl. 21–27.

MacLeod, N. 2003. The causes of Phanerozoic extinctions. *In* L. Rothschild and A. Lister, eds., Evolution on Planet Earth. Academic Press. London. p. 253–277.

MacLeod, N., & G. Keller. 1996. Cretaceous-Tertiary Mass Extinctions: Biotic and Environmental Changes. W. W. Norton & Company. New York. 575 p.

MacLeod, N., P. F. Rawson, P. L. Forey, F. T. Banner, M. K. BouDagher-Fadel, P. R. Bown, J. A. Burnett, P. Chambers, S. Culver, S. E. Evans, C. Jeffrey, M. A. Kaminski, A. R. Lord, A. C. Milner, A. R. Milner, N. Morris, E. Owen, B. R. Rosen, A. B. Smith, P. D. Taylor, E. Urquhart, and J. R. Young. 1997. The Cretaceous-Tertiary biotic transition. Journal of the Geological Society of London 154:265–292.

Maillieux, Eugène. 1939. La faune des schistes de Barvaux-sur-Ourthe (Frasnien Supérieur). Musée Royal d'Histoire Naturelle de Belgique, Bulletin 15(53):1–8, fig. 1–6.

Makridin, V. P. 1955. Nekotorye Iurskie rinkhonellidy evropeiskoi chasti SSSR [Some Jurassic rhynchonellids from the European part of the USSR]. Zapiski Geologicheskogo Fakulteta Khar'kovskogo Gosudarstvennogo Universiteta imeni A.M. Gor'kogo 12:81–91, 3 pl.

Makridin, V. P. 1964. Brakhiopody Iurskikh Otlozhenii Russkoi Platformy i Nekotorukh Prilezhashchikh k nei Oblastei [Brachiopods from the Jurassic deposits of the Russian Platform and some adjoining regions]. Ministerstvo Vysshego i Srednego Spetsialnogo Obrasovaniia USSR, Kharkovskii Gozudarstvennyi Universitet imeni A.M. Gorkogo Nauchno-Issledovatelskii Sektor. Moscow. 395 p., 25 pl.

Mallatt, J., & C. J. Winchell. 2002. Testing the new animal phylogeny: First use of combined large-subunit and small-subunit rRNA gene sequences to classify the protostomes. Molecular Biology and Evolution 19:289–301.

Manceñido, M. O. 1983. A new terebratulid genus from Western Argentina and its homoeomorphs (Brachiopoda, Early Jurassic). Ameghiniana 20(3–4):347–365.

Manceñido, M. O. 1998. Revaluación de los tipos de crura de los Rhynchonellida post-paleozoicos (Brachiopoda).—VII Congreso Argentino de Paleontología y Bioestratigrafía, Resúmenes. Bahía Blanca, Argentina. p. 46.

Manceñido, M. O. 2000. Crural types among post-Paleozoic Rhynchonellida (Brachiopoda). The Millennium Brachiopod Congress, 10–14 July 2000, London, Abstracts. The Natural History Museum. London. p. 57.

Manceñido, M. O., & Miguel Griffin. 1988. Distribution and palaeoenvironmental significance of the genus *Bouchardia* (Brachiopoda, Terebratellidina): Its bearing on the Cenozoic evolution of the South Atlantic. Revista Brasileira de Geociências 18(2):201–211, 3 fig., 2 pl.

Manceñido, M. O., & E. F. Owen. 2001. Post-Paleozoic Rhynchonellida (Brachiopoda): Classification and evolutionary background. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. The Systematic Association Special Volume Series 63. London. p. 189–200.

Manceñido, M. O., E. F. Owen, A. S. Dagys, & Sun Dong-Li. 2002. Norelloidea. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1308–1325.

Manceñido, M. O., E. F. Owen, N. M. Savage, & A. S. Dagys. 2002. Dimerelloidea. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1236–1245.

Mansuy, H. 1914. Etude des faunes paléozoïques et mésozoïques des feuilles de Phu-Nho-Quan et de Son-Tay (Tonkin). Mémoires du Service Géologique de l'Indochine 3(2):43–85, 6 pl.

Mansuy, H. 1916. Etude complémentaire des faunes paléozoïques et triasiques dans l'Est du Tonkin (feuille de That-Khé, Pho-Bong-gia, Lang-Son). Mémoires du service Géologique de l'Indochine 5(4):39–71, 2 pl.

Marek, L., & Vladimír Havlíček. 1967. The articulate brachiopods of the Kosov Formation (Upper Ashgillian). Věstník Ústředního ústavu geologického 42:275–284, pl. 1–4.

Marin, F., R. Amons., N. Guichard., M. Stigter., A. Hecker., G. Luquet., P. Layrolle., G. Alcaraz., C. Riondet, & P. Westbroek. 2005. Caspartin and calprismin, two proteins of the shell calcitic prisms of the Mediterranean fan mussel *Pinna nobilis*. Journal of Biological Chemistry 280:33,895–33,908.

Marin, F., P. Corstjens., B. de Gaulejac, E. D. Vrind-De Jong, & P. Westbroek. 2000. Mucins and molluscan calcification—Molecular characterization of mucoperlin, a novel mucin-like protein from the nacreous shell layer of the fan mussel *Pinna nobilis* (Bivalvia, Pteriomorphia). Journal of Biological Chemistry 275:20,667–20,675.

Marin, F., Y. Dauphin., M. Smith., Y. Isa., G. Muyzer, & P. Westbroek. 1996. Skeletal matrices, muci, and the origin of invertebrate calcification. Proceedings of the National Academy of Sciences 93:1554–1559.

Marshall, J. D., & P. D. Middleton. 1990. Changes in marine isotopic composition and the late Ordovician glaciation. Journal of the Geological Society, London 147:1–4.

Marshall, J. D., D. Pirrie, A. Clarke, C. P. Nolan, & J. Sharman. 1996. Stable-isotopic composition of skeletal carbonates from living Antarctic marine invertebrates. Lethaia 29:203–212.

Martínez Chacón, M. L., & C. F. Winkler Prins. 2000. New Rugosochonetidae (Brachiopoda) from the upper Bashkirian and Moscovian of the Cantabrian Mountains (N Spain). Revista Española de Paleontología 15(2):219–232.

Massy, A. L. 1925. The Brachiopoda of the coasts of Ireland. Proceedings of the Royal Irish Academy (section B) 37:37–46.

Mawson, Ruth, & J. A. Talent. 1999. Silicified Early Devonian (Lochkovian) brachiopods from Windellama, southeastern Australia. Senckenbergiana lethaea 79:145–189, 11 pl.

Maxwell, W. G. H. 1954. *Strophalosia* in the Permian of Queensland. Journal of Paleontology 28:533–559, pl. 54–57.

Maxwell, W. G. H. 1964. The geology of the Yarrol region. Part 1. Biostratigraphy. University of Queensland, Department of Geology, Papers 5(9):1–79, 14 pl.

Mawe, J. 1823. Linnean System of Conchology. London. p. 65, pl. 16.

McArthur, J. M., D. T. Donovan, M. F. Thirlwall, B. W. Fouke, & D. Mattey. 2000. Strontium isotope profile of the early Toarcian (Jurassic) Ocean Anoxia Event, the duration of ammonite biozones, and belemnite paleotemperatures. Earth and Planetary Science Letters 179:269–285.

McCammon, H. M. 1973. The ecology of *Magellania venosa*, an articulate brachiopod. Journal of Paleontology 47(2):266–278, 6 fig.

McCammon, H. M., & Ralph Buchsbaum. 1968. Size and shape variation of three Recent brachiopods from the Strait of Magellan. *In* W. L. Schmitt and G. A. Llano, eds., Biology of the Antarctic seas, Antarctic Research Series 11(3):215–225, 8 fig.

McClintock, J. B., M, M. Slattery, & C. W. Thayer. 1993. Energy content and chemical defense of the articulate brachiopod *Liothyrella Uva* (Jackson, 1912) from the Antarctic Peninsula. Journal of Experimental Marine Biology and Ecology 169(1):103–116.

McClung, Graham. 1978. Morphology, Palaeoecology and Biostratigraphy of *Ingelarella* (Brachiopoda: Spiriferida) in the Bowen and Sydney Basins of Eastern Australia. Geological Survey of Queensland, Publication 365, Palaeontological Paper 40:17–60.

McConnaughey, T. A. 1989a. ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates: I. Patterns. Geochimica et Cosmochimica Acta 53:151–162.

McConnaughey, T. A. 1989b. ^{13}C and ^{18}O isotopic disequilibrium in biological carbonates: II. *In vitro* simulation of kinetic isotope effects. Geochimica et Cosmochimica Acta 53:163–171.

McConnaughey, T. A., J. Burdett, J. F. Whelan, & C. K. Paull. 1997. Carbon isotopes in biological carbonates: Respiration and photosynthesis. Geochimica et Cosmochimica Acta 61:611–622.

McCrea, J. M. 1950. On the isotopic chemistry of carbonates and a paleotemperature scale. The Journal of Chemical Physics 18:849–857.

McGhee, G. R. 1980. Shell form in the biconvex articulate Brachiopoda—A geometric analysis. Paleobiology 6(1):57–76.

McKellar, R. G. 1965. An Upper Carboniferous brachiopod fauna from the Monto District, Queensland. Geological Survey of Queensland (Paleontological Papers 1), Publication 328:1–15, 5 pl.

McKinney, C. R., J. M. McCrea, S. Epstein, H. A. Allen, & H. C. Urey. 1950. Improvements in mass spectrometers for the measurements of small differences in isotope abundance ratios. Reviews of Scientific Instruments 21:724–730.

McLean, D. M. 1985. Mantle degassing unification of the trans-K-T geobiological record. *In* M. K. Hecht, B. Wallace, & G. T. Prance, eds., Evolutionary Biology, vol. 9. Plenum Press. New York. p. 287–313.

Meglitsch, P. A., & F. R. Schram. 1991. Invertebrate Zoology, 3rd ed. Oxford University Press. New York. 623 p.

Meidlinger, K., P. A. Tyler, & L. S. Peck. 1998. Reproductive patterns in the Antarctic brachiopod *Liothyrella uva*. Marine Biology 132:153–162.

Meile, Brigitte, & Daniel Pajaud. 1971. Présence de Brachiopodes dans le Grand Banc des Bahamas. Comptes rendus des séances de l'Académie des Sciences 273:469–472, 2 fig., 1 pl.

Mélou, Michel, Lhacène Oulebsir, & Florentin Paris. 1999. Brachiopodes et chitinozoaires ordoviciens dans le NE du Sahara algérien: Implications stratigraphiques et paléogéographiques. Geobios 32:823–839.

Menakova, G. N. 1991. Ordoviskaya sistema. Brakhiopody [Ordovician System. Brachiopods]. Atlas iskopaemoi fauny i flory Tajikistana. Ordovik, Silur, Devon. Donish. Dyushanbe. 272 p., 156 pl. In Russian.

Meneghini, C. G., & G. G. Capellini. 1880. Sulla Memoria del Dott. Mario Canavari i Brakhiopodi degli Strati a Terebratula aspasia Mgh. sull. Appeninus Centrale. Atti della Reale Accademia dei Lincei, Transiunti (series 3) 4:199–201.

Menke, C. T. 1828. Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur. G. Uslar. Pyrmonti. 91 p.

Mergl, Michal. 1983. New brachiopods (Cambrian—Ordovician) from Algeria and Morocco (Mediterranean Province). Casopis pro Mineralogii a Geologii 28:337–348.

Mergl, Michal. 1984. The fauna of the upper Tremadocian of Central Bohemia. Sbornik Geologickych věd, Paleontologie 26:9–46.

Mergl, Michal. 1995. New lingulate brachiopods from the Milina Formation and the base of Klabava Formation (late Tremadoc–early Arenig), Central Bohemia. Věstník Českého geologického ústavu 70(2):101–114, 2 fig., 4 pl.

Mergl, Michal. 1996a. New lingulate brachiopods from the top of the Klabava Formation (Lower Ordovician, Bohemia). Journal of the Czech Geological Society 41(1–2):43–54, 1 fig., 4 pl.

Mergl, Michal. 1996b. Discinid brachiopods from the Kopanina Formation (Silurian) of Amerika quarries near Morina, Barrandian, Central Bohemia. Casopis Národniho muzea Rada prirodovedna 165(1–4):121–126, pl. 1–4.

Mergl, Michal. 1997a. Obolid brachiopods with burrowing sculptures in the Lower Ordovician of Bohemia. Věstník Českého geologického ústavu 72(2):127–139.

Mergl, Michal. 1997b. New and rare lingulate brachiopods from lower part of the Klabava Formation (Arenig, Lower Ordovician) of Prague Basin, Bohemia. Journal of the Czech Geological Society 42(1–2):95–104.

Mergl, Michal. 1998. Generic status of two lingulacean brachiopods from the Králův Dvůr Formation, Upper Ordovician (Central Bohemia). Věstník Českého geologického ústavu 73(3):223–227.

Mergl, Michal. 2001a. Lingulate brachiopods of the Silurian and Devonian of the Barrandian (Bohemia, Czech Republic). Acta Musei Nationalis Pragae (Series B, Historia Naturalis) 57(12):1–49, 12 fig., 36 pl.

Mergl, Michal. 2001b. Extinction of some lingulate brachiopod families: New stratigraphical data from the Silurian and Devonian of Central Bohemia. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. Systematic Association Special Volume Series 63:345–351.

Mergl, Michal. 2002. Linguliformean and craniiformean brachiopods of the Ordovician (Třenice to Dobrotivá formations) of the Barrandian, Bohemia. Acta Musei Nationalis Praguae (Series B, Historia Naturalis) 58(1–2):1–82, 18 fig., 42 pl.

Merla, Giovanni. 1930. La fauna del Calcare a Bellerophon della regione dolomitica. Memoria dell'Instituto Geologico della Regia Universita di Padova 9:221 p., 3 fig., 11 pl.

Michalík, Jozef. 1993. Growth and structure of some Rhaetian rhynchonellid shells from the central western Carpathians. *In* J. Pálfy & A. Vörös, eds., Mesozoic Brachiopods of Alpine Europe. Hungarian Geological Society. Budapest. p. 101–108.

Michenfelder, M., G. Fu., C. Lawrence., J. C. Weaver., B. A. Wustman., L. Taranto., J. S. Evans, & D. E. Morse. 2003. Characterization of two molluscan crystal-modulating biomineralization proteins and identification of putative mineral binding domains. Biopolymers 70: 522–533.

von Middendorff, A. T. 1849a. Vorläufige Anzeige Bisher Unbekannter Mollusken, als Vorarbeit zu einer Malacozoologia Rossica. Mémoires de l'Académie Impériale des Sciences de St. Petersbourg (series 6) 6:13–22.

von Middendorff, A. T. 1849b. Beiträge zu einer Malacozoologia Rossica. Aufzählung und Beschreibung der zur Meeres Fauna Russlands gehörigen Zweischaler. Mémoires de l'Académie Impériale des Sciences de St.-Pétersbourg (6th series) 4 (part 3, no. 38):517–519.

Mii, Horng-Sheng, & Ethan L. Grossman. 1994. Late Pennsylvanian seasonality reflected in the ^{18}O and elemental composition of a brachiopod shell. Geology 22:661–664.

Mii, H.-S., E. L. Grossman, T. E. Yancy, B. I. Chuvashov, and A. Egorov. 2001. Isotope records of brachiopod shells from the Russian Platform: Evidence for the onset of mid-Carboniferous glaciation. Chemical Geology 175:133–147.

Miller, A. N. 2004. The Ordovician Radiation: Towards a New Global Synthesis. *In* B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 380–388.

Miller, S. R., S. Aigustine, T. L. Olson, R. E. Blankenship, J. Selker, & A. M. Wood. 2005. Discovery of a free-living chlorophyll d-producing cyanobacterium with a hybrid protebacterial/cyanobacterial small-subunit rRNA gene. Proceedings of the National Academy of Sciences 102:850–855.

Missarzhevsky, V. V. 1970 [1969]. Description of hyolithids, gastropods, hyolithelminths, camenides and forms of an obscure taxonomic position. *In* M. R. Raaben, ed., The Tommotian Stage and the Cambrian Lower Boundary Problem. Akademiya Nauka SSSR. Moscow. p. 103–175.

Mitchell, W. I. 1977. The Ordovician brachiopods from Pomeroy, Co. Tyrone. Palaeontographical Society Monograph 130:138 p., 28 pl.

Modzalevskaya, T. L. 1979. K sistematike paleozoiskikh atiridid [Systematics of Paleozoic athyridids]. Paleontologicheskii Zhurnal 1979(2):48–63, 11 fig., pl. 4.

Modzalevskaya, T. L. 1981. Brakhiopody [Brachiopods]. Biostratigraficheskii Obzor Fauny i Opisanie Nekotorykh Kharakternykh Predstavitelei. *In* L. V. Nekhorosheva, ed., Ob'iasnitel'naia Zapiska k Skheme Stratigrafii Verkhnesiluriiskikh Otlozhenii Vaigachsko-Iuzhnonovosemel'skogo Regiona [Explanatory note on stratigraphy chart of upper Silurian deposits of Vaigach-South Novaya Zemlya region. Biostratigraphical survey and description of some typical representatives]. Vsesoiuznyi Nauchno-Issledovatel'skii Institut Geologii i Mineral'nykh Resursov Mirovogo Okeana. Leningrad. p. 146–157.

Modzalevskaya, T. L. 1994. The middle Ludfordian event in brachiopod evolution in the European province. *In* H. P. Shonlaub & L. H. Kreutzer, eds., Field Meeting in the Southern Alps, Austria 1994 (In memoriam, Dr Hermann Jaeger). IUGS Subcommission on Silurian Stratigraphy, Geologische Bundesanstalt, 30. Wien. p. 147.

Modzalevskaya, T. L. 1997a. The middle Ludfordian event in the Silurian evolution of brachiopods of the European province. Stratigrafiya, Geologicheskaya Korrelyatsiya 5(3):3–9.
In Russian, English translation in Stratigraphy and Geological Correlation 5(3):205–211.

Modzalevskaya, T. L. 1997b. Upper Silurian brachiopods from type sections in Pechora and the Central Urals. *In* G. A. Stukalina, ed., Atlas of Palaeozoic benthic fauna of the north-east of European Russia. Ostracods, brachiopods, rugose corals. VSEGEI. St. Petersburg. p. 34–53.
In Russian.

Modzalevskaya, T. L., O. P. Kovalevskii, A. F. Abushik, & others. 1994. The basis of the Ludlowian zonal subdivisions of Russia and adjacent territories. *In* A. N. Oleinikov, ed., Zonal subdivisions and interregional correlation of Paleozoic and Mesozoic deposits of Russia and adjacent territories, vol. 1, Paleozoic. VSEGEI. St. Petersburg. 158 p.
In Russian.

Montañez, I. P., D. A. Osleger, J. L. Banner, L. Mack, & M. L. Musgrove. 2000. Evolution of the Sr and C isotope composition of Cambrian oceans. GSA Today 10:1–5.

Moore, R. C. 1952. Brachiopoda. *In* R. C. Moore, C. G. Lalicker, & A. G. Fischer, Invertebrate Fossils. McGraw-Hill. New York. p. 197–267.

Moore, R.C., ed. 1965. Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & the University of Kansas Press. New York & Lawrence. 927 p., 746 fig.

Morris, John. 1845. Brachiopoda. *In* P. E. de Strzeleki, ed., Physical description of New South Wales and Van Diemen's Land. Brown, Green and Longman. London. 462 p., 19 pl.

Morrisey, J. H. 1981. Silver stain for proteins in polyacrylamide gels: A modified procedure with enhanced uniform sensitivity. Analytical Biochemistry 117:307–310.

Morse, E. S. 1902. Observations on living Brachiopoda. Memoirs of the Boston Society of Natural History 5(8):313–386.

Morton, S. G. 1828. Description of the fossil shells which characterize the Atlantic Secondary Formation of New-Jersey and Delaware; including four new species. Academy of Natural Sciences of Philadelphia, Journal 6(1):72–100, pl. 3.

Motchurova-Dekova, Neda. 2001. Taxonomic and phylogenetic aspects of the shell ultrastructure of nine Cretaceous rhynchonellide brachiopod genera. Paleontological Research 5(4):319–330.

Motchurova-Dekova, Neda, Michiko Saito, & Kazuyoshi Endo. 2002. The Recent rhynchonellide brachiopod *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa, Japan. Paleontological Research 6(3):299–319, 14 fig.

Motchurova-Dekova, Neda, & E. Simon. 2007. *Homaletarhynchia* Simon & Owen, 2001, a genus transferred to the Basiliolidae (Pugnacoidea, Rhynchonellida, Brachiopoda). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 77:117–129.

Motchurova-Dekova, Neda, & Emma Taddei-Ruggiero. 2000. First occurrence of the brachiopod family Erymnariidae Cooper in the Upper Cretaceous of southern Italy. Palaeontology 43(1):173–197, pl. 1–5.

Muir-Wood, H. M. 1930. The classification of the British Carboniferous brachiopod subfamily Productinae. Annals and Magazine of Natural History (series 10) 5(25):100–108.

Muir-Wood, H. M. 1936. On the Liassic brachiopod genera *Orthoidea* and *Orthotoma*. Annals and Magazine of Natural History (London) (series 10) 17(98):221-242.

Muir-Wood, H. M. 1955. A History of the Classification of the Phylum Brachiopoda. British Museum (Natural History). London. v + 124 p., 12 fig.

Muir-Wood, H. M. 1959. Report on the Brachiopoda of the John Murray Expedition. *In* The John Murray Expedition 1933–34, Scientific Reports 10(6):283–317, 4 fig., 5 pl.

Muir-Wood, H. M. 1960. Homeomorphy in Recent Brachiopoda: *Abyssothyris* and *Neorhynchia*. The Annals and Magazine of Natural History (series 13) 3:521–528, 1 pl.

Muir-Wood, H. M. 1962. On the Morphology and Classification of the brachiopod suborder Chonetoidea. British Museum (Natural History), Monograph. viii + 132 p., 24 fig., 16 pl.

Muir-Wood, Helen M. 1965. Mesozoic and Cenozoic Terebratulidina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 2. Geological Society of America & Paleontological Institute. New York and Lawrence, Kansas. p. 762–816.

Muir-Wood, H. M., & G. A. Cooper. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). Geological Society of America Memoir 81:447 p., 8 fig., 135 pl.

Müller, F. 1860. Beschreibung einer Brachiopodenlarve. Archiv für Anatomie und Physiologie, Leipzig for 1860:72–80.

Müller, O. F. 1776. Zoologiae Danicae Prodromus seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium. Typis Hallageriis. Copenhagen. xxxii + 282 p.

Mulley, J., & P. W. H. Holland. 2004. Small genome, big insights. Nature 431:916–917.

Munier-Chalmas, M. 1881. Sur quelques genres des Brachiopodes. Bulletin Société Géologique France 8(4):279–280.

von Münster, Georg. 1839. Beiträge zur Petrefacten-Kunde. Der Buchner'schen Buchhandlung. Bayreuth. 124 p., 19 pl.

Nalivkin, D. V. 1979. Brakhiopody Turneiskogo Iarusa Urala. [Brachiopods from the Tournaisian Stage of the Urals]. Akademiia Nauk SSSR, Otdelenie Geologii Geofiziki i Geokhimii. Nauka. Leningrad. 248 p., 65 pl.

Nazarov, B. B. & L. E. Popov. 1980. Stratigrafiya i fauna kremnistokarbonatnykh tolshch ordovika Kazakhstana. Geologicheskiy Institut Akademii Nauk SSSR, Trudy 331:190 p., 60 fig., 32 pl.

Neall, V. E. 1970. Notes on the ecology and paleoecology of *Neothyris*, an endemic New Zealand brachiopod. New Zealand Journal of Marine and Freshwater Research 4(2):117–125, 2 fig.

Neall, V. E. 1972. Systematics of the endemic New Zealand brachiopod *Neothyris*. Journal of the Royal Society of New Zealand 2(2):229–247, 6 fig.

Nekvasilová, Olga. 1973. The brachiopod genus *Bohemirhynchia* gen. n. and *Cyclothyris* McCoy (Rhynchonellidae) from the Upper Cretaceous of Bohemia. Sbornik Geologickych věd, Paleontologie 15:75–117, pl. 1–12.

Nelson, Gareth. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. Systematic Zoology 27(3):324–345.

Neville, A. C. 1993. Biology of Fibrous Composites: Development Beyond the Cell Membrane. Cambridge University Press. Cambridge, UK. 224 p.

Nielsen, A. T. 1992. Ecostratigraphy and the recognition of the Arenigian (early Ordovician) sea-level changes. *In* B. D. Webby & J. R. Laurie, Global Perspectives on Ordovician Geology. A. A. Balkema. Rotterdam. p. 355–356.

Nielsen, Claus. 1985. Animal phylogeny in the light of the trochaea theory. Biological Journal of the Linnean Society 25:243–299.

Nielsen, C. 1991. The development of the brachiopod *Crania* (*Neocrania*) *anomala* (O.F. Müller) and its phylogenetic significance. Acta Zoologica (Stockholm) 72:7–28.

Nielsen, Claus. 1995. Animal Evolution: Interrelationships of the Living Phyla. Oxford University Press. Oxford. 467 p.

Nielsen, Claus. 2001. Animal Evolution: Interrelationships of the Living Phyla, 2nd edition. Oxford University Press. Oxford. 467 p.

Nielsen, C. 2002. The phylogenetic position of Entoprocta, Ectoprocta, Phoronida and Brachiopoda. Integrative and Comparative Biology 42:685–691.

Nielsen, Claus, N. Scharff, & D. Eibye-Jacobsen. 1996. Cladistic analysis of the animal kingdom. Biological Journal of the Linnean Society 57:385–410.

Nier, A. O. 1940. A mass spectrometer for routine isotope abundance measurements. Reviews of Scientific Instruments 11:212–216.

Nier, A. O. 1947. A mass spectrometer for isotope and gas analysis. Reviews of Scientific Instruments 18:398–411.

Nikiforova, O. I. 1970. Brakhiopody Grebenskogo Gorizonta Vaigacha (Pozdnii Silur) [Brachiopods from the Greben' horizon of Vaigach (late Silurian)]. *In* S. V. Cherkesova, ed., Stratigrafiia i Fauna Siluriiskikh Otlozhenii Vaigacha (sbornik statei) [Stratigraphy and faunas of the Silurian deposits of Vaigach (collected articles)]. Nauchno-Issledovatel'skii Institut Geologii Arktiki. Ministerstvo Geologii SSSR. Leningrad. p. 97–149, 7 pl.

Nikitin, I. F., & L. E. Popov. 1996. Strophomenid and triplesiid brachiopods from an Upper Ordovician carbonate mound in central Kazakhstan. Alcheringa 20:1–20.

Nikitin, I. F., L. E. Popov, & L. E. Holmer. 1996. Late Ordovician brachiopod assemblage of Hiberno-Salairian type Central Kazakhstan. GFF 118:83–96.

Nikitina, O. I., L. E. Popov, R. B. Neuman, M. G. Bassett, & L. E. Holmer. 2006. Mid Ordovician (Darriwilian) brachiopods of South Kazakhstan. National Museum of Wales Geological Series 25:145–222, 41 fig.

Nilsson, S. 1827. Petreficata Suecana formationis Cretaceae, descripta et iconibus illustrata. Lund. 39 p., 10 pl.

Nislow, C. 1994. Cellular dynamics during the early development of an articulate brachiopod, *Terebratalia transversa*. *In* W. H. Wilson Jr., S. A. Stricker, & G. L. Shinn, eds., Reproduction and development of marine invertebrates. The Johns Hopkins University Press. Baltimore. p. 118–128.

Noguchi, Y., K. Endo, F. Tajima, & R. Ueshima. 2000. The mitochondrial genome of the brachiopod *Laqueus rubellus.* Genetics 155:245–259.

Nomura, S., & K. M. Hatai. 1936. *Diestothyris tisimana,* a new species of Brachiopoda from the Northern Pacific. The Venus 6(3):131–134.

Nylander, J. A. A. 2004. MrModeltest 2.0. Evolutionary Biology Centre, Uppsala University: Program distributed by the author.

Oehlert, D.–P. 1887. Brachiopodes (Appendice). *In* Paul Fischer, Manuel de conchyliologie et de paléontologie conchyliologique, ou Histoire naturelle des mollusques vivants et fossiles, pt. 11. F. Savy. Paris. p. 1189–1334, fig. 892–1138, pl. 15.

O'Neil, J. R., R. N. Clayton, & T. K. Mayeda. 1969. Oxygen isotope fractionation in divalent metal carbonates. Journal of Chemical Physics 51:5547–5558.

Öpik, A. A. 1933. Über Plectamboniten. Universitatis Tartuensis (Dorpatensis) Acta et Commentationes (series A) 24(7):1–79, pl. 1–12.

Öpik, A. A 1934. Über Klitamboniten. Universitatis Tartuensis (Dorpatensis) Acta et Commentationes (series A) 26(5):1–239, fig. 1–55, 48 pl.

Oraspõld, A. L. 1956. New brachiopods of the Johvi, Keila and Vasalemma horizons. Trudy Instityta Geologii Akademiia Nauk Estonskoi SSR 1:41–67, pl. 1–4.
In Russian.

d'Orbigny, Alcide. 1847. Considérations zoologiques et géologiques sur les brachiopodes ou palliobranches, parts 1–2. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris (2nd series) 25(5):193–195; 25(7):266–269.

Ortiz, J. D., A. C. Mix, W. Rugh, J. M. Watkins, & R. W. Collier. 1996. Deep-dwelling planktonic foraminifera of the northeastern Pacific Ocean reveal environmental control of oxygen and carbon isotopic disequilibria. Geochimica et Cosmochimica Acta 60:4509–4523.

Ostrow, D. G., S. R. Wing, P. V. Mladenov, & M. S. Roy. 2001. Genetic differentiation of *Terebratella sanguinea* in the New Zealand fiords: A dispersal barrier in the marine environment? *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. The Systematics Association Special Volume Series 63:150–159, 1 fig.

Ovcharenko, V. N. 1983. Iurskie Brakhiopody Pamira [Jurassic brachiopods of the Pamirs]. Akademia Nauk Tadzhikskoi SSR, Institut Geologii. Dushanbe. p. 1–196, pl. 1–19.

Ovtsharenko, V. N. 1993. [Two new genera of the Late Jurassic brachiopods in the Pamirs]. Izvestiia Akademii Nauk Respubliki Tadzhikistan Otdelenie Nauk o Zemle 1(1):14–19.

Padden, M., H. Weissert, and M. de Rafelis. 2001. Evidence for Late Jurassic release of methane from gas hydrates. Geology 29:223–226.

Paeckelmann, Werner. 1942. Beiträge zur Kenntnis devonischer Spiriferen. Abhandlungen des Reichamts für Bodenforschung (Neue Folge) 197:1–188, 93 fig., 8 pl.

Page, R. D. M., & E. C. Holmes. 1998. Molecular evolution: A phylogenetic approach. Blackwell Science. Oxford. p. 1–346.

Pajaud, Daniel. 1970. Monographie des Thécidées. Mémoires de la Société Géologique de France (new series) 49(112):349 p., 140 fig., 16 pl.

Pajaud, Daniel. 1974. Écologie de Thécidées. Lethaia 7:203–218, 6 fig.

Pallas, P. S. 1776. Miscellanea Zoologica, quibus imprimis et obscurae Animalium species descriuntus. P. van Cleef. Hagae comitum. xi + 224 p., pl. 1–14.

Palmer, A. R. 2004. Symmetry breaking and the evolution of development. Science 306:828–833.

Pan C.-M. & N. Watabe. 1988. Shell growth of *Glottidia pyramidata* Stimpson (Brachiopoda: Inarticulata). Journal of Experimental Marine Biology and Ecology 119:43–53.

Pan C.-M. & N. Watabe. 1989. Periostracum formation and shell regeneration in the lingulid *Glottidia pyramidata* (Brachiopoda: Inarticulata). Transactions of the American Microscopy Society 108:283–298.

Papillon, D., Y. Perez, X. Caubit, & Y. Le Parco. 2004. Identification of chaetognaths as protostomes is supported by analysis of their mitochondrial genome. Molecular Biology and Evolution 21:2111–2129.

Parfrey, S. M. 1983. Redescription of the Permian aulostegid brachiopod *Taeniothaerus subquadratus* (Morris, 1845), the type species of *Taeniothaerus*. Memoir of the Australasian Association of Palaeontologists 1(Dorothy Hill Jubilee Memoire):289–296.

Parkinson, D., G. B. Curry, M. Cusack, & A. E. Fallick. 2005. Shell structure, patterns and trends of oxygen and carbon stable isotopes in modern brachiopod shells. Chemical Geology 219:193–235.

Passamaneck, Y., & K. M. Halanych. 2006. Lophotrochozoan phylogeny assessed with LSU and SSU data: Evidence of lophophorate polyphyly. Molecular Phylogenetics and Evolution 40(1):20–28.

Paterson, J. R., & G. A. Brock. 2003. Early Ordovician orthide brachiopods from Mount Arrowsmith, Northwestern New South Wales, Australia. Records of the Australian Museum 55:221–230.

Patterson, Colin. 1981. Significance of fossils in determining evolutionary relationships. Annual Review of Ecology and Systematics 12:195–223.

Peck, L. S., S. Brockington, & T. A. Brey. 1997. Growth and metabolism in the Antarctic brachiopod *Liothyrella uva*. Philosophical Transactions of the Royal Society of London (series B, Biological Sciences) 352:851–858.

Peck, L. S., & L. J. Holmes. 1989. Seasonal and ontogenetic changes in tissue size in the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). Journal of Experimental Marine Biology and Ecology 134:25–36.

Peck, L. S., K. Meidlinger, & P. A. Tyler. 2001 Development and settlement characteristics of the Antarctic brachiopod *Liothyrella uva* (Broderip, 1833). *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods—Past and Present. Taylor and Francis. London. p. 80–90.

Peck, L. S., & K. Robinson. 1994. Pelagic development in the brooding Antarctic brachiopod *Liothyrella uva*. Marine Biology 120:279–286.

von Peetz, H. 1901. Materialy k poznaniiu fauny Devonskikh otlozhenii okrain Kuznetskogo uglenosnogo basseina [Beiträge zur Kenntniss der Fauna aus den devonischen Schichten am Rande des Steinkohlenbassins von Kuznetz]. Travaux Section Geologique du Cabinet de sa Majesté St. Pétersbourg 4:1–394, 6 pl.

Pennington, J. T., M. N. Tamburri, & J. P. Barry. 1999. Development, temperature tolerance, and settlement preference of embryos and larvae of the articulate brachiopod *Laqueus californianus*. Biological Bulletin 196:245–256.

Percival, E. 1944. A contribution to the life-history of the brachiopod *Terebratella inconspicua* Sowerby. Transactions of the Royal Society of New Zealand 74:1–23.

Percival, E. 1960. A contribution to the life history of the brachiopod *Tegulorhynchia nigricans*. Quarterly Review of Microscopical Science 101:439–457.

Percival, I. G. 1995. *Eodinobolus* and related trimerellid brachiopods from the Late Ordovician of New South Wales. Memoirs of the Association of Australasian Palaeontologists 18:41–60, fig. 1–9.

Perez-Huerta, A, M. Cusack, and J. England. 2007. Crystallography and diagenesis in fossil craniid brachiopods. Palaeontology 50:757–763.

Peterson, K. J., & D. J. Eernisse. 2001. Animal phylogeny and the ancestry of bilaterians: Inferences from morphology and 18S rDNA gene sequences. Evolution and Development 3:170–205.

Pettitt, N. E. 1950. A Monograph of the Rhynchonellidae of the British Chalk. Part I. Palaeontographical Society of London, Monograph 103(450):i–vi + 1–26, pl. 1–2.
Published for 1949.

Phillips, John. 1841. Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and west

Somerset. Geological Survey of Great Britain, Memoir 1. Longman & Co. London. xii + 231 p., 60 pl.

Phillips, J., & J. W. Salter. 1848. Palaeontological appendix to Professor John Phillips' memoir on the Malvern Hills compared with the Palaeozoic districts of Allerly, etc. Memoirs of Geological Survey of Great Britain 2:331–386, pl. 4–30.

Pitrat, C. W. 1965. Spiriferidina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence, Kansas. p. 667–728.

Poletaev, V. I. 1997. A revision of the genus *Neospirifer* Fredericks, 1924 and a description of *Lutuginia*, a new genus in the subfamily Neospiriferinae. Paleontological Journal 31(3):302–311.

Poletaev, V. I. 1999. Revision of *Palaeochoristites* and description of a new Early Carboniferous spiriferid genus *Phragmobrachythyris*. Paleontological Journal 33(3):254–262.
Translated from Paleontologicheskii Zhurnal 1999(3):41–49.

Poletaev, V. I. 2000. *Donispirifer* and *Tegulispirifer*—New Middle to Late Carboniferous spiriferids from Eurasia. Paleontological Journal 34(3):278–286.

Poletaev, V. I. 2001. *Triangularia* gen. nov. and other new Carboniferous spiriferids and spiriferinids from Eurasia. Paleontological Journal 35(5):491–497.
Translated from Paleontologicheskii Zhurnal 2001(5):42–48.

Pope, J. K. 1976. Comparative morphology and shell histology of the Ordovician Strophomenacea (Brachiopoda). Palaeontographica Americana 49:127–213.

Popiel-Barczyk, E. 1968. Upper Cretaceous terebratulids (Brachiopoda) from the Middle Vistula Gorge. Prace Muzeum Ziemi 12: 3–86.

Popov, L. E. 1980. New brachiopod species from the Middle Ordovician of the Chu-Ili Hills. Ezhegodnik Vsesoyuznovo Palaeontolicheskova Obshchestvo 23:139–158.

Popov, L. Ye. 1992. The Cambrian radiation of brachiopods. *In* J. H. Lipps & P. W. Signor, eds., Origin and Early Evolution of the Metazoa. Plenum Press. New York. p. 399–423.

Popov, L. E. 2000a. Late Ordovician (Caradoc) linguliformean microbrachiopods from north-central Kazakhstan. Alcheringa 24:257–275, 8 fig.

Popov, L. E. 2000b. Late Ordovician (Ashgill) microbrachiopods from Zharyk beds, north-central Kazakhstan. Geobios 33(4):419–435.

Popov, L. Ye., M. G. Bassett, & L. E. Holmer. 2000. Class Craniata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 158–168.

Popov, L. E., M. G. Bassett, L. E. Holmer, & J. Laurie. 1993. Phylogenetic analysis of higher taxa of Brachiopoda. Lethaia 26:1–5.

Popov, L. E., & L. R. M. Cocks. 2006. Late Ordovician brachiopods from the Dulankara Formation of the Chu-Ili Range, Kazakhstan: Their systematics, palaeoecology and palaebiogeography. Palaeontology 49:247–283, pl. 1–6.

Popov, L. E., L. R. M. Cocks, & I. F. Nikitin. 2002. Upper Ordovician brachiopods from the Anderken formation, Kazakhstan: Their ecology and systematics. Bulletin of the Natural History Museum London (Geology) 58:13–79, 14 pl.

Popov, L. E., & L. E. Holmer. 1994. Cambrian-Ordovician lingulate brachiopods from Scandinavia, Kazakhstan, and South Ural Mountains. Fossils and Strata 35:156 p., 115 fig.

Popov, L. E., & L. E. Holmer. 2000a. Class Craniata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (revised), vol. 2. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 158–192.

Popov, L. Ye., & L. E. Holmer. 2000b. Trimerellida and Chileata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 184–200.

Popov, L. Ye., & L. E. Holmer. 2000c. Class Obolellata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 201–208.

Popov, L.E., L. E. Holmer, & M. G. Bassett. 1996. Radiation of the earliest calcareous brachiopods. *In* P. Copper and J. Jin, eds., Brachiopods: Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, 1995. Balkema. Rotterdam. p. 209–213.

Popov, L. E., L. E. Holmer, & V. Ju. Gorjansky. 1996. Middle Cambrian lingulate brachiopods from Tarbagatay Range, Kazakhstan. Acta Palaeontologica Polonica 41(3):299–317.

Popov, L., L. E. Holmer, & V. Yu. Gorjansky. 1997. Late Ordovician and Early Silurian trimerellide brachiopods from Kazakstan. Journal of Paleontology 71:584–598.

Popov, L. E., L. E. Holmer, & J. F. Miller. 2002. Lingulate brachiopods from the Cambrian-Ordovician boundary beds of Utah. Journal of Paleontology 76:211–228.

Popov, L. Ye., L. E. Holmer, A. J. Rowell, & John Peel. 1997. Early Cambrian brachiopods from North Greenland. Palaeontology 40(2):337–354, 7 fig., 1 pl.

Popov, L. E., I. F. Nikitin, & L. R. M. Cocks. 2000. Late Ordovician brachiopods from the Otar Member of the Chu-Ili Range, south Kazakhstan. Palaeontology 43:833–870, 6 pl.

Popov, Leonid E., I. F. Nikitin, & E. V. Sokiran. 1999. The earliest smooth atrypides and athyridides (Brachiopoda) from the Ordovician of Kazakhstan. Palaeontology 42:625–661.

Popov, L. Ye., & Yu. A. Tikhonov. 1990. Rannekembriiskie brakhiopody iz iuzhnoi Kirgizii [Early Cambrian brachiopods from south Kirgizii]. Paleontologicheskii Zhurnal 1990(3):33–44, fig. 1–2, pl. 3–4.

Popov, L.Ye, & G. T. Ushatinskaya. 1987. Novye dannye o mikrostrukture rakoviny bezzamkovykh brakhiopod otriada Paterinida [New data on the microstructure of the shell of inarticulate brachiopods of the order Paterinida]. Akademiia Nauk SSSR, Doklady (Moscow) 293(5):1,228–1,231.

Popov, Leonid E., Olev Vinn, & Olga I. Nikitina. 2001. Brachiopods of the redefined family Tritoechiidae from the Ordovician of Kazakhstan and South Urals. Geobios 34(2):131–155.

Popov, L. Ye., & Alwyn Williams. 2000. Class Kutorginata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. The Geological Society of America and Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 208–215.

Popp, B. N., T. F. Anderson, & P. A. Sandberg. 1986a. Brachiopods as indicators of original isotopic compositions in some Paleozoic limestones. Geological Society of America Bulletin 97:1262–1269.

Popp, B. N., T. F. Anderson, & P. A. Sandberg. 1986b. Textural, elemental and isotopic variations among constituents in middle Devonian limestones, North America. Journal of Sedimentary Petrology 56:715–727.

Porter, S. M. 2004. Halkieriids in Middle Cambrian phosphatic limestones from Australia. Journal of Paleontology 78:574–590.

Posenato, Renato. 1998. The gen. *Comelicania* Frech, 1901 (Brachiopoda) from the Southern Alps: Morphology and classification. Rivista Italiana di Paleontologia e Stratigrafia 104:43–68.

Posenato, Renato. 2001. The athyridoids of the transitional beds between Bellerophon and Werfen Formations (uppermost Permian, southern Alps, Italy). Rivista Italiana di Paleontologia e Stratigrafia 107:197–226.

Pourtalès, L.F. de, 1867 [1868]. Contributions to the fauna of the Gulf Stream at great depths. Bulletin of the Museum of Comparative Zoology, Harvard University 1(6):103–120.
1st series 1867, 2nd series 1868: 121–142.

Prendergast, K. L. 1943. Permian Productidinae and Strophalosiinae of Western Australia. Journal of the Royal Society of Western Australia 28:1–73.

Pross, A. 1980. Untersuchungen zur Gliederung von *Lingula anatina* (Brachiopoda).—(Archimerie bei Brachiopoden). Zoologische Jahrbücher, Abteilung für Anatomie und Ontogenie der Tiere 103:250–263.

Prud'homme, B., N. Lartillot, G. Balavoine, A. Adoutte, & M. Vervoort. 2002. Phylogenetic analysis of the Wnt gene family: Insights from lophotrochozoan members. Current Biology 12:1395–1400.

Pushkin, V. I. 1996. *Pripyatispirifer*, a new lower Famennian genus from Belarus. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 66:43–51, 2 fig., 1 tab., 1 pl.

Puura, I., & Nemliher, J. 2001. Apatite varieties in Recent and fossil linguloid shells. *In* C. H. C. Brunton, L. R. M. Cocks, and S. L. Long, eds., Brachiopods Past and Present. The Systematics Association Special Volume Series 63. Taylor & Francis. London. p. 7–16.

Qian W. L., & J. Roberts. 1995. Brachiopods of the Early Carboniferous *Schellwienella burlingtonensis* Zone in eastern Australia. Alcheringa 19:255-289.

Qian Y., & Stefan Bengtson. 1989. Paleontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. Fossils and Strata 24:1–156.

Qing H., C. R. Barnes, D. Buhl, and J. Veizer. 1998. The strontium isotope composition of Ordovician and Silurian brachiopods and conodonts: Relationships to geological events and implications for coeval seawater. Geochemica et Cosmochimica Acta 62:1721–1723.

Quing H., & J. Veizer. 1994. Oxygen and carbon isotopic composition of Ordovician brachiopods: Implications for coeval seawater. Geochimica et Cosmochimica Acta 58:4429–4442.

Quenstedt, F. A. 1868–1871. Die Brachiopoden. *In* Petrefactenkunde Deutschlands, vol. 2(1). Fuess. Leipzig. p. 1–748, 61 pl.
p. 1–160:1868, p. 161–464:1869, p. 465–748:1870, pl. 37–61:1871.

Racheboeuf, P. R. 2000. Chonetidina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (revised), vol. 2. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 362–423.

Racheboeuf, P. R. 2001. The chonetoidean fauna of the Kersadiou Formation (Givetian, Brittany). Neues Jahrbuch für Geologie und Paläontologie 10:577–593.

Racheboeuf, P. R., & Thanh Tong-Dzuy. 2000. Lower Devonian chonetoidean brachiopods from Bac Bo, North Viêt Nam. Palaeontology 43(6):1039–1068.

Radulović, Vladan, & B. Radulović. 2002. Internal homeomorphy in some Lower Cretaceous brachiopod genera (Terebratellidina) from the Carpatho-Balkanides, Eastern Serbia. Eclogae Geologicae Helvetiae 95(3):401–413.

Radulović, Vladan, B. Radulović, & D. Rabrenović. 2002. A new dallinide (Brachiopoda) genus (*Pictetella*) from the early Cretaceous eastern Serbia. Revue de Paléobiologie 21(2):789–793.

Radulović, Vladan, Draginja Urošević, & Nenad Banjac. 1992. Upper Triassic brachiopods from the Yugoslavian Carpatho-Balkanides (Stara Planina Mountain). Senckenbergiana lethaea 72:61–76, pl. 1–3.

Rahimpour-Bonab, H., Y. Bone, & R. Moussavi-Harami. 1997. Stable isotope aspects of modern molluscs, brachiopods, and marine cements from cool-water carbonates, Lacepede Shelf, South Australia. Geochimica et Cosmochimica Acta 61:207–218.

Rao, C. P. 1996. Elemental composition of marine calcite from modern temperate brachiopods, bryozoans and bulk carbonates, Eastern Tasmania, Australia. Carbonates and Evaporites 11:1–18.

Rau, K. 1905. Die Brachiopoden des mittleren Lias Schwabens mit Ausschluss der Spiriferinen. Geologische und Palaeontologische, Abhandlungen (Berlin) 6(5):1–94.

Raup, D. M. 1976. Species diversity in the Phanerozoic: A tabulation. Paleobiology 2:279–288.

Reed, C. G. 1987. Phylum Brachiopoda. *In* M. F. Strathmann, ed., Reproduction and development of marine invertebrates of the northern Pacific coast. University of Washington Press. Seattle. p. 486–496.

Reed, F. R. C. 1915. Supplementary Memoir on new Ordovician and Silurian fossils from the Northern Shan States. Palaeontologia Indica, Calcutta (new series) 6 (1):1–98, pl. 1–12.

Reed, F. R. C. 1931. New fossils from the *Productus* limestones of the Salt Range, with notes on other species. Palaeontologia Indica (new series) 17:1–56, pl. 1–8.

Reed, F. R. C. 1944. Brachiopoda and Mollusca from the *Productus* limestones of the Salt Range. Memoirs of Geological Survey of India, Palaeontologia Indica (new series) 23(2):678 p., 65 pl.

Remane, J. 2003. Chronostratigraphic correlations: their importance for the definition of geochronologic units. Palaeogeography, Palaeoclimatology, Palaeoecology 196:7–18.

Richardson, J. R. 1973. Studies on Australian Cainozoic Brachiopods 2. The family Laqueidae (Terebratellidae). Proceedings of the Royal Society of Victoria 85:117–126, 6 pl.

Richardson, J. R. 1975. Loop development and the classification of terebratellacean brachiopods. Palaeontology 18(2):285–314, fig. 1–4, pl. 44.

Richardson, J. R. 1981. Recent brachiopods from New Zealand—Background to the study cruises of 1977–79. New Zealand Journal of Zoology 8:133–143, 1 fig.

Richardson, J. R. 1987. Brachiopods from carbonate sands of the Australian Shelf. Proceedings of the Royal Society of Victoria 99(1):37–50, 6 fig.

Richardson, J. R. 1994. Origins and dispersal of a brachiopod family—The systematics, biogeography and evolution of the family Terebratellidae. Proceedings of the Royal Society of Victoria 106:17–29, 4 fig.

Richardson, J. R. 1997a. Ecology of articulated brachiopods. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 441–462, 19 fig.

Richardson, J. R. 1997b. Biogeography of articulated brachiopods. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 463–472, 1 fig.

Rioult, Michel. 1971. *Argyrotheca cistellula* (Searles-Wood) (Brachiopode, Terebratellacea) au large des côtes du Calvados. Bulletin de la Société Linnéenne de Normandie 102:26–28, 1 fig.

Risso, A. 1826. Histoire naturelle des principales productions de l'Europe méridionale, et particulièrement de celles des environs de Nice et des Alpes Maritimes. IV. Aperçu sur l'Histoire Naturelle des mollusques et des coquilles de l'Europe Méridionale, vol. 7. F. G. Levrault. Paris. 439 p., pl. 1–12.

Roberts, John. 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf basin, northwestern Australia. Bureau of Mineral Resources (BMR) Bulletin of Australian Geology and Geophysics 122:319 p.

Robson, S. P., G. S. Nowlan, & B. R. Pratt. 2003. Middle to Upper Cambrian Linguliformean brachiopods from Deadwood Formation of subsurface Alberta and Saskatchewan, Canada. Journal of Paleontology 77(2):201–211.

Rodland, D. L., M. Kowalewski, D. L. Dettman, K. W. Flessa, V. Atudorei, & Z. D. Sharp. 2003. High-resolution analysis of $\delta^{18}O$ in the biogenic phosphate of modern and fossil lingulid brachiopods. The Journal of Geology 111:441–453.

Roemer, F. A. 1850. Beiträge zur Kenntnis des nordwestlichen Harzgebirges. Palaeontographica 3:1–67.

Rokas, A., B. L. Williams, N. King, & S. B. Carroll. 2003. Genome-scale approaches to resolving incongruence in molecular phylogenies. Nature 425:798–803.

Rong Jia-yu. 1984. Brachiopods of latest Ordovician in the Yichang District, western Hubei, central China. *In* Stratigraphy and Palaeontology of Systemic Boundaries in China, Ordovician-Silurian Boundary, vol. 1. Nanjing Institute of Geology and Palaeontology, Academia Sinica. Anhui Science and Technology Publishing House. Anhui. p. 111–176, 14 pl.

Rong Jia-yu, Fernando Alvarez, T. L. Modzalevskaya, & Zhang Yan. 2004. Revision of the Athyrisininae, Siluro-Devonian brachiopods from China and Russia. Palaeontology 47:811–857.

Rong Jia-yu, & L. R. M. Cocks. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and "stropheodontoid" brachiopods. Palaeontology 37:651–694, pl. 1–7.

Rong Jia-Yu, & Zhan Ren-Bin. 1996. Brachidia of late Ordovician and Silurian eospiriferines (brachiopoda) and the origin of the spiriferides. Palaeontology 39(4):941–977.

Rõõmusoks, A. 1963. Strophomenoidea of the Ordovician and Silurian from Estonia, 2. New genera from the Harju Series. Eesti NSV Teaduste Akadeemia Toimetised (Keemia Bioloogia) 12 (3):231–241, pl. 1–2.
In Russian.

Rõõmusoks, A. 1985. The genera *Trigrammaria* and *Microtrypa* (Strophomenidae) in the Ordovician of Baltoscandia. Proceedings of the Academy of Sciences of the Estonian SSR, Geology 34:133–140, pl. 1–4.

Rõõmusoks, A. 1993. Four new brachiopod genera of the subfamily Oepikinae (Strophomenacea) from the Ordovician of Estonia. Proceedings of the Academy of Sciences of Estonia, Geology 42:48–57, pl. 1–4.

Rõõmusoks, A. 2004. Ordovician strophomenoid brachiopods of northern Estonia. Fossilia Baltica 3:1–151, pl. 1–34.

de Rosa, Renaud. 2001. Molecular data indicate the protostome affinity of brachiopods. Systematic Biology 50(6):848–859.

de Rosa, Renaud. 2002. Molecular data indicate the protostome affinity of brachiopods. Systematic Biology 50:848–859.

de Rosa, Renaud, J. K. Grenier, T. Andreeva, C. E. Cook, A. Adoutte, M. Akam, S. B. Carroll, & G. Balavoine. 1999. Hox genes in brachiopods and priapulids and protostome evolution. Nature 399:772–776.

Rosenberg, G. D., W. W. Hughes, & R. D. Tkachuck. 1988. Intermediary metabolism and shell growth in the brachiopod *Terebratalia transversa*. Lethaia 21:219–230.

Rösler, A. 1954. Die Fauna des rheinischen unter-Devons 1. *Stropheodonta* cf. *taeniolata* (Sandb.) aus dem Unter-Ems von Oberstadtfeld und ein neuer Fund von *Pyrogocystis octogona* R. Richter (Edioaster). Notizblatt des hessischen Landesamtes für Bodenforschung 82:30–37, 1 pl.

Rotai, A. P. 1931. Brachiopods and stratigraphy of the Lower Carboniferous of the Donetz Basin. Glavnogo Geologo-Razvedochnogo Upravleniia, Trudy [Transactions of the Geological and Prospecting Service of the U.S.S.R.] 73:35–144.
In Russian with English summary.

Rotai, A. P. 1951. Brakhiopodi srednego karbona donetskogo basseina, chast' 1, Spiriferidae. Vsesoiuznii Nauchno-issledovatel'skii Geologicheskii Institut (VSEGEI), Ministerstva Geologii. Moscow. 179 p.

Rowell, A. J. 1960. Some early stages in the development of the brachiopod *Crania anomala* (O. F. Müller). Annals and Magazine of Natural History 13:35–52.

Rowell, A. J. 1965. Order Paterinida. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 1. The Geological Society of America and University of Kansas Press. New York & Lawrence, Kansas. p. 293–295.

Rowell, A. J. 1981a. The Cambrian radiation: Monophyletic or polyphyletic origins? *In* M. E. Taylor, ed., Short Papers for the Second International Symposium on the Cambrian System. U. S. Geological Survey Open File Report 81-743:184–187.

Rowell, A. J. 1981b. The origin of the Brachiopods. *In* T. W. Broadhead, ed., Lophophorates, Notes for a Short Course. University of Tennessee. Knoxville. p. 97–109.

Rowell, A. J. 1982. The monophyletic origin of the Brachiopoda. Lethaia 15:299–307.

Rowell, A. J., & N. E. Caruso. 1985. The evolutionary significance of *Nisusia sulcata*, an early articulate brachiopod. Journal of Paleontology 59:1227–1242, fig. 1–9.

Rudwick, M. J. S. 1962a. Filter feeding mechanisms in some brachiopods from New Zealand. Journal of the Linnean Society, Zoology 44:592–615.

Rudwick, M. J. S. 1962b. Notes on the ecology of brachiopods in New Zealand. Transactions of the Royal Society of New Zealand, Zoology 1(25):327–335, 3 fig.

Rudwick, M. J. S. 1970. Living and fossil brachiopods. Hutchinson University Library. London. 199 p., 99 fig.

Ruiz-Trillo, I., J. Paps, M. Loukota, C. Ribera, U. Jondelius, J. Baguñà, & M. Riutort. 2002. A phylogenetic analysis of myosin heavy chain type II sequences corroborates that *Acoela* and *Neodermatida* are basal bilaterians. Proceedings of the National Academy of Sciences 99:11,246–11,251.

Ruiz-Trillo, I., M. Ruitort, H. M. Fourcade, J. Baguna, & J. L. Boore. 2004. Mitochondrial genome data support the basal position of Acoelomorpha and the polyphyly of the Platyhelminthes. Molecular Phylogenetics and Evolution 33:321–332.

Rukavishnikova, T. B. 1956. Brakhiopody ordovika Chu-Iliiskikh Gor [Ordovician Brachiopods from Kazakhstan]. *In* B. M. Keller and others, Ordovik Kazakhstana, II. Stratigrafiia Ordovika Chu-Iliiskikh Gor. Akademiia Nauk SSSR, Geologicheskii Institut, Trudy (Ordovik Kazakhstan II) (Moscow) 1: 105–168, 5 pl.
In Russian.

Runnegar, B. N. 1982. The Cambrian Explosion—Animals or fossils? Journal of the Geological Society of Australia 29(3-4):395–411.

Runnegar, B. N. 2000. Body building in *Halkieria* and comparisons with chitons and other mollusks. Geological Society of America, Abstracts with Programs 32:A72.

Rush, P. F., & H. S. Chafetz. 1990. Fabric-retentive, non-luminescent brachiopods as indicators of original $\delta^{13}C$ and $\delta^{18}O$ composition: A test. Journal of Sedimentary Petrology 60:968–981.

Rye, D. M., & M. A. Sommer II. 1980. Reconstructing paleotemperatures and paleo-salinity regimes with oxygen isotopes. *In* D. C. Rhoads & R. A. Lutz, eds., Topics in Geobiology, 1 Skeletal Growth of Aquatic Organisms. Plenum Press. New York. p. 169–202.

Rzhonsnitskaia, M. A. 1956. Systematization of Rhynchonellida. *In* E. Guzmán & others, eds., Resumenes de Los Trabajos Presentados. International Geological Congress, Mexico, Report 20:125–126.

Rzhonsnitskaia, M. A. 1959. K sistematike rinkhonellid [On the systematics of the rhynchonellids]. Paleontologicheskii Zhurnal 1959(1):25–36.

Rzhonsnitskaia, M. A. 1974. Brakhiopodi [Brachiopods]. *In* Yu. S. Biske, V. B. Goryanov, N. M. Petrosyan, & M. A. Rzhonsnitskaia, Materialy po faune i flore dzhidalinckoi svity (srednii paleozoi, Alaiskii khrebet) [Some materials on the fauna and flora of the Djidala formation (Middle Paleozoic Alai Range)]. Voprosy Stratigrafii 1:54–62, fig. 4–7, pl. 2.

Saito, Michiko. 1996. Early loop ontogeny of some Recent laqueid brachiopods. Transactions and Proceedings of the Palaeontological Society of Japan (new series) 183:485–499, 7 fig.

Saito, Michiko. 1998. Brachiopod phylogeny inferred from mitochondrial COI sequences. Doctor of Philosophy thesis. Tokyo University. Tokyo. p. 1–109.

Saito, Michiko, & K. Endo. 2001. Molecular phylogeny and morphological evolution of laqueoid brachiopods. Paleontological Research 5:87–100.

Saito, Michiko, K. Endo, & B. L. Cohen. 2001. Molecular phylogenetics and evolution of long-looped brachiopods. *In* C. H. C. Brunton, R. Cocks, & S.

Long, eds., Brachiopods Past and Present. Taylor and Francis. London. p. 129–137.

Saito, Michiko, S. Kojima, & K. Endo. 2000. Mitochondrial COI sequences of brachiopods: Genetic code shared with protostomes; limits of utility for phylogenetic reconstruction. Molecular Phylogenetics and Evolution 15:331–344.

Saito, Michiko, & Jun-ichi Tazawa. 2002. *Hemithiris woodwardi* (A. Adams) (Rhynchonellida, Brachiopoda) from the Pleistocene Shichiba Formation, Sado Island, central Japan. Science Reports of Niigata University (series E, Geology) 17:7–15, 5 fig.

Saiz Salinas, J. I. 1989. Verzeichnis der rezenten Brachiopoden (Brachiopoda) von den iberischen Küsten und den angrenzenden Meeren. Bonner Zoologische Beiträge 40(2):141–154.

Salmon, E. S. 1942. Mohawkian Rafinesquininae. Journal of Paleontology 16:564–603.

Salter, J. W., & H. F. Blanford. 1865. Palaeontology of Niti in the Northern Himalaya, being descriptions of the Palaeozoic and Secondary Fossils collected by Col. Richard Strachey, 8 vol. Cutter, Military Orphan Press. Calcutta. 112 p., 23 pl.

Samtleben, C., A. Munnecke, & T. Bickert. 2000. Development of facies and C/O-isotopes in transects through the Ludlow of Gotland: Evidence for global and local influences on a shallow-marine environment. Facies 43:1–38.

Samtleben, C., A. Munnecke, T. Bickert, & J. Patzold. 1996. The Silurian of Gotland (Sweden): Facies interpretation based on stable isotopes in brachiopod shells. Geologische Rundschau 85:278–292.

Samtleben, C., A. Munnecke, T. Bickert, & J. Pätzold. 2001. Shell succession, assemblage and species dependent effects on C/O-isotopic composition of brachiopods—Examples from the Silurian of Gotland. Chemical Geology 175:61–107.

Sanderson, M. J., & M. J. Donoghue. 1996. The relationship between homoplasy and confidence in a phylogenetic tree. *In* M. J. Sanderson & L. Hufford, eds., Homoplasy: The recurrence of similarity in evolution. Academic Press. San Diego. p. 67–89.

Sandy, M. R. 1998. Loop ontogeny of the Late Triassic (Norian) terebratulid brachiopod *Pseudorhaetina antimoniensis* Sandy from Sonora, Mexico and its taxonomic significance. Journal of Paleontology 72(1):28–35.

Sanson, G. F. O., S. Y. Kawashita, S. Brunstein, & M. R. S. Briones. 2002. Experimental phylogeny of neutrally evolving DNA sequences generated by a bifurcate series of nested polymerase chain reactions. Molecular Biology and Evolution 19:170–178.

Sartenaer, Paul. 1966. Commentaires sur le genre nominal *Adolfia* Gürich, G., 1909 et sur le nom générique *Guerichella* (Brachiopoda, Spiriferacea). Bulletin de la Société belge de Géologie, Paléontologie et Hydrologie 75(3):380–389.

Sartenaer, Paul. 1979. Deux nouveaux genres de rhynchonellides Frasniens précédémment inclus dans le genre *Calvinaria* (Brachiopoda). Géobios 12(4):535–547, 2 pl.

Sartenaer, Paul. 1984. Deux genres rhynchonellides nouveaux de la fin du Frasnien. Institut Royal des Sciences Naturelles de Belgique, Bulletin (Sciences de la Terre) 55(8):1–16.

Sartenaer, Paul. 1994a. *Canavirila,* nouveau genre calvinariide (rhynchonellide, brachiopode) de la partie moyenne du Frasnien. Institut Royal des Sciences Naturelles de Belgique, Bulletin (Sciences de la Terre) 64:97–108, 2 pl.

Sartenaer, Paul. 1994b. *Tiocyrspis*, a new late Frasnian cyrtiopsid genus from Germany and Belgium. *In* P. Königshof & R. Werner, eds., Willi Ziegler-Festschrift II. Courier Forschungsinstitut Senckenberg 169:29–43, 5 fig., 1 pl., 1 table.

Sartenaer, Paul. 1997. *Novaplatirostrum*, late Famennian rhynchonellid brachiopod genus from Sauerland and Thuringia (Germany). Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 67:25–37.

Sartenaer, Paul. 1998. *Leptoterorhynchus*, new middle Famennian rhynchonellid genus from Poland and Germany. Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 68:121–128.

Sartenaer, Paul. 1999a. *Tetragonorhynchus*, new late Famennian rhynchonellid genus from Maïder, southern Morocco, and Tetragonorhynchidae, n. fam. Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 69:67–75.

Sartenaer, Paul. 1999b. A new mid-Famennian rhynchonellid (brachiopod) genus from the Canning Basin, western Australia. Société Géologique du Nord, Annales (deuxième série) 7:79–84.

Sartenaer, Paul. 1999c. A new rhynchonellid (brachiopod) genus from the middle Frasnian of the Dinant Basin (Belgium). Senkenbergiana lethaea 79(1):275–279.

Sartenaer, Paul. 2000. *Phacoiderhynchus*, a new middle Famennian rhynchonellid genus from the Anti-Atlas, Morocco, and Phacoiderhynchidae n. fam. Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 70:75–88.

Sartenaer, Paul. 2001 [2000]. Revision of the rhynchonellid brachiopod genus *Ripidiorhynchus* Sartenaer. Geologica Belgica 3(3/4):191–213.

Sartenaer, Paul. 2003. *Tullypothyridina*, new late Givetian rhynchonellid (brachiopod) genus. Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 73:29–51, 1 pl.

Sartenaer, Paul, & G. Plodowski. 1996. Restatement of the late Tournaisian *Spirifer tornacensis* de Koninck, 1883 on the base of the original collection. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 66:53–71.

Sartenaer, Paul, V. I. Pushkin, & O. E. Kotlyar. 1997. Two early Famennian rhynchonellid species from the Pripyat' (Belarus) and Dnepr-Donets (Ukraine) Depressions. Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, Bulletin 67:39–55.

Sarytcheva, T. G. 1960. Brakhiopody. *In* T. G. Sarytcheva, asst. ed., Mshanki, Brakhiopody [Bryozoa, Brachiopoda], Y. A. Orlov, ed., Osnovy Paleontologii, vol. 7. Akademiia Nauk SSSR. Moscow. p. 115–324, pl. 1–75.
In Russian.

Sarytcheva, T. G., ed. 1977. Pozdnepaleozoiskie Produktidy Sibiri i arktiki [Late Palaeozoic Productida of Siberia and arctic regions]. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 161:1–220, pl. 1–27.

Sarytcheva, T. G., & A. N. Sokolskaya. 1959. O klassifikatsin lozhnoporistykh brakhiopod [On the classification of pseudopunctate brachiopods]. Akademiia Nauk SSSR, Doklady (Moscow) 125(1):181–184.

Savage, N. M. 1972. Some observations on the behaviour of the Recent brachiopod *Megerlina pisum* under laboratory conditions. Lethaia 5:61–67, 4 fig.

Savage, N. M. 1996. Classification of Paleozoic rhynchonellid brachiopods. *In* P. Copper & J. Jin, eds., Brachiopods. A. A. Balkema. Rotterdam. p. 249–260.

Savage, N. M., M. O. Manceñido, E. F. Owen, S. J. Carlson, R. E. Grant, A. S. Dagys, & Sun Dong-Li. 2002. Order Rhynchonellida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1027–1376, 233 fig.

Savazzi, Enrico. 1991. Burrowing in the inarticulate brachiopod *Lingula anatina*. Palaeogeography, Palaeoclimatology, Palaeoecology 85:101–106.

Scacchi, A., and R. A. Philippi. 1844. Enumeratio Molluscorum Siciliae, vol. 2. Halle. 303 p., 18 pl.

Schägger, H., & G. Von Jagow. 1987. Tricine-sodium dodecyl sulfate-polyacrylamide gel electrophoresis for the separation of proteins in the range from 1 to 100 kDa. Analytical Biochemistry 166:368–379.

von Schauroth, C. 1856. Ein neuer Beitrag zur Paläontologie des deutschen Zechsteingebirges. Zeitschrift der deutschen geologishen Gesellschaft 8:211–245, 1 pl.

Schindewolf, O. H. 1955. Über einige kambrische Gattungen inartikulater Brachiopoden. Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie 12:538–557, 7 fig.

von Schlottheim [sic], E. F. 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *In* C. C. Leonard, ed., Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neuesten Entdeckungen, vol. 7, no.1. Hermannschen Buchhandlung. Frankfurt am Main. P. 1-134, 4 pl.

von Schlotheim, E. F. 1820. Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung einer Sammlung versteinerter und fossiler Überreste der Tier- und Pflanzenreichs der Vorwelt Erläutert, vol. 1. Bekker. Gotha. 437 p., 54 pl.

Schmidt, Friedrich. 1888. Über eine neuendeckte untercambrische Fauna in Estland. Académie Impériale des Sciences, St. Petersbourg, Mémoires (series 7) 36(2):1–27, 2 pl.

Schmidt, Herta. 1965. Neue Befunde an Paläozoischen Rhynchonellacea (Brachiopoda). Senckenbergiana lethaea 46(1):1–25, 1 pl.

Schram, F. R. 1991. Cladistic analysis of metazoan phyla and the placement of fossil Problematica. *In* A. M. Simonetta & Simon Conway Morris, eds., The Early Evolution of Metazoa and the Significance of Problematic Taxa. Cambridge University Press. Cambridge, UK. p. 35–46.

Schuchert, Charles. 1893. A classification of the Brachiopoda. American Geologist 11(3):141–167.

Schuchert, Charles. 1896. Brachiopoda. *In* K. A. von Zittel, Text-book of Palaeontology, vol. 1, 1st ed., translated and edited by C. R. Eastman. Macmillan & Co., Ltd. London. p. 291–343, fig. 489–587.

Schuchert, Charles. 1911. Paleogeographic and geologic significance of Recent Brachiopoda. Bulletin of the Geological Society of America 22:258–275.

Schuchert, Charles. 1913. Class 2. Brachiopoda. *In* K. A. von Zittel, Text-book of Palaeontology, vol. 1, part 1, 2nd ed., translated and edited by Charles R. Eastman. MacMillan & Co., Ltd. London. p. 355–420, fig. 526–636.

Schuchert, Charles. 1929. Classification of brachiopod genera, fossils and Recent. *In* Charles Schuchert & C. M. LeVene, Brachiopoda (Generum et Genotyporum Index et Bibliographia). Fossilium Catalogus I: Animalia, vol. 42. W. Junk. Berlin. p. 10–25.

Schuchert, Charles, & G. A. Cooper. 1931. Synopsis of the brachiopod genera of the suborders Orthoidea and Pentameroidea, with notes on the Telotremata. American Journal of Science (series 5) 22:241–255.

Schuchert, Charles, & G. A. Cooper. 1932. Brachiopod genera of the suborders Orthoidea and Pentameroidea. Memoirs of the Peabody Museum of Natural History 4(1):xii + 270 p., pl. A, 1–29.

Schuchert, Charles, & C. M. LeVene. 1929. Brachiopoda (Generum et Genotyporum Index et Bibliographia). *In* J. F. Pompeckj, ed., Fossilium Catalogus, vol. I: Animalia, Pars 42. W. Junk. Berlin. p. 1–140.

Schumann, D. 1970. Inaequivalver Schalenbau bei *Crania anomala.* Lethaia 3(4):413–421, 7 pl.

Searles-Wood, 1841. Annals and Magazine of Natural History (eries 1) 6:253.

Seaver, E. C., D. A. Paulson, S. Q. Irvine, & M. Q. Martindale. 2001. The spatial and temporal expression of Ch-en, the engrailed gene in the polychaete *Chaetopterus*, does not support a role in body axis segmentation. Developmental Biology 236:195–209.

Senowbari-Daryan, B., & R. P. Reid. 1986. Upper Triassic sponges (Sphinctozoa) from southern Yukon, Stikinia terrane. Canadian Journal of Earth Sciences 24:882–902.

Sepkoski, J. J. 1975. Stratigraphic biases in the analysis of taxonomic diversity. Paleobiology 1:343–355.

Sepkoski, J. J. 1995. The Ordovician radiations: Diversification and extinction shown by global genus-level data. *In* J. D. Cooper, M. L. Droser, and S. C. Finney, eds., Ordovician Odyssey: Short Papers for the Seventh International Symposium on the Ordovician System. The Pacific Section, Society for Sedimentary Geology (SEPM), Book 77. Fullerton, California. p. 393–396.

Severgina, L. G. 1978. Brakhiopody i stratigrafiya verkhnego ordovika Gorno Altaia, Salaira i Gornoi Shorii [Brachiopods and stratigraphy of the Upper Ordovician of mountainous Altai region, Salair and

mountainous Shoriia]. Akademiia Nauk SSSR, Sibirskoe Otdelenie, Insitut Geologii i Geofiziki (IGIG), Trudy 405:3–41.
In Russian.

Sheehan, P. M. 1977. Species diversity in the Phanerozoic: A reflection of labor by systematists? Paleobiology 3:325–328.

Sheehan, P. M. 2001. The Late Ordovician mass extinction. Annual Reviews of Earth and Planetary Sciences 29:331–364.

Shen Shi, & N. W. Archbold. 2003. Lopingian (Late Permian) brachiopods from the Qubuerga Formation at the Qubu section in the Mt. Qomolangma region, southern Tibet, China. Palaeontographica (abt. A) 268:101 p.

Shen Shuzhong, & N.W. Archbold. 2002. Chonetoidea (Brachiopoda) from the Lopingian (Late Permian) of South China. Alcheringa 25:327–349.

Shen S.-Z., N. W. Archbold, Shi G. R., & Chen Z.-Q. 2000. Permian brachiopods from the Selong Xishan section, Xizang (Tibet), China. Part 1: Stratigraphy, Strophomenida, Productida, and Rhynchonellida. Geobios 33(6):725–752.

Shen S. Z. C., Cao C.-Q., C. M. Henderson, Wang X-D, Shi G. R., Wang Y., & Wang W. 2006. End-Permian mass extinction patterns in the northern peri-Gondwanan region. Palaeoworld 15:3–30.

Shen Shu-zhong, & He Xi-lin. 1994. Changhsingian brachiopod fauna from Guiding, Guizhou. Acta Palaeontologica Sinica 33(4):440–454, 2 pl.
In Chinese with English summary.

Shen S. Z., & Shi G. R. 1996. Diversity and extinction patterns of Permian Brachiopoda of South China. Historical Biology 12:93–110.

Shen Shu-zhong, Shi G. R., & N. W. Archbold. 2003a. Lopingian (Late Permian) brachiopods from the Qubuerga Formation at the Qubu section in the Mt. Qomolangma region, southern Tibet, China. Palaeontographica (abt. A) 268:49–101.

Shen Shu-zhong, Shi G. R., & N. W. Archbold. 2003b. A Wuchaipingian (Late Permian) brachiopod fauna from an exotic block in the Indus-Tsangpo suture zone, southern Tibet, and its palaeobiogeographical and tectonic implications. Palaeontology 46(2):225–256.

Shi, G. R. 1998. *Nahoniella*, a new name for *Yukonella* Shi and Waterhouse, 1996 (Spiriferida, Brachiopoda). Journal of Paleontology 72(5):935.

Shi G. R., & Shen Shu-zhong. 1997. A late Permian brachiopod fauna from Selong, southern Xizang (Tibet), China. Proceedings of the Royal Society of Victoria, 109(1): 37–56.

Shi G. R., Shen Shu-zhong, & B. W. Archbold. 1999. *Gruntea* gen. nov., a new Permian spirigerellid (Brachiopoda) genus from Selong, southern Tibet, China. Acta Palaeontologica Sinica, 38: 346–352.

Shi, G. R., & J. B. Waterhouse. 1996. Lower Permian brachiopods and molluscs from the upper Jungle Creek Formation, northern Yukon Territory, Canada. Geological Survey of Canada, Bulletin 424:1–242.

Shields, G. A., G. A. F. Carden, and J. Veizer. 2003. Sr, C, and O isotope geochemistry of Ordovician brachiopods: A major isotopic event around the Middle-Later Ordovician transition. Geochemica et Cosmochimica Acta 67:2005–2025.

Shimizu, K., J. Cha, G. D. Stucky, & D. E. Morse. 1998. Silicatein α: Cathepsin L-like protein in sponge biosilica. Proceedings of the National Academy of Science, USA 95:6,234–6,238.

Siblík, Milos. 2000. New data on the Hettangian brachiopod fauna of the Northern Calcareous Alps (Austria, Bavaria). Abhandlungen der Geologischen Bundesanstalt 56(2): 419–438.
Published for December 1999, accessed to the B.M. Library on 4 October 2000, also a leaflet of the Geological Survey in Vienna, p. 28, records effective publication in year 2000.

Siblík, Milos. 2002. New genus (*Superbirhyncha* gen. n.) for a rhynchonellid (Brachiopoda) from the Alpine Upper Triassic. Slovak Geological Magazine 8(1):101–103.

Simanauskas, T. 1996. Braquiópodes (Productidea) del Pérmico de la Cuenca Tepuel-Genoa, Chubut, Argentina. Ameghiniana (Revista Asociación Paleontológica Argentina) 33(4):377–383.

Simon, Eric, & E. F. Owen. 2001. A first step in the revision of the genus *Cretirhynchia* Pettitt, 1950. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 71:53–118, pl. 1–8.

Simon, Eric, & Gregory Willems. 1999. *Gwynia capsula* (Jeffreys, 1859) and other Recent brachiopods from submarine caves in Croatia. Bullétin de l'Institut Royal des Sciences naturelles de Belgique, Biologie 69:15–21, 2 fig. 1 pl.

Skovsted, C. B., & L. E. Holmer. 2000. Systematic position of the problematic Early Cambrian brachiopod *Mickwitzia*. The Millenium Brachiopod Congress, Abstracts. Natural History Museum, London. unpaginated, p. xx.

Skovsted, C. B., & L. E. Holmer. 2003. The Early Cambrian (Botomian) stem group brachiopod *Mickwitzia* from Northeast Greenland. Acta Palaeontologica Polonica 48(1):1–20.

Skovsted, C. B., & L. E. Holmer. 2005. Early Cambrian brachiopods from North-East Greenland. Palaeontology 48(2)325–345.

Slate, J., & N. J. Gemmell. 2004. Eve'n'Steve: Recombination of human mitochondrial DNA. Trends in Ecology and Evolution 19:561–563.

Sliusareva [Grigor'eva], A. D. 1958. O kazanskikh spiriferakh [On the Kazanian spirifers]. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 118(3):581–583.

Smirnova, T. N. 1972. Rannemelovye brackhiopody Kryma i Severnogo Kavkaza [Early Cretaceous brachiopoda of Crimea and the Northern Caucasus]. Nauka. Moscow. p. 1–143.

Smirnova, T. N. 1979. Mikrostruktura rakoviny nekotorykh rannemelovykh tetsideidnykh brakhiopod [Shell microstructure in Early Cretaceous thecidean brachiopods]. Paleontologicheskii Zhurnal 1979(3):79–86, 2 pl.

Smirnova, T. N. 1984. Rannemelovye brakhiopody (Morfologiia, sistematika, filogeniia, znachenie dlia biostratigrafii i paleozoogeografii). Izdatel'stvo "Nauka." Moscow. p. 1–200, pl. 1–24.

Smirnova, T. N. 1997. Shell structure of Upper Jurassic and Lower Cretaceous craniids (Brachiopoda) and its systematic significance. Journal of Paleontology 71(6):998–1007.

Smirnova, T. N. 2001. New late Hauterivian terebratulids from the southwestern Crimea. Journal of Paleontology 35(6):598–605.

Smirnova, T. N. 2004a. The lower Kazanian (upper Permian) terebratulid assemblage of the family Beecheriidae fam. nov. (Brachiopoda) from the east of the Russian Platform. Paleontologicheskii Zhurnal 38(2):166–171.

Smirnova, T. N. 2004b. A new genus and revision of known species of early Kazanian (Upper Permian) terebratulids from the Eastern Russian Platform. Paleontologicheskii Zhurnal 38(4):24–30.

Smirnova, T. N., A. A. Madison, & N. K. Esaulova. 2004. New Lower Kazanian (Upper Permian) terebratulids (Brachiopoda) from the northeastern Russian Platform: Family Dielasmatidae Schuchert, 1913. Paleontologicheskii Zhurnal 38(1):39–44.

Smirnova, T. N., & Galina T. Ushatinskaya. 2001. New lingulids (Brachiopoda) from the Lower Cretaceous of European Russia, with notes in the microstructure of their shells. Paleontologicheskii Zhurnal 2001(4):51–59.

Smith, A. B. 2001. Large scale heterogeneity of the fossil record, implications for Phanerozoic biodiversity studies. Philosophical Transactions of the Royal Society, London B356:1–17.

Smith, A. B., A. S. Gale, & N. Monks. 2001. Sea-level change and rock record bias in the Cretaceous: A problem for extinction and biodiversity studies. Paleobiology 27:241–253.

Smith, E. A. 1907. Brachiopoda. National Antarctic Expedition 1901–1904, vol. 2. London. 2 p.

Sokolskaya, A. N. 1954. Strofomenidy Russkoi Platformy [Strophomenidae of the Russian Platform]. Akademiia Nauk SSSR, Paleontologeskii Institut, Trudy 51:191 p., 18 pl.
In Russian.

Sokolskaya, A. N. 1960. Otriad Strophomenida. *In* T. G. Sarytcheva, asst. ed., Mshanki, Brakhiopody [Bryozoa, Brachiopoda], Y. A. Orlov, ed., Osnovy Paleontologii, vol. 7. Akademiia Nauk SSSR. Moscow. p. 206–220, pl. 27–32.
In Russian.

Solander, D. C. 1789. *In* G. Dixon, A Voyage round the World. p. 355, fig. 3, pl. 11.

Sorensen, M. V., P. Funch, E. Willerslev, A. J. Hansen, & J. Olesen. 2000. On the phylogeny of the Metazoa in the light of the Cycliophora and Micrognathozoa. Zoologischer Anzeiger 239:297–318.

Sowerby, G. B. 1844. Description of fossil shells from the Palaeozoic formation of Van Diemen‘s Land. *In* C. Darwin, Geological observations on the volcanic islands visited during the voyage of H.M.S. Beagle. Geological voyage of the Beagle pt. 2, Appendix. Smith Elder and Co. London. p. 158–160.

Sowerby, G. B. 1846. Descriptions of thirteen new species of brachiopods. Proceedings of the Zoological Society of London 14:91–95.

Sowerby, G. B. 1847. The Recent Brachiopoda. Thesaurus Conchyliorum, vol. 1, no. 17. London. p. 362, fig. 91–92, pl. 71.

Sowerby, James. 1812–1815. The Mineral Conchology of Great Britain, vol. 1. Published by the author. London. iv + 1–234, pl. 1–102.

Sowerby, James. 1815–1818. The Mineral Conchology of Great Britain, vol. 2. Benjamin Meredith. London. p. 1–235, pl. 103–203.

Spjeldnæs, Nils. 1957. The Middle Ordovician of the Oslo Region, Norway 8. Brachiopoda of the Suborder Strophomenoidea. Norsk Geologisk Tidsskrift 37:1–214, pl. 1–14.

Stache, Guido. 1878. Beiträge zur Fauna der Bellerophonkalke Südtirols. Nr. II. Pelecypoden und Brachiopoden. Jahrbuch der Kaiserlich-Köninglichen Geologischen Reichsanstalt 28:93–168, 1–4 pl.

Stainbrook, M. A. 1942. Brachiopoda of the Cedar Valley beds of Iowa. Journal of Paleontology 16(5):604–619.

Stainbrook, M. A. 1945. Brachiopoda of the Independence Shale of Iowa. Geological Society of America, Memoir 14:1–74, 6 pl.

Stankiewicz, B. A., P. F. Van Bergen, I. J. Duncan, J. F. Carter, D. E. G. Briggs, & R. P. Evershed. 1996. Recognition of chitin and proteins in invertebrate cuticles using analytical pyrolysis/gas chromatography and pyrolysis/gas chromatography/mass spectrometry. Rapid Communications in Mass Spectrometry 10:1747–1757.

Stanley, G.D., Jr., C. Gonzalez-Leon, M. R. Sandy, B. Senowbari- Daryan, P. Doyle, M. Tamura, & D. H. Erwin. 1994. Upper Triassic invertebrates from the Antimonio Formation, Sonora, Mexico. Journal of Paleontology (Paleontological Society Memoir 36) 68(4):1–33, 11 pl.

Stanley, S. M., & L. A. Hardie. 1999. Palaeontology links plate tectonics and geochemistry to sedimentology. GSA Today 9:1–7.

Stanton, R. J., D. L. Jeffery, & W. M. Ahr. 2002. Early Mississippian climate based on oxygen isotope compositions of brachiopods, Alamogordo Member of the Lake Valley Formation, south-central New Mexico. Geological Society of America Bulletin 114:4–11.

Stechmann, A., & M. Schlegel. 1999. Analysis of the complete mitochondrial DNA sequence of the brachiopod *Terebratulina retusa* places Brachiopoda within the protostomes. Proceedings of the Royal Society, London (series B) 266:2043–2052.

Stehli, F. G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. Bulletin of the American Museum of Natural History 105:257–358, fig. 1–55, pl. 17–27.

Stepanov, D. L. 1934. Brakhiopody mshankovykh izvestniakov Kolvinskogo raiona (Severnii Ural) part 1. Strophomenacea [The Brachiopoda of the Bryozoa Limestones of the Kolwa River Region (Northern Ural), part 1: Strophomenacea]. Neftianoi Geologo-Razvedochnyi Institut (NGRI), Trudy (series A) 37:1–63, 4 pl.

Stepanov, D. L., M. V. Kulikov, & A. A. Sultanaev. 1975. Stratigrafiia I brakhiopody verkhnepermskikh otlojenii poluostrava Kanin [Stratigraphy and brachiopods from the Upper Permian sediments of the Kanin Peninsula]. Vestnik Leningradskogo Universiteta, Geologia i Geografiia 6(1):51–65, 3 pl.

Stiller, J. W., & L. Harrell. 2005. The largest subunit or RNA polymerase II from the Glaucocystophyta: Functional constraint and short-branch exclusion in deep eukaryotic phylogeny. BMC Evolutionary Biology 5:71, doi: 10.1186/1471-2148-5-71.

Stoll, H. M., J. Ruiz Encinar, Ignacio Garcia Alonso, Y. Rosenthal, I. Probert, & C. Klaas. 2001. A first look at paleotemperature prospects from Mg in coccolith carbonate: Cleaning techniques and culture measurements. Geochemistry, Geophysics, Geosystems 2:Paper number 2000GC000144.

Streng, M. 1999. Early Middle Cambrian representatives of the superfamily Acrotretoidea (Brachiopoda) from Morocco. Zeitschrift der Deutschen Geologischen Gesellschaft 150(1):27–87.

de Strezelecki, P. E. 1845. Physical Description of New South Wales and Van Dieman's Land. Longman, Brown & Co. London. 462 p., 19 pl.

Stricker, S. A., & M. W. Folsom. 1997. Ooocyte maturation in the brachiopod *Terebratalia transversa*: role of follicle cell-oocyte attachments during ovulation and germinal vesicle breakdown. Biological Bulletin 193:324–340.

Stricker, S. A., & C. G. Reed. 1985a. The ontogeny of shell secretion in *Terebratalia transversa* (Brachiopoda, Articulata). I. Development of the mantle. Journal of Morphology 183(3):233–250.

Stricker, S.A., & C. G. Reed. 1985b. The ontogeny of shell secretion in *Terebratalia transversa* (Brachiopoda, Articulata). II. Formation of the protegulum and juvenile shell. Journal of Morphology 183:251–271.

Stricker, S. A., & C. G. Reed. 1985c. The protegulum and juvenile shell of a Recent articulate brachiopod: Patterns of growth and chemical composition. Lethaia 18:295–303.

Strusz, D. L., I. G. Percival, A. J. Wright, J. W. Pickett, & A. Byrnes. 1998. A giant new Trimerellide brachiopod from the Wenlock (Early Silurian) of New South Wales, Australia. Records of the Australian Museum 50:171–186.

Struve, Wolfgang. 1978. Fixo-sessile Brachiopoden aus dem Rheinischen Devon: *Schuchertellopsis* (*Krejcigrafella*) und *Auchmerella* (Strophomenida). Senckenbergiana lethaea 59:93–115, 3 pl.

Stubblefield, C. J., & O. M. B. Bulman. 1927. The Shineton Shales of the Erekin district: With notes on their development in other parts of Shropshire and Herefordshire. Quarterly Journal of the Geological Society of London 83:96–146, pl. 3–5.

Stüder, T. 1889. Die Forschungsreise S.M.S. "Gazelle" in den Jahren 1874 bis 1876. III. Zoologie und Geologie. Mittler and Sohn. Berlin. 322 p., 33 pl.

Suess, Eduard. 1854. Über die Brachiopoden der Kössener Schichten. Denkschriften der königlichen Akademie der Wissenschaften, mathematisch-naturwissenschaftlichen Klasse 7(2):29–65, pl. 1–4.

Sun Dong-li. 1981. [The Mesozoic brachiopods of Xizang]. *In* [Palaeontology of Xizang, Book III (The Series of the Scientific Expedition to the Qinghai-Xizang Plateau)]. Science Press. Beijing. p. 177–253, 14 pl. In Chinese with English summary.

Sun Dong-Li. 1987. [Early Cretaceous brachiopods from Baingoin and Xainza, Northern Xizang]. Nanjing Institute of Geology and Palaeontology, Bulletin 11:63–103, 7 pl.

Sun Dongli, & Chen Xiuqin. 1998. Devonian brachiopods from the Karakorum-Kunlun region. Paleontology of the Karakorum-Kunlun Mountains 4:163–214.

Sun Dong-Li, & Wang Zhi. 1984. [Brachiopoda]. *In* [Northwestern Regional Atlas of Paleontology, Xinjiang Province—Part 2 (Mesozoic and Cenozoic)], vol. 3. Beijing. p. 94–99, pl. 23.

Sun Dongli, & Zhang Zixin. 1998. [Jurassic brachiopods from the Karakorum region and its paleobiogeographical significance.] Palaeontology of the Karakorum-Kunlun Mountains 4:215–283, 11 pl. In Chinese with English summary.

Sun Weiguo, & Hou Xianguang. 1987. Early Cambrian medusae from Chengjiang, Yunnan, China. Acta Paleontologica Sinica 26:257–271.

Sun Yualin, Ma Xueping, Andrzej Baliński, & Yubo Zang. 2004. A new meristid brachiopod genus from the Lower Carboniferous of Guizhou, China. Journal of Paleontology 78:240–244.

Sutton, M. D., M. G. Bassett, & L. Cherns. 1999. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh Basin; Part 1. Monograph of the Palaeontographical Society 153:1–60, pl. 1–8.

Sutton, M. D., M. G. Bassett, & L. Cherns. 2000. Lingulate brachiopods from the Lower Ordovician of the Anglo-Welsh Basin; Part 2. Monograph of the Palaeontographical Society 154:61–114, pl. 9–23.

Suzuki, T., C. Mizuta, K. Uda, K. Ishida, K. Mizuta, S. Sona, D. M. Compaan, & W. R. Ellington. 2004. Evolution and divergence of the genes for cytoplasmic, mitochondrial, and flagellar creatine kinases. Journal of Molecular Evolution 59:218–226.

Swart, P. K. 1983. Carbon and oxygen isotope fractionation in Scleractinian corals: A review. Earth Science Reviews 19:51–80.

Taboada, A. C. 2004. Braquiópodos y bioestratigrafía del Carbonífero del Cordón del Naranjo (subcuenca Calingasta-Uspallata), Argentina. Ameghiniana 41(3):405–422.

Taddei-Ruggiero, Emma, & Tommaso Ungaro. 1984. *Sardorhynchia crassa* gen. nov., sp. nov. (Brachiopoda), from Jurassic of Sardinia. Bolletino della Societá Paleontologica Italiana 22(3):225–245, pl. 1–7. Published for 1983.

Tcherkesova, S. V. 1997. New rhynchonellid brachiopods from the upper Famennian of central Taimyr. Paleontologicheskii Zhurnal 3(1997):48–53. In Russian.

Tcherkesova, S. V. 1998. New rhynchonellid brachiopods from the Frasnian of the south-west of Novaya Zemlya. Paleontologicheskii Zhurnal 2(1998):40–46. In Russian.

Tcherkesova, S. V. 1999. Frasnian rhynchonellid brachiopods from William Island (Severnyi Island of Novaya Zemlya). Paleontologicheskii Zhurnal 4(1999):38–43. In Russian.

Tchorszhewsky, E. S. 1990. K sistematike iurskikh sil'katnykh Terebratulida (Brachiopoda) [On systematics of Jurassic sulcate Terebratulida]. Paleontologicheskii Sbornik 27:31–39.

Tchoumatchenco, P. V. 1986. *Tiaretithyris* gen. n. (Dallinidae, Brachiopoda) du Jurassique superieur des environs de la ville de Tiaret (Algerie du Nord). Geologica Balcanica 16(6):113–121, 1 pl.

Tchoumatchenco, P. V. 1987. Nouveaux taxa brachiopodes du Jurassique de l'Ouarsenis occidental (Algerie du Nord) [New brachiopod taxa from the Jurassic Sediments of Western Ouarsenis (North Algeria)]. Geologica Balcanica 17(1):47–62, 4 pl.

Telford, M. 2002. Cladistic analysis of molecular characters: the good, the bad and the ugly. Contributions to Zoology 71:93–100.

Temple, J. T. 1965. Upper Ordovician brachiopods from Poland and Britain. Acta Palaeontologica Polonica 10:379–427, 21 pl.

Tenison-Woods, J. E. 1878. On some new marine Mollusca. Transactions of the Royal Society of Victoria 14:55–65.

Termier, Henri, & G. Termier. 1949. Essai sur l'évolution des Spiriféridés. Maroc. Division des Mines et de la Géologie, Service Géologique, Notes et Mémoires 74B:85–112.

Tessmar-Raible, K., & D. Arendt. 2003. Emerging systems: Between vertebrates and arthropods, the Lophotrochozoa. Current Opinion in Genetics & Development 13:331–340.

Thayer, C. W. 1975. Size-frequency and population structure of brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 17:139–148, 4 fig.

Thayer, C. W., & R. A. Allmon. 1991. Unpalatable thecideid brachiopods from Palau: Ecological and evolutionary implications. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through Time. Proceedings of the 2nd International Brachiopod Congress, University of Otago, Dunedin, New Zealand, 5–9 February, 1990. Balkema. Rotterdam. p. 253–260.

Thayer, C. W., & H. M. Steele-Petrovic. 1975. Burrowing of the lingulid brachiopod *Glottidia pyramidata*: Its ecologic and paleoecologic significance. Lethaia 8:209–221.

Thompson, J. D., T. J. Gibson, F. Plewniak, F. Jeanmougin, & D. G. Higgins. 1997. The CLUSTAL_X windows interface: Flexible strategies for multiple sequence alignment aided by quality analysis tools. Nucleic Acids Research 25:4876–4882.

Thomson, J. A. 1915. On a new genus and species of the Thecideiinae. Geological Magazine (decade VI) 2:461–464, fig. 1.

Thomson, J. A. 1916. Additions to the knowledge of the Recent and Tertiary Brachiopoda of New Zealand and Australia. New Zealand Institute, Transactions and Proceedings 48:41–47, 1 pl.

Thomson, J. A. 1918a. Australasian Antarctic Expedition, 1911–14, Under the Leadership of Sir Douglas Mawson, D.Sc., B.E., Brachiopoda. Scientific Reports (series C) 4(3):1–76, 4 pl.

Thomson, J. A. 1918b. The genus *Bouchardia* (Brachiopoda) and the age of the younger beds of Seymour Island, West Antarctic. Geological Magazine (Dec.6) 5(648):258–263.

Thomson, J. A. 1918c. Brachiopoda. *In* J. Park, The geology of the Otamaru Districts, North Otago. New Zealand Geological Survey Bulletin (new series) 20:117–119.

Thomson, J. A. 1918d. Brachiopoda. Australasian Antarctic Expedition, 1911–1914. Scientific Reports (series C, Zoology and Botany) 4(3):76 p. 4 pl.

Thomson, J. A. 1926. A revision of the subfamilies of the Terebratulidae (Brachiopoda). Annals and Magazine of Natural History (series 9) 18(107):523–530.

Thomson, J. A. 1927. Brachiopod morphology and genera (Recent and Tertiary). New Zealand Board of Science and Art, Manual No. 7:333 p., 103 fig., 2 pl.

Tomita, K., S. Yokobori, T. Oshima, T. Ueda, & K. Watanabe. 2002. The cephalopod *Loligo bleekeri* mitochondrial genome: Multiplied noncoding regions and transposition of tRNA genes. Journal of Molecular Evolution 54:486–500.

Tommasi, L. R. 1970. Sôbre o Braquiópode *Bouchardia rosea* (Mawe, 1823). Boletim do Instituto Oceanografico, São Paulo 19:33–42, 11 fig.

Trautschold, H. 1876. Die Kalkbrueche von Mjatschkowa. Forsetzuzng. Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou 13(5):325–374.

Trueman, E. R., & T. M. Wong. 1987. The role of the coelom as a hydrostatic skeleton in lingulid brachiopods. Journal of Zoology 213(2):221–232, fig. 1–3.

Tunnicliffe, Verena, & Kerry Wilson. 1988. Brachiopod populations: Distribution in fjords of British Columbia (Canada) and tolerance of low oxygen concentrations. Marine Ecology—Progress Series 47:117–128, 7 fig.

Twenhofel, W. H. 1928. Geology of Anticosti Island. Geological Survey of Canada, Memoir (Ottawa) 154:1–351, 60 pl.

Tyazheva, A. P. 1972. Novye devonskie atiratsei Urala [New Devonian athyraceids from the Urals]. *In* I. A. Zanina, ed., Novye Vidy Drevnikh Rastenii i Bespozvonochnykh SSSR, vol. 3. Akademia Nauk SSSR, Bashkirskii Filial Institut Geologii. Moscow. p. 205–207.

Ulrich, E. O., & G. A. Cooper. 1936. New genera and species of Ozarkian and Canadian brachiopods. Journal of Paleontology 10:616–631.

Ulrich, E. O., & G. A. Cooper. 1938. Ozarkian and Canadian Brachiopoda. Geological Society of America, Special Paper 13:323 p., 14 fig., 58 pl.

Urey, H. C. 1947. The thermodynamic properties of isotopic substances. Journal of Chemical Society April:562–581.

Urey, H. C., H. A. Lowenstam, S. Epstein, & C. R. McKinney. 1951. Measurement of paleotemperatures and temperatures of the Upper Cretaceous of England, Denmark and the Southeastern United States. Bulletin of the Geological Society of America 62:399–416.

Ushatinskaya, G. T. 1997. Novye sredne- i pozdnekembriiskiye lingulidy i paterinidy (brakhiopody) severa Sibirskoi platformy [New Middle and Late Cambrian lingulids and paterinids (brachiopods) of northern Siberian Platform]. Paleontologicheskii Zhurnal 31(4):50–57, 2 pl.

Ushatinskaya, G. T. 1998. "Zubastyye" bezzamkovye brakhiopody iz srednego kembriya Sibiri i Kazakhstana [The "teeth-bearing" inarticulated brachiopods from the Middle Cambrian of Siberia and Kazakhstan. Paleontologicheskii Zhurnal 1998(5):38–42, 2 fig., 1 pl.

Ushatinskaya, G. T. 2001. Tannuolinids. *In* E. M. Alexander, J. B. Jago, A. Y. Rozanov, & A. Y. Zhuravlev, eds., The Cambrian Biostratigraphy of the Stansbury Basin, South Australia. IAPC NAUKA/Interperiodica, Moscow. p. 117–120.

Ushatinskaya, G. T. 2002. Genus *Micrina* (small shelly fossils) from the Lower Cambrian of South Australia: Morphology, microstructures, and possible relation to halkieriids. Paleontological Journal 36:9–19.

Ushatinskaya, G. T., & L. E. Holmer. 2001. Brachiopods. *In* E. M. Alexander, J. B. Jago, A. Yu. Rozanov, & A. Yu. Zhuravlev, eds., The Cambrian biostratigraphy of the Stansbury basin, South Australia. Transactions of the Palaeontological Institute 282:120–132.

Valentine, J. L., & G. A. Brock. 2003. A new siphonotretid brachiopod from the Silurian of Central-western New South Wales, Australia. Records of the Australian Museum 55:231–244.

Valentine, J. W. 1975. Adaptive strategies and the origin of grades and ground-plans. American Zoologist 15:391–404.

Valentine, J. W. 2004. On the Origin of Phyla. University of Chicago Press. Chicago. 614 p.

Valentine, J. W., David Jablonski, & D. H. Erwin. 1999. Fossils, molecules, and embryos: New perspectives on the Cambrian explosion. Development 126:851–859.

Veizer, J. 1983a. Chemical diagenesis of carbonates: Theory and application of trace element technique. *In* M. A. Arthur, T. F. Anderson, I. R. Kaplan, J. Veizer, & L. S. Land, eds., Stable Isotopes in Sedimentary Geology, SEPM Short Course Notes, No. 10. Society of Economic Paleontologists and Mineralologists. Tulsa, Oklahoma. p. 3.1–3.100.

Veizer, J. 1983b. Trace elements and isotopes in sedimentary carbonates. *In* R. J. Reeder, ed., Carbonates: Mineralogy and Chemistry. Reviews in Mineralogy. Mineralogical Society of America. Washington, D.C. p. 265–393.

Veizer, J. 1989. Strontium Isotopes in seawater through time. Annual Review of Earth and Planetary Sciences 17:141–167.

Veizer, J., D. Ala, K. Azmy, P. Bruckschen, D. Buhl, F. Bruhn, G. A. F. Carden, A. Diener, S. Ebneth, Y. Godderis, T. Jasper, C. Korte, F. Pawellek, O. G. Podlaha, & H. Strauss. 1999. $^{87}Sr/^{86}Sr$, $\delta^{13}C$ and $\delta^{18}O$ evolution of Phanerozoic seawater. Chemical Geology 161:59–88.

Veizer, J., P. Fritz, & B. Jones. 1986. Geochemistry of brachiopods: Oxygen and carbon isotopic records of Paleozoic oceans. Geochimica et Cosmochimica Acta 50:1679–1696.

Vélain, C. R. 1877. Passage de Venus sur le Soleil (Décembre, 1874), Expédition Francaise aux île Saint-Paul et Amsterdam, Zoologie: Observations générales sur la Faune des Mollusques. Archives de Zoologie Expérimental et Générale. 143 p., 3 pl.

Vendrasco, M. J., T. E. Wood, & Bruce Runnegar. 2004. Articulated Palaeozoic fossil with 17 plates greatly expands disparity of early chitons. Nature 429:288–291.

Verco, J. C. 1910. The Brachiopods of South Australia. Transactions of the Royal Society of South Australia 34: 89–99.

de Verneuil, Édouard. 1845. Paléontologie, Mollusques, Brachiopodes. *In* R. I. Murchison, Edouard de Verneuil, & A. de Keyserling, eds., Géologie de la Russie d'Europe et des Montagnes de l'Oural, vol. 2, no. 3, Paléontologie. John Murray. London. p. 17–395, 43 pl.

de Verneuil, Édouard. 1850. Note sur les fossiles dévoniens du district de Sabero (León). Bulletin de la Société géologique de France (2nd series) 7:155–186, pl. 3–4.

de Verneuil, Édouard, & E. J. A. D. d'Archiac. 1845. Note sur les fossiles du terrain paléozoïque des Asturies. Bulletin de la Société géologique de France (2nd series) 2:458–480, pl. 13–15.

Villas, Enrique, & L. R. M. Cocks. 1996. The first early Silurian brachiopod fauna from the Iberian Peninsula. Journal of Paleontology 70:571–588.

Vinther, Jakob, & Claus Nielsen. 2005. The Early Cambrian *Halkieria* is a mollusk. Zoologica Scripta 34:81–89.

Vörös, Attila. 1983. Some new genera of Brachiopoda from the Mediterranean Jurassic. Annales Historico-Naturales Musei Nationalis Hungarici 75:5–25, fig. 1–21.

Waagen, W. H. 1883. Salt Range fossils. Vol. 1, Part 4. *Productus* limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), fasc. 2:391–546.

Waagen, W. H. 1884. Salt Range fossils, vol. I, part 4. *Productus* Limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), fasc. 3–4:547–728, pl. 50–81.

Waagen, W. H. 1885. Salt Range fossils, vol. I, part 4. *Productus* Limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), fasc. 5:729–770, pl. 82–86.

Waagen, W. H. 1891. Salt Range Fossils, vol. IV, part 2. Geological results. Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), fasc. 4:89–242, pl. 1–8.

Wagner, P. J. 1998. A likelihood approach for evaluating estimates of phylogenetic relationships among fossil taxa. Paleobiology 24(4):430–449.

Wahlenberg, G. 1821. Petreficata telluris suecanae examinata. Nova Acta Regiae Societatis Scientiarum Upsaliensis 8:1–116, 293–297, pl. 1–7.

Walcott, C. D. 1884. Paleontology of the Eureka district, Nevada. United States Geological Survey, Monograph 8:298 p., 24 pl.

Walcott, C. D. 1908. Cambrian geology and paleontology, no. 3—Cambrian Brachiopoda, descriptions of new genera and species; no. 4—Classification and terminology of the Cambrian Brachiopoda. Smithsonian Miscellaneous Collections 53:53–165, pl. 7–12.

Wallberg, A., M. Tholleson, J. S. Farris, & U. Jondelius. 2004. The phylogenetic position of the comb jellies (Ctenophora) and the importance of taxonomic sampling. Cladistics 20:558–578.

Walsh, S. L. 2001. Notes on geochronological and chronostratigraphic units. Geological Society of America Bulletin 113:704–713.

Walsh, S. L. 2003. Notes on geochronological and chronostratigraphic units: Reply. Geological Society of America Bulletin 115:1,017–1,019.

Walton, Derek, Maggie Cusack, & Gordon B. Curry. 1993. Implications of the amino acid composition of Recent New Zealand brachiopods. Palaeontology 36:883–896.

Wan Zheng-quan. 1980. New observations on the Devonian Guanxi formation in northern part of Longmenshan Range, Sichuan Province with comment on the boundary between Lower and Middle Devonian. Professional Papers in Stratigraphy and Palaeontology, Chinese Academy of Geological Sciences 9:89–120, pl. 26–37.
In Chinese with English abstract.

Wang Yu, Yu Chang-min, & Wu Qi. 1974. Advances in the Devonian biostratigraphy of South China. Nanjing Institute of Geology and Palaeontology Memoirs, Academia Sinica 6:1–45, pl. 1–19.
In Chinese.

Wardlaw, Bruce, R. E. Grant, & C. H. C. Brunton. Richthofenioidea. 2000. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 3. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 610–619.

Watabe, N., & C.-M. Pan. 1984. Phosphatic Shell Formation in atremate brachiopods. American Zoologist 24:977–985.

Waterhouse, J. B. 1964. Permian brachiopods of New Zealand. New Zealand Geological Survey, Palaeontological Bulletin 35:1–287.

Waterhouse, J. B. 1966. Lower Carboniferous and Upper Permian brachiopods from Nepal. Jahrbuch der Geologische Bundesanstalt 12:5–99, 16 pl.

Waterhouse, J. B. 1967. Proposal of series and stages for the Permian in New Zealand. Royal Society of New Zealand (Geology), Transactions (Earth Sciences) 5:161–180.

Waterhouse, J. B. 1968. The classification and descriptions of Permian Spiriferida (Brachiopoda) from New Zealand. Palaeontographica (Abt. A) 129(1-3):1–94, 18 pl.

Waterhouse, J. B. 1969. Permian Strophalosiidae (Brachiopoda) from the Canadian Arctic Archipelago. Journal of Paleontology 43:28–40, 4 pl.

Waterhouse, J. B. 1973. New brachiopod genera from the New Zealand Permian. Royal Society of New Zealand Journal 3(1):35–42, 2 fig., 6 pl.

Waterhouse, J. B. 1975. New Permian and Triassic brachiopod taxa. University of Queensland, Department of Geology, Papers 7(1):1–23, 2 pl.

Waterhouse, J. B. 1978. Permian Brachiopoda and Mollusca from northwest Nepal. Palaeontographica (Abt. A) 160(1-6):1–175, 26 pl.

Waterhouse, J. B. 1982. New Zealand Permian brachiopod systematics, zonation, and palaeoecology. New Zealand Geological Survey, Palaeontological Bulletin 48:158 p., 23 pl.

Waterhouse, J. B. 1983. Permian brachiopods from Pija Member, Senja Formation, in Manang district of Nepal, with new brachiopod genera and species from other regions. Indian Geologists' Association, Bulletin 16(2):111–151.

Waterhouse, J. B. 1986. New Late Palaeozoic invertebrate taxa. Indian Geologists' Association, Bulletin (Chandigarh) 19:1–8.

Waterhouse, J. B. 1987. Late Paleozoic Brachiopoda (Athyrida, Spiriferida and Terebratulida) from the southeast Bowen Basin, east Australia. Palaeontographica (Abt. A) 196(1-3):1–56, 13 pl.

Waterhouse, J. B. 1988. *Megalosia,* a new strophalosiid (Brachiopoda) genus from the Late Permian Nisal Member, Manang District, Nepal. Journal of Paleontology 62:41–45, 1 pl.

Waterhouse, J. B. 1998. Ingelarelloidea (Spiriferida: Brachiopoda) from Australia and New Zealand, and reclassification of Ingelarellidae and Notospiriferidae. Earthwise 1:1–48.

Waterhouse, J. B. 2001. Late Paleozoic brachiopods and molluscs from Wairaki Downs, New Zealand. Earthwise 3:1–195.

Waterhouse, J. B. 2002a. Stratigraphical succession and structure of Wairaki Downs New Zealand. Earthwise 4:260 p.

Waterhouse, J. B. 2002b. Classification within Productinina and Strophalosidina (Brachiopoda). Earthwise 5:1–62.

Waterhouse, J. B. 2004. Permian and Triassic stratigraphy and fossils of the Himalaya in northern Nepal. Earthwise 6:1–259, 13 pl.

Waterhouse, J. B., & D. J. C. Briggs. 1986. Late Palaeozoic Scyphozoa and Brachiopods (Inarticulata, Strophomenida, Productida and Rhynchonellida) from the southwest Bowen Basin, Australia. Palaeontographica (Abt. A) 193(1–4):1–76, pl. 1–15.

Waterhouse, J. B., D. J. C. Briggs, & S. M. Parfrey. 1983. Major faunal assemblages in the Early Permian Tiverton formation near Homevale Homestead, northern Bowen basin, Queensland. *In* C. B. Foster, ed., Permian Geology of Queensland. Geological Society of Australia. Brisbane. p. 121–138.

Waterhouse, J. B., & Sangat Piyasin. 1970. Mid-Permian brachiopods from Khao Phrik, Thailand. Palaeontographica (Abt. A) 135:83–197, 22 fig., 19 pl.

Waterhouse J. B., & J. Waddington. 1982. Systematic descriptions, paleoecology and correlations of the Late Paleozoic subfamily Spiriferellinae Waterhouse (Brachiopoda) from the Yukon Territory and Canadian Arctic Archipelago. Geological Survey of Canada, Bulletin 289:1–72, 8 pl.

Watkins, Rodney. 1999. Silurian of the Great Lakes Region, Part 4: Llandovery (Aeronian) brachiopods of the Burnt Bluff Group, northeastern Wisconsin and northern Michigan. Milwaukee Public Museum Contributions in Biology and Geology 92:1–29.

Webby, B. D., R. A. Cooper, S. Bergstrom, & F. Paris. 2004. Stratigraphic Framework and Time Slices. *In* B. D. Webby, F. Paris, M. L. Droser, & I. G. Percival, eds., The Great Ordovician Biodiversification Event. Columbia University Press. New York. p. 41–47.

Webby, B. D., F. Paris, M. L. Droser, & I. G. Percival. 2004. The Great Ordovician Biodiversification Event. Columbia University Press. New York. 484 p.

Weber, J. N., & D. M. Raup. 1966. Fractionation of the stable isotopes of carbon and oxygen in marine organisms—The Echinoidea. Part 1. Variation of C^{13} and O^{18} content within individuals. Geochimica et Cosmochimica Acta 30:33–70.

Weber, J. N., & P. M. J. Woodhead. 1970. Carbon and oxygen isotope fractionation in the skeletal carbonate of reef building corals. Chemical Geology 6:93–117.

Wedekind, Rudolf. 1926. Die Devonische Formation. *In* W. H. Salomon, ed., Grundzüge der Geologie, vol. 2, Erdgeschichte. Stuttgart. p. 194–226, 5 fig., 6 pl.

Wenzel, B., & M. M. Joachimski. 1996. Carbon and oxygen isotopic composition of Silurian brachiopods (Gotland/Sweden): Palaeoceanographic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 122:143–166.

Wenzel, B., C. Lécuyer, & M. M. Joachimski. 2000. Comparing oxygen isotope records of Silurian calcite and phosphate $\delta^{18}O$ compositions of brachiopods and conodonts. Geochimica et Cosmochimica Acta 64:1859–1872.

Wesenberg-Lund, Elise. 1938. Brachiopoda. *In* The Zoology of Iceland. Ejnar Munksgaard. Copenhagen and Reykjavik. 11 p., 3 fig.

Wesenberg-Lund, Elise. 1939. Recent Norwegian Brachiopods. Det Kongelige NorskeVidenskabers Selskab, Forhandlinger 11(52):201–204, 1 fig.

Wesenberg-Lund, Elise. 1940a. Brachiopoda. *In* A. S. Jensen, W. Lundbeck, Th. Mortensen, and R. Spèarck, eds., The Zoology of the Faroes 59:8 p., 2 fig.

Wesenberg-Lund, Elise. 1940b. Brachiopods from the waters west of Greenland. The Godthaab Expedition 1928. Meddelelser om Grønland 80(6):24 p., 9 fig.

Wesenberg-Lund, Elise. 1941. Brachiopoda. The Danish Ingolf-Expedition 4 (12):17 p., 3 fig., 10 charts.

White, C. A. 1879. Paleontological Papers No.9; Fossils of the Jura-Trias of Southeastern Idaho. United States Geological Survey of the Territories, Bulletin 5(1):105–117.

Whitehouse, F. W. 1928. Notes on the Upper Palaeozoic marine horixons in eastern and western Australia. Australian Association for the Advancement of Science, Report 18:281–283.

Whittington, H. B. 1980. The significance of the fauna of the Burgess Shale, Middle Cambrian, British Columbia. Proceedings of the Geologists' Association 91:127–148.

Wignall, P. B. 2001. Large igneous provinces and mass extinctions. Earth Science Reviews 53:1–33.

Wignall, P. B., & A. Hallam. 1992. Anoxia as a cause of the Permo-Triassic mass extinction: Facies evidence from northern Italy and the western United States. Palaeogeography, Palaeoclimatology, Palaeoecology 93:21–46.

Williams, Alwyn. 1953. The classification of the strophomenoid brachiopods. Washington Academy of Sciences Journal 43:1–13.

Williams, Alwyn. 1955. Shell structure of the brachiopod *Lacazella mediterraneum* (Risso). Nature 175:1123–1124.

Williams, Alwyn. 1956. The calcareous shell of the Brachiopoda and its importance to their classification. Biological Reviews of the Cambridge Philosophical Society 31:243–287.

Williams, Alwyn. 1965a. Evolution and Phylogeny. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 1. The Geological Society of America and University of Kansas Press. New York and Lawrence. p. 164–197.

Williams, Alwyn. 1965b. Stratigraphic distribution. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 237–250.

Williams, Alwyn. 1965c. Suborder Strophomenidina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 362–412.

Williams, Alwyn. 1968a. Evolution of the shell structure of articulate brachiopods. Special Papers in Palaeontology 2:1–55.

Williams, Alwyn. 1968b. Shell structure of the billingsellacean brachiopods. Palaeontology 11:486–490, pl. 91–92.

Williams, Alwyn. 1968c. A history of skeletal secretion among articulate brachiopods. Lethaia 1(3):268–287.

Williams, Alwyn. 1970a. Origin of laminar-shelled articulate brachiopods. Lethaia 3:329–342.

Williams, Alwyn. 1970b. Spiral growth of the laminar shell of the brachiopod *Crania*. Calcified Tissue Research 6:11–19.

Williams, Alwyn. 1971. Comments on the growth of the shell of articulate brachiopods. *In* J. Thomas Dutro, Jr., ed., Paleozoic Perspectives: A Paleontological Tribute to G. Arthur Cooper. Smithsonian Contributions to Paleobiology 3:47–67.

Williams, Alwyn. 1973. The secretion and structural evolution of the shell of thecideidine brachiopods. Royal Society of London, Philosophical Transactions (series B) 264(865):439–478.

Williams, Alwyn. 1974. Ordovician Brachiopoda from the Shelve District, Shropshire. Bulletin of the British Museum (Natural History) Geology, Supplement 11:1–163, pl. 1–28.

Williams, Alwyn. 1990. Biomineralization in the Lophophorates. *In* J. G. Carter, ed., Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends, vol. 1. Van Nostrand Reinhold. New York. p. 67–82.

Williams, Alwyn. 1996. Introduction: Amended excerpts from the opening address. In Paul Copper and Jisuo Jin, eds., Brachiopods. Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2-5 September, 1995. p. 1–5.

Williams, Alwyn. 1997. Shell Structure. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 267–320.

Williams, Alwyn. 2002. Coordinating author's preface. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H, Brachiopoda, revised, vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. xxvi–xxx.

Williams, Alwyn. 2003. Microscopic imprints on the juvenile shells of Palaeozoic linguliform brachiopods. Palaeontology 46(1):67–92.

Williams, Alwyn, & C. H. C. Brunton. 1993. Role of shell structure in the classification of the orthotetidine brachiopods. Palaeontology 36:931–966.

Williams, Alwyn, & C. H. C. Brunton. 1997. Morphological and anatomical terms applied to brachiopods. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 423–440.

Williams, Alwyn, & C. H. C. Brunton. 2000. Suborder Orthotetidina. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part H (Revised), vol. 3. Geological Society of America and Paleontological Isntitute. Boulder, Colorado & Lawrence, Kansas. p. 644–689.

Williams, Alwyn, C. H. C. Brunton, and L. R. M. Cocks. 2000. Strophomenata. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H (Revised), Vol. 2. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 215-216.

Williams, Alwyn, C. H. C. Brunton, & D. I. MacKinnon. 1997. Morphology. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. p. 321–422.

Williams, Alwyn, S. J. Carlson, & C. H. C. Brunton. 2000. Brachiopod classification. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 2. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 1–29.

Williams, Alwyn, S. J. Carlson, & C. H. C. Brunton. 2002. Outline of suprafamilial classification and authorship. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 4. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. xxxiii–xxxix.

Williams, Alwyn, S. J. Carlson, C. H. C. Brunton, L. E. Holmer, & L. E. Popov. 1996. A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London (series B) 351:1171–1193, 6 fig.

Williams, Alwyn, B. L. Cohen, Maggie Cusack, & S. L. Long. 2000. Provenance of Atlantic lingulid brachiopods. Palaeontology 43:999–1018.

Williams, Alwyn, & Maggie Cusack. 1999. Evolution of a rhythmic lamination in the organophosphatic shells of brachiopods. Journal of Structural Biology 126:227–240.

Williams, Alwyn, & M. Cusack. 2001. Evolutionary and diagenetic changes in the chemico-structure of the shell of the cranioid brachiopods. Palaeontology 44:875–903.

Williams, Alwyn, Maggie Cusack, & K. Brown. 1999. Growth of protein-doped rhombohedra in the calcitic shell of craniid brachiopods. Proceedings of the Royal Society (series B) 266(1428):1601–1607.

Williams, Alwyn, Maggie Cusack, & J. O. Buckman. 1998. Chemico-structural phylogeny of the discinoid brachiopod shell. Philosophical Transactions of the Royal Society of London (series B) 353(1378):2005–2038.

Williams, Alwyn, Maggie Cusack, J. O. Buckman, & Thomas Stachel. 1998. Siliceous tablets in the larval shells of apatitic discinid brachiopods. Science 279:2094–2096.

Williams, Alwyn, M. Cusack, & S. Mackay. 1994. Collagenous chitinophosphatic shell of the brachiopod *Lingula*. Philosophical Transactions of the Royal Society of London (series B) 346:223–266.

Williams, Alwyn, & David A. T. Harper. 2000. Protorthida and Orthida. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 3. Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 709–782.

Williams, Alwyn, & R. A. Hewitt. 1977. The delthyrial covers of some living brachiopods. Proceedings of the Royal Society of London (series B) 197:105–129, pl. 1–7.

Williams, Alwyn, & L. E. Holmer. 1992. Ornamentation and shell structure of acrotretid brachiopods. Palaeontology (London) 35(3):657–692, 7 pl.

Williams, Alwyn, & L. E. Holmer. 2002. Shell structure and inferred growth, functions and affinities of the sclerites of the problematic *Micrina.* Palaeontology 45:845–873.

Williams, Alwyn, L. E. Holmer, & M. Cusack. 2004. Chemico-structure of the organophosphatic shell of siphonotretide brachiopods. Palaeontology 47(5):1313–1337.

Williams, Alwyn, M. A. James, C. C. Emig, Sarah Mackay, & M. C. Rhodes. 1997. Anatomy. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda (Revised), vol. 1. The Geological Society of America & Paleontological Institute. Boulder, Colorado & Lawrence, Kansas. p. 7–188.

Williams, Alwyn, Carsten Lüter, & Maggie Cusack. 2001. The nature of siliceous mosaics forming the first shell of the brachiopod *Discinisca*. Journal of Structural Biology 134(1):25–34.

Williams, Alwyn, & Sarah MacKay. 1979. Differentiation of the brachiopod periostracum. Palaeontology 22:721–736.

Williams, Alwyn, L. E. Popov, & L. E. Holmer. 1998. The diversity and phylogeny of the paterinate brachiopods. Palaeontology 41:221–262.

Williams, Alwyn, L. Popov, L. Holmer, & M. Cusack. 1998. The diversity and phylogeny of the paterinate brachiopods. Palaeontology 41:221–262.

Williams, Alwyn, & A. J. Rowell. 1965a. Brachiopod anatomy. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence, Kansas. p. 6–57.

Williams, Alwyn, & A. J. Rowell. 1965b. Brachiopod morphology. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H: Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 57–155, fig. 59–138.

Williams, Alwyn, & A. J. Rowell. 1965c. Evolution and phylogeny. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. Geological Society of America & University of Kansas Press. New York & Lawrence. p. 164–197.

Williams, Alwyn, & A. J. Rowell. 1965d. Classification. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda, vol. 1. The Geological Society of America and University of Kansas Press. New York & Lawrence, Kansas. p. 214–236.

Williams, Alwyn, & A. D. Wright. 1961. The origin of the loop in articulate brachiopods. Palaeontology 4:149–176, fig. 1–13.

Williams, Alwyn, & A. D. Wright. 1965. Suborder Orthidina. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 300–305.

Williams, Alwyn, & A. D. Wright. 1970. Shell structure of the Craniacea and other calcareous inarticulate brachiopods. Special Papers in Palaeontology 7:1–51.

Willmer, P. G. 1990. Invertebrate Relationships: Patterns in Animal Evolution. Cambridge University Press, Cambridge, England. 414 p.

Wilson, A. E. 1945. *Strophomena* and its homomorphs *Trigrammaria* and *Microtrypa* from the Ottawa Limestone of the Ottawa-St. Lawrence Lowlands. Transactions of the Royal Society of Canada (series 3) 39(4):121–150, pl. 1–2.

Wiman, Carl. 1902. 2. Studien uber das Nordbaltische Silurgebiet. I. Olenellussandstein, Obolussandstein und Ceratopygeschiefer. Bulletin of the Geological Institution of the University of Uppsala 6:12–76, pl. 1–4.

Wiman, C. 1903. Studien über das nordbaltische Silurgebiet. I. Olenellussandstein, Obolussandstein und Ceratopygeschiefer. Bulletin of the Geological Institution of the University of Upsala 6:12–76.

Winchell, C. J., J. Sullivan, C. B. Cameron, B. J. Swalla, & J. Mallatt. 2002. Evaluating hypotheses of deuterostome phylogeny and chordate evolution with new LSU and SSU ribosomal DNA data. Molecular Biology and Evolution 19:762–776.

Wind, J. 1953. Kridtaflejringer i Jylland. Fauna och Flora (Stockholm) 59(4–5):73–84.

Witman, J. D., & R. A. Cooper. 1983. Disturbance and contrasting patterns of population structure in the brachiopod *Terebratulina septentrionalis* (Couthouy) from two subtidal habitats. Journal of Experimental Marine Biology and Ecology 73:57–79, 10 fig.

Wolf, Y. I., I. B. Rogozin, & E. V. Koonin. 2004. Coelomata and not Ecdysozoa: Evidence from genome-wide phylogenetic analysis. Genome Research 14:29–36.

Wongwanich, T., A. J. Boucot, C. H. C. Brunton, M. R. House, & P. R. Racheboeuf. 2004. Namurian fossils (Brachiopods, Goniatites) from Satun Province, Southern Thailand. Journal of Paleontology 78(6):1072–1089.

Wood, T. S., & M. L. Lore. 2005. The higher phylogeny of phylactolaemate bryozoans inferred from 18S ribosomal DNA sequences. *In* H. I. Moyano, G. J. M. Cancino, & P. N. Wyse Jackson, eds., Bryozoan Studies, 2004. Taylor & Francis Group. London. p. 361–367.

Woodward, S. P. 1851–1856. A Manual of the Mollusca. John Weale. London. 488 p., 24 pl.

Woodward, S. P. 1855. Description of a new species of Recent *Rhynchonella*. The Annals and Magazine of Natural History (second series) 16(8):444, 1 pl.

Wray, G. A., J. S. Levinton, & L. H. Shapiro. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. Science 274:568–573.

Wright, A. D. 1965. Superfamily Enteletacea. *In* R. C. Moore, ed., Treatise on Invertebrate Paleontology. Part H, Brachiopoda. The Geological Society of America & University of Kansas Press. New York & Lawrence. p. 328–346.

Wright, A. D. 1970. A note on the shell structure of the triplesiacean brachiopods. Lethaia 3:423–426.

Wright, A. D. 1979. Brachiopod radiation. *In* M. R. House, ed., The Origin of Major Invertebrate Groups. Academic Press. London. p. 235–252.

Wright, A. D. 1981. The external surface of *Dictyonella* and of other pitted brachiopods. Palaeontology 24:443–482, 13 fig., 10 pl.

Xu Gui-rong. 1990. Phenetic-cladistic systematics and geographic patterns of Triassic rhynchonellids. *In* D. I. MacKinnon, D. E. Lee, & J. D. Campbell, eds., Brachiopods through time. Proceedings of the 2nd International Brachiopod Congress. A. A. Balkema. Rotterdam. p. 67–79.

Xu Guirong, & R. E. Grant. 1996. Reef-dwelling brachiopods from the Late Permian of the central Yangtze River area, China. Brachiopods, Proceedings of the Third International Brachiopod Congress, Sudbury, Ontario, Canada, 2–5 September 1995. A. A. Balkema. Rotterdam and Brookfield, Vermont. p. 305–311.

Xu G. R., & Li L. Z. 2002. On a new genus, *Zhuzhaiia*, of trimerelloid brachiopods from Sanqushan Formation (Middle Ashgill of Late Ordovician), Yushan Area, Jiangxi Province, southeast China. Acta Palaeontologica Sinica 41(3):19–427, fig. 1–3, pl. 1–2.

Xu Gui-Rong, & Liu Guang-Cai. 1983. [Brachiopods]. *In* Zun-Yi Yang & others, eds., [Triassic of the South Qilian Mountains]. Geological Publishing House. Beijing. p. 84–128.
In Chinese with English summary.

Xu Han-Kui, Rong Jia-Yu, & Liu Di-Yong. 1974. Brachiopoda (Ordovician). *In* A Handbook of the Stratigraphy and Palaeontology in Southwest China. Science Press. Beijing. p. 144–154, pl. 64–66.

Xu Qing-jian, Wan Zheng-quan, & Chen Yuan-ren. 1978. Brachiopoda. *In* Institute of Geological Sciences of south-western China, ed. Paleontological Atlas of southwestern China, Sichuan Province, vol. 1, Sinian–Devonian. Geological Publishing House. Beijing. p. 284–381, pl. 115–151.
In Chinese.

Xu Qing-Jie. 1978. [Brachiopoda]. *In* [Paleontological Atlas of Southwestern China, Sichuan Province], vol. 2. Beijing. p. 270–314, pl. 93–103.

Yabe, Hisakatsu, & Kotora Hatai. 1934. The Recent brachiopod fauna of Japan (1). New genera and subgenera. Proceedings of the Imperial Academy of Japan 10(9):586–589.

Yabe, H., & Ichiro Hayasaka. 1920. Palaeontology of Southern China, vol. 3. Geographical Research in China, Tokyo Geographical Society. Tokyo. 222 p.

Yadrenkina, A. G. 1977. Problemy stratigrafii Ordovika i Silura Sibiri. Akademiia Nauk SSSR Sibirskoe Otdelenie, Institut Geologii i Geofiziki, Trudy 372:1–140, 15 pl.

Yatsu, Naukidé. 1902 On the development of *Lingula anatina.* Journal of the College of Science, Imperial University, Tokyo, Japan 17(4):1–112, pl. 1–8.

Ye Song-Ling, & Yang Sheng-Qiu. 1979. [Brachiopods from the Bagon Lake Series, Northern Tibet]. Acta Palaeontologica Sinica 18(1):64–71, 1 pl.

Yochelson, E. L. 1993. Molluscan affinity of coeloscleritophorans. Lethaia 26:47–48.

Zavodowsky, V. M. 1960. New species of Permian brachiopods from the Kolyma River valley and Okhosk coast. Mater. Geol. Polez. Iskop Servero-Vostoka SSSR (Magadan) 14:61–73.

Zeng Qing-luan. 1987. [Brachiopoda]. *In* Wang Xiaofeng & others, Biostratigraphy of the Yangtze Gorge Area (2). Early Palaeozoic Era. Geological Publishing House. Beijing. 614 p., pl. 8–18.
In Chinese, with English summary on p. 489–555.

Zeng Quing-luan, & Hu Chang-ming. 1997. Discovery of new early Llandoverian brachiopod fauna from Wangjiara of Yushan County, Jiangxi and its significance. Acta Palaeontologica Sinica 36:1–17, 3 pl.

Zezina, O. N. 1970. Brachiopod distribution in the Recent ocean, with reference to problems of zoogeographic zoning. Paleontologicheskii Zhurnal 2:3–17.
In Russian.

Zezina, O. N. 1975a. Recent Caribbean deep-sea brachiopod fauna, the sources and the conditions of its formation. Akademiia Nauk CCCP, Moscow 188–195, 3 fig. In Russian with English abstract.

Zezina, O. N. 1975b. On some deep-sea brachiopods from the Gay Head–Bermuda transect. Deep-Sea Research 22:903–912, 9 fig.

Zezina, O. N. 1976a. The ecology and distribution of present-day brachiopods. Akademiia Nauk CCCP. Moscow. 138 p., 19 fig.
In Russian.

Zezina, O. N. 1976b. [A new genus of Recent terebratelloid brachiopod from the sublittoral of the Kurilo-Kamchatka region.] *In* Donnaia Fauna Kraevykh Morei SSSR [Bottom Fauna of the USSR Fringing Seas]. Akademia Nauk SSSR, P. P. Shirshov Institute of Oceanology. Moscsow. p. 101–105, 1 pl.
In Russian with English abstract.

Zezina, O. N. 1979. Novye dannye o brakhiopodakh dal'nevostochnyka SSSR. *In* Biologiia Shel'fa Kuril'skikh Ostrovov. Izdatel'stvo 'Nauka.' Moscow. p. 222–233.

Zezina, O. N. 1980. Structure, population growth and some biological characteristics of coldwater brachiopods from the southern hemisphere. *In* Ecological Research of the shelf. Oceanological Institute, Akademiia Nauk CCCP. Moscow. p. 9–35.

Zezina, O. N. 1981a. Recent deep-sea Brachiopoda from the western Pacific. Galathea Report 15:7–20, 4 fig., 4 pl.

Zezina, O. N. 1981b. The composition and the ways of formation of the thalassobathyal brachiopod fauna. *In* A. P. Zuznetsov & N. A. Mironov, eds., Benthos of the submarine mountains Marcus-Necker and adjacent Pacific regions. Akademiia Nauk CCCP. Moscow. p. 141–149, 1 pl.
In Russian with English abstract.

Zezina, O. N. 1981c. New and rare cancellothyroid brachiopods in the bathyal and abyssal ocean. *In* Deep-water benthic fauna of the Pacific Ocean. Trudy Instituta Okeanologie, Akademiia Nauk CCCP, Moscow 115:155–164.
In Russian.

Zezina, O. N. 1985. Living brachiopods and problems of the north bathyal oceans. Akademiia Nauk CCCP. Moscow. 247 p., 31 fig.
In Russian.

Zezina, O. N. 1987. Brachiopods collected by BENTHEDI-Cruise in the Mozambique Channel. Bulletin du Muséum national d'Histoire naturelle (series 4) 9(section A, no. 3):551–563, 3 fig.

Zezina, O. N. 1990. Composition and distribution of articulate brachiopods from the underwater rises of the eastern Pacific. Akademiia Nauk CCCP, Moscow 124:264–268, 1 fig.
In Russian with English abstract.

Zezina, O. N. 1991. New species of cancellothyroid brachiopods from the "Atlantis" cruise to the Mid-Atlantic Ridge. Zoologicheski Zhurnal 70(6):152–153.
In Russian.

Zezina, O. N. 1997a. Biogeography of the Bathyal Zone. Advances in Marine Biology 32:389–426, 11 fig.

Zezina, O. N. 1997b. Recent brachiopods in the composition of the biofiltering biota of Russian Seas. Akademiia Nauk. Moscow. 83 p, 46 fig.
In Russian.

Zezina, O. N. 2000. Russian collections of the deep-sea brachiopods in the Atlantic Ocean. *In* A. P. Kuznetsov and O. N. Zezina, eds., Benthos of the Russian seas and the northern Atlantic. Akademiia Nauk. Moscow. 26–36.
In Russian with English abstract.

Zezina, O. N. 2001a. Global surface-water circulation and the main features of brachiopod biogeography. *In* C. H. C. Brunton, L. R. M. Cocks, & S. L. Long, eds., Brachiopods Past and Present. The Systematics Association Special Volume Series 63:102–107, 2 fig.

Zezina, O. N. 2001b. Articulate brachiopods near Vietnam shores in the belt of suspension-feeders at the continental slope of Asia. *In* A. P. Kuznetsov and O. N. Zezina, eds., Composition and structure of the marine bottom biota. Akademiia Nauk. Moscow. p. 63–68, 2 fig.
In Russian with English abstract.

Zezina, O. N. 2005. On the systematic position of some Recent brachiopod species from the Norfolk Ridge (West Pacific). Invertebrate Zoology 2:29–33.

Zhan L. P. 1979. Brachiopods. *In* H. F. Hou, L. P. Zhan, & B. W. Chen, eds., The coal-bearing strata and fossils of late Permian from Guangtung. Geological Publishing House. Beijing. p. 61–100, 10 pl.
In Chinese.

Zhan Ren-bin, & L. R. M. Cocks. 1998. Late Ordovician brachiopods from the South China Plate and their palaeogeographical significance. Special Papers in Palaeontology 59:1–70, 9 pl.

Zhan Ren-bin, & Jin Jisuo. 2005. Brachiopods from the Dashaba Formation (Middle Ordovician) of Sichuan Province, south-west China. Special Papers in Palaeontology 74:1–63, pl. 1–16.

Zhan Ren-bin, & Rong Jia-yu. 1994. A new strophomenoid genus from middle Ashgill rocks (Ordovician) of Xiazhen, Yushan, N.E. Jiangxi, East China. Acta Palaeontologica Sinica 33:416–428, 1 pl.

Zhan Ren-bin, & Rong Jia-yu. 1995. Four new Late Ordovician brachiopod genera from the Zhejiang-Jiangxi border region, East China. Acta Palaeontologica Sinica 34(5):549–574.

Zhang X., Hou X., & C. C. Emig. 2003. Evidence of lophophore diversity in Early Cambrian Brachiopoda. Proceedings of the Royal Society of London (Supplement B, Biology Letters) 270:65–98.

Zhang Yan. 1983. [Late Palaeozoic Brachiopods]. *In* Zhang Yan, Fu Li-pu, & Ding Pei-zhen, Palaeontological Atlas of Northwest China, Shaanxi, Gansu and Ningxia Provinces, vol. 2. Geological Publishing House. Beijing. p. 244–425, pl. 88–143.
In Chinese.

Zhang Yan. 1987. Devonian brachiopod from Luqu-Tewo area of West Qinling Mountains, China. *In* Xi'an Institute of Geology and Mineral Resources, and Nanjing Institute of Geology and Palaeontology, Academia Sinica, eds., Late Silurian-Devonian strata and fossils from Luqu-Tewo area of west Qinling Mountains, China, vol. 2. Nanjing University Press. Nanjing. p. 95–164, pl. 102–120.
In Chinese, with English summary.

Zhang Yan, & Fu Li-pu. 1983. [Devonian Brachiopoda]. *In* Palaeontological Atlas of Shaanxi-Gansu-Ningxia, vol. 2. Geological Publishing House. Beijing. p. 244–425, pl. 88–143.
In Chinese.

Zhang Z., Han J., Zhang X., Liu J., & Shu D. 2004. Soft tissue preservation in the Lower Cambrian linguloid brachiopod from South China. Acta Palaeontologica Polonica 49(2):259–266.

Zhang Z. F., Han J., Zhang X. L., Liu J. N., & Shu S. G. 2003. Pediculate brachiopod *Diandongia pista* from the Lower Cambrian of South China. Acta Geologica Sinica 77(3):288–293.

Zhang Zhifei, Shu Degan, Han Jian, & Liu Jianni. 2006. New data on the rare Chengjiang (Lower Cambrian, South China) Linguloid brachiopod *Xianshanella haikouensis*. Journal of Paleontology 80(2):203–211.

von Zittel, K. A. 1870. Ueber den Brachial-Apparate bei einigen jurassischen Terebratuliden und ueber eine neue Brachiopodengattung Dimerella. Palaeontographica 17(5):211–222, pl. 41.

Zrzavý, J. 2003. Gastrotricha and metazoan phylogeny. Zoologica Scripta 32:61–81.

Zrzavý, Jan, Stanislav Mihulka, Pavel Kepka, Aleš Bedzêk, & David Tietz. 1998. Phylogeny of the metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14:249–285.

Zuykov, M. A., & Eva Egerquist. 2005. A new *Platystrophia*-like brachiopod genus from the Ordovician Boda Limestone of Dalarna, Sweden. GFF 127:1–5.

COMPREHENSIVE INDEX
PART H, BRACHIOPODA (REVISED), VOLUMES 1–6*

---

*page numbers in italics refer to content in Volume 1: Introduction.