TREATISE ON
INVERTEBRATE PALEONTOLOGY

Part H
BRACHIOPODA
Revised

Volume 2:
Linguliformea, Craniiformea, and Rhynchonelliformea (part)

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PART H, Revised

BRACHIOPODA

VOLUMES 2 & 3:

Linguliformea, Craniiformea, and Rhynchonelliformea (part)

Alwyn Williams, S. J. Carlson, C. H. C. Brunton, L. E. Holmer, L. E. Popov, Michal Mergl, J. R. Laurie, M. G. Bassett, L. R. M. Cocks, Rong Jia-yu, S. S. Lazarev, R. E. Grant, P. R. Racheboeuf, Jin Yu-gan, B. R. Wardlaw, D. A. T. Harper, A. D. Wright, and Madis Rubel

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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, Porifera, xviii + 122 p., 89 fig., 1955.

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Part G. Bryozoa, xii + 253 p., 175 fig., 1953.

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EDITORIAL PREFACE

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. These volumes, Part H, Revised, Brachiopoda, Volumes 2 and 3, have been prepared by such a team of specialists whose work was coordinated by Sir Alwyn Williams at The University of Glasgow. Editorial matters specific to these volumes are discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1985 in the *International Code of Zoological Nomenclature,* hereinafter referred to as the *Code,* provide procedures for answering such questions. The prime objective of the *Code* is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of thought and action of systematists. Priority of names is a basic principle of the *Code;* but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, revised the *Code* in 1999 to enhance further nomenclatorial stability. Its publication came too late to allow incorporation in these volumes. In any event the revised *Code* is specified as taking effect at the start of 2000. In spite of the revisions, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise,* especially in these volumes. 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 propose 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, p. 73), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in 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 volumes, in which authors have used fewer terms for such names. The reader is referred to the *Code* (Articles 10 to 20) for further details on availability of names. Here, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the *Code.* All zoological names that fail to comply with mandatory provisions of the *Code* are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the *Treatise,* although not explicitly differentiated in the *Code.* Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see *nomina nuda* below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code,* Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code,* Article 13a), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code,* Article 13b). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

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

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

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the *Treatise* deals with 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.

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

FAMILY-GROUP NAMES

Family-Group Names: Authorship and Date

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

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

Family-Group Names: Use of *nomen translatum*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) names, but all family-group taxa are defined as coordinate (*Code,* Article 36, p. 77): "A name established for a taxon at any rank in the family group is deemed to be simultaneously established with the same author and date for taxa based upon the same name-bearing type (type genus) at other ranks in the family group, with appropriate mandatory change of suffix [Art. 34a]." Such changes of rank and concomitant changes of endings as elevation of a tribe to subfamily rank or of a subfamily to family rank, if introduced subsequent to designation of a subfamily or family based on the same nominotypical genus, are *nomina translata.* In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum,* abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration.

Family HEXAGENITIDAE Lameere, 1917

[*nom. transl.* Demoulin, 1954, p. 566, *ex* Hexagenitinae Lameere, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code.* The latter is merely the individual who first defined some 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.

Superfamily AGNOSTOIDEA M'Coy, 1849

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

Family-Group Names: Use of *nomen correctum*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addition, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

Family STREPTELASMATIDAE Nicholson, 1889

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

Family PALAEOSCORPIDAE Lehmann, 1944

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

Family-Group Names: Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for family and subfamily, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a 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, p. 79), in which case ". . . it must be replaced either by the next oldest available name from among its synonyms, including those of its subordinate taxa, or, if there is no such name, by a new replacement name based on the valid name of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code* (p. 81), however, specifies that for subsequent application of the rule of priority, the family-group name ". . . should be cited with its own author and date, followed by the date of the replaced name in parentheses." Many family-group names that have been in use for a long time are *nomina nuda,* since they fail to satisfy criteria of availability (*Code,* Article 11f). These demand replacement by valid names.

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

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

SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

International rules of zoological nomenclature as given in the *Code* affect only lower-rank categories: subspecies to superfamily. Suprafamilial categories (suborder to phylum) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th International Congress of Zoology convened in 1958, thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision that was supported by a wide majority of the participants in the colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, a class or order defined by an author at a given date, using chosen morphologic characters (*e.g.,* gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (*e.g.,* hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. 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 33a and Glossary, p. 254) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

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

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

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

Prionocyclus MEEK, 1871b, p. 298 [**Ammonites serratocarinatus* MEEK, 1871a, p. 429, *non* STOLICZKA, 1964, p. 57; =*Prionocyclus wyomingensis* MEEK, 1876, p. 452].

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication except that diacritical marks have been removed. Where other mandatory changes are required, these are introduced later in the text, typically in 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 automatically becomes the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later SD designation is necessary. Examples of the use of SD as employed in the *Treatise* follow.

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

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

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

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code,* Article 13b). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

HOMONYMS

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

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

In like manner, a replacement generic name that is needed may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

Mysterium De Laubenfels, herein, *nom. nov. pro Mystrium* Schrammen, 1936, p. 183, *non* Roger, 1862 [**Mystrium porosum* Schrammen, 1936, p. 183; OD].

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

Synonymous Homonyms

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

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

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae Richter & Richter, 1925, based on *Scutellum* Pusch, 1833, a trilobite. This name is a junior homonym of Scutellidae Gray, 1825, based on the echinoid genus *Scutella* Lamarck, 1816. The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

SYNONYMS

In the *Treatise,* citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are 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.

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, might also be spelled Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the *Treatise* editorial staff has decided to retain the roman spelling that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, 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 THESE VOLUMES

Some languages, in these volumes most notably the Polish and Czech languages, are enriched with the use of diacritical marks that provide enhanced alphabetical diversity. While celebrating diversity, we have nevertheless elected to omit such marks from Polish and Czech geographical terms used in the *Treatise*. We continue to insert diacritical marks in authors' names and in such geological series names as Přídolí. Two factors have led us to this editorial decision. First, we in the *Treatise* editorial office typeset electronically all the pages, and such diacritical marks must be inserted by hand into the final computer-prepared pages. This is a costly and time-consuming operation that is fraught with the possibility of introducing errors. Second, in the burgeoning information age of the new millennium, databases and schemes for information retrieval will be of critical importance in managing paleontological information. Stability and uniformity of terminology are requisites of database-management systems, and the use of diacritical marks and computer technology are likely to remain incompatible for some time to come. We hope that linguistic purists will be tolerant of this transgression, which we have undertaken solely in the interest of expediency, accuracy, and information retrieval.

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 these volumes, we have taken special pains to acknowledge authorship of small subsections. Any reader citing the volumes is 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.

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 these volumes through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team including Jack Keim with photography and computer graphics and Jean Burgess with general support. Jill Krebs, the remaining member of the Paleontological Institute staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with the brachiopod *Treatise.*

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

Finally, I am pleased to extend once again on behalf of the members of the staff of the Paleontological Institute, both past and present, our most sincere thanks to Sir Alwyn Williams for the unwavering scholarship, dedication to the task, and scrupulous attention to detail that have marked his involvement with this project from the outset and, indeed, his entire career as a specialist on the Brachiopoda.

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Roger L. Kaesler
Lawrence, Kansas
January 1, 2000

STRATIGRAPHIC DIVISIONS

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

- **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**
    - Přídolí 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

COORDINATING AUTHOR'S PREFACE

ALWYN WILLIAMS
[University of Glasgow]

These complementary volumes 2 and 3 and those that follow describe about 5,000 brachiopod taxa belonging to all ranks of the classificatory hierarchy down to subgenera. The full text is intended to diagnose all taxa known in 1995 and nearly all those subsequently erected up to the year of publication of the last volume, where they will be assembled as a concluding supplement. The descriptions have been written by the thirty-four authors listed in the outline of suprafamilial classification (p. 22). Two contributors, Richard E. Grant and Jess G. Johnson, died before their assignments had been completed. But they had already prepared and submitted substantial parts of their assignments, and it has been a collaborative act of remembrance to complete their revisions as homage to two outstanding brachiopodologists.

Responsibilities for the revision and integration of the classificatory descriptions of the Brachiopoda were clearly defined at the outset of the project. Senior authors and their collaborators were responsible for the taxonomic revision of their allotted groups from subgenera to orders inclusive. They have also provided a brief introduction to any group, normally of ordinal rank, warranting an illustrated guide to the basic diagnostic features of its morphology. The introductions have further afforded authors opportunity to air their own views on the classification and phylogeny of the groups being revised.

Throughout the period of preparation, day-to-day advice on procedures, data retrieval, relocation of taxa within the hierarchy, nomenclature, and so on was given by the coordinating author and deputies. As assignments were completed but before final versions had been delivered to the editorial office in Kansas, drafts were submitted to the coordinating author for scientific appraisal. A detailed scrutiny was also made of introductions and the description of a representative superfamily and all its constituent taxa to ensure that diagnoses were consistently presented and were broadly comparable throughout all contributions, in the weighting and sequential description of relevant characters.

In this way, new descriptions of twenty-five groups of taxa, each with an introduction, were assembled. Their integration within a supraordinal classification then became the responsibility of the coordinating author and deputies. A classification intended for this purpose had already been published (WILLIAMS & others, 1996). Its erection had been made possible by access to documents and advice, freely given by all contributors to this *Treatise,* who have generally accepted the classification as an appropriate framework for the taxonomic revision of the phylum (reservations on a few ordinal groupings are noted in relevant introductions). The classification is described in the opening chapter of this volume. Its adoption has entailed the preparation of new or amended diagnoses for the phylum, three subphyla, and eight classes, with comments on their synapomorphies, on affinities with other groups of equal rank, and on relationships among their constituent taxa.

The mode of presentation of so much information has been determined by the practicalities of publication and the observance of geological and taxonomic conventions. Volumes exceeding 600 pages in length are unwieldy as sources of reference and even more so as bench-top tools. Taxonomic descriptions of groups with long geological records are traditionally arranged according to the chronological order of appearance of their high-ranking taxa. The brachiopod fossil record is unexcelled among metazoans with skeletons, and the preponderance of extinct groups is strikingly evident in that all but three of the 26 orders comprising the phylum first appeared in Cambro-Ordovician times, while only five survive today. Even so, it seemed at first that the classification of this skewed record could be presented, with proper regard for geological and taxonomic protocol, without having to split the description of any of the many orders between consecutive volumes.

This aim has been frustrated by the inevitable mismatch between the size and geological distribution of supraordinal taxa. Six of the eight classes, including all four restricted to the Early Paleozoic, contain less than 10 percent of described genera compared with more than 20 percent and 60 percent (mainly of post-Ordovician age) respectively assigned to the strophomenates and higher rhynchonellates. Indeed, preliminary estimates of format showed that the Linguliformea and Craniiformea could be described in a text of well under 200 pages, less than one-tenth of that required for the Rhynchonelliformea. Accordingly a volume was planned to hold descriptions not only of all linguliforms and craniiforms but also of some early rhynchonelliforms. The inclusion of such groups in one book of standard size, however, would split the strophomenate text between two, ostensibly self-contained volumes. Even so, it was decided to publish two such volumes numbered consecutively but issued simultaneously, like overweight twins after a long gestation, whose seniority is merely a matter of delivery. This ploy would enable the account of the rhynchonelliform subphylum to be interrupted at a significant node in its genealogy. The most obvious apportionment was to close Volume 3 with the description of the rhynchonelliform orthides and to open Volume 4 with a chapter on the pentamerides, the stem group of the rhynchonellides and all later rhynchonellates.

Finally, a small number of typographic, transpositional and taxonomic errors, and terminological ambiguities have been been found in Volume 1 (Kaesler, 1997). The only one requiring immediate correction is the mislabelling of shell folding in Figure 289 (1997, p. 328), which has been correctly relabelled on p. xxvi of this volume. The other errors should not cause difficulty even for the general reader and, as errors could well occur in this and succeeding volumes, it has been decided to issue a full list of errata in the supplement to Volume 5.

ACKNOWLEDGMENTS

The acknowledgments cited in Volume 1 of Part H(R) (Kaesler, 1997, p. 5–6) were intended to express heartfelt appreciation for the help received by all authors during preparation of their contributions to the entire revision. Assistance of every kind continues to flow, however, from new sources, even in answer to editorial queries, and merits special mention in this foreword.

For the last two years, there has been virtually unceasing communication between Kansas and Glasgow and the coordinating author and his collaborators by telephone, fax, and electronic and surface mail in the form of circular and individual documents as well as scripts in hard copy and on disk. Pivotal to the smooth running of this global exchange has been Sheila Harvey of Glasgow University. Her quick-witted initiative and blithe efficiency continue to keep everyone well supplied with accurate data, expeditiously dispatched; we are all indebted to her.

On the scientific side, many of us are also indebted to the late Vladimír Havlíček, formerly of the Czechoslovakian Geological Survey, for the unconditional use of his superb private collection of fossils and photographs, and to him and G. Arthur Cooper, formerly of the United States National Museum, for invaluable advice on many problems relating to brachiopod taxonomy. Sarah Long of the Natural History Museum, London has been widely consulted about obscure literature and has unstintingly arranged loans of, and access to, brachiopod specimens as have J. Thomas Dutro, Jr., and Jann Thompson of the Smithsonian Institution, Washington D.C.; we are pleased to thank them for their services. The taxonomic descriptions of most contributors have greatly benefitted not only from personal communications but also from individual loans of specimens and photographs from paleontologists and a host of institutions including those listed below. The sources of those that have been used for illustration are acknowledged in the appropriate figure captions in the text.

Finally some contributors have received previously unreported grants in support of their *Treatise* work and wish to thank the funding bodies. The grants include those from the Royal Society of London and the Chinese Academy of Science to Rong Jia-yu for travel to, and study in, London; the National Natural Science Fund of China (grant 480070) to Jin Yu-gan, Rong Jia-yu, and Hou Hong-fei for research in *Treatise* themes; the Natural Environment Research Council (grant GR3/09604) to A. Williams for research on shell structure; and the Royal Society of London (grant RSRG16604) to A. Williams for upgrading computer facilities.

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.

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
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
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
DNGM: Servicio Nacional Minero Geológico, Buenos Aires, Argentina
DP, DPO: Oviedo University, Spain
DPO: see DP
DPUCM: Departamento de Paleontologia, Universidad Complutense, Madrid, Spain
ENSM, FSI, FSL, SSL, TA: Université Claude Bernard, Lyon I, Villeurbanne, France
FD: Geological College of Eastern China, Fuzhou, China
FSI: see ENSM
FSL: see ENSM
GB: Xian Institute of Geology and Mineral Resources, Xian, China
GIN KAZ: Institute of Geology, Kazahk Academy of Sciences, Alma-Ata, Kazakhstan
GIN TAD: Institute of Geology, Dushanbe, Tadzhikistan
GIN UZ: Institute of Geology, Uzbek Academy of Sciences, Tashkent, Uzbekistan
GLAHM: Hunterian Museum, Glasgow University, Scotland, United Kingdom
GMC, IV: Geological Museum of China, Beijing, China
GMUT: see TUG
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
GS YA: see CGS
HB: Bureau of Geology and Mineral Resources of Hunan Province, Hunan, China
HIGS: Hangzhou Institute for Geological Science, Hangzhou, China
HM: see GLAHM

HNHMB: Hungarian Natural History Museum, Budapest, Hungary
HUB: see MB
IGAS: Institute of Geology, Chinese Academy of Sciences, Beijing, China
IGiG: Institute of Geology and Geophysics, Siberian Branch, Academy of Sciences, Akademgorodok, Russia
IGN: Institute of Geological Sciences, Kiev, Ukraine
IGR: Institute of Geology, University of Rennes, Rennes, France
IGS GSE: Institute of Geological Sciences, Edinburgh, United Kingdom
IGS GSM: see BGS
Inst. Geol.: Geological Institute, Bishkek, Kyrgyzstan
IO: P. P. Shirshov Institute of Oceanology, Moscow, Russia
IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
IV: see GMC
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
LGE: St. Petersburg State University, St. Petersburg, Russia
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
MCMB: Department of Geology, University of Beijing, Beijing, China
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MGRI: Moscow Geological Prospecting Institute, Moscow, Russia
MGU: Moscow State University, Russia
MIP: Invertebrate Paleontology Department, La Plata Natural Sciences Museum, La Plata, Argentina
MLP: La Plata Natural Sciences Museum, La Plata, Argentina
MM: Moravian Museum, Brno, Czech Republic
MMF: Geological and Mining Museum, Department of Mines, Sydney, Australia
MONZ: see NMNZ
MNHN: Muséum National d'Histoire Naturelle, Paris, France
Muz IG: Geological Museum of the Geological Institute, Warsaw, Poland
MV: see NMVP
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NM: National Museum, Prague, Czech Republic
NMNZ: Te Papa, Museum of New Zealand, Wellington, New Zealand
NMVP: Victoria Museum, Melbourne, Victoria, Australia
NMW: National Museum of Wales, Cardiff, United Kingdom
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
PIN: Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia
PIN RAS: see PIN
PIW: Paleontological Institute, Würzburg University, Würzburg, Germany
PM (formerly PMU): Palaeontological Museum, Uppsala University, Uppsala, Sweden
PMO: Paleontologisk Museum, University of Oslo, Norway
PRI: Paleontological Research Institute, Ithaca, New York, USA
QMF: Queensland Museum, South Brisbane, Australia
RM, RMS: Swedish Museum of Natural History, Stockholm, Sweden
ROM: Royal Ontario Museum, Toronto, Ontario, Canada
SAM.P: South Australian Museum, Adelaide, South Australia
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
SSL: see ESNM
SUI: University of Iowa, Department of Geology, Iowa City, USA
SUP: University of Sydney, New South Wales, Australia
TA: see ESNM
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

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

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

UCF: The University, Calgary, Canada

UCM: University of Canterbury, Christchurch, New Zealand

UD: University of Dijon, Dijon, France

UHR: Hokkaido University, Sapporo, Japan

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

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

XIGMR: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China

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

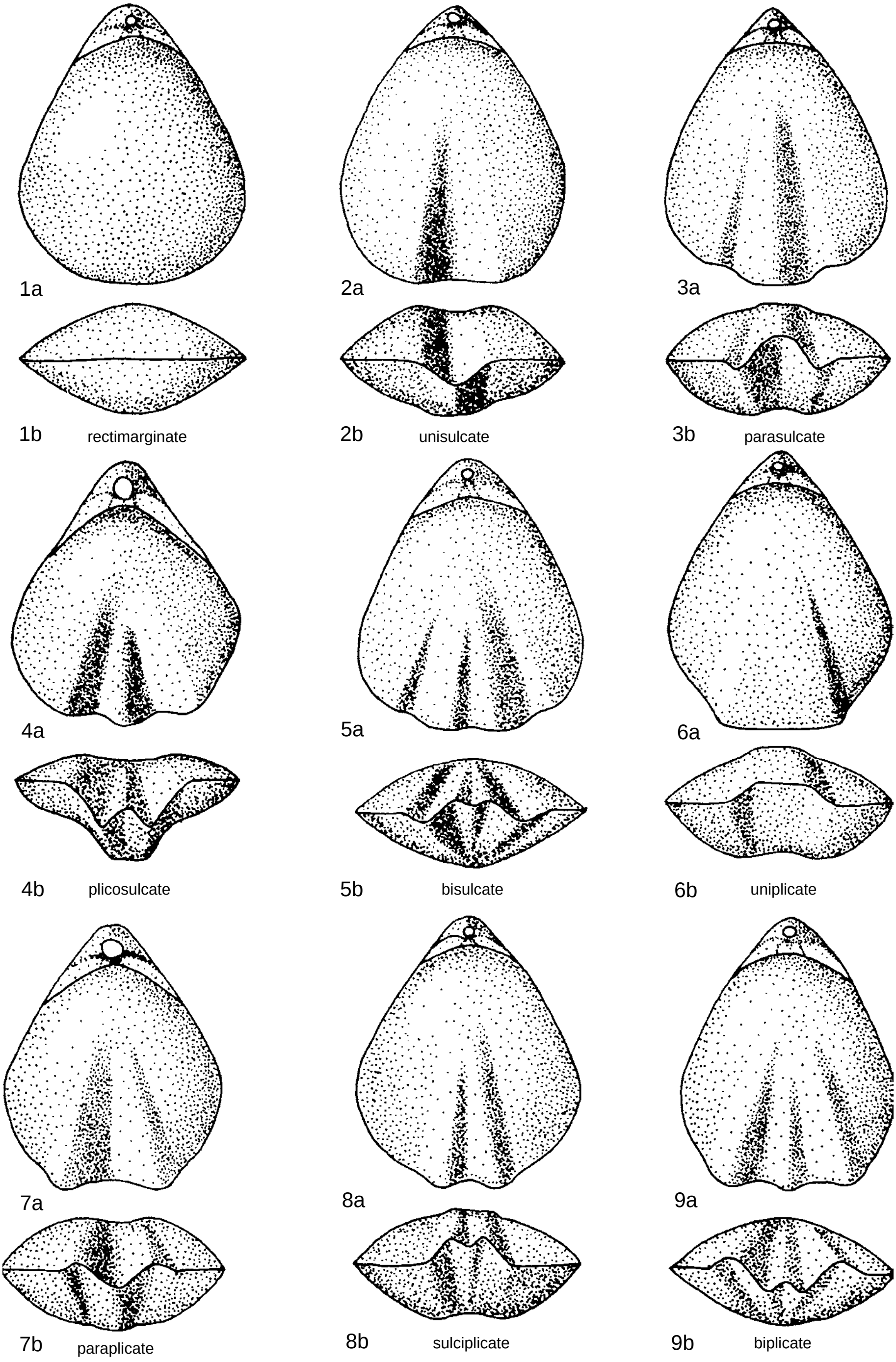

FIG. 289. Types of alternate folding; *1,* rectimarginate; *2–5,* forms of folding that are basically sulcate; *6–9,* forms of folding that are basically plicate (adapted from Williams & Rowell, 1965b).
[Note: this figure was corrected from the version in Volume 1, 1997, p. 328.]

BRACHIOPOD CLASSIFICATION

ALWYN WILLIAMS,[1] SANDRA J. CARLSON,[2] and C. HOWARD C. BRUNTON[3]

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HISTORICAL REVIEW

The chapter on the classification of the Brachiopoda for the first edition of the *Treatise on Invertebrate Paleontology* (WILLIAMS & ROWELL, 1965c, p. 214–234) also outlined the more influential taxonomic schemes that had been used over the previous 150 or so years for grouping species assigned to the phylum. Some of the classifications were little more than catalogues. DAVIDSON (1884), after a lifetime of unrivalled study of living and especially fossil brachiopods, would commit himself only to assigning the 139 genera he recognized to 28 suprageneric groupings, segregated into two orders established by KING in 1873 but essentially equivalent to the Inarticulata and Articulata of HUXLEY (1869). Incidental comments on the lack of fossil evidence for the theory of evolution suggest that DAVIDSON found no relationships among the groups that were strong enough to warrant the erection of any phylogenetic hierarchy. He did, however, carefully discriminate between family (-idae) and subfamily (-inae) and was among the first to recognize the need for a superfamilial rank. In bringing together all the loop- and spire-bearing brachiopods he used the collective nouns Terebratulacea and Spiriferacea but spoiled the effect by referring to these as families.

Other classifications proposed in the nineteenth century were more elaborate attempts to establish hierarchies on basic morphological and anatomical changes. That of GRAY (1848), which was based on the disposition of the lophophore and the structure of the shell, was well in advance of its time. GRAY interpreted the anatomy of extinct groups with commendable assurance. He recognized the relationship between rhynchonellides, pentamerides, and spiriferides and, in concluding that an unsupported lophophore was typical of orthides, strophomenides, and productides, was able to provide an integrated classification of living and extinct species.

WAAGEN's classification (1882–1885) featured inarticulated suborders, based on the presence and attitude of the pedicle, and articulated suborders, founded mainly on the nature of lophophore supports. The groupings were not new but were used with a greater understanding of their taxonomic importance than hitherto. He was the first to attempt any subordinal arrangement of the inarticulated brachiopods (recognized by him as the Lyopomata of OWEN, 1858); and he divided the articulated brachiopods (Arthropomata) into four suborders. Inconsistencies in the classification were evident even in the light of contemporary knowledge; yet modified versions of it survived up to 1949 (TERMIER & TERMIER, 1949b).

Many other intraphyletic classifications of the Brachiopoda were proposed in the nineteenth century but only two have survived in popular usage more or less to the present day. One was based on the presence or absence of teeth and sockets for the articulation of the valves. This distinction was first used by DESHAYES (in LAMARCK, 1836) to segregate species with free (libres) or conjoined (articules) valves and later by OWEN (1858) as one of the prime differences in establishing his Lyopomata and Arthropomata orders. Yet the self-explanatory *nomina* of Inarticulata and Articulata proposed by HUXLEY (1869) for two classes of brachiopods based on this distinction has prevailed to the present time.

The other classification widely used well into the twentieth century was that of BEECHER (1891, 1892). It was inspired by the Haekelian theory of evolution as was confirmed by BEECHER's (1891, p. 343) opening remarks on elucidating the evolutionary history of phyla by applying the "principles of growth, acceleration of development, and mechanical genesis" in the light of the "geological sequence of genera and species." In effect, he believed that his study of a relatively few, strategically chosen stocks would provide a classificatory framework consistent with brachiopod phylogeny.

According to BEECHER (1891), the generalized morphology of the brachiopod protegulum represents the most primitive condition of the shell and is similar to that of adult *Paterina,* the "early primordial form" (1891, p. 346). Subsequent radiation of the phylum involved an increasing dissimilarity in the valves and a ventral migration of the pedicle. Although BEECHER recognized the skeletal support for the lophophore as a distinctive characteristic of the dorsal valve, he maintained that all such internal structures grew independently of the valves and could be ignored in any attempt at determining the evolution of the brachiopod shell. In contrast, he regarded the type of pedicle opening and even the length of the pedicle, as having so affected shell growth that four distinct groups emerged during brachiopod evolution. The groups were accorded ordinal status with the Atremata and Neotremata embracing all inarticulated brachiopods and the Protremata and Telotremata all articulated brachiopods. As pedicle disposition favored the derivation of the protremates (*Strophomena*) from the neotremates (*Discinisca*) and the telotremates (*Rhynchonella*) from the atremates (*Lingula*), BEECHER rejected the Articulata and Inarticulata as formal taxa. His later comparative review (1892) of the embryology of brachiopods assigned to his new orders seemed to vindicate his supposed phylogenetic classification. In particular, he interpreted KOVALEVSKY's study (1874) of the development of the protrematous *Lacazella* as showing the pseudodeltidium to originate independently of the ventral valve.

Although BEECHER's (1891) classification was widely adopted, it was seldom used in the way its author intended. HALL and CLARKE (1892, 1894a) retained the Inarticulata and Articulata and adopted three of BEECHER's orders in a mixture with three suborders of WAAGEN (1882–1885). Even SCHUCHERT, the prime promoter of BEECHER's classification, initially (1893) retained the articulated and inarticulated classes; but by 1897 he had completely revised the brachiopod classification, then embracing more than 6,000 species, to conform with his understanding of BEECHER's version of brachiopod phylogeny.

SCHUCHERT's (1897) continuing use of an amended BEECHER classification perpetuated many inconsistencies and indeed added to them. By 1897, WALCOTT had shown that, unlike the brachiopod protegulum, *Paterina* has a cardinal area. Yet SCHUCHERT persisted in assuming that the brachiopod ancestor was like the protegulum, and he continued to use the term *Paterina* to denote this theoretical stage in brachiopod evolution. The third shell, identified by BEECHER in *Lacazella* and named prodeltidium by HALL and CLARKE (1892, 1894a), was declared to be homologous with biomineralized constrictions of the discinid pedicle opening and the posteromedial thickening of the dorsal valve of *Lingula.* SCHUCHERT also maintained that articulation had developed in many atremates and that the telotremates evolved from the atremates and not from the protrematous orthids as postulated by HALL and CLARKE (1892, 1894a). Despite growing evidence contradicting his assumptions, SCHUCHERT did not admit to any suspicions about the validity of his phylogenetic classification until 1932 when, with COOPER as co-author, he held it likely that the telotremates arose from the Protremata and that the prodeltidium had been misinterpreted (SCHUCHERT & COOPER, 1932).

The mainstay of the Beecher-Schuchert classification (SCHUCHERT, 1893, 1897) after the exposure of its inherent fallacies was, paradoxically, THOMSON's (1927) critique on brachiopod morphology and systematics. He showed that embryological research contradicted the generalizations propounded by BEECHER (1891) and SCHUCHERT (1893); and that their classifications had been flawed by their disregard for changes in the delthyrium, articulation, and shell structure. THOMSON (1927) also concluded that differences in the development of the pedicle are far more fundamental than the nature of the pedicle opening. Such differences, in association with other distinctive features, prompted him to propose two new subclasses, the Gastrocaulia and Pygocaulia, which were more or less synonymous with the Inarticulata and Articulata respectively.

With respect to brachiopod classification as a whole, the erection of these new subclasses was actually less significant than THOMSON's (1927) revision of BEECHER's (1891, 1892) orders, which led to a radical regrouping of constituent families and the introduction of a new order, the Palaeotremata for early brachiopods like the kutorginids, with a delthyrium and incompletely developed articulation. These amendments were incompatible with the assumptions on which BEECHER's (1891) orders were founded. Yet, in contrast to his willingness to erect new subclasses, THOMSON (1927) retained all BEECHER's (1891) orders, albeit with amended diagnoses. This ambivalence, in the wake of THOMSON's well-reasoned criticisms, was a signal for excessive caution from other paleontologists and greatly extended the life of a classification that had ceased to have any intrinsic merit.

The reaction to the classification proposed by THOMSON (1927) was mainly to use it selectively. Thus in 1944, COOPER used a version and briefly listed reasons for introducing some amendments. He reverted to the use of Inarticulata and Articulata but retained the Atremata and Neotremata more or less as amended by THOMSON (1927). The only articulated order to survive, however, was the Palaeotremata. The remaining articulated genera were assembled into superfamilies, which in turn were grouped together according to the impunctate, punctate, or pseudopunctate nature of their shells. COOPER (1944) emphasized that such an arrangement was not intended as a genetic classification but as an informal guide to quick identification of taxa.

In her history of brachiopod classification, MUIR-WOOD (1955) went further toward the abolition of BEECHER's classification. She discarded the Palaeotremata, assigning the kutorginids to the Orthoidea, and predicted that a comprehensive revision of the inarticulated brachiopods would lead to the rejection of the Atremata and Neotremata, although she retained them in her outline classification. She also rejected the use of shell structure or any other single character for ordinal classification and used only suborders and superfamilies to accommodate the 108 families of articulated brachiopods recognized at the time.

In 1956, WILLIAMS reviewed the more important classifications of the articulated brachiopods in the light of the secretion, structure, and growth of the calcitic shell. Previous classifications were shown to be at variance with processes of shell secretion or brachiopod phylogeny. It was concluded that no satisfactory ordinal arrangement could be made by using a few selected features of shell morphogeny. WILLIAMS (1956), therefore, advocated that the only way to erect a classification that is both compatible with the evolution of the brachiopod shell and utilitarian in usage is to assemble superfamilies from families and families from genera, with continual morphological comparison serving as a paleontological measure of affinity. Such groups have to be built up separately because features persisting unmodified in one group and, therefore, having a high taxonomic value, could appear only sporadically or be subject to extreme variability in another group and so possess a low taxonomic value. Chronostratigraphic consideration also had to be taken into account. Classifications can be affected by the range of a genus compared with that of the group as a whole because the variability of even persistent characters was frequently an inverse function of time. Significant chronostratigraphic gaps between the ranges of groups could also signal convergence, as in the case of cemented thecideidines, the alleged descendants of the Paleozoic protrematous strophomenides.

These considerations led WILLIAMS (1956) to emphasize the value of superfamilies that, by trial and error, had become taxa made up of demonstrably related stocks. He further contended that the superfamilies of articulated brachiopods, with few exceptions, could be marshalled into six groups, each typified by a well-known brachiopod (*Orthis, Strophomena, Pentamerus, Rhynchonella, Spirifer, Terebratula*), epitomizing the generalized morphology of its group.

The proposal to abandon the orders proposed by BEECHER (1891, 1982) and THOMSON (1927) and to erect a classification on generic foundations by continual morphological comparison, as outlined above, was adopted for both brachiopod treatises published in the 1960s.

In the *Osnovy Paleontologii,* SARYTCHEVA (1960) discarded the Atremata and Neotremata and allocated the inarticulated brachiopods to six orders (Rustellida, Lingulida, Craniida, Acrotretida, Siphonotretida, and Kutorginida). The articulated superfamilies were assembled into eight orders. Six of them accorded formal status to the groups identified by WILLIAMS (1956; Orthida, Strophomenida, Pentamerida, Rhynchonellida, Spiriferida, Terebratulida); the additional two were the Productida and Atrypida.

The classification adopted by WILLIAMS and ROWELL (1965c) for the first edition of the *Treatise on Invertebrate Paleontology* followed the same procedure, but the outcome was different. The inarticulated orders proposed in the Russian *Treatise* were amended in the following way. The Craniida was considered invalid on the grounds that its members were too closely related to the acrotretides to warrant ordinal recognition. The Siphonotretida was disbanded with the siphonotretids assigned to the Acrotretida, which led to the erection of a new order, the Obolellida, for residual carbonate-shelled taxa. The organophosphatic-shelled paterinids, with their well-developed cardinal areas, were removed from the Kutorginida and promoted to ordinal status as the Paterinida. As for the articulated orders established by SARYTCHEVA (1960), the Productida and Atrypida were demoted to suborders on the grounds that the taxonomic distances between them and the Strophomenidina and Spiriferidina respectively were significantly less than those among any of the other orders then being recognized.

WILLIAMS and ROWELL (1965c) contended that the ten orders defined in the first edition of the *Treatise* could be arranged in a gradient of change from the Lingulida to the Terebratulida. They identified five grades (1965c, p. 227) that could have served as the basis of subclasses, although they considered such a move premature. They did, however, retain the two classes, Inarticulata and Articulata, to accommodate ten orders, 20 suborders, 48 superfamilies, 202 families, 232 subfamilies, and 1,700 or so genera.

Within a year of the publication of the *Treatise* on the Brachiopoda in 1965, a phylogenetic analysis of extant members of the phylum had been published by HENNIG (1966, p. 145–154). Some of the data used for the analysis were incorrect; even so, HENNIG was prompted to suggest that the inarticulated, carbonate-shelled craniids are more closely related to articulated, carbonate-shelled brachiopods than to such inarticulated, phosphatic-shelled species as the lingulids. This point had, in fact, already been raised within the *Treatise* itself by JOPE (1965, p. 159) as a result of her biochemical studies of the brachiopod shell. In effect, the attempt to integrate a classification based on valve articulation with one intended to reflect the broad pathways of brachiopod evolution was already under scrutiny. Phylogenetic analysis of recent brachiopods by ROWELL (1981a, 1981b, 1982), however, reaffirmed the supraordinal grouping of the *Treatise.*

Later reviews had the advantages of access to new data on Early Paleozoic, carbonate-shelled inarticulated species and to computer programs facilitating virtually inexhaustible experiments in phylogenetic analyses. GORJANSKY and POPOV (1985, 1986), after appraising a mixture of reinterpretations of the development and anatomy of living species and of well-preserved skeletal features of extinct groups, concluded that phosphatic-shelled, inarticulated stocks are a distinct class of lophophorates (Lingulata) that is outside a restricted clade of carbonate-shelled forms that constituted their amended Brachiopoda. This view, entailing bivalve homoplasy among early lophophorates, had been abandoned before the publication of an account by NIELSEN (1991) of the development of *Crania,* which supported a close affinity between the craniids and other carbonate-shelled species but refuted brachiopod diphyly.

The dispute over craniid affinity is really a challenge to the use of a single character complex, in this instance shell articulation, to define the higher ranks of a classification of a phylum with a well-recorded genealogy extending throughout the Phanerozoic. It culminated with recent publications of cladograms constructed from universally accessible biological data characterizing seven extant superfamilies. The broad-frame phylogeny of CARLSON (1991, 1995) showed brachiopods to be monophyletic with craniids as primitive inarticulated brachiopods. Those of POPOV and others (1993) and HOLMER and others (1995) supported the division of the monophyletic Brachiopoda into two classes, the Lingulata and a new class Calciata for all carbonate-shelled species (including the craniids as the most primitive member of that group).

Notwithstanding some initial differences of opinion on brachiopod phylogenies, five contributors to this *Treatise* collaborated to erect a supraordinal classification that is generally acceptable to all those involved in the revision of the phylum (WILLIAMS & others, 1996). The classification had to accommodate more than 4,500 genera compared with less than 1,700 included in the first edition of the *Treatise.* Fortunately the authors had been freely given access to relevant studies of several other contributors, which included descriptions of new taxa especially from the Paleozoic successions of Asia and Australia and new research in traditional as well as molecular biology of the phylum.

The resultant supraordinal classification (WILLIAMS & others, 1996), consisting of three subphyla and eight classes, has been adopted for this revision of brachiopod taxonomy. Some amendments have been introduced and are discussed in the following section, which is virtually a transcription of the results and conclusions of the 1996 paper. Diagnoses of the supraordinal taxa compiled in 1996 have also been adopted with some changes. They have been incorporated at appropriate junctures in the taxonomic descriptions of the Brachiopoda in this and subsequent volumes.

BASIS FOR CLASSIFICATION

Methods

The diversity of the new information available for the 1996 study re-emphasized the dilemma facing past attempts to classify the Brachiopoda phylogenetically, namely how to reconcile two kinds of diagnostic data. More than 95 percent of all described genera are extinct, and brachiopods are especially prolific as fossils in older Phanerozoic successions. They and the higher taxa based on them are distinguished solely on the basis of shell variation with the inevitable complications arising from repeated homoplasy. The numerically insignificant recent genera are also largely distinguished using shell morphology, but at suprageneric levels anatomical, embryological, and, lately, genetic differences have become increasingly important. Of the six recent superfamilial to ordinal groups currently recognized—the linguloids, discinoids, cranioids, rhynchonellides, thecideidines, and terebratulides—the first four can be traced back directly to Cambro-Ordovician ancestors that were contemporaneous with 31 extinct groups of superfamilial to ordinal status. There are taxonomic as well as procedural advantages to deriving phylogenies for the two groups of superfamilies separately. In particular, a comparison of genealogies, based on independently assembled character sets and extrapolated from contemporaneous groups at the first Paleozoic branches and at the present day tips of the brachiopod evolutionary tree, would test the merits of a compounded phylogeny as a basis for a supraordinal classification.

The data were phylogenetically analyzed by the PAUP 3.1.1 program (SWOFFORD, 1993), supplemented by the MacClade 3.0 program (MADDISON & MADDISON, 1992). Most characters describing recent and Cambro-Ordovician taxa were set up as multistate characters and, to reduce the effects of homoplasy, were scale weighted. All characters were unordered during analyses, enabling polarity to be determined exclusively by outgroup methods although the choice of outgroups was not straightforward.

The protostomous sister group of the Brachiopoda has not yet been genetically identified with certainty, so it was appropriate to use representatives of all other lophophorates in the analysis of recent groups. They were *Phoronis* and representatives of the bryozoan tubuliporate and ctenostomate classes with organocalcitic and chitinoproteinaceous zooecia respectively, both of which first appeared in the Ordovician. Fifty-five characters (Table 1) were used to analyze present-day relationships among seven brachiopods, a phoronid, a tubuliporate, and a ctenostome listed in Figure 1. The characters comprehensively describe pertinent morphological, anatomical, and developmental states of the lophophorates concerned. The list differs little from others that have been recently used in analyses except for the inclusion of more information on the integument and mantle, which were summarized by 11 characters instead of the 2 or 3 used in previous analyses. Many comparative studies of the integument have been done within the last thirty years and have provided new insights into relationships between extinct and recent taxa as well as among living species.

Except for the Terebratulida and Thecideidina, all 28 brachiopod orders (or suborders) recognized in 1996 are represented in Cambro-Ordovician successions. These Early Paleozoic groups are distinguished exclusively by shell morphology and structure (Table 2) and were represented by 33 orders, suborders, and superfamilies in the analysis (see Fig. 3). The use of the other, nonbivalved lophophorates as outgroups gives little guidance on the polarity of morphological characters distinguishing Early Paleozoic brachiopods. On the other hand, only the stratigraphically oldest brachiopods are likely to include species that could reasonably serve as an ancestral group. The oldest known brachiopods (Tommotian to Botomian in age) are the organophosphatic-shelled cryptotretids followed closely by the carbonate-shelled obolellides, chileides, and kutorginides, which well represent the diversification of the phylum during Early Cambrian radiation. All four stocks were used (with other lophophorates) in trial analyses to identify the most appropriate outgroup.

The Cambro-Ordovician taxa were defined by 69 characters (Table 2). Twelve characters, which are also used for recent taxa, describe the composition, structure, and form of the shell, the nature of the mantle canal systems, the disposition of the gonads, and the nature and attachment of the pedicle and muscle systems. The rest are morphological features of the shell, which were subject to repeated homoplasy (WILLIAMS & others, 1996, p. 1177–1181).

GENEALOGIES

Recent Brachiopods

The conflicting interpretations of genetic data on relationships between brachiopods and other lophophorates prompted analyses of the brachiopods in varying combinations with *Phoronis* or tubuliporate and ctenostomate bryozoans as outgroups. The position of the craniid branch within a lophophorate tree is sensitive to the choice of outgroups (Fig. 1). No single cladogram could, therefore, satisfactorily represent the biological data (Table 1); and the one with *Phoronis* and both bryozoans as outgroups was chosen only because it retained represen-

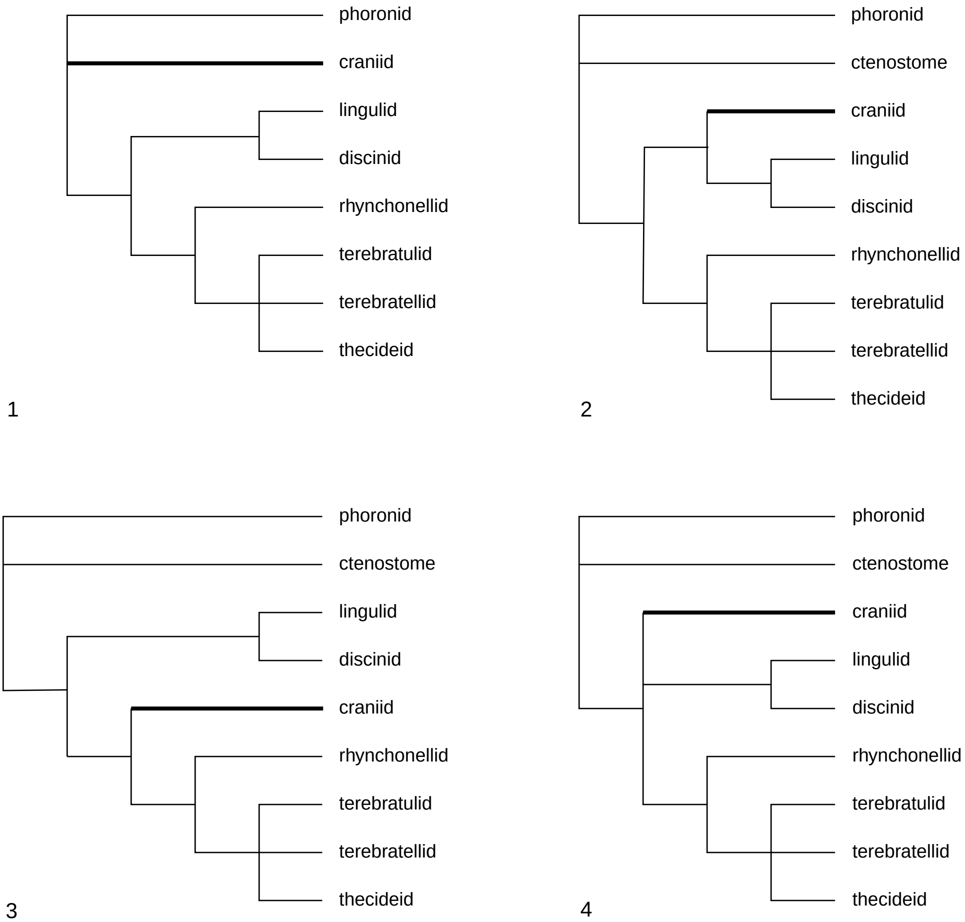

Fig. 1. Four trees derived by branch and bound analyses of data in Table 1 (matrix in Williams & others, 1996, p. 1187) with various combinations of other lophophorates as outgroups; variations in brachiopod branches are restricted to relocations of craniids and regroupings of terebratellid-thecideid polytomy within rhynchonellid clade; *1,* location of craniid branch in three of six trees generated by phoronid outgroup (position of craniid branch in other three trees relative to all other brachiopods is identical with that shown in *2*); *2,3,* location of craniid branch in three of six trees derived with phoronid and ctenostome bryozoan as outgroups; *4,* strict consensus of six trees represented by cladograms *2* and *3* (Williams & others, 1996).

tatives of all lophophorate phyla. The consensus of the three trees derived by branch and bound analysis is shown in Figure 2.

All three trees providing the consensus cladogram in Figure 2 contained the rhynchonellides as a sister group of a thecideid-terebratulide polytomy. Synapomorphies of this rhynchonellate clade include an astrophic shell articulated by cyrtomatodont teeth and sockets, a calcitic exoskeleton with a fibrous secondary layer, a reversal of the mantle rudiment during larval development and the closure of the posterior arc of the mantle cavity with a concomitant fusion of mantle lobes, a pedicle developing from a rudiment, and an intestine without an anus.

The lingulids and discinids form another, lingulate clade characterized by such synapomorphies as a shell composed of chitin, proteins, glycosaminoglycans (GAGs), and apatite in stratiform successions; a double row of tentacles along the entire length of the lophophore; and gonads restricted to the body cavity.

TABLE 1. The states of 55 characters used in phylogenetic analyses of recent brachiopods and other lophophorates identified in Figures 1 and 2 (new).

EXTERNAL COVER

1. general form: agglutinated tubes (0); zoecia only throughout (1); larval bivalves, adult zoecia (2); bivalved (3).
2. bivalves: not developed (0); inarticulated (1); articulated (2).
3. hinge line: no adult bivalves (0); not developed (1); strophic (2); astrophic (3).
4. valve growth: none (0); holoperipheral (1); mixoperipheral (2); hemiperipheral (3).

SHELL COMPOSITION AND STRUCTURE

5. periostracum: absent (0); simple (1); with infrastructure (2); with elaborate superstructure (3); with both (4).
6. infrastructures: lacking periostracum (0); thin GAGs (1); GAGs with proteinaceous fibrils (2); vesicular GAGs with proteinaceous fibrils (3); GAGs with chitinous and proteinaceous fibrils (4); GAGs with chitinous and proteinaceous tubes (5).
7. superstructure: lacking periostracum (0); fibrillar (1); sporadic vesicles (2); folded laminae (3); laminated vanes (4); labyrinth (5).
8. biomineral components: absent (0); stratiform apatite (1); laminar (tabular) calcite (2); fibrous calcite (3); foliated and laminar calcite (4).
9. organic components: mucus (0); mainly GAGs, chitin, and collagen (1); glycoprotein (2).
10. endoskeletal spiculation: absent (0); present (1).

MANTLE

11. mantles: absent (0); present (1).
12. inner mantle lobe: no mantle (0); present (1); absent (2).
13. inner epithelium secreting periostracum: absent (0); yes (1); no (2).
14. lobate cells: no mantle lobe (0); absent (1); present (2).
15. vesicular cells: absent (0); present (1); palisade cells (2).
16. periostracal slot: no outer mantle lobes (0); absent (1); present (2).
17. setae: present (0); absent from postlarval mantles (1); not developed (2).
18. canals or punctae: absent (0); canals (1); punctae without brushes (2); endopunctae with brushes (3).
19. outer epithelial protrusions: present (0); absent (1).
20. *vascula terminalia* of mantle canals: no mantle (0); peripheral (1); peripheral and interomedial (2).
21. mantle sinuses with gonads: no mantle (0); absent (1); present (2).
22. marginal sinuses: no mantle (0); absent (1); present (2).
23. mantle cavity: none (0); restricted to anterior (1); continuous posteriorly (2).

PEDICLE

24. pedicle: not developed (0); lost in postlarval forms (1); present (2); craniid thickened posterior epithelium (3).
25. origin: none (0); from posterior body wall (1); ventral of posterior body wall (2); rudiment (3).
26. pedicle core: none (0); coelomic cavity (1); connective tissue (2).
27. pedicle muscles: none (0); internal (1); external (2).

MUSCLE SYSTEM (DORSAL ATTACHMENT)

28. muscles of body wall: circular (0); parietal sets (1); dispersed (2).
29. adductor attachments: none (0); grouped, quadripartite (1); open, quadripartite (2); medial and posterolateral pairs (3); medial pair and single umbonal (4).
30. diductor-oblique attachments: none (0); one pair umbonal (1); three pairs of obliques (2); four pairs of obliques (3); one pair of obliques (4).

The craniids, as a sister group of the lingulate clade, are also distinct, especially in the tabular growth of the laminar secondary layer of their calcitic shell and the lack of a differentiated pedicle even during larval development when the initial attachment area of the ventral valve consists of an area of thickened, microvillous, pedicle epithelium (NIELSEN, 1991).

The equivocal relationship of the craniid with the lingulate and rhynchonellate clades, as shown in Figures 1 and 2, suggests uncertain phylogenetic affinities to both clades. An enlarged lingulate clade containing the craniids would be characterized by such apparent synapomorphies as a circumferential mantle cavity, a muscle system consisting of obliques and two pairs of adductors, the presence of a transient median tentacle in the early growth of the lophophore, and, within that organ, the median division of the brachial canals into two separate cavities. Appar-

TABLE 1. *(Continued).*

COELOMIC, CIRCULATORY, EXCRETORY SYSTEMS
31. body cavity divided by mesentery: yes (0); no (1).
32. gastroparietal bands: absent (0); present (1).
33. circulatory system: absent (0); present (1).
34. blood type: hemoglobin (0); hemerythrin (1); neither (2).
35. mixonephridia: absent (0); one pair (1); two pairs (2).
36. nephrostomes: not applicable (0); turned laterally (1); turned dorsally or medially (2).

NERVOUS SYSTEM
37. supraenteric ganglion: unknown (0); present (1); absent (2).
38. subenteric ganglion: nerve ring only (0); single (1); paired (2).

LOPHOPHORE
39. site of lophophore: in mantle cavity (0); in zoecium (1); at surface (2).
54. adult lophophore: trocholophe (0); spirolophe (1); plectolophe (2); ptycholophe (3).
55. median tentacle of lophophore: absent throughout ontogeny (0); present initially, then lost (1).
40. tentacles: single row (0); double row in post-trocholophous stages (1); double row throughout (2).
41. lophophore cavities and canals: intercommunicate (0); separated (1).
42. great brachial canals: absent (0); open into body cavity (1); sealed from body cavity (2); two separate cavities (3).
43. small brachial canals: absent (0); open into body cavity (1); open into central canal (2).
44. lophophore retractor system: absent (0); present (1).
45. retractor muscles: absent (0); single muscle (1); muscle complex (2).
46. brachial muscles: absent (0); present (1).

DIGESTIVE SYSTEM
47. alimentary tract: with anus (0); without anus (1).
48. intestine disposition: ending dorsoanteriorly (0); ending posteriorly (1); curving ventrally (2); ending laterally to right (3).
49. diverticular ducts: two (0); three (1); four (2); none (3).

EMBRYOLOGY AND DEVELOPMENT
50. larvae: planktotrophic (0); lecithotrophic (1).
51. coelom formation: schizocoelic (0); modified enterocoelic (1).
52. mantle development: without reversal (0); with reversal (1).
53. sperm morphology: ectaquasperm (0); entaquasperm (1).

ent synapomorphies of a rhynchonellate clade incorporating the craniids would include a proteinaceous calcitic shell with an inner epithelium not involved in the secretion of the periostracum, a single row of tentacles on trocholophous lophophores, gonads suspended in mantle sinuses, and lecithotrophic larvae. Some of these characters can be discerned in fossil brachiopods by studies of either the chemico-structure of the shell or anatomical impressions on valve interiors.

Cambro-Ordovician Brachiopods

An exploratory use of the earliest known brachiopods (the paterinides, obolellides, chileides, and kutorginides) and other lophophorates in combination and singly as outgroups to other Cambro-Ordovician brachiopods as a whole resulted in a variety of trees, mostly inconsistent with the geological record or previously prepared analyses of some of the ordinal taxa. The most compatible cladograms involved the paterinides, either singly or with the obolellides and kutorginides as outgroups. In these cladograms the paterinides (with other organophosphate-shelled brachiopods) were polytomously basal to a very large clade consisting of exclusively carbonate-shelled species. The use of *Phoronis* as the sole outgroup, however, released the paterinides from this role and enabled important assumptions to be made on the polarity of many characters distinguishing Cambro-Ordovician groups, as the paterinide shell is extraordinarily diverse in its composition and morphology. A single tree (Fig. 3) with a retention index of 0.79

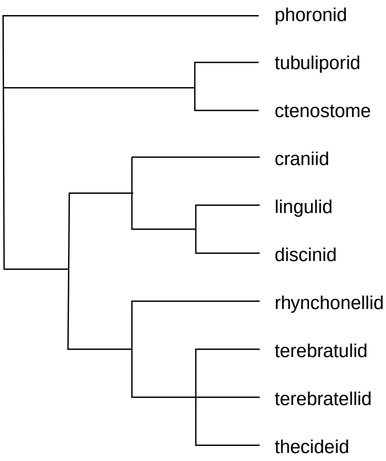

FIG. 2. Strict consensus of three trees derived by branch and bound analysis of data in Table 1 (matrix in WILLIAMS & others, 1996, p. 1187) with phoronid and tubuliporate and ctenostomate bryozoans serving as outgroups (Williams & others, 1996).

was identified in a heuristic search of a matrix of 34 taxa and 69 scale-weighted characters.

The stratigraphic compatibility of the tree topology in Figure 3 was tested by calculating a stratigraphic consistency index (SCI= 0.61; HUELSENBECK, 1994) and by stratocladistic analysis. The procedure (FISHER, 1992; MADDISON & MADDISON, 1992) of adding stratigraphic range data to the original character matrix as a designated stratigraphic character resulted in a few minor changes in the topology of Figure 3. In general, however, the stratigraphic tests suggest that the tree topology is highly robust with respect to both morphological and stratigraphical data.

In the cladogram (Fig. 3), the paterinides are shown as a sister group of a lingulate clade. Both groups are characterized by an organophospate, inarticulated shell although that of the paterinides is also strophic with interareas indented posteromedianly by a variably covered delthyrium and notothyrium (WILLIAMS, POPOV, & others, 1998). Moreover, the interiors of the paterinide valves also bear impressions of gonads, canal systems, and posteromedian muscle scars, which appear to be similar to those of the orthides. No foramen has yet been found, but they were attached to other living organisms (WILLIAMS, POPOV, & others, 1998), probably by a pedicle of ventral origin but emerging between the valves. The interareas could have been linked by a periostracal hinge secreted by fused mantle lobes, which would not have precluded a posterior body wall. It is noteworthy that, although the paterinide larval valves were defined by halos characteristic of a planktotrophic existence, their lobate micromorphology suggests that larvae had two pairs of setal sacs in the manner of the lecithotrophic larvae of articulated, calcite-shelled brachiopods (WILLIAMS, POPOV, & others, 1998).

The organophosphate-shelled brachiopods, other than the paterinides, are monophyletic although relationships within this lingulate clade are still in some doubt (HOLMER & POPOV, 1996b). Synapomorphies of the clade include a canaliculate shell fabric; a dispersed, specialized musculature that controlled a three-dimensional movement of the inarticulated valves; the confinement of the gonads to the body cavity; and the permeation of the mantles by baculate canal systems with interiomedial as well as marginal fringes of *vascula terminalia.*

Two extinct orders, the Siphonotretida and Acrotretida, along with the Lingulida, compose the Cambro-Ordovician lingulate clade, which has been accorded a supraordinal status. An interesting aspect of the analysis is the support for discinoids as having originally been a sister group of the remaining taxa within the clade. This would imply that the pedicle notch is an apomorphy of the linguloids and that both superfamilial branches evolved from a stem group with an elongate cylindroid extension of chitin-secreting epithelium and coelom serving as a pedicle. An orbiculid (*Orbiculoidea*) with such a pedicle has recently been found in the Lower Devonian Hunsrück Slate (KAESLER, 1997, fig. 60).

The analysis further indicated that all other Cambro-Ordovician brachiopods were

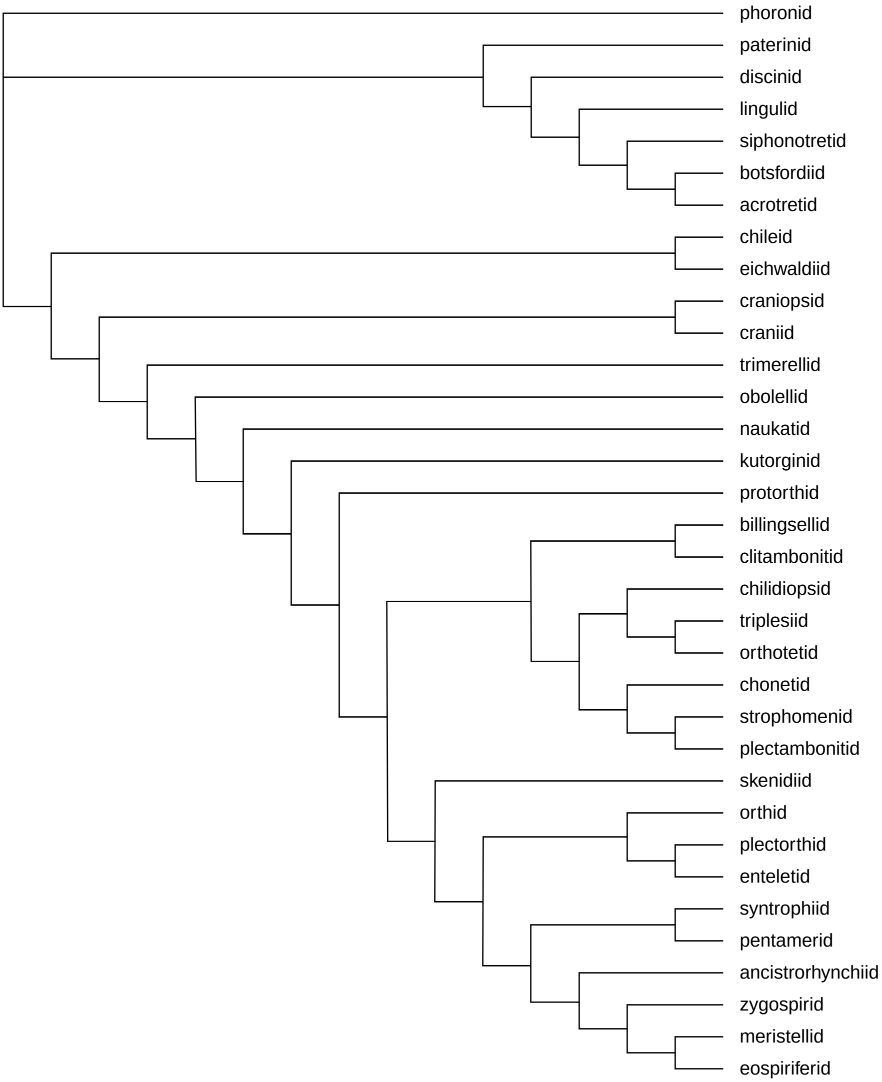

FIG. 3. Single tree derived in heuristic search involving stepwise random addition of taxa in ten replicates, for which character states in Table 2 (matrix in WILLIAMS & others, 1996, p. 1190) were scale weighted (adapted from Williams & others, 1996).

derived from a group with an impunctate carbonate shell preeminently characterized by a calcitic, fibrous secondary layer as suggested by ROWELL and CARUSO (1985, p. 1239). The assumption is consistent with the stratigraphic ranges of Early Cambrian carbonate-shelled species. The chileides are the earliest known calcite-shelled brachiopods with a strophic hinge line (POPOV & TIKHONOV, 1990) and include the Lower Cambrian *Kotujella,* which has a fibrous secondary layer, as have contemporaneous kutorginids (WILLIAMS, 1968b).

The fibrous fabric, however, was not universally developed. Apart from its polyphyletic replacement by cross-bladed lamination in Ordovician strophomenides and chonetidines (WILLIAMS, 1970; BRUNTON, 1972), it is

TABLE 2. The states of 69 characters used in phylogenetic analysis of Cambro-Ordovician brachiopods and phoronid, as listed in Figure 3 (new).

SHELL STRUCTURE

1. secondary layer: fibrous (0); foliated (1); tabular laminar (2); cross-bladed laminar (3); recrystallized, possibly aragonitic (4); stratiform (5); no shell (6).
2. perforation: impunctate (0); extropunctate (1); endopunctate (2); punctate (3); caniculate (4); no shell (5).
3. pseudopunctation: absent (0); present in some species (1); pseudopunctate (2); taleolate pseudopunctate (3); extropunctate (4); no shell (5).
4. aditicules: absent (0); present (1); no shell (2).

SHELL SHAPE

5. outline: subcircular-oval (0); subquadrate (1); transversely semioval (2); elongately semioval (3); protean (4); rostrate (5); conical (6); ostreiform (7); no shell (8).
6. neanic profile: biconvex (0); concavoconvex (1); convexoconcave (2); no shell (3).
7. profile (long.): biconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); concavoconvex (4); convexoconcave (5); resupinate (6); geniculate (7); planoconical (8); no shell (9).
8. profile (trans.): rectimarginate (0); unisulcate (1); sharply unisulcate (2); uniplicate (3); sharply uniplicate (4); strangulate (5); no shell (6).

ORNAMENTATION

9. radial: smooth (0); costate (1); coarsely costellate (2); ramicostellate (3); fascicostellate (4); multicostellate (5); parvicostellate (6); no shell (7).
10. capillae: absent (0); sporadically present (1); present (2); no shell (3).
11. concentric: growth lines (0); imbricate (1); lamellose (2); spiny bands (3); nodular lamellose (4); filate (5); reticulate (6); no shell (7).
12. superficial: absent (0); honeycomb (1); pustulose (2); radiating pits (3); postlarval pustules (4); no shell (5).

DELTHYRIUM

13. pedicle opening: ventral valve (0); supra-apical (1); posterior cleft (2); absent (3); between valves (4); no shell (5).
14. posterior cleft: absent (0); delthyrial (1); other (2); secondarily lost (3); no shell (4).
15. delthyrium: not developed (0); rudimentary (1); widely divergent (2); subparallel, narrowly divergent (3); no shell (4).
16. delthyrial cover: open delthyrium (0); apical plate (1); deltidial plates (2); deltidium (3); convex pseudodeltidium (4); pseudodeltidium with keel (monticule) (5); concave pseudodeltidium (6); no delthyrium (7); homeodeltidium (8); no shell (9).
17. foramen (ontogeny): absent (0) delthyrial (1); supra-apical (2); ventral (3); in young shells only (4); secondarily lost (5); not developed (6); no shell (7).
18. pedicle callist: absent (0); present, adnate (1); present as apical plate (2); pedicle collar (3); not developed (4); no shell (5).
19. notothyrium: absent (0); rudimentary (1); widely divergent (2); subparallel, narrowly divergent (3); no shell (4).
20. notothyrial cover: absent (0); antigydium (1); chilidial plates (2); chilidium (3); grooved plates (4); no notothyrium (5); secondarily lost (6); no shell (7).

CARDINAL AREAS, INTERAREAS, PSEUDOINTERAREAS

21. ventral: absent (0); vestigial (1); present (2); pyramidal-conical (3); lost-ginglymus (4); protean (5); no shell (6).
22. disposition: absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6); no shell (7).
23. dorsal: absent (0); vestigial (1); present (2); no shell (3).
24. disposition: absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6); no shell (7).

ARTICULATION

25. ventral articulating structures: absent or rudimentary (0); simple, pointed (1); transverse plate (2); delthyrial ridges (3); flexed cardinal margin (kutorginid) (4); cardinal sockets (5); no shell (6).
26. delthyrial ridges: no ridges (0); deltidiodont (1); deltidiodont with crural fossettes (2); transverse (3); transverse denticulate (4); cyrtomatodont (5); no shell (6).
27. dental plates: absent or rudimentary (0); present (1); replaced by free spondylium (2); no shell (3).
28. dorsal articulating sockets: absent (0); present (1); denticular pits (2); for delthyrial ridges (3); oblique furrows (4); propareas (5); hinge plate (6); no shell (7).
29. socket buttress: no sockets (0); hollows (1); nubs (2); plates or rods, parallel with hinge line (3); brachiophores (4); brachiophores and plates (5); brachiophores and fulcral plates (6); inner socket ridges (7); no shell (8).
30. brachiophores-crura: absent (0); brachiophore rods or blades (1); crura (2); anderidia (3); no shell (4).

TABLE 2. *(Continued).*

31. brachiophore supporting plates: absent (0); parallel (1); convergent (2); as septalium (3); divergent (4); no brachiophores (5); no shell (6).
32. fulcral plates: absent (0); present (1); no brachiophores (2); no shell (3).
33. hinge line-cardinal margin: not developed (0); astrophic (1); strophic (2); no shell (3).

MUSCULATURE

34. ventral adductors: dispersed posteriorly-anteriorly (0); grouped posteromedianly (1); posterior pair attached to apical part in the umbonal area, anterior pair vestigial or reduced (2); no shell (3).
35. dorsal adductors: median and posterolateral pairs (0); grouped quadripartite (1); linear (2); elongate, radiating (petaloid) (3); dispersed quadipartite (4); dispersed (5); vestigial or lost (6); no shell (7).
36. ventral diductors: not developed (0); interspersed with adductors (1); flanking-enclosing adductors (2); asymmetrical (3); attached to homeodeltidium or delthyrial margins (4); no shell (5).
37. dorsal diductor impressions: not developed (0); posteromedian plate or cavity (1); notothyrial platform or cardinal process (2); notothyrium or cardinal process (3); no shell (4).
38. ventral scar impressions: on valve floor (0); on callist or pseudospondylium (1); on raised structures (2); no shell (3).
39. raised structures: none (0); spondylium simplex-triplex (1); free spondylium (2); colleplax (3); raised platform (4); adductor chamber (5); myocoelidium (6); sessile spondylium (7); camarophorium (8); no shell (9).
40. notothyrial platform: absent or rudimentary (0); transverse plate (1); platform (2); platform and notothyrial ridges (3); not developed (4); no shell (5).
41. cardinal process: absent or rudimentary (0); median ridge (1); differentiated median ridge (2); variations of two lobes (3); median and submedian ridges (4); forked (5); undercut trifid (6); bilobate (7); no notothyrial structures (8); no shell (9).
42. dorsal median partition: absent to low ridge (0); septum (1); no shell (2).
43. subperipheral rim: absent (0); present (1); sporadic (2); geniculation (3); no shell (4).

MANTLE CANALS

44. ventral: saccate-convergent *vascula media* (0); saccate-divergent *vascula media* (1); digitate (2); lemniscate (3); pinnate (4); baculate (5); absent (6); bifurcate (7); no bivalved mantle (8).
45. dorsal: saccate (0); digitate (1); lemniscate (2); pinnate (3); apocopate (4); baculate (5); absent (6); bifurcate (7); no bivalved mantle (8).

ADDENDA

46. valve growth: holoperipheral (0); mixoperipheral (1); hemiperipheral (2); ventral valve mixoperipheral, dorsal valve hemiperipheral (3); ventral valve variable, dorsal valve mixoperipheral (4); no shell (5).
47. colleplax: absent (0); present (1); no shell (2).
48. ventral pseudointerarea: absent (0); present (1); not differentiated (2); other structures (3); no shell (4).
49. attachment scar: absent (0); cicatrix (1); encrusting (2); no shell (3).
50. hollow spines: absent (0); along hinge line (1); concentric rows (2); no shell (3).
51. brachial markings: absent (0); sporadically developed (1); no shell (2).
52. crural extensions: absent (0); spiralia (1); no shell (2).
53. orientation of spiralia: no spiralia (0); medial (1); dorsal (2); lateral (3); no shell (4).
54. jugum: absent (0); incomplete (1); complete (2); resorbed (3); no spiralia (4); no shell (5).
55. hinge plate: absent (0); present (1); divided by cardinal pit (2); with raised boss (3); no shell (4).
56. crural bases: absent (0); present (1); no crura (2); no shell (3).
57. shell mineral: carbonate (0); phosphate (1); no shell (2).
58. larval shell: absent (0); present (1).
59. larval shell ornamentation: smooth (0); pitted (1); pustulose (2); no larval shell (3).
60. larval shell spines: absent (0); present (1); no larval shell (2).
61. transverse muscle scars: absent (0); present (1); attached ventrally to inner side of (acrotretoid) pseudointerarea (2); no shell (3).
62. ventral cardinal muscle scars: absent (0); present (1); different muscle system (2); no shell (3).
63. dorsal cardinal muscle scars: absent (0); present (1); different muscle system (2); no shell (3).
64. outside lateral muscle scars: present (0); absent (1); combined with middle lateral muscle scars (2); no shell (3).
65. dorsal scars of gastroparietal bands: absent (0); present (1); no shell (2).
66. listrium: absent (0); present (1); no shell (2).
67. *vascula terminalia:* peripheral only (0); peripheral and medial (1); no bivalved mantle (2).
68. adjustor muscles: absent (0); present (1); no pedicle (2).
69. gonads: in body cavity (0); extending into mantle (1); no mantle (2).

unknown in carbonate-shelled inarticulated brachiopods except possibly for the eichwaldioids (Wright, 1981). The secondary layer of *Trematobolus,* which is assumed to typify the fabric of all obolellides (including the naukatidines), has been described as laminar (Williams & Wright, 1970, p. 45). The constituents of the layer, however, are lenticular rather than parallel sided in cross section. Such folii were probably membrane bound in life, in the manner of ensheathed fibers rather than the spirally growing tablets of craniids, which were intercalated between proteinaceous sheets.

In contrast to the foliated shell of the obolellides, the secondary layers of three orders, currently classified together (Gorjansky & Popov, 1985), are either truly laminar successions of tablets, as in craniides and craniopsides (Williams & Wright, 1970), or are invariably recrystallized, as in the trimerellides and possibly aragonitic in the original state (Jaanusson, 1966). All three orders are widely regarded as having first appeared in the Ordovician, but Jin and Wang (1992) have described *Heliomedusa* from the Lower Cambrian (?Botomian) of China, which is probably an early craniopside. The secondary fabrics of carbonate-shelled inarticulated groups may, therefore, have originated more or less contemporaneously. Yet neither the derivation of obolellide folii from fibers nor the secretion of an aragonitic secondary layer in trimerelloids are as fundamental a transformation as the development of the spirally secreted laminae of the craniides. Even the lamination, forming the cross-bladed fabric of strophomenide shells, consists of arrays of lath-shaped constituents that had evolved independently from fibers in the chonetidines (Brunton, 1972) and billingselloids (Williams, 1970). Consequently there is a strong possibility that the craniide-craniopside tabular lamination evolved independently of membrane-bound fibers.

The mode of attachment of Cambro-Ordovician brachiopods to the substrate was extremely variable. Cladistic evidence favors the organ of attachment of the stem group as an outgrowth of the outer epithelium of the ventral mantle. This origin is characteristic of living species of discinoids and craniides even though the latter are cemented by a central pad of ventral ectoderm without trace of any outgrowth. The ventral perforations of the chileides and the later, related eichwaldioids are also consistent with the development of a cuticular pad arising from the ventral mantle (Williams, Popov, & others, 1998) and are usually associated with a colleplax (Wright, 1981) or homologous structure.

These prototypic pedicles also varied in location relative to the shell and even encroached on the junction between the outer and inner epithelium of the ventral valve, as is shown by the morphology of the early lingulide shell. The pedicle of most linguloids emerged between the valves as an outgrowth of the inner epithelium (posterior body wall), according to Yatsu's study (1902) of recent *Lingula.* But this origin may not have been characteristic of the lingulellotretids and dysoristids with pedicle openings entirely restricted to the ventral valves, which are similar to those of most acrotretoids. Various openings in the carbonate shells of Cambro-Ordovician brachiopods have been interpreted as pedicle apertures. The delthyria of the chileides could not have accommodated a pedicle if the large perforation in the ventral valve contained an adhesive cuticular pad. Instead the notch could have indicated the location of the anus on the posterior body wall as postulated by Rowell and Caruso (1985) for the delthyrial-notothyrial gape of the kutorginide *Nisusia.* In the latter group, a small supra-apical foramen probably contained a peduncular structure as did an internal tube with an external supra-apical opening found in early obolellides (Geyer & Mergl, 1995). Such an organ would have acted as an adhesive anchor but would not have served as an axis of rotation for the shell as in recent species. Indeed, no adjustor muscle scars have been recognized within the muscle impressions of protorthides, billingselloids, and strophomenides (L. R. M. Cocks, personal communication, 1996). Among the clitambonitidines, evidence for adjustor scars in *Clinambon* (see Öpik, 1934, pl. xvll.1) is compromised by the sealing of the pedicle foramen later in the ontogeny of this genus (A. D. Wright, personal communication, 1996); and the scars so identified are probably lateral lobes of the diductor muscles, like those differentiated in many orthidines and strophomenides. Schuchert and Cooper (1932, p. 111) cited pedicle attachment scars in *Hemipronites* and *Deltatreta,* but such impressions would have been made by the cuticular cover of the pedicle and would not have indicated the presence of adjustors. Moreover, Wright (1994b) has figured the impressions of *vascula terminalia* along the margins of the ventral interareas of several clitambonitidines. They indicate the presence, *in vivo,* of a posterior body wall that would have precluded the development of a pedicle from a rudiment. The evidence for true adjustor scars in the triplesiidines is equally equivocal. Wright (1963a, p. 746) identified two impressions within the ventral muscle field as adjustor scars. They are, however, situated well posterior of the internal opening of a long pedicle tube, sporadically developed in triplesiidines, and could not have operated as adjustors.

Unquestionable impressions of ventral adjustor muscle bases are found in early Middle Cambrian orthide species assigned to the eoorthids and bohemiellids. Indeed, adjustor scars and pedicle callists are normally impressed on the ventral interiors of all orthidines (excluding the billingselloids) and syntrophiidines. This kind of ventral muscle base, however, was more or less restricted to the umbonal chamber, whereas that of recent brachiopods is impressed well to the anterior. Anatomical reconstruction suggests that, although the orthidine pedicle probably developed from a rudiment, it had a negligible base that was largely external to the shell. In contrast, the anteriorly placed ventral muscle bases of rhynchonellides, atrypides, spiriferides, and terebratulides have always afforded space in the umbonal chamber for the pedicle capsule, an assumed manifestation of mantle reversal (Williams & Wright, 1963, p. 16).

The evolution of valve articulation, involving teeth and sockets in the delthyrial and notothyrial regions, is another differentiating aspect of the Cambro-Ordovician radiation of carbonate-shelled brachiopods. According to the model (Fig. 3), articulatory devices were not developed in the ancestral brachiopod and are unknown in the phosphate-shelled groups or the carbonate-shelled craniides, craniopsides, trimerellides, and chileides. Likely descendants of the chileides, however, the dictyonellides, are characterized by a cardinal process flanked by a pair of furrows that receive rudimentary teeth of the ventral valve, and by posteromedian muscle scars feasibly interpreted as diductor bases. The Dictyonellida include the post-Cambrian eichwaldiids and the Late Paleozoic isogrammids, which share an articulatory system dominated by a cardinal process. In contrast, the articulation of the trimerellides was effected by a dorsal hinge plate fitting into a cardinal socket (Norford & Steele, 1969).

The articulatory device, developed in later obolellidines, consists of a pair of submedian denticles on either side of a narrow delthyrium fitting into small dorsal sockets; the muscle scar arrangement suggests that internal obliques functioned as diductors (Popov, 1992; Geyer & Mergl, 1995). The obolellidine articulation is essentially the same as that of the naukatidines except that the teeth of the latter are situated on a platform (anterise) (Popov, 1992).

Primitive articulatory devices, flanking the delthyrial and notothyrial openings and associated with diductor muscle systems, also evolved independently in the kutorginides as a pair of broadly curved edges to the ventral interarea fitting on obtusely triangular plates in the dorsal valve (Cooper, 1936; Rowell & Caruso, 1985) and in the protorthides as small teeth at the junctions of the delthyrium and the free spondylium, which fit laterally of rudimentary outgrowths at the notothyrial edges (Cooper, 1976).

The most successful articulatory device ever to have evolved was the orthoid type of hinge teeth and dental sockets. It first appeared among Early Cambrian species and is ancestral to the system characteristic of recent articulated species, but its precise origin has yet to be determined. The Lower Cambrian *Leioria* (Cooper, 1976) has a protorthide spondylium but deltidiodont teeth (dorsal projections of ridges bounding the delthyrium) and sockets (defined by erect bladelike brachiophores), in the manner of orthides. In contrast, the teeth of the Middle Cambrian bohemiellids are transverse and normally well lateral of the delthyrium, while those of billingselloids and strophomenoids are also essentially transverse (but immediately lateral of the delthyrium) and fit into shallow sockets defined by flat-lying ridges.

The orthide deltidiodont teeth and sockets are also characteristic of the pentamerides. But the intricate interlocking device of cyrtomatodont teeth and sockets first appeared in the astrophic rhynchonellides and are a synapomorphic complex shared with atrypides, athyridides, spiriferides, spiriferinides, terebratulides, and thecideidines.

One other complex of morphological features should play an important part in the supraordinal classification of brachiopods. Skeletal supports of the lophophore have developed independently during the evolution of many groups. Outgrowths from the floors of dorsal valves in the form of plates and platforms (but not necessarily septa partitioning the mantle cavity) probably gave some support to part or all of the lophophore in some acrotretides, strophomenides, and orthides after these groups had become well established (Williams & Rowell, 1965c). In contrast, apophyses arising from the dorsal hinge line where they are normally extensions of inner socket ridges constitute a transformation series in the elaboration of lophophore supports. Comparison of the disposition of the inner socket ridges of Middle and Upper Cambrian billingsellids and eoorthids shows that those of the former were flat lying, whereas those of the latter projected ventrally as brachiophores (Williams & Hurst, 1977). The billingselloid socket ridges are precursory to those of the strophomenides (*s.l.*), which functioned only as the inner containing walls of the dental sockets. Among the orthides, brachiophores also served as attachment areas for the dorsal adjustors, and in such Ordovician genera as *Phragmorthis* and *Skenidioides* extended sufficiently anteriorly to have likely supported the mouth segment of the lophophore (Williams & Rowell, 1965c).

The growth of apophyses (crura) supporting the mouth segment of the lophophore in the modern style, however, first occurred in Early Ordovician camerelloids and rhynchonellides and accompanied transformations of ancestral syntrophiidine cardinalia and articulation, notably the loss of all traces of a notothyrial platform and the differential secretion and resorption of cyrtomatodont teeth and sockets. The further elaboration of skeletal supports of the lophophore in the form of calcareous spiralia first characterized the later appearing atrypides and then, as descendants from that group, Late Ordovician athyridides and spiriferide eospiriferids.

No other features of Cambro-Ordovician brachiopods clearly delineate broad phylogenetic trends in shell morphology. Muscle differentiation, as deduced from the distribution of scars on valve interiors, took place but is better reflected in the development of articulation and the pedicle. Such ancillary structures as spondylia or deltidia developed many times and are not reliable diagnostic features at the supraordinal level. Even mantle canal systems were subject to repeated homoplasy in carbonate-shelled species, especially as a result of changes brought about by the enlargement of gonadal sacs during sexual maturity.

TABLE 3. The states of 19 synapomorphies, identified in phylogenetic analysis of recent and Cambro-Ordovician brachiopods and used to analyze suprafamilial groups and recent phoronid listed in Figure 4 (new).

SHELL

1. composition: chitinophosphatic (0); carbonate (1); no shell (2).
2. structure: stratiform (0); fibrous (and foliated) (1); tabular laminar (2); cross-bladed laminar (3); recrystallized (4); no shell (5).

MORPHOLOGY

3. shell growth: holoperipheral (0); mixoperipheral (1); hemiperipheral (2); no bivalved shell (3).
4. cardinal areas: absent (0); pseudointerareas (1); strophic interareas (2); astrophic interareas (3); no bivalved shell (4).
5. pedicle opening: absent (0); ventral valve floor (1); supra-apical (2); posterior cleft (3); delthyrial (4); between valves (5); no bivalved shell (6).
6. articulatory devices: absent (0); other kinds (1); deltidiodont teeth and sockets (2); cyrtomatodont teeth and sockets (3); no bivalved shell (4).
7. lophophore supports: absent (0); inner socket ridges (1); brachiophores (2); crura (3); crura and spiralia (4); no bivalved shell (5).

ANATOMY

8. pedicle: absent (0); from body wall (1); from rudiment (2).
9. posterior body wall: present (0); absent (with fused mantle lobes) (1); not applicable (2).
10. muscles operating articulation: none (0); regrouped internal obliques (1); diductors (2); no bivalved shell (3).
11. muscles operating pedicle: no pedicle (0); absent (1); present (2).
12. interomedial *vascula terminalia:* absent (0); present (1); no bivalved mantle (2).
13. gonadal distribution: restricted to body cavity (0); also in mantle sinuses (1).
14. anus: present (0); absent (1).
15. tentacles: doubled (0); doubled in post-trocholophous segments (1); single row (2).
16. shell perforations: absent (0); canals (1); punctae (2); pseudopunctae (3); endopunctae (4); no bivalved shell (5).
17. mantle reversal: no (0); yes (1); no bivalved mantle (2).
18. planktotrophic larval shell: present (0); postlarval shell only (1); no shell (2).
19. lobate cells in mantle lobe: absent (0); present (1); no bivalved mantle (2).

Reconciliation of Recent and Cambro-Ordovician Genealogies

The genealogies derived by analyses of the characteristics of recent and Early Paleozoic brachiopods are compatible and can be reconciled at supraordinal levels. Nineteen synapomorphies of ordinal or supraordinal significance were identified (Table 3) with seven related exclusively to the morphology and chemico-structure of the shell. Moreover, only two of the remaining twelve have left no trace in the fossil record. They are the distribution of tentacles on lophophore ridges and the presence of lobate cells in the outer mantle lobe (even the presence of an anus has been deduced from presumed fecal evidence in the kutorginides (ROWELL & CARUSO, 1985). Fourteen groups of brachiopods were analyzed in relation to *Phoronis.* Three, the lingulid, craniid, and rhynchonellid clades, involve both recent and extinct groups and contain two to six orders. Four of the wholly extinct groups, the paterinids, trimerellids, kutorginids, and protorthids, are single orders, while the rest consist of no more than two orders, according to present taxonomic practices. Even these, however, are variable in morphology and shell structure so that all fossil groups were coded for up to three multistate and up to six missing character states, which together constitute nearly one-quarter of the total characterization of the entire ingroup.

Even with the exclusion of tentacular distribution and lobate cell differentiation, the variability or uncertainty of character states generated a large number of trees (438 in a heuristic search involving stepwise random addition of taxa in 10 replicates). Various supraordinal groupings have been derived from a 50-percent, majority-rule consensus

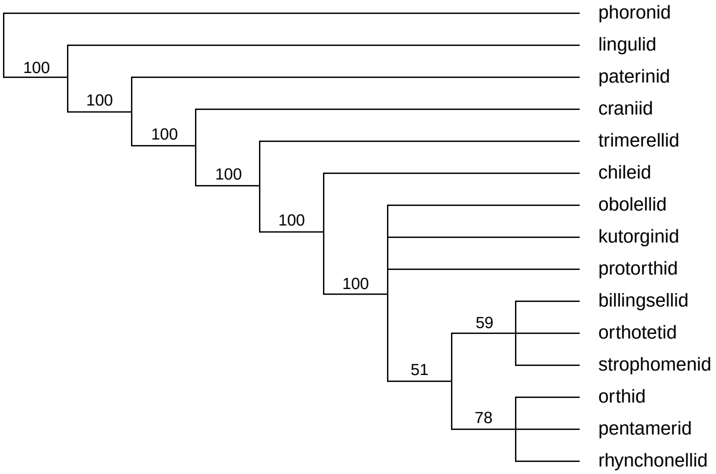

FIG. 4. Majority rule consensus of 438 trees derived in heuristic search of data in Table 3 (matrix in Williams & others, 1996, p. 1191) involving stepwise random addition of taxa in ten replicates with phoronid as outgroup (Williams & others, 1996).

(Fig. 4) including an obolellid-rhynchonellid clade; a paraphyletic group including the paterinids and chileids; and a lingulid sister group to all other brachiopods. Such grouping is also evident when *Phoronis* is eliminated as an outgroup and relationships among the ingroup are represented as an unrooted tree (Fig. 5). Two of these units are distinctive. The lingulid group is characterized by an organophosphatic shell with a stratiform secondary layer and lacks any articulation of the valves. The obolellid-rhynchonellid clade is distinguished by the fibrous secondary layer of an organocarbonate shell and the development of a diductor muscle system signalling valve articulation. For classificatory purposes, the paraphyletic contents of the third group could be redistributed. The paterinids with an organophosphatic stratiform shell fit with the lingulids; the fibrous-shelled chileids could be regarded as a sister group to the obolellid-rhynchonellid clade, and the craniids (with trimerellids) could be distinguished as having an organocarbonate (variably aragonitic) laminar shell and lacking evidence of a pedicle or cuticular pad.

With regard to the obolellid-rhynchonellid clade, the true tooth and socket arrangement is a synapomorphy only of the billingsellid-rhynchonellid subclade (Fig. 4). Morphological evidence of the development of an adjustor-controlled pedicle from a rudiment and the loss of the posterior body wall and anus is first found in the orthid-pentamerid-rhynchonellid group; while the development of an astrophic shell and crura in support of the mouth segment of the lophophore and evidence of mantle reversal are restricted to the rhynchonellid constituent, the youngest group to emerge during Cambro-Ordovician times.

THE SUPRAORDINAL CLASSIFICATION

The constraints governing the erection of a phylogenetic classification are explicit and are not met by any one of the cladograms illustrated in Figures 1 to 5. It would, therefore, be unwise at this juncture to erect a classification on any one of these trees. Rooting difficulties, which are part of the problem, could be resolved by adopting an unrooted tree (Fig. 5). Yet even this analysis could not be transformed into a strictly phylogenetic classification appropriate to all available chronostratigraphic and biological data. On the other hand, the classification erected in 1996 (Williams & others, 1996, p. 1184) can accommodate all currently recognized brachiopod taxa. It is also flexible enough to incorporate changes resulting from future refinements of outgroup and character data, mainly through a better understanding of genetic and embryological variability among extant species. Even so the major taxonomic categories of the classification are unlikely to be drastically changed for the following reasons.

There is firm evidence to support a continuing recognition of the subphylum Linguliformea as a monophyletic group (Fig. 1, 3; Carlson, 1995; Cohen & Gawthrop, 1996).

The subphylum Craniiformea is taxonomically defensible because the phylogenetic position of the craniid group is so uncertain. The craniids appear as one branch of an unresolved polytomy in some cladograms (Fig. 1) and as a paraphyletic group at the base of the Linguliformea (Fig. 1) or of the Rhynchonelliformea (Fig. 1, 3). These variable relationships could represent real and as yet unexplained character conflicts rather than differing interpretations of existing data. For the time being at least, the craniids and related groups are most conveniently accommodated in a separate subphylum.

The third subphylum is founded on the rhynchonellate clade, which is a constant feature of all cladograms although variably associated with other branches (Fig. 1–5). These branches include a number of separate, extinct plesions, mostly of Early Paleozoic age. They are the paterinids, chileids, obolellids, kutorginids, and strophomenids (*s.l.*), all of which have been given class status. The present assignment of these plesions among the subphyla is shown in Figure 6.

The Linguliformea consists of all brachiopods with organophosphatic shells that also covered their planktotrophic larvae. No linguliforms ever developed biomineralized devices for shell articulation, although the grouping of the paterinid ventral muscle bases suggests valve movement about a strophic hinge line controlled by a periostracal hinge (Williams, Popov, & others, 1998) serving as a ligament. Other features of the short-lived paterinate class, which are more characteristic of carbonate-shelled brachiopods are mantle impressions of exclusively marginal *vascula terminalia* and gonadal sacs and a lobate, larval dorsal valve that may have covered two pairs of setal sacs. The synapomorphies of the Lingulata clade of three orders include the canaliculate condition of the stratiform shell, a mantle permeated by interomedial as well as marginal *vascula terminalia* and gonads restricted to the body cavity.

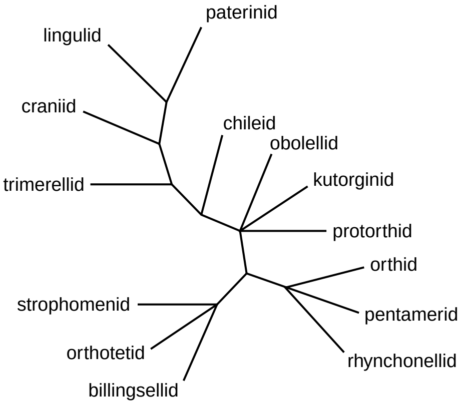

Fig. 5. Unrooted representation of relationships among taxa in Figure 4 (Williams & others, 1996).

The core of the Craniiformea is a clade consisting of two orders, the inarticulated Craniida and Craniopsida, which share with the articulated Trimerellida the synapomorphies of a nonfibrous carbonate shell and a lack of pedicle; together they compose the class Craniata.

The Chileata (including the Dictyonellidina), in contrast, have a fibrous secondary shell and a perforated ventral valve floor, which is believed to have housed a cuticular pad serving as a pedicle holdfast. The

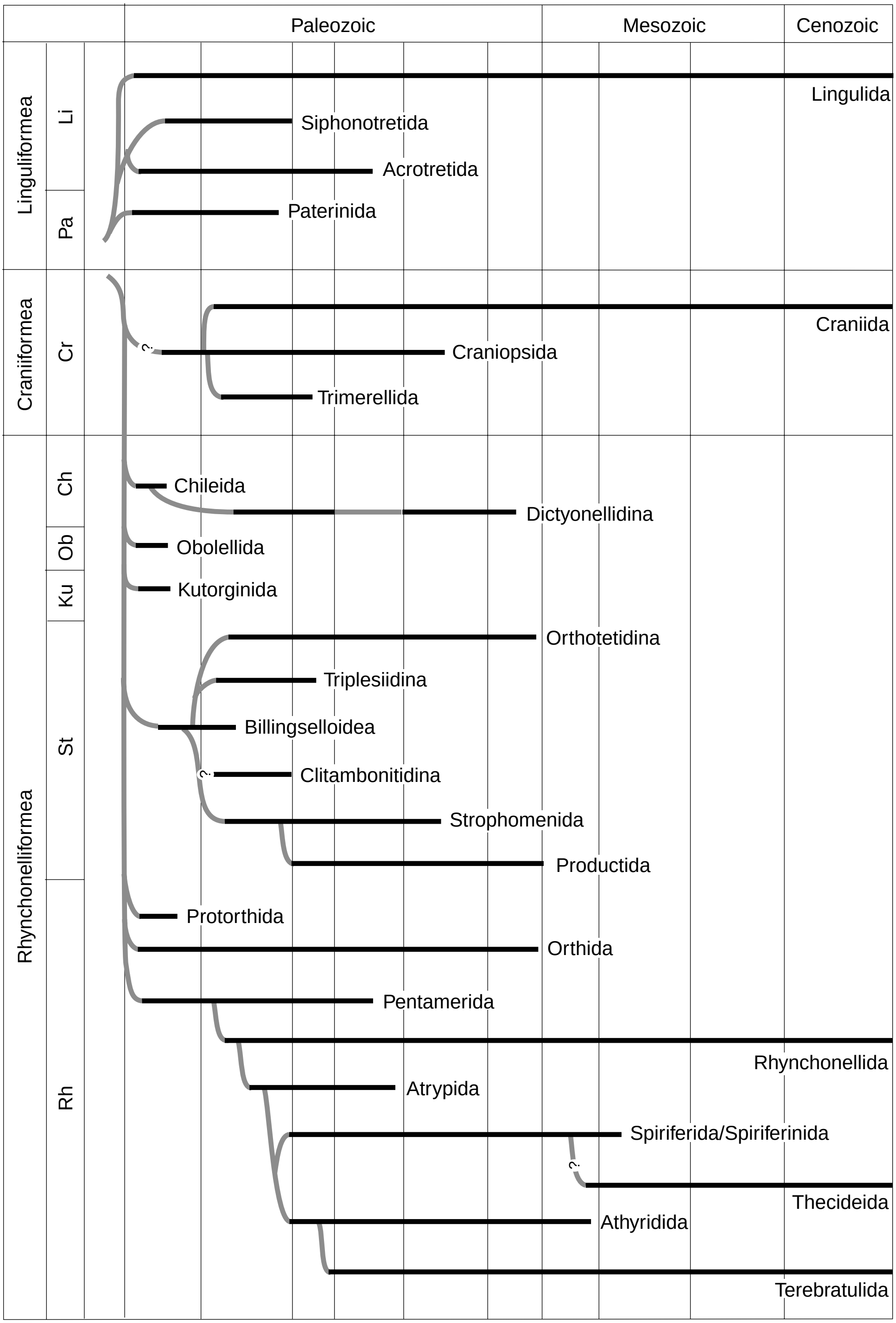

FIG. 6. *For explanation, see facing page.*

cladistic position of the chileates relative to the craniates is equivocal. The Chileata appear as a paraphyletic associate of the craniid-trimerellid branches in Figure 3 but as a sister group to the obolellid-rhynchonellid clade in Figure 4. On balance, the chileates have been included in the Rhynchonelliformea.

The Rhynchonelliformea, the largest subphylum with 19 of the 27 recognized orders, is well founded on several important clades including the Rhynchonellata, which embraces all recent articulated species. The subphylum shares with the Craniiformea the characteristic protegulum of a lecithotrophic larva so that the principal rhynchonelliform synapomorphies are the fibrous secondary layer of an organocarbonate shell, the presence of a pedicle, and the development of a recognizable diductor muscle system controlling the opening of the valves about a hinge axis defined by interareas.

The three classes Obolellata, Kutorginata, and Strophomenata share a supra-apical pedicle representing a specialized outgrowth of the posteromedian sector of the ventral mantle. The first two classes are further distinguished by simple articulatory devices and the last by deltidiodont teeth and dental sockets bounded by ridges. This classic tooth and socket arrangement is also characteristic of the Orthida as was a novel type of pedicle controlled by adjustor muscles, which occupied the delthyrial opening and almost certainly developed from a rudiment. The strophomenate clade, which underwent a loss of pedicle and articulation in Late Paleozoic productides, was further involved in the only major transformation affecting the fibrous secondary layer. The typical strophomenate cross-bladed lamination, however, was polyphyletic and possibly indicated a chemico-structural change in the shell of the stem group that led to an inherent tendency for bladelike fibers repeatedly to amalgamate laterally into laminae.

The taxonomic location of the protorthid plesion is equivocal. Protorthides could have possessed a pedicle rudiment but had a weakly developed articulatory device that could have evolved independently of deltidiodont teeth and sockets, although probably from the same stem plan. On the evidence of the cardinalia of *Leioria,* however, the order has been grouped with the rhynchonellates. The inclusion of the skenidioids in this class greatly extends its geological range.

The transformations defining the rhynchonellate Orthida were the foundation of the modern articulated brachiopod. In addition to the inferred development of a pedicle rudiment, other synapomorphies are likely to have been the loss of the posterior body wall, which presumably persisted in the Strophomenata, and the loss of the anus. Projecting brachiophores were also a new development of the orthides and pentamerides, while in the latter group an astrophic shell emerged for the first time.

The main synapomorphies of the other orders composing the Rhynchonellata, which range from the rhynchonellides and spire-bearers to the terebratulides and thecideidines, are mantle reversal and those leading to skeletal supports for the lophophore in the form of crura, spiralia, and loops. Endoskeletal spiculation, however, first appeared in some spiriferides and may be homologous with that characteristic of terebratulides and thecideidines, while endopunctation with a distal microvillous brush is a synapomorphy of later spiriferides, terebratulides, and thecideidines.

FIG. 6. The proposed supraordinal classification of Brachiopoda superimposed on a geological chart with lines representing geological systemic boundaries proportionately spaced on vertical radiometric time scale of 545 Ma and showing chronostratigraphic ranges of principal taxa within three subphyla composed of eight classes; *Li,* Lingulata; *Pa,* Paterinata; *Cr,* Craniata; *Ch,* Chileata; *Ob,* Obolellata; *Ku,* Kutorginata; *St,* Strophomenata; *Rh,* Rhynchonellata (Williams & others, 1996).

OUTLINE OF SUPRAFAMILIAL CLASSIFICATION AND AUTHORSHIP

The following outline of the classification of the Brachiopoda lists all suprafamilial taxa recognized and described in this and subsequent volumes on the phylum. The thirty-four contributors listed below were responsible for authorship of diagnoses for the listed taxa. In the case of orders, suborders, and superfamilies, the authors were also responsible for descriptions of all lower ranking taxa down to genera and subgenera.

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. Lower 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–Upper Ordovician.
L. E. Holmer & L. E. Popov
Siphonotretoidea. Middle Cambrian–Upper 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. Lower Ordovician–Holocene.
M. G. Bassett
Trimerellida. Lower Ordovician–upper Silurian.
L. E. Popov & L. E. Holmer
Trimerelloidea. Lower Ordovician–upper Silurian.
L. E. Popov & L. E. Holmer
Rhynchonelliformea. Lower Cambrian–Holocene.
Alwyn Williams, S. J. Carlson, & C. H. C. Brunton
Chileata. Lower Cambrian–Upper Permian.
L. E. Popov & L. E. Holmer
Chileida. 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 Triassic.
        - Alwyn Williams, C. H. C. Brunton, & L. R. M. Cocks
  - Strophomenida. Lower Ordovician–Upper Carboniferous.
        - L. R. M. Cocks & Rong Jia-yu
      - Strophomenoidea. Lower Ordovician–Upper Carboniferous.
        - L. R. M. Cocks & Rong Jia-yu
      - Plectambonitoidea. Lower Ordovician–Middle Devonian.
        - L. R. M. Cocks & Rong Jia-yu
    - Uncertain.
        - Alwyn Williams & C. H. C. Brunton
  - Productida. Upper Ordivician–Upper Permian, ?Lower Triassic.
        - C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
    - Chonetidina. Upper Ordovician–Lower Triassic.
        - P. R. Racheboeuf
      - Chonetoidea. Upper Ordovician–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
    - Strophalosiidina. Lower Devonian–Upper Permian.
        - C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
      - 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
  - Orthotetida. Lower Ordovician–Upper Permian.
        - Alwyn Williams, C. H. C. Brunton, & A. D. Wright
    - Orthotetidina. Lower 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. 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. Middle Cambrian–Lower Devonian.
Alwyn Williams & D. A. T. Harper
Plectorthoidea. Lower Cambrian–upper Silurian.
Alwyn Williams & D. A. T. Harper
Dalmanellidina. Lower Ordovician–Upper Permian.
D. A. T. Harper
Dalmanelloidea. Lower Ordovician–Upper Devonian.
D. A. T. Harper
Enteletoidea. Lower Ordovician–Upper Permian.
D. A. T. Harper
Uncertain.
Alwyn Williams & D. A. T. Harper
Pentamerida. ?Lower Cambrian, Middle Cambrian–Upper Devonian.
S. J. Carlson, A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
Syntrophiidina. ?Lower Cambrian, Middle Cambrian–Lower Devonian.
S. J. Carlson & Rong Jia-yu
Porambonitoidea. ?Lower Cambrian, Middle Cambrian–lower Silurian.
S. J. Carlson & Rong Jia-yu
Camerelloidea. Lower Ordovician–Lower Devonian.
S. J. Carlson & Rong Jia-yu
Pentameridina. Upper Ordovician–Upper Devonian.
A. J. Boucot, Rong Jia-yu, & R. B. Blodgett
Pentameroidea. Upper Ordovician–upper Silurian.
A. J. Boucot & Rong Jia-yu
Stricklandioidea. lower Silurian–upper Silurian.
A. J. Boucot & Rong Jia-yu
Gypiduloidea. lower Silurian–Upper Devonian.
R. B. Blodgett, A. J. Boucot, & Rong Jia-yu
Clorindoidea. upper 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. Upper Ordovician–Lower Carboniferous.
    N. M. Savage
  Uncinuloidea. lower Silurian–Upper Devonian.
    N. M. Savage
  Camarotoechioidea. lower Silurian–Lower Carboniferous.
    N. M. Savage
  Rhynchotetradoidea. Upper Devonian–Middle Jurassic.
    N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
  Lambdarinoidea. Upper Devonian–Upper Carboniferous.
    N. M. Savage
  Wellerelloidea. Lower Carboniferous–Lower Jurassic.
    N. M. Savage, M. O. Manceñido, E. F. Owen, A. S. Dagys, & Sun Dong-li
  Rhynchoporoidea. Lower Carboniferous–Upper Permian.
    N. M. Savage
  Dimerelloidea. Upper Devonian–Holocene.
    N. M. Savage, E. F. Owen, M. O. Manceñido, & A. S. Dagys
  Stenoscismatoidea. Lower Devonian–Upper Permian.
    S. J. Carlson & R. E. Grant
  Rhynchonelloidea. Lower Triassic–Upper Cretaceous.
    E. F. Owen & M. O. Manceñido
  Pugnacoidea. Lower Devonian–Holocene.
    N. M. Savage, M. O. Manceñido, E. F. Owen, & A. S. Dagys
  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
Atrypida. Lower Ordovician–Upper Devonian.
    Paul Copper
  Zygospiridina. Lower Ordovician–upper Silurian.
    Paul Copper
  Zygospiroidea. Lower Ordovician–upper Silurian.
    Paul Copper
  Atrypidina. Upper Ordovician–Upper Devonian.
    Paul Copper
  Atrypoidea. Upper Ordovician–Upper Devonian.
    Paul Copper
  Punctatrypoidea. lower Silurian–Lower Devonian.
    Paul Copper
  Lissatrypidina. ?Lower Ordovician, Upper Ordovician–Upper Devonian.
    Paul Copper
  Lissatrypoidea. ?Lower Ordovician, Upper Ordovician–Upper Devonian.
    Paul Copper
  Davidsoniidina. upper Silurian–Middle Devonian.
    Paul Copper
  Davidsonioidea. upper Silurian–Middle Devonian.
    Paul Copper
  Palaferelloidea. upper Silurian–Middle Devonian.
    Paul Copper
Athyridida. Upper Ordovician–Lower Jurassic.
    Fernando Alvarez
  Athyrididina. Upper Ordovician–Upper Triassic, ?Upper Jurassic.
    Fernando Alvarez & Rong Jia-yu
  Meristelloidea. Upper Ordovician–Lower Carboniferous.
    Fernando Alvarez & Rong Jia-yu
  Athyridoidea. ?Upper Ordovician, lower Silurian–Upper Triassic; ?Upper Jurassic.
    Fernando Alvarez & Rong Jia-yu
  Nucleospiroidea. ?Upper Ordovician, lower Silurian–Lower Permian.
    Fernando Alvarez & Rong Jia-yu

- Retzielloidea. lower Silurian–Lower Devonian.
  - Fernando Alvarez & Rong Jia-yu
- Retziidina. lower Silurian–Upper Triassic.
  - Fernando Alvarez & Rong Jia-yu
  - Retzioidea. lower Silurian–Upper Triassic.
    - Fernando Alvarez & Rong Jia-yu
  - Rhynchospirinoidea. lower Silurian–Middle Devonian.
    - Fernando Alvarez & Rong Jia-yu
  - Mongolospiroidea. Lower Devonian.
    - Fernando Alvarez & Rong Jia-yu
- Koninckinidina. Middle Triassic–Lower Jurassic.
  - D. I. MacKinnon
  - Koninckinoidea. Middle Triassic–Lower Jurassic.
    - D. I. MacKinnon

- Spiriferida. Upper Ordovician–Upper Permian.
  - J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-Fei
  - Spiriferidina. Upper Ordovician–Upper Permian.
    - J. L. Carter, J. G. Johnson, Rémy Gourvennec, & Hou Hong-Fei
    - Cyrtioidea. Upper Ordovician–Lower Devonian.
      - J. G. Johnson & Hou Hong-Fei
    - Spinelloidea. upper Silurian–Upper Devonian.
      - J. G. Johnson
    - Theodossioidea. Lower Devonian–Lower Carboniferous, ?Upper Carboniferous.
      - J. G. Johnson, J. L. Carter, & Hou Hong-Fei
    - Cyrtospiriferoidea. Lower Devonian–Upper Devonian.
      - J. G. Johnson
    - Ambocoelioidea. upper Silurian–Upper Permian.
      - J. G. Johnson, J. L. Carter, & Hou Hong-Fei
    - Martinioidea. upper Silurian–Upper Permian.
      - J. L. Carter & Rémy Gourvennec
    - Spiriferoidea. Upper Devonian–Upper Permian.
      - J. L. Carter
    - Brachythyridoidea. Upper Devonian–Upper Permian.
      - J. L. Carter
    - Paekelmanelloidea. Upper Devonian–Upper Permian.
      - J. L. Carter
  - Delthyridina. lower Silurian–Upper Permian.
    - J. G. Johnson, Rémy Gourvennec, J. L. Carter, & Hou Hong-Fei
    - Delthyridoidea. lower Silurian–Middle Devonian.
      - J. G. Johnson & Hou Hong-Fei
    - Reticularioidea. lower Silurian–Upper Permian.
      - Rémy Gourvennec, J. G. Johnson, & J. L. Carter
- 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–Lower Carboniferous.
      - J. G. Johnson
    - Suessioidea. Lower Carboniferous–Lower Jurassic.
      - J. L. Carter
    - Spondylospiroidea. Upper Triassic.
      - J. L. Carter
    - Pennospiriferinoidea. Upper Devonian–Lower Jurassic.
      - J. L. Carter
    - Spiriferinoidea. Middle Triassic–Lower Jurassic.
      - J. L. Carter
    - Syringothyridoidea. Upper Devonian–Lower Permian.
      - J. L. Carter

- Thecideida. Upper Triassic–Holocene.
  - P. G. Baker
  - Thecideidina. 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, A. J. Boucot, T. N. Smirnova, A. S. Dagys, Jin Yu-gan, & Sun Dong-li
  - Centronellidina. Lower Devonian–Upper Permian.
    - A. J. Boucot & Jin Yu-gan
    - Stringocephaloidea. Lower Devonian–Upper Permian.
      - A. J. Boucot & Jin Yu-gan
  - Terebratulidina. Lower Devonian–Holocene.
    - D. E. Lee, A. J. Boucot, A. S. Dagys, T. N. Smirnova, & Sun Dong-li
    - Dielasmatoidea. Lower Devonian–Lower Jurassic.
      - A. J. Boucot, Jin Yu-gan, D. E. Lee, Sun Dong-li, & A. S. Dagys
    - Cryptonelloidea. Lower Devonian–Lower Triassic.
      - A. J. Boucot & Jin Yu-gan
    - Terebratuloidea. Upper Triassic–Holocene.
      - D. E. Lee, T. N. Smirnova, Sun Dong-li, & A. S. Dagys
    - Loboidothyridoidea. Upper 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
    - Loboidothyridoidea. Lower Jurassic–Upper Cretaceous.
      - D. E. Lee, T. N. Smirnova, & A. S. Dagys
  - Terebratellidina. 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 & A. S. Dagys
    - Kingenoidea. Middle Triassic–Holocene.
      - D. I. MacKinnon, D. E. Lee, T. N. Smirnova, & A. S. Dagys
    - Laqueoidea. Lower Jurassic–Holocene.
      - D. I. MacKinnon, T. N. Smirnova, & 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. Paleocene–Holocene.
      - D. I. MacKinnon & D. E. Lee
    - Kraussinoidea. Miocene–Holocene.
      - D. E. Lee & D. I. MacKinnon
  - Uncertain.
    - Gwynioidea. Lower Jurassic–Holocene.
      - D. I. MacKinnon
  - *Incertae sedis*
    - Plicanoplitoidea (taxonomic rank uncertain). upper Silurian–Middle Devonian.
      - P. R. Racheboeuf
    - Cadomelloidea (taxonomic rank uncertain). Lower Jurassic.
      - D. I. MacKinnon

BRACHIOPODA

Alwyn Williams,[1] Sandra J. Carlson,[2] and C. Howard C. Brunton[3]

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Phylum BRACHIOPODA Duméril, 1806

[Brachiopoda Duméril, 1806, p. 154] [=Palliobraches de Blainville, 1814, p. 179; Spirobrachiophora Gray, 1821, p. 238; Palliobrachiata de Blainville, 1824, p. 298; Brachionopoda Agassiz, 1848, p. 145; Brachionacephala Bronn, 1862, p. 224; Brachionoconchae Bronn, 1862, p. 228]

Solitary, marine, bivalved, coelomate invertebrates bilaterally symmetrical about median plane normal to surface of separation between valves; shell organophosphatic or organocarbonate, attached to substrate by muscular stalk (pedicle) or cuticular pad or secondarily cemented or free and composed of commonly larger ventral (pedicle) valve and dorsal (brachial) valve lined by folded extensions (mantle) of body wall pervaded by canaliferous extensions of coelom; each normally with marginal fringe of chitinous setae; all epithelia monolayered, diverse monociliated cells with epistome possibly represented by brachial fold in front of mouth, feeding organ (lophophore) as tentacular, ciliated tubular extensions of coelom, variably disposed and suspended between mantles; alimentary canal with or without anus; nervous system subepithelial, principal ganglion subenteric, located below esophagus; one, rarely two, pairs of metanephridia also acting as gonoducts in main body cavity (metacoel); circulatory (haemal) system open, commonly with dorsal contractile vesicle; coelom schizocoelic or enterocoelic; mostly dioecious. *Lower Cambrian–Holocene.*

The term Brachiopodes was first used by Cuvier in 1805 for the acephalous molluscs *Lingula, Orbicula,* and *Terebratula,* but was not formalized until 1806 when Duméril proposed Brachiopoda as an order of Mollusca. This notion of a close molluscan affinity for brachiopods prevailed for much of the nineteenth century and was evident as late as 1934 in the Russian edition of Zittel's *Textbook of Palaeontology*. Other relationships, however, were advocated as the more obscure coelomates became better known. In 1853, Huxley coined the name Molluscoidea for brachiopods and the newly understood polyzoans (bryozoans). By 1870, Morse had concluded that brachiopods are more closely related to annelids than to molluscs and cited the possession of setae as part of the evidence of common ancestry. Later comparative studies of anatomy and larval development, especially those of *Phoronis* and brachiopods by Caldwell (1882), led Hatschek (1888) to propose a new phylum, the Tentaculata, for brachiopods, bryozoans, and phoronids. By the time this group had been more appropriately renamed "Lophophorata" (Hyman, 1959, p. 229), the brachiopods, as well as the bryozoans and phoronids, were being widely recognized as distinct phyla (Schuchert & LeVene, 1929; Hyman, 1940; Cooper, 1944). Indeed, in light of his studies of the life history of a terebratulide, Percival at one time (1944) even concluded that articulated brachiopods with organocarbonate shells are so different from inarticulated species with organophosphatic exoskeletons as to warrant the recognition of two phyla.

The long-held recognition of the Brachiopoda as a phylum has seldom been disputed by paleontologists or biologists. The shells of brachiopods have always been instantly distinguishable from those of other metazoans throughout a geological record unexcelled in its completeness and duration, while the biology and development of living species are as distinctive as their shell morphology. Brachiopod monophyly, however, has been questioned by Valentine (1975) and Wright (1979), who contended that articulated and various inarticulated stocks evolved independently from phoronid-like ancestors, an interpretation refuted by Rowell (1981a). Gorjansky and Popov (1986) also favored bivalve homoplasy when they envisaged the lophophorates as a clade of phoronids, bryozoans, and the organophosphatic-shelled brachiopods, with the organocarbonate-shelled brachiopods as a sister group. This classification had been abandoned before the publication of an account by Nielsen (1991) of the development of *Crania,* which supported a close affinity between the craniids and other carbonate-shelled species but refuted brachiopod diphyly.

This willingness to reconsider relationships among lophophorates is symptomatic of the controversy surrounding the precise rooting of the Brachiopoda (as well as the Phoronida and Bryozoa) within metazoan phylogeny. For almost a century, the lophophorates were widely regarded as protostomes, and attempts have even been made to restore Hatschek's original rank of phylum for the group (his Tentaculata), with the brachiopods, bryozoans, and phoronids reduced in hierarchical status to classes (Emig, 1984). More recently, Conway Morris and Peel (1995, p. 343–344) concluded that brachiopods evolved from extinct protostomes, the Lower Cambrian articulated halkieriids. This radical proposal is presently too speculative for us to accept the halkieriids as the sister group of the brachiopods.

A deuterostomous origin of some or all lophophorates has also attracted support especially within the last 50 years. Thus, reservations on how to interpret the development of the brachiopod gut and coelom prompted Hyman (1959, p. 230) to suggest that lophophorates "form some sort of link between the Protostoma and Deuterostoma." Nielsen (1995, p. 6), on the basis of studies and reinterpretations of lophophorate larval development, has also argued against the monophyly of the lophophorates and has assigned the bryozoans to the protostomes and the brachiopods and phoronids to the deuterostomes. In his view, many features, like the lophophore, which are common to all three taxa, are not synapomorphies but homoplasies. The prevalent opinion among zoologists, however, favors all lophophorates as being deuterostomes (Zimmer, 1964; Brusca & Brusca, 1990; Schram, 1991; Meglitsch & Schram, 1991; Eernisse, Albert, & Anderson, 1992).

These conflicting views, based on classical biological data, may be resolved by molecular evidence, particularly through the use of ribosomal RNA to determine metazoan molecular phylogeny (Conway Morris, 1993). So far, the unanimous conclusion, based on comparisons of sequences of 18S rRNAs using *Lingula* to represent brachiopods, is that the lophophorates are protostomes (Field & others, 1988; Ghiselin, 1988; Patterson, 1989; Lake, 1990; Adoutte & Phillipe, 1993), although relationships of taxa within the protostomes are still uncertain.

More detailed genetic studies of the lophophorates, however, are beginning to raise severe intraphyletic taxonomic problems. An analysis of sequences from one articulated and one inarticulated species of brachiopod, a phoronid, and a bryozoan showed the articulated species and the phoronid as sister taxa, that, together with the inarticulated brachiopods, molluscs, and polychaete annelids, form a sister clade to the bryozoans (Halanych & others, 1995). In contradiction to this perceived diphyletic origin of the Brachiopoda, a more comprehensive 18S rRNA study of more than 30 species representing all recent brachiopod superfamilies showed them to be monophyletic (Cohen & Gawthrop, 1996). Even so, Cohen and Gawthrop are unequivocal in nesting the phoronids within the brachiopod clade, either as a sister group of all inarticulated species or of the craniids alone. Their data rather weakly identified molluscs (possibly with annelids *inter alia*) as sister group(s) of the brachiopods and phoronids, but were inadequate to show the relationship of the bryozoans.

In the light of these confirmatory studies, brachiopods are regarded as forming a clade meriting recognition as a phylum. The resultant classification is, we believe, flexible enough to accommodate other lophophorates, like phoronids, should they eventually be assigned to the phylum. Meanwhile, it accommodates three subphyla and eight classes, diagnosed and discussed at their appropriate ranks in the classificatory hierarchy.

LINGULIFORMEA

ALWYN WILLIAMS,[1] SANDRA J. CARLSON,[2] and C. HOWARD C. BRUNTON[3]

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Subphylum LINGULIFORMEA Williams & others, 1996

[Linguliformea WILLIAMS & others, 1996, p. 1192]

Brachiopods with organophosphatic stratiform shells, inarticulated or with rudimentary articulation not involving teeth and sockets, outer mantle lobe without lobate cells; posterior body wall present or inferred for extinct species; pedicle emerging between valves or supra-apically with extension of coelomic cavity as core; alimentary tract with anus; lophophore of living species initially with median tentacle, lost during growth, tentacles in double row throughout ontogeny; larvae planktotrophic with variously ornamented shell, developed without mantle reversal. *Lower Cambrian (Tommotian)–Holocene.*

Living linguliforms are members of a clade, the Lingulata, that share with its sister group, the Paterinata, two synapomorphies that are either self-evident or can be inferred in extinct species. These synapomorphies are an organophosphatic shell, composed of variable aggregates of apatitic granules in a matrix of glycosaminoglycans (GAGs), β-chitin, and proteins; and a pedicle of varying complexity but consisting essentially of a tubular extension, with a coelomic core, of the ventral body wall, which is separated from its dorsal counterpart by a strip of inner epithelium (posterior body wall).

In many other features the paterinates are like the rhynchonelliforms and are distinguishable from the lingulates at class level. These features include the development of true interareas (albeit without a biomineralized articulatory device), the presence of posteromedial muscle sets instead of obliquely operating systems, the development of mantle gonocoels and the exclusively marginal *vascula terminalia,* and the morphology of the larval shell.

LINGULATA

LARS E. HOLMER and LEONID E. POPOV

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[Bohemian materials prepared by MICHAL MERGL, Západočeská Univerzita, Plzeň, Czech Republic]

Class LINGULATA Gorjansky & Popov, 1985

[Lingulata GORJANSKY & POPOV, 1985, p. 13]

Pedicle of living species with coelomic cavities, developing as outgrowth of posterior part of ventral mantle lobe; dorsal and ventral mantle lobes completely separated in adults; posterior body wall usually well developed; musculature usually composed of single or paired umbonal muscle, three or four pairs of oblique muscles (reduced in Acrotretida) and paired central muscles; lophophore with large and small brachial canal and two rows of filaments during trochophe stage; mechanism of shell opening hydraulic, by means of well-developed dermal muscles in anterior body wall; digestive tract open, recurved, U-shaped, with anus placed anteriorly, near right nephridiopore; nervous system epidermal with only one subenteric ganglion and peripheral mantle nerves; sensory organs represented by statocysts; gonads on free edges of peritoneal bands; mantle canals usually with *vascula terminalia* directed peripherally and medially (except in Paterinida). *Lower Cambrian (upper Atdabanian)–Holocene.*

The Lingulata was established originally by GORJANSKY and POPOV (1985, 1986) as a separate clade outside the Brachiopoda; however, they are better included as a monophyletic group within the Brachiopoda (HOLMER, 1989a, 1989b; POPOV & others, 1993;

Holmer & others, 1995). The problems of the relationship between the organophosphatic and carbonate-shelled inarticulated stocks is discussed above (Williams, Carlson, & Brunton, Brachiopod Classification, p. 1).

Several cladistic analyses of lingulate genera have produced inconclusive results as to the relationships among the various groups (especially for the genera of the Linguloidea); only the analysis of the Acrotretida (see Fig. 50; Table 7–9) and Siphonotretida (see Fig. 76; Table 10–12) resulted in partly resolved trees that are presented below. This problem requires further study; the subdivision at the family level adopted in the previous edition of the *Treatise* (Rowell, 1965a) is largely accepted, with minor modification.

The 23 recognized extinct and extant families of the Lingulida, Acrotretida, and Siphonotretida were analyzed using 40 unweighted, unordered characters (see Holmer & Popov, 1996b for further details). The two families (Paterinidae and Cryptotretidae) of the Paterinida, which are the oldest known organophosphatic-shelled inarticulated brachiopods, were selected as outgroups. The analysis generated 354 equally parsimonious trees 104 steps long, with a consistency index of 0.712 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; Swofford, 1993). The strict consensus tree (see Fig. 38; Table 4–6) is poorly resolved but gives support for the Acrotretida (including only the Acrotretoidea) as a potential monophyletic order. The Lingulida (and the Linguloidea) as defined below cannot be confirmed as a monophyletic group. It is possible that the Lingulida may represent a stem-group from which the Siphonotretida and Acrotretida were derived, but this needs further study.

The only extant organophosphatic-shelled stocks, the linguloids and discinoids, share many characters, including type of musculature, pedicle, digestive tract, mantle canal system, ontogeny, and shell structure; many of these characters can also be traced in their fossil representatives. The Discinoidea is here considered as a superfamily within the Lingulida (see Fig. 38).

The lingulate muscle system is more complex than that of other brachiopods; all recent and many fossil groups have three or four pairs of oblique muscles occupying a peripheral position in the body cavity (Fig. 7, 39, 51). These muscles control the rotation and sliding movements of the valves and probably directly reflect the absence of true articulation; in that respect the muscle system is similar to that of the carbonate-shelled inarticulated group. Recent craniides, however, have only one oblique muscle (oblique internal) that can be compared with that of recent lingulides (see below; see Fig. 89).

The discinoid anterior and posterior adductors and the linguloid umbonal and central muscles (see Fig. 7, 39) may be homologous with the cranioid adductors (see Fig. 89), and these muscles may possibly also be primitive for all brachiopods, but the polarity of this character is highly uncertain.

The muscle system of the extinct Acrotretida and Siphonotretida is probably reduced and modified by comparison with other lingulates. As noted below, the interpretation of the preserved scars has varied, and the earliest evolution and origin of these groups is far from certain. The position of the Dysoristidae is also very uncertain; the family is here placed within the Lingulida in view of the similarities in shell structure.

Williams and Rowell (1965a) and Rowell (1977) compared the musculature of the extinct acrotretoids and siphonotretoids with that of recent discinoids, but it is also possible to homologize the scars with those of linguloids (see Fig. 51, 75). The extinct botsfordiids and acrothelids were previously placed within the Acrotretida, but the arrangement of muscle scars as well as other features (see Fig. 44) suggest that they should be classified with the Lingulida (see Fig. 38).

The presence of pitting on the larval shell in the acrotheloids and the acrotretoids apparently does not represent a synapomorphy for the Acrotretida as proposed by Rowell (1986) and Holmer (1989b); moreover, the larval shell of the former group is usually comparatively larger (more than 0.3 mm across) than that of the acrotretoids. HOLMER (1989b) noted that the size of the larval shell does not appear to be correlated with the size of the adult but remains fairly constant within different lingulate groups.

The body wall of recent lingulates has well-developed dermal muscles, which are absent in all brachiopods with a carbonate shell. These muscles are responsible for the hydraulic shell-opening mechanism and were probably present also in all extinct organophosphatic-shelled brachiopods, with the possible exception of the paterinates.

The pedicle of living lingulates originates as an outgrowth of the ventral mantle lobe and contains muscles and coelomic cavities. A pedicle opening or groove is invariably present at some stage in the ontogeny of all extinct and extant lingulate stocks, including the encrusting acrotretoids (*Eoconulus* and *Undiferina*) and the free-lying elkaniid linguloid *Volborthia.*

The posterior body wall of lingulates is usually well developed, and the mantle lobes are completely separated. In recent *Lingula,* however, the first-formed shell originates as an organic plate secreted over a single epithelial area at the end of the embryonic stage, and the valves become separated later in ontogeny (YATSU, 1902).

The mantle canal system is usually baculate, with *vascula lateralia* in both valves and *vascula media* in the dorsal valve; the *vascula terminalia* branch both peripherally and medially from the main vascular trunks (Fig. 7).

LINGULIDA

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Order LINGULIDA Waagen, 1885

[*nom. transl.* KUHN, 1949, p. 99, *ex* suborder Lingulacea WAAGEN, 1885, p. 754; *nom. correct.* GORJANSKY, 1960, p. 173, *pro* order Lingulacea KUHN, 1949, p. 99; *emend.* HOLMER & POPOV, herein] [=Mesocaulia WAAGEN, 1885, p. 754, *partim;* Atremata BEECHER, 1891, p. 354, *partim*] [*incl.* Discinida WAAGEN, 1885]

Larval shell usually large (more than 0.3 mm across), smooth or with pitted microornamentation; pedicle emerging posteriorly between valves or through foramen; musculature composed of single or paired umbonal muscle (posterior adductor in Discinoidea), three or four pairs of oblique muscles, and paired central muscles (anterior adductor in Discinoidea); mantle canal system baculate or bifurcate; dorsal *vascula media* usually developed; shell structure with baculate laminae (KAESLER, 1997, fig. 238). *Lower Cambrian (upper Atdabanian)–Holocene.*

The concept of the order is expanded here to include the Discinoidea and Acrotheloidea.

Superfamily LINGULOIDEA Menke, 1828

[*nom. correct.* ROBERTS in ROBERTS & JELL, 1990, p. 305, *pro* Lingulacea SCHUCHERT, 1896, p. 306, *nom. transl. ex* Lingulidae GRAY, 1840, p. 155, *nom. correct. pro* Lingulaceae MENKE, 1828, p. 56, *nom. imperf.*] [*incl.* Obolacea KING, 1846, *nom. transl.* SCHUCHERT, 1896, p. 305, *ex* Obolidae KING, 1846, p. 28]

Shell generally biconvex; surface of larval shell smooth or with pitted microornamentation; both valves with marginal beaks (except Paterulidae); pedicle usually emerging between valves, more rarely through foramen (Lingulellotretidae and Dysoristidae); both valves usually with well-developed pseudointerareas; ventral visceral area bisected by pair of V-shaped grooves, representing impressions of pedicle nerve; dorsal visceral area usually with tonguelike, median, anterior projection; musculature composed of single or paired umbonal muscle, paired transmedian, anterior lateral, outside lateral, and middle lateral oblique muscles and paired central muscles; mantle canal system baculate or bifurcate. *Lower Cambrian (upper Atdabanian)–Holocene.*

The superfamily Linguloidea, as defined here, is not supported as a monophyletic group in our cladistic analysis; the relationships between many of the included families could not be resolved (see Fig. 38). The cladistic analysis on the generic level produced numerous trees that are even more unresolved, with a highly unstable topology. This is probably due partly to the fact that many lingulids have a rather limited number of available characters, many of which are still poorly known from most taxa. The Lingulellinae has been included into the Obolinae in view of the very small differences between the two subfamilies; and the poorly known, monotypic family Andobolidae Kozłowski (1930) is here considered to represent a problematic group of uncertain affinity.

The earliest known linguloideans belong to the Obolidae, and include "*Lingulella,*" from the upper Atdabanian of north-central Siberia (Pelman, 1977) and *Palaeoschmidtites* from the "*Fallotaspis*" Biozone of Canada (Ushatinskaya in Voronova and others, 1987). These genera already exhibit typical linguloidean characters, including well-developed pseudointerareas in both valves, a well-defined visceral area in the posterior half of the valves, and a distinctive, tonguelike, median, anterior projection in the dorsal valve. The muscle pattern of the earliest obolids are nearly identical with that of virtually all younger linguloideans, consisting of six pairs of symmetrically arranged scars (Fig. 7). Moreover, the dorsal visceral area of many Early Paleozoic linguloideans shows traces of what appear to represent the attachment scars of the gastroparietal bands, directly posterior to the central muscle scars (Fig. 7), and similar scars can be observed on recent specimens. This may indicate that the earliest linguloideans already had a digestive tract nearly identical to that of the recent Lingulidae. Furthermore, almost all known fossil linguloideans have a well-preserved pair of V-shaped grooves bisecting the ventral visceral area (Fig. 7); identical grooves are present in shells of recent Lingulidae, where they represent impressions of the pedicle nerve (Mickwitz, 1909; Holmer, 1991a).

In contrast to the Obolidae, the Zhanatellidae have a larval and postlarval shell with finely pitted microornamentation as well as a ventral beak with semicircular emarginature. The family appeared at about the same time as the Obolidae, in the late Atdabanian (Popov & Ushatinskaya, 1992). As noted by Popov (1992) and Popov and Ushatinskaya (1992), the zhanatellids may be related to the Discinoidea, appearing first in the Early Ordovician; the morphological step from a deep emarginature to a discinoid pedicle notch is not great. A similar type of emarginature is also known in the Botomian obolid *Kyrshabaktella,* but it lacks pitted microornamentation. Pitted larval shells also characterize the Eoobolidae, which are first recorded from the Botomian, but here the postlarval shell is finely pustulose, and this combination of characters makes it possible that the eoobolids are related to the Botsfordioidea.

Two families of linguloideans, the Lingulellotretidae and the Dysoristidae, may have developed an acrotretid-like pedicle foramen independently (see Fig. 38); as noted above, it is possible that the acrotretids and siphonotretids might have been derived from such a stem group of linguloideans, but this is as yet uncertain (see also Fig. 76). The oldest of the families, the Lingulellotretidae, had already appeared in the Botomian and is characterized by the presence of a pedicle foramen as well as an internal pedicle tube. From the unique, soft-body preservation at Chengjiang, China (Jin, Hou, & Wang, 1993), it is clear that *Lingulellotreta* (referred to as "*Lingulepis*") had a long pedicle much like that of recent Lingulidae, but it emerged from a foramen. The family Dysoristidae, appearing only in the Late Cambrian, also has a pedicle foramen, but unlike in the lingulellotretids it is placed anterior to the ventral beak, and it was sometimes enlarged through resorption of the shell. Also unlike the Lingulellotretidae, the larval and postlarval shell of the dysoristids is pitted, which might indicate a relationship with the Zhanatellidae.

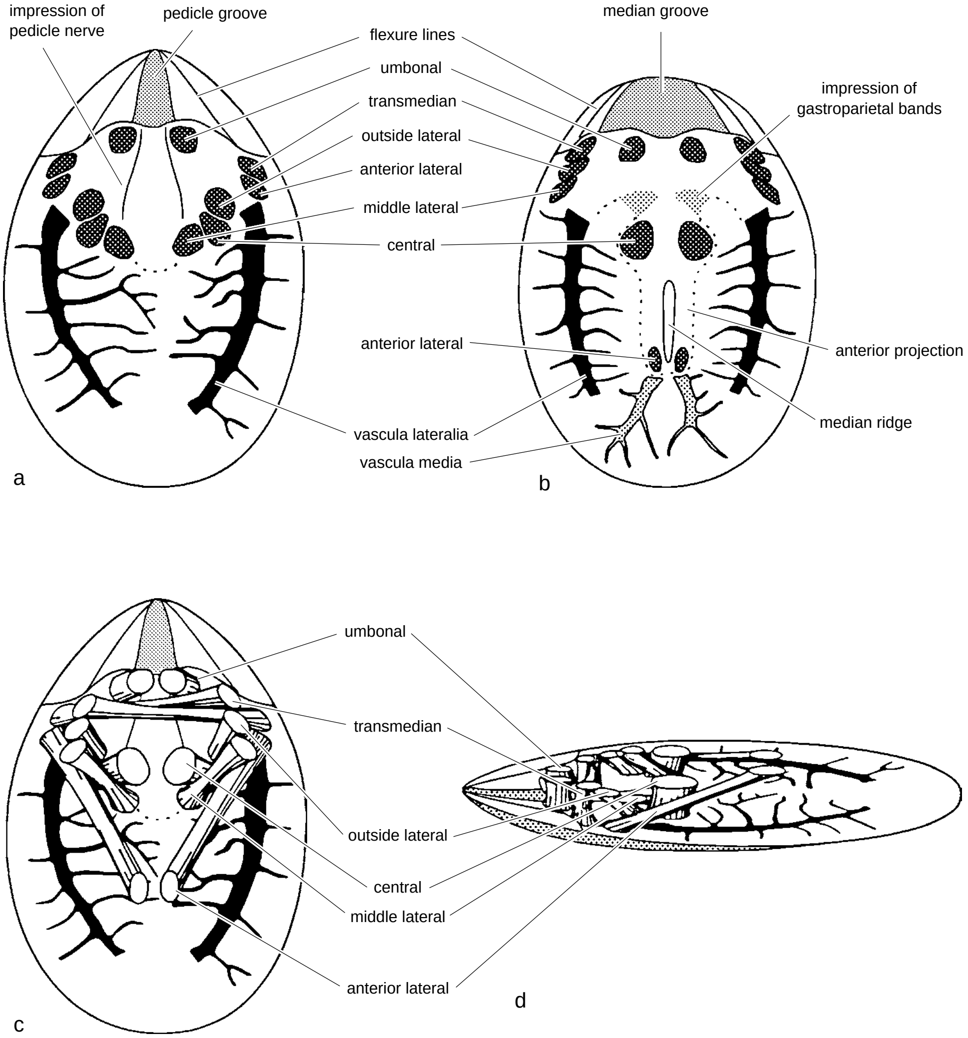

FIG. 7. Schematic illustration of musculature and mantle canal system of *Oepikites; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

During the Middle and Late Cambrian the taxonomic diversity of linguloideans increased significantly, particularly within the Obolidae. Most Cambrian obolids have smooth shells with a subdued ornamentation of concentric growth lines (*Ungula, Obolus,* etc.), and only some genera like *Westonia* and *Rebrovia* are more strongly ornamented with undulating rugae or zigzag growth ridges; the latter type of ornamentation in *Westonia* was interpreted as possible burrowing sculptures by SAVAZZI (1986), and it is likely that the genus had an infaunal life habit. Other Middle and Late Cambrian obolids (like *Ungula* and *Obolus*), however, have been interpreted as epifaunal (POPOV & others, 1989).

The Elkaniidae (*Elkania* and *Broeggeria*) first appeared during the Late Cambrian. Within this family, there is a tendency toward strongly biconvex shells with high visceral platforms; a similar type of morphology occurs within the monotypic family Aulonotretidae as well. The elkaniids are also distinguished by having a pitted larval and postlarval shell similar to that of the Zhanatellidae.

The most important diversification in the evolution of the linguloideans took place early in the Ordovician. Within the Obolidae, both the subfamilies Glossellinae and Elliptoglossinae appeared at the beginning of the Ordovician along with the families Lingulasmatidae, Aulonotretidae, Pseudolingulidae, and Paterulidae.

The family Pseudolingulidae is probably related closely to the linguloidean stock from which the recent family Lingulidae was derived; indeed our analysis indicates that they may form a monophyletic group (see Fig. 38). The pseudolingulids are characterized by many features found also in the Lingulidae, notably the following: converging *vascula lateralia* with possible bifurcation, poorly developed or absent dorsal *vascula media,* and reduced pseudointerareas. Other characters, however, indicate that the pseudolingulids are related to the Obolidae, including having a paired umbonal muscle that is bisected by the pedicle nerve, as well as having a symmetrical transmedian muscle (HOLMER, 1991a).

The origin of the micromorphic family Paterulidae is unknown, but it is possible that paedomorphism was involved (POPOV, ZEZINA, & NÕLVAK, 1982, p. 103). Both valves in the paterulids lack pseudointerareas and have small pitted larval shells much like those of the acrotretids; the postlarval shell has distinctive pitting with rhomboid pits. The interior has a typical lingulid set of muscle scars, including traces of the pedicle nerve. *Paterula* is distributed worldwide in most types of facies, and it is possible that these extremely thin-shelled brachiopods may have had a prolonged planktonic life habit, but the adults belonged to the epibenthos; Silurian *Paterula* (referred to as *Craniops*) has been found attached around the oscular margin of sponges (LENZ, 1993). According to our cladistic analysis (Fig. 38) they may be related closely to the Discinoidea, but this possibility requires further study.

Many groups of linguloideans underwent a major extinction within the Caradoc to Ashgill interval, including, among others, the Lingulasmatidae, Zhanatellidae, and Elkaniidae, as well as the most of the subfamily Obolinae and Glossellinae. Two poorly known genera (*Trigonoglossa* and *Lachrymula*) of the latter appear to have survived into the Carboniferous.

The earliest genera belonging possibly to the Lingulidae are *Apsilingula* and *Barroisella,* from the Late Devonian; the umbonal muscle of both these genera apparently was undivided, and the V-shaped grooves of the pedicle nerve in *Barroisella* appear to curve around the ventral umbonal scar, much as in recent Lingulidae. The possible impressions of the transmedian muscle in *Apsilingula* and *Barroisella* are difficult to interpret, but A. J. WILLIAMS (1977) proposed that *Apsilingula* had an asymmetrical and divided transmedian muscle as in the recent genera. Undoubted Lingulidae appeared first in the Carboniferous (*Lingularia*) and show fairly clear imprints of an asymmetrical transmedian muscle; however, the impression of the pedicle nerve seems to bisect the heart-shaped ventral umbonal muscle (BIERNAT & EMIG, 1993). Many Late Paleozoic and Mesozoic lingulids may be better referred to *Lingularia,* but generic assignment of most described species still remains a problem in view of the rather minute differences in internal and external morphology between *Lingula* and *Lingularia.* According to the restricted definition of *Lingula* by BIERNAT and EMIG (1993), this genus seems first to have appeared in the Late Cretaceous or early Cenozoic together with *Glottidia.*

Family LINGULIDAE Menke, 1828

[*nom. correct.* GRAY, 1840, p. 155, *pro* Lingulaceae MENKE, 1828, p. 56, *nom. imperf.*]

Shell elongate oval, subrectangular to spatulate, gently and subequally biconvex, equivalved; larval shell smooth; ventral valve with triangular ventral depression or groove for passage of pedicle; ventral pseudointerarea vestigial, lacking flexure lines, rarely forming well-defined, triangular propareas; dorsal valve with small, undivided pseudointerarea not extending as plate into valve;

muscle system with asymmetrical transmedian and unpaired umbonal muscles; pedicle nerve curving around umbonal muscle; posterolateral margins of visceral area in both valves strongly concave or straight; dorsal visceral area with narrow anterior projection extending anteriorly beyond midvalve; dorsal central and anterior lateral muscle scars usually closely spaced; mantle canal system bifurcate in living forms; *vascula lateralia* of both valves converging anteriorly; *vascula media* vestigial or absent. Living forms with long flexible pedicle; lophophore spirolophous, with apices of spires medially directed. *?Upper Devonian, Carboniferous–Holocene.*

Lingula Bruguière, 1797, pl. 250 [**L. anatina* Lamarck, 1801, p. 141; ICZN opinion no. 1355, 1985] [=*Pharetra* Bolten, 1798, p. 159 (type, *P. monoculoides*); *Ligula* Cuvier, 1798, p. 435; *Ligularius* Duméril, 1806, p. 170; *Lingularius* Schuchert & LeVene, 1929, p. 76]. Shell elongate oval to subrectangular; ventral pseudointerarea with wide triangular pedicle groove; ventral visceral area extending to midvalve, with impression of pedicle nerve curving around unpaired umbonal muscle scar; dorsal interior with visceral area extending somewhat anterior to midvalve; dorsal central and anterior lateral muscle scars closely spaced, bisected by weak median septum; *vascula media* absent. Shell of living species poorly mineralized laterally. *?Cretaceous, Tertiary–Holocene:* ?cosmopolitan (exact stratigraphic and geographic distribution of fossil forms is very uncertain).——Fig. 8,*1a–f.* **L. anatina* Lamarck, Holocene; *a,b,* dorsal valve exterior, both valves lateral view, Moreton Bay, Australia, ×0.8 (Emig, 1982); *c,d,* ventral valve interior, dorsal valve interior, ×0.62; *e,f,* ventral visceral area, dorsal visceral area, Viti Levu, Fiji, USNM 76709, ×1.9 (new).——Fig. 8,*1g,h. L. adamsi* Dall, Holocene, Chihli, China; dorsal, ventral pseudointerarea, RMS Br 137380, ×3.8 (new).

?**Apsilingula** A. J. Williams, 1977, p. 403 [**A. parkesensis;* OD]. Elongate oval with subparallel lateral margins; dorsal and ventral pseudointerareas poorly known; both valves strongly thickened posteriorly, with deeply impressed muscle scars; ventral visceral area extending to midvalve; transmedian scars possibly asymmetrical; ventral *vascula lateralia* strongly convergent, becoming subparallel anteriorly; dorsal visceral area extending anteriorly beyond midvalve, with anterior lateral and central muscle scars widely spaced; dorsal median septum wide, extending from central muscle scars and almost reaching anterior margin; dorsal vascular system unknown. *?Upper Devonian:* Australia (New South Wales).——Fig. 8,*2a,b.* **A. parkesensis,* Mandagery Sandstone, Hervey Group, Parkes; *a,* holotype, latex cast of ventral internal mold, ANU 34486A, ×2.8; *b,* paratype, latex cast of dorsal internal mold, ANU 34486C, ×2.1 (new).

?**Barroisella** Hall & Clarke, 1892, p. 62 [**B. campbelli* Cooper, 1942, p. 228, *nom. nov. pro Lingula subspatulata* Meek & Worthen, 1868, p. 437, *non* Hall & Meek, 1856; OD] [=*Barroisella* Clarke, 1889, p. 43, *nom. nud.*]. Shell elongate oval; ventral pseudointerarea with small but prominent, solid propareas; ventral visceral field extending to midvalve, with V-shaped impression of pedicle nerve possibly passing lateral to poorly impressed, unpaired umbonal muscle scar; ventral transmedian scars apparently asymmetrical; dorsal visceral area extending far anterior to midvalve, bisected by low, broad median ridge, bifurcating near midvalve; second low ridge intercalated between bifurcation, probably bearing anterior lateral muscle scars; ventral *vascula lateralia* submedian, short, converging anteriorly; dorsal *vascula lateralia* subperipheral, parallel in posterior half; *vascula media* apparently absent. *?Upper Devonian, Lower Carboniferous:* USA, Poland.——Fig. 9,*1a–e.* **B. campbelli* Cooper, Barroisella beds, Upper Devonian, Ohio River, New Albany, Indiana; *a,* ventral valve exterior, USNM 459667a, ×6.2; *b,* ventral valve interior, ×6.7; *c,* oblique posterior view of ventral valve interior, USNM 459667b, ×12.5; *d,* dorsal valve interior, ×6.2; *e,* oblique posterior view of dorsal valve interior, USNM 459667b, ×16.7 (new).

Glottidia Dall, 1870, p. 157 [**Lingula albida* Hinds, 1844, p. 71; OD]. Shell strongly elongate; ventral pseudointerarea small, with vestigial propareas and pedicle groove; ventral visceral area extending somewhat anterior to midvalve, with posterolateral margins bounded by two divergent septa, serving as places of attachment for oblique muscles and support of body wall; pedicle nerve curving around unpaired umbonal muscle scar; dorsal visceral area with median septum extending from umbonal to transmedian muscles; mantle canal system with papillae; *vascula media* absent. *?Cretaceous, Tertiary–Holocene:* ?Antarctica, *Cretaceous;* Europe, *Tertiary;* North America, *Tertiary–Holocene;* South America, *Holocene.*——Fig. 9,*2a–c.* **G. albida* (Hinds), Holocene, Anaheim Bay, California; *a,* dorsal valve exterior, ×1.8; *b,c,* ventral, dorsal valve interior, MCZ 4423, ×2.8 (new).

?**Langella** Mendes, 1961, p. 2 [**Lingula imbituvensis* de Oliveira, 1930, p. 18; OD]. Similar to *Barroisella,* but with much shorter dorsal median ridge, and lacking anterior intercalated ridge. *Carboniferous–Permian:* Brazil.——Fig. 10*a,b.* **L. imbituvensis* (Oliveira), Tubarâo Series, Paraná; *a,* ventral internal mold, DNGM 4251, ×6; *b,* dorsal internal mold, DGM 3555, ×6 (Mendes, 1961).

Lingularia Biernat & Emig, 1993, p. 10 [**L. similis;* OD]. Shell elongate oval with subparallel lateral margins; ventral pseudointerarea small, with broad triangular pedicle groove and vestigial propareas; umbonal muscle scar heart-shaped, bisected by impression of pedicle nerve; dorsal visceral area extending anteriorly beyond midlength, with short median ridge bisecting anterior lateral muscle scars,

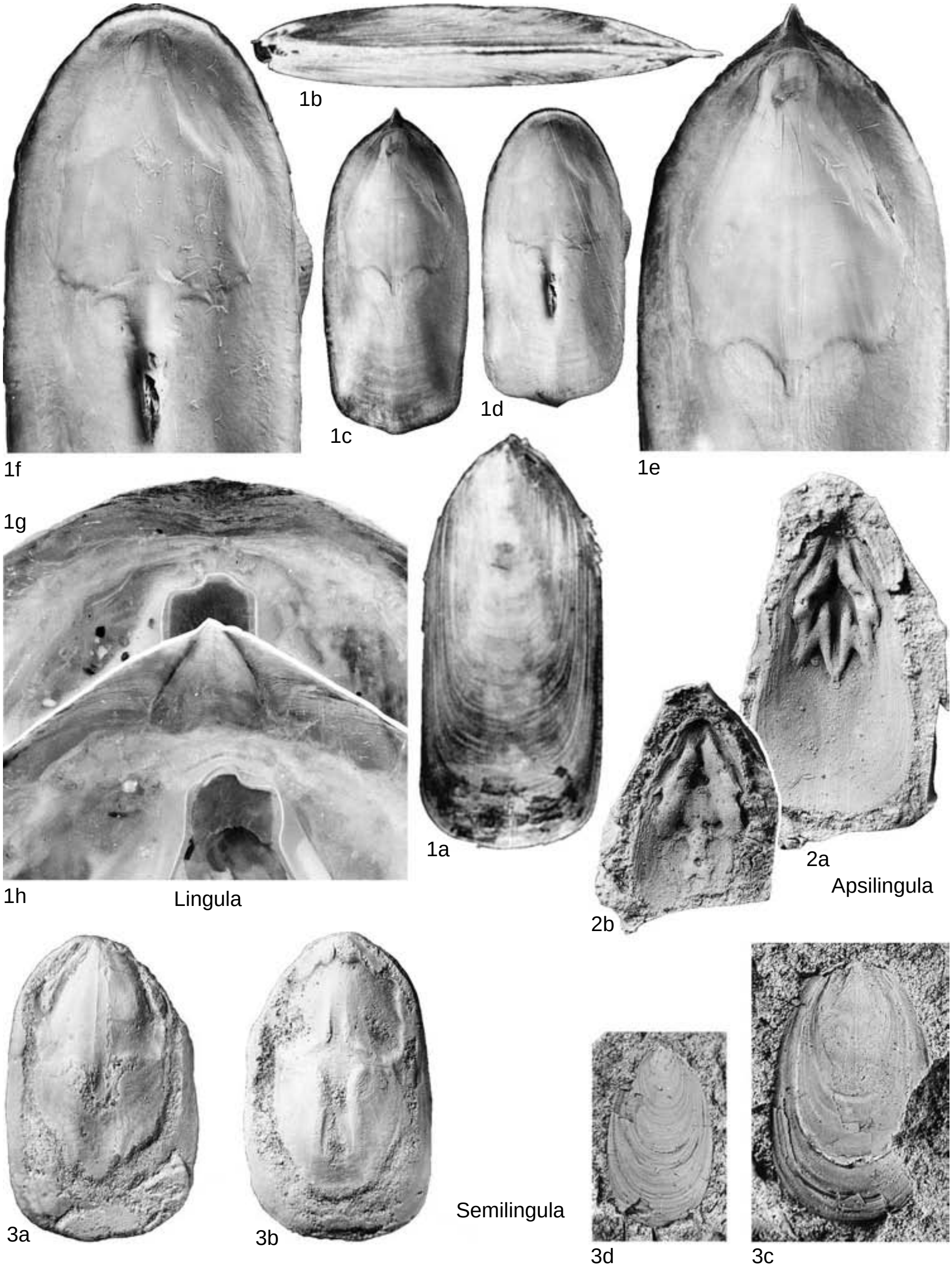

FIG. 8. Lingulidae (p. 36–39).

vascula lateralia in both valves convergent, but generally somewhat shorter in ventral valve. *Carboniferous–Cretaceous, ?Tertiary:* Europe, *Carboniferous–Cretaceous;* North America, *Triassic–Cretaceous;* ?South America, *Cretaceous–Tertiary;* Australia, ?Antarctica, Egypt, Kazakhstan, *Cretaceous;* Bear Island, Spitsbergen, *Triassic–Jurassic;* Russia, ?Japan, New Zealand, northern Siberia, Pakistan, *Triassic.*——FIG. 9,*3a–d.* **L. similis,* Brentskardhaugen beds, Toarcian–Aalenian, Wimanfjellet, Spitsbergen; *a,* holotype, internal mold of dorsal valve, ZPAL Br XXIV/385, ×1.7; *b,* paratype, internal mold of dorsal valve, ZPAL Br XXIV/432, ×2.5; *c,* paratype, internal mold of

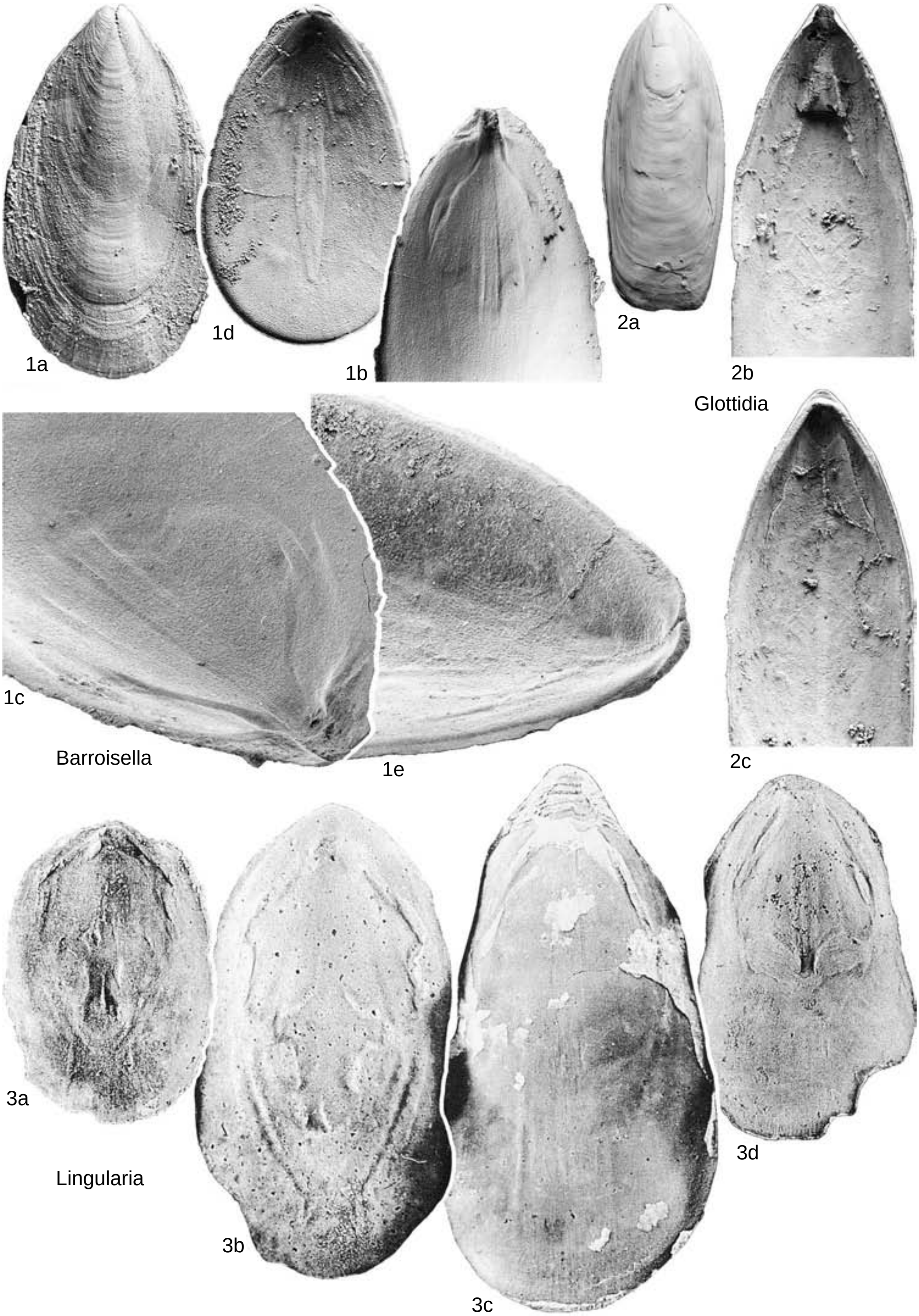

FIG. 9. Lingulidae (p. 36–38).

ventral valve, ZPAL Br XXIV/418, ×2.5; *d,* paratype, internal mold of ventral valve, ZPAL Br XXIV/416, ×2.5 (Biernat & Emig, 1993).

Semilingula POPOV in EGOROV & POPOV, 1990, p. 113 [**Lingula arctica* MILORADOVICH, 1936, p. 37; OD]. Similar to *Lingularia,* but with vestigial dorsal *vas-*

cula media. Permian: Russia (Komi, Novaya Zemlya, Siberia), Australia.——Fig. 8,*3a,b.* **S. arctica* (Miloradovich), Kungurian, Kozhim River, Komi, Russia; ventral, dorsal view of internal mold, CNIGR 3/9644, ×2.5 (Ifanova, 1972).——Fig. 8,*3c,d. S. taimyrensis* (Einor), Lower Permian, Daldyn River, central Siberia, Russia; *c,* internal mold of ventral valve, CNIGR 2/12675, ×2.5; *d,* dorsal valve exterior, CNIGR 7/12675, ×2.5 (Egorov & Popov, 1990).

Family PSEUDOLINGULIDAE Holmer, 1991

[*nom. transl.* Holmer & Popov, herein, *ex* Pseudolingulinae Holmer, 1991a, p. 17]

Shell elongate, subrectangular to elongate subelliptical, subequivalved to equivalved; ventral pseudointerarea with small, triangular propareas lacking flexure lines; dorsal posterior margin thickened, forming reduced, undivided, anacline to catacline pseudointerarea, never extending as plate into valve; both valves with paired umbonal muscle scars; ventral valve with impression of pedicle nerve bisecting umbonal scar; dorsal scars of central and anterior lateral muscles closely spaced; mantle canal system baculate or possibly bifurcate, *vascula lateralia* converging anteriorly; *vascula media* absent. *Ordovician (Llanvirn)–Lower Carboniferous.*

Pseudolingula Mickwitz, 1909, p. 771 [**Crania quadrata* von Eichwald, 1829, p. 273; OD]. Shell elongate subrectangular; ventral pseudointerarea with narrow, deep pedicle groove; ventral visceral area extending anteriorly beyond midvalve; oblique muscle scars placed on broadly divergent ridges; dorsal visceral area bisected by broad median septum, extending from beak to anterior lateral muscle scars; dorsal central and anterior lateral muscle scars placed close together; *vascula lateralia* of both valves short, submedian, slightly converging; *vascula media* absent; inner surface of both valves with conspicuous wrinkling directly lateral to *vascula lateralia. Ordovician (Llanvirn–Ashgill):* North America, Great Britain, Sweden, Estonia, Lithuania, northwestern Russia, Ukraine (Podolia), Kazakhstan.——Fig. 11,*1a–f.* **P. quadrata* (von Eichwald), lower Ashgill, Estonia; *a,b,* ventral internal mold, lateral view of both valves, ×0.6; *c,* anterior part of ventral internal mold showing mantle canals, Hiiumaa Island, RMS Br 135782, ×1.7; *d,e,* interior of dorsal, ventral valve, Hiiumaa Island, RMS Br 65960, ×1.7; *f,* posterior view of both valves, showing pseudointerareas, Lehtse, BMNH B 86354, ×3.3 (new).

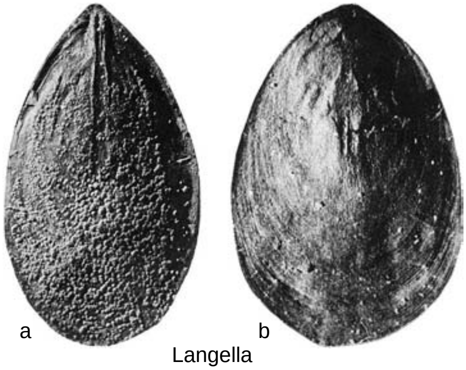

Fig. 10. Lingulidae (p. 36).

Bicarinatina Batrukova, 1969, p. 59 [**Lingula bicarinata* Kutorga, 1837, p. 38; OD [=*Liralingua* Graham, 1970, p. 153 (type, *L. indicis* Graham, 1970)]. Shell subrectangular to elongate subelliptical, ornamented by growth lines or concentric rugellae; both valves with two or three broad, radial replications; ventral pseudointerarea short, with deep, narrow pedicle groove; ventral visceral area large, rhomboidal, extending to midvalve; dorsal visceral area bisected by long median ridge, with wide, semielliptical anterior projection extending anterior to midvalve; central muscle scars large, situated close to anterior lateral muscle scars. *Middle Devonian–Lower Carboniferous:* Estonia, Latvia, Lithuania, northwestern Russia, Scotland, USA (Alaska).——Fig. 11,*2a–d.* **B. bicarinata* (Kutorga), Narova Formation, Eifelian, Pechora and Luga River, northwestern Russia; *a,* ventral valve exterior, RMS Br 136342, ×2.5; *b,* dorsal valve exterior, RMS Br 136343, ×2.5; *c,* internal mold of dorsal valve, ×1.7; *d,* dorsal valve interior, CNIGR 1/6933, ×1.7 (new).

?Tarutiglossa Havlíček, 1984, p. 63 [**T. platyfaba;* OD]. Shell elongate subrectangular with slightly concave anterior margin; ventral pseudointerarea poorly known; dorsal pseudointerarea anacline; ventral visceral area weakly impressed, not extending to midvalve; dorsal visceral field with narrow, anterior projection, extending anteriorly beyond midvalve; dorsal anterior lateral and central muscles closely spaced; mantle canal system unknown. *Devonian (Frasnian–Famennian):* Libya.——Fig. 12,*1a,b.* **T. platyfaba,* Tarut Formation, Famennian, Jabal Fezzan; *a,* holotype, dorsal external mold, ×3.3; *b,* dorsal internal mold, ×5.8 (Havlíček & Röhlich, 1987). [Michal Mergl]

?Wadiglossa Havlíček, 1984, p. 63 [**W. supramarginalis;* OD]. Shell elongate oval, subequivalved; ventral pseudointerarea small, divided by shallow, broadly triangular pedicle groove; dorsal pseudointerarea catacline, poorly defined; ventral visceral area weakly impressed, extending to midvalve, with weak median ridge or pair of slender ridges extending anteriorly beyond visceral field; dorsal visceral area poorly defined, bisected by low median ridge, extending anteriorly beyond midvalve; dorsal central muscles scars large subcircular; ventral mantle canals unknown; dorsal *vascula* *lateralia* submedian, slightly converging. *Devonian (Frasnian)–Lower Carboniferous (Tournaisian):* Libya.——FIG. 12,*2a–c.* **W. supramarginalis; a,* holotype, internal mold of dorsal valve, ×5; *b,* lateral view of *a,* ×6; *c,* internal mold of ventral valve, ×5 (new).——FIG. 12,*2d. W. wadigena* HAVLÍČEK; holotype, internal mold of ventral valve, ×7.5 (new). [MICHAL MERGL]

Family OBOLIDAE King, 1846

[Obolidae KING, 1846, p. 28] [*incl.* Experilingulidae USHATINSKAYA, 1992; Kyrshabaktellidae HOLMER & POPOV, herein, *nom. correct. pro* Kyrshabactellidae USHATINSKAYA, 1992, p. 83]

Shell unequivalved or subequivalved, variable in outline; larval shell smooth; ventral pseudointerarea usually with deep pedicle groove; ventral propareas usually with well-developed flexure lines; dorsal pseudointerarea variably developed; pedicle emerging between valves; muscle system with paired umbonal muscle scars; dorsal visceral area invariably with well-developed, tongue-like, median, anterior projection; mantle canal system baculate with well-developed *vascula media;* ventral *vascula lateralia* usually divergent in posterior half or arcuate, converging anteriorly. An undescribed upper Atdabanian genus in subfamily Obolinae (PELMAN, 1977) extends the stratigraphic range of this family and subfamily. *Lower Cambrian (upper Atdabanian)–Lower Carboniferous.*

Subfamily OBOLINAE King, 1846

[*nom. transl.* DALL, 1870, p. 154, *ex* Obolidae KING, 1846, p. 28] [*incl.* Lingulellinae SCHUCHERT, 1893]

Shell rounded, elongate, suboval to subtriangular, unequivalved; ventral pseudointerarea well developed, raised or continuous with valve floor; dorsal pseudointerarea with median groove or undivided. *Lower Cambrian (upper Atdabanian)–Lower Carboniferous.*

Obolus VON EICHWALD, 1829, p. 274 [**O. apollinis;* SD DAVIDSON, 1853, p. 135] [=*Obulus* QUENSTEDT, 1868, p. 732]. Shell circular to rounded triangular, dorsibiconvex to subequally biconvex; ventral propareas with deep, narrow pedicle groove; dorsal pseudointerarea lacking flexure lines; visceral area of both valves weakly thickened, extending to midvalve; dorsal median ridge vestigial or absent; *vascula lateralia* of both valves submarginal, arcuate. *Middle Cambrian–Ordovician (Tremadoc):* Russia (Ingria), Estonia.——FIG. 13,*1a–d.* **O. apollinis* VON EICHWALD, Tosna Formation, *Cordylodus proavus* Biozone, Lava River, Ingria; *a,* ventral valve exterior, CNIGR 5/12348, ×3.3; *b,* ventral valve interior, TAGI BR 1703, ×3.3; *c,* dorsal valve exterior, CNIGR 8/12348, ×3.3 (Popov & others, 1989); *d,* dorsal valve interior, TAGI BR 1706, ×3.3 (Kaljo & others, 1986).

Agalatassia POPOV & HOLMER, 1994, p. 51 [**A. triangularis;* OD]. Shell elongate triangular, ornamented by fine rugellae, forming zigzag pattern; ventral pseudointerarea small, triangular, with shallow, broadly triangular pedicle groove, and reduced propareas; ventral visceral area subtriangular, slightly thickened anteriorly, extending to midlength; ventral *vascula lateralia* submarginal; dorsal pseudointerarea poorly developed, not raised above valve floor; dorsal umbonal scar undivided, placed on platform; dorsal visceral area with narrow median projection, extending somewhat anterior to midlength; dorsal *vascula lateralia* submarginal and long; *vascula media* long. *Ordovician (lower Arenig):* Kazakhstan (Kendyktas Range).——FIG. 13,*2a–e.* **A. triangularis,* Kendyktas Range, Agalatas River; *a,* ventral valve exterior, Agalatas Formation, RMS Br 135982, ×4.2; *b,* dorsal valve exterior, Kurdai Formation, RMS Br 135977, ×2.5; *c,* ventral internal mold, Kurdai Formation, RMS Br 135974, ×2.5; *d,* dorsal internal mold, Kurdai Formation, RMS Br 135979, ×2.5; *e,* holotype, dorsal valve interior, Agalatas Formation, RMS Br 135982, ×2.5 (Popov & Holmer, 1994).

Aksarinaia KONEVA, 1992, p. 92 [**A. triquetra;* OD]. Shell subtriangular, flatly biconvex; pseudointerareas of both valves with flexure lines; ventral pseudointerarea orthocline with deep, subtriangular pedicle groove and strongly raised, narrow propareas; dorsal pseudointerarea moderately high, with broad median groove and narrow, elevated propareas; dorsal visceral area slightly thickened, extending anterior to midvalve; dorsal *vascula media* marginal, arcuate. *Middle Cambrian:* Kazakhstan (Malyi Karatau), Russia (eastern Siberia).——FIG. 13,*3a–f.* **A. triquetra,* Amgaian, Kyrshabakty River; *a,* ventral valve exterior, ×13.8; *b,* lateral view, ×16.7; *c,* larval shell, RMS Br 136344, ×50; *d,* oblique view of ventral interior, RMS Br 136345, ×75; *e,* dorsal valve interior, ×33.3; *f,* oblique view of dorsal interior, RMS Br 136347, ×66.7 (new).

Anomaloglossa PERCIVAL, 1978, p. 125 [**A. porca;* OD]. Shell elongate oval, slightly unequivalved; ventral pseudointerarea with wide triangular pedicle groove, bisected by low median plication; dorsal pseudointerarea poorly developed and undifferentiated; ventral visceral area with short median ridge in posterior part; dorsal visceral area with weakly defined median ridge. *Ordovician (upper Caradoc–lower Ashgill):* Australia (New South Wales).——FIG. 14,*1a–d.* **A. porca,* Goonumbla Volcanics, Eastonian, New South Wales; *a,* latex cast of ventral internal mold, ×0.8; *b,* ventral pseudointerearea and pedicle groove, MMF 16096, ×2.5; *c,* latex cast of dorsal internal mold, SUP 41483, ×0.8; *d,* latex cast of dorsal internal mold, SUP 62455, ×0.8 (Percival, 1978).

Apatobolus POPOV in NAZAROV & POPOV, 1980, p. 81

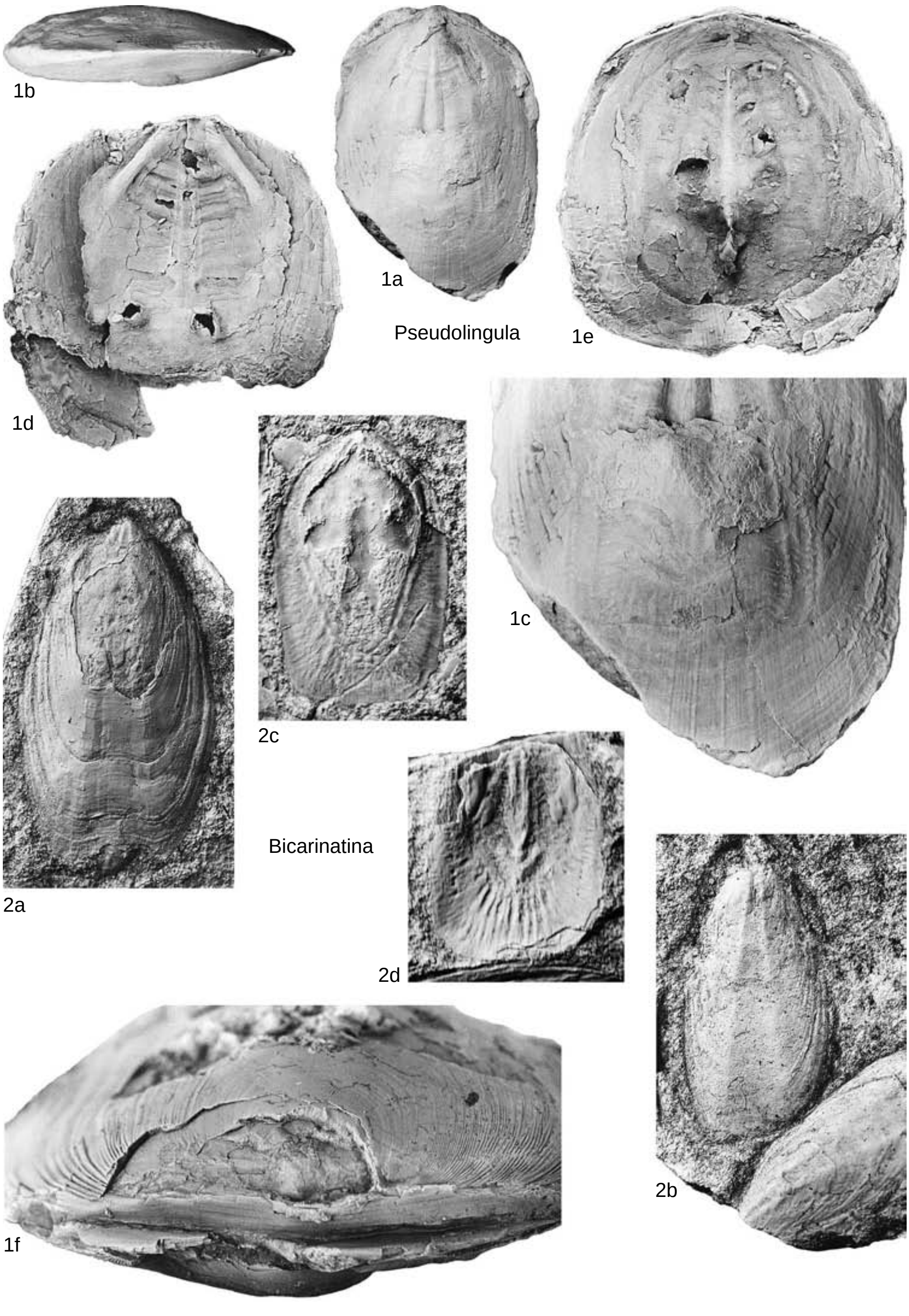

FIG. 11. Pseudolingulidae (p. 39).

[**A. plicatus;* OD] [=*Paldiskites* HAVLÍČEK, 1982, p. 34 (type, *Lingula sulcata* BARRANDE, 1879, pl. 106; OD)]. Shell oval to subcircular, thin shelled, ornamented by growth lines and low irregular radial plications; pseudointerareas of both valves low and short, lacking flexure lines; ventral pseudointerarea

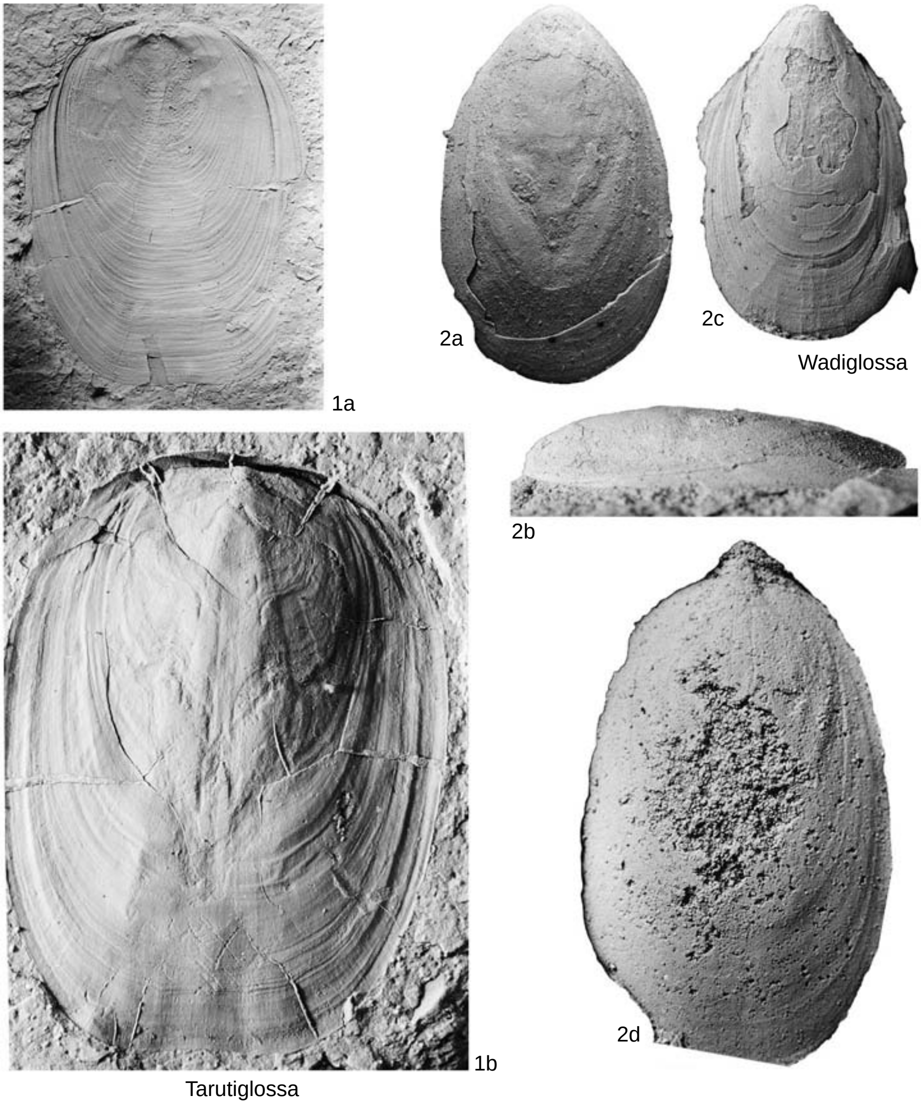

FIG. 12. Pseudolingulidae (p. 39–40).

with shallow pedicle groove; ventral umbonal muscle scars divided by two short, parallel ridges. *Ordovician (Arenig–lower Caradoc):* Kazakhstan, *lower Caradoc;* Bohemia, *Arenig;* Sweden, England, *Llanvirn.*——FIG. 14,*3a–e.* **A. plicatus,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Chingiz Range; *a,* holotype, ventral valve exterior, CNIGR 3/11352, ×4.2; *b,* dorsal valve exterior, CNIGR 7/11352, ×4.2 (Nazarov & Popov, 1980); *c,* dorsal valve interior, ×37.5; *d,* lateral view of dorsal pseudointerarea, RMS Br 136348, ×50; *e,* ventral interior, RMS Br 136349, ×45.8 (new).

Barbatulella WILLIAMS & LOCKLEY, 1983, p. 393 [**B. lacunosa;* OD]. Similar to *Apatobolus,* but lacking radial ornamentation, and with marginal spines; ventral pseudointerarea with well-defined flexure lines. *Ordovician (Ashgill):* Scotland.——FIG. 15,*2a,b.* **B. lacunosa,* upper Hartfell Shale, *Dicellograptus complanatus* Biozone, Dob's Linn; *a,* dorsal valve exterior, ×7; *b,* holotype, detail of lateral commissure with spines, HM 14655, ×14.6 (Williams & Lockley, 1983).

Chakassilingula USHATINSKAYA, 1992, p. 81 [**C. erbiensis;* OD]. Shell subpentagonal, slightly unquivalved; ventral pedicle groove narrow, with well-defined median furrow, bounded laterally by two subparallel plications; ventral propareas strongly raised, with well-defined flexure lines; dor-

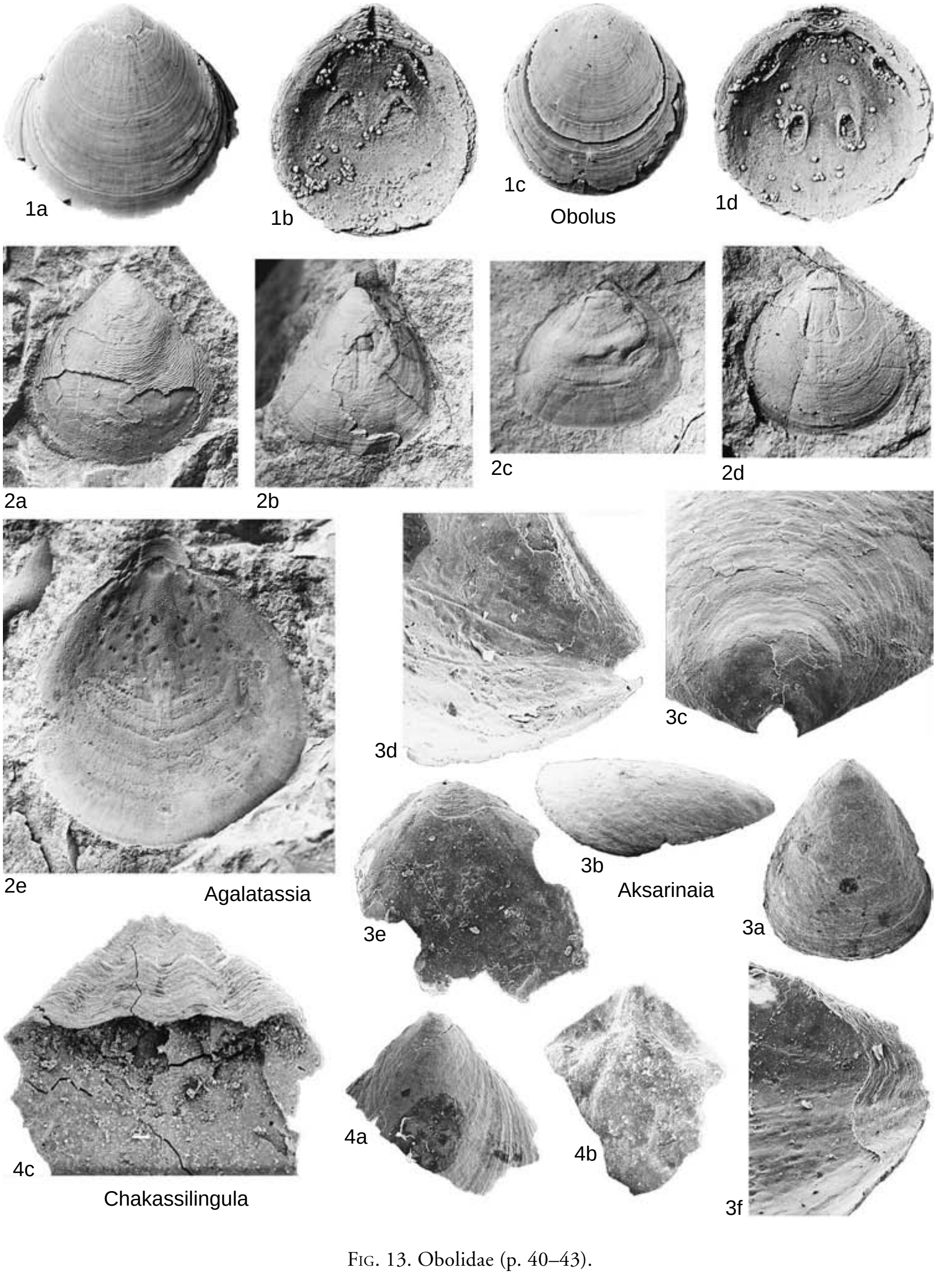

FIG. 13. Obolidae (p. 40–43).

sal pseudointerarea high, subtriangular with two broad, submedian plications; ventral visceral area slightly raised anteriorly, extending to midvalve; dorsal interior with low median ridge. *Middle Cambrian (Amgaian):* Russia (Altai).——FIG. 13,*4a–c.* **C. erbiensis,* Amgaian, *Opistocephalus–Schistocephalus* Biozone, Batenev Ridge, Altai; *a,* ventral valve exterior, PIN 4377/208, ×16.7; *b,* ventral valve interior, PIN 4377/203, ×25; *c,* dorsal valve interior, PIN 4377/210, ×25 (Ushatinskaya, 1992).

Dicellomus HALL, 1871a, p. 3 [**Lingula polita* HALL, 1861a, p. 24; ICZN, 1965a, opinion no. 721]. Shell small, subcircular to subtriangular, unequivalved; ventral pseudointerarea with narrow pedicle groove; dorsal pseudointerarea vestigial; ventral visceral area thickened anteriorly; dorsal anterior

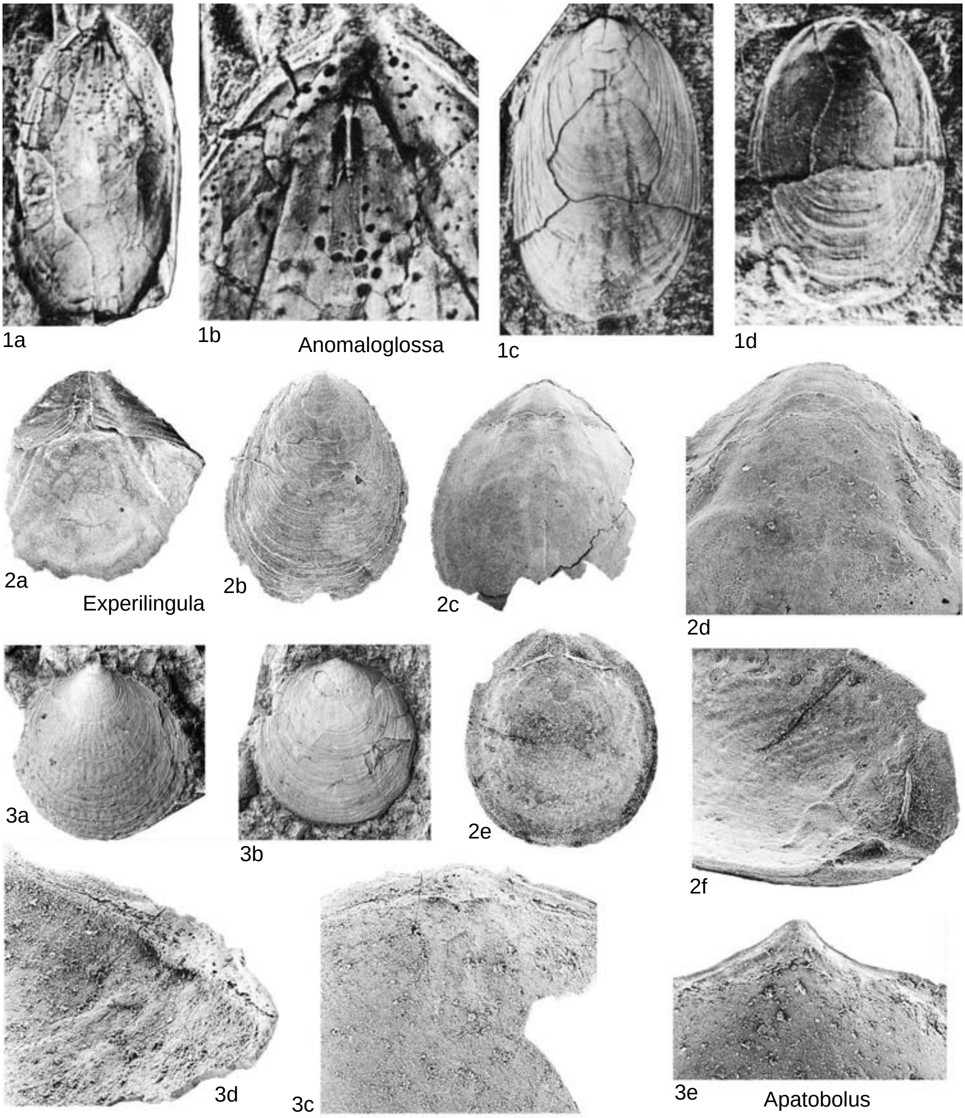

Fig. 14. Obolidae (p. 40–46).

lateral and central muscle scars closely spaced; dorsal visceral area extending slightly anterior to midvalve; ventral *vascula lateralia* submedian, straight and somewhat divergent in posterior half; dorsal *vascula lateralia* subperipheral; dorsal *vascula media* long and divergent. *?Middle Cambrian, Upper Cambrian:* North America, *Cedaria–Crepicephalus* Zones.——Fig. 15,*3a–h. D. ?amblia* Bell, 1944, Gros Ventre Group, Sheridan County, Wyoming; *a,b,* ventral valve exterior, lateral view, USNM 459668a, ×5.4; *c,* dorsal valve exterior, ×6.7; *d,* lateral view of dorsal valve, USNM 459668b, ×8.3; *e,* dorsal valve visceral area with central muscle scars, ×12.5; *f,* dorsal pseudointerarea, ×20.1; *g,* dorsal valve interior, USNM 459668c, ×5.4; *h,* ventral valve interior, USNM 459668d, ×5.4 (new).

Euobolus Mickwitz, 1896, p. 129 [**Obolus (Euobolus) elegans;* SD Popov & Khazanovitch in Popov and others, 1989, p. 102]. Shell subcircular, with parvicostellate radial ornamentation; ventral pseudointerarea with well-defined, narrow, pedicle groove; dorsal valve unknown. *Upper Cambrian:* Estonia, Ingria.——Fig. 15,*4a,b.* **E. elegans* (Mickwitz), Tosna Formation (redeposited), western Ingria (core 190); ventral valve exterior, interior, CNIGR 24/12348, ×12.5 (Popov and others, 1989).

Expellobolus Havlíček, 1982, p. 25 [**Lingula expulsa* Barrande, 1879, pl. 110; OD]. Shell elongate

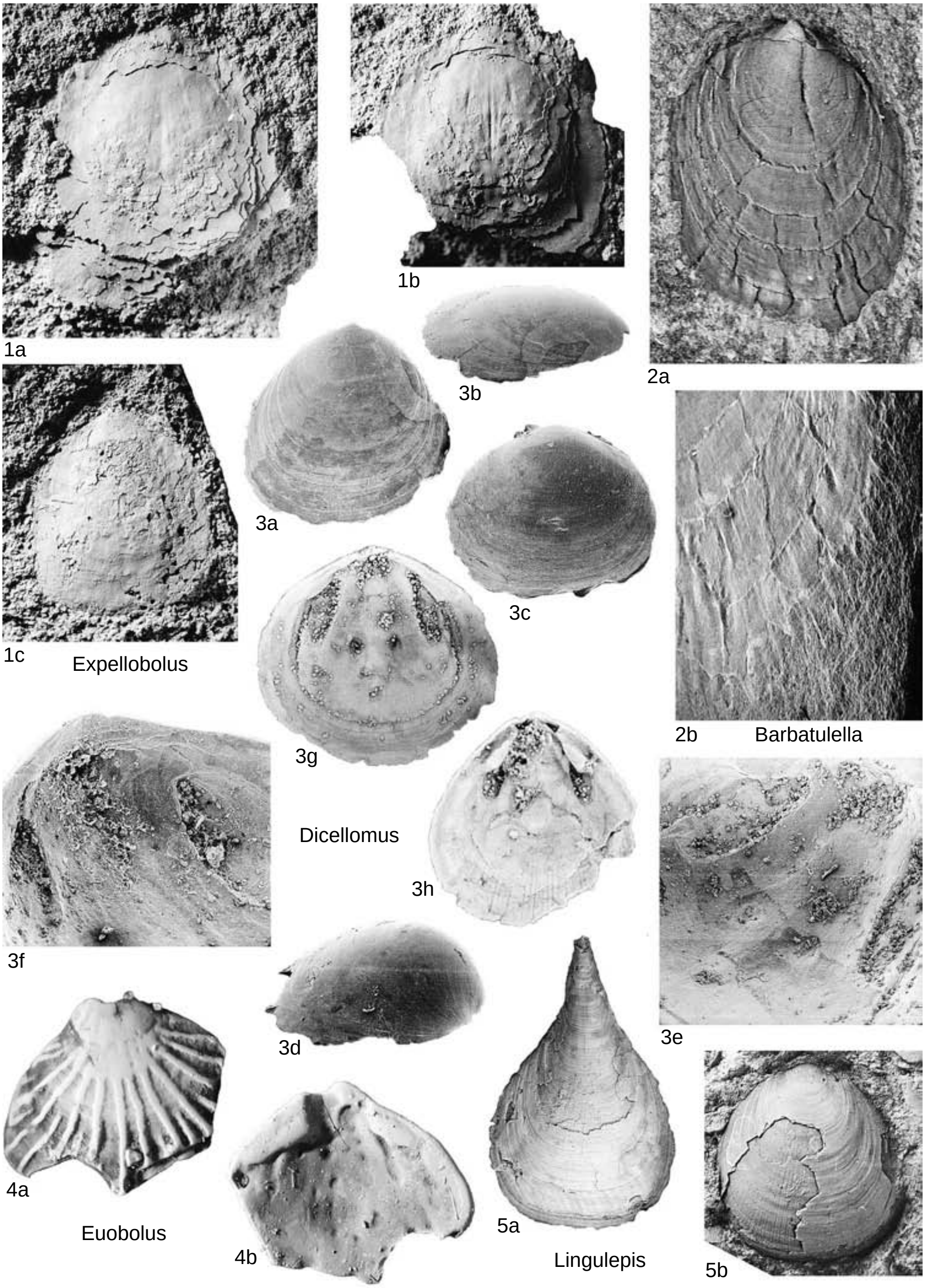

FIG. 15. Obolidae (p. 43–50).

subrectangular; ornamentation with thin, radial capillae; ventral pseudointerarea with narrow, shallow pedicle groove; dorsal pseudointerarea forming crescent-shaped strip along posterior margin; dorsal visceral area narrow, and not extending to midvalve, bisected by low median ridge; dorsal anterior lateral and central muscle scars closely spaced; *vascula lateralia* of both valves submarginal, divergent in posterior half. *Ordovician (Tremadoc–Arening, ?Llanvirn):* Bohemia, *?Tremadoc–lower Arenig;* Wales, *Tremadoc;* ?Baltoscandia, *Arenig–?Llanvirn.*——Fig. 15,*1a–c.* **E. expulsus* (Barrande), Trenice Formation, Bohemia; *a,* ventral internal mold, Krusna hora, OMR VH 3130, ×2.1; *b,* dorsal internal mold, Otrocín, NM L 30790, ×2.1; *c,* dorsal internal mold, Bukov, NM L 28821, ×2.1 (new). [Michal Mergl]

Experilingula Koneva & Popov, 1983, p. 113 [**E. divulgata;* OD]. Shell subequally biconvex, unequivalved, elongate; ventral pseudointerarea apsacline; anteromedian parts of ventral propareas deflected strongly dorsally, to form triangular opening; pedicle groove deep, bounded laterally by ridges, and bisected by narrow furrow; flexure lines well developed in both valves; dorsal pseudointerarea anacline, with concave median groove, elevated above valve floor; ventral visceral area not extending to midlength; dorsal visceral area small, bisected by low median ridge, with narrow anterior projection extending to midlength; dorsal *vascula lateralia* peripherally placed, arcuate; dorsal *vascula media* long, moderately divergent. *Upper Cambrian:* Kazakhstan.——Fig. 14,*2a–d.* **E. divulgata, Rhaptagnostus trisulcus* Biozone, Batyrbay; *a,* ventral valve interior, RMS Br 136350, ×9.2; *b,* dorsal valve exterior, RMS Br 136351, ×11.7; *c,* dorsal valve interior, ×8.3; *d,* detail of dorsal pseudointerarea, RMS Br 136380, ×37.5 (new).——Fig. 14,*2e,f. E.* sp. cf. *E. divulgata* Koneva & Popov, Kujandy Formation, Olenty River; *e,* ventral valve interior, ×10; *f,* oblique lateral view of ventral pseudointerarea, RMS Br 136231, ×19.2 (Holmer & Popov, 1994).

Fordinia Walcott, 1908, p. 64 [**Obolus (Fordinia) perfecta;* OD]. Shell suboval, slightly unequivalved; both valves with shallow sulcus; ventral pseudointerarea lacking flexure lines, with narrow, deep pedicle groove bisected by furrow; dorsal pseudointerarea raised, undivided, flattened; ventral visceral area slightly thickened, extending to midvalve, divided by two broad, divergent ridges; dorsal visceral area slightly thickened, bisected by low median ridge, with narrow, long, anterior projection extending almost to anterior margin; dorsal central muscle scars small; ventral *vascula lateralia* submedian, converging; dorsal *vascula lateralia* submarginal, slightly arcuate. *Middle Cambrian–Upper Cambrian:* North America.——Fig. 16,*1a–e.* **F. perfecta* (Walcott), Weeks Limestone, Middle Cambrian, Weeks Canyon, House Range, Utah; *a,* paratype, ventral valve exterior, USNM 51947b, ×5.8; *b,* paratype, dorsal valve exterior, USNM 51947c, ×5.8; *c,* paratype, dorsal valve interior, USNM 51947d, ×5; *d,* ventral valve visceral area and pseudointerarea, USNM 459669b, ×8.3; *e,* oblique posterior view of ventral pseudointerarea and pedicle groove, USNM 459669b, ×18 (new).

Foveola Gorjansky, 1969, p. 30 [**F. maarduensis;* OD] [=*Faveolla* Popov in Nazarov & Popov, 1980, p. 81]. Shell rounded, unequivalved; thin shelled; postlarval shell coarsely pitted; ventral pseudointerarea with deep, narrow pedicle groove; ventral propareas elevated, lacking flexure lines; ventral and dorsal interior poorly known. *Ordovician (?Tremadoc, Arenig–Llanvirn, ?Llandeilo):* Estonia, *lower Arenig (Paroistodus proteus* Zone*)–upper Llanvirn;* ?Ireland, ?Kazakhstan, *Arenig;* ?USA (Alabama), *?Llandeilo.*——Fig. 17,*1a–d.* **F. maarduensis,* Leetse Formation, Hunneberg, Estonia; *a,* ventral valve exterior, RMS Br 136352, ×3.3 (new); *b,* dorsal valve exterior, Maardu quarry, CNIGR 52/9960, ×2.5 (Gorjansky, 1969); *c,* ventral valve exterior, oblique view, ×41.7; *d,* detail of ornamentation of ventral valve, Keila-Joa, RMS Br 136353, ×100 (new).

?Gorjanskya Tenjakova, 1980, p. 131 [**G. tselinogradica;* OD]. Shell subtriangular to suboval, unequivalved; ventral pseudointerarea elongated, widely triangular with well-developed pedicle groove and flexure lines; dorsal pseudointerarea with narrow median groove, and flexure lines; ventral visceral area thickened anteriorly, rhomboidal in outline, extending to midvalve; dorsal visceral area moderately thickened, bisected by weak median ridge, with long anterior projection extending to midvalve; *vascula lateralia* of both valves marginal, arcuate; *vascula media* long, divergent. *Ordovician (Llanvirn),* central Kazakhstan. No satisfactory material available for illustrations.

Kyrshabaktella Koneva, 1986a, p. 52 [**K. certa;* OD] [=*Kyrshabactella* Ushatinskaya, 1992, p. 83]. Shell elongate oval or suboval, subequally biconvex, slightly unequivalved; ventral beak with large, semicircular emarginature; ventral pseudointerarea with wide, subrectangular pedicle groove and short, raised propareas with flexure lines; dorsal visceral area with wide median ridge in posterior half, and long median projection, extending anterior to midlength; ventral *vascula lateralia* submedian, straight, slightly divergent in posterior half; dorsal *vascula lateralia* submarginal; *vascula media* short, slightly divergent. *Lower Cambrian (Botomian)–Middle Cambrian:* Russia (Siberia, Altai), Kazakhstan (Malyi Karatau), Kirghizia, Australia (Northern Territory).——Fig. 18,*1a–e.* **K. certa,* Aktas Formation, Amgaian, Kyrshabakty River, Kazakhstan; *a,* ventral valve exterior, RMS Br 136354, ×33.3; *b,* ventral valve interior, ×27.1; *c,* posterior oblique view showing emarginature, RMS Br 136355, ×41.7; *d,* dorsal valve exterior, RMS Br 136356, ×23; *e,* dorsal valve interior, RMS Br 136357, ×23 (new).

Leontiella Yadrenkina, 1982, p. 73 [**L. gloriosa;* OD] [=*Khalfinella* Yadrenkina, 1982, p. 211, *obj.*] Similar to *Lingulella,* but with radial, papillose microornamentation, and short, crescent-shaped dorsal pseudointerarea; dorsal visceral field extending anterior to midvalve, bisected by long, broad median ridge. *Ordovician (Llanvirn):* Russia (Siberia).——Fig. 16,*2a–d.* **L. gloriosa,* Guragur Formation, Kulumbe River; *a,* dorsal valve interior, IGiG 712/10, ×1.7; *b,* dorsal valve exterior, IGiG 712/6, ×1.7; *c,* ornamentation of ventral valve, IGiG 712/7, ×6.7; *d,* ventral valve exterior, IGiG 712/13, ×1.7 (Yadrenkina, 1982).

Leptembolon Mickwitz, 1896, p. 130 [**Obolus (Leptembolon) lingulaeformis;* OD]. Shell elongate

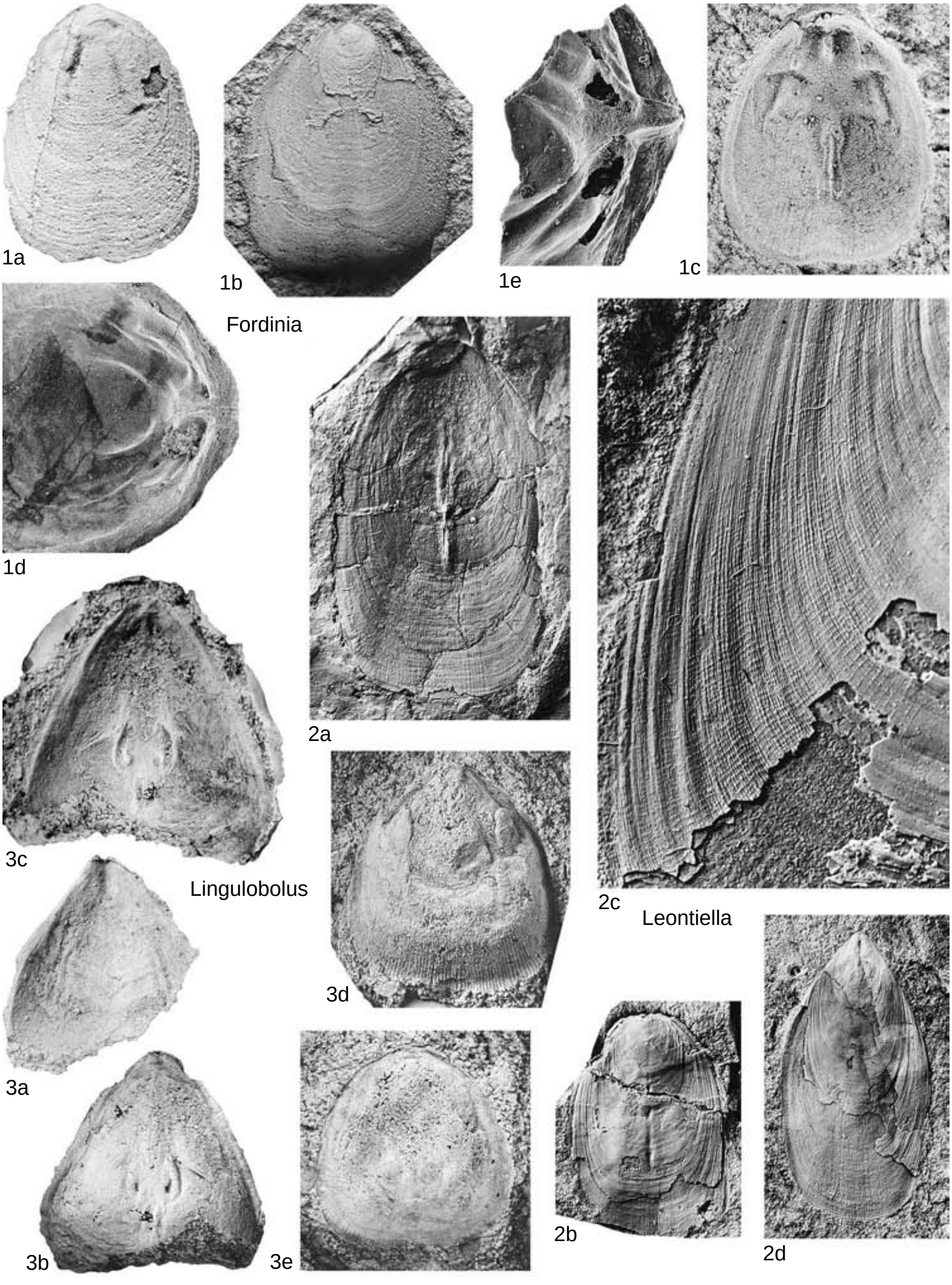

FIG. 16. Obolidae (p. 46–50).

oval to subtriangular, subacuminate; ventral pseudointerarea with narrow, triangular pedicle groove and well-defined flexure lines; ventral visceral area thickened anteriorly, rhomboidal, extending to midvalve; dorsal visceral area slightly thickened anteriorly, bisected by low median ridge, with long, anterior projection, extending close to anterior margin; *vascula lateralia* of both valves submarginal and slightly arcuate. *Ordovician (?Tremadoc, Arenig):* Bohemia, Poland, Estonia, Russia (Ingria, Southern Urals).——FIG. 18,*3a–d*. **L. lingulaeformis* (MICKWITZ), Leetse Formation, lower Arenig

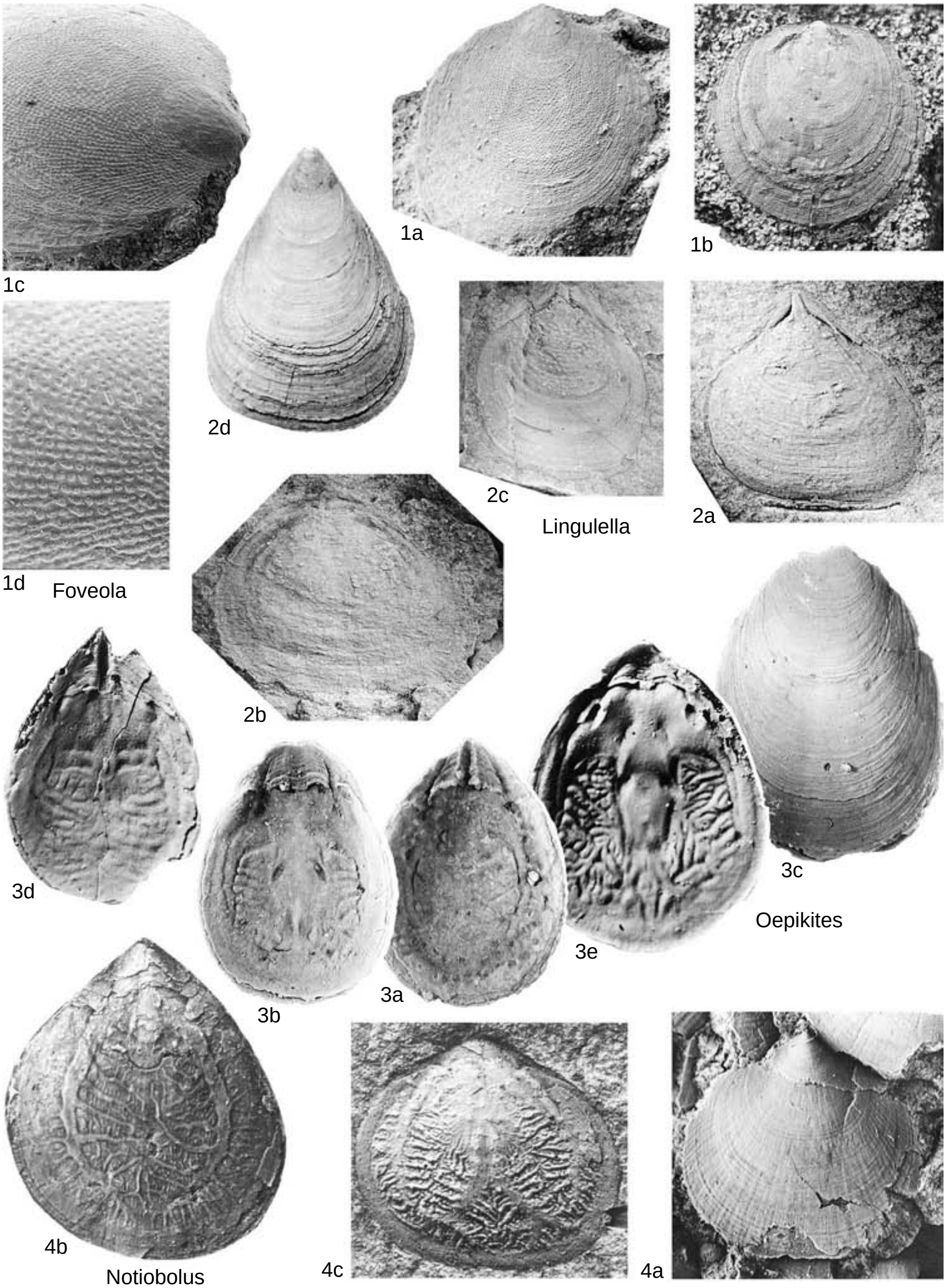

FIG. 17. Obolidae (p. 46–50).

(*Paroistodus proteus* Zone), Estonia; *a,* ventral valve exterior, RMS Br 136258, ×2; *b,* ventral valve interior, Iru, TAGI BR 3505, ×1.7; *c,* dorsal valve exterior, RMS Br 136359, ×1.7; *d,* dorsal valve interior, Leetse, TAGI BR 3506, ×2.1 (new).

Lindinella MERGL & ŠLEHOFEROVÁ, 1990, p. 74 [**L. kordulei;* OD]. Shell strongly acuminate, equivalved, with ornamentation of pronounced rugae that become coalescent laterally; ventral pseudointerarea long with prominent flexure lines and

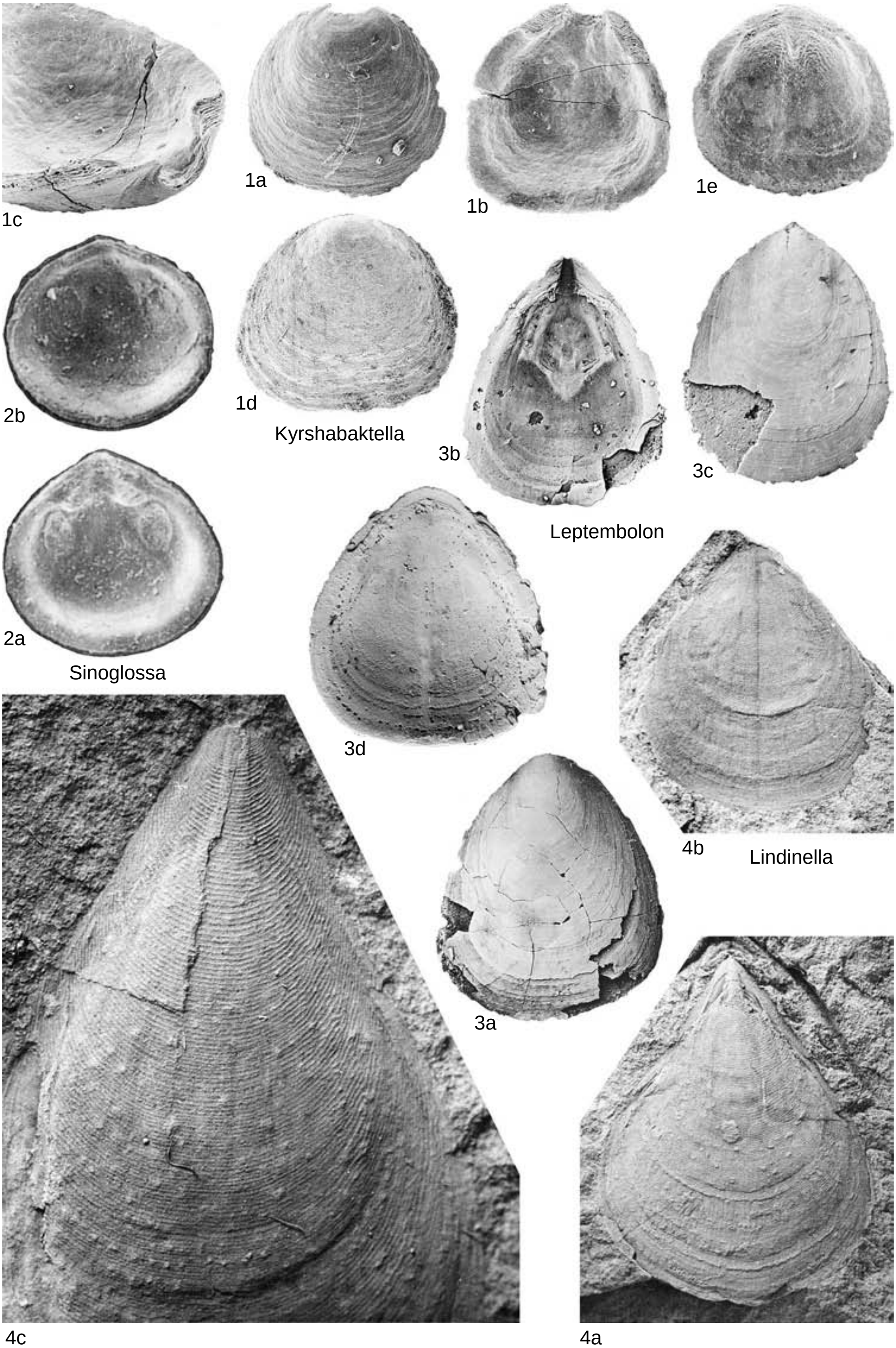

FIG. 18. Obolidae (p. 46–52).

deep, narrow pedicle groove; dorsal interior with fine, long median septum, extending almost to anterior margin; dorsal visceral area extending anterior to midvalve. _?upper Lower Cambrian, Middle Cambrian:_ Bohemia, ?Sweden.——Fig. 18,_4a–c._ *_L. kordulei,_ Jince Formation, Brdy Mountains; _a,_ paratype, ventral composite mold, GS YA 1285, ×3.2; _b,_ paratype, dorsal composite mold, GS YA 1290, ×3.2; _c,_ holotype, latex cast of ventral exterior, GS YA 1290, ×8.3 (Mergl & Šlehoferová, 1990). [Michal Mergl]

Lingulella Salter, 1866, p. 333 [*_Lingula davisii_ M'Coy, 1851, p. 405; SD Dall, 1870, p. 159]. Shell elongate oval to subtriangular, thin shelled, subacuminate; ventral pseudointerarea with narrow, triangular pedicle groove; ventral propareas with well-defined flexure lines; visceral areas of both valves weakly impressed; dorsal visceral area with low median ridge, extending anterior to midvalve; anterior lateral and central muscle scars closely spaced; _vascula lateralia_ peripherally placed. _Upper Cambrian–Ordovician:_ ?cosmopolitan (exact stratigraphic and geographic range very uncertain at present).——Fig. 17,_2a–c._ *_L. davisii_ (M'Coy), Lingula Flags, Merioneth Series, northern Wales; _a,_ ventral internal mold, USNM 51740b, ×2.1; _b,_ dorsal internal mold, USNM 51740d, ×2.1; _c,_ ventral internal mold, NMW 24.479.G9, ×1.7 (new).——Fig. 17,_2d. L. antiquissima_ (Jeremejew), Tosna Formation, _Cordylodus proavus_ Biozone, Syas River, Ingria; ventral valve exterior, neotype, CNIGR 180/12348, ×2.5 (Popov & others, 1989).

Lingulepis Hall, 1863c, p. 129 [*_Lingula pinnaformis_ Owen, 1852, p. 583; SD Dall, 1870, p. 161]. Shell strongly acuminate, subtriangular, unequivalved; ventral beak strongly elongate; pseudointerarea elongate triangular, with narrow pedicle groove and flexure lines; dorsal pseudointerarea poorly known; ventral visceral area short, not extending to midvalve; dorsal visceral area slightly thickened, extending to midvalve, bisected by two divergent ridges; ventral _vascula lateralia_ strongly arcuate. _Middle Cambrian–Upper Cambrian, ?Ordovician:_ North America, ?Europe, Greenland, Siberia, ?China (exact stratigraphic and geographic range quite uncertain at present).——Fig. 15,_5a,b._ *_L. pinnaformis_ (Owen); Upper Cambrian, Wisconsin; _a,_ ventral valve exterior, USNM 51888d, ×2.3; _b,_ dorsal valve exterior, AMNH 39076 B, ×2.3 (new).

Lingulobolus Matthew, 1895, p. 260 [*_?Lingulella affinis_ Billings, 1872, p. 468; OD] [=_Sphaerobolus_ Matthew, 1895, p. 263 (type, _?Lingulella spissa_ Billings, 1872, p. 468)]. Shell subtriangular, strongly biconvex, with radial ornamentation of fine striae; ventral pseudointerarea narrow, subtriangular with broadly triangular pedicle groove; dorsal pseudointerarea vestigial, undivided; ventral visceral area slightly thickened anteriorly; dorsal visceral area weakly defined, extending anterior to midlength; dorsal anterior lateral and central muscle scars closely spaced; ventral _vascula lateralia_ straight, subperipheral, divergent proximally; dorsal _vascula lateralia_ peripheral, arcuate. _Lower Ordovician:_ Canada (Newfoundland), ?Europe (France, Great Britain), ?North Africa (Algeria).——Fig. 16,_3a–c._ *_L. affinis_ (Billings), Bell Island Group, Bell Island, Conception Bay, Newfoundland; _a,_ latex cast of ventral internal mold, USNM 51673b, ×1.2; _b,_ dorsal internal mold, ×1; _c,_ latex cast of dorsal internal mold, USNM 51679a, ×1.2 (new).——Fig. 16,_3d,e. L. spissus_ (Billings), Bell Island Group, Bell Island, Conception Bay, Newfoundland; _d,_ ventral internal mold, USNM 51679k, ×1.7; _e,_ dorsal internal mold, USNM 51678e, ×1.5 (new).

Notiobolus Popov in Popov & Soloviev, 1981, p. 67 [*_N. tenuis;_ OD]. Shell rounded to subtriangular, thin-shelled, unequivalved; pseudointerareas of both valves with flexure lines; ventral pseudointerarea with flattened propareas and deep, narrow pedicle groove; ventral visceral area subtriangular, not extending to midvalve; dorsal visceral area bisected by low median ridge, bounded laterally by two ridges, with anterior projection extending slightly anterior to midvalve; _vascula lateralia_ of both valves peripheral, arcuate; _vascula media_ long, widely divergent. _Middle Cambrian:_ Antarctica.——Fig. 17,_4a–c._ *_N. tenuis,_ erratic boulder, Middle Cambrian, Shackleton Range; _a,_ ventral valve exterior, RMS Br 136360, ×3.8 (new); _b,_ ventral internal mold, CNIGR 26/11378, ×4.2; _c,_ holotype, dorsal internal mold, CNIGR 25/11378, ×4.2 (Popov & Soloviev, 1981).

Oepikites Khazanovitch & Popov in Khazanovich, Popov, & Melnikova, 1984, p. 40 [*_O. macilentus;_ OD]. Shell subacuminate, elongate oval to subtriangular, unequivalved; propareas of both valves high, with well-defined flexure lines; visceral areas of both valves slightly thickened, bisected by short median ridge, with long anterior projection; _vascula lateralia_ of both valves submarginal, arcuate; _vascula media_ short, divergent. _Middle Cambrian–Upper Cambrian:_ Estonia, Russia (Ingria, Moscow basin, Altai), Sweden, ?USA (Texas).——Fig. 17,_3a–c._ *_O. macilentus,_ Sablinka Formation, Middle Cambrian, Ingria; _a,_ ventral valve interior, Sarya River, CNIGR 61/12348, ×6.7; _b,_ dorsal valve interior, Sarya River, CNIGR 62/12348, ×6.7; _c,_ dorsal valve exterior, Tosna River, CNIGR 58/12348, ×6.7 (Popov & others, 1989).——Fig. 17,_3d,e. O. triquetrus_ Popov & Khazanovitch, Ladoga Formation, Upper Cambrian, Syas River, Ingria; _d,_ ventral valve interior, CNIGR 67/12348, ×5; _e,_ holotype, dorsal valve interior, CNIGR 72/12348, ×6.7 (Popov & others, 1989).

Palaeobolus Matthew, 1899, p. 201 [*_P. bretonensis;_ OD] [=_?Obolopsis_ Saito, 1936, p. 349 (type, _O. margaritae;_ OD)]. Externally similar to _Notiobolus,_ but with more strongly developed concentric ornamentation; both valves lacking lateral ridges; both valves with almost parallel, submedian _vascula lateralia. Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):_ Canada (Nova Scotia), Kazakhstan (Malyi Karatau Range), China, ?Korea.——Fig. 19,_2a–c._ *_P. bretonensis,_ Bourinot Group, Cape Breton, Canada; _a,_ ventral valve exterior, USNM 51664a, ×2.2; _b,_ partly exfoliated dorsal valve, USNM 51664b, ×2.1; _c,_ partly exfoliated ventral valve, ROM CM (A), ×2.2 (new).

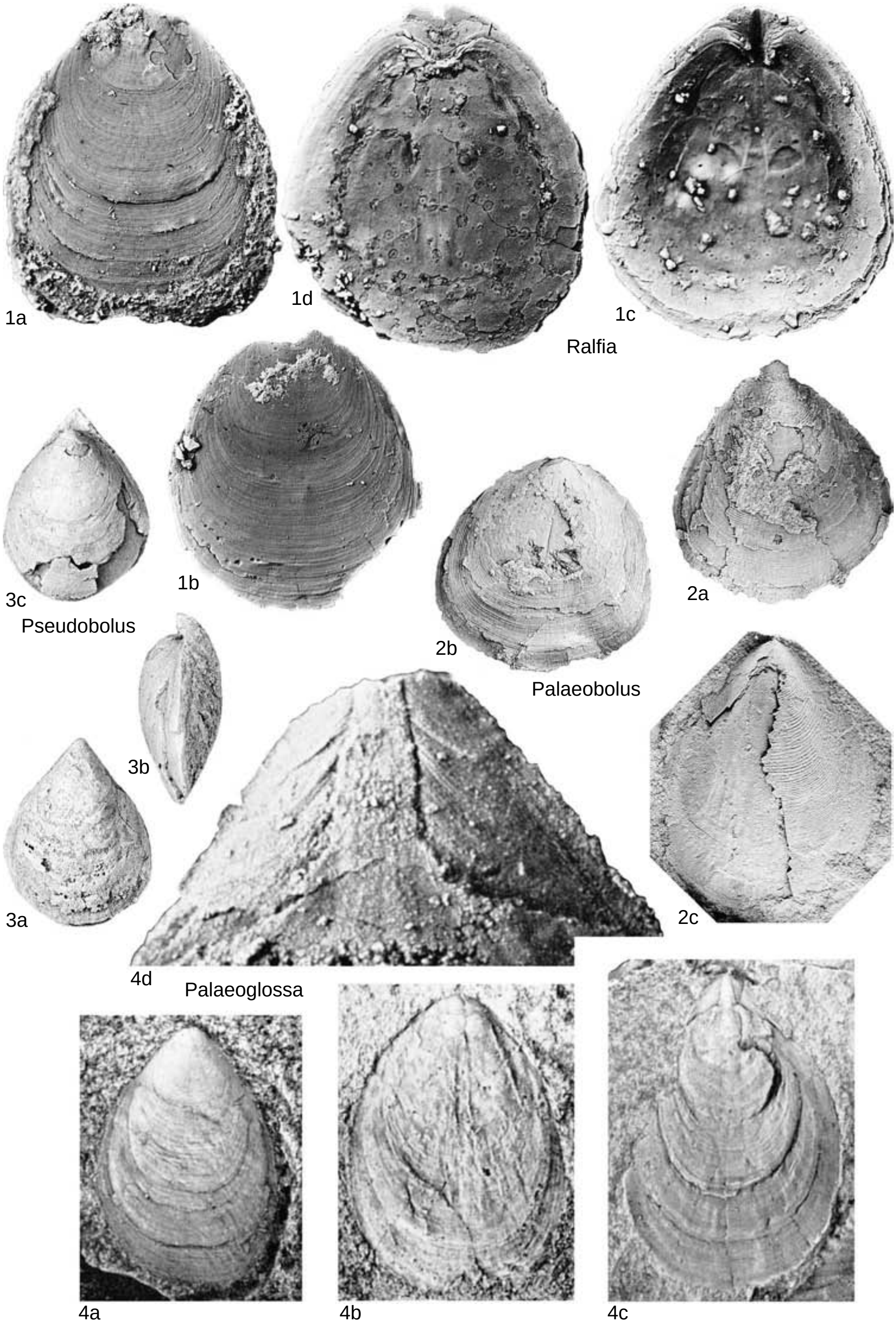

FIG. 19. Obolidae (p. 50–52).

Palaeoglossa COCKERELL, 1911, p. 96, *nom. nov. pro Glossina* PHILLIPS, 1848, p. 370, *non* WIEDEMANN, 1830 [**Lingula attenuata* SOWERBY in MURCHISON, 1839, p. 641; OD] [=*Palaeoglossina* DUNBAR & CONDRA, 1932, p. 35]. Similar to *Lingulella,* but with oval more biconvex and elongate. May be junior synonym of *Lingulella. Ordovician (upper Tremadoc–Caradoc):* Great Britain, *Arenig–Caradoc;* USA, *Llanvirn–Caradoc;* Bohemia, *?Upper Tremadoc–Caradoc;* Russia, Southern Urals, *upper Tremadoc.*——FIG. 19,*4a–d.* **P. attenuata* (SOWERBY), Meadowtown Beds, Llandeilo, Lower Wood Brook, Shropshire, Great Britain; *a,* ventral valve exterior, latex cast, BMNH BB 37112, ×3.8; *b,* dorsal valve internal mold, BMNH BB 37118b, ×3; *c,* ventral valve internal mold, BMNH BB 37115, ×2.3; *d,* detail of ventral pseudointerarea, BMNH BB 37111a, ×14.4 (Williams, 1974).

Palaeoschmidtites KONEVA, 1979, p. 35 [**P. minimus;* OD]. Shell small, elongate oval, slightly unequivalved; ventral pseudointerarea with broad, subtriangular pedicle groove; dorsal pseudointerarea with wide median groove, and reduced propareas; ventral visceral area slightly thickened anteriorly, extending to midvalve; dorsal visceral area completely bisected by long median ridge, with anterior projection extending slightly anterior to midvalve; ventral *vascula lateralia* submedian, straight, and slightly divergent in posterior half; dorsal *vascula lateralia* submarginal, arcuate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* Kazakhstan, Australia, Canada, Yukon. No satisfactory material available for illustration.

Pseudobolus COOPER, 1956, p. 194 [**Palaeoglossa gibbosa* WILLARD, 1928, p. 256; OD]. Shell oval, dorsibiconvex; ventral pseudointerarea anacline; ventral beak incurved; interior characters unknown. *Ordovician (Llandeilo–Caradoc):* USA (Virginia).——FIG. 19,*3a–c.* **P. gibbosus* (WILLARD), Murat Formation, Virginia; pedicle, ventral exterior, both valves lateral, brachial ventral exterior, USNM 109422a, ×2 (Cooper, 1956).

Ralfia POPOV & KHAZANOVITCH in POPOV & others, 1989, p. 126 [**Ungula ovata* PANDER, 1830, p. 59; OD]. Shell triangular, rounded, subequivalved; ventral pseudointerarea small, rhomboidal, with narrow, deep pedicle groove and subparallel flexure lines; dorsal pseudointerarea reduced, rhomboidal; ventral visceral area slightly thickened, extending to midvalve; dorsal visceral area with long median projection extending anterior to midlength; ventral *vascula lateralia* subparallel, submarginal; dorsal *vascula media* short, divergent. *Upper Cambrian, ?Ordovician (Tremadoc):* Russia, Ingria, *Upper Cambrian;* ?Sweden, *Tremadoc.*——FIG. 19,*1a–d.* **R. ovata* (PANDER), Ladoga Formation, Izhora River, Ingria; *a,* ventral valve exterior, CNIGR 206/12348, ×6.7; *b,* dorsal valve exterior, CNIGR 202/12348, ×6.7; *c,* ventral valve interior, holotype, CNIGR 203/12348, ×6.7; *d,* dorsal valve interior, CNIGR 203/12348, ×6.7 (Popov & others, 1989).

Rebrovia POPOV & KHAZANOVITCH in POPOV & others, 1989, p. 112 [**R. chernetskae;* OD]. Shell acuminate, elongate oval to subtriangular, subequibiconvex, unequivalved; ornamentation of fine undulating rugae; pseudointerareas of both valves lacking flexure lines; ventral pseudointerarea with narrow pedicle groove, bounded laterally by low ridges; dorsal pseudointerarea undivided; dorsal visceral area with narrow anterior projection extending anterior to midvalve; *vascula lateralia* of both valves marginal, slightly divergent in posterior half; dorsal *vascula media* short, slightly divergent to subparallel. *Upper Cambrian:* Estonia, Russia (Ingria, White Sea).——FIG. 20,*2a–e.* **R. chernetskae,* Ladoga Formation, Syas River, Ingria; *a,* holotype, dorsal valve exterior, CNIGR 85/12348, ×12.5 (Popov & others, 1989); *b,* ventral valve interior, ×18; *c,* oblique lateral view of ventral pseudointerarea, ×23, RMS Br 136361 (new); *d,* dorsal valve interior, CNIGR 84/12348, ×8.3 (Popov & others, 1989); *e,* detail of ornamentation, RMS Br 136363, ×100 (new).

Schmidtites SCHUCHERT & LEVENE, 1929, p. 121, *nom. nov. pro Schmidtia* VON VOLBORTH, 1869, p. 208, *non* BALSAMO-CRIVELLI, 1863 [**Schmidtia celata* VON VOLBORTH, 1869, p. 209; OD]. Shell elongate oval or subtriangular, ventribiconvex, thick-shelled; ventral pseudointerarea with deep narrow pedicle groove; ventral propareas elevated, slightly concave, with flexure lines; dorsal pseudointerareas with concave median groove and reduced, elevated propareas; visceral areas of both valves thickened; shallow heart-shaped depression in ventral valve; dorsal visceral area with long median projection bisected by low median ridge; *vascula lateralia* of both valves subparallel, marginally; dorsal *vascula media* short, widely divergent. *Upper Cambrian:* Estonia, Russia (Ingria), Sweden.——FIG. 20,*4a–c.* **S. celatus* (VON VOLBORTH), *Cordylodus andresi* Biozone, Turjekelder Rivulet, Estonia; *a,* ventral valve exterior (covered by the encrusting problematic *Marcusodictyon priscum* (BASSLER), TAGI BR 1711, ×6.7; *b,* ventral valve interior, TAGI BR 1709, ×6.7 (Kaljo & others, 1986); *c,* dorsal valve interior, CNIGR 98/12348, ×6.7 (Popov & others, 1989).

?Sinoglossa MEI, 1993, p. 415 [**S. amygdalina;* OD]. Shell small, subcircular; ventral pseudointerarea high, triangular; ventral propareas with pair of deep, oblique grooves; posterolateral muscle fields in both valves large, ovoid; ventral *vascula lateralia* submedian, widely divergent in proximal part; dorsal visceral area with weak median ridge. *Middle Cambrian–Upper Cambrian:* northern China (Hebei).——FIG. 18,*2a,b.* **S. amygdalina,* Zhangxia Formation, Middle Cambrian, Wanxian County; *a,* holotype, ventral valve interior, MCMB 91063, ×30; *b,* paratype, dorsal valve interior, MCMB 91064, ×30 (Mei, 1993).

Spinilingula COOPER, 1956, p. 210 [**S. intralamellata;* OD]. Outline and internal morphology similar to *Lingulella,* but with lamellose ornamention with short prone spines along anterior edge of lamellae. *Ordovician (upper Arenig–Llandeilo):* USA (Alabama, Nevada), Sweden, Kazakhstan.——FIG. 20,*1a–f.* **S. intralamellata,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* holotype, dorsal

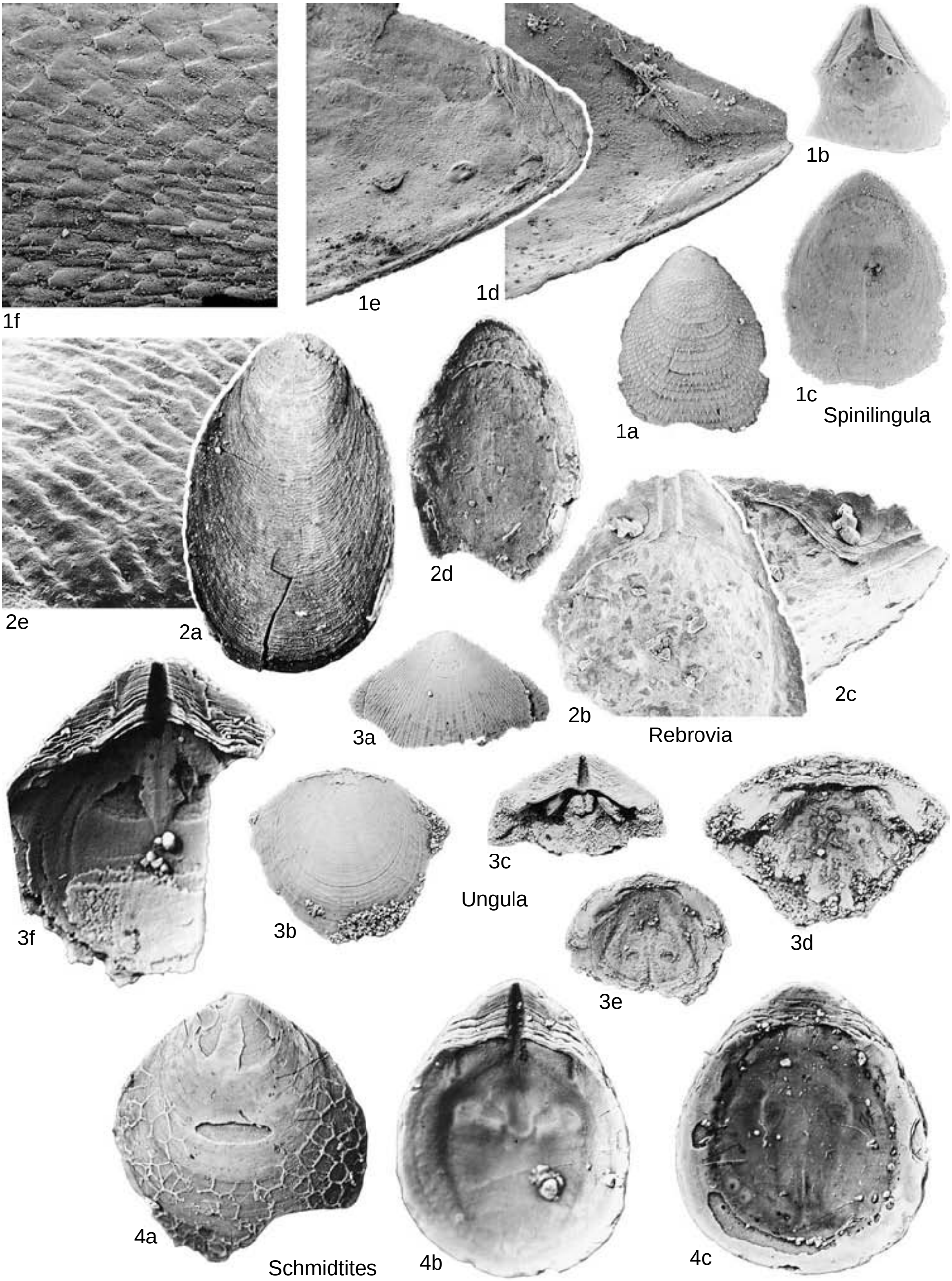

FIG. 20. Obolidae (p. 52–54).

valve exterior, USNM 116784a, ×8.3; *b,* paratype, ventral valve interior, USNM 116784f, ×8.3; *c,* paratype, dorsal valve interior, USNM 116784h, ×8.3 (Cooper, 1956); *d,* oblique lateral view of ventral pseudointerarea, USNM 459670a, ×23.3; *e,* oblique lateral view of dorsal pseudointerarea, USNM 459670b, ×18.3; *f,* detail of ornamentation, USNM 459670c, ×41.7 (new).

?Squamilingulella Xu, 1978, p. 284 [**S. zhonghuaensis;* OD]. Shell elongate oval, with distinctive ornamentation forming chevron pattern; ventral beak somewhat acute; pseudointerareas and internal characters of both valves inadequately known. *Ordovician (Tremadoc):* southern China.

Trigonoglossa DUNBAR & CONDRA, 1932, p. 35 [**Lingula nebrascensis* MEEK, 1872a, p. 158; OD]. Shell elongate triangular, ornamented by strongly raised rugae, separated by broad flat interspaces; dorsal pseudointerarea well developed, undivided; dorsal visceral area with broad anterior projection, extending close to the anterior margin, and bisected by long median ridge; large, elongate, suboval central muscle scars placed in the middle of valve, anterior lateral muscle scars placed close to the anterior valve margin; dorsal *vascula lateralia* subperipheral, subparallel; *vascula media* very short, subparallel. *?Silurian, Lower Carboniferous:* North America, Great Britain, *Lower Carboniferous;* ?Estonia, *Silurian.*——FIG. 21,*3a.* **T. nebrascensis* (MEEK), Graham, Texas; ventral valve exterior, USNM 459673, ×1.4 (Rowell, 1965a).——FIG. 21,*3b,c. T. spatiosa* (HALL), Milesbury, Pennsylvania, USNM 459672; *b,* latex cast of dorsal external mold, ×1.7; *c,* latex cast of dorsal internal mold, ×1.7 (new).

Ungula PANDER, 1830, p. 57 [**U. convexa;* SD ROWELL, 1965a, p. 266] [=*Ungulites* QUENSTEDT, 1837, p. 143]. Shell dorsibiconvex, subcircular to suboval; smooth or with concentric rugae; posterior half of shell strongly thickened; pseudointerareas of both valves with flexure lines; ventral pseudointerarea with narrow, deep pedicle groove, which may be sealed in adults; dorsal pseudointerarea wide, with somewhat concave median groove, elevated above valve floor; ventral visceral area elevated anteriorly, forming low platform with heart-shaped, median depression; dorsal visceral area slightly thickened; ventral and dorsal *vascula lateralia* arcuate, peripherally placed; dorsal *vascula media* short, widely divergent. *Upper Cambrian:* Estonia, Lithuania, Russia (Ingria), Sweden.——FIG. 20,*3a–f.* **U. convexa,* Ladoga Formation, Ingria; *a,* ventral valve exterior, CNIGR 128/12348, ×2.5; *b,* dorsal valve exterior, CNIGR 120/12348, ×2.5; *c,* ventral valve interior, CNIGR 137/12348, ×1.7; *d,* dorsal valve interior, CNIGR 118/12348, ×2.5; *e,* dorsal valve interior of juvenile, Izhora River, CNIGR 129/12348, ×2.5; *f,* ventral valve interior, Lava River, CNIGR 114/12348, ×3.3 (Popov & others, 1989).

Westonia WALCOTT, 1901, p. 683 [**Lingula aurora* HALL, 1861a, p. 24; OD]. Shell elongate suboval to subtriangular, gently biconvex, unequivalved, ornamented by fine, concentric growth lines crossed by irregular, transverse lines, forming zigzag lines in posterior half of valve; ventral pseudointerarea with narrow, triangular pedicle groove and slightly elevated propareas with flexure lines; dorsal pseudointerarea with flexure lines and median groove; visceral areas weakly impressed in both valves; dorsal visceral area with median projection extending anterior to midlength; dorsal central and anterior lateral muscle scars widely spaced; dorsal median ridge variably developed; *vascula lateralia* in both valves submarginal, arcuate. *Middle Cambrian–Upper Cambrian:* Canada, USA, Russia, Spain, China, Australia.——FIG. 21,*1a–d.* **W. aurora* (HALL), St. Croix Sandstone, Upper Cambrian, Wisconsin; *a,* latex cast of ventral internal mold, USNM 51681c, ×1.7; *b,* ventral internal mold, USNM 51681a, ×1.7; *c,* latex cast of dorsal external mold, USNM 51681d, ×1.7 (new); *d,* detail of ornamentation of external mold of ventral valve, USNM 459674, ×8.3 (Savazzi, 1986).

?Westonisca HAVLÍČEK, 1982, p. 28 [**Lingula lamellosa* BARRANDE, 1879, pl. 106; OD]. Shell equally biconvex or slightly dorsibiconvex, elongate oval; ornamentation by concentric rugae, crossed by irregular, transverse lines, forming irregular zigzag lines; ventral pseudointerarea apsacline, lacking flexure lines, with shallow pedicle groove; dorsal pseudointerarea crescent shaped, forming narrow strip along posterior margin; ventral visceral area short, rhomboidal, not extending to midvalve; dorsal visceral area with long anterior projection, extending almost to anterior margin; ventral *vascula lateralia* submedian, arcuate; dorsal *vascula lateralia* subperipheral, subparallel; dorsal *vascula media* short, widely divergent. *Lower Ordovician:* Bohemia.——FIG. 21,*2a–c.* **W. lamellosa* (BARRANDE), Trenice Formation, Libecov; *a,* partly exfoliated ventral valve, OMR VH 3193, ×5; *b,* dorsal valve exterior, OMR VH 2990a, ×3.3; *c,* dorsal valve exterior, OMR VH 2990b, ×5 (new). [MICHAL MERGL]

Subfamily GLOSSELLINAE
Cooper, 1956

[Glossellinae COOPER, 1956, p. 213]

Shell elongate, slightly unequivalved, postlarval ornamentation commonly papillose; dorsal posterior margin more or less thickened, but lacking pseudointerarea; ventral pseudointerarea well developed, with elevated propareas. *Ordovician (Arenig–Ashgill), ?Lower Carboniferous.*

Glossella COOPER, 1956, p. 228 [**G. papillosa;* OD]. Shell elongate oval, with well-developed radial papillose ornamentation; ventral pseudointerarea with broad triangular groove; visceral area of both valves not thickened; ventral visceral area not extending to midvalve; dorsal visceral area with anterior projection extending somewhat anterior to midvalve, bisected by weak median septum; ventral *vascula lateralia* submarginal, subparallel; dorsal *vascula lateralia* submarginal, slightly converging; dorsal *vascula media* not known. *Ordovician (Arenig–Caradoc):* USA, Scotland, Sweden, Poland, Estonia, Russia (Ingria).——FIG. 22,*1a–h.* **G. papillosa,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,b,* ventral valve interior, exterior, ×4.2; *c,* holotype, detail of papillose ornamentation, USNM 116787b, ×6.7 (Cooper, 1956); *d,* detail of ventral pseudointerarea, USNM 459687a, ×12.5; *e,* detail of dorsal larval shell, ×9.2; *f,* oblique lateral view of dorsal larval shell, ×12.5; *g,* detail of edge of dorsal larval shell, ×41.2; *h,* detail of papillose ornamentation, USNM 459687b, ×271 (new).——FIG.

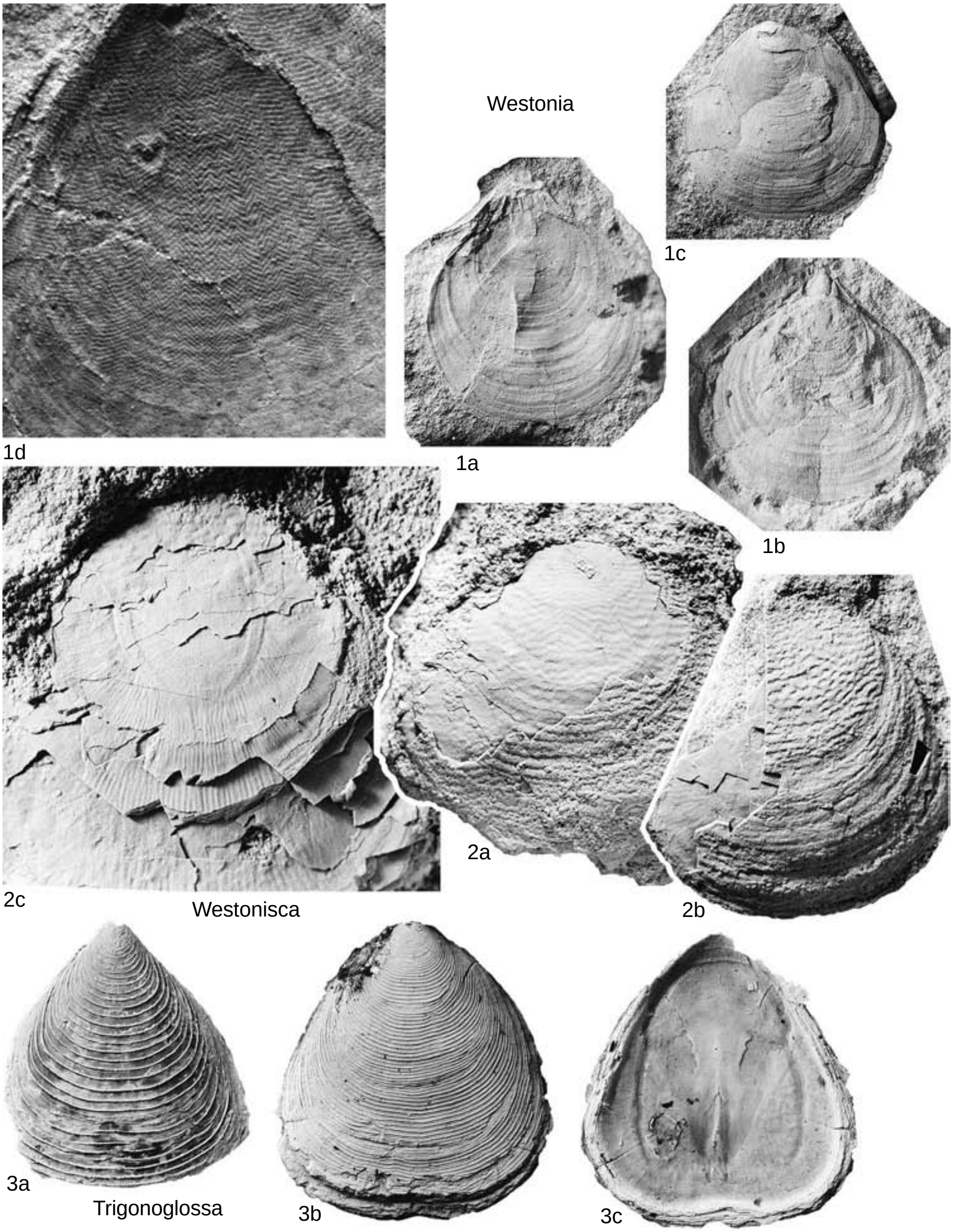

Fig. 21. Obolidae (p. 54).

22,*1i,j. G. liumbona* Cooper, Bromide Formation, Poolville Member, Caradoc, Spring Creek, Oklahoma; paratype, ventral valve exterior, lateral view of both valves, USNM 116786, ×3.3 (Cooper, 1956).

?Anx Havlíček, 1980a, p. 301 [**A. angens;* OD]. Shell minute, subequally biconvex; ventral valve acuminate, much longer than dorsal valve; ventral pseudointerarea large, with shallow, triangular to parallel-sided pedicle groove; interior characters poorly known. [Genus poorly understood; might be juvenile]. *Ordovician (Caradoc–Ashgill):* Bohemia.——Fig. 22,*5. A. ater* (Havlíček), Bohdalec Formation, Prague; paratype, internal mold of ventral

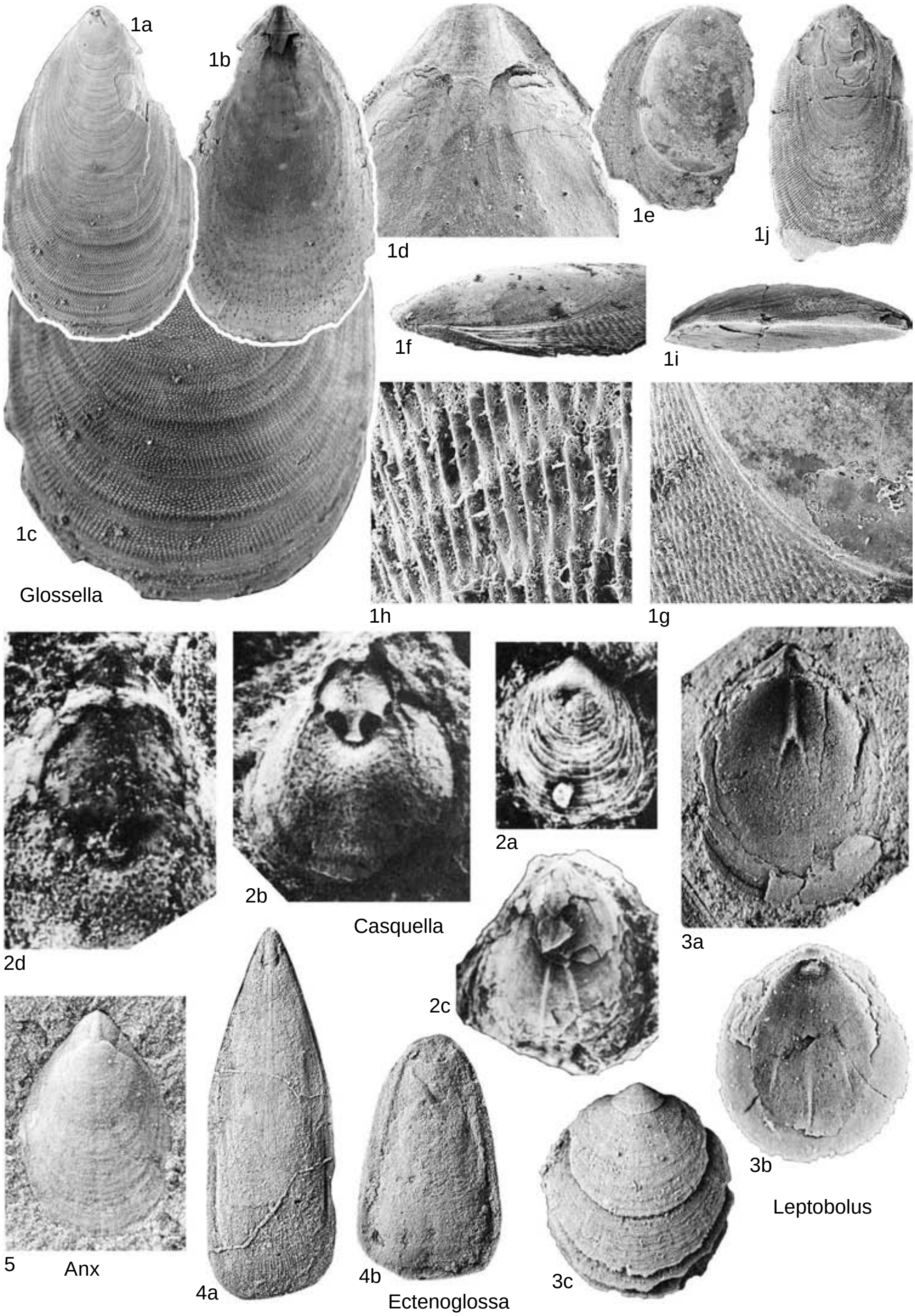

FIG. 22. Obolidae (p. 54–57).

valve, OMR VH 3349, ×11.7 (new). [MICHAL MERGL]

Casquella PERCIVAL, 1978, p. 128 [**C. bifida;* OD]. Shell thick, subtriangular, subacuminate; ornamented by fine, concentric rugae; ventral pseudointerarea with wide triangular pedicle groove and poorly developed flexure lines; ventral visceral area strongly thickened, not extending to midvalve; dorsal visceral area elongate oval, extending to midvalve; ventral *vascula lateralia* submedian, slightly divergent; dorsal *vascula lateralia* submarginal; dorsal *vascula media* long, slightly divergent. *Ordovician (upper Caradoc–lower Ashgill):* Australia (New South Wales).——FIG. 22,*2a–d.* **C. bifida,* Goonumbla Volcanics, Eastonian, New South Wales; *a,* paratype, latex cast of dorsal external mold, SUP 614472, ×1.7; *b,* holotype, ventral internal mold, SUP 61504, ×1.7; *c,* dorsal internal mold, SUP 62468, ×1.7; *d,* latex cast of ventral internal mold, SUP 61500, ×3.3 (Percival, 1978).

?Ectenoglossa SINCLAIR, 1945, p. 63 [**Lingula lesueuri* ROUAULT, 1850, p. 727; OD]. Shell strongly elongate and narrow; ventral pseudointerarea orthocline, strongly triangular, with reduced propareas; ventral visceral area with two short, subparallel ridges in posterior part; dorsal interior and vascular marks in both valves unknown. [Genus poorly understood.] *Ordovician (Arenig):* France, Great Britain.——FIG. 22,*4a,b.* **E. lesueuri* (ROUAULT), Arenig, pebbles in Triassic Budleigh Salterton Pebble Bed, Devon; *a,* internal mold of ventral valve, ×1.2; *b,* internal mold of dorsal valve, ×1.2 (Rowell, 1965a).

Fezzanoglossa HAVLÍČEK in HAVLÍČEK & MASSA, 1973, p. 273 [**F. fezzanica;* OD]. Shell elongate oval, with median plication; ornamentation of fine, closely spaced rugae and fine radial striation; visceral areas of both valves poorly defined; dorsal visceral area extending slightly anterior to midvalve, bisected by long median ridge. *Ordovician (Caradoc):* Libya.——FIG. 23,*2a,b.* **F. fezzanica,* Melez Chograne Formation, Djebel Fezzan; *a,* latex cast of ventral exterior, CFP UA 374/1, ×2.1 (Havlíček & Massa, 1973); *b,* external mold showing ornamentation, ×10 (new). [MICHAL MERGL]

Glyptoglossella COOPER, 1960, p. 601, *nom. nov. pro Glyptoglossa* COOPER, 1956, p. 226, *non* BRENSKE, 1895 [**Glyptoglossa cavellosa* COOPER, 1956, p. 227; OD]. Shell elongate oval; ornamentation of concentric lamellae scalloped along their anterior margins; dorsal interior with median ridge reaching midvalve; muscle scars and vascular system unknown. *Ordovician (Caradoc):* USA (Maryland, Virginia, Pennsylvania), Scotland.——FIG. 23,*1a–d.* **G. cavellosa* (COOPER), Shippensburg Formation, Pennsylvania; *a,* dorsal valve exterior, ×3.3; *b,* lateral view of both valves, ×1.7; *c,* holotype, detail of ornamentation, USNM 109273, ×5; *d,* dorsal valve exterior, USNM 109272d, ×1.7 (Cooper, 1956).

?Lachrymula GRAHAM, 1970, p. 158 [**L. inusitata;* OD]. Shell moderately convex, subtriangular to subovate, subacuminate; ornamented by concentric rugae and fine, radial striae; ventral pseudointerarea well defined, with deep triangular pedicle groove, lacking flexure lines; internal characters unknown. *?Lower Carboniferous:* Great Britain.——FIG. 23,*4a,b.* **L. inusitata,* Orchard Limestone, Scotland; ventral valve exterior, dorsal valve exterior, IGS GSE 13933, ×4.2 (new).——FIG. 23,*4c. L. latior* (M'COY), Motherwell Bridge; ventral valve exterior, IGS GSE 12393, ×7.2 (Graham, 1970).

Leptobolus HALL, 1871b, p. 2 [**L. lepis;* SD DALL, 1877, p. 42] [=*Leptobulus* HALL, 1871b, *nom. neg.*]. Shell small, elongate oval; ventral pseudointerarea with deep triangular pedicle groove; ventral visceral area thickened antriorly, bisected by median ridge, bifurcating near anterior end; dorsal visceral area with one to three low ridges. *Ordovician (Llanvirn–Ashgill):* North America, Bohemia, Sweden, Ireland.——FIG. 22,*3a,b.* **L. lepis,* West Covington, Kentucky; *a,* ventral valve interior, USNM 45239a, ×13.3; *b,* dorsal valve interior, USNM 45239b, ×13.3 (Cooper, 1956).——FIG. 22,*3c. L. insignis* HALL, Eden Formation, St. Thomas, Kentucky; dorsal valve exterior, USNM 71887c, ×13.3 (Cooper, 1956).

?Libyaeglossa HAVLÍČEK in HAVLÍČEK & MASSA, 1973, p. 275 [**L. collombi;* OD]. Shell of medium size, unequivalved, dorsibiconvex, elongate subtriangular; ventral pseudointerarea large with deep pedicle groove; ornamentation of fine concentric rugae. Interior poorly known. *Ordovician (Caradoc):* Libya.——FIG. 24,*4a,b.* **L. collombi,* Melez Chograne Formation; *a,* paratype, latex cast of ventral external mold, Oued Kedawal, CFP UA 225/24, ×1.7; *b,* paratype, latex cast of dorsal external mold, Djebel Fezzan, CFP UA 374/5, ×1.7 (Havlíček & Massa, 1973). [MICHAL MERGL]

Pachyglossella COOPER, 1960, p. 601, *nom. nov. pro Pachyglossa* COOPER, 1956, p. 223, *non* HODGSON, 1843, *nec* FAUVEL, 1868 [**Pachyglossa dorsiconvexa* COOPER, 1956, 225; OD]. Shell elongate oval, dorsibiconvex; ornamented by concentric rugae; postlarval shell with pitted microornamentation; ventral pseudointerarea with deep pedicle groove; dorsal visceral area slightly thickened, with narrow anterior projction extending slightly anterior to midvalve; *vascula lateralia* in both valves submarginal. *Ordovician (Llandeilo–Caradoc):* USA (Alabama, Oklahoma, Minnesota, Wisconsin, Virginia), Scotland.——FIG. 24,*1a–d.* **P. dorsiconvexa* (COOPER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* ventral valve exterior, USNM 459675a, ×2.7; *b,* ventral valve interior, USNM 459675b, ×5.8; *c,* dorsal valve interior, USNM 459675c, ×7.5; *d,* detail of pitted microornamentation, USNM 459675d, ×150 (new).——FIG. 24,*1e. P. biconvexa* (COOPER), Bromide Formation, Hickory Creek, Oklahoma; dorsal valve interior, USNM 459676a, ×2.5 (new).

Plectoglossa COOPER, 1956, p. 222 [**P. oklahomensis;* OD]. Shell elongate oval, dorsibiconvex; ornamented by concentric rugae; ventral pseudointerarea

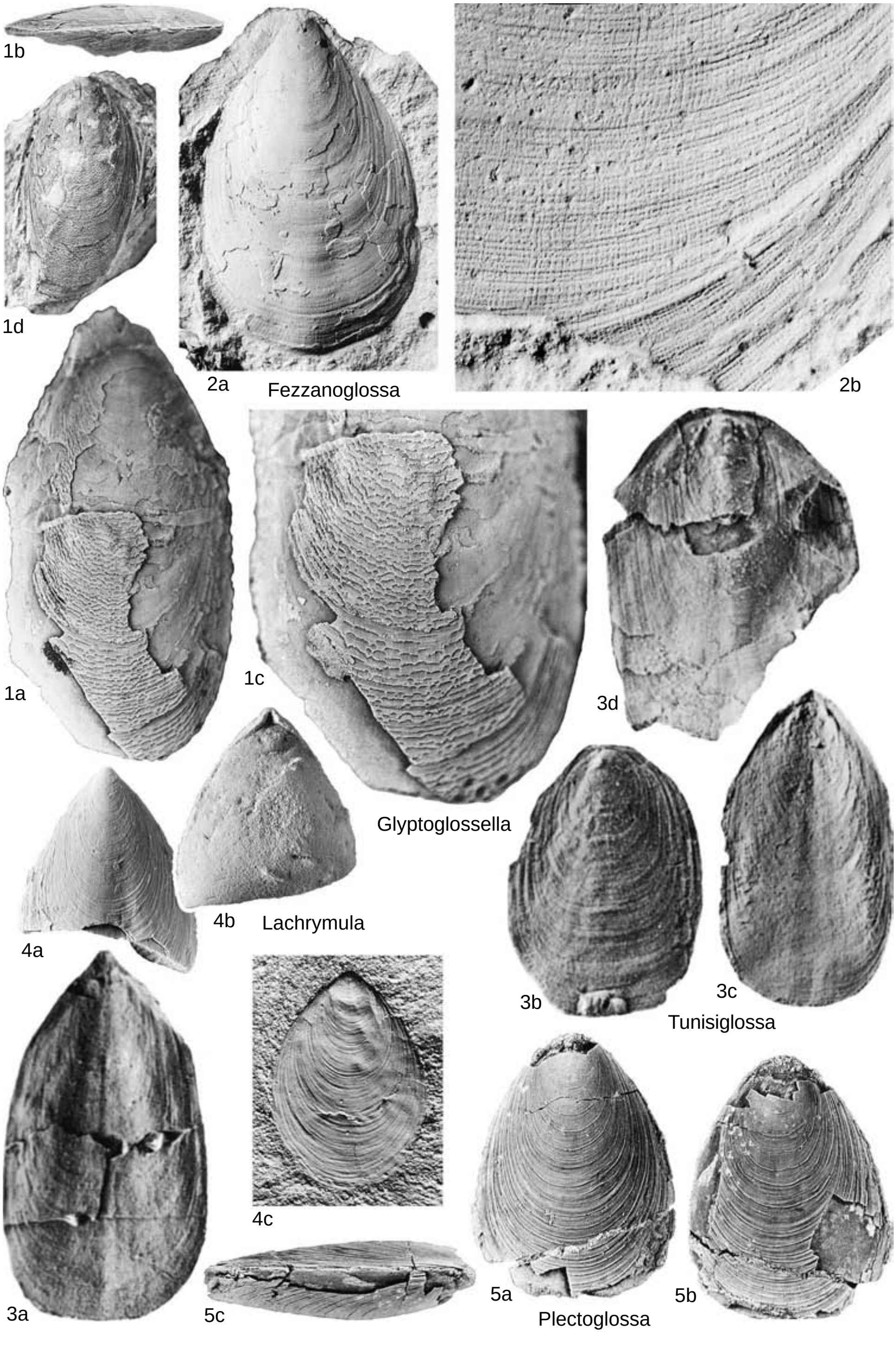

FIG. 23. Obolidae (p. 57–60).

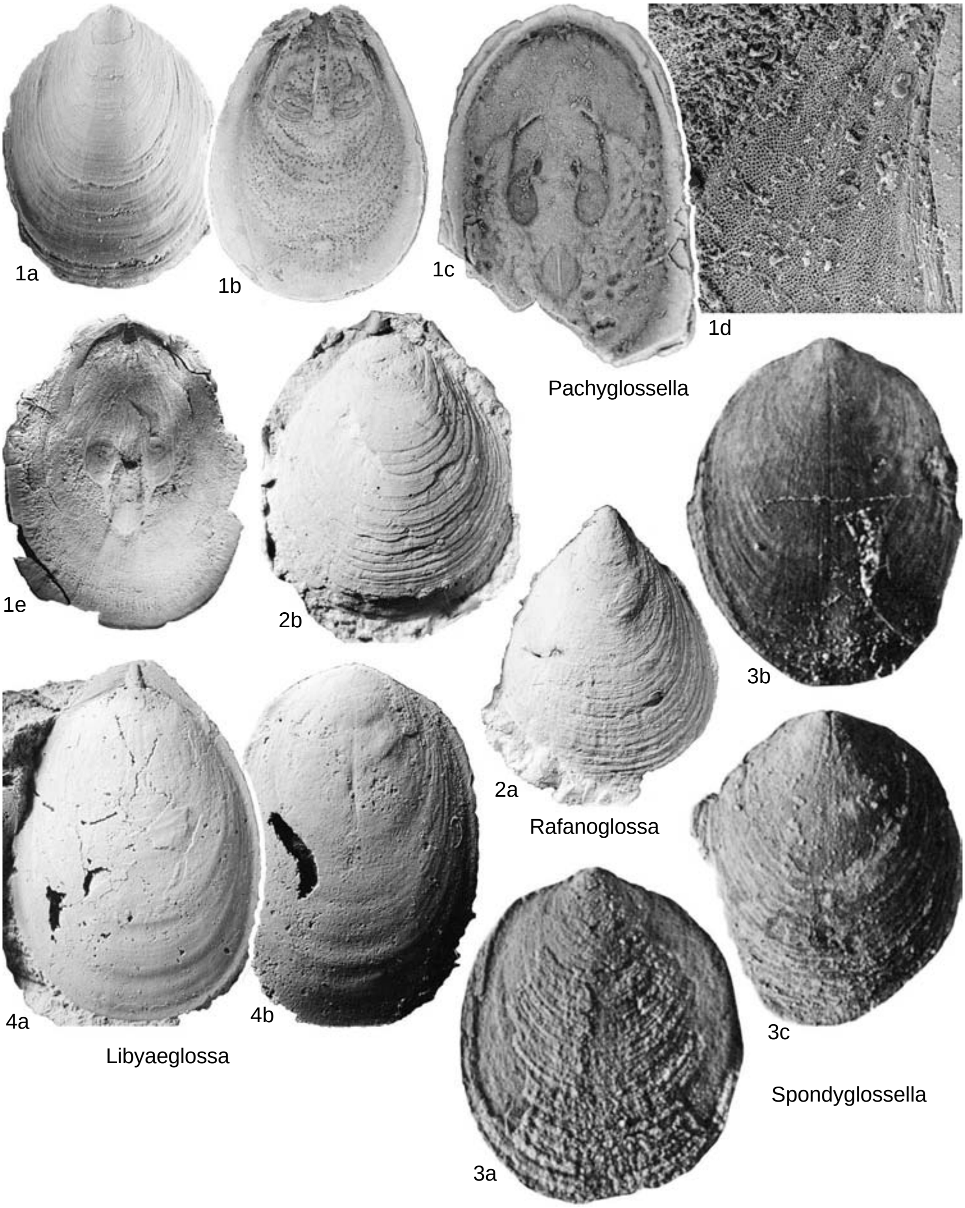

FIG. 24. Obolidae (p. 57–60).

divided medianly by low fold; interior characters of both valves unknown. *Ordovician (?Arenig, Caradoc, ?Ashgill):* Great Britain and Ireland, *?Arenig;* USA, Oklahoma, Virginia, *Caradoc;* ?South Africa.——FIG. 23,*5a–c.* **P. oklahomensis,* Bromide Formation, Pooleville Member, Spring Creek, Oklahoma; ventral valve exterior, dorsal valve exterior, lateral view of both valves, USNM 116783, ×4.2 (Cooper, 1956).

Rafanoglossa HAVLÍČEK, 1980b, p. 4 [**Lingula impar* BARRANDE, 1879, pl. 103; OD]. Similar to *Glossella,* but lacking papillose ornamentation; dorsal visceral area completely bisected by well-developed median ridge. *Ordovician (Arenig–Ashgill):* France, *Arenig;* Bohemia, *Arenig–Llanvirn.*——FIG. 24,*2a,b.* **R. impar* (BARRANDE), Dobrotivá Formation, Bohemia; *a,* ventral internal mold, Prague, OMR VH 3188b, ×5.8; *b,* dorsal internal mold, Malé Prílepy, OMR

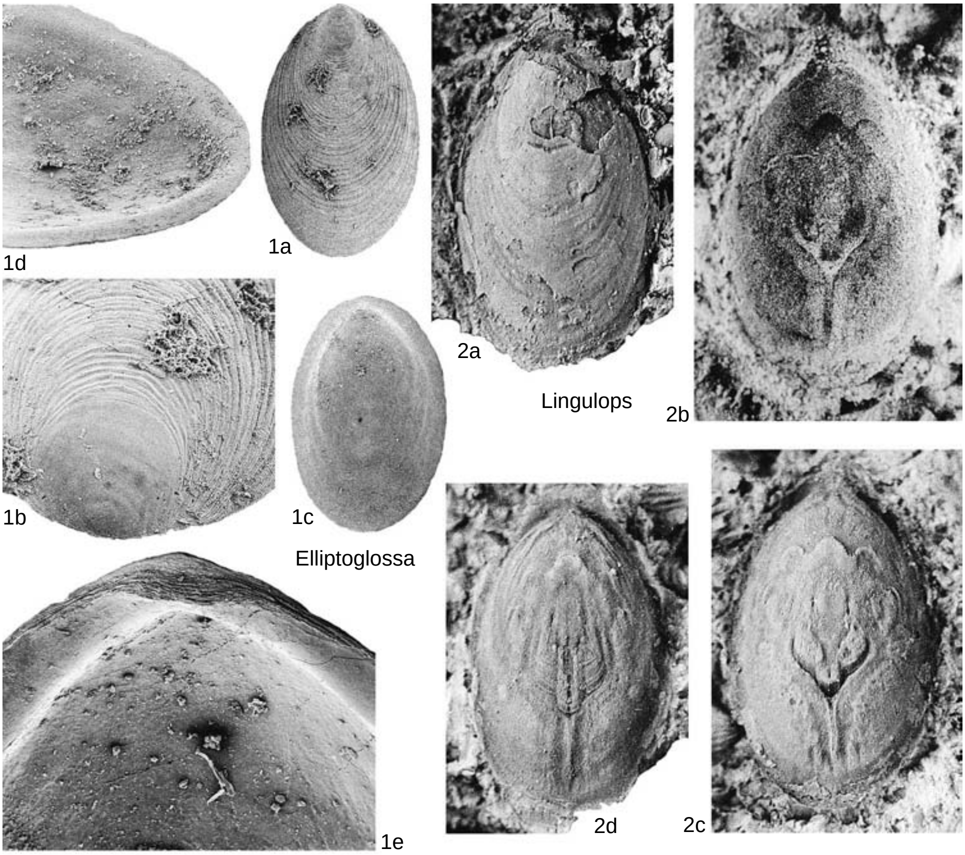

FIG. 25. Obolidae (p. 60–61).

VH 3187a, ×6.7 (Havlíček, 1982). [Michal Mergl]

?Spondyglossella Havlíček, 1980b, p. 5 [**S. spondylifera;* OD]. Shell slightly elongate oval; ventral pseudointerarea small with vestigial propareas, elevated above valve floor, and supported anteriorly by short median ridge; other characters unknown. *Ordovician (?Tremadoc, Arenig–Llanvirn):* France.——Fig. 24,*3a–c.* **S. spondylifera,* Arenig, Montagne Noire, France; *a,* paratype, ventral valve, ×9.2; *b,* paratype, internal mold of dorsal valve, ×8.3; *c,* holotype, internal mold of ventral valve, ×8.3 (Havlíček, 1980b). [Michal Mergl]

?Tunisiglossa Massa, Havlíček, & Bonnefous, 1977, p. 13 [**T. tripolitanea;* OD]. Shell equivalved, subrectangular in outline; ventral pseudointerarea minute, with fine pedicle groove; ornamentation of fine concentric rugae of uneven size. *Ordovician (Tremadoc):* Tunisia, Libya.——Fig. 23,*3a–d.* **T. tripolitanea,* Sanrhar Formation, Rhadabes basin; *a,* paratype, external mold of ventral valve, ×2.4; *b,* paratype, dorsal valve exterior, ×3.1; *c,* paratype, internal mold of ventral valve, ×2.4; *d,* paratype, internal mold of dorsal valve, ×1.8 (Massa, Havlíček, & Bonnefous, 1977). [Michal Mergl]

Subfamily ELLIPTOGLOSSINAE Popov & Holmer, 1994

[Elliptoglossinae Popov & Holmer, 1994, p. 54]

Shell equivalved, elongate oval; larval shell smooth; pseudointerareas in both valves vestigial; visceral areas of both valves extending anterior to midvalve; both valves with distinct limbus. *Ordovician (Tremadoc)–Silurian (Ludlow).*

Elliptoglossa Cooper, 1956, p. 241 [**?Leptobolus ovalis* Bassler, 1919, p. 230; OD]. Visceral fields of both valves weakly impressed, not thickened. *Ordovician (Tremadoc–lower Ashgill):* Poland, *?Tremadoc, Arenig;* Great Britain, Ireland, Sweden, Estonia, Ingria, *Tremadoc–Llanvirn;* Kazakhstan, *Tremadoc–Caradoc;* Russia, Southern Urals, *Arenig–Llanvirn;* USA, Great Britain, Ireland, *Arenig–Caradoc;* Australia, *Caradoc–lower Ashgill.*——FIG. 25,*1a–d.* **E. ovalis* (BASSLER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×11.2; *b,* posterior view of dorsal larval shell, USNM 459676a, ×41.7; *c,* dorsal valve interior, ×11.2; *d,* dorsal interior, oblique lateral view, USNM 459676b, ×33.3 (new).——FIG. 25,*1e. E. sylvanica* COOPER, Shundy Formation, lower Llanvirn, Sary-Kumy, central Kazakhstan; detail of ventral posterior margin with vestigial pseudointerarea, RMS Br 136364, ×30.8 (new).

Lingulops HALL, 1872a, p. 245 [**L. whitfieldi;* OD] [=*Ligulops* HALL, 1871b, p. 2; ICZN opinion no. 1151, 1980]. Externally similar to *Elliptoglossa,* but with visceral fields of both valves forming low platforms; central and anterior lateral muscle scars closely spaced. *Ordovician (Caradoc)–Silurian (Ludlow):* North America, *Caradoc–Ludlow;* Estonia, *Ashgill.*——FIG. 25,*2a–d. L. norwoodi* (JAMES), Lexington Limestone, Kentucky; *a,* dorsal valve exterior, West Covington, USNM 45219a, ×10; *b,c,* internal mold of dorsal valve, latex cast, Ludlow, USNM 15863, ×10; *d,* dorsal internal mold, West Covington, USNM 45219a, ×10 (Cooper, 1956).

Family EOOBOLIDAE
Holmer, Popov, & Wrona, 1996

[Eoobolidae HOLMER, POPOV, & WRONA, 1996, p. 41]

Shell dorsibiconvex, somewhat inequivalved, elongate oval to subtriangular; larval shell well defined, with pitted microornamentation; postlarval shell finely pustulose; ventral pseudointerarea elevated above valve floor, with deep pedicle groove and well-developed flexure lines; dorsal pseudointerarea divided, raised above valve floor; muscle system with paired umbonal muscle scars divided by V-shaped impression of pedicle nerve; dorsal visceral field with well-developed anterior projection extending to midlength; mantle canal system baculate with well-developed *vascula media. Lower Cambrian (Botomian)–Upper Cambrian.*

Eoobolus MATTHEW, 1902, p. 97 [**Obolus (Eoobolus) triparilis* MATTHEW, 1902, p. 94; SD ROWELL, 1965a, p. 263)] [=*Clivosilingula* USHATINSKAYA, 1993b, p. 133 (type, *Lingulella clivosa* PELMAN, 1983, p. 125; OD)]. Shell inequivalved, dorsibiconvex, elongate suboval to subcircular; pedicle groove deep, narrow, subtriangular; both valves with well-developed flexure lines; dorsal pseudointerarea moderately high with broad median groove; visceral areas of both valves slightly thickened anteriorly; dorsal valve usually with fine median ridge and pair of submedian ridges bisecting visceral field; ventral *vascula media* submarginal, arcuate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* Canada, Nova Scotia, *lower Middle Cambrian;* Pakistan, Salt Range, *Botomian;* Russia, Siberia, *Botomian–Amgaian;* Australia, South Australia, *Toyonian.*——FIG. 26,*1a–e.* **E. triparilis* (MATTHEW); Bourinot Group, Cape Breton, Canada; *a,* ventral valve exterior, USNM 57013, ×4.2; *b,* dorsal valve exterior, ROM 510 CM (A), ×4.2; *c,* ventral valve exterior, USNM 51855a, ×4.2; *d,* internal mold of ventral valve, USNM 57013c, ×3.3; *e,* dorsal internal mold, USNM 57013d, ×3.8 (new).——FIG. 26,*1f–h. E. clivosus* (PELMAN); Amgaian, Kharbusuonka River, Siberia; *f,* dorsal valve exterior, ×33.3, PIN 4290/51; *g,* ornamentation of larval shell, ×2250; *h,* ornamentation of postlarval shell, PIN 4290/50, ×225 (Ushatinskaya, 1993b).——FIG. 26,*1i,j. E. elata* (PELMAN), Amgaian, Olenek River, Siberia; *i,* dorsal valve interior, PIN 4290/59, ×16.7; *j,* ventral valve interior, PIN 4290/60, ×16.7 (Ushatinskaya, 1993b).

Vassilkovia POPOV & KHAZANOVITCH in POPOV & others, 1989, p. 123 [**V. granulata;* OD]. Shell equibiconvex, inequivalved; ornament of growth lines crossed by irregular, transverse lines and small, closely spaced granules; pseudointerarea of both valves well developed; pedicle groove deep, narrow; interior characters of both valves weakly impressed. *Upper Cambrian:* Russia (Ingria).——FIG. 26,*2a–c.* **V. granulata,* Ladoga Formation, Lava River, Ingria; *a,* holotype, ventral valve interior, CNIGR 176/12348, ×2.5; *b,c,* paratype, dorsal valve exterior, interior, CNIGR 177/12348, ×2.5 (Popov & others, 1989).——FIG. 26,*2d,e. V.* sp., Tosna Formation, Ingria (Lava River); *d,* ventral valve exterior, ×2.5; *e,* detail of ornamentation, CNIGR 178/12348, ×6.7 (Popov & others, 1989).

Family ZHANATELLIDAE
Koneva, 1986

[Zhanatellidae KONEVA, 1986a, p. 49]

Shell subcircular to elongate; larval and postlarval shell with finely pitted microornamentation; pedicle groove well developed, deep; ventral flexure lines variably developed; ventral beak commonly with semicircular emarginature; dorsal pseudointerarea divided by median groove or undivided, muscle system with paired ventral umbonal muscle scars divided by V-shaped impression of pedicle nerve; pleurocoel weakly developed; both valves with baculate mantle canal system; *vascula media* present. *Lower Cambrian (upper Atdabanian)–Ordovician (Ashgill), ?Silurian.*

Zhanatella KONEVA, 1986a, p. 50 [**Z. rotunda;* OD]. Shell subequally biconvex, circular, with ventral

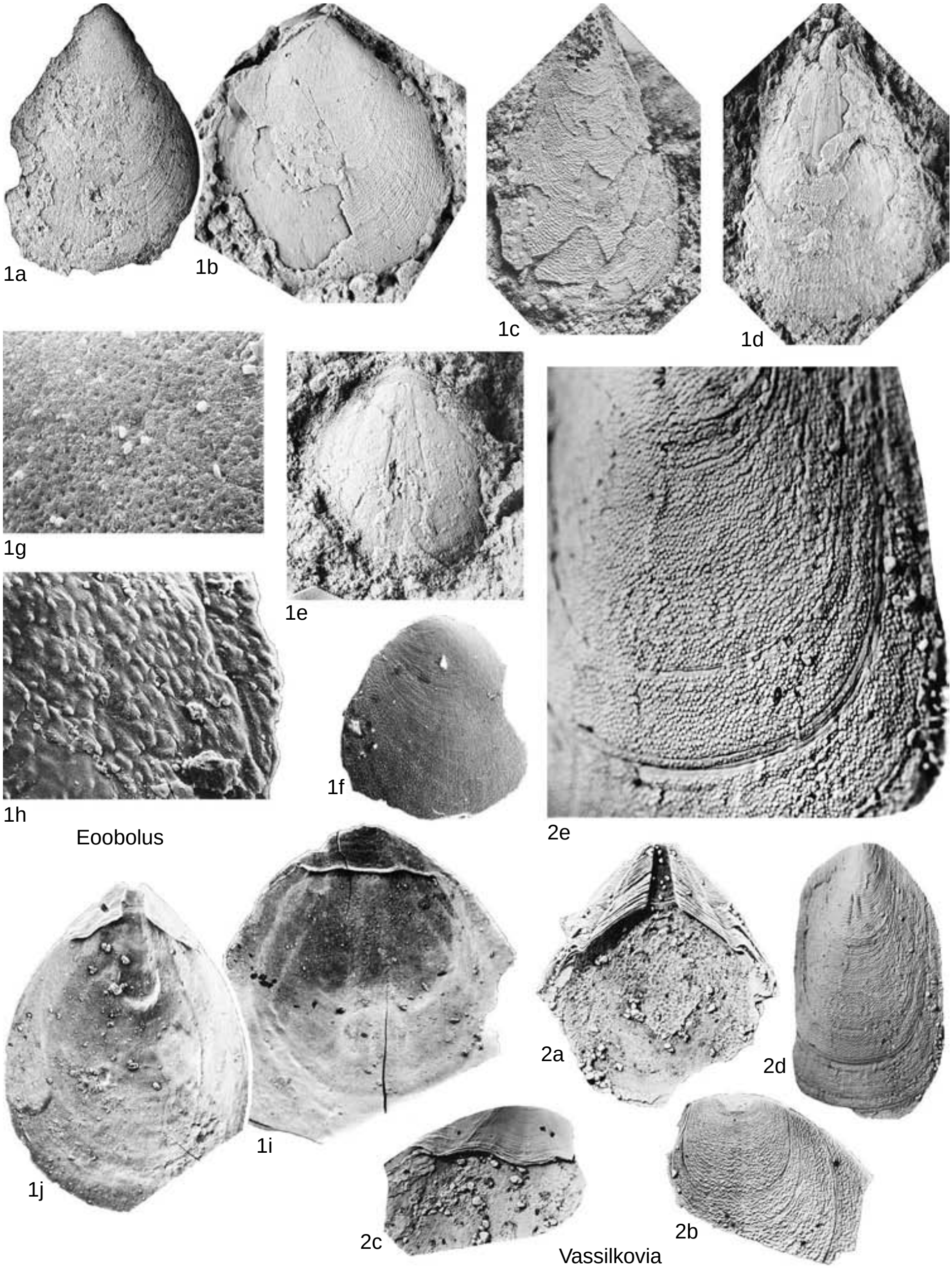

FIG. 26. Eoobolidae (p. 61).

emarginature; ornament of regularly spaced, high, concentric rugae; ventral pseudointerarea wide, with deep, narrow pedicle groove and flattened, elevated propareas, with flexure lines; dorsal pseudointerarea with wide median groove; ventral visceral field slightly thickened anteriorly, not extending to midvalve; dorsal visceral field small, with narrrow, anterior projection, not extending to midvalve, and bordered laterally by low ridges; ventral *vascula lateralia* submedian, widely divergent in posterior half and arcuate anteriorly; dorsal *vascula lateralia* subperipheral, arcuate; *vascula media* long, diver-

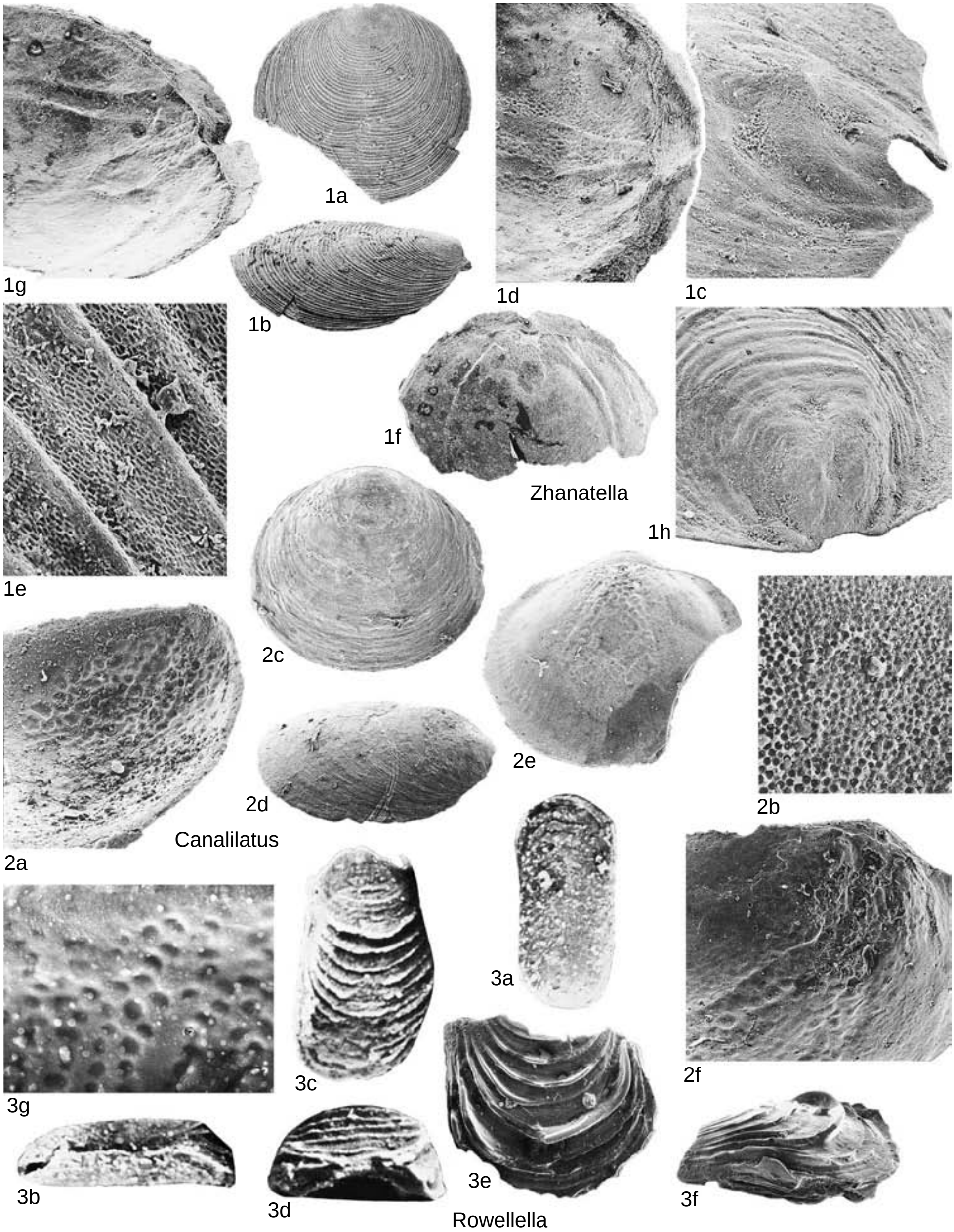

FIG. 27. Zhanatellidae (p. 61–66).

gent. *Upper Cambrian:* Kazakhstan, ?Australia, Antarctica, North America.——FIG. 27,*1a–h.* **Z. rotunda,* Kujandy Formation, Satpak, north-central Kazakhstan; *a,* ventral valve exterior, ×5.4; *b,* lateral view, RMS Br 136041, ×6.2; *c,* oblique view of ventral larval shell with emarginature, RMS Br 136044, ×83.3; *d,* oblique lateral view of dorsal pseudointerarea and visceral area, RMS Br 136046, ×25; *e,* detail of pitted microornamentation of dorsal valve, RMS Br 136050, ×229; *f,* ventral valve interior, ×10; *g,* oblique view of ventral pseudointerarea and visceral area, RMS Br 136045, ×19.2; *h,* oblique posterior view of dorsal larval shell, RMS Br 136047, ×41.7 (Holmer & Popov, 1994).

?Canalilatus PELMAN, 1983, p. 126 [**C. paululus;* OD] [=*Pelmania* KONEVA, 1992, p. 89 (type, *P. perrara;* OD)]. Shell small, subcircular; ventral pseudointerarea small; pedicle groove wide, shallow; dorsal pseudointerarea vestigial, undivided; ventral visceral field slightly thickened posteromedially, not extending to midlength; dorsal visceral field slightly thickened posteriorly with broad anterior projection, extending anteriorly beyond midlength, bounded laterally by ridges and bisected by fine median ridge. [Genus poorly understood, may represent juvenile zhanatellid]. *Middle Cambrian (Amgaian):* Russia (Siberia), Kazakhstan (Malyi Karatau).——FIG. 27,*2a,b.* **C. paululus,* Kuonamka Formation, Amgaian, Kuonamka River, Siberia; *a,* oblique lateral view of dorsal valve interior, RMS Br 136365, ×62.5; *b,* detail of pitted microornamentation of dorsal larval shell, RMS Br 136366, ×625 (new). ——FIG. 27,*2c–f. C. perrarus* (KONEVA), Aktas Formation, Amgaian, Kyrshabakty River; *c,* ventral valve exterior, ×33.3; *d,* lateral view, RMS Br 136367, ×37.5; *e,* dorsal valve interior, ×31.2; *f,* oblique view of dorsal interior, RMS Br 136368, ×62.5 (new).

Fossuliella POPOV & USHATINSKAYA, 1992, p. 66 [**Lingulella linguata* PELMAN, 1977, p. 39; OD]. Shell elongate suboval, weakly biconvex; ventral pseudointerarea with deep pedicle groove and elevated propareas with flexure lines; ventral beak with deep emarginature; dorsal pseudointerarea moderately high, with wide median groove and vestigial propareas; ventral visceral field small, subtriangular, not extending to midvalve; ventral *vascula lateralia* submarginal, straight to slightly arcuate; dorsal visceral field slightly thickened, with *anterior* projection extending *anteriorly* beyond midvalve; dorsal *vascula lateralia* marginal, arcuate. *Lower Cambrian (upper Atdabanian)–Upper Cambrian:* Russia, Siberia, *upper Atdabanian–Middle Cambrian;* Kazakhstan, *Upper Cambrian.*——FIG. 28,*1a–f. F. konevae* POPOV & HOLMER, Kujandy Formation, Upper Cambrian, Satpak, north-central Kazakhstan; *a,* ventral valve exterior, RMS Br 136032, ×10; *b,* dorsal valve exterior, ×13.3; *c,* detail of pitted microornamentation of dorsal valve, RMS Br 136031, ×417; *d,* lateral view of dorsal valve, RMS Br 136029, ×18.3; *e,* ventral pseudointerarea and pedicle groove, RMS Br 136036, ×31.7; *f,* dorsal valve interior, RMS Br 136030, ×17.5 (Holmer & Popov, 1994).

Hyperobolus HAVLÍČEK, 1982, p. 15 [**Lingula feistmanteli* BARRANDE, 1879, pl. 106; OD]. Shell subequally biconvex to dorsibiconvex, subtriangular to subpentagonal; ornament of fine, evenly spaced, concentric rugae; larval and postlarval shell with pitted microornamentation; pseudointerareas of both valves orthocline, raised highly above valve floor; pedicle groove narrow, deep; ventral visceral field thickened, rhomboidal, not extending to midvalve; dorsal visceral field with wide anterior projection, extending to or somewhat anterior to midvalve; anterior lateral muscle scars large, close to central scars; ventral *vascula lateralia* submedian, slightly divergent in posterior half; dorsal *vascula lateralia* submarginal, slightly divergent; *vascula media* short, widely divergent. *Ordovician (?Tremadoc, ?Arenig, lower Llanvirn):* Bohemia, *?Tremadoc;* Kazakhstan, Southern Urals, *?Arenig;* Malyi Karatau, *lower Llanvirn.*——FIG. 29,*3a,b.* **H. feistmanteli* (BARRANDE), Trenice, Bohemia; *a,* latex cast of ventral internal mold, Holyvrch, OMR VH 3133a; ×1.6; *b,* latex cast of dorsal internal mold, Obis, OMR VH 3144a, ×1.6 (Havlíček, 1982). [MICHAL MERGL]

Paldiskia GORJANSKY, 1969, p. 28 [**P. obscuricostata;* OD]. Shell subequibiconvex, subtriangular; ornament of narrow, raised concentric rugae and radial ribs in apical region of both valves; larval and postlarval shell with pitted microornamentation; pedicle groove broadly triangular; ventral flexure lines poorly defined; ventral visceral area weakly impressed. Dorsal interior unknown. *?Upper Cambrian, Ordovician (?Tremadoc, lower Arenig):* Estonia, *upper Tremadoc–lower Arenig;* ?Russia, Moscow basin, eastern White Sea coast, *?Upper Cambrian.*——FIG. 29,*2a–c.* **P. obscuricostata,* Leetse Formation, Estonia, Maardu quarry; *a,* holotype, ventral valve exterior, CNIGR 43/9960, ×2.5; *b,* ventral valve interior, CNIGR 58/9960, ×2.5; *c,* ventral valve exterior, CNIGR 9960, ×2.5 (Gorjansky, 1969).

Rosobolus HAVLÍČEK, 1982, p. 18 [**R. robertinus;* OD]. Shell subtriangular to suboval, slightly elongated; pitted microornamentation; pseudointerareas of both valves wide, strongly raised and shelflike; pedicle groove narrow, deep; dorsal pseudointerarea anacline, undivided; ventral visceral field subtriangular, slightly elevated anteriorly; dorsal visceral field bounded laterally by slender ridges; dorsal central and anterior lateral muscle scars large, elongate, bisected by median ridge; ventral *vascula lateralia* submarginal, straight, parallel anteriorly, slightly divergent posteriorly; dorsal *vascula lateralia* marginal; *vascula media* long, slightly divergent. *Ordovician (?Tremadoc, Arenig, ?Llanvirn):* Bohemia, *?Tremadoc;* ?Sweden, *Llanvirn.*——FIG. 29,*1a–d.* **R. robertinus,* Trenice, Holoubkov, Bohemia; *a,* ventral internal mold, OMR VH 3064b, ×5.8 (new); *b,* dorsal internal mold, OMR VH 3080b, ×5.8; *c,* latex cast of dorsal external mold, OMR VH 703, ×5.8 (Havlíček, 1982); *d,* detail of microornamentation, ×112 (new). [MICHAL MERGL]

Rowellella WRIGHT, 1963b, p. 233 [**R. minuta;* OD]. Shell dorsibiconvex, elongate oval to subrectangular; ornament of concentric rugae, becoming lamellose peripherally; apical region of both valves usually poorly preserved; ventral pseudointerarea with wide pedicle groove and narrow, elevated propareas lacking flexure lines; dorsal valve geniculate ventrally; with low, undivided pseudointerarea; ventral visceral field slightly thickened anteriorly, not extending to midvalve; dorsal visceral field with thickened anterior platform bearing central and anterior lateral muscle scars, placed far anterior of midvalve; *vascula lateralia* of both valves peripheral;

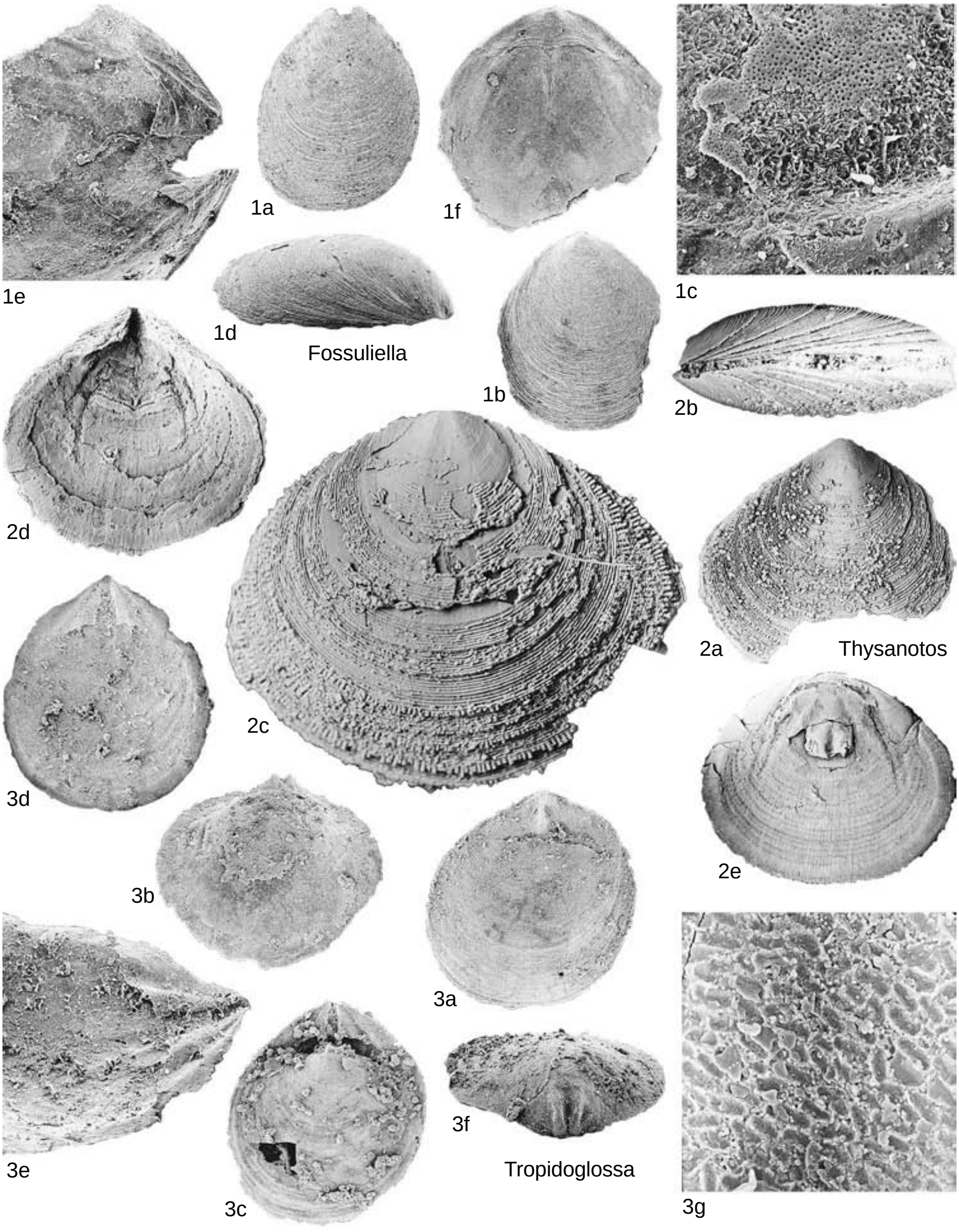

FIG. 28. Zhanatellidae (p. 64–67).

vascula media short, divergent. *Ordovician (Tremadoc–Ashgill), ?Silurian:* Poland, *Tremadoc–Llanvirn;* Sweden, *Tremadoc–Caradoc, ?Silurian;* Bohemia, Russia, Ingria, Southern Urals, *Arenig–Llanvirn;* USA, Alabama, Nevada, *Arenig–Llandeilo;* Estonia, *Arenig–Ashgill;* Kazakhstan, *Llanvirn–Ashgill;* Ireland, *Ashgill.*——FIG. 27,*3a–d.* **R. minuta,* Portrane Limestone, Ashgill, Portrane County, Ireland; *a,b,* holotype, ventral, lateral view of both valves, BMNH BB 28223, ×25; *c,* dorsal valve exterior, BMNH BB 28225, ×25; *d,* anterior of dorsal valve exterior, BMNH BB 28226 (Wright, 1963b).——FIG. 27,*3e–g. R. rugosa* GORJANSKY, Obukhovo Formation, Llanvirn, Pskov district, Pechory Core, Russia; *e,f,* dorsal valve exterior, oblique lateral view, ×17.5; *g,* detail of pitted

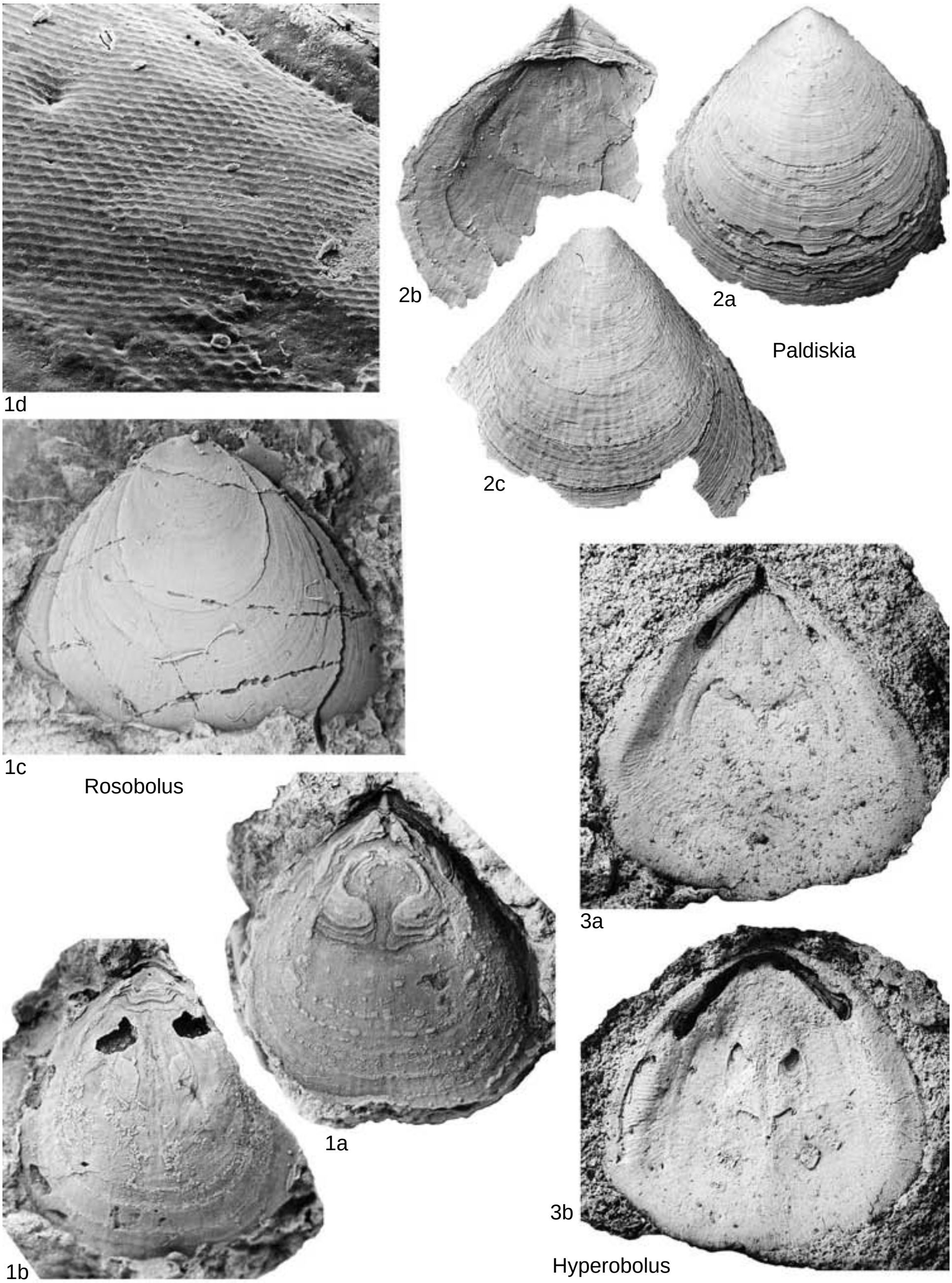

FIG. 29. Zhanatellidae (p. 64).

microornamentation, RMS Br 136370, ×417 (new).

Thysanotos Mickwitz, 1896, p. 130 [**Obolus siluricus* von Eichwald, 1840, p. 195; OD] [=*Mickwitzella* Walcott, 1908, p. 70, obj.; *Thysanotus* Koliha, 1926, p. 317; *Thysanobolus* Havlíček, 1982, p. 21 (type, *T. lingulides;* OD)]. Shell suboval, subequivally biconvex to somewhat dorsibiconvex; ornament of high, widely spaced rugae, superposed on concentric lamellae with marginal spines; larval and postlarval shell with pitted microornamentation; pseudointerarea of both valves with well-defined flexure lines; ventral pseudointerarea orthocline; pedicle groove narrow, triangular, deep; dorsal pseudointerarea low, anacline, with well-defined median groove; ventral interior with subtriangular visceral field, slightly raised anteriorly, not extending to midvalve; dorsal interior with well-defined visceral area; anterior projection bounded laterally by low ridges, and extending anteriorly beyond midlength; dorsal central muscle scars large, elongate suboval, divided by groove; ventral *vascula lateralia* submarginal, straight, widely divergent anteriorly; dorsal *vascula lateralia* submarginal; *vascula media* poorly impressed. *Ordovician (?Tremadoc, Arenig, ?Llanvirn):* Germany, Bavaria, Thuringia, *?Tremadoc, ?Arenig;* Bohemia, *?Tremadoc–lower Arenig;* Kazakhstan, *Arenig;* Poland, Holy Cross Mountains, ?Serbia, *?Arenig;* Estonia, Russia, Urals, *Arenig, ?Llanvirn.*——FIG. 28,*2a–e.* **T. siluricus* (VON EICHWALD), Leetse beds, Estonia; *a,b,* ventral view, lateral view of both valves, Hundikuristik, TAGI BR 3501, ×1.2; *c,* dorsal valve exterior, Leetse, LMT 6574t, ×2.9; *d,* ventral valve interior, Mäeküla, TAGI BR 3503, ×1.2; *e,* dorsal valve interior, Leetse, TAGI BR 3510, ×1.2 (new).

Tropidoglossa ROWELL, 1966, p. 31 [**Linnarssonella modesta* WALCOTT, 1908, p. 90; OD]. Shell small and thin, elongate oval, dorsibiconvex; larval and postlarval shell with pitted microornamentation; ventral beak with distinctive, short keel; ventral pseudointerarea with deep pedicle groove and well-developed flexure lines; beak of dorsal valve with two short, divergent ridges; dorsal pseudointerarea narrow, with poorly developed median groove; visceral field and mantle canals not clearly impressed. *Upper Cambrian:* USA (Utah), *Dunderbergia* Biozone.——FIG. 28,*3a–g.* **T. modesta* (WALCOTT), Orr Formation, House Range, USNM loc. 30k, Utah; *a,* ventral valve exterior, USNM 459677a, ×19.6; *b,* dorsal valve interior, USNM 459677b, ×19.6; *c,* dorsal view of complete shell, USNM 459677c, ×13.8; *d,* ventral valve interior, ×10; *e,* oblique lateral view of ventral pseudointerarea, USNM 459677d, ×20.8; *f,* posterior view of dorsal valve, USNM 459677e, ×22.9; *g,* detail of pitted microornamentation, USNM 459677f, ×425 (new).

Family ELKANIIDAE
Walcott & Schuchert, 1908

[*nom. transl.* SCHUCHERT & LEVENE, 1929, p. 12, *ex* Elkaniinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 144]

Shell subtriangular to subcircular, dorsibiconvex or subequally biconvex, with maximum thickness posteriorly; larval and postlarval shell with finely pitted microornamentation; ventral propareas wide, with well-defined flexure lines; visceral fields of both valves strongly thickened, forming elevated platforms, not extending anteriorly beyond midvalve; dorsal visceral field with well-developed anterior projection; muscle system with paired umbonal muscle; *vascula lateralia* of both valves widely divergent in posterior half, arcuate; *vascula media* long, widely divergent. *Upper Cambrian–Ordovician (lower Ashgill).*

Elkania FORD, 1886b, p. 325, *nom. nov. pro Billingsia* FORD, 1886a, p. 466, *non* DE KONINCK, 1876 [**Obolella desiderata* BILLINGS, 1862a, p. 69; OD]. Shell moderately to strongly biconvex, subcircular; ornament of fine concentric rugae; dorsal beak strongly incurved, covered by ventral pseudointeraea; ventral propareas weakly anacline; dorsal pseudointerarea anacline, crescent shaped, forming low, wide strip along margin; pedicle groove narrow, deep. *Upper Cambrian–Ordovician (Llanvirn):* USA, Nevada, Alaska, *Upper Cambrian or Lower Ordovician;* Canada, Quebec, *Lower Ordovician;* Kazakhstan, *Llanvirn.*——FIG. 30,*2a,b.* **E. desiderata* (BILLINGS), Levis Shale, Levis, Quebec; *a,* dorsal internal mold, USNM 51943d, ×3.8; *b,* ventral internal mold, USNM 51943b, ×4.8 (Ulrich & Cooper, 1938).——FIG. 30,*2c–e. E. alaskensis* ULRICH & COOPER, Squaw Mountain, Yukon, Alaska; *c,* ventral view of both valves, GSC 9121, ×4.2; *d,* ventral internal mold, GSC 9121b, ×3.6; *e,* dorsal view of both valves, GSC 9121, ×4.2 (Ulrich & Cooper, 1938).——FIG. 30,*2f,g. E. hamburgensis* (WALCOTT), Goodwin Formation, Eureka district, Hamburg Ridge, Nevada; posterior view of both valves, lateral view of both valves, USNM 17286b, ×4.8 (Ulrich & Cooper, 1938).

Broeggeria WALCOTT, 1902, p. 605, *nom. correct.* ULRICH & COOPER, 1936b, p. 618, *pro Bröggeria* WALCOTT, 1902, p. 605, *nom. imperf.* [**Obolella salteri* HOLL, 1865, p. 102; OD]. Shell rounded to subtriangular, moderately biconvex, with slightly longer ventral valve; larval and postlarval shell ornamented by subcircular pits; ventral pseudointerarea broadly triangular with widely triangular pedicle groove; dorsal pseudointerarea crescent shaped, with wide median groove; visceral areas of both valves moderately thickened, not extending to midvalve. *Upper Cambrian–Ordovician (lower Llanvirn):* Great Britain, *Upper Cambrian–Tremadoc;* Sweden, Norway, Denmark, *Upper Cambrian–Arenig;* Kazakhstan, *Upper Cambrian–lower Llanvirn;* ?Argentina, Canada, Nova Scotia, *Tremadoc;* ?Belgium, *?Tremadoc;* ?Bohemia, *?Tremadoc–lower Arenig.*——FIG. 30,*3a–e.* **B. salteri* (HOLL); *a,* ventral valve exterior, ×5; *b,* pitted microornament of ventral valve, Bjørkåsholmen Formation, Tremadoc, Ottenby, Sweden, RMS Br 133940, ×500 (Popov & Holmer, 1994); *c,* ventral valve interior, latex cast, Tremadoc, *Clonograptus tenellus* Biozone, Cwm Crymlyn, South Wales, IGS RU 8949, ×8.3 (Owens &

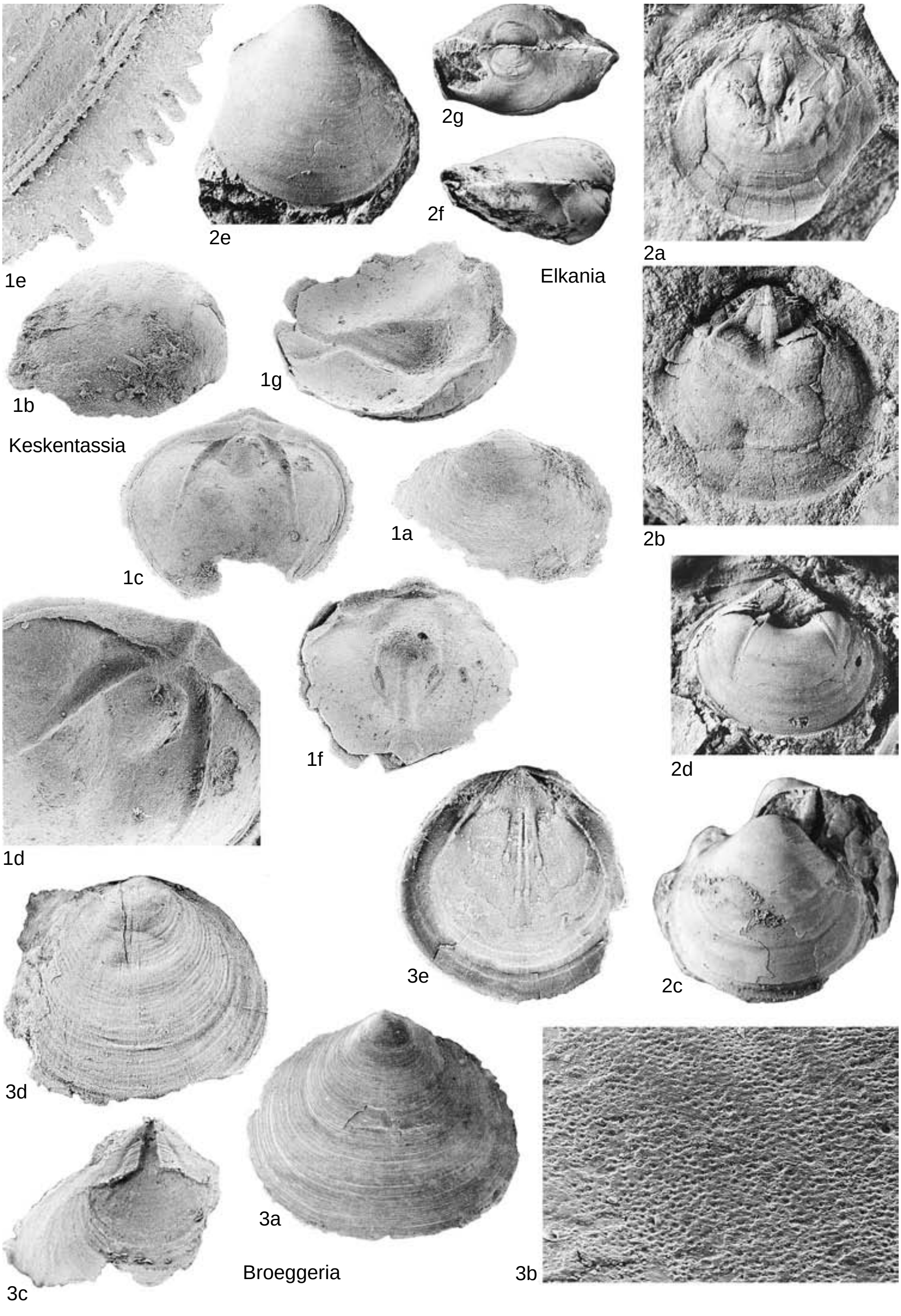

FIG. 30. Elkaniidae (p. 67–69).

others, 1982); *d,* dorsal valve exterior, White-Leaved-Oak Shales, Merioneth Series, Malvern Hills, South Wales, IGS GSM 32733, ×6.7 (Owens & others, 1982); *e,* dorsal internal mold, lower Tremadoc Shales, Clyn-côch, South Wales, NMW 77.1G.46, ×6.7 (Owens & others, 1982).

Elkanisca Havlíček, 1982, p. 51 [**Obolus klouceki* Koliha, 1918, p. 133; OD]. Shell strongly dorsibiconvex, rounded; postlarval shell ornamented by concentric rugae; microornamentation with lenticular pits; ventral pseudointerarea wide, apsacline, with widely triangular pedicle groove; dorsal pseudointerarea low, crescent shaped; interior of both valves as in *Elkania. Ordovician (?Tremadoc, lower Arenig):* Bohemia.——Fig. 31,*1a,b.* **E. klouceki* (Koliha); holotype, dorsal external mold, dorsal internal mold, Klabava Formation, Zebrák, NM L18156, ×4.2 (Havlíček, 1982).——Fig. 31,*1c. E. obesa* (Havlíček); detail of pitted microornamentation, OMR VH 65778, ×200 (new).——Fig. 31,*1d. E. lineola* Havlíček; ventral internal mold, Klabava Formation, ×4.2 (new). [Michal Mergl]

Keskentassia Popov & Holmer, 1994, p. 66 [**K. multispinulosa;* OD]. Shell strongly biconvex, slightly inequivalved; ventral pseudointerarea forming crescent-shaped strip; ventral propareas strongly elevated, flat, lacking flexure lines; ventral *vascula lateralia* submedial; dorsal pseudointerarea reduced, mainly consisting of wide median groove; dorsal transmedian, outside lateral, and middle lateral muscle scars placed on separate muscle platforms along posterolateral margins of visceral area; postlarval shell with finely pitted microornament, and spinose valve margin. *Ordovician (lower Arenig):* Kazakhstan (Kendyktas Range).——Fig. 30,*1a–g.* **K. multispinulosa,* Agalatas Formation, Kendyktas Range, Agalatas River, Kazakhstan; *a,* holotype, ventral valve exterior, ×7.5; *b,* holotype, ventral valve lateral view, RMS Br 136026, ×10; *c,* ventral valve interior, ×8.3; *d,* oblique view of visceral area and pseudointerarea, ×16.3; *e,* marginal spines, RMS Br 136021, ×67; *f,* dorsal valve interior, ×11.3; *g,* oblique lateral view of interior, RMS Br 136023, ×13.8 (Popov & Holmer, 1994).

Lamanskya Moberg & Segerberg, 1906, p. 71 [**L. splendens;* OD] [=*Dictyobolus* Williams & Curry, 1985, p. 189 (type, *D. transversus;* OD)]. Shell strongly biconvex, more than half as thick as wide, with wide truncated posterior margin; exterior smooth or with subdued rugae; microornamentation of lenticular pits; ventral pseudointerarea low, apsacline, with deep, triangular pedicle groove bounded laterally by strong plications; dorsal pseudointerarea strongly incurved medially, with vestigial median groove; visceral platforms of both valves as in *Broeggeria. Ordovician (Tremadoc–Llanvirn):* Sweden, Norway, *Tremadoc–Arenig;* Estonia, Ireland, *Arenig;* Russia, Ingria, Southern Urals, *Arenig–Llanvirn.*——Fig. 31,*2a–e.* **L. splendens; a,* ventral pseudointerarea, pedicle groove, RMS 133942, ×25.8; *b,* pitted microornamentation of ventral valve, Latorp Limestone, *Megistaspis armata* Biozone, Uddagården quarry, Västergötland, Sweden, RMS 133940, ×425; *c,d,* holotype, dorsal valve exterior, lateral view, Bjørkåsholmen Formation, Ottenby, Öland, Sweden, LO 1795T, ×4; *e,* partly exfoliated dorsal valve showing visceral platform and *vascula media,* Latorp Limestone, *Megistaspis planilimbata* Biozone, Ottenby, Öland, Sweden, RMS Br 133692, ×5.7 (Holmer, 1993).

Monobolina Salter, 1866, p. 334 [**Lingula plumbea* Salter in Murchison, 1859, p. 50; OD] [=*Monobilina* Rowell, 1965a, p. 270]. Shape of shell and interior characters similar to *Broeggeria,* but with distinctive ornamentation of concentric fila and radial costellae. *Ordovician (Arenig–Llandeilo):* Great Britain.——Fig. 32,*2a–e.* **M. plumbea* (Salter), Mytton Flags, Arenig, Shropshire; *a,* latex cast of ventral external mold, ×5; *b,* detail of ventral ornamentation, BMNH BB 35468, ×10; *c,* latex cast of dorsal external mold, BMNH BB 35470a, ×4.5; *d,* latex cast of ventral internal mold, BMNH BB 35473a, ×2.2; *e,* latex cast of dorsal internal mold, BMNH BB 35469a, ×2.3 (Williams, 1974).

?Pseudodicellomus Bell in Bell & Ellinwood, 1962, p. 407 [**Dicellomus mosaicus* Bell, 1941, p. 216; OD]. Shell dorsibiconvex, subcircular; larval and postlarval shell with pitted microornamentation; pedicle groove deep, broadly triangular; ventral propareas narrow with flexure lines; dorsal pseudointerarea low, with wide median groove; interior of both valves with low visceral platforms; ventral *vascula lateralia* submedian, widely divergent posteriorly. *Upper Cambrian:* USA (Texas, Montana), *Conaspis–Ptychaspis–Prosaukia* Biozones.——Fig. 32,*1a–d.* **P. mosaicus* (Bell), Morgan Creek Limestone, Texas; *a,* ventral valve interior, USNM 125574, ×5; *b,* dorsal valve interior, USNM 125576, ×5; *c,* ventral valve interior, oblique anterior view, ×9.2; *d,* detail of pitted microornamentation of ventral valve, USNM 459678a, ×200 (new).

Tilasia Holmer, 1991b, p. 197 [**T. rugosa;* OD]. Shell transversely suboval, moderately to subequally biconvex; ornament of concentric rugae, and with microornament of regular rhomboidal pits; ventral pseudointerarea with wide propareas and deep, triangular pedicle groove, bounded laterally by plications; dorsal pseudointerarea with widely triangular median groove and narrow propareas; ventral interior poorly known; dorsal interior with short visceral platform, bisected by weak median ridge; dorsal central and anterior lateral muscle scars closely spaced. *Ordovician (upper Llandeilo–lower Ashgill):* ?USA, Alabama, *Llandeilo;* Sweden, *upper Llandeilo–lower Ashgill;* Kazakhstan, Chu-Ili Range, *Caradoc.*——Fig. 31,*3a–d.* **T. rugosa,* Boda Limestone, Siljan District, Sweden; *a,b,* ventral valve exterior, lateral view of both valves, ×2.5; *c,* holotype, internal mold of dorsal valve, Jutjärn, RMS Br

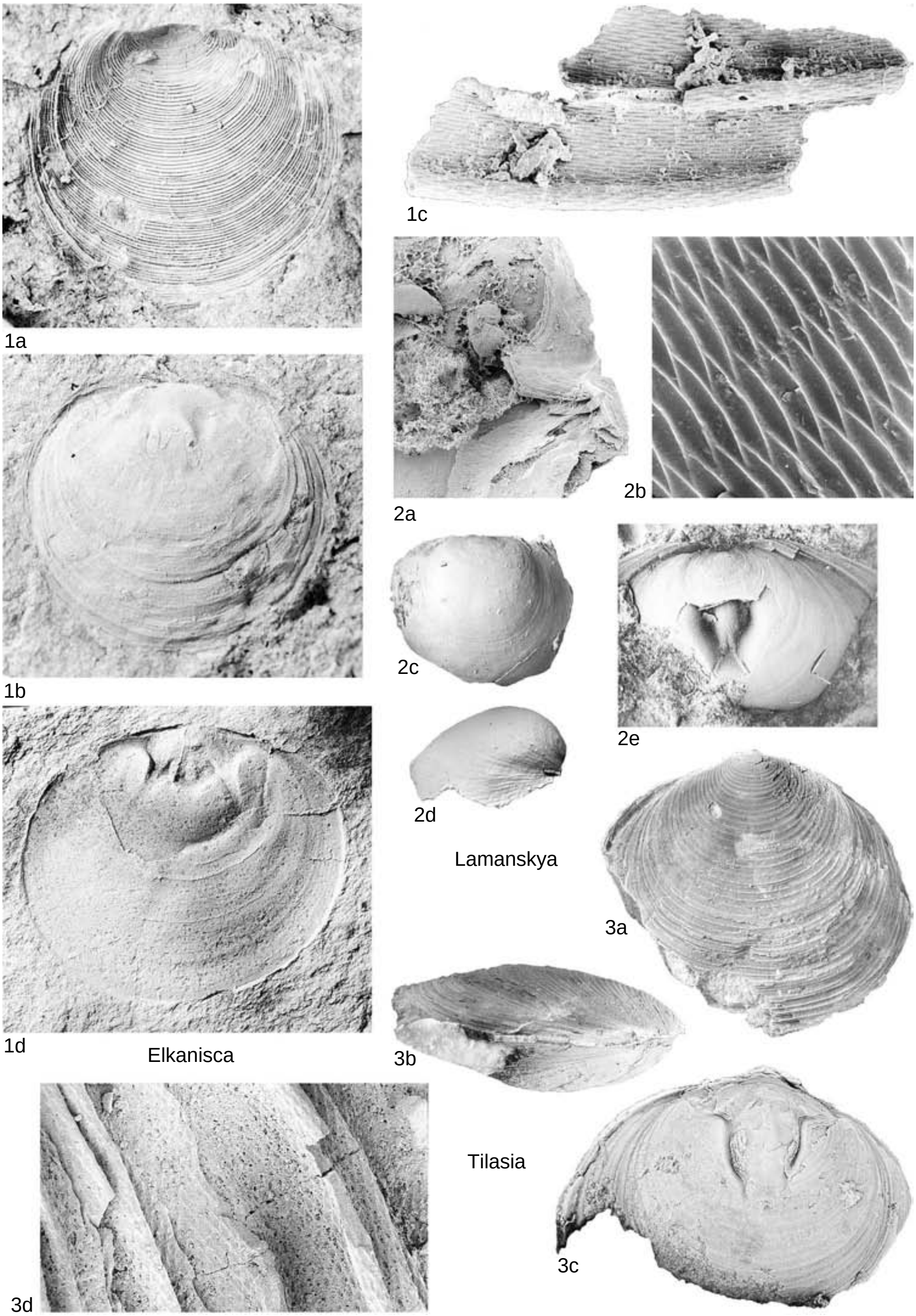

FIG. 31. Elkaniidae (p. 69–72).

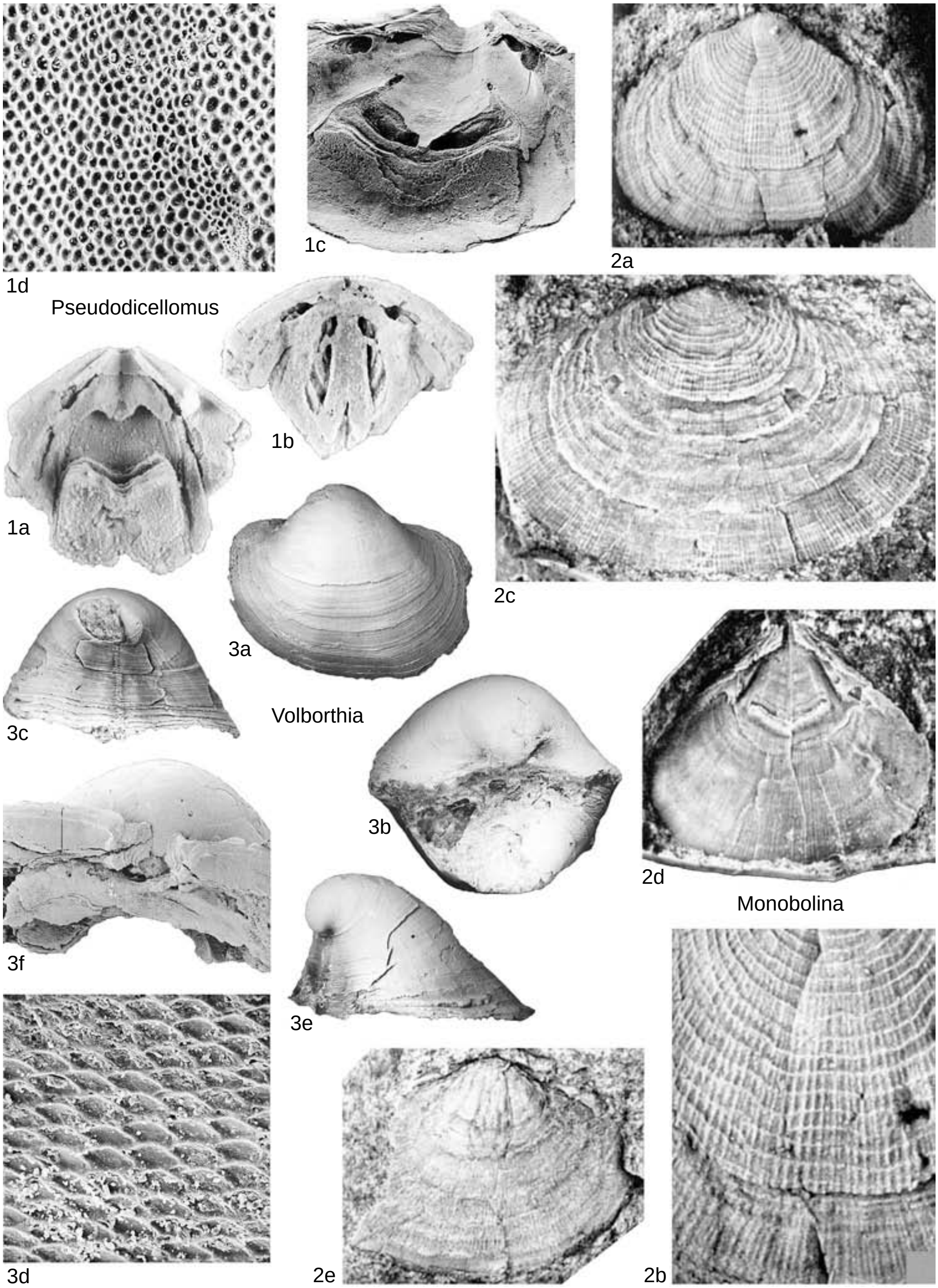

FIG. 32. Elkaniidae (p. 69–72).

133686, ×2.2; *d,* detail of pitted microornamentation, Skålberget, RMS Br 133691, ×50 (Holmer, 1991b).

Volborthia von Möller, 1870, p. 409 [**Acrotreta recurva* Kutorga, 1848, p. 277; OD]. Shell dorsibiconvex, with conical dorsal valve, strongly inequivalved; larval shell with circular pits, postlarval shell ornamented by rhomboidal pits; ventral pseudointrarea rudimentary, anacline with a narrow, deep pedicle groove; dorsal pseudointerarea high, triangular, procline, divided by low ridge; visceral platforms in both valves poorly mineralized; other interior characters poorly known. *Ordovician (upper Arenig–lower Llanvirn):* Sweden, Russia (Ingria).——Fig. 32,*3a–f.* **V. recurva* (Kutorga), upper Arenig–lower Llanvirn, *Asaphus expansus* Biozone, Ingria; *a,b,* neotype, ventral valve exterior, posterior view of both valves, Lava River, RMS Br 136305, ×1.7; *c,* dorsal valve posterior view, ×1.7; *d,* detail of pitted microornamentation, Putilovo quarry, RMS Br 136341, ×179; *e,* dorsal valve, lateral view, Putilovo quarry, RMS Br 136307, ×1.7; *f,* detail of pedicle groove, Volkhov River, RMS Br 136308, ×8.3 (Holmer & Popov, 1995).

Family AULONOTRETIDAE new family

[Aulonotretidae Holmer & Popov, herein]

Shell very thick, strongly biconvex, lamellose; ornamented by undulating, evenly spaced rugae; postlarval shell with microornamentation of fine rhomboidal pits; ventral pseudointerarea well developed, lacking flexure lines, with narrow, deep pedicle groove; dorsal pseudointerarea flattened, with straight posterior margin and poorly defined median groove; visceral area of both valves strongly thickened, extending to midvalve; dorsal central and anterior lateral muscle scars closely placed, bisected by low median ridge; *vascula lateralia* of both valves submedian, slightly convergent; *vascula media* absent. *Ordovician (upper Arenig–lower Llanvirn).*

Aulonotreta Kutorga, 1848, p. 260 [**A. sculpta;* SD Hall & Clarke, 1892, p. 82; =*Obolus antiquissimus* von Eichwald, 1843, p. 143] [=*Acritis* von Volborth, 1869, p. 212, obj.; *Rohonodus* Schallreuter, 1983, p. 108 (type, *R. vastorfensis;* OD)]. Characters as for family. *Ordovician (upper Arenig–lower Llanvirn):* Sweden, *lower Llanvirn;* Estonia, Russia, Ingria, *upper Arenig.*——Fig. 33,*1a–g.* **A. antiquissima* (von Eichwald), upper Arenig, Estonia; *a,* ventral valve exterior, Mäeküla, RMS Br 133729, ×2.5; *b,* lateral view of both valves, Leetse, LMT 1201ql:51, ×1.8; *c,* dorsal valve interior, Tallinn, RMS Br 133538, ×3.1; *d,* dorsal valve exterior, Ingria, BMNH B 5999, ×1.7; *e,* ventral valve interior, Tallinn, RMS Br 65717, ×4.2; *f,* detail of ornamentation of dorsal valve, ×41.7; *g,* detail of pitted microornamentation, RMS Br 65709, ×112 (new).

Family LINGULELLOTRETIDAE Koneva & Popov, 1983

[Lingulellotretidae Koneva & Popov, 1983, p. 116]

Shell elongate oval to subtriangular; larval shell smooth; pseudointerareas of both valves well developed; ventral pseudointerarea with elongate oval pedicle foramen; ventral interior with internal pedicle tube; muscle system with paired umbonal muscle; mantle canal system baculate with *vascula media;* ventral *vascula lateralia* straight and divergent in posterior half; dorsal *vascula lateralia* peripheral. *Lower Cambrian (Botomian)–Ordovician (Tremadoc).*

Lingulellotreta Koneva in Gorjansky & Koneva, 1983, p. 132 [**L. ergalievi;* OD; =*Lingulepis malongensis* Rong, 1974, p. 114]. Shell elongate oval to subtriangular; ventral pseudointerarea orthocline with well-developed flexure lines; dorsal pseudointerarea with wide, concave median groove and short propareas; visceral areas of both valves not thickened; ventral visceral area extended to midvalve; dorsal visceral area with anterior projection extending slightly anterior to midvalve. *Lower Cambrian (Botomian–Toyonian):* Kazakhstan, China (Yunnan).——Fig. 34,*1a–d.* **L. malongensis* (Rong); *a,* dorsal view of external mold, with impression of pedicle, Chiungchussu Formation, Chengjiang, NIGP 113916, ×4.2; *b,* external mold of ventral valve, NIGP 113922, ×12.9 (Jin, Hou, & Wang, 1993); *c,* ventral valve interior, MANK 2224/34, ×16.7; *d,* dorsal valve interior, Ushbass River, MANK 2224/36, ×16.7 (Gorjansky & Koneva, 1983).

Aboriginella Koneva in Koneva & Popov, 1983, p. 121 [**A. denudata;* OD]. Shell elongate oval, moderately to strongly biconvex; ventral pseudointerarea lacking flexure lines; dorsal pseudointerarea flat, undivided, highly elevated; ventral visceral field raised, forming platform, extending to midvalve; dorsal visceral field strongly thickened posteriorly, with low, narrow anterior projection, extended to midvalve; dorsal central and anterior lateral muscle scars small, closely spaced. *Upper Cambrian:* Kazakhstan.——Fig. 34,*2a–d.* **A. denudata,* Zhumabai Formation, Malyi Karatau; *a,* detail of ventral pseudointerarea with pedicle foramen, MANK 427/247, ×8.3; *b,* ventral internal mold, MANK 427/119, ×5; *c,* dorsal pseudointerarea, MANK 427/248, ×16.7 (Koneva & Popov, 1983); *d,* dorsal internal mold, MANK 427/123, ×5 (new).

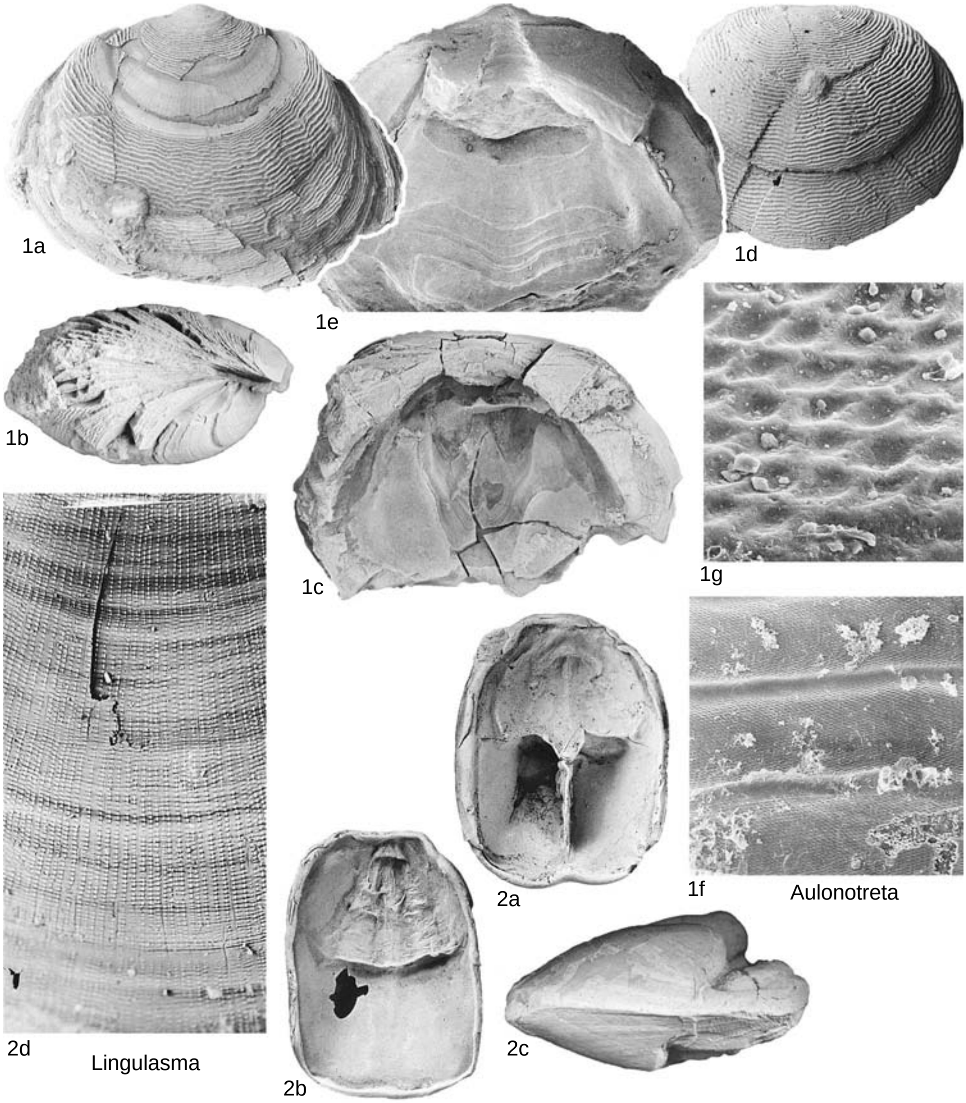

FIG. 33. Aulonotretidae and Lingulasmatidae (p. 72–75).

Mirilingula POPOV in KONEVA & POPOV, 1983, p. 116 [**M. mutabilis;* OD]. Exterior and pseudointerareas similar to *Aboriginella,* but with shallow sulcus in both valves; both valves lacking lacking visceral platforms; dorsal interior with low median ridge. *Upper Cambrian–Ordovician (Tremadoc):* Kazakhstan.——FIG. 34,*4a–c.* **M. mutabilis, Cordylodus proavus* Biozone, Batyrbai, Malyi Karatau; *a,* ventral valve exterior, CNIGR 27/11991, ×2.5; *b,* dorsal valve exterior, CNIGR 29/11991, ×2.5 (Koneva & Popov, 1983); *c,* detail of ventral pseudointerarea with pedicle foramen, RMS Br 136369, ×31.7 (new).——FIG. 34,*4d. M.* sp., Selety Limestone, Upper Cambrian, Selety River; dorsal valve interior, RMS Br 136034, ×22.9 (Popov & Holmer, 1994).

Vaculina KONEVA, 1992, p. 90 [**V. obscura;* OD]. Shell elongate oval, subequally to somewhat dorsibiconvex; ventral propareas highly elevated with flexure lines; dorsal pseudointerarea with shallow median groove; ventral visceral area forming low rhomboidal platform, slightly raised anteriorly, extending to midvalve; ventral *vascula lateralia* straight, slightly divergent, submarginal; dorsal visceral area forming low, subtriangular platform with

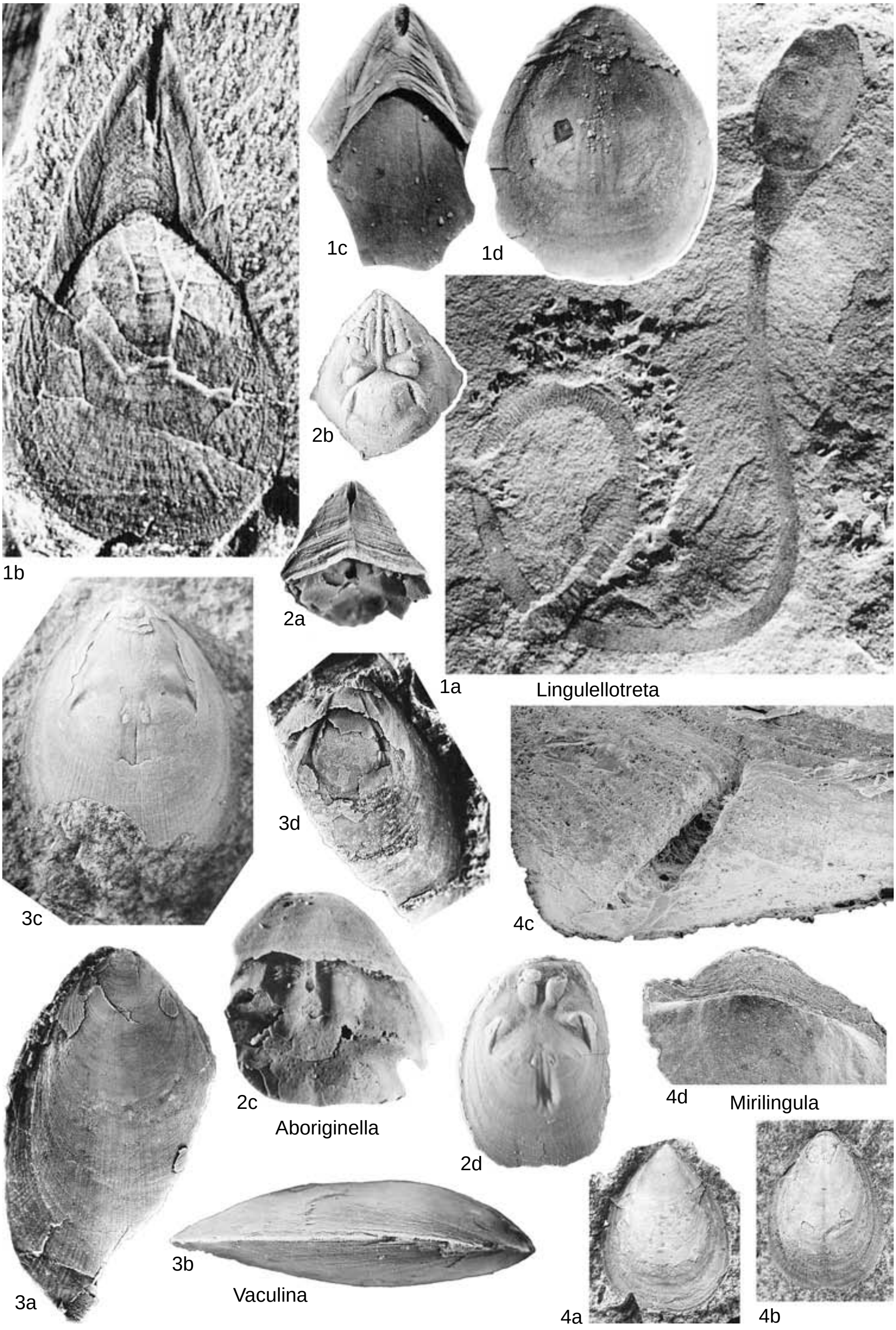

FIG. 34. Lingulellotretidae (p. 72–75).

narrow anterior projection, extending anteriorly beyond midvalve and bisected by median ridge; dorsal *vascula lateralia* marginal, slightly arcuate. *Middle Cambrian (Amgaian)–Upper Cambrian:* Kazakhstan.——FIG. 34,3*a–d.* **V. obscura,* Zhumabai Formation, Upper Cambrian, Malyi Karatau, Kyrshabakty River; *a,b,* holotype, ventral valve exterior, lateral view of both valves, MANK 427/583, ×2.5; *c,* dorsal internal mold, MANK 427/584, ×2.5; *d,* ventral internal mold, MANK 427/578, ×3.3 (Koneva, 1992).

Family LINGULASMATIDAE Winchell & Schuchert, 1893

[Lingulasmatidae WINCHELL & SCHUCHERT, 1893, p. 353]

Shell dorsibiconvex, elongate oval to subrectangular; ornament of radial striae composed of pustules; both valves with three low radial folds; ventral pseudointerarea vestigial with minute pedicle groove, dorsal pseudointerarea absent; visceral fields of both valves highly elevated, forming platforms; dorsal visceral platform supported anteriorly by high median septum; muscle system with paired umbonal muscle; mantle canal system baculate; *vascula lateralia* in both valves straight, subparallel, submarginal. *Ordovician (Llanvirn–Ashgill).*

Lingulasma ULRICH, 1889, p. 383 [**L. schucherti;* OD] [=*Lingulelasma* MILLER, 1889, p. 351]. Characters as for family. *Ordovician (Llanvirn–Ashgill):* Sweden, Norway, *Llanvirn;* Russia (Ingria), *Llanvirn–Llandeilo;* Estonia, *Llanvirn–Caradoc;* Lithuania, *Llandeilo–Caradoc;* Great Britain, Ireland, *Llandeilo–Ashgill;* Canada, Ontario, Quebec, USA, *Caradoc–Ashgill.*——FIG. 33,*2a,b.* **L. schucherti,* Ashgill, Wilmington, Illinois; *a,* cast of dorsal internal mold, ×0.8; *b,* cast of ventral internal mold, USNM 45194, ×0.8 (Rowell, 1965a).——FIG. 33,*2c. L. galenense* WINCHELL & SCHUCHERT, Decorah Formation, middle Caradoc, Decorah, USNM loc. no. 303, Iowa; lateral view of internal mold of both valves, USNM 459769, ×1.7 (new).——FIG. 33,*2d. L. compactum* COOPER, Oranda Formation, lower Caradoc, Linville Station, Virginia; holotype, detail of pustulose ornamentation, USNM 109347, ×6.7 (Cooper, 1956).

Family PATERULIDAE Cooper, 1956

[Paterulidae COOPER, 1956, p. 236]

Shell elongate oval, dorsibiconvex, inequivalved; both valves with submarginal apex and limbus; larval and postlarval shell small, with pitted microornamentation; both valves lacking pseudointerarea; ventral valve with narrow pedicle notch; visceral fields of both valves large, extended anterior to midvalve; muscle system with paired umbonal muscle bisected by impression of pedicle nerve; mantle canal system baculate with *vascula media;* both valves with submarginal, arcuate *vascula lateralia;* pleurocoel well developed. *Ordovician (Arenig)–Silurian, ?Devonian.*

Paterula BARRANDE, 1879, pl. 110 [**P. bohemica;* OD]. Characters as for family. *Ordovician (Arenig)–Silurian, ?Devonian:* USA, Canada, *Arenig–Silurian;* Bohemia, *Llanvirn–Caradoc;* Russia, *Arenig–Caradoc;* Sweden, Norway, Denmark, Poland, Lithuania, Estonia, Kazakhstan, *Arenig–Ashgill;* Great Britain, Ireland, *Llanvirn–Ashgill;* Australia, *Caradoc–Ashgill;* ?Thailand, *?Devonian.*——FIG. 35*a–h. P. perfecta* COOPER; *a,* ventral valve interior, Oranda Formation, lower Caradoc, Linville Station, Virginia, USNM 109404g, ×25 (Cooper, 1956); *b,* ventral valve exterior, ×20.8; *c,* oblique posterior view of ventral valve, ×26.7; *d,* detail of ventral larval shell and pedicle notch, ×125; *e,* microornamentation of ventral larval shell, ×1142; *f,* microornamentation of postlarval shell, USNM 459680a, ×333; *g,* dorsal valve exterior, USNM 459680b, ×42.7; *h,* detail of interior pedicle notch, Pratt Ferry beds, Llandeilo, Alabama, USNM 459680c, ×62.5 (new).——FIG. 35*i. P. circina* HAVLÍČEK, Dobrotivá Formation, Bohemia (Liben-Bílá skála); paratype, dorsal internal mold, OMR VH 3239, ×9.2 (Havlíček, 1982).

Family DYSORISTIDAE Popov & Ushatinskaya, 1992

[Dysoristidae POPOV & USHATINSKAYA, 1992, p. 66]

Shell subcircular to elongate oval; larval and postlarval shell with pitted microornamentation; ventral valve with circular foramen extending anteriorly through resorption; posterior part of foramen closed by plate; pseudointerarea flat, undivided; dorsal pseudointerarea with median groove and well-developed propareas; dorsal visceral field with anterior projection extending anteriorly beyond midvalve; muscle system with paired umbonal muscle; mantle canal system baculate with *vascula media. Upper Cambrian–Ordovician (Arenig).*

Dysoristus BELL, 1944, p. 146 [**D. lochmanae;* OD] [=*Dysozistus* GORJANSKY, 1960, p. 182]. Shell biconvex, subtriangular, elongate oval; pedicle foramen

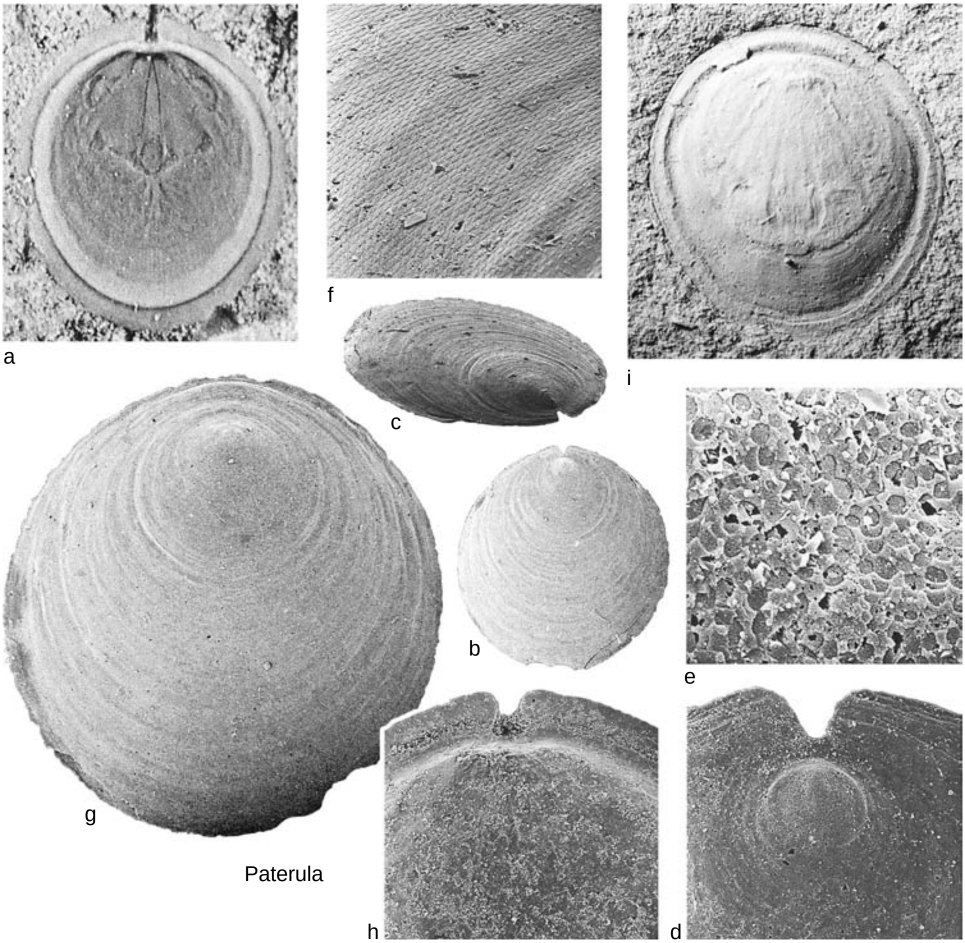

FIG. 35. Paterulidae (p. 75).

widely subtriangular, covered apically by plate; ventral visceral field not extending to midvalve; dorsal visceral field with narrow anterior projection, extending anteriorly beyond midvalve, and bisected by weak median ridge; *vascula lateralia* of both valves marginal, arcuate; *vascula media* divergent. *Upper Cambrian:* USA, Kazakhstan.——FIG. 36,*1a–f.* **D. lochmanae,* Dresbachian, *Dunderbergia* Zone, Nevada; *a,* ventral valve exterior, ×20; *b,* lateral view, ×22.5; *c,* oblique posterior view of pedicle foramen, RMS Br 136267, ×41.7; *d,* ventral valve interior, RMS Br 136266, ×18.3; *e,* dorsal valve exterior, ×18.3; *f,* lateral view, RMS Br 136265, ×25 (new).——FIG. 36,*1g–i. D. orientalis* POPOV & HOLMER, Aksak-Kujandy Mountain; *g,* ventral interior, pseudointerarea, lateral view, RMS Br 136059, ×20.8; *h,* dorsal interior, ×20; *i,* lateral view of dorsal interior, RMS Br 136061, ×33.3 (Popov & Holmer, 1994).

Ferrobolus HAVLÍČEK, 1982, p. 71 [**F. catharinus;* OD]. Shell subcircular; pedicle track elongate triangular, with rounded pedicle foramen; ventral visceral area small, not extending to midvalve; ventral *vascula lateralia* submedian. *Upper Cambrian–Ordovician (Arenig):* Kazakhstan; Bohemia, *?Tremadoc–lower Arenig.*——FIG. 36,*2a–c.* **F. catharinus,* Trenice Formation, Holoubkov, Bohemia; *a,* holotype, latex cast of ventral external mold, NM L 18125, ×6.7; *b,* ventral internal mold, OMR VH 3067, ×6.7 (Havlíček, 1982); *c,* dorsal internal mold, OMR VH 3066a, ×6.7 (new).——FIG. 36,*2d–f. F. fragilis* POPOV & HOLMER, Olenty Formation, Sasyksor Lake, Kazakhstan; *d,* detail of ventral pseudointerarea and internal pedicle foramen, RMS Br 136064, ×62.5; *e,* ventral valve exterior, ×26.7; *f,* detail of pitted microornamentation of ventral valve, RMS Br 136066, ×417 (Popov & Holmer, 1994).

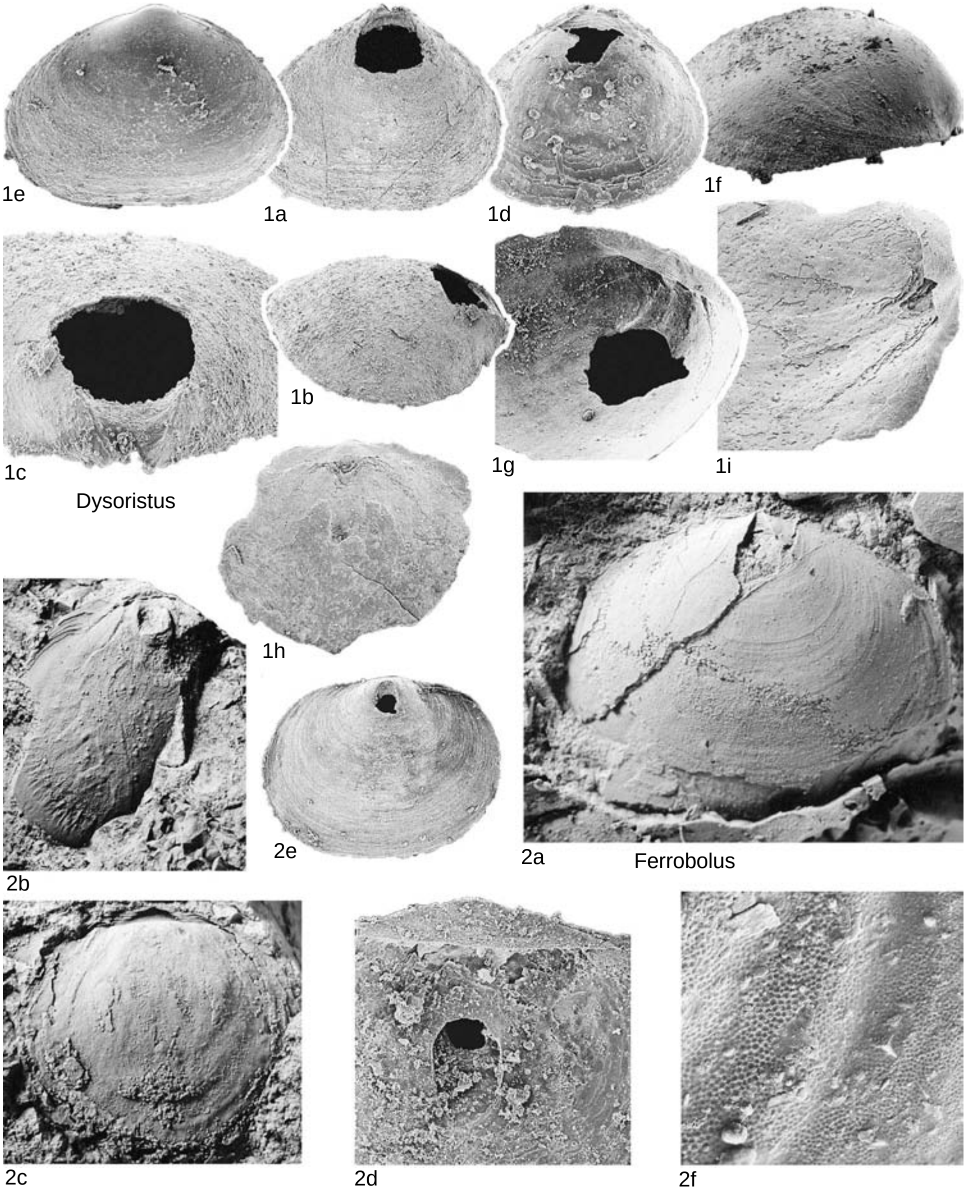

FIG. 36. Dysoristidae (p. 75–76).

Family UNCERTAIN

Bistramia VON HOEK, 1912, p. 247 [**B. elegans;* OD] [=?*Pizarroa* VON HOEK, 1912, p. 246 (type, *P. quichuana*); *Tunarites* COOPER & MUIR-WOOD, 1951, p. 196, *nom. nov. pro Tunaria* VON HOEK, 1912, p. 247 (type, *Tunaria cochambina*), *non* LINK, 1807]. Shell dorsibiconvex, subtriangular, with fine rugae; ventral valve with acuminate beak; ventral pseudointerarea small, subtriangular, with narrow pedicle groove; dorsal pseudointerarea forming narrow strip along short posterior margin; dorsal visceral area slightly thickened, rhomboidal, extending anteriorly beyond midvalve and bisected by fine median ridge; *vascula lateralia* of both valves submarginal, straight and divergent proximally; *vascula media* short, subparallel. *Ordovician (?Caradoc):* Bolivia.——FIG. 37,*3a–d.* **B. elegans,* Bolivia; *a,*

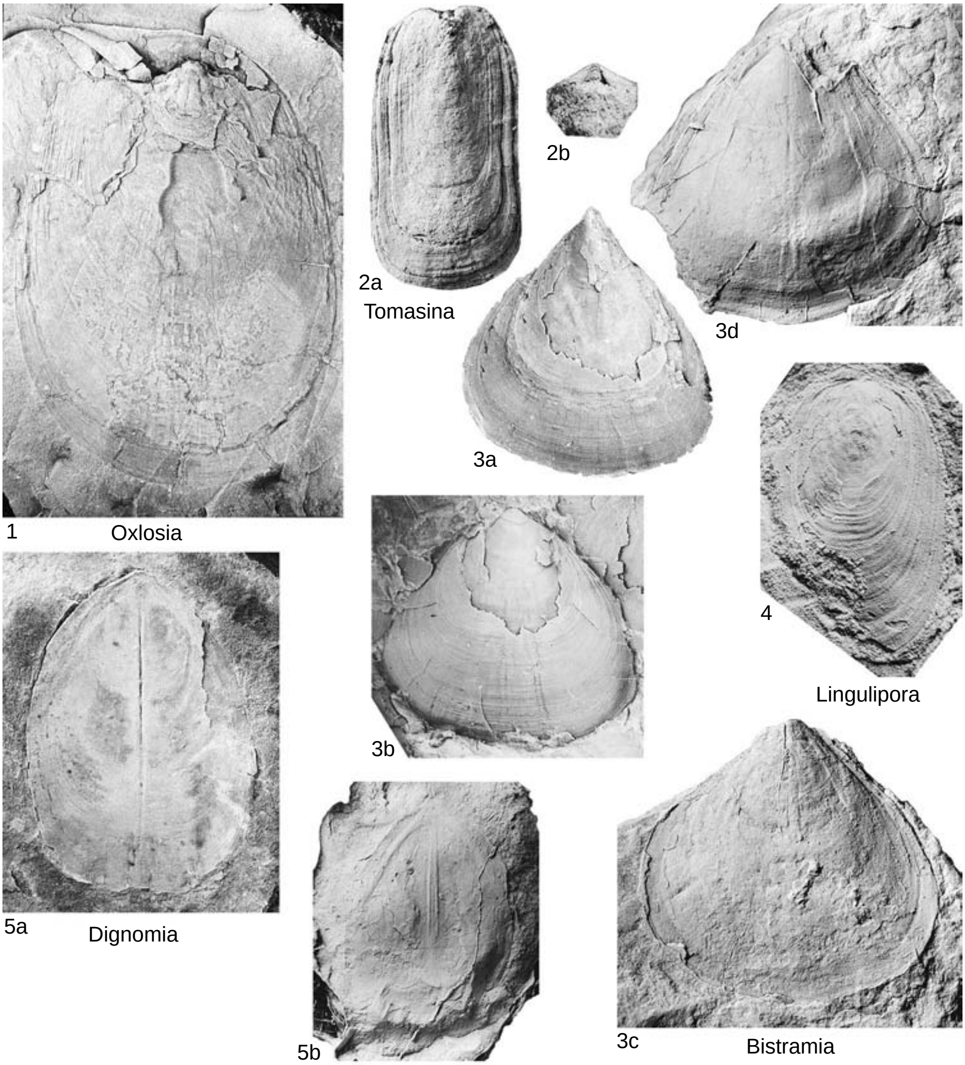

FIG. 37. Uncertain (p. 77–79).

ventral valve exterior, USNM 459681a, ×2.1; *b,* dorsal valve exterior, USNM 459681b, ×2.1; *c,* ventral internal mold, USNM 459681c, ×2.1; *d,* dorsal ventral internal mold, USNM 459681c, ×2.1 (new).

Dignomia HALL, 1871a, p. 2 [**Lingula alveata* HALL, 1863a, p. 23; SM HALL, 1872a, pl. 13]. Shell subtriangular to suboval; ventral interior with two widely divergent ridges posteriorly (may be impression of pedicle nerve); dorsal interior with long median ridge. All other characters inadequately known. *Middle Devonian:* USA (New York, Ohio).——FIG. 37,*5a,b.* **D. alveata* (HALL), Hamilton Group, New York; *a,* latex cast of ventral internal mold, latex cast, Cayuga Lake, Ludlowville, AMNH 36787, ×0.8 (new); *b,* dorsal internal mold, Seneca Lake, USNM 91851, ×0.8 (Rowell, 1965a).

Laima GRAVITIS, 1981, p. 448 [**L. latgalica;* OD]. Shell elongate suboval to subrectangular, equally biconvex. All other characters unknown. *Middle Devonian:* Latvia.

Lingulipora GIRTY, 1898, p. 387 [**Lingula (Lingulipora) williamsana;* OD]. Shell elongate oval; coarsely punctate; ventral pseudointerarea well developed, with deep, triangular pedicle groove and elevated propareas, lacking flexure lines; dorsal pseudointerarea absent; interior of both valves poorly known. *Middle Devonian–Upper Carboniferous:* USA (Virginia, New Mexico, Oklahoma, Kentucky, Texas), Poland, Russia.——Fig. 37,*4*. **L. williamsana* (Girty), Upper Devonian, Virginia; dorsal valve exterior, USNM 97988a, ×3.3 (Rowell, 1965a).

Lunoglossa Xu & Xie, 1985, p. 469 [**L. puqiensis;* OD]. Shell elongate oval; ventral pseudointerarea well developed, with pedicle groove; interiors of both valves poorly known. *Upper Permian:* China.

Oxlosia Ulrich & Cooper, 1936b, p. 619, *nom. nov. pro Eunoa* Clarke, 1902, p. 606, *non* Malmgren, 1867 [**Eunoa accola* Clarke, 1902, p. 607; OD]. Shell weakly biconvex, elongate oval, with fine rugae; both valves with submarginal apex; interior of both valves and ventral valve inadequately known. *Ordovician (Arenig–Llanvirn):* Canada (Quebec), *Arenig;* Kazakhstan, *Llanvirn.*——Fig. 37,*1*. **O. accola* (Clarke), Levis Shale, Quebec (Levis), Canada; dorsal valve exterior, USNM 71832, ×8.3 (Ulrich & Cooper, 1938).

Timalina Batrukova, 1969, p. 70 [**T. miranda;* OD]. Genus poorly known; pseudointerarea and interior characters unknown. *Upper Devonian:* Russia (Komi).

Tomasina Hall & Clarke, 1892, p. 65 [**Lingula criei* Davidson in Guillier, 1881, p. 372; OD] [=*Tomasina* Hall, 1891, p. 15, *nom. nud.*]. Shell elongate subrectangular; ventral beak distinctly elevated above plane of commissure; triangular opening beneath beak. *Ordovician (Arenig):* France, Great Britain.——Fig. 37,*2a,b*. **T. criei* (Davidson), Sarthe; latex cast of ventral valve external mold, posterior view of pseudointerarea, ×1.2 (Rowell, 1965a).

Superfamily DISCINOIDEA Gray, 1840

[*nom. correct.* Harper & others, 1993, p. 430, *ex* Discinacea Gray, 1840, *nom. imperf., nom. transl.* Schuchert, 1896, p. 309, *ex* Discinidae Gray, 1840, p. 155]

Growth of ventral valve holoperipheral; larval shell smooth, large (about 0.5 mm across), lacking pedicle notch; pedicle opening in young, postlarval stages forming triangular notch in posterior margin of ventral valve; adult pedicle opening may be closed posteriorly or extend to margin of shell; anterior end of track of pedicle opening usually closed by listrium; ventral valve lacking well-defined pseudointerarea; muscle system with paired posterior and anterior adductors and three pairs of oblique muscles; posterolateral muscle fields in ventral valve situated posterior to umbo; mantle canal system bifurcate in recent stocks; *vascula media* well developed. *Ordovician–Holocene.*

The Discinoidea have been classified previously with the Acrotretoidea, from which they were thought to have originated (Williams & Rowell, 1965a). This assumption was based mainly on the presence of an acrotretoidean pedicle foramen in both groups; however, as noted by several authors (e.g., Chuang, 1971b, 1977; Wright, 1979; Popov & Nõlvak, 1987; Iwata, 1982; Holmer, 1987, 1989b) fossil and recent discinoideans seem to share more characters with the linguloideans, most notably the following: (1) ontogeny—both groups generally have a comparatively large, smooth, circular to transversely suboval larval shell, generally about 0.5 mm across, which lacks a pedicle notch (Chuang, 1977; Holmer, 1989b); (2) anatomy—the discinoidean musculature with paired posterior and anterior adductors and three pairs of oblique muscles as well as the bifurcate mantle canals of the recent discinoideans show a great deal of resemblance to those of linguloideans (Helmcke, 1939); (3) shell structure—both groups have baculate laminae (Iwata, 1982; Holmer, 1989b; Williams, Mackay, & Cusack, 1992); (4) ornamentation—the postlarval shell of many fossil discinoideans and some linguloideans have an identical type of distinctive, pitted microornamentation (Holmer, 1989b) probably representing a cast of the infrastructure of the periostracum (Williams & Curry, 1991).

The elevation of the superfamily to ordinal rank was proposed by Wright (1979), Popov (in Nazarov & Popov, 1980) and Holmer (1989b), but our cladistic analysis (Fig. 38) suggests that the discinoideans might be better considered as a superfamily within the Lingulida. Moreover, the analysis indicates also that the discinoideans are possibly a sister group to the Paterulidae, with which they share some potential synapomorphies (Table 4–6). Thus, it seems that the discinoideans may have been derived directly from within the Lingulida, but the earliest history of the discinoideans is still poorly known; the Zhanatellidae has also been proposed as a possible ancestral stock for the group (Popov, 1992; Popov & Ushatinskaya, 1992).

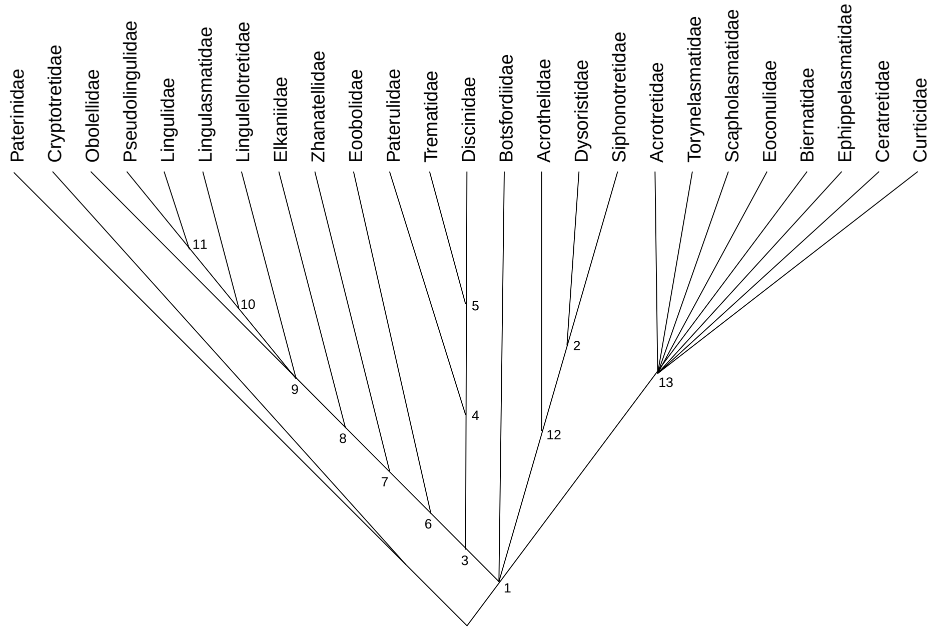

FIG. 38. Strict consensus tree of 354 equally parsimonious cladograms; numbered nodes supported by character states listed in Table 4; see also Table 5–6 (new).

Details of the relationship between the two families Trematidae and Discinidae are also not known; the latter family appears to be somewhat older, and the first recorded possible discinid is the poorly known *Orbiculoidea? subovalis* BIERNAT from the Tremadoc of Poland (BIERNAT, 1973). The oldest undoubted member of the Discinidae is from the Arenig of Baltoscandia, belonging to *Schizotreta sensu lato*, while the earliest trematid (*Schizocrania*) is from the Llanvirn (WILLIAMS, 1974).

The Trematidae is distinguished from the Discinidae mainly by a combination of characters, including postlarval ornamentation of superficial pits (lacking in *Schizocrania* and *Schizobolus*) and a posteriorly unrestricted pedicle opening (except in *Drabodiscina*). The trematid postlarval pits are larger, around 0.05 to 0.5 mm in diameter, than those of many Paleozoic discinids (*Schizotreta, Orbiculoidea,* and *Acrosaccus*), which are generally less than 4 mm in diameter; the only types of postlarval pits that are similar occur in the lingulid *Foveola* and in the enigmatic paterinids (WRIGHT, 1981). The interpretation of the trematid pits is uncertain; WRIGHT (1981) noted that it is unlikely that the pits contained organic material other than the periostracum and that their structure suggests that they may reflect undula-

TABLE 4. Synapomorphy scheme for internal nodes of cladogram shown in Figure 38 (new).

Node	Character states
1	10:4 14:1 15:0 21:0 29:0 30:1
2	3:1 5:1
3	10:3 35:0
4	4:1 7:1
5	10:0 12:1 14:0
6	1:1 4:0
7	3:0 7:2
8	5:0 7:0
9	9:1 18:1 19:1 30:0
10	1:0 2:0
11	9:0 12:0 17:1 18:0 19:1
12	1:3 2:0 11:1 21:1 22:1 28:1 29:1
13	9:3 16:1 21:2 22:2 25:2 27:2 28:2 33:0 0:2

TABLE 5. List of coded characters used in cladistic analysis (Fig. 38) of families of organophosphatic brachiopods (new).

1. convexity: biconvex (0); dorsibiconvex (1); ventribiconvex or planoconvex (2); convexoplane (3).
2. relative size of valves: equivalved (0); inequivalved (1).
3. ornamentation of larval shell: smooth (0); pitted (1); pustulose (2).
4. ventral larval tubercles: absent (0); present (1).
5. boundary of larval shell: poorly defined (0); marked by elevated rim (1); marked by elevated rim and change in microornamentation (2).
6. larval pedicle opening: marginal notch in larval shell (0); opening within larval shell (1).
7. granulation: absent (0); present (1); radial rows of granules (2).
8. hollow spines: absent (0); present (1).
9. ventral pseudointerarea: absent (0); present, shelflike (1); vestigial (2); not differentiated (3).
10. adult pedicle opening: delthyrial (0); elongate pedicle foramen on pseudointerarea (1); elongate pedicle track on posterior slope (2); foramen situated posterior to umbo (3); small apical foramen (4); foramen situated anterior to umbo (5); secondary delthyrium (6).
11. listrium: absent (0); present (1).
12. pedicle groove: absent (0); present (1); present in juveniles, transformed into internal pedicle tube in adults (2).
13. transmedian muscle scars: paired symmetrical (0); asymmetrical (1); on inner side on acrotretoid ventral pseudointerarea (2).
14. posterolateral muscle platforms: absent (0); present, posterolateral (1); present, posteromedian (2).
15. homeodeltidium: absent (0); present (1); vestigial (2).
16. acrotretoid ventral pseudointerarea: absent (0); present (1).
17. dorsal umbo: marginal (0); submarginal (1); subcentral (2).
18. dorsal pseudointerarea: absent (0); present (1).
19. posterior body wall: close to posterior margin (0); at a distance from posterior margin (1).
20. mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
21. ventral posterolateral muscle fields: anterolateral to apex (0); posterolateral to apex (1); situated on inner sides of acrotretoid pseudointerarea (2); situated on the inner sides of homeodeltidium (3).
22. ventral posterior adductor muscle scars: paired, posteromedian (0); paired, posterolateral (1); paired, subcentral (2); absent (3); forming single scar (4).
23. ventral *vascula media:* absent (0); present (1).
24. dorsal visceral field: weakly defined or slightly thickened anteriorly (0); forming elevated platform (1).
25. ventral anterior muscle field: weakly defined or slightly raised (0); forming solid muscle platform (1); on apical process (2).
26. apical process (if present): low ridge anterior to pedicle tube (0); occluding apex (1); wide ridge perforated by pedicle tube (2); wide, subtriangular, anterior and lateral to foramen (3); wide, subtriangular, anterior to foramen (4); bosslike (5); vestigial to absent (6); high septum (7); high ridge anterior to foramen (8).
27. posterolateral muscle fields: weakly defined to slightly raised (0); forming platforms (1); forming cardinal scars (2).
28. outside lateral muscle scars: present (0); absent (1); combined with middle lateral scars (2).
29. mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
30. dorsal *vascula media:* absent (0); present, short (1); present, long (2).
31. median buttress: absent (0); present (1).
32. dorsal median septum or ridge (in acrotretoideans): absent (0); low triangular (1); high triangular (2).
33. dorsal anterior adductor scars: absent (0); present (1).
34. shell structure: baculate (0); granular (1); columnar (2).
35. resorption around pedicle foramen: absent (0); present (1).
36. pitted postlarval microornamentation: absent (0); present (1).
37. profile of ventral valve: gently convex (0); strongly convex to conical (1); low conical, catacline with subcentral apex (2); high conical, procline to catacline (3); high conical, apsacline to procline (4); adopting shape of substrate (5).
38. shape of acrotretoid pseudointerarea: well defined laterally (0); convex in cross section, poorly defined laterally (1); flattened, well defined laterally (2).
39. pedicle nerve impression: absent (0); bisecting umbonal muscle scars (1); passing lateral to umbonal muscle scars (2).
40. dorsal larval tubercles: absent (0); present (1).

tions of the mantle edge. The ontogeny of most trematids is poorly studied; according to CHUANG (1971b), *Trematis* has an embryonic shell (around 0.18 mm wide) as well as a larval shell (around 0.47 mm wide), but traces of the embryonic shell have not been

TABLE 6. Character-state matrix used in PAUP analysis (Fig. 38) of characters as listed in Table 5. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Paterinidae	2	1	2	0	2	0	0	0	1	0	0	0	9	0	1	0	0	1	0	2
Cryptotretidae	2	1	9	0	9	0	0	0	1	0	0	0	9	0	1	0	0	1	0	9
Obolidae	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	9	0
Pseudolingulidae	0	0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	1	1	0
Lingulidae	0	0	0	0	0	0	0	0	2	0	0	1	1	0	0	0	0	1	1	1
Lingulellotretidae	1	1	0	0	0	0	0	0	1	1	0	2	0	9	0	0	0	1	0	0
Lingulasmatidae	1	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	1	0
Elkaniidae	1	1	0	0	1	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0
Zhanatellidae	1	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0
Dysoristidae	2	1	1	0	1	0	0	0	1	5	0	0	0	0	0	0	0	1	0	0
Paterulidae	1	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0
Eoobolidae	1	1	1	0	2	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0
Botsfordiidae	2	1	1	1	2	0	1	0	2	0	0	1	0	0	0	0	0	1	0	0
Acrothelidae	2	1	1	1	2	0	1	0	3	3	0	0	0	1	0	0	9	1	0	0
Siphonotretidae	2	0	0	0	0	0	0	1	1	5	0	0	0	0	0	0	0	1	0	0
Trematidae	3	0	0	0	9	0	0	0	3	2	1	0	0	0	0	0	1	0	1	0
Discinidae	9	0	0	0	2	0	0	0	3	2	1	0	0	0	0	0	1	0	1	1
Acrotretidae	2	1	1	0	2	9	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Torynelasmatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Scaphelasmatidae	2	1	1	0	2	0	0	0	3	4	0	0	2	0	0	1	0	1	0	0
Ceratretidae	2	1	1	0	2	0	0	0	3	2	0	0	2	1	0	1	0	1	0	0
Ephippelasmatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9
Eoconulidae	2	1	1	0	2	0	0	0	3	4	0	0	2	0	0	1	9	9	0	0
Curticiidae	2	1	1	0	2	0	0	0	3	6	0	0	2	0	0	1	0	1	0	0
Biernatidae	2	1	1	0	2	1	0	0	3	4	0	0	2	0	0	1	0	1	0	9

observed from any other trematid. The only detailed study of the trematid muscle system (*Trematis*) indicates that it was closely similar to that of the Discinidae (Chuang, 1971b), but in most forms the muscle scars are weakly impressed.

Rowell (1965a) subdivided the Discinidae into three subfamilies, Orbiculoideinae, Disciniscinae, and Discininae, based mainly on differences in the presence or absence of an internal pedicle tube and a posteriorly unrestricted pedicle notch. This practice is not followed here; as far as can be determined at present, the development of these characters is variable within genera like *Roemerella, Lindstroemella,* and *Lingulodiscina.* The detailed morphology of most fossil discinids, however, remains extremely poorly known. The Paleozoic genera *Orbiculoidea, Schizotreta,* and *Acrosaccus* seem to share the distinctive pitted postlarval microornamentation, which might be used to distinguish the Orbiculoideinae, but the distribution of this character within the Discinidae is not yet known.

It is accepted generally that the posterior and anterior adductors of recent discinids are the homologues of the lingulid umbonal and central muscles (Williams & Rowell, 1965a), but the exact correlation of the three pairs of oblique muscles of the discinids with the four pairs in lingulids is somewhat uncertain; the discinid oblique posterior probably corresponds to the lingulid transmedian muscle and the oblique internal may be the equivalent to the lingulid middle lateral muscle (on the assumption that the outside lateral muscle is reduced in the discinides), while the oblique lateral muscle of the discinids may correspond with the anterior lateral muscle of the lingulids (see Fig. 39). The muscle system of most fossil discinids is not well known; it is best known in *Schizotreta* and *Lochkothele* (Popov & Ushatinskaya, 1992; Havlíček & Mergl, 1988). As pointed out by Popov and Ushatinskaya

Table 6. *(Continued).*

Character no.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Paterinidae	3	9	1	0	0	9	0	9	3	1	0	9	9	9	9	0	1	9	0	0
Cryptotretidae	3	9	9	0	0	9	0	9	9	1	0	9	9	9	9	0	1	9	0	0
Obolidae	0	0	0	9	9	9	9	0	0	1	0	9	1	0	0	0	0	9	1	0
Pseudolingulidae	0	0	0	0	0	9	0	0	0	0	0	9	1	0	0	0	0	9	1	0
Lingulidae	0	4	0	0	0	9	0	0	1	0	0	9	1	9	0	0	0	9	2	0
Lingulellotretidae	0	0	0	9	9	9	0	0	0	1	0	9	1	0	0	0	0	9	1	0
Lingulasmatidae	0	0	0	1	1	9	0	0	0	9	0	9	1	0	0	0	0	9	1	0
Elkaniidae	0	0	0	1	1	9	1	0	0	1	0	9	1	0	0	1	1	9	1	0
Zhanatellidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	1	0	9	1	0
Dysoristidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	1	1	0	9	0	0
Paterulidae	0	0	0	0	0	9	0	0	0	1	0	9	1	9	0	1	0	9	1	0
Eoobolidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	1	0	9	1	0
Botsfordiidae	0	0	0	0	0	9	0	0	0	1	0	9	1	0	0	0	0	9	1	1
Acrothelidae	9	9	0	0	0	9	0	0	0	1	0	9	1	0	0	0	1	9	0	1
Siphonotretidae	0	0	0	0	0	9	0	0	0	1	0	9	1	1	1	0	0	9	0	0
Trematidae	1	1	0	0	0	9	0	1	9	9	0	9	1	0	0	0	0	9	0	0
Discinidae	1	1	0	0	0	9	0	1	1	1	0	9	1	0	0	1	1	9	1	0
Acrotretidae	2	2	0	0	2	9	2	2	0	1	1	9	9	2	0	0	1	9	0	0
Torynelasmatidae	2	2	0	0	2	1	2	2	9	9	1	1	0	2	0	0	3	2	0	0
Scaphelasmatidae	2	9	0	0	2	6	2	9	9	9	0	2	9	2	0	0	2	1	0	0
Ceratretidae	2	2	0	0	2	7	2	2	0	9	1	1	0	2	0	0	1	0	0	0
Ephippelasmatidae	2	2	0	0	2	1	2	2	9	9	0	1	0	2	0	0	4	0	0	0
Eoconulidae	2	2	0	0	2	6	2	9	9	9	0	9	9	2	0	0	5	1	0	0
Curticiidae	2	2	0	0	2	4	2	9	9	9	1	0	9	9	1	0	1	0	0	0
Biernatidae	2	3	0	0	2	6	2	2	2	1	0	1	0	2	0	0	4	1	0	0

(1992, fig. 9), the relative position of the muscle scars in these two genera appears to be very similar to those of most Paleozoic linguloideans; among other things, the dorsal visceral area of *Schizotreta* has a linguloidean, anterior projection bearing the scars of the oblique lateral muscle, which occupies exactly the same position as the dorsal anterior lateral muscles in the linguloideans (Fig. 39).

Family TREMATIDAE Schuchert, 1893

[Trematidae Schuchert, 1893, p. 149] [=Ptychopeltidae Horný, 1961, p. 299]

Shell usually ornamented with large, superficial pits; beak of dorsal valve marginal, protruding beyond ventral valve; pedicle opening usually extending to posterior margin of ventral valve in all growth stages. *Ordovician–Devonian.*

Trematis Sharpe, 1848, p. 66 [**Orbicula terminalis* Emmons, 1842, p. 395; SD Davidson, 1853, p. 130]. Shell dorsibiconvex, circular to suboval; ornament of small, rounded to rectangular, superficial pits variably arranged, commonly in rough quincunx or in rows radiating from beak; ventral valve with subcentral apex, margins of pedicle notch straight or concave toward midline; dorsal pseudointerarea not raised above valve floor; dorsal median ridge low, variably developed, separating two bean-shaped composite muscle scars. *Ordovician (Llandeilo–Ashgill), ?Silurian:* Great Britain, Ireland, Kazakhstan, *Llandeilo–Ashgill;* Jordan, *Caradoc–Ashgill;* USA, Canada, *Caradoc–Ashgill, ?Silurian;* Bohemia, Norway, South Africa, *Ashgill.*——Fig. 40,*1a,b.* **T. terminalis* (Emmons), Trenton Group, Caradoc, New York; *a,* ventral internal mold, Trenton Falls, USNM 92255, ×3.3; *b,* dorsal internal mold, Black Creek, USNM 459682, ×3.3 (new).——Fig. 40,*1c,d. T. millipunctata* Hall, Wagnesville Formation, Ashgill, Wagnesville, Ohio; dorsal valve exterior, ventral valve exterior, USNM 40441, ×2.5 (new).

Drabodiscina Havlíček, 1972, p. 231 [**Discina grandis* Barrande, 1879, pl. 97.1; OD]. Similar to *Trematis,* but larger, planoconvex, with only rectangular pits; pedicle opening not reaching posterior valve margin. *Ordovician (Caradoc–Ashgill):* Bohemia.——Fig. 40,*3a–c.* **D. grandis* (Barrande), Letná Formation, Caradoc, Prague basin; *a,* ventral internal mold, NM, ×1.2; *b,* dorsal external mold, NM, ×1.2; *c,* detail of ornamentation, ×5 (new).

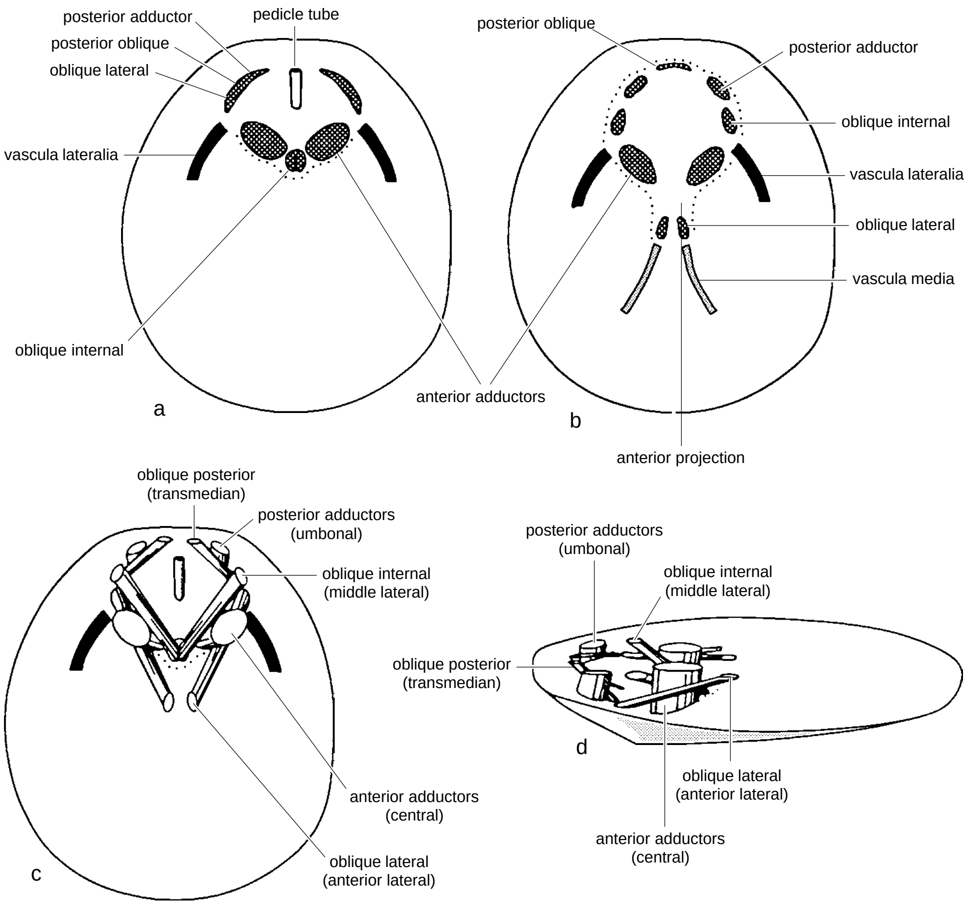

Fig. 39. Schematic illustration of musculature and mantle canal system of *Schizotreta; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

Schizocrania Hall & Whitfield, 1875, p. 71 [*?*Orbicula filosa* Hall, 1847, p. 99; OD] [=*Ptychopeltis* Perner, 1903, p. 42 (type, *P. incola;* OD); *Orbiculothyris* Wolfart in Wolfart, Bender, & Stein, 1968, p. 528 (type, *O. costellata;* OD)]. Shell subcircular to subtriangular, convexoplane to convexoconcave; dorsal valve ornamented by fine costellae; ventral valve less costellate or lacking costellae; ventral valve circular in outline; pedicle opening broadly triangular, with straight margins; listrium small; posterior margin of dorsal valve slightly thickened. *Ordovician–Lower Devonian:* Peru, *Ordovician–Silurian;* Ireland, *upper Llanvirn–Ludlow;* Bohemia, *Llandeilo–early Caradoc;* Jordan, *Caradoc–Ashgill;* USA, Canada, *Caradoc–Lower Devonian;* Libya, *Ashgill;* Sweden, Estonia, Lithuania, *Silurian;* Great Britain, France, *upper Silurian–Lower Devonian;* Ukraine (Podolia), *Lower Devonian.*——Fig. 40,*2a–d.* **S. filosa* (Hall), Caradoc–Ashgill, USA; *a,* dorsal valve exterior, ×1.7; *b,* detail of ornamentation of dorsal valve, Trenton Group, Middleville, New York, AMNH 29755, ×4.2 (new); *c,* cluster of attached valves, Maysville, Ohio, USNM 459683, ×1.2 (Rowell, 1965a); *d,* dorsal internal mold, AMNH 29753, ×2.5 (new).

?Schizobolus Ulrich, 1886, p. 25 [**Discina truncata* Hall, 1863a, p. 28; OD; =*Lingula concentrica* Vanuxem, 1842, p. 168] [=*Ljaschenkovia* Batrukova, 1969, p. 71 (type, *L. udmurtica;* OD)]. Shell elongate oval, weakly biconvex; both valves with beak placed posteriorly, not marginal; pedicle opening forming triangular notch extending from beak to posterior margin, lacking listrium; dorsal valve with short, straight posterior margin; dorsal interior with low ridge extending to midvalve. *Devonian:* USA, Uruguay, Brazil, Russia (Komi), Poland.——Fig. 40,*4a,b.* **S. concentricus* (Vanuxem), Middle Devonian, Poor Valley, Tennessee; *a,* ventral internal mold, USNM 459685a, ×4.2; *b,* dorsal external

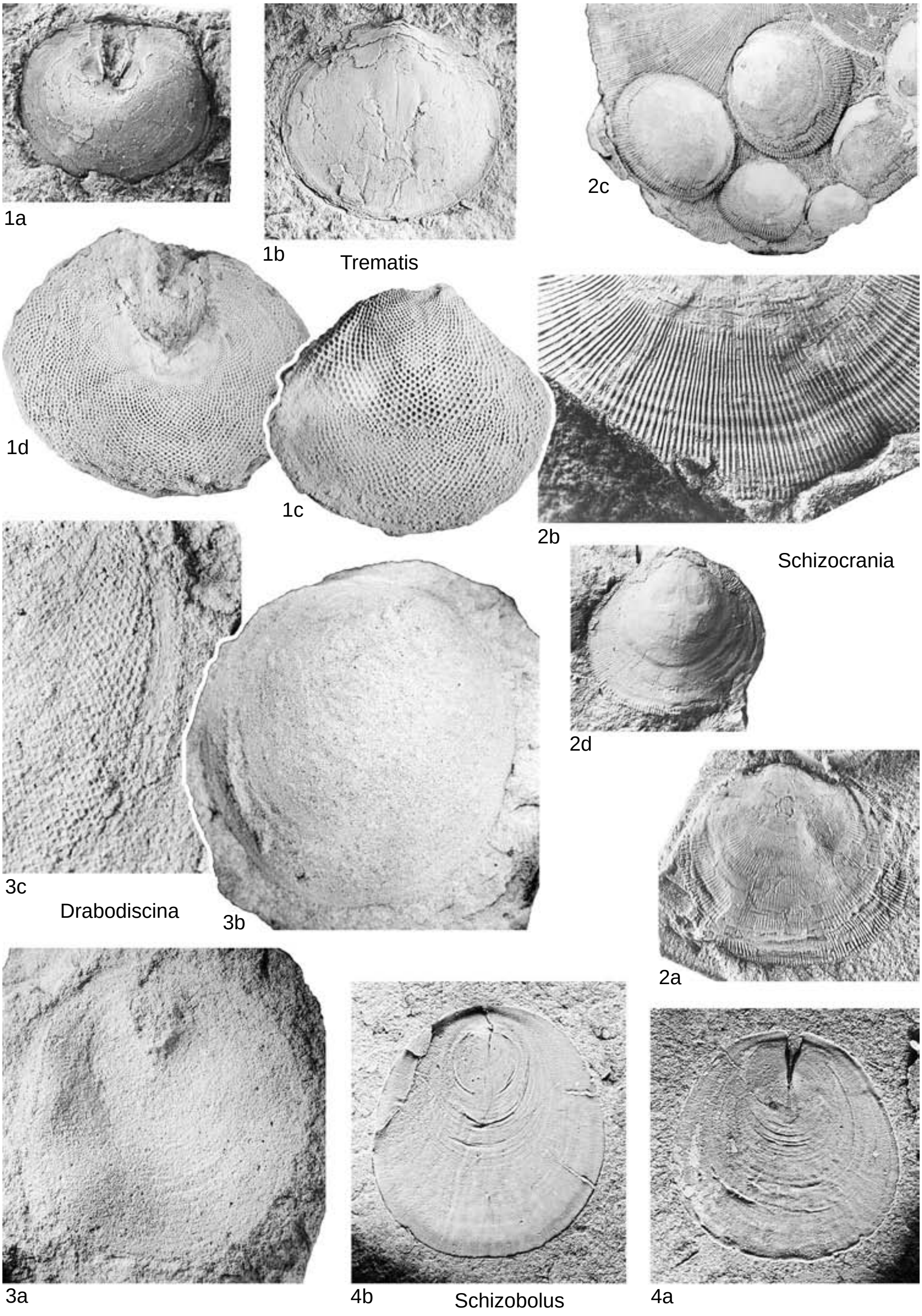

FIG. 40. Trematidae (p. 83–85).

mold, USNM 459685b, ×4.2 (new).

Tethyrete HAVLÍČEK, 1994, p. 63 [**T. frigerum;* OD]. Similar to convexoplane *Trematis,* but with reticulate ornament of radial costellae with crossbars. *Ordovician (upper Ashgill):* Bohemia. Satisfactory material not available for illustration.

Family DISCINIDAE Gray, 1840

[Discinidae GRAY, 1840, p. 155] [=Orbiculidae M'COY, 1844, p. 103] [*incl.* Orbiculoideinae SCHUCHERT & LEVENE, 1929, p. 13; Disciniscinae SCHUCHERT & LEVENE, 1929, p. 13; Acrosaccidae WILLARD, 1928, p. 258]

Dorsal valve with holoperipheral growth, usually conical to subconical; postlarval shell with pitted microornamentation in many fossil forms; pedicle opening variably developed, open posteriorly or closed by narrow band of periostracum or listrium; internal pedicle tube may be present; mantle canal system in both valves bifurcate in recent species, but poorly known in most fossil forms; lophophore in recent species spirolophe or schizolophe. *Ordovician (?Tremadoc, Arenig)–Holocene.*

Discina LAMARCK, 1819, p. 236 [**D. ostreoides;* OD; =*Crania striata* SCHUMACHER, 1817, p. 102]. Shell irregularly subcircular, biconvex to convexoconcave; ventral valve cemented to substrate, pedicle opening may be sealed in adults; both valves with subcentral apex; ornament of concentric growth lines and fine costellae; ventral interior with high, subtriangular median septum (probably attachment site of oblique internal muscle) extending short distance posteriorly of apex, partially closing pedicle opening, and almost forming pedicle tube; lophophore spirolophous. *Holocene:* western Africa.——FIG. 41,*1a–f.* **D. striata* (SCHUMACHER), Holocene, western Africa; *a,* dorsal valve exterior, ×5; *b,* detail of dorsal apex, ×7.5 (new); *c,* ventral valve exterior, Cape Palmas, USNM 5962, ×3.3; *d,* dorsal valve interior, ×4.2; *e,* ventral valve interior, ×4.2; *f,* lateral oblique view of ventral visceral area, Gambia, RMS Br 136372, ×8.3 (new).

Acrosaccus WILLARD, 1928, p. 258 [**A. shuleri;* OD]. Shell ventribiconvex to planoconvex, subcircular; postlarval shell with pitted microornamentation superposed on elevated, concentric fila; both valves with beak posterior, not marginal; ventral valve low to high conical; pedicle track narrow, mainly closed by listrium; foramen at posterior end of listrium, continued as internal tube; dorsal valve flattened. *Ordovician (Llanvirn–Ashgill):* cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 41,*2a–c.* **A. shuleri,* Rich Valley Formation, Caradoc, Virginia; *a,b,* ventral valve exterior, lateral view, USNM 109699a, ×3.3; *c,* dorsal valve exterior, USNM 109699c, ×3.3 (Cooper, 1956).——FIG. 41,*2d–h. A. willardi* (COOPER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *d,* ventral valve exterior, ×9.2; *e,* lateral view of ventral valve, ×20.8; *f,* detail of ventral larval shell, USNM 459688a, ×54.2; *g,* oblique lateral view of dorsal apex, ×19.5/61.2; *h,* detail of postlarval pitted microornamentation of dorsal valve, USNM 459688b, ×112 (new).

Chrustenotreta HAVLÍČEK, 1994, p. 60 [**C. chrustenica* HAVLÍČEK, 1994, p. 61; OD]. Similar to *Schizotreta,* but with subcentral ventral umbo and lacking internal pedicle tube. *Ordovician (Caradoc):* Bohemia.

Discinisca DALL, 1871b, p. 37 [**Orbicula lamellosa* BRODERIP, 1833, p. 124; OD]. Shell dorsibiconvex to convexoconcave, subcircular; ornamentation of fine growth lines that may become lamellose peripherally, with or without fine ribs; ventral valve with large depressed area around pedicle track, internally with small triangular median septum extending posteriorly from apex on to listrium; lophophore in recent forms spirolophous. *?Triassic, Lower Jurassic–Holocene:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 42,*2a–g.* **D. lamellosa* (BRODERIP), Holocene, Callao, Peru; *a,* ventral valve exterior, ×1.4; *b,* oblique posterior view, ×1.7; *c,* dorsal valve exterior, ×1.4; *d,* lateral view, ×1.8; *e,* ventral valve interior, ×1.2; *f,* dorsal valve interior, USNM 17826, ×1.2 (new); *g,* cluster of valves, ×0.7 (Rowell, 1965a).

Discradisca STENZEL, 1964, p. 627 [**Orbicula antillarum* D'ORBIGNY, 1845, p. 368; OD]. Similar to *Discinisca* but with wide, transversely suboval pedicle track, closed apically by semicircular, gently concave listrium; ornamentation of fine costellae and growth lamellae. *Lower Tertiary (Danian)–Holocene:* Gulf of Mexico, Caribbean, Brazil.——FIG. 41,*3a–c.* **D. antillarum* (D'ORBIGNY), Holocene; *a,* ventral view of both valves, ×3.3; *b,* detail of ventral umbonal area, ×75; *c,* dorsal valve exterior, USNM 442685, ×3 (new).

Kosoidea HAVLÍČEK & MERGL, 1988, p. 171 [**K. fissurella;* OD]. Shell similar to *Lindstroemella* but smaller, convexoplane to convexoconcave, with submarginal dorsal beak; lacking dorsal median septum and ridges bounding dorsal anterior adductor scars. *Silurian (Ludlow):* Bohemia, Estonia.——FIG. 43,*1a,b.* **K. fissurella,* Kopanina Formation, Bohemia; *a,* holotype, ventral valve interior, OMR VH 4534c, ×10.8; *b,* paratype, dorsal valve exterior, OMR VH 4531a, ×7.5 (Havlíček & Mergl, 1988). [MICHAL MERGL]

Lindstroemella HALL & CLARKE, 1890, p. 134 [**L. aspidium;* OD] [=*Lindstromella* CLARKE, 1889, p. 43, *nom. nud.; Lindstoemelia* DUNBAR & CONDRA, 1932, p. 49]. Shell dorsibiconvex, ornament of well-developed, concentric fila; ventral valve with central apex; pedicle track long, narrow, not completely closed posteriorly; dorsal valve with subcentral apex; dorsal interior with low median ridge anterior to apex, two lateral ridges bounding anterior adductor scars and converging anteriorly. *Middle Devonian–Carboniferous:* USA (New York, Nebraska, Ohio, Kansas, Kentucky), *Middle Devonian–Lower Carboniferous;* ?Peru, ?Russia (Urals), *Carboniferous;* ?Belgium, *Upper Carboniferous.*——FIG. 43,*3a,b.* **L. aspidium,* Hamilton beds, Middle Devonian, Hamilton, New York; *a,* ventral external mold, NYSM 1483, ×0.6; *b,* dorsal internal mold, NYSM 1482, ×0.6 (new).

Lingulodiscina WHITFIELD, 1890, p. 121 [**Lingula exilis* HALL, 1860b, p. 77; OD]. Genus poorly known. Shell dorsibiconvex to convexoplane, elongate oval; pedicle track broad, transversely suboval; dorsal valve with submarginal beak; internal charac-

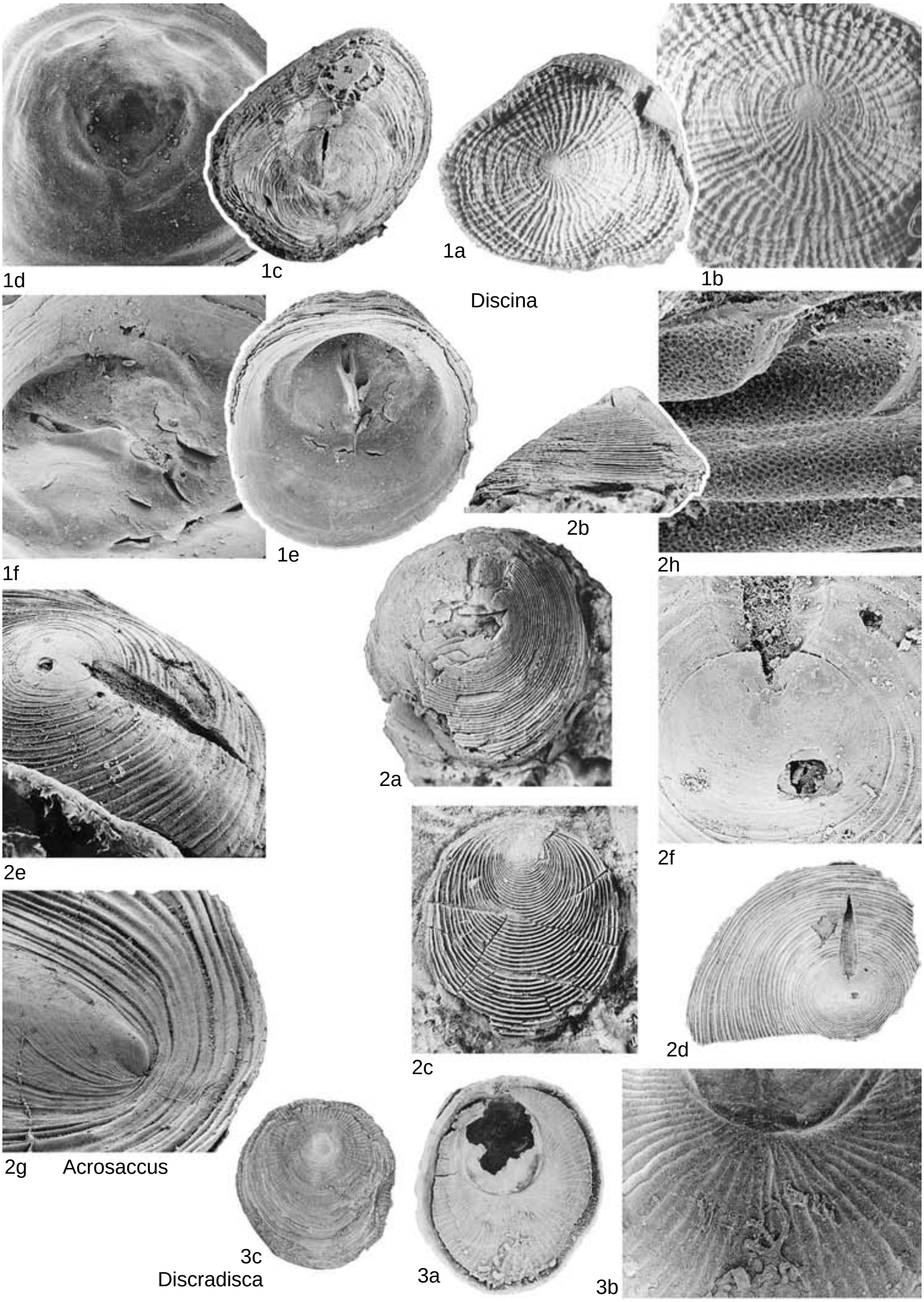

FIG. 41. Discinidae (p. 86).

ters inadequately known. *?Silurian, Devonian, ?Carboniferous, ?Permian:* ?Germany, *Silurian;* ?Ghana, ?New Zealand, *Devonian;* USA, *Devonian, ?Carboniferous;* ?Peru, ?Brazil, *?Carboniferous;* ?European Russia, *Permian.*——FIG. 42,*4a,b.* **L. exilis* (HALL), Middle Devonian, Hamilton, New York; *a,* ventral valve exterior, AMNH 36776, ×1.9; *b,* dorsal valve exterior, AMNH 36779, ×1.9 (new).

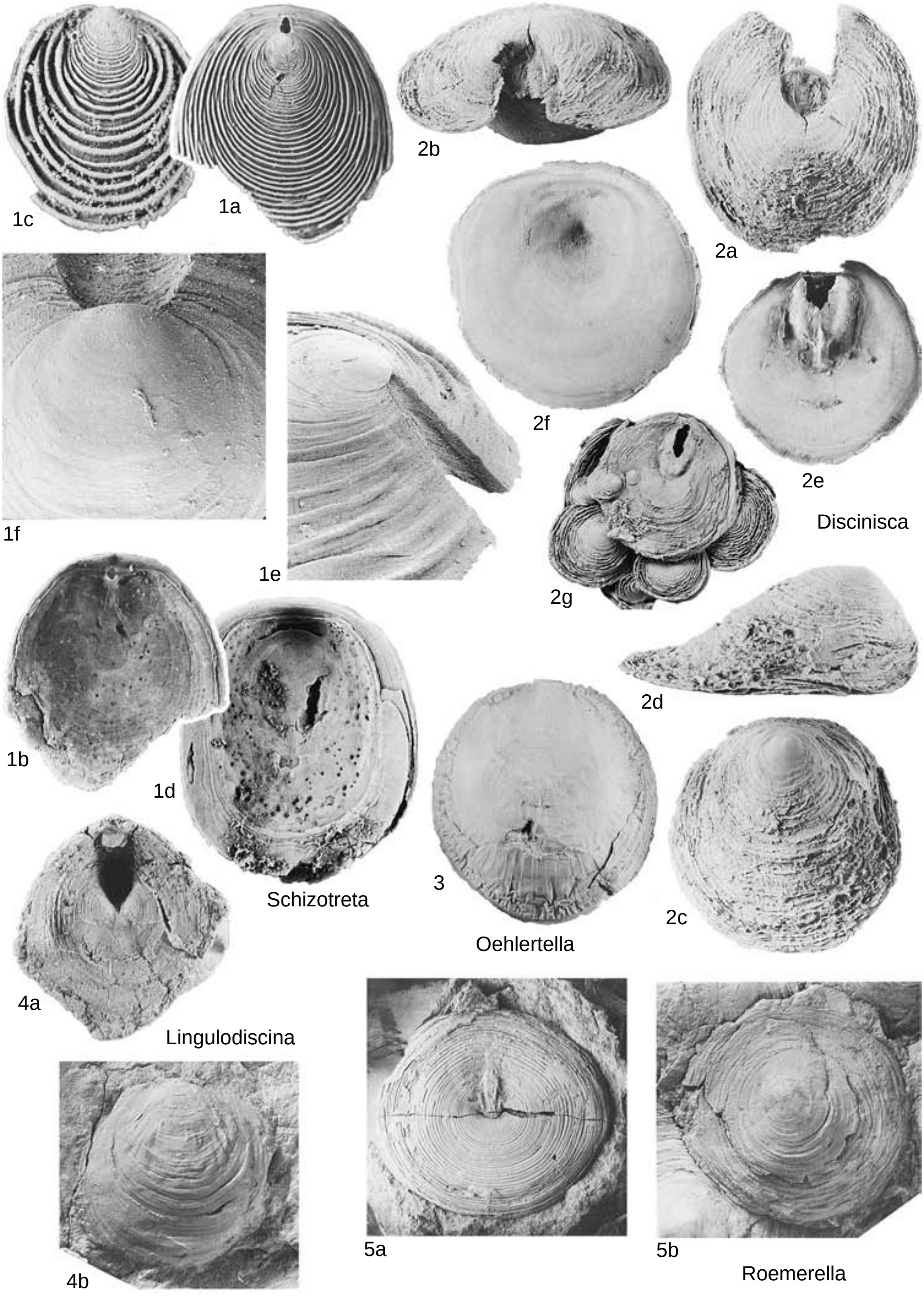

FIG. 42. Discinidae (p. 86–90).

Lochkothele HAVLÍČEK & MERGL, 1988, p. 169 [**Discina intermedia* BARRANDE, 1879, pl. 99, fig. 4.2; OD]. Shell ventribiconvex, subcircular; ventral valve with subcentral apex; pedicle track short, with small, circular pedicle foramen posterior to apex; dorsal valve with submarginal umbo; internal pedicle tube long, opening near posterior margin; ventral anterior adductor scars highly elevated, situated

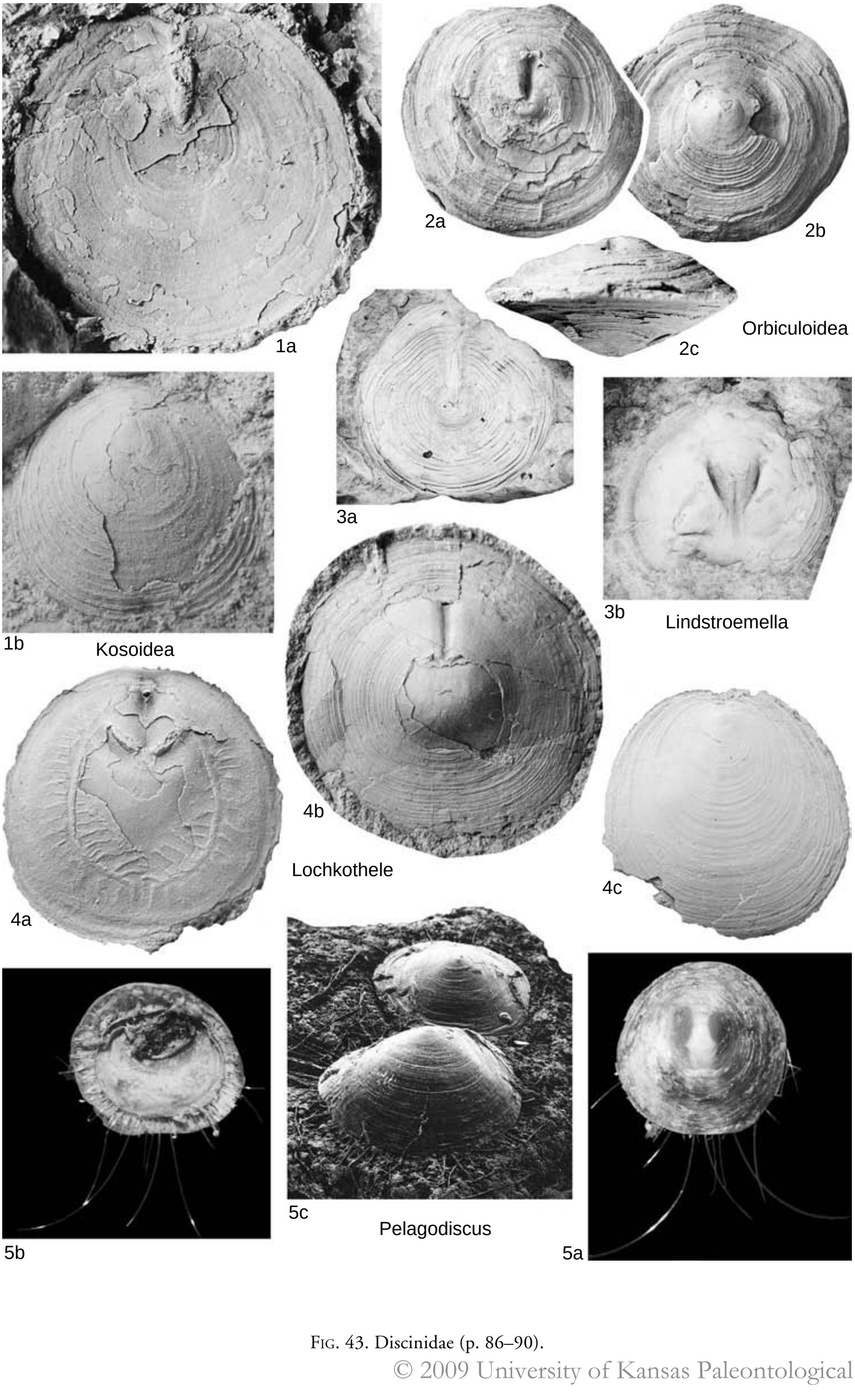

FIG. 43. Discinidae (p. 86–90).

in umbonal area; dorsal visceral area raised anteriorly; *vascula lateralia* in both valves submarginal, arcuate; *vascula media* long, subparallel. *Lower Devonian (Lochkovian):* Bohemia.——FIG. 43,*4a–c.* **L. intermedia* (BARRANDE), Radotín Limestone, Kosor; *a,* ventral internal mold, OMR VH 4510f, ×5.4; *b,* dorsal valve exterior, OMR VH 4521c, ×5.4; *c,* ventral valve exterior, OMR VH 4510e, ×8.3 (Havlíček & Mergl, 1988).

?Oehlertella HALL & CLARKE, 1890, p. 133 [**Discina pleurites* MEEK, 1875, p. 278; OD] [=*Oehlertella* CLARKE, 1889, p. 43, *nom. nud.*]. Genus poorly known. Shell dorsibiconvex; ventral valve similar to *Discinisca,* but pedicle track parallel-sided and ventral interior lacking median septum; dorsal apex submarginal. *?Silurian, Devonian–Carboniferous:* ?Estonia, *Silurian;* Libya, *Devonian–Carboniferous;* USA (New York, Ohio), Scotland, *Carboniferous.* ——FIG. 42,*3.* **O. pleurites* (MEEK), Cuyahoga Formation, Upper Carboniferous, Trumbull County, Ohio; dorsal valve exterior, OSU 22336, ×1.3 (new).

Orbiculoidea D'ORBIGNY, 1847, p. 269 [**Orbicula forbesii* DAVIDSON, 1848, p. 334; ICZN opinion 722, 1965b]. Shell strongly dorsibiconvex to convexoplane, subcircular; ornament of both valves usually with well-developed, concentric fila; dorsal valve conical to subconical, apex variably positioned; ventral valve low subconical to gently concave, pedicle track narrow, closed anteriorly by listrium; foramen at posterior end of listrium, continued as internal tube to open in front of posterior margin. *?Ordovician, Silurian–Permian:* cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 43,*2a–c.* **O. ?forbesii* (DAVIDSON), Wenlock, England; ventral valve exterior, dorsal valve exterior, lateral view of both valves, ×4 (Rowell, 1965a).

Pelagodiscus DALL, 1908, p. 440 [**Discina atlantica* KING, 1868, p. 170; OD]. Similar to *Discinisca* but smaller, very thin-shelled; lophophore schizolophous. *?Miocene, Holocene:* cosmopolitan.——FIG. 43,*5a–c.* **P. atlanticus* (KING), Holocene; *a,b,* dorsal, ventral valve exterior (photographed underwater), North Atlantic Ocean (Rowell, 1965a); *c,* oblique lateral view of two attached shells, northeastern Pacific Ocean, USNM 384198, ×5 (new).

Roemerella HALL & CLARKE, 1890, p. 137 [**Orbicula grandis* VANUXEM, 1842, p. 152; OD] [=*Roemerella* CLARKE, 1889, p. 43, *nom. nud.*]. Genus poorly known. Shell large, convexoconcave; ventral valve with central apex and pedicle track on broadly elevated area; dorsal valve high conical with subcentral apex. *Devonian:* USA (New York, Indiana, Oklahoma, Kentucky, Pennsylvania, Ohio, Michigan); ?South Africa, ?Belgium, ?Germany. ——FIG. 42,*5a,b.* **R. grandis* (VANUXEM), Hamilton Group, New York; *a,* ventral external mold, USNM 26064, ×0.8; *b,* dorsal valve exterior, AMNH 5139, ×1.2 (new).

Schizotreta KUTORGA, 1848, p. 272 [**Orbicula elliptica* KUTORGA, 1846, p. 123; OD]. Shell convexoplane to ventribiconvex, elongate oval; postlarval shell with pitted microornamentation, superposed on elevated, concentric fila; both valves with submarginal beaks; ventral valve low, subconical; pedicle track short, mainly closed by listrium, with small foramen slightly posterior to apex, continued as internal tube; dorsal valve flattened with submarginal apex. *Ordovician (Arenig)–Silurian:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 42,*1a–f. S. corrugata* COOPER, Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,b,* ventral valve exterior, interior, specimen lost, ×5; *c,* dorsal valve exterior, USNM 116808k, ×6.7; *d,* dorsal valve interior, USNM 116808e, ×3.3 (Cooper, 1956); *e,* oblique lateral view of ventral valve, ×20.8; *f,* detail of ventral larval shell, USNM 459686, ×54.2 (new).

Schizotretinia HAVLÍČEK, 1994, p. 61 [**S. euxina* HAVLÍČEK, 1994, p. 62; OD]. Shell subcircular, convexoplane; ornamented by highly raised concentric rugellae; ventral valve with subcentral umbo and subtriangular median notch in posterior margin; pedicle track elongate elliptical, does not reach posterior valve margin; dorsal valve with submarginal umbo. *Ordovician (upper Ashgill):* Bohemia. [MICHAL MERGL]

Superfamily ACROTHELOIDEA Walcott & Schuchert, 1908

[*nom. correct.* HOLMER & POPOV, herein, *pro* superfamily Acrothelacea, *nom. transl.* USHATINSKAYA, 1994, p. 41, *ex* Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146]

Shell with short, convex posterior margin; postlarval ornament of fine, evenly distributed granules or pustules; larval shell pitted, with apical spines or tubercles; ventral valve convex or low conical; ventral pseudointerarea vestigial or lacking; pedicle emerging through delthyrium or foramen posterior to apex; dorsal pseudointerarea vestigial or lacking; muscle system linguloidean, with paired umbonal muscle; mantle canal system of both valves baculate; *vascula media* well developed. *Lower Cambrian (upper Atdabanian)–Lower Ordovician (Arenig, ?Llandeilo).*

The close relationship between the Botsfordiidae and Acrothelidae has long been recognized (ROWELL, 1965a). As noted by ROWELL (1965a) it is probable that the botsfordiids were ancestral to the acrothelides; moreover, it now seems possible to trace an almost continuous gradual transition from the latest botsfordiids (*Karathele*) with a deep, but unrestricted delthyrial pedicle opening and well-defined ventral pseudointerarea to early acrothelids (*Eothele*) with a low, subconical ventral valve, a reduced

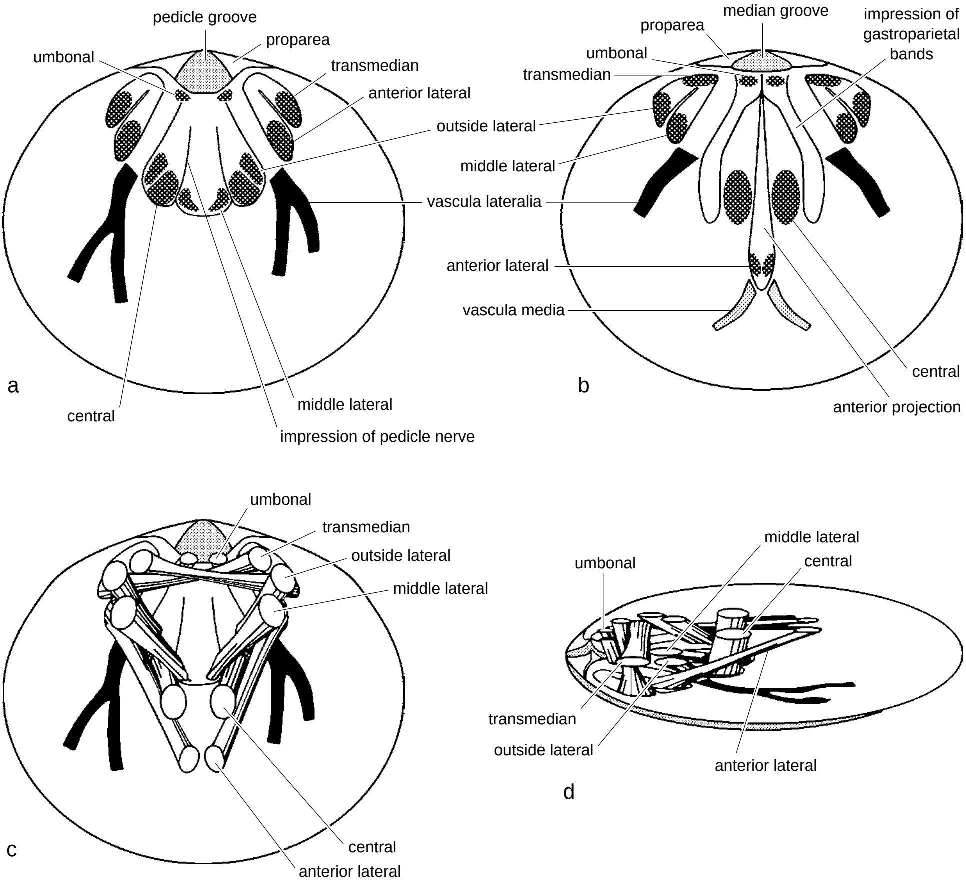

FIG. 44. Schematic illustration of musculature and mantle canal system of *Edreja; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

pseudointerarea (transformed into pedicle tube), and an elongate, suboval pedicle foramen formed in the postlarval stage (HOLMER & POPOV, 1996b).

The muscle system of botsfordiids is very similar to that of Lower Paleozoic Obolidae (WALCOTT, 1912; POPOV, 1992); the earliest known genera, *Botsfordia* and *Edreja,* have scars that appear to match a full set of obolid muscles (Fig. 44), while the number of muscles in the acrothelids was probably reduced. The scars of a linguloidean type of V-shaped pedicle nerve in *Botsfordia* and *Edreja* (Fig. 44) also may indicate a close relationship between the two groups.

The shell structure of botsfordiids has not yet been studied adequately but includes baculate laminae (HOLMER, 1989b; POPOV & HOLMER, 1994).

The earliest evolution of the group is still poorly known. Although the botsfordiids and acrothelids have some characters in common with the acrotretoideans, such as a pitted larval shell and a pedicle foramen (in acrothelids), it is clear that they also exhibit many lingulid features, such as baculate shell structure (USHATINSKAYA, 1994). As noted above, they might be related closely to the lingulid family Eoobolidae, which is also characterized by a pitted larval shell and a pustulose-granular postlarval ornamentation. WILLIAMS and ROWELL (1965a) proposed that the acrothelids probably were ancestral to the discinids, but in view of the considerable differences in their ontogenies, this is unlikely (CHUANG, 1971a; HOLMER, 1989b).

Family ACROTHELIDAE Walcott & Schuchert, 1908

[*nom. transl.* ROWELL, 1965a, p. 280, *ex* Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146; *incl.* Schizopolidacea SCHINDEWOLF, 1955, p. 556]

Shell ventribiconvex; ventral valve low conical to subconical; pedicle foramen circular, placed immediately posterior to apex, not enclosed within larval shell; ventral posterolateral muscle fields situated slightly posterior to pedicle opening; ventral larval shell with one pair of spines and sometimes with median tubercle; dorsal larval shell with one or two pairs of spines. *Lower Cambrian–Lower Ordovician (Arenig, ?Llandeilo).*

Subfamily ACROTHELINAE Walcott & Schuchert, 1908

[Acrothelinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 146]

Dorsal valve plane to gently convex, with marginal beak, dorsal pseudointerarea forming crescent-shaped rim; dorsal interior with low median ridge; internal pedicle tube usually present. *Lower Cambrian–Ordovician (Arenig).*

Acrothele LINNARSSON, 1876, p. 20 [**A. coriacea;* SD OEHLERT, 1887b, p. 1270] [=*Dearbornia* WALCOTT, 1908, p. 78 (type, *D. clarki*); *Redlichella* WALCOTT, 1908, p. 89 (type, *Acrotreta granulata* LINNARSSON, 1876, p. 24); *Glyptacrothele* TERMIER & TERMIER, 1974, p. 45 (type, *G. courtessolei*)]. Ornament of fine, concentric growth lines, usually with additional irregular wavy ridges bearing minute granules; dorsal pseudointerarea forming obtusely triangular plate not raised above valve floor; internal pedicle tube absent; ventral larval shell with median tubercle. *?Lower Cambrian, Middle Cambrian–Upper Cambrian:* ?cosmopolitan (exact stratigraphic and geographic range is very uncertain).——FIG. 45,*1a–l.* **A. coriacea,* Middle Cambrian; *a,* ventral valve exterior, Bornholm, Denmark, USNM 51983a, ×6.3; *b,* ventral valve interior, USNM 18208a, ×6.3; *c,* dorsal valve interior, Scania (Andrarum), Sweden, USNM 18208d, ×6.3; *d,* dorsal valve exterior, ×11; *e,* lateral view of dorsal valve, ×18; *f,* lateral view of dorsal larval shell, ×62; *g,* detail of dorsal larval spine and pitting, SGU 8498, ×229; *h,* detail of dorsal pseudointerarea, SGU 8499, ×17.5; *i,* ventral valve exterior, ×19.2; *j,* detail of ventral larval shell, ×62.5; *k,* posterior view of ventral valve, SGU 8500, ×42; *l,* ventral valve interior, Östergötland (Knivinge), Sweden, SGU 8501, ×33.3 (new).——FIG. 45,*1m–o. A. granulata* (LINNARSSON), Middle Cambrian, *Paradoxides oelandicus* Biozone, Öland (Borgholm), Sweden; *m,* dorsal valve exterior, USNM 511991c, ×3.3; *n,* ventral valve exterior, USNM 511991a, ×3.3; *o,* dorsal valve interior, USNM 511991d, ×3.3 (new).

Eothele ROWELL, 1980, p. 17 [**E. spurri;* OD]. Shell with commissure flexed strongly ventrally; ventral valve low subconical, with sharply pointed apex somewhat anterior to posterior margin; pedicle foramen relatively large, elongate lens shaped; dorsal beak strongly depressed below posterolateral flanks of valve; ventral interior with short pedicle tube; ventral larval shell with median tubercle. *upper Lower Cambrian–lower Middle Cambrian:* USA (Nevada), Canada (Yukon), *upper Lower Cambrian;* Australia (New South Wales), *Amgaian.*——FIG. 46,*2a–e.* **E. spurri,* Lower Cambrian, *Bonnia–Olenellus* Biozone, Mount Ely, Nevada; *a,* dorsal valve exterior, ×20.8; *b,* paratype, posterior view of dorsal valve, KUMIP 115531, ×52.5; *c,* paratype, dorsal valve interior, KUMIP 115530, ×20.8; *d,e,* ventral valve exterior, lateral view, KUMIP 115528, ×20.8 (Rowell, 1980).

Orbithele SDZUY, 1955, p. 9 [**Discina contraria* BARRANDE, 1868, p. 104; OD]. Externally similar to *Acrothele* but with marginal spines; internal pedicle tube supported anteriorly by short septum. *upper Middle Cambrian–Ordovician (Arenig):* Greenland, *upper Middle Cambrian;* Australia, USA, *lower Upper Cambrian;* Denmark, *Tremadoc;* Germany, Morocco, Mauritania, *?Tremadoc;* Norway, Poland, Russia (Southern Urals), Sweden, *Tremadoc–Arenig;* Estonia, *Arenig;* Bohemia, *?Tremadoc–lower Arenig.*——FIG. 46,*1a–i. O. ceratopygarum* (BRØGGER); *a,* ventral valve exterior, ×7.5; *b,* oblique lateral view of ventral valve, ×10; *c,* detail of marginal spines of dorsal valve, RMS Br 20791a, ×33.3; *d,* dorsal valve exterior, ×6.2; *e,* detail of dorsal larval shell, ×79.2; *f,* detail of granular postlarval ornamentation, LO 6564t, ×131; *g,* ventral larval shell and pedicle foramen, LO 6565t, ×62.5; *h,* ventral valve interior, LO 1787t, Bjørkåsholmen Limestone, Tremadoc, Öland (Ottenby), Sweden, ×7; *i,* dorsal valve interior, Kidryas Formation, Tremadoc, Southern Urals (Tyrmantau Ridge), Russia, RMS Br 136299, ×10 (Popov & Holmer, 1994).

Schizopholis WAAGEN, 1885, p. 752 [**S. rugosa;* OD] [=*Discinolepis* WAAGEN, 1885, p. 749 (type, *D. granulata*)]. Shell ventribiconvex, subcircular; ventral valve with submarginal beak; pedicle opening long, narrow slit immediately posterior to apex, not extending to posterior margin; ventral interior with broad, subparallel, submedian *vascula lateralia;* dorsal interior with long, broad median ridge, extending anteriorly beyond midvalve; other internal characters poorly known. *Lower Cambrian:* Pakistan, ?Kazakhstan.——FIG. 45,*2a–d.* **S. rugosa, Neobolus* Beds, Salt Range, Pakistan; *a,b,* ventral valve exterior, posterior view, ×5; *c,* dorsal internal mold, ×5; *d,* dorsal valve exterior, ×5 (Rowell, 1965a).

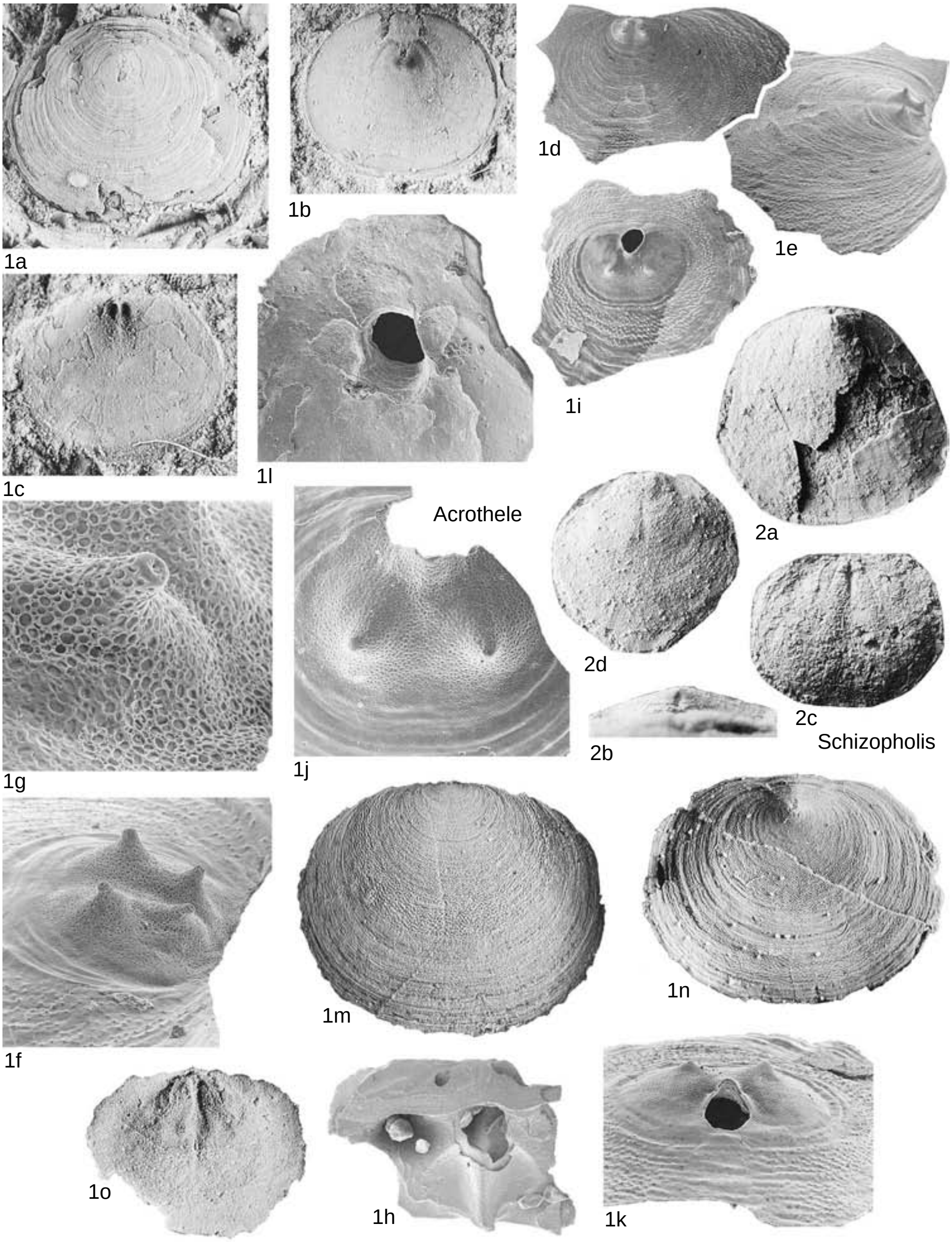

FIG. 45. Acrothelidae (p. 92).

Spinulothele ROWELL, 1977, p. 76 [**?Siphonotreta dubia* WALCOTT, 1912, p. 625; OD]. Genus poorly known. Externally similar to *Acrothele* but with posteriorly placed ventral beak, and slightly lamellose, concentric, growth frills crossed by fine impersistent ribs, producing low, radially arranged, spinelike nodes. *Lower Cambrian:* USA (Nevada).

Subfamily CONODISCINAE Rowell, 1965

[Conodiscinae ROWELL, 1965a, p. 281]

Dorsal valve depressed conical, beak subcentral. *Upper Cambrian, ?Lower Ordovician.*

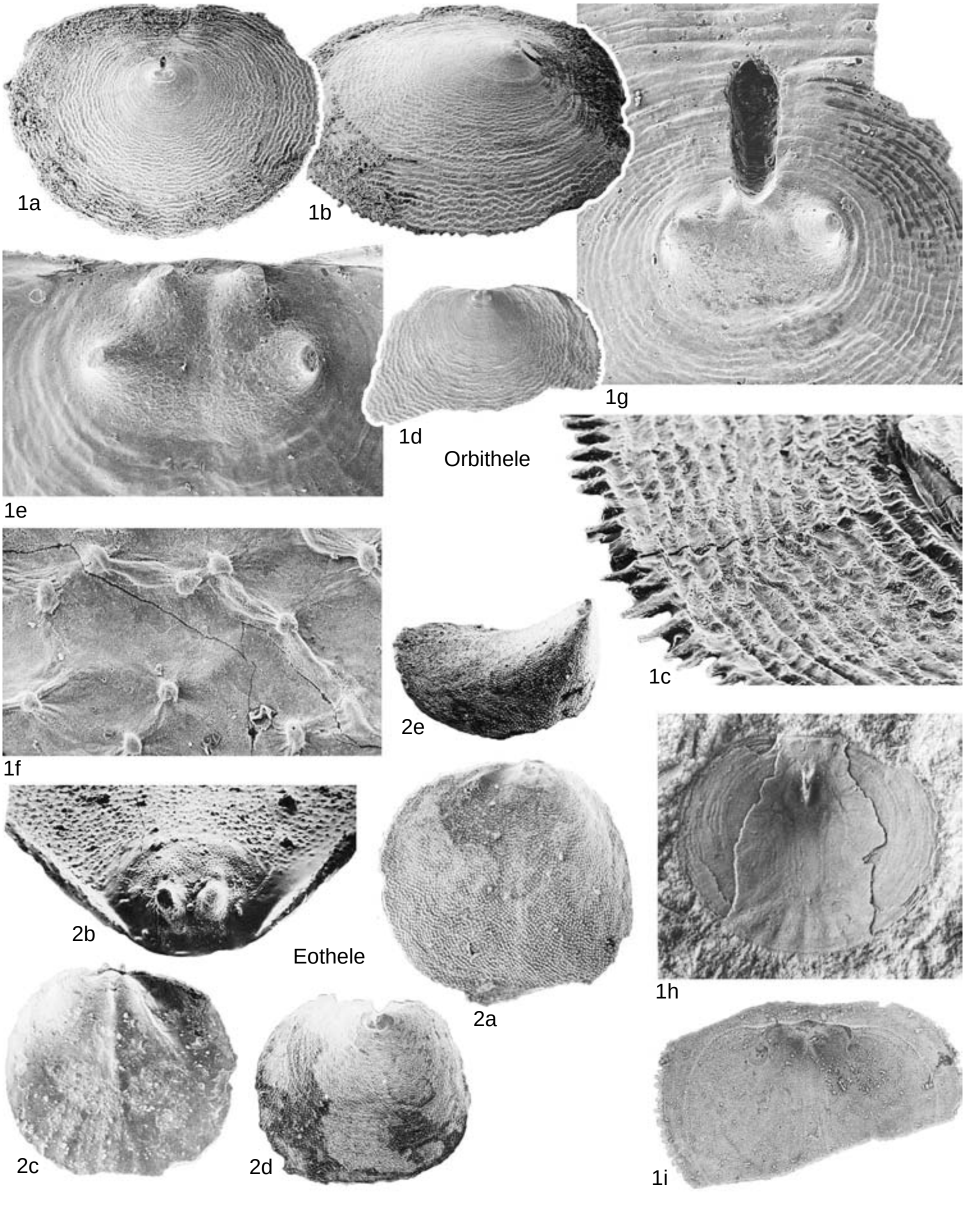

FIG. 46. Acrothelidae (p. 92).

Conodiscus Ulrich & Cooper, 1936b, p. 619 [**Acrothele burlingi* Kobayashi, 1935a, p. 45; OD]. Ventral valve similar to *Acrothele;* dorsal interior with low median ridge extending posteriorly from apex. *Upper Cambrian, ?Lower Ordovician:* USA (Alaska).——Fig. 47,*1a–d.* **C. burlingi* (Kobayashi), Upper Cambrian or Lower Ordovician, Hard Luck Creek, Alaska; *a,* dorsal valve exterior, USNM 92830b, ×3.3; *b,* cast of ventral valve exterior, USNM 92830a, ×4.2; *c,* dorsal valve interior, USNM 92829, ×3.3; *d,* ventral valve interior, USNM 92829a, ×3.3 (Ulrich & Cooper, 1938).

?Discotreta Ulrich & Cooper, 1936b, p. 619 [**Acrothele levisensis* Walcott, 1908, p. 85; OD]. Shell transversely suboval; both valves with apex positioned posteriorly; pedicle foramen small, situated immediately behind the apex and bounded laterally by two short folds; ventral interior with short internal pedicle tube and weakly defined median ridge bisecting visceral area; dorsal interior with elongate suboval central muscle scars and small paired anterior lateral muscle scars, at about

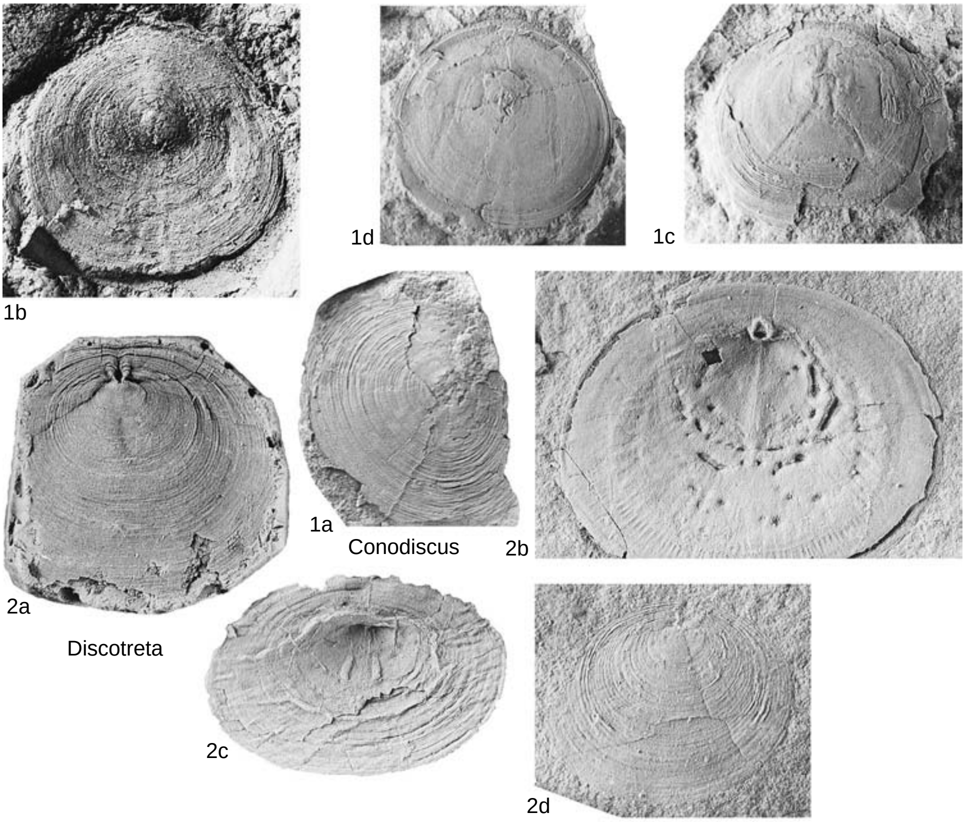

FIG. 47. Acrothelidae (p. 94–95).

midvalve. *Ordovician (Arenig):* Canada (Quebec). ——FIG. 47,*2a–d.* **D. levisensis* (WALCOTT), Levis Shale, Levis, Quebec; *a,* ventral valve exterior, USNM 92832a, ×5; *b,* ventral valve interior, USNM 92832d, ×2.9; *c,* dorsal valve interior, USNM 92832f, ×2.1; *d,* ventral valve exterior, USNM 92832b, ×4.2 (Ulrich & Cooper, 1938).

Family BOTSFORDIIDAE Schindewolf, 1955

[*nom. transl.* ROWELL, 1965a, p. 281, *ex* superfamily Botsfordiacea SCHINDEWOLF, 1955, p. 545] [*incl.* subfamily Neobolinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 144]

Shell biconvex; ventral pseudointerarea vestigial, divided by deep pedicle groove forming triangular delthyrium; dorsal pseudointerarea vestigial, divided by median groove; muscle system probably similar to that of obolids, consisting of paired umbonal, transmedian, outside lateral, internal lateral, anterior lateral, and central muscles; *vascula lateralia* straight, submedian, divergent in both valves; larval shell with one to three apical tubercles in ventral valve and two in dorsal valve. *Lower Cambrian (upper Atdabanian)–Middle Cambrian (Amgaian).*

Botsfordia MATTHEW, 1891, p. 148 [**Obolus pulcher* MATTHEW, 1889, p. 306; OD] [=*Mobergia* REDLICH, 1899, p. 5 (type, *M. granulata*)]. Shell subcircular; ventral pseudointerarea catacline; ventral interior with small, slightly thickened visceral field, with three anterior lobelike projections, not extending to midvalve; dorsal interior with narrow anterior projection extending to midvalve, bisected by median ridge; ventral larval shell with single median tubercle. *Lower Cambrian–Middle Cambrian:* Pakistan, ?Korea, ?Australia, USA (New York, Vermont), *Lower Cambrian;* Canada (Quebec, Labrador, New Brunswick), ?Spain, *Lower Cambrian–Middle Cambrian;* Norway, Sweden, *Lower Cambrian, ?lower Middle Cambrian;* ?Greenland, *upper Lower Cambrian;* Russia (Siberia), *upper Atdabanian–Amgaian;* Kazakhstan, *Botomian–Toyonian;* ?Mongolia, ?China, *Middle Cambrian;* Bohemia, Morocco, *lower Middle Cambrian.*——FIG. 48,*1a,b.* **B. pulchra* (MATTHEW), Hanford Brook Formation, upper Lower Cambrian, Catons Island, New

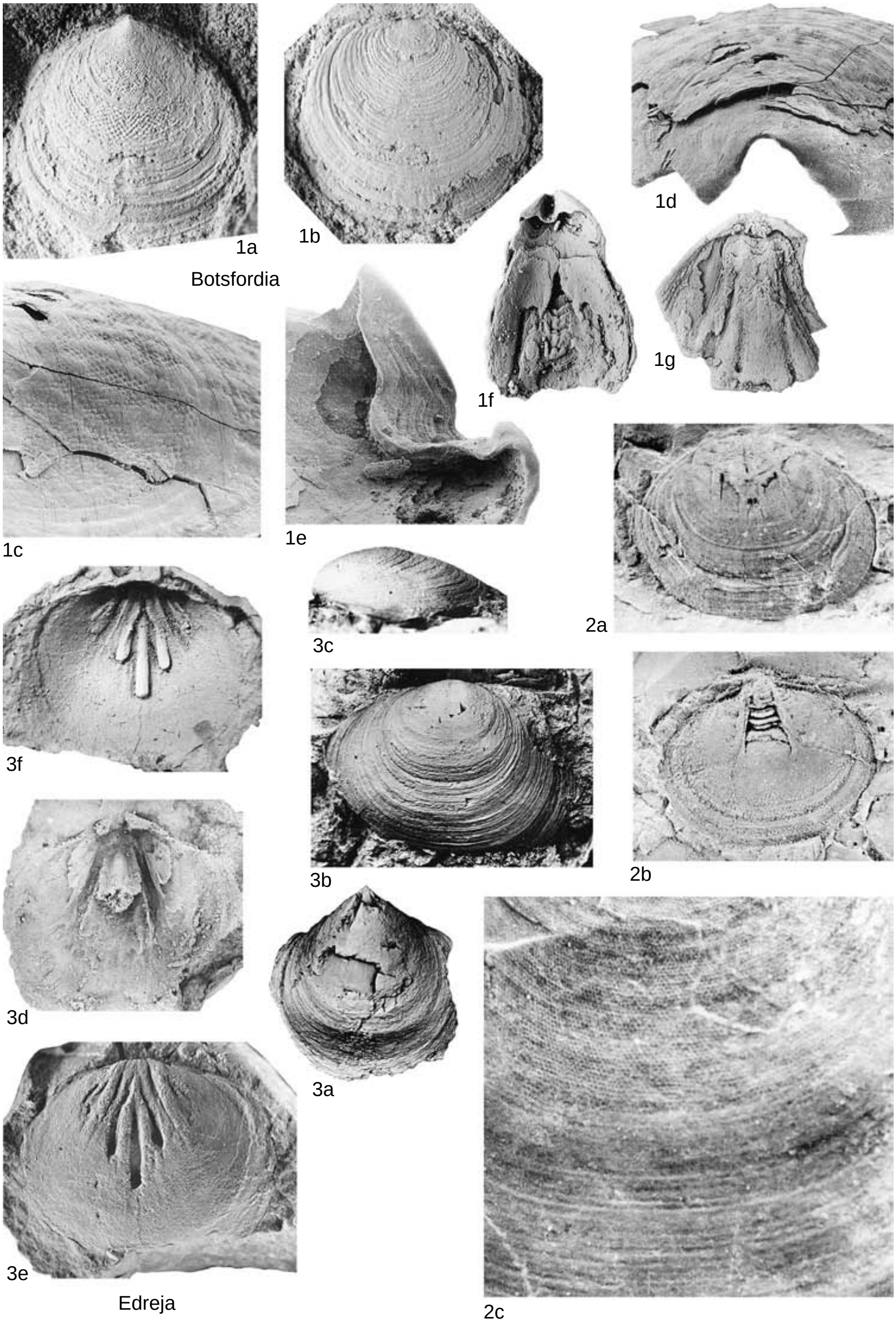

FIG. 48. Botsfordiidae (p. 95–97).

Brunswick, Canada, USNM loc. no. 308d; *a,* ventral valve exterior, ROM 164(C), ×3.3; *b,* dorsal valve exterior, ROM 164(B), ×3.3 (new).——Fig. 48,*1c–g. B. caelata* (Hall), Lower Cambrian, Troy, New York, USNM loc. no. 2b, USNM 34617; *c,* detail of ventral valve ornamentation, ×18.3; *d,* posterior view of ventral valve, ×13.3; *e,* ventral pseudointerarea and pedicle groove, ×17.5; *f,* interior of ventral valve, ×4.2; *g,* dorsal valve interior, ×4.2 (new).

?Bomina Korovnikov & Ushatinskaya, 1994, p. 128 [**B. tuvaensis* Korovnikov & Ushatinskaya, 1994, p. 130; OD]. Shell ventribiconvex, subcircular; umbonal area finely pustulose with weakly developed radial ornament, smooth peripherally; dorsal larval shell with single pair of tubercles; ventral interior with slightly raised visceral area; dorsal interior with low posterolateral muscle platforms and fine median ridge. Genus inadequately known, originally referred to the Paterinida. *Lower Cambrian (Botomian):* Russia (Tuva).

Diandongia Rong, 1974, p. 113 [**D. pista;* OD]. Externally similar to and possibly congeneric with *Edreja,* but differs in having shorter ventral visceral platform, not extending to midlength; pseudointerareas of both valves and dorsal interior inadequately known. *Lower Cambrian:* South China. ——Fig. 48,*2a–c.* **D. pista,* upper Chiungchussu Formation, Wuding, Yunnan; *a,* holotype, dorsal internal mold, NIGP 22149, ×2.5; *b,* paratype, ventral internal mold, NIGP 22146, ×2.5; *c,* paratype, dorsal external mold, ornamentation, NIGP 22150, ×16.7 (Rong, 1974).

Edreja Koneva, 1979, p. 49 [**E. crassa;* OD]. Shell subcircular, lamellose peripherally; ventral pseudointerarea orthocline to apsacline with well-developed propareas; dorsal pseudointerarea forming narrow, crescent-shaped rim; ventral visceral field forming narrow, elevated, three-lobed platform, extending to midvalve; dorsal interior with long, low median septum extending to midvalve; dorsal central muscle scars placed on elevated ridges, directly lateral to septum; dorsal posterolateral muscle field forming low, elongate, slightly divergent platforms. *Lower Cambrian (upper Atdabanian–Botomian):* Australia (Northern Territory), *upper Atdabanian;* Kazakhstan, *Botomian.*——Fig. 48,*3a–f.* **E. crassa,* Edrei beds, Botomian, Edrei Mountains; *a,* paratype, ventral valve exterior, MANK 2138/149, ×8.3; *b,c,* paratype, dorsal valve exterior, lateral view, MANK 2138/154, ×2.5 (Koneva, 1979); *d,* latex cast of ventral internal mold, RMS Br 136374, ×2.9 (new); *e,f,* paratype, dorsal internal mold, latex cast of dorsal internal mold, MANK 2138/159, ×2.5 (Koneva, 1979).

Glyptias Walcott, 1901, p. 675 [*?*Lingula favosa* Linnarsson, 1869, p. 356; OD]. Shell thick, lamellose posteriorly, subtriangular; ventral valve subacuminate; ventral propareas vestigial; ventral visceral field very short, slightly thickened anteriorly, not extending to midvalve; dorsal interior with broad median ridge and narrow anterior projection extending to midvalve; dorsal posterolateral muscle fields placed on elevated, slightly diverging ridges. *Lower Cambrian:* Sweden, ?Norway.——Fig. 49,*2a–e.* **G. favosa* (Linnarsson), Lingulide Sandstone, Sweden; *a,* ventral valve exterior, USNM 35264, ×5.8; *b,* dorsal valve exterior, USNM 25264b, ×5.4; *c,* ventral internal mold, Lugnås, Västergötland, USNM 35264c, ×4.6; *d,* dorsal internal mold, SGU 84502, ×6.2; *e,* detail of ventral umbonal area, Gävle (glacial erratic), SGU 84503, ×12.5 (new).

Karathele Koneva, 1986b, p. 206 [**K. coronata;* OD]. Shell subequibiconvex, subcircular; ventral pseudointerarea catacline, lacking propareas; delthyrium semioval; dorsal valve slightly sulcate; ventral visceral field very small and short, only slightly thickened; dorsal median ridge not extending to midvalve; ventral larval shell with three tubercles. *Lower Cambrian (Toyonian)–Middle Cambrian (Amgaian):* Kazakhstan, Australia (Northern Territory, South Australia), Antarctica.——Fig. 49,*1a–d.* **K. coronata,* Amgaian, Kyrshabakty, Malyi Karatau; *a–c,* ventral valve exterior, posterior view, interior, MANK 427/365, ×17.5; *d,* ventral larval shell, MANK 427/375, ×42 (Koneva, 1986b).

Neobolus Waagen, 1885, p. 756 [**N. warthi;* SD Oehlert, 1887b, p. 1263] [=*Lakhmina* Oehlert, 1887b, p. 1265, *nom. nov. pro Davidsonella* Waagen, 1885, p. 762 (type, *D. linguloides*), *non* Munier-Chalmas, 1880, *nec* Fredericks, 1926]. Similar to *Botsfordia,* but differs in having well-developed dorsal visceral platform. *Lower Cambrian:* Pakistan, ?Germany, ?Australia.——Fig. 49,*3a–d.* **N. warthi* Waagen, *Neobolus* Beds, Salt Range, Pakistan; *a,* ventral valve exterior, ×2.5; *b,* posterior view of ventral valve, ×3.3; *c,* dorsal valve exterior, ×3.3; *d,* dorsal valve interior, ×3.3 (Rowell, 1965a).

Order ACROTRETIDA Kuhn, 1949

[*nom. correct.* Gorjansky, 1960, p. 178, *pro* order Acrotretacea Kuhn, 1949, p. 101; *emend.,* Holmer & Popov, herein] [=Neotremata Beecher, 1891, p. 354, *partim*]

Shell usually ventribiconvex; ventral valve commonly conical to subconical, more rarely convex; larval shell small (less than 0.3 mm across) with pitted microornamentation; apical pedicle foramen, formed during or shortly after larval stage; ventral cardinal muscle scars placed on posterior slope of valve; ventral umbonal scars (apical pits) located subapically, near pedicle opening; dorsal cardinal muscle scars near pseudointerarea, usually thickened and well defined; mantle canal system baculate or pinnate; dorsal triangular median septum usually present; shell structure columnar or camerate. *Lower Cambrian–Middle Devonian, ?Upper Devonian.*

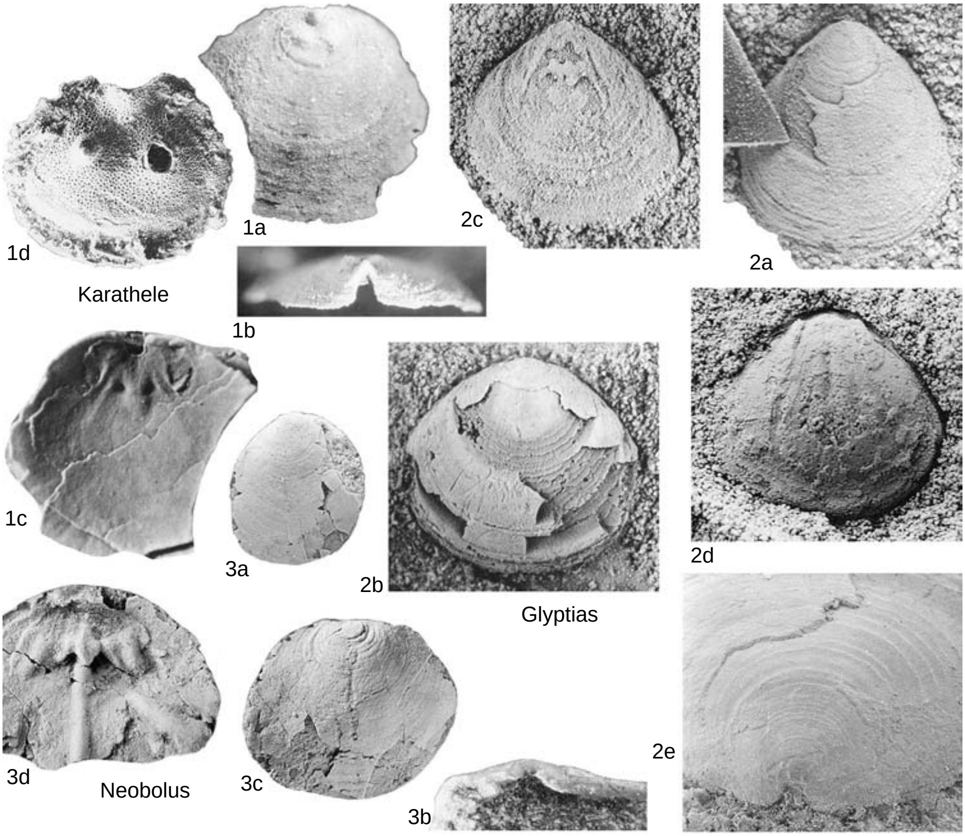

FIG. 49. Botsfordiidae (p. 97).

ROWELL (1965a) included the discinoids, the siphonotretoids, and the calcareous cranioids within the acrotretides. Following our cladistic analysis (see Fig. 38), however, the Acrotretida is here restricted to include only the superfamily Acrotretoidea; this node is supported in two analyses (Fig. 50; Table 7).

Superfamily ACROTRETOIDEA Schuchert, 1893

[*nom. transl.* SCHUCHERT, 1896, p. 308, *ex* Acrotretidae SCHUCHERT, 1893, p. 150; *emend.,* HOLMER & POPOV, herein]

Characters as for order. *Lower Cambrian–Middle Devonian, ?Upper Devonian.*

Thirty-three selected acrotretoidean genera were analyzed using 41 unweighted, unordered characters, with an outgroup consisting of five paterinid, siphonotretid, botsfordioidean, and lingulid genera (Table 8–9). Twenty-seven equally parsimonious trees 129 steps long were generated with a consistency index of 0.620 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The strict consensus tree (Fig. 50) is partly unresolved and the internal topology of the acrotretoid clade is uncertain and problematic. The Acrotretidae, as defined here, is not supported as a monophyletic group by the analysis; it might partly represent a paraphyletic stem group from which the other families, the Scaphelasmatidae, Biernatidae, Ephippelasmatidae, Ceratretidae, and Torynelasmatidae were derived (Fig. 50).

The origin and earliest evolution of the acrotretoids are still poorly known; the earliest known genera from the late Atdabanian

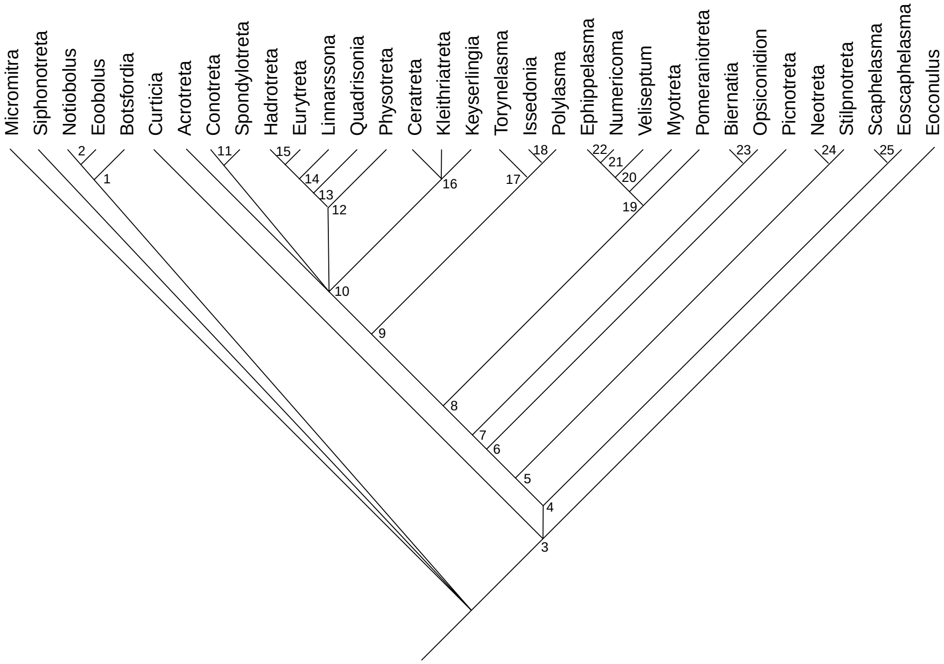

Fig. 50. Strict consensus tree of 27 equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 7 (new).

are the same age as the earliest botsfordioids and linguloids. The acrotretoids have generally been considered to be related closely to the botsfordiids and acrothelids (e.g., Williams & Rowell, 1965a), and this is still a possibility, although it is not supported in any of our cladistic analyses (see Fig. 38, 50).

The Cambrian acrotretoids are not particularly diverse taxonomically, seemingly belonging mostly to the Acrotretidae (*sensu lato*) and Ceratretidae, both being characterized by biconvex to moderately ventribiconvex shells, with a well-developed apical process and thickened muscles scars. The main diversification appears to take place at around the Late Cambrian to Early Ordovician transition, when most of the acrotretoid families, such as the Torynelasmatidae, Ephippelasmatidae, Eoconulidae, and others first appeared.

It is difficult to homologize the acrotretoidean muscle system with that of other lingulates. Williams and Rowell (1965a, p. 127, fig. 96, 114) proposed that the

Table 7. Synapomorphy scheme for internal nodes of cladogram shown in Figure 50 (new).

Node	Character states					
1	2:1	3:1	9:1			
2	1:2	8:1	20:2	30:1		
3	7:0	10:2	21:1	22:2	24:2	41:2
4	32:1					
5	10:3	13:1	25:4	28:1		
6	33:1					
7	16:4	25:0				
8	26:2	28:2				
9	14:0	16:3	40:1			
10	15:1	25:7	26:4			
11	12:1	14:1	15:2	19:1	39:1	
12	16:1	25:3	26:5			
13	33:3	34:1				
14	25:5	26:0				
15	5:1					
16	10:2	13:0	16:1	23:1		
17	14:2	36:1				
18	38:1					
19	1:3	12:1	36:3			
20	15:1					
21	34:1					
22	36:2	37:1				
23	21:0	24:0	35:1	36:2	39:1	
24	1:0	2:0	14:3			
25	15:1	16:2				

TABLE 8. Character-state matrix used in PAUP analysis (Fig. 50) of characters as listed in Table 9. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Micromitra	1	2	0	2	0	0	1	0	0	0	0	0	0	9	9	1	0	1	2	9
Siphonotreta	1	2	0	0	0	1	1	0	0	1	1	0	0	9	9	0	0	0	0	1
Notiobolus	2	1	0	0	0	0	1	1	1	0	0	0	0	9	9	0	0	0	0	2
Eoobolus	2	1	1	1	0	0	1	1	1	0	0	0	0	9	9	0	0	0	0	2
Botsfordia	1	1	1	1	0	0	2	0	1	0	0	0	0	9	9	0	1	0	0	0
Curticia	1	1	0	1	0	0	0	9	9	4	1	0	0	3	0	0	0	0	0	0
Acrotreta	1	2	0	1	1	0	0	9	0	3	0	0	0	0	1	3	0	0	1	0
Conotreta	1	2	0	1	0	0	0	9	0	3	0	1	1	1	2	3	0	0	1	0
Hadrotreta	1	2	0	1	1	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Eurytreta	1	2	0	1	1	0	0	9	0	3	0	1	0	0	2	1	0	0	0	0
Linnarssonia	1	2	0	1	0	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Neotreta	0	0	0	1	0	0	0	9	0	3	0	0	1	3	0	0	0	0	9	9
Physotreta	1	2	0	1	0	0	0	9	0	3	0	0	1	0	1	1	0	0	0	0
Picnotreta	1	2	0	1	0	0	0	9	0	3	0	0	1	1	1	0	0	0	0	0
Quadrisonia	1	2	0	1	0	0	0	9	0	3	0	1	1	1	1	2	0	0	0	0
Spondylotreta	1	2	0	1	0	0	0	9	0	3	0	1	1	1	2	3	0	0	9	9
Stilpnotreta	0	1	0	1	0	0	0	9	0	3	0	0	1	3	2	0	0	0	9	9
Eoconulus	0	2	0	1	0	0	0	9	0	5	0	0	0	1	0	5	0	0	0	0
Scaphelasma	1	2	0	1	0	0	0	9	0	2	0	0	0	1	1	2	0	0	9	9
Eoscaphelasma	1	2	0	1	0	0	0	9	0	2	0	0	0	1	1	2	0	0	9	9
Torynelasma	1	2	0	1	9	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Issedonia	3	2	0	1	0	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Polylasma	1	2	0	1	0	0	0	9	0	3	0	0	1	2	0	3	0	0	9	9
Ephippelasma	3	2	0	1	0	0	0	9	0	3	0	1	1	0	1	4	0	0	9	9
Veliseptum	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Pomeraniotreta	3	2	0	1	0	0	0	9	0	3	0	1	1	1	0	4	0	0	9	9
Numericoma	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Myotreta	3	2	0	1	0	0	0	9	0	3	0	1	1	1	1	4	0	0	9	9
Biernatia	1	2	0	1	0	0	0	9	0	3	0	0	1	1	0	4	0	0	9	9
Opsiconidion	1	2	0	1	0	0	0	9	0	3	0	0	1	1	0	4	0	0	9	9
Ceratreta	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0
Kleithriatreta	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0
Keyserlingia	1	2	0	1	0	0	0	9	0	2	0	0	0	0	1	1	0	0	0	0

musculature consisted of anterior and posterior adductors (as in craniids and discinoids), with one pair of cardinal muscles attached to the large posterior scars of both valves in addition to a pair of smaller anterocentral muscles extending from the ventral apical pits to the dorsal anterior scars lateral to the median septum. This model, however, does not account for the dorsal median buttress and ventral apical process, both showing muscle scars. Accepting that the musculature of the Acrotretoidea is of the general craniid-discinoid type, it would seem that both the ventral-dorsal cardinal scars as well as the scars on the median buttress and apical pits correspond to the posterior adductor, while the dorsal anterocentral scars and the scars on the apical process are the equivalent to the anterior adductor.

An alternative model for reconstructing acrotretoid musculature was proposed by POPOV (1992, fig. 3), who suggested that the conical ventral valve may represent a linguloid ventral valve that is rolled up along the posterior margin. The botsfordiids would then appear to have a morphology intermediate between that of the Obolidae and Acrotretidae, in having an incompletely rolled-up ventral valve (see Fig. 44). The acrotretoid pedicle foramen would have been formed by the linguloid pedicle groove, but the linguloid propareas are reduced to partly form the intertrough; if this is so, the acrotretoid ventral pseudointerarea might

TABLE 8. *(Continued).*

Character no.	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Micromitra	0	1	0	0	9	0	0	2	0	0	0	0	0	0	0	9	9	9	2	0	9
Siphonotreta	0	0	0	1	9	1	0	2	1	0	0	0	0	0	0	9	9	9	0	0	1
Notiobolus	0	0	0	0	9	0	0	2	1	1	0	0	0	0	0	9	9	9	0	0	0
Eoobolus	0	0	0	0	9	0	0	2	1	1	0	0	0	0	0	9	9	9	0	0	0
Botsfordia	0	0	0	0	9	0	0	2	1	0	1	0	0	0	0	9	9	9	0	0	0
Curticia	1	2	0	2	9	0	0	2	1	0	0	0	0	9	9	9	9	9	0	0	9
Acrotreta	1	2	0	2	7	4	0	2	1	0	0	1	1	0	0	9	9	9	9	1	2
Conotreta	1	2	0	2	8	0	0	2	1	0	0	1	1	0	0	0	9	9	1	1	2
Hadrotreta	1	2	9	2	5	0	0	2	1	0	0	1	3	1	0	9	0	0	0	1	2
Eurytreta	1	2	0	2	4	0	0	2	1	0	0	1	3	9	9	9	9	9	0	1	2
Linnarssonia	1	2	0	2	5	0	0	1	2	0	0	1	3	9	9	9	9	9	0	1	2
Neotreta	9	2	0	2	6	0	0	1	2	0	0	1	0	9	9	9	9	9	9	0	2
Physotreta	1	2	0	2	3	5	0	2	1	0	0	1	1	0	0	0	9	9	9	1	2
Picnotreta	9	2	0	2	4	0	0	1	2	0	0	1	1	0	0	0	9	9	9	0	2
Quadrisonia	1	2	0	2	3	5	0	2	1	0	0	1	3	9	9	9	9	9	9	1	2
Spondylotreta	1	2	0	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	1	1	2
Stilpnotreta	9	2	0	2	4	0	0	1	1	0	0	1	0	9	9	9	9	9	9	1	2
Eoconulus	9	2	0	2	6	0	1	0	9	0	0	0	0	9	9	9	9	9	9	0	2
Scaphelasma	9	2	0	2	6	0	0	2	1	0	0	1	2	0	0	0	9	9	9	0	2
Eoscaphelasma	9	2	0	2	6	3	0	2	1	0	0	1	0	9	9	9	9	9	9	0	2
Torynelasma	9	2	0	2	0	2	0	2	1	0	0	1	1	0	0	1	0	0	9	1	2
Issedonia	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	1	0	1	9	1	2
Polylasma	0	2	0	2	0	2	0	2	1	0	0	1	1	0	0	1	1	1	9	1	2
Ephippelasma	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	2	1	0	9	0	2
Veliseptum	0	2	0	0	9	0	0	2	1	0	0	1	1	1	0	3	0	0	9	0	2
Pomeraniotreta	1	2	0	2	1	5	0	2	1	0	0	1	0	9	9	9	9	9	9	0	2
Numericoma	1	2	0	2	0	2	0	2	1	0	0	1	1	1	0	2	1	0	9	0	2
Myotreta	1	2	0	2	0	2	0	2	1	0	0	1	1	0	0	3	0	0	9	0	2
Biernatia	0	2	0	0	9	0	0	1	1	0	0	1	1	0	1	4	0	0	9	0	2
Opsiconidion	0	2	0	0	9	0	0	1	1	0	0	1	1	0	1	2	0	0	1	0	2
Ceratreta	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	0	1	2
Kleithriatreta	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	3	0	0	0	1	2
Keyserlingia	1	2	1	2	7	4	0	2	1	0	0	1	1	0	0	0	9	9	0	1	2

not be homologous with that of the linguloids.

As a result of the acquisition of a conical valve shape, the ventral posterolateral muscle fields, with the equivalents of the linguloid transmedian and anterior lateral muscles, migrated up on to the posterior slope of the acrotretoid valve to form the ventral cardinal scars; the dorsal cardinal scars sometimes show possible traces of two muscles, and may have been the sites of equivalents of either the transmedian, outside lateral, or middle lateral. The ventral umbonal muscle scars then formed the acrotretoid apical pits posterolateral to the pedicle foramen, and this muscle was probably attached to the dorsal median buttress. The acrotretoid apical process is invariably situated between the proximal ends of the ventral *vascula lateralia* and undoubtedly represents a muscle platform with up to two pairs of muscle scars (e.g., *Hadrotreta, Ceratreta,* and *Keyserlingia*), which are possibly homologous with the linguloid outside lateral, middle lateral, and central muscles, while the dorsal anterocentral muscle scar may have served as the attachment site for the central and anterior lateral muscles (Fig. 51).

The acrotretoids undoubtedly had a smaller number of muscles by comparison with the linguloids, and it is likely that, for example, the central muscles were absent in most forms, especially in extremely highly conical taxa that lack or have a reduced apical

TABLE 9. List of coded characters used in cladistic analysis (Fig. 50) of genera within order Acrotretida (new).

1. convexity: equibiconvex (0); ventribiconvex (1); dorsibiconvex (2); planoconvex or concavoconvex (3).
2. relative size of valves: equivalved (0); inequivalved (1); strongly inequivalved (2).
3. granular ornamentation: absent (0); present (1).
4. larval shell: smooth (0); pitted (1); pustulose (2).
5. dorsal sulcus: absent (0); present (1).
6. hollow spines: absent (0); present (1).
7. ventral pseudointerarea: acrotretoid (0); well developed (1); narrow, apsacline or catacline (2).
8. flexure lines: absent (0); present (1).
9. pedicle groove: absent (0); present (1).
10. enclosed pedicle foramen: absent (0); posterior to beak (1); anterior to beak (2); apical (3); present in juveniles, delthyrial in adults (4); present in juveniles, closed in adults (5).
11. resorption around foramen: absent (0); present (1).
12. external pedicle tube: absent (0); present (1).
13. larval pedicle opening: marginal notch in larval shell (0); within larval shell (1).
14. acrotretoid pseudointerarea (if present): convex in cross section, well defined laterally (0); convex in cross section, poorly defined laterally (1); flattened, well defined laterally (2); vestigial (3).
15. acrotretoid pseudointerarea (if present): undivided (0); divided by intertrough (1); divided by interridge (2).
16. profile of ventral valve: gently convex (0); strongly convex to conical (1); conical, catacline with subcentral apex (2); high conical, procline to catacline (3); high conical, apsacline to procline (4); adopting shape of substrate (5).
17. ventral larval spines: absent (0); present (1).
18. homeodeltidium: absent (0); present (1).
19. ventral mantle canals: baculate (0); pinnate (1); saccate (2).
20. ventral *vascula lateralia:* submedian, divergent proximally, or arcuate (0); submedian, arcuate (1); subperipheral or peripheral, straight or arcuate (2).
21. apical pits: absent (0); present (1).
22. ventral posterolateral muscle fields: anterior to pedicle opening (0); on inner sides of homeodeltidium (1); on inner sides of acrotretoid pseudointerarea (2).
23. ventral posterolateral muscle platform: absent (0); present (1).
24. ventral anterior muscle platform: absent (0); present (1); present, forming apical process (2).
25. apical process (if present): low ridge anterior to pedicle tube (0); occluding apex (1); wide ridge perforated by pedicle tube (2); wide, subtriangular, anterior and lateral to foramen (3); wide, subtriangular, anterior to foramen (4); bosslike (5); vestigial (6); high septum (7); high ridge anterior to foramen (8).
26. internal pedicle tube: absent (0); along anterior slope of valve (1); along posterior slope of valve (2); free (3); supported by septum (4); surrounded by apical process (5).
27. dorsal umbo: marginal (0); anterior to margin (1).
28. dorsal pseudointerarea: absent (0); vestigial (1); well developed (2).
29. median groove: absent (0); narrow (1); wide (2).
30. dorsal flexure lines: absent (0); present (1).
31. dorsal larval spines: absent (0); present (1).
32. dorsal posterolateral muscle fields: weakly defined, not thickened (0); thickened, forming cardinal scars (1).
33. dorsal median septum: absent (0); submedian (1); near anterior margin (2); low ridge (3).
34. dorsal median septum with spines along anterior slope: absent (0); present (1).
35. dorsal median septum with concave anterior margin: absent (0); present (1).
36. surmounting plate: absent (0); dorsally concave (1); saddle shaped (2); flat (3); dorsally convex (4).
37. surmounting plates with spines: absent (0); present (1).
38. surmounting plate with dorsally directed plates along lower surface: absent (0); present (1).
39. dorsal mantle canals: baculate (0); bifurcate (1); pinnate (2); saccate (3).
40. median buttress: absent (0); present (1).
41. shell structure: baculate (0); microgranular (1); columnar or camerate (2).

process (e.g., *Biernatia*); moreover, the middle lateral and outside lateral muscles might have been united into a single muscle running from the dorsal cardinal muscle fields to the apical process.

Assuming that this interpretation of acrotretoid muscles is correct, it is clear that the same muscle was attached to areas of very unequal size in opposite valves; thus it is unlikely that they had columnar muscles like

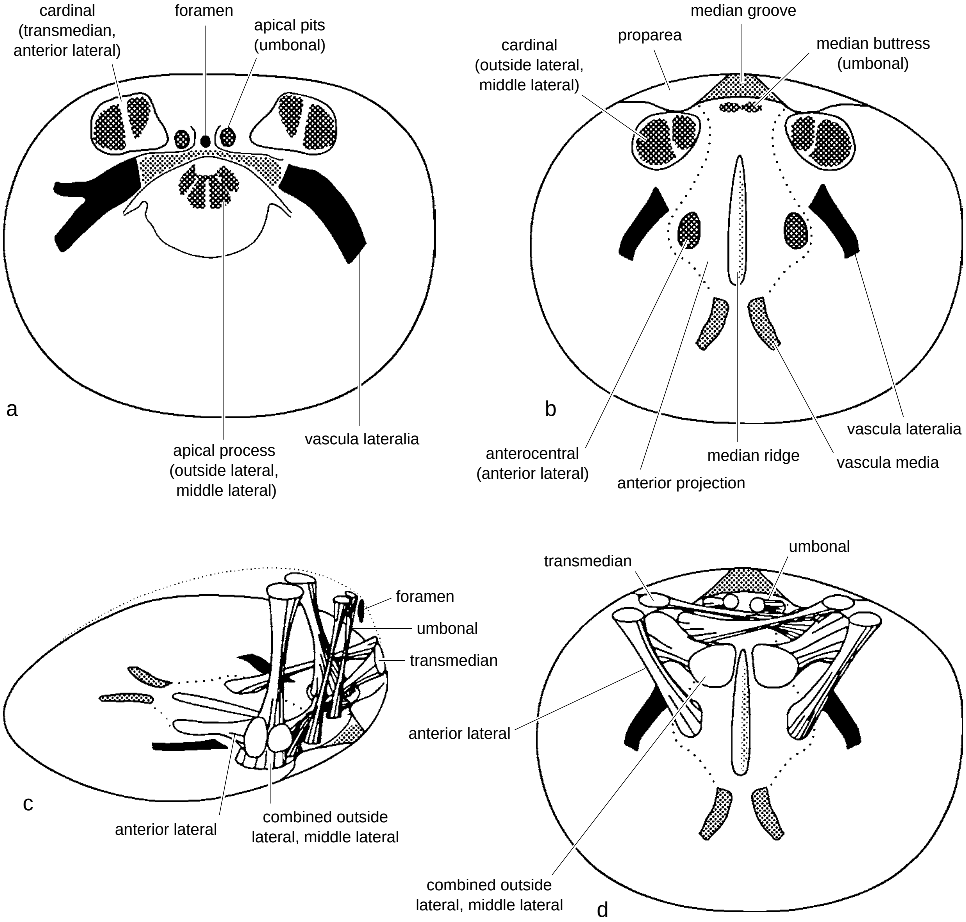

FIG. 51. Schematic illustration of musculature and mantle canal system of *Hadrotreta; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed laterally, ventrally (new).

those of all recent linguloids and discinoids, but instead the muscles might have been tendonized. Tendonization might also have been related to the high convexity of the shell.

Family ACROTRETIDAE Schuchert, 1893

[Acrotretidae SCHUCHERT, 1893, p. 150] [*incl.* Linnarssoniinae ROWELL, 1965a, p. 277; Anabolotretidae USHATINSKAYA, 1994, p. 48; Kotujotretidae USHATINSKAYA, 1994, p. 50]

Ventral valve conical, more rarely convex; ventral pseudointerarea commonly bisected by intertrough or interridge; pedicle foramen circular or elongate oval, apical or immediately posterior to beak; foramen completely or partly within larval shell; apical process variable, usually with muscle platform directly anterior to pedicle tube; dorsal interior usually with median septum or ridge; median buttress commonly present; cardinal muscle fields usually thickened, becoming wider anterolaterally. *Lower Cambrian–Silurian (Wenlock).*

Acrotreta KUTORGA, 1848, p. 275 [**A. subconica;* SD DAVIDSON, 1853, p. 133]. Shell finely pustulose with wide posterior margin; ventral valve highly conical; pseudointerarea well defined, apsacline to catacline or weakly procline; foramen not enclosed within larval shell; dorsal pseudointerarea with wide median groove and propareas; apical process forming high septum and muscular platform, perforated by pedicle tube that usually occupies more than half valve height; strongly impressed pinnate mantle canals, with three pairs of trunks; dorsal interior with triangular median septum, median buttress. *Ordovician (?Tremadoc, Arenig–Llandeilo):* Bohemia, *?Tremadoc, Arenig;* Poland, *Arenig;* Estonia, Russia (Ingria, Southern Urals), Sweden, *Arenig–Llanvirn;* USA, Alabama, *Llandeilo.*——FIG. 52,*1a–g.* **A. subconica,* Billingen Stage; *a,b,* ventral valve, posterior view, lateral view, Päite beds, Lava River, Vassilkovo, Ingria, Russia, CNIGR 134/9960, ×8.3 (Gorjansky, 1969); *c,* dorsal valve exterior, ×13.8; *d,* oblique lateral view of dorsal valve, ×16.2; *e,* detail of pitted ornamentation of dorsal larval shell, Päite beds, Mäekalda, Tallinn, Estonia, RMS Br 133894, ×1133; *f,* ventral valve interior, Mäeküla beds, Mäeküla, Estonia, RMS Br 133890, ×9.2; *g,* dorsal valve interior, Päite beds, Mäekalda, Tallinn, Estonia, RMS Br 133895, ×11.2 (Holmer & Popov, 1994).

Acrothyra MATTHEW, 1901, p. 303 [**Acrotreta proavia* MATTHEW, 1899, p. 203; SD WALCOTT, 1912, p. 716]. Shell ventribiconvex with short, convex posterior margin; ventral pseudointerarea well defined, apsacline; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea vestigial, concave undivided plate; ventral interior with elongate triangular apical process, thickened anteriorly, located anterior to foramen; apical pits anterior to foramen on lateral sides of apical process; dorsal valve with low triangular median ridge; median buttress elongated. *Middle Cambrian:* USA (California, Nevada, Idaho), Canada (Nova Scotia), ?France, ?England, Russia (?Novaya Zemlya, Altai).——FIG. 52,*2a–e. A. urania* (WALCOTT), Middle Cambrian, Utah, USNM loc. 55u; *a–d,* ventral valve exterior, posterior view, lateral view, interior, USNM 139491, ×12.5; *e,* dorsal valve interior, USNM 139493, ×12.5 (Rowell, 1966).

Aktassia POPOV in NAZAROV & POPOV, 1976, p. 37 [**A. triangularis;* OD]. Shell elongate triangular with short, convex posterior margin; ventral valve narrow, conical; pseudointerarea orthocline, poorly defined laterally, undivided; external pedicle tube with minute foramen, enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea poorly developed, undivided; apical process absent; dorsal interior with moderately high, triangular, bladelike median septum; dorsal median buttress absent; cardinal muscle fields poorly defined. *Ordovician (Llandeilo):* Sweden, Kazakhstan (Chingiz Range).——FIG. 52,*3a,b.* **A. triangularis,* Bestamak Formation, Chingiz Range, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136390, ×62.5; *b,* dorsal valve interior, RMS Br 136391, ×41.7 (new).——FIG. 52,*3c,d. A.* sp. cf. *A. triangularis* POPOV, Gullhögen Formation, Skövde, Västergötland; *c,* ventral valve, lateral view, ×162; *d,* ventral valve interior, RMS Br 132788, ×83.3 (Holmer, 1989b).

Amictocracens HENDERSON & MACKINNON, 1981, p. 295 [**A. teres;* OD]. Shell subcircular with short, weakly concave posterior margin; ventral valve low, conical; pseudointerarea procline, poorly defined laterally with fine interridge; foramen enclosed within larval shell; dorsal valve weakly convex with poorly defined pseudointerarea, forming concave, undivided plate; apical process forming bosslike projection anterior to internal foramen; dorsal interior with moderately high, triangular, bladelike median septum; dorsal median buttress poorly developed. *Middle Cambrian:* Australia (Queensland), New Zealand; ?northern China (Hebei).——FIG. 52,*5a–d.* **A. teres,* Mailchange Limestone, *Goniagnostus nathorsti* Biozone, Georgina basin, Queensland; *a,* dorsal valve interior, JCF 10718, ×22.5; *b,c,* ventral valve exterior, lateral view of both valves, JCF 10719, ×35; *d,* ventral valve interior, JCF 10717, ×20.8 (Henderson & MacKinnon, 1981).

Anabolotreta ROWELL & HENDERSON, 1978, p. 8 [**A. tegula;* OD]. Shell transversely oval with short, weakly concave posterior margin; ornament of distinctive growth lamellae; ventral valve low conical; ventral pseudointerarea procline, poorly defined laterally with intertrough poorly defined or absent; foramen directly posterior to beak, not enclosed within larval shell; dorsal valve moderately convex; dorsal pseudointerarea poorly defined, undivided, concave; apical process elongate, subtriangular, anterior to foramen; dorsal median ridge sometimes developed. *upper Middle Cambrian–Upper Cambrian:* Greenland, *upper Middle Cambrian;* USA (Great Basin), *Dresbachian;* Russia (Novaya Zemlya, Siberia), Kazakhstan, *upper Mayaian–Upper Cambrian;* Australia (Queensland, New South Wales), New Zealand.——FIG. 52,*4a–f.* **A. tegula,* Mungerebar Limestone, western Queensland, Australia; *a,* dorsal valve exterior, CPC 17935, ×33.3; *b,* dorsal valve interior, JCF 10312, ×30; *c,* holotype, ventral valve interior, JCF 10311, ×33.3; *d,* ventral valve exterior, CPC 17934, ×33.3; *e,f,* lateral view of both valves, posterior view, CPC 17937, ×50 (Rowell & Henderson, 1978).

Anelotreta PELMAN in ERMAK & PELMAN, 1986, p. 198 [**A. magna;* OD]. Shell large for family, transversely oval; foramen large, transversely oval, not enclosed within larval shell, directly posterior to beak; ventral pseudointerarea procline with well-defined intertrough; dorsal valve flattened; dorsal propareas well defined, narrow; ventral cardinal muscle field forming low platform; apical process subtriangular, forming high median boss directly anterior to foramen; dorsal interior with small cardinal muscle fields and well-defined anterocentral scars; dorsal median buttress well developed; dorsal median ridge low; both valves with baculate mantle canals. *Middle Cambrian (Mayaian):* Russia (north-central Siberia).——FIG. 53,*2a–c.* **A. magna,* Mayaktakh Formation, Lena River at Chekurovka, Siberia; *a,* detail of ventral valve exterior, ×25; *b,* lateral view of ventral valve, RMS Br 136392, ×12.5; *c,* ventral valve interior, RMS Br 136393, ×8.3 (new).

Angulotreta PALMER, 1954, p. 769 [**A. triangularis;* OD]. Shell with weakly convex posterior margin; ventral pseudointerarea procline to weakly apsacline with intertrough; foramen enclosed within larval shell; dorsal pseudointerarea with wide median groove; apical process well developed, long, forming

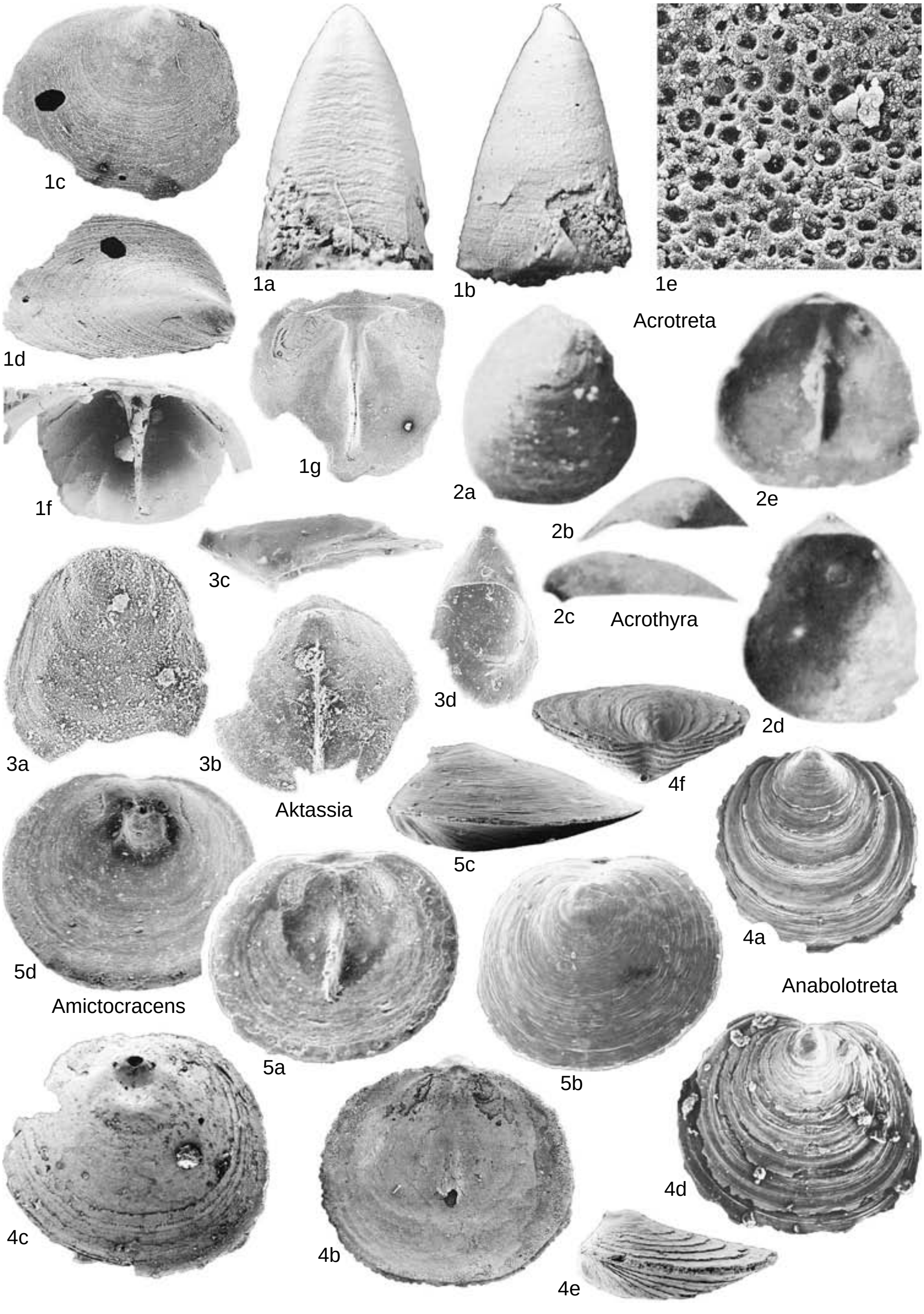

FIG. 52. Acrotretidae (p. 103–104).

broad ridge along posterior slope, partly enclosing internal pedicle tube anteriorly; apical pits well developed, deep, placed posterior to internal foramen; dorsal triangular median septum high, may be digitate; dorsal median buttress and anterocentral muscle scars present. *?Middle Cambrian, Upper*

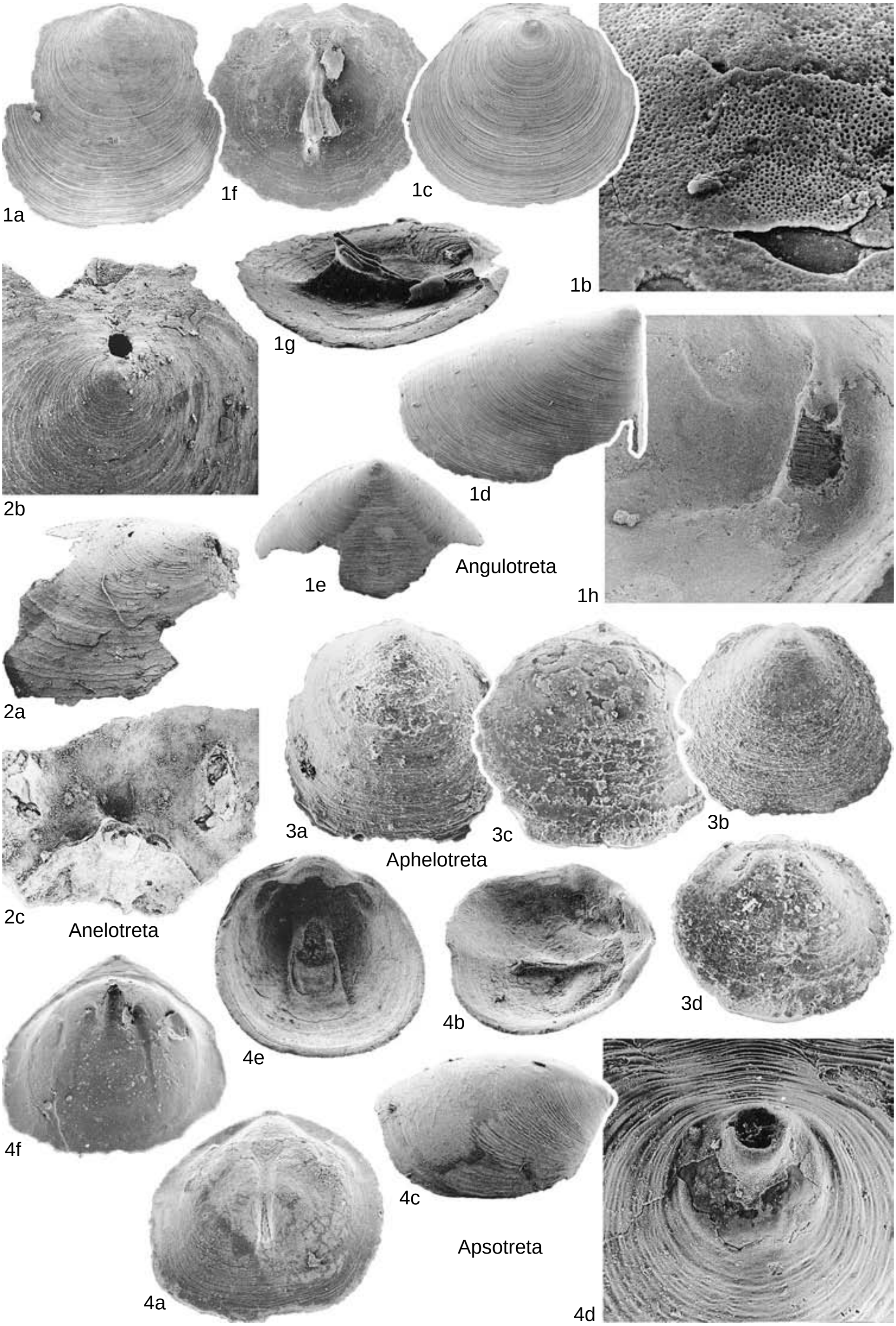

FIG. 53. Acrotretidae (p. 104–107).

Cambrian: USA (Texas, Montana, Wyoming, Missouri), Estonia, Russia (Ingria, ?Siberia, Novaya Zemlya), *lower Upper Cambrian;* West Antarctica; ?northern China (Hebei).——FIG. 53,*1a–h*. **A. triangularis,* Dresbachian, *Aphelaspis* Biozone, central Texas; *a,* dorsal valve exterior, ×18.3; *b,* detail of pitted ornamentation of the dorsal larval shell, USNM 459689a, ×558; *c,* ventral valve exterior, ×16.7; *d,* lateral view of ventral valve, ×20; *e,* posterior view of ventral valve, USNM 459689b, ×18.3; *f,* dorsal valve interior, ×18.3; *g,* oblique lateral view of dorsal valve, USNM 459689c, ×23.3; *h,* ventral valve interior, USNM 459689d, ×29.2 (new).

Aphelotreta ROWELL, 1980, p. 10 [**A. minuta;* OD]. Shell biconvex, subcircular with short, weakly concave posterior margin; ventral pseudointerarea low catacline to moderately apsacline with indistinct intertrough; foramen small, not enclosed within larval shell; dorsal pseudointerarea with short anacline to orthocline propareas and wide median groove; apical process vestigial, forming low, elongate triangular thickening anterior to foramen; dorsal interior with poorly developed median ridge and median buttress. *lower Middle Cambrian–lower Upper Cambrian:* USA (Nevada), Russia (north-central Siberia), ?Australia (New South Wales).——FIG. 53,*3a–d*. **A. minuta,* Pioche Shale, *Albertella* Biozone, Highland Range, Nevada; *a,* ventral valve exterior, KUMIP 115472, ×41.7; *b,* dorsal valve exterior, KUMIP 115511, ×41.7; *c,* ventral valve interior, KUMIP 115469, ×41.7; *d,* dorsal valve interior, KUMIP 115471, ×41.7 (Rowell, 1980).

Apsotreta PALMER, 1954, p. 770 [**A. expansa;* OD]. Shell subcircular with short, weakly convex anterior margin; ventral valve strongly convex to low subconical; pseudointerarea low, apsacline with interridge; short external pedicle tube enclosed within larval shell; dorsal pseudointerarea well developed with broadly triangular median groove and short orthocline to anacline propareas; broad, ridgelike apical process mainly on anterior slope, long, parallel-sided or expanding anteriorly; dorsal interior with low triangular median septum, elongate median buttress. *Upper Cambrian:* USA (Missouri, Texas).——FIG. 53,*4a–f*. **A. expansa,* upper Dresbachian, *Dunderbergia* Biozone, central Texas; *a,b,* dorsal valve interior, oblique lateral view, RMS Br 136394, ×16.7; *c,* lateral view of ventral valve exterior, ×20; *d,* detail of ventral larval shell, RMS Br 136395, ×123; *e,* oblique anterior view of ventral valve interior, RMS Br 136397, ×40; *f,* ventral valve interior, RMS Br 136396, ×20 (new).

Araktina KONEVA, 1992, p. 94 [**A. intermedia;* OD]. Shell subcircular to transversely suboval with wide, straight posterior margin; ventral valve low conical; pseudointerarea catacline to procline with poorly defined intertrough; foramen elongate, lens shaped, enclosed within larval shell; dorsal pseudointerarea wide, straight with shallow median groove; apical process broad, subtriangular, anterior to foramen; ventral mantle canals baculate; dorsal cardinal muscle fields small, thickened; dorsal median buttress small; dorsal median ridge low, triangular. *Middle Cambrian (Mayaian)–Upper Cambrian:* Kazakhstan, Russia (eastern Siberia).——FIG. 54,*3a–d*. **A. intermedia,* Upper Cambrian, *Glyptagnostus stolidotus* Biozone, Malyi Karatau, Kazakhstan; *a,* ventral valve exterior, RMS Br 136398, ×25; *b,* detail of ventral larval shell, RMS Br 136399, ×91; *c,* ventral valve interior, RMS Br 136400, ×19.2 (new); *d,* dorsal valve interior, MANK 726/486, ×13.3 (Koneva, 1992).

Canthylotreta ROWELL, 1966, p. 5 [**Acrotreta marjumensis* WALCOTT, 1908, p. 94; OD]. Shell subcircular; ventral valve moderately convex with weakly incurved beak; pseudointerarea low, apsacline with intertrough; foramen immediately posterior of beak, not enlosed within larval shell; dorsal pseudointerarea well defined with broad median groove and short anacline propareas; apical process subtriangular, partly enclosing pedicle tube; apical pits small, directly adjacent to foramen; dorsal interior with thin, moderately high triangular septum and median buttress; dorsal anterocentral muscle scars well defined. *upper Middle Cambrian, ?Upper Cambrian:* USA (Utah, Nevada), Greenland, *upper Middle Cambrian;* ?northern China (Hebei), *upper Middle Cambrian–Upper Cambrian.*——FIG. 54,*1a–h*. **C. marjumensis* (WALCOTT), upper Middle Cambrian, *Cedaria* Biozone, Utah, USNM loc. 11n; *a,* dorsal valve exterior, USNM 459690a, ×11.2; *b,c,* ventral valve exterior, lateral view, ×11.2; *d,* oblique posterior view of ventral pseudointerarea, USNM 459690b, ×45.8; *e,* dorsal valve interior, ×13.8; *f,* lateral view of dorsal valve, ×16.7; *g,* oblique lateral view of dorsal pseudointerarea, USNM 459690c, ×45.8; *h,* oblique lateral view of ventral valve interior, showing the apical process, USNM 459690d, ×27.1 (new).

Conotreta WALCOTT, 1889, p. 365 [**C. rusti;* OD] [=*Geinitzia* CLARKE, 1889, p. 43, *nom. nud.*]. Ventral valve externally similar to *Angulotreta,* but usually with fine interridge; ventral mantle canals pinnate; apical process forming low ridge along anterior slope of valve; dorsal median septum high, triangular, usually with anterior denticles or spines; dorsal interior with large cardinal muscle scars and median buttress. *Ordovician (Arenig–Caradoc):* USA, Ireland, Sweden, Russia (Ingria), Estonia, Kazakhstan, ?China.——FIG. 55,*1a–g*. **C. rusti,* Denley Limestone, Trenton Falls, New York; *a,* dorsal valve exterior, ×41.7; *b,* detail of dorsal larval shell, OSU 48101, ×162; *c,* oblique view of dorsal pseudointerarea, OSU 48102, ×33.3; *d,* ventral valve exterior, ×31.7; *e,* oblique view of larval shell and foramen, OSU 48103, ×100; *f,* detail of apical process, OSU 48104, ×20.8; *g,* paratype, latex cast of ventral internal mold, showing apical process and pinnate mantle canals, MCZ 8840, ×20.8 (new).——FIG. 55,*1h–l*. *C. siljanensis* HOLMER, Furudal-Dalby limestones, Llandeilo, Siljan district, Sweden; *h,* paratype, dorsal valve exterior, RMS Br

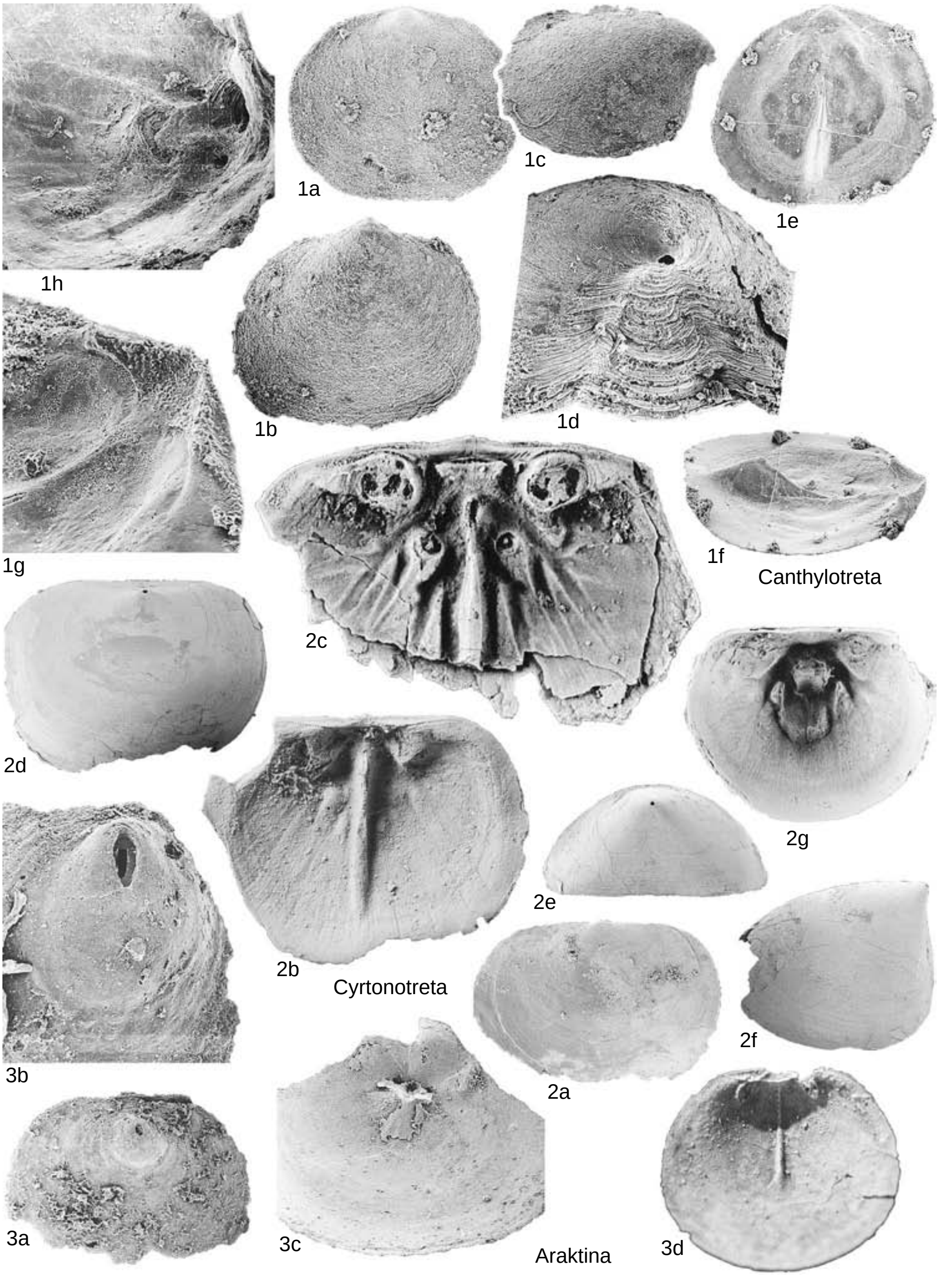

FIG. 54. Acrotretidae (p. 107–110).

132467, ×22.9; *i,j,* holotype, dorsal valve interior, lateral view, RMS Br 132374, ×25; *k,l,* paratype, ventral valve, lateral view, posterior view, RMS Br 132445, ×12.5 (Holmer, 1989b).

Cyrtonotreta HOLMER, 1989b, p. 93 [**Conotreta depressa* COOPER, 1956, p. 251; OD]. Shell subcircular to transversely oval with straight, wide posterior margin; ventral valve moderately conical,

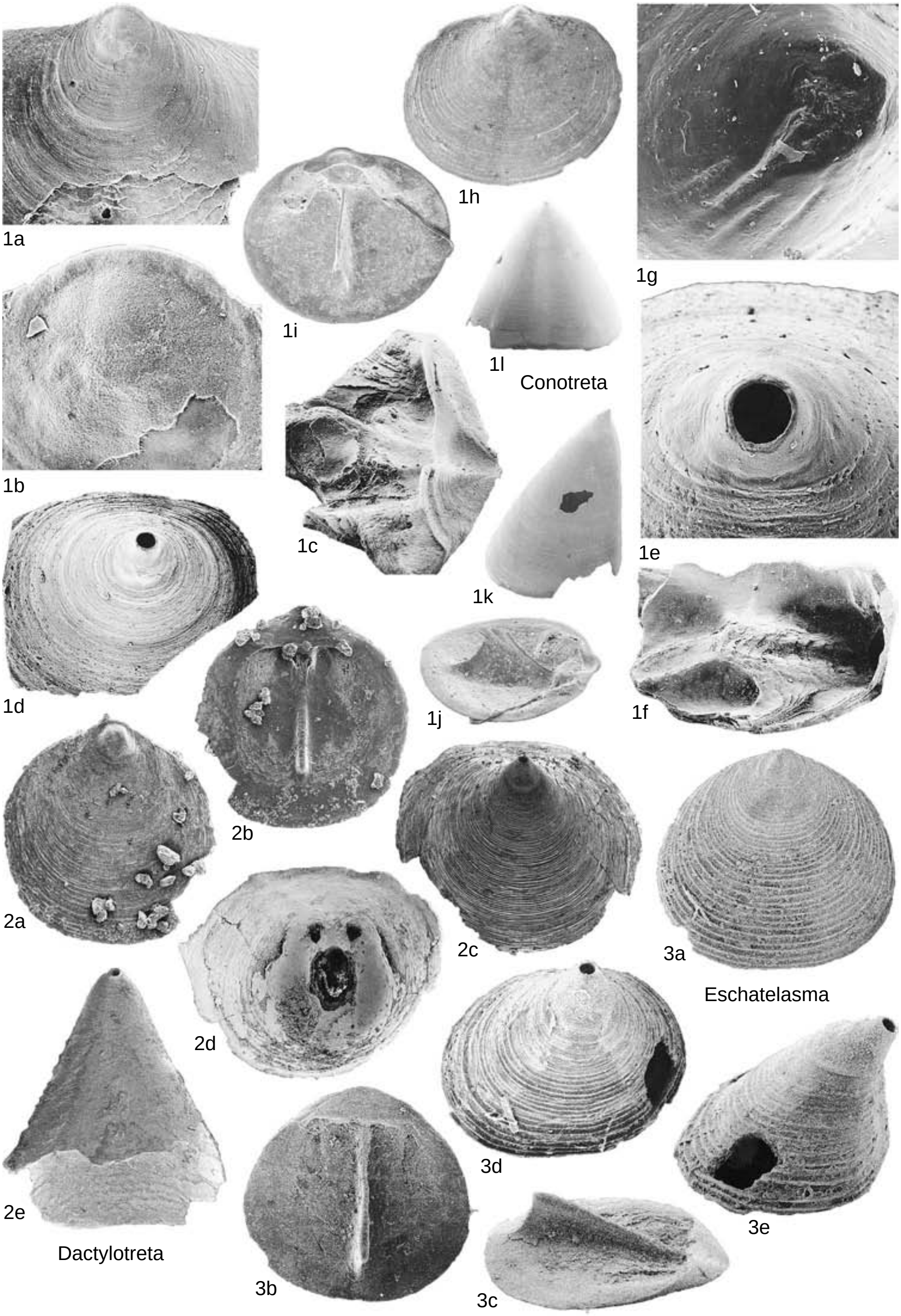

FIG. 55. Acrotretidae (p. 107–110).

procline to apsacline; ventral pseudointerarea commonly with interridge; foramen enclosed within larval shell; dorsal valve weakly convex, sulcate; dorsal pseudointerarea wide, orthocline to anacline with median groove; apical process forming broad, thickened ridge anterior and lateral to interior foramen; pinnate mantle canal deeply impressed; dorsal interior with long triangular median septum and broad median buttress. *Ordovician (Arenig–Llandeilo):* USA (Alabama), Sweden, Kazakhstan.——FIG. 54,*2a–g.* **C. depressa* (COOPER), Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, USNM 459691a, ×5; *b,* dorsal valve interior, USNM 459691b, ×6.5 (new); *c,* dorsal valve interior, USNM 116815k, ×7.5 (Cooper, 1956); *d,* ventral valve exterior, ×5.4; *e,* posterior view of ventral valve, ×4.6; *f,* oblique lateral view of ventral valve, USNM 459691c, ×5.4 (new); *g,* holotype, ventral valve interior, USNM 116815e, ×5 (Cooper, 1956).

Dactylotreta ROWELL & HENDERSON, 1978, p. 3 [**D. redunca;* OD]. Shell subcircular with convex posterior margin; ventral valve highly conical; ventral pseudointerarea catacline to weakly procline, poorly defined laterally with narrow intertrough; foramen enclosed within larval shell; dorsal pseudointerarea long and high with well-developed median groove and anacline to orthocline propareas; apical process large, completely occluding apex; apical pits posterolateral to foramen; dorsal interior with low triangular median septum and median buttress. *upper Middle Cambrian–Ordovician (Tremadoc):* Greenland, *upper Middle Cambrian;* USA (Great Basin), *upper Dresbachian–lower Franconian;* Kazakhstan, Kirghizia, *Upper Cambrian;* Russia (Southern Urals), Sweden, Norway, *Tremadoc;* Australia (Queensland), *Middle Cambrian (Mayaian)–Upper Cambrian;* West Antarctica, *Upper Cambrian.*——FIG. 55,*2a–e.* **D. redunca,* Upper Cambrian, Georgina Basin, Queensland; *a,b,* holotype, dorsal valve exterior, interior, JCF 10309, ×33.3; *c,d,* paratype, ventral valve exterior, interior, JCF 10304, ×33.3; *e,* paratype, ventral valve, posterior view, JCF 10307, ×41.7 (Rowell & Henderson, 1978).

Dicondylotreta MEI, 1993, p. 410 [**D. parallela;* OD]. Shell ventribiconvex, subcircular; ventral pseudointerarea weakly apsacline; foramen not enclosed within larval shell; dorsal pseudointerarea with median groove; apical process forming median ridge between posterior and anterior slopes of valve, perforated posteriorly by pedicle tube; dorsal interior with low, triangular median sepum. *upper Middle Cambrian:* northern China (Hebei).——FIG. 56,*1a–e.* **D. parallela,* Middle Cambrian (Mayaian), *Taitzuia–Damesella* Biozones, Qingxing, Wanxian County; *a,* paratype, dorsal valve exterior, MCMB 91011, ×25; *b,* paratype, dorsal valve interior, MCMB 91009, ×25; *c,* paratype, ventral valve exterior, MCMB 91013, ×25; *d,* holotype, ventral valve interior, MCMB 91008, ×25; *e,* paratype, detail of ventral larval shell, MCMB 91131, ×217 (Mei, 1993).

Ditreta BIERNAT, 1973, p. 65 [**D. dividua;* OD]. Shell rounded, with straight posterior margin; ventral valve moderately conical; pseudointerarea poorly defined laterally; dorsal valve weakly convex; dorsal pseudointerarea with median groove; apical process broad; dorsal median ridge low, short. Genus poorly understood. *Ordovician (Tremadoc):* Poland.

Eschatelasma POPOV, 1981, p. 34 [**E. rugosum;* OD]. Shell subcircular with convex posterior margin; ornament of evenly spaced rugae; ventral valve moderately conical; pseudointerarea poorly defined laterally, procline to catacline with weak intertrough; foramen enclosed within larval shell; dorsal valve flat; dorsal pseudointerarea with shallow, broadly triangular median groove; apical process vestigial or lacking; dorsal median septum long, triangular; dorsal cardinal muscle field large, extending to midvalve. *Silurian (Wenlock):* Estonia.——FIG. 55,*3a–e.* **E. rugosum,* Parmaja Formation, Jaani Stage, Ohesaare Core, Saaremaa, Estonia; *a,* paratype, dorsal valve exterior, TAGI BR 1612, ×30; *b,* dorsal valve interior, ×23.3; *c,* holotype, oblique lateral view of dorsal valve, TAGI BR 1615, ×27.5; *d,* ventral valve exterior, ×50.8; *e,* paratype, lateral view of ventral valve, TAGI BR 1618, ×55 (new).

Eurytreta ROWELL, 1966, p. 9 [**Acrotreta curvata* WALCOTT, 1902, p. 584; OD] [=*Euritreta* POPOV in NAZAROV & POPOV, 1980, p. 91]. Shell subcircular to transversely oval with short, weakly convex posterior margin; ventral valve convex to subconical; ventral pseudointerarea apsacline to catacline, poorly defined laterally with poorly defined intertrough or interridge; foramen usually forming short tube, enclosed within larval shell; dorsal valve weakly convex, sulcate with low pseudointerarea divided by wide median groove; apical process subtriangular, anterior to foramen, bearing semicircular depression; dorsal interior with triangular median ridge or septum; dorsal cardinal muscle fields short, small, rounded, relatively close together; median buttress wide; dorsal anterocentral muscle scars usually well defined, small, rounded. *Upper Cambrian–Ordovician (lower Caradoc):* USA, Canada, *Upper Cambrian–Ordovician (lower Llanvirn);* Great Britain, Norway, Sweden, Denmark, *Upper Cambrian–Tremadoc;* Russia (Ingria, Southern Urals), *Upper Cambrian–Arenig;* Kazakhstan, *Upper Cambrian–lower Caradoc;* Estonia, *Tremadoc;* Poland, *Tremadoc–Llanvirn.*——FIG. 56,*2a–g.* **E. curvata* (WALCOTT), Pogonip Limestone, ?Tremadoc, Eureka district, Nevada, USNM loc. 203a; *a,* dorsal valve exterior, USNM 459664a, ×10.8; *b,* dorsal valve interior, USNM 459664c, ×12.5; *c,* oblique lateral view of dorsal interior, USNM 459664d, ×15; *d,e,* ventral valve exterior, posterior view, USNM 459664e, ×16.7; *f,* lateral view of ventral valve, USNM 459664f, ×20.8; *g,* ventral valve interior, USNM 459664g, ×20 (new).

Fascicoma POPOV in NAZAROV & POPOV, 1980, p. 92 [**F. obscura;* OD]. Shell subcircular with short, convex posterior margin; ventral valve conical; ventral pseudointerarea procline, poorly defined laterally

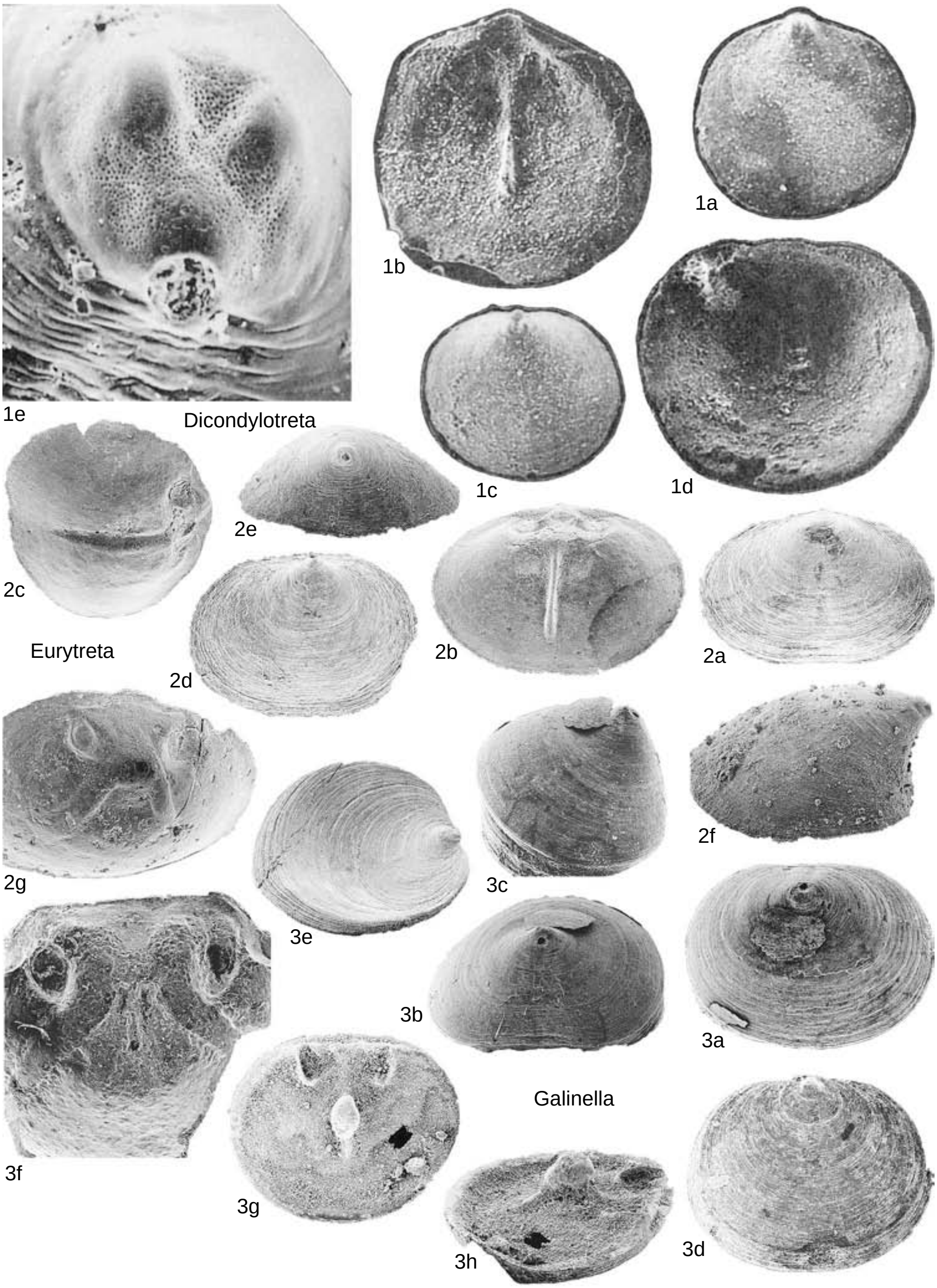

FIG. 56. Acrotretidae (p. 110–112).

with interridge; foramen forming short, external pedicle tube, enclosed within larval shell; dorsal valve weakly convex, weakly sulcate; dorsal pseudointerarea orthocline to anacline with median groove; apical process forming broad ridge posterior to foramen, completely occluding apex in gerontic specimens; dorsal median septum high, triangular, strongly spinose; dorsal interior with small, rounded cardinal muscle scars and median buttress; ventral mantle canals pinnate. *Ordovician (upper Arenig):* Kazakhstan. Satisfactory material not available for illustration.

Galinella Popov & Holmer, 1994, p. 108 [**Acrotreta retrorsa* Lermontova, 1951, p. 5; OD]. Ventral valve widely conical, strongly geniculated dorsally; ventral pseudointerarea procline to catacline, undivided; pedicle foramen within larval shell; dorsal valve geniculated ventrally in adults; ventral interior with ridgelike apical process, expanding posteriorly; ventral mantle canal system baculate with *vascula lateralia* slightly divergent anteriorly; dorsal median septum low, triangular, sometimes with bulbous projection; dorsal cardinal muscle fields small, subcircular, deeply impressed. *Upper Cambrian:* north-central Kazakhstan (Kujandy Formation).——Fig. 56,*3a–h.* **G. retrorsa* (Lermontova), Cambrian olistoliths in Satpak Formation, Kujandy Mountain, Kazakhstan; *a–c,* ventral valve exterior, posterior view, lateral view, RMS Br 136134, ×20; *d,* dorsal valve exterior, ×20; *e,* oblique lateral view, RMS Br 136124, ×17; *f,* ventral valve interior, RMS 136132, ×27.5; *g,h,* dorsal valve interior, lateral view, RMS 136125, ×18 (Popov & Holmer, 1994).

Hadrotreta Rowell, 1966, p. 12 [**Acrotreta primaea* Walcott, 1902, p. 593; OD]. Shell transversely oval with short, rounded posterior margin; ventral apex moderately convex to subconical; ventral pseudointerarea catacline to gently procline with shallow intertrough; foramen not enclosed within larval shell; dorsal valve gently convex with broad, shallow median sulcus; dorsal pseudointerarea narrowly triangular, orthocline to anacline with shallow median groove; apical process forming rounded boss anterior to internal foramen; apical pits immediately lateral of pedicle tube; dorsal median ridge low; mantle canals baculate. *upper Lower Cambrian–Middle Cambrian:* USA (Nevada), *upper Lower Cambrian–lower Middle Cambrian;* Russia (Novaya Zemlya, Altai), Kirghizia, Uzbekistan, *Amgaian;* Kazakhstan, *Amgaian–Mayaian;* Australia, *lower Amgaian.*——Fig. 57,*1a–f.* **H. primaea* (Walcott), Pioche Shale, upper *Bonnia–Olenellus*–pre-*Albertella* Biozones, Nevada, USNM loc. 316; *a,* dorsal valve exterior, USNM 459692a, ×8.3; *b,* dorsal valve interior, USNM 459692b, ×8.3; *c,* anterior view of ventral pseudointerarea, USNM 459692c, ×7.5; *d,* detail of apical process, USNM 459692d, ×13.3 (new); *e,* ventral valve exterior, KUMIP 115512, ×15.8; *f,* ventral valve interior, KUMIP 115525, ×15.8 (Rowell, 1980).

Hansotreta Krause & Rowell, 1975, p. 46 [**H. acrobela;* OD]. Shell subcircular with short, convex posterior margin; ventral valve high, narrowly conical; foramen apical, enclosed within larval shell; ventral pseudointerarea poorly defined, procline to apsacline with narrow interridge; dorsal valve flattened to somewhat concave; dorsal pseudointerarea raised with triangular median groove and strongly anacline propareas; ventral apex occluded by elongate triangular apical process, anterior to internal foramen; dorsal interior with elongated cardinal muscle fields and anterocentral muscle scars; dorsal median ridge well developed. *Ordovician (upper Llanvirn):* USA (Nevada).——Fig. 57,*2a–f.* **H. acrobela,* Antelope Valley Limestone, Meiklejohn Peak; *a,* dorsal valve exterior, ×29.2; *b,* detail of dorsal larval shell, USNM 250200a, ×229; *c,* ventral valve exterior, ×13.1; *d,* posterior view of ventral valve, USNM 250200b, ×18.3; *e,* oblique lateral view of dorsal interior, USNM 250200c, ×20; *f,* ventral valve interior, USNM 250200d, ×16.7 (new).

Hisingerella Henningsmoen in Waern, Thorslund, & Henningsmoen, 1948, p. 388 [*?*Atrypa nitens* von Hisinger, 1837, p. 77; OD]. Shell subcircular with short, weakly convex posterior margin; ventral pseudointerarea procline to apsacline with interridge; foramen forming short tube, enclosed within larval shell; dorsal valve flattened, somewhat sulcate; dorsal pseudointerarea orthocline to anacline with wide median groove; apical process vestigial to absent; dorsal interior with raised cardinal muscle fields, divided by broad median buttress; dorsal median septum triangular with single upper septal rod. *Ordovician (?upper Llanvirn, Llandeilo–Ashgill):* ?USA (Nevada), *upper Llanvirn;* Sweden, *?Llanvirn, Llandeilo–lower Ashgill;* ?Scotland, *Caradoc;* Norway, *upper Caradoc;* Estonia, Lithuania, *Caradoc–Ashgill;* Australia (New South Wales), *upper Caradoc–lower Ashgill;* Ireland, *Ashgill.*——Fig. 57,*3a–h. H. tenuis* Holmer, Bestorp Limestone, *Pleurograptus linearis* Biozone, Västergötland (Skövde), Sweden; *a–c,* holotype, dorsal valve exterior, oblique lateral view of exterior, oblique lateral view of interior, RMS Br 128522, ×20.8 (Holmer, 1986); *d,* dorsal valve interior, RMS Br 136401, ×20 (new); *e,* ventral valve exterior, ×27.5; *f,* lateral view of ventral valve, RMS Br 128521, ×30.8; *g,* oblique posterior view of both valves, RMS Br 128516, ×75 (Holmer, 1986); *h,* ventral valve interior, RMS Br 136402, ×31.7 (new).

Kotylotreta Koneva, 1990, p. 49 [**K. undata;* OD]. Shell transversely oval with fine rugae; ventral valve low conical; ventral pseudointerarea procline with intertrough weakly defined laterally; foramen not enclosed within larval shell; dorsal pseudointerarea vestigial with wide, shallow median groove; apical process broad, extending between posterior and anterior slope of valve and perforated posteriorly by short pedicle tube; apical pits deeply impressed, directly lateral to foramen; ventral mantle canals baculate; cardinal muscle fields transversely oval, weakly thickened; anterocentral scars situated on low ridge; dorsal median ridge low. *Middle Cambrian (Amgaian–Mayaian):* Kazakhstan (Malyi Karatau).——Fig. 58,*1a–f.* **K. undata,* Aktas lower Zhumabai formations, Kyrshabakty River; *a,* dorsal valve exterior, RMS Br 135403, ×50; *b,* dorsal valve interior, ×41.7; *c,* oblique lateral view of dorsal interior, RMS Br 135404, ×62.5; *d,* lateral view of ventral exterior, ×41.7; *e,* detail of ventral larval shell, RMS Br 136405, ×150; *f,* oblique lateral view of ventral interior, RMS Br 136406, ×75 (new).

Linnarssonella Walcott, 1902, p. 601 [**L. girtyi;* OD]. Shell subcircular to elongate oval with

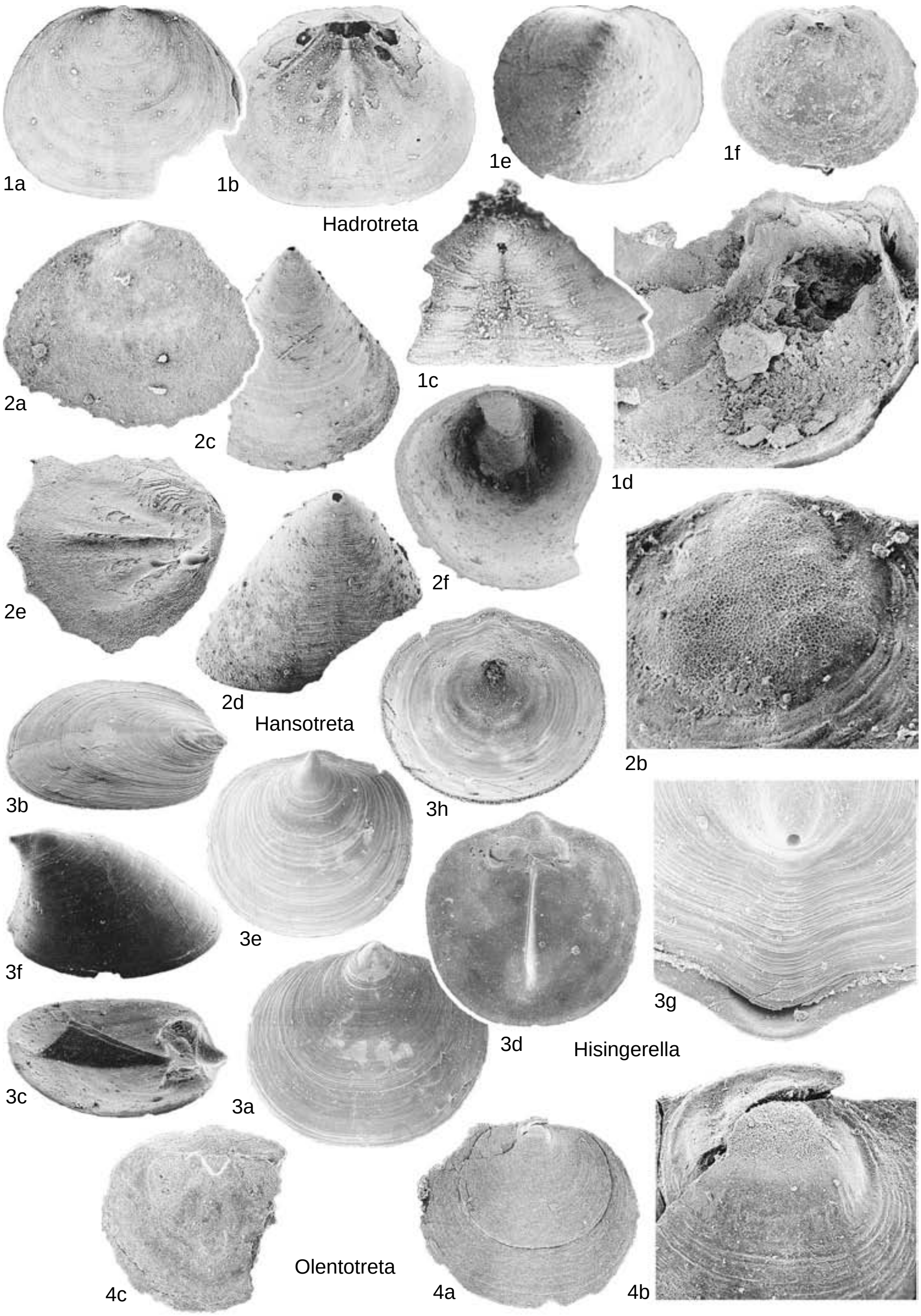

FIG. 57. Acrotretidae (p. 112–115).

rounded posterior margin; ventral valve moderately convex; ventral pseudointerarea low, apsacline, undivided; foramen enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea orthocline with broad median groove; posterolateral margins of dorsal propareas with deep grooves; api-

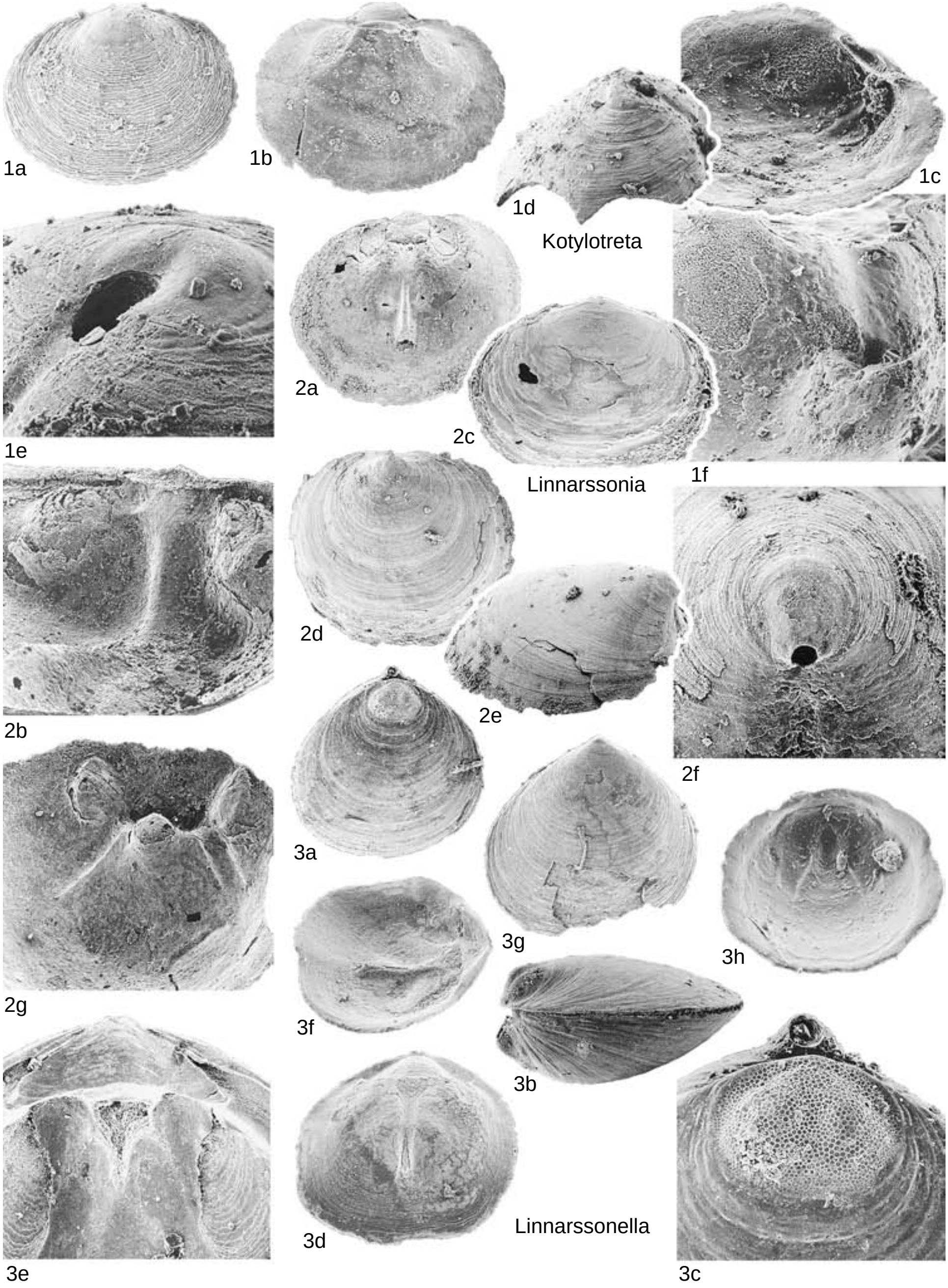

FIG. 58. Acrotretidae (p. 112–115).

cal process elongate triangular, perforated by foramen; dorsal median ridge low. *Upper Cambrian (upper Dresbachian–Franconian):* USA, Canada. ——FIG. 58,*3a–h.* **L. girtyi,* Franconian (*Elvinia* Biozone), South Dakota, USNM loc. 88a; *a,* dorsal view of both valves, ×41.7; *b,* lateral view of both valves, ×54.2; *c,* oblique posterior view of both valves, USNM 459694a, ×138; *d,* dorsal valve interior, ×15; *e,* detail of dorsal pseudointerarea, ×33.3; *f,* oblique lateral view of dorsal interior, USNM 459694b, ×15; *g,* ventral valve exterior, USNM 459694c, ×15; *h,* oblique anterior view of ventral interior, USNM 459694d, ×20.8 (new).

Linnarssonia Walcott, 1885, p. 115 [**Obolella transversa* Hartt in Dawson, 1868, p. 644; OD] [=*Pegmatreta* Bell, 1941, p. 231 (type, *P. perplexa*)]. Shell subcircular to transversely oval with short, convex posterior margin; ventral valve convex to low subconical; ventral pseudointerarea catacline to procline, rarely apsacline with intertrough; foramen not enclosed within larval shell; dorsal valve gently convex with vestigial, undivided pseudointerarea; apical process high, bosslike, anterior to foramen; dorsal interior with high median ridge and median buttress; anterocentral scars well defined. *Lower Cambrian–Middle Cambrian:* ?Germany, *Lower Cambrian;* Great Britain, Russia (Siberia), Kazakhstan, Kirghizia, *Lower Cambrian–Middle Cambrian;* Sweden, Norway, *?Lower Cambrian, Middle Cambrian;* ?Mexico (Sonora), USA (Utah, Montana, Alaska), Canada, ?China, West Antarctica, *Middle Cambrian;* Greenland, *upper Middle Cambrian;* Australia, New Zealand.——Fig. 58,*2a–g. L. ophirensis* (Walcott), Middle Cambrian, lower *Bolaspidella* or *Bathyuriscus–Elrathia* Biozones, Utah, USNM loc. 3e; *a,* dorsal valve interior, ×12.5; *b,* oblique posterior view of dorsal interior, USNM 459693a, ×31.7; *c,* dorsal valve exterior, USNM 459693b, ×13.1; *d,* ventral valve exterior, ×16.7; *e,* oblique lateral view of ventral exterior, ×20; *f,* oblique posterior view of ventral umbo, USNM 459693c, ×66.7; *g,* ventral valve interior, USNM 459693d, ×25 (new).

Longipegma Popov & Holmer, 1994, p. 110 [**L. gorjanskii* Popov & Holmer, 1994, p. 111; OD] [=*Kotujotreta* Ushatinskaya, 1994, p. 51 (type, *K. memorabilis;* OD)]. Shell distinctly inequivalved; ventral valve transversely suboval, low conical; ventral pseudointerarea procline to catacline, divided by intertrough; dorsal valve elongate subtriangular, with elongate subtriangular pseudointerarea, usually occupying more than half of valve width; median groove widely subtriangular; apical process high, ridgelike; dorsal cardinal muscle scars closely spaced; dorsal median ridge or septum starting directly anterior to pseudointerarea; postlarval shell ornamented by evenly spaced rugellae. *Upper Cambrian–Ordovician (Tremadoc):* Russia (north-central Siberia), *Upper Cambrian;* Sweden, *Tremadoc.*——Fig. 59,*1a–h.***L. gorjanskii,* Upper Cambrian, Kety Regional Stage, Botorchuk Rivulet, north-central Siberia; *a,* ventral valve exterior, ×25; *b,* lateral view, ×26.7; *c,* ornamentation of postlarval shell, RMS Br 136273, ×54.2; *d,* dorsal valve exterior, RMS Br 136270, ×12.5; *e,* ornamentation of dorsal larval shell, RMS Br 136276, ×833; *f,* ventral interior showing apical process, RMS Br 136276, ×42.7; *g,* holotype, dorsal valve interior, ×12.2; *h,* oblique lateral view of interior, RMS Br 136271, ×12.2 (Popov & Holmer, 1994).

Neotreta Sobolev, 1976, p. 132 [**N. tumida;* OD]. Shell subequally biconvex, transversely oval with wide, straight posterior margin; ventral pseudointerarea vestigial; foramen enclosed within larval shell; dorsal pseudointerarea vestigial, concave, undivided plate; apical process poorly developed; dorsal interior with thickened cardinal muscle fields and variably developed median ridge, lacking median buttress. *Middle Cambrian–lower Upper Cambrian:* England, *upper Middle Cambrian;* Sweden, *Middle Cambrian;* Russia (southeastern Siberia), Kazakhstan, Kirghizia, Australia (Queensland), northern China (Hebei).——Fig. 59,*3a–c.* **N. tumida,* Upper Cambrian, ?*Glyptagnostus reticulatus* Biozone, Dzhagdy Range (Verkhniaia Dzavodi River), Siberia; *a,* dorsal valve interior, RMS Br 135922, ×37.5; *b,* ventral valve exterior, ×37.5; *c,* detail of ventral larval shell, RMS Br 135923, ×101 (Popov, Berg-Madsen, & Holmer, 1994).——Fig. 59,*3d–f. N. kargailensis* Popov, Berg-Madsen, & Holmer, Kargaily Formation, northern Tien Shan, Kargaily River, Kirghizia; *d,* dorsal valve exterior, ×31.2; *e,* oblique lateral view of dorsal exterior, RMS Br 135926, ×37.5; *f,* ventral valve interior, RMS Br 135928, ×37.5 (Popov, Berg-Madsen, & Holmer, 1994).——Fig. 59,*3g. N. davidi* Popov, Berg-Madsen, & Holmer, Mungerebar Limestone, western Queensland; holotype, detail of ventral pseudointerarea and larval shell, QMF 25634, ×83.3 (Popov, Berg-Madsen, & Holmer, 1994).

Olentotreta Koneva, Popov, & Ushatinskaya in Koneva & others, 1990, p. 161 [**O. olentensis;* OD]. Shell transversely oval with straight posterior margin; ventral valve conical; ventral pseudointerarea catacline, flattened; foramen enclosed within larval shell; dorsal valve weakly convex, flattened peripherally; dorsal pseudointerarea anacline, wide with median groove; apical process low, occluding apex of valve, perforated by short pedicle tube; dorsal median ridge low with anterocentral muscle scars at posterior end; dorsal median buttress well defined. *Upper Cambrian:* Kazakhstan.——Fig. 57,*4a–c.* **O. olentensis,* Kujandy Formation, Semiz-Bugu Mountain, north-central Kazakhstan; *a,* dorsal valve exterior, ×23.3; *b,* detail of dorsal larval shell, RMS Br 136407, ×138; *c,* dorsal valve interior, RMS Br 136408, ×27.5 (new).

Opisthotreta Palmer, 1954, p. 771 [**O. depressa;* OD]. Shell almost equibiconvex, subcircular with short, rounded posterior margin; ventral pseudointerarea low, apsacline; dorsal valve moderately convex with wide median groove and vestigial propareas; apical process low, expanding anteriorly; dorsal median ridge vestigial to absent. *Middle Cambrian–Upper Cambrian:* USA (Texas), Russia (southeastern Siberia), northern China (Hebei).——Fig. 59,*2a–d.* **O. depressa,* middle Dresbachian, *Coosella* Biozone, Arizona; *a,* ventral valve exterior, ×25; *b,* lateral view of ventral exterior, ×31.7; *c,* posterior view of ventral larval shell, RMS Br 136409, ×100; *d,* dorsal valve exterior, RMS Br 136410, ×27.5 (new).

Ottenbyella Popov & Holmer, 1994, p. 114 [**Acrotreta carinata* Moberg & Segerberg, 1906, p. 66; OD]. Ventral valve highly conical with maximum height at beak; ventral pseudointerarea invariably procline, with distinct interridge; external pedicle

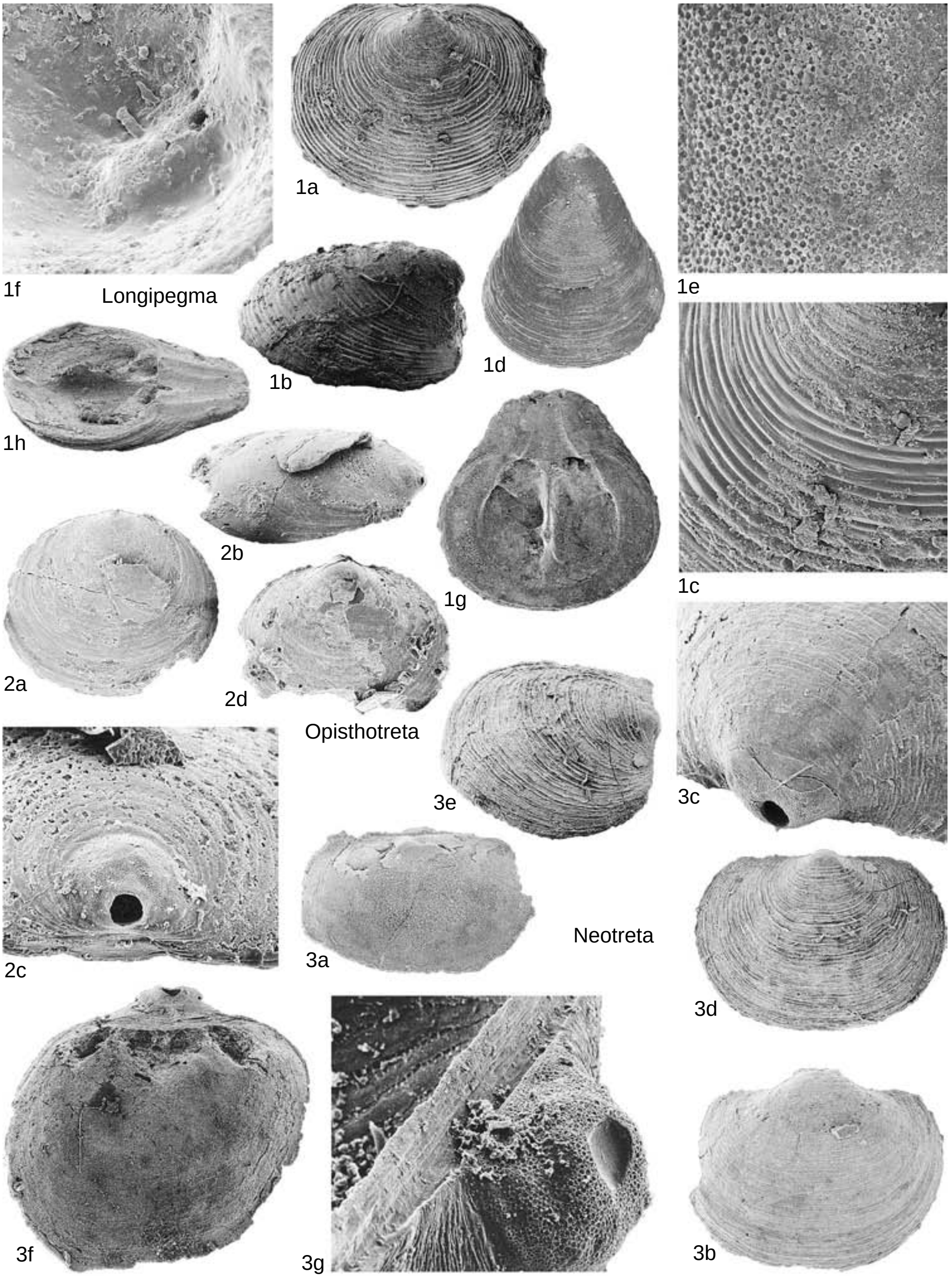

FIG. 59. Acrotretidae (p. 115).

tube very short; dorsal valve flattened, broadly sulcate; dorsal pseudointerarea wide but short, broadly subtriangular; apical process small and low; ventral *vascula lateralia* well developed, straight; dorsal median ridge very low; median buttress poorly developed; dorsal cardinal muscle fields small and short, transversely elongate suboval in outline. *Ordovician (upper Tremadoc):* Sweden, Norway.——FIG. 60,*2a–g*. **O. carinata* (MOBERG & SEGERBERG, 1906); *a–c,* Bjørkåsholmen Limestone, Oslo region,

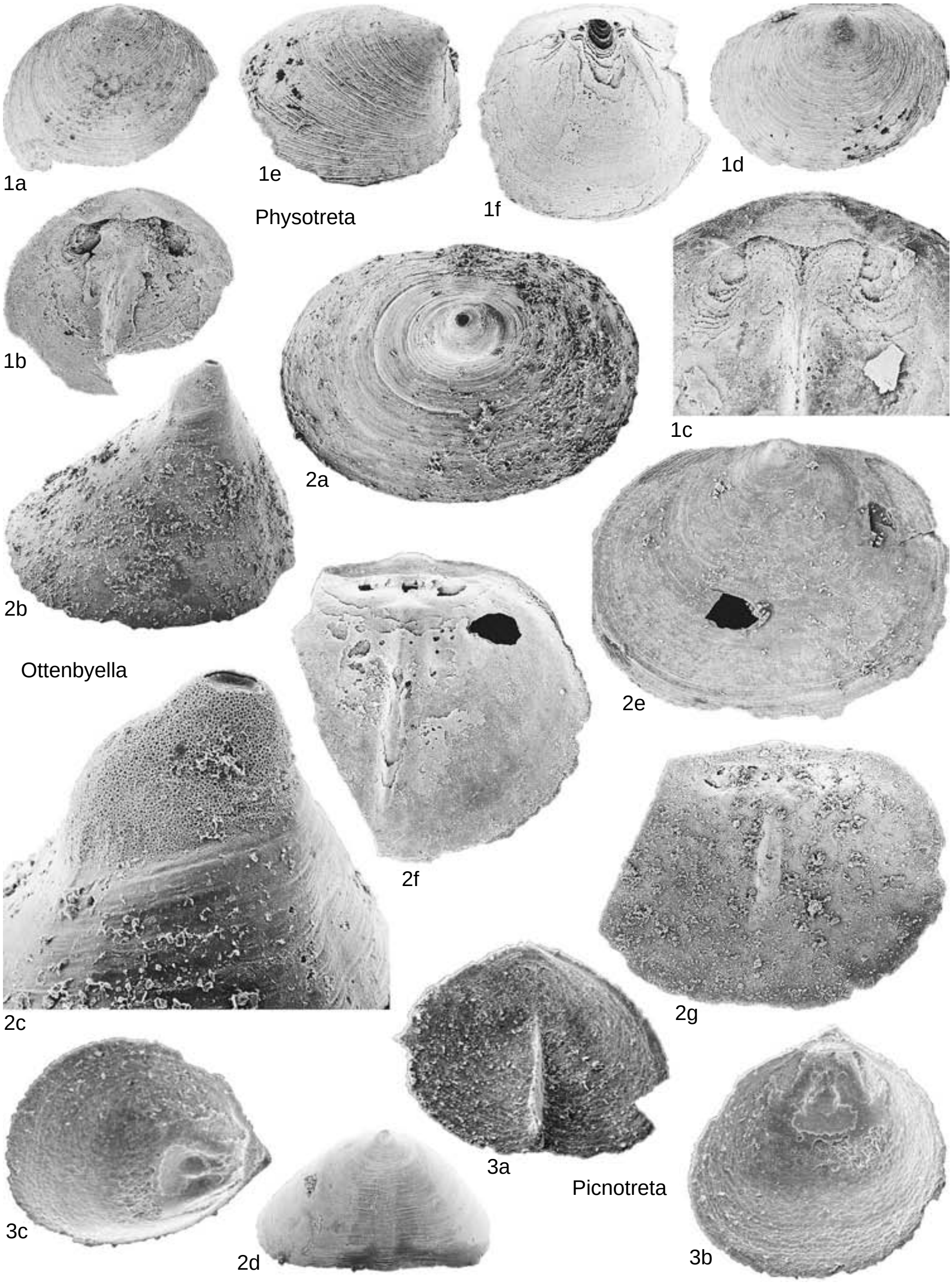

FIG. 60. Acrotretidae (p. 115–118).

Norway, RMS Br 135908; *a,* ventral valve exterior, ×46.7; *b,* lateral view, ×50; *c,* lateral view of the larval shell, ×188; *d,* ventral valve, posterior view, Ottenby, Sweden, LO 6561t, ×14.2; *e,* dorsal valve exterior, Bjørkåsholmen Limestone, Oslo region, Norway, RMS Br 135905, ×24.2; *f,* dorsal valve interior, Ottenby, Sweden, LO 6559t, ×26.7; *g,* dorsal valve interior, Bjørkåsholmen Limestone, Oslo region, Norway, RMS 135899, ×22.5 (Popov & Holmer, 1994).

Physotreta Rowell, 1966, p. 19 [**Acrotreta spinosa* Walcott, 1905, p. 302; OD]. Shell subcircular with straight to gently convex posterior margin; ornament of closely spaced rugae; ventral valve moderately conical; ventral pseudointerarea poorly defined, procline to catacline with weak intertrough; foramen at margin of larval shell; dorsal pseudointerarea relatively long, anacline with broadly triangular median groove; apical process occluding apex, perforated by wide pedicle tube; apical pits lateral to foramen; dorsal interior with triangular median septum and median buttress; dorsal anterocentral muscle scars well defined. *Middle Cambrian (Mayaian)–Upper Cambrian, ?Ordovician (Tremadoc–Llandeilo)*: Russia (Altai), *Mayaian;* USA (Nevada), *Dresbachian;* ?Australia (New South Wales), *Upper Cambrian;* ?Kazakhstan, *Tremadoc;* ?Sweden, *Llandeilo.*——Fig. 60,*1a–f.* **P. spinosa* (Walcott), Upper Cambrian, *Dunderbergia* Zone, Nevada, USNM loc. 61; *a,* dorsal valve exterior, USNM 459695a, ×9.2; *b,* dorsal valve interior, ×9.2; *c,* detail of dorsal cardinal muscle fields and pseudointerarea, USNM 459695b, ×22.5; *d,* ventral valve exterior, ×11.2; *e,* lateral view of ventral exterior, USNM 459695c, ×15; *f,* ventral valve interior, USNM 459695d, ×12.5 (new).

Picnotreta Henderson & MacKinnon, 1981, p. 301 [**P. debilis;* OD]. Shell almost equibiconvex, subcircular to subtriangular with narrow, convex posterior margin; ventral pseudointerarea apsacline, short, depressed; dorsal valve moderately convex; dorsal pseudointerarea vestigial, undivided; apical process low, elongate subtriangular, anterior to foramen; dorsal interior with low triangular median septum, lacking median buttress. *Middle Cambrian–lower Upper Cambrian:* USA; Greenland, *upper Middle Cambrian;* ?Antarctica (northern Victoria Land), Kirghizia, Kazakhstan, Australia (Queensland), New Zealand.——Fig. 60,*3a–c.* **P. debilis,* Bottom Rock Limestone, Tasman Formation, Cobb Valley, northwestern Nelson, New Zealand; *a,* dorsal valve interior, UCM 888, ×31.7; *b,c,* ventral valve interior, oblique lateral view of ventral interior, UCM 887, ×35 (Henderson & MacKinnon, 1981).

Prototreta Bell, 1938, p. 405 [**P. trapeza;* OD] [?=*Homotreta* Bell, 1941, p. 230 (type, *H. interupta;* OD)]. Shell subcircular to transversely oval with weakly convex posterior margin; ornament of fine rugae; ventral valve conical to highly conical; ventral pseudointerarea procline to apsacline with intertrough; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea long, anacline with broad triangular median groove; apical process broad, ridgelike, penetrated by pedicle tube; apical pits posterolateral to foramen; dorsal median septum triangular, sometimes digitate or with thickened rod or platform near top; dorsal median buttress narrow, elongate. *Lower Cambrian, Middle Cambrian:* Kazakhstan; ?Germany, *Lower Cambrian;* USA (Montana, Utah), Greenland, *upper Middle Cambrian;* Russia (Novaya Zemlya, Altai, ?Siberia), *Mayaian;* ?China; ?West Antarctica.——Fig. 61,*2a–h. P. attenuata* (Meek), Swazy Limestone, Middle Cambrian, Topaz Mountain, Utah; *a,* dorsal valve exterior, ×20.8; *b,* detail of dorsal larval shell, RMS Br 136411, ×91.7; *c,* dorsal valve interior, RMS Br 136412, ×10; *d,* dorsal valve interior, ×12.5; *e,* detail of digitate dorsal median septum, RMS Br 133660, ×41.7; *f,* oblique posterior view of ventral exterior, RMS Br 136413, ×15.8; *g,* ventral valve exterior, RMS Br 136414, ×22.5; *h,* detail of ventral valve interior, RMS Br 136415, ×26.7 (new).

Quadrisonia Rowell & Henderson, 1978, p. 6 [**Q. minor;* OD]. Shell transversely oval with relatively short, straight posterior margin; ventral valve low subconical to conical; ventral pseudointerarea procline to catacline, undivided or with very shallow intertrough; dorsal valve weakly convex; dorsal pseudointerarea short, orthocline with wide median groove; apical process elongate subtriangular, perforated by pedicle tube; dorsal median ridge variably developed; dorsal cardinal muscle fields small, subcircular, close to each other; dorsal anterocentral scars well defined. *Upper Cambrian:* ?Sweden, Australia, West Antarctica, USA (Great Basin), Kazakhstan.——Fig. 62,*1a–e.* **Q. minor,* Orr Formation, *Elvinia* Zone, Steamboat Pass, Utah; *a,b,* dorsal valve exterior, interior, KUMIP 115506, ×20.8; *c,* holotype, ventral valve lateral view, KUMIP 115501, ×20.8; *d,e,* ventral valve interior, exterior, KUMIP 115502, ×21.7 (Rowell & Henderson, 1978).

Rhondellina Rowell, 1986, p. 1059 [**R. dorei;* OD]. Shell weakly dorsibiconvex, transversely oval with short, gently convex posterior margin; larval shell with regularly spaced pits of varying size; ventral pseudointerarea vestigial, apsacline; foramen within larval shell; dorsal pseudointerarea minute with vestigial propareas; ventral interior with long, ridgelike apical process anterior to foramen; dorsal interior lacking median ridge and buttress. *upper Middle Cambrian–lower Upper Cambrian:* Greenland, *upper Middle Cambrian;* USA (Great Basin), *Dresbachian;* Kazakhstan (Malyi Karatau), *Dresbachian;* ?Russia (north-central Siberia), *Mayaian–Dresbachian.*——Fig. 61,*1a–e.* **R. dorei,* Hamburg Limestone, *Crepicephalus* Biozone, McGill, Nevada; *a,* dorsal valve interior, ×33.3; *b,* detail of dorsal interior, KUMIP 118204, ×66.7; *c,* ventral valve exterior, KUMIP 118206, ×29.2; *d,* ventral valve interior, ×33.3; *e,* detail of apical process, KUMIP 118207, ×66.7 (Rowell, 1986).

Satpakella Koneva, Popov, & Ushatinskaya in Koneva & others, 1990, p. 162 [**S. inconstans;* OD]. Shell transversely oval; ventral valve subcylindrical; pseudointerarea procline to apsacline, poorly defined laterally with weak intertrough; foramen enclosed within larval shell; dorsal pseudointerarea anacline or orthocline with wide median groove; apical process small, perforated by short pedicle tube; dorsal median septum triangular, strongly thickened with bulbous projection at top; median

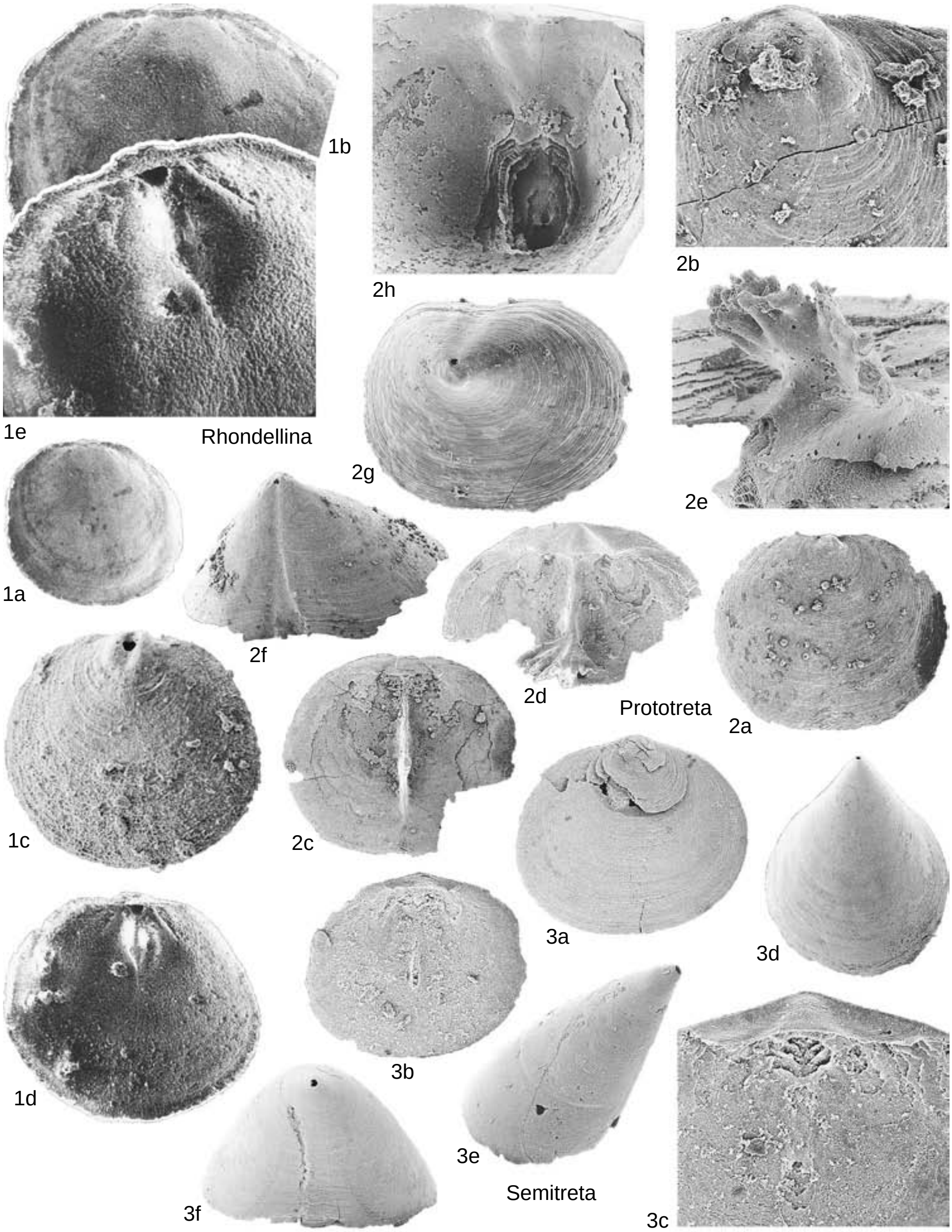

FIG. 61. Acrotretidae (p. 118–120).

buttress present; dorsal cardinal muscle field forming thickened platform. *Upper Cambrian:* Kazakhstan.——FIG. 63,*2a–c.* **S. inconstans,* Kujandy Formation, Erzhan, northeast-central Kazakhstan; *a,* dorsal valve exterior, RMS Br 136416, ×25; *b,* dorsal valve interior, ×20.8; *c,* oblique lateral view of dorsal interior, RMS Br 136417, ×25 (new).

Semitreta BIERNAT, 1973, p. 75 [**S. maior;* OD]. Similar to *Hansotreta,* but with poorly developed apical process and poorly divided ventral pseudointerarea. *Upper Cambrian–Ordovician (Tremadoc–lower Arenig):* Poland, Russia (north-central Siberia, ?Southern Urals), ?Estonia, ?Great Britain.——FIG. 61,*3a–f.* **S. maior,* Tremadoc chalcedonites,

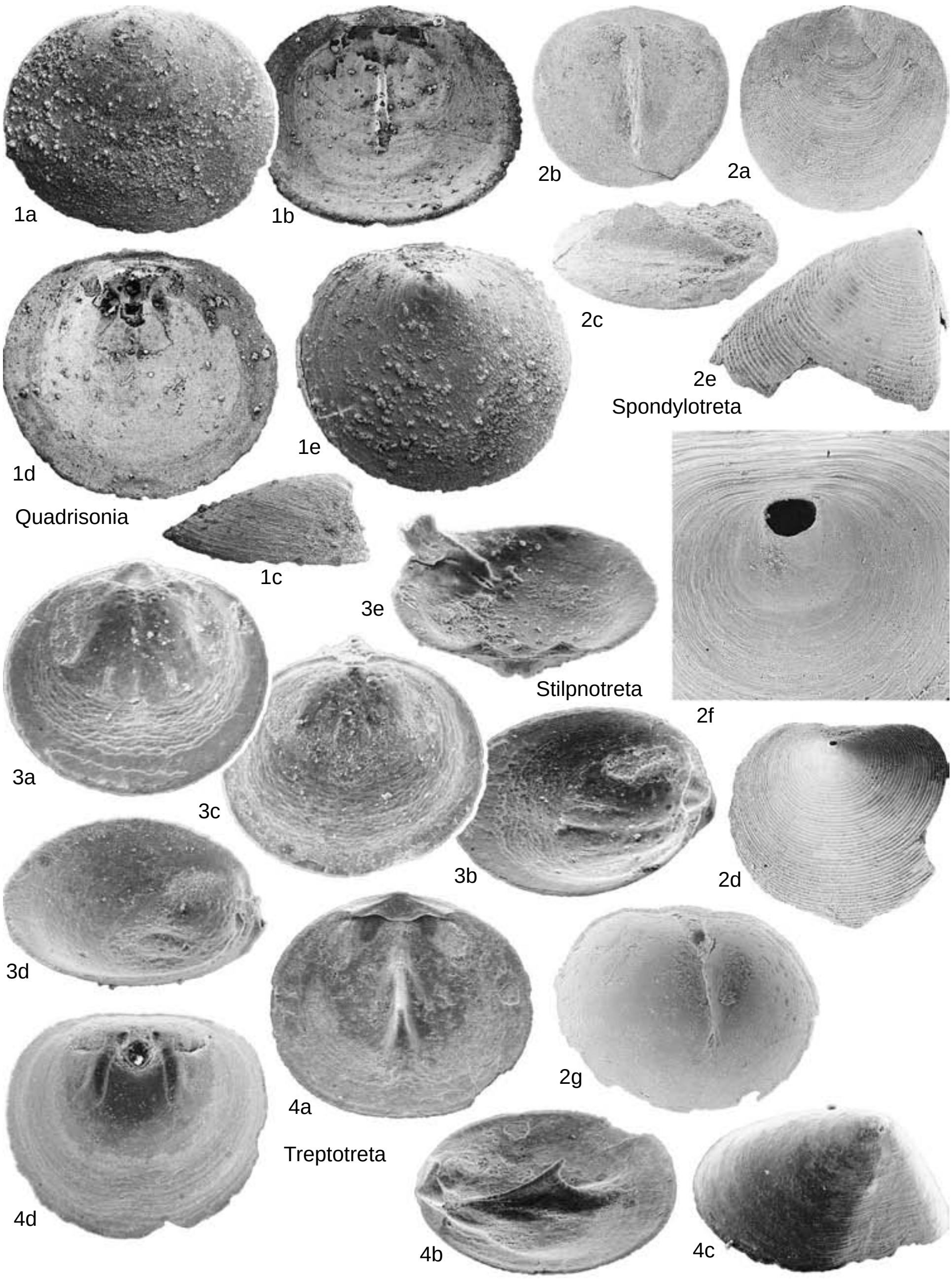

FIG. 62. Acrotretidae (p. 118–121).

Wysoczki, Holy Cross Mountains, Poland; *a,* dorsal valve exterior, RMS Br 136418, ×25; *b,* dorsal valve interior, RMS Br 136419, ×27.5; *c,* detail of dorsal pseudointerarea, RMS Br 136420, ×50; *d,* ventral valve exterior, RMS Br 136421, ×11.2; *e,* lateral view of ventral exterior, RMS Br 136422, ×27.5; *f,* posterior view of ventral exterior, RMS Br 136423, ×13.1 (new).

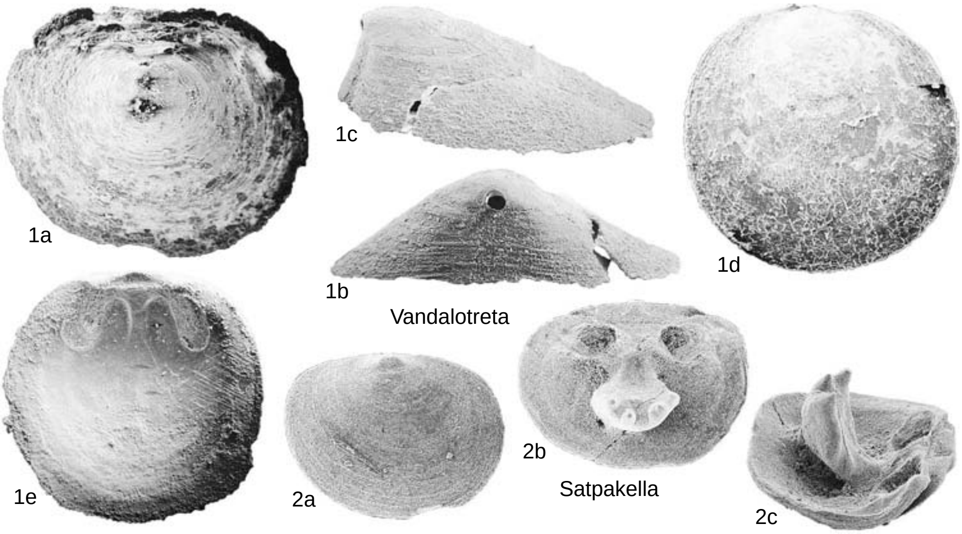

Fig. 63. Acrotretidae (p. 118–122).

Spondylotreta Cooper, 1956, p. 255 [**S. concentrica;* OD]. Shell transversely oval with straight posterior margin; ornament of fine rugae; ventral valve highly conical; ventral pseudointerarea well defined, catacline to slightly procline with interridge; foramen forming short tube, enclosed within larval shell; dorsal valve gently convex, sulcate; dorsal pseudointerarea wide with median groove; internal pedicle tube along posterior slope of valve, continued as forked ridge, supported apically by median septum; dorsal interior with long, triangular median septum and median buttress. *Ordovician (Llanvirn–Ashgill):* USA (Alabama, Nevada, ?Virginia), *Llanvirn–Llandeilo;* Sweden, *Llandeilo–lower Caradoc;* Kazakhstan, *Caradoc;* Estonia, *upper Caradoc–Ashgill;* Ireland, *Ashgill.*——Fig. 62,*2a–g.* **S. concentrica,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×9.2; *b,* dorsal valve interior, ×8.3; *c,* oblique lateral view of dorsal interior, RMS Br 133934, ×10; *d,* ventral valve exterior, ×11.2; *e,* lateral view of ventral exterior, ×12.5; *f,* detail of ventral larval shell, RMS Br 133935, ×75 (Holmer & Popov, 1994); *g,* ventral valve interior, RMS Br 136418, ×33.3 (new).

Stilpnotreta Henderson & MacKinnon, 1981, p. 297 [**S . magna;* OD]. Shell almost equibiconvex, subcircular to transversely oval with short, convex posterior margin; ventral pseudointerarea vestigial; foramen enclosed within larval shell; dorsal pseudointerarea orthocline with wide median groove and vestigial propareas; apical process subtriangular, occluding apex, extending to midvalve; dorsal visceral field with narrow anterior projection extending to midvalve, bisected by low median ridge; dorsal median buttress absent. *Middle Cambrian–Upper Cambrian:* Kazakhstan, Kirghizia, Russia (Novaya Zemlya, Siberia), Antarctica, Sweden, Australia (Queensland), New Zealand; Great Britain, *Middle Cambrian.*——Fig. 62,*3a–e.* **S. magna; a,b,* holotype, dorsal valve interior, oblique lateral view, Mungerebar Limestone, western Queensland, Australia, JCF 10720, ×41.7; *c,d,* ventral valve interior, oblique lateral view, JCF 10721, ×45.8; *e,* oblique posterior view of dorsal interior, Tasman Formation, northwestern Nelson (Cobb Valley), New Zealand, UCM 878, ×41.7 (Henderson & MacKinnon, 1981).

Treptotreta Henderson & MacKinnon, 1981, p. 293 [**T. jucunda;* OD]. Shell transversely oval with straight to weakly convex, moderately wide posterior margin; ventral valve conical; pseudointerarea procline with intertrough vestigial or absent; foramen enclosed within larval shell; dorsal valve weakly convex or flattened; dorsal pseudointerarea wide, orthocline with median groove; apical process widening anteriorly, sometimes forming ridge, perforated by pedicle tube; dorsal median septum high, triangular. *Middle Cambrian–Upper Cambrian:* Australia (Queensland, ?New South Wales), New Zealand, West Antarctica, Russia (Novaya Zemlya, Siberia), Kazakhstan, *Upper Cambrian;* ?northern China (Hebei).——Fig. 62,*4a–d.***T. jucunda,* Mungerebar Limestone, western Queensland, Australia; *a,b,* dorsal valve interior, oblique lateral view, JCF 10716, ×18.3; *c,* oblique posterior view of ventral exterior, JCF 10715, ×19.2; *d,* holotype, ventral valve interior, JCF 10714, ×16.7 (Henderson & MacKinnon, 1981).

Vandalotreta Mergl, 1988, p. 292 [**V. vafra;* OD] [=*Luhotreta* Mergl & Šlehoferová, 1990, p. 95 (type, *L. pompeckji*)]. Shell transversely oval to subcircular with narrow, convex posterior margin;

ventral valve wide conical; ventral pseudointerarea procline to catacline, poorly defined laterally with intertrough; foramen not enclosed within larval shell; dorsal valve weakly convex; dorsal pseudointerarea short with broadly triangular median groove; apical process forming bosslike thickening anterior to internal foramen; dorsal visceral field with narrow anterior projection, bisected by vestigial median ridge; dorsal median buttress developed. *upper Lower Cambrian–lower Middle Cambrian*: Sweden; Kazakhstan, Antarctica (King George Island), *Toyonian;* Australia (South Australia, Northern Territory), *Toyonian–lower Amgaian;* Morocco, *Amgaian;* Bohemia, *lower Middle Cambrian.*——FIG. 63,*1a–e.* **V. vafra,* Middle Cambrian, Amgaian, High Atlas Mountains (Yagour inlier), Morocco; *a,* ventral valve exterior, GSP MM 343, ×29.2; *b,c,* posterior view of ventral exterior, lateral view, GSP MM 338, ×41.7; *d,* dorsal valve exterior, GSP MM 346, ×29.2; *e,* dorsal valve interior, GSP MM 336, ×25 (Mergl, 1988).

Family SCAPHELASMATIDAE Rowell, 1965

[*nom. transl.* KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 163, *ex* Scaphelasmatinae ROWELL, 1965a, p. 278]

Shell biconvex to concavoconvex with straight or weakly concave posterior margin; ornament of coarse, regularly spaced rugae, lamellose peripherally; ventral pseudointerarea with widely triangular intertrough; foramen not enclosed within larval shell; apical process vestigial to absent, usually forming low projection anterior to foramen; apical pits small, directly lateral to apical process; dorsal median septum triangular, bladelike, arising near midvalve and extending almost to anterior margin, or absent; dorsal anterocentral muscle scars directly lateral to septum. *Middle Cambrian (Amgaian)–upper Silurian.*

Scaphelasma COOPER, 1956, p. 259 [**S. septatum;* OD]. Ventral valve low conical to conical; ventral pseudointerarea poorly defined, procline; foramen large, oval; apical process variably developed; dorsal valve with high median septum; median buttress absent. *Ordovician (Arenig–Ashgill):* southern China, *Arenig–Llanvirn;* Poland, *Arenig–Llanvirn, ?Ashgill;* Sweden, Kazakhstan, *Arenig–Ashgill;* Ireland, *upper Arenig–Ashgill;* USA (Alabama, Nevada, Iowa), *Llanvirn–Ashgill;* Estonia, Russia (Ingria), *upper Arenig–lower Llanvirn.*——FIG. 64,*1a–d.* **S. septatum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×31.7; *b,* detail of dorsal larval shell, RMS Br 136419, ×112; *c,* oblique lateral view of dorsal interior, RMS Br 136420, ×30; *d,* oblique lateral view of ventral interior, RMS Br 136421, ×20 (new).——FIG. 64,*1e,f. S. mica* POPOV, Karakan Limestone, upper Arenig, northern Betpak-Dala, Kazakhstan; *e,* dorsal valve interior, RMS Br 133672, ×33.3; *f,* ventral valve exterior, RMS Br 133673, ×33.3 (Holmer, 1989b).

Artiotreta IRELAND, 1961, p. 1138 [**A. parva;* OD]. Similar to *Scaphelasma,* but smaller; foramen circular; dorsal pseudointerarea with vestigial median groove and propareas. May be junior synonym of *Scaphelasma. upper Silurian:* USA (Oklahoma, Missouri, Illinois).——FIG. 64,*2a–e.* **A. parva,* Chimney Hill Limestone, Arbuckle Mountains, Oklahoma; *a,* dorsal valve exterior, USNM 459696a, ×50; *b,* dorsal valve interior, ×50; *c,* detail of dorsal pseudointerarea, USNM 459696b, ×165; *d,* ventral valve exterior, ×50; *e,* detail of ventral larval shell, ×151.7 (new).

Batenevotreta USHATINSKAYA, 1992, p. 87 [**B. formosa;* OD]. Shell transversely oval with fine rugae; ventral valve low conical; ventral pseudointerarea procline to catacline, poorly defined laterally with shallow, wide intertrough; foramen circular; dorsal valve moderately convex; dorsal pseudointerarea low, anacline with shallow median groove; apical process broad, semicircular, anterior to short pedicle tube; dorsal interior with small median buttress and low median ridge; dorsal cardinal muscle fields large, transversely oval, thickened. *Middle Cambrian (Amgaian):* Russia (Altai). Satisfactory material not available for illustration.

Eoscaphelasma KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 165 [**E. satpakensis;* OD]. Shell transversely oval with weakly concave posterior margin; ornament of fine rugae, sometimes lamellose peripherally; ventral valve low conical; ventral pseudointerarea procline, poorly defined laterally with broad intertrough; foramen elongate oval; dorsal valve weakly convex; dorsal pseudointerarea low, orthocline with median groove; apical process vestigial, perforated by foramen or short pedicle tube; dorsal median ridge vestigial to absent. *Upper Cambrian:* Kazakhstan.——FIG. 65,*2a–f.* **E. satpakensis,* Kujandy Formation, Olenty River, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136199, ×27.5; *b,* dorsal valve interior, ×25; *c,* detail of dorsal pseudointerarea, RMS Br 136192, ×62.5; *d,* ventral valve exterior, RMS Br 136196, ×41.7; *e,* oblique lateral view of ventral exterior, RMS Br 136334, ×37.5; *f,* detail of ventral larval shell, RMS Br 136197, ×125 (Popov & Holmer, 1994).

Rhysotreta COOPER, 1956, p. 258 [**R. corrugata;* OD]. Shell with ornament of strong rugae; ventral valve highly conical; ventral pseudointerarea flattened, procline to catacline; foramen unusually large, rounded triangular; dorsal valve flattened; dorsal pseudointerarea wide and long, flattened with poorly defined median groove; dorsal apical process lacking; dorsal interior with high, triangular median septum and variably developed median buttress. *Ordovician (Arenig–Caradoc):* North America (Nevada, Alabama), Kazakhstan.——FIG. 64,*3a–g.* **R.*

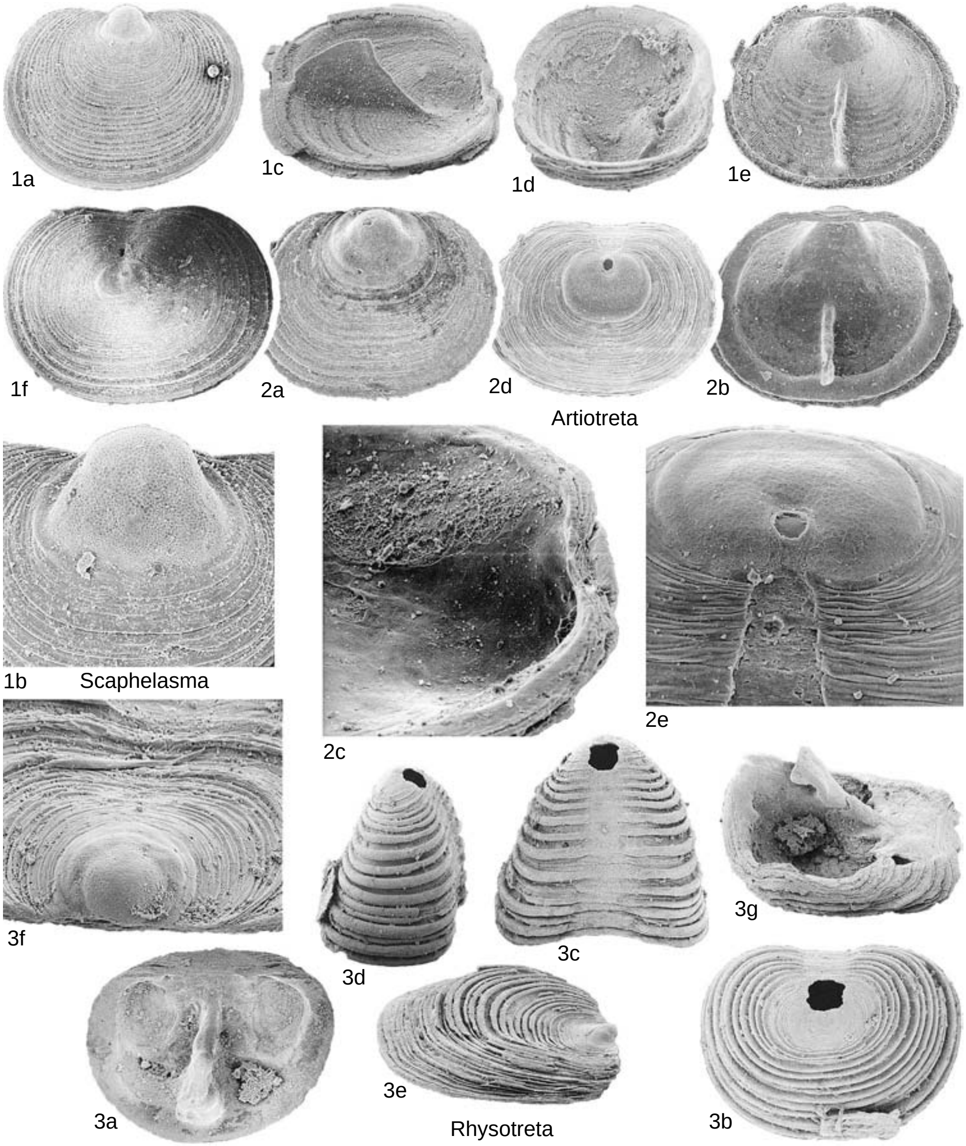

FIG. 64. Scaphelasmatidae (p. 122–123).

corrugata, Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve interior, USNM 459697a, ×13.8; *b,* ventral valve exterior, ×20.8; *c,* posterior view of ventral exterior, ×17.9; *d,* lateral view of ventral exterior, USNM 459697b, ×15; *e,* oblique lateral view of dorsal valve exterior, ×17.9; *f,* detail of dorsal larval shell, USNM 459697c, ×83.3; *g,* oblique lateral view of dorsal interior, USNM 459697d, ×20.8 (new).

?Tobejalotreta KONEVA, POPOV, & USHATINSKAYA in KONEVA & others, 1990, p. 163 [**T. aseptata;* OD]. Shell with straight posterior margin; ornament of rugae; ventral valve highly conical; ventral pseudointerarea procline with intertrough; foramen large, elongate subtriangular; dorsal valve flattened; dorsal pseudointerarea flattened with shallow, widely triangular median groove; apical process absent; dorsal interior with broad median buttress, lacking median septum. *Upper Cambrian:* Kazakhstan.——FIG. 65,*1a,b.* **T. aseptata,* Olenty River; *a,* dorsal valve exterior, RMS Br 136422, ×27.5; *b,* dorsal valve interior, RMS Br 136423, ×25 (new).

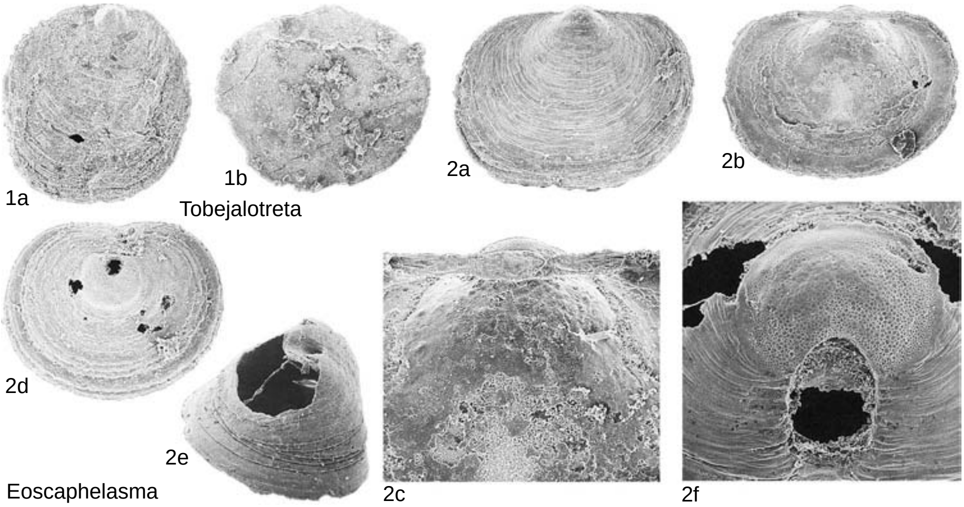

FIG. 65. Scaphelasmatidae (p. 122–123).

Family TORYNELASMATIDAE Rowell, 1965

[*nom. transl.* HOLMER & POPOV, herein, *ex* Torynelasmatinae ROWELL, 1965a, p. 279; *emend.,* HOLMER, 1989b, p. 106]

Shell with wide, straight posterior margin; ventral valve subpyramidal; ventral pseudointerarea flat, procline to apsacline, undivided; foramen enclosed within larval shell; dorsal pseudointerarea wide, poorly divided; ventral interior with low, ridgelike apical process supporting pedicle tube; dorsal valve with high, triangular median septum, commonly with variably developed surmounting platform; broad median buttress elevated above median groove; dorsal anterocentral scars absent. *Ordovician (Arenig)–Silurian.*

Torynelasma COOPER, 1956, p. 257 [**T. toryniferum;* OD]. Ventral pseudointerarea catacline to weakly apsacline; dorsal median septum high with flat to dorsally concave surmounting platform. *Ordovician (Arenig–lower Caradoc):* USA (Alabama, Nevada), Sweden, Kazakhstan, Russia (Pskov district), southern China.——FIG. 66,*1a–h.* **T. toryniferum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×19.6; *b,* oblique lateral view of dorsal exterior, USNM 459698a, ×20.8; *c,* dorsal valve interior, ×17.9; *d,* oblique lateral view of dorsal interior, ×27.5; *e,* detail of dorsal median septum, USNM 459698b, ×31.7; *f,* ventral valve exterior, ×16.7; *g,* lateral view of ventral exterior, ×16.7; *h,* detail of ventral larval shell, USNM 459698c, ×162 (new).

Acrotretella IRELAND, 1961, p. 1139 [**A. siluriana;* OD]. Ventral valve wide conical; ventral pseudointerarea procline to catacline; apical process and internal pedicle tube absent; dorsal pseudointerarea undivided; dorsal median septum low to high with dorsally concave surmounting platform; dorsal larval shell bulbous. *Ordovician (Caradoc)–upper Silurian:* Sweden, *Caradoc–lower Silurian;* Ireland, *Ashgill;* USA (Oklahoma, Missouri, Illinois), *upper Silurian.*——FIG. 66,*3a,b.* **A. siluriana,* Chimney Hill Limestone, Arbuckle Mountains, Oklahoma; *a,* dorsal valve exterior, USNM 459699a, ×45.8; *b,* dorsal valve interior, USNM 459699b, ×41.7 (new).——FIG. 66,*3c–e. A.* sp., Bestorp Limestone, *Pleurograptus linearis* Biozone, Västergötland (Skövde), Sweden; *c,* ventral valve exterior, ×66.7; *d,* lateral view of ventral exterior, ×75; *e,* detail of pitted dorsal larval microornament, RMS Br 128506, ×1508 (Holmer, 1986).

Cristicoma POPOV in NAZAROV & POPOV, 1980, p. 89 [**C. sincera;* OD]. Externally like *Torynelasma;* apical process forming septum, supported anteriorly by long pedicle tube, occluding apex in gerontic forms; dorsal median septum high, triangular with numerous spines. *Ordovician (upper Arenig):* Kazakhstan.——FIG. 66,*4a–d.* **C. sincera,* Karakan Limestone, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136424, ×37.5; *b,* dorsal valve interior, ×19.6; *c,* lateral view of dorsal exterior, RMS Br 136425, ×25; *d,* ventral valve interior, RMS Br 136426, ×27.5 (new).

Issedonia POPOV in NAZAROV & POPOV, 1980, p. 103 [**I. spinosa;* OD]. Externally like *Torynelasma;* dorsal median septum with spines and dorsally concave surmounting platform. *Ordovician (lower Llanvirn):* central Kazakhstan.——FIG. 66,*2a–g.* **I. spinosa,* Shundy Formation, Sary-Kumy, Kazakhstan; *a,* dorsal valve exterior, RMS Br 136427, ×27.5; *b,* oblique lateral view of dorsal interior, ×20.8; *c,* dorsal valve interior, ×17.9; *d,* detail of dorsal median septum, RMS Br 136428, ×37.5; *e,* ventral valve exte-

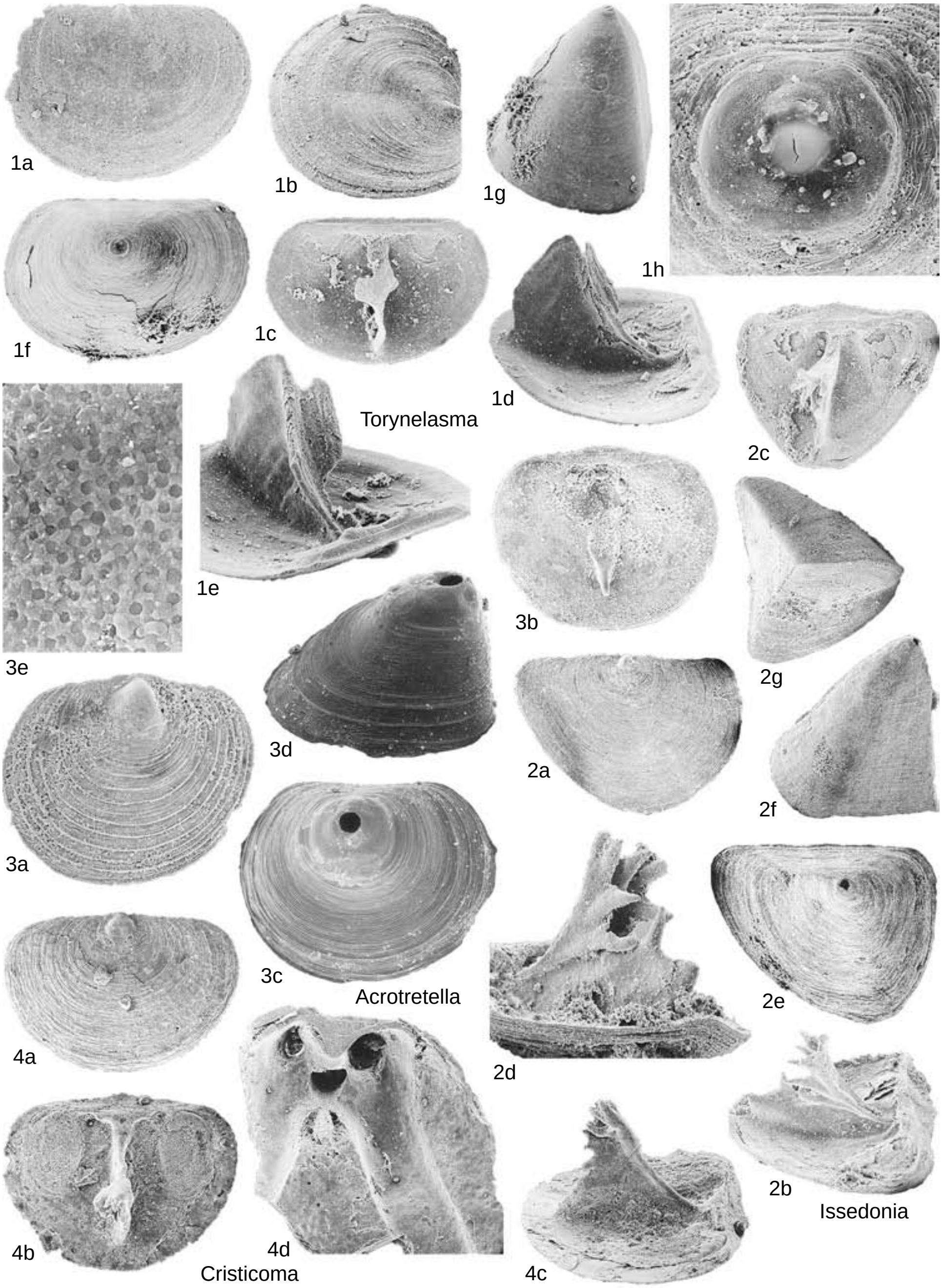

FIG. 66. Torynelasmatidae (p. 124–125).

rior, ×25; *f,* oblique posterior view of ventral exterior, RMS Br 136429, ×17.9; *g,* oblique lateral view of both valves, RMS Br 136430, ×17.9 (new).

Mylloconotreta WILLIAMS & CURRY, 1985, p. 203 [**M. elimata;* OD]. Similar to *Torynelasma,* but with subcylindrical, geniculate ventral valve. *Ordovician (upper Arenig):* Ireland.——FIG. 67,*1a–d.* **M. elimata,* Tourmakeady Limestone, Mayo, Ireland; *a,* paratype, dorsal valve exterior, BMNH BB 95422, ×20; *b,* holotype, dorsal valve interior, BMNH BB

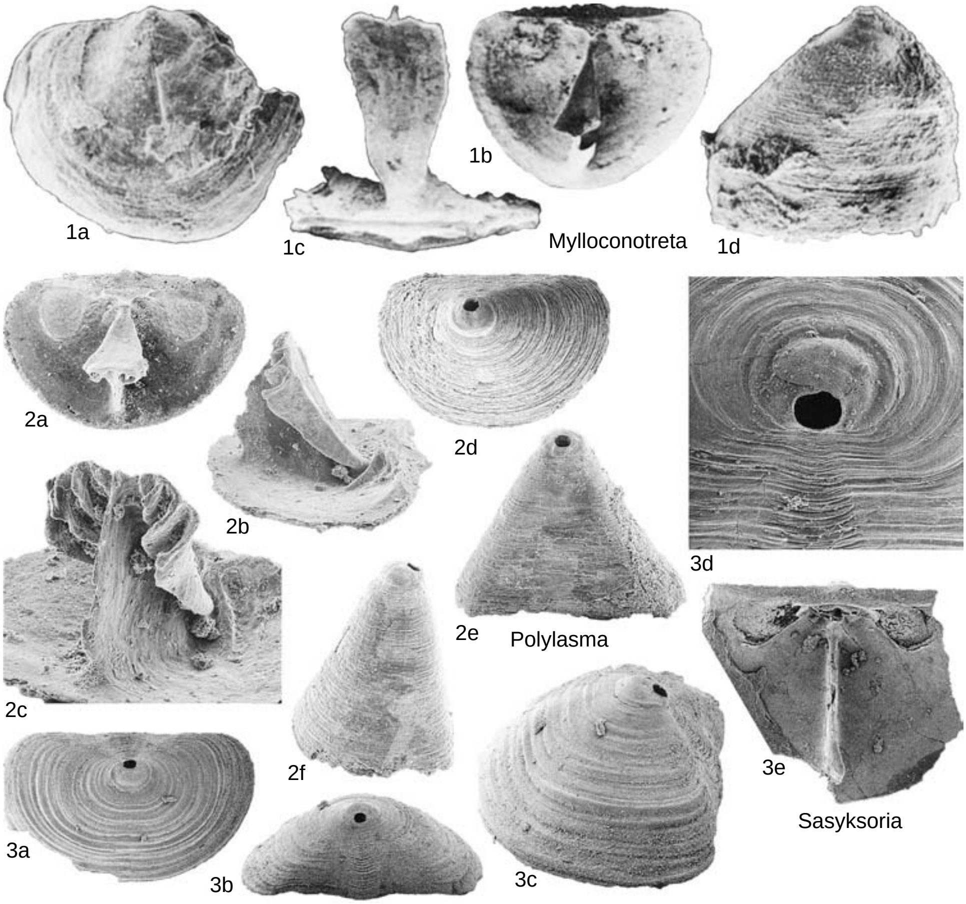

FIG. 67. Torynelasmatidae (p. 125–126).

95420, ×13.3; *c,* paratype, detail of dorsal median septum, BMNH BB 95357, ×25.8; *d,* paratype, lateral view of ventral exterior, BMNH BB 95423, ×11.7 (Williams & Curry, 1985).

?Paratreta BIERNAT, 1973, p. 68 [**P. similis;* OD]. Ventral valve subconical; ventral pseudointerarea catacline to procline; dorsal valve gently convex; dorsal pseudointerarea with median groove; apical process subtriangular, anterior to foramen; dorsal interior with high, triangular median septum and large, thickened cardinal muscle fields. Genus poorly known. *Ordovician (Arenig–Llanvirn):* Poland.

Polylasma POPOV in NAZAROV & POPOV, 1980, p. 105 [**P. subsciduum;* OD]. Similar to *Torynelasma* but with concave surmounting plate bearing numerous dorsally directed lateral plates along its lower surface. *Ordovician (upper Arenig–Llanvirn):* Kazakhstan.——FIG. 67,*2a–f.* **P. subsciduum,* Karakan Limestone, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve interior, ×25; *b,* oblique lateral view of dorsal interior, ×41.7; *c,* detail of dorsal median septum, RMS Br 136431, ×66.7; *d–f,* ventral valve exterior, posterior view, lateral view, RMS Br 136432, ×33.3 (new).

Sasyksoria POPOV & HOLMER, 1994, p. 135 [**S. rugosa;* OD]. Ventral valve low conical; ventral pseudointerarea flattened, procline to catacline, divided by wide interridge; dorsal pseudointerarea wide; dorsal median groove wide, poorly defined; apical process low, ridgelike, penetrated posteriorly by internal pedicle foramen; dorsal median septum simple, triangular; cardinal buttress high, wide; postlarval shell covered by strong, evenly spaced lamellae. *Ordovician (lower Arenig):* north-central Kazakhstan.——FIG. 67,*3a–e.* **S. rugosa,* Ordovician, Olenty Formation, Lake Sasyksor; *a,* holotype, ventral valve exterior, ×20.8; *b,* posterior view, ×20.8; *c,* lateral view, ×33.3; *d,* larval shell, RMS Br 136252, ×83.3; *e,* dorsal valve interior, RMS Br 136251, ×23.3 (Popov & Holmer, 1994).

Family EPHIPPELASMATIDAE Rowell, 1965

[*nom. transl.* HOLMER & POPOV, herein, *ex* Ephippelasmatinae ROWELL, 1965a, p. 279] [*incl.* Myotretinae BIERNAT, 1973, p. 80]

Shell with narrow, straight posterior margin; ornament of fine rugae; ventral valve usually narrow, highly conical; pseudointerarea catacline to strongly apsacline with intertrough; foramen enclosed within larval shell, usually forming tube; dorsal valve weakly convex to concave; dorsal pseudointerarea with short, lens-shaped median groove; ventral interior usually with pedicle tube along posterior slope; apical process vestigial, usually forming low ridge near apex; dorsal median septum variably developed; dorsal median buttress commonly absent. *Upper Cambrian–Ordovician (Ashgill).*

Ephippelasma COOPER, 1956, p. 261 [**E. minutum;* OD]. Ventral valve narrow, high conical; pseudointerarea catacline to weakly apsacline with intertrough; dorsal valve with symmetrical, saddlelike median septum. *Ordovician (Llandeilo–Ashgill):* USA (Alabama), *Llandeilo;* Sweden, *upper Llandeilo;* Kazakhstan, *Llandeilo–Caradoc;* Ireland, ?China (Yangtze), *Ashgill.*——FIG. 68,*1a–h.* **E. minutum,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, RMS Br 136433, ×41.7; *b,* dorsal valve interior, ×41.7; *c,* oblique lateral view of dorsal interior, RMS Br 136434, ×50; *d,* detail of dorsal median septum, RMS Br 136435, ×66.7; *e,f,* ventral valve exterior, posterior view, ×41.7; *g,* lateral view of ventral exterior, ×33.3; *h,* detail of ventral larval shell, USNM 459700a, ×125 (new).

Akmolina POPOV & HOLMER, 1994, p. 125 [**A. olentensis;* OD]. Ventral valve widely conical; ventral pseudointerarea usually catacline, more rarely somewhat procline or apsacline; intertrough wide and shallow with median plication; pedicle foramen at end of short pedicle tube, enclosed within larval shell; dorsal pseudointerarea low, divided by median groove; ventral interior with short internal pedicle tube fused with posterior valve slope; apical process forming low elevation anterior and lateral to pedicle tube, becoming slightly ridged anteriorly; median buttress and dorsal median ridge weakly developed or absent. *Upper Cambrian–Ordovician:* Kazakhstan, *Drepanoistodus proteus* Biozone.——FIG. 68,*2a–i.* **A. olentensis,* Kujandy Formation, Aksak-Kujandy Mountain, Kazakhstan; *a,* ventral valve exterior, ×33.3; *b,* lateral view, ×41.7; *c,* lateral view of larval shell, RMS Br 136164, ×125; *d,* holotype, posterior view of conjoined valves, RMS Br 136169, ×45.8; *e,f,* dorsal valve exterior, ×27.5, lateral view, ×50, RMS Br 136167; *g,* ventral valve interior showing apical process, RMS Br 136171, ×83.3; *h,* dorsal valve interior, ×27.5; *i,* oblique lateral view of pseudointerarea, ×110 (Popov & Holmer, 1994).

Lurgiticoma POPOV in NAZAROV & POPOV, 1980, p. 99 [**L. singularis;* OD]. Shell transversely oval; ventral valve wide conical; ventral pseudointerarea procline with interridge; dorsal valve moderately convex; apical process occluding apex; dorsal median septum high, folded asymmetrically, strongly spinose; median buttress present. *Ordovician (lower Llanvirn):* Kazakhstan.——FIG. 69,*1a–g.* **L. singularis,* Shundy Formation, Sary-Kumy, central Kazakhstan; *a,* dorsal exterior, ×19.6; *b,* oblique lateral view of dorsal exterior, RMS Br 136436, ×25; *c,* dorsal interior, ×19.6; *d,* oblique lateral view of dorsal interior, RMS Br 136437, ×26.7; *e,* ventral valve exterior, ×19.6; *f,* posterior view of ventral exterior, ×20.8; *g,* lateral view of ventral exterior, RMS Br 136438, ×25 (new).

Mamatia POPOV & HOLMER, 1994, p. 128 [**Paratreta retracta* POPOV in NAZAROV & POPOV, 1980, p. 95; OD]. Ventral valve conical; ventral pseudointerarea undivided, catacline to apsacline; pedicle foramen forming short external pedicle tube, within larval shell; dorsal valve evenly convex, with wide, narrow pseudointerarea, and well developed propareas; apical process completely occluding apex, perforated by short internal pedicle tube; ventral *vascula lateralia* baculate; median buttress well developed; dorsal median septum triangular, low to moderately high, with a single septal rod; dorsal cardinal muscle fields strongly impressed. *Ordovician (lower Arenig):* Russia (Southern Urals), Kazakhstan.——FIG. 69,*3a–g.* **M. retracta* (POPOV); *a,* ventral valve exterior, Olenty Formation, Lake Sasyksor, Kazakhstan, ×33.3; *b,* lateral view, Olenty Formation, Lake Sasyksor, Kazakhstan, ×41.7; *c,* posterior view, Olenty Formation, Lake Sasyksor, Kazakhstan, ×37.5, RMS Br 136181; *d,* dorsal valve exterior, Olenty Formation, Lake Sasyksor, Kazakhstan, RMS Br 136174, ×33.3; *e,* ventral valve interior, RMS Br 136187 Koagash Formation, Karabutak River, Southern Urals, ×33.3; *f,* dorsal valve interior Koagash Formation, Karabutak River, Southern Urals, ×41.7; *g,* lateral view Koagash Formation, Karabutak River, Southern Urals, RMS Br 136177, ×33.3 (Popov & Holmer, 1994).

Myotreta GORJANSKY, 1969, p. 67 [**M. crassa;* OD]. Shell transversly oval; ventral pseudointerarea catacline to apsacline with intertrough; dorsal median septum high, triangular, simple or folded, generally with upper rod. *Ordovician (Arenig–Llanvirn):* Sweden, Poland, Estonia, Russia (Ingria, Pskov district), Lithuania.——FIG. 68,*3a–e.* **M. crassa,* Kunda Stage, Pechory core, Pskov district; *a,* dorsal valve interior, ×45.8; *b,* oblique lateral view of dorsal interior, RMS Br 136439, ×54.2; *c,* ventral valve exterior, ×41.7; *d,* lateral view of ventral exterior,

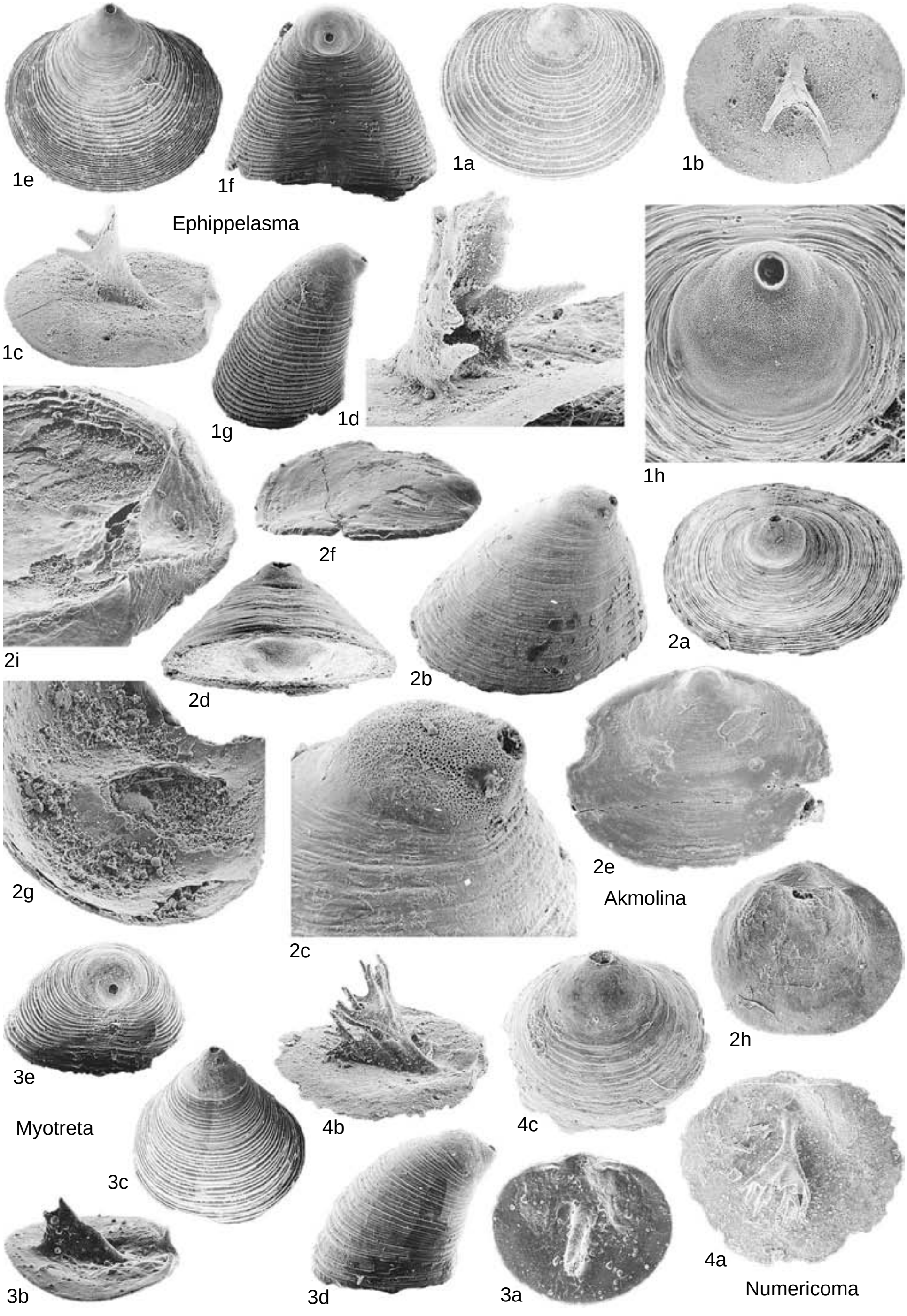

FIG. 68. Ephippelasmatidae (p. 127–129).

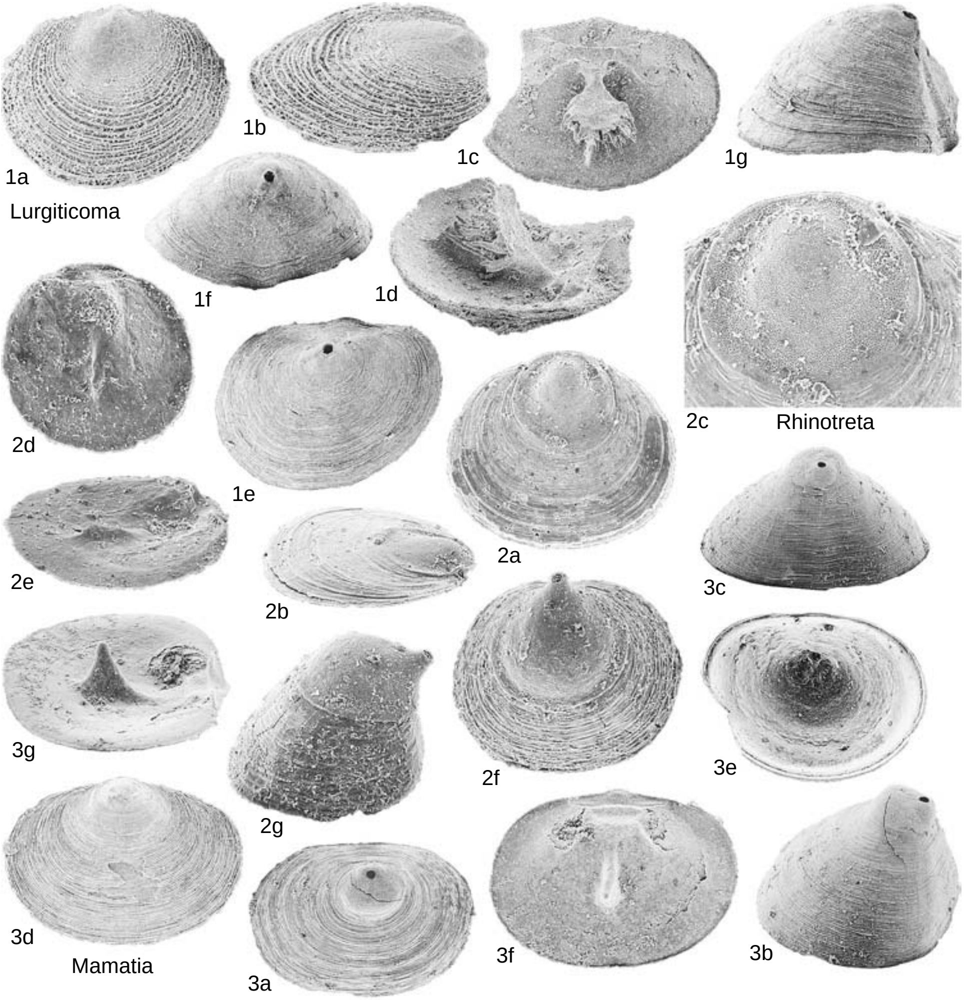

FIG. 69. Ephippelasmatidae (p. 127–130).

×45.8; *e,* posterior view of ventral exterior, RMS Br 136440, ×50 (new).

Numericoma POPOV in NAZAROV & POPOV, 1980, p. 100 [**N. ornata;* OD]. Externally like *Ephippelasma;* dorsal median septum folded asymmetrically with numerous spines. *Ordovician (Arenig–Llandeilo):* Bohemia, *Arenig;* Poland, Russia (Ingria, Pskov district), Estonia, Lithuania, southern China, *Arenig–Llanvirn;* Kazakhstan, Sweden, *Arenig–Llandeilo;* USA (Nevada), *Llanvirn.*——FIG. 68,*4a–c.* **N. ornata,* Karakan Limestone, upper Arenig, northern Betpak-Dala, Kazakhstan; *a,* dorsal valve interior, ×41.7; *b,* oblique lateral view of dorsal interior, RMS Br 136441, ×45.8; *c,* ventral valve exterior, RMS Br 136442, ×66.7 (new).

Pomeraniotreta BEDNARCZYK, 1986, p. 415 [**P. biernatae;* OD] [=*Anatreta* MEI, 1993, p. 405 (type, *A. transversa*)]. Externally similar to *Numericoma,* but more narrow, high conical; apical process occluding apex; dorsal median septum absent. *Upper Cambrian–Ordovician (Arenig):* Kazakhstan, *Upper Cambrian;* Poland, Norway, Sweden, *Tremadoc–Arenig;* Bohemia, *Arenig;* northern China (Hebei).——FIG. 70,*2a–h.* **P. biernatae,* Bjørkåsholmen Limestone, upper Tremadoc, Sweden; *a,b,* dorsal valve exterior, lateral view, RMS Br 129085, ×33.3; *c,* dorsal valve interior, RMS Br 129086, ×33.3; *d,* ventral valve exterior, RMS Br 129089, ×33.3; *e,f,* lateral view of ventral exterior, posterior view, Flagabro, Scania, RMS Br 128088, ×19.6; *g,*

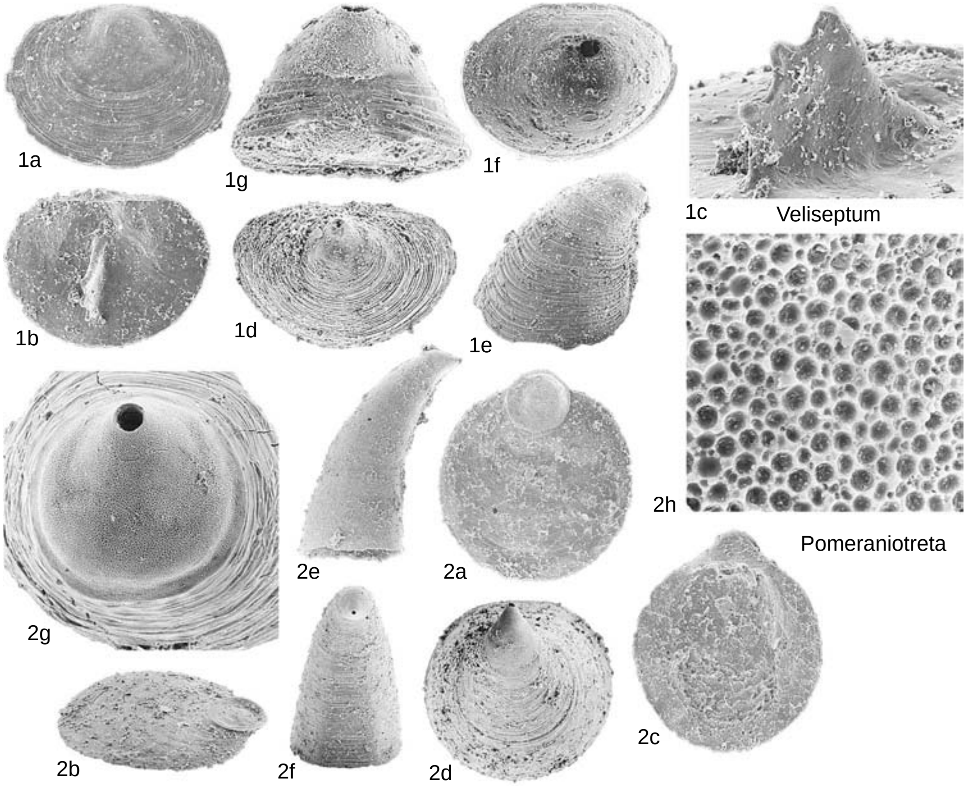

FIG. 70. Ephippelasmatidae (p. 129–130).

ventral larval shell, ×138; *h,* detail of pitted larval microornamentation, Ottenby, Öland, RMS Br 136282, ×1400 (Popov & Holmer, 1994).

Rhinotreta HOLMER, 1986, p. 113 [**R. muscularis;* OD]. Shell subcircular; ventral valve with long exterior pedicle tube; dorsal valve flat; dorsal median ridge low. *Ordovician (Caradoc–Ashgill):* Sweden, Estonia, Ireland.——FIG. 69,*2a–g.* **R. muscularis, Dicranograptus clingani* Biozone, Västergötland (Skövde), Sweden; *a,* dorsal valve exterior, ×62.5; *b,* oblique lateral view of dorsal exterior, ×75; *c,* holotype, detail of dorsal larval shell, RMS Br 128556, ×138; *d,* dorsal valve interior, ×66.7; *e,* paratype, oblique lateral view of dorsal interior, RMS Br 128555, ×75; *f,g,* paratype, ventral valve exterior, oblique lateral view, RMS Br 128564, ×75 (Holmer, 1986).

Veliseptum POPOV in NAZAROV & POPOV, 1976, p. 38 [**V. fragile;* OD]. Externally similar to *Numericoma,* but dorsal median septum high, triangular with spines along anterior slope and upper rod or surmounting plate. *Ordovician (Llandeilo–Ashgill):* Ireland, Sweden, Kazakhstan.——FIG. 70,*1a–g. V. strictum* HOLMER, *Dicranograptus clingani* Biozone, Västergötland (Skövde), Sweden; *a,* paratype, dorsal valve exterior, RMS Br 128549, ×66.7; *b,* dorsal valve interior, ×41.7; *c,* holotype, detail of dorsal median septum, RMS Br 128532, ×150; *d,e,* paratype, ventral valve exterior, lateral view, RMS Br 128528, ×37.5; *f,* ventral valve interior, RMS Br 136443, ×66.7; *g,* paratype, posterior view of both valves, RMS Br 128532, ×66.7 (Holmer, 1986).

Family BIERNATIDAE Holmer, 1989

[*nom. transl.* HOLMER & POPOV, herein, *ex* Biernatinae HOLMER, 1989b, p. 131]

Shell with narrow, convex posterior margin; ventral valve narrow, highly conical; ventral pseudointerarea strongly apsacline, poorly defined laterally; intertrough poorly developed or absent; dorsal pseudointerarea small, divided; apical process absent; dorsal interior with high triangular median septum bearing dorsally convex surmounting plate or rod on posterior slope; anterior slope of septum undercut; dorsal anterocentral scars absent. *Ordovician (upper Tremadoc)–Middle Devonian, ?Upper Devonian.*

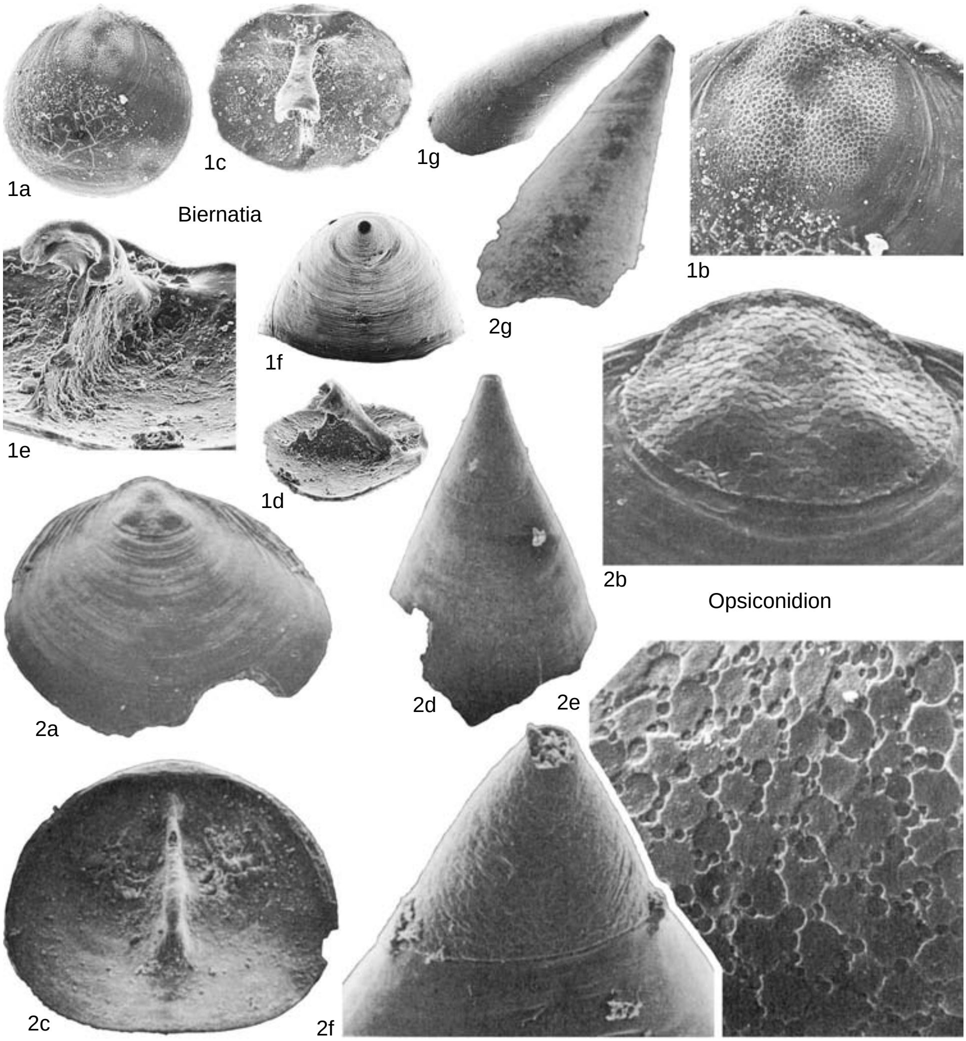

FIG. 71. Biernatidae (p. 131–132).

Biernatia HOLMER, 1989b, p. 133 [**Torynelasma minor rossicum* GORJANSKY, 1969, p. 71; OD]. Dorsal interior with strongly dorsally convex surmounting plate. *Ordovician (Tremadoc–Ashgill):* Sweden, *Tremadoc–Ashgill;* southern China, *Arenig–Llanvirn;* Russia (Ingria, Pskov district), Estonia, Lithuania, Poland, *Arenig–Caradoc;* USA (Alabama, Nevada), *Llanvirn–Llandeilo;* Kazakhstan, *Llanvirn–Ashgill;* Libya, *Caradoc.*——FIG. 71,*1a–g.* **B. rossica* (GORJANSKY), Kunda Stage, Pechory core, Pskov district; *a,* dorsal valve exterior, ×58.3; *b,* detail of dorsal larval shell, ×162; *c,d,* dorsal valve interior, lateral view, ×54.2; *e,* detail of dorsal median septum, RMS Br 133684, ×125; *f,* oblique posterior view of ventral exterior, ×50; *g,* lateral view of ventral exterior, RMS Br 133685, ×31.7 (Holmer, 1989b).

Opsiconidion LUDVIGSEN, 1974, p. 143 [**O. arcticon;* OD] [=*Caenotreta* COCKS, 1979, p. 94 (type, *Caenotreta aldridgei*]. Similar to *Biernatia* but dorsal median septum with rodlike projection or flat surmounting plate. *Ordovician (Ashgill)–Middle Devonian, ?Upper Devonian:* Estonia, *Ashgill–Wenlock;* England, *Llandovery;* Bohemia, *Llandovery–Lochkovian;* Sweden, *Llandovery–Wenlock;* Poland, *Wenlock;* Russia (Novaya Zemlya), *Lower Devonian;* USA (Alaska), Canada (Yukon Territory, Ontario), Australia (Victoria, New South Wales), *Lower Devonian–Middle Devonian;* Germany, Austria, *Lower Devonian, ?Upper Devonian.*——FIG. 71,*2a–g.* **O.*

arcticon, Canada; *a,* dorsal valve exterior, ×73.3; *b,* detail of dorsal larval shell, ROM 37373, ×271; *c,* dorsal valve interior, ROM 37376, ×64.2; *d,* ventral valve exterior, ×65; *e,* detail of larval pitted microornamentation, ROM 37377, ×933; *f,* detail of ventral larval shell, Onondaga Formation, Middle Devonian, Ontario, ROM 37378, ×210; *g,* ventral valve exterior, Michelle Formation, lower Emsian, Yukon Territory, ROM 37381, ×55.8 (von Bitter & Ludvigsen, 1979).

Family CERATRETIDAE Rowell, 1965

[*nom. transl.* Ushatinskaya in Ushatinskaya, Gidaspov, & Riazantsev, 1986, p. 38, *ex* Ceratretinae Rowell, 1965a, p. 278]

Shell ventribiconvex; posterior margin weakly convex; ventral pseudointerarea procline to catacline, poorly defined laterally with intertrough; foramen usually large, elongate oval, not enclosed within larval shell; dorsal pseudointerarea wide with broad median groove; apical process high, ridgelike, sometimes forming septum, perforated by pedicle tube; dorsal interior with triangular median septum or ridge; cardinal muscle scars of both valves elevated, platformlike; dorsal anterocentral scars well defined. *upper Lower Cambrian–Upper Cambrian.*

Ceratreta Bell, 1941, p. 233 [**C. hebes;* OD] Shell transversely oval with moderately wide posterior margin; ornament of evenly spaced rugae; ventral valve strongly convex to subconical; ventral pseudointerarea procline to apsacline with intertrough; foramen, elongate, lens shaped; apical process long, ridgelike, supporting pedicle tube along posterior slope; dorsal median septum long, triangular. *Upper Cambrian:* USA (Montana, Wyoming, Texas), Sweden, Finland (Åland Islands), Estonia, Russia (Ingria, southeast Siberia).——Fig. 72,*1a–g.* **C. hebes,* middle Franconian, *Conaspis* Biozone, Montana; *a,* dorsal valve exterior, RMS Br 136443, ×17.9; *b,* dorsal valve interior, ×17.9; *c,* oblique lateral view of dorsal interior, RMS Br 136444, ×20.8; *d,* ventral exterior, ×15; *e,* lateral view of ventral exterior, ×17.9; *f,* posterior view of ventral exterior, RMS Br 136445, ×16.2; *g,* ventral valve interior, RMS Br 136446, ×13.8 (new).

Bozshakolia Ushatinskaya in Ushatinskaya, Gidaspov, & Riazantsev, 1986, p. 38 [**B. coniformis;* OD]. Shell subcircular with short, weakly convex posterior margin; ventral pseudointerarea procline, divided by narrow intertrough; foramen relatively small, elongate oval; apical process swollen, ridgelike; dorsal interior with poorly developed median septum or high ridge; dorsal median buttress wide. *upper Lower Cambrian–Middle Cambrian:* Sweden, *upper Lower Cambrian;* central Kazakhstan, *Middle Cambrian.*——Fig. 72,*2a–d.* **B. coniformis,* Kysyl-Kojandy Formation, Maya River, Bozshakol, Shiderty and Olenty Rivers; *a,* dorsal valve exterior, PIN 4113/30, ×22.5; *b,* dorsal valve interior, PIN 4113/13, ×18.3; *c,* ventral valve posterior view, PIN 4113/5, ×22.5; *d,* ventral valve interior, PIN 4113/2, ×25.8 (Ushatinskaya, Gidaspov, & Riazantsev, 1986).

Erbotreta Holmer & Ushatinskaya, 1994, p. 207 [**E. singularis;* OD]. Shell subrectangular; ventral valve highly conical; ventral pseudointerarea, procline to catacline, divided by broad, weakly defined intertrough; pedicle foramen elongate lenticular; dorsal valve flattened; dorsal pseudointerarea with wide median groove and narrow propareas; ventral interior with apical process occluding apex, penetrated by pedicle tube; dorsal median ridge poorly developed. *Middle Cambrian (Amgaian):* Russia (Altai).——Fig. 73,*1a–h.* **E. singularis,* Sladky Korenya Formation, Batenev Ridge; *a,* dorsal valve exterior, PIN 4377/1, ×6.7; *b,c,* dorsal valve interior, ×8.3, pseudointerarea, ×16.7, PIN 4377/9; *d,e,* ventral valve exterior, lateral view, RMS 126342, ×11.2; *f,* holotype, ventral valve, posterior view, PIN 4377/5, ×17.5; *g,* ventral larval shell and pedicle foramen, RMS 126342, ×75; *h,* ventral valve interior, PIN 4377/14, ×27.5 (Holmer & Ushatinskaya, 1994).

Keyserlingia Pander in von Helmersen, 1861, col. 46 [**Orbicula reversa* de Verneuil, 1845, p. 289; SD Dall, 1871a, p. 75] [=*Kayserlingia* Beecher, 1891, p. 354; *Clistotrema* Rowell, 1963, p. 35, *nom. nov. pro Orbicella* d'Orbigny, 1847, p. 269 (type, *Orbicula buchii* de Verneuil, 1845, p. 288), *non* Dana, 1846, p. 204]. Shell subcircular; ventral valve low conical with thickened rim of lamellose shell along posterior margin; ventral pseudointerarea procline to catacline with broad intertrough; foramen elongate, lens shaped; apical process forming high, thickened septum with spoonlike anterior projection; cardinal muscle fields of both valves forming strongly elevated, sometimes undercut platforms; dorsal median septum low, triangular. *Upper Cambrian:* Russia (Ingria, Moscow basin), Estonia, Sweden.——Fig. 73,*2a–e.* **K. reversa* (de Verneuil); *a,* dorsal valve interior, RMS Br 136447, ×15; *b,* ventral valve interior, RMS Br 136448, ×12.5; *c,* ventral valve exterior, Ladoga Formation, Ingria (Dudergof), Russia, RMS Br 136449, ×10 (new); *d,e,* oblique posterior view of ventral exterior, lateral view, Obolus sandstone, south Bothnian Sea (Finngrundet Core), Sweden, PM B582, ×12.5 (Puura & Holmer, 1993).——Fig. 73,*2f–i. K. buchii* (de Verneuil), Maardu beds, *Cordylodus andresi* Biozone, Estonia; *f,* dorsal valve exterior, Turjekelder, TAGI BR 1713, ×6.9; *g,* dorsal valve interior, Ülgase, CNIGR 242/12348, ×9.2; *h,* ventral valve interior, Valkla, CNIGR 241/12348, ×5.5 (Popov & others, 1989); *i,* detail of apical process, Jägala Juga, RMS Br 67185, ×15 (new).

Kleithriatreta Roberts in Roberts & Jell, 1990, p. 289 [**K. lamellosa;* OD]. Similar to *Ceratreta* but with more procline ventral valve; deeply excavated dorsal cardinal muscle fields; dorsal median septum with blunt, spinose process. *Lower Cambrian*

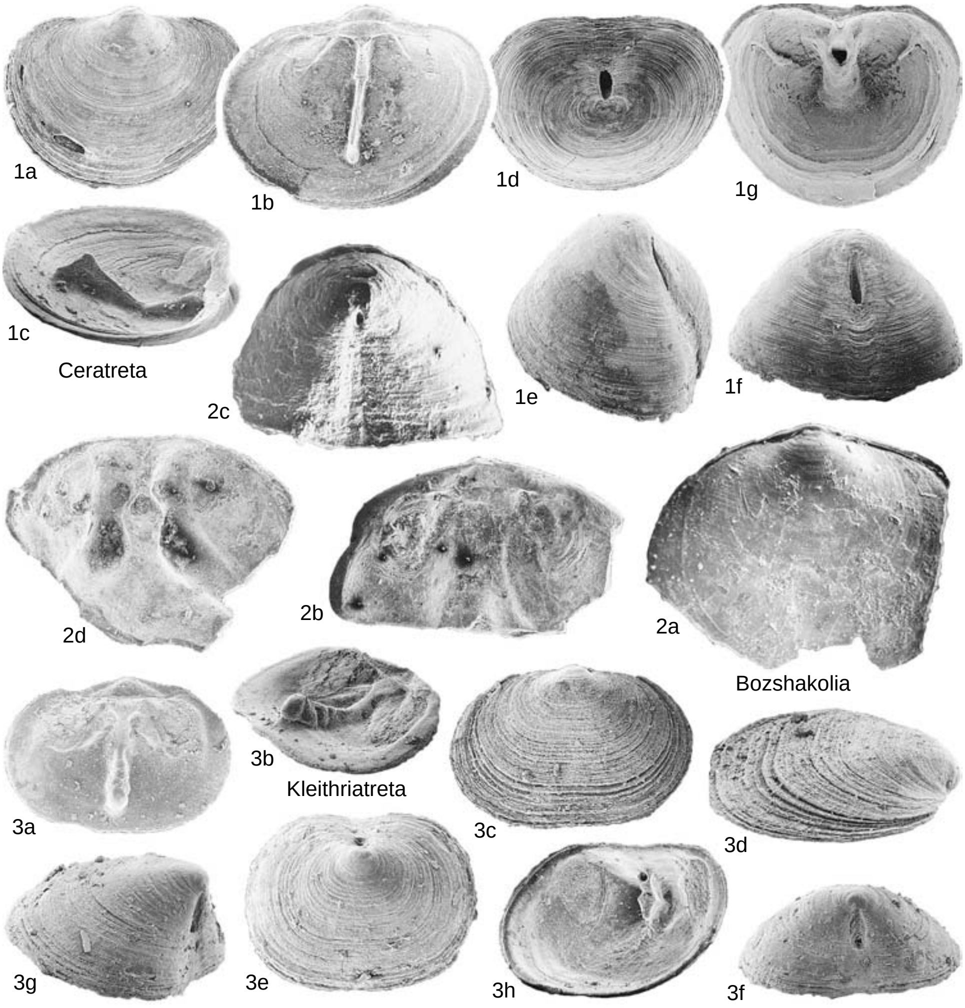

FIG. 72. Ceratretidae (p. 132–133).

(?Toyonian), Middle Cambrian: Australia (New South Wales), *lower Amgaian;* Kirghizia (northern Tien Shan), Kazakhstan.——FIG. 72,*3a–h.* **K. lamellosa,* Coonigan Formation, Mootwingee area, New South Wales, Australia; *a,b,* dorsal valve interior, oblique lateral view, ×20; *c,* dorsal valve exterior, ×15; *d,* oblique lateral view of dorsal exterior, ×18.8; *e,* ventral valve exterior, ×15; *f,* oblique posterior view of ventral exterior, ×15; *g,* oblique lateral view of ventral exterior, ×18.3; *h,* ventral valve interior, ×13.8 (new).

Family EOCONULIDAE Rowell, 1965

[Eoconulidae ROWELL, 1965a, p. 291]

Shell asymmetrical with fine rugae; ventral valve encrusting; pedicle opening may be sealed internally; ventral pseudointerarea absent; dorsal pseudointerarea commonly absent; apical process bosslike, anterior to foramen. *Ordovician (Arenig–Ashgill).*

Eoconulus COOPER, 1956, p. 282 [**E. rectangulatus;* OD]. Dorsal valve conical, usually with subcentral apex; cardinal muscle fields of both valves generally strongly thickened. *Ordovician (Arenig–Ashgill):* USA (Alabama, Nevada), Bohemia, *Arenig;* Russia (Ingria, Southern Urals), southern China, *Arenig–Llanvirn;* Sweden, Kazakhstan, *Arenig–Caradoc;* Estonia, Poland, *Arenig–Ashgill;* Ireland, *Ashgill.*——FIG. 74,*1a–c.* **E. rectangulatus,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×20.8; *b,* posterior view of dorsal exterior,

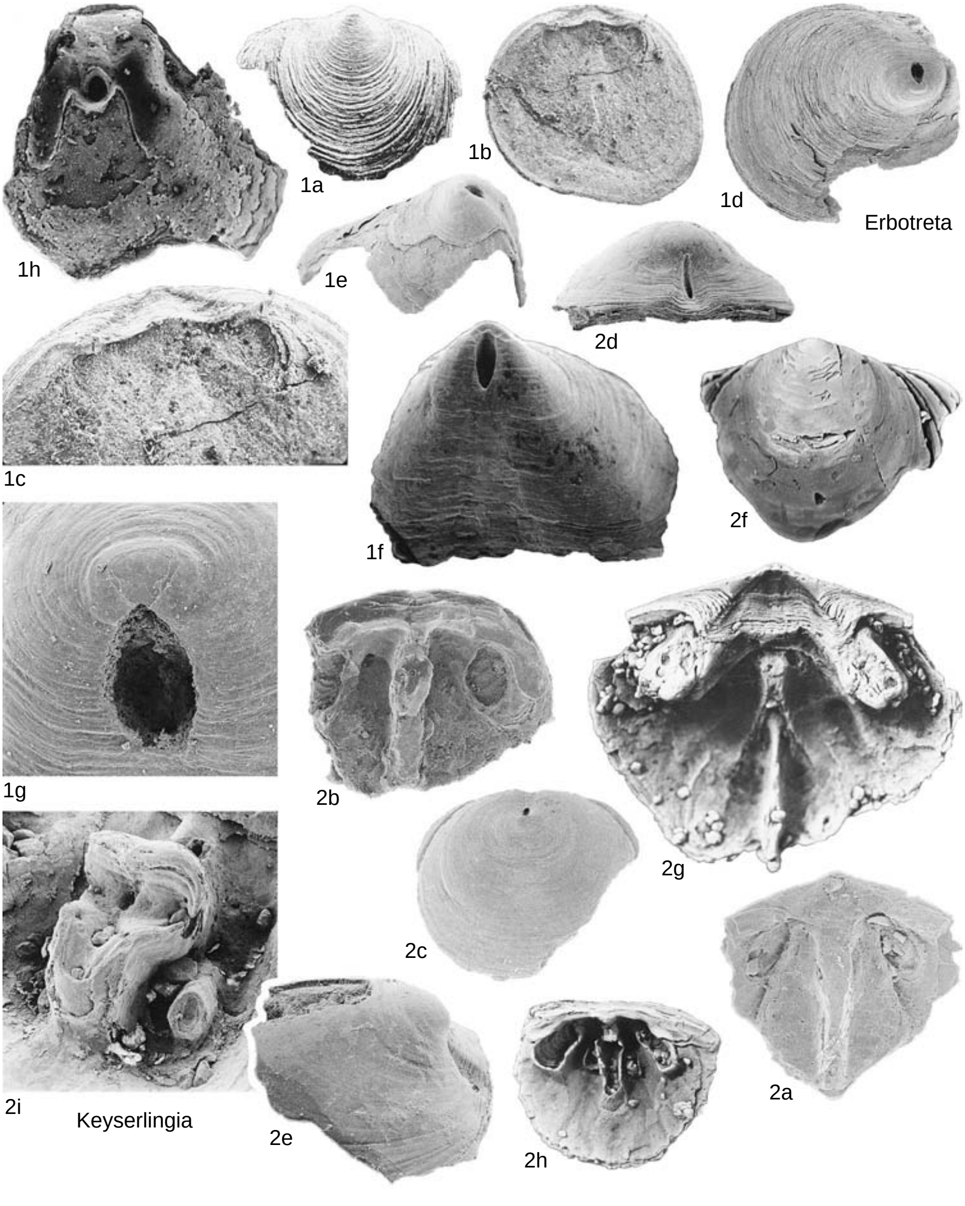

FIG. 73. Ceratretidae (p. 132).

USNM Br 117977a, ×16.7; *c,* dorsal valve interior, USNM Br 117977b, ×16.7 (new).——FIG. 74,*1d,e. E.* sp. cf. *E. clivosus* POPOV, Skärlöv Limestone, Llanvirn, Siljan district, Sweden; *d,* ventral valve interior, ×20.8; *e,* ventral valve oblique lateral view, RMS Br 128960, ×25 (Holmer, 1989b).——FIG. 74,*1f. E.* sp. cf. *E. semiregularis* BIERNAT, Gullhögen Limestone, Llandeilo, Siljan district, Sweden; ventral valve exterior, RMS Br 132719e, ×33.3 (Holmer, 1989b).

Otariconulus HOLMER & POPOV, herein, *nom. nov. pro Otariella* POPOV & HOLMER, 1994, p. 141, *non* WATERHOUSE, 1978 [**Otariella prisca* POPOV & HOLMER, 1994, p. 141; OD]. Shell inequally biconvex, usually more or less asymmetrical; pedicle foramen partly outside larval shell; dorsal valve convex with marginal beak; dorsal pseudointerarea well defined; apical process anterior to internal foramen; ventral cardinal muscle fields large, thickened, placed posterolaterally; dorsal cardinal muscle fields

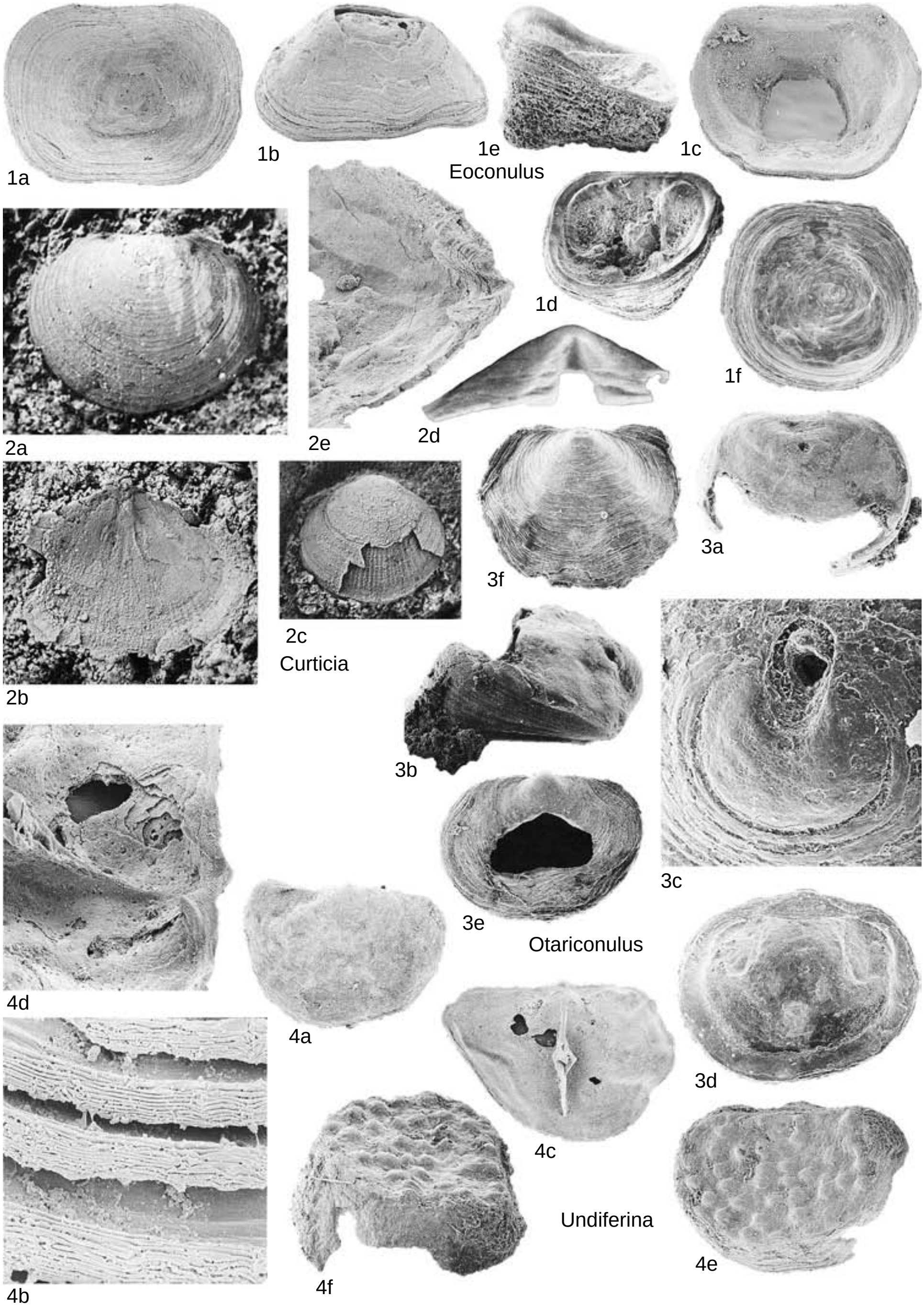

FIG. 74. Eoconulidae and Curticiidae (p. 133–136).

large, elongate oval; dorsal median ridge usually present. *Ordovician (Tremadoc–lower Arenig):* Kazakhstan, Russia (Southern Urals), Sweden.——

FIG. 74,*3a–f.* **O. priscus* (POPOV & HOLMER), Aksak-Kujandy, north-central Kazakhstan; *a,b,* holotype, ventral valve, exterior, lateral view, Satpak

Formation, RMS Br 136211, ×32.7; *c,* ventral larval shell and pedicle foramen, olistolith in Olenty Formation, RMS Br 136212, ×150; *d,* dorsal valve interior, RMS Br 136210, ×37.5; *e,* dorsal valve exterior, Satpak Formation, RMS Br 136213, ×32.7; *f,* dorsal valve exterior, olistolith in Olenty Formation, RMS Br 136214, ×32.7 (Popov & Holmer, 1994).

Undiferina Cooper, 1956, p. 262 [**U. rugosa;* OD]. Ventral valve like *Eoconulus,* but higher; dorsal valve with marginal beak; dorsal pseudointerarea orthocline to anacline with median groove; dorsal interior with high, triangular median septum with rod or narrow thickened surmounting plate. *Ordovician (upper Arenig–Llandeilo):* USA (Nevada, Alabama), central Kazakhstan.——Fig. 74,*4a–d.* **U. rugosa,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* dorsal valve exterior, ×10; *b,* detail of ornamentation, USNM 116833a, ×150; *c,* dorsal valve interior, ×11.2; *d,* detail of dorsal pseudointerarea, USNM 116833b, ×33.3 (new).——Fig. 74,*4e,f. U. nevadensis* Rowell & Krause, Shundy Formation, Llanvirn, Sary-Kumy, central Kazakhstan; *e,* ventral valve exterior, ×13.8; *f,* oblique lateral view, RMS Br 136450, ×17.9 (new).

Family CURTICIIDAE
Walcott & Schuchert, 1908

[Curticiidae Walcott & Schuchert in Walcott, 1908, p. 143]

Shell ventribiconvex, transversely oval with weakly convex posterior margin; ventral valve moderately convex; foramen enlarged by resorption, forming triangular opening; ventral pseudointerarea with broad median groove; dorsal median ridge low. *upper Middle Cambrian–Upper Cambrian.*

Curticia Walcott, 1905, p. 319 [**C. elegantula;* OD]. Characters as for family. *upper Middle Cambrian–Upper Cambrian:* USA (Montana, Minnesota), Greenland, ?England.——Fig. 74,*2a–c.* **C. elegantula,* St. Croix Sandstone, Upper Cambrian, Taylors Falls, Minnesota; *a,* ventral valve exterior, USNM Br 51402a, ×7.1; *b,* dorsal valve interior, USNM Br 51902e, ×6.7; *c,* ventral valve exterior, USNM Br 5192d, ×3.3 (Rowell & Bell, 1961).——Fig. 74,*2d,e. C. minuta* Bell, Upper Cambrian, *Crepicephalus* Biozone, Half Moon Pass, Big Snowy Mountain, Montana; *d,* ventral valve, posterior view, UT 12393, ×23.3 (Rowell & Bell, 1961); *e,* detail of ventral pseudointerarea, USNM 459701a, ×31.2 (new).

Family UNCERTAIN

Craniotreta Termier & Monod, 1978, p. 149 [**C. caltepensis;* OD][=*Craniotrata* Termier & Monod, 1978, p. 149, *nom. null.; Graniotreta* Termier & Monod, 1978, p. 149, *nom. null.*]. Genus poorly known. Described as siphonotretid, but with acrotretid-like shell structure, apical process and muscle scars. May be synonym of *Linnarssonia. Middle Cambrian:* Turkey (western Taurus Mountains).

Dzhagdicus Sobolev, 1992, p. 107 [**D. sentus;* OD]. Shell subquadrate with wide, straight posterior margin, lamellose peripherally; ventral valve unknown; dorsal valve gently convex with marginal beak; dorsal pseudointerarea orthocline; dorsal interior with short median ridge and large, thickened, transversely oval cardinal muscle fields. *Upper Cambrian:* Russia (southeastern Siberia). Satisfactory material not available for illustration.

Schizotretoides Termier & Monod, 1978, p. 151 [**S. tauricus;* OD]. Genus poorly known. Acrotretid-like. *Ordovician:* Turkey (western Taurus Mountains).

Order SIPHONOTRETIDA
Kuhn, 1949

[*nom. correct.* Gorjansky, 1960, p. 180, *pro* order Siphonotretacea Kuhn, 1949, p. 101, *nom. imperf.*]

Shell with hollow spines, usually ventribiconvex, inequivalved; larval and postlarval shell lacking pitted microornament; shell structure microgranular; growth of ventral valve mixoperipheral or holoperipheral; pedicle foramen apical, circular, or extending anteriorly through resorption, producing elongate triangular 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)–Ordovician (upper Ashgill).*

The scope of the Siphonotretida as interpreted here closely follows the original concept of Kuhn (1949) and differs from that of Gorjansky (1960), who also included the Obolellidae with calcium carbonate shells.

Superfamily
SIPHONOTRETOIDEA
Kutorga, 1848

[*nom. correct.* Harper & others, 1993, p. 430, *pro* Siphonotretacea Walcott & Schuchert in Walcott, 1908, p. 145, *nom. imperf., nom. transl. ex* Siphonotretidae Dall, 1877, p. 62, *nom. correct. pro* family Siphonotretaeae Kutorga, 1848, p. 253, *nom. imperf.*]

Characters as for order. *upper Middle Cambrian (Mayaian)–Ordovician (upper Ashgill).*

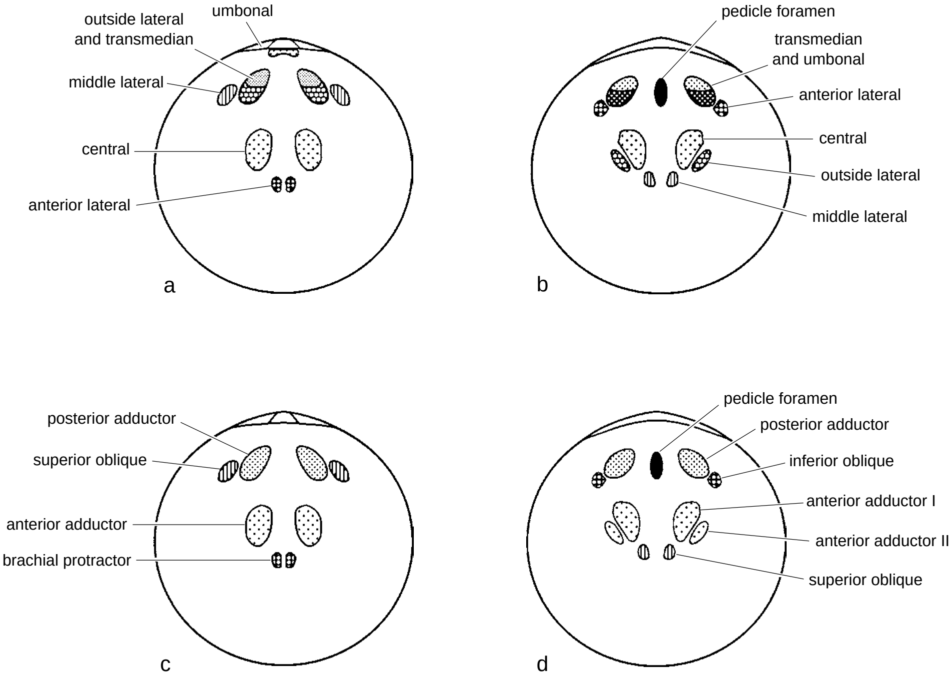

FIG. 75. Alternative interpretations of musculature of *Schizambon australis; a,b,* based on linguloidean type of musculature (new); *c,d,* based on discinoidean type of musculature (Rowell, 1977).

The only character that defines the siphonotretoids as a monophyletic clade is the presence of hollow spines. The siphonotretoids have a fairly simple shell morphology, and the most important taxonomic characters are related to the morphology of the pedicle foramen, internal pedicle tube, pseudointerareas, and type of spinose ornamentation. The interior morphology is unfortunately inadequately known for most taxa. This is due in part to the lack of detailed studies on the group, but in many forms (e.g., *Eosiphonotreta, Alichovia*) the innermost shell layer is poorly mineralized, and such characters as muscle scars and mantle canals are usually not well defined.

The siphonotretoids have generally been classified previously as an acrotretide superfamily (ROWELL, 1965a). Data now available, however, suggest that they may be related more closely to the lingulides; most importantly they differ from the acrotretides in lacking a small, pitted larval shell as well as a columnar shell structure (HOLMER, 1989b). The siphonotretoidean shell structure is not well known but seems to be made up mostly of microgranular apatite (BIERNAT & WILLIAMS, 1971; POPOV & NŌLVAK, 1987). The only character possibly uniting them with the Acrotretida is the pedicle foramen, but a similar type of foramen is now also known from the lingulide family Lingulellotretidae (KONEVA & POPOV, 1983).

Most siphonotretoid taxa (excluding *Acanthambonia* and *Celdobolus*) are characterized by a pedicle foramen that becomes enlarged by varying degrees of resorption; however, this type of resorption is known also from the Acrotretida (Curticiidae; ROWELL & BELL, 1961) and Lingulida (Dysoristidae; POPOV & USHATINSKAYA, 1992).

The siphonotretoid muscle system has not been studied in detail; it is best known from *Schizambon* and in part also from *Celdobolus* and *Siphonobolus* (HAVLÍČEK, 1982). CHUANG (1971a) attempted to reconstruct the muscle

TABLE 10. Character-state matrix used in PAUP analysis (Fig. 76) of characters as listed in Table 11; missing data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Obolinae	2	1	0	0	0	0	0	0	0	0	0	0	2	1	1	1	1	0	0
Lingulellotreta	2	2	0	0	0	0	0	4	0	1	1	0	2	1	1	2	1	0	0
Dysoristus	1	1	0	0	0	0	0	3	2	0	0	0	2	1	0	2	1	1	1
Ferrobolus	1	2	0	0	0	0	0	3	2	0	0	0	2	1	0	2	1	1	1
Acanthambonia	0	0	1	0	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0
Celdobolus	0	0	1	0	0	0	0	1	0	1	1	0	2	1	1	1	0	0	0
Helmersenia	1	1	1	0	1	0	2	1	0	1	1	0	2	1	1	0	0	0	0
Alichovia	0	0	5	1	1	1	2	1	0	0	3	0	9	9	9	9	0	0	0
Eosiphonotreta	1	1	2	0	2	0	2	2	0	0	2	0	2	0	0	0	0	0	0
Cyrbasiotreta	1	1	4	0	2	1	3	3	2	0	0	1	2	1	0	3	0	0	0
Gorchakovia	1	2	1	1	2	0	3	3	1	0	0	0	1	1	0	3	0	0	0
Karnotreta	1	1	3	0	2	1	2	3	1	0	3	1	2	0	0	1	0	0	0
Multispinula	1	1	4	0	2	1	2	3	2	0	3	0	2	1	0	0	0	0	0
Nushbiella	1	2	4	2	2	1	3	3	2	0	3	1	1	1	0	3	0	0	0
Siphonobolus	1	1	1	0	2	0	2	2	0	1	2	0	2	1	1	1	0	0	0
Schizambon	2	1	1	2	0	0	0	3	2	1	0	0	2	1	1	0	0	0	0
Siphonotreta	1	2	1	0	0	0	1	2	0	2	4	0	2	1	2	1	0	0	0

system of *Schizambon* to support his view that the perforated valve of siphonotretoids and acrotretoids is the dorsal one. ROWELL (1977) proposed a more likely reconstruction of the same genus, which supports the more traditional view, with the perforate valve as ventral (Fig. 75c,d). The reconstructions by CHUANG and ROWELL are both based on the assumption that the muscle system of *Schizambon* is closely comparable with that of the Discinida; however, as shown by HAVLÍČEK (1982) it is equally possible to deduce the siphonotretoid muscle system from that of early Paleozoic Lingulida (Fig. 75a,b). The shape of the visceral area in the siphonotretoids is closely similar to that of most lingulides. ROWELL (1977) proposed that the two pairs of muscle scars in the elongate anterior projection from the dorsal visceral area in *Schizambon* are homologous with the anterior adductors and brachial protractors in discinids (Fig. 75c). These pairs of scars, however, may also be compared with the dorsal central and anterior lateral muscles of lingulides (Fig. 75a). CHUANG (1971a) identified a possible scar placed directly anterior to the dorsal pseudointerarea (i.e., in the imperforate valve, to use his terminology) in *Schizambon* as the attachment scar of the pedicle; however, if it is present it is more likely to be the trace of the dorsal umbonal muscle scars (Fig. 75a), and similar scars have been identified in *Siphonobolus* by HAVLÍČEK (1982) and in *Siphonotreta.* With the view adopted here, it is likely that the large, paired posterolateral muscle scars in the dorsal valve of *Schizambon* are homologous with the transmedian and outside lateral muscle and that the muscle scars in the median anterior part of the ventral valve may have been the attachment site of the central, middle lateral, and internal oblique muscles (Fig. 75a,b).

The mantle canals of the Siphonotretoidea are also known imperfectly in most taxa, but appear to be closely similar to those of most lower Paleozoic lingulides. They are best known from *Celdobolus, Siphonobolus* (HAVLÍČEK, 1982), and *Schizambon* (ROWELL, 1962a), where the dorsal and ventral *vascula lateralia* are developed; the dorsal *vascula media* are known only from the latter two genera.

The earliest history of the siphonotretoids is still very obscure and poorly represented in the fossil record; the earliest known genera, *Schizambon* (AKSARINA & PELMAN, 1978) and *Gorchakovia* (POPOV & others, 1989), from the upper Middle and Upper Cambrian, both have a large pedicle foramen formed through resorption. The earliest siphono-

TABLE 11. List of coded characters used in cladistic analysis (Fig. 76) of genera within superfamily Siphonotretoidea (new).

1. convexity: equibiconvex (0); ventribiconvex (1); dorsibiconvex (2).
2. relative valve size: equivalved (0); unequivalved (1); stongly unequivalved (2).
3. hollow spines: absent (0); one size (1); two sizes (2); one size of spines arranged along edge of lamellae (3); two sizes of spines arranged along edge of lamellae (4); spines bifurcating (5).
4. radial ornamentation: absent (0); fine striation (1); costellae (2).
5. ventral pseudointerarea: flat, well defined laterally (0); rudimentary (1); convex, poorly defined laterally (2).
6. ventral pseudointerarea with median ridge: absent (0); present (1).
7. inclination of ventral pseudointerarea: orthocline (0); anacline (1); apsacline (2); procline to catacline (3).
8. pedicle track and foramen: absent (0); apical (1); small, placed slightly anterior to apex (2); broad subtriangular, extending anterior to beak (3); situated on pseudointerarea (4).
9. pedicle track with posterior plate: absent (0); vestigial (1); long, subtriangular (2).
10. ventral visceral field: poorly defined (0); slightly thickened anteriorly (1); forming thickened platform (2).
11. internal pedicle tube: absent (0); flattened, along valve floor (1); long, cylindrical (2); short, cylindrical (3); cylindrical, within visceral platform (4).
12. dorsal sulcus: absent (0); present (1).
13. dorsal pseudointerarea: absent (0); rudimentary (1); well developed (2).
14. dorsal median groove: absent (0); present (1).
15. dorsal visceral field: weakly defined (0); slightly thickened anteriorly (1); with anterior lateral and central muscle scars forming elevated platform (2).
16. dorsal median ridge: absent (0); bisecting all of visceral field (1); bisecting central and anterior lateral muscle scars (2); bisecting umbonal muscle scars (3).
17. baculae: absent (0); present (1).
18. larval shell: not pitted (0); pitted (1).
19. postlarval shell: not pitted (0); pitted (1).

tretoids may have been related closely with the Lingulellotretidae or Dysoristidae. The siphonotretoids have their main range in the Ordovician and the youngest indisputable species (*Multispinula drummuckensis* HARPER, 1984) is from the upper Ashgill (upper Rawtheyan) of Scotland; the taxonomic position of the only possible Silurian species ("*Siphonotreta*" *anglica* MORRIS, 1850) from the Wenlock of England was questioned by ROWELL (1962a).

A cladistic analysis of 13 siphonotretoid genera (excluding only the poorly known *Mesotreta* and *Quasithambonia*) was performed using 19 unweighted, unordered characters (Table 10–11) with an outgroup consisting of *Lingulellotreta, Dysoristus, Ferrobolus,* and the subfamily Obolinae. Seven trees 70 steps long were generated with a consistency index of 0.571 (branch-and-bound search, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The resulting strict consensus tree (Fig. 76) supports the view that the siphonotretoids form a monophyletic group.

Family SIPHONOTRETIDAE Kutorga, 1848

[*nom. correct.* DALL, 1877, p. 62, *pro* family Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*] [*incl.* Acanthamboniinae COOPER, 1956, p. 211; Schizamboninae HAVLÍČEK, 1982, p. 70]

Characters as for superfamily. *upper Middle Cambrian (Mayaian)–Ordovician (upper Ashgill).*

Dysoristus and *Ferrobolus* were placed within the Siphonotretidae by ROWELL (1962a) and HAVLÍČEK (1982). POPOV and USHATINSKAYA (1992) noted that the baculate shell structure, pitted microornamentation of the larval and postlarval shells, as well as the lack of hollow spines in both these genera indicate that they belong to the Lingulida.

Siphonotreta DE VERNEUIL, 1845, p. 286 [**Crania unguiculata* VON EICHWALD, 1829, p. 274; SD DAVIDSON, 1853, p. 131]. Shell ventri- or equibiconvex, elongate oval, ornamented by undulating fila superposed on thick, widely spaced lamellae, with very closely spaced, evenly distributed, short spines of uniform size; foramen circular, apical; ventral pseudointerarea large, apsacline, orthocline to anacline, undivided, and flattened, with concave median depression; dorsal pseudointerarea orthocline, shelflike, fitting closely into median depression in ventral pseudointerarea; median groove wide, poorly defined, with propareas reduced;

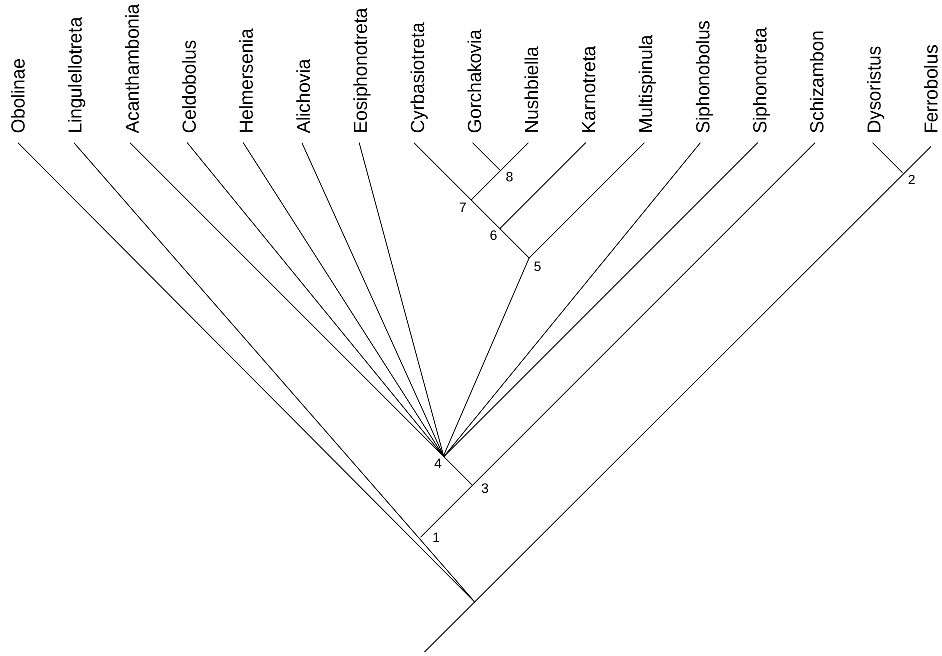

FIG. 76. Strict consensus tree of 7 equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 12 (new).

visceral area of both valves thickened, forming platforms; internal pedicle tube long, possibly closed in adults, emerging through visceral platform, with possible umbonal muscle scar; dorsal anterior lateral muscle scars placed between central muscle scars, and bisected by low median ridge. *Ordovician (Arenig–lower Caradoc):* Russia (Ingria), Estonia, Sweden.——FIG. 77,*1a–f.* **S. unguiculata* (VON EICHWALD); *a,b,* ventral valve exterior, dorsal valve exterior, ×1.7; *c,* lateral view of both valves, lower Llanvirn, Kunda, GMK 3975, ×2.9; *d,* posterior view of ventral valve exterior, ×4.2; *e,* detail of ventral pedicle opening, lower Llanvirn, Volkhov River, Ingria, BMNH B 14159, ×12.5; *f,* detail of visceral area and pedicle tube of ventral valve interior, Arenig, Iswos at Volkhov River, Ingria, RMS Br 73882, ×4.2 (new).——FIG. 77,*1g,h. S. intermedia* GORJANSKY, Llandeilo–lower Caradoc; *g,* dorsal valve interior, Kukruse, Estonia, RMS Br 133503, ×2.5; *h,* detail of spinose ornamentation of dorsal valve exterior, Kohtla-Järve, Estonia, RMS Br 133696, ×5 (new).

Acanthambonia COOPER, 1956, p. 211 [**A. minutissima;* OD]. Shell close to equibiconvex, with evenly spaced spines of uniform size; foramen apical, circular, minute; ventral pseudointerarea short, widely triangular, orthocline to anacline; dorsal pseudointerarea vestigial; ventral interior with flattened pedicle tube attached to valve floor; visceral areas of both valves poorly defined. *Ordovician (Arenig–Ashgill)*: Sweden, Ireland, Bohemia, *Arenig–Ashgill;* USA (Alabama, Virginia), *Llandeilo–Caradoc;* Estonia, *Ashgill.*——FIG. 77,*2a–f.* **A. minutissima,* Pratt Ferry beds, Llandeilo, Pratt Ferry, Alabama; *a,* ventral valve exterior, ×15; *b,* ventral valve, lateral view, USNM 116796a, ×17.5; *c,* ventral pseudointerarea and internal pedicle tube, USNM 116796b, ×75; *d,* dorsal valve exterior, ×14.2; *e,* dorsal valve, lateral view, USNM 116796c, ×15; *f,* dorsal valve interior, USNM 116796d, ×15 (new).——FIG. 77,*2g,h. A. delicata* HOLMER, Siljan district, Sweden; *g,* paratype, ventral larval shell and pedicle opening,

TABLE 12. Synapomorphy scheme for internal nodes of cladogram shown in Figure 76 (new).

Node	Character states						
1	10:1	11:1					
2	1:1	9:2	15:0	18:1	19:1		
3	3:1	16:0	17:0				
4	1:1	7:1	8:2	10:0			
5	3:4	5:2	6:1	8:3	9:2	11:3	15:0
6	12:1	16:1					
7	7:3	11:0	16:3				
8	2:2	4:1	13:1				

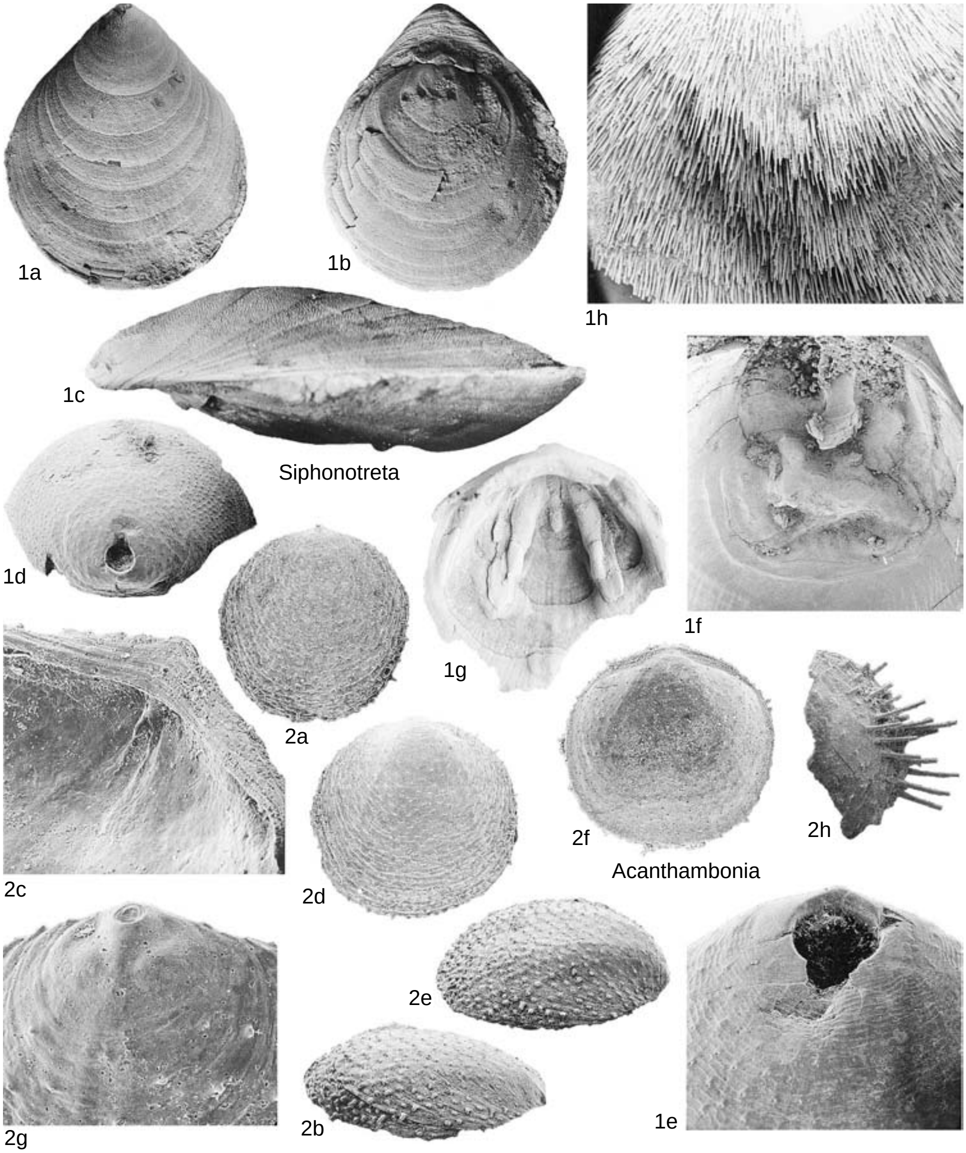

FIG. 77. Siphonotretidae (p. 139–141).

Kårgärde Limestone, Llanvirn, RMS Br 128935, ×92; *h,* paratype, fragmentary valve with spines, Folkeslunda Limestone, Llanvirn, RMS Br 129048b, ×25 (Holmer, 1989b).

Alichovia GORJANSKY, 1969, p. 97 [**A. ramispinosa;* OD]. Shell close to equibiconvex and equivalved, subtriangular, ornamented by widely spaced lamellae, with widely spaced, bifurcating (ramispinose) uniform spines; foramen circular, apical; ventral pseudointerarea low, highly apsacline, slightly convex, and divided by median plication; dorsal pseudointerarea with broad median plication in median groove, fitting closely into plication in ventral pseudointerarea; internal pedicle tube short, possibly closed in adults; other interior characters poorly known. *Ordovician (Tremadoc–Caradoc):* northeastern Russia, Estonia, *Caradoc;* Poland, *Tremadoc.*——FIG. 78,*1a–f.* **A. ramispinosa,* Viru Series; *a,b,* ventral valve exterior, dorsal valve exterior, ×1.7; *c,* lateral view of both valves, Idavere Stage (CIII), Pskov District (Sebezh Core 219; 430 m), RMS Br 136335, ×2.1; *d,* ventral valve interior,

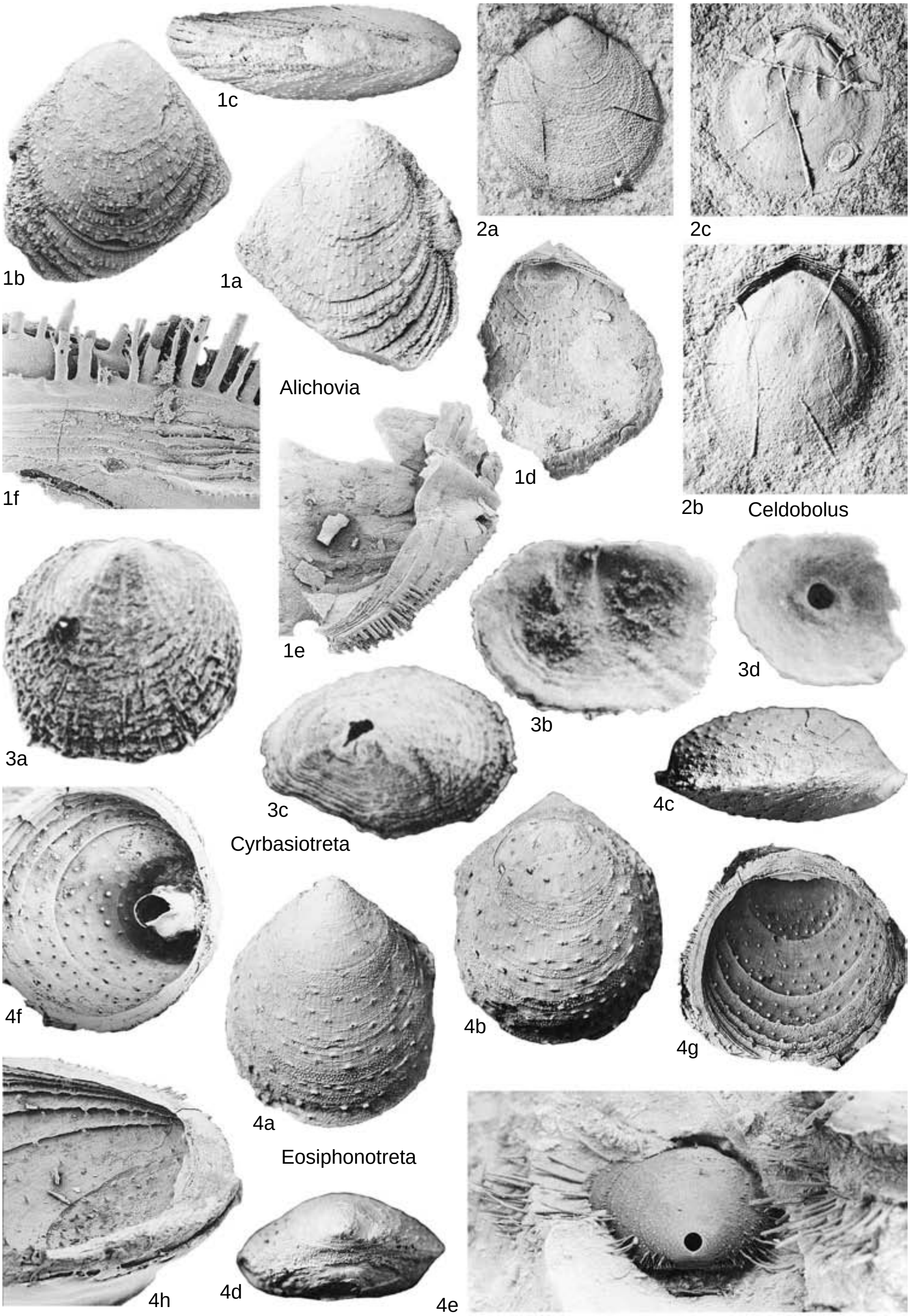

FIG. 78. Siphonotretidae (p. 141–143).

RMS Br 136336, ×1.7; *e,* dorsal pseudointerarea, oblique lateral view, ×5; *f,* detail of ramispinose ornamentation, RMS Br 136337, middle Caradoc, Aluvere quarry, Estonia, ×25 (new).

Celdobolus Havlíček, 1982, p. 63 [**Obolus complexus* Barrande, 1879, pl. 113; OD]. Shell subcircular to elongate-oval, almost equibiconvex, ornamented by closely spaced thin lamellae, with evenly spaced spines of uniform size; foramen minute, circular, apical; ventral pseudointerarea low, flattened, apsacline, undivided; dorsal pseudointerarea undivided, wide, anacline to almost orthocline, striated; internal pedicle tube may be sealed in adults; ventral visceral area slightly thickened, rhomboidal, and extending to midvalve; dorsal visceral area with possible scars of central and anterior lateral muscles, bisected by median ridge; *vascula lateralia* of both valves marginal, arcuate. *Ordovician (Arenig):* Bohemia, ?Poland.——Fig. 78,*2a–c. C. mirandus* (Barrande), Klabava Formation, Strasice, Bohemia; *a,* latex cast of ventral external mold, OMR VH 65771, ×8.3; *b,* ventral internal mold, OMR VH 65772, ×5; *c,* dorsal internal mold, OMR VH 65770, ×8.3 (new).

Cyrbasiotreta Williams & Curry, 1985, p. 208 [**C. cirrata;* OD]. Shell transversely oval to subcircular, with conical ventral valve and gently convex, sulcate dorsal valve; ornamented by lamellae, with marginal row of fine, evenly spaced spines of two sizes; pedicle track elongate oval, tapering posteriorly, covered posteriorly by concave plate; ventral pseudointerarea procline, divided by faint ridge; dorsal valve weakly sulcate; dorsal pseudointerarea narrow, undivided; visceral areas of both valves poorly defined; internal pedicle tube absent. *Ordovician (upper Arenig):* Ireland.——Fig. 78,*3a–d.* **C. cirrata,* Tourmakeady Limestone, Mayo, Ireland; *a,* holotype, dorsal valve exterior, BMNH BB 95436, ×13.3, *b,* paratype, oblique view of dorsal valve interior, BMNH BB 95438, ×14.2; *c,* oblique view of ventral valve exterior, BMNH BB 95437, ×11.7; *d,* paratype, oblique view of ventral valve interior, BMNH BB 95439, ×15 (Williams & Curry, 1985).

Eosiphonotreta Havlíček, 1982, p. 57 [**Terebratula verrucosa* von Eichwald, 1840, p. 163; OD]. Shell ventribiconvex, elongate oval, lamellose, ornamented by widely spaced, thick, very long spines and more numerous thin, short spines; ventral pseudointerarea apsacline to catacline, undivided; foramen small, apical; dorsal pseudointerarea orthocline, divided by wide, shallow median groove; ventral interior with long conical pedicle tube, sometimes enclosed by umbonal muscle platform; dorsal interior with elevated umbonal muscle platform; other interior characters unknown. *Ordovician (Tremadoc–early Llanvirn:* Bohemia, *Tremadoc–Arenig;* Russia (Ingria), Estonia, *Arenig–lower Llanvirn.*——Fig. 78,*4a–h.* **E. verrucosa* (von Eichwald), Arenig; *a–d,* ventral valve exterior, dorsal valve exterior, lateral view of both valves, posterior view of both valves, Volkhov River, Ingria, BMNH B 5959, ×2.9; *e,* posterior view of ventral valve exterior with preserved spines, Mäekalda, Tallinn, RMS Br 135726, ×2.1; *f,* ventral valve interior, Mäekalda, Tallinn, RMS Br 133509 ×4.2; *g,* dorsal valve interior, ×4.2; *h,* lateral view of dorsal valve interior, Mäekalda, Tallinn, RMS Br 133509, ×6.2 (new).

Gorchakovia Popov & Khazanovitch in Popov & others, 1989, p. 135 [**G. granulata;* OD]. Shell ventribiconvex, ornamented by fine, evenly spaced spines of uniform size; pedicle track large, widely triangular, with small posterior plate; ventral pseudointerarea procline to catacline, undivided, and poorly defined laterally; dorsal pseudointerarea vestigial; internal pedicle tube lacking; interior characters poorly defined. *Upper Cambrian:* Russia (Ingria).——Fig. 79,*1a,b.* **G. granulata,* Volkhov River; *a,* holotype, dorsal exterior oblique view, CNIGR 258/12348, ×62.5; *b,* paratype, ventral valve exterior, CNIGR 261/12348, ×50 (Popov & others, 1989).

Helmersenia Pander in von Helmersen, 1861, column 48 [**Siphonotreta ladogensis* Jeremejew, 1856, p. 73; SD Walcott, 1912, p. 367]. Similar to *Acanthambonia,* but ornamented with widely spaced spines; ventral pseudointerarea low, apsacline; dorsal pseudointeraea wide, shelflike, poorly divided, with anacline propareas; internal pedicle tube short, closed in adults; ventral visceral area slightly thickened; *vascula lateralia* of both valves submarginal, arcuate. *Upper Cambrian–Ordovician:* Russia (Ingria), *Cordylodus proavus* Biozone; Estonia, *Cordylodus angulatus–C. rotundatus Biozone.*——Fig. 79,*3a–e.* **H. ladogensis* (Jeremejew), Tosna Formation, Ingria, Russia; *a,* ventral valve exterior, ×8.3; *b,* ventral larval shell and foramen, ×22.5; *c,* lateral view of ventral valve exterior, Volkhov River, RMS Br 136338, ×8.3 (new); *d,* dorsal valve interior, Kotly Village, CNIGR 253/12348, ×8.3; *e,* dorsal valve exterior, Volkhov River, CNIGR 254/12348, ×8.3 (Popov & others, 1989).

Karnotreta Williams & Curry, 1985, p. 211 [**K. adnata;* OD]. Shell subcircular, ventribiconvex, lamellose peripherally, with marginal rows of flattened spines; foramen large, subcircular, tapering slightly posteriorly; ventral pseudointerarea narrow, triangular, apsacline, divided by low ridge; dorsal valve weakly sulcate; dorsal pseudointerarea undivided, arched medially to form convex fold; ventral interior with short pedicle tube; dorsal visceral area extending slighly anterior to center, bisected by weak median ridge. *Ordovician (upper Arenig):* Ireland.——Fig. 79,*4a–d.* **K. adnata,* Tourmakeady Limestone, Mayo, Ireland; *a,* holotype, ventral valve exterior, BMNH BB 95414; *b,* paratype, ventral valve interior, BMNH BB 95416; *c,* paratype, dorsal valve exterior, BMNH BB 95415; *d,* paratype, dorsal valve interior, BMNH BB 95417, all ×7.5 (Williams & Curry, 1985).

Mesotreta Kutorga, 1848, p. 271 [**Siphonotreta tentorium* Kutorga, 1848, p. 270; OD]. Shell subcircular, with evenly spaced spines of two sizes; ventral valve low conical, with subcentral apex; foramen small, somewhat anterior to apex; dorsal

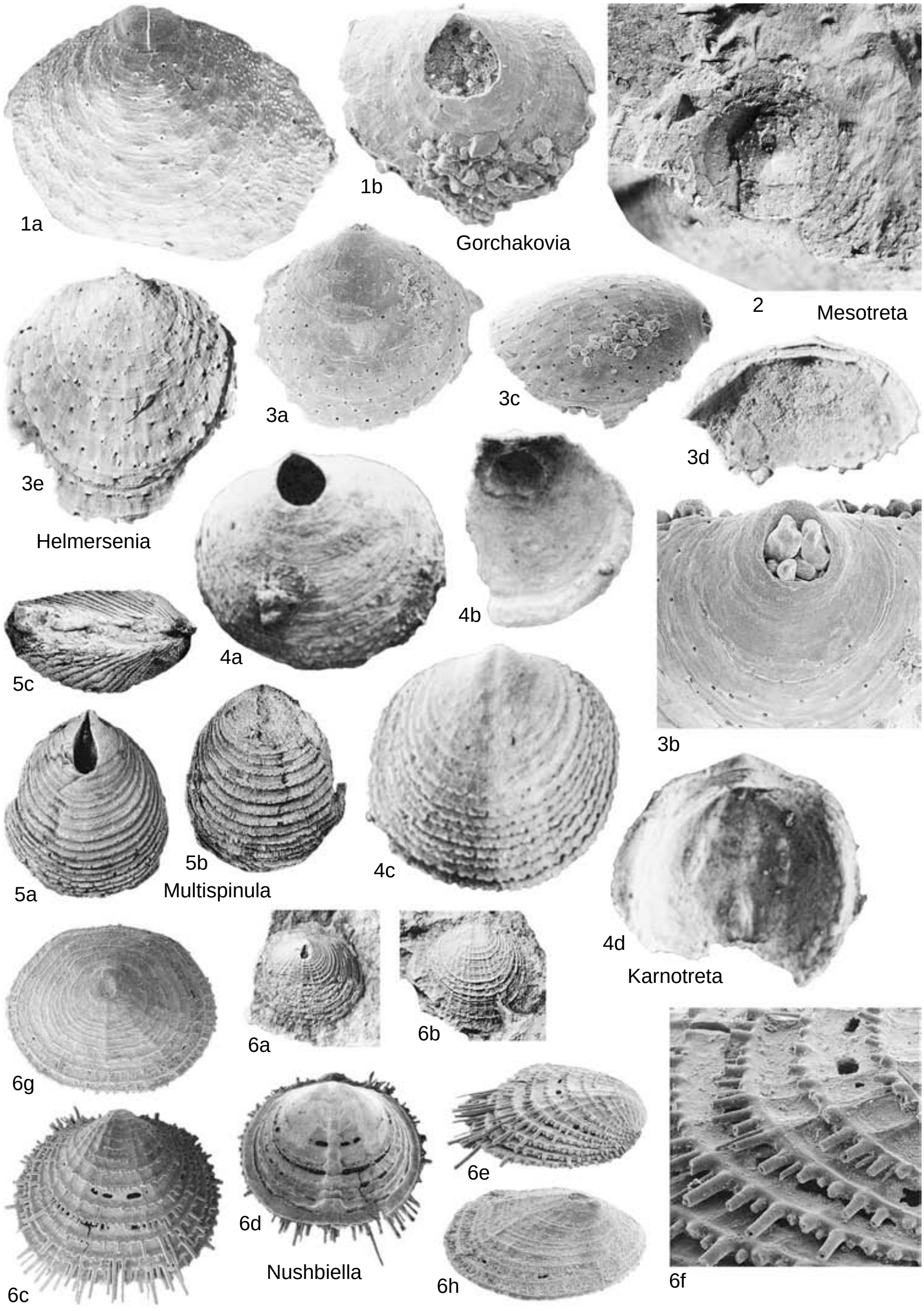

FIG. 79. Siphonotretidae (p. 143–145).

valve unknown. *Ordovician (Arenig):* Russia (Ingria).——FIG. 79,*2*. **M. tentorium* (KUTORGA), Arenig, Babino quarry; ventral valve exterior, RMS Br 136339, ×2.5 (new).

Multispinula ROWELL, 1962a, p. 147 [**Schizambon macrothyris* COOPER, 1956, p. 267; OD]. Shell thick, subcircular to elongate suboval, ornamented by strongly developed, evenly spaced lamellae, each bearing marginal spines of two sizes; ventral pseudointerarea low apsacline to procline; dorsal pseudointerarea low orthocline, divided by median groove; pedicle opening externally like *Schizambon,* but with internal pedicle tube. *Ordovician (upper Arenig–upper Ashgill):* Ireland, *upper Arenig;* Canada (Quebec), *Llanvirn;* USA (Virginia, Nevada, Oklahoma, Tennessee), *Llanvirn–Caradoc;* Kazakhstan, *Llandeilo;* Great Britain (Scotland), *Llandeilo–upper Ashgill;* Russia (Taimyr), *Ashgill.*——FIG. 79,*5a–c.* **M. macrothyris* (COOPER), Wardell Formation, Virginia; holotype, ventral valve exterior, dorsal valve exterior, lateral view of both valves, USNM 98204a, ×1.7 (Cooper, 1956).

Nushbiella POPOV in KOLOBOVA & POPOV, 1986, p. 252 [**Multispinula dubia* POPOV, 1977, p. 104; OD]. Externally similar to *Cyrbasiotreta,* but with ornamentation of radial costellae, internal pedicle tube; dorsal pseudointerarea absent; visceral areas of both valves weakly impressed; dorsal interior with two large muscle scars on either side of thick median ridge. *Ordovician (upper Arenig–Caradoc):* Kazakhstan; Sweden, *Llanvirn–Caradoc;* USA (Virginia, Alabama), *Llandeilo–Caradoc.*——FIG. 79,*6a–b.* **N. dubia* (POPOV), Anderken Formation, Chu-Ili Range, Kazakhstan; *a,* ventral valve exterior, CNIGR 26/12361, ×5; *b,* dorsal valve exterior, CNIGR 2/12361, ×5 (Kolobova & Popov, 1986).——FIG. 79,*6c–h. N. lillianae* HOLMER, Dalby Limestone, Siljan District, Sweden; *c,* dorsal valve exterior, ×10; *d,* dorsal valve interior, ×11.2; *e,* dorsal valve exterior, oblique lateral view, ×11.2; *f,* holotype, dorsal valve exterior, detail of ornamentation, RMS Br 132543, ×42; *g,* ventral valve exterior, ×19.6; *h,* paratype, ventral valve exterior, oblique lateral view, RMS Br 132493, ×23 (Holmer, 1989b).

?Quasithambonia BEDNARCZYK & BIERNAT, 1978, p. 303 [**Q. rarispinosa;* OD]. Genus poorly understood; possibly juvenile of *Eosiphonotreta. Ordovician (Arenig):* Poland.

Schizambon WALCOTT, 1884, p. 69 [**S. typicalis;* SD OEHLERT, 1887b, p. 1266] [=*Schizambonia* OEHLERT, 1887b, p. 1266]. Shell dorsibiconvex; ornament of closely spaced rugellae, short discontinuous costellae and evenly spaced, fine spines; ventral pseudointerarea low, undivided, apsacline to orthocline; pedicle track elongate triangular, posterior part covered by plate; dorsal pseudointerarea low, with poorly defined median groove; visceral areas of both valves slightly thickened; dorsal visceral area extending anteriorly to midvalve, with central and anterior lateral muscle scars; *vascula lateralia* of both valves marginal, arcuate. *upper Middle Cambrian (Mayaian)–Ordovician (Arenig):* Canada (New Brunswick, ?British Columbia), *Upper Cambrian–?Lower Ordovician;* Russia (Altai), *Mayaian;* USA (Nevada, Colorado, Utah, Pennsylvania, Alaska), Argentina (Jujuy Province), ?Greenland, *Lower Ordovician;* West Antarctica, *Upper Cambrian.*——FIG. 80,*1a–f.* **S. typicalis,* Pogonip Limestone, Eureka district, Nevada; *a,* ventral valve exterior, ×9.2; *b,* detail of ornamentation, USNM 459671a, ×45.8; *c,* ventral valve interior showing pseudointerarea and internal foramen, USNM 459671b, ×31; *d,* lateral view of ventral valve exterior, ×10; *e,* detail of pedicle track, USNM 459671c, ×41.7 (new); *f,* dorsal valve interior, USNM 143025d, ×10 (Rowell, 1962a).

Siphonobolus HAVLÍČEK, 1982, p. 61 [**Siphonotreta simulans* RŮŽIČKA, 1927, p. 7; OD]. Shell ventribiconvex, elongate oval, ornamented by lamellae with evenly spaced spines of uniform size; foramen moderately large, subcircular; ventral pseudointerarea, low, undivided, poorly defined; dorsal pseudointerarea large, orthocline, divided by wide, poorly defined median groove; ventral interior with long pedicle tube and slightly thickened visceral area extending to midvalve; dorsal visceral area with long, broad anterior projection, extending almost to anterior margin, bisected by low median ridge, with well-defined scars of central and anterior lateral muscles; dorsal umbonal set on platform; *vascula lateralia* of both valves marginal, arcuate. *Ordovician (Tremadoc–Arenig):* Bohemia, *Tremadoc;* Southern Urals, *Arenig.*——FIG. 80,*3a,b.* **S. simulans* (RŮŽIČKA); *a,* ventral internal mold, OMR VH 2083a, ×8.3; *b,* dorsal internal mold, Trenice Formation, Bohemia (Holoubkov), OMR VH 3059d, ×8.3 (new).——FIG. 80,*3c–e. S. uralensis* (LERMONTOVA), Akbulaksai Formation, Alimbet Farm, Southern Urals; *c,* ventral valve exterior, RMS Br 136074, ×6.7; *d,* ventral valve interior, oblique anterior view, RMS Br 136080, ×12.5; *e,* detail of foramen, RMS Br 136079, ×62.5 (new).

Siphonotretella POPOV & HOLMER, 1994, p. 84 [**S. jani;* OD]. Shell ventribiconvex and subcircular; ventral valve subconical; ventral pseudointerarea procline to slightly apsacline, poorly defined laterally; pedicle foramen apical, small, rounded, not enlarged through resorption; dorsal valve gently convex, with maximum height somewhat anterior to apex; dorsal pseudointerarea extremely reduced, mainly consisting of median groove; shell surface covered by fine hollow spines of about equal size; internal characters of both valves poorly known. *Ordovician (Tremadoc–early Arenig):* Poland (Holy Cross Mountains), *Tremadoc;* Sweden, Norway, *upper Tremadoc;* Kazakhstan (Southern Urals, north-central Kazakhstan), *early Arenig.*——FIG. 80,*2a–c.***S. jani,* Bjørkåsholmen Limestone, Sweden; *a,b,* holotype, ventral valve, lateral view, ×62.5, larval shell, LO 6525T, ×167; *c,* dorsal valve interior, LO 6524t, ×62.5 (Popov & Holmer, 1994).——FIG. 80,*2d,e. S.* sp., Koagash Formation, Karabutak River, Southern Urals; *d,* ventral valve exterior, ×25; *e,* oblique lateral view, RMS Br 136083, ×30.8 (Popov & Holmer, 1994).

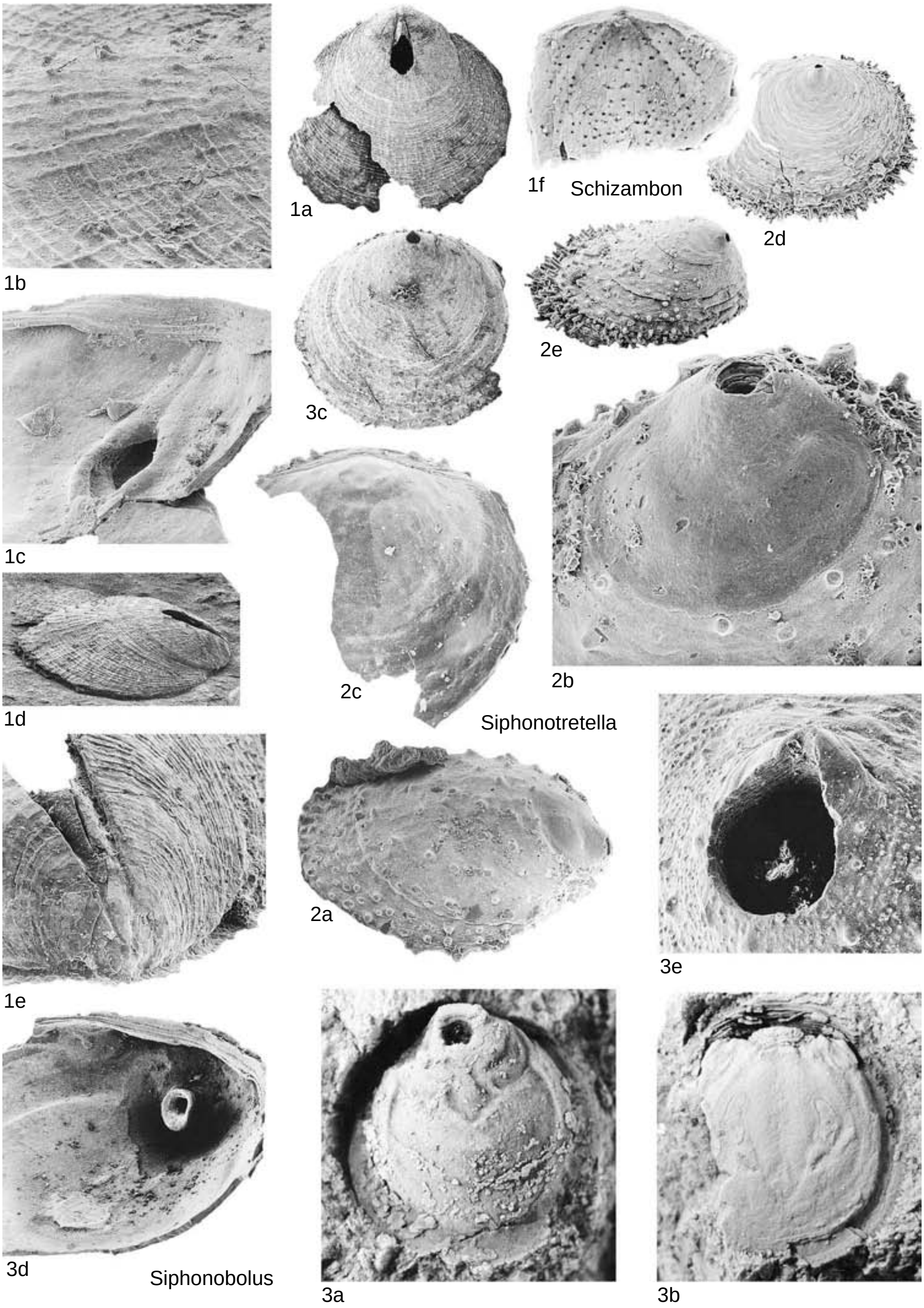

FIG. 80. Siphonotretidae (p. 145).

PATERINATA

J. R. Laurie

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Class PATERINATA Williams & others, 1996

[Paterinata Williams & others, 1996, p. 1192]

Larval shell pustulose; strophic cardinal margins lacking setae, possibly associated with fused mantle lobes; incipient, divergent notothyrium and delthyrium covered by variably developed homeodeltidium; paired dorsal adductor muscles grouped medially and posterolaterally, diductor muscles possibly attached ventrally to homeochilidium or delthyrial margin and inserted dorsally in posteromedian cavity; saccate, rarely pinnate mantle canal system possibly accommodating gonads. *Lower Cambrian (Tommotian)–Upper Ordovician.*

Order PATERINIDA Rowell, 1965

[Paterinida Rowell, 1965a, p. 293]

Shell usually ventribiconvex, with straight or nearly straight hinge line. Ventral valve convex to hemiconical, pseudointerarea usually divided by triangular delthyrium, with or without variably developed homeodeltidium. Dorsal valve usually weakly convex, pseudointerarea divided by broad notothyrium, partially closed by homeochilidium. Ventral musculature includes a pair of large, triangular apical scars. Dorsal musculature includes two pairs of scars, anteromedial and posterolateral. Ventral mantle canal systems pinnate or saccate where known. Dorsal mantle canal systems saccate where known. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

The Paterinida were one of the earliest, but never a dominant brachiopod stock, with the oldest specimens coming from the Tommotian of the Siberian Platform. They have always been difficult to place taxonomically, no doubt in part due to their orthoid-like appearance, coupled with the lack of knowledge of their interior. Recent discoveries have shown that the Paterinida are a more morphologically diverse group than had been suspected, with ventral valves ranging from pyramidal with a procline pseudointerarea and a large, convex homeodeltidium to moderately convex with an orthocline pseudointerarea marked by a median intertrough, while dorsal valves range from those lacking an interarea to those with a low, planar interarea, wide notothyrium, and homeochilidium. Their ornament is predominantly concentric, with fine concentric fila being characteristic of the cryptotretids and some paterinids, in the latter commonly broken into drapes by radial sets of nick points. The closely packed depressions developed in paterinids such as *Micromitra, Dictyonina,* and others are homologous, having originated as offset concave arcs of the concentric fila. Radial ornament is rarely developed in paterinates, with many of the recorded capillae and costellae being traces of radially successive nick points that break the concentric fila into drapes (Williams, Popov, & others, 1998).

MUSCULATURE

Williams and Rowell (1965a, p. 127) and Rowell (1965a, p. 294) assessed what was known of the musculature of this group and concluded that the scars of both valves were narrowly triangular and radiated from their respective valve apices. Rowell (1980, p. 18) studied etched material of *Dictyonina pannula* (White) and considered that the ventral muscle field was elongate triangular and divided by two subparallel mantle canals. Laurie (1987) examined specimens of two

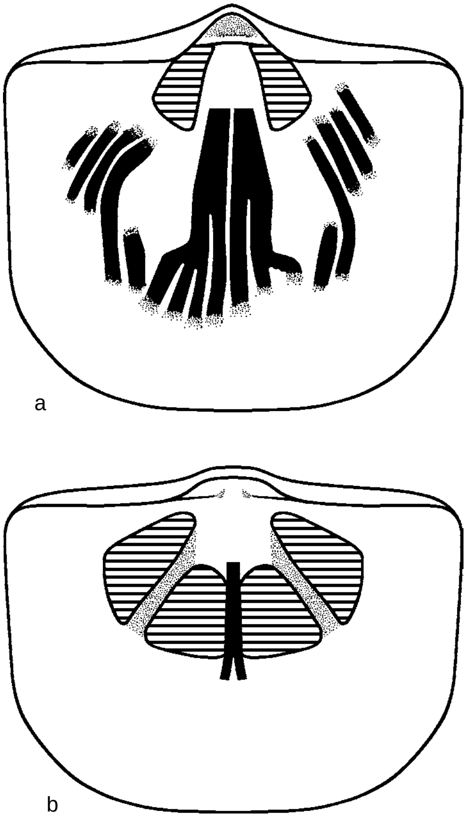

FIG. 81. Interpretation of musculature and mantle canal systems of *Askepasma toddense* Laurie, 1986; *a,* ventral valve, muscle scars *hatched,* mantle canals *black; b,* dorsal valve, muscle scars *hatched,* vascula media *black,* dorsal vascula myaria *stippled* (new).

well-preserved species, *Askepasma toddense* (Fig. 81) and *Paterina* sp. (Fig. 82), and by comparison showed that the ventral musculature included a pair of apical, triangular scars, which were probably separated from one another by the proximal portions of a pair of *vascula media.* Williams, Popov, and others (1998) consider that, in addition to these scars, another pair are also present, bounded laterally by ridges along the delthyrial margins and lying mostly on the inside of the homeodeltidium.

On the other hand, the dorsal musculature was shown to include two pairs of scars on the floor of the valve: the anteromedian pair separated from a low median ridge by the proximal parts of a pair of *vascula media;* and the posterolateral pair located in front of the lateral extremities of the notothyrium. It was also suggested by Laurie (1987, p. 264) that a transverse, often bilobate pit in the apex of the homeochilidium was a muscle attachment site, homologous with the diductors of articulated brachiopods. However, Williams, Popov, and others (1998) have suggested that these paterinide diductors could be homologous with the posterior adductors of discinoids, while the adductors may correspond to the anterior adductors and oblique laterals of discinoids.

MANTLE CANALS

The mantle canal system of the Paterinida is also not very well understood. Rowell (1980) and Laurie (1987) have shown that the ventral valve contains two subparallel *vascula media.* In *Askepasma toddense* they are flanked by indistinct *en echelon* markings (Fig. 81a) that Laurie (1987) interpreted as probably saccate *vascula genitalia* because of the general similarity to the early orthoids. However, further examination has shown that it is unlikely that the ventral mantle canal system of *Askepasma toddense* is saccate. Indeed, it is considered more likely that the ventral mantle canal system of this species is pinnate, in some respects similar to the condition displayed by *Conotreta* (compare Fig. 81a with Williams & Rowell, 1965a, fig. 138e) although detailed comparisons are impossible because of the generally poor preservation of the mantle canal system in *Askepasma toddense.* The ventral mantle canal system of *Paterina* sp. (Fig. 82a) differs considerably from that of *Askepasma,* in that it appears to have a pair of strong *vascula media* that distally curve outward to become concentric, enveloping a pair of large, reniform areas interpreted by Laurie (1987) as saccate *vascula genitalia.* This assertion has been supported by Williams, Popov, and others (1998) who noted that these areas have a finely nodular microtopography, a common feature of shell floor underlying gonads.

The dorsal mantle canal system in *Askepasma toddense* (Fig. 81b) is unclear, but that of *Paterina* sp. (Fig. 82b) was shown by LAURIE (1987) to consist of a pair of broad *vascula media* that separated the anteromedian pair of muscle scars from the median ridge. As these canals leave the muscle field, they also curve laterally to become concentric, conforming to the saccate condition. These envelop small reniform areas extending from between the anterior and posterior dorsal muscle scars but are not as well defined as those in the ventral valve.

SHELL STRUCTURE

POPOV and USHATINSKAYA (1987) and USHATINSKAYA and others (1988) examined the shell structure of *Cryptotreta neguertchenensis* and *Micromitra* sp. and concluded that the shell consisted of between two and eight lamellae, each comprising closely packed subhexagonal prisms with their long axes normal to the surface of the lamella. This they considered to be the primary structure of the paterinid shell. WILLIAMS, MACKAY, and CUSACK (1992, fig. 41), however, illustrated aggregates of spheroidal apatite in a fracture surface of *Dictyonina* sp. cf. *D. ornatella* and considered (p. 102) that the original structure of paterinid shell material was more likely to have been spheroidal, in common with that of recent lingulids, discinids, and Paleozoic acrotretids. They believed the prisms discovered by POPOV and USHATINSKAYA (1987) to be recrystallized casts of secreting epithelium similar to those found in linguloids by CURRY and WILLIAMS (1983). This was confirmed by WILLIAMS, POPOV, and others (1998).

The more detailed study of paterinide shell structure recently undertaken by WILLIAMS, POPOV, and others (1998) has shown that the paterinide shell was secreted in the orthodox succession of periostracum, primary, and secondary layers. X-ray diffraction techniques have shown that in four paterinids and one cryptotretid the mineral comprising the shell was carbonate hydroxylapatite.

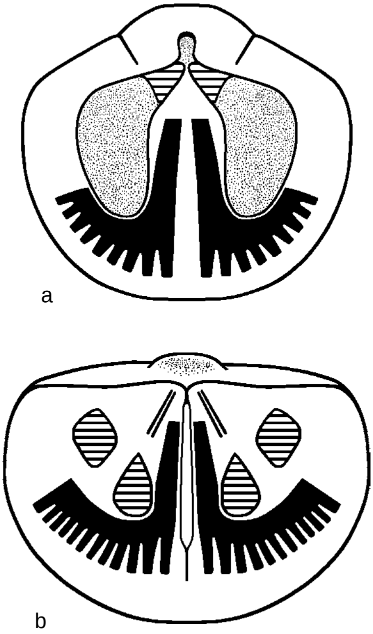

FIG. 82. Interpretation of musculature and mantle canal systems of *Paterina* sp. (see Laurie, 1987); *a,* ventral valve; *b,* dorsal valve; muscle scars *hatched;* vascula media *black;* ventral reniform areas *stippled* (new).

As expected, no preserved periostracum has been discovered with certainty. The primary layer in several paterinids is a thin, homogeneous, compact, vertically cleaved lamina ranging in thickness from 2.5 to 10.5 µm (1.8 µm in *Cryptotreta*) and is not always clearly distinguishable as it commonly grades into the secondary layer. It consists of spherules of apatite from 40 to 60 nm in diameter aggregated into mosaics over 200 nm in diameter or recrystallized into plates about 1 µm in size.

In *Cryptotreta undosa* the secondary layer is stratified, comprising phosphatized so-called membranes 80 to 100 nm thick, usually alternating with apatitic laminae up to 2 µm thick. Internally, these membranes are usually indented by subhexagonal depressions that WILLIAMS, POPOV, and others (1998) considered to be impressions of cells of the mantle epithelium; a succession of these impressions simulate the hexagonal columns reported by POPOV and USHATINSKAYA

(1987) and USHATINSKAYA and others (1988). The apatitic laminae vary in thickness and were believed by WILLIAMS, POPOV, and others (1998) to have been spherulitic, although they are now mostly recrystallized into acicular prisms. In the posteromedian section of larger shells, the apatitic laminae may pass into lenticular chambers up to 25 µm high with walls of orthogonally oriented acicular apatite surrounding aggregates of clays and apatitic prisms.

LARVAL SHELL MORPHOLOGY

Paterinid larval valves are defined by their well-developed halo, are about 600 to 700 µm wide and tuberculate, smooth (*Dictyonites, Lacunites*) or with close-packed depressions (*Askepasma*). WILLIAMS, POPOV, and others (1998) have examined well-preserved *Micromitra* sp. cf. *M. ornatella* from Turkey that are largely covered in hemispherical tubercles 4.5 to 6 µm in diameter, separated from one another by troughs 1.5 µm wide. These tubercles fade marginally, becoming sporadic before disappearing on the halo. The larval dorsal valve is inflated into a posteromedian mound and four distal lobes bounded by a median cleft and a pair of anterolateral clefts and associated complex folds. The larval ventral valve is also quadrilobate, but the lobes are less well defined and do not extend distally as far as those of the dorsal valve; hence they do not complement the dorsal lobes. The posteromedian lobe of the dorsal valve is assumed by WILLIAMS, POPOV, and others (1998) to have accommodated the digestive system and the peripheral lobes each to have borne a sac of larval setae.

RELATIONSHIPS

Although POPOV and others (1993, fig. 1b) and HOLMER and others (1995, p. 732) placed them firmly within the Lingulata because of their phosphatic shell, their relationships within that group are uncertain, because their musculature and mantle canal systems differ from those of other phosphatic brachiopods.

For a long time, paterinid genera have been unsatisfactorily differentiated on the basis of various aspects of their external ornament. This is due to the exceedingly sparse knowledge of their interior morphology and shell structure and to the fact that they never dominate fossil faunas, consequently generating only sporadic interest. Although all genera assigned to the group are similar in broad morphology, the considerable variation in the development of the pseudointerareas and the delthyrial covers engenders doubt as to their monophyly.

Superfamily PATERINOIDEA Schuchert, 1893

[*nom. correct.* LAURIE, herein, *pro* Paterinacea SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 11, *nom. imperf., nom. transl. ex* Paterinidae SCHUCHERT, 1893, p. 148, *nom. imperf.*] [*incl.* Dictyoninacea COOPER, 1956, p. 187]

Characters as for order. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

Family PATERINIDAE Schuchert, 1893

[Paterinidae SCHUCHERT, 1893, p. 148] [*incl.* Micromitridae SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 11]

Hinge line straight or nearly straight; ventral pseudointerarea variably defined, varying in height, usually catacline to procline, sometimes apsacline, usually flat; later forms all have ornament of radially arranged pits or perforations. Both ventral and dorsal mantle canal systems saccate where known. *Lower Cambrian (Tommotian)–Upper Ordovician (Ashgill).*

Paterina BEECHER, 1891, p. 345 [**Obolus labradoricus* BILLINGS, 1861a, p. 6; OD]. Transversely ovate to subquadrate, ventribiconvex; hinge line nearly straight, ventral pseudointerarea variably defined, high, apsacline or catacline; homeodeltidium unknown; dorsal pseudointerarea low, ?catacline, homeochilidium unknown; ornament of irregular, fine, concentric fila, commonly broken by nick points into sets of drapes. *upper Lower Cambrian–Middle Cambrian:* England, France, Spain, USA, Canada (Newfoundland), *upper Lower Cambrian;* Siberia, *Middle Cambrian.*——FIG. 83,*1a–d.* **P. labradorica* (BILLINGS), Newfoundland, Canada; *a,* ventral valve exterior, normal view, ×4; *b,* syntype, ventral valve exterior, detail of ornament, GSC 381, ×12; *c,* ventral valve exterior, normal view, ×4; *d,* syntype, ventral valve exterior, detail of ornament, GSC 381a, ×12 (new).

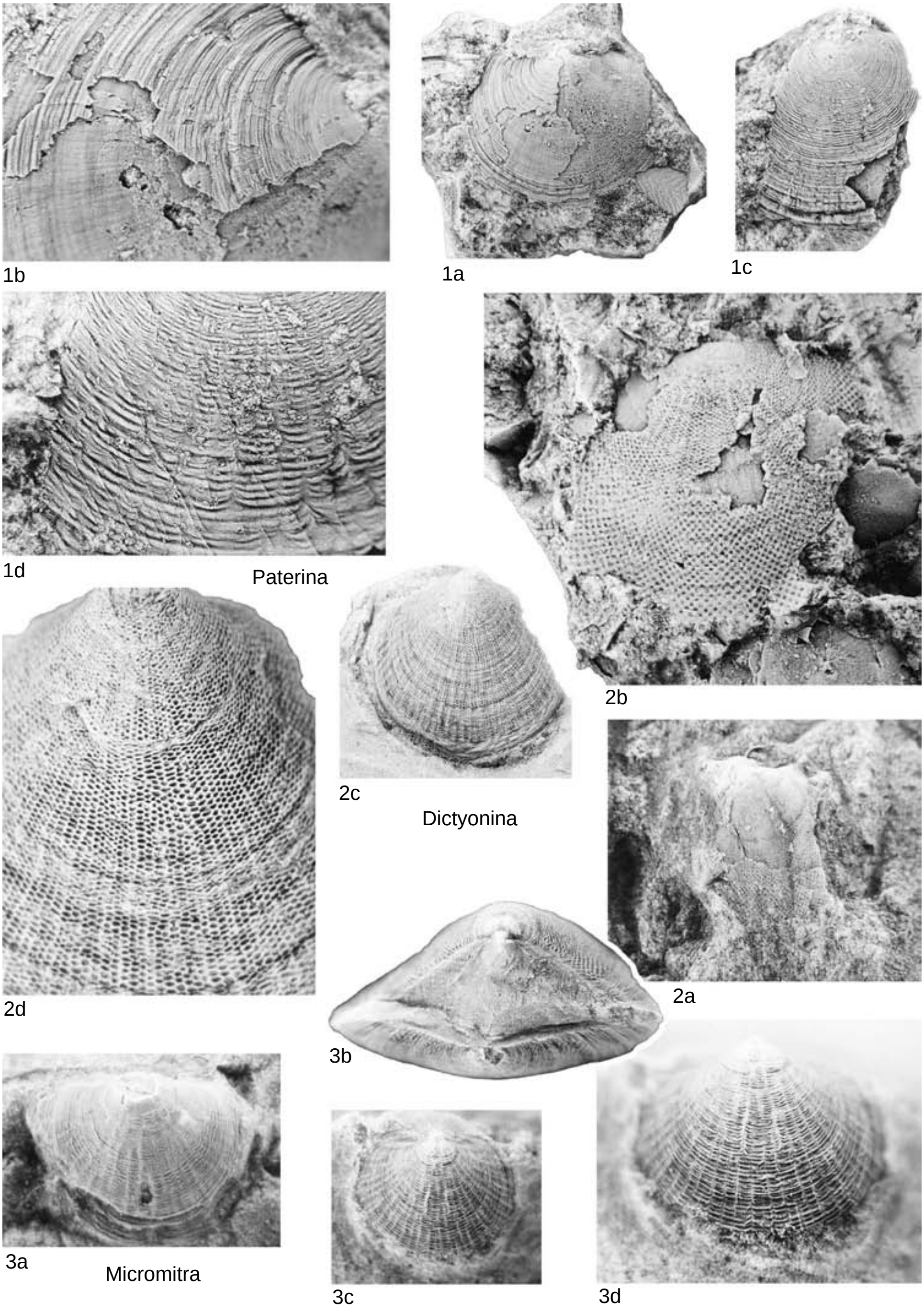

FIG. 83. Paterinidae (p. 150–153).

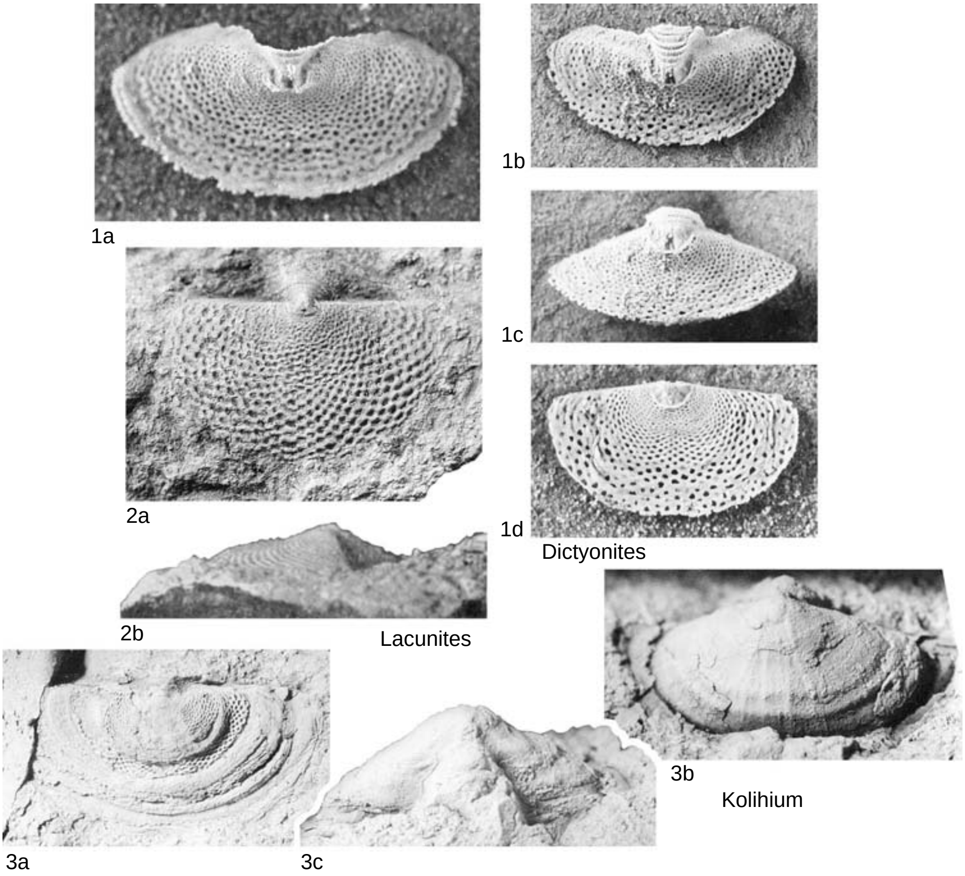

FIG. 84. Paterinidae (p. 152–153).

Dictyonina COOPER, 1942, p. 228, *nom. nov. pro Iphidella* WALCOTT, 1912, p. 359, *non* WALCOTT, 1905 [**Trematis pannulus* WHITE, 1874, p. 6; OD]. Transversely ovate, ventribiconvex; hinge line nearly straight; ventral valve strongly convex with prominent beak; ventral pseudointerarea variably defined, high, apsacline, with homeodeltidium short; dorsal valve moderately convex with low pseudointerarea; ornament of fine radiating rows of subhexagonal pits, increasing in size distally. *Lower Cambrian–Upper Cambrian:* ?France, central Kazakhstan, *Lower Cambrian;* Nevada, *upper Lower Cambrian–lower Middle Cambrian;* Turkmenistan, Kirghizia, Mexico, Arizona, Montana, *Middle Cambrian;* New South Wales, Idaho, Utah, *lower Middle Cambrian;* Siberian Platform, *Amgaian;* southern Kazakhstan, Russian Asia, *Amgaian–Mayaian;* Denmark (Bornholm), Norway, *Jincella brachymetopa* Zone; Antarctica, Germany, *Upper Cambrian;* Wyoming, *Cedaria* Zone; Texas, *Aphelaspis* Zone.——FIG. 83,*2a,b.* **D. pannula* (WHITE), Pioche Shale, Nevada; *a,* holotype, ?ventral valve exterior, USNM 15331a, ×10; *b,* dorsal valve exterior, USNM 15333b, ×10 (new).——FIG. 83,*2c,d. D. hexagona* (BELL), lower Meagher Limestone, Montana; *c,* ventral valve exterior, ×5; *d,* syntype, detail of ornament, UM 20816a, ×15 (new).

Dictyonites COOPER, 1956, p. 187 [**D. perforata;* OD]. Transversely semiovate, ventribiconvex, posterior margin nearly straight; ventral valve pyramidal, ventral pseudointerarea clearly defined, high, procline, with homeodeltidium well developed; dorsal valve weakly convex; dorsal pseudointerarea very low, poorly defined, homeochilidium absent; shell deeply pitted or perforate, with depressions arranged radially on proximal portion of valve, irregularly on distal portion of valve, pits increasing in size distally. *Lower Ordovician–Upper Ordovician (Ashgill):* Montana, Kazakhstan, *Lower Ordovician;* Alabama, Sweden, *lower Middle Ordovician;* Ireland, *Ashgill.*——FIG. 84,*1a–d.* **D. perforata,* Pratt Ferry Formation, Alabama; *a,* holotype, ventral valve exterior, USNM 116830L, ×10; *b,c,* paratype, ventral valve in normal view, anteroventral view, USNM 116830J,

×10; *d,* paratype, dorsal valve exterior, USNM 116830I, ×10 (Cooper, 1956).

Kolihium Havlíček, 1982, p. 55 [**Kutorgina kolihai* Růžička, 1927, p. 5; OD]. Transversely semiovate, ventribiconvex with straight posterior margin; ventral valve pyramidal, with strong concentric rugae; ventral pseudointerarea clearly defined, catacline to procline, with large, strongly convex homeodeltidium; dorsal valve weakly convex with low, catacline pseudointerarea; homeochilidium narrow and strongly convex apically, broad and upturned distally; shell finely and densely pitted, with pits arranged radially, becoming larger distally. *Lower Ordovician (Tremadoc):* Czech Republic (Bohemia).——Fig. 84,*3a–c.* **K. kolihai* (Růžička), Trenice Formation, Holoubkov, Bohemia; *a,* dorsal valve exterior, NM L18129, ×8 (Havlíček, 1982); *b,c,* ventral valve internal mold in anteroventral view, posterior view, CGS VH816A, ×8 (new).

Lacunites Gorjansky, 1969, p. 103 [**L. balaschovae;* OD]. Semicircular in outline, ventribiconvex with straight posterior margin; ventral valve pyramidal; ventral pseudointerarea clearly defined, procline, with large, strongly convex homeodeltidium; dorsal valve weakly convex; dorsal pseudointerarea low; homeochilidium well defined; shell densely pitted with pits arranged radially and becoming larger distally. *Lower Ordovician (Tremadoc):* Southern Urals, northwestern Russia (St. Petersburg area), Czech Republic (Bohemia).——Fig. 84,*2a,b.* **L. balaschovae,* Leetse Horizon, St. Petersburg region; *a,* ventral valve exterior, normal view, ×4; *b,* holotype, ventral valve exterior, lateral view, CNIGR 247/9960, ×3 (Gorjansky, 1969).

Micromitra Meek, 1873, p. 479 [**Iphidea sculptilis* Meek, 1873, p. 479; OD] [=*Iphidella* Walcott, 1905, p. 304, *nom. nov. pro Iphidea* Billings, 1872, p. 477 (type, *I. bella;* OD), *non* Bayley, 1865; *Icodonta* Bell, 1941, p. 212 (type, *I. typica;* OD); ?*Walcottina* Cobbold, 1921, p. 334 (type, *W. lapworthi;* OD)]. Transversely ovate to subcircular, ventribiconvex; hinge line nearly straight; ventral pseudointerarea variably defined, high, apsacline, catacline or procline; homeodeltidium small to large; dorsal pseudointerarea usually well defined, low, anacline to catacline; homeochilidium small, apical; ornament of sharply defined, evenly spaced concentric fila, with or without fine radial costellae, which in some species break up the concentric fila into short segments that are usually convex adapically. *Lower Cambrian–Upper Cambrian:* Sweden, England, Yunnan, Anhui, British Columbia, Northwest Territories, Nova Scotia, *Lower Cambrian;* Siberia, Tien Shan, Kazakhstan, Kirghizia, Idaho, Montana, Nevada, Utah, Mexico, Greenland, Denmark (Bornholm), northeastern China, Inner Mongolia, Ningxia, Korea, New Zealand, Queensland, Northern Territory, New South Wales, *Amgaian;* Russian Asia, Kazakhstan, Antarctica, Missouri, Pennsylvania, Wyoming, *Upper Cambrian.*——Fig. 83,*3a–d.* **M. sculptilis* (Meek), Gallatin County, Montana; *a,* holotype, ventral valve exterior, USNM 7864a, ×10; *b,* posterior view of conjoined valves, UM 20818a, ×10; *c,* ventral valve exterior, normal view, ×10; *d,* ventral valve exterior, detail of ornament, UM 20814a, ×15 (new).

Family CRYPTOTRETIDAE Pelman, 1979

[Cryptotretidae Pelman, 1979, p. 38]

Hinge line straight, ventral pseudointerarea clearly defined, high, apsacline to orthocline, flat to concave; ornament of irregular growth lines; ventral mantle canal system probably pinnate; dorsal mantle canal system unknown. *Lower Cambrian (Tommotian–Botomian).*

Cryptotreta Pelman, 1977, p. 53 [**C. neguertchenensis;* OD]. Transversely ovate, biconvex with straight hinge line; ventral valve moderately convex with prominent beak; ventral pseudointerarea well defined, high, orthocline, with narrow median ridge; dorsal valve moderately convex; dorsal pseudointerarea very low; ornament of fine concentric growth lines, lamellose distally, with fine radial striae. *Lower Cambrian (Tommotian):* Russia (Siberian Platform).——Fig. 85*–d.* **C. neguertchenensis,* Aldan River, eastern Siberia; *a,* conjoined valves, dorsal view, ×10 (Pelman, 1977); *b,* conjoined valves, ventral view, IGiG 492/15, ×10 (new); *c,* holotype, conjoined valves, ventral view, IGiG 492/9/3-1, ×5; *d,* dorsal valve exterior, IGiG 492/15/8-1, ×10 (Pelman, 1977).

Aldanotreta Pelman, 1977, p. 51 [**A. sunnaginensis;* OD]. Transversely ovate, biconvex, ventral valve broadly sulcate, hinge line straight; ventral pseudointerarea well defined, high, apsacline; delthyrium open; dorsal pseudointerarea well defined, high, hypercline; ornament of irregularly developed, concentric growth lamellae and fine radial lirae. *Lower Cambrian (Tommotian):* Russia (Siberian Platform).——Fig. 86,*4a–c.* **A. sunnaginensis,* Aldan River, eastern Siberia; *a,b,* dorsal valve, dorsal, posterior view, IGiG 492/6/3-13, ×5; *c,* holotype, conjoined valves, anterior view, IGiG 492/7/2-3, ×7 (Pelman, 1977).

Askepasma Laurie, 1986, p. 449 [**A. toddense;* OD]. Subquadrate, ventribiconvex, ventral valve weakly, broadly sulcate, hinge line straight; ventral pseudointerarea well defined, high, slightly concave, apsacline; homeodeltidium absent; dorsal pseudointerarea well defined, planar, anacline to catacline; homeochilidium well developed, small, apical; ornament of irregularly developed, concentric growth lamellae; microornament of irregularly arranged, polygonal pits. *Lower Cambrian (Atdabanian):* Australia (Northern Territory, South Australia).——Fig. 86,*1a–e.* **A. toddense,* Todd River Dolomite, near Deep Well, Northern Territory; *a–c,* ventral valve exterior, interior, holotype, lateral view, CPC

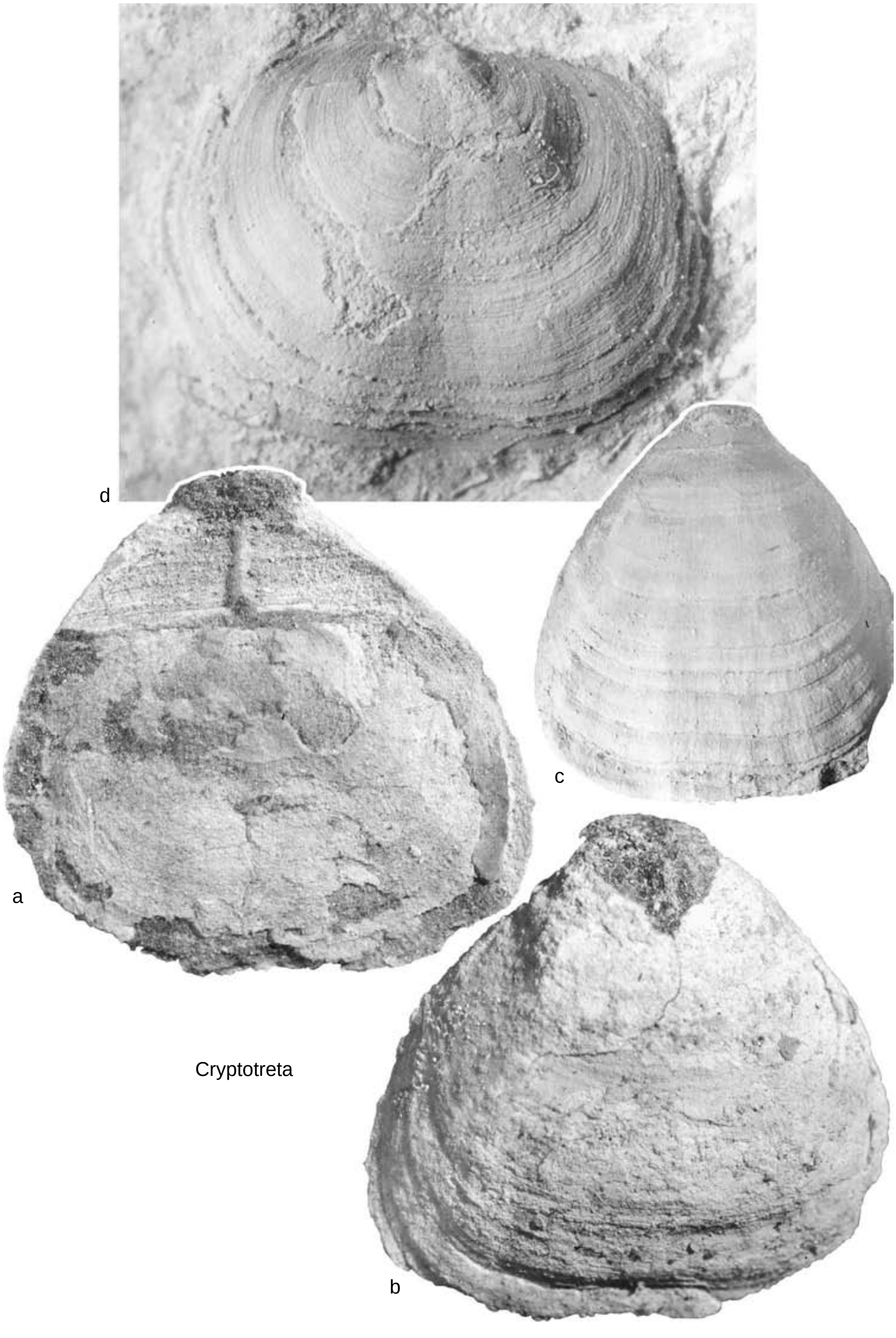

FIG. 85. Cryptotretidae (p. 153).

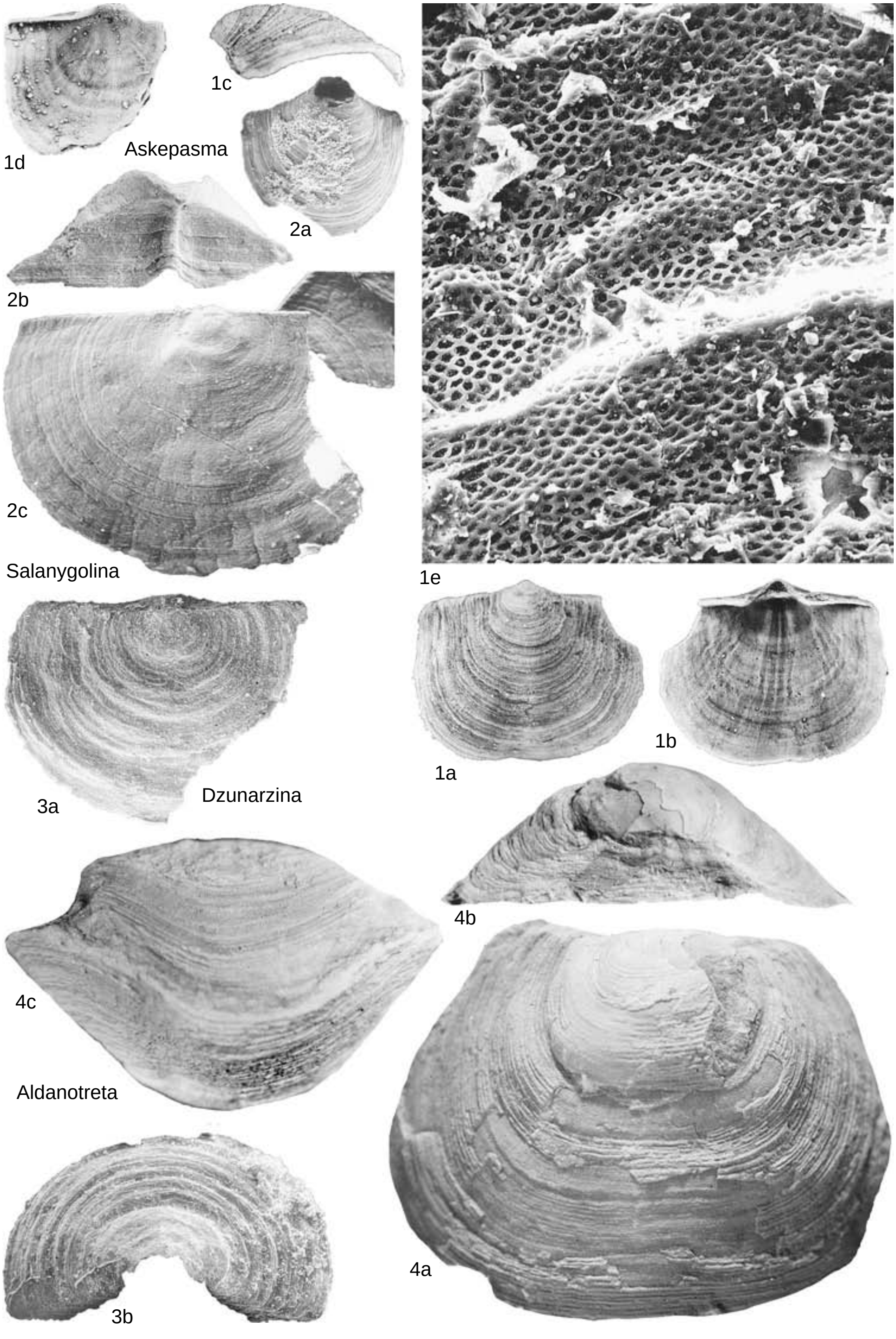

FIG. 86. Cryptotretidae (p. 153–156).

23642, ×5; *d,* paratype, dorsal interior, CPC 23656, ×5 (Laurie, 1986); *e,* detail of microornament, CPC 23726, ×200 (new).

Dzunarzina Ushatinskaya, 1993a, p. 116 [*D. elenae; OD]. Similar to *Askepasma* but smaller, with planar ventral pseudointerarea; hypercline dorsal pseudointerarea, broad, weakly convex homeochilidium; lacking both ventral sulcus and microornament of pits. *Lower Cambrian (Atdabanian):* western Mongolia.——Fig. 86,*3a,b.* **D. elenae,* Mount Dzun-Arza area, western Mongolia; a, dorsal valve exterior, PIN 3302/5049, ×22; b, ventral valve exterior, posterior oblique view, PIN 3302/5048, ×30 (Ushatinskaya, 1993a).

Salanygolina Ushatinskaya, 1987, p. 63 [**S. obliqua;* OD]. Semiovate with hinge line straight, long; ventral valve strongly convex; ventral pseudointerarea well defined, high, nearly flat, apsacline; homeodeltidium narrow, strongly convex, completely covering delthyrium; large supra-apical foramen present; dorsal valve weakly convex; pseudointerarea low, anacline; homeochilidium small, convex; ornament of uneven, discontinuous growth lines. *Lower Cambrian (Botomian):* western Mongolia.——Fig. 86,*2a–c.* **S. obliqua,* Salany-Gol Section, western Mongolia; *a,* holotype, ventral valve exterior, PIN 3302/5013, ×12; *b,* ventral valve, posterior view, PIN 3302/5014, ×18 (Ushatinskaya, 1987); *c,* dorsal valve exterior, PIN 3302/5019, ×25 (new).

BRACHIOPOD-LIKE FOSSILS

The following genera have at some time been referred to the Brachiopoda. The eponymous genus of the Tianzhushanellidae was assigned to the phylum with confidence by Liu (1979) while Conway Morris and Bengtson (in Bengtson & others, 1990) considered a brachiopod affinity possible. *Mickwitzia,* on the other hand, has long been considered a brachiopod (Linnarsson, 1869; Walcott, 1912; Rowell, 1965a; Goryansky, 1969; Rowell, 1977; McMenamin, 1992), commonly being referred to the Paterinida. The punctate, three-layered phosphatic shell, however, is unlike that of any other phosphatic brachiopod; consequently the genus is tentatively excluded from the Brachiopoda.

Family MICKWITZIIDAE
Goryansky, 1969

[Mickwitziidae Goryansky, 1969, p. 104]

Phosphatic, bivalved, one valve planar to slightly convex with submarginal apex, the other a low cone with apex at or near posterior margin, punctate. *Lower Cambrian.*

Mickwitzia Schmidt, 1888, p. 24 [**?Lingula monilifera* Linnarsson, 1869, p. 344; OD] [=*Causea* Wiman, 1902, p. 53 (type, *C. formosa;* OD)]. Characters as for family. *Lower Cambrian:* USA (California, Nevada), Canada (Alberta, British Columbia, Nova Scotia), Mexico, Sweden, Finland, Estonia, Lithuania.——Fig. 87,*1a–d.* **M. monilifera* (Linnarsson), Sweden; *a,* planar valve, exterior, normal view, ×2; *b,* planar valve, detail of punctation, RM Br 1592, ×8; *c,* convex valve, exterior, normal view, ×1; *d,* convex valve, lateral view, SGU Aa 172, ×1 (new).

Family TIANZHUSHANELLIDAE
Conway Morris, 1990

[Tianzhushanellidae Conway Morris in Bengtson & others, 1990, p. 164]

Probably calcareous, bivalved, biconvex, each valve with pair of recessed cavities near posterior end. *Lower Cambrian (Tommotian–Atdabanian).*

Tianzhushanella Liu, 1979, p. 508 [**T. ovata;* OD]. Genus poorly understood, not sufficiently illustrated. [Conway Morris (in Bengtson & others, 1990, p. 164) considered this to be closely related to, but distinct from *Apistoconcha* and *Aroonia.*] *Lower Cambrian (Tommotian):* Hubei, Shaanxi, China.

Apistoconcha Conway Morris in Bengtson & others, 1990, p. 171 [**A. apheles;* OD]. Interior of each valve has posterior plate with median or paired recesses and elongate toothlike structures, in one valve arcuately arranged about the midline, in the other, located laterally. *Lower Cambrian (Atdabanian):* Australia (South Australia).——Fig. 87,*3a,b.* **A. apheles,* Parara Limestone, Horse Gully; *a,* holotype, dorsal valve interior, SAM.P 30771, ×90; *b,* ventral valve interior, SAM.P 30777, ×60 (Bengtson & others, 1990).

Aroonia Bengtson in Bengtson & others, 1990, p. 181 [**A. seposita;* OD]. Interior of one valve with small conical median pit formed by inward deviation of posterior valve margin; other valve with bosslike callosity in corresponding position. *Lower Cambrian (Atdabanian):* Australia (South Australia).——Fig. 87,*2a,b.* **A. seposita* Bengtson, Ajax Limestone, Mount Scott Range; valve with posterior pit, exterior, holotype, interior, ×40, SAMP 30793 (Bengtson & others, 1990).

Other genera assigned to the Brachiopoda and not thus far shown to be otherwise include: *Scambocris* Liu, 1979, p. 507 (type, *S. hordeolu;* OD); *Acidotocarena* Liu, 1979, p. 507 (type, *A. oxyria;* OD); *Artimyctella* Liu,

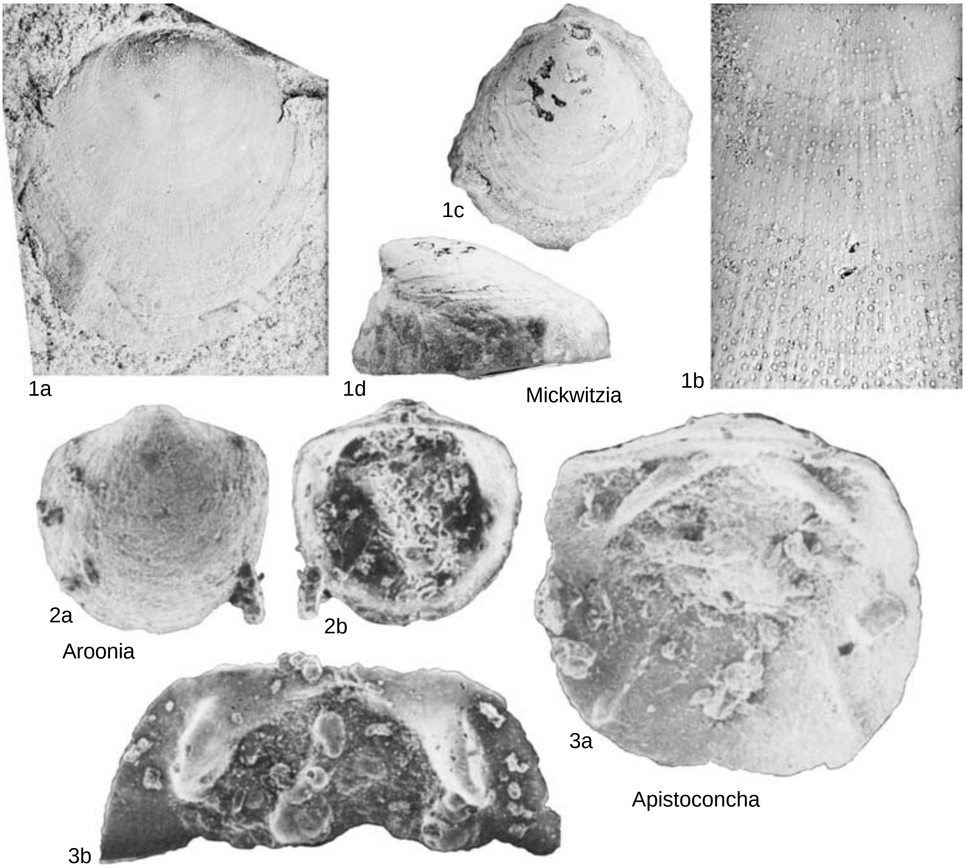

FIG. 87. Mickwitziidae and Tianzhushanellidae (p. 156).

1979, p. 508 (type, *A. yichangensis;* OD); *Protobolus* Liu, 1979, p. 508 (type, *P. olivaeformis;* OD); *Plicatolingula* Liu, 1979, p. 510 (type, *P. caelata;* OD); *Psamathopalass* Liu, 1979, p. 510 (type, *P. amphidoz;* OD); *Yuanjiapingella* Yue in Xing & others, 1984, p. 169 (type, *Y. longa;* OD); *Dolichomocelypha* Liu, 1987, p. 375 (type, *D. nympha;* OD); *Heosomocelypha* Liu, 1987, p. 372 (type, *H. elongata;* OD). All these genera are too poorly understood to be confidently assigned to any phylum.

CRANIIFORMEA

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Subphylum CRANIIFORMEA Popov & others, 1993

[*nom. transl. et correct.* WILLIAMS & others, 1996, p. 1192, *pro* subclass Craniformea POPOV & others, 1993, p. 2]

Brachiopods with calcitic or possibly aragonitic inarticulated shells with laminar (tabular) secondary layers; posterior body wall complete, inner mantle lobes not developed at valve margins, pedicle not developed, shell free lying or with encrusting ventral valve cemented by larval epithelium; muscle system with a single pair of internal oblique and with paired outside lateral muscles attached anteriorly to the body wall; alimentary tract more or less axial with anus medially on posterior body wall; lophophore initially with median tentacle lost during growth, tentacles in double row in post-trocholophous growth stages only; nervous system in base of epidermis with paired subenteric ganglia; mantle canal systems with *vascula terminalia* peripheral only, normally pinnate, containing gonads; larva lecithotrophic without shell. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Holocene.*

So far as is known, the unique feature of craniiforms is the tabular nature of the laminar secondary layer of the shell, which could also have been characteristic of the presumed aragonitic shells of trimerellides. Other features, which in combination are diagnostic of the subphylum Craniiformea, include the orthodoxly inarticulated condition of the shell (and its attendant muscle system) and the presence of an anus, which are typical of the linguliforms; shell composition and a single row of tentacles on the trocholophous lophophore, on the other hand, are shared with the rhynchonelliforms.

CRANIATA

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Class CRANIATA Williams & others, 1996

[Craniata WILLIAMS & others, 1996, p. 1192]

Characters as for subphylum. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Holocene.*

The classification of the calcareous-shelled inarticulated brachiopods has long been problematical; the trimerellides were assigned to the Lingulida and the craniides to the Acrotretida by ROWELL (1965a), while HELMCKE (1939) and HENNIG (1966) proposed that the morphology and anatomy of Holocene craniides indicate that they are more closely related to the articulated stocks now comprising the rhynchonellate and strophomenate members of the Rhynchonelliformea. The craniopsides have been referred by some authors to the Cranioidea (GORJANSKY, 1960; WILLIAMS, 1963) and by others to the Linguloidea (ROWELL, 1965a); COOPER (1956) placed them in the Paterulidae (within the Trimerelloidea). This confusing array of conflicting interpretations is probably due to the fact that it has been difficult previously to interpret the muscle scars on the extinct craniopsides and trimerellides, which have distinctive muscle platforms somewhat resembling those of some lingulide taxa such as *Lingulasma* and *Lingulops.* Moreover, the earliest evolutionary record of the three carbonate-shelled groups has been obscure; the earliest known true craniides, craniopsides, and trimerellides were long accepted as being from the Ordovician, making it possible to assume that they were derived from organophosphate-

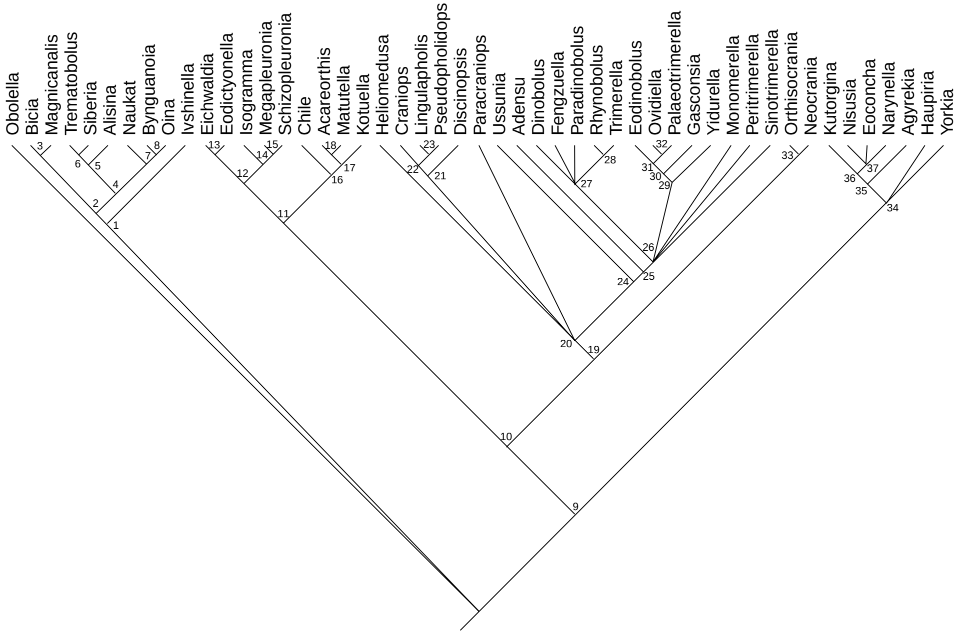

FIG. 88. Consensus tree (fifty-percent majority rule of 720 equally most parsimonious cladograms); numbered nodes supported by character states listed in Table 13 (new).

shelled ancestors at about that time (e.g., WILLIAMS & ROWELL, 1965b, fig. 141). A further problem has been the comparatively poor understanding of the ontogeny of the only surviving Holocene carbonate-shelled stock, the Craniida.

GORJANSKY and POPOV (1985, 1986), POPOV and others (1993), HOLMER and others (1995), and POPOV, HOLMER, and BASSETT (1996) proposed a classification in which the craniides, trimerellides, and craniopsides are sister groups within a monophyletic clade. Notwithstanding the equivocal relationships of the craniides as highlighted by some analyses (CARLSON, 1995; WILLIAMS & others, 1996), there is now a consensus of support for this model derived from a growing body of evidence (HOLMER & others, 1995; WILLIAMS & others, 1996). Support for this model now comes from a growing body of evidence: (1) the range of the nonpediculate, carbonate-shelled stocks has been extended down into the Lower Cambrian, through the discovery of the craniopside-like *Heliomedusa* from China (JIN & WANG, 1992); the problematical *Discinopsis* from the Middle Cambrian of Canada may also belong this group (POPOV, HOLMER, & BASSETT, 1996, p. 210); (2) the biochemistry of Holocene Craniida indicates that they may be quite unrelated to discinides and other organophosphate-shelled inarticulated brachiopods (JOPE, 1986; TUROSS & FISHER, 1989); (3) *Neocrania* lacks all trace of a pedicle throughout ontogeny, and the larva has no similarity to that of lingulides and discinides but is more similar to that of the articulated brachiopods in being lecithotrophic and lacking a protegulum and larval shell (NIELSEN, 1991); it is also clear that there is no trace of a larval shell and pedicle in the extinct trimerellides and craniopsides; (4) new, well-preserved material of trimerellides now shows that it is possible to interpret the muscle scars using Holocene craniides as a model (GORJANSKY & POPOV, 1985, 1986). It is also difficult to explain why the evolutionary transition from a phosphate-shelled

TABLE 13. List of coded characters used in cladistic analysis (Fig. 88) of carbonate-shelled inarticulated brachiopods (new).

1. outline: subcircular (0); elongate oval (1); transversely oval (2); elongate semioval (3); transversely semioval (4); transversely subrectangular (5).
2. profile: equibiconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); convexoplane (4).
3. anterior commissure: rectimarginate (0); sulcate (1); uniplicate (2); bisulcate (3).
4. radial ornamentation: smooth (0); smooth apically, costellate peripherally (1); costate (2); coarsely costellate (3); finelly costellate (4); striated (5).
5. concentric ornamentation: fila (0); fine rugae (1); strong rugae (2).
6. growth lamellae: absent (0); present (1).
7. pustulose-spinose ornamentation: absent (0); pustulose (1); spinose (2).
8. pitted ornamentation: absent (0); present (1).
9. posterior commissure: straight wide (0); straight short (1); broadly convex; (2); short, convex (3).
10. delthyrial-notothyrial opening: narrow delthyrium (0); wide delthyrium and notothyrium (1); absent (2).
11. growth of dorsal valve: hemiperipheral (0); holoperipheral or mixoperipheral (1).
12. concave homeodeltidium: absent (0); narrow (1); wide (2).
13. pseudodeltidium: absent (0); apical (1); large, convex (2); concave (3).
14. chilidium: absent (0); forming single plate (1); forming two plates (2).
15. trimerellid ventral cardinal area: absent (0); low (1); high (2); vestigial (3).
16. inclication of trimerellid ventral cardinal area: orthocline or anacline (0); apsacline (1).
17. ventral interarea (width-length): absent (0); low, less than 50% (1); high, more than 50% (2).
18. inclination of ventral interarea: anacline (0); orthocline (1); apsacline (2); procline to catacline (3).
19. dorsal interarea (width-length): absent (0); low, less than 50% (1); high, more than 50% (2).
20. inclination of dorsal interarea: anacline (0); orthocline (1).
21. ventral pseudointerarea: absent (0); poorly defined laterally (1); well defined laterally (2).
22. dorsal pseudointerarea: absent (0); poorly defined laterally (1); well defined laterally (2).
23. pedicle opening: absent (0); delthyrial (1); posterior to apex (2); apical (3); anterior to apex (4).
24. ventral umbonal perforation: absent (0); small, apical (1); enlarged through resorption (2).
25. paired denticles: absent (0); consisting of secondary shell, located on delthyrial margins (1); located on anterise (2); consisting partly of primary shell, located on delthyrial margins (3).
26. sockets: absent (0); on sides of notothyrial cavity (1).
27. furrows along lateral sides of pseudodeltidium: absent (0); present (1).
28. hinge socket: absent (0); vestigial (1); well developed (2).
29. hinge plate: absent (0); vestigial (1); well developed (2).
30. kutorginid articulation: absent (0); present (1).
31. sockets and socket ridges composed partly of primary shell: absent (0); present (1).
32. oblique lateral muscles: absent (0); present (1).
33. internal oblique muscles: attached posterolaterally to dorsal valve (0); attached posteromedianly, but not serving as diductors (1); attached posteromedianly, serving as diductors (2).
34. *levator ani*: absent (0); present (1).
35. ventral muscle platform: absent (0); solid (1); free anteriorly (2); slightly vaulted anteriorly (3); strongly vaulted anteriorly (4).
36. dorsal muscle platform: absent (0); solid (1); slightly vaulted anteriorly (2); strongly vaulted anteriorly (3).
37. umbonal cavities: absent (0); vestigial (1); well defined (2).
38. cardinal process: absent (0); present (1).
39. ventral median structure: absent (0); ridge (1); septum (2); groove (3).
40. dorsal median structure: absent (0); ridge (1); septum (2); groove (3).
41. notothyrial platform: absent (0); present (1).
42. ventral median ridge or septum anterior to visceral area: absent (0); present (1).
43. dorsal median ridge or septum anterior to visceral area: absent (0); present (1).
44. ventral mantle canals: pinnate (0); bifurcate (1); baculate (2).
45. ventral *vascula lateralia:* absent (0); present (1).
46. ventral *vascula media:* absent (0); present (1).
47. dorsal mantle canals: pinnate (0); bifurcate (1); baculate (2).
48. dorsal *vascula lateralia:* absent (0); present (1).
49. dorsal *vascula media:* absent (0); present (1).
50. dorsal secondary shell layer: laminar (0); fibrous (1); shell aragonitic (2).
51. endopunctation: absent (0); simple pores (1); bifurcating pores.
52. attachment scar: absent (0); cicatrix (1); encrusting (2).
53. colleplax: absent (0); present (1).
54. dorsal adductors: dispersed (0); radial (1); quadripartite (2).

ancestor to a carbonate shell in each of the three groups should have involved the repeated loss of a pedicle and larval shell; the change to an encrusting or free-lying mode of life occurred several times within the organophosphatic acrotretoids (*Eoconulus*) and linguloids (*Volborthia*), and in each of these groups traces of a pedicle and larval shell persist through ontogeny.

An analysis of 49 genera of carbonate-shelled brachiopods, including 23 trimerellides, craniopsides, and craniides, was performed using 54 unweighted, unordered characters, using the Obolellida as the root (Table 13, 15); these include the oldest known carbonate-shelled inarticulated brachiopods (PELMAN, 1977; POPOV, HOLMER, & BASSETT, 1996). Seven hundred twenty equally parsimonious trees 209 steps long were generated with a consistency index of 0.507 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The consensus tree (Fig. 88; Table 14) is highly unresolved but gives support to the identity of the Trimerellida and Craniida as monophyletic orders. The Craniopsida as defined here, however, is not supported as a monophyletic group in our cladistic analysis; it possibly represents a paraphyletic stem-group.

Using the model proposed by GORJANSKY and POPOV (1985), the musculature of the craniopsides and trimerellides may have been closely similar to that of Holocene *Neocrania,* consisting of paired anterior and posterior adductors, oblique internal, and an unpaired median muscle (*levator* and *protrusor ani*); the oblique lateral muscles attached dorsally to the anterior body wall. In most craniiforms, the latter muscles may have served as a diductor by creating hydrostatic pressure in the body cavity, comparable with the model proposed erroneously by GUTMANN, VOGEL, and ZORN (1978) for the lingulides. Only the trimerellides seem to have developed a system with a diductor muscle analogous with that in rhynchonelliform articulated brachiopods (GORJANSKY & POPOV, 1985).

TABLE 14. Synapomorphy scheme for internal nodes of cladogram shown in Figure 88 (new).

Node	Character states						
1	25:3	35:1					
2	40:1						
3	1:1						
4	13:3	23:2	25:1	26:1	39:0		
5	2:2	6:1	23:3	54:2			
6	4:0	35:0	39:3				
7	1:2	4:2	25:2				
8	2:1						
9	4:0	39:0	41:0	44:0	46:1	47:0	50:1
10	19:0	20:0	32:1	51:1			
11	1:4	9:0	24:2	53:1			
12	32:0	38:2	40:2	43:1			
13	1:3	9:3	13:3	39:2			
14	2:3	5:2	18:0				
15	1:5	4:2	41:1				
16	2:1	11:0	33:1				
17	1:5	3:2					
18	4:2	53:0					
19	10:2	17:0	23:0	33:0	34:1	50:0	54:0
20	1:1	9:3	44:2	47:2	51:0		
21	35:1	36:1					
22	6:1						
23	21:1	22:1					
24	9:2	12:2	15:1	28:1	29:1	33:1	50:2
25	2:1	28:2	29:2	33:2	39:1		
26	12:1	35:3	36:2	43:1			
27	37:1	39:0	42:1				
28	12:2	35:4	36:1				
29	1:2	36:1					
30	6:1	35:1	43:0				
31	16:0	39:0	49:0				
32	1:0	15:2	44:1	47:1			
33	40:1	46:0					
34	9:2	10:1	13:2	27:1	30:1	45:0	48:0
35	17:2	20:1					
36	1:5	2:2	7:1	24:1			
37	3:1	4:4	7:2	9:0	31:1	41:1	

The mantle canal system of many craniiforms is relatively poorly known; it has been described from most craniides and a few trimerellides, but with the exception of the problematical *Heliomedusa* it is completely unknown for the craniopsides. Holocene craniides have only a single pair of main trunks in both valves, corresponding to the *vascula lateralia,* but some Lower Paleozoic forms (e.g., *Pseudocrania;* Fig. 89) have a dorsal *vascula media.* The trimerellides appear to have a mantle canal system similar to that of

TABLE 15. Character-state matrix used in PAUP analysis (Fig. 88) of characters as listed in Table 13. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Obolella	0	0	0	5	0	1	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	0	0	0
Bicia	1	0	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	3	0	0
Ivshinella	0	1	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	3	0	0
Magnicanalis	1	0	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	9	0	0
Trematobolus	0	2	0	0	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	4	0	1	1	0
Alisina	0	2	0	5	0	1	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	3	0	1	1	0
Siberia	0	2	0	0	0	1	0	0	1	0	1	0	3	0	0	9	1	3	1	1	0	0	3	0	1	1	0
Naukat	2	0	2	2	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	2	0	2	1	0
Bunguanoia	2	1	1	2	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	2	0	2	1	0
Oina	2	1	0	0	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	0	0	2	1	0
Eichwaldia	3	0	0	0	0	0	0	0	3	0	1	0	3	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Dictyonella	3	0	0	0	0	1	0	1	3	0	1	0	3	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Isogramma	4	3	0	0	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Megapleuronia	5	3	0	2	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Schizopleuronia	5	3	1	2	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Chile	4	2	0	1	0	0	0	0	0	0	0	0	1	0	0	9	1	1	0	9	0	0	1	2	0	0	0
Acareorthis	5	3	3	2	0	1	0	0	0	0	0	0	2	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Matutella	5	1	2	4	0	0	0	0	0	0	0	0	0	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Kotuella	5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Kutorgina	6	2	0	0	2	1	1	0	2	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Yorkia	0	0	0	0	0	0	0	0	2	1	1	0	2	0	0	9	1	2	1	1	0	0	1	1	0	0	1
Haupiria	0	0	0	0	0	0	0	0	2	1	1	0	2	0	0	9	1	2	1	1	0	0	1	0	0	0	1
Agyrekia	0	0	0	5	1	0	0	0	2	1	1	0	2	1	0	9	2	3	2	0	0	0	1	0	0	0	1
Nisusia	5	2	0	4	0	0	2	0	0	1	1	0	2	0	0	9	2	3	1	0	0	0	1	1	0	0	1
Eoconcha	5	2	1	3	0	0	0	0	0	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Narynella	5	2	1	4	0	0	2	0	0	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Heliomedusa	0	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	0	0	0	0	0	9
Craniops	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Discinopsis	0	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Lingulapholis	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	1	0	0	0	0	9
Paracraniops	1	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Pseudopholidops	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	1	0	0	0	0	9
Ussunia	1	0	0	0	0	0	0	0	2	2	1	2	9	9	3	1	0	9	0	9	0	0	0	0	0	0	9
Adensu	1	1	0	0	0	0	0	0	2	2	1	2	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Dinobolus	0	0	0	0	0	1	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Eodinobolus	2	1	0	0	0	1	0	0	2	2	1	1	9	9	1	0	0	9	0	9	0	0	0	0	0	0	9
Fengzuella	0	1	0	0	0	0	0	0	2	2	1	1	9	9	1	9	0	9	0	9	0	0	0	0	0	0	9
Gasconsia	2	4	0	0	0	1	0	0	0	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Monomerella	1	1	0	0	0	1	0	0	2	2	1	2	9	9	2	1	0	9	0	9	0	0	0	0	0	0	9
Ovidiella	0	1	0	0	0	1	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Palaeotrimerella	1	1	0	0	0	1	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Paradinobolus	1	1	0	0	0	0	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Peritrimerella	0	4	0	0	0	0	0	0	2	2	1	2	9	9	1	9	0	9	0	9	0	0	0	0	0	0	9
Rhynobolus	1	1	0	0	0	0	0	0	2	2	1	2	9	9	2	1	0	9	0	9	0	0	0	0	0	0	9
Sinotrimerella	1	1	0	0	0	0	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Trimerella	1	1	0	0	0	0	0	0	2	2	1	2	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Yidurella	2	0	0	0	0	0	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Orthisocrania	0	0	0	3	0	0	0	0	1	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Neocrania	0	4	0	0	0	0	0	0	1	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9

the craniides, but it differs in some genera (*Palaeotrimerella*) that have *vascula media* in the ventral valve, while others (*Monomerella* and *Gasconsia*) appear to have *vascula media* in both valves (HOLMER & POPOV in WILLIAMS, BRUNTON, & MACKINNON, 1997, fig. 386.2).

Heliomedusa is characterized by the presence of dorsal *vascula media* and *vascula lateralia;* the ventral mantle canals are poorly known, but apparently the *vascula lateralia* are developed (JIN & WANG, 1992).

Marginal mantle setae were long thought to be absent in craniides, but NIELSEN (1991) has now demonstrated their presence in juvenile *Neocrania.* Firm evidence of setae is generally lacking for most fossil craniiformeans, but they have been described from *Helio-*

TABLE 15. *(Continued).*

Character no.	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Obolella	0	0	0	0	9	1	0	0	0	0	0	3	0	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Bicia	0	0	0	0	9	2	0	1	0	0	0	3	1	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Ivshinella	0	0	0	0	9	2	0	1	0	0	0	3	0	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Magnicanalis	0	0	0	0	9	2	0	1	0	0	0	1	1	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Trematobolus	0	0	0	0	9	2	0	0	0	0	0	3	1	1	0	0	2	1	0	2	1	1	0	0	0	1	2
Alisina	0	0	0	0	9	2	0	1	0	0	0	0	1	1	0	0	2	1	0	2	1	1	9	0	0	0	2
Siberia	0	0	0	0	9	2	0	0	0	0	0	3	1	1	0	0	2	1	0	2	1	1	9	0	0	0	2
Naukat	0	0	0	0	0	2	0	1	1	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Bunguanoia	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Oina	0	0	0	0	0	2	0	2	0	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Eichwaldia	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	1	9	9	9	9	9	9	9	9	0	1	9
Dictyonella	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	1	9	9	9	9	9	9	1	1	0	1	9
Isogramma	0	0	0	0	0	2	0	0	0	0	1	0	2	0	0	1	9	9	9	9	9	9	9	9	0	1	9
Megapleuronia	0	0	0	0	0	2	0	9	3	0	1	9	1	1	0	1	9	9	9	0	9	9	9	9	0	1	9
Schizopleuronia	0	0	0	0	0	2	0	0	0	0	1	0	2	1	0	1	9	9	9	9	9	9	9	9	0	1	9
Chile	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	9	9	9	1	9	9	9	0	1	1
Acareorthis	0	0	0	0	9	1	0	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	9
Matutella	0	0	0	0	9	9	0	0	0	0	0	0	0	0	0	0	0	9	9	0	9	9	9	9	0	0	9
Kotuella	0	0	0	0	9	9	0	0	9	0	9	0	0	9	0	9	9	9	9	9	9	9	1	1	0	1	9
Kutorgina	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	1
Yorkia	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	9	0	1	0	0	9	9	9	0	0	9
Haupiria	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	9
Agyrekia	0	0	1	0	9	2	0	0	0	0	0	0	1	0	0	0	9	9	9	0	9	9	9	9	0	0	1
Nisusia	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0	9	9	0	9	9	1	0	0	0	1
Eoconcha	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	9	9	9	9	9	9	9	0	0	0	9
Narynella	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0	9	9	0	9	9	1	0	0	0	1
Heliomedusa	0	0	9	9	1	0	9	0	0	0	0	0	0	0	0	0	2	1	9	2	1	1	9	9	0	0	0
Craniops	0	0	9	9	1	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	0	0	1	0	0
Discinopsis	0	0	9	9	9	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	0
Lingulapholis	0	0	9	9	1	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Paracraniops	0	0	9	9	1	0	9	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Pseudopholidops	0	0	9	9	1	0	9	0	0	0	0	1	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Ussunia	1	1	9	9	1	1	1	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	2	9	0	0	0
Adensu	2	2	9	9	0	2	1	0	0	0	0	1	0	0	0	0	0	1	1	9	9	9	2	9	0	0	0
Dinobolus	2	2	9	9	1	2	1	4	2	1	0	0	0	0	1	1	9	9	9	2	1	9	2	9	0	0	0
Eodinobolus	2	2	9	9	1	2	1	1	1	0	0	0	0	0	0	0	2	1	1	2	1	0	2	9	0	0	0
Fengzuella	2	2	9	9	9	2	9	3	2	1	0	1	1	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Gasconsia	1	1	9	9	1	2	1	1	1	0	0	1	0	0	0	0	2	1	9	2	1	1	2	9	0	0	0
Monomerella	2	2	9	9	1	2	1	1	2	2	0	1	0	0	0	1	2	1	1	9	9	9	2	9	0	0	0
Ovidiella	2	2	9	9	1	2	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	2	9	0	0	0
Palaeotrimerella	2	2	9	9	1	2	1	1	1	0	0	1	1	0	0	1	1	1	1	1	1	0	2	9	0	0	0
Paradinobolus	2	2	9	9	9	2	9	3	2	1	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Peritrimerella	2	2	9	9	9	2	9	3	2	0	0	0	0	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Rhynobolus	2	2	9	9	9	2	9	4	1	1	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Sinotrimerella	2	2	9	9	9	2	9	3	2	0	0	9	0	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Trimerella	2	2	9	9	1	2	1	4	3	2	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Yidurella	2	2	9	9	9	2	9	3	1	0	0	1	1	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Orthisocrania	0	0	9	9	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0
Neocrania	0	0	9	9	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	2	0	0

medusa (JIN & WANG, 1992). JIN and WANG (1992) concluded that *Heliomedusa* might be an early representative of a lineage of nonpediculate brachiopods independent from that of the lingulides. With the model adopted here it is likely that the morphology of such a craniopside-like brachiopod may have been close to that of the earliest common ancestor of the craniiforms.

The main radiation of the craniiforms apparently took place during the Early Ordovician, although their origin remains obscure. The Trimerellida tend to form large, heavy shells that appear to have been aragonitic in composition (JAANUSSON, 1966). This group also has a unique articulatory structure, consisting of a dorsal hinge plate fitting tightly into a ventral cardinal socket.

This type of morphology is present already in the earliest trimerellides, the Ussuniidae of Llandeilo age; these shells are among the largest known Ordovician brachiopods. According to GORJANSKY and POPOV (1986) the Ussuniidae may be related closely to the craniopsides, and although the former can be over ten times larger than the latter, they show similarities in the shape of the pseudointerareas as well as the development of the visceral areas and main muscle scars.

CRANIOPSIDA

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Order CRANIOPSIDA Gorjansky & Popov, 1985

[Craniopsida GORJANSKY & POPOV, 1985, p. 12]

Shell biconvex, elongate oval to subcircular; visceral area of both valves extending anterior to midvalve; scars of dorsal oblique internal muscles situated posterolaterally; cemented at apical region of ventral valve, or free lying; shell calcitic, impunctate. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

The morphology of craniopsides is simple, and taxa within the order can be defined only on characters such as the presence or absence of pseudointerareas, visceral platforms, median ridges, position of the umbo, and presence of attachment scar (cicatrix). The shell is usually equally biconvex, with the umbo situated marginally or posteriorly. Only some craniopsids (*Lingulapholis, Pseudopholidops*) have well-developed pseudointerareas.

The craniopside muscle system is here modeled after that of the Craniida (Fig. 90); however, alternative reconstructions, based mainly on the pattern of muscles present in lingulides, have also been proposed. MERGL (1986), for example, suggested that the unpaired posteromedian scar might correspond to the lingulide umbonal muscle, but with the view adopted here it corresponds to the unpaired median muscle (*levator* and *protrusor ani*) of craniides (Fig. 90). According to MERGL, the remaining three paired dorsal and four ventral muscle scars can be correlated with the lingulide transmedian, anterior lateral, middle lateral, and central muscle scars; but the transmedian and central scars are also comparable with the craniide anterior and posterior adductors; the dorsal middle lateral scars may correspond to the craniide internal oblique muscles that were attached to the anterior part of the ventral median ridge. The ventral anterior lateral scars may have represented the oblique lateral muscles that were attached to the anterior body wall, while the dorsal anterior lateral may be similar to the brachial protractor muscles of craniides (Fig. 90).

Superfamily CRANIOPSOIDEA Williams, 1963

[*nom. transl.* HARPER in HARPER & others, 1993, p. 430, *ex* Craniopsidae WILLIAMS, 1963, p. 346]

Characters as for order. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

Family CRANIOPSIDAE Williams, 1963

[Craniopsidae WILLIAMS, 1963, p. 346] [=Pholidopsidae GORJANSKY, 1960, p. 177]

Characters as for superfamily. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

Craniops HALL, 1859b, p. 84 [**?Orbicula squamiformis* HALL, 1843a, p. 108; OD] [=*Pholidops* HALL, 1859a, p. 489, obj.]. Shell subequally biconvex, elongate oval, lamellose; both valves with growth holoperipheral, umbones posterior to center; visceral areas of both valves elevated anteriorly, forming low platforms; both valves with limbus; attached apically by cementation. *Ordovician (Caradoc)–Lower Carboniferous (Tournaisian):* Canada, *?Upper Ordovician, Silurian–Devonian;* USA, *?Upper Ordovician, Silurian–Tournaisian;* Poland, *Caradoc–Silurian;* China, Australia, Brazil, *Silurian–*

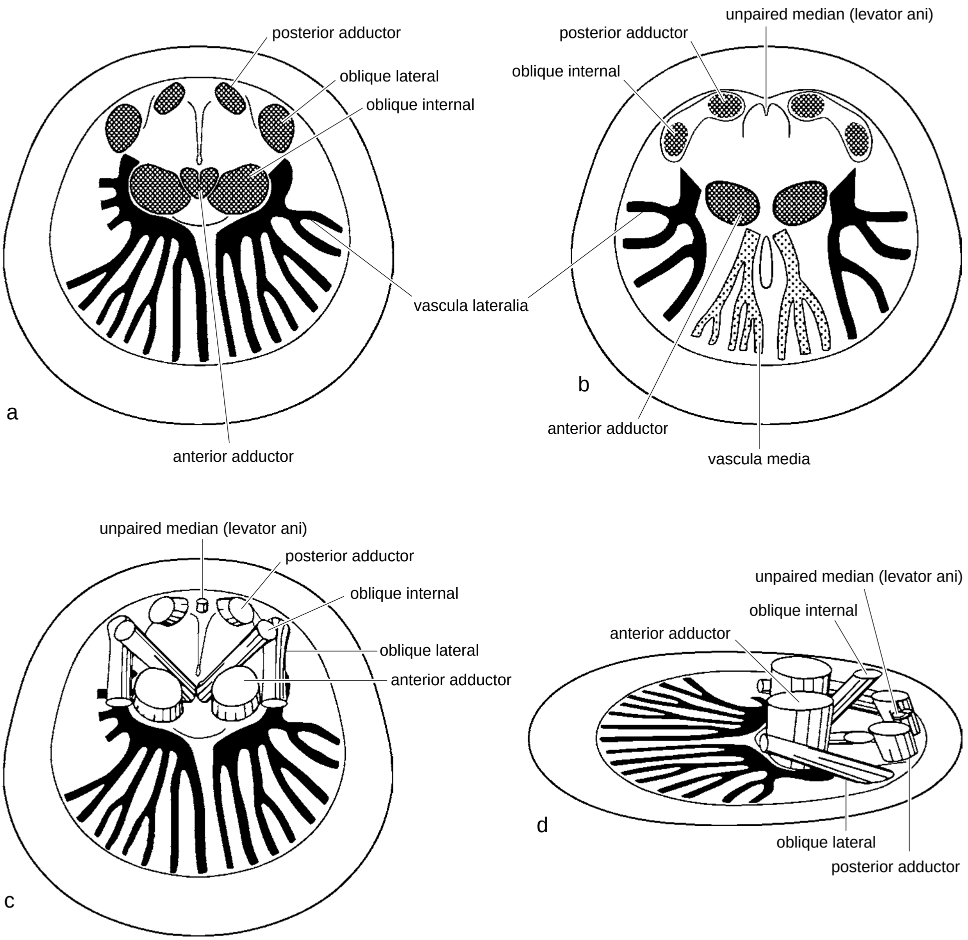

FIG. 89. Schematic illustration of musculature and mantle canal system of *Pseudocrania; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (Bassett, new).

Devonian; Portugal, Great Britain, Sweden, Bohemia, Estonia, *Silurian;* Colombia, *Devonian.* ——FIG. 91,*3a–e. C. implicata* (SOWERBY), Wenlock, Mulde beds, Fröjel, Gotland, Sweden; *a,* dorsal valve exterior, RM Br 24306a, ×15; *b,* lateral view of both valves, RM Br 24306b, ×25; *c,* ventral valve interior, ×19.2; *d,* oblique lateral view of ventral interior, RM Br 24306c, ×37.5; *e,* dorsal valve interior, RM Br 24306d, ×26.7 (new).

?Discinopsis MATTHEW in HALL & CLARKE, 1892, p. 105 [**?Acrotreta gulielmi* MATTHEW, 1886, p. 37; OD]. Genus inadequately known; shell probably biconvex, flattened, subcircular; growth apparently holoperipheral in both valves, umbones posterior to center; interiors of both valves poorly known, but with low visceral platforms bounded laterally by ridges. *Middle Cambrian:* Canada (New Brunswick).——FIG. 91,*1a–c. *D. gulielmi* (MATTHEW), Seely Limestone, New Brunswick (St. John), Canada, paralectotypes; *a,* internal mold, ROM 642CM(D); *b,* external mold, ROM 642CM(F); *c,* internal mold, ROM 642CM(E), ×8.3 (new).

?Heliomedusa SUN & HOU, 1987, p. 261[269] [**H. orienta;* OD]. Shell biconvex, inequivalved, subcircular; mixoperipheral growth in ventral valve, with beak marginal, and well-defined pseudointerarea; holoperipheral growth in dorsal valve, apex placed posterior to center; visceral area of both valves thickened slightly anteriorly, extending anterior to center; mantle canal system of both valves baculate; dorsal mantle canals with *vascula media* and *vascula lateralia. Lower Cambrian (?Botomian):* China (Yunnan).——FIG. 92,*1a–d. *H. orienta,* Chiungchussu Formation, Chengjiang; *a,* internal cast of both valves, NIGP 113927, ×2.5; *b,* dorsal internal mold, NIGP 100301, ×6.7; *c,* dorsal internal mold, NIGP 113930, ×6.7; *d,* setae around the margin of dorsal and ventral valves, NIGP 100282, ×6.7 (Jin & Wang, 1992).

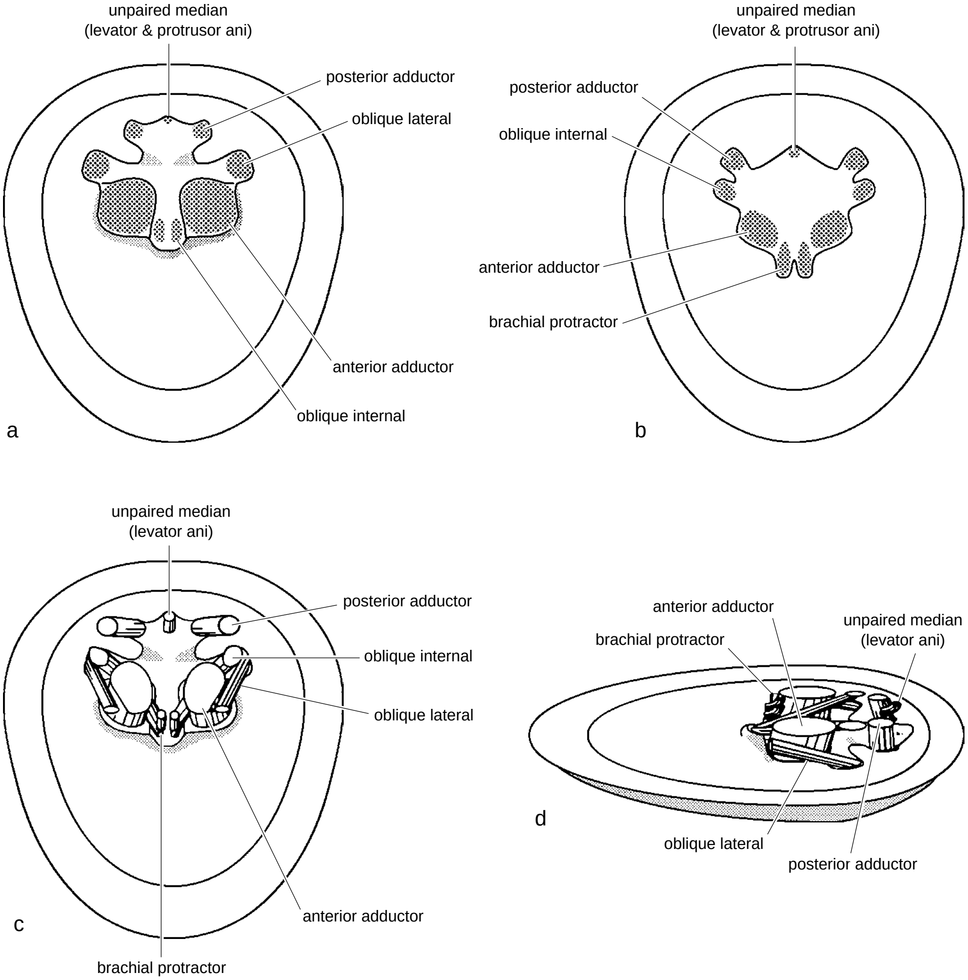

FIG. 90. Schematic illustration of musculature of *Craniops; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

Lingulapholis SCHUCHERT, 1913b, p. 295 [**Pholidops terminalis* HALL, 1859a, p. 490; OD]. Shell subequally biconvex, elongate oval, lamellose; mixoperipheral growth in both valves, marginal beaks, and well-developed pseudointerareas; visceral areas of both valves elevated anteriorly, forming low platforms; both valves with limbus; free lying. *Devonian:* USA, Colombia.——FIG. 91,*2a.* **L. terminalis* (HALL), Becraft Mountain, New York (Hudson), USA; cast of dorsal internal mold, NYSM 1745, ×4.2 (new).——FIG. 91,*2b–f. L. calceola* (HALL & CLARKE), Camden Chert Quarry, Tennessee, USA; *b,* ventral valve exterior, USNM 459665c, ×8.3; *c,* ventral valve interior, USNM 459665d, ×10; *d,e,* dorsal valve exterior, oblique lateral view, USNM 459665a, ×10; *f,* dorsal valve interior, USNM 459665b, ×10 (new).

Paracraniops WILLIAMS, 1963, p. 346 [**Craniops pararia* WILLIAMS, 1962, p. 88; OD]. Externally similar to *Craniops,* but lacking cicatrix and dorsal visceral platform; dorsal interior with two low ridges. *Ordovician (Caradoc)–Silurian (Llandovery):* Turkey, China, *Caradoc;* Kazakhstan, *Caradoc–Llandovery;* Great Britain, *Caradoc–?Llandovery;* Sweden, Russia (Taimyr), *Ashgill;* Canada (Nova Scotia), *Llandovery.*——FIG. 92,*2a–c.* **P. pararia* (WILLIAMS), Lower Ardmillan Series, Girvan, Scotland; *a,* paratype, ventral internal mold, BMNH BMNH 29799, ×8.3; *b,* paratype, dorsal external mold, ×8.3; *c,* holotype, dorsal internal mold, BMNH BB 26709, ×8.3 (Williams, 1962).

Pseudopholidops BEKKER, 1921, p. 64 [**Pholidops scutellata;* OD] [=*Sanxiaella* RONG & CHANG in CHANG, 1981, p. 558[565] (type, *Paracraniops*

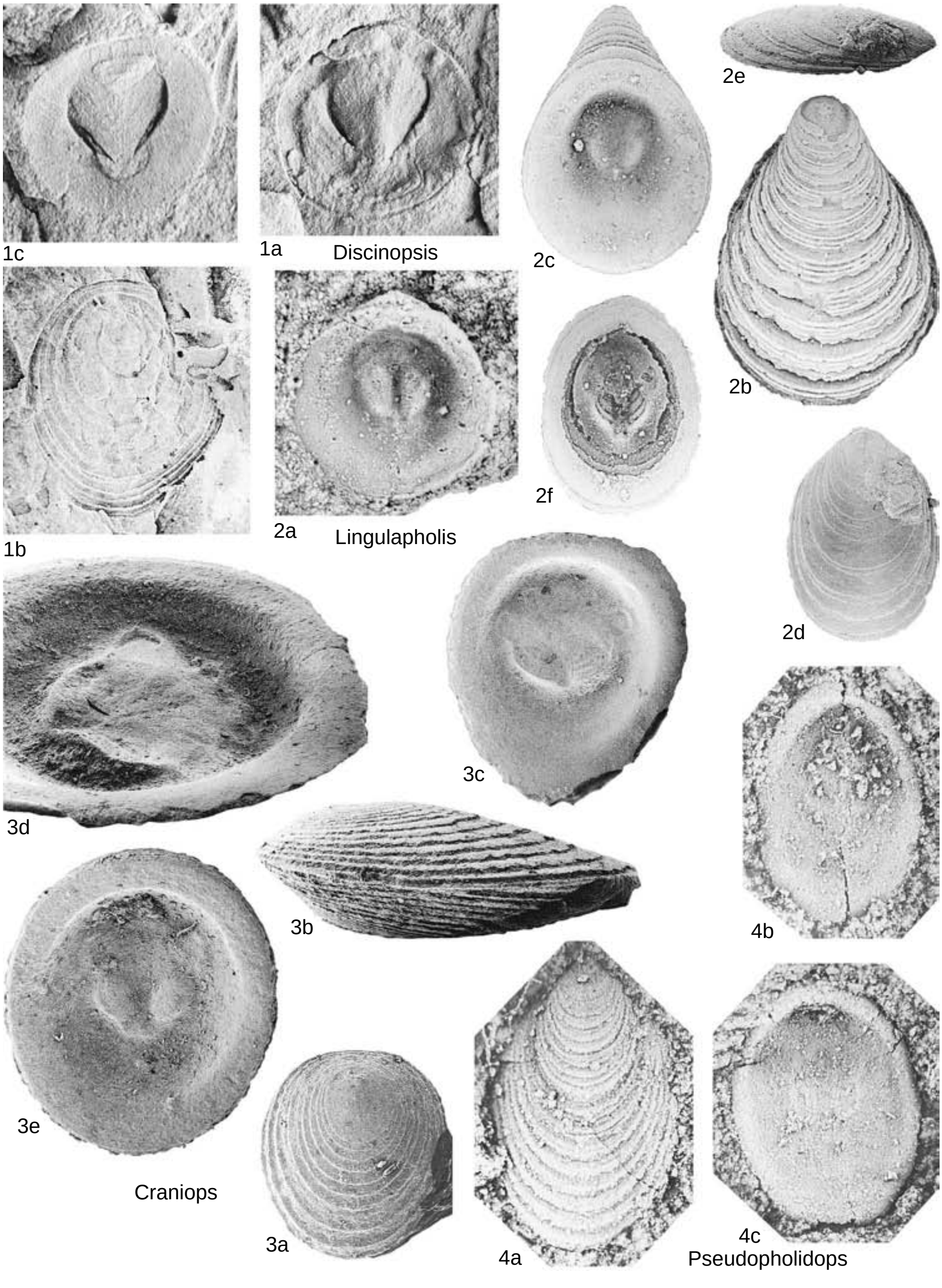

FIG. 91. Craniopsidae (p. 164–167).

partibilis RONG, 1979, p. 2)]. Externally like *Lingulapholis,* but with ventral median ridge and less thickened visceral areas. *Ordovician (Llandeilo–Ashgill):* Estonia, Lithuania, Bohemia, China.——FIG. 91,*4a–c.* **P. scutellata* (BEKKER), Kohtla-Järve, Estonia; *a,* dorsal valve exterior, TAGI BR 3507, ×17.5; *b,* dorsal valve interior, TAGI BR 3508, ×15.8; *c,* ventral valve interior, TAGI BR 3509, ×16.7 (new).

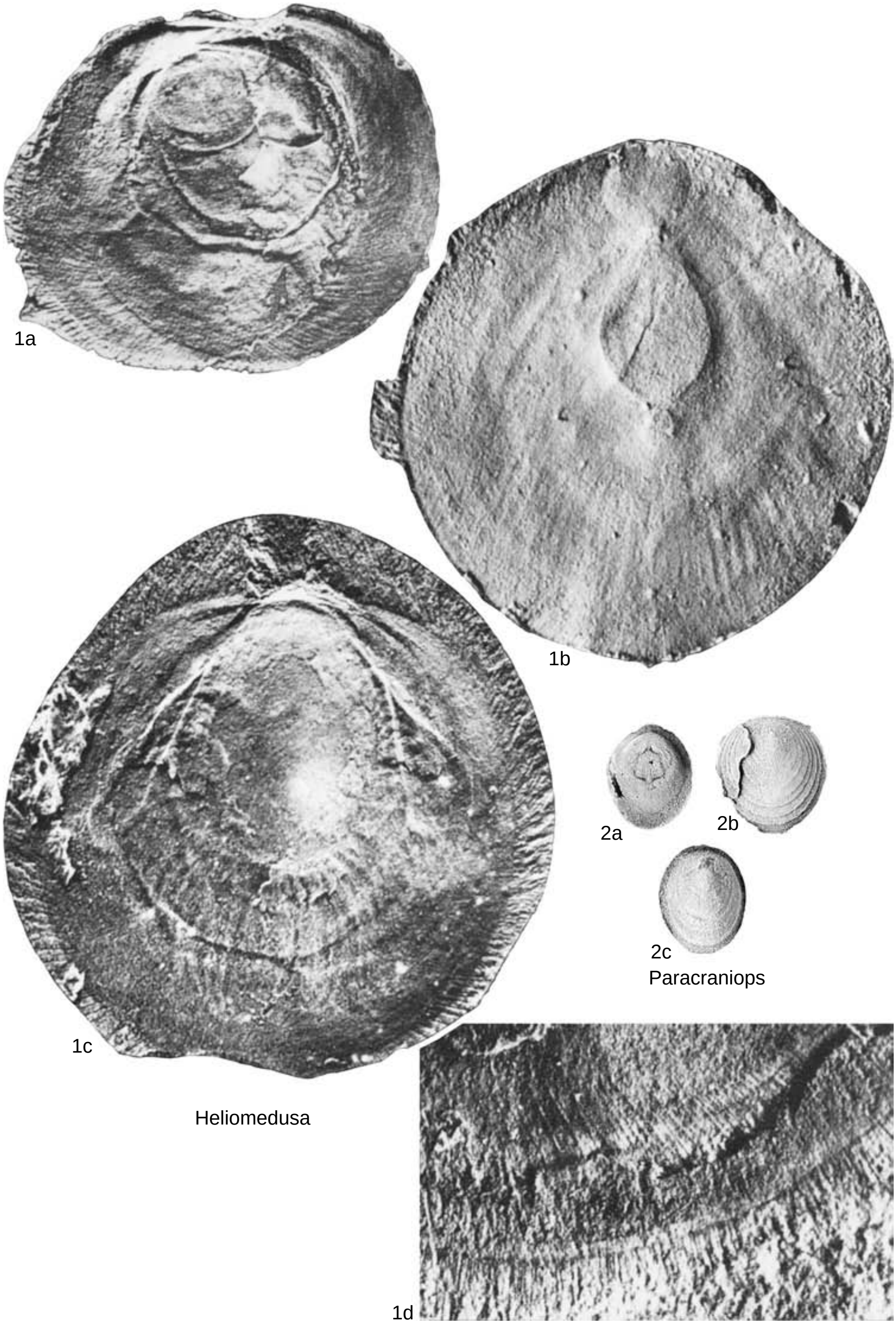

FIG. 92. Craniopsidae (p. 165–166).

CRANIIDA

MICHAEL G. BASSETT

[National Museum of Wales]

Order CRANIIDA Waagen, 1885

[*nom. transl. et correct.* KUHN, 1949, p. 99, *ex* suborder Craniacea WAAGEN, 1885, p. 744] [=Gasteropegmata WAAGEN, 1885, p. 744, *partim;* Gastropegmata HALL & CLARKE, 1894a, p. 326, *partim;* Craniidina ROWELL, 1965a, p. 288, *partim*]

Dorsal valve invariably calcified, punctate; ventral valve in some taxa without secondary shell or entirely periostracal; mantle setae present in recent forms; shell growth generally holoperipheral, rarely mixoperipheral; dorsal valve convex to subconical, ventral valve plane to convex or encrusting; dorsal body wall of recent forms attached to dorsal valve in five separate areas; attachment scars of dorsal internal oblique muscles situated posterolaterally; mantle canal system pinnate, only rarely with *vascula media. Ordovician (upper Arenig)–Holocene.*

The earlier record of a single species of craniide from the Middle Cambrian (*?Crania columbiana* WALCOTT, 1889) is now known to be unfounded (BASSETT, unpublished). In the oldest known genus (*Pseudocrania*) from the Lower Ordovician, the pattern of the musculature and vascular system (Fig. 93) already heralds that of recent *Neocrania* and indicates a remarkably stable anatomical organization throughout the preserved history of the group.

Similar stability is recorded in the structural evolution of the dorsal valve, composed of primary acicular and secondary laminar calcitic layers permeated by punctae, and whose fabric is probably close to that of the craniide ancestor (WILLIAMS & WRIGHT, 1970). By contrast, the history of ventral shell secretion displays considerable variation, including the loss of punctation in one genus (*Petrocrania*). Such variation was initiated following the loss of a pedicle in the craniide prototype and the subsequent adoption of a ventrally cemented or encrusting mode of life by some genera (WILLIAMS & WRIGHT, 1970, p. 48; see also below).

NIELSEN's (1991) study of larval development in *Neocrania* confirms that a pedicle is

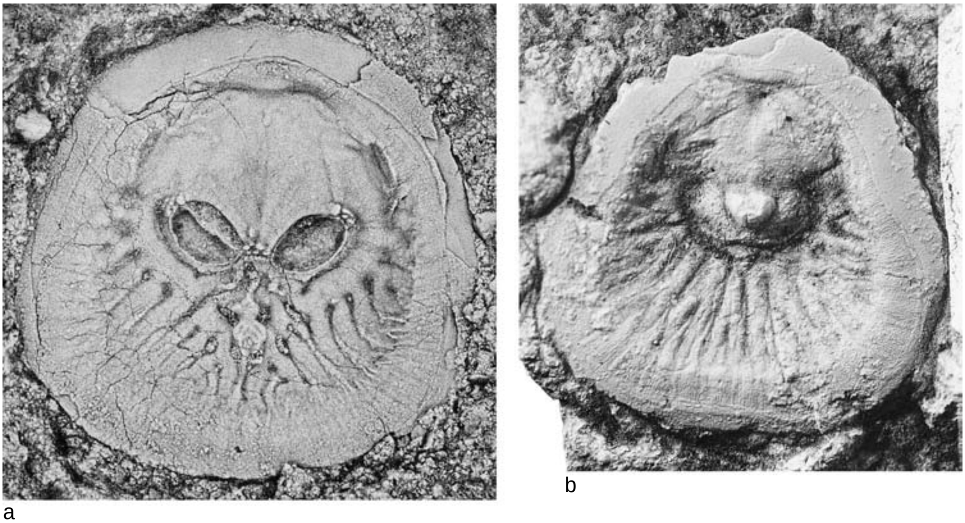

FIG. 93. Dorsal and ventral musculature and vascular systems of *Pseudocrania petropolitana* (PANDER); *a,* dorsal interior, Volkhov, Ordovician, Hälluden, Öland, Sweden, RM Br15082, ×2.7 (new); *b,* ventral interior, Volkhov, Ordovician, Voronino, Ingria, Russia, VSEGEI 113/9960, ×3 (Gorjansky, 1969).

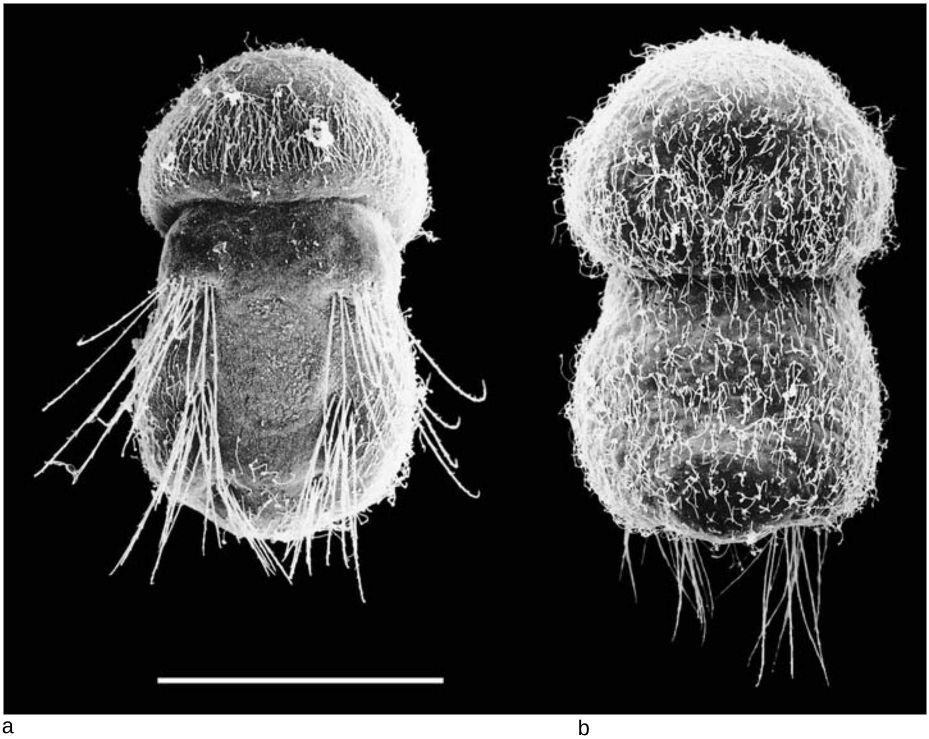

FIG. 94. Fully grown larvae of *Neocrania anomala* (MÜLLER) in *a,* dorsal and *b,* ventral views, showing setae and absence of larval shell; Holocene, off west coast of Sweden, scale bar: 100 mm (Nielsen, 1991).

lacking throughout ontogeny, and that, as in articulated brachiopods, no larval shell is developed (Fig. 94). His identification of marginal larval setae (Fig. 95) gives strong support to the view of brachiopod monophyly. The complex metamorphosis involved in larval development and settlement includes some change in direction of alignment of the setae, which suggests that some kind of mantle reversion takes place and which also supports a close relationship between the craniides and articulated rhynchonelliform stocks.

Superfamily CRANIOIDEA
Menke, 1828

[*nom. correct.* HARPER in HARPER & others, 1993, p. 431, *pro* Craniacea SCHUCHERT, 1896, p. 310, *nom. imperf.; nom. transl. ex* Craniidae KING, 1846, p. 28; *nom. correct. pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*]

Characters as for order. *Ordovician (upper Arenig)–Holocene.*

Classification of the craniides within a single family is further recognition of their evolutionary stability. The Eoconulidae, previously assigned provisionally to this group (ROWELL, 1965a, p. 288), have organophosphatic shells and are now included in the Acrotretoidea (ROWELL & KRAUSE, 1973, p. 798; HOLMER, 1989b, p. 147). The establishment of a separate family to accommodate the free-lying *Pseudocrania* and *Orthisocrania* (POPOV in POPOV & PUSHKIN, 1986, p. 16) is unwarranted; although both these genera have a fully developed secondary laminar shell layer in the ventral valve, unlike that of encrusting taxa (WILLIAMS & WRIGHT, 1970, p. 42), the secretory regime of the dorsal valve is identical to that of all other craniides. Modifications of ventral shell fabric reflect accommodation to a cementing or encrusting life strategy that took place a number of times in the history of the craniides; this life strategy has no taxonomic significance.

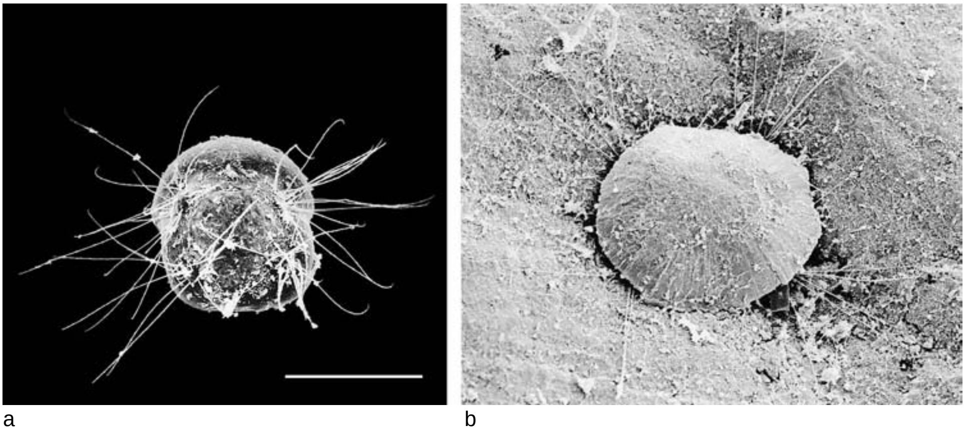

FIG. 95. Development of setae in early ontogentic stages of *Neocrania anomala* (Müller), showing *a,* early larval stage of dorsal valve, and *b,* juvenile with early shell about three days after settling; Holocene, off west coast of Sweden, scale bar: 100 mm (Nielsen, 1991).

Family CRANIIDAE Menke, 1828

[*nom. correct.* Gray, 1840, p. 155, *pro* Craniaceae Menke, 1828, p. 56, *nom. imperf.*] [=family Craniacea Menke, 1830, p. 96; Craniadae Forbes, 1838, p. 38] [*incl.* Valdiviathyrididae, *nom. correct.* Rowell, 1965a, p. 289, *pro* Valdiviathyridae Helmcke, 1940, p. 235, *nom. imperf.;* Pseudocraniidae Popov in Popov & Pushkin, 1986, p. 16]

Characters as for order. *Ordovician (upper Arenig)–Holocene.*

Crania Retzius, 1781, p. 72 [**Anomia craniolaris* Linnaeus, 1758, p. 700; SD Schmidt, 1818, p. 71]. Dorsal valve subconical to conical; ventral valve convex, attached posteriorly at large cicatrix; beaks posterocentral; dorsal posterior face steep; pseudointerarea commonly developed; dorsal posterior margin straight; smooth with only faint growth laminae; ventral musculature deeply incised, posterior scars marginal, directed posteriorly, often perforating the valve externally; anterior scars central, united across rounded median ridge, with bounding rim; dorsal posterior adductors large, thickened, weak myophragm extending into anterior half of valve; well-developed, thickened, pustulose limbus. *Upper Cretaceous (Campanian–Maastrichtian):* Sweden, Denmark, France, Netherlands, Belgium, western Russia.——Fig. 96,*1a–k.* **C. craniolaris* (Linnaeus); *a–c,* paralectotype, dorsal valve interior, exterior, lateral, lower Campanian chalk, Ivö, Scania, southern Sweden, LS 183C, ×3 (Lee & Brunton, 1986); *d,e,* ventral valve interior, exterior, lower Campanian chalk, Kristianstad, Scania, southern Sweden, PM Sk96, ×3; *f,g,* ventral valve interior, exterior with musculature perforating the posterior tip of the valve, lower Campanian chalk, Kristianstad, PM Sk97, ×3; *h,i,* ventral valve interior, exterior with large cicatrix, lower Campanian chalk, Ivö, RM Br 102250, ×3; *j,k,* dorsal valve interior, lateral, Senonian, Barnakälla, Scania, RM Br 94816, ×3 (new).

Acanthocrania Williams, 1943, p. 71 [**Crania spiculata* Rowley, 1908, p. 74; OD] [=?*Choniopora* von Schauroth, 1854, p. 546 (type, *C. radiata*); ?*Punctopatella* Grubbs, 1939, p. 559 (type, *P. corallifera*); *Celidocrania* Liu, Zhu, & Xue, 1985, p. 9[40] (type, *C. luohoensis*)]. Dorsal valve convex to subconical; ornament of fine papillae disposed concentrically with coarser, hollow spines; beak excentric; posterior face normally steep; anterior adductor scars generally larger than posterior pair; muscle field bisected by weak myophragm; valve margin not thickened; limbus developed rarely; encrusting; ventral valve unknown. *Ordovician (Caradoc [upper Champlainian])–Lower Carboniferous:* cosmopolitan.——Fig. 97,*1a–c. A. spinosa* Rodriguez & Gutschick, Sappington Formation, unit E (lower Mississippian), Antelope Valley, western Montana; *a,b,* holotype, dorsal valve exterior, lateral, UND 352, ×3; *c,* paratype, dorsal valve exterior, UND 353, ×3 (Rodriguez & Gutschick, 1967).——Fig. 97,*1d–g. A. papillifera* (Roemer), Ashgill, near Llanfyllin, North Wales; *d–f,* latex cast of dorsal valve exterior, internal mold, lateral, ×3; *g,* detail of ornamentation on anterolateral surface, BMNH BB34089, ×5 (Wright, 1972).

Ancistrocrania Dall, 1877, p. 13, *nom. subst. pro Cranopsis* Dall, 1871b, p. 27, *non* Adams, 1860 [**Crania parisiensis* Defrance, 1818, p. 313; OD]. Ventral valve attached across entire surface and commonly simulating ornament of host; dorsal beak central; anterior face convex; posterior face long, concave; anterior dorsal adductors borne partly on two widely divergent, posterlaterally directed processes separated by short, high septum extending anteriorly as slender ridge; ventral anterior scars central, deeply incised; ventral rim commonly thickened, elevated as crest. *Upper Cretaceous (Coniacian–Maastrichtian), lower Paleogene (?Danian):* France, Belgium, Netherlands, Sweden,

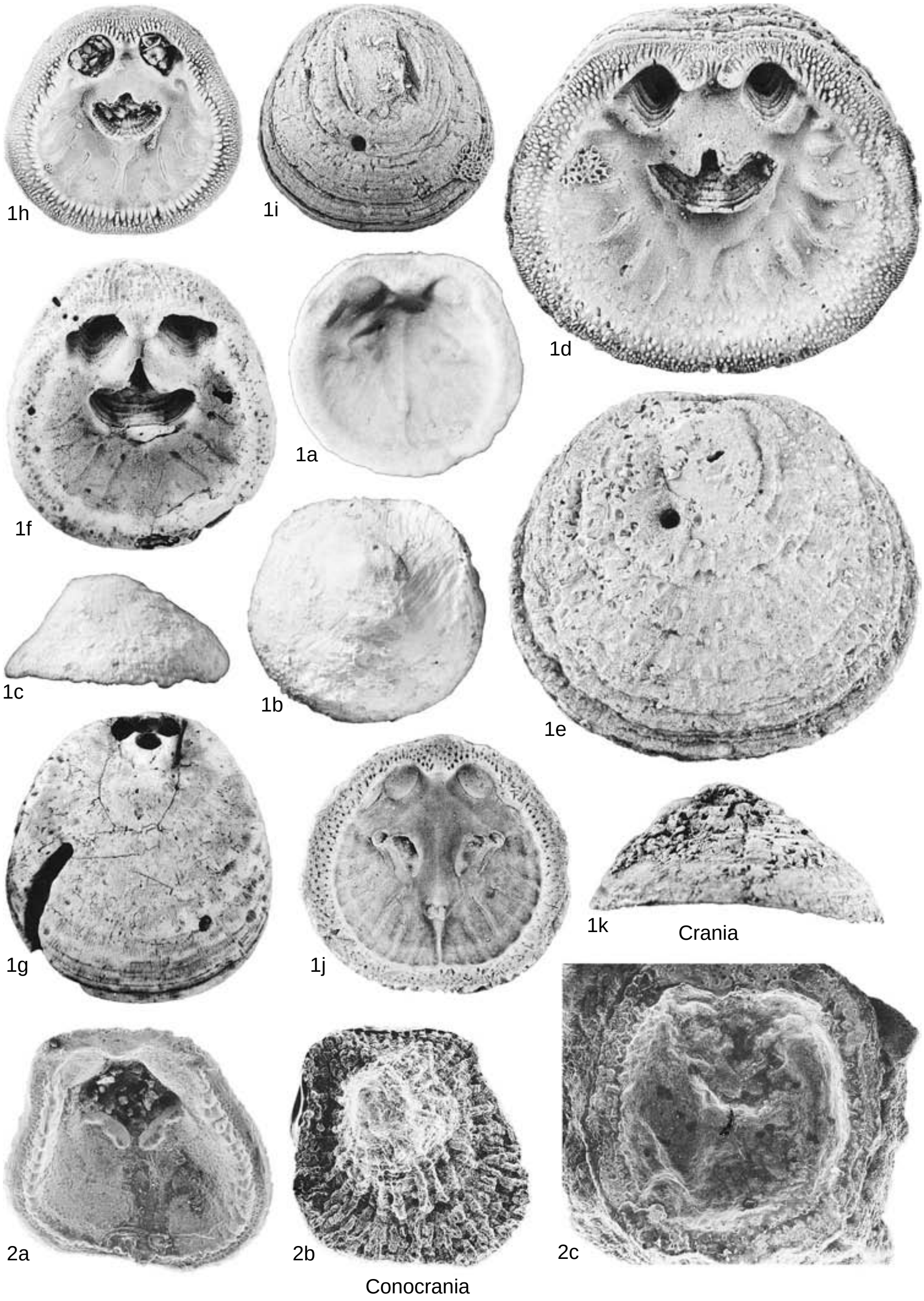

FIG. 96. Craniidae (p. 171–174).

England, North America.——FIG. 97,_2a–f. *A. parisiensis_ (DEFRANCE), upper Chalk, Senonian, England; *a,b,* dorsal valve exterior, lateral, Trimingham, Norfolk, SM B34482, ×2; *c,d,* dorsal valve interior, oblique posterolateral showing processes, Trimingham, Norfolk, SM B34483b, ×2; *e,* ventral valve interior, Norwich, SM B1067, ×2; *f,* ventral valve interior, Gravesend, Kent, SM B807, ×2 (new).

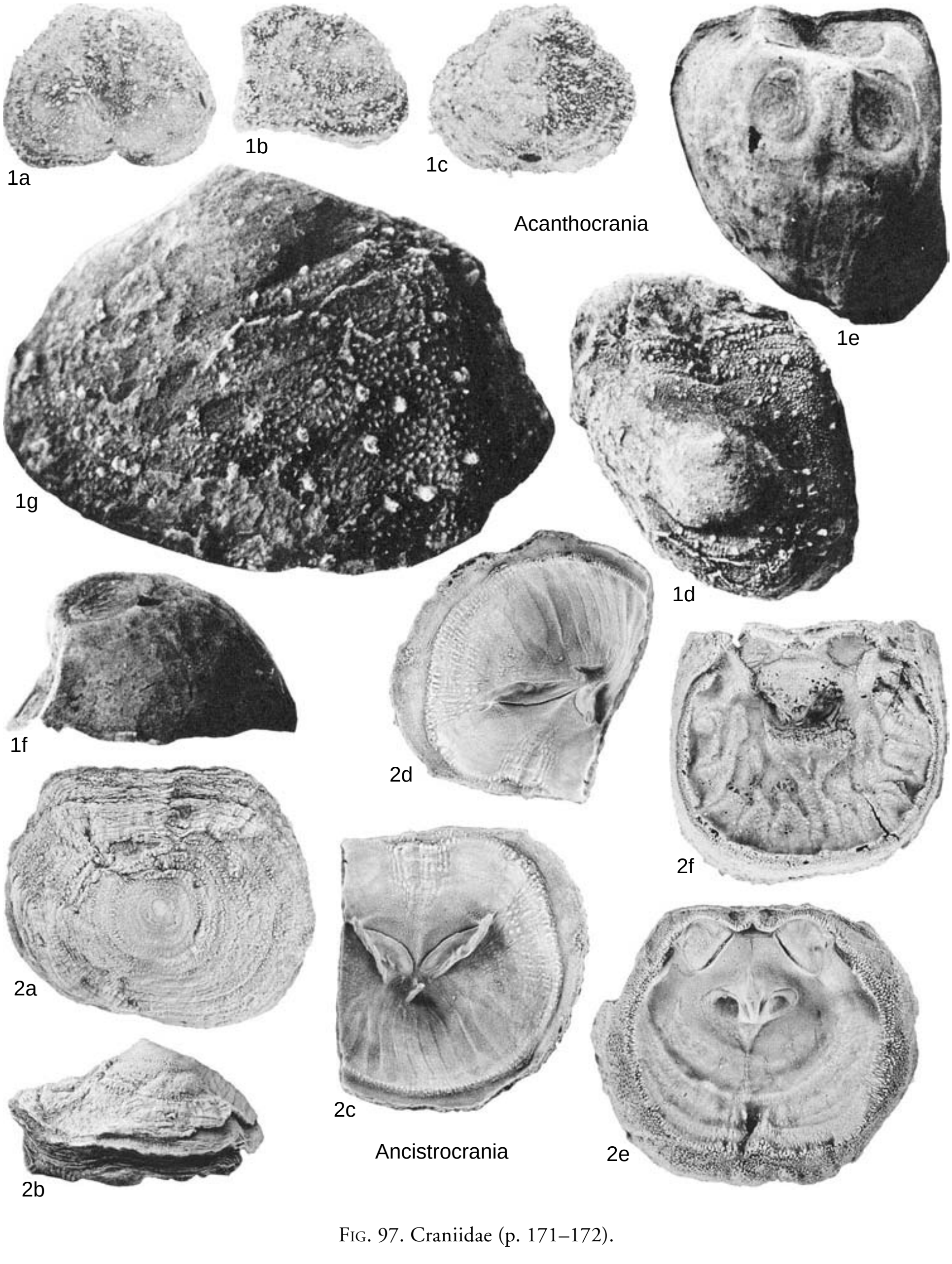

FIG. 97. Craniidae (p. 171–172).

Craniscus DALL, 1871b, p. 27 [**Crania tripartita* VON MÜNSTER, 1840, p. 297; OD]. Dorsal valve weakly to strongly convex; beak excentric; ventral valve of type species unknown, flat in other species, attached by entire surface; smooth with fine growth laminae; ventral musculature unknown; dorsal anterior adductor scars raised on two strong ridges, united with a medium septum or ridge to divide valve into three chambers; valve margins not thickened. *Upper Jurassic (lower Oxfordian)–Holocene:* Europe, Australia, Japan, Indo-Pacific seas.——FIG. 98,*1a–c.* **C. tripartita* (VON MÜNSTER), lower Oxfordian limestone (loose pebble), Thurnau, northern Bavaria, Germany; *a,* lectotype, dorsal valve interior, BSM AS VII 171, ×5; *b,c,* paralectotype, dorsal valve exterior, lateral, BSM AS VII 172, ×5 (Rowell, 1965a).

Conocrania SMIRNOVA, 1996, p. 262 [**Craniscus spinacostatum* SMIRNOVA, 1972, p. 23; OD]. Micromorphic; dorsal valve strongly convex to

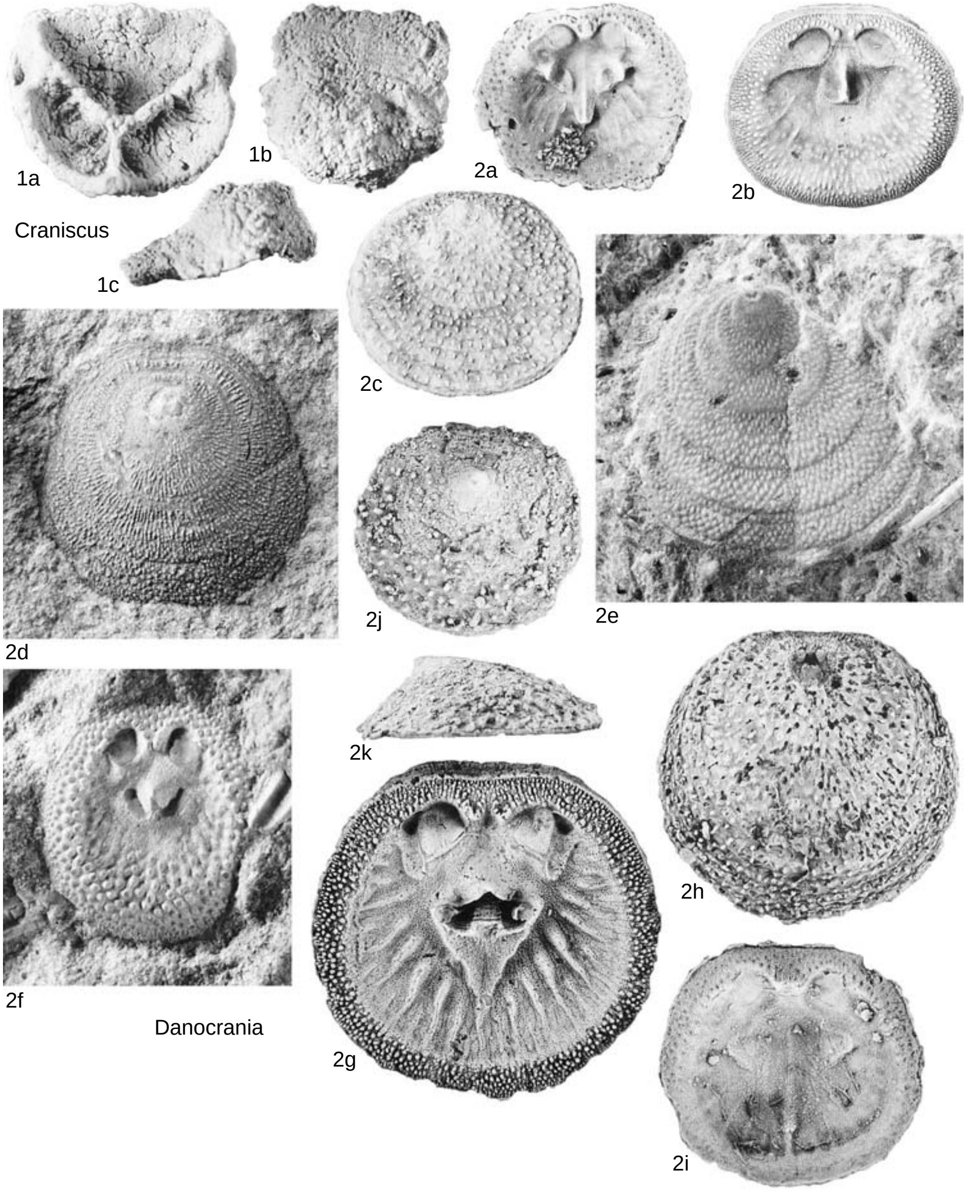

FIG. 98. Craniidae (p. 173–176).

subconical; beak close to straight posterior margin; ventral valve weakly convex, cemented across entire surface; coarsely costellate ribs elevated distally at thickened valve margins; dorsal posterior adductor scars large, abutting valve margin; anterior scars raised, crescentic to oval; ventral muscle scars small, slender with weak platform in front of anterior pair; subperipheral rim tuberculate; limbus flat to concave. *Lower Cretaceous (Berriasian–upper Valanginian):* Ukraine, Czech Republic.——FIG. 96,*2a–c*. **C. spinacostata* (SMIRNOVA), Berriasian sponge reef, Kuchki, Burulcha river, Crimea, Ukraine, topotypes; *a,* dorsal valve interior, CNIGR N168/12942, ×20; *b,* dorsal valve exterior, CNIGR N169/12942, ×20; *c,* ventral valve interior, CNIGR N174/12942, ×20 (Smirnova, 1996).

Danocrania ROSENKRANTZ, 1964, p. 515 [**Crania tuberculata* NILSSON, 1826, p. 326; OD; *nom. conserv.,* ICZN, 1988c, p. 63, Opinion 1469, *pro Craniolites brattenburgicus* SCHLOTHEIM, 1820, p. 246] [=*Westralicrania* COCKBAIN, 1967, p. 119 (type, *W. allani*)]. Convexiplane; dorsal valve rarely

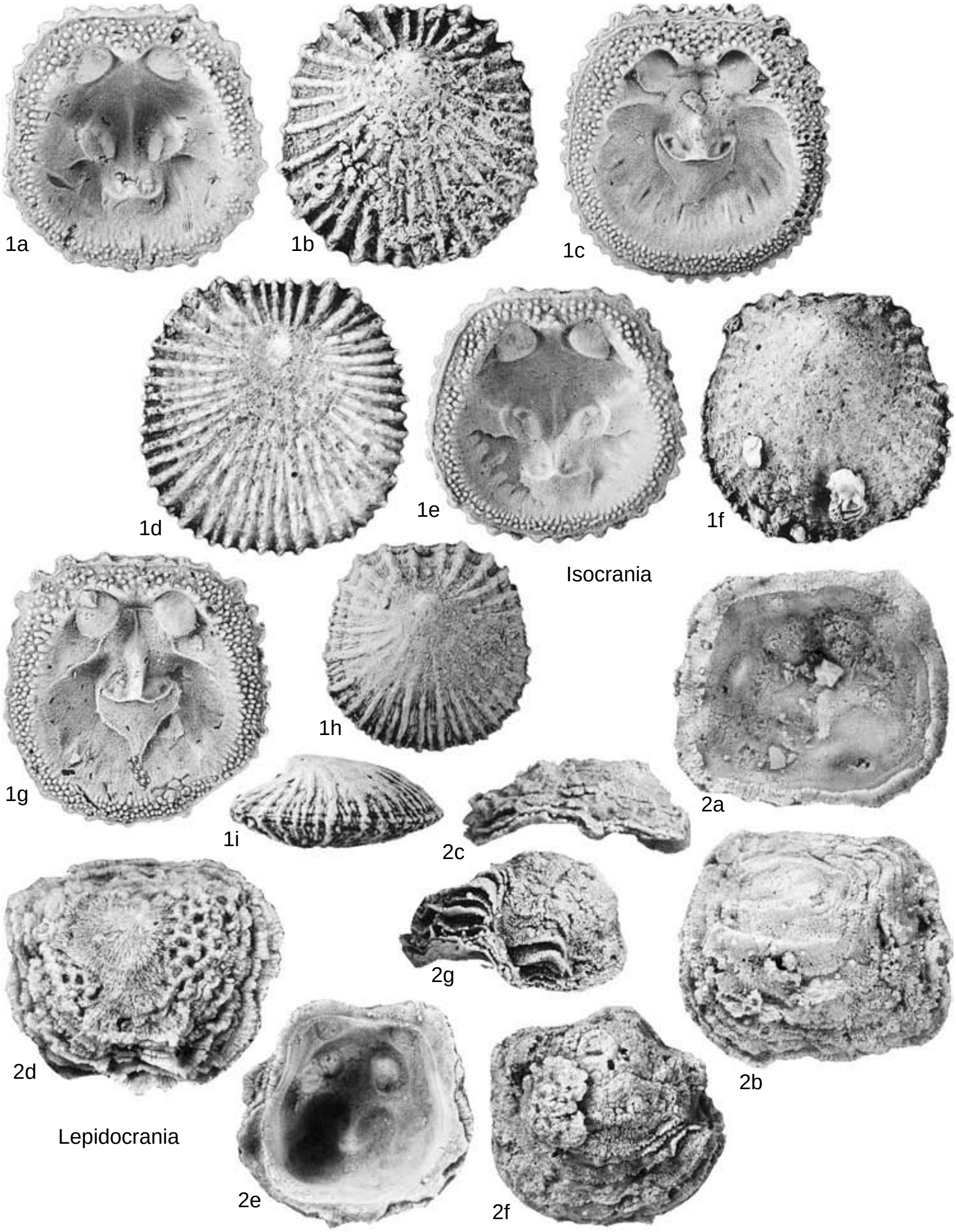

FIG. 99. Craniidae (p. 176–178).

subconical; ventral valve sometimes weakly concave; ornament pustulose to spinose; beaks set posteriorly; cicatrix at ventral umbo; pseudointerarea generally present; interiors commonly tuberculate; dorsal interior with articulatory ridge separating large, marginal posterior adductors; anterior scars widely separated, borne on low converging plates; short broad ridge extending anteriorly; short septum divides small anterior ventral scars; marginal rim rounded or as limbus. *Upper Cretaceous (Maastrichtian)–lower Paleogene (Danian, ?Thanetian):* Sweden, Denmark, Belgium, Netherlands, Austria, Ukraine, Crimea, western Australia.——FIG. 98,*2a–f.* **D. tuberculata* (NILSSON), Danian, Denmark; *a,* dorsal valve interior, Faxe, BMNH BD3367, ×3; *b,c,* ventral valve interior, exterior, Faxe, BMNH BD3366, ×3; *d,* dorsal valve exterior, Saltholm Limestone, Copenhagen, BMNH

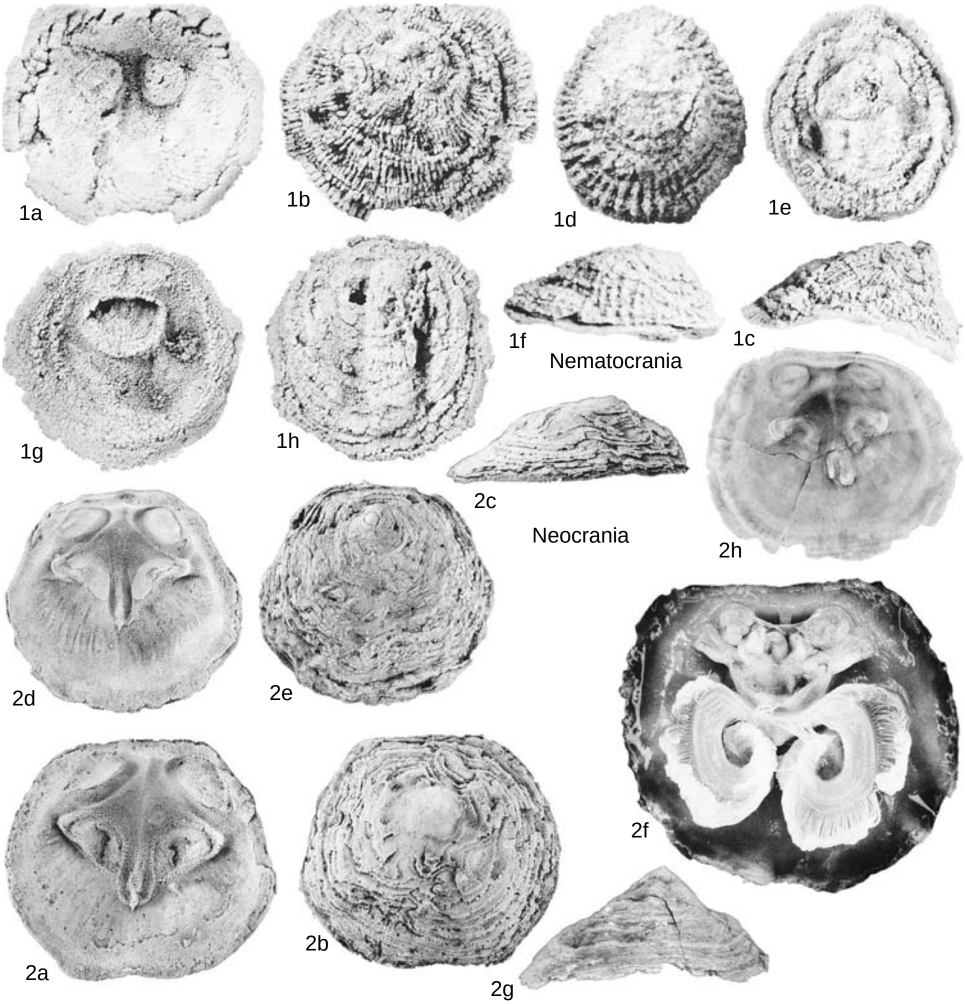

FIG. 100. Craniidae (p. 178–180).

B80856, ×3; *e,* ventral valve exterior, Saltholm Limestone, Copenhagen, BMNH B80850, ×3; *f,* ventral valve interior, Saltholm Limestone, Copenhagen, BMNH B80858, ×3 (Lee & Brunton, 1986).——FIG. 98,*2g–k. D. spinulosa* NILSSON, Senonian, Kjugestrand, Scania, southern Sweden; *g,h,* ventral valve interior, exterior, PM Sk110, ×3; *i–k,* dorsal valve interior, exterior, lateral, PM Sk111, ×3 (new).

Isocrania JAEKEL, 1902, p. 1062 [**Crania egnabergensis* RETZIUS, 1781, p. 75; SD SCHUCHERT & LEVENE, 1929, p. 69]. Subequally biconvex to subconical, dorsal curvature generally stronger; beaks excentric or well toward commonly straight posterior margin; attached at umbonal cicatrix in early growth, mostly free lying as adults; coarsely costellate; dorsal posterior adductors large, separated by broad articulatory ridge; anterior scars smaller, paired, broad median ridge extending well toward anterior margin; ventral posterior adductors large, well separated; anterior scars small, alongside short septum extending anteriorly as tapering ridge; limbus wide, coarsely pustulose. *Upper Cretaceous (lower Campanian)–lower Paleogene (Danian):* Sweden, Denmark, Netherlands, England, Africa, Asia.——FIG. 99,*1a–i. *I. egnabergensis* (RETZIUS), lower Campanian chalk, southern Sweden; *a,b,* dorsal valve interior, exterior, Ignaberga, Scania, PM Sk115, ×4; *c,d,* ventral valve interior, exterior, Ignaberga, Scania, PM Sk116, ×4; *e,f,* dorsal valve interior, exterior, Ignaberga, Scania, PM Sk117, ×4; *g,* ventral valve interior, Ignaberga, Scania, PM Sk118, ×4; *h,i,* ventral, lateral views of complete shell, Maltesholm, Scania, RM Br 97732, ×4 (new).

Lepidocrania COOPER & GRANT, 1974, p. 246 [**L. tardispinosa;* OD]. Dorsal valve gently convex to

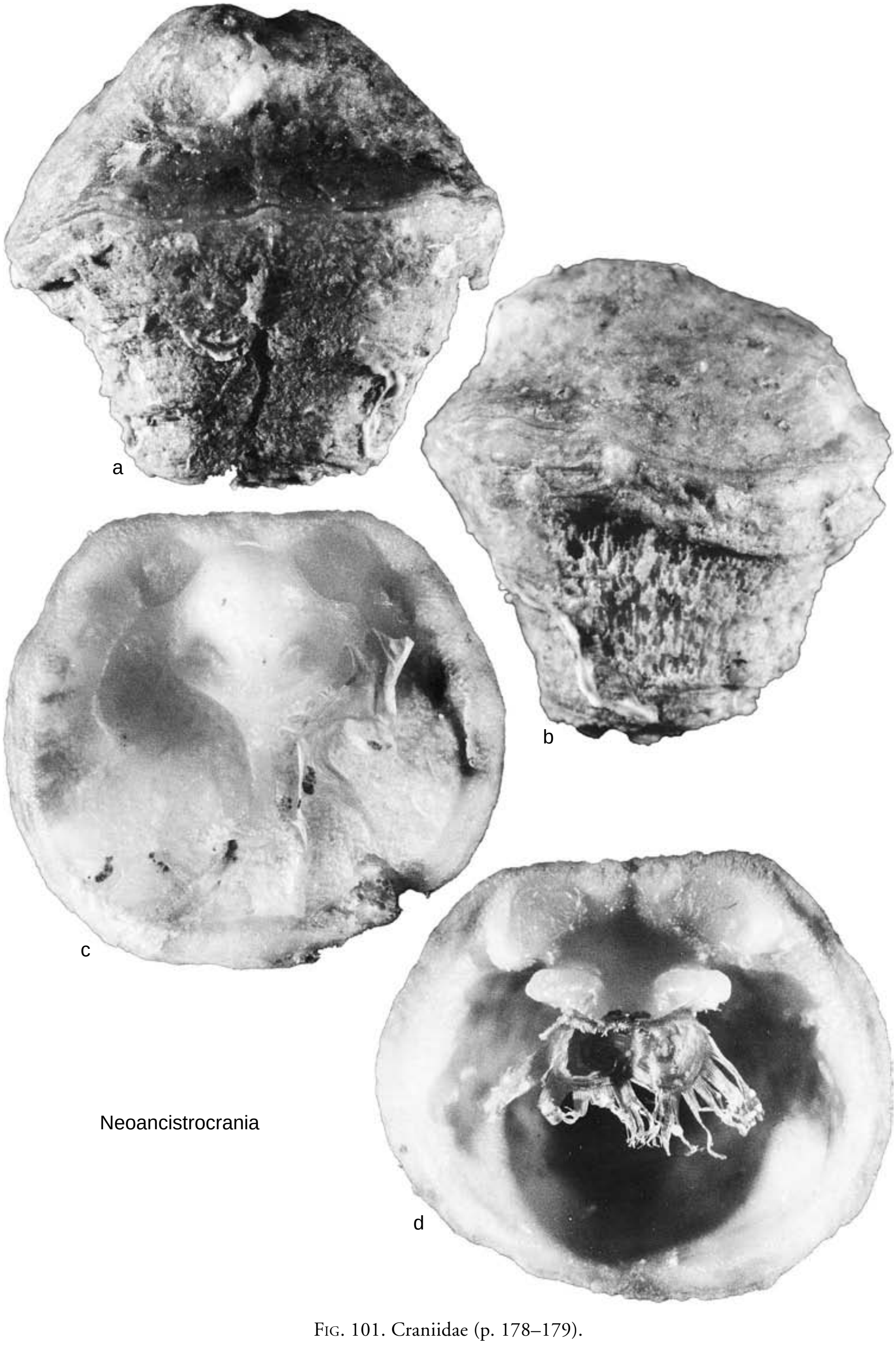

FIG. 101. Craniidae (p. 178–179).

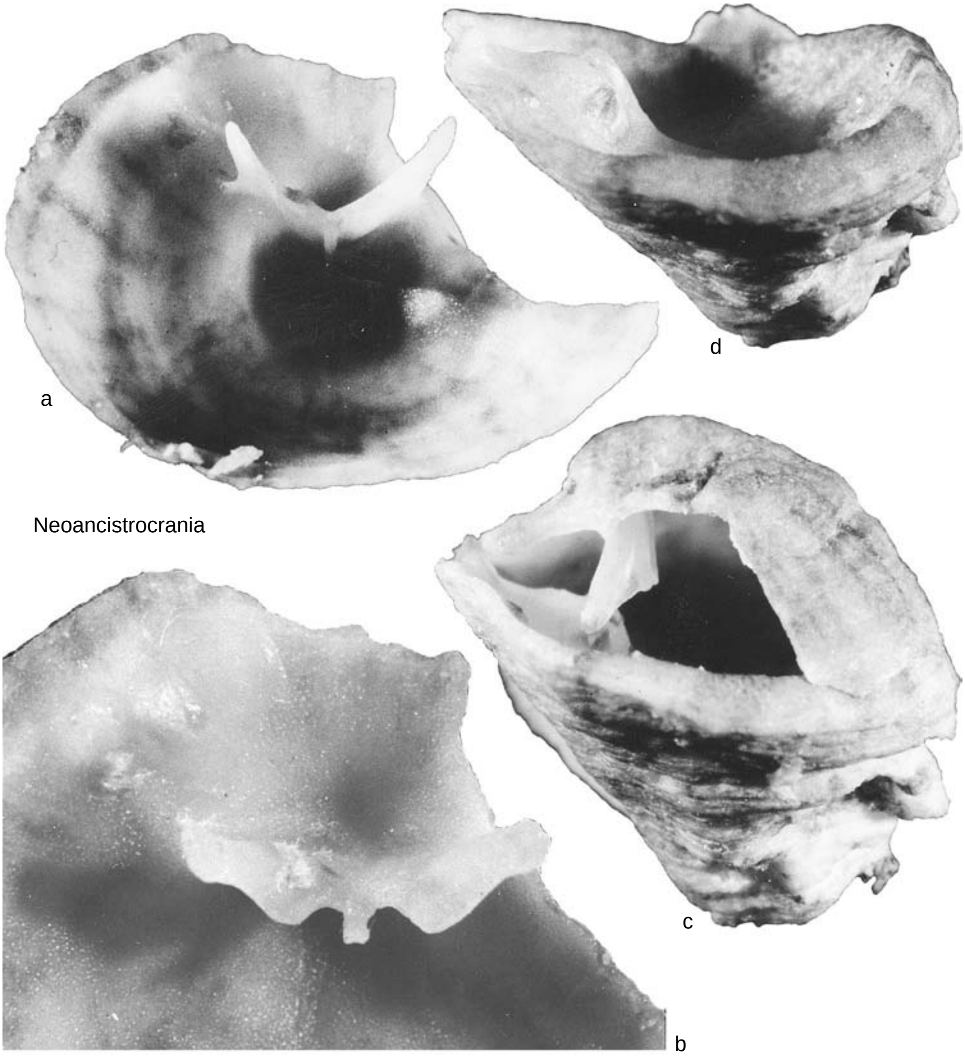

FIG. 102. Craniidae (p. 178–179).

conical, strongly lamellose or scaly with scattered, stout spines; beak excentric; posterior adductor scars marginal; oblique laterals, anterior adductors commonly subequal, thickened; limbus variably wide, thickened; encrusting; ventral valve unknown. *Lower Permian:* USA (western Texas).——FIG. 99,*2a–g*. **L. tardispinosa,* Road Canyon Formation, Wolfcampian, western Texas; *a–c,* holotype, dorsal valve interior, exterior, lateral, USNM 152582a, ×4; *d,* paratype, dorsal valve exterior, USNM 151395a, ×6; *e–g,* paratype, dorsal valve interior, exterior, lateral, USNM 152583, ×4 (Cooper & Grant, 1974).

Nematocrania GRANT, 1976, p. 31 [**N. crassa;* OD]. Ventral valve calcified, cemented posterocentrally at cicatrix, plane or simulating substrate morphology; dorsal valve convex to low conical with posterocentral beak, steep posterior face; costellate with widely spaced growth laminae; dorsal anterior adductors large, thickened; posterior scars small, marginal; ventral anterior adductors deeply incised with bounding rim; limbus narrow, finely pustulose. *Lower Permian (upper Artinskian):* southern Thailand.——FIG. 100,*1a–h*. **N. crassa,* Rat Buri Limestone, upper Artinskian, Ko Muk; *a–c,* holotype, dorsal valve interior, exterior, lateral, USNM 211603, ×4; *d–f,* paratype, dorsal exterior, ventral exterior, lateral, USNM 211595, ×5.5; *g,h,* paratype, ventral valve interior, exterior, USNM 211612, ×4 (Grant, 1976).

Neoancistrocrania LAURIN, 1992, p. 344 [**N. norfolki;* OD]. Biconical, inequivalved, ventral apex flattened

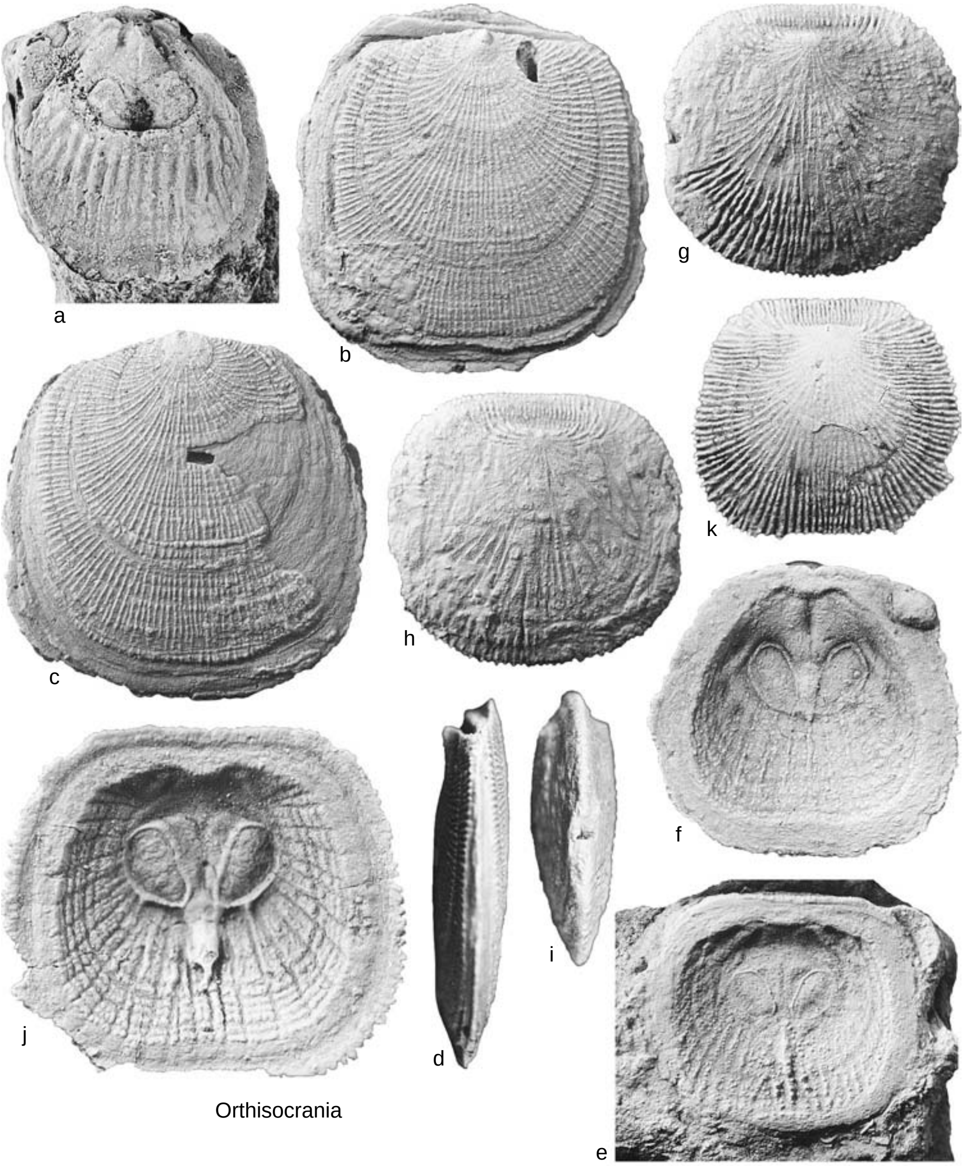

Fig. 103. Craniidae (p. 180–181).

as attachment cicatrix; dorsal beak posterocentral, smooth with faint growth laminae; ventral posterior muscle scars large, marginal, separated by a stout rounded swelling; dorsal interior with pair of rounded knobs alongside posterior adductors, bearing oblique muscles, extending up into ventral valve; otherwise resembling *Ancistrocrania* but with reduced septum between processes; marginal rim not thickened. [Precise affinities of this genus, known only from two specimens, remain unclear; it is possibly a mature *Valdiviathyris* or a synonym of *Ancistrocrania*]. *Holocene:* South Pacific.——Fig. 101*a–d*. **N. norfolki,* Holocene, Norfolk Ridge, South Pacific (233 m); holotype, posterior, lateral, ventral interior, dorsal interior, MNHN, ×4.5 (Laurin, 1992).——Fig. 102*a–d*. **N. norfolki,* Holocene, Norfolk Ridge, South Pacific (233 m); paratype, dorsal valve interior, anterior vertical view of processes, lateral view of conjoined valves showing disposition of dorsal processes, oblique view of ventral valve illustrating height of posterior knobs, UD, ×5 (Laurin, 1992).

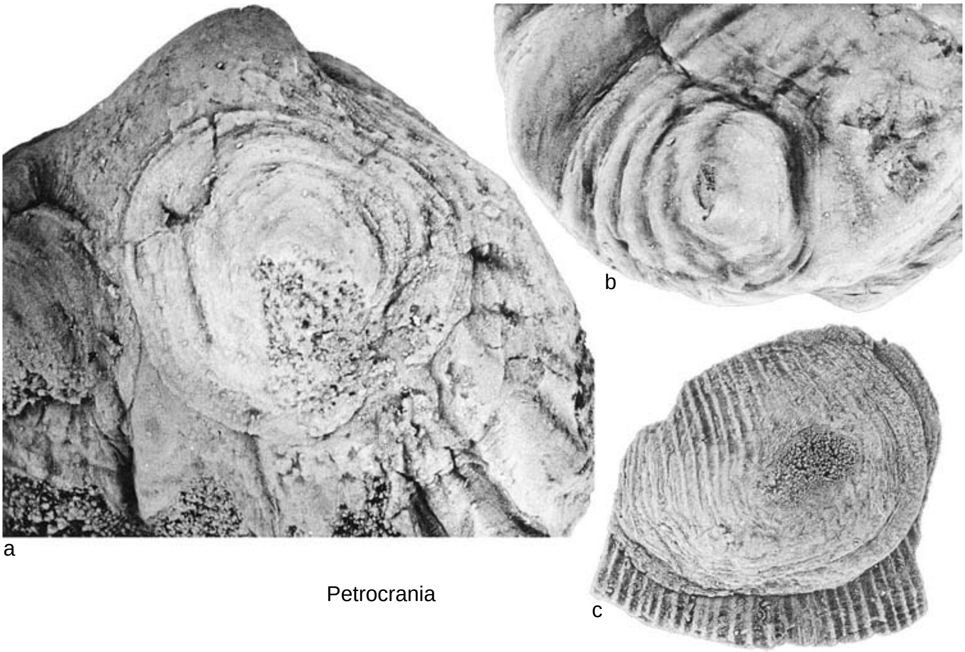

Fig. 104. Craniidae (p. 181–182).

Neocrania Lee & Brunton, 1986, p. 150 [**Patella anomala* Müller, 1776, p. 237; OD; ICZN plenary powers, 1988b, p. 62, Opinion 1468] [=*Criopus* Poli, 1791, p. 34 (type, *C. fimbriatus* Poli, 1795, p. 189), ICZN plenary powers, 1988a, p. 61, opinion 1467; *Criopoderma* Poli, 1795, p. 255, ICZN plenary powers, 1988a, p. 61, opinion 1467; *Orbicula* Cuvier, 1798, p. 435, obj., ICZN plenary powers, 1988b, p. 62, opinion 1468; *Orbicularius* Duméril, 1806, p. 170; *Cryopus* Deshayes in Lamarck, 1836, p. 314, ICZN plenary powers, 1988a, p. 61, opinion 1467; *Criopododerma* Agassiz, 1848, p. 301, ICZN plenary powers, 1988a, p. 61, opinion 1467]. Dorsal valve convex to conical; beak subcentral to posterocentral, smooth, finely pustulose or rarely finely costellate; posterior margin commonly straight; recent species with dendroid shell punctation; dorsal posterior adductor scars large, rounded, thickened, widely separated; anterior scars commonly crescentic, raised above valve floor; weak myophragm bisects muscle field; encrusting; ventral valve uncalcified in recent species, otherwise sometimes thin; ventral posterior adductor scars large, anterior scars united medially; marginal mantle setae observed in recent forms; valve margins variably thickened, with limbus or faint submarginal rim. *Paleogene (Eocene)–Holocene:* cosmopolitan.——Fig. 100,*2a–h*. **N. anomala* (Müller), Holocene; *a–c,* dorsal valve interior, exterior, lateral, off western coast of Sweden, north of Hunnebostrand (60 to 120 m), NMW 98.10G.1, ×3; *d,e,* dorsal valve interior, exterior, off western coast of Sweden, north of Hunnebostrand (60 to 120 m), NMW 98.10G.2, ×3; *f,* dorsal interior with body preserved, off southwestern Yttre Vattenholmen, Kosterfjorden, western Sweden (40 to 65 m), NMW 98.11G.1, ×4 (new); *g,h,* lateral view of conical dorsal valve, dorsal interior with asymmetrical protractor scar, Øresund, Denmark, BMNH ZB3955a, ×2 (Lee & Brunton, 1986).

Orthisocrania Rowell, 1963, p.39 [**Pseudocrania divaricata* M'Coy, 1851, p. 388; OD]. Free lying; biplanate to weakly biconvex, beaks initially marginal, growth mixoperipheral, may become holoperipheral through ontogeny; ventral pseudointerarea apsacline to catacline; dorsal pseudointerarea anacline; multicostellate; anterior adductor scars usually considerably larger than posterior scars in both valves; mantle canal system includes paired *vascula media;* limbus wide, smooth. *Ordovician (Llandeilo–Ashgill):* England, Sweden, Estonia, Russia (Ingria), Kazakhstan.——Fig. 103*a*. **O. divaricata* (M'Coy), Caradoc Series, Longvillian, Bryn Melyn, Bala, North Wales; syntype, ventral valve internal mold, SM A41949, ×2 (new).——Fig. 103*b–f. O. planissima* (von Eichwald), middle Ordovician, Ingria; *b–d,* dorsal, ventral, lateral, CNIGR 114/9960, ×3; *e,f,* dorsal, ventral interiors, CNIGR 116/9960, 115/9960, ×2 (Gorjansky, 1969).——Fig. 103*g–k. O. depressa* (von Eichwald), middle Ordovician; *g–i,* ventral, dorsal, lateral, Estonia, CNIGR 118/9960, ×2; *j,* dorsal inte-

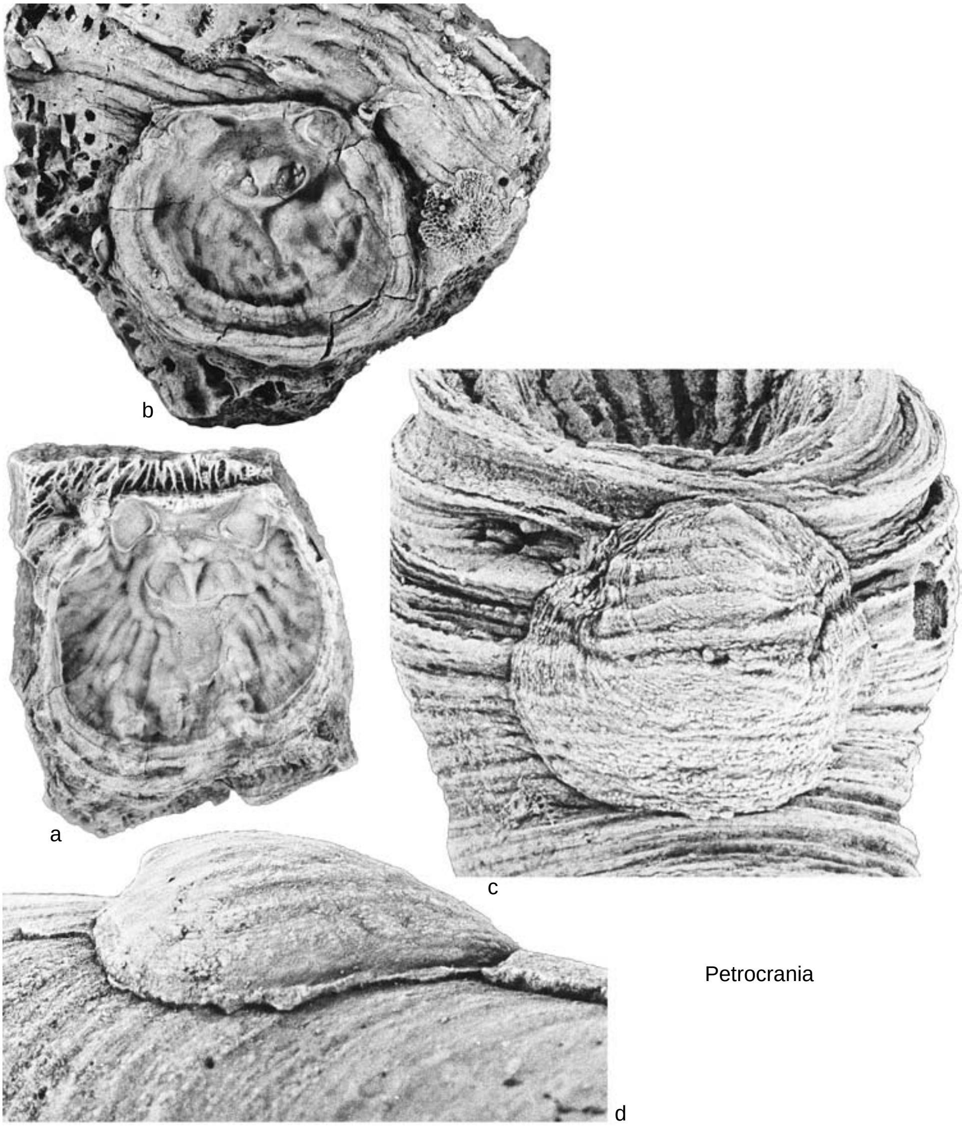

FIG. 105. Craniidae (p. 181–182).

rior, Ingria, CNIGR 119/9960, ×3; *k,* dorsal exterior, Ingria, CNIGR 119/9960, ×2 (Gorjansky, 1969).

Petrocrania RAYMOND, 1911, p. 229, *nom. subst. pro Craniella* OEHLERT, 1888, p. 101, *non* VON SCHLOTHEIM, 1820 [**Craniella meduanensis* OEHLERT, 1888, p. 102; OD] [=*Philhedrella* KOZŁOWSKI, 1929, p. 28 (type, *Philhedra (Philhedrella) mimetica*); *Lissocrania* WILLIAMS, 1943, p. 71 (type, *Crania dodgei* ROWLEY, 1908, p. 73); *Petrocraniella* PETROV, 1968, p. 74 (type, *P. grandissima*)]. Dorsal valve convex to subconical; beak subcentral to posterocentral; ornament only of concentric growth laminae or simulating morphology of the host; dorsal posterior adductor scars typically larger than anterior scars, but not exclusively; *vascula lateralia* commonly prominent, sigmoidal; valve margin not thickened, limbus narrow when developed; encrusting; ventral valve not known. *Lower Ordovician (upper Arenig)–Lower Carboniferous:* cosmopolitan.——FIG. 104*a–c. P. mimetica* (KOZŁOWSKI), Borshchov horizon, Lochkovian, Podolia, Ukraine; *a,b,* dorsal valves on host rhynchonelloidean shell, USNM 84331, ×4; *c,* dorsal valve, NMW 80.14G.3, ×3 (new).——FIG. 105*a–d. P.* sp., Wenlock, Gotland, Sweden; *a,b,* dorsal interiors, Halla

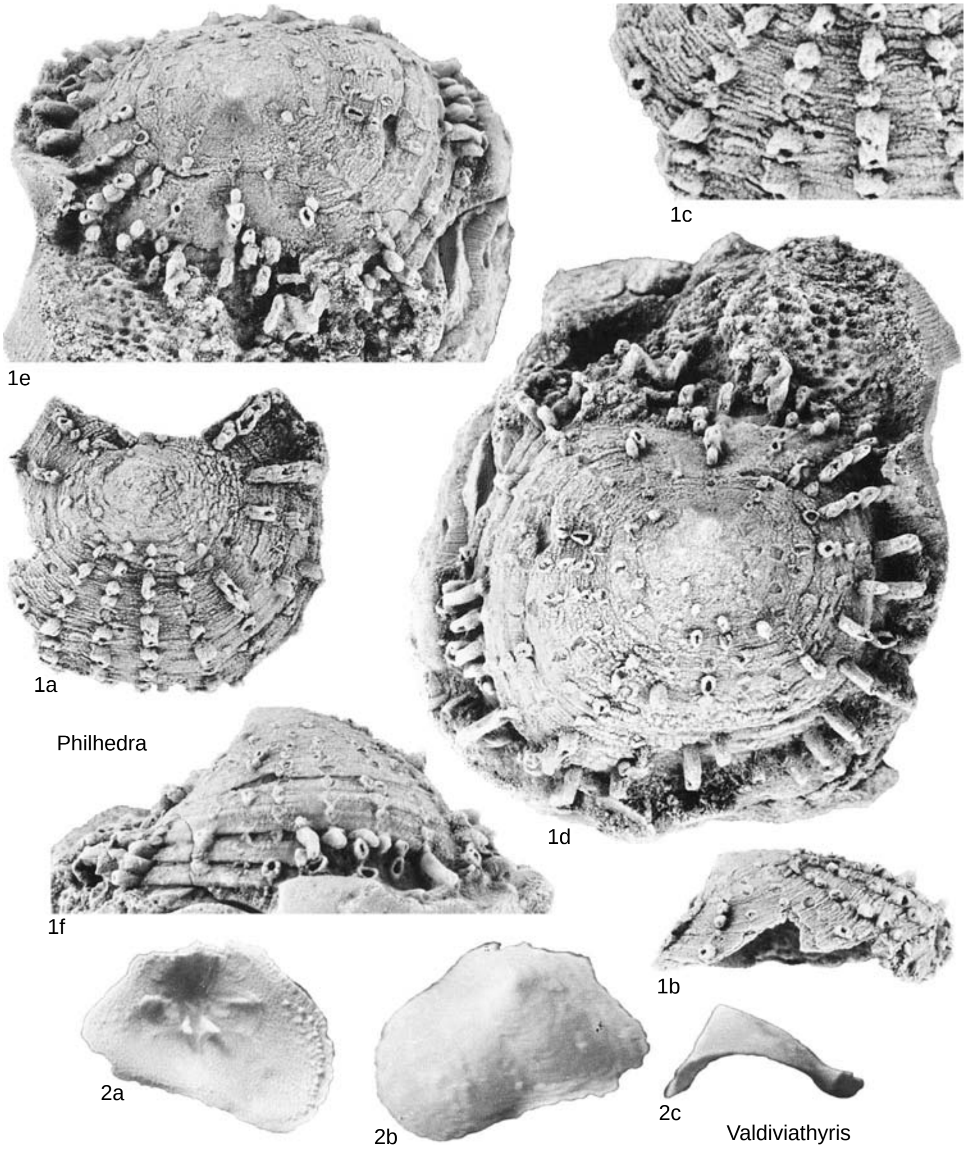

FIG. 106. Craniidae (p. 182–183).

Formation, SGU Type Collection, ×3; *c,* dorsal view, upper Visby Formation, RM Br 108374, ×3; *d,* lateral view, upper Visby Formation, RM Br 108240, ×3 (new).

Philhedra KOKEN, 1889, p. 465, *non Philhedra* SCHMIDT, 1939 [**P. baltica;* OD] [=*Philedra* BEKKER, 1921, p. 34]. Dorsal valve subconical; beak well posterior with steep, concave posterior face; ornament of thick, radially aligned hollow spines, concentric growth laminae; musculature unknown; encrusting; ventral valve unknown. *Ordovician (Llanvirn–Caradoc):* eastern Baltic (Ingria, Estonia).——FIG 106,*1a–f.* **P. baltica,* Viruan, Kukruse horizon, Kohtla-Jārve, Kuttjejõu, northern Estonia; *a,b,* dorsal valve exterior, lateral, ×4; *c,* detail of ornament, TAGI BR 1311, ×6; *d–f,* dorsal valve exterior, posterior, lateral, TAGI BR 1313, ×4 (new).

Pseudocrania M'COY, 1851, p. 387 [**Orbicula antiquissima* VON EICHWALD, 1840, p. 169; =*Crania petropolitana* PANDER, 1830, p. 100, subj.; SD DAVIDSON, 1853, expl. pl. 9] [=*Palaeocrania* VON EICH-

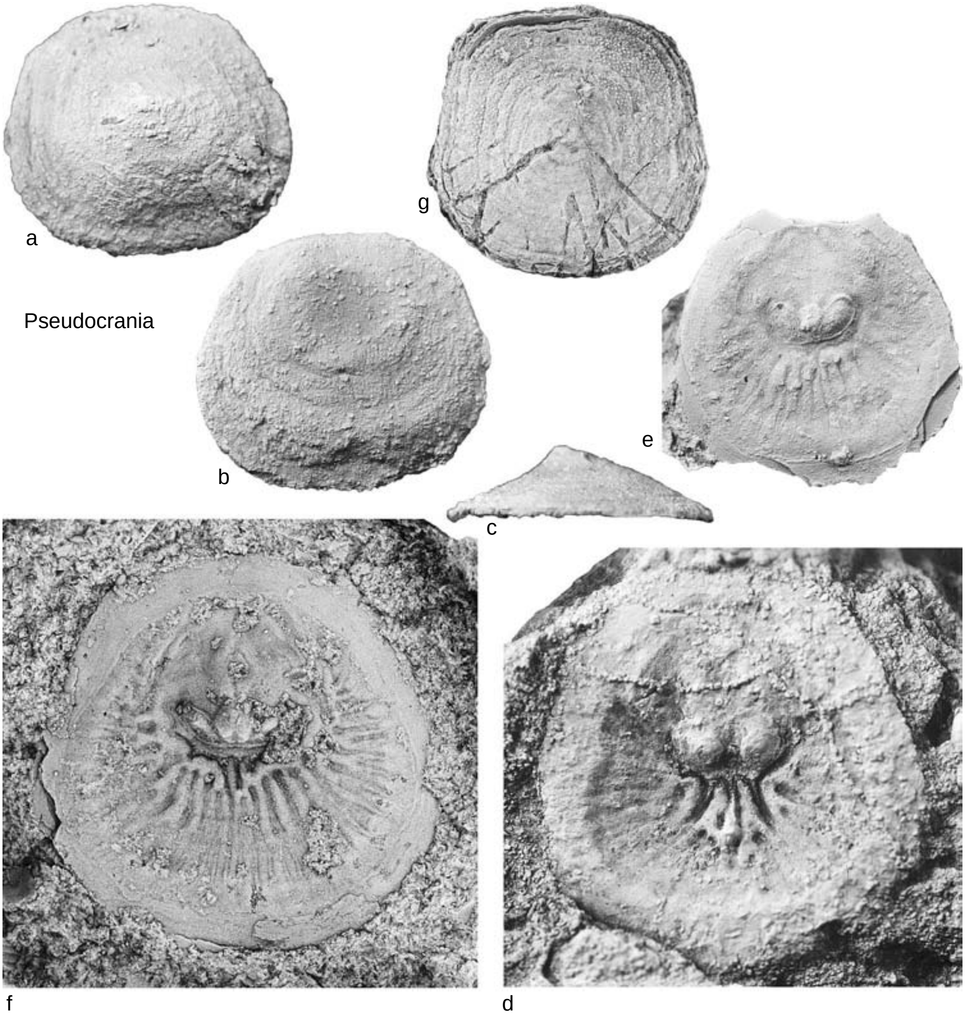

FIG. 107. Craniidae (p. 182–183).

WALD, 1854, p. 20, obj.]. Free lying; dorsal valve convex to subconical; ventral valve plane to subconical; beaks subcentral; growth holoperipheral; ornament of randomly spaced fine papillae, growth laminae; internally similar to *Orthisocrania,* including development of *vascula media. Lower Ordovician (upper Arenig):* Sweden, Russia (Ingria), Estonia, northern Germany.——FIG. 107*a–g.* **P. petropolitana,* Volkhov; *a–c,* dorsal, ventral, lateral views of conjoined valves, Ingria, CNIGR 108/9960, ×2; *d,* dorsal valve interior, Ingria, CNIGR 109/9960, ×2; *e,* ventral valve interior, Ingria, CNIGR 112/9960, ×2 (Gorjansky, 1969); *f,* ventral interior, Öland, Sweden, RM Br 15016, ×2; *g,* ventral valve exterior, Hälludden, Öland, SGU Type Collection, ×1.5 (new).

Valdiviathyris HELMCKE, 1940, p. 237 [**V. quenstedti;* OD]. Ventral valve unknown; dorsal valve thin-shelled, conical; beak posterocentral with steep posterior face; ornament of fine growth laminae only; internally similar to *Ancistrocrania* but lacking septum, with processes less divergent, more ventrally directed. [*Valdiviathyris* remains imperfectly known from a single, probable juvenile valve (ROWELL, 1962b); it is not unlikely that it could be a synonym of *Ancistrocrania,* and until more material of the type species is found it is recommended that the generic name should not be used for other taxa]. *Holocene:* southern Indian Ocean.——FIG. 106,2*a–c.* **V. quenstedti;* holotype, dorsal valve interior, exterior, lateral, MB 198, ×8 (Rowell, 1962b).

TRIMERELLIDA

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Order TRIMERELLIDA Gorjansky & Popov, 1985

[Trimerellida GORJANSKY & POPOV, 1985, p. 12]

Shell thick, unusually large, probably aragonitic; free lying; unequally biconvex, growth mixoperipheral in both valves; usually smooth; ventral cardinal interarea commonly well developed, articulatory structure comprising ventral cardinal socket and dorsal hinge plate (apart from Ussuniidae); mantle lobes probably not fused along posterior margin; musculature apparently composed of paired posterior and anterior adductors, and outside lateral muscles; paired internal oblique muscles attached to posterior end of dorsal hinge plate (except in *Gasconsia*); mantle canal system baculate, bifurcate, or pinnate, sometimes with *vascula lateralia* and *vascula media* in both valves. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Trimerellides are characterized by inequibiconvex, sometimes almost spheroidal, thick shells, with mixoperipheral growth in both valves; they are among the largest known Early Paleozoic brachiopods and probably had an aragonitic shell (JAANUSSON, 1966). They adopted a free-living mode of life, lacking all evidence of a pedicle throughout ontogeny. Trimerellides are commonly found in massive reeflike accumulations of numerous individuals of the same species, vertically inclined, umbo downward; a typical such occurrence of *Eodinobolus* was described by WEBBY and PERCIVAL (1983) from the Upper Ordovician of Australia.

The shells of most trimerellides are usually almost smooth, and only *Costitrimerella* has radial ornamentation. The shape of the shell probably correlates strongly with the unique type of articulation, which consists of a dorsal hinge plate that fits tightly into a cardinal socket in the ventral valve, with a concave homeodeltidium in the center of the ventral interarea (Fig. 108); these structures effectively fixed the axis of rotation in a manner analogous to that of the articulated brachiopods.

The trimerellides also have unusual muscle scars; it is unlikely that the muscle system is comparable with that of the lingulides as proposed originally by DAVIDSON and KING (1872). NORFORD and STEELE (1969) showed that the muscle scars on some unusually well-preserved *Eodinobolus* are completely different from those of lingulides; they reconstructed a musculature consisting mainly of two paired large adductors and two smaller diductors working behind the axis of rotation. GORJANSKY and POPOV (1985, 1986) described the muscle system from *Eodinobolus, Ovidiella,* and *Palaeotrimerella* and proposed an alternative reconstruction based mainly on the craniide muscle system (Fig. 108); they also recognized that the trimerellides might have had a shell-opening mechanism with directly working diductors, but in contrast to NORFORD and STEELE (1969) they proposed that the oblique internal muscles may have been attached to the dorsal hinge plate, which is placed behind the axis of rotation (Fig. 108).

The muscle system of *Gasconsia* seems to have been slightly different; it is the only strophic trimerellide with a wide posterior margin, and the dorsal hinge plate is apparently situated anterior to the rotation axis. As noted by HANKEN and HARPER (1985) and MERGL (1988) this indicates that a diductor muscle could not function in the manner proposed for other trimerellids. MERGL (1988) proposed that it had a hydraulic shell opening mechanism with the outside lateral muscles attached to the anterior body wall.

Most trimerellids have muscle platforms in the anterior region of the visceral area of one or both valves. In most Ordovician genera (such as *Eodinobolus* and *Ovidiella*) these platforms are simple thickenings beneath the anterior muscle fields, while most Silurian

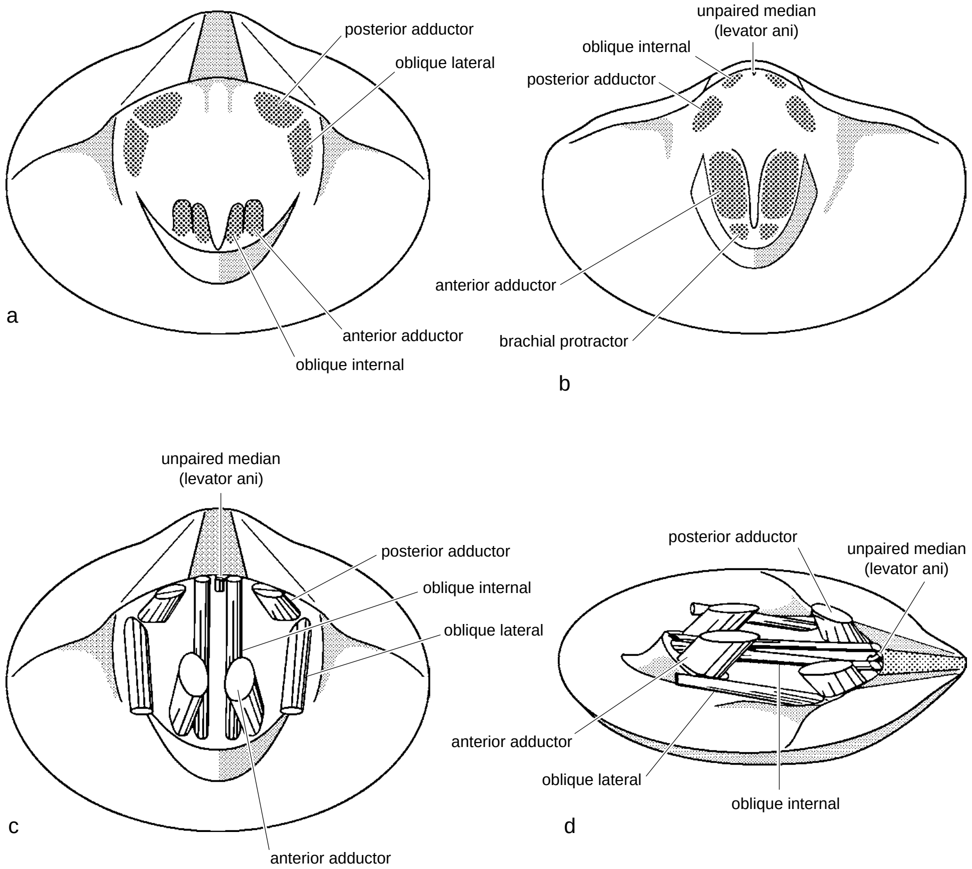

FIG. 108. Schematic illustration of musculature of *Eodinobolus; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

forms have distinctly raised, vaulted platforms that are hollow anteriorly.

Superfamily TRIMERELLOIDEA Davidson & King, 1872

[*nom. correct.* HARPER & others, 1993, p. 430, *pro* Trimerellacea SCHUCHERT & LEVENE, 1929, p. 12, *nom. imperf.; nom. transl. ex* Trimerellidae DAVIDSON & KING, 1872, p. 442]

Characters as for order. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Family TRIMERELLIDAE Davidson & King, 1872

[Trimerellidae DAVIDSON & KING, 1872, p. 442]

Shell with well-developed visceral platforms in one or both valves; lateral oblique muscle scars commonly present in ventral valve; mantle canal system bifurcate or baculate. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Trimerella BILLINGS, 1862c, p. 166 [**T. grandis;* SD DALL, 1870, p. 160] [=*Gotlandia* DALL, 1870, p. 160 (type, *G. lindstroemi;* OD); *Machaerocolella* LI & HAN, 1980, p. 15 (type, *M. zhoujiashanensis;* OD); *Prosoponella* LI, 1984, p. 778[780] (type, *P. jiangshanensis;* OD)]. Shell dorsibiconvex, elongate triangular; ventral valve flattened; ventral interarea high, triangular, apsacline, with deep concave homeodeltidium occupying more than half of interarea; dorsal valve strongly convex, beak incurved; ventral umbonal cavities small or vestigial; both valves with distinctly raised visceral platforms, extending anterior to center; visceral platforms with deep vaults, separated by median partition, extending anterior to platform; dorsal hinge plate high, strongly incurved; dorsal *vascula lateralia* broad, slightly divergent, lacking trace of bifurcation.

Ordovician (Ashgill)–Silurian (Wenlock): China, *Ashgill;* Kazakhstan, *Llandovery;* USA, Canada, Sweden (Gotland), Australia, Russia (Altai), *Wenlock.*——FIG. 109,*1a,b.* **T. grandis,* Guelph Limestone, Hespeler, Ontario, syntypes, GSC 2803; *a,* dorsal view of internal mold of both valves, ×0.6; *b,* oblique posterior view of both valves, ×0.7 (new).——FIG. 109,*1c–e. T. lindstroemi* DALL, Högklint beds, Gotland, Sweden; *c,* detail of articulatory structure of both valves, Visby, Galgberget, RM Br 24466, ×1.2; *d,e,* ventral valve interior, exterior, BMNH B 5958, ×0.8 (new).——FIG. 109,*1f. T. acuminata* BILLINGS, Guelph Limestone, Hespeler, Ontario; cast of ventral internal mold, BMNH B 14308, ×0.8 (new).——FIG. 109,*1g. T. ohioensis* MEEK, Niagara Group, Otwa County, Ohio; posterior view of internal mold of both valves, BMNH B 5959, ×0.8 (new).

Costitrimerella RONG & LI, 1993, p. 131[138] [**C. costellata;* OD]. Shell subcircular, costellate; ventral valve unknown; dorsal visceral platform solid, transversely oval, extending anteriorly to midvalve. *Ordovician (Ashgill):* China (Zhejiang).——FIG. 109,*3a–c.* **C. costellata,* Huangnekang Formation, Jiangshan, NIGP 119155; *a,* holotype, latex cast of dorsal external mold, NIGP 119155, ×4.2; *b,* latex cast of dorsal internal mold, ×3.3; *c,* holotype, lateral view, NIGP 119155, ×4.2 (Rong & Li, 1993).

Dinobolus HALL, 1871a, p. 4 [**Obolus conradi* HALL, 1867b, p. 368; OD] [=*Conradia* HALL, 1872b, p. 107, obj.]. Shell subequally biconvex, subcircular; lamellose peripherally; ventral pseudointerarea widely triangular with narrow homeodeltidium; ventral umbonal cavities vestigial; ventral visceral platform rhomboidal, somewhat hollow anteriorly, extending to midvalve and supported anteriorly by short median septum; dorsal visceral platform extending somewhat anteriorly to midvalve, supported anteriorly by short median septum; dorsal hinge plate short, low, slightly incurved. *Silurian (Llandovery–Wenlock):* USA, Canada, Great Britain, Ireland, Sweden (Gotland), Estonia, Russia (Siberia), Kazakhstan, China.——FIG. 109,*2a,b.* **D. conradi* (HALL), Cedarville, Ohio; *a,b,* ventral view of internal mold of both valves, lateral view, USNM 459666, ×0.8 (new).——FIG. 109,*2c. D. davidsoni* (SALTER); lectotype, dorsal view of internal mold of both valves, BMNH B 16510, ×1.2 (new).

Eodinobolus ROWELL, 1963, p. 37 [**Obolellina magnifica* BILLINGS, 1871c, p. 329; OD]. Shell subequally biconvex to weakly dorsibiconvex, subtriangular to transversely suboval; lamellose peripherally; ventral pseudointerarea orthocline, triangular, of variable height, with widely triangular, narrow homeodeltidium; visceral platforms of both valves massive, low elongated suboval, extending to or somewhat anterior of midvalve, sometimes with weak median ridge; ventral umbonal cavities absent; mantle canal system baculate; *vascula lateralia* of both valves short, subparallel or slightly convergent, lacking evidence of bifurcation; ventral *vascula media* subparallel. *Ordovician (Caradoc–Ashgill):* USA, Canada, Ireland, Great Britain, Estonia, Kazakhstan, Russia (Siberia, Urals), ?Uzbekistan, Australia.——FIG. 109,*4a–e.* **E. magnificus* (BILLINGS), Rockland Formation, Ontario; *a,* ventral valve exterior, USNM 116800a, ×1.2; *b,* ventral valve interior, USNM 116800d, ×1.2; *c,d,* dorsal valve exterior, oblique lateral view, USNM 116800b, ×1 (new); *e,* dorsal valve interior, GSC 1161b, ×1.2 (Cooper, 1956).

Fengzuella LI & HAN, 1980, p. 17 [**F. zhejiangensis;* OD]. Shell subpentagonal, dorsibiconvex; ventral pseudointerarea moderately high, with widely triangular, shallow, narrow homeodeltidium; ventral umbonal cavities poorly developed; ventral visceral platform broadly rhomboidal, bisected by low median ridge, slightly vaulted anteriorly, extending anteriorly to midvalve, supported anteriorly by short median septum; shallow cardinal socket bounded anteriorly by broad cardinal buttress, supported by low median ridge; dorsal interior with widely triangular, short, slightly vaulted anteriorly visceral platform, not extending to midvalve; supported by long median ridge that extends to anterior margin. *Ordovician (Ashgill):* China (Zhejiang).——FIG. 110,*1a,b.* **F. zhejiangensis;* Huangnekang Formation, Jiangshan, holotype, FD 144; *a,* ventral internal mold, ×3; *b,* dorsal internal mold, ×2.5 (Li & Han, 1980).

Gasconsia NORTHROP, 1939, p. 161 [**G. schucherti;* OD]. Shell convexiplane to convexiconcave; transversely suboval with long, straight posterior margin; ornament of indistinct low radial ribs, fine, concentric rugae; may be lamellose peripherally; ventral cardinal interarea low, apsacline, with narrow, poorly defined homeodeltidium; visceral platforms of both valves low, solid; median ridges of both valves vestigial or absent; dorsal hinge plate broad, low, bounded posteriorly by transverse furrow; mantle canal systems of both valves baculate with dorsal *vascula media. Ordovician (Ashgill)–Silurian (Ludlow):* Norway, Sweden, Kazakhstan, *Ashgill;* USA, *Wenlock;* Canada, Bohemia, *Ludlow.*——FIG. 110,*2a.* **G. schucherti,* Gascons and Bouleaux Formations, Quebec; paralectotype, dorsal internal mold, YPM 13312, ×1.7 (Hanken & Harper, 1985).——FIG. 110,*2b,c. G. worsleyi* HANKEN & HARPER, Bønsnes Formation, Rawtheyan, Ringerike, Oslo; *b,* holotype, ventral valve interior, PMO 13091, ×0.8, *c,* latex cast of dorsal internal mold, PMO 104.000, ×0.8 (Hanken & Harper, 1985). ——FIG. 110,*2d. G.* sp., Delphi, Indiana, USNM 62258; latex cast of dorsal internal mold, ×0.7 (new).

?Gyroselenella LI, 1985, p. 581, *nom. nov. pro Selenella* LI, 1984, p. 779, *non Selenella* HALL & CLARKE, 1894a [**Selenella circularis* LI, 1984, p. 779]. Genus poorly understood; known only from one valve, described as ventral but probably dorsal. *Ordovician (Ashgill):* China (Zhejiang).

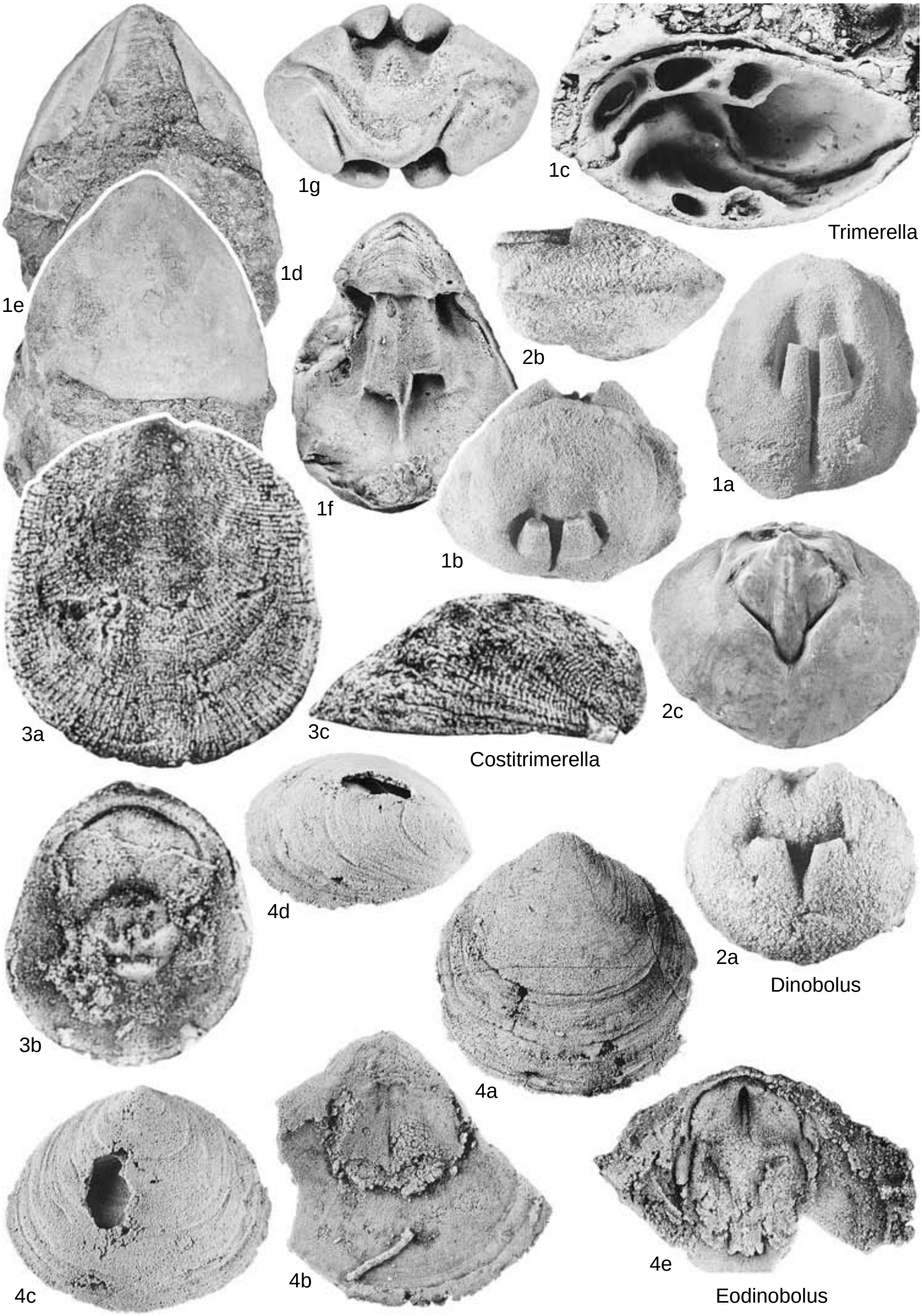

FIG. 109. Trimerellidae (p. 185–186).

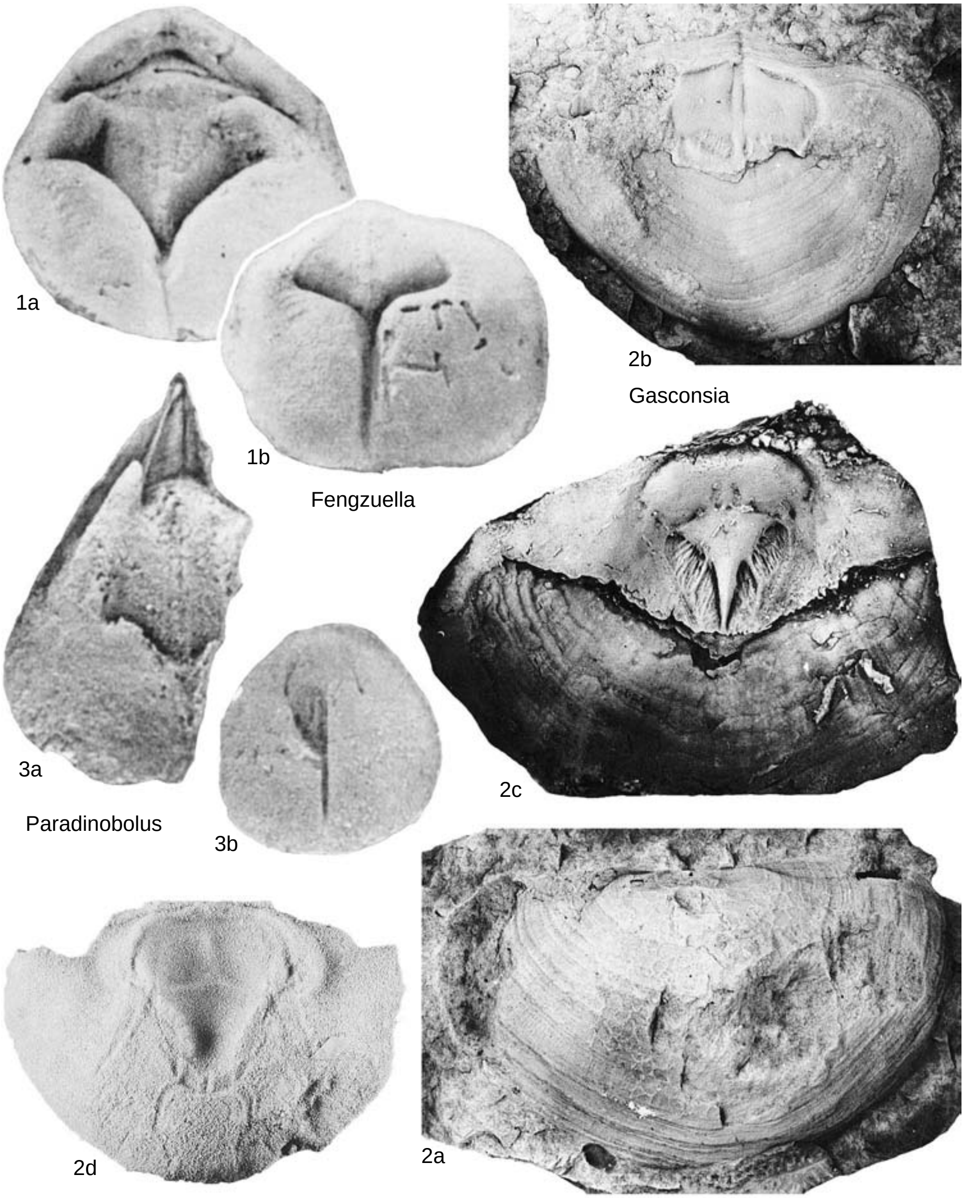

FIG. 110. Trimerellidae (p. 186–190).

Monomerella BILLINGS, 1871b, p. 220 [**M. prisca;* SD DAVIDSON & KING, 1874, p. 155]. Shell elongate subtriangular; sometimes ornamented by fine, concentric rugae; may be lamellose peripherally; ventral cardinal interarea apsacline, high, triangular, with broad, shallow homeodeltidium; dorsal valve moderately convex with incurved beak; ventral interior with deep umbonal cavities; ventral visceral platform slightly vaulted to solid, extending anteriorly to midvalve, bisected by median ridge that may be transformed anteriorly into high septum; dorsal visceral platforms vaulted anteriorly, supported by variably developed median ridge; ventral mantle canals baculate with well-defined *vascula media* and *vascula lateralia. Ordovician (Caradoc)–Silurian (Wenlock):* Australia, *Caradoc;* ?Kazakhstan, China, *Ashgill;* eastern USA, Canada, Sweden (Gotland), Estonia, *Wenlock.*——FIG. 111,*1a,b.* **M. prisca,*

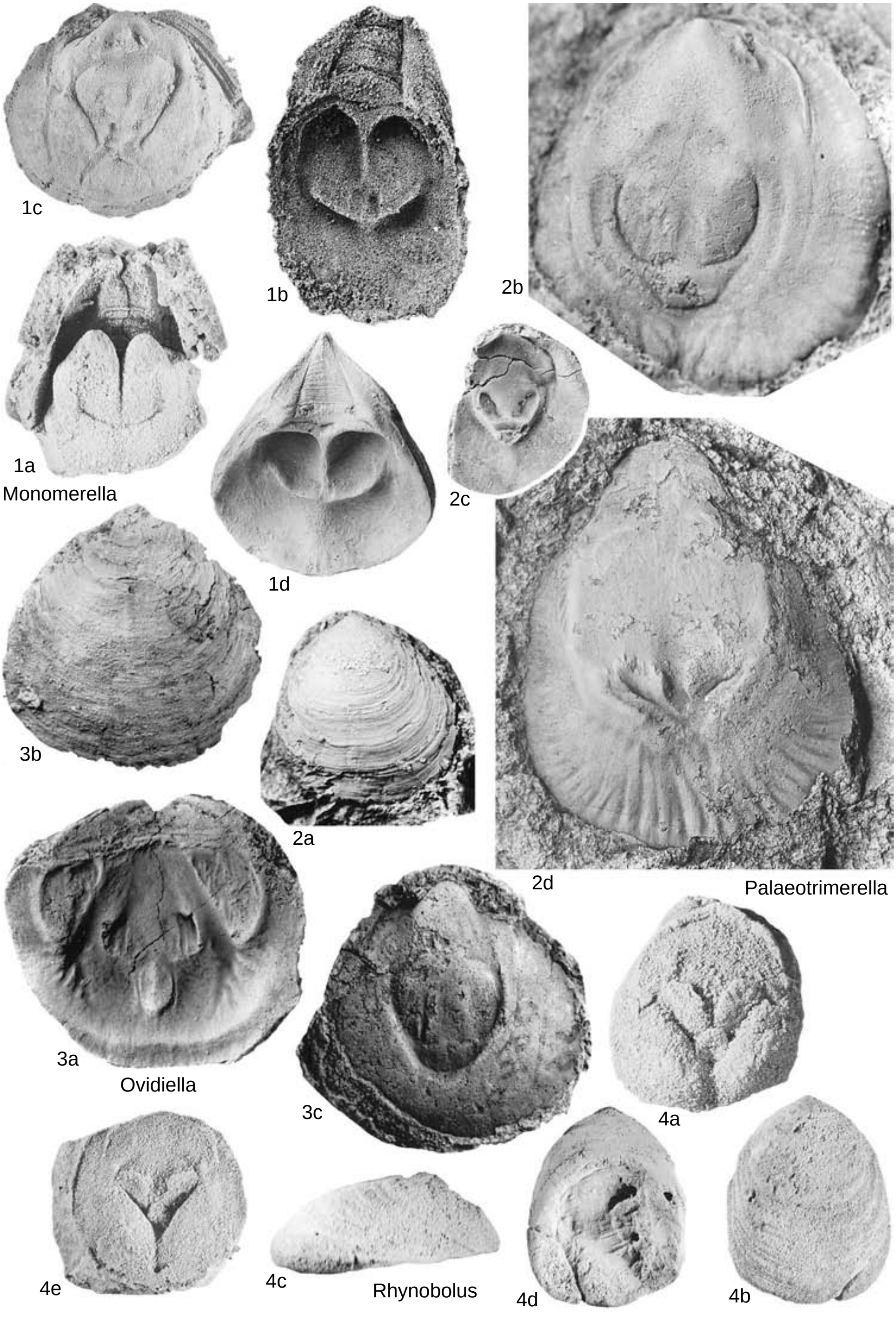

FIG. 111. Trimerellidae (p. 188–191).

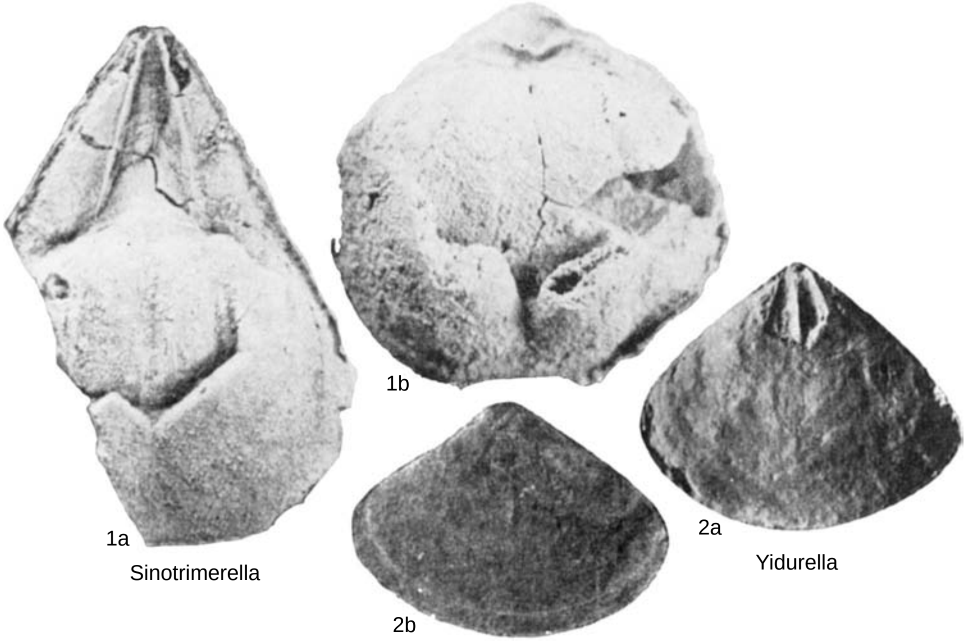

FIG. 112. Trimerellidae (p. 191).

Guelph Formation, Hespeler, Ontario; *a,* syntype, ventral internal mold, GSC 2811d, ×0.8; *b,* latex cast of ventral internal mold, USNM 67179, ×0.8 (new).——FIG. 111,*1c. M. greeni* HALL & CLARKE, Niagara Limestone, Rising Sun, Ohio; holotype, dorsal internal mold, OSU 7322, ×0.8 (new).——FIG. 111,*1d. M. walmstedti* DAVIDSON & KING, 1872, Slite beds, Fårön, Lanså, Gotland; ventral valve interior, RM Br 24443, ×0.8 (new).

Ovidiella NIKITIN & POPOV, 1984, p. 130 [**O. plana;* OD]. Shell dorsibiconvex with wide, straight posterior margin; subcircular; lamellose peripherally; ventral cardinal interarea moderately high, orthocline with very broad homeodeltidium and reduced propareas; dorsal valve moderately convex, beak slightly incurved; ventral interior with low, solid visceral platform, extending far anteriorly to midvalve; ventral scars of outside lateral and posterior adductor muscles on thickened, elongate semioval platforms; dorsal interior with solid, elongate oval visceral platform; ventral *vascula lateralia* with vestigial bifurcation; ventral *vascula media* short, subparallel; dorsal *vascula lateralia* bifurcate, with anterior branches slightly arcuate, convergent. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan. ——FIG. 111,*3a–c.* **O. plana,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,* holotype, ventral valve interior, CNIGR 15/12095, ×1.4; *b,* ventral valve exterior, CNIGR 17/12095, ×1.4; *c,* dorsal internal mold, CNIGR 19/12095, ×1.4 (Nikitin & Popov, 1984).

Palaeotrimerella LI & HAN, 1980, p. 10 [**P. orientalis;* OD]. Shell dorsibiconvex, elongate subtriangular; ornamented by irregular concentric rugellae, lamellose peripherally; ventral cardinal interarea high, orthocline, with shallow, relatively narrow homeodeltidium; dorsal valve moderately convex; ventral interior lacking umbonal cavities; visceral platforms of both valves low, solid, extending anteriorly to center, bisected by fine median ridges; dorsal visceral platform supported anteriorly by median septum; hinge plate low, thickened; mantle canal system bifurcate in both valves, with short subparallel *vascula media* in ventral valve. *Ordovician (Llandeilo–Ashgill):* Kazakhstan, China (Zhejiang).——FIG. 111,*2a–d. P. superba* NIKITIN & POPOV, Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,* dorsal valve exterior, CNIGR 13/12095, ×1.7; *b,* dorsal internal mold, CNIGR 8/12095, ×1.7; *c,* dorsal valve interior, CNIGR 8a/12095, ×1.7; *d,* ventral internal mold, CNIGR 1/11921, ×1.7 (Nikitin & Popov, 1984).

Paradinobolus LI & HAN, 1980, p. 19 [**P. sinensis;* OD]. Shell elongate oval; ventral cardinal interarea triangular, moderately high with narrow homeodeltidium; ventral interior without umbonal cavities; visceral platforms of both valves long, narrow, vaulted anteriorly, extending slightly anteriorly to midvalve, supported anteriorly by median septum. May be juvenile *Sinotrimerella. Ordovician (Ashgill):* China (Zhejiang).——FIG. 110,*3a,b.* **P. sinensis,* Huangnekang Formation, Jiangshan, Zhejiang, holotype, FD 152; *a,* ventral internal mold, ×2.5; *b,* dorsal internal mold, ×2.5 (Li & Han, 1980).

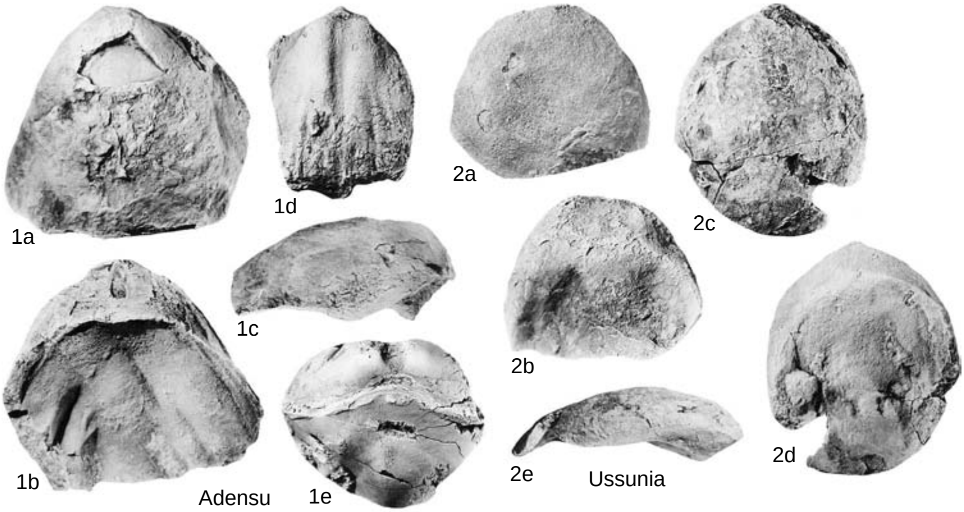

FIG. 113. Adensuidae and Ussuniidae (p. 191–192).

Peritrimerella LIANG, 1983, p. 257 [**P. chunanensis;* OD]. Similar to *Fengzuella* but convexoplane, lacking ventral umbonal cavities and median septum or ridge; short visceral platforms of both valves not extending to midvalve. *Ordovician (Ashgill):* China (Zhejiang).

Rhynobolus HALL, 1871a, p. 5 [**Obolus galtensis* BILLINGS, 1862c, p. 168; SD DALL, 1877, p. 61] [=*Obolellina* BILLINGS, 1871b, p. 222, obj.; *Rhinobolus* HALL & CLARKE, 1892, p. 44]. Shell elongate oval; ventral cardinal interarea high, triangular with broad homeodeltidium; ventral umbonal cavities vestigial; ventral visceral platform very low, solid; dorsal hinge plate small, slightly convex, bounded posteriorly by transverse furrow; dorsal visceral platform moderately high, slightly vaulted anteriorly; visceral platforms in each valve may be supported by weak median ridge. *Silurian (Wenlock):* USA, Canada, Sweden (Gotland).——FIG. 111,*4a–e.* **R. galtensis* (BILLINGS), Guelph Limestone, Ontario; *a,* holotype, dorsal view of internal mold of both valves, Galt, Canada, GSC 2818a, ×0.8; *b–d,* dorsal valve exterior, lateral view, interior, GSC 2820a, ×0.8; *e,* dorsal internal mold, Durham, Hespeler, GSC 2820b, ×0.8 (new).

Sinotrimerella LI & HAN, 1980, p. 13 [**S. jiangshanensis;* OD]. Shell elongate oval to subtriangular, dorsibiconvex; ventral cardinal interarea high, triangular, with broad, shallow to moderately deep homeodeltidium; visceral platforms of both valves extending anteriorly to midvalve, slightly vaulted, each bisected medially by fine ridge; dorsal visceral platform supported anteriorly by short median septum. *Ordovician (Ashgill):* China (Zhejiang).——FIG. 112,*1a,b.* **S. jiangshanensis,* Huangnekang Formation, Jiangshan; *a,* holotype, ventral internal mold, FD 149, ×1.3; *b,* paratype, dorsal internal mold, FD 148, ×1.5 (Li & Han, 1980).

Yidurella ZENG, 1987, p. 210 [**Y. yiduensis;* OD]. Shell subequally biconvex, transversely oval; ventral cardinal interarea short, triangular; ventral interior with an elongate, solid visceral platform bisected by fine median ridge, supported anteriorly by short septum; dorsal interior with long median septum anterior to narrow, solid visceral platform. *lower Silurian:* China.——FIG. 112,*2a,b.* **Y. yiduensis,* Shamao Formation, Tizikou, Yidu; *a,* paratype, ventral internal mold, IV 45872, ×0.8; *b,* paratype, dorsal internal mold, IV 45876, ×0.8 (Zeng, 1987).

Family ADENSUIDAE
Popov & Rukavishnikova, 1986

[Adensuidae POPOV & RUKAVISHNIKOVA, 1986, p. 58]

Shell strongly biconvex to spheroidal; elongate oval; ventral pseudointerarea low; both valves thickened posteriorly, lacking visceral platforms; lateral oblique muscles absent; ventral mantle canal system pinnate, ventral *vascula media* well developed. *Ordovician (upper Caradoc–lower Ashgill).*

Adensu POPOV & RUKAVISHNIKOVA, 1986, p. 58 [**A. monstratum;* OD]. Shell slightly ventribiconvex; ventral valve with strongly incurved posterior margin; ventral interior with broad, low median ridge bisecting visceral field; dorsal hinge plate massive, semielliptical, strongly incurved; dorsal anterior, posterior adductor muscles separated by deep, broad, widely divergent furrows; ventral *vascula lateralia, vascula media* very short. *Ordovician (upper Caradoc–lower Ashgill):* Kazakhstan.——FIG. 113,*1a–e.* **A. monstratum,* Dulankara Formation, Adensu River, Chu-Ili Range; *a–c,* holotype, dorsal valve exterior, interior, lateral view, CNIGR 1/

11544, ×0.4; *d,* paratype, ventral internal mold, CNIGR 9/11544, ×0.4; *e,* paratype, posterior view of internal mold of both valves, CNIGR 6/11544, ×0.4 (Popov & Rukavishnikova, 1986).

Family USSUNIIDAE
Nikitin & Popov, 1984

[Ussuniidae Nikitin & Popov, 1984, p. 127]

Posterior margin rounded; articulatory structures poorly developed; visceral platforms absent in both valves; ventral pseudointerarea vestigial. *Ordovician (Llandeilo–lower Caradoc).*

Ussunia Nikitin & Popov, 1984, p. 127 [**U. incredibilis;* OD]. Shell subequally biconvex, elongate oval; both valves thickened posteriorly; ventral interior with shallow, broad, median depression along posterior margin; ventral visceral field poorly defined, with two broad depressions diverging anteriorly; dorsal hinge plate vestigial; dorsal visceral field extending anteriorly to midvalve. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan.——Fig. 113,*2a–e.* **U. incredibilis,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,b,* paratype, dorsal valve exterior, interior, CNIGR 3/12095, ×0.8; *c–e,* paratype, ventral valve exterior, interior, lateral view, CNIGR 2/12095, ×0.8 (Nikitin & Popov, 1984).

RHYNCHONELLIFORMEA

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[[1]The University of Glasgow; [2]The University of California, Davis; and [3]formerly of the Natural History Museum, London]

Subphylum RHYNCHONELLIFORMEA Williams & others, 1996

[Rhynchonelliformea WILLIAMS & others, 1996, p. 1192]

Brachiopods with articulated calcitic shells, secondary layer basically fibrous; outer mantle lobe variably indented by periostracal slot between vesicular and lobate cells; hinge formed by margins of posterior interareas secreted by fused mantle lobes; articulatory structures essentially a pair of ventral teeth and dorsal sockets on either side of median indentations (delthyrium and notothyrium respectively) of interareas; pedicle of later groups developing from rudiment and occupying delthyrial area, filled with connective tissue, controlled by adjustor muscles; adductor muscles normally located posteromedially, diductor muscles flanking adductors ventrally, inserted in notothyrial region dorsally; alimentary tract without anus in living species; lophophore without median tentacle, tentacles double in post-trocholophous stages of growth; lophophore supported in later groups by calcitic extensions from dorsal hinge in form of crura, spiralia, or loops; mantle canal systems variable in branching, containing gonads, without marginal sinuses; larvae lecithotrophic, without shell, embryonic mantle in later groups undergoing reversal. *Lower Cambrian (Atdabanian)–Holocene.*

The rhynchonelliforms are the largest group of brachiopods and have been the dominant subphylum since Late Cambrian times, although only one of the five constituent classes is represented by living species. The definitive synapomorphy is the fibrous, secondary layer in a calcitic shell. The development of interareas, notched by a delthyrium and notothyrium, is shared with the linguliform paterinates. Similarly there is evidence to suggest that a functional anus persisted within the rhynchonelliforms at least to the emergence of the kutorginates and that the development of a pedicle from a rudiment is a synapomorphy of the only extant class, the Rhynchonellata.

CHILEATA

LEONID E. POPOV and LARS E. HOLMER

[VSEGEI, St. Petersburg; and University of Uppsala]

Class CHILEATA Williams & others, 1996

[Chileata WILLIAMS & others, 1996, p. 1192]

Shell strophic (with exception of Eichwaldiidae), ventral valve with mixoperipheral growth, dorsal valve with hemiperipheral growth; mantle lobes possibly fused posteriorly; ventral valve with cardinal interarea; ventral umbo with perforation enlarged anteriorly by resorption, usually covered posteriorly by colleplax; mantle canals pinnate. *Lower Cambrian (Botomian)–Permian.*

Order CHILEIDA Popov & Tikhonov, 1990

[Chileida POPOV & TIKHONOV, 1990, p. 39]

Strophic shell lacking hinge structures; ventral interarea flattened, widely triangular with delthyrium open or covered by variably developed convex pseudodeltidium; ventral umbonal perforation large subtriangular, sometimes covered posteriorly by colleplax; visceral fields in both valves placed close to posterior shell margin; musculature with posterior and anterior adductors; internal oblique muscles attached to apical part of

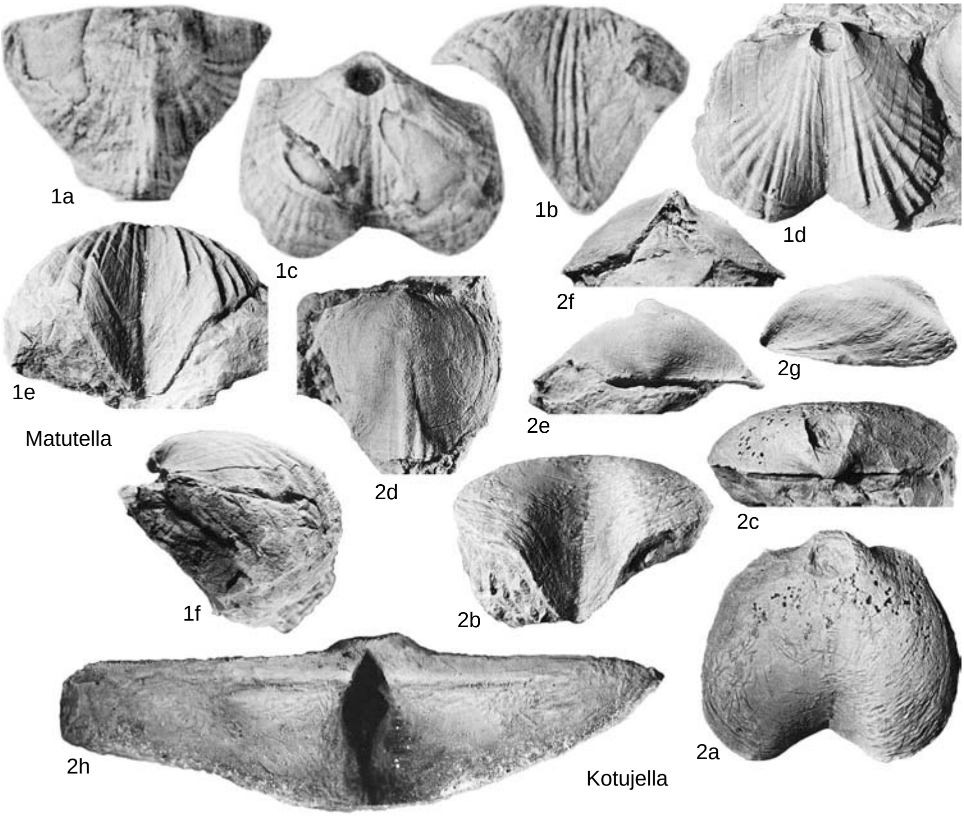

FIG. 114. Matutellidae (p. 195–196).

dorsal valve. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

The chileides first appeared in the Botomian and include the earliest known calcitic brachiopods with a strophic shell. Chileides lack any trace of articulatory structures along the posterior margin, and it is possible that the axis of rotation was fixed entirely by fused mantle lobes (POPOV & TIKHONOV, 1990; POPOV, 1992; HOLMER & POPOV, 1996b). Chileides also have an unusually large ventral umbonal perforation, which is enlarged by resorption and sometimes covered posteriorly by a plate. The plate is more or less identical in morphology to the colleplax described by WRIGHT (1981) in eichwaldioids. The function of the ventral perforation is not understood fully, but it is unlikely that it served as a pedicle opening, both because of its anterior position and due to the fact that the chileides also have a delthyrium. If it is homologous with a colleplax, it is possible that it was the site of an organic pad secreted by the outer epithelium, as proposed by WRIGHT (1981). POPOV and TIKHONOV (1990) and POPOV (1992) speculated that the perforation may have served as part of an hydraulic shell-opening mechanism. Chileide shell structure is known only from *Kotujella,* and according to WILLIAMS (1990) this may represent the oldest known endopunctate brachiopod with a fibrous secondary layer. The muscle system of the chileides is poorly understood; according to POPOV and TIKHONOV (1990), a set of internal oblique muscles may have attached posteromedially to the dorsal valve. Their location suggests that they are possibly ho-

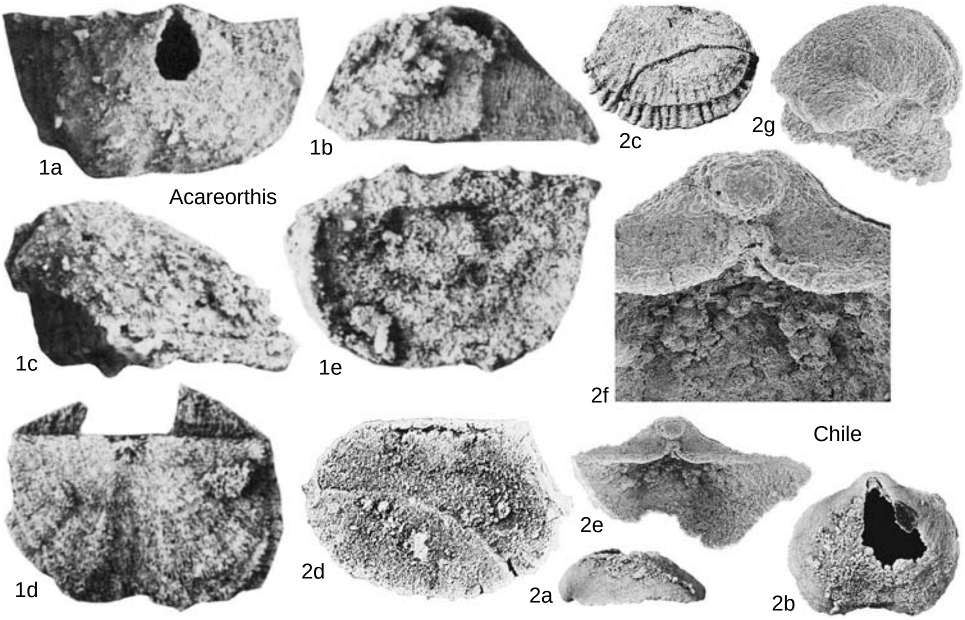

FIG. 115. Chileidae (p. 196).

mologous with the diductors of articulated brachiopods including obolellides, but because they are situated anterior to the axis of rotation they cannot have aided in shell opening. It is probable that chileides opened their shell by contraction of outside lateral muscles attached anteriorly to the body wall, comparable with the arrangement in recent craniides. In the Matutellidae, both valves have pinnate mantle canals; in *Chile* there are three pairs of main trunks in the ventral valve and only one pair in the dorsal valve.

Superfamily MATUTELLOIDEA Andreeva, 1962

[*nom. correct.* HOLMER & POPOV, herein, *pro* Matutellacea ANDREEVA, 1987, p. 33, *nom. transl. ex* Matutellidae ANDREEVA, 1962, p. 90]

Characters as for order. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

Family MATUTELLIDAE Andreeva, 1962

[Matutellidae ANDREEVA, 1962, p. 90]

Shell dorsibiconvex, anterior commissure uniplicate; ventral valve with sulcus, open triangular delthyrium, which may be covered apically by convex pseudodeltidium; broad triangular opening anterior to beak not extending to midvalve, covered posteriorly by small concave plate; dorsal valve with strong median fold; mantle canal system of ventral valve pinnate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

Matutella COOPER, 1951, p. 6 [**M. clarki;* OD]. Shell subquadrate in outline, costellate, sporadically imbricate; homeodeltidium small, apical. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* USA, Russia (Siberia, Altai).——FIG. 114,*1a–c.* **M. clarki,* Shady Formation, northeast of Austinville, Virginia; *a,* dorsal valve exterior, USNM 111689k, ×1.7; *b,* anterior view of ventral valve, USNM 111689d, ×1.7; *c,* holotype, ventral valve exterior, USNM 111689n, ×1.7 (Cooper, 1951).——FIG. 114,*1d–f. M. grata* ANDREEVA, Toyonian, Rassokha River, Siberia; ventral valve exterior, anterior view, lateral view, CNIGR 8202, ×1.7 (new).

Kotujella ANDREEVA, 1962, p. 94 [**K. calva;* OD]. Shell externally similar to *Matutella,* but smooth and lacking pseudodeltidium. *Lower Cambrian (Toyonian):* Russia (Siberia).——FIG. 114,*2a–h.* **K. calva,* Rassokha River, Siberia; *a–c,* ventral valve exterior, anterior view, posterior view, CNIGR 8202, ×1.7; *d–g,* dorsal valve exterior, posterior view, anterior view, lateral view, CNIGR 8202,

×1.7 (new); *h,* ventral valve interior, CNIGR 24/8202, ×5 (Andreeva, 1962).

Family CHILEIDAE Popov & Tikhonov, 1990

[Chileidae POPOV & TIKHONOV, 1990, p. 39]

Shell inequibiconvex, or planoconvex; anterior commissure rectimarginate; pseudodeltidium commonly present; large, subtriangular perforation anterior to beak extending to midvalve. *Lower Cambrian (Botomian)–Middle Cambrian (lower Amgaian).*

Chile POPOV & TIKHONOV, 1990, p. 39 [**C. mirabilis;* OD]. Shell ventribiconvex, semielliptical; smooth apically, costellate peripherally; ventral interarea low, orthocline; delthyrium small, covered apically by convex pseudodeltidium; large, elongate triangular perforation extending anteriorly to midvalve, covered apically by colleplax; ventral mantle canals with two or three pairs of main trunks; dorsal *vascula lateralia* widely divergent. *Lower Cambrian (Botomian):* south Kirghizia.——FIG. 115,*2a–g.* **C. mirabilis,* southern Tien Shan Range, Chachme River; *a,b,* holotype, lateral view of ventral valve exterior, exterior, CNIGR 3/12589, ×3.3; *c,* dorsal valve exterior, ×3.3; *d,* paratype, dorsal valve interior, CNIGR 7/12589, ×4.2 (Popov & Tikhonov, 1990); *e,* ventral valve interior, ×7.5; *f,* paratype, detail of ventral interarea, delthyrium, RMS Br 136454, ×22.9; *g,* paratype, lateral view of ventral valve exterior, RMS Br 136455, ×12.5 (new).

Acareorthis ROBERTS in ROBERTS & JELL, 1990, p. 268 [**A. jelli;* OD]. Shell planoconvex, bisulcate, subrectangular; ornament of costae and concentric lamellae; ventral interarea high triangular, catacline to apsacline, bisected by narrow, convex pseudodeltidium; dorsal interior with transverse ridge along posterior margin, divided medially by thickened internal oblique muscle scars; dorsal posterior, anterior adductor scars deeply impressed. *Lower Cambrian (Toyonian)–Middle Cambrian (lower Amgaian):* Greenland, *Toyonian;* Australia (New South Wales), *lower Amgaian.*——FIG. 115,*1a–e.* **A. jelli,* Coonigan Formation, Mootwingee area, New South Wales; *a,* holotype, ventral valve exterior, AMF 79654, ×12.5; *b,* paratype, ventral valve, posterior view, AMF 79657, ×10; *c,* paratype, ventral valve, lateral view, AMF 79658, ×12.5; *d,* paratype, dorsal valve exterior, AMF 79659, ×12.5; *e,* paratype, dorsal valve interior, AMF 79663, ×15 (Roberts & Jell, 1990).

DICTYONELLIDA

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Order DICTYONELLIDA Cooper, 1956

[*nom. transl.* HOLMER, herein, *ex* Dictyonellidina ROWELL, 1965b, p. 359, *nom. correct. pro* suborder Dictyonelloidea COOPER, 1956, p. 947]

Ventral interarea variably developed; ventral perforation extending anterior to umbo through resorption and covered by colleplax; delthyrium open or covered by concave pseudodeltidium; dorsal valve with cardinal process, high median septum; dorsal mantle canals pinnate. *Upper Ordovician (Caradoc)–Lower Permian (Artinskian).*

The systematic position of the Eichwaldiidae and Isogrammidae has long remained uncertain (ROWELL, 1965b; WRIGHT, 1981); they have been considered to be closely related to each other and this is also supported by our cladistic analysis (see Fig. 89). The inferred relationship between the eichwaldiids and isogrammids is based mainly on the presence of a smooth, triangular area at the umbo, which is enlarged by shell resorption and covered posteriorly by a plate, having a slitlike opening to the interior (Fig. 116.2a, 116.3a). This peculiar structure was termed the colleplax by WRIGHT (1981) and was known previously only from the dictyonellides; however, a similar structure is now also known to be present in the Chileida (Fig. 116.1a). If it is homologous, the dictyonellides may form a monophyletic group together with the Cambrian Chileida, as suggested by cladistic analysis (see Fig. 89). WRIGHT (1981) assumed that the colleplax was the site of an organic pad secreted by the outer epithelium, rather than serving as a passage for the pedicle. The isogrammids and eichwaldiids differ from each other in other aspects of their morphology; the Eichwaldiidae has a nonstrophic shell with a concave pseudodeltidium, while the Isogram-

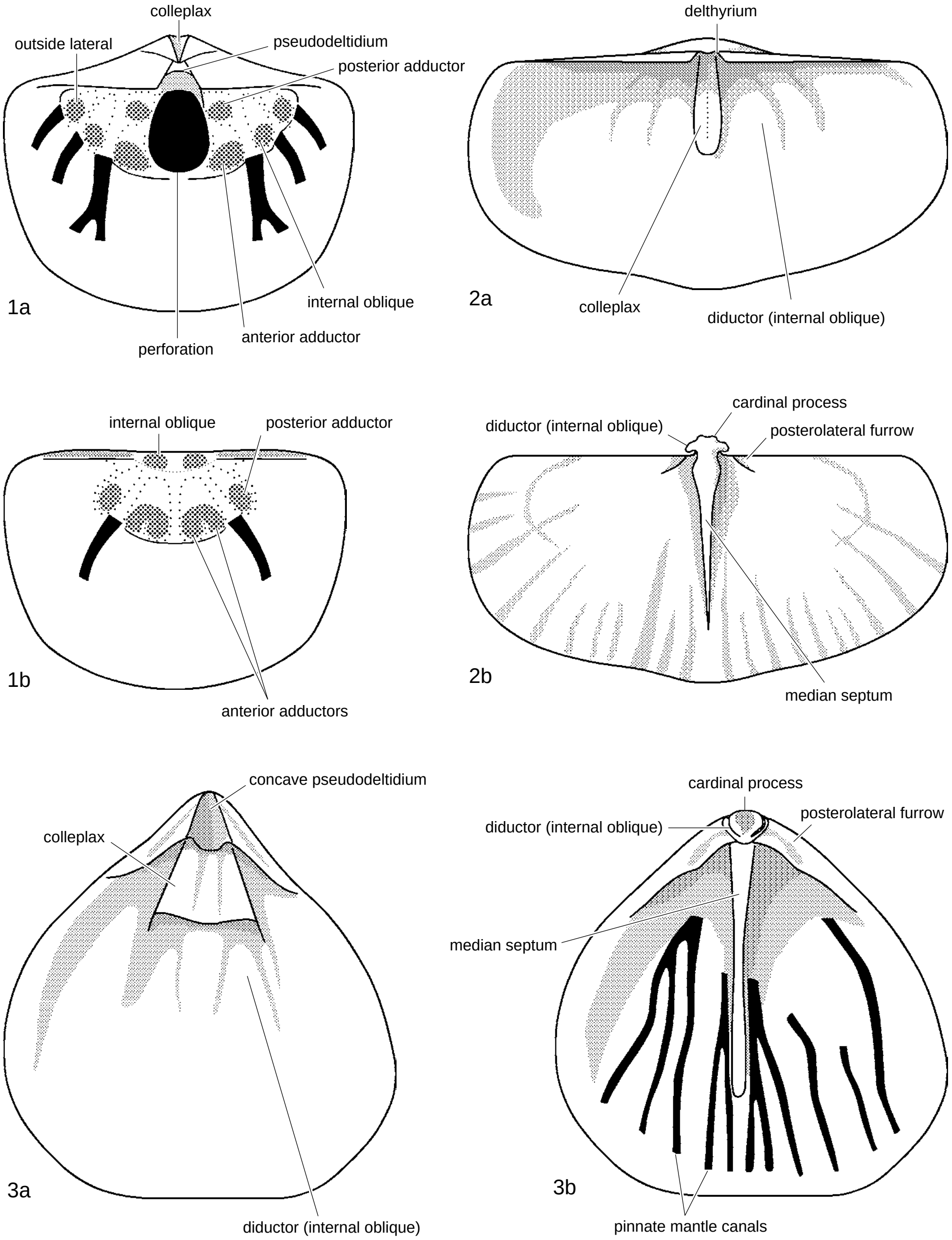

FIG. 116. Schematic illustration of musculature, mantle canal system, and articulation of Dictyonellida and Chileida; *1a,b,* ventral, dorsal valve of *Chile; 2a,b,* ventral, dorsal valve of *Isogramma; 3a,b,* ventral, dorsal valve of *Eodictyonella* (new).

midae is characterized by a strophic shell with a triangular delthyrium (Fig. 116.2–116.3). The muscle system is inadequately known in both families, but the presence of a cardinal process in both groups (Fig. 116.2b, 116.3b) suggests that they may have had diductor muscles as in articulated brachiopods (ROWELL, 1965a); in some

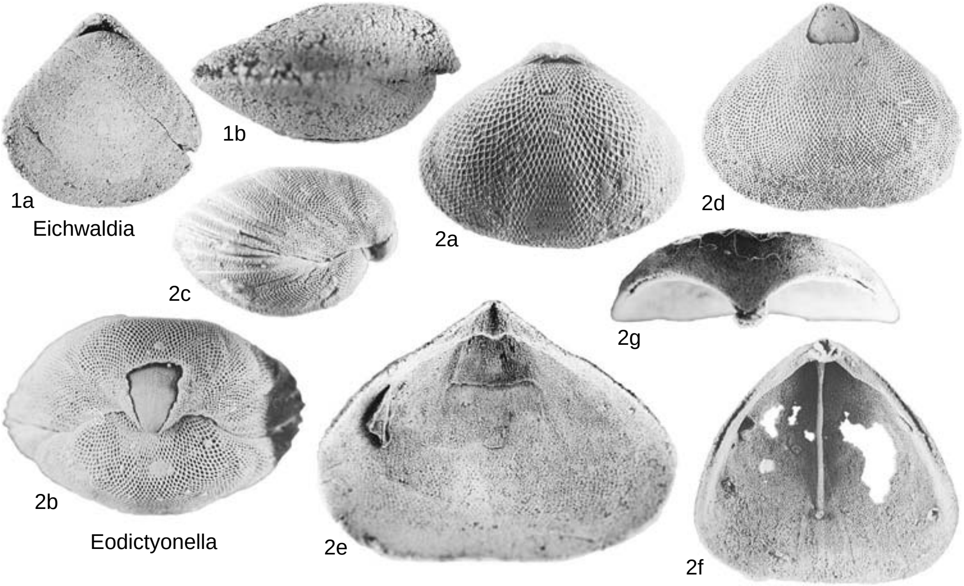

FIG. 117. Eichwaldiidae (p. 198–200).

isogrammids (*Megapleuronia*), the dorsal attachment of the diductor muscle is located on a high platform. They differ from the articulated brachiopods, however, in having a different type of articulation; in the Eichwaldiidae, the lateral movements of the valves are restricted both by furrows on the posterolateral margins of the dorsal valve as well as an incurved dorsal beak, fitting tightly into the concave pseudodeltidium (Fig. 116.2ab). In the Isogrammidae, the articulatory structures include small posterolateral furrows located lateral to the cardinal process (Fig. 116.3ab). The shell of eichwaldiids is endopunctate and has a fibrous secondary layer (WRIGHT, 1981), while the original shell structure in the Isogrammidae is unknown. It would seem that the latter are preserved invariably as internal molds and casts or have become silicified; this type of preservation may suggest that the shell of isogrammids was originally aragonitic, but further work is needed to clarify this problem. The mantle canals of isogrammids are poorly known and known only from the dorsal valve of *Megapleuronia,* which has a pinnate condition. In the Eichwaldiidae, the dorsal mantle canals of *Eodictyonella* also appear to be pinnate (Fig. 116.2b).

Superfamily EICHWALDIOIDEA Schuchert, 1893

[*nom. correct.* HARPER & others, 1993, p. 435, *pro* Eichwaldiacea ROWELL, 1965b, p. 359, *nom. transl. ex* Eichwaldiidae SCHUCHERT, 1893, p. 155]

Characters as for order. *Upper Ordovician (Caradoc)–Lower Permian (Artinskian).*

Family EICHWALDIIDAE Schuchert, 1893

[Eichwaldiidae SCHUCHERT, 1893, p. 155]

Shell biconvex, triangular; ventral interarea high, subtriangular with reduced propareas; pseudodeltidium broad, concave; dorsal posterolateral margins with long, oblique furrows, serving as articulatory structures; shell punctate with fibrous secondary layer. *Upper Ordovician (Caradoc)–Lower Devonian.*

Eichwaldia BILLINGS, 1858, p. 190 [**E. subtrigonalis;* OD]. Ornament of fine fila; dorsal median septum prominent, extending close to anterior margin, with cardinal process forming boss at posterior end of septum; musculature unknown. *Ordovician*

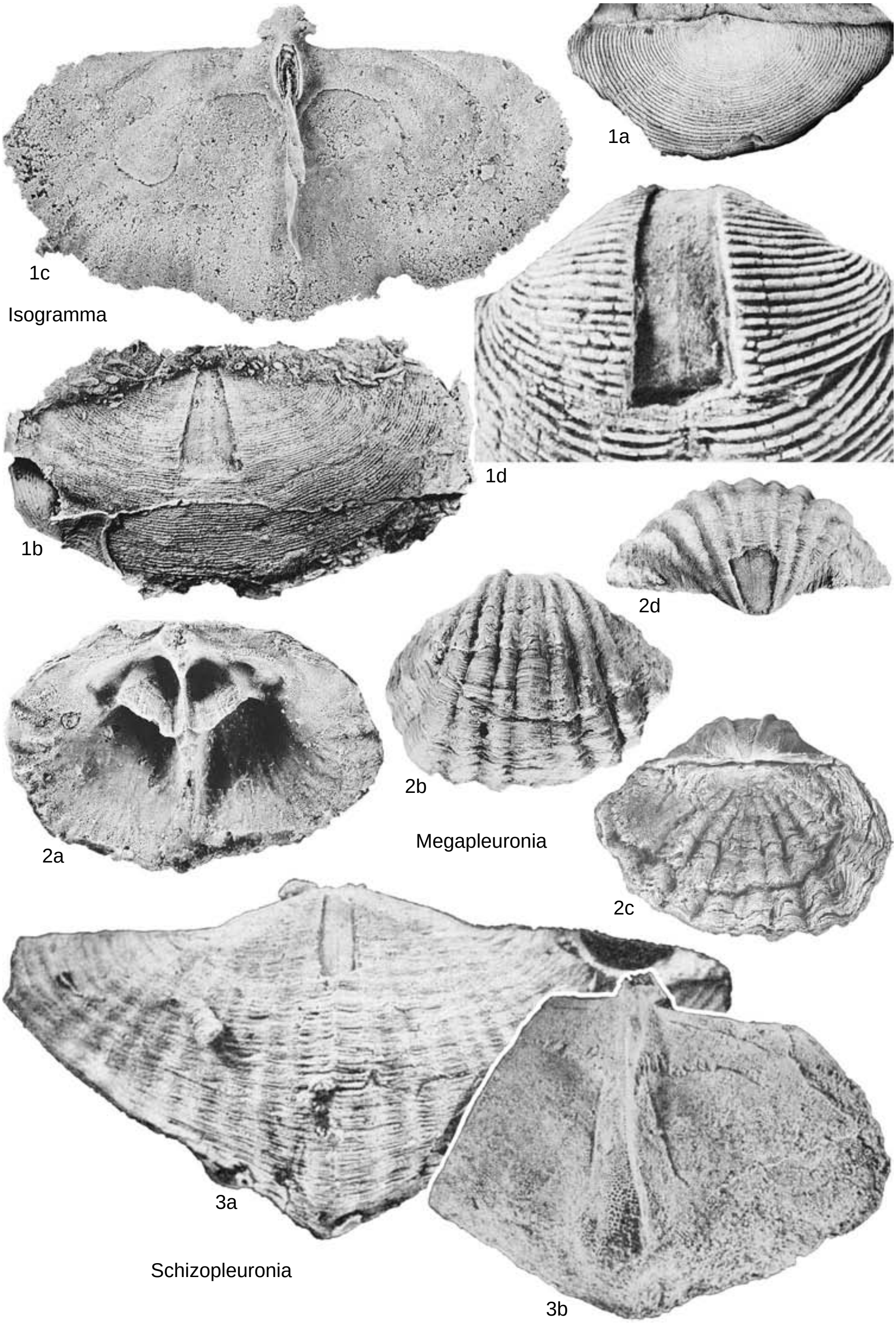

FIG. 118. Isogrammidae (p. 200).

(Caradoc): Canada (Ontario, Quebec).——FIG. 117,*1a,b.* **E. subtrigonalis,* Ottawa Formation, Allumette Island, Quebec; *a,* dorsal view of both valves, ×1.7; *b,* oblique lateral view of both valves, GSC 1145, ×3.3 (new).

Eodictyonella WRIGHT, 1994a, p. 908, *nom. nov. pro Dictyonella* HALL, 1867a, p. 274, *non Dictyonella* SCHMIDT, 1868, p. 10 [**Atrypa coralifera* HALL, 1852, p. 281; OD] [=*Dyctionella* OEHLERT, 1887b, p. 1267]. Similar to *Eichwaldia,* but with ornament of coarse pits, formed by intersecting, offset radiating rows of narrow ridges. *Ordovician (Ashgill)–Lower Devonian:* USA, Canada, *Ashgill–Silurian;* Great Britain, Sweden, Estonia, Bohemia, Russia (Altai), Ukraine (Podolia), China, *Silurian;* Kazakhstan, *Silurian–Lower Devonian.*——FIG. 117,*2a–c. D. reticulata* (HALL), Waldron Shale, Silurian, Waldron, Indiana; *a,* dorsal view of both valves, AMNH 36636, ×2.5; *b,* posterior view of both valves, ×2.7; *c,* lateral view of both valves, USNM 303732, ×2.1 (new).——FIG. 117,*2d–g. D. gibbosa* (HALL), Decatur Formation, Silurian, Linden, Tennessee; *d,* ventral valve exterior, USNM 459702a, ×2.9; *e,* ventral valve interior, USNM 459702b, ×4.7; *f,* dorsal valve interior, ×2.5; *g,* posterior view, dorsal valve interior, USNM 459702c, ×2.8 (new).

Family ISOGRAMMIDAE
Schuchert, 1929

[Isogrammidae SCHUCHERT, 1929, p. 18] [*incl.* Megapleuroniinae LIAO, 1983, p. 637]

Shells transversely suboval; ventral interarea wide, flattened; delthyrium open, triangular; cardinal process with well-developed shaft; posterolateral furrows small, located lateral to cardinal process. *Carboniferous–Permian.*

Isogramma MEEK & WORTHEN, 1870, p. 36 [*?*Chonetes millipunctatus* MEEK & WORTHEN, 1870, p. 35; OD] [=*Aulacorhynchus* VON DITTMAR, 1872, p. 2, *non* GOULD, 1834; *Aulacorhyna* STRAND, 1928, p. 37, *nom. nov. pro Aulacorhynchus* VON DITTMAR, 1872 (type, *Aulacorhynchus pachti* VON DITTMAR, 1872, p. 2), *non* GOULD, 1834]. Large, concavoconvex; ornament of strong, concentric, elevated fila; myophore strong; shaft bifurcating around dorsal median ridge. *Carboniferous–Permian:* Great Britain, Austria, Germany, Spain, Poland, Kazakhstan, Uzbekistan, *Carboniferous;* USA, European Russia, Ukraine, China, *Carboniferous–Permian;* Japan, *Permian.*——FIG. 118,*1a,b. I. texanum* COOPER, Gaptank Formation, Carboniferous, Marathon, western Texas; *a,* dorsal external mold, ×1.1; *b,* holotype, ventral external mold, USNM 111688a, ×1.1 (Cooper, 1952a).——FIG. 118,*1c. I. lobatum* COOPER & GRANT, Cathedral Mountain Formation, Permian, western Texas; dorsal interior, USNM 151384, ×0.8 (Cooper & Grant, 1974).——FIG. 118,*1d. I. salteri* BRAND, Hotwells Limestone, Carboniferous, Compton Martin, Somerset; detail of colleplax, BGS Zo1525, ×5 (Wright, 1981).

Megapleuronia COOPER, 1952a, p. 117 [**Productus fabianii* GRECO, 1947, p. 1; OD]. Biconvex or concavoconvex; costate, with discontinuous, raised fila; ventral interior unknown; dorsal muscle platform free, supported by median septum. *Permian:* Italy (Sicily).——FIG. 118,*2a.* **M. fabianii* (GRECO), Sosio Limestone, Pietra di Salamone, Sosio Valley; dorsal valve interior, USNM 116346, ×1.2 (Cooper, 1952a).——FIG. 118,*2b–d. M. grecoi* COOPER, Sosio Limestone, Pietra di Salamone, Sosio Valley; holotype, ventral view, dorsal view, posterior view of both valves, USNM 116347b, ×1.2 (Cooper, 1952a).

Schizopleuronia LIAO, 1983, p. 637 [**S. grandis;* OD]. Externally similar to *Megapleuronia,* but sulcate, lacking dorsal muscle platform. *Permian:* China.——FIG. 118,*3a,b.* **S. grandis,* Heshan Formation, Guangxi; *a,* holotype, ventral view, NIGP 70460, ×0.8; *b,* paratype, dorsal valve interior, NIGP 70462, ×0.8 (Liao, 1983).

OBOLELLATA

LEONID E. POPOV and LARS E. HOLMER
[VSEGEI, St. Petersburg; and University of Uppsala]

Class OBOLELLATA
Williams & others, 1996

[Obolellata WILLIAMS & others, 1996, p. 1192]

Shell biconvex, foliated, impunctate; both valves with hemiperipheral growth and well-defined interareas; ventral interarea with delthyrium, usually covered by concave pseudodeltidium, rarely open; articulatory structures variably developed; musculature probably with internal oblique muscles attached to dorsal valve posteromedianly. *Lower Cambrian–Middle Cambrian (Amgaian).*

Order OBOLELLIDA
Rowell, 1965

[Obolellida ROWELL, 1965a, p. 291]

Anterior commissure rectimarginate or slightly sulcate; ventral interarea low and relatively short; delthyrium open, or covered by convex pseudodeltidium; paired denticles, if present, lacking supporting structures; mantle canal system baculate in both valves, with ventral and dorsal *vascula lateralia* and dorsal *vascula media;* impunctate with laminar secondary layer. *Lower Cambrian–Middle Cambrian (Amgaian).*

The obolellides were usually united previously with the siphonotretoids, but ROWELL (1962a, 1965a) recognized them as a separate superfamily and order. The possible monophyly of the order could not be confirmed by our cladistic analysis, where they were used as an outgroup; the same analysis suggests that the Naukatidina forms a monophyletic group within the Obolellida as well as the Trematobolidae (see Fig. 89). The obolellides include the earliest known calcitic brachiopods and are known from the lower Atdabanian (PELMAN, 1977); the poorly known late Tommotian obolellide *Nochoroiella* (GRIGORIEVA, MELNIKOVA, & PELMAN, 1983) is here considered to be of problematic affinity. The group includes both forms that lack articulation, as well as those that have primitive articulation, consisting of paired ventral denticles and dorsal sockets (Fig. 119). The denticles are first known from forms within the Obolellidae, where they are composed partly of primary shell, while the Trematobolidae and Naukatida have denticles consisting entirely of secondary shell (POPOV, HOLMER, & BASSETT, 1996). The denticles lack supporting structures in all Obolellida, but in Naukatida they are supported by an arcuate plate below the interarea, the anterise (Fig. 119.3a). An open delthyrium is present only in the Obolellidae; in all other obolellides the delthyrium is covered by a concave pseudodeltidium (Fig. 119). According to GORJANSKY and POPOV (1985, 1986), the muscle system in the Obolellida is closely comparable with that of other articulated brachiopods in having anterior and posterior adductor scars, which form a quadripartite muscle field in the dorsal valve; and a single pair of oblique muscles, the internal oblique muscles, attached dorsally to a small area at the bottom of the notothyrial cavity (Fig. 119). In *Obolella,* the ventral muscle scars are located peripherally within the visceral area, but in most genera they form a single muscle field, with the adductor scars located medially. In articulated obolellides, the attachment scar of the internal oblique muscles is located posterior to the axis of rotation, suggesting that they may have served as diductors (Fig. 119).

Superfamily OBOLELLOIDEA
Walcott & Schuchert, 1908

[*nom. correct.* HARPER in HARPER & others, 1993, p. 431, *pro* Obolellacea GORJANSKY, 1960, p. 180, *nom. imperf., nom. transl. ex* Obolellidae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 145]

Characters as for order. *Lower Cambrian–Middle Cambrian (Amgaian).*

Family OBOLELLIDAE
Walcott & Schuchert, 1908

[Obolellidae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 145]

Ornament of fine, radial capillae; ventral valve with open delthyrium; articulation lacking or vestigial, with paired denticles on delthyrial margins, composed partly of primary shell; dorsal adductor scars radially arranged; ventral *vascula lateralia* submedian, divergent; dorsal *vascula lateralia* submarginal. *Lower Cambrian.*

Obolella BILLINGS, 1861b, p. 6 [**O. chromatica;* SD DALL, 1870, p. 163]. Shell weakly biconvex, subcircular or elongate oval; ornament of fine striae, lamellose peripherally; ventral interarea low, narrow, apsacline to catacline; ventral beak marginal; dorsal interarea low, orthocline; ventral visceral field forming low, solid platform, bisected by shallow median groove. *Lower Cambrian (Atdabanian, ?Botomian):* USA, Canada, Greenland, Russia (Siberia, Altai), ?Norway, China, Spain, Australia.——FIG. 120,*2a–c.* **O. chromatica,* Labrador, Canada; *a,* ventral valve interior, GSC 395i, ×4.2 (new); *b,* dorsal valve exterior, USNM 14891c, ×3.3 (Rowell, 1962a); *c,* dorsal interior, GSC 395m, ×4.2 (new).——FIG.

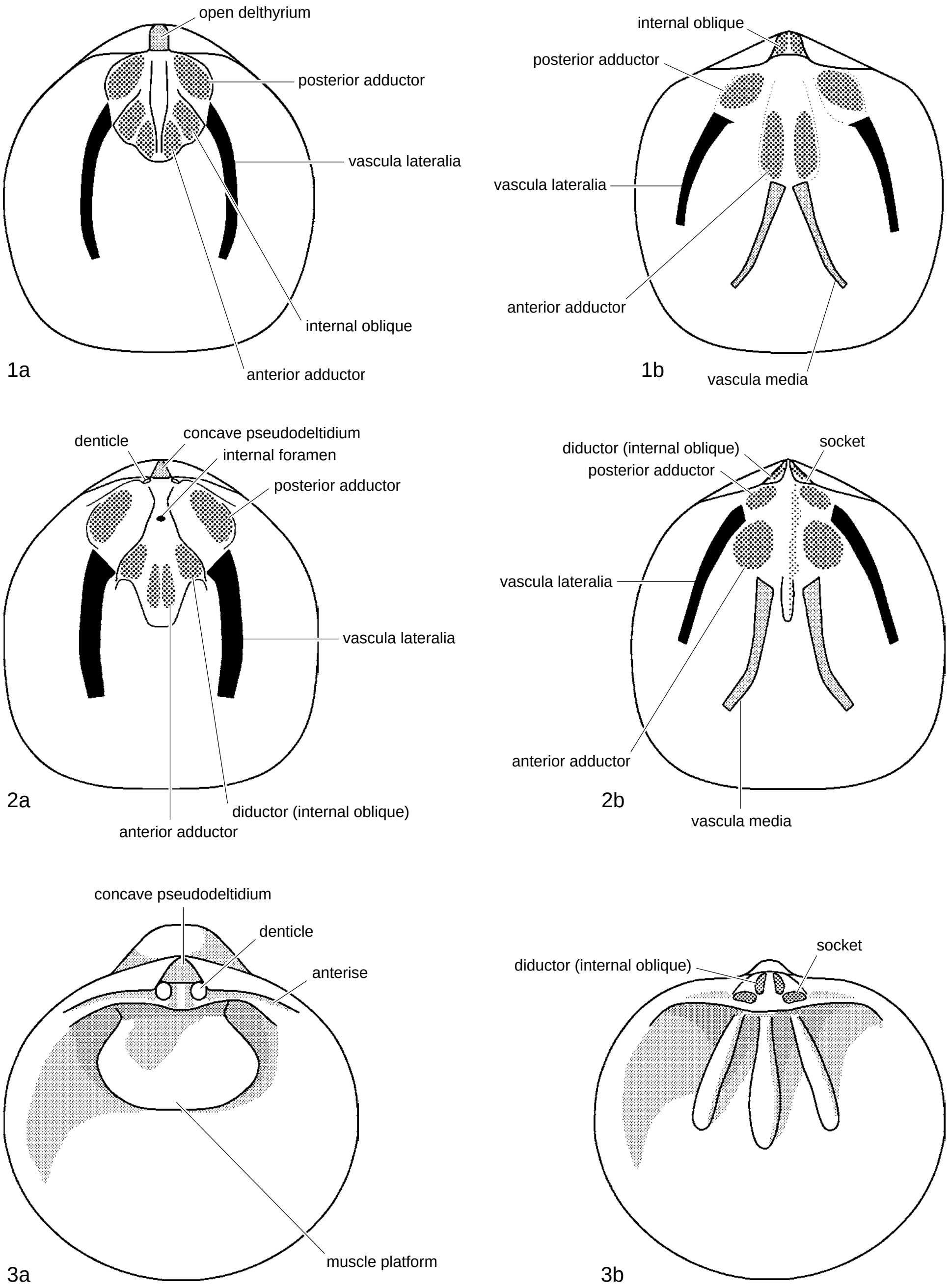

FIG. 119. Schematic illustration of musculature, mantle canal system, and articulation of Obolellida; *1a,b,* ventral, dorsal valve of *Obolella; 2a,b,* ventral, dorsal valve of *Trematobolus; 3a,b,* ventral, dorsal valve of *Oina* (new).

120,*2d–f. O. crassa* (HALL), Troy, New York; *d,* ventral valve interior, USNM 51951f, ×3.3; *e,* dorsal internal mold, USNM 51951, ×3.3; *f,* ventral valve exterior, USNM 14691, ×2.5 (new).

Bicia WALCOTT, 1901, p. 676 [**Obolella gemma* BILLINGS, 1871b, p. 218; OD]. Shell subtriangular or ovate; ornament of weak, radial striae; ventral beak subacuminate; ventral interarea relatively high,

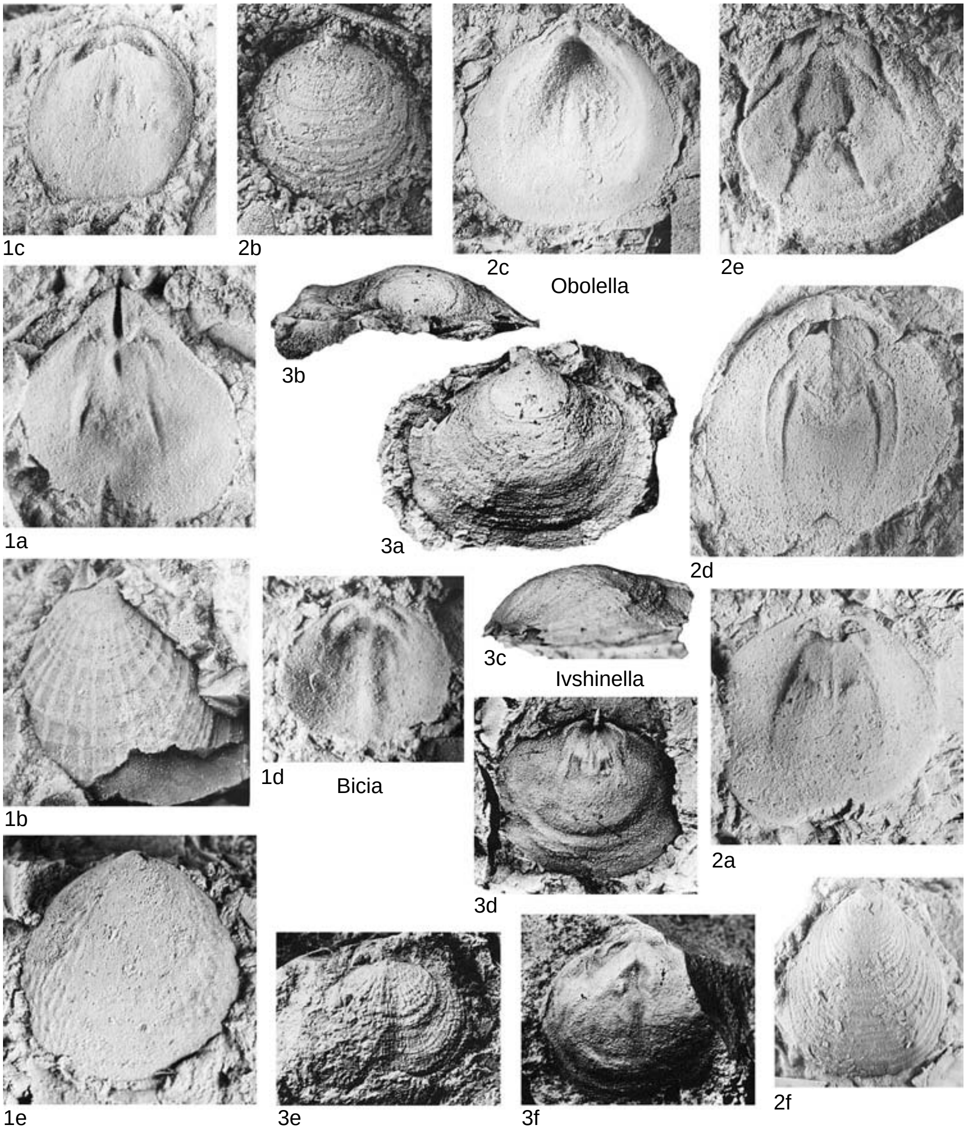

FIG. 120. Obolellidae (p. 201–204).

orthocline, triangular, with delthyrium, bearing small denticles; dorsal pseudointerarea low, orthocline; ventral visceral field thickened, extending to midvalve, with median depression; dorsal median ridge broad, extending from beak; ventral *vascula lateralia* submedian, widely divergent. *Lower Cambrian:* USA, Russia (southeastern Siberia).——FIG. 120,*1a–e.* **B. gemma* (BILLINGS), Troy, New York; *a,* ventral valve interior, GSC 387d, ×6.7; *b,* ventral valve exterior, USNM 51900, ×6.1; *c,* dorsal internal mold, USNM 51900d, ×5; *d,* dorsal valve interior, USNM 14889f, ×5; *e,* dorsal valve exterior, GSC 387, ×6.7 (new).

Brevipelta GEYER, 1994, p. 996 [**B. chouberti* GEYER, 1994, p. 997; OD]. Ventral valve with deep delthyrial opening; ventral visceral field poorly defined; dorsal median septum poorly defined; dorsal adductor scars poorly defined; ventral *vascula lateralia* submedian, divergent. *Lower Cambrian:* Morocco, *Choubertella* and *Daguinaspis* Zones.——FIG. 121,*1a–d.* **B. chouberti,* Lower Cambrian, Amouslek Formation, western Anti-Atlas

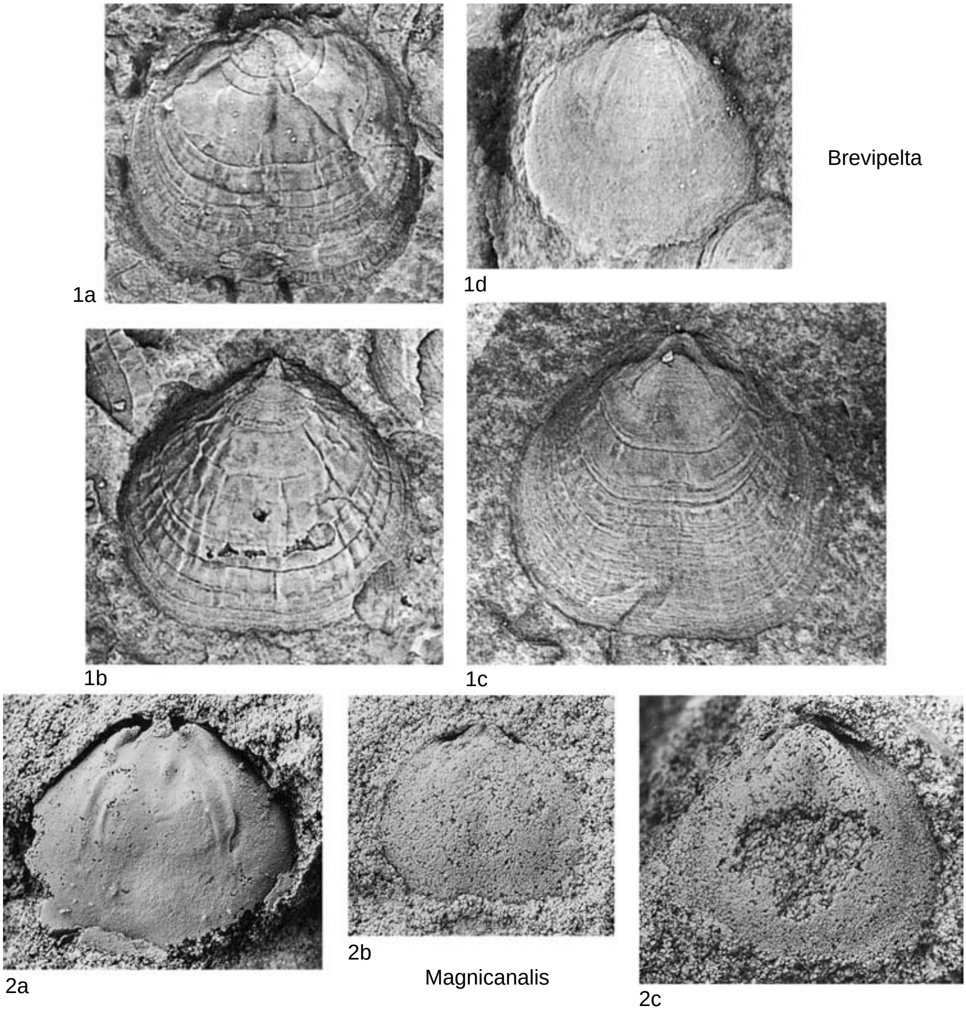

FIG. 121. Obolellidae (p. 203–205).

Mountains; *a,* dorsal valve exterior, IGR 19994g, ×6; *b,* ventral valve exterior, PIW 93119b, ×6; *c,* dorsal internal mold, PIW 93119q, ×6; *d,* ventral internal mold, PIW 93118a, ×6 (Geyer, 1994).

Ivshinella KONEVA, 1979, p. 54 [**I. modesta;* OD]. Shell almost equibiconvex, subcircular, or transversely oval; ornament of radial striae; ventral interarea orthocline, with low, triangular delthyrium, bearing small denticles; dorsal valve slightly sulcate; dorsal interarea low, orthocline; ventral visceral field moderately thickened, extending anteriorly to midvalve; dorsal visceral field broad, elongate oval, slightly thickened, extending to midvalve; ventral *vascula lateralia* submedian, slightly divergent. *Lower Cambrian (Botomian):* central Kazakhstan.——FIG. 120,*3a–f.* **I. modesta,* Edrej Beds, Edrej Mountains; *a–c,* holotype, ventral valve exterior, posterior view, lateral view, MANK 2138/198, ×3.3; *d,* ventral internal mold, MANK 2138/204, ×3.3; *e,* dorsal valve exterior, MANK 2138/211, ×3.3; *f,* dorsal internal mold, MANK 2138/210, ×3.3 (Koneva, 1979).

Magnicanalis ROWELL, 1962a, p. 140 [**Obolella mobergi* WALCOTT, 1901, p. 673; OD]. Shell gently biconvex, elongate to transversely oval; ornament of fine radial striae; ventral interarea low, apsacline, with delthyrium; dorsal interarea orthocline; ventral visceral field slightly thickened in posterior third, bisected by median groove; dorsal visceral field poorly defined, bisected by low median ridge; dorsal internal oblique muscles scars on strongly elevated notothyrial platform, bisected by low, median plication; dorsal posterior adductor scars on two widely divergent, ridgelike elevations; ventral

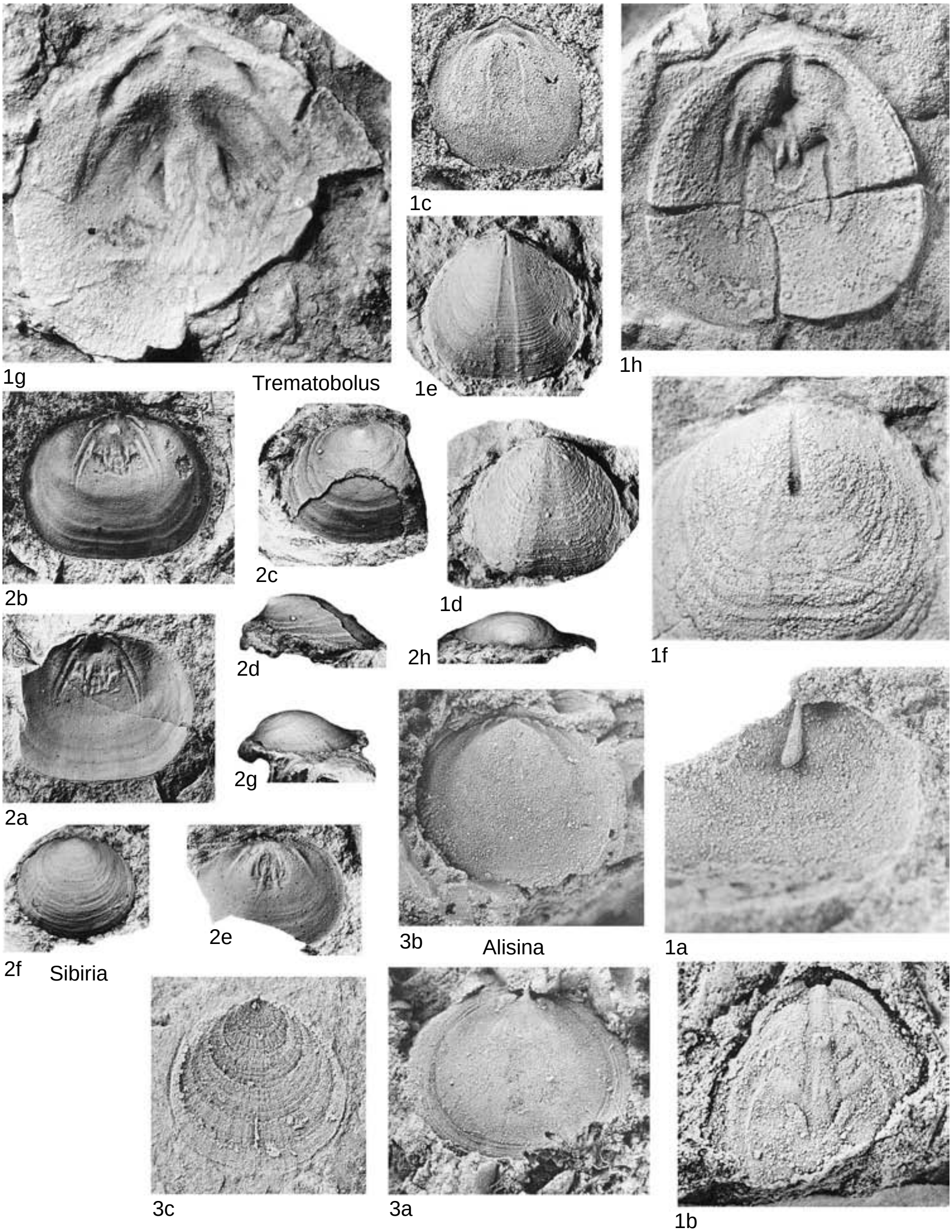

Fig. 122. Trematobolidae (p. 206).

vascula lateralia submedian, subparallel. *Lower Cambrian:* Sweden, Russia (southeastern Siberia).——Fig. 121,*2a–c*. **M. mobergi* (Walcott), Lingulid Sandstone, Sularp, Scania; *a,* ventral internal mold, LO 6575t, ×3.3; *b,* dorsal internal mold, LO 6576t, ×2.9; *c,* dorsal internal mold, LO 6577t, ×4.2 (new).

Family TREMATOBOLIDAE new family

[Trematobolidae Popov & Holmer, herein]

Strophic articulation with paired, ventral denticles, composed of secondary shell; sometimes with dorsal sockets; delthyrium

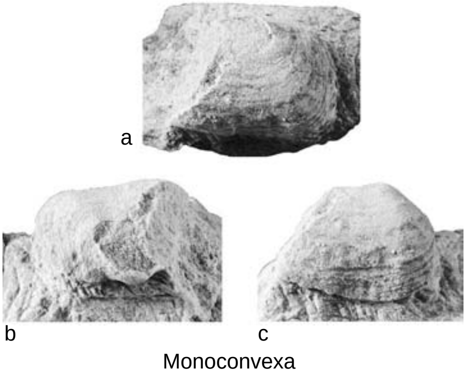

Fig. 123. Uncertain (p. 206).

covered by concave pseudodeltidium; pedicle emerging through foramen, located apical or anterior to beak. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian).*

Trematobolus Matthew, 1893, p. 276 [**T. insignis;* OD] [=*Protosiphon* Matthew, 1897, p. 70 (type, *P. kempanum*); *Protosyphon* Gorjansky, 1960, p. 181; *Lamellodonta* Vogel, 1962, p. 216 (type, *L. simplex*)]. Shell almost equibiconvex to somewhat dorsibiconvex, elongate or transversely oval; ventral interarea low; apsacline, with narrow, concave pseudodeltidium; pedicle foramen small, rounded, anterior to beak; pedicle track narrow, triangular, covered by concave plate; dorsal interarea low, orthocline or gently anacline; ventral visceral area strongly thickened, with broad median furrow posterior to foramen; notothyrial cavity sometimes with small sockets; dorsal diductor scars sometimes bisected by low median ridge; ventral *vascula lateralia* submedian, subparallel; dorsal *vascula lateralia* straight, widely divergent. *Lower Cambrian (Toyonian)–Middle Cambrian (Amgaian):* USA, Canada, Spain, Morocco, Russia (Siberia, Altai).——Fig. 122,*1a–c. T. kempanum* (Matthew), Lower Cambrian, Long Island, New Brunswick; *a,* ventral external mold, USNM 52212n, ×3.3; *b,* ventral internal mold, USNM 52212c, ×3.6; *c,* dorsal internal mold, USNM 52212k, ×1.7 (Rowell, 1962a).——Fig. 122,*1d–h. T. pristinus bicostatus* Gorjansky, Toyonian, Rassokha River, Siberia; *d,* paratype, dorsal valve exterior, CNIGR 11/8362, ×1.7; *e,* holotype, ventral valve exterior, CNIGR 1/8362, ×1.7; *f,* detail of ventral umbonal area, CNIGR 5/8362, ×5 (Gorjansky, Egorova, & Savitskii, 1964); *g,* dorsal valve interior, CNIGR 15/8362, ×4.2; *h,* paratype, ventral valve interior, CNIGR 9/8362, ×4.2 (Gorjansky & Popov, 1986).

Alisina Rowell, 1962a, p. 141 [**Obolella atlantica* Walcott, 1890, p. 36; OD]. Shell gently ventribiconvex, subcircular, sometimes with fine striae; ventral interarea apsacline to catacline; concave pseudodeltidium with median plication; foramen rounded, apical; dorsal valve sometimes gently sulcate; dorsal interarea low, triangular, orthocline, with open notothyrium, bearing sockets, bounded by low ridges; ventral visceral field thickened anteriorly; dorsal adductor scars arranged radially, with smaller posterior scars; ventral *vascula lateralia,* submedian subparallel, or slightly divergent; dorsal *vascula lateralia* submarginal, widely divergent; dorsal *vascula media* long, widely divergent. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian):* USA, Canada, Russia (Siberia, Altai), Great Britain.——Fig. 122,*3a–c.* **A. atlantica* (Walcott), Lower Cambrian; *a,* ventral internal mold, Conception Bay, Newfoundland, USNM 18322a, ×5; *b,* dorsal internal mold, Bristol County, Massachusetts, USNM 143123, ×5; *c,* ventral external mold, Trinity Bay, Newfoundland, USNM 51998b, ×3.3 (Rowell, 1962a).

Sibiria Gorjansky in Pelman, 1977, p. 47 [**S. magna;* OD]. Shell ventribiconvex, subcircular, smooth apically, lamellose peripherally; ventral valve subconical; ventral interarea procline to catacline, with deep, concave pseudodeltidium with median plication; beak anterior to margin; pedicle foramen small, apical; dorsal valve may be slightly sulcate; dorsal interarea low, orthocline; ventral visceral field somewhat thickened; notothyrial platform low, broadly triangular, bearing small sockets on its lateral sides; dorsal visceral area sightly raised, extending anteriorly to midvalve; ventral *vascula lateralia* submedian, straight, slightly divergent; dorsal *vascula lateralia* submarginal, widely divergent; *vascula media* long, divergent. *Lower Cambrian (Atdabanian):* Russia (eastern Siberia).——Fig. 122,*2a–e.* **S. magna,* Kotuy River; *a,b,* paratype, ventral valve interior, internal mold, CNIGR 2/10933, ×1.7; *c,d,* holotype, ventral valve exterior, lateral view, CNIGR 1/10933, ×1.7; *e,* paratype, dorsal internal mold, CNIGR 3/10933, ×1.7 (Gorjansky, 1977).——Fig. 122,*2f–h. S. glabra* Gorjansky, Kotuy River; paratype, dorsal exterior, lateral view, posterior view, CNIGR 7/10933, ×1.7 (Gorjansky, 1977).

Superfamily UNCERTAIN

Monoconvexa Pelman, 1977, p. 49 [**M. monoconvexa;* OD]. Shell ventribiconvex, transversely suboval; beaks of both valves marginal; interareas, internal characters of both valves unknown. *Lower Cambrian (upper Atdabanian):* Russia (Siberia).——Fig. 123*a–c.* **M. monoconvexa,* Lena River; ventral exterior, posterior view, anterior view, IGiG 392/31, ×3 (new).

Nochoroiella Pelman in Grigorieva, Melnikova, & Pelman, 1983, p. 54 [**N. isitica;* OD]. Shell small, biconvex, transversely elliptical to subtriangular; both valves with marginal beaks, lacking interareas.

Genus poorly known, may be an operculum. *Lower Cambrian (upper Tommotian):* Russia (Siberia).

Order NAUKATIDA Popov & Tikhonov, 1990

[Naukatida POPOV & TIKHONOV, 1990, p. 40]

Shell biconvex, smooth or with radial ornament; ventral interarea with concave pseudodeltidium, which may be perforated apically by elongate oval foramen; ventral visceral platform high, may be free peripherally; articulation with pair of closely spaced, ventral denticles, located on anterise, dorsal sockets on lateral sides of notothyrial platform; dorsal adductor scars arranged radially. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

In the Naukatida, the ventral muscle field is located on a high platform, and in some genera, like *Oina,* this platform is free distally (see Fig. 119.3a), thus making it comparable with the ventral spondylium-like structure of protorthoids, like *Arctohedra* and *Glyptoria* (POPOV, 1992).

Superfamily NAUKATOIDEA Popov & Tikhonov, 1990

[*nom. transl.* HARPER in HARPER & others, 1993, p. 431, *ex* Naukatidae POPOV & TIKHONOV, 1990, p. 41]

Characters as for suborder. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

Family NAUKATIDAE Popov & Tikhonov, 1990

[Naukatidae POPOV & TIKHONOV, 1990, p. 41]

Characters as for superfamily. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

Naukat POPOV & TIKHONOV, 1990, p. 41 [**N. proprium;* OD]. Shell dorsibiconvex, transverse oval, smooth apically, coarsely costellate peripherally; anterior commissure uniplicate; ventral interarea apsacline; pseudodeltidium concave, perforated apically by elongate-oval pedicle foramen; ventral visceral platform small, strongly thickened anteriorly; dorsal interior with median septum, anterior adductor scars located on high, broad ridges lateral to septum. *Lower Cambrian (Botomian):* southern Kirghizia.——FIG. 124,*3a–d.* **N. proprium,* Chachme River, southern Tien Shan Range; *a,* oblique posterior view of both valves, ×22.9; *b,* dorsal view of both valves, ×19.6; *c,* holotype, oblique lateral view of both valves, CNIGR 10/12589, ×22.9 (new); *d,* paratype, ventral exterior, CNIGR 11/12589, ×16.7 (Popov & Tikhonov, 1990).

Bojarinovia AKSARINA in AKSARINA & PELMAN, 1978, p. 106 [**B. levigata;* OD]. Shell ventribiconvex, transversely oval; anterior commissure rectimarginate; ventral interarea low, narrow, apsacline; pedicle opening, interior poorly known; dorsal valve (described originally as ventral) with anterior and posterior adductor scars forming elevated tripartite platform, divided by two deep furrows; *vascula media* straight, widely divergent. *upper Lower Cambrian:* Russia (Altai). Satisfactory material not available for illustration.

Bynguanoia ROBERTS in ROBERTS & JELL, 1990, p. 281 [**B. perplexa;* OD]. Shell ventribiconvex, subcircular; anterior commissure sulcate; ornament of coarse, radial costae; ventral interarea low, narrow, apsacline; concave pseudodeltidium perforated apically by elongate-oval pedicle foramen; dorsal valve with vestigial interarea and shallow sulcus; ventral interior with strongly thickened anterior visceral platform; notothyrial platform narrow, strongly elevated; dorsal posterior adductor scars forming separate elevated platforms close to posterior margin. *Middle Cambrian (lower Amgaian):* Australia (New South Wales).——FIG. 124,*1a–g.* **B. perplexa,* Coonigan Formation, Mootwingee area; *a–e,* paratype, ventral, dorsal, posterior, anterior, lateral views of both valves, AMF 79714, ×3.3; *f,* holotype, ventral valve interior, AMF 79716, ×3.3; *g,* paratype, dorsal valve interior, AMF 79718, ×3.3 (Roberts & Jell, 1990).

Oina POPOV & TIKHONOV, 1990, p. 42 [**O. rotunda;* OD]. Shell subequibiconvex, transverse oval; anterior commissure rectimarginate; ventral interarea low, short, apsacline; delthyrium completely closed by concave pseudodeltidium; dorsal interarea small, orthocline; ventral visceral platform strongly elevated, free distally; notothyrial platform strongly elevated; dorsal interior with three broad, high septa not extending to midvalve. *Lower Cambrian (Botomian):* southern Kirghizia.——FIG. 124,*2a–g.* **O. rotunda,* Chachme River, southern Tien Shan Range; *a,* holotype, ventral valve interior, CNIGR 14/12589, ×3.3; *b,* paratype, ventral valve exterior, CNIGR 18/12589, ×3.3 (Popov & Tikhonov, 1990); *c,* dorsal valve exterior, CNIGR 17/12589, ×3.3; *d,* paratype, oblique lateral view of ventral valve interior, RMS Br 136451, ×13.8; *e,* oblique lateral view of ventral valve exterior, ×6.2; *f,* paratype, oblique posterior view of ventral valve exterior, RMS Br 136452, ×8.3; *g,* paratype, dorsal valve interior, RMS Br 136453, ×13.8 (new).

?Swantonia WALCOTT, 1905, p. 296 [**Camerella antiquata* BILLINGS, 1861b, p. 10; OD]. Shell subtriangular, with rectimarginate anterior commissure; ornament of coarse, rounded ribs; ventral interarea with concave pseudodeltidium; other characters unknown. *Lower Cambrian:* USA (Nevada, Vermont).

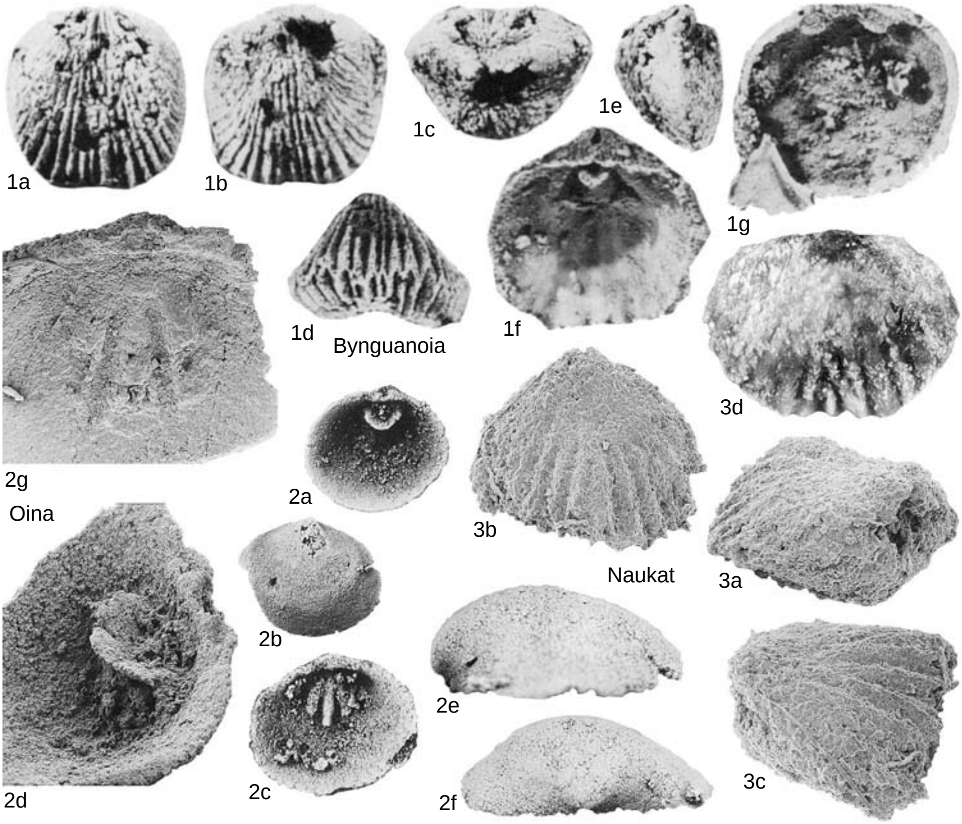

FIG. 124. Naukatidae (p. 207).

KUTORGINATA

LEONID E. POPOV and ALWYN WILLIAMS

[VSEGEI, St. Petersburg; and The University of Glasgow]

Class KUTORGINATA Williams & others, 1996

[Kutorginata WILLIAMS & others, 1996, p. 1193]

Shell strophic, ventribiconvex; anterior margin rectimarginate, rarely sulcate; posterior margin wide, straight, with large median opening; delthyrium widely triangular, covered by convex pseudodeltidium, bounded laterally by furrows; beak with small, rounded apical foramen; dorsal interarea divided by wide notothyrium; both valves with slightly thickened, weakly defined visceral area situated close to posterior margin; dorsal adductor scars radially disposed, dorsal diductor scars impressed on floor of notothyrial cavity; cardinal process absent; articulation by edges of interareas, without teeth and dental sockets; mantle canal systems pinnate; digestive tract probably open with anus placed posteromedianly between valves; shell structure fibrous impunctate. *Lower Cambrian–Middle Cambrian.*

The strophic, articulated shells of the Kutorginata rotated on simple hinge mechanisms that are different from those of other rhynchonelliforms. The hinge mechanisms of *Nisusia* and *Kutorgina* (Fig. 125), which

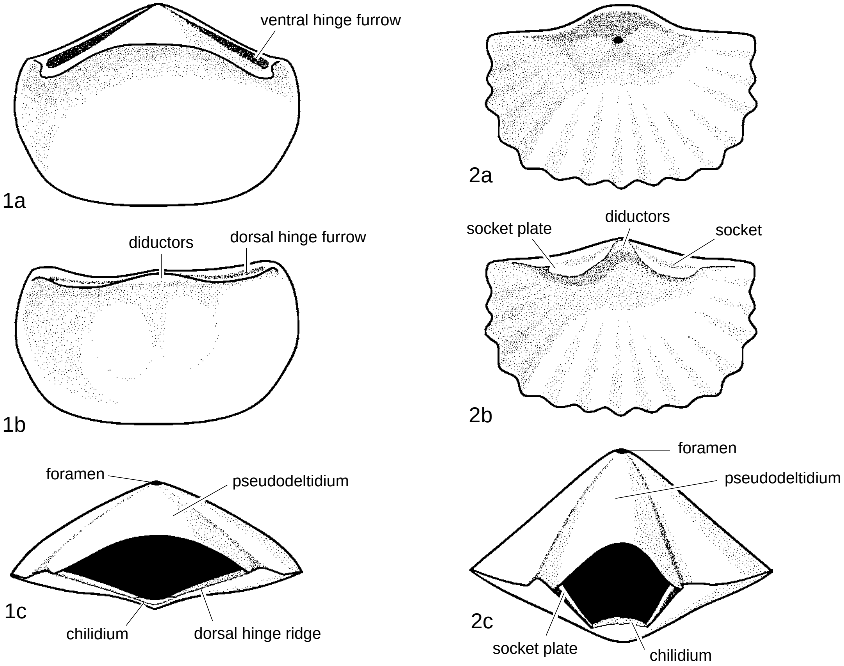

FIG. 125. Diagrammatic representation of kutorginide articulation; *1a–c, Kutorgina,* interiors of ventral and dorsal valves and posterior view of shell; *2a–c, Nisusia,* interiors of ventral and dorsal valves and posterior view of shell (adapted from Holmer & Popov, 1996).

are best known (Rowell & Caruso, 1985; Popov & Tikhonov, 1990; Roberts & Jell, 1990; Popov and others, 1997), illustrate the variability of these primitive devices. In *Nisusia,* the lateral margins of the pseudodeltidium fit into deep sockets at the ends of a groove separating the dorsal interarea from a narrow socket plate continuous with the chilidium. In *Kutorgina,* a deep groove (ventral hinge groove) also separates the ventral interarea from the pseudodeltidium. This furrow accommodated the ends of the narrow lateral sectors of the dorsal interarea, which was also separated by a hinge furrow from a dorsal hinge ridge continuous with a chilidium. The differences between these two interlocking devices are minor as they merely reflect the strength of flexuring developing between the delthyrial and notothyrial covers and their respective interareas. Indeed the discovery by Popov and Tikhonov (1990) of a rudimentary kutorginid hinge device in juvenile specimens of *Nisusia* confirms the homology of the mechanisms.

With respect to brachiopod phylogeny, the discovery by Rowell and Caruso (1985) of silicified specimens of their *Nisusia sulcata*

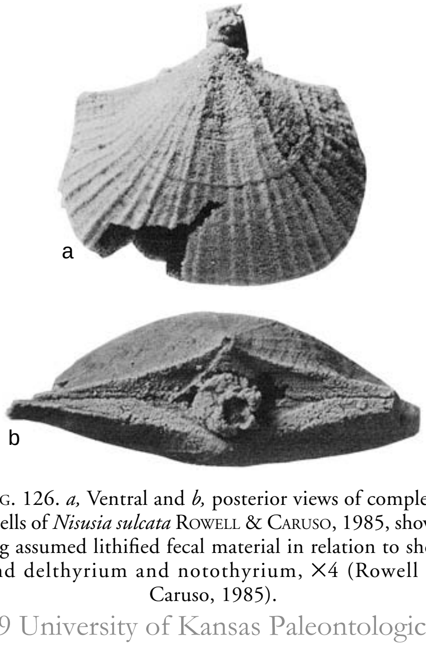

FIG. 126. *a,* Ventral and *b,* posterior views of complete shells of *Nisusia sulcata* Rowell & Caruso, 1985, showing assumed lithified fecal material in relation to shell and delthyrium and notothyrium, ×4 (Rowell & Caruso, 1985).

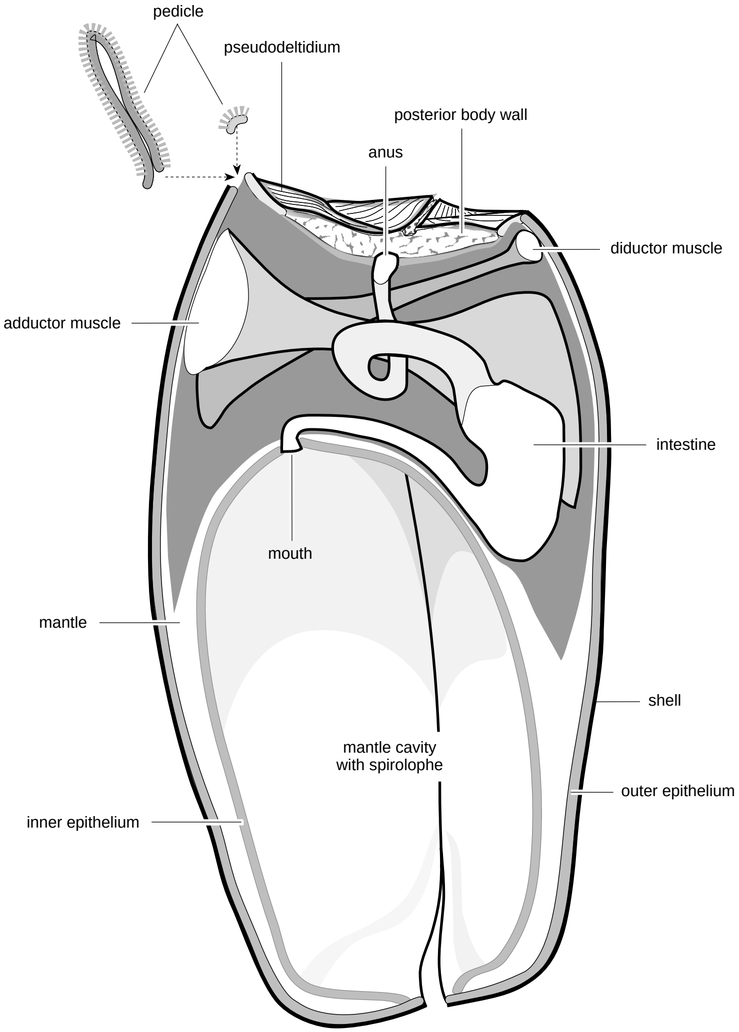

FIG. 127. Diagrammatic reconstruction of integument, pedicle, musculature, and intestine of nisusiids based on interpretation of *Nisusia sulcata* by ROWELL and CARUSO (1985); pedicle shown as varying from fully functional organ with chitinous cuticle to vestigial patch of poorly differentiated pedicle epithelium secreting chitinomucus cementing cover resulting in deformation of some kutorginid shells (new).

with cylindroid structures emerging from the opening subtended by the delthyrium and notothyrium (Fig. 126), is highly significant. The presence of a supra-apical foramen in the ventral valve precludes these structures from being pedicles and there are compelling reasons for accepting the authors' interpretation of them as fossilized feces. This would be consistent with the kutorginates having an anus located on a posterior body wall in the manner characteristic of living discinids and craniids (Fig. 127).

The secondary layer of *Nisusia* (Fig. 128) is typically fibrous; and this fabric is assumed to be characteristic of the kutorginates as a whole.

Order KUTORGINIDA Kuhn, 1949

[*nom. transl.* GORJANSKY, 1960, p. 181, *pro* order Kutorginacea KUHN, 1949, p. 99] [=Paleotremata THOMSON, 1927, p. 118; *incl.* order Rustellida KUHN, 1949, p. 99]

Characters as for class. *Lower Cambrian–Middle Cambrian.*

Superfamily KUTORGINOIDEA Schuchert, 1893

[*nom. correct.* POPOV & WILLIAMS, herein, *pro* Kutorginacea WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 144, *nom. transl. ex* Kutorginidae SCHUCHERT, 1893, p. 151] [*incl.* Rustellacea WALCOTT, 1908, p. 143, *partim*]

Shell with articulation characterized by two triangular plates formed by dorsal interarea, bearing oblique ridges on the inner sides, which fit into deep furrows formed by ridges along inner sides of ventral interarea and lateral extensions of pseudodeltidium. *Lower Cambrian–Middle Cambrian.*

Family KUTORGINIDAE Schuchert, 1893

[Kutorginidae SCHUCHERT, 1893, p. 151] [*incl.* Rustellidae WALCOTT, 1908, p. 143; ?Schuchertinidae WALCOTT, 1908, p. 145; Yorkiidae ROWELL, 1962a, p. 144; Agyrekiidae KONEVA, 1979, p. 59]

Shell ventribiconvex; ventral interarea narrow, poorly defined laterally; dorsal valve with marginal beak; notothyrium open; mantle canal system with two principal canals on both valves, radiating anteriorly. *Lower Cambrian–Middle Cambrian.*

Kutorgina BILLINGS, 1861b, p. 8 [**K. cingulata;* OD] [=*Koturgina* BILLINGS, 1861b, p. 8, *nom. imperf.; ?Rustella* WALCOTT, 1905, p. 311 (type, *R. edisoni*)]. Shell slightly elongate to transverse oval in outline with irregular ventral profile; strongly lamellose peripherally, with granular microornament; ventral cardinal area strongly apsacline to anacline. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian):* Canada, USA, Greenland, Sardinia, Russia (Siberia, southern Urals), Kazakhstan, Kirghizia, Israel, Australia (New South Wales).——FIG. 129,*1a–g. K. catenata* KONEVA, Lower Cambrian, Botomian, right side of Chachme River, southern Kirghizia; *a,* ventral valve exterior, ×10; *b,* posterior view, ×11; *c,* lateral view, RM 137376, ×11; *d,* dorsal valve exterior, ×9; *e,* posterior view, RM 137377, ×10; *f,* dorsal valve interior, RM 137378, ×10; *g,* incomplete ventral valve interior, RM 137379, ×10 (new).

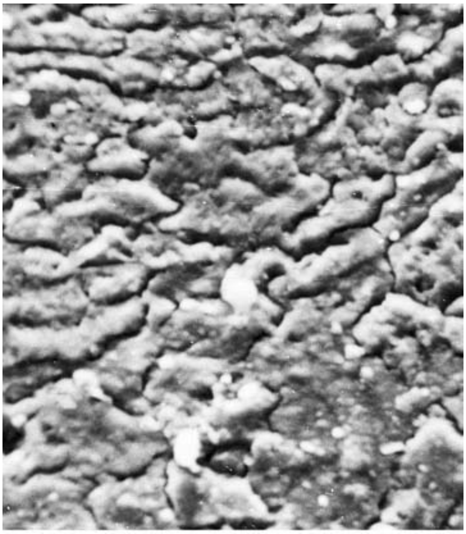

FIG. 128. SEM micrograph of polished and etched section of secondary layer of the shell of *Nisusia* sp. cf. *N. kotujensis* ANDREEVA (1962, p. 87) showing variably recrystallized fibers, ×1200 (new).

Agyrekia KONEVA, 1979, p. 60 [**A. alta;* OD]. Shell biconvex ornamented by fila and radial striations; ventral interarea high, triangular, catacline, or procline; beak slightly incurved, pseudodeltidium broad, gently convex; dorsal valve moderately to strongly convex with broad open notothyrium, short triangular interarea; ventral interior with short median septum near apex. *Lower Cambrian (Botomian)–Middle Cambrian (lower Amgaian):* Kazakhstan, Australia (New South Wales), Russia (southwestern Siberia), Greenland.——FIG. 129,*2a–f.* **A. alta,* Botomian, Kazakhstan, Agyrek Mountains; *a–c,* ventral valve exterior, lateral view, posterior view, KAS 2138/257, ×3; *d–f,* ventral valve (illustrated as a dorsal valve by KONEVA, 1979) exterior, posterior view, lateral view, KAS 2138/258, ×3 (Koneva, 1979).

Haupiria MACKINNON, 1983, p. 101 [**H. tasmani;* OD]. Similar to *Yorkia,* but lacking apical foramen and internal tube. *Middle Cambrian:* New Zealand. Illustrated specimens not as informative as diagnosis.

Schuchertina WALCOTT, 1905, p. 323 [**S. cambria;* OD]. Genus poorly known; shell subequally biconvex, smooth or filate; interarea, interior of ventral valve unknown; dorsal interior with short median ridge and pinnate mantle canals. *Middle Cambrian:* North America.

Yorkia WALCOTT, 1897, p. 714 [**Y. wanneri;* OD] [=*Quebecia* WALCOTT, 1905, p. 320 (type, *Obolella circe* BILLINGS, 1871b, p. 219)]. Shell subcircular or

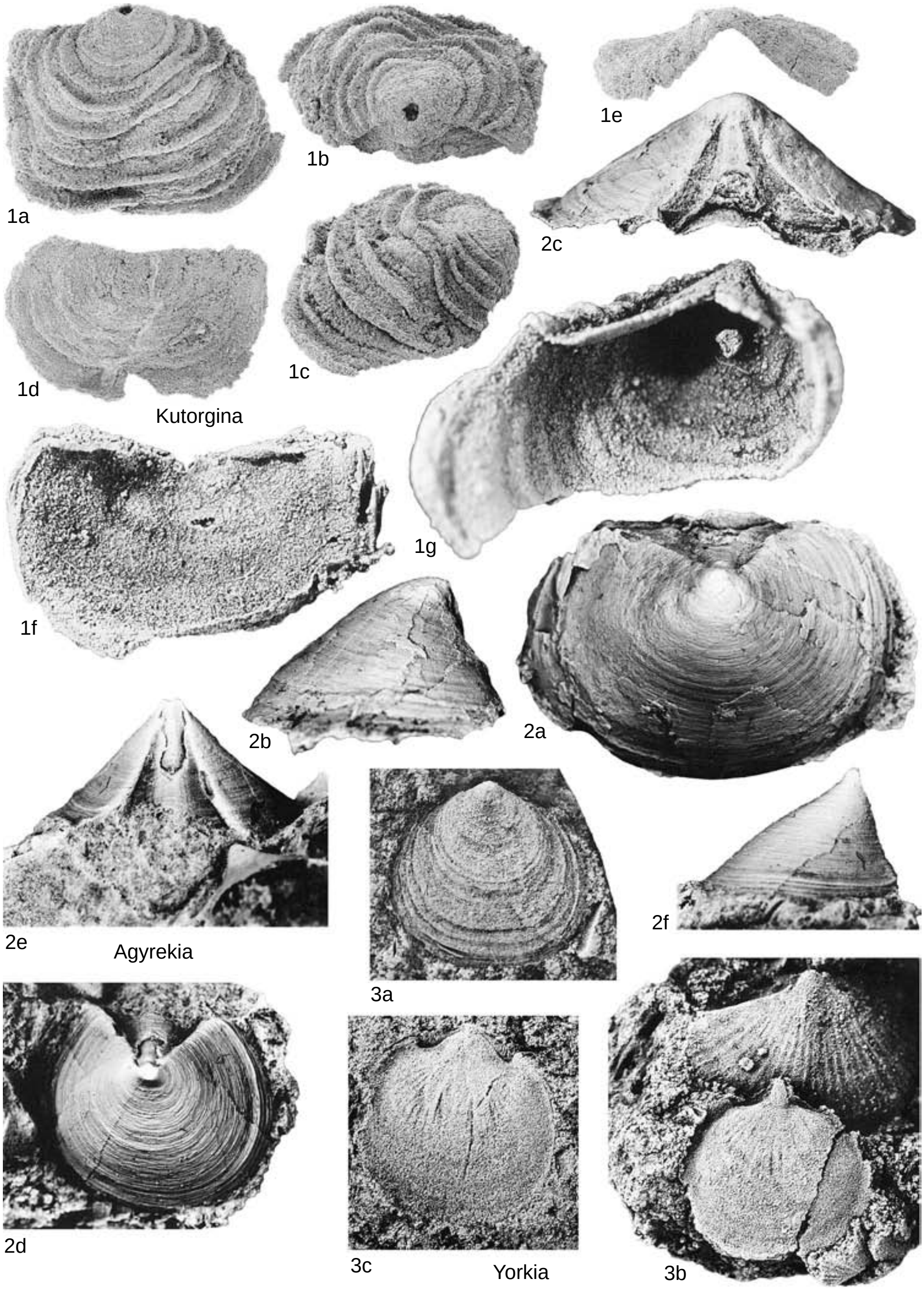

FIG. 129. Kutorginidae (p. 211–213).

subtriangular in outline, smooth; ventral interarea low, apsacline, or rarely catacline; ventral beak small, perforated by minute foramen extending internally as subconical tube; dorsal valve with broad notothyrium, narrow triangular propareas; muscle scars, mantle canals in both valves imperfectly known. *Lower Cambrian:* USA (New York, Pennsylvania), eastern Canada, Russia (Altai).——FIG.

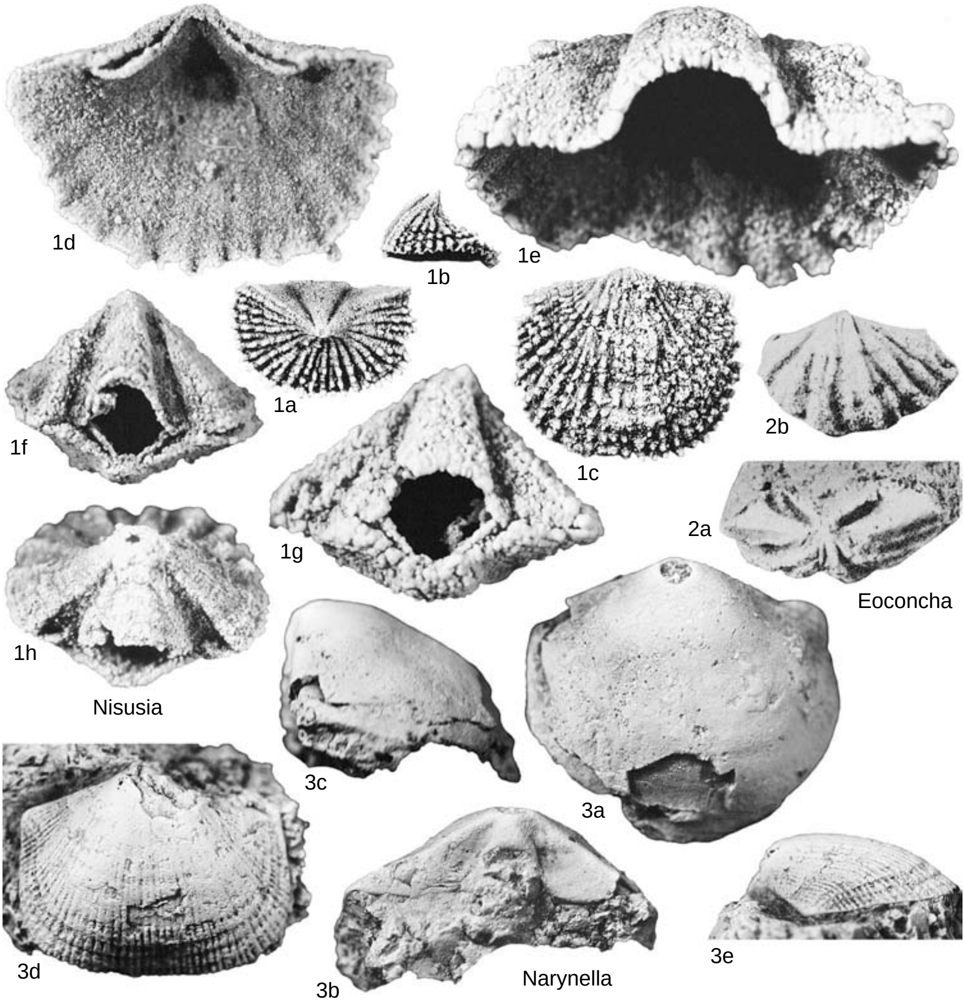

Fig. 130. Nisusiidae (p. 213–214).

129,*3a–c.* **Y. wanneri,* Lower Cambrian; *a,* ventral valve exterior, latex cast, Codorus Creek near Emigsville, Pennsylvania, USNM 26433a, ×2; *b,* ventral internal mold, 3 miles northwest of York, Pennsylvania, USNM 139470, ×2; *c,* dorsal internal mold, Codorus Creek near Emigsville, Pennsylvania, USNM 26433h, ×2 (Rowell, 1962a).

Superfamily NISUSIOIDEA
Walcott & Schuchert, 1908

[*nom. correct.* Popov & Williams, herein, *pro* Nisusiacea Andreeva, 1987, p. 32, *nom. transl. ex* Nisusiidae Schuchert & Cooper, 1931, p. 242; *nom. transl. ex* Nisusiinae Walcott & Schuchert in Walcott, 1908, p. 147]

Articulation effected by two lateral plates bounding elongate dorsal sockets into which the dorsal edges of ventral interarea fit; diductor muscles attached dorsally to elevated notothyrial platform; mantle canal system of both valves pinnate. *Lower Cambrian–Middle Cambrian.*

Family NISUSIIDAE
Walcott & Schuchert, 1908

[*nom. transl.* Schuchert & Cooper, 1931, p. 242, *ex* Nisusiinae Walcott & Schuchert in Walcott, 1908, p. 147]

Characters as for superfamily. *Lower Cambrian–Middle Cambrian.*

Nisusia Walcott, 1905, p. 247 [**Orthisina festinata* Billings, 1861b, p. 10; OD]. Shell ventribiconvex; transverse rectangular or semioval in outline; ornamented by costellae normally bearing numerous

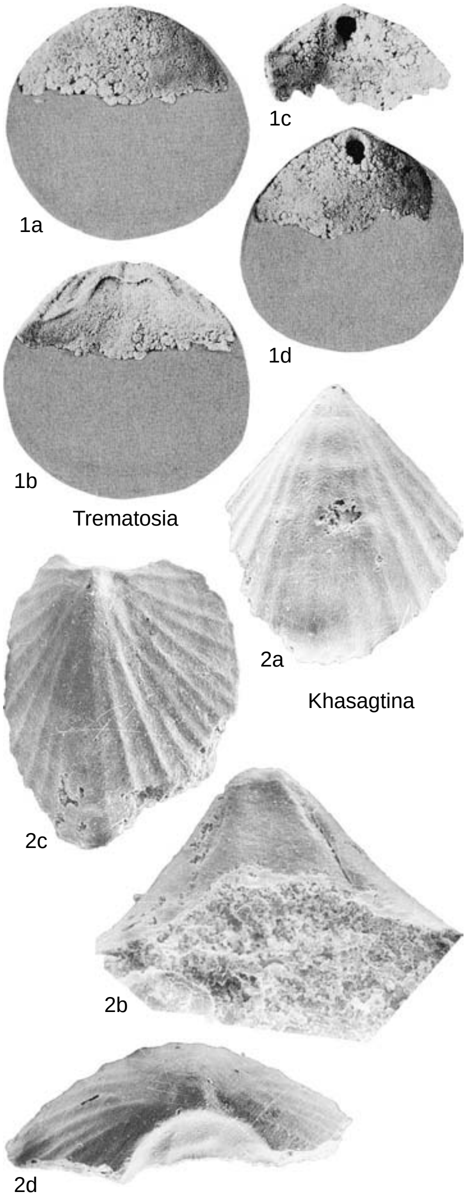

Fig. 131. Nisusiidae (p. 214–215).

small, hollow spines; anterior margin rectimarginate or slightly sulcate; interarea high, triangular, procline to apsacline; dorsal interior with transverse, elevated notothyrial platform; dorsal adductor muscle scars may be discretely impressed on two pairs by prominent ridges. *Lower Cambrian (Botomian)–Middle Cambrian:* USA, Canada, Greenland, Russia (Siberia), Kazakhstan, Australia.——Fig.130,*1a–h. N. alaica* Popov & Tikhonov; Botomian, right side of Chachme River, southern Kirghizia; *a,b,* ventral valve exterior, lateral view, CNIGR 31/12589, ×3; *c,* dorsal valve exterior, CNIGR 18/12589, ×3 (Popov & Tikhonov, 1990); *d,* dorsal valve, interior, ×10; *e,* ventral valve, posterior view, RM, no number, ×15 (new); *f,* complete shell of juvenile specimen, posterior view, CNIGR 34/12589, ×10 (Popov & Tikhonov, 1990); *g,* complete shell of juvenile specimen, posterior view, RM, no number, ×15 (new); *h,* complete shell of juvenile specimen, posterior view, CNIGR 33/12589, ×15 (Popov & Tikhonov, 1990).

Eoconcha Cooper, 1951, p. 4 [**E. austini;* OD]. Shell coarsely costellate, with ventral median sulcus, dorsal fold; no spines; ventral interarea apsacline; interior of both valves imperfectly known. *Lower Cambrian–Middle Cambrian:* USA (Virginia).——Fig. 130,*2a,b.* **E. austini,* Lower Cambrian, Virginia; *a,* dorsal valve exterior, posterior view, ×1.5; *b,* ventral internal mold, ×2 (Cooper, 1951).

Narynella Andreeva, 1987, p. 34 [**Nisusia ferganensis* Andreeva, 1962, p. 89; OD]. Shell finely costellate, with variably developed median sulcus, dorsal fold, similar to *Nisusia,* but lacking spines. *Lower Cambrian (Toyonian)–Middle Cambrian:* USA, Uzbekistan, Australia.——Fig. 130,*3a–e.* **N. ferganensis* (Andreeva), Amgaian, Madygen, Fergana Valley, Uzbekistan; *a–c,* ventral valve exterior, posterior view, lateral view, CNIGR 7/8202, ×3; *d,e,* dorsal valve, exterior, lateral view, CNIGR 9/8202, ×3 (Andreeva, 1962).

Khasagtina Ushatinskaya, 1987, p. 66 [**K. primaria;* OD]. Shell ventribiconvex, elongate suboval in outline, costellate, with narrow, slightly incurved posterior margin; ventral valve with apical foramen, narrow apsacline interarea occupied mainly by convex pseudodeltidium; dorsal valve with orthocline interarea and two pairs of muscle scars. [This genus is provisionally assigned to the Kutorginida until more is known about its internal features]. *Lower Cambrian (?Tommotian, Atdabanian):* Mongolia, France.——Fig. 131,*2a–d.* **K. primaria,* Atdabanian, Bajangol Formation; Salany-Gol Rivulet, western Mongolia; *a,* holotype, ventral internal mold, PIN 3302/5007, ×15; *b,* ventral internal mold, posterior view, PIN 3302/5005, ×54; *c,* dorsal internal mold, PIN 3302/5001, ×13; *d,* dorsal internal mold, posterior view, PIN 3302/5007, ×20 (Ushatinskaya, 1987).

Trematosia Cooper, 1976, p. 276 [**Obolus radifer* Richter & Richter, 1941, p. 22; OD]. Shell biconvex, elongate oval to subcircular in outline, with rectimarginate anterior margin; smooth, lamellose peripherally; ventral valve with large subcircular foramen placed anteriorly to beak and narrow pseudodeltidium; dorsal valve with narrow, divided interarea bounding widely diverging furrows; internal characters of both valves poorly known. [This genus is doubtfully assigned to the Kutorginata. The holotype and several syntypes of *Trematosia radifer* (COOPER, 1976, pl. 3, fig. 1–6, 32) are characterized by a large foramen anterior to the ventral beak, a poorly defined ventral interarea, and a different kind of dorsal interarea with distinctive hinge structures. Such features are unknown in kutorginids. Other specimens also assigned to *T. radifer* are those identified as *Trematosia* sp. 1 (COOPER, 1976, pl. 1, fig. 39–41), probably better identified as *Yorkia*]. *Lower Cambrian:* Israel, Jordan.——FIG. 131,*1a–d.* **T. radifer* (RICHTER & RICHTER), Nimra Formation, Ghor-es-Safi, Jordan; *a,b,* incomplete dorsal valve exterior, interior, BMNH BB 61421, ×2; *c,d,* incomplete ventral valve interior, exterior, BMNH BB 61422, ×2 (Cooper, 1976).

STROPHOMENATA

ALWYN WILLIAMS,[1] C. HOWARD C. BRUNTON,[2] and L. R. M. COCKS[3]

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Class STROPHOMENATA Williams & others, 1996

[Strophomenata WILLIAMS & others, 1996, p. 1193]

Rhynchonelliform brachiopods with secondary shell composed preeminently of cross-bladed laminae but also of fibers or laminar laths in older groups; impunctate in early stocks but typically pseudopunctate with or without taleolae or rarely extropunctate; shell outline and profile variable, but essentially planar to weakly concavo-convex in strophomenides; strophic hinge line, commonly with high ventral interarea and reduced dorsal interarea; delthyrium and notothyrium variably covered by pseudodeltidium and chilidium; supra-apical foramen normally developed in larval shells but becoming lost in adults; some species cemented at the umbo; tubular spines uniquely developed in productides; deltidiodont teeth simple, transverse or peglike, lost in strophodontids and post-Famennian productidines, dental sockets commonly defined by low, flat-lying ridges parallel with hinge line; dorsal bases of diductor muscles inserted on notothyrial platform or normally on prominent cardinal process of varied morphology; ventral bases attached laterally of medially placed adductor scars; lophophore supports rare, posteriorly as brachiophores or medially as raised dorsal ridges; mantle canal systems saccate to pinnate, poorly known in later groups. *Middle Cambrian (Amgaian)–Upper Permian (Tatarian).*

More than 1,500 genera, ranging throughout the Paleozoic era, have been assigned to the Strophomenata and are major constituents of many faunas, some in rock-forming quantities. They include some of the most bizarre species of the phylum so that the class embraces a number of groups characterized by autapomorphies meriting suprafamilial recognition as in the Lyttoniidina and Richthofenioidea.

The most inclusive morphological feature of the Strophomenata is a supra-apical or apical foramen, at least in juveniles, that became sealed in adult valves of many later groups. It is assumed that such a foramen accommodated an apically situated peduncular outgrowth of the ventral mantle that acted solely as an adhesive anchor and, in the absence of adjustor scars, never as an axis of rotation for the shell. The outgrowth is regarded as homologous with that inferred for the Obolellata and Kutorginata.

Articulatory devices are also widely used in strophomenate classification; but the deltidiodont teeth and socket ridge apparatus, found in all older stocks, is not greatly different from that of early rhynchonellates (orthides) except in one respect. Early strophomenate socket ridges are weak and flat lying, a synapomorphic condition precursory to taxonomically significant transformations like the loss of dentition in the later productides or its secondary elaboration in the later orthotetidines.

Shell structure and pseudopunctation have previously played a crucial taxonomic role in distinguishing strophomenates from other brachiopods. Cross-bladed lamination, however, is demonstrably homoplastic with, for example, the chonetidine fabric of lath-like secondary fibers appearing some time after its development in Early Ordovician strophomenoids, triplesiidines, and orthotetidines, all in contrast to the more orthodox fibrous secondary layers of plectambonitoids. This contrast is also true of the laminar-shelled billingselloids and the fibrous-shelled clitambonitidines, both of which have been provisionally assigned to the same order (Billingsellida). Similarly, pseudopunctation, so characteristic of plectambonitoids and strophomenoids, was not fully established in the orthotetidines until Devonian times, although sporadic traces of a form of pseudopunctation have been found in the otherwise impunctate triplesiidines and older orthotetidines (chilidiopsoids).

Such variability, which is matched in the elaboration of cardinalia, the distribution of spinose outgrowths on the shell and so on, suggests that homoplasy is a serious handicap to a phylogenetic classification of the Strophomenata.

STROPHOMENIDA

L. R. M. Cocks and Rong Jia-yu

[The Natural History Museum, London; and Academia Sinica, Nanjing]

Order STROPHOMENIDA Öpik, 1934

[*nom. transl.* Moore, 1952, p. 221, *ex* suborder Strophomenoidea Öpik, 1934, p. 75]

Strophomenate brachiopods with pseudopunctate shell structure, normally with taleolae; spines absent; shell outline normally with relatively wide hinge line, variable profile from concavoconvex to convexoconcave, also biconvex; delthyrium and notothyrium variably covered by pseudodeltidium and chilidium; some species cemented at the umbo; teeth usually present but sometimes absent and replaced in function by hinge line denticles; cardinal process bifid or trifid; mantle canal systems saccate to pinnate where seen. *Lower Ordovician (Tremadoc)–Carboniferous (Namurian).*

Since the revision of the supraordinal classification of the Brachiopoda (Williams & others, 1996), the order Strophomenida is now much more restricted than in the previous *Treatise* (Moore, 1965), in which it also included the chonetids, productids, davidsonids, oldhaminids, and lyttoniids as well as the strophomenids. The order is here restricted to two central superfamilies, the Strophomenoidea and the Plectambonitoidea, neither of which has any external spines (unlike the chonetidines and productidines) and both of which invariably have pseudopunctate shell structure (unlike the orthotetidines). The irregular shapes of the oldhaminids and lyttoniids are very different from the general bilateral symmetry of the Strophomenida. The key variables within the order are discussed under the two superfamilies below. The Strophomenoidea were derived from the Plectambonitoidea, probably in early Arenig time, and the Plectambonitoidea probably evolved from the Billingselloidea at about the Cambro-Ordovician boundary. Both the included superfamilies were abundant and diverse during Ordovician and early Silurian times, but the Plectambonitoidea dwindled as the Silurian progressed, with a small number lingering into the Eifelian. The Strophomenoidea also flourished during most of the Devonian but were badly depleted by the Frasnian-Famennian extinction, with the few remaining representatives becoming extinct near the end of the Namurian.

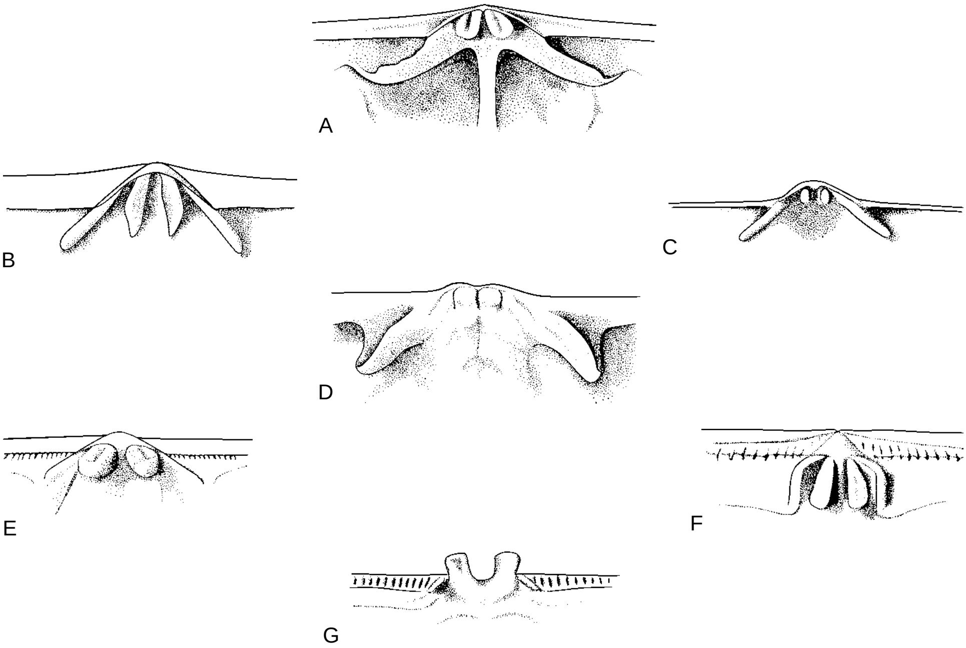

FIG. 132. Differing cardinalia types among Strophomenoidea; *A,* based on *Strophomena* (Strophomenidae); *B,* based on *Kjerulfina* (Rafinesquinidae); *C,* based on *Bystromena* (Glyptomenidae); *D,* based on *Christiania* (Christianiidae); *E,* based on *Amphistrophia* (Amphistrophiidae); *F,* based on *Leptostrophia* (Leptostrophiidae); *G,* based on *Strophodonta* (Strophodontidae) (new).

Superfamily STROPHOMENOIDEA King, 1846

[*nom. correct.* COCKS & RONG, herein, *pro* Strophomenacea SCHUCHERT, 1896, p. 312, *nom. transl. ex* Strophomenidae KING, 1846, p. 28]

Outline semicircular with greatest width usually at hinge line; external spines absent; slender profile varying from concavoconvex to convexoconcave, sometimes geniculate; supra-apical foramen open or closed in adults, pedicle tube sometimes present in juveniles; interareas, pseudodeltidium, and chilidium present in most stocks; articulation either of teeth and sockets or denticulations, occasionally both; bifid cardinal process. An undescribed Arenig genus in family Strophomenidae (RONG & COCKS, 1994) extends the stratigraphic range of this superfamily and family. *Ordovician (Arenig)–Carboniferous (Namurian).*

This superfamily differs chiefly from the other superfamily in the suborder, the Plectambonitoidea (below) in possessing bifid rather than single or trifid cardinal process lobes. Some previous authors, although not in the previous edition of the *Treatise* (MOORE, 1965), have subdivided the group into two superfamilies; one, the Strophomenoidea (previously termed the Strophomenacea) with smooth hinge lines and the other (often termed Stropheodontacea) with denticulate hinge lines. After close analysis, RONG and COCKS (1994) determined that denticulation arose independently and polyphyletically in at least three stocks of the Strophomenoidea, and thus the stropheodontids have been subsumed as a number of separate families within the Strophomenoidea here. Apart from the presence or absence of denticulated hinge lines, the key feature for familial differentiation within the superfamily has again been the form of the cardinal process (Fig. 132). RONG and COCKS (1994) defined four types, which they termed A to D, for the nondenticulate families and a further three types (E to G) for the denticulate families. A complication is that during the later Silurian and Devonian history of the denticulate families, the cardinal process changed and evolved within the various stocks, as originally described by WILLIAMS (1953a). In earlier classifications much familial weight was attributed to the valve profile, *e.g.,* the normal convexity of the Rafinesquinidae, the resupinate Strophomenidae, and the geniculate Leptaenidae; however, the valve profile is now considered to be a merely generic or occasionally a subfamilial character.

The development of the hinge line denticulation is of great importance, both for phylogeny and for classification. After the differentiation of the cardinalia, some of the Strophomenidae underwent early experimentation in the development of denticulation. There are many Caradoc-Ashgill taxa that bear crenulations and even denticles. Weakness, irregularity, and instability of development of the denticles and crenulations in the Strophomenidae indicate that their adaptive experimentation in this feature was unsuccessful, and no taxon of the family Strophomenidae gave rise to any strophodontoids. Within the Rafinesquinidae crenulations can be developed sporadically in the same population: sometimes the crenulations are quite strong, but usually they are weak. Despite the development of crenulations in several genera, however, the development of true denticulation in the *Leptaena* subgroup was also unsuccessful, and no strophodontoids were derived from the Leptaeninae.

The earliest known strophomenoids with crenulations (mainly pits) on the anteromedian faces of the teeth and on the posterior faces of the socket ridges are known in rocks of Llanvirn age, for example "*Macrocoelia*" *llandeiloensis elongata,* which is a rafinesquinid. Thus the rafinesquinids were possibly the first family to experiment in the development of denticulation, and this occurred in a very early stage of their evolutionary history. During the first stage of denticular development denticles are present only in the ventral valve and are usually regular but weak.

In the second stage, during late Caradoc and Ashgill times, there was a stable development of both crenulations and denticles in the rafinesquinid ventral valve, emerging from beneath the lamellar layer on either side of the delthyrium. Both denticles and crenulations are seen in the ventral valves on the denticular plates and the median anterior part of the teeth. These should have counterparts in the dorsal valve. Although there are counterpart crenulations on the posterior face of the socket ridge in the dorsal valve, however, there are no counterpart denticles to those on the ventral valve denticular plate.

The third stage in the evolution of denticulation was mainly in early and middle Llandovery times, when many taxa evolved that bear true denticles on the hinge lines of both valves for the first time, although others bear denticles only in the ventral valve and they are absent in the dorsal valve apart from crenulated socket ridges. There are three stocks in which denticles occur in both valves: *Eopholidostrophia, Eostrophonella,* and *Palaeoleptostrophia.* Establishment of denticulation is usually associated with an open delthyrium, loss of dental plates, a faintly impressed muscle field with no bounding ridges in the ventral valve, and a weakly impressed muscle field lacking any traces of transmuscle septa in the dorsal valve.

In the fourth stage (mainly in the late Llandovery), the establishment of denticulation was completed and almost all taxa of the denticulate families bear denticles in both ventral and dorsal valves. As time went by, denticular plates became larger in general, with more denticles on them, and the denticles started to spread gradually and progressively along the hinge line. The general trend in evolution of denticulation in the Silurian was that the more denticles present, the younger the age of the taxon in the same stock, assuming that the absolute size was comparable. We do not put any great systematic value on the absolute number of the denticles or on the proportion of the hinge line occupied by them at any time in the history

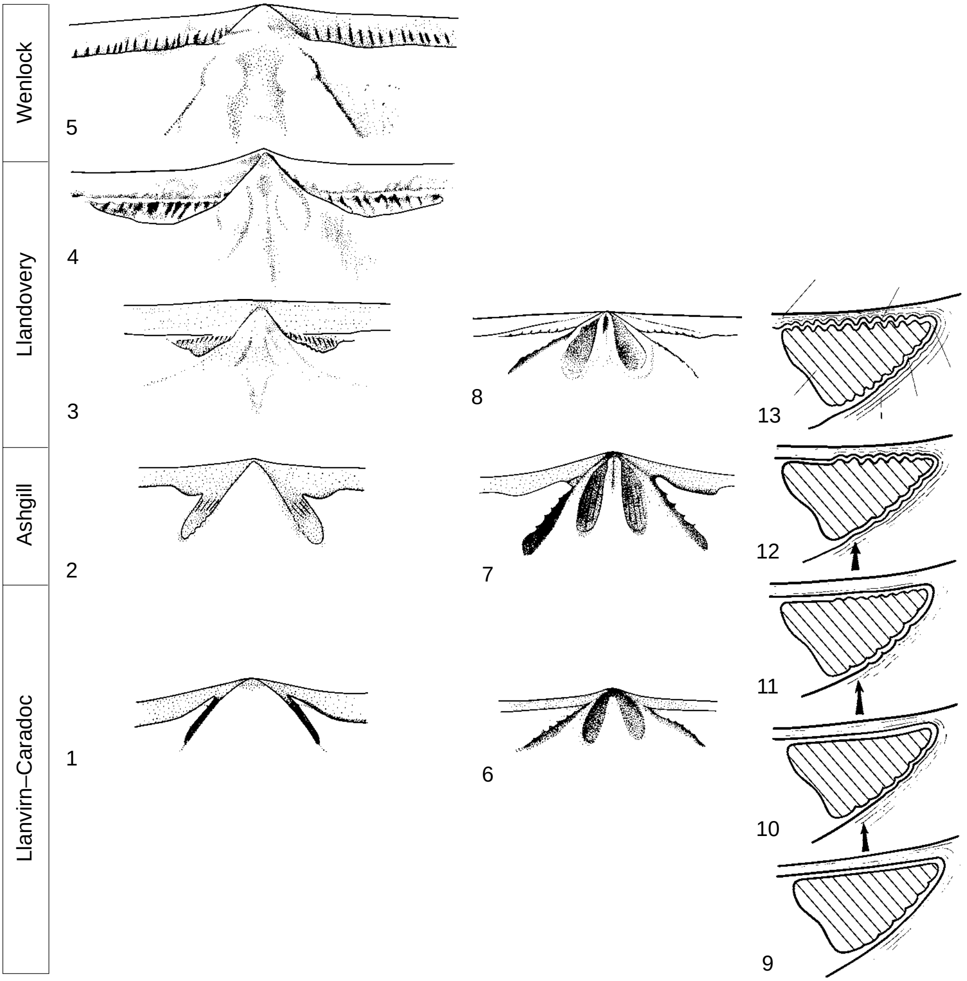

FIG. 133. Evolution of articulation in Strophomenoidea in Late Ordovician and early Silurian; *1–8,* internal molds; *1,6, Macrocoelia; 2,7, Eostropheodonta; 3,8, Palaeoleptostrophia; 4, Brachyprion; 5, Mesoleptostrophia filosa; 9–13,* schematic sections through strophomenoidean ventral hinge line, socket ridge, and dental plate showing development first of crenulations and subsequently denticles (Rong & Cocks, 1994).

of the stock, since, as noted by WILLIAMS (1953a), the increasing denticulation of the hinge line was progressive ontogenetically as well as phylogenetically. It is a general evolutionary trend, however, that early forms have fewer denticles in adult stages and later forms more numerous denticles.

The order Strophomenida (including plectambonitoids and strophomenoids) possess deltidiodont rather than the cyrtomatodont hinge teeth, which are more efficient in articulation than deltidiodont teeth (JAANUSSON, 1971). To have the function of keeping the position of the axis of rotation fixed along a long hinge line in strophomenoid evolutionary history, it was necessary to form accessory structures, such as crenulations and denticles, which were developed to fulfill the same function when the teeth became reduced. Thus the denticles functioned as interlocking devices to prevent the valves from skewing sideways. Almost no group with cyrtomatodont teeth possesses denticles along the hinge line. The establishment of denticulation, which seems to have been a new advantageous construction, led to a radiation in the Silurian and Devonian. Although the denticulate families survived the latest Ordovician ice age, however, they did not escape the Frasnian-Famennian mass extinction. This was perhaps because either (1) in the early stage of their evolutionary history they had great vitality and their novelties, especially the establishment of denticulation, were very favorable to their life habits; or (2) in the later stages of their history they did not adjust to the changing environments and, although they developed existing structures, such as strong forked, posteriorly directed cardinal process lobes, there was not enough space between the two valves for a more developed cardinal process.

The loss of dental plates in different denticulate stocks also occurred at different times, but mostly before the Wenlock. The earliest known taxon lacking dental plates is *Origostrophia.* The loss of dental plates, which progressed by simple shortening (rather than by a flaring toward and subsequent merger with the denticular plates and then the hinge line), may be considered an important trend in strophodontoid evolutionary history (WILLIAMS, 1953a; see also Fig. 133). The evolution and stratigraphical ranges of the families within the Strophomenoidea are shown in Figure 134 (RONG & COCKS, 1994).

Family STROPHOMENIDAE King, 1846

[Strophomenidae KING, 1846, p. 28]

Outline semicircular to transverse; cardinal process lobes robust and often subcircular, situated on the posterior end of a notothyrial platform; discrete, strong socket ridges often curved around laterally at their ends. *Ordovician (Arenig)–Silurian (Ludlow).*

Subfamily STROPHOMENINAE King, 1846

[*nom. transl.* GILL, 1871, p. 26, *ex* Strophomenidae KING, 1846, p. 28]

Differs from Furcitellinae in that muscle-bounding ridges in dorsal valve and side septa absent or very weak. *Ordovician (Llanvirn–Ashgill).*

Strophomena RAFINESQUE in DE BLAINVILLE, 1824, p. 302 [**Leptaena planumbona* HALL, 1847, p. 112; SD ICZN Opinion 1671, 1992] [=*Rugomena* RŌŌMUSOKS, 1993b, p. 115 (type, *R. adilensis*)]. Profile gently resupinate; ornament variable from parvicostellate to costellate; prominent pseudodeltidium; small chilidium; teeth strong, sometimes with irregular denticles, crenulations; dental plates extending into elevated bounding ridges largely surrounding the subcircular to rhomboidal ventral muscle field; adductor scars not enclosed by diductor scars; ventral myophragm sometimes present; socket ridges sometimes crenulated; strong, short median ridge coming from the posterior edge of notothyrium; ridge sometimes forked anteriorly; dorsal muscle field gently impressed, with weak bounding ridges sometimes present laterally; occasional weak transmuscle ridges sometimes present, often absent. *Ordovician (Caradoc–Ashgill):* North America, Europe.

- S. (**Strophomena**). Similar to *S. (Keilamena)* but with squatter, more triangular cardinal process lobes and dorsal side septa often weakly developed; similar to *S. (Tetraphalerella)* but generally larger, with flaring although small ventral adductor muscle scars and more anterolaterally directed socket plates rather than recurving back to the hinge line. *Ordovician (Caradoc–Ashgill):* North America, Scotland.——FIG. 135,*1a–f.* **S. (S.) planumbona* (HALL), Trenton Group, Caradoc, Cincinnati, Ohio; *a–c,* lectotype, ventral, posterior, lateral views of conjoined valves, AMNH 30247, ×1.5; *d,e,* ventral, anterior views of ventral interior, AMNH 30248, ×1.5; *f,* dorsal interior, AMNH 918/5, ×1.5 (Rong & Cocks, 1994).——FIG. 135,*1g. S. adilensis* (RŌŌMUSOKS), ventral interior, Adila Formation, Pirgu Stage, Ashgill, Vardi, Estonia, TAGI BR 1531, ×1.5 (Rōōmusoks, 1993b).
- S. (**Keilamena**) RŌŌMUSOKS, 1993b, p. 114 [**Actinomena occidens* MANNIL in ORASPOLD, 1956, p. 59; OD]. Similar to *S. (Strophomena),* but with erect cardinal process lobes, no hint of dorsal side septa. *Ordovician (Caradoc):* Baltic. ——FIG. 135,*3a–c.* **S. (K.) occidens* (MANNIL), Keila Stage, middle Caradoc; *a,* ventral exterior, Jälgimägi, Estonia, TAGI BR 2387, ×1; *b,* holotype, ventral interior, Keila, Estonia, TAGI BR 3091, ×1; *c,* dorsal interior, Kulna, Estonia, TAGI BR 2380, ×1.5 (Rōōmusoks, 1993b).
- S. (**Tetraphalerella**) WANG, 1949, p. 28 [**T. cooperi;* OD]. Similar to *S. (Strophomena),* but with small ventral adductor muscle scars completely enclosed by diductor scars; socket plates more recurved laterally back toward the hinge line; dorsal transmuscle ridges not known. *Ordovician (Ashgill):* North America.——FIG. 135,*2a–c.* **S.*

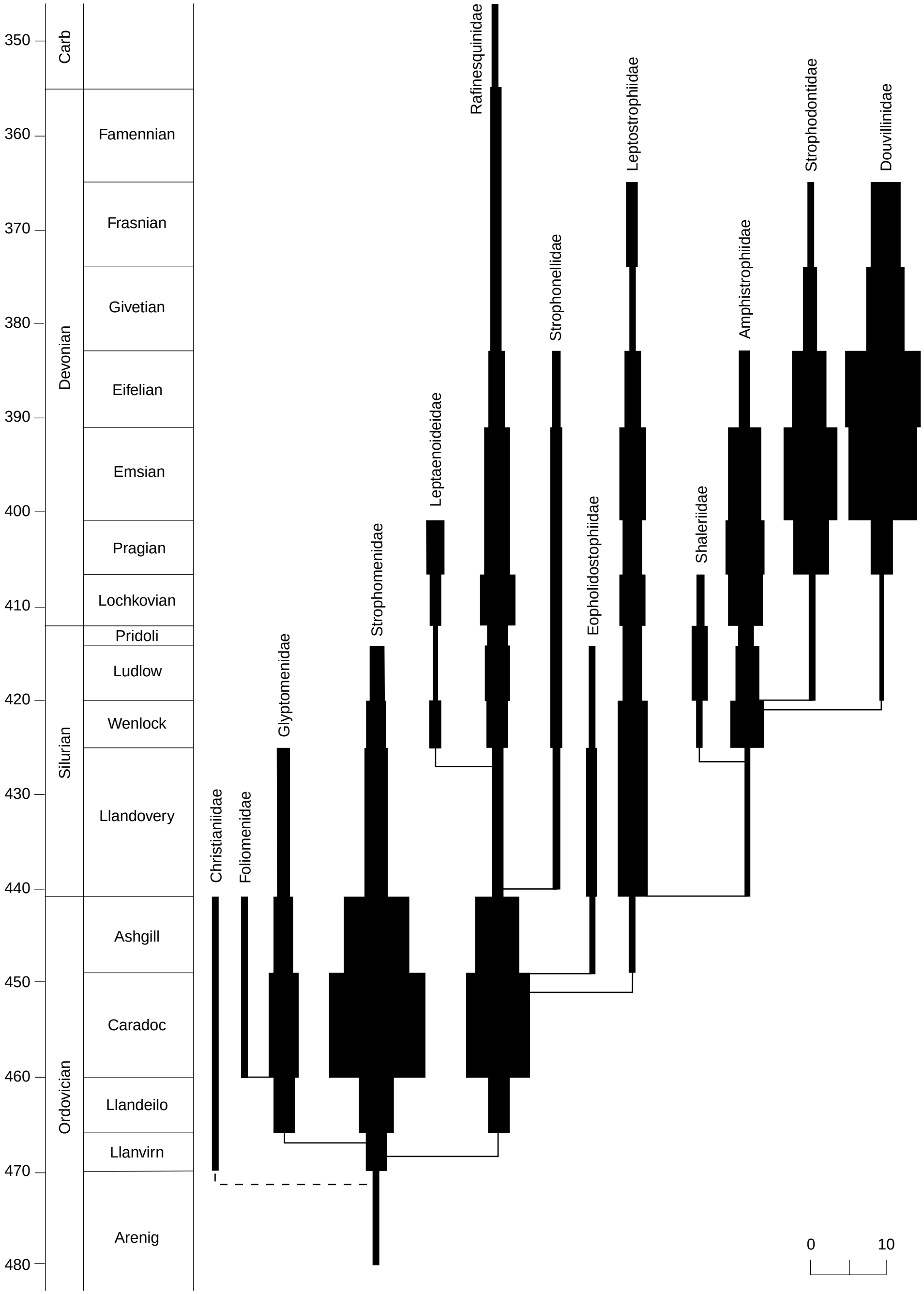

FIG. 134. Stratigraphic ranges and postulated relationship of families of Strophomenoidea; absolute ages in million years shown on left; widths of column representing each family indicate relative number of genera in each series (Ordovician and Silurian) or stage (Devonian) (Rong & Cocks, 1994).

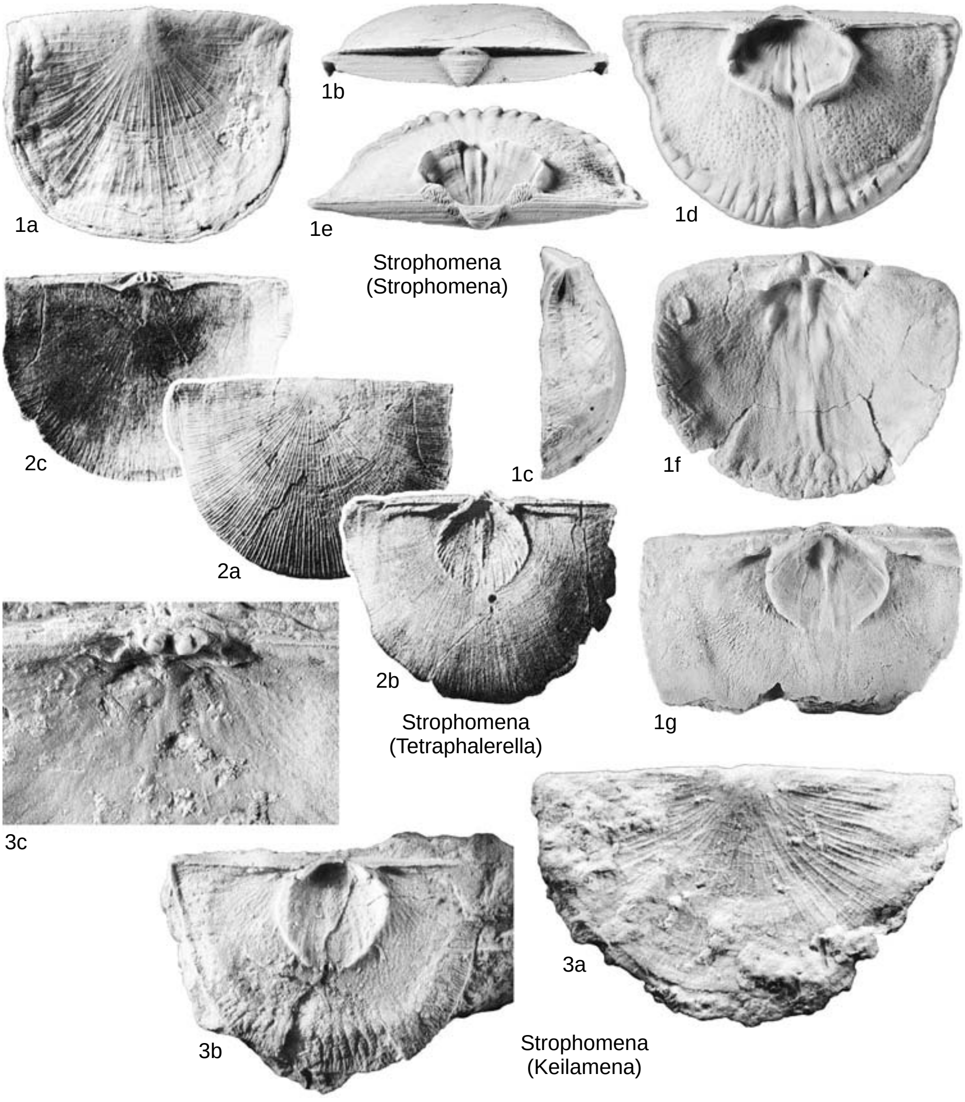

FIG. 135. Strophomenidae (p. 220–222).

(T.) cooperi, upper Elgin Limestone, lower Ashgill, Orleans, Winneshiek County, Iowa; holotype, dorsal exterior, ventral interior, dorsal interior, SUI 1860, ×1 (Wang, 1949).

Actinomena ÖPIK, 1930, p. 166 [**Strophomena (A.) orta;* OD]. Profile gently resupinate; ornament unequally parvicostellate with rugae only posterolaterally; with pseudodeltidium, chilidium; prominent teeth with irregular denticles on dorsal face; thick dental plates continuous anteriorly with curved to straight bounding ridges on lateral parts of subquadrate to subcircular ventral muscle field; faint dorsal transmuscle ridges; muscle-bounding ridges, side septa weakly developed in some species. *Ordovician (Llandeilo–Caradoc):* Europe.——FIG. 136,*1a–d.* **A. orta,* Kukruse Formation C2β, upper Llandeilo; *a,* dorsal exterior, Käva, TAGI BR 201, ×1.5; *b,* ventral interior, Kukers, northwest of Jewe, Estonia, BMNH B 10881, ×1.5; *c,* ventral interior, Käva, TAGI BR 1504, ×1.5; *d,* dorsal interior, Käva, ×1.5 (new).

Drummuckina BANCROFT, 1949, p. 11 [**Stropheodonta donax* REED, 1917, p. 892; OD]. Profile concavo-convex; ornament costellate; small deltidial plates;

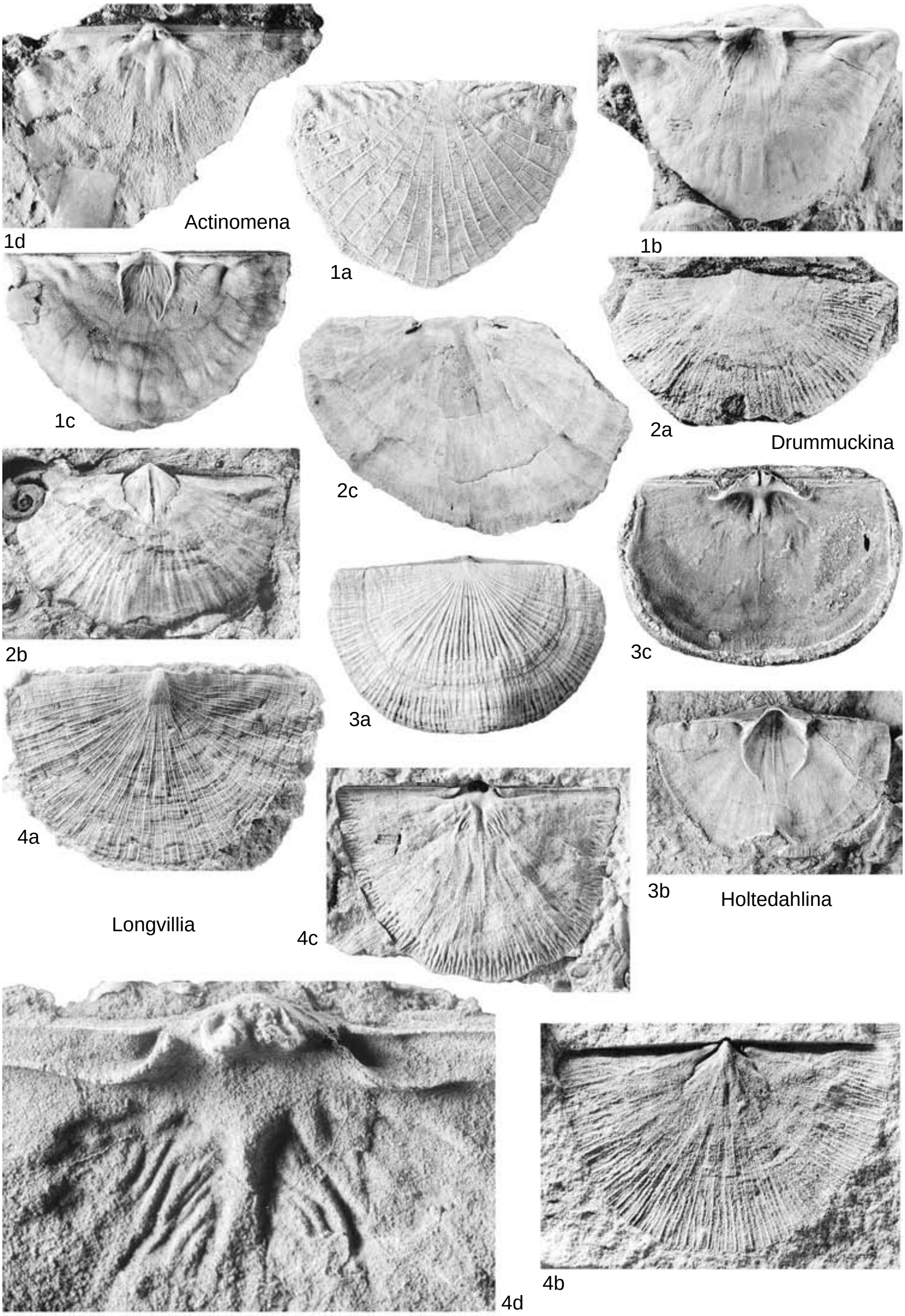

FIG. 136. Strophomenidae (p. 222–224).

large chilidium; teeth with weak, irregular denticles; short dental plates continuous with elevated bounding ridges nearly enclosing trapezoidal ventral muscle field; myophragm present; socket ridges flaring laterally subparallel to hinge line; dorsal muscle field poorly impressed; small thin dorsal median ridge. *Ordovician (Ashgill):* Scotland.——FIG. 136,*2a–c*. **D. donax* (REED), Starfish Bed, Drummuck Group, Rawtheyan, Thraive Glen, Girvan, Strathclyde, Scotland; *a,* ventral exterior, BMNH B 72915, ×1.5; *b,* lectotype, ventral internal mold, BMNH B 72906, ×1.5; *c,* dorsal internal mold, BMNH B 72916, ×1.5 (new).

Esilia NIKITIN & POPOV, 1985, p. 38 [**E. tchetvericovae;* OD]. Profile biconvex, with strong dorsal fold, ventral sulcus; ornament unequally costellate, with bifurcation, intercalation; strong pseudodeltidium, chilidium; dental plates continuous with elongate elliptical bounding ridges enclosing ventral muscle field except anteriorly; cardinal process robust, with lobes close together, situated on strong notothyrial platform; socket ridges fused to base of cardinal process lobes curving posteriorly, extending laterally very close to hinge line; dorsal muscle field faint; dorsal median ridge present. *Ordovician (Llandeilo–Caradoc):* Kazakhstan.——FIG. 137,*3a–e*. **E. tchetvericovae,* ?Andriushenskaya Formation, middle Ordovician, Ishim River, ?North Kuprianovka, central Kazakhstan; *a,* latex cast of dorsal exterior, CNIGR 32/12209, ×2; *b,c,* dorsal, lateral views of dorsal exterior, BMNH BC 12930, ×1.5; *d,* latex cast of ventral interior, CNIGR 17/12209, ×2; *e,* latex cast of dorsal interior, CNIGR 21/12209, ×2 (new).

Holtedahlina FOERSTE, 1924, p. 122 [**Leptaena sulcata* DE VERNEUIL, 1848b, p. 350; OD]. Profile gently dorsibiconvex with strong ventral sulcus, dorsal fold anteriorly; ornament of unequal costellae; large pseudodeltidium; small chilidial plates; interior as in *Strophomena,* but dorsal transmuscle ridges weakly developed. *Ordovician (upper Llandeilo–lower Ashgill):* North America, Baltic, Kazakhstan, China.——FIG. 136,*3a–c*. **H. sulcata* (DE VERNEUIL), Whitewater Formation, upper Caradoc–lower Ashgill, Camden, Ohio; *a,* dorsal view of conjoined valves, USNM 117747a, ×1.5; *b,* ventral interior, USNM 117744, ×1.5; *c,* dorsal interior, USNM 117747b, ×1.5 (Cooper, 1956).

Infurca PERCIVAL, 1979a, p. 185 [**I. tessellata;* OD]. Profile convexoplanar to dorsibiconvex; ornament multicostellate with conspicuous growth lamellae; small pseudodeltidium, chilidium; crenulate teeth supported by divergent dental plates with short bounding ridges to pentagonal muscle field, which is open anteriorly; cardinalia as in *Strophomena;* thin dorsal median ridge. *Ordovician (Caradoc):* Australia.——FIG. 137,*2a–c*. **I. tessellata,* Sandstone in Goonumbla Volcanoes, upper Caradoc, Currajong Park Homestead, Gunningbland, New South Wales, Australia; *a,* latex of ventral exterior mold, SUP 62566, ×3; *b,* latex of ventral internal mold, SUP 62564, ×2; *c,* holotype, latex of dorsal internal mold, SUP 62560, ×2 (Percival, 1979a).

Longvillia BANCROFT, 1933, p. 3 [**Orthis grandis* J. DE C. SOWERBY, 1839, p. 638; OD]. Profile very gently resupinate; unequally parvicostellate ornament; small pseudodeltidium, chilidium; short divergent dental plates continuous with short bounding ridges only posterolateral to muscle field, which is open anteriorly; strong cardinal process with lobes close together; short thin socket ridges curving anteriorly, then laterally subparallel with hinge line; short dorsal median ridge present. *Ordovician (Llandeilo–Ashgill):* Europe, Asia.——FIG. 136,*4a–d*. **L. grandis* (J. DE C. SOWERBY), Cheney Longville Flags, Caradoc, Marsh Wood, Marshbrook, Shropshire, England; *a,b,* latex casts of ventral external, internal molds, BMNH B 8528, ×1 (new); *c,* dorsal internal mold, ×1; *d,* magnification of latex cast of cardinalia, BMNH BB 30638, ×5 (Rong & Cocks, 1994).

Pseudostrophomena RŌŌMUSOKS, 1963, p. 237 [**P. reclinis;* OD]. Profile resupinate as in *Strophomena;* ornament unequally costellate; small pseudodeltidium, chilidium; differs from *Strophomena* in short straight bounding ridges only posterolaterally to ventral muscle field,which is open anterolaterally, anteriorly; distinctive recurved socket plates; dorsal muscle field poorly impressed. *Ordovician (Caradoc):* Baltic.——FIG. 137,*4a–d*. **P. reclinis,* Rägavere Formation, upper Caradoc; *a,* dorsal exterior, Voore, Estonia, BMNH BB 91298, ×1.5; *b,* ventral interior, Rägavere, Estonia, BMNH BC 12945, ×1.5; *c,* ventral interior, Voore, BMNH BB 91296, ×1.5; *d,* dorsal interior, Voore, BMNH BB 91297, ×1.5 (new). [Note added in proof: not orthotetidine, see page 674.]

Trotlandella NEUMAN in NEUMAN & BRUTON, 1974, p. 95 [**T. loki;* OD]. Profile dorsibiconvex; multicostellate ornament; pseudodeltidium large; chilidium small; dental plates extending anteriorly to bound short oval ventral muscle field; cardinal process lobes delicate, but socket ridges short, strong, curved laterally subparallel to hinge line; dorsal muscle field poorly impressed. *Ordovician (Llanvirn):* Baltic.——FIG. 137,*1a–d*. **T. loki,* Whiterock, Llanvirn, siltstone block, Trotland Farm, Hølonda area, Trøndelag, Norway; *a,b,* ventral, posterior views of latex cast of conjoined valves, PMO 89083, ×1.5; *c,* ventral internal mold, PMO 89088, ×1.5; *d,* holotype, latex cast of dorsal interior, PMO 89080, ×1 (Neuman & Bruton, 1974).

Subfamily FURCITELLINAE Williams, 1965

[Furcitellinae WILLIAMS, 1965d, p. 384]

Dorsal valve muscle field with muscle-bounding ridges; dorsal side septa often developed, although can be weak in some members of population. *Ordovician (Llanvirn)–Silurian (Ludlow).*

Furcitella COOPER, 1956, p. 875 [**F. plicata;* OD]. Profile dorsibiconvex with deeper dorsal valve; ventral valve often flat to concave anteriorly; ornament

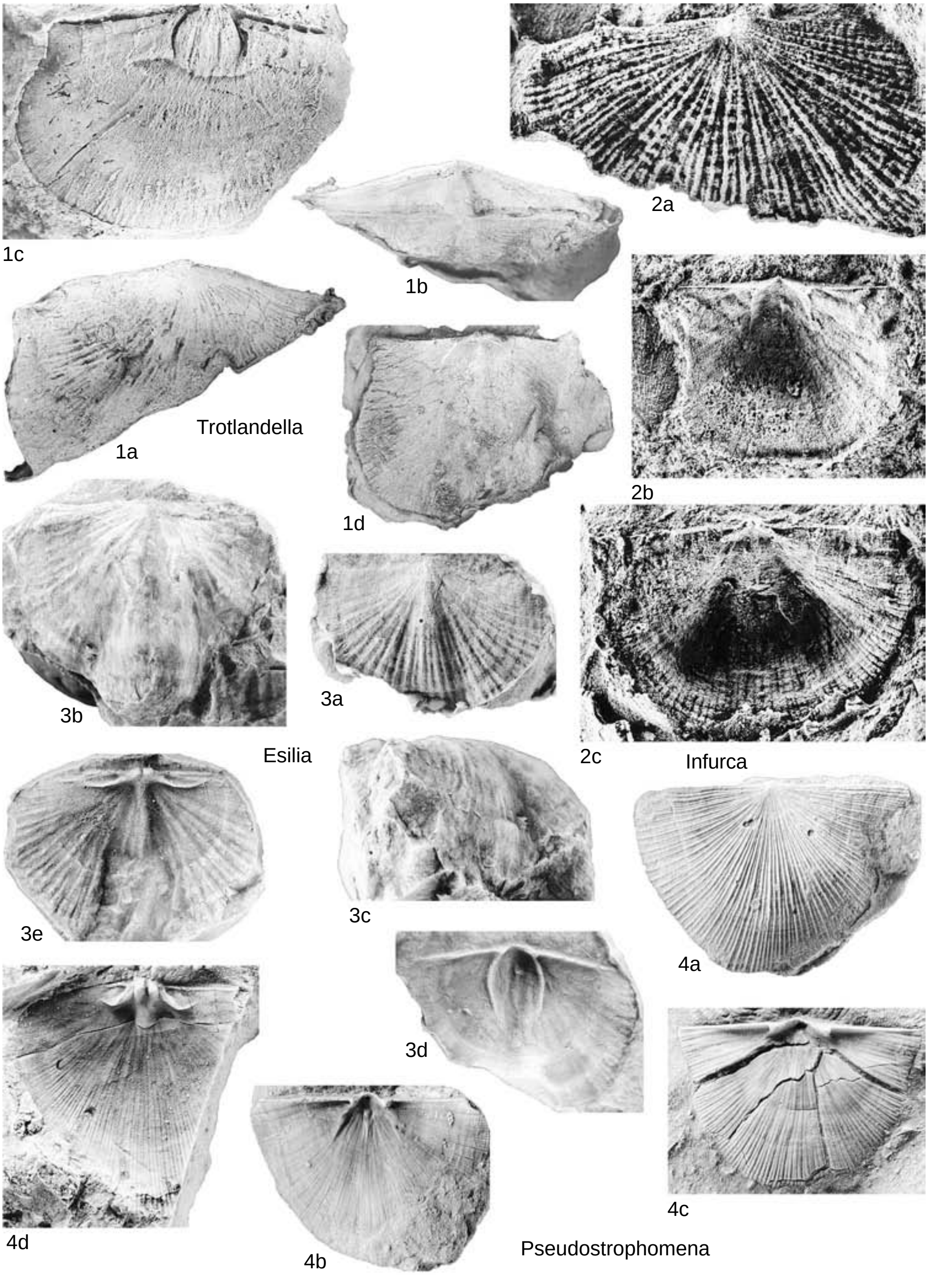

FIG. 137. Strophomenidae (p. 224).

costellate; strongly convex pseudodeltidium, chilidium; short but stout dental plates extending into curved bounding ridges enclosing trapezoidal ventral muscle field except anteriorly; cardinal process lobes united with dorsal median ridge; transmuscle ridges well developed, close to socket

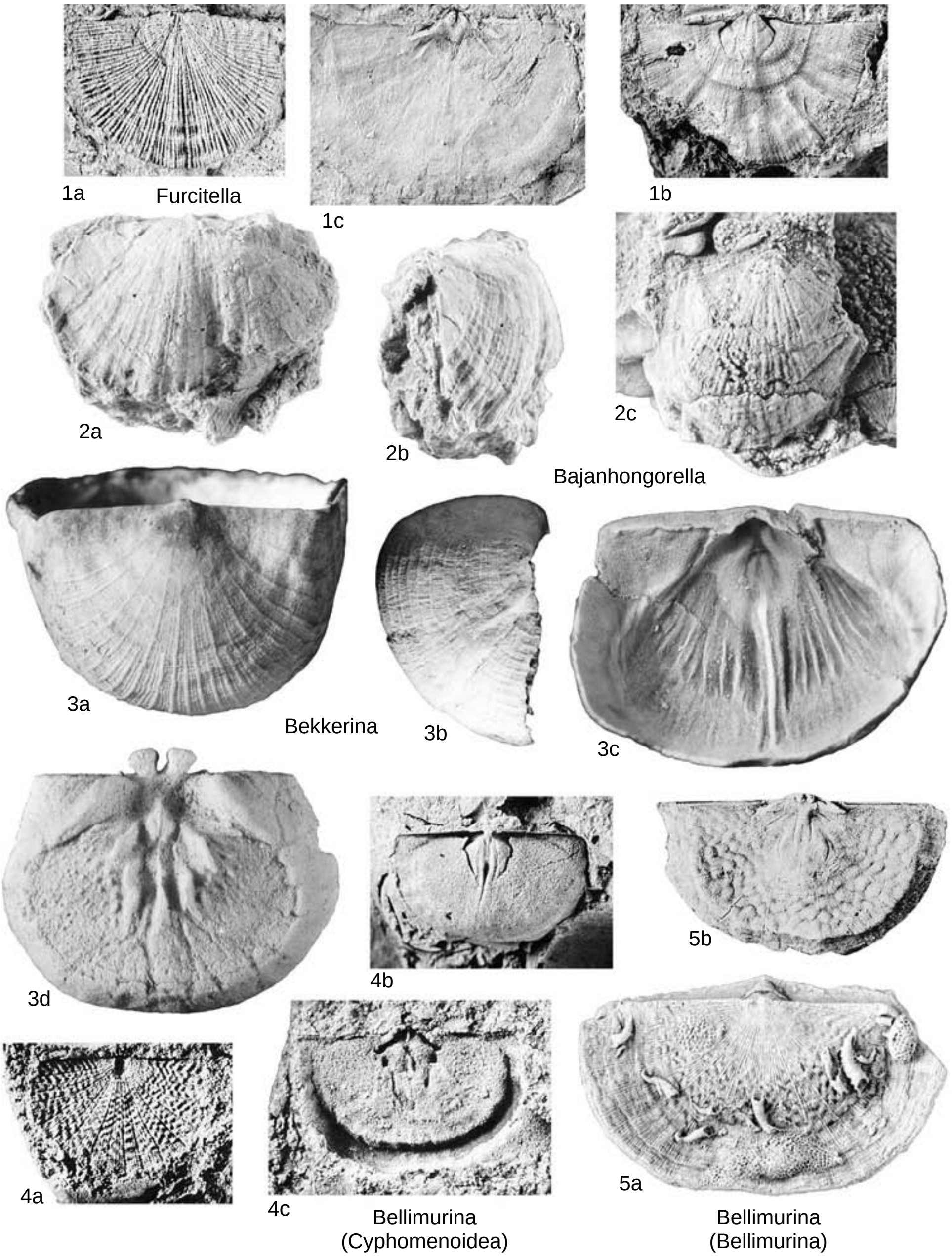

FIG. 138. Strophomenidae (p. 224–227).

ridges; small thin median ridge variably developed in valve center bifurcating anteriorly; side septa variably developed, but often absent. *Ordovician (Caradoc–Ashgill):* North America.——FIG. 138,*1a–c.* **F. plicata,* Oranda Formation, Caradoc, Linville Station, Virginia; *a,* plasticine cast of ventral exterior, USNM 117750d, ×2; *b,* ventral internal mold, USNM 117750c, ×2; *c,* plasticine cast of dorsal interior, USNM 117751c, ×2 (Cooper, 1956).

?Bajanhongorella Rozman, 1977, p. 124 [**B. bajanhongorica;* OD]. Small; subcircular outline, profile strongly dorsibiconvex; fasciculate ornament; interior poorly known, apart from strong dental plates, dorsal median septum; hence family uncertain. *Ordovician (Ashgill):* Mongolia.——Fig. 138,*2a–c.* **B. bajanhongorica,* lower Ashgill, Bayan Khongor, Mongolia; *a,b,* dorsal, lateral views of dorsal exterior, BMNH BB 75086, ×3; *c,* partly exfoliated ventral valve, BMNH BB 75087, ×3 (new).

Bekkerina Rõõmusoks, 1993a, p. 50 [**Rafinesquina dorsata* Bekker, 1921, p. 73; OD]. Ventral valve profile strongly convex; dorsal profile flat, geniculate; unequally parvicostellate ornament; pseudodeltidium vestigial; chilidium small; flaring dental plates extending anterolaterally into edge of large, distinctive ventral muscle field without bounding ridges but impressed into valve floor, with radial striae; long narrow ventral median septum; prominent cardinal process lobes directed ventroposteriorly; discrete thin socket plates; anterior dorsal side septa high, long; dorsal subperipheral rim present. *Ordovician (Llandeilo–Caradoc):* Baltic. ——Fig. 138,*3a–d.* **B. dorsata* (Bekker), Kukruse Stage, Llandeilo–Caradoc, Kohtla-Järve, Estonia; *a,b,* ventral, lateral views of conjoined valves, TAGI BR 227, ×4; *c,* ventral interior, TAGI BR 236, ×4; *d,* dorsal interior, TAGI BR 229, ×4 (Rõõmusoks, 1993a).

Bellimurina Cooper, 1956, p. 854 [**Leptaena charlottae* Winchell & Schuchert, 1892, p. 288; OD]. Profile biconvex centrally, concavoconvex in adults, gently geniculate dorsally; distinctive ornament of small concentric rugae interrupted by costellae; large pseudodeltidium; smaller chilidium; short divergent dental plates extending into curved bounding ridges to ventral muscle field, open anteriorly; cardinalia as in *Furcitella;* short dorsal median ridge often forked anteriorly, but variably developed; variably developed dorsal transmuscle ridges. *Ordovician (Caradoc)–Silurian (Telychian):* cosmopolitan.

B. (**Bellimurina**). Similar to *B. (Cyphomenoidea)* but with continuous dorsal transmuscle ridges and lower dorsal subperipheral rim. *Ordovician (Caradoc):* North America, Kazakhstan, China.——Fig. 138,*5a,b.* **B. (B.) charlottae* (Winchell & Schuchert), Decorah Formation, Guttenberg Member, Caradoc, St. Paul, Minnesota; *a,* dorsal view of conjoined valves, YPM S3620a, ×2; *b,* dorsal interior, YPM S3619, ×2 (Cooper, 1956).

B. (**Cyphomenoidea**) Cocks, 1968, p. 316 [**Leptaena wisgoriensis* Lamont & Gilbert, 1945, p. 660; OD]. Similar to *B. (Bellimurina)* but dorsal transmuscle ridges vestigial to dotlike; dorsal side septa strong, high subperipheral rim present. *Silurian (Aeronian–Telychian):* Europe, North America.——Fig. 138,*4a–c.* **B. (C.) wisgoriensis* (Lamont & Gilbert), Wych Beds, upper Llandovery, Coneygore Coppice, Alfrick, Worcestershire, England; *a,* dorsal external mold, OUM C5612, ×2; *b,* ventral internal mold, OUM C5638, ×2; *c,* dorsal internal mold, OUM C5631, ×2 (Cocks, 1968).

Biparetis Amsden, 1974, p. 54 [**B. paucirugosus;* OD]. Profile concavoconvex, with strong dorsal geniculation; ornament unequally parvicostellate with weak, irregular rugae sometimes developed; large pseudodeltidium; small chilidium; teeth strong with occasional irregular denticles, crenulations; flaring dental plates with pair of short transverse ridges connecting them with hinge line; strong curved elevated bounding ridges to ventral muscle field except anteriorly; diductor scars enclosing adductor scars; distinctive curved pair of united side septa, dorsal muscle-bounding ridges extending anteriorly from anterolateral end of socket ridges. *Ordovician (Ashgill):* North America.——Fig. 139,*1a–d.* **B. paucirigosus,* Leemon Formation, upper Ashgill, Cape Girardeau County, Missouri; *a,b,* holotype, dorsal, lateral views of conjoined valves, OKGS 6707, ×1.5; *c,* ventral interior, OKGS 6703, ×1.5; *d,* dorsal interior, OKGS 6716, ×1.5 (new).

Dactylogonia Ulrich & Cooper, 1942, p. 623 [**D. geniculata;* OD] [=*Blyskavomena* Havlíček, 1976, p. 369 (type, *D. blyskavensis* Havlíček, 1967, p. 85; OD); *Cyphomena* Cooper, 1956, p. 840 (type, *Leptaena homostriata* Butts, 1942, p. 110; OD)]. Profile concavoconvex, dorsally geniculate; ornament finely costellate to parvicostellate; large pseudodeltidium; small chilidium; short dental plates with curved muscle-bounding ridges variably developed from strong to absent in some specimens; short myophragm present or absent; cardinal process lobes ventrally directed; socket ridges widely divergent; dorsal median ridge variably developed; dorsal transmuscle ridges, side septa well developed; dorsal subperipheral rim. *Ordovician (Caradoc):* North America, Europe.——Fig. 139,*2a–c.* **D. geniculata,* Little Oak Formation, Caradoc, Cahaba Valley, Alabama; *a,* dorsal view of conjoined valves, USNM 117588a, ×2; *b,* ventral interior, ×1; *c,* dorsal interior, USNM 108202, ×3 (Cooper, 1956). ——Fig. 139,*2d,e. D. homostriata* (Butts), Oranda Formation, Caradoc, Strasburg, Virginia; *d,* ventral view of conjoined valves, USNM 117623a, ×3; *e,* dorsal interior, USNM 117624, ×3 (Cooper, 1956).——Fig. 139,*2f,g. D. blyskavensis* (Havlíček), Letná Formation, lower Caradoc, Blyskava Hill, Chrustenice, Czech Republic; *f,* ventral internal mold, ×2; *g,* holotype, dorsal internal mold, OMR VH 337a, ×1.5 (Havlíček, 1976).

?Dzhebaglina Misius, 1986, p. 169 [**D. kelpensis;* OD; Ichkebash Formation (Middle Ordovician), Orto-Nura River, Nura Mountains, northern Kirghizia]. Profile biconvex, with slight dorsal fold, ventral sulcus; ornament unequally parvicostellate; small interarea; small subparallel dental plates posterolaterally bounding small ventral muscle field with elevated bounding ridges uniting anteriorly to form a spondylium-like structure; cardinal process obscure, thus family assignment uncertain; short

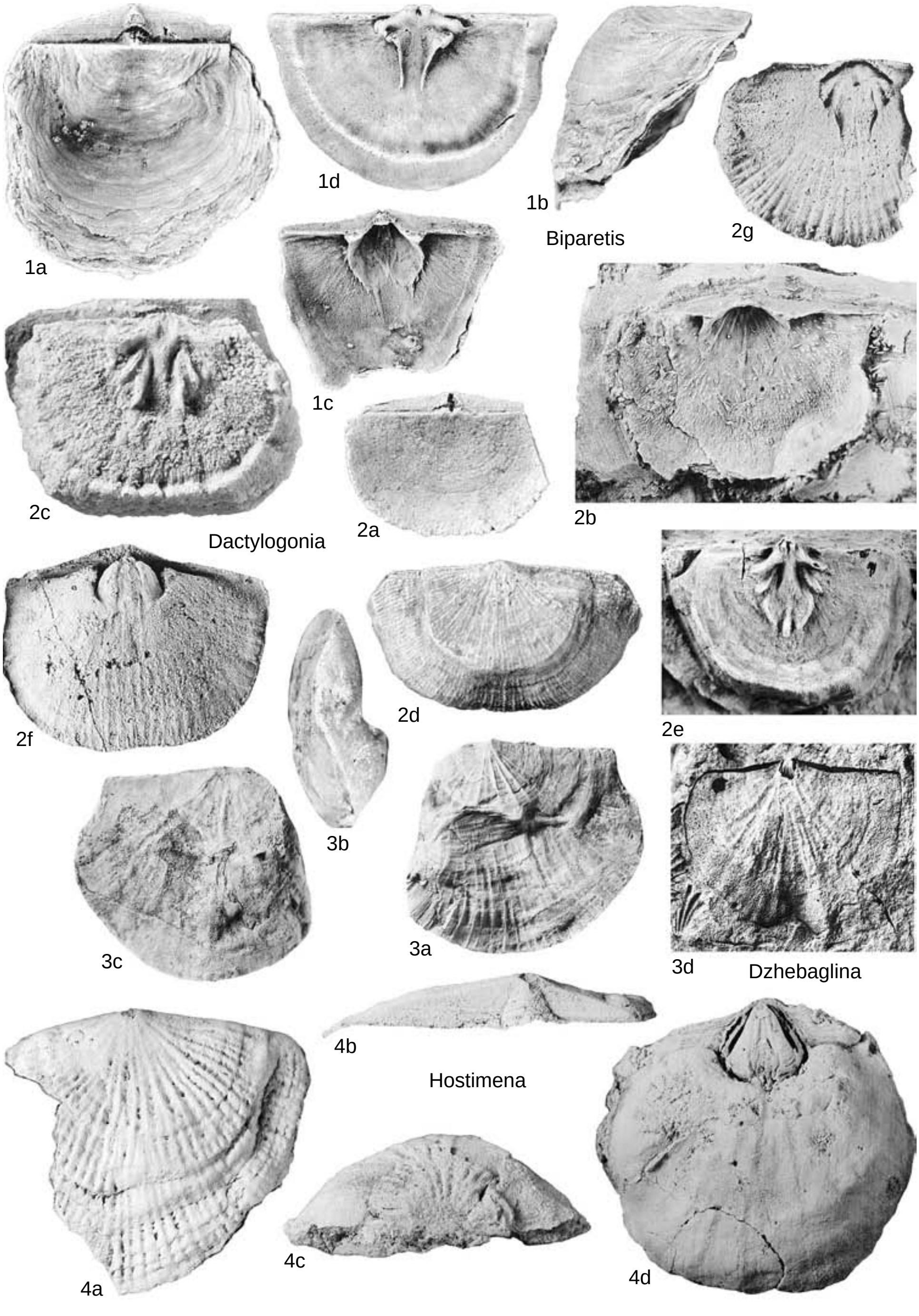

FIG. 139. Strophomenidae (p. 227–229).

socket ridges, relatively small dorsal muscle field with side septa; short central dorsal median septum poorly developed. *Ordovician (Caradoc–Ashgill):* Asia.——Fig. 139,*3a–d. D.* sp., Dulankara Formation, lower Ashgill, Dulankara, Kazakhstan; *a–c,* ventral, lateral, dorsal views of conjoined valves, ×2; *d,* ventral internal mold, ×2 (Popov, new).

Geniculina Rõõmusoks, 1993a, p. 53 [**Strophomena pseudoalternata* Schmidt, 1858, p. 214; OD]. Transverse outline; gently concavoconvex profile, geniculate anteriorly with a trail of variable length; unequally parvicostellate ornament with irregular oblique wrinkles posterolaterally; prominent pseudodeltidium, chilidium; subcircular to trapezoidal ventral muscle field with bounding ridges; short ventral myophragm; ventroposteriorly directed robust cardinal process lobes; socket plates curving laterally to become subparallel with hinge line, crenulate posteriorly in center; one strong pair of dorsal side septa with other minor pairs variably developed; thin dorsal median septum extending anteriorly from myophragm; subperipheral rim present. *Ordovician (Ashgill):* Baltic, North America.——Fig. 140,*1a–c.* **G. pseudoalternata* (Schmidt), Pirgu Stage, middle Ashgill, Estonia; *a,* ventral exterior, Piirsalu, TAGI BR 1463, ×1.5; *b,* ventral internal mold, Röa, TAGI BR 1539, ×1.5; *c,* lectotype, dorsal interior, Vardi, TAGI BR 1460, ×1.5 (Rõõmusoks, 1993a).

?Hostimena Havlíček in Havlíček & Štorch, 1990, p. 69 [**Strophomena hirundo explanans* Barrande, 1879, pl. 47, fig. 11.3–11.5, 11.7–11.9; OD]. Profile strongly dorsibiconvex, with ventral valve flat posteriorly, moderately convex anteriorly; geniculate dorsally in some adult specimens; large pseudodeltidium; ventral muscle field relatively small, completely bounded by ridges; dorsal interior unknown. *Silurian (Telychian–Sheinwoodian):* Europe.——Fig. 139,*4a–d.* **H. explanans* (Barrande), Tuffaceous limestone in Motol Formation, Wenlock, Listice, near Beroun, Bohemia, Czech Republic; *a,b,* ventral, posterior views of ventral exterior, OMR VH 4280a, ×1.5; *c,* posterior view of dorsal exterior, OMR VH 4280b, ×1.5; *d,* ventral internal mold, OMR VH 1945, ×1.5 (Havlíček & Štorch, 1990).

Iberomena Villas, 1985, p. 97 [**Strophomena sardoa* Vinassa, 1927, p. 481; OD]. Profile flat to gently resupinate; ornament mainly unequally parvicostellate; pseudodeltidium small; chilidium reduced or absent; short thick dental plates joined to weak bounding ridges only developed in posterolateral part of subspherical to pentagonal ventral muscle field; short myophragm; short dorsal transmuscle ridges well developed, sometimes united with thin side septa. *Ordovician (Caradoc–Ashgill):* Europe.——Fig. 140,*2a–e.* **I. sardoa* (Vinassa); *a,* latex cast of ventral exterior, Fombuena Formation, upper Caradoc, Luesma, Cadenas Ibéricas Orientales, Spain, DP 2300, ×1.5; *b,c,* ventral internal mold, latex cast, Portixeddu Formation, upper Caradoc–lower Ashgill, Portixeddu, Sardinia, Italy, ×1.5; *d,e,* dorsal internal mold, ×1.5, enlargement of latex cast of cardinalia, Fombuena Formation, upper Caradoc, Luesma, Cadenas Ibéricas Orientales, Spain, DB 2309, ×6 (Villas, 1985).

Katastrophomena Cocks, 1968, p. 293 [**Strophomena antiquata woodlandensis* Reed, 1917, p. 902; OD]. Resupinate with variable ventral geniculation, dorsal fold, ventral sulcus often developed anteriorly; irregularly and variably costellate ornament; large pseudodeltidium, chilidium; teeth with irregular denticles, crenulations sometimes developed; short dental plates merging with curved bounding ridges to relatively small subcircular ventral muscle field, not joined anteriorly; myophragm variably developed; short dorsal transmuscle ridges usually present, side septa often present; short dorsal median ridge present posteriorly; additional small central ridge sometimes developed between side septa. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.

K. (**Katastrophomena**). Similar to *K. (Costistrophomena)* but with finer (but still irregular) radial costellae. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.——Fig. 141,*1a–d.* **K. (K.) woodlandensis* (Reed), Woodland Formation, Llandovery, Rhuddanian, Woodland Point, Girvan, Strathclyde, Scotland; *a,* dorsal exterior, BMNH B 73012, ×1.5; *b,c,* lectotype, ventral interior, latex cast, BMNH B 54490, ×1.5; *d,* dorsal internal mold, BMNH BB 31425, ×1.5 (Cocks, 1968).

K. (**Costistrophomena**) Sheehan, 1987, p. 41 [**C. costata;* OD]. Similar to *K. (Katastrophomena)* except with coarser radial ornament, with strong, widely spaced growth lines. *Ordovician (Ashgill):* Europe.——Fig. 141,*2a–e.* **K. (C.) costata,* Lower Fosse Formation, Ashgill, Vitrival-Bruyère, Ardennes, Belgium; *a,* ventral external mold, IRScNB 1608, ×1.5; *b,* ventral internal mold, IRScNB 1612, ×2; *c,* ventral internal mold, IRScNB 1615, ×2; *d,* holotype, dorsal internal mold, IRScNB 1610, ×2; *e,* dorsal internal mold, IRScNB 1613, ×2 (Sheehan, 1987).

Kirkina Salmon, 1942, p. 598 [**K. millardensis;* OD]. Profile gently concavoconvex; ornament of fine parvicostellae; ventral interior unknown apart from dental plates present; socket ridges widely divergent, curving posterolaterally; dorsal muscle field diamond shaped with two or more pairs of side septa; poorly defined weak, broad myophragm present, but no dorsal median septum. *Ordovician (Llanvirn–Llandeilo):* North America.——Fig. 142,*2a,b.* **K. millardensis,* Pogonip Group,

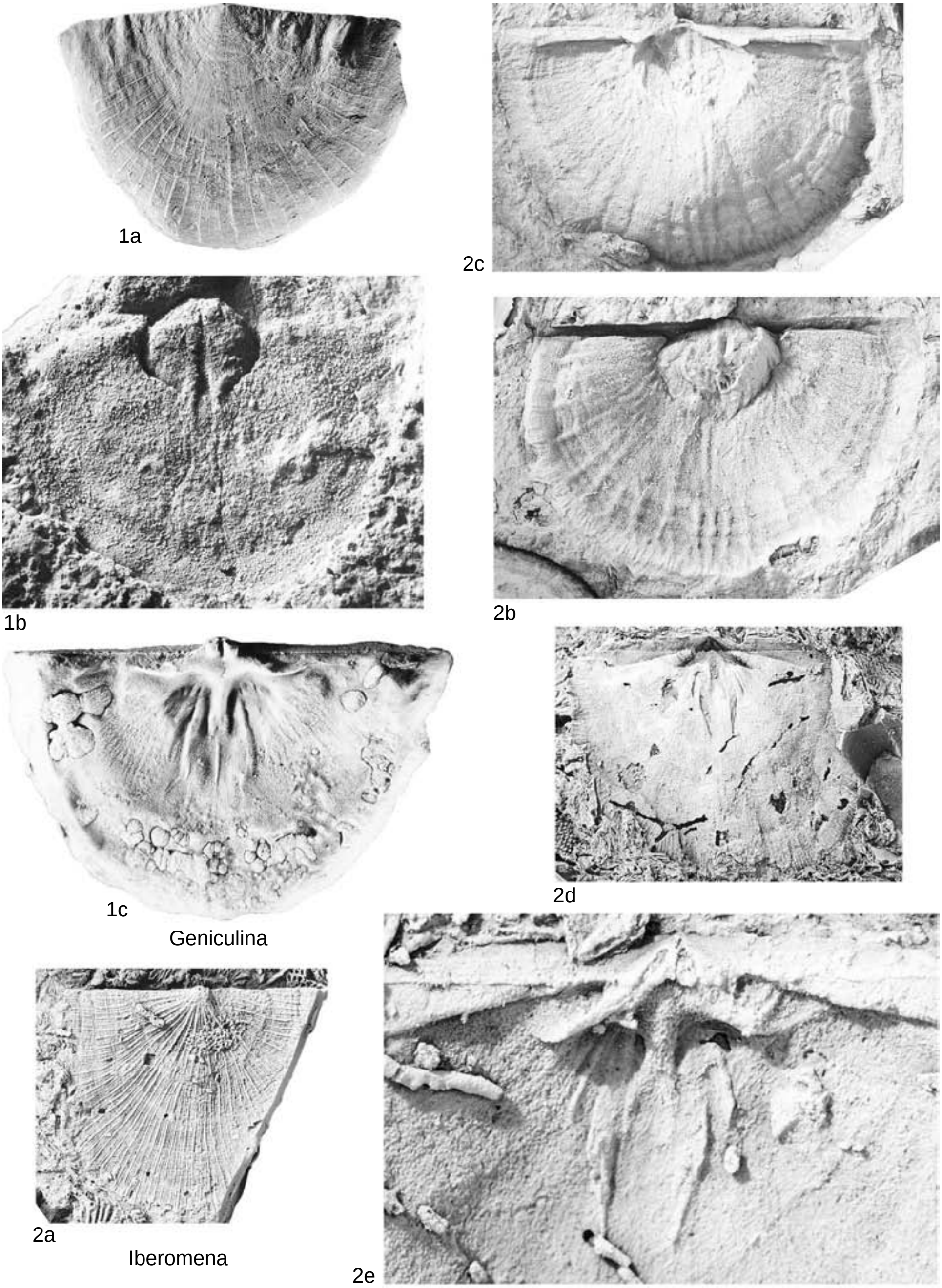

Fig. 140. Strophomenidae (p. 229).

Llanvirn, Point of Rocks, Millard County, Utah; *a,* partly exfoliated ventral exterior, AMNH CU 25918, ×1.5; *b,* holotype, dorsal interior, AMNH CU 25917, ×2 (new).

Laevicyphomena Cocks, 1968, p. 317 [**Cyphomena (L.) feliciter;* OD]. Outline transverse, profile dorsibiconvex, geniculate; radial ornament absent; small pseudodeltidium, chilidium; muscle-

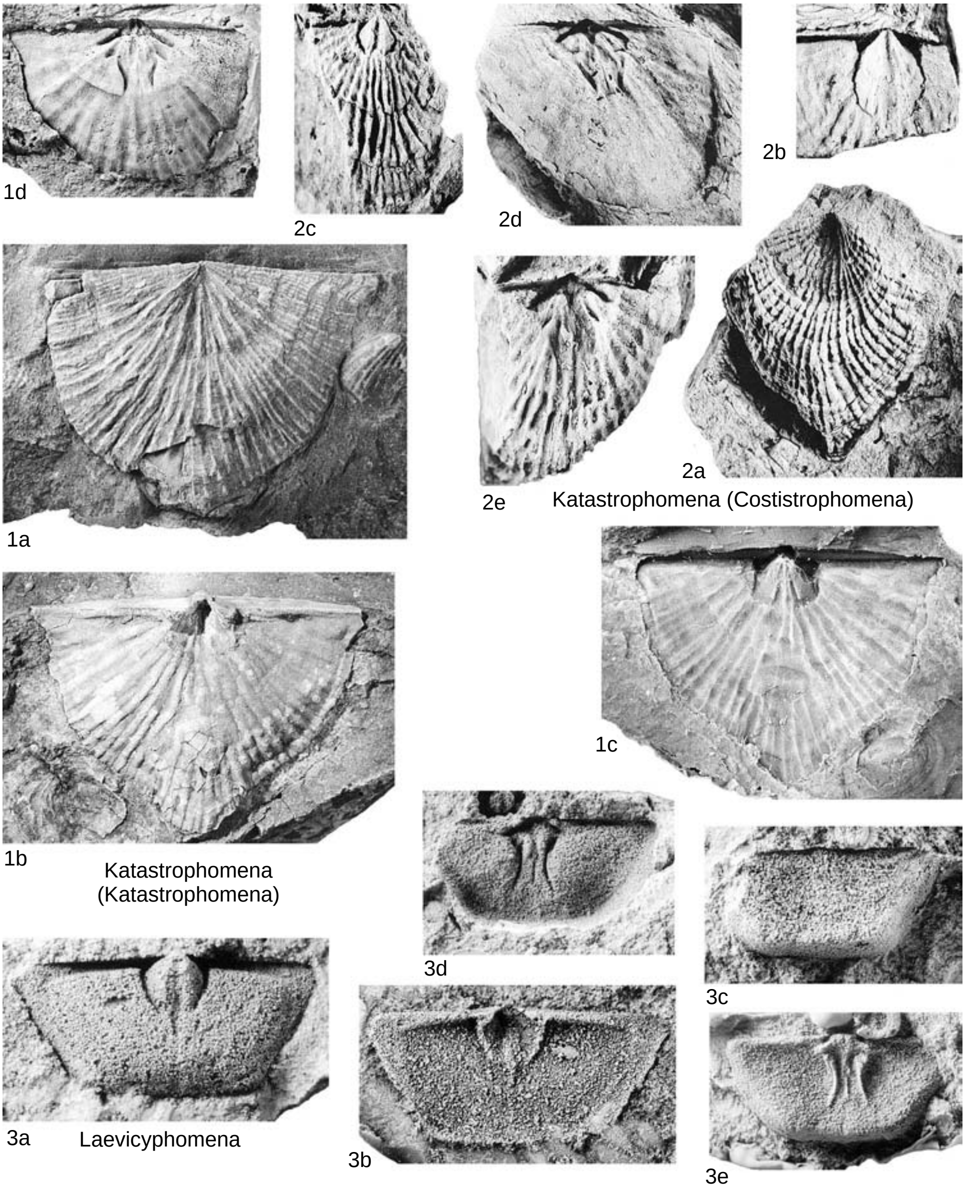

Fig. 141. Strophomenidae (p. 229–231).

bounding ridges enclosing small, often bilobed ventral muscle field; myophragm often present; erect cardinal process; short straight socket plates; distinctive pair of concave dorsal side septa as in *Biparetis,* united posteriorly with short muscle-bounding ridges. *Silurian (Aeronian):* Europe.——Fig. 141,*3a–e.* **L. feliciter,* Bog Quartzite, Aeronian, Bog Mine, Shropshire, England; *a,b,* holotype, ventral internal mold, latex cast, BMNH BB 31346, ×3; *c–e,* dorsal external, internal molds, latex cast of dorsal interior, BMNH BB 31352, ×2 (new).

Luhaia Rõõmusoks, 1956, p. 1091 [**L. vardi;* OD]. Profile convexoconcave, geniculate in ventral direction; rugae irregular, variably developed but sometimes over whole shell, not broken by irregular parvicostellae; large pseudodeltidium; smaller chilidium; strong teeth uniting anterolaterally with

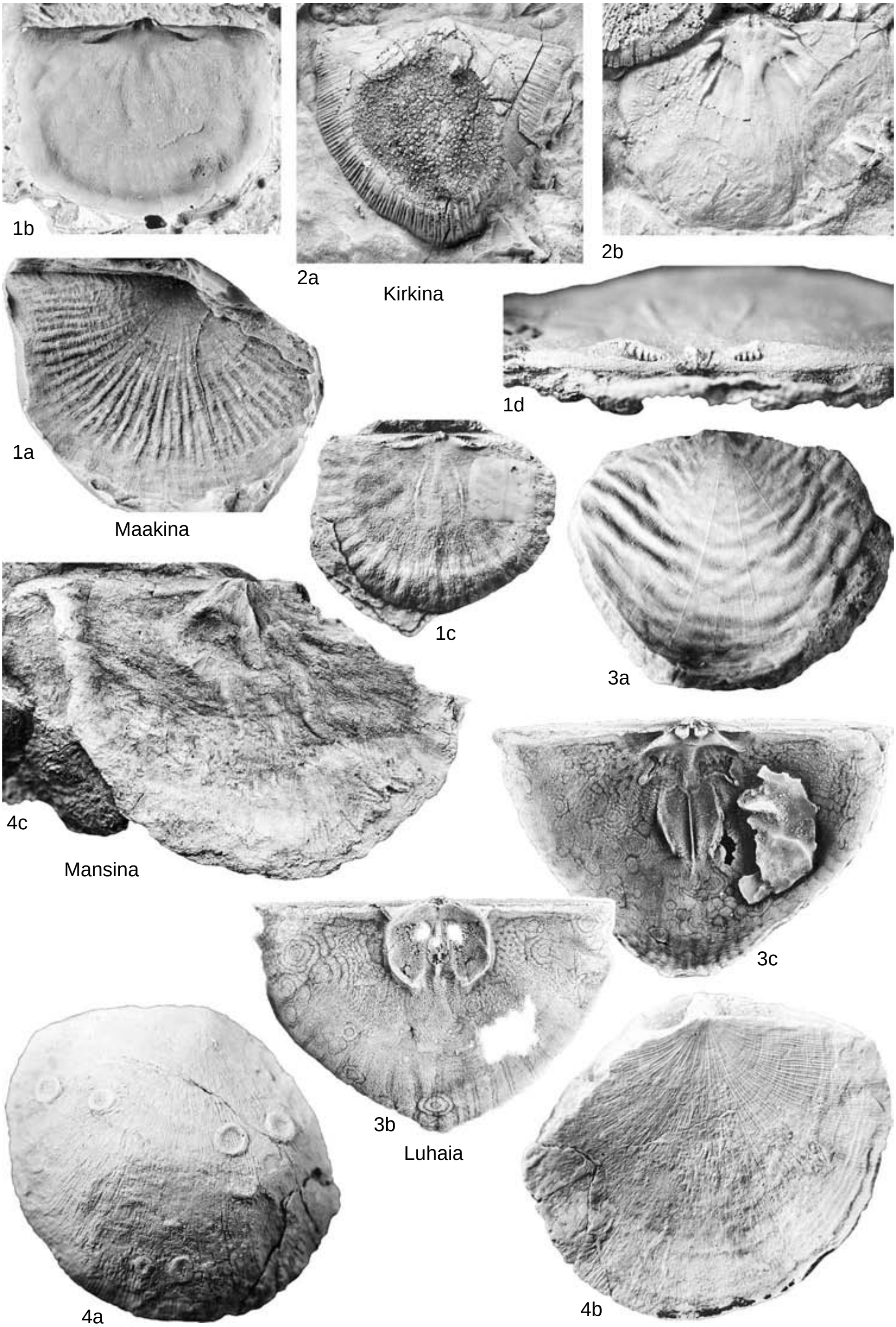

FIG. 142. Strophomenidae (p. 229–233).

pronounced muscle-bounding ridges that curve around subquadrangular ventral muscle field, progress posteriorly before merging with valve floor without uniting; short ventral median septum; socket ridges short, stout, small notothyrial platform developed; pair of curved side septa in dorsal valve center, as well as thin central median septum anterior of short, broad myophragm. *Ordovician (Ashgill):* Baltic.——FIG. 142,*3a–c.* **L. vardi; a,* ventral exterior, Pirgu Formation, Ashgill, Khoskholm, Estonia, TAGI BR 1607, ×2 (Rõõmusoks, new); *b,* ventral interior, Ashgill, Estonia, PM 1010a, ×2; *c,* dorsal interior, Ashgill, Estonia, PM 1010b, ×2 (Jaanusson, new).

Maakina ANDREEVA in NIKIFOROVA & ANDREEVA, 1961, p. 170 [**Oepikina (M.) kulinnensis;* OD]. Semicircular outline; ventral valve with gently convex profile; dorsal valve flat with gentle geniculation anteriorly; distinctive ornament of strong to median rounded costellae; small pseudodeltidium; large chilidium; ventral interior poorly known; very divergent crenulated socket ridges curving laterally subparallel with hinge line; dorsal muscle field poorly impressed, but with thin, curved side septa, no median septum. *Ordovician (Caradoc):* northern Asia.——FIG. 142,*1a–d.* **M. kulinnensis,* Baksansk Horizon, Mangazei Stage, Caradoc, Siberian Platform, Russia; *a,* holotype, latex cast of ventral exterior, CNIGR 7453/420, ×2; *b,* latex cast of dorsal internal mold, CNIGR 7453/416, ×2 (new); *c,* dorsal view of dorsal interior, CNIGR 7453/418, ×2; *d,* posterior view of dorsal interior, CNIGR 7453/418, ×5 (Popov, new).

?Mansina ANDREEVA, 1977, p. 116 [**M. uralica;* OD]. Large with concavoconvex profile, subcircular outline; unequally parvicostellate ornament; large chilidium; ventral interior unknown; cardinal process poorly known, hence family uncertain; short socket ridges, small notothyrial platform; pair of dorsal side septa variably developed, curved posteriorly, subparallel anteriorly; small dorsal median septum poorly developed for short distance centrally. *Ordovician (Caradoc):* Russia.——FIG. 142,*4a–c.* **M. uralica,* Shchygoisk Formation, middle Ordovician, River Khosin, subpolar Urals, Russia; *a,b,* holotype, ventral, dorsal views of conjoined valves, CNIGR 24/10852, ×1.5; *c,* dorsal interior, CNIGR 25/10852, ×2 (Popov, new).

Molongcola PERCIVAL, 1991, p. 153 [**M. variabilis;* OD]. Profile planoconvex to unequally biconvex, not geniculate; ornament coarsely multicostellate; strong pseudodeltidium; very small chilidium; dental plates continuous anteriorly with bounding ridges that are sometimes short, sometimes curved to enclose most of muscle field; cardinalia prominent with ventral facing cardinal process lobes; dorsal median ridge short, small, sometimes absent; distinctive dorsal transmuscle ridges connected anteriorly to anterior ends of curved muscle-bounding ridges, continuing anteriorly as side septa, between which is small central ridge. *Ordovician (Caradoc):* Australia.——FIG. 143,*1a–c.* **M. variabilis,* Trilobite Hill Limestone Member, Cliefden Caves Limestone, Caradoc, Licking Hole Creek, New South Wales, Australia; *a,* dorsal exterior, SUP 68569, ×2; *b,* ventral interior, SUP 68562, ×1.5; *c,* oblique view of dorsal interior, SUP 68563, ×2 (Percival, 1991).

Murinella COOPER, 1956, p. 844 [**M. partita;* OD]. Planoconvex but variably biconvex to concavoconvex profile; costellate to unequally parvicostellate ornament; large interarea, pseudodeltidium, very small discrete chilidial plates; ventral muscle field short, subcircular with variably developed muscle-bounding ridges; adductors separated by median septum extending anteriorly beyond muscle field; short stout socket ridges, strong notothyrial platform; thin central dorsal median septum, one or two pairs of subparallel side septa weakly developed; elevated subperipheral rim in dorsal valve, sometimes with variably developed corresponding subperipheral groove in ventral valve. *Ordovician (Llandeilo–Caradoc):* North America.——FIG. 143,*3a,b.* **M. partita,* Mountain Lake Member, Bromide Formation, Llandeilo–Caradoc, Sulphur, Murray County, Oklahoma; *a,* ventral interior, BMNH BC 12841, ×2; *b,* dorsal interior, BMNH BC 12842, ×2 (new).

Oepikina SALMON, 1942, p. 589 [**O. septata;* OD] [=*Oepikinella* WILSON, 1944, p. 199 (type, *O. affinis;* OD)]. Transverse outline; concavoconvex profile with weak geniculation developed in older specimens; unequally parvicostellate ornament; small pseudodeltidium; vestigial chilidium; crenulate teeth; dental plates short, weak; ventral muscle field poorly impressed; notothyrial platform well developed, extending anteriorly into variably developed, usually prominent dorsal median septum; two or more pairs of strong transmuscle septa; distinctive dorsal subperipheral rim. *Ordovician (Llandeilo–lower Ashgill):* North America, Baltic.——FIG. 143,*2a–e.* **O. septata, Doleroides* Zone, Lebanon Formation, Caradoc, Knox Brook, near Murfreesboro, Tennessee; *a,b,* ventral, dorsal views of conjoined valves, USNM 117828, ×2; *c,* ventral interior, USNM 117829b, ×2 (Cooper, 1956); *d,* holotype, dorsal interior, USNM 117829c, ×2 (new); *e,* ventral interior, USNM 117827b, ×2 (Cooper, 1956).

?Oslomena SPJELDNAES, 1957, p. 161 [**O. osloensis;* OD]. Small shells with strongly concavoconvex profile; parvicostellate ornament; large pseudodeltidium, chilidium; ventral muscle field bounded posterolaterally by dental plates merging anteriorly with curved muscle-bounding ridges not uniting anteriorly; cardinal process poorly known, hence family uncertain; widely divergent socket plates; poorly impressed dorsal muscle field with weak median septum, side septa. *Ordovician (Caradoc):* Baltic.——FIG. 143,*5a,b.* **O. osloensis,* Arnestad Formation, lower Caradoc; *a,* dorsal view of conjoined valves, Skien, Norway, PMO L153, ×2; *b,* lateral view of ventral valve, BMNH BC 13036, Billingstad, Norway, ×2 (new).

Panderites RÕÕMUSOKS, 1993a, p. 49 [**Plectambonites imbrex* PANDER, 1830, p. 91; OD]. Concavoconvex

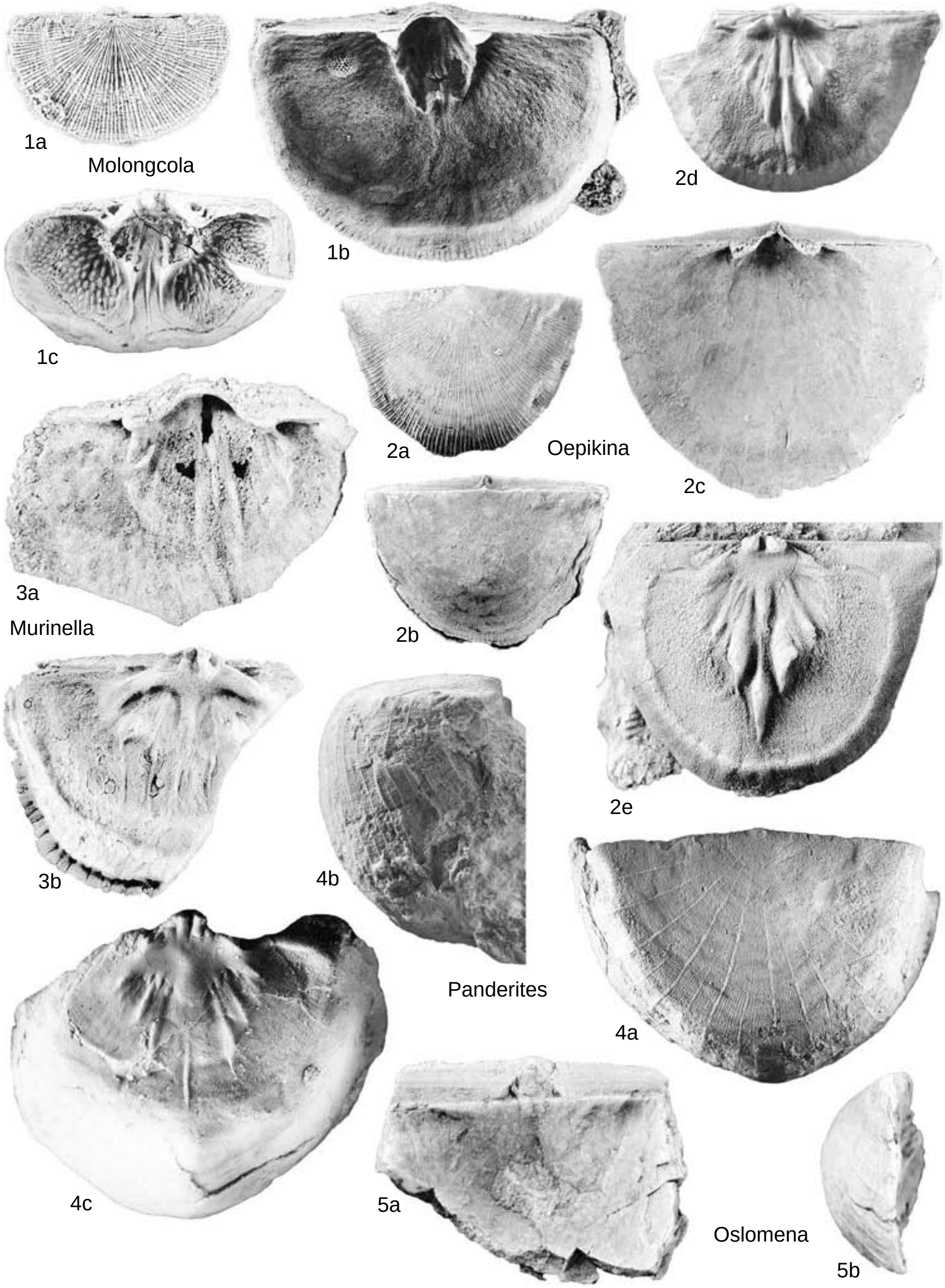

Fig. 143. Strophomenidae (p. 233–235).

profile with sharp dorsal geniculation, long trail; unequally parvicostellate ornament; small pseudodeltidium; large chilidium; subcircular ventral muscle field, faintly impressed, with no bounding ridges; erect, ventroposteriorly directed, relatively small cardinal process lobes; broad low myophragm extending anteriorly into thin dorsal median septum; two or more pairs of thin transmuscle septa. *Ordovician (Llanvirn):* Baltic.——Fig. 143,*4a–c*. **P. imbrex* (Pander), Aseri Stage, upper Llanvirn,

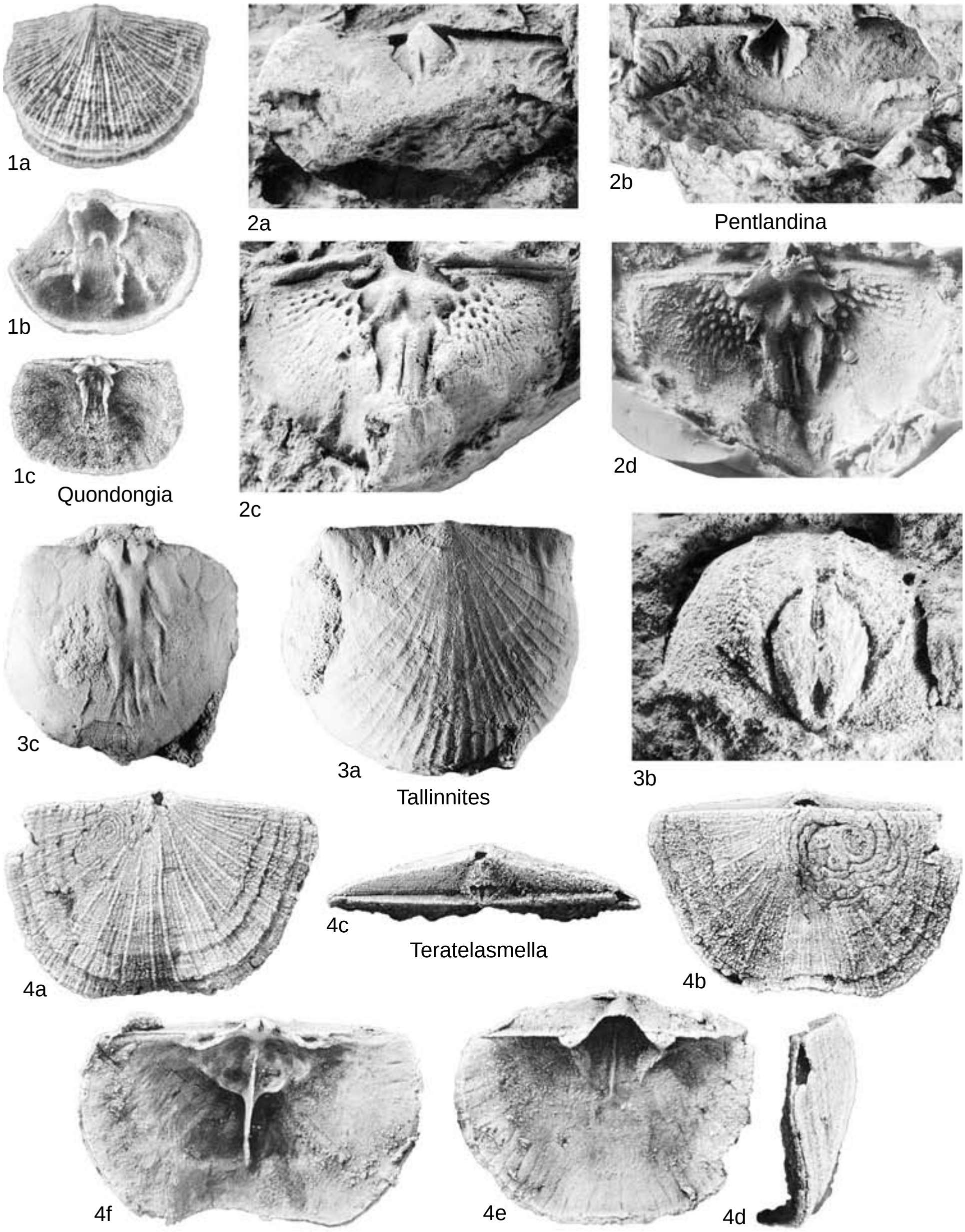

Fig. 144. Strophomenidae (p. 235–237).

Pavlovsk, St. Petersburg, Russia; *a,* ventral view of conjoined valves, ×2; *b,* lateral view of conjoined valves, BMNH B 3959, ×1.5 (new); *c,* dorsal interior, RMS Br 131660, ×2 (Rõõmusoks, 1993a).

Pentlandina Bancroft, 1949, p. 13 [**Strophomena (P.) tartana;* OD]. Transverse to subtriangular outline; biconvex profile with strong dorsal fold, ventral sulcus; parvicostellate ornament that breaks distinctive small, regular rugae; open delthyrium with small pseudodeltidial plates, vestigial chilidium; strong teeth, dental plates merging with elevated muscle-bounding ridges not quite uniting anteriorly; strong, short, curved socket ridges, short notothyrial platform; prominent dorsal side septa, small central median ridge. *Silurian (Telychian–Wenlock):* Europe, North America, China.——Fig. 144,*2a–d.* **P.*

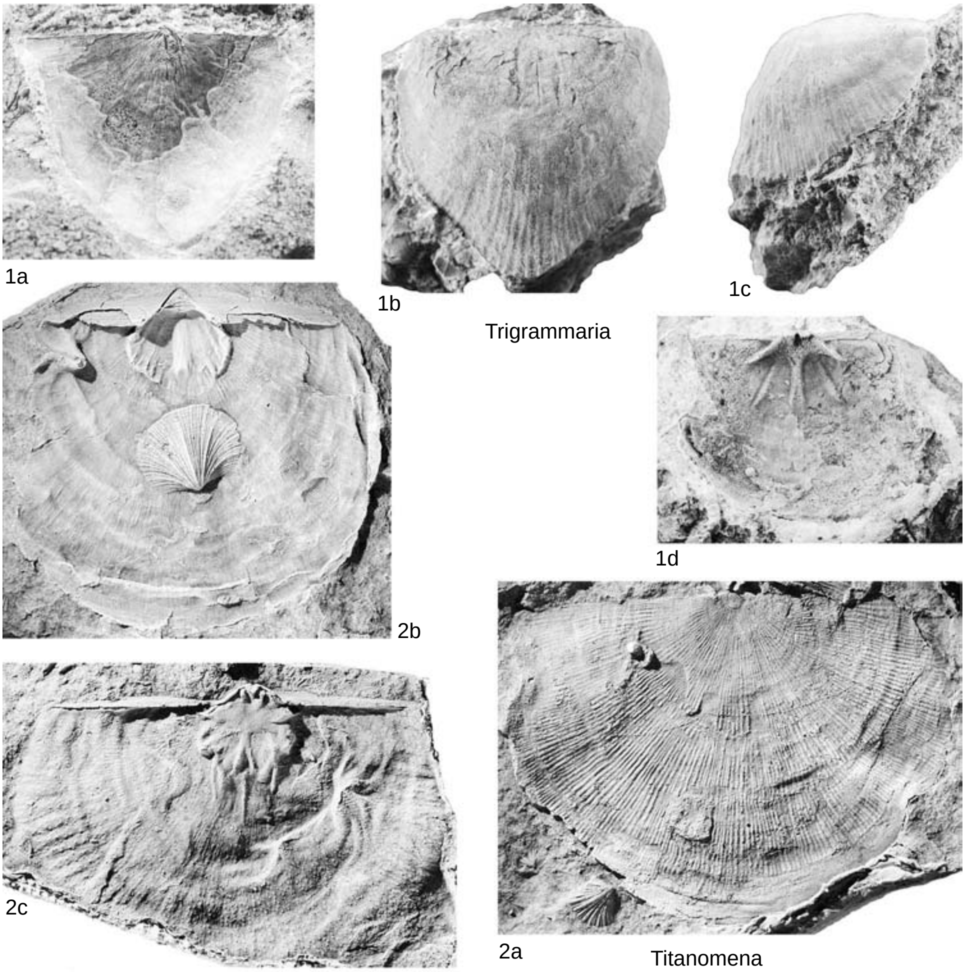

FIG. 145. Strophomenidae (p. 237).

tartana, Llandovery (Telychian) Beds, North Esk Inlier, Pentland Hills, Borders region, Scotland; *a,b,* ventral internal mold, latex cast, BMNH B 8485, ×2; *c,d,* dorsal internal mold, latex cast, BMNH BB 31450, ×3 (new).

Quondongia PERCIVAL, 1991, p. 151 [**Q. alitis;* OD]. Small shells with planoconvex to biconvex profile, occasional rounded plications anteriorly; unequally parvicostellate ornament; prominent pseudodeltidium, small chilidium; thin dental plates merging with anteriorly directed muscle-bounding ridges; ventral muscle field open anteriorly; short socket ridges; prominent elevated curved dorsal side septa; thin short central median ridge. *Ordovician (Caradoc):* Australia.——FIG. 144,*1a–c.* **Q. alitis,* Quondong Limestone, Caradoc, Bowan Park, New South Wales, Australia; *a,* ventral exterior, SUP 68595, ×4; *b,* ventral interior, SUP 68596, ×4; *c,* dorsal interior, SUP 69478, ×4 (Percival, 1991).

Tallinnites RÕÕMUSOKS, 1993a, p. 50 [**Oepikina? imbrexoidea* SOKOLSKAYA, 1954, p. 51; OD]. Subrectangular to semicircular outline; ventral valve evenly, strongly convex, dorsal valve more gently concave; unequally parvicostellate ornament; pseudodeltidium small; chilidium large; long elliptical ventral muscle field with bounding ridges not quite uniting anteriorly; ventroposteriorly directed, prominent cardinal process lobes; weak socket ridges; broad notothyrial platform posteriorly; centrally, anteriorly in dorsal valve there are variably developed, rather irregular but generally weak side septa, median ridge. *Ordovician (Llanvirn–Llandeilo):* Baltic.——FIG. 144,*3a–c.* **T. imbrexoidea* (SOKOLSKAYA), Uhaku Stage, lower Llandeilo, Estonia; *a,* ventral exterior, Kohtla-Järve, TAGI BR 1572, ×1.5; *b,* ventral internal mold, Loo, ×2; *c,* dorsal interior, Lasnamägi, TAGI BR 1574, ×1.5 (Rõõmusoks, 1993a).

Teratelasmella Laurie, 1991, p. 84 [**T. plicata;* OD]. Planoconvex to biconvex profile with ventral sulcus, dorsal fold; relatively large ventral interarea with well-developed pseudodeltidium; pair of small chilidial plates; unequally parvicostellate ornament; stout teeth; stout dental plates; poorly impressed ventral muscle field laterally bounded by short muscle-bounding ridges; small ventral median septum; widely divergent curving socket ridges; relatively small dorsal muscle field with bounding ridges, short transmuscle ridges; thin but prominent, relatively long, dorsal median septum. *Ordovician (Llandeilo):* Australia.——Fig. 144,*4a–f.* **T. plicata,* Upper Cashions Creek Limestone, Llandeilo, Settlement Road, Tasmania, Australia; *a–d,* holotype, ventral, dorsal, posterior, lateral views of conjoined valves, UTGD 99641, ×4; *e,* ventral interior, UTGD 99648, ×5; *f,* dorsal interior, UTGD 99669, ×4 (Laurie, 1991).

?Titanomena Bergström, 1968, p. 16 [**T. grandis;* OD]. Large, with compressed plano- to concavoconvex profile; equally parvicostellate ornament; small pseudodeltidium, chilidium; short dental plates merging anteriorly with bounding ridges to diamond-shaped ventral muscle field; relatively small, erect cardinal process lobes as in some glyptomenids, thus family position uncertain; chilidium present; dorsal muscle field with poorly developed, thin median, transmuscle septa. *Ordovician (Ashgill):* Baltic.——Fig. 145,*2a–c.* **T. grandis,* upper *Dalmanitina* Beds, Ashgill, Allebergsände, Västergötland, Sweden; *a,* latex cast of dorsal exterior, RMS Br 10929, ×1.5; *b,* latex cast of ventral internal mold, RMS Br 10944, ×1; *c,* holotype, latex cast of dorsal internal mold, LO 4257, ×1.5 (Bergström, 1968).

Trigrammaria Wilson, 1945, p. 140 [**T. trigonalis;* OD] [=*Microtrypa* Wilson, 1945, p. 144 (type, *M. altilis;* OD)]. Resupinate profile, with variably developed dorsal fold, ventral sulcus near anterior margin; ornament usually parvicostellate; ventral interior poorly known; socket ridges divergent; fine dorsal side septa, median septum variably developed; median septum sometimes bifurcating anteriorly as in *Furcitella. Ordovician (Llandeilo):* North America.——Fig. 145,*1a–c.* **T. trigonalis,* Ottawa Limestone, Llanvirn, Ottawa, Ontaria, Canada; *a,* partially exfoliated conjoined valves, GSC 7614b, ×1.5; *b,c,* holotype, dorsal, lateral views of dorsal internal mold, GSC 7614, ×1.5 (new).——Fig. 145,*1d. T. altilis* (Wilson), Ottawa Limestone, Llanvirn, Rockland, Ontario, Canada; holotype, dorsal interior, GSC 7649, ×2 (new).

Family RAFINESQUINIDAE
Schuchert, 1893

[*nom. transl.* Pope, 1976, p. 151, *ex* Rafinesquininae Schuchert, 1893, p. 153] [=Elliptostrophiidae Havlíček, 1967, p. 111; Leptaenidae Hall & Clarke, 1894a, p. 354]

Outline usually transverse; cardinal process lobes usually elongate or platelike in shape, entirely discrete throughout ontogeny; notothyrial platform variably developed; socket ridges straight, often thinner, smaller than in the Strophomenidae. *Ordovician (Llanvirn)–Carboniferous (Namurian).*

Subfamily RAFINESQUININAE
Schuchert, 1893

[Rafinesquininae Schuchert, 1893, p. 153]

Rafinesquinids lacking dorsal geniculation, often lacking rugae (except posterolaterally in gerontic specimens). *Ordovician (Llandeilo)–Silurian (Ludlow).*

Rafinesquina Hall & Clarke, 1892, p. 281 [**Leptaena alternata* Conrad, 1838, p. 115; OD]. Concavoconvex profile, with dorsal valve initially very gently concave but with increased curvature anteriorly; unequally parvicostellate ornament; pseudodeltidium, larger chilidium filling delthyrium; relatively short, divergent dental plates; ventral muscle field flabellate, with no bounding ridges; ponderous triangular cardinal process lobes in adults flanked by short delicate socket ridges often with crenulations; weak dorsal median septum present, merging posteriorly with low myophragm. *Ordovician (Caradoc–Ashgill):* cosmopolitan.——Fig. 146,*2a–e.* **R. alternata* (Conrad), Hudson River Group, Caradoc, Cincinnati, Ohio; *a,* dorsal view of conjoined valves, BMNH BC 56160, ×1; *b,* ventral interior, BMNH BC 13035, ×1; *c,* dorsal interior, BMNH BC 13549, ×1 (new); *d,* latex cast of cardinal area, muscle field, BMNH B 39912, ×2; *e,* enlarged view of cardinal area, BMNH B 39912, ×4 (Cocks, new).

Colaptomena Cooper, 1956, p. 889 [**C. leptostrophoidea;* OD] [=*Macrocoelia* Cooper, 1956, p. 890 (type, *M. obesa;* OD)]. Large, with compressed plano- to concavoconvex profile; vestigial pseudodeltidium; small chilidium; dental plates rudimentary or obsolescent; flabellate ventral muscle field well impressed, but without bounding ridges; triangular, lobate cardinal process lobes; thin, small, divergent socket plates; short thin dorsal median septum extending anteriorly from myophragm; transmuscle septa poorly developed. *Ordovician (Llandeilo–Caradoc):* North America, Europe, Asia.——Fig. 147,*1a–c.* **C. leptostrophoidea,* Martinsburg formation, Caradoc, Green Mount Church, Broadway Quadrangle, Virginia; *a,* ventral exterior, USNM 117763a, ×1; *b,* ventral internal mold, USNM 117762a, ×1; *c,* dorsal interior, USNM 117763b, ×1 (Cooper, 1956).——Fig. 147,*1d–f. C. obesa,* Arline Formation, Llandeilo–Caradoc, Friendsville, Concord, Tennessee; *d,* holotype, ventral exterior, USNM 117783a, ×1; *e,* ventral interior, USNM 117782b, ×1; *f,* dorsal interior, USNM 117782a, ×2 (Cooper, 1956).

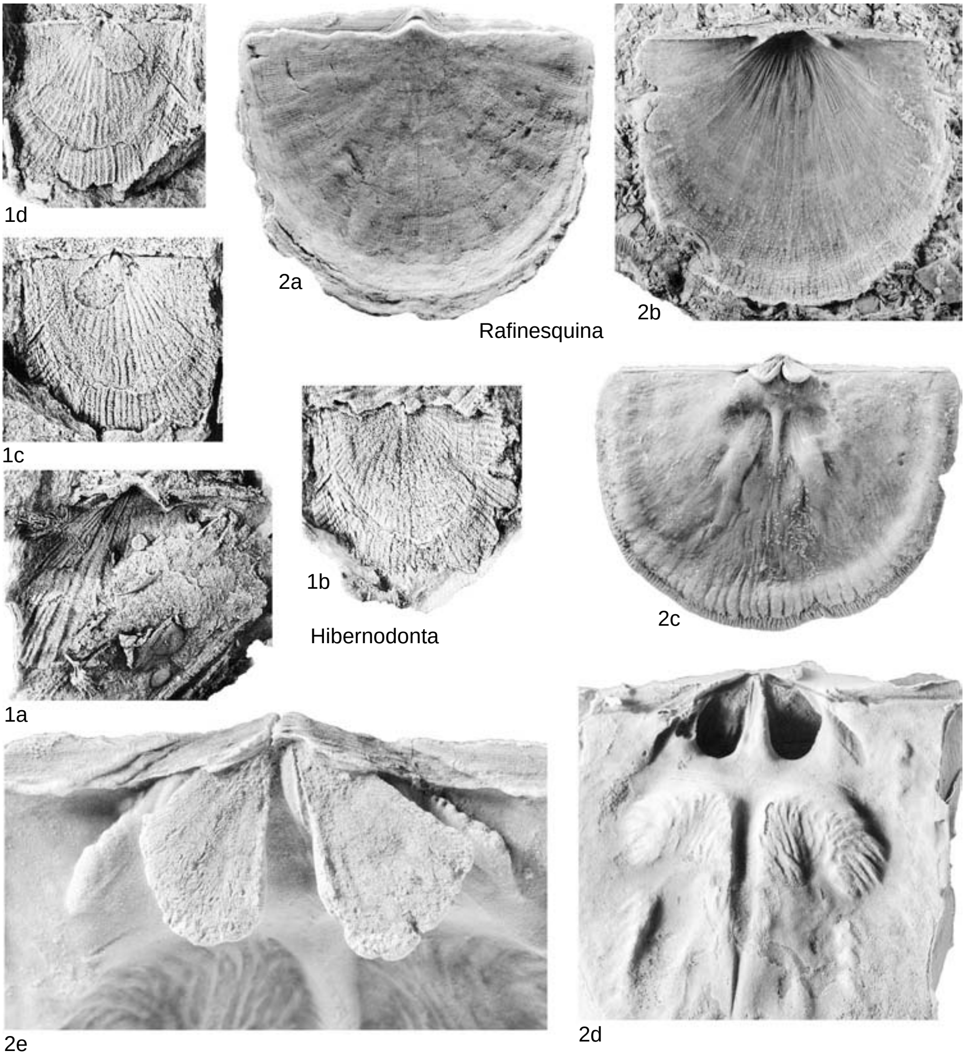

FIG. 146. Rafinesquinidae (p. 237–239).

Hedstroemina BANCROFT, 1929, p. 58 [**H. fragilis;* OD] [=*Rakverina* RŐŐMUSOKS, 1993c, p. 161 (type, *?Oepikina inaequiclina* ALICHOVA, 1951, p. 58)]. Concavoconvex profile, weakly geniculate anteriorly; relatively fine, irregularly parvicostellate ornament with impersistent concentric wrinkles; vestigial pseudodeltidium; small chilidium; strong, divergent dental plates, but poorly impressed muscle fields with no bounding ridges; robust, narrowly divergent cardinal process lobes, but short, weak socket ridges; faint myophragm, but no dorsal septa. *Ordovician (Caradoc):* Europe.——FIG. 148,*2a–c.* **H. fragilis,* Cheney Longville Flags, Caradoc, Woolston House, Shropshire, England; *a,* dorsal external mold, BMNH BB 69460, ×1.5; *b,* lectotype, ventral internal mold, BMNH BB 14380, ×1.5; *c,* dorsal internal mold, BMNH BB 73550, ×3 (new).——FIG. 148,*2d,e. H. inaequiclina* (ALICHOVA), Rägavere Formation, Caradoc, Rägavere, Estonia; *d,* ventral exterior, GMUT Br 1560, ×2; *e,* dorsal interior, GMUT Br 1630, ×2 (Rőőmusoks, 1993c).

?Hibernodonta HARPER & MITCHELL in HARPER & others, 1985, p. 300 [**H. praeco;* OD]. Small, planoconvex profile; relatively coarse parvicostellate ornament; no pseudodeltidium; with chilidium; no denticles on hinge line, but crenulations on teeth; intermediate between rafinesquinids, leptostrophiids, hence family position uncertain; thin, widely divergent dental plates present; poorly impressed

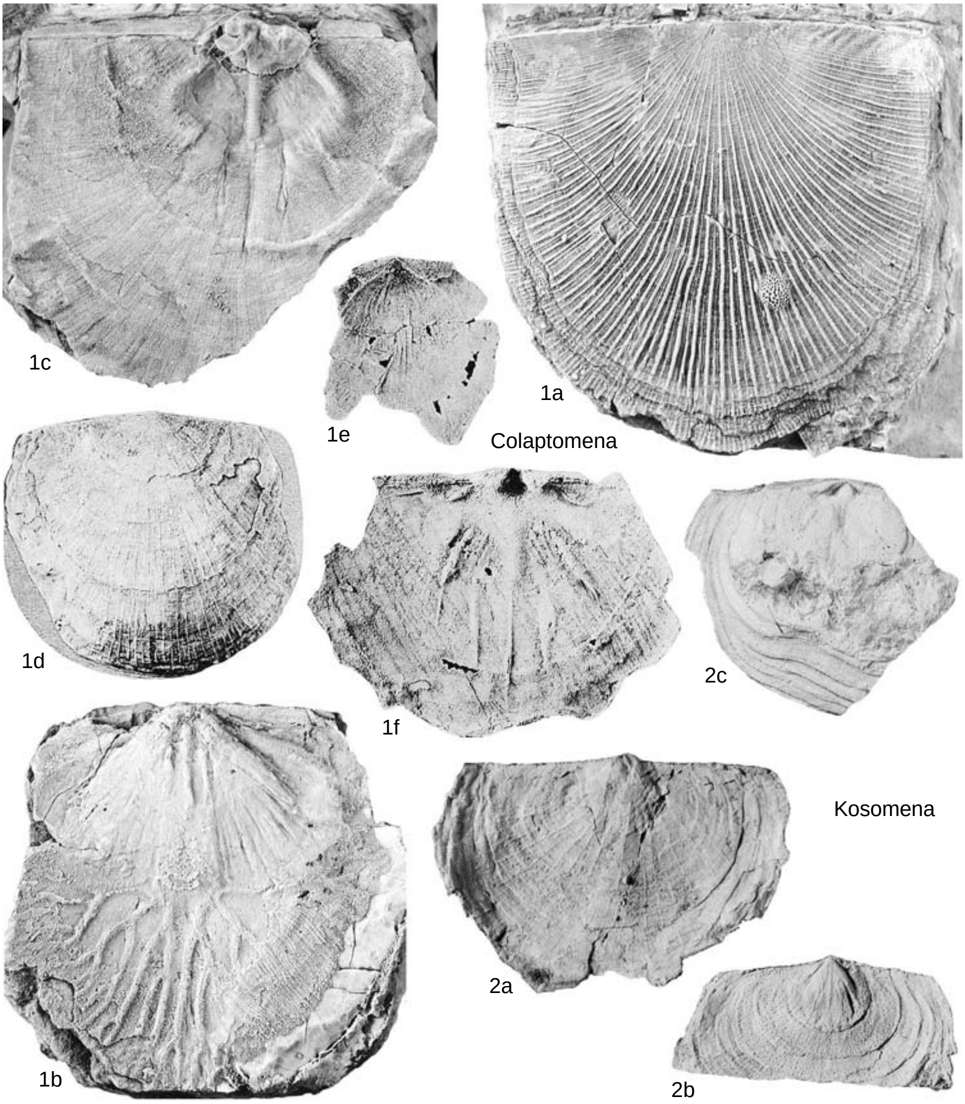

FIG. 147. Rafinesquinidae (p. 237–242).

ventral muscle field with no bounding ridges; small, discrete cardinal process lobes; short, slender crenulated socket ridges; dorsal muscle field poorly impressed. *Ordovician (Caradoc):* Ireland.——FIG. 146,*1a–d.* **H. praeco,* Clashford House Formation, middle Caradoc, Herbertstown, County Meath, Ireland; *a,* holotype, latex of ventral interior, BMNH BC 9197, ×4; *b–d,* exterior, internal mold, latex of dorsal valve, BMNH BC 9195, ×4 (Harper & others, 1985).

Kjaerina BANCROFT, 1929, p. 43 [**K. typa;* OD]. Gently concavoconvex profile with occasional dorsal geniculation posteriorly; parvicostellate ornament with accentuated median costella, often with posterolateral rugae; vestigial pseudodeltidium; small chilidium; prominent dental plates anterolaterally leading to muscle-bounding ridges enclosing weakly impressed triangular ventral muscle field; delicate cardinalia with dorsal socket ridges present but separate from elongate cardinal process lobes; weakly impressed dorsal muscle field with trans-muscle septa absent. *Ordovician (Caradoc):* Britain.——FIG. 149,*1a–d.* **K. typa,* Cheney Longville Flags, Caradoc, Burrell's Coppice, Cheney Longville, Shropshire, England; *a,* ventral external mold, BMNH BB 30650, ×1.5; *b,* lectotype,

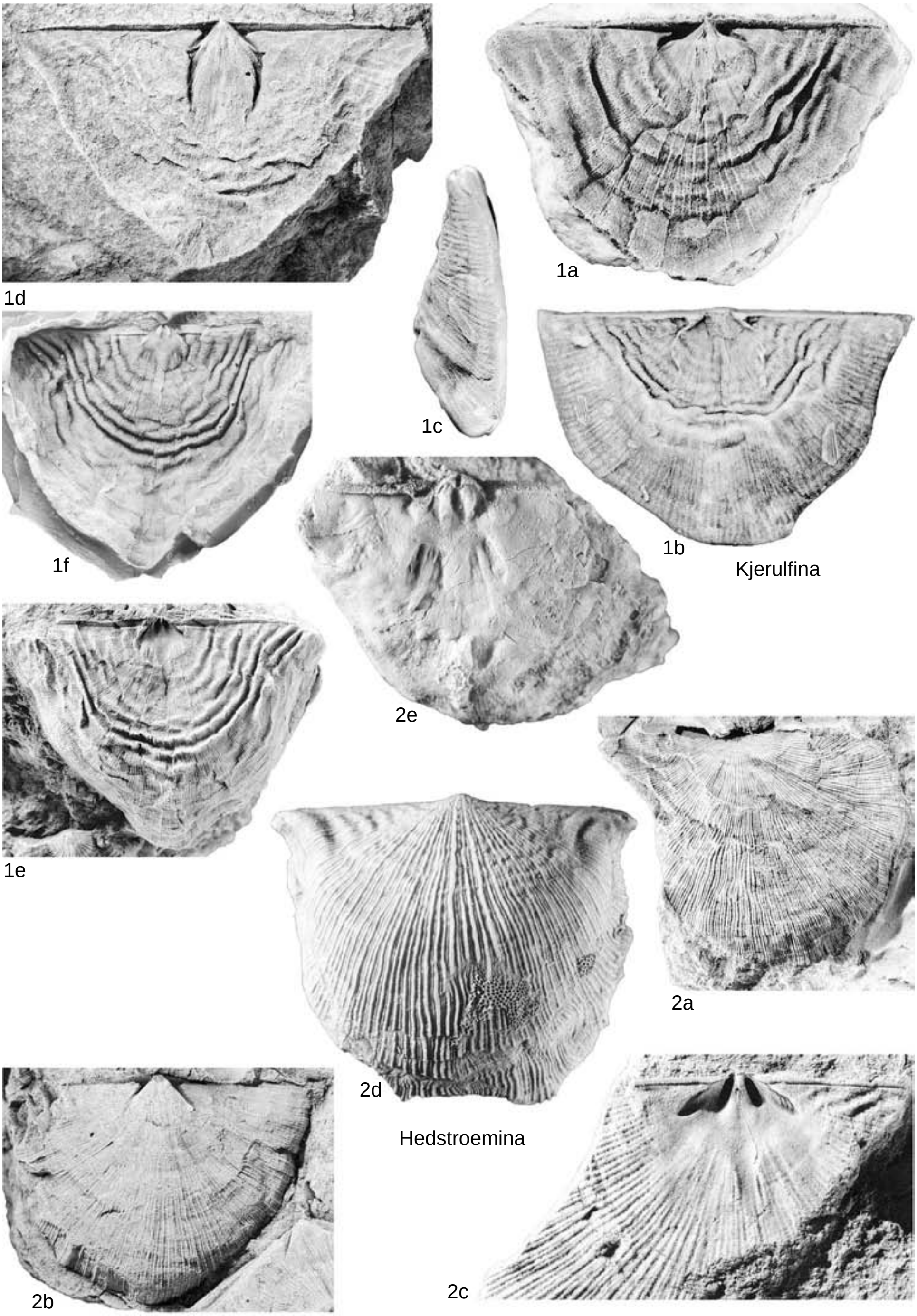

FIG. 148. Rafinesquinidae (p. 239–241).

ventral internal mold, BMNH BB 14383, ×1.5; *c,* dorsal internal mold, ×2; *d,* enlargement of latex cast of cardinal area, BMNH BC 13405, ×8 (new).

Kjerulfina BANCROFT, 1929, p. 59 [**K. trigonalis;* OD]. Posterior part of ventral valve with convex profile, dorsal valve flat or gently concave, then both valves anteriorly geniculate in a ventral direction; ornament usually unequally parvicostellate with fine to coarse irregular rugae; small pseudodeltidium, chilidium; short, thin flaring dental plates; ventral muscle field elongate to subcircular, muscle-bounding ridges variably developed; cardinal process lobes elongate; socket ridges widely divergent; dorsal muscle field poorly defined. *Ordovician (Caradoc–Ashgill):* Europe.——FIG. 148,*1a–f.* **K. trigonalis,* Cheney Longville Flags, Caradoc, Marsh Wood, Marshbrook, Shropshire, England; *a,* ventral internal mold, BMNH BB 9148, ×2; *b,* ventral view of plaster cast of ventral interior, BMNH BB 73908, ×1.5; *c,* lateral view of plaster cast of ventral interior, BMNH BB 73908, ×1.5; *d,* lectotype, ventral internal mold, BMNH BB 73834, ×1.5; *e,* dorsal internal mold, ×1.5; *f,* latex cast, BMNH BB 73901, ×1.5 (new).

Kosomena HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 71 [**K. kosia;* OD]. Ventral valve with gently convex profile posteriorly, but resupinate anteriorly; dorsal valve posteriorly planar but anteriorly convex; dental plates present, but no muscle-bounding ridges; muscle fields poorly impressed; divergent cardinal process lobes, short socket ridges; dorsal median septum absent. *Silurian (Ludlow):* Europe.——FIG. 147,*2a–c.* **K. kosia,* Upper Kopininá Formation, upper Ludlow, Kosov Quarry, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 4227, ×1.5; *b,* ventral internal mold, OMR VH 4229, ×1.5; *c,* dorsal internal mold, OMR VH 4228, ×1.5 (Havlíček & Štorch, 1990).

Megamyonia WANG, 1949, p. 32 [**M. knighti;* OD]. Small; concavoconvex profile, with dorsal valve initially very gently concave but with increased curvature anteriorly; finely costellate, sometimes with prominent central costa; pseudodeltidium small; chilidium large; with dental plates; relatively large, very impressed ventral muscle field distinctive from all other Rafinesquinidae, flabellate, with irregular transmuscle septa; socket ridges faint, short; dorsal myophragm prominent but no median septum. *Ordovician (Ashgill):* North America.——FIG. 149,*4a–c.* **M. knighti,* Fort Atkinson Member, Maquoketa Shale, Ashgill, Ossian, Winneshiek County, Iowa; *a,* dorsal exterior, SUI 1868, ×2; *b,* holotype, ventral interior, SUI 1869, ×2; *c,* dorsal interior, SUI 1870, ×2 (Wang, 1949).

Odoratus ZHU, 1985, p. 39[51] [**O. wangi;* OD]. Profile gently concavoconvex, but geniculation ventrally directed; ornament unequally parvicostellate; dental plates short; rounded ventral muscle field with low bounding ridges posterolaterally; dorsal median ridge well developed. *Ordovician (Caradoc–Ashgill):* China.——FIG. 149,*3a,b.* **O. wangi,* Maimushan Member, Wulongtun Formation, upper Caradoc–lower Ashgill, Wulongtun, Huma County, eastern Greater Khingan Mountains, Heilongjiang Province, northeastern China; *a,* latex cast of ventral internal mold, SIGM 70167, ×2; *b,* latex cast of dorsal internal mold, SIGM 70178, ×2 (Rong & Zhu, new).

Rhipidomena COOPER, 1956, p. 866 [**Strophomena tennesseensis* WILLARD, 1928, p. 285; OD]. Profile initially convexoconcave but resupinate anteriorly; low pseudodeltidium; small chilidial plates; abbreviated divergent dental plates, strongly impressed large flabellate ventral muscle field without bounding ridges; large lobate cardinal process lobes; short socket ridges; broad myophragm extending short distance anteriorly; two or three pairs of fine united dorsal transmuscle, side septa sometimes present. *Ordovician (Llandeilo–Caradoc):* North America.——FIG. 149,*2a–e.* **R. tennesseensis* (WILLARD), Benbolt Formation, Llandeilo; *a,b,* ventral, lateral views of conjoined valves, New Harmony, Heiskell, Virginia, BMNH BC 12840, ×1.5 (new); *c,* posterior view of conjoined valves, Rye Cove, Clinchport, Virginia, USNM 117683a, ×1 (Cooper, 1956); *d,* ventral interior, New Harmony, Heiskell, BMNH BC 12838, ×1.5 (new); *e,* dorsal interior, Mount Eager Church, Tennessee, USNM 117692a, ×2 (Cooper, 1956).

Subfamily LEPTAENINAE
Hall & Clarke, 1894

[*nom. transl.* COCKS & RONG, herein, *ex* Leptaenidae HALL & CLARKE, 1894a, p. 354] [=Elliptostrophiidae HAVLÍČEK, 1967, p. 111]

Rafinesquinids with dorsal geniculation; usually with concentric rugae over whole shell. *Ordovician (Llanvirn)–Carboniferous (Namurian).*

Leptaena DALMAN, 1828, p. 94 [**L. rugosa;* SD KING, 1846, p. 28] [=*Astamena* RÕÕMUSOKS, 1989, p. 114 (type, *A. inaequalis;* OD); *Kurnamena* RÕÕMUSOKS, 1989, p. 114 (type, *L. taxilla* ORASPÕLD, 1956, p. 51; OD); *Leptaenella* FREDERICKS, 1918, p. 89 (type, *L. rhomboidalis ventricosa* HALL & CLARKE, 1892, pl. 15A, fig. 43; OD; Oriskany Sandstone (Lower Devonian), Cumberland, Maryland, USA); *Leptaenopoma* MAREK & HAVLÍČEK, 1967, p. 282 (type, *L. trifidum;* OD); ?*Leptaenulopsis* HAUPT, 1878, p. 31 (type, *L. simplex;* SD HALL & CLARKE, 1892, p. 294; Wenlock, Germany); *Oandumena* RÕÕMUSOKS, 1989, p. 116 (type, *L. fluviatilis* ORASPÕLD, 1956, p. 54; OD; Oandu Series (upper Caradoc), Rakvere, Estonia); *Orhoria* HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 73 (type, *O. provellerosa;* OD; Kopaniná Formation (Ludfordian), Bohemia, Czech Republic); *Schmidtomena* RÕÕMUSOKS, 1989, p. 115 (type, *L. acuteplicata* SCHMIDT, 1908, p. 726; OD); *Simileptaena* RÕÕMUSOKS, 1989, p. 114 (type, *S. paucirugata;* OD); ?*Turgenostrophia* ALEKSEEVA in ALEKSEEVA & ERLANGER, 1983, p. 29 (type, *T. rara;* OD; upper

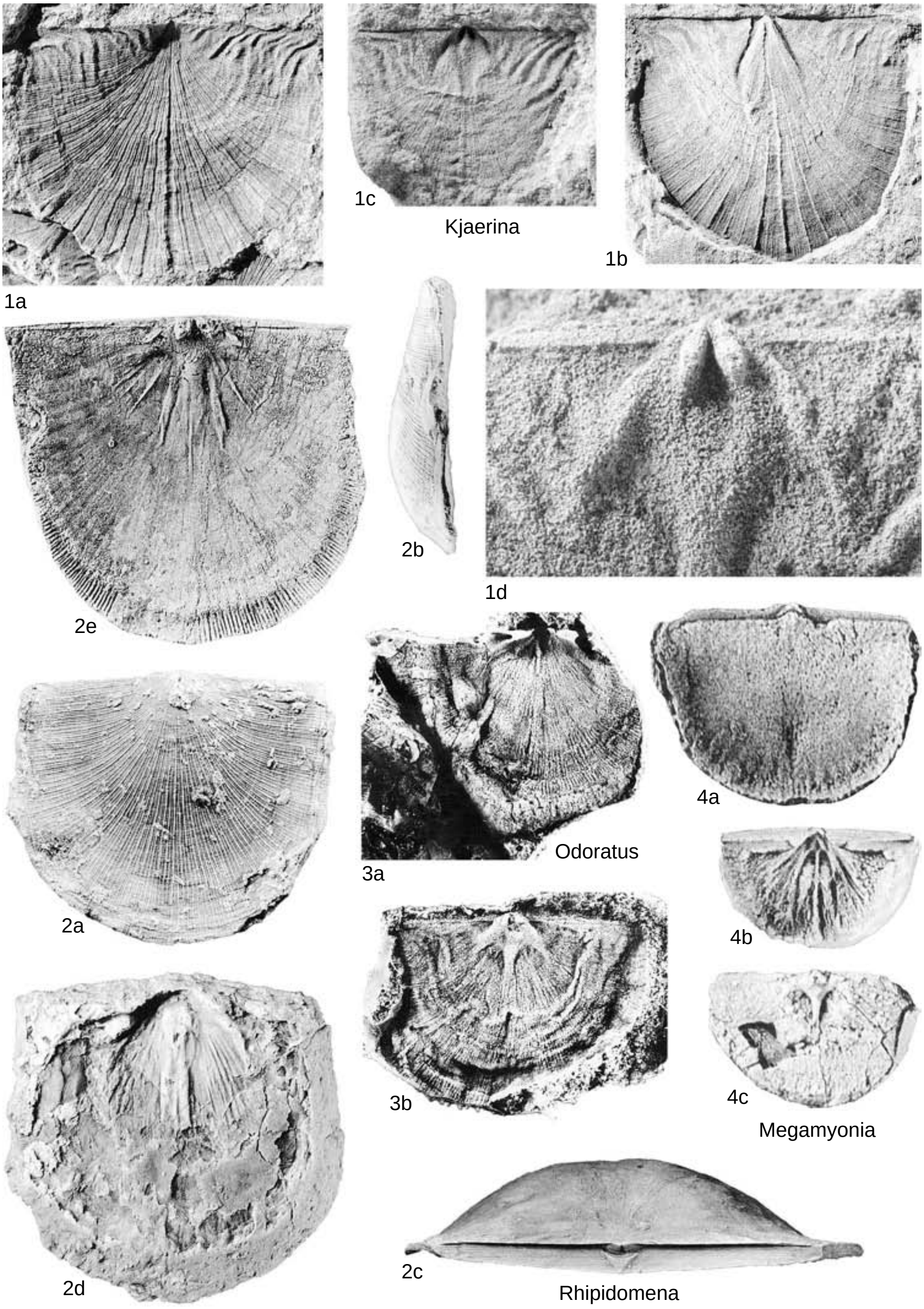

FIG. 149. Rafinesquinidae (p. 239–242).

Silurian, Yamatu-Gol river, northwestern Mongolia)]. Outline usually transverse, rounded anteriorly; profile concavoconvex with sharp anterior dorsal geniculation; ornament costellate to unequally parvicostellate; concentric rugae variable but usually well developed; small pseudodeltidium; large chilidium; short dental plates; ventral muscle field varies from subcircular to elongate with bounding ridges usually developed posterolaterally, sometimes curving round anteriorly; cardinal process lobes elongate, ventrally directed; socket ridges present but usually weak, sometimes with crenulations; dorsal muscle field variably impressed with median ridge often present; transmuscle ridges, diaphragm variably developed in dorsal valve. *Ordovician (Llanvirn)–Devonian (Pragian, ?Emsian).*

L. (**Leptaena**). Similar to *L. (Septomena)* but lacking the distinctive two pairs of dorsal transmuscle ridges. *Ordovician (Caradoc)–Devonian (Pragian, ?Emsian):* cosmopolitan.——Fig. 150,*1a–e.* **L. (L.) rugosa, Dalmanitina* Beds, Ashgill, Alleberg, Västergötland, Sweden; *a,b,* ventral, lateral views of ventral internal mold, BMNH B 13594, ×1.5; *c,d,* dorsal internal mold, ×1.5, latex cast of it, BMNH BB 67944, ×1.5; *e,* latex cast of juvenile dorsal internal mold, BMNH BB 67946, ×2 (new).——Fig. 150,*1f. L. (L.) inaequalis* (Rõõmusoks), Johvi Beds, lower Caradoc, Anija, Estonia; holotype, ventral exterior, TAGI BR 1346, ×1.5 (Rõõmusoks, 1989).——Fig. 150,*1g. L. (L.) taxilla* Oraspõld, Johvi Stage, lower Caradoc, Alliku, Estonia; dorsal interior, ×2 (Rõõmusoks, 1989).——Fig. 150,*1h. L. (L.) acuteplicata* Schmidt, Porkuni Stage, upper Ashgill, Estonia; ventral interior, TAGI BR 1335, ×1.7 (Rõõmusoks, 1989).——Fig. 150,*1i,j. L. (L.) paucirugata* (Rõõmusoks), Vormsi Stage, Ashgill, Kõrgessaare, Estonia; holotype, ventral, lateral views of ventral valve, TAGI BR 1349, ×1.5 (Rõõmusoks, 1989).——Fig. 150,*1k. L. (L.) trifidum* (Marek & Havlíček), Kosov Formation, Ashgill, Bechovice, Czech Republic; dorsal internal mold, OMR VH 354e, ×3 (Havlíček, new).

L. (**Septomena**) Rõõmusoks, 1989, p. 115 [**L. juvenilis* Öpik, 1930, p. 173; OD]. Similar to *L. (Leptaena)* but with two well-developed pairs of transmuscle ridges in dorsal valve, outer pair divergent, inner pair subparallel, united with side septa, continuing anteriorly for over half valve length. *Ordovician (Llanvirn–Caradoc):* Baltic.——Fig. 150,*2a–c.* **L. (S.) juvenilis* (Öpik), Viivikonna Formation, Kukruse Stage C2β, upper Llandeilo, Estonia; *a,* holotype, ventral exterior, Käva, TAGI BR 207, ×2; *b,* ventral interior, Kohtla-Järve, TAGI BR 212, ×2; *c,* dorsal interior, Küttejõu, TAGI BR 1319, ×2 (Rõõmusoks, 1989).

?Bracteoleptaena Havlíček, 1963, p. 224 [**Strophomena bracteola* Barrande, 1879, pl. 45, fig. 17, 18, 20–24, pl. 53, fig. 1; OD]. Costellate; profile gently geniculate dorsally with regular or irregular rugae; small interarea with pseudodeltidium, chilidium; short, thin, widely divergent dental plates; weak muscle-bounding ridges leading to relatively small subcircular ventral muscle field; cardinal process lobes small, rather obscure (thus could be glyptomenid if lobes posterior to hinge line, rather than rafinesquinid); socket ridges small, widely divergent, subparallel to hinge line; dorsal muscle field ill defined. *Silurian (Wenlock–Ludlow):* Europe.——Fig. 151,*1a,b.* **B. bracteola* (Barrande), Liten Formation, Wenlock; *a,* ventral, dorsal internal molds, Mezoun, OMR VH 380b, ×2; *b,* lectotype, ventral internal mold, Borek, Suchomasty, Czech Republic, NM CE 236, ×2 (Havlíček, 1967).

Glossoleptaena Havlíček, 1967, p. 115 [**Strophomena emarginata* Barrande, 1879, pl. 45, fig. 8–9; OD] [=*Ludfordina* Kelly, 1967, p. 599 (type, *L. pixis;* OD)]. Outline subquadrate; profile as in *Rugoleptaena,* with anterior margin concave; ornament of faint costellae, weak rugae; lacks dental plates; small oval ventral muscle field bounded posterolaterally by low curved ridges; cardinal process lobes delicate, slightly elongate, directed ventrally; socket ridges short, well developed. *Silurian (Ludlow)–Devonian (Lochkovian–Eifelian):* Europe.——Fig. 152,*3a,b.* **G. emarginata* (Barrande), Lochkov Limestone, Lochkovian, Karlík, Bohemia, Czech Republic; ventral external, internal molds, OMR VH 385, ×2.6 (Havlíček, 1967).

Harjumena Rõõmusoks, 1993c, p. 162 [**Strophomena schmidti* Gagel, 1890, p. 42; OD]. Similar to *Leptaena* in profile, but more subtriangular in outline; ornament unequally parvicostellate with irregular concentric corrugations on disc; vestigial pseudodeltidium, large chilidium; elongate ventral muscle field open anteriorly; long cardinal process lobes, short dental plates; dorsal muscle field poorly impressed. *Ordovician (Ashgill):* Baltic.——Fig. 151,*2a–c.* **H. schmidti* (Gagel), Saunja Formation, Nabala Stage, lower Ashgill, glacial boulders, Estonia; *a,* partly exfoliated dorsal valve, ×1; *b,* ventral internal mold, ×1; *c,* dorsal interior, RMS Br 13609, ×3 (Rõõmusoks, 1993c).

Hingganoleptaena Zhu, 1985, p. 41 [**Leptaena nenjiangensis* Su, 1980, p. 274; OD]. Similar to *Leptaena* in profile, ornamentation, but with concave pair of long dorsal valve side septa prominent, originating from just anterior of pair of very short muscle-bounding ridges. *Ordovician (Caradoc–Ashgill):* China.——Fig. 151,*3a–d.* **H. nenjiangensis* (Su), Wulongtun Formation, upper Caradoc–lower Ashgill, Wulongtun, Huma County, Heilongjiang Province, China; *a,* dorsal external mold, SIGM 70130, ×3; *b,* ventral internal mold, SIGM 70140, ×3; *c,d,* dorsal internal molds, SIGM 70126-7, ×3 (Su, new).

Hollardina Racheboeuf & Garcia-Alcade in Racheboeuf, Carls, & Garcia-Alcade, 1982, p. 46 [**H. plana;* OD]. Profile concavoconvex, geniculate; multicostellate ornament; rugae absent except weak near hinge line; small pseudodeltidium; large

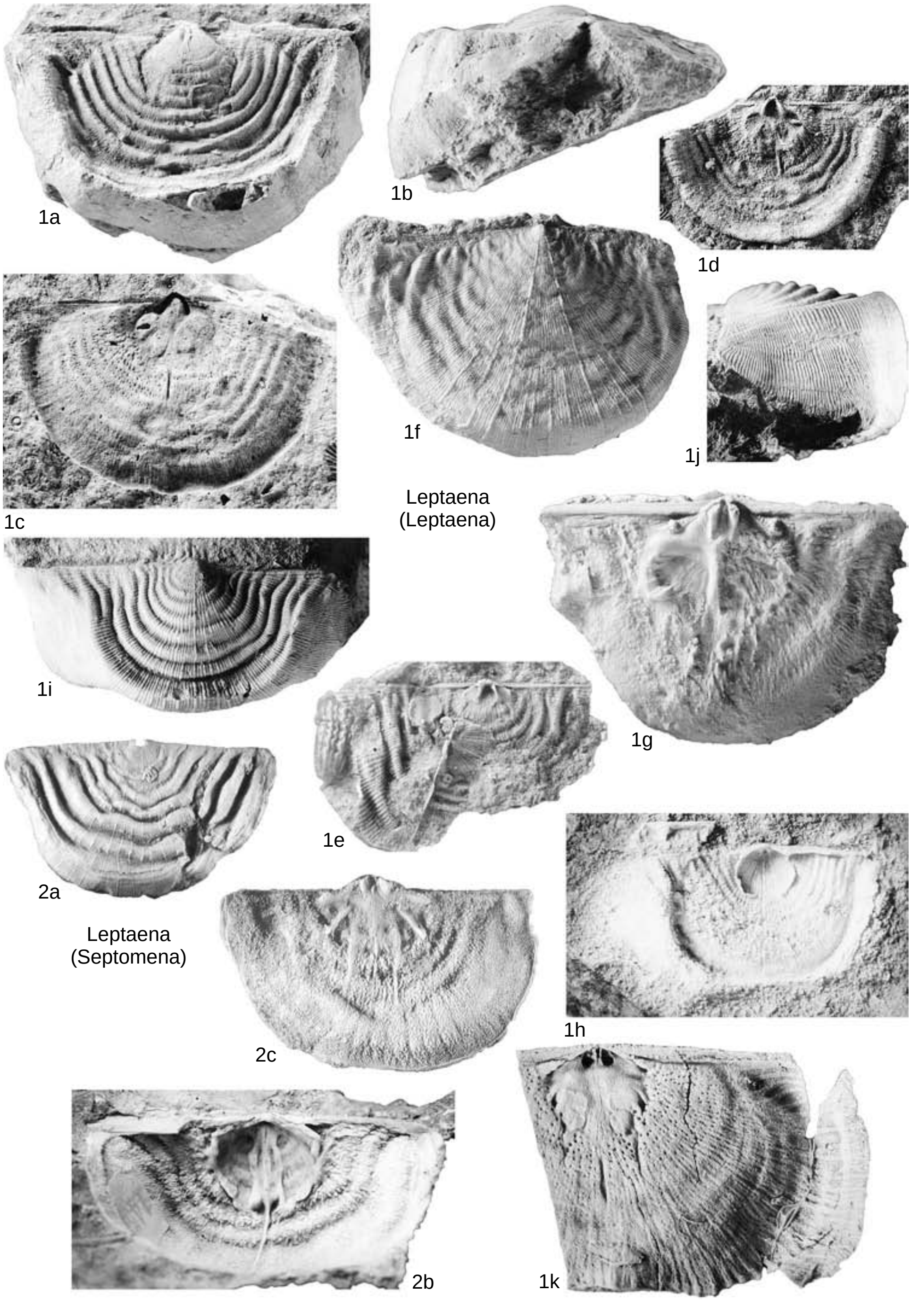

FIG. 150. Rafinesquinidae (p. 242).

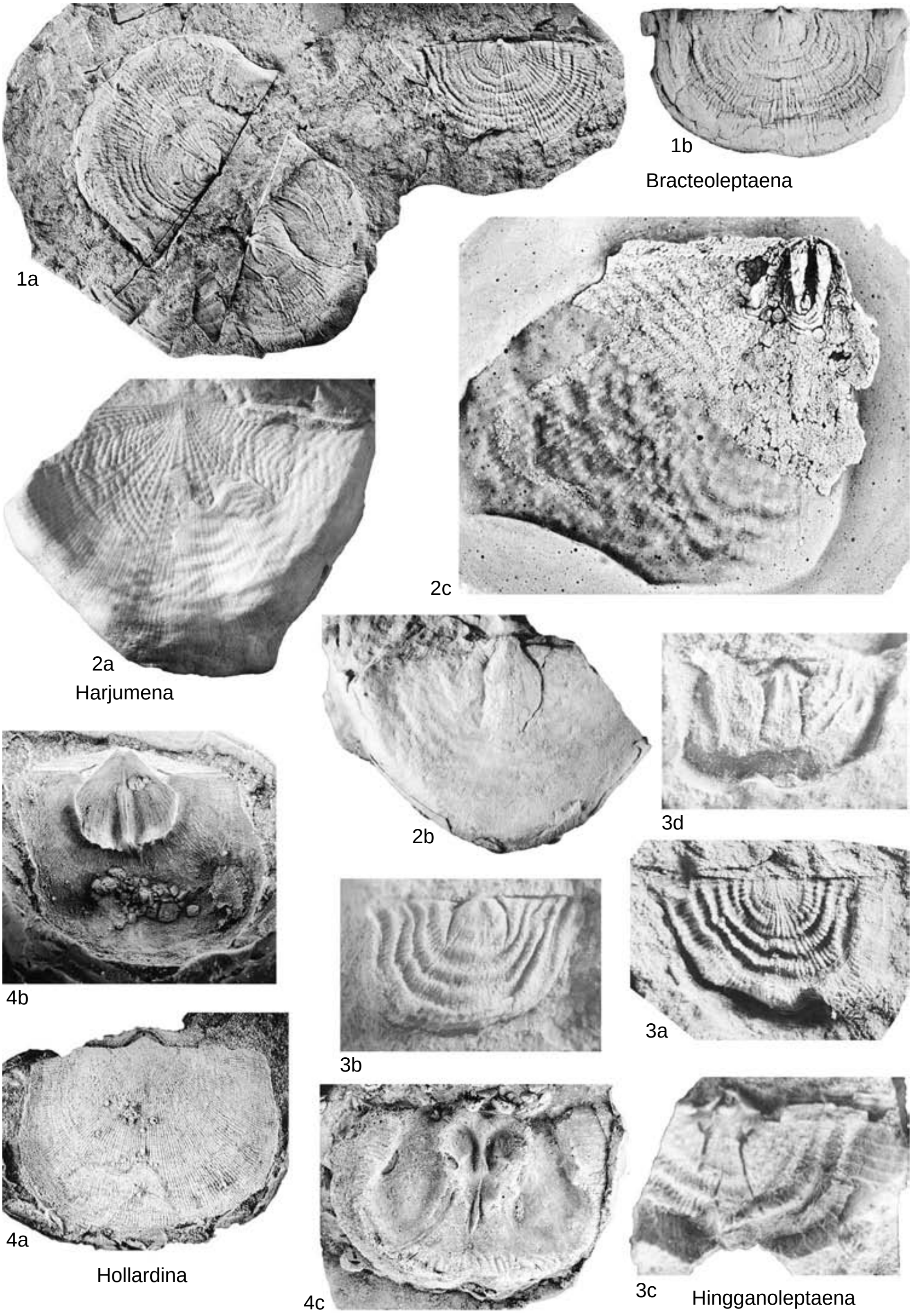

FIG. 151. Rafinesquinidae (p. 243–246).

chilidium; ventral muscle platform completely surrounded by ridges, partly elevated; dorsal muscle-bounding ridges also developed; thin dorsal median septum. *Devonian (Lochkovian):* Europe.——Fig. 151,*4a–c.* **H. plana,* Kerdéniel Member, Landévennec Formation, Lochkovian, Pointe du Corbeau, Finistère, Brittany, France; *a,* dorsal view of conjoined valves, LPB 8918, ×1; *b,* latex cast of ventral internal mold, LPB 8919, ×1; *c,* latex cast of dorsal internal mold, LPB 8917, ×1 (Racheboeuf, new).

Kiaeromena Spjeldnaes, 1957, p. 183 [**Leptaena kjerulfi* Holtedahl, 1916, p. 72; OD] [=*Estonomena* Rõõmusoks, 1989, p. 113 (type, *Leptaena estonensis* Bekker, 1921; OD)]. Gentle geniculation; unequally parvicostellate, rugate ornament; pseudodeltidium, chilidium large; dental plates leading to posterolateral muscle-bounding ridges; ventral valve muscle field subcircular; cardinalia as in *Kjerulfina;* dorsal transmuscle ridges variably developed. *Ordovician (Llandeilo–Ashgill).*

K. (**Kiaeromena**). Similar to *K. (Bekkeromena),* but without elevated muscle-bounding ridges and with subcirular rather than elongate ventral muscle field. *Ordovician (Llandeilo–Caradoc):* Baltic.——Fig. 152,*1a–d.* **K. (K.) kjerulfi* (Holtedahl), Frognerkiln Formation, middle Caradoc, Norway; *a,b,* ventral, lateral views of ventral internal mold, Lindøya, Oslo, PMO 66964, ×1; *c,* lectotype, dorsal interior, Gasøya, Oslo-Asker district, PMO L128, ×1; *d,* dorsal internal mold, Lindøya, PMO 67014, ×1 (new).——Fig. 152,*1e,f. K. (K.) estonensis* (Bekker), Kukruse Formation, Llandeilo, Estonia; *e,* ventral exterior, Kukruse, BMNH BB 5220, ×1 (new); *f,* dorsal interior, Vanamõisa, TAGI BR 219, ×1 (Rõõmusoks, 1989).

K. (**Bekkeromena**) Rõõmusoks, 1963, p. 235 [**Strophomena semipartita* Roemer, 1861, pl. 1, fig. 5–9; OD]. Similar to *K. (Kiaeromena)* but with elevated muscle-bounding ridges encircling ventral valve muscle field elongate rather than subcircular; dorsal transmuscle ridges usually absent. *Ordovician (Ashgill):* Baltic.——Fig. 152,*2a,b.* **K. (B.) semipartita* (Roemer), Pirgu Formation, Ashgill, Pirgu, Estonia; *a,* ventral exterior, TAGI BR 1295, ×1.5 (Rõõmusoks, 1963); *b,* ventral exterior, BMNH BB 91342, ×1.5 (new).——Fig. 152,*2c,d.* **K. (B.)* sp. aff. *K. (B.) semipartita* (Roemer), Kuti, Estonia; *c,* ventral interior, TAGI BR 1297, ×1.5; *d,* partially exfoliated conjoined valves showing cardinalia, dorsal muscle field, TAGI BR 1296, ×1.5 (Rõõmusoks, 1963).

Lepidoleptaena Havlíček, 1963, p. 224 [**Strophomena rhomboidalis lepidula* Barrande, 1879, pl. 41, fig. 10; OD]. Transverse outline; similar to *Leptaena* but with strong ridges bounding visceral area in both valves, merging with valve hinge line lateral to vestigial dental plates, well-developed socket ridges. *Silurian (Ludlow)–Devonian (Emsian):* Europe.——Fig. 153,*1a–d.* **L. lepidula* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* dorsal external mold, NM L6657, ×1; *b,c,* ventral, anterior views of ventral internal mold, OMR VH 373a, ×1; *d,* dorsal internal mold, OMR VH 374, ×1 (Havlíček, 1967).

Leptaenopyxis Havlíček, 1963, p. 224 [**Leptaena bouei* Barrande, 1848, p. 237; OD] [=*Yujiangia* Xu, 1991, p. 314 (type, *Leptaenopyxis intermedia* Hou & Xian, 1975, p. 20; OD)]. Transverse, subquadrate outline; concavoconvex profile with anterior margin usually concave, lateral margins raised ventrally above disc before dorsal geniculation; costellate ornament with well-developed rugae; short pseudodeltidium, chilidium; ventral muscle field subcircular, bounded by ridges; dorsal muscle field bounded by variably developed ridges; dorsal median septum usually present; diaphragm variable. *Devonian (Pragian–Emsian):* Europe, Asia.

L. (**Leptaenopyxis**). More transverse than *L. (Hefengia)* but with relatively smaller ventral muscle field and with no ventral median septum anterior of the muscle field. *Devonian (Pragian–Emsian):* Europe.——Fig. 153,*2a–d.* **L. (L.) bouei* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,b,* dorsal, anterior views of conjoined valves, NM CF385, ×1; *c,* ventral internal mold, OMR VH 372b, ×1; *d,* dorsal internal mold, OMR VH 372a, ×1 (Havlíček, 1967).——Fig. 153,*2e. L. (L.) intermedia* (Hou & Xian), Yukiang Formation, lower Emsian, Liujiang, Heng Xian County, southern Guangxi Province, China; dorsal view of conjoined valves, NIGP 87820, ×1 (Xu, 1991).

L. (**Hefengia**) Xu, 1991, p. 313 [**L. (H.) hefengensis;* OD]. Similar to *L. (Leptaenopyxis),* but with larger ventral muscle field occupying more than half disc; dorsal median septum very long, extending to anterior margin of disc. *Devonian (Emsian):* China.——Fig. 153,*3a–d.* **L. (H.) hefengensis,* Mangkelu Formation, Emsian, Mangkelu, Hoboksar County, western Junggar, Xingjiang Province, China; *a,b,* holotype, ventral, lateral views of internal mold of conjoined valves, NIGP 111514, ×1; *c,d,* ventral, dorsal views of internal mold of conjoined valves, NIGP 111512, ×1 (new).

Leptagonia M'Coy, 1844, p. 116 [**Producta analoga* Phillips, 1836, p. 215; OD] [?=*Adiaphragma* Xian in Xu, Wan, & Chen, 1978, p. 299 (type, *A. ganxiensis;* M; Xian gives "*Adiaphragma yukiangensis* Xian (MS)" as type species, but it is a *nomen nudum* and *Adiaphragma ganxiensis* Wan is only species described within new genus; however, interiors are unknown; Ganxi Formation (lower Emsian), Ganxi, Beichuan County, northern Sichuan, China); *Pseudoleptaena* Miloradovich, 1947, p. 96

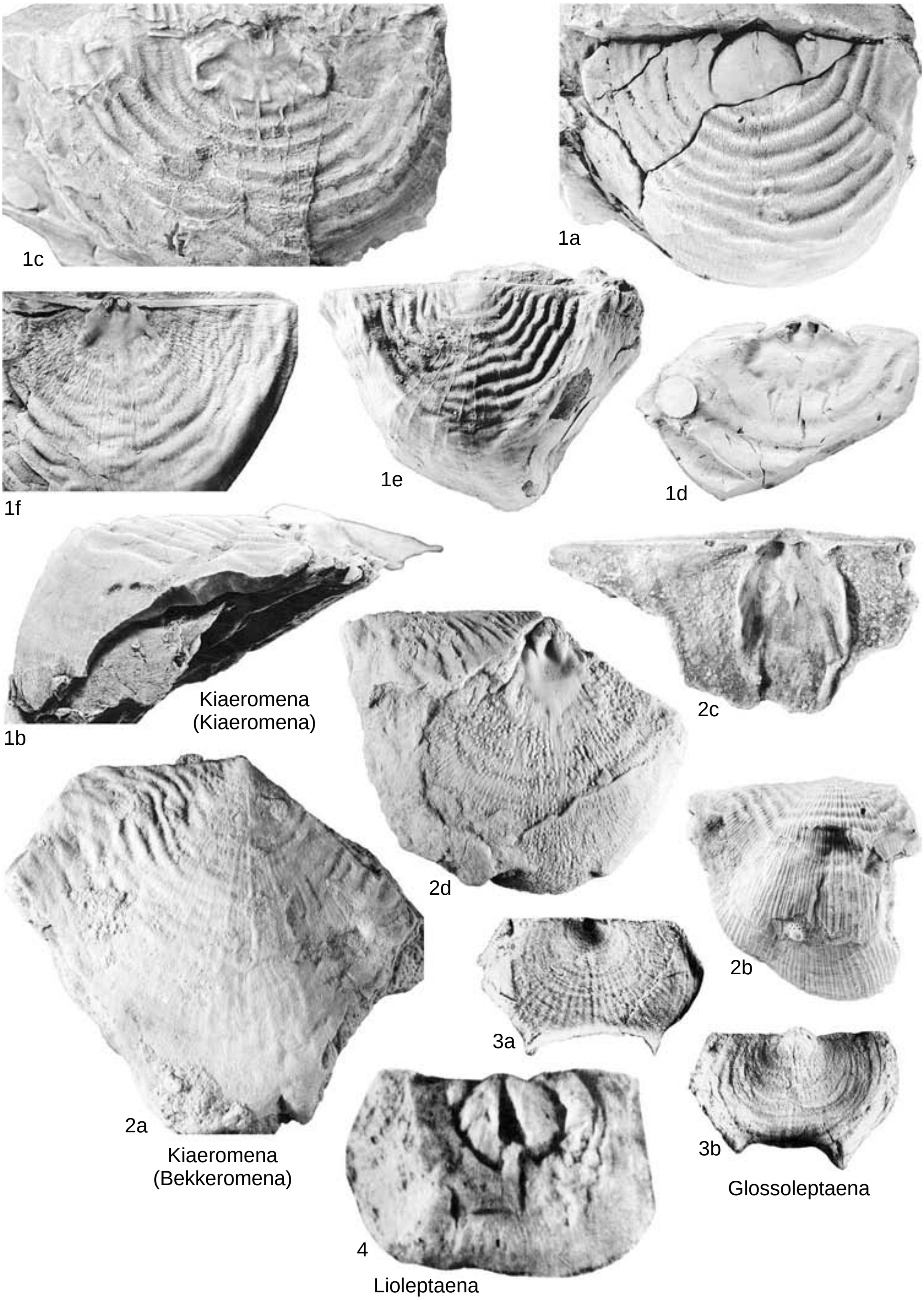

FIG. 152. Rafinesquinidae (p. 243–250).

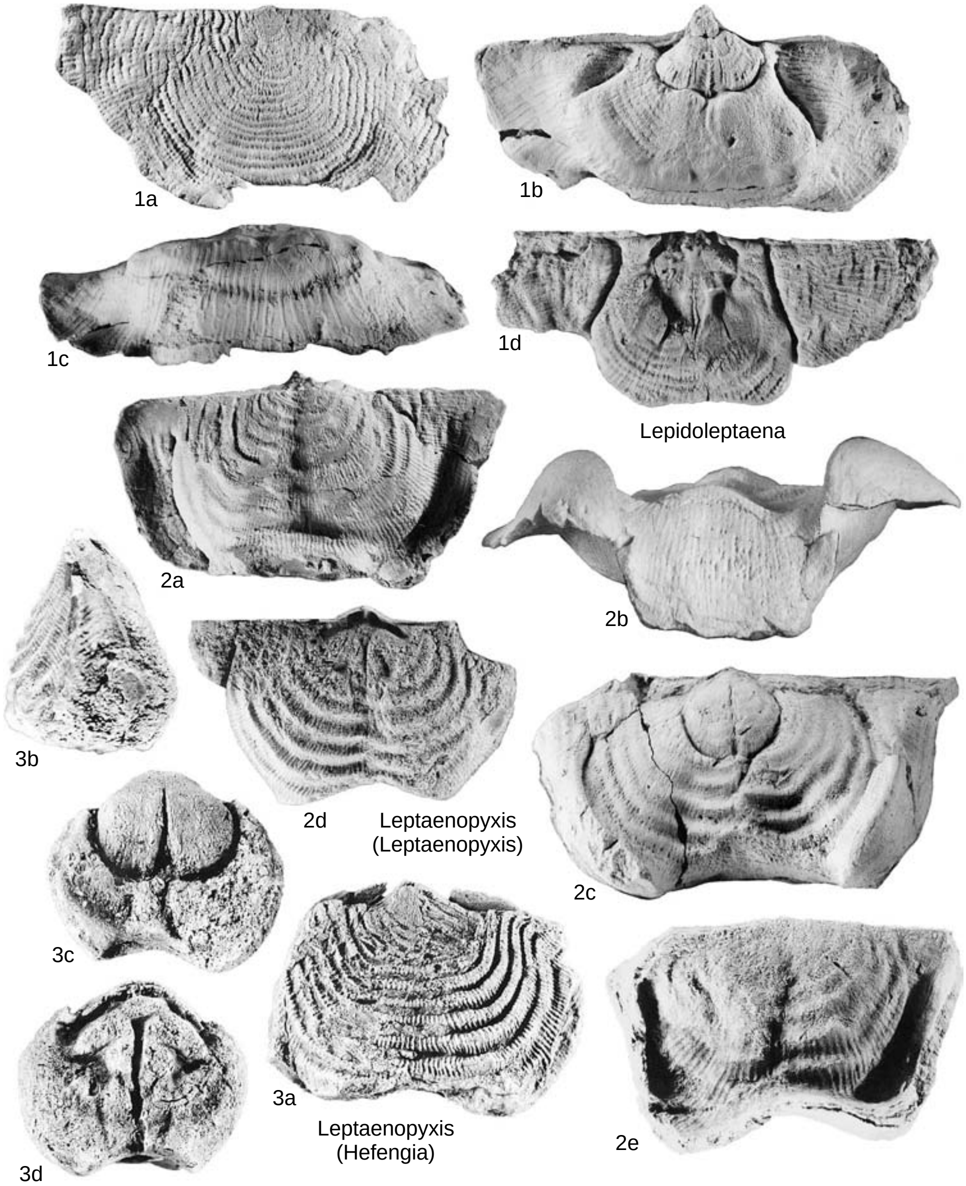

FIG. 153. Rafinesquinidae (p. 246).

(type, *Leptaena distorta* J. DE C. SOWERBY, 1840 in 1840–1846, p. 10); ?*Semileptagonia* KARAPETOV, 1971, p. 60 (type, *S. pamirica;* OD; upper Famennian, Pamir Mountains, Tadzhikistan)]. Similar to *Leptaena,* but with both ventral, dorsal muscle field platforms elevated clear of valve floor; more substantial cardinal process. *Devonian (Emsian)–Carboniferous (Namurian):* cosmopolitan.——FIG. 154,*1a–d.* **L. analoga* (PHILLIPS); *a,b,* lectotype, ventral, lateral views of conjoined valves, Carboniferous Limestone, Viséan, Bolland, Yorkshire, BMNH B 8936, ×1.5; *c,* ventral interior, Redesdale Formation, Viséan, Redesdale, Cumbria, England, BMNH B 46524, ×2; *d,* dorsal interior,

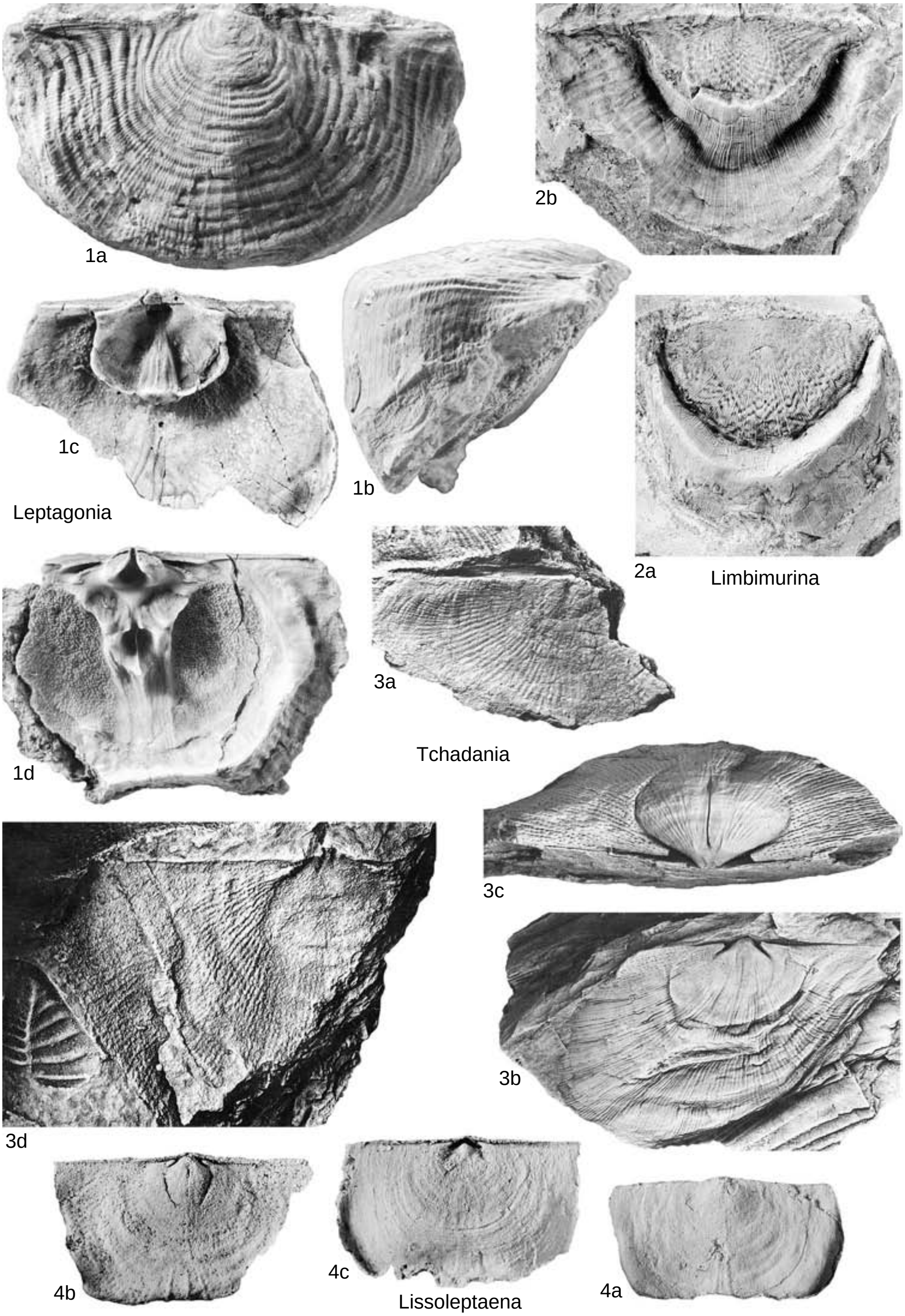

FIG. 154. Rafinesquinidae (p. 246–252).

Redesdale Formation, Viséan, Redesdale, Cumbria, England, BMNH B 43708, ×1.5 (new).

Limbimurina Cooper, 1956, p. 851 [**L. insueta;* OD]. Profile gently biconvex posteriorly with ventral geniculation followed by dorsal geniculation; distinctive ornament of small rugae interrupted by costellae, sometimes achieving interference pattern; strong divergent dental plates, leading to elevated bounding ridges surrounding subcircular ventral muscle field divided by low median ridge; thin widely diverging socket ridges; dorsal transmuscle ridges. *Ordovician (Caradoc–lower Ashgill):* North America, Scotland, Kazakhstan.——Fig. 154,*2a,b.* **L. insueta,* Rodman Member, Nealmont Formation, Caradoc, Holidaysburg, Pennsylvania; *a,* holotype, ventral exterior, USNM 117659a, ×2; *b,* dorsal exterior, USNM 117660b, ×2 (Cooper, 1956).

?Lioleptaena Xian in Xian & Jiang, 1978, p. 264 [**L. kailiensis;* OD]. Similar to *Leptaena* but without ornament on disc; dorsal interior unknown, thus family uncertain. *Silurian (Llandovery):* China.——Fig. 152,*4.* **L. kailiensis,* Wengxiang Formation, upper Telychian, Wengxiang, Kaili County, Guizhou Province, southwestern China; holotype, ventral internal mold, GB 354, ×1 (Xian & Jiang, 1978).

Lissoleptaena Havlíček, 1992, p. 171 [**L. lissodermis;* OD]. Ornament of radial costellae absent except near median plane; similar to *Leptaena* but with no radial ornament laterally, small number of faint median costellae, faint rugae. *Devonian (Lochkovian):* Europe.——Fig. 154,*4a–c.* **L. lissodermis,* Kotys Limestone, Lochkovian, Lobolitová strán, Reporyje, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 5166a, ×2; *b,* ventral internal mold, OMR VH 4696a, ×2; *c,* dorsal internal mold, OMR VH 5163a, ×2.5 (Havlíček, 1992).

Mackerrovia Cocks, 1968, p. 319 [**Brachyprion arenaceus lobatus* Lamont & Gilbert, 1945, p. 667; OD]. Concavoconvex profile with dorsal geniculation varying from sharp to more gentle; faint ornament of unequal parvicostellae, fine, irregular rugae weakly developed; teeth, dental plates continuous with long distinctive subparallel muscle-bounding ridges more than half valve length; cardinal process lobes elongate, erect; short flaring socket ridges with fine crenulations; dorsal muscle field faintly impressed with pair of long parallel side septa; central median ridge developed in central part of valve. *Silurian (Telychian):* Europe.——Fig. 155,*3a–d.* **M. lobata* (Lamont & Gilbert); *a,b,* external, internal molds of dorsal valve, Hughley Shales, Telychian, Devil's Dingle, Shropshire, England, BMNH BC 50573, ×1.5 (new); *c,* ventral internal mold, Damery Beds, Telychian, Tortworth, Avon, England, BUM 12180, ×1.5; *d,* latex cast of ventral interior, Damery Beds, Telychian, Tortworth, Avon, England, BUM 12159, ×1.5 (Cocks, 1968).

Notoleptaena Gill, 1951, p. 191 [**N. linguifera;* OD]. Ventral profile planar, dorsal convex, but with substantial dorsally directed sulcus, fold; similar to *Leptaenopyxis* but lateral margins flat, not raised ventrally; dorsally geniculate anteriorly, laterally; no pseudodeltidium; small chilidium; ventral muscle field elevated, enclosed by muscle-bounding ridges; ventral peripheral rim developed; dorsal muscle field small, enclosed posterolaterally; thin but prominent dorsal median septum. *Devonian (?Emsian):* Australia.——Fig. 155,*1a–c.* **N. linguifera,* Mount Ida Beds, Lower Devonian, Dargile Parish, Heathcote district, Victoria, Australia; *a,* latex of ventral exterior, NMVP P59527, ×1.5; *b,* holotype, latex of ventral interior, NMVP P59523, ×1; *c,* latex of dorsal interior, NMVP P59526, ×1 (new).

Rugoleptaena Havlíček, 1956, p. 558 [**R. hornyi;* OD] [?=*Elliptostrophia* Havlíček, 1963, p. 225 (type, *E. elliptica*); *Yunnanoleptaena* Jahnke & Shi, 1989, p. 153 (type, *Y. shidianensis;* OD)]. Transverse outline with shell raised ventrally at lateral margin; dorsal geniculation, short trail developed only in adults; similar to *Glossoleptaena* except radial ornament lacking apart from single median costella; small pseudodeltidium; large chilidium; dental plates very short or absent leading to muscle-bounding ridges posterolaterally defining small subcircular ventral muscle field; socket ridges, dorsal valve muscle field weakly developed. *Devonian (Pragian–Emsian):* Europe, China.——Fig. 155,*2a–d.* **R. hornyi; a,* dorsal exterior, Zlíchov Limestone, Emsian, Hlubocepy, Prague, Czech Republic, OMR VH 101a, ×2; *b,* ventral internal mold, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 35, ×2; *c,* latex cast of ventral interior, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 34, ×2; *d,* dorsal internal mold, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 32, ×2 (Havlíček, 1967).——Fig. 155,*2e,f. R. elliptica* Havlíček, Daleje Shales, Emsian, Hlubocepy, Prague, Czech Republic; *e,* ventral internal mold, OMR VH 381c, ×2; *f,* dorsal internal mold, OMR VH 381a, ×2 (Havlíček, 1967).——Fig. 155,*2g,h. R. shidianensis* (Jahnke & Shi), Xiangyangsi Formation, Pragian, Dazhaimen, Yunnan, China; *g,* holotype, ventral internal mold, CIGMR 919-68, ×2; *h,* dorsal internal mold, CIGMR 919-107, ×2 (Jahnke & Shi, 1989).

Scamnomena Bassett, 1977, p. 134 [**Strophomena rugata* Lindström, 1861, p. 371; OD]. Small, with geniculation weak or absent; prominent apical foramen; radial ornament absent or very weak; concentric rugae variably developed or absent; large pseudodeltidium; small chilidium; teeth relatively large; low median ventral ridge; cardinal process lobes stout, divergent; socket ridges widely divergent. *Silurian (Wenlock):* Europe.——Fig. 155,*4a–d.* **S. rugata* (Lindström), upper Visby Beds,

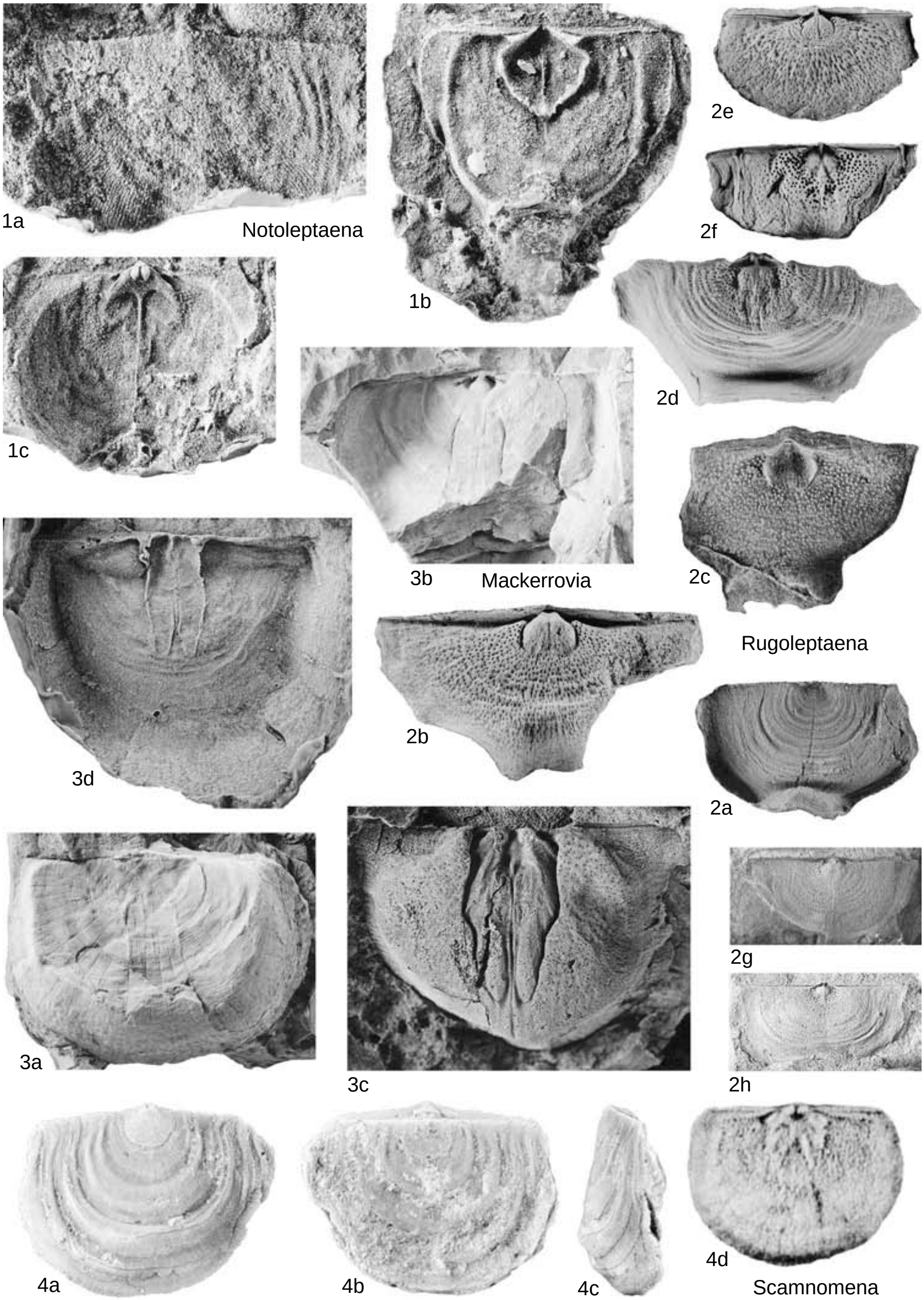

FIG. 155. Rafinesquinidae (p. 250–252).

Sheinwoodian, Visby, Gotland, Sweden; *a–c,* ventral, dorsal, side views of conjoined valves, BMNH B13498, ×4 (new); *d,* dorsal interior, RMS Br 102333, ×4 (Bassett, 1977).

?Tchadania Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 85 [**T. insignis;* OD]. Profile convexoconcave; ornament multicostellate; pseudodeltidium, chilidium small; with dental plates, curved muscle-bounding ridges laterally, but poorly impressed ventral muscle field open anteriorly; short, variably developed ventral median ridge; cardinal process lobes small, position obscure (and thus may be glyptomenid rather than rafinesquinid); poorly impressed dorsal muscle field; no dorsal median septum or side septa. *Silurian (Ludlow):* Russia.——Fig. 154,*3a–d.* **T. insignis,* Pichishuysk Formation, Ludlow, Pichi-Shuy, Tuva, Russia; *a,* dorsal external mold, IGiG 35/6884, ×2; *b,* holotype, ventral internal mold, IGiG 34/6884, ×1.5; *c,* holotype, ventral internal mold, IGiG 34a/6884, ×1.5; *d,* dorsal internal mold, IGiG 37/6884, ×2 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Family GLYPTOMENIDAE Williams, 1965

[*nom. transl.* Rong & Cocks, 1994, p. 664, *ex* Glyptomeninae Williams, 1965d, p. 388]

Outline usually transverse; small cardinal process lobes at or largely posterior to hinge line; socket ridges fused directly onto lateral bases of cardinal process lobes; notothyrial platform usually absent; concave area variably occurs immediately anterior to cardinal process lobes. *Ordovician (Llanvirn)–Silurian (Llandovery).*

Subfamily GLYPTOMENINAE Williams, 1965

[Glyptomeninae Williams 1965d, p. 388]

Lacking side septa; lacking dorsal median septum. *Ordovician (Llanvirn)–Silurian (Llandovery).*

Glyptomena Cooper, 1956, p. 881 [**G. sculpturata;* OD]. Profile gently concavoconvex; ornament unequally parvicostellate; small pseudodeltidium; short dental plates; poorly defined small subcircular ventral muscle field open anteriorly; widely divergent, prominent socket ridges; notothyrial platform weak; dorsal muscle field poorly impressed, with usually absent but sometimes sporadic, faint transmuscle septa; faint dorsal central median septum variably developed. *Ordovician (Llandeilo–Caradoc):* North America, Scotland, Kazakhstan, China.——Fig. 156,*3a–c.* **G. sculpturata,* Chatham Hill Formation, Llandeilo, Sharon Springs, Burkes Garden Quadrangle, Virginia; *a,b,* exterior, interior views of ventral valve, USNM 117856a, ×3; *c,* dorsal interior, USNM 117856b, ×3 (Cooper, 1956).

Bystromena Williams, 1974, p. 146 [**B. perplexa;* OD]. Small, concavoconvex profile; ornament of variably developed, sometimes unequal parvicostellae; large protegulum, foramen truncating ventral beak; large arched chilidium; small pseudodeltidium; short divergent dental plates; ventral muscle field poorly impressed, open anteriorly; delicate cardinalia; short, very divergent socket ridges; poorly impressed dorsal muscle field with short faint transmuscle septa; thin dorsal central median septum present in some specimens, absent in others. *Ordovician (Caradoc):* England.——Fig. 156,*5a–c.* **B. perplexa,* Spy Wood Grit, Costonian, Shelve, Shropshire, England; *a,b,* dorsal external, internal molds, BMNH BB 35367, ×5; *c,* holotype, ventral internal mold, BMNH BB 35363, ×3 (new).

?Hesperinia Cooper, 1956, p. 822 [**H. kirki;* OD]. Plano- to slightly concavoconvex outline; parvicostellate ornament; substantial pseudodeltidium; small chilidium; oblique dental plates present; ventral muscle field unknown; cardinal process obscure, thus familial position uncertain; very divergent socket plates curving laterally to run parallel to hinge line. Irregular notothyrial platform developed; hint of valve thickening on platform, but no dorsal septa clearly developed; dorsal subperipheral rim present. *Ordovician (Llanvirn–Llandeilo):* North America.——Fig. 156,*2a,b.* **H. kirki,* Tank Hill Formation, Llanvirn–Llandeilo, Monument Canyon, Nevada; *a,* holotype, dorsal exterior of conjoined valves, USNM 117626a, ×3; *b,* dorsal interior, USNM 117627a, ×3 (Cooper, 1956).

Linostrophomena Rong, Xu, & Yang, 1974, p. 203 [**L. convexa;* OD]. Ventral valve convex profile, dorsal valve initially convex, then concave anterolaterally; parvicostellate ornament; small pseudodeltidium; vestigal chilidium; teeth strong; true dental plates absent, well-defined elevated ventral muscle field with curved bounding ridges; cardinal process lobes separate, fused to widely divergent but short curved socket ridges; two pairs of adductor scars differentiated in relatively small dorsal muscle field. *Silurian (Telychian):* China.——Fig. 157,*1a–c.* **L. convexa,* upper Xiushan Formation, upper Telychian, Rongxi, Xiushan County, Sichuan Province; *a,b,* latex casts of ventral internal molds, NIGP 22344-5, ×2, *c,* holotype, latex cast of dorsal internal mold, NIGP 22347, ×1.5 (new).

?Mjoesina Spjeldnaes, 1957, p. 137 [**Rafinesquina mjoesensis* Holtedahl, 1916, p. 19; OD]. Profile concavoconvex; ornament unequally parvicostellate; strong but short dental plates extending into lateral curved muscle-bounding ridges; dorsal valve interior, hence familial assignment unknown. [Types untraced in PMO; Spjeldnaes figures too poor to

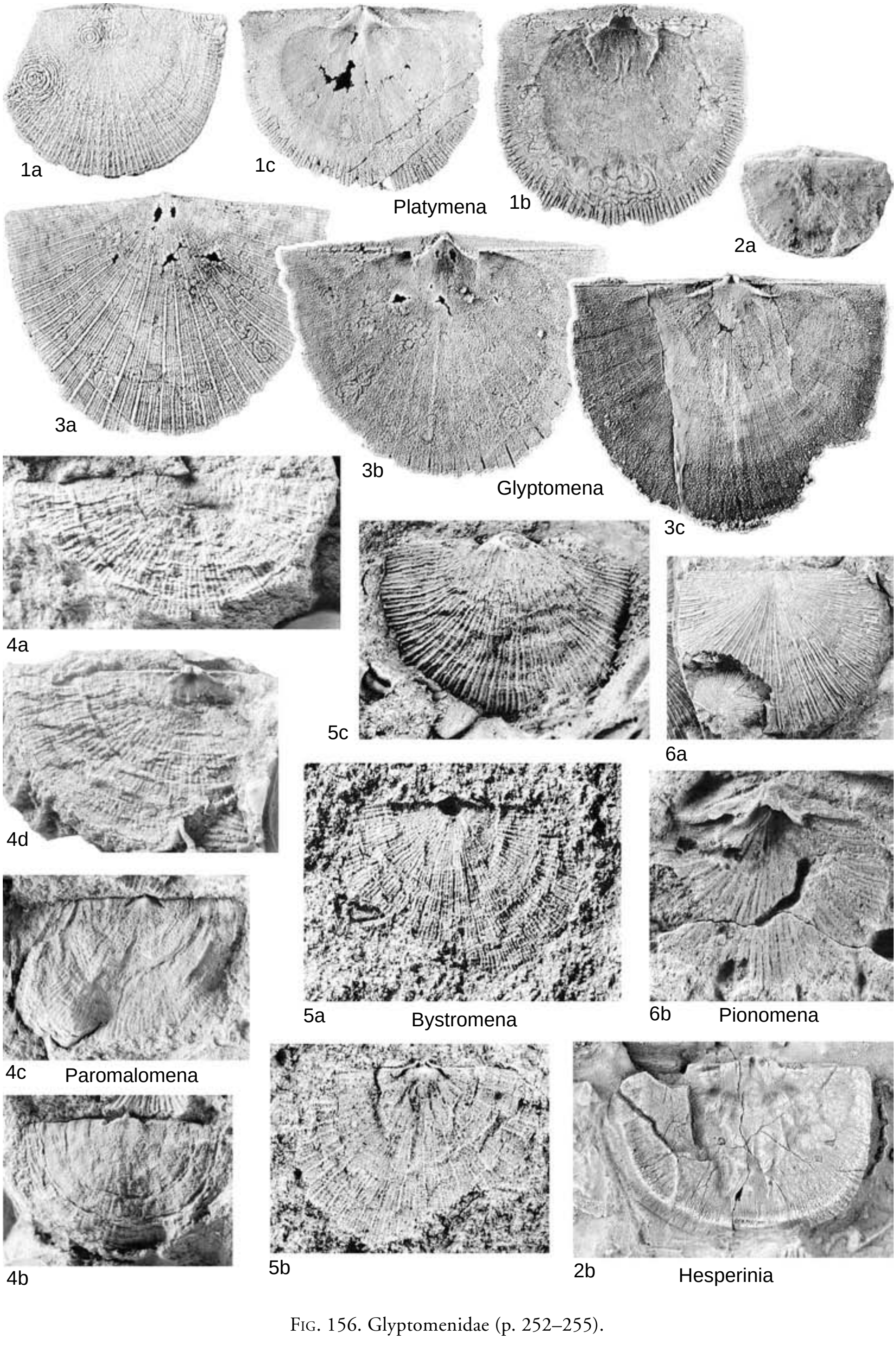

FIG. 156. Glyptomenidae (p. 252–255).

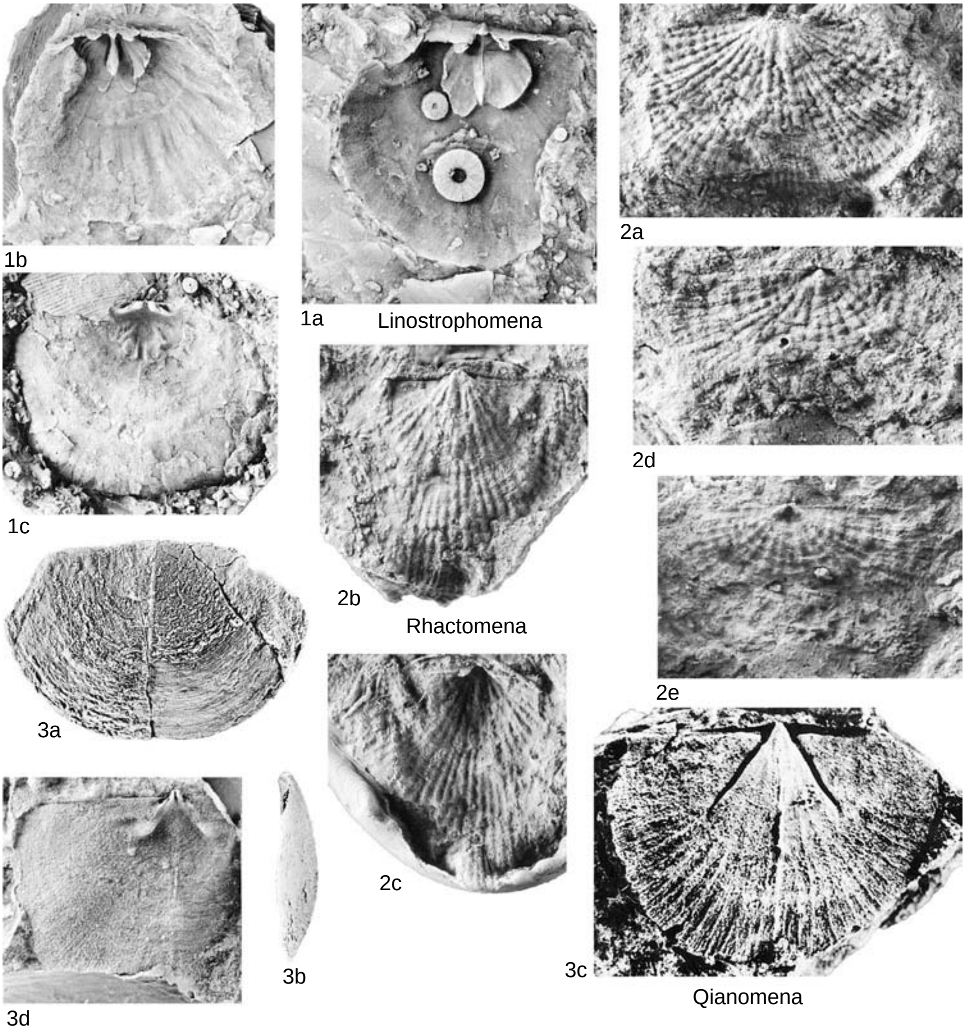

FIG. 157. Glyptomenidae (p. 252–256).

illustrate; could be *nomen dubium.*] *Ordovician (Caradoc):* Baltic, Upper Mjøsa Limestone, upper Caradoc, Helgøya, Hamar-Nes district, Norway.

Paromalomena RONG, 1984, p. 150 [**Platymena polonica* TEMPLE, 1965, p. 407; OD]. Relatively wide outline; planoconvex profile, with anterior fold, sulcus; finely costellate ornament; small pseudodeltidium; large chilidium; short, widely divergent dental plates; poorly impressed small ventral muscle field; small, short but widely divergent socket ridges; small, poorly impressed dorsal muscle field with no septa, although pair of short transmuscle ridges sometimes present. *Ordovician (Ashgill):* cosmopolitan.——FIG. 156,*4a–d*. **P. polonica* (TEMPLE), Dalmanitina Beds, Ashgill, Stawy, near Kagow, Holy Cross Mountains, Poland; *a,* ventral external mold, BMNH BB 29216, ×3; *b,* ventral internal mold, BMNH BB 30010, ×3; *c,* holotype, dorsal internal mold, BMNH BB 30009, ×3; *d,* latex cast of dorsal internal mold, BMNH BB 29216, ×3 (new).

?Pionomena COOPER, 1956, p. 901 [**P. neumani;* OD]. Similar to *Glyptomena,* but gently biconvex, with shorter, more obsolescent dental plates; small pseudodeltidium, larger chilidium; dorsal interior, hence family assignment, poorly known. *Ordovician (Llandeilo–Caradoc):* North America, Scotland. ——FIG. 156,*6a,b*. **P. neumani,* New Market Formation, Llandeilo–Caradoc, Williamsport, Maryland; *a,* dorsal exterior, USNM 117756c, ×2; *b,* ventral interior, USNM 117755, ×3 (Cooper, 1956).

Platymena Cooper, 1956, p. 879 [**P. plana;* OD]. Planoconvex to slightly concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium, chilidium small; stout teeth leading anteriorly to thin dental plates flaring laterally, coalescing with curved muscle-bounding ridges directed inward, merging anteriorly with valve floor; short, stout socket ridges merging with prominent thick but short notothyrial platform; dorsal muscle field poorly impressed with no septa; faint subperipheral ventral, dorsal rims poorly developed in some adults. *Ordovician (Caradoc–lower Ashgill):* North America, Kazakhstan.——Fig. 156,*1a–c.* **P. plana,* Arline Formation, Caradoc, Friendsville, Tennessee; *a,* dorsal exterior, USNM 117759c, ×2; *b,* ventral interior, USNM 117759a, ×2; *c,* dorsal interior, USNM 117759e, ×2 (Cooper, 1956).

Pomeromena Mitchell, 1977, p. 112 [**P. transversa;* OD]. Small with transverse outline, concavoconvex profile; pronounced ventral sulcus, smaller dorsal fold; faint parvicostellate ornament; small pseudodeltidium; larger chilidium; small ventral process; no dental plates; faint muscle-bounding ridges defining small bilobed ventral muscle field; widely divergent socket ridges, weak notothyrial platform; dorsal muscle field poorly impressed; no dorsal median septum or side septa. *Ordovician (Ashgill):* Ireland.——Fig. 158,*2a–e.* **P. transversa,* Killey Bridge Formation, Ashgill, Killey Bridge, Pomeroy, County Tyrone, Northern Ireland; *a–c,* holotype, latex cast of ventral external mold, ventral internal mold, latex cast, BGS NIG 887, ×2.5; *d,* latex of ventral internal mold, BGS GU 1041, ×2.5; *e,* dorsal internal mold, BGS GU 1093, ×3 (new).

?Proboscisambon Havlíček & Mergl, 1982, p. 44 [**Strophomena quaesita* Barrande, 1879, p. 101; OD]. Transverse outline, biplanar to very gently concavoconvex profile; very faint parvicostellate ornament, with accentuated median costella; small pseudodeltidium, chilidium; very short, thin widely divergent dental plates; poorly impressed muscle fields in both valves; cardinal process lobes delicate, widely separated, on hinge line; socket ridges not visible. *Ordovician (Ashgill):* Europe.——Fig. 158,*1a,b.* **P. quaesita* (Barrande), Králuv Dvur Formation, Ashgill, Jezerka, Bohemia, Czech Republic; *a,* ventral internal mold, MM 039, ×6; *b,* dorsal internal mold, MM 041, ×6 (Mergl, new).

Qianomena Rong & Yang, 1981, p. 173 [**Q. unicosta;* OD]. Profile moderately concavoconvex; radial ornament absent or very faint apart from single prominent central costa; no true dental plates but very prominent, straight ventral muscle-bounding ridges posterolaterally to ventral muscle field, open anteriorly; cardinal process lobes projected posteriorly; socket ridges short; dorsal muscle field poorly impressed. *Silurian (Llandovery):* China.——Fig. 157,*3a–d.* **Q. unicosta,* lower Xiangshuyuan Formation, upper Rhuddanian–

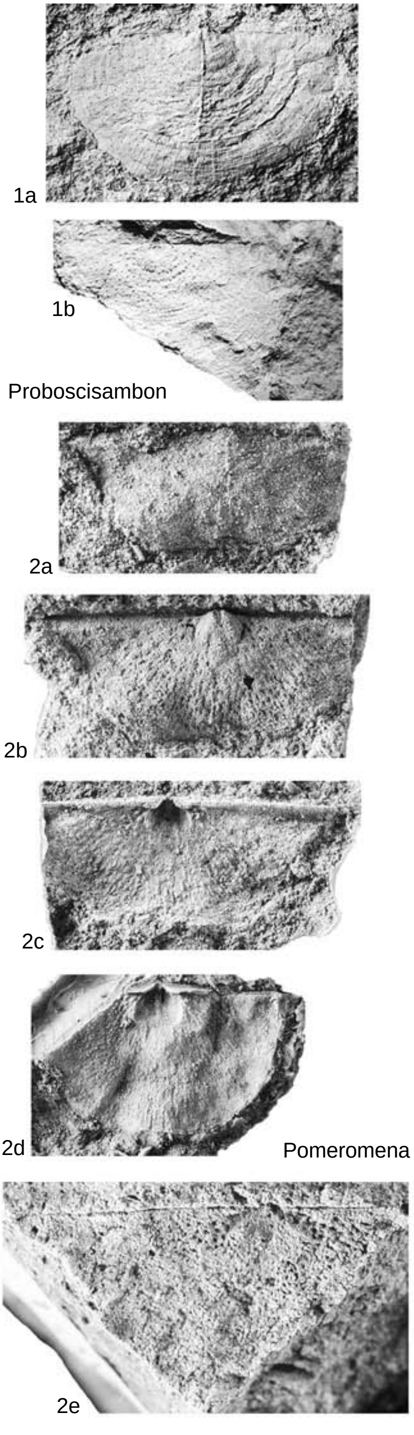

Fig. 158. Glyptomenidae (p. 255).

lower Aeronian; *a,b,* holotype, ventral, lateral views of conjoined valves, Yingwuxi, Sinan County, NIGP 43873, ×2; *c,* ventral internal mold, Hongyan reservoir, Sinan County, northeastern Guizhou Province, China, NIGP 43870, ×2; *d,* latex cast of dorsal internal mold, Hongyan Reservoir, Sinan County, northeastern Guizhou Province, China, NIGP 43868, ×3 (new).

Rhactomena MITCHELL, 1977, p. 111 [**R. splendens;* OD]. Planoconvex profile with ventral sulcus, weaker dorsal fold; distinctive ornament of relatively strong costae forming small nodes where strong growth lines cross them; weak rugae; small convex chilidium with median groove; small teeth, no dental plates; both muscle fields poorly impressed; short divergent socket ridges; no dorsal median septum or side septa. *Ordovician (Ashgill):* Ireland.——FIG. 157,*2a–e.* **R. splendens,* Killey Bridge Formation, Ashgill, Killey Bridge, Pomeroy, County Tyrone, Northern Ireland; *a,* dorsal exterior, BGS GU 1076, ×6; *b,c,* internal mold, latex of ventral interior, BGS GU 1071, ×6; *d,e,* internal mold, latex of dorsal interior, BGS GU 1070, ×6 (new).

Subfamily TERATELASMINAE
Pope, 1976

[*nom. transl.* RONG & COCKS, 1994, p. 664, *ex* tribe Teratelasmini POPE, 1976, p. 153]

Similar to the Glyptomeninae but differs in possessing muscle-bounding ridges, or united transmuscle ridges and side septa; high dorsal median septum. *Ordovician (Llandeilo–Ashgill).*

Teratelasma COOPER, 1956, p. 823 [**T. neumani;* OD]. Profile planoconvex to gently biconvex, with dorsal median sulcus; unequally parvicostellate ornament; short flaring dental plates posterolaterally bounding short, bilobed ventral muscle field, poorly impressed; short curved socket ridges; dorsal muscle field poorly impressed but with posterolateral muscle-bounding ridges; prominent but short elevated dorsal side septa, with lateral protrusions in older specimens; very large elevated dorsal median septum extending for four-fifths of valve length. *Ordovician (Llandeilo–Caradoc):* North America.——FIG. 159,*1a–d.* **T. neumani,* Sevier Formation, Llandeilo–Caradoc, Old Kagley Church, Binfield Quadrangle, Tennessee; *a,* plasticine cast of dorsal exterior, USNM 117938a, ×3; *b,* plasticine cast of ventral interior, USNM 117938l, ×3; *c,d,* dorsal internal mold, latex cast, USNM 117938m, ×4 (Cooper, 1956).

Tashanomena ZHAN & RONG, 1994, p. 418 [**T. variabilis;* OD]. Concavo- to planoconvex profile; thin dental plates merging anteriorly into curved bounding ridges enclosing small ventral muscle field except anteriorly; small cardinal process lobes united with short, thin socket ridges; dorsal muscle field with posterolateral oblique curved bounding ridges, elevated anteriorly; elongated dorsal side septa, prominent median septum in dorsal valve center only. *Ordovician (Ashgill):* China.——FIG. 159,*2a–d.* **T. variabilis,* Xiazhen Formation, middle Ashgill, Tashan, Yushan, Jiangxi Province, China; *a,* dorsal external mold, NIGP 121549, ×10; *b,* ventral internal mold, NIGP 121542, ×10; *c,* holotype, dorsal internal mold, NIGP 121550, ×10; *d,* holotype, dorsal internal mold, NIGP 121553, ×10 (Zhan & Rong, 1994).

Family FOLIOMENIDAE
Williams, 1965

[Foliomenidae WILLIAMS, 1965d, p. 391]

Without radial ornament, lacking dental plates, with small, bilobed ventral muscle field; cardinal process as in Glyptomenidae, but with pair of close, narrowly divergent dorsal valve side septa. *Ordovician (Caradoc–Ashgill).*

Foliomena HAVLÍČEK, 1952, p. 413 [**Strophomena folium* BARRANDE, 1879, pl. 55; OD] [=*Jielingia* ZENG, 1987, p. 235 (type, *J. jielingensis;* OD)]. Transverse outline, biplanar to very gently concavoconvex profile; pedicle sheath often prominent; small interarea with very small pseudodeltidium; ventral muscle field bilobed, weakly impressed; short myophragm; bladelike socket ridges broadly divergent to become subparallel to hinge line. *Ordovician (Caradoc–Ashgill):* cosmopolitan.——FIG. 160,*1a–c.* **F. folium* (BARRANDE), Králuv Dvur Formation, Ashgill, Králuv Dvur, Czech Republic; *a,* ventral external mold, NM CD1566, ×2; *b,* lectotype, ventral internal mold, NM CD1565a, ×2.5; *c,* dorsal internal mold, NM CD1565b, ×2 (Havlíček, 1967).——FIG. 160,*1d. F. jielingensis* (ZENG), Miaopo Formation, lower Caradoc, Jieling, Yichang County, Hubei Province, China, dorsal internal mold, YIGM IV45822, ×5 (Zeng, new).

Family CHRISTIANIIDAE
Williams, 1953

[Christianiidae WILLIAMS, 1953b, p. 9]

Low cardinal process with lobes very close together, fused at their bases; socket plates often elevated anteriorly from valve floor; two pairs of distinctive large dorsal side septa. *Ordovician (Llanvirn–Ashgill).*

Christiania HALL & CLARKE, 1892, p. 298 [**Leptaena subquadrata* HALL, 1883, pl. 46, fig. 32, 33; OD] [=*Christianella* LIANG in LIU, XU, & LIANG, 1983, p. 277 (type, *C. zhitangensis;* OD)]. Outline usually elongate in adults; concavoconvex profile with

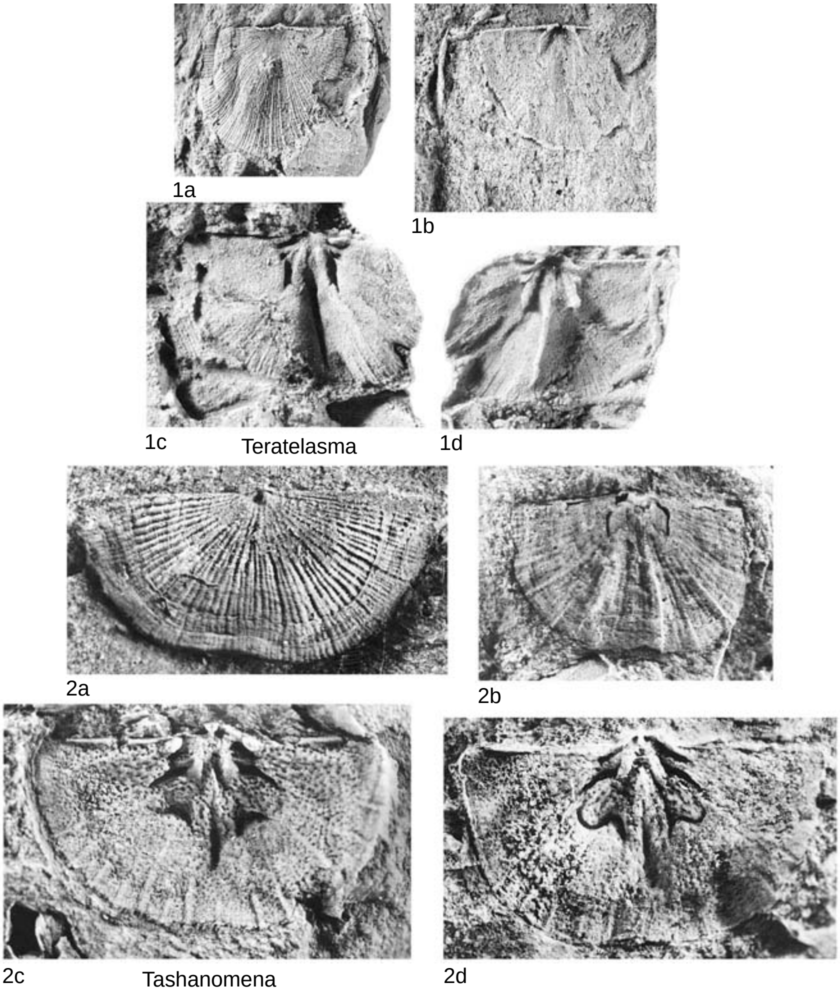

FIG. 159. Glyptomenidae (p. 256).

strong convexity, especially near umbo; apical foramen persistent throughout ontogeny; no radial ornament; largely open delthyrium, but with small pseudodeltidium, chilidium; teeth simple, supported by receding dental plates; well-impressed bilobed ventral muscle field bounded laterally by weak low ridges; anterior part of muscle field continuous with vascula media leading to digitate mantle canals; small transverse plates sometimes developed between two prominent pairs of dorsal valve side septa. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.——FIG. 160,*2a–d.* **C. subquadrata* (HALL), Caradoc; *a,b,* dorsal, lateral views of conjoined valves, Lenoir Formation, Friendsville, Tennessee, BMNH B 78727, ×3; *c,d,* dorsal, posterior views of dorsal interior, Athens Formation, Perry County, Tennessee, AMNH 37883, ×3 (new).——FIG. 160,*2e–g. C. zhitangensis* (LIANG), Huangnikang Formation, lower Ashgill, Zhitang, Quxian County, Zhejiang Province, eastern China; *e,* dorsal external mold, HIGS 2703, ×3; *f,* holotype, ventral internal mold, HIGS 2701, ×3; *g,* dorsal internal mold, HIGS 2702, ×3 (Liu, Xu, & Liang, 1983).

Nubialba NEUMAN, 1994, p. 1231 [**N. forbesi;* OD]. Similar to *Christiania,* but with ornament of fine, widely spaced costae, one medially located. *Ordovician (Ashgill):* North America.——FIG. 160,*3a–c.* **N. forbesi,* Pyle Mountain Argillite, Ashgill, Aroostook County, Maine, USA; *a,* dorsal external mold, USNM 465231, ×5; *b,* ventral internal mold, USNM 465242, ×5; *c,* holotype, dorsal internal mold, USNM 455231, ×5 (Neuman, 1994).

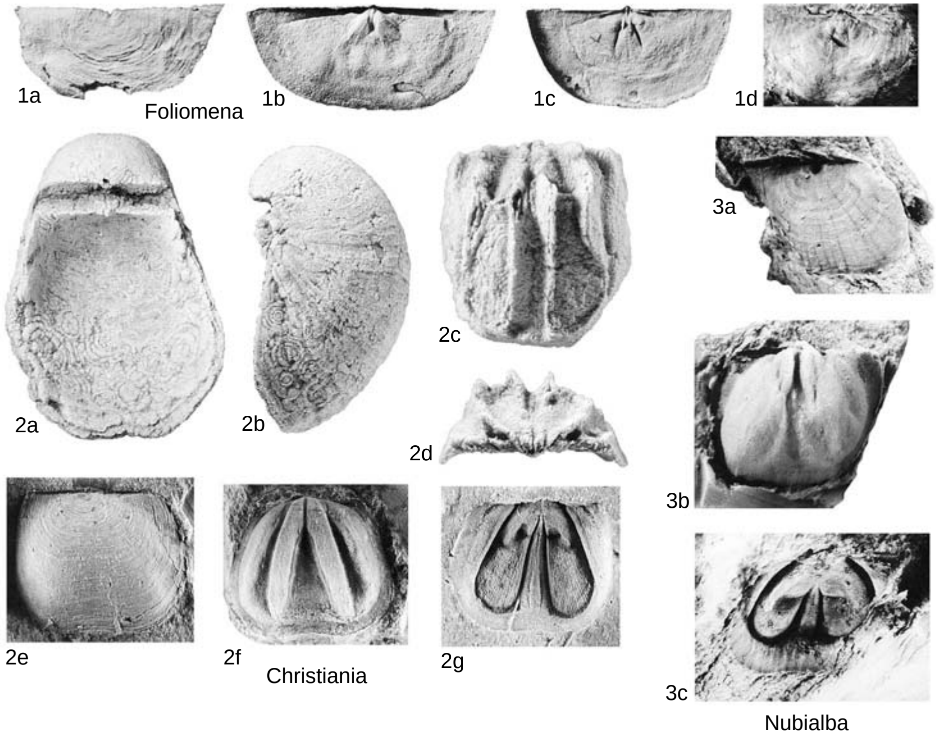

FIG. 160. Foliomenidae and Christianiidae (p. 256–257).

Family LEPTAENOIDEIDAE Williams, 1953

[*nom. transl.* Rong & Cocks, 1994, p. 665, *ex* Leptaenoideinae Williams, 1953b, p. 8] [=Liljevallinae Williams, 1953b, p. 9]

Bizarre forms with ventral valve attached to substrate by cementation; dorsal interiors only known in *Leptaenisca,* which has strong, ventrally directed cardinal process lobes. *Silurian (upper Llandovery)–Devonian (Emsian).*

Leptaenoidea Hedstrom, 1917, p. 2 [**L. silurica;* OD]. Ventral valve cemented over complete disc prior to geniculation; ornament finely costellate, rugose; ventral muscle field short, broad with strong elevated lateral bounding ridges; myophragm present; dorsal valve unknown. *Silurian (Wenlock):* Baltic.——Fig. 161,*1.* **L. silurica,* Halla Beds, Wenlock, Horsne Canal, Gotland, Sweden; lectotype, ventral interior, Swedish Geological Survey, ×4 (Bassett & Cocks, 1974).

Leptaenisca Beecher, 1890a, p. 239 [**Leptaena concava* Hall, 1857, p. 47; OD]. Ventral valve attached in umbonal area in younger growth stages only; profile concavoconvex with unequally parvicostellate ornament; elongate bilobed ventral muscle field bounded laterally by strong plates; ventral median septum; strong cardinal process lobes posteroventrally directed; thin low short socket ridges present close to cardinal process; distinctive planospiral brachial ridges originating anterolateral to cardinalia. *Devonian (Pragian–Emsian):* North America.——Fig. 161,*2a–e.* **L. concava* (Hall), lower Helderburg Group, Lower Devonian, Albany County, New York; *a–c,* ventral, lateral, internal views of ventral valve, YPM 28116, ×2; *d,* dorsal internal mold, YPM 24859, ×2; *e,* dorsal interior showing cardinalia, YPM 28115, ×2 (Bassett, new).

Leptaenomendax García-Alcalde in García-Alcalde & Martínez-Chacón, 1978, p. 255 [**L. chaconae;* OD]. Asymmetrically cemented by ventral umbo, otherwise regular outline; ornament of costellae, rugae; elevated ventral muscle field bounded anteriorly, laterally by united bounding ridges; cardinal process lobes high, delicate, directed posteroventrally; low socket ridges straight, narrow; dorsal muscle field elevated; dorsal subperipheral rim. *Devonian (Emsian):* Europe.——Fig. 161,*3a–d.* **L. chaconae,* Grupo la Vid, upper Emsian, Colle Church, Sabero, Spain; *a,b,* holotype, conjoined valves, dorsal, ventral views, with ventral valve cemented to bryozoan, DPO 431, ×2; *c,* ventral interior, DPO 433, ×2; *d,* dorsal interior, DPO

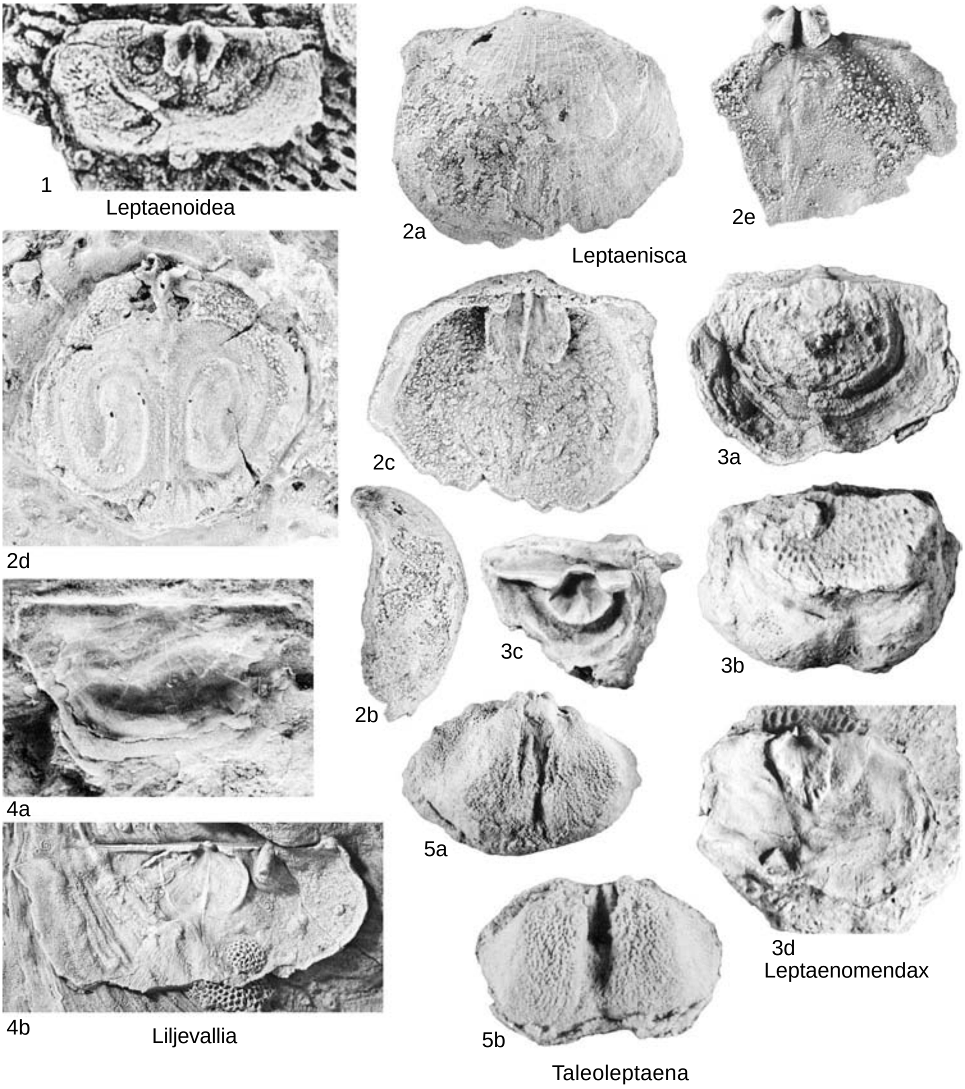

FIG. 161. Leptaenoideidae (p. 258–259).

6259, ×2 (García-Alcalde & Martínez-Chacón, 1978).

Liljevallia HEDSTROM, 1917, p. 9 [*L. gotlandica; OD]. Irregular profile, outline with cementation to match substrate, but usually transverse; unequally parvicostellate ornament; irregular oblique denticles present on dorsal facets of teeth; dental plates continuous with curved high bounding ridges around ventral muscle field; myophragm variably developed; dorsal interior unknown. *Silurian (upper Llandovery–lower Wenlock):* Baltic.——FIG. 161,*4a,b.* *L. gotlandica, upper Visby Beds, lower Wenlock; *a,* dorsal exterior, Stenkwrkehuks Fyr, ×2 (new); *b,* lectotype, ventral interior encrusted on stromatoporoid, Nygardsback, Gotland, Sweden, Swedish Geological Survey, ×2 (Bassett & Cocks, 1974).

?Taleoleptaena HAVLÍČEK, 1967, p. 121 [*T. taleolata; OD]. Profile strongly convex but irregular; attachment scar not known; thick shelled, lacking ornament; dental plates parallel, close together; ventral median septum; dorsal valve unknown, thus familial position uncertain. *Devonian (Emsian):* Europe.——FIG. 161,*5a,b.* *T. taleolata, Zlichov Limestones, Emsian, Praha-Hlubocepy, Czech Republic; *a,* partly exfoliated ventral valve, OMR VH 497b, ×3; *b,* holotype, ventral internal mold, OMR VH 497e, ×5 (Havlíček, 1967).

Family AMPHISTROPHIIDAE Harper, 1973

[*nom. transl.* HARPER & BOUCOT, 1978, p. 154, *ex* Amphistrophiinae HARPER, 1973, p. 36] [=Maoristrophiidae USHATINSKAYA & ALEKSEEVA, 1983, p. 37]

Hinge line denticulate; lacking dental plates; ventral valve muscle field semielliptical in outline, bounded laterally by curved muscle-bounding ridges (except *Eoamphistrophia*); variable cardinal process; dorsal muscle field bounded posterolaterally by low ridges extending anteriorly from socket ridges; no dorsal side septa. *Silurian (Telychian)–Devonian (Eifelian).*

Subfamily AMPHISTROPHIINAE Harper, 1973

[Amphistrophiinae HARPER, 1973, p. 36]

Differs from Mesodouvillininae in having resupinate profile. *Silurian (Telychian)–Devonian (Emsian).*

Amphistrophia HALL & CLARKE, 1892, p. 292 [**Strophomena striata* HALL, 1843a, p. 104; OD] [=*Strophonellites* HAVLÍČEK, 1967, p. 184 (type, *Leptaena patricia* BARRANDE, 1848, p. 245; OD)]. Resupinate, with curved to geniculate profile; ornament unequally parvicostellate to costellate; strong bounding ridges posterior, lateral to suboval ventral muscle field; weak ventral median septum; cardinal process lobes short, posteroventrally directed, situated on hinge line; weakly impressed dorsal muscle field. *Silurian (Telychian)–Devonian (Lochkovian).*

A. (**Amphistrophia**). Similar to *A. (Pembrostrophia)* but with unequally costellate to finely costellate ornament; similar to *A. (Amphistrophiella)* but with relatively gentle and evenly curved geniculation. *Silurian (Telychian–Ludfordian):* cosmopolitan.——FIG. 162,*1a–c.* **A. (A.) striata* (HALL), Wenlock; *a,* syntype, dorsal exterior, Niagara Group, Lockport, New York, AMNH 31255, ×1.5; *b,* ventral interior, Waldron Shale, Waldron, Indiana, AMNH 40780, ×1.5; *c,* dorsal interior, Waldron Shale, Waldron, Indiana, AMNH 40779, ×1.5 (new).——FIG. 162,*1d–f. A. (A.) patricia* (BARRANDE), Motol Formation, Wenlock, Svaty Jan pod Skalou, Bohemia, Czech Republic; *d,* dorsal exterior mold, ×1.5; *e,* ventral internal mold, OMR VH 457b, ×2; *f,* dorsal internal mold, OMR VH 457a, ×1.5 (Havlíček, 1967).

A. (**Amphistrophiella**) HARPER & BOUCOT, 1978, p. 157 [**Orthis funiculata* M'COY, 1846, p. 30; OD] [=*Amphistrophiella (Amsdenostrophiella)* HARPER & BOUCOT, 1978, p. 158 (type, *Strophonella prolongata* FOERSTE, 1909a, p. 85; OD)]. Similar to *A. (Amphistrophia)* but with more sharply geniculate profile. *Silurian (Telychian)–Devonian (Lochkovian):* cosmopolitan.——FIG. 162,*3a–e.* **A. (A.) funiculata* (M'COY), Much Wenlock Limestone Formation, Homerian, Dudley, western Midlands, England; *a–c,* exterior of conjoined valves, *a,* ventral view, *b,* oblique dorsal view, ×1.5, *c,* center of interarea, BMNH B 5692, ×8; *d,* ventral interior, BMNH BC 13419, ×2; *e,* dorsal interior, BMNH BC 13420, ×2 (new).

A. (**Pembrostrophia**) BASSETT, 1971, p. 325 [**A. (P.) freshwaterensis;* OD]. Similar to *A. (Amphistrophia),* but with ornament stronger and more uniformly costellate. *Silurian (Wenlock):* Europe.——FIG. 162,*2a–e.* **A. (P.) freshwaterensis,* Gray Sandstone Group, lower Wenlock, Freshwater East Bay, Dyfed, Wales; *a,* latex of ventral exterior; *b,c,* ventral internal mold, latex cast, BMNH BC 41356, ×1.5; *d,e,* dorsal internal mold, latex cast, BMNH BC 41362, ×1.5 (new).

Devonamphistrophia HARPER & BOUCOT, 1978, p. 159 [**Strophodonta alveata* HALL, 1863a, p. 36; OD]. Gently resupinate profile; uniformly costellate ornament; cardinal process lobes strongly posteriorly directed; straight posterolateral bounding ridges to subtriangular, bilobed ventral muscle field; possible dorsal median septum; faint myophragm; dorsal muscle field weakly impressed. *Devonian (?Lochkovian, Pragian–Emsian):* North America.——FIG. 163,*1a–c.* **D. alveata* (HALL), Schoharie Grit, Emsian, Clarkesville, Albany County, New York; *a,b,* ventral internal mold, latex cast, NYSM 2053, ×1.5; *c,* latex cast of dorsal interior, NYSM 2054, ×2 (new).

Eoamphistrophia HARPER & BOUCOT, 1978, p. 154 [**Amphistrophia whittardi* COCKS, 1967, p. 261; OD]. Profile gently resupinate with anterior rounded geniculation; unequally parvicostellate ornament; weakly impressed muscle fields in both valves; no ventral valve muscle-bounding ridges; cardinal process ventrally directed, but short. *Silurian (Telychian):* Europe.——FIG. 163,*2a,b.* **E. whittardi* (COCKS), Hughley Shale, Telychian, Domas, Shropshire; *a,* ventral internal mold, OUM C13514, ×2.5; *b,* dorsal internal mold, OUM C13536, ×2.5 (Cocks, 1967).

Subfamily MESODOUVILLININAE Harper & Boucot, 1978

[Mesodouvillininae HARPER & BOUCOT, 1978, p. 124]

Similar to Amphistrophiinae, but concavoconvex profile. *Silurian (?Telychian, Sheinwoodian)–Devonian (Eifelian).*

Mesodouvillina WILLIAMS, 1950, p. 281 [**Stropheodonta subinterstrialis seretensis* KOZŁOWSKI, 1929, p. 96; OD] [=*Mesodouviella* HARPER & BOUCOT, 1978, p. 124 (type, *Mclearnites invasor* JOHNSON, 1970a,

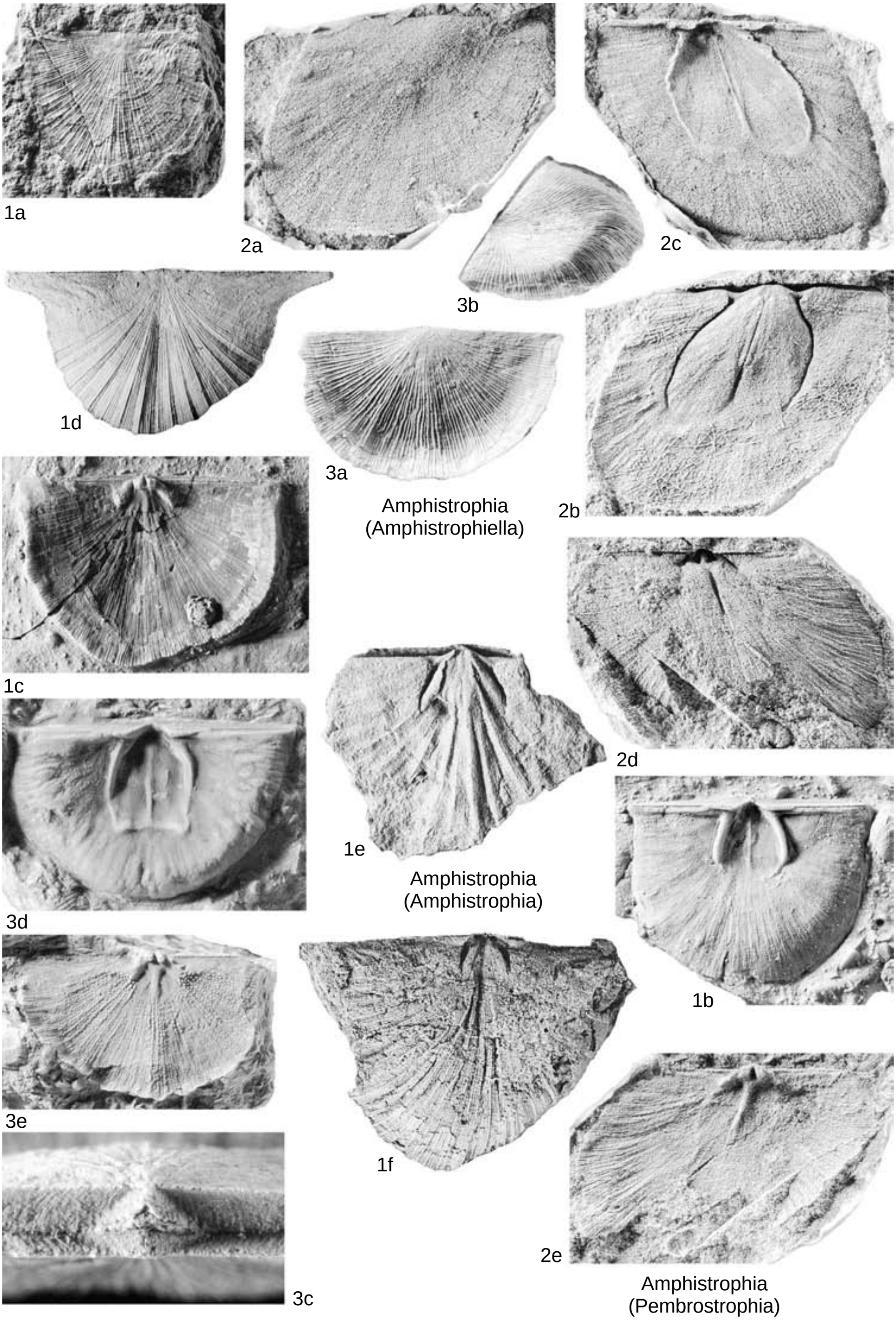

FIG. 162. Amphistrophiidae (p. 260).

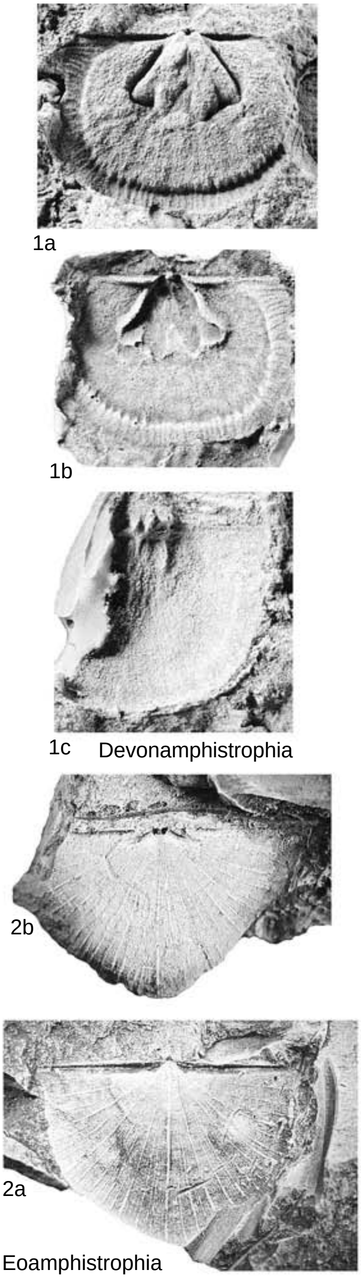

Fig. 163. Amphistrophiidae (p. 260).

p. 118; OD); ?*Planodouvillina* Harper & Boucot, 1978, p. 145 (type, *P. cortezi;* OD; *Eurekaspirifer pinyonensis* Zone (Emsian), Cortez Mountains, Nevada)]. Strongly to gently concavoconvex profile; unequally parvicostellate ornament; small interarea with pseudodeltidium, small chilidium; denticles along half to two-thirds of hinge line; straight or slightly curved muscle-bounding ridges to subtriangular ventral muscle field, open anteriorly; cardinal process posteroventrally to posteriorly directed; short thin divergent socket plates; weak curved dorsal muscle-bounding ridges; dorsal side septa usually absent; dorsal subperipheral rim variably developed. *Silurian (Sheinwoodian)–Devonian (Eifelian):* cosmopolitan.——Fig. 164,*1a–d.* **M. subinterstrialis seretensis* (Kozłowski), Bogdanovka Beds, Bogdanovka, Podolia, Ukraine; *a–c,* neotype, ventral, dorsal, lateral views of conjoined valves, CNIGR 33/11475, ×1.5; *d,* ventral interior, CNIGR 32/11475, ×1.5 (Bassett, new).——Fig. 164,*1e. M. s. subinterstrialis,* Mitkov Beds, Borshchov Stage, Lochkovian, Lanovtsy, Podolia, Ukraine; dorsal interior, CNIGR 30/11475, ×1.5 (Bassett, new).——Fig. 164,*1f–h. M. invasor* (Johnson), *Acrospirifer kobehana* Zone, Emsian, Sulphur Spring Range, Great Basin, Nevada; *f,g,* holotype, ventral exterior, interior, USNM 156938, ×1.5; *h,* dorsal interior, USNM 156941, ×1.5 (Johnson, new).

Desistrophia Talent in Gratsianova, Shishkina, & Talent, 1988, p. 94 [**Maoristrophia papilio* Strusz, 1983, p. 165; OD]. Transverse outline; concavoconvex profile with large ventral fold, dorsal sulcus; similar to *Maoristrophia* but with parvicostellate ornament, narrower triangular ventral muscle field with shorter, smaller socket ridges which, with cardinal process lobes, situated on notothyrial platform; dorsal muscle-bounding ridges more sharply developed, pair of short transmuscle ridges present in gerontic specimens. *Silurian (Wenlock, ?Ludlow):* Australasia.——Fig. 165,*2a–c.* **D. papilio* (Strusz), Canberra Formation, Wenlock, Canberra, Australian Capital Territory, Australia; *a,* latex cast of ventral exterior, CPC 21488, ×4; *b,* latex cast of ventral interior, CPC 21480, ×4; *c,* holotype, latex cast of dorsal interior, CPC 21485, ×4 (Strusz, new).

Eomaoristrophia Ushatinskaya in Ushatinskaya & Alekseeva, 1983, p. 38 [**E. kobdensis;* OD]. Similar to *Maoristrophia* but with cardinal process on posterior part of notothyrial plate between two socket ridges, with no trace of dorsal transmuscle septa or subperipheral ridge. *Silurian (?Wenlock, Ludlow):* Mongolia.——Fig. 164,*3a,b.* **E. kobdensis,* Wenlock–Ludlow, Buliantu-Gol River, western Mongolia; *a,* holotype, internal mold of ventral valve, PIN 3950/1, ×2; *b,* internal mold of dorsal valve, PIN 3950/3, ×1 (Ushatinskaya & Alekseeva, 1983).

Gladiostrophia Havlíček, 1967, p. 141 [**Leptaena verneuili* Barrande, 1848, p. 219; OD]. Large; strongly concavoconvex profile; strong, coarse, uniform costellate ornament; subtriangular ventral muscle field with strong straight bounding ridges posterolaterally only; erect cardinal process lobes directed ventroposteriorly; prominent curved dorsal muscle-bounding ridges posterolaterally; weak dorsal median septum. *Silurian (Ludlow)–Devonian*

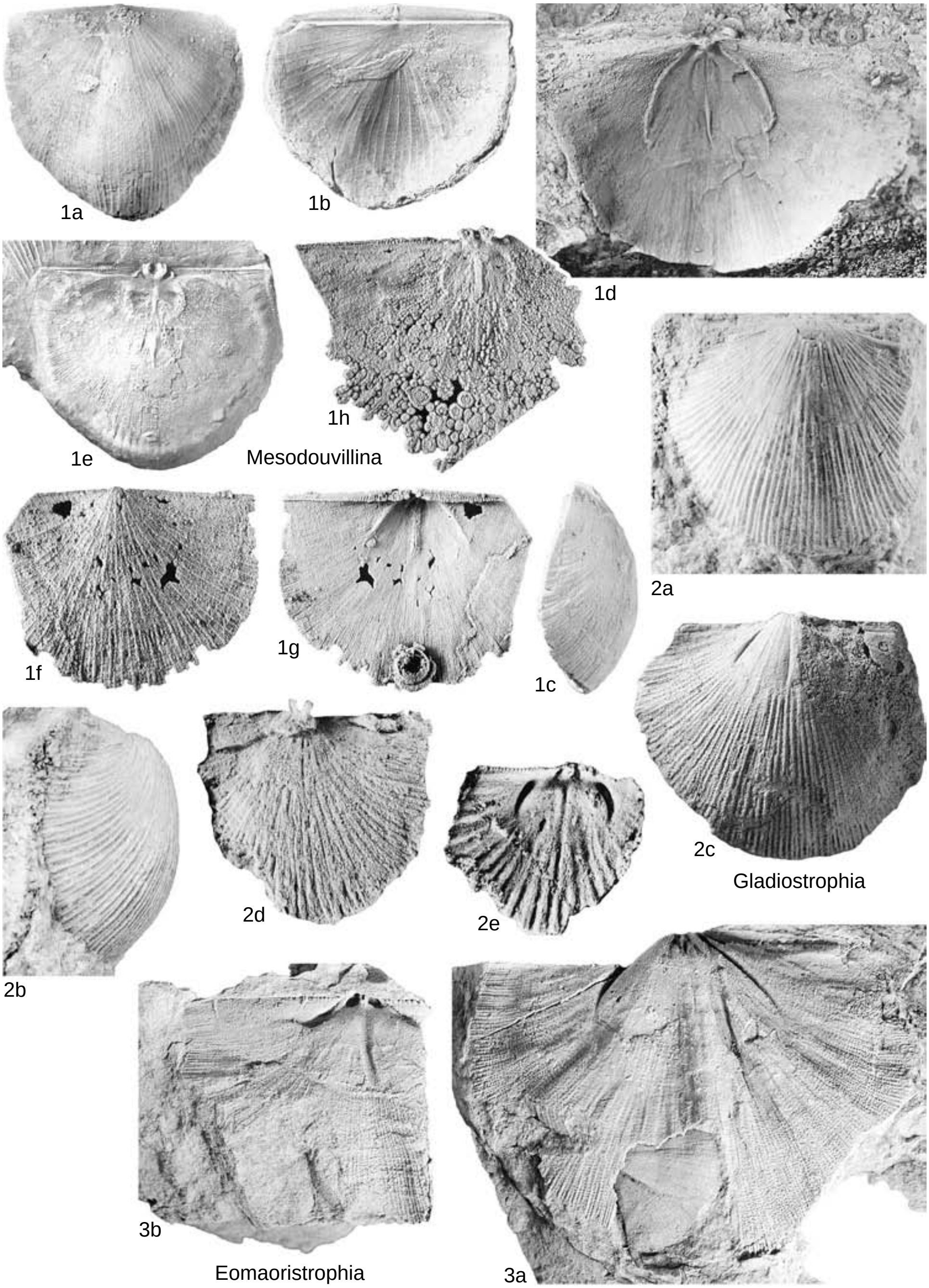

FIG. 164. Amphistrophiidae (p. 260–264).

(Emsian): Europe, Asia.——FIG. 164,*2a–e.* **G. verneuili* (BARRANDE), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,b,* ventral, lateral views of ventral exterior, BMNH BB 54620, ×1 (new); *c,* ventral interior, OMR VH 411a, ×1; *d,* dorsal external mold, OMR VH 410a,

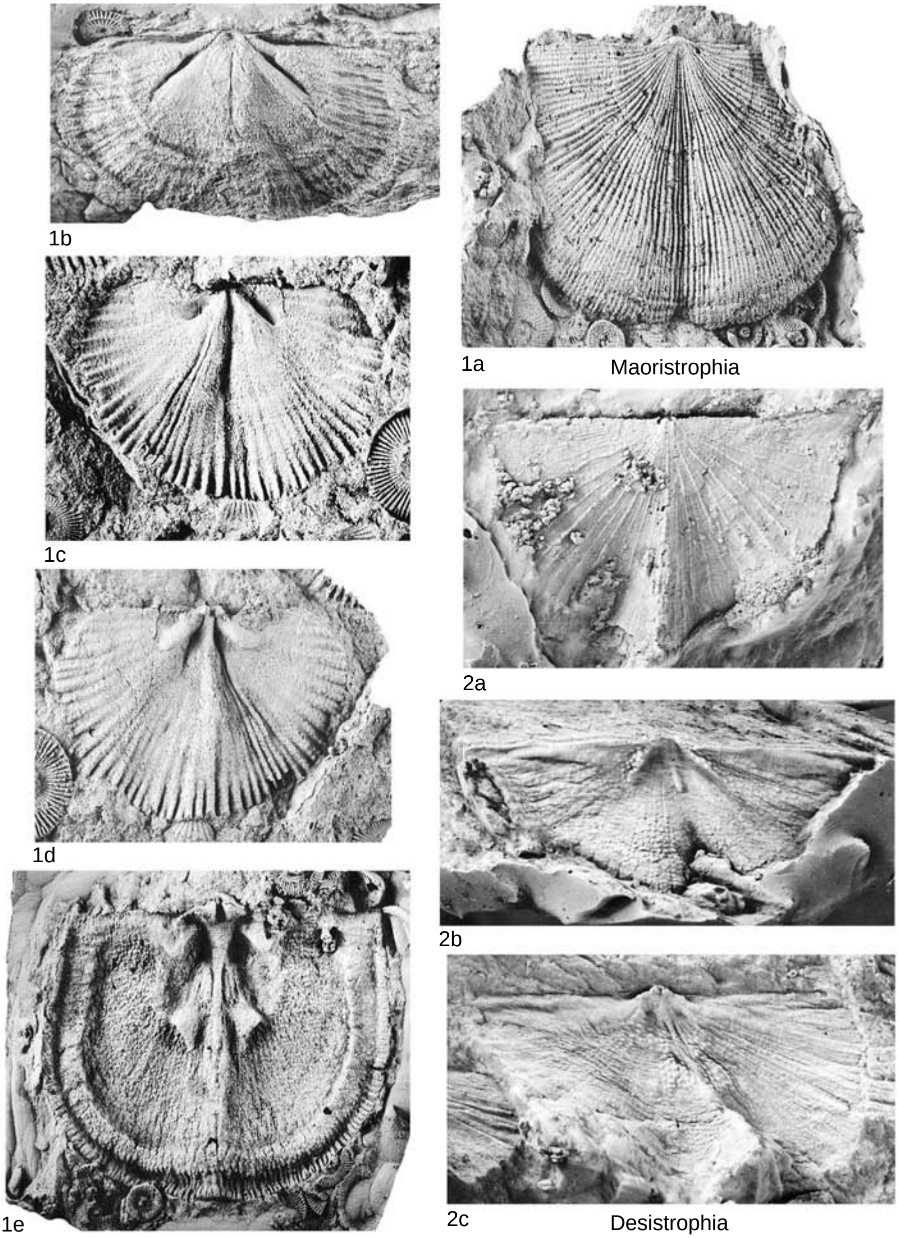

FIG. 165. Amphistrophiidae (p. 262–266).

×1.5; *e,* dorsal internal mold, OMR VH 410c, ×2 (Havlíček, 1967).

?Jakutostrophia MANANKOV, 1991, p. 65 [**J. undata;* OD]. Distinctive ornament of strong raised costellae with fine radial costellae, with rugae interrupted by primary costellae; interiors poorly known, thus familial position uncertain. *Devonian (Eifelian):* Asia.——FIG. 166,*4a,b.* **J. undata,* Middle Sakin Formation, Eifelian, River Khobochalo, eastern Yakutia, Russia; *a,* partly exfoliated

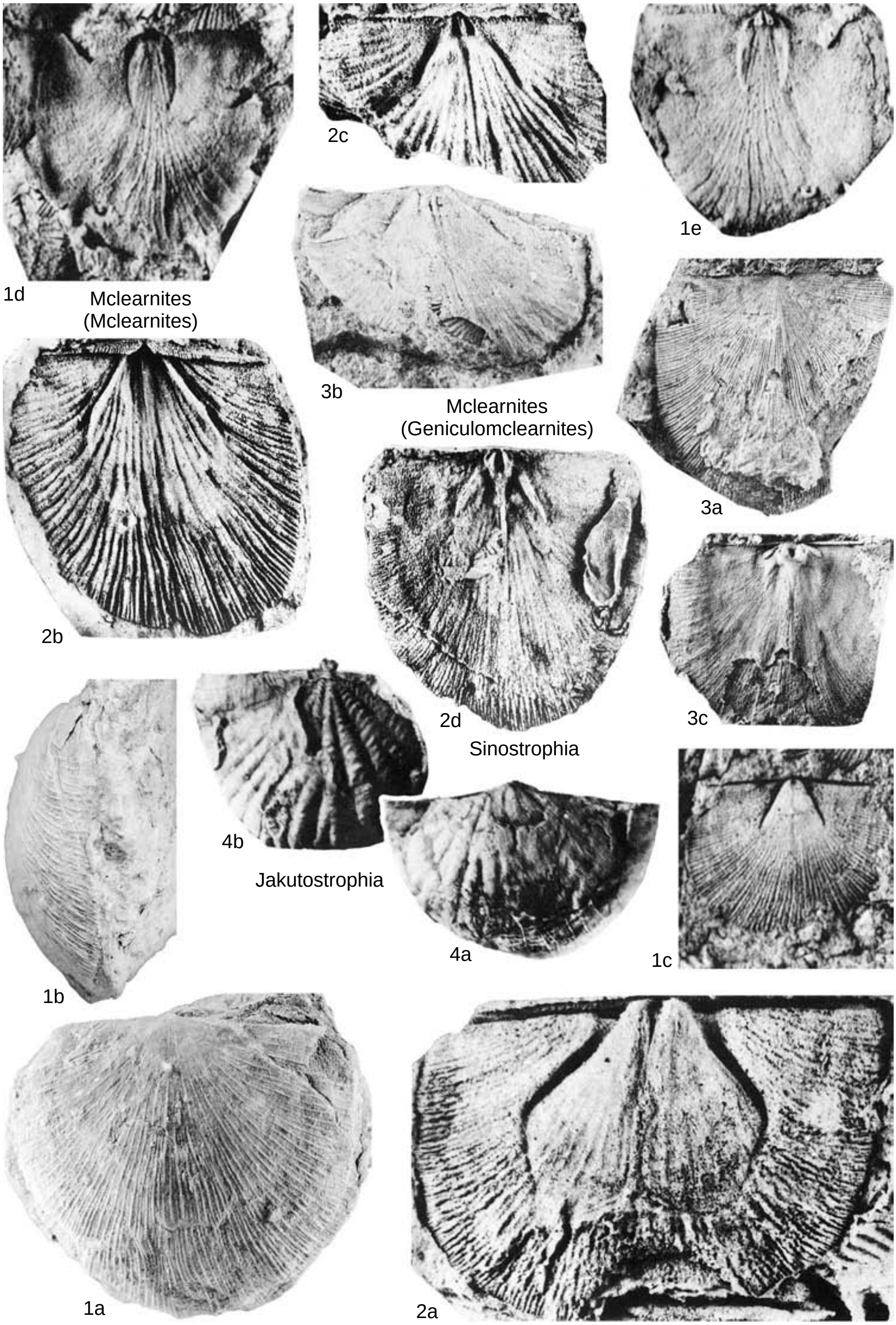

FIG. 166. Amphistrophiidae (p. 264–266).

ventral valve, CNIGR 4114/634, ×1.5; *b,* holotype, partly exfoliated dorsal valve, CNIGR 4114/633, ×1 (Manankov, 1991).

Maoristrophia Allan, 1947, p. 440 [**M. neozelanica;* OD]. Semielliptical, planoconvex profile with ventral fold, dorsal sulcus; ornament costellate; denticles along less than half hinge line; triangular ventral muscle field bounded posterolaterally with largely straight ridges that curve around a short distance anteriorly; muscle field poorly impressed anteriorly; cardinal process on hinge line, strong, ventrally directed, joined to posterior end of median ridge, which extends for at least half valve length; strong socket ridges that curve, extending laterally for variable distance; dorsal transmuscle ridges, subperipheral ridge variably developed in both valves, more common in gerontic specimens. *Devonian (Emsian):* Australasia, Mongolia.——Fig. 165,*1a–e.* **M. neozelanica,* Reefton Beds, Emsian, Lankey Creek, Reefton, New Zealand; *a,* latex cast of dorsal exterior, USNM 153136, ×1.5; *b,* internal mold of ventral valve, USNM 153137, ×1.25; *c,d,* internal mold of dorsal valve, latex cast, USNM 153138, ×2; *e,* latex cast of dorsal internal mold, USNM 153135, ×1.25 (Johnson, new).

Mclearnites Caster, 1945, p. 319, *nom. nov. pro Mclearnia* Caster, 1939, p. 28, *non* Crickmay, 1930 [**Brachyprion mertoni* McLearn, 1924, p. 61; OD] [=*Mclearnitesella* Harper & Boucot, 1978, p. 131 (type, *Mclearnites (M.) hickoxi;* OD)]. Concavoconvex profile similar to *Mesodouvillina;* ornament usually uniformly costellate; denticles along one-third to one-half of hinge line; subtriangular ventral muscle field with strong bounding ridges posterolaterally only; open anteriorly; relatively small, erect cardinal process; strong, slightly curved dorsal valve muscle-bounding ridges. *Silurian (?Telychian, Wenlock)–Devonian (Lochkovian):* cosmopolitan.

M. (**Mclearnites**). Similar to *M. (Geniculomclearnites)* but without dorsal geniculation. *Silurian (?Telychian, Wenlock)–Devonian (Lochkovian):* cosmopolitan.——Fig. 166,*1a–c.* **M. (M.) mertoni* (McLearn), Stonehouse Formation, Přídolí–Lochkovian, Arisaig, Nova Scotia, Canada; *a,* ventral internal mold, GSC 19341, ×1; *b,c,* dorsal internal mold, latex cast, GSC 19344, ×1.5 (Harper & Boucot, 1978).——Fig. 166,*1d,e. M. (M.) newsomensis* (Foerste), Waldron Shale, Wenlock, Newsom, Nashville, Tennessee; ventral, lateral views of ventral exterior, BMNH BB 31482, ×1.5 (new).

M. (**Geniculomclearnites**) Harper & Boucot, 1978, p. 133 [**M. (G.) genicularia;* OD]. Similar to *M. (Mclearnites)* but with dorsally directed geniculate anterior margins; denticles slightly more than halfway along hinge line. *Devonian (Lochkovian):* North America.——Fig. 166,*3a–c.* **M. (G.) genicularia,* Dalhousie Formation equivalent, Lochkovian, New Brunswick, Canada; *a,* dorsal external mold, USNM 220606, ×1.5; *b,* ventral internal mold, USNM 220607, ×1.5; *c,* latex cast of dorsal internal mold, USNM 220605, ×1.5 (Harper & Boucot, 1978).

Sinostrophia Hamada, 1971, p. 52 [**S. kondoi;* OD]. Moderately concavoconvex profile; ornament coarsely costellate (although can become abruptly fine near valve margin); denticulate along entire hinge line; prominent straight bounding ridges posterolateral to bilobed ventral muscle field, open anteriorly; relatively small erect cardinal process lobes; socket ridges abbreviated, located posterolateral to cardinal process lobes; dorsal muscle-bounding ridges mostly straight posterolaterally. *Devonian (Pragian–Emsian):* China.——Fig. 166,*2a–d.* **S. kondoi,* Huolongmen Formation, lower Emsian, Jinshui, Lesser Khingan District, Heilongjiang, northeastern China; *a,* holotype, ventral interior mold, 130KE1, repository unknown, ×1.5; *b,* latex cast of ventral interior, 220KG1, repository unknown, ×1; *c,* dorsal interior mold, O56HF3, repository unknown, ×1; *d,* latex cast of dorsal interior, 223KGI, repository unknown, ×1 (Hamada, new).

Family DOUVILLINIDAE Caster, 1939

[*nom. transl.* Sokolskaya, 1960, p. 214, *ex* Douvillininae Stainbrook, 1945, p. 20, *nom. transl. ex* tribe Douvillinini Caster, 1939, p. 70] [=Telaeoshaleriidae Harper & Boucot, 1978, p. 153]

Hinge line denticulate; lacking dental plates [except *Douvillinella (Crinistrophia)*]; ventral muscle field variable, subcircular to bilobed, well impressed, usually with bounding ridges laterally, anteriorly; cardinal process lobes directed ventroposteriorly, posteriorly; socket ridges present but small; dorsal side septa. *Silurian (Ludlow)–Devonian (Frasnian).*

Subfamily DOUVILLININAE Caster, 1939

[*nom. transl.* Stainbrook, 1945, p. 20, *ex* Douvillinini Caster, 1939, p. 70]

Relatively transverse ventral muscle field elevated, with prominent overhanging muscle-bounding ridges meeting anteriorly; dorsal median septum bifurcates anteriorly. *Devonian (?Eifelian–Frasnian).*

Douvillina Oehlert, 1887b, p. 1282 [**Orthis dutertrei* Murchison, 1840, p. 253 (attributed to de Verneuil by Oehlert); OD]. Strongly concavoconvex profile; ornament parvicostellate; denticles over most of hinge line; elevated, very curved bounding ridges surrounding distinctive subcircular but relatively small ventral muscle field; erect cardinal process lobes; diverging dorsal side septa with cavity between them anteriorly. *Devonian (Frasnian):* cosmopolitan.——Fig. 167,*1a–d.* **D. dutertrei* (Murchison), Ferques Limestone Forma-

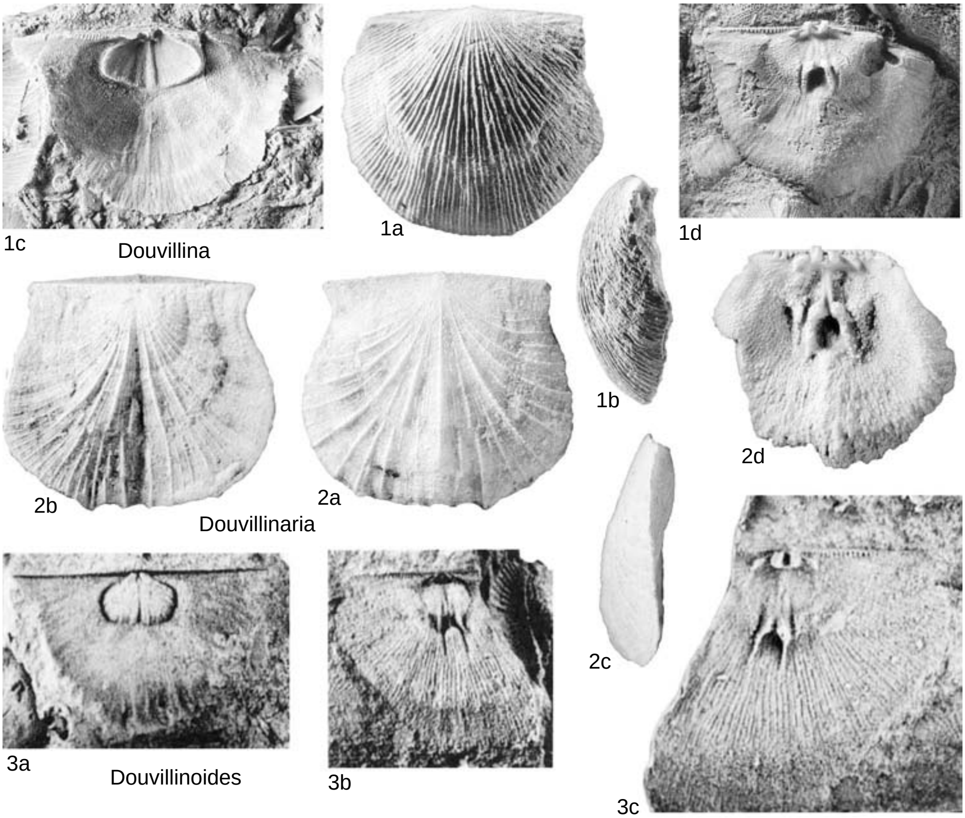

FIG. 167. Douvillinidae (p. 266–267).

tion, Frasnian, Ferques, Boulonnais, France; *a,b,* ventral, lateral views of conjoined valves, BMNH BC 13416, ×1.5; *c,* ventral interior, BMNH BC 13417, ×1.5; *d,* dorsal interior, BMNH BC 13418, ×1.5 (new).

Douvillinaria STAINBROOK, 1945, p. 22 [**Stropheodonta variabilis* CALVIN, 1878, p. 727; OD]. Biconvex profile, but with ventral fold, dorsal sulcus; ornament of curving unequal parvicostellae to uniform costellae; denticles along entire hinge line; elevated bounding ridges around relatively small subcircular to bilobed ventral muscle field; erect ventrally, posteriorly directed cardinal process lobes; dorsal myophragm bifurcating anterior to two septa with hollow between them. *Devonian (?Eifelian, Givetian–Frasnian):* North America, ?Spain.——FIG. 167,*2a–d.* **D. variabilis* (CALVIN), Independence Shale, Frasnian, Middle Amana, Iowa; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH BB 57970, ×3; *d,* dorsal interior, BMNH BB 57971, ×3 (new).

Douvillinoides HARPER & BOUCOT, 1978, p. 152 [**Douvillinella? crickmayi* PEDDER, 1960, p. 212; OD]. Similar to *Douvillinaria* but profile thin, gently resupinate without fold or sulcus; ornament usually uniformly costellate. *Devonian (Frasnian):* North America.——FIG. 167,*3a–c. D.* sp., Chemung Group, Frasnian, Nichols, New York; *a,* ventral internal mold, USNM 220633, ×1; *b,* ventral internal mold, ×1; *c,* ventral latex cast, USNM 220634, ×1.5 (Harper & Boucot, 1978).

Subfamily PROTODOUVILLININAE
Harper & Boucot, 1978

[Protodouvillininae HARPER & BOUCOT, 1978, p. 138] [=Douvinellinellinae HARPER & BOUCOT, 1978, p. 146; Teichostrophiinae HARPER & BOUCOT, 1978, p. 43]

Maximum width of dorsal muscle field near posterior of valve, in contrast to Leptodontellinae; ventral muscle field strongly impressed, usually semielliptical, but with tendency to elongation in some genera, bounded laterally by muscle-bounding ridges in most genera, however, these bounding ridges not elevated, unlike Douvillininae; dorsal side septa mostly straight but sometimes diverging anteriorly; second pair of side septa rarely developed. *Silurian (Ludlow)–Devonian (Frasnian).*

Protodouvillina Harper & Boucot, 1978, p. 138 [**Strophomena inaequistriata* Conrad, 1842, p. 254; OD]. Profile strongly concavoconvex; unequally parvicostellate ornament; ventral muscle field bounded by short but strong curved ridges posterolaterally, with anterior margin open; small erect cardinal process lobes; dorsal myophragm continuous with base of cardinal process continuing anteriorly, bifurcating into pair of short but prominent side septa that may be relatively straight or may curve inward. *Silurian–Devonian (Přídolí–Givetian):* cosmopolitan.——Fig. 168,*1a–c*. **P. inaequistriata* (Conrad), Hamilton Group, Eifelian, Moscow, Livingston, New York; *a,* ventral exterior, AMNH 37215, ×2; *b,* ventral interior, AMNH 37218, ×2; *c,* dorsal interior, AMNH 37217, ×2 (new).

Bojodouvillina Havlíček, 1967, p. 171 [**Leptaena phillipsii* Barrande, 1848, p. 226; OD]. Profile moderately concavoconvex; unequally parvicostellate ornament; denticles along two-thirds of hinge; ventral diductor field separated by well-developed median septum; muscle-bounding ridges poorly developed around bilobed muscle field; erect, posteriorly directed cardinal process; dorsal interior relatively simple, with pair of short, straight side septa; curved dorsal muscle-bounding ridges weakly developed; no dorsal median septum. *Devonian (Pragian–Emsian):* Europe, ?Mongolia.——Fig. 168,*2a–d*. **B. phillipsii* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* lectotype, ventral interior, NM L6747, ×1.5; *b,* conjoined valves showing dorsal internal mold, OMR VH 444a, ×1.5; *c,* damaged conjoined valves, including cardinal process, OMR VH 444b, ×1.5; *d,* ventral internal mold, Zlíchov Limestones, Emsian, U kaplicky, Praha-Hlubocepy, Bohemia, Czech Republic, OMR VH 93a, ×1.5 (Havlíček, 1967).

?Contradouvillina Gratsianova, 1975, p. 48 [**C. salairica;* OD]. Transverse, gently planoconvex profile, anteriorly geniculate ventrally; elongate ventral muscle field with diductors close together, enclosing adductor scars; dorsal interior poorly known, hence generic status and family position uncertain. *Devonian (Pragian):* Asia, Malobachat Beds, Mount Gurevska region, northeastern Salair, Altai-Sayan, Russia.

Cymostrophia Caster, 1939, p. 39 [**Leptaena stephani* Barrande, 1848, p. 230; OD] [=*Corrugatella* Khalfin, 1948, p. 236, obj.]. Variable outline; variably convex profile, geniculate ventral valve; dorsal valve initially flat, geniculate anteriorly; distinctive ornament of rugae interrupted by primary costellae; relatively large, suboval ventral muscle field bounded by low ridges posterolaterally only; ventral myophragm developed; small, erect cardinal process lobes; dorsal muscle field bounded posterolaterally by low ridges; one pair of low dorsal side septa, small median ridge in valve center. *Silurian (Ludlow)–Devonian (Givetian):* cosmopolitan.

- **C.** (**Cymostrophia**). Transverse outline; strongly convex profile; ornament of very pronounced interrrupted rugae. *Devonian (Lochkovian–Givetian):* cosmopolitan.——Fig. 168,*3a–c*. **C. (C.) stephani* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* ventral exterior, NM CF382, ×1 (Havlíček, 1967); *b,* ventral interior, BMNH BC 13007, ×1.5 (new); *c,* dorsal interior, OMR VH 398a, ×1 (Havlíček, 1967).
- **C.** (**Protocymostrophia**) Harper & Boucot, 1978, p. 127 [**Strophomena ivanensis* Barrande, 1879, pl. 52, fig. IV 1–4, 9–12; OD]. Similar to *C. (Cymostrophia)* but having suboval rather than transverse outline, gently concavoconvex profile, less pronounced interrupted rugae in ornament. *Silurian (Ludlow)–Devonian (Eifelian):* cosmopolitan.——Fig. 168,*4a–c*. **C. (P.) ivanensis* (Barrande), Kotys Limestone, Lochkovian, Svaty Jan pod Skalou, Bohemia, Czech Republic; *a,* ventral exterior, OMR VH 439a, ×1.5; *b,* ventral interior, OMR VH 439d, ×2; *c,* dorsal internal mold, OMR VH 439c, ×1.5 (Havlíček, 1967).

Douvillinella Spriestersbach, 1925, p. 432 [**Stropheodonta filifer* Schmidt, 1913, p. 313; OD; locality: *cultrijugatus* zone (Eifelian), ?Attendorn-Elsper, Doppelmulde, Germany] [=*Fibulistrophia* García-Alcalde, 1972, p. 43 (type, *F. fibula;* OD)]. Profile gently resupinate to gently concavoconvex; ornament uniformly costellate; denticulate along most of hinge line; bilobed ventral diductor muscle field widely separated by broad triangular space, bounded laterally by faint muscle-bounding ridges that are sometimes also present anteriorly; socket ridges long, widely divergent, not joined to cardinal process lobes; pair of long, thin, curved dorsal side septa; short dorsal median ridge may be developed centrally; subperipheral rims variably present in both valves. *Devonian (Emsian–Eifelian):* Europe.

- **D.** (**Douvillinella**). Similar to *D. (Crinistrophia)* but with muscle-bounding ridges always developed, although sometimes faint. *Devonian (Emsian–Eifelian):* Europe.——Fig. 169,*1a–d*. *D. (D.) fibula* (García-Alcade), Moniello Formation, Emsian, Les Areñes, Avilés, Asturias, Spain; *a,b,* holotype, ventral, dorsal views of conjoined valves, DPO 2489, ×1.5; *c,* ventral interior, DPO 2546, ×2; *d,* dorsal interior, DPO 2563, ×2 (García-Alcade, 1972).
- **D.** (**Crinistrophia**) Havlíček, 1967, p. 134 [**C. crinita;* OD]. Similar to *D. (Douvillinella)* but gently concavoconvex profile; ornament unequally parvicostellate to costellate; short dental plates may be developed; relatively large bilobed ventral muscle field without bounding ridges;

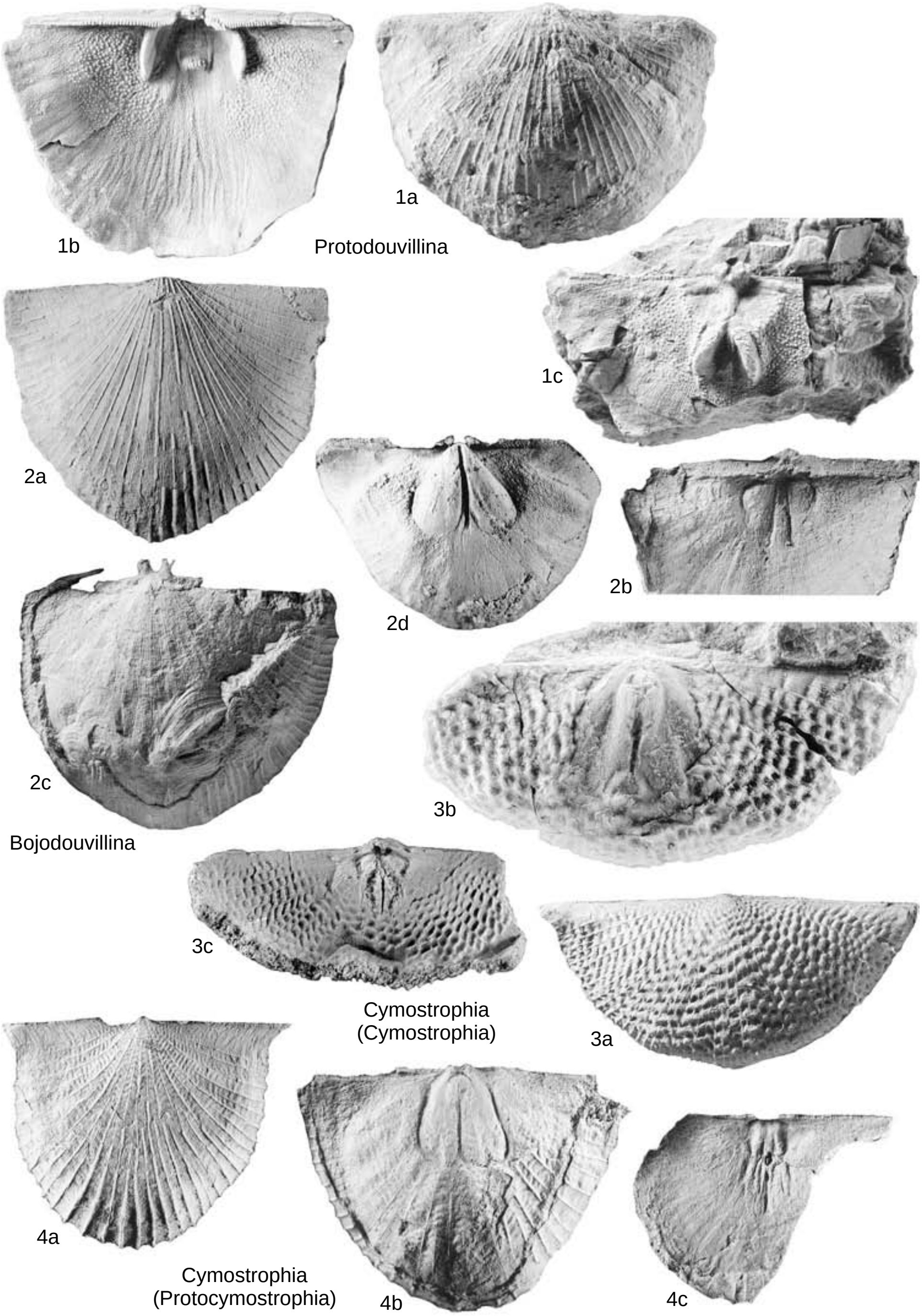

FIG. 168. Douvillinidae (p. 268).

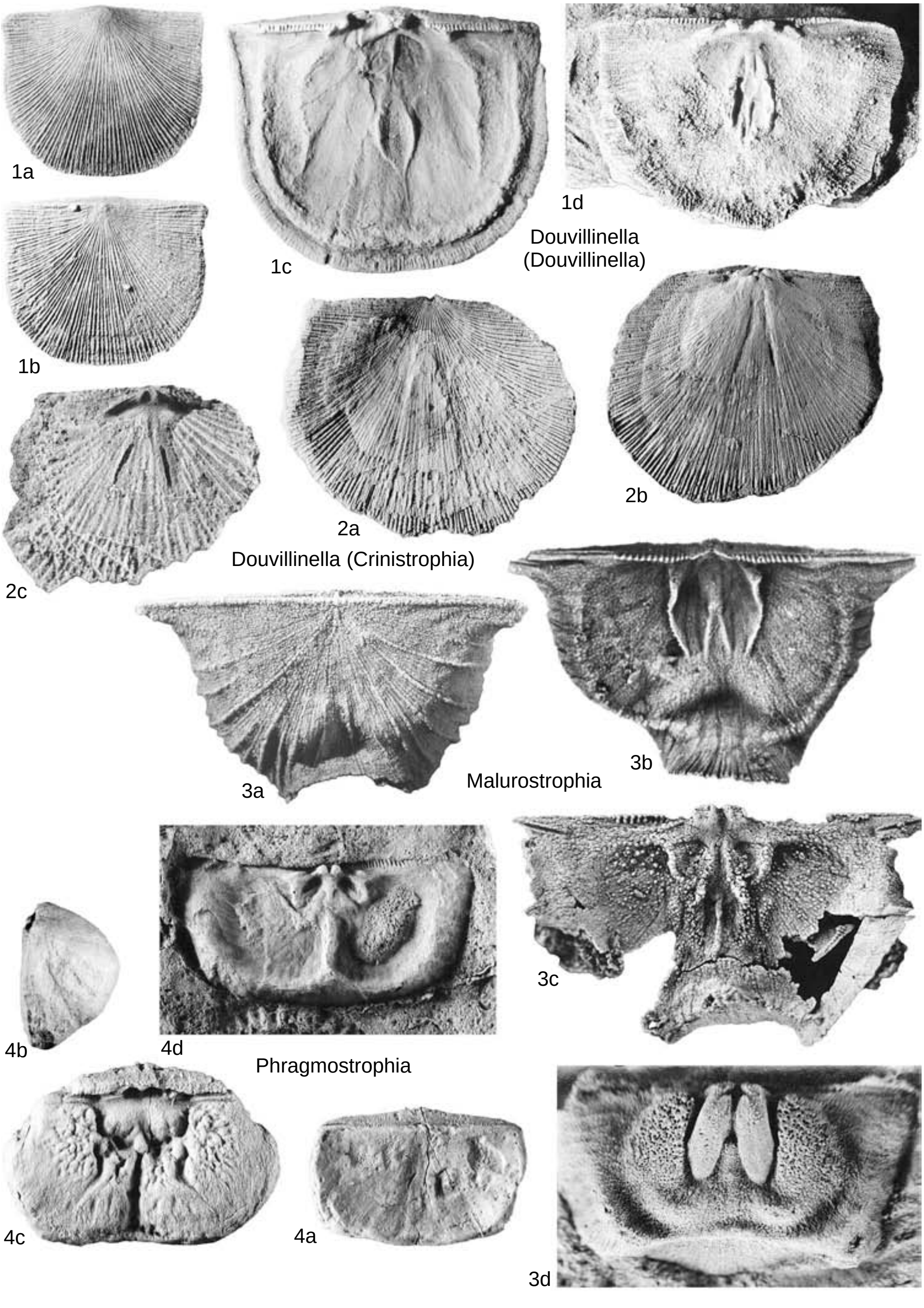

FIG. 169. Douvillinidae (p. 268–274).

short erect cardinal process with prominent socket ridges flaring anterolaterally; short, straight dorsal transmuscle septa variably developed. *Devonian (Emsian):* Europe.——FIG. 169,*2a–c. *D. (C.) crinita,* Zlíchov Limestone, Emsian, Praha-Hlubocepy, Bohemia, Czech Republic; *a,b,* ventral interior, exterior molds, OMR VH 405c, ×1.5; *c,* dorsal interior mold, OMR VH 406b, ×3.7 (Havlíček, 1967).

Hercostrophia Williams, 1950, p. 277 [**H. alpenensis;* OD]. Gently to moderately concavoconvex profile; unequally parvicostellate ornament; bilobed to subtriangular ventral muscle field bounded by two pairs of lateral, median bounding ridges sometimes united posteriorly to form arch; dorsal muscle field not situated on elevated platform, bounding ridges absent; pair of strong dorsal side septa. *Devonian (Givetian–Frasnian):* North America, Australia.——Fig. 170,*1a,b.* **H. alpenensis,* Alpena Limestone, Givetian, Alpena, Michigan; *a,* ventral interior, USNM 116017, ×2; *b,* dorsal view of conjoined valves, USNM 116018, ×2 (Williams, 1953a).——Fig. 170,*1c. H.* sp., Givetian, New York; dorsal interior, ×2 (Williams, 1953a).

Malurostrophia Campbell & Talent, 1967, p. 309 [**M. flabellicauda;* OD] [=*Sinoshaleria* Xian in Xian & Jiang, 1978, p. 268 (type, *S. guangshunensis;* OD)]. Profile gently resupinate, geniculate; quadrate outline, indented anterior margin; ornament unequally parvicostellate; ventral muscle field bilobed, elongate, bounded laterally by subparallel but slightly curved ridges; myophragm well developed, bifurcating anteriorly; ventral subperipheral rim; large, erect, posteriorly directed cardinal process lobes; dorsal muscle field bounded laterally, posteriorly by ridges; one pair of dorsal side septa, additional pair sometimes developed laterally; short dorsal median ridge developed centrally, sometimes extending anteriorly. *Devonian (Emsian–Givetian):* Australia, China.——Fig. 169,*3a–c.* **M. flabellicauda, Receptaculites* Limestone, Emsian–Eifelian, Bloomfield Station, Taemas, New South Wales, Australia; *a,* holotype, dorsal view of conjoined valves, ANU 14620, ×4; *b,* ventral interior, ANU 14987, ×4; *c,* dorsal interior, ANU 14983, ×4 (Campbell & Talent, 1967).——Fig. 169,*3d. M. guangshunensis* (Xian), Dushan Formation, Givetian, Tianqibao, Guangshun, Changshung County, Guizhou Province, China; holotype, ventral internal mold, GB 371, ×2 (Xian & Jiang, 1978).

Megastrophiella Harper & Boucot, 1978, p. 19 [**Stropheodonta iddingsi* Merriam, 1940, p. 79; OD]. Profile strongly concavoconvex; parvicostellate to costellate ornament; ventral muscle field bilobed to oval with weak bounding ridges mainly developed posterolaterally; central ventral median ridge present; cardinal process lobes posteriorly directed, not joined at their bases; socket ridges widely divergent, separate from cardinal process lobes; dorsal muscle field elevated on platform, with well-developed transmuscle septa, bounding ridges; central dorsal median septum extended anteriorly. *Devonian (Emsian–Eifelian):* North America.——Fig. 170,*2a–f.* **M. iddingsi* (Merriam), *Spirifer pinyonensis* Zone, lower Nevada Formation, Emsian, Lone Mountain, Roberts Mountains, Nevada; *a,b,* holotype, ventral, posterior views of conjoined valves, USNM 96370, ×1.5; *c,d,* ventral, posterior views of ventral internal mold, USNM 156961, ×1.5; *e,f,* dorsal internal mold, latex cast, USNM 156962, ×2 (Johnson, new).

?Moravostrophia Havlíček, 1962, p. 471 [**Strophomena interstrialis moravica* Šmycka, 1897, p. 19; OD]. Small shell with subrectangular outline; concavoconvex profile; parvicostellate ornament, sometimes with fine rugae between costellae; ventral interior unknown, hence queried familial assignment; cardinal process lobes separate, strongly posteriorly directed; socket ridges small, widely divergent; dorsal adductor muscle field weakly impressed with strong bounding ridges curved inward; short central dorsal median septum, with pair of short side septa between it and muscle field; dorsal subperipheral rim well developed. *Devonian (Givetian):* Europe.——Fig. 170,*4a–e.* **M. moravica* (Šmycka), Givetian Beds, Celechovice na Hané, Moravia, Czech Republic; *a,* lectotype, ventral exterior, Brno 10939, ×2; *b,c,* dorsal, ventral views of conjoined valves, OMR VH 522a, ×2; *d,* dorsal interior, Figner collection, ×2; *e,* enlargement of cardinalia, OMR VH 522b, ×4.5 (Havlíček, 1967).

Nadiastrophia Talent, 1963, p. 62 [**N. superba;* OD] [?=*Xenostrophia* Wang in Wang, Yu, & Wu, 1974, p. 37 (type, *Shaleria yukiangensis* Wang, 1956, p. 149; OD)]. Profile gently concavoconvex, sharply geniculate in both valves; ornament unequally parvicostellate; hinge line denticulate along most of width; bilobed ventral muscle field chiefly elongate; muscle-bounding ridges present laterally, sometimes weakly anteriorly; ventral subperipheral rim developed in gerontic specimens; erect, posteriorly directed cardinal process lobes; myophragm variably developed; dorsal side septa vary from strong to very weak; dorsal muscle field on elevated platform with short bounding ridges present posterolaterally; dorsal median septum variably developed centrally, occasionally anteriorly, but sometimes absent; variably developed dorsal subperipheral rim. *Devonian (Emsian–Eifelian):* Australasia, China, Canada.——Fig. 170,*3a,b.* **N. superba,* Kilgower Member, Tabberabbera Formation, Emsian, Mitchell River, south of Tabberabbera, Victoria, Australia; *a,* ventral internal mold, GSV 5889a, ×3; *b,* dorsal internal mold, GSV 56578a, ×3 (Harper & Boucot, 1978).——Fig. 170,*3c–f. N. yukiangensis* (Wang), Liujing Member, Yukiang Formation, lower Emsian, Liujing railway station, Hengxian County, southern Guangxi, China; *c,d,* dorsal, lateral views of conjoined valves, BMNH BC 12833, ×2; *e,* ventral interior, BMNH BC 12834, ×2; *f,* dorsal interior, NIGP 23618, ×2 (new).

Paucistrophia Wang & Zhu, 1979, p. 23 [**Radiomena concinnusa* Wang in Wang, Yu, & Wu, 1974, p. 38; OD]. Profile concavoconvex, geniculate; ornament unequally parvicostellate; hinge line denticulate over most of valve width; large bilobed ventral muscle field, with strong bounding ridges anterior from dental plates surrounding entire field; dorsal valve similar to *Nadiastrophia. Devonian (Emsian):* China.——Fig. 172,*2a,b.* **P. concinnusa* (Wang),

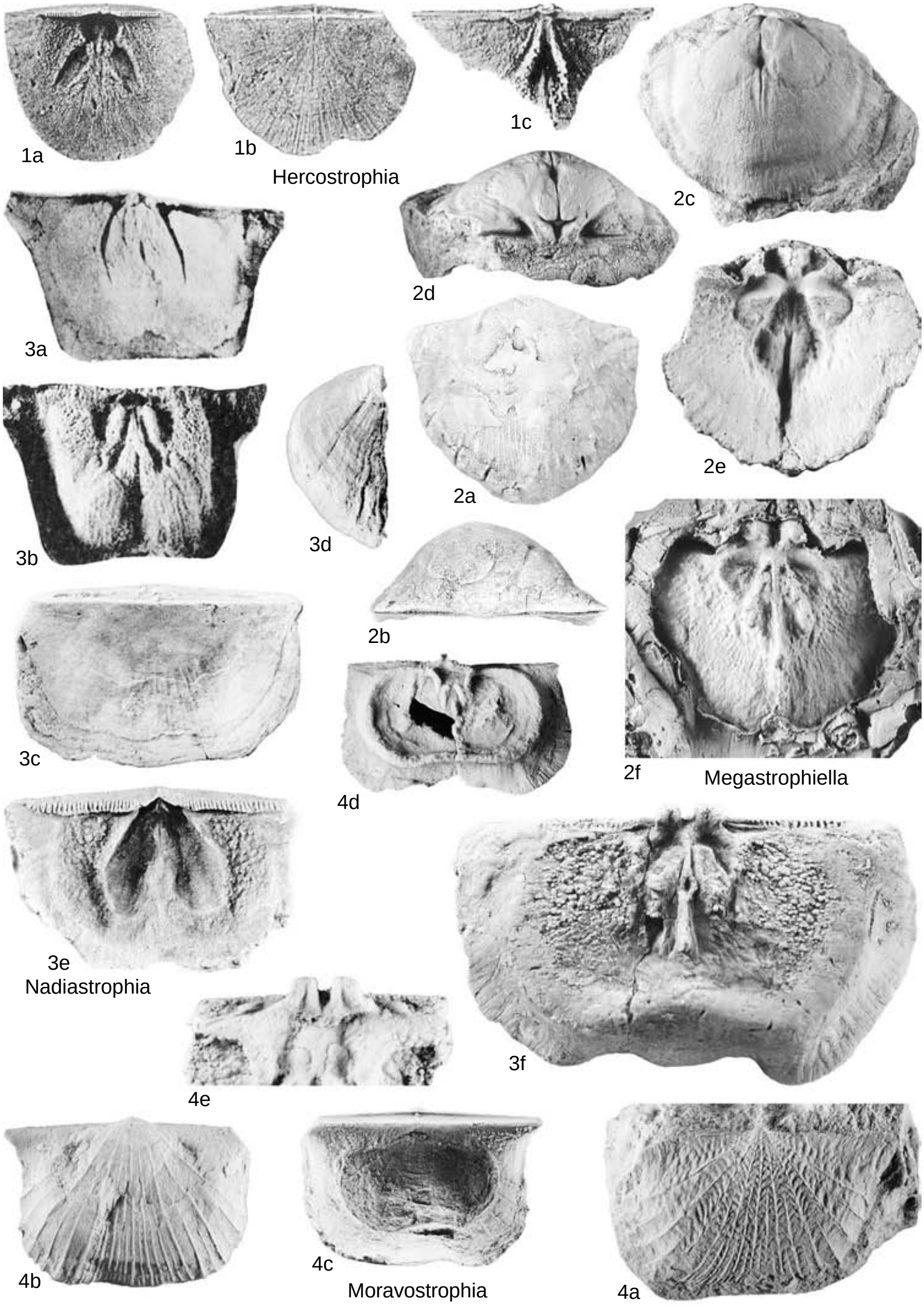

FIG. 170. Douvillinidae (p. 271).

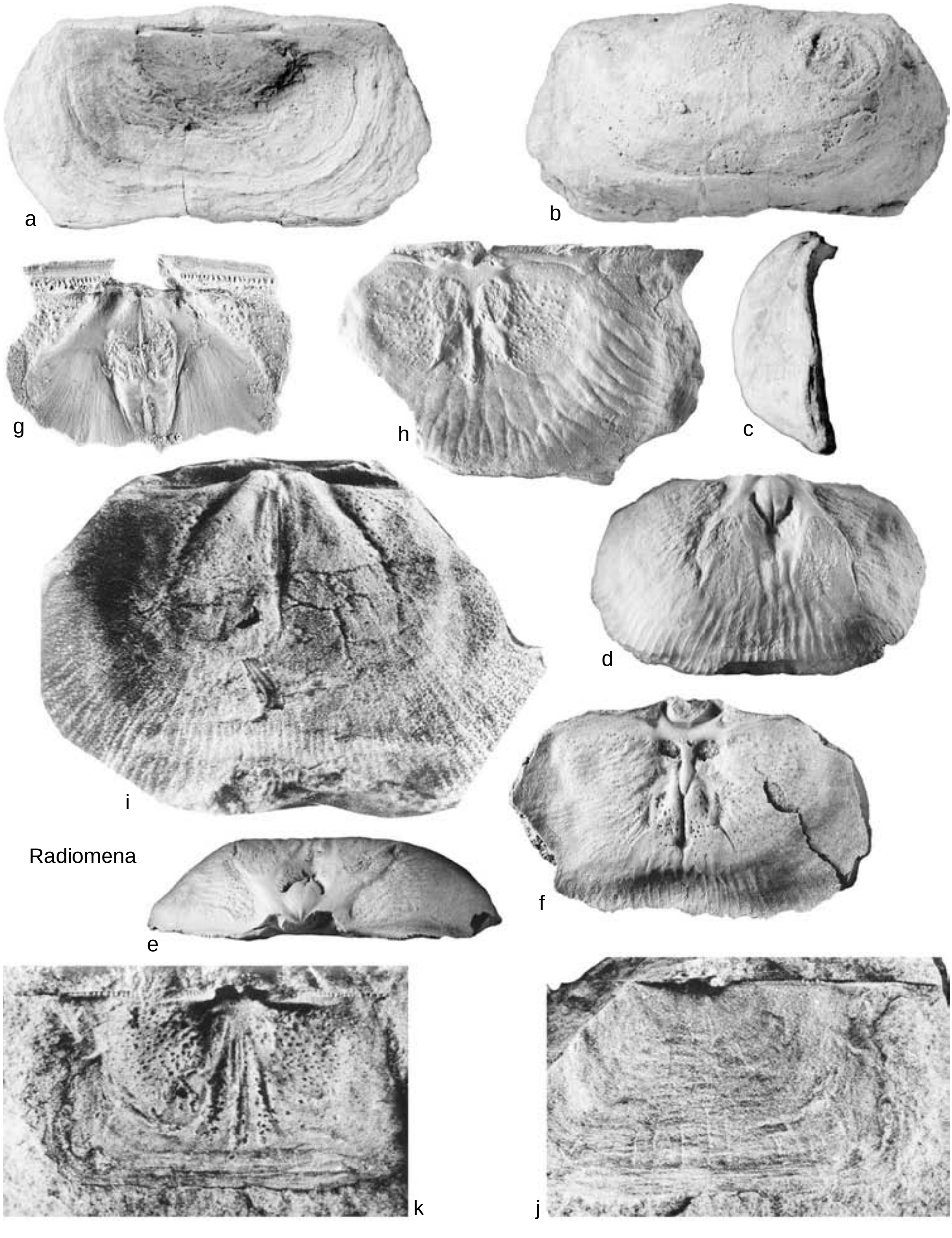

FIG. 171. Douvillinidae (p. 274).

Sipai Formation, upper Emsian, Sipai Village, Luzhai, Guangxi Province, China; holotype, ventral, dorsal views of internal mold of conjoined valves, NIGP 23657, ×1.5 (new).

Phragmostrophia HARPER, JOHNSON, & BOUCOT, 1967, p. 428 [**P. merriami;* OD]. Ventral valve strongly convex profile, dorsal valve flat; fine, unequally parvicostellate ornament; denticles along most of valve width; ventral muscle field bounded laterally by ridges; dorsal muscle field raised on elevated platform with bounding ridges; one or two pairs of dorsal side septa present; ventral dorsal median septum relatively strong, sometimes extending anteriorly to join subperipheral rim. *Devonian (Emsian–Eifelian):* North America, Russia.——FIG. 169,*4a–d*. **P. merriami, Eurekaspirifer pinyonensis* Zone, Emsian; *a,* dorsal view of conjoined valves, Sulphur Spring Range, ×2; *b,* lateral view of conjoined valves, northern Roberts Mountains, Eureka County, Nevada, USNM 140410, ×1.5; *c,* holotype, dorsal internal mold, Sulphur Spring Range, USNM 140409, ×2; *d,* latex cast of dorsal internal mold, Sulphur Spring Range, ×2 (Harper, Johnson, & Boucot, 1967).

Radiomena HAVLÍČEK, 1962, p. 471 [**Orthis irregularis* ROEMER, 1844, p. 75; OD] [=*Chuanostrophia* XIAN in XIAN & others, 1988, p. 207 (type, *C. scitula;* OD)]. Ventral valve moderately to strongly convex profile, dorsal valve first flat but geniculate anteriorly; unequally parvicostellate weak ornament; denticles along most of valve width; ventral muscle field weakly impressed anteriorly, bilobed diductor scars separated by low, wide myophragm; erect, posteriorly directed cardinal process lobes; dorsal muscle field bounded by low ridges; one pair of dorsal side septa present, anterior ends sometimes curve out laterally; weak dorsal median ridge developed centrally. *Devonian (Emsian–Givetian):* Europe, Asia.——FIG. 171*a–h*. **R. irregularis* (ROEMER); *a–c,* dorsal, ventral, lateral views of conjoined valves, Eifelian Beds, Gerolstein, BMNH BC 12831, ×2 (new); *d–f,* ventral, posterior, dorsal views of conjoined valves, Eifelian Beds, Eifel, Germany, SMF 19119, ×1 (Johnson, new); *g,* interior of incomplete ventral valve, Givetian, Celechovice na Hané, Moravia, Czech Republic, OMR VH 402a, ×1.6; *h,* dorsal interior, Givetian, Celechovice na Hané, Moravia, Czech Republic, OMR VH 404c, ×1.7 (Havlíček, 1967).——FIG. 171*i–k*. *R. scitula* (XIAN), Shiliangzi Member, Yangmaba Formation, upper Emsian, Jiangyou, Beichuan County, northern Sichuan Province, China; *i,* ventral internal mold, ×1; *j,k,* holotype, internal, external mold of dorsal valve, ×1.5 (Xian & others, 1988).

Taemostrophia CHATTERTON, 1973, p. 43 [**T. patmorei;* OD]. Alate, subquadrate outline; flat profile but with sharply geniculate margin; unequally parvicostellate ornament; variable ventral muscle field with bounding ridges directed toward center at first, then anteriorly flare out laterally before curving back to unite anteriorly; other specimens simply curving laterally, open anteriorly; adductor muscles entirely enclosed by diductors; erect cardinal process lobes directed ventrally or posteroventrally; dorsal muscle-bounding ridges strong both laterally and anteriorly; central dorsal median ridge present; one pair of dorsal side septa variably developed; similar to *Malurostrophia* but ventral muscle field less bilobed. *Devonian (Emsian–Eifelian):* Australia.——FIG. 172,*3a–c*. **T. patmorei,* Warroo Limestone, Emsian, Hume Park, Yass, New South Wales, Australia; *a,b,* holotype, ventral exterior, interior, ANU 18922, ×1.5; *c,* dorsal interior, ANU 18923e, ×2 (Campbell, new).

Teichostrophia HARPER, JOHNSON, & BOUCOT, 1967, p. 420 [**Strophomena lepis* BRONN, 1837, p. 87; OD] [?=*Ancylostrophia* HARPER, JOHNSON, & BOUCOT, 1967, p. 423 (type, *A. kondelensis;* OD)]. Outline subquadrate; ventral valve strongly convex profile, dorsal valve flat posteriorly, sharply geniculate, with raised interior subperipheral rim; ornament smooth or very faint unequal parvicostellae; bilobed ventral muscle field strongly impressed but without raised muscle-bounding ridges; socket ridges very small; dorsal muscle field impressed onto elevated platform with encircling muscle-bounding ridges, variably developed side septa; short dorsal median septum sometimes developed anteriorly. *Devonian (Emsian–Givetian):* Europe, Asia.——FIG. 172,*1a–d*. **T. lepis* (BRONN), Siegenian, Emsian Beds, Gerolstein, Eifel, Germany; *a,* ventral view of conjoined valves, BMNH BC 12830, ×2; *b,* dorsal view of conjoined valves, BMNH BC 12828, ×2; *c,* internal mold of ventral valve, BMNH BC 12829, ×2 (new); *d,* internal mold of conjoined valves, USNM 145566, ×2 (Harper & Boucot, 1978).

Telaeoshaleria WILLIAMS, 1950, p. 281 [**Shaleria (T.) sulcata;* OD] [?=*Kinelina* LJASCHENKO, 1969, p. 35 (type, *K. eifelensis;* OD)]. Ventral valve strongly convex profile, dorsal valve flat posteriorly, geniculate anteriorly; unequally parvicostellate ornament; ventral muscle field with long, parallel-sided diductor scars bounded laterally by strong bounding ridges, divided by myophragm that forks anteriorly; dorsal muscle field on elevated but relatively small, low platform; central pair of dorsal side septa always present, sometimes additional pair also developed laterally; short dorsal median ridge centrally. *Devonian (Eifelian–Givetian):* Europe, Asia, Algeria.——FIG. 172,*4a–c*. **T. sulcata,* Calceola beds, Eifelian, Lissingen, Eifel, Germany; *a,* interior mold of ventral valve, USNM 116031, ×2; *b,* holotype, dorsal view of conjoined valves, USNM 116030, ×2; *c,* interior mold of dorsal valve, USNM 116032, ×1.5 (Williams, 1953a).

Tsaganella OLENEVA, 1994, p. 50 [**T. plana;* OD]. Ventral valve weakly convex profile, dorsal valve nearly flat; relatively fine unequally parvicostellate ornament; denticles along half valve width; ventral muscle field bilobed, surrounded by well-developed bounding ridges; small ventral process; cardinal process erect; flaring, medium-sized socket ridges; small side septa variably developed within relatively small dorsal muscle field; fine dorsal median septum sometimes present centrally. *Devonian (Givetian):* Asia.——FIG. 172,*5a–d*. **T. plana,* Khatygolsk Formation, Givetian, Khar-Tolgoi, Altai Mountains, Mongolia; *a,* dorsal external mold, PAN 4427/146, ×1.5; *b,c,* holotype, ventral internal mold, latex cast, PAN 4427/210, ×1.5; *d,* dorsal internal mold, PAN 4427/188, ×1.3 (Oleneva, 1994).

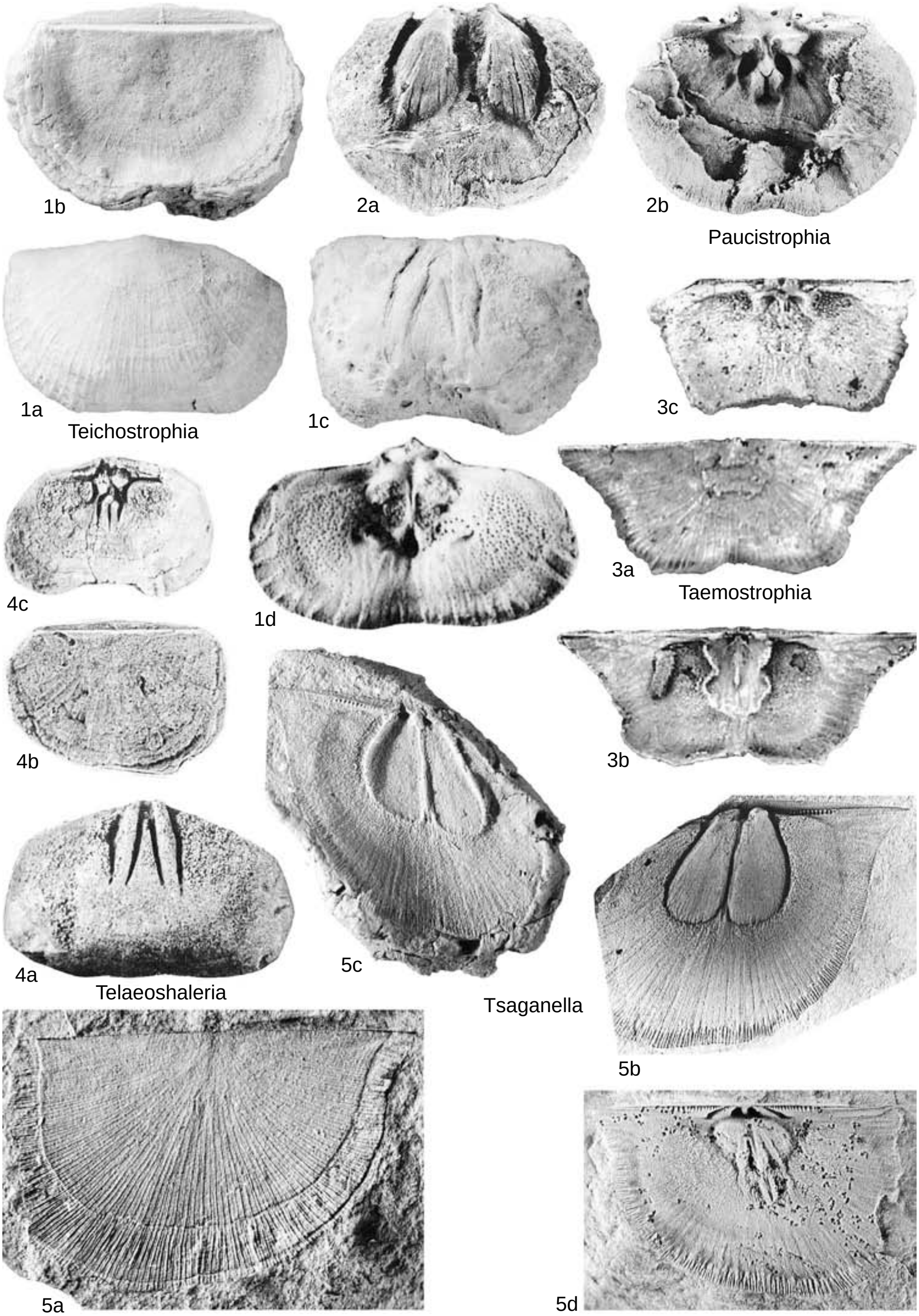

FIG. 172. Douvillinidae (p. 271–274).

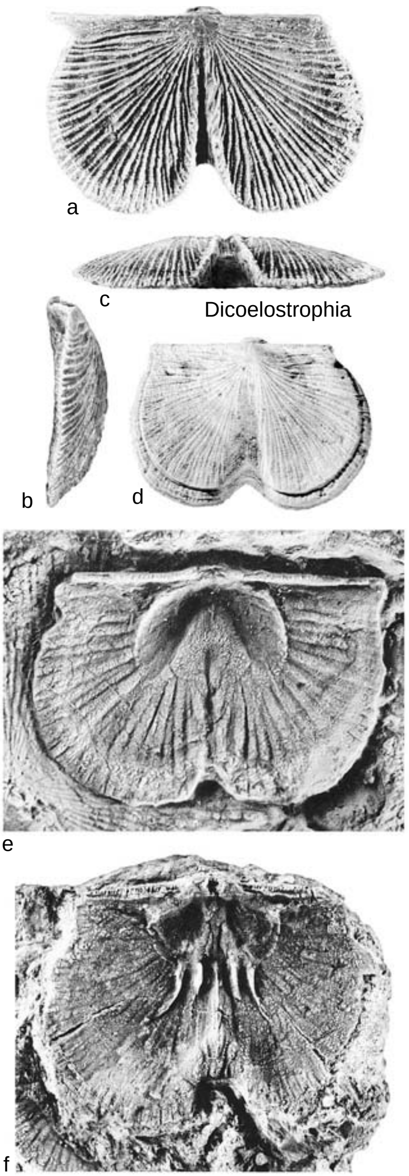

FIG. 173. Douvillinidae (p. 276).

Subfamily DICOELOSTROPHIINAE Wang & Rong, 1986

[Dicoelostrophiinae WANG & RONG, 1986, p. 98]

Characters same as for Douvillinidae, with sharply indented, bilobed anterior commissure due to prominent long narrow sulcus in each valve; two pairs of dorsal side septa. *Devonian (Emsian).*

Dicoelostrophia WANG, 1955a, p. 104 [**D. punctatum;* OD]. Profile mostly gently resupinate to shallowly biconvex; ornament variable, ranging from unequally parvicostellate to fascicostellate, usually costellate; denticles along most of hinge width; bilobed ventral muscle field with strong bounding ridges posterolaterally, separated anteriorly by broad central area; dorsal muscle field bounded laterally, posteriorly by ridges; two pairs of high, strong dorsal side septa, median septum. *Devonian (Emsian):* China.——FIG. 173*a–f.* **D. punctatum,* Yukiang Formation, lower Emsian, Liujing, Hengxian, Guangxi Province, China; *a–c,* holotype, dorsal, lateral, anterior views of conjoined valves, ×1.5; *d,* dorsal view of conjoined valves, BMNH BC 12848, ×1.5; *e,* ventral valve interior, NIGP 87917, ×2; *f,* dorsal valve interior, NIGP 23611, ×2 (new).

Subfamily LEPTODONTELLINAE Williams, 1965

[Leptodontellinae WILLIAMS, 1965d, p. 403]

Profile gently to strongly concavoconvex, usually geniculate in varying degrees; ventral muscle field long, bilobed, separated by relatively broad flat area anterior to diductor scars; cardinal process lobes directed posteriorly; distinct short socket ridges almost parallel with lateral margins of cardinal process lobes, turning laterally to form low ridges parallel to hinge line; differs from Douvillininae in general absence of dorsal valve side septa and in widest part of dorsal muscle field, occurring anteriorly rather than posteriorly. *Devonian (Emsian–Frasnian).*

Leptodontella KHALFIN, 1948, p. 253 [**Leptaena caudata* SCHNUR, 1854, p. 224; OD] [=*Glossostrophia* WILLIAMS, 1950, p. 282, obj.; *Altaestrophia* BUBLICHENKO, 1956, p. 96 (type, *Leptodontella acuta* KHALFIN, 1948, p. 255; OD]. Profile biplanar in central disc, then gently resupinate, sharply geniculate ventrally; fold, sulcus present in concave anterior margin; unequally parvicostellate ornament; large, bilobed, weakly impressed ventral muscle field; strong dorsal muscle-bounding ridges; dorsal side septa absent or weakly developed; thin dorsal median septum with prominent thickening centrally. *Devonian (Eifelian–Givetian):* Europe, Africa, Asia.——FIG. 174,*4a–e.* **L. caudata* (SCHNUR), Eifelian; *a,b,* internal molds of ventral, dorsal interiors, Blankenheim Limestone, Gerolstein, Eifel, Germany, USNM 116391a, ×1.5; *c,d,* dorsal, ×1, and anterior views, ×1.5, of conjoined valves, Blankenheim Limestone, Gerolstein, Eifel, Germany, USNM 116391b (Williams, 1953a); *e,* dorsal interior, Padaukpin Limestone, Padaukpin, near Maymyo, northern Shan States, Burma, SM 2654, ×1.25 (Johnson, new).——FIG. 174,*4f. L. acuta,*

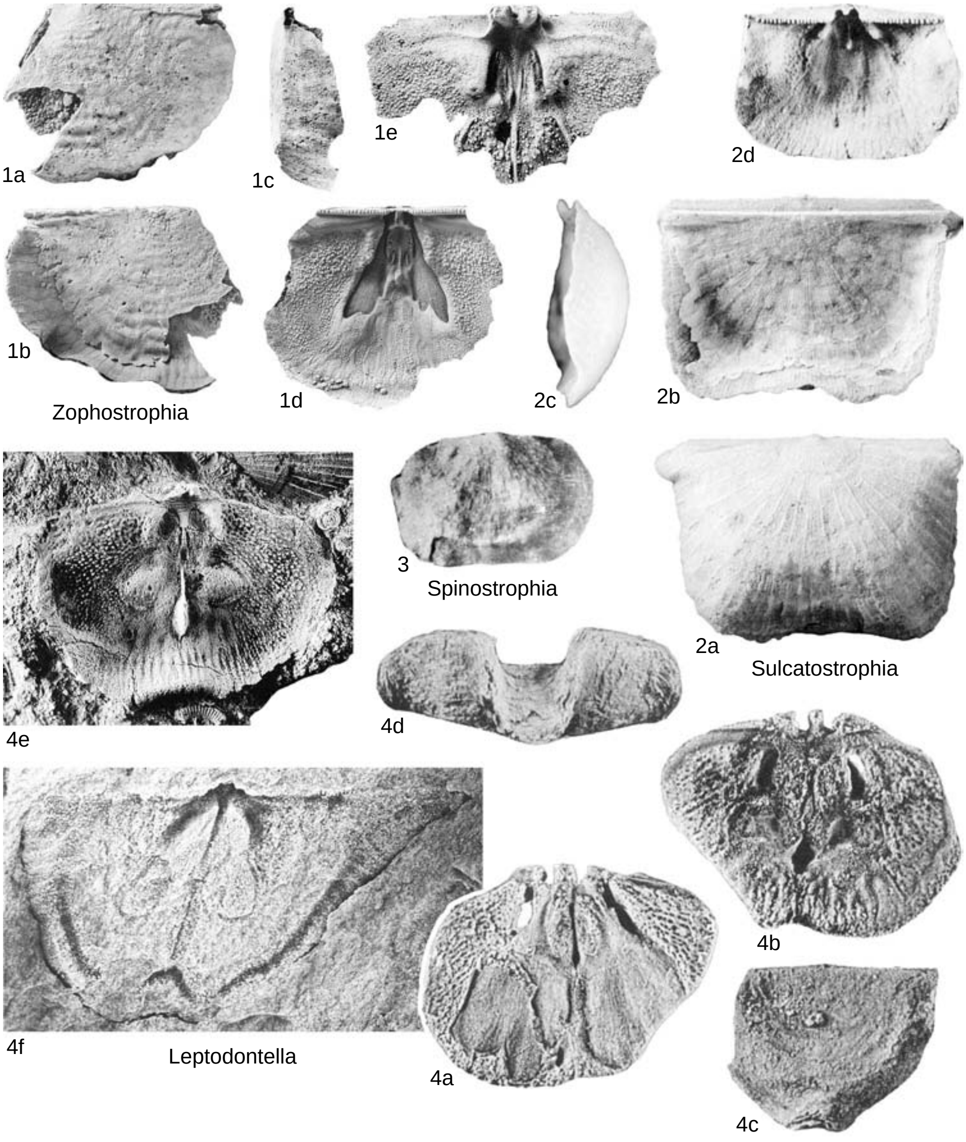

Fig. 174. Douvillinidae (p. 276–278).

Medvedev Formation, upper Emsian, Medvedev, Gorny Altai, Russia; dorsal internal mold, PAN 1/244, ×2 (Gratsianova, new).

Parastrophonella Bublichenko, 1956, p. 93 [**Strophomena anaglypha* Kayser, 1871, p. 628; OD]. Planoconvex to gently resupinate profile; similar to *Leptodontella,* but without anterior fold, sulcus; unequally parvicostellate ornament; triangular, bilobed ventral muscle field, well impressed but without bounding ridges; erect, ventrally directed cardinal process lobes; dorsal muscle field well impressed posteriorly, open anteriorly; weak dorsal myophragm posteriorly only; dorsal side septa absent. *Devonian (Emsian–Givetian):* Europe, northern Africa.——Fig. 175*a–d*. **P. anaglypha* (Kayser), Rommersheimer Shale, Eifelian, Eifel, Germany; *a,* latex of ventral exterior, Gees, SMF 19154, ×3; *b,* ventral interior, Rommersheim, Prümer Mulde, SMF 19154, ×3; *c,d,* mold, latex cast of dorsal interior, Rommersheim, Prümer Mulde, SMF 19160, ×3 (Johnson, new).

?**Spinostrophia** Jiang in Xian & Jiang, 1978, p. 267 [**S. ellipsoidea;* OD]. Ornament of interrupted costellae as in *Nervostrophia,* but profile strongly

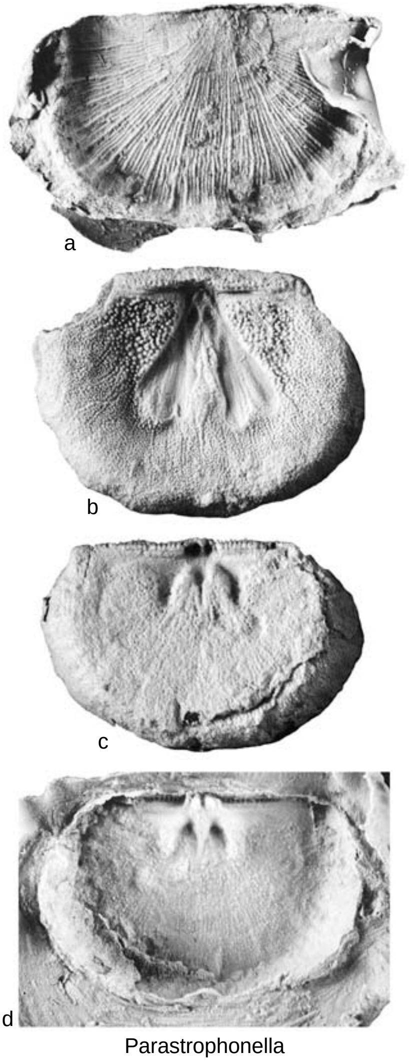

FIG. 175. Douvillinidae (p. 277).

concavoconvex, dorsally geniculate (unlike *Nervostrophia*); ventral muscle field bilobed; dorsal interior unknown, hence queried assignment to this subfamily. *Devonian (Eifelian):* China.——FIG. 174,*3*. **S. ellipsoidea,* Longdongshui Formation, Eifelian, Pinghuangshan, Dushan County, Guizhou Province; holotype, ventral exterior, GB 127, ×1 (Xian & Jiang, 1978).

Sulcatostrophia CASTER, 1939, p. 81 [**Leptostrophia camerata* FENTON & FENTON, 1924, p. 96; OD] [=*Pseudodouvillina* STAINBROOK, 1945, p. 26 (type, *P. euglyphea;* OD)]. Quadrate outline; profile strongly concavoconvex; ventral valve sulcus occasionally present; costellate to unequally parvicostellate ornament, with some individual ventral valve costellae occasionally variably strong along their length, as in *Nervostrophia;* poorly impressed ventral muscle field, but with prominent short flaring muscle-bounding ridges posteroventrally only, mimicking dental plates; short ventral median septum posteriorly only; dorsal side septa absent or sometimes faintly developed. *Devonian (Frasnian):* North America, Russia.——FIG. 174,*2a–d*. **S. camerata* (FENTON & FENTON), Hackberry Formation, Frasnian, Mason City, Iowa; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH B 18905, ×3 (new); *d,* ventral valve interior, USNM 220529, ×2 (Harper & Boucot, 1978).

Zophostrophia VEEVERS, 1959, p. 63 [**Z. ungamica;* OD]. Profile dorsally geniculate; ornament uniformly costellate with weak rugae; deeply impressed bilobed ventral muscle field with short ventral median septum; dorsal muscle field strongly impressed, especially posteriorly; thin dorsal median septum centrally only. *Devonian (Frasnian):* Australia.——FIG. 174,*1a–e*. **Z. ungamica,* Sadler Formation, Frasnian, Sadler Ridge, Fitzroy basin; *a–c,* holotype, ventral, dorsal, lateral views of conjoined valves, CPC 2942, ×1; *d,* ventral interior, CPC 2941, ×1.23; *e,* dorsal interior, CPC 2940, ×1.77 (Strusz, new).

Family LEPTOSTROPHIIDAE
Caster, 1939

[*nom. transl.* SOKOLSKAYA, 1960, p. 215, *ex* Leptostrophiinae CASTER, 1939, p. 27] [=Eostropheodontidae HAVLÍČEK, 1967, p. 80; Nervostrophiinae HARPER & BOUCOT, 1978, p. 89; Mesoleptostrophiinae HARPER & BOUCOT, 1978, p. 66; Brachyprioninae HARPER & BOUCOT, 1978, p. 13]

Profile biplanate or gently concavoconvex; hinge line usually denticulate; triangular ventral muscle field, bounded posterolaterally by ridges (sometimes lacking in older forms) sometimes partitioned by radial ridges (unique in Strophomenoidea), open anteriorly; cardinal process lobes usually ventrally directed, although rarely posteriorly or posteroventrally directed; socket ridges usually present; side septa in dorsal valve generally absent. *Ordovician (Ashgill)–Devonian (Frasnian).*

Leptostrophia HALL & CLARKE, 1892, p. 288 [**Stropheodonta magnifica* HALL, 1857, p. 54; OD] [=*Magniventra* HARPER & BOUCOT, 1978, p. 77 (type, *Strophomena magniventra* HALL, 1857, p. 54; OD)]. Semicircular outline; profile biplanate to gently concavoconvex; ornament usually unequally costellate; hinge line entirely denticulate; ventral valve with distinctive ventral process or tubular

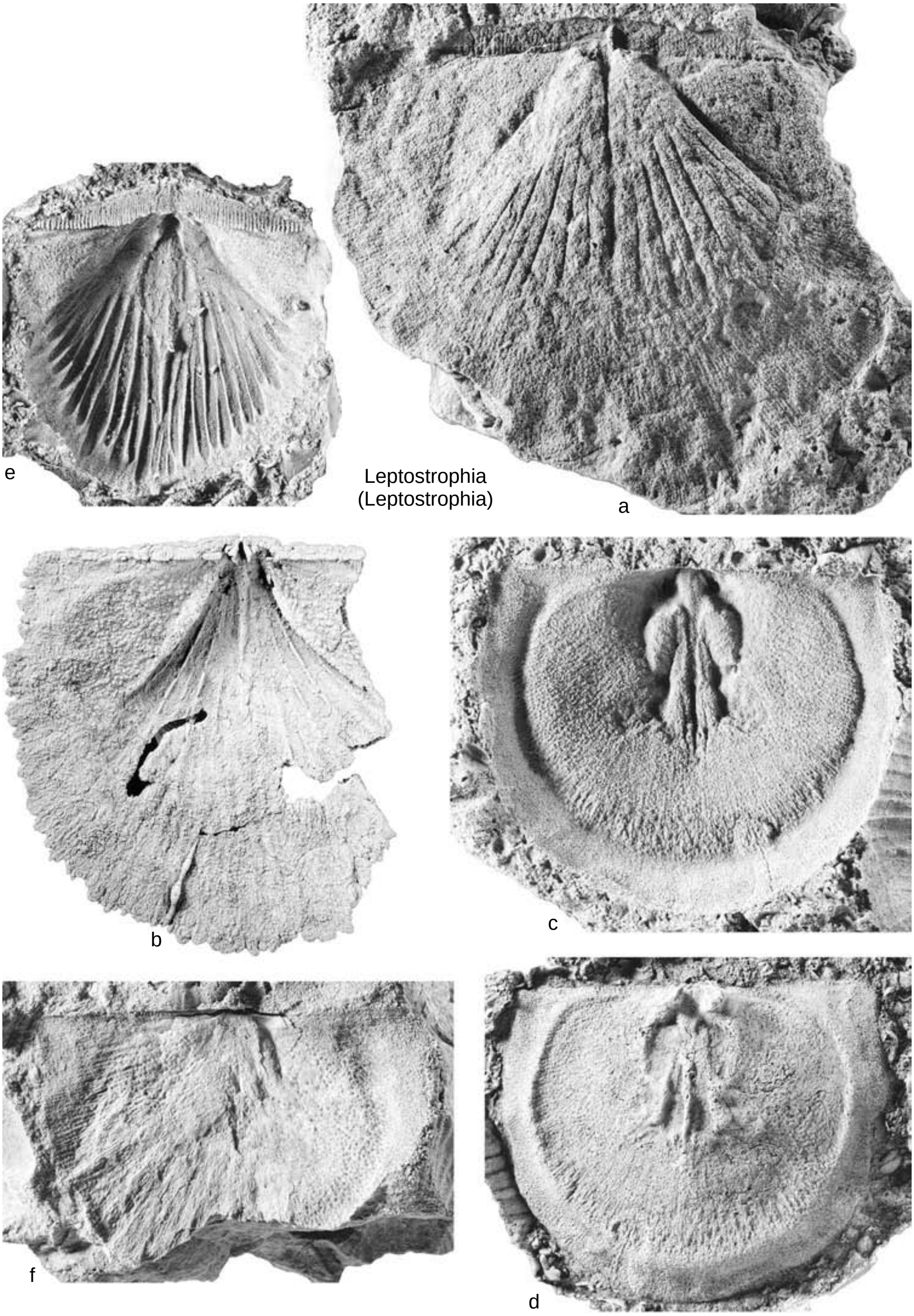

FIG. 176. Leptostrophiidae (p. 280).

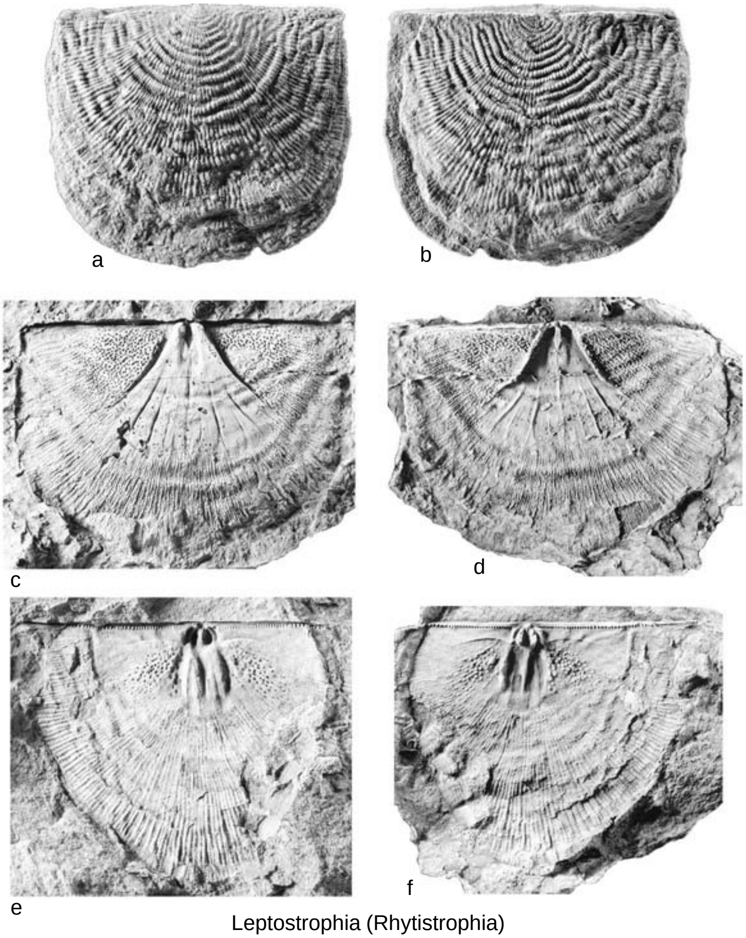

Fig. 177. Leptostrophiidae (p. 280–281).

chamber; ventral muscle field with bounding ridges posterolaterally only, partitioned by low radial ridges; cardinal process lobes elongate to ponderous but separated at their base, ventrally to posteroventrally directed; socket plates small, situated posterolaterally, close to cardinal process lobes, often curved subparallel with lobes; dorsal muscle-bounding ridges may be present laterally, posteriorly; small central dorsal septum variably developed; dorsal subperipheral rim variably present. *Devonian (Pragian–Emsian):* cosmopolitan.

L. (**Leptostrophia**). Similar to *L. (Rhytistrophia)* but lacking rugae except minimally at alae; distinctive tubular chamber in place of ventral process. *Devonian (Pragian–Emsian):* North America.——Fig. 176*a–d*. **L. (L.) magnifica* (Hall), Oriskany Sandstone, Pragian; *a,* lectotype, internal mold of ventral valve, Schoharie County, New York, AMNH 34789, ×0.75; *b,* ventral interior, Cumberland, Maryland, AMNH 34794, ×1; *c,d,* internal mold, latex cast of dorsal valve, Schoharie County, New York, BMNH BC 13063, ×1 (new).——Fig. 176*e,f. L. (L.) magniventra* (Hall), Oriskany Sandstone, Pragian, Schoharie, Schoharie County, New York; *e,* syntype, latex cast of mold of ventral valve, AMNH 34780, ×1; *f,* partly exfoliated dorsal valve, showing mold of cardinal process, AMNH 34782, ×1 (new).

L. (**Rhytistrophia**) Caster, 1939, p. 86 [**Stropheodonta beckii* Hall, 1859a, p. 191; OD]. Similar to *L. (Leptostrophia),* but with ornament of variably developed, discontinuous concentric rugae; ventral process instead of tubular chamber. *Silurian (Ludlow)–Devonian (Emsian):* North America, Europe, Mongolia.——Fig. 177*a–f.* **L. (R.) beckii* (Hall), Helderberg Group, Pragian; *a,b,* lectotype, ventral, dorsal views of

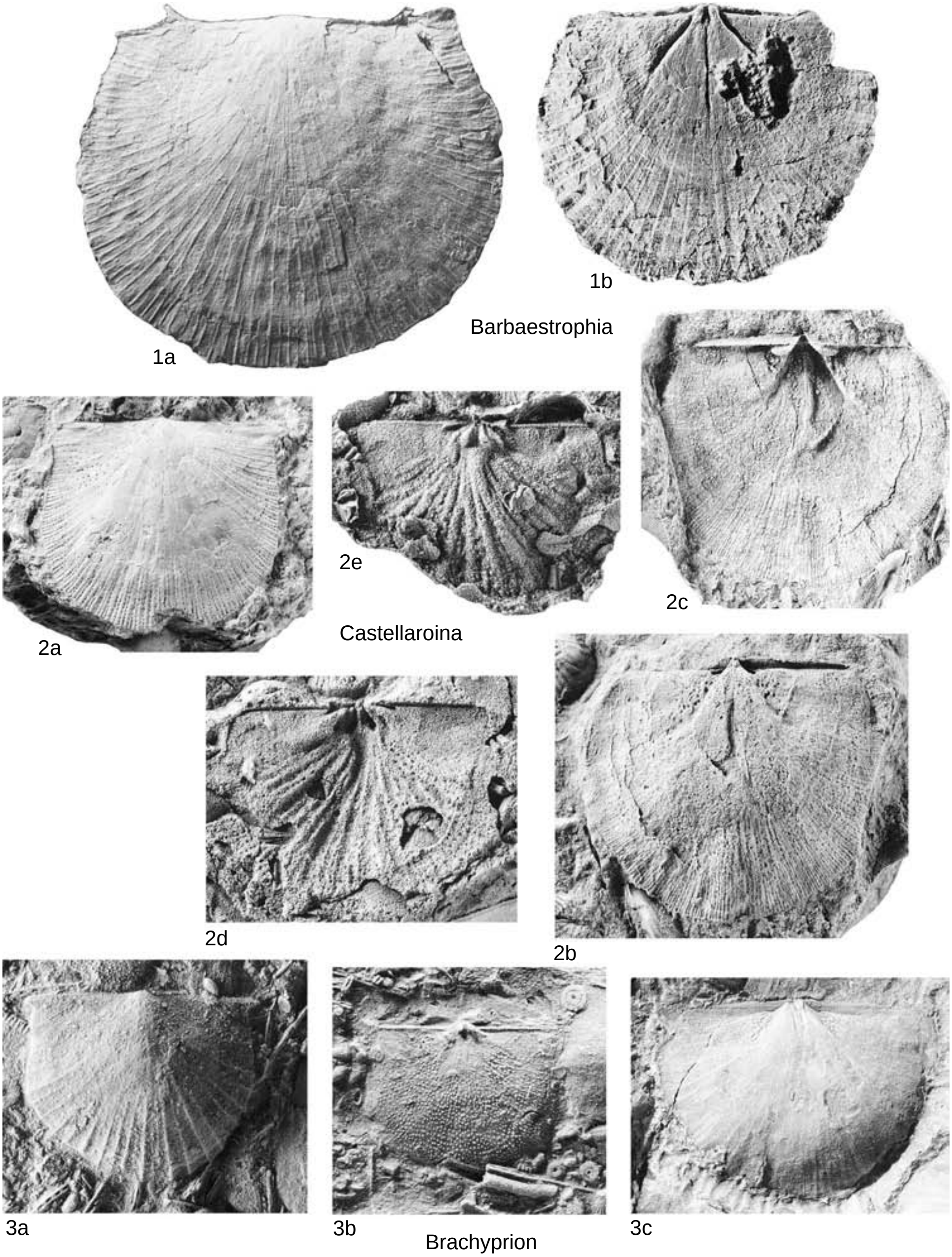

FIG. 178. Leptostrophiidae (p. 282).

conjoined valves, Schoharie, New York, AMNH 33162, ×1; *c,d,* ventral internal mold, latex cast, Becraft's Mountain, Columbia, New York, AMNH 33166, ×1; *e,f,* dorsal internal mold, latex cast, Becraft's Mountain, Columbia, New York, AMNH 33167, ×1 (new).

?**Barbaestrophia** Havlíček, 1965a, p. 7 [**Strophomena praestans* Barrande, 1879, pl. 51–IV, fig. 1–7; OD]. Two to three pairs of curved spines extending posterolaterally from hinge line; family designation uncertain because dorsal interior unknown, but ventral muscle field typically leptostrophiid in its posterolateral bounding ridges and in its triangularity. *Devonian (Lochkovian):* Europe.——Fig. 178,*1a,b.* **B. praestans* (Barrande), Kotys Limestones, Lochkovian, Svaty Jan pod Skalou, Czech Republic; *a,* lectotype, ventral exterior, NM L6672, ×1.5; *b,* internal mold of ventral interior, OMR VH 427, ×1.5 (Havlíček, 1967).

Brachyprion Shaler, 1865, p. 63 [**Strophomena leda* Billings, 1860, p. 55; OD]. Profile gently to moderately concavoconvex; ornament mainly unequally parvicostellate, but may be costellate; denticles on denticular plates in ventral valve, small number on dorsal hinge line; dental plates absent; ventral muscle field usually triangular, but may be gently curved posterolaterally; muscle-bounding ridges weak or absent; cardinal process lobes erect, small, suboval, not united at their base; socket ridges thin, widely divergent; dorsal muscle field poorly impressed. *Silurian (Aeronian–Ludlow):* cosmopolitan.——Fig. 178,*3a,b.* **B. leda* (Billings), Jupiter Formation, Telychian, Anticosti Island, Quebec, Canada; *a,* lectotype, ventral exterior, ×2; *b,* dorsal interior, GSC 2442, ×2 (new).——Fig. 178,*3c. B.* sp., Vik Formation, Telychian, Porsgrunn, Norway; ventral internal mold, BMNH BC 6894, ×1.5 (new).

Castellaroina Boucot in Amos, 1972, p. 11 [**Tropidoleptus fascifer* Kayser, 1897, p. 291; OD]. Profile gently concavoconvex; unequally parvicostellate ornament; strong teeth with crenulations fused to vestigial dental plates; very finely denticulate for up to half hinge width; muscle-bounding ridges weak or absent although triangular ventral muscle field well impressed posterolaterally; strong cardinal process lobes positioned completely anterior to hinge line, not united at their base; short flaring socket ridges; dorsal muscle field poorly impressed. *Silurian (Ludlow, ?Přídolí):* Argentina.——Fig. 178,*2a–e.* **C. fascifer* (Kayser), Los Espejos Formation, Ludlow, Agua Negra, San Juan, Argentina; *a,* ventral exterior, BAU 7693, ×1.5; *b,c,* ventral internal mold, latex cast, BAU 7694, ×1.5; *d,e,* dorsal internal mold, latex cast, BAU 7700, ×2 (new).

Chynistrophia Havlíček, 1977b, p. 301 [**C. foliola;* OD]. Small subrectangular outline; planoconvex profile; similar to *Leptostrophia* apart from narrower diductor scars, no radial ridges in ventral muscle field, dorsal muscle field relatively small. *Devonian (Pragian):* Europe.——Fig. 179,*1a–c.* **C. foliola,* Chotec Limestone, Pragian, Chynice, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 2601, ×3.5; *b,* ventral internal mold, ×3.5; *c,* dorsal internal mold, ×4 (Havlíček, 1977b).

Eomegastrophia Cocks, 1967, p. 260 [**Megastrophia (E.) ethica;* OD]. Profile concavoconvex; ornament from unequally parvicostellate to uniformly costellate; dental plates present in parts or all of population; denticular plates with small number of denticles; ventral muscle field moderately impressed, muscle-bounding ridges absent; cardinal process lobes narrow, ventrally directed, not joined at bases; short anterolateral socket plates present; dorsal muscle field weakly impressed. *Silurian (Aeronian):* Europe, ?North America.——Fig. 180,*2a–c.* **E. ethica,* Pentamerus Beds, Aeronian, Morrellswood, Shropshire, England; *a,* holotype, mold of ventral interior, GSM 102715, ×1; *b,* mold of dorsal interior, GSM 102717, ×1; *c,* mold of dorsal interior, BMNH BC 13415, ×1.5 (Cocks, 1967).

Eostropheodonta Bancroft, 1949, p. 9 [**Orthis hirnantensis* M'Coy, 1851, p. 395; OD] [=*Aphanomena* Bergström, 1968, p. 13 (type, *A. schmalenseei;* OD); *Eoleptostrophia* Harper & Boucot in Amos, 1972, p. 11, *nom. nud.; Neokjaerina* Levy & Nullo, 1974, p. 191 (type, *Kjaerina (N.) florentina*); *Pirgumena* Rõõmusoks, 1993c, p. 163 (type, *P. martnai;* OD)]. Planoconvex to gently concavoconvex profile; ornament variable from unequally parvicostellate to fascicostellate, sometimes in same population; small denticular plates with few denticles; no denticles on hinge line; short but strong dental plates present, with crenulations; ventral process generally absent; muscle field in both valves obscure or faintly impressed; erect cardinal process lobes elongate, separated at their bases; socket ridges widely divergent; dorsal septa absent. *Ordovician (Ashgill)–Silurian (Wenlock):* cosmopolitan.——Fig. 181*a–d.* **E. hirnantensis* (M'Coy), Ashgill; *a,* latex of dorsal exterior, Husbergøya Formation, Rambergøya, Oslo, Norway, BMNH BB 93972, ×1.5; *b,c,* dorsal internal mold, latex cast, Husbergøya Formation, Rambergøya, Oslo, Norway, BMNH BB 94003, ×2; *d,* ventral internal mold, Hirnant Formation, Aber Hirnant, near Bala, Gwynedd, Wales, BMNH B 89573, ×1.5 (new).——Fig. 181*e–g. E. schmalenseei* (Bergström), lower *Dalmanitina* Beds, Ashgill; *e,* latex cast of external mold of conjoined valves, Stommen, Västergötland, Sweden, LO 4249, ×1.5 (Bergström, 1968); *f,* ventral internal mold, Stommen, BMNH B 90684, ×1 (new); *g,* holotype, latex cast of dorsal internal mold, Allebergsände, Västergötland, Sweden, LO 4248, ×1 (Bergström, 1968).——Fig. 181*h,i. E. martnai* (Rõõmusoks), Adila Formation, Pirgu Stage, Ashgill, Härküla, Aruküla, Estonia; *h,* ventral external mold, GMUT Br 1492, ×1; *i,* dorsal internal mold, GMUT Br 1477, ×1 (Rõõmusoks, 1993c).——Fig. 181*j,k. E. florentina* (Levy & Nullo), Don Braulio Formation, Ashgill, Villicun Range, San Juan Province, Argentina; *j,* holotype, latex cast of ventral exterior, DNGM 14994, ×2; *k,* latex cast of ventral exterior,

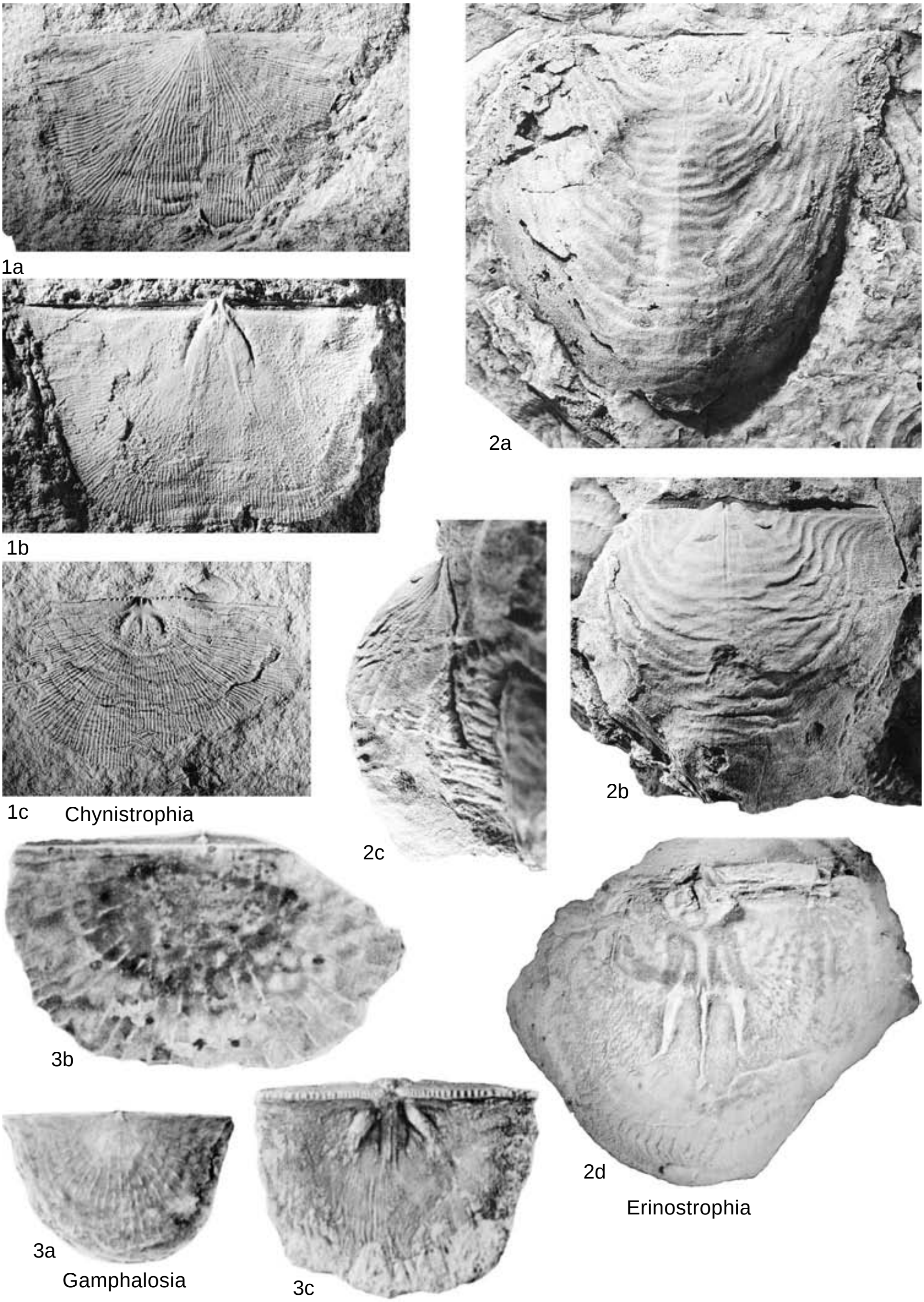

FIG. 179. Leptostrophiidae (p. 282–286).

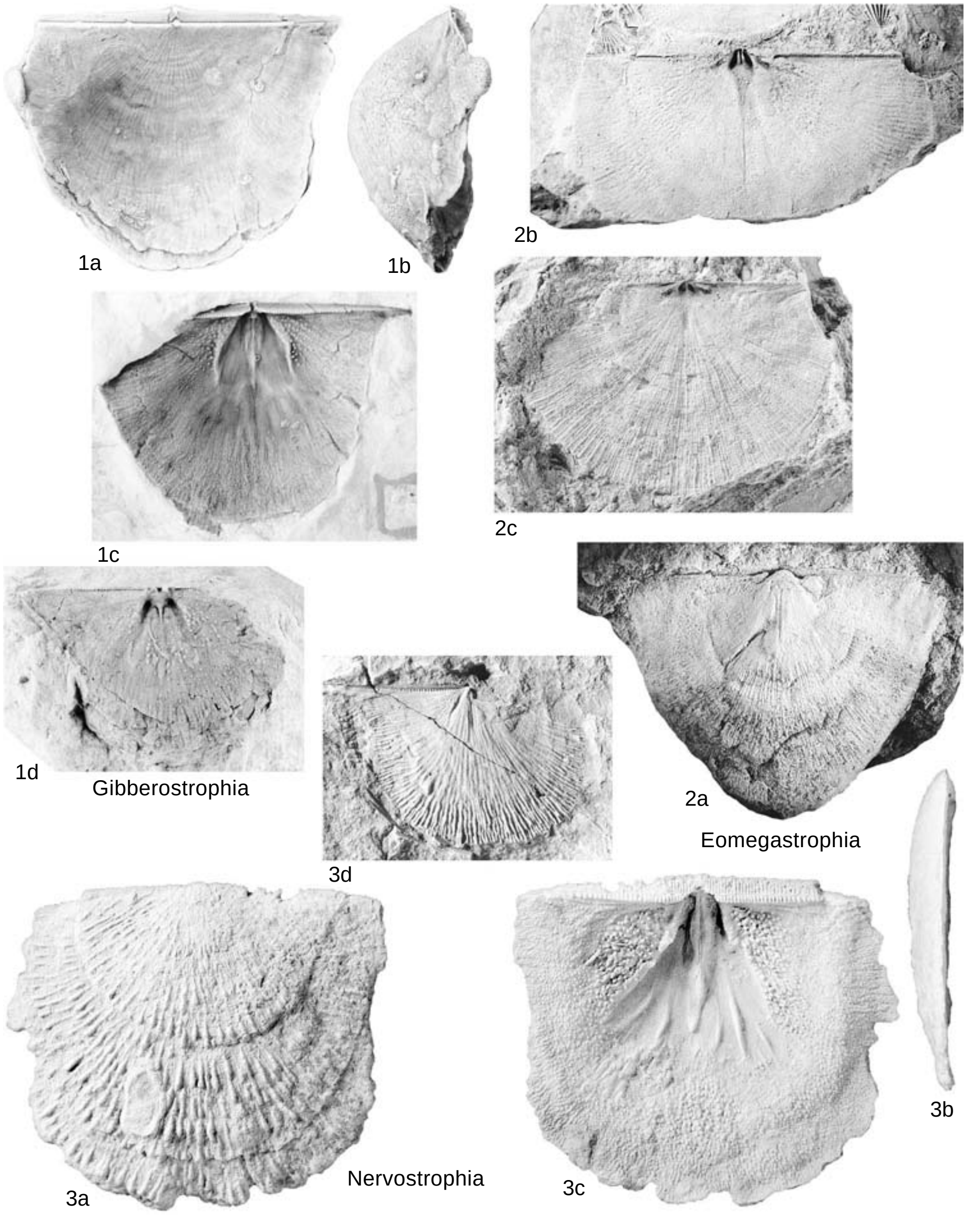

FIG. 180. Leptostrophiidae (p. 282–286).

dorsal interior, *ex* DNGM 14995, ×5 (Benedetto, new).

Erinostrophia COCKS & WORSLEY, 1993, p. 44 [**Orthis undata* M'COY, 1846, p. 36; OD]. Strongly concavoconvex profile; similar to *Protomegastrophia,* but with pronounced but discontinuous rugae over whole shell; rounded rather than bladelike cardinal process lobes. *Silurian (Telychian):* Europe.——FIG. 179,*2a–d.* **E. undata,* Telychian; *a,* external mold of dorsal valve, Porsgrunn Formation, Skien, Norway, BMNH BC 6806, ×1.5; *b,c,* ventral, lateral views of ventral internal mold, Bruflat Formation, Sogn, Hadeland, Norway, BMNH BC 6686, ×1.5; *d,* dorsal interior, lower Visby Beds, Visby, Gotland, Sweden, BMNH B 13611, ×1 (Cocks & Worsley, 1993).

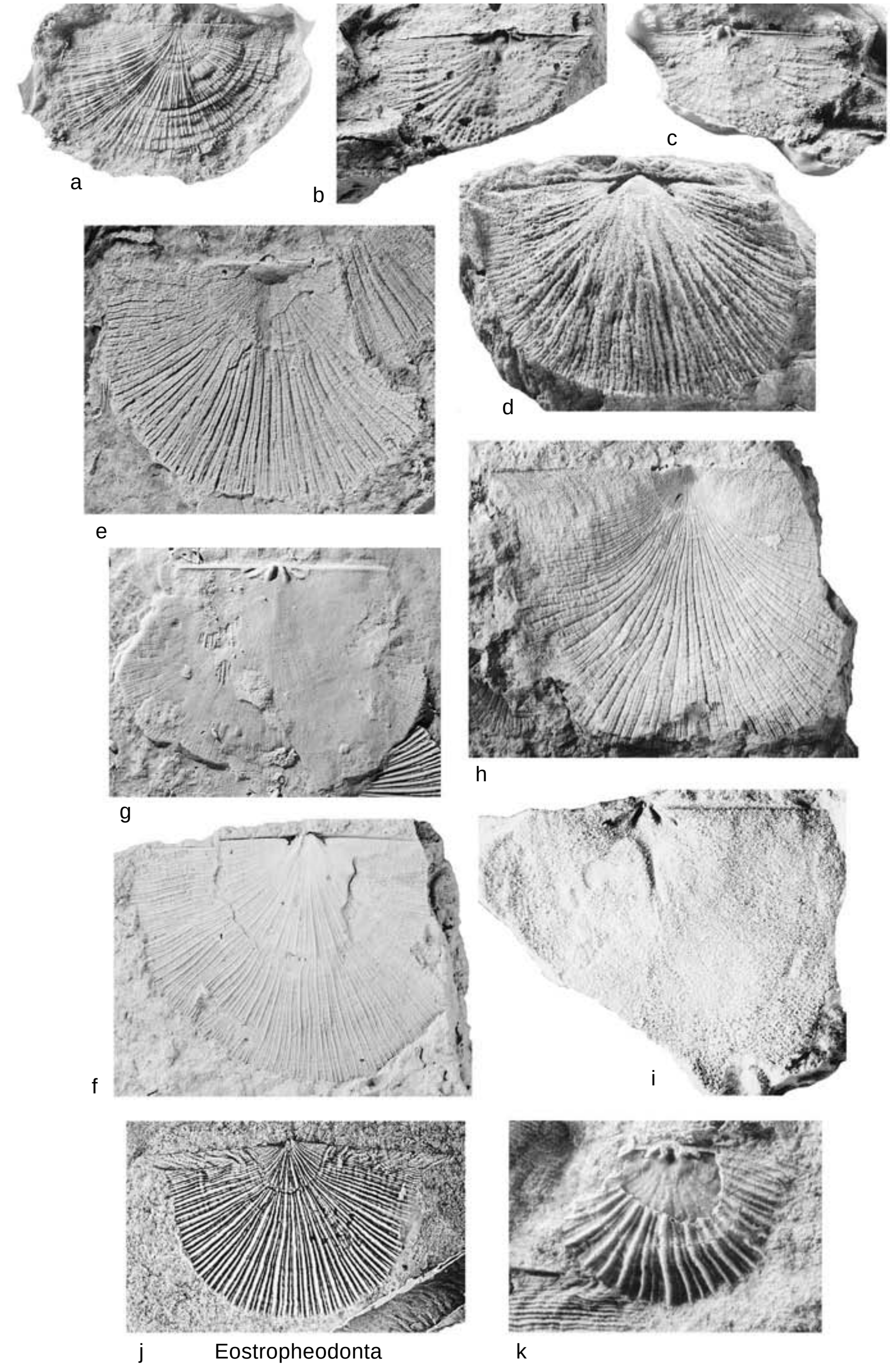

FIG. 181. Leptostrophiidae (p. 282).

Gamphalosia STAINBROOK, 1945, p. 33 [**G. tenuissima;* OD]. Profile gently resupinate; ornament with costellae of variable strength as in *Nervostrophia* but more pronounced on ventral than dorsal valve; weak rugae also developed sporadically. *Devonian (Frasnian):* North America, Europe.——FIG.

179,*3a–c.* **G. tenuissima,* Independence Shale, Frasnian, Brandon, Iowa; *a,* ventral valve exterior, SUI MAS 858b, ×2; *b,* dorsal view of exterior of conjoined valves, SUI MAS 859B, ×3; *c,* ventral valve interior, SUI MAS 859, ×3 (Harper & Boucot, 1978).

Gibberostrophia Harper & Boucot, 1978, p. 79 [**Stropheodonta gibbera* Amsden, 1958, p. 73; OD]. Profile strongly concavoconvex; ornament uniformly costellate; denticulation over most of hinge line; muscle field deeply impressed in both valves laterally, posteriorly, becoming fainter anteriorly; with slightly curved bounding ridges posterolaterally in ventral valve; ventral process well developed; myophragm present in both valves; cardinal process lobes elongate, close together but not united; socket ridges abbreviated, close to but separate from cardinal process lobes. *Devonian (Lochkovian):* North America.——Fig. 180,*1a–d.* **G. gibbera* (Amsden), Haragan Formation, Lochkovian, Hunton, Arbuckle Mountains, Oklahoma; *a,b,* holotype, dorsal, lateral views of conjoined valves, OKGS 930, ×1.5; *c,* ventral interior, OKGS 927, ×1.5; *d,* dorsal interior, OKGS 924, ×1.5 (new).

Mesoleptostrophia Harper & Boucot, 1978, p. 68 [**M. kartalensis;* OD, *nom. nov. pro Stropheodonta (Leptostrophia) explanata* Paeckelmann & Sieverts, 1932, *non* Sowerby, 1842 in 1840–1846, p. 40; Kartal-schichten (Emsian), Turkey] [=*Leptostrophiella* Harper & Boucot, 1978, p. 74 (type, *Leptaena explanata* Sowerby, 1842, p. 409; OD); *Mitchellella* Strusz, 1984, p. 126 (type, *Stropheodonta quadrata* Mitchell, 1923, p. 469; OD)]. Outline semicircular to subquadrate; profile biplanate to gently concavoconvex; ornament unequally parvicostellate to uniformly costellate; denticulate over most of valve width; small ventral process present; subtriangular to bilobed ventral muscle field with bounding ridges variably developed posterolaterally; variable, usually small, cardinal process lobes. *Silurian (Telychian)–Devonian (Eifelian):* cosmopolitan.

- M. (**Mesoleptostrophia**). Relatively small cardinal process lobes, ventroposteriorly directed, close posteriorly, convergent anteriorly, continuous with median ridge. *Silurian (Telychian)–Devonian (Emsian):* cosmopolitan.——Fig. 182,*2a–c. M. (M.) quadrata* (Mitchell), Bowning Beds, Ludlow, Bowning Railway Station, New South Wales, Australia; *a,b,* latex cast of external, internal molds of ventral valve, CPC 24006, ×2; *c,* latex cast of dorsal internal mold, AMF 28820, ×5 (Strusz, new).——Fig. 182, *2d,e. M. (M.) explanata* Sowerby, Coblenzian, Emsian; *d,* internal mold of ventral valve, Daun, BMNH B 42798, ×1; *e,* internal mold of dorsal valve, Grünbach, Germany, BMNH B 24570, ×1 (new).
- M. (**Paraleptostrophia**) Harper & Boucot, 1978, p. 70 [**Leptostrophia clarkei* Chatterton, 1973, p. 58; OD]. Ventral valve as in *M. (Mesoleptostrophia),* but cardinal process lobes strongly posteriorly directed with thin socket ridges parallel to lateral margins of cardinal process lobes, turning to extend laterally as low ridges subparallel to hinge line; dorsal median septum present; curved bounding ridges posterolateral to dorsal muscle field. *Devonian (Emsian–Eifelian):* Australia, Burma.——Fig. 182,*1a–c.* **M. (P.) clarkei* (Chatterton), Warroo Limestone, Emsian, Yass, New South Wales, Australia; *a,b,* holotype, exterior, interior views of ventral valve, ANU 18934, ×1; *c,* dorsal interior, ANU 18935e, ×1.5 (Campbell, new).

Nervostrophia Caster, 1939, p. 79 [**Strophomena nervosa* Hall, 1843a, p. 266; OD]. Profile gently concavoconvex to planoconvex; distinctive ornament of radial costellae that are intermittently discontinuous over whole shell; hinge line completely denticulate; triangular ventral muscle field similar to *Leptostrophia* with some radial ridges, open anteriorly; ventral process continuous with myophragm; ponderous but short cardinal process lobes ventrally, posteriorly directed, short socket plates subparallel with cardinal process lobes; prominent dorsal muscle-bounding ridges. *Devonian (?Givetian, Frasnian):* cosmopolitan.——Fig. 180,*3a–d.* **N. nervosa* (Hall), Frasnian; *a–c,* external, lateral, internal views of ventral valves, Hackberry Formation, Frasnian, Rockford, Iowa, BMNH B 41544, ×1.5; *d,* syntype, ventral internal mold, Chemung Group, Bath, New York, AMNH 37205, ×1 (new).

Palaeoleptostrophia Rong & Cocks, 1994, p. 683 [**Stropheodonta jamesoni* Reed, 1917, p. 893; OD]. Profile biplanate to gently concavoconvex; ornament of gently curved unequal parvicostellae; no dental plates; denticles confined to small denticular plates in ventral valve interlocking with corresponding denticles on dorsal hinge line; muscle field poorly impressed in both valves, bounding ridges absent; ventral process weakly developed; thin short myophragm present; cardinal process lobes anteroventrally directed, divergent; thin platelike socket ridges with crenulations on posterior facets. *Silurian (Rhuddanian–Aeronian):* Europe, ?North America.——Fig. 183,*4a–c.* **P. jamesoni* (Reed), Woodland Formation, Rhuddanian, Woodland Point, near Girvan, Strathclyde, Scotland; *a,* ventral internal mold, BMNH BC 2454, ×1.5; *b,c,* dorsal internal mold, latex cast, BMNH BC 2471, ×1.5 (Rong & Cocks, 1994).

Protoleptostrophia Caster, 1939, p. 75 [**Strophomena blainvillii* Billings, 1874, p. 28; OD] [=*Siberistrophia* Astashkina, 1970, p. 131 (type, *Brachyprion speranskii* Khalfin, 1948, p. 274; OD); *Tastaria* Havlíček, 1965a, p. 6 (type, *Leptostrophia tasta* Rukavishnikova, 1961, p. 52; OD)]. Similar to *L. (Leptostrophia),* but with strong ventral process, without radial ridges in ventral muscle field; socket ridges absent in most specimens, although very faint in few members of populations. *Devonian (Lochkovian–Frasnian):* cosmopolitan.——Fig.

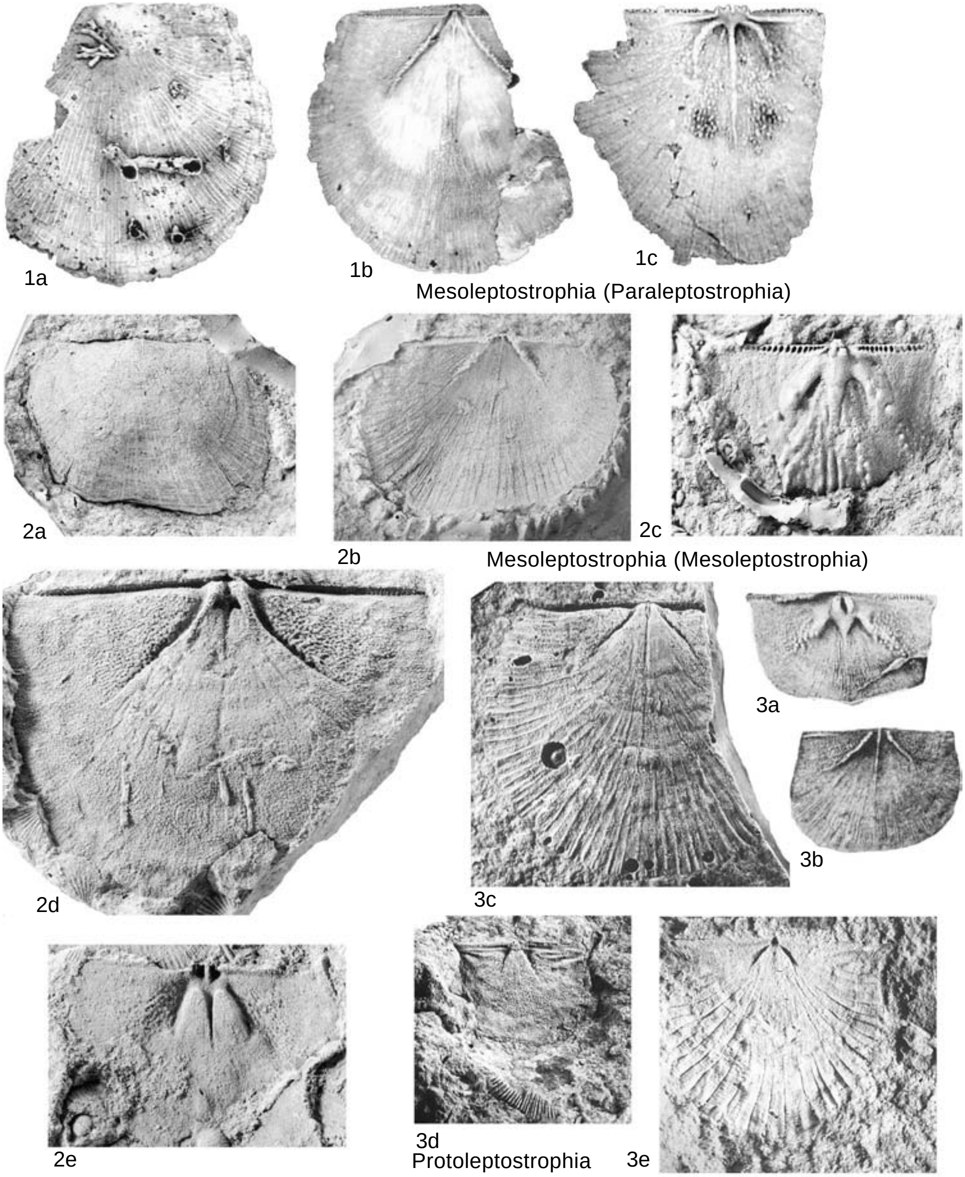

FIG. 182. Leptostrophiidae (p. 286–287).

182,*3a,b*. **P. blainvillii* (BILLINGS), Gaspé Sandstones (Devonian), St. John River, York Township, Gaspé, Quebec, Canada; *a,* plasticine cast of mold of dorsal interior, USNM 112091a, ×1; *b,* plasticine cast of mold of ventral interior, USNM 112091b, ×1 (Williams, 1953a).——FIG. 182,*3c–e. P. tasta* (RUKAVISHNIKOVA), Karazhirik Formation, Lochkovian; *c,* holotype, ventral internal mold, Tastuibulak well, MANK 67/9, ×1; *d,* ventral internal mold, Kogan well, north Pribalkash, Kazakhstan, MANK 67/13, ×1; *e,* dorsal internal mold, Tastuibulak well, MANK 67/17, ×1 (Rukavishnikova, 1961).

Protomegastrophia CASTER, 1939, p. 36 [**Leptaena profunda* HALL, 1852, p. 61; OD]. Profile moderately to strongly concavoconvex; ornament usually parvicostellate but rarely subuniformly costellate; denticles on denticular plates may stretch laterally

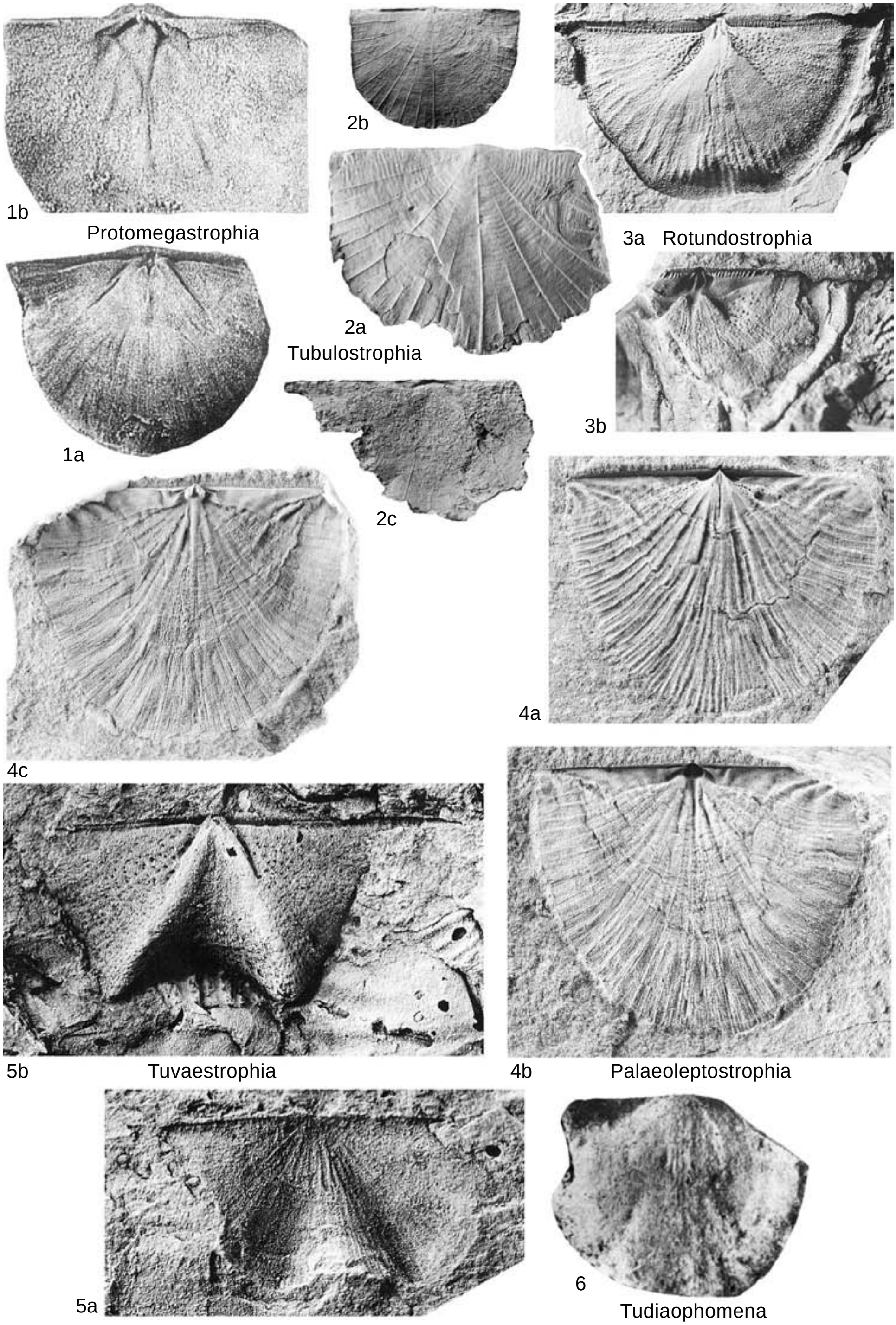

FIG. 183. Leptostrophiidae (p. 286–289).

up to one-third of hinge line; ventral muscle field bounding ridges developed for short distance posterolaterally; small but distinct ventral process, myophragm present; strong cardinal process lobes divergent, separated at base, directed ventrally; cardinal process pit present; socket ridges short; dorsal muscle field with faint bounding ridges posterolaterally. *Silurian (Telychian)–Devonian (Lochkovian):* cosmopolitan.——Fig. 183,*1a,b.* **P. profunda* (Hall), Racine Formation, Wenlock, Racine, Wisconsin; *a,* ventral internal mold, USNM 11637a, ×0.75; *b,* dorsal internal mold, USNM 116372b, ×1.5 (Williams, 1953a).

Rotundostrophia Gratsianova in Gratsianova, Zinchenko, & Kul'kov, 1960, p. 439 [**Leptodontella rotundata* Khalfin, 1948, p. 278; OD]. Similar to *Leptostrophia* but more transverse outline, no ventral muscle field radial ridges, ventrally geniculate near anterior margin; cardinal process lobes ventrally directed; dorsal muscle-bounding ridges strong for short distance posterolaterally. *Devonian (Emsian):* Russia.——Fig. 183,*3a,b.* **P. rotundata* (Khalfin), Kondratev Formation, lower Emsian, Kondratev, Altai Mountains, Russia; *a,* internal mold of ventral valve, TsGM 377/29, ×2; *b,* internal mold of dorsal valve, TsGM 377/26, ×3 (Gratsianova, new).

?Tubulostrophia Havlíček, 1967, p. 139 [**Leptaena fugax* Barrande, 1848, p. 233; OD]. Profile flat to gently concavoconvex; semicircular outline; ornament unequally parvicostellate, sometimes with fine rugae developed posteriorly; delicate pedicle tube preserved; small, very fine cardinal process lobes, but ventral interior poorly known and family uncertain, although hinge line denticulate for about one-third of its width; poorly impressed muscle fields. *Devonian (Pragian–Emsian):* Europe.——Fig. 183,*2a–c.* **T. fugax* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* ventral valve exterior, OMR VH 448a, ×1.5; *b,* internal mold of ventral valve, OMR VH 449b, ×1.5; *c,* brachial valve internal mold, OMR VH 499a, ×1.5 (Havlíček, 1967).

?Tudiaophomena Xian in Xian & Jiang, 1978, p. 266 [**T. plicata;* OD]. Interiors poorly known, perhaps leptostrophiid due to outline, profile, but treated here as a *nomen dubium. Silurian (Telychian):* China.——Fig. 183,*6.* **T. plicata,* Xiushan Formation, upper Telychian, Tudi-ao, Yanhe County, Guizhou Province, China; ventral valve internal mold, GB 353, ×1 (Xian & Jiang, 1978).

Tuvaechonetes Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 114 [**T. insolitus;* OD]. Triangular ventral muscle field, lack of spines, clear denticulation reveal its leptostrophiid rather than chonetid affinities; ornament unequally costellate; long lateral hinge line extensions. *Silurian (Přídolí):* Russia.——Fig. 184,*2a,b.* **T. insolitus,* Přídolí beds, Pichi-Shuy, Tuva, Russia; *a,* internal mold of ventral valve, IGiG SO 116, ×3; *b,* internal mold of dorsal valve, IGiG SO 117, ×2 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Tuvaestrophia Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 100 [**T. elegantula;* OD]. Transverse outline with extended alae, distinctive triangular ventral sulcus, dorsal fold; ornament of fine costellae; triangular ventral muscle field with strong posterolateral bounding ridges, open anteriorly; dorsal valve interior poorly known. *Silurian (Ludlow, ?Přídolí):* Russia.——Fig. 183,*5a,b.* **T. elegantula,* Pichishuysk Formation, Ludlow, Pichi-Shuy, Tuva, Russia; *a,* mold of ventral exterior, IGiG SO N78a, ×4; *b,* holotype, mold of ventral interior, IGiG SO N78, ×4 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Velostrophia Havlíček, 1965a, p. 7 [**Strophomena insolita* Barrande, 1879, pl. 52, fig. 1, pl. 128, fig. 3, pl. 143, fig. VI–3; OD]. Distinctive outline of spinelike projections curving posterolaterally from lateral extremities, also irregular plications around anterior commissure; variably geniculate profile; ventral muscle field narrowly divergent for family, with small muscle-bounding ridges, open anteriorly; myophragm present; cardinalia as in *Mesoleptostrophia;* curved dorsal muscle-bounding ridges posterolaterally. *Devonian (Pragian–Emsian):* Europe.——Fig. 184,*1a–c.* **V. insolita* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* lectotype, ventral exterior, NM L6459, ×1.5; *b,* ventral interior, OMR VH 426a, ×1.5; *c,* dorsal internal mold, OMR VH 429c, ×2 (Havlíček, 1967).

Viodostrophia Villas & Cocks, 1996, p. 579 [**V. alcaldei;* OD]. Planoconvex to gently concavoconvex profile; uniformly parvicostellate ornament; no dental plates, with denticles restricted to denticular plates in ventral valve, posterior edge of divergent socket ridges in dorsal valve; subtriangular ventral muscle field with short straight posterolateral bounding ridges; open anteriorly; similar to *Palaeoleptostrophia,* but with muscle-bounding ridges; similar to *Eostropheodonta,* but no dental plates. *Silurian (Telychian):* Spain.——Fig. 184,*3a–e.* **V. alcaldei,* El Castro Formation, Telychian, Viodo, Asturias, Spain; *a–c,* holotype, latex, internal mold, latex of ventral interior, DPO 29362, ×3; *d,e,* internal mold, latex of dorsal interior, DPO 29368, ×3 (Villas & Cocks, 1996).

Family EOPHOLIDOSTROPHIIDAE
Rong & Cocks, 1994

[Eopholidostrophiidae Rong & Cocks, 1994, p. 690]

Profile moderately to strongly concavoconvex; denticles on hinge line or denticular plates; triangular ventral muscle field very weakly impressed, open anteriorly, with no muscle-bounding ridges except for short distance posterolaterally; no radial ridges in muscle field, unlike some Leptostrophiidae; cardinal process lobes small, separate,

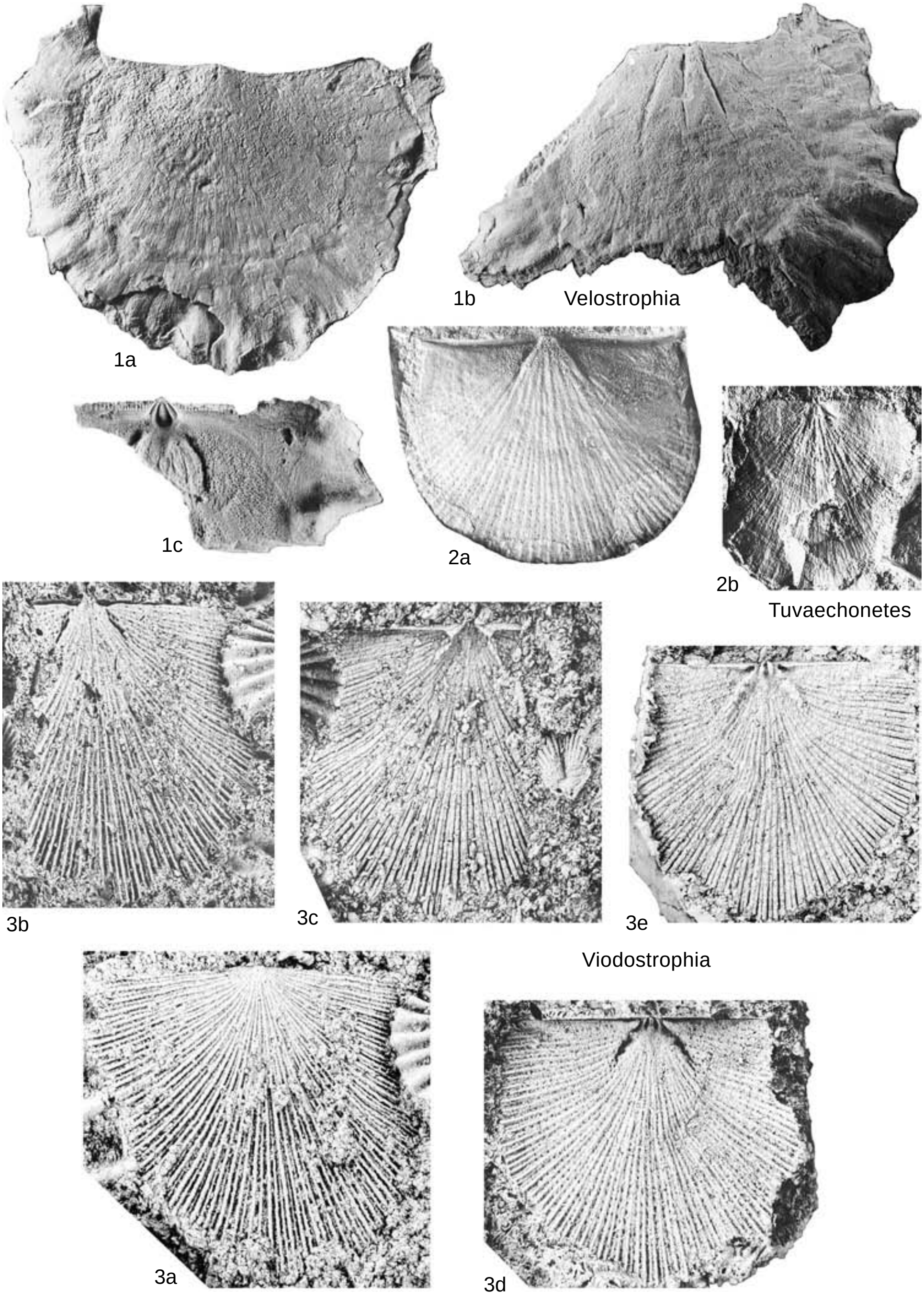

FIG. 184. Leptostrophiidae (p. 289).

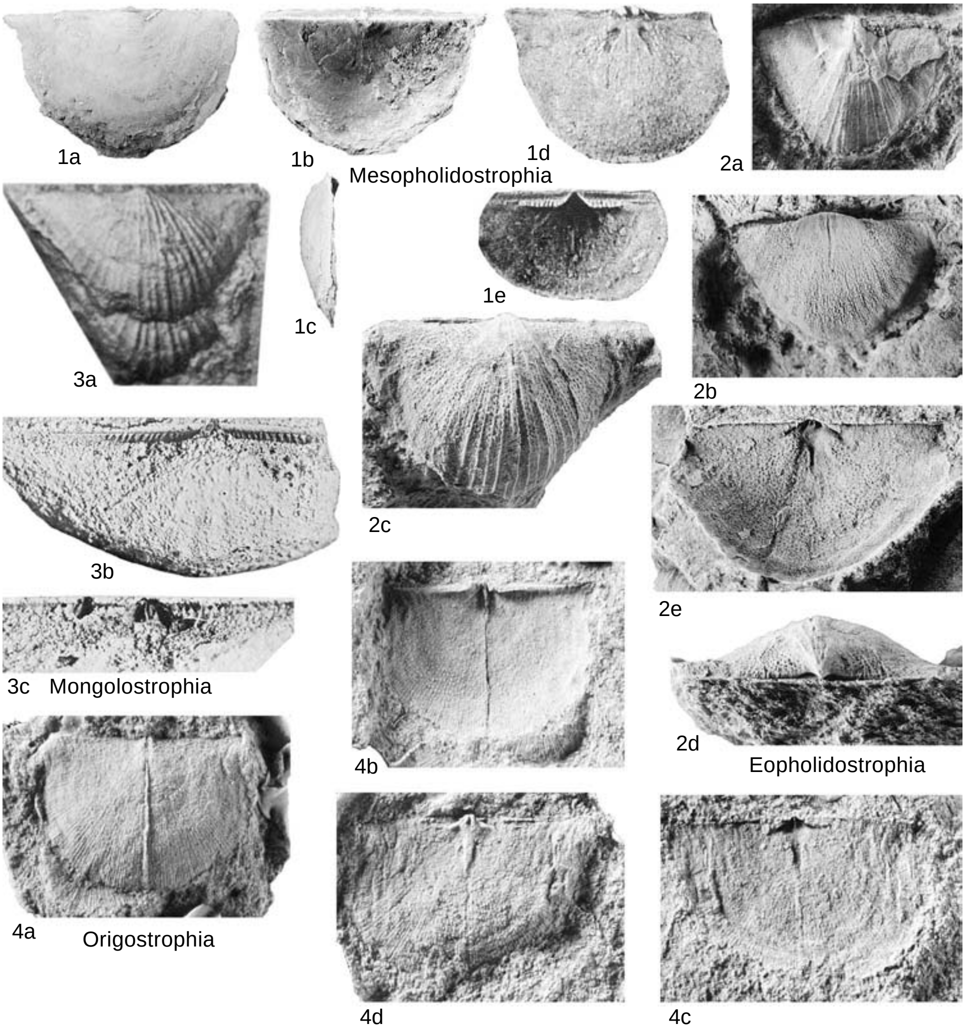

FIG. 185. Eopholidostrophiidae (p. 291–292).

ventrally directed; short thin socket ridges; dorsal side septa absent. *Ordovician (Ashgill)–Silurian (Ludlow).*

Eopholidostrophia HARPER, JOHNSON, & BOUCOT, 1967, p. 411 [**Stropheodonta sefinensis* WILLIAMS, 1951, p. 124; OD]. Profile concavoconvex, usually transverse, with thin body cavity; ornament finely costellate to unequally parvicostellate, sometimes with accentuated median rib; denticles on denticular plate; few denticles may be present along short distance of dorsal hinge line near umbo; ventral muscle field weakly impressed, without bounding ridges; cardinal process lobes elongate, ventrally directed, situated between thin, short socket ridges; dorsal muscle field very weakly impressed; weak dorsal myophragm posteriorly only. *Ordovician (Ashgill)–Silurian (Telychian):* cosmospolitan.——FIG. 185,*2a–e*. **E. sefinensis* (WILLIAMS), Rhydings Formation, Aeronian, River Sefin, Llandovery, Dyfed, Wales; *a,* partly exfoliated ventral exterior, BMNH BB 95809, ×3; *b,* holotype, internal mold of ventral valve, SM 30051, ×2; *c,d,* ventral, posterior views of ventral internal mold, BMNH BB 95813, ×3; *e,* internal mold of dorsal valve, BMNH BB 95790, ×3 (new).

Mesopholidostrophia Williams, 1950, p. 278 [**Pholidostrophia (M.) nitens;* OD] [=*Mesolissostrophia* Williams, 1950, p. 280 (type, *Lissostrophia (M.) pellucida;* OD, from same type locality as *P. (M.) nitens*)]. Similar to *Eopholidostrophia* in outline, profile, but ornament weak or almost absent; pedicle tube often preserved; nacreous shell often developed; denticulation spread along one-third to half of hinge line; ventral process present; cardinal process small, erect; dorsal muscle field weakly impressed posteriorly, open anteriorly; weak dorsal myophragm. *Silurian (Telychian–Ludlow):* cosmopolitan.——Fig. 185,*1a–e.* **M. nitens* (Williams), Mulde Marl, Homerian, Klintehamn, Gotland, Sweden; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH BC 12836, ×3 (new); *d,* ventral interior, USNM 116024b, ×3; *e,* dorsal interior, USNM 116024c, ×3 (Willliams, 1953a).

Mongolostrophia Rozman & Rong, 1993, p. 39 [**?Leptodonta ludmilae* Rozman, 1992, p. 19; OD]. Similar to *Origostrophia,* but with ornament of coarse wavy costellae with wide interspaces, prominent growth lines. *Silurian (Llandovery):* Mongolia.——Fig. 185,*3a–c.* **M. ludmilae* (Rozman), Baidarik Formation, Aeronian, Gobi Altai, Mongolia; *a,* ventral exterior, PAN 3980/1343, ×2; *b,* ventral internal mold, PAN 3980/1850, ×5; *c,* dorsal internal mold, PAN 3980/1847, ×10 (Rozman & Rong, 1993).

Origostrophia Mitchell, 1977, p. 115 [**O. fragilis;* OD]. Transverse outline, gently concavoconvex profile; fine parvicostellate ornament with single enhanced median costella; hinge line bearing narrow but very wide denticular plates, each bearing 5 to 16 denticles, extending along hinge line for up to half its width; no dental plates; dorsal interior as in *Eopholidostrophia. Ordovician (Ashgill):* Ireland. ——Fig. 185,*4a–d.* **O. fragilis,* Killey Bridge Formation, Ashgill, Pomeroy, Northern Ireland; *a,b,* holotype, latex casts of ventral exterior, interior, GSM GU998-9, ×4; *c,d,* internal mold of dorsal valve, latex cast, GSM GU1007, ×4 (new).

Family STROPHODONTIDAE

Caster, 1939

[*nom. correct.* Rong & Cocks, 1994, p. 666, *pro* Stropheodontidae Caster, 1939, p. 26] [=Pholidostrophiidae Sokolskaya, 1960, p. 215, *nom. transl. pro* Pholidostrophiinae Stainbrook, 1943, p. 44; Lissostrophiidae Harper & Boucot, 1978, p. 38]

Hinge line denticulate; ventral muscle field strongly impressed, but muscle-bounding ridges absent anteriorly, usually laterally; ventral muscle field subcircular to suboval; dorsal muscle field subelliptical, usually elevated on platform with bounding ridges; central dorsal median ridge or septum often present; dorsal side septa usually, but not always, developed. *Silurian (Ludlow)–Devonian (Frasnian).*

Strophodonta Hall, 1850, p. 348 [**Strophomena demissa* Conrad, 1842, p. 258; OD] [=*Cymbistropheodonta* Harper & Boucot, 1978, p. 38 (type, *Strophodonta cymbiformis* Swallow, 1860, p. 635; OD)]. Profile moderately to strongly concavoconvex; uniformly costellate ornamentation, varying from fine to coarse; entire hinge line denticulate; ventral muscle field moderately impressed, bilobed, but with no bounding ridges; adductor, diductor scars clearly differentiated; radial ridges variably developed in anterior part of diductor scars; cardinal process lobes strong, posteriorly directed, usually joined at their bases to form U-shaped structure; socket ridges very small, divergent; variably elevated dorsal muscle field with two pairs of adductor scars, lateral pair larger than median pair; prominent muscle-bounding ridges; short central dorsal median septum, short dorsal side ridges variably developed; subperipheral rim usually present. *Silurian (Přídolí)–Devonian (Frasnian):* North America, Europe.

S. (**Strophodonta**). Similar to *S. (Asturistrophia)* but with weaker socket ridges and elevated dorsal muscle field. *Silurian (Přídolí)–Devonian (Frasnian):* North America, Europe.——Fig. 186,*2a–e.* **S. (S.) demissa* (Conrad); *a–c,* ventral, dorsal, lateral views of conjoined valves, Hamilton Group, Eifelian–Givetian, Arkona, Ontario, Canada, BMNH B 75070, ×1.5; *d,* ventral interior, Hamilton Group, Eifelian–Givetian, Sylvania, Ohio, BMNH BB 23316, ×1; *e,* dorsal interior, Upper Ferron Point Formation (Givetian), Alpena County, Michigan, BMNH BB 16568, ×1.5 (new).——Fig. 186,*2f,g. S. (S.) cymbiformis* (Swallow), Hamilton Group, Frasnian, Fulton, Missouri; *f,g,* ventral, lateral views of ventral exterior, BMNH B 39797, ×1.5 (new).

S. (**Asturistrophia**) García-Alcade, 1992, p. 72 [**A. insolita;* OD]. Similar to *S. (Strophodonta)* but stronger socket ridges, dorsal muscle field not elevated; dorsal subperipheral rim more marked. *Devonian (Emsian)*: Europe.——Fig. 186,*1a–c.* **S. (A.) insolita,* La Ladrona Formation, upper Emsian, La Vela, Arnao, Avilés, Asturias, Spain; *a,* dorsal exterior, DPO 26399, ×1; *b,* ventral interior, DPO 27119, ×2; *c,* dorsal interior, DPO 26400, ×1 (García-Alcade, 1992).

Arbizustrophia García-Alcalde, 1972, p. 57 [**A. diaphragmata;* OD]. Small size; concavoconvex to planoconvex profile; evenly parvicostellate ornament; convex pseudodeltidium; weakly curved ventral muscle-bounding ridges posterolaterally; muscle field open anteriorly; dorsal interior as in

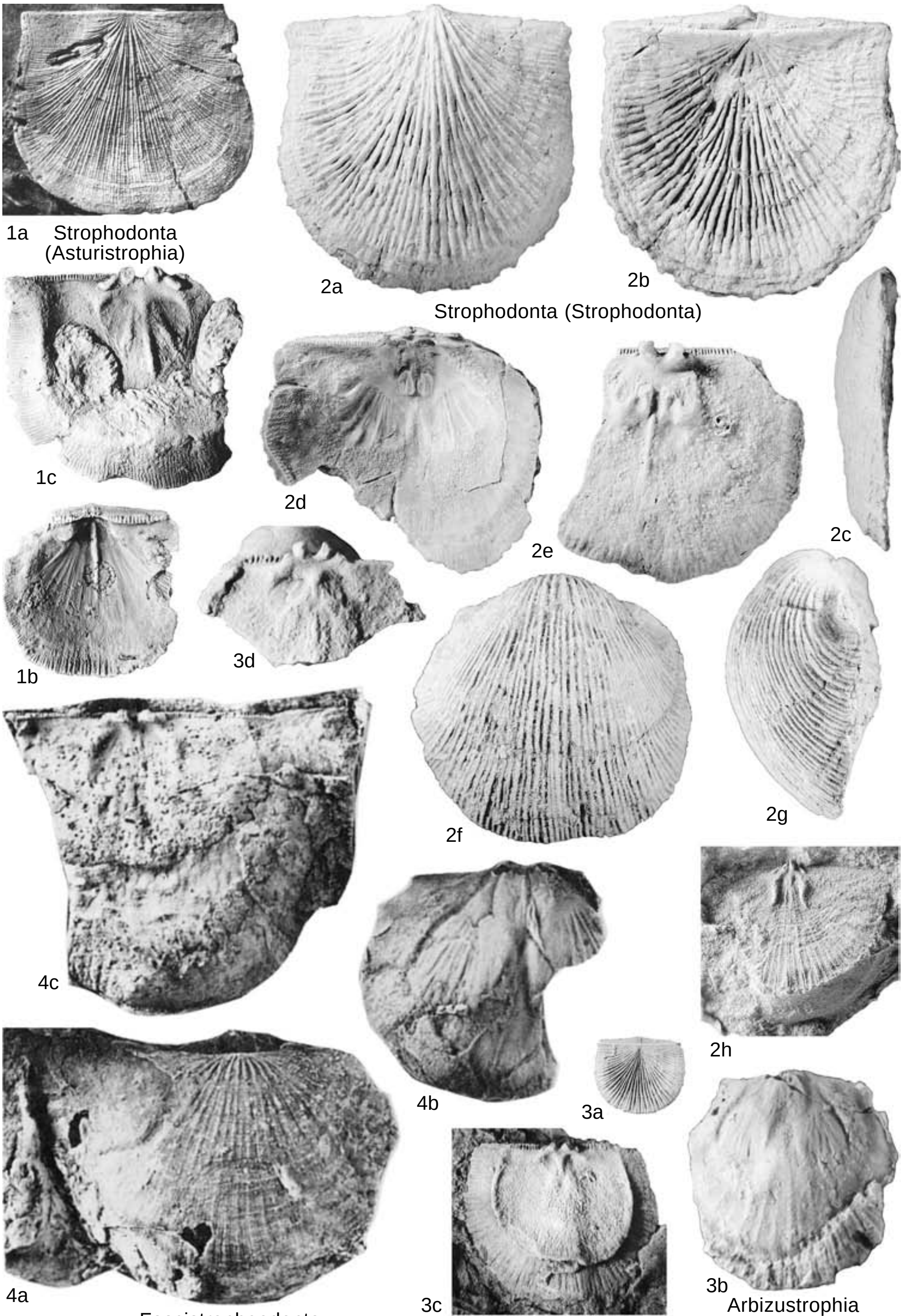

FIG. 186. Strophodontidae (p. 292–294).

Strophodonta except denticles extending only half valve width, dorsal muscle-bounding ridges scarcely developed, diaphragm more pronounced. *Devonian (Emsian):* Europe.——FIG. 186,*3a–d*. **A. diaphragmata,* Aguion Formation, Emsian; *a,* holotype, dorsal view of conjoined valves, Avilés, DPO 2622, ×1; *b,* ventral internal mold, Avilés, DPO 2663, ×2; *c,* dorsal interior, Luanco, Asturias, Spain, DPO 26563, ×2; *d,* fragment of dorsal interior showing cardinalia, Avilés, DPO 26747, ×3 (García-Alcalde, 1972).

Boucotstrophia JAHNKE, 1981, p. 150 [**Stropheodonta herculea* DREVERMAN, 1904, p. 276; OD]. Profile concavoconvex, weakly dorsally geniculate; ornament unequally parvicostellate to finely costellate; denticles half valve width; ventral muscle field circular, with weak bounding ridges laterally, posteriorly, prominent radial ridges present within muscle field; cardinal process lobes large, close together, ventrally directed; small socket ridges flaring anterolaterally from near cardinal process lobes; elevated, elongate dorsal muscle field with prominent bounding ridges; central dorsal median ridge, faint side septa present. *Devonian (Pragian–Emsian):* Europe.——FIG. 187,*1a–c*. **B. herculea* (DREVERMAN), Seifener Shale, Emsian, Altenkirchen, Germany; *a,* latex cast of dorsal exterior, SMF 66/424, ×1; *b,* ventral internal mold, SMF 72/43, ×0.75; *c,* latex cast of dorsal internal mold, SMF 163/4, ×1 (Jahnke, 1981).

Dictyostrophia CASTER, 1939, p. 40 [**D. cooperi;* OD]. Strongly concavoconvex profile, sometimes weakly geniculate; ornament of coarse angular plications imposed on finer unequal parvicostellae; hinge line entirely denticulate; small short ventral median ridge present; cardinal process lobes posteriorly directed, joined at their bases; socket ridges thin, widely separated from cardinal process lobes; muscle-bounding ridges well developed in dorsal valve; variable muscle platform. *Devonian (Pragian–Eifelian):* cosmopolitan.

D. (**Dictyostrophia**). Similar to *D. (Plicostropheodonta),* but without elevated dorsal muscle platform, dorsal subperipheral rim. *Devonian (Emsian):* South America.——FIG. 187,*3a,b*. **D. (D.) cooperi,* beds of Emsian age, Floresta, Colombia; *a,* dorsal exterior mold, USNM 220648, ×1; *b,* dorsal view of internal mold of conjoined valves, USNM 220649, ×1 (Harper & Boucot, 1978).

D. (**Plicostropheodonta**) SOKOLSKAYA, 1960, p. 214 [**Orthis murchisoni* DE VERNEUIL & D'ARCHIAC in D'ARCHIAC & DE VERNEUIL, 1842, p. 371; OD]. Similar to *D. (Dictyostrophia),* but stronger plications, stronger dorsal muscle platform, dorsal subperipheral rim. *Devonian (Pragian–Eifelian):* Europe, Africa, New Zealand.——FIG. 187,*4a,b*. **D. (P.) murchisoni* (DE VERNEUIL & D'ARCHIAC), Siegenian Beds, Humerich, Oberstadfeld, Eifel, Germany; posterior, ventral views of ventral internal mold, BMNH B 40574, ×1.5 (new).

Fascistropheodonta HARPER & BOUCOT, 1978, p. 24 [**Orthis sedgwicki* D'ARCHIAC & DE VERNEUIL, 1842, p. 371; OD]. Strongly concavoconvex profile; ornament of angular plications, commonly forming fascicostellate bundles, superimposed on fine uniform costellae; large bilobed ventral muscle field with bounding ridges posterolaterally; interior as in *Dictyostrophia* but dorsal muscle field not raised, except posterolaterally, bounding ridges weaker; central dorsal median ridge variably present. *Devonian (Pragian–Eifelian):* Europe.——FIG. 186,*4a–c*. **F. sedgwicki* (D'ARCHIAC & DE VERNEUIL), Wiltzer Schichten, upper Emsian, Daleiden, Eifel, Germany; *a,b,* dorsal external mold, ventral view of internal mold of conjoined valves, USNM 220753, ×1.5; *c,* latex cast of dorsal internal mold, USNM 220757, ×1.5 (Harper & Boucot, 1978).

Galateastrophia HARPER & BOUCOT, 1978, p. 25 [**Stropheodonta galatea* BILLINGS, 1874, p. 20; OD]. Strongly concavoconvex profile; distinctive ornament of strong plications on central part of both valves, anteriorly, laterally weaker, with fine parvicostellae present; hinge line entirely denticulate; variably impressed, large bilobed ventral muscle field, ventral median septum; cardinal process lobes posterior to hinge line, directed posteriorly; divergent socket ridges faint, short; dorsal muscle field small with distinctive transmuscle ridges and muscle-bounding ridges; central dorsal median ridge; dorsal side ridges. *Devonian (Emsian–Givetian):* North America.——FIG. 188,*1a–c*. **G. galatea* (BILLINGS), Grande Grève Limestone, lower Emsian, Indian Cove, Gaspé Bay, Quebec, Canada; *a,* dorsal view of conjoined valves, USNM 220705, ×3; *b,* ventral interior, USNM 220708, ×3; *c,* dorsal interior, USNM 220701, ×3 (Harper & Boucot, 1978).

Gorgostrophia HAVLÍČEK, 1967, p. 136 [**Leptaena neutra* BARRANDE, 1848, p. 231; OD]. Moderately concavoconvex profile; uniformly costellate or unequally parvicostellate ornamentation; denticulation over two-thirds valve width; ventral muscle field large, extending to two-thirds length; diductor, adductor scars separated by narrow myophragm that bifurcates anteriorly; short, wide cardinal process lobes posteroventrally directed; dorsal muscle field weakly impressed; long narrow, dorsal median septum extending anteriorly from near cardinal process. *Devonian (Pragian–Emsian):* Europe.——FIG. 187,*2a–d*. **G. neutra* (BARRANDE), Pragian, Koneprusy, Czech Republic; *a,* ventral exterior, Vinarice Limestone, Pragian, Certovy schody, OMR VH 416, ×1.4; *b,* ventral interior, Koneprusy Limestone, NM L6743, ×1.5; *c,* ventral internal mold, Koneprusy Limestone, OMR VH 415a, ×1.5; *d,* dorsal internal mold, Vinarice Limestone, Certovy schody, OMR VH 416b, ×2 (Havlíček, 1967).

Khangaestrophia MENDBAJAR, 1994, p. 40 [**K. raissae;* OD]. Strongly concavoconvex profile; ornament of coarse costellae with sharp crests interspersed with fine parvicostellae; very small dental plates; ventral muscle field bilobed to subcircular; lateral muscle-bounding ridges that only originate near hinge line separately from and lateral to dental plates; very fine ventral median septum; weak myophragm devel-

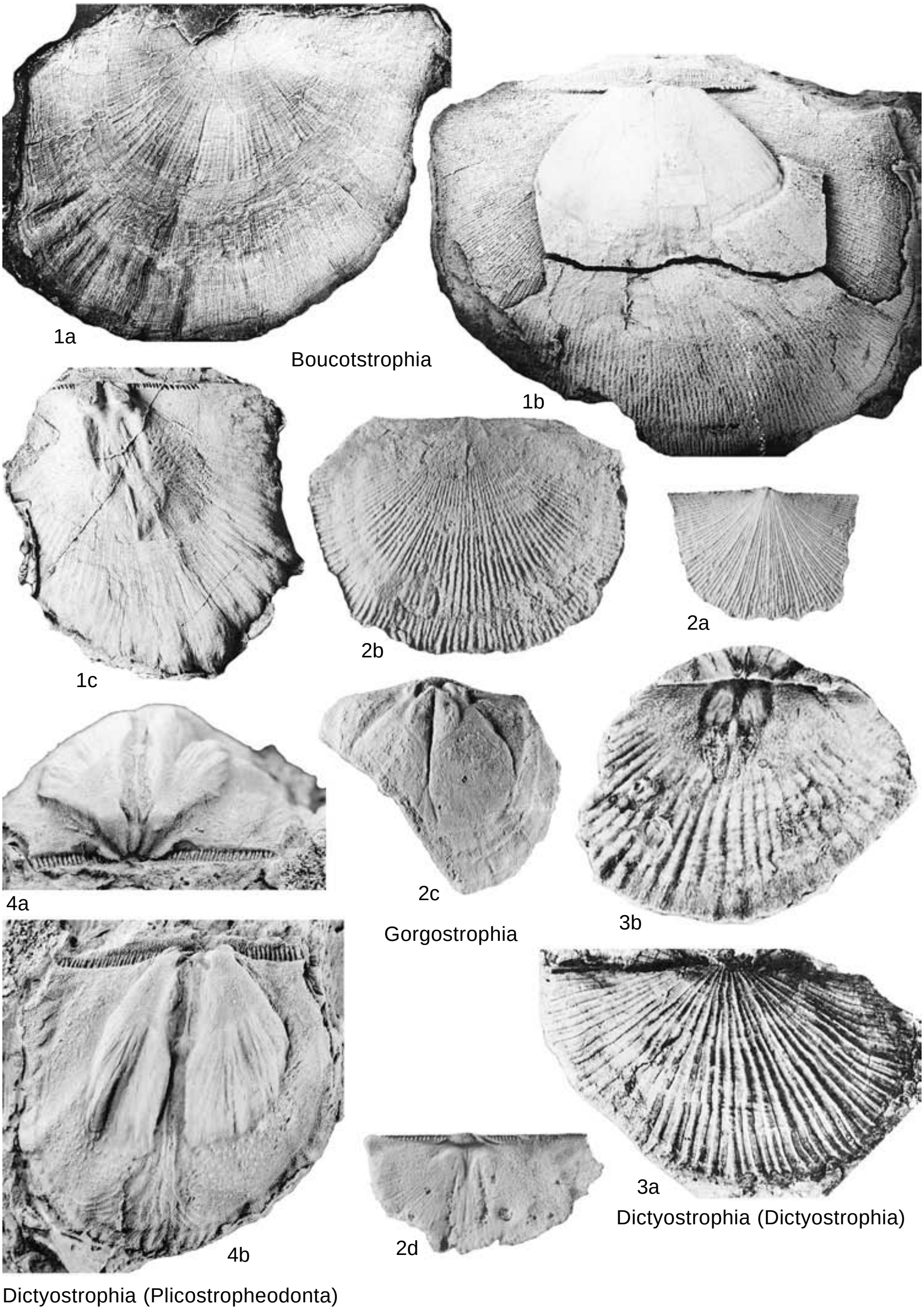

FIG. 187. Strophodontidae (p. 294).

oped posteriorly; cardinal process lobes erect, directed posteroventrally; dorsal muscle field with lateral curved bounding ridges, bisected by median septum reaching to half valve length. *Devonian (Emsian):* Mongolia.——FIG. 188,*2a–d*. **K. raissae,* Chulinsk Formation, Emsian, Terchin-Tsagaan-Nuur, Mongolia; *a,* ventral exterior mold, PAN 4131/13, ×1.5; *b,* enlarged to show ornament, PAN

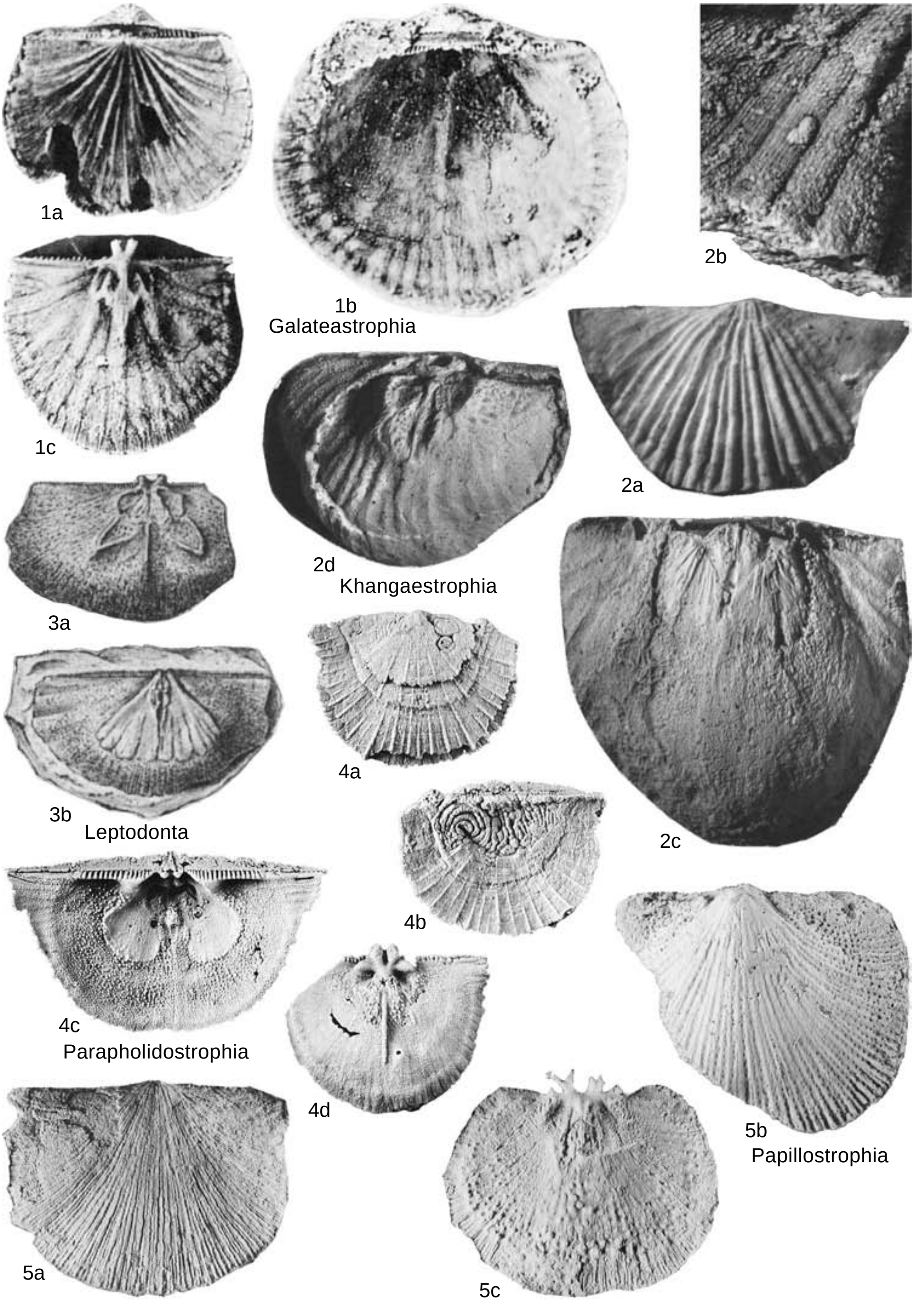

FIG. 188. Strophodontidae (p. 294–297).

4131/10, ×7; *c,* ventral internal mold, PAN 4131/14, ×1.5; *d,* holotype, latex cast of dorsal internal mold, PAN 4131/12, ×1.5 (Alekseeva, new).

?Leptodonta KHALFIN, 1955, p. 237, *nom. nov. pro Oehlertia* KHALFIN, 1948, p. 256, *non* PERNER, 1907 [*?*Leptaena leblanci* ROUAULT, 1851, p. 393; OD].

Strongly concavoconvex profile; ornament of uniform coarse costellae; ventral muscle field strongly impressed posteriorly but not anteriorly; muscle-bounding ridges absent; cardinal lobes posteriorly directed, extended posterior to hinge line; socket ridges absent; dorsal muscle field weakly impressed; central dorsal median ridge variably developed; weak side ridges present; topotype material not located, so revision is needed; hence queried family assignment. *Devonian (Pragian–Eifelian):* Europe, Turkey.——Fig. 188,*3a,b.* **L. leblanci* (Rouault), Emsian beds, Izé, Rennes, France; *a,* ventral internal mold, ×2; *b,* dorsal interior, ×1 (Oehlert, 1886).

Lissostrophia Amsden, 1949, p. 202 [**L. cooperi;* OD]. Minute; strongly concavoconvex profile shells with conspicuous ventral umbo; subcircular in outline; no ornament; ventral muscle field small, slightly divergent; cardinal process lobes pronglike, united at base, posteriorly directed beyond hinge line; socket ridges absent; dorsal muscle field weakly impressed, with thick bounding ridges posterolaterally; thick pair of dorsal transmuscle ridges slightly divergent. *Silurian (Ludlow):* North America.——Fig. 189,*2a–d.* **L. cooperi,* Henryhouse Formation, Ludlow, Ada, Pontotoc County, Oklahoma; *a,b,* dorsal, lateral views of conjoined valves, BMNH BC 13001, ×3 (new); *c,* ventral interior, USNM 115379, ×3; *d,* dorsal interior, USNM 115382, ×3 (Williams, 1953a).

Megastrophia Caster, 1939, p. 37 [**Stropheodonta concava* Hall, 1857, p. 140; OD]. Large shells, with strongly concavoconvex profile; ornament costellate to unequally parvicostellate; denticulate along two-thirds of hinge line; ventral muscle field varying from elongate to transverse, muscle-bounding ridges absent except in few gerontic individuals; cardinal process lobes massive, wide, joined at their base to form U-shaped structure, projecting posterior to hinge line; socket ridges small, thin, widely divergent; elevated dorsal muscle field with strong bounding ridges; small central dorsal septum; two very short dorsal side septa. *Devonian (Emsian–Givetian):* North America, Asia (Altai-Sayan).——Fig. 189,*1a–e.* **M. concava* (Hall), Givetian; *a,b,* ventral, lateral views of conjoined valves, Hamilton Group, York, AMNH 37197, ×1; *c,* ventral interior, Hamilton Group, Canandaigua Lake, AMNH 37196, ×1; *d,* dorsal interior, Hamilton Group, Darien, New York, BMNH B 9580, ×1; *e,* partial dorsal interior showing cardinal process, Silica Shale, Travers Group, Sylvania, Ohio, BMNH BB 16709, ×1.5 (new).

Minutostropheodonta Harper & Boucot, 1978, p. 30 [**Leptaena subtransversa* Schnur, 1854, p. 223; OD]. Small shells with transverse outline; profile strongly concavoconvex; distinctive ornament of widely spaced costellae separated by broad arched or flat areas on ventral valve, corresponding slightly concave areas on dorsal valve; dorsal valve may have superimposed coarse plications centrally but not anteriorly; denticles over half valve width; ventral muscle field not bounded by ridges, strongly impressed, extending up to two-thirds valve length; cardinal process lobes posteriorly directed, overhanging hinge line; socket ridges widely divergent; dorsal muscle field elevated on prominent platform; central dorsal median septum extends from platform to subperipheral ridge. *Devonian (Eifelian):* Germany.——Fig. 190,*2a–d.* **M. subtransversa* (Schnur), Rommersheimer Schichten, Eifelian, Gerolstein, Eifel, Germany; *a,b,* ventral, lateral views of conjoined valves, BMNH B 39638, ×4 (new); *c,* ventral interior, USNM 220822, ×3; *d,* dorsal interior, USNM 220802, ×5 (Harper & Boucot, 1978).

?Neumanella Harper & Boucot, 1978, p. 29 [**N. varimya;* OD]. Similar to *Leptodonta* in outline, profile, ornament, but with narrower ventral muscle field; lacking central dorsal median septum, dorsal side septa; family uncertain. *Silurian (Ludlow, ?Přídolí):* North America.——Fig. 191,*2a–c.* **N. varimya,* Přídolí beds, Scraggly Lake, Maine; *a,* latex of external mold of conjoined valves, USNM 220732, ×3; *b,* latex of ventral internal mold, USNM 220725, ×3; *c,* latex of dorsal internal mold, USNM 220736, ×1.5 (Harper & Boucot, 1978).

Papillostrophia Havlíček, 1967, p. 132 [**Leptaena consobrina* Barrande, 1848, p. 218; OD]. Concavoconvex profile with geniculation; similar to *Gorgostrophia,* but with dental plates, distinctive papillae on dorsal median, subperipheral ridges. *Devonian (Emsian):* Europe.——Fig. 188,*5a–c.* **P. consobrina* (Barrande); *a,* ventral exterior, Koneprusy Limestone, Pragian, Koneprusy, NM CF395; *b,* ventral internal mold, Koneprusy Limestone, Pragian, Koneprusy, OMR VH 407b, ×2.4; *c,* lectotype, dorsal interior, Zlíchov Limestone, Emsian, U kaplícky, Praha-Hlubocepy, Bohemia, Czech Republic, NM CF395, ×1.5 (Havlíček, 1967).

Parapholidostrophia Johnson, 1971, p. 309 [**P. harperi;* OD]. Outline semicircular; profile concavoconvex; unequally parvicostellate ornament; denticulate over more than half width; bilobed, well-impressed ventral muscle field; similar to *Pholidostrophia,* but shell not nacreous; short socket plates fused to lateral bases of cardinal process lobes; prominent thin dorsal median septum. *Devonian (Emsian–Eifelian):* North America.——Fig. 188,*4a–d.* **P. harperi, Warrenella kirki* Zone of Denay Limestone, Eifelian, Roberts Creek Ranch, southern Roberts Mountains, Nevada; *a,b,* ventral, dorsal views of conjoined valves, USNM 157355, ×2; *c,* holotype, ventral interior, USNM 157354, ×2; *d,* dorsal interior, USNM 157366, ×2 (Johnson, new).

Pholidostrophia Hall & Clarke, 1892, p. 287 [**Strophomena nacrea* Hall, 1857, p. 144; OD]. Transverse, semielliptical outline, moderately concavoconvex profile; commonly smooth, but some specimens with faint traces of radial ornament; distinctive nacreous shell; hinge line denticulate over half valve width; bilobed ventral muscle field impressed, but with no bounding ridges; cardinal process lobes united at their bases, posteriorly directed; socket ridges absent; dorsal muscle field

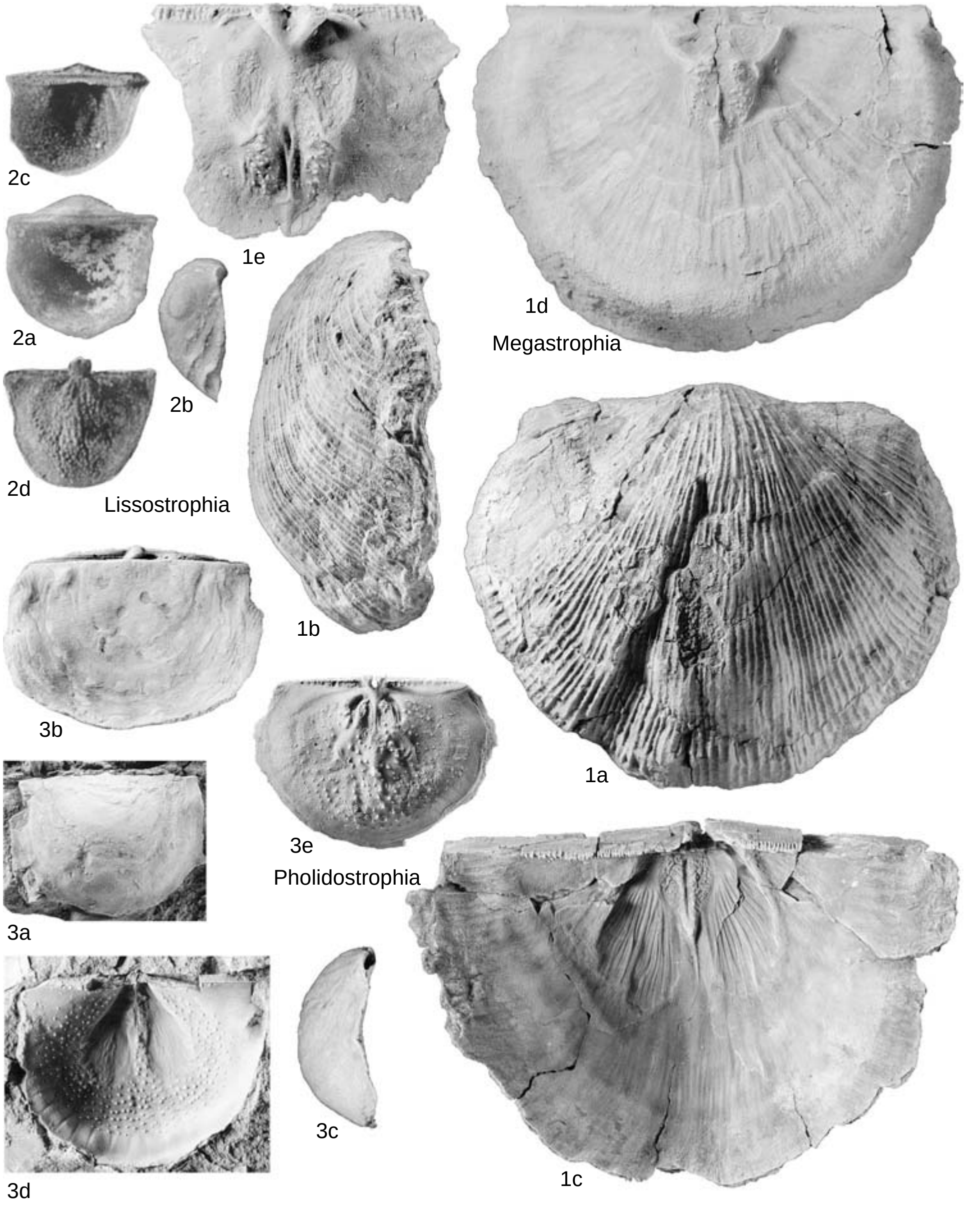

FIG. 189. Strophodontidae (p. 297–298).

differentiated into two pairs; central dorsal median ridge; side ridges variably developed. *Devonian (Emsian–Frasnian):* North America, Europe.——FIG. 189,*3a–e*. **P. nacrea* (HALL), Hamilton Group, Givetian; *a,* ventral exterior, Gennessee Valley, AMNH 37211, ×2; *b,c,* dorsal, lateral views of conjoined valves, York, BMNH B 9579, ×2; *d,* ventral interior, Canandaigua Lake, New York, AMNH 37213, ×2; *e,* dorsal interior, Gennessee Valley, AMNH 37211, ×2 (new).

Pterostrophia GARRATT, 1985, p. 523 [**P. carinatus;* OD]. Strongly convex profile with sharply deflected trail; distinctive parvicostellate ornament with weak small interrupted rugae between primary costellae; denticulate over two-thirds of hinge line; small dental plates; subtriangular to bilobed ventral muscle

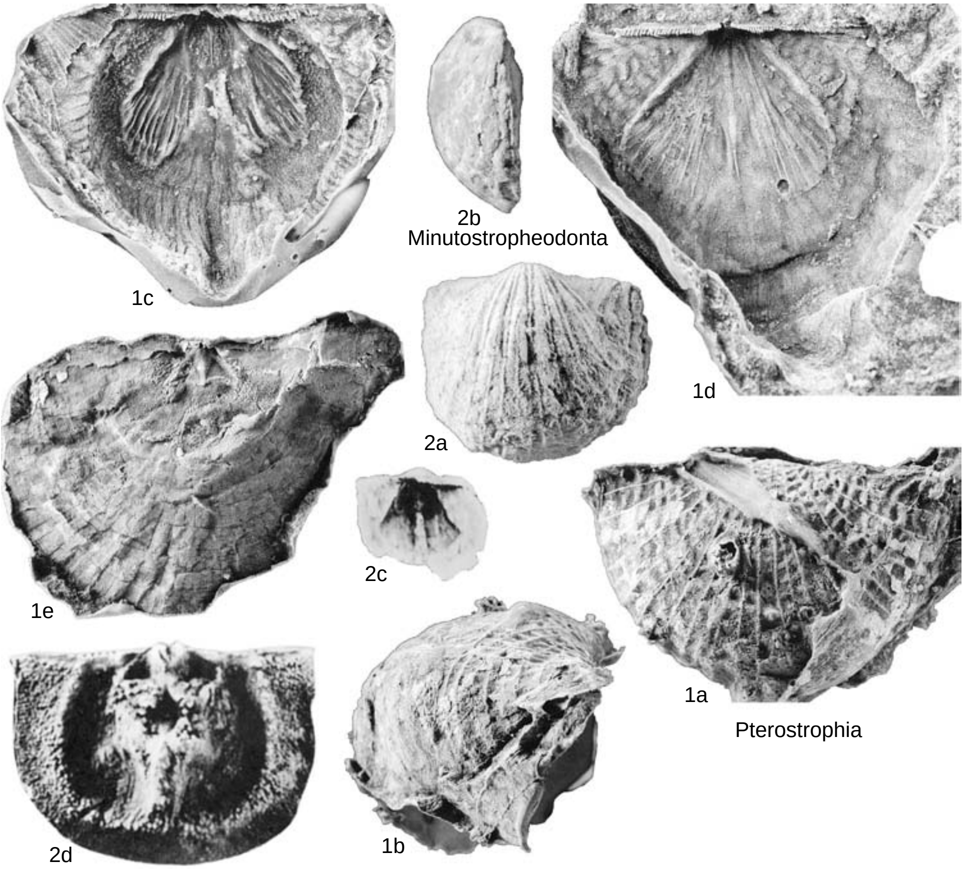

FIG. 190. Strophodontidae (p. 297–299).

field large, flabellate, but variably impressed, particularly centrally; dorsal muscle field faintly impressed, with rare muscle-bounding ridges; short dorsal myophragm; dorsal side septa absent. *Lower Devonian:* Australasia.——FIG. 190,*1a–e.* **P. carinatus,* Humevale Formation, Lower Devonian, Mooroolbark, Lilydale, Victoria, Australia; *a–c,* holotype, external, lateral, internal views of latexes of ventral valve, NMVP P1474, ×1.5; *d,* latex of ventral interior, NMVP P49770, ×1.5; *e,* latex of dorsal interior, NMVP P49496, ×1.5 (new).

Strophonelloides CASTER, 1939, p. 106 [**Strophodonta reversa* HALL, 1858a, p. 494; OD] [?=*Chemungia* CASTER, 1939, p. 106 (type, *Stropheodonta caelata* HALL, 1867c, p. 112; OD)]. Profile resupinate, ventrally gently geniculate except in young individuals (only resupinate genus in family); costellate ornament; denticulate over almost entire hinge line width; ventral muscle field as in *Strophodonta* but with muscle-bounding ridges varying from strong, elevated to absent; weak central furrow developed in ventral subperipheral rim corresponding with median ridge in anterior part of dorsal valve; dorsal muscle field elevated on platform with bounding ridges; weak dorsal subperipheral rim. *Devonian (Frasnian):* North America.——FIG. 191,*1a–e.* **S. reversa* (HALL), Hackberry Formation, Frasnian, Rockford, Iowa; *a,* ventral view of conjoined valves, NYSM 2092, ×1.5; *b,* lateral view of conjoined valves, BMNH B 41670, ×1; *c,* ventral interior, NYSM 2095, ×1.5; *d,* ventral interior, BMNH B 41456, ×2; *e,* dorsal interior, NYSM 2094, ×2 (new).——FIG. 191,*1f–h. S. caelata* (HALL), Chemung Group, Frasnian; *f,* latex cast of ventral internal mold, Blossburg, Pennsylvania, AMNH 37220, ×1; *g,h,* dorsal internal mold, latex cast, Waverly, New York, NYSM 2088, ×1.5 (new).

?Trilobostrophia SHISHKINA, 1983, p. 1229 [*Megastrophia bobilevi* SHISHKINA in GRASIANOVA & SHISHKINA, 1977, p. 34; OD]. Outline transverse, strongly concavoconvex profile, trilobate with anterior fold, sulcus; costellate ornament; large ventral muscle field with bounding ridges posterolaterally; ventral median ridge present; massive cardinal

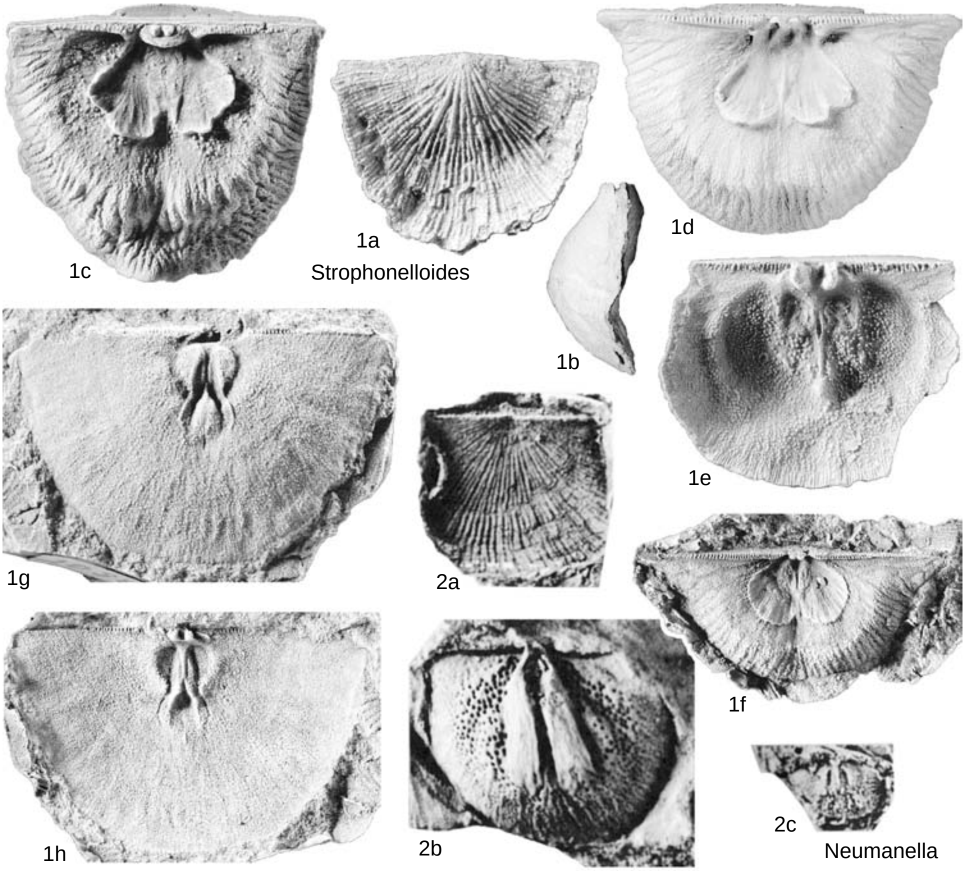

FIG. 191. Strophodontidae (p. 297–299).

process lobes; socket ridges flaring laterally subparallel with hinge line; strongly impressed dorsal muscle field with two pairs of adductor scars differentiated; short central dorsal median septum; requires revision. *Devonian (Emsian):* Siberia.

Family SHALERIIDAE Williams, 1965

[*nom. transl.* HAVLÍČEK, 1967, p. 174, *ex* Shaleriinae WILLIAMS, 1965d, p. 402]

Denticulate hinge line; parallel-sided, elongate diductor muscle scars in ventral valve, bounded laterally by ridges; dorsal median ridge (myophragm) usually present, commonly bifurcating anteriorly. *Silurian (Wenlock)–Devonian (Lochkovian).*

Shaleria CASTER, 1939, p. 33 [**Strophomena gilpeni* DAWSON, 1881, p. 336; OD] [=*Shaleria (Protoshaleria)* HARPER & BOUCOT, 1978, p. 162 (type, *Strophomena ornatella* DAVIDSON, 1871, p. 309; OD)]. Gently concavoconvex profile; not geniculate; ornament unequally parvicostellate, often with small rugae within parvicostellae; denticulate along half valve width; prominent ventral muscle-bounding ridges posterolaterally only, with additional oblique muscle ridges, small ventral process; erect to anteriorly facing cardinal process lobes; short, flaring socket ridges; one or two pairs of dorsal side septa. *Silurian (Ludlow)–Devonian (Lochkovian):* North America, Europe.

S. (**Shaleria**). Similar to *S. (Janiomya)* but with two pairs of relatively large dorsal side septa. *Silurian (Ludlow)–Devonian (Lochkovian):* North America, Europe.——FIG. 192,*3a–d*. **S. (S.) gilpeni* (DAWSON), Stonehouse Formation, Přídolí–Lochkovian, Arisaig, Nova Scotia, Canada; *a,b,* mold, latex cast of ventral interior, USNM 10201, ×2; *c,d,* mold, latex cast of dorsal interior, GSC 19355, ×2 (Harper, 1973).——FIG. 192,*3e–h*. *S. (S.) ornatella* (DAVIDSON), Ludfordian; *e,f,* latex casts of ventral exterior, interior, Llangibby Formation, near Usk, Gwent,

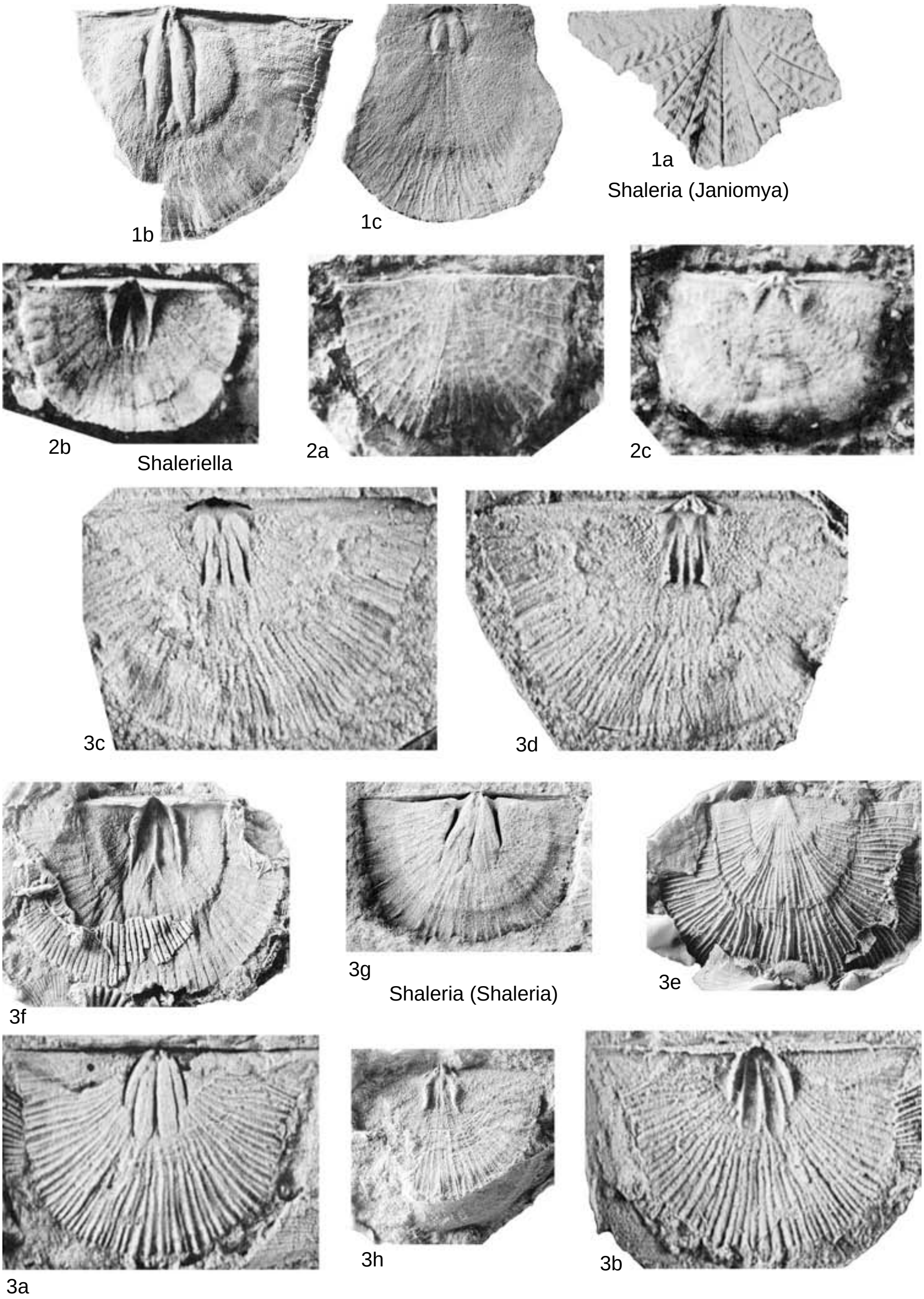

FIG. 192. Shaleriidae (p. 300–302).

Wales, BMNH BC 13115, ×2; *g,* internal mold of ventral valve, Whitcliffe Formation, Ludlow, Shropshire, England, BMNH B 842, ×2; *h,* latex cast of dorsal interior, Llangibby Formation, near Usk, Gwent, Wales, BMNH BC 13112, ×2 (new).

S. (**Janiomya**) Havlíček, 1967, p. 174 [**J. parallelomya;* OD]. Ornament unequally parvicostellate to uniformly costellate; similar to *S. (Shaleria)* but with only single pair of weak, abbreviated lateral dorsal side septa. *Silurian (Ludlow–Přídolí):* Europe.——Fig. 192,*1a,b.* **S. (J.) parallelomya,* Pozary Formation, Přídolí, Svaty Jan pod Skalou, Bohemia, Czech Republic; *a,* holotype, ventral internal mold, OMR VH 445b, ×1.5; *b,* dorsal internal mold, OMR VH 445a, ×1.5 (Havlíček, 1967).——Fig. 192,*1c. S. (J.) flexa* (Havlíček); ventral external mold, Kopaniná Formation, Ludlow, Morina, OMR VH 4230, ×4 (Havlíček, 1967).

Shaleriella Harper & Boucot, 1978, p. 160 [**S. delicata;* OD]. Ornament of distinctive zigzag rugae interrupted by primary costellae over most of central area of valve, but often absent anteriorly; similar to *S. (Shaleria)* but dorsal side septa absent, gently geniculate dorsally. *Silurian (Wenlock–Přídolí):* cosmopolitan.——Fig. 192,*2a–c.* **S. delicata,* Hemse Marl, Gorstian, Hemse Station, Gotland, Sweden; *a,* holotype, ventral exterior, USNM 220911, ×3; *b,* ventral interior, USNM 220913, ×3; *c,* dorsal interior, USNM 220914, ×3 (Harper & Boucot, 1978).

Family STROPHONELLIDAE Caster, 1939

[*nom. transl.* Sokolskaya, 1960, p. 215, *ex* Strophonellinae Caster, 1939, p. 98]

Resupinate profile; hinge line denticulate; ventral muscle field subquadrate, with muscle-bounding ridges well developed except in *Eostrophonella. Silurian (Rhuddanian)–Devonian (Emsian).*

Strophonella Hall, 1879, p. 153 [**Strophomena semifasciata* Hall, 1863b, p. 210; OD] [=*Costistrophonella* Harper & Boucot, 1978, p. 99 (type, *Strophomena punctulifera* Conrad, 1838, p. 117; OD); *Strophoprion* Twenhofel, 1914, p. 25 (type, *Brachyprion geniculatum* Shaler, 1865, p. 63; OD)]. Ornament variably costellate; hinge line denticulate over most of valve width; no dental plates; ventral muscle field subquadrate, usually with well-developed muscle-bounding ridges except anteriorly at valve center; cardinal process lobes short, swollen, directed posteroventrally; dorsal muscle field weakly impressed. *Silurian (Wenlock)–Devonian (Emsian):* cosmopolitan.

S. (**Strophonella**). Similar to *S. (Quasistrophonella),* but with finely costellate or parvicostellate ornament not separated by smooth interspaces. *Silurian (Wenlock)–Devonian (Emsian):* cosmopolitan.——Fig. 193,*2a.* **S. (S.) semifasciata* (Hall), Niagara Group, Wenlock, Waldron, Indiana; lectotype, dorsal exterior, AMNH 1932, ×1 (new).——Fig. 193,*2b–e. S. (S.) punctulifera* (Conrad), Lochkovian; *b,c,* dorsal, lateral views of partly exfoliated dorsal valve, lower Helderberg Group, Port Colburn, Ontario, Canada, AMNH 33070, ×1; *d,* internal mold of ventral valve, lower Helderberg Group, Schoharie, New York, BMNH B 9290, ×1; *e,* dorsal interior, BMNH B 74973, ×1 (new).

S. (**Quasistrophonella**) Harper & Boucot, 1978, p. 98 [**Leptaena bohemica* Barrande, 1848, p. 243; OD]. Similar to *S. (Strophonella),* but with broad smooth interspaces between costellae. *Silurian (Ludlow)–Devonian (Emsian):* Europe.——Fig. 193,*1a,b.* **S. (Q.) bohemica* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* dorsal exterior, NM L6686, ×1; *b,* internal mold of dorsal valve, OMR VH 508, ×1 (Havlíček, 1967).

Eostrophonella Williams, 1950, p. 281 [**Strophonella davidsoni* Holtedahl, 1916, p. 64; OD]. Outline, profile as in *Strophonella;* dental plates; denticles confined to denticular plates in ventral valve, variably developed on posterior margins of sockets in dorsal valve; muscle field faintly impressed in both valves; cardinal process lobes elongate as in *Kjerulfina. Silurian (Rhuddanian–Aeronian):* Europe.——Fig. 193,*3a–e. E. eothen* (Bancroft), Haverford Mudstone Formation, Rhuddanian, Gasworks, Haverfordwest, Dyfed, Wales; *a,b,* exterior, interior dorsal molds, BMNH BB 771016, ×1; *c,* ventral internal mold, BMNH BB 71005, ×1; *d,* latex cast of dorsal internal mold, ×1.5; *e,* enlargement of cardinalia, BMNH BC 50617, ×6 (new).

Family UNCERTAIN

Douvinella Ljaschenko, 1985, p. 12 [**D. parva;* OD]. Concavoconvex profile, unequally parvicostellate ornament; ventral interior with denticulate hinge line, muscle field expanded anteriorly as in *Parastrophonella;* dorsal interior unknown. *Devonian (Frasnian):* Timan, Russia.

Gunnarella Spjeldnaes, 1957, p. 149 [**Strophomena (G.) delta;* OD]. Resupinate; ornament of rugae interrupted by costellae; dorsal valve interior unknown, but possibly within Strophomenidae. *Ordovician (Caradoc):* Baltic.——Fig. 194,*2a,b.* **G. delta,* Solvang Formation, upper Caradoc, Gasøya, Oslo district, Norway; dorsal, lateral views of dorsal valve, PMO L63, ×1.5 (new).

Idioglyptus Northrop, 1939, p. 172 [**I. stigmatus;* OD]. Exteriors of type specimens have ornament of interrupted rugae as in *Cymostrophia,* but interiors unknown, thus genus considered *nomen dubium. middle Silurian:* West Point Formation, middle Silurian, West Point, Port Daniel region, Chaleur Bay, Gaspé Peninsula, Quebec, Canada.

Playfairia Reed, 1917, p. 866 [**Strophomena deltoidea* Conrad, 1839, p. 64; OD]. Profile concavoconvex, with parvicostellate ornament; dorsal valve interior unknown, but possibly within Rafinesquinidae. *Ordovician (Caradoc):* North America.——Fig. 194,*3a,b.* **P. deltoidea* (Conrad), Trenton Group, Caradoc, Trenton Falls, New York; *a,* lectotype, dorsal exterior, AMNH 701A, ×1.5; *b,* partly exfoliated ventral exterior, AMNH 701B, ×1.5 (new).

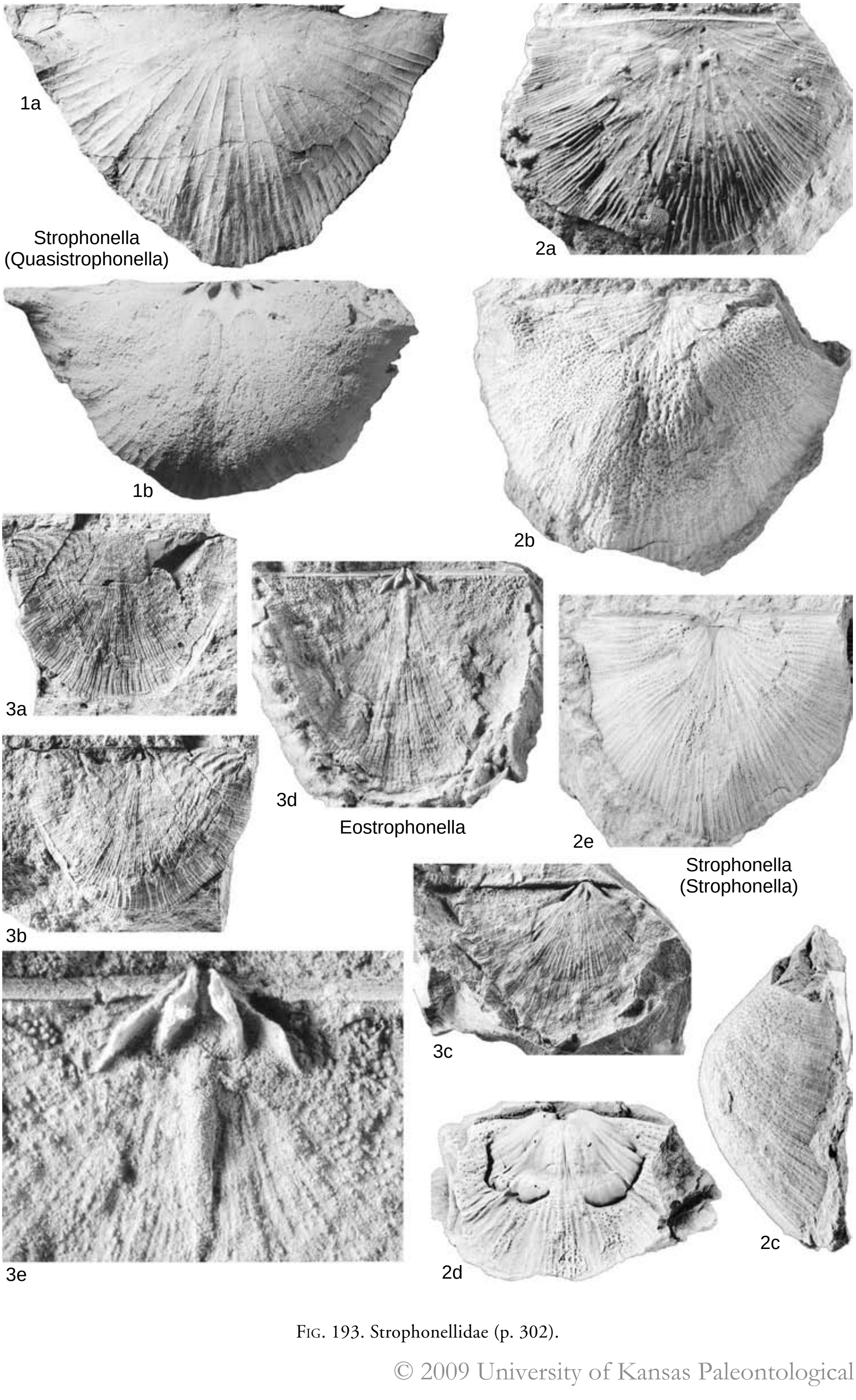

FIG. 193. Strophonellidae (p. 302).

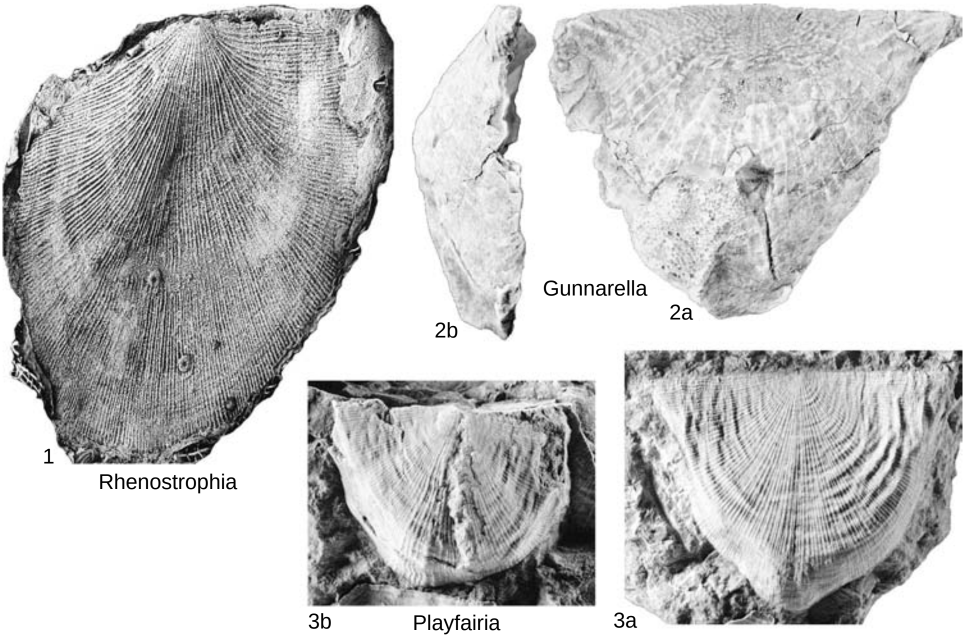

FIG. 194. Uncertain (p. 302–304).

Rhenostrophia BOUCOT, 1960b, p. 483 [**Orthis subarachnoidea* D'ARCHIAC & DE VERNEUIL, 1842, p. 372; OD]. Only holotype, exterior of ventral valve, known; although undoubtedly strophomenoid, without knowledge of interior must remain a *nomen dubium. Lower Devonian (Emsian):* Germany.——FIG. 194,*1.* **R. subarachnoidea* (D'ARCHIAC & DE VERNEUIL), Laubacher Schichten, upper Emsian, Kemmenau, near Ems, Nassau, Germany; holotype, ventral exterior, École de Mines, Orsay, ×1 (Jahnke, new).

Syntrophodonta STRUVE, 1982, p. 198 [**S. paeckelmanni;* OD]. Although hinge line denticulate, uncertain if genus (known only from single ventral valve internal mold) is within Strophomenida since shell structure unknown; ventral muscle field elevated, bounded anterolaterally by pair of raised plates not quite meeting centrally; even if strophomenoid, family unknown. *Devonian (Givetian):* Grossilbeck Member, Mergelsberg Formation, Gross-Illbeck, Ratingen, Germany.

Superfamily PLECTAMBONITOIDEA Jones, 1928

[*nom. transl.* COOPER & WILLIAMS, 1952, p. 332, *ex* Plectambonitinae JONES, 1928, p. 394]

Shell fibrous, pseudopunctate; shell outline generally semicircular with straight hinge line; profile normally concavoconvex, occasionally resupinate; ornamentation variable, but generally unequally parvicostellate; external spines absent; supra-apical pedicle foramen present, although usually closed, nonfunctional in adults; pseudodeltidium and chilidium present to variable degrees; articulation chiefly of simple teeth (usually supported by short dental plates), sockets, hinge line denticles rarely developed; ventral muscle field usually bilobed with muscle-bounding ridges varying from strong to absent; cardinal process with simple median ridge, sometimes with subsidiary lateral ridges to become trifid, never bifid (although there are a few genera with no cardinal process); dorsal valve including variably developed or absent median septum, paired side septa; dorsal muscle field often on elevated bema (originating posterocentrally) or platform (originating posterolaterally); mantle canals often present but variable in form. *Ordovician (Tremadoc)–Devonian (Eifelian).*

Revision of this superfamily has revealed a relatively limited range of morphologies within it. The valve profile, for example, varies between concavoconvex and convexo-

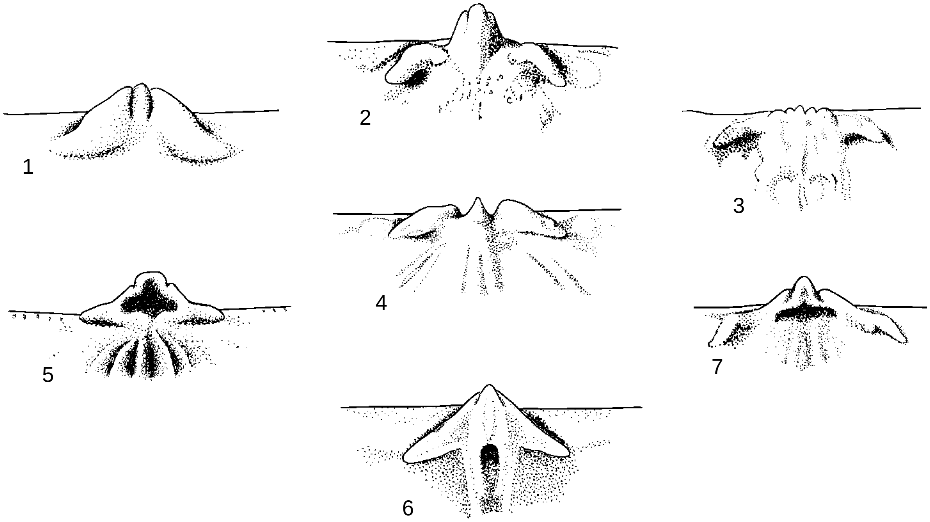

FIG. 195. Cardinal processes of various Plectambonitoidea; *1,4,* simple, ankylosed anteriorly to valve floor (*1,* Taffiidae: *Spanodonta,* ×6; *4,* Bimuriidae: *Bimuria,* ×4); *2,3,* trifid, ankylosed anteriorly to valve floor (Leptellinidae: *2, Leptelloidea,* ×6; *3, Leptellina,* ×6); *5–7,* trifid, undercut anteriorly (Sowerbyellidae: *5, Eoplectodonta,* ×6; *6, Gunningblandella,* ×7; *7, Sowerbyella,* ×7) (new).

concave (resupinate) and can determine differences only between genera, and ornament too is very repetitive. Similarly the presence or absence of a pseudodeltidium in the ventral valve or a chilidium in the dorsal valve, even though sometimes difficult to determine with the vagaries of preservation, seems of little classificatory value above generic rank. The ventral valve interior is also relatively conservative, with, in many stocks, a bilobed muscle field confined posterocentrally by the space between the simple teeth. The presence or absence of dental plates in the superfamily is only of significance at the generic level, and not always then. It is only in the dorsal valve that a variety of structures can be found that are useful for suprageneric classification and identification. Chief is the cardinal process, which varies from family to family between being simple, with a ridge growing from the notothyrial floor, to trifid, *i.e.,* with an extra pair of ridges on either side of the central ridge, and finally what is termed here trifid and undercut, in which the central ridge and its partners are not ankylosed anteriorly to the valve floor, but supported laterally (FIG. 195). Another key feature is the presence or absence of a bema, a thickened pad of secondary shell originating posterocentrally, sometimes as an extension of socket ridges, and upon which the dorsal valve muscle field and other structures are located. The bema is not to be confused with the platform, which in contrast originates posterolaterally and is much closer to the anterior valve margin than the bema. Some plectambonitoids, e.g., *Leangella* (FIG. 196) have both bema and platform. Thus the platform represents chiefly the area occupied by the lophophore, while the bema serves as the area for attachment and elevation of the dorsal muscle field. The dorsal muscle field may be transversely or obliquely divided. The final feature used to distinguish between families is the presence or absence of dorsal side septa, which are paired septa running obliquely across the interior of the dorsal valve.

Family PLECTAMBONITIDAE
Jones, 1928

[*nom. transl.* KOZŁOWSKI, 1929, p. 108, *ex* Plectambonitinae JONES, 1928, p. 394]

Transverse outline, width always greatest at cardinal extremities; concavoconvex to gently resupinate profile; dental plates

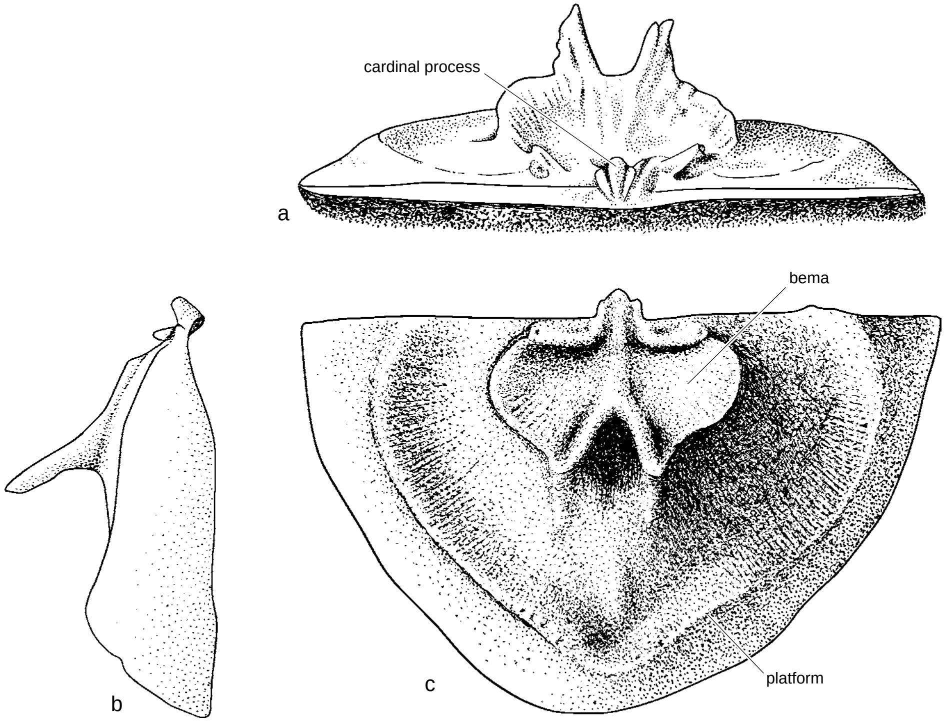

FIG. 196. Dorsal interior of *Leangella (L.) gibbosa* showing trifid cardinal process ankylosed anteriorly to valve floor, elevated bema, and edge of prominent platform; *a–c,* posterior, lateral, dorsal views, ×9 (Cocks & Rong, 1989).

usually present; simple cardinal process, not undercut; no bema; side septa usually present. *Ordovician (Tremadoc–lower Caradoc).*

Subfamily PLECTAMBONITINAE Jones, 1928

[Plectambonitinae Jones, 1928, p. 394] [=Plectellinae Schuchert & Cooper, 1931, p. 245, assigned to Clitambonitidae]

Differs from Taphrodontinae in possessing hinge line denticles and in having simple dorsal median septum. *Ordovician (Tremadoc–Llandeilo).*

Plectambonites Pander, 1830, p. 90 [**P. planissimus;* SD Hall & Clarke, 1892, p. 296]. Concavoconvex profile; distinctive unequally parvicostellate ornament but not with granular texture; small chilidium, pseudodeltidium not filling delthyrium; denticles over half valve width; dental plates present, confining posterolateral part of ventral muscle field that is flabellate, open anteriorly; similar to *Plectella* but more convex (sometimes geniculate), with side septa in dorsal valve more pronounced, more numerous, more complex; weak dorsal platform present. *Ordovician (Llanvirn–Llandeilo):* Baltic.——FIG. 197,*1a–e.* **P. planissimus,* Aseri Horizon, upper Llanvirn; *a–c,* ventral, dorsal, lateral views of conjoined valves, Pavlovsk, TAGI BR 345, ×3; *d,* ventral interior, Pavlovsk, TAGI BR 346, ×3; *e,* dorsal interior, Putilovo, St. Petersburg, Russia, BMNH BC 13030, ×3 (new).

?Akelina Severgina, 1967, p. 133 [**A. akelina;* OD] [=*Humaella* Zhu, 1982, p. 53 (type, *H. huangbanjiensis*)]. Concavoconvex to planoconvex profile; reticulate ornamentation; no dental plates; faintly impressed bilobed ventral muscle field; strong dorsal median septum, with ridges in dorsal valve interpreted as side septa; familial assignment uncertain due to variable morphology in the few assigned specimens. *Ordovician (Tremadoc):* Asia.——FIG. 197,*3a–d.* **A. akelina,* Algan Formation, upper Tremadoc, River Akel, Kusnetz Alatau, Altai Mountains, Russia; *a,* ventral interior, CNIGR 424/1323, ×4; *b,* ventral exterior, CNIGR 1030/11323, ×3; *c,* dorsal interior, CNIGR 1027/1323, ×3; *d,* dorsal interior, CNIGR 427/1323, ×4 (Cocks & Rong, 1989).——FIG. 197,*3e,f. A. huangbanjiensis,* Huangbanjishan Formation, Tremadoc, Fulintun, west of Xinglong, Huma County, Heilongjiang Province, China; *e,* ventral internal mold, SIGM LBr 81047, ×4; *f,* dorsal internal mold, SIGM LBr 81041, ×4 (Zhu, 1982).

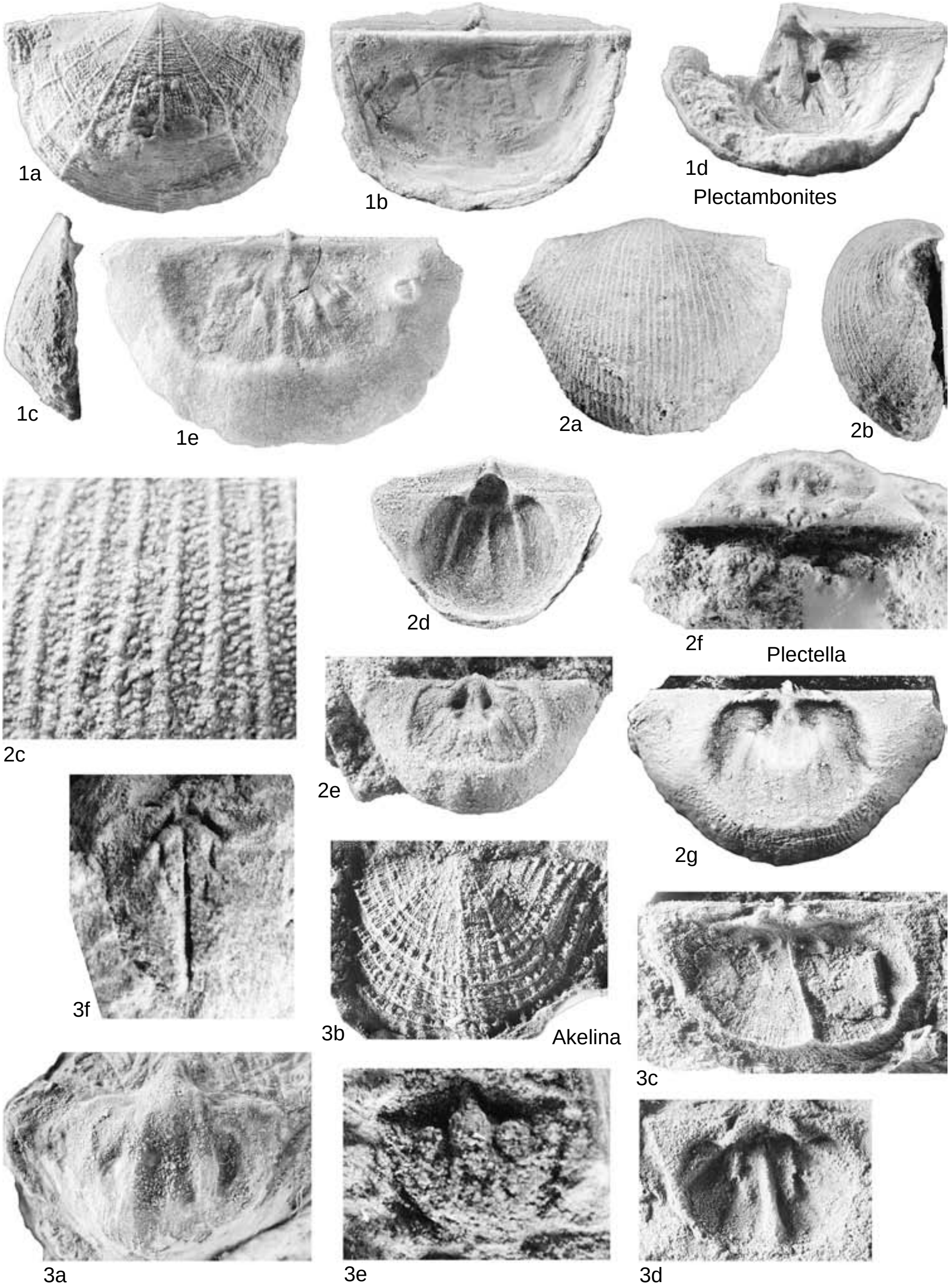

FIG. 197. Plectambonitidae (p. 306–308).

Ingria ÖPIK, 1930, p. 57 [**Orthisina nefedyevi* VON EICHWALD, 1855, pl. 36, fig. 13; OD] [=*Palinorthis* ULRICH & COOPER, 1936b, p. 625 (type, *P. cloudi;* OD)]. Flat to gently resupinate profile; unequally parvicostellate ornament; narrow chilidium, pseudodeltidium not filling delthyrium; denticles over half valve width; dental plates present with short straight or slightly curved ventral muscle-

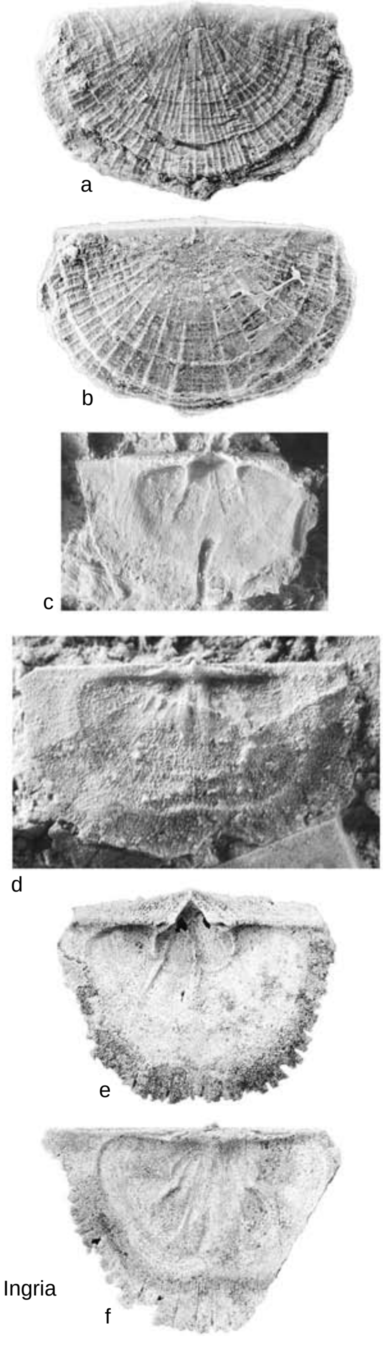

Fig. 198. Plectambonitidae (p. 307–308).

bounding ridges laterally only; muscle field poorly impressed anteriorly; socket plates short, ridgelike, widely divergent, subparallel with hinge line; complex side septa similar to *Plectambonites;* weak dorsal platform present. *Ordovician (Arenig–Llanvirn):* Baltic, North America, Tuva, northern Asia.——Fig. 198*a–d.* **I. nefedyevi* (von Eichwald); *a,b,* ventral, dorsal views of conjoined valves, Volkhov Horizon, upper Arenig, Obukova Village, St. Petersburg, Russia, BMNH BC 12876, ×2; *c,* ventral interior, Jagala-Joa, Estonia, ×2.5; *d,* dorsal interior, Kunda Stage, upper Arenig, Ingria, Russia, TAGI BR 314, ×4 (new).——Fig. 198*e,f. I. cloudi, Orthidiella* Zone, lower Llanvirn, Frenchman's Flat, Nevada; *e,* ventral interior, BMNH BC 10310, ×2; *f,* dorsal interior, BMNH BC 10306, ×2 (new).

Plectella Lamansky, 1905, p. 156 [**Plectambonites uncinata* Pander, 1830, p. 91; OD]. Concavoconvex profile with incurved beak; equally parvicostellate, granular ornament; small pseudodeltidium, small chilidium; short dental plates; ventral median septum anterior of muscle field, pair of ventral side septa extending from anterior edge of dental plates; pronounced ventral diaphragm, dorsal platform; similar to *Plectambonites* but with distinctive granular ornament, less pronounced side septa. *Ordovician (Arenig):* Baltic.——Fig. 197,*2a–g.* **P. uncinata* (Pander), Leetse Formation, lower Arenig; *a,b,* ventral, lateral views of ventral exterior, ×2.5; *c,* enlargement of ornament, Popovka river, St. Petersburg, Russia, BMNH BC 12854, ×10; *d,* ventral interior, Mäeküla, Estonia, TAGI BR 336, ×2; *e,* dorsal view of dorsal interior, Mäeküla, Estonia, TAGI BR 338, ×2; *f,* posterior view of dorsal interior, St. Zakluha River, St. Petersburg, Russia, BMNH BC 12855, ×3; *g,* dorsal view of dorsal interior, Popovka River, St. Petersburg, Russia, KIGLGU 155/691. 693, ×2 (new).

Subfamily TAPHRODONTINAE
Cooper, 1956

[*nom. transl.* Williams, 1965d, p. 376, *ex* Taphrodontidae Cooper, 1956, p. 740] [=Isophragminae Cooper, 1956, p. 733]

Differs from Plectambonitinae in possessing prominent pair of fused septa centrally in dorsal valve and in lacking hinge line denticles. *Ordovician (Llanvirn–Caradoc).*

Taphrodonta Cooper, 1956, p. 740 [**T. parallela;* OD]. Concavoconvex profile; unequally parvicostellate ornament; similar to *Isophragma* but with no resupination, smaller, more subcircular ventral valve muscle field; subperipheral thickened ridge variably developed in ventral valve, with corresponding platform in dorsal valve, both anteriorly interrupted by central fused septa; cardinal process narrow, high; two small plates between cardinal process and interarea; side septa vestigial, often absent, except for strong central pair fused together along length, homologizing wide medium septum. *Ordovician (Llanvirn, ?Llandeilo, ?Caradoc):* North America, Asia.

T. (**Taphrodonta**). Similar to *T. (Nanambonites),* but with no chilidium in dorsal valve. *Ordovi-*

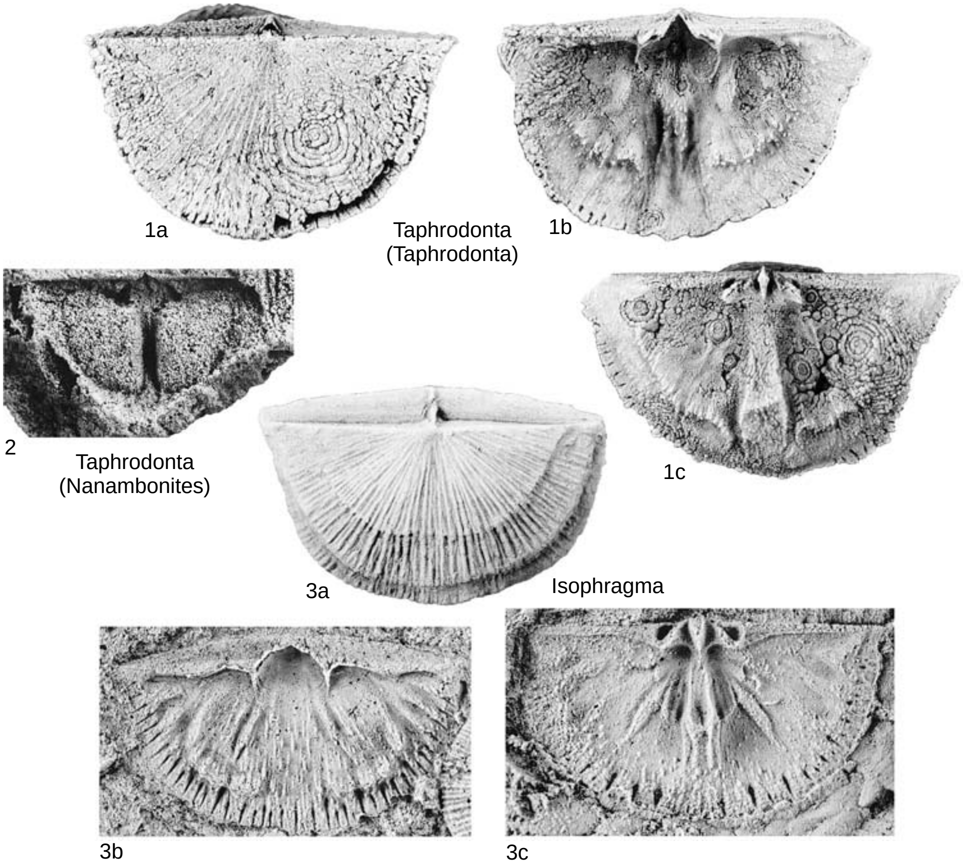

FIG. 199. Plectambonitidae (p. 308–309).

cian (Llanvirn, ?Llandeilo, ?Caradoc): North America, Kazakhstan.——FIG. 199,*1a–c.* **T. (T.) parallela,* Antelope Valley Formation, upper Llanvirn, Ikes Canyon, Nevada; *a,* holotype, dorsal view of conjoined valves, USNM 117562e, ×3; *b,* ventral interior, USNM 117562g, ×3; *c,* dorsal interior, USNM 117562f, ×3 (Cooper, 1956).

T. (**Nanambonites**) LIU, 1976, p. 145 [**N. paucus;* OD]. Similar to *T. (Taphrodonta)* but with chilidium in dorsal valve. *Ordovician (Llanvirn):* Asia.——FIG. 199,*2.* **T. (N.) paucus,* lower formation of Jiacun Group, Llanvirn, Mount Jolmo Lungma area, Tibet, China; holotype, dorsal internal mold, NIGP 23173, ×3 (Liu, 1976).

Isophragma COOPER, 1956, p. 733 [**I. ricevillense;* OD]. Flat to slightly resupinate profile; finely costellate to unequally parvicostellate ornament; dental plates short; ventral muscle field subquadrate with wide adductor traces; faint ventral subperipheral rim variably present; strong, low, wide cardinal process; no accessory plates between cardinal process, interarea; side septa variably developed, usually absent apart from strong, centrally fused pair. *Ordovician (Llanvirn–Caradoc):* North America, Scotland, Tuva, Kazakhstan.——FIG. 199,*3a–c.* **I. ricevillense,* Athens Formation, lower Caradoc, Riceville, Tennessee; *a,* holotype, dorsal view of conjoined valves, USNM 110918a, ×3; *b,* ventral interior, USNM 110923a, ×4; *c,* dorsal interior, USNM 110923b, ×4 (Cooper, 1956).

Family TAFFIIDAE
Schuchert & Cooper, 1931

[*nom. transl.* ULRICH & COOPER, 1936b, p. 625, *ex* Taffiinae SCHUCHERT & COOPER, 1931, p. 243]

Outline quadrate to transverse; profile concavoconvex to resupinate; variable ornament from multicostellate to unequally parvicostellate; short dental plates usually present; simple cardinal process ankylosed anteriorly to valve floor (occasionally absent);

no bema; weak dorsal median septum variably developed, but no side septa. *Ordovician (?Tremadoc, Arenig–Llandeilo).*

Subfamily TAFFIINAE Schuchert & Cooper, 1931

[Taffiinae SCHUCHERT & COOPER, 1931, p. 243] [=Aporthophylinae LIU, 1976, p. 143; Spanodontinae COCKS & RONG, 1989, p. 98]

Profile concavoconvex; with platform. *Ordovician (Arenig–Llandeilo).*

Taffia BUTTS, 1926, p. 99 [**T. planoconvexa;* OD] [=*Chaloupskia* NEUMAN in NEUMAN & BRUTON, 1989, p. 61 (type, *C. scabrella;* OD)]. Planoconvex profile; parvicostellate ornament; large apsacline interarea, large pseudodeltidium, small chilidium also present; ventral muscle scar small, open anteriorly; usually without simple cardinal process (but rarely present); weak myophragm developed to half valve length; weak subperipheral rim variably developed. *Ordovician (Arenig–Llanvirn):* North America, Argentina, Norway, Australia.——FIG. 200,*1a–d.* **T. planoconvexa,* Odenville Formation, lower Arenig; *a,* dorsal view of conjoined valves, St. Clair County, USNM 71461b, ×4; *b,c,* holotype, dorsal exterior, interior, St. Clair County, USNM 91586, ×3; *d,* ventral interior, Vandiver, Alabama, USNM 91590a, ×3 (Cooper, 1956).——FIG. 200,*1e–h. T. scabrella* (NEUMAN), Hølonda Limestone, Arenig–Llanvirn, Katugleåsen, Trondheim, Norway; *e,* ventral exterior, PMO 116659, ×2; *f,* ventral internal mold, PMO 116661, ×2; *g,h,* dorsal internal mold, latex cast, PMO 116664, ×2 (Neuman & Bruton, 1989).

Aporthophyla ULRICH & COOPER, 1936b, p. 625 [**A. typa*; OD]. Gently concavoconvex to planoconvex profile; differs from *Taffia* in its unequally parvicostellate ornament, smaller interarea; chilidium present, pseudodeltidium reduced or absent; strong dental plates, short ventral muscle-bounding ridges; cardinal process always present; dorsal muscle field weak: short dorsal myophragm to quarter valve length. *Ordovician (Arenig–Llanvirn):* North America, Asia, Australia.——FIG. 200,*3a–d.* **A. typa,* Antelope Valley Formation, Llanvirn, Ikes Canyon, Nevada; *a–c,* latex cast of dorsal exterior, dorsal internal mold, latex cast, USNM 92866e, ×1.5; *d,* ventral internal mold, USNM 117566, ×1.5 (Cooper, 1956).

Aporthophylina LIU, 1976, p. 144 [**A. intermedia;* OD]. Similar to *Aporthophyla* but lacking dental plates in ventral valve, with stronger subperipheral rim in both valves. *Ordovician (Arenig–Llanvirn):* China.——FIG. 200,*2a–c.* **A. intermedia,* Jiacun Formation, Llanvirn, Zhaya, Dingri County, southern Tibet, China; *a,* ventral external mold, NIGP 23171, ×1; *b,* ventral internal mold, NIGP 23170 ×2; *c,* holotype, dorsal internal mold, NIGP 23169, ×1 (Liu, 1976).

Spanodonta PRENDERGAST, 1935, p. 12 [**S. hoskingiae;* OD] [=*Archambona* COOPER, 1988, p. 186 (type, *A. floweri;* OD)]. Concavoconvex profile; fine unequally parvicostellate ornament; ventral interarea apsacline, dorsal hypercline; pseudodeltidium, chilidium apparently vestigial; short dental plates, muscle-bounding ridges mostly surrounding bilobed ventral muscle field; cardinal process not trilobed (*contra* WILLIAMS, 1965d, p. 375), consists of simple ridge; prominent socket ridges curved anterolaterally; distinctive dalmanelloid-like dorsal muscle field, with median septum, transverse ridge separating two pairs of muscle scars; prominent dorsal subperipheral rim. *Ordovician (Llanvirn–Llandeilo):* Australia, Malaya.——FIG. 201,*3a–d.* **S. hoskingiae,* Gap Creek Formation, Llanvirn–Llandeilo, Gap Spring, Price's Creek, Emmanuel Range, Western Australia; *a,* ventral exterior, BMNH BC 10604, ×4; *b,* conjoined valves showing ventral interior, BMNH BC 7242, ×4; *c,d,* dorsal interior, BMNH BC 10605, ×3 (Cocks & Rong, 1989).

Tourmakeadia WILLIAMS & CURRY, 1985, p. 252 [**T. fimbriata;* OD]. Concavoconvex profile; costellate to parvicostellate ornament; prominent apsacline interarea, open notothyrium; short divergent dental plates; small, thin cardinal process; very divergent socket plates; with distinctive elevated, striated, bilobed platforms in both valves. *Ordovician (Arenig–Llanvirn):* North America, Europe.

T. (**Tourmakeadia**). Similar to *T. (Bockelia)* but with open delthyrium, less prominent dorsal myophragm, and stronger ventral subperipheral rim. *Ordovician (Arenig):* North America, Ireland.——FIG. 201,*1a–c.* **T. (T.) fimbriata,* Tourmakeady Formation, upper Arenig, County Mayo, Ireland; *a,* ventral exterior, BMNH BB 95539, ×4; *b,* ventral interior, BMNH BB 95542, ×4; *c,* holotype, dorsal interior, BMNH BB 95538, ×5 (Williams & Curry, 1985).

T. (**Bockelia**) NEUMAN in NEUMAN & BRUTON, 1989, p. 63 [**B. angusticostata;* OD]. Similar to *T. (Tourmakeadia)* but with pseudodeltidium, more prominent dorsal myophragm merging anteriorly with bilobed platform; ventral subperipheral rim only weakly developed. *Ordovician (Arenig–Llanvirn):* Baltic.——FIG. 201,*2a–d.* **T. (B.) angusticostata,* Hølanda Formation, Arenig–Llanvirn, Trondheim, Norway; *a–c,* latex cast of dorsal exterior, dorsal internal mold, latex cast of dorsal valve, PMO 116671, ×2; *d,* ventral internal mold, PMO 116674, ×2 (Neuman & Bruton, 1989).

Subfamily AHTIELLINAE Öpik, 1933

[Ahtiellinae ÖPIK, 1933a, p. 19]

Resupinate profile; with platform (or diaphragm). *Ordovician (Arenig–Llanvirn).*

Ahtiella ÖPIK, 1932, p. 37 [**A. lirata;* OD]. Profile resupinate, geniculate; unequally parvicostellate, often unequally rugate ornament; catacline ventral interarea; anacline dorsal interarea; widely spaced ventral dental plates, muscle-bounding ridges con-

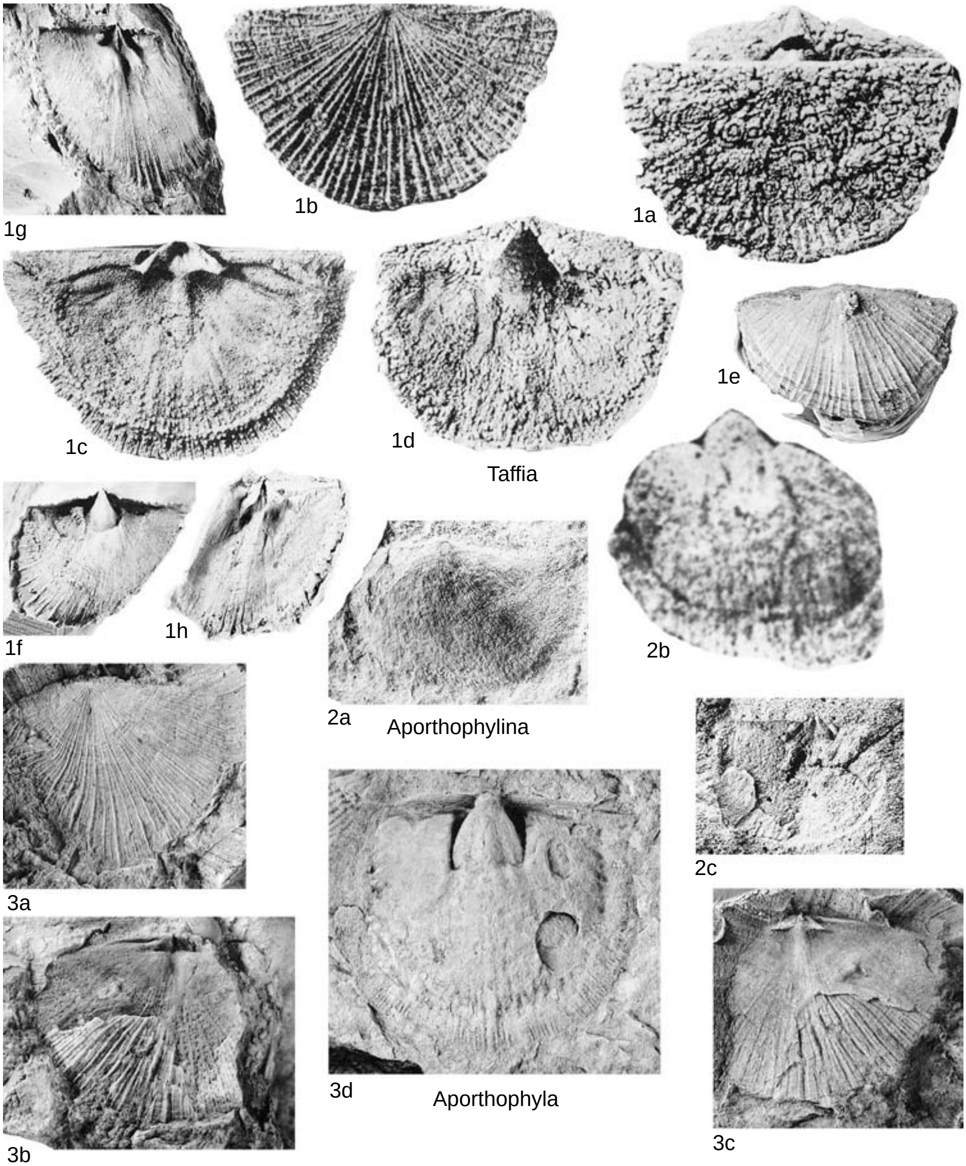

FIG. 200. Taffiidae (p. 310).

verging anteriorly before merging with valve floor; small thin cardinal process, relatively fine socket plates posteriorly that are more robust anteriorly; dorsal myophragm weak to absent; no dorsal median septum. *Ordovician (Arenig–Llanvirn):* northwestern Europe, North America, South America.——FIG. 202,*1a,b*. **A. lirata,* Kunda Stage, Llanvirn, Tsitri, Estonia; *a,* ventral interior, ×2 (Williams, 1965d); *b,* dorsal interior, ×1.8 (Rõõmusoks, new).——FIG. 202,*1c,d*. *A. jaanussoni* (HESSLAND), Arenig–Llanvirn, Sweden; dorsal exterior, internal mold, ×1 (Williams, 1965d).

Borua WILLIAMS & CURRY, 1985, p. 250 [**B. modesta;* OD]. Smooth apart from faint peripheral parvicostellae, occasional impersistent rugae in some specimens; ventral interarea apsacline to orthocline; dorsal interarea anacline; arched pseudodeltidium, chilidium not covering entire delthyrium; short dental plates, very weak ventral muscle-bounding ridges; elevated ventral subperipheral rim; low small

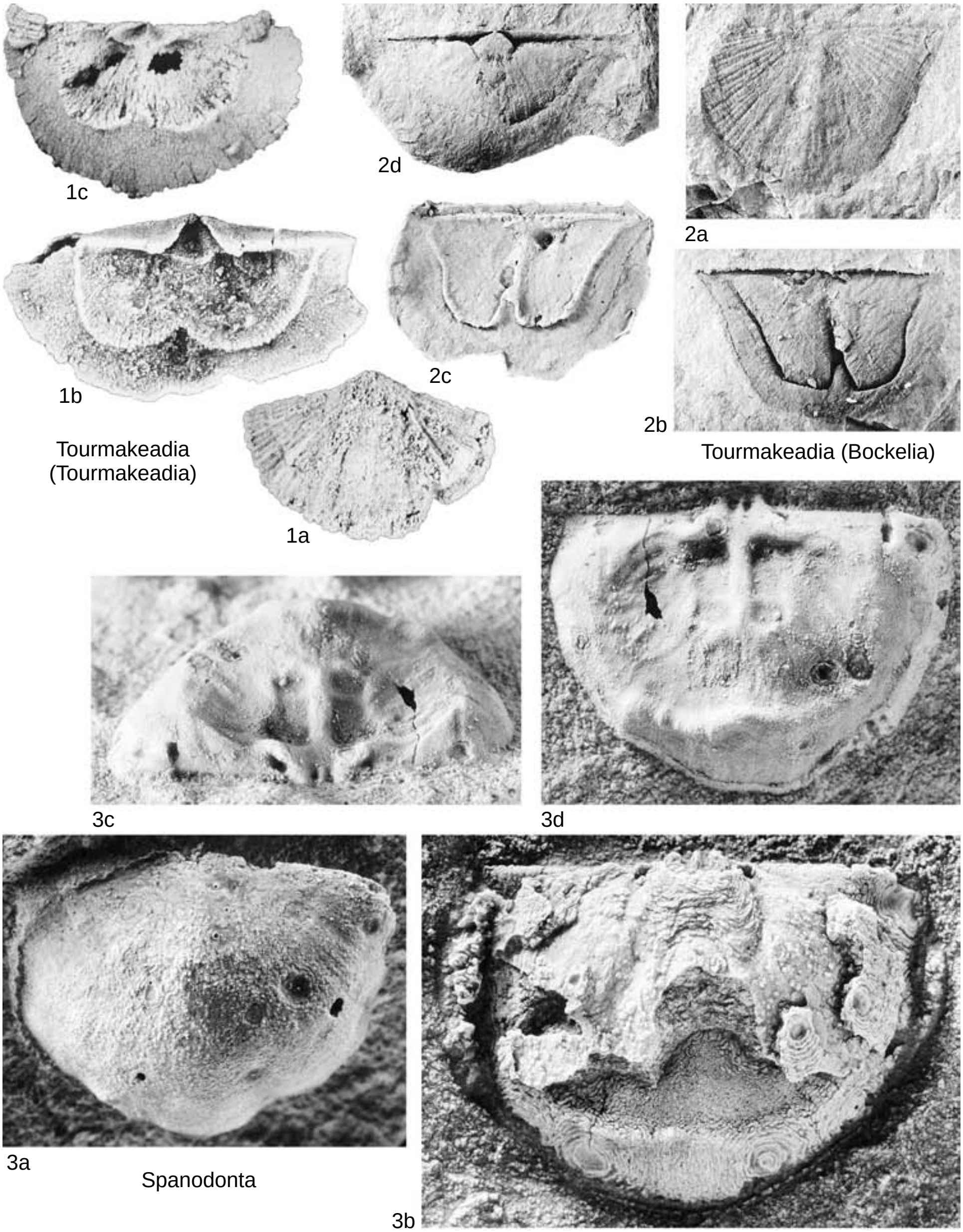

FIG. 201. Taffiidae (p. 310).

cardinal process; elevated small socket plates; short myophragm in dorsal valve, but no dorsal valve median septum; dorsal valve diaphragm present. *Ordovician (Arenig):* North America, Ireland.——FIG. 202,*3a–d.* **B. modesta,* Tourmakeady Limestone, upper Arenig, Srah Bridge, County Mayo, Ireland; *a,* dorsal exterior, BMNH BB 95537, ×4; *b,* ventral interior, BMNH BB 95532, ×3; *c,* holotype, dorsal interior, BMNH BB 95531, ×3; *d,* dorsal interior, BMNH BB 95533, ×3 (Williams & Curry, 1985).

Guttasella NEUMAN, 1976, p. 31 [**G. gutta;* OD]. Doubly geniculate profile as in *Inversella (Reinversella);* fine unequally parvicostellate ornament; no

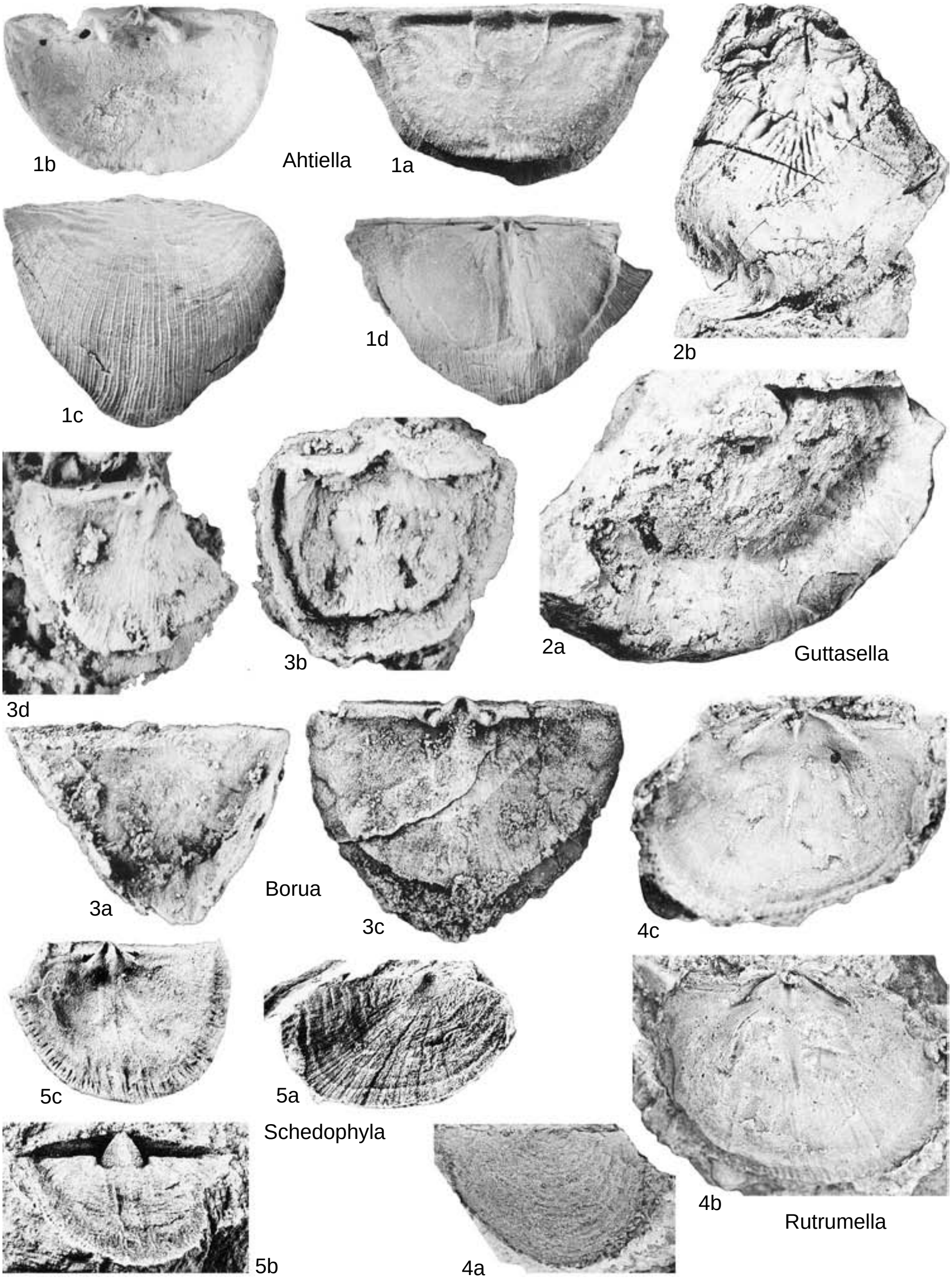

FIG. 202. Taffiidae (p. 310–314).

rugae; apsacline ventral interarea; short dental plates posterolateral to weakly impressed bilobed ventral muscle field; prominent but narrow bladelike cardinal process; variably impressed irregular dorsal muscle-bounding ridges; no dorsal median septum; subperipheral rims absent (apart from double geniculation). *Ordovician (Llanvirn):* North America.——FIG. 202,*2a,b.* **G. gutta,* Virgin Arm Tuffs, Llanvirn, Virgin Arm, Newfoundland, Canada; *a,* ventral internal mold, GSC 35059,

×1.5; *b,* holotype, dorsal internal mold, GSC 35058, ×1.5 (Neuman, 1976).

Inversella ÖPIK, 1933a, p. 21 [**I. borealis;* OD]. Strongly geniculate in ventral direction, sometimes with more than one deflection; unequally parvicostellate ornament with persistent rugae over valve; small interarea; short dental plates leading anteriorly to muscle-bounding ridges define relatively small bilobed ventral muscle field; prominent bladelike cardinal process, socket plates; no dorsal median septum. *Ordovician (Arenig–Llanvirn):* Europe, South America, North America.

I. (**Inversella**). Similar to *I. (Reinversella)* but with only one deflection at anterior and lateral valve borders and less continuous rugae. *Ordovician (Llanvirn):* Baltic, North America.——FIG. 203,*1a–c.* **I. (I.) borealis,* Echinosphaeriten Limestone, Aseri Stage, upper Llanvirn, Eesti, Estonia; *a,* dorsal exterior, BMNH BC 12877, ×1.5 (new); *b,* ventral internal mold, ×1.5; *c,* dorsal exterior, dissolved away posteromedianly to show mold of cardinalia, ×1.5 (Williams, 1965d).

I. (**Reinversella**) BATES, 1968, p. 169 [**R. monensis;* OD]. Similar to *I. (Inversella)* but with an extra second deflection of anterior, lateral borders, with more continuous rugae. *Ordovician (Arenig–Llanvirn):* Wales, South America.——FIG. 203,*2a–d.* **I. (R.) monensis,* Treiorwerth Formation, Arenig, Ffynnon-y-mab, Anglesey, Wales; *a–c,* holotype, latex of dorsal exterior, internal mold, latex cast, BMNH BB 30574, ×2; *d,* latex cast of ventral interior, BMNH BB 30575, ×2 (new).

?Rutrumella HARPER in BRUTON & HARPER, 1981, p. 163 [**R. implexa;* OD]. Resupinate profile; subquadrate outline, not geniculate; differs from *Schedophyla* in having discontinuous rugae but no radial ornament; ventral interior unknown, familial assignment uncertain; relatively large socket plates, low dorsal median septum to half valve length; dorsal muscle field poorly impressed. *Ordovician (Llanvirn):* Baltic.——FIG. 202,*4a–c.* **R. implexa,* clasts in Otta Conglomerate, lower Llanvirn, Otta, Norway; *a,* holotype, dorsal exterior, PMO 105.803, ×1; *b,c,* mold, latex of dorsal interior, PMO 105.804, ×2 (Bruton & Harper, 1981).

Sanjuanella BENEDETTO & HERRERA, 1987, p. 103 [**S. plicata;* OD]. Biconvex to planoconvex profile; similar to *Borua* but with marked parvicostellate ornament; prominent pseudodeltidium; short dental plates, curved muscle-bounding ridges nearly encircling relatively small ventral muscle field; small bladelike socket ridges; myophragm, but no dorsal valve median septum; dorsal muscle field poorly impressed; no dorsal platform. *Ordovician (Llanvirn):* South America.——FIG. 203,*3a–e.* **S. plicata,* upper San Juan Formation, Llanvirn, Quebrada Honda, Cerro Viejo, San Juan Province, Argentina; *a,b,* ventral, dorsal views of conjoined valves, CORD-PZ 8760, ×1.5; *c,* ventral internal mold, CORD-PZ 8766, ×1.5; *d,* dorsal internal mold, ×1.4; *e,* latex cast, ×3 (Benedetto & Herrera, 1993).

Schedophyla NEUMAN, 1971, p. 120 [**S. potteri;* OD]. Similar to *Aporthophyla* but resupinate profile; differs from *Rutrumella* in having radial ornamentation, no rugae; large apsacline ventral interarea, with low-arched pseudodeltidium; short stout dental plates, small curved muscle-bounding ridges nearly enclosing short subcircular ventral muscle field; bulbous cardinal process; bladelike socket ridges; median septum absent; subperipheral rim weakly developed. *Ordovician (Arenig–Llanvirn):* North America, China.——FIG. 202,*5a–c.* **S. potteri,* Tuffaceous Sandstone, ?Llanvirn, Hayden Brook, York County, New Brunswick, Canada; *a,* ventral exterior, GSC 24796, ×2; *b,* ventral internal mold, GSC 24795, ×2; *c,* holotype, latex cast of dorsal interior, GSC 24793, ×2 (Neuman, 1971).

Subfamily PELONOMIINAE
Cocks & Rong, 1989

[Pelonomiinae COCKS & RONG, 1989, p. 98]

Not resupinate, although fairly flat profiles; no platform. *Ordovician (Llanvirn).*

Pelonomia COOPER, 1956, p. 699 [**Orthis delicatula* BILLINGS, 1865 in 1861–1865, p. 217; OD]. Subrectangular outline; profile planoconvex with slight ventral fold with corresponding dorsal sulcus; unequally parvicostellate ornament; small interareas with rudimentary pseudodeltidium but larger chilidium; short dental plates posterolaterally bounding small ventral muscle field; small cardinal process; bladelike socket ridges; median ridge absent but larger pseudopunctae developed on dorsal sulcus. *Ordovician (Llanvirn):* North America.——FIG. 204,*1a–c.* **P. delicatula* (BILLINGS), Table Head Formation, Llanvirn, Table Head, Newfoundland, Canada; *a,* ventral exterior, ×4 (new); *b,c,* dorsal internal mold, latex cast, USNM 117557, ×3 (Cooper, 1956).

Subfamily LEPTELLINAE
Williams, 1965

[Leptellinae WILLIAMS, 1965d, p. 376]

Characters as for family, but without cardinal process. *Ordovician (?Tremadoc–Llanvirn).*

Leptella HALL & CLARKE, 1892, p. 293 [**Leptaena sordida* BILLINGS, 1862 in 1861–1865, p. 74; OD] [=*Leptella (Eosericoidea)* ZENG, 1987, p. 228 (type, *L. hubeiensis* ZENG, 1977, p. 57; OD); *Niquivilia* BENEDETTO & HERRERA, 1993, p. 50 (type, *N. extensa*)]. Concavoconvex profile; unequally parvicostellate ornament; large interareas with small pseudodeltidium, chilidium; relatively small, but well-impressed bilobed ventral muscle field between

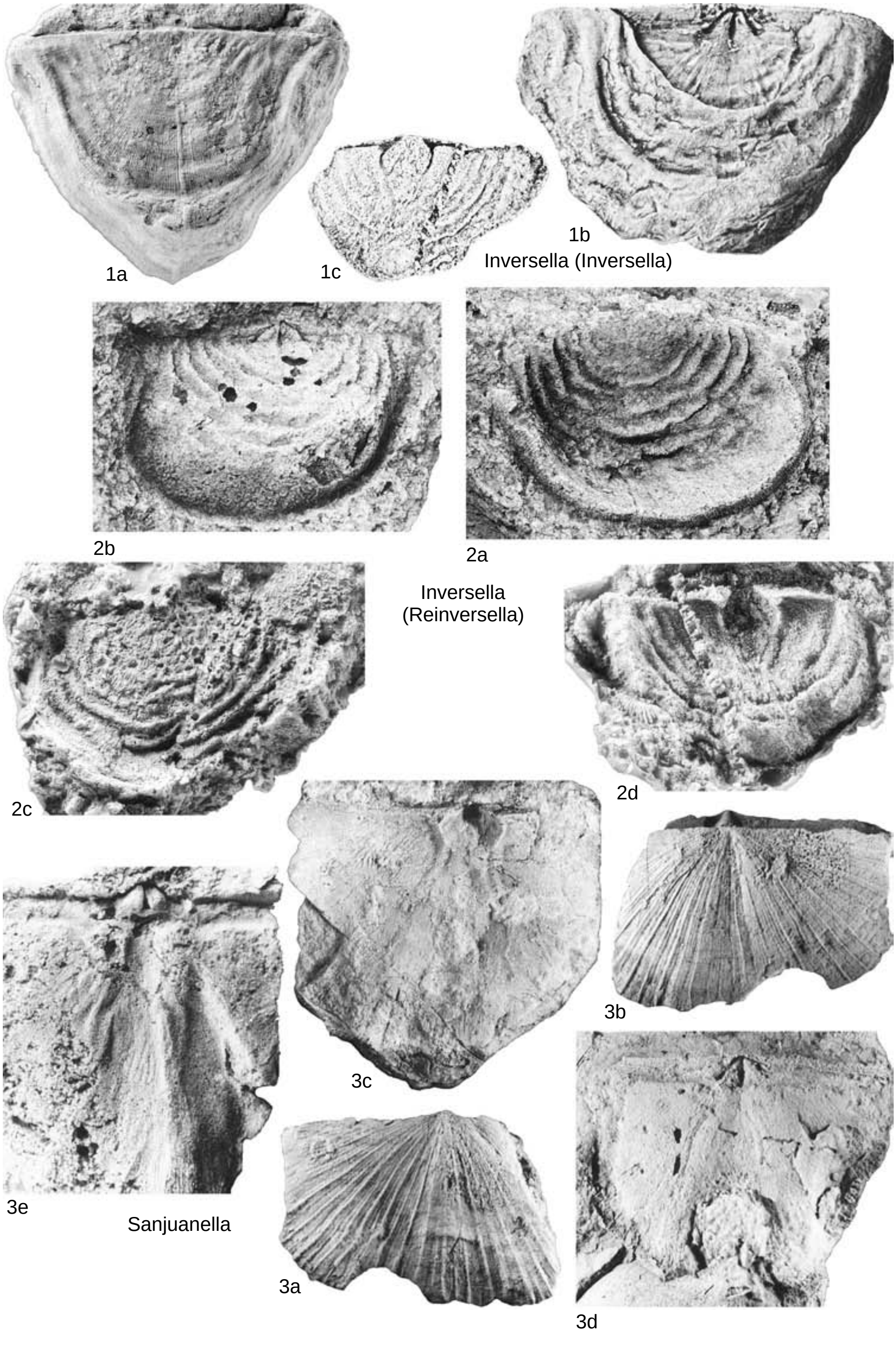

FIG. 203. Taffiidae (p. 314).

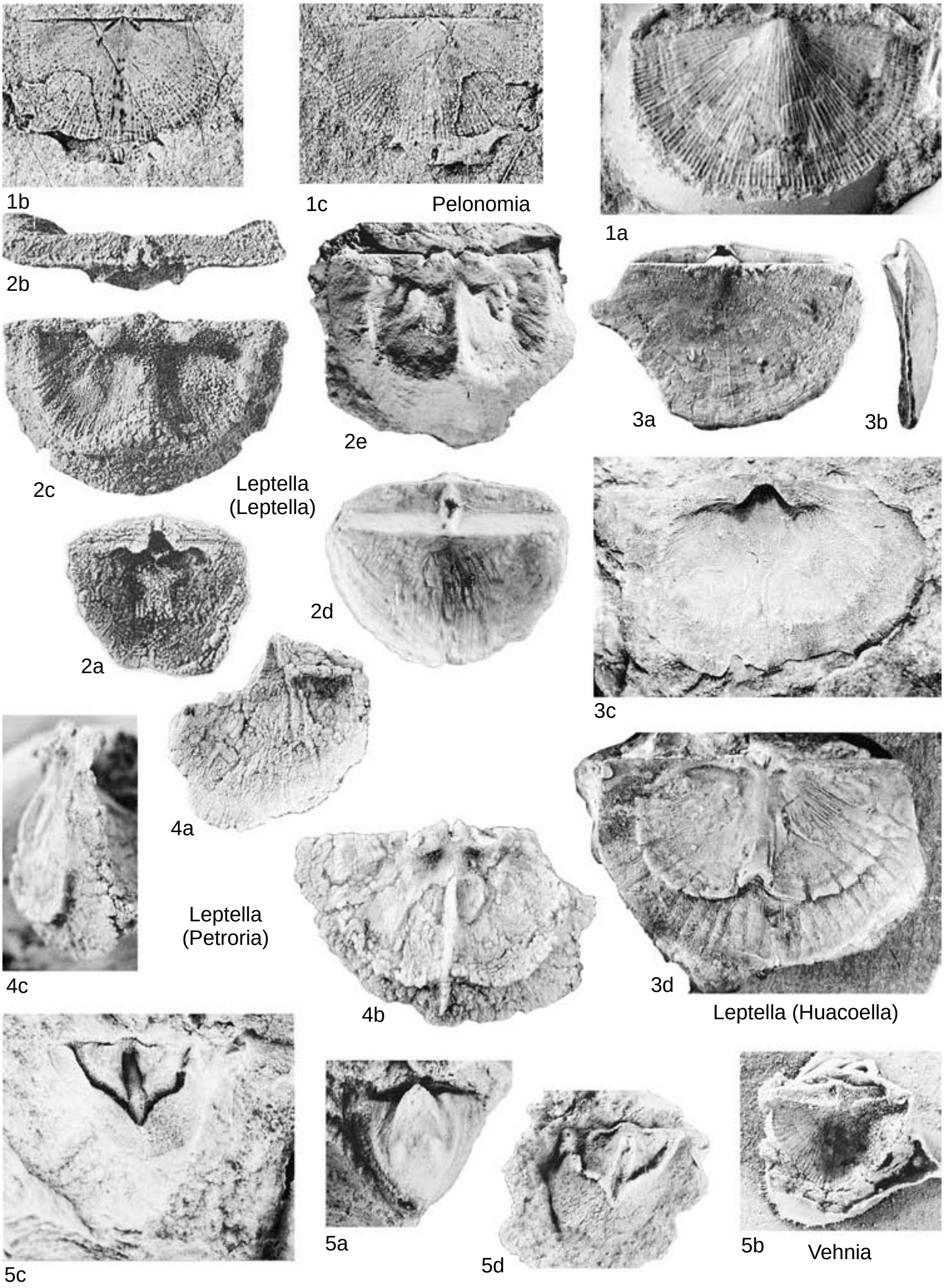

FIG. 204. Taffiidae (p. 314–317).

short dental plates; field limited anteriorly by variably developed broad median callosity; robust socket ridges curving posterolaterally; dorsal median septum merging anteriorly with bilobed platform but may continue anterior to it; may possess one or two pairs of short lateral ridges at posterolateral margin of platform. *Ordovician (?Tremadoc, Arenig–Llanvirn):* cosmopolitan.

L. (Leptella). Diagnosis as for genus, but more convex than *L. (Huacoella)* and with hypercline dorsal interarea. Differs from *L. (Petroria)* in the median septum being confined by platform anteriorly and in possessing a median ventral callosity. *Ordovician (?Tremadoc, Arenig–Llanvirn):* North America, South America, Ireland, China.——FIG. 204,*2a–c.* **L. (L.) sordida* (BILLINGS), Lévis Shale, Arenig–Llanvirn, Point Lévis, Quebec, Canada; *a,* ventral interior, GSC 9069, ×3; *b,c,* posterior, dorsal views of dorsal interior, USNM 90752b, ×6 (Ulrich & Cooper, 1938).——FIG. 204,*2d,e. L. (L.) hubeiensis* ZENG, Dawan Formation, Arenig, Yichang, western Hubei Province, China; *d,* dorsal view of conjoined valves, YIGM IV45222, ×3; *e,* dorsal interior, YIGM IV46023, ×3 (Zeng, 1977).

L. (Huacoella) BENEDETTO & HERRERA, 1993, p. 46 [**H. radiata;* OD]. Similar to *L. (Leptella),* but larger, less convex in profile, with orthocline rather than hypercline dorsal interarea, less robust teeth, socket plates. *Ordovician (Arenig):* Argentina.——FIG. 204,*3a–d.* **L. (H.) radiata,* San Juan Limestone, upper Arenig, Huaco, San Juan, Argentina; *a,b,* dorsal, lateral views of conjoined valves, CORD-PZ UNC 288, ×1.5; *c,* ventral interior, CORD-PZ UNC 287, ×1.5; *d,* holotype, dorsal interior, CORD-PZ UNC 281, ×1.5 (Benedetto & Herrera, 1993).

L. (Petroria) WILSON, 1926, p. 27 [**P. rugosa;* OD]. Similar to *L. (Leptella)* but lacking median ventral callosity, with median septum continuing anteriorly of raised platform in dorsal valve. *Ordovician (Arenig–Llanvirn):* North America, South America, Kazakhstan.——FIG. 204,*4a–c.* **L. (P.) rugosa,* Beaverfoot Formation, Arenig, Palliser Pass, British Columbia, Canada; *a,* ventral interior, ×3; *b,c,* dorsal, lateral views of dorsal interior, GSC 6754a, ×4 (Cooper, 1956).

Vehnia NEUMAN in NEUMAN & BRUTON, 1989, p. 65 [**Chonetoidea triangularis* REED, 1932a, p. 137; OD]. Very concavoconvex profile; finely costellate ornament; interareas coplanar, pseudodeltidium, chilidial plates developed; very short dental plates, weak muscle-bounding ridges defining short bilobed ventral muscle field; cardinal process variably developed, often absent; widely flaring thin socket ridges; median septum bifurcating, with two halves running subparallel anteriorly, but not beyond high elevated platform extending anteriorly. *Ordovician (Arenig–Llanvirn):* Norway.——FIG. 204,*5a–d.* **V. triangularis* (REED), Hølanda Formation, Arenig–Llanvirn, Damtjern, Trondheim, Norway; *a,* ventral internal mold, PMO 116690, ×5; *b,* latex cast of conjoined valves, PMO 11681, ×5; *c,d,* dorsal internal mold, latex cast, PMO 116689, ×5 (Neuman & Bruton, 1989).

Family BIMURIIDAE Cooper, 1956

[Bimuriidae COOPER, 1956, p. 764, *partim*] [=Craspedeliinae COCKS & RONG, 1989, p. 145]

Strongly concavoconvex profile; dental plates poorly developed or absent; cardinal process simple, not undercut, sometimes fused with socket ridges; with bema, side septa. *Ordovician (Llandeilo–middle Ashgill).*

Bimuria ULRICH & COOPER, 1942, p. 622 [**B. superba;* OD]. Concavoconvex profile with incurved beak; no ornament, but comae sometimes developed; small pseudodeltidium, chilidium absent; widely spaced, very divergent teeth, curved socket plates; ventral muscle field poorly impressed, open anteriorly; cardinal process varies from wedgelike to absent; widely flaring socket plates varying from straight, stout to curving anterolaterally; dorsal side septa varying from one to two pairs; long dorsal median septum. *Ordovician (Llandeilo–middle Ashgill):* cosmopolitan.

B. (Bimuria). Differs from *B. (Cooperea)* in its less elongate outline and in its elongate, divided bema in adults. *Ordovician (Llandeilo–middle Ashgill):* cosmopolitan.——FIG. 205,*1a–e.* **B. (B.) superba,* Arline Formation, Llandeilo, Friendsville, Tennessee; *a,b,* ventral, dorsal views of conjoined valves, BMNH BC 7270, ×2; *c,* ventral interior, BMNH BC 13421, ×2; *d,e,* posterior, dorsal views of dorsal interior, BMNH BC 7269, ×2 (Cocks & Rong, 1989).

B. (Cooperea) COCKS & RONG, 1989, p. 147 [**B. siphonata* COOPER, 1956, p. 770; OD]. Profile concavoconvex; outline very laterally elongate; pedicle tube sometimes present; differs from *B. (Bimuria)* in its bilobed subcircular bema in adults, often elevated anteriorly, laterally. *Ordovician (Llandeilo–Caradoc):* North America.——FIG. 205,*2a–c.* **B. (C). siphonata* (COOPER), Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* holotype, external view of conjoined valves (specimen also shows pedicle tube), USNM 117470a, ×10 (Cooper, 1956); *b,* ventral interior, BMNH BC 10303, ×10 (Cocks & Rong, 1989); *c,* dorsal interior, USNM 117470e, ×10 (Cooper, 1956).

Craspedelia COOPER, 1956, p. 772 [**C. marginata;* OD]. Similar to *Bimuria,* but with geniculate profile with additional anterior deflection; fold, sulcus; no ornament known; bema sometimes elevated anteriorly. *Ordovician (Llandeilo–Caradoc):* North America, Scotland, Kazakhstan.——FIG. 205,*3a–d.* **C. marginata,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,b,* ventral exterior, interior, USNM 117474a, ×6; *c,* dorsal exterior, USNM 117474e, ×5; *d,* dorsal interior, USNM 117474d, ×7 (Cooper, 1956).

Family SYNDIELASMATIDAE Cooper, 1956

[Syndielasmatidae COOPER, 1956, p. 742]

Concavoconvex to planoconvex profile; dental plates poorly developed, often absent; trifid cardinal process; no bema; side septa usually developed. *Ordovician (Llanvirn–Caradoc).*

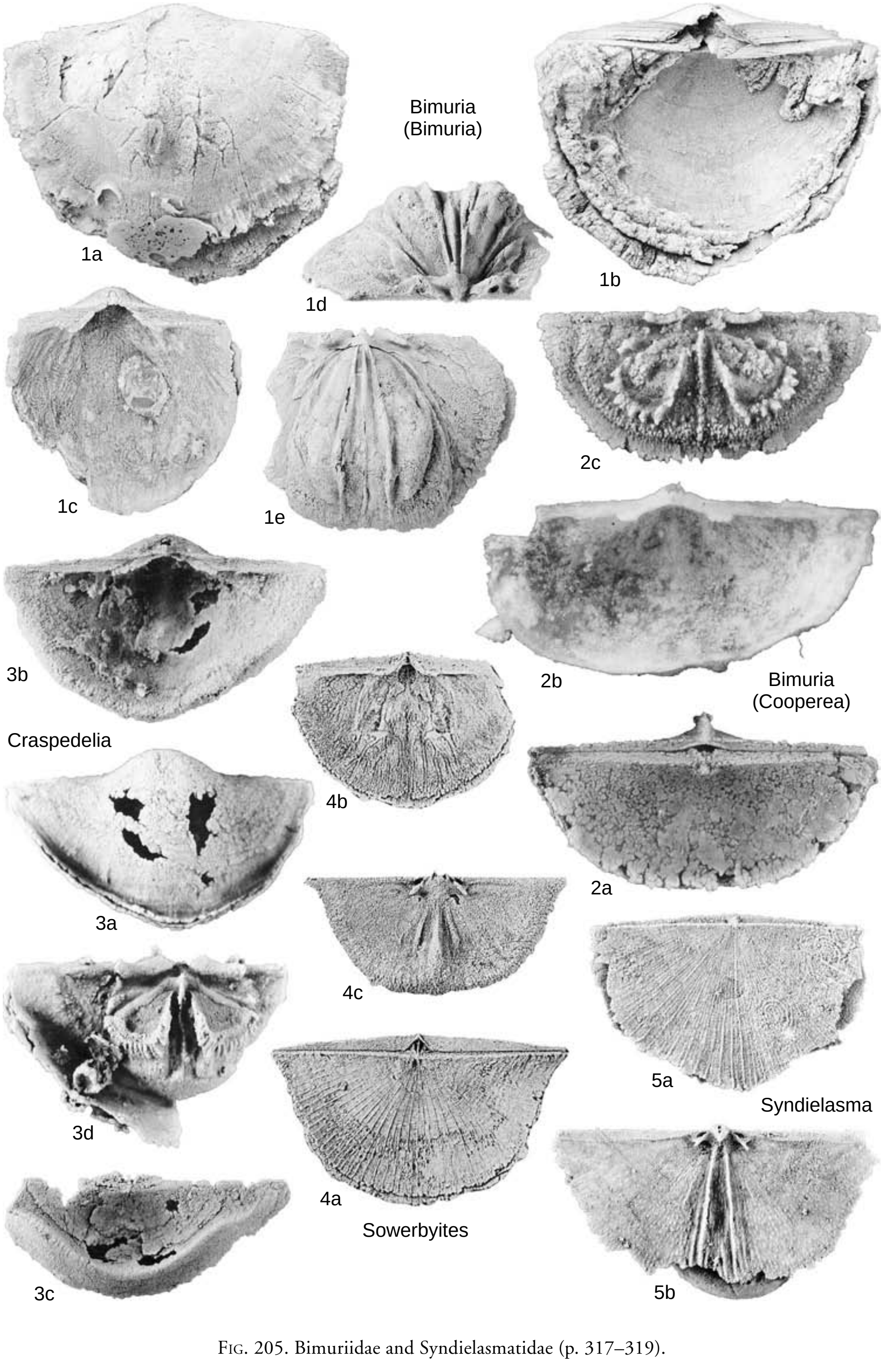

FIG. 205. Bimuriidae and Syndielasmatidae (p. 317–319).

Syndielasma COOPER, 1956, p. 742 [**S. biseptatum;* OD]. Gently concavoconvex to planoconvex profile; unequally parvicostellate ornament; interarea small; pseudodeltidium reduced or absent; ventral interior poorly known, but without dental plates; muscle fields poorly impressed; bulbous cardinal process not fused anterolaterally to thin socket plates; very short thin dorsal median septum developed posteriorly in some specimens only; two prominent long side septa; similar to *Sowerbyites* but without dorsal median septum. *Ordovician (Llanvirn):* North America.——FIG. 205,*5a,b.* **S. biseptatum,* upper Pogonip Group, Llanvirn, Ikes Canyon, Nevada; *a,* dorsal view of conjoined valves, USNM 117565e, ×3; *b,* dorsal interior, USNM 117565h, ×4 (Cooper, 1956).

Sowerbyites TEICHERT, 1937, p. 66 [**S. medioseptatus;* OD]. Concavoconvex profile; unequally parvicostellate ornament with accentuated costellae narrowly spaced; thickened concentric lamellae common distally; delthyrium largely open, but small pseudodeltidium, small chilidial plates; ventral adductor scar small, within delthyrial cavity; diductor scars long, broad, divergent, ending in callosities; cardinal process fused with brachiophore bases; similar to *Syndielasma,* but median septum present in dorsal valve; side septa variably developed. *Ordovician (Llandeilo–Caradoc):* North America, Ireland, Mongolia, Australia.——FIG. 205,*4a–c. S. triseptatus* (WILLARD), Lincolnshire Formation, Caradoc, Clinch Valley, Tennessee; *a,* dorsal view of conjoined valves, USNM 117415b, ×2; *b,* ventral interior, USNM 117415j, ×2; *c,* dorsal interior, USNM 117415a, ×2 (Cooper, 1956).

Family LEPTELLINIDAE
Ulrich & Cooper, 1936

[*nom. transl.* COOPER, 1956, p. 744, *ex* Leptellininae ULRICH & COOPER, 1936b, p. 626] [=Titanambonitidae LAURIE, 1991, p. 55]

Profile concavoconvex to resupinate; dental plates present; trifid cardinal process fused anteriorly to valve floor (not undercut); no side septa present; no bema present (although clear muscle-bounding ridges occasionally seen). *Ordovician (upper Arenig)–Silurian (upper Llandovery).*

Subfamily LEPTELLININAE
Ulrich & Cooper, 1936

[Leptellininae ULRICH & COOPER, 1936b, p. 626]

Restricted ventral valve muscle field. *Ordovician (?Arenig, Llanvirn)–Silurian (Telychian).*

Leptellina ULRICH & COOPER, 1936b, p. 626 [**L. tennesseensis;* OD] [=*Urbimena* HAVLÍČEK, 1976, p. 367 (type, *U. mareki;* OD); *Qianjiangella* LIANG in LIU, XU, & LIANG, 1983, p. 274 (type, *Q. qianjiangensis;* OD]. Concavoconvex profile; unequally parvicostellate ornament, sometimes with comae; relatively large interarea; small pseudodeltidium in apex of delthyrium; chilidium absent; small dental plates, bounding ridges posterolateral to bilobed ventral valve muscle field (often less than quarter valve length); subperipheral rims sometimes present; thin central ridge to cardinal process set low relative to hinge line, with lateral components less prominent (only thin central process projecting posteriorly from hinge line; even this is sometimes entirely anterior to hinge line); median septum elevated anteriorly to merge with variably elevated platform. *Ordovician (?Arenig, Llanvirn)–Silurian (Telychian):* cosmopolitan.

L. (**Leptellina**). Similar to *L. (Merciella)* but with narrower cardinal process, less elevated and narrower platform and a single dorsal subperipheral rim. *Ordovician (?Arenig, Llanvirn–Ashgill):* cosmopolitan.——FIG. 206,*1a–c.* **L. (L.) tennesseensis,* Arline Formation, Llandeilo, Friendsville, Tennessee; *a,* dorsal view of conjoined valves, USNM 117453b, ×4 (Cooper, 1956); *b,* posterior view of dorsal interior, BMNH BB 1228, ×4; *c,* lateral view of dorsal interior, BMNH BB 1228, ×3.5 (Cocks & Rong, 1989).——FIG. 206,*1d,e. L. (L.) mareki* (HAVLÍČEK), Liben Formation, lower Caradoc, Motol, Prague, Czech Republic; *d,* ventral internal mold, ×5; *e,* dorsal internal mold, ×5 (Havlíček, 1976).——FIG. 206,*1f–i. L. (L.) qianjiangensis* (LIANG), Changwu Formation, middle Ashgill, Jianglütang, Chunan County, western Zhejiang Province, China; *f,* dorsal view of external mold of conjoined valves, showing interarea, HIGS 04351, ×2; *g,h,* holotype, internal mold of ventral valve, HIGS 04312, ×2; *i,* dorsal view of internal mold of conjoined valves, HIGS 04322, ×1.8 (Liu, Xu, & Liang, 1983).

L. (**Merciella**) LAMONT & GILBERT, 1945, p. 655 [**Leptella (Merciella) vesper;* OD]. Concavoconvex profile; unequally parvicostellate ornament; differs from *L. (Leptellina)* in having broader cardinal process, in having more elevated, wider platform, with an extra subperipheral rim in dorsal valve. *Silurian (Llandovery):* Europe, China.——FIG. 206,*2a–d.* **L. (M.) vesper,* Wych Formation, Telychian, Alfrick, Worcestershire, England; *a,* partially exfoliated ventral valve, showing ornament to left, interior to right, BU 373, ×3; *b,* ventral interior mold, BU 368, ×3; *c,d,* mold, latex cast of dorsal interior, BU 370, ×3 (new).

Acculina MISIUS in MISIUS & USHATINSKAYA, 1977, p. 113 [**A. acculica;* OD]. Gently resupinate profile; unequally parvicostellate ornament; pseudodeltidium over more than half ventral delthyrium; dental plates leading to muscle-bounding ridges surrounding bilobed ventral muscle field not enclosed anteriorly; no ventral valve myophragm; short, prominent socket ridges; myophragm elevated

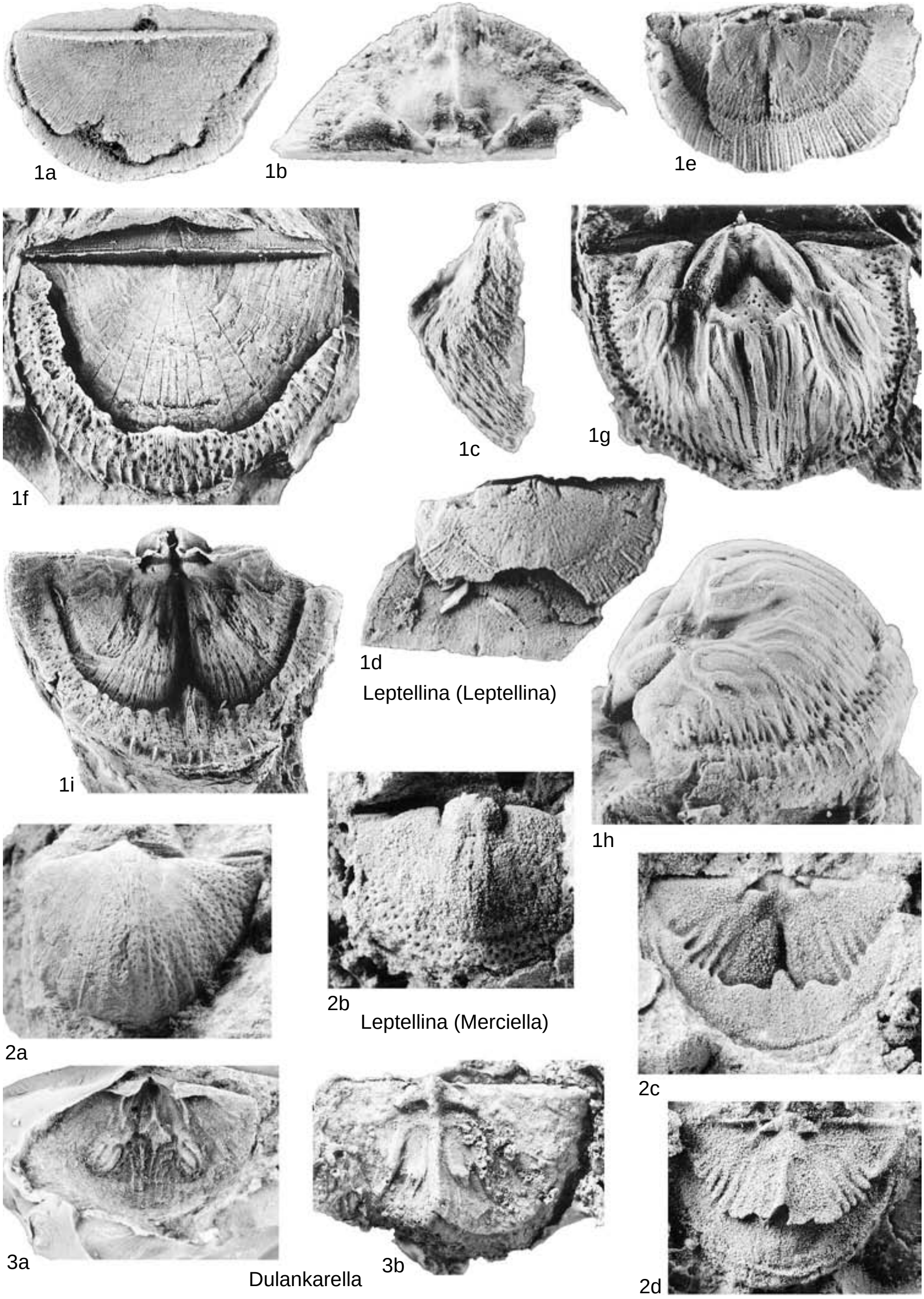

FIG. 206. Leptellinidae (p. 319–322).

anterior to dorsal median septum leading to quadrate dorsal platform, bilobed anteriorly. *Ordovician (Llandeilo–Caradoc):* Central Asia.——FIG. 207,*1a–f. *A. acculica; a,* dorsal view of conjoined valves, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia,

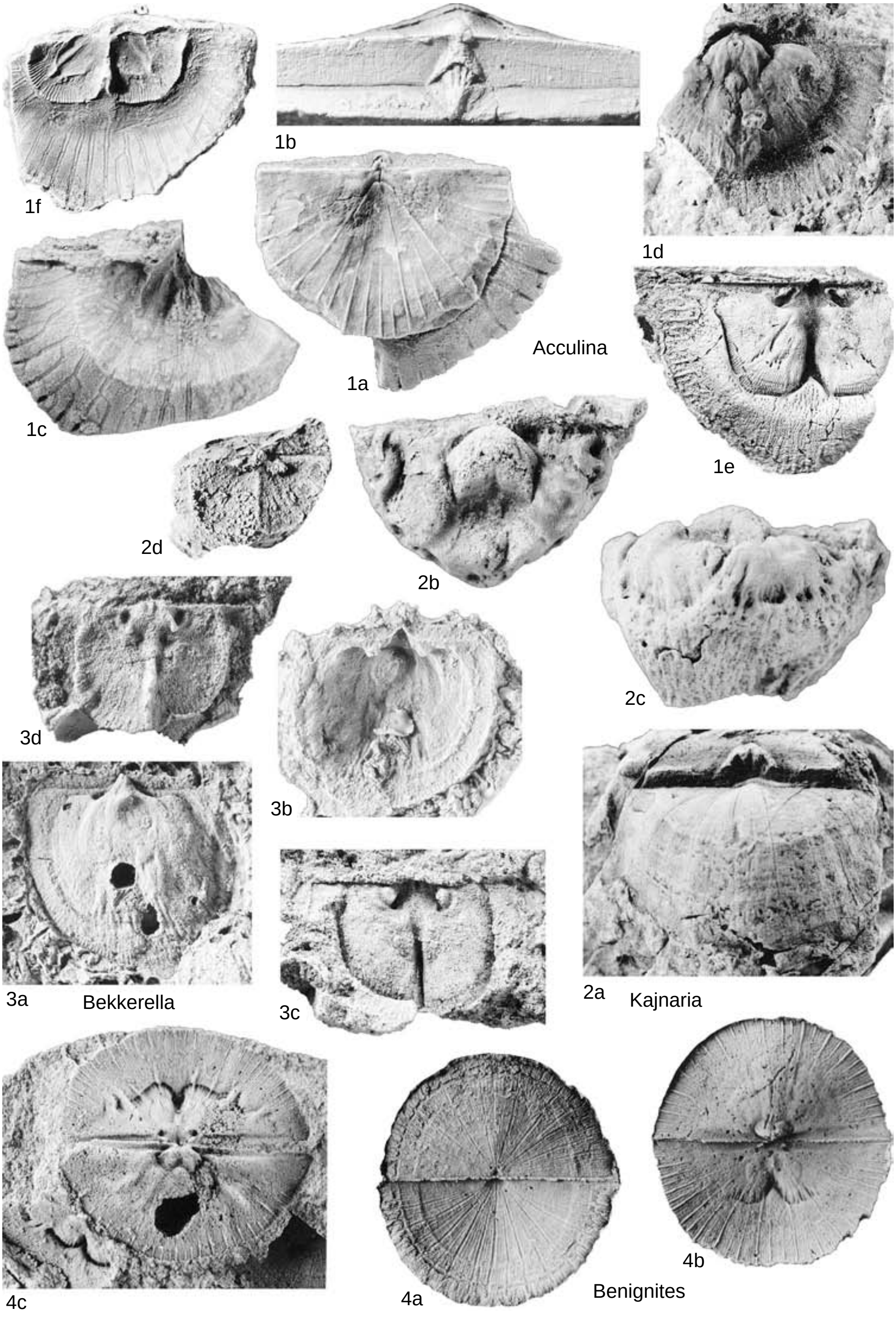

FIG. 207. Leptellinidae (p. 319–322).

BMNH BC 12907, ×3 (new); *b,* interarea of conjoined valves, Anderken Formation, Caradoc, Burultas, Kazakhstan, ×5 (Popov, new); *c,* ventral interior, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia, BMNH BC 12903, ×2; *d,* internal mold, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia, BMNH BC 12896, ×2 (new); *e,f,* dorsal internal mold, dorsal interior, Anderken Formation, Caradoc, Burultas, Kazakhstan, ×2 (Popov, new).

Bekkerella Reed, 1936, p. 38 [**Orthis subcrateroides* Reed, 1906, p. 63; OD]. Concavoconvex profile; fine radial ornament; pseudodeltidium, chilidium not known; prominent teeth with minimal dental plates; ventral muscle scars divergent, restricted by variably developed muscle-bounding ridges; weak ventral subperipheral ridge; small simple cardinal process; short, stout, curved socket ridges; prominent dorsal median septum developed anteriorly from myophragm, dividing prominent quadrate platform anteriorly. *Ordovician (Caradoc):* Burma.——Fig. 207,*3a–d.* **B. subcrateroides* (Reed), Naungkangyi Beds, Caradoc, Chaungzon, Northern Shan States, Burma; *a,b,* ventral internal mold, latex cast, SM 3128, ×2.5; *c,d,* dorsal internal mold, latex cast, BMNH BB 37750, ×2 (new).

Benignites Havlíček, 1952, p. 412 [**Strophomena primula* Barrande, 1879, pl. 52, fig. 3; OD]. Transverse outline; gently concavoconvex profile; unequally parvicostellate ornament; small bilobed ventral muscle field enclosed anteriorly; no ventral valve median septum; simple cardinal process, small socket ridges; wide but relatively small bilobed platform in posterior of center of dorsal valve, interrupted by mantle canals. *Ordovician (Llandeilo):* Europe.——Fig. 207,*4a–c.* **B. primula,* Dobrotivá Shales, Llandeilo, Malé Prílepy, Bohemia, Czech Republic; *a,b,* external, internal molds of conjoined valves, ×4; *c,* internal mold of conjoined valves, ×3 (Havlíček, 1976).

Dulankarella Rukavishnikova, 1956, p. 135 [**D. magna;* OD]. Concavoconvex profile; exterior, ventral interior as in *Leptellina,* except for larger bilobed ventral muscle field extending to half valve length or more; dorsal interior with striated lateral lobes of cardinal process distinct from brachiophores; pronounced socket ridges, muscle-bounding ridges; prominent dorsal median septum not extending anteriorly of diaphragm. *Ordovician (Caradoc–Ashgill):* Kazakhstan.——Fig. 206,*3a,b.* **D. magna; a,* latex cast of ventral internal mold, Otarsky Horizon, Caradoc, CNIGR 12375/200, ×1.5; *b,* latex cast of dorsal interior, Dulankara Formation, upper Caradoc, Dulankara, Chu-Ili Mountains, Kazakhstan, ×2 (new).

Kajnaria Nikitin & Popov in Klenina, Nikitin, & Popov, 1984, p. 144 [**K. derupta;* OD] [=*Pseudoleptellina* Andreev, 1992, p. 112 (type, *P. similis;* OD)]. Strongly concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium, no chilidium; massive teeth, no dental plates; strong muscle-bounding ridges in ventral valve, with two curved ridges variably developed anteriorly (the diaphragm of Nikitin & Popov, 1984); variably developed ventral valve myophragm; dorsal interior with robust dental plates, prominent median septum, platform. *Ordovician (Llandeilo–Ashgill):* Kazakhstan.——Fig. 207,*2a–d.* **K. derupta,* upper Bestamakskaya Formation, Erkebidaikski Horizon, middle Ordovician, New Archal Hill, Chinghiz Mountains, Kazakhstan; *a,* dorsal external mold, BMNH BC 12931, ×3; *b,c,* ventral internal mold, BMNH BC 12932, ×3 (new); *d,* latex cast of dorsal internal mold, CNIGR 110/12095, ×2 (Klenina, Nikitin, & Popov, 1984).

Leptelloidea Jones, 1928, p. 385 [**Plectambonites schmidti* var. *leptelloides* Bekker, 1921, p. 68; OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; very small deltidial plates, small chilidium; distinctive articulation including pits, accessory teeth in ends of dental plates, corresponding structures in dorsal valve; large bilobed ventral muscle scars extending to about half valve length (much longer than *Leptellina* but not so wide as in *Dulankarella*), adductor scars enclosed by diductor scars; large cardinal process projecting posteriorly from hinge line, but cardinal process separate from socket plates; dorsal median septum merging with bilobed elevated platform. *Ordovician (Llanvirn–Caradoc):* Europe, Burma.——Fig. 208,*1a–f.* **L. leptelloides* (Bekker), Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia; *a,* dorsal view of conjoined valves, USNM 84257c, ×3 (Cooper, 1956); *b,c,* ventral interior, viewed ventrally, from anterior, TAGI BR 93, ×3 (new); *d–f,* dorsal interior viewed laterally, ×3, dorsally, ×3, posteriorly, ×5, BMNH BB 5169 (Cocks & Rong, 1989).

Mabella Klenina in Klenina, Nikitin, & Popov, 1984, p. 69 [**Leptellina (M.) semiovalis;* OD] [=*Wiradjuriella* Percival, 1991, p. 138 (type, *W. halis;* OD)]. Very convex ventral profile, slightly concave dorsal profile; very fine parvicostellate ornament; pseudodeltidium filling most of delthyrium; chilidium absent; stout flaring teeth; vestigial dental plates leading to bounding ridges lateral to bilobed ventral muscle field; prominent cardinal process, flaring socket ridges; dorsal interior as in *Leptellina* but with prominent median septum anteriorly enlarging, tubular, sometimes bifurcating, but not extending anteriorly from platform rim; platform may be elevated. *Ordovician (Caradoc–Ashgill):* Kazakhstan, Australia, ?Burma.——Fig. 208,*2a–e. M. multicosta* (Rukavishnikova), lower Kulunbulak Formation, Dulankara Horizon, lower Ashgill, Kulunbulak River, Kazakhstan; *a,b,* ventral internal mold, latex cast, BMNH BC 12935a, ×5; *c,d,* dorsal internal mold, latex cast, BMNH BC 12935b, ×5; *e,* latex cast of dorsal interior, BMNH BC 12934, ×5 (new).——Fig. 208,*2f–i. M. halis* (Percival), Billabong Limestone, middle Caradoc, Parkes, New South Wales, Australia; *f,g,* dorsal, posterior views of conjoined valves, SUP 67527, ×3; *h,* ventral inte-

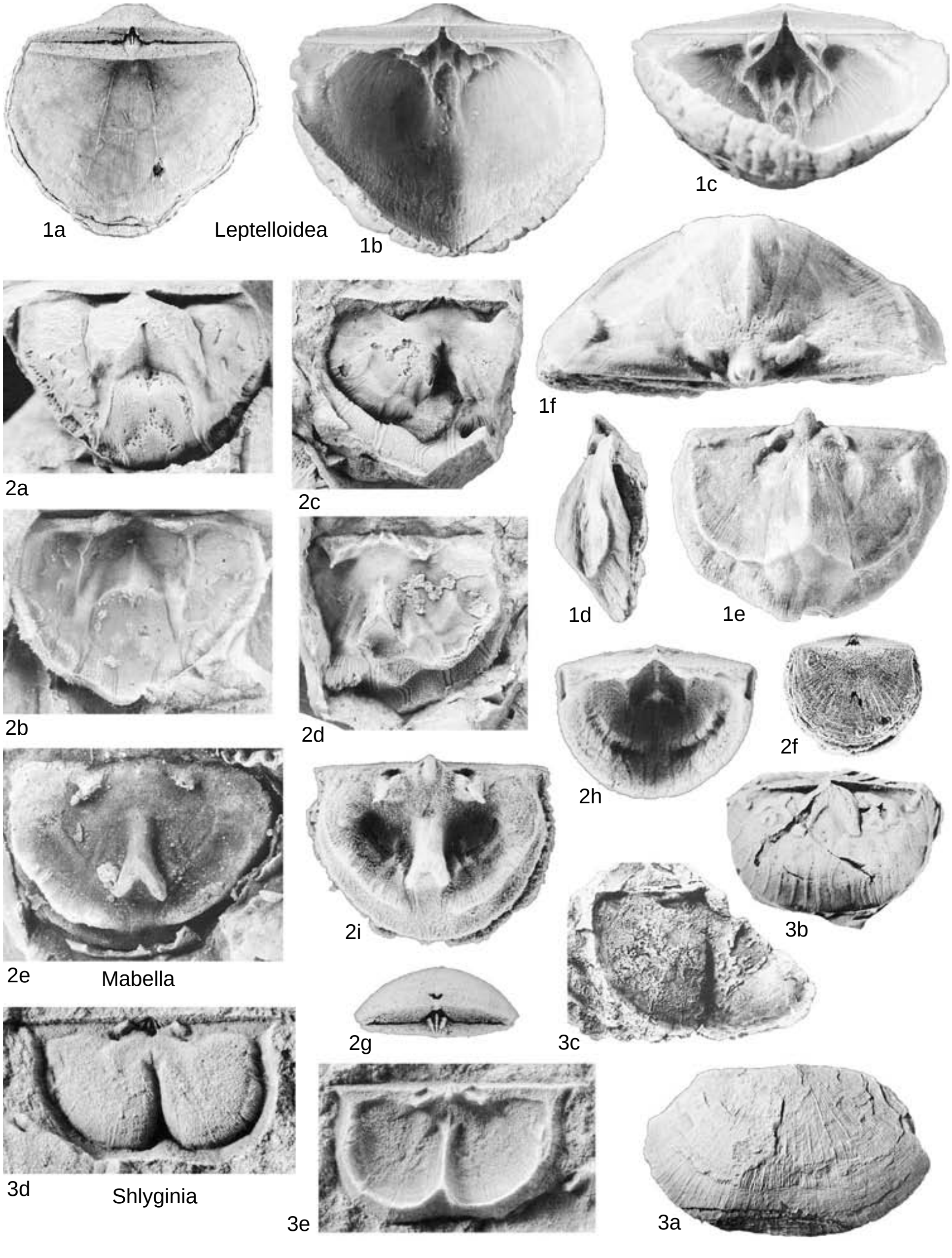

FIG. 208. Leptellinidae (p. 322–324).

rior, SUP 67512, ×5; *i,* holotype, dorsal interior, SUP 67491, ×5 (Percival, 1991).

Reversella LIANG in LIU, XU, & LIANG, 1983, p. 274 [**R. trigonoformis;* OD]. Profile resupinate, strongly geniculate ventrally; unequally parvicostellate ornament; teeth, dental plates posterior to ventral muscle field with strong bounding ridges, meeting anteriorly, with central strong myophragm within muscle field; prominent cardinal process, socket plates, large median septum extending anteriorly to

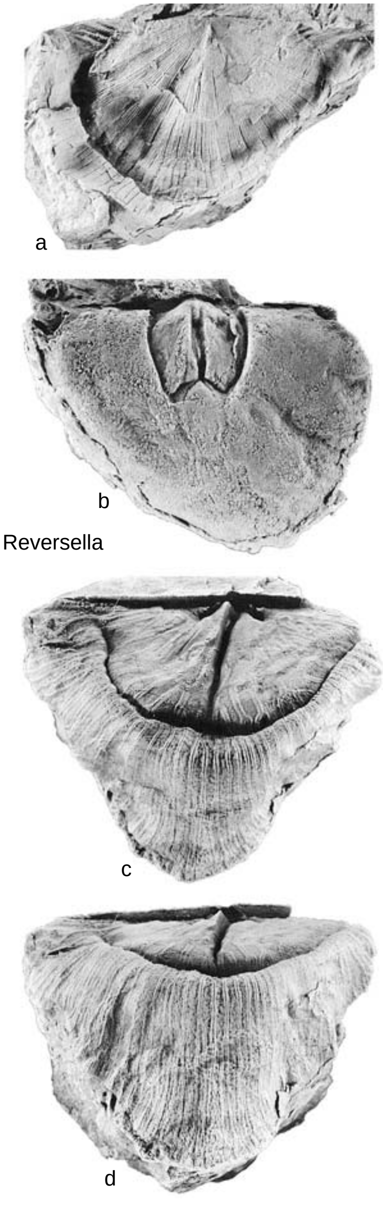

FIG. 209. Leptellinidae (p. 323–324).

merge with platform; dorsal platform with diaphragm, not bilobed anteriorly. *Ordovician (Ashgill):* China.——FIG. 209*a–d.* **R. trigonoformis,* Changwu Formation, middle Ashgill, Jianglütang, Chunan County, western Zhejiang, China; *a,* dorsal external mold, HIGS 04332, ×1; *b,* ventral internal mold, HIGS 04328, ×1.4; *c,d,* holotype, dorsal internal mold viewed obliquely, anteriorly, HIGS 04327, ×1 (Liu, Xu, & Liang, 1983).

Shlyginia NIKITIN & POPOV, 1983, p. 237 [**S. declivis;* OD]. Concavoconvex profile; differs from *Leptellina* in possessing large muscle field in ventral valve to about half valve length or more; adductor muscle scars usually enclosed by diductor scars in ventral valve; cardinal process projecting slightly or not at all posteriorly from hinge line as in *Leptellina. Ordovician (Llandeilo–lower Ashgill):* Kazakhstan.——FIG. 208,*3a–c.* **S. declivis,* Andryushinka Formation, Llandeilo–Caradoc, Ishim River, Kazakhstan; *a,* holotype, ventral exterior, CNIGR 31/11990, ×3; *b,* ventral internal mold, CNIGR 34/11990, ×3; *c,* dorsal internal mold, CNIGR 35/11990, ×3 (Nikitin & Popov, 1983).——FIG. 208,*3d,e. S. extraordinaria* (RUKAVISHNIKOVA), Dulankara Formation, Caradoc, Dulankara, Kazakhstan; dorsal internal mold, latex cast, BMNH BC 12897, ×3 (new).

Subfamily
PALAEOSTROPHOMENINAE
Cocks & Rong, 1989

[Palaeostrophomeninae COCKS & RONG, 1989, p. 107]

Profile concavoconvex to resupinate; large open ventral valve muscle field; usually with deeply impressed mantle canal markings in both valves. *Ordovician (Arenig–Caradoc).*

Palaeostrophomena HOLTEDAHL, 1916, p. 43 [**Strophomena concava* SCHMIDT, 1858, p. 215; OD]. Gently resupinate profile; unequally parvicostellate ornament with posterolateral rugae common; small pseudodeltidium, larger chilidium; small teeth with reduced dental plates leading to posterolateral bounding ridges around triangular ventral muscle field open anteriorly; prominent cardinal process, small socket ridges; central myophragm becoming striated anteriorly; platform absent; dorsal interior as in *Apatomorpha. Ordovician (Llanvirn–Caradoc):* cosmopolitan.——FIG. 210,*1a–c.* **P. concava* (SCHMIDT), Llanvirn; *a,* dorsal exterior, Hunduum Formation, Tallinn, BMNH BB 91269, ×2 (new); *b,c,* ventral and dorsal interiors, Uhaku Stage, Erra, Estonia, ×2 (Rõõmusoks, new).

Apatomorpha COOPER, 1956, p. 709 [**Rafinesquina pulchella* RAYMOND, 1928, p. 296; OD]. Concavoconvex to planoconvex profile; unequally parvicostellate ornament; narrow pseudodeltidium developed; widely divergent teeth; dental plates present; large prominent ventral muscle field with short muscle-bounding ridges, muscle scars flabellate anteriorly; prominent cardinal process, small socket ridges; prominent but divided dorsal myophragm; small dorsal muscle field with oblique ridges; no platform. *Ordovician (Llanvirn–Caradoc):* North America, Australia.——FIG. 210,*2a–d.* **A. pulchella* (RAYMOND), Athens Formation, upper Llandeilo–lower Caradoc, Tennessee; *a,* dorsal view of exterior of conjoined valves, USNM 110895c, ×3; *b,* ventral internal mold, BMNH BC 12849, ×2; *c,* ventral interior, USNM 110896a, ×3 (Cooper, 1956); *d,* dorsal interior, USNM 110896c, ×3 (new).

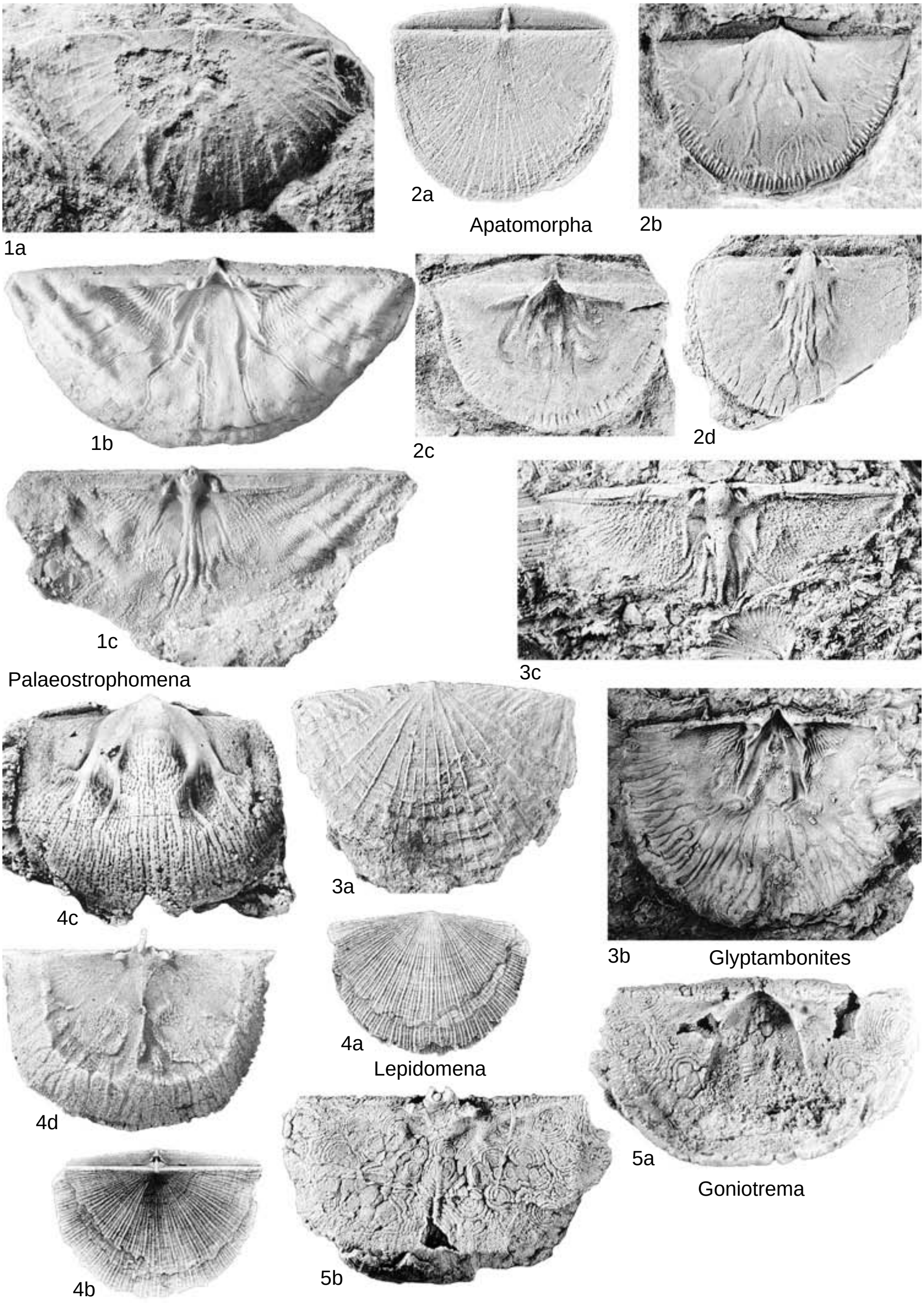

FIG. 210. Leptellinidae (p. 324–326).

Glyptambonites COOPER, 1956, p. 712 [**G. musculosus;* OD]. Gently concavoconvex profile; unequally parvicostellate ornament with much accentuated costellae, posterolateral rugae common; small pseudodeltidium, moderate chilidium; small teeth, dental plates leading to strong lateral muscle-bounding ridges; bilobed ventral muscle field relatively open anteriorly; bulbous cardinal process; very small socket ridges; large myophragm leading anteriorly to relatively small dorsal median septum; posterolateral dorsal muscle-bounding ridges in adults; no platform (although no entire dorsal valve yet illustrated); similar to *Apatomorpha* but with ventral valve muscle field narrower, longer muscle-bounding ridges. *Ordovician (Llanvirn–Caradoc):* North America, Scotland, Kazakhstan.——FIG. 210,*3a–c.* **G. musculosus,* Oranda Formation, lower Caradoc, Linville Station, Virginia; *a,* ventral exterior, USNM 117391, ×2; *b,* latex cast of ventral internal mold, USNM 117390a, ×1; *c,* latex cast of dorsal interior, USNM 117388c, ×2 (Cooper, 1956).

?Goniotrema ULRICH & COOPER, 1936b, p. 626 [**G. perplexum;* OD]. Concavoconvex profile; ornament uncertain; strong teeth; strong muscle-bounding ridges, triangular ventral muscle field open anteriorly; prominent erect cardinal process but very small socket ridges; weak myophragm; no bema but faint traces of possible side septa (and thus possible inclusion in Syndielasmatidae); weak platform present; not certainly leptellinid. *Ordovician (Llanvirn):* North America.——FIG. 210,*5a,b.* **G. perplexum,* upper Pogonip Group, upper Llanvirn, Ikes Canyon, Nevada; *a,b,* holotype, ventral, dorsal interiors, USNM 92872, ×2 (Cooper, 1956).

Ishimia NIKITIN, 1974, p. 59 [**I. ishimensis;* OD]. Large with convex ventral valve, flat dorsal valve becoming concave anteriorly; unequally parvicostellate ornament, sometimes with comae; pseudodeltidium, chilidium present; substantial teeth but dental plates short or absent; well-impressed triangular ventral muscle field with no bounding ridges, open anteriorly; prominent cardinal process, socket plates curving anterolaterally; prominent dorsal median septum merging anteriorly with elevated platform; similar to *Toquimia,* but with concavoconvex profile, stronger median septum, stronger dorsal platform. *Ordovician (Llanvirn–lower Caradoc):* Asia.——FIG. 211,*1a,b.* **I. ishimensis,* Andryshenskaya Formation, Llandeilo, Ishim River, Kazakhstan; *a,* latex cast of ventral interior, CNIGR 1614/14, ×1; *b,* holotype, latex cast of dorsal interior, CNIGR 1614/15, ×1 (new).

Lepidomena LAURIE, 1991, p. 55 [**L. pulchra;* OD]. Concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium, chilidium; ventral interarea orthocline or apsacline; dorsal interarea hypercline; dental plates absent; ventral muscle field bilobed; similar to *Apatomorpha* but high bladelike cardinal process, delicate bladelike socket ridges free distally; dorsal median septum, low dorsal platform rim developed. *Ordovician (Caradoc):* Australia.——FIG. 210,*4a–d.* **L. pulchra,* lower Benjamin Limestone, Caradoc, Settlement Road, Florentine Valley, Tasmania, Australia; *a,b,* ventral, dorsal views of conjoined valves, UTGD 99913, ×2; *c,* ventral internal mold, UTGD 99911, ×2; *d,* holotype, dorsal interior, UTGD 99906, ×2 (Laurie, 1991).

Onegia ANDREEV, 1993, p. 51 [**O. vitrea;* OD]. Small transverse shells with concavoconvex profile; unequally parvicostellate ornament with anterior extensions of three major costellae; poorly impressed ventral muscle field; ventral subperipheral rim; stubby socket plates; dorsal median septum leading to elevated bilobed dorsal valve platform. *Ordovician (Arenig):* Russia.——FIG. 211,*2a.* **O. vitrea,* uppermost Volkhov Formation, upper Arenig, Volkhov River, St. Petersburg, Russia; dorsal interior, PAN 4459/4, ×9 (Andreev, 1993).——FIG. 211,*2b–d. O. geometrica* (KUTORGA), uppermost Volkhov Formation, upper Arenig, River Lava, St. Petersburg, Russia; *b,c,* ventral, dorsal views of conjoined valves, BMNH BC 51234, ×10; *d,* ventral interior, BMNH BC 51235, ×10 (Popov, new).

Titanambonites COOPER, 1956, p. 717 [**T. medius;* OD]. Concavoconvex profile; ornament unequally parvicostellate, but with finer parvicostellae crossed by regular concentric lamellae; ventral muscle field flabellate; interior as in *Apatomorpha* but with variably developed platform; cardinal process bulbous; posterior dorsal valve adductor scars separated by transverse rather than oblique ridges leading to *vascula myaria. Ordovician (Llandeilo–Caradoc):* North America, Kazakhstan.——FIG. 211,*3a–d.* **T. medius,* Athens Formation, Llandeilo–Caradoc, Christiansburg, Tennessee; *a,* dorsal view of conjoined valves, USNM 117429c, ×1; *b,* ventral internal mold, USNM 117429f, ×2; *c,d,* latex cast, natural mold of dorsal interior, USNM 117429g, ×2 (Cooper, 1956).

Toquimia ULRICH & COOPER, 1936b, p. 626 [**T. kirki;* OD]. Gently concavoconvex to planoconvex profile initially, but resupination develops anteriorly in larger specimens; unequally parvicostellate ornament; large pseudodeltidium, small chilidium variably developed; large but poorly impressed ventral muscle field; ventral subperipheral rim; bulbous cardinal process with massive central component, small lateral processes; short, erect socket ridges; weak myophragm extending anteriorly into thin, low median septum; mantle canals often well impressed; similar to *Apatomorpha* but with weak platform. *Ordovician (Llanvirn–Llandeilo, ?Caradoc):* cosmopolitan.——FIG. 212,*2a–c.* **T. kirki,* upper Pogonip Group, Llanvirn, Ikes Canyon, Nevada; *a,* interarea of conjoined valves, USNM 117567h, ×3; *b,* latex of ventral internal mold, USNM 117567a, ×1.5; *c,* latex of dorsal internal mold, USNM 117567d, ×2 (Cooper, 1956).

Ujukites ANDREEVA, 1985, p. 41 [**U. altaicus;* OD]. Profile planoconvex to slightly resupinate; very upright interarea with small pseudodeltidium, chilidium; very short dental plates, no bounding ridges to triangular, flabellate weakly impressed ventral muscle field; cardinal process weak, but definitely leptellinid (i.e., trifid, not undercut); short dorsal median septum developed in valve center only; very weakly developed dorsal platform. *middle Ordovician:* Tuva, Russia.——FIG. 212,*1a–d.* **U. altaicus,* ?Stretinski Formation, middle Ordovician, River Tuloi, Altai Mountains, Russia; *a,b,* holotype, con-

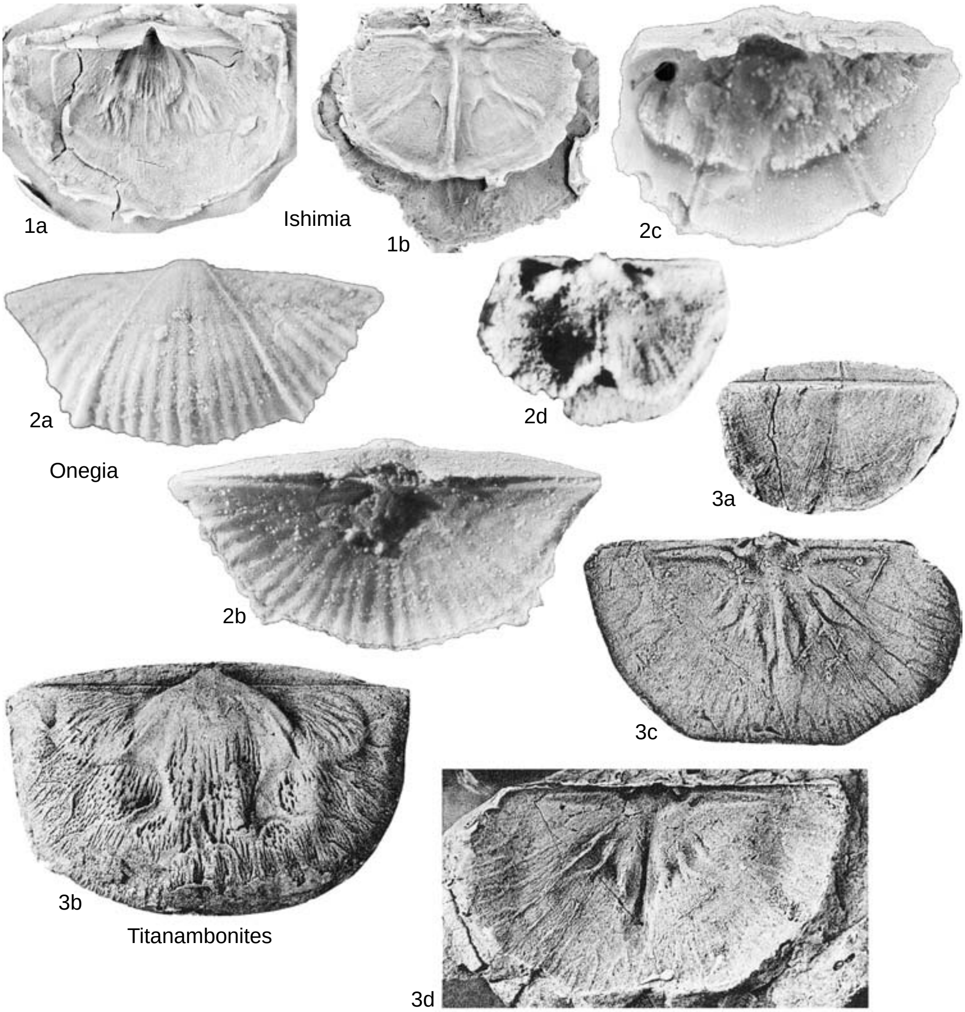

FIG. 211. Leptellinidae (p. 326).

joined valves, CNIGR 70/11865, ×4; *c,* ventral interior, CNIGR 76/11865, ×4; *d,* dorsal internal mold, CNIGR 74/11865, ×4 (Popov, new).

Family GRORUDIIDAE
Cocks & Rong, 1989

[Grorudiidae COCKS & RONG, 1989, p. 112]

Concavoconvex profile; dental plates present; cardinal process trifid, not undercut; bema present; side septa present, but sometimes merged or weakly developed; platform variably developed. *Ordovician (lower Llanvirn–upper Caradoc).*

Grorudia SPJELDNAES, 1957, p. 61 [**G. grorudi;* OD] [=*Alwynella* SPJELDNAES, 1957, p. 85 (type, *A. osloensis;* OD)]. Very transverse outline; gently concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidium unknown; small teeth; poorly impressed ventral muscle field with no bounding ridges; prominent bulbous cardinal process with very small socket ridges; similar to *Tetraodontella, Calyptolepta* but with no platform, side septa not extending beyond small but elevated bema; short strong median septum also present, but not anterior of bema. *Ordovician (Caradoc):* Baltic.——FIG. 213,*3a–c.* **G. grorudi,* Zone 4aβ, lower Caradoc, Tåsen Station, Oslo, Norway; *a,* latex cast of dorsal exterior, PMO 66940, ×4; *b,c,* holotype, dorsal internal mold, latex cast, PMO 66940, ×6 (Cocks & Rong, 1989).

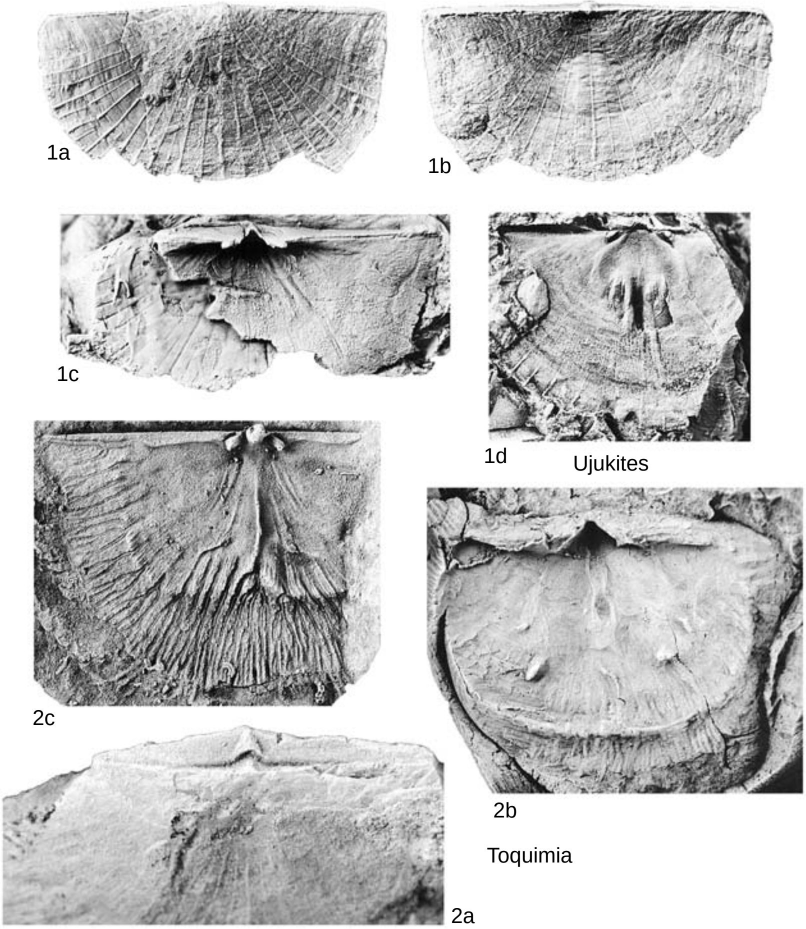

FIG. 212. Leptellinidae (p. 326–327).

Calyptolepta NEUMAN, 1976, p. 35 [**C. diaphragma;* OD] [=*Anechophragma* NEUMAN, 1976, p. 37 (type, *A. rarum;* OD); *Ujukella* ANDREEV, 1993, p. 52 (type, *U. alexandrae;* middle Malinovsk Formation (Llanvirn), Tevel-tal, Tuva, Russia); *Yuanbaella* FU, 1982, p. 116 (type, *Tetraodontella truncata* FU, 1975, p. 108; OD)]. Small; strongly concavoconvex profile; ventral interarea apsacline with small pseudodeltidium; dorsal interarea catacline to hypercline with small chilidium; short wide teeth with dental plates absent or reduced to slight thickening at sides of muscle field; short bilobed ventral muscle field; ventral subperipheral rim; simple bladelike cardinal process; flaring socket ridges; dorsal myophragm elevated anteriorly into median septum rising anteriorly to merge with elevated platform; similar to *Tetraodontella* but with two distinct side septa in median part of dorsal valve although with some variability; in some specimens septa nearly merged into median septum. *Ordovician (Llanvirn):* North America, Tuva, China.——FIG. 214*a–e.* **C. diaphragma,* Virgin Arm Formation, Llanvirn, Virgin Arm, New World Island, Newfoundland, Canada; *a,* dorsal view of conjoined valves, GSC 35067, ×2; *b,c,* latex cast of internal mold, ventral interior, GSC 35071, ×2 (Neuman, 1976); *d,e,* latex cast of internal mold, dorsal interior, GSC 35068a, ×3 (Cocks & Rong, 1989).——FIG. 214*f–i. C. rarum,* Virgin Arm Formation, Llanvirn, Virgin Arm, New World Island, Newfoundland, Canada; *f,g,* molds of ventral, dorsal exteriors, GSC 35078, ×3; *h,i,* holotype, latex cast of dorsal interior, GSC 35077, ×3 (Neuman, 1976).——FIG. 214*j–m. C. truncata,* Xiliangsi Formation, lower Llanvirn, Dangmengou, Yuanba, Nanzheng County, southern Shaanxi Province, China; *j,k,* exterior of ventral, dorsal valves, GB 141, GB 142, ×12; *l,* internal mold of ventral valve, GB 143, ×9; *m,* internal mold of dorsal valve, GB 145, ×12 (Fu, 1982).

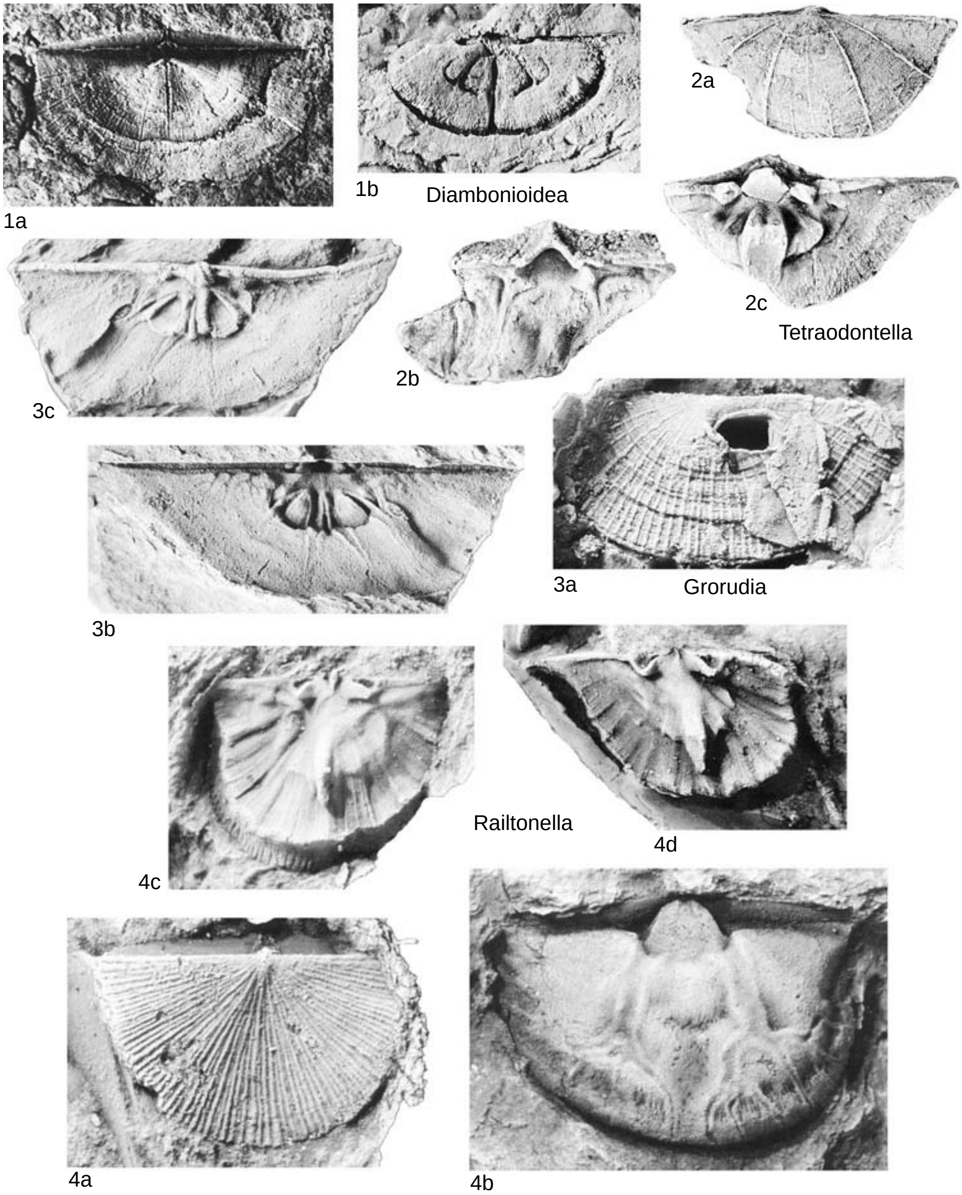

FIG. 213. Grorudiidae (p. 327–331).

Diambonioidea ZENG, 1987, p. 230 [**D. transversa;* OD]. Concavoconvex profile; unequally parvicostellate ornament; deltidial plates covering only small part of delthyrium; similar to *Calyptolepta,* but dorsal valve flat, with wider dorsal valve muscle field; short side septa constrained within muscle field; prominent dorsal median septum merging anteriorly with platform. *Ordovician (Llandeilo–Caradoc):* China.——FIG. 213,*1a,b.* **D. transversa,* Miaopo Formation, upper Llandeilo–lower Caradoc, Huanghuachang, Yichang County, western Hubei, China; *a,* external mold of conjoined valves, YIGM IV45808, ×4; *b,* dorsal internal mold, YIGM IV45807, ×4 (Zeng, 1987).

Railtonella LAURIE, 1991, p. 63 [**R. scanloni;* OD]. Ventral valve convex; dorsal valve flat but concave anteriorly; small pseudodeltidium, chilidium; large teeth with vestigial dental plates, poorly impressed

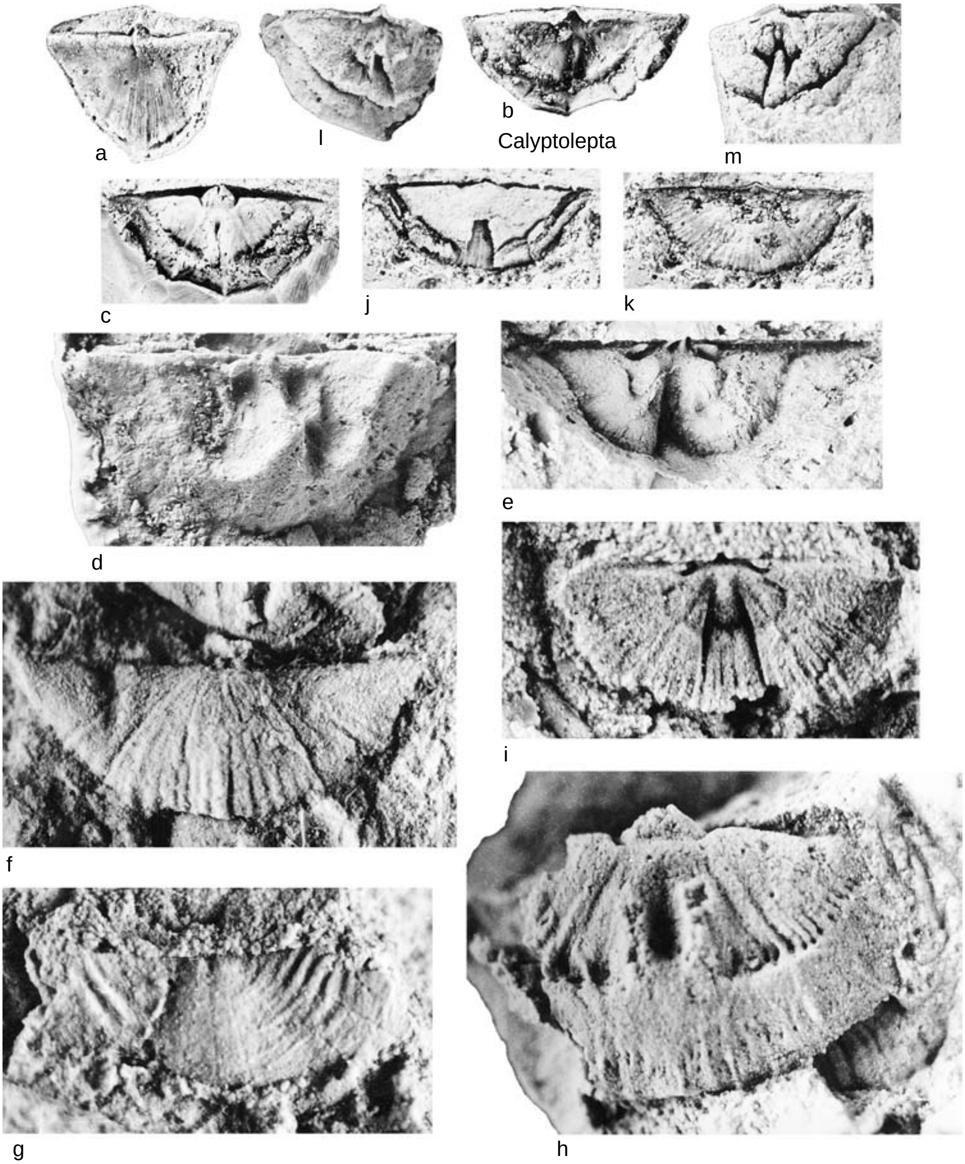

FIG. 214. Grorudiidae (p. 328).

ventral muscle field; prominent saccate ventral mantle canals; variable but relatively small bladelike cardinal process; similar to *Calyptolepta,* but with thick, well-developed dorsal median septum extending beyond bema; prominent variably elevated dorsal platform. *Ordovician (Llanvirn):* Australia.——FIG. 213,*4a–d.* **R. scanloni,* Karmberg Limestone, Llanvirn, Railton, Tasmania, Australia; *a,* dorsal view of latex cast of conjoined valves, UTGD 99822, ×6; *b,* ventral internal mold, UTGD 99837, ×6; *c,* holotype, latex cast of dorsal valves, UTGD 99825, ×6; *d,* latex cast of dorsal valves, UTGD 120293, ×6 (Laurie, 1991).

Tetraodontella JAANUSSON, 1962, p. 1 [**T. biseptata;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; small teeth, dental plates; relatively small ventral muscle field; dorsal interior as in *Calyptolepta* but with strong central pair of septa fused together along their length, homologizing a wide median septum, except where they divide anteriorly; further short side septa constrained within muscle field, bema; weak platform present. *Ordovician (Llanvirn–Caradoc):* Baltic, China.——FIG. 213,*2a–c.* **T. biseptata,* Dalby Limestone, middle Caradoc, Böda Hamn borehole, Öland, Sweden; *a,* holotype, ventral exterior, RMS Öl 1040, ×5; *b,* ventral interior, RMS Öl 1037, ×7; *c,* dorsal interior, ×4 (Williams, 1965d).

Family LEPTESTIIDAE Öpik, 1933

[*nom. transl.* WILLIAMS, 1953b, p. 6, *ex* Leptestiinae ÖPIK, 1933a, p. 24]

Concavoconvex profile; dental plates present; with bema, no side septa; trifid cardinal process not undercut. *Ordovician (?Arenig, Llanvirn)–Silurian (Ludlow).*

Leptestia BEKKER, 1922, p. 362 [**L. musculosa;* OD]. Concavoconvex profile; fine, unequally parvicostellate ornament; with pseudodeltidium, chilidium; teeth small, dental plates lacking; ventral muscle field subcircular, well impressed though without raised muscle-bounding ridges; erect cardinal process, small socket ridges, variably developed myophragm leading anteriorly to weak dorsal median septum; with elongate bema; median septum through bema merging anteriorly with lobes of platform. *Ordovician (?Arenig, Llanvirn–Caradoc):* Europe, Asia.——FIG. 215,*1a–d.* **L. musculosa; a,* ventral exterior, Uhaku Stage, Llandeilo, Uhaku, Estonia, BMNH BB 33356, ×1.5 (new); *b,* ventral interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, ×2 (Rõõmusoks, new); *c,* dorsal view of dorsal interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, BMNH BB 5189, ×1.5; *d,* posterior view of dorsal interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, BMNH BB 5189, ×2 (Cocks & Rong, 1989).

Bilobia COOPER, 1956, p. 759 [**B. hemisphaerica;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium short or absent; thin chilidium present; stubby bilobed teeth, obsolescent dental plates; ventral muscle field strongly bilobed with divergent diductors; broad median ridge sporadically developed anterior to ventral scar, generally as coalescent tubercles; cardinal process erect; divided, elevated bema, undercut anteriorly, separated centrally by small discrete median septum; variably developed platform with diaphragm or peripheral rim. *Ordovician (Caradoc):* cosmopolitan.——FIG. 216,*2a–d.* **B. hemisphaerica,* Oranda Formation, lower Caradoc, Strasburg Quadrangle, Virginia; *a,* holotype, dorsal view of exterior of conjoined valves, USNM 111099b, ×4; *b,* ventral internal mold, USNM 111099d, ×5; *c,* conjoined valves, including mold of dorsal interior, USNM 111099c, ×4; *d,* dorsal interior, USNM 111099f, ×5 (Cooper, 1956).——FIG. 216,*2e,f. B. musca* (ÖPIK) Kukruse Formation (lower Caradoc), Kohtla-Järve, Estonia; *e,f,* posterior, ×7, lateral views of dorsal interior, ×5, BMNH BB 5202 (Cocks & Rong, 1989).

Leangella ÖPIK, 1933a, p. 42 [**Plectambonites scissa* (DAVIDSON, 1871) var. *triangularis* HOLTEDAHL, 1916, p. 84; OD] [=*Diambonia* COOPER & KINDLE, 1936, p. 356 (type, *Plectambonites gibbosa* WINCHELL & SCHUCHERT, 1892, p. 288; OD); *Opikella* AMSDEN, 1968, p. 48 (type, *L. (O.) dissiticostella;* OD); *Tufoleptina* HAVLÍČEK, 1961, p. 447 (type, *T. tufogena;* OD)]. Strongly concavoconvex profile; unequally parvicostellate ornament; large orthocline interarea; strong teeth with small dental plates; ventral muscle field small, bilobed, with pronounced muscle-bounding ridges; subperipheral rim variably present in ventral valve; ventral median septum varying from strong to absent; erect cardinal process, laterally flaring socket ridges; weak myophragm; dorsal median septum absent; elevated bema bilobed, undercut anteriorly; platform or discontinuous row of enhanced septules; diaphragm or peripheral rim near valve margin. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.

L. (Leangella). Similar to *L. (Leptestiina)* but with discrete platform. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.——FIG. 216,*3a–d.* **L. (L.) scissa* (DAVIDSON), upper Haverford Mudstone Formation, Rhuddanian, Gasworks, Haverfordwest, Dyfed, Wales; *a,* latex of conjoined valves, BMNH BB 70996, ×5; *b,* dorsal exterior latex, BMNH BB 31826, ×5 (new); *c,d,* mold, latex of dorsal interior, BMNH BB 32167, ×6 (Cocks & Rong, 1989).——FIG. 216,*3e,f. L. (L.) tufogena,* Liten Formation, Homerian, Hlinik, Svaty Jan pod Skalou, Bohemia, Czech Republic; *e,* ventral internal mold, OMR VH 290, ×5; *f,* dorsal internal mold, OMR VH 285, ×5 (Havlíček, 1967).——FIG. 216,*3g. L. (L.) gibbosa,* Stewartville Formation, lower Ashgill, Stewartville, Minnesota; dorsal interior, BMNH BC 7272, ×5 (Cocks & Rong, 1989).

L. (Leptestiina) HAVLÍČEK, 1952, p. 412 [**Benignites (Leptestiina) prantli;* OD]. Similar to *L. (Leangella)* except that dorsal valve platform is made up anteriorly of discrete septules not merged to form typical continuous platform. *Ordovician (Caradoc–Ashgill):* Europe, ?China.——FIG. 216,*1a,b.* **L. (L.) prantli* HAVLÍČEK, Králuv Dvur Formation, middle Ashgill, Králuv Dvur, Bohemia, Czech Republic; *a,b,* internal mold of conjoined valves, external mold of dorsal valve, NM CD 1557, ×5 (Havlíček, 1967).

Rurambonites COCKS & RONG, 1989, p. 118 [**Plectambonites ruralis* REED, 1917, p. 879; OD]. Concavoconvex profile; unequally parvicostellate ornament; delthyrium largely open, with small pseudodeltidium, pair of chilidial plates; strong teeth, denticulate hinge line; ventral muscle field relatively small; bilobed with encircling muscle-bounding ridges; strong erect cardinal process; bladelike, widely divergent socket ridges; bema transverse, not bilobed, in contrast to bilobed elongate bema of *Sampo;* small dorsal median septum

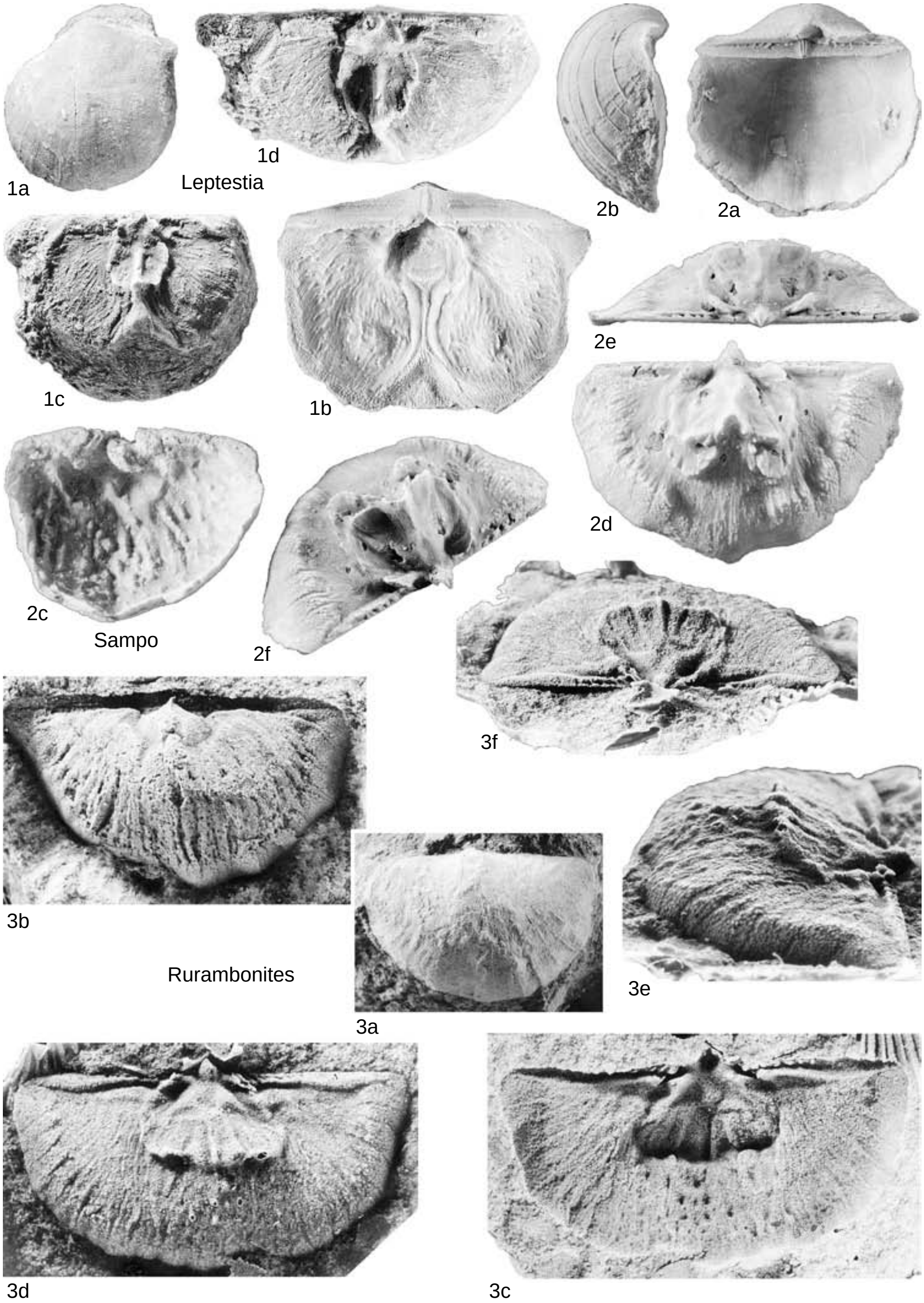

FIG. 215. Lepestiidae (p. 331–334).

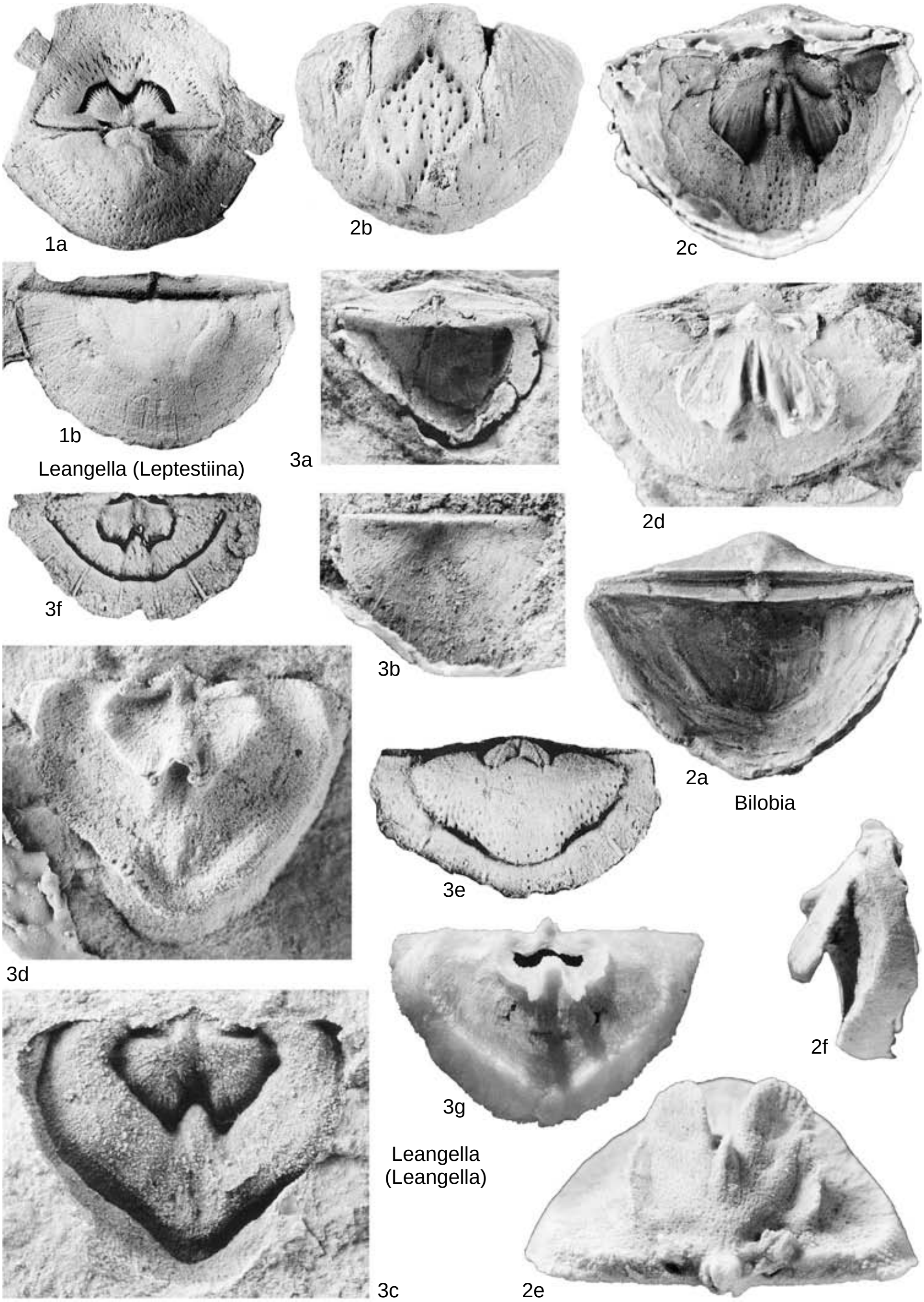

FIG. 216. Leptestiidae (p. 331).

confined to bema. *Ordovician (Ashgill):* Scotland, North America.——FIG. 215,*3a–f.* **R. ruralis* (REED), southern Threave Formation, Rawtheyan, Starfish Bed, Girvan, Strathclyde, Scotland; *a,* ventral exterior, BMNH BC 50914, ×2; *b,* ventral internal mold, BMNH BC 7202, ×3; *c–f,* dorsal internal mold, dorsal, lateral, posterior views of latex cast, BMNH BC 7200, ×3 (Cocks & Rong, 1989).

Sampo ÖPIK, 1933a, p. 35 [**S. hiiuensis;* OD]. Concavoconvex profile; unequally parvicostellate ornament; hinge line denticulate; ventral muscle field bilobed; cardinal process erect; bema elongate (in contrast to *Rurambonites*), bilobed, undercut; similar to *Bilobia* apart from denticulate hinge line. *Ordovician (Caradoc–Ashgill):* Baltic.——FIG. 215,*2a–f.* **S. hiiuensis,* Vormsi Stage, lower Ashgill; *a,b,* dorsal, lateral views of conjoined valves, Hiiuma, TAGI BR 1235, ×2; *c,* ventral interior, Körgessaare, Estonia, TAGI BR 1236, ×3; *d–f,* dorsal interior viewed dorsally, posteriorly, obliquely, Körgessaare, Estonia, TAGI BR 361, ×3 (new).

Family XENAMBONITIDAE Cooper, 1956

[*nom. transl.* COCKS & RONG, 1989, p. 120, *ex* Xenambonitinae COOPER, 1956, p. 813]

Concavoconvex to planoconvex profile; with dental plates; cardinal process undercut; variably developed bema; no side septa. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Subfamily XENAMBONITINAE Cooper, 1956

[Xenambonitinae COOPER, 1956, p. 813]

Similar to Aegiromeninae, but with platform; bema elevated. *Ordovician (Llandeilo–Ashgill).*

Xenambonites COOPER, 1956, p. 813 [**X. undosus;* OD]. Strongly concavoconvex profile with ventral fold, dorsal sulcus; parvicostellate ornament with occasional stronger costellae; geniculate anteriorly in ventral direction; apparently open delthyrium; strong teeth; vestigial dental plates; small bilobed ventral valve muscle field, elevated except at posterior ends of mantle canals, ventral subperipheral rim; small cardinal process lobes; substantial but short curved socket plates; short elevated myophragm, too broad to be termed septum, confined within elevated bema; weak platform mirroring ventral subperipheral rim. *Ordovician (Llandeilo–Caradoc):* North America, Scotland.——FIG. 217,*2a–c.* **X. undosus,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* ventral exterior, USNM 117468-l, ×6; *b,* ventral interior, USNM 117468a, ×6; *c,* holotype, dorsal interior, USNM 117468h, ×7 (Cooper, 1956).

Metambonites ZHAN & RONG, 1995, p. 552 [**M. meritus;* OD]. Dorsibiconvex profile; unequally parvicostellate ornament with no rugae; teeth small, dental plates absent; ventral denticles, dorsal fossettes irregularly developed; distinctive ventral platform, elevated in most specimens, surrounding bilobed muscle field, short stout ventral myophragm; cardinal process massive, projecting posteroventrally; socket ridges short, thick, high; bema strongly elevated, undercut, significantly smaller than ventral platform. *Ordovician (Ashgill):* China, Kazakhstan.——FIG. 217,*1a–d.* **M. meritus,* Xiazhen Formation, middle Ashgill, Daqiao, Jiangshan County, Zhejiang Province, China; *a,b,* ventral internal mold, ×5, latex cast, ×5, NIGP 124512; *c,d,* holotype, dorsal internal mold, ×4, latex cast, ×5, NIGP 124515 (Zhan & Rong, 1995).

Synambonites ZHAN & RONG, 1995, p. 552 [**S. biconvexus;* OD]. Ventribiconvex profile with elevated ventral marginal deflection and trough, corresponding narrow, high dorsal rim; fine multicostellate ornament, irregular rugae; similar to *Xenambonites* but differs in profile, in lacking fold, sulcus; elongated, bilobed, relatively small ventral muscle field, with strong teeth, dental plates; massive cardinal process projecting ventrally; elevated bema; subperipheral rim in ventral valve, corresponding dorsal trough. *Ordovician (Ashgill):* China.——FIG. 217,*3a–d.* **S. biconvexus,* Xiazhen Formation, middle Ashgill, Daqiao, Jingshan County, Zhejiang Province; *a,* latex cast of dorsal exterior, NIGP 124511, ×6; *b,* ventral internal mold, NIGP 124514, ×4; *c,d,* holotype, dorsal internal mold, latex cast, NIGP 124515, ×5 (Zhan & Rong, 1995).

Subfamily AEGIROMENINAE Havlíček, 1961

[Aegiromeninae HAVLÍČEK, 1961, p. 450]

Similar to Xenambonitinae, but without platform; variably developed bema, sometimes represented merely by line of enlarged septules, but never elevated. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Aegiromena HAVLÍČEK, 1961, p. 450 [**Leptaena aquila* BARRANDE, 1848, p. 228; OD]. Gently concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; small teeth, dental plates; weak muscle-bounding ridges posterolateral only to elongate, bilobed ventral muscle field; widely flaring short socket ridges, bema variably developed, absent in some specimens; weakly impressed dorsal muscle field; similar to *Aegiria,* but with dental plates. *Ordovician (Llanvirn–Ashgill):* Europe, northern Africa, Bolivia.——FIG. 218,*1a–d.* **A. aquila* (BARRANDE), Zahorany Formation, middle Caradoc, Bohemia, Czech Republic; *a,* latex cast of ventral exterior, BMNH BB 3340, ×3; *b,c,* ventral internal mold, latex cast, BMNH BB 13658, ×3; *d,* dorsal internal mold, BMNH BC 7212, ×4 (new).

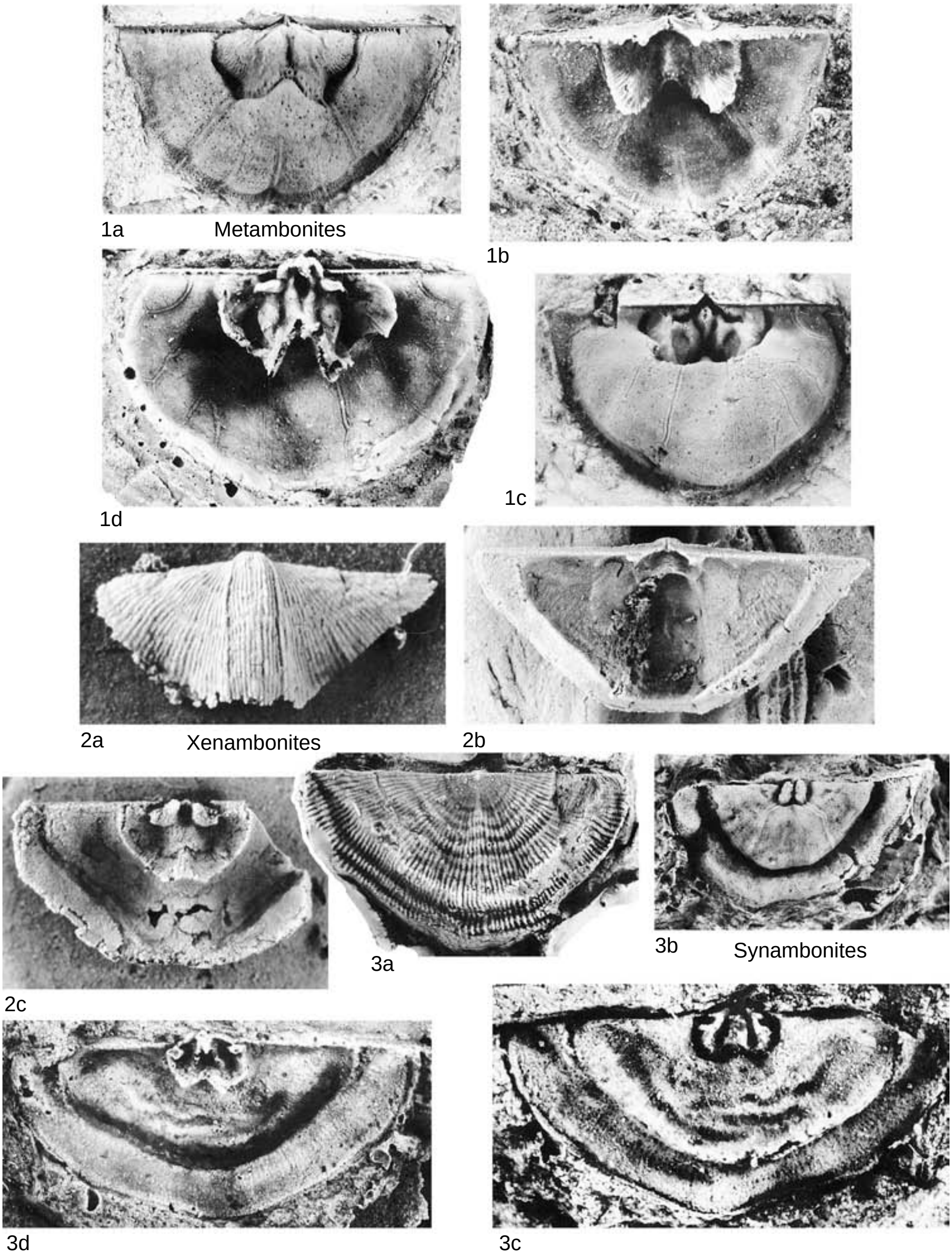

FIG. 217. Xenambonitidae (p. 334).

Aegiria ÖPIK, 1933a, p. 55 [**A. norvegica;* OD] [=*Aegironetes* HAVLÍČEK, 1967, p. 46 (type, *Strophomena tristis* BARRANDE, 1879, pl. 70, fig. 6.1; OD)]. Gently concavoconvex profile; parvicostellate ornament; delthyrium closed by large pseudodeltidium, chilidium; relatively short, variably impressed, bilobed ventral muscle field; erect cardinal process; differs from *Mezounia* in relatively transverse bema, not bilobed anteriorly; bema always present; short central median septum transecting anterior end of bema; platform sometimes indicated merely by elongate pseudopunctae. *Ordovician (Ashgill)–Silurian (Llandovery):* Europe, China.——FIG. 218,*3a–e.* **A. norvegica,* Solvik Formation,

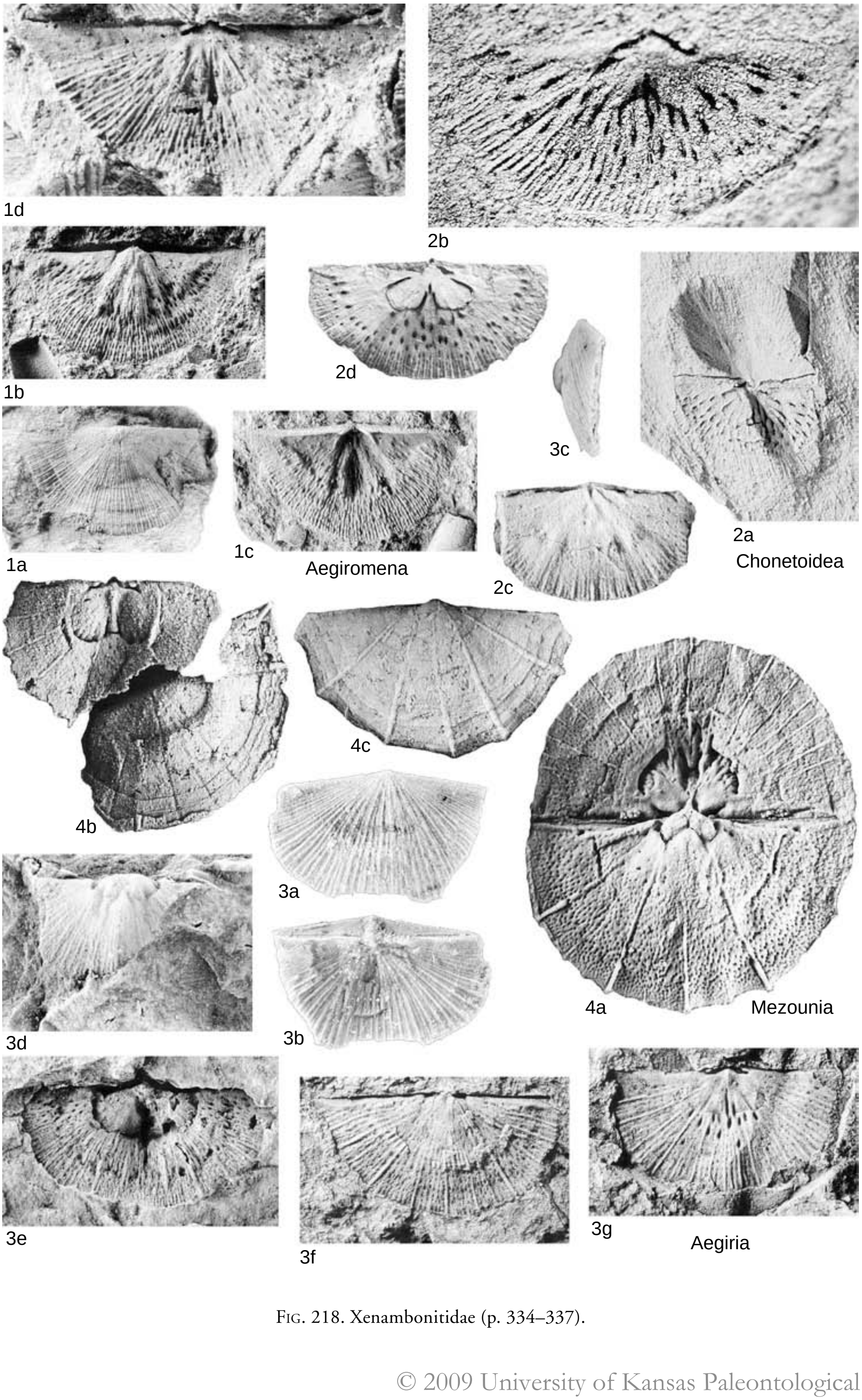

FIG. 218. Xenambonitidae (p. 334–337).

Rhuddanian, Leangen, Asker, Norway; *a–c,* ventral, dorsal, lateral views of conjoined valves, PMO 40690, ×4; *d,* ventral internal mold, PMO 40689, ×4; *e,* dorsal internal mold, PMO 40688, ×4 (new).——FIG. 218,*3f,g. A. tristis,* Králuv Dvur Formation, lower–middle Ashgill, Jezerka, Michli, Prague, Czech Republic; *f,* ventral internal mold, ×7; *g,* dorsal internal mold, ×7 (Mergl, new).

Chonetoidea JONES, 1928, p. 393 [**Plectambonites papillosa* REED, 1905, p. 451; OD] [=*Sericoidea* LINDSTRÖM, 1953, p. 134 (type, *Leptaena sericea* var. *restricta* HADDING, 1913, p. 62; OD); ?*Sentolunia* HAVLÍČEK, 1967, p. 53 (type, *S. senta;* OD)]. Gently concavoconvex profile; parvicostellate ornament, sometimes with unequal parvicostellae; small interarea; small arched pseudodeltidium; no chilidium; widely divergent teeth, socket plates; bilobed but weakly impressed ventral muscle field; similar to *Jonesea,* but with elongated septules, rather than circular papillae; bema sometimes present, sometimes delineated only by larger septules. *Ordovician (Llandeilo–Ashgill):* cosmopolitan.——FIG. 218,*2a,b.* **C. papillosa* (REED), Slade, Redhill Mudstone Formation, middle Ashgill, Upper Slade, near Haverfordwest, Dyfed, Wales; *a,* internal mold of conjoined valves, SM A11313, ×4; *b,* lectotype, dorsal internal mold, SM A11311, ×10 (Cocks & Rong, 1989).——FIG. 218,*2c,d. C. senta,* Králuv Dvur shales, lower–middle Ashgill, Králuv Dvur, Czech Republic; holotype, ventral, dorsal internal molds, OMR VH 276, ×4 (Havlíček, 1967).

Epelidoaegiria STRUSZ, 1982, p. 115 [**Aegiria (E.) chilidifera;* OD]. Similar to *Aegiria* but with unequally parvicostellate ornament, hinge line denticulate, small pseudodeltidium, chilidium. *Silurian (Wenlock, ?Ludlow):* Australia, Japan.——FIG. 219,*3a–d.* **E. chilidifera,* Walker Volcanics, Wenlock, Canberra, A.C.T., Australia; *a,* dorsal view of latex cast of conjoined valves, CPC 20365, ×4; *b,* magnified view of latex cast of interarea, CPC 20387, ×10; *c,* latex cast of ventral interior, CPC 20359, ×4; *d,* latex cast of dorsal interior, CPC 20949, ×4 (Strusz, 1982).

Jonesea COCKS & RONG, 1989, p. 127 [**Leptaena grayi* DAVIDSON, 1849, p. 271; OD] [=*Dionaegiria* HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 65, obj.]. Gently concavoconvex profile; distinctive sharply crested parvicostellate ornament; vestigial dental plates, bilobed ventral muscle field; sometimes septules with pair of prominent tubercles posterolaterally inside ventral valve; similar to *Chonetoidea,* but with circular papillae rather than elongated; bema sometimes suggested by raised tubercles but not always developed. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.——FIG. 220*a–d.* **J. grayi* (DAVIDSON); *a,* latex cast of external molds of conjoined valves, lower Bringewood Beds, upper Ludlow, Ludlow, Shropshire, England, BMNH BC 10343, ×12; *b,c,* dorsal internal mold, latex cast, lower Bringewood Beds, upper Ludlow, Ludlow, Shropshire, England, BMNH BC 10375, ×12; *d,* upper Leintwardine Beds, Ludlow, Ludlow, Shropshire, England, ventral internal mold, BMNH BC 10340, ×12 (Cocks & Rong, 1989).

Mezounia HAVLÍČEK, 1967, p. 31 [**Strophomena bicuspis* BARRANDE, 1879, pl. 128, fig. 1–5; OD]. Gently concavoconvex profile; semicircular outline; unequally parvicostellate ornament; prominent flaring teeth, bounding ridges around relatively small bilobed ventral muscle field; similar to *Aegiria* but with small bema bilobed anteriorly; no dorsal median septum. *Silurian (Wenlock):* Europe.——FIG. 218,*4a–d.* **M. bicuspis* (BARRANDE), Motol Formation, Wenlock, Borek, Mezoun, Bohemia, Czech Republic; *a,* internal mold of conjoined valves, OMR VH 514, ×7.3; *b,c,* internal, external molds of two dorsal valves, OMR VH 513d, ×7.7; *d,* ventral exterior, ×5.5 (Havlíček, 1967).

Multiridgia ZENG, 1987, p. 234 [**M. elegans;* OD]. Gently concavoconvex to planoconvex profile; unequally parvicostellate ornament; dental plates lacking; row of septules developed, enclosing poorly impressed muscle fields in both valves; dorsal valve septules as in *Chonetoidea,* but without anterior bilobation; short dorsal median septum. *Ordovician (Llandeilo–Caradoc):* China.——FIG. 219,*2a,b.* **M. elegans,* Miaopo Formation, upper Llandeilo–lower Caradoc; *a,* holotype, ventral internal mold, Jieling, YIGM IV45746, ×7; *b,* dorsal internal mold, Huanhuachang, Yichang County, Hubei Province, YIGM IV45740, ×9 (Zeng, 1987).

Nabiaoia XU, 1979, p. 370 [**N. pusilla;* OD]. Planoconvex profile; thin shelled; almost imperceptable parvicostellate radial ornament with irregular rugae; short, flaring teeth, socket ridges; no bema, platform, or side septa; dorsal muscle field of elevated pustules in irregular but subradial rows; dorsal median septum variably present, stronger posteriorly, centrally. *Devonian (Eifelian):* China.——FIG. 219,*1a–d.* **N. pusilla,* Tangxiang Formation, Eifelian, Luofu of Nandan, Guangxi Province; *a,b,* ventral internal mold, latex cast, NIGP 81012, ×10 (Xu, new); *c,d,* holotype, dorsal internal mold, latex cast, NIGP 41251, ×7 (Xu, 1979).

Family HESPEROMENIDAE
Cooper, 1956

[*nom. transl.* COCKS & RONG, 1989, p. 127, *ex* Hesperomeninae COOPER, 1956, p. 744] [=Anoptambonitidae RÕÕMUSOKS, 1963, p. 231]

Concavoconvex to resupinate profile; dental plates weakly present or absent; cardinal process undercut; no bema; no side septa; with platform. *Ordovician (Llanvirn–Ashgill).*

Hesperomena COOPER, 1956, p. 744 [**H. leptellinoidea;* OD]. Concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium, but no chilidium known; short flaring teeth; large, wide but poorly impressed ventral muscle field; large erect cardinal process; short socket ridges; weak

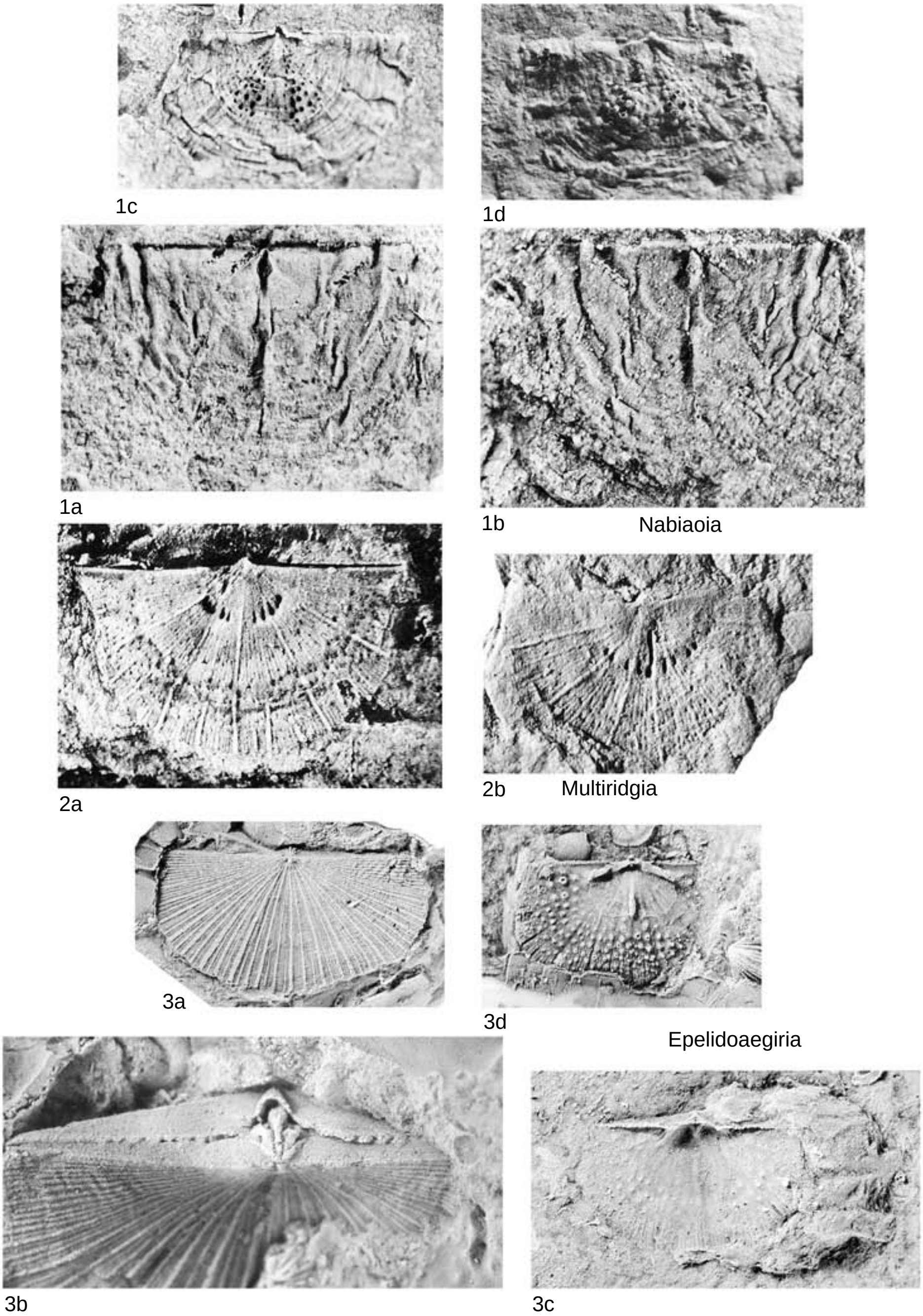

FIG. 219. Xenambonitidae (p. 337).

dorsal median septum bifurcating anteriorly to unite with weak platform. *Ordovician (Llanvirn):* North America.——FIG. 221,*1a–c.* **H. leptellinoidea,* Antelope Valley Limestone, Pogonip Group, upper Llanvirn, Ikes Canyon, Roberts Mountains, Nevada; holotype, dorsal exterior, ventral interior, dorsal interior views of conjoined valves, USNM 117560, ×3 (Cooper, 1956).

Anoptambonites Williams, 1962, p. 170 [**Leptaena grayae* Davidson, 1883, p. 171; OD] Concavoconvex profile; parvicostellate ornament; large rectimarginate to procline interarea; open delthyrium; variable, sometimes large, chilidium; prominent teeth; short dental plates; small ventral muscle field restricted by bilobed muscle-bounding ridges; no ventral median septum; no posterolateral tubercles in ventral valve; large cardinal process striated posteriorly; flaring socket ridges; strong median septum merging anteriorly with elevated bilobed platform. *Ordovician (Llandeilo–Ashgill):* North America, Scotland, Ireland, Asia.——Fig. 221,*2a–e.* **A. grayae* (Davidson), Craighead Limestone, upper Caradoc, Craighead, Girvan, Strathclyde, Scotland; *a,b,* lectotype, dorsal, lateral views of conjoined valves, BMNH B 73408, ×4 (new); *c,d,* posterior, downward views of ventral interior, BMNH BB 15868, ×3 (Cocks & Rong, 1989); *e,* dorsal interior, BMNH BB 15869, ×3.5 (new).

Aulie Nikitin & Popov in Klenina, Nikitin, & Popov, 1984, p. 148 [**A. convexa;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; similar to *Anoptambonites* but with pseudodeltidium present, ventral valve muscle-bounding ridges semicircular, not bilobed, with dorsal valve median septum extending a little anteriorly of platform. *Ordovician (Caradoc):* Kazakhstan.——Fig. 222,*1a–d.* **A. convexa,* middle Erkebidaiski Horizon, Caradoc, Chinghiz Mountains; *a,b,* latex cast of exterior of conjoined valves with enlargement of interarea, CNIGR 104/12095, ×2, ×5; *c,* ventral internal mold, CNIGR 99/12095, ×3; *d,* dorsal internal mold, CNIGR 100/12095, ×3 (Popov, new).

Chaganella Nikitin, 1974, p. 65 [**C. chaganensis;* OD] [=*Tylambonites* Percival, 1991, p. 143 (type, *T. speciosa;* OD)]. Similar to *Anoptambonites* but biconvex to weakly resupinate profile anteriorly; unequally parvicostellate ornament; open delthyrium, large discrete chilidial plates; ventral muscle field bilobed; prominent callosities in ventral interior; erect cardinal process; flaring socket plates; weakly impressed bema; strong dorsal median septum merging anteriorly with bilobed platform. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan, Australia.——Fig. 222,*2a–d.* **C. chaganensis,* lower Bestamak Formation, Llandeilo, Chagan River, Chinghiz Mountains, Kazakhstan; *a,* holotype, ventral exterior, CNIGR 1614/45, ×2; *b,* ventral internal mold, KAS 1614/41, ×2; *c,* dorsal internal mold, KAS 1614/43, ×2 (Nikitin, 1974); *d,* latex cast of dorsal interior, CNIGR 133/12095, ×2.5 (new).——Fig. 222,*2e–h. T. speciosa,* Cliefden Caves Limestone, Caradoc, Walli, New South Wales, Australia; *e,* posterior view of conjoined valves, SUP 68483, ×5; *f,g,* holotype, ventral exterior, interior, SUP 68462, ×2; *h,* dorsal interior, SUP 68469, ×3 (Percival, 1991).

Kassinella Borissiak, 1956, p. 50 [**K. globosa;* OD] [=*Durranella* Percival, 1979b, p. 96 (type, *D. septata;* OD)]. Concavoconvex to planoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; posterolateral tubercles usually present in ventral interior; short ventral median septum always present; similar to *Aulie* but with peripheral rim developed, ventral muscle-bounding ridges very elongate, bilobed; no dental plates; erect cardinal process with laterally flaring socket ridges; dorsal septum; dorsal peripheral rim

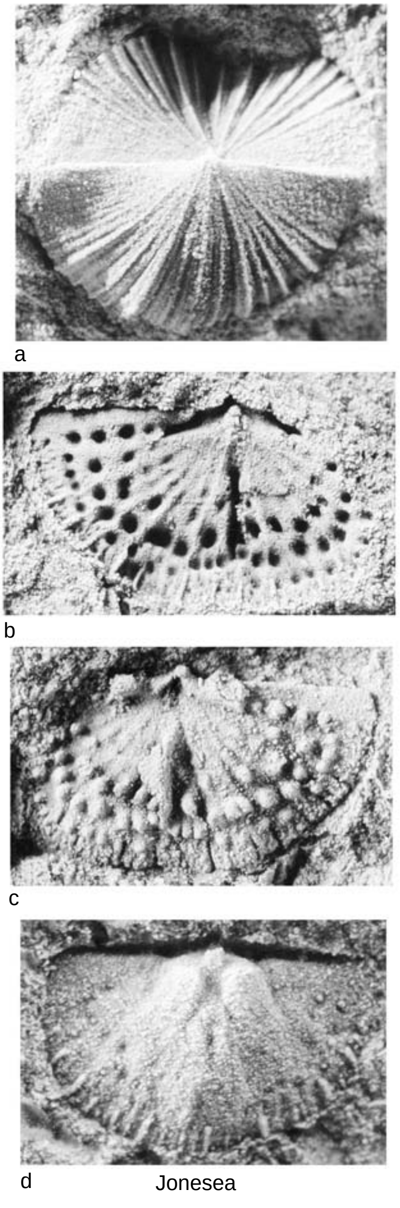

Fig. 220. Xenambonitidae (p. 337).

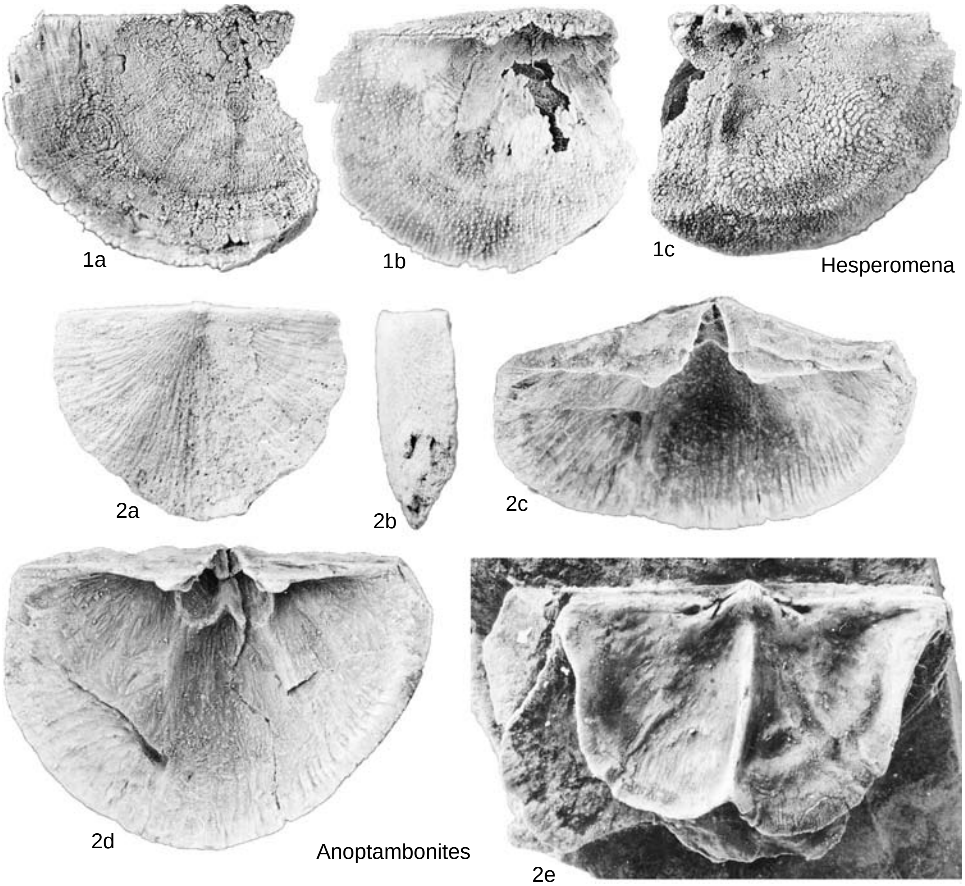

FIG. 221. Hesperomenidae (p. 337–339).

variably developed. *Ordovician (Caradoc–Ashgill):* Kazakhstan, China, Australia, Europe.

K. (**Kassinella**). Similar to *K. (Trimurellina)* but with dorsal median septum not extending anteriorly of platform. *Ordovician (Caradoc–Ashgill):* Asia, Australia, Europe.——FIG. 223,*1a*. **K. (K.) globosa,* Kulunbulak Formation, Dulankara Horizon, lower Ashgill, Kulunbulak River, Tarbagatai Range, Kazakhstan; ventral internal mold, BMNH BC 12934, ×5 (new).——FIG. 223,*1b*. *K. (K.)* sp., Changwu Formation, middle Ashgill, Jiangshan County, Zhejiang Province, China; dorsal internal mold, NIGP 101834, ×10 (Cocks & Rong, 1989).——FIG. 223,*1c,d*. *K. (K.) septata,* Goonumbla Volcanics, upper Caradoc, Gunningbland, New South Wales, Australia; *c,* latex cast of dorsal interior, SUP 61570, ×5; *d,* dorsal internal mold, SUP 61562, ×5 (Percival, 1979b).

K. (**Trimurellina**) MITCHELL, 1977, p. 74 [**T. superba;* OD]. Concavoconvex profile; semicircular outline; similar to *K. (Kassinella)* but with dorsal valve median septum extending anteriorly of platform (but not of peripheral rim). *Ordovician (Ashgill):* Ireland, Scotland.——FIG. 223,*2a–d*. **K. (T.) superba,* Killey Bridge Formation, middle Ashgill, Pomeroy, County Tyrone, Northern Ireland; *a,* dorsal external latex, GSM GU 1112, ×15; *b,* ventral internal mold, GSM GU 1113, ×15; *c,* dorsal internal mold, GSM GU 1124, ×15; *d,* holotype, dorsal internal latex, GSM GU 1109, ×15 (new).

Family SOWERBYELLIDAE Öpik, 1930

[*nom. transl.* COOPER, 1956, p. 744, *ex* Sowerbyellinae ÖPIK, 1930, p. 60]
[=Dubioleptinidae HAVLÍČEK, 1967, p. 70]

Concavoconvex to resupinate profile; weak dental plates usually developed, sometimes absent; undercut cardinal process; side septa; bema usually developed. *Ordovician (Llanvirn)–Devonian (Eifelian).*

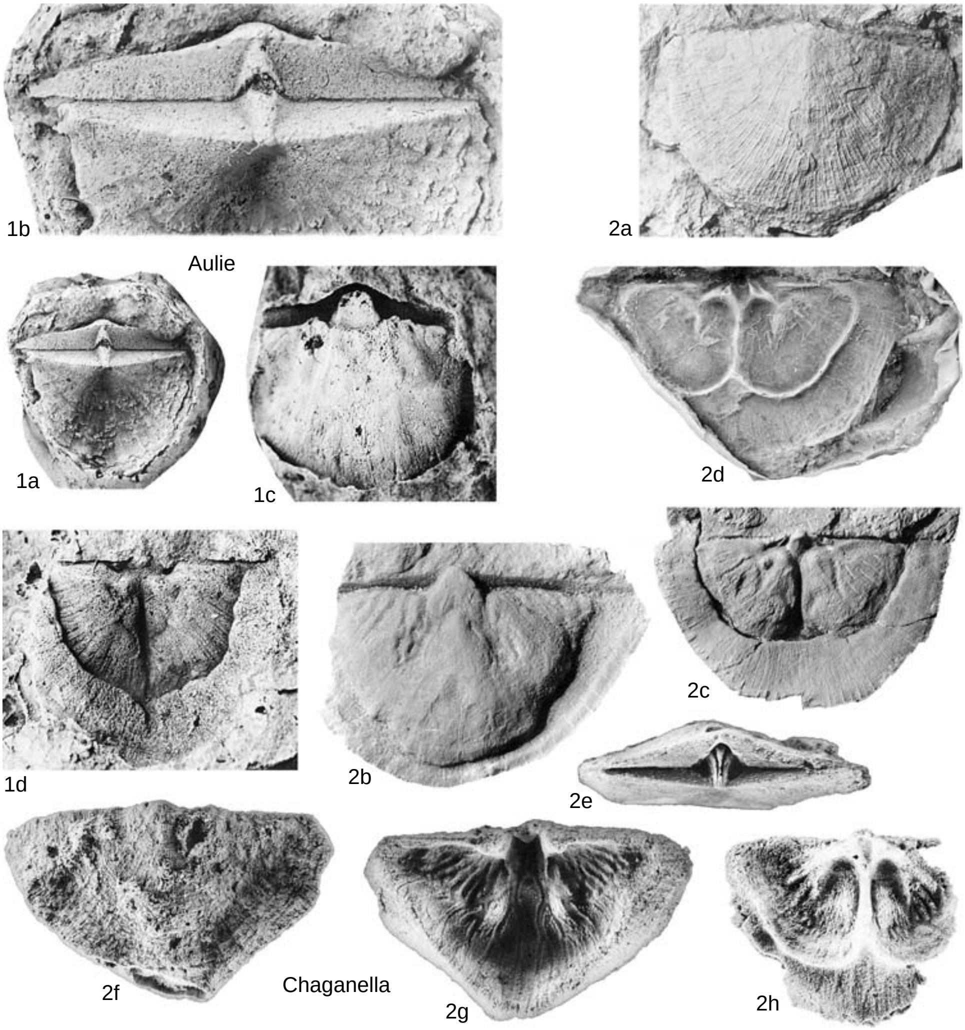

Fig. 222. Hesperomenidae (p. 339).

Subfamily SOWERBYELLINAE Öpik, 1930

[Sowerbyellinae Öpik, 1930, p. 60]

Bema divided; cardinal process differentiated. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Sowerbyella Jones, 1928, p. 384 [**Leptaena sericea* J. de C. Sowerby, 1839, p. 636; OD] [=*Sowerbyella (Viruella)* Rõõmusoks, 1959, p. 14 (type, *S. liliifera* Öpik, 1930, p. 148; OD)]. Concavoconvex profile; parvicostellate to unequally parvicostellate ornament; small arched pseudodeltidium; no chilidium; short teeth; no denticles on hinge line; short but widely diverging dental plates; bilobed ventral muscle field open anteriorly, with posterolateral muscle-bounding ridges; thin short ventral median septum posteriorly; small cardinal process; wide flaring socket plates; bema variable, usually present but occasionally absent; median septum in dorsal valve variably developed, usually absent; similar to *Anisopleurella* but with prominent pair of central side septa, which sometimes form edge of bema and are sometimes developed above it. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.

S. (**Sowerbyella**). Similar to *S. (Rugosowerbyella),* but rugae absent or confined to simple rugae at cardinal extremities. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.——Fig. 224,*1a–d.* **S. (S.) sericea* (J. de C. Sowerby), Horderley Sandstone Formation, Longvillian, Onny Valley, Shropshire, England; *a,* ventral internal mold,

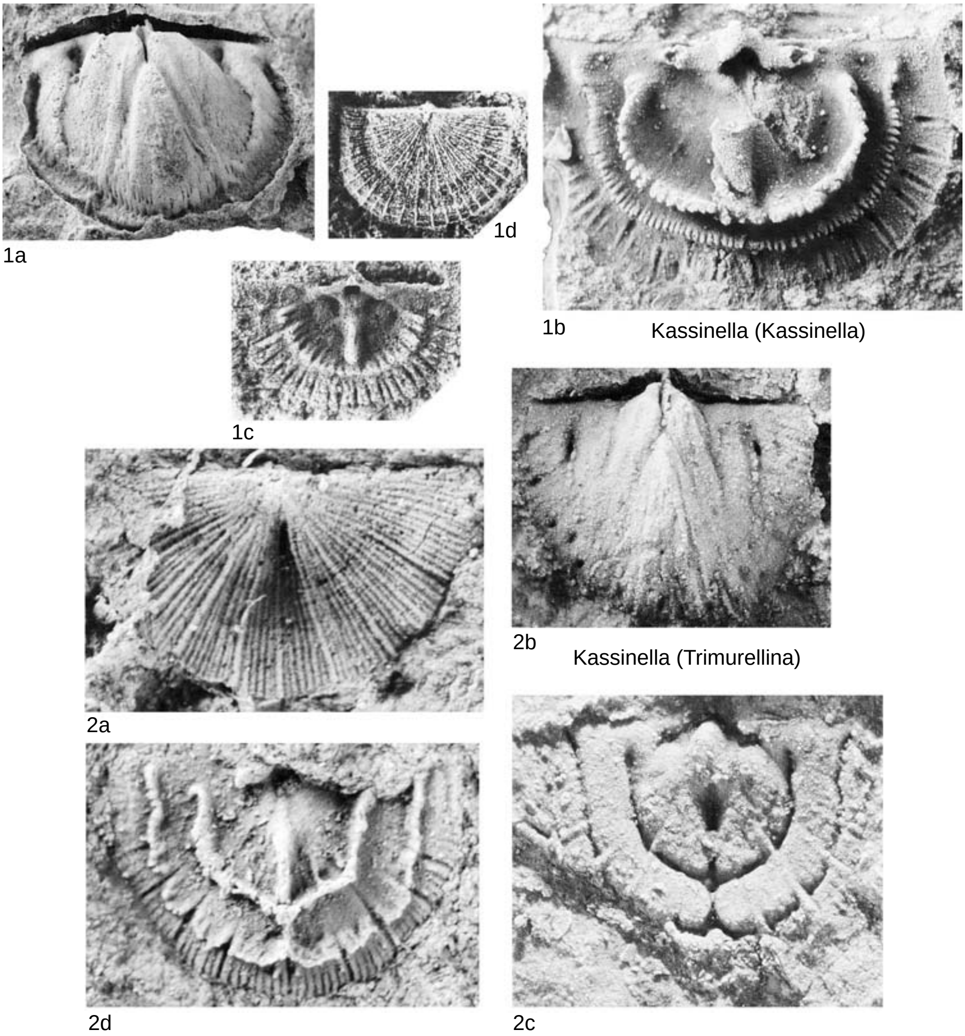

Fig. 223. Hesperomenidae (p. 340).

BMNH BC 7302, ×3; *b,* latex cast of dorsal interior, BMNH BC 6052, ×5; *c,d,* posterior, oblique lateral views of latex cast of dorsal interior, BMNH BC 6051, ×4 (Cocks & Rong, 1989).——Fig. 224,*1e–h. S. (S.) liliifera,* Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia; *e,* dorsal view of conjoined valves, BMNH BB 5147, ×5; *f,* ventral exterior, BMNH BB 5148, ×3; *g,* ventral interior, BMNH BB 5151, ×4; *h,* dorsal interior, BMNH BB 5149, ×5 (Cocks & Rong, 1989).

S. (Rugosowerbyella) Mitchell, 1977, p. 83 [**Ptychoglyptus ambiguus* Reed, 1952, p. 56; OD; =*Plectambonites subcorrugatella* Reed, 1917, p. 886; OD]. Similar to *S. (Sowerbyella)* but with distinctive ornament of concentric rugae truncated, offset by accentuated costae. *Ordovician (?Llanvirn, Ashgill):* cosmopolitan.——Fig. 224,*2a–c.* **S. (R.) subcorrugatella,* Killey Bridge Formation, lower Ashgill, Pomeroy, County Tyrone, Northern Ireland; *a,* external mold of conjoined valves, BMNH BC 12219, ×4; *b,* ventral internal mold, BMNH BB 67729, ×4; *c,* dorsal internal mold, BMNH BB 67728, ×4 (new).

Anisopleurella Cooper, 1956, p. 804 [**A. tricostellata;* OD] [=*Pseudoanisopeurella* Wang in Wang & Yan, 1978, p. 222 (type, *P. aletheta;* OD; upper Miaopo Formation (lower Caradoc), Fenxiang, Yichang County, western Hubei Province, China)]. Wide outline; gently concavoconvex profile; unequally parvicostellate ornament often with only three

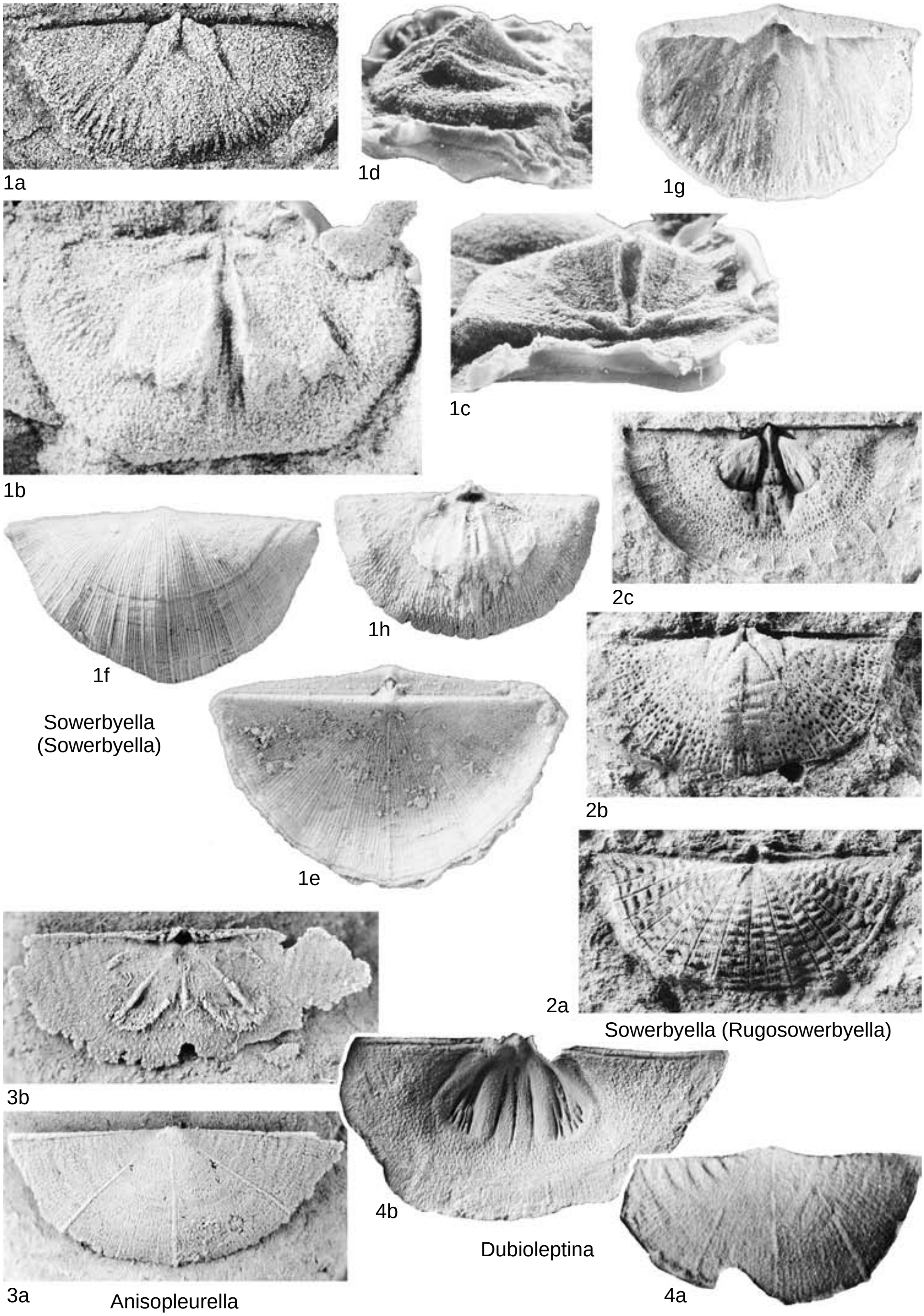

FIG. 224. Sowerbyellidae (p. 341–344).

prominent costellae; with pseudodeltidium, chilidium; teeth small, no denticles on hinge line; ventral muscle field small, bilobed, with divergent diductors, adductors borne on low median ridge; small cardinal process with laterally elongate socket ridges; prominent lateral side septa confined within bilobed, suboval bema; dorsal median septum; similar to *Sowerbyella* but no prominent paired central side septa developed. *Ordovician (Llandeilo)–Silurian (Llandovery):* cosmopolitan.——Fig. 224,*3a,b.* **A. tricostellata,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* holotype, ventral exterior, USNM 117475b, ×9; *b,* dorsal interior, USNM 117475a, ×9 (Cooper, 1956).

Dubioleptina Havlíček, 1967, p. 70 [**Strophomena expulsa* Barrande, 1879, pl. 53, fig. 4; OD]. Concavoconvex profile; unequally parvicostellate ornament; hinge line not denticulate; similar to *Sowerbyella* but with no teeth or socket plates. *Silurian (Wenlock):* Europe.——Fig. 224,*4a,b.* **D. expulsa,* Liten Formation, Wenlock, Lodenice, Bohemia, Czech Republic; *a,* ventral exterior, NM L6476, ×6; *b,* dorsal internal mold, OMR VH 332, ×4 (Havlíček, 1967).

Eochonetes Reed, 1917, p. 916 [**Chonetes (Eochonetes) advena* Reed, 1917, p. 915; OD] [=*Thaerodonta* Wang, 1949, p. 19 (type, *T. aspera;* OD]. Similar to *Sowerbyella* but with denticles on lateral parts of dorsal valve hinge line only, opposing small sockets on ventral valve hinge line; canals in ventral valve hinge line variably developed, usually absent. *Ordovician (Caradoc–Ashgill):* Scotland, North America, Baltic, northern Africa.——Fig. 225,*1a–d.* **E. advena,* Starfish Bed, South Threave, upper Rawtheyan, Girvan, Strathclyde, Scotland; *a,* ventral internal mold, BMNH BC 10817, ×5; *b,* dorsal internal mold, BMNH B 73919, ×3; *c,d,* dorsal internal mold obliquely tilted to show lateral denticles, latex cast, BMNH BC 10291, ×5 (Cocks & Rong, 1989).

Eoplectodonta Kozłowski, 1929, p. 112 [**Sowerbyella precursor* Jones, 1928, p. 437; OD; =*Leptaena duplicata* J. de C. Sowerby, 1839, p. 636 (Cocks, 1970, p. 166)] [=*Ygera* Havlíček, 1961, p. 449 (type, *Y. ygerens;* OD; =*Leptaena transversalis sowerbyana* Barrande, 1848, p. 225)]. Transverse outline; concavoconvex profile with incurved beak; parvicostellate to unequally parvicostellate ornament; open delthyrium, chilidial plates usual, but sometimes an entire chilidium; similar to *Sowerbyella* but with denticulate hinge line in central area of ventral valve, corresponding fossettes in dorsal valve hinge line; flaring bilobed ventral muscle field with strong dental plates, bounding ridges posterolaterally; variably developed, thin, short, ventral median septum posteriorly; erect cardinal process, socket plates; bilobed bema often raised off valve floor laterally, with from one to three pairs of prominent side septa; fine small dorsal median septum variably present in valve center only. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.

E. (**Eoplectodonta**). Differs from *E. (Kozlowskites)* in ventral muscle scars that touch centrally (although they are partly divided by the thin, short median septum) and from *E. (Ygerodiscus)* in lack of shell undulations. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.——Fig. 225,*3a.* **E. (E.) duplicata,* upper Haverford Mudstone Formation, Rhuddanian, Haverfordwest, Dyfed, Wales; *a,* ventral internal mold, BMNH BB 31674, ×3 (Cocks, 1970).——Fig. 225,*3b–d. E. (E.) transversalis* (Wahlenberg), lower Visby Marl, Telychian, Nyhamn, Visby, Gotland, Sweden; *b,* dorsal view of conjoined valves, BMNH BB 34820, ×3; *c,* ventral interior, BMNH BB 34829, ×3; *d,* dorsal interior, BMNH BB 32425, ×3 (Cocks, 1970).——Fig. 225,*3e,f. E. (E.) sowerbyana,* Liten Formation, Wenlock, Svaty Jan pod Skalou, Bohemia, Czech Republic; *e,* ventral internal mold, OMR VH 324, ×1.8; *f,* dorsal internal mold, OMR VH 320, ×2 (Havlíček, 1967).

E. (**Kozlowskites**) Havlíček, 1952, p. 406 [**Strophomena nuntia* Barrande, 1879, pl. 49, fig. 3; OD]. Similar to *E. (Eoplectodonta)* but ventral muscle scars not united centrally; ventral valve mantle canal markings simple, subparallel; bilobed dorsal muscle field less than half valve length, unlike *E. (Eoplectodonta). Ordovician (Caradoc–Ashgill):* Europe, China.——Fig. 225,*4a–c.* **E. (K.) nuntia* (Barrande), Králuv Dvur Formation, Ashgill, Králuv Dvur, Bohemia, Czech Republic; *a,* external mold of conjoined valves, NM CD 1568, ×4; *b,* ventral internal mold, NM CH 314, ×4; *c,* dorsal internal mold, NM CD 1557, ×4 (Havlíček, 1967).

E. (**Ygerodiscus**) Havlíček, 1967, p. 62 [**Leptaena transversalis* var. *undulata* Salter in Phillips & Salter, 1848, p. 372; OD] [=*E. (Paranisopleurella)* Zhang, 1989b, p. 102 (type, *E. (P.) cooperi;* OD)]. Similar to *E. (Eoplectodonta)* but with distinctive shell undulations and with less massive bema. *Silurian (Llandovery–Wenlock):* Europe, North America.——Fig. 225,*2a–d.* **E. (Y.) undulata* (Salter), V_2C Beds, Rhuddanian, Mathyrafal, Meifod, Wales; *a,* dorsal external mold, BMNH BB 31925, ×3; *b,* ventral internal mold, BMNH BB 32109, ×3; *c,d,* dorsal internal mold, latex cast, BMNH BB 31917, ×5 (new).

Gunningblandella Percival, 1979b, p. 111 [**G. resupinata;* OD]. Similar to *Sowerbyella* but resupinate in profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; hinge line not denticulate; short dental plates; bilobed ventral muscle field divided by short thin median septum posteriorly; erect cardinal process, flaring socket plates; bema less than half valve length; dorsal side septa weakly developed. *Ordovician (Caradoc):* Australia, ?Norway.——Fig. 226,*2a–e.* **G. resupinata,* Goonumbla Volcanics, upper Caradoc, Gunningbland, New South Wales, Australia; *a,* latex cast of dorsal exterior, SUP 61490, ×2.5; *b,* latex cast of ventral interior, SUP 61510, ×2.5; *c,* holotype, dorsal internal mold, ×2.5; *d,* latex cast, SUP 61487, ×3; *e,* latex cast of dorsal interior, SUP 61503, ×5 (Percival, 1979b).

Plectodonta Kozłowski, 1929, p. 112 [**P. mariae;* OD]. Quadrate outline; gently concavoconvex

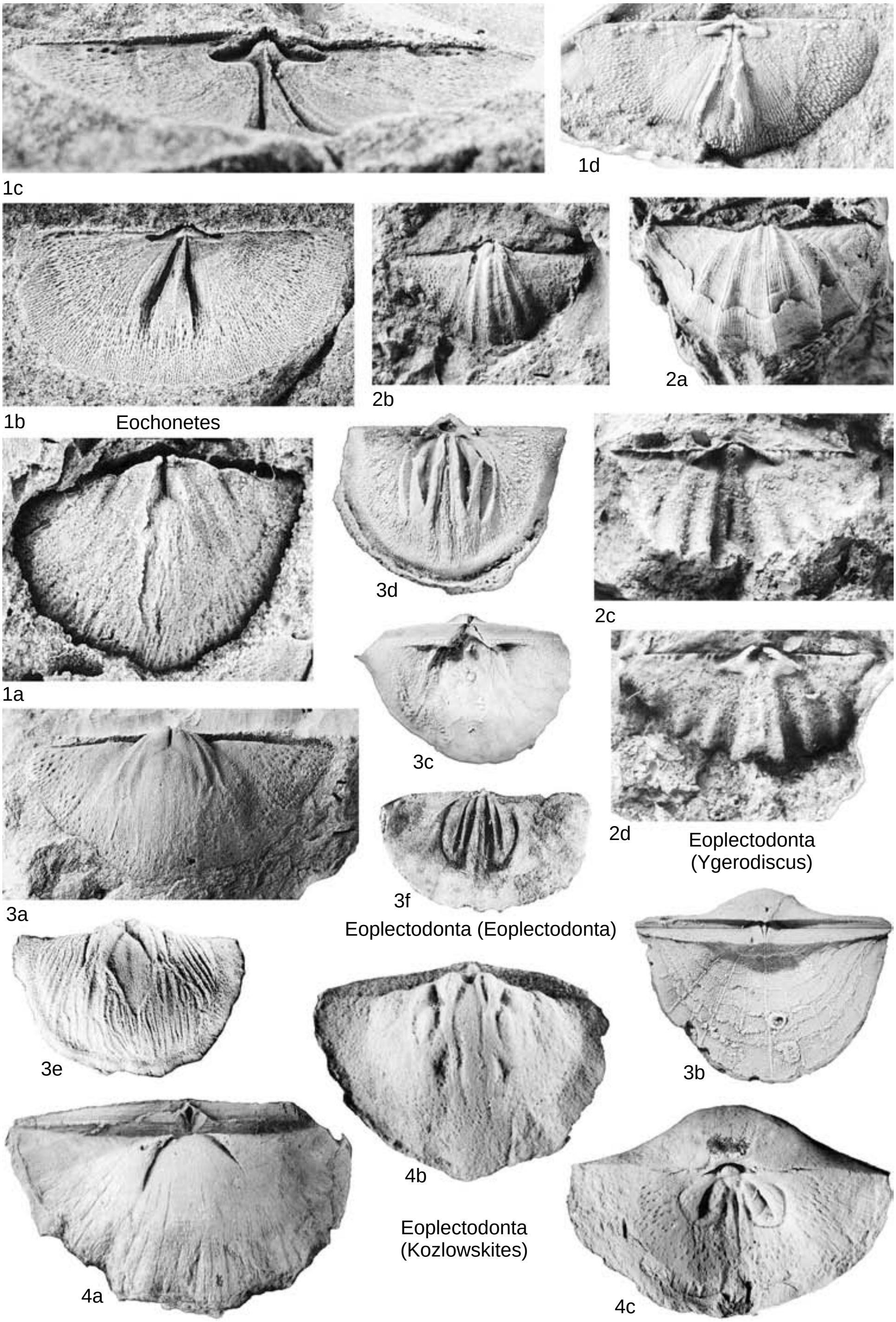

FIG. 225. Sowerbyellidae (p. 344).

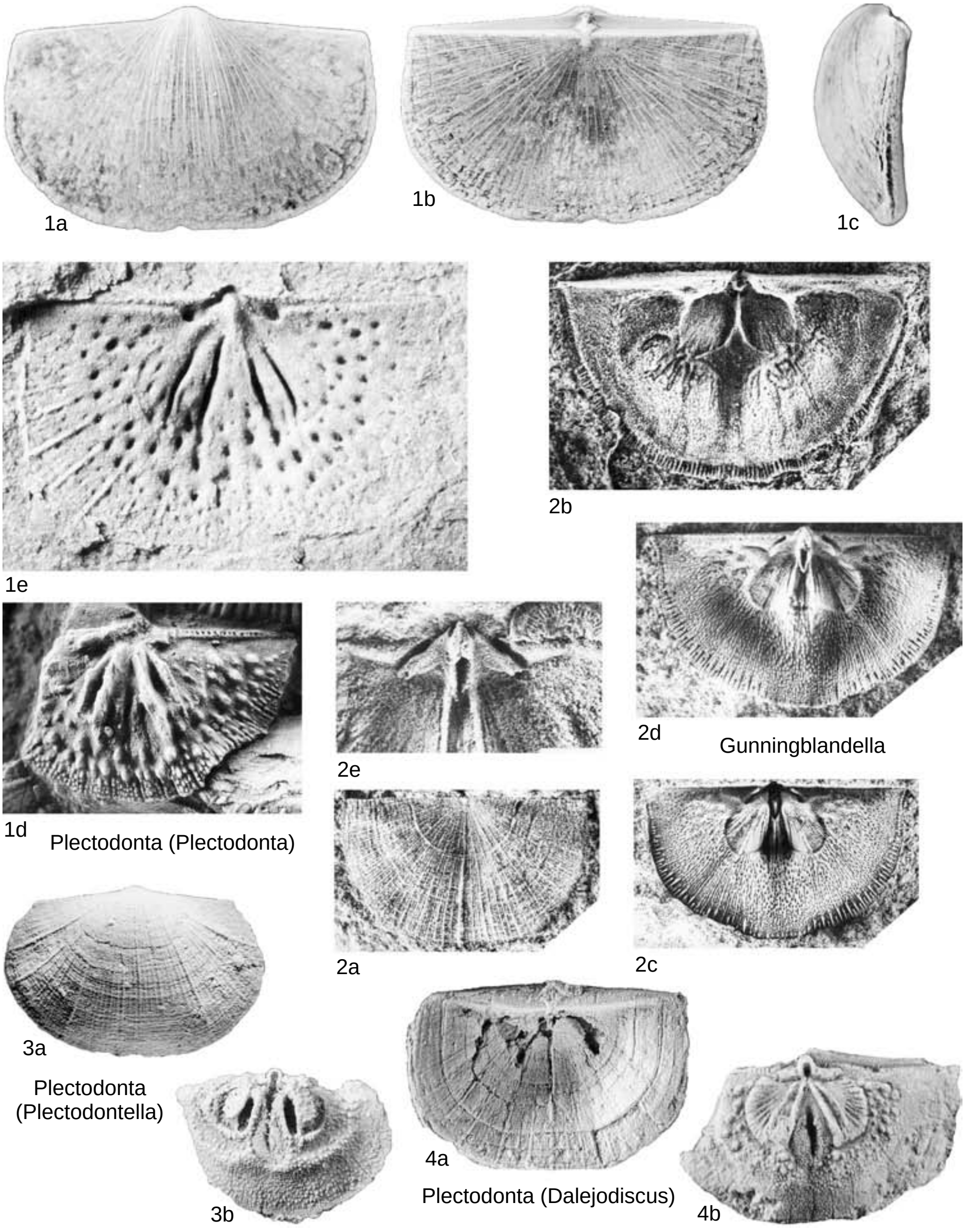

FIG. 226. Sowerbyellidae (p. 344–347).

profile; parvicostellate ornament; hinge line denticulate; small pseudodeltidium, chilidial plates; small teeth, stubby socket plates; small bilobed ventral muscle field; bema variably developed; dorsal median septum, platform absent; similar to *Eoplectodonta* except with stronger pseudodeltidium, less incurved beak, more quadrate, less alate valve extremities, coarse papillae on dorsal valve interior. *Silurian (Přídolí)–Devonian (Eifelian):* cosmopolitan.

P. (Plectodonta). Similar to *P. (Dalejodiscus)* but with bema weak or absent, and differing from *P. (Plectodontella)* in the absence of side septa. *Silurian (Přídolí)–Devonian (Eifelian):* cosmopolitan.——FIG. 226,*1a–e*. **P. (P.) mariae,* Taina Formation, Borshchov Group, Lochkovian, Rukhotin, Krzywcze, Podolia, Ukraine; *a–c,* exterior views of conjoined valves, BMNH BB 81378, ×5 (new); *d,* dorsal interior, BMNH B 81370, ×6; *e,* dorsal internal mold, BMNH BB 65810, ×8 (Cocks & Rong, 1989).

P. (**Dalejodiscus**) Havlíček, 1961, p. 449 [**Strophomena comitans* Barrande, 1879, pl. 56; OD]. Similar to *P. (Plectodonta)* but with elevated, radially striated bema, short central dorsal median septum. *Devonian (Pragian–Eifelian):* Europe, ?Asia.——Fig. 226,*3a,b.* **P. (D.) comitans* (Barrande), Daleje Shales, Eifelian, Praha-Hlubocepy, Czech Republic; *a,* exterior of conjoined valves, OMR VH 318, ×4; *b,* dorsal interior, OMR VH 284, ×4 (Havlíček, 1967).

P. (**Plectodontella**) Havlíček, 1953, p. 8 [**P. redunca;* OD]. Similar to *P. (Plectodonta)* but with strong raised bema, distinctive pair of strong side septa posterior of valve center; weak platform present. *Devonian (Eifelian):* Europe. ——Fig. 226,*4a,b.* **P. (P.) redunca,* Trebotov Limestone Formation, lower Eifelian, Holyne, Prague, Czech Republic; *a,* ventral exterior, OMR VH 26, ×3.7; *b,* dorsal interior, OMR VH 25, ×3.5 (Havlíček, 1967).

Subfamily PTYCHOGLYPTINAE Cooper, 1956

[Ptychoglyptinae Cooper, 1956, p. 815]

Weak bema, not divided; cardinal process differentiated. *Ordovician (?Llandeilo, Caradoc–Ashgill).*

Ptychoglyptus Willard, 1928, p. 283 [**P. virginiensis;* OD]. Concavoconvex to planoconvex profile, shell often delicate; distinctive ornament of small rugae interrupted by costellae; small arched pseudodeltidium; chilidial plates; flaring teeth with short dental plates; poorly impressed muscle fields; small, erect cardinal process lobes; flaring socket plates; bema poorly impressed; one or two pairs of short weak side septa variably developed. *Ordovician (?Llandeilo, Caradoc–Ashgill):* cosmopolitan.——Fig. 227*a–d.* **P. virginiensis; a,* ventral exterior, Edinburg Formation, Caradoc, Harrisonburg, Virginia, USNM 98231b, ×3; *b,* ventral interior, Edinburg Formation, Caradoc, Harrisonburg, Virginia, USNM 98231b1, ×3; *c,* dorsal interior, Effna-Rich Valley Formation, lower Caradoc, Porterfield Quarry, Virginia, USNM 111042b, ×4; *d,* dorsal interior, Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama, USNM 117398c, ×4 (Cooper, 1956).

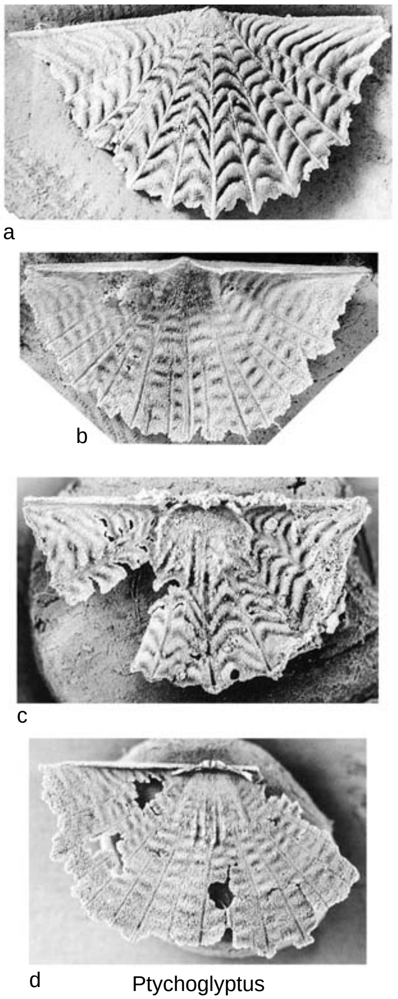

Fig. 227. Sowerbyellidae (p. 347).

PLECTAMBONITOIDEAN GENERA UNASSIGNED TO FAMILIES

Leptoptilum Öpik, 1930, p. 130 [**Leptestia (Leptoptilum) bekkeri;* OD]. Only broken fragments available showing merely pseudopunctate, convex ventral valve, parvicostellate ornament; perhaps synonym of *Leptestia,* but considered *nomen dubium* here. *Ordovician (Caradoc):* Kukruse Formation, Kohtla, Estonia.

Paucicostella Cooper, 1956, p. 711 [**P. canadensis;* OD]. Parvicostellate ornament, gently convex ventral valve, nearly flat dorsal valve; interior unknown, apart from short dental plates, relatively wide ventral muscle field; *nomen dubium. Ordovician (Arenig–Llanvirn):* Canada.——Fig. 228,*1.* **P. canadensis,* Mystic Conglomerate, Arenig–Llanvirn, Mystic, Quebec, Canada; ventral exterior, USNM 117395a, ×3 (Cooper, 1956).

Ukoa Öpik, 1932, p. 33 [**U. ornata;* OD]. Large; resupinate, weakly geniculate profile; unequally parvicostellate ornament; ventral muscle field triangular, open anteriorly; dorsal interior unknown,

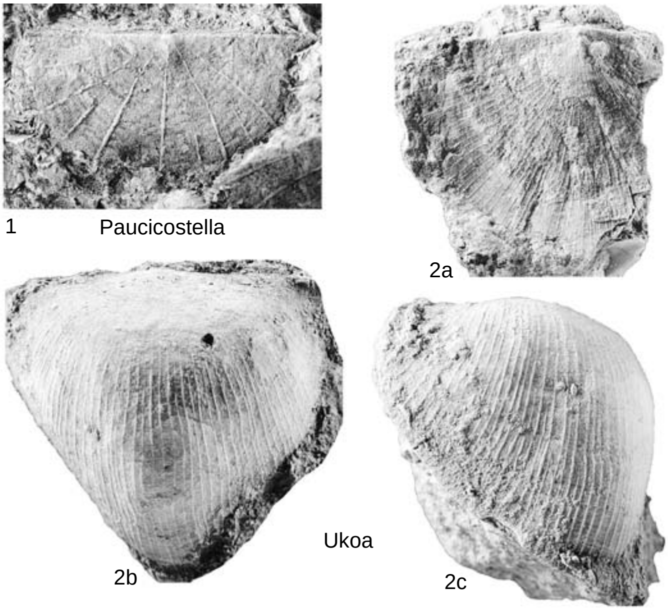

FIG. 228. Unassigned (p. 347–348).

thus may be strophomenine. *Ordovician (Arenig–Llanvirn):* Baltic.——FIG. 228,*2a–c.* **U. ornata; a,* ventral exterior, Kunda Horizon, lower Llanvirn, Lava River, St. Petersburg, Russia, BMNH BC 12858, ×1; *b,c,* dorsal exterior, Kunda Horizon, upper Arenig, Lynna River, St. Petersburg, Russia, BMNH BC 12857, ×1 (new).

UNCERTAIN

ALWYN WILLIAMS and C. HOWARD C. BRUNTON
[The University of Glasgow; and formerly of the Natural History Museum, London]

Suborder UNCERTAIN

Family EOCRAMATIIDAE Williams, 1974

[Eocramatiidae WILLIAMS, 1974, p. 127]

Subquadrate, costellate; apsacline ventral interarea with submesothyrid foramen and long, convex pseudodeltidium; narrow, hypercline dorsal interarea with small, convex chilidium; teeth unsupported, ventral muscle scar indistinct but more or less limited to delthyrial cavity; divergent chilidial plates filling notothyrium, ankylosed to socket ridges or plates parallel with hinge line, dorsal adductor scars quadripartite about low myophragm; shell impunctate. *Lower Ordovician (Llanvirn).*

Eocramatia WILLIAMS, 1974, p. 128 [**E. dissimulata;* OD]. Planoconvex, gently uniplicate, finely costellate by branching and intercalation. [This genus has many generalized features in common with the billingselloids and clitambonitoids. But the absence of dental plates and notothyrial platform and the presence of divergent plates filling the notothyrium (in a manner more reminiscent of the chilidial plates of the leptellids than the bilobed cardinal process of strophomenids) suggest that it belongs to the Strophomenida. Within that order, the Orthotetidina and the Plectambonitoidea are the most likely taxonomic repositories for *Eocramatia.* If the structures occupying the notothyrium prove to be the cardinal process lobes, the genus could be placed with the orthotetoids, although the profile of the

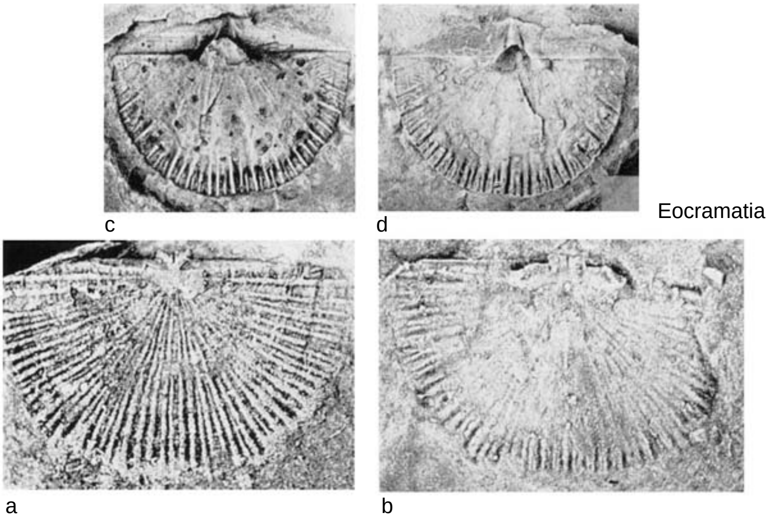

FIG. 229. Uncertain (p. 348–349).

dorsal valve would militate against such an assignment as would the attitude of the socket ridges and the absence of dental plates. The impunctate condition of the shell has been inferred from the condition of the molds of specimens, which are preseved in fine shale. In any event, both the Orthotetidina and the Plectambonitoidea accommodate impunctate stocks.] *Lower Ordovician (Llanvirn):* England.——FIG. 229*a–d.* **E. dissimulata;* Hope Shales, Brithdir Farm, Shropshire, Llanvirn; *a,b,* paratype, latex casts of dorsal valve exterior, interior, BMNH BB35489a, BMNH BB35489b, ×5.8; *c,d,* holotype, latex mold, cast of ventral valve interior, BMNH BB35488a, ×3.5 (Williams, 1974).

PRODUCTIDA

C. H. C. Brunton[1], S. S. Lazarev[2], and R. E. Grant[3]

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Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959

[Productida Sarytcheva & Sokolskaya, 1959, p. 182]

This large and diverse order includes the biggest and most unusual brachiopods known. Characterization can, therefore, be difficult, but the order is described as follows.

Small to gigantic strophomenates with dorsal valves markedly smaller than ventral; corpus cavity in profile commonly concavo-convex to planoconvex, rarely conical or even resupinate; ears and trails commonly prominent, in some the latter elaborated into bordering structures, such as gutters; spines tubular and normally covering ventral valves, but may be restricted to hinge line; may also be present on dorsal valves, rarely absent, as in lyttonioids and some richthofenioids; radial ribbing common, rugae less so; dental plates absent; cardinal process normally present, prominent, some with a proximal shaft, bilobed with posteriorly facing recessed myophores; brachial ridges or more elaborate brachial structures variably present; anderidia present in chonetidines and earliest true productides; mantle canal markings rare; internal surfaces commonly endospinose; shell structure crested to cross-bladed laminar with pseudopunctae having taleolae, fine internal tuberculation common; in some large-sized taxa shell thickening produced a prismatic appearance in section. *Upper Ordovician (Cautleyan)–Upper Permian, ?Lower Triassic.*

Within the Productida are included those strophomenates that developed tubular spines. These developed at valve margins but continued growth after being left behind the margin. Some remained alive, containing growth tissue, during long periods of ontogeny. These spines are unlike those found in some rhynchonellides or other orders. We include chonetidines, true productidines, strophalosiidines, which include aulostegoids and richthofenioids, and the lyttoniidines. Rarely the spines were lost, especially in cemented species during the Permian.

PRODUCTIDA EXCLUDING THE CHONETIDINA

History

Classification of this group has always been problematical, with specialists such as Thomas Davidson (1861) commenting on the existing confusion and Girty (1909, p. 230) remarking upon "the abundant intermediate stages" to be found between what would be considered as distinct species. In 1918 Janischewsky's opinion was that productids were the most complex of brachiopods and incapable of being clearly classified. In 1928, however, Muir-Wood gathered 41 species and varieties together and discussed the use of 8 genera within what would today probably be recognized as 4 different families, but only representing a small proportion of the Productida. Sarytcheva (1937, 1949), Sokolskaya (1948), Sarytcheva and Sokolskaya (1952), and Sarytcheva and others (1963) published descriptive works. Sarytcheva, Licharew, and Sokolskaja (1960) wrote the Productida section of the Russian *Treatise on Brachiopods and Bryozoans* (*Osnovy*), which provided a classification of the whole of the Productida, including the Chonetacea. The *Osnovy* included lyttonioids but not the few genera based on *Gemmellaroia,* which Williams (1953b) had placed with the orthotetaceans. Also in 1960, however, and a few months prior to publication of the Russian *Osnovy,* Muir-Wood and Cooper (1960) published a monograph on the Productoidea, a superbly illustrated book, thanks to Cooper's photographic expertise, and one that described 167 genera, divided between 11 families within the Productacea and 8 within the Strophalosiacea, including the conical Richthofeniidae and Scacchinellidae. They reintroduced the Gemmellaroiinae into the

Richthofeniidae because of their anchoring spines. Their work formed the basis, presented by MUIR-WOOD, for the Productidina section of the brachiopod *Treatise on Invertebrate Paleontology* (WILLIAMS & others in MOORE, 1965). At that time the suborder was divided into two superfamilies, following the 1960 pattern, and WILLIAMS added the Oldhaminidina (including the Lyttonioidea). Not surprisingly the *Treatise* and its forerunner (MUIR-WOOD & COOPER, 1960) stimulated a spate of studies so that by the early 1990s the number of nominal genera had risen to about 500, many of which could not easily be fitted into either the Russian (SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960) or international (MOORE, 1965) published classifications.

The uncertain taxonomic position of the gemmellaroiids has again been challenged by GRANT (1993a), who usefully pointed out the normal operation of the dorsal valve in *Gemmellaroia* but assigned the group of four genera back to the orthotetides, believing them to lack spines and have koskinoid perforations. GRANT (1993a) stressed the taxonomic importance of koskinoid ventral umbonal perforations, but their true nature has been questioned by WILLIAMS and BRUNTON (1993), who suggest they are secondary borings. Further study reveals that *Loczyella* belongs with the Permianellinae of the Lyttonioidea, while the probable spinose exterior of *Gemmellaroia* means it should remain in the Richthofenioidea. The fate of the remaining two genera is unclear, but for the time being we retain *Tectaria* and *Cyndalia* in the Productida, although the latter only questionably.

Various problems attended previous classifications. First, the early evolution of the group, in the Early and Middle Devonian, was poorly known, so it was impossible to determine clear lineages. Second, and partly because of the above, groupings were the result of similar morphologies rather than lineages or the study of variations in morphological features in time and space. Although in the 1965 *Treatise* homeomorphy was featured and the similarities between some Carboniferous and Permian genera were listed, the separation of genera to different families lacked clear explanation. Third, some of the characters selected as important in the 1965 classification have proven to be variable and hence difficult to use; for example, the cardinal process changed during ontogeny and by adulthood is also variable in detail. On the other hand the shape and depth of the corpus cavity (see below) were rejected as a useful character. This was because in grouping genera with superficial similarities, without considering ancestry, taxa of different lineages were brought together that had different adult corpus cavity depths. Here we find corpus cavity depth a valuable characteristic when considered in conjunction with other characters of the shell and its evolution.

Much excellent descriptive work has been published during the last 30 years, and this, together with the earlier monographs, has allowed us to take a new look at the classification of the Productida. We accept the importance of corpus shape and the forms of growth stressed by Russian brachiopod specialists but also the value of internal and external features such as ribbing, rugation, spine distributions and styles, lamellae, the various ridges bounding the corpus cavity internally or positions of muscle scars, as well as the basic adult form of the cardinal process.

Since the 1965 edition of the brachiopod *Treatise* there have been few attempts to reclassify productides, and those of COOPER and GRANT (1975) or WATERHOUSE (1978), based largely on Permian faunas, made some changes. The former retained the Productidina with four superfamilies (Strophalosiacea, Aulostegacea, Richthofeniacea, and Productacea). WATERHOUSE (1978) raised the group to ordinal level with two suborders, the Productidina (divided into Productellacea, Productacea, and Linoproductacea) and Strophalosiidina (divided into Strophalosiacea, Richthofeniacea, and Aulostegacea, into which he included some genera assigned here to the Echinoconchoidea in the Productidina). LIANG (1990), also studying Permian brachiopods, proposed a classification for the phylum that, like Cooper (1944), divided the inarticulated and articulated brachiopods into impunctate and punctate divisions, including two orders of productides, in the belief that they too included an endopunctate group; this scheme has not gained support, and it is felt (in the absence of any direct electron-microscopic study) that his punctate structures in productides are a form of pseudopunctation.

Present situation

The number of pre-Frasnian, Devonian productidine genera has increased from about 3, described in 1965, to 11 by 1993. This information has allowed the reconstruction of three major lines of evolution in the Productidina: the Linoproductoidea, Productoidea, and Echinoconchoidea, all of which proliferated near the Devonian to Carboniferous boundary into many more families and subfamilies. This evidence allows a phylogenetic classification by building lineages of species and genera. This technique led to the recognition of many homeomorphic parallel lineages with different origins, and in consequence some large groups have been divided into smaller taxa. For example, the Marginiferidae of the 1965 *Treatise* involved 4 subfamilies and a total of about 21 genera united by somewhat similar morphologies, namely, tendencies toward smallness, sparse but symmetrically situated spines, and internal marginal ridges. In detail, however, diagnoses within subfamilies proved to be inconsistent. We now recognize that those 21 genera are distributed in taxa having their origins in 4 different subfamilies and 2 families of the new classification (see Brunton, Lazarev, & Grant, 1995).

Studies of the brachiopod genome by Cohen and Gawthrop in the first volume of the revision of the brachiopod *Treatise* (1997, p. 189) indicate that the genome is small as compared to some other invertebrates, implying that it is probably not rich in repetitive sequences. The relationship between genome size and diversity of morphology, however, remains to be established; so for the present we can only speculate on any direct relationship between a small genome size and tendency toward repetitions of morphological features through time. In practice a consequence of the recognition of many reintroductions of morphologies in the same or different lineages is that we cannot fit our identified suprageneric taxa within the 4 levels of classification available between the suborder and subfamily while maintaining anything close to a phylogenetic structure. For instance one of the longest ranging and most diverse groups in the Productoidea is the Productellidae, starting in the Early Devonian and becoming extinct at the end of the Permian; it consists of 5 subfamilies, all probably with independent origins from the Productellinae stem group, and then about 20 subgroups ranging from 3 to about 20 genera (in a total of over 100 genera), which we cluster into tribes (see Brunton, Lazarev, & Grant, 1995, and Brunton & Lazarev, 1997). This category has been used occasionally in the past for brachiopods and, more commonly, in other organisms for subfamilial generic groupings; it is recognized by the International Commission on Zoological Nomenclature with the termination -ini.

Morphology

Depth and shape of the corpus and its relationship to ears and trails are useful characters. Definitions of terms, however, such as visceral disk, body or visceral cavity, and trail, have been used differently by authors and lack precision (but see Morphological and Anatomical Terms Applied to Brachiopods, Williams, Brunton, & others, 1997, p. 423). Growth studies of deep productidines demonstrate that ventral and dorsal valves grew at different speeds, that ventral trails correspond in a stable relationship only with dorsal trails in adulthood, and that the former originated posteriorly at the anterior margin of what has been called the ventral visceral disk. It is important to be able to define unequivocally the complete shell cavity exclusive of its peripheral cavities, where the ears and trails are located, so as to provide a measure of its depth. Thus the corpus (Fig. 230, and see Brunton, Lazarev, & Grant,

1995) includes the body (or visceral) cavity plus the mantle cavity. The term can be used for the description of external surfaces or this cavity between the valves. Peripheral cavities are marginal to and commonly partially separated from the corpus by marginal structures, usually ridges of secondary shell material.

The ventral trail, *sensu lato,* started growth on the ventral corpus at a point marked on the shell lateral profile (commonly best seen in median section) by a tightening of the spiral growth curve that, in different species, produced anything from a slight change in curve to a true geniculation. At this geniculation point the ventral surface ornamentation commonly changed to one that continued to the anterior margin. As adults the ventral and dorsal trails grew more or less parallel to each other, forming the slitlike gape through which seawater was circulated to the mantle cavity. The ventral trail can be differentiated into two regions: posteriorly the region of preadult growth, which started at the geniculation point and was confined to the corpus; and the true adult functional ventral trail extending beyond the corpus. The dorsal and ventral visceral disks become specifically defined as those areas of the corpus posterior to the origins of trails. Normally, in deep shells, the anterior margin of the ventral visceral disk can be defined by a radius of curvature centered on the hinge axis equal to the dorsal visceral disk length (Fig. 230). The situation differs in shallow, strongly concavoconvex shells, because the two valves follow closely similar growth curves and in consequence are approximately equal in surface length. Any change in their growth spiral, seen in lateral profile, was slight and occurred at about the same position on both valves; consequently the visceral and trail areas of these shells are poorly differentiated and of similar curved lengths.

As in living brachiopods, the corpus cavity of productides can be divided into the posterior body cavity containing the body organs of the animal, and the anteriorly placed mantle cavity containing the lophophore. All evidence indicates the presence of a normal, anterior body wall composed of inner mantle epithelium (Williams, 1956), which in all probability was ciliated where it lined the mantle cavity. The disposition of the anterior body wall, separating the two cavities and in all probability accommodating the median mouth section of the lophophore, has been questioned for over a century. Until recently there has commonly been an assumption that this body wall extended posterolaterally toward the hinge extremities (e.g., Brunton, 1982). Lazarev (1985) suggested a more centrally confined position for the body cavity in buxtoniids. This interpretation was based on the presence of paired ridges anterior to the cardinal process, which possibly supported the body wall, and the rather similar microornamentation of the dorsal valve interior both anterior and posterior to the brachial ridges (widely accepted as areas from which the lophophore was suspended), perhaps indicating that both areas accommodated the mantle cavity. This microornamentation is a mixture of small pits and tubercles, which have been likened to shagreen, and occurs also in some ventral valve umbos, as in some productids. Since then, study of other productides and strophomenides supports the view that the body cavity was confined closely around the cardinalia and dorsal muscle scars, with lateral and anterior regions of the body wall connecting across the corpus cavity just

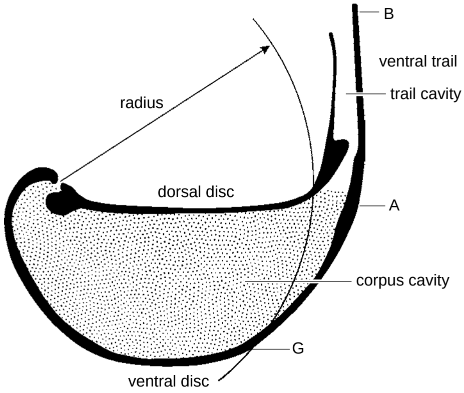

Fig. 230. Median section of adult productidine with deep corpus cavity; from points *A* to *B,* adult ventral trail; from *G* to *A,* anterior region of corpus from point of geniculation (*G*), representing earlier ventral trail growth; the region posterior to *G* is ventral disc; radius from hinge axis representing dorsal disc length prior to geniculation (new).

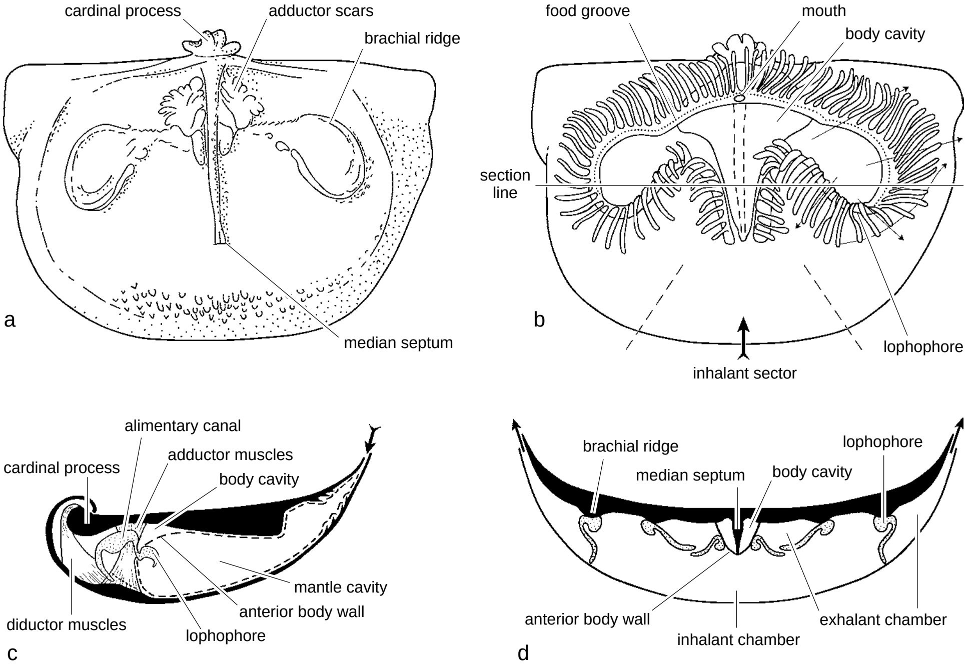

FIG. 231. *a,* dorsal valve interior of productoid, based on *Reticulatia; b,* stylized reconstruction of lophophore and body cavity region (*shaded*); *c,* median longitudinal section of shell showing inferred main musculature, mantle epithelium, and body wall with lophophore and alimentary canal; *d,* cross section of shell indicating ventromedian inhalant and more dorsally situated exhalant water chambers separated by lophophore. Inhalant *arrows* have tails; water current entered anteromedianly, down narrow trail region, into ventral part of mantle cavity from where it passed between tentacles, from food groove side, to exhalant chamber and lateral margins of shell (new).

anterior to the positions of the diductor muscles (Fig. 231a,b). This disposition of the body cavity leaves more space posterolaterally for extensions of the mantle cavity behind the posterodorsal attachment areas of the lophophore, thus allowing the posterior elements of the lophophore to have passed water posteriorly between their tentacles in the same direction (relative to the tentacles) as in all known living brachiopods. This position of the body wall implies that the mantle epithelium formed much of the posterior hinge margin. These surfaces probably were not fused, leaving the posterior margin potentially open to the sea, especially as the valves moved relative to each other during growth, tending to leave gaps at the posterior margin. These were closed by the growth of a variety of shelly ridges, such as cardinal ridges, the ginglymus or interarea, the lophidium, and modifications of the external surface of the cardinal process within the delthyrium of some strophalosiidines. Many of these structures helped articulate the valves as well as provide better seals at the hinge line.

The concept of the mantle cavity extending posteriorly has been applied in other possible strophomenates, such as clitambonitaceans (WRIGHT, 1994b), in which mantle canal-like markings were recognized on internal surfaces of the interareas.

Mantle canals are rarely, poorly, or questionably preserved in productides. In chonetidines, traces of vascular trunks were described by MUIR-WOOD (1962) in the middle of ventral valves of *Neochonetes;* and, although these ridges are unlike the depressions left by mantle canals in well-authenticated genera, similar structures can be found in several Carboniferous and Permian genera. In productidines ROBERTS (1971) described fragmentary traces of canals in the dorsal

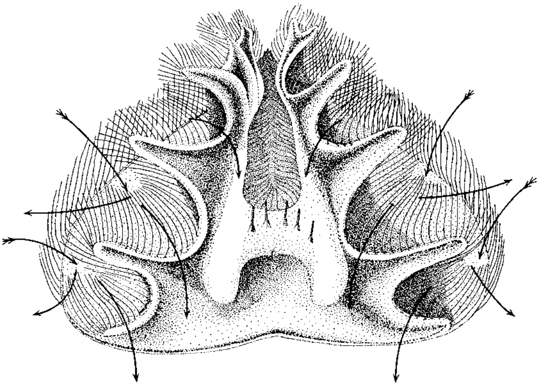

FIG. 232. Falafer calcified brachidium and reconstructed lophophore of small Permian aulostegid lacking trails; shells probably opened as in living thecideidines, capable of raising dorsal valves widely to expose lophophore and able to create a lateral inhalant water current (adapted from Grant, 1972).

valves of *Lomatiphora,* but these may be the internal representations of external ribbing in these thin-shelled specimens. BRUNTON (1966), in a general discussion on productoid morphology, wrote of a possible pinnate system associated with the marginal ribbing of adult shells. In more recent years the internal disk areas of many productidines, characteristically patterned by minute tubercles and pits, are interpreted as underlying the positions of gonadal tissue in the mantles. If so, at least some productidines had spreading saccate canal systems, which may have terminated distally in fine radiating canals between the radially aligned endospines and tubercles commonly seen at visceral disk margins and on trails. There seems to be no evidence for median canals or canals surrounding the gonocoel. The remaining groups of Productida have even less evidence of mantle canal systems.

In the Productida the form of the lophophore and pattern of water circulation within the mantle cavity remained enigmatical for a long time; even the function of the brachial ridges was questioned. Now it is generally agreed that these ridges reflect the attachment areas of a simple schizolophe or the basal course of a more strongly folded ptycholophous falafer type of lophophore, as described by GRANT (1972). The falafer style of lophophore is known in small, deep corpus strophalosiids and was supported on a calcified brachidium (Fig. 232). Whether this type of lophophore was universal in all productides with deep corpus cavities is unclear, but there is no direct evidence in pre-Permian species; and it may be that it was confined to small attached species lacking long trails. In these small species an efficient water circulation system would have entered laterally with the main exhalant current anteromedianly. Currently there is no universal agreement on the possible water circulation systems in productides. In chonetids and productides with a shallow corpus, however, (perhaps also in other deep species with trails) the shallow cavity could not have accommodated a falafer lophophore; and a simple schizolophe, following the brachial ridges, is more likely (Fig. 231b). Assuming that fossil brachiopod lophophores worked as do all those in living species, that is, with water passed between the lophophore tentacles from the brachial (food) groove surface to the outer surface, the disposition of tentacles around the schizolophe requires the inhalant current to have been anteromedian with the exhalant currents laterally positioned, as suggested by BRUNTON for chonetids (1972) and some productides (1982; Fig. 231d). A water circulation system like this is seen in living juvenile species during their schizolophous growth stage, although by adulthood the circulation changed to the median exhalant current typical of plectolophous species. The alternative view, with a median exhalant current, has been

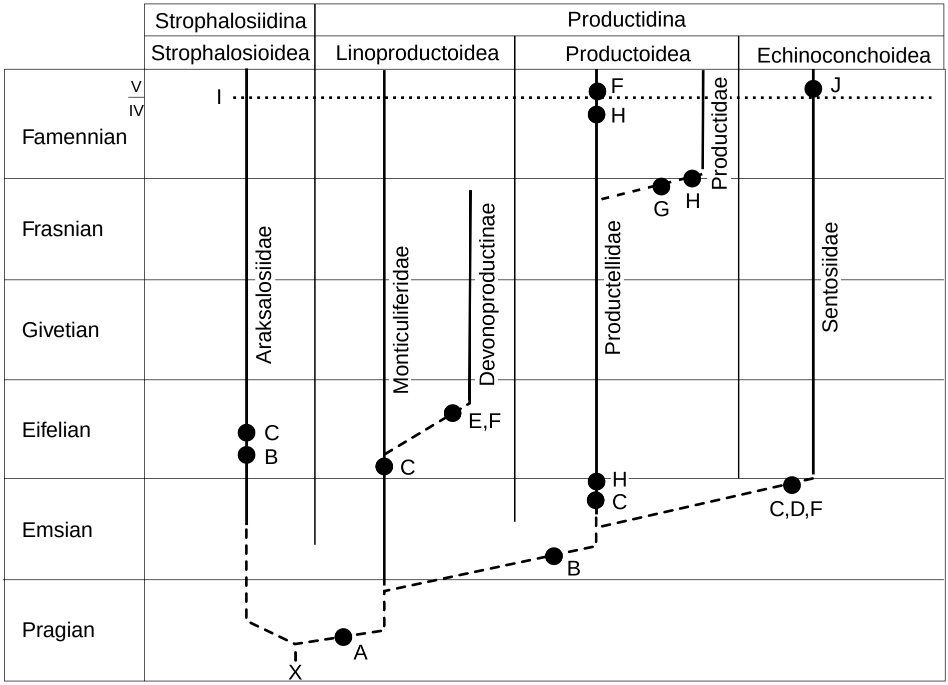

FIG. 233. Major morphological changes during Devonian of Productida, giving rise to Productidina and Strophalosiidina and their superfamilies and families; character changes identified by letters *A* to *J; A,* loss of interareas; *B,* loss of fine, chonetid-like ribbing; *C,* loss of anderidia; *D,* development of dorsal spines (unimportant in strophalosiidines); *E,* development of serial dorsal lamellae; *F,* development of marginal structures; *G,* development of deep corpus cavity; *H,* introduction of anterior ribbing; *I,* loss of toothed articulation in Productidina; *J,* first differentiation of spines into bands; *X,* chonetidine ancestor from which spread of spines over ventral valve gave rise to Productidina and Strophalosidina (new).

suggested by Lazarev (1996) in the Yakovleviini. (For development and function of lophophores, see the lophophore section of the chapter on anatomy in the first volume of the Brachiopoda revision, Williams & others, 1997, p. 110–120.)

Recently differences between the cardinal processes of productides and some other strophomenates as compared to the cardinal processes of many other rhynchonelliforms were discussed by Brunton, Alvarez, and MacKinnon (1996). An important characteristic of the cardinal process of productides is the traces, commonly preserved on their external (dorsal) faces, of relic myophores indicating the dorsal attachment positions of paired diductor muscles during ontogeny.

Morphological changes

Early Devonian productides retained some chonetidine characteristics, such as anderidia found in *Ralia, Eoproductella,* and *Chattertonia* in the Strophalosioidea, Linoproductoidea, and Productoidea respectively and a fine radial ribbing that persisted throughout most of the linoproductoids (Fig. 233). These shared characters indicate a common ancestry (monophyly in the sense of Simpson, 1961) for the whole group. Spines were restricted to the hinge line in chonetidines, but spread to the rest of the ventral valve in true productides. At an early stage, probably within the Lochkovian or Pragian, loss of the interarea differentiated the Productidina from the Strophalosiidina. This separation was further marked by the tendencies for the cardinal process in productidines to grow posterodorsally, curving into the ventral umbo, while that of strophalosiidines grew posteroventrally (Fig. 234). In the Emsian (e.g., *Chattertonia,* an early productellid in the Productoidea) the ancestral fine radial ribbing was lost and anterior ribbing developed, which became coarse in the latest Emsian (e.g., *Spinulicosta*). Specimens in the late Famennian developed ribbing that started more posteriorly, and by the middle Tournaisian it originated near the umbo, as in some lineages of the Productidae. By the Eifelian spines had developed on dorsal valves and *Caucasiproductus* (in the Sentosiidae) introduced the Echinoconchoidea. Lazarev (1989) described the systematics of Devonian Strophalosiidina, and in 1990 he published details of the evolution and systematics of the Productidina.

Late in the Famennian, between the European Zones IV and V, important changes occurred. Until then productidines retained a toothed articulation, similar to that of the strophalosiidines, but from then on teeth and sockets were lost from all productidine lineages (Fig. 233). Early in the Famennian, within the diverse Productoidea, the Productidae arose from their stem group, the Productellinae, by a deepening of the corpus cavity in the relatively smooth leioproductines, which evolved in the Early Carboniferous into the ribbed and reticulate genera of the Dictyoclostinae and Productinae. Early in the Early Carboniferous some of these deep productids, the Buxtoniinae, also developed spinose dorsal valves. These trends toward spinose dorsal valves and deeper corpus cavities are also seen in some Early Carboniferous Productellinae, in some Plicatiferinae, and in Marginiferinae. At much the same time corpus depth increased in the Echinoconchoidea and slightly later (Viséan) in the Linoproductoidea, but although it was a widespread trend in the former, in the linoproductoids shallow genera of the Monticuliferidae continued through the Permian. Similar trends are seen in the Productellidae and Productidae.

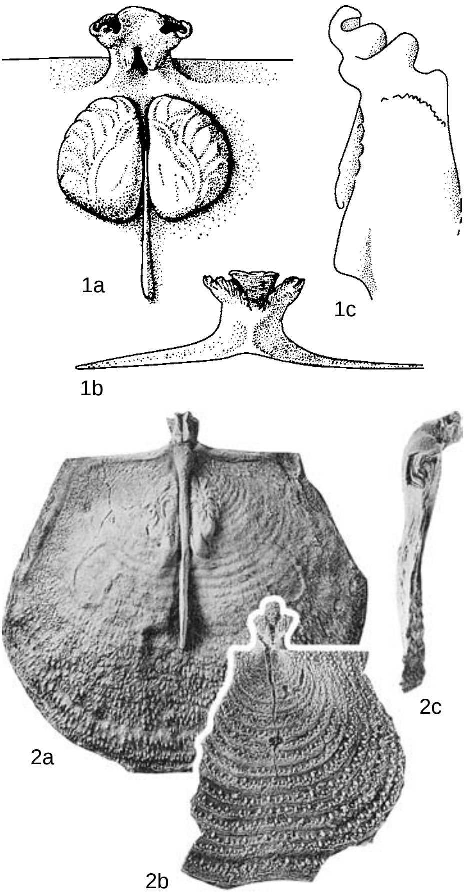

Fig. 234. Cardinalia showing dispositions of cardinal processes; *1a,* internal, *1b,* external (adapted from Muir-Wood & Cooper, 1960), and *1c,* lateral views (new), typical of strophalosiidines, based on *Edriosteges,* with posteroventrally directed cardinal process; *2a,* internal, *2b,* external, and *2c,* lateral views typical of productidines, based on *Echinaria,* with posterodorsally directed cardinal process (adapted from Muir-Wood & Cooper, 1960).

By the Early Carboniferous most characteristics had been introduced into the Productidina. More varied and widespread ecological conditions in the Viséan and again in the Early Permian seem to have resulted in a proliferation of diversity, commonly resulting from recombinations of characters, character evolution, or loss. In most lineages these changes occurred several times, leading to much parallelism. Within Carboniferous and Permian Productidina a few novelties arose, such as nasute or tubiform trails, gigantism, external monticules, or the direct evidence for the acquisition of a complex ptycholophe suspended from the falafer brachidium in some Permian species with deep corpus cavities. These changes in development of the lophophore were probably in response to the need for greater capacity in the food- and oxygen-capturing mechanism of the lophophore. This depends on cilia covering the tentacles, so the greater number of tentacles capable of being housed on the lophophore, the greater its food-gathering capacity. In order to increase feeding area the tentacles had to lengthen or the lophophore had to lengthen to accommodate more tentacles and become folded within the mantle cavity. This required a deepening of the shell. The unresolved question is whether a simple schizolophe, perhaps with long tentacles, persisted in deep shells with the falafer type of lophophore restricted to its known occurence in small Permian strophalosiidine species, or whether an unsupported ptycholophe could have evolved along with the deepening of the corpus cavity in the latest Devonian?

It is in the Strophalosiidina and lyttoniidines that the most unusual and extreme morphologies are found. The Strophalosioidea remained relatively conservative from their Early Devonian origin; interareas were reduced in many of the Araksalosiidae and in the Chonopectidae, in which spine cover was also reduced, but for the rest there were variations in spine cover and style, radial and concentric ornamentation. The Aulostegoidea, with its origin in the early Carboniferous, lost its toothed articulation, developed shallow and deep species, and some developed elaborated trails as flanges, gutters, and even complex needlelike spinose margins, such as in the Lower Permian *Chonosteges.*

Richthofenioids, characterized by their conical shapes in which the dorsal valve commonly was positioned within the ventral cone, seem to have had their origin in a mid-Carboniferous aulostegoid (SUTHERLAND, 1996; refer to the section on the Richthofenioidea, herein, p. 610). Diversity in the form of ventral valve marginal growth is also seen in some richthofeniids that developed a characteristic meshwork covering the aperture of the cone, called the coscinidium. This structure created a protected area of sea water into which the lophophore was extended while feeding and is characteristic of several later genera in most families. A consistent feature within the superfamily is the form of articulation in which knobs (tegula) at the lateral extremities of narrow dorsal hinge lines fit into corresponding cavities at the dorsal edge of the posterior margin of the ventral corpus cavity. Associated with their conical shape is the myocoelidium in ventral valves of the Richthofeniidae, which probably accommodated the ventral ends of the diductor and adductor muscles (RUDWICK & COWEN, 1968). In other families this structure is replaced by a median septum or muscle platform.

In the Late Carboniferous the most extreme modifications occurred, probably in a strophalosiidine, giving rise to the Lyttoniidina. The relationships of this group were discussed by GRANT (1972) where it was noted that the late Triassic Bactryniidae was unrelated to the lyttoniids and removed to the Thecideidina. Thus now it is almost certain that few, if any, post-Permian productides existed (but see SHEN & SHI, 1996). The morphology and phylogeny of the lyttoniidines are outlined by WILLIAMS, HARPER, and GRANT in the introduction to that suborder (herein, p. 619).

We recognize many problems remaining in the classification of the Productida, and in particular the Strophalosiidina has yet to be studied phylogenetically in order to unravel the lineages from homeomorphic groupings.

Terminology

Terms herein emended or added since 1965, in the first edition of the brachiopod *Treatise,* follow.

Bordering structures. An informal general term covering any structure developed at the valve or trail margins in adulthood, such as flanges (Morphological and Anatomical Terms, WILLIAMS, BRUNTON, & others, 1997, p. 430) or gutters.

Cardinal ridge (Morphological and Anatomical Terms, WILLIAMS, BRUNTON, & others, 1997, p. 426). Ridge extending along the dorsal valve posterior margin from the cardinal process base (Fig. 235.2), as compared to lateral ridges, which diverge from the hinge line (Fig. 235.1).

Corpus (Morphological and Anatomical

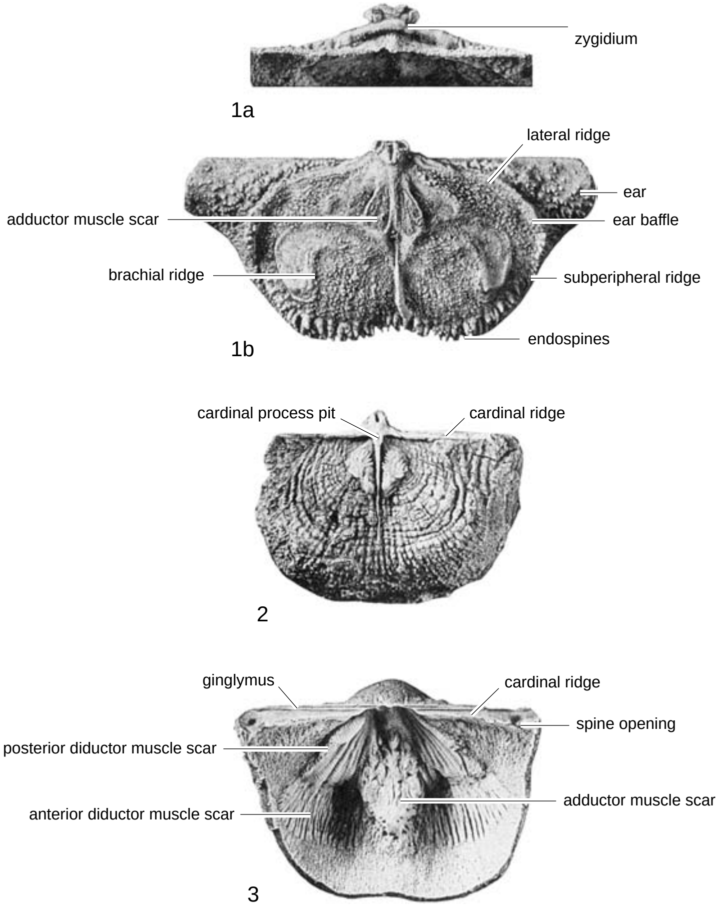

FIG. 235. Productidine internal morphology; *1a, Paucispinifera* dorsal valve, exterior of cardinal process, *1b,* interior; *2, Buxtonia* dorsal valve interior; *3, Inflatia* ventral valve interior; ginglymus here weakly developed; ear baffle and subperipheral ridge form marginal structures of dorsal valve corpus (new).

Terms, WILLIAMS, BRUNTON, & others, 1997, p. 427). Those areas of the valves enclosing the corpus cavity, the area occupied by the body cavity (p. 425) and mantle (p. 433) cavities, but excluding the peripheral cavities separating the dorsal and ventral ears and trails (Fig. 230).

Marginal structures. An informal description including structures forming part of the margins to the corpus cavity, helping to differentiate it from the ears and trails. Such structures are not at the valve edges. The term includes lateral ridges, ear baffles, and any marginal or subperipheral ridges or structures such as cinctures.

Peripheral cavities. A general informal description for any cavity distal to the corpus cavity and narrowly enclosed by ears and trails in productides and some strophomenoids or by other shell extensions in groups such as athyridids.

Many productide features are linked: strongly developed lateral ridges and ear baffles commonly correlate with well-differentiated corpus and peripheral cavities; prominent dorsal lateral ridges correlate with lines of external ventral spines diverging from the hinge line or marking the posterior limit of spines on the ventral valve.

In diagnoses we use size terms as general indicators in some taxa. These relate to the maximum width of the corpus, not including

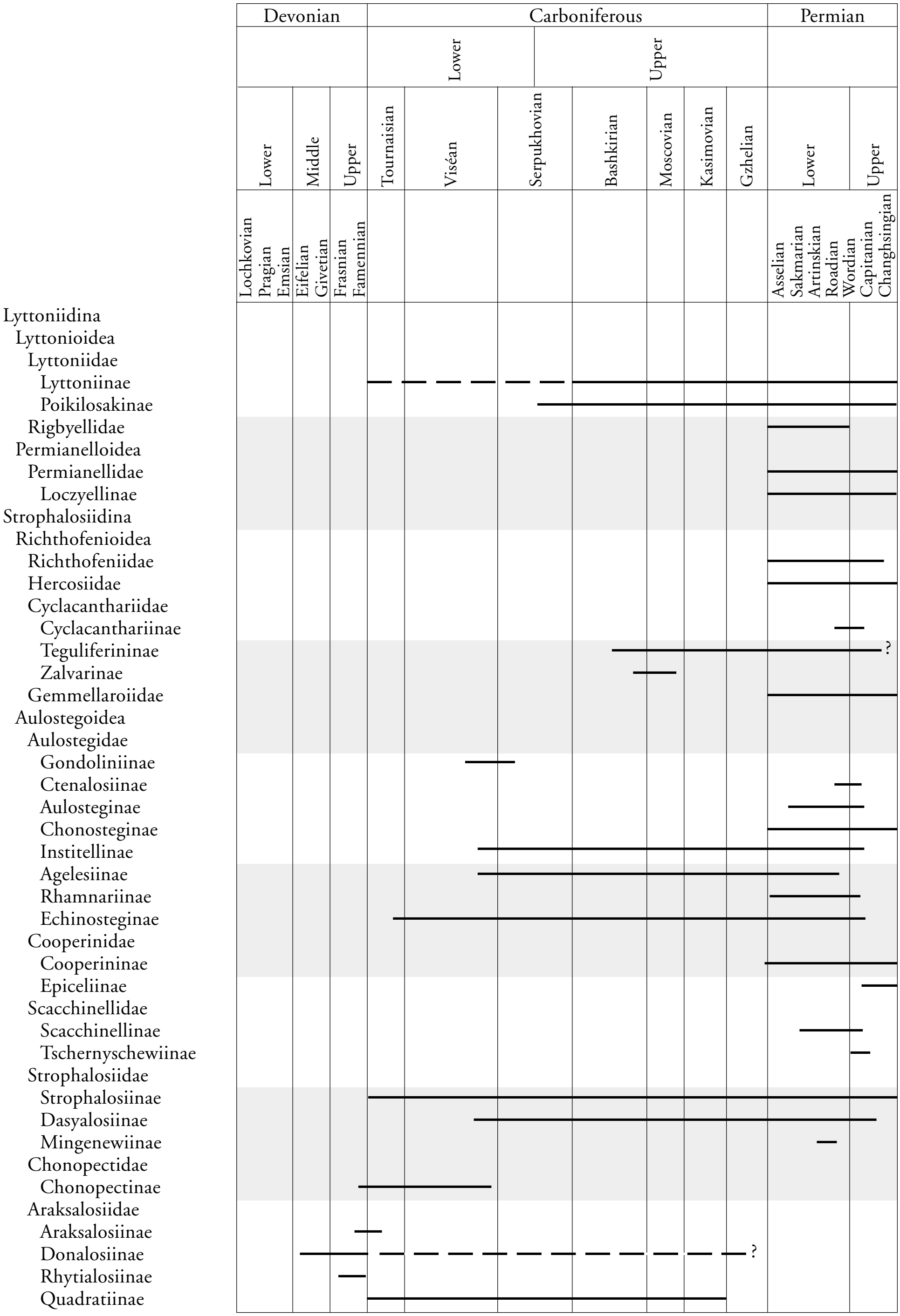

FIG. 236. Resume of classification of non-chonetidine Productida to subfamily levels and their stratigraphic distributions; *, Productininae ranges questionably into the Triassic (new).

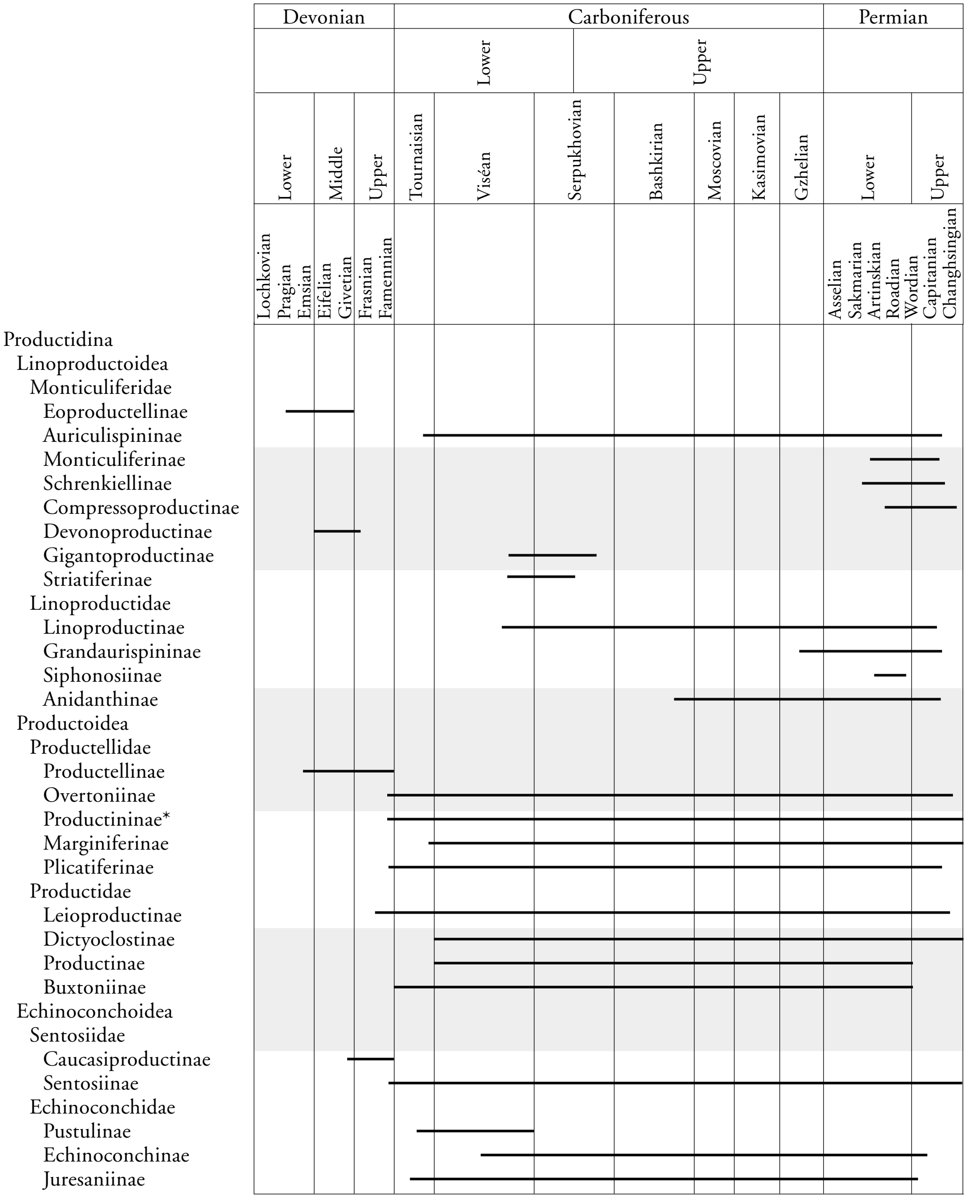

FIG. 236. *Continued.*

ears. We find this measure to be the most consistent, and it can be used on broken shells even when their peripheral cavities have been lost. The size terms used are: small: shells up to 20 mm wide; medium: shells more than 20 mm and up to 50 mm wide; large: shells more than 50 mm and up to 100 mm wide; and gigantic: shells over 100 mm wide. Corpus depth is assessed as the maximum dorsal corpus length divided by the maximum depth; where this ratio is less than 3 the shell is termed deep, if about 3 it is moderate, if the ratio is over 3 the corpus cavity is shallow.

Using the Classification

Generic diagnoses commonly make reference to another long-established genus, usually the taxon name bearer. In some a genus may be described as similar to another genus, in which case it is felt that the two are closely similar and likely, with added information, to prove to be subjective synonyms. When translations from Russian or Chinese to English are readily available, the English translation pages are included and enclosed in brackets.

At the onset of work on the Productida, genera were assigned so that RACHEBOEUF took charge of all chonetidines; regarding the Productidina and Strophalosiidina, BRUNTON and LAZAREV took charge of the pre-Permian; and GRANT dealt with Permian genera, his speciality for about thirty years. Although this apportionment was not conducive to phylogenetic analysis, at a meeting in London in 1993 an outline classification was discussed and agreed upon. In December 1994 the sudden death of GRANT necessitated all Permian genera going to the assignment of BRUNTON and LAZAREV, who found much remaining to be investigated in these less familiar taxa. Consequently, and in order to minimize delay in publication of this volume of the *Treatise,* some of the more obscure Permian genera are not treated as fully as we would wish.

Generic stratigraphic ranges follow the IUGS (see Fig. 236) chart despite the increasingly common practice of considering the Roadian as the basal stage of the Upper Permian, coming between the Kungurian and the Kazanian.

ACKNOWLEDGMENTS

Grateful thanks are due to Sarah Long (Natural History Museum, London) for preparing the list of references and maintaining the computer-based files and without whose considerable support this contribution would have been delayed. We thank Bruce Wardlaw (USGS, Denver) and Alwyn Williams for accepting the tasks of completing the Richthofenioidea and Lyttoniidina respectively, following Richard Grant's death. Tom Dutro (Smithsonian, Washington) kindly sent to London various files and illustrations of Permian genera. Colleagues, too numerous to name, have helped in providing valuable information, and CHCB is grateful to the Natural History Museum, London, for facilities provided since his retirement.

CHONETIDINA

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Suborder CHONETIDINA Muir-Wood, 1955

[*nom. correct.* MUIR-WOOD, 1965a, p. 420, *pro* suborder Chonetoidea MUIR-WOOD, 1955, p. 68]

Productides with concavoconvex to planoconvex profiles, resupinate in some; spines tubular, posteriorly directed, or spine apertures only, on ventral valves posterior margin only; shell surface with radial costae, and costellae, or smooth, rarely lamellose in some; interareas present; toothed articulation or denticulate hinge line; cardinal process bilobed, directed posteriorly, supported by a median septum or anteriorly bounded by a cardinal process pit; accessory septa in some; anderidia present, faint to strongly developed; brachial ridges absent or weakly developed. *Upper Ordovician (Cautleyan)–Permian, ?Lower Triassic.*

The suborder Chonetidina, as here constituted, is an extinct Paleozoic group of articulated brachiopods. The range of the suborder is from Late Ordovician (Ashgill, Cautleyan to Rawtheyan) to Late Permian and possibly the earliest Triassic, a period of about 200 million years, during which they had a worldwide distribution (Fig. 237). They were especially prolific during Devonian to Permian times. The external morphology of the chonetidine shell is highly conservative from the uppermost Ordovician to the Upper Permian, and most of the morphological innovations and evolutionary tendencies among characters were developed as early as the

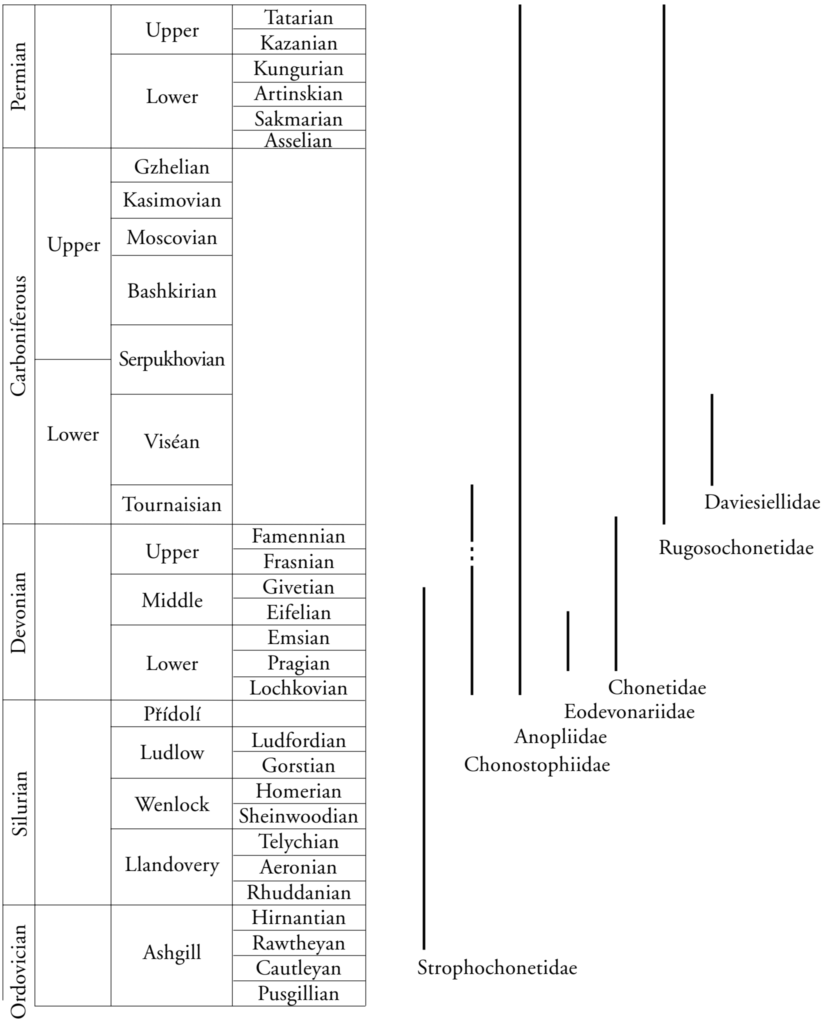

FIG. 237. Chronostratigraphic range of chonetoidean families (new).

Early Devonian (Emsian). They can be found in rocks deposited in all types of marine environments other than reefs; they evolved rapidly; and they are usually abundant. Such characters make them very useful for biostratigraphic purposes and paleogeographic reconstructions.

Known as early as 1820, the chonetidines have been studied more intensively during the last 30 years than ever before. In the first edition of the Brachiopoda *Treatise* (MOORE, 1965) the suborder Chonetidina included two superfamilies: Chonetacea and Cadomellacea. The order to which the superfamily Cadomellacea belongs is now uncertain. The first edition of the *Treatise* listed 32 genera assigned to 11 subfamilies (Cadomellacea excluded) and 4 families. After the revision of the genus *Semenewia* (Semenewiidae), now assigned to the suborder Strophalosiidina, the suborder included more than 1,200 species belonging to 162 genera assigned to 15 subfamilies and 7 families, namely Strophochonetidae, Chonostrophiidae, Anopliidae, Eodevonariidae, Chonetidae, Rugosochonetidae, and Daviesiellidae (Fig. 237).

The exterior of a typical member of the Chonetidina exhibits a concavoconvex strophic shell, subrectangular in outline with a maximum width at or just anterior to the hinge line, with a row of oblique spines, symmetrically inserted on the posterior edge of the ventral valve, and a weakly curved, commonly apsacline ventral interarea that is longer than the usually hypercline dorsal interarea (Fig. 238). A pseudodeltidium and chilidium are present, with variably developed cardinal crests below the chilidium. The shell surface is usually costellate. Variations include convexity, the planoconvex profile of strophochonetids as well as the convexoconcave, resupinate profile of the chonostrophiids; the outline varies, with length:width ratios usually between 0.6 and 1.0; the reduced or mucronate hinge lines of *Chonetes* and *Dyoros* respectively; the rectimarginate or sulcate anterior commissure; the ventral sulcus of *Dagnachonetes,* associated with the dorsal median fold of *Dyoros,* with its superimposed median plication of *Mesolobus;* and the size of radial ornamentation, with or without median enlarged costae, or the absence of radial ornamentation in *Anoplia* and *Tornquistia.* The most important external difference, however, is the morphology of spines, their orientation, and their distribution along the posterior edge of the ventral valve (Fig. 239). Spines are commonly straight, oblique, posterolaterally directed, and symmetrically arranged as in *Protochonetes;* they are orthomorph perpendicular (*Ctenochonetes*), oblique, or parallel (*Longispina*). They can, however, also be variably curved, cyrtomorph intraversed or extraversed (*Renaudia, Eodevonaria* respectively), or even geniculated (*Devonochonetes*); their angle with the hinge line varies from 0° to 90°. Moreover, spines can be asymmetrically inserted during juvenile stages, as in *Ctenochonetes,* or even at adult stages (*Asymmetrochonetes, Chlupacina, Semicaplinoplia*). Spine characters have been described previously (Racheboeuf, 1981b).

The largest species occur in the Lower Carboniferous, and they belong to the genus *Delepinea.* They may attain a width of 30 cm and rival the gigantoproductid productidines. During the Early Devonian (Emsian) a first tendency toward relative gigantism developed with shells attaining a width of about 5 cm (*e.g., Ctenochonetes, Loreleiella, Pleurochonetes*). Shell size decreased at the end of the Devonian. Shell size is better referred to as the length of the shell, which is often better preserved, rather than to the width of the shell. Specimens are referred to as very small when they are less than 5 mm long, small when between 5 and 10 mm, medium-sized between 10 and 20 mm, large between 20 and 30 mm, and very large when the length exceeds 30 mm, which corresponds to a width of about 50 mm. Most shells are between 5 and 20 mm long, with a corresponding width between 5 and 30 mm, according to their outline. The length is measured along the longitudinal axis from the most posterior part of the ventral umbo to the anterior margin. The width is the maximum width of the shell. It is measured along the hinge or anterior to the hinge line. Thickness is measured along an axis at right angles to length and width. Convexity is expressed by the length to thickness ratio. The spine implantation on the posterior margin of the ventral valve is described by the distance of each spine from the umbo in millimeters (Racheboeuf, 1981b). In dorsal valve interiors, the angles (in degrees) between inner socket ridges, anderidia, and accessory septa are often used to provide diagnoses.

The shell structure is typically pseudopunctate. Internally, an important morphological feature common to most of the chonetidine shells is the presence of a pair of anderidia in the dorsal valve interior; they are interpreted as lophophore supports. In the earliest representatives (*Archeochonetes*) anderidia may be absent or imperceptible.

The ventral muscle impressions of the chonetidines are confined to the posterior half of the ventral valve and are longitudinally divided by a myophragm (Fig. 238). Adductor scars are relatively small,

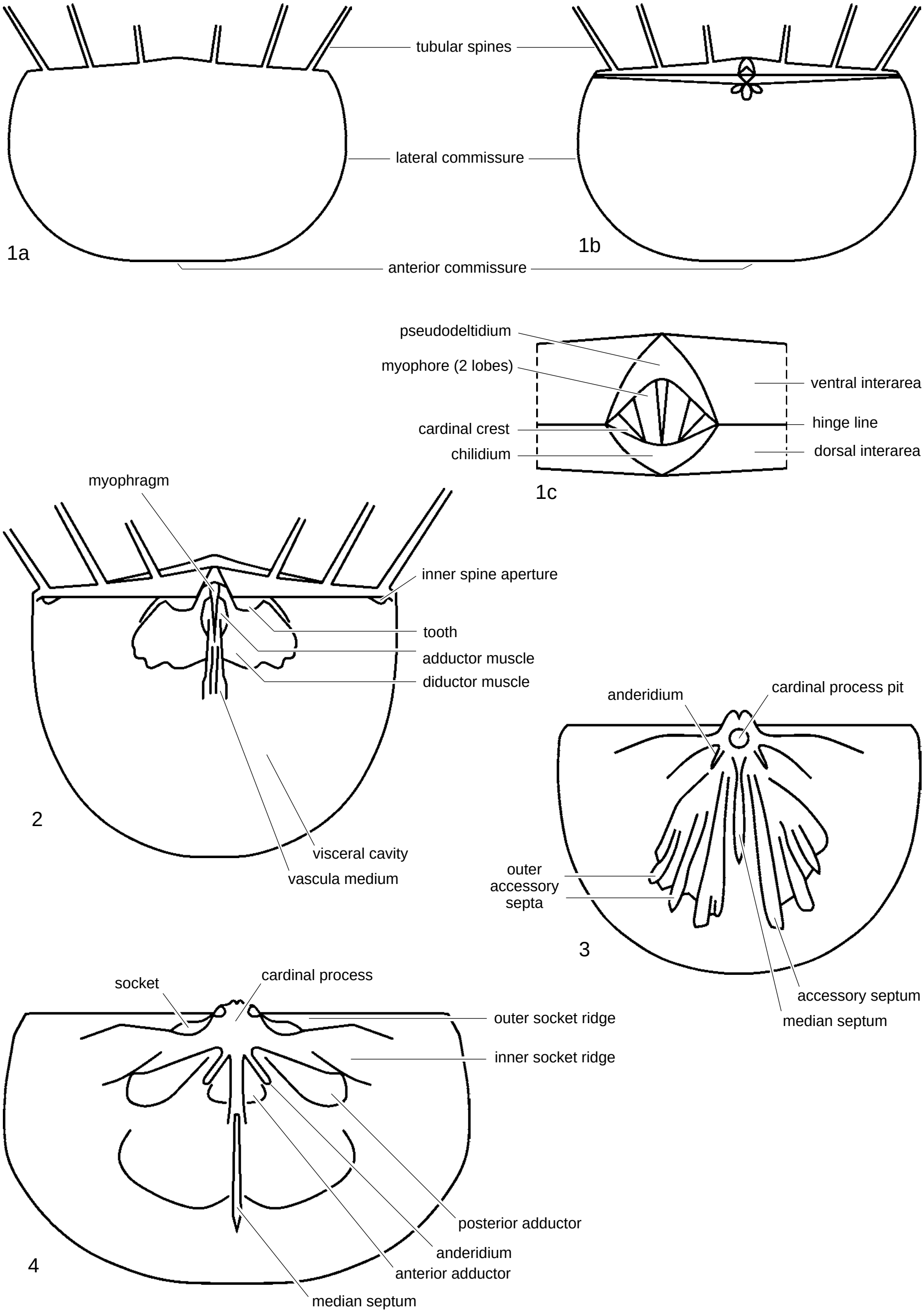

FIG. 238. Diagrammatic representation of morphology of chonetoidean shell; *1,* external morphology of complete articulated shell; *1a,* ventral view; *1b,* dorsal view; *1c,* detail of dorsal view; *2–4,* internal morphology; *2,* ventral valve interior; *3,* dorsal valve interior of anopliid type; *4,* dorsal valve interior of strophochonetid type (new).

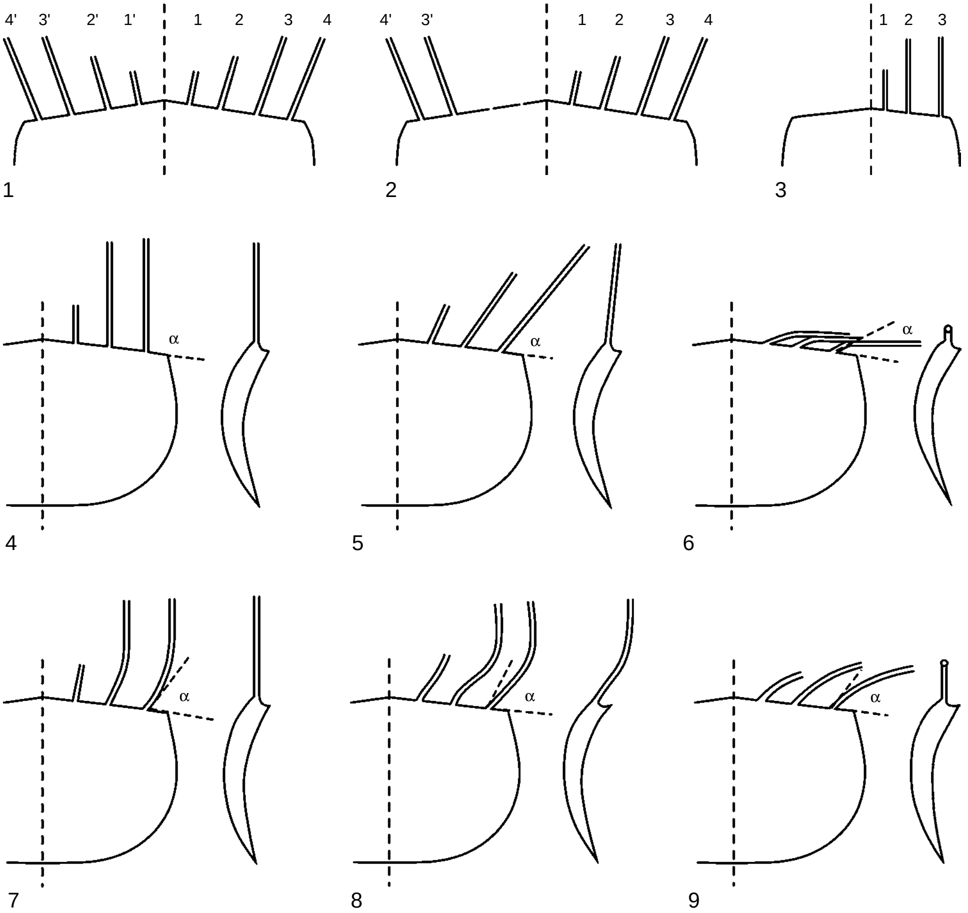

FIG. 239. *1–3,* Distribution of spines along posterior margins and corresponding formulae; *4–9,* descriptions of spine morphology and orientations; *4,* orthomorph perpendicular; *5,* orthomorph oblique; *6,* orthomorph parallel; *7,* cyrtomorph intraversed; *8,* cyrtomorph geniculate intraversed; *9,* cyrtomorph extraversed (new).

subrounded, elliptical or subtriangular, narrow, elongate, and adjacent to the myophragm. They are surrounded by diductor scars, usually subtriangular in outline, anteriorly rounded, and may be radially grooved. The mantle canal system is reduced to one pair of variably developed *vascula media* originating anterior of the adductors. The hinge is usually smooth, but denticles, probably reminiscent of a plectambonitoid ancestor, are developed in several genera. A denticulate hinge line characterizes the family Eodevonariidae, but it sporadically occurs in other families such as the Middle Devonian genus *Devonaria* (Anopliidae) and the Permian *Striochonetes.*

The dorsal valve interior exhibits two main types of morphological features (Fig. 238). The first one shows a median septum, and the second shows one or several pairs of accessory septa, commonly without a median septum, or with a reduced median septum or a breviseptum. Variations affect both morphological types. The median septum is commonly absent or very reduced in primitive forms in juveniles and in such paedomorphic shells as *Strophochonetes, Ctenochonetes,* and *Chlupacina* respectively. When developed, the median septum may support the cardinal process as in *Ctenochonetes;* in *Dagnachonetes* this is not so. In the latter genus, a cardinal process pit commonly developed between the cardinal process and the median septum. The median septum is sometimes reduced to a breviseptum. Accessory septa characterize the families Anopliidae and Chonetidae. They are variable in number, size, and morphology and are commonly bladelike, smooth, or variably spinose. The cardinal process morphology is a constant feature among chonetidines and is invariably bilobed. Variations affect size, outline, and morphology of the two lobes of the myophore, which are narrow and medially coalescent or posterolaterally widened and deeply separated as in *Chonetes* and *Loreleiella* respectively. A quadrilobate myophore is commonly described but refers only to the paired outer walls of each lobe of the myophore.

The strophochonetids are one of the most homogenous groups among chonetidines and undoubtedly represent one of the ancestral stocks. They range from the Upper Ordovician to the Middle Devonian (Eifelian). Externally, they are mainly characterized by a fine radial ornament, the presence of a variably developed ventral median enlarged costa (*e.g., Ctenochonetes*), or several radially arranged enlarged costae (*e.g., Archeochonetes, Strophochonetes*), associated with a planoconvex to moderately concavoconvex longitudinal profile (an exception being the markedly concavoconvex shell of *Leptochonetes*). The lack of enlarged costae and the development of coarser radial costellae allow differentiation of the Protochonetinae from the Strophochonetinae. Additional diagnostic features of both subfamilies are high-angled to perpendicular spines and primitive features in interiors of both valves; the interior of the dorsal valve with a weakly developed median septum and inner socket ridges during the Silurian, becoming usually well developed from the Lower Devonian, except for small, paedomorphic forms such as *Chlupacina;* and interior of the ventral valve with a similar progressive development of muscle scars, myophragm, and *vascula media.* The sporadic appearance of small forms, commonly with asymmetrically arranged spines, related with environmental changes during the Devonian and corresponding to intra-Devonian biotic events, is interpreted in terms of heterochrony.

The chonostrophiids may also exhibit one or several enlarged costae (*Chonostrophia*), but they are easily distinguished from strophochonetids, to which they are probably closely allied, by their resupinate, convexoconcave, longitudinal profile. Except for the Lower Carboniferous *Tulcumbella,* they range from Lower to Middle Devonian (Givetian).

The family Anopliidae is commonly regarded as a group with very small, smooth or costate shells with one or several pairs of accessory septa in the interior of the dorsal valve. There are two subfamilies, Anopliinae with smooth exteriors, and Caenanopliinae with radial ornament, but such a definition is not satisfactory because it is purely phenetic. The shell size is not a reliable character at the family level. The large size of *Airtonia* was considered to preclude its assignment to the family Anopliidae, but size increase between the Lower Devonian *Plicanoplia* and the Lower Carboniferous *Airtonia* is no more than a factor of 12, *i.e.,* almost the same as that between the smallest Silurian and the largest Lower Devonian Strophochonetinae (factor of 11). It is likely that some small Devonian shells included within the family Anopliidae are paedomorphic derivatives of the Chonetidae.

The family Eodevonariidae is typically restricted to Lower and Middle Devonian (Pragian to Eifelian). The main characteristics of its representatives are the denticulate nature of the hinge line and the variable development of accessory septa. Both features are probably reminiscent of the plectambonitoids. A denticulate hinge line, however, may also occur in such other families as anopliids (*Devonaria*) and possibly rugosochonetids (*Striochonetes*).

The Devonian family Chonetidae includes the subfamilies Chonetinae, Dagnachonetinae, Retichonetinae, Devonochonetinae, and Notiochonetinae. The family is externally characterized by the development of concentric fila, which appear by Middle Devonian times, and, internally, by usually weakly divergent anderidia in the dorsal valve interior. Except for the oldest group, the chonetines, the dorsal valve inner features are commonly reduced to a median septum or breviseptum. Accessory septa are, as a rule, poorly developed, bladelike, spinose accessory septa, often developed in the anterior half of the shell only (*Chonetes, Longispina*). Accessory septa tended to diminish in size during the Early Devonian and have disappeared by the Middle Devonian.

Rugosochonetidae represents the largest family among chonetidines, but phyletic relationships are not evident within the family, which will probably have to be divided. The family ranges from the Lower Carboniferous to Upper Permian and includes the subfamilies Rugosochonetinae, Capillomesolobinae, Plicochonetinae, Delepineinae, Svalbardiinae, Undulellinae, Lamellosiinae, and Quinquenellidae. This group is characterized by a global common tendency to develop a ventral sulcus associated with a corresponding dorsal fold, sometimes complicated by the development of a ventral median ridge. The exterior of the shell may be radially ornamented, smooth, or lamellose (*Lamellosia*). Internally rugosochonetids lack dorsal accessory septa; anderidia are usually relatively large and prominent, and the cardinal process is anteriorly bounded by a pit.

Following MUIR-WOOD (1962, 1965a), the family Daviesiellidae is restricted to the Carboniferous large shells of *Daviesiella.* The family is herein retained within chonetidines only questionably because its representatives exhibit several characters that make them apparently more closely allied to productidines than to chonetidines. Among these characters are the thickened ventral valve with reduced interarea, as well as the lack of a spine row, pseudodeltidium, and anderidia.

After early attachment by means of the pedicle, most of the chonetidine shells rested on the sea bottom with the dorsal valve uppermost, the extremities of the hinge spines serving for attachment by cementation with mucopolysaccharides to particles. It seems likely that many juveniles and some paedomorphic forms had an epiplanktonic mode of life, such as the Early Devonian representatives of the family Strophochonetidae.

The conservative morphology of the chonetidine shell leads to a number of homeomorphs characterized by similar external form, spines, and ornament associated with dissimilar internal structures mainly in the dorsal valve (*e.g., Chonetes, Dagnachonetes,* and *Devonochonetes*).

The classification employed here is based on external characters, including shell form, convexity, ornament, morphology, orientation, and implantation of spines; internally, the main characters are the morphology of the muscle field and hinge teeth in the ventral valve, and the morphology of the dorsal valve interior.

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Superfamily CHONETOIDEA Bronn, 1862

[*nom. transl.* RACHEBOEUF, herein, *ex* Chonetacea SCHROCK & TWENHOFEL, 1953, p. 317, *nom. transl. ex* Chonetidae BRONN, 1862, p. 301]

Shell very small (3 mm) to very large (200 mm), concavoconvex to resupinate, with hollow spine row normally developed along posterior margin of ventral valve only; when spines not externally developed, canal apertures visible; when spines absent, corresponding canal apertures also absent; spines vary in number, orientation, morphology, and disposition on both sides of posterior ventral margin; sulcus and fold absent or variably developed; anterior commissure rectimarginate, sulcate, or parasulcate; functional pedicle in early growth stages only;

shell smooth, sometimes lamellose, usually costellate with branching or intercalating costellae; enlarged costae present in some genera; interarea present in both valves with variably developed pseudodeltidium and chilidium, more rarely with chilidial plates; ventral interior with variably developed myophragm dividing relatively large muscle field with small adductors and large, smooth or flabellate diductors; *vascula media* sporadically preserved; hinge with a pair of variably developed hinge teeth, sometimes longitudinally striate, or hinge line denticulate with or without vestigial hinge teeth; dorsal interior typically with a pair of variably developed anderidia; cardinal process always present, variable in shape and size, more or less strongly bilobed internally; myophore with two lobes, variably developed but always longitudinally grooved, and medianly adjacent or distinctly separated; median septum often absent in juveniles, developing with growth as longitudinal ridge or breviseptum or lacking; accessory septa developed in some families, bladelike or formed by fused pustules; cardinal process anteriorly limited by pit or supported by median septum; inner socket ridges variably developed, always supporting cardinal process; lophophore possibly of trocholophe, ptycholophe, spirolophe, or mesolophe type, supported by anderidia; brachial ridges absent or variably developed; shell structure laminar, pseudopunctate. *Upper Ordovician (Cautleyan)–Permian, ?Lower Triassic.*

Family STROPHOCHONETIDAE Muir-Wood, 1962

[*nom. transl.* RACHEBOEUF, 1981b, p. 45, *ex* Strophochonetinae MUIR-WOOD, 1962, p. 40]

Shell small to large, transverse, finely costellate, planoconvex to markedly concavoconvex; median enlarged costa restricted to beak or reaching anterior margin, rarely absent; growth lines usually ill defined; interareas flat with well-developed pseudodeltidium, chilidium; hinge spines long, high-angled, commonly orthomorph perpendicular, sometimes cyrtomorph intraverse or orthomorph oblique; spines symmetrically or variously asymmetrically inserted on posterior ventral margin, sometimes lacking on one side of valve; ventral valve interior with short myophragm; relatively stout hinge teeth; dorsal valve interior with strong cardinal process, usually wider than long, deeply bilobed; myophore posteriorly displayed, two lobes being laterally flanked by short chilidial crests fusing anteriorly with shaft of cardinal process; cardinal process pit present during Silurian, persisting in juvenile and paedomorphic Devonian taxa; sockets anteriorly bounded by variably developed inner socket ridges, short and posteriorly curved, long and parallel to hinge line or anteriorly highly divergent at about 150°; sockets sometimes overhung in their mesial part by lateral horizontal expansions of cardinal process; dorsal median septum absent or well developed; no accessory septa; anderidia usually relatively small, anteriorly divergent at 35° to 90° and not posteriorly fused to cardinal process in oldest forms; brachial ridges commonly not developed. *Upper Ordovician (Cautleyan)–lower Middle Devonian.*

Subfamily STROPHOCHONETINAE Muir-Wood, 1962

[Strophochonetinae MUIR-WOOD, 1962, p. 40]

Strophochonetids with ventral median enlarged costa always present but variably developed; spines orthomorph perpendicular or cyrtomorph intraverse, symetrically or asymmetrically arranged. *Upper Ordovician (Cautleyan)–Middle Devonian (Eifelian).*

Strophochonetes MUIR-WOOD, 1962, p. 40 [**Chonetes cingulatus* LINDSTRÖM, 1861, p. 374; OD]. Shell small, plano- to moderately concavoconvex; well-developed median enlarged costa; long, symmetrically arranged high-angled spines varying from intraverse cyrtomorph proximally to orthomorph vertical distally; cardinal process strongly bilobed internally, anteriorly bounded by cardinal process pit; no median septum; anderidia long, narrow, anteriorly divergent at 60° and isolated on valve floor; inner socket ridges short, thin, as two rounded ridges almost parallel to hinge. *lower Silurian (upper Llandovery–Wenlock):* Sweden, Bohemia, Spain, Great Britain, Anticosti, Algeria.——FIG. 240,*3a–c*. **S. cingulatus* (LINDSTRÖM), Silurian, Baltic; ventral view, dorsal view, dorsal valve interior, ×4 (Muir-Wood, 1962).

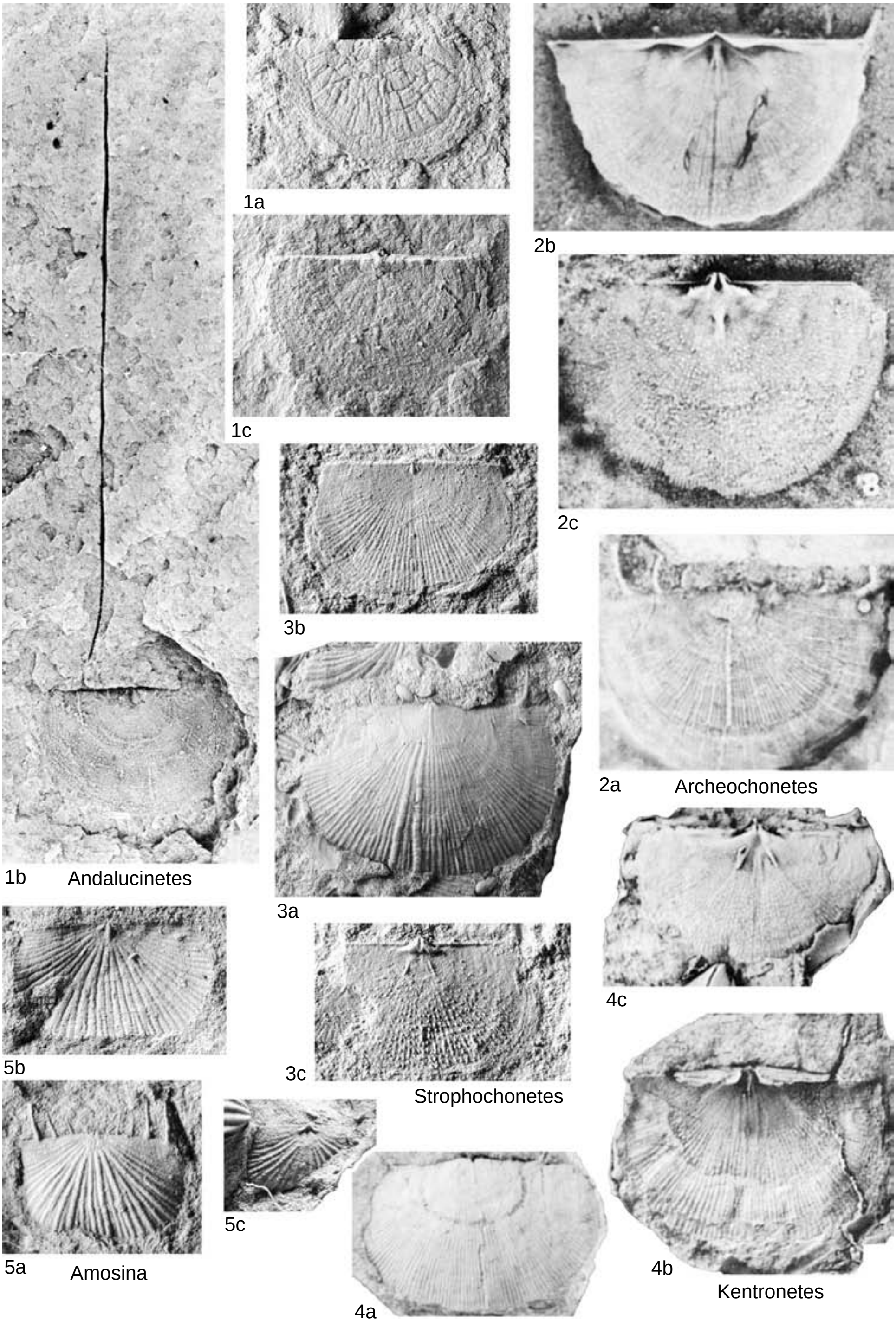


FIG. 240. Strophochonetidae (p. 369–374).

Amosina Boucot, 1975, p. 359 [**Chonetes fuertensis* Kayser, 1897, p. 300; OD]. Shell small, almost planoconvex to concavoconvex transversely elongate to subrectangular in outline; ventral sulcus present or absent, with or without longitudinal ridge; median enlarged costa absent or reaching anterior commissure; orthomorph symmetrically arranged spines, vertical or high-angled; no dorsal median septum; inner socket ridges poorly developed, supporting wide, short cardinal process; reduced anderidia anteriorly divergent at 90°, not fused posteriorly. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian):* Argentina, Bolivia.——Fig. 240,*5a–c.* **A. fuertensis* (Kayser), Ludlow–Přídolí, Argentina; ventral view, dorsal view, dorsal valve interior, ×4 (Benedetto & others, 1992).

Andalucinetes Racheboeuf, 1985, p. 660 [**A. hastatus;* OD]. Very small, thin, almost planoconvex shell; median enlarged costa restricted to posteromedian part of ventral valve; anteriorly, surface of shell becoming parchmentlike; very long vertical spines, either on right or left side; hinge teeth laterally elongated, parallel to hinge line; myophragm long, thin; dorsal interior with low, narrow inner socket ridges, narrow, elongate cardinal process pit; anderidia reduced, widely spaced, anteriorly divergent at 90°; no median septum. *Lower Devonian (Pragian):* Spain.——Fig. 240,*1a–c.* **A. hastatus; a,* ventral valve exterior; *b,* external mold of complete shell; *c,* dorsal valve exterior, ×4 (Racheboeuf, 1985).

Archeochonetes Racheboeuf & Copper, 1986, p. 1303 [**Chonetes (Eodevonaria) primigenius* Twenhofel, 1914, p. 26; OD]. Shell small; median enlarged costa present with several variably developed secondary enlarged costae; spines cyrtomorph intraverse to orthomorph, high-angled, symmetrically arranged and progressively infilled during growth, then not connected with shell interior; teeth, anterior wall of sockets longitudinally crenulated; anderidia poorly developed, anteriorly divergent at 35°; cardinal process deeply bilobed internally; median septum low, short. *Upper Ordovician (Cautleyan)–Silurian (Wenlock):* Anticosti Island, New Brunswick.——Fig. 240,*2a–c.* **A. primigenius* (Twenhofel), Ashgill, Anticosti; ventral valve exterior, ventral valve interior, dorsal valve interior, ×4 (Racheboeuf & Copper, 1986).

Asymmetrochonetes Smith, 1980, p. 49 [**A. spinalonga;* OD]. Shell small with variably developed median enlarged costa; orthomorph perpendicular spines on right side of pedicle valve only, very rarely on left side only; inner socket ridges, median septum, anderidia faintly developed but present. *Lower Devonian (Lochkovian–Pragian):* Canadian Arctic Archipelago, southern France, Spain, Bohemia, Australia (New South Wales).——Fig. 241,*3a–c.* **A. spinalonga,* Lochkovian, Canadian Arctic Archipelago; ventral valve, ventral valve interior, dorsal valve interior, ×4 (Smith, 1980).

Australostrophia Caster, 1939, p. 83 [**Leptostrophia?? mesembria* Clarke, 1913, p. 286; OD]. Medium, plano- to concavoconvex shell; maximum width at midlength; radial ornamentation parvicostellate, crossed by dense fila; median enlarged costa present in early stages only; spines orthomorph oblique, symetric and low-angled. *Lower Devonian (Lochkovian–Emsian):* Brazil, Argentina, Bolivia, Guinea.——Fig. 241,*1a–c. A. clarkei* Racheboeuf & Herrera, Pragian, Bolivia; *a,* ventral valve, ×4; *b,* dorsal side of an articulated shell, ×3; *c,* dorsal valve interior, ×3 (Racheboeuf & Herrera, 1994).

Babinia Racheboeuf & Branisa, 1985, p. 1435 [**B. parvula;* OD]. Shell small, transversely elongate, weakly concavoconvex; orthomorph vertical, symmetrically arranged spines; no dorsal median septum; narrow, elevated rounded ridgelike inner socket ridges anteriorly divergent at 160°, supporting wide, short cardinal process anteriorly bounded by weak cardinal process pit; thin anderidia isolated on valve floor, anteriorly divergent at 70°. *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Bolivia, Argentina, Brazil, Quebec.——Fig. 241,*4a,b.* **B. parvula,* Emsian, Bolivia; ventral valve exterior, interiors of articulated specimen, ×4 (Racheboeuf & Branisa, 1985).

Borealinetes Racheboeuf & Lespérance, 1995, p. 21 [**B. comestus;* OD]. Shell small to medium; spines cyrtomorph intraverse, symmetrically arranged; median enlarged costa reaching anterior margin of ventral valve; ventral valve interior with semicircular to semielliptical adductor scars; dorsal valve interior with inner socket ridges typically overhanging sockets posteriorly. *Lower Devonian (Pragian–Emsian):* Quebec.——Fig. 241,*2a–d.* **B. comestus,* Pragian, Quebec; *a,* ventral valve, ×4; *b,* ventral valve interior, ×4; *c,d,* articulated shell, dorsal side, dorsal valve interior, ×4 (Racheboeuf & Lespérance, 1995).

Chlupacina Havlíček & Racheboeuf, 1979, p. 86 [**C. longispina;* OD] [=*Hemichonetes* Havlíček & Racheboeuf, 1979, p. 83, *nom. nud.; Hemichonetes* Racheboeuf, 1981b, *non* Li, Gu, & Su, 1980, p. 343, obj.; *Philippotia* Racheboeuf, 1982, p. 1024; obj.]. Very small plano- to concavoconvex shell; radial ornamentation often restricted to periphery of valves; median enlarged costa well developed; two to three long spines on one side only; usually oblique in their proximal part, then becoming orthomorph vertical; dorsal valve interior without median septum; cardinal process short, wide, supported by narrow, rounded ridgelike inner socket ridges anteriorly divergent at about 145°; anterior margin of cardinal process, socket ridges almost vertical above valve floor; cardinal process pit variably developed, often longitudinally elongate; anderidia short, thin, isolated on valve floor, anteriorly divergent at 50°. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Bohemia, Armorican Massif, Spain, Canadian Arctic Archipelago, Australia, ?China.——Fig. 242,*4a–d. C. belairensis* (Racheboeuf), Emsian, southwestern Europe; *a,* ventral valve exterior, ×5; *b,* dorsal valve interior, ×5; *c,* detail of

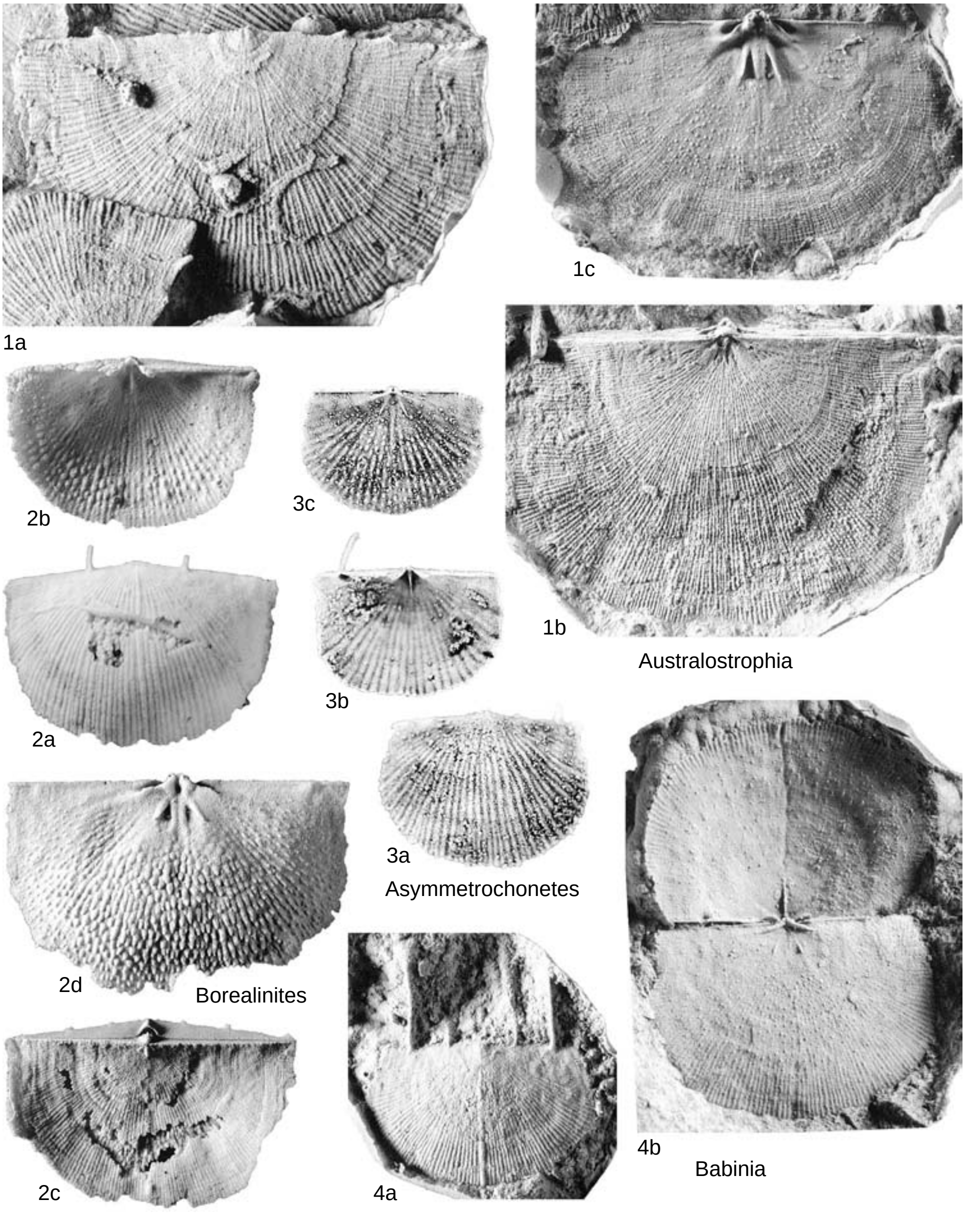


FIG. 241. Strophochonetidae (p. 371).

cardinal process, ×12; *d,* ventral valve with spines, ×5 (Racheboeuf, 1982).

Ctenochonetes RACHEBOEUF, 1976, p. 52 [**Chonetes tenuicostata* OEHLERT, 1877, p. 599; OD]. Shell small to medium, weakly to markedly concavoconvex; variably developed median enlarged costa; spines orthomorph perpendicular; juveniles spines asymmetrically arranged, then symmetrical in adults, two spines closest from umbo always lacking on one side (commonly the left one, Fig. 243); inner socket ridges, dorsal septum and anderidia well developed, fusing posteriorly and supporting cardinal process; median wall of sockets overhung by two horizontal, platelike expansions. *Lower Devonian (upper Lochkovian–lower Emsian):* Germany, France, Spain, Morocco.——FIG. 242,*1a–d.* **C. tenuicostatus* (OEHLERT), Pragian, Armorican Massif ; *a,* ventral valve; *b,* articulated shell in dorsal view; *c,*

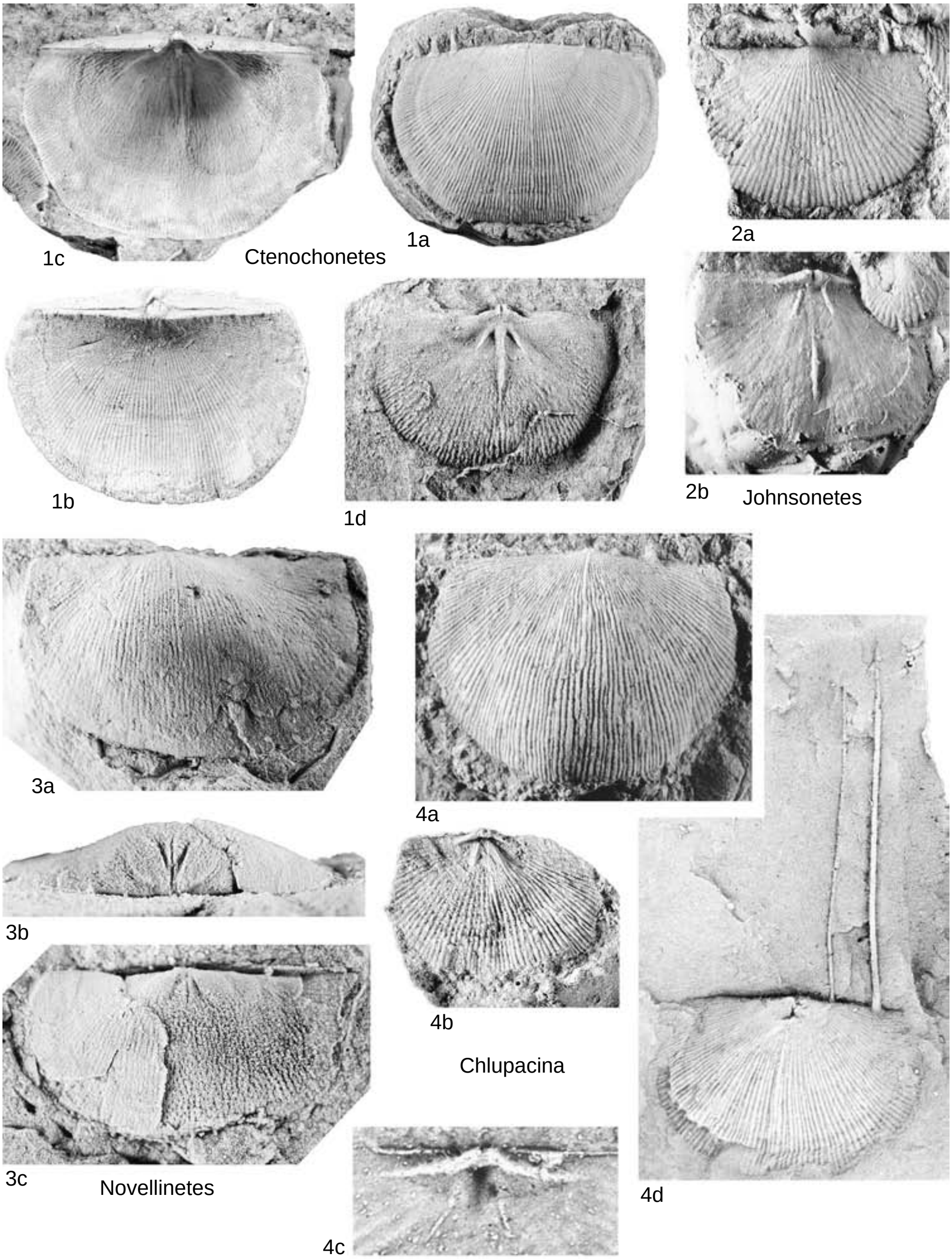


FIG. 242. Strophochonetidae (p. 371–376).

ventral valve interior; *d,* dorsal valve interior, ×2 (Racheboeuf, 1976).

Dawsonelloides BOUCOT & HARPER, 1968, p. 165 [**Chonetes canadensis* BILLINGS, 1874, p. 17; OD]. Shell medium to large, almost plano- to gently concavoconvex; surface finely costellate with narrow median enlarged costa; ventral interarea apsacline; dorsal interarea anacline to hypercline; pseudodeltidium, chilidial plates; orthomorph high-angled to perpendicular spines; dorsal interior with long, prominent median septum supporting cardinal process; anderidia variably developed; long, narrow inner socket ridges parallel to hinge line; interior of ventral, or both valve interiors, with radial grooves.

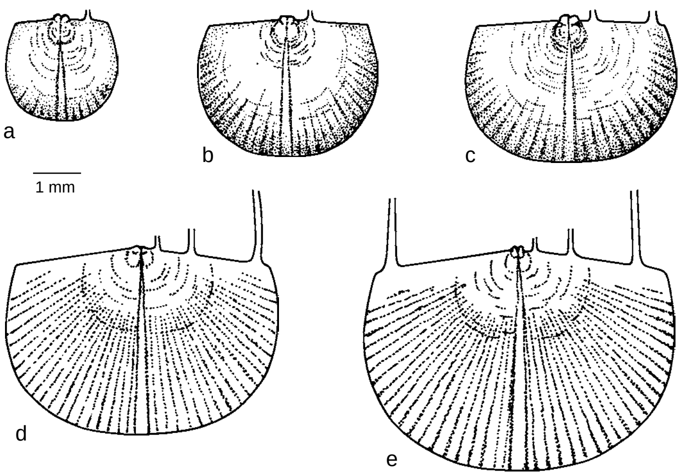


FIG. 243. Strophochonetidae (Strophochonetinae); *a–e,* ontogenetic development of spines on ventral valve of *Ctenochonetes tenuicostatus* (OEHLERT) (new).

upper Silurian (Ludlow)–Lower Devonian (Pragian): Maine, Quebec.——FIG. 244,*1a–c.* **D. canadensis* (BILLINGS), Pragian, Quebec; *a,* ventral valve, ×1.5 (Racheboeuf & Lespérance, 1995); *b,* ventral valve interior, ×1.5 (Boucot & Harper, 1968); *c,* dorsal valve interior, ×1.5 (Racheboeuf & Lespérance, 1995).

Johnsonetes RACHEBOEUF, 1987, p. 7 [**Chonetes filistriata* WALCOTT, 1884, p. 127; OD]. Shell small to medium, markedly concavoconvex, transverse in outline; when present, median enlarged costa developed on beak only; spines orthomorph vertical, asymmetrically arranged, more spines on one side; homologous spines appearing first on opposite side; long, thin dorsal median septum supporting stout, short, wide cardinal process; inner socket ridges low, rounded, anteriorly divergent at 130° to 140°; anderidia short, anteriorly divergent at 45° to 50°, posteriorly fused with cardinal process. *Lower Devonian (Pragian–Emsian):* Canadian Arctic Archipelago, Australia (New South Wales).——FIG. 242,*2a,b.* **J. filistriata* (WALCOTT), Pragian, Canadian Arctic Archipelago; *a,* ventral valve exterior, ×3; *b,* dorsal valve interior, ×4 (Racheboeuf, 1987).

Kentronetes RACHEBOEUF & HERRERA, 1994, p. 552 [**Chonetes rücki* ULRICH, 1893, p. 79; OD]. Shell medium; median enlarged costa commonly reduced to posterior part of ventral valve; spines cyrtomorph intraverse, symmetrically arranged; ventral valve interior with long *vascula media;* posterior muscle bounding ridges bending anteriorly; well-differentiated muscle scars with typically droplike adductors; dorsal valve interior with isolated anderidia; variably developed median septum not supporting cardinalia; short, curved inner socket ridges supporting lobes of deeply bilobed cardinal process. *Lower Devonian (Pragian–Emsian):* Bolivia, Argentina, South Africa.——FIG. 240,*4a–c.* **K. ruecki* (ULRICH), Pragian, Bolivia; ventral exterior, ventral interior, dorsal interior, ×2 (Racheboeuf & Branisa, 1985).

Leptochonetes HAVLÍČEK & RACHEBOEUF, 1979, p. 89 [**Chonetes tardus* BARRANDE, 1879, pl. 46; OD]. Shell small, strongly concavoconvex, very thin, maximum width at hinge line; long median enlarged costa; orthomorph oblique spines, low to medium angled, symmetrically arranged; interareas linear; ventral muscle field small, ill defined; dorsal interior without median septum; inner socket ridges relatively well developed, supporting small cardinal process; anderidia isolated on valve floor, anteriorly divergent at 40°. *Lower Devonian (Pragian–Emsian):* Bohemia.——FIG. 244,*2a,b.* **L. tardus* (BARRANDE), Pragian, Bohemia; *a,* ventral valve, ventral view, ×4; *b,* lateral view, ×5 (Havlíček & Racheboeuf, 1979).——FIG. 244,*2c. L. hostinensis* (BARRANDE), Emsian, Bohemia; dorsal valve internal mold, ×5 (Havlíček & Racheboeuf, 1979).

Novellinetes HAVLÍČEK & RACHEBOEUF, 1979, p. 87 [**Chonetes novellus* BARRANDE, 1879, pl. 46; OD]. Shell small to medium size, transversely elongate, subrectangular in outline; ornamentation very fine with weak median enlarged costa; spines orthomorph almost vertical; two spines on one side, one on other; ventral muscle field wide, well impressed with nonadjacent adductors; inner socket ridges long, narrow, almost parallel to hinge line; anderidia very small; no median septum; small cardinal process anteriorly bounded by deep, narrow cardinal process pit. *Lower Devonian (Emsian):* Bohemia.

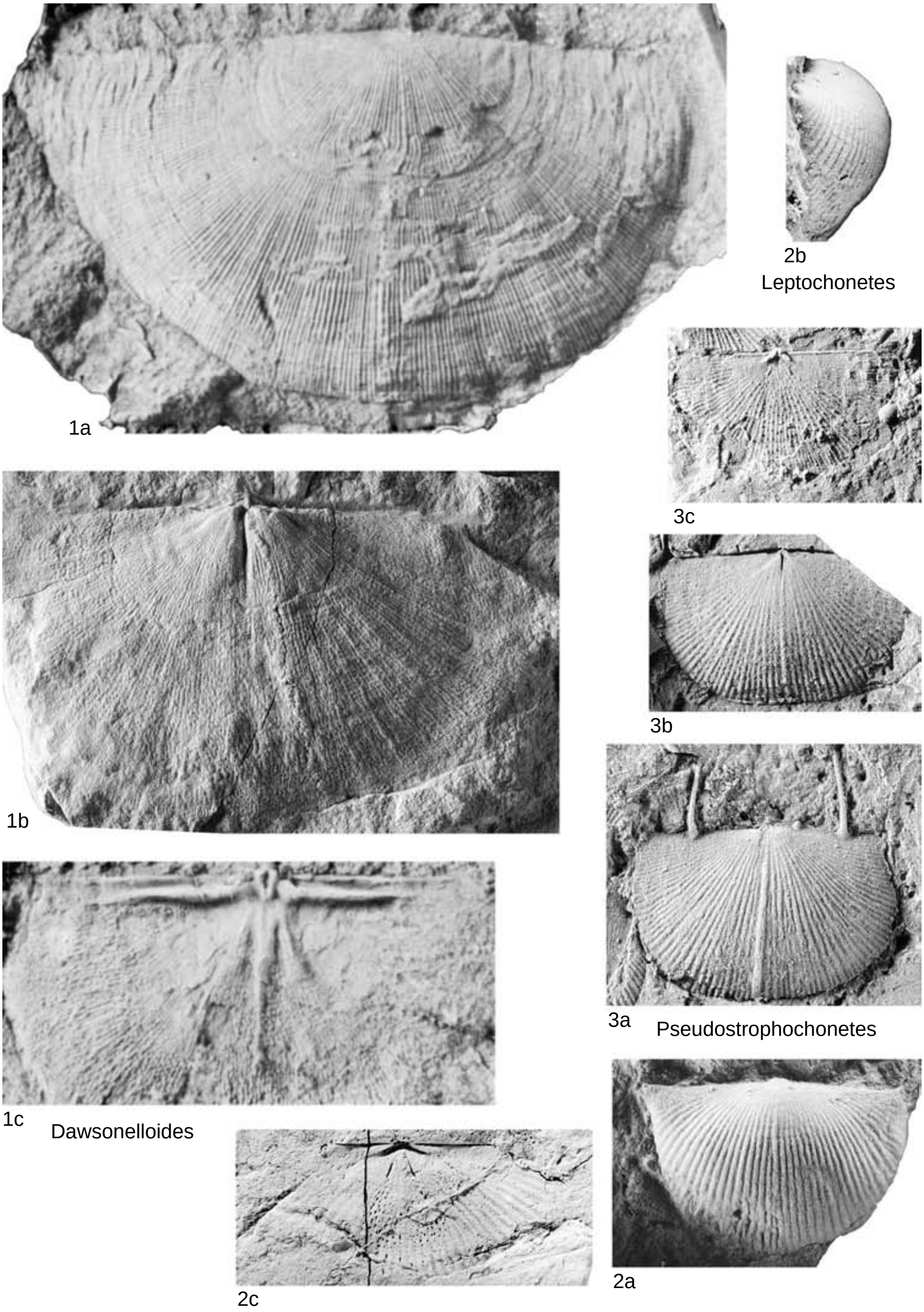


FIG. 244. Strophochonetidae (p. 373–376).

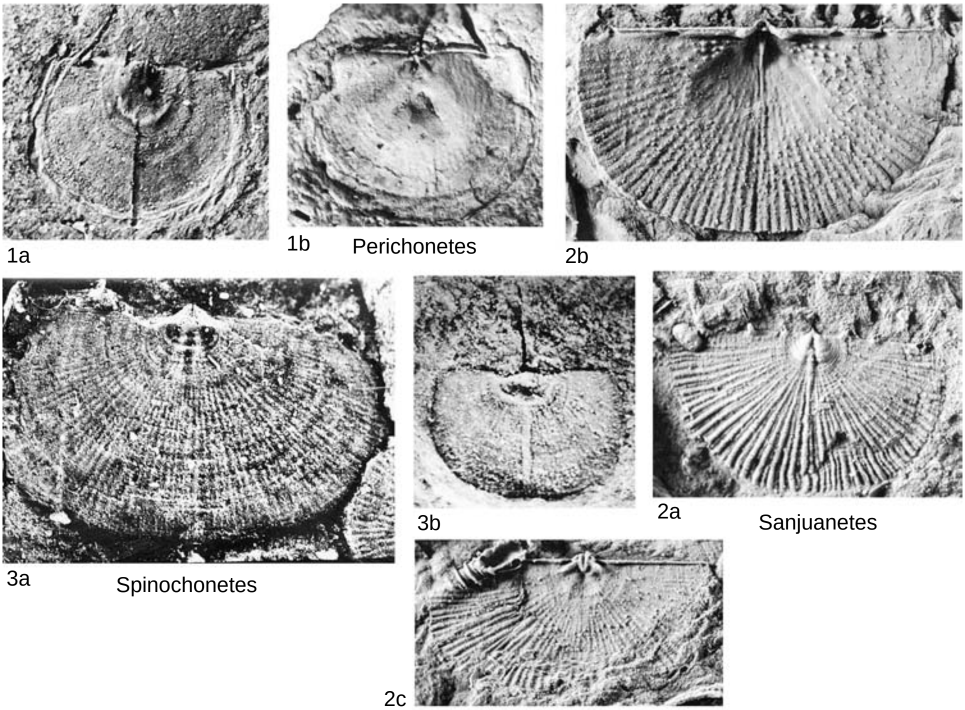


FIG. 245. Strophochonetidae (p. 376–377).

——FIG. 242,*3a–c*. **N. novellus* (BARRANDE), Emsian, Bohemia; *a,* ventral valve exterior; *b,c,* ventral valve interior, posterior and ventral views, ×5 (Havlícek & Racheboeuf, 1979).

Perichonetes XU, 1979, p. 372[380] [**P. mirabilis;* OD]. Very small, almost planoconvex thin shell, subquadrate to weakly transverse in outline; prominent median enlarged costa; fine radial costellae crossed by concentric growth lines; one or two, orthomorph vertical spines, usually on right side only; ventral interior with narrow ridge surrounding muscle field and anteriorly fusing with myophragm; dorsal interior without median septum; long, narrow socket ridges coalescing with small cardinal process. [*Perichonetes* differs from *Chlupacina* in the presence of a narrow ridge surrounding the ventral muscle only. This feature may be no more than an artefact due to the flattening of specimens, and possibly related to an ontogenetic discontinuity in the shell fabric. *Perichonetes* is retained as a distinct genus, awaiting further data about the ventral valve interior.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* southern China (Guangxi), northeastern Vietnam.——FIG. 245,*1a,b*. **P. mirabilis;* ventral valve external mold, dorsal valve external mold, ×10 (Xu, 1979).

Pseudostrophochonetes RACHEBOEUF, 1981b, p. 40 [**Chonetes mediocostalis* KOZŁOWSKI, 1929, p. 120; OD]. Externally similar to *Strophochonetes* except in spine morphology, arrangement; orthomorph vertical spines, two first juvenile spines lacking on one side of valve; internally close to *Strophochonetes* but with narrow elongate cardinal process pit, anteriorly divergent inner socket ridges. *Lower Devonian (Lochkovian):* Podolia.——FIG. 244,*3a–c*. **P. mediocostalis* (KOZŁOWSKI), Lochkovian, Podolia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×4 (Racheboeuf, 1981b).

Sanjuanetes RACHEBOEUF & HERRERA, 1994, p. 543 [**S. dalenzae;* OD]. Shell transverse, plano- to weakly concavoconvex; ventral interarea steeply apsacline to catacline; dorsal interarea catacline; pseudodeltidium, chilidium large, prominent; spines high angled, weakly cyrtomorph intraverse, symmetrically arranged; radial costae, costellae rounded, intercalating ventrally, bifurcating dorsally, crossed by fila; ventral valve interior with long pad parallel to hinge; anderidia not fused posteriorly with cardinal process; no median septum; deeply bilobed cardinal process supported by short inner socket ridges subparallel to hinge. *Silurian (Ludlow)–Devonian (Lochkovian):* Argentina, Bolivia.——FIG. 245,*2a–c*. **S. dalenzae,* Lochkovian, Bolivia; ventral valve exterior, ventral valve interior, dorsal valve interior, ×5 (Racheboeuf & Herrera, 1994).

Spinochonetes RONG, XU, & YANG, 1974, p. 203 [**S. notata;* OD][=*Shiqianella* XIAN in XIAN & JIANG, 1978, p. 272, obj.; *Megaspinochonetes* YANG &

Rong, 1982, p. 434, obj.]. Shell small, gently to strongly concavoconvex; only one orthomorph vertical spine originating from ventral umbo; median enlarged costa well developed; ventral, dorsal muscle field more or less impressed with variably developed surrounding ridges. *lower Silurian (upper Llandovery–lower Wenlock):* southern China (Sichuan, Guizhou, Hunan, Hubei).——Fig. 245,*3a.* **S. notata,* Telychian, central China; ventral valve internal mold, ×6 (Rong, Xu, & Yang, 1974).——Fig. 245,*3b. S. subrectangularis* (Yang & Rong), Telychian, central China; dorsal valve interior, ×5 (Rong, Xu, & Yang, 1974).

Subfamily PROTOCHONETINAE new subfamily

[Protochonetinae Racheboeuf, herein]

Small to medium, plano- to concavoconvex shell; pseudodeltidium, chilidium, or chilidial plates present; median enlarged costa usually absent or weakly developed; spines symmetrically arranged, orthomorph oblique, low to high angled; dorsal interior with median septum, weakly divergent anderidia; inner socket ridges varying from short, curved to long, narrow, parallel to hinge line. *Silurian (Wenlock)–Lower Devonian (Emsian).*

Protochonetes Muir-Wood, 1962, p. 50 [**P. ludloviensis;* OD]. Shell small to medium, transverse, almost plano- to concavoconvex; surface costellate; pseudodeltidium, chilidium present; long, variably developed dorsal median septum supporting cardinal process; short curved inner socket ridges; cardinal process internally deeply bilobed; short, free anderidia anteriorly divergent at 40° to 45°. *Silurian (Wenlock–Přídolí):* England, Sweden, Russia, Quebec, USA (New York).——Fig. 246,*6a,b. *P. ludloviensis,* Wenlock, England; ventral valve, dorsal valve interior, ×3 (Muir-Wood, 1962).

Eoplicanoplia Boucot & Harper, 1968, p. 168 [**Chonetes colliculus* Foerste, 1909c, p. 24; OD]. Shell small, strongly concavoconvex; surface costellate; ventral interarea orthocline with pseudodeltidium; dorsal interarea unknown; dorsal interior with long inner socket ridges slightly divergent from hinge line, well-developed anderidia, faint median septum. *upper Silurian (Ludlow–Přídolí):* northeastern USA.——Fig. 246,*2a–c. *E. collicula* (Foerste), Ludlow, North America; ventral valve, ventral, posterior views, ventral valve interior, ×4 (Boucot & Harper, 1968).

Hypselonetes Racheboeuf, 1981b, p. 43 [**Strophochonetes (Hypselonetes) vinearum;* OD]. Shell small; median enlarged costa often ill developed; inner socket ridges, median septum, anderidia posteriorly fused, supporting stout cardinal process. *upper Silurian (Ludlow–Přídolí):* France, Spain.——Fig. 246,*1a–c. *H. vinearum,* Přídolí, Spain; ventral valve exterior, ventral valve interior, dorsal valve exterior, ×4 (Racheboeuf, 1981b).——Fig. 246,*1d. H. arauzensis* Racheboeuf, Přídolí, Spain; dorsal valve interior, ×5 (Racheboeuf, 1981b).

Nabarredia Havlíček & Racheboeuf, 1979, p. 96 [**Chonetes minor* Barrande, 1879, pl. 46; OD]. Shell small, subrectangular in outline, with ventral valve longitudinally weakly depressed; radial ornamentation of rounded costellae; median enlarged costa restricted to posterior half of juvenile shells only; visceral disk surrounded by wide, low, rounded ridge; dorsal interior with short anderidia anteriorly divergent at 35° to 40°, reduced inner socket ridges posteriorly overhanging sockets, anteriorly divergent at 115° to 125°; no cardinal process pit; median septum lacking or reduced to low, narrow ridge. *upper Silurian (Přídolí)–Lower Devonian (Lochkovian):* Bohemia, China.——Fig. 246,*5. *N. minor* (Barrande), Lochkovian, Bohemia; partly exfoliated ventral valve, ×4.5 (Havlíček & Racheboeuf, 1979).

Quadrikentron Boucot & Gauri, 1966, p. 1023 [**Chonetes hudsonica camdenensis* Dunbar, 1920, p. 131; OD]. Shell small to medium, concavoconvex; ornamentation finely costellate; no median enlarged costa; ventral interior with subcircular muscle field posteriorly bounded by curved ridges; adductors well developed; *vascula media* wide, long; dorsal interior with stout, internally deeply bilobed cardinal process; median septum wide, low, commonly longitudinally grooved, sometimes extending anteriorly as high, narrow breviseptum; anderidia relatively small but well differentiated, anteriorly divergent at 55° to 70°; inner socket ridges variably developed, laterally widening, tapering, anteriorly divergent at 130° to 150°; no cardinal process pit but depressed area between cardinal process and median septum. *Lower Devonian (Pragian–Emsian):* USA (Maine, Tennessee, New York), Argentina, Bolivia.——Fig. 246,*4a,b. *Q. camdenensis* (Dunbar), Emsian, North America; ventral valve, dorsal valve interior, ×4 (Boucot & Gauri, 1966).

Shagamella Boucot & Harper, 1968, p. 167 [**S. ludloviensis;* OD]. Shell very small, moderately to markedly concavoconvex; surface looking smooth but generally faintly costellate at periphery of shell, with variably developed median enlarged costa; dorsal interior with strong anderidia, cardinal process pit; breviseptum rarely developed; no accessory septa. *Silurian (Wenlock–Ludlow):* Great Britain, Bohemia.——Fig. 246,*3a–c. *S. ludloviensis,* Ludlow, Great Britain; ventral valve exterior, ventral valve interior, dorsal valve interior, ×5 (Boucot & Harper, 1968).

Subfamily PARACHONETINAE Johnson, 1970

[Parachonetinae Johnson, 1970a, p. 135]

Shell medium to large, robust; radial ornamentation costate, often sinuous, irregular; posterolateral costae originating along

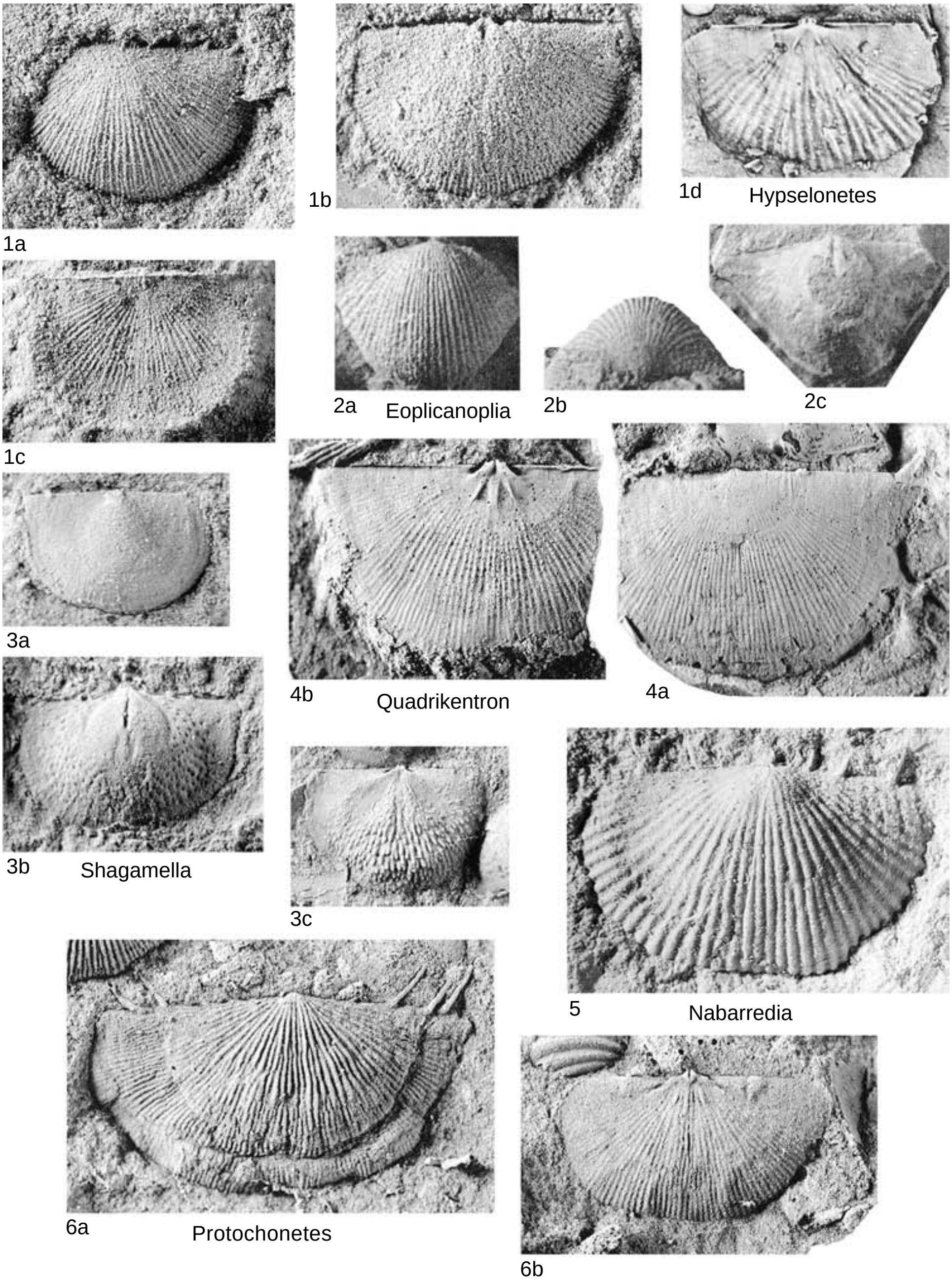


FIG. 246. Strophochonetidae (p. 377).

posterior margin of valves; orthomorph spines high-angled to perpendicular; large, deep dorsal cardinal process pit; anderidia long, slightly divergent anteriorly; variably developed median septum; no accessory septa. *Silurian (Ludlow)–Middle Devonian.*

Parachonetes JOHNSON, 1966b, p. 365 [**Chonetes macrostriata* WALCOTT, 1884, p. 126; OD]. Shell

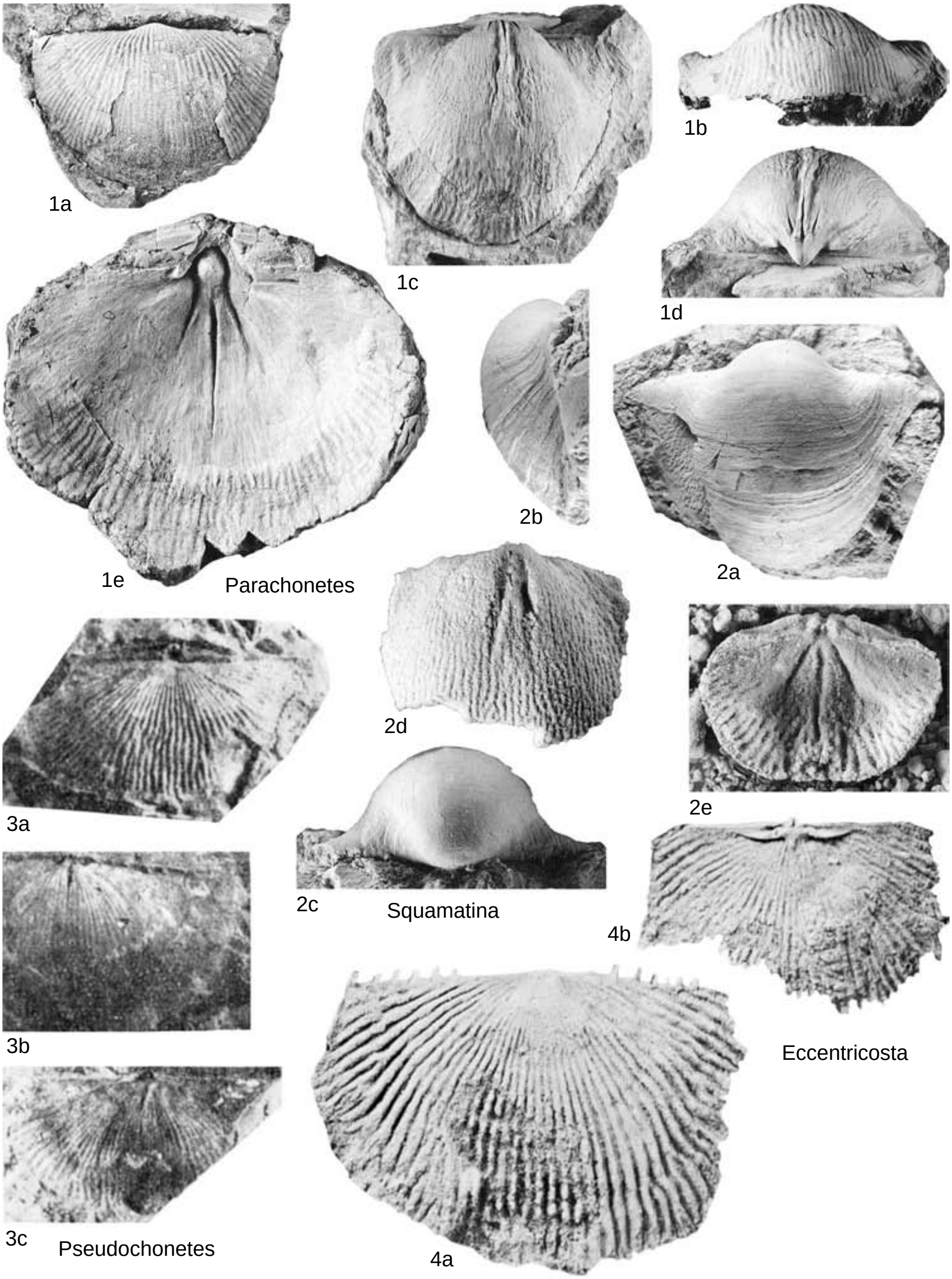


FIG. 247. Strophochonetidae (p. 378–380).

medium to large, strongly concavoconvex; radial rounded, irregular costae; spines orthomorph, high angled to perpendicular, symmetrically arranged; dorsal valve interior with wide, more or less deep cardinal process pit between bases of two lobes of cardinal process; long anderidia anteriorly divergent at 35°, posteriorly fused with cardinal process lobes; well-developed median septum; low, ill-defined inner socket ridges anteriorly divergent at 100° to 130°. *Lower Devonian (Pragian–Emsian):* USA

(Nevada, Alaska), Canadian Arctic Archipelago, Australia (New South Wales), ?France, Bohemia, Russian platform, northeastern China, Vietnam.——FIG. 247,*1a–e*. **P. macrostriatus* (WALCOTT), Emsian, Nevada; *a,b,* ventral valve exterior, ventral, anterior views, ×1; *c,d,* ventral valve interior, ventral, posterior views, ×1.5; *e,* dorsal valve mold, ×2 (Johnson, 1966b).

Eccentricosta BERDAN, 1963, p. 254 [**Chonetes jerseyensis* WELLER, 1900, p. 8; OD]. Shell medium, transverse, moderately concavoconvex; spines orthomorph perpendicular, symmetrically arranged; radial ornamentation of costae, posterolateral costae originating along posterior margin; ventral interior with short, wide hinge teeth; stout, short median septum; dorsal interior with small internally bilobed cardinal process; inner socket ridges narrow, rounded, weakly curved posteriorly, extending along hinge line; median septum low, short; anderidia long, low, narrow, anteriorly divergent at 35° to 40°. *Silurian (Ludlow–Přídolí):* North America.——FIG. 247,*4a,b*. * *E. jerseyensis* (WELLER), Přídolí, North America; ventral valve, dorsal valve interior, ×3 (Berdan, 1972).

Pseudochonetes SU, 1976, p. 183 [**P. flexoplicatus;* OD]. Medium to large, moderately concavoconvex; radial rounded, sinuous, irregular costellae; ventral valve interior with short myophragm; muscle field large, well impressed, radially striate; dorsal valve interior without cardinal process pit; median septum posteriorly low, wide, narrowing, tapering anteriorly; low, narrow, ill-defined inner socket ridges anteriorly divergent at about 150°. *?Lower Devonian, Middle Devonian:* Inner Mongolia.——FIG. 247,*3a–c*. **P. flexoplicatus; a,* dorsal side of an articulated shell, ×2; *b,* ventral valve internal mold, ×2; *c,* dorsal valve internal mold, ×2 (Su, 1976).

Squamatina HAVLÍČEK & RACHEBOEUF, 1979, p. 109 [**Chonetes squamatula* BARRANDE, 1848, p. 249; OD]. Small, thick, strongly concavoconvex shell with depressed flanks, well-differentiated ears; maximum width at hinge line; ventral interarea apsacline, flat; dorsal interarea weakly hypercline; pseudodeltidium, chilidium not observed; shell surface lamellose, without radial ornamentation; symmetrically arranged orthomorph oblique, high-angled spines; ventral muscle field posteriorly situated; very short myophragm; pair of strong, long, poorly divergent vascular trunks; long, wide dorsal median septum supporting small bilobed cardinal process; very long, stout anderidia anteriorly divergent at 55°; low, long inner socket ridges. [Although smooth, *Squamatina* is herein questionably placed within the Parachonetinae due to its inner features: the morphology of ventral muscle scars and *vascula media;* and the stout dorsal median septum and anderidia]. *Lower Devonian (Pragian):* Czech Republic.——FIG. 247,*2a–e*. **S. squamatula* (BARRANDE), Pragian, *Nowakia acuaria* Zone, Bohemia; *a–c,* ventral valve, ventral, lateral, posterior views; *d,* ventral valve interior; *e,* dorsal valve interior, ×3 (Havlíček & Racheboeuf, 1979).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

[Chonostrophiidae MUIR-WOOD, 1962, p. 95]

Shell small to large, resupinate; ventral valve concave to almost flat; dorsal valve moderately convex; outline moderately to strongly transverse, subsemicircular to suboval; ventral interarea flat, anacline to strongly catacline with variably developed, but present, wide pseudodeltidium; dorsal interarea flat, strongly anacline, with chilidium or chilidial plates; numerous spines orthomorph perpendicular or oblique, high-angled, symmetrically arranged; radial ornamentation costellate or parvicostellate with very fine concentric fila; ventral interior with stout oblique hinge teeth; muscle field relatively large, variably impressed in valve floor, divided by short to long myophragm; dorsal interior with faint to long, well-differentiated anderidia; median septum absent or strongly developed; inner socket ridges straight, parallel to hinge line, or short, bending posteriorly, or short, anteriorly divergent; cardinal process wide, short, not extending beyond posterior margin, always elevated above valve floor; cardinal process internally bilobed but lobes adjacent medianly; myophore with two triangular, wide, longitudinally deeply grooved lobes directed posteriorly. *Lower Devonian (Lochkovian)–Lower Carboniferous (Tournaisian).*

Chonostrophia HALL & CLARKE, 1892, p. 310 [**Chonetes reversa* WHITFIELD, 1882, p. 213; OD]. Shell small to medium; radial ornamentation parvicostellate, with low, narrow costellae; spines orthomorph oblique, symmetrically arranged; chilidium present; no dorsal median septum; anderidia ill defined; inner socket ridges short, bending posteriorly, surrounding sockets. *upper Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* North America (Appalachian Mountains), South America (Bolivia, Argentina).——FIG. 248,*2a*. **C. reversa* (WHITFIELD), ventral valve exterior, original of HALL & CLARKE, 1892, NYSM 1241, ×10 (Racheboeuf & Lespérance, 1995).——FIG. 248,*2b–d*. *C. dawsoni* (BILLINGS), Emsian, Québec; *b,* dorsal valve interior, ×3; *c,* ventral valve exterior, ×2; *d,* ventral valve interior, ×2 (Racheboeuf & Lespérance, 1995).

Chonostrophiella BOUCOT & AMSDEN, 1964, p. 881 [**Chonetes complanata* HALL, 1857, p. 56; OD].

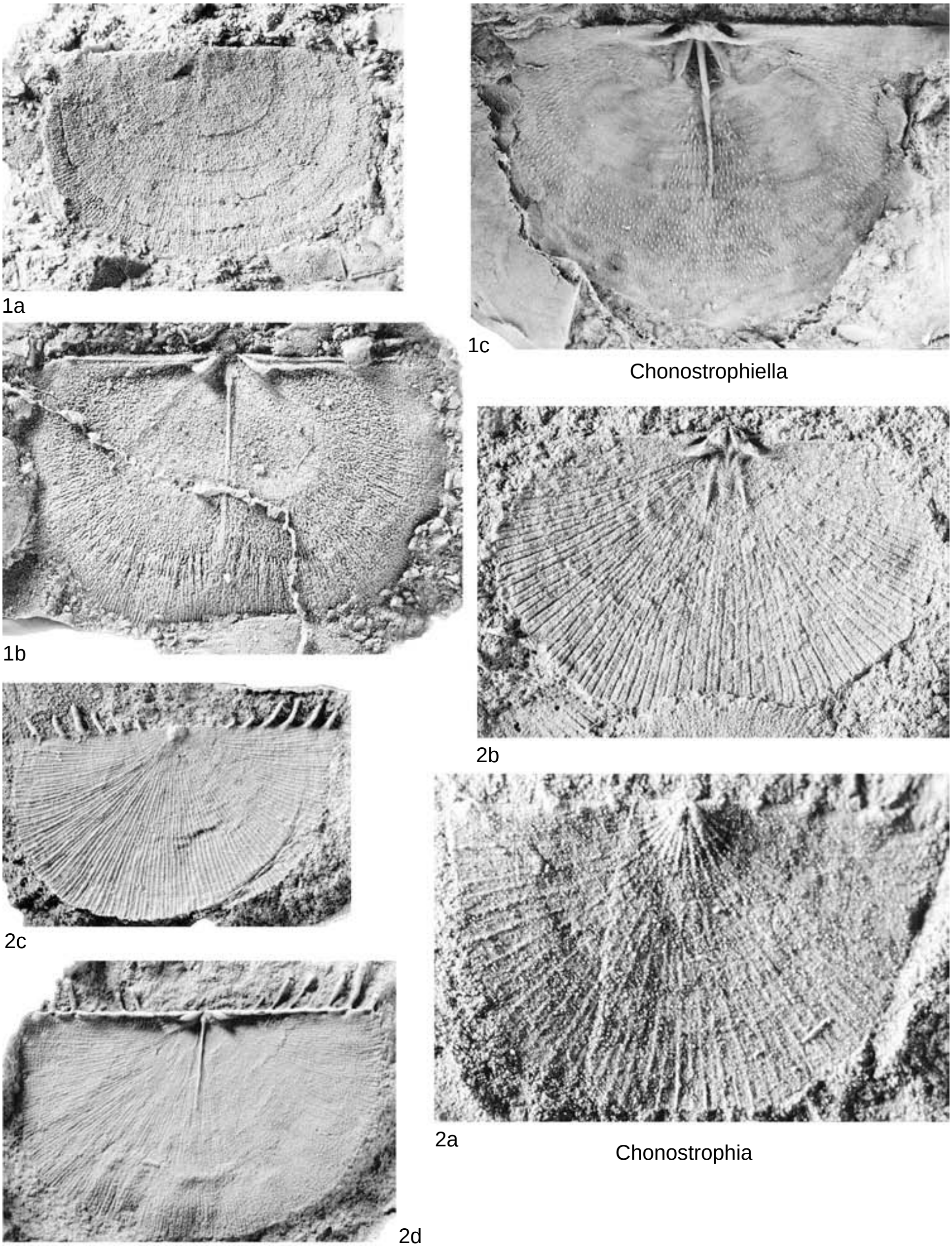


FIG. 248. Chonostrophiidae (p. 380–382).

Shell small to large; radial ornamentation finely costellate; spines orthomorph perpendicular, symmetrically arranged; dorsal interior with long median septum; long elevated anderidia anteriorly divergent at 50°; anterior margin of cardinal process, anterior edge of inner socket ridges almost vertical above valve floor; inner socket ridges short, narrow, rounded. *Lower Devonian (upper Lochkovian–lower Emsian):* North America (Appalachian Mountains, Canadian Arctic Archipelago), northeastern

China.——FIG. 248,*1a,b.* **C. complanata* (HALL), originals of HALL; ventral valve exterior, ventral valve interior, ×2 (Boucot & Amsden, 1964).——FIG. 248,*1c. C. briceae* RACHEBOEUF, Emsian, Canadian Arctic; dorsal valve interior, ×2 (Racheboeuf, 1987).

Tulcumbella CAMPBELL in CAMPBELL & ENGEL, 1963, p. 68 [**T. microstriata;* OD]. Shell small to medium, slightly resupinate; similar to *Chonostrophiella,* but with very short ventral median septum; dorsal interior with short, narrow median septum; inner socket ridges long, straight, parallel to hinge line; anderidia unknown. *Lower Carboniferous (Tournaisian):* Australia (New South Wales). Material not suitable for illustration.

Family ANOPLIIDAE Muir-Wood, 1962

[*nom. transl.* BOUCOT & HARPER, 1968, p. 167, *ex* Anopliinae MUIR-WOOD, 1962, p. 32]

Shell very small to small, commonly as long as wide, usually strongly concavoconvex; shell surface smooth, capillate or costellate; pseudodeltidium and chilidium present; ventral area commonly concave; spines lacking or present, low-angled to vertical, always orthomorph, symmetrically or asymmetrically arranged; ventral muscle field usually deeply impressed in valve floor; hinge line denticulate in one genus; dorsal interior with pair of generally high-angled anderidia; one or several pairs of bladelike accessory septa sometimes replaced by sinuous irregular crests, or by stout, radially arranged, more or less fused endospines; median septum usually less well developed than accessory septa, lacking or replaced by breviseptum; cardinal process pit commonly present. [The classification adopted herein is still classical, purely phenetic, and without any phylogenetical implication. Due to their small size (among other characters), most genera included in this family seem likely to be no more than paedomorphic forms evolved from the family Chonetidae during the Devonian or from the family Rugosochonetidae during the Carboniferous, for example. A complete and detailed revision of the family Anopliidae is urgently needed.] *Devonian (Lochkovian)–Permian (Tatarian).*

Subfamily ANOPLIINAE Muir-Wood, 1962

[Anopliinae MUIR-WOOD, 1962, p. 32]

Small, strongly concavoconvex anopliids possessing smooth external shell. *Devonian (Lochkovian)–Permian (Tatarian).*

Anoplia HALL & CLARKE, 1892, p. 309 [**Leptaena nucleata* HALL, 1857, p. 47; OD]. Shell very small, strongly concavoconvex; outline subtriangular to elongate; profile strongly arched transversely; spines not developed; spine apertures symmetrically arranged on posterior margin of ventral valve; dorsal interior with one to four pairs of variably developed accessory septa; median septum supporting cardinal process in oldest forms; cardinal process pit present in younger forms as in juveniles; in any case, median septum short, not extending beyond half valve length; anderidia relatively small, anteriorly divergent at 70°. *Lower Devonian (Lochkovian–upper Emsian):* USA, Europe.——FIG. 249,*1a–d.* **A. nucleata* (HALL), Camden Chert, USA; ventral valve exterior, dorsal valve exterior, ventral valve interior, dorsal valve interior, ×3.5 (Hall & Clarke, 1892).

Anopliella RACHEBOEUF, 1998, p. 52, *nom. nov. pro Tuberella* VOGEL, XU, & LANGENSTRASSEN, 1989, p. 36, *non Tuberella* LEE, 1987, echinoconchoid productid [**Tuberella tangxiangensis* VOGEL, XU, & LANGENSTRASSEN, 1989, p. 36; OD]. Shell very small, semicircular, and markedly concavoconvex; surface smooth; spines unknown; ventral interior without dental plates and septum; dorsal interior without median and lateral septa, but with numerous elongate, fusing tubercles in the midportion of the valve. *Lower Devonian (upper Emsian):* southern China.——FIG. 250,*1a,b.* **A. tangxiangensis* (VOGEL, XU, & LANGENSTRASSEN), upper Emsian, southern China; dorsal valve interiors, ×15 (Vogel, Xu, & Langenstrassen, 1989).

Anopliopsis GIRTY, 1938a, p. 281 [**Chonetina subcarinata* GIRTY, 1926, p. 27; OD]. Shell very small, subtriangular in outline with usually well-developed ears; profile deeply concavoconvex longitudinally; ventral valve with narrow, shallow sulcus; surface smooth with few prominent growth lines; spines orthomorph oblique, high-angled, symmetrically arranged; ventral interior with short median septum continued anteriorly by row of pustules that may coalesce; dorsal interior without median septum; several pairs of variably developed accessory septa; cardinal process small, anteriorly bounded by relatively large cardinal process pit; anderidia small. *Carboniferous (Viséan–Namurian):* USA.——FIG. 249,*2a,b.* **A. subcarinata* (GIRTY), lower Viséan, USA; dorsal valve interior, ventral valve internal mold, ×5 (Girty, 1938a).

Chonetina KROTOW, 1888, p. 500, *nom. nov. pro Chonetella* KROTOW, 1885, p. 274, 309, *non*

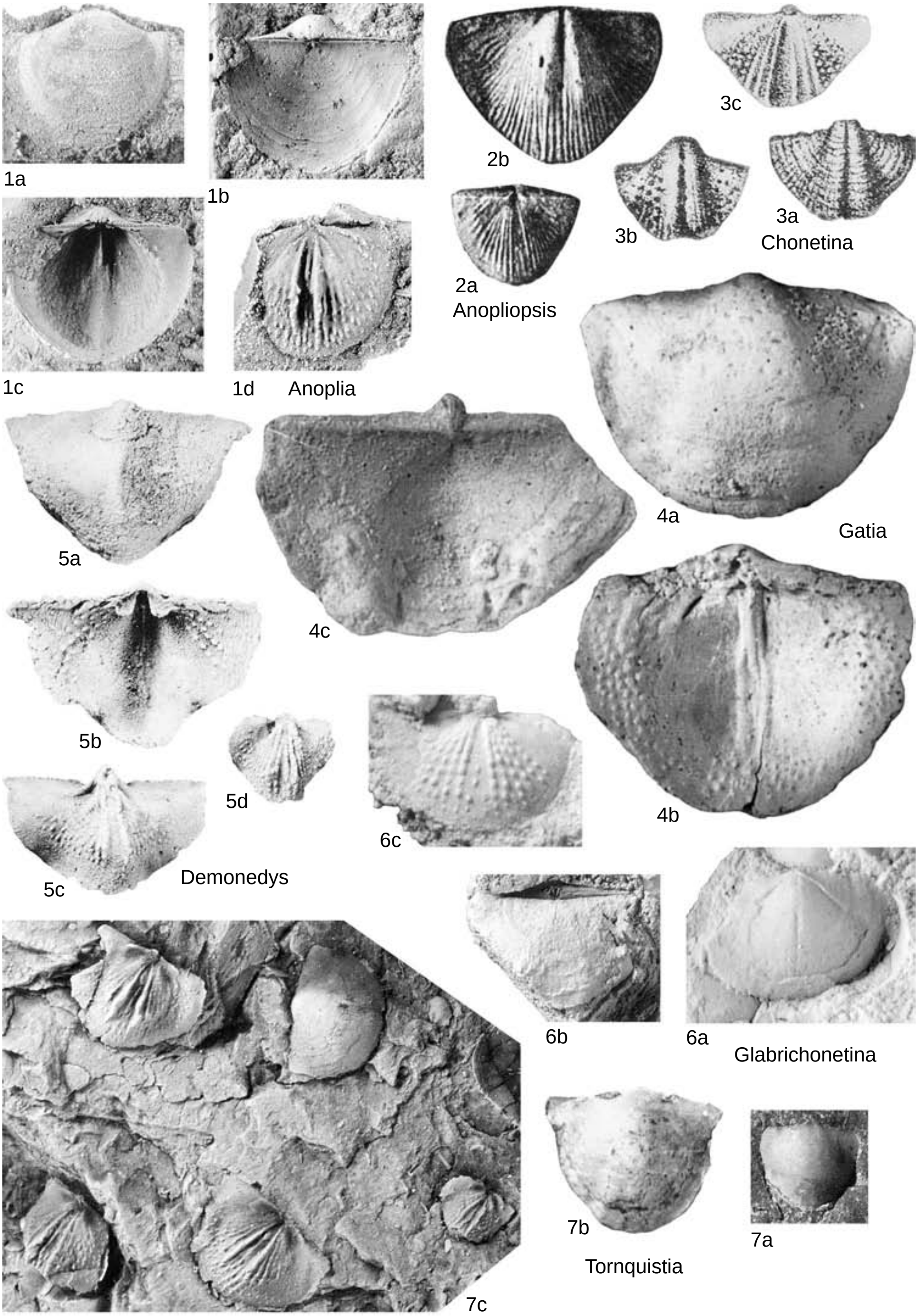
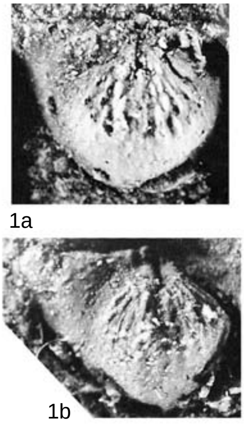
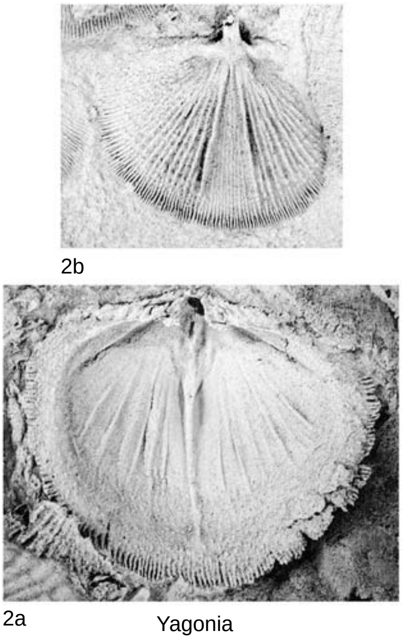


FIG. 249. Anopliidae (p. 382–385).



Anopliella



Yagonia

FIG. 250. Anopliidae (p. 382–385).

WAAGEN, 1884, p. 613, obj. [**Chonetella artiensis* KROTOW, 1885, p. 275; OD]. Shell small, highly concavoconvex with dorsal median fold, deep ventral sulcus; shell smooth with growth lines; spines developed; dorsal valve interior with several platelike septa formed from fused papillae; no median septum. *Upper Carboniferous (Stephanian)–Permian (Kazanian):* Europe, Asia.——FIG. 249,*3a–c.* **C. artiensis* (KROTOW), Russia, Urals; ventral valve, ventral valve internal mold, dorsal valve interior, ×3 (Krotow, 1885).

Demonedys GRANT, 1976, p. 66 [**D. fastigiata;* OD]. Shell small, typically transversely subtrigonal in outline; shell strongly concavoconvex, almost trilobate with large median ventral fold, corresponding dorsal sulcus; surface smooth, pseudocapillate, with few lamellose concentric growth lines; spines orthomorph oblique, symmetrically arranged; ventral interior with short median septum; dorsal interior medianly folded with short anderidia, pair of long divergent accessory septa; cardinal process wide, posteriorly elevated above valve floor, supported by straight, narrow inner socket ridges anteriorly divergent at 100° to 105°, deep anterior pit. *Permian (Artinskian–Tatarian):* Thailand, Nepal, Western Australia.——FIG. 249,*5a–d.* **D. fastigiata,* Permian, Thailand; ventral valve exterior, interior, dorsal valve interior, juvenile dorsal interior, ×4 (Grant, 1976).

Gatia ARCHBOLD, 1993, p. 4 [**G. superba;* OD]. Large, smooth anopliid-shaped shells, widest at hinge; ventral valve interior with short myophragm posteriorly, parallel vascular trunks extending to valve anterior on either side of myophragm; dorsal valve interior with short anderidia extending to form rounded, club-shaped brachiophores; short median septum arising anterior to shallow cardinal process pit, separated from short median septum by narrow depressed region; short accessory septa (or ridges) developed anterior to median septum, apparently by fusion of row of papillae. *Permian (Artinskian):* Western Australia.——FIG. 249,*4a–c.* * *G. superba,* Artinskian, Carnarvon basin, Western Australia; ventral valve exterior, interior, dorsal valve interior, ×3.5 (Archbold, 1993).

Glabrichonetina WATERHOUSE, 1978, p. 130 [**G. kuwaensis;* OD]. Shell small, moderately concavoconvex, with almost flat dorsal valve, ventral valve slightly swollen medianly; no fold nor sulcus; ventral interarea short, concave; dorsal interarea almost linear; no radial ornamentation; surface covered with very fine concentric lamellae; about ten pairs of spines orthomorph oblique, symmetrically arranged; ventral interior with low, long median septum; dorsal interior without median septum, accessory septa, but with several radial, anteriorly divergent rows of pustules. *Upper Permian (Tatarian):* northwestern Nepal.——FIG. 249,*6a–c.* **G. kuwaensis,* Tatarian, Nepal; *a,* partly exfoliated ventral valve; *b,* dorsal exterior of articulated shell; *c,* dorsal valve interior, ×6 (Waterhouse, 1978).

Tornquistia PAECKELMANN, 1930, p. 227 [**Leptaena (Chonetes) polita* M'COY, 1855, p. 427; OD] [=*Paeckelmannia* LICHAREW, 1934b, p. 509, obj.]. Very small to small, highly concavoconvex medianly; greatest width along hinge line with well-differentiated ears; shell surface smooth, pseudocapillate when decorticated; few growth lines; spines orthomorph oblique, symmetrically arranged; ventral interior with long, narrow septum; dorsal interior with short, ill-defined anderidia anteriorly divergent at 40° to 50°; pair of long, narrow accessory septa anteriorly divergent at 25° to 35°; median septum absent or reduced to short anteriorly placed median ridge; inner socket ridges short, straight, narrow; cardinal process small, anteriorly bounded by cardinal process pit. *Upper Devonian–Permian:* Great Britain, Ireland, France, Spain, Germany, Thailand.——FIG. 249,*7a–c.* **T. polita* (M'COY), Lower Carboniferous, Scotland; *a,b,* ventral valves showing spine row, ×4; *c,* slab with four dorsal valve interiors, ventral valve cast, ×4 (Paeckelmann, 1930).

Yagonia ROBERTS, HUNT, & THOMPSON, 1976, p. 210 [**Y. gibberensis;* OD]. Shell medium, moderately concavoconvex; no radial ornamentation; surface pseudocapillate when decorticated; narrow concentric growth lines; ventral interarea apsacline; dorsal interarea linear; pseudodeltidium, chilidium small; spines unknown; ventral interior with long median septum, flabellate diductors; dorsal interior with strong median septum supporting elongate cardinal process in largest shell, no pit; small anderidia anteriorly divergent at 60°; usually two pairs of long, spinose accessory septa and variably developed additional septa formed by fused endospines. *Carboniferous (upper Viséan–Westphalian):* eastern Australia.——FIG. 250,*2a,b.* **Y. gibberensis,* Viséan, eastern Australia; ventral valve interior, dorsal valve interior, ×2 (Roberts, Hunt, & Thompson, 1976).

Subfamily CAENANOPLIINAE Archbold, 1980

[Caenanopliinae ARCHBOLD, 1980a, p. 189]

Small to medium-sized, concavoconvex anopliids with costate or costellate exterior. *Devonian (Lochkovian)–Permian (Kungurian).*

Caenanoplia CARTER, 1968, p. 1143 [**C. burlingtonensis;* OD]. Shell small, strongly concavoconvex, subsemicircular to subtriangular in outline; ears well differentiated; spines orthomorph oblique, high-angled, symmetrically arranged; ventral interarea apsacline, flat to curved, with small pseudodeltidium; dorsal interarea hypercline, with chilidium; radial ornamentation of low rounded costellae crossed by lamellose growth lines; long, narrow ventral median septum; dorsal interior with large cardinal process pit, no median septum nor accessory septa; anderidia long, narrow, anteriorly divergent at 80°; surface covered with sparse endospines arranged in radial rows. *Lower Carboniferous (Tournaisian–Namurian):* North America.——FIG. 251,*1a–d.* **C. burlingtonensis,* Burlington Limestone, Missouri; *a–c,* articulated shell, ventral, lateral, dorsal views; *d,* dorsal valve interior, ×4 (Carter, 1968).

Arcuaminetes BIZZARRO, 1995, p. 158 [**Chonetes scitula* HALL, 1857, p. 107; OD]. Shell small, strongly concavoconvex, elliptical in outline with maximum width toward midline; radial ornamentation costellate; spines cyrtomorph intraversed, symmetrically arranged; dorsal valve interior with low median septum supporting low cardinal process; accessory septa low angled; anderidia well developed, high angled at 70°. *Middle Devonian (upper Eifelian–Givetian):* USA, France, Spain, Niger, Mauritania.——FIG. 251,*3a,b.* **A. scitulus* (HALL), Hamilton Group, Givetian, USA; ventral valve exterior, dorsal valve interior, ×6.6 (Bizzarro, 1995).

Caplinoplia HAVLÍČEK & RACHEBOEUF, 1979, p. 102 [**C. pragensis;* OD]. Shell very small, strongly concavoconvex; spines orthomorph perpendicular, symmetrically arranged; dorsal interior with cardinal process pit, well-developed anderidia anteriorly divergent at 60° to 70°; two pairs of strong, bladelike accessory septa; external septa shorter, lengthening anderidia; well-developed breviseptum originating at midlength of valve. *Lower Devonian (Pragian–Emsian):* France, Spain, Bohemia, Russia, Canadian Arctic Archipelago.——FIG. 251,*2a–c.* **C. pragensis,* Koneprusy Limestone, Pragian, Bohemia; *a,* ventral valve exterior; *b,* ventral valve internal mold; *c,* dorsal valve internal mold, ×10 (Havlíček & Racheboeuf, 1979).

Celtanoplia RACHEBOEUF, 1981b, p. 95 [**Chonetes boblayei* DE VERNEUIL, 1850, p. 783; OD]. Shell very small, strongly concavoconvex; radial costellae tending to increase symmetrically both by bifurcation and intercalation; spines orthomorph oblique, symmetrically arranged, middle to high angled; cardinal process pit present in juveniles; short median septum supporting cardinal process in adults; anderidia relatively small but stout, anteriorly divergent at 80°; two or three pairs of well-developed, bladelike accessory septa. *Lower Devonian (Pragian–lower Emsian):* Rhenish Slate Mountains, Armorican Massif, Spain, Morocco, Algeria.——FIG. 251,*4a–e.* **C. boblayei* DE VERNEUIL, Saint Céneré Formation, Pragian, Armorican Massif; *a,* ventral valve exterior; *b,* dorsal side of articulated shell; *c,* ventral valve internal mold; *d,* ventral valve interior; *e,* dorsal valve interior, ×4 (Racheboeuf, 1981b).

Corbicularia LJASCHENKO, 1973, p. 29 [**Chonetes menneri* LJASCHENKO, 1958b, p. 119; OD]. Shell very small, ornamented with small fine costae; structure of shell with strongly concentrically wrinkled layers; spines symmetrically arranged, almost perpendicular; dorsal valve interior with well-developed cardinal process pit; median septum, accessory septa absent or reduced to low, almost indistinct structures. *Upper Devonian:* northern Europe, Russian Platform. Material not suitable for illustration (Ljaschenko, 1973).

Costachonetes WATERHOUSE, 1975, p. 2 [**Chonetes uralica* MÖLLER var. *pygmaea* VON LOCZY, 1897, p. 64; OD]. Caenanopliids with swollen ventral valve with narrow ventral sulcus at least posteriorly; dorsal interior with thin median septum, small anderidia. *Upper Carboniferous (Kasimovian)–Lower Permian (Sakmarian):* Thailand. Material not suitable for illustration (Waterhouse, 1975).

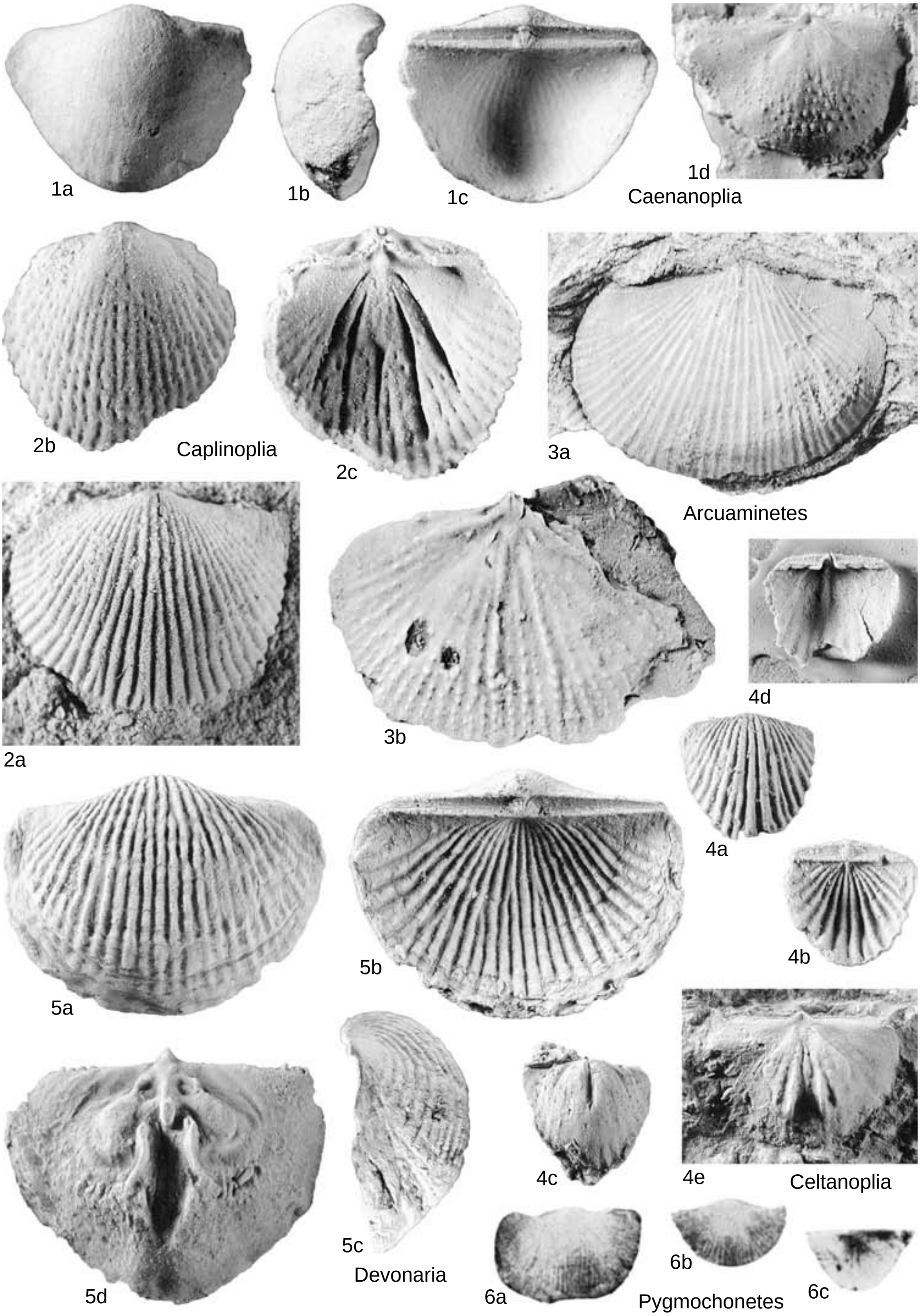


FIG. 251. Anopliidae (p. 385–387).

Costachonetina Waterhouse, 1981, p. 63 [**C. krotowi;* OD][=*Chonetina* sp. Grant, 1976, p. 65]. Small subtriangular shell with arched ventral valve bearing sulcus; dorsal valve with corresponding fold; ears large; shell surface ornamented by strong costae; no spines developed but few spine apertures on posterior margin of ventral valve; dorsal median septum short, anteriorly elevated, with 2 to 4 pairs of spinose accessory septa. [Afanas'eva (1988, p. 89) regarded *Costachonetina* as a junior synonym of *Chonetinella* Ramsbottom, 1952. The relatively strong radial ribbing, the development of the short, anteriorly elevated dorsal median septum, as well as the development of 2 to 4 spinose accessory septa, all characters lacking in *Chonetinella,* preclude such a synonymy.] *Lower Permian (Artinskian–Kungurian):* southern Thailand. Material not suitable for illustration (Waterhouse, 1981).

Devonaria Biernat, 1966, p. 77 [**Chonetes zeuschneri* Sobolev, 1909, p. 444; OD][=*Plicodevonaria* Boucot & Harper, 1968, p. 162, obj.]. Shell small, rounded or weakly elongate in outline, usually strongly concavoconvex; surface costellate; no spines developed but canal apertures alternating on each side of umbo; hinge denticulate; cardinal process internally ventrally gibbous; short median septum supporting cardinal process; anderidia posteriorly fusing with septum, anteriorly divergent at 80°; one pair of long, narrow, bladelike accessory septa usually longitudinally curved medianly. *Middle Devonian (Eifelian–Givetian):* Poland, Nakichevan, Rhenish Slate Mountains, Armorican Massif, northern Africa (Tindouf syncline).——Fig. 251,*5a–d.* **D. zeuschneri* (Sobolev), Skaly beds, Givetian, Poland; ventral valve exterior, dorsal exterior, lateral profile, dorsal valve interior, ×3 (Racheboeuf, new).

Globosochonetes Brunton, 1968, p. 48 [**G. parseptus;* OD]. Shell very small, strongly concavoconvex; strong radial ornamentation; ventral interarea orthocline with small pseudodeltidium; dorsal interarea almost linear; spines cyrtomorph bending medianly, disymmetrically arranged with two more spines on left side; ventral interior with short laterally elongated hinge teeth parallel to hinge line; dorsal interior showing short lobate median breviseptum in gerontic shells; long, narrow inner socket ridges supporting small cardinal process with small pit; anderidia reduced, anteriorly divergent at about 90°; accessory septa long, bladelike, anteriorly divergent at 10° to 15°. *Upper Devonian (Famennian)–Carboniferous (Moscovian):* Europe.——Fig. 252,*1a–d.* **G. parseptus,* Viséan, Fermanagh, Ireland; *a,b,* ventral valve, exterior, interior; *c,* lateral profile; *d,* dorsal valve interior, ×7.5 (Brunton, 1968).

Klocinetes Bizzarro, 1995, p. 162 [**Chonetes lepidus* Hall, 1857, p. 108; OD]. Shell small with flattened cardinal extremities; ornamentation of fine, angular costellae, with two enlarged costellae originating at beak of ventral valve; ventral valve interior with longitudinally divided myophragm; dorsal valve interior with pair of accessory septa; anderidia well developed, anteriorly divergent at 60°, not connected with cardinal process; short breviseptum, cardinal process pit present. *Middle Devonian (Eifelian):* USA.——Fig. 252,*3a–c.* **K. lepidus* (Hall), Eifelian, Marcellus Formation of Hamilton Group; *a,* ventral valve exterior, ×7; *b,* articulated shell, dorsal view, ×5.4; *c,* dorsal valve interior, ×7.5 (Bizzarro, 1995).

Permochonetes Afanas'eva, 1977a, p. 148 [**P. pamiricus;* OD]. Shell relatively large for family; exterior finely costellate; spines orthomorph oblique, low angled; dorsal valve interior without accessory septa, median septum; anderidia reduced; rows of radial papillae present. *Permian (Artinskian):* Pamirs.——Fig. 252,*4a–c.* **P. pamiricus,* Artinskian, Pamirs; ventral valve exterior, ventral valve internal cast, dorsal valve interior, ×3 (Afanas'eva, 1977a).

Plicanoplia Boucot & Harper, 1968, p. 169, *non Plicanoplia* Havlíček, 1973, p. 337, obj. [**Chonetes fornacula* Dunbar, 1920, p. 130; OD] [=*Cyrtoniscus* Boucot & Harper, 1968, p. 172, subj.]. Shell very small, commonly strongly concavoconvex; radial costellae or costae relatively strong for shell size; no spines developed but symmetrically arranged canal apertures along posterior margin of ventral valve; dorsal interior with elevated anderidia anteriorly divergent at 90°; median septum fusing posteriorly with inner cristae, supporting cardinal process; accessory septa well developed. *Lower Devonian (Pragian–Emsian):* eastern North America, Armorican Massif, Spain, northern Africa.——Fig. 252,*2a–d.* **P. fornacula* (Dunbar), Camden Chert, Tennessee; juvenile dorsal valve interior, adult dorsal valve interior, ventral valve exterior, ventral valve interior, ×5 (Boucot & Harper, 1968).

Pygmochonetes Jing & Hu, 1978, p. 111[126] [**P. jingxianensis;* OD]. Shell small, subsemicircular, strongly concavoconvex; shell surface costellate; costellae bifurcating, intercalating laterally; spines orthomorph oblique, symmetrically arranged; ventral valve interior with low myophragm, radial rows of coarse endospines; dorsal valve interior with cardinal process pit, reduced breviseptum, at least one pair of accessory septa sometimes reaching anterior margin. *Lower Permian:* southern China.——Fig. 251,*6a–c.* **P. jingxianensis,* Lower Permian, southern China; ventral valve exterior, ventral valve interior, dorsal valve internal mold, ×3 (Jing & Hu, 1978).

Semicaplinoplia Racheboeuf, 1995, p. 555 [**Plicanoplia sotoi* Garcia-Alcalde & Racheboeuf, 1978, p. 852; OD]. Externally similar to *Caplinoplia* but without spines on one side (usually left one) of ventral valve; dorsal valve interior with accessory septa displayed as in *Celtanoplia. Lower*

Devonian (Lochkovian): Spain, France, Algeria.——Fig. 252,*7a,b.* **S. sotoi* (Garcia-Alcalde & Racheboeuf), Lochkovian, Nieva Formation, northwestern Spain; ventral valve exterior, dorsal valve interior, ×4 (Racheboeuf, 1995).

Songzichonetes Yang Xue-chang, 1984, p. 210[332] [**S. sanxiaensis;* OD]. Differs externally from *Pygmochonetes* by its less arched longitudinal profile, radial costellae bifurcating in middle part of shell, development of growth lines; internally, dorsal valve interior exhibits long inner socket ridges, but no median septum. *Permian:* southern China.——Fig. 252,*6a–c.* **S. sanxiaensis,* Permian, southern China; ventral valve exterior, lateral profile, dorsal valve interior, ×5 (Yang Xue-chang, 1984).

Subglobosochonetes Afanas'eva, 1976, p. 67 [**C. (Rugosochonetes) malevkensis* Sokolskaya, 1950, p. 23; OD]. Similar to *Globosochonetes,* but dorsal valve interior without accessory septa; anderidia anteriorly divergent at 40° to 50°; no median septum. *Lower Carboniferous (Tournaisian):* Russian Platform.——Fig. 252,*5a–e.* **S. malevkensis* (Sokolskaya), Tournaisian, Malevkian Horizon, Russian Platform; *a,b,* articulated shell, ventral, lateral views, ×6; *c,* ventral valve interior, ×3; *d,* ventral valve with preserved spines, ×3; *e,* dorsal valve interior, ×3 (Afanas'eva, 1976).

Subfamily HOLYNETINAE Racheboeuf, 1981

[Holynetinae Racheboeuf, 1981b, p. 109]

Small shell weakly concavoconvex to strongly arched; tranverse, subequidimensional to semicircular in outline; shell surface costate to costellate; spines orthomorph oblique to vertical, symmetrically or asymmetrically arranged; ventral valve interior with short, wide, transversely elongated teeth; dorsal valve interior with cardinal process pit, no median septum and one, or several, pair of accessory septa; anderidia low, short, not fused posteriorly; inner socket ridges short, poorly developed. *Devonian (Emsian)–Lower Carboniferous (Viséan).*

Holynetes Havlíček & Racheboeuf, 1979, p. 97 [**H. holynensis;* OD]. Shell weakly to strongly concavoconvex, transversely elongate; spines orthomorph perpendicular on right side of ventral valve only; dorsal interior without median septum; cardinal process pit small, deep, narrow; usually one pair of narrow, bladelike accessory septa extending from cardinal process pit almost to anterior margin; anderidia isolated on valve floor, anteriorly divergent at 50° to 60°. *Middle Devonian (Eifelian, Givetian):* Armorican Massif, Rhenish Slate Mountains, Spain, Bohemia.——Fig. 253,*4a.* **H. holynensis,* Eifelian, Europe; ventral valve exterior, ×6.5 (Havlíček & Racheboeuf, 1979).——Fig. 253,*4b–d. H. stephaniae* Racheboeuf, Givetian, Kersadiou Formation, Armorican Massif; ventral valve exterior, ventral valve interior, dorsal valve interior, ×6 (Racheboeuf, 1981b).

Herrerella Racheboeuf, 1995, p. 559 [**H. zarelae;* OD]. Very small, transversely elongate, moderately concavoconvex; radial ornamentation of very low, almost indistinct costellae crossed by concentric, faint growth lines; erect, dissymmetrically arranged spines; ventral myophragm reduced; teeth laterally elongate, parallel to ventral interarea; dorsal valve interior with short, wide cardinal process, with pit, but no median septum; long inner socket ridges anteriorly divergent at 150°; anderidia almost imperceptible; no accessory septa, but two radial rows of strong endospines. *Upper Devonian (Famennian):* Morocco (Tafilalt).——Fig. 253,*5a–c.* **H. zarelae,* Famennian, Tafilalt, Morocco; *a,* ventral valve exterior, ×18; *b,* holotype, ventral valve interior, FLS 413819, ×18; *c,* dorsal valve interior, ×18 (Racheboeuf, 1995).

Malayanoplia Hamada, 1969, p. 255 [**M. demiluna;* OD]. Shell transverse, gently concavoconvex; shell surface capillate; spines orthomorph vertical; dorsal valve interior with faint anderidia; no median septum; inner socket ridges narrow, parallel to hinge; one pair of prominent, high accessory septa; several pairs of less developed accessory septa on either side of first pair. *Upper Devonian:* Malayan Peninsula.——Fig. 253,*2.* **M. demiluna;* dorsal valve interior, ×5 (Hamada, 1969).

Saharonetes Havlíček, 1984, p. 84 [**S. saharensis;* OD]. Shell gently concavoconvex; radial ornamentation costellate; costellae increase by bifurcation on ventral valve, by implantation in dorsal valve; spines orthomorph oblique, symmetrically arranged; ventral interarea flat, apsacline; dorsal one flat, almost linear, hypercline; pseudodeltidium present; chilidium unknown; small, oblique hinge teeth; interior dorsal without median septum; anderidia reduced, isolated on valve floor, anteriorly divergent at 90°; cardinal process longitudinally depressed ventrally; inner socket ridges short, strongly bending posteriorly to fuse with cardinal process; pair of long, thin accessory septa, low, gently divergent at 25° to 45°, extending about two-thirds valve length. *Lower Carboniferous (Tournaisian–Viséan):* Libya, Ghana.——Fig. 253,*1a,b. S. ghanaensis* Racheboeuf & others, ?Tournaisian, Ghana; ventral valve exterior, dorsal valve interior, ×5 (Havlíček, 1984).

Septachonetes Chatterton, 1973, p. 76 [**S. melanus;* OD]. Shell very small, transversely elongate; surface capillate; two orthomorph perpendicular spines on right side of ventral valve only; dorsal interior with deep cardinal process pit, faint anderidia anteriorly divergent at 70° to 80°; no median septum; three to five pairs of irregular sinuous accessory septa developed in anteromedian part of valve only. *Devonian*

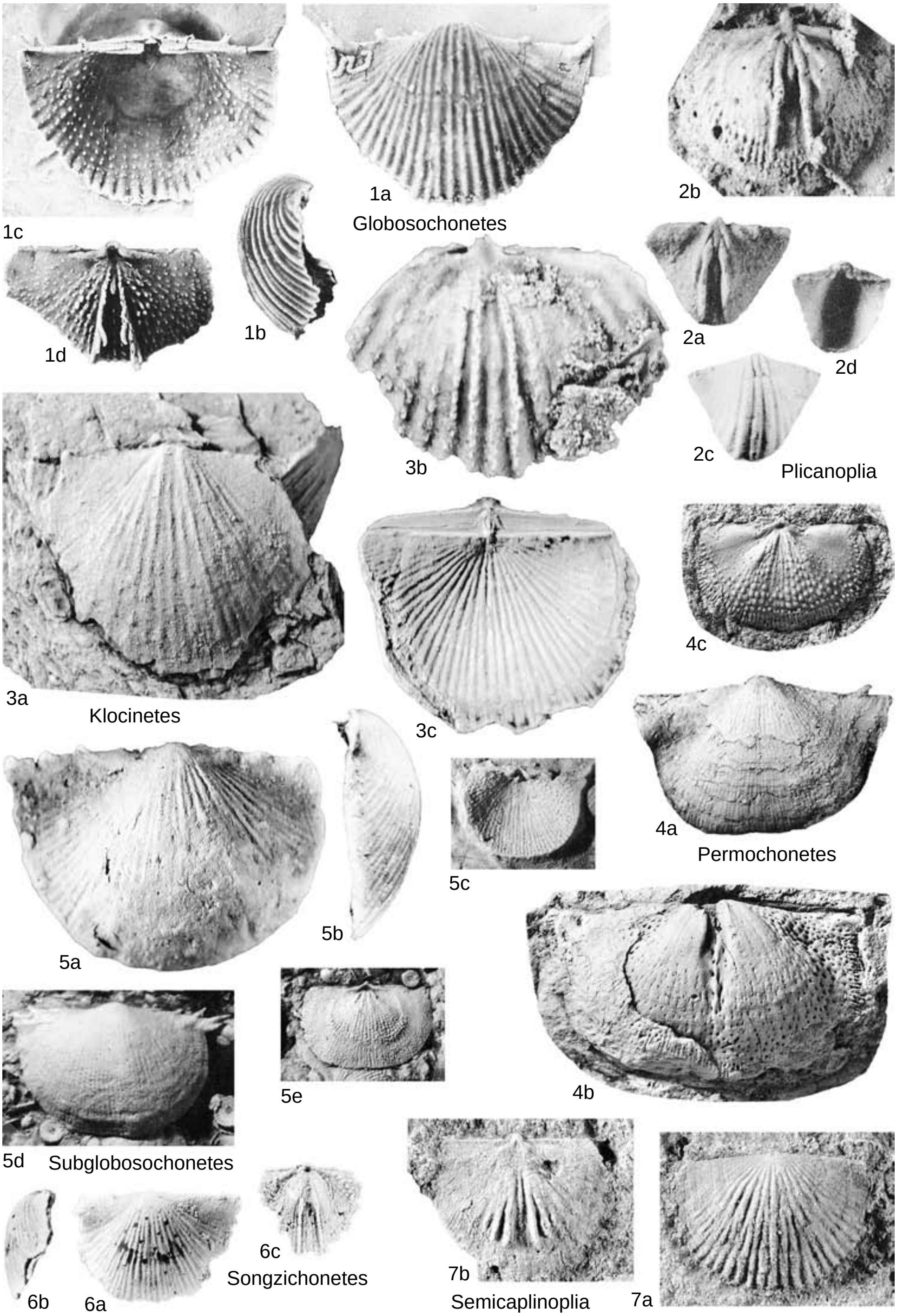


FIG. 252. Anopliidae (p. 387–388).

(?upper Emsian, ?lower Eifelian): Australia (New South Wales).——FIG. 253,*6a–c.* **S. melanus,* upper Emsian, Australia, New South Wales; *a,b,* ventral valve, exterior, interior, ×5.7; *c,* dorsal valve interior, ×10 (Chatterton, 1973).

Trichochonetes ROBERTS, 1976, p. 22 [**T. perpendicularis;* OD]. Similar to *Saharonetes,* but with orthomorph perpendicular spines; radial ornamentation capillate; dorsal interior with narrow inner socket ridges extending laterally almost parallel to posterior margin. *Lower Carboniferous (Viséan):* Australia (New South Wales).——FIG. 253,*3a,b.* **T. perpendicularis,* Viséan, Australia, New South Wales; ventral valve exterior, interior of an articulated shell, ×3 (Roberts, 1976).

Subfamily AIRTONIINAE
Muir-Wood, 1962

[Airtoniinae MUIR-WOOD, 1962, p. 107]

Shell with thickened ventral valve; ventral interarea low; no dorsal interarea; adductor scars not dendritic; dorsal valve interior with breviseptum, strong anderidia posteriorly fused with strong, posteriorly projected cardinal process. *Lower Carboniferous (Viséan).*

Airtonia COPE, 1934, p. 273 [**A. hudsoni;* OD]. Shell medium, markedly concavoconvex, finely capillate; pseudodeltidium reduced or posterior callosity; cardinal process lobes widely divergent posterolaterally; periphery of brachial platform with strong radial accessory septalike ridges. *Lower Carboniferous (Viséan):* England, ?Belgium, ?France.——FIG. 254*a–e.* **A. hudsoni,* Viséan, England, Yorkshire; *a–c,* ventral valve, ventral, lateral, interior, ×1; *d,e,* dorsal valve, interior, exterior, ×1 (Cope, 1934).

Family EODEVONARIIDAE
Sokolskaja, 1960

[Eodevonariidae SOKOLSKAJA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 223]

Shell small to large, capillate to rarely costate, moderately to markedly concavoconvex; ventral valve sometimes weakly sulcate; ventral interarea flat to more or less concave, weakly apsacline to anacline; dorsal interarea usually short, flat, hypercline; pseudodeltidium, chilidium present; spines inserted on posterior ventral margin, either symmetrically or not; spines closest to umbo sometimes lacking on one side; spines absent or variably developed, short, almost orthomorph perpendicular or long and cyrtomorph, bending medianly or laterally; ventral interior with myophragm, muscle field usually well developed; hinge line typically denticulate but variably developed; denticles extending all along hinge of both valves, or restricted to median part of both valves, or well developed on ventral valve only; vestigial hinge teeth present especially when hinge line not completely denticulate; dorsal median septum usually long, low, variably developed, supporting cardinal process; anderidia well differentiated, anteriorly divergent between 40° and 90°; inner socket ridges long, narrow, widely divergent anteriorly from 130° to 165°; accessory septa ill-defined, often reduced to low ridges in anteromedian part of valve, sometimes bending laterally; cardinal process variably developed in shape, size; short, small with posteriorly directed myophore, or internally geniculated with dorsally directed myophore, or strongly bilobed, widened posteriorly. *Lower Devonian (Pragian)–Middle Devonian (Eifelian).*

Eodevonaria BREGER, 1906, p. 534 [**Chonetes arcuatus* HALL, 1857, p. 76; SD SCHUCHERT & LEVENE, 1929, p. 57]. Shell small to medium, variably concavoconvex in profile, moderately transverse in outline; radial ornamentation capillate to costate; spines symmetrically arranged, cyrtomorph bending laterally; ventral interarea flat to very weakly concave, apsacline; cardinal process short, subtriangular in ventral view, weakly bilobed internally; anderidia slightly divergent anteriorly at 40° to 50°; inner socket ridges at about 130° to 145°; accessory septa restricted to anterior part. *Lower Devonian (Pragian–Emsian):* North America (Appalachian Mountains).——FIG. 255,*1a–c.* **E. arcuata* (HALL), Camden Chert, Tennessee, USA; ventral internal mold, ventral valve exterior, dorsal valve interior, ×2 (Breger, 1906).

Davoustia RACHEBOEUF, 1976, p. 68 [**Chonetes davousti* OEHLERT, 1887a, p. 66; OD]. Shell small, strongly concavoconvex, more or less transversely elongate; spines always very short, orthomorph almost perpendicular; spines asymmetrically arranged; hinge line denticulate with two vestigial hinge teeth; denticles always present in median part of ventral valve, sometimes lacking in dorsal valve of oldest species; dorsal interior with long median septum supporting cardinal process, ill-defined, variably developed accessory septa; cardinal process ventrally connected with swollen callus; anderidia long,

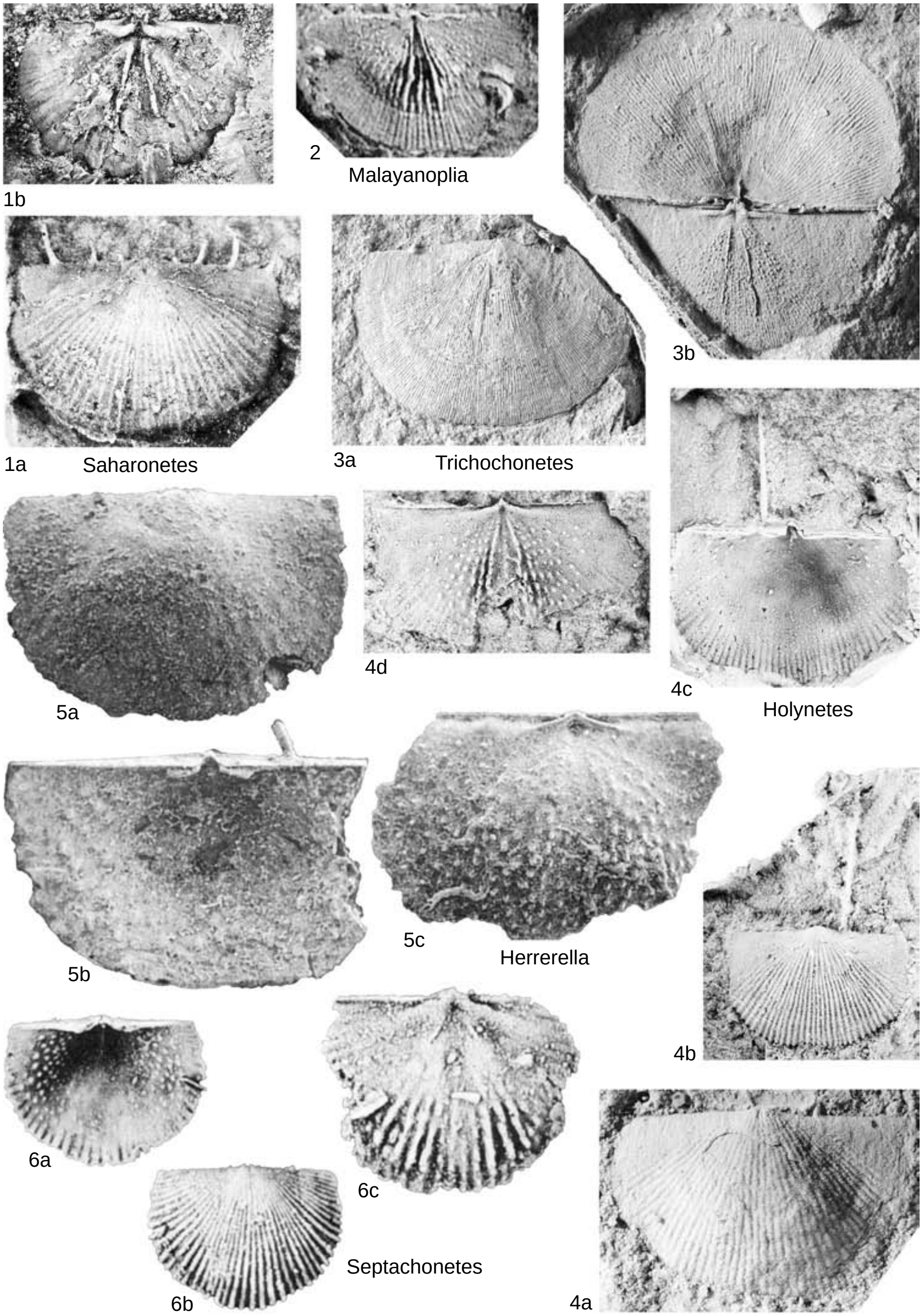


FIG. 253. Anopliidae (p. 388–390).

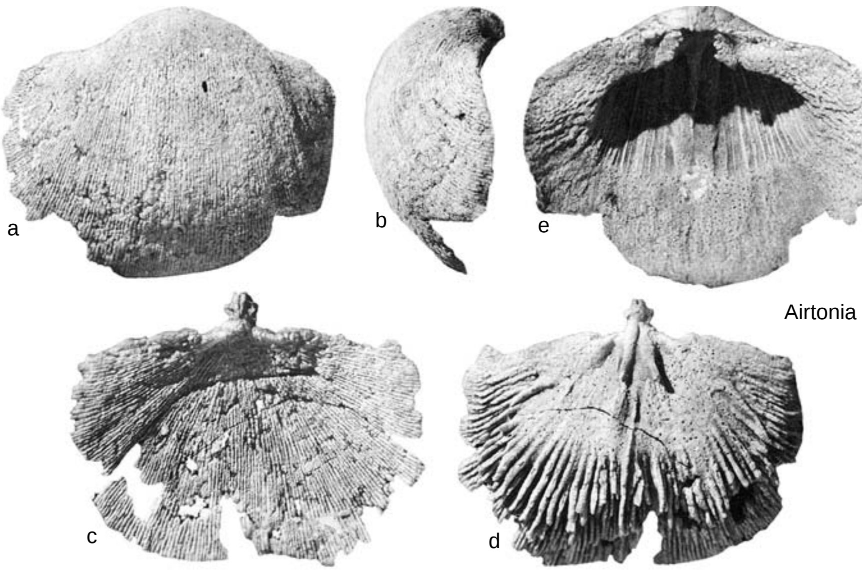


FIG. 254. Anopliidae (p. 390).

elevated, anteriorly divergent at 80° to 90°; cardinal process geniculated, bending dorsally, with myophore directed dorsally. *Lower Devonian (Pragian):* Armorican Massif, Spain, Morocco.——FIG. 255,*3a–c.* **D. davousti* (OEHLERT), Pragian, Saint Céneré Formation, Armorican Massif; juvenile ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×6 (Racheboeuf, 1976).

Lomaella HERRERA, 1995, p. 127 [**L. primoris;* OD]. Medium to large, transverse shell, resembling *Loreleiella* in its posterolaterally widened cardinal process lobes, but without developed spines. *Lower Devonian (Pragian–Emsian):* Argentine Precordillera (Herrera, 1995).

Loreleiella RACHEBOEUF, 1986, p. 643 [**Eodevonaria jahnkei* RACHEBOEUF, 1981b, p. 192; OD]. Similar to *Eodevonaria* but shell often larger, transversely elongate; maximum width at hinge line, ears triangular, often well developed; cardinal process stout, deeply bilobed; lobes massive, widening, diverging posterolaterally, deeply grooved longitudinally; myophore directed posteriorly, sticking out of posterior margin. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Armorican Massif, Rhenish Slate Mountains, Spain, Morocco, Algeria.——FIG. 255,*4a,b.* **L. jahnkei* (RACHEBOEUF), Emsian, Spain; ventral valve exterior, dorsal valve interior, ×2 (Racheboeuf, 1986).

Renaudia RACHEBOEUF, 1976, p. 71 [**Eodevonaria (Renaudia) mainensis;* OD]. Similar to *Eodevonaria* but shell medium, transversely elongate, strongly arched longitudinally; ventral valve more or less sulcate; spines cyrtomorph bending medianly, symmetrically arranged; interareas relatively short. *Lower Devonian (upper Pragian–lower Emsian):* Armorican Massif, Spain, Morocco.——FIG. 255,*2a–d.* **R. mainensis* (RACHEBOEUF), upper Pragian, Montguyon Formation, Armorican Massif; *a,* ventral valve exterior; *b,* dorsal side of articulated shell with spines; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Racheboeuf, 1976).

Family CHONETIDAE Bronn, 1862

[Chonetidae BRONN, 1862, p. 301]

Shell small to large, usually transverse, planoconvex to variably concavoconvex; shell surface smooth to costate; radial ornamentation sometimes restricted to posteromedian part of shell; concentric undulating fila present in some genera; spines commonly oblique, often numerous, high-angled to parallel to hinge line, symmetrically or asymmetrically arranged; ventral valve interior with well-developed, often transversely elongate, longitudinally striate hinge teeth; long, thin myophragm dividing large, variably impressed muscle field; *vascula media* weak or indistinct; dorsal valve interior with cardinal process anteriorly bounded by cardinal process pit, or elevated above valve floor, or

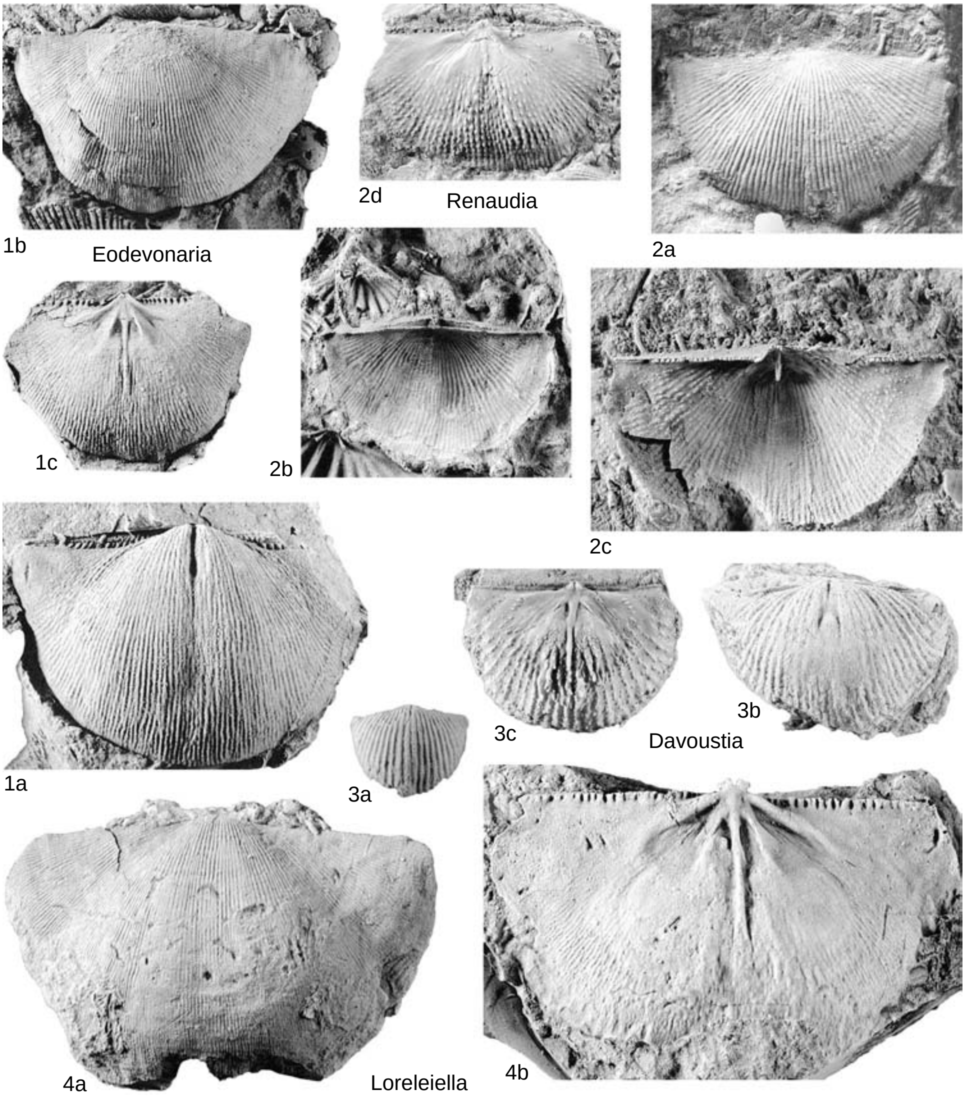


Fig. 255. Eodevonariidae (p. 390–392).

supported by median septum; cardinal process laterally flanked by commonly short, narrow, posteriorly bent inner socket ridges; median septum variably developed, sometimes reduced to breviseptum; pair of spinose or bladelike accessory septa developed in subfamily Chonetinae; anderidia usually weakly divergent anteriorly. *Lower Devonian (Pragian)–Upper Devonian (Frasnian, ?Famennian).*

Subfamily CHONETINAE Bronn, 1862

[*nom. transl.* Waagen, 1884, p. 612, *ex* Chonetidae Bronn, 1862, p. 301]

Small to medium chonetids, costate to capillate, without concentric fila; spines numerous, short, symmetrically arranged;

dorsal valve interior with short, low cardinal process, variably developed cardinal process pit; median septum ill developed, low, narrow, with one pair of variably differentiated accessory septa, usually spinose; long, low anteriorly weakly divergent anderidia. *Lower Devonian (Pragian–Emsian).*

Chonetes Fischer de Waldheim, 1830, pl. 26, fig. 8–9 [**Terebratulites sarcinulatus* von Schlotheim, 1820, p. 256; SD de Verneuil, 1845, p. 238]. Shell small to medium, transversely elongate; profile from almost planoconvex to moderately concavoconvex; beak small, narrow; ventral interarea apsacline, dorsal interarea hypercline; pseudodeltidium, chilidium present; spines low angled, orthomorph oblique geniculate, symmetrically arranged; radial ornamentation capillate or costellate originating at umbo, tapering toward margins looking smooth or finely lamellose; ventral interior with long, narrow median septum; strong laterally elongate hinge teeth obliquely placed; teeth, sockets longitudinally striate; dorsal interior with long, narrow median septum supporting cardinal process; short, posteriorly curved inner socket ridges; anderidia long, anteriorly divergent at 40°, posteriorly fused; shaft of cardinal process sometimes depressed medianly, but no true cardinal process pit; long, usually ill-defined accessory septa formed by fused endospines, anteriorly divergent at about 20°. *Lower Devonian (Pragian–Emsian):* Europe.——Fig. 256,*1a–d.* **C. sarcinulatus* (von Schlotheim), Emsian, Rhenish Slate Mountains; *a,* ventral valve exterior; *b,* dorsal valve interior; *c,* incomplete ventral valve exterior with spine bases; *d,* ventral valve internal mold, ×2 (Fischer de Waldheim, 1830).

Boicinetes Havlíček & Racheboeuf, 1979, p. 73 [**Chonetes bohemicus* Barrande, 1879, pl. 46, fig. II, 1–5; OD] [=*Chalimochonetes* Baranov, 1980, p. 142, obj.]. Shell medium, weakly concavoconvex; spines orthomorph oblique at about 70° to 80°, symmetrically arranged; ventral interarea apsacline, weakly concave, with small pseudodeltidium; dorsal interarea hypercline, flat, short, with inconspicuous chilidium; radial ornamentation very finely capillate (about 10 per mm); lamellose concentric growth lines; ventral interior with short myophragm; dorsal interior with long median septum, cardinal process pit, long anderidia anteriorly divergent at 35° to 45°; inner socket ridges high, narrow. *Lower Devonian (Pragian–Emsian):* Czech Republic, northeastern Russia.——Fig. 256,*2a–d.* **B. bohemicus* (Barrande), Pragian, Koneprusy Limestone, Czech Republic; *a,b,* ventral valve exterior, lateral profile; *c,* ventral valve internal mold; *d,* partly exfoliated dorsal valve interior, ×2 (Havlíček & Racheboeuf, 1979).

Plebejochonetes Boucot & Harper, 1968, p. 159 [**Chonetes plebeja* Schnur, 1854, p. 226; OD]. Resembles *Chonetes,* but shell usually smaller, more strongly concavoconvex; radial ornamentation of costellae or costae, posterolateral costae crossing posterior margin of valves; spines orthomorph oblique, symmetrically arranged; ventral valve interior with short myophragm, anteriorly rounded teeth; dorsal valve with short median septum; cardinal process pit developed in oldest representatives; cardinal process deeply bilobed internally; several pairs of ill-defined accessory septa in oldest forms, one pair of bladelike accessory septa in last representatives. *Lower Devonian (Pragian–Emsian):* Europe.——Fig. 256,*3a–d. P. semiradiatus* (Sowerby), Emsian, Rhenish Slate Mountains; *a,b,* ventral valve exterior, lateral profile; *c,* ventral valve internal mold; *d,* dorsal valve external mold, ×2 (Boucot & Harper, 1968).

Subfamily DAGNACHONETINAE Racheboeuf, 1981

[Dagnachonetinae Racheboeuf, 1981b, p. 153]

Small to large chonetids with numerous undulating fila crossing radial ornamentation; dorsal valve interior with large, posteriorly widened cardinal process not supported by median septum; breviseptum often well developed; no accessory septa; anderidia usually long, well developed, weakly divergent anteriorly. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Dagnachonetes Afanas'eva, 1978b, p. 66 [**D. caucasius;* OD]. Shell medium, weakly to moderately concavoconvex, transversely elongate; ventral sulcus, dorsal fold sometimes poorly developed in more arched species; spines orthomorph oblique, symmetrically arranged; ventral interarea apsacline, with wide pseudodeltidium; dorsal interarea catacline, with chilidium; radial ornamentation of numerous low costellae increasing rapidly in number, mainly by bifurcation in ventral valve; costellae narrowing toward periphery of shell when their numbers increase, crossed by very fine concentric fila; ventral interior with umbonal thickening, narrow, high median septum extending to midlength; hinge teeth laterally elongate, semioval; wide, internally bilobed cardinal process anteriorly bounded by cardinal process pit; inner socket ridges variable in length, extending almost parallel to hinge line; long, low, rounded median septum; anderidia long, straight or slightly bending medianly, anteriorly divergent at 50° to 70°; adductors usually well delimited. *Middle Devonian (Eifelian–Givetian):* Poland, Russia, France, Spain, China.——Fig. 257,*1a,b.* **D. caucasius,* Eifelian, Russia; ventral valve, dorsal valve interior, ×3 (Afanas'eva, 1978b).

Frankiella Racheboeuf, 1983, p. 607 [**F. drewitzi;* OD]. Shell small, transverse with leptaenoid morphology; longitudinal profile regularly concavo-

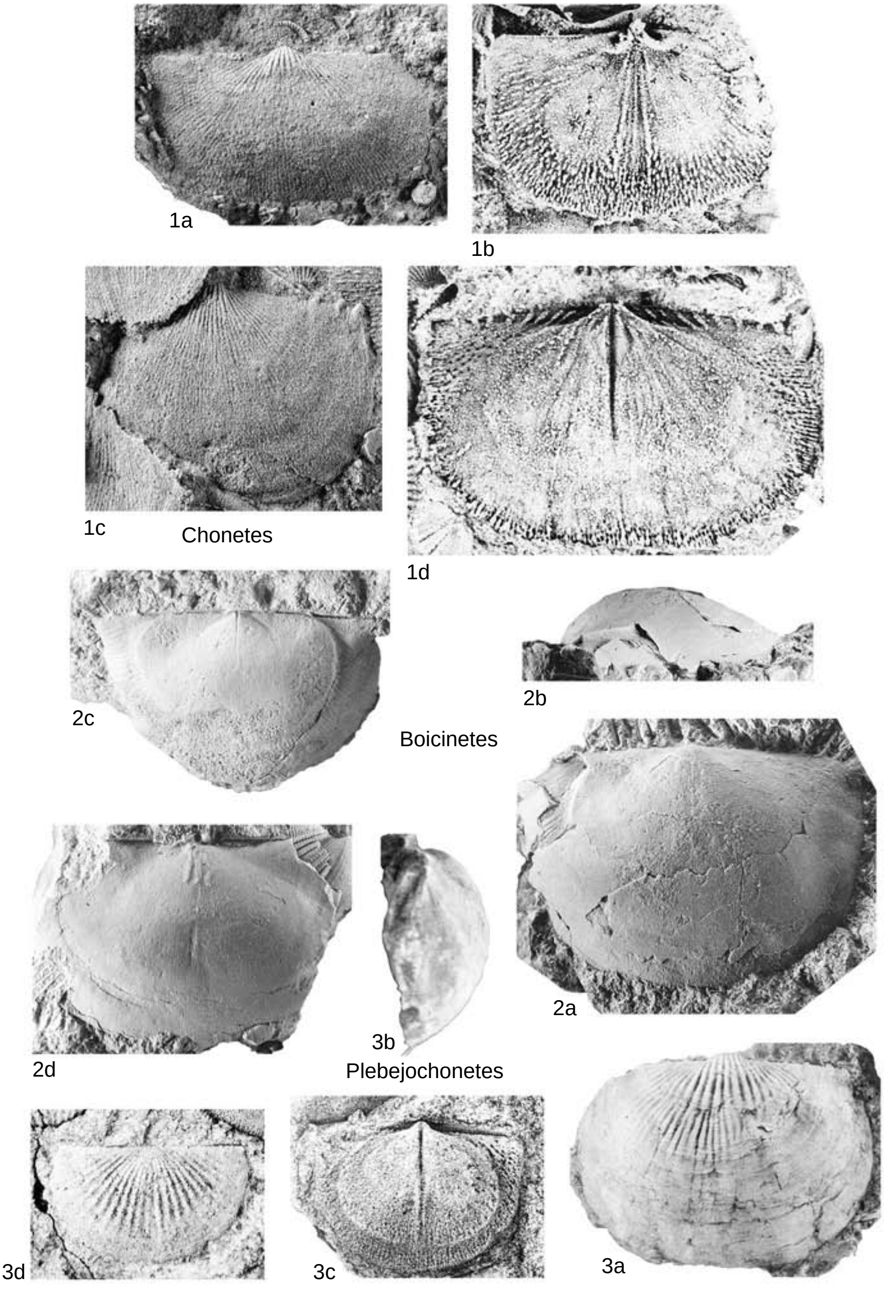


FIG. 256. Chonetidae (p. 394).

convex; from umbo, profile becoming anterolaterally planoconvex then resupinate, determining trail in anterior view; margin of both valves bending dorsally; ventral interarea flat, apsacline with wide delthyrium covered by pseudodeltidium; dorsal interarea flat, hypercline; chilidium unknown; radial ornamentation costellate; costellae increasing ventrally by implantation, dorsally by bifurcation; spines orthomorph oblique, symmetrically arranged; ventral interior with short median septum; hinge teeth stout but small, anteriorly rounded; dorsal interior with wide, short, internally deeply bilobed cardinal process anteriorly bounded by large cardinal process pit; anderidia relatively long; breviseptum present; inner socket ridges low, widening laterally, supporting cardinal process medianly. *Middle Devonian (Eifelian):* Armorican Massif, Rhenish Slate Mountains.——Fig. 257,*2a,b.* **F. drewitzi,* Eifelian, Saint-Fiacre Formation, Armorican Massif; well-preserved ventral valve exterior, ventral valve with spines, ×3 (Racheboeuf, 1983).

Luanquella Garcia-Alcalde & Racheboeuf, 1978, p. 847 [**L. cantabriensis;* OD] [=*Dagnachonetes (Luanquella)* Racheboeuf, 1981b, p. 155]. Differs from *Dagnachonetes* by its radial ornamentation with costellae anteriorly widening, or not, crossed by few perceptible concentric fila; dorsal interarea always hypercline instead of catacline; inner socket ridges narrower, anteriorly less divergent. *Lower Devonian (Emsian):* France, Spain.——Fig. 257,*3a–d.* **L. cantabriensis,* Emsian, Cantabrian Mountains, Spain; *a–c,* ventral valve, exterior, profile, interior; *d,* dorsal valve interior, ×1.5 (Garcia-Alcalde & Racheboeuf, 1978).

Mamutinetes Havlíček, 1990, p. 132 [**M. latipleura;* OD]. Small, moderately concavoconvex shell with wide, very low radial costellae originating anterior of beak, widening anteriorly; orthomorph oblique, symetrically arranged hinge spines; deep elongate-oval cardinal process pit; long, low, narrow breviseptum; no accessory septa; anderidia ill defined; long, straight inner socket ridges parallel to hinge line. *Lower Devonian (Emsian):* Bohemia.——Fig. 258,*1.* **M. latipleura,* Eifelian, Czech Republic; ventral valve exterior, ×4 (Havlíček, 1990).

Nurochonetes Ushatinskaya, 1977, p. 42 [**Chonetes akkultukensis* Ushatinskaya, 1966, p. 92; OD]. Shell medium to large, transverse; gentle ventral sulcus, weak dorsal fold usually present; radial ornamentation of bifurcating costellae; spines orthomorph, almost vertical, symmetrically arranged; pseudodeltidium, widely separated chilidial plates; ventral valve interior with short myophragm, massive lamellar teeth; dorsal valve interior with narrow median septum supporting cardinal process; anderidia anteriorly divergent at 40° to 50°; strong, curved, inner socket ridges. *Lower Devonian (Emsian):* Kazakhstan.——Fig. 257,*4.* **N. akkultukensis* (Ushatinskaya), Emsian, Kazakhstan; ventral, dorsal valve internal molds, ×3 (Ushatinskaya, 1977).

Pradochonetes Pardo & Garcia-Alcalde, 1984, p. 104 [**P. muelleri;* OD]. Shell small, weakly transverse, moderately concavoconvex; radial ornamentation of rounded costellae regularly dichotomizing ventrally, intercalating dorsally; spines orthomorph, high angled, symmetrically arranged; ventral valve interior with very short myophragm, strong endospines in posterolateral areas; dorsal valve interior with breviseptum in juveniles, stout median septum supporting cardinal process in largest shells; anderidia long, narrow, widely divergent anteriorly, not fusing posteriorly; inner socket ridges thickening, elevating during ontogeny, almost parallel to hinge. *Upper Devonian (Frasnian):* Spain.——Fig. 258,*2a–c.* **P. muelleri,* Frasnian, southern Spain; *a,b,* ventral valve exterior, dorsal valve interior; *c,* ventral valve exteriors, dorsal valve interiors, ×3 (Pardo & Garcia-Alcalde, 1984).

Rhyssochonetes Johnson, 1970b, p. 2095 [**R. aurora solox;* OD][=*Cedulia* Racheboeuf, 1979, p. 256, obj.]. Shell small, transversely elongate, moderately concavoconvex; radial ornamentation of rounded costellae crossed by fine, closely spaced fila; orthomorph oblique, high-angled, symmetrically arranged spines; periphery of ventral interior ornamented with concentric undulating ridges, corresponding to fila; variably developed cardinal process pit; inner socket ridges variably elongate, almost parallel to hinge line; anderidia relatively short, anteriorly divergent at 60° to 70°; septum poorly developed, sometimes absent or extending anteriorly as breviseptum; no accessory septa. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* North America, northern France.——Fig. 257,*5a–d.* **R. solox,* Givetian, Nevada; *a,b,* ventral valve exterior, interior; *c,d,* dorsal valve interiors, ×4 (Johnson, 1970b).

Sinochonetes Wang, Boucot, & Rong, 1981, p. 288[293] [**Chonetes minutisulcatus* Hou & Xian, 1975, p. 25; OD]. Shell small to medium, often uniplicate; ventral sulcus, dorsal fold variably developed; ventral interarea apsacline, flat; dorsal interarea narrow, hypercline; pseudodeltidium, chilidium present; orthomorph oblique symmetrically arranged spines; radial ornamentation capillate to costellate; ventral myophragm very short; hinge teeth massive; dorsal interior with long median septum often elevated anteriorly, supporting cardinal process ventrally connected with swollen callus; anderidia anteriorly divergent at 60°; inner socket ridges long, variably developed, anteriorly divergent at 150° to 160°. *Lower Devonian (Pragian–Emsian):* southern China, Canadian Arctic Archipelago.——Fig. 258,*3a–c.* **S. minutisulcatus* (Hou & Xian), upper Pragian, southern China; *a,b,* ventral valve, exterior, profile; *c,* dorsal valve interior, ×3 (Wang, Boucot, & Rong, 1981).

Subfamily DEVONOCHONETINAE Muir-Wood, 1962

[Devonochonetinae Muir-Wood, 1962, p. 43]

Small to large chonetids, weakly to markedly concavoconvex; shell surface with

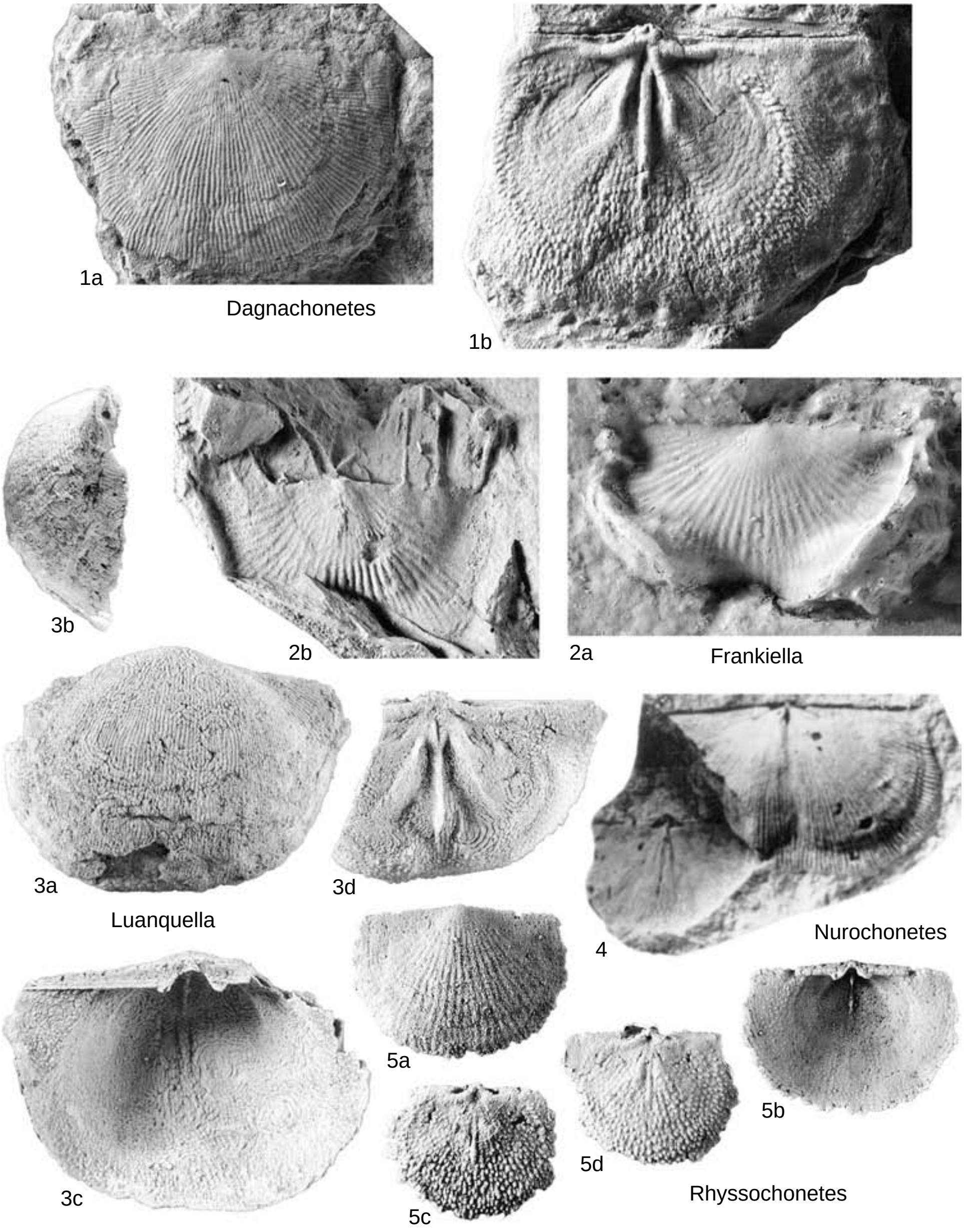


FIG. 257. Chonetidae (p. 394–396).

numerous costae or costellae without concentric fila; spines orthomorph oblique to cyrtomorph; large, weakly prominent pseudodeltidium; chilidium small; ventral valve interior with large, well-impressed muscle field; dorsal valve interior with long median septum supporting elevated, relatively long, narrow, cardinal process; no true

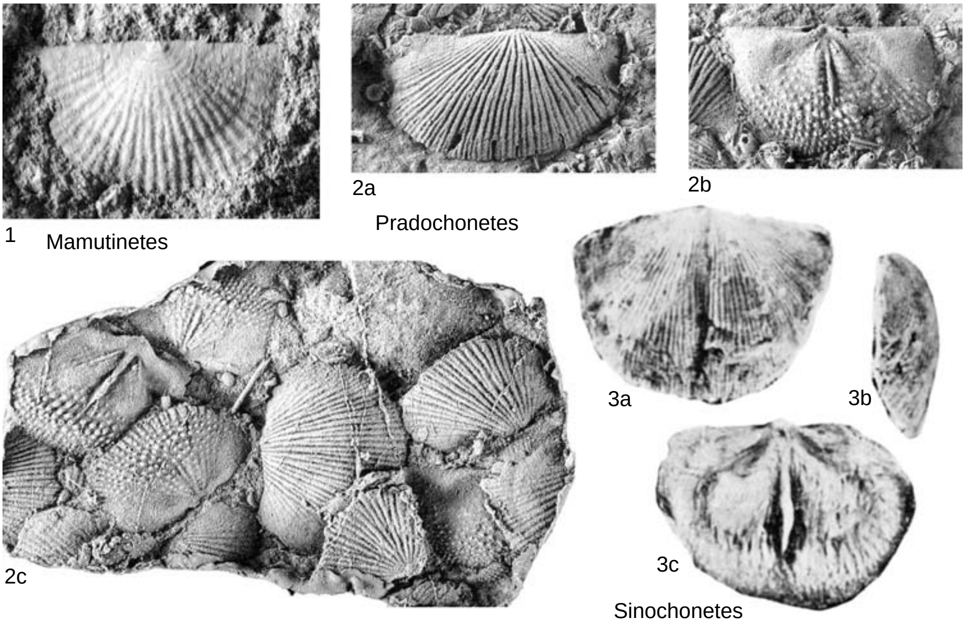


FIG. 258. Chonetidae (p. 396).

accessory septa; anderidia posteriorly fused with cardinal process; inner socket ridges relatively developed for family. *Lower Devonian (Emsian)–Upper Devonian (Frasnian).*

Devonochonetes MUIR-WOOD, 1962, p. 43 [**Chonetes coronatus* HALL, 1857, p. 146; OD; *nom. nov. pro Strophomena carinata* CONRAD, 1842, p. 257, *non* CONRAD, 1839, p. 64]. Shell small to medium, transverse, moderately concavoconvex; shell surface capillate to costellate; spines orthomorph oblique, low angled; dorsal valve interior with long median septum supporting the long, elevated cardinal process; anderidia weakly anteriorly divergent. *Middle Devonian (Eifelian–Givetian):* North America.——FIG. 259,*1a–e*. **D. coronatus* (HALL), Hamilton Group, Kashong Shales, New York; *a–c,* ventral valve, ventral, lateral, anterior views; *d,e,* dorsal valve exterior, interior, ×2.5 (Muir-Wood, 1962).

Aseptonetes ISAACSON, 1977, p. 177 [**A. boucoti;* OD]. Shell small to medium, moderately concavoconvex, equidimensional to weakly transverse; radial costellae, interspaces variably V-shaped in cross section; spines orthomorph oblique high angled to vertical, symmetrically arranged; juvenile dorsal valve interior with weak median septum, accessory septalike radial rows of strong endospines; adult dorsal valve interior with long, narrow median septum. *Middle Devonian (Eifelian–Givetian):* South America (Bolivia).——FIG. 259,*3a–e*. **A. boucoti,* Eifelian, uppermost Icla, Huamampampa Formations, Bolivia; *a,* internal mold of articulated shell; *b,* ventral valve; *c,d,* latex cast of both valves; *e,* ventral valve exterior, latex cast, ×2 (Racheboeuf & Branisa, 1985).

Hallinetes RACHEBOEUF & FELDMAN, 1990, p. 4 [**Strophomena lineata* CONRAD, 1839, p. 64; OD]. Shell small, markedly concavoconvex when adult; spines orthomorph perpendicular, disymmetrically arranged; radial ornamentation of low-rounded costellae often narrowing anteriorly as their numbers increase; ventral interarea apsacline, concave; dorsal interarea almost linear, hypercline; pseudodeltidium, chilidium not observed; ventral interior with long myophragm and large, deeply impressed muscle field; dorsal interior swollen with long median septum not supporting cardinal process; cardinal process pit in juveniles; posteromedian part of valve deeply depressed in adults; anderidia anteriorly divergent at 50° to 55°, posteriorly fused with wide, long inner socket ridges; no accessory septa; adductors deeply impressed. *Middle Devonian (Eifelian):* New York.——FIG. 259,*2a–c*. **H. lineatus* (CONRAD), Seneca Member, Onondaga Limestone, New York; ventral valve exterior, ventral valve interior, dorsal valve interior, ×3 (Racheboeuf & Feldman, 1990).

Huananochonetes WANG, BOUCOT, & RONG, 1981, p. 290[295] [**Parachonetes ovalis* HOU & XIAN, 1975, p. 27; OD]. Shell small, highly concavoconvex;

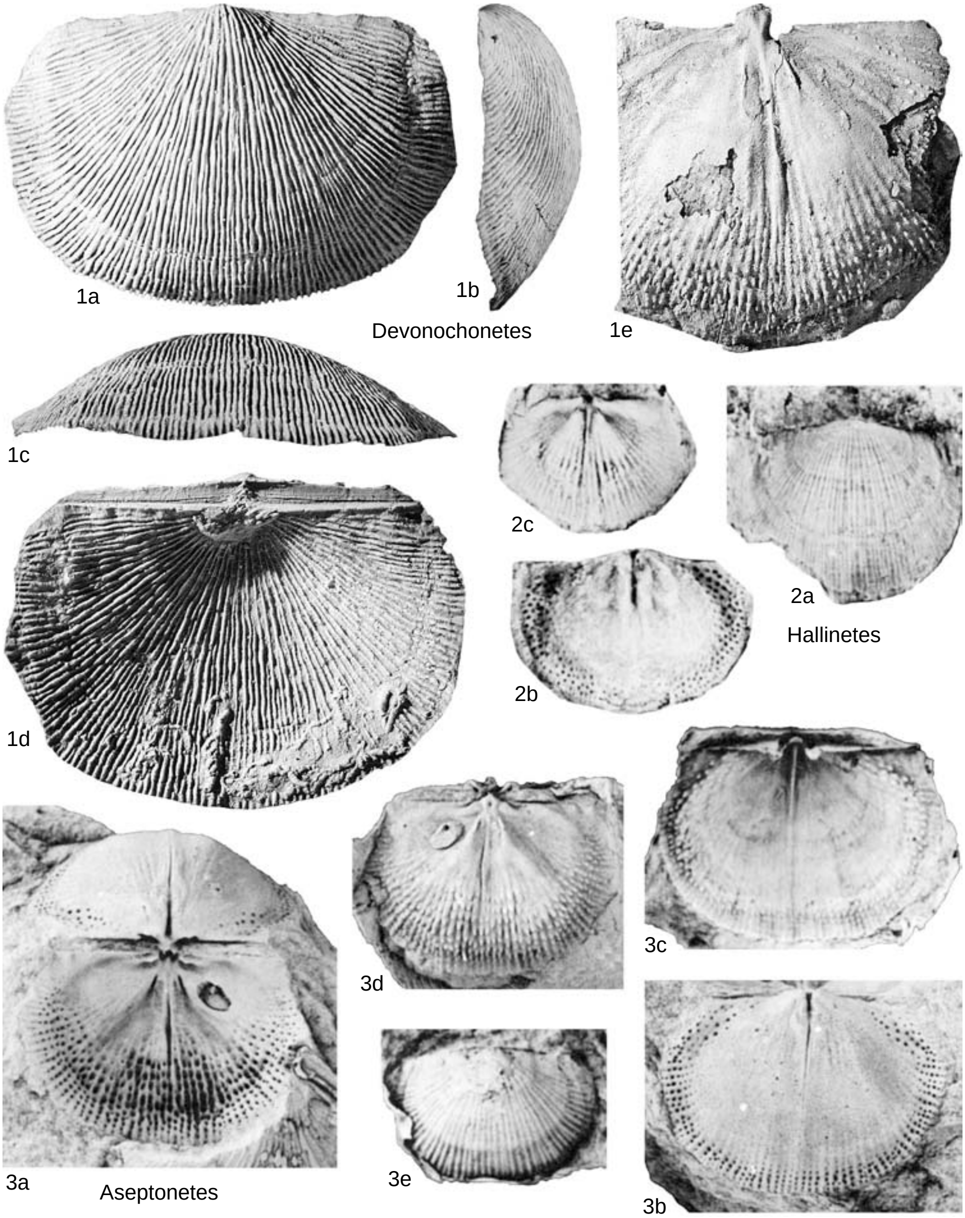


FIG. 259. Chonetidae (p. 398).

orthomorph oblique, high-angled spines at about 50°; radial ornamentation of narrow, rounded costellae; large, convex pseudodeltidium; chilidium reduced, almost indistinct; ventral interior with short myophragm, short, ill-developed hinge teeth; dorsal interior with long median septum supporting cardinal process; short anderidia anteriorly highly divergent at 80°; long, narrow inner socket ridges almost parallel to posterior margin. *Lower Devonian (Emsian):* southern China.——FIG. 260,*1a–c.* **H. ovalis* (HOU & XIAN), lower Emsian, Yukiang Formation, central Guangxi; *a,b,* ventral valve, ventral, lateral views; *c,* dorsal valve interior, ×3 (Wang, Boucot, & Rong, 1981).

Longispina COOPER, 1942, p. 230 [**Chonetes emmetensis* WINCHELL, 1866, p. 92; OD]. Shell small, usually strongly concavoconvex; anterior margin regularly rounded; small umbo prominent, often strongly curved posteriorly; ventral interarea concave, anacline; dorsal interarea more or less concave, hypercline; pseudodeltidium long, narrow; chilidium small; radial ornamentation costellate to costate; few strong growth lines usually present; spines orthomorph parallel to hinge line, symmetrically arranged; ventral interior with short, stout median septum; hinge teeth relatively small, anteriorly rounded; dorsal interior with variably developed median septum supporting long, narrow cardinal process; myophore long, narrow, dorsally directed; inner socket ridges low, short; anderidia small, anteriorly divergent at 50° to 70°; pair of variably developed accessory septa in anterior part of valve, anteriorly divergent at 20° to 30°. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* North America (Appalachian Mountains), Venezuela, Bolivia, Morocco, Algeria, Spain, France.——FIG. 260,*5a–d.* **L. emmetensis* (WINCHELL), Middle Devonian, Hamilton Group, New York, USA; ventral valve internal mold, ventral valve exterior, articulated shell in dorsal view, dorsal valve interior, ×3 (Cooper, 1942).

Montsenetes RACHEBOEUF, 1992, p. 37 [**Devonochonetes notius* BENEDETTO, 1984, p. 60; OD]. Shell medium, subequidimensional or weakly transverse, strongly concavoconvex; radial ornamentation relatively strong; spines orthomorph oblique, symmetrically arranged; ventral valve interior with long myophragm dividing large, radially striate, muscle field with semielliptical adductors; dorsal valve interior with strong median septum, anteriorly elevated, supporting large, posteriorly elongated, elevated cardinal process; anderidia weakly divergent anteriorly. *Middle Devonian (Eifelian–Givetian):* North America (Appalachian Mountains), Venezuela, Bolivia, Sahara.——FIG. 260,*2a–c.* **M. notius* (BENEDETTO), Middle Devonian, Caño del Oeste Formation, Sierra de Perija, Venezuela; ventral valve, ventral, lateral views, dorsal valve interior, ×2 (Benedetto, 1984).

Striatochonetes MIKRJUKOV, 1968, p. 90 [**Strophonema setigera* HALL, 1843a, p. 180; OD]. Shell very small, subsemicircular; shell surface finely costellate; spines cyrtomorph intraverse, symmetrically arranged; dorsal valve interior with shallow cardinal process pit, no median septum, one pair of narrow, low accessory septa; anderidia very reduced; inner socket ridges relatively strong. [When he described the new genus, MIKRJUKOV mentioned the concentric fila crossing the radial ribs and the intervals. This character could not be observed in the North American shells.] *Middle Devonian (Eifelian):* North America, Russia.——FIG. 260,*4a–c.* **S. setigera* (HALL), Middle Devonian, Chemung Group, New York; ventral valve exterior, partly exfoliated ventral valve, dorsal valve interior, ×4 (Mikrjukov, 1968).

Xinjiangochonetes XU, 1991, p. 317[330] [**X. pygmaeus;* OD]. Shell small to medium, moderately concavoconvex, subsemicircular in outline; shell surface costellate; spines low angled; ventral valve interior with large teeth, very long myophragm; dorsal valve interior with short, weak median septum. [Due to the preservation of the type material, this monospecific genus remains poorly known. The lack of dorsal accessory septa, however, makes likely its assignment to the Devonochonetinae.] *?Lower Devonian (Emsian), Middle Devonian (Eifelian):* China (northern Xinjiang).——FIG. 260,*3a,b.* **X. pygmaeus,* ?upper Lower Devonian, Eifelian, northern Xinjiang; ventral valve internal molds, dorsal valve interior, ×1.5 (Xu, 1991).

Subfamily NOTIOCHONETINAE Racheboeuf, 1992

[Notiochonetinae RACHEBOEUF, 1992, p. 42]

Shell medium to large, transverse, nearly planoconvex to markedly concavoconvex; ventral interarea orthocline or apsacline, flat or weakly concave, with pseudodeltidium; dorsal interarea anacline, with strong, distinct chilidial plates; radial ornamentation costellate, without fila; spines orthomorph oblique, low angled, symmetrically arranged; ventral interior with strong, short, often laterally elongate hinge teeth; myophragm long, dividing large muscle field; diductors usually flabellate; dorsal interior with stout cardinal process, strongly bilobed internally, prominent above valve floor; myophore varying from posteriorly to dorsally oriented; strong anderidia anteriorly divergent at 20° to 45°; long, narrow median septum usually supporting cardinal process developing during ontogenesis; accessory septa distinct in juveniles, tapering with growth, often absent in largest shells. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Notiochonetes MUIR-WOOD, 1962, p. 48 [**Chonetes skottsbergi* CLARKE, 1913, p. 29; OD]. Shell medium to large, transverse, plano- to slightly concavoconvex; pseudodeltidium, disjunct chilidial plates; external spines unknown; ventral valve interior with large elongate teeth, large muscle field; large cardinal process, elevated, with myophore projecting ventrally; median septum low, narrow, pos-

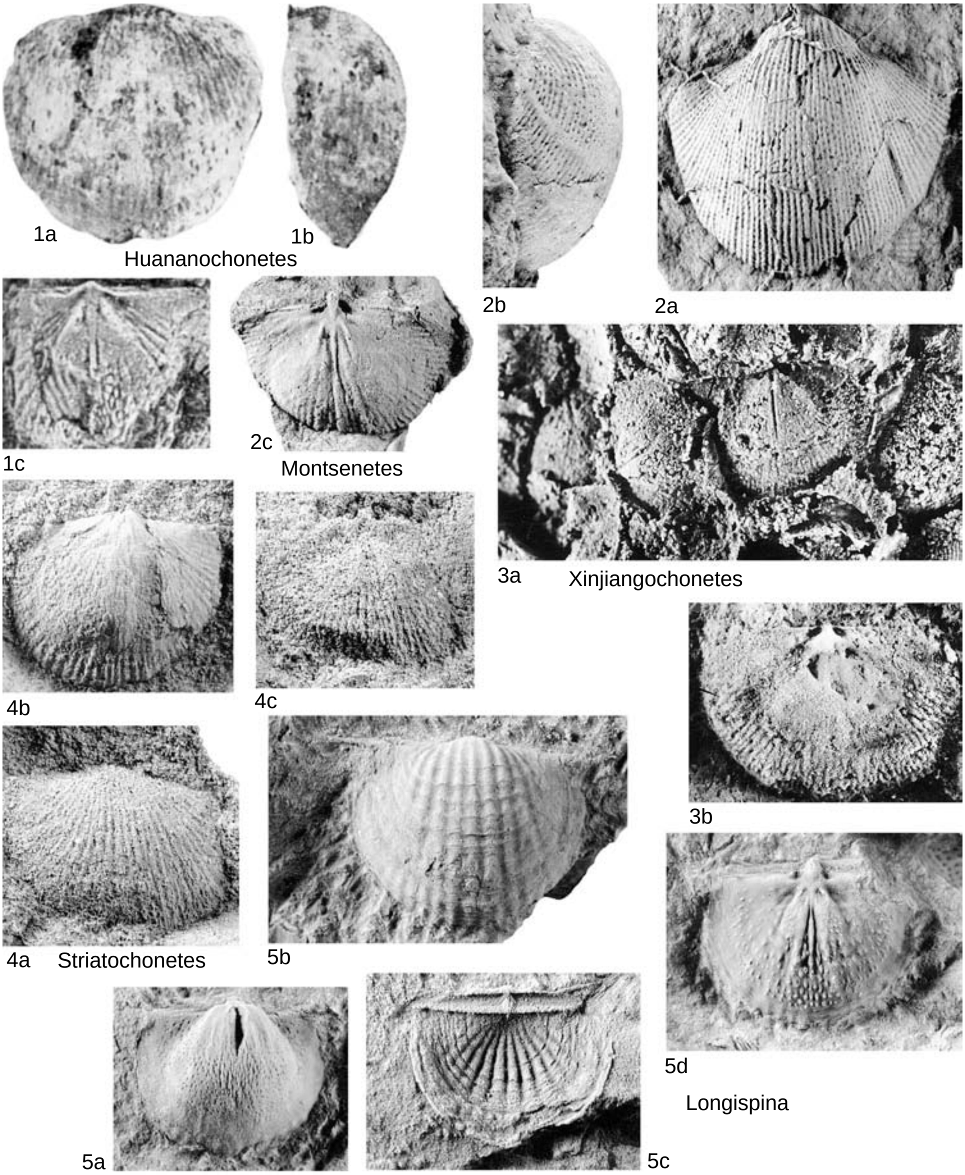


FIG. 260. Chonetidae (p. 398–400).

teriorly thickened; long, strong anderidia; inner socket ridges straight. *Middle Devonian (Eifelian):* Falkland Islands, ?Brazil, South Africa.——FIG. 261,*1a,b.* *_N. skottsbergi_ (CLARKE), western Cape, Bokkeveld Group, South Africa; ventral valve internal mold, dorsal valve interior, ×1.5 (Hiller, 1987).

Allanetes BOUCOT & JOHNSON, 1967, p. 142 [*_A. neozelanica;_ OD]. Shell medium to large, markedly concavoconvex; radial ornamentation of coarse costae, costellae; disjunct chilidial plates; few spines ?symmetrically arranged, orthomorph ?perpendicular; ventral myophragm high, bladelike; dorsal valve interior with median septum, stout anderidia;

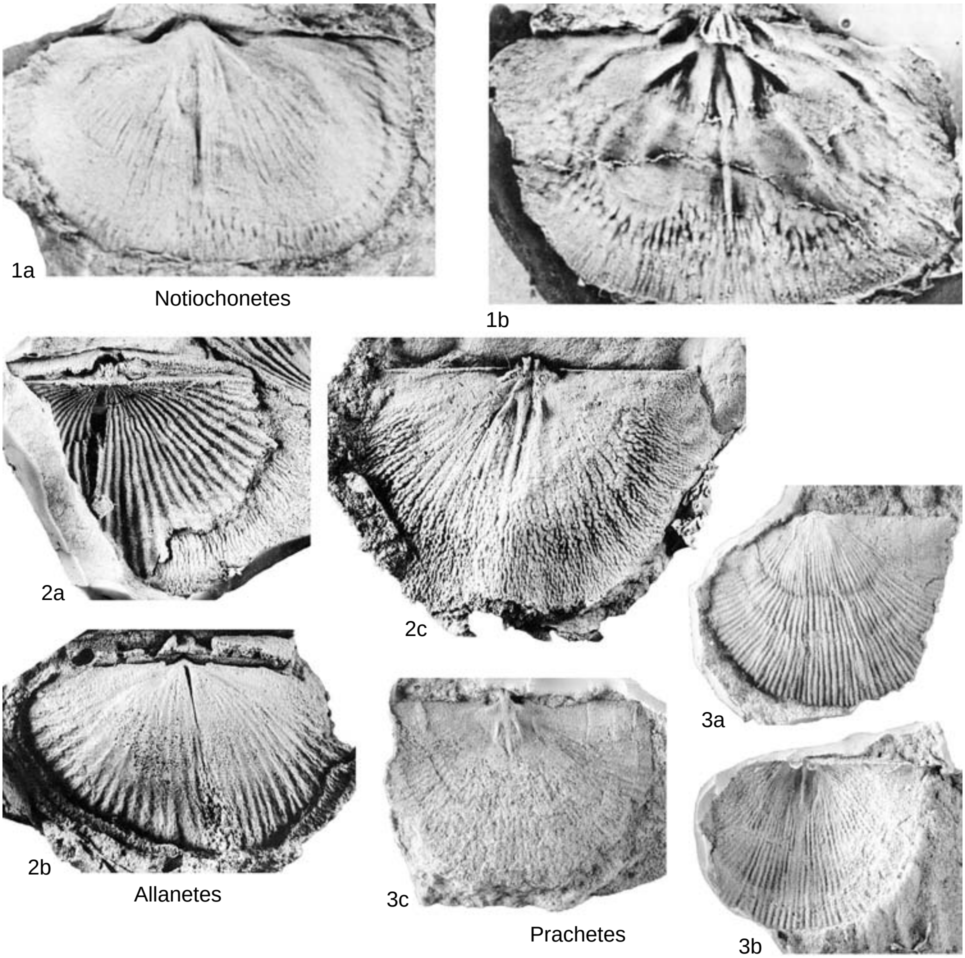


FIG. 261. Chonetidae (p. 400–403).

cardinal process deeply bilobed, elevated above valve floor, anteriorly bounded by cardinal process pit; inner socket ridges short, narrow. *Lower Devonian (Emsian):* New Zealand.——FIG. 261,*2a–c*. **A. neozelanica,* lower Emsian, Reefton beds, New Zealand; dorsal side of articulated shell, ventral valve internal mold, dorsal valve interior, ×2 (Boucot & Johnson, 1967).

Pleurochonetes ISAACSON, 1977, p. 175 [**Chonetes (Pleurochonetes) lauriata;* OD][=*Gamonetes* ISAACSON, 1977, p. 168, obj.; *Aseptonetes* ISAACSON, 1977, p. 177, obj.]. Differs from *Notiochonetes* in its dorsal valve interior; anderidia less developed, more divergent anteriorly; inner socket ridges shorter, posteriorly curved, more posteriorly situated, more divergent anteriorly; median septum supporting cardinal process; myophore projecting posteriorly; spines orthomorph oblique, symmetrically arranged. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Bolivia, Argentina, South Africa.——FIG. 262*a*. *P. falklandicus* (MORRIS & SHARPE), Emsian, Falkland islands; dorsal valve interior, ×2 (Hiller, 1987).——FIG. 262*b–e*. *P. anteloi* (ISAACSON), Eifelian, upper Icla Formation, Bolivia; *b–d,* dorsal valve interior, ventral valve interior, adult dorsal valve interior; *e,* ventral valve exterior, ×2 (Racheboeuf, 1992).

Prachetes BIZZARRO, 1995, p. 175 [**Pleurochonetes? condori* RACHEBOEUF, 1992, p. 49; OD]. Shell medium, slightly transverse to equidimensional, moderately concavoconvex, with flattened cardinal extremities; maximum width at hinge line; spines symmetrical, orthomorph oblique; ornamentation of dense, narrow, angular costellae; ventral valve interior with posterior ridges anteriorly divergent at 70° to 80°; dorsal valve interior with small cardinal

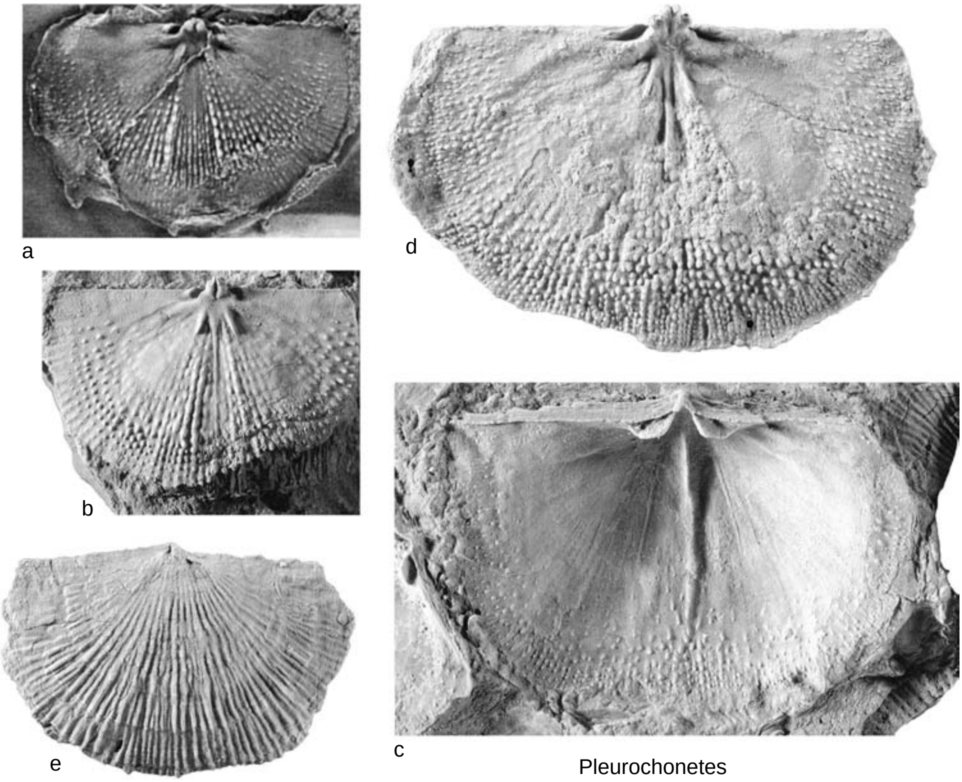


FIG. 262. Chonetidae (p. 402).

process, short median septum, anderidia anteriorly weakly divergent, less than 40°. *Middle Devonian (Givetian):* North America (Appalachian Mountains), Bolivia.——FIG. 261,*3a–c.* **Prachetes condori* (RACHEBOEUF), Givetian, Cruz Loma Sandstone, Bolivia; ventral valve exterior, ventral valve interior, dorsal valve interior, ×2 (Bizzarro, 1995).

Subfamily RETICHONETINAE Muir-Wood, 1962

[Retichonetinae MUIR-WOOD, 1962, p. 62]

Shell small, subequidimensional; dorsal valve interior without cardinal process pit; median septum supporting cardinal process; inner socket ridges, anderidia reduced; no accessory septa; no brachial ridges. [This subfamily is retained herein to include genera for which the phylogenetic relationships are unclear. They can be provisionally regarded as neotenic forms; further investigations would possibly suggest their assignment to the subfamily Devonochonetinae.] *Upper Devonian (Frasnian, ?Famennian).*

Retichonetes MUIR-WOOD, 1962, p. 62 [**Chonetes armata* BOUCHARD-CHANTEREAUX in DE VERNEUIL, 1845, p. 241; OD]. Shell small, usually weakly transverse in outline, markedly concavoconvex; ventral interarea apsacline, posteriorly concave; dorsal interarea hypercline; small, convex pseudodeltidium, chilidium; radial ornamentation of low, narrow costellae; few lamellose concentric growth lines; spines orthomorph oblique, low to high angled from umbo to cardinal extremities; ventral interior with small rounded hinge teeth, short myophragm; posterolateral margins of visceral cavity with two radial rows of strong pustules; dorsal interior with stout median septum supporting cardinal process, no pit; small but strong anderidia anteriorly divergent at 80° to 90°; inner socket ridges relatively long, anteriorly divergent at 160°, bearing radial row of pits for articulation with posterior pustules of ventral valve. *Upper Devonian (Frasnian, ?Famennian):* Europe, Australia; USA (New Mexico), *?Famennian.*——FIG. 263,*1a–c.* **R. armatus* (BOUCHARD-CHANTEREAUX), Frasnian,

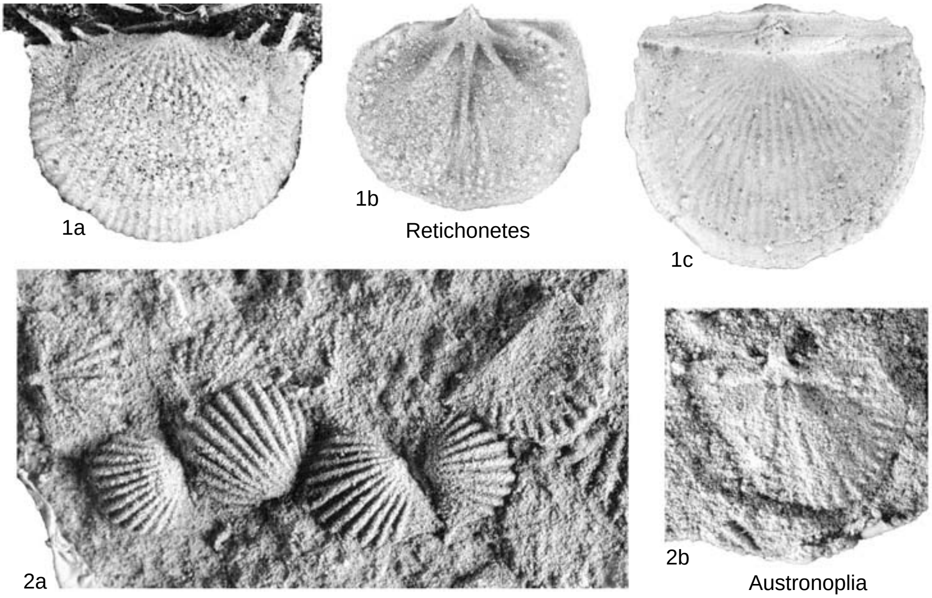


FIG. 263. Chonetidae (p. 403–404).

upper *Asymmetricus* Zone, northern France; ventral valve exterior, dorsal side of articulated shell, dorsal valve interior, ×5 (Racheboeuf, 1979).

Austronoplia ISAACSON, 1977, p. 178 [**Chonetes stuebeli* ULRICH, 1893, p. 80; OD]. Shell small, moderately concavoconvex, subsemicircular; shell surface with subtriangular to rounded costae; ventral valve exterior with median fold in largest shells; spines orthomorph oblique, symmetrically arranged; dorsal valve interior with median septum supporting posteriorly elongate cardinal process; no cardinal process pit; anderidia short, widely divergent anteriorly; inner socket ridges short, posteriorly curved; no accessory septa; interior of both valves with strong endospines. [The overall shell morphology and the lack of cardinal process pit and accessory septa make *Austranoplia* a member of the Retichonetinae rather than Costanopliinae.] *Upper Devonian (Frasnian):* Bolivia.——FIG. 263,*2a,b*. **A. stuebeli* (ULRICH), Frasnian, Bolivia; ventral valve exteriors, dorsal valve interior, ×5 (Racheboeuf, 1992).

Family RUGOSOCHONETIDAE Muir-Wood, 1962

[*nom. transl.* COOPER & GRANT, 1975, p. 1212, *ex* Rugosochonetinae MUIR-WOOD, 1962, p. 32]

Shell small to large, costate, capillate, smooth or lamellose, plano- to strongly concavoconvex; ventral sulcus absent to strongly developed, with corresponding dorsal fold; spines symmetrically arranged, orthomorph oblique to perpendicular; pseudodeltidium, chilidium usually present; variably developed ventral myophragm, always high posteriorly; dorsal interior with long median septum; no accessory septa; anderidia always prominent, anteriorly moderately divergent; internally bilobed cardinal process anteriorly bounded by cardinal process pit. *Carboniferous–Permian, ?Lower Triassic.*

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

[Rugosochonetinae MUIR-WOOD, 1962, p. 32]

Small to large rugosochonetids with radially capillate or costate external ornament; ventral sulcus weakly to strongly developed; dorsal fold present in several genera; spines usually orthomorph oblique, at low to moderate angle; brachial ridges often well developed. *Carboniferous–Permian, ?Lower Triassic.*

Rugosochonetes SOKOLSKAYA, 1950, p. 23 [**Orthis hardrensis* PHILLIPS, 1841, p. 138; OD] [=*Nix* EASTON, 1962, p. 45, obj.]. Shell small, plano- to slightly concavoconvex; dorsal interarea reflexed; pseudodeltidium, chilidium developed; shell capillate; spines orthomorph oblique, at 45° to 60°, symmetrically arranged; dorsal median septum half of valve length, inner socket ridges curved. *Lower Carboniferous (Tournaisian)–Upper Carboniferous (Gzhelian):* Europe, Asia, Australia, North America, Africa.——FIG. 264,*1a–d. R. celticus* MUIR-WOOD, Namurian, Scotland; *a,* ventral valve exterior, ×3; *b,* ventral valve interior, ×4; *c,d,* dorsal valve interiors, ×2 (Muir-Wood, 1962).

Alatochonetes LIANG, 1990, p. 144[460] [**A. alata;* OD]. Shell small, strongly transverse, subtrapezoidal, with acute to alate cardinal extremities; shell surface with coarse radial costae crossed by strong concentric rugae with prominent tubercles at junction; ventral valve interior with long, low myophragm; dorsal valve interior poorly known. *middle Permian:* southern China.——FIG. 264,*2. *A. alatus,* middle Permian, southern China; dorsal view of articulated shell, internal mold, ×3.5 (Liang, 1990).

Arctochonetes IFANOVA, 1968, p. 29 [**Chonetina? postartiensis* USTRITSKY, 1960, p. 112; OD]. Shell small, concavoconvex; ventral sulcus weak or absent; shell surface finely costellate; spines orthomorph oblique, symmetrically arranged; ventral valve interior with short myophragm, pair of strong vascular trunks, anteriorly divergent at 60°; dorsal valve interior with ill-defined median septum, pair of long, low accessory septa. *Lower Permian (Artinskian–Kungurian):* Pechora Basin.——FIG. 264,*3a–c. *A. postartiensis* (USTRITSKY), Artinskian, Pechora Basin; ventral valve internal molds, ventral valve exterior, dorsal valve internal mold, ×2 (Ifanova, 1968).

Chonetinella RAMSBOTTOM, 1952, p. 13 [**Chonetes flemingi* NORWOOD & PRATTEN, 1855b, p. 26; OD]. Small, bilobate, highly concavoconvex shell with deep median sulcus, high fold; pseudodeltidium, chilidium ill developed or absent; shell surface capillate; dorsal valve interior with small bilobed cardinal process, alveolus; long, anteriorly elevated median septum; long inner socket ridges, parallel to hinge. *Upper Carboniferous–Lower Permian (Kungurian):* Europe, North America, South America, *Pennsylvanian;* North America, Asia, *Wolfcampian–Leonardian.*——FIG. 264,*6a–d. *C. flemingi* (NORWOOD & PRATTEN), Pennsylvanian, Texas; *a,b,* articulated shell, ventral, dorsal views; *c,* ventral valve interior; *d,* dorsal valve interior, ×3 (Ramsbottom, 1952).

Fanichonetes XU & GRANT, 1994, p. 29 [**F. campigia;* OD]. Small to medium, transverse shell; shell surface strongly costellate; ventral sulcus and corresponding dorsal fold developed; numerous spine canals but outer spines not observed; ventral valve interior with short myophragm, coarse isolated endospines posterolaterally; dorsal valve interior poorly known, with cardinal process pit. [Among the diagnostic characters the authors quoted the ". . . spines mostly inclined toward midline." Judging from the specimens illustrated in their figure 16, it appears clearly that these features are not the spines but molds of the spine canals inside the posterior margin of the decalcified ventral valve. Their orientation toward midline conforms with all chonetoids and is only due to the growth process.] *Upper Permian (Tatarian):* southern China.——FIG. 264,*7a,b. *F. campigia,* Upper Permian, southern China; *a,* ventral valve exterior; *b,* holotype, ventral valve interior, ×3 (Xu & Grant, 1994).

Fusichonetes LIAO in ZHAO & others, 1981, p. 52[83] [**Plicochonetes nayongensis* LIAO, 1980, p. 252; OD]. Shell small, transverse with ventral sulcus, dorsal fold; shell surface with strong simple costae; spines low angled; ventral valve interior with rows of endospines; dorsal valve interior with median septum. *Upper Permian, ?Lower Triassic:* China.——FIG. 264,*8a–c. *F. nayongensis* (LIAO), uppermost Permian–?lowermost Triassic, southern China; ventral valve exterior, dorsal exterior of articulated shell, ventral valve interior, ×4 (Liao, 1981).

Isochonetes AISENVERG, 1985, p. 41 [**I. larinoensis;* OD]. Shell medium, transverse; ventral valve regularly convex; ornament of uniform, fine, regular costellae; spine bases medium angled, 45° to 60°; ventral valve interior with short myophragm, long vascular trunks; adductor scars small, oval; diductor scars large, triangular; dorsal valve interior with cardinal process pit, median septum, distinct brachial ridges. *Lower Carboniferous (lower Bashkirian):* Donets Basin.——FIG. 264,*4a–d. *I. larinoensis,* lower Bashkirian, western Donets Basin; *a,b,* articulated shell, ventral, dorsal views; *c,d,* ventral valve interior, dorsal valve interior, ×2 (Aisenverg, 1985).

Jakutochonetes AFANAS'EVA, 1977a, p. 31 [**J. jacuticus;* OD]. Shell large, transverse, without sulcus, but narrow furrow anteriorly developed in both valves; pseudodeltidium developed; surface ornamented by very thin, intercalating, branching costellae with prominent growth lines; spines low angled, posterolaterally oriented; ventral myophragm not extending beyond midlength; oval adductor scars; *vascula media* developed; hinge teeth laterally elongated; dorsal valve interior with relatively large cardinal process pit, laterally widened cardinal process, myophore; median septum stout in posterior half of valve; inner socket ridges high, narrow, posteriorly bent. *Upper Carboniferous:* Arctic Siberia.——FIG. 264,*5a–d. *J. jacuticus;* ventral valve internal mold, ventral valve external mold, dorsal valve internal mold, dorsal external mold of articulated shell, ×2 (Afanas'eva, 1977a).

Komukia WATERHOUSE, 1982b, p. 343 [**K. solita;* OD]. Shell thickened, transverse; surface ornamented by low capillae interrupted by low growth lines; spine bases symmetrical; ventral valve interior with strong, long myophragm, two long, broad

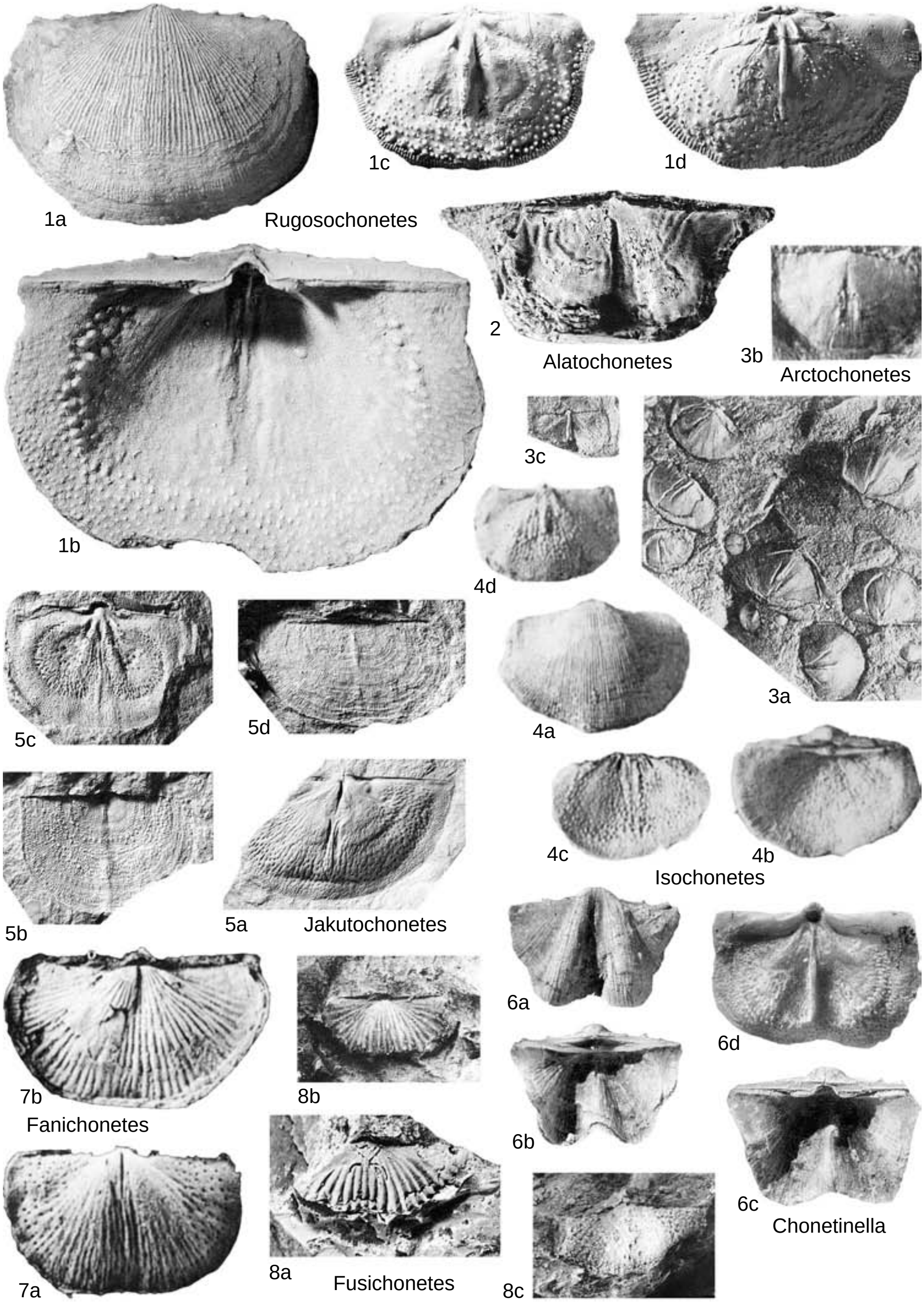


FIG. 264. Rugosochonetidae (p. 405).

vascular trunks; dorsal valve interior with cardinal process pit in largest shells; median septum well developed; strong inner socket ridges; brachial platform well delimited by spinose ridge. *Lower Permian:* Thailand.——FIG. 265,*1a–d.* **K. solita,* Lower Permian, Thailand; *a,b,* articulated shells, dorsal view; *c,d,* ventral valve internal mold, dorsal valve internal mold, ×1.5 (Waterhouse, 1982b).

Neochonetes MUIR-WOOD, 1962, p. 87 [**Chonetes dominus* KING, 1938, p. 259; OD] [=*Quadranetes* SADLICK, 1963, p. 721, obj.]. Small to large sized, almost plano- to moderately concavoconvex rugosochonetids with finely capillate external ornament, feebly to distinctly developed sulcus; low to moderately angled spines; ventral valve interior with prominent myophragm; vascular trunks parallel, deeply impressed; dorsal interior with cardinal process pit, anderidia, median septum, brachial ridges; inner socket ridges well developed; outer socket ridges may be present. *Upper Carboniferous–Upper Permian.*

N. (**Neochonetes**) MUIR-WOOD, 1962, p. 87 [**Chonetes dominus* KING, 1938, p. 259; OD] [=*Quadranetes* SADLICK, 1963, p. 721, obj.]. Small- to medium-sized, slightly concavoconvex; ventral valve may be sulcate; pseudodeltidium vestigial or absent, chilidium present; exterior capillate or smooth anteriorly; spines numerous, oblique, symmetrically arranged; dorsal median septum anteriorly elevated; inner, outer socket ridges commonly developed. *Upper Carboniferous–Upper Permian:* cosmopolitan.——FIG. 265,*2a–d.* **N. (N.) dominus* (KING), Pennsylvanian, Texas; *a,b,* articulated shell, ventral, dorsal views; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (King, 1938).

N. (**Sommeriella**) ARCHBOLD, 1982, p. 10 [**Chonetes pratti* DAVIDSON, 1859a, p. 116; OD] [=*N. (Sommeria)* ARCHBOLD, 1981b, p. 113; obj.]. Similar to *N. (Neochonetes)* but sulcus usually conspicuously developed, gentle fold often developed in dorsal valve, greater convexity in ventral valve, hinge spines at about 40° to 45°; maximum width of mature shells usually anterior of hinge; interiors as for *N. (Neochonetes). Lower Permian (Sakmarian–Kungurian):* Western Australia.——FIG. 265,*3a–e.* **N. (S.) pratti* (DAVIDSON), Holmwood Shales, Irwin River, uppermost Sakmarian–Artinskian; *a,b*, ventral, dorsal sides of articulated shell; *c–e,* dorsal valve interiors, ×2 (Archbold, 1981b).

Paramesolobus AFANAS'EVA, 1975, p. 101 [**P. ivanovae;* OD]. Differs from *Mesolobus* by its shell surface ornamented with relatively strong bifurcating costellae. *Upper Carboniferous (Moscovian–Gzhelian):* Russia.——FIG. 265,*4a–d.* **P. ivanovae,* Kasimovian, Russian Platform; *a,* ventral valve exterior; *b,c,* dorsal valves, exterior, interior; *d,* ventral valve interior, ×2 (Afanas'eva, 1975).

Schistochonetes ROBERTS, 1971, p. 54 [**S. abruptus;* OD]. Shell medium sized, auriculate, mainly characterized by its ornamentation; surface coarsely costate posteriorly, becoming finely or indistinctly costellate anteriorly; costae bifurcating, rarely trifurcating then intercalating from umbo to shell margin; spines symmetrically arranged, orthomorph oblique, low angled (25°); median septum not supporting cardinal process, pit shallow; anderidia anteriorly divergent at 60° to 70°; short, narrow inner socket ridges. *Lower Carboniferous (Viséan):* Australia.——FIG. 266,*1a–d.* **S. abruptus,* Utting Calcarenite, Viséan, northwestern Australia; *a,b,* articulated shell, ventral, lateral views; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Roberts, 1971).

Sokolskya AISENVERG, 1980, p. 55 [**S. calmiusensis;* OD]. Shell medium, thin walled, weakly concavoconvex, transverse, with maximum width at hinge line; shell surface capillate; spines not observed; ventral valve interior with narrow myophragm, small oval adductor scars, large, triangular diductor scars; dorsal valve interior with posteriorly curved short inner socket ridges; no cardinal process pit; short, low median septum, anderidia posteriorly fused with cardinalia. *Upper Carboniferous (lower Kinderscoutian):* Russia (Donets Basin).——FIG. 266,*3a–c.* **S. calmiusiensis,* lower Kinderscoutian, Donets Basin, Russia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×2 (Aisenverg, 1980).

Waagenites PAECKELMANN, 1930, p. 223 [**Chonetes grandicostus* WAAGEN, 1884, p. 638; OD] [=*Dienerella* REED, 1931, p. 18, obj.]. Small, quadrate, ventral valve highly convex, with deep median sulcus; no pseudodeltidium; umbo much incurved; valves with very few coarse costae, or costellate, rarely capillate; ears large, smooth; dorsal septum medianly developed; short socket ridges. *Upper Permian:* Pakistan, Timor, ?North America, Arctic (Spitzbergen).——FIG. 265,*5a–d.* **W. grandicostus* (WAAGEN), upper *Productus* Limestone, Pakistan; *a,* ventral valve exterior, ×1; *b–d,* enlarged ventral, posterior, lateral views, ×2 (Muir-Wood, 1962).

Waterhouseiella ARCHBOLD, 1983a, p. 70 [**Waagenites speciosus* WATERHOUSE & PIYASIN, 1970, p. 112; OD]. Small, distinctly concavoconvex, moderately transverse rugosochonetids with strongly developed, radial, costellate ornament; sulcus weakly developed or obsolescent; dorsal fold low; dorsal interior with strongly developed cardinal process pit, socket plates, lateral septa, median septum; ventral valve with myophragm, variably developed vascular trunks parallel to myophragm. *Permian:* Thailand, Indonesia, Pakistan, Afghanistan.——FIG. 266,*2a–d.* **W. speciosus* (WATERHOUSE & PIYASIN), Kazanian, southern Thailand; *a,b,* ventral valve, ventral, lateral views, ×3; *c,* dorsal view of articulated shell, ×3; *d,*

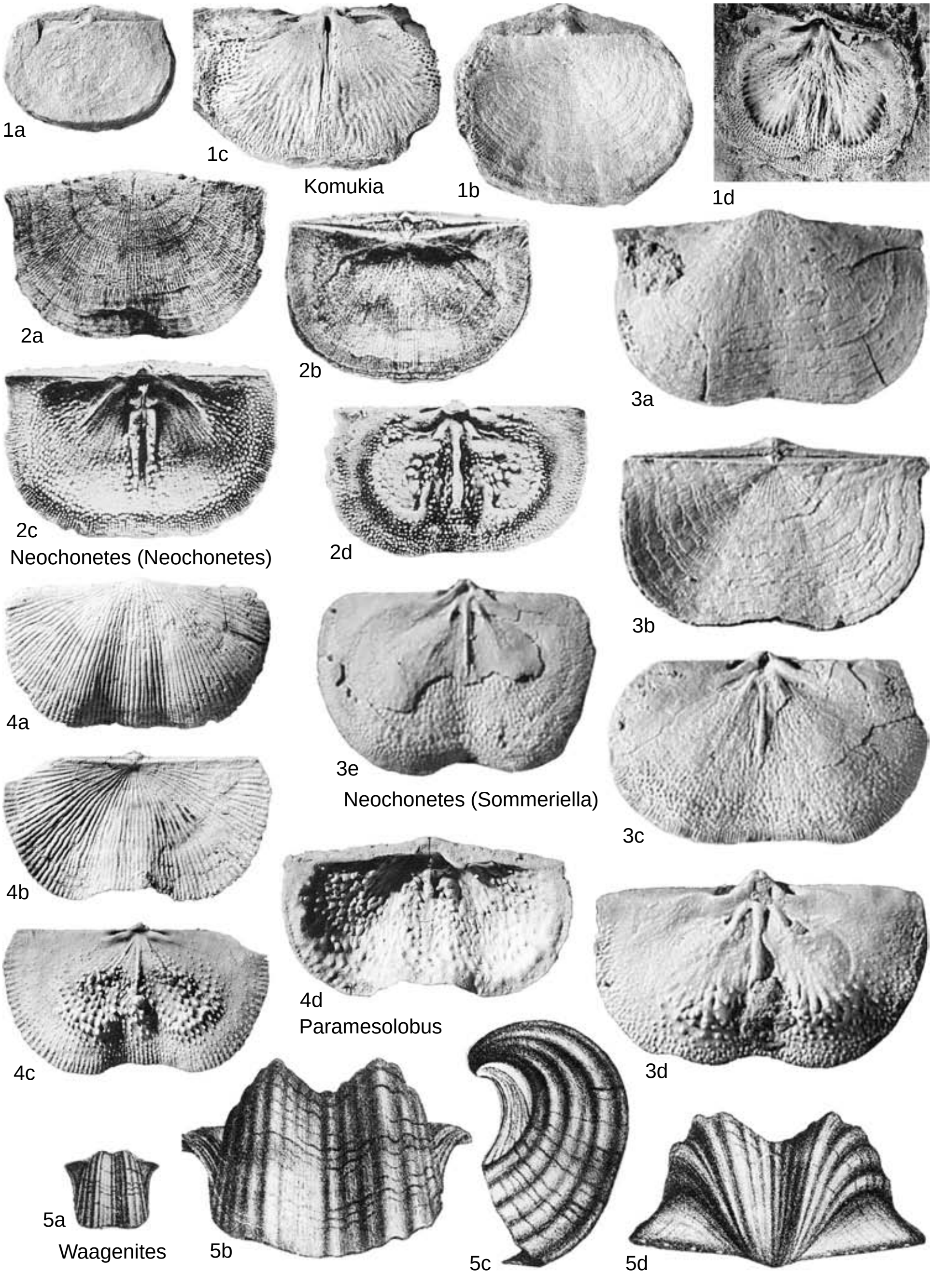


FIG. 265. Rugosochonetidae (p. 405–407).

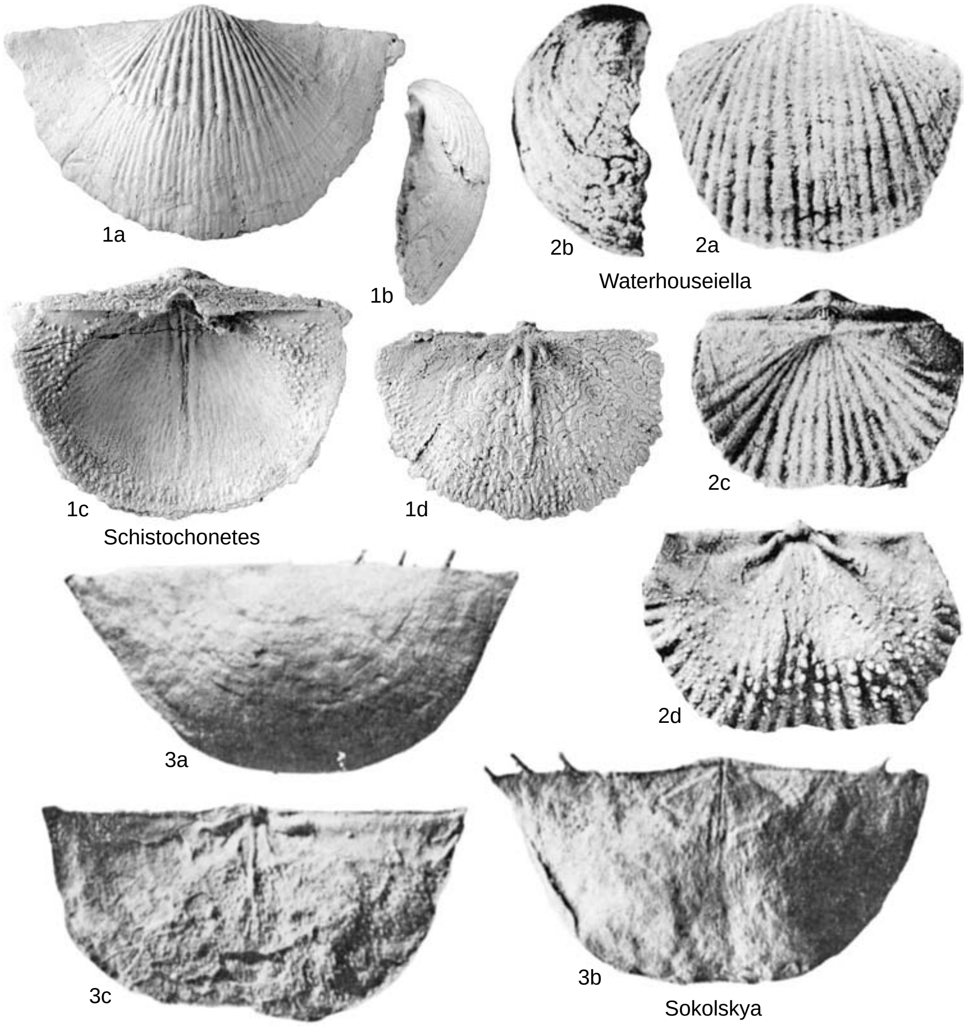


FIG. 266. Rugosochonetidae (p. 407–409).

dorsal valve interior, ×4 (Waterhouse & Piyasin, 1970).

Subfamily CAPILLOMESOLOBINAE Pečar, 1986

[Capillomesolobinae PEČAR, 1986, p. 16]

Small, capillate or smooth Rugosochonetidae; median lobe present or absent in ventral median sulcus. *Upper Carboniferous (Moscovian)–Permian.*

Capillomesolobus PEČAR, 1986, p. 18 [**C. karavankensis;* OD]. Small, finely capillate Rugosochonetidae; median lobe present or absent in ventral median sulcus; spines orthomorph oblique, high angled to vertical. *Upper Carboniferous (Moscovian)–Permian:* North America, Europe (Carnian Alps).——FIG. 267,*1a–d.* **C. karavankensis,* Gzhelian, Karavanke Mountains; *a,* ventral valve, ×2; *b,c,* ventral valve, exterior, interior, ×2; *d,* dorsal valve, internal mold, ×2 (Pečar, 1986).

Mesolobus DUNBAR & CONDRA, 1932, p. 134 [**Chonetes mesolobus* NORWOOD & PRATTEN, 1855b,

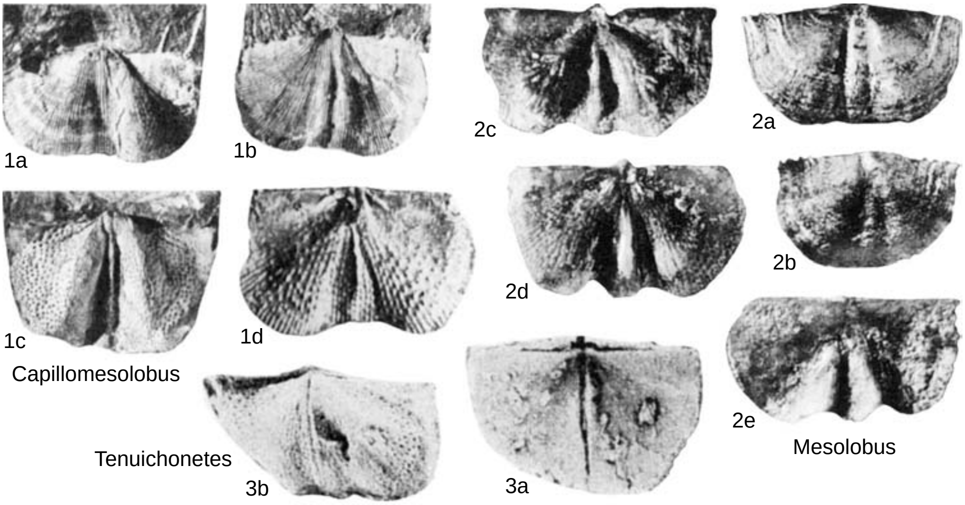


FIG. 267. Rugosochonetidae (p. 409–410).

p. 27; OD]. Small, valves moderately concavoconvex, normally with ventral sulcus bearing median fold, dorsal fold bearing median sulcus; pseudodeltidium, chilidium present; shell capillate or smooth, commonly lamellose; spines oblique, symmetrically arranged; dorsal median septum long, anteriorly elevated, serrated; inner socket ridges parallel to hinge. *Upper Carboniferous:* North America.——FIG. 267,*2a–e*. **M. mesolobus* (NORWOOD & PRATTEN), Missouri; *a,b,* ventral valves, ×2; *c,* dorsal valve interior, ×2; *d,e,* dorsal valve, interior, exterior, ×2 (Muir-Wood, 1962).

Tenuichonetes JING & HU, 1978, p. 109[125] [**Chonetes tenuilirata* CHAO, 1928, p. 26; OD]. Shell medium, trapezoidal; shell surface capillate; ventral valve moderately convex; deep ventral sulcus originating at beak, with single plication in sulcus; spines orthomorph oblique, symmetrically arranged; ventral valve interior with long myophragm; dorsal valve interior with cardinal process pit; long median septum; long, straight inner socket ridges parallel to hinge, short anderidia; no brachial ridges. *Lower Permian:* China.——FIG. 267,*3a,b.* **T. tenuilirata* (CHAO), Lower Permian, China; dorsal valve internal mold, ventral valve internal mold, ×2 (Jing & Hu, 1978).

Subfamily DELEPINEINAE Muir-Wood, 1962

[Delepineinae MUIR-WOOD, 1962, p. 33]

Shell medium to large, almost plano- to markedly concavoconvex, transverse in outline; ventral valve thickened; radial ornamentation capillate to costellate; ventral interarea flat, apsacline to orthocline; dorsal interarea hypercline; pseudodeltidium, chilidium present, usually wide; numerous, symmetrically arranged spine canals crossing posterior margin of ventral valve; spines usually poorly developed, orthomorph oblique or irregularly curved, low to medium angled; dorsal median septum long, narrow, widening, tapering posteriorly, not supporting cardinal process; cardinal process short, widened, with anterior margin almost vertical above valve floor, more or less concave anteriorly, bounded by cardinal process pit; short, weakly developed, slightly divergent anderidia; inner socket ridges short, posteriorly concave, almost parallel to hinge line. *Lower Carboniferous (Tournaisian)–Upper Permian.*

Delepinea MUIR-WOOD, 1962, p. 99 [**Productus comoides* J. SOWERBY, 1822 in 1821–1822, p. 31; OD]. Large, markedly transverse in outline, with posteriorly thickened ventral valve; longitudinal profile strongly arched posteriorly; radial ornamentation capillate to costellate; spines orthomorph oblique when preserved. *Lower Carboniferous (Tournaisian–Viséan):* France, Belgium, Germany, Great Britain, Russia, northern Africa, Asia, Australia.——FIG. 268*a,b.* **D. comoides* (SOWERBY), Viséan, Westmorland, England; articulated shell, ventral, dorsal views, ×1 (Muir-Wood, 1962).——Fig. 268*c,d. D. destinezi* (Vaughan), Viséan, Fermanagh, Northern Ireland; ventral valve interior, accessory adductor scars, ×1 (Muir-Wood, 1962).——Fig. 268*e,f. D. carinatus* (Garwood), Viséan, Westmorland, England; ventral valve exterior, dorsal valve interior, ×1 (Muir-Wood, 1962).

Gibbochonetes Aisenverg, 1971, p. 70 [**Delepinea (Gibbochonetes) forniculata;* OD]. Shell thin, medium to large, strongly concavoconvex; surface capillate with almost indistinct concentric fila; ventral valve interior with short myophragm, large diductors, poorly impressed adductors; dorsal valve interior with low cardinal process; median lobes of myophore higher than lateral ones; small cardinal process pit present; median septum, anderidia fairly well developed. [The author initially compared his new subgenus to *Delepinea,* and it is provisionally left here within the subfamily Delepineinae, but the presence of cardinal process pit would possibly imply a close relationship to the subfamily Rugosochonetinae.] *Lower Carboniferous (upper Tournaisian–lower Viséan):* Russian Platform.——Fig. 269,*1a–d.* **G. forniculata,* upper Tournaisian, Donetz Basin, Russia; *a–c,* ventral valve exterior, ventral, lateral, posterior views, ×2; *d,* dorsal valve interior, ×2 (Aisenverg, 1971).

Megachonetes Sokolskaya, 1950, p. 42 [**Chonetes siblyi* Thomas, 1919, p. 612 (also Paeckelmann, 1930, p. 274); OD; *nom. nov. pro Chonetes compressa* Sibly, 1908, p. 78, *non* Waagen, 1884, p. 630]. Medium to large, almost plano- to moderately concavoconvex; ventral valve slightly thickened; surface finely capillate; irregularly curved spines, extending at 45 to 60°. *Lower Carboniferous (Tournaisian–upper Viséan):* Belgium, France, Germany, Great Britain, Ireland, Russia, northern Africa, Asia, Australia.——Fig. 269,*3a–e.* **M. siblyi* (Thomas), Lower Carboniferous, Viséan, England; *a–c,* articulated shell, ventral, dorsal, lateral views, ×1.25; *d,* ventral valve posterior part with interarea, pseudodeltidium; *e,* ventral valve interior with accessory adductor scars, ×2 (Muir-Wood, 1962).

Mongolochonetes Afanas'eva, 1991, p. 98 [**M. inaequalis;* OD]. Differs from *Megachonetes* in its smaller size, its slightly concavoconvex longitudinal profile, development of ventral sulcus, dorsal fold, and lower-angled spines at 30° to 35°. *Upper Permian:* southern Mongolia. Material not suitable for illustration.

Petalochonetes Afanas'eva in Afanas'eva & others, 1988, p. 52 [**P. altaicus;* OD]. Large, with well-developed ventral sulcus; spines medium angled, at 50° to 60°; radial ornamentation of thin, dense costellae crossed by fila; dorsal valve interior without cardinal process pit; median septum not supporting cardinal process; no brachial ridges; anderidia not fused posteriorly, anteriorly divergent at 60° to 70°. [The development of the ventral sulcus would better fit with the subfamily Rugosochonetinae. The subfamilial assignment cannot be stated without detailed revision of the type species.] *Lower Carboniferous:* southern Mongolia.——Fig. 269,*2a–d.* **P. altaicus; a,b,* ventral internal molds, ×2; *c,* dorsal valve internal mold, ×2; *d,* internal mold of the cardinalia, ×6 (Afanas'eva & others, 1988b).

Subfamily PLICOCHONETINAE Sokolskaja, 1960

[Plicochonetinae Sokolskaja in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 222]

Small, strongly cconcavoconvex, costellate to costate rugosochonetids; hinge spines oblique, high angled; fold, sulcus absent; interior generalized, often poorly known. *Carboniferous–Permian.*

Plicochonetes Paeckelmann, 1930, p. 222 [**Chonetes buchianus* de Koninck, 1843, p. 208; OD]. Shell small to medium; ventral valve medianly arched; pseudodeltidium small or absent; shell surface costate, rarely bifurcating, with numerous growth lines; spines high angled (55° to 70°); dorsal valve with well-developed median septum, or without; short, curved, inner socket ridges. *Lower Carboniferous–Upper Carboniferous (Namurian):* Europe, Asia, northern Africa, Australia, North America.——Fig. 270,*1a–c.* **P. buchianus* (de Koninck), lower Namurian, Yorkshire; *a,* ventral valve exterior, ×1.5 (de Koninck, 1847b); *b,* ventral valve interior, ×3 (Muir-Wood, 1962); *c,* dorsal valve interior, ×3 (de Koninck, 1847b).

Hemichonetes Li, Gu, & Su, 1980, p. 343, *non Hemichonetes* Racheboeuf, 1981a [**H. hemipleura;* OD]. Differs externally from *Plicochonetes* by radial ornamentation restricted to posteromedian part of shell, and by development, or not, of low sulcus, fold; internally by short dorsal median septum, large cardinal process pit, long, parallel, inner socket ridges. *Lower Permian:* northeastern China.——Fig. 270,*5a,b.* **H. hemipleura,* Lower Permian, northeastern China; dorsal valve internal mold, external mold, ×2 (Li, Gu, & Su, 1980).

Prorugaria Waterhouse, 1982a, p. 40 [**P. thailandica;* OD]. Small shell with moderately developed sulcus, fold; hinge wide; strong costae, costellae bifurcating on flanks of sulcus, fold; dorsal valve interior with short median septum, anderidia; inner surface with strong radially arranged endospines forming at least one pair of accessory septalike ridges. *Lower Carboniferous:* Thailand.——Fig. 270,*3a,b.* **P. thailandica;* ventral valve exterior, incomplete dorsal valve interior, ×6 (Waterhouse, 1982a).

Rugaria Cooper & Grant, 1969, p. 4 [**Chonetes hessensis* King, 1931, p. 61; OD]. Small, strongly costate shell; spines oblique; dorsal valve interior with short, well-developed median septum; large cardinal process with deep cardinal process pit; broad, strongly endospinose anterior slope in dorsal

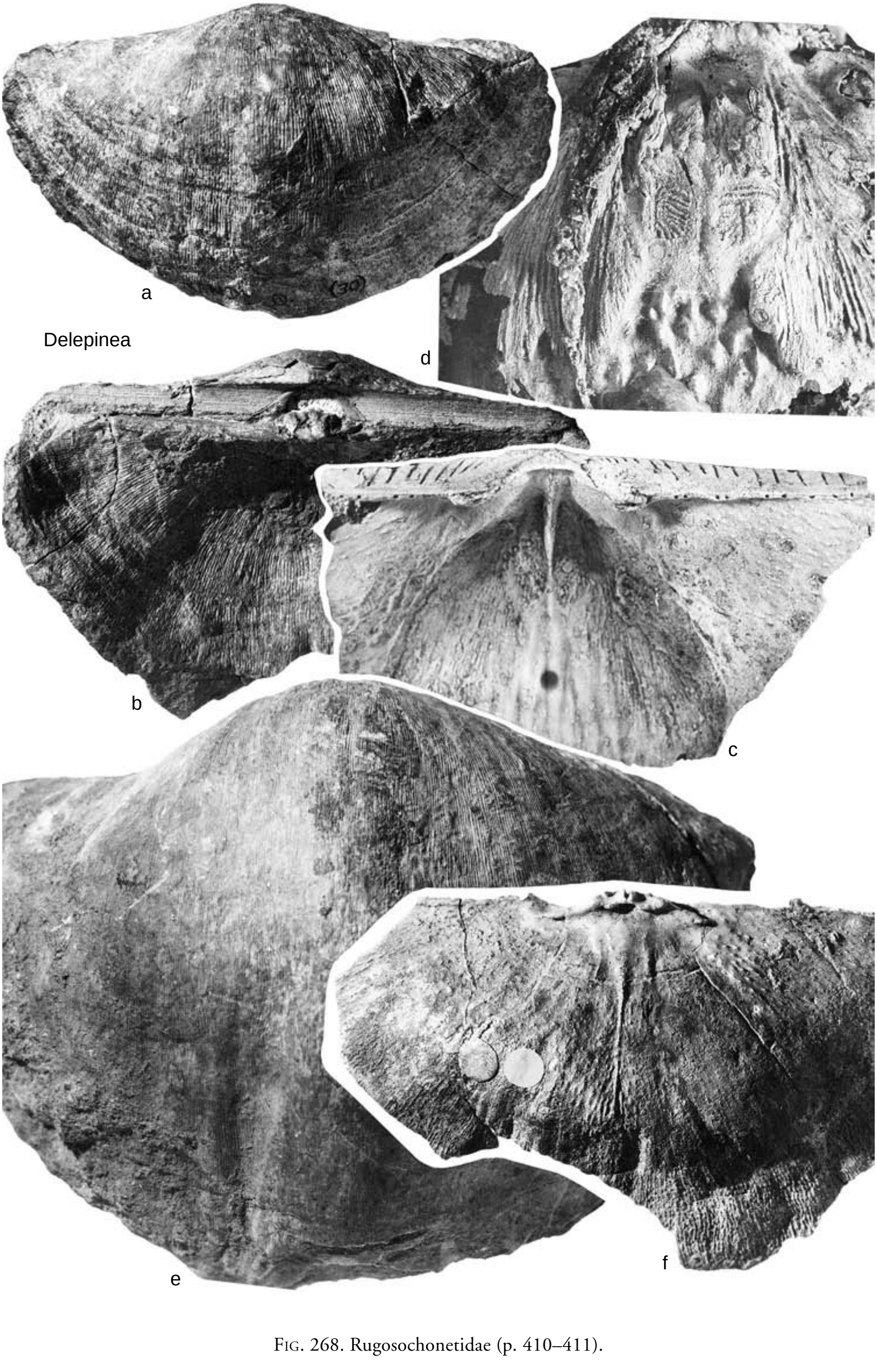


FIG. 268. Rugosochonetidae (p. 410–411).

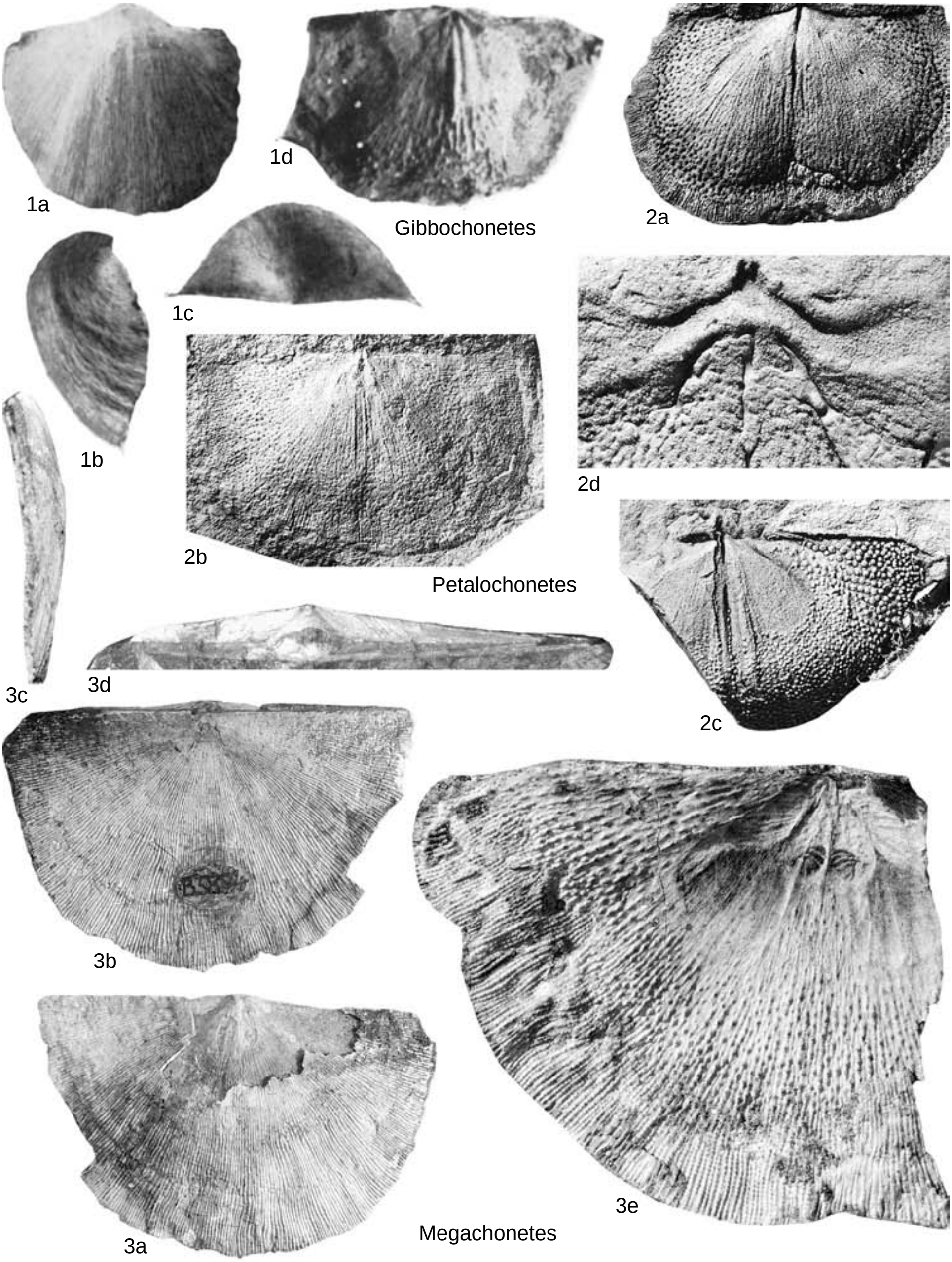


FIG. 269. Rugosochonetidae (p. 411).

valve. *Permian (Asselian):* USA (Texas).——FIG. 270,*2a–d.* **R. hessensis* (KING), Asselian, Hess Canyon; *a,b,* articulated shell, ventral, dorsal views, ×4; *c,d,* dorsal valve interiors, ×4 (Cooper & Grant, 1969).

Sulcirugaria WATERHOUSE, 1983b, p. 112 [**S. transversa;* OD]. Shell transverse to subelongate with well-developed fold, sulcus; shell surface covered with strong bifurcating costellae; spines not observed; ventral valve interior with short

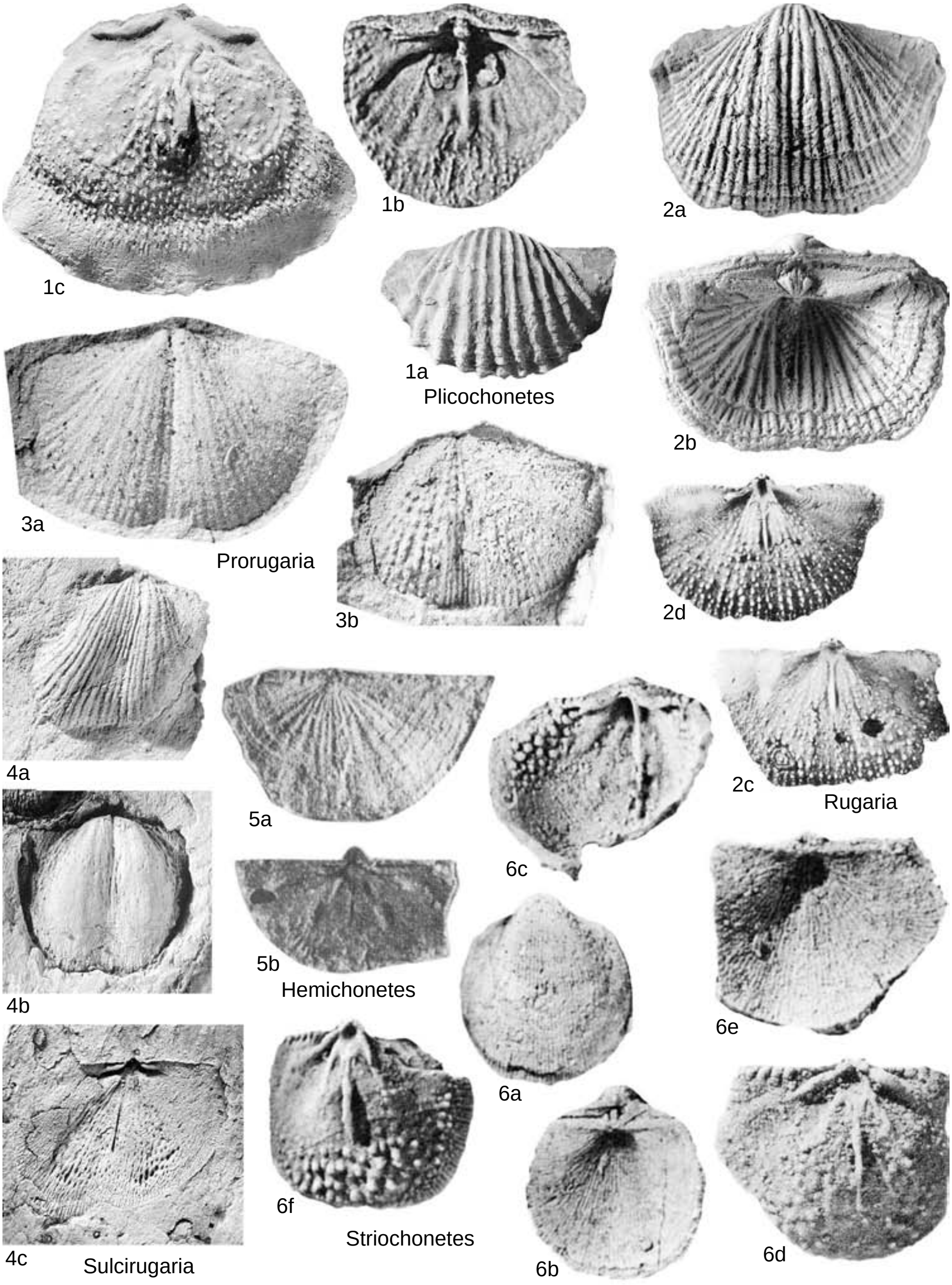


FIG. 270. Rugosochonetidae (p. 411–415).

myophragm, low vascular trunks; dorsal valve interior with low median septum, well-developed adductor scars. *Upper Permian (Tatarian):* Nepal.——FIG. 270,*4a–c.* **S. transversa;* ventral valve exterior, ventral valve internal mold, dorsal valve internal mold, ×2 (Waterhouse, 1983b).

Subfamily STRIOCHONETINAE Waterhouse & Piyasin, 1970

[Striochonetinae Waterhouse & Piyasin, 1970, p. 106]

Hinge denticulated chonetids; without sulcus, fold; ventral valve interior with long, bladelike myophragm; dorsal valve interior with cardinal process pit, median septum or breviseptum, strong anderidia, short, oblique inner socket ridges; no accessory septa. *middle Permian.*

Striochonetes Waterhouse & Piyasin, 1970, p. 106 [**S. scutella;* OD] [=*Ratburia* Yanagida, 1970, p. 85, obj.]. Small, markedly concavoconvex subcircular shell; shell surface capillate; spines developed in juvenile forms only; posterolateral parts of ventral valve interior with strong endospines; dorsal valve interior with small cardinal process, median septum arising anteriorly; strong anderidia; large anterior adductor scars. *middle Permian:* Thailand.——Fig. 270,*6a–f.* **S. scutella; a,b,* articulated shell, ventral, dorsal views, ×3; *c,* incomplete ventral valve interior, ×3; *d,e,* dorsal valve interior, exterior, ×4; *f,* dorsal valve interior, ×4 (Waterhouse & Piyasin, 1970).

Subfamily SVALBARDIINAE Archbold, 1982

[Svalbardiinae Archbold, 1982, p. 4]

Small to medium sized, externally smooth rugosochonetids; dorsal exterior pseudocapillate when worn; spines orthomorph oblique at low to moderate angle. *Lower Carboniferous–Upper Permian (Tatarian).*

Svalbardia Barchatova, 1970, p. 78 [**Chonetes capitolinus* Toula, 1875; OD]. Small, planoconvex to weakly concavoconvex; short, orthomorph oblique, low-angled spines; ventral valve coarsely pseudopunctate; dorsal interior with anteriorly prominent median septum, anderidia posteriorly fusing anterior to cardinal process pit; brachial ridges well defined; recurved anterior portions raised in mature individuals. *Permian (Kungurian–Kazanian):* Russia, Spitzbergen, Canadian Arctic, Australia.——Fig. 271,*1a–d. S. thomasi* Archbold, Baker Formation, Kungurian, Western Australia; *a,b,* articulated shell, dorsal, ventral views, ×3.5; *c,* ventral valve interior, ×4; *d,* dorsal valve interior, ×4.5 (Archbold, 1981c).

Capillonia Waterhouse, 1973, p. 37 [**Lissochonetes brevisulcus* Waterhouse, 1964, p. 21; OD]. Shell medium; ventral valve smooth, dorsal valve capillate; spines orthomorph oblique, symmetrically arranged; dorsal valve interior with thin median septum, short anderidia; brachial ridges with raised recurved anterior portions. [Archbold (1982, p. 4) interpreted the original illustrations of Waterhouse (1964) and thought that the dorsal valve was smooth instead of capillate, although Waterhouse (1973) concluded that the ornament was original and not worn. Without further information the description of capillate dorsal valve is maintained here.] *middle Permian:* New Zealand.——Fig. 271,*2a–c.* **Capillonia brevisulcus* (Waterhouse), Arthurton Group, ?Kazanian, South Island, New Zealand; articulated shell, dorsal side, ventral valve interior, incomplete dorsal valve interior, ×2 (Waterhouse, 1964).

Chonetinetes Cooper & Grant, 1969, p. 3 [**C. reversus;* OD]. Small, smooth, alate, dorsally deeply concave, anteriorly tapering shell; ventral sulcus, dorsal fold better developed in the umbonal region; dorsal valve interior with short median septum; erect cardinal process having deep cardinal process pit; anderidia reduced but anterior slope of dorsal valve deeply sulcate, lateral regions elevated. *Upper Permian (Kazanian–Tatarian):* USA (Texas).——Fig. 271,*5a–e.* **C. reversus,* Road Canyon Formation, upper Artinskian, Texas; *a,* ventral valve exterior, ×3; *b,* articulated shell, dorsal side, ×4; *c,* ventral valve interior, ×3; *d,e,* dorsal valve interiors, ×3 (Cooper & Grant, 1975).

Dyoros Stehli, 1954, p. 312 [**Chonetes consaguineus* Girty, 1929, p. 409; OD] [=*Stauromata* Hoover, 1981, p. 51, obj.]. Wide-hinged smooth shells with sulcus varying from deep to barely visible; ventral valve interior, visceral region usually strongly fringed by spines on anterolateral side. *Lower Permian (Sakmarian)–Upper Permian (Kazanian).*

D. (**Dyoros**) Stehli, 1954, p. 312 [**Chonetes consanguineus* Girty, 1929, p. 409; OD]. Strong angular ears, deep ventral sulcus. *Permian:* USA (Texas).——Fig. 272,*1a–c.* **D. (D.) consanguineus* (Girty), Bone Spring and Skinner Ranch Formations, Asselian, Texas; *a,* articulated shell, dorsal side, ×2; *b,* ventral valve interior, ×2; *c,* dorsal valve interior, ×4 (Cooper & Grant, 1975).

D. (**Lissosia**) Cooper & Grant, 1975, p. 1241 [**D. (L.) concavus;* OD]. Wide hinge, strong ears but sulcus conspicuously developed in late adult stages. *Permian (Artinskian–Kazanian):* USA (Texas).——Fig. 273*a–c.* **D. (L.) concavus,* Word Formation, Kazanian, Texas; ventral valve exterior, ventral valve interior, dorsal valve interior, ×4 (new).

D. (**Tetragonetes**) Cooper & Grant, 1975, p. 1246 [**D. (T.) quadrangulatus;* OD]. Relatively narrow hinged, reduced ears, rectangular outline, strong sulcus, moderately developed interior details. *Permian (Artinskian–Kazanian):* USA (Texas).——Fig. 272,*2a–d.* **D. (T.) quadrangulatus,* Word Formation, Kazanian, Texas; *a–c,* ventral valve, exterior, anterior, internal view, ×3; *d,* dorsal valve interior, ×3 (new).

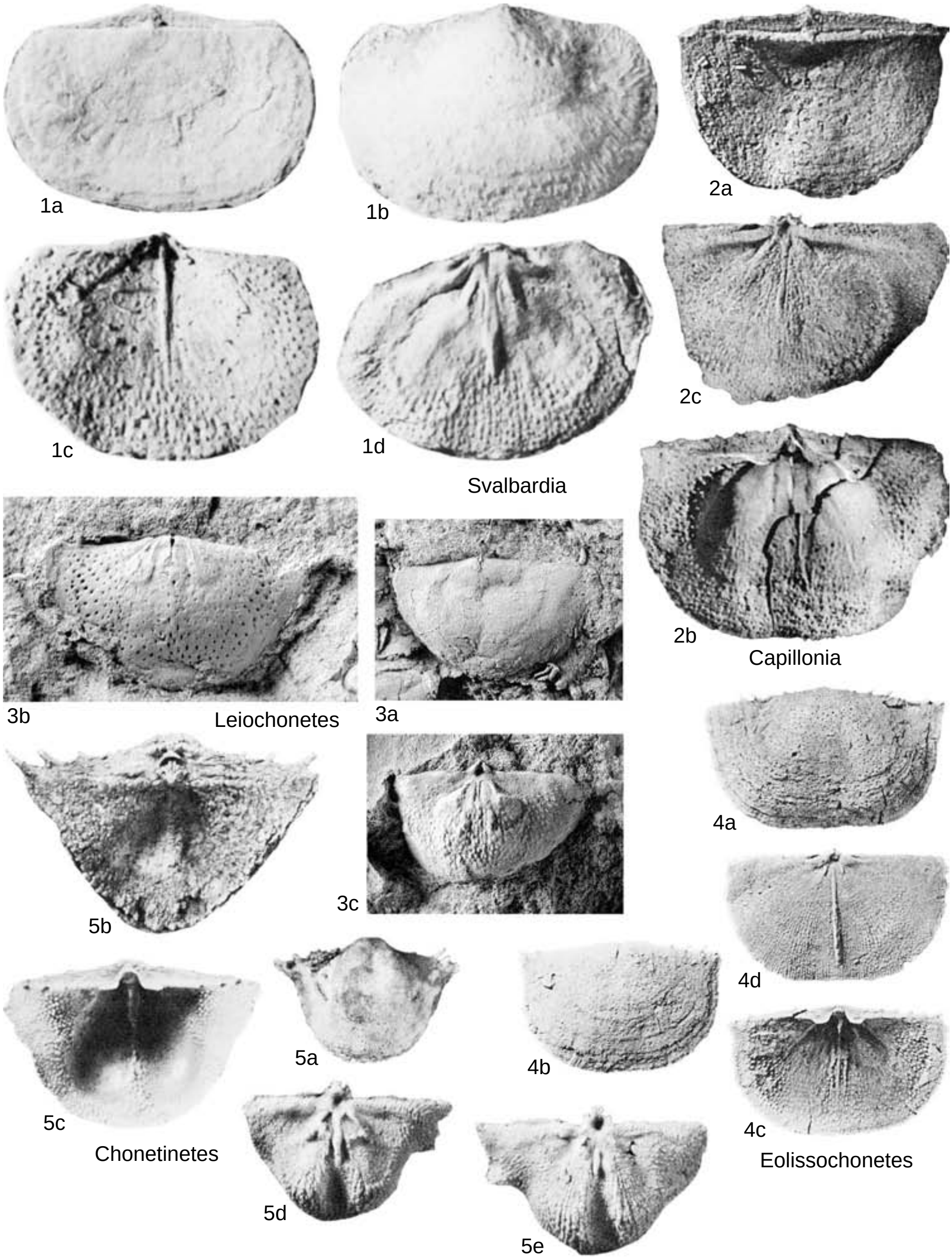


FIG. 271. Rugosochonetidae (p. 415–417).

Eolissochonetes HOARE, 1960, p. 220 [**Chonetes laevis* KEYES, 1888, p. 229, *non* DAVIDSON, 1866; OD; =*Eolissochonetes keyesi* MUIR-WOOD, 1962, p. 76; OD]. Differs from *Svalbardia* by the very short anderidia that usually do not fuse with median septum posteriorly, and by poorly developed brachial ridges; dorsal valve interior with long, anteriorly elevated median septum. *Lower Carboniferous (Namurian):* North America.——FIG. 271,4*a–d*. **E. keyesi* (MUIR-WOOD), Namurian, Missouri; *a,b,*

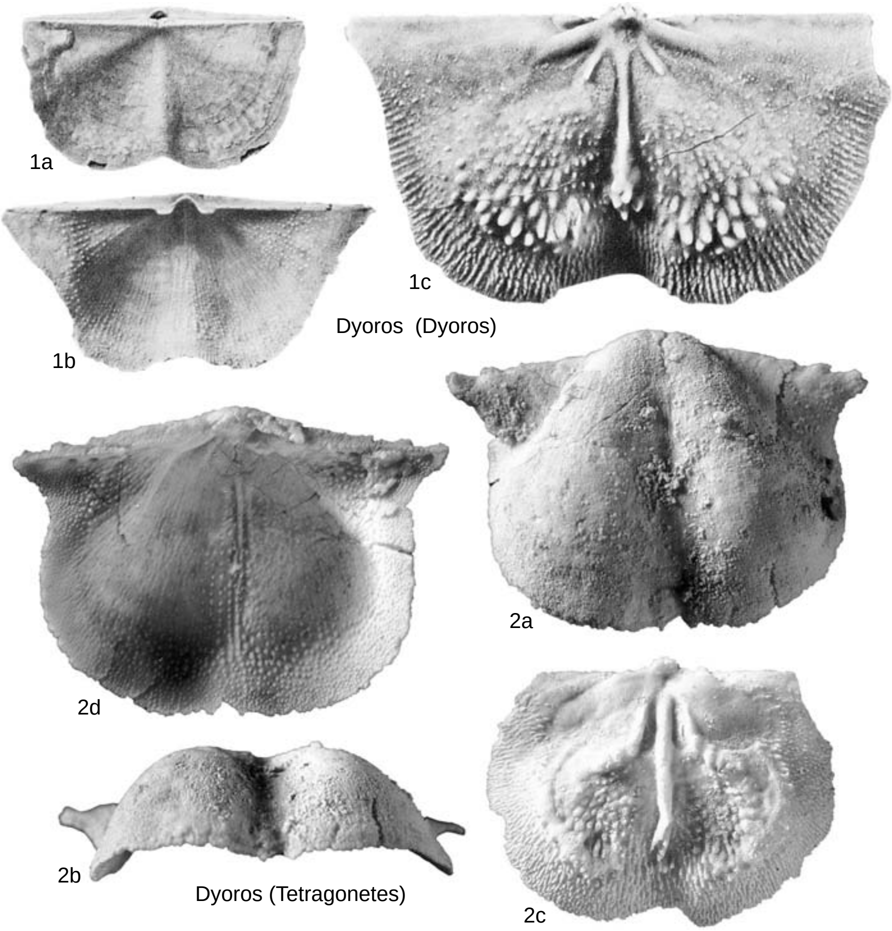


FIG. 272. Rugosochonetidae (p. 415).

ventral valve exteriors, ×2; *c,* ventral valve interior, ×2; *d,* dorsal valve interior, ×2 (Hoare, 1960).

Komiella Barchatova, 1970, p. 62 [**Chonetes omolonensis* Licharew, 1934c, p. 11; OD]. Differs from *Lissochonetes* by its stout anderidia, strong median septum fused anteriorly of deep cardinal process pit; shell subquadrate; dorsal valve interior with poorly defined brachial ridges. [Archbold (1981c, p. 3) discussed the relationships between *Svalbardia* and *Komiella.* Afanas'eva (1988) regarded *Komiella* as junior synonym of *Lissochonetes,* but the author follows Archbold's 1982 opinion, considering *Komiella* useful for separating a group of species with strongly developed dorsal internal structures from *Lissochonetes.* To synonymize these genera would be premature.] *Upper Carboniferous (Moscovian)–Permian (Kazanian):* Russia.

Leiochonetes Roberts, 1976, p. 26 [**L. salisburyensis;* OD]. Small, moderately to strongly concavoconvex; spines orthomorph oblique, almost perpendicular, symmetrically arranged; dorsal valve interior with short median septum; cardinal process pit well developed; anderidia widely divergent anteriorly. *Lower Carboniferous (Viséan):* eastern Australia.——FIG. 271,*3a–c.* **L. salisburyensis,* Viséan, eastern Australia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×3 (Roberts, 1976).

Leurosina Cooper & Grant, 1975, p. 1260 [**L. marginata;* OD]. Small, widely rectangular in outline; anterior commissure unfolded or broadly deflected dorsally; spines orthomorph oblique. *Lower Permian (Sakmarian–Kungurian):* USA (Texas). ——FIG. 274,*1a–d.* * *L. marginata,* Word Formation, Kazanian, Texas; *a–c,* ventral valve, exterior, interior, anterior view, ×3; *d,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Lissochonetes Dunbar & Condra, 1932, p. 169 [**Chonetes geinitzianus* Waagen, 1884, p. 621; OD; *nom. nov. pro Chonetes glabra* Geinitz, 1866, p. 60, *non* Hall, 1857, p. 117]. Shell transverse, slightly

Fig. 273. Rugosochonetidae (p. 415).

concavoconvex, weakly sulcate; spines orthomorph oblique (40°), symmetrically arranged; delicate dorsal valve internal structures with low, narrow median septum, or breviseptum, and anderidia not fusing posteriorly; cardinal process pit present. *Upper Carboniferous (Namurian)–Permian:* Europe, Asia, northern Africa, North America, Asia; Australia, *Namurian–Permian.*——Fig. 274,*2a–c.* **L. geinitzianus* (Waagen), upper Pennsylvanian, Nebraska; *a,* ventral valve exterior, ×3.5; *b,* articulated shell, dorsal side, ×3; *c,* dorsal valve interior, ×3 (Dunbar & Condra, 1932).

Quadrochonetes Stehli, 1954, p. 309 [**Q. girtyi;* OD; *nom. nov. pro Chonetes quadratus* Girty, 1929, p.

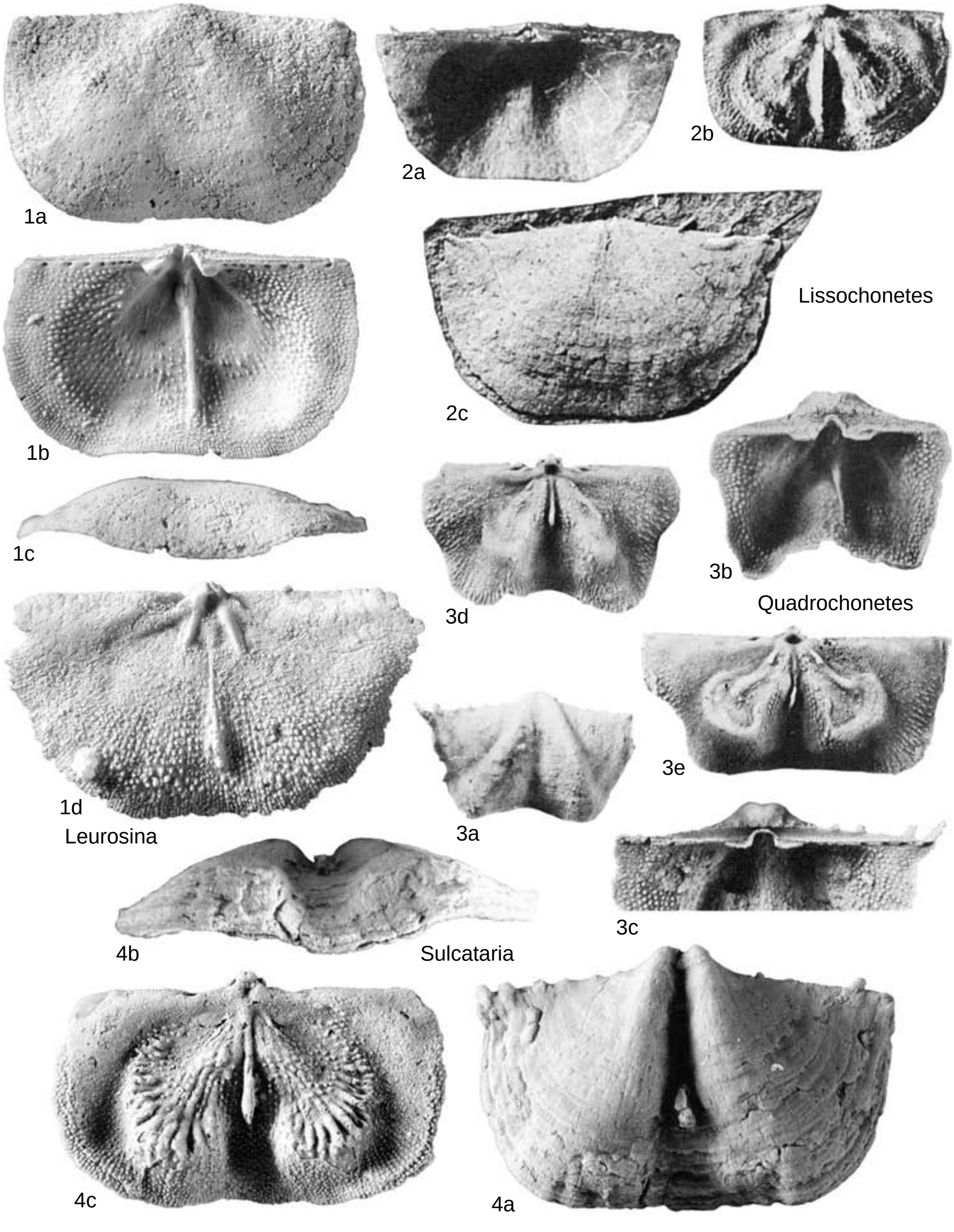


FIG. 274. Rugosochonetidae (p. 417–420).

407, *non Chonetes uralica quadratus* BOLKHOVITINIVA & MARKOV, 1926, p. 26, *nec* NIKITIN, 1890]. Small, quadrate, strongly concavoconvex, smooth shell; prominent dorsal fold, deep ventral sulcus; ears large; spines orthomorph oblique, high angled; dorsal valve interior with low, short median septum; brachial ridges obscure or absent; short, curved inner socket ridges; anderidia anteriorly widely divergent. *Carboniferous–Lower Permian:* USA.——FIG. 274,*3a–e.* **Q. girtyi*, Bone Spring Formation, Artinskian, Texas; *a,* ventral valve exterior, ×2; *b,* ventral valve interior, ×3; *c,* posterior part of ventral valve, ×4; *d,e,* dorsal valve interiors, ×3 (Cooper & Grant, 1975).

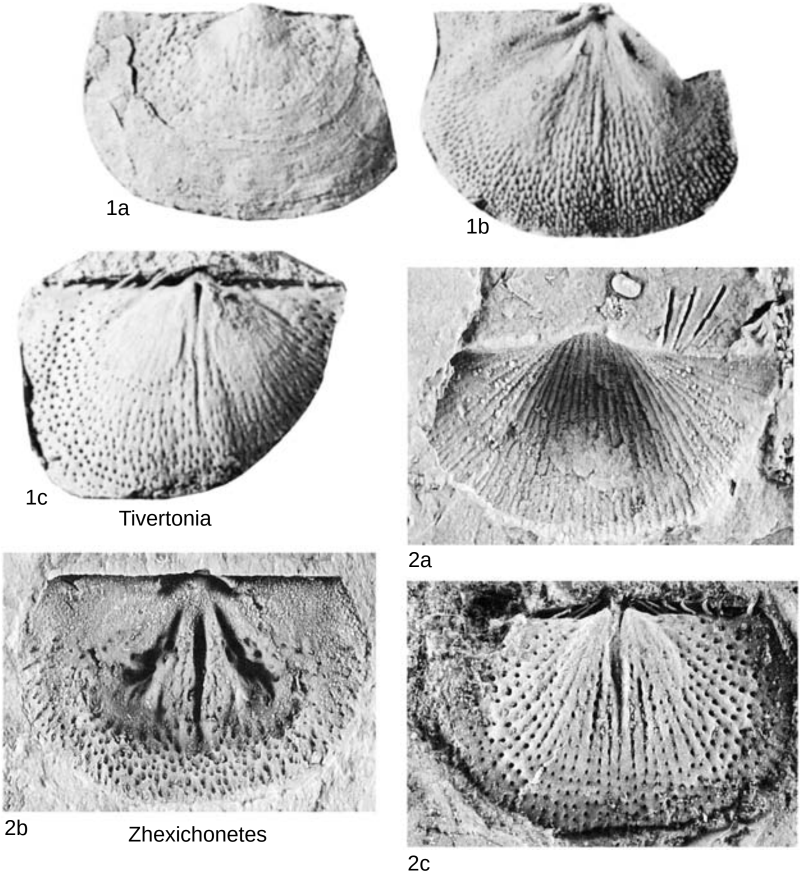


FIG. 275. Rugosochonetidae (p. 420).

Sulcataria COOPER & GRANT, 1969, p. 5 [**Chonetina? rostrata* DUNBAR & CONDRA, 1932, p. 150; OD]. Small, smooth shell with deeply sulcate ventral valve; dorsal valve weakly concave with strong median fold; ventral valve interior with broad, elevated adductor ridge, flattened margins; dorsal valve interior with thick median septum, strongly lobed anterior visceral region. *Lower Permian (Asselian):* USA (Texas).——FIG. 274,*4a–c*. **S. rostrata* (DUNBAR & CONDRA), Graham Formation, Asselian, Texas; *a,b,* ventral valve, ventral, anterior views, ×4; *c,* dorsal valve interior, ×4 (Cooper & Grant, 1969).

Tivertonia ARCHBOLD, 1983a, p. 71 [**Lissochonetes yarrolensis* MAXWELL, 1954a, p. 35; OD]. Shell smooth, gently concavoconvex; ventral valve with short, thin spines at moderate angle to hinge; mature dorsal valve interior with distinct cardinal process pit, lateral septa, long median septum; maximum width of shell of immature individuals at midlength of valves, lending semicircular outline to shell; sulcus absent or ill defined. *Lower Permian (Sakmarian):* eastern Australia, Argentina.——FIG. 275,*1a–c*. **T. yarrolensis* (MAXWELL), Yarrol Formation, Queensland; *a,* ventral valve exterior, ×4; *b,* dorsal valve interior, ×3.25; *c,* ventral valve internal mold, ×3.75 (Archbold, 1983a).

Zhexichonetes LIANG, 1982, p. 201 [**Z. longispina;* OD]. Small, costellate shell without sulcus, fold; spines long, vertical near umbo, posterolaterally directed near angles; dorsal valve interior with stout median septum not supporting cardinal process; strongly developed anderidia, high, anteriorly thickened. *Lower Permian:* China (Zhejiang).——FIG. 275,*2a–c*. **Z. longispina,* Jia Shan Formation, Lower Permian; ventral valve external mold, dorsal valve internal mold, ventral valve internal mold, ×4.7 (Liang, 1990).

Subfamily UNDULELLINAE
Cooper & Grant, 1975

[Undulellinae COOPER & GRANT, 1975, p. 1286]

Small smooth rugosochonetids; exterior of dorsal valve pseudocapillate when worn;

spines orthomorph, oblique or perpendicular, symmetrically arranged; brachial ridges, dorsal median septum prominent; cardinal process small. *Permian (Sakmarian–Kungurian).*

Undulella Cooper & Grant, 1969, p. 5 [**U. undulata;* OD]. Small, slightly concavoconvex, subrectangular in outline with cardinal extremities at 90°; anteromedian margin of shell deflected dorsally; spines orthomorph, almost perpendicular. *Lower Permian (Artinskian–Kungurian):* USA (Texas).——Fig. 276,*1a–c.* **U. undulata,* Word Formation, Texas; ventral valve exterior, interior, dorsal valve interior, ×4 (Cooper & Grant, 1969).

Micraphelia Cooper & Grant, 1969, p. 4 [**M. scitula;* OD]. Small, unfolded, narrow-hinged rugosochonetids with orthomorph oblique spines; interior with thickened, spinose anterolateral visceral region. *Lower Permian (Sakmarian–Artinskian):* USA (Texas).——Fig. 276,*2a–c.* **M. scitula,* Bell Canyon Formation, Texas; ventral valve exterior, interior, dorsal valve interior, ×4 (Cooper & Grant, 1969).

Subfamily LAMELLOSIINAE
Cooper & Grant, 1975

[Lamellosiinae Cooper & Grant, 1975, p. 1270]

Concentrically lamellose rugosochonetids without radial ornament; pseudocapillate shell when worn. *Permian.*

Lamellosia Cooper & Grant, 1975, p. 1270 [**L. lamellosa;* OD]. Small, subtrapezoidal; spines orthomorph oblique, symmetrically arranged. *Upper Permian (Kazanian–Tatarian):* USA (Texas).——Fig. 276,*4a,b.* **L. lamellosa;* Guadalupian, Texas; ventral valve exterior, interior, ×3 (Cooper & Grant, 1975).

Parademonedys Yang Xue-chang, 1984, p. 208[332] [**P. huananensis;* OD]. Small, subtrapezoidal, strongly concavoconvex; spines present but not described; interiors unknown. [The author compared this new genus with *Demonedys* and placed it within the Anopliinae, but it seems provisionally better placed within the Lamellosiinae because of the nature of its ornamentation, which is similar to that of *Lamellosia.*] *Lower Permian:* southern China.——Fig. 276,*3.* **P. huananensis,* southern China; ventral valve exterior, ×3 (Yang Xue-chang, 1984).

Subfamily QUINQUENELLINAE
Archbold, 1981

[Quinquenellinae Archbold, 1981a, p. 205]

Small, subquadrate, with smooth exterior; shell surface not pseudocapillate when worn; ventral sulcus absent or ill defined; spines symmetrically arranged; dorsal interior with short anderidia, pair of long accessory septa, variably developed median septum. *Permian.*

Quinquenella Waterhouse, 1975, p. 2 [**Q. glabra;* OD]. Transverse, subquadrate to subtrapezoidal, with maximum width at hinge line; orthomorph oblique spines; dorsal valve interior with variably developed, thin median septum, long, thin accessory septa, short, strong anderidia usually fused posteriorly; cardinal process pit variably developed. *Permian (Artinskian–Tatarian):* Australia, Indonesia, Himalaya, ?Burma, ?Malaysia, ?Afghanistan.——Fig. 276,*5a–d.* *Q. magnifica* Archbold, Aifat Formation, Irian Jaya, Permian, Indonesia; *a,* dorsal side of articulated shell, latex, ×4; *b,* ventral valve internal mold, ×4; *c,* dorsal valve internal mold, ×4.5; *d,* juvenile dorsal valve internal mold, ×8 (Archbold, 1981d).

Sandrella Waterhouse, 1985, p. 212 [**S. platina;* OD]. Smaller medium, smooth shell, almost planoconvex; spines not observed; ventral valve interior with short, narrow myophragm; dorsal valve interior with cardinal process pit, low, ill-developed median septum, long anderidia, five pairs of low, narrow accessory septa. *Permian:* Himalayas, *Lamnimargus himalayaensis* Zone.——Fig. 276,*6a–c.* *S. platina, Gungri formation, Permian, *Lamnimargus himalayensis* Zone, western Himalayas; *a,* ventral valve internal mold, ×1.5; *b,* dorsal valve interior, latex, ×2; *c,* dorsal valve interior, latex, ×3 (Waterhouse, 1985).

Family DAVIESIELLIDAE
Sokolskaja, 1960

[Daviesiellidae Sokolskaja in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 223]

Large shell with thickened ventral valve; very low interareas; no spine row; adductor scars partly or wholly dendritic; detached rounded accessory adductor scars present; dorsal valve interior without cardinal process pit; brachial ridges anteriorly directed. *Lower Carboniferous (Viséan).*

Daviesiella Waagen, 1884, p. 613 [**Productus llangollensis* Davidson, 1863, p. 277; SD Oehlert, 1887b, p. 1280]. Large, highly concavoconvex shell; ventral valve massive, much thickened; pseudodeltidium lacking, chilidium present; ventral valve interior with dendritic adductor scars; dorsal valve interior with massive median septum supporting cardinal process. [*Daviesiella* differs from all other chonetoidean genera in its shell shape (much thickened ventral valve, very low interareas), as well as in the lack of spine row, pseudodeltidium and anderidia. Moreover the adductor scars are typically dendritic. In this sense the position of *Daviesiella* within the Chonetoidea remains uncertain and it would probably be better assigned to the superfamily Productoidea.] *Lower Carboniferous*

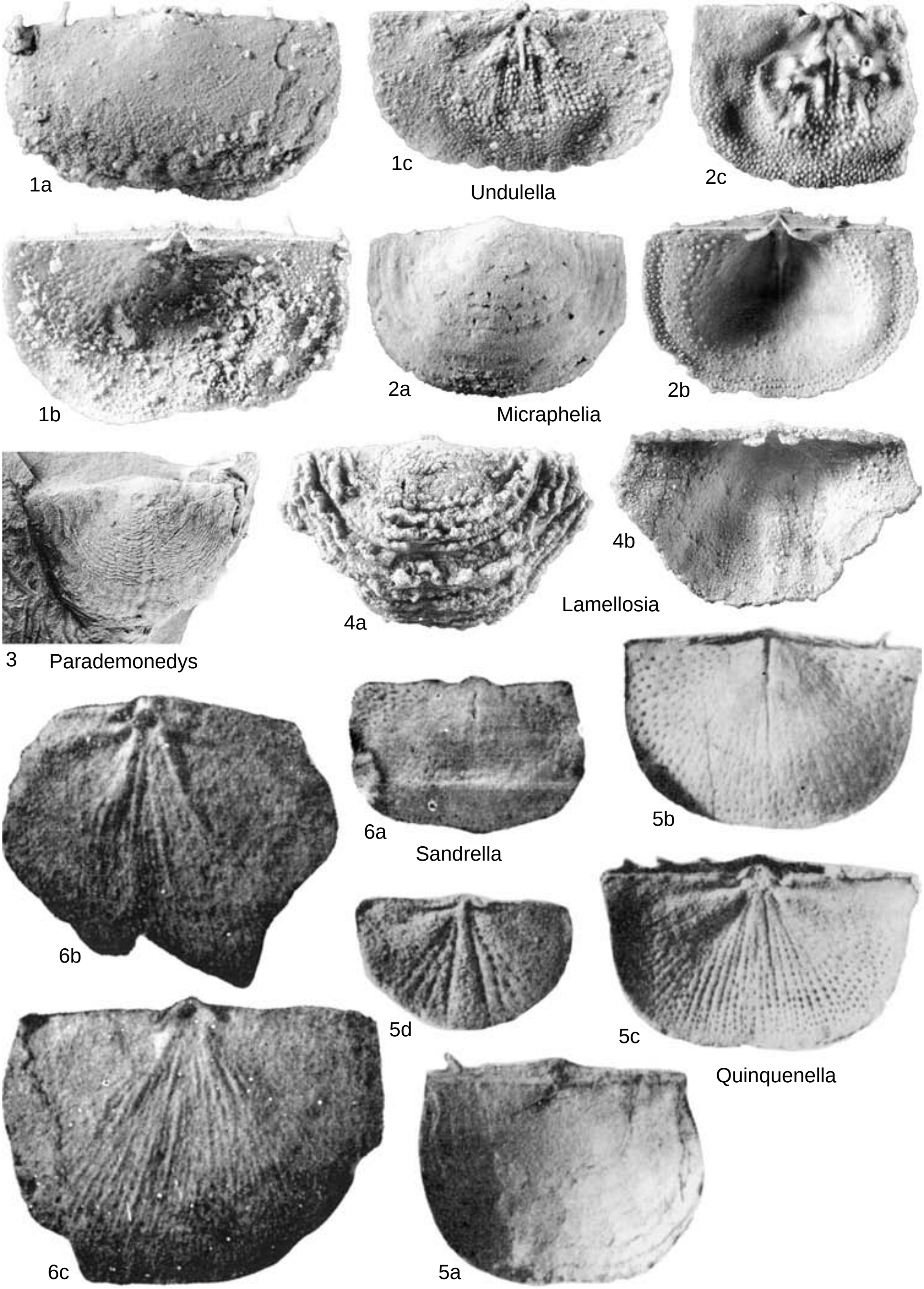


FIG. 276. Rugosochonetidae (p. 421).

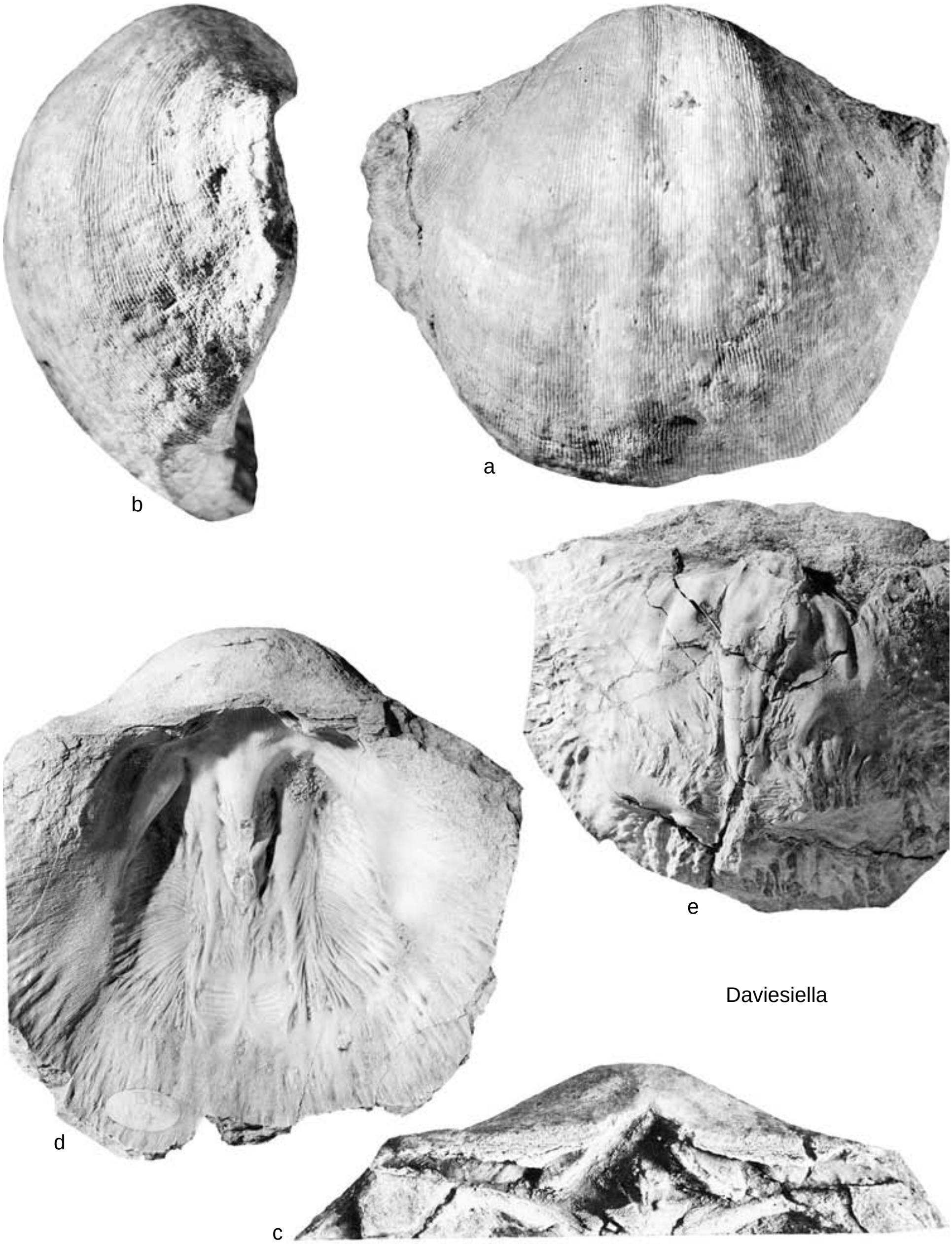


FIG. 277. Rugosochonetidae (p. 421–423).

(Viséan): England, Wales.——FIG. 277*a–e.* **D. llangollensis* (DAVIDSON), Wales (Denbighshire); *a,b,* ventral valve, ventral, lateral views, ×1; *c,* interarea showing hinge teeth, chilidium of damaged specimen, ×2; *d,* ventral valve interior, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood, 1962).

TREATISE ON INVERTEBRATE PALEONTOLOGY

Part H

BRACHIOPODA

Revised

Volume 3: Linguliformea, Craniiformea, and Rhynchonelliformea (part)

ALWYN WILLIAMS, C. H. C. BRUNTON, and S. J. CARLSON with
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PRODUCTIDINA

C. H. C. Brunton,[1] S. S. Lazarev,[2] R. E. Grant,[3] and Jin Yu-gan[4]

[[1]formerly of the Natural History Museum, London; [2]Palaeontological Institute, Moscow; [3]deceased; and [4]Nanjing Institute of Geology and Palaeontology]

Suborder PRODUCTIDINA Waagen, 1883

[*nom. correct.* Muir-Wood, 1965b, p. 448, *pro* suborder Productacea Waagen, 1883, p. 447; *sensu* Lazarev, 1990, p. 77]

Productides lacking interareas or with ginglymus only; toothed articulation absent after uppermost Devonian; cardinal process directed posteriorly or posterodorsally, not ventrally; brachial ridges commonly reniform, confined. [This group comprises the more characteristic productides that normally lived unattached on relatively soft substrates, stabilized by their straight or gently curved spines. There is a tendency within each superfamily for stratigraphically older representatives to have shallow corpus cavities that became deep in younger taxa. Trails may be long but lack elaboration, other than for rare anteromedian plication.] *Lower Devonian (Pragian)–Upper Permian (Changhsingian), ?Lower Triassic.*

Superfamily PRODUCTOIDEA Gray, 1840

[*nom. transl.* Maillieux, 1941, p. 7, *ex* Productidae Gray, 1840, p. 151]

Productidines with long trails, other than in early forms; ornamentation diverse, commonly ribbed, spines may be absent from near ventral hinge, otherwise widely to closely spaced; dorsal spines in some. *Lower Devonian (Emsian)–Upper Permian (Changhsingian), ?Lower Triassic.*

Family PRODUCTELLIDAE Schuchert, 1929

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 145, *ex* Productellinae Schuchert in Schuchert & LeVene, 1929, p. 17]

Shell small to medium sized; dorsal corpus concave, or rarely, only slightly concave; ribbing absent from beak or totally; spines varied, commonly on ventral valve only, commonly absent from hinge region; corpus cavity shallow, or rarely, deep in Carboniferous or Permian; teeth absent after uppermost Devonian; lateral ridges appearing in lower Tournaisian. *Lower Devonian (Emsian)–Upper Permian (Changhsingian), ?Lower Triassic).*

Subfamily PRODUCTELLINAE Schuchert, 1929

[Productellinae Schuchert in Schuchert & LeVene, 1929, p. 17]

Ribs rarely developed, then only anteriorly; spines evenly distributed over ventral valve only; corpus shallow; teeth present; lateral ridges, ear baffles lacking; cardinal process lobes divergent, V-shaped dorsally, with pit; dorsal adductor scars commonly nondendritic. *Lower Devonian (Emsian)–Upper Devonian (Famennian).*

Productella Hall, 1867c, p. 153 [**Productus subaculeatus* Murchison, 1840, p. 255; SD Oehlert, 1887b, p. 1279]. Width 10 to 20 mm; concavoconvex, with spines evenly distributed on ventral valve only, spine bases commonly not elongate; rugae weak posterolaterally, no ribbing. *Middle Devonian (Givetian)–Upper Devonian (Frasnian, ?Famennian):* Eurasia.——Fig. 278,*1a–e.* **P. subaculeata* (Murchison), upper Frasnian, France (Boulonnais); *a–d,* shell viewed posteriorly, laterally, ventrally, dorsally, ×2; *e,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Chattertonia Johnson, 1976, p. 789 [**Spinulicosta campbelli* Chatterton, 1973, p. 78; OD]. Similar to *Spinulicosta,* but with anderidia. *Lower Devonian (Emsian):* Australia.——Fig. 278,*2a–f.* **C. campbelli* (Chatterton), Emsian, New South Wales; *a,b,* holotype, viewed ventrally, dorsally, ANU 18950, ×3 (new); *c,* ventral valve lateral view, ×3; *d,* ventral valve exterior, ×2.2; *e,* ventral valve interior showing teeth, ×3; *f,* dorsal valve interior showing anderidia, *arrow,* ×4 (Chatterton, 1973).

Helaspis Imbrie, 1959, p. 400 [**H. luma;* OD]. Resembles *Spinulicosta,* but exagerated elongate spine bases simulate ribs posteriorly, ribbed anteriorly. *Middle Devonian (Givetian):* North America.——Fig. 278,*3a–c.* **H. luma,* Givetian, Michigan; *a,b,* ventral, dorsal exteriors of shell, ×2; *c,* dorsal valve interior, ×2 (Imbrie, 1959).

Sinoproductella Wang, 1955b, p. 349 [**Productella hemispherica* Tien, 1938, p. 19; OD]. Poorly known; gently concavoconvex with short trail, shallow corpus; ?short interareas or ginglymus; spines long on ears, low angled on rest of ventral valve, rugae weak dorsally, plus dimples; ?teeth. *upper Upper Devonian (Famennian):* China.——Fig.

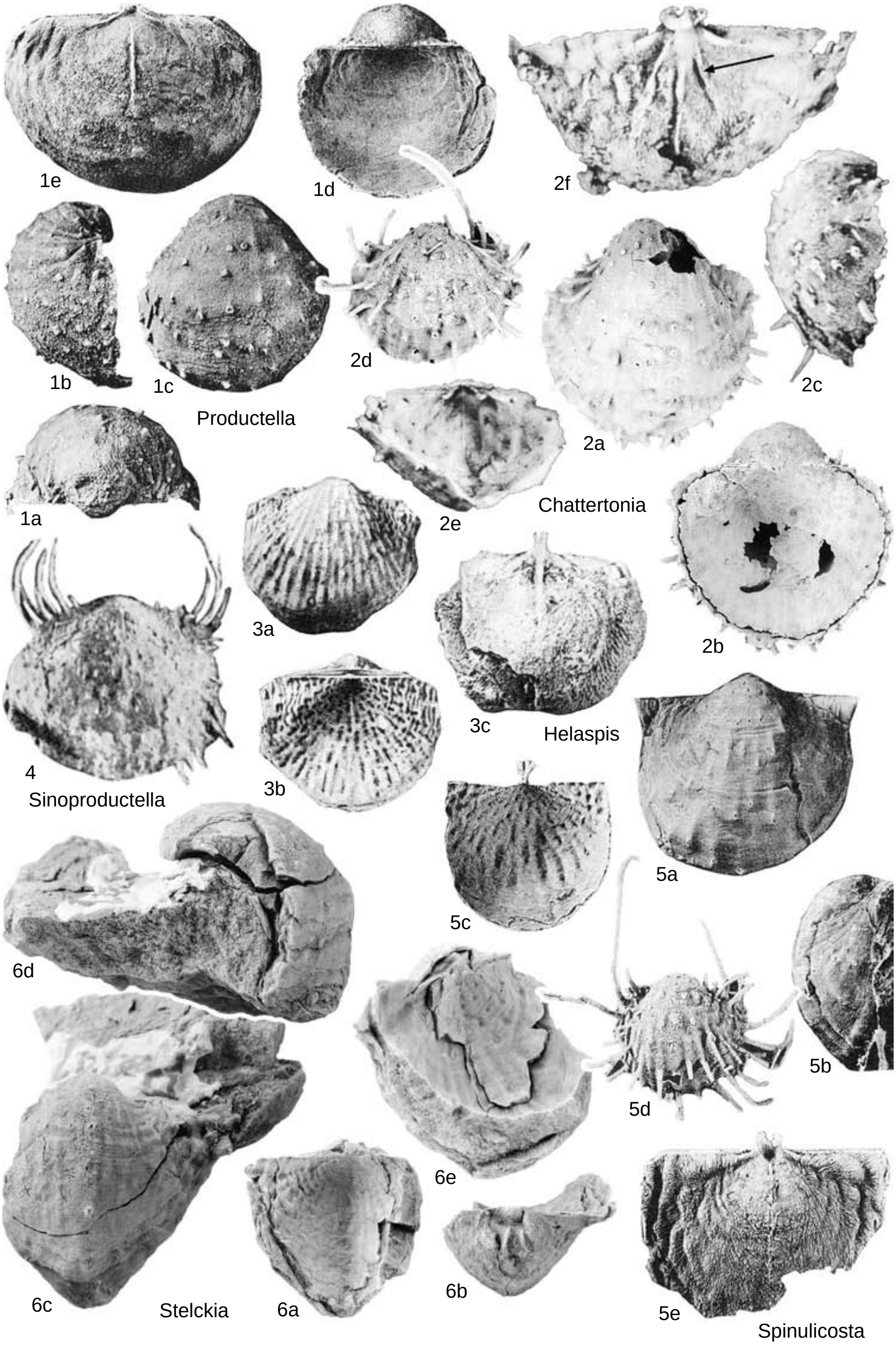


FIG. 278. Productellidae (p. 424–426).

278,*4.* **S. hemispherica* (Tien), Famennian, Hsiknangshan Limestone, Hunan; ventral valve exterior, ×1 (Wang, 1955b).

Spinulicosta Nalivkin, 1937, p. 49 [**Productus spinulicostus* Hall, 1857, p. 173, OD]. Small; outline subrounded, strongly concavoconvex profile; weakly lamellose, spines as *Productella,* but with elongate spine ridges posterior to spines, ribbing anteriorly; dorsal valve dimpled. *Lower Devonian–Middle Devonian (Eifelian):* North America, Europe, Australia, ?Asia.——Fig. 278,*5a,b.* **S. spinulicosta* (Hall), Eifelian, New York; *a,b,* lectotype, ventral valve exterior, lateral views, AMNH 4377a, ×2 (Muir-Wood & Cooper, 1960).——Fig. 278,*5c. S.* sp. cf. *S. spinulicosta* (Hall), Lower Devonian, Ohio; dorsal valve exterior, ×2 (Muir-Wood & Cooper, 1960).——Fig. 278,*5d,e. S.* sp. cf. *S. navicella* (Hall), Middle Devonian, Nevada; *d,* silicified ventral valve exterior, ×2; *e,* incomplete silicified dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Stelckia Crickmay, 1963, p. 21 [**S. galearius;* OD]. Poorly known; outline semicircular to subtriangular; highly arched medianly; ears flat; radial ridges faint, possibly spine bases; rugae on ears, weak on venter, dorsal valve; spines at ears, medianly, recumbent on venter. *Middle Devonian (Givetian):* Canada.——Fig. 278,*6a–e.* **S. galearius,* Givetian, Ramparts Formation, Northwest Territories; *a,b,* holotype, incomplete corpus viewed dorsally, posteriorly, showing paired dorsal ridges, PRI 27111, ×1; *c,d,* ventral, lateral views of incomplete specimen, ×1.5; *e,* dorsolateral view of posteromedian region, ×2 (new).

Subfamily PRODUCTININAE
Muir-Wood & Cooper, 1960

[Productininae Muir-Wood & Cooper, 1960, p. 181]

Wide-hinged productellids commonly ribbed, especially ventrally; few spines on ventral valve only, absent from hinge region; corpus cavity shallow, except some Paramarginiferini; brachial ridges, where present, with anterior lobe axes directed anteromedianly. *Upper Devonian (Famennian)–Upper Permian (Changhsingian), ?Lower Triassic.*

Tribe PRODUCTININI
Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 926, *ex* Productininae Muir-Wood & Cooper, 1960, p. 181]

Ribbing on ventral valve, concentric lamellae prominent on dorsal valve; ventral profile an ideal spiral; no sulcus; brachial ridges unknown. *Upper Devonian (Famennian)–Lower Carboniferous (Asbian).*

Productina Sutton, 1938, p. 551 [**Productus sampsoni* Weller, 1909, p. 300; OD]. Small; subrounded outline with small ears, strongly concavoconvex with inflated umbo; ribbing regular, relatively fine, interrupted anteriorly by lamellae, especially dorsally. *Upper Devonian–Lower Carboniferous (lower Hastarian):* North America, Europe, Australia, ?northern Africa.——Fig. 279,*1a–e.* **P. sampsoni* (Weller), Hastarian; *a,b,* ventral valve viewed ventrally, laterally, Texas, ×2; *c,* ventral valve viewed posteriorly, Texas, ×2; *d,e,* dorsal view of shell, dorsal valve interior, Caballero Formation, New Mexico, ×3 (Muir-Wood & Cooper, 1960).

Argentiproductus Cooper & Muir-Wood, 1951, p. 195, *nom. nov. pro Thomasella* Paul, 1942, p. 191, *non* Fredericks, 1928 [**Producta margaritacea* Phillips, 1836, p. 215; OD] [=*Thomasia* Fredericks, 1928, p. 783, *non* Poche, 1908, *nec* Rübsaamen, 1910, *nec* Wilson, 1910, *nec* Lambert, 1918; *Thomasina* Paeckelmann, 1931, p. 181, *non* Newstead & Carter, 1911]. Transverse posteriorly; ribbing wide, flattened, branching, slightly lamellose, few ventral spines only. *Lower Carboniferous (Viséan):* Europe, northern Africa.——Fig. 279,*2a–f.* **A. margaritacea* (Phillips), Asbian; *a,* neotype, ventral valve exterior, north Wales, BMNH BB 13616, selected by Brunton & Mundy, 1993, ×1; *b,c,* ventral, dorsal views of shell, silicified specimens, Fermanagh, British Isles, ×1.5; *d,* ventral view of young valve with median spine, silicified specimen, Fermanagh, ×1.5; *e,* ventral valve interior, silicified specimen, Fermanagh, ×2.5; *f,* dorsal valve interior, silicified specimen, Fermanagh, ×1.5 (new).

Dorsirugatia Lazarev in Lazarev & Suur'suren, 1992, p. 63 [**D. tsagankhalgensis;* OD]. Wide ears; weak ventral ribbing; row of three spines on each flank; dorsal lamellae plus weak anterior ribbing. *Upper Devonian (upper Famennian):* Mongolia.——Fig. 279,*3a–d.* **D. tsagankhalgensis,* uppermost Famennian, Gobi Altai; *a,* holotype, viewed ventrally, PIN 3385/1523, ×3; *b–d,* ventral valve viewed anteroventrally, posteriorly, laterally, ×3 (Brunton & Mundy, 1993).

Productellina Reed, 1943, p. 99 [**Productus (Productellina) fremingtonensis;* OD]. Ears small; ventral valve only ribbed, dorsal valve lamellose; possibly only single pair of ventral flank spines. *Upper Devonian (Famennian)–Lower Carboniferous (lower Tournaisian):* southern Britain.——Fig. 279,*4a–d.* **P. fremingtonensis,* lower Tournaisian, Pilton Beds, Devon; *a,b,* holotype, dorsal valve external mold, latex replica, OUM E287, ×2; *c,d,* ventral valve internal mold viewed ventrally, laterally, note spine base, *arrowed,* ×2 (new).

Tribe CHONETELLINI Licharew, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 926, *ex* Chonetellidae Licharew in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 226] [=Haydenellinae Jing & Hu, 1978, p. 113]

Outline subtriangular, may have ginglymus; lateral profile deeply concavoconvex

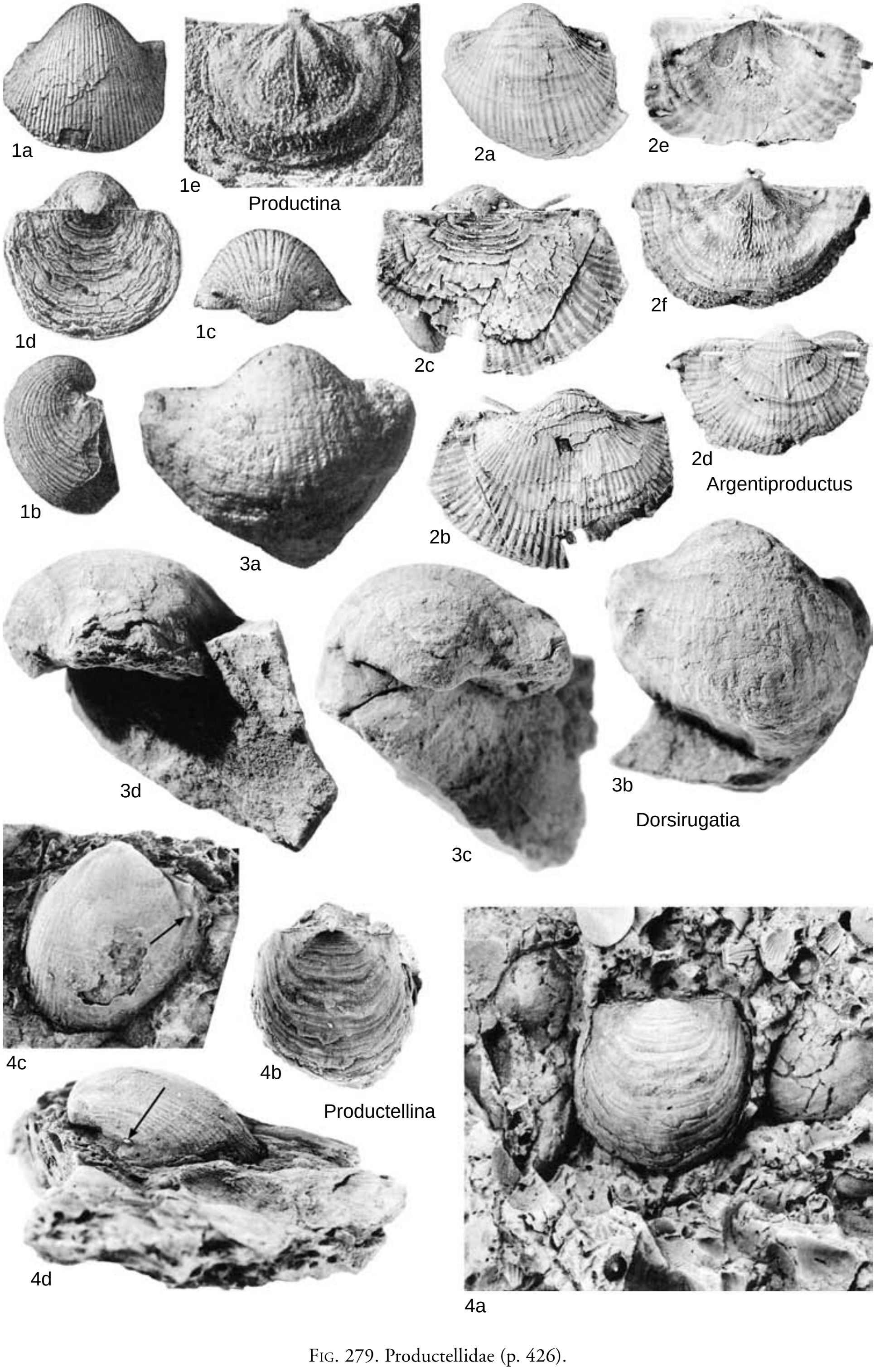


Fig. 279. Productellidae (p. 426).

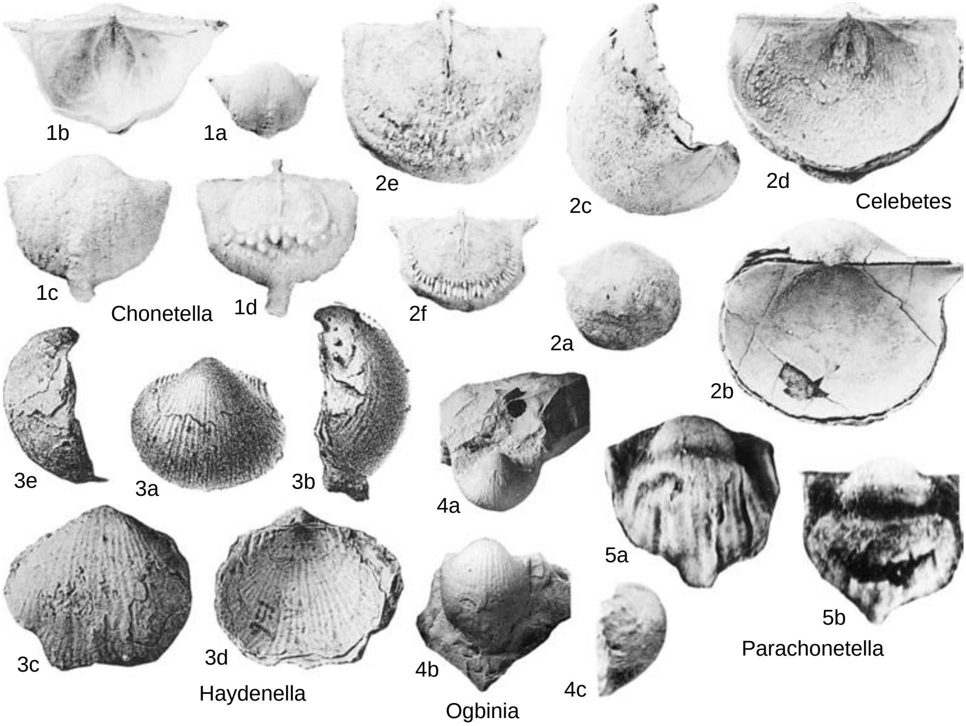


FIG. 280. Productellidae (p. 428–429).

with shallow corpus cavity; ribbing weak or absent; commonly nasute, with spines only flanking umbo. *Lower Permian (Artinskian)–Upper Permian (Changhsingian).*

Chonetella WAAGEN, 1884, p. 613, 657, *non Chonetella* KROTOW, 1885, p. 274, =*Chonetina* KROTOW, 1888, p. 500 [**C. nasuta;* OD]. Subcircular to transverse chonetiform, strongly nasute outline; ventral ginglymus; ribbing absent or weak; spines extend posterolaterally from hinge line, ?absent from corpus; cardinal process long, but narrow; lateral ridges divergent from hinge, long brachial ridges bordered anteriorly by strong endospines. *upper Lower Permian (Kungurian)–Upper Permian (Capitanian):* Pakistan (Salt Range).——FIG. 280,*1a–d.* **C. nasuta,* Permian, Kalabagh member, Khisor Range; *a,* ventral valve exterior, ×1; *b,* ventral valve interior, ×2; *c,* ventral valve exterior, ×2; *d,* dorsal valve interior, ×2 (Grant, 1976).

Celebetes GRANT, 1976, p. 137 [**C. gymnus;* OD]. Concavoconvex profile with weak geniculation; ribbing absent, concentric ornament weak or absent; spines few near hinge, few or absent elsewhere; anterior margin commonly not nasute; cardinal process narrow to trifid with short shaft; tubercles widespread, endospines at anterior margin of visceral disk. *Lower Permian (Artinskian):* Thailand.——FIG. 280,*2a–f.* **C. gymnus,* Artinskian, Phangnga; *a,* holotype, viewed ventrally, ×1; *b,c,* holotype, viewed dorsally, laterally, USNM 212444, ×2; *d,* ventral valve interior, ×2; *e,* dorsal valve interior, ×2; *f,* dorsal valve interior, ×1 (Grant, 1976).

Haydenella REED, 1944, p. 78 [**Productus kiangsiensis* KAYSER, 1883, p. 185; OD] [=*Striatospica* WATERHOUSE, 1975, p. 11 (type, *Striatifera kayseri* CHAO, 1927b, pl. 13, fig. 9; OD)]. Smaller medium-sized corpus with short simple trails, broad outline; short ginglymus common; ribbing weak, absent at umbos; rugae only on ears; spines separate corpus from posterior ear regions, thin spines scattered on ventral corpus; ventral diductor scars prominent; cardinal process dorsally trifid; lateral ridges weak, no marginal ridges. *upper Lower Permian (Roadian)–Upper Permian (Tatarian):* China, Asia, Transcaucasia.——FIG. 280,*3a–e.* **H. kiangsiensis* (KAYSER); *a,b,* ventral valve exterior, lateral view of shell showing flank spines, Permian, Jiangxi, ×1; *c–e,* ventral, dorsal, lateral views of shell, middle *Productus* Limestone, Salt Range, Pakistan, ×1 (Muir-Wood & Cooper, 1960).

Ogbinia SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 229 [**O. dzhagrensis;* OD]. Small, around 10 mm wide, elongate outline; ginglymus; ribbing low, lacking rugae; spines in row near hinge only;

cardinal process unifid, supported by shell thickening anteriorly; median septum short. *upper Lower Permian (Roadian):* Transcaucasus.——FIG. 280,*4a–c.* **O. dzhagrensis,* Ufimian, Transcaucasus; holotype, viewed posteriorly, ventrally, laterally, PIN 2071/65, ×1 (Sarytcheva & Sokolskaya, 1965).

?Parachonetella LIAO, 1980, p. 260 [**P. zhongyingensis;* OD]. Resembles *Chonetella,* but differs in having irregular ribs on trail, ventral cincture at corpus margin. *upper Upper Permian (Changhsingian):* China.——FIG. 280,*5a,b.* **P. zhongyingensis,* Changhsingian, Guizhou; *a,* holotype, anteroventral view, NIGP 43650, ×2; *b,* anteroventral view of another specimen, ×2 (new).

Planihaydenella CHANG, 1987, p. 757[764] [**P. anqingensis;* OD]. Poorly known, possible synonym of *Haydenella,* but ribbing reportedly well developed. *?Upper Permian:* China.

Tribe PARAMARGINIFERINI
Lazarev, 1986

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 926, *ex* Paramarginiferinae LAZAREV, 1986c, p. 23]

Radial ribbing and, in some, posteriorly reticulate; ventral profile distorted, ventral trail (when present) commonly becoming anteriorly nasute; ventral marginal ridges commonly developed. *Lower Carboniferous (Viséan)–Upper Permian (Changhsingian), ?Lower Triassic.*

Paramarginifera FREDERICKS, 1916, p. 61 [**Marginifera clarkei* CHERNYSCHEV, 1902, p. 328; OD]. Medium size with pentagonal outline; profile concavoconvex, long trail with broadly nasute extension; median sulcus originates at umbo; ribbing complete, rugae weak on disks; six spines symmetrically disposed on ears, flanks, venter; cincture bordering ventral corpus; interior unknown. *Lower Permian (Asselian–Artinskian):* Ural Mountains, Inner Mongolia, northern China.——FIG. 281,*1a–d.* **P. clarkei* (TSCHERNYSCHEW), Permian, *Schwagerina* Limestone, Ural Mountains; *a,b,* anteroventral view, anterior view, ×1; *c,d,* posteroventral view, lateral view, ×1 (Muir-Wood & Cooper, 1960).

Alitaria COOPER & MUIR-WOOD, 1967, p. 808, *nom. nov. pro Alifera* MUIR-WOOD & COOPER, 1960, p. 207 (type, *Productus expansus* DE KONINCK, 1842, p. 159, *non* PANDER, 1830) [**Alifera konincki* MUIR-WOOD & COOPER, 1960, p. 208; OD]. Transverse outline with large strongly differentiated ears; disks reticulate, commonly two pairs of thick halteroid spines on flanks; strong ventral marginal ridges. *Lower Carboniferous (Viséan):* Europe, northern Africa, northern Asia.——FIG. 281,*2a–f.* **A. konincki* (MUIR-WOOD & COOPER), Viséan, Visé, Belgium; *a,* oblique lateral view of internal mold showing marginal ridge, ×2; *b,c,* ventral view of internal mold, replica of its dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960); *d–f,* anterior, posterior, lateral views of ventral valve exterior, ×1.5 (new).

Bibatiola GRANT, 1976, p. 136 [**B. costata;* OD]. Outline broadly triangular with nasute anterior margin; deeply concavoconvex; ribbing originates posteriorly on disks; spines few, two or three on each flank, up to six on venter; cardinal process trifid, sessile; lateral ridges extend weakly to separate ears; endospines short, few. *Lower Permian (Artinskian):* Thailand.——FIG. 281,*3a–e.* **B. costata,* Artinskian, Ko Muk; *a–c,* holotype, viewed ventrally, dorsally, laterally, USNM 212423, ×2; *d,e,* dorsal valve interior, viewed laterally, ×2 (Grant, 1976).

Bothrionia COOPER & GRANT, 1975, p. 984 [**B. nasuta;* OD]. Outline nasute; median ribs may be lacking at sulcus, on trail may branch anterior to spine bases; spines few, one large spine on each ear, others over ventral valve; posterior sulcus becoming nasute anteriorly at adult margin; ventral ear baffles continued anteriorly to form low ridge around corpus; cardinal process sessile, trifid; median septum short, thin; endospines numerous, long. *Permian (Wordian):* USA.——FIG. 281,*4a–e.* **B. nasuta,* Permian, Word Formation, Texas; *a–c,* holotype, viewed ventrally, dorsally, laterally, USNM 149637a, ×1; *d,* ventral valve interior, ×2; *e,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Cathaysia CHING in WANG, CHING, & FANG, 1966, p. 327 [**Productus chonetoides* CHAO, 1927b, p. 62; OD]. Small with transverse to quadrate outline, concavoconvex profile; ears distinct, sulcus shallow or absent; ribbing branched, rugae on ears, near hinge only; single large spine on each ear, one or two on each side of trail; ventral muscle scars smooth with slightly excavated adductor scars, prostrate endospines; dorsal interior with numerous endospines. *Permian (Artinskian–Changhsingian), Lower Triassic (?lower Scythian):* southern China, Caucasus.——FIG. 282,*1a–d.* **C. chonetoides* (CHAO), Permian Coal Series, Jiangsu Province; *a,b,* ventral views of two incomplete specimens, Changhsingian, Zhejiang Province, ×1 (new); *c,* replica of dorsal valve interior, Fujian Province, ×2; *d,* ventral valve exterior, ×2 (Xu & Grant, 1994).

Cymoproductus XU, 1987, p. 227 [**C. callicostella;* OD]. Poorly known; medium size, transverse with hinge equal to maximum width; ventral disk weakly convex, geniculate with short trail; ribbing fine, ears with irregular rugae only; spines strong, in rows separating ears; interiors unknown. *Upper Permian (Changhsingian):* China.——FIG. 282,*6a,b.* **C. callicostella,* Changhsingian, China; *a,* ventral valve exterior, ×1; *b,* incomplete dorsal valve exterior with dimples opposite ventral spine positions, ×1 (Xu, 1987).

Eomarginiferina BRUNTON, 1966, p. 229 [**Eomarginifera (E.) trispina;* OD]. Small, around 10 mm wide; ventral profile with tight spiral, trail rarely slightly nasute; reticulate posteriorly, few (commonly three) thick symmetrical ventral spines; corpus relatively deep; no median sulcus; no anterior ventral

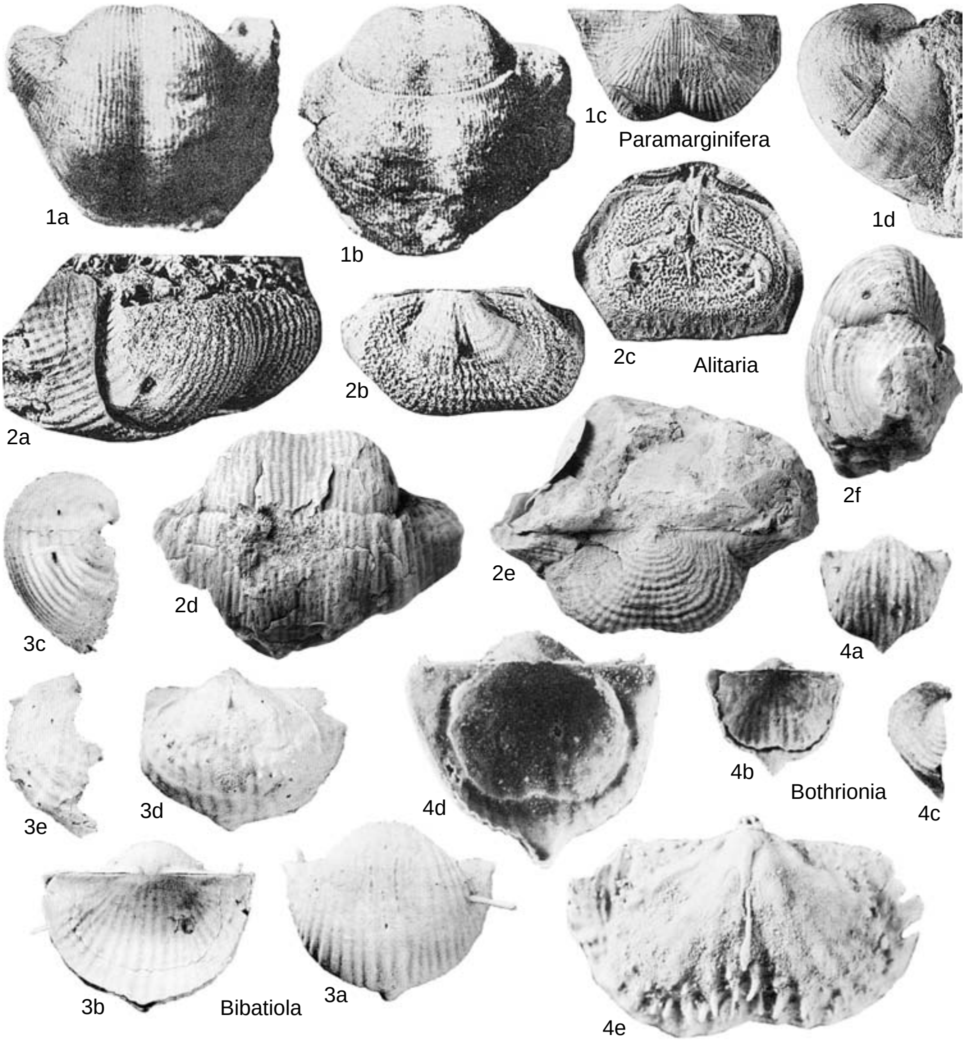


Fig. 281. Productellidae (p. 429).

marginal ridges. *Carboniferous (Viséan, ?lower Moscovian):* Europe, ?China.——Fig. 282,*2a–h.* **E. trispina* (Brunton), Asbian, Fermanagh, British Isles, silicified specimens; *a,* holotype viewed dorsally, showing position of ear baffles, BMNH BB 52890, ×4; *b–d,* ventral valve viewed ventrally, laterally, internally, showing median spine cavity, *arrow,* ×3; *e,f,* dorsal valve interior viewed ventrally, posteroventrally, ×4; *g,* young ventral valve exterior with three major spines, ×3; *h,* juvenile ventral valve with pedicle sheath, ×15 (Brunton, 1966).

Huatangia Liao & Meng, 1986, p. 78[91] [**H. sulcatifera;* OD]. Small transverse shell with narrow anterior sulcus; ribbing irregular on corpus, fine on trail; rugae strong posterolaterally on ventral valve, reticulate posteriorly on dorsal disk; ventral marginal ridge; cardinal process narrow (?unifid). *Upper Permian (Changhsingian):* China.——Fig. 282,*4a–d.* **H. sulcatifera,* Changhsingian, Hunan; *a,* holotype, lateral view, NIGP 74198, ×1; *b,* anteroventral view, NIGP 74198, ×2; *c,* ventral valve exterior, ×1; *d,* external mold of dorsal valve, ×1.5 (new).

?Paryphella Liao in Zhao & others, 1981, p. 53[83] [**Cathaysia sulcatifera* Liao, 1980, p. 261; OD] [=*Spinoparyphella* Liang, 1990, p. 11, *nom. nud.* (type, *S. zhinanensis;* OD)]. Small, widest at hinge with large flat ears; ginglymus short; dorsal disk weakly concave; ribbing simple, weak posteriorly; rugae strong on ears; two pairs of spines at hinge;

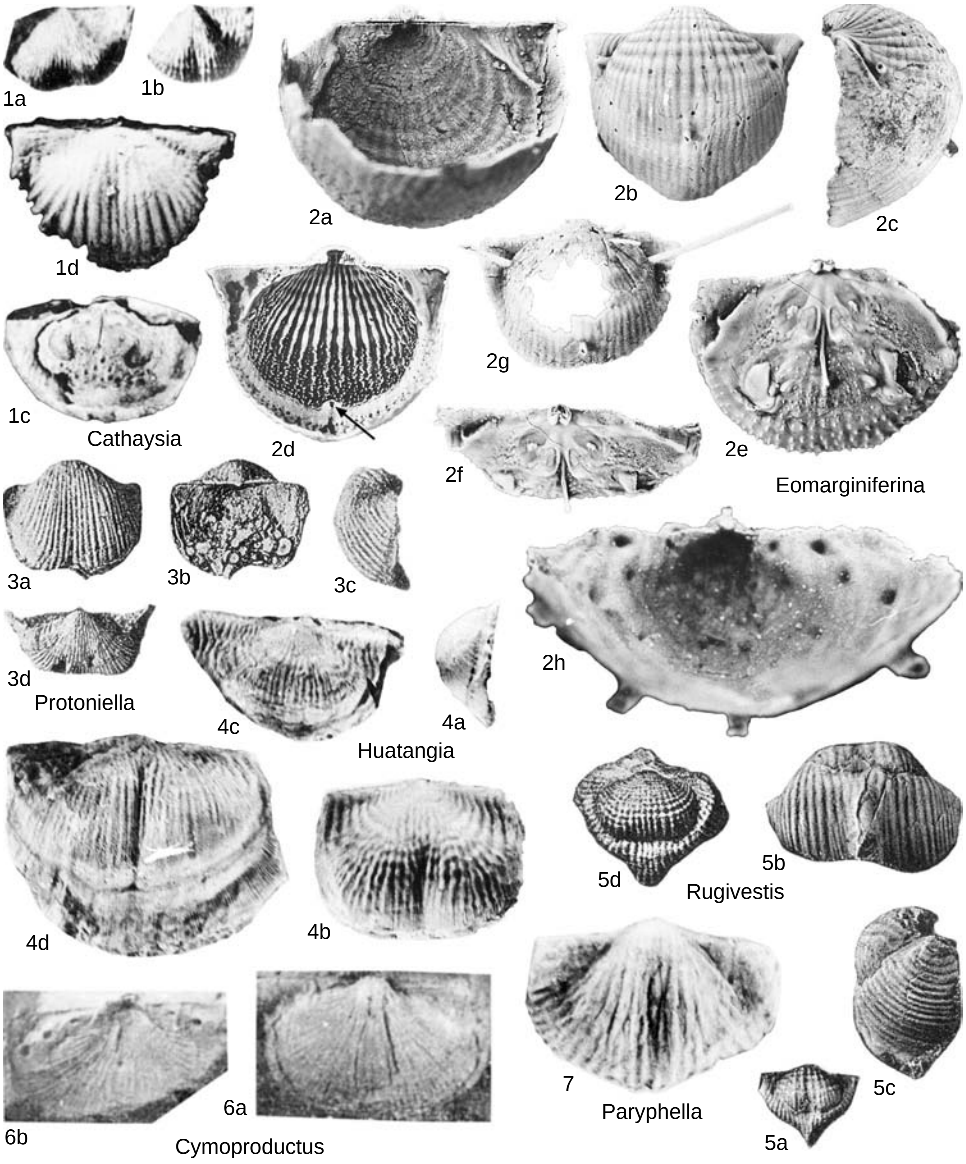


Fig. 282. Productellidae (p. 429–432).

cardinal process narrow, elongate; low median septum extending to midlength of valve. *upper Upper Permian (Changhsingian), ?Lower Triassic:* southern China.——Fig. 282,*7.* **P. sulcatifera* (Liao), upper Upper Permian, Guizhou; ventral valve exterior, ×3 (new).

?Protoniella Bell, 1929, p. 110 [**P. beedii;* OD]. Small; outline rounded, profile concavoconvex, slight median sulcus on ventral trail; ribbing starts near beak, bearing fine scattered spines ventrally; dorsal valve ribbed, weakly lamellose anterolaterally, no rugae; cardinal ridges, ear baffles. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* central, eastern North America.——Fig. 282,*3a–d.* **P. beedi,* Lower Carboniferous, upper Windsor, Nova Scotia; *a–c,* holotype, viewed ventrally, dorsally, laterally, GSC 7954d, ×1; *d,* posterior view of ventral valve, ×1 (Muir-Wood & Cooper, 1960).

Rugivestis Muir-Wood & Cooper, 1960, p. 235 [*?*Proboscidella carinata* Muir-Wood & Cooper in

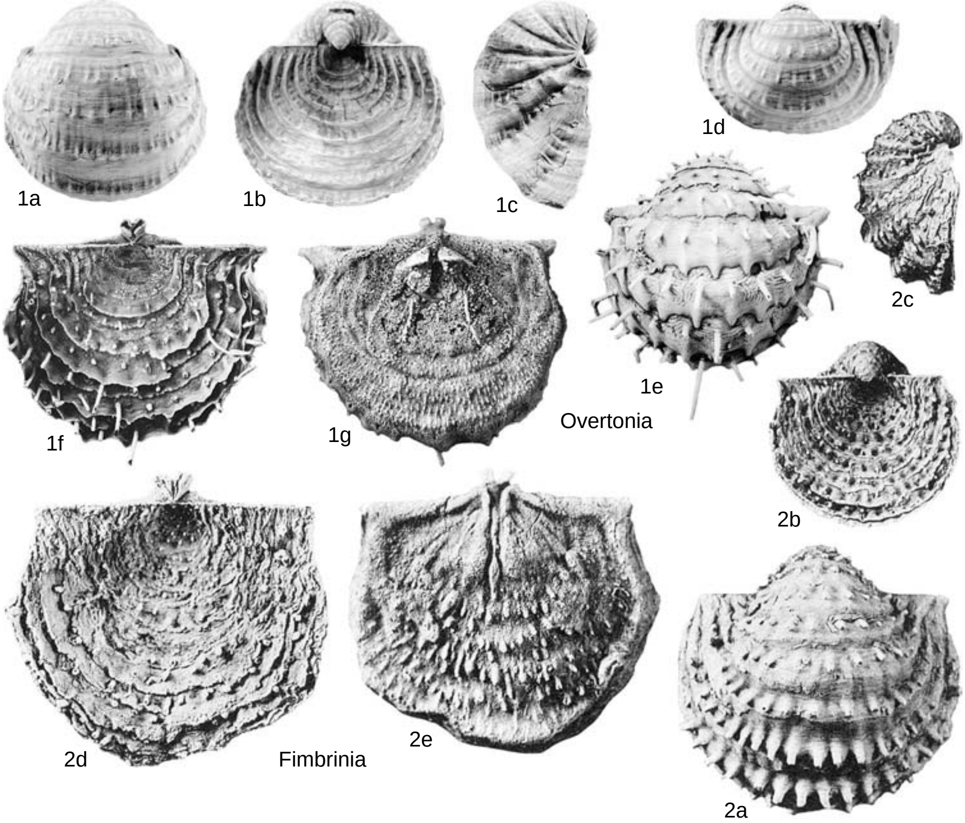


FIG. 283. Productellidae (p. 432–433).

COOPER, 1957, p. 36; OD]. Small, trigonal outline with trail folded into broad nasute extension; short flanges at start of trail continuous with ears; disks concavoconvex, reticulate; ribbing well developed on trails; spines few, symmetrically placed; marginal ridges in both valves. *Lower Permian (Asselian–Artinskian, ?Kungurian):* North America, Russia.——FIG. 282,*5a–c.* **R. carinata* (MUIR-WOOD & COOPER), Permian, Coyote Butte Formation, Oregon; *a,* holotype, viewed ventrally, USNM 124156a, ×1; *b,c,* holotype, viewed anteriorly, laterally, USNM 124156a, ×2 (Muir-Wood & Cooper, 1960).——FIG. 282,*5d. R. kutorgae* (TSCHERNYSCHEW), Lower Permian, *Schwagerina* Limestone, southern Ural Mountains; ventral view, ×1 (Muir-Wood & Cooper, 1960).

Subfamily OVERTONIINAE
Muir-Wood & Cooper, 1960

[Overtoniinae MUIR-WOOD & COOPER, 1960, p. 183] [=Avoniidae SARYTCHEVA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 226, *partim*]

Ribs absent or rarely confined anteriorly on trails; spines scattered equally on both valves, but absent from ventral hinge; corpus depth varied. *Upper Devonian (upper Famennian)–Upper Permian (Tatarian).*

Tribe OVERTONIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 926, *ex* Overtoniinae MUIR-WOOD & COOPER, 1960, p. 183]

Strong rounded rugae bearing spines; corpus cavity deep; dorsal adductor scars raised. *Lower Carboniferous (upper Viséan)–Lower Permian (Asselian).*

Overtonia THOMAS, 1914, p. 259 [**Producta fimbriata* J. DE C. SOWERBY, 1824 in 1823–1825, p. 85; OD]. Small to medium; ventral spines associated with rugae from crests, short prostrate spines at lamellose anterior margins; dorsal spines erect in bands between series of short trails; dorsal adductor platforms raised. *Lower Carboniferous (upper Viséan):* Europe, ?Asia, ?northern Africa.——FIG. 283,*1a–g.* **O. fimbriata* (J. DE C. SOWERBY); *a–d,* ventral, dorsal, lateral, posterior views of shell, Asbian, York-

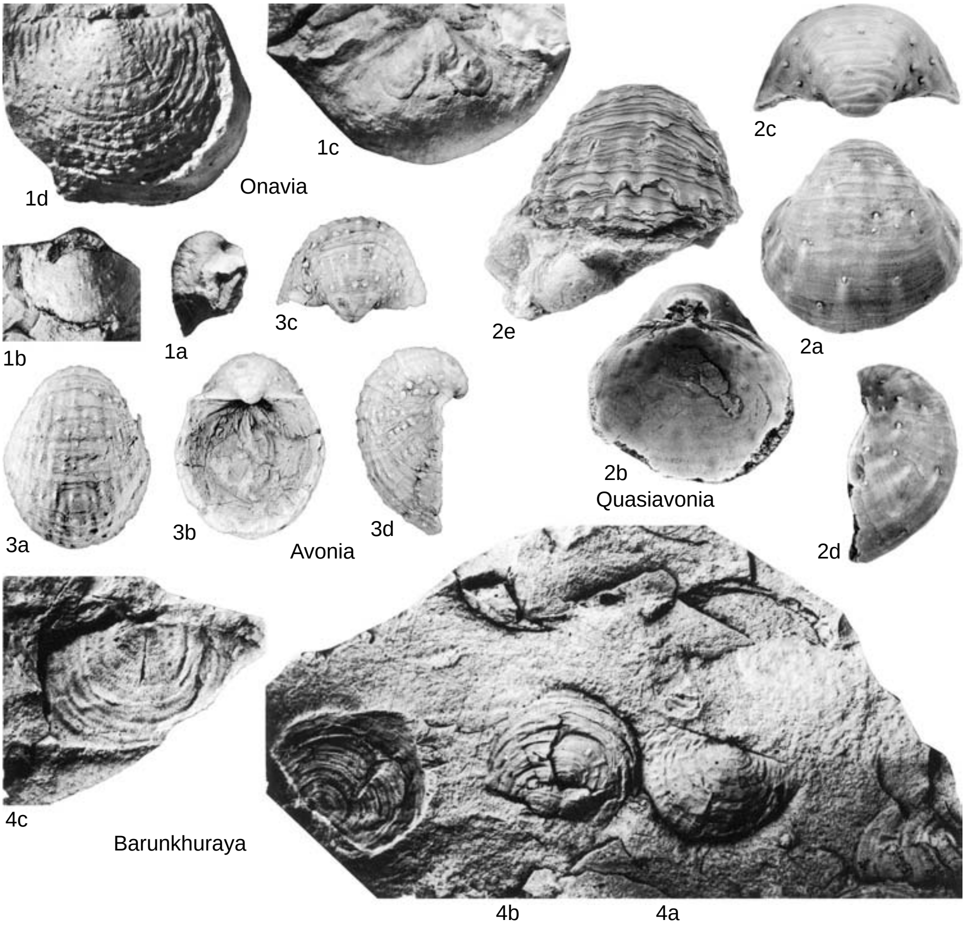


FIG. 284. Productellidae (p. 433–434).

shire, ×1 (new); *e–g,* ventral valve exterior, dorsal valve exterior, interior, silicified specimens, Fermanagh, ×2 (Brunton, 1966).

Fimbrinia COOPER, 1972, p. 450, *nom. nov. pro Fimbriaria* MUIR-WOOD & COOPER, 1960, p. 186, *non* FROELICH, 1802 [**Overtonia plummeri* KING, 1938, p. 276; OD]. Similar to *Overtonia* but small; spine bands single, from crests of rugae; dorsal adductor scars commonly not elevated. *Upper Carboniferous (Kasimovian)–Lower Permian (Asselian):* North America.——FIG. 283,*2a–e.* **F. plummeri* (KING), Finnis Shale, Texas; *a,* ventral, ×3; *b,c,* dorsal, lateral views of shell, ×2; *d,e,* dorsal valve exterior, interior, ×4 (Muir-Wood & Cooper, 1960).

Tribe AVONIINI Sarytcheva, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 926, *ex* Avoniidae SARYTCHEVA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 226]

Concentric ornament of broad irregular lamellose bands; ventral lateral profile an ideal spiral; corpus cavity shallow to moderate. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Serpukhovian).*

Avonia THOMAS, 1914, p. 259 [**Productus youngianus* DAVIDSON, 1860, p. 180; OD]. Outline somewhat elongate; concentric ornament of weak irregular lamellae, ribbing weak, only anteriorly; lateral ridges to inner side of ears. *Lower Carboniferous (Viséan–lower Serpukhovian):* Europe, Asia.——FIG. 284,*3a–d.* **A. youngiana* (DAVIDSON), Brigantian, Stirlingshire; *a–d,* lectotype, viewed ventrally, dorsally, posteriorly, laterally, BMNH B 45680, ×1.5 (new).

Barunkhuraya LAZAREV in BRUNTON & LAZAREV, 1997, p. 385 [**B. indrengynensis;* OD]. Small, slightly wider than long; nongeniculate; rugae on both valves, slightly lamellose; spines ventral, with swollen bases, row near hinge; cardinal process pit; lateral ridges weak, very short, but strongly divergent. *Upper Devonian (upper Famennian):* Mongolia

(Indrengyn-Nuru Mountains).——FIG. 284,*4a–c*. **B. indrengynensis,* upper Famennian, Indrengyn-Nuru Mountains; *a,b,* slab showing holotype, dorsal valve external mold (right), ventral valve external mold (left), PIN N 3385/1104, ×2; *c,* dorsal valve internal mold, ×2 (Brunton & Lazarev, 1997).

Onavia LAZAREV in BRUNTON & LAZAREV, 1997, p. 387 [**O. barunkhurensis;* OD]. Small, nongeniculate; rugae, spines on both valves; lateral ridges very short, weak. *Lower Carboniferous (Tournaisian):* Mongolia.——FIG. 284,*1a–d*. **O. barunkhurensis,* Tournaisian, Khuren-Ula Mountains; *a,* holotype, viewed laterally, PIN N 3385/1358, ×1; *b,* ventral view of specimen with most of ventral valve missing, ×1; *c,* ventral valve internal mold, ×2; *d,* dorsal valve external mold, ×2 (Brunton & Lazarev, 1997).

Quasiavonia BRUNTON, 1966, p. 219 [**Productus aculeatus* J. SOWERBY, 1814 in 1812–1815, p. 156; OD]. Ventral umbo inflated; both valves irregularly lamellose, spines with slightly swollen bases ventrally, fine dorsally; corpus cavity moderate. *Lower Carboniferous (Viséan):* Europe, western Asia, northern Africa.——FIG. 284,*2a–e*. **Q. aculeata* (J. SOWERBY); *a–d,* lectotype, viewed ventrally, dorsally, posteriorly, laterally, Viséan, Derbyshire, BMNH B 60992, ×2; *e,* specimen viewed anteriorly, showing lamellae, Brigantian, Derbyshire, ×2 (new).

Tribe COSTISPINIFERINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 926, *ex* Costispiniferinae MUIR-WOOD & COOPER, 1960, p. 217] [=Tubersulculinae WATERHOUSE in BAMBER & WATERHOUSE, 1971, p. 205]

Concentric ornament weak; ribbing may be present on trails; ventral profile geniculate, with shallow to deep corpus cavity. *Upper Carboniferous (Gzhelian)–Upper Permian (Tatarian).*

Costispinifera MUIR-WOOD & COOPER, 1960, p. 217 [**C. texana;* OD; =*Avonia walcottiana costata* R. E. KING, 1931, p. 85]. Small, transverse corpus with geniculate profile, deep cavity, elongate trails; rugae irregular on posterior disks; ribbing developed on trails; spines evenly distributed over ventral valve, thinner on dorsal valve; cardinal process with short shaft; lateral ridges extend across ears; long endospines border brachial areas anteriorly and laterally. *upper Lower Permian (Roadian)–lower Upper Permian (lower Kazanian):* USA.——FIG. 285,*1a–f*. **C. texana,* Kazanian, Word Limestone, Texas; *a–d,* holotype, viewed anteriorly, posteriorly, dorsally, laterally, USNM 124150a, ×1; *e,* ventral valve partial interior, ×2; *f,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Comuquia GRANT, 1976, p. 97 [**C. modesta;* OD]. Small, elongate ovate; concavoconvex profile with shallow corpus; ribbing absent, some growth lines prominent; spines evenly distributed on ventral valve, dorsal spines fine; cardinal process bilobed, weakly quadrifid; median ridge weak, short; brachial ridges not developed. *Lower Permian (Artinskian):* Thailand, Himalaya, northern Tibet.——FIG. 285,*2a–e*. **C. modesta,* Artinskian, Ko Muk, Thailand; *a–c,* holotype, ventral valve viewed ventrally, internally, laterally, USNM 212136, ×3; *d,* dorsal view of complete shell, ×3; *e,* young dorsal valve interior, ×3 (Grant, 1976).

Darlinuria LI & GU, 1976, p. 245 [**D. liaoningensis;* OD]. Small, subcircular corpus outline with small, well-differentiated ears; ventral profile weakly convex; dorsal valve concave; corpus cavity shallow; spines prostrate, small, in groups on ears, scattered on disk, concentrically in broad bands anteriorly; dorsal spines reportedly few; interiors poorly known. *Upper Permian (Kazanian–Tatarian):* Inner Mongolia, China.——FIG. 285,*3a–e*. **D. liaoningensis,* Upper Permian, Liaoning Province; *a,b,* holotype, ventral, posterior views (with ventral valve uppermost), SIGM 7K20, ×2.5; *c,d,* ventral, lateral views of specimen, ×3; *e,* internal mold of ventral valve, ×2 (new).

Dorashamia SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 217 [**D. abichi;* OD]. Small chonetiform shell with thick-walled valves; ornament of weak rugae becoming lamellose anteriorly; spine row near hinge, rare thin spines over venter, three spines separate dorsal ears; cardinal process sessile, bilobed; lateral ridges separate ears, disappear anteriorly. *Upper Permian (upper Capitanian):* Transcaucasus, ?North Caucasus, Kashmir.——FIG. 285,*5a–d*. **D. abichi,* upper Capitanian, Transcaucasus; *a,b,* holotype viewed ventrally, dorsally, PIN 2072/42, ×4; *c,* holotype viewed laterally, PIN 2072/42, ×1; *d,* incomplete dorsal valve exterior, ×4 (Sarytcheva & Sokolskaya, 1965).

Dyschrestia GRANT, 1976, p. 101 [**D. spodia;* OD]. Broadly subovate, widest near midlength; beak inflated; spines equally and widely scattered on ventral disk, thicker in groups on flanks and on concentric lamellae on trail; dorsal spines slender; lateral ridges extend to separate ears weakly; endospines numerous in broad band around brachial ridges. *Lower Permian (upper Artinskian):* Thailand, Western Australia, Indonesia.——FIG. 286,*1a–e*. **D. spodia,* upper Artinskian, Ko Muk, Thailand; *a–c,* holotype viewed ventrally, dorsally, laterally, USNM 212164, ×2; *d,* incomplete ventral valve interior, ×4; *e,* dorsal valve interior, ×2 (Grant, 1976).

Echinauriella LAZAREV in BRUNTON & LAZAREV, 1997, p. 387 [**Krotovia jisuensiformis* SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 216; OD]. Small, around 10 mm wide, strongly convex profile; spines fine posteriorly, densely distributed on both valves; plications incipient on trail; dorsal lateral ridges prominent, adductor scars narrow, elongate. *upper Lower Permian (Roadian)–Upper Permian (Kazanian):* Transcaucasus.——FIG. 285,*4a–d*. **E. jisuensiformis* (SARYTCHEVA), Roadian, River Vedi; *a,b,* holotype, viewed ventrally, laterally, PIN 2071/

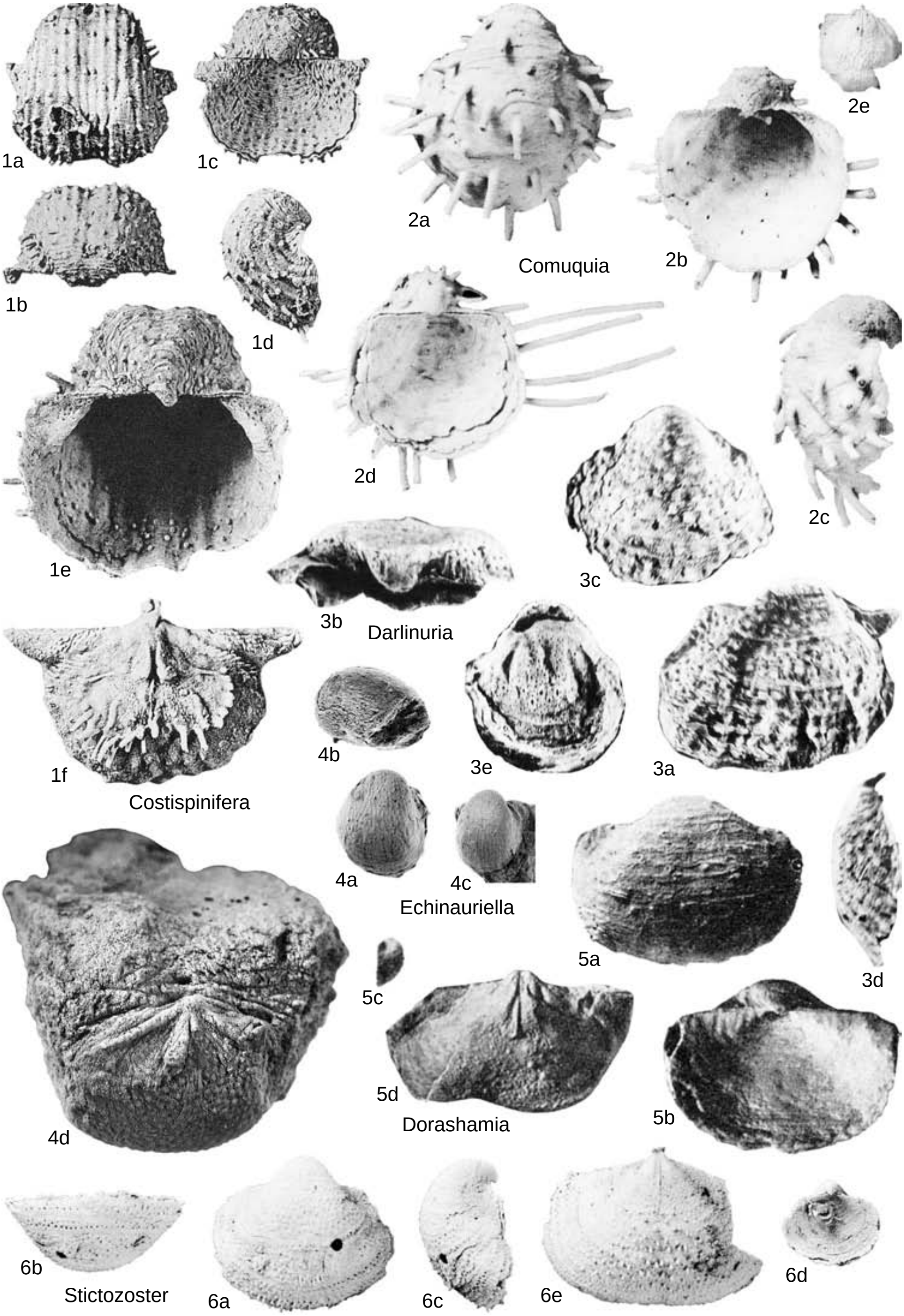


FIG. 285. Productellidae (p. 434–436).

78, ×1; *c,* ventral view of specimen, ×1; *d,* dorsal valve interior, ×3 (Sarytcheva & Sokolskaya, 1965).

Echinauris Muir-Wood & Cooper, 1960, p. 221 [**E. lateralis;* OD]. Small, subcircular outline, with small, well-differentiated ears; ventral corpus strongly inflated in transverse profile, cavity moderately deep; exterior smooth, but for erect spines covering both valves, clusters of thicker spines on flanks; ear baffles ventrally; dorsal lateral ridges separate ears, long endospines anterolaterally. *Lower Permian (Sakmarian)–lower Upper Permian (Wordian):* USA, Tibet.——Fig. 286,*2a–e.* **E. lateralis,* Upper Permian, Word Limestone, Texas; *a,* holotype, ventral view, USNM 124052a, ×1 (Muir-Wood & Cooper, 1960); *b,* dorsal view of specimen, ×1.5; *c,* lateral view of specimen, ×1.5; *d,* ventral view of shell with much of ventral valve missing, ×1 (Cooper & Grant, 1975); *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

?Lethamia Waterhouse, 1973, p. 38 [**L. ligurritus;* OD]. Poorly defined; medium size, concavoconvex with shallow corpus cavity; spines seemingly erect on both valves; ribbing absent, rugae weak. If with geniculate profile, would be better accommodated in the Levipustulini of the Plicatiferinae. *Lower Permian–lower Upper Permian (Kazanian):* New Zealand, ?Australia.

Neoplicatifera Ching, Liao, & Hou, 1974, p. 309 [**Plicatifera huangi* Ustritsky in Ustritsky, Hu, & Chan, 1960, p. 26; OD]. Small to medium transverse corpus with long trail; ventral profile with weakly convex disk, weakly geniculate; flanks steep, nearly parallel; dorsal disk gently concave geniculate; corpus cavity moderately deep; rugae on both disks; weakly ribbed or smooth; spines fine, posteriorly on rugae, scattered anteriorly, curved row between umbonal slope and ears; dorsal valve with fine short spines; cardinal process bilobate; median septum long; lateral ridges, marginal ridges lost anteriorly. [Assigned to the Semicostellini of the Plicatiferinae if with strong geniculation and ribbing on trail; Ustritsky decided (1960) that the species described by Huang (1932, p. 38–41) was not *Plicatifera minor* (Schellwien) and renamed it *P. huangi.*]. *upper Lower Permian–Upper Permian (Kazanian):* China, Salt Range.——Fig. 286,*4a–d.* **N. huangi* (Ustritsky), Permian, China (Guizhou Province); *a–c,* shell viewed posteriorly, anteriorly, laterally, ×1; *d,* dorsal valve interior, ×1 (Huang, 1932).

Paraplicatifera Zhao & Tan, 1984a, p. 26[30] [**P. regularis;* OD]. Resembles *Neoplicatifera,* but differs in its clearly defined anterior ribbing; dorsal valve unknown, but assumed spinose. *Lower Permian (Artinskian)–lower Upper Permian (Wordian):* China.——Fig. 286,*3a–c.* **P. regularis,* Permian, China; holotype, viewed posteriorly, anteriorly, laterally, HB 257, ×2 (Zhao & Tan, 1984a).

Pseudoavonia Wang in Zhang, Fu, & Ding, 1983, p. 312 [**Avonia lopingensiformis* Ustritsky in Ustritsky, Hu, & Chan, 1960, p. 28; OD]. Poorly known, resembles *Costispinifera,* but lacks concentric ornament on ventral umbo, perhaps fewer dorsal spines; apparently has stronger marginal ridges at sides of dorsal disk. *Lower Permian (Artinskian):* China.——Fig. 286,*6a,b.* **P. lopingensiformis* (Ustritsky), Chihsian, Xinjiang; ventral valve viewed anteriorly, posteriorly, ×1 (Zhang, Fu, & Ding, 1983).

Stictozoster Grant, 1976, p. 96 [**S. leptus;* OD]. Small, outline circular; evenly concavoconvex; ribs, rugae absent, but with weak lamellose ornament; spines fine, of equal dimensions, arranged on variable concentric bands on both valves; cardinal process small with variable pit; median septum thin, short; endospines extensive in both valves. *Lower Permian (Artinskian):* Thailand, western and eastern Timor, Indonesia, Western Australia, western Malaysia.——Fig. 285,*6a–e.* **S. leptus,* Permian, Ko Muk, Thailand; *a–c,* holotype, viewed ventrally, anteriorly, laterally, ×2; *d,* dorsally, USNM 212105, ×1; *e,* dorsal valve interior, ×2 (Grant, 1976).

Tubersulculus Waterhouse in Bamber & Waterhouse, 1971, p. 208 [**T. maximus;* OD]. Medium size, deeply concavoconvex profile; ventral sulcus and dorsal fold produce tubiform median trail; ribbing absent, concentric ornament of weak lamellae; spines with swollen bases, densely spaced on both valves, concentrically arranged anteriorly; cardinal process bilobed, quadrifid; adductor scars indistinct; lateral ridges separate ears; disk interior strongly endospinose. *upper Upper Carboniferous (Gzhelian)–Lower Permian (Artinskian):* Canada, Russia.——Fig. 286,*5a–e.* **T. maximus,* Lower Permian, Jungle Creek Formation, Yukon Territory; *a,b,* holotype, internal mold viewed ventrally, dorsally, GSC 26393, ×1; *c,* ventral valve exterior, ×1; *d,* replica of dorsal exterior, ×1; *e,* incomplete mold of ventral valve interior, ×1 (Bamber & Waterhouse, 1971).

Zhuaconcha Liang, 1990, p. 183[463] [**Z. hirsutispins;* OD]. Poorly preserved material. Small to medium size with weakly concavoconvex profile; hinge slightly less than maximum width; spines fine, closely covering both valves; ribbing, concentric ornament absent; dorsal marginal ridge, raised adductor scars; apart from marginal ridge genus similar to *Echinauriella.* Illustrations inadequate for publication. *Upper Permian (Kazanian):* China.

Tribe INSTITIFERINI
Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 927, *ex* Institiferinae Muir-Wood & Cooper, 1960, p. 203]

Minute to small shells with relatively deep corpus cavity, bearing concentric ornament, coarse ribbing on trails strongly deflected as flanges or gutters; spines on ventral corpus only. *Lower Carboniferous (Viséan).*

Institifera Muir-Wood & Cooper, 1960, p. 203 [**Productus tessellatus* de Koninck, 1847b, p. 110;

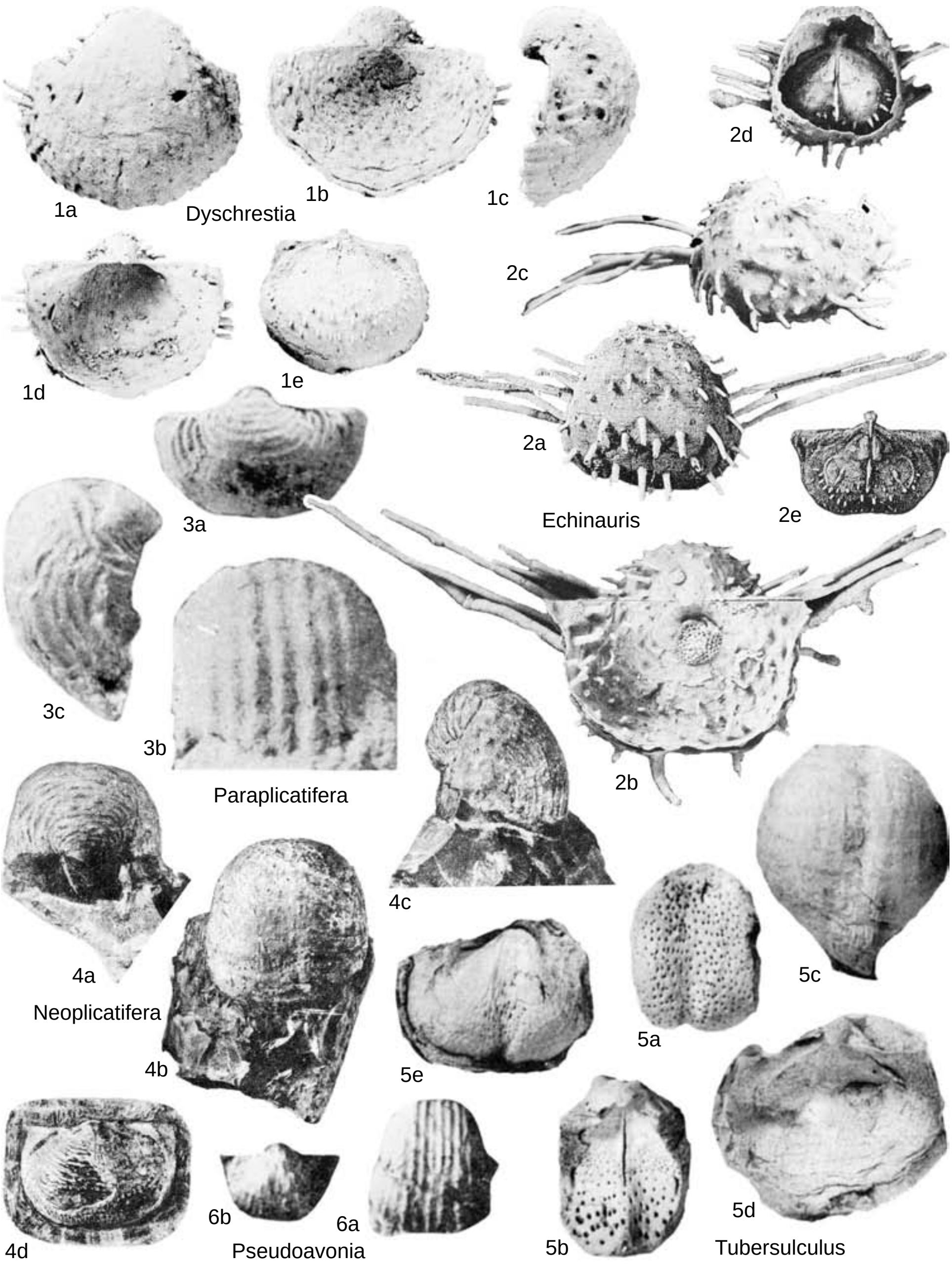


FIG. 286. Productellidae (p. 434–436).

OD]. Deep corpus, but slightly concave dorsal valve; ribbing variable, but clear anteriorly and especially on elaborate bordering structures that roll dorsally inward, ventrally outward; spines fine from concentric swollen bases. *Lower Carboniferous (Viséan):* western Europe.——FIG. 287,*2a–e*. **I. tessellata* (DE KONINCK), Viséan, Ireland; *a,* shell viewed ventrally with section of recurved flange

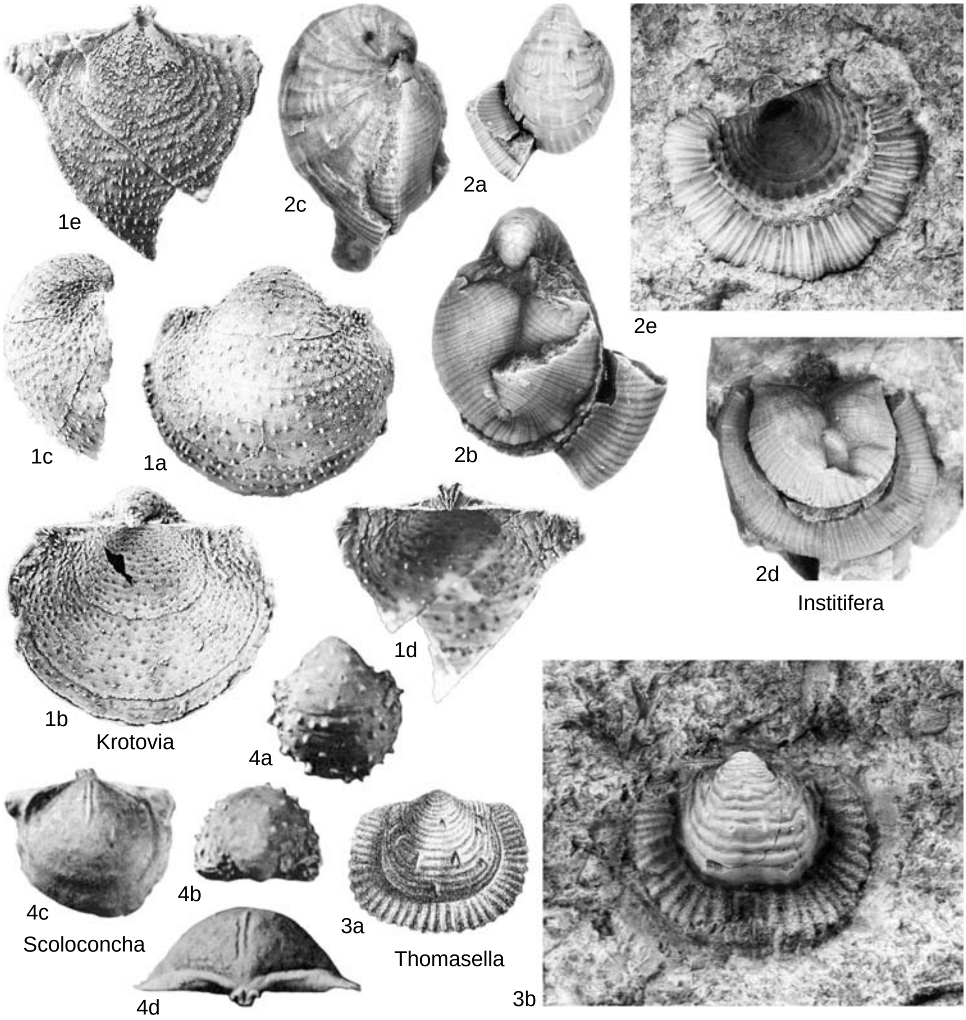


FIG. 287. Productellidae (p. 436–439).

preserved, Cork, ×2; *b,c,* shell viewed dorsally, laterally with its inwardly turned dorsal flange, anteriorly recurved ventral flange, Cork, ×3; *d,* dorsal view of shell with complete dorsal, ventral flanges, Cork, ×3; *e,* dorsal view of corpus (flange missing) plus ventral flange, Kildare, ×2 (new).

?Thomasella FREDERICKS, 1928, p. 778 [**Productus wrighti* DAVIDSON, 1861, p. 162; OD]. Very small, corpus around 5 mm width; rugose visceral disk, ribbed flange; spines few from ventral rugae. *Lower Carboniferous (Viséan):* British Isles.——FIG. 287,*3a,b.* **T. wrighti* (DAVIDSON), Viséan, Cork, Ireland; *a,* drawing of ventral exterior, with flange, ×3 (Davidson, 1861); *b,* lectotype, same specimen, BMNH B 40097, ×4 (new).

Tribe KROTOVIINI
Brunton, Lazarev, & Grant, 1995

[Krotoviini BRUNTON, LAZAREV, & GRANT, 1995, p. 926]

Concentric ornament weak or lacking; ventral profile an ideal spiral; shallow corpus cavity. *Lower Carboniferous (Viséan)–Upper Carboniferous (Serpukhovian, ?Bashkirian).*

Krotovia FREDERICKS, 1928, p. 779 [**Productus spinulosus* J. SOWERBY, 1814 in 1812–1815, p. 155; OD]. Spine bases swollen (tuberculate), dense, quincuncially arranged; thin shelled; weakly developed marginal ridges; cardinal process quadrifid.

Lower Carboniferous (Viséan)–lower Upper Carboniferous (Serpukhovian, ?Bashkirian): Eurasia, northern Africa.——FIG. 287,*1a–e.* **K. spinulosa* (J. SOWERBY), silicified specimens, Asbian, Fermanagh, British Isles; *a–c,* shell viewed ventrally, dorsally, laterally, ×2.3; *d,e,* incomplete dorsal valve viewed posterodorsally, internally, ×3.6 (Brunton, 1966).

Scoloconcha GORDON, 1966, p. 583 [**Productus indianensis* HALL, 1858b, p. 13; OD]. Small, around 6 mm wide; spines less dense than *Krotovia,* may be roughly concentric; cardinal process trifid, strong marginal structures. *Lower Carboniferous (middle Viséan):* USA.——FIG. 287,*4a–d.* **S. indianensis* (HALL), middle Viséan, Indiana; *a,b,* ventral, posterior views of shell, ×3; *c,* internal view of dorsal valve, ×3; *d,* posterior view of dorsal valve interior, ×4 (Gordon, 1966).

Subfamily MARGINIFERINAE Stehli, 1954

[Marginiferinae STEHLI, 1954, p. 321, *partim*]

Ribbing normally dominates (may be reduced in Permian) concentric ornament; ventral profile commonly geniculate at start of trail growth; corpus cavity commonly shallow, becoming deep in Permian. *Lower Carboniferous (upper Tournaisian)–Upper Permian (Changhsingian).*

Tribe MARGINIFERINI Stehli, 1954

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 927, *ex* Marginiferinae STEHLI, 1954, p. 321, *partim*]

Ventral spines, rarely on both valves; always ribbed, but weak; commonly series of few dorsal trails, corpus cavity deep. *Lower Permian (Artinskian)–Upper Permian (Changhsingian).*

Marginifera WAAGEN, 1884, p. 713 [**M. typica;* OD] [=*Strigospina* LIAO, 1979, p. 535 (type, *S. lineata;* OD)]. Outline subquadrate with well-differentiated, wide ears; ventral profile strongly convex near geniculation, dorsal disk weakly concave with series of two to three trails; ribbing commonly weak, reticulate disks; spines in prominent rows along flanks plus others widely scattered on venter, none at hinge; ear baffles in both valves; dorsal lateral ridges strongly divergent, continue straight across ears, becoming marginal ridge; endospines in single row anterior to brachial ridges. *Lower Permian (upper Artinskian)–lower Upper Permian (Kazanian):* Himalayas, southeastern Asia, north, northeastern China.——FIG. 288,*1a–e.* **M. typica,* Permian, Wargal Limestone, Pakistan, Khisor Range; *a,b,* posterior, anteroventral views of ventral valve, ×1.5; *c,* dorsal view of shell, ×2; *d,* lateral view of shell, ×2; *e,* dorsal valve interior, ×2 (Grant, 1968).

Entacanthadus GRANT, 1993b, p. 13 [**E. chioticus;* OD]. Small, moderately deep cavity resembling *Marginifera* in shape, but lacking ribbing and with small ears; dorsal valve weakly concave, geniculate, with series of closely spaced trails; spines in row at flanks, widely scattered over ventral corpus; dorsal adductor scars slightly arched medianly over start of short median septum. *upper Lower Permian (Kungurian):* Greece.——FIG. 288,*3a–e.* **E. chioticus,* Kungurian, Khios Island; *a,* holotype, viewed ventrally, USNM 402157, ×2; *b,* dorsal view of shell, ×2; *c,d,* ventral valve viewed laterally, internally, ×2; *e,* dorsal valve interior, ×2 (Grant, 1993b).

?Jipuproductus SUN, 1983, p. 123 [**J. jipuensis;* OD]. Poorly known, seemingly similar to *Marginifera,* but condition of dorsal trails unknown, probably differing in its small ears, prominent rugae on flanks, dorsal cardinal ridges. *upper Lower Permian (Artinskian):* Xizang, Tibet.

Otariella WATERHOUSE, 1978, p. 30 [**Marginifera otaria* GRANT, 1976, p. 115; OD]. Resembles *Marginifera,* but differs with trail overhanging dorsal disk, in lacking ribs, although there are elongate spine bases on trail; widely extended concavoconvex ears with unusually deep auricular cavities, somewhat twisted appearance; dorsal valve seemingly with only one trail; spine row on flanks less prominent; dorsal interior with more numerous endospines. *Lower Permian (Artinskian–lower Kungurian):* Thailand.——FIG. 288,*2a–e.* **O. otaria* (GRANT), Permian, Khao Chang; *a,b,* holotype viewed ventrally, laterally, USNM 212259, ×2; *c,* holotype viewed dorsally, USNM 212259, ×1; *d,* shell viewed anteroventrally, ×2; *e,* dorsal valve interior, ×2 (Grant, 1976).

Probolionia COOPER, 1957, p. 27 [**P. posteroreticulata;* OD]. Small with well-differentiated ears forming widest part of shell; ventral profile with weakly convex disk, geniculation, convex trail; median sulcus from median disk; dorsal disk gently concave, geniculate, with several dorsal trails; ribbing originates near beak, with rugae forming reticulation; spines symmetrical on ears, venter, and row along flanks, no dorsal spines; lateral, marginal ridges complete. *upper Lower Permian (Kungurian)–lower Upper Permian (Kazanian):* USA, Pamir.——FIG. 289,*2a–d.* **P. posteroreticulata,* Permian, Coyote Butte Formation, Oregon; *a–c,* holotype, viewed posteriorly, anteriorly, laterally, USNM 125369, ×2; *d,* drawing of longitudinal section showing dorsal trails, ×2 (Muir-Wood & Cooper, 1960).

Spinomarginifera HUANG, 1932, p. 16 [**S. kueichowensis;* OD] [=*Rugosomarginifera* XU, 1987, p. 224 (type, *Marginifera jisuensis* CHAO, 1927b, p. 149; OD); *Haydenoides* CHAN in YANG DE-LI & others, 1977, p. 352 (type, *H. orientalis;* OD)]. Small to medium, with wide hinge; weakly concavoconvex with long ventral trail anterior to geniculation, dorsal trail short; ribbing absent, but elongate spine bases; rugae irregular, narrow; spines commonly densely spaced, fine, but in some widely spaced

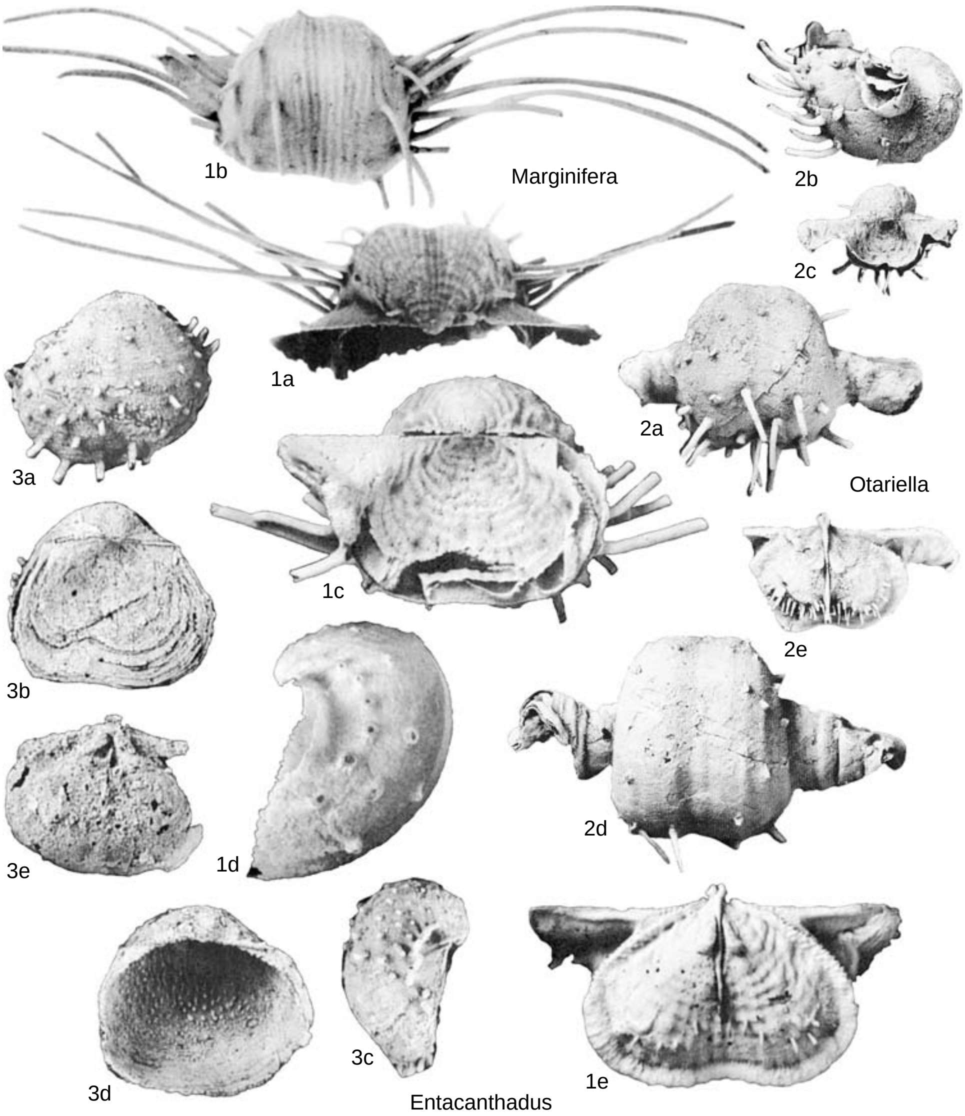


FIG. 288. Productellidae (p. 439).

anteriorly; dorsal valve with variably developed fine spines (the type species reported as lacking dorsal spines); marginal ridges strong in both valves, but ventrally incomplete anteriorly. *upper Lower Permian (upper Roadian)–Upper Permian (Changhsingian):* China, Japan, Afghanistan, Middle East.——FIG. 289,*1a–f.* **S. kueichowensis,* Permian Coal Series, Guizhou, China; *a–c,* ventral, posterior, lateral views, ×1; *d,* ventral view with remnants of long spines, ×1; *e,* exfoliated dorsal valve interior, ×1; *f,* internal mold of dorsal valve, ×1 (Huang, 1932).

Tribe BREILEENIINI Brunton, 1997

[Breileeniini BRUNTON in BRUNTON & LAZAREV, 1997, p. 389]

Spines on both valves, ribs commonly start anteriorly on corpus with elongate spine bases posteriorly. *Lower Carboniferous (upper Tournaisian)–Upper Carboniferous (upper Moscovian).*

Breileenia BRUNTON in BRUNTON & LAZAREV, 1997, p. 389 [**Productus davidsoni* JAROSZ, 1917, p. 88;

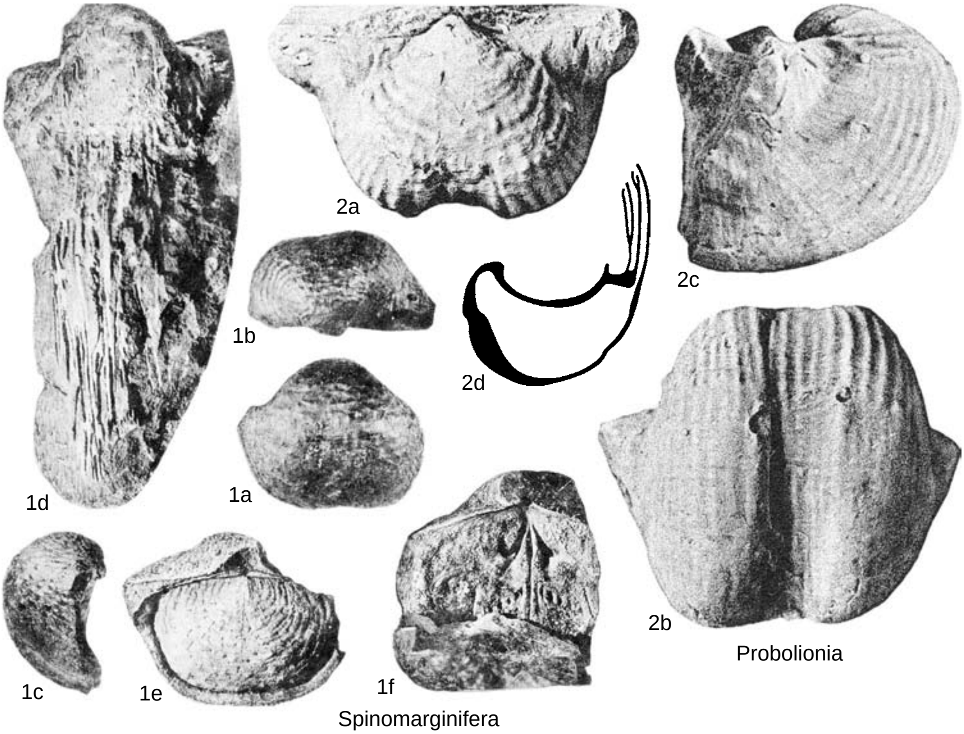


Fig. 289. Productellidae (p. 439–440).

OD]. Outline subrounded, corpus cavity moderately deep; spines distributed on both valves, ventrally with elongate bases or weak ribs originating at about half corpus length; growth lamellae weak, but may become prominent anteroventrally. *Lower Carboniferous (upper Tournaisian)–Upper Carboniferous (Serpukhovian):* western Europe, ?China, Canada. ——Fig. 290,*1a–e*. **B. davidsoni* (Jarosz); *a,b,* lectotype, viewed ventrally, laterally, Asbian, Derbyshire, British Isles, BGS 72461, ×1; *c,* external mold of dorsal valve, Asbian, Derbyshire, ×1; *d,* lateral view of shell, Asbian, Derbyshire, ×1.5; *e,* ventral view of shell with broken ventral trail, Staffordshire, ×1.5 (Brunton & Lazarev, 1997). ——Fig. 290,*1f,g*. *B. radiata* Brunton, Brigantian, Derbyshire; corpus viewed ventrally, dorsally, showing lateral ridges, ×2 (Brunton & Lazarev, 1997).

Desmoinesia Hoare, 1960, p. 226 [**Productus muricatus* Norwood & Pratten, 1855a, p. 14, *non* Phillips, 1836; OD; =*Marginifera muricatina* Dunbar & Condra, 1932, p. 222] [=*Rudinia* Muir-Wood & Cooper, 1960, p. 229, obj.]. Outline transverse, ventral umbo weakly inflated, irregularly rugose, weakly ribbed on corpus, trails; ventral spines on ribs, becoming concentric on anterior corpus and trail; dorsal spines sparse, reduced in later species; ventral ear baffles, subperipheral ridge. *Upper Carboniferous (upper Moscovian):* North America.——Fig. 290,*2a–f*. **D. muricatina* (Dunbar & Condra), Desmoinesian, Oklahoma; *a,* ventral view of shell, ×2; *b,c,* posterior, dorsal views of shell, ×2; *d,* lateral view of shell, ×1; *e,* ventral valve interior, ×2; *f,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Sandia Sutherland & Harlow, 1973, p. 41 [**S. brevis;* OD]. Radial ribbing relatively strong, posterior reticulation; dorsal spines thin plus few thick ones anteriorly. *Upper Carboniferous (middle Moscovian):* southern North America.——Fig. 290,*3a–f*. **S. brevis,* middle Moscovian, New Mexico; *a,b,* holotype viewed ventrally, laterally, OU 7688, ×1; *c–e,* holotype viewed anteriorly, posteriorly, dorsally, ×2; *f,* dorsal valve interior, ×2 (Sutherland & Harlow, 1973).

Tribe INCISIINI Grant, 1976

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 927, *ex* Incisiidae Grant, 1976, p. 103]

Outline commonly anteriorly bilobate; ventral spines only, ribbing absent; hinge narrow; lateral profile not geniculate. *Lower Permian (upper Artinskian)–Upper Permian (Changhsingian).*

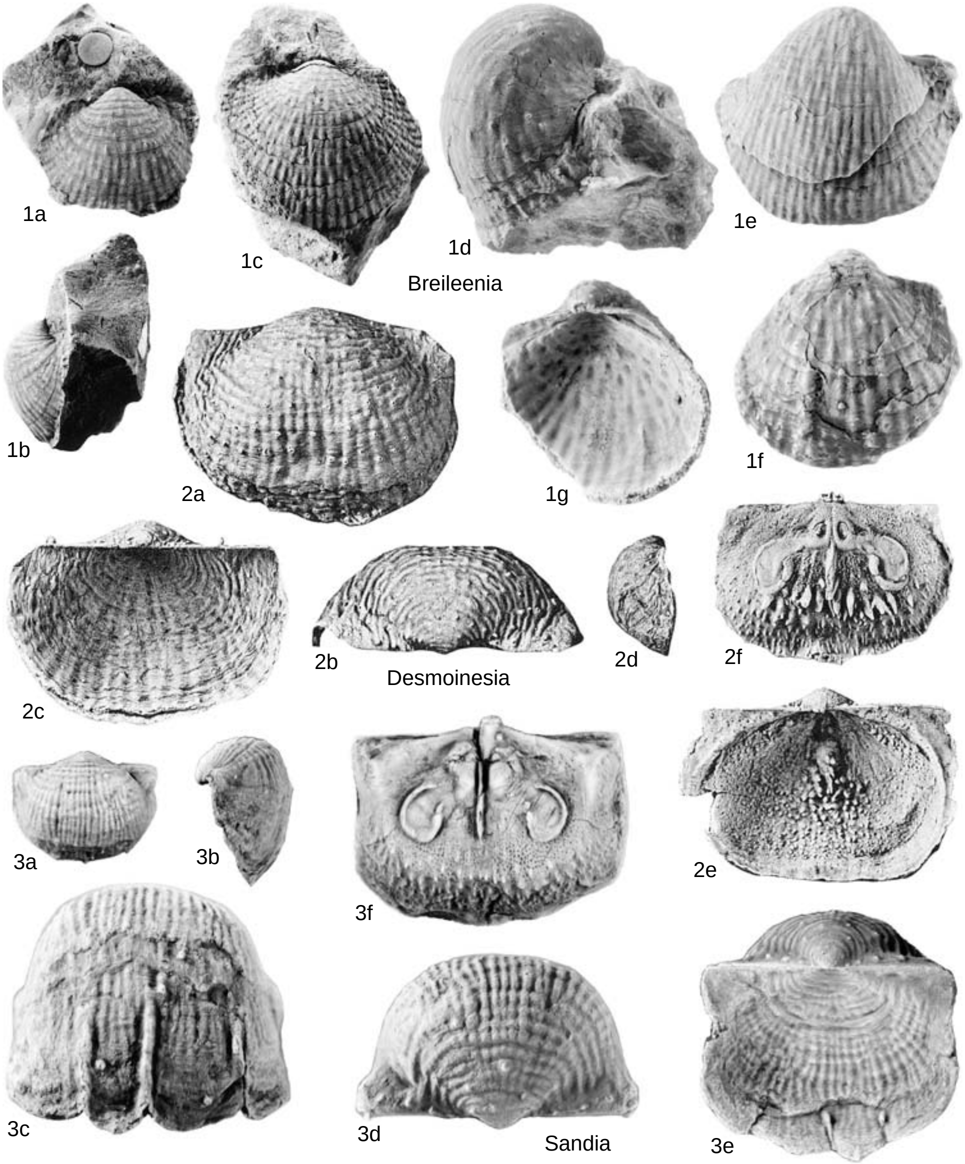


FIG. 290. Productellidae (p. 440–441).

Incisius GRANT, 1976, p. 103 [**I. concisus;* OD]. Outline narrow, widening anteriorly forming weakly bilobed anterior margin; profile nongeniculate, with strongly incurved ventral umbo; halteroid spines in row on each flank, scattered over venter, absent from sulcus and from dorsal valve; cardinal process small, bilobed; brachial ridges enclose elongate lobes occupying most of dorsal disk. *Lower Permian (upper Artinskian)–Upper Permian (Changhsingian):* Thailand, southern China, Greece.——FIG. 291,*3a–d.* **I. concisus,* Permian, Ko Muk, Thailand; *a,* holotype viewed ventrally, USNM 212184, ×4; *b,* holotype viewed dorsally, USNM 212184, ×1.5; *c,* shell viewed laterally, ×3; *d,* dorsal valve interior, ×3 (Grant, 1976).

Cyrtalosia TERMIER & TERMIER, 1970, p. 455 [*C. circinata;* OD]. Poorly preserved and known, difficult to differentiate from *Incisius* other than by its reported lack of ventral spines. *Upper Permian (Tatarian):* Cambodia.——FIG. 291,*1a,b.* **C.*

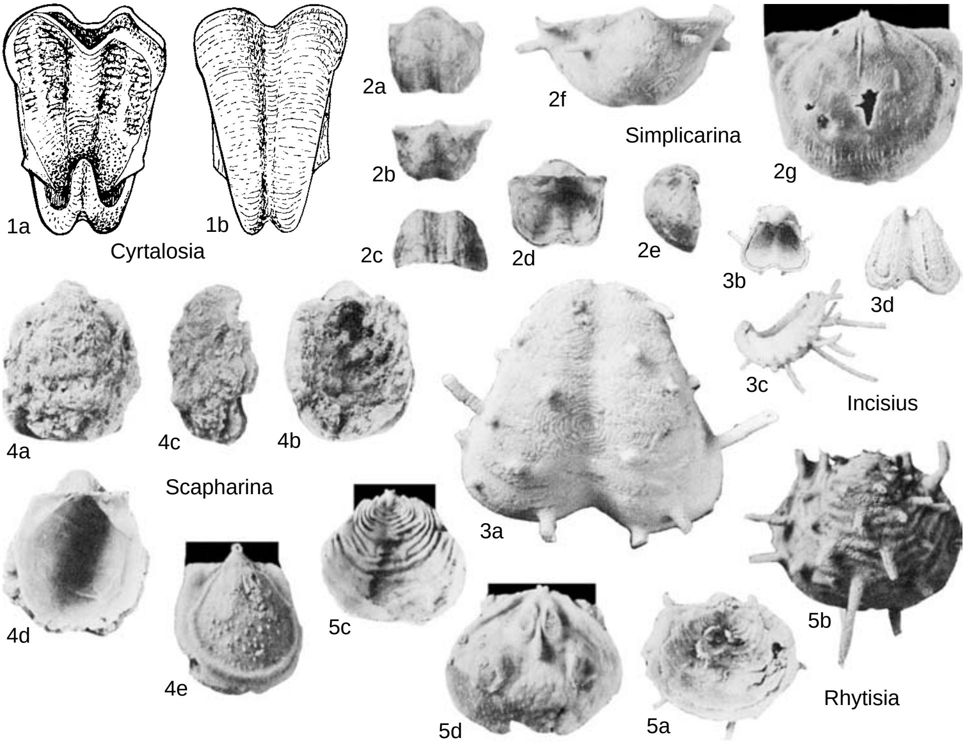


FIG. 291. Productellidae (p. 442–443).

circinata, Dzhulfian, Phnom Anseh; drawings of dorsal, ventral views, ×3 (Termier & Termier, 1970).

Rhytisia COOPER & GRANT, 1975, p. 967 [**R. rugosa;* OD]. Small, around 8 mm wide, rounded, concavo-convex profile, no anterior sulcus; rugae on both valves, no ribbing; spines relatively strong, scattered on ventral valve only; cardinal process sessile, bilobed; lateral ridges strongly divergent, separating ears, disappear anterolaterally; median septum short, tuberculate anteromedianly. *Lower Permian (Kungurian)–lower Upper Permian (Wordian):* USA.——FIG. 291,*5a–d.* **R. rugosa,* Permian, Road Canyon Formation, Texas; *a,* holotype, viewed dorsally, USNM 152703c, ×2; *b,* ventral valve exterior, ×3; *c,* dorsal valve exterior, ×2; *d,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Scapharina COOPER & GRANT, 1975, p. 895 [**S. rugosa;* OD]. Small, elongate with rounded anterior margin; spines few, probably confined near posterior margin; shell commonly roughly lamellose; ear baffles in ventral valve; cardinal process small, supported by lateral ridges separating ears and continued as complete marginal ridge. *Upper Permian (Capitanian):* USA.——FIG. 291,*4a–e.* **S. rugosa,* Permian, Bell Canyon Formation, Texas; *a–c,* holotype, viewed ventrally, dorsally, laterally, USNM 152657d, ×3; *d,* ventral valve interior, ×3; *e,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Simplicarina COOPER & GRANT, 1975, p. 966 [**S. incompta;* OD]. Small, outline subquadrate with small ears, rounded anterior margin; hinge approximately equal to maximum width; exteriors smooth with variable median sulcus; spines few, one or two on lateral slopes, venter; cardinal process small, sessile, bilobate; median septum short; lateral ridges at high angle from hinge, extend as marginal ridge, weak anteriorly, but with endospines. *upper Lower Permian (Roadian):* USA.——FIG. 291,*2a–g.* **S. incompta,* Permian, Road Canyon Formation, Texas; *a–e,* holotype viewed ventrally, posteriorly, anteriorly, dorsally, laterally, USNM 153927a, ×1; *f,* ventral valve viewed posteriorly, ×2; *g,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

Tribe PAUCISPINIFERINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 927, *ex* Paucispiniferinae MUIR-WOOD & COOPER, 1960, p. 319, *partim*] [=Hystriculininae LAZAREV, 1986c, p. 23; Caucasoproductinae G. KOTLYAR, 1989, p. 121, *partim;* Jiguliconchinae LAZAREV, 1986c, p. 22]

Commonly widest at hinge, with ventral median sulcus; always ribbed, ventral spines only; corpus cavity may be deep. *Upper Carboniferous (Kasimovian)–Upper Permian (Tatarian).*

Paucispinifera Muir-Wood & Cooper, 1960, p. 319 [**P. auriculata;* OD]. Medium size, transverse outline with large ears forming widest part of shell; ribbing most strongly developed in geniculation region, lost at trail margin; rugae absent; about six spines symmetrically placed on ears, flanks, venter, smaller spines in rows separating ears from corpus; cardinal process sessile, broad with zygidium; lateral ridges strong, continued as complete marginal ridge. *upper Lower Permian (Roadian)–lower Upper Permian (Wordian):* southern USA.——Fig. 292,*1a–e.* **P. auriculata,* Permian, Word Formation, Texas; *a,b,* holotype viewed anteriorly, posteroventrally, USNM 124054g, ×1; *c,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960); *d,e,* shell viewed dorsally, laterally, ×1 (Cooper & Grant, 1975).

Anemonaria Cooper & Grant, 1969, p. 8 [**A. inflata;* OD; =*Marginifera sublaevis* King, 1931, p. 89, *partim*]. Subrectangular, ears extended; deeply concavoconvex; sulcus distinct; nearly smooth except for indistinct ribs on trail; spines few, in row on each flank, scattered over venter, visceral disk; ventral interior with small ear baffles; sessile cardinal process with zygidium. *Lower Permian (Sakmarian–Roadian):* USA, north and northeastern China.——Fig. 292,*2a–d.* **A. inflata,* Permian, Cathedral Mountain Formation, Texas; *a,* ventral valve exterior, ×1; *b,* dorsal view of complete specimen, ×1; *c,d,* dorsal valve viewed internally, ×2, posteriorly, ×4 (Cooper & Grant, 1975).

Azygidium Waterhouse, 1983c, p. 153 [**Horridonia mitis* Hill, 1950, p. 17; OD]. Similar to *Anemonaria,* but with longer trail, no zygidium, but similarly weak or no ribbing. *Lower Permian:* eastern Australia (Dresden Formation).

Caricula Grant, 1976, p. 128 [**C. salebrosa;* OD]. Small, transverse, ears extended, geniculate; visceral disks strongly rugose, weakly ribbed, ribbing almost lost on trails; sulcus prominent; spines few, up to four across ears, six on venter; cardinal process internally V-shaped, on short shaft; median septum raised anteriorly; lateral ridges extend as low marginal ridges around corpus; brachial ridges prominent. *Lower Permian (Artinskian):* Thailand.——Fig. 293,*1a–e.* **C. salebrosa,* Artinskian, Ko Muk; *a–c,* holotype viewed ventrally, dorsally, laterally, USNM 212368, ×3; *d,e,* ventral valve interior, dorsal valve interior, ×3 (Grant, 1976).

Caucasoproductus G. Kotlyar, 1989, p. 121 [**P. (Productus) dichotomocostatus* Licharew, 1937, p 39; OD]. Small, asymmetric, trails may flare; plano- to weakly concavoconvex corpus; ribbing thin with dichotomous branching; visceral disks reticulate; spine row near hinge, widely scattered over valve; marginal ridge around dorsal cavity. *Upper Permian (Tatarian):* North Caucasus.——Fig. 292,*4a–d.* **C. dichotomocostatus* (Licharew), Dzhulfian, Urushten; *a–c,* ventral, dorsal, lateral views of incomplete specimen, ×1; *d,* posteroventral view of incomplete specimen, ×1 (Licharew, 1937).

Costiferina Muir-Wood & Cooper, 1960, p. 277 [**Productus indicus* Waagen, 1884, p. 687; OD]. Larger medium size, transverse in ventral outline, with well-defined ears; ventral profile strongly, but evenly convex; dorsal disk almost flat, geniculate with trail; ribbing originates near umbo, widening to coarsely irregular on trail; disks reticulate; spines large, on ears, in row separating ears and on trail; dorsal lateral ridges bend sharply to separate ears, continue as marginal ridge; adductor scars large with anterior and posterior components; long median septum; valves thick shelled. *upper Lower Permian (Artinskian)–Upper Permian (Kazanian):* Pakistan, Western Australia, southeastern Asia, China.——Fig. 292,*3a–c.* **C. indica* (Waagen), Upper Permian, upper *Productus* Limestone, Salt Range, Pakistan; ventral valve viewed posteroventrally, anteriorly, laterally, ×1 (Muir-Wood & Cooper, 1960).——Fig. 292,*3d–f. C. vishnu* (Waagen), Permian, upper *Productus* Limestone, Salt Range, Pakistan; *d,* ventral valve interior, ×1; *e,f,* dorsal valve interior, lateral view, ×1 (Muir-Wood & Cooper, 1960).

Elliottella Stehli, 1955, p. 711, *nom. nov. pro Psilonotus* Stehli, 1954, p. 323, *non* Walker, 1834 [**Psilonotus transversalis* Stehli, 1954, p. 324; OD]. Small, somewhat transverse shells, corpus cavity commonly moderately deep; ventral median sulcus; ventral disk convex, profile geniculate; ribbing strong, originating posteriorly on disks; spines widely scattered, arising from ribs; weak divergent lateral ridges extend across ears; median septum reaches margin of disk. *Lower Permian (Artinskian):* southern USA.——Fig. 293,*2a,b.* **E. transversalis* (Stehli), Lower Permian, Bone Spring Formation, Texas; ventral valve viewed ventrally, laterally, ×1 (Stehli, 1954).——Fig. 293,*2c,d. E. minima* (Stehli), Lower Permian, Bone Spring Formation, Texas; shell viewed dorsally, dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Hystriculina Muir-Wood & Cooper, 1960, p. 210 [**H. texana;* OD]. Ventral spines sparse, include row on each umbonal flank; concentric ornament posteriorly, weak; lateral ridges strongly divergent, continued as ear baffles. *Upper Carboniferous (upper Kasimovian)–Permian:* North America, central Europe.——Fig. 293,*3a–f.* **H. texana,* upper Kasimovian–Gzhelian, Texas; *a–d,* holotype viewed ventrally, posteriorly, dorsally, laterally, USNM 124034a, ×2; *e,f,* dorsal valve interior, posterior, ×3 (Muir-Wood & Cooper, 1960).

Jiguliconcha Lazarev, 1990, p. 81 [**Hystriculina gracilicosta* Lazarev, 1984, p. 71; OD]. Similar to *Hystriculina,* but lateral ridges weak, close to hinge. *Upper Carboniferous (Kasimovian):* eastern Europe.——Fig. 293,*5a–d.* **J. gracilicosta* (Lazarev), Kasimovian, Moscow basin; *a,* anteroventral view of ventral valve, ×1; *b,c,* ventral, lateral views of ventral valve, ×1; *d,* dorsal valve interior, median septum broken, ×3 (new).

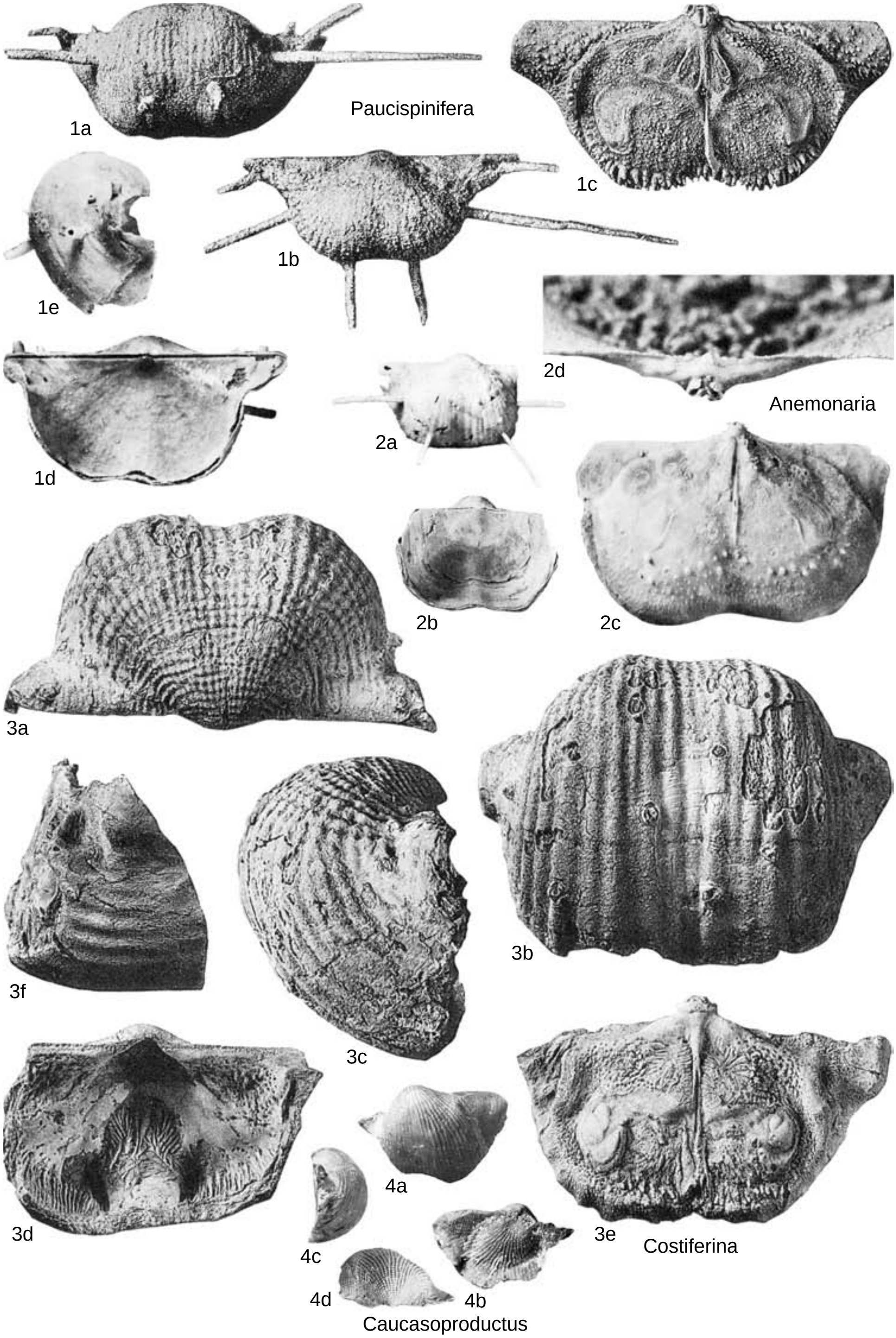


FIG. 292. Productellidae (p. 444).

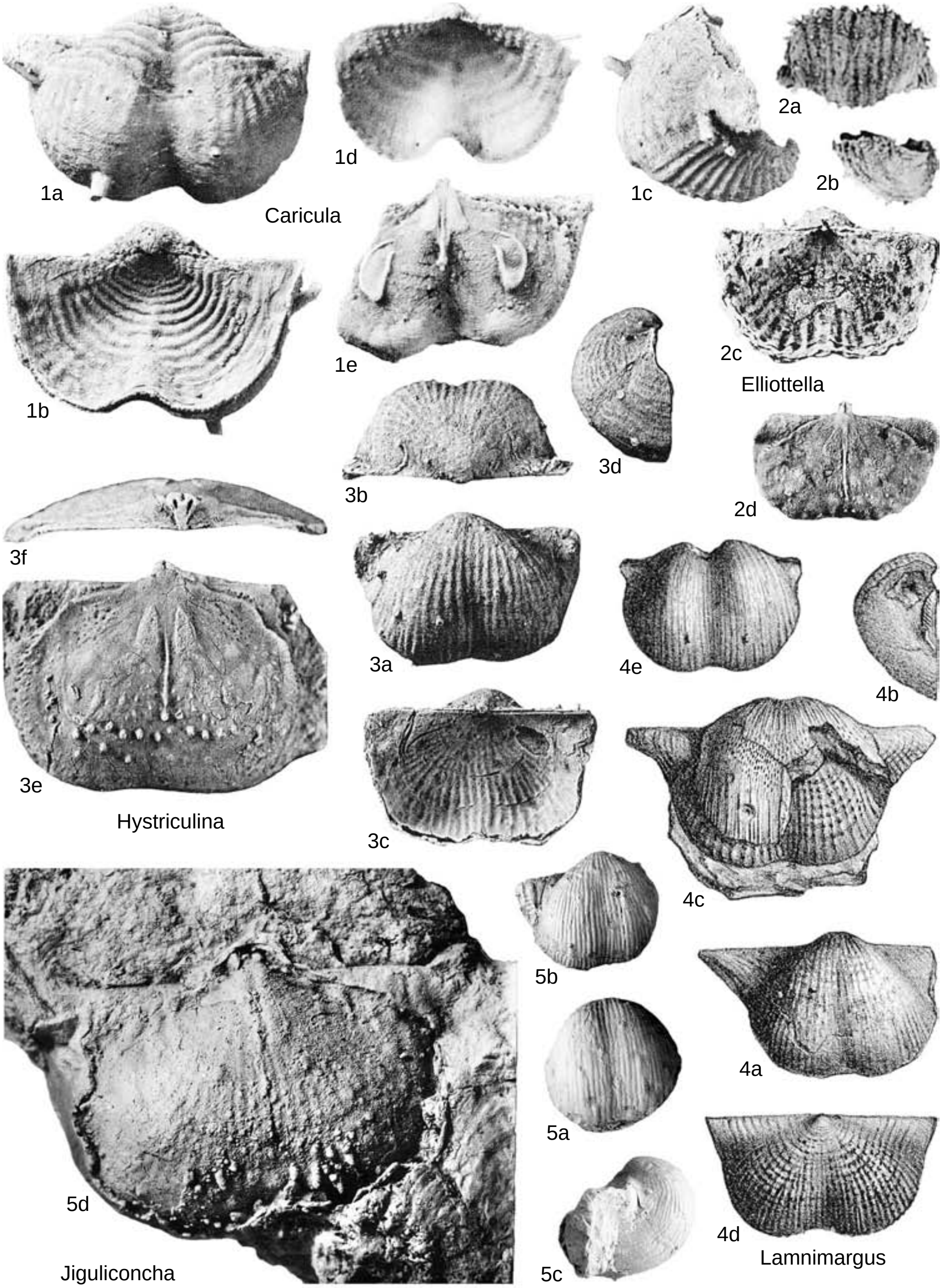


FIG. 293. Productellidae (p. 444–447).

Lamnimargus WATERHOUSE, 1975, p. 10 [**Marginifera himalayensis* DIENER, 1899, p. 39; OD]. Transverse with large ears forming wide hinge line; median sulcus originates near beak; disk reticulate; spines in row near hinge, in row on flanks, plus about two on venter; ventral interior with striated adductor scars; dorsal lateral ridges become complete marginal ridge. *upper Lower Permian (Kungurian):* Himalayas, Nepal, Pamirs.——Fig. 293,*4a–e.* **L. himalayensis* (Diener), upper Lower Permian; *a,b,* lectotype (selected by Waterhouse, 1975) viewed ventrally, laterally, Kashmir, ×1; *c,* ventral view of shell with exfoliated, partially missing ventral valve, Spiti, ×1; *d,e,* external mold of dorsal valve, anteroventral view of shell, Spiti, ×1 (Diener, 1899).

Lampangella Waterhouse, 1983a, p. 121 [**L. lata;* OD]. Transverse outline with large ears; short ginglymus; ribbing prominent anteriorly; spines in row near hinge, row at ears, sparse on ventral corpus; low ear baffles. *Upper Permian (Tatarian):* Thailand.——Fig. 294,*1a–c.* **L. lata,* Upper Permian, Huali Tak Formation, northwestern Thailand; *a,* holotype, incomplete ventral valve exterior, TBR 441, ×2; *b,* ventral valve exterior, ×3; *c,* dorsal valve external mold, ×2.5 (Waterhouse, 1983a).

Liosotella Cooper, 1953, p. 36 [**L. rugosa;* OD]. Small to medium size with broad, shallow median sulcus; gently concavoconvex corpus, geniculate, long trails; steep flanks; ribbing strong only on trail; spines in curved rows at base of flanks, scattered variably on rest of valve; zygidium commonly present; dispositions of lateral ridges, extensions across ears variable; one or two rows of strong endospines anterior to well-marked brachial ridges, surfaces tuberculate. *upper Lower Permian (Roadian)–lower Upper Permian (lower Kazanian):* central, North America, northern and northeastern China.——Fig. 294,*2a–d.* **L. rugosa,* Upper Permian, Monos Formation, Sonora, Mexico; holotype viewed posteriorly, anteriorly, dorsally, laterally, USNM 115458, ×1 (Muir-Wood & Cooper, 1960).——Fig. 294,*2e–f. L. irregularis* Cooper & Grant, Upper Permian, Word Formation, Texas; dorsal valve exterior, interior, ×1 (Cooper & Grant, 1975).

Nudauris Stehli, 1954, p. 317 [**N. diabloensis;* OD]. Medium size, weakly concavoconvex profile; ears well developed at widest part of shell; weak ventral sulcus, dorsal fold; ribbing weak to obscure; rugae on both disks; spines in row near hinge, scattered on ventral valve; lateral ridges short, close to hinge; cardinal process trifid, median septum long, thin. *Lower Permian (Asselian–Kungurian):* USA.——Fig. 294,*4a–e.* **N. diabloensis,* Permian, Bone Spring Formation, Texas; *a–c,* ventral valve viewed ventrally, anteriorly, laterally, ×1; *d,* dorsal valve exterior, ×1; *e,* dorsal valve interior, ×1 (Cooper & Grant, 1975).

Oncosarina Cooper & Grant, 1969, p. 9 [**O. spinocostata;* OD]. Small, strongly concavoconvex profile with steep flanks; ventral sulcus weak or absent; disk smooth, ribbing originating anteriorly on disks, prominent on trail; spines thick in clusters on anterior ears, thinner on umbonal regions, lateral slopes, crests of costae; dorsal adductor scars on platforms overhanging medianly; cardinal process broad, variably bilobed, quadrifid; lateral ridges extend to separate ears. *Lower Permian (Artinskian–lower Kungurian):* USA.——Fig. 294,*3a–d.* **O. spinocostata,* Permian, Skinner Ranch Formation, Texas; *a,* holotype viewed ventrally, USNM 149824, ×2; *b,* holotype viewed laterally, USNM 149824, ×1; *c,* shell viewed dorsally, ×2; *d,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Retimarginifera Waterhouse, 1970, p. 123 [**R. perforata;* OD]. Small, transverse, widest at hinge; profile deeply concavoconvex, deep ventral sulcus; visceral disk reticulate with clear ribbing commonly extending along trail; six major spines, in pairs on ears, venter; sessile, trifid cardinal process; lateral ridges extend as marginal ridge that may be lost anteriorly. *Lower Permian (Artinskian–Kungurian):* Western Australia, Thailand, Himalayas, northern China.——Fig. 295,*1a–d.* **R. perforata,* Permian, Byro Group, Western Australia, Carnavon Basin; *a,* holotype viewed ventrally, U.W.A. 59282, ×2; *b,* ventral valve exterior, ×2 (Waterhouse, 1970); *c,* dorsal view of shell, ×1.5; *d,* dorsal valve interior, ×1.5 (Archbold, 1984).——Fig. 295,*1e–g. R. celeteria* Grant, Permian, Ko Muk, Thailand; *e,* dorsal view of shell, ×1; *f,g,* shell viewed ventrally, laterally, ×1 (Grant, 1976).

Shanxiproductus Duan & Li, 1985, p. 232 [**S. shanxiensis;* OD]. Resembling *Hystriculina,* but medianly sulcate, rugose on visceral disks, may form distal spine ridges on ventral trail; ventral internal marginal ridges. *Upper Carboniferous (Gzhelian)–Lower Permian (Asselian):* China.——Fig. 295,*2a–c.* **S. shanxiensis,* Asselian, Shanxi; anterior, posterior, lateral views of ventral valve, ×2 (Duan & Li, 1985).

Spinarella Cooper & Grant, 1975, p. 1058 [**S. perfecta;* OD]. Medium, outline rectangular, but with extended ears; deeply concavoconvex; ribbing low, variable over anterior disks, trails; rugae in posterior region producing varied degree of reticulation; spines in row across ears, scattered widely over ventral valve; ventral adductor scars sunken; cardinal process small, sessile, trifid to quadrifid; median ridge long; brachial ridges strong; inner surface strongly endospinose. *upper Lower Permian (Roadian):* USA.——Fig. 295,*3a–f.* **S. perfecta,* Permian, Road Canyon Formation, Texas; *a–c,* holotype, viewed ventrally, dorsally, laterally, USNM 148844a, ×1; *d,* ventral valve interior, ×1; *e,* ventral valve viewed posteriorly, ×1; *f,* dorsal valve interior, ×1 (Cooper & Grant, 1975).

Transennatia Waterhouse, 1975, p. 10 [**Productus gratiosus* Waagen, 1884, p. 691; OD] [=*Gratiosina* Grant, 1976, p. 131, obj.; *Asioproductus* Chan (Zhan) in Hou, Zhan, & Chen, 1979, p. 85 (type, *A. bellus;* OD); *Kurtomarginifera* Xu, 1987, p. 225 (type, *K. spinata;* OD)]. Small, outline subquadrate with small ears; ribs strongly defined, commonly converging into sulcus; rugae strong, producing reticulation on both disks; spines in row separating ears, scattered on disk, trail; cardinal process sessile quadrifid. *Lower Permian (?Kungurian), Upper Permian (Kazanian):* Himalayas, Thailand, China, Timor, Western Australia, Greece, Sicily.——Fig. 295,*4a–e.* **T. gratiosa* (Waagen), Upper Permian, Wargal Formation, Salt Range, Pakistan; *a,b,* ventral, dorsal views, ×1; *c–e,* lateral, ventral interior, dorsal interior, ×2 (Grant, 1976).——Fig.

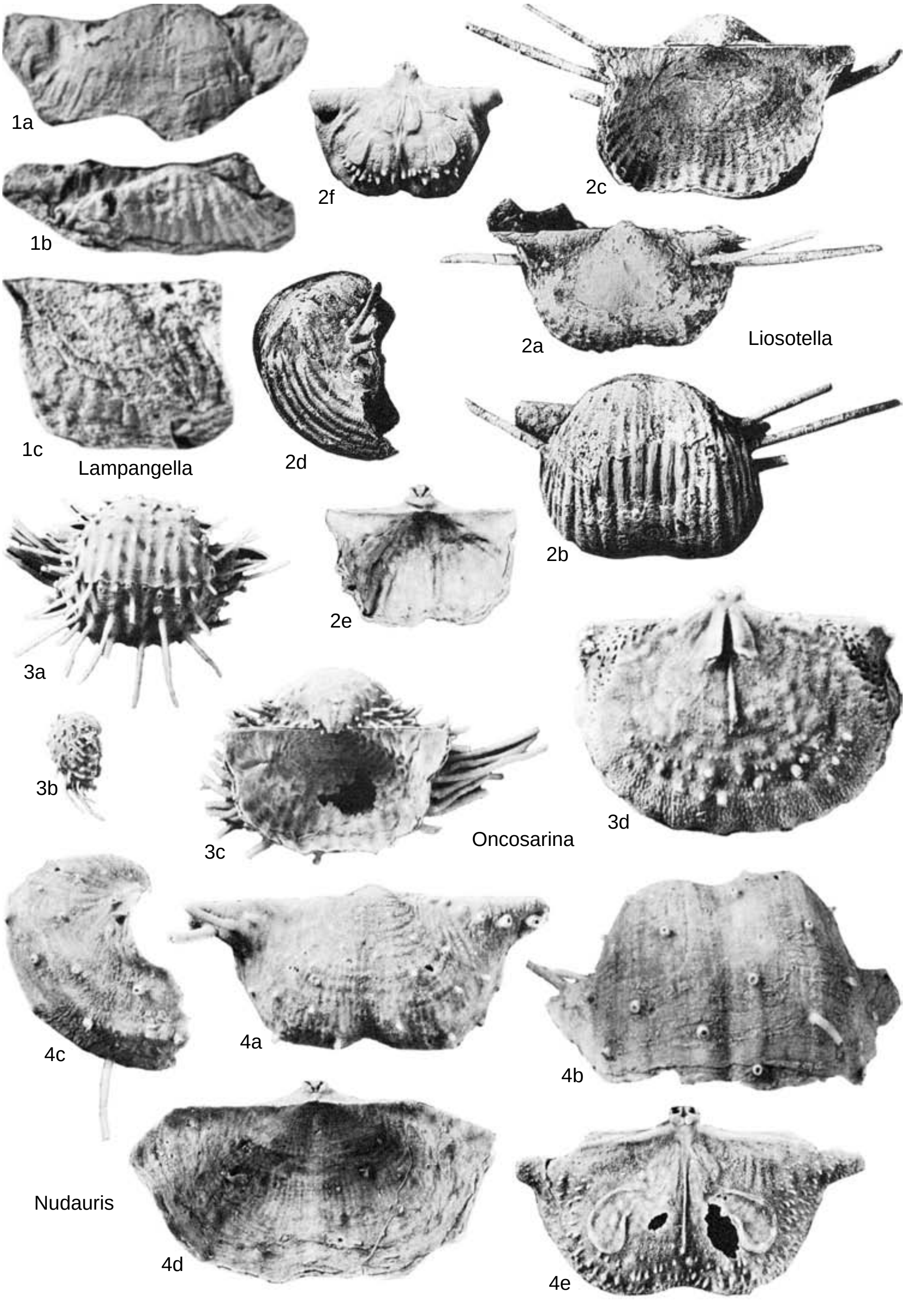


FIG. 294. Productellidae (p. 447).

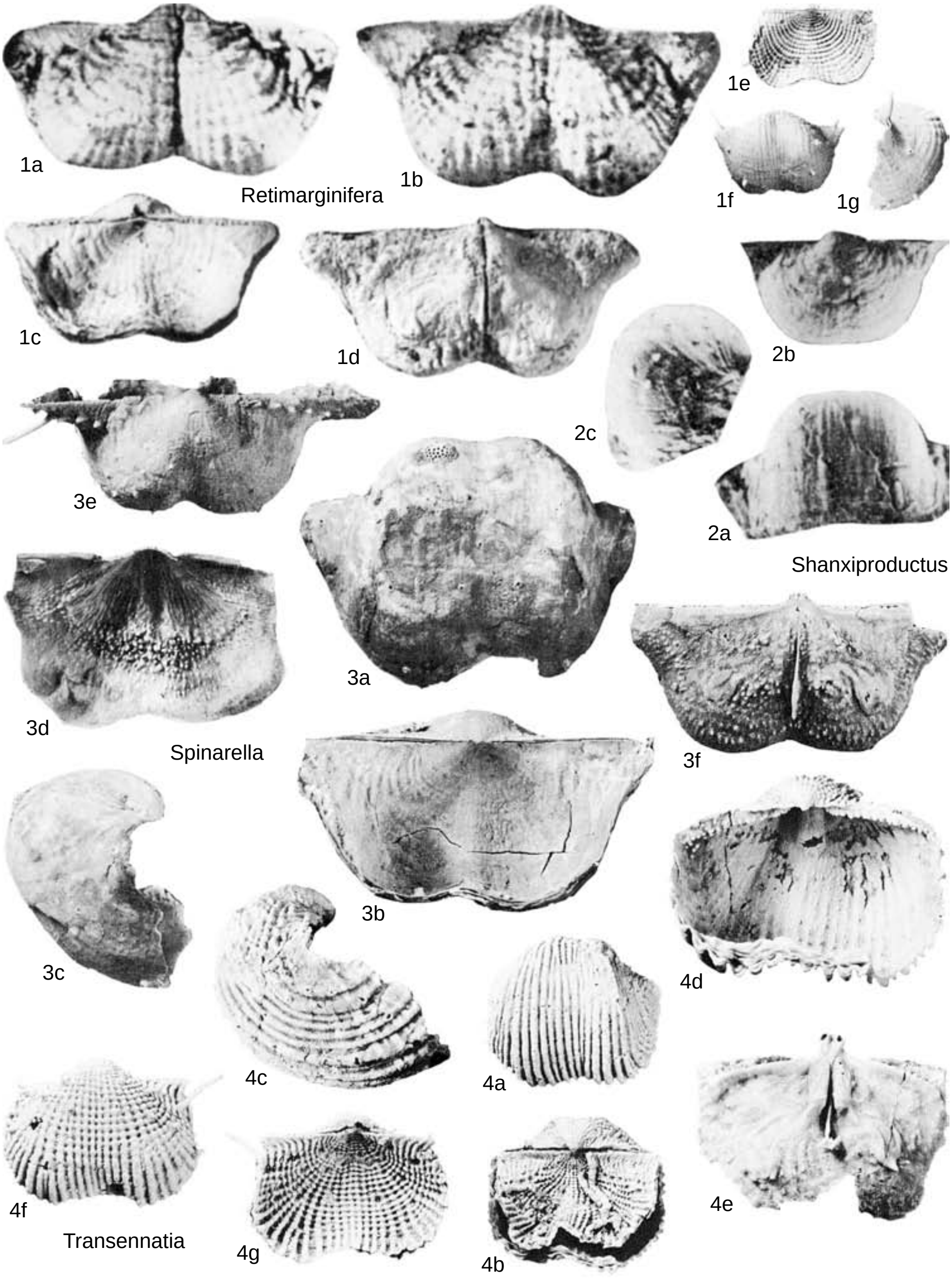


FIG. 295. Productellidae (p. 447–449).

295,*4f,g. T. insculpta* (GRANT) Permian, Ko Muk, Thailand; ventral, dorsal views of shell, ×2 (Grant, 1976).

Xestosia COOPER & GRANT, 1975, p. 1063 [**X. obsolescens;* OD]. Resembling *Spinarella,* but with clumps of spines on ears, internally with endospines

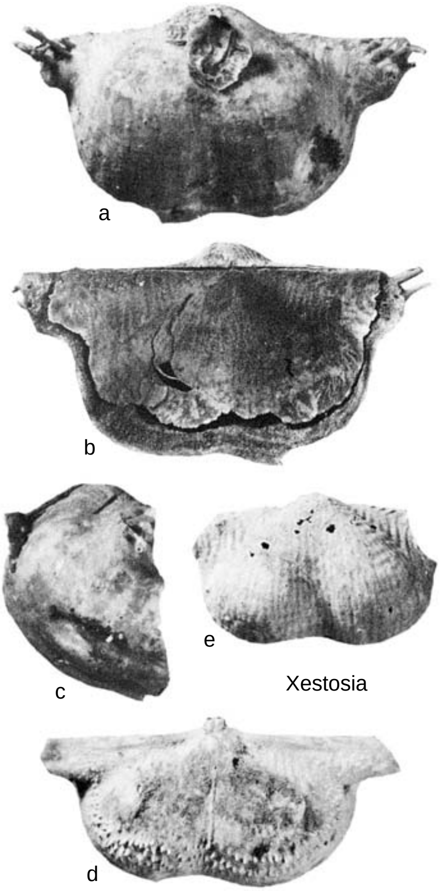


FIG. 296. Productellidae (p. 449–450).

distributed only marginally. *upper Lower Permian (Kungurian):* USA.——FIG. 296*a–c.* **X. obsolescens,* Permian, Cathederal Mountain Formation, Texas; holotype, viewed ventrally, dorsally, laterally, USNM 148861b, ×1 (Cooper & Grant, 1975). ——FIG. 296*d,e. X. schucherti* (KING); dorsal valve interior, ventral valve exterior, ×1 (Cooper & Grant, 1975).

Subfamily PLICATIFERINAE
Muir-Wood & Cooper, 1960

[Plicatiferinae MUIR-WOOD & COOPER, 1960, p. 201]

Shell geniculated, with ventral disk only gently convex; corpus cavity moderately shallow to rarely deep anteriorly; ribbing lacking, weak or only anteriorly on trails; concentric ornament normally strong, especially rugae; spines sparsely or densely distributed on ventral valves, commonly including near hinge, rarely on both. *Upper Devonian (upper Famennian)–Upper Permian (Kazanian).*

Tribe PLICATIFERINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 927, *ex* Plicatiferinae MUIR-WOOD & COOPER, 1960, p. 201]

Corpus cavity moderately deep, trail long; ribbing absent or weak, only on trails; rugae or lamellae strongly developed on corpus; ear baffles in dorsal valve, rarely also in ventral valve. *Carboniferous (middle Viséan–Bashkirian), ?Upper Carboniferous.*

Plicatifera CHAO, 1927b, p. 25 [**Productus plicatilis* J. DE C. SOWERBY, 1824 in 1823–1825, p. 85; OD]. Transverse outline; rugae strongly developed on corpus, ribbing absent or incipient, narrow, may extend over trail; stout spines near hinge, on flanks, few anteriorly, smaller ones scattered on rugae. *Lower Carboniferous (middle Viséan–upper Viséan):* Eurasia, northern Africa.——FIG. 297,*1a–c.* **P. plicatilis* (J. DE C. SOWERBY), Viséan, Derbyshire, British Isles; lectotype, viewed anteroventrally, dorsally, posteriorly, BMNH B 60960, ×2 (new).——FIG. 297,*1d–f. P. pseudoplicatilis* (MUIR-WOOD, 1928), Asbian, Fermanagh, silicified specimens; *d,* dorsal valve interior, ×1.5; *e,* interiors of two incomplete articulated valves viewed anteriorly, ×1.5; *f,* incomplete juvenile ventral valve exterior showing pedicle sheath, *arrow,* clasping spines, ×10 (Brunton & Mundy, 1993).

Absenticosta LAZAREV, 1991, p. 58 [**A. uldzejtuensis* SUUR'SUREN & LAZAREV in LAZAREV, 1991, p. 58; OD]. Rugae thin, undulose, irregular; spines thin, densely arranged ventrally, dorsal spines few, thicker anteriorly; lateral ridges continue weakly to anterior margin. *Lower Carboniferous (?middle Viséan, upper Viséan):* Transbaikalia, Mongolia.——FIG. 297,*4a–d.* **A. uldzejtuensis* (SUUR'SUREN & LAZAREV), middle Viséan–upper Viséan, Mongolia; *a,b,* incomplete shell viewed anteroventrally, posteriorly, ×1.5 (new); *c,* external mold of dorsal valve, ×1; *d,* anterolateral view of external mold of dorsal valve, ×1 (Lazarev, 1991).

Aseptella MARTÍNEZ CHACÓN & WINKLER PRINS, 1977, p. 18 [**A. asturica;* OD]. Small, up to 14 mm wide, transverse shell; rugae narrow but clear or lamellose, no ribs; ventral spines stout, in two radiating rows on each flank; dorsal interior with strong lateral ridges and ear baffles. *Carboniferous (lower Serpukhovian–Bashkirian), ?Upper Carboniferous:* Spain, Argentina, Thailand.——FIG. 297,*2a–d.* **A. asturica,* lower Bashkirian, Oviedo; *a,* external mold of ventral valve, ×8.5; *b,* internal mold of ventral valve, ×4; *c,* external mold of dorsal valve, ×4; *d,* internal mold of dorsal valve, ×7 (Martínez Chacón & Winkler Prins, 1977).

Crossacanthia GORDON, 1966, p. 580 [**C. perlamellosa;* OD]. Small; rounded shells, no ribbing, con-

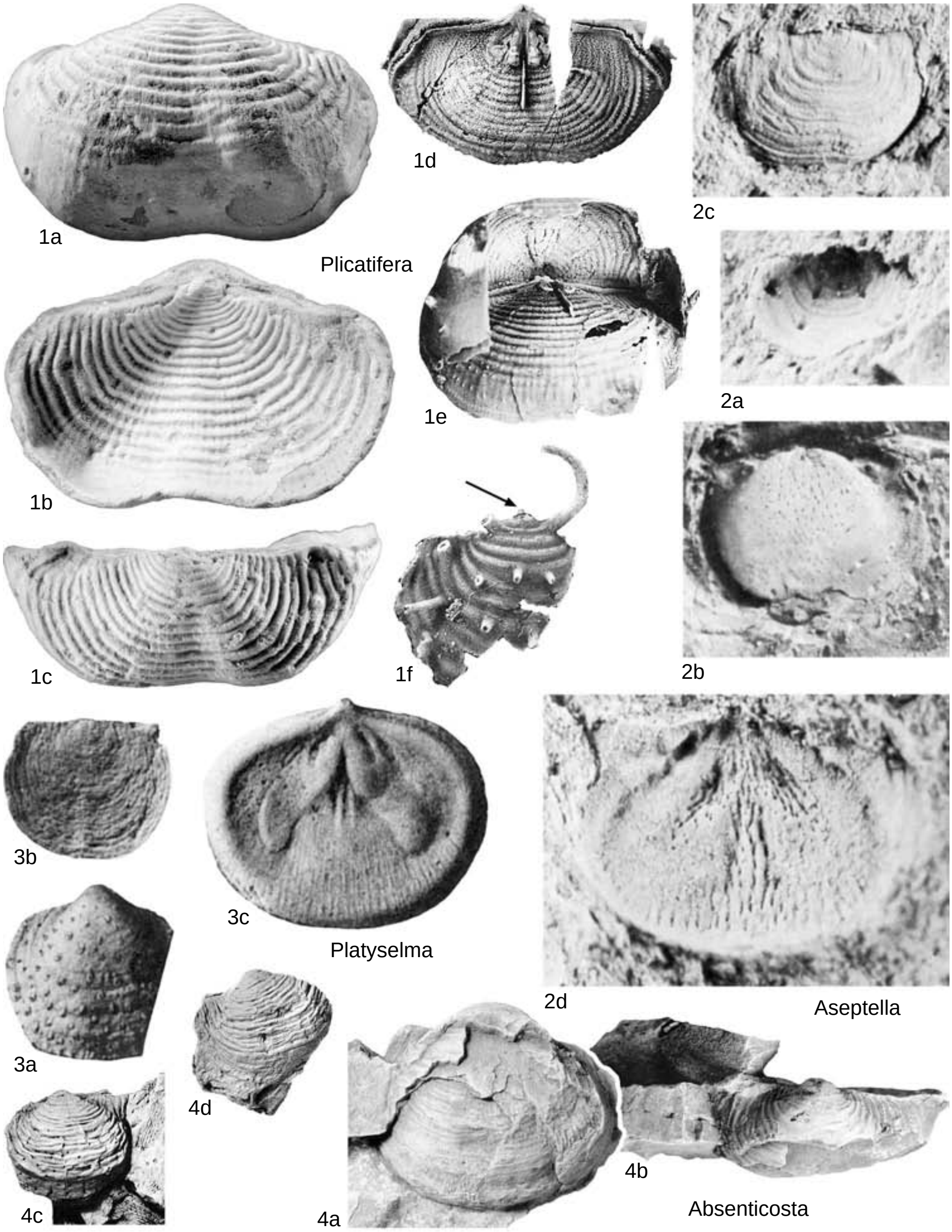


FIG. 297. Productellidae (p. 450–452).

centric lamellae on both valves bearing numerous spines, but only anteriorly on dorsal valve; dorsal complete subperipheral ridge. *Lower Carboniferous (middle Viséan):* USA.——FIG. 298,*2a–e.* **C. perlamellosa,* middle Viséan, Missouri; *a,* holotype viewed ventrally, USNM 120637, ×1; *b,c,* anteriorly, laterally, USNM 120637, ×2; *d,* dorsal valve exterior, ×2; *e,* dorsal valve interior, ×2 (Gordon, 1966).

Ferganoproductus GALITSKAYA, 1977, p. 33 [**Productus ferganensis* JANISCHEWSKY, 1918, p. 41; OD]. Rugae narrow, irregular posteriorly, forming some reticulation with spine bases; spines fine covering ventral valve, plus rows near hinge, at flanks, rarely and

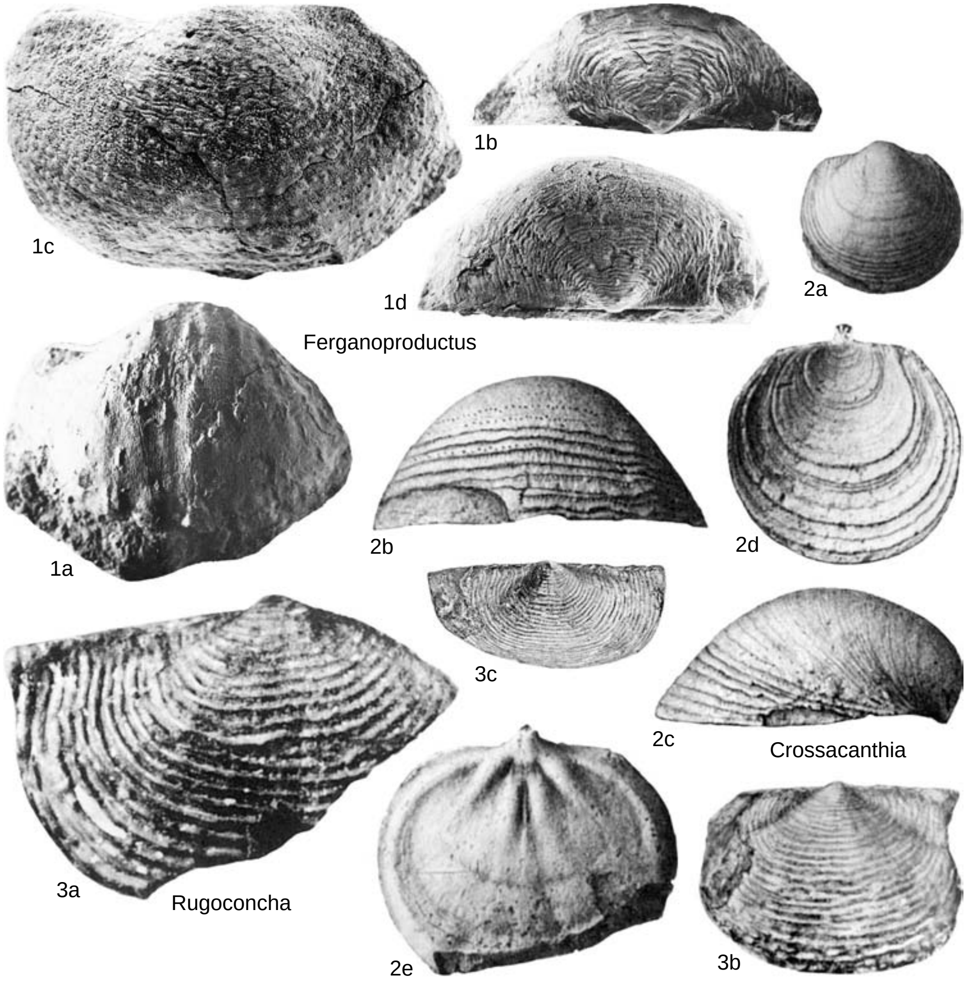


Fig. 298. Productellidae (p. 450–452).

thicker on dorsal valve. *Carboniferous (upper Viséan–Serpukhovian):* eastern Europe, Asia.——Fig. 298,*1a–d.* **F. ferganensis* (Janischewsky), Serpukhovian, Kirghizia; *a,b,* ventral exterior viewed ventrally, posteriorly, ×1; *c,d,* external mold of dorsal valve viewed dorsally, posteriorly, ×1 (Galitskaya, 1977).

Platyselma Gordon, 1966, p. 575 [**P. echinatum;* OD]. Planoconvex with moderately deep corpus cavity; weak lamellae on both valves, spines in weak concentric bands confined to ventral valve (or perhaps fine ones on dorsal valves); strong subperipheral ridges. *Lower Carboniferous (middle Viséan):* southern USA.——Fig. 297,*3a–c.* **P. echinatum,* middle Viséan, Oklahoma; *a,* incomplete ventral valve exterior, ×2; *b,* dorsal valve exterior, ×1; *c,* dorsal valve interior, ×2 (Gordon, 1966).

?Rugoconcha Jin & Sun, 1981, p. 132 [**Plicatifera chaoi* Grabau, 1936, p. 171; OD]. Resembles *Plicatifera,* but seemingly lacking trails, with rugae covering ventral valve; small cicatrix; ginglymus may be present. *Upper Carboniferous (lower Bashkirian):* southern China.——Fig. 298,*3a–c.* **R. chaoi* (Grabau), lower Bashkirian, Guangxi; *a,* ventral valve exterior (holotype No. 5384 lost during WWII; neotype, NIGP 48674, held at Nanjing Institute of Geology & Paleontology), ×2; *b,c,* ventral valve exterior viewed ventrally, posteroventrally, ×1 (Grabau, 1936).

Tribe LEVIPUSTULINI Lazarev, 1985

[*nom. transl.* Brunton, Lazarev, & Grant, herein, *ex* Levipustulinae Lazarev, 1985, p. 72]

Dorsal valves with short trails, corpus cavity variable; rugae weak or lacking but spines numerous with pustulose bases, commonly on both valves, but lost dorsally in Permian; marginal structures, peripheral cavities reduced or absent. *Lower Carboniferous (upper Viséan)–Lower Permian (Kungurian).*

Levipustula MAXWELL, 1951, p. 10 [**L. levis;* OD]. Gently concavoconvex profile, shallow to moderate corpus cavity; pustulose quincuncial spine bases covering ventral valve, spines long, slender, including on ears; lateral ridges short. *Carboniferous (Serpukhovian, ?Bashkirian):* Australia, South America.——FIG. 299,*3a–c.* **L. levis; a,b,* holotype, dorsal valve external mold, latex replica of ventral valve exterior, Moscovian, Queensland, UQF 11900a,b, ×1.5 (new); *c,* latex replica of dorsal valve interior, New South Wales, ×2 (Muir-Wood & Cooper, 1960).

Bulahdelia ROBERTS in ROBERTS, HUNT, & THOMPSON, 1976, p. 213 [**B. myallensis;* OD]. Ventral spine row near hinge, elongate spine bases posteriorly, lacking anteriorly where spines concentrically arranged; dorsal spines anteriorly only on lamellose bands; cardinal process pit present. *Lower Carboniferous (upper Viséan):* Australia.——FIG. 299,*1a–e.* **B. myallensis,* upper Viséan, New South Wales; *a,* holotype, latex replica of ventral valve exterior, AMF 57742, ×1.5; *b,* internal mold of ventral valve interior, ×1.5; *c,* latex replica of dorsal valve exterior, ×1.5; *d,* latex replica of dorsal valve interior, ×1.5; *e,* latex replica of dorsal valve interior, ×1.5 (Roberts, Hunt, & Thompson, 1976).

Impiacus LAZAREV & SUUR'SUREN in AFANASJEVA & others, 1988, p. 53 [**I. dzhinsetuensis;* OD] [=*Nudymia* LAZAREV, 1990, p. 93 (type, *Bailliena nudymiensis* SARYTCHEVA, 1977, p. 116)]. Medium to large shells; corpus depth variable; rugae weak, irregular; spines varied on both valves, with increasing density on ears in stratigraphically younger species; cardinal ridges diverge from hinge laterally, may extend as ear baffles. *Lower Carboniferous (upper Viséan):* northeastern Asia.——FIG. 299,*2a–c.* **I. dzhinsetuensis,* upper Viséan, Gobi Altai, Mongolia; *a,b,* ventral valve internal mold viewed posteriorly, anteriorly, ×1 (new); *c,* dorsal valve exterior, ×1 (new). ——FIG. 299,*2d,e. I. arateliensis* LAZAREV, upper Viséan, Ara-Teli-Gol River; *d,* holotype, external mold of ventral valve, PIN 3385/1250, ×1; *e,* incomplete dorsal valve interior, ×2 (Lazarev, 1991).

Jakutoproductus KASCHIRTZEV, 1959, p. 28 [**Marginifera verchoyanica* FREDERICKS, 1931, p. 211; OD]. Medium size, transverse, with well-differentiated ears; ventral disk weakly convex, dorsal disk almost flat; rugae irregular on corpus of both valves, commonly undulose; spine bases scattered ventrally, elongate posteriorly, rounded and concentrically arranged on trail; cardinal process pit separates median septum; lateral ridges in both valves, dorsally continuous as weak marginal ridge. *Lower Permian (Asselian–Kungurian):* northern Canada, Siberia, Mongolia, northern Asia.——FIG. 300,*1a–e.* **J. verchoyanica* (FREDERICKS), ?Sakmarian–Artinskian, northeastern Russia, Verkhoyan; *a,b,* lectotype, abraded ventral valve viewed ventrally, laterally, TsNIGRA 45/10902, selected by SOLOMINA, 1981, ×1 (new); *c,d,* shell viewed ventrally, laterally, ×1; *e,* dorsal valve internal mold, ×1 (Solomina, 1981).

Lanipustula KLETS, 1983, p. 75[71] [**Pustula baicalensis* MASLENNIKOV, 1960, p. 341; OD]. Similar to *Levipustula,* but with dense dorsal spines; cardinal ridges, buttress plates. *Lower Carboniferous (?upper Viséan)–upper Upper Carboniferous:* Russia, Transbaikal, Mongolia.——FIG. 300,*2a–d.* **L. baicalensis* (MASLENNIKOV), Upper Carboniferous, Transbaikalia; *a,* neotype, ventral valve exterior, PIN 3979/1, ×1; *b,* ventral valve internal cast, ×2; *c,* dorsal valve external mold, ×3; *d,* dorsal valve internal cast, ×3 (Klets, 1983).

Onopordumaria WATERHOUSE in BAMBER & WATERHOUSE, 1971, p. 205 [**O. punctura;* OD]. Poorly known, resembles *Levipustula,* but has more, thinner ventral spines, swollen dorsal spine bases; dorsal interior with strong endospines anteriorly. *Upper Carboniferous (middle Moscovian):* Canada. ——FIG. 301*a–c.* **O. punctura,* middle Moscovian, Yukon; *a,* holotype, incomplete ventral valve exterior, GSC 26396, ×1; *b,* broken ventral valve internal casts, ×1; *c,* dorsal valve internal cast, ×1 (Bamber & Waterhouse, 1971).

Piatnitzkya TABOADA, 1993, p. 591 [**P. borrelloi;* OD]. Small, resembles *Jakutoproductus,* but lacks concentric rugae, strong rounded spine bases on trail. [The presence of fine ribbing would place this genus in the Auriculispininae]. *Lower Permian (Asselian):* Argentina.——FIG. 300,*4a–d.* **P. borrelloi,* Permian, Rio Genoa Formation, Chubat Province; *a,* ventral valve exterior, ×1.5; *b,* dorsal valve external mold, ×2; *c,d,* latex replicas of dorsal valve interiors, ×1.5 (Taboada, 1993).

Verchojania ABRAMOV, 1970, p. 112 [**Jakutoproductus cheraskowi* KASCHIRTZEV, 1959, p. 30; OD]. Similar to *Jakutoproductus* but without dorsal spines, with weakly developed or lacking concentric rugae; ventral sulcus variable. *Upper Carboniferous (Bashkirian–Moscovian):* northern Asia.——FIG. 300,*3a–c.* **V. cheraskowi* (KASCHIRTZEV), Bashkirian–Moscovian, Yakutsk; *a,b,* internal mold of ventral valve viewed ventrally, anterolaterally, ×1 (new); *c,* ventral valve, shell missing umbonally, viewed posteriorly, ×1 (Abramov, 1970).

Tribe LEVITUSIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, herein, *ex* Levitusiinae MUIR-WOOD & COOPER, 1960, p. 295]

Relatively large shells with long trails, moderate to deep corpus cavities; ribbing absent or weak fine radial striations; rugae, spines weak, sparsely developed; spine row anterior to ears, commonly a ventral median row on weak ridge; weak cardinal ridges, no marginal ridges. *Lower Carboniferous (Tournaisian–upper Viséan).*

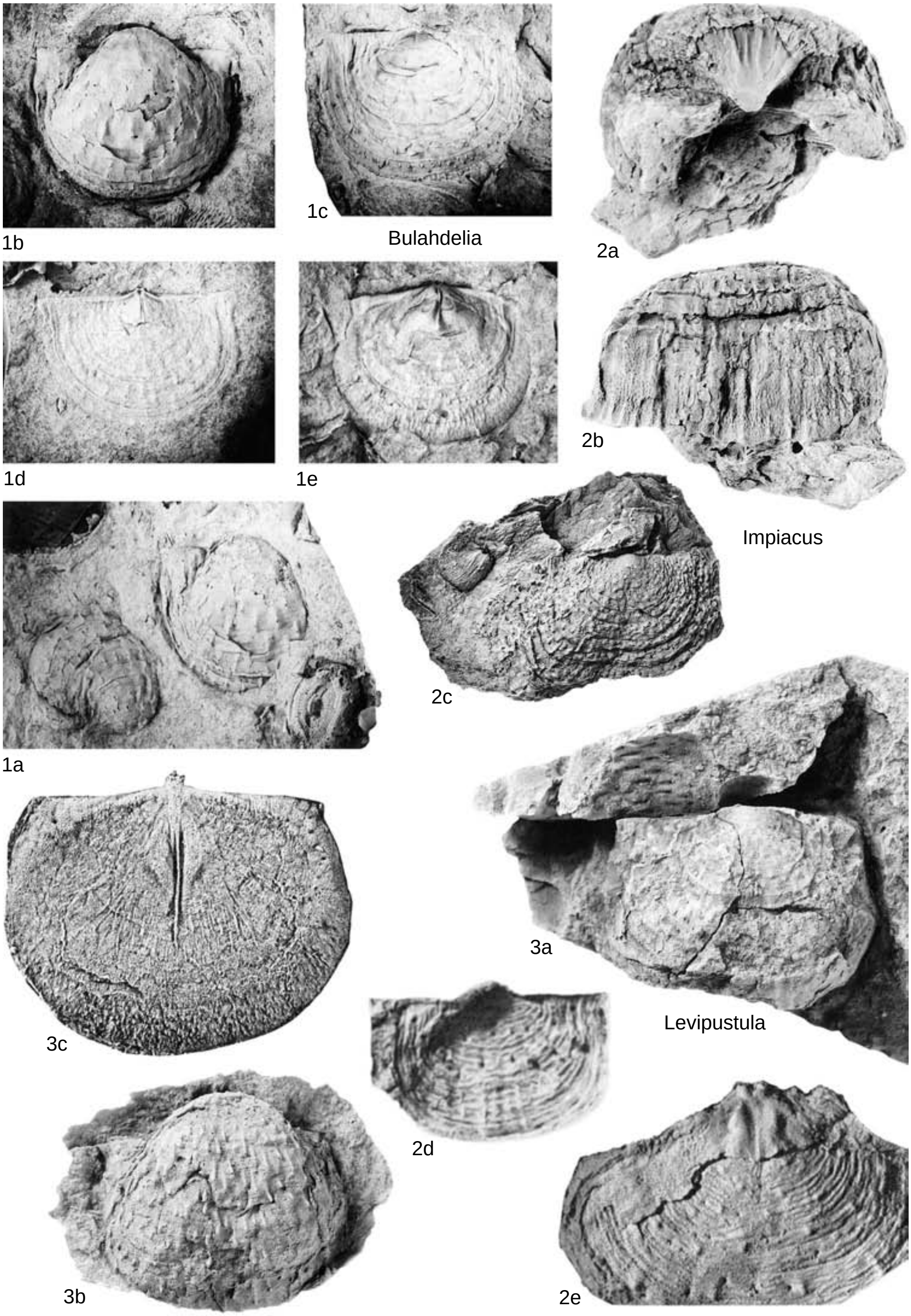


FIG. 299. Productellidae (p. 453).

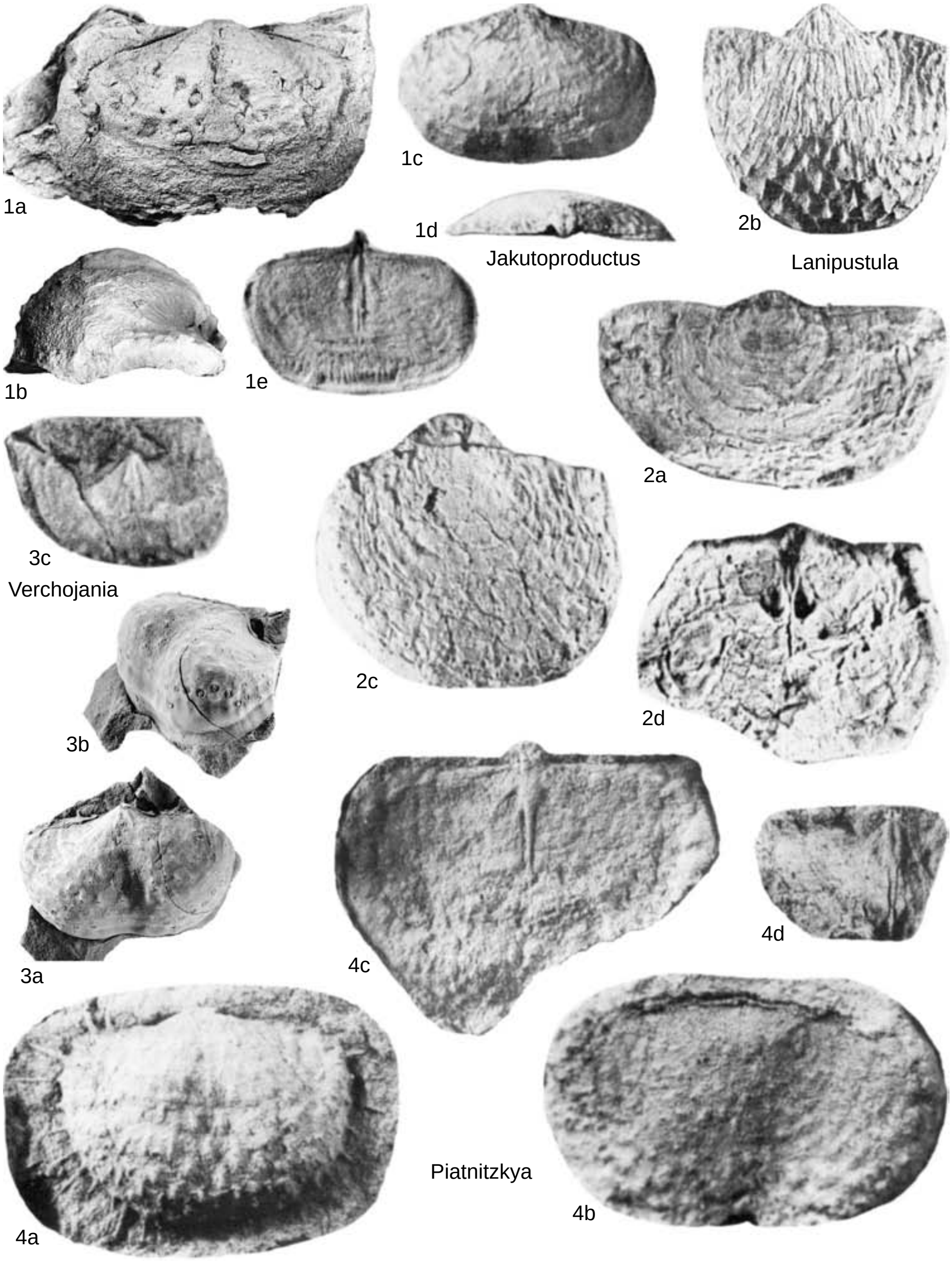


FIG. 300. Productellidae (p. 453).

Levitusia MUIR-WOOD & COOPER, 1960, p. 295 [**Productus humerosus* J. SOWERBY, 1822 in 1821–1822, p. 21; OD; =*P. christiani* DE KONINCK, 1847a, p. 274]. Commonly large with thick walled ventral valve, trail long, spreading; fine radial ornament on some species, may also have median ridge with

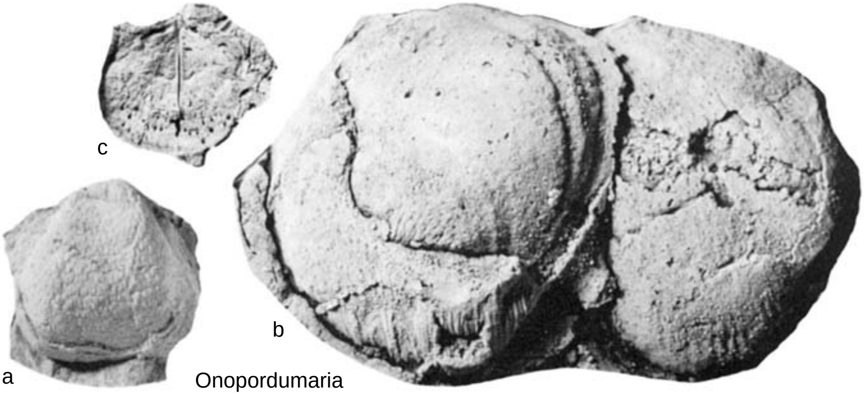


FIG. 301. Productellidae (p. 453).

spines; corpus cavity shallow; ventral brachial pits in some species. *Lower Carboniferous (Viséan):* Europe, Ural Mountains, ?Middle Asia (Kirghizia).——FIG. 302*a–f.* **L. humerosa* (J. SOWERBY); *a,b,* holotype, ventral valve internal mold viewed anteriorly, laterally, lower Viséan, Derbyshire, British Isles, BMNH B 60959, ×1; *c,d,* ventral valve exterior viewed anteriorly, laterally, Staffordshire, ×0.75 (Brunton, 1979); *e,* dorsal valve interior, Staffordshire, ×1; *f,* ventral valve exterior viewed posteroventrally, Visé, Belgium, ×1 (Muir-Wood & Cooper, 1960).——FIG. 302*g.* Specimen called *P. christiani* by DE KONINCK; detail anteromedianly, showing median spines, fine radial ornament, Visé, Belgium, UPS D812, ×2.5 (Brunton, 1979).

Acanthoplecta MUIR-WOOD & COOPER, 1960, p. 170 [**Producta mesoloba* PHILLIPS, 1836, p. 215; OD]. Medium sized, around 30 mm wide; concavoconvex with long trails, may have gutter; commonly weak median fold bearing spines, dorsal sulcus; other spines scattered; body cavity shallow to deep. *Lower Carboniferous (Viséan):* Eurasia, northern Africa.——FIG. 303,*1a–f.* **A. mesoloba* (PHILLIPS); *a,* lectotype, ventral valve exterior viewed anteriorly, Asbian, Yorkshire, BMNH B427, ×1.5; *b,* lectotype, ventral valve exterior viewed anterolaterally, Asbian, Yorkshire, ×1; *c,* ventral valve exterior viewed posteriorly, Asbian, Yorkshire, ×1 (new); *d,* complete shell viewed dorsally, Asbian, Yorkshire, ×1 (Muir-Wood & Cooper, 1960); *e,f,* silicified dorsal valve with gutter viewed ventrally, laterally, Fermanagh, ×1.25 (Brunton, 1966).

Admodorugosus BRUNTON & MUNDY, 1993, p. 111 [**A. cracoensis;* OD]. Small to medium sized; prominent rugae covering entire valves, no ribbing; larger spines in rows near hinge and medianly. *Lower Carboniferous (Asbian):* western Europe.——FIG. 303,*2a–e.* **A. cracoensis; a,b,* holotype, shell with broken ventral valve, showing some of dorsal valve, viewed ventrally, posteriorly, Asbian, Yorkshire, BMNH BD 2447, ×2; *c,* oblique view of shell with ventral trail missing, Staffordshire, ×2; *d,* anterolateral view of complete ventral valve, Staffordshire, ×2; *e,* anterior view of ventral valve showing median spines, Staffordshire, ×2 (Brunton & Mundy, 1993).

Geniculifera MUIR-WOOD & COOPER, 1960, p. 187 [**Avonia boonensis* BRANSON, 1938, p. 40; OD]. Small, around 12 mm wide; planoconvex, deep corpus plus simple trails; rugae posteriorly on disks, trails smooth; spines few, scattered on ventral valve. *Lower Carboniferous (Hastarian–Viséan):* North America, Europe.——FIG. 304,*1a–d.* **G. boonensis* (BRANSON), Hastarian, New Mexico; *a–c,* ventral valve exterior viewed ventrally, posteriorly, laterally, ×2; *d,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).——FIG. 304,*1e. G. keyserlingiana* (DE KONINCK), Viséan, Visé, Belgium; latex replica of dorsal valve interior, ×3.5 (Brunton & Mundy, 1993).

Kadraliproductus GALITSKAYA, 1977, p. 36 [**Productus (Plicatifera) kadralensis* GLADTCHENKO, 1955, p. 15; OD]. Posterior nodose reticulation of impersistent median ribbing with rugae; spines at hinge, scattered ventrally; corpus deep. *Lower Carboniferous (upper Tournaisian):* Kirghizia, western Europe.——FIG. 303,*3a–d.* **K. kadralensis* (GLADTCHENKO), upper Tournaisian, Kirghizia; *a,b,* holotype, ventral valve viewed posteroventrally, anteriorly, Inst. Geol. 81/3, ×1; *c,* complete ventral valve viewed laterally, ×1; *d,* shell with part of ventral valve missing, viewed anteriorly showing deep corpus, ×1 (Galitskaya, 1977).

Spinorugifera ROBERTS, 1976, p. 50 [**S. chichesterensis;* OD]. Small; gently concavoconvex profile without clear trails; entirely rugose, slightly lamellose ventrally, with spines near hinge, scattered on ventral rugae, spines commonly lacking dorsally; lateral ridges short. *Lower Carboniferous (upper Viséan):* Australia.——FIG. 304,*2a–d.* **S. chichesterensis,* upper Viséan, New South Wales; *a,b,* holotype, latex replicas of ventral valve exterior, dorsal valve exterior, AMF 57025a,b, ×2; *c,d,* latex replicas of dorsal valve exterior, interior, ×2 (Roberts, 1976).

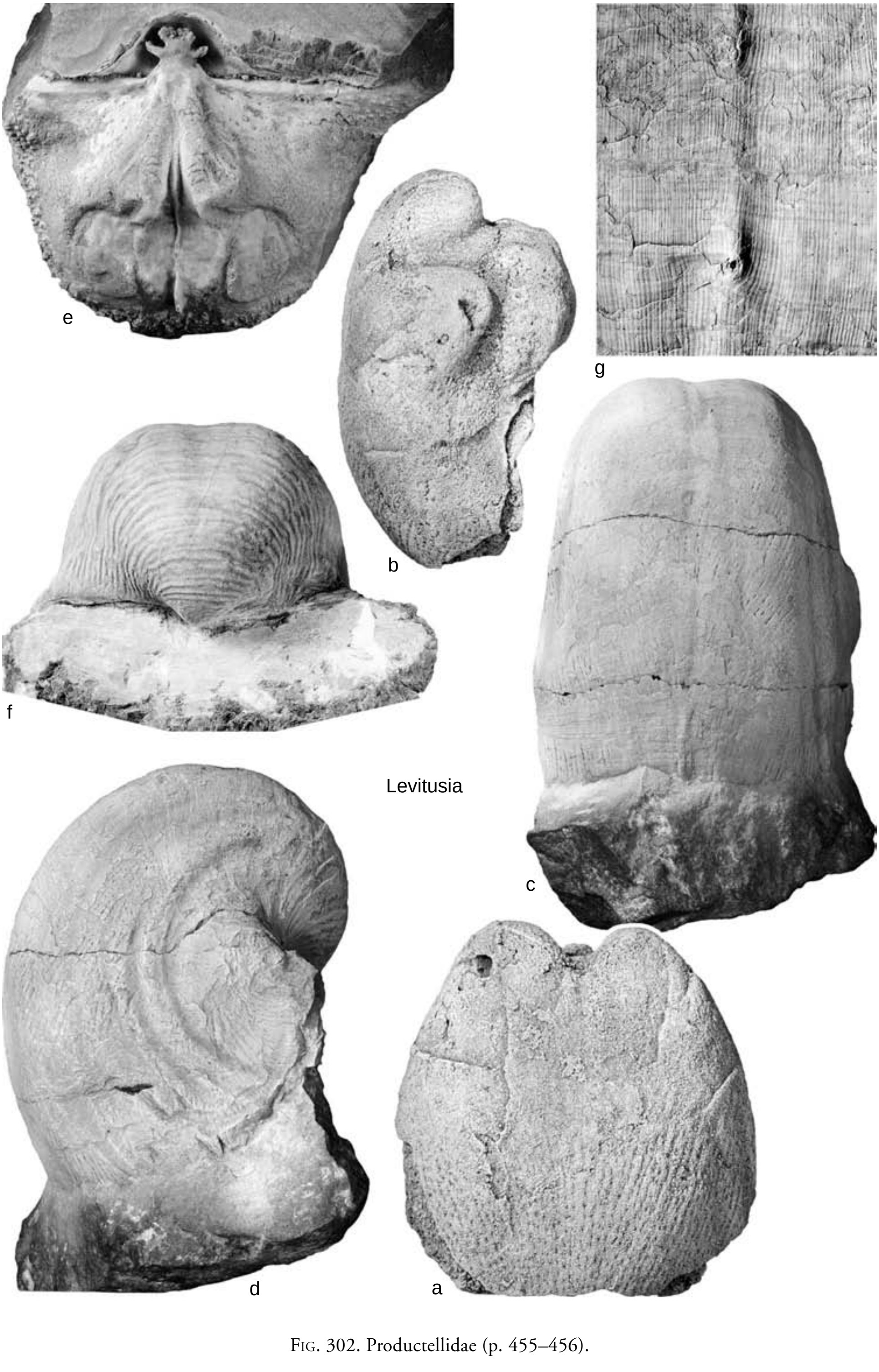


FIG. 302. Productellidae (p. 455–456).

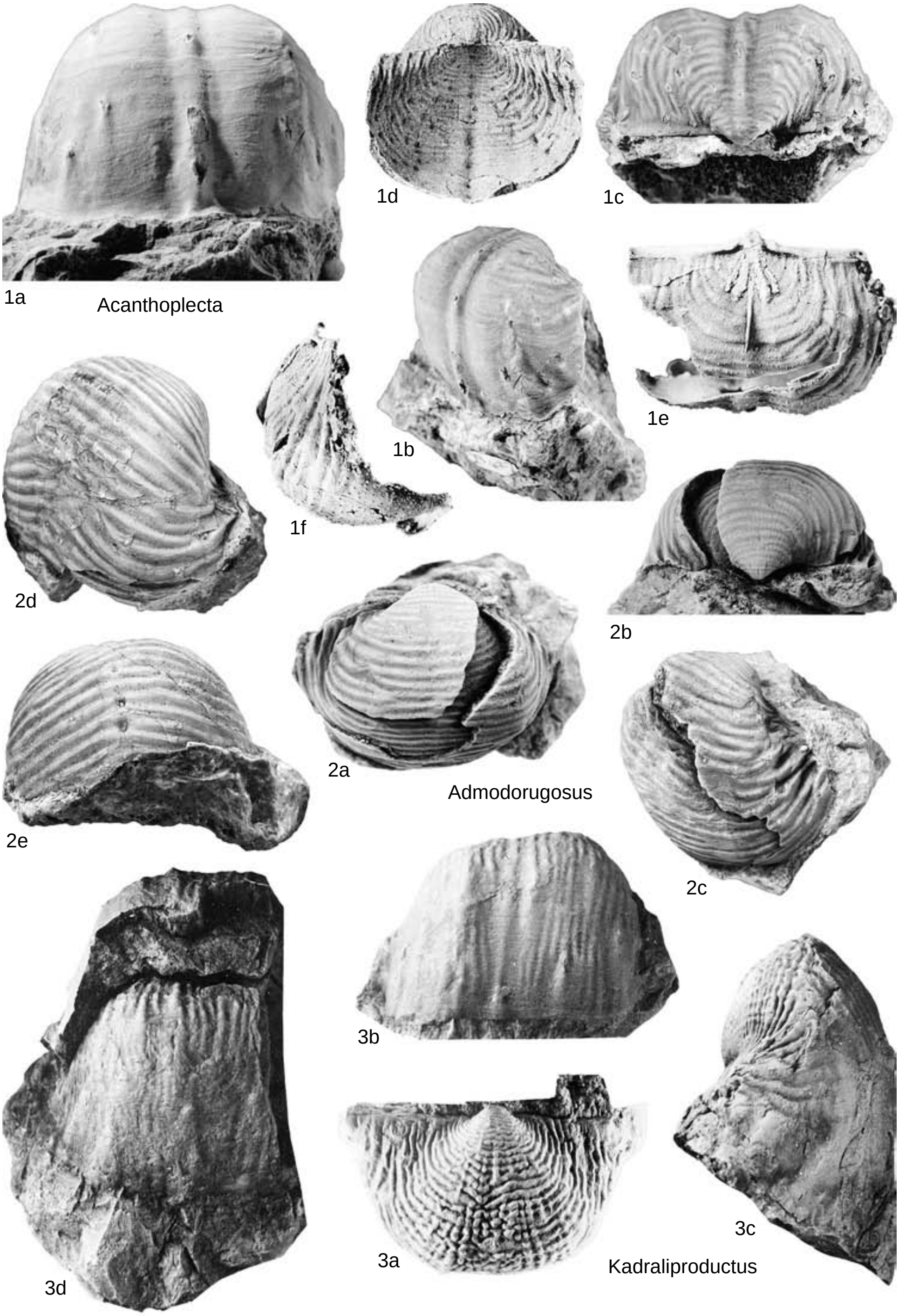


FIG. 303. Productellidae (p. 456).

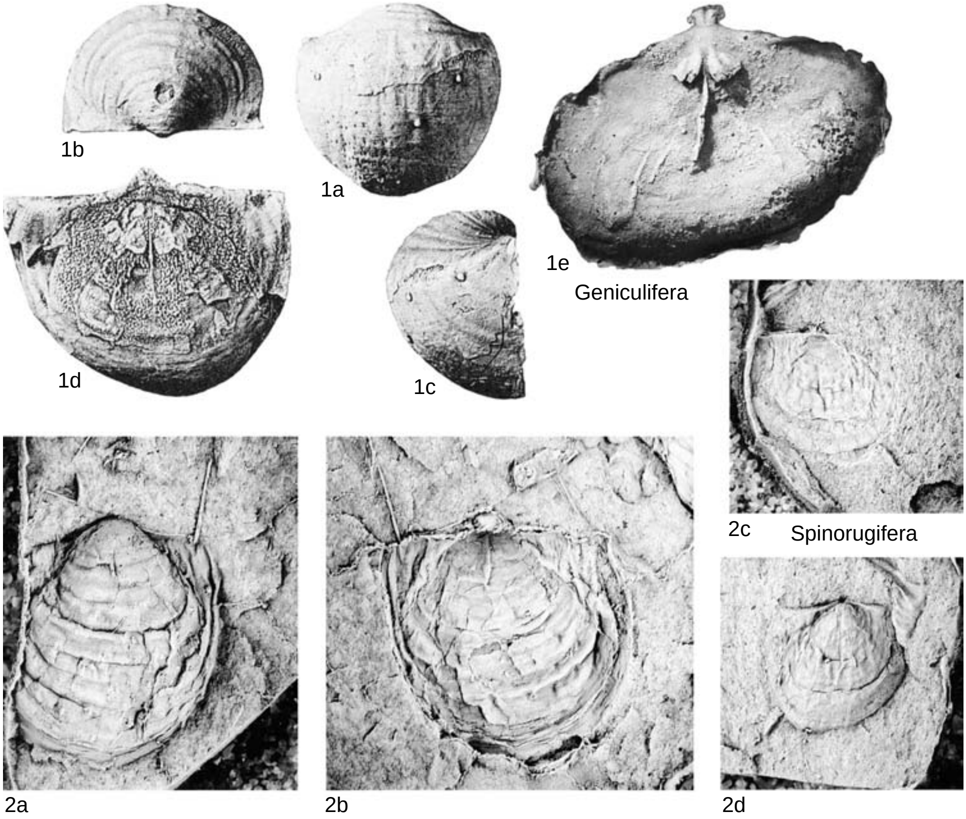


Fig. 304. Productellidae (p. 456).

Tribe RUGAURINI Lazarev, 1990

[*nom. transl.* Brunton, Lazarev, & Grant, herein, *ex* Rugaurinae Lazarev, 1990, p. 88]

Corpus cavity shallow; trail absent or very short; no ribbing, dense spines covering ventral valve, rarely on dorsal valves anteriorly; teeth in oldest taxa; no ear baffles or submarginal ridges. *Upper Devonian (upper Famennian)–Lower Carboniferous (upper Viséan).*

Rugauris Muir-Wood & Cooper, 1960, p. 193 [**R. paucispina;* OD]. Medium size; semicircular outline, gently concavoconvex profile; rugae numerous, narrow, covering disks; fine low-angled spines cover ventral valve; dorsal valve dimpled, few spines; lateral ridges subparallel to hinge. *Lower Carboniferous (Hastarian):* USA, Russia, eastern Australia, Canada, ?San Salvador.——Fig. 305,*1a–f.* **R. paucispina,* Hastarian, Iowa; *a–d,* holotype, ventral, anterior, posterior, lateral views of ventral valve, USNM 79477a, ×1; *e,* replica of dorsal valve exterior, ×1; *f,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Carringtonia Brunton & Mundy, 1986, p. 2 [**Productus carringtoniana* Davidson, 1863, p. 274; OD]. Transverse, markedly but irregularly rugose, ventral spines only, at hinge, widely on rugae. *Lower Carboniferous (upper Viséan):* western Europe.——Fig. 305,*2a–d.* **C. carringtoniana* (Davidson); *a,* lectotype, ventral valve exterior, Asbian, Staffordshire, BMNH B 5743, ×1; *b,* external mold of dorsal valve showing dimples of ventral hinge spines, Asbian, Staffordshire, ×1.5; *c,d,* posterolateral, dorsal views of shell, Yorkshire, ×1.5 (new).

Iniproductus Lazarev, 1990, p. 88 [**Pustula ?inica* Sarytcheva in Beznossnova & others, 1962, p. 151; OD]. Resembles *Rugauris,* but larger, rugae less regular, no dorsal spines; two or three rows of thicker spines near hinge, elongate quincuncial spine bases except on trails where spine bases small, concentric; cardinal ridges short. *Upper Devonian (upper Famennian):* Russia.——Fig. 306*a–e.* **I.*

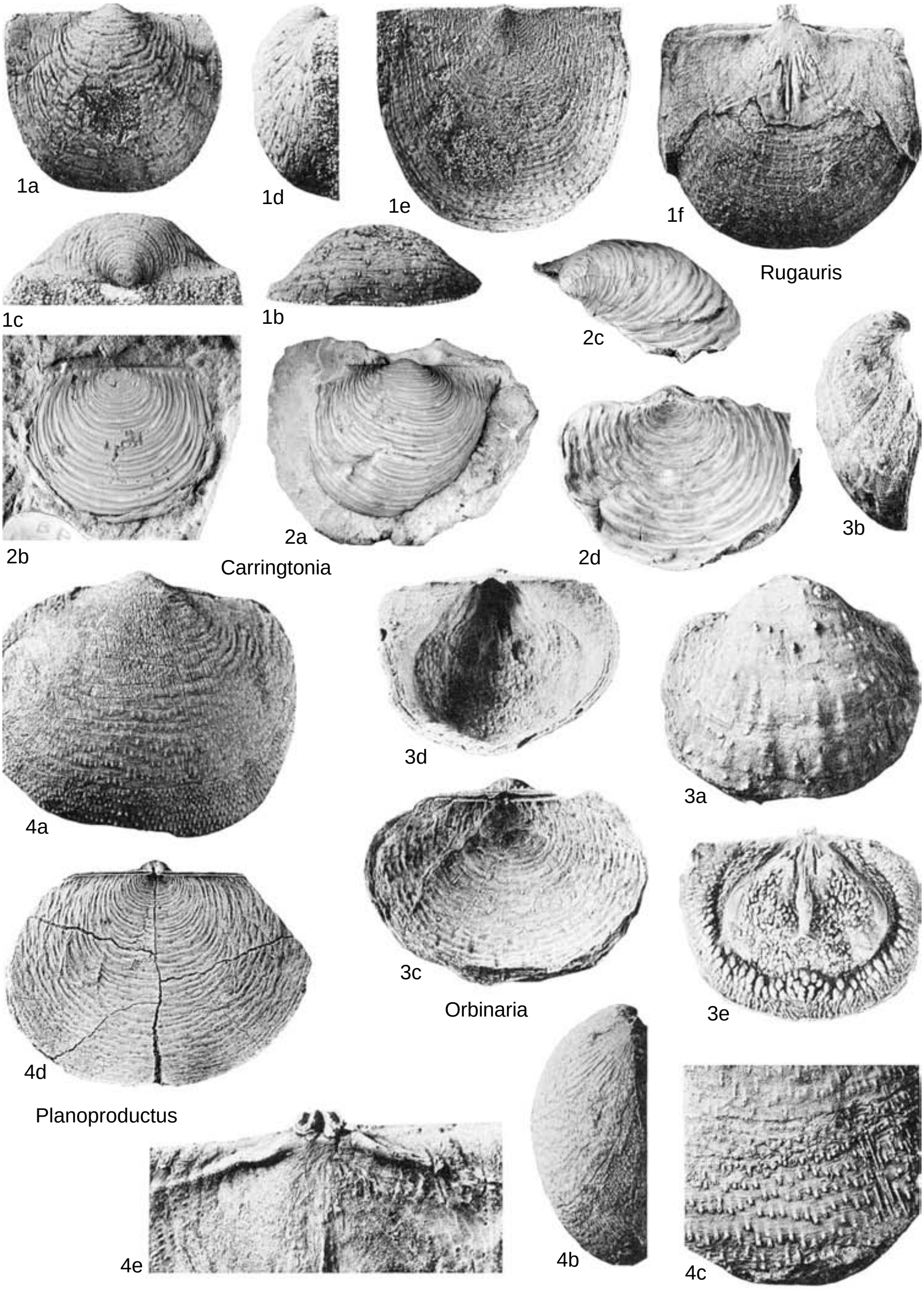


FIG. 305. Productellidae (p. 459–461).

inicus (SARYTCHEVA), upper Famennian, Kuzbass; *a,b,* ventral, lateral views of ventral valve, ×1; *c,* dorsal exterior of incomplete shell, ×1; *d,* spines extending from near lateral margin of ventral valve, ×2.5; *e,* incomplete dorsal valve interior, ×1 (Sarytcheva & others, 1963).

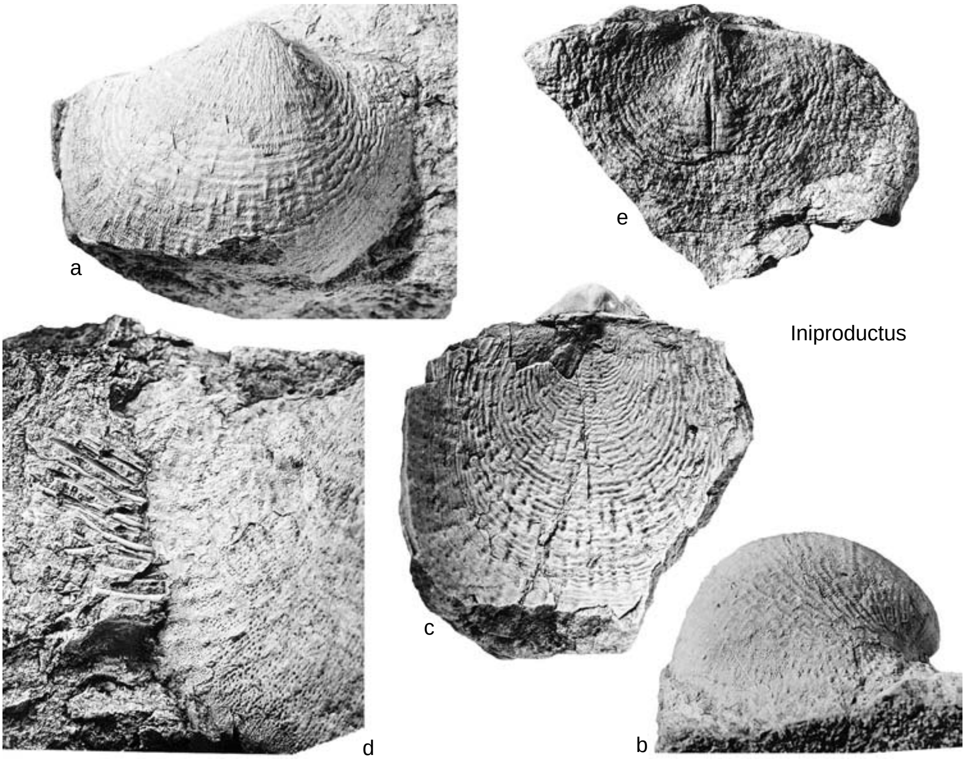


FIG. 306. Productellidae (p. 459–460).

Orbinaria MUIR-WOOD & COOPER, 1960, p. 149 [**Productella pyxidata* HALL, 1858a, p. 498; OD]. Weakly concavoconvex profile; concentric ornament, especially on dorsal valve; dorsal spines sparse, fine; ventral spines with slight pustules; teeth minute; dorsal interior with strongly papillose subperipheral ridge. *Upper Devonian (upper Famennian), Lower Carboniferous (?Hastarian):* North America, ?Europe, ?northern Africa.——FIG. 305,*3a–e*. **O. pyxidata* (HALL), upper Famennian, possibly to lower Hastarian, Louisiana Limestone, Missouri; *a,* ventral valve exterior, ×2; *b,c,* lateral view, dorsal view of shell, ×2; *d,e,* ventral valve interior, dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Planoproductus STAINBROOK, 1947, p. 310 [**Productella hillsboroensis* KINDLE, 1909, p. 19; OD]. Medium sized; rugae weak ventrally, stronger dorsally; spines on ventral valve only, fine, numerous with short ridges; lateral ridges short, divergent. *Upper Devonian (upper Famennian):* southern USA, France, ?Japan.——FIG. 305,*4a–e*. **P. hillsboroensis* (KINDLE), uppermost Famennian, New Mexico; *a,b,* ventral valve exterior viewed ventrally, laterally, ×1; *c,* detail of ornament, ×2; *d,* dorsal valve exterior, ×1; *e,* posterior region of dorsal valve interior, ×4 (Muir-Wood & Cooper, 1960).

Tribe SEMICOSTELLINI
Nalivkin, 1979

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 927, *ex* Semicostellinae NALIVKIN, 1979, p. 67]

Corpus cavity deep; costae on long trails; lateral, marginal ridges commonly well developed in both valves. *Lower Carboniferous (Tournaisian)–Upper Permian (Kazanian).*

Semicostella MUIR-WOOD & COOPER, 1960, p. 195 [**Avonia oklahomensis* SNIDER, 1915, p. 83; OD]. Rugae weak, with elongated spine bases on ventral disk, clear ribs anteriorly, spines in row on flanks; dorsal valve rugose, sparsely spinose, geniculate with clear ribs on trail; divergent lateral ridges, marginal structures. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* southern USA, Ural Mountains, northern Asia.——FIG. 307,*1a–e*. **S. oklahomensis* (SNIDER), upper Viséan–lower Serpukhovian, Oklahoma; *a–c,* ventral valve viewed ventrally, posteriorly, laterally, ×1; *d,* shell viewed dorsally, ×1; *e,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Cinctifera MUIR-WOOD & COOPER, 1960, p. 165 [**Productus medusa* DE KONINCK, 1842, p. 166;

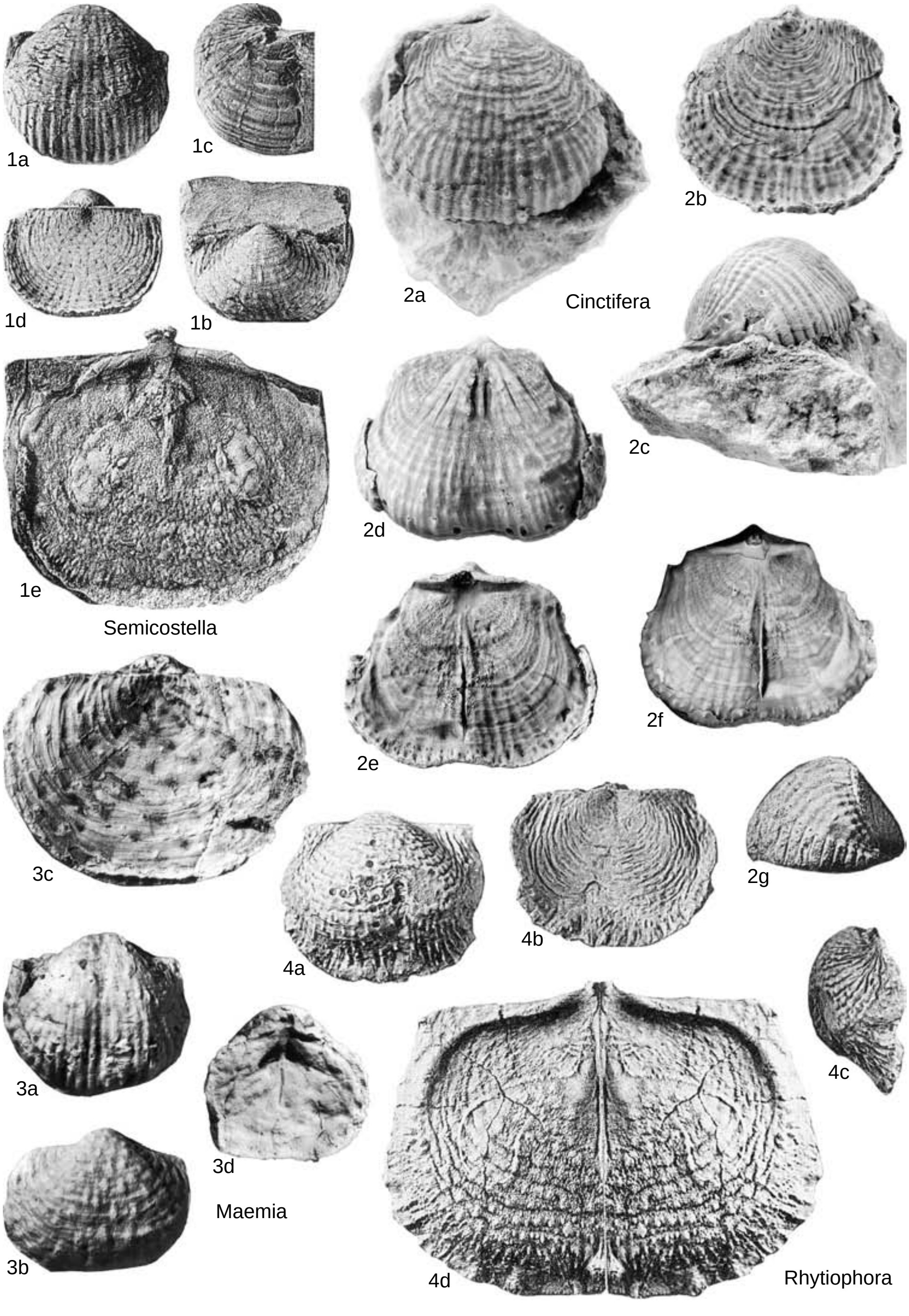


FIG. 307. Productellidae (p. 461–464).

OD]. Ventral valve disk flattened, ribbing complete, other than beaks; cinctures especially at margin of disk, spinose outgrowths from ventral valve margin. *Lower Carboniferous (Viséan):* Europe.——FIG. 307,*2a–g.* **C. medusa* (DE KONINCK); *a–c,* shell viewed ventrally, dorsally, ventral valve viewed later-

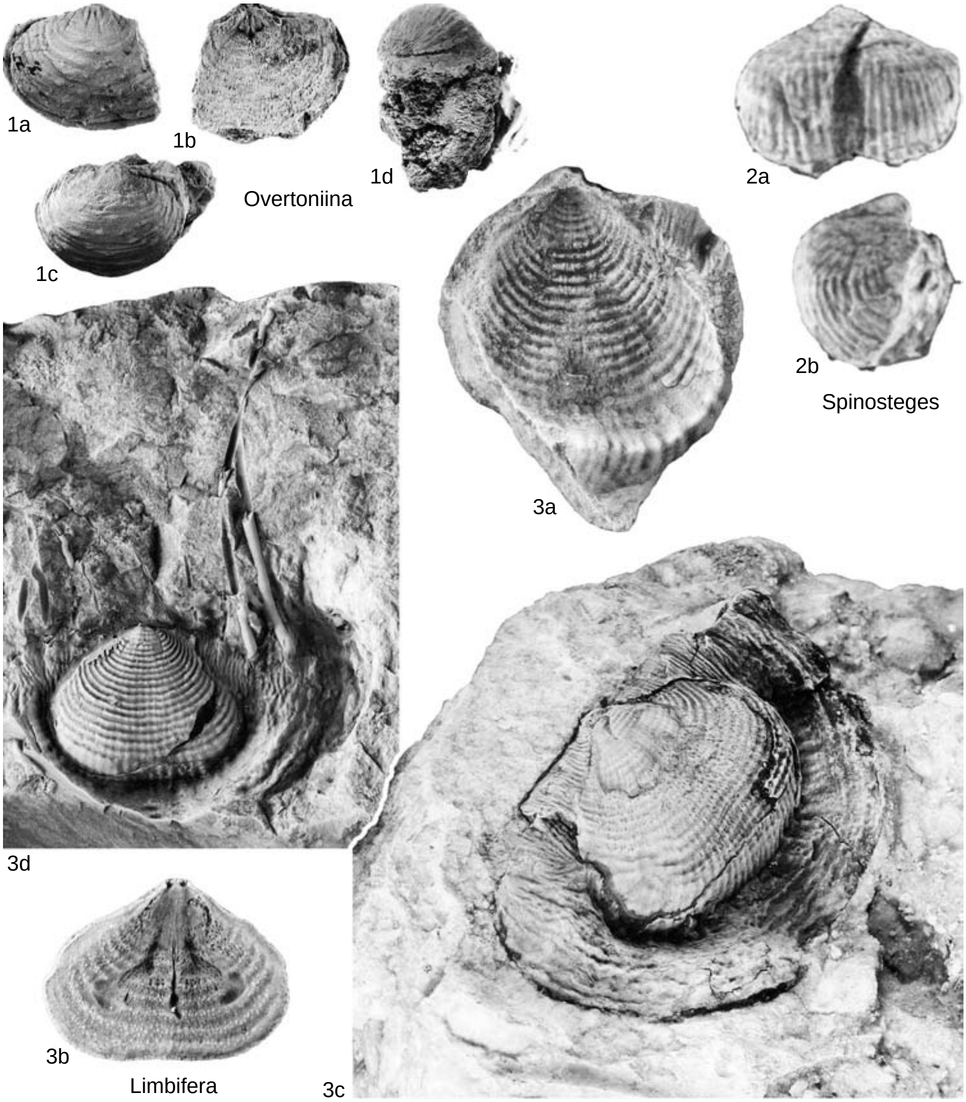


FIG. 308. Productellidae (p. 463–464).

ally, Asbian, Derbyshire, British Isles, ×2; *d–f,* internal mold viewed ventrally, dorsally plus latex replica of dorsal interior, Asbian, Derbyshire, ×2 (new); *g,* ventral valve internal mold showing marginal spines, Visé, Belgium, ×3 (Muir-Wood & Cooper, 1960).

Limbifera BRUNTON & MUNDY, 1988b, p. 69 [**Productus griffithianus* DE KONINCK, 1847b, p. 74; OD]. Small; corpus outline triangular with large flattened ears; weakly concavoconvex with shallow corpus, ventrally geniculated gutter; ribbing entire with rugae posteriorly; paired row of stout attachment spines across ears; lateral ridges, ear baffles strong. *Lower Carboniferous (upper Viséan):* western Europe.——FIG. 308,*3a–d.* **L. griffithiana* (DE KONINCK); *a,* lectotype, incomplete internal mold viewed anterodorsally, Viséan, Visé, Belgium, BMNH BD 3376, ×3; *b,* internal mold of dorsal valve, Viséan, Visé, ×3; *c,* oblique view of ventral valve exterior with gutter, Asbian, Yorkshire, ×2; *d,* incomplete ventral valve exterior with posterior attachment spines, Asbian, Yorkshire, ×1.5 (Brunton & Mundy, 1988b).

Maemia LAZAREV in BRUNTON & LAZAREV, 1997, p. 391 [**M. chaykensis;* OD]. Small to medium with rectangular outline; both valves geniculate with moderate to deep corpus cavity; rugae weak on both disks; ribbing on trails only; spines on both valves;

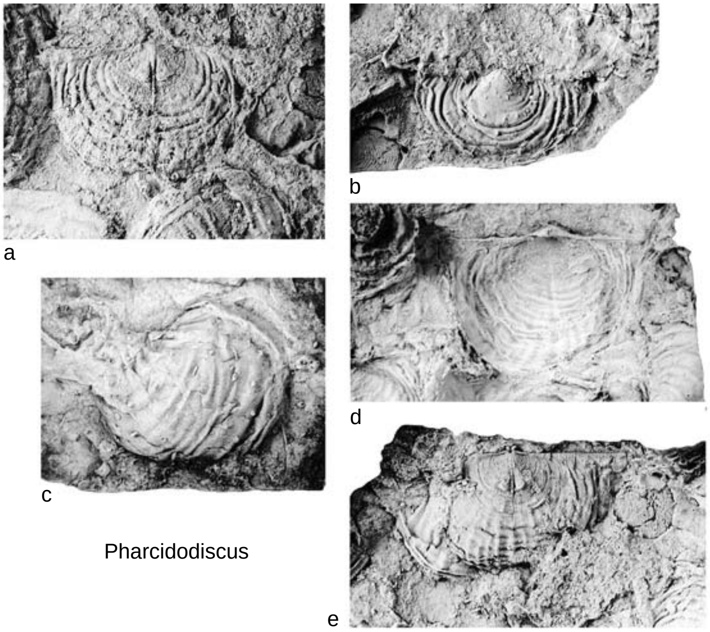


Fig. 309. Productellidae (p. 464).

ventral lateral and marginal ridges weak; dorsal cardinal ridges continue as ear baffles, weak submarginal ridges; adductor scars raised with medianly curving crests. *Upper Carboniferous:* Arctic Russia.——Fig. 307,*3a–c.* **M. chaykensis,* upper Bashkirian–lower Kasimovian, Yugorsky Peninsula, Mongolia; *a,* holotype, viewed ventrally, PIN N2802/1168, ×1; *b,* ventral valve exterior, ×1; *c,* dorsal valve exterior, ×2 (Brunton & Lazarev, 1997).——Fig. 307,*3d. M. nana* Lazarev, upper Moscovian–lower Kasimovian; dorsal valve internal mold, ×2 (Brunton & Lazarev, 1997).

Overtoniina Grunt in Grunt & Dmitriev, 1973, p. 94 [**O. mamazairica;* OD]. Small, planoconvex corpus with geniculation to trails; ventral disk weakly but densely rugose, with rounded spine bases; trail with broad ribs; lateral ridges, median septum short; adductor platforms overhang anteromedianly. *Lower Permian (Artinskian):* Pamir, Afghanistan.——Fig. 308,*1a–d.* **O. mamazairica,* Artinskian, southeastern Pamir; *a,b,* holotype, internal mold viewed ventrally, dorsally, PIN 2228/590, ×1; *c,d,* specimen viewed ventrally, laterally, ×1 (Grunt & Dmitriev, 1973).

Pharcidodiscus Roberts, 1976, p. 46 [**P. boulderensis;* OD]. Rugae, ribbing weaker than *Semicostella;* ears prominent, corpus cavity moderately deep; spine rows just anterior to hinge; cardinal ridges, but ear baffles absent. *Lower Carboniferous (upper Tournaisian):* Australia.——Fig. 309*a–e.* **P. boulderensis,* upper Tournaisian, Queensland; *a,* holotype, latex replica of dorsal valve interior, GSQ F10269, ×1.5; *b,* latex replica of posterior region of ventral valve exterior, ×1.5; *c,* latex replica of anterior region of ventral valve exterior, ×1.5; *d,* latex replica of dorsal valve exterior, ×1.5; *e,* latex replica of dorsal valve interior, ×2 (Roberts, 1976).

Rhytiophora Muir-Wood & Cooper, 1960, p. 192 [**Productus blairi* Miller, 1891, p. 689; OD]. Subquadrate outline; rugae irregular, weak ventromedianly, trail short, ribbed; spine ridges ventrally, especially anteriorly; spines numerous, dorsally only anteriorly; lateral ridges extend to separate ears from corpus. *Lower Carboniferous (middle Hastarian):* USA, Central America, northwestern Australia, ?central China.——Fig. 307,*4a–d.* **R. blairi* (Miller), middle Hastarian, Missouri; *a–c,* ventral, dorsal, lateral views of shell, ×1; *d,* half of dorsal valve interior completed by mirror image, ×2 (Muir-Wood & Cooper, 1960).

Spinosteges Liang, 1990, p. 155[461] [**S. sinensis;* OD]. Small, outline subquadrate with hinge slightly less than maximum width; ventral disk flattened, trail sulcate; elongate spine bases on ventral disk, relatively fine ribbing on trail; dorsal valve interiors unknown. *Upper Permian (Kazanian):* China.——Fig. 308,*2a,b.* **S. sinensis,* Permian, Lengwu Formation, Zhejiang; anteroventral, lateral views, ×2 (Liang, 1990).

Tribe YAKOVLEVIINI Waterhouse, 1975

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 927, *ex* Yakovleviinae Waterhouse, 1975, p. 11] [=Inflatiidae Sarytcheva in Sarytcheva, ed., 1977, p. 102]

Commonly medium sized with thick-shelled ventral valve, moderately deep corpus

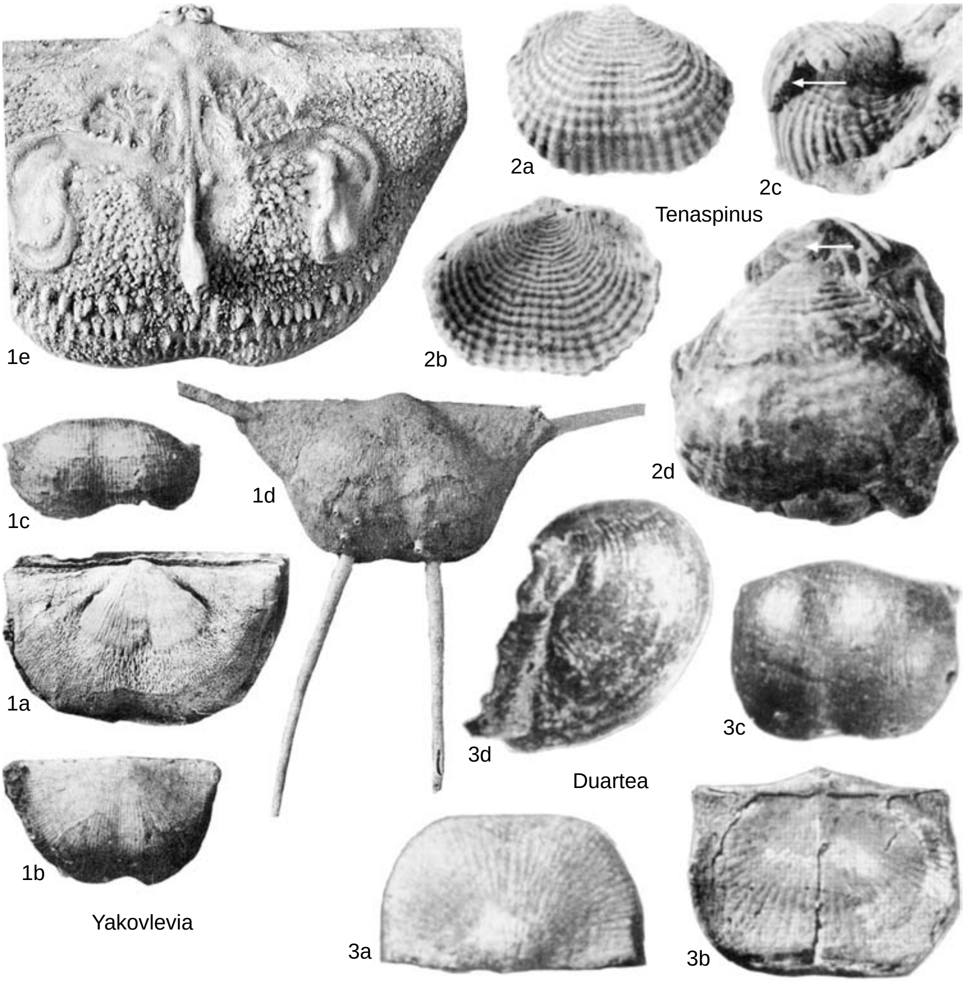


FIG. 310. Productellidae (p. 465–467).

cavity, becoming shallow in younger genera; ribbing on trails and all but posterior regions of corpus, commonly with four to six thick ventral spines; common trend to reduce ear cavities and extend anterior peripheral cavity. *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).*

Yakovlevia FREDERICKS, 1925, p. 7 [**Y. kaluzinensis;* OD] [=*Muirwoodia* LICHAREW, 1947, p. 188, *partim* (type, *Productus mammatus* KEYSERLING, 1846, p. 206; OD)]. Medium to large, outline pentagonal to subquadrate; ventral profile with flattened disk, strong geniculation, long trail; corpus cavity shallow; commonly median sulcus, starting posteriorly on disk; ribbing fine, weak; spines in rows of increasing size near hinge, plus few others, commonly four symmetrically placed; muscle fields strongly impressed; cardinal process sessile, broad; lateral ridges close to hinge, strongly angled separating small ears; anterior disk thickened or with endospines. *Lower Permian (Sakmarian)–Upper Permian (Kazanian):* Siberia, Arctic regions, Mongolia, China, Japan, USA.——FIG. 310,*1a.* **Y. kaluzinensis,* upper Lower Permian, eastern Siberia; ventral valve internal mold, ×0.7 (Wiman, 1914).——FIG. 310,*1b,c. Y. mammata* (KEYSERLING), Lower Permian, northern Russia; ventral valve viewed ventrally, anteriorly, ×1 (Licharew, 1947).——FIG. 310,*1d,e. Y. multistriata* (MEEK), Lower Permian, Texas; *d,* ventral valve exterior, ×1; *e,* dorsal valve interior, ×2 (Licharew, 1947).

Duartea MENDES, 1959, p. 58 [**Productus batesianus* DERBY, 1874, p. 54; OD] [=*Muirwoodia* LICHAREW, 1947, p. 188, *partim; Paramuirwoodia* ZHANG in ZHANG & others, 1983, p. 298]. Resembles

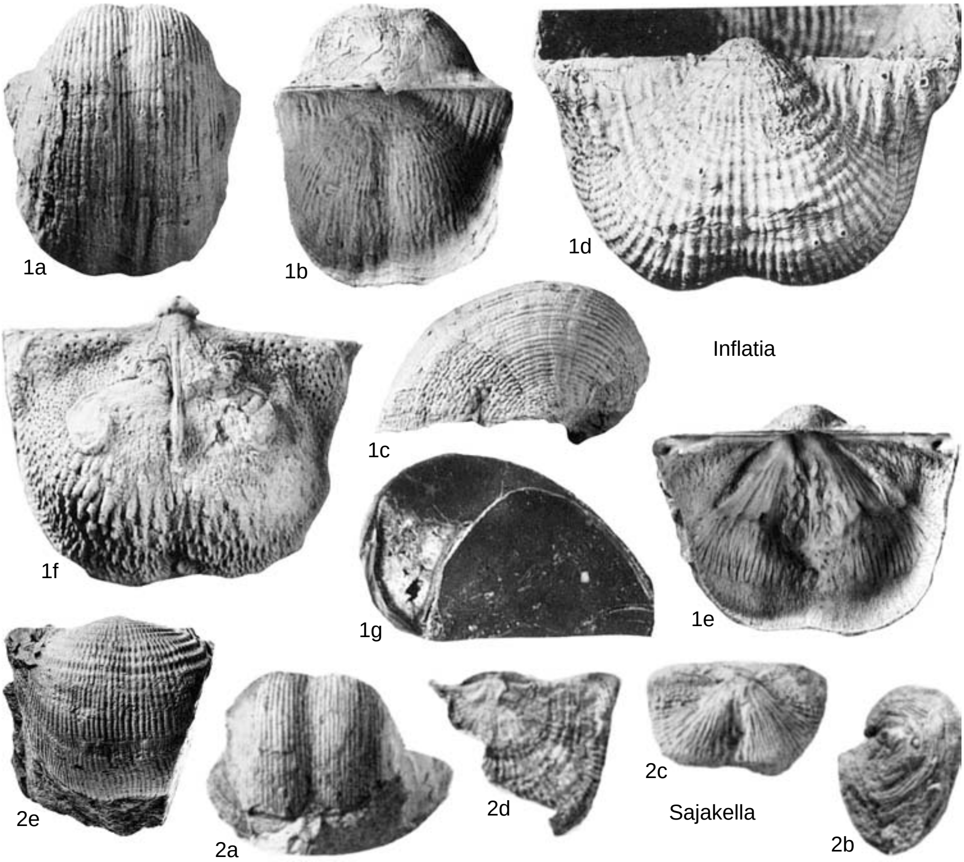


Fig. 311. Productellidae (p. 466–467).

Yakovlevia externally, but moderately deep corpus; spines in weak row separating ears, slight posterior reticulation, ribs become weak anteriorly. *Upper Carboniferous:* South America, Eurasia.——Fig. 310,*3a–d.* **D. batesiana* (Derby), lower part of Upper Carboniferous, Para Province, Brazil; *a,b,* shell viewed posteriorly, dorsally, ×1.5; *c,* ventral valve exterior, ×1; *d,* lateral view of ventral valve, ×1 (Mendes, 1959).

Inflatia Muir-Wood & Cooper, 1960, p. 226 [**Productus inflatus* McChesney, 1860, p. 40; OD] [=*Adairia* Gordon, Henry, & Treworgy, 1993, p. 20 (type, *A. adairensis* Drake, 1897, p. 402)]. Outline somewhat elongate with long trail, corpus deep; spines in row diverging from hinge, sparsely covering valve, especially anteriorly; dorsal valve strongly geniculate, no series of trails; ventral muscle fields strongly differentiated; dorsal interior thickened marginally. *Lower Carboniferous (upper Viséan)–Upper Carboniferous (lower Bashkirian):* North America, Asia, Australia.——Fig. 311,*1a–g.* **I. inflata* (McChesney), upper Viséan, Oklahoma; *a–c,* complete shell viewed ventrally, dorsally, laterally, ×1 (Gordon, Henry, & Treworgy, 1993); *d,* ventral valve exterior viewed posteriorly, ×2 (Muir-Wood & Cooper, 1960); *e,* ventral valve interior, ×1.5; *f,* dorsal valve interior, ×1.5; *g,* median section of shell showing corpus cavity, ×1 (Gordon, Henry, & Treworgy, 1993).

Sajakella Nasikanova in Sarytcheva, 1968, p. 141 [**S. formosa;* OD]. Small to medium; closely resembling *Inflatia,* but ears more prominent, ribbing commonly finer, trail spines thicker, cardinal process supported by ridges connecting to adductor scars. *Lower Carboniferous (upper Viséan)–Upper Carboniferous (Bashkirian):* Boreal Asia.——Fig. 311,*2a–d.* **S. formosa,* Bashkirian, Keregetassk Series, Kazakhstan; *a,* holotype, ventral valve exterior viewed anteriorly, PIN 1506/88, ×1; *b,* ventral valve viewed laterally, ×1; *c,* ventral valve internal cast, ×1; *d,* incomplete dorsal valve interior, ×1 (Sarytcheva, 1968).——Fig. 311,*2e. S. dzhinsetu-*

ensis Lazarev, upper Viséan, Gobi Altai, Mongolia; ventral valve exterior, ×1 (Lazarev & Suur'suren, 1992).

Tenaspinus Brunton & Mundy, 1994, p. 120 [**T. smarti;* OD]. Small, rounded elliptical outline with well-differentiated ears; ribbing starts close to umbos, widens anteriorly, disks reticulate; clasping spines at hinge, anterior ear margins, sparsely scattered on ventral disk. *Lower Carboniferous (upper Viséan):* British Isles.——Fig. 310,*2a–d.* **T. smarti; a,b,* holotype, corpus plus part of one ear viewed ventrally, dorsally, Asbian, Yorkshire, BMNH BD 9544, ×2; *c,* lateral view of a shell with part of ventral valve missing to show corpus depth (*arrow*), Derbyshire, ×2; *d,* ventral view of shell clasping crinoid columnal (*arrow*), Derbyshire, ×3 (Brunton & Mundy, 1994).

Subfamily UNCERTAIN

Liolimbella Li Li in Ding Yunjie & others, 1991, p. 155[184] [**L. spanoptycha;* OD]. Resembles small *Rhytibulus,* elongate oval outline with hinge less than maximum width; rugae fine, slightly increasingly separated anteriorly toward nonrugose margin; spines at hinge and scattered from rugae on ventral valve; dorsal valve and interiors unknown. *Lower Permian:* China.——Fig. 312*a.* **L. spanoptycha,* Lower Permian, Quinling; ventral valve, ×3 (Ding & others, 1991).——Fig. 312*b. L. polyptycha;* ventral valve, ×3 (Ding & others, 1991).

Family PRODUCTIDAE Gray, 1840

[Productidae Gray, 1840, p. 151]

Deep corpus cavity; spine row(s) near hinge; teeth only in oldest genera. *Upper Devonian (Famennian)–Upper Permian (Tatarian).*

Subfamily PRODUCTINAE Gray, 1840

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Productidae Gray, 1840, p. 151, *partim*]

Small to medium size; profile geniculate with trails long, may have bordering structures; ribbing entire, reticulate posteriorly; spines commonly only on ventral valve; marginal structures well developed, including ear baffles. *Lower Carboniferous (lower Viséan)–Lower Permian.*

Tribe PRODUCTINI Gray, 1840

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Productidae Gray, 1840, p. 151, *partim*]

Ribbing relatively fine; spines thin, numerous on ears; diaphragm associated with series of dorsal trails; dorsal adductor scars may be raised on platforms. *Lower Carboniferous (Viséan)–Upper Carboniferous (Moscovian).*

Fig. 312. Productellidae (p. 467).

Productus J. Sowerby, 1814 in 1812–1815, p. 153 [**Anomites productus* Martin, 1809, p. 9 (validated ICZN, 1956a, Opinion 419, p. 75); OD] [=*Producta* Conybeare & Phillips, 1822, p. 357; *Protonia* Link, 1830, p. 449, *non* Rafinesque, 1814, obj.; *Pyxis* von Chemnitz, 1784, p. 301, nonbinomial); *Hubeiproductus* Yang De-li, 1984, p. 229[331] (type, *H. guanyinyanensis;* OD)]. Medium size; corpus deep, ventral trail long, spreading; dorsal valve geniculated, dorsal diaphragm restricted to one third anteriorly; dorsal cardinal ridges tend to diverge as lateral ridges, becoming subperipheral ridge, adductor scars slightly raised. *Carboniferous (upper Viséan–Serpukhovian, ?Bashkirian):* Eurasia, northern Africa, southern China, ?North America.——Fig. 313,*1a–e.* **P. productus* (Martin), upper Viséan, Derbyshire; *a–d,* complete holotype, ventral, lateral views, BMNH B 40952, dorsal, posterior views of detached corpus region, ×1; *e,* anterior view of ventral valve, ×1 (new).——Fig. 313,*1f. P. carbonarius* (de Koninck), lower Serpukhovian, Yorkshire; latex replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Carlinia Gordon, 1971, p. 258 [**Productus phillipsi* Norwood & Pratten, 1855a, p. 8; OD]. Resembles *Diaphragmus,* but short trails, lacks strong reticulation posteriorly, ribbing commonly coarse; spines on ears, lacking clumps on flanks; wide zone of diaphragms. *Lower Carboniferous (lower Serpukhovian):* North America.——Fig. 313,*3a–e.* **C. phillipsi* (Norwood & Pratten), upper Chesterian, Utah; *a,b,* ventral, lateral views of specimen, ×1; *c,* dorsal view of shell, ×1; *d,* posterior view of ventral valve, ×1.5; *e,* dorsal valve interior, ×1 (Gordon, 1971).

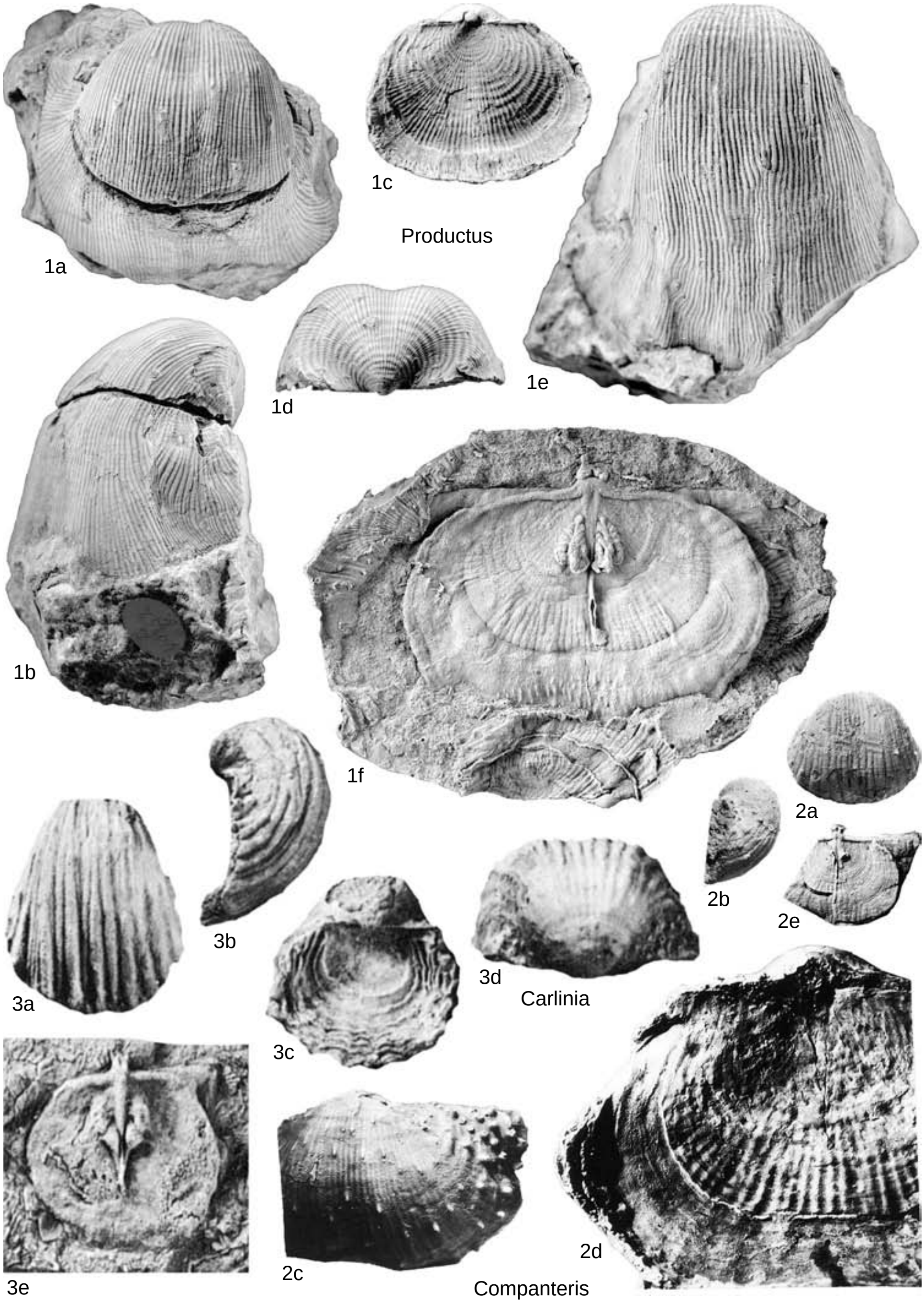


FIG. 313. Productidae (p. 467–469).

Companteris Lazarev, 1981, p. 79 [**C. aljutovensis;* OD]. Small size; dorsal diaphragm with two trails; dorsal adductor scar platforms overhang laterally. *Upper Carboniferous (upper Bashkirian–lower Moscovian):* eastern Europe.——Fig. 313,*2a–e.* **C. aljutovensis,* upper Bashkirian–lower Moscovian, Moscow Basin; *a,b,* ventral, lateral views of ventral valve, ×1; *c,* ventral valve exterior with cardinal extremity, spine bases preserved, ×2; *d,* dorsal valve exterior showing the ornament, microornament of diaphragm with traces of fragmented trails, ×5; *e,* dorsal valve interior, ×1 (Lazarev, 1981).

Diaphragmus Girty, 1910, p. 217 [**Productus elegans* Norwood & Pratten, 1855a, p. 13, *non* M'Coy, 1884; OD; =*Productus cestriensis* Worthen, 1860, p. 570]. Resembles *Productus,* but with series of dorsal diaphragms, trails leaving short flat external dorsal disk. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* North America.——Fig. 314,*1a–f.* **P. elegans* (Norwood & Pratten), upper Viséan–lower Serpukhovian; *a,* ventral view of ventral valve, Oklahoma, ×1; *b,c,* dorsal, lateral views of complete specimen, Oklahoma, ×1; *d,* spine bases on flank, Oklahoma, ×2; *e,* longitudinal section of specimen showing two diaphragms, two successive dorsal trails, Oklahoma, ×2; *f,* dorsal valve interior, Illinois, ×4 (Muir-Wood & Cooper, 1960).

Dowhatania Waterhouse in Waterhouse & Gupta, 1979, p. 127 [**Productus dowhatensis* Diener, 1915, p. 27; OD] [=*Parabuxtonia* Yang & Zhang, 1982, p. 304 (type, *P. kongjingensis;* OD); *Shishapangmaella* Yang in Yang & Fan, 1983, p. 273 (type, *S. shishapangaensis;* OD); obj.]. Poorly known; medium size; numerous fine spines, especially on ventral ears, flanks, absent dorsally; possibly with dorsal diaphragms; cardinal ridges. *?Lower Carboniferous (Viséan), Upper Carbonferous (Moscovian):* Himalayas, ?China.——Fig. 314,*2a–c.* **D. dowhatensis* (Diener), ?Bashkirian, Kashmir; *a,* ventral valve exterior with fringing spines, ×1; *b,* ventral valve exterior, ×1; *c,* incomplete dorsal valve interior, ×1 (Diener, 1915).

Lopasnia Ilkhovsky in Lazarev, 1990, p. 103 [**Thomasina(?) adhaerescens* Ivanova in Ivanov, 1935, p. 112; OD]. Small to medium size; outline rather transverse; ribbing strong, coarse anteriorly; two dorsal trails, short diaphragm; cardinal process supported by adductor ridges. *Upper Carboniferous (Moscovian):* Russia.——Fig. 314,*3a,b.* **L. adhaerescens* (Ivanova), Moscovian, Moscow basin; *a,* ventral view of ventral valve, ×2 (Ivanov, 1935); *b,* exfoliated dorsal valve exterior showing adductor ridges, ×3 (new).

?Marginirugus Sutton, 1938, p. 559 [**Productus magnus* Meek & Worthen, 1862, p. 142; OD]. Large; weakly plano- to concavoconvex lateral profile with short trails, moderate to deep corpus; fine ribbing entire, rugae posterolaterally, no reticulation; spines only ventrally, thick row close to hinge, posteriorly directed, fine spines sparse on corpus; cardinal process trifid, lateral ridges continue as weak subperipheral rim. *Lower Carboniferous (lower Viséan):* central North America.——Fig. 315*a–f.* **M. magnus* (Meek & Worthen), lower Viséan; *a,b,* posterior, lateral views of ventral valve, Illinois, ×1; *c,* posterior view of dorsal valve showing cardinal process, Illinois, ×1; *d,* posteroventral view of ventral valve interior, Illinois, ×1; *e,f,* dorsal valve interior, ventral view of ventral valve, Oklahoma, ×1 (Muir-Wood & Cooper, 1960).

Tribe KOZLOWSKIINI
Brunton, Lazarev, & Grant, 1995

[Kozlowskiini Brunton, Lazarev, & Grant, 1995, p. 928]

Spines variable, but may include few thick halteroid spines; zygidium may be present; marginal ridges associated with series of many dorsal trails. *Lower Carboniferous (Viséan)–Lower Permian (Sakmarian).*

Kozlowskia Fredericks, 1933, p. 29 [**Productus capaci* d'Orbigny, 1842, p. 50; OD]. Small, outline transverse with well-developed ears forming widest part of shell; planoconvex corpus, commonly with reticulate disks; ribbing may disappear anteriorly; spines variable from few, thick, and symmetrically arranged to more numerous scattered spines; zygidium present; endospines in single row at anterior margin of disk. *Upper Carboniferous (Bashkirian)–Lower Permian (Sakmarian):* cosmopolitan.——Fig. 316,*2a–c.* **K. capaci* (d'Orbigny), Lower Permian, Capinota, Bolivia; *a,b,* ventral valve posteriorly, laterally, ×2; *c,* ventral valve interior, ×2 (Muir-Wood & Cooper, 1960).——Fig. 316,*2d–f. K. splendens* (Norwood & Pratten), Upper Carboniferous, Magdalena Formation, New Mexico; *d,* dorsal view, ×1; *e,* anteroventral view, ×2; *f,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Eomarginifera Muir-Wood, 1930, p. 103 [**Productus longispinus* J. Sowerby, 1814 in 1812–1815, p. 154; OD] [=*Lissomarginifera* Lane, 1962, p. 901 (type, *L. nuda;* OD)]. Small, around 15 mm wide; ears small, zygidium absent; six symmetrical, stout spines; commonly weak median sulcus; dorsal submarginal ridges weak anteriorly, absent ventrally. *Lower Carboniferous (Viséan–lower Serpukhovian), ?Upper Carboniferous (?lower Moscovian):* Eurasia, northern Africa, ?North America.——Fig. 316,*3a–d.* **E. longispina* (J. Sowerby), upper Viséan, Ayrshire, Scotland; ventral, dorsal, lateral, posterior views of complete specimen, ×2 (new).——Fig. 316,*3e,f. E. lobata* (J. Sowerby); *e,* internal mold of ventral valve, Pendleian, Northumberland, British Isles, ×2; *f,* dorsal valve interior, Brigantian, ×2 (new).

Minispina Waterhouse, 1982a, p. 45 [**M. alata;* OD]. Similar to *Kozlowskia,* possibly differing by

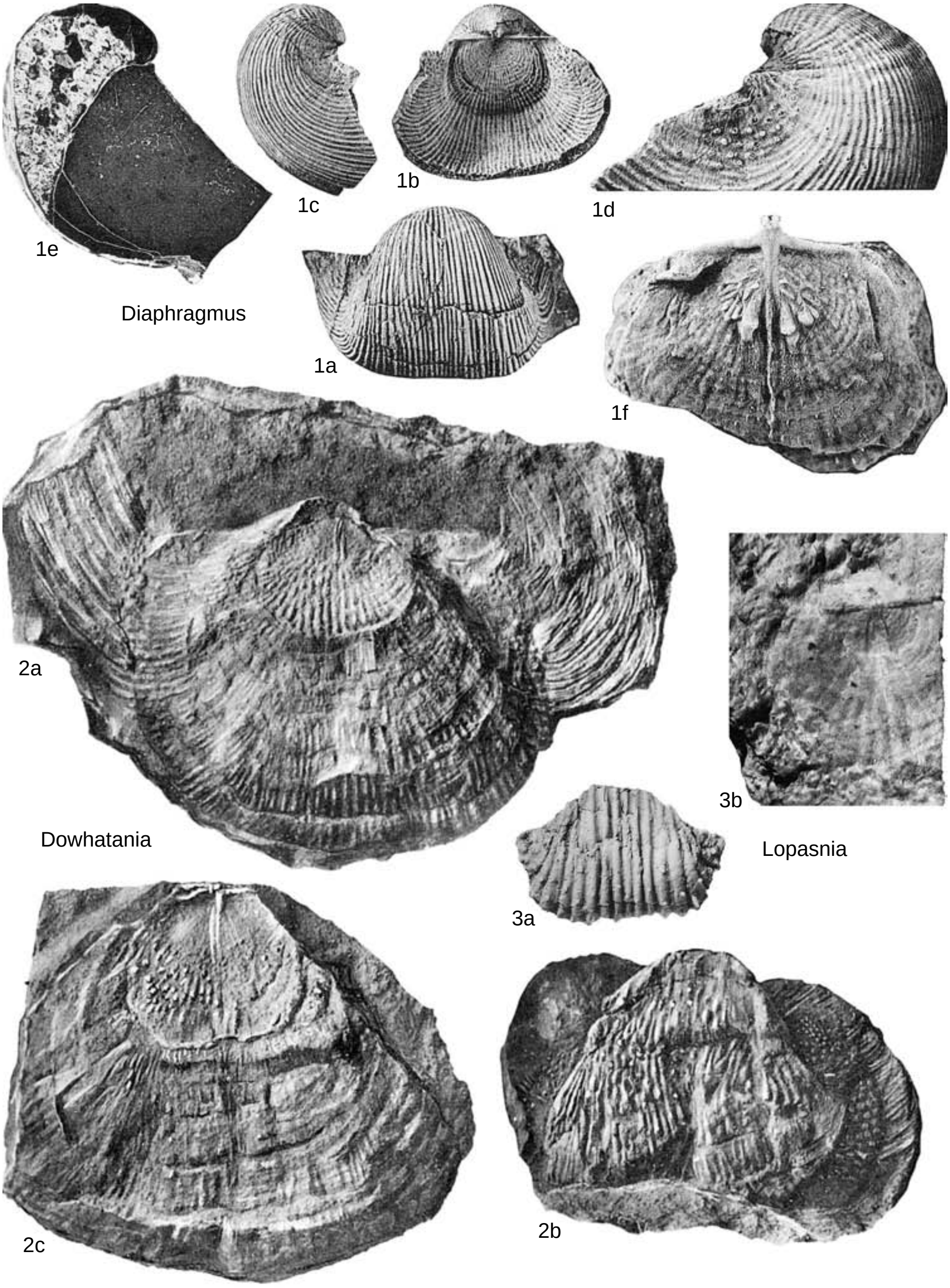
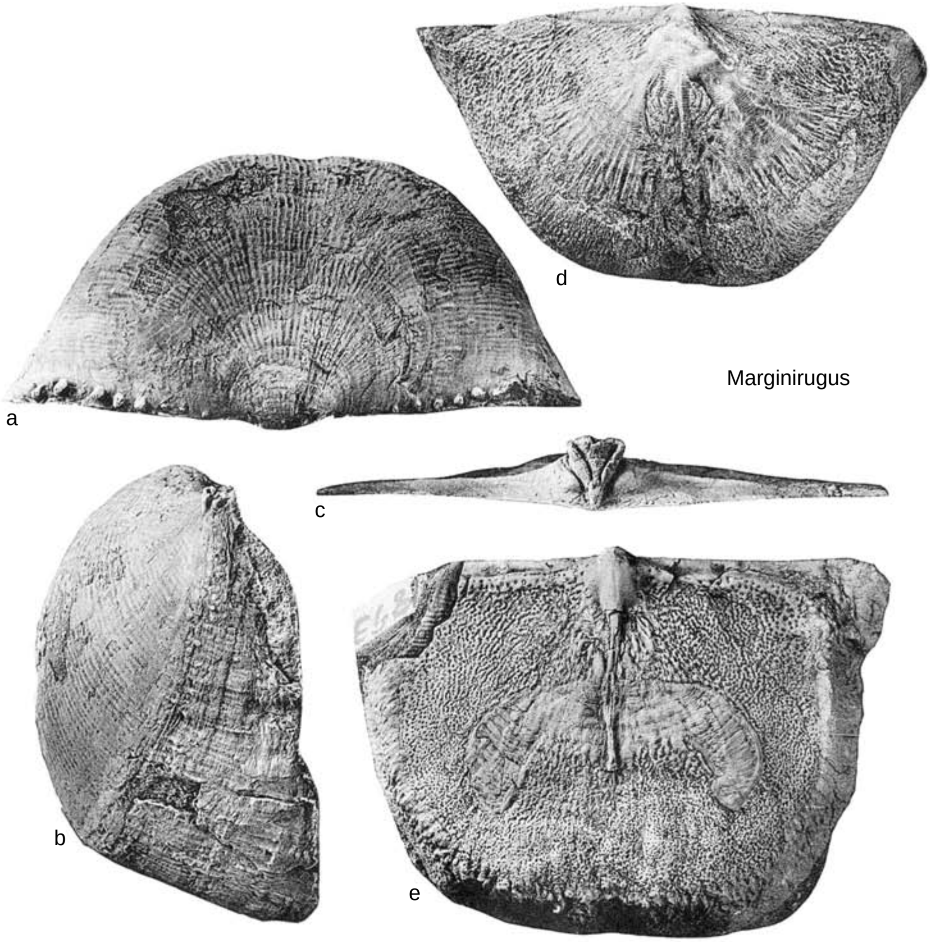


FIG. 314. Productidae (p. 469).

having no dorsal trails. *Upper Carboniferous (Kasimovian–Gzhelian):* southeastern Asia.——FIG. 316,*1a–c.* **M. alata,* upper Upper Carboniferous, northeastern Thailand; *a,* ventral valve exterior, ×2.2; *b,* ventral valve internal mold, ×3.5; *c,* dorsal valve internal mold, ×3 (Waterhouse, 1982a).



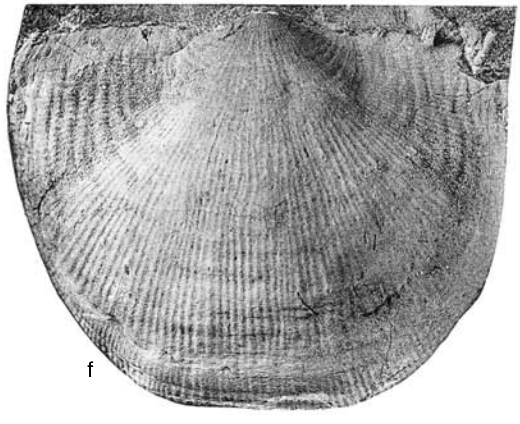


Fig. 315. Productidae (p. 469).

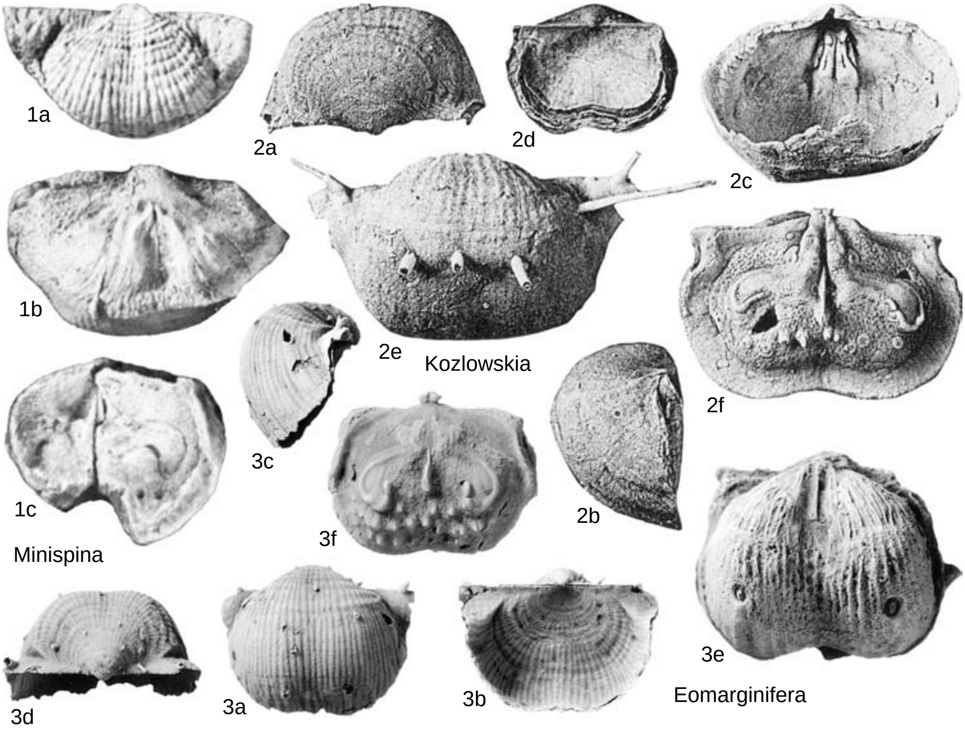


Fig. 316. Productidae (p. 469–470).

Tribe RETARIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Retariinae Muir-Wood & Cooper, 1960, p. 230]

Trail nonlamellose, may be tubiform; row of thick spines at base of ventral flank, sparse or absent from dorsal valves; dorsal adductor scars commonly positioned relatively anteriorly, with pitted, tuberculate surface ornamentation in ventral umbo. *Lower Carboniferous (lower Viséan)–Lower Permian.*

Kutorginella Ivanova, 1951, p. 329 [**K. mosquensis;* OD] [=*Retaria* Muir-Wood & Cooper, 1960, p. 230 (type, *R. umbonata;* OD); *Neoproboscidella* Ivanova, 1949, *nom. nud.; Calliomarginatia* Ching in Zhang & Ching, 1976, p. 181 (type, *C. himalayensis;* OD); *Aspinosella* Waterhouse, 1982a, p. 47 (type, *Kutorginella uddeni* Cooper & Grant, 1975, p. 1029; OD)]. Ventral median sulcus prominent, may form extended (nasute) trail medianly; ears large, almost flat; cardinal or lateral ridges continuous with ear baffles, extending as endospinous marginal ridge. [A *Retaria* group of species with widely divergent lateral ridges, poorly differentiated from ear baffles, may be separable from the *mosquensis* group of species with cardinal or lateral ridges close to the hinge line]. *Upper Carboniferous (Kasimovian)–Lower Permian:* eastern Europe, middle Asia, North America, China.——Fig. 317,*1a–d.* **K. mosquensis,* Kasimovian–Gzhelian, Moscow Basin; *a,* anterior view of specimen lacking nasute trail, ×1; *b,* ventroanterior view of specimen showing nasute trail, ×1 (Muir-Wood & Cooper, 1960); *c,* posterior view of ventral valve, ×1.2; *d,* dorsal valve interior, ×1.5 (Sarytcheva, 1971).——Fig. 317,*1e,f. K. umbonata* (Muir-Wood & Cooper), Leonardian, Texas; *e,* lateral view of shell, ×1; *f,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Antiquatonia Miloradovich, 1945, p. 496 [**Productus antiquatus* J. Sowerby, 1821 in 1821–1822, p. 15; OD]. Ventral spine ridge flanking ears with internal complimentary lateral ridges; ventral spines thick, halteroid. *Carboniferous (Viséan–Serpukhovian):* cosmopolitan.——Fig. 317,*2a,b.* **A. antiquata* (J. Sowerby), Viséan, Derbyshire; lectotype selected by Muir-Wood, 1928, anterior, lateral views of specimen lacking ears, BMNH B 60956, ×1 (new).——Fig. 317,*2c–f. A. hindi* (Muir-Wood), lower Brigantian, Derbyshire; *c,d,* holotype, posterior, lateral views, BMNH B 47860, ×1 (Muir-Wood, 1928); *e,f,* posterior view, showing part of internal mold, oblique lateral view of ventral valve, ×1 (new).

Kelamelia Zhang Zi-xin in Zhang & others, 1983, p. 305 [**K. typica;* OD]. Poorly known; ventral spines

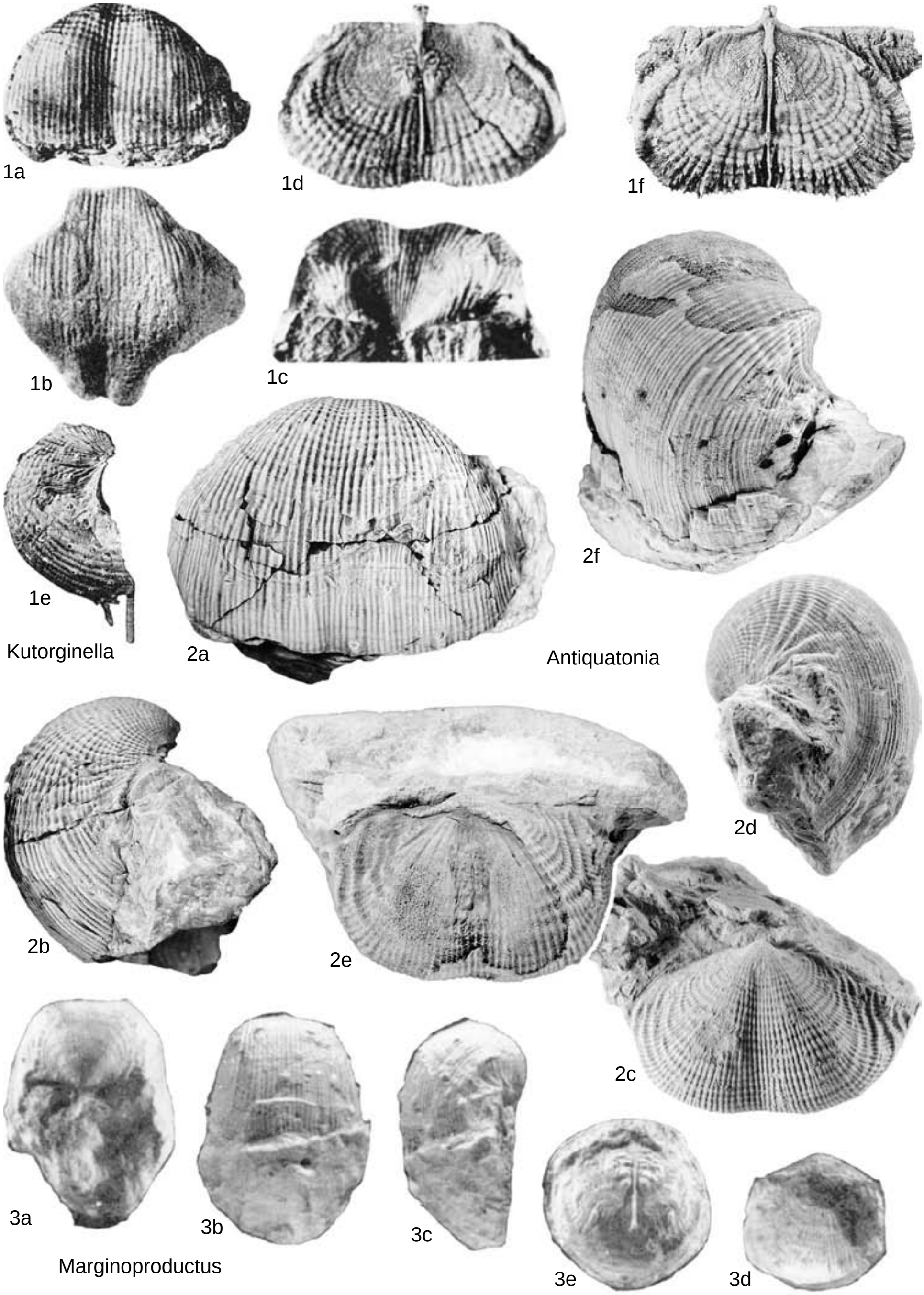


Fig. 317. Productidae (p. 472–475).

at hinge, flank to ear junction; lateral ridges ?short, slightly divergent, not extended as ear baffles. *Upper Carboniferous (Moscovian):* northern China. ——Fig. 318,*1a–d.* **K. typica,* Moscovian, Xinjiang; anterior, dorsal, lateral, posterior views of complete specimen, ×1 (Zhang & others, 1983).

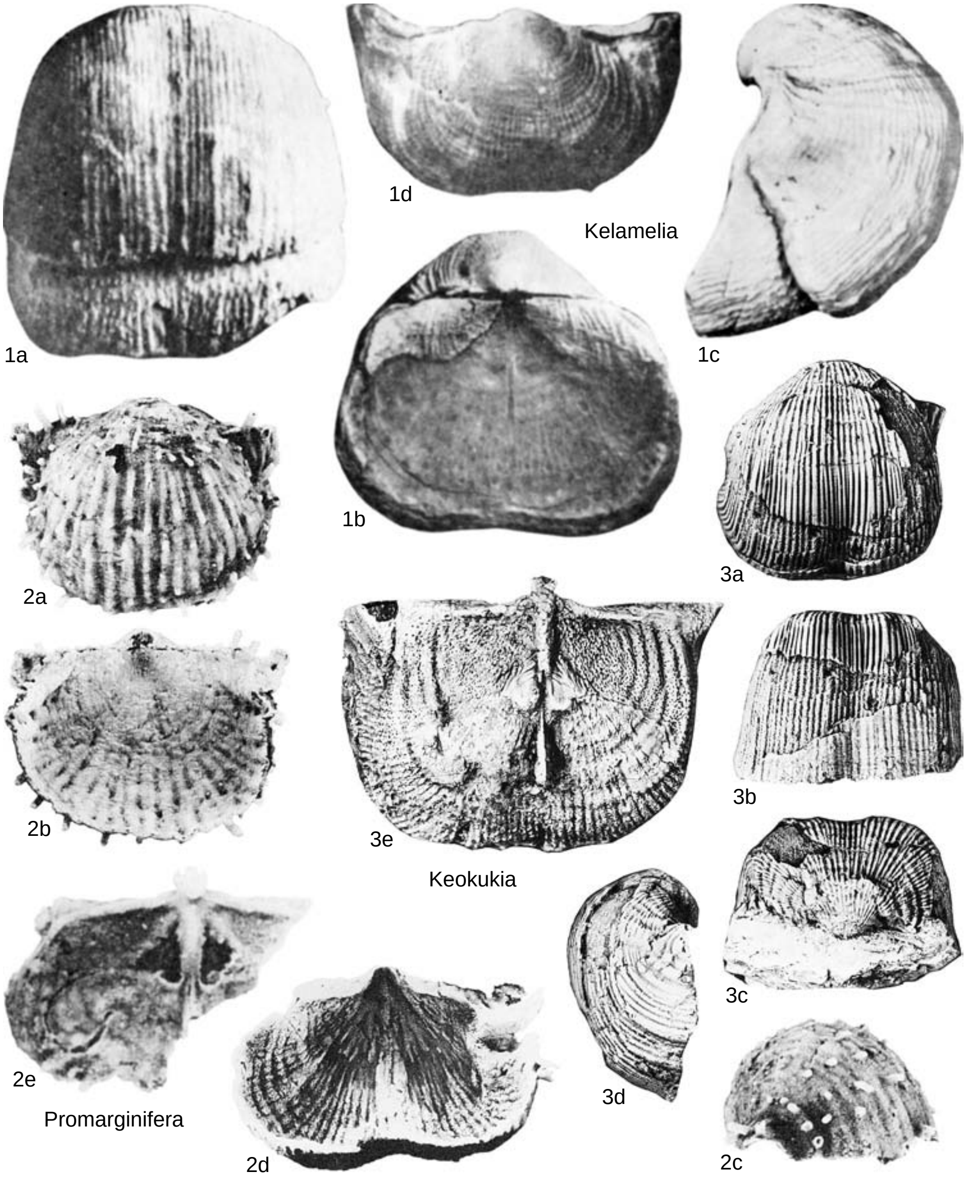


FIG. 318. Productidae (p. 472–475).

Keokukia CARTER, 1990, p. 229 [**K. sulcata;* OD]. Medium size; ears small, pointed; spine row diverges slightly from ventral hinge, others on flanks, trail, no dorsal spines; lateral ridges close to hinge, no marginal ridges. *Lower Carboniferous (lower Viséan):* central North America.——FIG. 318,*3a–e.* **K. sulcata,* lower Viséan, Illinois; *a–d,* holotype, ventral, anterior, posterior, lateral views, CMNH 34891, ×1; *e,* dorsal valve interior, ×1.5 (Carter, 1990).

Marginoproductus TAN ZHEN-XIU, 1986, p. 435[443] [**M. hunanensis;* OD]. Small to medium sized, around 20 mm wide; deep corpus with long trail; dorsal spines reportedly absent, but if present should be assigned to the Tolmatchoffiinae; closely resembles *Marginatia. Lower Carboniferous (lower*

Viséan): southern China.——FIG. 317,*3a–e.* **M. hunanensis,* lower Viséan, Hunan; *a,* holotype, posterior view, HB 318, ×1; *b,c,* anterior, lateral views of ventral valve, ×1; *d,* dorsal valve exterior, ×1; *e,* dorsal valve interior, ×1 (Tan, 1986).

Promarginifera SHIELLS, 1966, p. 428 [**P. trearnensis;* OD]. Small; corpus deep, ears well differentiated, trail simple; spines numerous, covering ventral valve, few and fine dorsally; lateral ridges close to hinge. *Lower Carboniferous (upper Viséan):* British Isles.——FIG. 318,*2a–e.* **P. trearnensis,* Asbian, Ayrshire; *a–c,* holotype, ventral, dorsal, lateral views, HM L6202, ×2; *d,* ventral valve interior, ×2; *e,* dorsal valve interior, ×2.5 (Shiells, 1966).

Svalbardoproductus USTRITSKY, 1962b, p. 82 [**S. stratoauritus;* OD]. Similar to *Thamnosia,* but said to differ by lacking spine clusters on ears; ribbing weak, indistinct anteriorly. *upper Lower Permian (Kungurian):* Spitzbergen.

Tesuquea SUTHERLAND & HARLOW, 1973, p. 53 [**T. formosa;* OD]. Small to medium size; corpus deep; spines only ventrally, small over reticulate disk, single or double rows prominent on flanks, continued onto trail; cardinal process small, sessile, cardinal ridges angle sharply at ears, continue as ear baffles. *lower Upper Carboniferous (Bashkirian):* southern North America.——FIG. 319,*2a–e.* **T. formosa,* Bashkirian, New Mexico; *a,* holotype, ventral view, OU 7659, ×1; *b,c,* posterior, lateral views, ×2; *d,* dorsal valve exterior, ×2; *e,* dorsal valve interior, ×2 (Sutherland & Harlow, 1973).

Thamnosia COOPER & GRANT, 1969, p. 10 [**T. anterospinosa;* OD] [=?*Neopugilis* LI in DING & others, 1991, p. 159[186] (type, *N. typicus;* OD); *Thuleproductus* SARYTCHEVA & WATERHOUSE, 1972, p. 67 (type, *T. crassauritus;* OD)]. Medium, widest at hinge; ventral disk gently convex, geniculate with long trail, medianly sulcate; spines on both valves, ventral valve with clusters of thicker spines on lateral slopes and anterior trail, dorsal spines small, thin; ear baffles in both valves, dorsally as extensions of cardinal ridges that diverge from hinge; marginal ridge becoming overgrown by row of endospines anteriorly. [The inclusion of *Neopugilis* from the Lower Permian of Shaanxi, China, may extend the range from the uppermost Carboniferous; interiors are poorly known.] *?upper Upper Carboniferous (?Gzhelian), upper Lower Permian (Roadian):* USA, Arctic Canada, eastern Greenland, Arctic Eurasia, ?China.——FIG. 319,*1a–e.* **T. anterospinosa,* Lower Permian, Cathedral Mountain Formation, Texas; *a–c,* holotype, viewed ventrally, dorsally, laterally, USNM 149852, ×1; *d,* ventral valve interior, ×1; *e,* dorsal valve interior, ×1 (Cooper & Grant, 1975).

Tubaria MUIR-WOOD & COOPER, 1960, p. 236 [**Productus genuinus* KUTORGA, 1844, p. 93; OD]. Resembles *Kutorginella,* but with larger convex ears and greatly extended anterior margin, forming tube; dorsal marginal ridge smooth. *Upper Carboniferous (Moscovian)–Lower Permian (Sakmarian):* Russia, Fergana.——FIG. 319,*3a–d.* **T. genuina* (KUTORGA), Schwagerina Limestone, Ural Mountains; *a,* shell viewed ventrally, ventral valve missing over right ear, ×1; *b,c,* shell viewed laterally, ventrally with ventral corpus removed, showing dorsal external mold, ×1 (Muir-Wood & Cooper, 1960); *d,* dorsal valve interior, ×1.5 (Sarytcheva, 1971).

Tribe SPYRIDIOPHORINI Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 928, *ex* Spyridiophoridae MUIR-WOOD & COOPER, 1960, p. 230]

Ribbing coarse, homogeneous anteriorly; spine row on each arched ear; no diaphragm or series of dorsal trails; dorsal adductor platforms well developed (spyridium). *Upper Carboniferous (Moscovian)–Lower Permian (Sakmarian, ?Artinskian).*

Spyridiophora COOPER & STEHLI, 1955, p. 471 [**S. distincta;* OD] [=*Spiridiophora* SARYTCHEVA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 234]. Medium size with transverse outline, ears large; ventral sulcus originating on umbo; dorsal disk almost flat, geniculate; spines include ear clusters, none dorsally; ear baffles in both valves strong; cardinal process sessile, bilobed, quadrifid; dorsal adductor scars raised, laterally directed platforms or true spyridium. *Lower Permian (Asselian–Sakmarian, ?Artinskian):* USA, southeastern Asia.——FIG. 320,*2a–e.* **S. distincta,* Lower Permian, Wolfcamp Formation, Texas; *a–c,* shell viewed ventrally, anteriorly, dorsally, ×1; *d,* dorsal valve viewed posteriorly showing spyridium, ×3 (Muir-Wood & Cooper, 1960); *e,* holotype, dorsal valve interior, USNM 124117, ×2 (Cooper & Grant, 1975).

Alexenia IVANOVA in IVANOV, 1935, p. 89 [**A. reticulata;* OD]. Externally similar to *Spyridiophora* but internal dorsal adductor platforms separated medianly, and less elevated. *Upper Carboniferous (Moscovian–Kasimovian):* Eurasia.——FIG. 320,*1a–c.* **A. reticulata,* Moscow basin; *a,* ventral valve exterior, Moscovian, ×2; *b,* ventral valve exterior, Moscovian, ×1 (Ivanova, 1935); *c,* dorsal valve interior, Kasimovian, ×1 (Lazarev, 1990).

Subfamily LEIOPRODUCTINAE Muir-Wood & Cooper, 1960

[Leioproductinae MUIR-WOOD & COOPER, 1960, p. 168]

Ribbing commonly absent or weak, never at beak; dorsal spines commonly absent; teeth absent in all but oldest genera. *Upper Devonian (Famennian)–Upper Permian (Capitanian).*

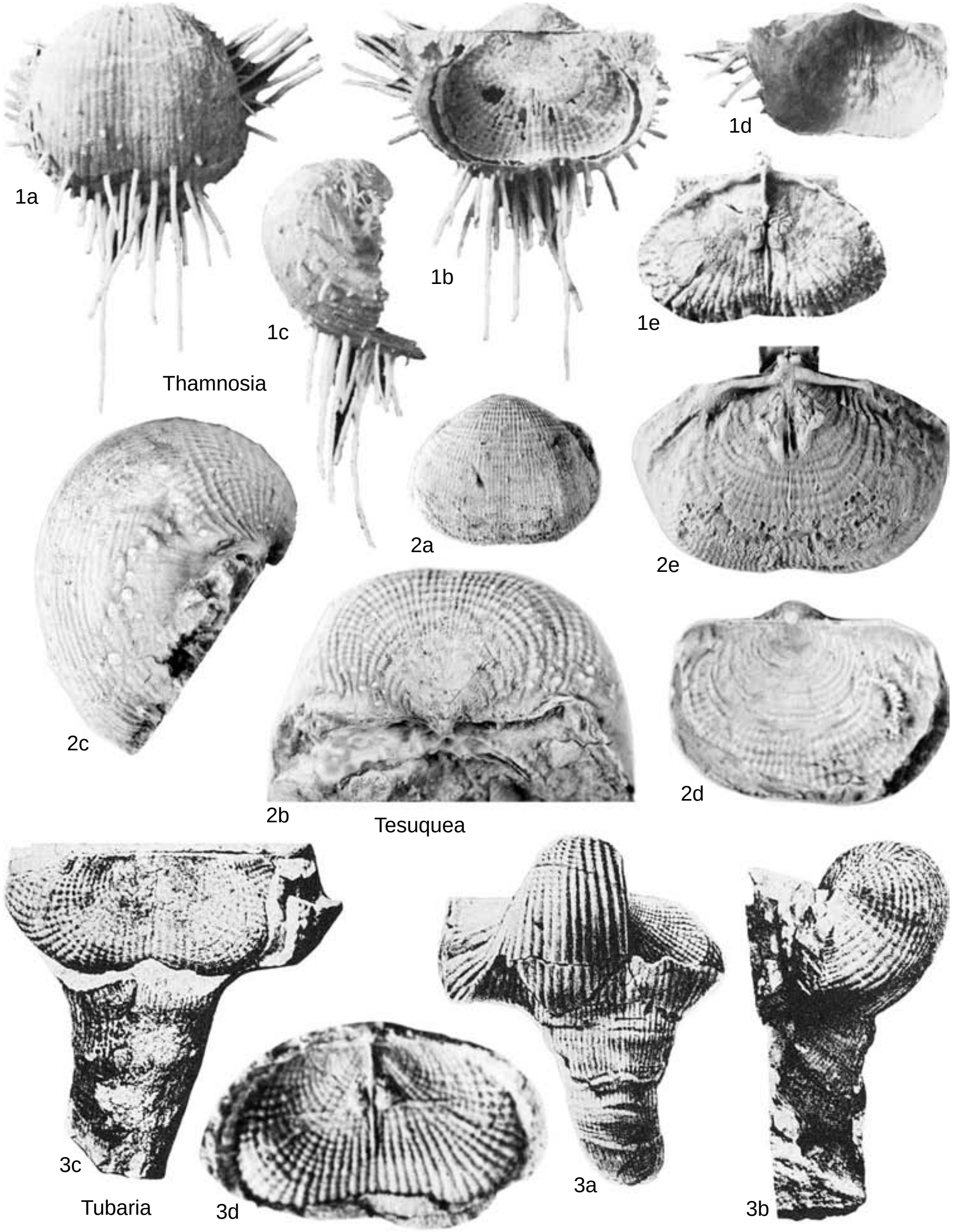


Fig. 319. Productidae (p. 475).

Tribe LEIOPRODUCTINI Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, herein, *ex* Leioproductinae Muir-Wood & Cooper, 1960, p. 168]

Small to medium sized; ribbing absent, but commonly with ventral median weak fold; ventral spines sparse, dorsal spines absent; teeth in early genera. *Upper Devonian (Famennian)–Lower Carboniferous (lower Viséan).*

Leioproductus Stainbrook, 1947, p. 307 [**Productella coloradoensis* var. *plicatus* Kindle, 1909, p. 18; OD].

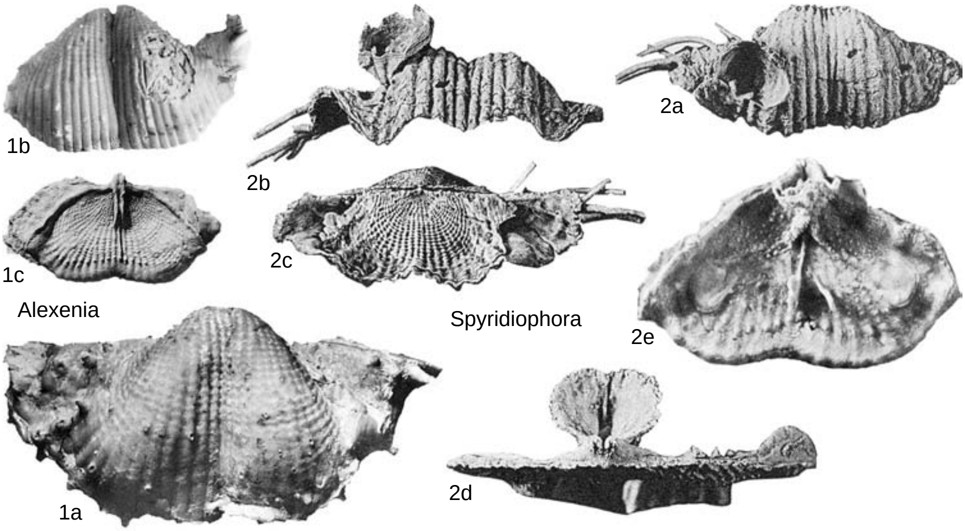


FIG. 320. Productidae (p. 475).

Spines sparse, evenly distributed roughly radially, commonly including ventral median row on low ridge; weak lateral ridges extend toward lateral margins, short accessory ridges posterior to adductor scars; cardinal process pit. *Upper Devonian (upper Famennian):* North America, Asia.——FIG. 321,*1a–f.* **L. plicatus* (KINDLE), uppermost Famennian, New Mexico; *a,* posterior view, ×1; *b,* anteroventral view, ×2; *c,* dorsal view, ×1; *d,* lateral view, ×2; *e,* dorsal valve interior, ×2; *f,* conjoined valves showing dorsal, ventral interiors, ×2 (Muir-Wood & Cooper, 1960).

Ardiviscus LAZAREV in LAZAREV & PUSHKIN, 1986, p. 42[35] [**A. naidovense* PUSHKIN in LAZAREV & PUSHKIN, 1986, p. 43[38]; OD]. Similar to *Leioproductus,* but with thinner spines, occurring more densely posterolaterally; teeth present, but no cardinal process pit. *Upper Devonian (lower Famennian):* Eurasia, ?North America.——FIG. 321,*5a–e.* **A. naidovense* PUSHKIN, lower Famennian, Belorussia, Gomel' region; *a,b,* holotype, ventral, lateral views, PIN N 4067/113, ×1; *c,* oblique lateral view of ventral valve exterior, ×1; *d,* dorsal view of shell, ×1; *e,* partial ventral valve internal mold showing muscle scars, ×3 (Lazarev & Pushkin, 1986).

Bispinoproductus STAINBROOK, 1947, p. 311 [**B. varispinosus;* OD]. Resembles *Leioproductus,* but with numerous ventral small spines, anteriorly on elongate bases, separated by slightly lamellose bands. *Upper Devonian (upper Famennian):* southern North America.——FIG. 321,*4a–d.* **B. varispinosus,* Famennian, New Mexico; *a,* dorsal view of complete specimen, ×1; *b,* ventral view of ventral valve, ×1; *c,* lateral view of ventral valve, note spines, ×1; *d,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Galeatella MUIR-WOOD & COOPER, 1960, p. 173 [**G. galeata;* OD]. Small; relatively shallow corpus; ventral disk weakly convex, gentle median sulcus; spines thin, at hinge, on indistinct rugae and anteriorly; cardinal process pit, accessory ridges posterior to adductor scars, no cardinal ridges. *Upper Devonian (upper Famennian):* North America.——FIG. 321,*2a–e.* **G. galeata,* uppermost Famennian, New Mexico; *a–c,* ventral, anterior, lateral views of ventral valve, ×1; *d,* dorsal view of nearly complete specimen, ×1; *e,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Grandiproductella LAZAREV in LAZAREV & SIMAKOV, 1987, p. 121[134] [**G. omolonensis* SIMAKOV in LAZAREV & SIMAKOV, 1987, p. 121[135]; OD]. Medium sized, around 30 mm wide; spines thin, in line at hinge, elsewhere rare; no ventromedian sulcus; teeth strong. *Upper Devonian (Famennian):* northeastern Asia.——FIG. 322,*1a–c.* **G. omolonensis* SIMAKOV, Famennian, Omolon Massif; *a,* holotype, ventral view, PIN N 4112/101, ×1; *b,* posterior view of ventral valve, ×1; *c,* posteroventral view of exfoliated ventral valve showing muscle scars, ×1 (Lazarev & Simakov, 1987).

?Hunanoproductus HOU HONG-FEI, 1965, p. 117 [**H. hunanensis;* OD]. Smaller medium size, outline subrounded; profile geniculate with flared trail; spines at hinge and rare, thin anteriorly; posterior rugae slight, corpus relatively shallow. *Lower Carboniferous (lower Tournaisian):* southern China.——FIG. 321,*3a–d.* **H. hunanensis,* lowermost Tournaisian, southern China; *a,b,* holotype, lateral, posterior views of ventral valve, IV 530, ×1; *c,d,* ventral, dorsal views of complete specimen, ×1 (Hou, 1965).

Kavesia LAZAREV in LAZAREV & SIMAKOV, 1987, p. 122[136] [**K. intrastriata* SIMAKOV in LAZAREV &

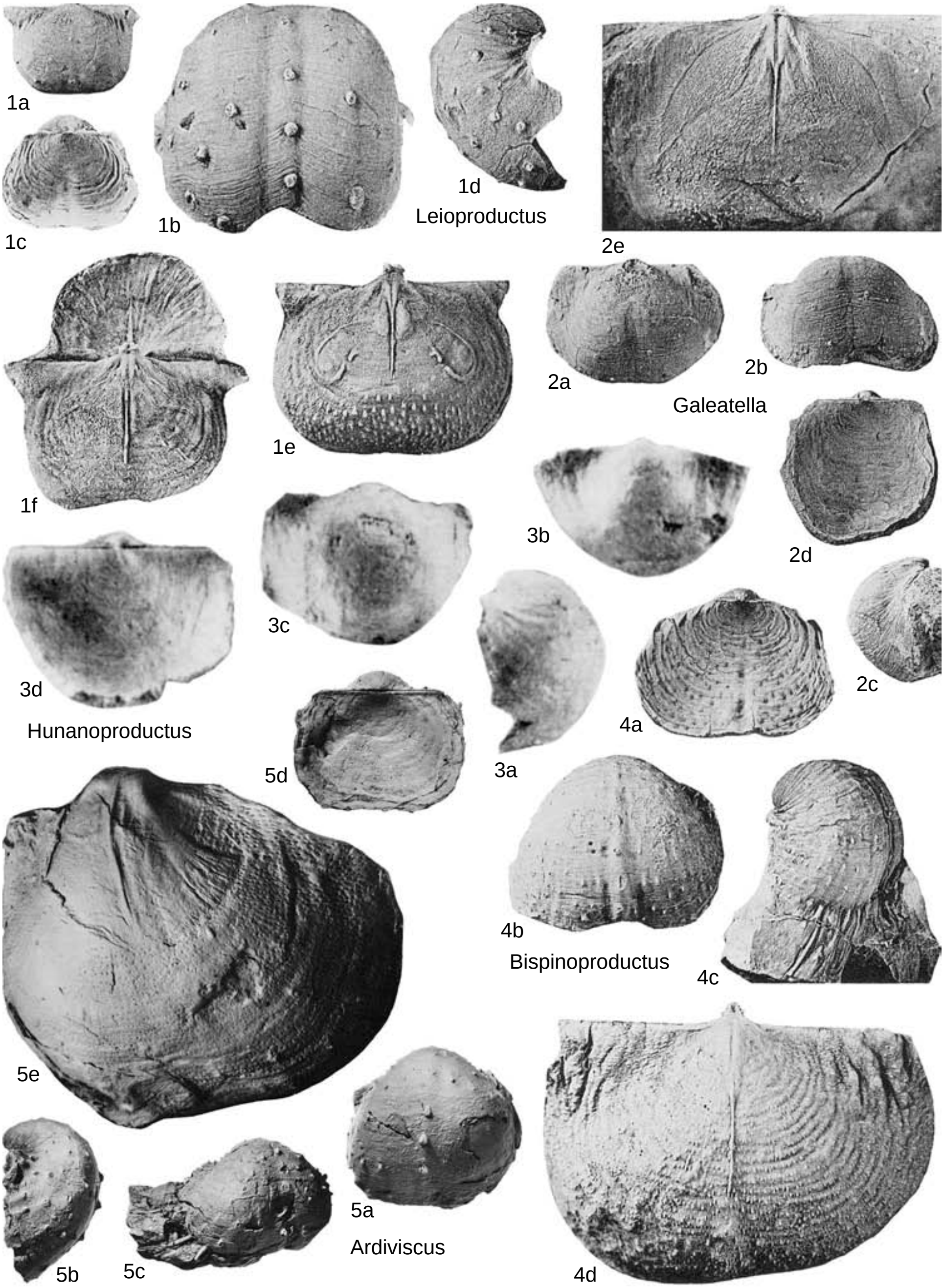


Fig. 321. Productidae (p. 476–477).

Simakov, 1987, p. 123[136]; OD]. Resembles *Grandiproductella,* but dorsal visceral disk more flat; teeth absent; no cardinal process pit. *?upper Upper Devonian, Lower Carboniferous (lower Tournaisian):* northeastern Asia.——Fig. 322,*4a–d*. **K. intrastriata* Simakov, ?uppermost Famennian–lower Tournaisian, Omolon Massif; *a,* holotype, dorsal view, showing cardinal process, PIN N 4112/104,

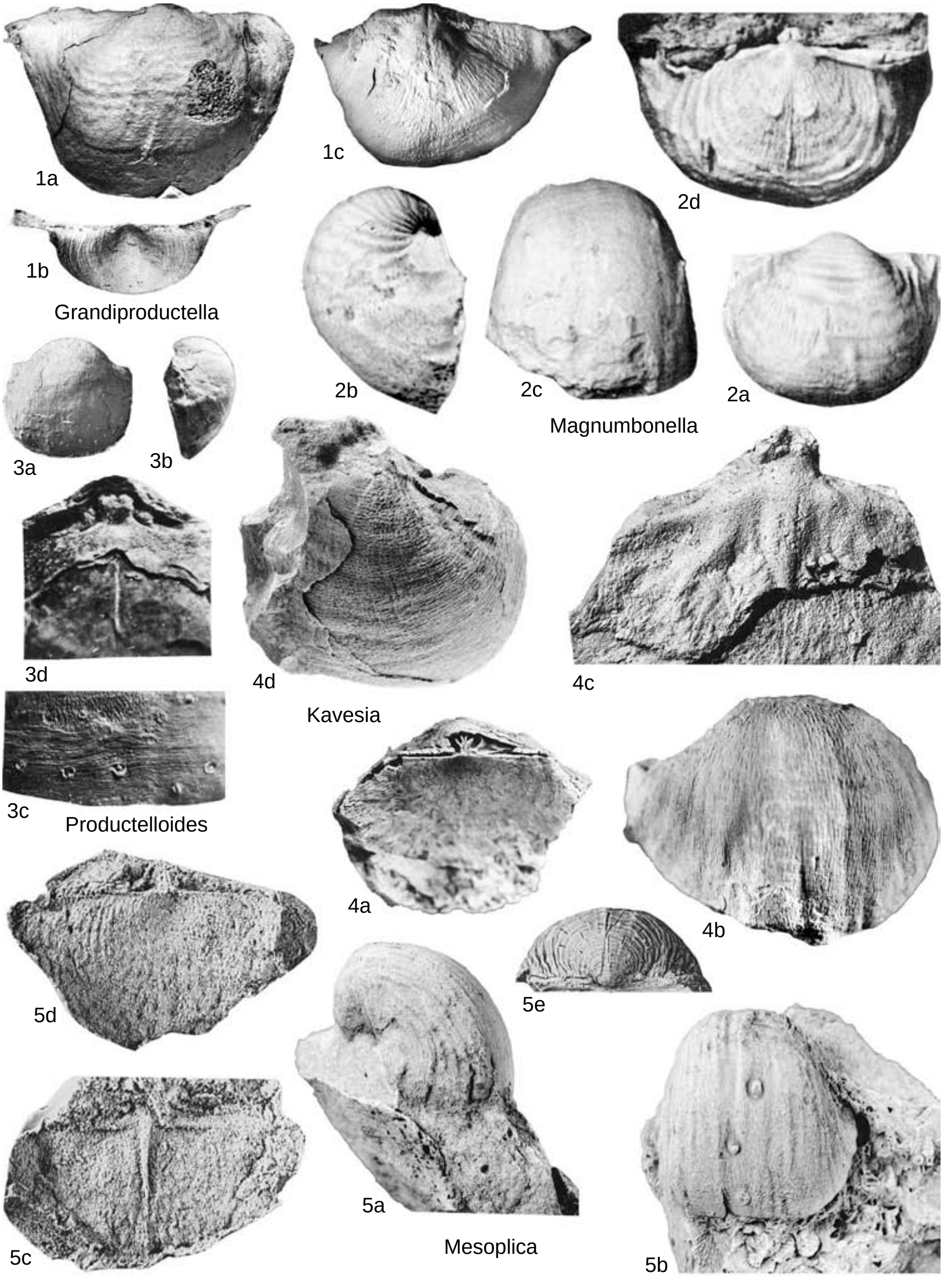


FIG. 322. Productidae (p. 477–480).

×1; *b,* internal cast of ventral valve, ×1; *c,* incomplete dorsal valve interior, ×3 (Lazarev & Simakov, 1987); *d,* anterolateral view of largely exfoliated valve, ×1 (new).

Magnumbonella CARTER, 1968, p. 1145 [**M. macrura;* OD]. Lateral profile strongly curved with deep corpus; rugae confined posteriorly, strong on flanks; spines rare, fine on dorsal valve, occasional elongate spine bases distal to spines; no cardinal process pit; lateral ridges diverge slightly from hinge, reaching ears. *Lower Carboniferous (Tournaisian–lower Viséan):* central North America.——FIG. 322,*2a–d.* **M. macrura,* lower Viséan, Missouri; *a,b,* ventral, lateral views of ventral valve, ×1.5; *c,* anterior view of ventral valve, ×1.5; *d,* dorsal valve interior, ×2 (Carter, 1968).

Mesoplica REED, 1943, p. 97 [**Leptaena praelonga* J. DE C. SOWERBY, 1840, pl. 53, fig. 29; OD]. Medium size; distinct ventral median fold bearing thicker spines in some; ribbing incipient anteriorly on corpus, trail; teeth absent; cardinal ridges short. *Upper Devonian (upper Famennian):* Europe, northern Africa, ?Asia.——FIG. 322,*5a–d.* **M. praelonga* (J. DE C. SOWERBY), uppermost Famennian, Devonshire; *a,b,* lateral, anterior views of ventral valve internal mold, ×1 (new); *c,d,* replicas of interior, exterior of posterior part of dorsal valve, ×2 (Muir-Wood & Cooper, 1960).——FIG. 322,*5e. M. simplicior* (NALIVKIN), Famennian, Kirghizia; posterior view of ventral valve, ×1 (Muir-Wood & Cooper, 1960).

Productelloides O. KOTLYAR, 1985, p. 112[97] [**P. gorobtsovensis;* OD]. Resembles *Leioproductus,* but without ventromedian fold, spines fine, widely scattered; teeth small. *Upper Devonian (upper Famennian):* Ukraine.——FIG. 322,*3a–d.* **P. gorobtsovensis,* upper Famennian, Poltava District; *a,b,* holotype, anteroventral, lateral views, IGN 2078/110, ×1; *c,* view of ventral valve surface at anterior margin, ×3; *d,* part of dorsal valve interior, ventral umbo showing teeth, ×5 (Kotlyar, 1985).

Tribe HORRIDONIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 928, *ex* Horridoniinae MUIR-WOOD & COOPER, 1960, p. 292]

Medium or commonly large, thick-walled valves; ribs weak or absent, one to three rows of halteroid spines commonly on ventral ears and, rarely, one row near dorsal hinge; rarely other dorsal spines; marginal structures commonly absent. *Lower Carboniferous (Serpukhovian)–Upper Permian.*

Horridonia CHAO, 1927b, p. 24 [**Productus horridus* J. SOWERBY, 1822 in 1821–1822, p. 17; OD] [?=*Sowerbina* FREDERICKS, 1928, p. 778 (type, *Productus timanicus* STUCKENBERG, 1905, p. 86; OD); *Pleurohorridonia* DUNBAR, 1955, p. 89 (type, *P. scoresbyensis;* OD)]. Medium size, outline pentagonal with wide hinge; weak median sulcus and dorsal fold; ribbing, rugae absent; spines in one to three rows on ears, few scattered on ventral valve, single row near dorsal hinge; dorsal lateral ridges extend to ears; dorsal muscle field rhombic; endospines around anterior margins of disk. *Upper Permian:* Europe, Arctic regions, ?Pakistan (Salt Range).——FIG. 323,*1a–f.* **H. horrida* (J. SOWERBY); *a–e,* shell viewed ventrally, posteriorly, anteriorly, laterally, dorsally, Zechstein, Thüringia, Germany, ×1; *f,* dorsal valve interior, Magnesian Limestone, Durham, ×1 (Muir-Wood & Cooper, 1960).

Bailliena NELSON & JOHNSON, 1968, p. 723 [**B. yukonensis;* OD]. Resembles *Horridonia,* but lacks dorsal spines near hinge, but with spines at dorsal geniculation zone; lamellose, especially dorsally; ribbed anteriorly on trail, anterior to thick spine bases. *Upper Carboniferous (Gzhelian)–Lower Permian (Asselian):* northern Canada.——FIG. 323,*2a–d.* **B. yukonensis,* Gzhelian–Asselian, Yukon Territory; *a,* holotype, viewed laterally, UCF 1088, ×1; *b,* holotype, close up of ventral hinge region, UCF 1088, ×2; *c,d,* ventral, dorsal views of specimen, ×1 (Nelson & Johnson, 1968).

Burovia USTRITSKY, 1980, p. 25 [**B. selanderensis;* OD]. Medium to large with variable outline, ears well differentiated; median sulcus originating on disk; prominent growth lines may form bands anteriorly; spines lacking at hinge, arranged in well-spaced rows on ventral valve and row at dorsal hinge with thick cluster on ears; cardinal process sessile, quadrifid; cardinal ridges weak or absent, marginal ridges strong laterally, continued anteriorly; shell substance thick, giving strong morphology with wide adductor scars. *upper Upper Permian:* Arctic regions.——FIG. 324*a–c.* **B. selanderensis,* Selander Formation, Selander Bay, Spitzbergen; *a,* holotype, ventral valve exterior, repository and number unknown, ×1; *b,* incomplete ventral valve with spine cluster, ×1; *c,* dorsal valve interior, ×1 (Ustritsky, 1980).——FIG. 324*d. B. maynei* (DUNBAR); anteroventral view of specimen, ×1 (Ustritsky, 1980).

Praehorridonia USTRITSKY, 1962a, p. 57 [**P. dorsoplicata;* OD]. Shape similar to *Horridonia,* but with thin spines scattered over ventral valve and anteriorly only on dorsal valve; incipient radial ribbing; lateral ridges thick, extended to separate ears. *Carboniferous (Serpukhovian–Bashkirian):* Arctic regions, Siberia, Canada.——FIG. 325,*1a–d.* **P. dorsoplicata,* lowermost Bashkirian, Kholodinn Formation, Taymyr; *a,b,* holotype, lateral, ventral views, VSEGEI 8363/176, ×1; *c,* ventral view showing incipient ribbing, VSEGEI 8363/176, ×2; *d,* dorsal valve interior, ×1 (Ustritsky, 1962a).

?Rugoclostus EASTON, 1962, p. 59 [**R. nivalis;* OD]. Similar to *Praehorridonia* but possibly differs in having ventral ginglymus and spines more densely covering dorsal ears. *lower Upper Carboniferous (lower Bashkirian):* central North America.——FIG. 325,*2a–c.* **R. nivalis,* lower Bashkirian, Cameron Creek Formation, Morrowan, Montana; holotype, dorsal, posterior, anteroventral views, USNM 118789, ×1 (Easton, 1962).

Tityrophoria WATERHOUSE in BAMBER & WATERHOUSE, 1971, p. 214 [**T. nelsoni;* OD]. Resembles *Praehorridonia,* but differs in lacking crowded spines

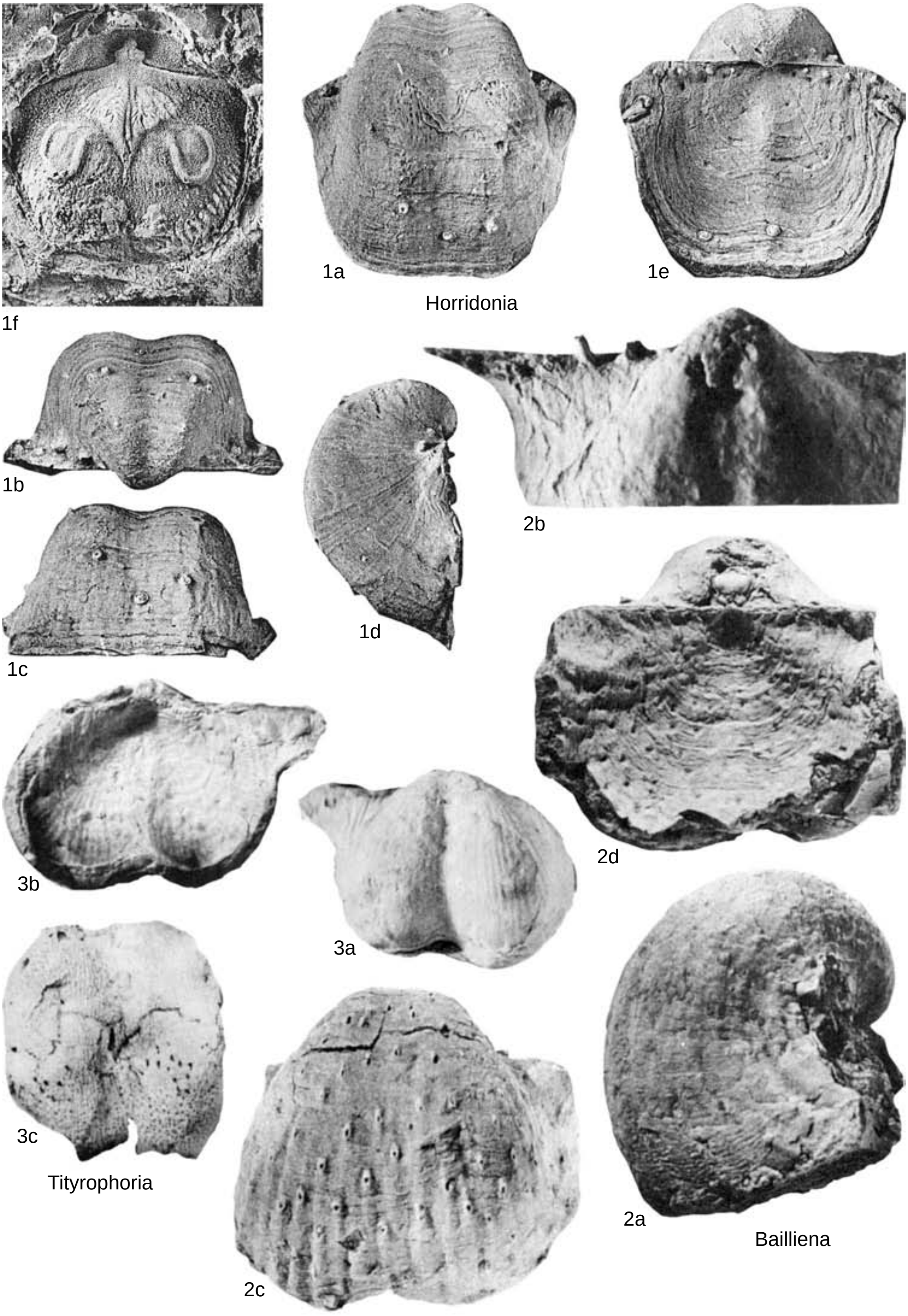


FIG. 323. Productidae (p. 480–483).

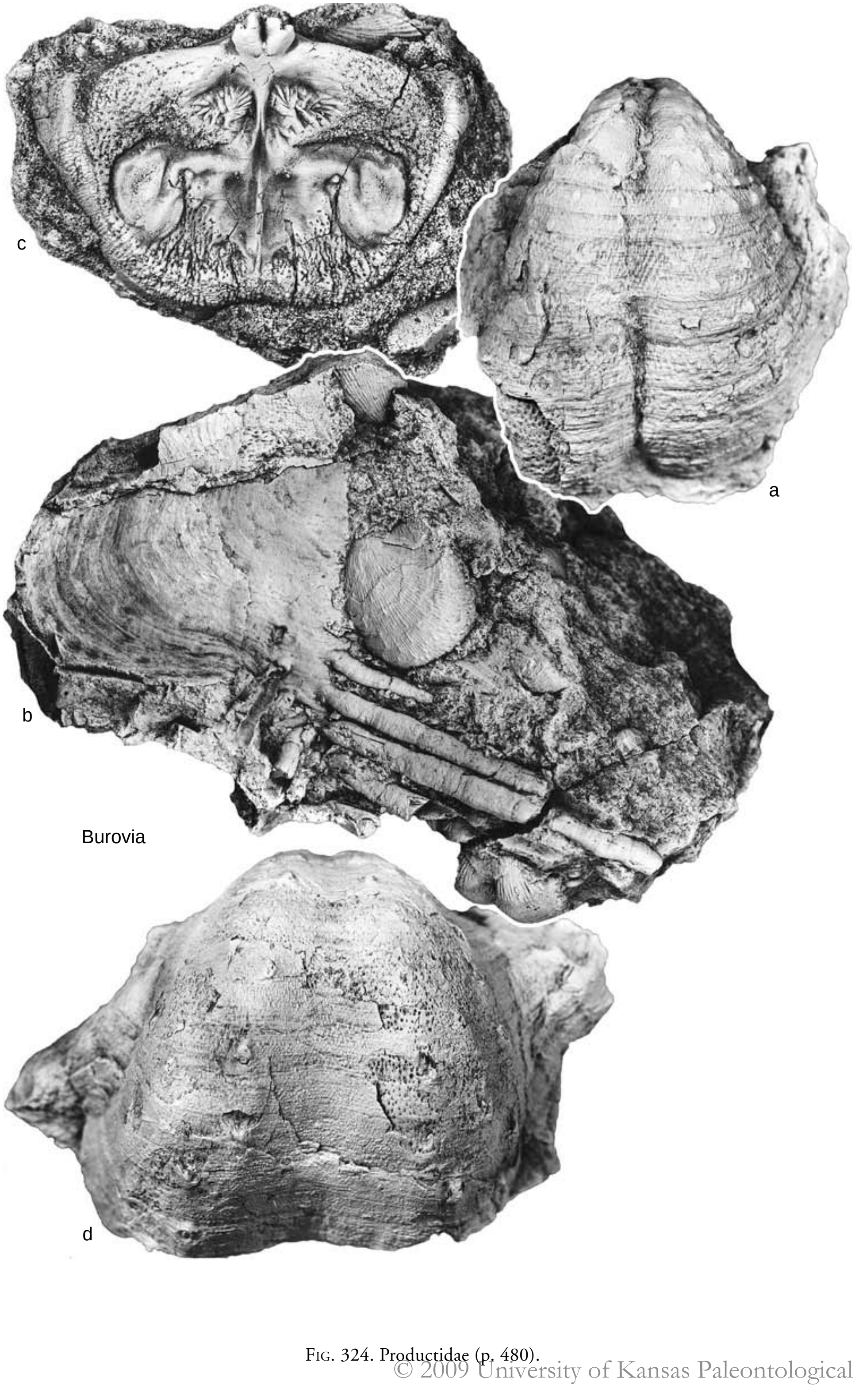


FIG. 324. Productidae (p. 480).

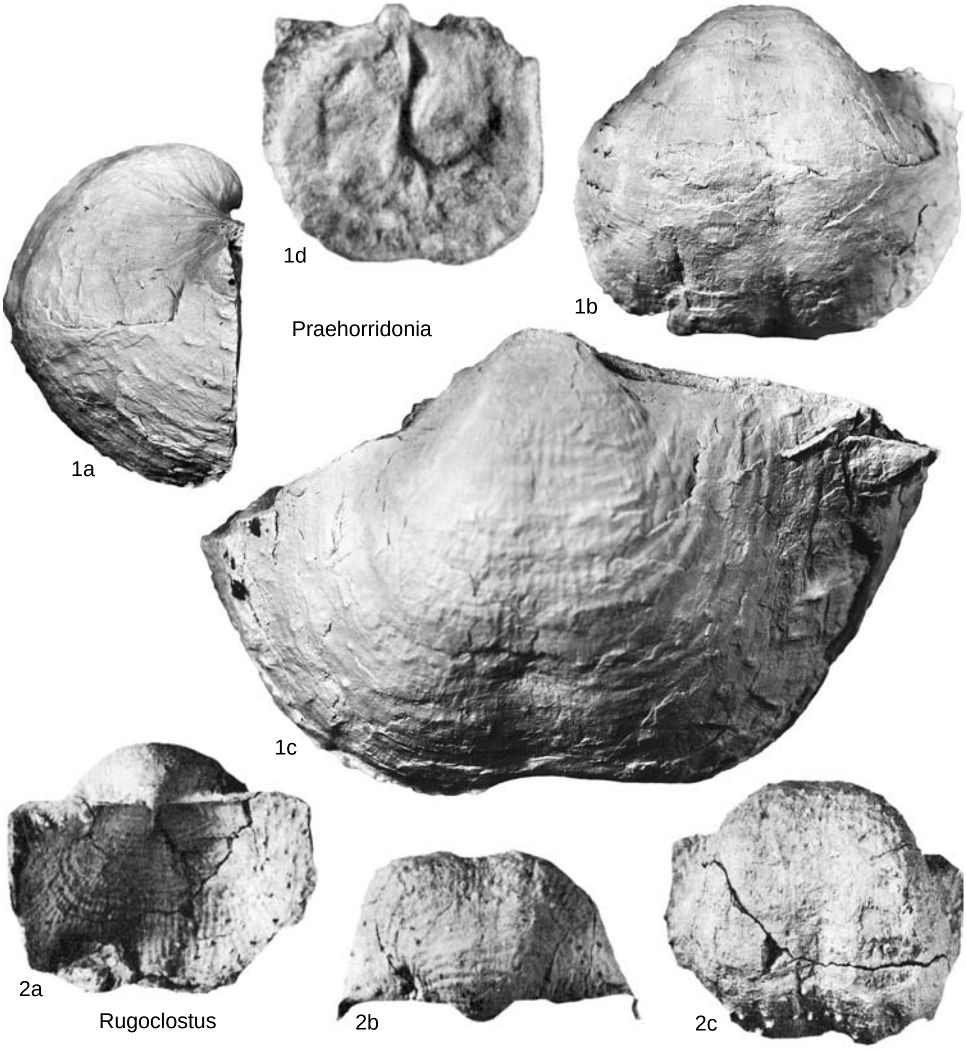


FIG. 325. Productidae (p. 480).

on ventral flange and trail, and in having only rare or absent dorsal spines. *Lower Permian:* Canada. ——FIG. 323,*3a–c.* **T. nelsoni,* Lower Permian, basal Tahkandit Formation, Yukon Territory; *a,b,* holotype, viewed ventrally, dorsally, GSC 26417, ×1; *c,* anteroventral view of internal cast, ×1 (Bamber & Waterhouse, 1971).

Tribe SEMIPRODUCTINI
McKellar, 1970

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 927, *ex* Semiproductinae MCKELLAR, 1970, p. 26] [=Lomatiphorinae ROBERTS, 1971, p. 84]

Medium size with deep corpus cavity, long trails; elongate spine bases arranged quincuncially on ventral disk, spines extending onto trail; ribs originate anteriorly on disks and always occur on trails; lateral ridges commonly short, no marginal structures; teeth in early genera. *Upper Devonian (Famennian)–Lower Carboniferous (lower Viséan).*

Semiproductus BUBLICHENKO, 1956, p. 99 [**S. minax;* OD]. Size medium, around 35 mm; outline subquadrate to elongate with broad sulcus anteriorly, ventral profile strongly convex; rugae weak or incomplete on disks with elongate spine bases; spines on weak ribs on ventral trail; lateral ridges prominent, but short. *upper Upper Devonian (upper Famennian)–lower Carboniferous (lower Tournaisian):* Ural Mountains, Asia, northern Australia.——

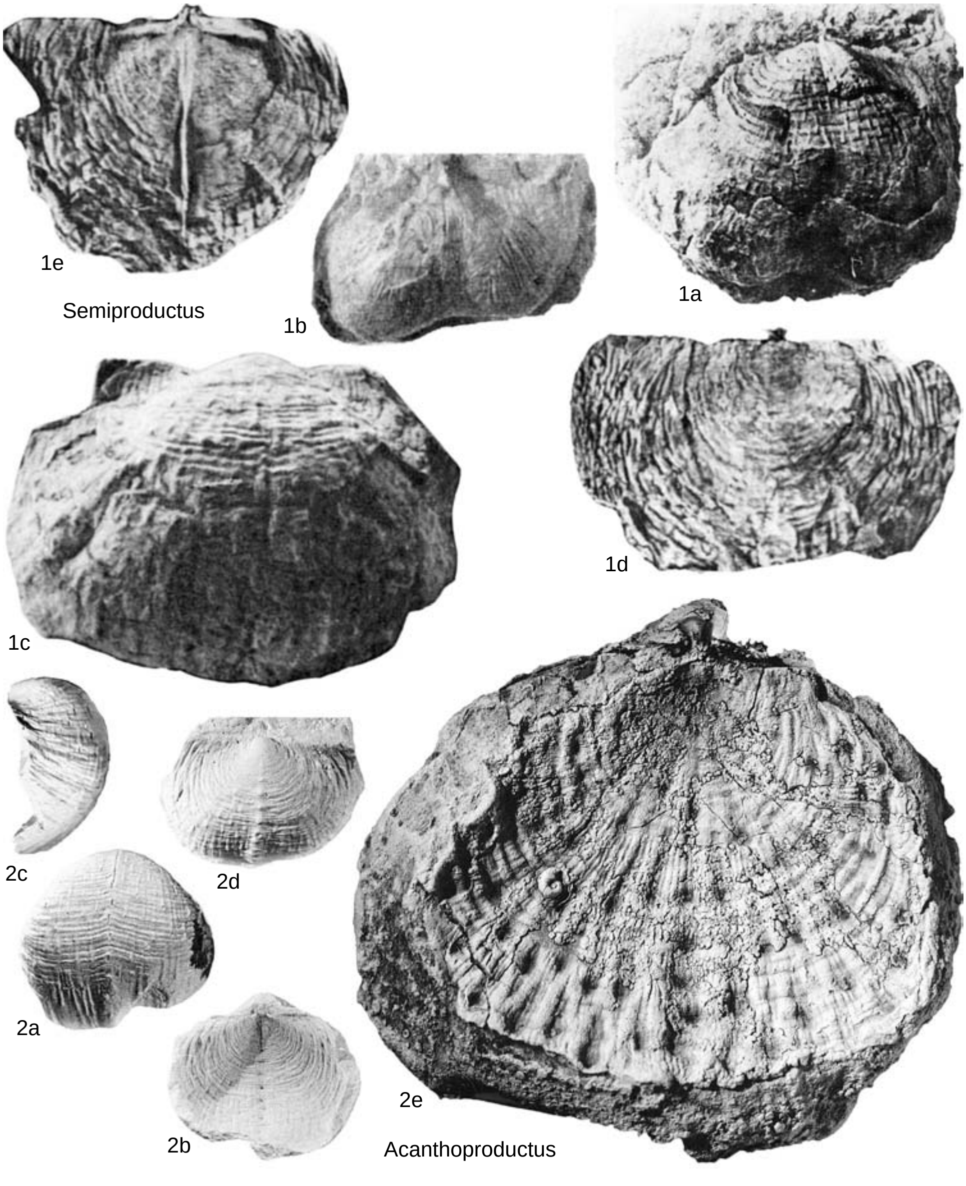


FIG. 326. Productidae (p. 483–485).

FIG. 326,*1a,b*. **S. minax,* lower Tournaisian, Kazakhstan; *a,* holotype, external mold of dorsal valve plus fragment of ventral valve to top right, ×0.8 (Bublichenko, 1956); *b,* internal mold of ventral valve, ×1 (Bublichenko, 1971).——FIG. 326,*1c–e*. *S. etheridgei* MCKELLAR, uppermost Famennian, Queensland; *c,* holotype, ventral valve exterior, GSQ F4088, ×1.5; *d,e,* replicas of dorsal valve exterior, interior, ×1.5 (McKellar, 1970).

Acanthoproductus MARTYNOVA, 1970, p. 59[49] [**A. bogdanovi;* OD]. Smaller medium size, 25 mm wide; rugae narrow on corpus, elongate spine bases become weak ridges only; dorsal valve with fine radial striations, median fold, sulcus; teeth. *Upper Devonian (Famennian):* Kazakhstan.——FIG. 326,*2a–e*. **A. bogdanovi,* Famennian, Kazakhstan; *a–c,* holotype, anteroventral, dorsal, lateral views, MGU 137/42, ×1; *d,* exfoliated dorsal valve interior, ×1 (Martynova, 1970); *e,* dorsal valve exterior, ×3 (Lazarev, 1990).

Lomatiphora Roberts, 1971, p. 84 [**L. aquila;* OD]. Ribbing complete, other than at beak, weaker on trail flanges of both valves; spines fine, scattered ventrally; sessile quadrifid cardinal process supported by adductor ridges; weak lateral ridges. *Lower Carboniferous (Tournaisian):* Australia.——Fig. 327,*1a–e.* **L. aquila,* lower Tournaisian, Bonaparte Gulf basin; *a,* latex replica of ventral valve exterior viewed posteroventrally, ×1.6; *b,* anteroventral view of ventral valve exterior, ×2; *c,* dorsal valve exterior, ×1.4; *d,* ventral valve internal mold, ×1.5; *e,* holotype, latex replica, dorsal valve interior, CPC 8261a, ×2 (Roberts, 1971).

Margaritiproductus Lazarev, 1986a, p. 67[47] [**Productus (Overtonia) celak* Nalivkin, 1937, p. 61; OD]. Small to medium size; moderately deep corpus, resembling *Semiproductus,* but ribbing confined to trails; teeth small. *Upper Devonian (upper Famennian):* central Asia.——Fig. 328,*3a,b.* **M. celak* (Nalivkin), upper Famennian, Kazakhstan; *a,* dorsal valve interior with fragment of ventral valve, small teeth, ×3; *b,* dorsal valve exterior, ×3 (Lazarev, 1986a).——Fig. 328,*3c. Margaritiproductus* sp.; part of dorsal valve interior showing socket, muscle scar, ×3 (new).

Nigerinoplica Lazarev, 1986a, p. 66[45] [**Plicatifera nigerina* Martynova, 1961, p. 87; OD]. Ribbing coarse, commonly confined anteriorly on trail; resembles *Spinocarinifera,* but with teeth. *Upper Devonian (Famennian):* Eurasia, ?North America.——Fig. 327,*3a–c.* **N. nigerina* (Martynova), upper Famennian, Kazakhstan; *a,* dorsal view of shell, ×3; *b,* partly exfoliated dorsal valve interior showing greatly reduced tooth, ×3 (Lazarev, 1986a); *c,* oblique view of dorsal interior, ×3 (Lazarev, 1990).

Seminucella Carter, 1987, p. 26 [**Spinocarinifera (Seminucella) parva;* OD]. Small, around 10 mm wide; resembles *Spinocarinifera,* but subparallel flanks, less even ribbing anteriorly; without peglike median lobe of cardinal process, perhaps larger cardinal process pit. *Lower Carboniferous (Tournaisian–lower Viséan):* northern North America.——Fig. 327,*2a–f.* **S. parva,* Tournaisian, western Alberta; *a–d,* holotype, viewed ventrally, anteriorly, posteriorly, laterally, GSC 63207, ×3; *e,* dorsal valve exterior, ×3; *f,* dorsal valve interior, ×3 (Carter, 1987).

Spinocarinifera Roberts, 1971, p. 100 [**S. adunata;* OD] [=*Nigeroplica* Nalivkin, 1975, p. 160 (type, *Productus niger* Gosselet, 1888, p. 632); ?*Productus flemingii* de Koninck, 1847a, p. 196, *non* Sowerby, 1812, p. 155, *sensu* Gosselet, 1880, pl. 6, fig. 16]. Small size; outline subquadrate with small but well-differentiated ears, profile strongly convex; dorsal valve weakly concave, geniculate with no spines; ribbing well formed anteriorly; cardinal process trifid with pit small, variable; cardinal ridges diverge from hinge close to ears. *Lower Carboniferous (lower Tournaisian):* Australia, Eurasia, northern Africa, North America.——Fig. 328,*1a–e.* **S. adunata,* Hastarian, Bonaparte Gulf, Australia; *a–d,* holotype viewed ventrally, dorsally, posteriorly, laterally, CPC 8564, ×2; *e,* dorsal valve interior, ×4 (Roberts, 1971).

Yanguania Yang Shi-pu, 1978, p. 107 [**Spinulicosta dushanensis* Yan Shi-pu, 1964, p. 87; OD]. Similar to *Spinocarinifera,* possibly differing by weak rugae posteriorly, weakly developed ribbing anteriorly. *Lower Carboniferous (Tournaisian):* southern China.——Fig. 328,*2a–d.* **Y. dushanensis,* lower Tournaisian, Yanguan, Guizhou; *a,* shell viewed anteroventrally, ×2; *b,* shell viewed dorsally, ×1; *c,d,* shell viewed anteriorly, laterally, ×1 (Yang Shi-pu, 1978).

Tribe TYLOPLECTINI
Termier & Termier, 1970

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Tyloplectidae Termier & Termier, 1970, p. 457]

Ribbed, other than at beak; additional striae dorsally; ventral spines large near hinge and on flanks, probably absent dorsally. *Lower Permian (Artinskian)–Upper Permian (Capitanian).*

Tyloplecta Muir-Wood & Cooper, 1960, p. 290 [**Productus scabriculus* mut. *nankingensis* Frech, 1911, p. 163; OD] [=*Nankinoproductus* Huang & Tseng, 1948, p. 254, *nom. nud.*]. Medium size, planoconvex with short adult trail; hinge equal to maximum width; elongate spine bases posteriorly, becoming ribs at midlength of corpus; rugae present posterolaterally on both valves; spines near hinge, scattered on venter; cardinal process with wide shaft; weak lateral ridges, ear baffles; shell substance thick. *Lower Permian (Artinskian–Kungurian):* China, southern Europe, ?Indonesia.——Fig. 329*a–g.* **T. nankingensis,* Lower Permian, Chihsian Formation, Sichuan; *a–c,* specimen viewed ventrally, posteriorly, laterally, ×1; *d,* shell viewed dorsally, ×1; *e,* ventral valve interior, ×1; *f,* dorsal valve interior, ×1; *g,* detail of dorsal valve external ornament, ×2 (Muir-Wood & Cooper, 1960).

Araxilevis Sarytcheva in Sarytcheva & Sokolskaya, 1965, p. 221 [**Productus intermedius* Abich, 1878, p. 27; OD]. Medium to large, ventral profile strongly convex with weak geniculation, anterior trail lamellose; median sulcus weak; ribbing absent, rugae weak on disks, ears; spine bases swollen, rounded posteriorly, elongate on ventral trail; dorsal valve weakly concave with short trail; cardinal process large, trifid; lateral ridges diverge slightly from hinge, continue weakly separating ears and to lateral margins; valves thick shelled, finely striate on exfoliated surfaces. *Upper Permian (upper Capitanian):* Transcaucasus.——Fig. 330,*1a–e.* **A. intermedius* (Abich), upper Capitanian, Transcaucasus; *a,b,* lectotype, viewed laterally, dorsally, LGE 24/99, ×1; *c,* anterior view, ×1; *d,* ventral view, ×1; *e,* dorsal valve interior, ×1 (Sarytcheva & Sokolskaya, 1965).

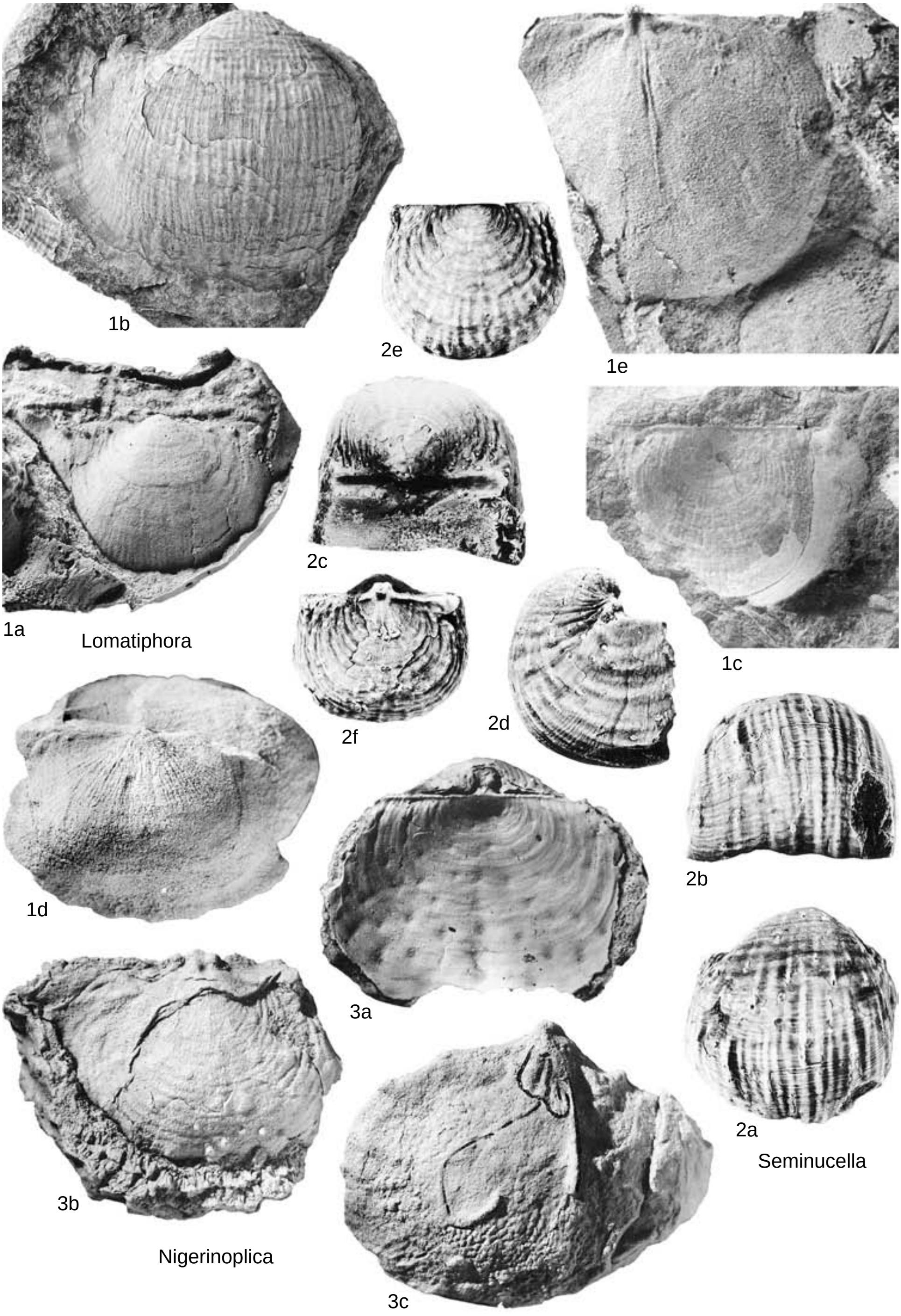


FIG. 327. Productidae (p. 485).

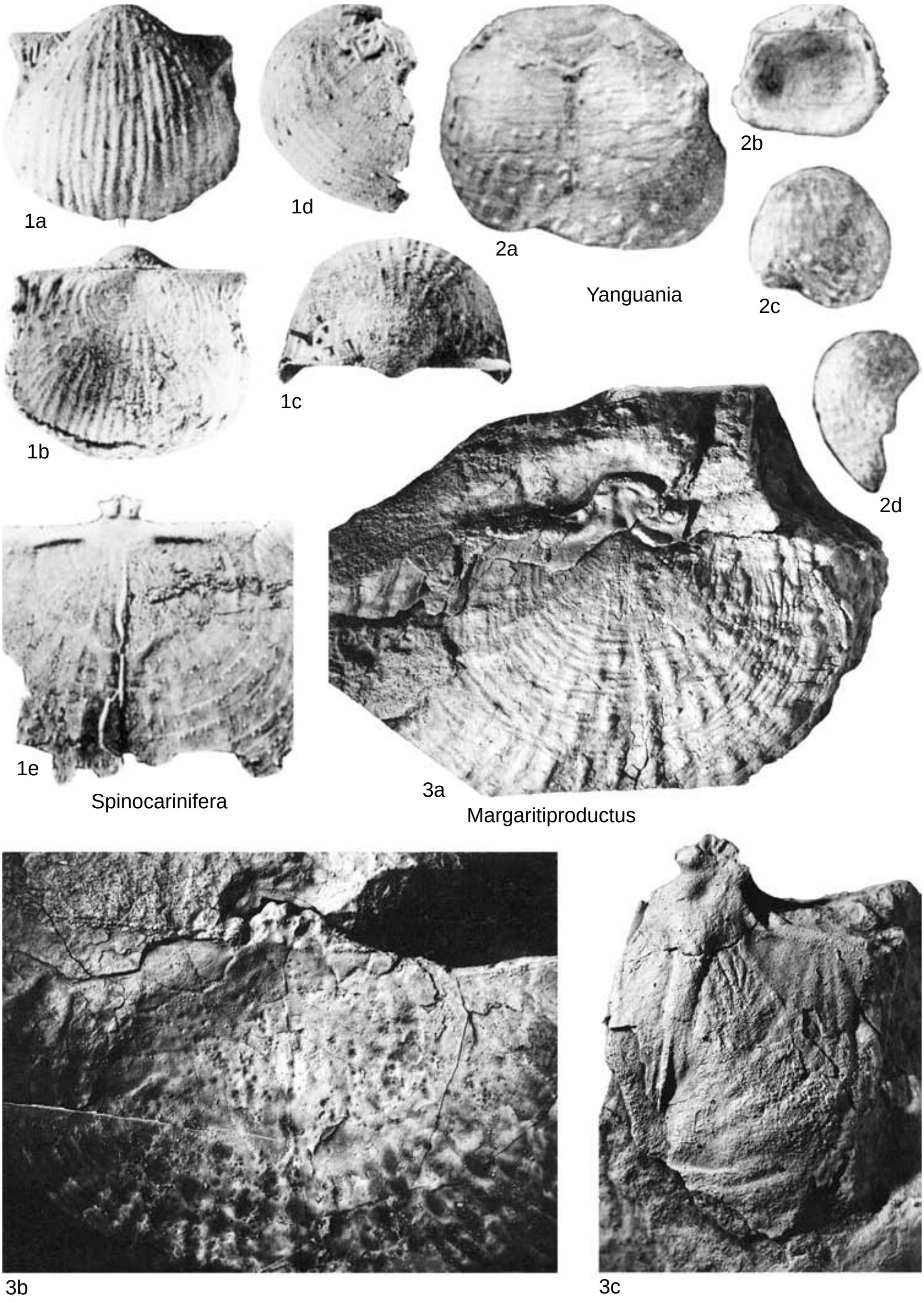


Fig. 328. Productidae (p. 485).

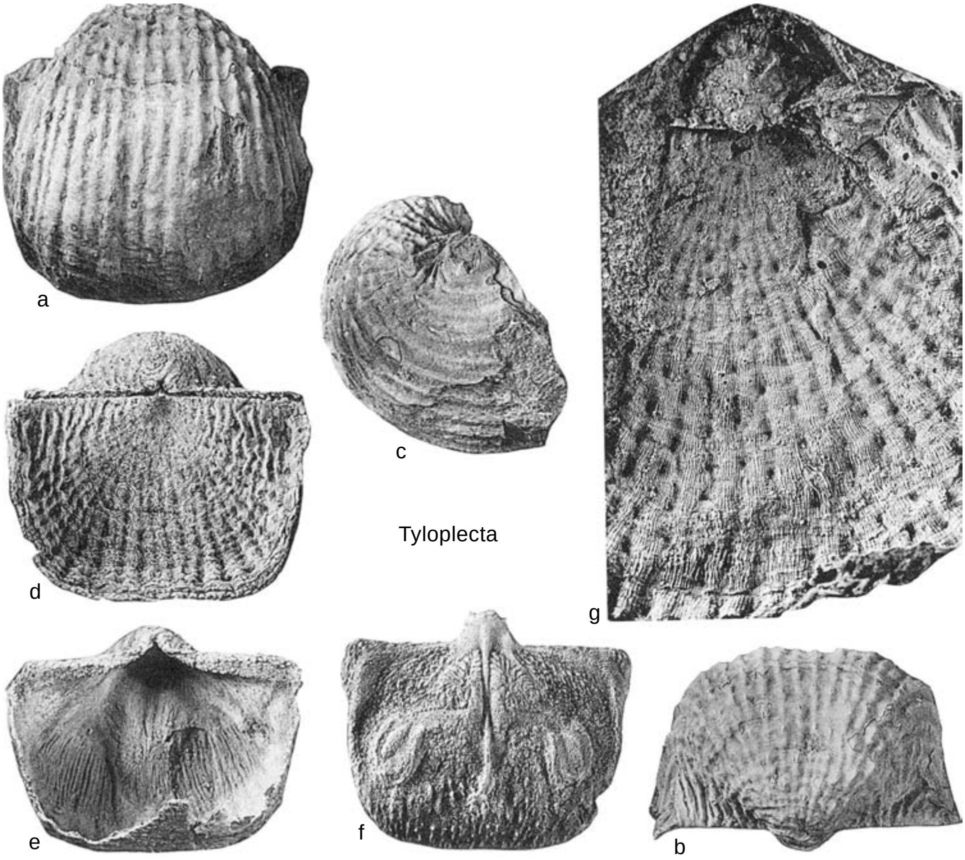


FIG. 329. Productidae (p. 485).

Pseudoantiquatonia ZHAN & WU, 1982, p. 98 [**P. mutabilis;* OD]. Medium size, planoconvex corpus with trails; spine distribution, ribbing as in *Tyloplecta,* but finer. *lower Upper Permian (Kazanian):* China (Xizang, Tibet).——FIG. 330,*2a–d.* **P. mutabilis,* Upper Permian, Xiala Formation, Xainza, Tibet; *a,b,* anterior, lateral views, ×1; *c,d,* deeply exfoliated dorsal valve interior, anterior, ×1 (Zhan & Wu, 1982).

Subfamily DICTYOCLOSTINAE Stehli, 1954

[Dictyoclostinae STEHLI, 1954, p. 316]

Medium to large size; 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. *Lower Carboniferous (Viséan)–Upper Permian (Tatarian).*

Dictyoclostus MUIR-WOOD, 1930, p. 103 [**Anomites semireticulatus* MARTIN, 1809, p. 7; OD]. Medium to commonly large; ribbing entire, ginglymus absent; spines clustered at ears, otherwise weak; cardinal ridges weak, not extended as ear baffles. *Lower Carboniferous (Viséan):* Europe, ?Asia, ?northern Africa.——FIG. 331*a–d.* **D. semireticulatus* (MARTIN), upper Viséan, Yorkshire; neotype, ventral, dorsal, posterior, lateral views, BMNH B45691, ×1 (new).——FIG. 331*e. D. pinguis* (MUIR-WOOD), upper Viséan, Yorkshire; wax replica of dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Auloprotonia MUIR-WOOD & COOPER, 1960, p. 273 [**A. aulacophora;* OD]. Somewhat resembling *Dictyoclostus* in ornament, but less strongly rugose, spines weaker, but with pair of strong spines on ears; trail with gutter; cardinal ridges extending to weak ear baffles. *Lower Carboniferous (middle Viséan):* North America.——FIG. 332,*1a–f.* **A. aulacophora,*

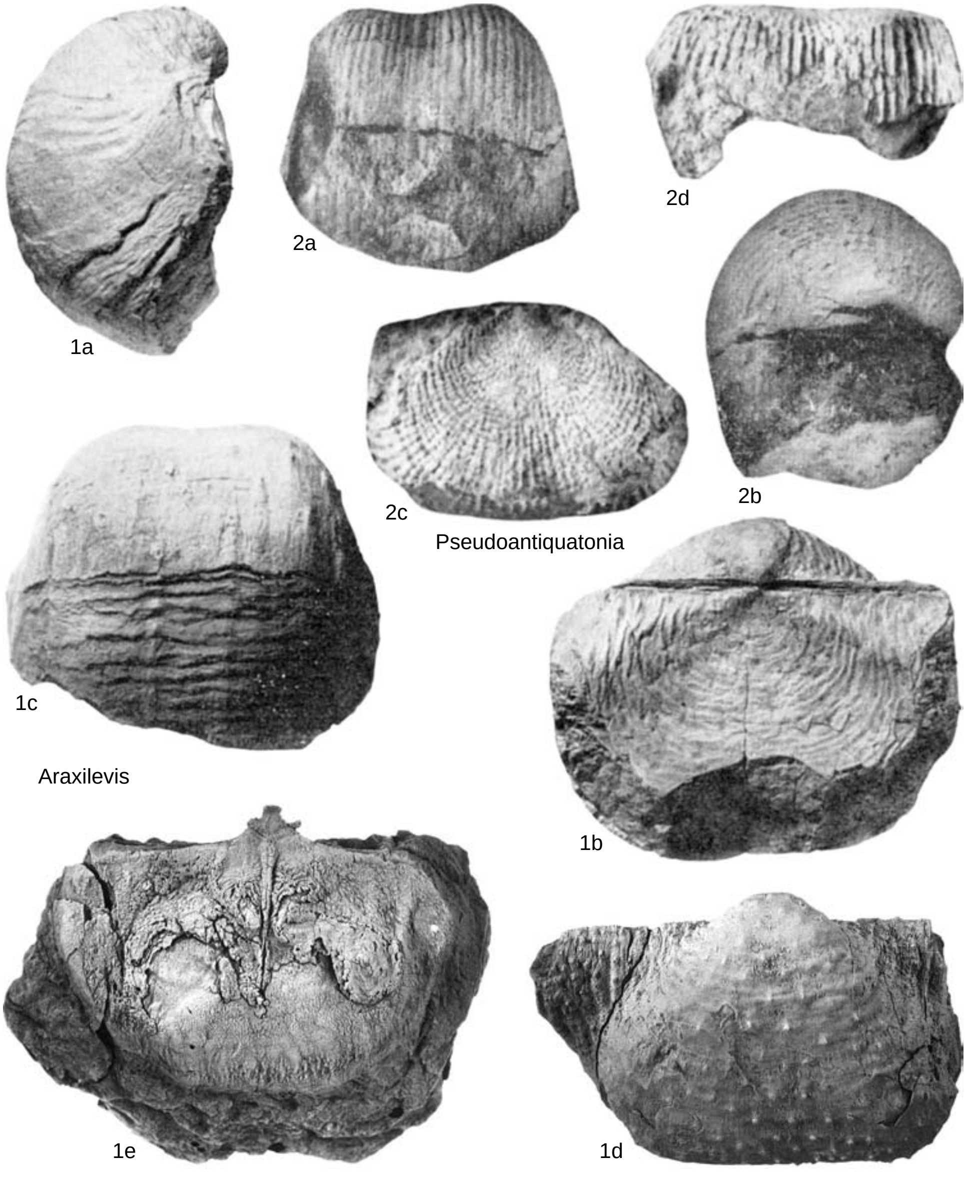


FIG. 330. Productidae (p. 485–488).

middle Viséan, Oklahoma; *a–c,* holotype, ventral, lateral, lateral oblique views, USNM 123976e, ×1; *d,* dorsal valve exterior, ×1; *e,* latex replica of dorsal valve interior, ×1; *f,* posterior view of ventral valve internal mold, ×1 (Muir-Wood & Cooper, 1960).

Callytharrella ARCHBOLD, 1985, p. 19 [**Dictyoclostus callytharrensis* PRENDERGAST, 1943, p. 13; OD]. Resembling *Stereochia,* but less strongly geniculate, weaker ear baffles, and with ribs on adult ears. *Lower Permian (Sakmarian):* Western Australia, Himalayas.——FIG. 333,*2a–e.* **C. callytharrensis* (PRENDERGAST), Lower Permian; *a,b,* ventral valve exterior, ventral valve viewed laterally, Jimba Jimba Calcarenite, Carnarvon Basin, Western Australia, ×1; *c–e,* ventral view, dorsal view, incomplete dorsal valve interior, Callytharra Formation, ×1 (Archbold, 1985).

Chaoiella FREDERICKS, 1933, p. 27 [**Productus semireticularis* var. *gruenewaldti* KROTOW, 1888, p. 546; OD]. Ears large; strong ventromedian sulcus,

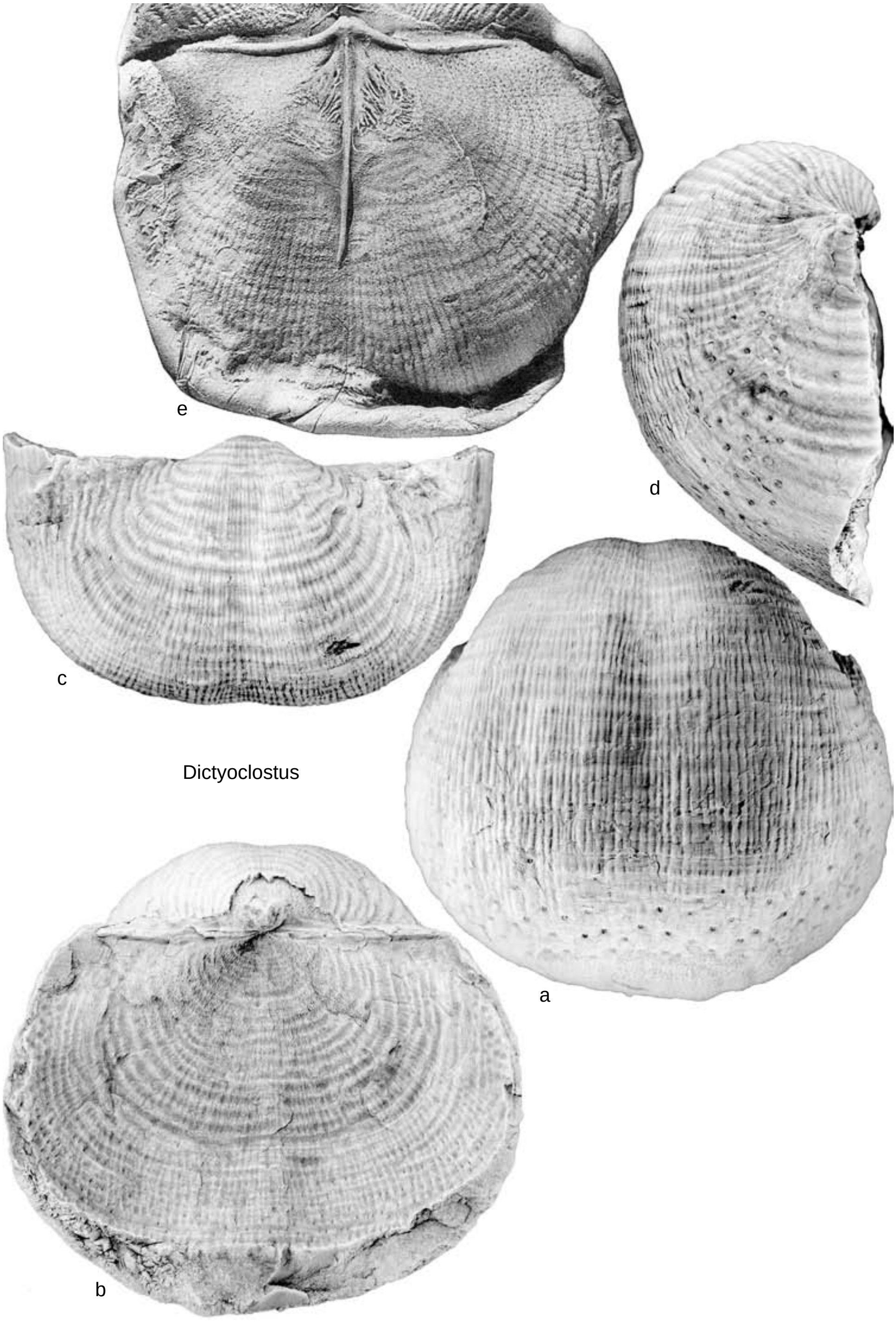


FIG. 331. Productidae (p. 488).

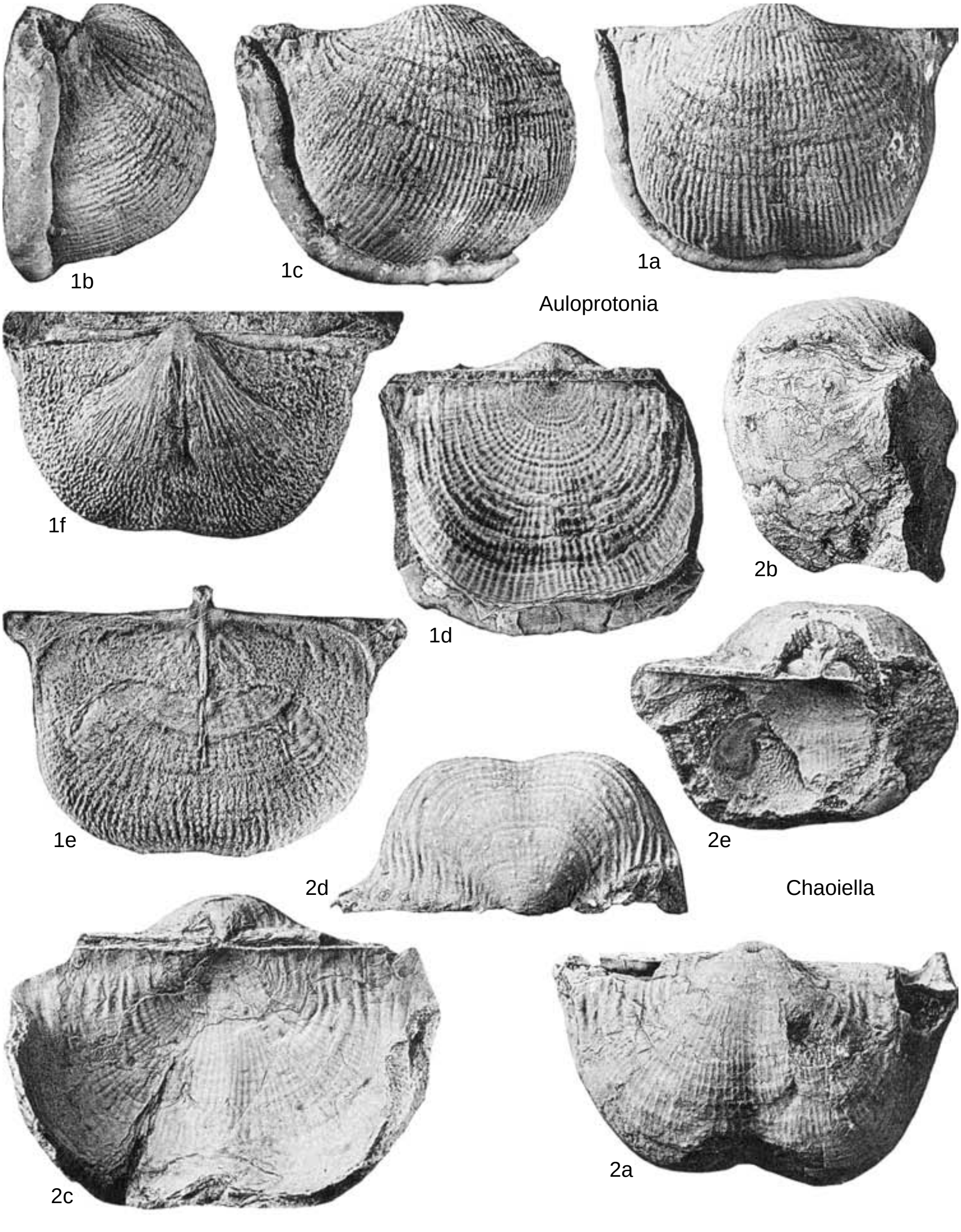


FIG. 332. Productidae (p. 488–491).

ribbing weak or absent on trails, reticulation relatively weak; strong cardinal ridges, dorsal adductor scars dendritic, placed relatively anteriorly. *Lower Permian (Artinskian):* Eurasia.——FIG. 332,*2a–e.* **C. gruenewaldti* (KROTOW), Artinskian, Russia; *a–c,* ventral, lateral, dorsal views of large specimen, ×1; *d,* posterior view of ventral exterior, ×1; *e,* posterodorsal view of specimen showing cardinal process, ×1 (Muir-Wood & Cooper, 1960).

Dasysaria COOPER & GRANT, 1969, p. 9 [**D. undulata;* OD]. Resembles *Reticulatia,* but with more densely scattered ventral spines and clusters on ears. *Lower Permian (Sakmarian):* USA.——FIG. 333,*1a–f.* **D. undulata,* Lower Permian, Hueco Formation, Texas;

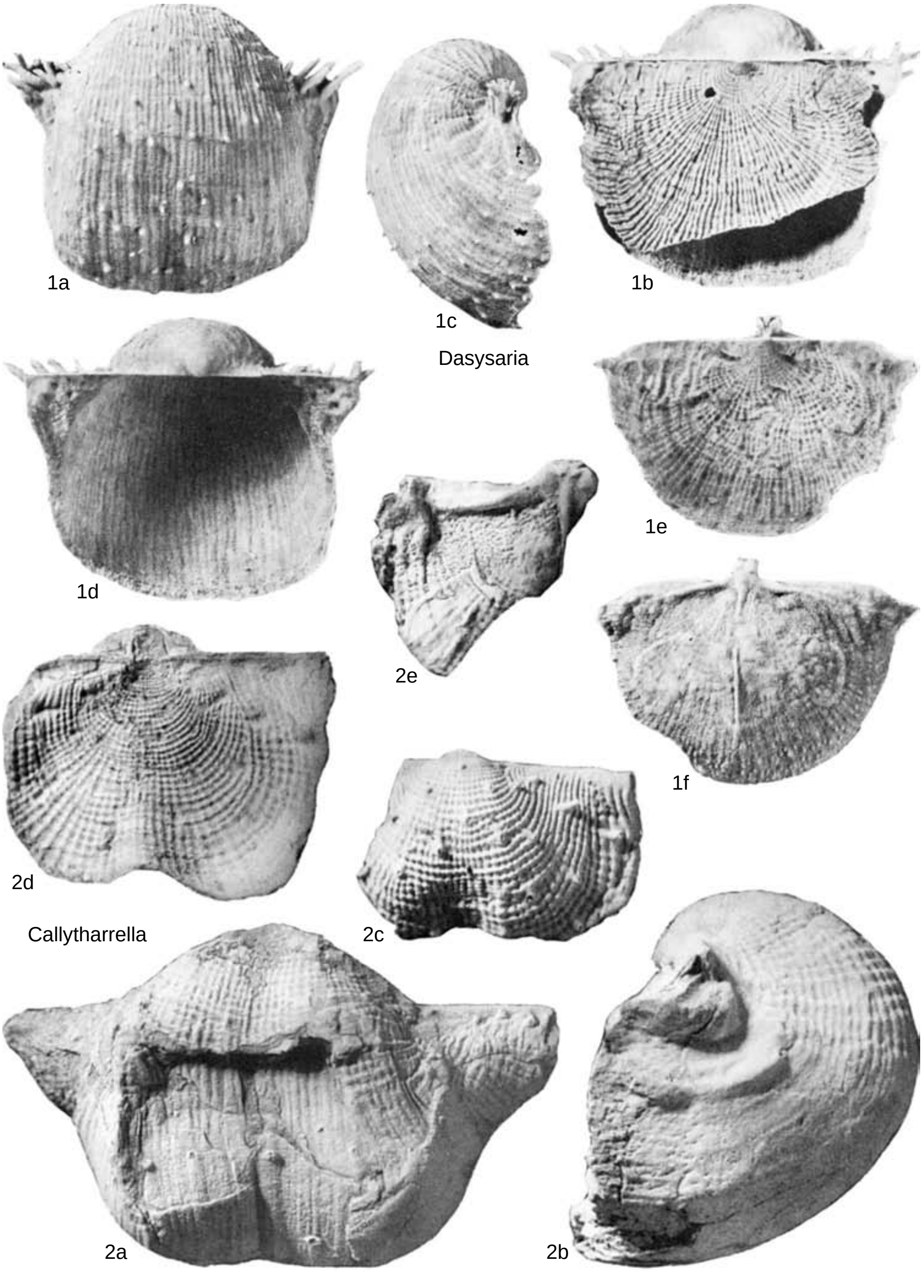


FIG. 333. Productidae (p. 489–492).

a–c, shell viewed ventrally, dorsally, laterally, ×1; *d,* ventral valve interior, ×1; *e,f,* dorsal valve exterior, interior, ×1 (Cooper & Grant, 1975).

Kunlunia WANG ZHI, 1983, p. 308 [**K. aspera;* OD]. Resembles *Liraplecta,* but differs in having large extended ears on which are clusters of spines. *Lower*

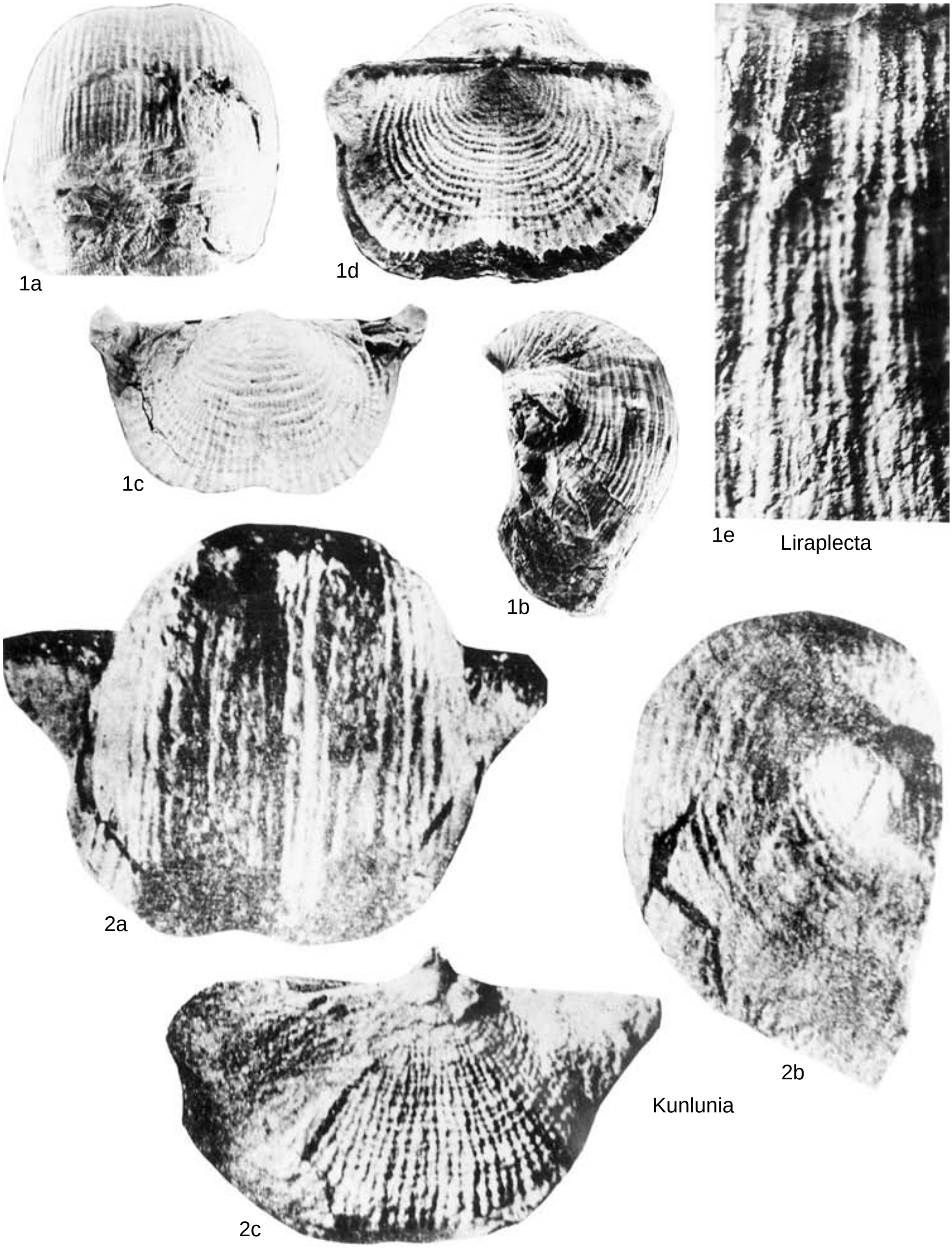


FIG. 334. Productidae (p. 492–494).

Permian (Asselian–Kungurian): China.——FIG. 334,*2a–c.* **K. aspera,* lower Chihsian, Kunlun Mountains, Xinjiang; *a,b,* holotype, ventral, lateral views, XBRB 355, repository unknown, ×1; *c,* incomplete dorsal valve interior showing part of external mold, ×1 (new).

Liraplecta JIN & SUN, 1981, p. 136 [**Productus richthofeni* CHAO, 1927b, p. 60; OD]. Resembles *Stereochia,* but has dorsal capillae plus normal ribbing. *Lower Permian (Asselian–Sakmarian):* China.——FIG. 334,*1a–e.* **L. richthofeni* (CHAO), Sakmarian, Lizha Formation, Tibet; *a,b,* anterior,

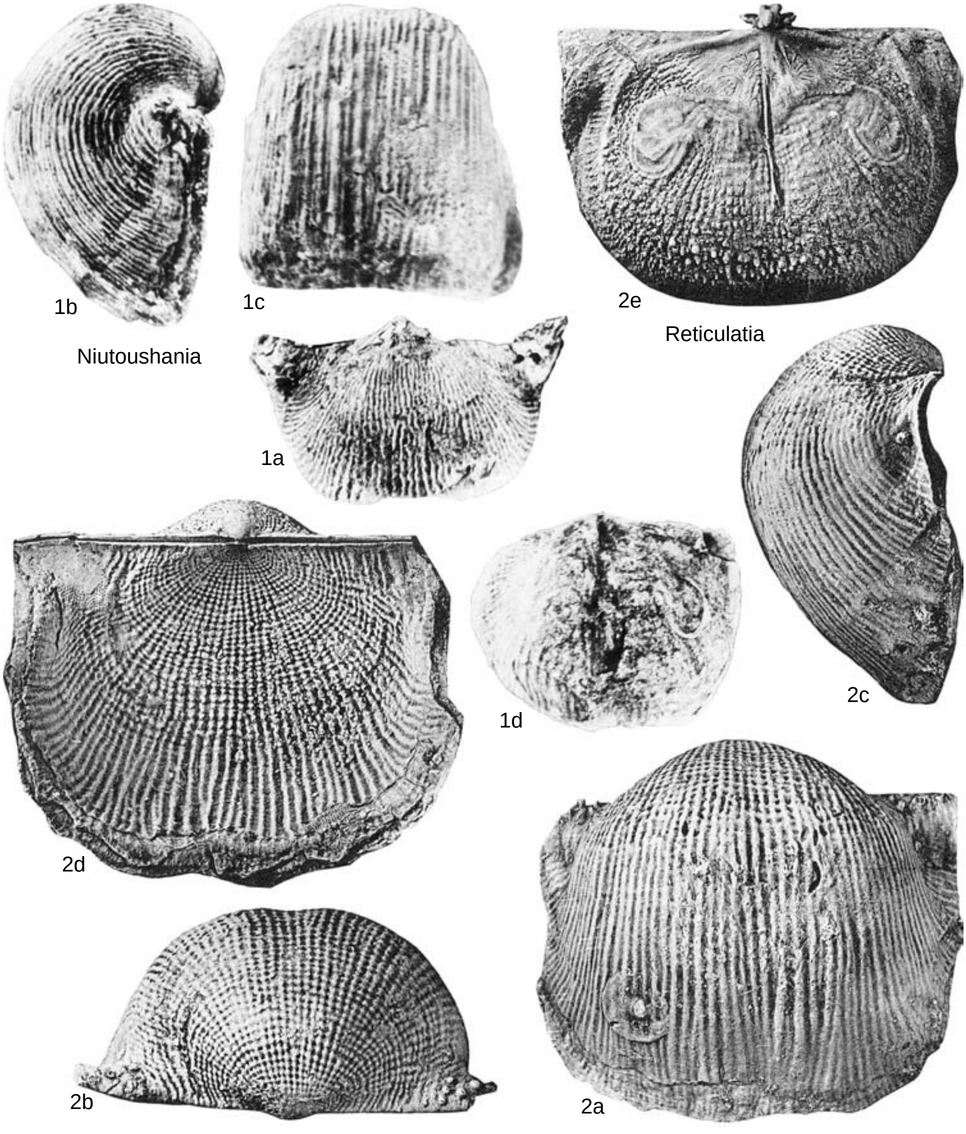


FIG. 335. Productidae (p. 494–496).

lateral views of specimen, ×1; *c,d,* ventral, dorsal views of shell, ×1; *e,* detail of dorsal external ornament, ×10 (Jin & Sun, 1981).

?**Niutoushania** LIAO, 1984, p. 281[284][**N. niutoushanensis;* OD]. Medium size, elongate with hinge wider than corpus width; profile strongly, evenly convex; median sulcus weak; dorsal valve with flattened posterior disk, geniculate, with trail; ribbing fine, somewhat irregular posteriorly, widening anteriorly; rugae seemingly absent; spines reported at hinge only; dorsal cardinal ridges extend as weak marginal ridge. Possibly a dictyoclostid but seemingly no reticulation. *Upper Permian (Tatarian):* China.——FIG. 335,*1a–d.* **N. niutoushanensis,* Longtan Formation, Anhui Province; *a,b,* holotype, viewed posteriorly, laterally, NIGP 71140, ×1; *c,* anterior view of shell, ×1; *d,* incomplete dorsal valve interior, ×1 (new).

Ozora CARTER, 1990, p. 226 [**O. genevievensis;* OD]. Spines ventral, near hinge, on flanks, rare on disk, but in concentric bands on trail with widened ribs; reticulation prominent posteriorly; adult dorsal disk with marginal ridges. *Lower Carboniferous (lower Viséan):* central North America.——FIG. 336,*1a–e.*

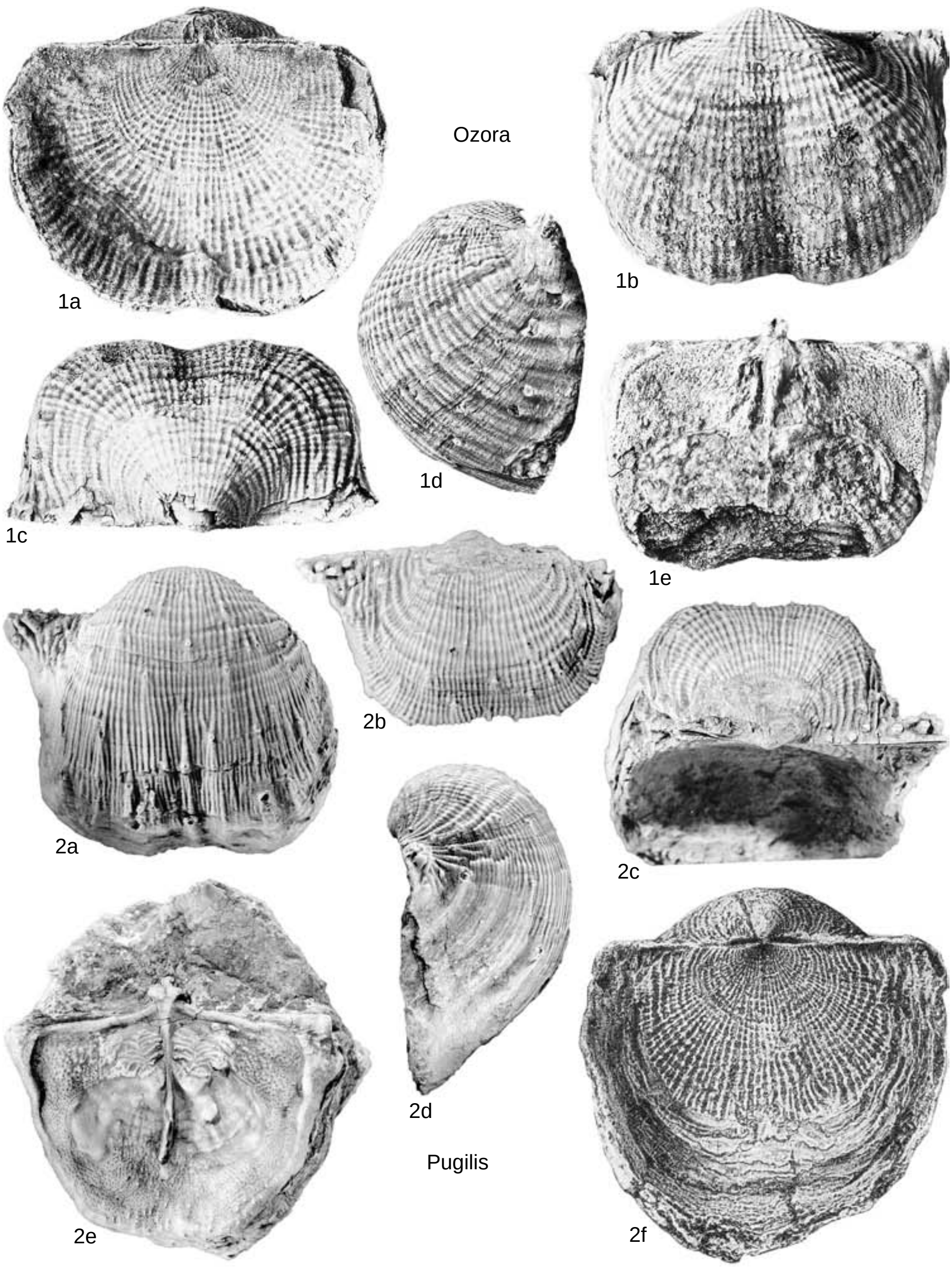


FIG. 336. Productidae (p. 494–496).

**O. genevievensis,* lower Viséan, Missouri; *a,* holotype, dorsal valve exterior, CMNH 34893, ×1; *b,c,* ventral valve exterior viewed ventrally, posteriorly, ×1; *d,* ventral valve viewed laterally, ×1; *e,* incomplete dorsal valve interior, ×1 (Carter, 1990).

Pugilis SARYTCHEVA, 1949, p. 104 [**Producta pugilis* PHILLIPS, 1836, p. 215; OD] [=*Pugilus* SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1952, p. 77, obj.]. Medium size; deep corpus; ribs regular posteriorly, but irregular and commonly weak on trails, enlarged or branched distal to spine bases; dorsal valve commonly lamellose on trail; lateral ridges strong, near hinge, continue as ear baffles and subperipheral ridge laterally. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* Europe, northern Africa.——FIG. 336,*2a–f.* **P. pugilis* (PHILLIPS); *a–d,* anterior, ventral, posterior, lateral views of shell, upper Viséan, north Wales, ×1; *e,* dorsal valve interior, Northumberland, ×1 (new); *f,* dorsal view of shell exterior showing series of dorsal trails, Serpukhovian, Renfrewshire, Scotland, ×1 (Muir-Wood & Cooper, 1960).

Reticulatia MUIR-WOOD & COOPER, 1960, p. 284 [**Productus huecoensis* KING, 1931, p. 68; OD]. Resembles *Dictyoclostus,* but differs in having ginglymus, lateral ridges near the hinge that may continue weakly as marginal ridges with endospines anteriorly. *Upper Carboniferous (Bashkirian)–Lower Permian (lower Artinskian):* North America, Europe, Asia.——FIG. 335,*2a–e.* **R. huecoensis* (KING), Lower Permian, Hughes Creek Shale, Nebraska; *a–d,* shell viewed ventrally, posteriorly, laterally, dorsally, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Rugatia MUIR-WOOD & COOPER, 1960, p. 285 [**Productus paraindicus* MCKEE, 1938, p. 241; OD]. Medium size, transverse with large, well-differentiated ears; median sulcus shallow, extending to valve margins; rugae weak on ears, some on dorsal disk; ribbing variable, originates anteriorly on disks, weak, irregular, coarse to strong anteriorly on corpus; spines thick, in lines separating umbo from ears, in clusters on ears, widely scattered on corpus, also with small spines; ventral adductor platform high; cardinal ridges lost at ears. *Lower Permian (Artinskian):* southern USA.——FIG. 337,*2a–e.* **R. paraindica* (MCKEE), Lower Permian, Leonard Formation, Texas; *a,b,* anterior, lateral views, ×1; *c,* dorsal view, ×1; *d,* dorsal valve interior, ×1; *e,* disarticulated dorsal, ventral valves, ×1 (Muir-Wood & Cooper, 1960).

Stereochia GRANT, 1976, p. 150 [**S. litostyla;* OD]. Medium size, widest at hinge; disks of both valves reticulate, trails costate; spines thick, but few, single on ears, venter; ventral adductor platforms raised, dendritic; diductor scars strongly striated; cardinal process trifid, shaft short, continuous with median septum; lateral ridges, ear baffles, latter strong in ventral valve. *Lower Permian (upper Artinskian):* Thailand, Indonesia, ?northeastern Asia.——FIG. 337,*1a–e.* **S. litostyla,* upper Artinskian, Ko Muk, Thailand; *a,b,* holotype, viewed laterally, dorsally, USNM 212592, ×0.75; *c,d,* ventral valve exterior, interior, ×1; *e,* dorsal valve interior, ×1 (Grant, 1976).

Subfamily BUXTONIINAE
Muir-Wood & Cooper, 1960

[Buxtoniinae MUIR-WOOD & COOPER, 1960, p. 255]

Size varied, but with corpus cavity deep; ribbing on trails, commonly on corpus; spines dense on both valves, but may be restricted anteriorly on dorsal valve; elongate cardinal process pit seldom absent; dorsal muscle scars separated from hinge region. *Lower Carboniferous (Tournaisian)–upper Lower Permian (Roadian).*

Tribe BUXTONIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 928, *ex* Buxtoniinae MUIR-WOOD & COOPER, 1960, p. 255] [=Kochiproductini LAZAREV, 1985, p. 67]

Dorsal trail commonly short, bordering structures (flanges) sporadic; ribs cover both valves, other than in Tournaisian, when smooth posteriorly; rugae irregular, may dominate ribs; spines on ventral valve uniformly distributed, commonly from swollen bases; buttress plates and pit present, but variable. *Lower Carboniferous (Tournaisian)–Lower Permian (Asselian, ?Sakmarian).*

Buxtonia THOMAS, 1914, p. 259 [**Anomites scabriculus* MARTIN, 1809, p. 8; OD, species declared invalid, ICZN, 1956a; =*Productus scabriculus* J. SOWERBY, 1814 in 1812–1815, p. 157; SD, ICZN, Opinion 420, 1956b, p. 143]. Medium size; ventral posterior ribbing characterized by swollen elongate spine bases; cardinal ridges to ears, cardinal process narrow, dorsally reflexed. *Carboniferous (Viséan–Serpukhovian):* Europe, America, Australia, ?Far East.——FIG. 338,*3a–c.* **B. scabricula* (J. SOWERBY), upper Viséan, Derbyshire; *a–c,* lectotype, ventral, dorsal, lateral views, BMNH B 60954, ×1 (new).——FIG. 338,*3d,e. Buxtonia* sp., Lower Carboniferous, Pendleian, Northumberland; *d,* dorsal view of internal mold, ×1; *e,* latex replica of dorsal valve interior, ×1.5 (new).

?Bellaclathrus WINTERS, 1963, p. 26 [**B. spinosus;* OD]. Medium size, corpus outline subquadrate; corpus profile almost planoconvex with strong dorsal geniculation; trails short; ventral sulcus weak; disks reticulate; spines fine on both valves plus rows of thick spines at ventral ears; cardinal process trifid with short shaft internally; lateral ridges reach ears, medium septum divided posteriorly. *Lower Permian:* USA.——FIG. 338,*1a–f.* **B. spinosus,* Lower Permian, Fort Apache Limestone, Arizona; *a–c,* holotype, viewed ventrally, dorsally, laterally, AMNH 27995/3:1, ×1; *d,* ventral view, ×1; *e,* part of dorsal valve interior, ×2; *f,* exterior showing cardinal process, ×3 (Winters, 1963).

Buxtonioides MENDES, 1959, p. 43 [**Productus amazonicus* KATZER, 1903, p. 264; OD] [=*Gemmulicosta* WATERHOUSE in BAMBER & WATERHOUSE, 1971, p. 210 (type, *G. gemma;* OD)]. Similar to *Kochiproductus,* but apparently lacking bordering flange, internal ventral posteromedian ridge, and without adult buttress plates. *Upper Carboniferous*

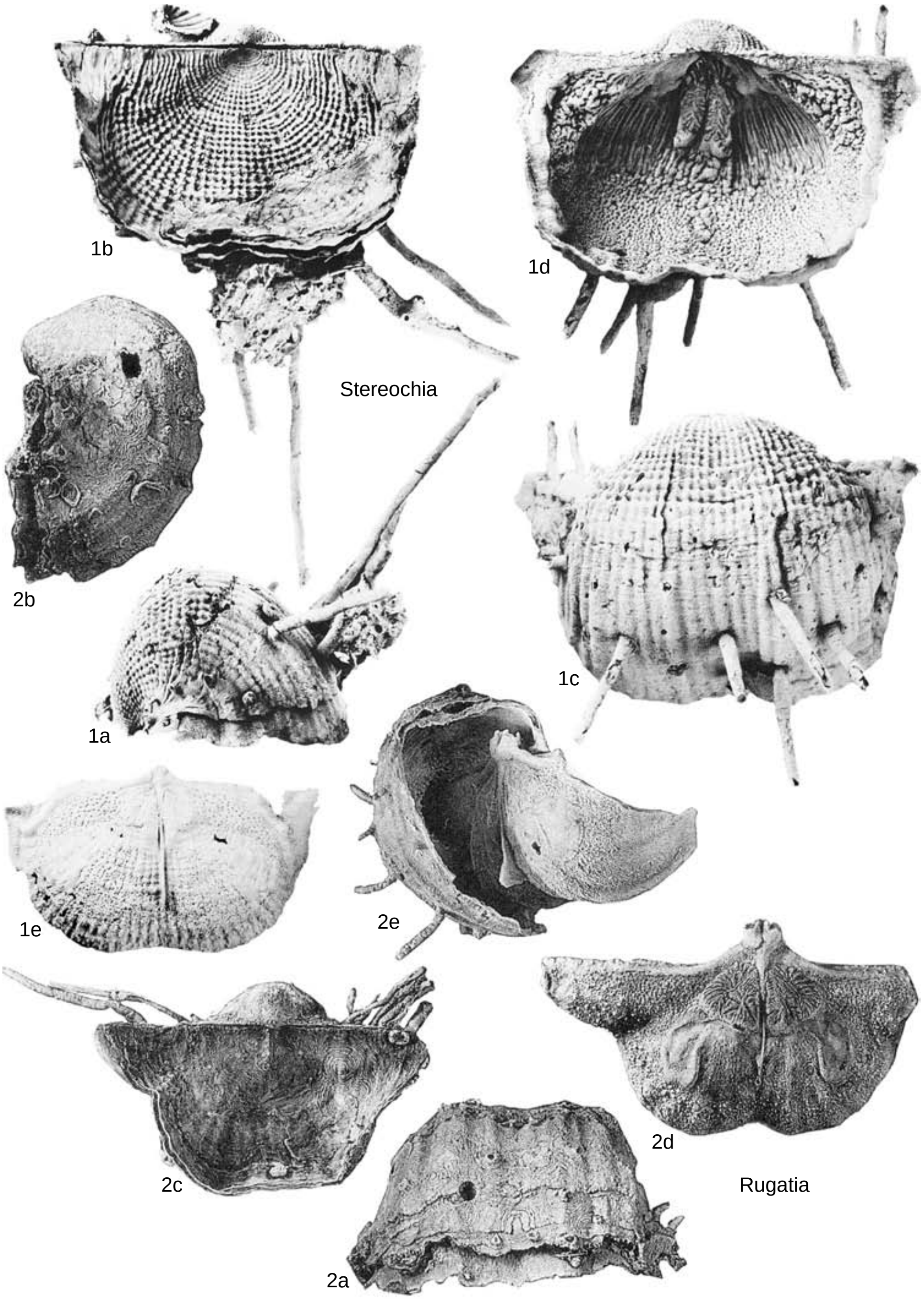


FIG. 337. Productidae (p. 496).

(Bashkirian–Gzhelian): South America, Canada, Russia.——FIG. 339*a–c.* **B. amazonicus* (KATZER), Morrowan–Desmoinesian, Brazil; *a,b,* ventral, dorsal views of complete specimen, ×1; *c,* details of ventral valve exterior, ×5 (Mendes, 1959).——FIG. 339*d. B. gemma* WATERHOUSE, Moscovian, western

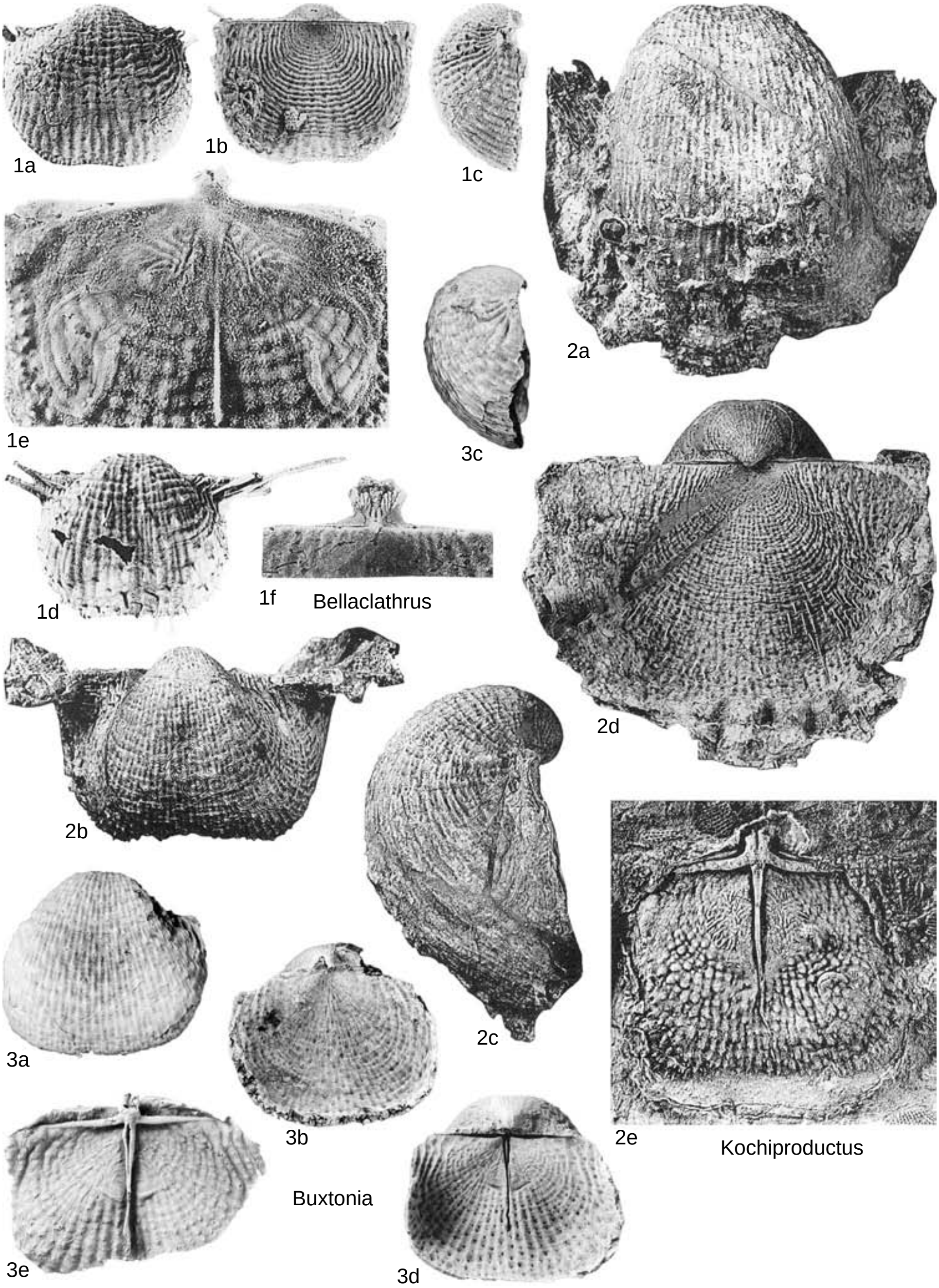


FIG. 338. Productidae (p. 496–500).

Alberta; ventral view of ventral valve, ×1 (Bamber & Waterhouse, 1971).——FIG. 339*e. B. gjeliensis* (IVANOV), Gzhelian, Gzel, near Moscow; dorsal valve exterior plus interior of ventral umbo showing cardinal process, lack of ventral ridge, ×1 (Lazarev, 1990).

Flexaria MUIR-WOOD & COOPER, 1960, p. 258 [**Productus arkansanus* GIRTY, 1910, p. 216; OD].

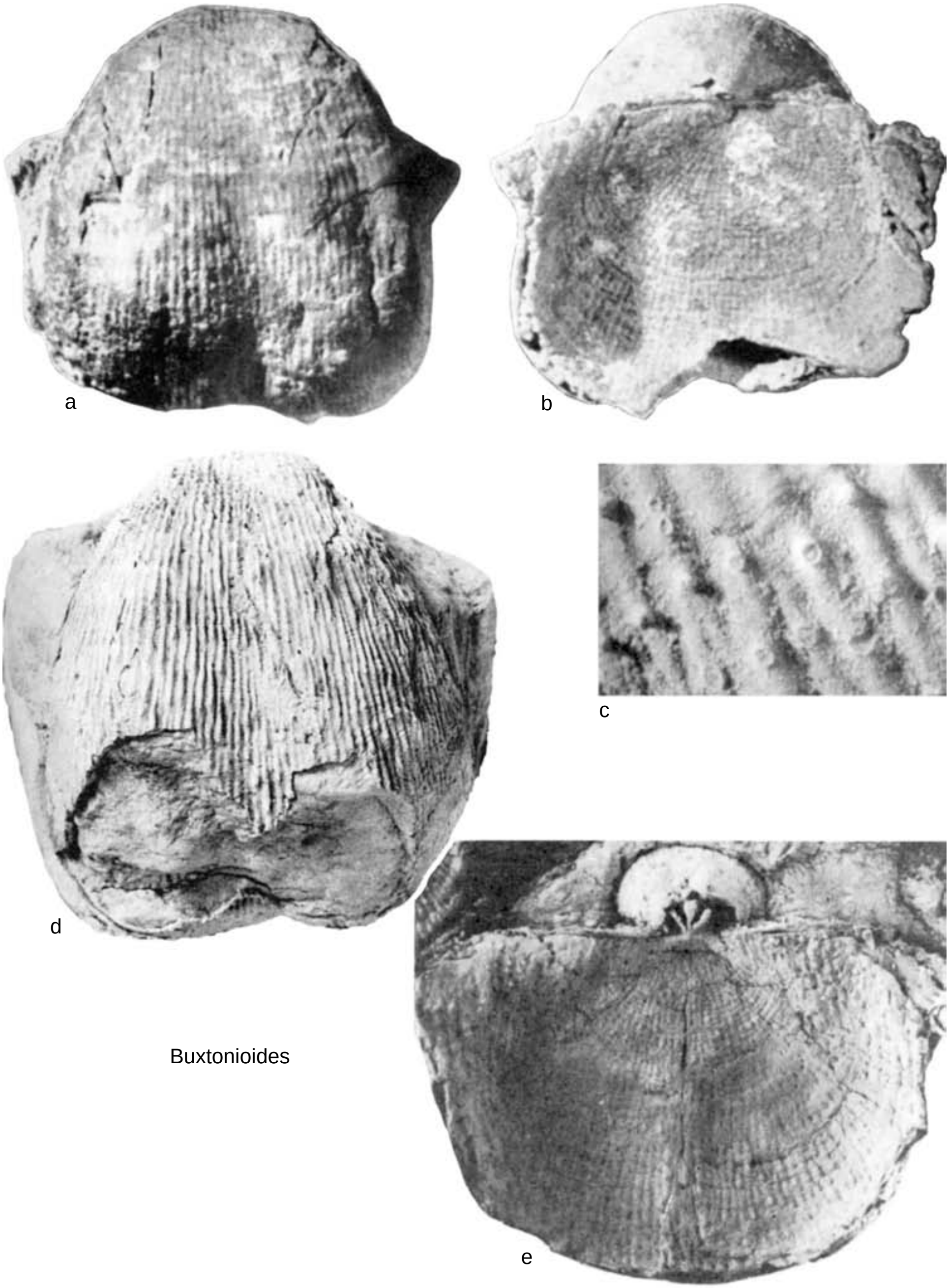


FIG. 339. Productidae (p. 496–498).

Resembles *Buxtonia,* but differing in its flat dorsal disk, geniculate trail; short lateral ridges, more elongate adductor muscle scars. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* North America.——FIG. 340,*2a–f.* **F. arkansana* (GIRTY), upper Viséan–lower Serpukhovian; *a,* dorsal view of complete specimen, Missouri, ×1; *b–d,* ventral, posterior, lateral views of complete specimen, Missouri,

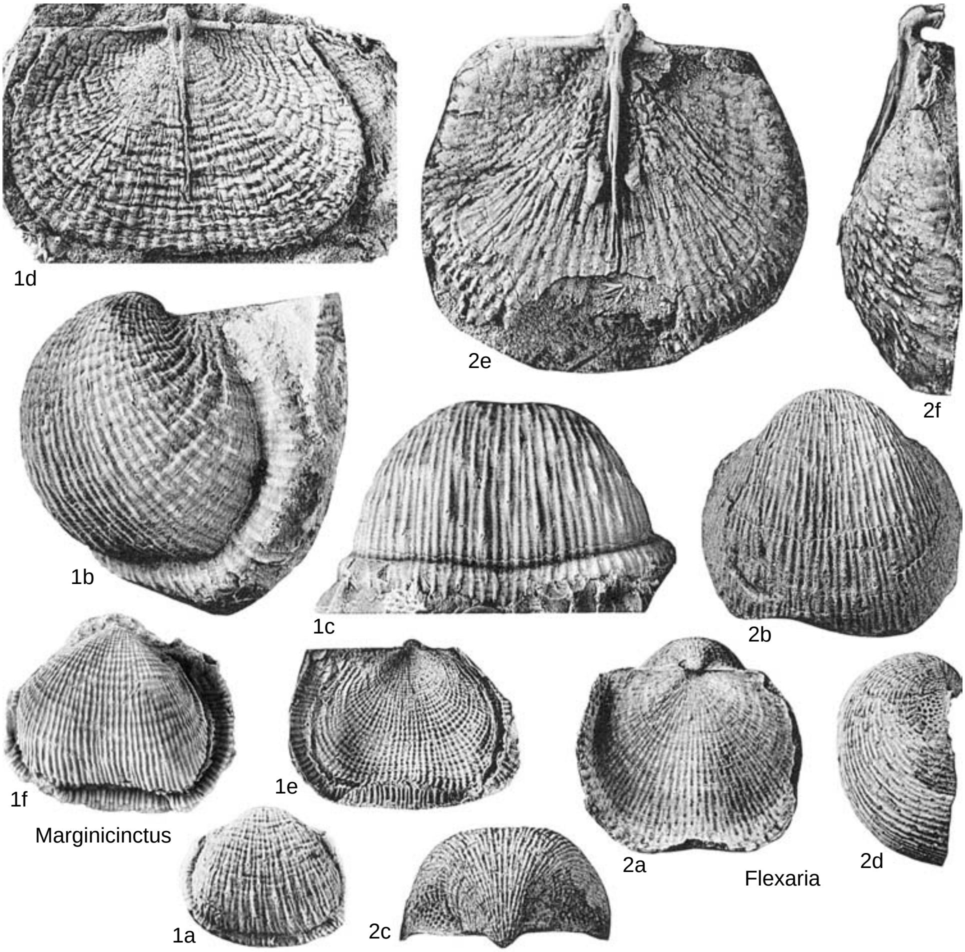


FIG. 340. Productidae (p. 498–501).

×1; *e,* dorsal valve interior, Oklahoma, ×2; *f,* lateral view of dorsal valve, Oklahoma, ×2 (Muir-Wood & Cooper, 1960).

Kochiproductus DUNBAR 1955, p. 107, *nom. nov. pro. Tschernyschewiella* FREDERICKS, 1924, p. 20, *non* VON TOLL, 1899 [**Productus porrectus* KUTORGA, 1844, p. 96; SD MUIR-WOOD & COOPER, 1960, p. 260]. Medium to large, with large ears, commonly with anterolateral flange; ribbing weak on ventral valve, accentuated by closely spaced elongate spine bases; rugae more prominent on dorsal valve; spines recumbent from swollen bases, semierect on ears and ventral trail, cover dorsal valve; low ventral median ridge from umbo to anterior of muscle field; cardinal ridges long, buttress plates with pit in adults. *Lower Permian (Asselian, ?lower Sakmarian):* Arctic regions, Mongolia, North and South America.——FIG. 338,*2a–e. K. peruvianus* (D'ORBIGNY), Lower Permian, Hueco Formation, Texas; *a–d,* shell viewed ventrally, posteriorly, laterally, dorsally, ×0.75; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Labriproductus COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Worthenella* GIRTY, 1938b, p. 442, *non* WALCOTT, 1911 [**Productus wortheni* HALL, 1858a, p. 638; OD]. Smaller than *Buxtonia,* but with stronger ribs, small bordering flange, no ventromedian sulcation. *Lower Carboniferous (upper Tournaisian–Viséan):* central North America.——FIG. 341,*1a–e.* **L. wortheni* (HALL), upper Tournaisian, Missouri; *a–d,* ventral, lateral, anterior, posterior views of specimen, ×2; *e,* latex replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Marginicinctus SUTTON, 1938, p. 561 [**Productus marginicinctus* PROUT, 1857, p. 43; OD]. Resembles *Buxtonia,* but smaller, with bordering reflexed flange, internal marginal ridges in both valves. *Lower Carboniferous (middle Viséan):* North

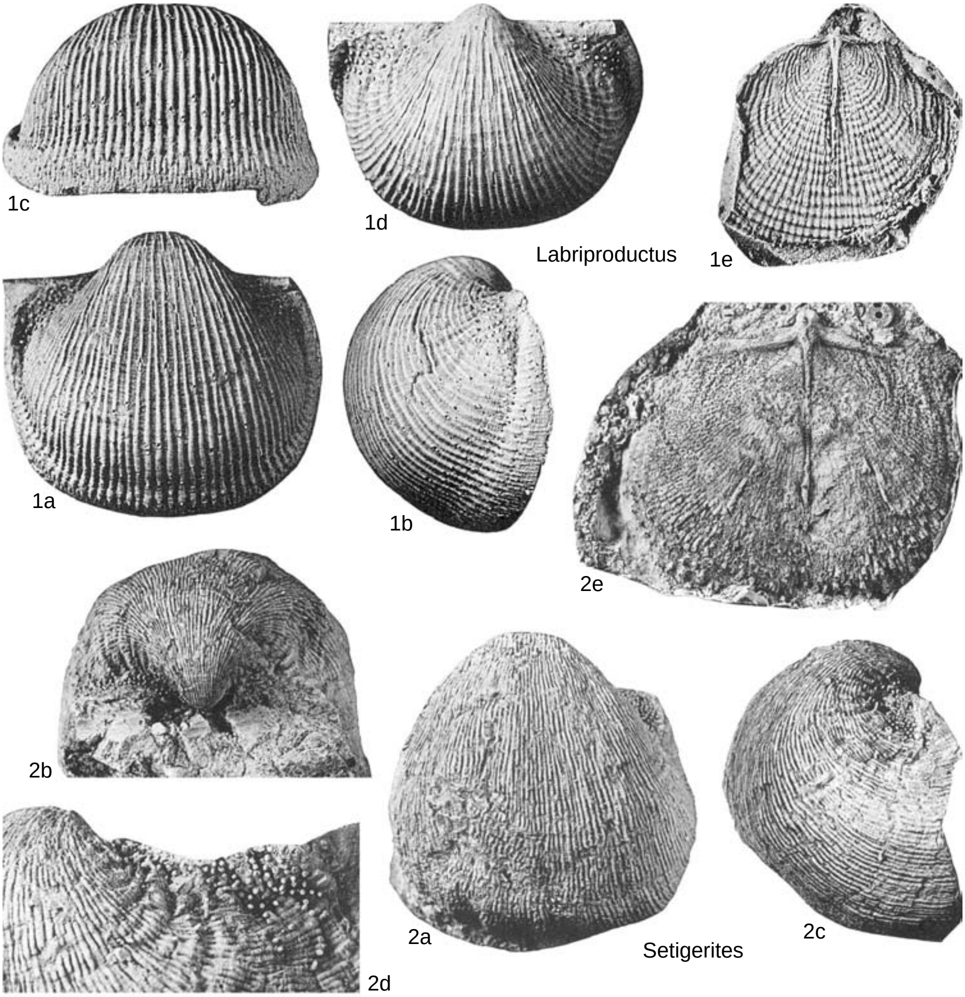


FIG. 341. Productidae (p. 500–501).

America, Europe.——FIG. 340,*1a–d*. **M. marginicinctus* (PROUT), middle Viséan; *a,* ventral valve exterior, Missouri, ×1; *b,c,* oblique lateral, anterior views of specimen, Iowa, ×2; *d,* latex replica of dorsal valve interior, Tennessee, ×2 (Muir Wood & Cooper, 1960).——FIG. 340,*1e,f*. *M. projectus* (MUIR-WOOD), Viséan, Cork; *e,* dorsal valve exterior, ×1; *f,* ventral view of shell with flange, ×1 (Muir-Wood & Cooper, 1960).

Setigerites GIRTY, 1939, p. 141, *nom. nov. pro Setigerella* GIRTY, 1938b, p. 434, *non* EHRENBERG, 1872 [**Productus setigerus* HALL, 1858a, p. 638; *=P. setiger, nom. correct.* MUIR-WOOD & COOPER, 1960, p. 197; OD]. Size medium; trail commonly with gutter, rugae at umbonal flanks weak; ribbing fine, entire, associated with slightly swollen spine bases; spine groups posteriorly and on ears; cardinal process pit small, lateral ridges only slightly divergent from hinge, no marginal ridges. *Lower Carboniferous (upper Tournaisian–lower Serpukhovian):* North America, Eurasia, ?northern Africa.——FIG. 341,*2a–e*. **S. setiger* (HALL), upper Tournaisian; *a–c,* ventral, posterior, lateral views of ventral valve, Indiana, ×1, *d,* posterolateral region showing spine bases on ears, Indiana, ×2; *e,* latex replica of dorsal valve interior, Missouri, ×2 (Muir-Wood & Cooper, 1960).

Tribe TOLMATCHOFFIINI
Sarytcheva, 1963

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 928, *ex* Tolmatchoffiidae SARYTCHEVA in SARYTCHEVA & others, 1963, p. 168] [Spinifronsinae WATERHOUSE, 1981, p. 82]

Dorsal trail of varied length; ribbing covering both valves, other than in lower

Tournaisian, when umbos smooth; rugae commonly absent, spines on ventral valve not uniformly distributed; commonly with elongate cardinal process pit. *Lower Carboniferous (Tournaisian)–upper Lower Permian (Roadian).*

Tolmatchoffia Fredericks, 1933, p. 28 [**Productus robustus* Tolmatchoff, 1924, p. 230; OD]. Medium size; almost planoconvex, deep corpus, gently spreading trail; ribbing entire, becoming wider, indistinct on ventral trail; rugae more distinct dorsally, reticulate; spines scattered on both valves, commonly concentric on ventral trail; cardinal process large, normally with pit, cardinal ridges may reach ears, no marginal ridges. *Lower Carboniferous (upper Tournaisian):* Eurasia, northern Africa, North America.——Fig. 342*a–e*. **T. robusta* (Tolmatchoff), Tournaisian, Kuzbass, central Asia; *a–c,* neotype, selected by Sarytcheva in Sarytcheva and others, 1963, ventral, lateral, posterior views of ventral valve, PIN 1493/149, ×1; *d,* dorsal valve exterior, ×1; *e,* dorsal valve interior, ×1 (Sarytcheva & others, 1963).

Acanthocosta Roberts, 1971, p. 104 [**A. teicherti;* OD]. Small to medium size, 20 to 25 mm wide; ribbing absent at beak, elongate spine bases posteriorly becoming regular ribs anteriorly with spines, thicker spines in rows on flanks, few and fine dorsally; cardinal ridges short. *Lower Carboniferous (Tournaisian):* Australia.——Fig. 343*a–f.* **A. teicherti,* Tournaisian, Bonaparte Gulf, Australia; *a–d,* holotype, ventral, lateral, posterior, anterior views, CPC 8645, ×2; *e,f,* interior, exterior views of dorsal valve showing spine bases, ×4 (Roberts, 1971).

Brasilioproductus Mendes, 1959, p. 48 [**Productus chandlessi* Derby, 1874, p. 51; OD]. Medium size; reticulate visceral disk, ribbing weak on trail; dorsal spines with row near hinge. *Upper Carboniferous (Bashkirian–Moscovian):* South America, southern North America.——Fig. 344,*1a–e*. **B. chandlessi* (Derby), Morrowan–Desmoinesian, Brazil; *a,b,* ventral, lateral views of complete specimen, ×1.7; *c,* dorsal view of complete specimen, ×1.3 (Mendes, 1959); *d,e,* ventral valve anterior view, dorsal valve interior, ×1 (Derby, 1874).

Libys Massa, Termier, & Termier, 1974, p. 175 [**L. hericinus;* OD]. Size reaches around 55 mm wide; resembles *Peniculauris,* but with dorsal spines restricted to margins and ears, not on hinge or umbo. *Lower Carboniferous (Viséan):* northern Africa.——Fig. 344,*2a*. **L. hericinus,* Holkerian, Libya; posterior view of ventral valve, ×1 (new).——Fig. 344,*2b–e*. *L. minor* Massa, Termier, & Termier, Viséan, Libya; *b–d,* holotype, ventral, dorsal, lateral views, TA 92/6, ×1; *e,* dorsal view of internal mold, ×1 (new).

Marginatia Muir-Wood & Cooper, 1960, p. 262 [**Productus fernglenensis* Weller, 1909, p. 299; OD] [=*Paramarginatia* Yang Shi-pu, 1978, p. 111 (type, *P. weinginensis;* OD)]. Small to medium size; reticulate posteriorly; dorsal spines rare, small; dorsal valve with variably positioned lateral ridges, commonly extending to lateral margins and commonly subperipheral rim. *Lower Carboniferous (lower Viséan):* North America, Europe, northern Africa, central China.——Fig. 344,*3a–d*. **M. fernglenensis* (Weller), lower Viséan, Missouri; *a–c,* posterior, anterior, lateral views of ventral valve, ×1; *d,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Peniculauris Muir-Wood & Cooper, 1960, p. 278 [**P. mckeei;* OD; *nom. nov. pro Productus ivesi* King, 1931, p. 69, *non* Newberry, 1861]. Medium to large, widest at hinge, with large ears; ginglymus incipient; ventral profile somewhat flattened posteriorly, geniculate and long trail; ribbing strong, swollen at densely positioned spine bases; disks weakly reticulate; spines in rows near hinge, clusters on ears and scattered over ventral valve, fine on dorsal valve; cardinal process trifid with large median sector; lateral ridges extend across ears; adductor scars wide; long median septum. *Lower Permian (Sakmarian–Roadian):* USA.——Fig. 345,*1a–e*. **P. mckeei,* Lower Permian, Leonard Formation, Texas; *a–d,* holotype, viewed ventrally, anteriorly, laterally, dorsally, USNM 123445, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Piloricilla Carter, 1987, p. 33 [**P. desmetensis;* OD]. Resembles *Acanthocosta,* but with flared lateral margins and some thicker ventral spines anteriorly; cardinal ridges widening laterally and uniting with obscure marginal rim. *Lower Carboniferous (lower Viséan):* Canada.——Fig. 345,*2a–g*. **P. desmetensis,* lower Viséan, western Alberta; *a–e,* holotype, ventral, anterior, lateral, posterior, dorsal views, GSC 63246, ×1; *f,* dorsal valve interior, ×2; *g,* posterior view of preceding specimen, ×3 (Carter, 1987).

Scissicosta Lazarev in Lazarev & Suur'suren, 1992, p. 65 [*S. gobiensis;* OD]. Resembles *Tolmatchoffia,* but smaller, more concave dorsal valve, ribbing absent at beaks, well defined on trails; dorsal spines rare, confined to zone of geniculation. *lower Lower Carboniferous (lower Tournaisian):* Mongolia.——Fig. 346,*1a–d*. **S. gobiensis,* Hastarian, Mongolia; *a,b,* holotype, ventral, lateral views, PIN N 3385/1080, ×1; *c,* ventral valve exterior, ×1; *d,* incomplete dorsal valve interior, ×1 (Lazarev & Suur'suren, 1992).——Fig. 346,*1e*. *S. busalaensis* Suur'suren; exterior mold of dorsal valve, ×1 (Lazarev & Suur'suren, 1992).

Spinifrons Stehli, 1954, p. 318 [**S. quadratus;* OD]. Medium size, resembling *Peniculauris,* but with clusters of thicker spines on ears and rarely anteriorly; cardinal process small; weakly developed lateral ridges close to hinge, and other internal morphology weak. *Lower Permian (upper Sakmarian–Artinskian):* southern USA.——Fig. 346,*3a–e*. **S. quadratus,* Lower Permian, Bone Spring Formation, Texas; *a,b,* shell viewed ventrally, posteriorly, ×1; *c,* lateral view, ×1; *d,e,* dorsal valve exterior, interior, ×1 (Muir-Wood & Cooper, 1960).

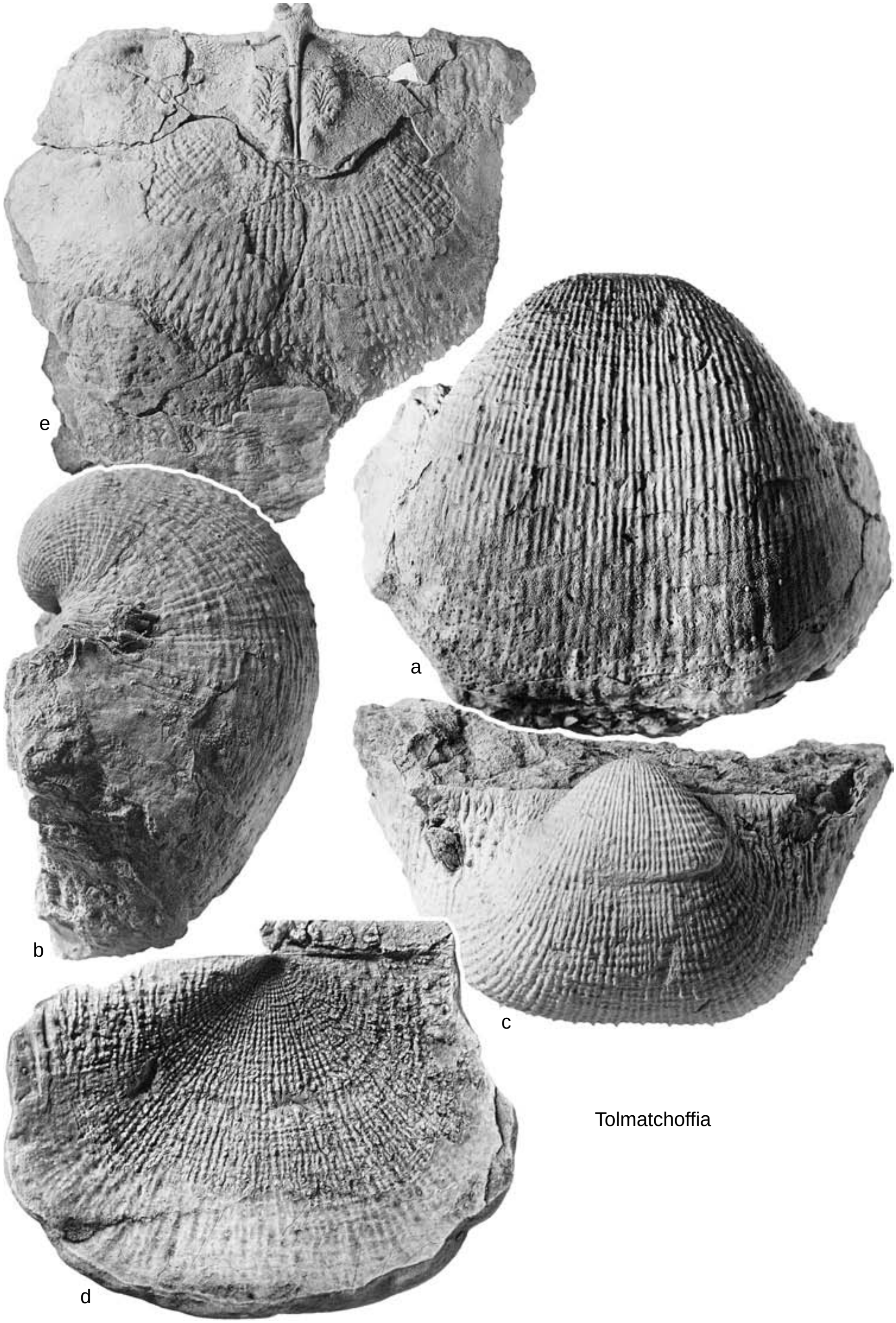


FIG. 342. Productidae (p. 502).

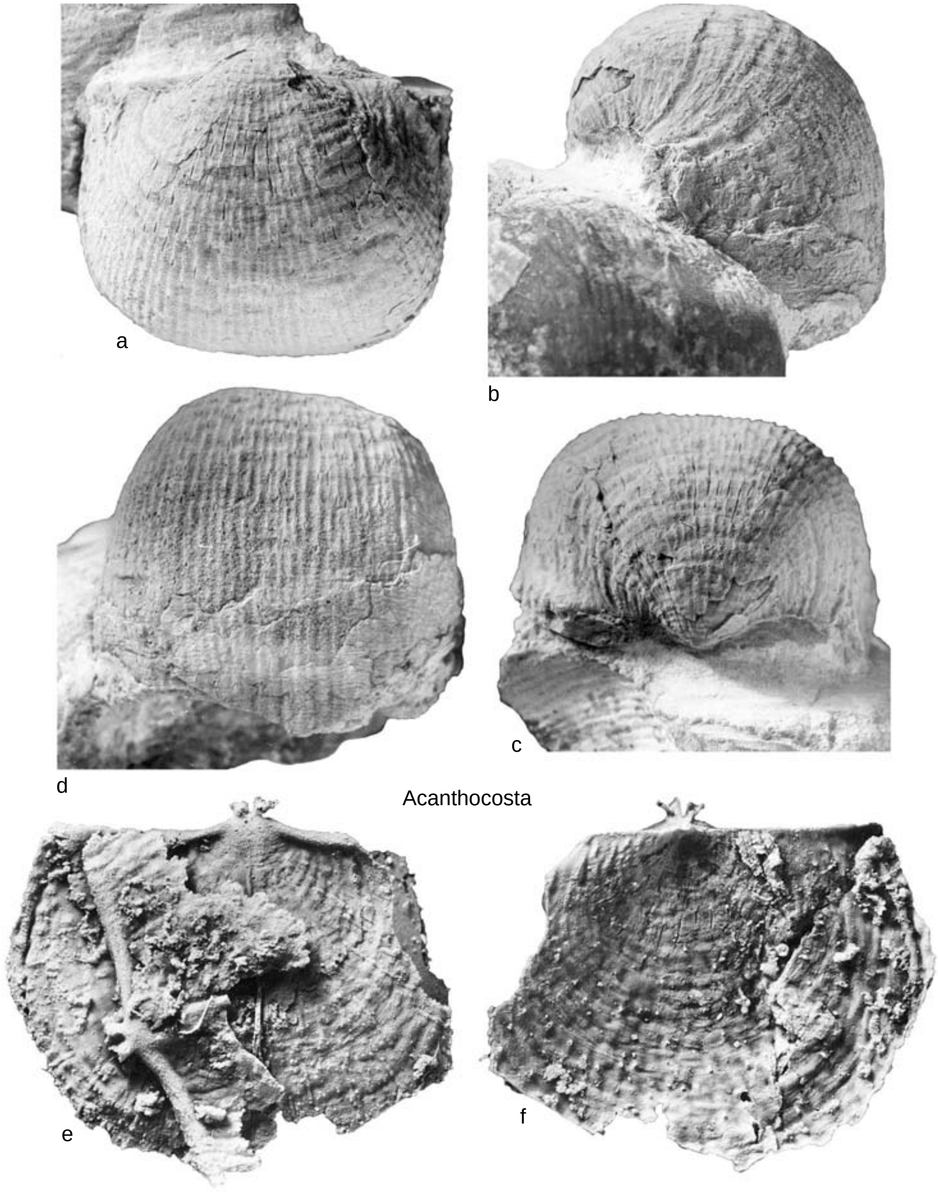


FIG. 343. Productidae (p. 502).

Squamaria MUIR-WOOD & COOPER, 1960, p. 287 [**S. moorei;* OD]. Medium size with wide hinge; ventral trail lamellose marginally; disks reticulate, but ribbing weak, irregular on trails; spines in prominent thick clusters on ears of both valves, widely scattered ventrally on accentuated ribs, sparse, fine dorsally; lateral, marginal ridges weak; shell substance thick. *Lower Permian:* USA.——FIG. 347,*1a–f.* **S. moorei,* Lower Permian, Talpa Formation, Texas; *a,b,* holotype, viewed anteriorly, dorsally, USNM 123987, ×1; *c,d,* posterior, lateral views of shell, ×1; *e,* incomplete ventral valve interior, ×1; *f,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Tomilia SARYTCHEVA in SARYTCHEVA & others, 1963, p. 220 [**T. khalfini;* OD]. Resembles *Tolmatchoffia,* but smaller, ribbing less well developed, sulcate, with thick-walled valves; cardinal process massive, protruding, supported by thick, short, divergent lat-

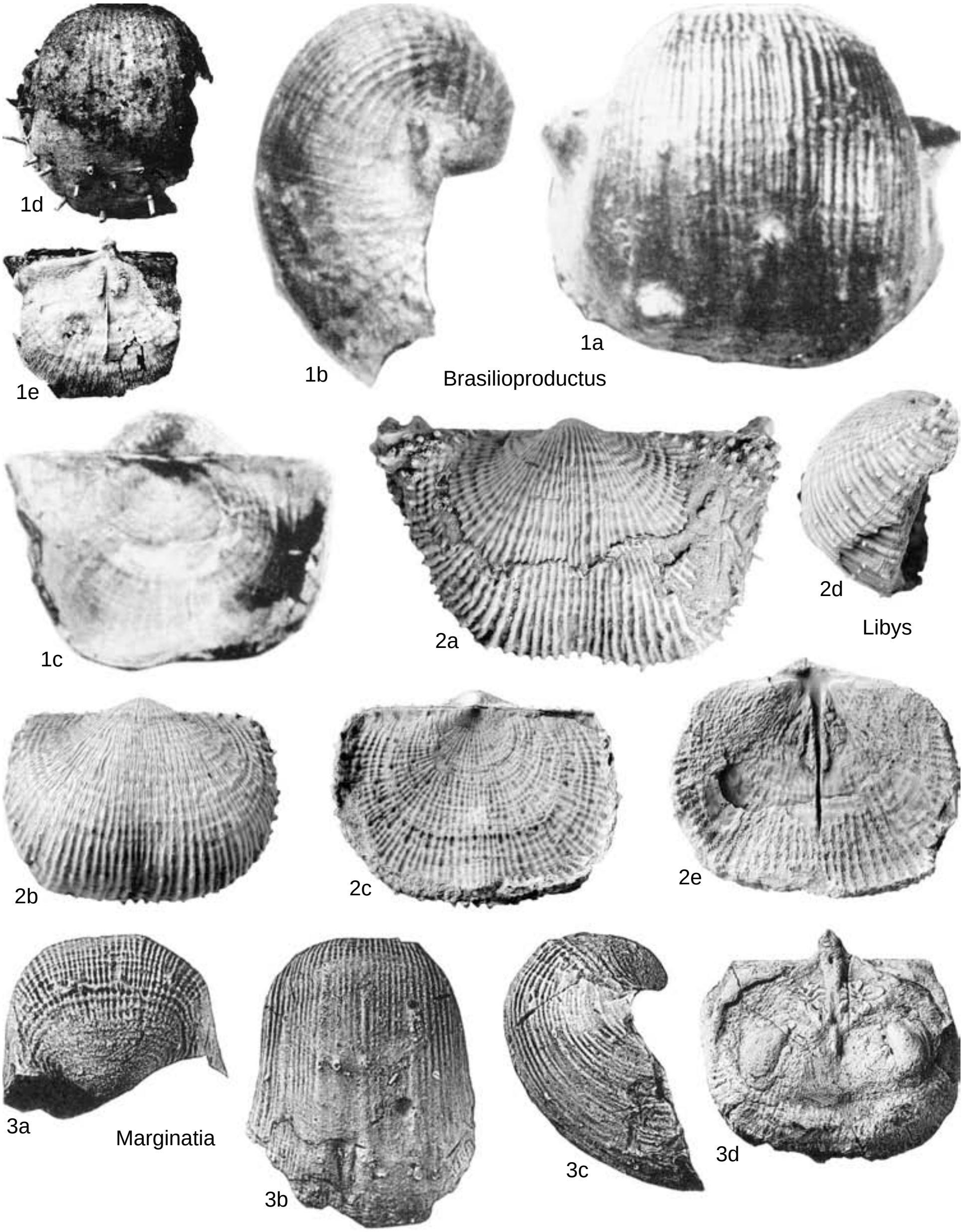


FIG. 344. Productidae (p. 502).

eral ridges. *Lower Carboniferous (lower Viséan):* Siberia.——FIG. 346,*2a–e.* **T. khalfini,* Viséan, Kuzbass, central Asia; *a,b,* ventral, posterior views of ventral valve, ×1; *c,* posterior view of ventral valve internal mold, ×1; *d,e,* holotype, lateral, dorsal views of internal mold, PIN N 1493/134, ×1 (Sarytcheva & others, 1963).

Tomiproductus SARYTCHEVA in SARYTCHEVA & others, 1963, p. 201 [**Productus elegantulus* TOLMATCHOFF, 1924, p. 244; OD]. Small; thin shelled, deep corpus, elongate ventral trail; ribbing entire, fine, weak reticulation on disks; spines sparsely scattered, thicker, somewhat concentric on ventral trail; paired ridges posterior to dorsal adductor scars, lateral

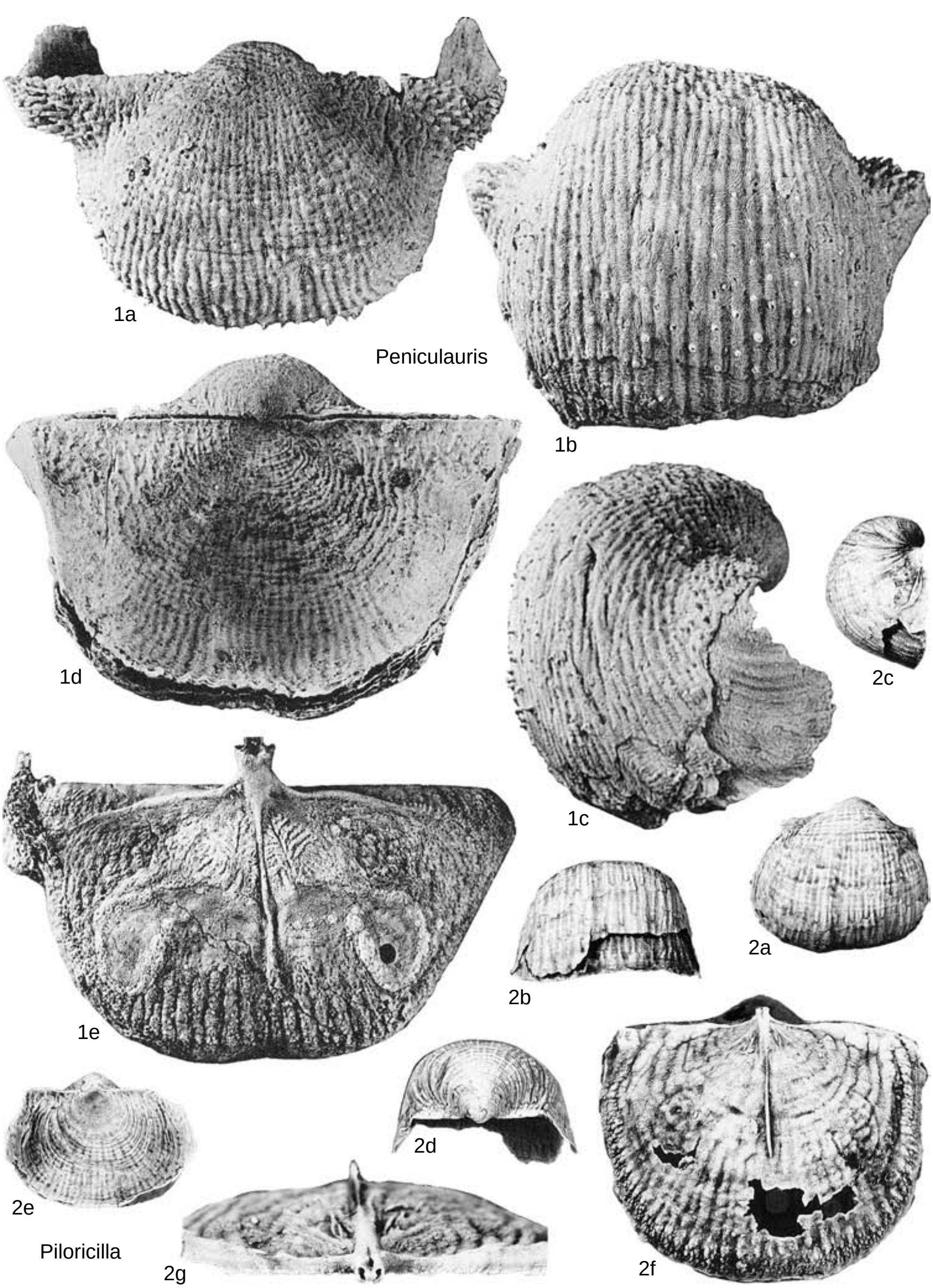


FIG. 345. Productidae (p. 502).

ridges reach ears. *Lower Carboniferous (lower Tournaisian):* Eurasia, North America, ?northern Africa.——FIG. 348,*2a–e.* **T. elegantulus* (TOLMATCHOFF), Tournaisian, Kuzbass, central Asia; *a–c,* neotype, dorsal, lateral, anterior views, PIN N 1493/238, ×1; *d,* posterior view of ventral valve,

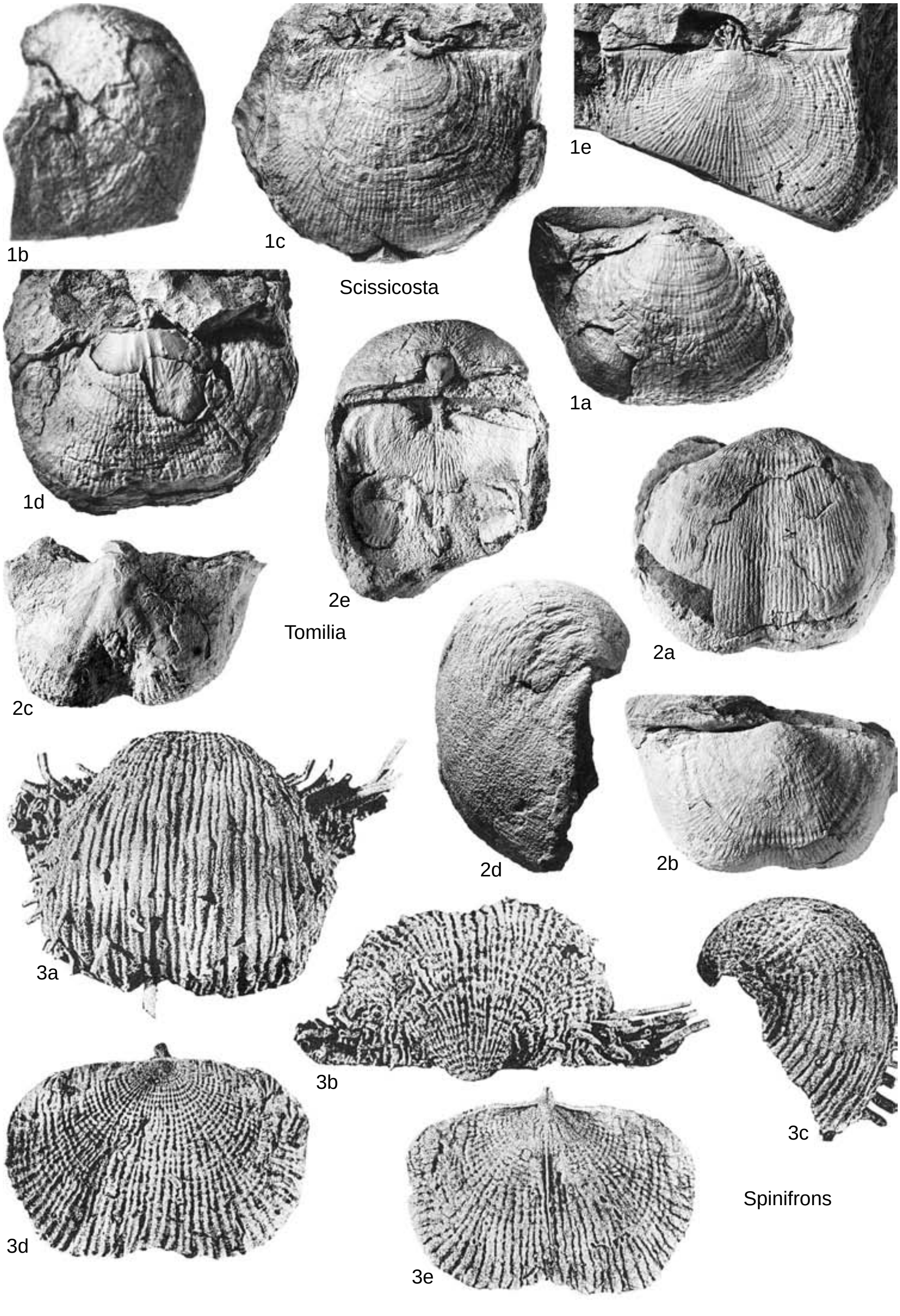


FIG. 346. Productidae (p. 502–505).

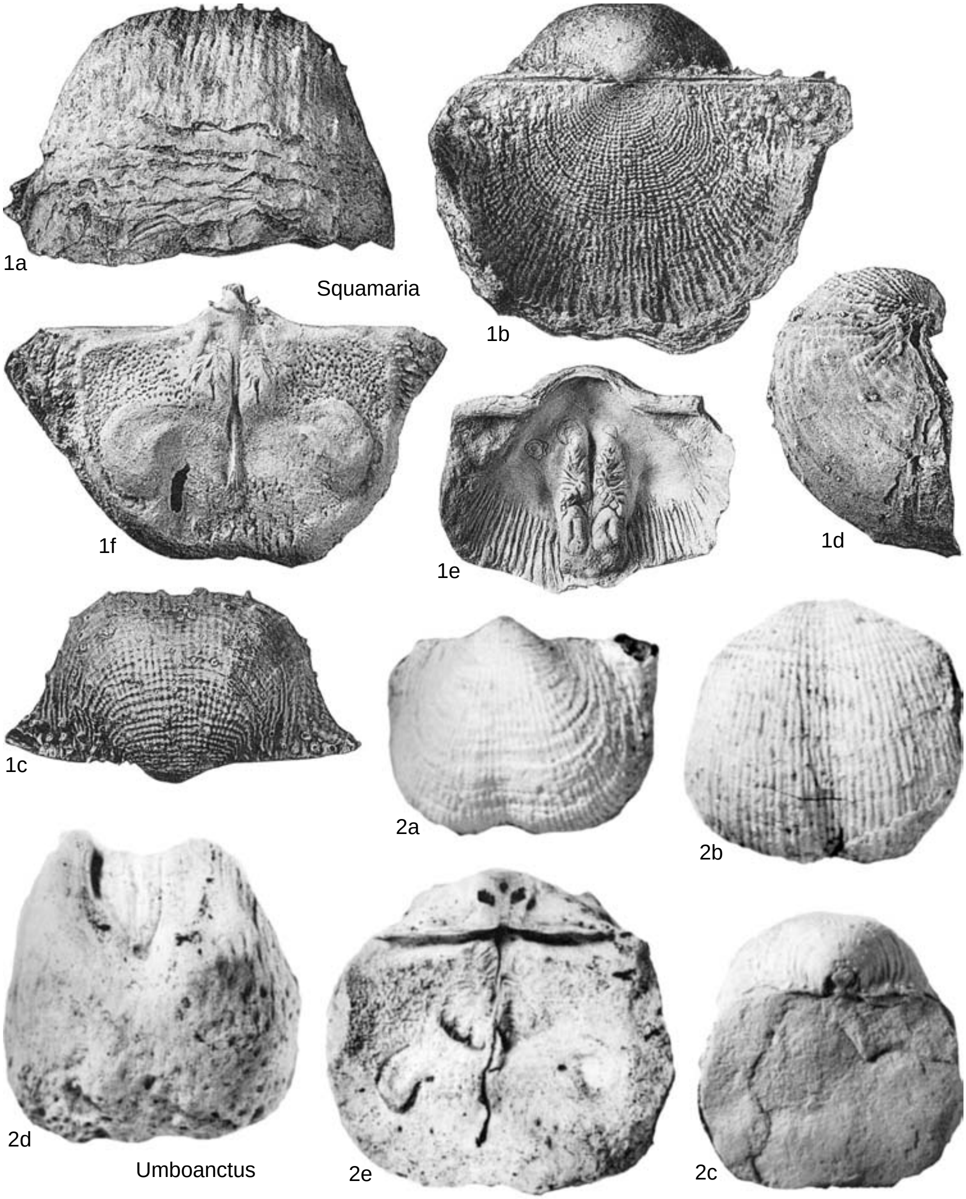


FIG. 347. Productidae (p. 504–508).

×1; *e,* dorsal valve interior, ×3 (Sarytcheva & others, 1963).

Umboanctus WATERHOUSE in BAMBER & WATERHOUSE, 1971, p. 212 [**U. spinosus;* OD]. Size medium; thick shelled with geniculated dorsal valve; ventral trail medianly sulcate, ribbing strong, clearly reticulate disks; spines numerous on both valves, concentric on ventral trail; cardinal ridges prominent, endospines large anteriorly; prominent ventral adductor scar platform. *Upper Carboniferous (lower Moscovian):* Canada.——FIG. 347,*2a–e.* **U. spinosus,* Moscovian, Yukon; *a,* ventral view of ventral valve, ×1; *b,c,* holotype, anterior, dorsal views, GSC 26411, ×1; *d,e,* ventral, dorsal views of internal cast, ×1 (Bamber & Waterhouse, 1971).

Xinshaoproductus TAN ZHEN-XIU, 1986, p. 433[442] [**X. xinshaoensis;* OD] [=*Neoyanguania* SHI XIAO-YING, 1988, p. 348[352] (type, *N. quadrata*)]. Similar to *Marginatia,* but with less well-defined ribbing, reticulation posteriorly; spines numerous from ventral elongate bases, not known dorsally; weak cardinal ridges plus ridges posterolaterally to adductor scars. *Lower Carboniferous (upper Tournaisian):* southern China.——Fig. 348,*1a–d.* **X. xinshaoensis,* Tournaisian, Hunan; *a–c,* holotype, lateral, anterior, posterior views, HB 302, ×1; *d,* dorsal valve interior, ×1 (Tan, 1986).

Superfamily ECHINOCONCHOIDEA Stehli, 1954

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Echinoconchidae Stehli, 1954, p. 326]

Productidines widest anterior to hinge, with corpus cavity deep in most families; trail commonly very short; spines covering both valves, including at hinge, commonly arranged in concentric bands, recumbent, forming dense mats; ribbing absent. *Middle Devonian (Givetian)–Upper Permian (Changhsingian).*

Family ECHINOCONCHIDAE Stehli, 1954

[Echinoconchidae Stehli, 1954, p. 326]

Corpus with planoconvex profile, cavity deep; dorsal trail commonly short; spines thin, commonly in concentric bands, recumbent. *Lower Carboniferous (Tournaisian)–Upper Permian (Kazanian).*

Subfamily ECHINOCONCHINAE Stehli, 1954

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 243, *ex* Echinoconchidae Stehli, 1954, p. 326]

Concentric bands well developed on both valves bearing spines differentiated in size; buttress plates, cardinal process pit absent. *Lower Carboniferous (upper Viséan)–Upper Permian (Kazanian).*

Tribe ECHINOCONCHINI Stehli, 1954

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 929, *ex* Echinoconchidae Stehli, 1954, p. 326]

Medium to large; concentric bands cuesta-like in profile, posterior part smooth, narrower than anteriorly where spines differentiated by size; one or two rows of thicker spines posteriorly, thinner rows anteriorly; dorsal adductor scars tend to become raised, crests curve laterally. *Lower Carboniferous (upper Viséan)–Lower Permian (Sakmarian).*

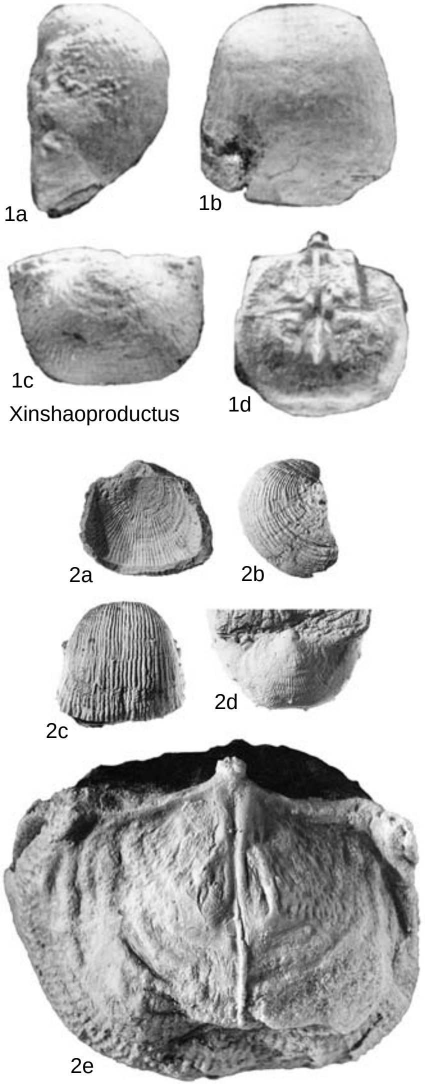


Fig. 348. Productidae (p. 505–509).

Echinoconchus Weller, 1914, p. 138 [**Anomites punctatus* Martin, 1809, pl. 37, fig. 6–8, declared invalid from 1948, ICZN, 1950; =*Productus punctatus* J. Sowerby, 1822 in 1821–1822, p. 22; SD Chao, 1927b, p. 63]. Outline transversely subcircular, dorsal valve weakly concave, minimal trails; cardinal process narrow, supported by cardinal ridges; adductor scars elongate, slightly raised

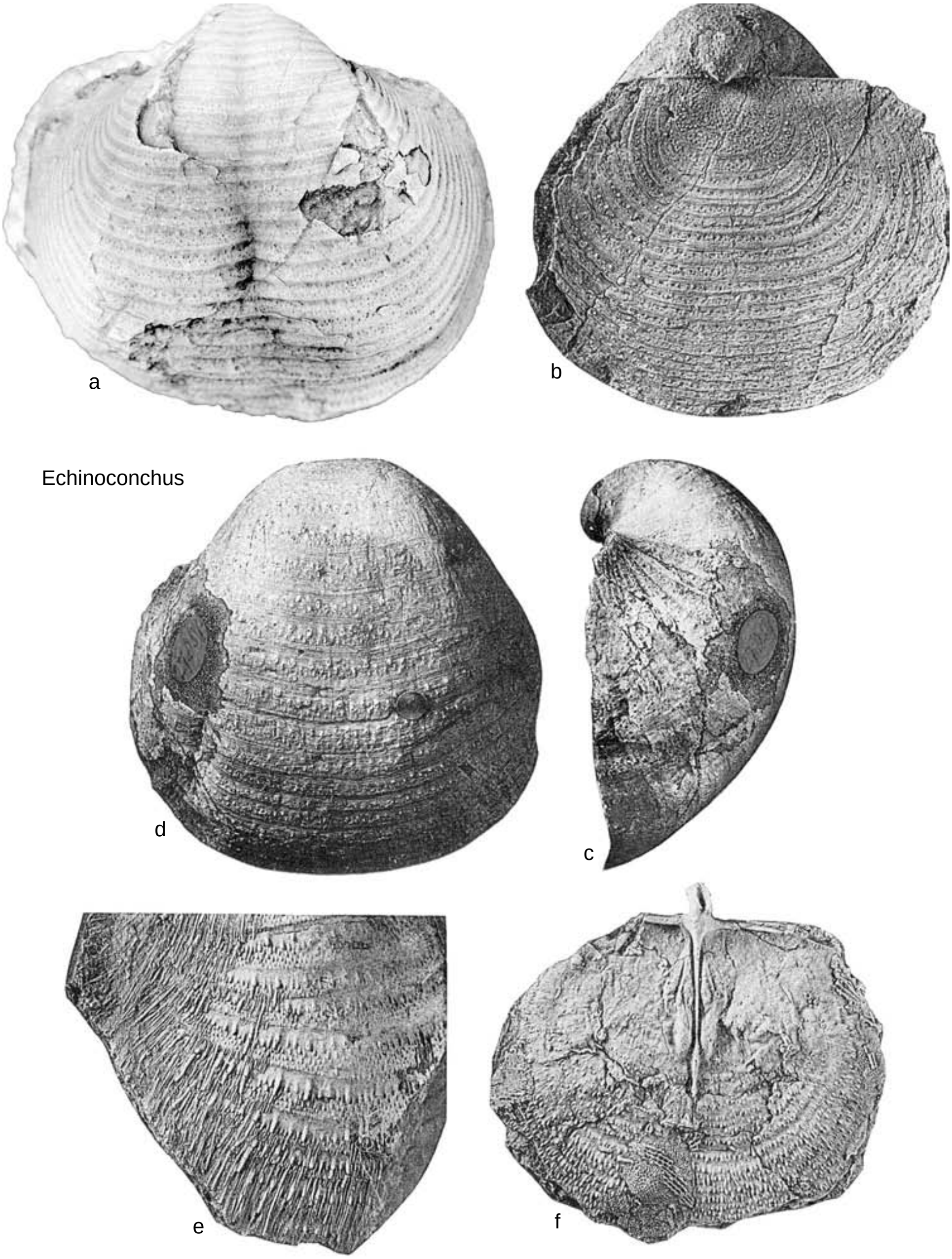


FIG. 349. Echinoconchidae (p. 509–510).

anteriorly. *Lower Carboniferous (upper Viséan):* cosmopolitan.——FIG. 349*a–e.* **E. punctatus* (J. SOWERBY), Asbian; *a,* lectotype, viewed ventrally, Derbyshire, British Isles, BMNH B 60966, ×1 (new); *b–d,* shell viewed dorsally, laterally, ventrally, Yorkshire, ×1; *e,* anterolateral detail of ventral exterior, Yorkshire, ×2 (Muir-Wood & Cooper, 1960).——FIG. 349*f.* **E. alternatus* (NORWOOD & PRATTEN), dorsal valve interior, Chesterian, Oklahoma, ×1 (Muir-Wood & Cooper, 1960).

Echinaria MUIR-WOOD & COOPER, 1960, p. 248 [**Productus semipunctatus* SHEPARD, 1838, p. 153; OD].

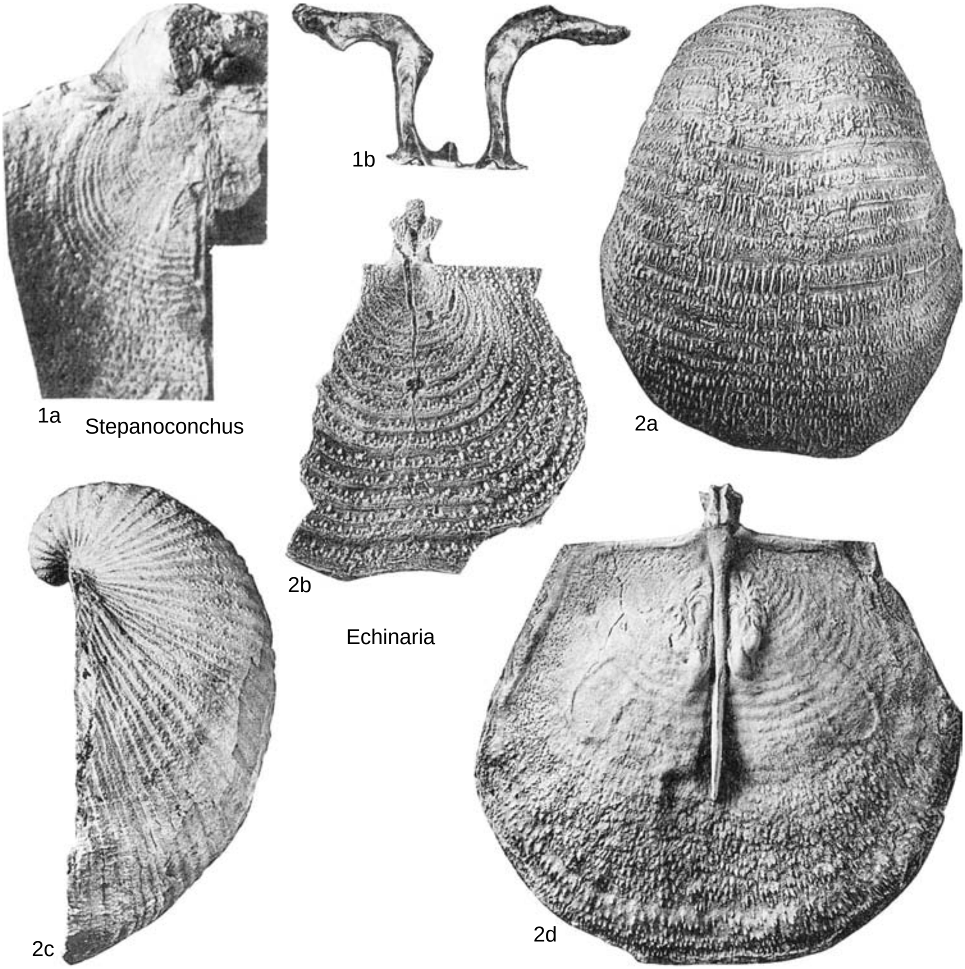


FIG. 350. Echinoconchidae (p. 510–511).

Medium to large; elongate outline widening anteriorly; cardinal ridges, strong median septum support narrow, trifid, cardinal process; ear baffles weak. *Upper Carboniferous (Gzhelian)–Lower Permian:* North America, northern South America, Eurasia.——FIG. 350,*2a–d.* **E. semipunctata* (SHEPARD), Virgilian; *a,* ventral valve exterior, Texas, ×1; *b,* incomplete dorsal valve exterior, Texas, ×2; *c,* shell viewed laterally, Kansas, ×1; *d,* dorsal valve interior, Illinois, ×1 (Muir-Wood & Cooper, 1960).

Stepanoconchus LAZAREV, 1985, p. 69[68] [**Echinoconchus postpunctatus* STEPANOV in VOLGIN, 1960, p. 62; OD]. Externally resembles *Echinoconchus,* but differs internally by having dorsal adductor scars on laterally curving muscle platforms. *upper Upper Carboniferous (upper Gzhelian)–Lower Permian (Sakmarian):* Ural Mountains.——FIG. 350,*1a,b.* **S. postpunctatus* (STEPANOV), Lower Permian, Ural Mountains; *a,* dorsal view of incomplete shell fractured at adductor platform, ×0.75; *b,* transverse section of dorsal adductor platform, valve internal surface to bottom, ×5 (Lazarev, 1990).

Tribe CALLIPROTONIINI
Lazarev, 1985

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 929, *ex* Calliprotoniinae LAZAREV, 1985, p. 71]

Medium size; concentric ornamentation of low, anteriorly, somewhat lamellose bands covered by evenly distributed recumbent spines on each band, grading from large to small anteriorly; lateral ridges strongly developed, extending as submarginal ridges. *Upper Carboniferous (Gzhelian)–Lower Permian (Sakmarian).*

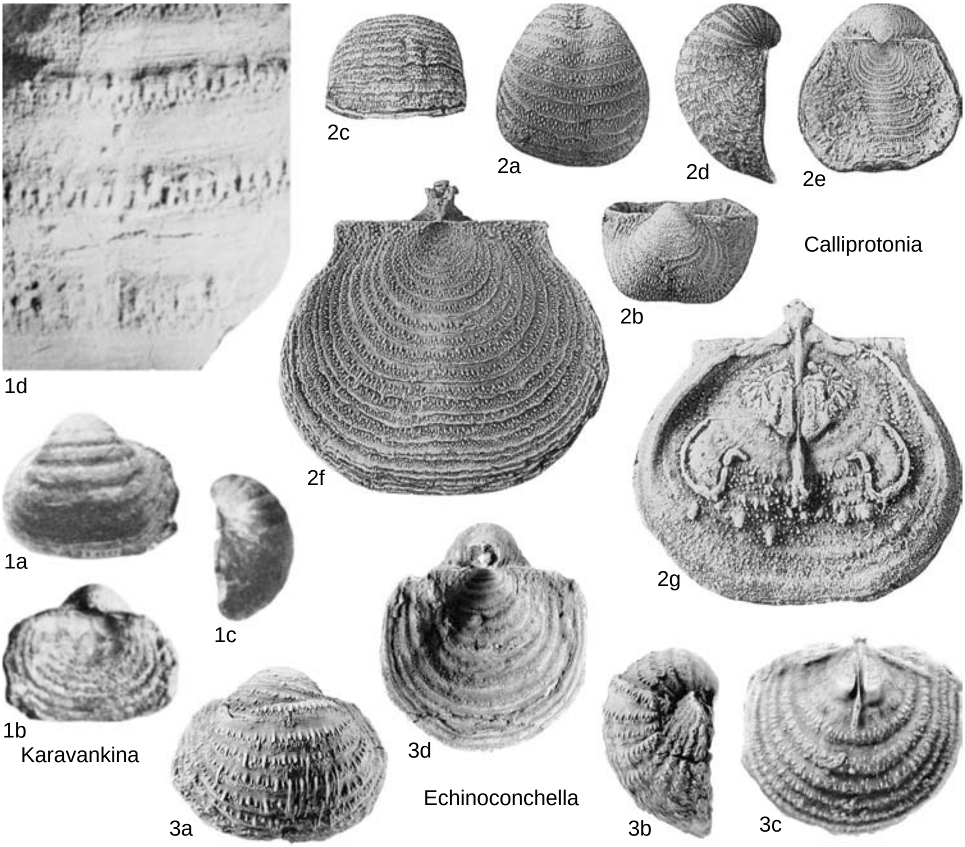


Fig. 351. Echinoconchidae (p. 512).

Calliprotonia Muir-Wood & Cooper, 1960, p. 246 [**C. renfrarum;* OD]. Small to medium size; planoconvex with short trails, commonly weak ventromedian sulcation; cardinal process trifid, strongly supported by lateral ridges. *Upper Carboniferous (Gzhelian)–Lower Permian (Sakmarian):* North America, South America, eastern Europe (Moscow basin, Ural Mountains), Asia, ?Spitzbergen.——Fig. 351,*2a–g*. **C. renfrarum,* Virgilian, Texas; *a–e,* shell viewed ventrally, posteriorly, anteriorly, laterally, dorsally, ×1; *f,g,* dorsal valve exterior, interior, ×2 (Muir-Wood & Cooper, 1960).

Tribe KARAVANKININI Ramovš, 1969

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 929, *ex* Karavankininae Ramovš, 1969, p. 261]

Small to medium size; high relief concentric bands, symmetrical in profile, tops bearing concentric rows of spines, distributed by size, separated by wider smooth bands; dorsal adductor scars raised, crests curved medianly after Serpukhovian. *Lower Carboniferous (Brigantian)–Upper Permian (Kazanian).*

Karavankina Ramovš, 1969, p. 261 [**K. typica;* OD] [=*Karavankina* Ramovš, 1966, p. 120, *nom. nud.*]. Small to medium size; outline commonly transversely subcircular; concentric bands with wide, spine-free regions; cardinal ridges weak, paired dorsal adductor platforms undercut anteromedianly. *Upper Carboniferous–Upper Permian (Kazanian):* Eurasia.——Fig. 351,*1a–d*. **K. typica,* Kazanian, northern Yugoslavia; *a–c,* holotype, viewed ventrally, dorsally, laterally, UL 3714/160, ×1; *d,* detail of ventral ornament, ×5 (Ramovš, 1969).

Echinoconchella Lazarev, 1985, p. 70[68] [**Productus elegans* M'Coy, 1844, p. 108; OD]. Resembles *Karavankina,* but without dorsal muscle platforms. *Lower Carboniferous (Brigantian–lower Serpukhovian):* Eurasia.——Fig. 351,*3a–c*. **E. elegans* (M'Coy), Brigantian, Scotland; *a,b,* shell viewed ventrally, laterally, ×2; *c,* dorsal valve interior, ×3 (new).——Fig. 351,*3d*. *E. venusta* (Thomas), lower Brigantian, Derbyshire; dorsal view of shell showing spine bases, ×2 (new).

Subfamily JURESANIINAE
Muir-Wood & Cooper, 1960

[Juresaniinae MUIR-WOOD & COOPER, 1960, p. 266]

Concentric bands absent or confined anteriorly; spines may be differentiated by size anteriorly; cardinal process pit, buttress plates present in Carboniferous juveniles only. *Lower Carboniferous (Tournaisian)–Upper Permian (Kazanian).*

Tribe JURESANIINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 929, *ex* Juresaniinae MUIR-WOOD & COOPER, 1960, p. 266] [=Bathymyoniinae LAZAREV, 1986c, p. 29]

Quincuncial pustules posteriorly, reducing in area through upper Permian; concentric bands of spines commonly on rest of valves; anteriorly rugose or lamellose. *Lower Carboniferous (upper Asbian)–upper Lower Permian (Roadian).*

Juresania FREDERICKS, 1928, p. 786 [**Productus juresanensis* CHERNYSCHEV, 1902, p. 276; OD]. Smaller medium size, subquadrate outline with hinge forming widest part; ventral profile weakly geniculate; median sulcation weak; ventral disk with elongate spine bases arranged quincuncially, anterior to disk (trail) nonrugose bands with differentiated spines, elongate thicker spines posteriorly, thinner recumbent spines anteriorly; buttress plates converge anteriorly to median septum. *upper Upper Carboniferous (Kasimovian)–Lower Permian (Asselian):* Arctic Eurasia, western Himalayas.——FIG. 352,*3a–e.* **J. juresanensis* (TSCHERNYSCHEW), *Schwagerina* Limestone, Juresan River, Russia; *a,b,* syntype, specimen viewed posteriorly, laterally, ×1 (Muir-Wood & Cooper, 1960); *c,* anteroventral view of ventral valve, ×1; *d,* detail of ventral trail, ×3 (Lazarev, 1990); *e,* dorsoposterior view of shell with dorsal valve removed, showing short convergent buttress plates (*arrow*), ×3 (new).

Ametoria COOPER & GRANT, 1975, p. 1055 [**A. residua;* OD]. Medium, hinge wide; spines of two sizes covering venter, clusters on ears and flanks, finer covering dorsal valve; buttress plates absent. *upper Lower Permian (Roadian):* USA.——FIG. 352,*1a–e.* **A. residua,* Road Canyon Formation, Texas; *a–c,* holotype, viewed ventrally, anteriorly, laterally, USNM 153476, ×1; *d,* incomplete dorsal valve exterior, ×1; *e,* incomplete dorsal valve interior, ×1.5 (Cooper & Grant, 1975).

Bathymyonia MUIR-WOOD & COOPER, 1960, p. 244 [**Productus nevadensis* MEEK, 1877, p. 64; OD]. Medium, subquadrate in dorsal outline; dorsal disk plane to gently concave with short trail; medium sulcation slight; spines mixed in size, varied inclinations; ventral disk with elongate swollen bases, anteriorly spines arranged in bands of several rows; cardinal process large, with shaft, buttress plates absent; cardinal ridges strong; ventral valve thick shelled posteriorly. *Lower Permian (?Artinskian, Kungurian):* USA, ?eastern China, ?Japan.——FIG. 353,*1a–g.* **B. nevadensis* (MEEK), Lower Permian, Phosphoria Formation; *a–d,* lectotype, viewed ventrally, posteriorly, anteriorly, laterally, Nevada, USNM 668a, ×1; *e,* dorsal valve exterior, Nevada, ×1; *f,* ventral valve internal mold, Nevada, ×1; *g,* dorsal valve interior, Wyoming, ×1 (Muir-Wood & Cooper, 1960).

Bilotina REED, 1944, p. 109 [**Strophalosia (Bilotina) subtecta;* OD] [=*Septasteges* WATERHOUSE & PIYASIN, 1970, p. 120 (type, *S. acanthus;* OD)]. Smaller medium size with subquadrate corpus outline, deep planoconvex profile with geniculate trails; small cicatrix may be present; ventral ginglymus; elongate spine ridges may simulate impersistent ribbing; spines strong, evenly scattered on ventral valve, thin on dorsal valve; cardinal process strong, supported by paired elevated adductor platforms; cardinal, marginal ridges strong. *Lower Permian (Artinskian):* western Pakistan, Thailand.——FIG. 352,*2a–c.* **B. subtecta,* Amb Formation, Khisor Range; *a,b,* ventral valve exterior viewed ventrally, laterally, ×1; *c,* incomplete dorsal valve interior, ×1 (Grant, 1976).——FIG. 352,*2d–g. B. acantha* (WATERHOUSE & PIYASIN), Rat Bui Limestone, southern Thailand; *d,e,* ventral valve viewed ventrally, posteriorly; ×2; *f,* dorsal valve exterior, ×1; *g,* dorsal valve interior, ×2 (Grant, 1976).

Buntoxia LAZAREV, 1986b, p. 94 [**Buxtonia scabricula* var. *mosquensis* IVANOV, 1935, p. 102; OD]. Dorsal valve almost flat; ventral spine bases swollen umbonally, rugae anteriorly with bands of differentiated spines; median septum grooved posteriorly. *upper Lower Carboniferous (upper Asbian)–Upper Carboniferous (Gzhelian):* Russia.——FIG. 354*a–d.* **B. mosquensis* (IVANOV), Moscovian, Myachkovian, Moscow basin; *a–c,* ventral valve exterior viewed anteroventrally, laterally, posteroventrally, ×1; *d,* dorsal valve interior, ×1 (new).——FIG. 354*e. B.* sp. aff. *B. mosquensis* (IVANOV), Kasimovian; detail of ventral ornament anteriorly, ×3 (Lazarev, 1990).——FIG. 354*f. B.* sp., Serpukhovian; detail of ventral valve posteroventrally, ×3 (Lazarev, 1990).

Cubacula LAZAREV, 1984, p. 73[70] [**Productus subpunctatus* NIKITIN, 1890, p. 58; OD]. Small to medium sized; slightly emarginate outline; resembles *Parajuresania,* but between every four or five recumbent spines erect spines project from middle of bands, each widely separated by narrow rugae originating at about half corpus length, commonly symmetrical in profile. *Upper Carboniferous (Kasimovian–lower Gzhelian):* eastern Europe.——FIG. 355,*1a–f.* **C. subpunctata* (NIKITIN), Kasimovian, Moscow basin; *a–c,* shell viewed ventrally, laterally, dorsally, ×1; *d,* detail of cardinal process dorsally, ×4; *e,* detail of ventral valve ornament, ×3; *f,* dorsal valve interior, ×1 (new).

Densepustula LAZAREV, 1982, p. 66[66] [**Flexaria russiensis* SEMENOVA, 1972, p. 26; OD]. Ornament

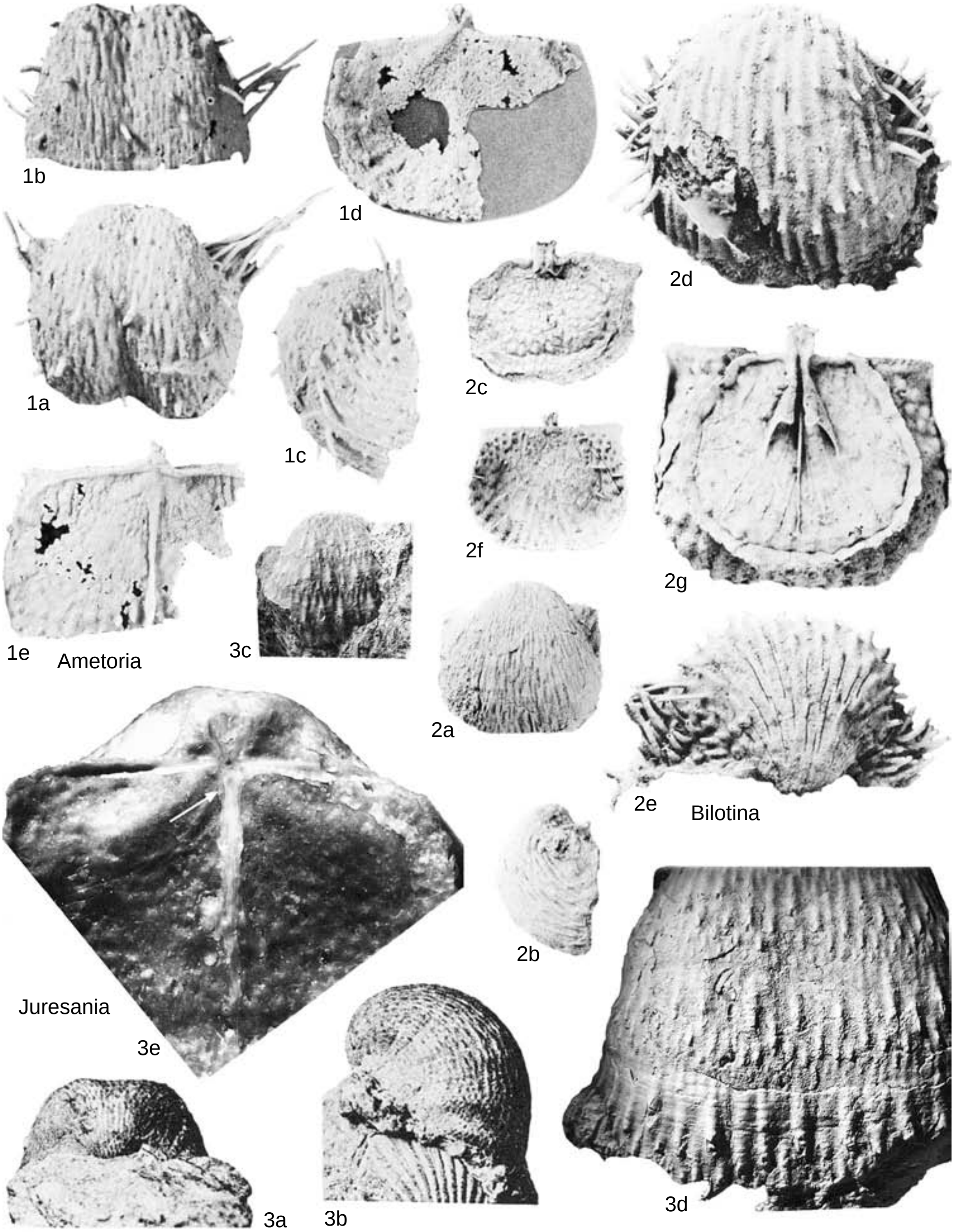


FIG. 352. Echinoconchidae (p. 513).

as in *Juresania* posteriorly, but lacks concentric bands anteriorly. *Upper Carboniferous (upper Bashkirian–lower Moscovian):* Russia.——FIG. 356,*1a–d.* **D. russiensis* (SEMENOVA), lower Moscovian, Moscow basin; *a,* ventral valve viewed anteriorly, ×3; *b,* dorsal valve exterior, ×1; *c,* detail of dorsal valve exterior, ×4; *d,* incomplete juvenile dorsal valve interior showing buttress plates, ×3 (Lazarev, 1982).

Parajuresania LAZAREV, 1982, p. 70 [**Productus nebrascensis* OWEN, 1852, p. 584; OD]. Resembles *Juresania* but differs in having small, uncommon ventral cicatrix; concentric bands with differentiated spines only anteriorly, anterior spines thin, recum-

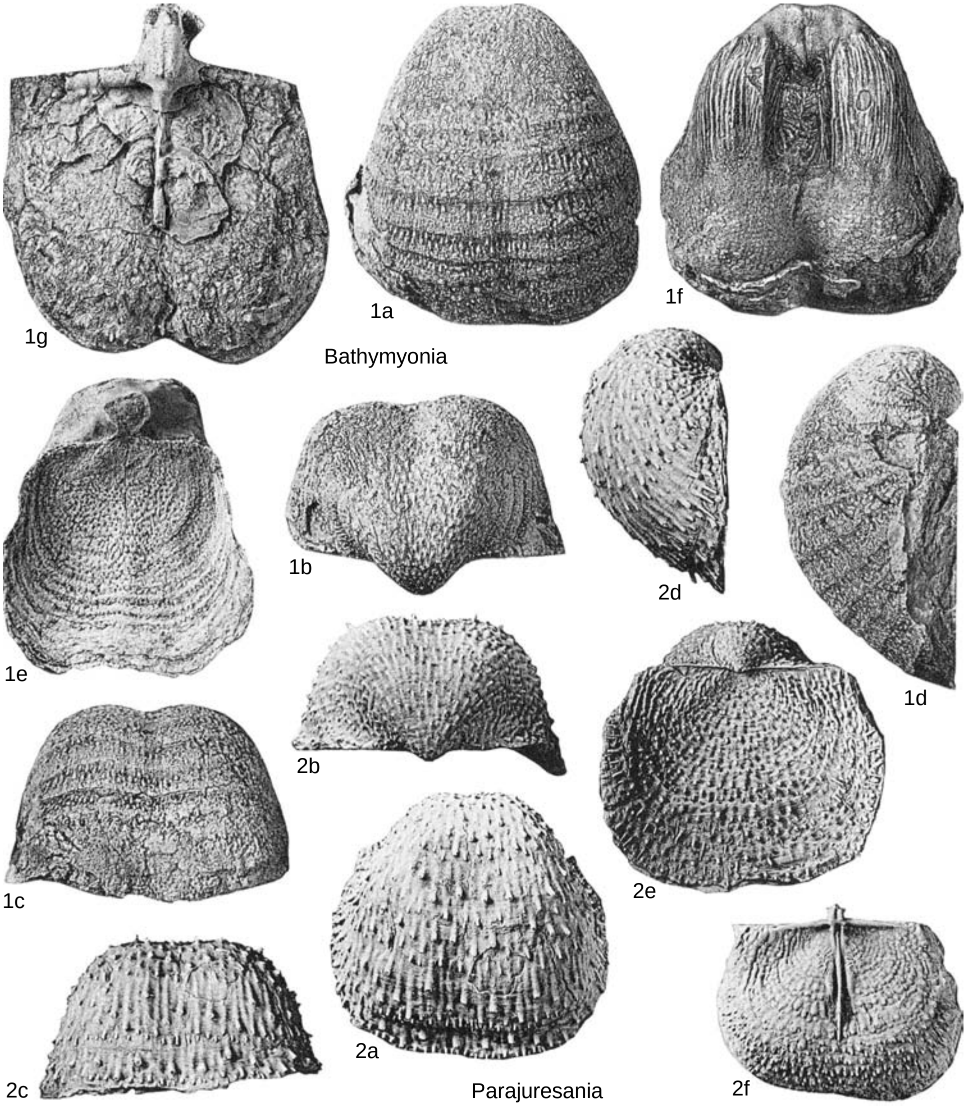


FIG. 353. Echinoconchidae (p. 513–515).

bent, posterior spines thicker, suberect; buttress plates subparallel as juvenile. *Upper Carboniferous (upper Kasimovian)–Lower Permian (Asselian):* North America, northern Europe.——FIG. 353,*2a–f.* **P. nebrascensis* (OWEN), Asselian, Kansas; *a–e,* shell viewed ventrally, posteriorly, anteriorly, laterally, dorsally, ×1; *f,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Pulchratia MUIR-WOOD & COOPER, 1960, p. 249 [**Productus symmetricus* MCCHESNEY, 1860, p. 35; OD]. Resembles *Parajuresania,* but spines more uniform in size, lacking strong spine bases; lateral ridges diverge slightly from hinge, buttress plates weak, convergent, or lost in adults. *Upper Carboniferous (Kasimovian–Gzhelian):* North America.——FIG. 355,*2a–e.* **P. symmetrica* (MCCHESNEY), Virgilian, Texas; *a–d,* shell viewed anteroventrally, laterally, dorsally, dorsolaterally, ×1 (new); *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Vediproductus SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 219 [**V. vediensis;* OD]. Medium size, resembles *Juresania,* but differs by having spine bands of strong relief covering ventral valve; cardinal ridges bend sharply across ears. *upper Lower Permian (Roadian):* Transcaucasus, China.——FIG. 356,*2a–e.* **V. vediensis,* Ufimian, Avush,

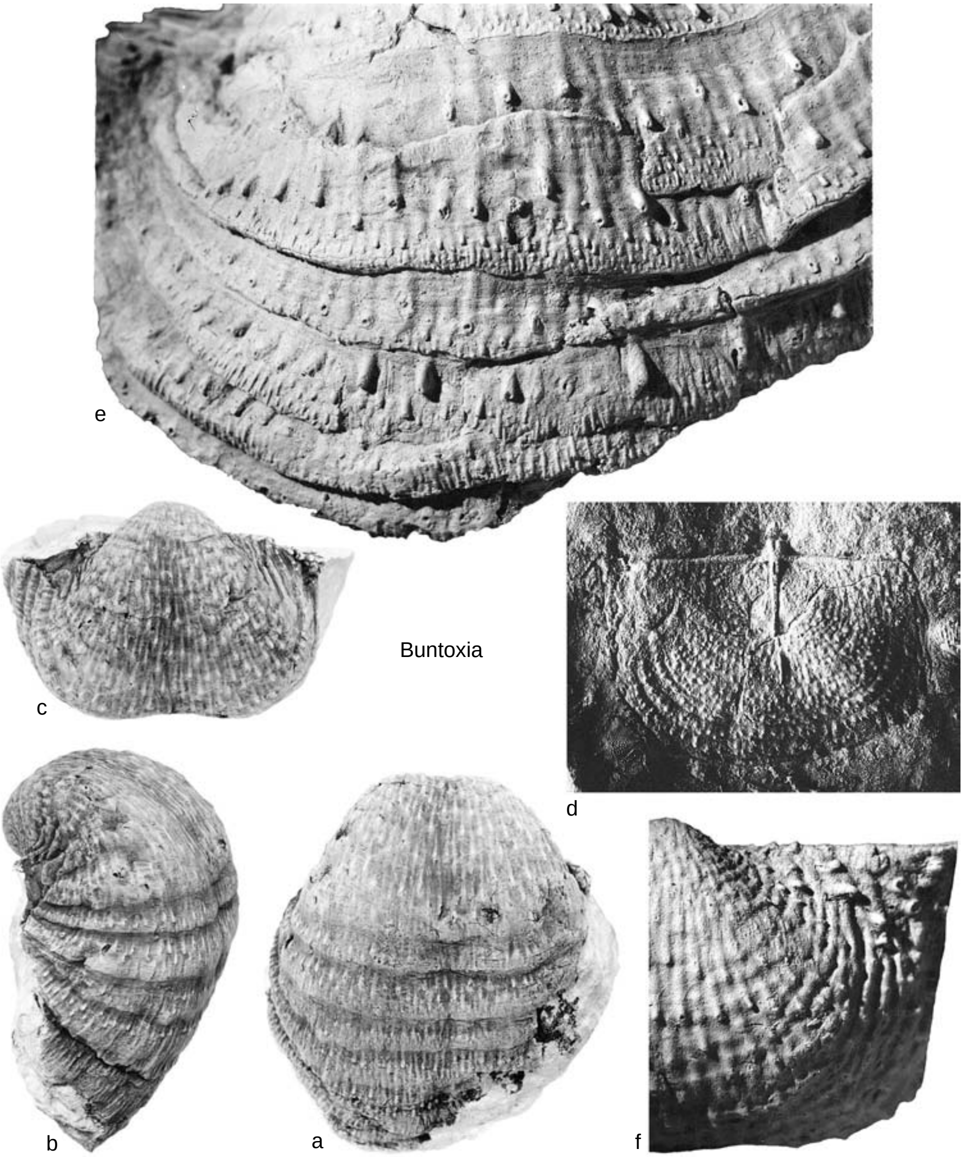


FIG. 354. Echinoconchidae (p. 513).

Transcaucasia; *a–c,* holotype, viewed ventrally, posteriorly, laterally, PIN 207/32, ×1; *d,* detail of ventral valve exterior, ×3; *e,* incomplete dorsal valve interior, ×1 (Sarytcheva & Sokolskaya, 1965).

Tribe WAAGENOCONCHINI
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 929, *ex* Waagenoconchinae MUIR-WOOD & COOPER, 1960, p. 252]

Corpus with small quincuncially arranged spines, dense mat of long peripheral spines; weak banding anteriorly; trails may be long. *Lower Carboniferous (Tournaisian)–Upper Permian.*

Waagenoconcha CHAO, 1927b, p. 24, 85 [**Productus humboldti* D'ORBIGNY, 1842, p. 54; OD] [=*Biplatyconcha* WATERHOUSE, 1983b, p. 125, *nom. nov. pro Platyconcha* WATERHOUSE, 1975, p. 8, *non* LONGSTAFF, 1933, gastropod (type, *P. grandis* WATERHOUSE, 1975, p. 8); *Ruthenia* FREDERIKS, 1928, p. 789 (type, *Productus irginae* STUCKENBERG, 1898, p. 340); *Wimanoconcha* WATERHOUSE, 1983b,

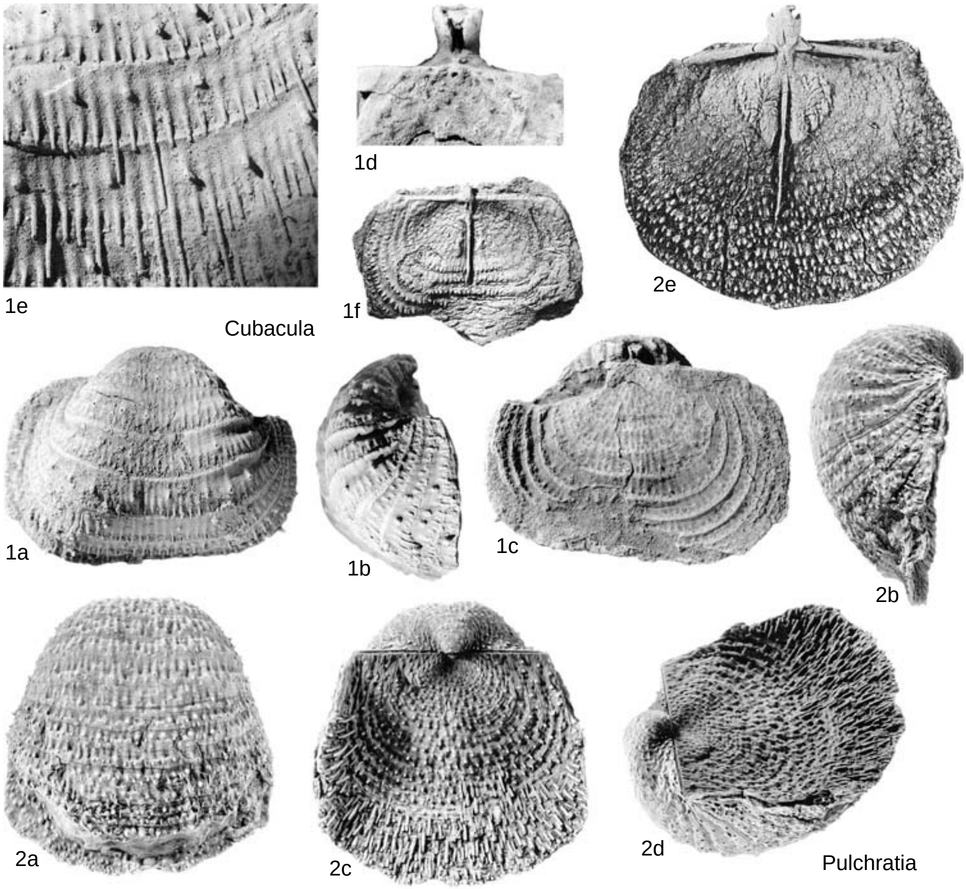


FIG. 355. Echinoconchidae (p. 513–515).

p. 125 (type, *Waagenoconcha wimani* FREDERIKS, 1934, p. 28)]. Medium to large shells; outline subrounded with hinge slightly less than maximum width; corpus planoconvex, with short trails; corpus covered by pustulose, slightly elongate spine bases arranged quincuncially; dorsal interior with no buttress plates. *Wimanoconcha* was reported as differing in having anteriorly thickened dorsal valve (but see ARCHBOLD, 1993, upper Capitanian of Australia). *Biplatyconcha* was reported as lacking dorsal spines. *upper Upper Carboniferous–Upper Permian:* cosmopolitan.

W. (**Waagenochocha**) CHAO, 1927b, p. 85 [**Productus humboldti* D'ORBIGNY, 1842, p. 54; OD]. *Waagenoconcha* with spreading flanks; ventral trail with smaller spines than corpus and with small rounded bases. *upper Upper Carboniferous–upper Lower Permian:* cosmopolitan.——FIG. 357,*1a–c*. **W. humboldti* (D'ORBIGNY), Lower Permian, Bolivia; shell viewed ventrally, dorsally, posteriorly, ×1 (Muir-Wood & Cooper, 1960).——FIG. 357,*1d*. *W. prophetica* (COOPER & GRANT), upper Finnis Shale, Gzhelian, Texas; detail of ventral valve exterior, ×2 (Muir-Wood & Cooper, 1960).——FIG. 357,*1e,f*. *W. magnifica* COOPER & GRANT, upper Lower Permian, Texas; dorsal valve exterior, part of interior, ×1 (Muir-Wood & Cooper, 1960).

W. (**Gruntoconcha**) ANGIOLINI, 1995, p. 206 [**W. (G.) macrotuberculata;* OD]. Differs from *Waagenoconcha* in having coarse, less elongate spine bases, weak differentiation of anterior nonswollen spine bases; weak rugae near start of ventral trail, steep lateral margins giving more strongly convex transverse profile. [*Septoproductus* FRECH, 1911, p. 132 (type, *Productus abichi* WAAGEN, 1884, p. 697) might be considered a senior synonym, but the type species was misidentified by FRECH and his genus belongs with *Tschernyschewia* STOYANOW, 1910; BRUNTON, 1997 (ICZN Case 3034)]. *upper Lower Permian (Roadian)–lower Upper Permian (Kazanian):* western Himalayas (Karakorum).——FIG. 357,*2a*. **W. (G.) macrotuberculata,* Ufimian, Karakorum; ventral valve exterior, ×1 (new).——FIG. 357,*2b–f*. *W. (G.) abichi*

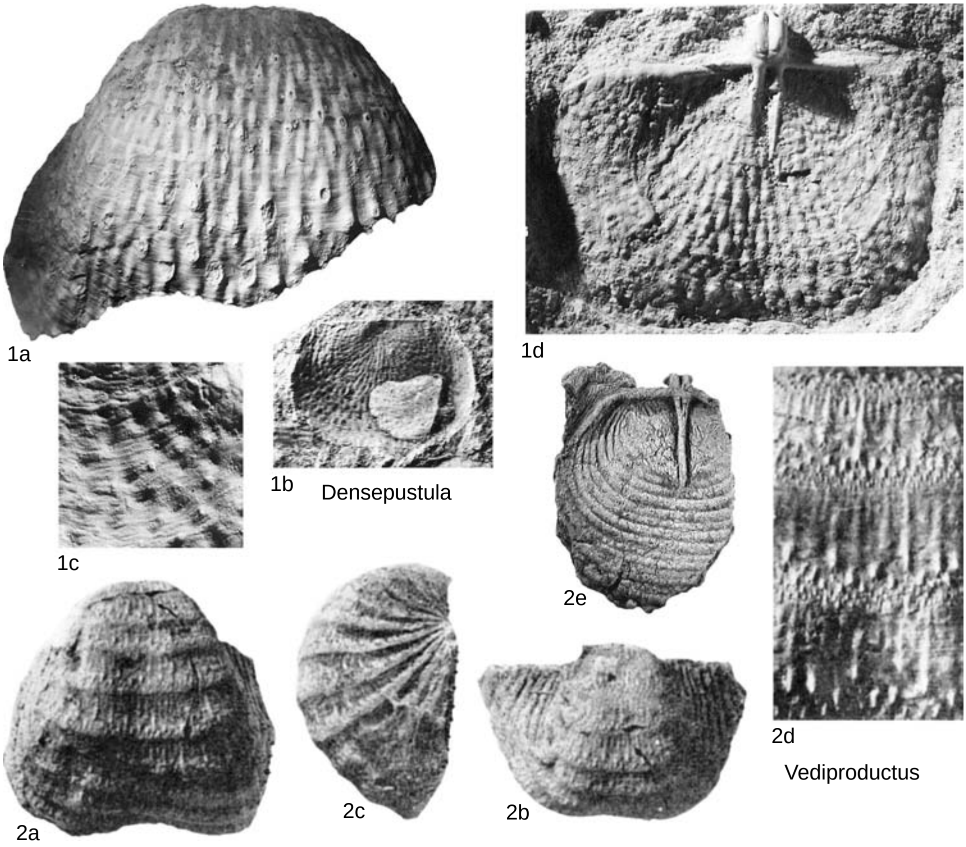


FIG. 356. Echinoconchidae (p. 513–516).

(WAAGEN), ?Kazanian, mid-*Productus* Limestone, Khisor Range; *b,c,* shell viewed ventrally, anteriorly, ×1 (Muir-Wood & Cooper, 1960); *d,* anteroventral view of shell, ×1.5; *e,* dorsal view of shell, ×1.25; *f,* dorsal valve interior, ×1.5 (Grant, 1966).

Balkhasheconcha LAZAREV, 1985, p. 68[66] [**Waagenoconcha balkhashensis* NASIKANOVA in SARYTCHEVA, 1968, p. 106; OD]. Similar to *Waagenoconcha* in ornament, but with buttress plates. *Upper Carboniferous (Bashkirian–Moscovian):* northeastern Arctic Russia.——FIG. 358,*2a–c.* **B. balkhashensis* (NASIKANOVA), Upper Carboniferous, Keregetassk Formation, Kazakhstan; *a,* holotype, ventral valve exterior, PIN 1506/1163, ×1; *b,* incomplete dorsal valve interior, ×1; *c,* detail of ventral external ornament, ×3 (Sarytcheva, 1968).

Buxtoniella ABRAMOV & GRIGORJEVA, 1986, p. 94 [**B. longispina;* OD]. Similar to *Balkhasheconcha* but no anterior band of thinner spines on ventral valve. *Lower Carboniferous (middle Viséan):* Russia.——FIG. 358,*1a–d.* **B. longispina,* middle Viséan, Sokolsk Beds, Verkhoyansk; *a,* holotype, anteroventral view of ventral valve, PIN 4002/858, ×1; *b,* ventral view of ventral exterior, ×1; *c,* dorsal view of incomplete specimen, ×1; *d,* incomplete dorsal valve interior, ×1 (Abramov & Grigorjeva, 1986).

Spinauris ROBERTS, 1971, p. 107 [**S. cristata;* OD]. Resembles *Waagenoconcha,* but lacks well-differentiated finer spines anteriorly; cardinal process shaft weak or lacking, pit variably present; cardinal ridges weak, short, may extend as weak ear baffles, submarginal ridge. *Lower Carboniferous (Tournaisian):* Western Australia.——FIG. 358,*3a–e.* **S. cristata,* lower Tournaisian, Bonaparte Gulf; *a–d,* shell viewed ventrally, posteriorly, laterally, dorsally, ×1; *e,* holotype, dorsal valve interior, CPC 8543, ×1 (Roberts, 1971).

Subfamily PUSTULINAE Waterhouse, 1981

[Pustulinae WATERHOUSE, 1981, p. 71]

Medium to large size; low rugae; spine base pustules may not be arranged in bands; buttress plates, cardinal process pit absent. *Lower Carboniferous (upper Tournaisian–Viséan).*

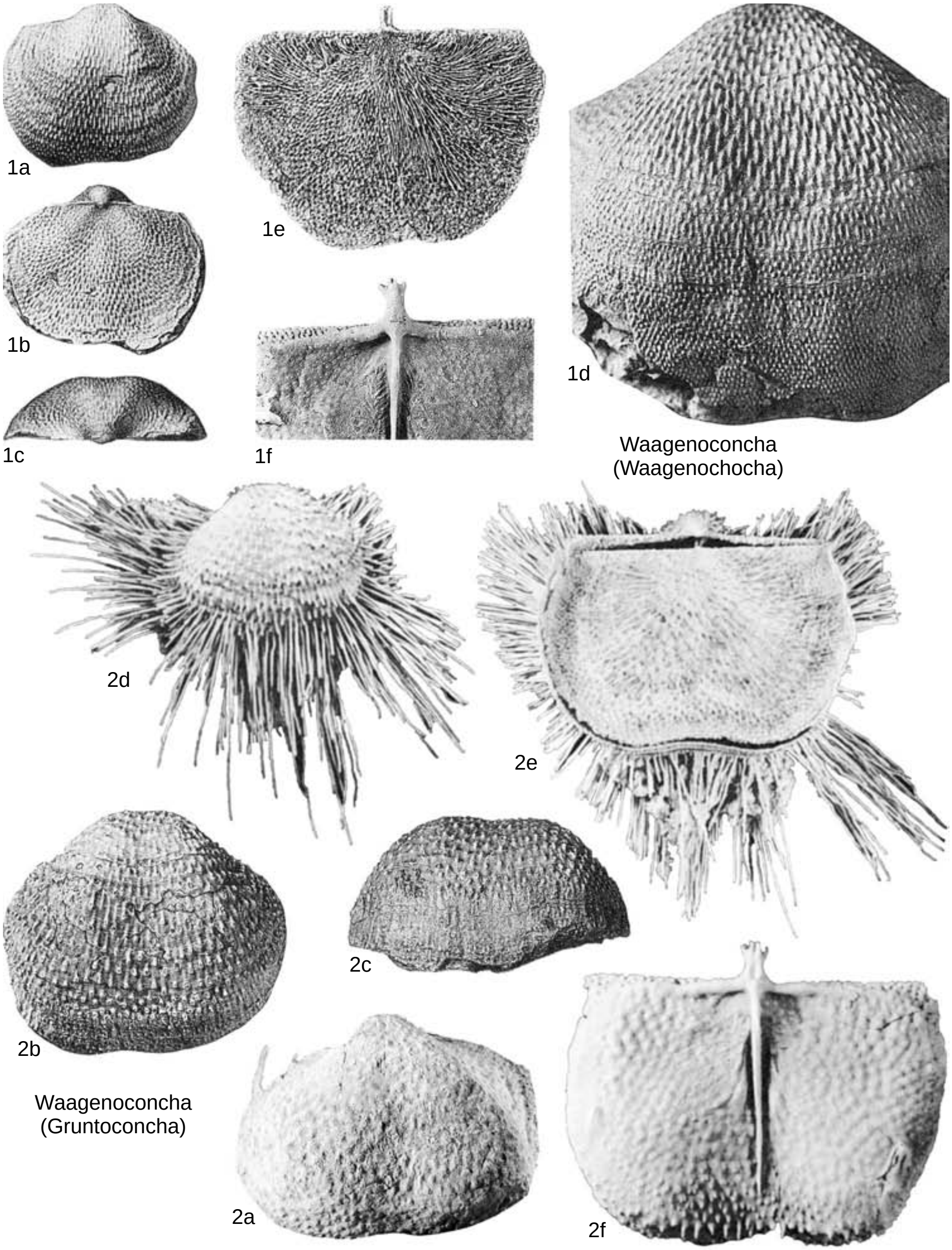


FIG. 357. Echinoconchidae (p. 517–518).

Pustula THOMAS, 1914, p. 259 [**Producta pustulosa* PHILLIPS, 1836, p. 216; OD]. Outline subrectangular with weak ventral sulcus, dorsal median fold, almost planoconvex, trails minimal; spine bases elongate, in irregular concentric bands with weak spine differentiation; cardinal process narrow, dorsal face trifid; cardinal ridges diminish toward ears, no marginal ridges. *Lower Carboniferous (Viséan):* Eurasia, northern Africa, ?North America.——FIG. 359,*1a–f.* **P. pustulosa* (PHILLIPS), Asbian–Brigantian; *a,* holotype, viewed anterolaterally, Lancashire, British Isles, BMNH B419, ×1; *b–e,* specimen viewed ventrally, posteriorly, laterally, dorsally, Staffordshire, ×1 (new); *f,*

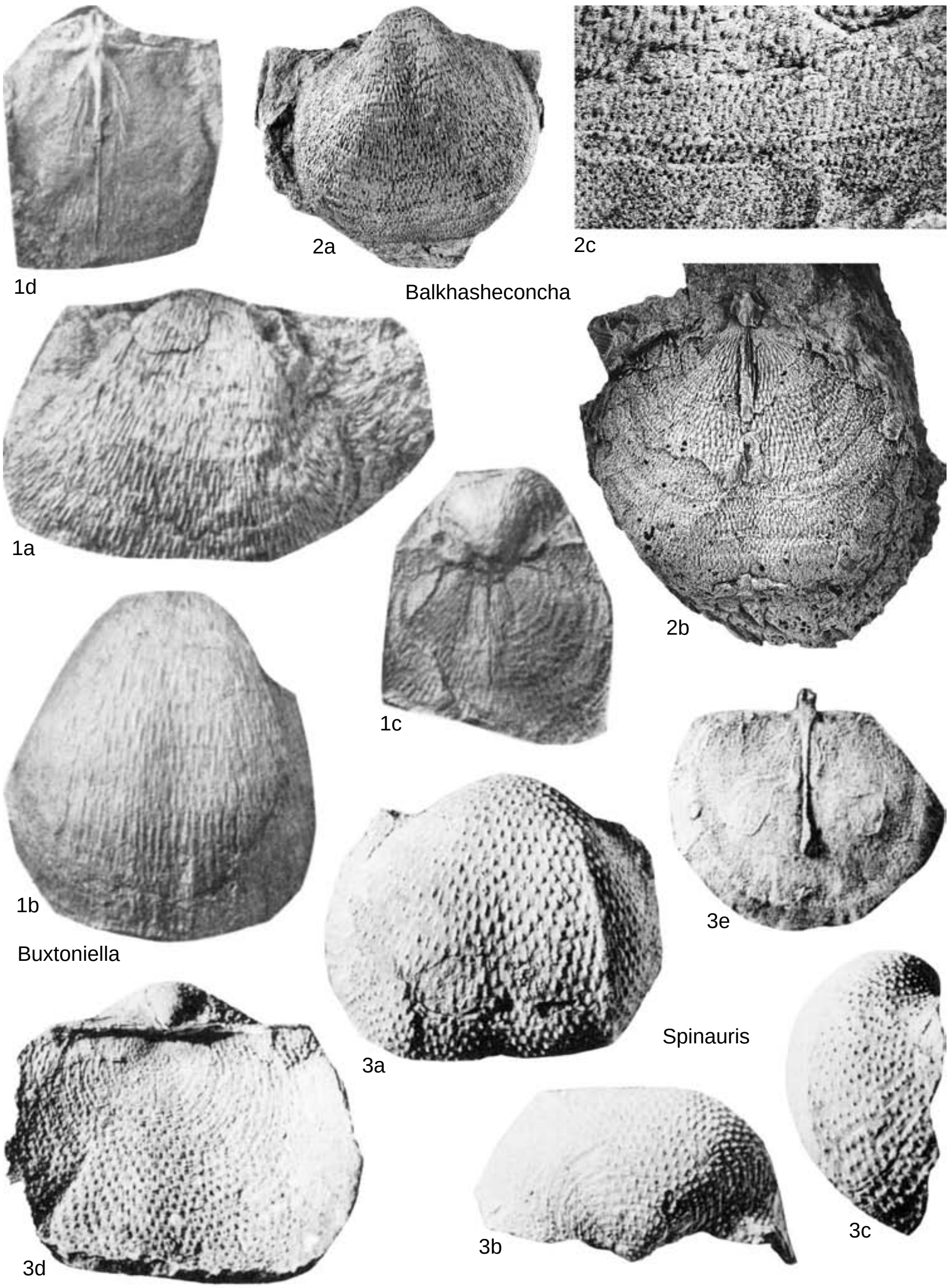


FIG. 358. Echinoconchidae (p. 518).

incomplete dorsal valve interior, Scotland, ×1 (Muir-Wood & Cooper, 1960).

?Etheridgina OEHLERT, 1887b, p. 1278 [**Productus complectens* ETHERIDGE, 1876, p. 462; OD]. Poorly known, possibly representing the young of more than one taxon; ventral valves around 3 mm wide, attached by clasping spines, rugae bearing scattered spines; associated dorsal valves, similarly rugose, spinose; quadrifid cardinal process supported by cardinal ridges, may also be buttress plates. *Lower*

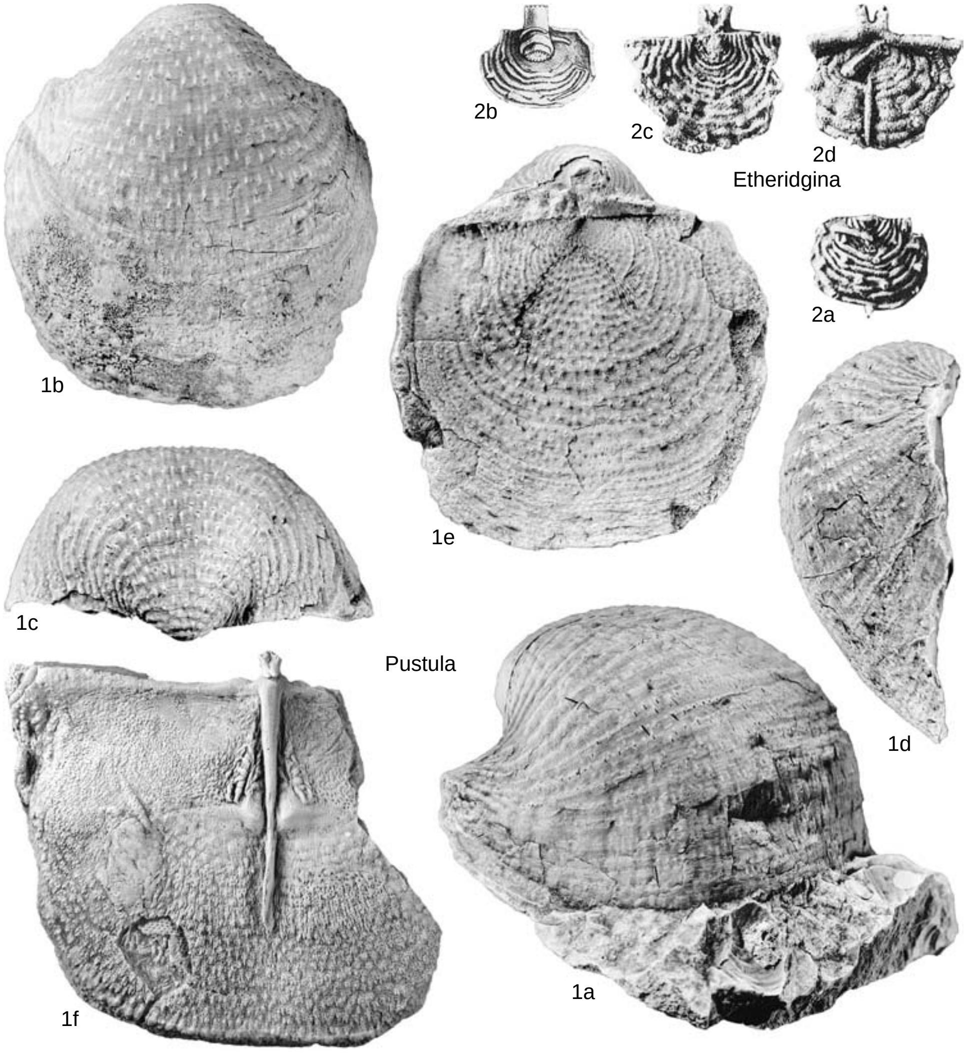


FIG. 359. Echinoconchidae (p. 519–521).

Carboniferous (Viséan): British Isles.——FIG. 359,*2a–d.* **E. complectens* (ETHERIDGE), Brigantian, East Lothian; *a,* ventral valve exterior, ×5; *b,* ventral valve clasping crinoid stem, ×7; *c,d,* incomplete dorsal valve exterior, interior, ×5 (Muir-Wood & Cooper, 1960).

Scutepustula SARYTCHEVA in SARYTCHEVA & others, 1963, p. 165 [**Productus (Waagenoconcha) scutelatus* BALASHOVA, 1955, p. 146; OD]. Size medium; outline subcircular, closely spaced rugae bearing well-differentiated bands of elongate spine bases; otherwise resembles *Pustula. Lower Carboniferous (upper Tournaisian):* Eurasia, North America.——FIG. 360,*1a–e.* **S. scutelata* (BALASHOVA), upper Tournaisian, southeastern Ural Mountains; *a,b,* shell viewed ventrally and with corpus removed, exposing part of dorsal valve external mold, ×1; *c,* ventral ornament viewed posterolaterally, ×3; *d,* ventral ornament viewed anteromedianly showing spine bases, ×5; *e,* ventral valve in lateral profile, ×1 (Sarytcheva & others, 1963).

?Septarinia MUIR-WOOD & COOPER, 1960, p. 251 [**Productus leuchtenbergensis* DE KONINCK, 1847a, p. 226; OD]. Ornamentation resembles *Pustula* on disks, but spines in concentric bands anteriorly, with more prominent dorsal median fold; ventral umbo interior with low median septum. *Lower Carboniferous (Asbian):* western Europe.——FIG. 360,*2a–f.* **S. leuchtenbergensis* (DE KONINCK), Asbian; *a,b,* lectotype, internal mold, viewed posteriorly, dorsally, Visé, Belgium, BMNH BD 193, ×1.5 (Mundy & Brunton, 1983); *c,* latex replica of posterior corpus cavity showing median septa, Visé, Belgium, ×1.5 (Muir-Wood & Cooper, 1960); *d–f,* shell viewed ventrally, laterally, anteriorly, Cork, Ireland, ×1 (Mundy & Brunton, 1983).

Family SENTOSIIDAE McKellar, 1970

[Sentosiidae McKellar, 1970, p. 27]

Echinoconchoids having shallow corpus cavity; concentric bands, spine differentiation commonly absent. *Middle Devonian (Givetian)–Upper Permian (Changhsingian).*

Subfamily SENTOSIINAE McKellar, 1970

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 928, *ex* Sentosiidae McKellar, 1970, p. 27]

Sentosiids without teeth; spines thin, may have elongate bases. *Upper Devonian (Famennian)–Upper Permian (Changhsingian).*

Tribe SENTOSIINI McKellar, 1970

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 929, *ex* Sentosiidae McKellar, 1970, p. 27]

Concentric rugae or lamellae may be as bands anteriorly. *Upper Devonian (Famennian)–Upper Permian (Changhsingian).*

Sentosia Muir-Wood & Cooper, 1960, p. 196 [**Krotovia praecursor* Stainbrook, 1947, p. 313; OD]. Size small to medium; outline transversely elliptical, ventral umbo small; rugae delicate, irregular, associated with fine prostrate spines from small rounded bases; cardinal process bilobed, quadrifid, lateral ridges short, only slightly divergent from hinge. *Upper Devonian (Famennian):* North America, ?northern Africa, Europe.——Fig. 361,*1a–e.* **S. praecursor* (Stainbrook), Famennian, New Mexico; *a–c,* shell viewed ventrally, posteriorly, laterally, ×1; *d,* shell viewed dorsally, ×2; *e,* part of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Alatoproductus Jing & Zhu in Jing & Hu, 1978, p. 120 [**A. truncatus;* OD] [=*Chenxianoproductus* Liao & Meng, 1986, p. 79 (type, *C. nitens;* OD); ?=*Chonostegoidella* Li & Yang in Li, Yang, & Feng, 1986, p. 219 (type, *C. longlinensis;* OD)]. Small to medium size, subtrigonal in outline with hinge less than maximum width; small cicatrix present in some; ventral median sulcus shallow; dorsal disk gently concave, trail short; short elongate spine bases with suberect fine spines becoming weakly arranged concentrically anteriorly; interiors poorly known, but with lateral ridges curving to lateral margins. *?Lower Permian, Upper Permian (Kazanian–Changhsingian):* China.——Fig. 361, *2a,b.* **A. truncatus,* Kunfeng Formation, Anhui; dorsal valve external mold, interior, ×1.5 (Jin & Hu, 1978).——Fig. 361,*2c,d. A. nitens* Liao & Meng, Upper Permian, Hunan; *c,* holotype, ventral valve exterior, NIGP 74181, ×1.5; *d,* external mold of dorsal valve, ×2 (new).

Jakutella Abramov, 1970, p. 119 [**J. sarytchevae;* OD]. Medium; ventral profile strongly convex; concentric ornament anteriorly lamellose, somewhat resembling *Stegacanthia;* no differentiation of spines, arranged quincuncially posteriorly; interiors unknown. *Upper Carboniferous (Moscovian–Kasimovian):* northern Asia.——Fig. 361,*4a–d.* **J. sarytchevae,* Moscovian, Yakutsk; *a,* anterior view of ventral valve exterior, ×1 (Abramov, 1970); *b,c,* posteroventral, lateral views of ventral valve, ×1; *d,* external mold of dorsal valve, ×1 (new).

Laminatia Muir-Wood & Cooper, 1960, p. 189 [**Productella laminata* Kindle, 1909, p. 18; OD]. Small; gently concavoconvex; concentric ornament strong, lamellose; spines differentiated into bands and by size; lateral ridges short, divergent. *Upper Devonian (Famennian):* southern North America, Australia, ?Kazakhstan.——Fig. 362,*1a–f.* **L. laminata* (Kindle), uppermost Famennian, New Mexico; *a,* ventral valve exterior, ×2; *b–e,* shell viewed anteriorly, laterally, posteriorly, dorsally, ×2; *f,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Malloproductus Tachibana, 1981, p. 62, *nom. nov. pro Nodella* Tachibana, 1964, p. 38 [**M. pexus;* OD]. Size medium; similar to *Sentosia,* but possibly with longer fine spines, extending almost radially; cardinal process elongate, median septum long, narrow. *Upper Devonian (Famennian):* Japan.——Fig. 362,*3a–c.* **M. pexus,* Famennian, northeastern Japan; *a,* ventral valve exterior with corona of spines, squashed, ×1; *b,* replica of dorsal valve exterior, including cardinal process, ×1.5; *c,* replica of dorsal valve interior, ×1 (new).

Markamia Jin Yu-gan & Shi Quan in Jin & others, 1985, p. 192 [**M. transversa;* OD] [=*Tuberella* Li in Li, Yang, & Feng, 1986, p. 222 (type, *T. typica;* OD); *Uraloconchus* Lazarev, 1990, p. 112 (type, *Productus jakovlevi* Chernyschev, 1902, p. 300; OD)]. Size small to medium; outline transverse, weakly concavoconvex; spines prostrate, coarse posteriorly on narrow lamellose bands separated by narrower bands of smooth shell; dorsal spines fine; interiors unknown. *Upper Carboniferous (Gzhelian)–Lower Permian (Artinskian):* China, Tibet, western Ural Mountains.——Fig. 362,*4a,b.* **M. transversa,* Gzhelian–Asselian, Xizang; *a,* ventral valve exterior, NIGP 60757, ×1; *b,* dorsal valve exterior, ×1 (Jin & others, 1985).

Productellana Stainbrook, 1950, p. 373 [**P. bifaria;* OD]. Small; outline subcircular, reportedly with short interarea, open delthyrium; rugae weak, irregular, slightly lamellose; spines widely spaced, weakly concentric. *Upper Devonian (Famennian):* North America, ?China.——Fig. 362,*2a–e.* **P. bifaria,* Famennian, Aplington, Iowa; *a–c,* holotype,

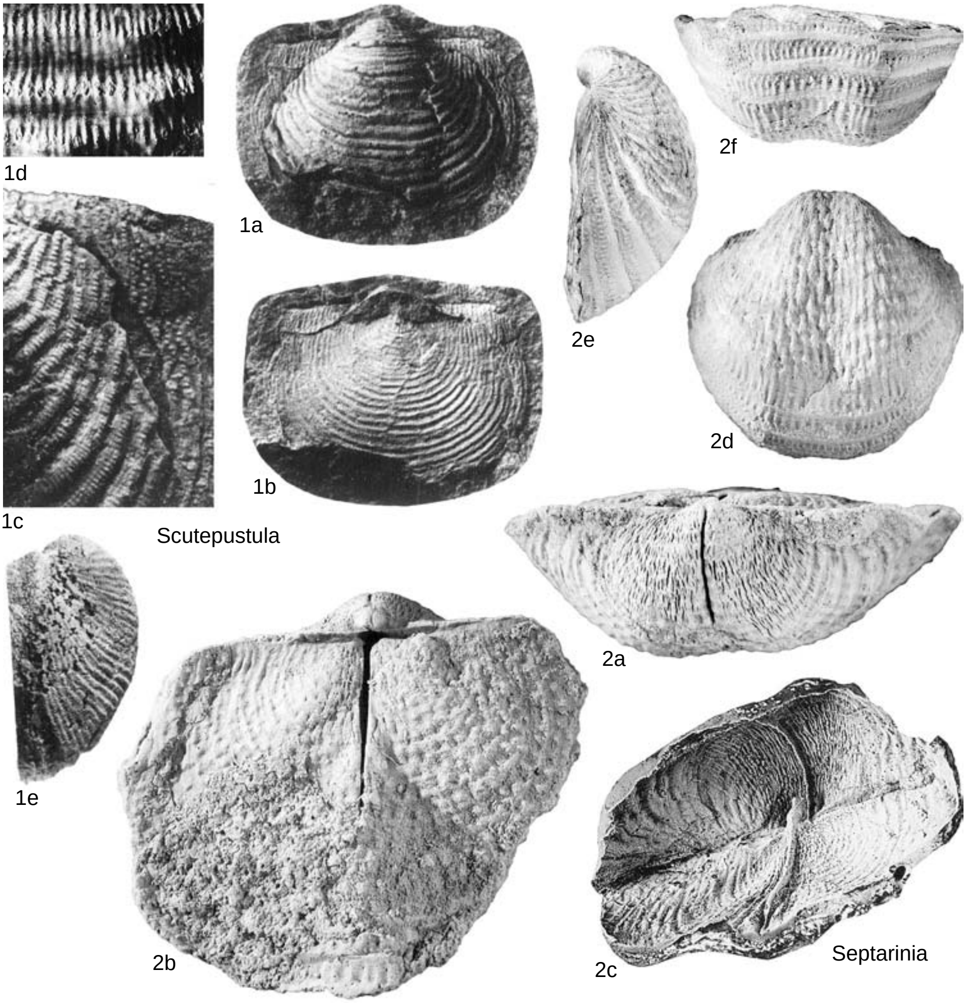


FIG. 360. Echinoconchidae (p. 521–522).

viewed ventrally, laterally, anteriorly, SUI 21656A, ×1; *d,* shell viewed dorsally, ×1.5; *e,* shell viewed dorsally, ×3 (new).

Sentosioides LAZAREV in LAZAREV & SUUR'SUREN, 1992, p. 69 [**S. tsagankhalginensis;* OD]. Ventral umbo moderately inflated; elongate spine-base pustules on both valves, ventral spines thicker than *Sentosia;* weak concentric ornament. *Upper Devonian (upper Famennian):* Russia, Asia.——FIG. 362,*5a–d.* **S. tsagankhalginensis,* uppermost Famennian, Gobi Altai, Mongolia; *a,* incomplete ventral valve exterior, ×2 (new); *b,* replica of incomplete dorsal valve exterior, ×1.5; *c,* part of dorsal valve interior plus external mold, ×1.6 (new); *d,* holotype, incomplete dorsal valve interior, PIN 3385/1050, ×1 (Lazarev & Suur'suren, 1992).

Stegacanthia MUIR-WOOD & COOPER, 1960, p. 198 [**S. bowsheri;* OD]. Size medium; concavoconvex with short trails, ornament lamellose, each band with elongate spine bases, spines prostrate; lateral ridges diverge toward ears. *Lower Carboniferous (upper Tournaisian–lower Viséan):* southern North America, ?northern Africa, Europe.——FIG. 361,*3a–e.* **S. bowsheri,* Ivorian, New Mexico; *a–d,* holotype, viewed ventrally, anteriorly, laterally, dorsally, USNM 123963, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Tribe BAGRASIINI Nalivkin, 1979

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 929, *ex* Bagrasiinae NALIVKIN, 1979, p. 109]

Elongate spine bases simulate ribs on both valves. *Lower Carboniferous (upper Tournaisian–lower Viséan).*

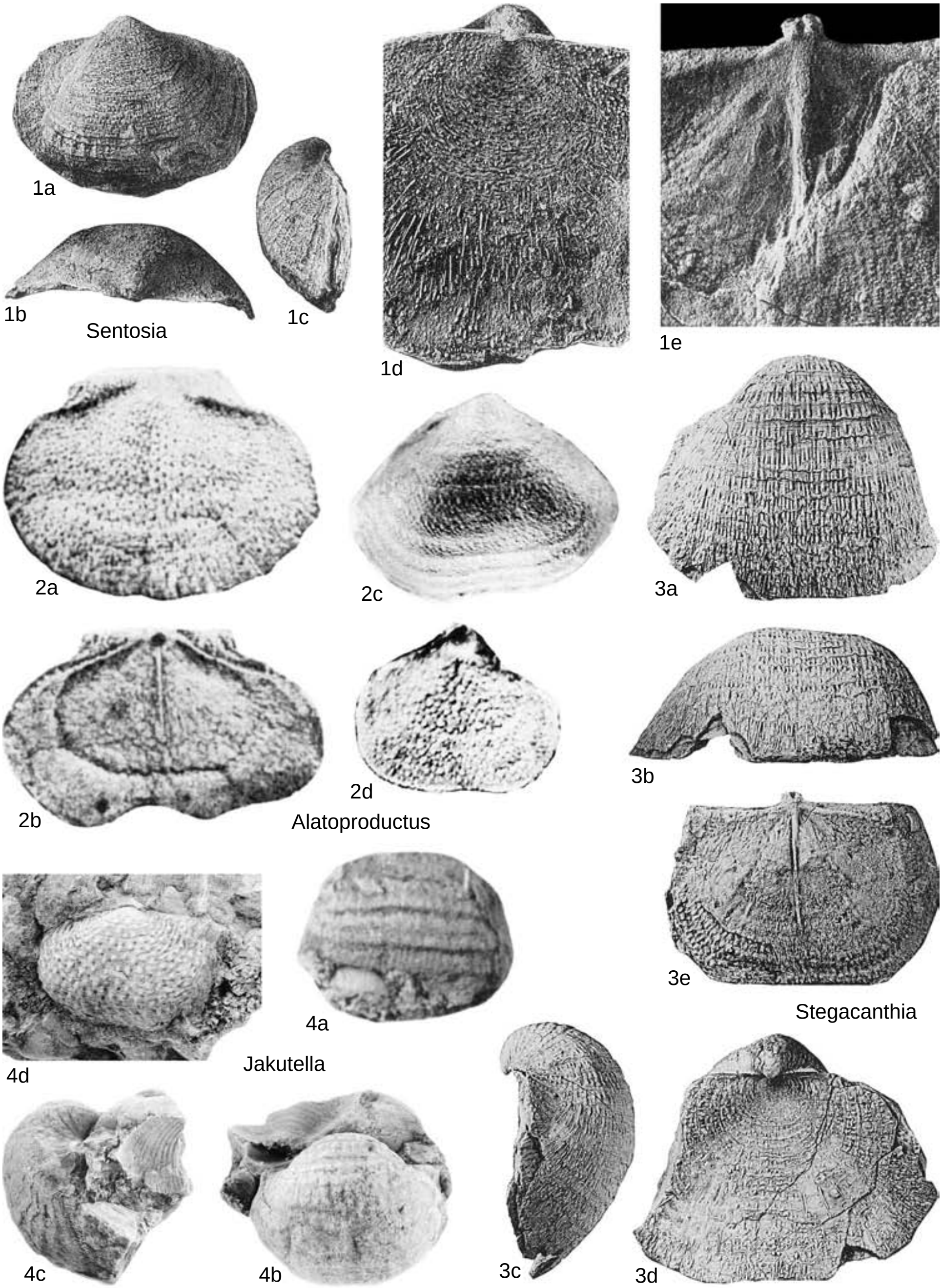


FIG. 361. Sentosiidae (p. 522–523).

Ericiatia MUIR-WOOD & COOPER, 1960, p. 172 [**Productus newberryi* HALL, 1857, p. 180; OD; =*Productella newberryi* HALL, 1883, pl. 49, fig. 1–3] [=*Bagrasia* NALIVKIN in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 231 (type, *Productus chonetiformis* KRESTOVNIKOV & KARPYSHEV, 1948, p. 48)]. Size small to medium; outline subcircular to transverse, elongate spine bases simulate ribbing over

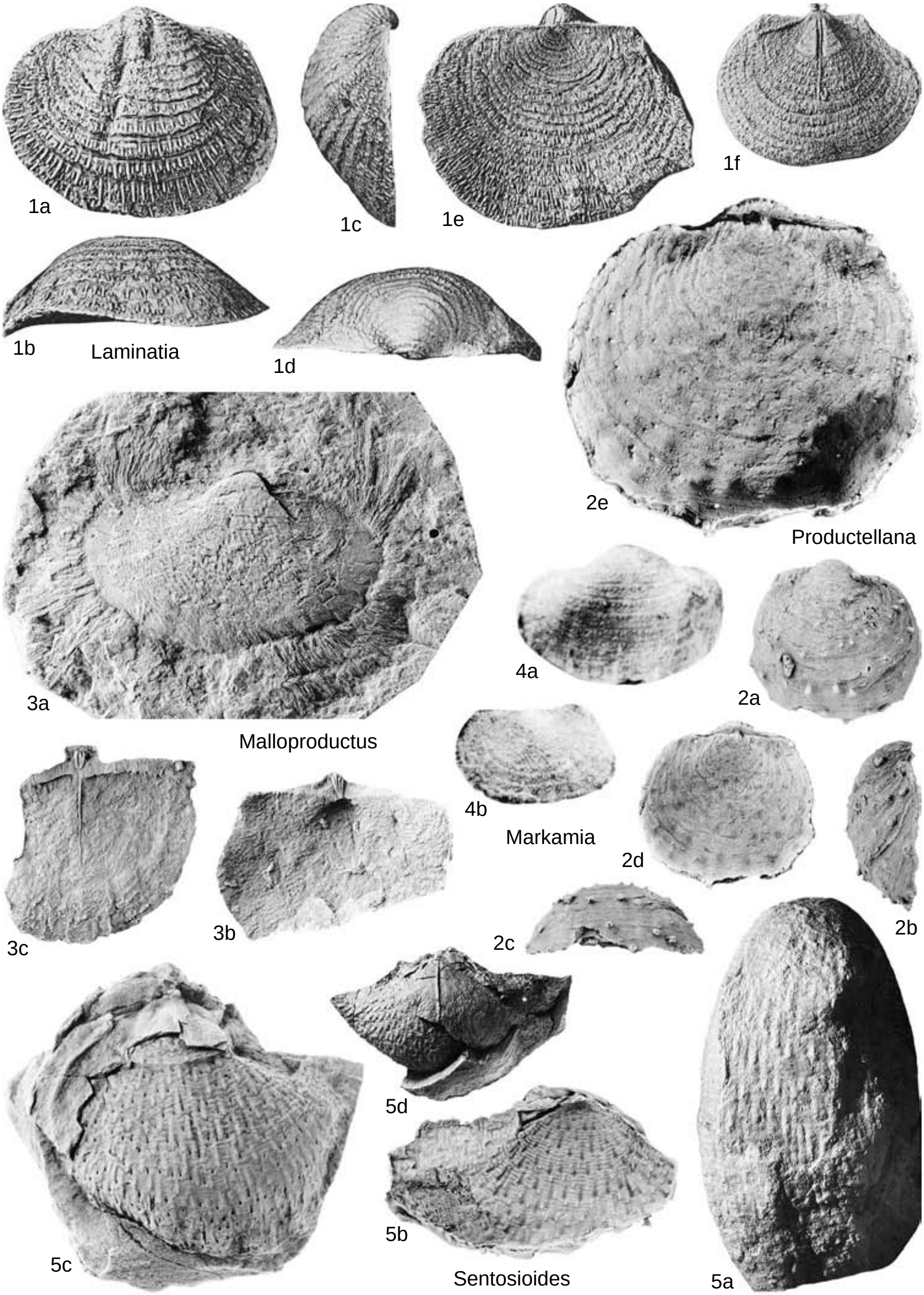


FIG. 362. Sentosiidae (p. 522–523).

complete shell; cardinal process weakly supported by short lateral ridges. *Lower Carboniferous (upper Tournaisian–lower Viséan):* western Ural Mountains, North America.——FIG. 363*a–d.* **E. newberryi* (HALL), upper Kinderhookian–lower Osagean, Ohio; *a,* ventral valve exterior, ×1; *b,* lateral profile

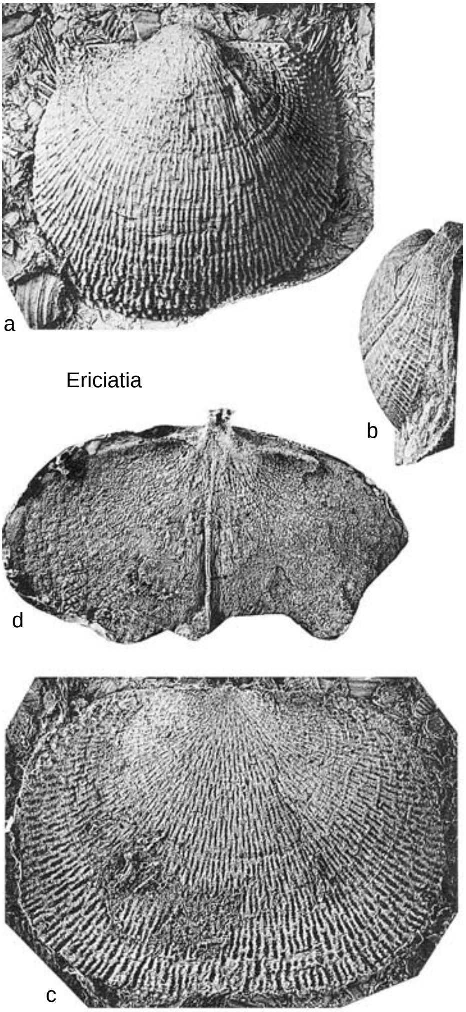


FIG. 363. Sentosiidae (p. 524–526).

of ventral valve, ×1; *c,* replica of dorsal valve exterior, ×1; *d,* replica of incomplete dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Subfamily CAUCASIPRODUCTINAE Lazarev, 1987

[Caucasiproductinae Lazarev, 1987, p. 49]

Sentosiids with teeth, sockets; ventral spines relatively thick, suberect; lateral ridges short, divergent anteriorly. *Middle Devonian (Givetian)–Upper Devonian (Famennian).*

Caucasiproductus Lazarev, 1987, p. 50[47] [**C. gretchishnikovae;* OD]. Size small; narrow ginglymus; thick-walled with up to 0.5 mm thick ventral spines; short ventral median septum; cardinal process strongly V-shaped. *Middle Devonian (Givetian):* Transcaucasia.——Fig. 364,*2a.* **C. gretchishnikovae,* Givetian, Transcaucasia; holotype, ventral valve exterior, PIN 4127/103, ×3 (Lazarev, 1987).——Fig. 364,*2b–e. Caucasiproductus* sp.; *b,c,* dorsal, posterior views of shell, ×3 (Lazarev, 1987); *d,* ventral valve internal mold plus shell anterolaterally, ×3; *e,* dorsal valve interior, ×3 (Lazarev, 1990).

Praewaagenoconcha Sokolskaya, 1948, p. 132 [**Productus orelianus* von Möller, 1871, p. 389; OD]. Small; thinner shelled than *Caucasiproductus,* spines relatively fine in roughly concentric arrangement, commonly with spine bearing median ridge; no ventral median septum. *Upper Devonian (Famennian):* eastern Europe.——Fig. 364,*3a–d.* **P. oreliana* (von Möller), Famennian, Moscow basin; *a,b,* ventral valve exterior viewed ventrally, laterally, ×2; *c,* shell viewed posteriorly, ×2; *d,* shell viewed dorsally showing spines, ×2 (new).

Strophoproductus Nalivkin, 1937, p. 46 [**Productella hystricula* Hall, 1867c, p. 178; OD]. Small; undulose concentric ornament; weak elongate spine bases, spines probably recumbent; cardinal process strongly bilobed internally, with pit and short socket ridges. *Upper Devonian (Frasnian):* North America, Eurasia.——Fig. 364,*1a–c.* **S. hystriculus* (Hall), Frasnian, New York; *a,* ventral valve exterior, ×2; *b,* dorsal valve exterior, ×2; *c,* dorsal valve interior on left, ×2 (Muir-Wood & Cooper, 1960).

Family UNCERTAIN

Septiconcha Termier & others, 1974, p. 125 [**S. taeniosa;* OD]. Insufficient morphology to assign, but if deep corpus cavity, then assigned to Juresaniinae. *Upper Permian (Kazanian):* Afghanistan.

Superfamily LINOPRODUCTOIDEA Stehli, 1954

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 929, *ex* Linoproductinae Stehli, 1954, p. 319] [=Striatoidea Nalivkin, 1979, p. 105]

Trail commonly long but simple; ribbing regular, entire, relatively fine, commonly delicately sinuose; ventral spines at hinge, diverse on rest of valve, never few, thick and symmetrical; dorsal valve without spines except grandaurispinins and some gigantoproductins. *Lower Devonian (Pragian)–Upper Permian (upper Tatarian).*

Family LINOPRODUCTIDAE Stehli, 1954

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 296, *ex* Linoproductinae Stehli, 1954, p. 319]

Linoproductoids with deep corpus cavity, distinct trails; commonly no dorsal spines.

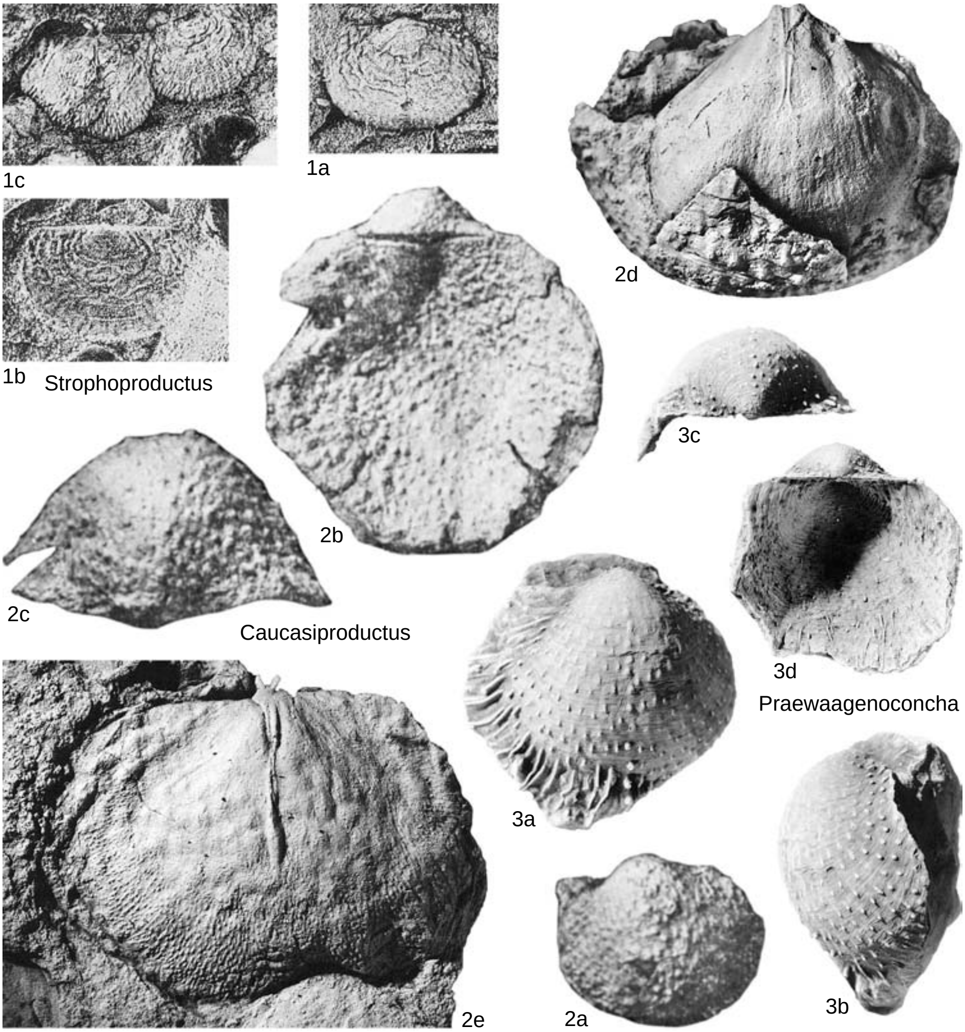


FIG. 364. Sentosiidae (p. 526).

Lower Carboniferous (middle Viséan)–Upper Permian (Tatarian).

Subfamily LINOPRODUCTINAE Stehli, 1954

[Linoproductinae STEHLI, 1954, p. 319] [=Fluctuariinae NALIVKIN, 1979, p. 107; Stepanoviellinae WATERHOUSE, 1975, p. 12]

Linoproductids without marginal structures or dorsal spines. *Lower Carboniferous (middle Viséan)–Upper Permian (Kazanian).*

Linoproductus CHAO, 1927b, p. 128 [**Productus cora* D'ORBIGNY, 1842, p. 55; OD] [=*Euproductus* WHITEHOUSE, 1928, p. 281, obj.; *Cora* FREDERICKS, 1928, p. 781, 790, obj; *Levisapicus* TONG in TONG & others, 1990, p. 66[100] (type, *L. giganteus*)]. Medium to large, outline elongate subcircular; ventral profile inflated posteriorly, dorsal corpus gently concave; hinge commonly widest part of shell; ribbing complete, tends to be distorted at spine bases, which are widely scattered ventrally; spines also closely set in one or two rows along hinge; rugae on ventral ears, flanks, dorsal corpus; cardinal process sessile, trifid, supported by lateral ridges; adductor scars, brachial ridges weakly marked. [*Levisapicus,* Zhigou Formation (Sakmarian) of Sichuan, is reported as having a group of spines on ears.] *upper Upper Carboniferous–Upper Permian (Kazanian):* cosmopolitan.——FIG. 365,*1a–f.* **L. cora* (D'ORBIGNY), Lower Permian, Bolivia (Cochabamba); *a–d,* shell viewed ventrally, posteriorly, dorsally, laterally, ×1; *e,* large example viewed

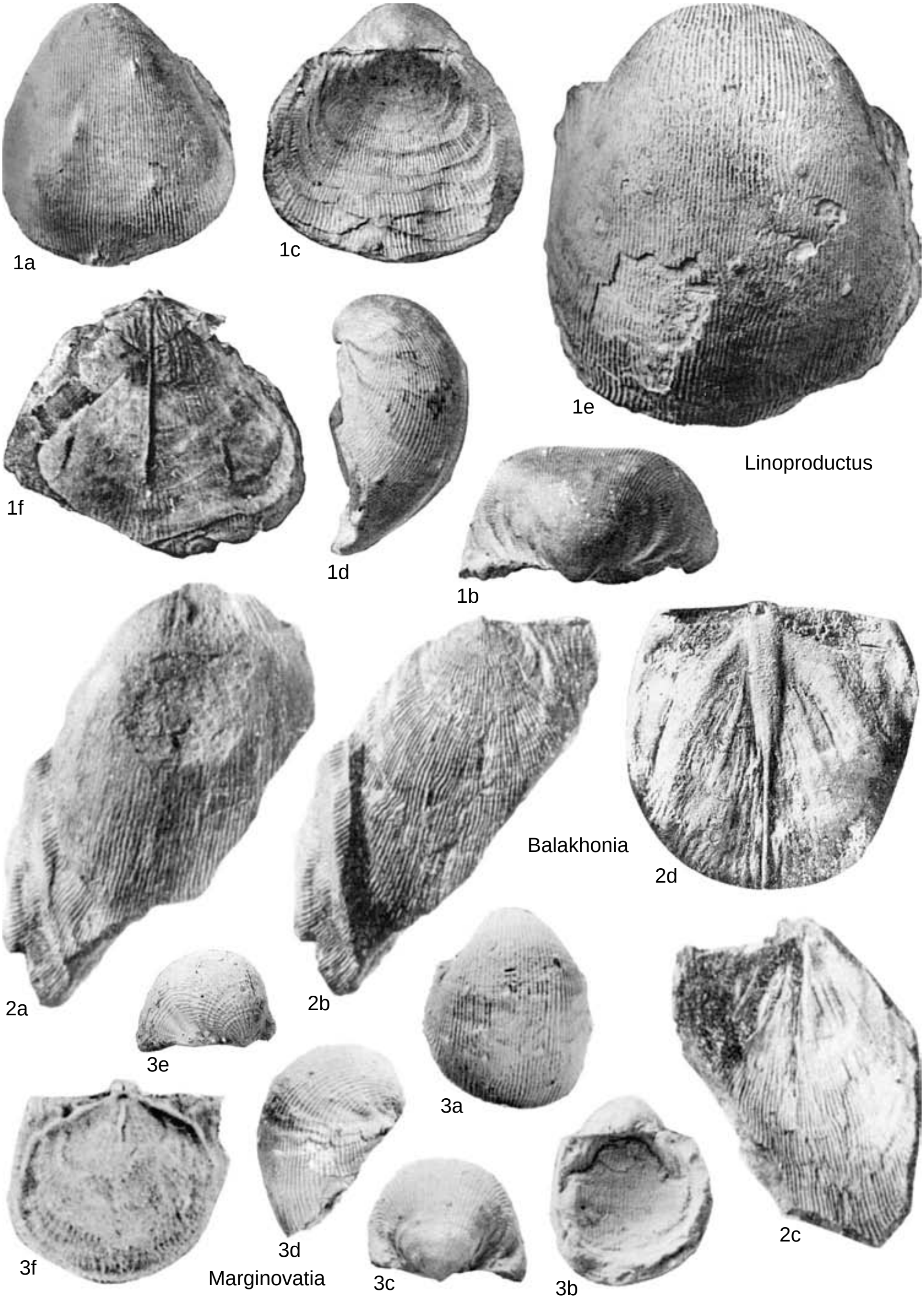


FIG. 365. Linoproductidae (p. 527–530).

ventrally, ×1; *f,* incomplete dorsal valve interior, ×1 (Kozłowski, 1914).

Balakhonia SARYTCHEVA in SARYTCHEVA & others, 1963, p. 231 [**B. ostrogensis;* OD]. Medium size; ventral profile convex with long trail, ears prominent, flanks gently sloping; spines at hinge, rarely on ventral corpus where finer than ribs; cardinal process sessile with well-separated lobes; dorsal adductor scars di-

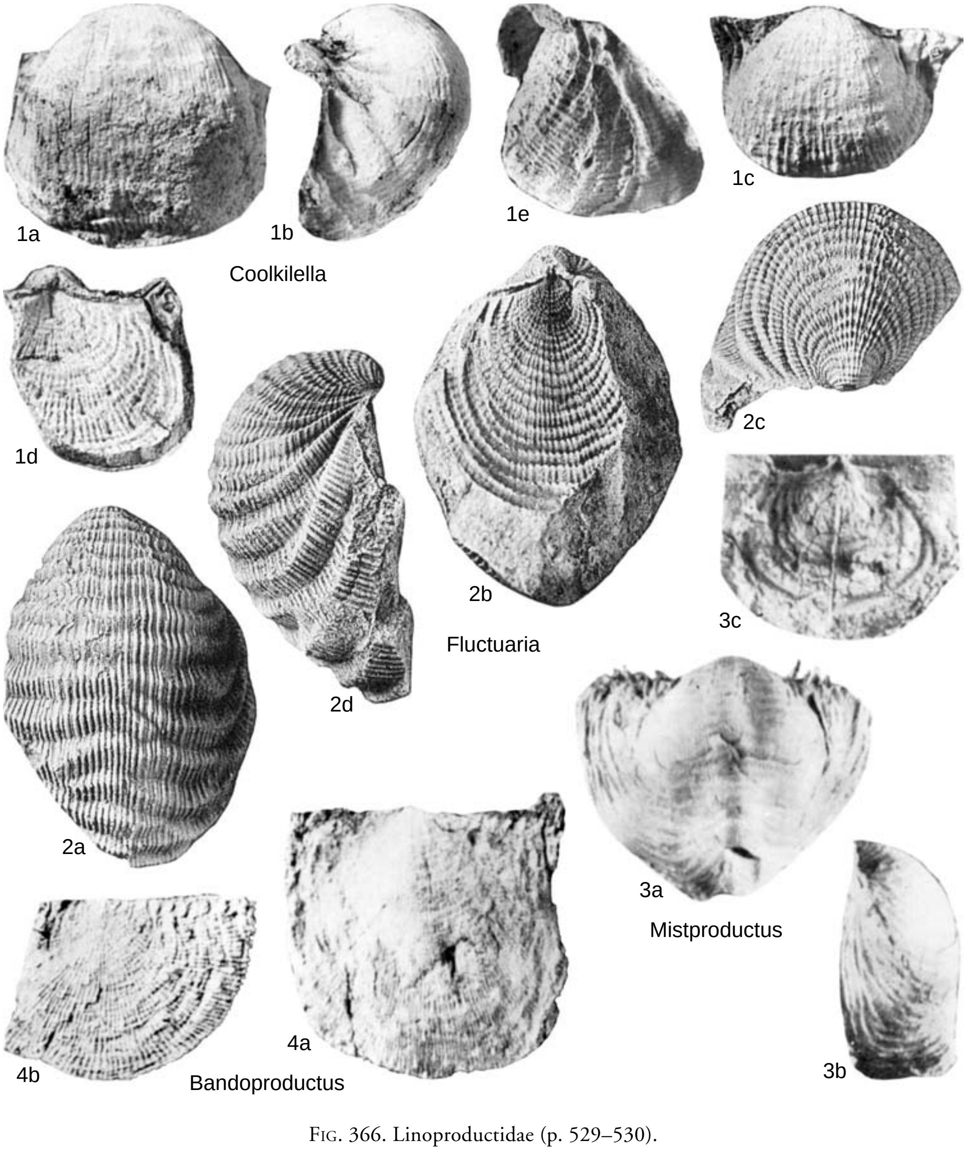


FIG. 366. Linoproductidae (p. 529–530).

vided, bordered posterolaterally by ridges. _upper Lower Carboniferous (upper Viséan–lower Serpukhovian), ?Upper Carboniferous (Bashkirian):_ Eurasia, ?northern Africa.——FIG. 365,_2a–d_. *_B. ostrogensis,_ upper Viséan–Serpukhovian, Ostrog Formation, Kuzbass; _a–c,_ holotype, internal mold of ventral valve, dorsal valve external, internal molds, PIN 1493/278, ×1; _d,_ incomplete dorsal valve interior, ×2 (Sarytcheva & others, 1963).

Bandoproductus JING & SUN, 1981, p. 138 [*_B. hemiglobica;_ OD]. Medium size, resembling _Linoproductus,_ but with fine ventral spines no wider than ribs on corpus, single row of hinge spines; trails short; thin shelled. _Upper Carboniferous (Gzhelian)–Lower Permian (Sakmarian):_ Tibet (Xizang).——FIG. 366,_4a,b_. *_B. hemiglobica,_ Lower Permian, Bando Group, Tibet; _a,_ ventral valve exterior, ×1; _b,_ external mold of incomplete dorsal valve, ×1 (Jin & Sun, 1981).

Coolkilella ARCHBOLD, 1993, p. 14 [*_Cancrinella coolkilyaensis_ ARCHBOLD, 1983b, p. 241; OD]. Resembles _Cancrinella,_ but with planoconvex corpus, strongly geniculate dorsal valve, long trails; rugae at ears, weak on disks; spines in two rows on ears, sparse on venter from weakly developed, elongate bases. _upper Lower Permian (upper Artinskian–lower Kungurian):_ Western Australia.——FIG. 366,_1a–e_. *_C. coolkilyaensis_ (ARCHBOLD), upper Lower

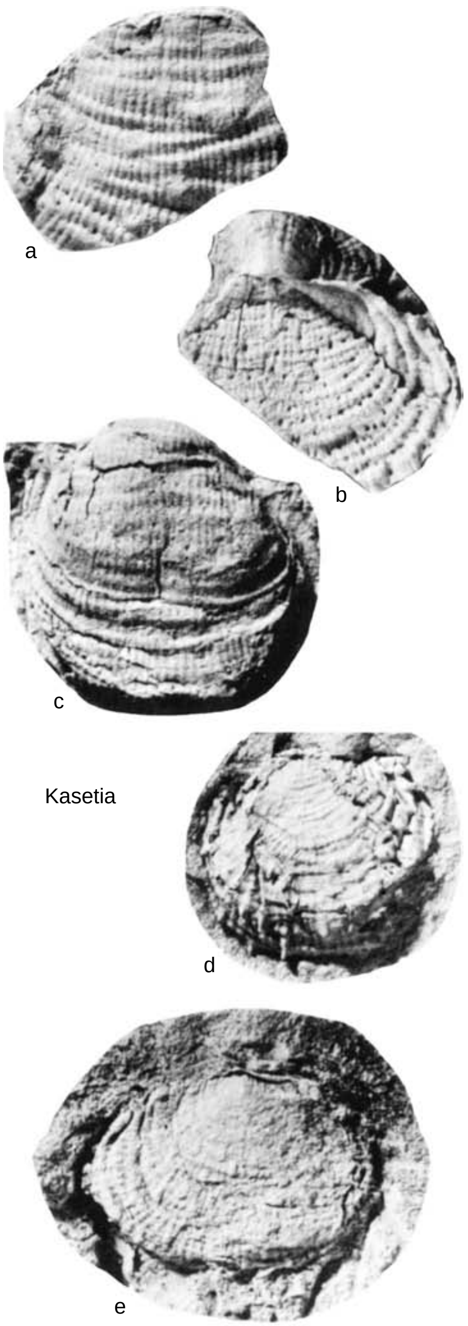


FIG. 367. Linoproductidae (p. 530).

Permian, Coolkilya Greywacke, Carnarvon basin; *a,b,* holotype, internal mold viewed anteroventrally, laterally, CPC 19920A, ×1.4; *c,* internal mold viewed posteroventrally, ×1.5; *d,* incomplete internal mold viewed dorsally, ×1.5; *e,* external mold of dorsal valve viewed laterally showing strong geniculation, ×1.4 (Archbold, 1983b).

Fluctuaria MUIR-WOOD & COOPER, 1960, p. 303 [**Productus undatus* DEFRANCE, 1826, p. 354; OD]. Small; elongate, nongeniculate profile; rugae prominent, entire, increasing in size anteriorly; spines at hinge, ears, otherwise rare; cardinal process small, sessile; cardinal ridges weak. *Lower Carboniferous (upper Viséan), ?Upper Carboniferous (?lower Moscovian):* Eurasia, ?North America.——FIG. 366,*2a–d.* **F. undata* (DEFRANCE), Asbian, Visé, Belgium; ventral, dorsal, posterior, lateral views of specimen, ×2 (Muir-Wood & Cooper, 1960).

Kasetia WATERHOUSE, 1981, p. 89 [**K. kaseti;* OD]. Resembles *Coolkilella,* but small with irregular discontinuous rugae; spines in clusters on ears, weakly developed spine bases. *Lower Permian (Artinskian):* southern Thailand.——FIG. 367*a–e.* **K. kaseti,* Lower Permian, Ko Yao Noi Formation, Thailand; *a,b,* holotype, incomplete internal mold of ventral, dorsal valves, TBR 287, ×3; *c,* ventral valve internal mold, ×3; *d,* replica of ventral valve exterior, ×3; *e,* exfoliated dorsal valve interior, ×3 (Waterhouse, 1981).

Marginovatia GORDON & HENRY, 1990, p. 533 [**Productus ovatus* var. *minor* SNIDER, 1915, p. 79; OD]. Small, less than 20 mm wide; spines in one or two rows near ventral hinge, others sparsely scattered; rugae at ears, less commonly complete on ventral disk; marginal ridges in both valves at start of trails. *Lower Carboniferous (middle Viséan)–Upper Carboniferous (Bashkirian):* USA, Arctic Canada. ——FIG. 365,*3a–f.* **M. minor* (SNIDER), Chesterian, Oklahoma; *a–d,* ventral, dorsal, posterior, lateral views of shell, ×2; *e,* posterolateral view of shell, ×2; *f,* dorsal valve interior, ×3 (Gordon & Henry, 1990).

?Mistproductus YANG DE-LI, 1991, p. 81[90] [**M. eucallusus;* OD]. Poorly known, similar to *Linoproductus,* but may be folded anteriorly, possibly resulting from shell damage, and reportedly with cicatrix surrounded by rhizoid spines on ears, flanks; corpus cavity deep. *Lower Permian (Artinskian–Kungurian):* southern China.——FIG. 366,*3a–c.* **M. eucallusus,* Lower Permian, Guangxi; *a,b,* ventral valve exterior, lateral view, ×1; *c,* dorsal valve interior, ×1.5 (Yang De-li, 1991).

Subfamily ANIDANTHINAE Waterhouse, 1968

[Anidanthinae WATERHOUSE, 1968a, p. 1172]

Linoproductids with well-developed ears, marginal structures; concentric lamellae (series of trails) commonly on dorsal valve; corpus cavity commonly deep. *Upper Carboniferous (Bashkirian)–Upper Permian (Capitanian).*

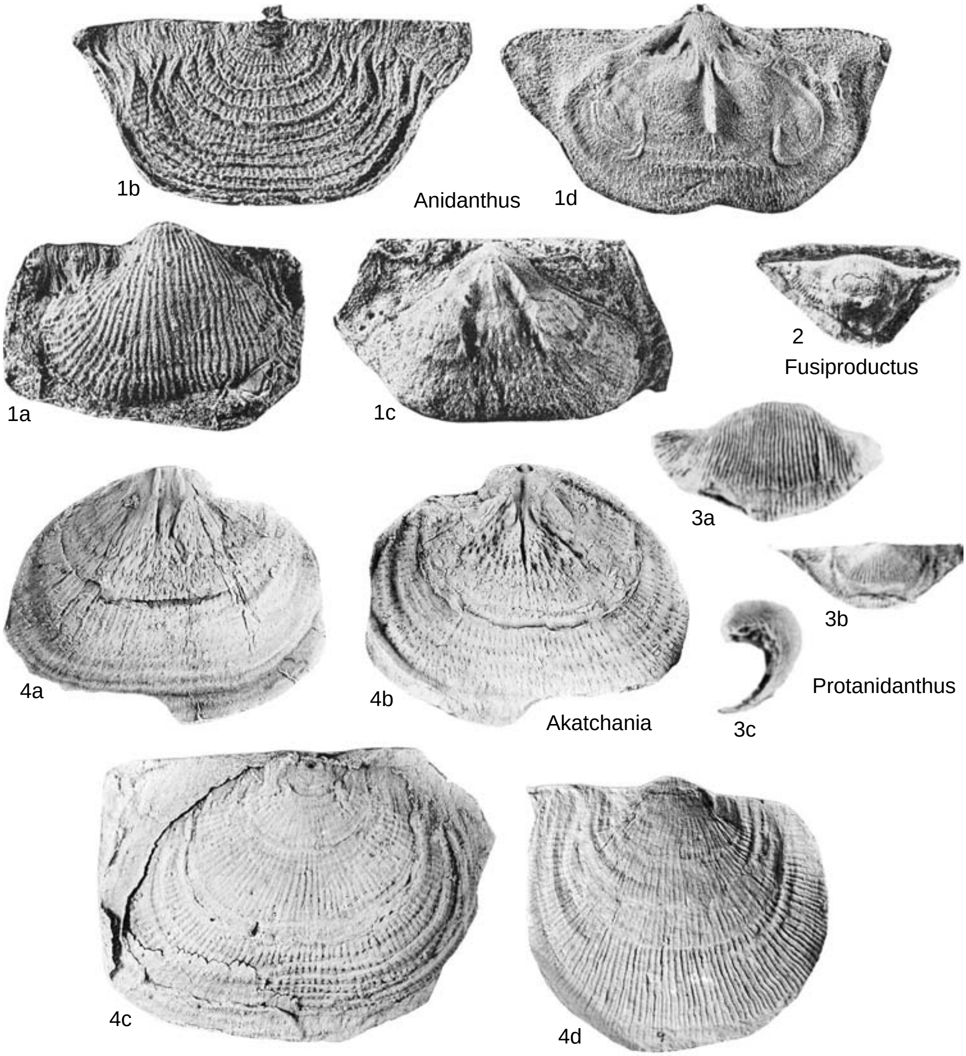


FIG. 368. Linoproductidae (p. 531–533).

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, 1924, p. 8)]. Medium size, transverse shells with large, well-differentiated ears forming maximum width; ribbing on both valves, except ears; rugae lamellose dorsally; spines in row near hinge, widely scattered on corpus, trail; dorsal interior with thickened shell posteromedianly, median septum about half disk length. *upper Lower Permian–lower Upper Permian:* Australia, northern and central Asia, central America.——FIG. 368,*1a–d*. **A. springsurensis* (BOOKER), New South Wales; *a,* ventral valve exterior, ×2; *b,* dorsal valve exterior, ×2; *c,* ventral valve interior, ×2; *d,* replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Akatchania KLETS in ABRAMOV & GRIGORJEVA, 1988, p. 135 [**A. plana;* OD]. Medium size, hinge width approximately equal to corpus width; cavity shallow; rugae on ventral flanks and ears, dorsal valve with widely separated lamellae; spines near hinge only, extending posterolaterally; median septum short; lateral, marginal ridges complete in both valves. *Lower Permian (Asselian):* central Siberia. ——FIG. 368,*4a–d*. **A. plana,* Lower Permian, Katchan Formation, southern Verkhoyan; *a,b,* holotype, internal mold viewed ventrally, dorsally,

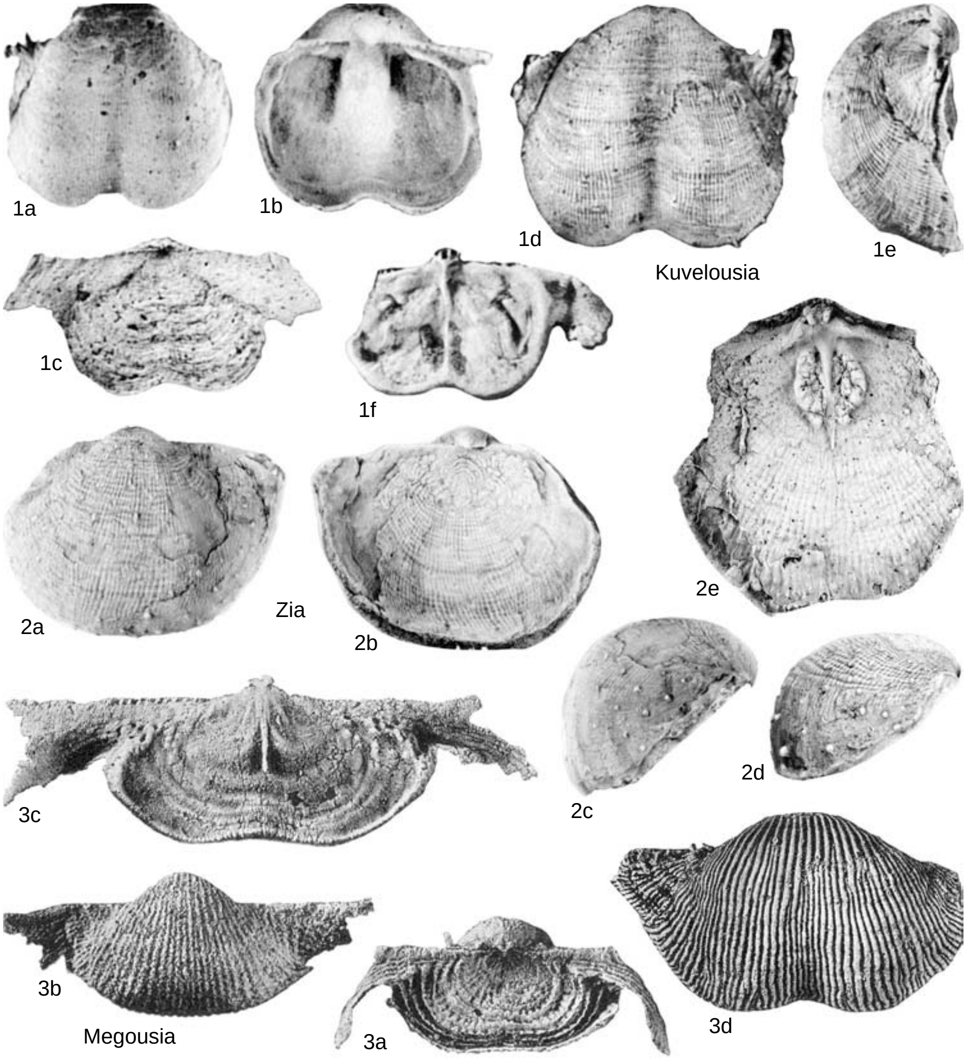


FIG. 369. Linoproductidae (p. 532–533).

M.Ch. 14019-1/50, ×2; *c,* dorsal valve external mold, ×2 (Abramov & Grigorjeva, 1988); *d,* ventral valve exterior, ×2 (new).

Fusiproductus WATERHOUSE, 1975, p. 12 [**Linoproductus fusiformis* HUANG, 1932, p. 45; OD]. Poorly known small shells with highly enrolled ventral valve; outline wide with subtubular ventral ears; ribbing fine; spines single on ears, lacking on venter. *Upper Permian (Capitanian):* China (Guizhou), ?Urals, ?Siberia.——FIG. 368,*2.* **F. fusiformis* (HUANG), Capitanian, Guizhou; ventral valve exterior, ×1 (HUANG, 1932).

Kuvelousia WATERHOUSE, 1968a, p. 1175 [**K. sphiva;* OD] [=*Nothokuvelousia* WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 62 (type, *N. aurifera*)]. Resembles *Megousia,* but larger with dorsal valve heavily thickened; median septum may reach marginal ridge. *Upper Permian (Kazanian):* Arctic Canada, USA, eastern Australia.——FIG. 369,*1a–f.* **K. sphiva,* Kazanian, Degerbols Formation, Arctic Canada; *a–c,* holotype, ventral valve exterior, interior, dorsal valve exterior, GSC 22910, ×1; *d,e,* ventral valve exterior, viewed laterally, ×1; *f,* dorsal valve interior, ×1 (Waterhouse, 1968a).

Megousia MUIR-WOOD & COOPER, 1960, p. 309 [**M. auriculata;* OD]. Resembles *Anidanthus,* but ribbing on extended ears curving anterodorsally. *lower Upper Permian:* North America, eastern Australia, Tasmania.——FIG. 369,*3a–c.* **M. auriculata,* Upper Permian, Word Limestone, Texas; *a,* holotype, viewed dorsally, USNM 124108b, ×2; *b,* ventral valve exterior, ×2; *c,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).——Fig. 369,*3d. M. alata* (Cooper), Monos Formation, Sonora, Mexico; ventral valve exterior, ×2 (Muir-Wood & Cooper, 1960).

Protanidanthus Liao, 1979, p. 536[544] [**P. elegans;* OD]. Similar to *Anidanthus,* but lacks dorsal lamellae. *Lower Permian:* China.——Fig. 368,*3a–c. *P. elegans,* Asselian, Guizhou; *a,* ventral valve exterior, ×1; *b,* dorsal valve exterior, ×1; *c,* lateral view of shell, ×1 (Liao, 1979).

Zia Sutherland & Harlow, 1973, p. 59 [**Z. novamexicana;* OD] [=*Semilunataproductus* Han Tong-xiang in Han & others, 1987, p. 317 (type, *S. semilunatus;* OD)] Medium size, around 30 mm wide; outline subcircular, profile geniculate with flattened ventral disk; disks reticulate, trails ribbed; spines scattered on ventral valve, but larger on trail; cardinal process sessile, lateral ridges diverge into ear baffles. [*Semilunataproductus,* Gzhelian to Asselian of Shanxi, China, is minute, around 4 mm wide, with flattened (?cicatrix) ventral disk and somewhat rugose dorsal tail.] *Upper Carboniferous (Bashkirian)–Lower Permian (Asselian):* southern USA.——Fig. 369,*2a–e. *Z. novamexicana,* Morrowan, New Mexico; *a–c,* holotype, viewed ventrally, dorsally, laterally, OU 7790, ×1; *d,* lateral view of ventral valve exterior, ×1; *e,* incomplete replica of dorsal valve interior, ×1.5 (Sutherland & Harlow, 1973).

Subfamily GRANDAURISPININAE Lazarev, 1986

[Grandaurispininae Lazarev, 1986c, p. 32] [=Paucispinauriinae Waterhouse in Waterhouse & Briggs, 1986, p. 2]

Linoproductids with thin spines also on dorsal corpus; ribbing may be reduced; marginal structures, series of trails absent. *Upper Carboniferous (Gzhelian)–Upper Permian (Tatarian).*

Grandaurispina Muir-Wood & Cooper, 1960, p. 305 [**C. kingorum;* OD]. Medium size with hinge at maximum width; dorsal disk weakly concave with short trail; ribbing fine (capillae) commonly indistinct, rugae weak on dorsal disk; spines thick, in clusters on ears and flanks, thin with slightly elongate bases quincuncially arranged ventrally; dorsal valve with dimples, thin suberect spines; cardinal process sessile, trifid, lacking pit; lateral ridges short, medium septum long. *Upper Permian (Kazanian):* USA.——Fig. 370,*1a–d. *G. kingorum,* Upper Permian, Word Formation, Texas; *a,* holotype, viewed dorsally, USNM 123454, ×1.5; *b,* ventral valve exterior, ×1; *c,d,* dorsal valve viewed externally showing capillae, internally, ×2 (Muir-Wood & Cooper, 1960).

Cancrinella Fredericks, 1928, p. 784 [**Productus cancrini* de Verneuil, 1845, p. 245; OD] [=*Platycancrinella* Waterhouse, 1983b, p. 126 (type, *P. grandauris*)]. Small to medium size, corpus almost planoconvex, deep cavity; spines with elongate swollen bases on ribs, evenly distributed, clusters on ears, spines fine on dorsal valves; rugae weak on both valves; cardinal process sessile; lateral ridges close to hinge; median septum commonly divided posteriorly. [*Platycancrinella,* from Upper Permian of Nepal, said to differ by having less crowded spines on ears and flanks.] *Upper Carboniferous (Gzhelian)–Upper Permian (Wordian):* cosmopolitan.——Fig. 370,*2a–d. *C. cancrini* (de Verneuil), Lower Permian, Arctic Russia; *a–c,* shell viewed ventrally, dorsally, laterally, ×1; *d,* part of dorsal valve interior, ×4 (Sarytcheva, 1977).——Fig. 370,*2e,f. C. subquadrata* Cooper & Grant, Upper Permian, Word Formation, Texas; *e,* dorsal valve exterior, ×2; *f,* dorsal valve interior, ×1 (Cooper & Grant, 1975).——Fig. 370,*2g,h. C. altissima* (R. H. King), Gzhelian, Wayland Shale, Texas; shell viewed ventrally, dorsally, ×1 (Muir-Wood & Cooper, 1960).

Holotricharina Cooper & Grant, 1975, p. 1173 [**H. hirsuta;* OD]. Resembles *Grandaurispina* with ventral spines of two sizes, but lacks ventral ribbing. *Lower Permian–lower Upper Permian:* USA.——Fig. 371,*1a–e. *H. hirsuta,* Lower Permian, Road Canyon Formation, Texas; *a,* holotype, ventral valve exterior, USNM 149896a, ×1; *b,c,* ventral valve exterior viewed ventrally, laterally, ×1; *d,* shell viewed dorsally, ×2; *e,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

Lyonia Archbold, 1983b, p. 244 [**Linoproductus cancriniformis* var. *lyoni* Prendergast, 1943, p. 24; OD]. Resembles *Cancrinella,* but with strong hinge spines, no ear clusters, dorsal spines developed anteriorly; cardinal process small, unusually sessile, unsupported by ridges, lacking clear lateral ridges. *Lower Permian (Sakmarian):* Western Australia, ?Himalayas.——Fig. 372,*1a–e. *L. lyoni* (Prendergast), Sakmarian, Lyons Group, Carnarvon basin; *a,* holotype, vental valve exterior, AMF 36530, ×1; *b,* ventral valve exterior, ×1; *c,* dorsal valve external mold, ×1; *d,* dorsal valve internal mold, ×1; *e,* replica of dorsal cardinalia, ×4.5 (Archbold, 1983b).

Paucispinauria Waterhouse, 1983b, p. 130 [**Terrakea concava* Waterhouse, 1964, p. 67; OD]. Similar to *Terrakea,* but possibly differing in its coarser ventral spines and band of coarse spines at base of dorsal trail. *upper Lower Permian–lower Upper Permian:* southern New Zealand, Australia.——Fig. 371,*2a–e. *P. concava* (Waterhouse), low Upper Permian, *Productus* Creek Limestone, Southland, New Zealand; *a,b,* holotype, ventral valve internal mold viewed posteriorly, replica of dorsal valve exterior, NZGS BR 200, ×2; *c,d,* ventral valve exterior viewed anteriorly, posteroventrally, ×2; *e,* replica of dorsal valve interior, ×2 (Waterhouse, 1964).

Stepanoviella Zavodowsky, 1960, p. 336 [**S. paracurvata;* OD]. Resembles *Globiella,* but with planoconvex deep corpus profile; outline more transverse, with recumbent, suberect spines on ventral valve, suberect spines on dorsal trail. *Upper Permian (Kazanian–Tatarian):* northeastern Russia.——Fig. 370,*3a–e. *S. paracurvata,* Kazanian,

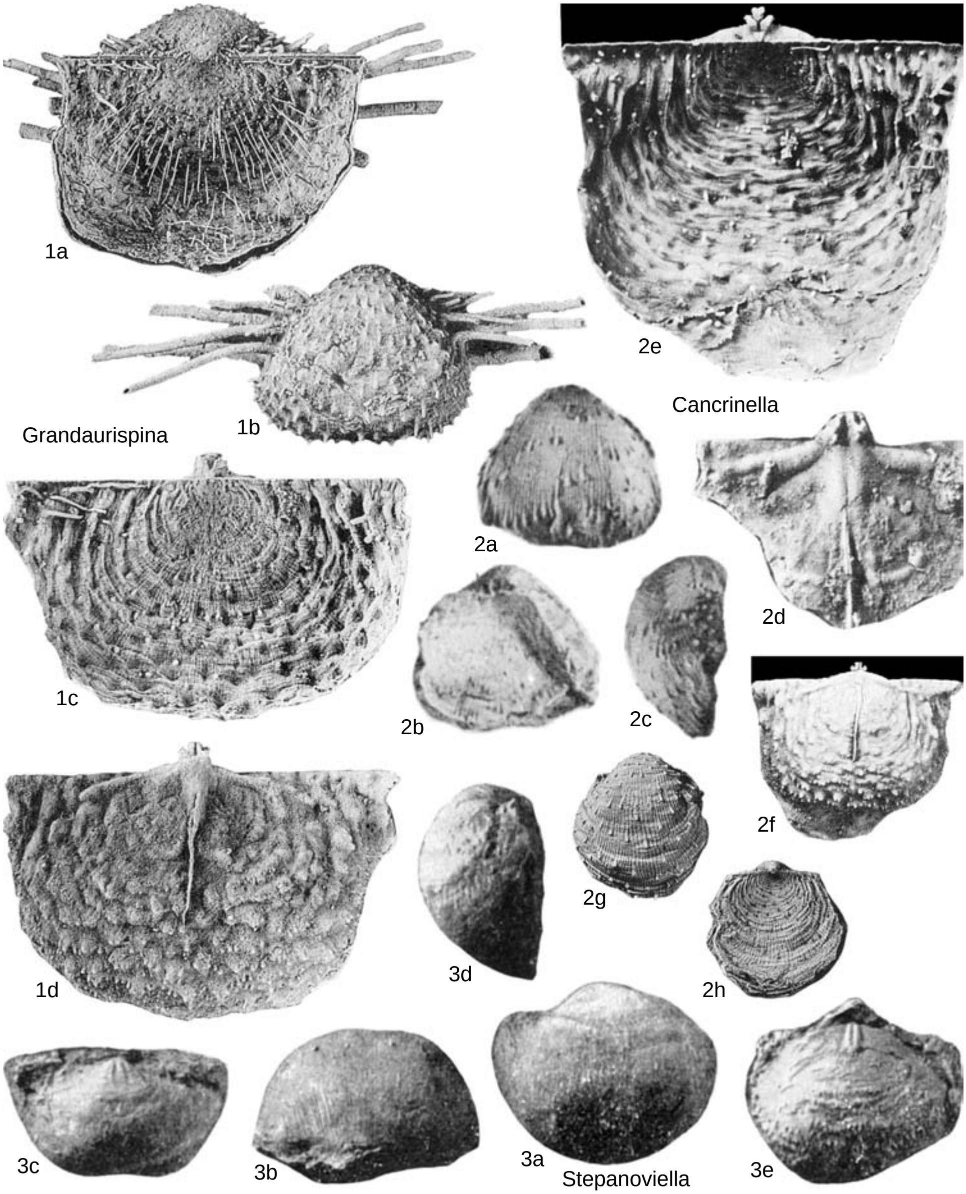


FIG. 370. Linoproductidae (p. 533–534).

Khivatch Horizon, Kolymo-Omolon; *a–d,* holotype, viewed ventrally, anteriorly, posteriorly, laterally, TsNIGRA 30/9081, ×1; *e,* dorsal valve interior, ×1 (Zavodowsky, 1960).

Terrakea BOOKER, 1930, p. 66 [**Productus brachythaerus* MORRIS in DE STREZELECKI, 1845, p. 284, *non* G. B. SOWERBY, 1844, p. 158; SD MAXWELL, 1956, p. 333] [=*Saetosina* WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 54 (type, *Terrakea multispinosa* DEAR, 1971, p. 18)]. Medium size, gently concavoconvex profile, moderate to deep corpus; ribbing on both valves, ventrally with swollen elongate spine bases with semirecumbent spines; spines on dorsal valve mainly anteriorly; dorsal lateral ridges slightly divergent from hinge; median ridge commonly weakly divided posteriorly. *Lower Permian–lower Upper Permian:* eastern Australia, New Zealand, Russian Arctic.——FIG. 372,*2a–d.* **T. brachythaerum* (MORRIS), upper Marine Series, New South Wales; *a,* ventral valve internal mold viewed

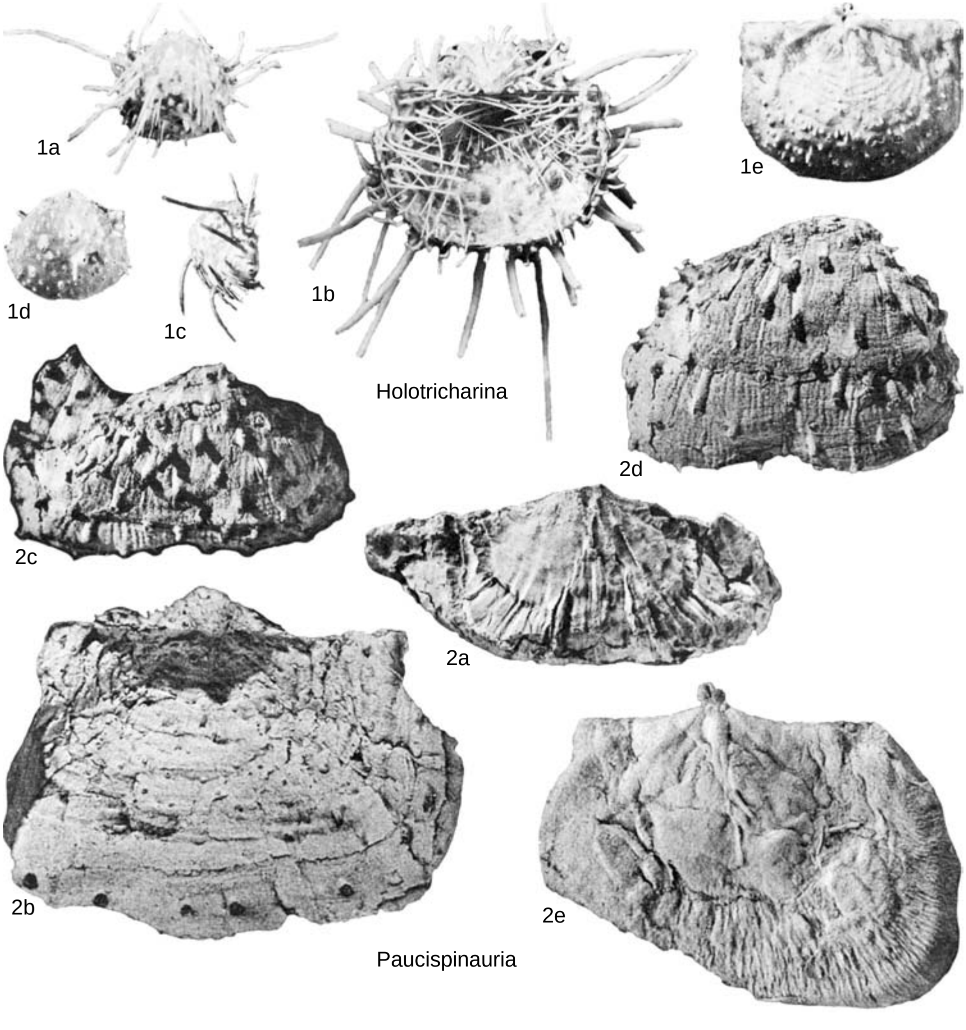


FIG. 371. Linoproductidae (p. 533).

laterally, ×1; *b,* exfoliated dorsal valve exterior, ×1; *c,* replica of shell viewed dorsally, ×1; *d,* replica of dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).——FIG. 372,*2e,f. T. fragile* (DANA); ventral valve internal mold, ventral valve exterior, ×1 (Muir-Wood & Cooper, 1960).

Subfamily SIPHONOSIINAE
Lazarev, 1986

[Siphonosiinae LAZAREV, 1986c, p. 32]

Linoproductids with elongate outline, short tubiform ventral trail; hinge narrower than maximum width; spines rhizoid, on ventral valve only; marginal structures at borders of both valves. *upper Lower Permian (Artinskian–Kungurian).*

Siphonosia COOPER & GRANT, 1975, p. 1188 [**S. alleni;* OD]. Small siphonate shells; beak with small cicatrix; weakly reticulate disks; spines posterolaterally on ventral valve; ventral diductor scars widely triangular; cardinal process sessile, narrow quadrifid; lateral ridges strongly divergent; brachial ridges elongate, reaching disk borders. *upper Lower Permian (Artinskian–Kungurian):* USA.——FIG. 373*a–f.* **S. alleni,* Cathedral Mountain Formation, Texas; *a–c,* holotype, ventral valve viewed ventrally, posteriorly, laterally, USNM 152789a, ×1.5; *d,* holotype, ventral valve viewed internally, USNM 152789a, ×1.5; *e,* dorsal valve exterior, ×2; *f,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

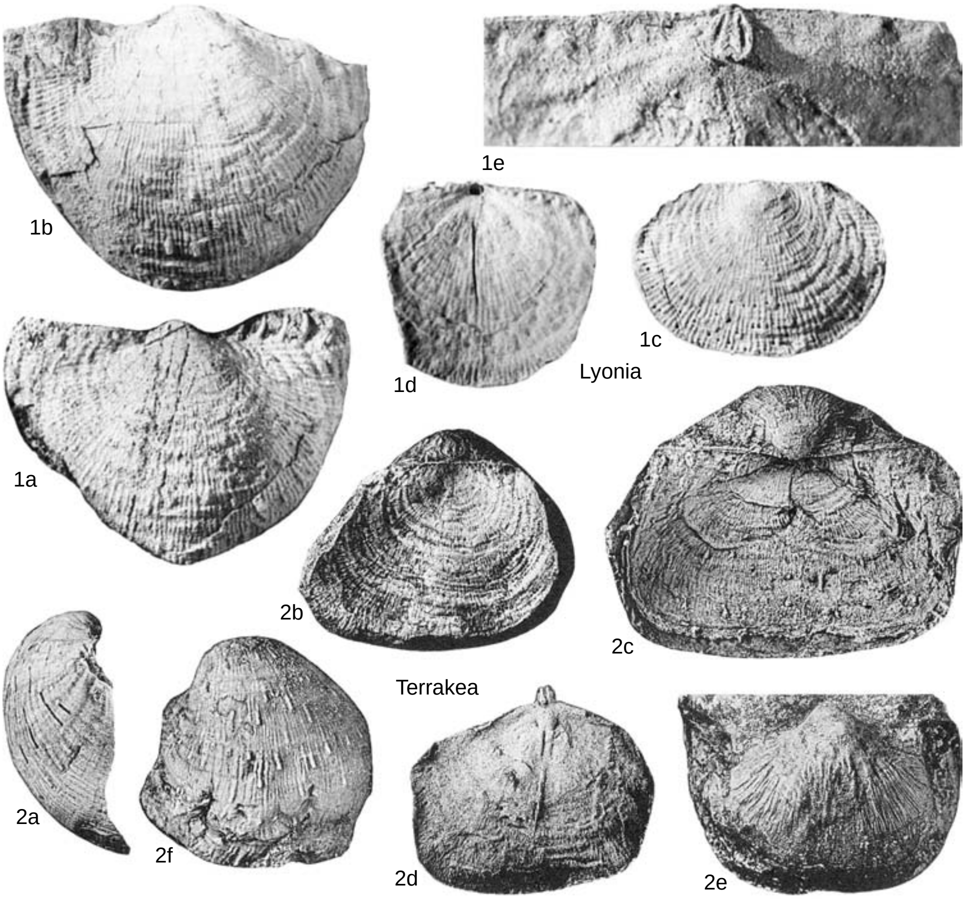


FIG. 372. Linoproductidae (p. 533–535).

Subfamily UNCERTAIN

Selloproductus TERMIER & others, 1974, p. 143 [**S. sellatus;* OD]. Poorly known elongate taxon with no information on characters of importance. Possibly a synonym of *Linoproductus. Upper Permian (Kazanian):* Afghanistan.

Family MONTICULIFERIDAE Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 929, *ex* Monticuliferinae MUIR-WOOD & COOPER, 1960, p. 327]

Linoproductoids with moderately shallow corpus cavity, rarely very shallow; rugae posterolaterally or irregularly widespread; spines on ventral valve, rarely restricted to hinge region; marginal structures normally absent. *Lower Devonian (Pragian)–Upper Permian (upper Tatarian).*

Subfamily MONTICULIFERINAE Muir-Wood & Cooper, 1960

[Monticuliferinae MUIR-WOOD & COOPER, 1960, p. 327]

Medium to large with weakly convex transverse profile; lateral shell profile flattened over disks, convex geniculation, trails; spines at hinge, scattered on venter; commonly with tubercles or monticules, capillae may be present. *Lower Permian (Artinskian)–Upper Permian (Kazanian).*

Monticulifera MUIR-WOOD & COOPER, 1960, p. 327 [**Productus intermedius* var. *sinensis* FRECH, 1911, p. 176; OD] [=*Sinoproductus* CHAN & LI, 1962, p. 477, obj.]. Medium size; monticules dense posteriorly, decreasing anteriorly, interrupted by irregular capillae; ill-defined ribs on trail; spines near hinge line, scattered on ventral valve; dorsal median septum narrow, almost reaching anterior edge of disk.

Lower Permian (Artinskian–Kungurian), Upper Permian (?Kazanian): central China, ?Indonesia.——FIG. 374,*2a–d.* **M. sinensis* (FRECH), Chihsian–Maokouan, Sichuan; *a,b,* ventral valve exterior, lateral views, ×1; *c,* detail of external ornament, ×3; *d,* incomplete dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Chilianshania YANG & TING in YANG & others, 1962, p. 85 [**C. chilianshanensis* TING in YANG & others, 1962, p. 86; OD] [=*Capillifera* JIN & YE in JIN & others, 1979, p. 86, invalid; =*Pseudomonticulifera* ZHAO & TAN, 1984b, p. 26 (type, *C. hunanensis* ZHAO & TAN in LIU, TAN, & DING, 1982, p. 189)]. Resembles *Monticulifera,* but lacks capillae ventrally and monticules; small spine tubercles present posteriorly. [*Capillifera* erected in incorrect belief that *Chilianshania* was junior homonym of a trilobite, however, spelling is different: *Qilianshania* CHU, 1960, p. 62.] *upper Lower Permian (Artinskian)–lower Upper Permian (Kazanian):* west central China.——FIG. 374,*1a–d.* **C. chilianshanensis* (DING), Chihsian–Maokouan, Qinghai; *a,b,* holotype, viewed posteriorly, anteriorly, IGAS 00178, ×1; *c,* ventral valve viewed posteroventrally, ×1; *d,* incomplete dorsal valve interior, ×1 (Yang & others, 1962).

?Paramonticulifera TONG, 1978, p. 234 [* *P. incosta;* OD] [=*Tongluella* LIANG, 1990, p. 202[466] (type, *T. basilica*)]. Medium to large transverse shells, around 50 mm, resembling *Monticulifera,* but lacking capillae and having tuberculate ornament, possibly not true monticules; no anterior ribbing. *lower Upper Permian:* China.——FIG. 375,*1a–d.* **P. incosta,* Upper Permian, Maokouan Formation, Sichuan; *a–c,* holotype, viewed ventrally, posteriorly, laterally, SB 4075, repository unknown, ×1; *d,* posterior view of ventral valve, ×1 (new).

Zhenania DING in ZHANG, FU, & DING, 1983, p. 293 [**Z. zhenanensis;* OD]. Poorly known; similar to *Monticulifera,* but with smaller tubercles or monticules; capillate, but with no anterior ribs. *upper Lower Permian (Roadian)–lower Upper Permian (Wordian):* China.——FIG. 375,*2a–c.* **Z. zhenanensis,* Upper Permian, Shuixiakou Formation, Shanxi; posterior, anterior, lateral views, ×1 (Zhang, Fu, & Ding, 1983).

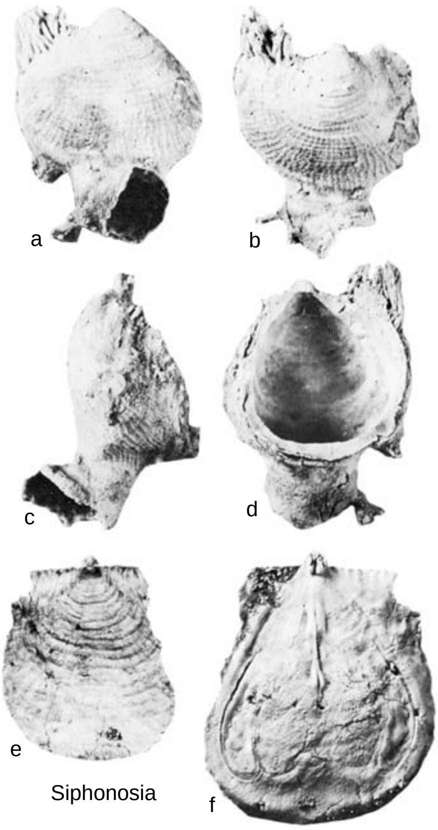


FIG. 373. Linoproductidae (p. 535).

Subfamily AURICULISPININAE Waterhouse, 1986

[Auriculispininae WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 57] [=Ovatiinae LAZAREV, 1990, p. 121]

Medium size with rounded to elongate outline; spines normally on ventral valve only, with clusters on ears; teeth, sockets absent; marginal structures commonly absent. *Lower Carboniferous (Tournaisian)–Upper Permian (Capitanian).*

Auriculispina WATERHOUSE, 1975, p. 13 [**Cancrinella levis* MAXWELL, 1964, p. 34; OD]. Medium size with narrow ventral umbo; both valves finely ribbed, moderately rugose; spines ventral only, dense along hinge, ears, quincuncially on venter; dorsal valve dimpled; ventral adductor scars smooth to striate. *Lower Permian:* eastern Australia.——FIG. 376,*1a–d.* **A. levis* (MAXWELL), Lower Permian, Burnett Formation, Yarrol basin; *a,* holotype, ventral valve internal mold, UQF 187056, ×1.5; *b,* incomplete ventral valve external mold, ×1.5 (Waterhouse & Briggs, 1986); *c,* dorsal valve internal mold, ×1.2; *d,* part of ventral valve exterior, ×1.2 (Maxwell, 1964).

Asperlinus WATERHOUSE & PIYASIN, 1970, p. 132 [**Productus asperulus* WAAGEN, 1884, p. 693; OD]. Small size with relatively strong ribbing; spines evenly distributed over ventral valve, producing dorsal dimples; weak lateral ridges in dorsal valve. *upper Lower Permian–Upper Permian (Capitanian):* western Pakistan, Thailand, Timor.——FIG. 376,*4a–d.* **A. asperulus* (WAAGEN), upper *Productus* Limestone, Capitanian, Salt Range, Pakistan; *a–c,* lectotype, viewed ventrally, dorsally, anteriorly, GSI F3732, ×1; *d,* incomplete dorsal valve interior, ×1 (Waagen, 1884).

Cancrinelloides USTRITSKY in USTRITSKY & TSCHERNJAK, 1963, p. 85 [**Productus obrutschewi* LICHAREW,

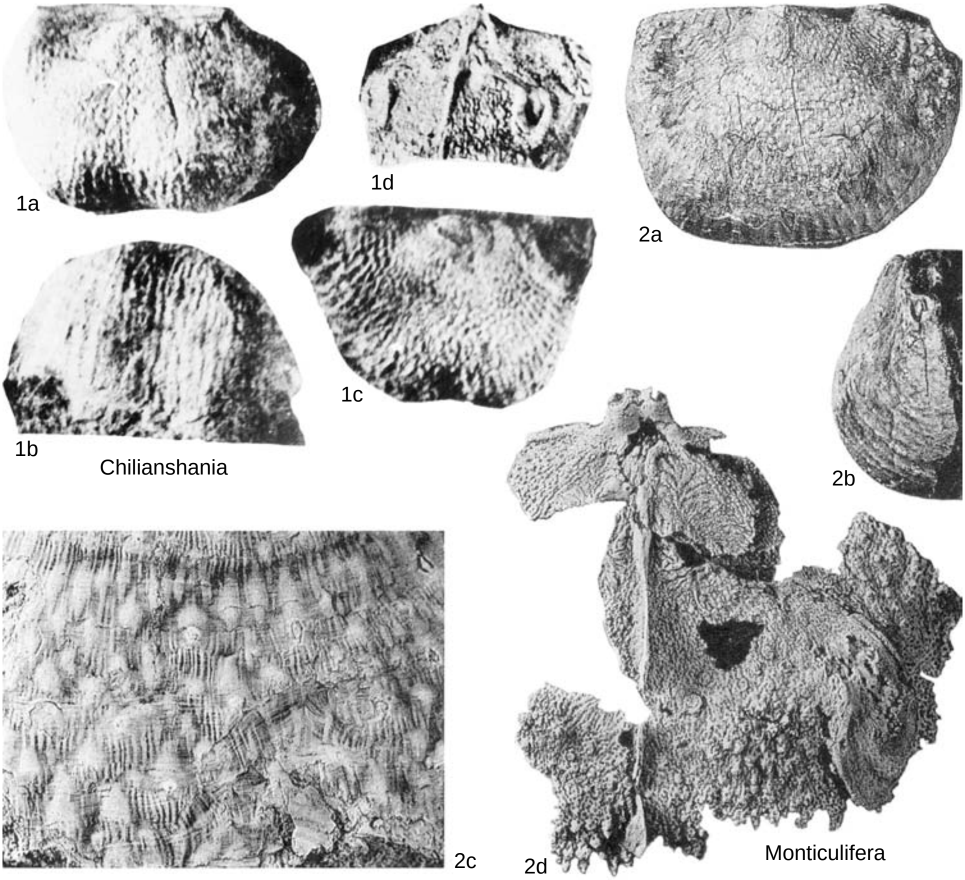


FIG. 374. Monticuliferidae (p. 536–537).

1934c, p. 24; OD]. Medium to large, transverse shell; profile gently convex with weak geniculation, short trail; corpus cavity becoming moderate in depth by adulthood; spine bases elongate except at hinge, anterior margin; spines evenly distributed, recumbent posteriorly, erect, more dense anteriorly; lateral ridges diverge from hinge, rather short; short ridges posterolaterally to dorsal adductor scars. *upper Lower Permian (Roadian):* Arctic, Transbaikalia, Mongolia.——FIG. 376,*3a–c.* **C. obrutschewi* (LICHAREW), Roadian, Omolonskya; *a,* holotype, incomplete ventral valve exterior, TsNIGRA 16/10901, ×1; *b,* lateral view of ventral valve, ×1; *c,* ventral valve exterior, ×1 (Sarytcheva, 1977).

Chianella WATERHOUSE, 1975, p. 13 [**Avonia? chianensis* CHAO, 1927b, p. 126; OD] [=*Longyania* ZHU, 1990, p. 71 (type, *L. magna*)]. Small to medium shells with wide hinge, well-defined ears; ventral disk flattish, curving into simple trail; ribbing strong; spines along ventral hinge, sparsely scattered; rugae on dorsal flanks. [*Longyania* is very poorly known, appearing to be somewhat larger, coming from lower Upper Permian of China (Maokouan).] *upper Lower Permian (Kungurian)–lower Upper Permian (Kazanian):* China.——FIG. 377,*1a–c.* **C. chianensis* (CHAO), Hsiaokiang Limestone, Jiangxi; *a,b,* holotype, viewed ventrally, laterally, NIGP 904, ×1; *c,* median longitudinal section of specimen, ×1 (Chao, 1927b).

Costatumulus WATERHOUSE in WATERHOUSE & BRIGGS, 1986, p. 58 [**Auriculispina tumidus* WATERHOUSE, BRIGGS, & PARFREY, 1983, p. 133; OD]. Similar to *Cancrinelloides* with double row of spines close to ventral hinge, but possibly with less regular rugae, elongate spine bases continuing to ventral valve margin. *Lower Permian (Artinskian):* Australia, central and ?eastern Himalayas.——FIG. 376,*2a–d.* **C. tumidus* (WATERHOUSE, BRIGGS, & PARFREY), Lower Permian, Elvinia Formation, Bowen basin, Australia; *a,* replica of ventral valve exterior, ×1.5; *b,* replica of incomplete ventral valve exterior, ×1.5; *c,* dorsal valve external mold, ×1.5; *d,* replica of dorsal valve interior, ×1.5 (Waterhouse & Briggs, 1986).

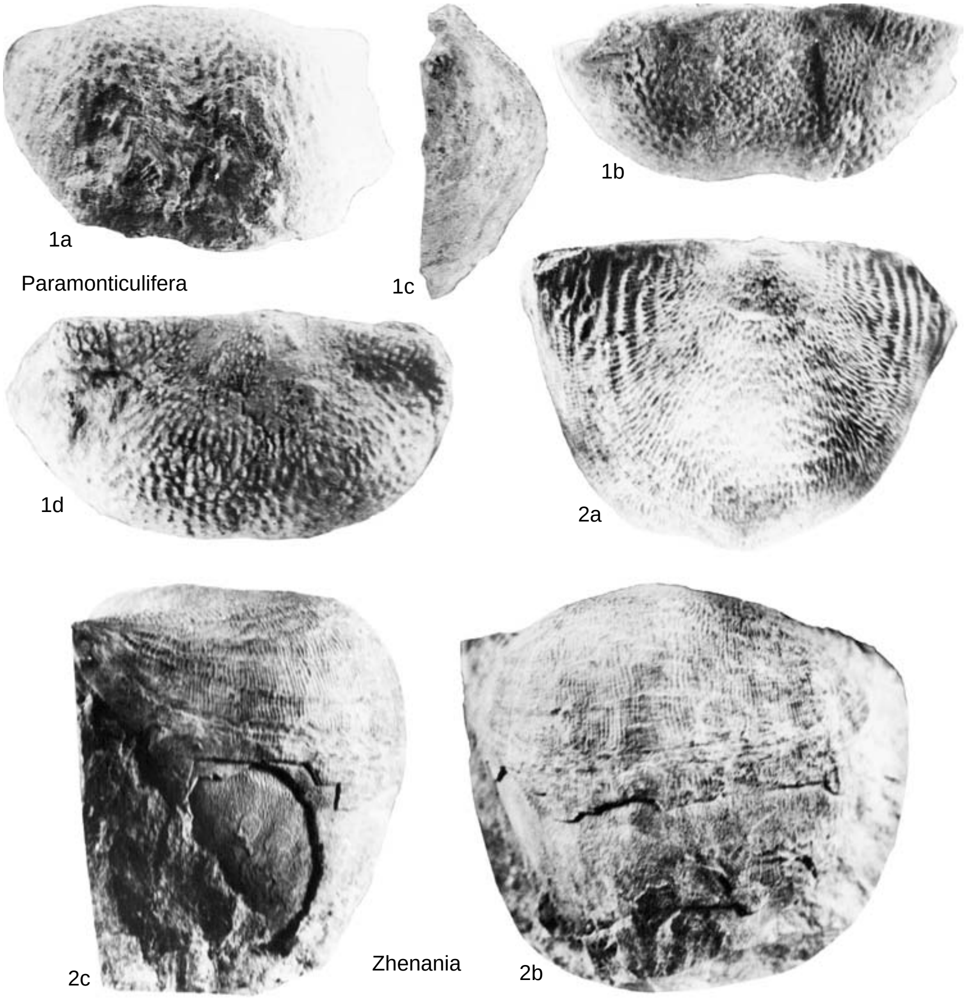


FIG. 375. Monticuliferidae (p. 537).

Filiconcha DEAR, 1969, p. 299 [**F. hillae;* OD]. Similar to *Cancrinelloides,* but with more abundant spines posteriorly, spines on dorsal valve also. *upper Lower Permian:* eastern Australia.——FIG. 377,*3a–e.* **F. hillae,* Flat Top Formation, Lower Permian, Bowen basin, Australia; *a,* holotype, viewed ventrally, GSQ F10996a, ×1; *b,* replica of ventral valve exterior, ×1; *c,* dorsal valve internal mold, ×1.5; *d,* replica of part of dorsal interior, ×3; *e,* dorsal valve external mold, ×2 (Dear, 1969).

Globiella MUIR-WOOD & COOPER, 1960, p. 304 [**Productus hemisphaerium* KUTORGA, 1844, p. 99; OD]. Smaller medium size shell, globose, anteriorly elongate; small, poorly differentiated ears at maximum width; anterior flanks steep, corpus cavity moderately shallow; ribbing fine, regular, covering shell; spines only at ventral hinge; ventral muscle field deeply impressed; ventral lateral ridges separate ears, fit with weak dorsal ridges; paired median ridges separate dorsal adductor fields. *Upper Permian (Kazanian):* Russia, Himalayan chain.——FIG. 377,*2a–g.* **G. hemisphaerium* (KUTORGA), Kazanian, Kama River, Russia; *a–c,* ventral valve viewed ventrally, laterally, internally, ×1; *d,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960); *e,f,* shell viewed ventrally, dorsally, ×1; *g,* posterior view of shell, ×1 (Grigorjewa, 1962).

Linoprotonia FERGUSON, 1971, p. 551 [**Productus hemisphaericus* J. SOWERBY, 1822 in 1821–1822, p. 31; OD] [=*Connectoproductus* DONAKOVA, 1974, p. 173 (type, *Productus probus* ROTAI, 1931, p. 53]. Size medium to large; gently concavoconvex profile,

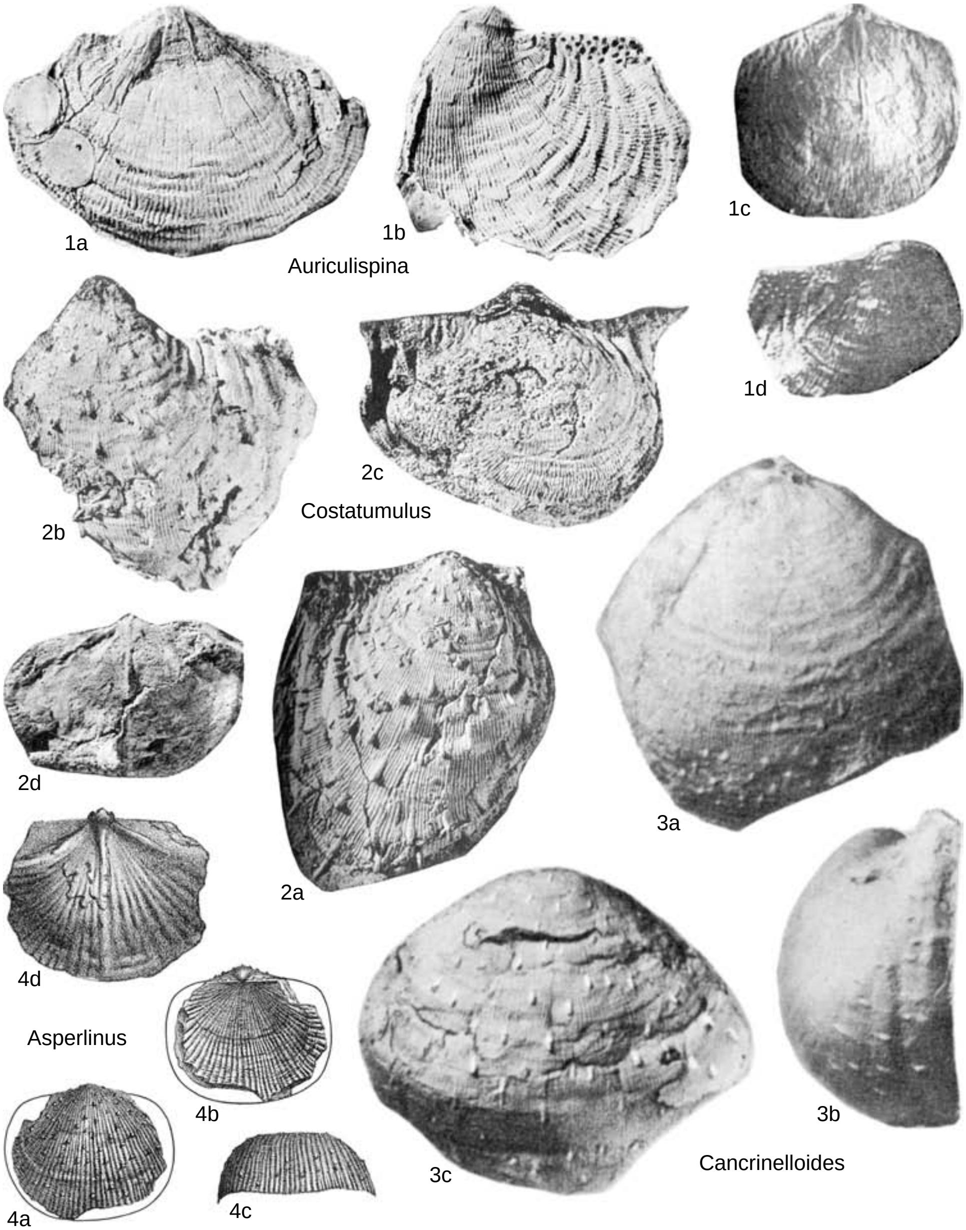


FIG. 376. Monticuliferidae (p. 537–538).

umbo weakly differentiated; rugae weakly developed; low cardinal process, commonly with pit; brachial cones low. *Lower Carboniferous (upper Tournaisian–Viséan):* Eurasia, northern Africa.——FIG. 378,*1a–e*. **L. hemisphaericus* (J. SOWERBY), Asbian; *a,* lectotype, viewed ventrally, southern Wales, BMNH B 44114, selected by PRENTICE, 1949, p. 265, ×1; *b,* dorsal valve exterior, southern Wales, ×1; *c,* ventral valve internal mold, Somerset, ×1; *d,* incomplete dorsal valve interior, northern Wales, ×1; *e,* details of posterolateral spines on ventral valve, Lancashire, ×3 (new).

Liraria COOPER & GRANT, 1975, p. 1156 [*L. lirata;* OD]. Resembles *Globiella,* but wider than long;

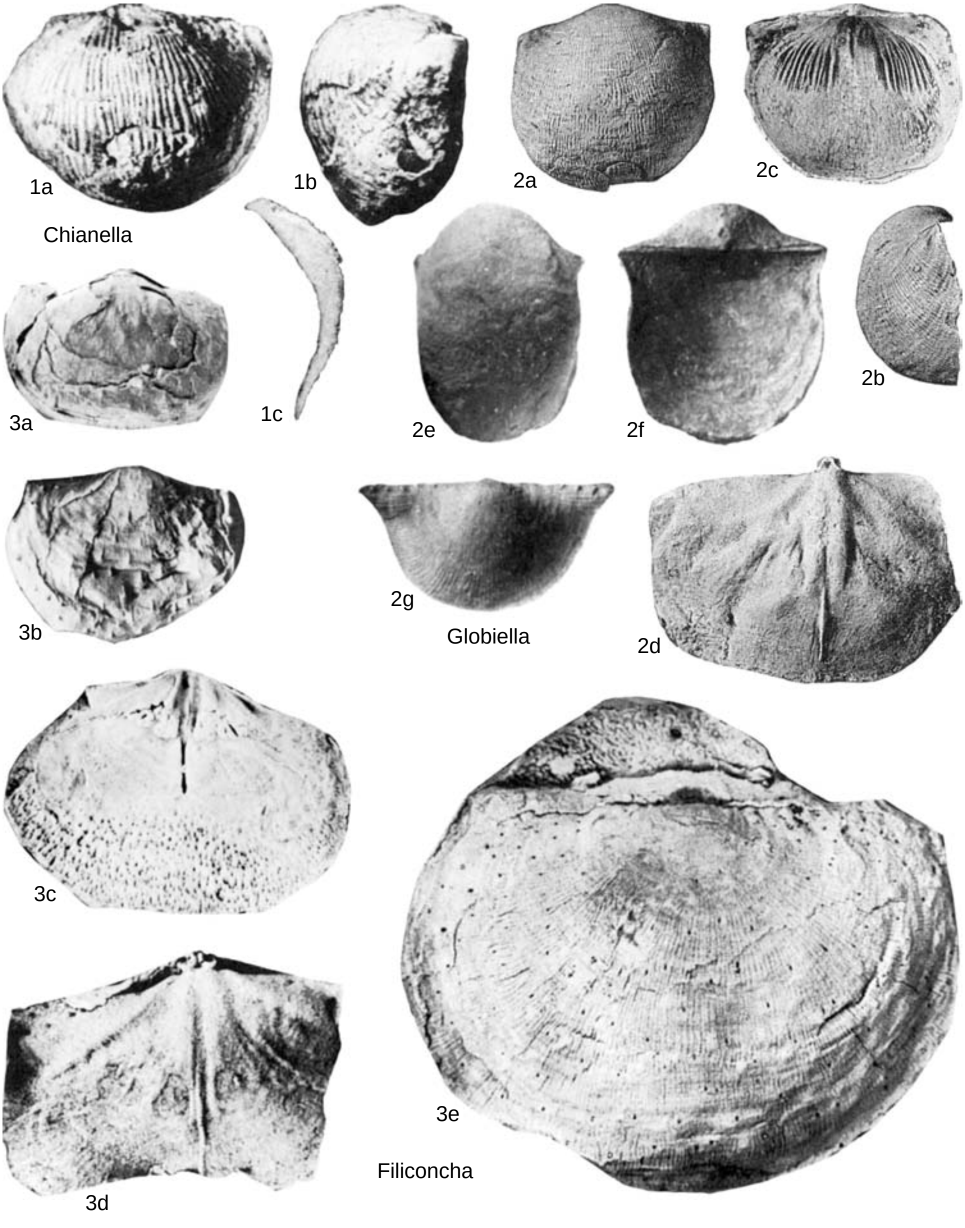


FIG. 377. Monticuliferidae (p. 538–539).

spines near hinge, few on venter; dorsal median septum more prominent; dorsal lateral ridges short, strong, divergent; adductor scars with raised median edges. *Lower Permian (Artinskian–Kungurian):* USA.——FIG. 378,*3a–f.* **L. lirata,* Bone Spring Formation, Texas; *a–d,* holotype, viewed ventrally, posteriorly, laterally, internally, USNM 152782a, ×1; *e,* dorsal valve exterior, ×2; *f,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Magadania GANELIN in GRIGORJEWA, GANELIN, & KOTLYAR, 1977, p. 153 [**Cancrinella? bajkurica* USTRITSKY in USTRITSKY & TSCHERNJAK, 1963, p. 65; OD]. Outline elongate, stongly concavoconvex with shallow corpus cavity; ribbing narrow, rugae on dorsal disk; spines only ventrally, elongate, slightly swollen bases, recumbent, becoming erect anteriorly; dorsal lateral ridges strongly divergent from hinge; median septum divided posteriorly; shell

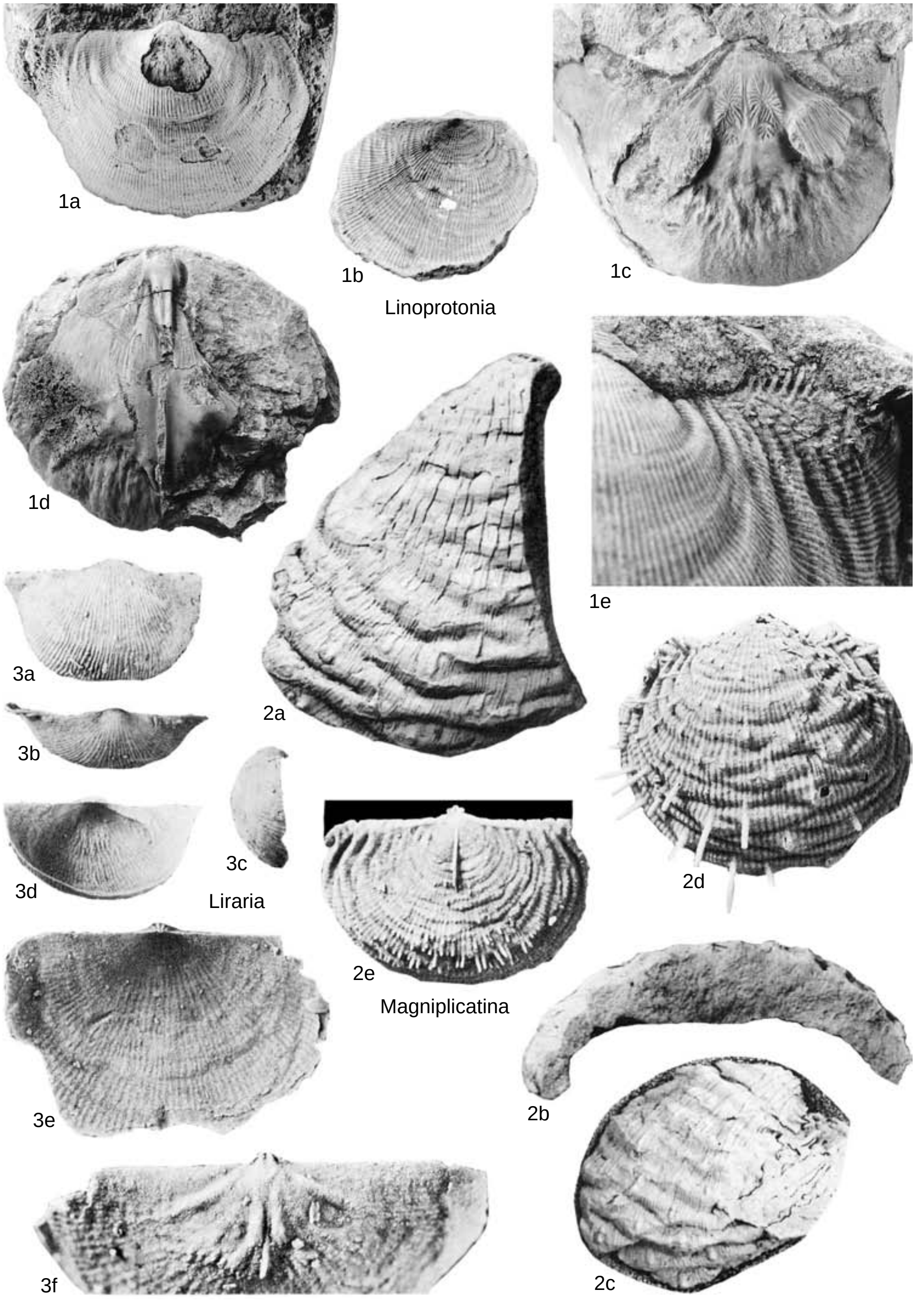


FIG. 378. Monticuliferidae (p. 539–544).

walls thick. *Upper Permian (?Kazanian):* Taymyr, ?northeastern Mongolia.——Fig. 379,*1a–d.* **M. bajkurica* (USTRITSKY), Upper Permian, upper Baykur Formation, River Sokolinaya, Russia; *a,b,* holotype, viewed ventrally, dorsally, TsNIGRA 126/8263, ×2; *c,* ventral valve internal mold, ×1

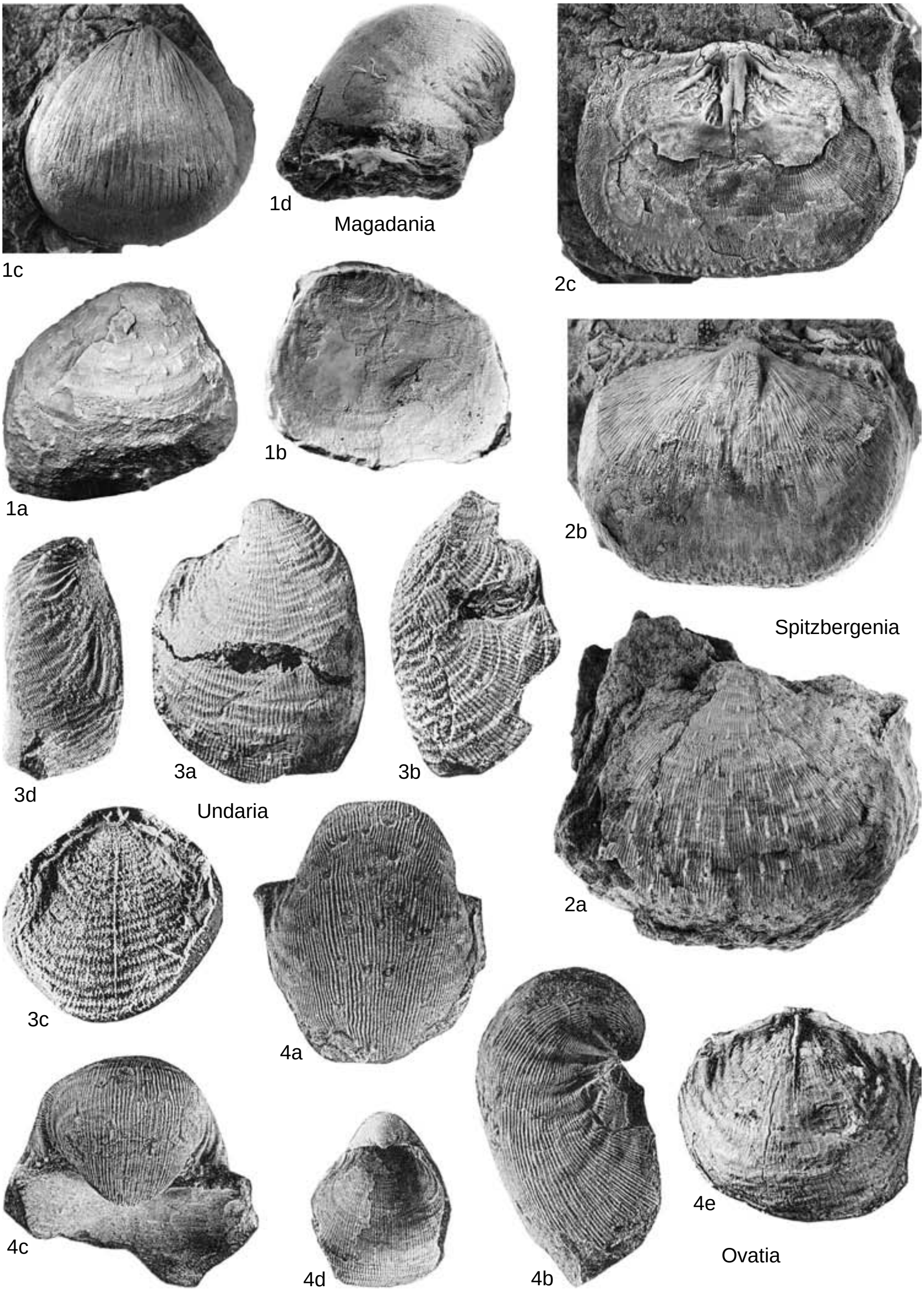


FIG. 379. Monticuliferidae (p. 541–546).

(Grigorjewa, Ganelin, & Kotlyar, 1977); *d,* ventral valve viewed laterally, ×1 (new).

Magniplicatina Waterhouse, 1983b, p. 130 [*_Cancrinella magniplica_ Campbell, 1953, p. 7; OD] [=*Helenaeproductus* Lazarev in Pavlova & others, 1991, p. 117 (type, *H. khubsugulensis*)]. Resembles *Cancrinella,* but with shallow corpus, strong rugae on ventral valve and relatively thick, widely

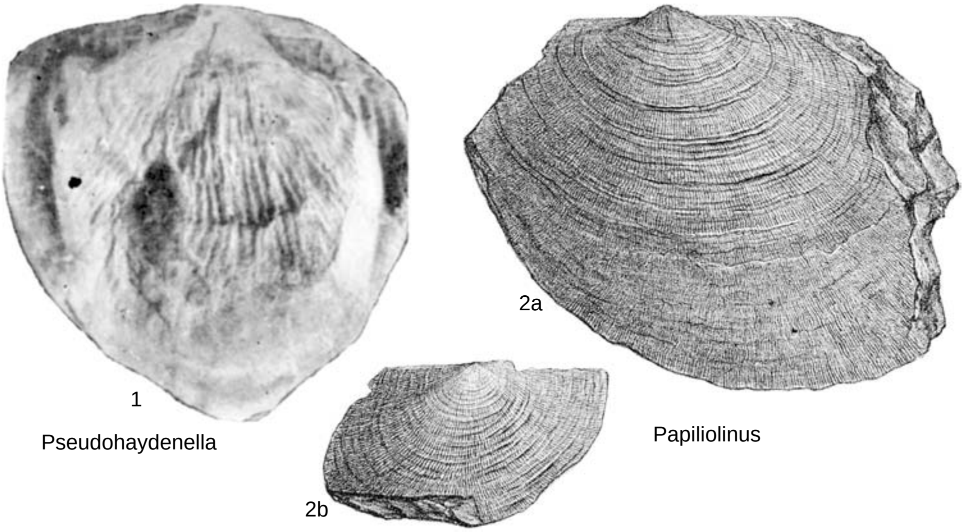


Fig. 380. Monticuliferidae (p. 544).

spaced ventral spines. *upper Lower Permian (Kungurian)–Upper Permian (Kazanian):* Australia, New Zealand, USA, Mongolia, Russian Arctic, ?China.——Fig. 378,*2a–c. M. halli* (Waterhouse), Mangarewa Formation, New Zealand; *a,b,* holotype, ventral, lateral views of incomplete internal mold, NZGS BR950, ×1; *c,* oblique view of ventral valve internal mold, ×1 (Waterhouse, 1982c).——Fig. 378,*2d,e. M. sparsispinosa* (Cooper & Grant), Bone Spring Formation, Texas; *d,* holotype, ventral valve exterior, USNM 152780a, ×2; *e,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

Ovatia Muir-Wood & Cooper, 1960, p. 311 [**O. elongata;* OD]. Small to medium sized; ventral profile close to ideal spiral with no geniculation, trail narrow, elongate; umbo narrow, but highly arched, strongly differentiated from ears where rugae are strong; one to two rows of spines near hinge, sparsely scattered on ventral valve where they commonly interrupt ribs; lateral ridges short. *Lower Carboniferous (Tournaisian)–Upper Carboniferous (Serpukhovian):* North America, Eurasia, northern Africa.——Fig. 379,*4a–e.* **O. elongata,* Chesterian, Oklahoma; *a–c,* holotype, viewed anteroventrally, laterally, posteriorly, USNM 124101a, ×1; *d,* dorsal view of small shell, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Papiliolinus Waterhouse & Gupta, 1977, p. 160 [**P. eishmakami;* OD, *nom. nov. pro Productus undatus* Diener, 1899, p. 23, *non* Defrance, 1826]. Poorly known; large; subsemicircular outline, profile curvature weak; ribbing fine for family, rugae fine and possibly covering valves; cardinal process seemingly trifid with broad median ridge. *upper Lower Carboniferous (upper Viséan):* northern India.——Fig. 380,*2a,b.* **P. eishmakami,* upper Viséan, Kashmir; two external casts of dorsal valves, ×1 (Diener, 1899).

Pseudohaydenella Liang, 1990, p. 174[462] [**P. huadongensis;* OD] [=*Lamiproductus* Liang, 1990, p. 205[467] (type, *L. typicus*)]. Poorly known, possible synonym of *Chianella.* Medium to large, subtriangular, somewhat nasute outline; no sulcus; rugae confined to ears; spines sparsely scattered on ribs; dorsal lateral ridges low, thick. *Upper Permian (upper Capitanian):* eastern China.——Fig. 380,*1.* **P. huadongensis,* upper Capitanian, Lengwu Formation, Zhejiang; ventral valve exterior, ×1.5 (Liang, 1990).

Spitzbergenia G. Kotlyar in Grigorjewa, Ganelin, & Kotlyar, 1977, p. 155 [**Productus loveni* Wiman, 1914, p. 72; OD]. Medium, subquadrate outline; prominent elongate spine bases on ventral disk resemble *Magniplicatina,* but lacks prominent rugae; spines recumbent, thin, concentric arrangement anteriorly, erect spines on ears, flanks, trail; ventral diductor scars enclose adductor scars anteriorly; cardinal process small, supported by medianly grooved median septum, strongly diverging short lateral ridges. *lower Upper Permian (Kazanian):* Spitzbergen, Novaya Zemlaya, Canada, Alaska, northern and northeastern European Russia.——Fig. 379,*2a–c.* **S. loveni,* Kazanian, Selander Formation, Spitzbergen; *a,* ventral valve exterior, ×1; *b,* ventral valve internal mold, ×1; *c,* dorsal valve interior, ×1 (Grigorjewa, Ganelin, & Kotlyar, 1977).

Teleoproductus Li Li in Li Li, Yang De-li, & Feng Ru-lin, 1986, p. 230 [**T. typicus;* OD]. Small to medium size, hinge widest part of shell, anterior margin strongly nasute, but not forming tube with dorsal trail; rugae strong on flanks, ears, dorsal disk; spines at hinge and few on ventral flanks; interiors unknown. *Lower Permian (Sakmarian)–lower Upper Permian (Wordian):* China.——Fig. 381,*3a–c.* **T. typicus,* Longyin Formation, Guangxi; holotype,

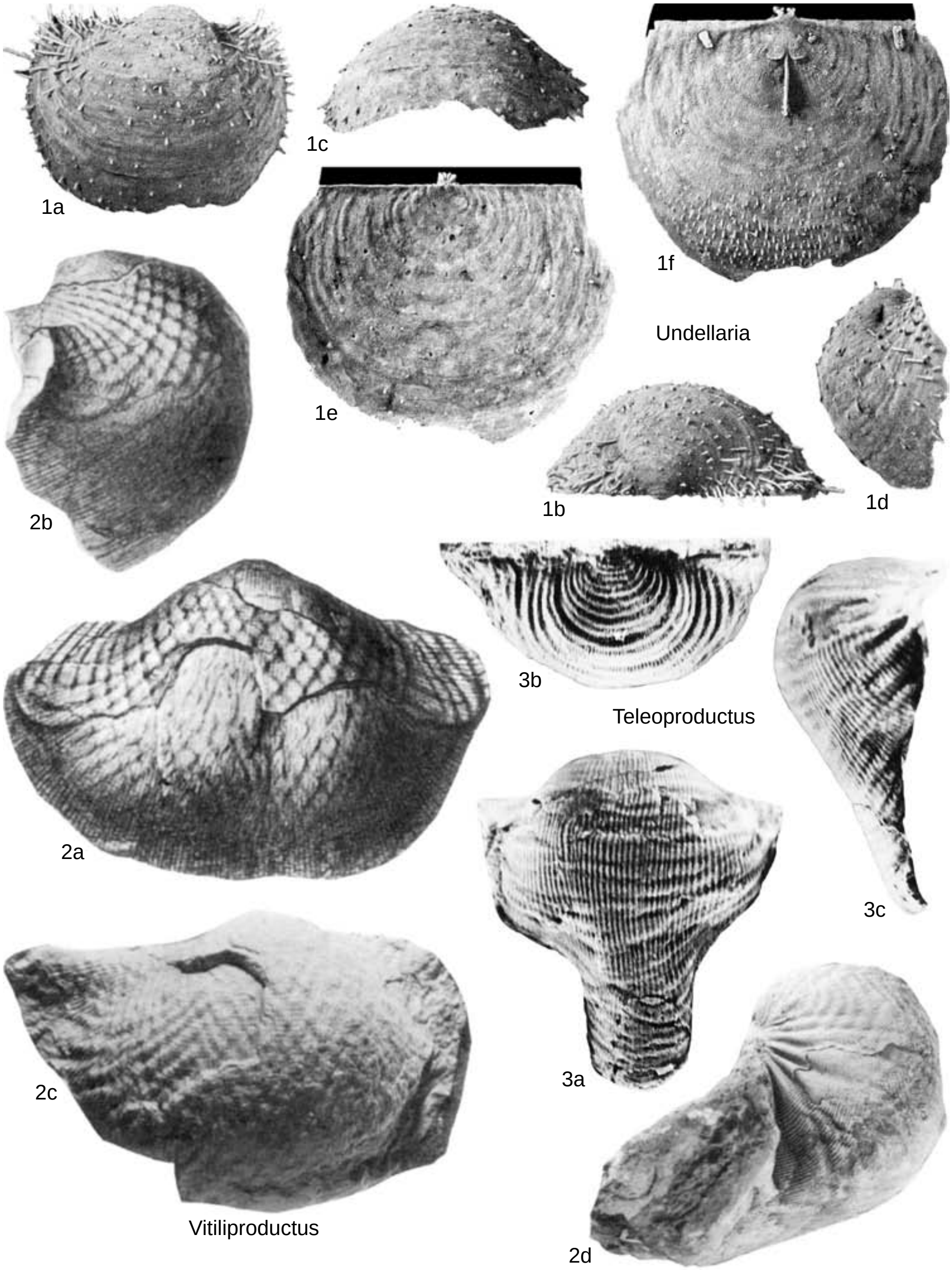


Fig. 381. Monticuliferidae (p. 544–546).

viewed anteroventrally, posteriorly, laterally, ?NGM 562176 (repository unknown), ×1.5 (new).

Undaria Muir-Wood & Cooper, 1960, p. 317 [**U. manxensis;* OD]. Small; trails elongate, tubiform; ribbing entire, prominent at rugae that cover corpus, trails posteriorly; spines at and close to hinge, widely scattered on ventral corpus; cardinal process bilobed, quadrifid; lateral ridges and short ear baffles, median septum long, but thin. *upper Lower Carboniferous (upper Viséan):* western Europe.——Fig. 379,*3a–c.* **U. manxensis,* Asbian, Isle of Man; *a,* incomplete ventral valve exterior, ×2; *b,* external mold of dorsal valve viewed laterally, ×2; *c,* replica of dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).——FIG. 379,*3d. U. erminea* (DE KONINCK), Viséan, Belgium; external mold of dorsal valve viewed laterally, ×1 (Muir-Wood & Cooper, 1960).

Undellaria COOPER & GRANT, 1975, p. 1157 [**U. magnifica;* OD]. Medium size with hinge slightly narrower than midwidth; transverse profile evenly convex; rugae weak on both valves; spines numerous, thin, short, less abundant on anterior venter; ventral muscle field relatively small; cardinal process small, sessile, bilobed, quadrifid; lateral ridges weak, short in both valves; adductor scars raised anteriorly. *upper Lower Permian (Artinskian–Kungurian):* USA.——FIG. 381,*1a–f.* **U. magnifica,* Bone Spring Formation, Texas; *a–d,* holotype, viewed ventrally, posteriorly, anteriorly, laterally, USNM 152783b, ×1; *e,f,* dorsal valve exterior, interior, ×1.5 (Cooper & Grant, 1975).

?Vitiliproductus CHING YU-GAN & LIAO ZHAO-TING, 1974, p. 278 [**Productus groeberi* KRENKEL, 1913, p. 42; OD]. Medium to large; intersecting oblique rugae forming tetrahedral elevations over corpus, rugae commonly strong at flanks; interiors unknown. *Lower Carboniferous (upper Viséan):* China, western Europe, Asia, Australia.——FIG. 381,*2a–c.* **V. groeberi* (KRENKEL); *a,b,* ventral, lateral views of shell, as figured by KRENKEL (1913), ?Asbian, Tien Shan, ×1; *c,* ventral valve exterior, upper Viséan, Guizhou, ×1 (Brunton & Mundy, 1988a).——FIG. 381,*2d. V. wedberensis* BRUNTON & MUNDY, ?Asbian, Kerry County, Ireland; lateral view of ventral valve, ×1 (Brunton & Mundy, 1988a).

Subfamily COMPRESSOPRODUCTINAE Jing & Hu, 1978

[Compressoproductinae JING & HU, 1978, p. 115]

Small or medium size, elongate outline, hinge narrow; corpus cavity moderately shallow; valves thin shelled with complete ribbing, rugae; spines rare, rhizoid; cardinal process single median ridge (unifid), lateral ridges weak. *Lower Permian–Upper Permian (upper Tatarian).*

Compressoproductus SARYTCHEVA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 231 [**Productus compressus* WAAGEN, 1884, p. 710; OD] [=*Substriatifera* KOTLYAR, 1964, p. 123 (type, *Productus (mytiloides) vladivostockensis* FREDERICKS, 1925, p. 17)]. Medium size, elongate trigonal outline resembling *Stratifera,* but commonly with narrow hinge, deeper corpus cavity, and rugae persisting over both valves; ventral lateral ridges weak; shell substance thin. *Upper Permian (Kazanian–upper Tatarian):* Pakistan, northern Caucasus, Transcaucasus, southeastern Asia.——FIG. 382,*1a–c.* **C. compressus* (WAAGEN), *Productus* Limestone, Salt Range, Pakistan; ventral valve exterior viewed ventrally and from both sides, ×0.8 (Waagen, 1884).

Fallaxoproductus LI, GU, & LI, 1982, p. 115[128] [**F. sutungensis;* OD]. Resembles *Compressoproductus,* but lacks ears and rugae confined to dorsal valve. *Lower Permian:* Inner Mongolia.——FIG. 382,*2a.* **F. sutungensis,* Lower Permian, Inner Mongolia; ventral valve exterior, ×1 (Li, Gu, & Li, 1982).——FIG. 382,*2b–d. F. dedorus,* Lower Permian, Inner Mongolia; *b,* dorsal valve exterior, ×1; *c,d,* internal molds of ventral, dorsal valves, ×1 (Li, Gu, & Li, 1982).

Sarytchevinella WATERHOUSE, 1983a, p. 126 [**Productus djulfensis* STOYANOW, 1915, p. 84; OD]. Resembles *Compressoproductus,* but may differ in having somewhat wider hinge line, in having spines on the venter, and weak or no rugae anteriorly. *Upper Permian (upper Capitanian):* Armenia, Caucasus, southern China, northern Thailand.——FIG. 382,*3a–c.* **S. djulfensis* (STOYANOW), upper Capitanian, Armenia; *a,b,* exterior viewed ventrally, laterally, ×1; *c,* posterior part of shell viewed dorsally, ×2 (Stoyanow, 1915).

Subfamily DEVONOPRODUCTINAE Muir-Wood & Cooper, 1960

[Devonoproductinae MUIR-WOOD & COOPER, 1960, p. 177]

Moderately shallow corpus cavity; fine ribbing especially on ventral valve; dorsal valves with concentric lamellae as traces of series of trails; cardinal process pit absent; ear baffles in ventral valve, weak dorsal lateral ridges; weak submarginal ridge in dorsal valve with papillae. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian).*

Devonoproductus STAINBROOK, 1943, p. 55 [**Productella walcotti* FENTON & FENTON, 1924, p. 119; OD, *nom. nov. pro Productus dissimilis* HALL, 1858a, p. 497, *non* DE KONINCK, 1847a, p. 225; =*P. (Productella) hallana* WALCOTT, 1884, p. 130, *partim*] [=*Striatoproductus* NALIVKIN, 1947, p. 75 (type, *Orthis sericea* VON BUCH, 1838, p. 68)]. Small; outline subcircular, cicatrix small, rare; spines suberect at hinge, widely scattered ventrally from bases wider than ribs; dorsal lamellae prominent; lateral ridges may continue anteriorly; median septum long, not supporting cardinal process. *Upper Devonian (Frasnian):* North America, Europe, central Asia.——FIG. 383,*1a–f.* **D. walcotti* (FENTON & FENTON), Frasnian, Iowa; *a,b,* shell viewed posteriorly, laterally, ×2; *c,* ventral valve exterior, ×2; *d,* ventral valve interior, ×2; *e,f,* dorsal valve exterior, interior, ×3 (Muir-Wood & Cooper, 1960).

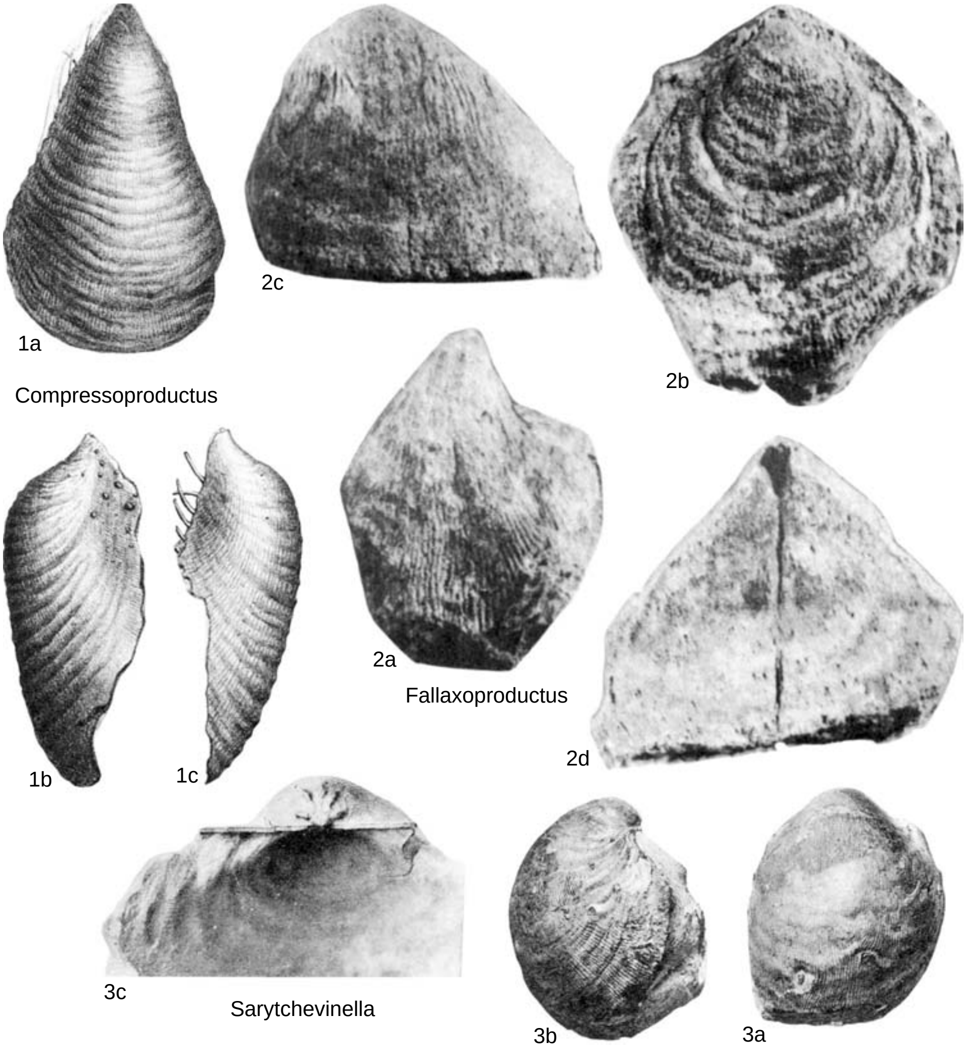


Fig. 382. Monticuliferidae (p. 546).

Chonopectoides Crickmay, 1963, p. 23 [**C. catamorphus;* OD]. Poorly known; small, around 4.5 mm wide, chonetiform shells with ventral ginglymus; ribs fine, obscure, on ventral valve only; dorsal valve lamellose; spines project posterolaterally from hinge only; teeth strong; socket ridges continue as weak ear baffles. *upper Middle Devonian:* Canada (Northwest Territories).——Fig. 383,*2a–d.* **C. catamorphus; a,* holotype, viewed ventrally, PRI 27124, ×10; *b,* ventral valve interior, ×10; *c,* dorsal valve exterior, ×10; *d,* dorsal valve interior, ×10 (new).

Poloniproductus Biernat & Lazarev, 1988, p. 66 [**Productella varians* Biernat, 1966, p. 66; OD]. Resembles *Devonoproductus,* but with suberect spines from slightly elongate bases and weak concentric lamellae on both valves; no ribbing; teeth small; brachial impressions wide on disk. *Middle Devonian (Eifelian):* eastern Europe.——Fig. 383,*3a–f.* **P. varians* (Biernat), Eifelian, Holy Cross Mountains; *a–c,* shell viewed ventrally, posteriorly, laterally, ×2 (new); *d,* shell viewed dorsally, ×2 (Lazarev, 1990); *e,* ventral valve interior, ×2 (new); *f,* dorsal valve interior, ×2.5 (Biernat, 1966).

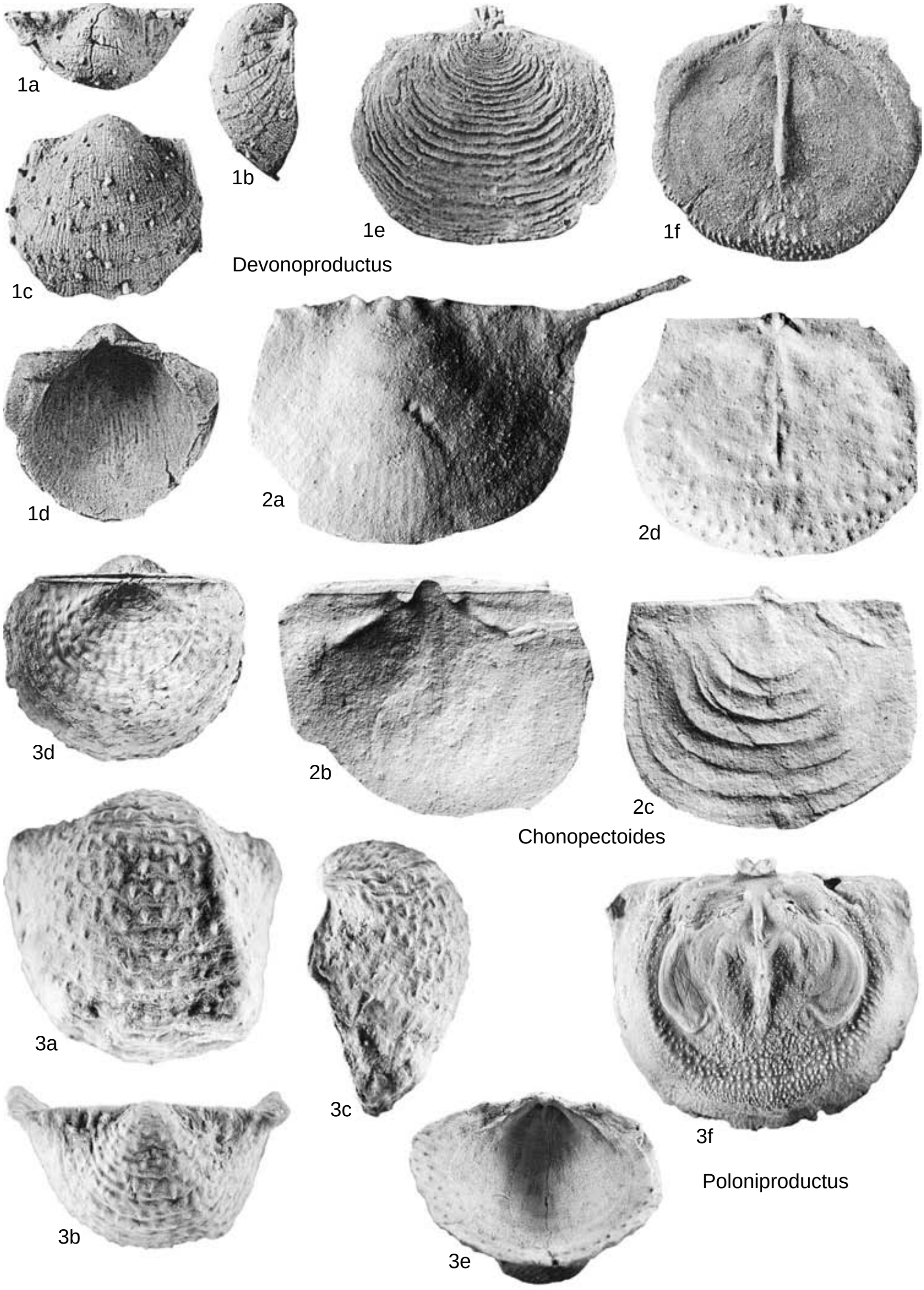


FIG. 383. Monticuliferidae (p. 546–547).

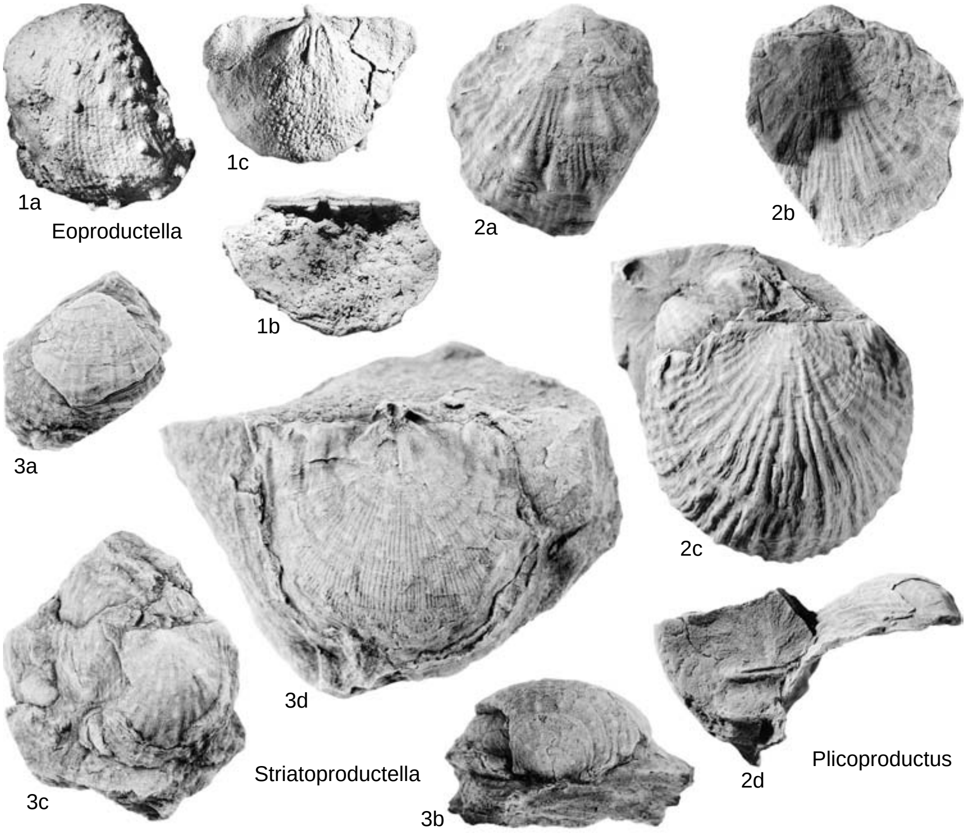


FIG. 384. Monticuliferidae (p. 549–550).

Subfamily EOPRODUCTELLINAE Lazarev, 1987

[Eoproductellinae Lazarev, 1987, p. 49]

Small or medium size; both valves or dorsal valve only with fine ribbing, spines on ventral valve only; teeth, sockets present. *Lower Devonian (Pragian)–Middle Devonian (upper Givetian).*

Eoproductella Rzhonsnitzkaya, 1980, p. 59 [**E. menakovae;* OD]. Small; hinge widest part of shell; profile strongly concavoconvex; ribbing weak on both valves, spines widespread from thick bases; anderidia present. *Lower Devonian (Pragian–Emsian):* middle Asia.——Fig. 384,*1a–c.* **E. menakovae,* Pragian, Tadjikistan; *a,* oblique lateral view of ventral valve, ×1; *b,* ventral valve viewed dorsally showing teeth, ×1.5; *c,* dorsal valve interior, one lobe of cardinal process missing, ×1.5 (Lazarev, 1990).

Plicoproductus Ljaschenko, 1969, p. 14 [**Productella mosolovica* Ljaschenko, 1958a, p. 93; OD]. Small; relatively coarsely costellate with additional fine striae especially dorsally; spines ventral, relatively coarse with irregular concentric arrangement. *Middle Devonian (Eifelian):* Russia.——Fig. 384,*2a–d.* **P. mosolovica* (Ljaschenko), Middle Devonian, Russia; *a,b,* ventral, dorsal views of shell, ×2; *c,d,* dorsal valve external mold, lateral view of shell with two spines, ×2 (new).

Striatoproductella Krylova, 1962, p. 54 [**Striatoproductus tunguensis* Nalivkin, 1960, p. 319; OD] [=*Hanaeproductus* Ficner & Havlíček, 1978, p. 65 (type, *Productus rittbergensis* Quenstedt, 1871, p. 613)]. Small with subcircular corpus; spine bases fine, elongate, only ventrally; dorsal valve with low

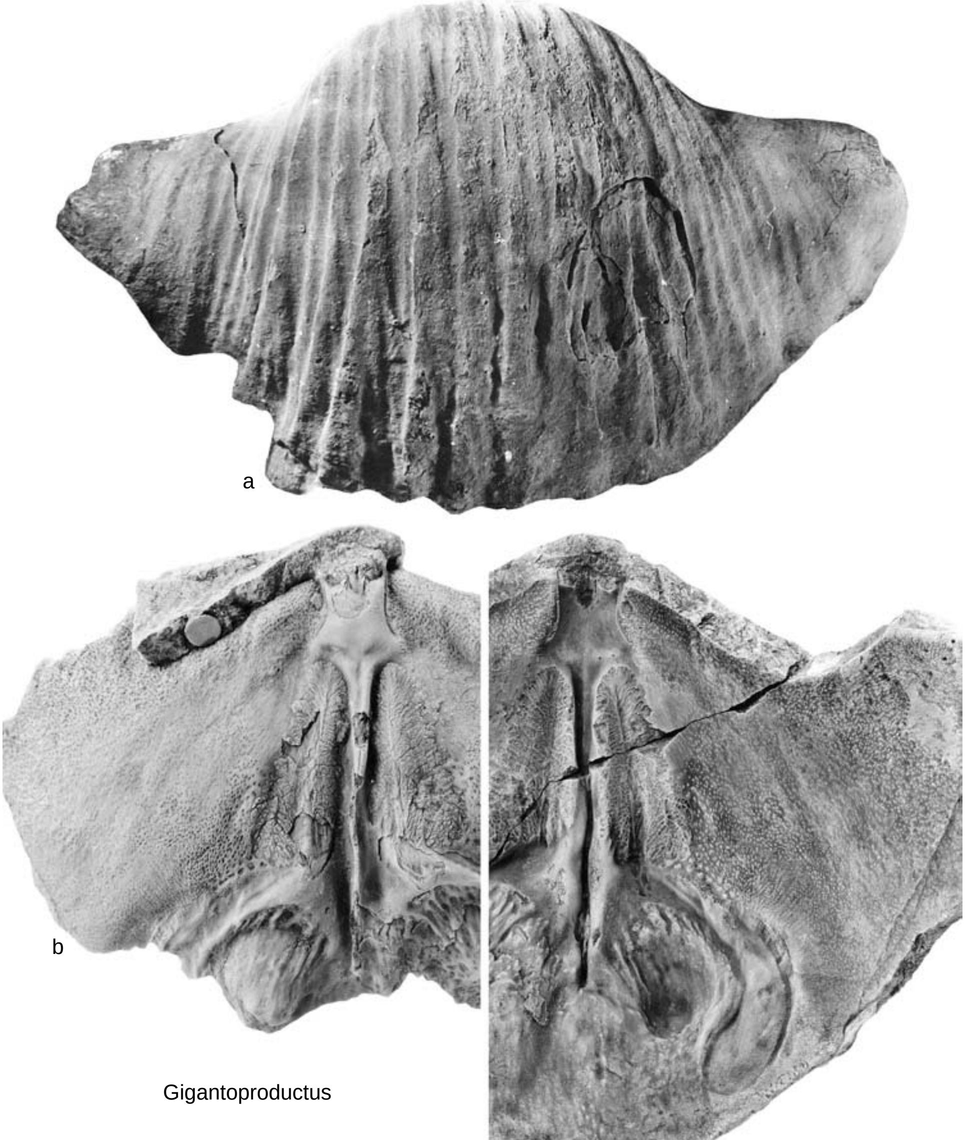


FIG. 385. Monticuliferidae (p. 551).

dichotomizing ribs; teeth small. *Middle Devonian (upper Givetian):* northern Eurasia.——FIG. 384,*3a–d.* **S. tunguensis* (NALIVKIN), upper Givetian, Siberia; *a,* ventral valve exterior viewed ventrally, ×1; *b,* ventral valve exterior viewed posteriorly, ×1.5; *c,* dorsal valve external mold, ×1; *d,* partly exfoliated dorsal valve interior, ×2 (new).

Subfamily GIGANTOPRODUCTINAE Muir-Wood & Cooper, 1960

[Gigantoproductinae MUIR-WOOD & COOPER, 1960, p. 330]

Gigantic, large or medium size, hinge at greatest width; corpus cavity very shallow;

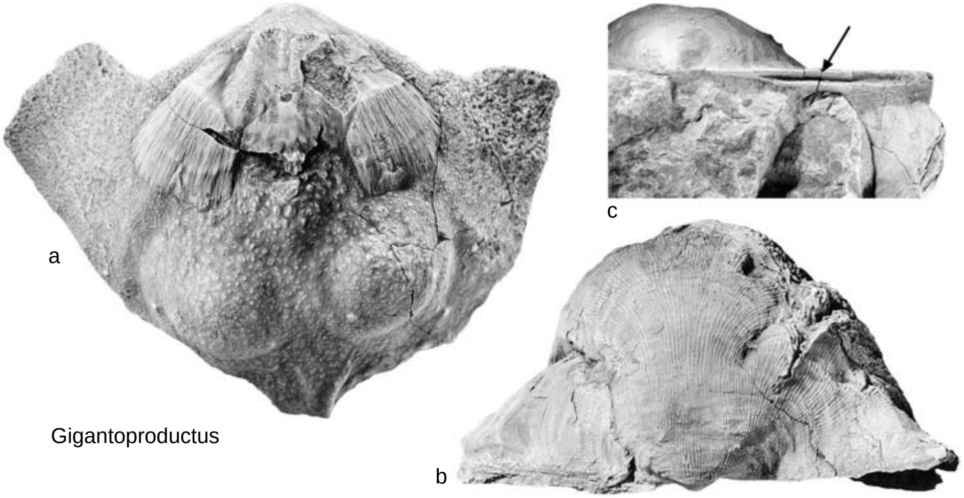


FIG. 386. Monticuliferidae (p. 551).

fully ribbed, spines on ventral valve, rarely also on dorsal valves; marginal structures commonly absent; cardinal process pit commonly present. *Lower Carboniferous (Viséan)–Upper Carboniferous (Serpukhovian).*

Tribe GIGANTOPRODUCTINI Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 930, *ex* Gigantoproductinae MUIR-WOOD & COOPER, 1960, p. 330] [=*Kansuellinae* MUIR-WOOD & COOPER, 1960, p. 336]

Large or gigantic, thick-walled ventral valves; ventral umbo not strongly incurved; commonly ribbed; spines commonly on ventral valve; cardinal process trifid with median ridge well developed or sole element; brachial cones commonly distinct. *Lower Carboniferous (Viséan)–Upper Carboniferous (Serpukhovian).*

Gigantoproductus PRENTICE, 1950, p. 437, *nom. nov. pro Gigantella* SARYTCHEVA, 1928, p. 13, *non* EKMAN, 1905 [**Anomites giganteus* MARTIN, 1793, pl. 15, fig. 1 (invalid, ICZN, 1950); =*Productus giganteus* J. SOWERBY, 1822 in 1821–1822, p. 19; SD MUIR-WOOD, 1951, p. 98 (species validated and SD confirmed, ICZN, 1956b, Opinion 420, p. 135)]. Commonly gigantic, transverse; ribbing entire, but commonly irregular and weakened at trail plications; spines rare; ventral valve thick-shelled with pits accommodating dorsal brachial cones; cardinal process trifid, sessile. *Lower Carboniferous (upper Viséan):* Eurasia, northern Africa.——FIG. 385*a–c*. **G. giganteus* (J. SOWERBY), upper Viséan; *a,* ventral valve exterior, England, ×0.6 (Muir-Wood, 1965b); *b,c,* incomplete dorsal valve interior, internal mold, northern Wales, ×1 (new).——FIG. 386*a–c*. **G. giganteus* (J. SOWERBY), upper Viséan; *a,* ventral valve internal mold, northern Wales, ×0.6; *b,c,* ventral valve viewed posteriorly, showing damaged shell, and dorsally showing short ginglymus (*arrow*), Scotland, ×0.5 (new).

Beleutella LITVINOVICH, 1967, p. 55 [**B. rara;* OD]. Outline subrounded; ventral profile flattened umbonally; ginglymus strongly developed; ribbing narrow; spines thin, sparse; valve walls thick; cardinal process prominent, trifid with fused median ridges dominant; brachial cones present. *Lower Carboniferous (lower Serpukhovian):* Kazakhstan.——FIG. 387,*1a–c*. **B. rara,* Serpukhovian, Kazakhstan, Dzhezgazgan district; *a,b,* holotype, viewed ventrally, laterally, MGU 31/342, ×1 (Litvinovich, 1967); *c,* incomplete ventral valve internal mold, ×1 (Litvinovich & Vorontsova, 1991).

Datangia YANG DE-LI in YANG DE-LI & others, 1977, p. 369 [**D. luzhaiensis* NI SHI-ZHAO in YANG & others, 1977, p. 369; OD] [=*Datangia* YANG SHI-PU, 1978, p. 122 (type, *D. weiningensis,* obj.; *Moderatoproductus* LITVINOVICH & VORONTSOVA, 1983, p. 86 (type, *Gigantella moderata* SCHWETSOV, 1922, p. 10]. Poorly known; large; outline subcircular to oval; ribbing strong, even, no plications; spines at hinge, on ears, scattered ventrally; brachial cones absent. *Lower Carboniferous (Viséan):* China, northern Africa.——FIG. 387,*2a–c*. **D. luzhaiensis* (NI SHI-ZHAO), Lower Carboniferous, Datang Stage, Guangxi; ventral, posterior, lateral views of specimen, ×1 (Yang & others, 1977).

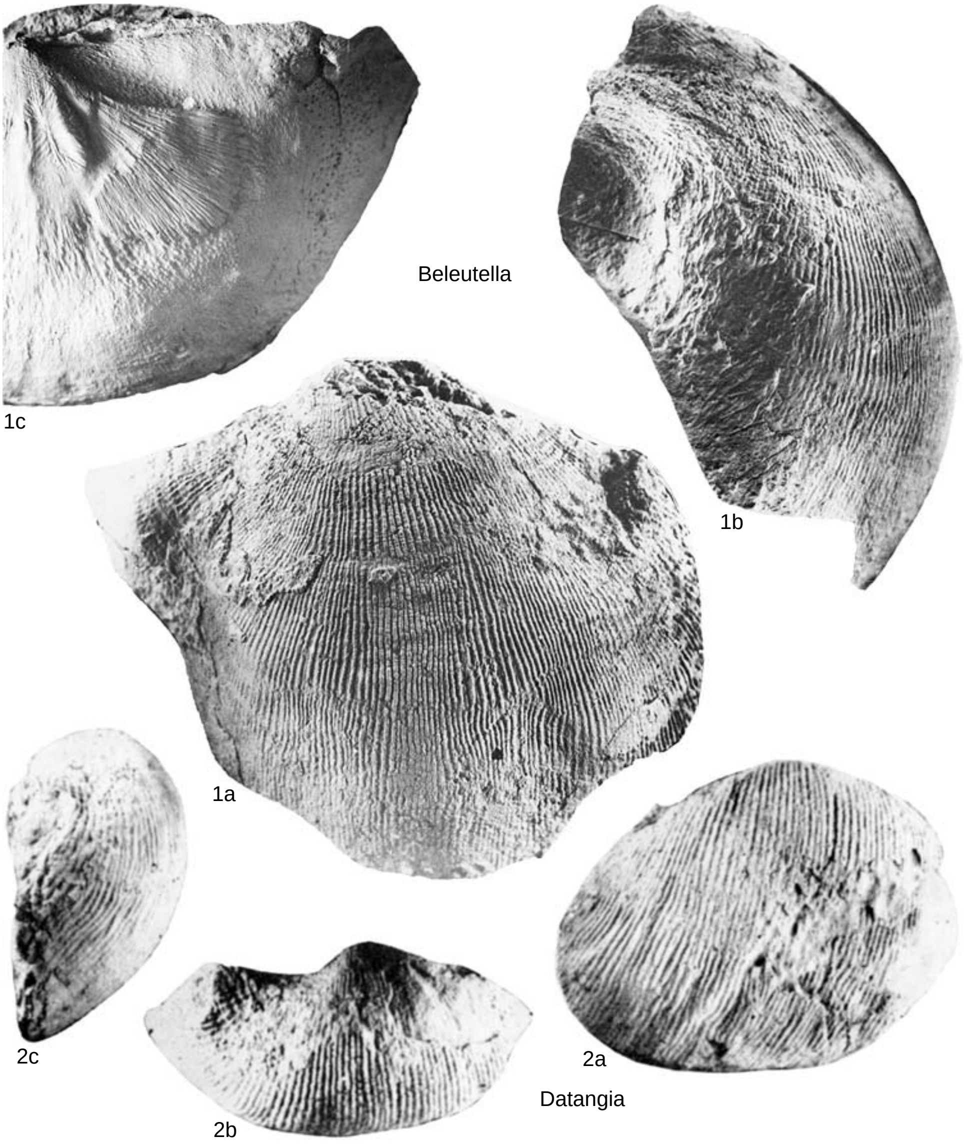


FIG. 387. Monticuliferidae (p. 551).

Globosoproductus LITVINOVICH & VORONTSOVA, 1983, p. 88 [**Gigantella magnifica* SCHIMANSKY, 1940, p. 106; OD]. Poorly known; large, somewhat ventrally inflated corpus; ribs fine posteriorly, where also reticulate, becoming coarser anteriorly; ventral spines sparse with thinner row near hinge, dorsal spines thin, rarely present; cardinal process narrow, bilobed; thin shelled, no brachial pits. *Lower Carboniferous (middle Viséan):* Russia.——FIG. 388,*1a–c*. **G. magnifica* (SCHIMANSKY), Lower Carboniferous, Tulsky, northern Urals; ventral valve viewed anteriorly, posteriorly, laterally, ×0.75 (Litvinovich & Vorontsova, 1991).

Kansuella CHAO, 1928, p. 67 [**Striatifera kansuensis* CHAO, 1927b, p. 108; OD] [=*Parakansuella* TAN ZHEN-XIU, 1987, p. 123 (type, *P. xinshaoensis;* OD)]. Transverse outline; weakly concavoconvex with weakly inflated ventral umbo and prominent ginglymus in both valves; rugae posteriorly, but weak anteromedianly; interiors as in *Gigantoproductus* but

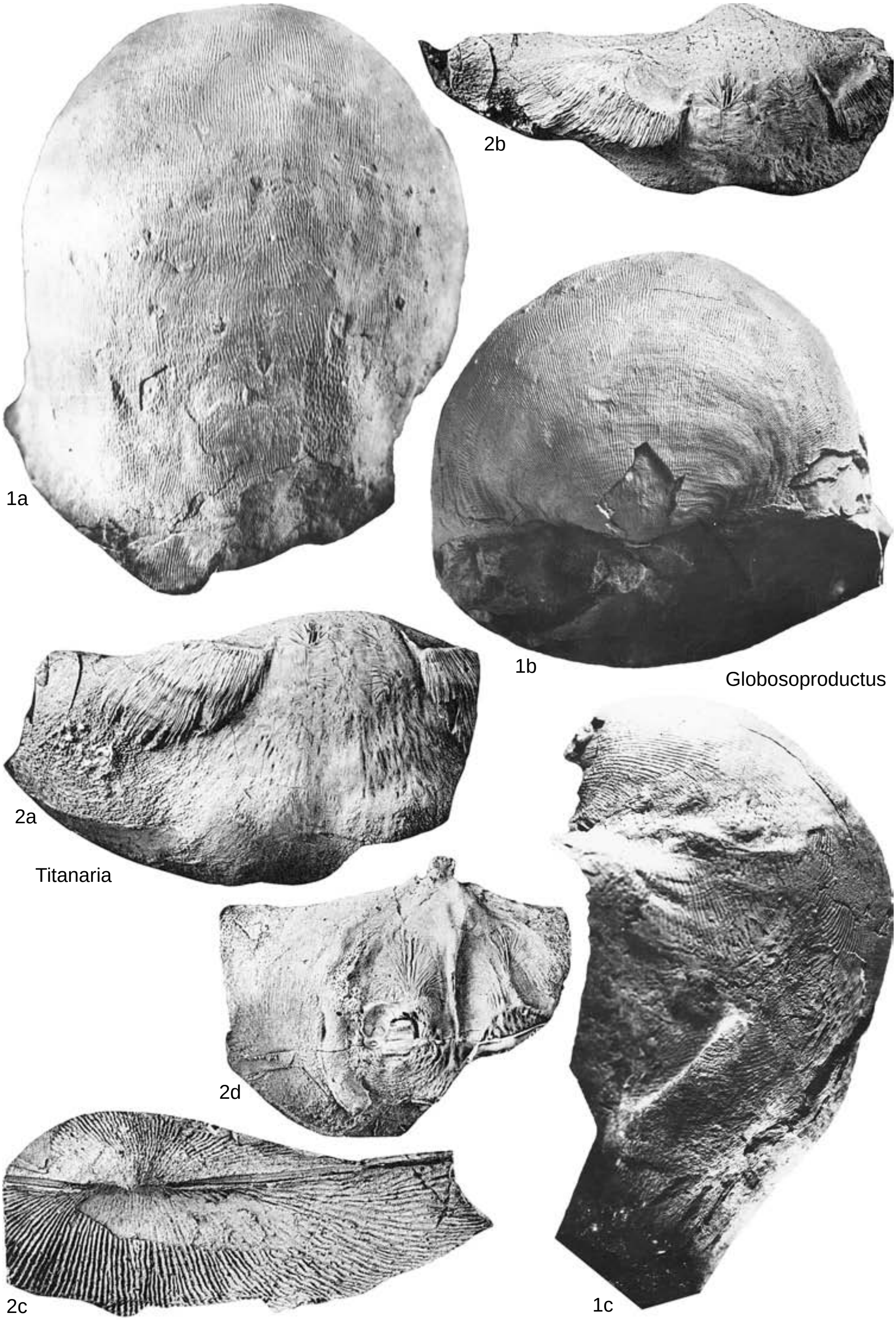


FIG. 388. Monticuliferidae (p. 552–555).

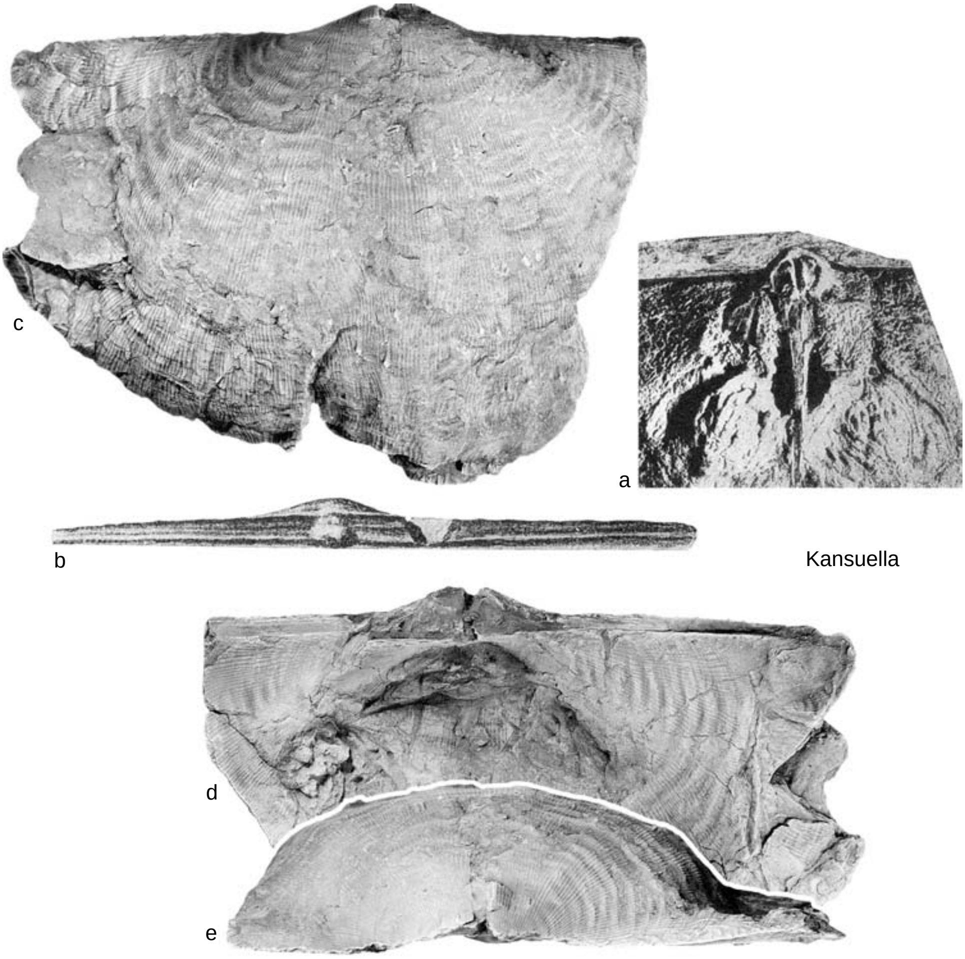


FIG. 389. Monticuliferidae (p. 552–554).

with bilobed cardinal process. [*Parakansuella* may differ in lacking rugae and more inflated ventral umbo.] *Lower Carboniferous (Viséan):* Eurasia.——FIG. 389*a,b.* **K. kansuensis,* Viséan, Kansu, China; *a,* incomplete dorsal valve internal mold, ×0.75; *b,* posterior view of shell with short ginglymus, ×0.75 (Muir-Wood & Cooper, 1960).——FIG. 389*c–e. Kansuella* sp., upper Viséan, Scotland; incomplete shell viewed ventrally, dorsally, posteriorly, ×0.75 (new).

Kueichowella YANG SHI-PU in FENG & JIANG, 1978, p. 267 [**K. kueichowensis;* OD] [=*Guizhouella* YANG SHI-PU, 1978, p. 124 (type, *G. guizhouensis* YANG SHI-PU, 1978, p. 125, obj.)]. Externally resembles *Kansuella,* but more strongly concavoconvex, no ginglymus; rugae cover valves fully; valves relatively thin shelled; cardinal process large, unifid. *Carboniferous (lower Serpukhovian):* China.——FIG. 390,*2a–c.* **K. kueichowensis,* lower Serpukhovian, Guizhou, originally figured as *G. guizhouensis; a,b,* holotype, viewed ventrally, posteriorly, MCMB F3-2297, ×0.5; *c,* ventral valve exterior viewed posteroventrally, ×1 (Yang Shi-pu, 1978).

Serbarinia MOROZOV, 1985, p. 115 [**Productus kalugensis* SARYTCHEVA, 1928, p. 61; OD]. Resembles *Gigantoproductus,* but thin shelled; cardinal process trifid with strong median ridge; posterolateral internal surfaces strongly pustulose. *Lower Carboniferous (lower upper Viséan):* Russia.——FIG. 391*a–d.* **S. kalugensis* (SARYTCHEVA), lower Alexin, Moscow basin; *a,b,* replica of holotype, viewed ventrally, posteriorly, MGRI 30/27, ×0.5 (new); *c,* ventral valve interior, ×1; *d,* dorsal valve interior, ×1 (Sarytcheva, 1928).

Titanaria MUIR-WOOD & COOPER, 1960, p. 334 [**T. costellata;* OD]. Gigantic or large; transverse, resem-

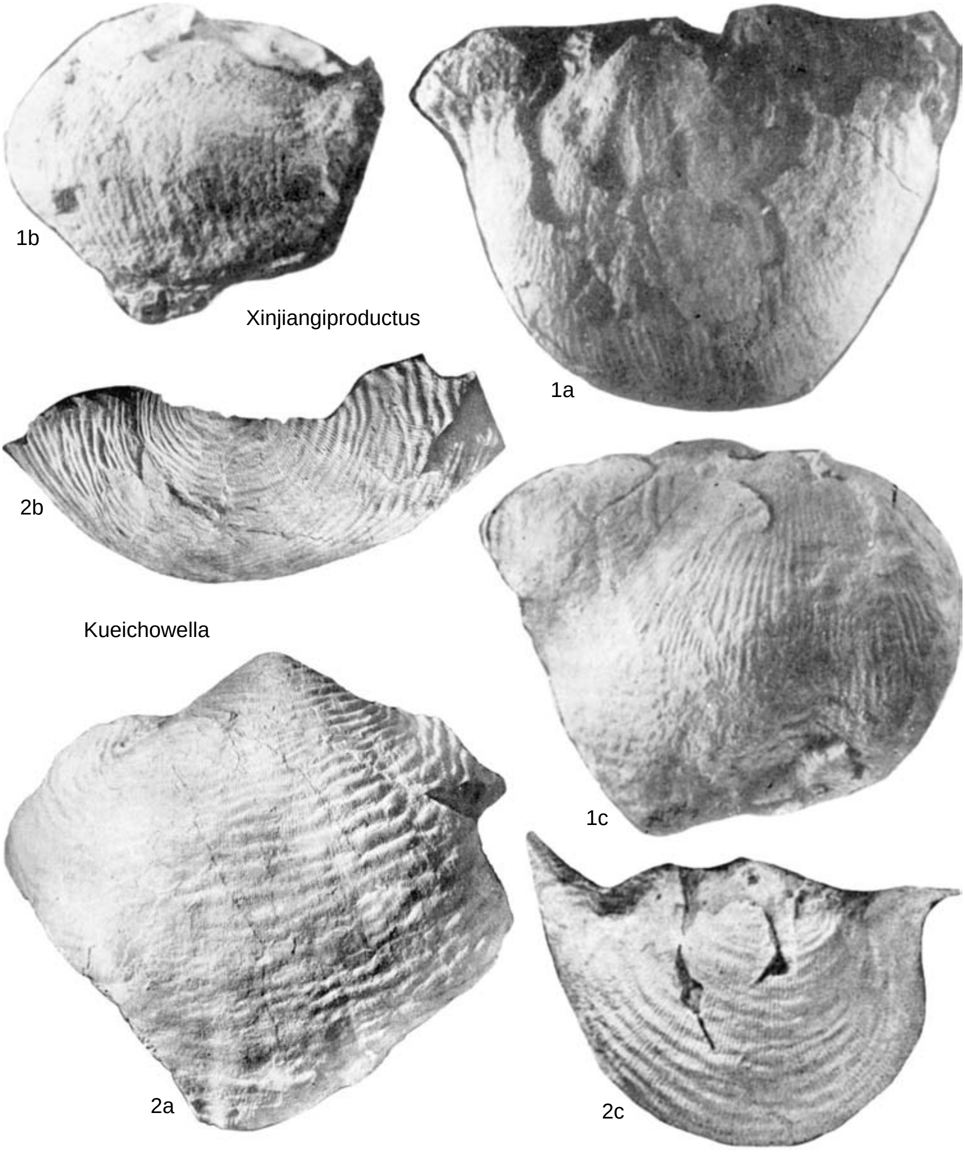


FIG. 390. Monticuliferidae (p. 554–556).

bling *Gigantoproductus,* but lacking rugae, anterior plications; ginglymus short; spines fine, widely distributed on both valves; ventral adductor scars between diductors; cardinal process trifid with strongly projecting median portion, brachial cones absent. *Lower Carboniferous (Viséan–lower Serpukhovian):* North America, North Africa.——FIG. 388,*2a–d.* **T. costellata,* Chesterian, California; *a,b,* holotype, internal mold, viewed ventrally, posteriorly, USNM 8040a, ×0.8; *c,d,* replica of external mold, viewed posterodorsally and replica of incomplete dorsal valve interior, USNM 8040a, ×0.8 (Muir-Wood & Cooper, 1960).

Xinjiangiproductus YAO & FU, 1987, p. 96[101] [**X. yamansuensis;* OD]. Medium size; resembling *Datangia,* but with thick-shelled ventral valve and brachial cones; dorsal valve thin shelled. *Lower Carboniferous (Viséan–lower Serpukhovian):* China.——FIG. 390,*1a–c.* **X. yamansuensis,* Lower Carboniferous, Xinjiang; *a,b,* holotype, partly exfoliated

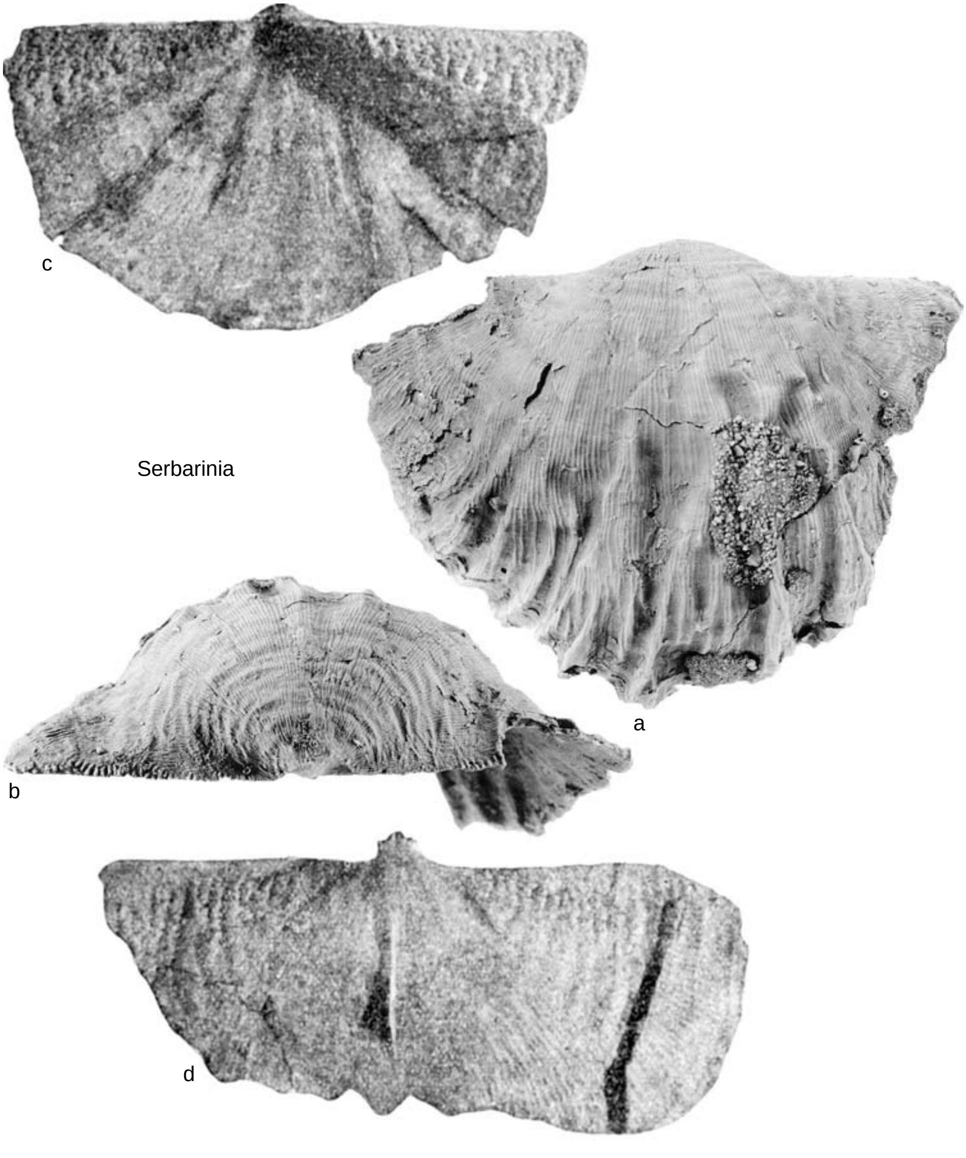


FIG. 391. Monticuliferidae (p. 554).

ventral valve viewed ventrally, laterally, ×1; *c,* exfoliated dorsal valve interior viewed anterolaterally, ×1 (Yao & Fu, 1987).

Tribe SEMIPLANINI Sarytcheva, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 930, Semiplanidae SARYTCHEVA in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 231]

Medium size to large, with very thin shell substance; ventral umbo strongly incurved; ribs of various widths; spines on both valves, some on ventral only; cardinal process bilobed or trifid, with median ridges poorly developed; no brachial cones. *Lower Carboniferous (middle Viséan–lower Serpukhovian).*

Semiplanus SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1952, p. 119 [**Productus semiplanus* SCHWETSOV,

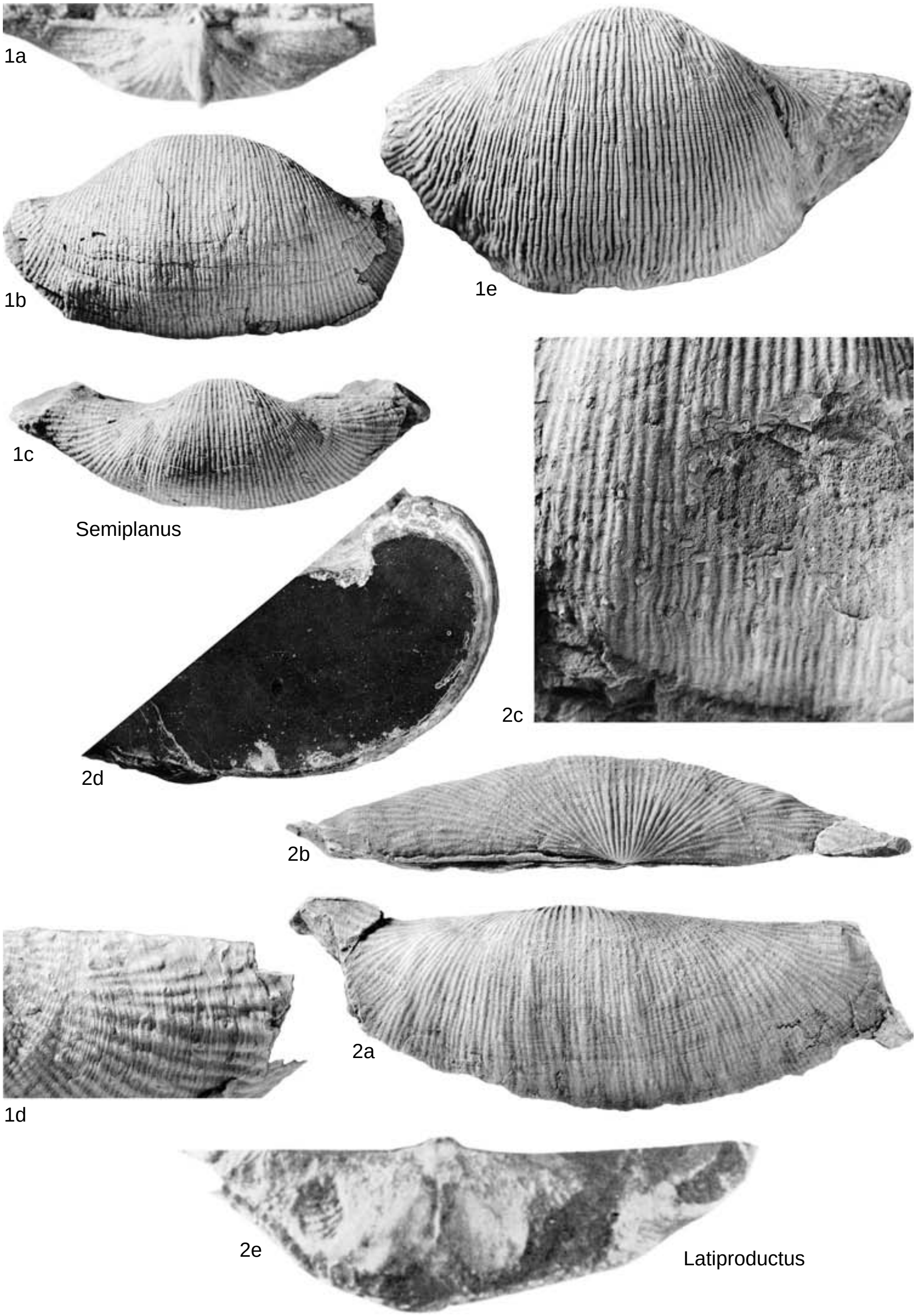


FIG. 392. Monticuliferidae (p. 556–559).

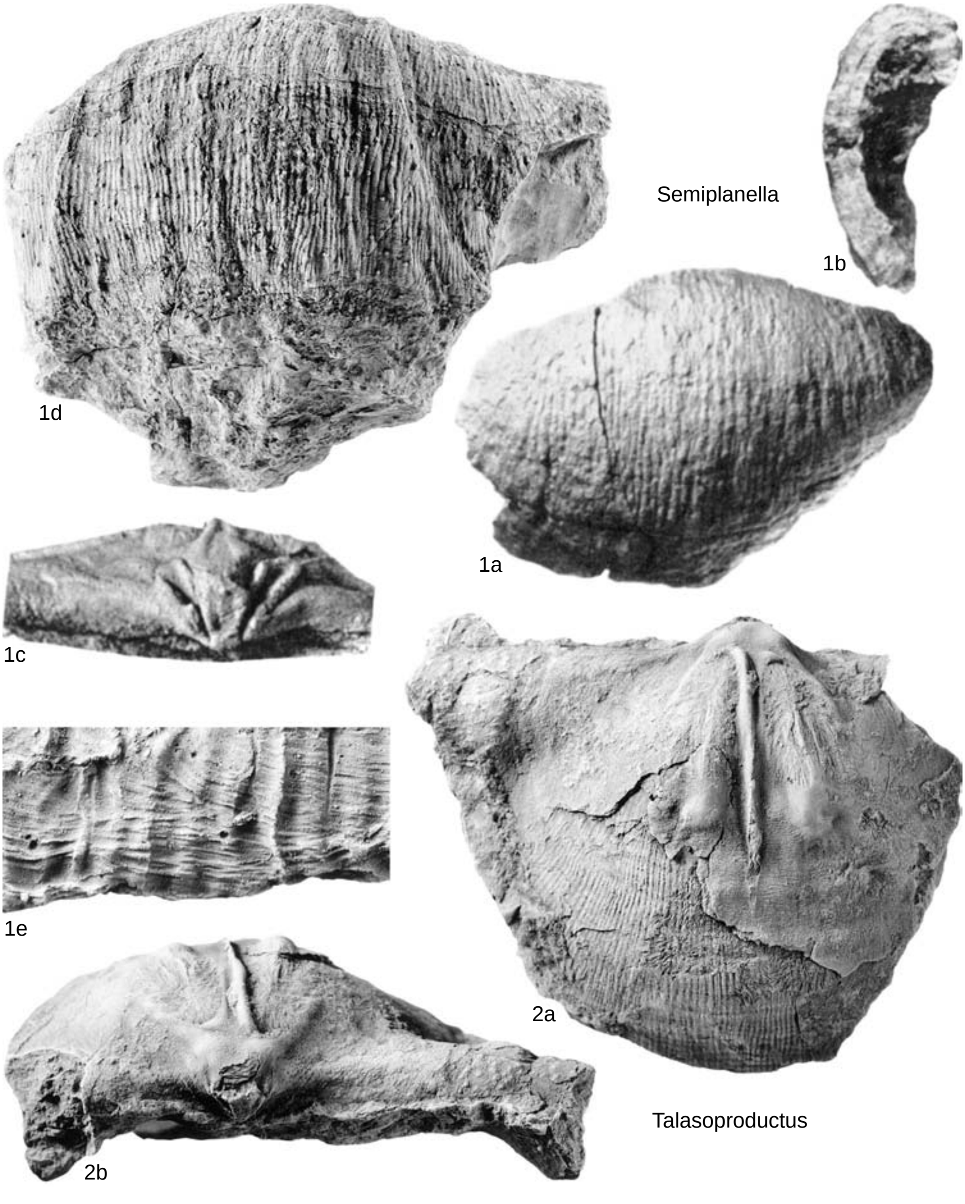


Fig. 393. Monticuliferidae (p. 559–560).

1922, p. 10; OD]. Medium to large; outline strongly transverse with poorly defined ears; ribbing distinct, entire; spines fine, numerous on both valves, less wide than ribs; cardinal process bilobed, becoming weakly trifid, supported by thick median septum; brachial ridges indistinct. *Lower Carboniferous (upper Viséan):* Eurasia.——Fig. 392,*1a–d*. **S. semiplanus* (Schwetsov), Asbian, Isle of Anglesey, north Wales; *a,* dorsal valve interior viewed posteriorly, ×1.5 (Sarytcheva & Legrand-Blain, 1977); *b,c,* ventral valve exterior viewed anteroventrally, posteroventrally, ×1; *d,* detail of ear showing ornament, spine bases, ×3 (new).——Fig. 392,*1e. Semiplanus* sp., Derbyshire; ventral valve exterior showing spine bases, ×1 (new).

Latiproductus Sarytcheva & Legrand-Blain, 1977, p. 75 [**Productus latissimus* J. Sowerby, 1822 in 1821–1822, pl. 330, fig. 2–3; OD]. Resembles *Semiplanus,* but lacking dorsal spines and with somewhat thicker ventral spines, ribbing; cardinal process trifid with short middle lobe. *Lower Carboniferous (Brigantian–lower Serpukhovian):* Eurasia, northern

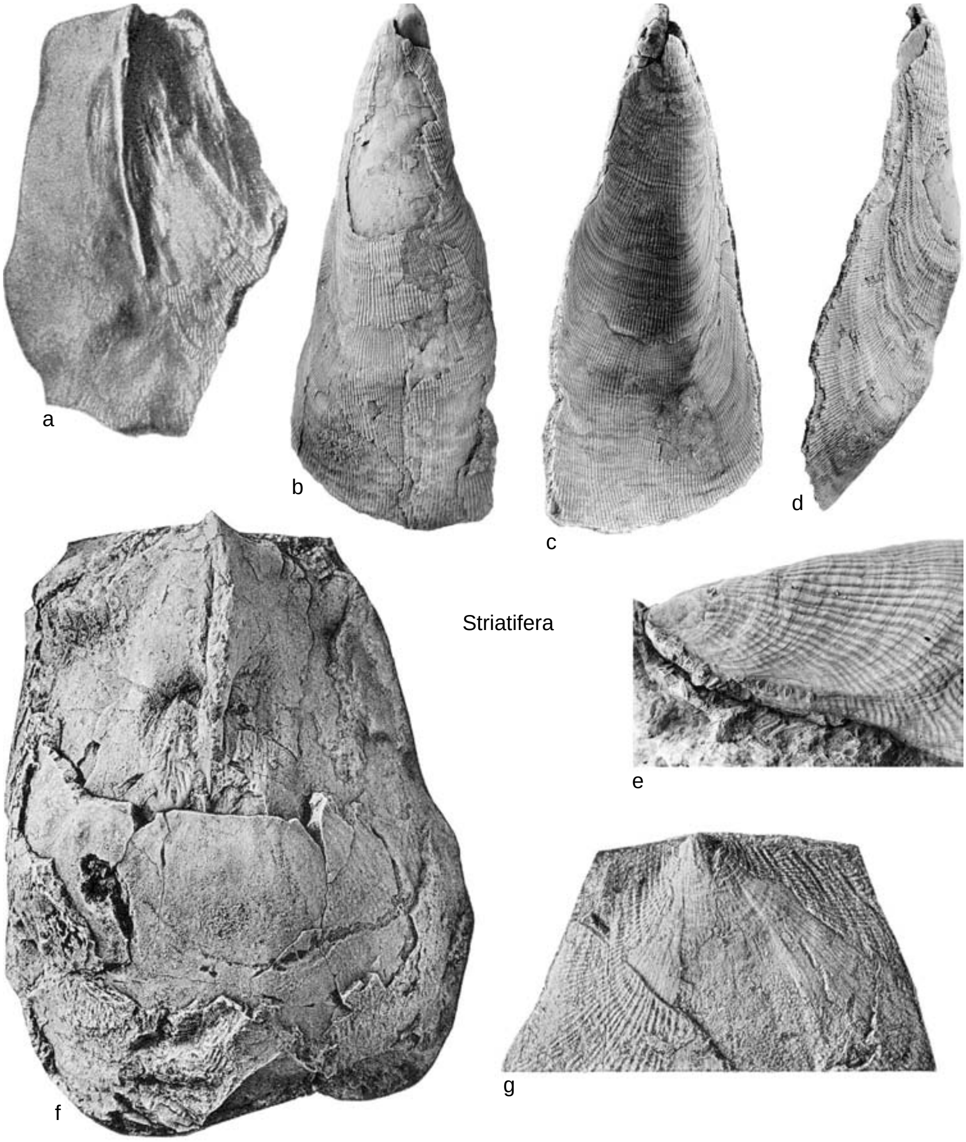


FIG. 394. Monticuliferidae (p. 560).

Africa.——FIG. 392,*2a–e.* **L. latissimus* (J. SOWERBY), Brigantian, Isle of Anglesey; *a,b,* external mold of dorsal valve viewed ventrally, posteriorly, ×1; *c,* external ornament with spine bases, ×2; *d,* median longitudinal section showing ventral profile, ×1 (new); *e,* dorsal valve interior, ×1 (Sarytcheva & Legrand-Blain, 1977).

Semiplanella SARYTCHEVA & LEGRAND-BLAIN, 1977, p. 79 [**S. carinthica* SARYTCHEVA in SARYTCHEVA & LEGRAND-BLAIN, 1977, p. 81; OD]. Resembles *Semiplanus,* but with thick-shelled valves and sessile cardinal process with strong but short median lobe; cardinal ridges obscure; spines fine, more common ventrally; brachial ridges well defined. *Lower Carboniferous (upper Viséan):* western Europe, ?central Asia, ?northern Africa.——FIG. 393,*1a–e.* **S. carinthica* (SARYTCHEVA), Brigantian, Carnic Alps, Austria; *a,b,* holotype, viewed ventrally, in section, PIN 3704/2, ×1; *c,* dorsal valve interior viewed posteriorly, ×3 (Sarytcheva & Legrand-Blain, 1977); *d,* anterior view of ventral valve exterior, ×1; *e,* segment of dorsal valve trail external mold with few spine bases, ×5 (new).

Talasoproductus LITVINOVICH & VORONTSOVA, 1983, p. 92 [**T. turlanensis;* OD]. Shell large but thin walled, lateral profile unusually gently convex;

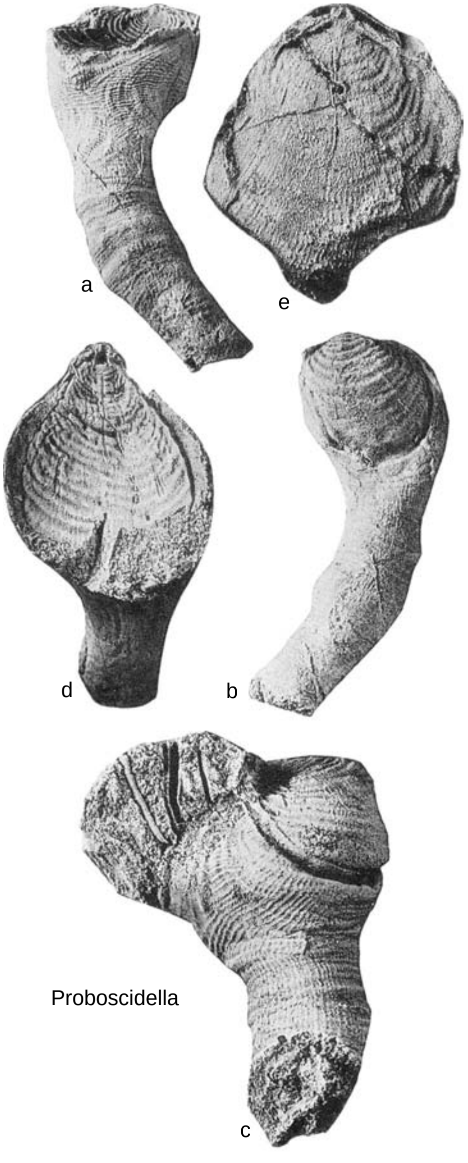


Fig. 395. Monticuliferidae (p. 560–562).

ribbing fine with narrow interspaces; spines confined to ventral hinge, ears; cardinal process with median, lateral portions equal; dorsal adductor scars bordered by ridges posterolaterally, lateral ridges short. *Lower Carboniferous (middle Viséan):* Kazakhstan.——Fig. 393,*2a,b.* **T. turlanensis,* middle Viséan, Kazakhstan; incomplete dorsal valve interior viewed ventrally, posteriorly, ×1 (new).

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 on ventral valve only. *Carboniferous (upper Viséan–Serpukhovian).*

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; cardinal process of single ridge continuous with median septum. *Carboniferous (upper Viséan–Serpukhovian).*

Striatifera Chao, 1927b, p. 94 [**Mytilus striatus* Fischer de Waldheim, 1837, p. 181; OD; *non Pileopsis striatus* Phillips, 1836, p. 224]. Elongate, tapering posteriorly, flattened shell; spines ventral, clustered at ears and scattered on costellae; cardinal process commonly unifid, supported by long median septum. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* Eurasia, northern Africa, North America.——Fig. 394*a–e.* **S. striata* (Fischer de Waldheim); *a,* dorsal valve interior, Asbian–Brigantian, Russia, ×1 (Muir-Wood & Cooper, 1960); *b–d,* corpus of specimen viewed ventrally, dorsally, laterally, upper Asbian, Belgium, ×0.75; *e,* lateral view of ventral umbo with spine bases marginally, British Isles, Yorkshire, ×3 (new).——Fig. 394*f,g.* *Striatifera* sp., Meramecian–Chesterian, Oregon; *f,* dorsal valve interior, ×1; *g,* partly exfoliated ventral valve viewed posteriorly, ×1 (Muir-Wood & Cooper, 1960).

Tribe PROBOSCIDELLINI Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 930, *ex* Proboscidellinae Muir-Wood & Cooper, 1960, p. 325]

Corpus cavity shallow; hinge narrower than maximum width; ventral trail long and forming tube, irregularly rugose; cardinal process bilobed, lateral, and submarginal ridges present. *Lower Carboniferous (upper Viséan).*

Proboscidella Oehlert, 1887b, p. 1277 [**Productus proboscideus* de Verneuil, 1840, p. 259; OD]. Corpus with weak rugae that may extend on ventral trail, forming long tube; spines strong at posterior margin, sparse or absent elsewhere. *Lower Carboniferous (upper Viséan):* Eurasia.——Fig. 395*a–e.* **P. proboscidea* (de Verneuil), upper Viséan, Belgium;

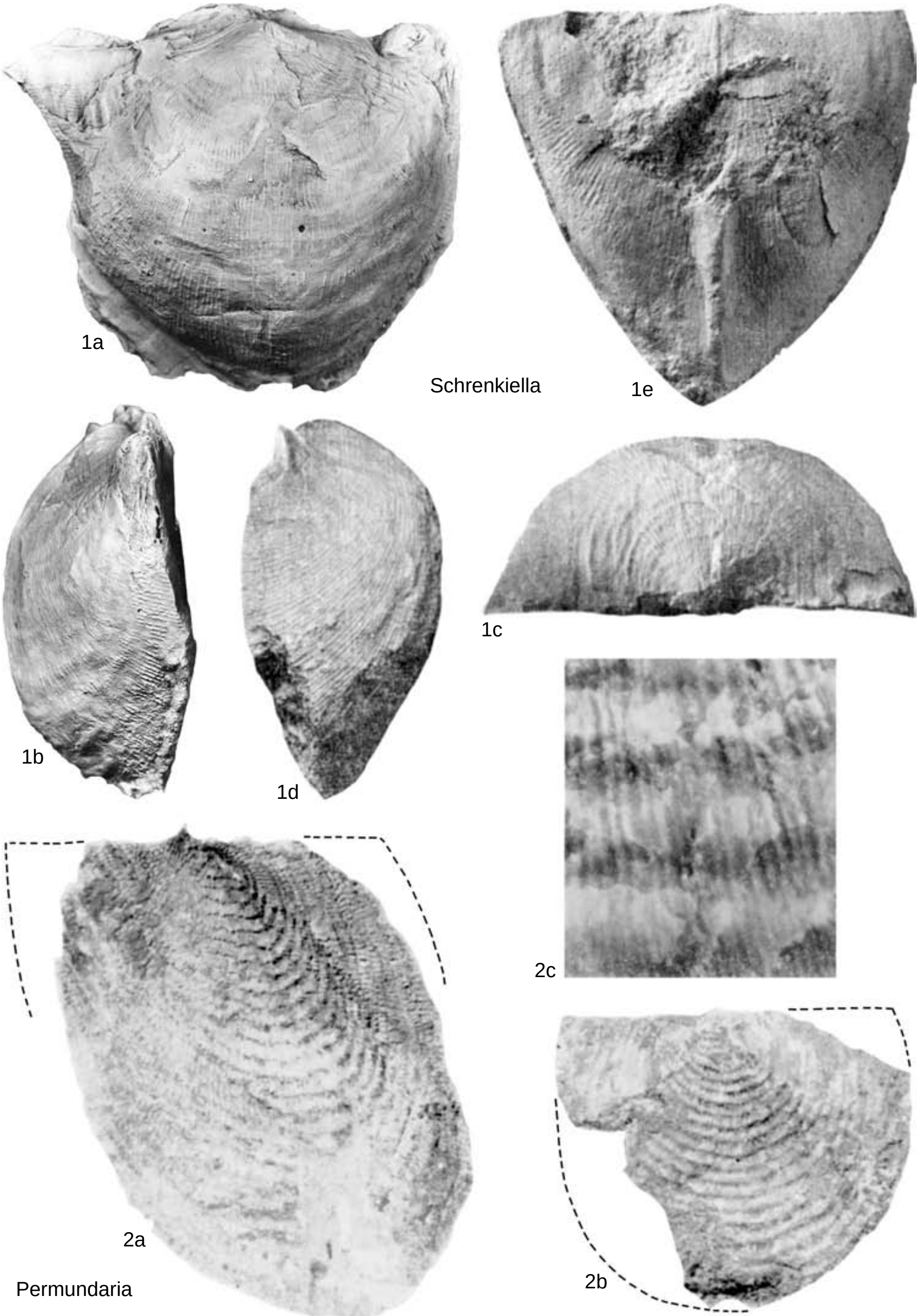


FIG. 396. Monticuliferidae (p. 562–563).

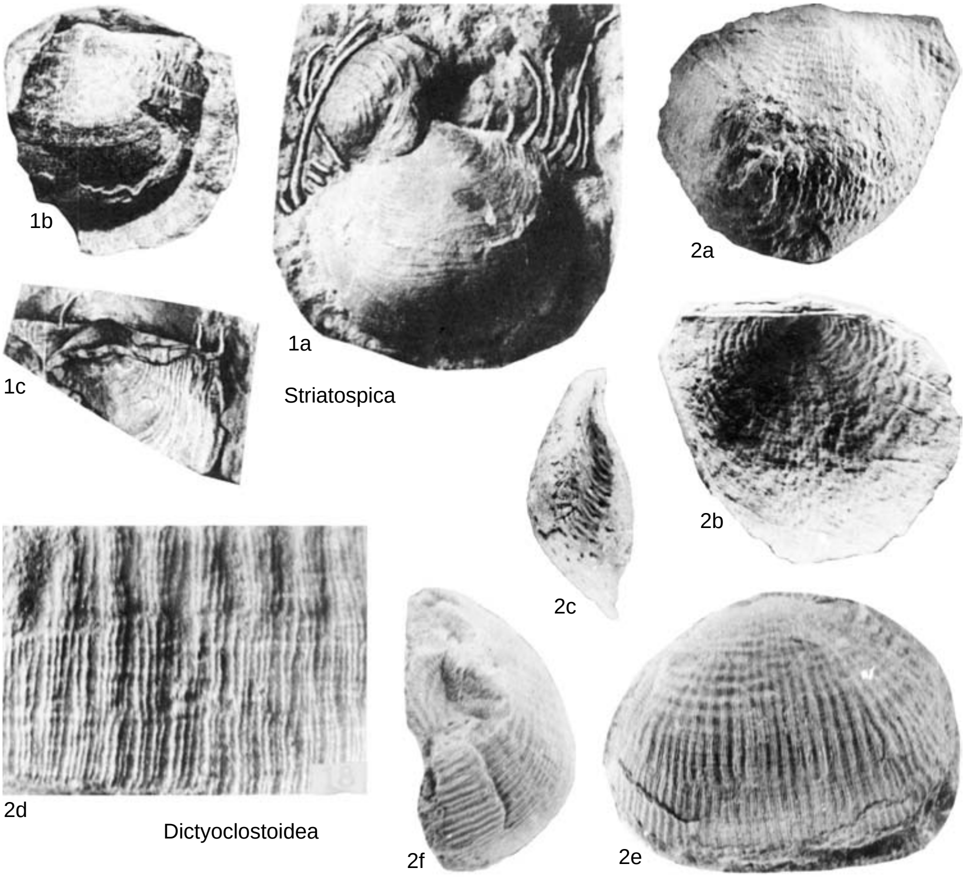


FIG. 397. Monticuliferidae (p. 562–563).

a,b, lateral, ventral views of almost complete specimen, ×3; *c,* oblique lateral view of shell with clasping spines, ×3; *d,* dorsal view of internal mold of shell, ×2; *e,* replica of dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Subfamily SCHRENKIELLINAE Lazarev, 1986

[Schrenkiellinae LAZAREV, 1986c, p. 30]

Medium size to large, with flattened ventral disk; spines in row near hinge margin only, ribs separated by wider interspaces, commonly with fine capillation; rugae may be present. *Lower Permian (Sakmarian)–Upper Permian (upper Capitanian).*

Schrenkiella BARCHATOVA, 1973, p. 97 [**Productus schrenki* STUCKENBERG, 1875, p. 88; OD] [=?*Achunoproductus* USTRITSKY, 1971, p. 21; *Indigia* BARCHATOVA, 1973, p. 100 (type, *I. ilibeica*)]. Medium to large, somewhat trapezoid to broadly trigonal with median ventral fold; visceral disks weakly curved; ribs fine, narrower than interspaces, tend to fluctuate in width; spines only recorded at ventral hinge. *Lower Permian (Sakmarian):* northern Russia, ?Australia.——FIG. 396,*1a,b.* **S. schrenki* (STUCKENBERG), Sakmarian, Timan; partly exfoliated ventral valve exterior viewed ventrally, laterally, ×1 (new).——FIG. 396,*1c,d. S. timanica* BARCHATOVA; specimen viewed posteriorly, laterally, ×1 (Barchatova, 1973).——FIG. 396,*1e. S. triangulata* (BARCHATOVA); exfoliated dorsal valve interior, ×1.5 (Barchatova, 1973).

Dictyoclostoidea JING & HU, 1978, p. 121 [**D. kiangsiensis* WANG & CHING in WANG, CHING, & FANG, 1966, p. 437; OD] [=*Dictyoclostoidea* WANG & CHING in WANG, CHING, & FANG, 1964, p. 264, *nom. imperf.; Dictyoclostoidea* WANG & CHING in WANG, CHING, & FANG, 1966, p. 437, *nom. imperf.;* ?=*Hypolinoproductus* LIANG in WANG & others, 1982, p. 212 (type, *H. changxingensis*)]. Closely resembles *Schrenkiella,* but possibly with more strongly developed rugae; capillae restricted to dor-

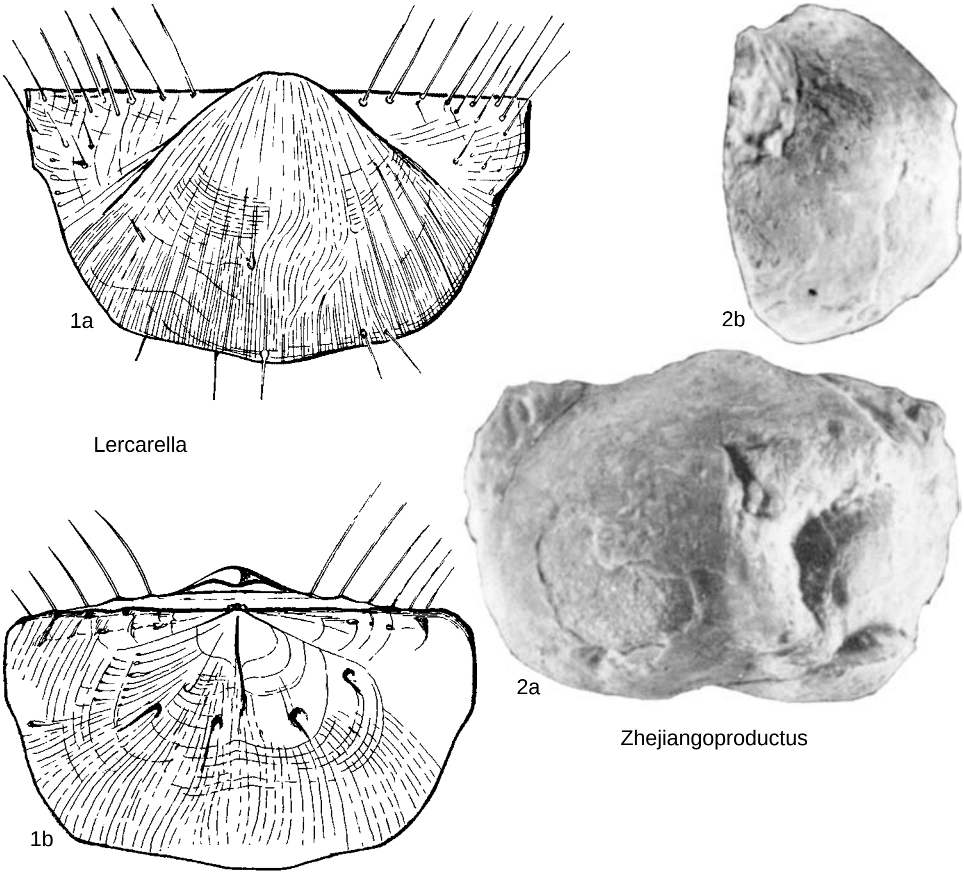


FIG. 398. Monticuliferidae (p. 563–564).

sal valve, rare spines on ventral valve; short ginglymus may be present. *upper Lower Permian (Artinskian)–lower Upper Permian (Kazanian):* eastcentral China.——FIG. 397,*2a–d.* **D. kiangsiensis* WANG & CHING, Xiaojiangbian Limestone, Jiangxi; *a–c,* specimen viewed ventrally, dorsally, laterally, ×1.5; *d,* detail of dorsal valve ornament, ×5 (new).——FIG. 397,*2e,f. D. changxingensis* (LIANG), Chihsian Formation, Anhui; holotype, internal mold of ventral valve viewed ventrally, laterally, ZI 52803, ×1.6 (new).

Permundaria NAKAMURA, KATO, & CHOI, 1970, p. 295 [**P. asiatica;* OD]. Poorly understood genus; medium to large with very weakly concavoconvex profile; rugae, fine ribbing cover shell, but no spines reported. *Upper Permian:* Japan, Cambodia, southern China, Kashmir, ?Iran.——FIG. 396,*2a.* **P. asiatica,* Upper Permian, Sisophon Limestone, Kitakami Mountains; holotype, ventral valve external mold, UHR 19015, ×1.4 (Nakamura, Kato, & Choi, 1970).——FIG. 396,*2b,c. P. sisophonensis* NAKAMURA, KATO, & CHOI; *b,* holotype, incomplete ventral valve exterior, UHR 19017, ×1.4; *c,* detail of ribbing, UHR 19017, ×10 (Nakamura, Kato, & Choi, 1970).

Striatospica WATERHOUSE, 1975, p. 11 [**Striatifera? kayseri* CHAO, 1927b, p. 115; OD]. Medium size with hinge forming widest part of shell; trail forming flange anteriorly, laterally; rugae fine on both disks; capillae on both valves, no costation; strong spine rows on ears, close to hinge only; interiors unknown. *Upper Permian (upper Capitanian):* China.——FIG. 397,*1a–c.* **S. kayseri* (CHAO), Loping Formation, Jiangxi; *a,* holotype, ventral valve exterior, ?NIGP 1104, ×1; *b,* ventral valve exterior, ×1; *c,* external mold of part of dorsal valve, ventral umbo, ×1 (Chao, 1927b).

Subfamily UNCERTAIN

Lercarella MASCLE & TERMIER, 1970, p. 188 [**L. sicana;* OD]. Poorly known, large, transverse, widest at hinge with ginglymus or interarea; weakly concavoconvex with shallow corpus; spines near ventral hinge, on ears and rarely on venter; interiors poorly known, cardinal process possibly ventrally

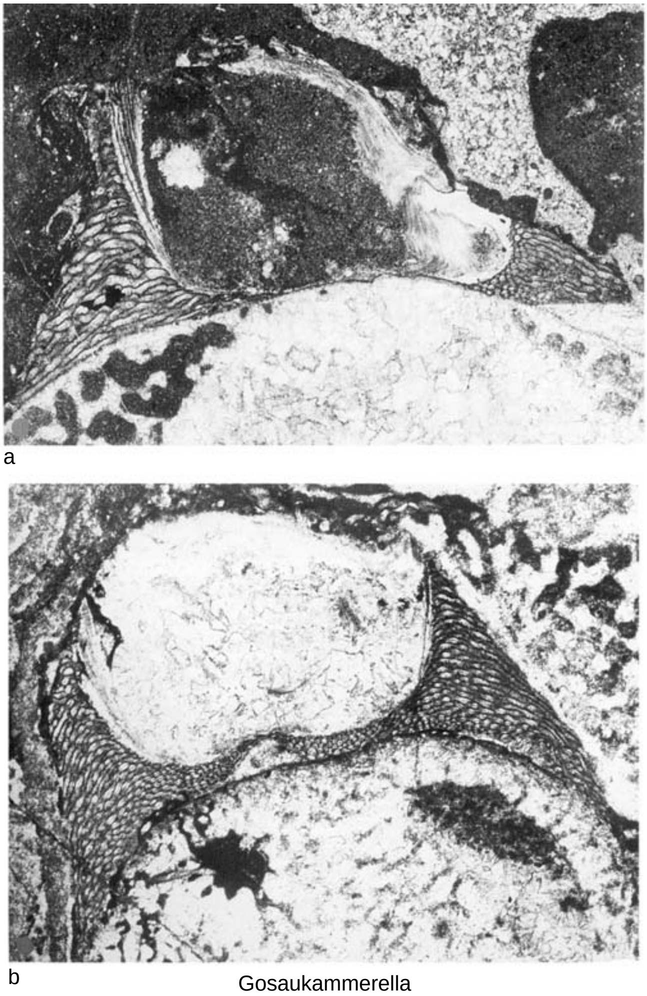


FIG. 399. Uncertain (p. 564–565).

directed, indicating relationship with the Strophalosiinae, otherwise possibly in Monticuliferidae. *Lower Permian:* Sicily.——FIG. 398,*1a,b.* **L. sicana,* Lower Permian, Lercara Friddi; *a,* reconstruction of ventral valve, ×1; *b,* reconstruction of dorsal valve, ×1 (Mascle & Termier, 1970).

Zhejiangoproductus LIANG WEN-PING, 1990, p. 196[464] [**Z. zhejiangensis;* OD]. Poorly known, large with hinge equal to maximum width; ventral disk flattened, with convex trail; sulcus originating on ventral disk; spines at hinge line and ears, reportedly absent alsewhere; exteriors reportedly smooth other than rugae on ears. *Upper Permian (Kazanian):* China.——FIG. 398,*2a,b.* **Z. zhejiangensis,* Kazanian, Lengwu Formation, Zhejiang; shell viewed ventrally and laterally, ×1.5 (Liang, 1990).

Superfamily UNCERTAIN

Gosaukammerella SENOWBARI-DARYAN & FLÜGEL, 1996, p. 92 [**G. eomesozoica;* OD; =?*Pycnoporidium eomesozicum* FLÜGEL, 1972, p. 968, possibly alga]. Minute, 2 to 3 mm wide, planoconvex corpus, thin valve walls, but ventrally with outgrowths of thick, symmetrical mass of tubules attaching to substrate; shell substance reportedly pseudopunctate, laminar; interiors unknown. [If a productide it is a long holdover that lived in a cryptic reef environment]. *?Upper Triassic (?Norian, ?Rhaetian):* alpine Mediterranean region.——FIG. 399*a,b.* **G. eomesozoica,* Dachstein Reef Limestone, Norian, Austria; *a,* oblique longitudinal section of both valves, ×15; *b,* transverse section of ventral valve and tubular attachment structure, ×15 (Senowbari-Daryan & Flügel, 1996).

Suborder STROPHALOSIIDINA Schuchert, 1913

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *ex* Strophalosiinae SCHUCHERT, 1913a, p. 391, *sensu* LAZAREV, 1989, *non* WATERHOUSE, 1978]

Productides with interareas in ventral valve only or both valves; commonly ventrally attached; profile includes conical shape; spines on ventral or both valves, rarely absent; toothed articulation retained or lost; cardinal process directed ventrally or posteroventrally, never dorsally.

This group of productides is tremendously varied in shape and habit, ranging from chonetid-like in profile to conical or flattened; attachment is by direct cementation of part of the ventral valve or by creeping, irregularly shaped spines. Carboniferous and Permian taxa tend to be adapted to live on hard substrates, commonly reef environments, and the various elaborations of trails appear to have been in response to these habitats. *Lower Devonian (Emsian)–Upper Permian (Changhsingian).*

Superfamily STROPHALOSIOIDEA Schuchert, 1913

[*nom. correct.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *pro* Strophalosiacea MUIR-WOOD & COOPER, 1960, p. 71, *nom. transl. ex* Strophalosiinae SCHUCHERT, 1913a, p. 391]

Cicatrix commonly developed; corpus cavity shallow; teeth retained; brachial ridges commonly extending to disk margins. *Lower Devonian (Emsian)–Upper Permian (Changhsingian).*

Family STROPHALOSIIDAE Schuchert, 1913

[*nom. transl.* STEHLI, 1954, p. 328, *ex* Strophalosiinae SCHUCHERT, 1913a, p. 391]

Outline rounded; strong rhizoid spines over ventral or both valves, may be bidirectional; planoconvex profile, but corpus cavity rather shallow; trails short. *Lower Carboniferous (Hastarian)–Upper Permian (Changhsingian).*

Subfamily STROPHALOSIINAE Schuchert, 1913

[Strophalosiinae SCHUCHERT, 1913a, p. 391] [=Heteralosiinae MUIR-WOOD & COOPER, 1960, p. 80; Truncateninae LIAO, 1982, p. 539; Licharewiellinae ARCHBOLD, 1986, p. 98]

Spines on ventral valve only; plano- to weakly concavoconvex profile. *Lower Carboniferous (Hastarian)–Upper Permian (Changhsingian).*

Strophalosia W. KING, 1844, p. 313 [**S. gerardi* W. KING, 1846, p. 92; SD MUIR-WOOD & COOPER, 1960, p. 74] [=*Leptaenalosia* W. KING, 1850, p. 93, *nom. nud.*]. Medium, slightly transverse subrounded outline with ill-defined small ears; hinge less than maximum width; ventral interarea wide but short; weak concavoconvex profile; concentric ornament weak ventrally, lamellose dorsally; weak capillation may be present on dorsal valve; spines cover ventral valve, suberect, semirecumbent; lateral ridges ventrally, separating ears; medium septum connected to cardinal process, interrupted at adductor scars, reaching two-thirds disk length. *Lower Permian (Sakmarian)–Upper Permian (Kazanian):* Himalayas, Australia ?Arctic Russia, China, Salt Range.——FIG. 400,*1a–c.* **S. gerardi* W. KING, Ladakh, Himalayas; *a,b,* lectotype, viewed ventrally, dorsally, FC D 267, ×1.5; *c,* incomplete dorsal valve interior, ×1.5 (Brunton, 1966).——FIG. 400,*1d–f. S. irwinensis* COLEMAN, Callytharra Formation, Carnarvon basin, Australia; *d,* ventral valve exterior, ×1.2; *e,* ventral valve internal mold, ×1.6; *f,* dorsal valve interior, ×2 (Archbold, 1986).

Coronalosia WATERHOUSE & GUPTA, 1978, p. 415 [*C. blijniensis;* OD]. Similar to *Strophalosia,* but with fine ventral spines, other than at hinge line; relatively smooth dorsal valve exterior. Published figures inadequate for illustration. *Lower Permian (?Sakmarian):* India.

Craspedalosia MUIR-WOOD & COOPER, 1960, p. 82 [**Orthothrix lamellosa* GEINITZ, 1848, p. 86; OD]. Resembles *Dasyalosia* ventrally, but with dorsal valve strongly lamellose, lacking spines. *upper Lower Permian (Roadian):* Europe.——FIG. 401,*1a–d.* **C. lamellosa* (GEINITZ), lower Zechstein, Gera, Germany; *a–c,* shell viewed ventrally, dorsally, laterally, ×2; *d,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Etherilosia ARCHBOLD, 1993, p. 11 [**Strophalosia etheridgei* PRENDERGAST, 1943, p. 43; OD]. Small, subcircular with hinge less than maximum width; resembling *Heteralosia,* but differing in its relatively larger cicatrix, distinct rhizoid spines, in having only ventral uniform, suberect spines. *Lower Permian*

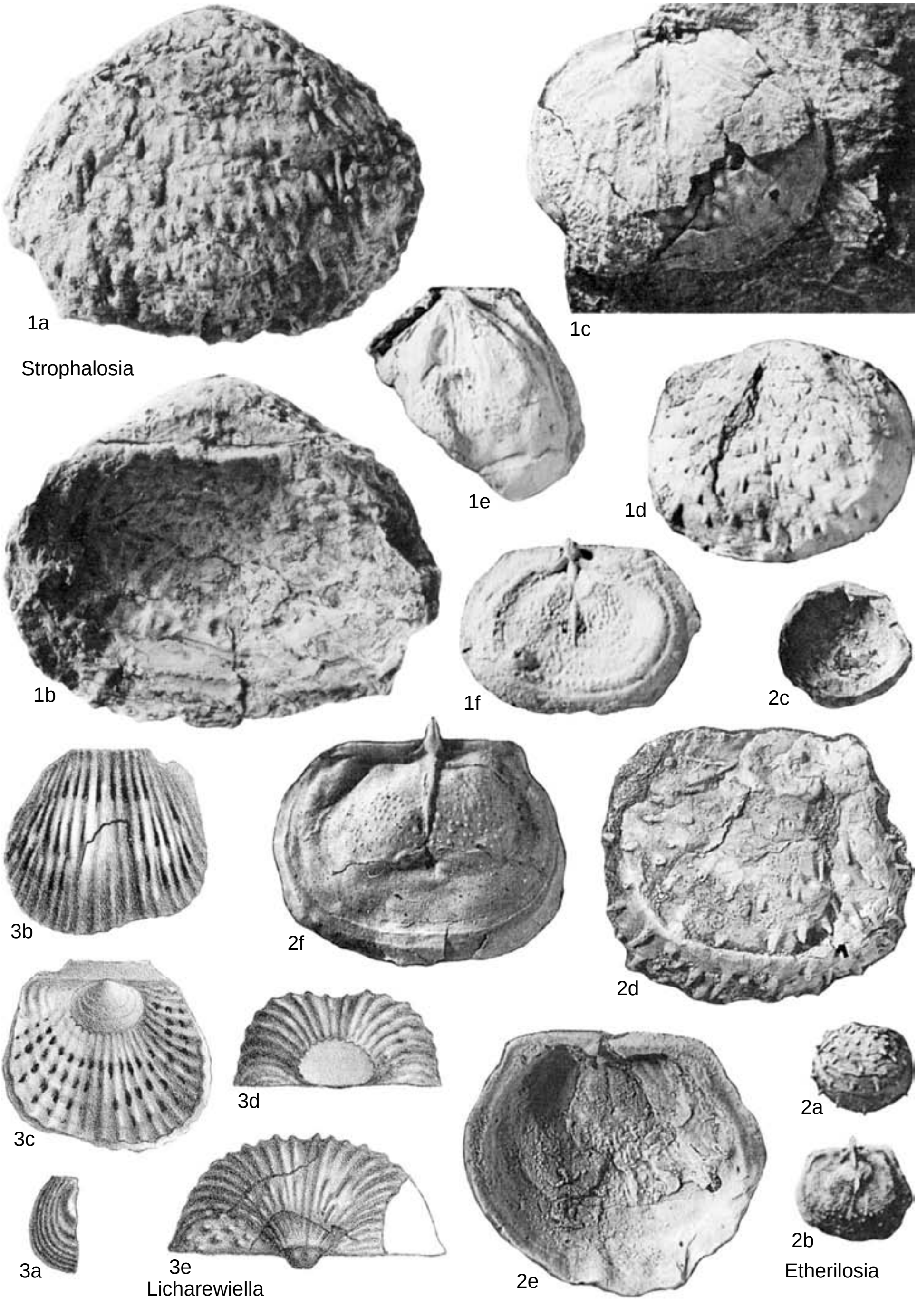


FIG. 400. Strophalosiidae (p. 565–569).

(upper Sakmarian–upper Artinskian): Western Australia.——FIG. 400,*2a–c.* **E. etheridgei* (PRENDERGAST), Callytharra Formation; *a,* ventral valve exterior, Carnarvon basin, ×1.5; *b,* dorsal valve interior, Carnarvon basin, ×2; *c,* ventral valve interior, Irwin basin, ×1.5 (Coleman, 1957).——FIG.

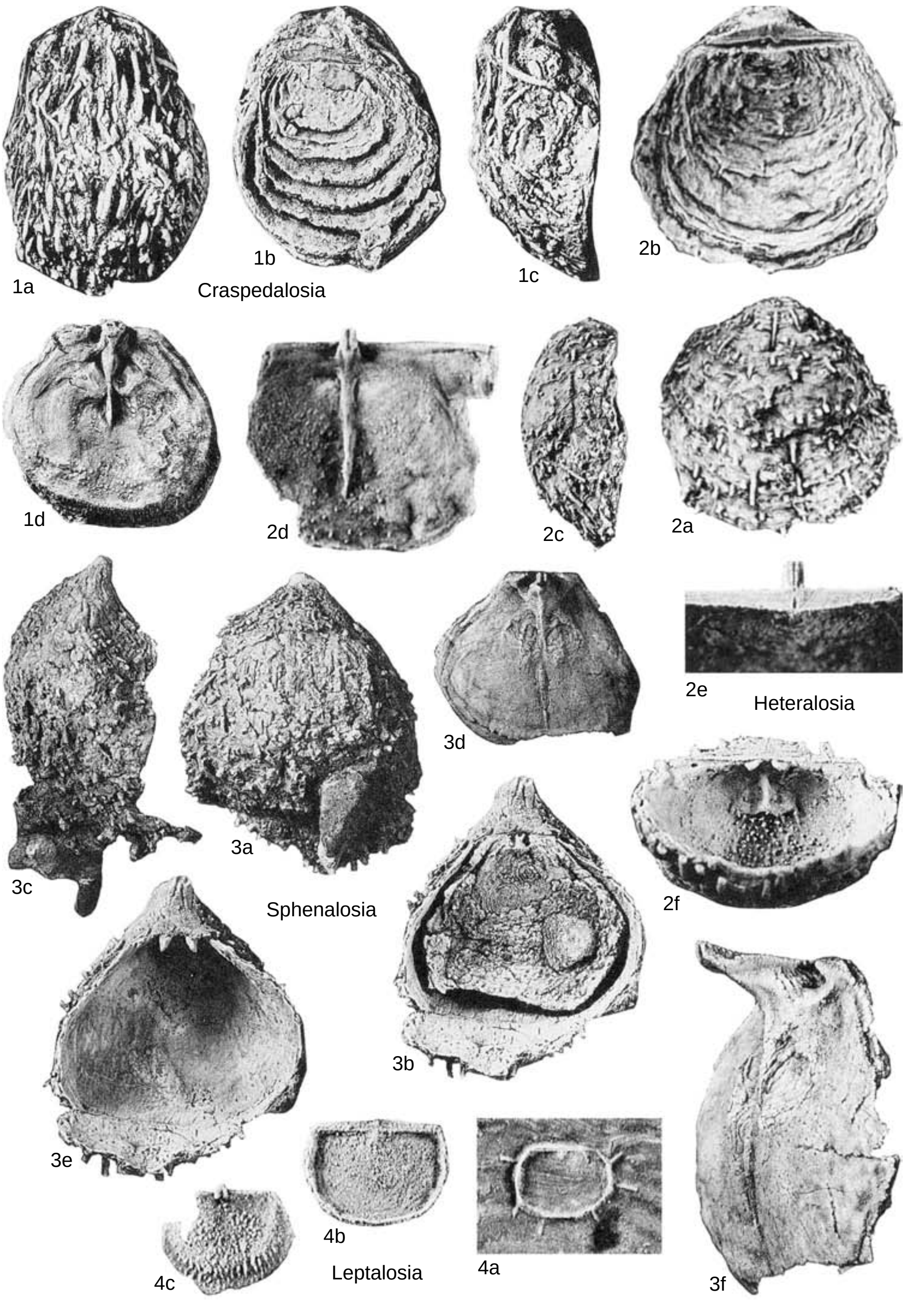


FIG. 401. Strophalosiidae (p. 565–569).

400,*2d–f. E. prendergastae* (COLEMAN), ?Cundlego Formation, Carnarvon basin; *d,* ventral valve exterior, ×3; *e,* ventral valve interior, ×3.2; *f,* dorsal valve interior, ×3.2 (Archbold, 1993).

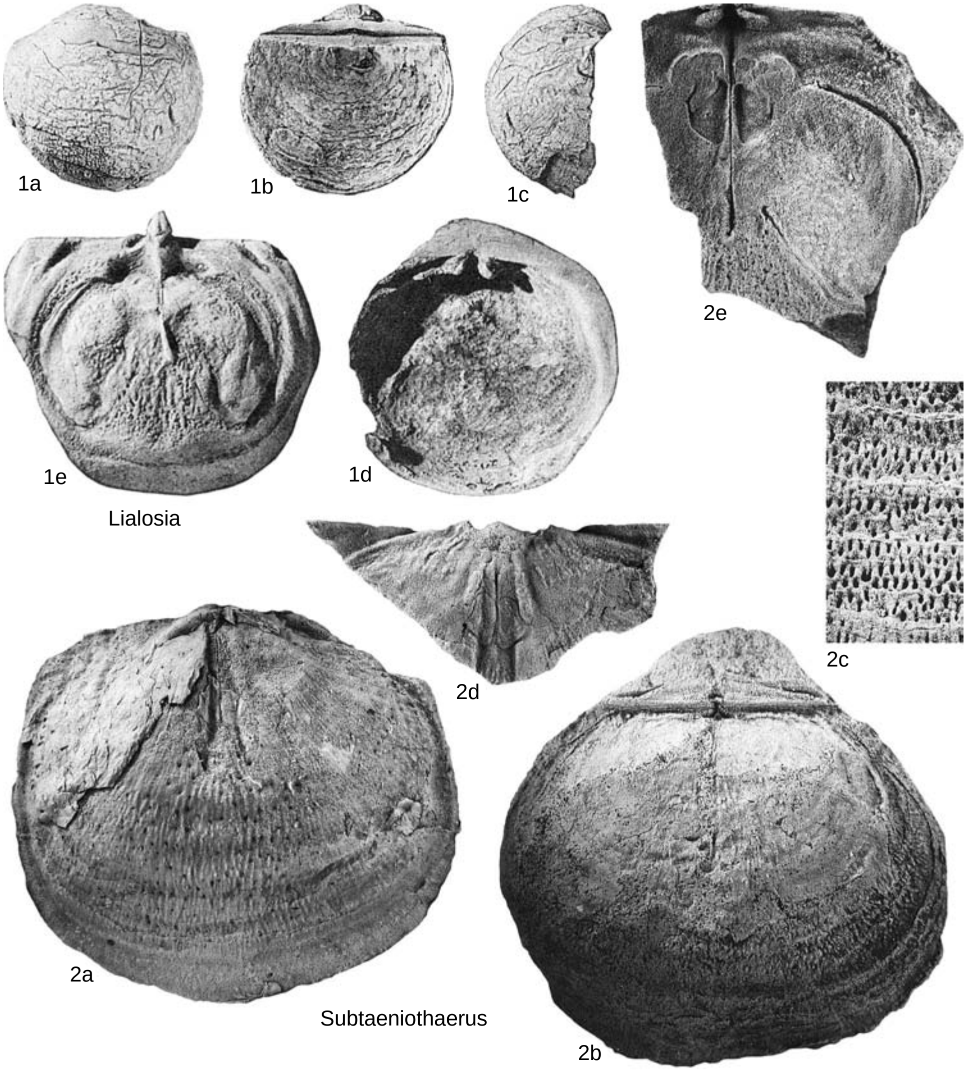


FIG. 402. Strophalosiidae (p. 569).

Heteralosia KING, 1938, p. 278 [**H. slocomi;* OD]. Small; subcircular, gently concavoconvex shells; cicatrix varied, spines bidirectional; both valves lamellose; socket ridges may extend to border adductor scars posteriorly, prominent median septum supports cardinal process. *Lower Carboniferous (Asbian)–lower Upper Permian:* North America, Europe.——FIG. 401,*2a–e.* **H. slocomi,* Gzhelian, Graham Formation, Texas; *a–c,* shell viewed ventrally, dorsally, laterally, ×2; *d,* incomplete dorsal valve interior, ×3; *e,* incomplete dorsal valve, posterior, ×4 (Muir-Wood & Cooper, 1960).——FIG. 401,*2f. H. hystricula* (GIRTY), Wordian, Texas; ventral valve interior showing teeth, muscle field, ×3 (Muir-Wood & Cooper, 1960).

Leptalosia DUNBAR & CONDRA, 1932, p. 260 [**Strophalosia scintilla* BEECHER, 1890b, p. 243; OD]. Minute, around 3 mm wide; interareas short; ventral valve almost fully cemented by cicatrix; few radiating spines from margins, smooth dorsal exterior; cardinal process bilobed anteroventrally, connecting with small socket ridges. [An unsatisfactory genus, possibly representing the young of other strophalosiids]. *Lower Carboniferous (Hastarian)–Upper Carboniferous:* North America, ?Russia.——FIG. 401,*4a–c.* **L. scintilla* (BEECHER), Hastarian, Louisiana Limestone, Missouri; *a,* dorsal view of attached shell, ×4; *b,* dorsal valve exterior, ×8; *c,* dorsal valve interior, ×8 (Muir-Wood & Cooper, 1960).

Lialosia Muir-Wood & Cooper, 1960, p. 86 [**Strophalosia kimberleyensis* Prendergast, 1943, p. 47; OD]. Medium, subcircular outline with hinge less than maximum width; interareas short on both valves, cicatrix present; disks gently concavoconvex with short trails; concentric lamellose ornament more prominent dorsally; capillae faint; spines only in rows at low angle to hinge; dorsal interior thickened around disk, with large brachial areas. *Lower Permian (Artinskian–Kungurian):* Western Australia.——Fig. 402,*1a–e.* **L. kimberleyensis* (Prendergast), Wandagee Formation, Carnarvon basin; *a–c,* shell viewed ventrally, dorsally, laterally, ×1; *d,* ventral valve interior, ×1.5; *e,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Licharewiella Ustritsky in Ustritsky, Hu Bin, & Chan, 1960, p. 47, *non* Sokolskaya, 1960, p. 219 (Orthotetidina) [**Strophalosia costata* Waagen, 1884, p. 655; OD] [=*Magniderbyia* Ting, 1965, p. 265; =*Costalosia* Waterhouse & Shah, 1966, p. 230, obj.; *Truncatenia* Liao, 1982, p. 539[542] (type, *T. heshanensis*)]. Small, dorsal corpus transversely subquadrate; ventral profile variable, modified by cicatrix almost perpendicular to short interarea; median sulcus from disk to margin; ribs strong, extending onto trails; rhizoid spines surrounding cicatrix, other spines only ventrally; dorsal interior with prominent marginal ridge; adductor scars probably raised on platforms. *lower Lower Permian–lower Upper Permian:* Pakistan, China, Caucasus.——Fig. 400,*3a–e.* **L. costata* (Waagen), lower *Productus* Limestone, Salt Range; *a,* partly exfoliated specimen viewed laterally, ×1; *b–d,* same specimen viewed ventrally, dorsally, posteriorly, ×2; *e,* incomplete specimen viewed posteriorly, ×2 (Waagen, 1884).

Liveringia Archbold, 1987, p. 30 [**L. magnifica;* OD]. Medium size, widest at midlength; interarea wide, short; capillae weak, but more conspicuous dorsally; spines in rows at hinge, ears, ventral spines few, short; dorsal surface with elongate dimples; marginal ridges in both valves, more prominent laterally; cardinal process short, thick, quadrifid; brachial ridges strong. *Upper Permian (upper Capitanian):* Western Australia.——Fig. 403,*1a–f.* **L. magnifica,* Hardman Formation, Canning Basin; *a,* holotype, dorsal valve external mold, CPC 26450, ×1.2; *b,* detail of ornament, ×3.2; *c,* ventral valve exterior, ×3.2; *d,* ventral valve internal mold viewed posteriorly, ×1.6; *e,* replica of ventral valve interior, ×1; *f,* dorsal valve interior, ×1 (Archbold, 1987).

Megalosia Waterhouse, 1988, p. 41 [**M. chuluensis;* OD]. Similar to *Marginalosia,* but dorsal spines reportedly absent. *upper Upper Permian (Changhsingian):* Nepal.——Fig. 403,*2a–c.* **M. chuluensis,* Nisal Formation, northcentral Nepal; *a,* holotype, viewed dorsally, UQF 76010, ×1; *b,* ventral valve exterior ×1; *c,* replica of dorsal valve interior, ×1 (Waterhouse, 1988).

Sphenalosia Muir-Wood & Cooper, 1960, p. 87 [**S. smedleyi;* OD]. Medium size, rounded trigonal outline without ears, narrow but high ventral interarea; weakly conavoconvex profile; ribbing, rugae absent; spines numerous ventrally, rhizoid posteriorly, semirecumbent elsewhere; teeth, sockets prominent; cardinal process narrow, long, extending ventrally below flat pseudodeltidium; median septum reaching across disk; marginal ridge weak. [This genus may prove to be more suitably assigned to the Gondolininae.] *Upper Permian (Kazanian):* central USA.——Fig. 401,*3a–f.* **S. smedleyi,* Phosphoria Formation, Wyoming; *a–c,* holotype, viewed ventrally, dorsally, laterally, ×1; *d,e,* dorsal valve interior, ventral valve interior, USNM 119089, ×1; *f,* oblique view of dorsal valve interior, USNM 119089, ×2 (Muir-Wood & Cooper, 1960).

Subtaeniothaerus Solomina, 1988, p. 40[39] [**S. lungersgauzeni;* OD]. Large, subcircular outline, hinge less than maximum width; ventral interarea short; spine base tubercles small, densely distributed on ventral valve only; no dorsal spines or dimples reported; marginal ridge in ventral valve; dorsal adductor scars with wide posterior, narrow anterior components. *lower Upper Permian:* northern Siberia.——Fig. 402,*2a–e.* **S. lungersgauzeni,* Dulgalakh horizon, Verkhoyan; *a,* holotype, incomplete dorsal valve interior, PIN 4218/100, ×1; *b,* dorsal valve external mold, ventral interarea, ×1; *c,* part of ventral valve external mold, ×2; *d,* incomplete ventral valve internal mold, ×1; *e,* incomplete dorsal valve internal mold, ×1 (Solomina, 1988).

Subfamily DASYALOSIINAE Brunton, 1966

[Dasyalosiinae Brunton, 1966, p. 192]

Spines on both valves; dorsal valve commonly flat. *Lower Carboniferous (upper Viséan)–Upper Permian (Capitanian).*

Dasyalosia Muir-Wood & Cooper, 1960, p. 76 [**Spondylus goldfussi* von Münster, 1839, p. 44; OD]. Small to medium size, subcircular outline with variable narrow hinge line; interarea short, pseudodeltidium flat to convex; cicatrix small or absent; spines densely cover both valves, erect, recumbent; teeth prominent, ventral ear baffles; dorsal ear baffles, marginal ridge weak. *upper Lower Carboniferous–lower Upper Permian:* western Europe.——Fig. 404,*1a–c.* **D. goldfussi* (von Münster), lower Upper Permian, Zechstein, Gera, Germany; *a,b,* shell viewed ventrally, dorsally, ×1; *c,* ventral valve viewed posteriorly showing interarea, teeth, ×3 (Muir-Wood & Cooper, 1960).——Fig. 404,*1d,e.* *D. lamnula* Brunton, Asbian, Fermanagh; incomplete dorsal valve exterior, interior, ×5 (Brunton, 1966).

Acanthalosia Waterhouse in Waterhouse & Briggs, 1986, p. 31 [**A. domina;* OD]. Size medium; gently concavoconvex with prominent ventral umbo; interareas, dorsal lophidium; ventral spines bidirectional, thicker than dorsal spines; no ribbing or lamellae; cardinal process large, supported by socket ridges. *Lower Permian (upper Artinskian):* eastern Australia.——Fig. 405,*1a–d.* **A. domina,* upper Lower Permian, Dresden Limestone, Bowen basin; *a,* holotype, viewed dorsally, UQF 73978, ×1; *b,* ventral valve external mold, ×1; *c,* dorsal valve

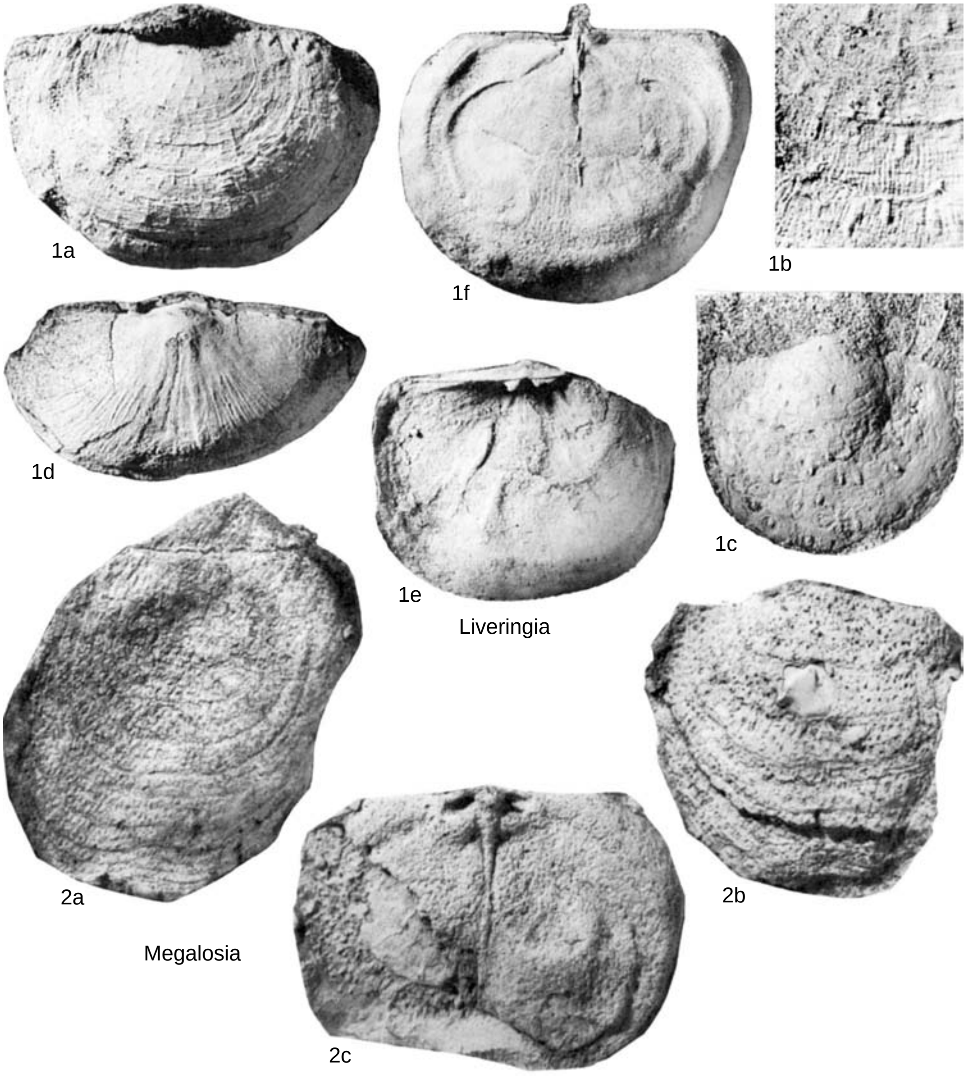


FIG. 403. Strophalosiidae (p. 569).

exterior, ×1; *d,* dorsal valve interior, ×1 (Waterhouse, 1986).

Arcticalosia WATERHOUSE, 1986, p. 2 [**Wyndhamia unispinosa* WATERHOUSE, 1969, p. 34; OD]. Similar to *Marginalosia,* but possibly differing in having more strongly concentrically ornamented dorsal exterior. *upper Lower Permian (lower Wordian)–Upper Permian (Capitanian):* Arctic Canada.——FIG. 404,*3a–c.* **A. unispinosa* (WATERHOUSE), Capitanian, Melville Island; *a,* holotype, ventral valve exterior, GSC 23818, ×1; *b,* dorsal valve exterior, ×1; *c,* dorsal valve interior with broken cardinal process, ×1 (Waterhouse, 1969).

?Costalosiella WATERHOUSE, 1983b, p. 119 [**Costalosia argentea* WATERHOUSE & SHAH, 1966, p. 233; OD]. Poorly known and some key characteristics not recorded; ventral valve inflated with elongate spine bases becoming ribs toward anterior margins; spines on both valves; dorsal disk weakly reticulate. No illustrations suitable for publication. *Lower Permian (?Kungurian), Upper Permian (Kazanian):* Iran (Malukabad).

Crossalosia MUIR-WOOD & COOPER, 1960, p. 75 [**Productus buchianus* DE KONINCK, 1847b, p. 129; OD]. Small, around 9 mm wide; subcircular; high ventral interarea, cicatrix unknown; both valves

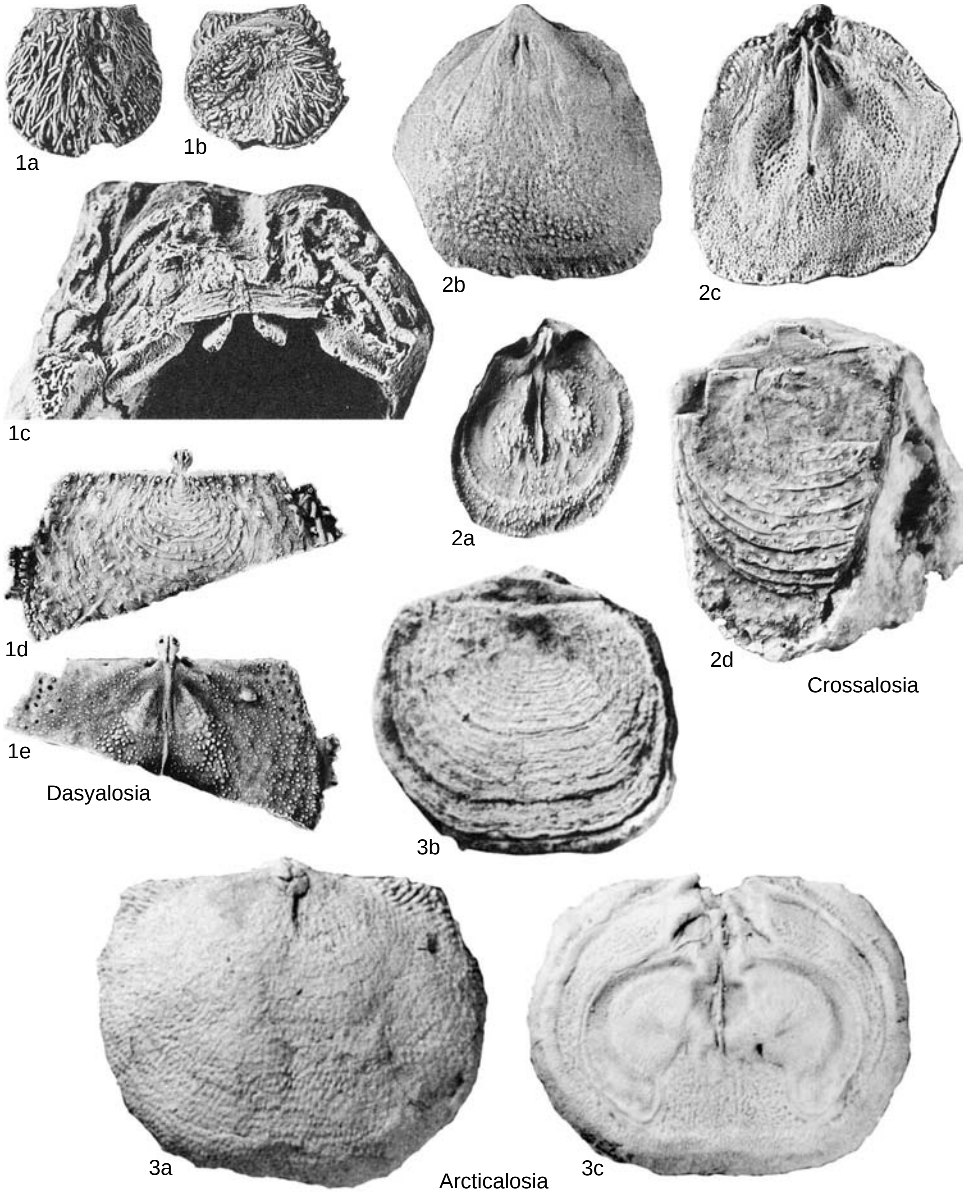


Fig. 404. Strophalosiidae (p. 569–571).

lamellose, with suberect spines; cardinal process narrow, projecting into ventral umbo, median septum over half disk length. *Lower Carboniferous (upper Viséan):* Europe.——Fig. 404,*2a–d.* **C. buchiana* (de Koninck), Asbian; *a,* lectotype, replica of dorsal valve interior, Visé, BMNH BD 197, ×3 (new); *b,c,* internal mold of shell viewed ventrally, dorsally, Visé, ×2 (Muir-Wood & Cooper, 1960); *d,* incomplete dorsal valve exterior, ventral interarea, North Yorkshire, ×4 (Brunton & Mundy, 1988b).

Echinalosia Waterhouse, 1967, p. 167, *nom. nov. pro Multispinula* Waterhouse, 1966, p. 11, *non* Rowell, 1962, p. 147 [**Strophalosia maxwelli* Waterhouse, 1964, p. 32; OD]. Similar to *Wyndhamia,* but somewhat smaller, with relatively less wide hinge line, giving more circular outline. *upper Lower Permian–lower Upper Permian:* eastern

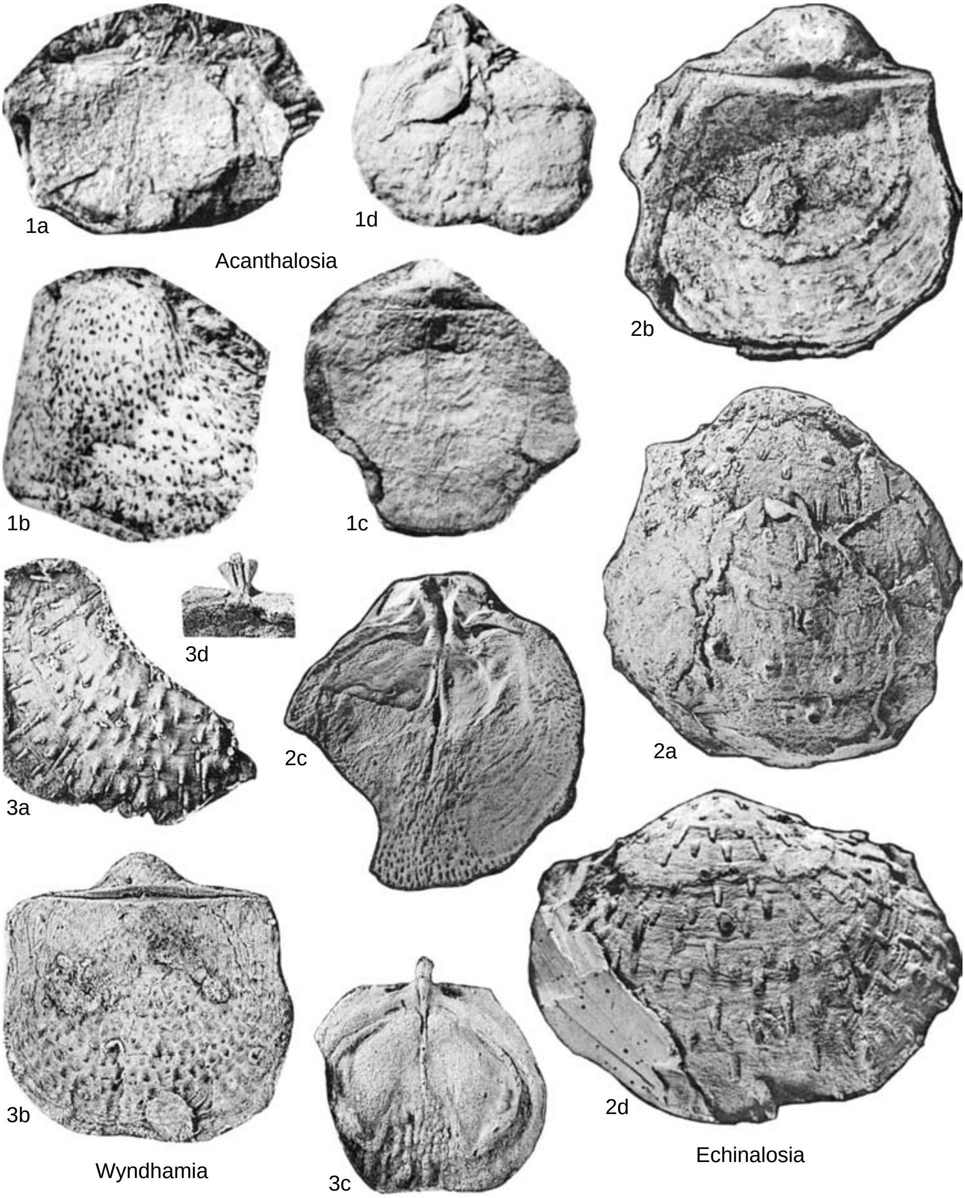


FIG. 405. Strophalosiidae (p. 569–574).

Australia, southern New Zealand, Nepal, Pakistan.——FIG. 405,*2a–d.* **E. maxwelli* (WATERHOUSE), *Productus* Creek Group, Southland, New Zealand; *a–c,* holotype, ventral, dorsal exteriors, dorsal valve internal mold, NZGS BR253, ×2; *d,* ventral valve exterior, ×2 (Waterhouse, 1964).

Hontorialosia MARTÍNEZ CHACÓN, 1979, p. 119 [**H. uniplicata;* OD]. Small, up to 10 mm wide; narrow ventral interarea; outline anteriorly emarginate, with ventral sulcus, dorsal fold; rugae weak posteriorly, somewhat lamellose anteriorly; spines relatively fine, bidirectional ventrally. *Upper Carboniferous (upper Moscovian):* southwestern Europe.——FIG. 406,*2a–d.* **H. uniplicata,* upper Moscovian, Bolsovian, northern Spain; *a,* holotype, dorsal valve exterior, DPO 8763, ×3.5; *b,* ventral valve viewed ventrally,

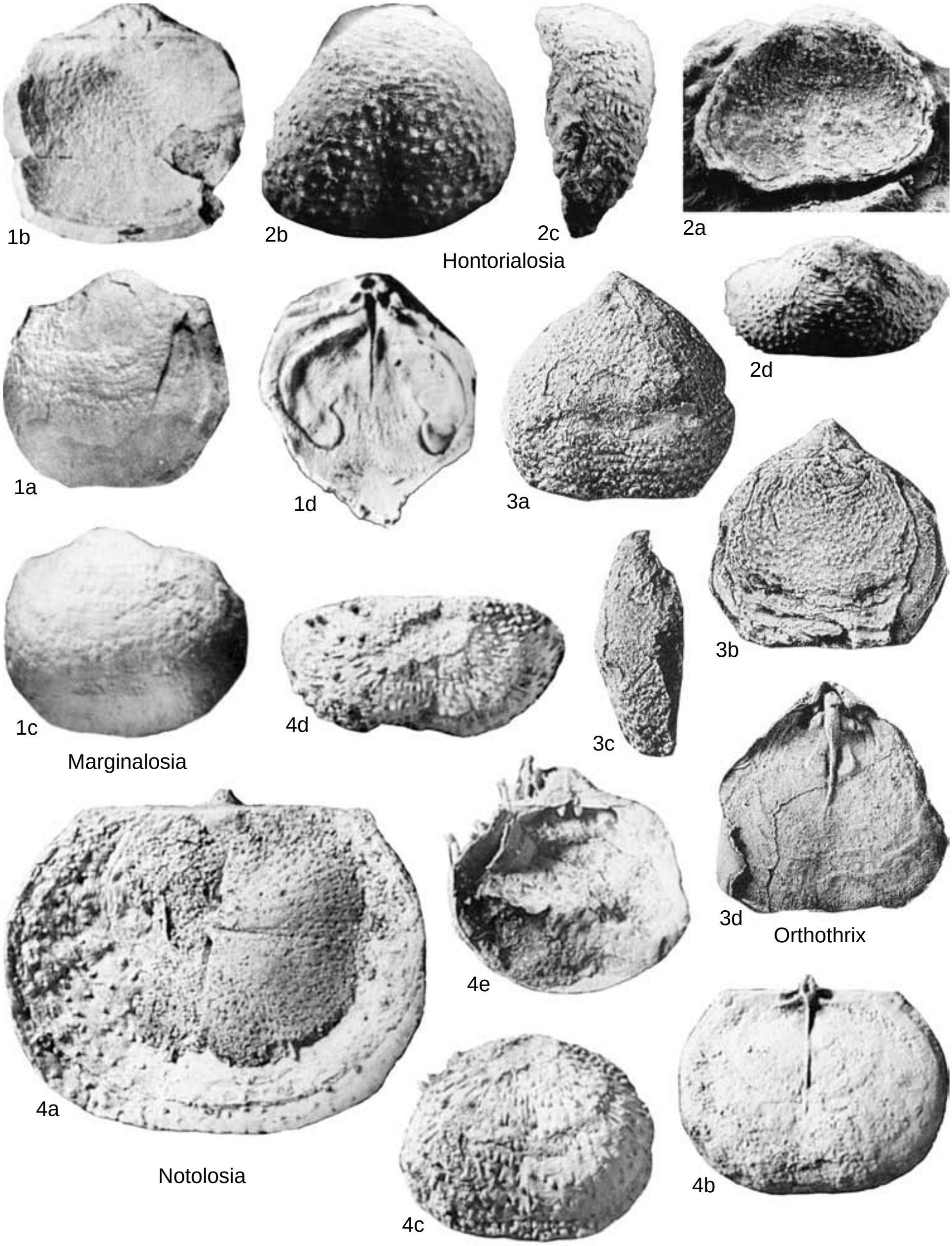


Fig. 406. Strophalosiidae (p. 572–574).

×3.5; *c,d,* ventral valve viewed laterally, posteriorly, ×3 (Martínez Chacón, 1979).

Marginalosia Waterhouse, 1978, p. 64 [**?Echinalosia kalikotei* Waterhouse, 1975, p. 4; OD]. Resembles *Wyndhamia* internally, but externally differs in having fine densely spaced spines on both valves. *Upper Permian (Capitanian):* northwestern Nepal, ?Russian Arctic, New Zealand.——Fig. 406,*1a–d. *M. kalikotei* (Waterhouse), Chhidruan, northwestern Nepal; *a,b,* holotype, viewed ventrally, dorsally,

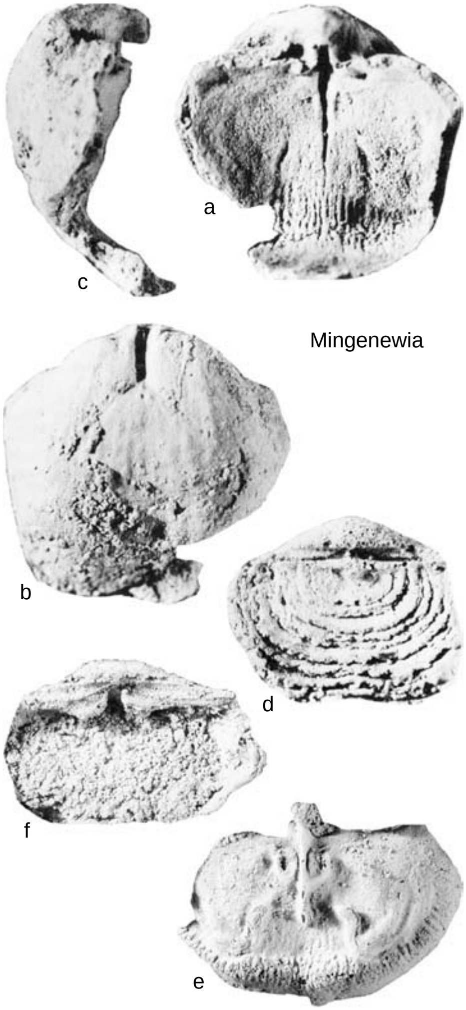


FIG. 407. Strophalosiidae (p. 574).

UQF 68854, ×1 (Waterhouse, 1978); *c,* ventral valve exterior, ×1; *d,* dorsal valve internal mold, ×1 (Waterhouse, 1975).

Notolosia ARCHBOLD, 1986, p. 114 [**Echinalosia (Notolosia) dickinsi;* OD]. Smaller, more rounded outline than *Echinalosia;* cicatrix larger, ventral recumbent spines more closely spaced. *Upper Permian (Capitanian):* Western Australia.——FIG. 406,*4a–e.* **N. dickinsi* (ARCHBOLD), Hardman Formation, Canning Basin; *a,b,* holotype, CPC 24451, dorsal valve viewed externally, ×3, internally, ×2; *c,* shell viewed ventrally, ×1.8; *d,* shell viewed posteriorly, ×2; *e,* ventral valve viewed internally, ×2 (Archbold, 1986).

Orthothrix GEINITZ, 1847, p. 84 [**Orthis excavata* GEINITZ, 1842, p. 578; SD DALL, 1877, p. 53]. Small, rounded subtrigonal, maximum width anteriorly, hinge narrow; interarea trigonal, short dorsally; dorsal valve gently convex with relatively deep corpus; dorsal valve lamellose anteriorly; spines fine, recumbent on both valves; cardinal process connected to prominent median septum posteriorly; adductor scars, brachial ridges well developed. *upper Lower Permian (Roadian)–Upper Permian (Kazanian):* Europe.——FIG. 406,*3a–d.* **O. excavata* (GEINITZ), mid-Zechstein, Thuringia; *a–c,* partly exfoliated specimen viewed ventrally, dorsally, laterally, ×2; *d,* replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Wyndhamia BOOKER, 1929, p. 24 [**Strophalosia (W.) dalwoodensis;* OD] [=*Branxtonia* BOOKER, 1929, p. 30 (type, *B. typica*); *Pseudostrophalosia* CLARKE, 1970, p. 987 (type, *S. brittoni* MAXWELL, 1954b, *partim*)]. Medium size, dorsal valve outline subquadrate, interareas short; concentric ornament rugose at ears, otherwise weak or rare lamellae; spines semierect but finer spines prostrate from short ridges, fine only on dorsal valve; cardinal process prominent, trifid; socket ridges short, extending as low marginal ridge; dorsal disk with thickened shell anteriorly. *lower Lower Permian–lower Upper Permian:* Australia, New Zealand; Siberia, Arctic Canada, *lower Upper Permian.*——FIG. 405,*3a–c.* **W. dalwoodensis* (BOOKER), ?Artinskian, Hobart, Tasmania; *a,* replica of part of ventral valve exterior, ×2; *b,* shell viewed dorsally, ×1; *c,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).——FIG. 405,*3d. W. jukesi* (ETHERIDGE); detail of cardinal process viewed posteriorly, ×1 (Muir-Wood & Cooper, 1960).

Subfamily MINGENEWIINAE
Archbold, 1980

[Mingenewiinae ARCHBOLD, 1980a, p. 253]

Spines absent; no cicatrix, dorsal valve lamellose. *Lower Permian (Artinskian).*

Mingenewia ARCHBOLD, 1980a, p. 255 [**M. anomala;* OD]. Small transverse shell; planoconvex, deep corpus with short trails; ventral interarea short, wide; ventral exterior smooth, dorsal exterior almost totally covered by prominent lamellae; brachial ridges prominent anteriorly, close to anterior end of median septum. *Lower Permian (middle Artinskian):* Western Australia.——FIG. 407*a–f.* **M. anomala,* Mingenew Formation, Perth Basin; *a–c,* holotype, viewed dorsally, ventrally, laterally, CPC 19145, ×4; *d,* dorsal valve exterior, ×4 (Archbold, 1980b); *e,* replica of dorsal valve interior, ×4.5; *f,* replica of ventral valve posterodorsally, ×5 (new).

Family CHONOPECTIDAE
Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 931, *ex* Chonopectinae MUIR-WOOD & COOPER, 1960, p. 157]

Concavoconvex profile, shallow corpus cavity; cicatrix varied; trails short; fine radial

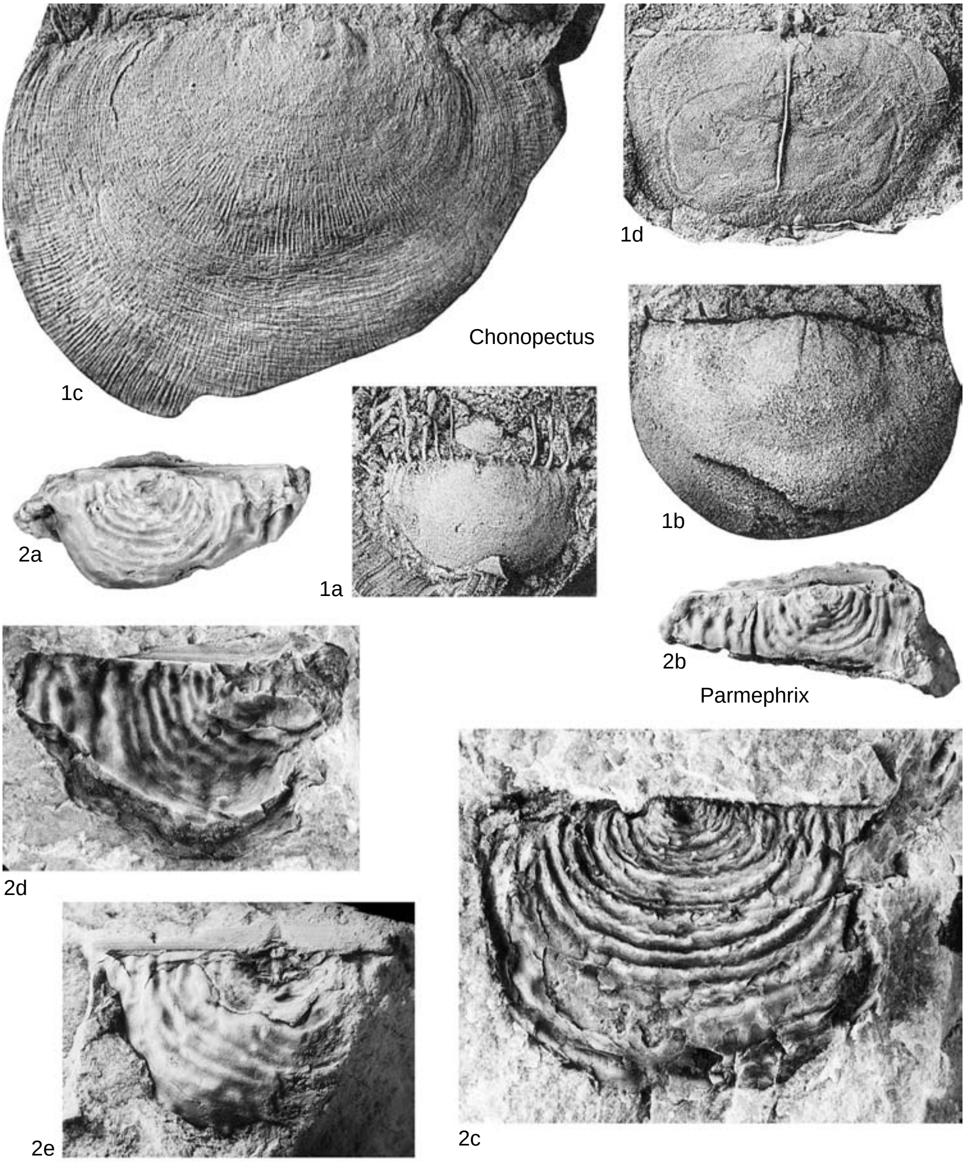


FIG. 408. Chonopectidae (p. 575–576).

ornament, rugae variable; hinge spines plus sparse, fine ventral corpus spines. *Upper Devonian–Lower Carboniferous (Brigantian).*

Chonopectus HALL & CLARKE, 1892, p. 312 [**Chonetes fischeri* NORWOOD & PRATTEN, 1855b, p. 25; OD]. Chonetoid in appearance with hinge spines, short ventral median ridge, but commonly with small cicatrix, additional rare ventral spines; capillae variable, rugae weak, irregular posterolaterally; cardinal process with small flanking sockets, anteromedian pit; long, low median septum. *Upper Devonian–Lower Carboniferous (Hastarian):* North America, western Europe.——FIG. 408,*1a–c*. **C. fischeri* (NORWOOD & PRATTEN), lower Kinderhookian, Iowa; *a,* external replica of ventral valve, ×1; *b,* internal mold of ventral valve, ×2; *c,* ventral valve exterior, ×4 (Muir-Wood & Cooper, 1960).——FIG. 408,*1d*. *Chonopectus* sp., Upper Devonian, New York; dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Dengalosia Manankov & Pavlova, 1981, p. 137 [**D. gobica;* OD]. Ventral umbo extending posteriorly of hinge, with prominent interarea; rugae irregular, discontinuous capillae; ventral spines at low angle from hinge, suberect elsewhere; dorsal spines rare, anteriorly; cardinal process narrow, elongate quadrifid, occupying deltidium. *Lower Carboniferous (Viséan):* northern Asia.——Fig. 409,*1a–f.* **D. gobica,* upper Viséan, southern Mongolia; *a,b,* internal mold viewed ventrally, dorsally, ×1.5; *c,* posterior view of shell showing interareas, ×1.5; *d,* detail of ventral exterior with fine capillae, ×3 (new); *e,* exfoliated dorsal valve, ×1; *f,* part of dorsal valve interior, ×3 (Manankov & Pavlova, 1981).

Parmephrix Brunton & Mundy in Brunton, Racheboeuf, & Mundy, 1994, p. 58 [**P. eileeni* Brunton & Mundy in Brunton, Racheboeuf, & Mundy, 1994, p. 58; OD, *P. eileenarum* Brunton, Lazarev, & Grant, herein; =*Palmerhytis stebdenensis* Brunton & Mundy, 1986, p. 6, *partim*)]. Resembles *Semenewia,* but flattened irregular disks; small cicatrix, rugae irregular, covering corpus, ventrally bearing scattered spines, no radial ornament; teeth small. *Lower Carboniferous (upper Viséan):* western Europe.——Fig. 408,*2a–e.* **P. eileenarum* Brunton, Lazarev, & Grant, Asbian, North Yorkshire; *a,b,* ventral, dorsal views of incomplete specimen, ×2; *c,* holotype, partly exfoliated ventral valve exterior showing small cicatrix, BMNH BD 2496, ×2; *d,* incomplete dorsal valve exterior, ×2; *e,* incomplete dorsal valve interior, external mold of ventral interarea, ×2 (Brunton, Racheboeuf, & Mundy, 1994).

Semenewia Paeckelmann, 1930, p. 217 [**Chonetes concentrica* de Koninck, 1847b, p. 186; OD] [=*Palmerhytis* Brunton & Mundy, 1986, p. 6, *partim*]. Cicatrix variable; rugae regular, strongly developed, covering both valves; spines at hinge, smaller on rugae; fine capillae; cardinal process supported by inner socket ridges, short median septum. *Lower Carboniferous (Asbian–Brigantian):* western Europe.——Fig. 409,*2a–e.* **S. concentrica* (de Koninck), Asbian–Brigantian, Visé; *a,* lectotype, replica of dorsal valve exterior, ventral interarea, ESNM 20034, ×2; *b,* slightly distorted dorsal valve exterior, ventral hinge spines, ×2; *c,* young ventral valve exterior, ×2; *d,* replica of two ventral valve interiors with hinge spines from lower attached to upper, ×2; *e,* replica of dorsal valve interior, articulated posterior region of ventral valve; note dorsal valve dimples posteriorly indicating ventral spines and fine external capillae, ×3 (Brunton, Racheboeuf, & Mundy, 1994).

Family ARAKSALOSIIDAE
Lazarev, 1989

[Araksalosiidae Lazarev, 1989, p. 34]

Interareas short; concavoconvex, shallow corpus cavity; radial ornamentation commonly absent; cardinal process with pit; cardinal, marginal ridges commonly absent. *Lower Devonian (Emsian)–Lower Carboniferous (Tournaisian), ?Upper Carboniferous (Gzhelian).*

Subfamily ARAKSALOSIINAE
Lazarev, 1989

[Araksalosiinae Lazarev, 1989, p. 35]

Pseudodeltidium, chilidium present; cicatrix reduced; mat of spines on ventral or both valves, commonly with stout rows at ventral hinge; elongate spine bases may form incipient ribs anteriorly; marginal structures absent. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian).*

Araksalosia Lazarev, 1989, p. 36[32] [**Waagenoconcha maxima* Abramjan, 1957, p. 33; OD]. Resembling *Hamlingella,* about 50 mm wide, but with no dorsal valve spines; spines finer than *Acanthatia. Upper Devonian (upper Famennian):* Transcaucasia, Mongolia.——Fig. 410,*1a–d.* **A. maxima* (Abramjan), uppermost Famennian, Transcaucasia; *a,* deeply exfoliated ventral valve exposing internal mold posteromedianly, ×1 (Lazarev, 1989); *b,* partly exfoliated ventral exterior showing spine bases, ×2 (new); *c,* dorsal valve interior, ×1; *d,* detail of cardinalia, teeth, sockets, ×2 (Lazarev, 1989).

Acanthatia Muir-Wood & Cooper, 1960, p. 158 [**Heteralosia nupera* Stainbrook, 1947, p. 309; OD]. Outline subcircular, cicatrix small; interareas, but reduced in dorsal valve, narrow arched pseudodeltidium; ventral spines strong at hinge, fine prostrate elsewhere, rare dorsally; cardinal process externally quadrifid, supported anteriorly by pair of short weak ridges. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* North America, western Europe, ?northern Africa, ?Asia.——Fig. 411,*1a–e.* **A. nupera* (Stainbrook), uppermost Famennian, New Mexico, Percha Shale; *a,* ventral valve exterior, ×1.5; *b,* shell viewed laterally, ×1; *c,* shell viewed dorsally, ×1; *d,* shell viewed posteriorly, ×2; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Hamlingella Reed, 1943, p. 78 [**Productella goergesi* Paeckelmann, 1931, p. 56; OD]. Resembling *Whidbornella,* but outline transversely subrounded, hinge line less than maximum width; ventral hinge spines curved with fine recumbent hairlike spines from delicate swollen bases covering valve, more erect spines dorsally; never ribbed; widely divergent ridges support cardinal process, border dorsal adductor scars posterolaterally. *Upper Devonian (upper Famennian):* Germany, England, ?Asia.——Fig. 410,*2a,b.* **H. goergesi* (Paeckelmann), Famennian, Etroeungt, Rhine; *a,* partly exfoliated ventral valve,

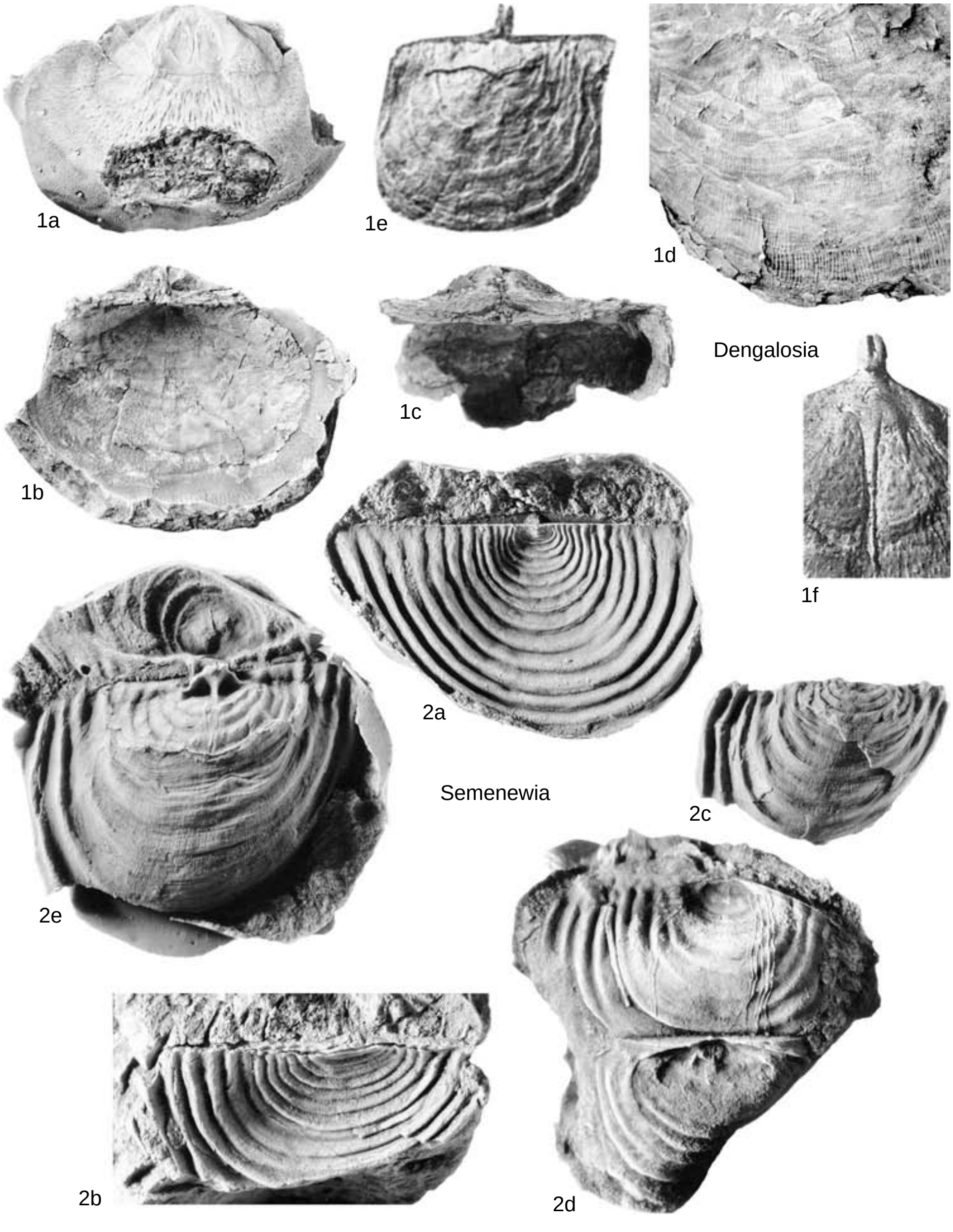


FIG. 409. Chonopectidae (p. 576).

×1; *b,* dorsal valve interior, ×1 (Paeckelmann, 1931).——FIG. 410,*2c,d. H. piltonensis* (REED), Pilton Beds, Devon; *c,* holotype, ventral valve internal mold, SM H 276, ×1; *d,* latex replica, ×1.5 (new).

Kahlella LEGRAND-BLAIN, 1995, p. 430 [**K. meyendorffi;* OD]. Resembles *Whidbornella* with strong row of hinge spines, but with no anterior ribbing or sign of dorsal spines; fine impersistent rugae posterolaterally; cardinalia weak, with pit, not

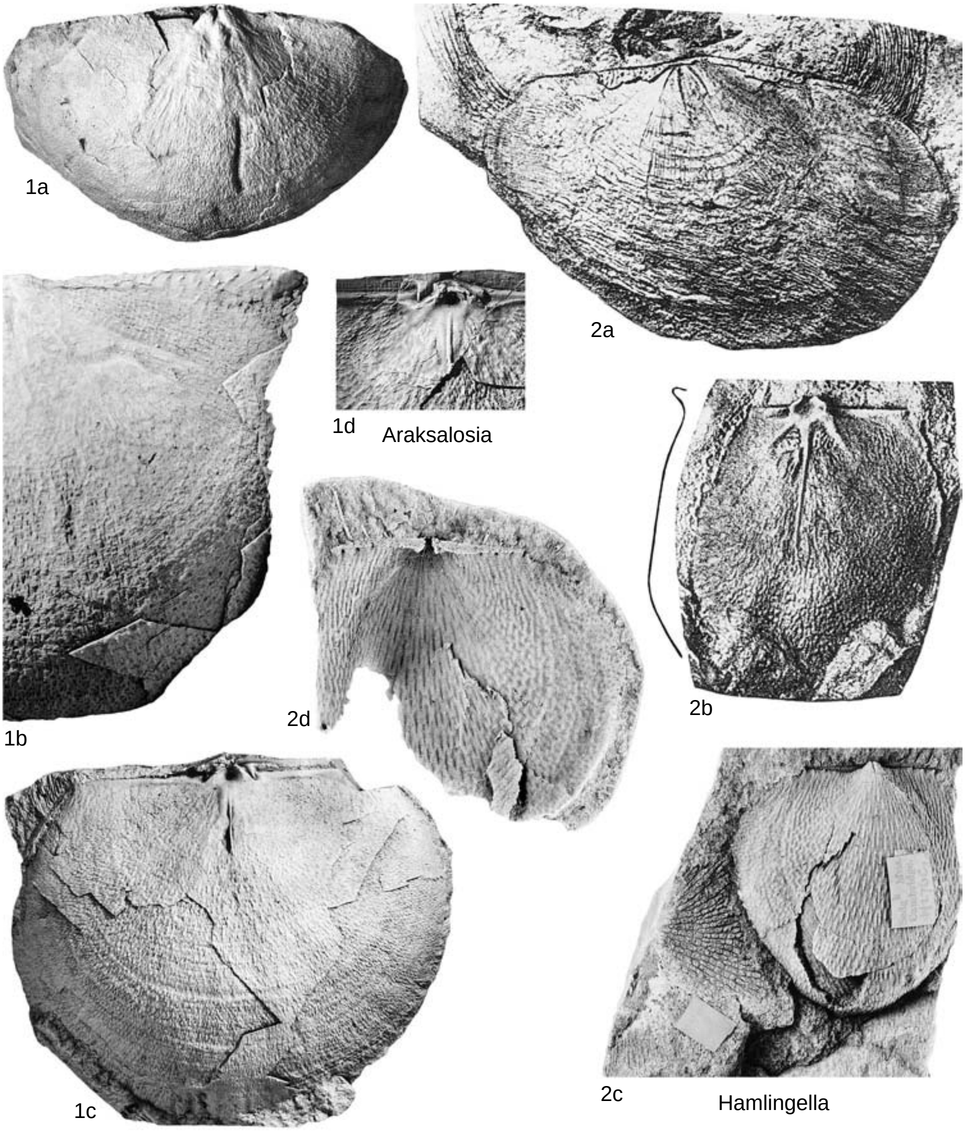


FIG. 410. Araksalosiidae (p. 576–577).

connected to short medium septum. *Upper Devonian (upper Famennian):* Algeria.——FIG. 411,*2a–d.* _*K. meyendorffi,_ upper Famennian, Famennian V–VI, Saharan Algeria; *a,* holotype, dorsal view of shell showing ventral hinge spines, SSL 413602a, ×1.3; *b,* incomplete ventral valve exterior, ×1; *c,* dorsal valve interior, ×1.3; *d,* deeply exfoliated dorsal valve exterior, ×1.3 (Legrand-Blain, 1995).

Ruthiphiala CARTER, 1988, p. 30 [_*Pustula bushbergensis_ BRANSON, 1938, p. 164; OD]. Medium sized; semicircular in outline, ventral valve with hinge spines plus finer prostrate spines from elongate swollen bases producing riblike ornament; inner socket ridges short, median septum extending anteriorly from shallow cardinal process pit. *Lower Carboniferous (Hastarian):* central North America.——FIG. 412,*2a–e.* _*R. bushbergensis_ (BRANSON), lower Kinderhookian, Missouri; *a,* lectotype, viewed posteriorly, UMC 4253, ×2; *b,c,* lectotype, viewed laterally, ventrally, ×1; *d,* dorsal valve interior, ×1; *e,* posteromedian area of dorsal valve interior with external mold of ventral interarea (*arrow*), ×2 (Carter, 1988).

Whidbornella REED, 1943, p. 71 [_*Leptaena caperata_ J. DE C. SOWERBY, 1840, pl. 53, fig. 4; OD]. Outline subcircular to elongate, wide hinge line; rugae ir-

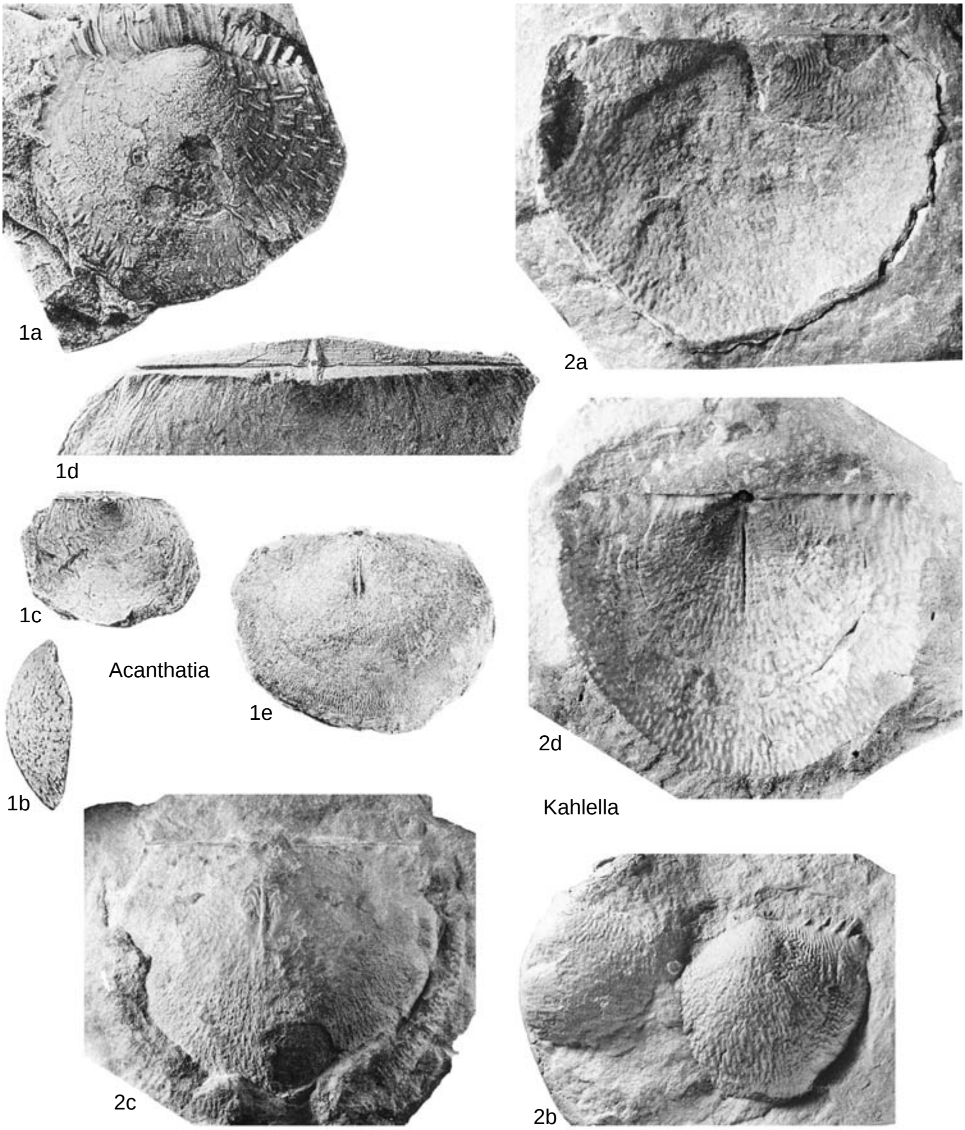


FIG. 411. Araksalosiidae (p. 576–578).

regular, mainly at ears; spines strong at ventral hinge, elongate spine bases tending to form incipient ribs anteromedianly; inner socket ridges at high angle to hinge supporting low cardinal process. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* western Europe, northern Africa, ?North America.——FIG. 412,*1a–d.* **W. caperata* (J. DE C. SOWERBY), uppermost Famennian, Pilton Beds, Devon; *a,* ventral valve external mold, ×1; *b,* replica of ventral valve interior, ×1.5 (new); *c,* dorsal valve external mold, ×1; *d,* replica of incomplete dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Subfamily DONALOSIINAE Lazarev, 1989

[Donalosiinae LAZAREV, 1989, p. 35]

Pseudodeltidium, chilidium present; cicatrix present, may be extensive; spines relatively thick, commonly only on ventral valve; concentric ornament may be lamellose; radial ornament rare on trails. *Lower Devonian (Emsian)–Upper Devonian (Famennian), ?Upper Carboniferous (Gzhelian).*

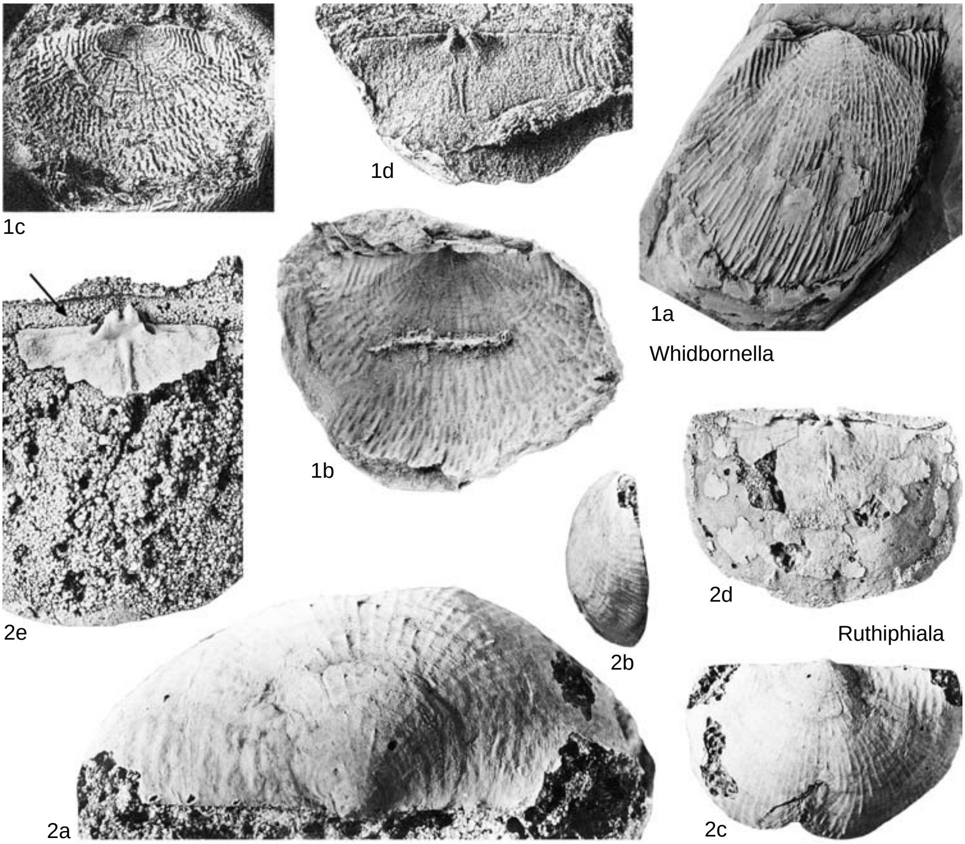


FIG. 412. Araksalosiidae (p. 578–579).

Donalosia LAZAREV, 1989, p. 35[31] [**Productella calva* var. *multispinosa* SOKOLSKAYA, 1948, p. 54; OD]. Convex pseudodeltidium; spines at hinge thicker than elsewhere, absent dorsally; rugae varied, more prominent on dorsal valve posteriorly; brachial ridges spreading widely. *Upper Devonian (Frasnian–Famennian):* eastern Europe, Transcaucasia.——FIG. 413,*1a–d*. **D. multispinosa* (SOKOLSKAYA), Famennian, Zadonsk beds, Russian platform; *a,* shell viewed ventrally, ×2; *b,* shell viewed dorsally, ×1; *c,* shell viewed posteriorly, ×2 (new); *d,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).——FIG. 413,*1e*. *D. caperatiformis* (ABRAMJAN), upper Famennian, Transcaucasia; drawing of ventral internal mold, ×1 (Lazarev, 1989).

?Auchmerella STRUVE, 1964, p. 521 [**A. irmingina;* OD]. Small; abnormal genus, only ventral valves known; strongly cemented by cicatrix, spines spreading radially; ventral interior resembles *Devonalosia,* but with narrow median ridge, weakly elevated diductor scars. *Middle Devonian (Eifelian):* Germany.——FIG. 413,*2*. **A. irmingina,* Eifelian, Eifel; replica of holotype, ventral valve interior, SMF 19227, ×3 (new).

Australosia MCKELLAR, 1970, p. 12 [**A. starensis;* OD]. Minute, around 8 mm wide; outline transverse; concavoconvex, commonly with relatively large cicatrix, long trails; ventral interarea with narrow arched pseudodeltidium; rugae weak on disks, costellate anteriorly; spines at hinge line, from ribs anteriorly; socket ridges at low angle to hinge, brachial ridges widely spreading. *Upper Devonian (Famennian):* Australia.——FIG. 413,*3a–c*. **A. starensis,* Famennian, Star Beds, Star basin, Queensland; *a,* holotype, replica of dorsal valve exterior, ventral interarea with hinge spines, GSQ F11324, ×3; *b,* ventral valve internal mold, ×4; *c,* replica of dorsal valve interior, ×4 (new).

Devonalosia MUIR-WOOD & COOPER, 1960, p. 83 [**D. wrightorum;* OD]. Small, outline subcircular; flat pseudodeltidium, no chilidium, cicatrix varied; ventral spines only, thick, attaching posteriorly, recumbent anteriorly, arranged concentrically; rugae weak, somewhat lamellose; strong teeth, impressed ventral

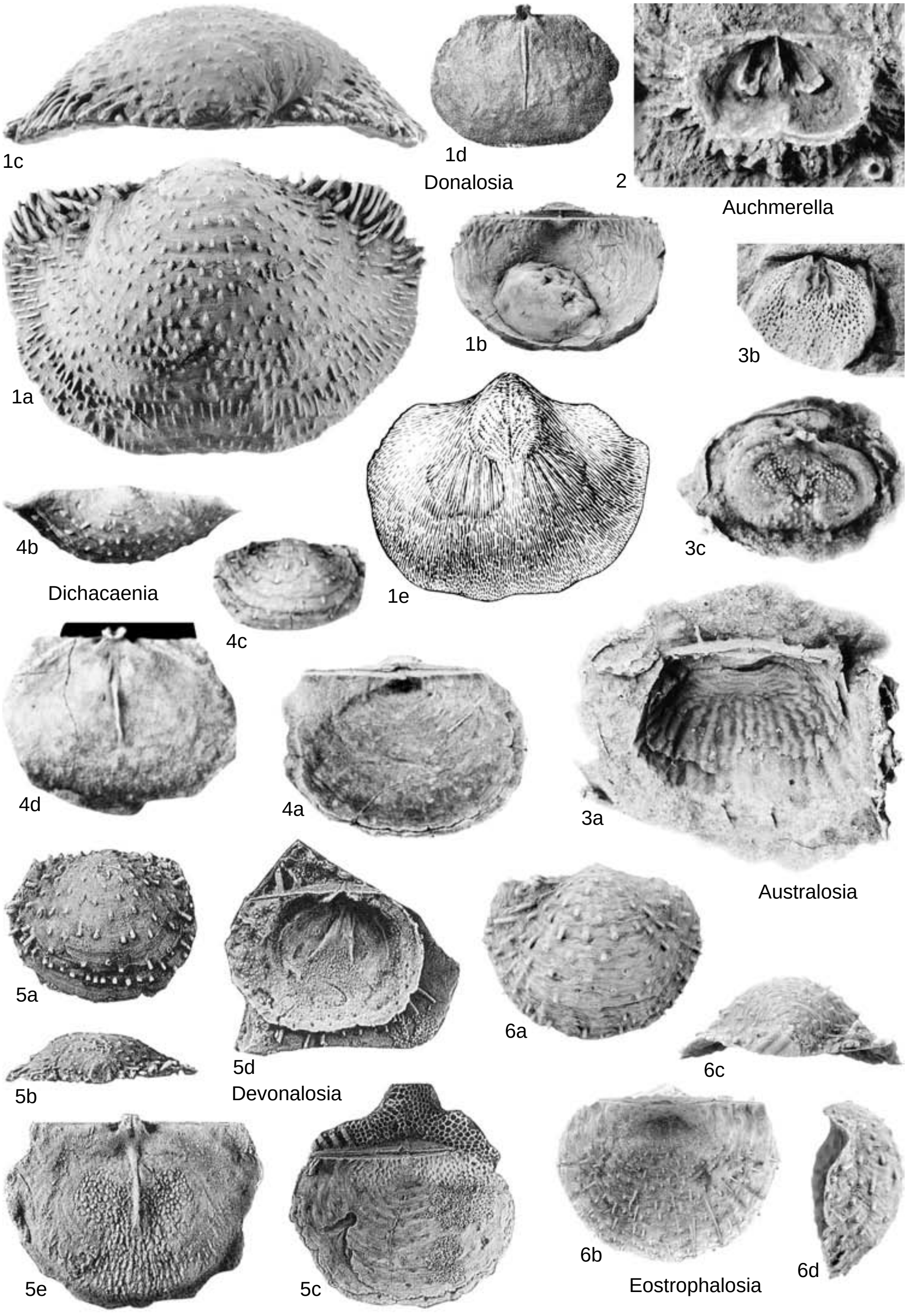


FIG. 413. Araksalosiidae (p. 580–582).

diductor scars; deep sockets, dorsal median septum, tuberculate between brachial impressions. *Middle Devonian (Eifelian–Givetian):* North America.——FIG. 413,*5a–e.* **D. wrightorum,* Givetian, Arkona Shale, Ontario; *a,b,* shell viewed ventrally, posteriorly, ×2; *c,* dorsal view of attached shell, ×3; *d,* ventral valve interior, ×3; *e,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Dichacaenia COOPER & DUTRO, 1982, p. 60 [**D. perplexa;* OD]. Small to medium sized; resembling *Devonalosia,* but with impersistent cicatrix, valve surfaces smooth to weakly lamellose; spines only ventrally, evenly and somewhat radially distributed, recumbent with short spine bases; cardinal process internally strongly bilobed, weak ear baffles, tuberculation fine. *Middle Devonian (Givetian):* southern USA, northern Africa, ?France.——FIG. 413,*4a,b.* **D. perplexa,* upper Givetian, Oñata Formation, New Mexico; holotype, viewed dorsally, posteriorly, USNM 200957a, ×1.5 (Cooper & Dutro, 1982).——FIG. 413,*4c,d. D. umbonata* COOPER & DUTRO; *c,* ventral valve exterior, ×1; *d,* dorsal valve interior, ×2 (Cooper & Dutro, 1982).

Dotswoodia MCKELLAR, 1970, p. 19 [**Whidbornella (D.) wyatti;* OD]. Outline transversely quadrate, around 30 mm wide; short ventral interarea, no cicatrix, short trails; rugae narrow, irregular on posterior visceral disks; spines on ventral valve only, recumbent from elongate spine bases becoming costate anteriorly, commonly with median spine row; dental sockets small, dorsal median septum prominent, supporting cardinal process. *Upper Devonian (Famennian):* Australia, western Europe.——FIG. 414,*2a–d.* **D. wyatti* (MCKELLAR), Famennian, *Sentosia minuta* Zone, Queensland; *a,* holotype, replica of ventral valve exterior, GSQ F 11477, ×1; *b,* dorsal valve exterior, ×1.5; *c,* replica of part of ventral valve interior, ×2; *d,* replica of incomplete dorsal valve interior, ×1.5 (McKellar, 1970).

?Enigmalosia CZARNIECKI, 1969, p. 271 [**E. sarytchevae;* OD]. Minute size; extensively cemented ventral valve, somewhat resembling *Australosia,* but with fine costellation, apparently no teeth, thin shell substance. *?Upper Carboniferous (?Gzhelian):* Spitzbergen.——FIG. 414,*1a–d.* **E. sarytchevae,* Gzhelian, western Spitzbergen; *a,b,* anterior, oblique ventral views of ventral valve exterior, ×4; *c,* oblique lateral view of ventral valve exterior, ×4 (new); *d,* drawing of dorsal valve interior, ×4 (Czarniecki, 1969).

Eostrophalosia STAINBROOK, 1943, p. 58 [**Strophalosia rockfordensis* HALL & CLARKE, 1892, p. 163; OD]. Small with circular outline; ventral interarea prominent medianly, apical arched pseudodeltidium, cicatrix small; spines at ventral hinge, recumbent elsewhere, fine on dorsal valve; rugae weak, lamellose; dorsal valve dimpled. *Upper Devonian (Frasnian):* North America, ?western Europe.——FIG. 413,*6a–d.* **E. rockfordensis* (HALL & CLARKE), Frasnian, Hackberry Formation, Rockford, Iowa; specimen viewed ventrally, dorsally, posteriorly, with fragment of shell attached, laterally, ×2 (new).

?Irboskites BEKKER, 1924, p. 48 [**I. fixatus;* OD]. Small; profile planoconvex, ventral valve strongly cemented by extensive cicatrix; short ventral interarea; spines apparently lacking, exteriors smooth; ventral interior resembles *Devonalosia* with anteriorly angled teeth; dorsal interior with strong inner plus outer socket ridges, brachial markings extensive. *Upper Devonian (Frasnian):* eastern Europe.——FIG. 415,*3a–c.* **I. fixatus,* lower Frasnian, Irboska Formation, Estonia; *a,* holotype, replica of ventral valve interior, TAGI BR 011, ×2; *b,* exterior of ventral valve with cicatrix to right (note that the pair of objects are possibly the tubes of coiled adherent worms), ×2; *c,* dorsal valve interior, ×2 (new).

Morganella MCKELLAR, 1970, p. 17 [**M. maxwelli;* OD]. Corpus width 30 to 35 mm; shells geniculate with sloping flanks, no median sulcation or folding; ventral interarea short; trail margin slightly flared; thick spines confined to hinge area, fine over ventral corpus; teeth small; cardinal process with pit between small socket ridges. *Upper Devonian (lower Famennian):* Australia.——FIG. 414,*3a–e.* **M. maxwelli,* lower Famennian, Queensland; *a,* lateral oblique view of replica of incomplete ventral valve exterior, ×1.5; *b,* external mold of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×1; *d,* latex replica of dorsal valve interior, ×2 (McKellar, 1970); *e,* latex replica of ventral valve interior showing small teeth, *arrowed,* ×2 (new).

Oligorhachis IMBRIE, 1959, p. 403 [**O. oligorhachis;* OD]. Similar to *Devonalosia,* but small, about 8 mm wide; small cicatrix, relatively thick spines. *Middle Devonian:* North America.——FIG. 415,*2a–e.* **O. oligorhachis,* Givetian, Traverse Group, Gravel Point Formation, Michigan; *a–d,* holotype, viewed ventrally, dorsally, laterally, posteriorly, USNM 125574, ×3; *e,* dorsal valve interior, ×3 (Imbrie, 1959).

Ralia LAZAREV, 1987, p. 48[44] [**R. primigenia;* OD]. Small; somewhat transverse, concavoconvex shell with moderately inflated ventral umbo; pseudodeltidium convex; spines at ventral hinge, widely scattered; dorsal valve with weak fine ribbing; anderidia present. *Lower Devonian (Emsian):* Mongolia.——FIG. 415,*1a,b.* **R. primigenia,* Emsian, Gobi Altai, Mongolia; *a,* holotype, dorsal exterior of shell with ventral interarea, PIN 4217/2, ×3; *b,* internal mold of ventral valve with shell fragments anterolaterally, ×3 (Lazarev, 1987).

Truncalosia IMBRIE, 1959, p. 401 [**T. gibbosa;* OD]. Resembles small *Heteralosia,* but lacking lamellose ornament; spines relatively thin, possibly not bidirectional. *Middle Devonian:* North America.——FIG. 415,*4a–e.* **T. gibbosa,* Givetian, Traverse Group, Gravel Point Formation, Michigan; *a–d,* holotype, viewed dorsally, ventrally, laterally, posteriorly, USNM 125568, ×2; *e,* dorsal valve interior, ×3 (Imbrie, 1959).

Subfamily QUADRATIINAE Lazarev, 1989

[Quadratiinae LAZAREV, 1989, p. 38(34)]

Pseudodeltidium, chilidium commonly absent; concentric ornament well developed,

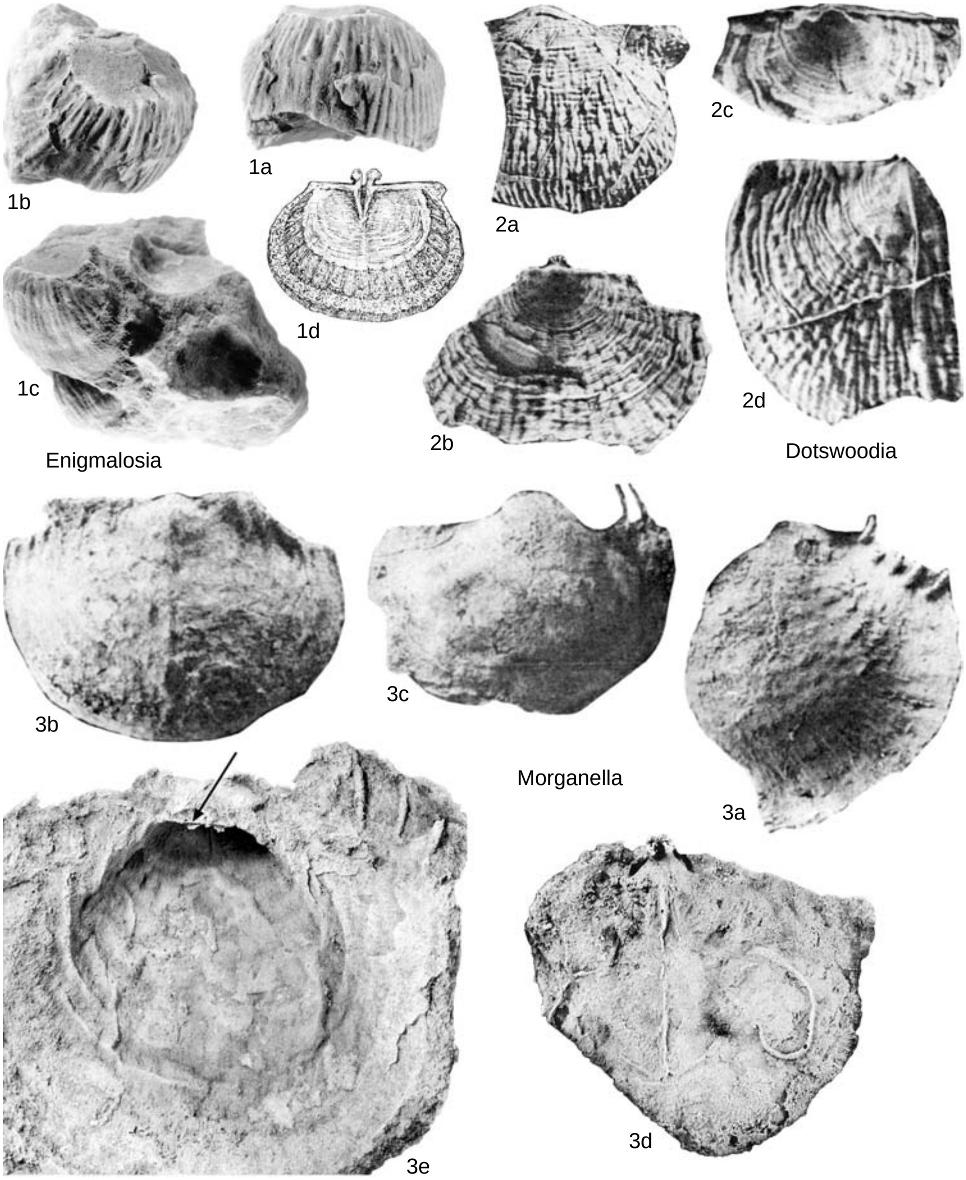


Fig. 414. Araksalosiidae (p. 582).

regular; spines at low angle, rare on dorsal valve; marginal ridges present. *Lower Carboniferous (Hastarian)–Upper Carboniferous (Kasimovian).*

Quadratia Muir-Wood & Cooper, 1960, p. 161 [**Productus hirsutiforme* Walcott, 1884, p. 133; OD]. Outline transversely subrectangular; interareas wide but short; rugae narrow, entire; ventral spines in row near hinge, elsewhere prostrate, concentric, rare dorsally; well-defined ventral muscle fields, lateral ridges extending across ears; cardinal process occupies delthyrium, small sockets, weak dorsal lateral ridges. *Lower Carboniferous (?Tournaisian, Viséan)–Upper Carboniferous (Serpukhovian):* North America.——Fig. 416,*1a–e*. **Q. hirsutiformis* (Walcott), lower Chesterian, Oklahoma; *a–c,* shell viewed ventrally, dorsally, posteriorly, ×1; *d,* posterior view of ventral internal mold, ×1.5; *e,* replica of dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

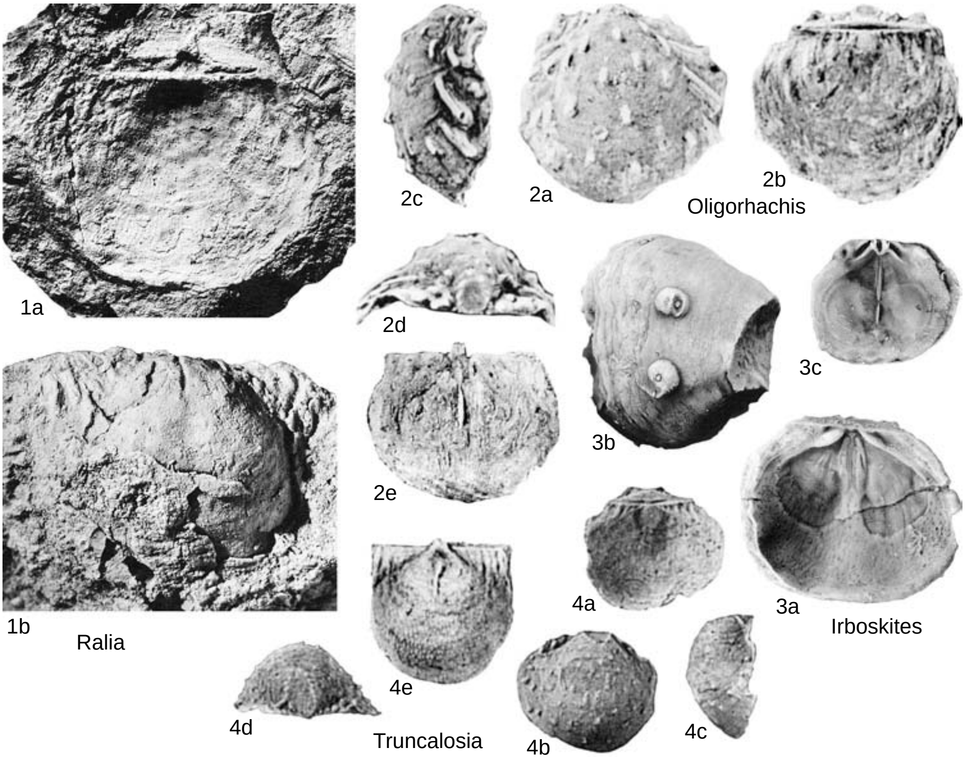


FIG. 415. Araksalosiidae (p. 582).

Chonetipustula PAECKELMANN, 1931, p. 31 [**Productus plicatus* SARRES, 1857, p. 20; OD]. Small, outline semicircular; interareas reduced; both valves rugose; ventral spines long, fine, straight at hinge line, recumbent elsewhere, but rare dorsally; short ventral umbonal myophragm, teeth and sockets small; cardinal process occupies delthyrium, marginal ridges unknown. *Lower Carboniferous (Viséan):* Europe, ?Asia.——FIG. 416,*3a,b.* **C. plicata* (SARRES), upper Viséan, Germany, Rhine; *a,* internal mold of ventral valve, ×1; *b,* ventral valve exterior, ×1 (Muir-Wood & Cooper, 1960).

Cyphotalosia CARTER, 1967, p. 281 [**C. masonensis;* OD]. Small; slightly inflated ventral umbo, differentiated small ears with dorsally flexed extensions; interareas with narrow pseudodeltidium, chilidium, cicatrix small; spines few near ventral hinge, plus scattered and curving on rest of valve, none dorsally; rugae, growth lamellae narrow and somewhat irregular. *Lower Carboniferous (Hastarian):* North America.——FIG. 416,*4a–e.* **C. masonensis,* upper Kinderhookian, Texas; *a,* holotype, viewed ventrally, USNM 154583, ×2; *b,* holotype, viewed dorsoposteriorly, USNM 154583, ×3; *c,d,* ventral valve internal mold viewed ventrally, laterally, ×2; *e,* exfoliated dorsal valve interior, ×2 (Carter, 1967).

Plicaea AISENVERG, 1992, p. 130[168] [**P. insignita;* OD]. Small, 5 mm wide; outline transversely quadrate, geniculate, trails with short flange or gutter; interarea short, cicatrix small; attached also by clasping spines near hinge, other spines rare on rugose corpus, trails smooth; wide sessile cardinal process supported by inner socket ridges subparallel to hinge. *Lower Carboniferous (middle Viséan):* Ukraine.——FIG. 416,*5a–d.* **D. insignita,* Holkerian, Tulsky, Donetz; *a,b,* ventral valve external mold, replica, ×5; *c,d,* dorsal valve internal mold, replica, ×5 (new).

Plicatiferina KALASHNIKOV, 1980, p. 45 [**Productus pseudoplicatilis* STEPANOV, 1948, p. 33; OD]. Resembles *Quadratia* in size, outline, but with prominent, narrow rugae on both valves; ventral median sulcus in some; spines fine on ventral valve; interiors almost unknown. *Upper Carboniferous (Kasimovian):* eastern Europe.——FIG. 416,*2a.* **P. pseudoplicatilis* (STEPANOV), Kasimovian, Bashkiria; ventral valve exterior, ×1 (Stepanov, 1948).——FIG. 416,*2b–d. P. neoplicatilis* (STEPANOV), northern Urals; *b,* ventral valve exterior, ×1; *c,* ventral valve

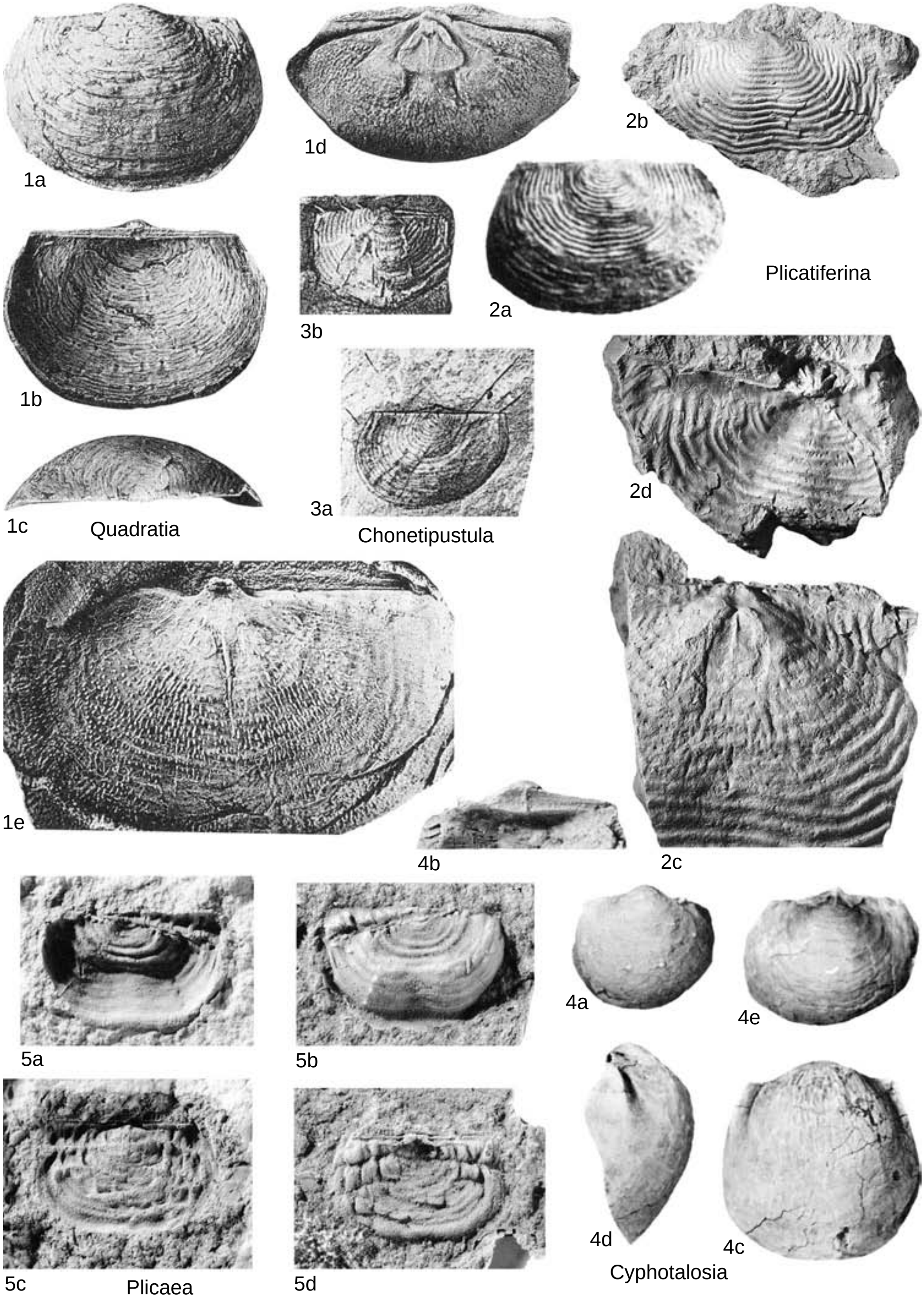


FIG. 416. Araksalosiidae (p. 583–586).

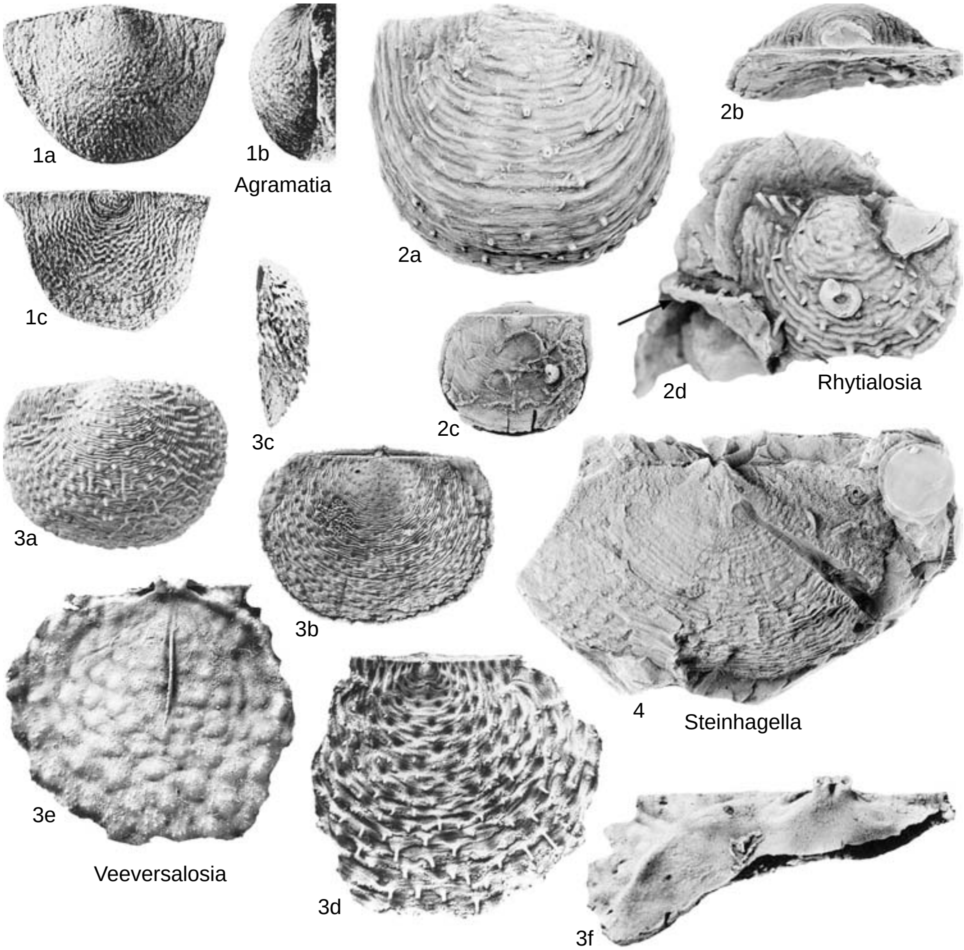


FIG. 417. Araksalosiidae (p. 586–587).

internal mold, ×1.5; *d,* incomplete dorsal valve exterior, ×2 (new).

Subfamily RHYTIALOSIINAE Lazarev, 1989

[Rhytialosiinae LAZAREV, 1989, p. 38(35)]

Cicatrix present; undulose rugae prominent but discontinuous; spines dense on ventral valve, fewer on dorsal valve. *Upper Devonian (middle Frasnian–Famennian).*

Rhytialosia LAZAREV, 1989, p. 38[35] [**Productus petini* NALIVKIN, 1930, p. 71; OD]. Maximum width at hinge, cicatrix present; ventral spines only, relatively thick, especially close to hinge; rugae more prominent ventrally, entire, undulose; dorsal median septum full length of disk. *Upper Devonian (middle Frasnian):* Europe.——FIG. 417,*2a–d.* **R. petini* (NALIVKIN), middle Frasnian, Russian Platform; *a,b,* shell viewed ventrally, posteriorly, ×2; *c,* shell viewed dorsally, ×1; *d,* two ventral valves, one externally, one incomplete dorsolaterally showing tooth, *arrowed,* ×2 (new).

Agramatia SOKOLSKAYA, 1948, p. 39 [**Productus agramati* NALIVKIN in MARKOWSKII & NALIVKIN, 1934, p. 21; OD]. Small; outline subsemicircular with adult hinge at maximum width; interareas reduced, cicatrix small; spines fine ventrally, unknown dorsally; rugae impersistent medianly, nodose, absent anteriorly where spine bases tend to be elongate. *Upper Devonian (lower Famennian):* Russia, ?North America.——FIG. 417,*1a–c.* **A. agramati* (NALIVKIN), lower Famennian, central Russia; *a,b,* ventral valve exterior viewed ventrally, laterally, ×2; *c,* dorsal valve exterior, ×2 (Muir-Wood & Cooper, 1960).

Steinhagella GOLDRING, 1957, p. 223 [**Leptaena membranacea* PHILLIPS, 1841, p. 60; OD]. Outline subsemicircular, resembles *Agramatia,* but undulose rugae more persistent medianly, lacking swollen spine bases; dorsal valve with fewer, erect spines. *Upper Devonian (Famennian):* Eurasia, northern Africa.——Fig. 417,*4.* **S. membranacea* (Phillips), Famennian V–VI, Cornwall; lectotype, internal mold of ventral valve, GSM 95430, ×2 (new).

Veeversalosia Lazarev, 1989, p. 39[35] [**Steinhagella numida* Veevers, 1959, p. 77; OD]. Cicatrix minute, short interareas, small apical pseudodeltidium; spines on both valves, lacking strong hinge spines; rugae fine; differs from *Steinhagella* by having inner socket ridges extended as lateral ridges, ear baffles; median septum short. *Upper Devonian (middle Frasnian):* Western Australia.——Fig. 417,*3a–f.* **V. numida* (Veevers), middle Frasnian, Fitzroy Basin; *a–c,* holotype, viewed ventrally, dorsally, laterally, CPC 2954, ×1; *d,e,* young dorsal valve exterior, interior, ×3.5; *f,* incomplete dorsal valve interior, ×2 (Veevers, 1959).

Superfamily AULOSTEGOIDEA Muir-Wood & Cooper, 1960

[*nom. transl.* Brunton, Lazarev, & Grant, 1995, p. 932, *ex* Aulostegidae Muir-Wood & Cooper, 1960, p. 94]

Probably attached permanently by spines or direct cementation; ventral interarea present, dorsal interarea small or absent, no chilidium; trails commonly elaborated or conical in Permian, when corpus cavity became deep; teeth absent; brachial ridges may be restricted. *Lower Carboniferous (Ivorian)–Upper Permian (Changhsingian).*

Family AULOSTEGIDAE Muir-Wood & Cooper, 1960

[Aulostegidae Muir-Wood & Cooper, 1960, p. 94]

Plano- to weakly concavoconvex profile, corpus moderate depth; commonly with ventral rhizoid spines; cardinal process trifid or quadrifid, adductor scars dendritic. *Lower Carboniferous (Ivorian)–Upper Permian (Changhsingian).*

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

[Aulosteginae Muir-Wood & Cooper, 1960, p. 95]

Elaborated trails; spines numerous on both valves; ribbing absent; shell material thick. *Lower Permian (Sakmarian)–Upper Permian (Capitanian).*

Aulosteges von Helmersen, 1847, p. 330–331 [**A. wangenheimi* de Verneuil, 1845, p. 194; OD; =*A. variabilis* von Helmersen, 1847, p. 330]. Medium size, variable to long, may be asymmetric; ventral interarea with elongate to subtrigonal outline; total profile weakly concavoconvex with variably developed cicatrix; concentric ornament weak or absent; spines densely distributed on both valves, of two sizes ventrally; dorsal interior with rhomboidal pit separating cardinal process from median septum. *Upper Permian (Kazanian):* northern Eurasia, ?Australia.——Fig. 418,*1a–d.* **A. wangenheimi* de Verneuil, Kazanian, Orenburg, Russia; *a–c,* shell viewed ventrally, dorsally, laterally, ×1; *d,* incomplete dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Lipanteris Briggs in Waterhouse & Briggs, 1986, p. 36 [**Aulosteges (Taeniothaerus) subquadratus* var. *cracowensis* Hill, 1950, p. 8; OD]. Resembles *Taeniothaerus,* but with somewhat narrower hinge line, lamellae only on dorsal trail, spines larger and more widely spaced on venter, commonly on radial ridges anteriorly. *Lower Permian (Artinskian–Kungurian):* eastern Australia.——Fig. 418,*2a,b.* **L. cracowensis* (Hill), Fairyland Formation, Bowen basin; *a,* ventral valve viewed laterally, ×1; *b,* ventral valve internal mold, ×1 (Waterhouse & Briggs, 1986).——Fig. 418,*2c–e. L. sparsispinosus* Briggs; *c,d,* holotype, ventral valve internal mold viewed laterally, its replica viewed anteroventrally, UQF 72797, ×1; *e,* replica of incomplete dorsal valve interior, ×1 (Waterhouse & Briggs, 1986).

Megasteges Waterhouse, 1975, p. 6 [**M. nepalensis;* OD]. Similar to *Wyatkina,* but reportedly with only one size of ventral spines; said to differ from *Taeniothaerus* by having longer interarea, thicker ventral spines, and ventral diductor scars that enclose adductor scars more closely anteriorly. *Upper Permian (Capitanian):* Himalayas (northwestern Nepal), ?eastern Australia.——Fig. 419,*2a,b.* **M. nepalensis,* Punjabian, Dolpo Region, Nepal; *a,* holotype, internal mold viewed dorsally, 314, repository unknown, ×1; *b,* internal mold viewed ventrally, ×1 (Waterhouse, 1975).

Reedoconcha G. Kotlyar, 1964, p. 124 [**Productus (Taeniotherus) permixtus* Reed, 1932b, p. 12; OD]. Medium size with elongate outline, maximum width anteriorly; interarea short, occupying about half hinge width; median sulcus weak, variable; beak acute; elongate spine bases simulate ribbing on ventral valve; spines cover both valves, ventrally strong, semirecumbent, dorsally fine; no anterior spine bands; cardinal process with paired ridges on shaft; median septum long; adductor scars well developed. *Lower Permian:* Oman, Afghanistan, Himalayas.——Fig. 419,*1a–f.* **R. permixta* (Reed), Sakmarian; *a,* ventral valve exterior, Agglomeritic Slate, Kashmir, ×0.75; *b,* ventral valve internal mold, Agglomeritic Slate, Kashmir, ×1; *c,* dorsal valve internal mold, Agglomeritic Slate, Kashmir, ×1 (Reed, 1932b); *d,* ventral valve viewed posteroventrally, Saiwan Formation, southern Oman, ×1; *e,* complete specimen viewed dorsally, Saiwan Formation, southern Oman, ×1; *f,* dorsal cardinalia viewed internally, Saiwan Formation, southern Oman, ×1 (new).

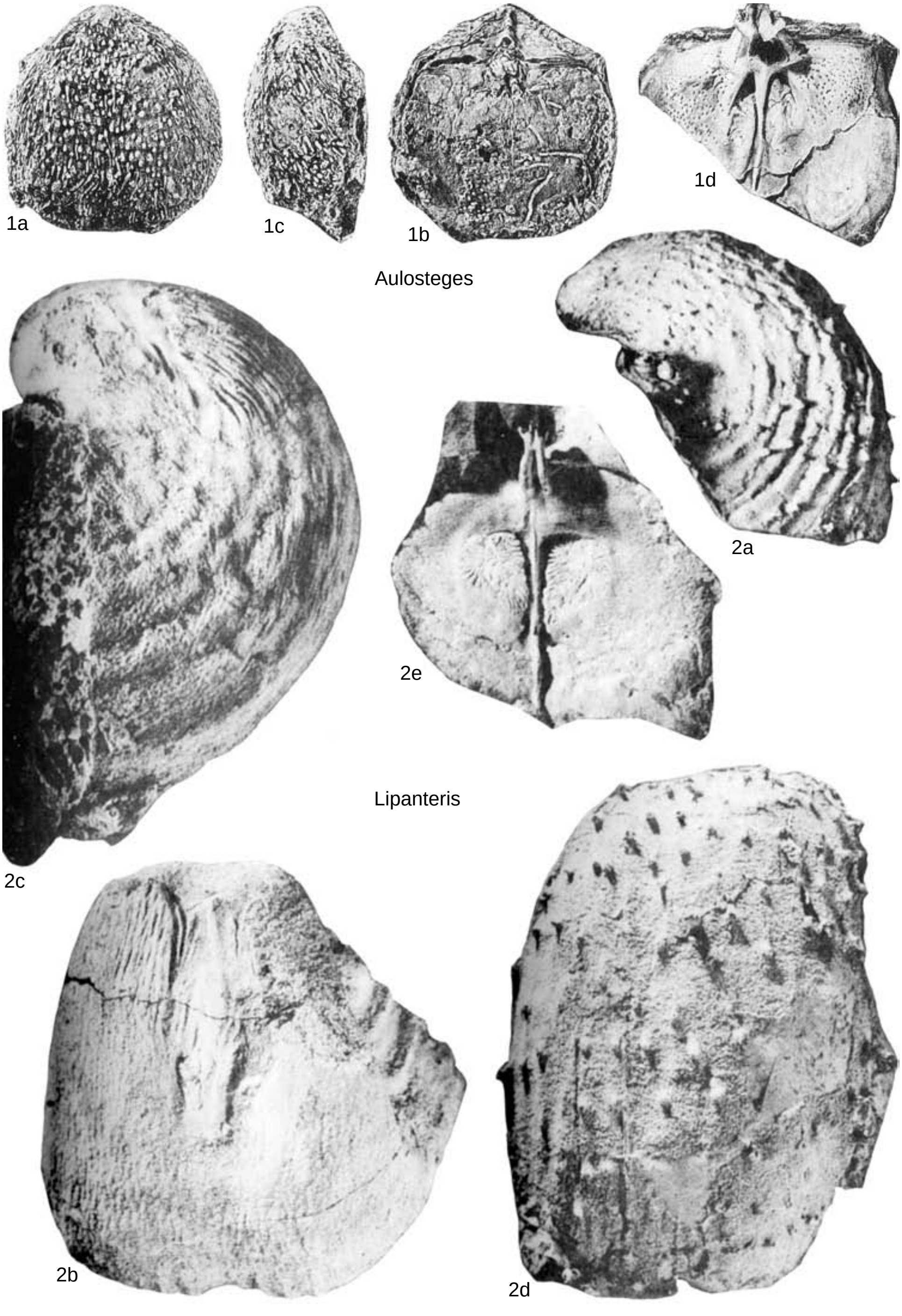


FIG. 418. Aulostegidae (p. 587).

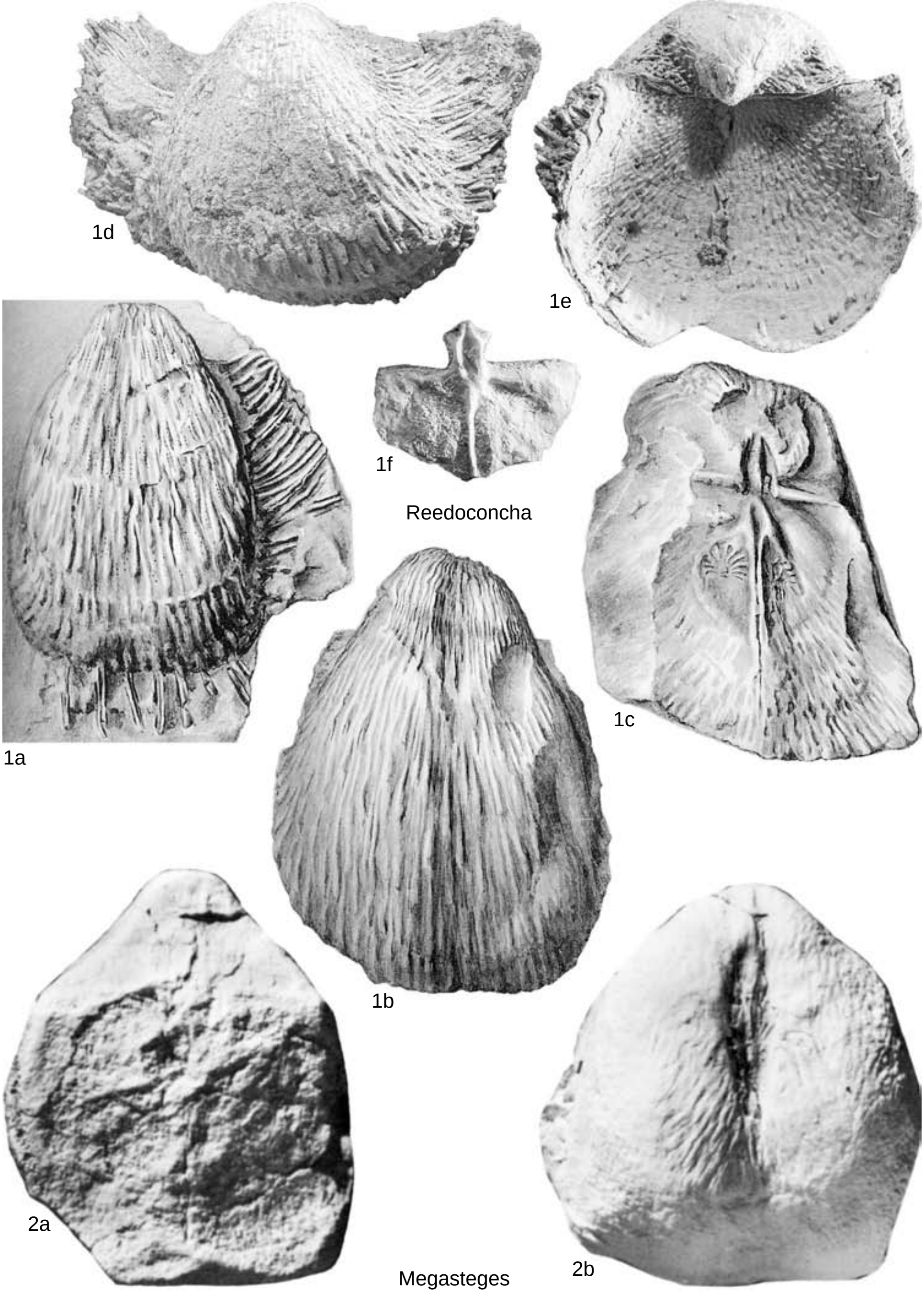


FIG. 419. Aulostegidae (p. 587).

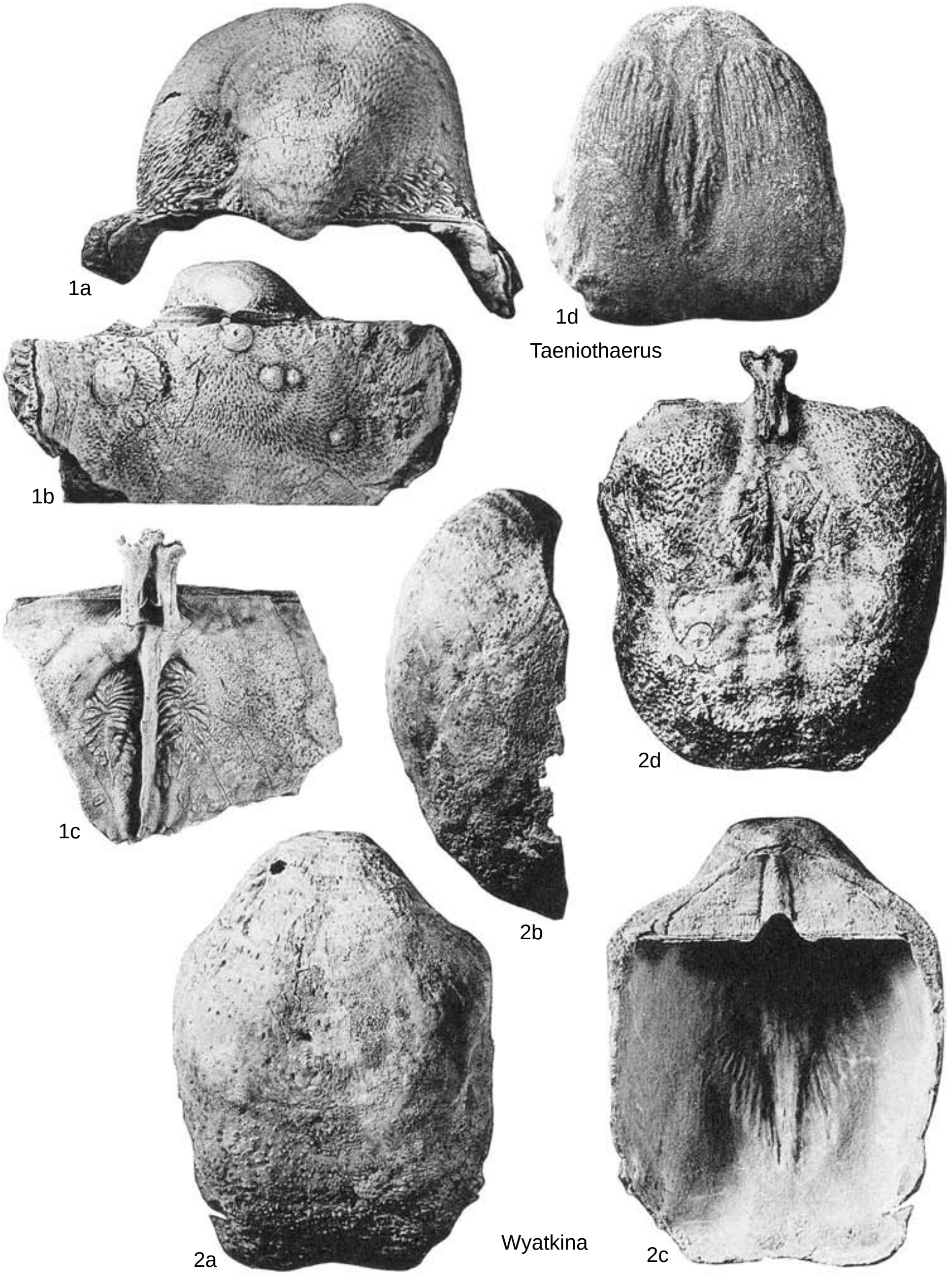


FIG. 420. Aulostegidae (p. 590–591).

Taeniothaerus WHITEHOUSE, 1928, p. 281 [**P. subquadratus* MORRIS in DE STREZELECKI, 1845, p. 248; OD]. Large with thick-shelled valves; transverse profile highly arched with steep flanks; interareas short, but wide; spines relatively fine, densely distributed on both valves with clusters of thicker spines on posterior flanks; ventral adductor scars positioned anteriorly; cardinal process shaft medianly sulcate, myophores large, trifid to quadrifid. *Lower Permian (Sakmarian–Artinskian):* Australia, ?Asia.——FIG. 420,*1a–d.* **T. subquadratus* (MORRIS); *a,b,* ventral valve viewed posteriorly, dorsally, Wandagee Series, Western Australia, ×0.75; *c,* incomplete dorsal valve interior, Wandagee Series, Western Australia, ×0.75; *d,* ventral valve internal mold, Gympie Beds, Queensland, ×0.75 (Muir-Wood & Cooper, 1960).

Wyatkina FREDERICKS, 1931, p. 211 [**Aulosteges gigas* NECHAEV, 1894, p. 155; OD]. Resembles *Aulosteges,* but larger, with wider, less variable ventral interarea almost equal to maximum width of shell; ventral profile more strongly and evenly convex; spines less thick, possibly absent from dorsal valves. *Upper Permian (Kazanian):* Eurasia.——FIG. 420,*2a–d.* **W. gigas* (NECHAEV), Wyatka River; *a–c,* ventral valve viewed ventrally, laterally, internally, ×1; *d,* dorsal valve interior, ×0.75 (Muir-Wood & Cooper, 1960).

Subfamily AGELESIINAE Cooper & Grant, 1975

[*nom. transl.* BRUNTON, GRANT, & LAZAREV, 1995, p. 932, Agelesiidae COOPER & GRANT, 1975, p. 890]

Corpus outline triangular; ventral interarea reduced; no dorsal spines but having strong concentric ornament; ear baffles strong; dorsal adductor platforms commonly raised. *Lower Carboniferous (upper Viséan)–Lower Permian (Artinskian).*

Agelesia COOPER & GRANT, 1969, p. 6 [**A. triagonalis* R. E. KING, 1931, p. 94; OD]. Small, commonly distorted; cluster of rhizoid spines confined to posterior half of ventral valve, creating dimples on dorsal valve; both valves finely rugose; cardinal process variable, commonly strongly bilobed; dorsal adductor scars raised, endospines anteriorly. *Lower Permian (Artinskian):* USA.——FIG. 421,*1a–d.* **A. triagonalis* R. E. KING, Cathedral Mountain Formation, Texas; *a–c,* complete specimen viewed ventrally, laterally, dorsally, ×2; *d,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

?Rhytibulbus LI LI in DING YUNJIE & others, 1991, p. 157[185] [**R. zhen'anensis;* OD]. Poorly known; small to medium, elongate outline with wide hinge line, well-defined ears; interarea short; ventral profile semicircular; costellae extending to trail between rugae on disks; spines on ventral valve only, with wide bases; interiors unknown. *Lower Permian:* China.——FIG. 421,*2a–c.* **R. zhenanensis,* Quinling Range; *a,b,* ventral valve viewed posteroventrally, laterally, ×1; *c,* dorsal valve exterior, ×1 (Ding & others, 1991).

Stipulina MUIR-WOOD & COOPER, 1960, p. 200 [**Productus deshayesianus* DE KONINCK, 1842, p. 193; OD]. Outline of corpus plus trails elongate, with well-differentiated ears; ventral interarea small, restricted medianly; long spines from swollen bases on ventral corpus; ear baffles strong; brachial markings elongate, commonly raised anteriorly. *Lower Carboniferous (upper Viséan):* western Europe.——FIG. 421,*3a–g.* **S. deshayesianus* (DE KONINCK); *a,* ventral valve internal mold viewed laterally, Visé, ×6; *b,c,* ventral valve internal mold viewed posteriorly, replica showing strong ear baffles, Visé, ×5 (Muir-Wood & Cooper, 1960); *d,* replica of dorsal valve interior, Visé, ×5; *e,f,* ventral valve exterior viewed ventrally, laterally, Asbian, Northern Yorkshire, ×4; *g,* part of dorsal valve exterior showing large ears, Asbian, Northern Yorkshire, ×4 (Brunton & Mundy, 1988b).

Subfamily CHONOSTEGINAE Muir-Wood & Cooper, 1960

[CHONOSTEGINAE MUIR-WOOD & COOPER, 1960, p. 113]

Small, with complex, valvelike, spinose corpus margin, strong geniculation, short trails; strong ribbing anteriorly. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Chonosteges MUIR-WOOD & COOPER, 1960, p. 113 [**Aulosteges magnicostatus* GIRTY, 1909, p. 278; OD]. Small, subcircular to subpentagonal outline; ventral interarea, umbo variable, depending on attachment; lophidium, zygidium present in some; planoconvex corpus profile with strong geniculation; ribbing strong anterior to geniculation; spines rhizoid on ventral disk, ribs; both trails reflexed ventrally, at corpus margin complex series of interdigitating spines and funnel-like processes. *Lower Permian (Artinskian):* southern USA, Russia, ?Malaysia.——FIG. 422,*4a.* **C. magnicostatus* (GIRTY), Delaware Mountain Formation, Texas; holotype, viewed dorsally, USNM 118548, ×3 (Cooper & Grant, 1975).——FIG. 422,*4b–e. C. variabilis* COOPER & GRANT, Cathedral Mountain Formation, Texas; *b,* detail of shell commissure anteriorly with ventral attachment spines below, ×3; *c,* dorsal valve exterior, ×1; *d,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960); *e,* ventral valve exterior, ×2 (Cooper & Grant, 1975).

Chonostegoides SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 212 [**C. ogbinensis;* OD]. Medium size, subquadrate outline with small ears; interarea short; corpus planoconvex, deep; trails reflexed, ribbed; spine bases slightly swollen, elongate on ventral corpus, dorsal spines larger anteriorly; marginal structures similar to *Chonosteges;* dorsal interior with complete marginal ridge. *upper Lower Permian (Roadian):* Transcaucasus.——FIG. 422,*1a–c.* **C. ogbinensis,* Ufimian, Gnishiksky Horizon, Ogbin; *a,b,* holotype, ventral exterior, largely exfoliated dorsal valve interior, PIN 2071/76, ×1; *c,* dorsal valve exterior, ×1 (Sarytcheva & Sokolskaya, 1965).——FIG. 422,*1d. C. armenicus* SARYTCHEVA; detail of external mold of dorsal valve flange, ×6 (Sarytcheva & Sokolskaya, 1965).

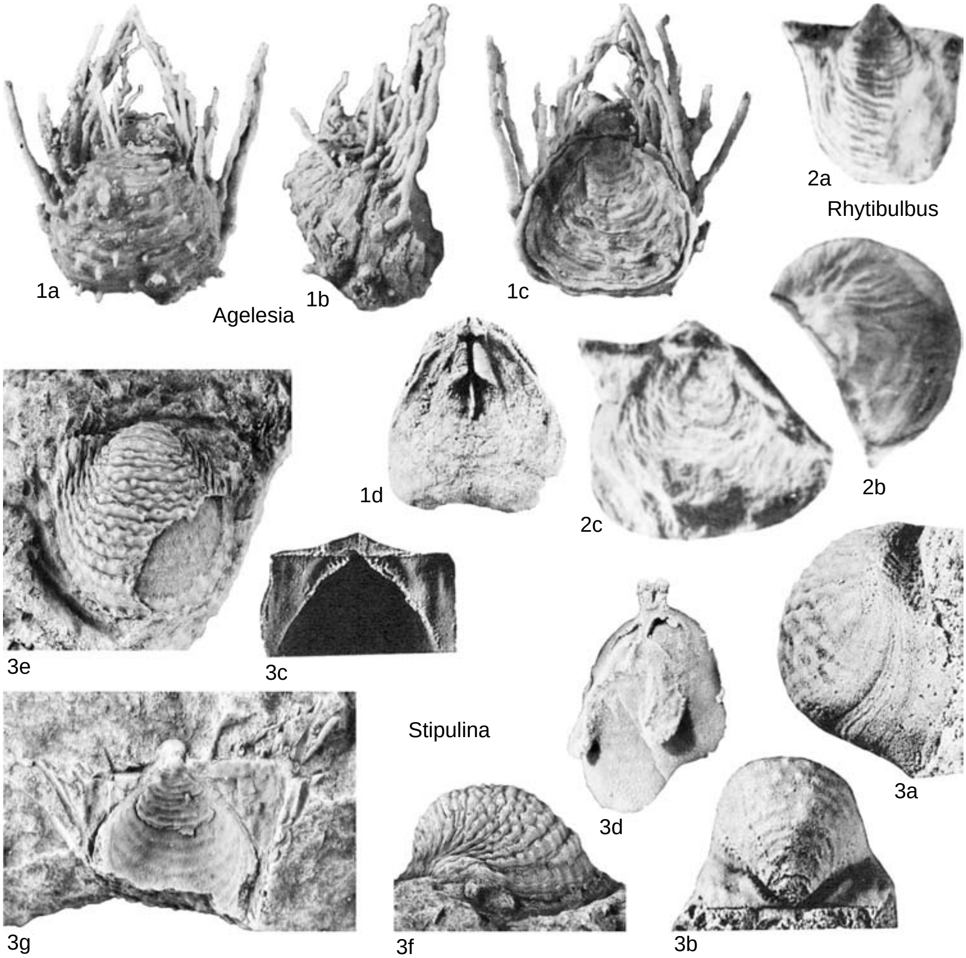


Fig. 421. Aulostegidae (p. 591).

Costisteges Liao, 1982, p. 540[543] [*_C. dongluoensis;_ OD]. Resembles *Chonosteges,* but lacks the complex spine, funnel arrangement bordering the corpus cavity. Published figures inadequate for illustration. *Upper Permian (Changhsingian):* China.

Urushtenia Licharew, 1935, p. 370 [*_Productus pseudomedusa_ Chernyschev, 1902, p. 293; OD]. Small, transverse with planoconvex flattened corpus, geniculate with trails; ventral interarea short, cicatrix small; ribbing starts on disks, prominent on trails; rugae narrow on disks; spines distributed on both disks, fine dorsally; spinose marginal ridges, gutters of trails resembling *Chonesteges. Lower Permian (Asselian–Sakmarian):* Russia, China.——Fig. 422,*3a–e.* *_U. pseudomedusa_ (Tschernyschew); *a,* specimen viewed ventrally, Sakmarian, Schwagerina Limestone, Ural Mountains, ×2; *b,* specimen viewed dorsally, Sakmarian, Schwagerina Limestone, Ural Mountains, ×1; *c,d,* specimen viewed posteriorly, laterally, Kasarmensky Kamen, Russia, ×2 (Muir-Wood & Cooper, 1960); *e,* dorsal valve interior, Kasarmensky Kamen, Russia, ×2.5 (Sarytcheva & Grunt, 1969).

Urushtenoidea Jing Yu-gan & Hu Shi-zhong, 1978, p. 116 [*_Urushtenia chaoi_ Ching Yu-gan, 1963; OD] [=*Uncisteges* Jing Yu-gan & Hu Shi-zhong, 1978, p. 117 (type, *Eomarginifera crenulatea* Ting Pei-chen in Yang Tsun-yi & others, 1962, p. 85; OD)]. Small, planoconvex corpus, geniculated to trails; ribbing originates on disks, prominent on trails; rugae impersistent, more prominent on ventral disk; spines erect on ribs; trail margins extending as interlocking spines similar to *Chonosteges;* cardinal process with basal pit; adductor field may be elevated; marginal ridge with row of spines. *upper Lower Permian:* southern China.——Fig. 422,*2a–c.* *_U. chaoi_ (Ching), ?Roadian, Hsiaojiangbian Formation, Jiangxi; *a,b,* specimen viewed anteriorly, laterally, ×1; *c,* specimen viewed anteriorly showing commissural spines, ×1 (new).——Fig.

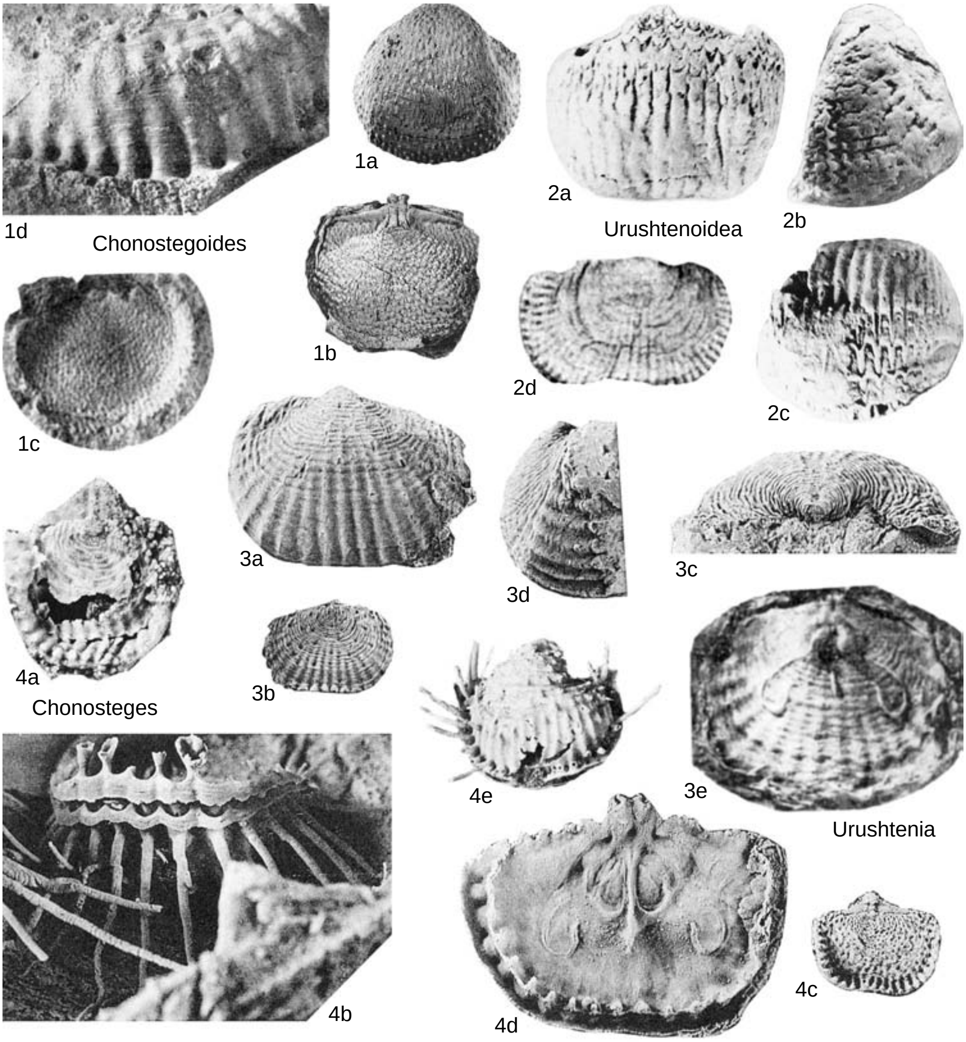


Fig. 422. Aulostegidae (p. 591–593).

422,*2d. U. chenanensis* (Chan), Kuhfeng Formation, Shangxi; ventral valve exterior, ×1.5 (Jing & Hu, 1978).

Subfamily CTENALOSIINAE Muir-Wood & Cooper, 1960

[Ctenalosiinae Muir-Wood & Cooper, 1960, p. 91]

Interarea short; ribbing varied, no dorsal spines; hinge lines denticulate. *Lower Permian (Roadian)–Upper Permian (Kazanian).*

Ctenalosia Cooper & Stehli, 1955, p. 470 *[*C. fixata;* OD]. Small, subcircular, with hinge of variable width; corpus planoconvex with anterior series of short dorsal trails; interarea short, with internal single row of denticles fitting dorsal hinge pits; ribbing variably developed on trails; both disks anteriorly rugose or lamellose; spines rhizoid on ventral corpus, posterior trail; cardinal process relatively strong; adductor platforms closely spaced with short median septum anteriorly. *Upper Permian (lower Kazanian):* USA.——Fig. 423,*1a–e.* **C. fixata,* Word Formation, Texas; *a,b,* holotype, viewed posteriorly, dorsally, USNM 124123a, ×3; *c,d,* attached ventral valve viewed anteriorly, internally, ×3; *e,* dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Mongolosia Manankov & Pavlova, 1976, p. 354 [**M. morenkovi;* OD]. Medium size, transverse outline; concavoconvex corpus, profile geniculate; no sulcus; cicatrix present; interarea short; concentric lamellae on dorsal valve, ribbing fine; spines in row at hinge,

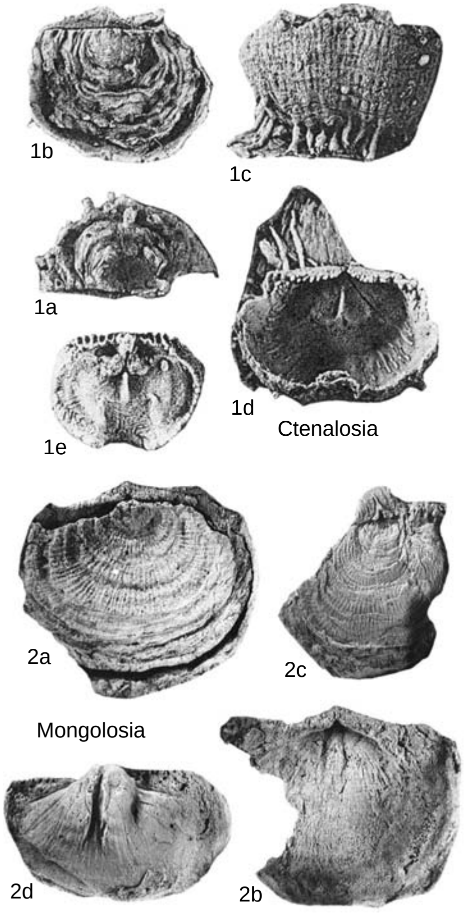


FIG. 423. Aulostegidae (p. 593–594).

scattered on ears, venter; up to 30 conical denticles at ventral hinge fitting pits on dorsal interior; cardinal process trifid with large median ridge, supported anteriorly by two ridges. *upper Lower Permian (Roadian)–lower Upper Permian:* central Mongolia.——FIG. 423,*2a–d*. **M. morenkovi; a,b,* holotype, viewed dorsally, showing dorsal valve exterior, ventral valve interior, PIN 3158/1, ×1; *c,* external mold of dorsal valve, ×1; *d,* internal mold of ventral valve, ×1 (Manankov & Pavlova, 1976).

Subfamily ECHINOSTEGINAE
Muir-Wood & Cooper, 1960

[Echinosteginae MUIR-WOOD & COOPER, 1960, p. 101]

Ventral interarea distinct, but variable; dorsal spines commonly absent; dorsal, ventral adductor scars prominent. *Lower Carboniferous (Tournaisian)–Upper Permian (Capitanian).*

Echinosteges MUIR-WOOD & COOPER, 1960, p. 101 [**Aulosteges tuberculatus* R. E. KING, 1931, p. 95; OD]. Medium size, subquadrate to elongate with strong but variable ventral interarea; corpus planoconvex, gently geniculate with anteriorly flanged trail; ventral disk with swollen spine bases, coarse ribbing on trail; spines rhizoid in clusters on ears and flanks, small, semirecumbent, evenly distributed over ventral valve; dorsal disk dimpled, spines rare; cardinal ridge parallel to hinge, forming sharp angle with complete marginal ridge. *lower Upper Permian:* USA.——FIG. 424,*1a–e*. **E. tuberculatus* (R. E. KING), Word Limestone, Texas; *a,* ventral valve exterior, ×1; *b,c,* ventral valve exterior, interior, ×1; *d,* shell viewed dorsally, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

Archaiosteges CARTER, 1991, p. 360 [**A. harperi;* OD]. Small; hinge less than maximum corpus width; ?without cicatrix; weakly concavoconvex, shallow with short trails; almost completely rugose; ventral swollen spine bases regularly distributed, spines fine; no ribbing; cardinal and marginal ridges; cardinal process thick, strongly supported by nonfunctional ridges resembling inner socket ridges. *Lower Carboniferous (Ivorian, ?Chadian):* USA.——FIG. 424,*2a–g*. **A. harperi,* lower Osagean, Iowa; *a–c,* holotype, viewed ventrally, anteriorly, laterally, CMNH 34953, ×2; *d,e,* ventral, posterodorsal views, ×3; *f,* young dorsal valve exterior, ×3; *g,* dorsal valve interior, ×2 (Carter, 1991).

Baissalosteges G. KOTLYAR, 1989, p. 119 [**B. gracilis;* OD]. Medium size, subquadrate outline, maximum width anteriorly; ventral interarea prominent; dorsal disk weakly concave, geniculate with short trail; corpus cavity shallow; capillation fine, indistinct on both valves; spines fine, recumbent, covering valve, rhizoid near hinge, cluster on ears; cardinal ridges, medium septum reach half dorsal disk length; shell material thin. *Upper Permian (Capitanian):* Transcaucasus, ?China.——FIG. 425,*3a–e*. **B. gracilis,* Khachikek Horizon, Transcaucasus; *a,b,* holotype, incomplete shell viewed ventrally, dorsally, TsNIGRA 36/12540, ×1; *c,* ventral valve exterior, ×1; *d,* shell viewed dorsally, ×1; *e,* detail of ventral valve exterior, ×3 (Kotlyar, 1989).

Edriosteges MUIR-WOOD & COOPER, 1960, p. 103 [**E. multispinosus;* OD] [=*Neoedriosteges* LIANG, 1990, p. 150[460] (type, *N. transversa;* OD)]. Medium, circular to subquadrate outline with short but wide ventral interarea; corpus gently concavoconvex with trails commonly having gutter; concentric ornament variably lamellose, especially dorsally; fine radial capillae commonly preserved on trails; ventral spines as in *Echinosteges,* but anteriorly tend to be distributed concentrically; no dorsal spines; interiors resemble *Echinosteges. Lower Permian:* USA, China, Tibet, Salt Range.——FIG. 425,*2a–e*. **E. multispinosus,* upper Leonard Formation, Texas; *a,b,* holotype, viewed ventrally, laterally, USNM 123906a, ×1; *c,* ventral valve interior, ×1; *d,* shell viewed dorsally, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood & Cooper, 1960).

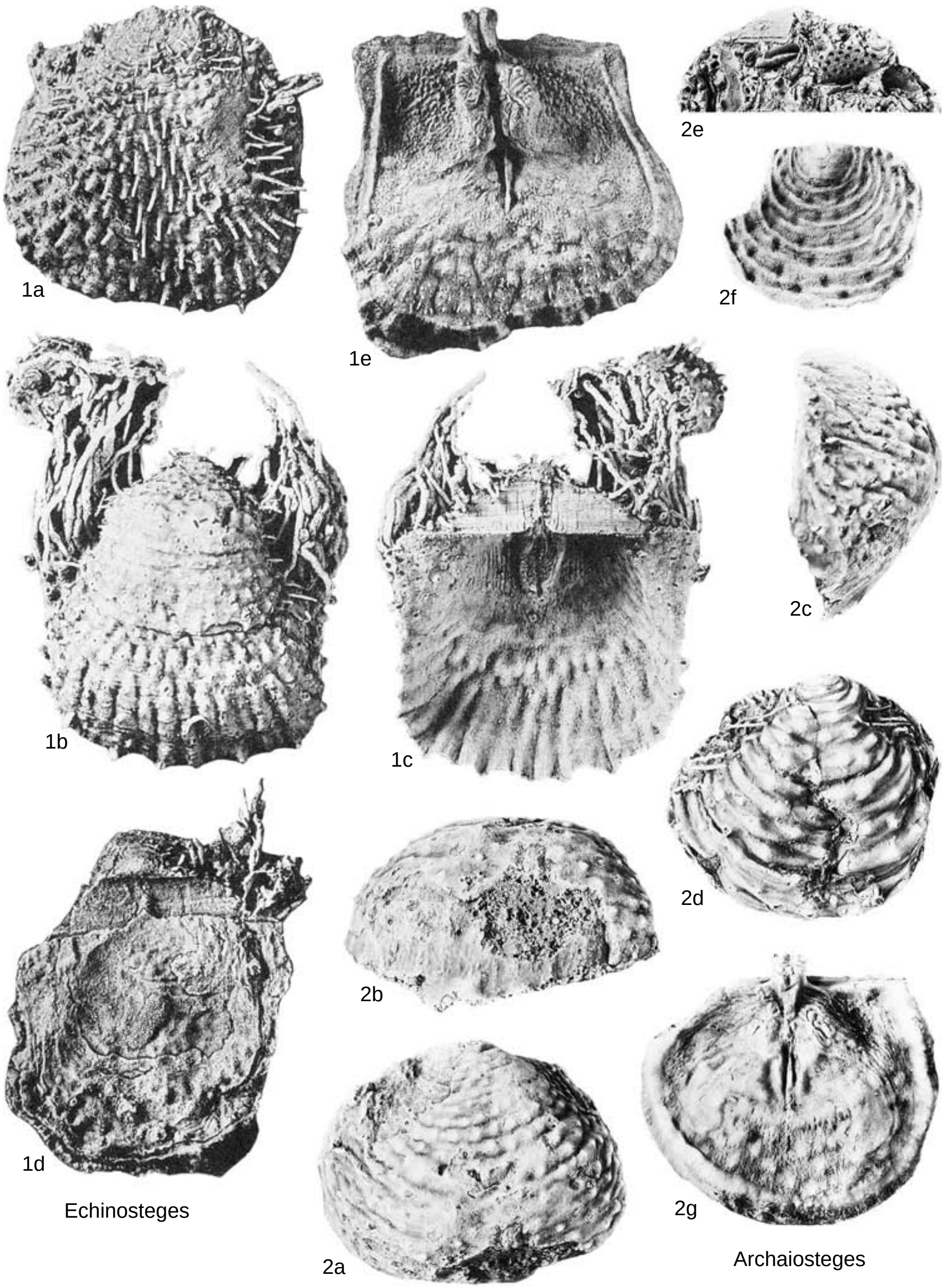


FIG. 424. Aulostegidae (p. 594).

Girlasia DE GREGORIO, 1930, p. 21 [**Strophalosia (Girlasia) superelegans;* OD]. Small, elongate outline, narrow hinge with short interarea; corpus weakly concavoconvex; exteriors smooth; spines evenly distributed on ventral valve, with slight rounded basal swellings, dorsal spines suberect, fine, rare; internal hinge lines denticulate. *Permian (Wordian):* Sicily. ——FIG. 426,*3a–c*. **G. superelegans* DE GREGORIO,

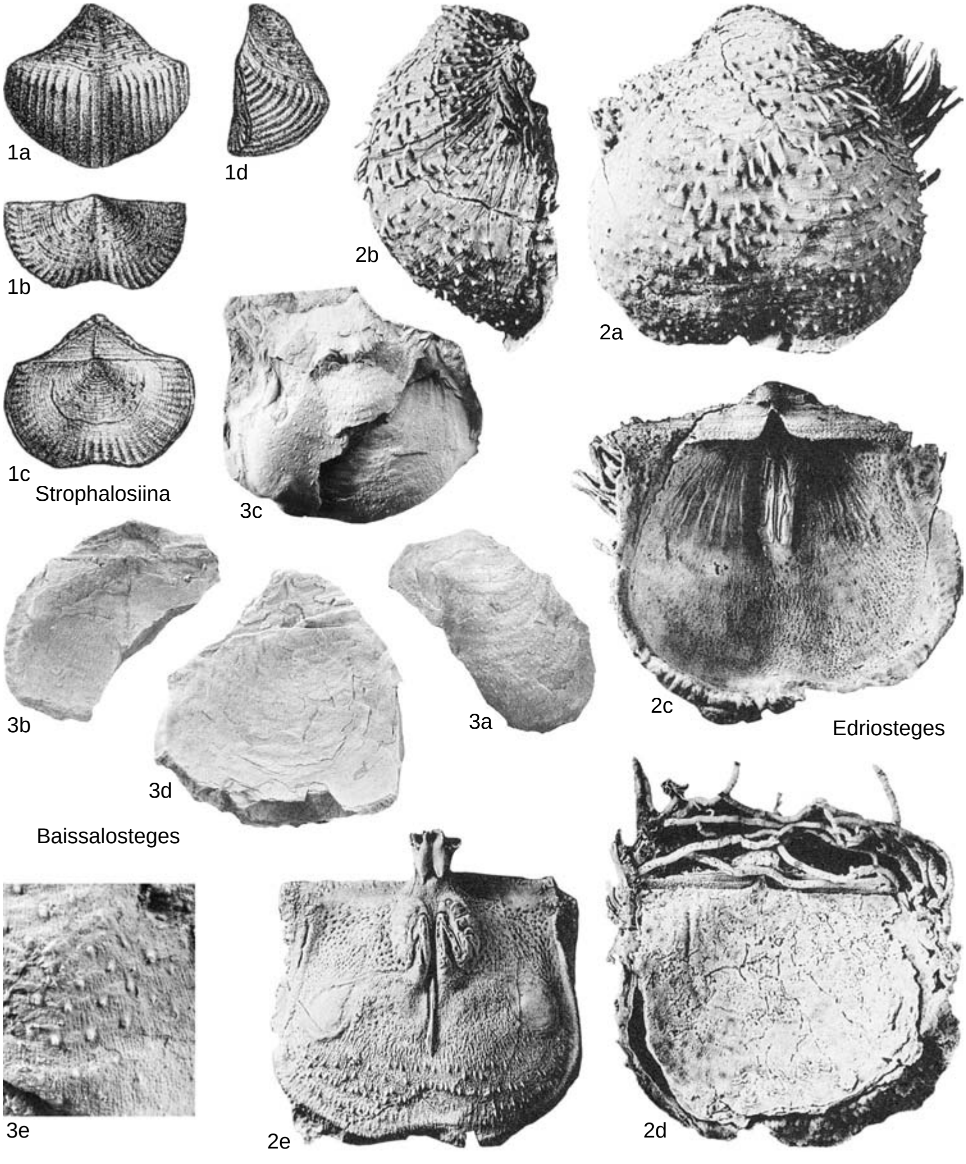


FIG. 425. Aulostegidae (p. 594–599).

Sosio Limestone, Palermo; *a,b,* shell viewed ventrally, dorsally, ×3; *c,* shell viewed laterally, ×2 (Muir-Wood & Cooper, 1960).

Howseia LOGAN, 1963, p. 756 [**Productus latirostratus* HOWSE, 1848, p. 256; OD]. Medium size, weakly sulcate shell; hinge narrower than width of midlength; ribbing absent, growth lines strong; spines in row on ventral flanks, few on venter; ventral adductor scars dendritic; dorsal scars striated; cardinal process bilobed, quadrifid, extending ventrally. *lower Upper Permian (lower Kazanian):* England.——FIG. 426,*1a–f.* **H. latirostrata* (HOWSE), middle Magnesian Limestone, County Durham; *a–c,* lectotype, viewed ventrally, dorsally, laterally, GSM 59737, ×1.5; *d,* posteriorly exfoliated ventral valve exterior, ×1.25; *e,* ventral valve internal mold plus shell on right ear, ×1.5; *f,* dorsal valve interior, cardinalia, ×3 (Logan, 1963).

Limbella STEHLI, 1954, p. 329 [**Aulosteges wolfcampensis* R. E. KING, 1931, p. 95; OD]. Me-

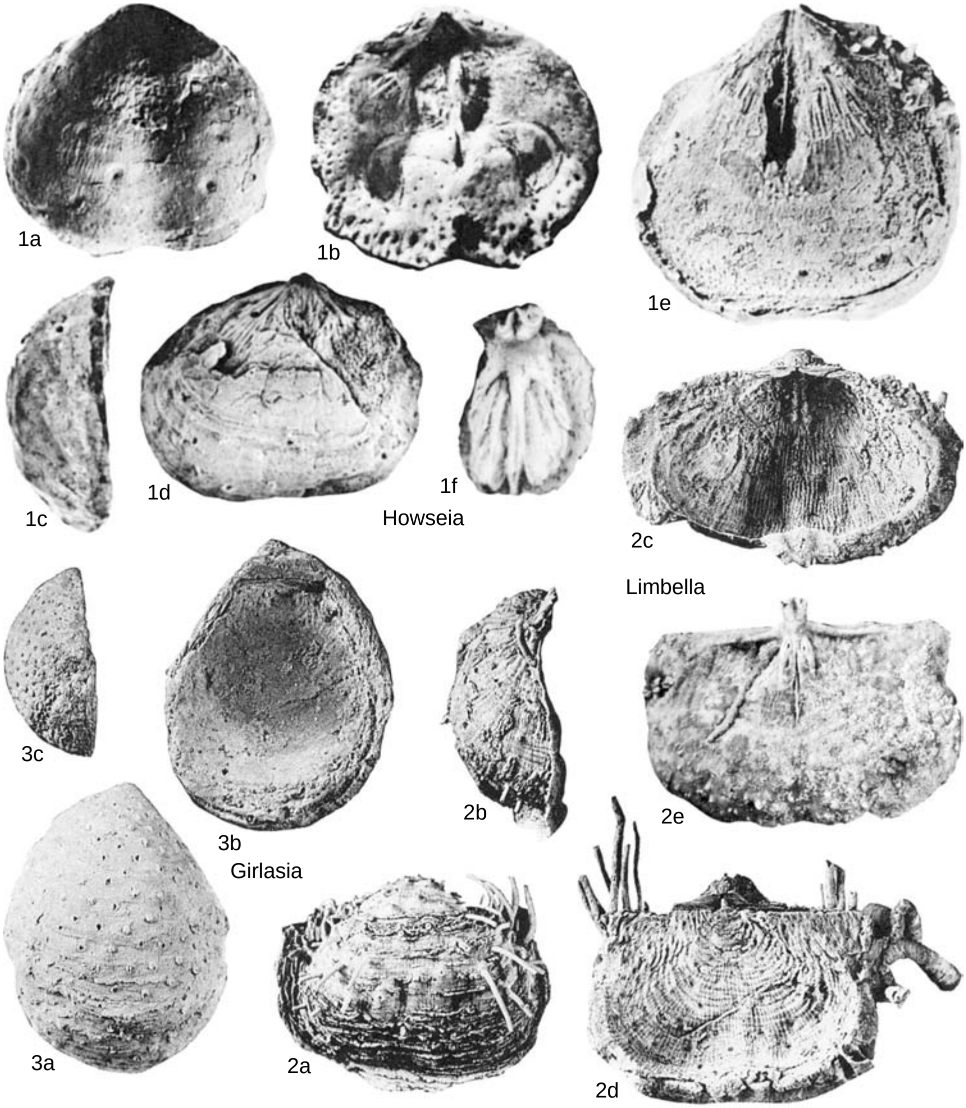


FIG. 426. Aulostegidae (p. 595–597).

dium size, resembling *Edriosteges,* but differing in its distictive fine ribbing, tendency to be lamellose, fewer ventral corpus spines; interareas, relationships of cardinal process to delthyrium vary in both genera; internally has short, well-developed cardinal ridges, lacking marginal ridges and with relatively weak, narrow dorsal adductor scars. *Upper Carboniferous–Lower Permian:* USA.——FIG. 426,*2a–e.* **L. wolfcampensis* (R. E. KING), Asselian, Neal Ranch Formation, Texas; *a,* ventral valve exterior, ×1; *b,* ventral valve viewed laterally, ×1; *c,* ventral valve interior, ×1; *d,* shell viewed dorsally, ×1 (Muir-Wood & Cooper, 1960); *e,* dorsal valve interior, ×1 (Cooper & Grant, 1975).

Sphenosteges MUIR-WOOD & COOPER, 1960, p. 108 [**Aulosteges hispidus* GIRTY, 1920, p. 644; OD]. Externally somewhat resembling *Sphenalosia,* but differs in having fine ribbing, narrow convex pseudodeltidium; no teeth; cardinal process less narrow, shorter. *Upper Permian (Kazanian):* central USA.——FIG. 427,*4a–f.* **S. hispidus* (GIRTY), Phosphoria Formation, Wyoming; *a,b,* holotype, viewed ventrally, laterally, USNM 119088, ×1; *c,* detail of ventral valve exterior, ×2; *d,* incomplete

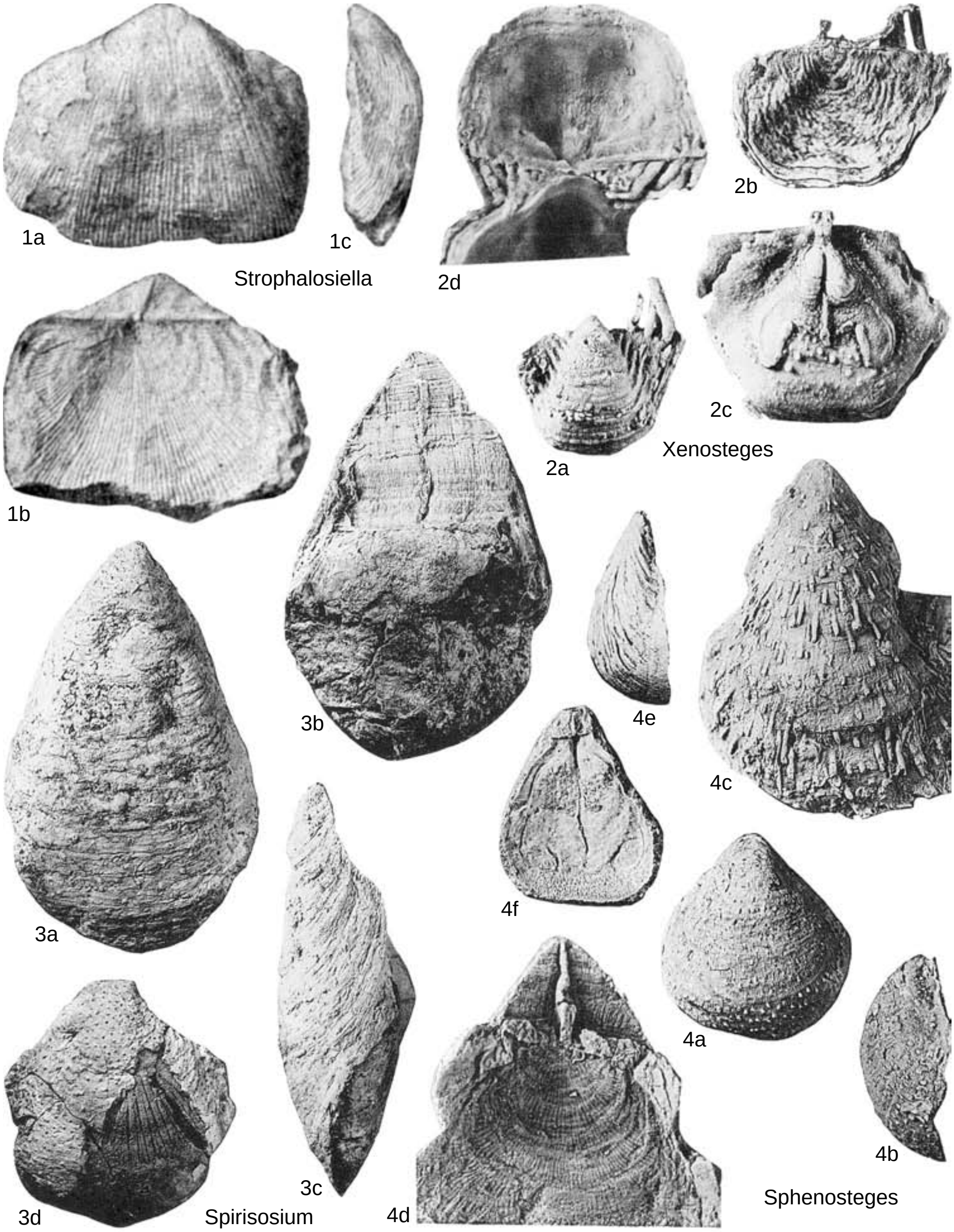


FIG. 427. Aulostegidae (p. 597–599).

dorsal view of shell, ×3; *e,* lateral view of ventral valve internal mold, ×1; *f,* internal mold of dorsal valve, ×1 (Muir-Wood & Cooper, 1960).

?Spirisosium DE GREGORIO, 1930, p. 23 [**S. primarium;* OD; =*Aulosteges karpinskyi* GEMMELLARO, 1892, p. 26]. Poorly known, medium size; elongate trigonal outline, no sulcus; interarea long, trigonal, narrow pseudodeltidium; concentric lamellose ornament weak; spines at edges of interarea, on flanks and small, distributed over ventral valve; reportedly rare on dorsal valve; interiors unknown. [This genus may prove to be more suitably assigned to the Gondolininae.] *?Permian (?Wordian):* Sicily.——FIG. 427,*3a–d.* **S. karpinskyi* (GEMMELLARO), Sosio Limestone, Sicily; *a–c,* shell viewed ventrally, dorsally, laterally, ×0.75; *d,* partly exfoliated ventral valve showing part of diductor scar, ×0.75 (Muir-Wood & Cooper, 1960).

?Strophalosiella LICHAREW, 1935, p. 372 [**S. coraeformis;* OD]. Medium size, broadly subcircular with hinge slightly less than maximum width, high trigonal interarea with narrow pseudodeltidium; ribbing fine, entire other than at beak; rugae posterolaterally on dorsal valve; spines reported from edges of interarea, flanks, and possibly scattered on ventral valve only; interiors unknown. *Lower Permian:* northern Europe, Russia.——FIG. 427,*1a–c.* **S. coraeformis,* Vymm basin, Russia; incomplete specimen viewed ventrally, dorsally, laterally, ×1 (Sarytcheva, Licharew, & Sokolskaja, 1960).

Strophalosiina LICHAREW, 1935, p. 369 [**Aulosteges tibeticus* DIENER, 1897, p. 35; OD]. Smaller medium size, pentagonal outline with high triangular interarea; median sulcus full length of valve; profile strongly geniculate; ribbing on trails only; rugae on disks, narrow; spines scattered on ventral disk; interiors unknown. *upper Lower Permian (Artinskian)–Upper Permian (Kazanian)*: Himalayas, Caucasus.——FIG. 425,*1a–d.* **S. tibeticus* (DIENER), Chitichum Limestone, Tibet, DIENER specimen; viewed anteroventrally, ventrally, dorsally, laterally, ×1 (Muir-Wood & Cooper, 1960).

Xenosteges MUIR-WOOD & COOPER, 1960, p. 111 [**X. adherens;* OD]. Small, subquadrate outline with prominent wide ears; interarea short; delthyrium open; lamellose concentric ornament, especially on dorsal valve; spines large, rhizoid on hinge, ears, and at umbo, lacking elsewhere; lateral ridges in both valves, dorsally variably connected to marginal ridge. *upper Lower Permian (Artinskian)–lower Upper Permian (lower Kazanian):* southern USA.——FIG. 427,*2a–d.* **X. adherens,* Cathedral Mountain Formation, Texas; *a,* ventral valve exterior, ×2; *b,* dorsal valve exterior, ×2; *c,* dorsal valve interior, ×4 (Muir-Wood & Cooper, 1960); *d,* attached ventral valve viewed internally, ×2 (Cooper & Grant, 1975).

Subfamily INSTITELLINAE
Muir-Wood & Cooper, 1960

[Institellinae MUIR-WOOD & COOPER, 1960, p. 117] [=Costellariinae MUIR-WOOD & COOPER, 1960, p. 123; Sinuatellidae MUIR-WOOD & COOPER, 1960, p. 124]

Corpus rugose to reticulate; trails commonly ribbed with bordering structures of flanges or gutters; dorsal spines commonly absent. *Lower Carboniferous (Viséan)–lower Upper Permian (Capitanian).*

Institina MUIR-WOOD & COOPER, 1960, p. 164 [**Productus marginalis* DE KONINCK, 1847a, p. 238; OD]. Rugae on visceral disks, ribbing on trail from geniculated cincture; cardinal process narrow, cardinal ridges reach ears. *Lower Carboniferous (upper Viséan):* Europe.——FIG. 428,*1a–f.* **I. marginalis* (DE KONINCK), Asbian, Visé; *a–d,* partially exfoliated shell viewed ventrally, dorsally, posteriorly, laterally, ×2; *e,* oblique lateral view of ventral valve exterior with trail, ×2 (new); *f,* replica of dorsal valve interior, ×3 (Muir-Wood & Cooper, 1960).

Costellarina COOPER & MUIR-WOOD, 1967, p. 808, *nom. nov. pro Costellaria* MUIR-WOOD & COOPER, 1960, p. 123, *non* SWAINSON, 1840 [**C. costellata* MUIR-WOOD & COOPER, 1960, p. 124; OD]. Small, around 10 mm wide, subquadrate outline, gently concavoconvex profile; interarea wide, short; cicatrix; ribbing starting anteriorly on reticulate disks; spines semirecumbent, scattered over ventral valve plus clusters on ears; cardinal process sessile, broadly bilobed. [The described specimens may not be adult.] *Lower Permian:* USA.——FIG. 428,*2a–g.* **C. costellata* MUIR-WOOD & COOPER, Talpa Formation, Texas; *a,* holotype, viewed dorsally, USNM 124110a, ×2; *b–d,* shell viewed ventrally, posteriorly, laterally, ×2; *e,* ventral valve exterior, ×3; *f,* dorsal valve interior, ×4; *g,* detail of cardinal process externally, ×6 (Muir-Wood & Cooper, 1960).

Craspedona COOPER & GRANT, 1975, p. 881 [**C. newelli;* OD]. Small circular corpus with wide hinge, tubiform anterior trails forming part of flanges; ventral interarea short; cicatrix minute; both disks weakly reticulate, ribbing becoming stronger anteriorly; spines rhizoid at posterior margins and ears, fine spines scattered on ventral corpus; lateral plus marginal ventral ridges; cardinal process small, sessile, partly overhung dorsally by zygidium extending as lateral ridges, ear baffles; near hinge irregular tubercles fit corresponding pits in ventral hinge region. *upper Lower Permian (Kungurian)–Upper Permian (Capitanian):* USA.——FIG. 429,*1a–e.* **C. newelli,* Bell Canyon Formation, Texas; *a,b,* holotype, viewed ventrally, dorsally, USNM 154172a, ×1; *c,* ventral valve exterior, ×1.5; *d,* ventral valve interior, ×1.5; *e,* dorsal valve interior, ×1.5 (Cooper & Grant, 1975).

Glyptosteges COOPER & GRANT, 1975, p. 876 [**G. intricatus;* OD]. Small, with small cicatrix; spines rhizoid posteriorly, recumbent on venter; both valves strongly, fully costate; ventral adductor scars elevated, surrounded by flabellate diductor scars; cardinal process small; lateral ridges extending straight across ears. *Lower Permian (Sakmarian–Artinskian):* USA.——FIG. 429,*3a–e.* **G. intricatus,* Skinner Ranch Formation, Texas; *a,b,* ventral valve viewed ventrally, laterally, ×1; *c,* attached ventral valve exterior, ×2; *d,e,* dorsal valve exterior, interior, ×1.5 (Cooper & Grant, 1975).

Institella COOPER, 1942, p. 230 [**Productus leonardensis* R. E. KING, 1931, p. 70; OD]. Medium size; ventral profile with disk weakly convex, geniculate with trail margin reflexed; median sulcus prominent, forming V-shaped fold in gutter; interarea short; cicatrix small; ribbing disappearing on gutter; spines thick, rhizoid at hinge, ears, smaller and scattered on venter; dorsal lateral ridges variable, may extend

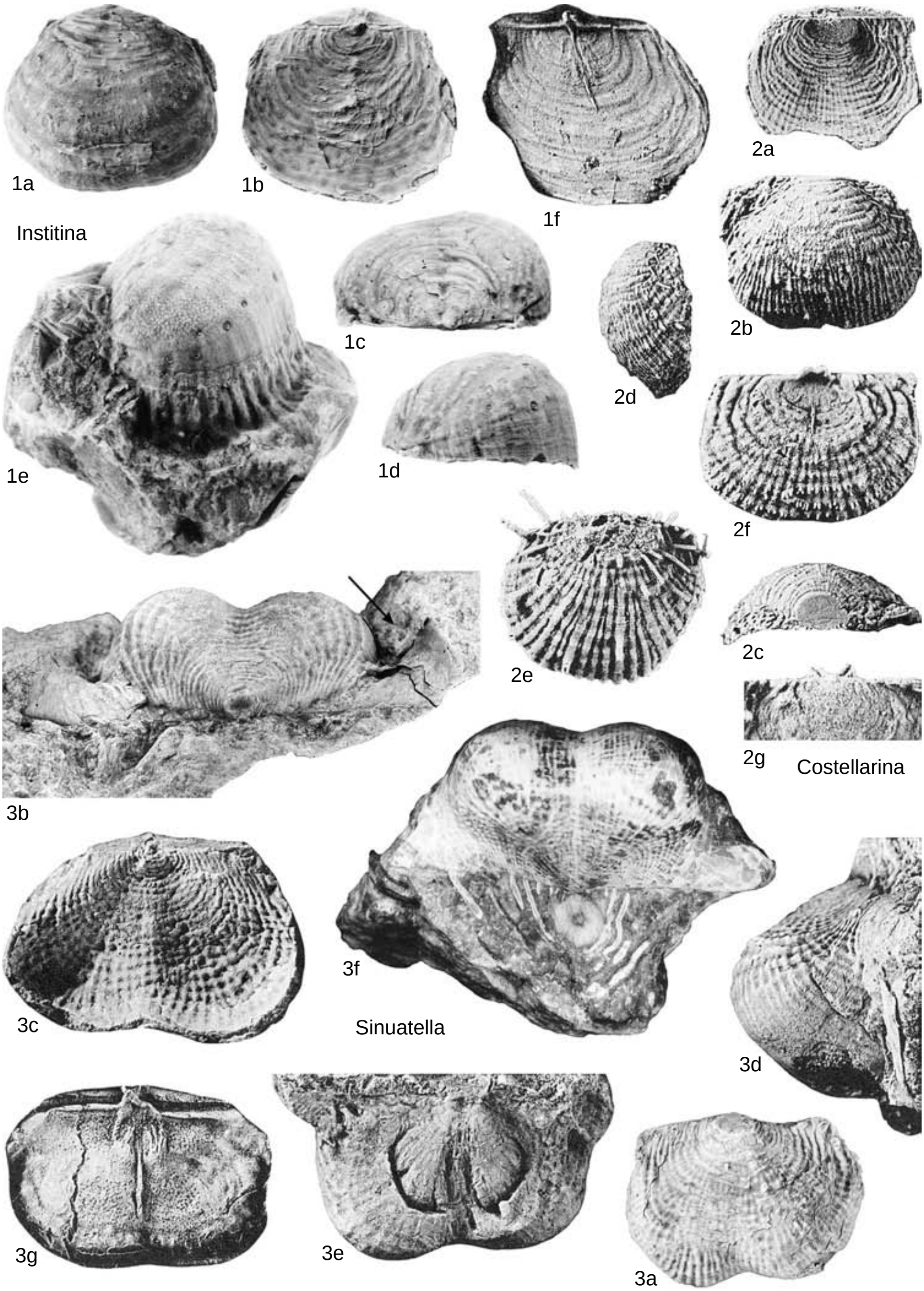


FIG. 428. Aulostegidae (p. 599–604).

to lateral margins. *upper Lower Permian–lower Upper Permian:* USA.——FIG. 429,*4a–e*. **I. leonardensis* (R. E. KING), Cathedral Mountain Formation, Texas; *a,* ventral valve exterior, ×1.5; *b,* lateral view of ventral valve, ×1; *c,* shell viewed dorsally, ×1; *d,* dorsal valve interior, ×1 (Muir-Wood & Cooper,

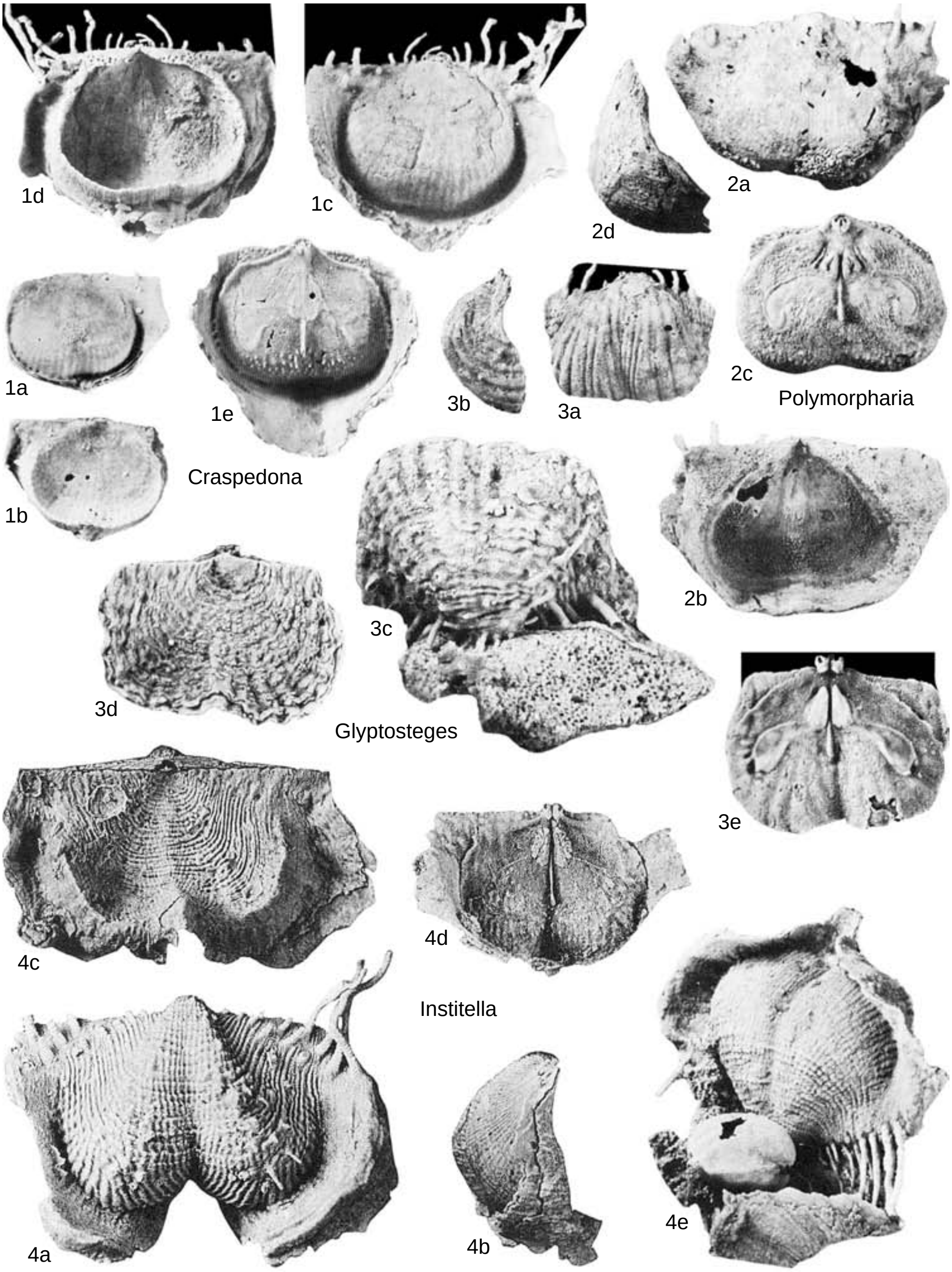


FIG. 429. Aulostegidae (p. 599–601).

1960); *e,* oblique view of attached shell, ×1 (Cooper & Grant, 1975).

Polymorpharia COOPER & GRANT, 1975, p. 1143 [**P. polymorpha;* OD]. Resembles *Crespedona,* but without strong median flanged trail; lacking rugae on disks; dorsal adductor scars shorter, strongly marked. *upper Lower Permian (Roadian)–lower Upper Permian (Wordian):* USA.——FIG. 429,*2a–d.* **P. polymorpha,* Cherry Canyon Formation, Texas; *a,b,* ventral valve exterior, interior, ×1; *c,* dorsal valve interior, ×1; *d,* dorsal valve viewed laterally, ×1 (Cooper & Grant, 1975).

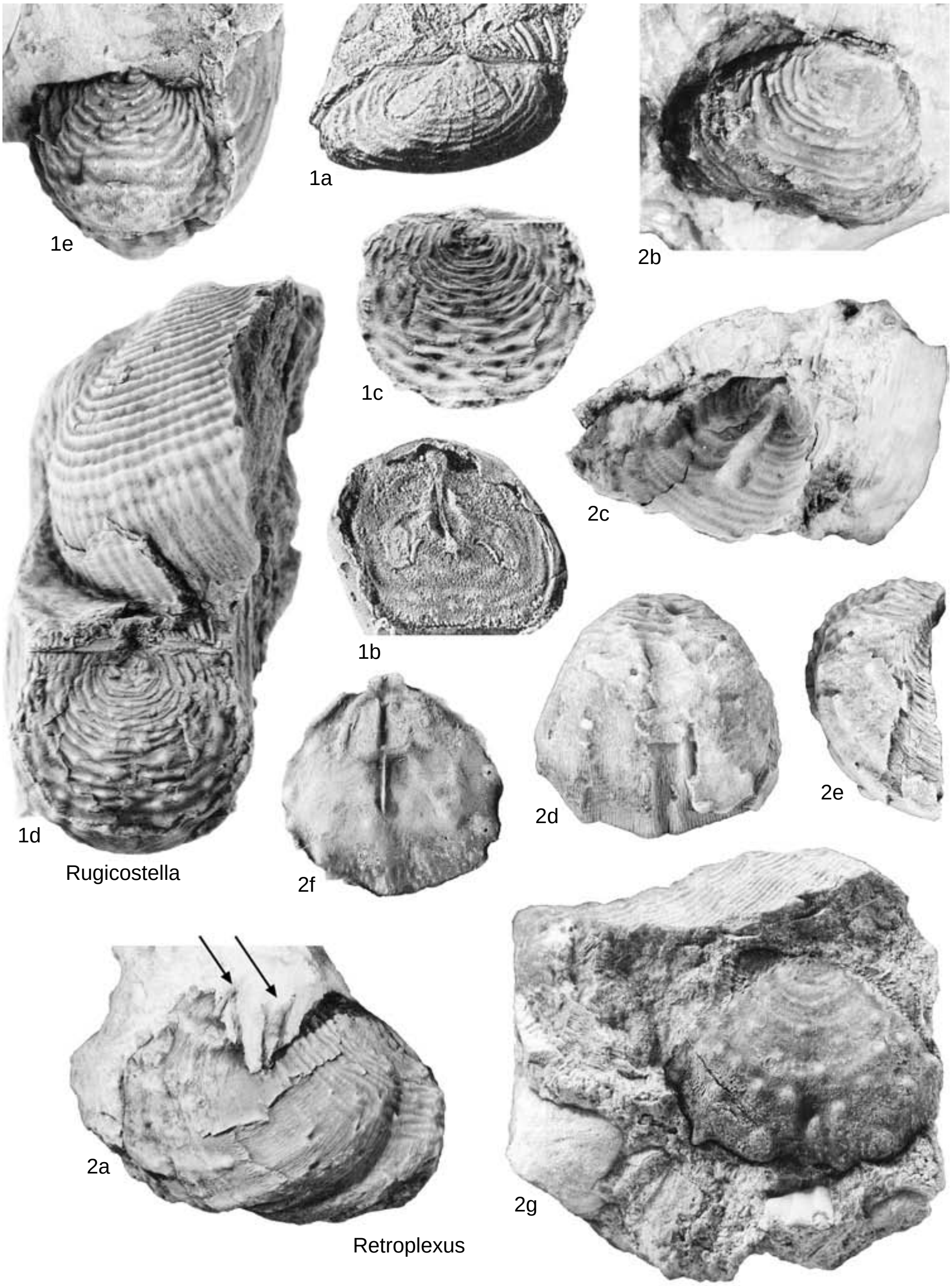


Fig. 430. Aulostegidae (p. 602–604).

Retroplexus Brunton & Mundy, 1988b, p. 74 [**R. parkhousensis;* OD]. Cicatrix small, variable; visceral disks strongly differentiated from ears, rugose; trails smooth with distal spine ridges, rhizoid spines long from hinge and flanks, other spines on ventral corpus and trail; dorsal adductor scars slightly elevated; ear baffles. *Lower Carboniferous (upper Viséan):* British Isles, ?western Europe.——Fig. 430,*2a–g.* **R. parkhousensis,* Asbian; *a,* holotype, viewed anterolaterally showing spines extending into matrix (*ar-*

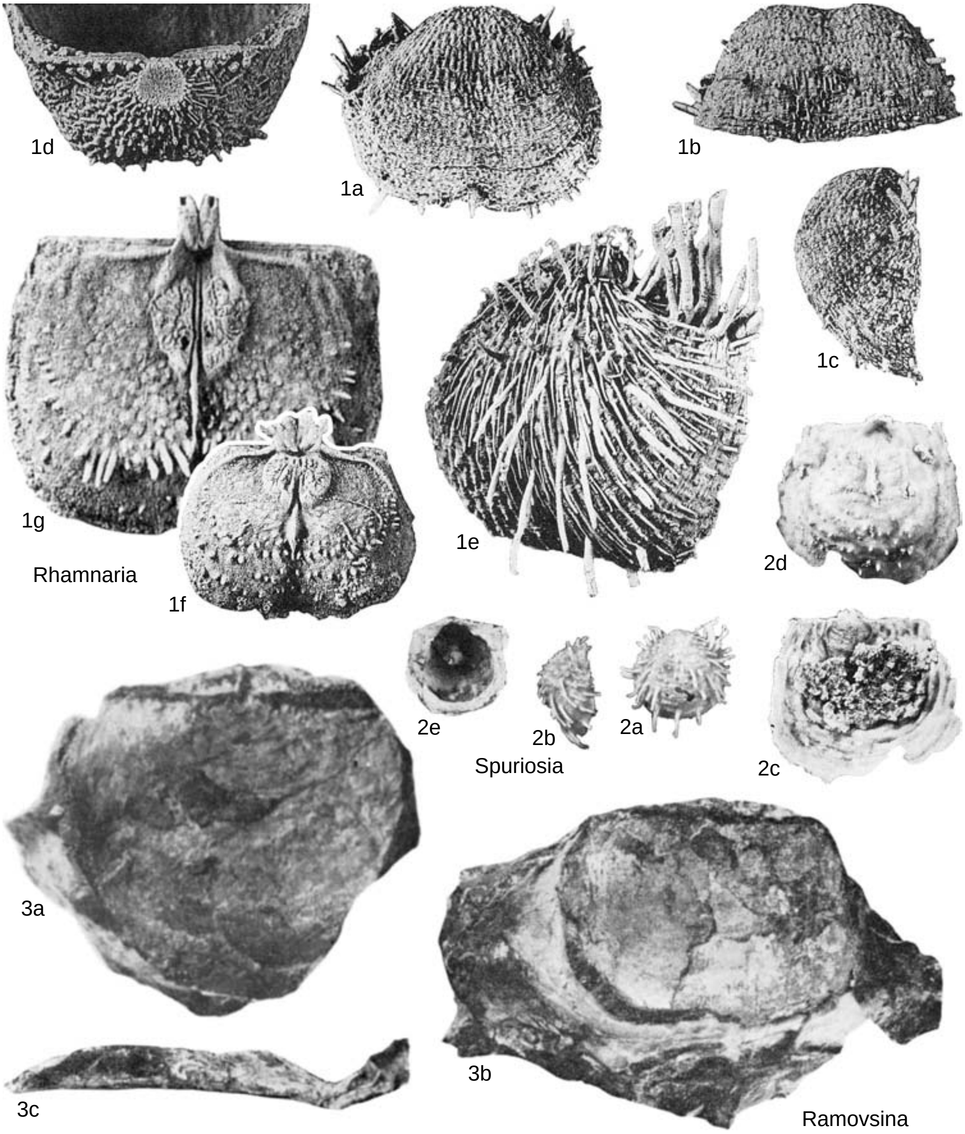


Fig. 431. Aulostegidae (p. 604–605).

rows), Derbyshire, BMNH BB58751, ×2; *b,* juvenile ventral valve with cicatrix adhering to *Tabulipora,* Derbyshire, ×3; *c,* incomplete ventral interior, Derbyshire, ×3; *d–f,* internal mold viewed anteriorly, laterally, and replica of dorsal valve corpus interior, Staffordshire, ×2; *g,* deeply exfoliated dorsal valve interior with pustules indicating ventral spine positions, Staffordshire, ×2 (Brunton & Mundy, 1988b).

Rugicostella Muir-Wood & Cooper, 1960, p. 166 [**Productus nystianus* de Koninck, 1842, p. 202; OD]. Small; strongly geniculate with short ventral interarea; ventral corpus with irregular rugae, swollen spine bases, attachment spines at ventral hinge; cincture, trail smooth to coarsely ribbed; cardinal process supported by short median ridge; cardinal ridges extend as ear baffles, subperipheral rim. *Lower Carboniferous (upper Viséan):* Europe, ?Far East.——Fig. 430,*1a–e.* **R. nystiana* (de Koninck); *a,* internal mold of ventral valve with hinge spines, upper Viséan, Visé, ×3; *b,* replica of dorsal valve interior, upper Viséan, Visé, ×4 (Muir-Wood & Cooper, 1960); *c,* dorsal view of complete corpus with *d,* showing its counterpart attached to

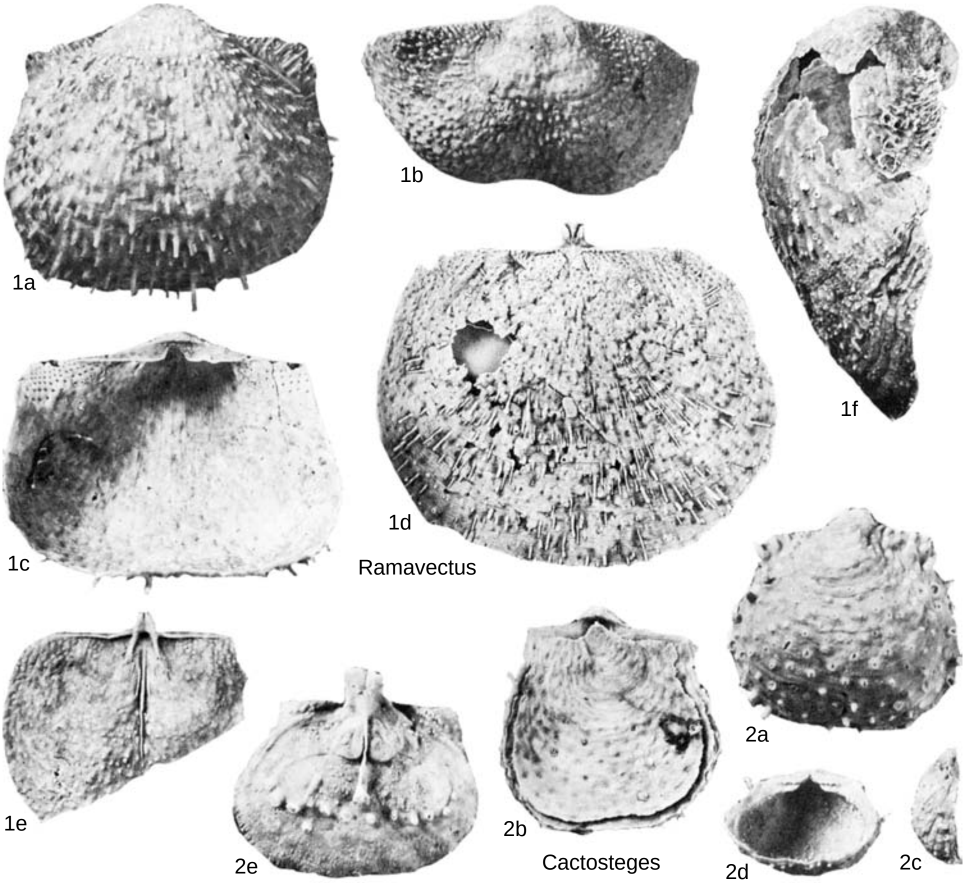


FIG. 432. Aulostegidae (p. 605).

Limbifera, Asbian, northern Yorkshire, ×3; *e,* ventral view of corpus and part of long trail, Asbian, northern Yorkshire, ×3 (new).

Sinuatella MUIR-WOOD, 1928, p. 37 [**Leptaena sinuata* DE KONINCK, 1851, p. 654; OD]. Ventral outline transverse, anteriorly sulcate; visceral disks reticulate, trails weakly ribbed with flange or gutters; cicatrix; attachment spines posteriorly and finer, rare corpus spines; ventral muscle field bordered anterolaterally by ridges. *Lower Carboniferous (Viséan–lower Namurian):* Eurasia. ——FIG. 428,*3a–g.* **S. sinuata* (DE KONINCK); *a,* ventral valve exterior with cicatrix, Asbian, North Yorkshire, ×1.5; *b,* posterior view of specimen with cicatrix, lateral gutter (*arrow*), Asbian, North Yorkshire, ×2 (new); *c,* dorsal valve exterior, Asbian, North Yorkshire, ×2; *d,* lateral view showing geniculate ventral valve, upper Viséan, Staffordshire, ×2; *e,* partial internal mold of ventral valve, upper Viséan, Staffordshire, ×2 (Muir-Wood & Cooper, 1960); *f,* ventral view of shell with spines clasping section of crinoid stem, Asbian, Derbyshire, ×1.5 (new); *g,* replica of young dorsal valve interior, Visé, ×2 (Muir-Wood & Cooper, 1960).

Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

[Rhamnariinae MUIR-WOOD & COOPER, 1960, p. 119] [=Ramovsiinidae SREMAC, 1986, p. 14]

Interarea reduced or rudimentary; spines on both valves; cardinal process commonly wide; dorsal adductor scars raised or on platforms. *Lower Permian (Asselian)–Upper Permian (Kazanian).*

Rhamnaria MUIR-WOOD & COOPER, 1960, p. 119 [**R. kingorum;* OD]. Medium, subcircular outline with weakly developed ears; commonly with cicatrix; sulcation weak; disks plano- to slightly concavo-convex with short dorsal trail; dorsal valve strongly dimpled; spine bases swollen on ventral disk, elongate anteriorly, spines thick in clusters at hinge and flanks, semierect and mixed with thin recumbent spines on rest of valve; cardinal process variable, wide; endospines strong anteriorly on disk. *lower Upper Permian:* southern USA.——FIG. 431,*1a–g*. **R. kingorum,* Word Limestone, Texas; *a–c,* holotype, ventral valve viewed ventrally, anteriorly, laterally, USNM 124072b, ×1; *d,* ventral valve viewed posteriorly, ×1; *e,* ventral valve viewed obliquely, ×1; *f,* dorsal valve interior, ×1; *g,* dorsal valve interior, ×2 (Muir-Wood & Cooper, 1960).

Cactosteges COOPER & GRANT, 1975, p. 850 [**C. anomalus;* OD]. Small, subcircular shells with reduced ventral interarea; concentric ornament weak; dorsal spines more fine than ventral spines; ventral adductor scars elevated on low platforms; cardinal process thick set, weakly bilobed; medium septum low, thin, extending almost to disk margin; endospines prominent anteriorly. *lower Upper Permian:* USA.——FIG. 432,*2a–e*. **C. anomalus,* Word Formation, Texas; *a,b,* holotype viewed ventrally, dorsally, USNM 151297a, ×2; *c,* holotype viewed laterally, USNM 151297a, ×1; *d,* ventral valve interior, ×1; *e,* dorsal valve interior, ×2 (Cooper & Grant, 1975).

Ramavectus STEHLI, 1954, p. 327 [**R. diabloensis;* OD]. Somewhat resembles *Reedoconcha* in size and shape, with concentric lamellae becoming marked toward ventral margin; ventral spine bases elongate posteriorly with semirecumbent spines, more erect spines at hinge and ears, dorsal spines fine and semirecumbent; cardinal process short, trifid, supported by pair of divergent ridges enclosing posterior edges of weak adductor scars; cardinal ridges barely reaching ears. *Lower Permian (Artinskian):* southern USA.——FIG. 432,*1a–f.* **R. diabloensis,* Bone Spring Formation, Texas; *a–c,* ventral valve viewed ventrally, posteriorly, internally, ×1; *d,* dorsal valve exterior, ×1; *e,* dorsal valve interior, ×1; *f,* lateral view of large ventral valve, ×0.75 (Cooper & Grant, 1975).

Ramovsina SREMAC, 1986, p. 14 [**R. likana;* OD]. Medium-sized corpus with laterally and anteriorly extended trails; ventral interarea short, approximately equal to corpus width; spines both coarse, fine on both valves, coarse on hinge, ears; cardinal process large, quadrifid. *lower Upper Permian (Kazanian):* Croatia.——FIG. 431,*3a–c*. **R. likana,* Murghabinian, Velebit Mountains; *a,* holotype, viewed dorsally, GPZ 1223, ×1; *b,c,* dorsal, lateral views of specimen with wide flange on right, ×0.75 (Sremac, 1986).

Spuriosia COOPER & GRANT, 1975, p. 898 [**S. circularis;* OD]. Small, around 5 mm wide, with minute cicatrix; ventral interarea very short, dorsal valve with irregular fine rugae, sparse spines. *Lower Permian (Asselian–Sakmarian):* USA.——FIG. 431,*2a–e*. **S. circularis,* Neal Ranch Formation, Texas; *a,b,* holotype, viewed ventrally, laterally, USNM 153490a, ×2; *c,d,* dorsal valve exterior, interior, ×4; *e,* ventral valve interior, ×2 (Cooper & Grant, 1975).

Subfamily GONDOLININAE
Jin Yu-gan, Brunton, & Lazarev, 1998

[Gondolininae JIN YU-GAN, BRUNTON, & LAZAREV, 1998, p. 8]

Elongate trigonal, homeomorph of *Striatifera,* but with long, narrow ventral interarea; spines rhizoid on ventral umbonal margins. *Lower Carboniferous (upper Viséan–lower Serpukhovian).*

Gondolina CHING YU-GAN & LIAO ZHAO-TING in WANG YU, CHING YU-GAN, & FANG DA-WEI, 1966, p. 412 [**G. weiningensis;* OD]. Resembles *Striatifera* in outline, but with extended ventral umbo, long triangular interarea; rugae irregular, interrupting ribbing; spines thin, rhizoid, in clusters on umbonal flanks and unknown elsewhere. *Lower Carboniferous (upper Viséan–lower Serpukhovian):* China.——FIG. 433*a–c*. **G. weiningensis,* lower Serpukhovian, Guizhou; holotype, viewed ventrally, dorsally, laterally, NIGP 22444, ×0.75 (Wang, Ching, & Fang, 1966).

Family COOPERINIDAE Pajaud, 1968

[*nom. transl.* COOPER & GRANT, 1975, p. 822, *ex* Cooperininae PAJAUD, 1968, p. 158]

Small elongate to bilobate outline, cemented by large cicatrix, spines, or both; fine spines commonly also on dorsal valves; hinge teeth, pseudodeltidium absent; dorsal interior with adductor platform, prominent brachial ridges. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Subfamily COOPERININAE
Pajaud, 1968

[Cooperininae PAJAUD, 1968, p. 158]

Size small for family; ventral interarea, cicatrix surrounded by rhizoid spines; dorsal muscle platforms short. *Lower Permian (Asselian)–Upper Permian (Changhsingian).*

Cooperina TERMIER, TERMIER, & PAJAUD, 1966, p. 332 [**C. inexpectata;* OD]. Minute, subquadrate; ventral exterior slightly lamellose, spinose; dorsal valve flat to slightly concave, some spinose; anterior commissure emarginate; ventral interior with long, low, median ridge; dorsal disk almost surrounded by brachial ridges; cardinal process weakly bilobed; adductor scars on platforms elevated anteriorly. *Permian (Wordian):* USA, Thailand.——FIG. 434,*1a–d*. **C. inexpectata,* Wordian, Texas; *a,b,* shell with large cicatrix viewed ventrally, dorsally, ×6; *c,* ventral valve interior, ×6; *d,* dorsal valve interior, ×6 (Cooper & Grant, 1975).

Ansehia TERMIER & TERMIER, 1970, p. 456 [**A. thecideiformis;* OD]. Small, around 5 mm wide,

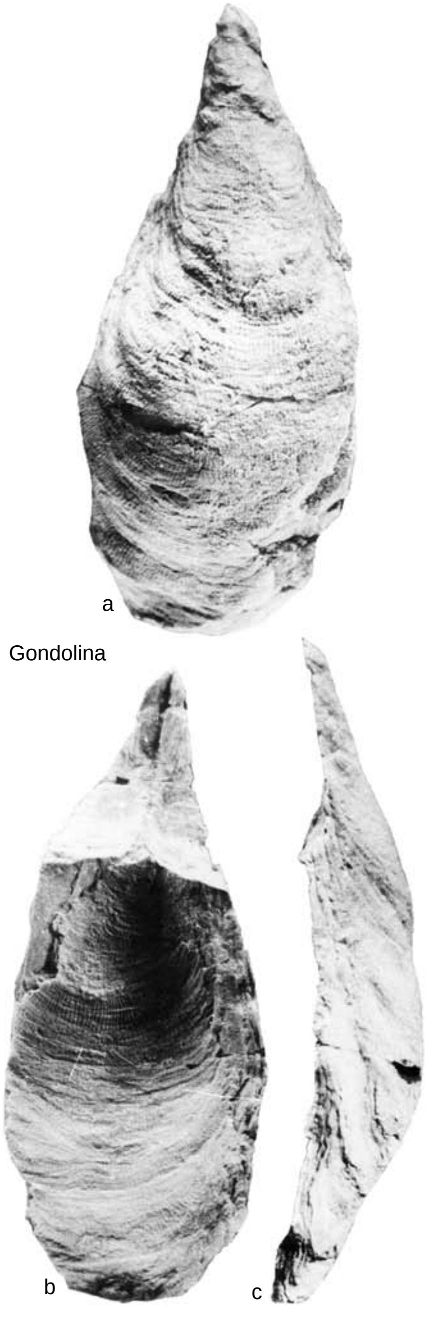


FIG. 433. Aulostegidae (p. 605).

elongate, but with small ears at wide hinge; ventral interarea prominent, flat; shell attached ventrally; strongly uniplicate with narrow, deep ventral sulcus, high dorsal fold; spines on ventral valve only, curved forward, semirecumbent; interiors unknown. *Upper Permian (Capitanian):* Cambodia.——FIG. 434,*4a,b.* **A. thecideiformis,* Dzhulfian, Pnom Ansch; holotype, viewed ventrally, dorsally, number and repository unknown, ×6 (Termier & Termier, 1970).

Atelestegastus COOPER & GRANT, 1975, p. 828 [**A. marginatus;* OD]. Minute, attached by cicatrix, rhizoid spines; outline subcircular, rectimarginate; ventral interarea variable, commonly narrow; dorsal disk flat with short geniculate trail; cardinal process bilobed, quadrifid with short shaft; lateral ridges separate ears; dorsal muscle scars slightly raised; brachial ridges large, bounded anteriorly by row of endospines. *Lower Permian (Asselian–Sakmarian):* USA.——FIG. 434,*2a–e.* **A. marginatus,* Neal Ranch Formation, Texas; *a–c,* holotype, viewed ventrally, laterally, dorsally, USNM 154135a, ×6; *d,* ventral valve exterior, ×6; *e,* dorsal valve interior, ×6 (Cooper & Grant, 1975).

Falafer GRANT, 1972, p. 216 [**F. epidelus;* OD]. Small with sporadic ventral sulcus; ventral interarea short, flat to concave; spines few, on ventral valve only; ventral interior with broad muscle platform having median notch; dorsal interior with paired crenulated ptycholophous brachidia arching posteriorly; cardinal process slender, quadrifid. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 434,*3a–f.* **F. epidelus,* Episkope Limestone, Idhra; *a,* holotype, slightly gaping, viewed anteriorly, USNM 169763, ×6; *b,* ventral valve interior, ×6; *c,* shell exterior viewed dorsally, ×6; *d,* dorsal valve interior viewed ventrally, ×6; *e,f,* anteroventral, lateral views of dorsal valve interior, brachidium, ×6 (Grant, 1972).

Subfamily EPICELIINAE Grant, 1972

[Epiceliinae GRANT, 1972, p. 223]

Large for family; hinge narrow with small interarea; ventral spines restricted around cicatrix; brachial ridges multilobed. *Upper Permian (?Capitanian, Changhsingian).*

Epicelia GRANT, 1972, p. 223 [**E. episcopiensis;* OD]. Small, outline bilobate; ventral valve deeply sulcate with large cicatrix; spines fused together around cicatrix; dorsal valve thick, strongly emarginate, exterior with short spines and paired pits reflecting internal brachiophore platforms; cardinal process small, trifid, extending ventrally. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 435,*1a–f.* **E. episcopiensis,* Episkopi Limestone, Idhra; *a–d,* holotype, viewed ventrally, dorsally, anteriorly, laterally, USNM 169751, ×6; *e,* ventral valve interior, ×6; *f,* dorsal valve interior, ×6 (Grant, 1972).

Ceocypea GRANT, 1972, p. 225 [**C. dischides;* OD]. Ventral valve bilobate with deep sulcus; cicatrix surrounded by fine flattened spines; cardinal process small, knoblike; brachial ridges strong, indicative of ptycholophe. *Upper Permian (?Capitanian, Changhsingian):* Thailand, Pakistan, Greece.——FIG. 435,*2a–c.* **C. dischides,* Episkopi Limestone,

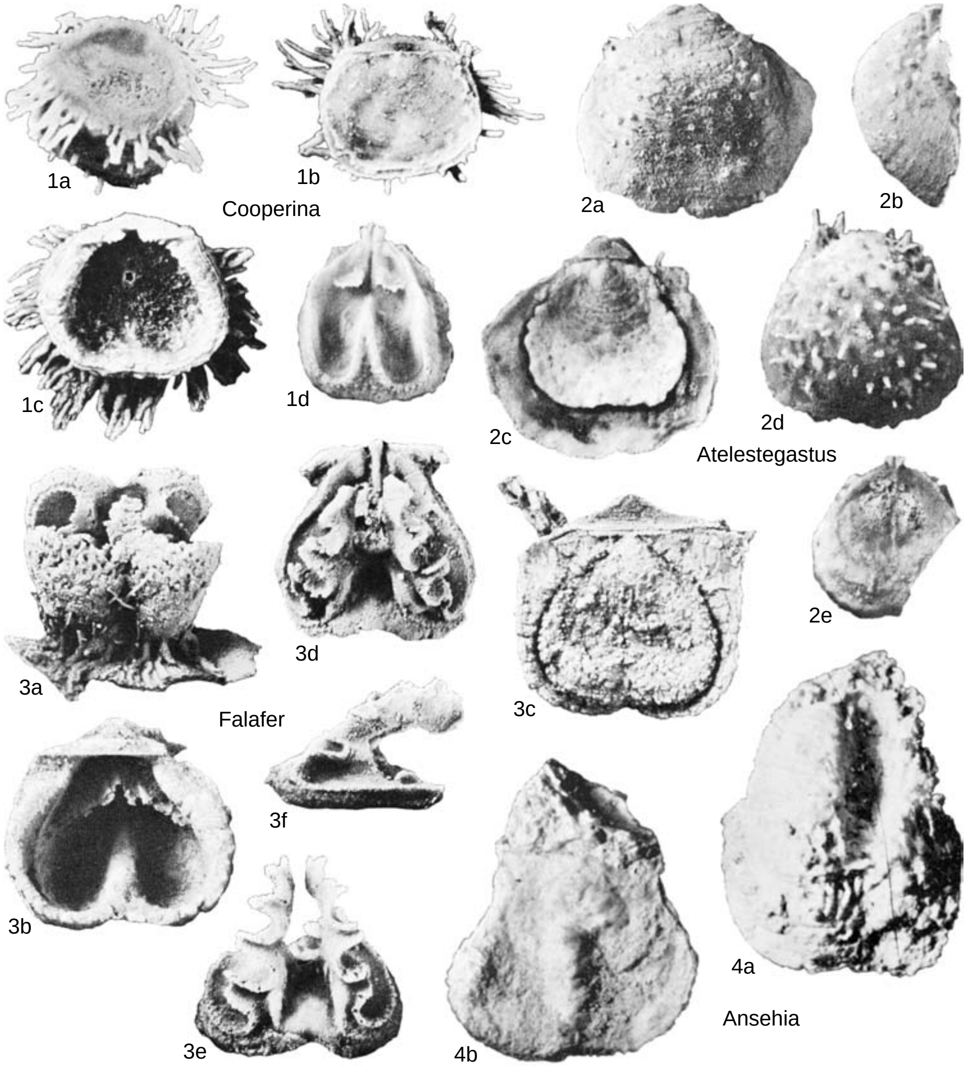


Fig. 434. Cooperinidae (p. 605–606).

Idhra; holotype, viewed ventrally, dorsally, laterally, USNM 169762, ×4 (Grant, 1972).——Fig. 435,*2d,e*. *C. chytrina* Grant, Changhsingian, Kalabagh to Wargal Limestones, Khisor Range; *d,* internal mold of ventral valve, ×4; *e,* incomplete dorsal valve interior, ×4 (Grant, 1972).

Family SCACCHINELLIDAE Licharew, 1928

[*nom. transl.* Williams, 1953b, p. 12, *ex* Scacchinellinae Licharew, 1928, p. 265]

Prominent ventral median septum, widely bilobed cardinal process. *Lower Permian–Upper Permian (Capitanian).*

Subfamily SCACCHINELLINAE Licharew, 1928

[Scacchinellinae Licharew, 1928, p. 265]

Ventral valve conical with transverse partitions apically; dorsal valve lidlike; deep corpus cavity. *Lower Permian–Upper Permian (Wordian).*

Scacchinella Gemmellaro, 1891, p. 22 (1897, p. 114) [**S. variabilis* Gemmellaro, 1897, p. 114; SD Schuchert in Schuchert & LeVene, 1929, p. 110]. Commonly deeply conical with weakly convex dorsal valve, prominent and wide ventral interarea occupying one side; spines rhizoid

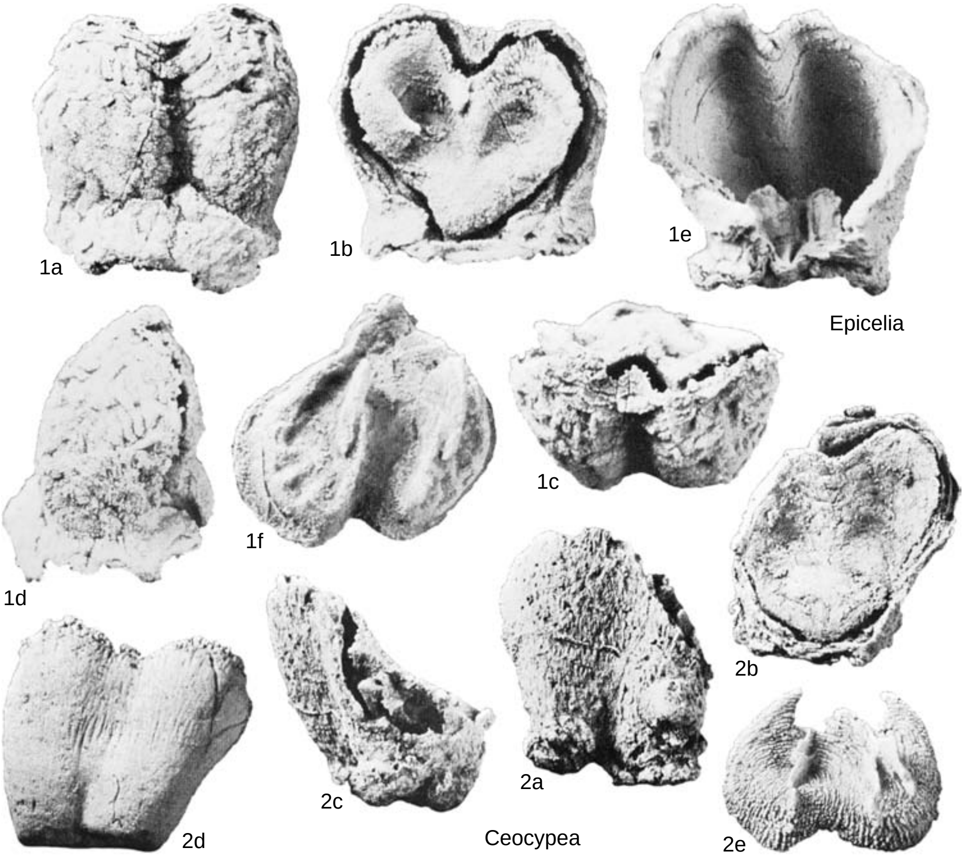


FIG. 435. Cooperinidae (p. 606–607).

ventrally, fine dorsally; dorsal adductor platforms overhang laterally. *Permian (Wordian):* North America, southern Europe, Russia.——FIG. 436,*1a.* **S. variabilis* GEMMELLARO, Sosio Limestone, Sicily; shell viewed posteriorly, ×3 (Rudwick & Cowen, 1968).——FIG. 436,*1b–d. S. americana* STEHLI, Hess Formation, Texas; *b,* attached specimen viewed anteriorly, ×1; *c,* posterior internal region of articulated valves showing cardinal process, ventral septum, ×1; *d,* dorsal valve interior, ×1.5 (Muir-Wood & Cooper, 1960).

Derbyella GRABAU, 1931, p. 269 [**D. bureri;* OD]. Poorly known, small to medium subconical outline with long, triangular ventral interarea; ribbing apparently interrupted by concentric ornament; ventral interior with median septum, myocoelidium. *Lower Permian:* Mongolia.——FIG. 436,*4a,b. *D. bureri,* Jisu Honguer Limestone, Jisu Honguer; *a,* holotype viewed ventrally, GSC 1416, ×1; *b,* holotype viewed dorsally, GSC 1416, ×2 (Grabau, 1931).

Subfamily TSCHERNYSCHEWIINAE Muir-Wood & Cooper, 1960

[Tschernyschewiinae MUIR-WOOD & COOPER, 1960, p. 126]

Concavoconvex profile; cicatrix common, plus support spines. *Upper Permian (Capitanian).*

Tschernyschewia STOYANOW, 1910, p. 853 [**T. typica;* OD]. Smaller medium size with subcircular corpus outline, short trails; cicatrix small, variable; hinge narrow with short interareas; external ornament somewhat resembling *Waagenoconcha,* but internally with high ventral median septum fitting between lobes of cardinal process. [*Septoproductus* FRECH, 1911, p. 132 (type, *Productus abichi* WAAGEN, 1884, p. 697 was misidentified by FRECH (1911) and suppression of his genus is sought; BRUNTON, 1997, ICZN Case 3034.] *Upper Permian (Capitanian):* southern Europe, China.——FIG. 436,*3a–e.* **T.*

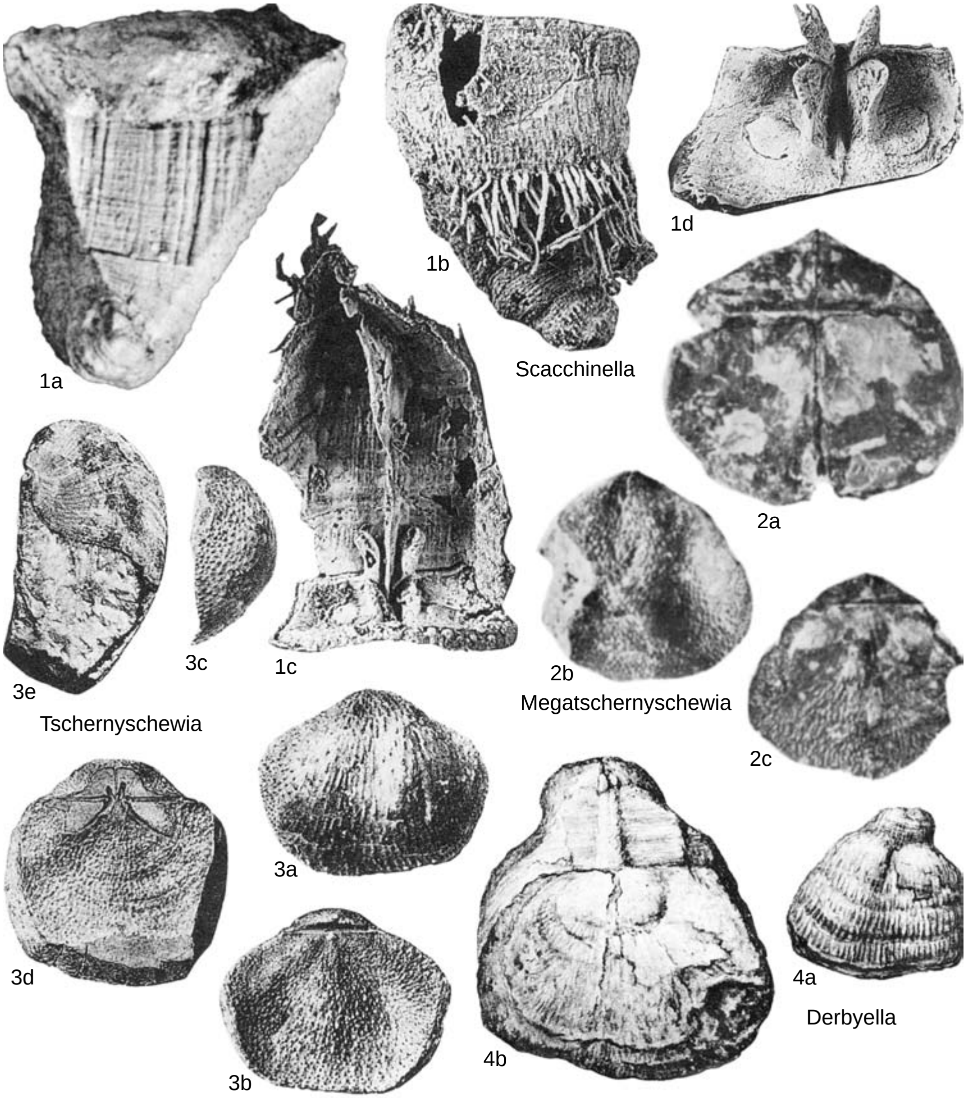


FIG. 436. Scacchinellidae (p. 607–609).

typica, Dzhulfian, Armenia; *a–c,* specimen viewed ventrally, dorsally, laterally, ×1; *d,* dorsal view of specimen cut at beak showing cardinal process, median septum, ×1; *e,* longitudinal section of specimen showing large ventral median septum, ×1 (Muir-Wood & Cooper, 1960).

Megatschernyschewia SREMAC, 1986, p. 19 [**M. longiseptata;* OD]. Similar to *Tschernyschewia,* but larger, around 40 mm wide, with longer, triangular ventral interarea. *Upper Permian (Kazanian):* Croatia.——FIG. 436,*2a–c.* **M. longiseptata,* Murghabian, Velebit Mountains; *a,* holotype, internal mold of specimen retaining pieces of shell, viewed dorsally, GPZ 1237, ×1; *b,c,* specimen viewed ventrally, dorsally, ×1 (Sremac, 1986).

RICHTHOFENIOIDEA

Bruce Wardlaw[1], R. E. Grant[2], and C. H. C. Brunton[3]

[[1]United States Geological Survey, Reston, Virginia; [2]deceased; and [3]formerly of the Natural History Museum, London]

Superfamily RICHTHOFENIOIDEA Waagen, 1885

[*nom. correct.* Brunton, Lazarev, & Grant, 1995, p. 933, *pro* Richthofeniacea Muir-Wood, 1955, p. 69, *nom. transl. ex* Richthofeniidae Waagen, 1885, p. 729]

Ventral valve conical or sphenoid, dorsal valve caplike or recessed below ventral margin; ventral valve attached to substrate directly or by rhizoid spines, or by both; interarea absent. *Upper Carboniferous–Upper Permian.*

Richthofenioids, with their coral-like appearance, are among the more unusual brachiopods but can be derived morphologically from more conventional productides. Among the Strophalosiidina there is a tendency toward long or elaborate ventral trails. Any initially attached form that continued to grow its ventral trail so as to curve up and posteriorly toward the umbo would, if rotated anteriorly and with the lateral margins of the trails fused posteriorly, display the basic shape of a richthofenioid. Just such an early richthofenioid was described as *Ardmosteges* by Sutherland (1996) from the early Upper Carboniferous Morrowan Series in Oklahoma, USA. This is the earliest known richthofenioid, and Sutherland (1996) described how a juvenile aulostegid stage with a ventral interarea grew into the adult-richthofenid conelike form with virtually no interarea showing. The juvenile shell provides good evidence for derivation from the Aulostegidae (Fig. 437).

The greatest diversification of the Richthofenioidea took place in the Permian, with steady expansion into the middle part of the period followed by decline toward the end of that period. Cooper and Grant (1975, p. 927) followed the classification by Muir-Wood and Cooper (1960) in excluding *Teguliferina* from the Richthofenioidea and placing it in the Strophalosioidea. Here it is reunited with the richthofenioids on the basis of its lack of an interarea in adults and the judgment that the cardinal process is neither sufficiently different from that of most Richthofenioidea nor sufficiently similar to that of most strophalosiidines to justify the earlier placement. As remarked by Cooper and Grant (1975), the position of *Teguliferina* in the Upper Carboniferous (Pennsylvanian) and Early Permian suggests that it may have been an ancestor of the richthofenioids. We unite *Ardmosteges* with *Teguliferina* and other teguliferines to form the stem group for the superfamily.

All richthofenioids lived attached, initially by the beak, and generally developed stabilizing spines early in their ontogeny. The rare *Collumatus* of the Texas Permian is stabilized by successive sheets of shell material rather than spines, but this is regarded as simply an aberration, not a deeply significant taxonomic character (Cooper & Grant, 1975, p. 961). *Zalvera,* after the first few mm of growth when it too resembled an aulostegid, is aspinose and appears to have been an early aberrant form.

The four families of the Richthofenioidea are separated by differing external shapes and in their ventral valve muscle attachment structures. The Gemmellaroiidae are less securely classified, having been placed at times with the orthotetidines (e.g., Williams, 1953b; Grant, 1993a) or with productides (e.g., Muir-Wood & Cooper, 1960; Muir-Wood in Moore, 1965). Discussion has centered mainly on the presence or absence of external spines; Grant (1993a) also stressed the importance of koskinoid umbonal perforations in ventral valves of *Tectarea* and *Cyndalia* in this group as well as in some orthotetidines. Williams and Brunton (1993) questioned the validity of koskinoid structures in taxonomy, and studies of *Gemmellaroia* from Italy have revealed

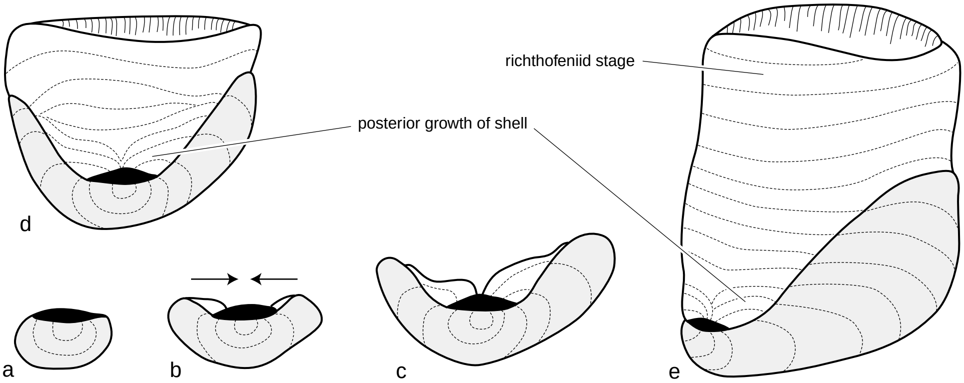


FIG. 437. *Ardmosteges orchamus* SUTHERLAND showing growth of ventral valve, viewed *a–d,* posteriorly and *e,* obliquely; early aulostegid stage *shaded;* interarea *black;* posterior growth of shell shows in early growth lines, indicated in *b* (*arrows*) and *c,* lead to posteromedian fusion dorsal to the interarea and continued annular growth formed the adult conical richthofeniid stage (*a–c,* new; *d,e,* adapted from Sutherland, 1996).

the bases of external spines. Therefore, we here include two of the four genera discussed by GRANT (1993a) as belonging to the Gemmellaroiidae; *Cyndalia* is included with less certainty; and *Loczyella* is assigned to the lyttoniidine superfamily Permianelloidea.

The rare and poorly illustrated forms *Striirichthofenia, Neorichthofenia,* and *Strophorichthofenia* are difficult to place. Both *Neorichthofenia* and *Strophorichthofenia* appear to have a ventral median septum that would place them in the Hercosiidae. The internal features of *Striirichthofenia* are not known, so it is placed with uncertainty in the Richthofeniidae, the common Asian richthofenioids.

The genus *Prorichthofenia* (KING, 1931, p. 97) based on *Crania permiana* SCHUMARD (1859, p. 395) is abandoned. SCHUMARD's specimens, lost in a fire, were never illustrated. KING (1931) placed specimens belonging to several currently recognized genera from western Texas in this genus, so it cannot be synonymized with any of them. The most abundant forms in the Glass Mountains of Texas are species of *Hercosia, Hercosestria,* and *Cyclacantharia.* KING (1931, pl. 28–30) illustrated specimens of all of them under the name *Prorichthofenia.* Details were explained by COOPER and GRANT (1975, p. 939, 963).

Family RICHTHOFENIIDAE Waagen, 1885

[Richthofeniidae WAAGEN, 1885, p. 729]

Conical, spines rhizoid, ventral myocoelidium. *Lower Permian–Upper Permian.*

Richthofenia KAYSER, 1881, p. 352 [**Anomia lawrenciana* DE KONINCK, 1863, p. 18; OD]. Aperture spines possibly similar to those of *Prorichthofenia, Hercosia, Hercosestria,* and *Cyclacantharia;* myocoelidium with three septa. *Lower Permian–Upper Permian:* Sicily, Russia, China, Japan, Pakistan, Timor.——FIG. 438,*3a–c.* **R. lawrenciana* (DE KONINCK), Pakistan; *a,* ventral valve interior with myocoelidium, ×0.85; *b,* dorsal valve exterior, ×0.85; *c,* ventral valve longitudinal section showing cystose shell structure, ×0.85 (Waagen, 1885).

Coscinarina MUIR-WOOD & COOPER, 1960, p. 138 [**Richthofenia communis* GEMMELLARO, 1894, p. 7; OD; described and illustrated by DI-STEFANO, 1914, p. 16]. Large, with cone much elongated, aperture covered by arched, reticulated meshwork of spines; myocoelidium with single septum, extending length of cup. *middle Permian:* Europe.——FIG. 438,*1a–c.* **C. communis* (GEMMELLARO), Sosio Limestone, Wordian, Sicily; *a,* dorsolateral view of large specimen, reticulate covering, ×0.85; *b,* specimen showing dorsal valve and myocoelidium, ×0.85 (Di-Stefano, 1914); *c,* dorsal valve interior, ×0.85 (Muir-Wood & Cooper, 1960).

Globosobucina WATERHOUSE & PIYASIN, 1970, p. 123 [**G. scopae;* OD]. Squat cone attached by beak and stout rhizoid spines; dorsal valve lidlike, convex, not recessed into ventral vestibule; ventral myocoelidium capacious, visible eternally, internally bilobate and containing median septum as in *Richthofenia;* dorsal interior with prominent cardinal process;

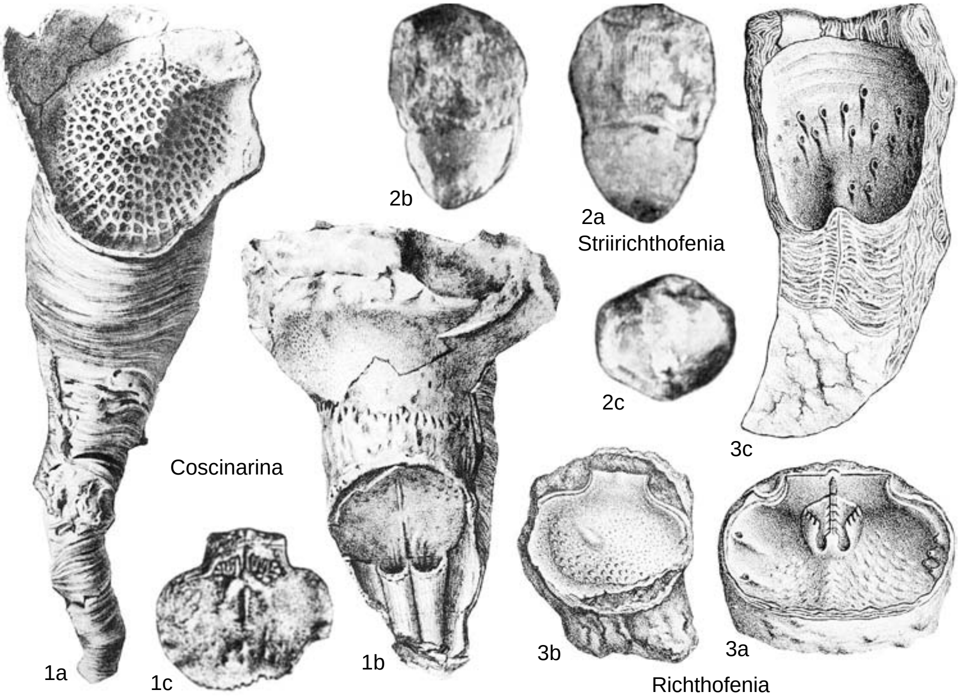


FIG. 438. Richthofeniidae (p. 611–612).

stout endospines, denticulate margin. *Lower Permian (Roadian)–Upper Permian (Wordian):* Thailand (Rat Buri).——FIG. 439,*2a–f.* **G. scopae,* holotype, UTC B538, Rat Buri Limestone; *a,* lateral view showing anterior face of ventral valve with large tubular spines, and inner surface of dorsal valve (above) bearing submarginal spines, ×1; *b,* view of internal ventral spines on anterior face of valve (below), looking through gap between two valves, ×1; *c,* posterior view of ventral valve, showing myocoelidium, growth lamellae, and tubular spines, ×1; *d,* lateral view, with dorsal valve above and ventral valve covered by tubular spines and growth lamellae, ×1; *e,f,* anterior view looking through gap between dorsal (above) and ventral valves; same view, tilted to show internal face of myocoelidium, ×1 (Waterhouse & Piyasin, 1970).

Seseloidia GRANT, 1993b, p. 10 [**S. phelbodes;* OD]. Conical, ventral valve walls thick, vesicular, with rough exterior; supporting spines few, scattered randomly; apertural spines absent; dorsal valve pustulose, resting on prominent shelf recessed within ventral aperture; hinge narrowed by proximal swellings of ventral shelf; ventral interior containing low, front-to-back swelling on floor; myocoelidium long, reaching from floor to just below hinge, containing high median septum arising from floor of myocoelidium and not reaching valve wall except at valve floor; muscle marks visible within myocoelidium; apical parts of high shells filled by cystose tissue. *Lower Permian: Verbeekina* Zone, Greece (Khios Island).——FIG. 439,*1a–d.* **S. phelbodes,* Kungurian, Khios; *a,* ventral interior showing myocoelidium and internal bases of spines, ×1.5; *b,* lateral view of juvenile with both valves, ×2; *c,d,* holotype, exterior views, side and posterior, USNM 402133, ×1 (Grant, 1993b).

Striirichthofenia LU TONG-CHEN, 1982, p. 609[611] [**S. mianchuensis;* OD]. Small, irregularly conical, base rounded, aperture widely flaring; dorsal valve lidlike, not recessed; pseudodeltidium internal, covered by outer shell layer; outer shell capillate. *Lower Permian:* China (Sichuan Province).——FIG. 438,*2a–c.* **S. mianchuensis;* Artinskian, Mianchu, Sichuan; *a,b,* anterior view, posterior view, ×1; *c,* holotype, upper view, ×1 (Lu, 1982).

Family HERCOSIIDAE
Cooper & Grant, 1975

[Hercosiidae COOPER & GRANT, 1975, p. 928]

Conical, spines rhizoid, ventral median septum. *Lower Permian–Upper Permian.*

Hercosia COOPER & GRANT, 1969, p. 7 [**Richthofenia uddeni* BÖSE, 1916; OD]. High cones, tend to cluster, mostly anchored by rhizoid spines, rarely by beak; aperture protected by spines on ventral anterior rim and complimentary long dorsal endospines,

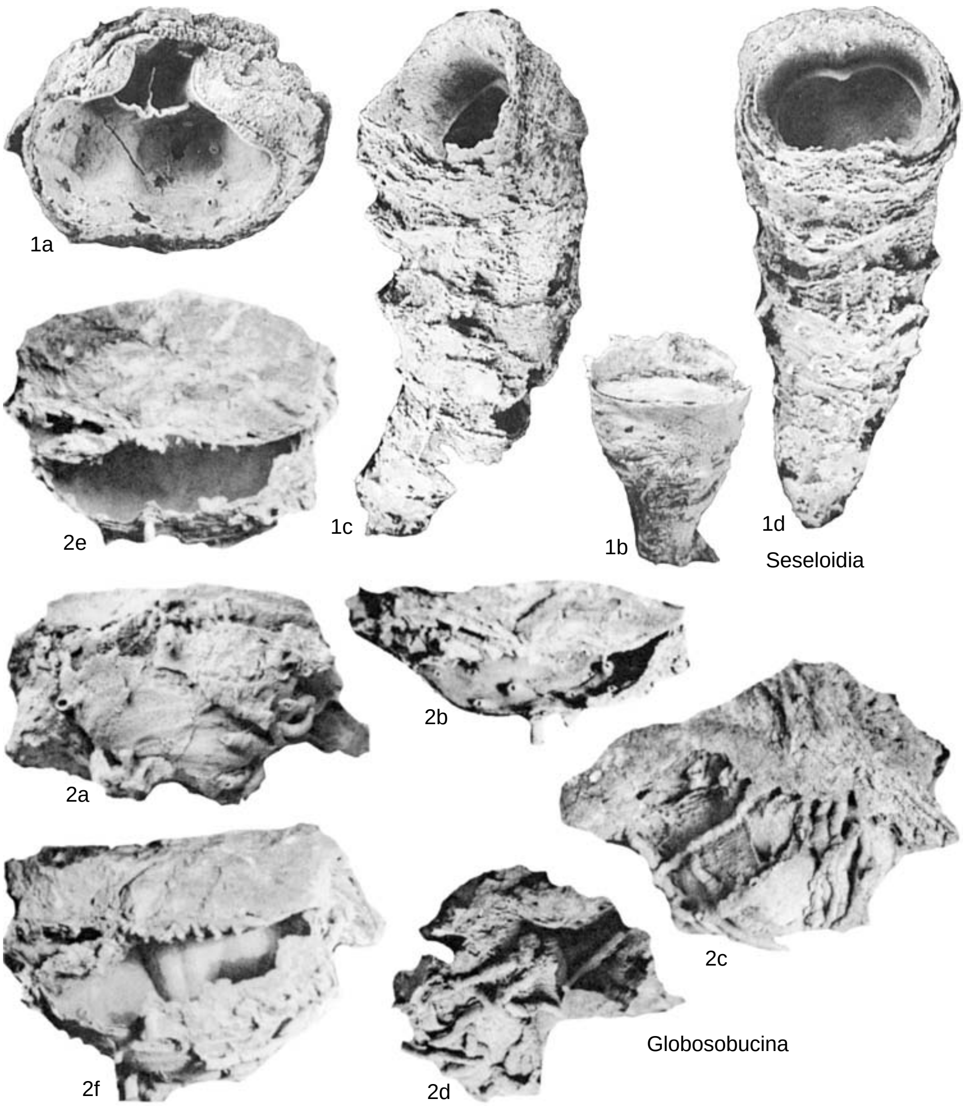


FIG. 439. Richthofeniidae (p. 611–612).

both crossing gape during feeding; ventral interior with high bladelike septum for muscle attachment in adults (juveniles have a myocoelidium as in *Richthofenia*); dorsal interior with bilobed cardinal process, visible adductor muscle marks, and aforesaid endospines. *Lower Permian (Artinskian–Kungurian):* USA (western Texas).——FIG. 440,*2a–d*. **H. uddeni* (BÖSE), Leonardian, western Texas; *a,b,* anterior, dorsal views of young adult, ×1; *c,* broken ventral valve showing median septum and growth track of hinge, ×1; *d,* interior of dorsal valve showing endospines and cardinal process, ×2 (Cooper & Grant, 1975).

Hercosestria COOPER & GRANT, 1969, p. 7 [**H. cribrosa;* OD]. Small cone tending to form clusters, hence typically distorted; attached by beak or numerous rhizoid spines; dorsal valve deeply recessed below low meshwork (coscinidium) protecting aperture (not highly domed as in *Sestropoma*); ventral interior with high, bladelike median septum; dorsal interior with all features reduced: endospines short and few, cardinal process low, short, bilobed. *Lower Permian (Artinskian–Roadian):* USA (western Texas).——FIG. 440,*3a–c*. **H. cribrosa,* Roadian, western Texas, *a,b,* side, dorsal view showing coscinidium over aperture, ×1; *c,* interior of dorsal

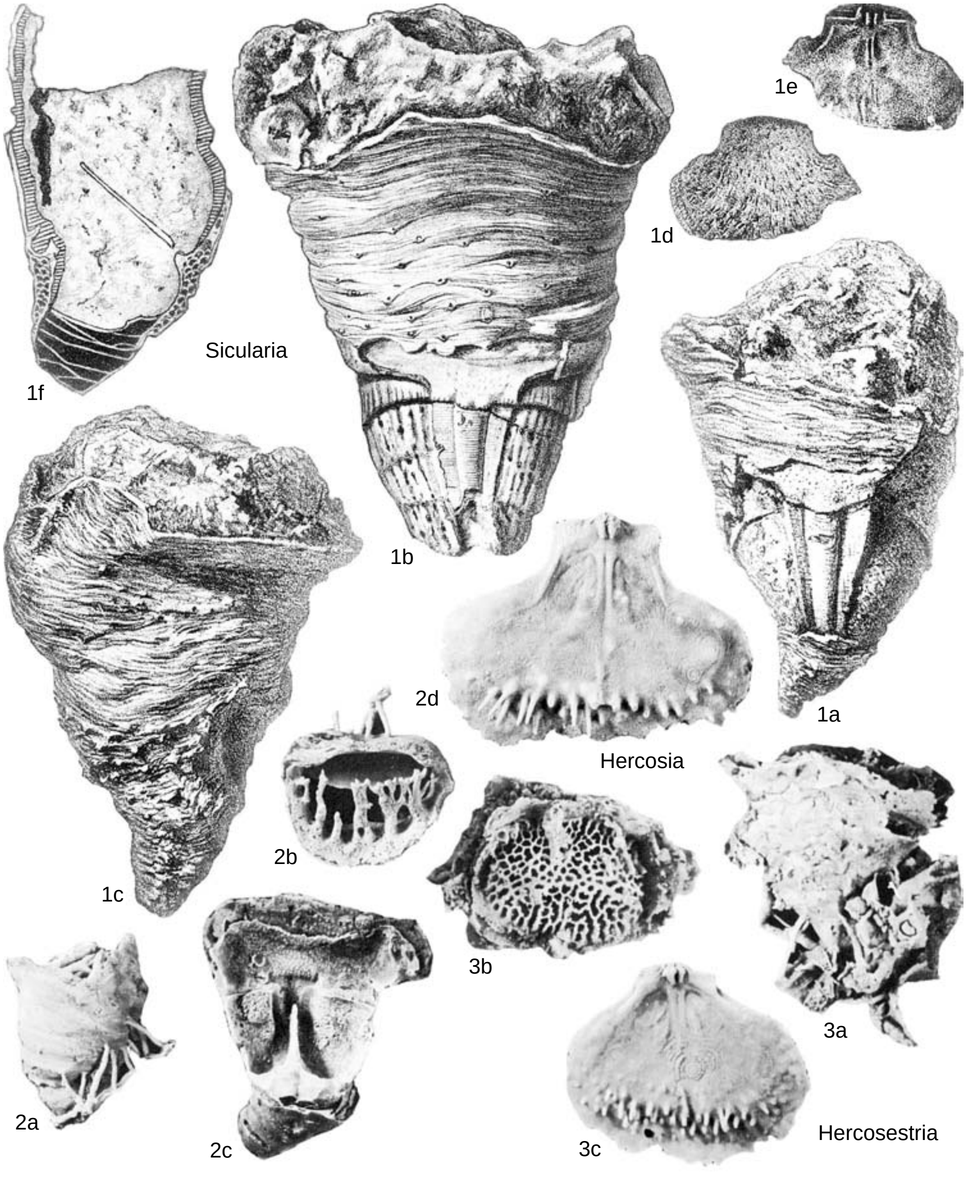


FIG. 440. Hercosiidae (p. 612–615).

valve showing lobate cardinal process and stunted endospines, ×1 (Cooper & Grant, 1969).

Neorichthofenia SHEN, HE, & ZHU, 1992, p. 180[193] [**Richthofenia mabutii* TAZAWA & ARAKI, 1984, p. 3; OD]. Ventral valve external features unknown, but anteriorly sulcate; interior has low anterior median ridge, numerous fine and irregular radial ribs on anterior sides of valves; dorsal interior with bilobed cardinal process, slender and long shafted, row of endospines two-thirds distance from posterior end. *Upper Permian (Changhsingian):* China, Japan.——FIG. 441,*2a–d*. **N. mabutii* (TAZAWA & ARAKI), Kanokura Formation, Kitakami Mountains, Japan, internal mold of conjoined valves; *a,* dorsal valve interior, ×2; *b–d,* ventral valve interior viewed anteriorly, posteriorly, ventrally, ×2 (Tazawa & Araki, 1984).

Sicularia GRANT, 1993b, p. 11 [**Richthofenia sicula* GEMMELLARO, 1894, p. 7; described and illustrated by DI-STEFANO, 1914, p. 22]. Conventionally conical richthofenioid lacking either coscinidium or, in adults, myocoelidium, but having long, low, thin median septum along inside of posterior wall of ventral valve. *Lower Permian–Upper Permian:* Sicily.——FIG. 440,*1a–f.* **S. sicula* (GEMMELLARO), Wordian, Sosio Limestone, Sicily; *a,* posterior view with exfoliated valve revealing internal trace of muscle field, ×1; *b,* posterior view, ×1; *c,* anterior view, ×1; *d,e,* external, internal view of dorsal valve, ×1; *f,* longitudinal section showing low median septum and dorsal valve, ×1 (Di-Stefano, 1914).

Strophorichthofenia TERMIER & others, 1974, p. 123 [**S. afghana;* OD]. Small, conical ventral valve with flat dorsal valve resting just below ventral margin (opercular); both valves with low median septa; ventral valve with scattered rhizoid spine bases, large cicatrix of attachment, growth lines, and rugae. *Upper Permian (Kazanian):* Afghanistan.——FIG. 441,*1.* **S. afghana,* lower Murghabian, Wardak, central Afghanistan; holotype, posterior view of complete specimen, ×2 (Termier & others, 1974).

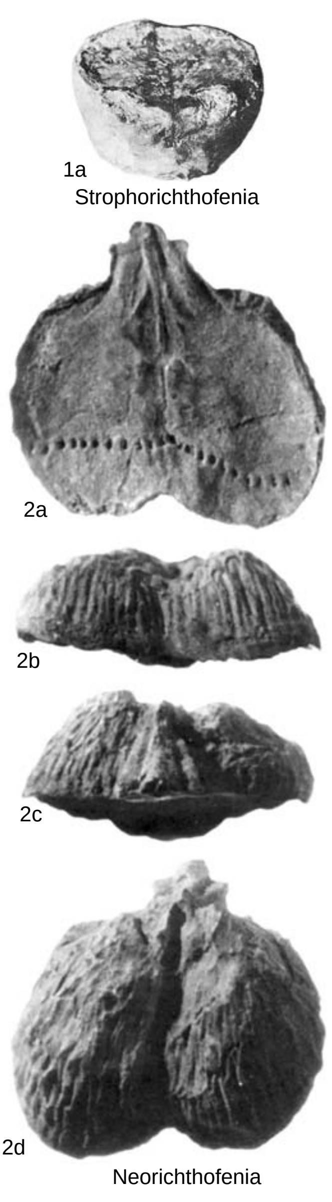


FIG. 441. Hercosiidae (p. 614–615).

Family CYCLACANTHARIIDAE Cooper & Grant, 1975

[Cyclacanthariidae COOPER & GRANT, 1975, p. 938]

Conical, spines rhizoid or absent, ventral muscle callosity. *Upper Carboniferous (Bashkirian)–Upper Permian (Capitanian).*

Subfamily CYCLACANTHARIINAE Cooper & Grant, 1975

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 933, *ex* Cyclacanthariidae COOPER & GRANT, 1975, p. 938]

Conical, with coscinidium or rim of protective spines; no rhizoid spines in *Collumatus. upper Lower Permian (Roadian)–Upper Permian (Capitanian).*

Cyclacantharia COOPER & GRANT, 1969, p. 7 [**C. kingorum;* OD]. High cone, commonly distorted by clustering; variably flared rim entirely surrounded by medianly directed protective spines; ventral valve attached by beak and many anchoring spines; ventral interior with thickened muscle area but no septa; dorsal interior with small bilobed cardinal process and few long stout endospines that cross ventral spines to protect during feeding. *Permian (Wordian):* USA (western Texas).——FIG. 442,*1a–d.* **C. kingorum,* Word Formation, western Texas; *a,* dorsal valve exterior, ×1; *b,* dorsal valve interior showing endospines, ×1; *c,d,* holotype, side and dorsal (apertural) views, USNM 153831, ×1 (Cooper & Grant, 1969).

Collumatus COOPER & GRANT, 1969, p. 6 [**C. solitarius;* OD]. Small squat cone of solitary habit, attached by base and concentric sheets of shelly tissue, lacking supporting spines; coscinidium of coarse meshwork of flattened anastomosing spines; ventral interior with low adductor thickening and flabellate diductor scars; dorsal interior with short bilobed cardinal process and dendritic adductor scars. *upper Lower Permian (Roadian):* USA (western Texas).——FIG. 442,*2a–f.* **C. solitarius,* Roadian, western Texas; *a–e,* holotype, side, posterodorsal, ventral, anterior, posterior views, USNM 153548a, ×2; *f,* dorsal oblique view into open shell showing dorsal valve interior with small cardinal process, ×1 (Cooper & Grant, 1974).

Sestropoma COOPER & GRANT, 1969, p. 8 [**S. cribriferum;* OD]. Variably conical, ventral valve long and tapering to short and squat; marginal rim narrow or flared; coscinidium highly arched with

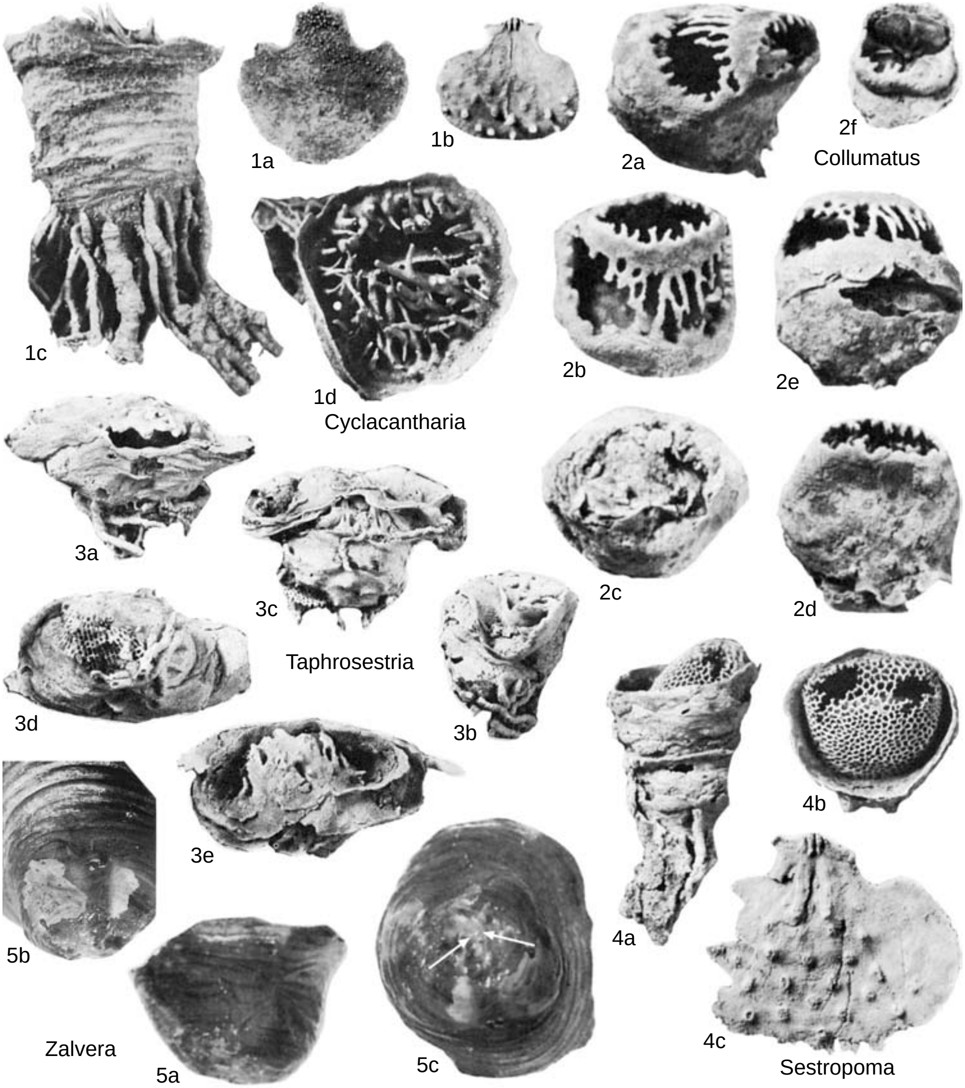


FIG. 442. Cyclacanthariidae (p. 615–617).

profile reflecting exactly the sweep of dorsal valve opening and remaining at full gape; general aspect like *Hercosestria* but with more regular and higher coscinidium, and lacking internal median septum. *Upper Permian (upper Wordian–Capitanian):* USA (western Texas), Mexico.——FIG. 442,*4a–c*. **S. cribriferum,* upper Wordian–Capitanian, western Texas; *a,b,* side, dorsal (apertural) views showing thick rhizoid spines and strongly elevated and rounded coscinidium over aperture, ×1; *c,* interior of dorsal valve, ×3 (Cooper & Grant, 1969).

Taphrosestria COOPER & GRANT, 1975, p. 954 [**T. peculiaris;* OD]. Squat cone with flaring marginal rim; external surface strongly rugose and squamose; attached at base and stabilized by strong spines of circular cross section; dorsal valve deeply recessed, protected by coscinidium of flattened anastomosing spines; ventral interior without septa but thickened muscle field showing attachment scars; dorsal interior nearly smooth, without endospines, brachial ridges rarely visible; cardinal process short, bilobed; muscle field thickened slightly. *upper Lower Permian (Roadian):* USA (western Texas).——FIG. 442,*3a–e*. **T. peculiaris,* Road Canyon Formation, western Texas; anterior, lateral, posterior, ventral, dorsal views, ×1 (Cooper & Grant, 1975).

Subfamily TEGULIFERININAE Muir-Wood & Cooper, 1960

[*nom. transl.* BRUNTON, LAZAREV, & GRANT, 1995, p. 933, *ex* Teguliferinidae MUIR-WOOD & COOPER, 1960, p. 92]

Sphenoid (obliquely conical), spines rhizoid; no coscinidium. *Upper Carboniferous (Bashkirian)–Lower Permian, ?Upper Permian.*

Teguliferina SCHUCHERT & LEVENE, 1929, p. 121, *nom. nov. pro Tegulifera* SCHELLWIEN, 1898, p. 362, *non* SAALMÜLLER, 1880 [**Tegulifera deformis* SCHELLWIEN, 1898, p. 362; OD]. Low oblique cone (sphenoid); ventral surface wrinkled and irregular; attached by ventral beak, anchored by strong circular or flattened spines reinforced by connecting shelly tissue; anterior edge of ventral cup bearing inwardly pointing protective spines; ventral interior with slightly thickened muscle field but no septa; dorsal interior with short bilobate cardinal process, each lobe with pit for diductor attachment; hinge narrow, with short articulating knob on each side; brachial ridges visible on some specimens. *Upper Carboniferous (Bashkirian)–Lower Permian, ?Upper Permian:* Yugoslavia, Japan, China, Russia, Ferghana, USA (Kansas, western Texas).——FIG. 443,*1a,b.* **T. deformis* (SCHELLWIEN), Lower Permian, Yugoslavia; *a,* dorsal valve exterior, elongate ventral valve above, ×1; *b,* dorsal valve internal mold, ×2 (Schellwien, 1898).

Acritosia COOPER & GRANT, 1969, p. 5 [**A. magna;* OD]. Low conical, oblique in youth, becoming more symmetrical with growth; ventral cup margin flared, bearing inwardly directed protective spines only anteriorly; valve attached by rhizoid spines of circular cross section; ventral interior without septum but with low median myophragm; dorsal muscle area slightly thickened; cardinal process short, erect; hinge apical; endospines few, stout. *Lower Permian:* USA (Texas).——FIG. 443,*2a,b.* **A. magna,* Lower Permian, western Texas; holotype, lateral view, dorsal view showing open dorsal valve in attached position (*arrow*), USNM 151739a, ×1 (Cooper & Grant, 1969).

Ardmosteges SUTHERLAND, 1996, p. 8 [**A. orchamus;* OD]. Sphenoid ventral valve having an early aulostegid growth stage with interarea closed by elytridium and lophidium, followed by a richthofeniid growth stage of progressive fusion of ventral valve posteriorly and dorsal to interarea, developing into a richthofeniid-like cone anchored by rhizoid spines. *Upper Carboniferous (Bashkirian):* USA (Oklahoma).——FIG. 443,*3a–c.* **A. orchamus,* holotype, OU 10260, upper Morrowan, Oklahoma; *a,* posterior view showing growth lines indicating infilling of shell above interarea (*arrow,* ventral valve broken laterally), ×2; *b,* dorsal view showing tilted dorsal valve in partly open position and protective endospines most frequently on anterior side, ×2; *c,* lateral view with juvenile spinose aulostegid stage below, ×2 (Sutherland, 1996).

Planispina STEHLI, 1954, p. 331 [**P. conida;* OD]. Similar to *Teguliferina,* but attachment spines fused together and to sides of cup by flat shelly tissue; anterior margin of cup with long protective spines. *Upper Carboniferous–Lower Permian:* North America.——FIG. 443,*8a–c.* **P. conida,* Lower Permian, western Texas; *a,* holotype, lateral view showing nested cones and flattened spines, AMNH 27313/1:1, ×1; *b,* ventral valve interior showing a few large protective spines, ×1; *c,* dorsal valve interior showing cardinal process, median ridge, and marginal endospines, ×1 (Stehli, 1954).

Proteguliferina LICHAREW in SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960, p. 236 [**Tegulifera rossica* IVANOV, 1925, p. 111; OD]. Similar to *Teguliferina* but spines along periphery of both valves, rudimentary ventral interarea covered by hoodlike later shell tissue; dorsal valve less deeply inserted. *Upper Carboniferous–Lower Permian:* Russia (Moscow basin, Donetz Basin), ?North America.——FIG. 443,*7a,b.* **P. rossica* (IVANOV), Upper Carboniferous, Moscow basin; *a,* dorsal view of complete shell with hood concealing ventral interarea, ×1; *b,* interarea exposed by removal of hood, ×1 (Ivanov, 1925).

Subfamily ZALVERINAE Brunton, 1996

[*nom. transl.* WARDLAW, GRANT, & BRUNTON, herein, *ex* Zalveridae BRUNTON, 1996, p. 53]

Conical, no external or apertural spines, and weakly attached. *Upper Carboniferous (Bashkirian–Moscovian).*

Zalvera BRUNTON, 1996, p. 53 [**Z. sibaica;* OD]. No external body spines or ventral marginal protective structures; broad rugae irregular; dorsal valve deep within ventral cone, corpus cavity shallow; short, subparallel, internal ventral ridges (*arrows*) associated with chamber near apical area involved in articulation of valves. *Upper Carboniferous (Bashkirian–Moscovian):* Russia (Urals), ?northern Spain.——FIG. 442,*5a–c.* **Z. sibaica,* Upper Bashkirian–lower Moscovian, Ural River; holotype, anterior, apical oblique, apical views, BMNH BD9653, ×1.5 (Brunton, 1996).

Family GEMMELLAROIIDAE Williams, 1953

[Gemmellaroiidae WILLIAMS, 1953b, p. 10]

Conical, with long ventral interarea; spines few, on ventral valve only or absent; dorsal valve caplike; ventral myocoelidium present. *Lower Permian–Upper Permian.*

Gemmellaroia COSSMANN, 1898, p. 77, *nom. nov. pro Megarhynchus* GEMMELLARO, 1894, p. 7, *non* DE LAPORTE, 1832 [**Megarhynchus marii* GEMMELLARO, 1894, p. 7; SD MABUTI, 1937, p. 16] [=*Megalorhynchus* DE GREGORIO, 1930, p. 23 (*errore pro Megarhynchus); Gemmellaroiella* MABUTI, 1937, p. 16 (type, *G. ozawai*)]. Exterior rugose and finely

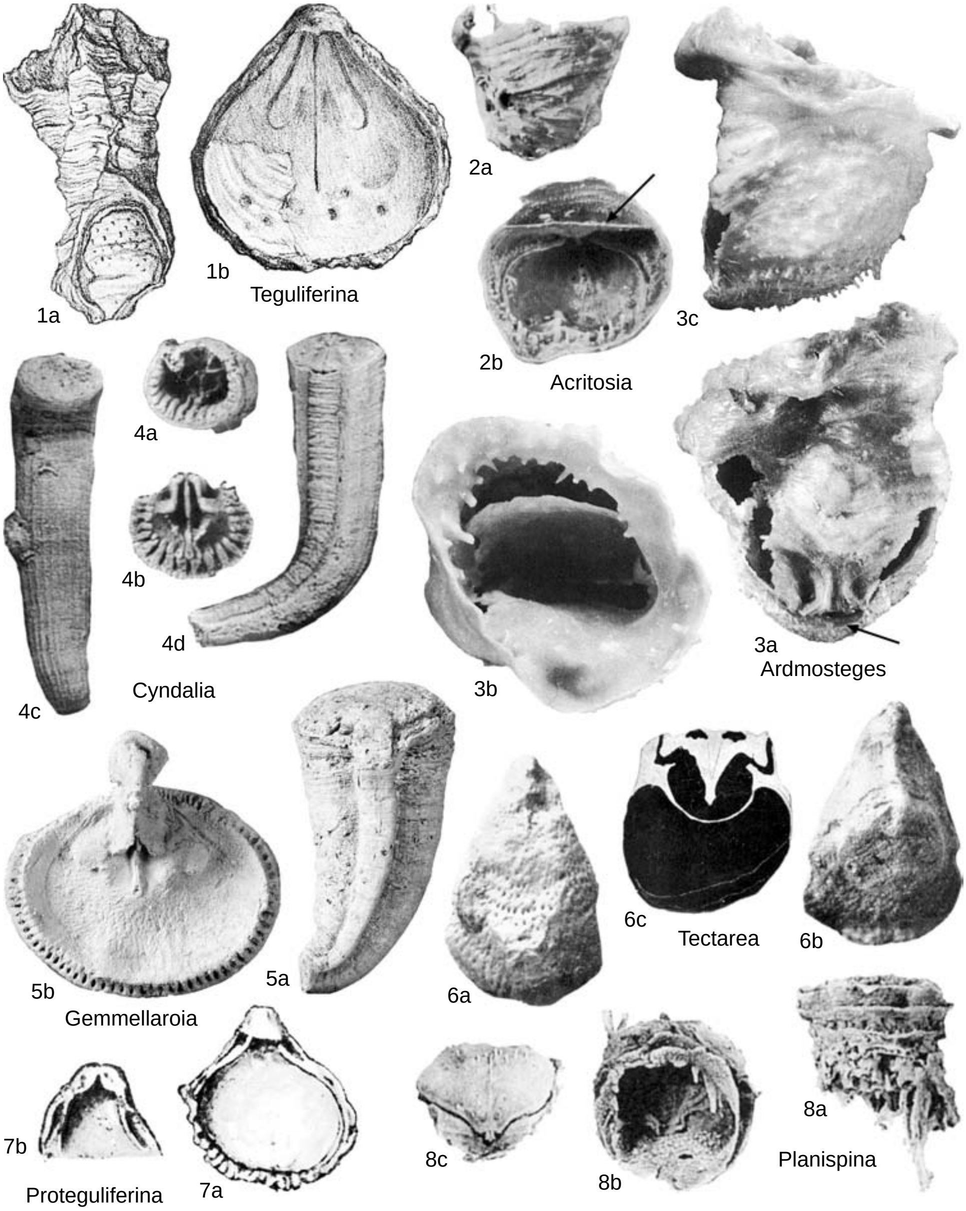


FIG. 443. Cyclacanthariidae and Gemmellaroiidae (p. 617–619).

spinose; myocoelidium long, anteriorly grooved and having internal median septum; internal margins of both valves denticulate. *Lower Permian–Upper Permian:* Europe, Asia.——FIG. 443,*5a,b.* **G. marii* (GEMMELLARO), Sosio Limestone, ?Kazanian, Sicily; *a,* posterior view showing conical ventral valve with pseudodeltidium and lidlike dorsal valve, ×1; *b,* dorsal valve interior with cardinal process and denticulate margin, ×2 (Gemmellaro, 1897).

Cyndalia GRANT, 1993a, p. 55 [**C. rudistiformis;* OD]. Minute, high conical shells with interarea and prominent convex pseudodeltidium extending from umbo to commissure; subcircular dorsal valve with weak radial costae; ventral costae weak; cicatrix apical, small, no spines recorded; teeth peglike and with myocoelidium; cardinal process lobes separated medianly, but continuous with sockets, prominent median septum and strong marginal crenulations; valve walls thick. *Upper Permian (?Capitanian, Changhsingian):* Greece.——FIG. 443,*4a–d.* **C. rudistiformis,* Capitanian, Episcopi Limestone, Hydra; *a,* ventral interior showing teeth, ×4; *b,* dorsal valve interior, ×6; *c,* holotype, anterior view of complete shell, USNM 460380, ×4; *d,* posterior view of complete shell, ×4 (Grant, 1993a).

Tectarea LICHAREW, 1928, p. 268 [**T. robinsoni;* OD]. Probably attached by umbo; exterior usually decorticated, probably capillate with intervening radially arranged pits; myocoelidium long, without septum or anterior groove, may be filled with secondary deposit; each valve with toothlike process and socket articulating with similar structures on other valve. *Lower Permian:* Europe (Caucasus).——FIG. 443,*6a–c.* **T. robinsoni; a,b,* ventral, dorsal views of specimen, ×3; *c,* transverse section showing cardinal process and myocoelidium, ×3 (Licharew, 1928).

LYTTONIIDINA

ALWYN WILLIAMS,[1] DAVID A. T. HARPER,[2] and R. E. GRANT[3]

[[1]The University of Glasgow; [2]University of Copenhagen; and [3]deceased]

Suborder LYTTONIIDINA new suborder

[Lyttoniidina WILLIAMS, HARPER, & GRANT, herein] [=Oldhaminidina WILLIAMS, 1965f, p. 510, *nom. nov. pro* suborder Oldhaminoidea WILLIAMS, 1953c, p. 286]

Grossly inequivalve productide brachiopods with the smaller dorsal valve consisting mainly of lobate brachidial plate; lacking rhizoid spines but rarely with spinose projections at ventral margin; ventral valve lacking interarea but with variably developed and disposed posterior flap of shell; hinge line normally covered by ventral shell, articulatory structures ill defined; secondary shell layer pseudopunctate. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

The morphology and classification of the lyttonioid brachiopods warrant a full discussion. Although vaguely suggestive of a strophalosiidine ancestry, the morphology is so bizarre as to continue to defy any confident interpretation of its details. This is true not only of certain morphological features of both valves but also of the shell structure and growth of the valves themselves. Consequently, the interpretation of shell morphology and the classification presented here, although benefitting from much new data since publication of the last *Treatise* account of the group (WILLIAMS, 1965f, p. 511–521), may yet undergo fundamental revision.

The shells are functionally bivalved, with the inner surface of the ventral valve everywhere extending well beyond the edge of the dorsal valve so that some of the ventral mantle margin, despite evidence for retractability, must have been permanently exposed during life. Moreover, the significantly smaller dorsal valve generally has a highly lobate outline resembling that of a ptycholophous lophophore, which led TERMIER and TERMIER (1949b) to postulate that the exposed part of the valve is a brachidium.

There is another line of evidence that supports this interpretation. The shell structure of the ventral valve is pseudopunctate, with a thin primary layer orthodoxly forming the entire outer surface of the valve (Fig. 444), which is characteristically ornamented by growth banding, growth disturbances, and evidence of shell repair.

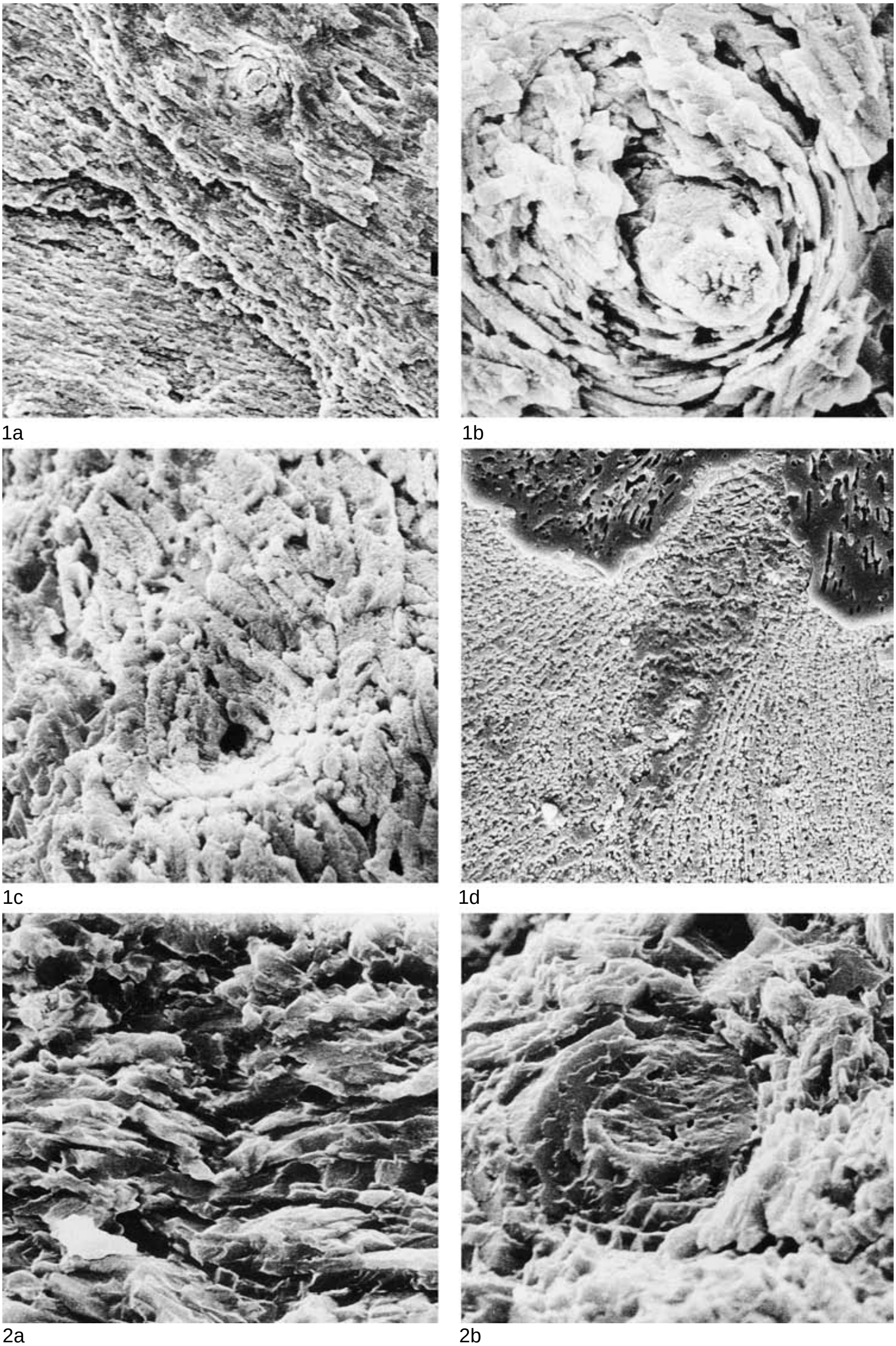


FIG. 444. *See explanation on facing page.*

In the structure generally identified as the dorsal valve, however, the primary layer is absent except for a small, posteriorly located, triangular area (Fig. 445) termed the false interarea by Rudwick and Cowen (1968). The rest of the valve is made up exclusively of secondary pseudopunctate calcite (Fig. 444.1a–c) so that *both* external and internal surfaces are pierced by taleolae to give a finely tuberculate appearance identical with that of the ventral internal surface (Williams, 1953c, 1973). It can be demonstrated in other articulated brachiopods that structures like lophophore supports that are composed only of secondary shell were secreted within invaginations of outer epithelium independent of the mantle edge. Consequently it was assumed that the part of the lyttonioid dorsal valve that is also composed only of secondary shell was not an exoskeletal cover but an internal skeletal support (internal plate) to a highly lobate mantle infold (Williams, 1953c). The assumption is confirmed by sections of internal plates. They show distinct pseudopunctate layers characterized by taleolae pointing ventrally and dorsally and separated by a thin brachiotest (Fig. 446.1). According to this interpretation, the true dorsal valve is vestigial, being represented by the false interarea composed of both outer primary shell and the inner secondary layer forming the cardinal process lobes and the posteromedian part of the articulatory device.

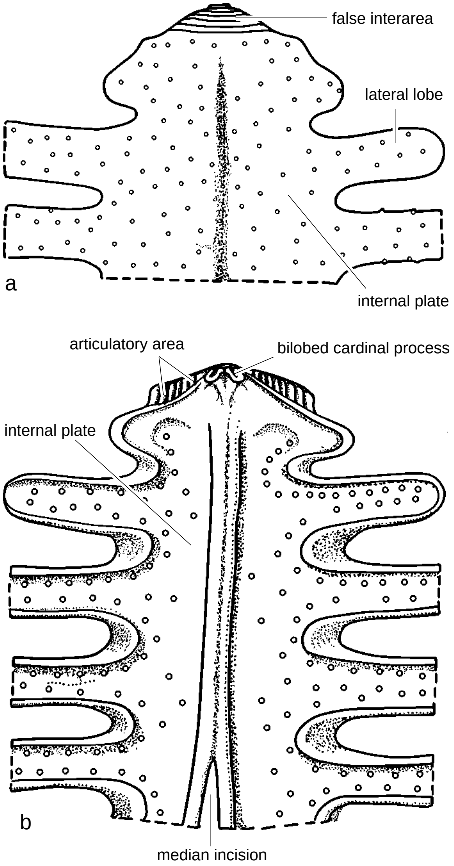


Fig. 445. Dorsal valve with internal plate of *Eolyttonia* sp., Permian, Texas; *a,* external and *b,* internal views (adapted from Williams, 1953).

The subsequent discovery by Grant (1972) of a calcified ptycholophous brachidium, arising from the floor of the dorsal valve of the strophalosioid *Falafer* and resembling the lobate dorsal valves of early stocks as well as immature lyttonioids, appears to confirm the interpretation of Termier and Termier (1949b) and Williams (1953c). By imparting rigidity to an investing infold of the mantle, the inferred internal plate could have given support to the lophophore. Immature specimens of the earliest-known lyttonioid, *Poikilosakos,* possess a subcircular internal

Fig. 444. Microstructure of lyttonioid shell; *1a–d, Oldhamina decipiens* (de Koninck), Permian, Salt Range, Pakistan; *1a,* general internal view (×300) of exfoliated lobe of dorsal valve showing pseudopunctae facing internally in upper right hand sector of micrograph and internal base of pseudopuncta facing externally in midregion along bottom with *1b,* another pseudopuncta, ×1400, *1c,* base of pseudopuncta, ×1300, and *1d,* etched resin-mounted section of pseudopuncta, ×3000; *2a,b,* fracture sections of ventral valve of *Poikilosakos petaloides* (Watson), upper Pennsylvanian, Kansas; *2a,* section showing thin primary layer along top, succeeded inwardly by laminae of secondary layer, ×1800; *2b,* core of pseudopuncta, ×2300 (new).

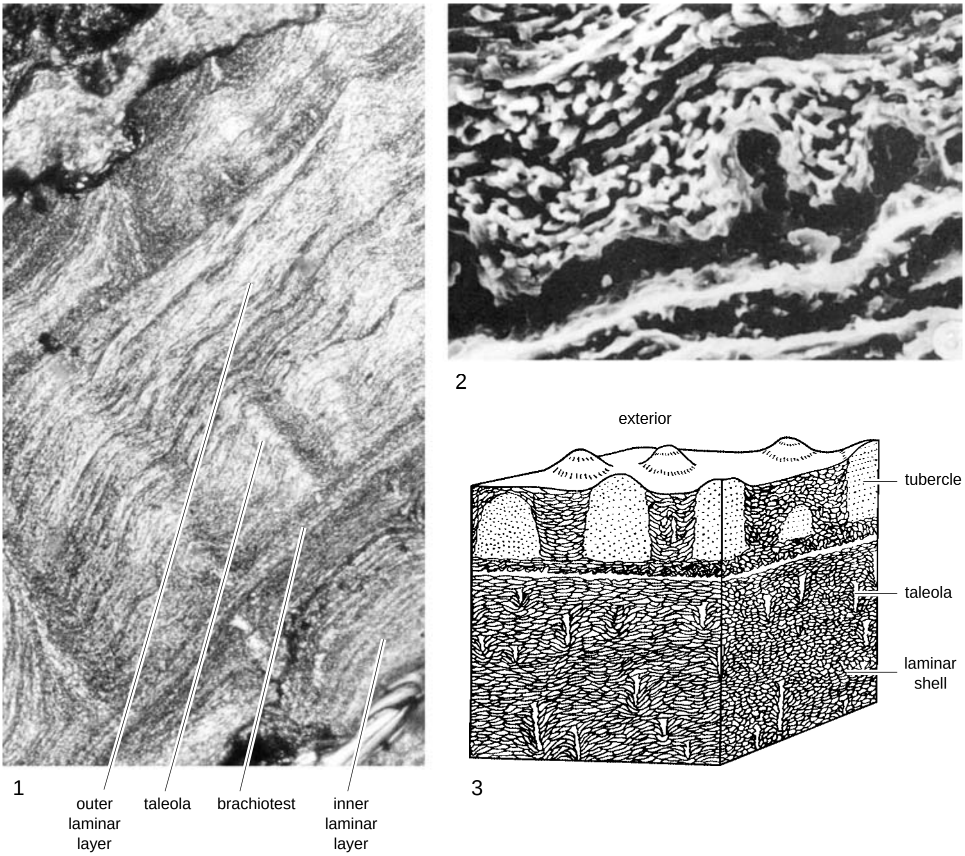


FIG. 446. *1,* Cellulose acetate peel of etched, resin-mounted section of dorsal valve of *Oldhamina decipiens* (DE KONINCK), Permian, Salt Range, Pakistan, showing brachiotest separating outer and inner laminar layers with taleolae, ×100 (new); *2,* SEM of section showing crenulated surfaces delineating interperiostracal gap (see FIG. 451) within ventral valve of *Dicystoconcha lapparenti* TERMIER & others, ×2300, Lower Permian, China; *3,* block diagram illustrating shell structure of permianellid (Wang & Jin, 1991).

plate with a median incision. Assuming the lophophore to have arisen from the mantle infold just within the edge of such a plate, it would have resembled the schizolophe; and with the development of lateral lobes to the internal plate, the feeding apparatus would have been transformed into a ptycholophe (Fig. 447).

The assumption that lyttonioid shells are virtually univalves in skeletal structure is by no means universally accepted. STEHLI (1956), for example, preferred to ascribe the anomalous distribution of primary shell to a physiological malfunction in an otherwise normally growing valve. The mantle lobes that are ultimately responsible for the growth of the shell are, however, differentiated from the same rudimentary mantle ring in living larvae; and, if this were also true for lyttonioid brachiopods, a fundamental difference in the shell structure of normally growing valves could hardly have arisen. Others, like G. A. COOPER (COOPER & GRANT, 1974, p. 384), have also continued to use dorsal or brachial valve for the entire dorsal structure purely on morphological grounds. The false interarea, although reminiscent of an obsolescent interarea and chilidium, however, is not homologous with them because growth was in an anterodorsal

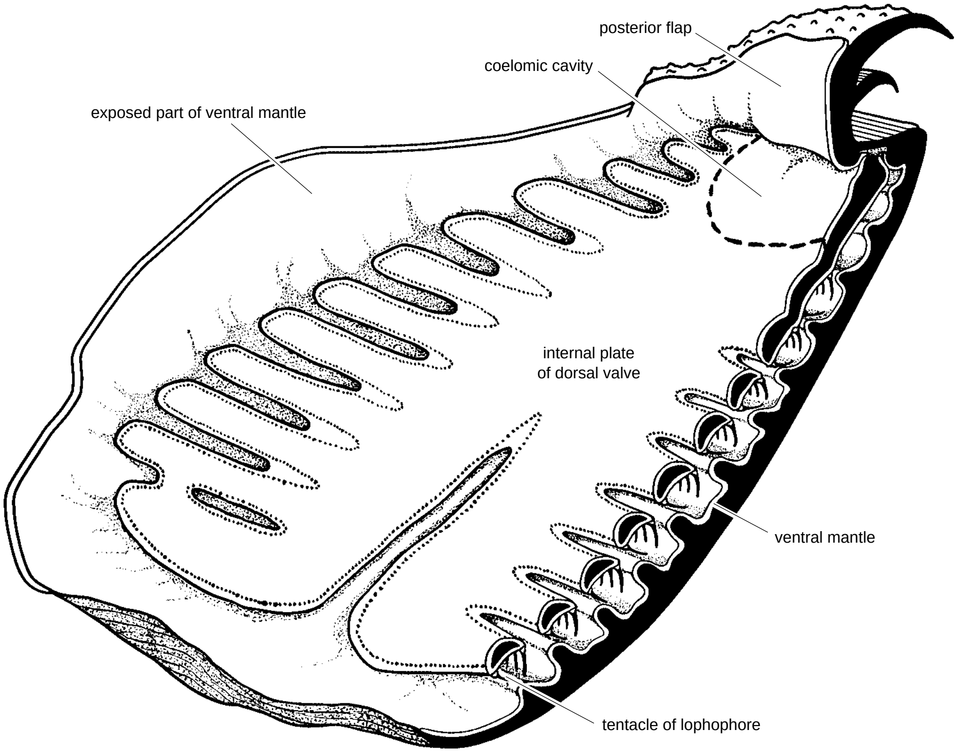


FIG. 447. Submedian view of *Eolyttonia* sp., Permian, Texas, reconstructed to show relationship between mantle lobes and shell (*solid black*) (Williams, 1953).

direction away from the cardinal process in a manner suggesting that expansion was controlled by a mantle edge coincident with the base of the triangle (WILLIAMS, 1953c).

The external and internal surfaces of the dorsal valve of permianellids are also tuberculate in a manner indicating that the valve is structurally homologous with that of lyttonioids and is likewise interpreted as an internal plate.

The morphology of the posterior part of the lyttonioid ventral valve is, in some respects, as anomalous as the structure of the dorsal valve. There is no interarea, but the posterior part of the ventral valve is extended anterodorsally as a flap (posterior flap) to overlie the dorsal valve, which is accommodated by a triangular impression (Fig. 448). This impression is also ornamented by growth lines parallel with the base and probably represents a zone of the posterior flap where secondary shell deposition was inhibited by the pressure of the heavily rutted periostracal cover to the dorsal valve. The flap is almost invariably sharply reflexed (reflexed zone) just anterior of the base of the impression and its attitude and shape can vary considerably. Specimens attached to a regular surface possess a flap that resembles a pair of ears extending laterally from the median reflexed area; in those that lay free on the sea floor throughout most of their lives the flap is greatly extroverted, so that the distal edge is usually in contact with the external surface of the ventral valve (Fig. 449); in those attached to irregular surfaces or crinoid stems the flap is closely adherent and molded to the substrate (Fig. 448); and, in at least two distinct stocks, *Keyserlingina* and *Pirgulia,* the flap grew forward with the rest of the ventral valve to form a deep cone (Fig. 450).

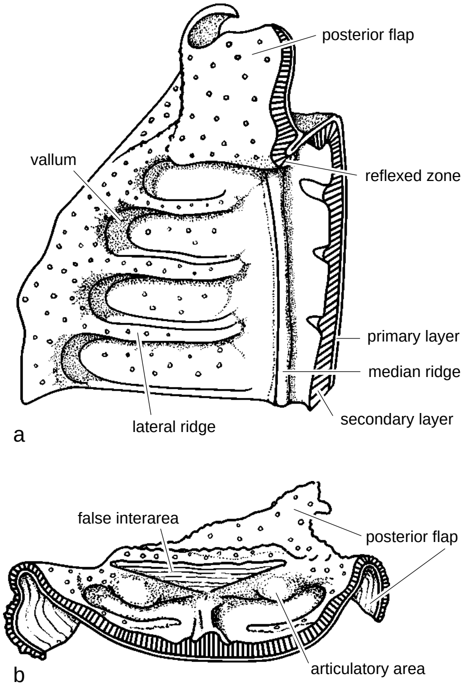


Fig. 448. Apical part of ventral valve of *Eolyttonia* sp., Permian, Texas, showing main morphological and structure features in *a,* submedian and *b,* anterior views (Williams, 1953).

Subsequent to the settling of spats, presumably by cementation of the apex of the ventral valve, the posterior flap assisted in fixation, as is well seen in lyttonioids attached to crinoid stems. It is envisaged as having been deposited by a posterior extension of the outer mantle lobe, capable of a rapid deposition of periostracum containing adhesive polymers and a thin film of shell. Evidently secretion by an extensible flap of the outer mantle lobe could be quickly terminated and the lobe then retracted along a rapidly exuded membrane in the manner of living species (Williams, 1971). Such retractions in quick succession would account for posterior flaps composed of paper-thin layers of shell consisting of both primary and secondary calcite that were commonly plastered one on top of another (Fig. 449).

The morphology of the permianellid ventral valve is not yet well known, but an everted posterior flap that assisted in attachment but without a strongly developed reflexed zone appears to have been characteristic of this group. The shell structure, however, appears to be identical with that of the dorsal valve. In effect the exteriors of both valves of permianellids are tuberculate and the entire shell has been interpreted as consisting of an outer tuberculate and an inner pseudopunctate zone with constituent tubercles and taleolae emerging at the external and internal surfaces respectively (Wang & Jin, 1991, p. 488) (Fig. 446.3). The tubercles are deeply embedded in laminar shell, which is disposed around them in the same way as laminae are around taleolae. The tubercles and taleolae appear to differ only in size and characterize two layers of laminar shell that were secreted by epithelial sheets facing each other. Yet the valve need not have been secreted within an epithelial fold in the manner inferred for the internal plate of the dorsal valve. Wang and Jin (1991, pl. III, fig. 1, 3) have illustrated the boundary between the outer and inner pseudopunctate layers as a space about 3 µm wide, bounded by crenulated surfaces. The crenulations appear to be sections of concentric, rounded folds with a wavelength of about 4 µm; and the surfaces bearing them are believed to have been the sites of the ventral periostracum (Fig. 446.2). On this assumption, the outer pseudopunctate tuberculate layer is homologous with the posterior flap of lyttonioids, folded back to become closely adherent to the exterior of the inner pseudopunctate layer representing the ventral valve in the othodox sense (Fig. 451).

Apart from the cardinal process, which, although highly variable, is essentially bilobed in the strophomenid fashion, lyttonioid internal features also show noteworthy departures from arrangements typical of other articulated brachiopods. The ventral valve has no teeth, but a pair of striated, convex surfaces (dental areas of Watson, 1917) occur in the apical region; and these articulate with a pair of similarly striated, oval concave surfaces (sockets) lying anterolaterally to the cardinal process lobes and extending down to the first pair of lateral lobes in the dorsal valve. Cooper and Grant (1974, p. 390) disputed this interpretation. Instead they regarded the complementary grooves and ridges found in the hinge regions as having functioned as *dorsal* teeth and *ventral* sockets. In the absence of annotated illustrations, their description of this device is confusing. In any event, it is academic to attempt to interpret lyttoniidine articulation in terms of an orthodox tooth-and-socket arrangement except, however, for the permianelloid arrangement. According to Wang and Jin (1991, p. 485), a bilobed cardinal process in the dorsal valve is flanked by well-defined sockets that received convex dental areas developed in the ventral valve.

Cooper and Grant (1974, p. 386) noted that the "hinge generally is fairly uniform throughout the Lyttoniidae" (except for *Choanodus*), and the generic descriptions given here are based on the assumption that there is a significant difference between the articulatory devices of lyttonioids and permianelloids.

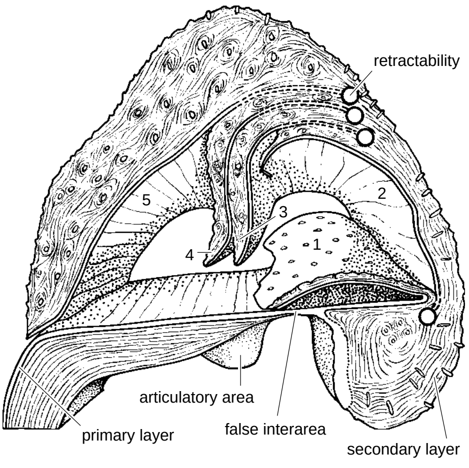


Fig. 449. Submedian portion of posterior flap of *Oldhamina decipiens* (de Koninck), Salt Range, Pakistan; numbers *1* to *5* denote successive layers of shell deposited by posterior flap; *circles* represent locations of minimum retractability of mantle flap necessary for deposition of each succeeding layer (Williams, 1953).

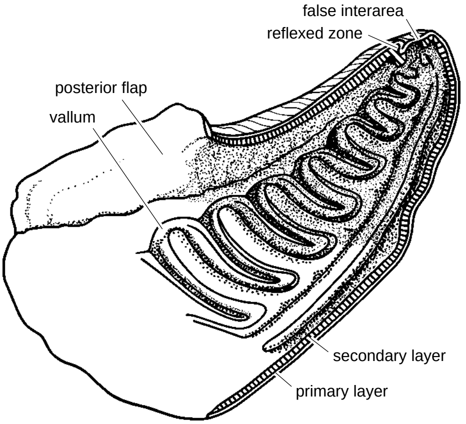


Fig. 450. Submedian view of interior of ventral valve of *Pirgulia* sp., Permian, Texas (Williams, 1953).

Muscle scars are preserved only sporadically throughout the entire suborder but include a pair of variably defined dorsal adductor scars on either side of the median ridge. The ventral impressions, on the other hand, can be asymmetrical in the lyttonioids, and the disposition of the ventral scars is indicative of two important groups (Stehli, 1956; Williams, 1965f; Cooper & Grant, 1974). In the first group (e.g., *Coscinophora*), a pair of large elongate adductor scars located submedianly are flanked by a pair of smaller, elongate diductors; this symmetrical field is commonly associated with median and submedian ridges. In the second group, which includes such forms as *Poikilosakos,* the right diductor is always larger than the left and is contained within an elongately semiconical sheath, while the adductor scars are obscure or represented by inconspicuous asymmetrical hollows located posteromedianly. This asymmetry is reflected in the uneven growth of the lobes of the cardinal process; that of *Poikilosakos,* for example, is unequally developed with the right lobe usually being the larger. Such asymmetry of scars may have been linked to a degeneracy of the muscle system. In any event, the dorsal valve was commonly so confined by the lateral walls of the ventral valve that it could not have slewed in the plane of articulation as believed by

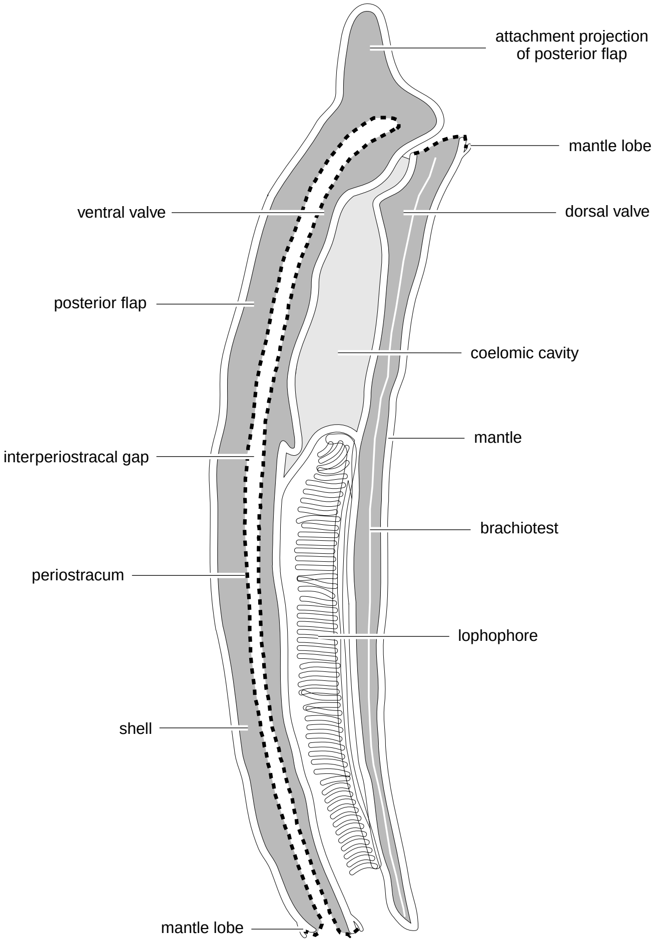


FIG. 451. Stylized submedian section of young permianellid shell showing inferred distribution of integument and soft parts *in vivo* (new).

WATSON (1917). Furthermore, the close proximity of the cardinal process lobes to the floor of the ventral valve and the physical constraint of the posterior flap immediately dorsal of the dorsal valve precludes any considerable movement normal to the plane of articulation (WILLIAMS, 1953c; RUDWICK & COWEN, 1968).

The permianelloid muscle system seems always to have been symmetrical (HE & ZHU, 1979; WANG & JIN, 1991), with the ventral scars impressed on and laterally to a narrow, hollow median platform.

In the earliest lyttonioid, *Poikilosakos,* a low bounding ridge lying well within the margin of the ventral valve completely surrounds the median area of the interior. The ridge was termed a flange by WATSON (1917) but was later renamed a vallum by COOPER and GRANT (1974, p. 385). There is little point to changing a well-established term in this way, although an additional term, like vallum, can serve a useful purpose. It is important, especially with regard to the permianelloids, to distinguish between the ridge and the marginal shell beyond; and it is here proposed to restrict the use of vallum for the ridge and flange for shell beyond.

During lyttonioid ontogeny and phylogeny, the vallum became increasingly looped

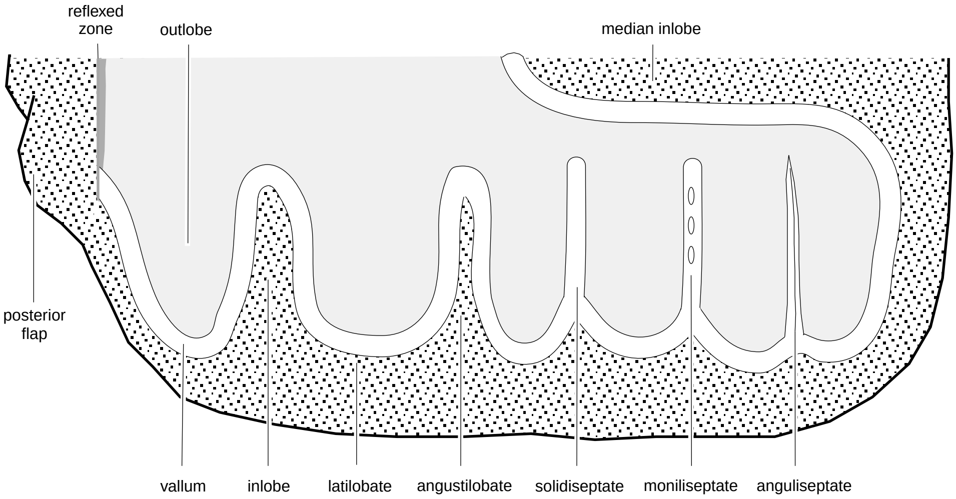


FIG. 452. Terminology used by COOPER and GRANT (1974, p. 385) to describe various stages in the compression of loops of vallum in ventral interior of lyttonioids (new).

with a complementary increase in the lobation of the dorsal valve. COOPER and GRANT (1974, p. 385) devised a complicated terminology to identify prescribed stages in the progressive compression of the loops of the vallum and their transformation into ridges and septa. Some of these terms are illustrated in Figure 452 but have not been used in any systematic way in the following descriptions of genera.

In young lyttonioid shells, the vallum was roughly subcircular in outline and was indented to form a median loop only; but during further growth involving resorption the vallum increased in size and became disposed as a small number of lateral loops in addition to the median one. Each loop was sufficiently open to include medianly a narrow strip of the valve floor bounded by an indented segment of the vallum (latilobate condition). The internal plate of the dorsal valve corresponded in outline to the disposition of the bounding ridge so that it was lobate and lay so close to the ventral valve that each lobe was seemingly isolated distally from its neighbor by a loop of the bounding vallum.

In later Lyttonioidea (e.g., *Keyserlingina, Paralyttonia*), the loops began to close by an increase in the size of adjacent segments of the vallum and their encroachment onto the intervening median strip of the valve floor (angustilobate condition) until, in extreme forms like *Oldhamina* and *Leptodus,* the ridge boundaries of each loop were completely united into one solid septal structure (solidiseptate condition) that may even develop a series of small crests (moniliseptate condition). In this manner the looped vallum of the earlier and more generalized Lyttonioidea was transformed into solid septa, the dorsal surfaces of which may be concave, bluntly convex, or sharp; and a pair of notches extending the length of the septa commonly developed to accommodate the edges of lobes to the internal plate.

Other modifications associated with evolution of the septal apparatus included an increase in the number of septa disposed symmetrically or asymmetrically about the median line, the progressive closure of the median incision of the dorsal valve, and the partial fusion of the lateral lobes by the growth of dissepiments.

The identification of the flange and vallum in the permianelloids is provisional. The valve margins of the permianelloid shell are more nearly coincident than those of the lyttonioids. But WANG and JIN (1991)

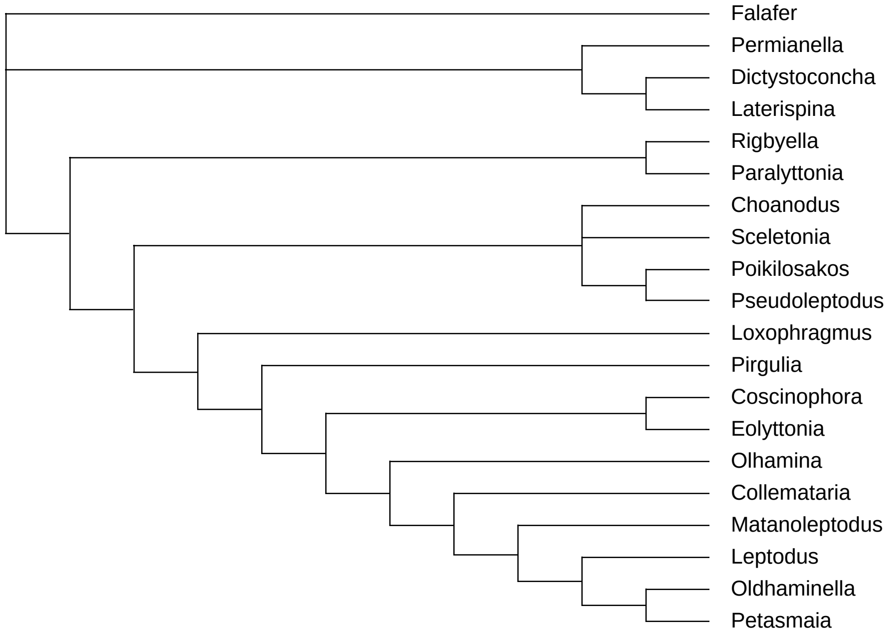


FIG. 453. Cladogram showing strict majority consensus of 39 trees derived by heuristic (stepwise random addition of taxa in 10 replicates) search of matrix composed of 20 genera, named in cladogram, and 30 characters, listed in Table 16 (new).

illustrate in diagrams and photographs a circumferential ridge in the permianellid ventral valve that has been identified as a vallum and a narrow surrounding flange that is extended as lateral spines in *Laterispina.* In this interpretation, the permianelloids and lyttonioids could have shared an ancestor with a distinctive bilobate shell.

The classification of the Lyttoniidina is still in a state of improvisation. All the lyttonioid genera described below are clearly related to one another but display degrees of morphological differences that normally call for some kind of convenient familial grouping. Thus, two families have long been recognized, the Poikilosakidae and the Oldhaminidae, based upon the symmetry of lobation (WILLIAMS, 1953c) or changes in the symmetry of the ventral muscle scars (STEHLI, 1956; COOPER & GRANT, 1974).

The permianelloids were initially recognized as a new order (HE & ZHU, 1979) but were subsequently reduced to familial rank (WANG & JIN, 1991) once their affinities with the lyttonioids had been established. Nonetheless, the permianelloids are quite distinctive and may yet be shown to be related to such aberrant genera as *Loczyella* and *Litocothia.* The phylogeny of the lyttonioids and permianelloids has been analyzed (SWOFFORD & BEGLE, 1993). The analysis, which excluded genera inadequately diagnosed or of doubtful affinities, was based on the characters defined in Table 16 and used the strophalosioid *Falafer* as an outgroup. The resultant majority consensus cladogram (Fig. 453) and the derived genealogy (Fig. 454) show that the lyttonioids consist of a group (the Rigbyellidae) with dorsal lobes parallel to the median plane of the valve rooted to a clade (the Lyttoniidae) that is composed of genera with laterally or radially disposed lobes, the Poikilosakinae and Lyttoniinae respectively. It also shows that *Falafer* and the permianelloids form a dichotomous stem group to the lyttonioids. When all the morphological characteristics of the excluded genera are known, a new group-

TABLE 16. States of 30 characters used in phylogenetic analysis of 19 genera in suborder Lyttoniidina, with strophalosioid *Falafer* as sister group, as shown in Figure 453 (new).

SHELL STRUCTURE

1. primary layer: present in both valves (0); reduced in dorsal valve (1); reduced in both valves (2).

SHELL SHAPE

2. size: small (<10 mm) (0); medium (1); large (>50 mm) (2).
3. outline: conforming to substrate (0); subcircular (1); transversely oval (2); elongately oval (3); fan shaped (4).
4. ventral valve: flat (0); cup shaped (1); conical (2); scooplike (3); convex (4).
5. ventral sulcus: present (0); absent (1).
6. posterior flap: absent (0); present (1).
7. growth of flap: absent (0); everted (1); forming cowl (2); forming long hood (3); rolled posteriorly (4); forming ringlike clasp (5).
8. attachment: beak (0); beak and spines (1); beak and posterior flap (2); entire ventral valve (3).
9. spines: present (0); absent (1); along lateral margin (2).
10. rhizoid spines: present (0); absent (1).
11. valve margins: coincident (0); dorsal within ventral (1).

VENTRAL INTERIOR

12. vallum: absent (0); open lobes (1); compressed lobes (2).
13. compressed lobes: absent (0); as grooved ridges (1); as septa (2); as sharp septa (3).
14. septal inclination: not applicable (0); vertical (1); inclined anteriorly (2).
15. septal segmentation: not applicable (0); continuous (1); beaded (2).

DORSAL VALVE

16. outline: unindented (0); bilobate (1); multilobate (2).
17. multilobation: undeveloped (0); elongately bilobate (1); laterally lobate (2); radially lobate (3); parallel lobate (4); laterally lobate, becoming radially lobate anteriorly (5); lateral lobes convex anteriorly (6).
18. number of lateral lobes: undeveloped (0); <10 (1); >10 (2).
19. lobe structure: not applicable (0); open (1); contiguous (2); punctured (3).
20. median slit: not applicable (0); open (1); virtually closed (2); punctured (3); open deep (4).

MUSCULATURE

21. ventral muscle platform: present (0); absent (1); hollow (2).
22. ventral diductor scars: symmetrical (0); asymmetrical (1).
23. diductor ridges: not developed (0); as sheath (1); discrete (2); as thickened boss (3).

ARTICULATION AND CARDINALIA

24. (bilobed) cardinal process: absent (0); single lobed (1); asymmetric bilobed (2); bilobed (3); quadrilobed (4).
25. articulatory processes: teeth and sockets (0); lyttonioid type (1); no dorsal articulating process (2); dental areas and sockets (3).
26. ventral interarea: present (0); absent (1).
27. dorsal valve: present (0); vestigial (1).
28. septal crenulation: absent (0); present (1); no septa (2).
29. cardinal process: essentially bilobed (0); fused, v-shaped (1).
30. reflexed zone: absent or vestigial (0); present (1).

ing is likely to emerge without necessarily compromising the suprageneric taxonomic hierarchy based on the data presently available (Fig. 454).

A great deal of nomenclatorial confusion has also arisen through an unwarranted action of WAAGEN (1883). The first described genus of the group was named *Leptodus* by KAYSER (1883) in the belief that the incomplete specimen he examined represented the remains of fish teeth. Shortly afterward, WAAGEN ascertained their true nature and, because the name *Leptodus* perpetuated a serious misidentification, suppressed it in favor of *Lyttonia* WAAGEN, the type species of which was subsequently designated by HALL and CLARKE (1894a). In the same publication, WAAGEN erected another genus (*Oldhamina*) and a new subfamily, the Lyttoniinae. Since then most European paleontologists (NOETLING, 1905; WANNER & SIEVERTS, 1935; LICHAREW, 1932; etc.) have used the familial name Lyttoniidae, whereas SCHUCHERT (1913a), presumably in order to

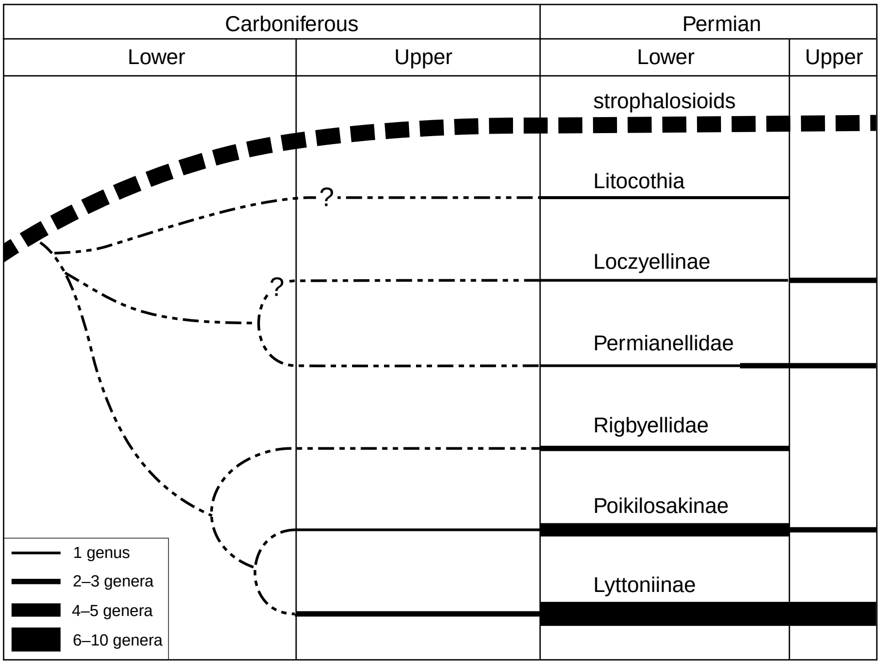


FIG. 454. Classification of Lyttoniidina, superimposed on an Upper Paleozoic chronostratigraphic chart, showing inferred relationship of taxa with one another and with assumed ancestral strophalosioid group represented by *Falafer* (new).

emphasize the invalid procedure adopted by WAAGEN, proposed Leptodinae as a suprageneric taxon in 1913, and (with LEVENE) established Oldhaminidae in 1929. In general, there is no doubt that the familial designation Lyttoniidae has been more widely used by paleontologists than either Oldhaminidae or Leptodinae (International Code of Zoological Nomenclature, STOLL & others, 1961, art. 40a) and was, therefore, adopted by WILLIAMS in 1965 (WILLIAMS, 1965f).

WILLIAMS (1953c, p. 286) had previously erected a new suborder for the group, the Oldhaminoidea, that was later corrected to Oldhaminidina (WILLIAMS, 1965f, p. 511). In effect, the superfamilial nomenclature of the Lyttoniidae remains confusingly hybrid. No rules of zoological nomenclature presently preclude the replacement of an ordinal (or subordinal) name by another deemed more suitable. In our opinion, it is now opportune to discard the name Oldhaminidina and replace it with Lyttoniidina, thereby bringing the suprageneric nomenclature of this group of brachiopods into a comprehensible progression through the taxonomic ranks.

Superfamily LYTTONIOIDEA Waagen, 1883

[*nom. transl.* LICHAREW in SARYTCHEVA, LICHAREW, & SOKOLSKAYA, 1960, p. 237, *ex* Lyttoniinae WAAGEN, 1883, p. 396]

Shape of shell irregular, exterior of ventral valve ornamented by growth lamellae and disturbances, that of dorsal valve by fine tubercles; posterior flap variably disposed but forming a narrow reflexed zone immediately dorsal of hinge of dorsal valve; ventral interior with circumferential ridge (vallum), intramarginal to wide flange, vallum initially disposed as open loops becoming compressed into septa, surrounding and interdigitating with lobate dorsal valve; lightly impressed muscle scars not supported by platforms; cardinal process essentially bilobed but commonly deformed. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Family LYTTONIIDAE Waagen, 1883

[*nom. transl.* NOETLING, 1905, p. 129, *ex* Lyttoniinae WAAGEN, 1883, p. 396] [=Oldhaminidae SCHUCHERT & LEVENE, 1929, p. 18]

Lobation of ventral vallum and dorsal valve consisting of median indentation with variable number of lobes (and septa) on either side, directed laterally or anterolaterally; ventral muscle field including large, submedian adductor scars flanked by pair of variably developed, smaller diductor impressions. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Subfamily LYTTONIINAE Waagen, 1883

[Lyttoniinae WAAGEN, 1883, p. 396] [=Leptodinae SCHUCHERT, 1913a, p. 387]

Commonly large lyttoniids with vallum of ventral valve compressed into more or less symmetrically arranged lateral, arcuate septa, inclined anteriorly with crenulated posterior sides; when present ventral diductor muscle scars and variably developed cardinal process symmetrical. *?Lower Carboniferous, Upper Carboniferous–Upper Permian.*

Leptodus KAYSER, 1883, p. 161 [**L. richthofeni;* OD] [=*Lyttonia* WAAGEN, 1883, p. 396 (type, *L. nobilis*); *Gubleria* TERMIER & TERMIER, 1960, p. 241 (type, *G. disjuncta*); *Spinolyttonia* SARYTCHEVA, 1964, p. 69 (type, *S. arakeljani*); *Lyttonia (Digitia)* DE GREGORIO, 1930, p. 32 (type, *L. (I.) princeps* var. *glomerata*); *Lyttonia (Irma)* DE GREGORIO, 1930, p. 32 (type, *L. (I.) bilobata*); *Lyttonia (Vincia)* DE GREGORIO, 1930, p. 31 (type, *L. (V.) asymmetrica*); ?*Lyttonia (Prisca)* DE GREGORIO, 1930, p. 31 (type, ?*L. (P.) fasciculata*); *Juxoldhamina* LIANG, 1990, p. 470 (type *L. imparilisa;* OD); *Semigublerina* LIANG, 1990, p. 469 (type *S. flabelata;* OD)]. Ventral valve scoop shaped, normally transversely oval, attached by beak and everted posterior flap; septa in ventral interior arcuate, normally sharp, tending to vertical disposition; muscle scars large, bounded laterally by high, medianly concave ridges; dorsal adductor scars elongate and impressed well anterior of hinge region; bilobed cardinal process elongate narrow. [The poor preservation of the type material of *L. richthofeni* and the almost simultaneous publication in 1883 of *Leptodus* and *Lyttonia* by KAYSER and WAAGEN respectively for congeneric species have played no small part in the subsequent proliferation of subjective synonyms. The genera and subgenera erected by DE GREGORIO, however, are poorly founded and inadequately described by any standard. Indeed, COOPER and GRANT (1974, p. 410) asserted that *Irma* and *Imperia* are algal forms. The subjective synonymy of *Spinolyttonia,* on the other hand, has been prompted by the rejection of COOPER and GRANT (1974, p. 387) of the family Spinolyttoniidae, erected by WILLIAMS (1965f, p. 521) for a lyttoniid with posterolateral spines. At the time, COOPER and GRANT, having never seen spinose oldhaminidines in the vast collections of mainly American material at their disposal, suggested that the Russian specimen had been misinterpreted. Subsequently the types of *Spinolyttonia arakeliani* SARYTCHEVA were examined at the Palaeontological Institute in Moscow by R. E. GRANT, who did not see any spines on the specimens (reported in correspondence 10 May, 1991). *Juxoldhamina* is intended for shells as in *Leptodus* with sharp septa as in *Oldhamina.* In view of the changes that ventral septa undergo during shell growth, we consider that the genus is not secure. In a like vein, the distinguishing feature of *Semigublerina,* sporadic culminations along the crest of the median septum, can occur in *Leptodus.*] *Permian:* Eurasia, USA (Texas), Australia.——FIG. 455,*3a,b.* **L. richthofeni,* Upper Permian, Lo-Ping, China; *a,* ventral view of partly exfoliated ventral valve, ×1; *b,* tilted view of partly exfoliated ventral valve, ×2 (Cooper & Grant, 1974).——FIG. 455,*3c,d. L. nobilis* WAAGEN, Upper Permian, Pakistan; *c,* ventral valve with attachment flap, ×1; *d,* partly conjoined valves attached to species of *Enteletes,* ×1 (Grant, 1976).

Cardinocrania WAAGEN, 1885, p. 745 [**C. indica;* OD] [=?*Pseudokeyserlingina* FREDERICKS, 1916, p. 64, hypothetical genus (FREDERICKS established a number of genera related to stages in the phylogeny of the group that had not actually been discovered as fossils.)]. Small subcircular ventral valve with raised, medianly indented anterior margin and everted posterior flap; raised submedian muscle scars developed posteriorly; dorsal valve unknown. [The validity of this genus is in dispute and cannot be confirmed until more topotypic material, including dorsal valves, has been collected. The *Cardinocrania* figured by WANNER and SIEVERTS (1935, pl. 6, fig. 1–2), which has an asymmetrical ventral muscle scar, has been identified as young *Pseudoleptodus* by COOPER and GRANT (1974, p. 410), who believed that the type ventral valves of *Cardinocrania* are young specimens of *Leptodus*]. *Permian:* Pakistan, Timor.

Collemataria COOPER & GRANT, 1974, p. 433 [**C. elongata;* OD]. Similar to *Leptodus* but normally subtriangular in outline with transverse, regularly arranged septa in ventral valve and more open lobes in dorsal valve; dorsal hinge region without articulatory processes, bilobed cardinal process with four myophore surfaces. *Permian:* USA (Texas), Venezuela, China.——FIG. 456,*1a–e.* **C. elongata,* Upper Permian, Word Formation, Texas; *a–c,* dorsal, lateral, ventral views of conjoined valves, ×1; *d,* dorsal view of partly conjoined valves, ×1; *e,*

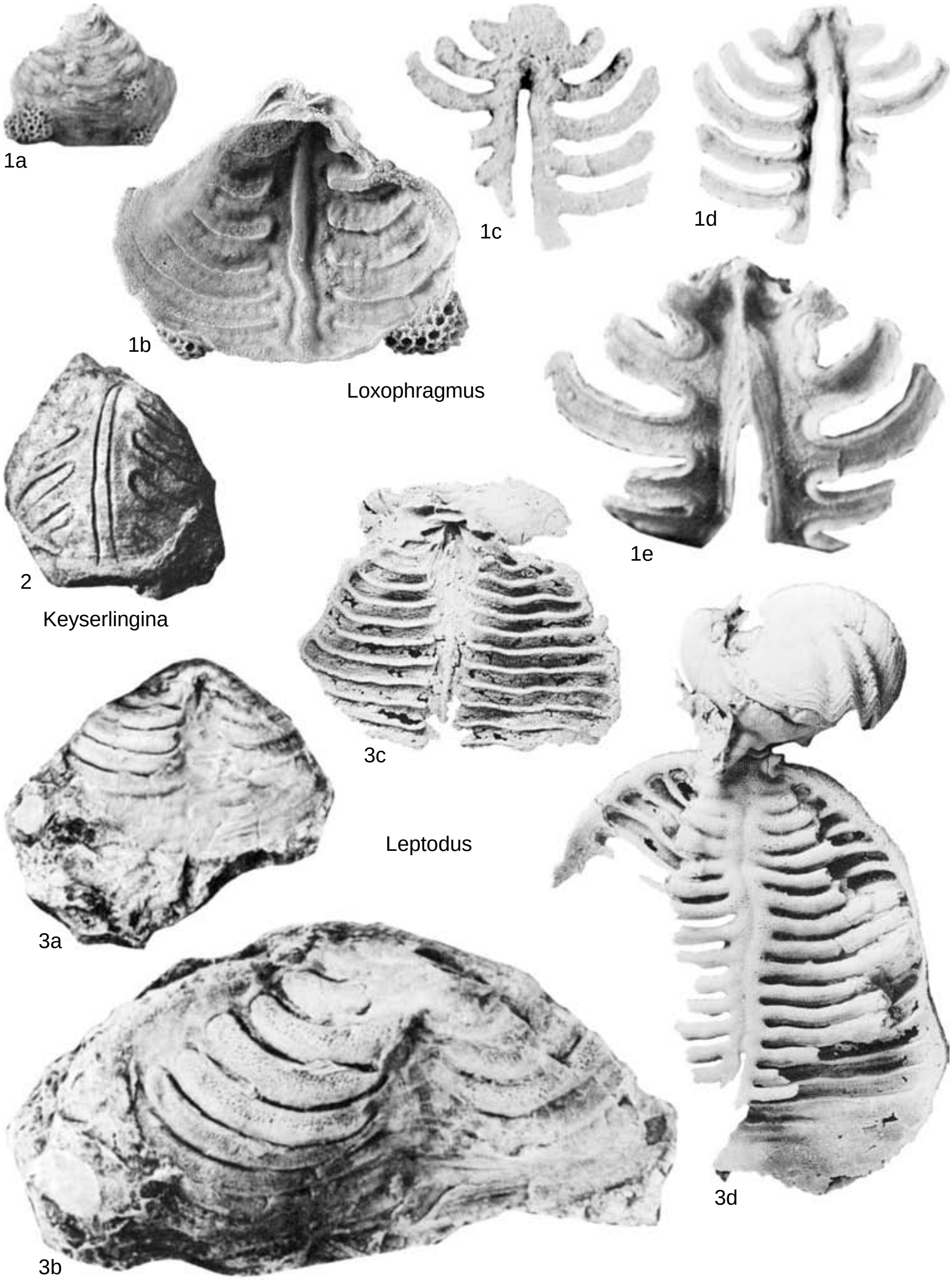


FIG. 455. Lyttoniidae (p. 631–634).

enlargement of posterior half of dorsal interior, ×3 (Cooper & Grant, 1974).

Coscinophora COOPER & STEHLI, 1955, p. 469 [**C. nodosa;* OD]. Similar to *Leptodus* but with numerous septa in ventral valve broken into discrete beads, more or less symmetrically disposed but commonly becoming radially aligned anteriorly; lobes of dorsal valve united by dissepiments to define a series of

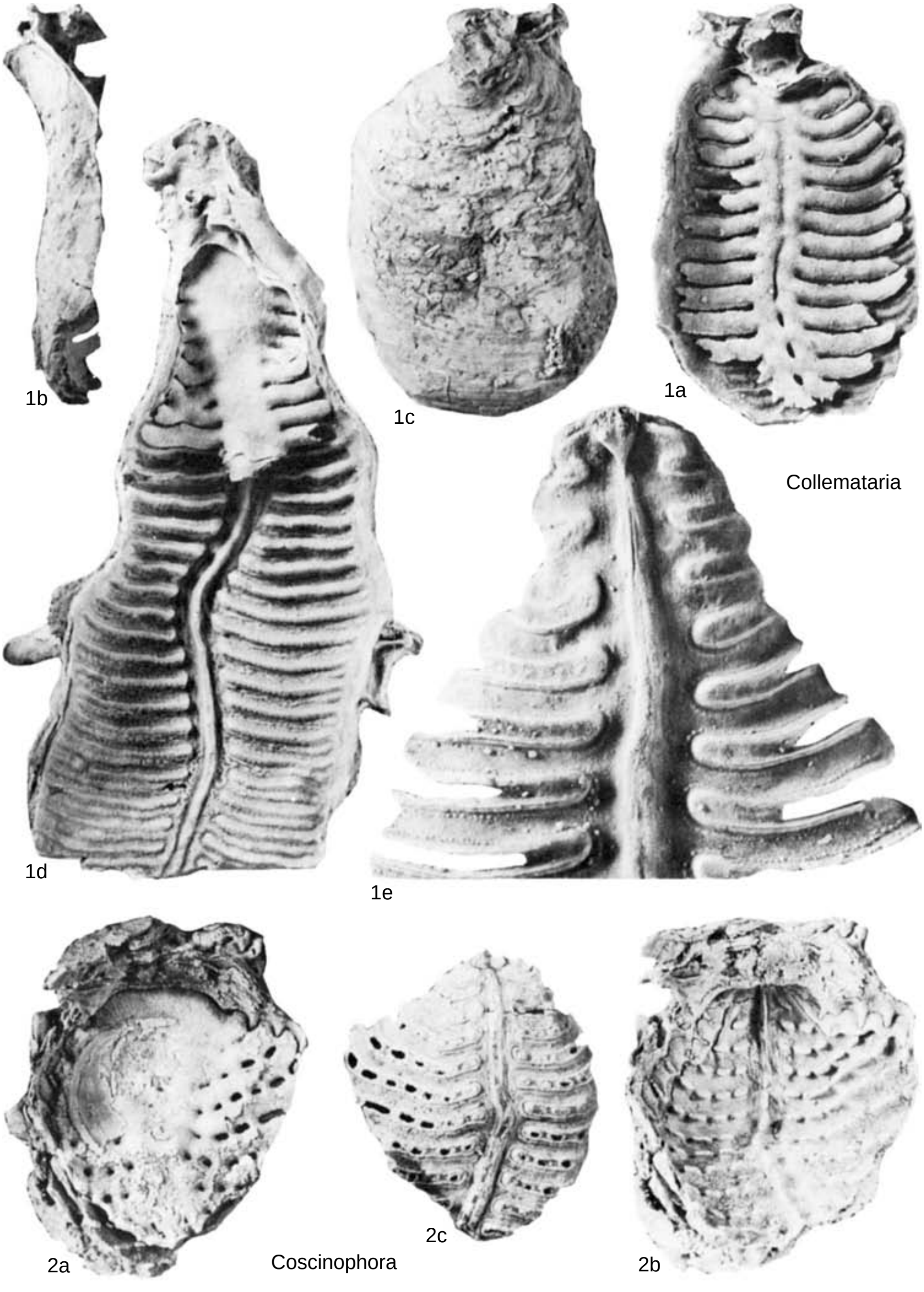


FIG. 456. Lyttoniidae (p. 631–633).

holes complementary to ventral beads. *Lower Permian:* USA (Texas).——FIG. 456,*2a–c*. **C. nodosa,* Lower Permian, Cathedral Mountain Formation, Texas; *a,* dorsal view of conjoined valves, ×1; *b,* ventral interior of same specimen, ×1; *c,* dorsal interior of same specimen, ×1 (Cooper & Grant, 1974).

Eolyttonia Fredericks, 1924, p. 25 [**Oldhamina (Lyttonia) mira* Fredericks, 1916, p. 74; OD] [=*Uralina* Schuchert & LeVene, 1929, p. 122 (type, *U. tastubaensis* Likharev, 1925), *nom. nov. pro Uralia* Likharev, 1925, p. 4, *non* Mulsant, Verreaux, & Verreaux, 1866; *Paraleptodus* Li & Gu in Li, Gu, & Su, 1980, p. 390 (type, *P. wuchangensis;* OD)]. Large with subconical ventral valve subcircular in outline, attached in part by everted posterior flap; numerous more or less symmetrically disposed lateral septa arcuate, thick with concave flat crests, median incision of dorsal valve slitlike and limited to anterior half; cardinal process having single shaft and bifid myophore. *Upper Carboniferous–Lower Permian:* Austria, Yugoslavia, *Upper Carboniferous;* northeastern China, Japan, Siberia, USA (Texas), Thailand, Timor, *Lower Permian.*——Fig. 457,*1a–c. E. chaotica* Cooper & Grant, Upper Permian, Road Canyon Formation, Texas; *a,b,* dorsal exterior, interior of posterior part of same valve, ×1; *c,* enlargement of posterior part of same valve, ×3 (Cooper & Grant, 1974).——Fig. 457,*1d,e. E. circularis* Cooper & Grant, Lower Permian, Cathedral Mountain Formation, Texas; interior, exterior of ventral valve, ×1 (Cooper & Grant, 1974).

Keyserlingina Chernyschev, 1902, p. 55 [**K. schellwieni;* OD] [=*Parakeyserlingina* Fredericks, 1916, p. 14 (type, *Keyserlingina darvasica* Chernyschev, 1914); *Chaoella* Likharev, 1931, p. 161 (type, *C. caucasica*)]. Small, subconical by forward growth of posterior flap, attached broadly along posterior surface; vallum of ventral valve folded into narrow loops forming up to 7 pairs of lateral ridges and low median ridge split at anterior end; dorsal valve unknown. [This genus is poorly known by only a ventral valve. Cooper and Grant (1974, p. 411) compared it with the poikilosakin *Pseudoleptodus* but, in the absence of any evidence of an asymmetrical ventral muscle field, left it among the lyttoniids as was done in the first edition of the Brachiopoda *Treatise* (Williams, 1965f, p. 518).] *?Lower Carboniferous, Upper Carboniferous–Lower Permian:* China (Guangdong, Guizhou), *?Lower Carboniferous;* Austria, *Upper Carboniferous;* China, ?Thailand, Russia (Urals, Caucasus), *Lower Permian.*——Fig. 455,*2. K. filicis* (Keyserling), Lower Permian, western Urals; internal mold of ventral valve, ×1 (Sarytcheva, Licharew, & Sokolskaya, 1960).

Loxophragmus Cooper & Grant, 1974, p. 432 [**L. ellipticus;* OD] [=*Palaeoldhamina* Liang in Wang & others, 1982, p. 230 (type, *P. kuzishanensis*)]. Subconical ventral valve with up to 10 or so pairs of crenulated, arcuate septa and deeply incised median slit; cardinal process slightly excentric. *Lower Permian:* USA, eastern China.——Fig. 455,*1a–e.* **L. ellipticus,* Lower Permian, Cathedral Mountain Formation, Texas; *a,* exterior of ventral valve, ×1; *b,* interior of ventral valve, ×2; *c,d,* exterior, interior of dorsal valve, ×2; *e,* dorsal interior, ×4 (Cooper & Grant, 1974).

Matanoleptodus Liao, 1983, p. 641 [**M. punctatus;* OD]. Ventral valve, suboval in outline, attached by much of external surface and everted posterior flap associated near its right anterior junction with valves, with few broken hollow spines; median septum strong, flanked by 5 or 6 pairs of arcuate, widely grooved lateral septa. [It is not clear from the illustrations whether the broken spines arise from the posterior flap. If they project inwardly from the *inner* surface of the posterior flap, they cannot be homologous with productide spines.] *Upper Permian:* China (Guangxi).——Fig. 457,*3a–c.* **M. punctatus,* Upper Permian, Guangxi Province; *a,* ventral interior, ×2; *b,* enlargement of posterolateral part of ventral valve showing spine arrangement, ×5; *c,* ventral interior attached to bryozoan, ×1 (new).

Oldhamina Waagen, 1883, p. 403 [**Bellerophon decipiens* de Koninck, 1863, p. 8; OD] [=*Waagenopora* Frech, 1902, p. 647 (type, *Oldhamina decipiens* de Koninck, 1863); *Oldhamella* Noetling, 1905, p. 129 (type, *Bellerophon decipiens* de Koninck); *Oldhamia* von Zittel, 1910, p. 280, *nom. null.*]. Ventral valve strongly convex, surface nearly smooth with fine growth banding; posterior flap recurved and rolled back in successive layers; internal septa medianly high, tapering laterally, sharp, inclined anteriorly, and strongly arcuate toward anterior to accommodate deep concavity of shell interior; dorsal valve with broad flattened hinge region and straight hinge line, cardinal process bilobed; median septum long, sharp, extending to anterior bifurcation of valve; lobes evenly spaced and more or less symmetrical, cambered with trailing edges anterior; external surface finely tuberculate. *Upper Permian:* Asia.——Fig. 458,*2a–c.* **O. decipiens* (de Koninck), Upper Permian, Pakistan; *a,b,* posterior, dorsal views of dorsal valve, ×3; *c,* ventral interior, ×3 (Waagen, 1883).

Oldhaminella Wanner in Wanner & Sieverts, 1935, p. 232 [**O. philocrina;* OD]. Transversely oval ventral valve strongly convex with everted posterior flap; median septum extending almost to apex of valve, flanked by 3 or 4 pairs of arcuate lateral ridges formed by fusion of compressed loops, with anterior sides strongly developed as fine ridges; ventral muscle scars bounded by lateral ridges. [This genus is based on 2 ventral valves only. Cooper and Grant (1974, p. 412) believed them to be immature *Leptodus.*] *Permian:* Timor.

Petasmaia Cooper & Grant, 1969, p. 10 [**P. expansa;* OD]. Large, flat, subcircular ventral valve with numerous, symmetrically disposed, transverse or gently arcuate, sharp septa; strong bilobed cardinal process with 4 myophore surfaces. *Permian:* USA (Texas).——Fig. 458,*1a–d.* **P. expansa,* Lower Permian, Cathedral Mountain Formation, Texas; *a,b,* exterior, interior of partly conjoined valves, ×0.66; *c,* dorsal interior, ×2; *d,* enlargement of posterior part of same valve, ×3 (Cooper & Grant, 1974).

Pirgulia Cooper & Muir-Wood, 1951, p. 195, *nom. nov. pro Pirgula* de Gregorio, 1930, *non Pirgula*

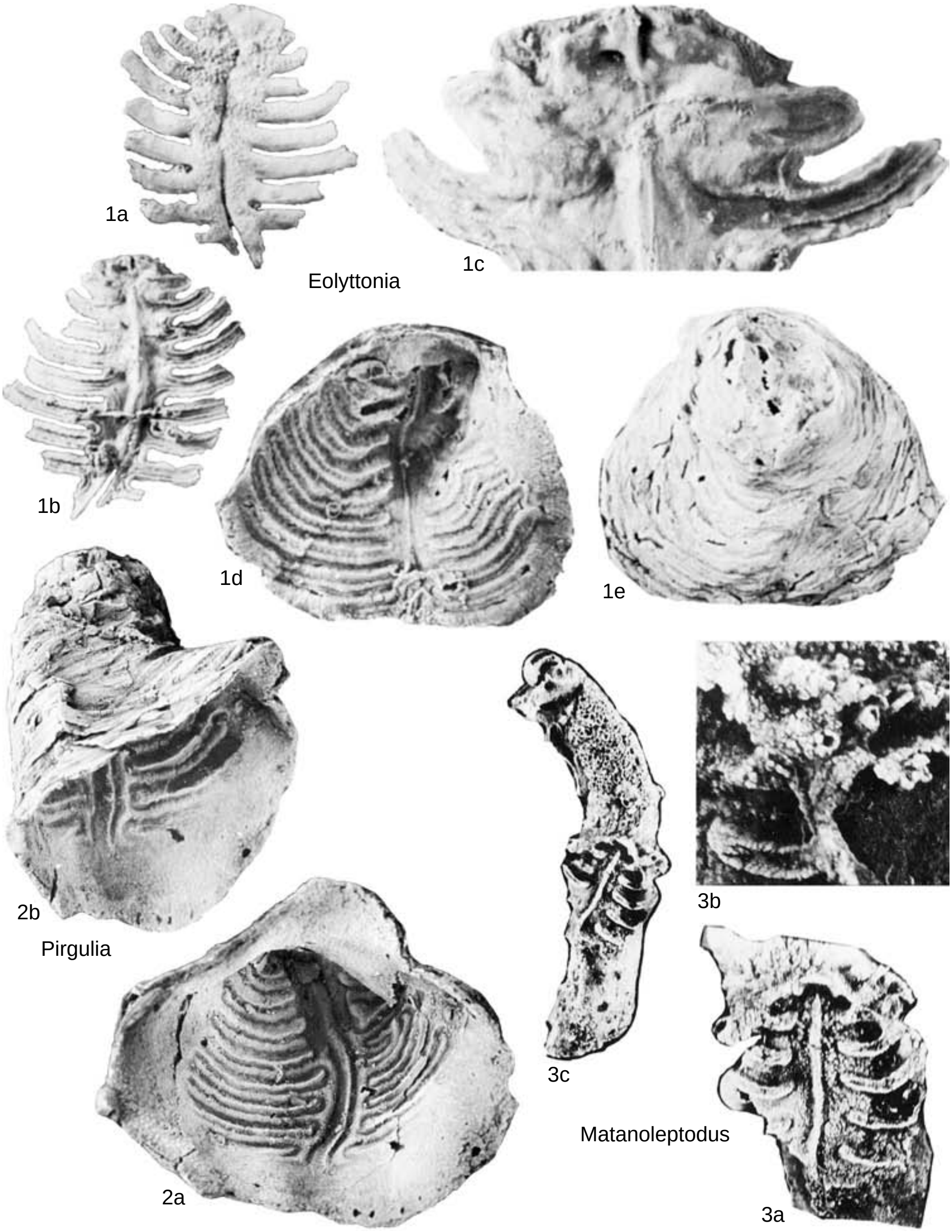


FIG. 457. Lyttoniidae (p. 634–635).

TESSMANN, 1921 [*?*Lyttonia (Pirgula) pediculata* DE GREGORIO, 1930, p. 30; OD]. Similar to *Leptodus* but with conical ventral valve attached apically and with blunt septa. *Permian:* Italy, USA (Texas).——FIG. 457,*2a,b. Pirgulia* sp., Lower Permian, Texas; dorsal, anterolateral views of ventral valve, ×1.5 (Williams, 1965f).

Subfamily POIKILOSAKINAE Williams, 1953

[*nom. transl.* WILLIAMS, HARPER, & GRANT, herein, *ex* family Poikilosakidae WILLIAMS, 1953c, p. 287]

Ventral diductor scar asymmetric with longer impression on right side; cardinal

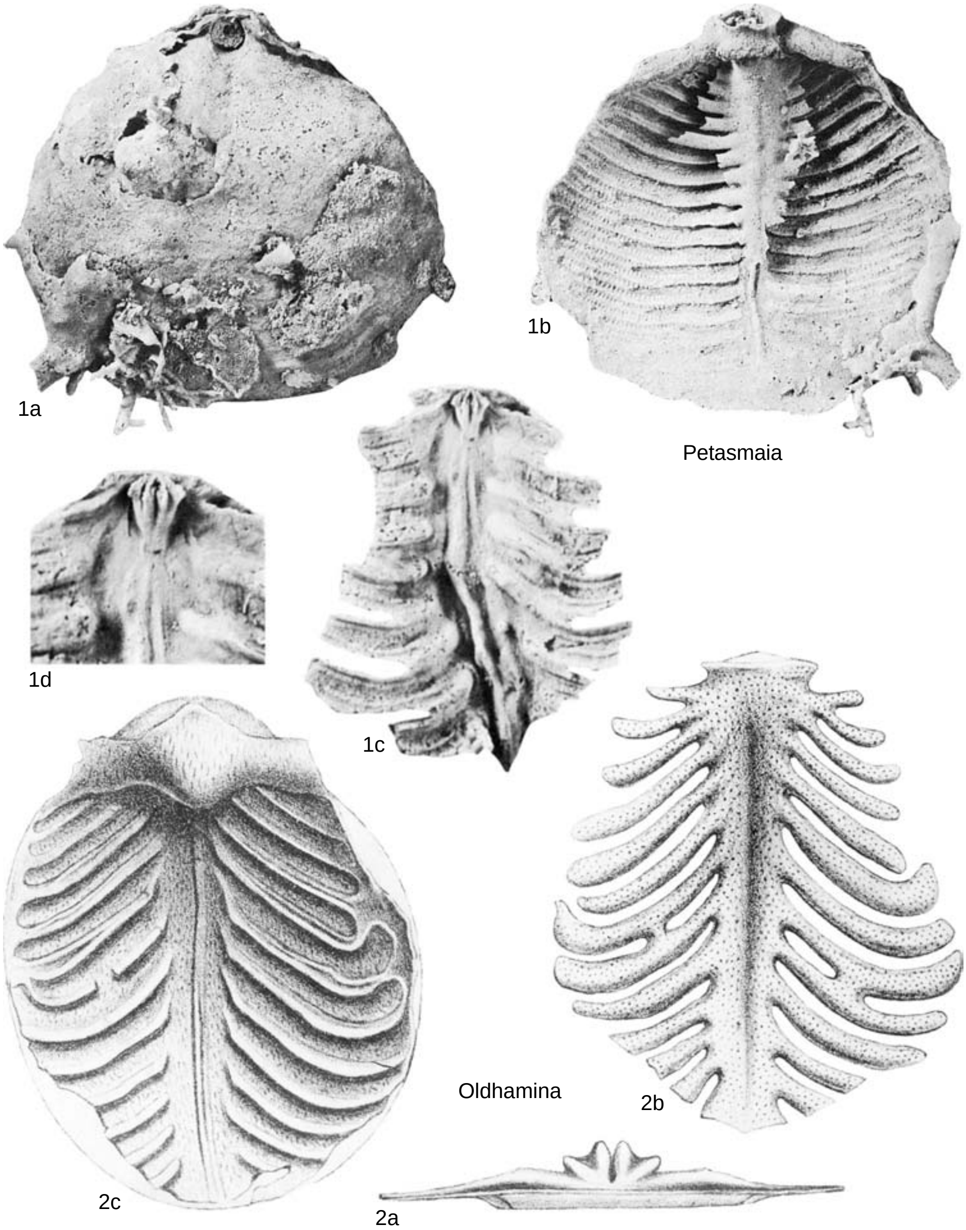


Fig. 458. Lyttoniidae (p. 634).

process deformed; dorsal valve deeply slit medianly. *Upper Carboniferous–Upper Permian.*

Poikilosakos Watson, 1917, p. 212 [**P. petaloides;* OD] [=?*Prokeyserlingina* Fredericks, 1916, p. 64, hypothetical genus (Fredericks established a number of genera related to stages in the phylogeny of the group that had not actually been discovered as fossils.)]. Small, ventral valve attached by entire surface and everted posterior flap; vallum disposed in small number of lobes pointing anteriorly and laterally, irregular and distorted; ventral muscle marks asymmetric, with left diductor weak and divergent from midline, with right being stronger and

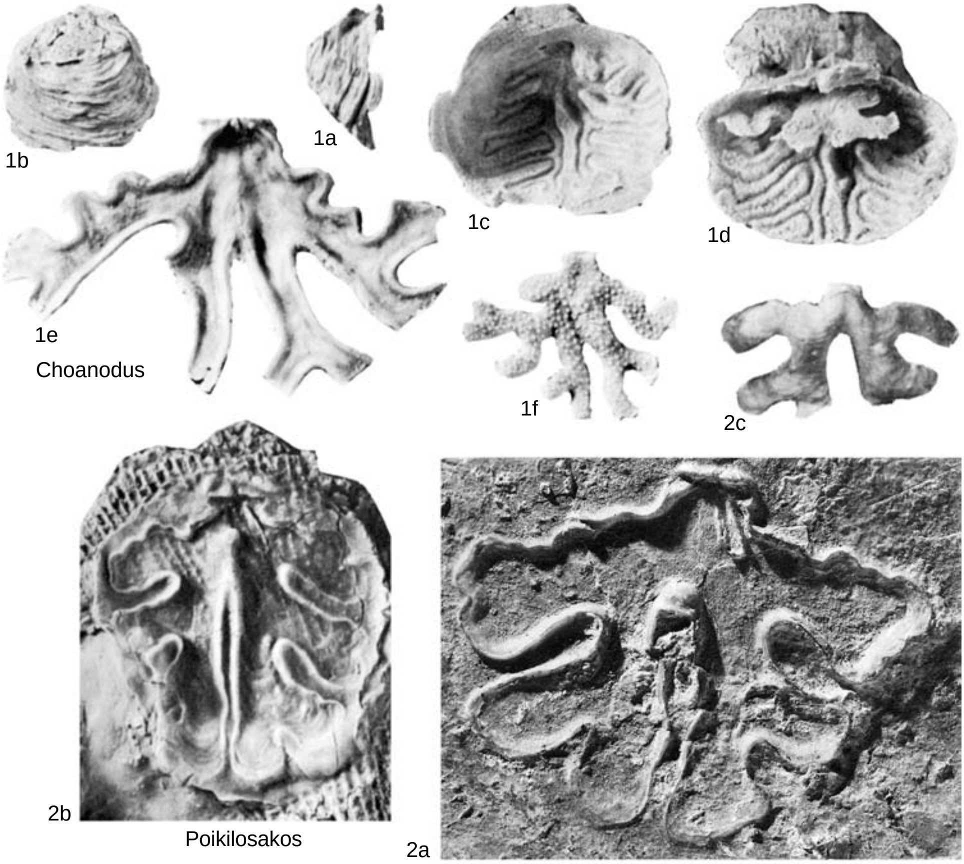


FIG. 459. Lyttoniidae (p. 636–637).

bounded by narrow sheath of shell. *Upper Carboniferous–middle Permian:* cosmopolitan, *Upper Carboniferous;* USA (Texas, New Mexico), *Lower Permian–middle Permian.*——FIG. 459,*2a–c.* **P. petaloides,* Upper Carboniferous; *a,* ventral interior, Graham Formation, Texas, ×3 (Williams, 1965f); *b,* elongate ventral interior, valve attached to fenestellid bryozoan colony, Graham Formation, Texas, ×2 (Cooper & Grant, 1974); *c,* dorsal exterior, Plattsmouth Limestone, Kansas, ×2 (Cooper & Grant, 1974).

Adriana DE GREGORIO, 1930, p. 32 [**A. osiensis;* OD] [=*Stita* DE GREGORIO, 1930, p. 32 (type, *Lyttonia (Stita) paupera;* OD)]. Ventral valve cone shaped; lobes and septa of ridge resembling vallum, on left side possibly single diductor scar. [The status of this genus, even as a brachiopod, has been challenged by RUDWICK and COWEN (1968, p. 153) and COOPER and GRANT (1974, p. 389), who were inclined to LIKHAREV's view (1964) that the vallum is an algal filament. More recently, however, the late R. E. GRANT tentatively identified an *Adriana*-like lyttonioid from the *Permian* of southern Thailand (1976, p. 161) and of Texas (written communication, May, 1991)]. *Permian:* Sicily, USA (?Texas), ?Thailand.

Choanodus COOPER & GRANT, 1974, p. 401 [**C. irregularis;* OD]. Subconical ventral valve with excessively wrinkled exterior, and internally with many, more or less paired, broad, lateral ridges; asymmetric bilobed cardinal process strongly developed. *Permian:* USA (Texas).——FIG. 459,*1a–f.* **C. irregularis,* Lower Permian, Cathedral Mountain Formation, Texas; *a,b,* lateral, ventral views of ventral exterior, ×1; *c,* interior of same valve, ×1.5; *d,* dorsal view of mature ventral valve with dorsal valve partly in place, ×2; *e,* interior dorsal valve, ×3; *f,* exterior of dorsal valve, ×2 (Cooper & Grant, 1974).

Pseudoleptodus STEHLI, 1956, p. 311 [**P. getawayensis;* OD]. Ventral valve subconical through forward growth of posterior flap, attached apically; lobes of vallum roughly symmetrical, compressed into 5 or more pairs of wide ridges; otherwise like *Poikilosakos. Lower Permian–Upper Permian:* USA, southern Thailand.——FIG. 460,*1a–e.* **P.*

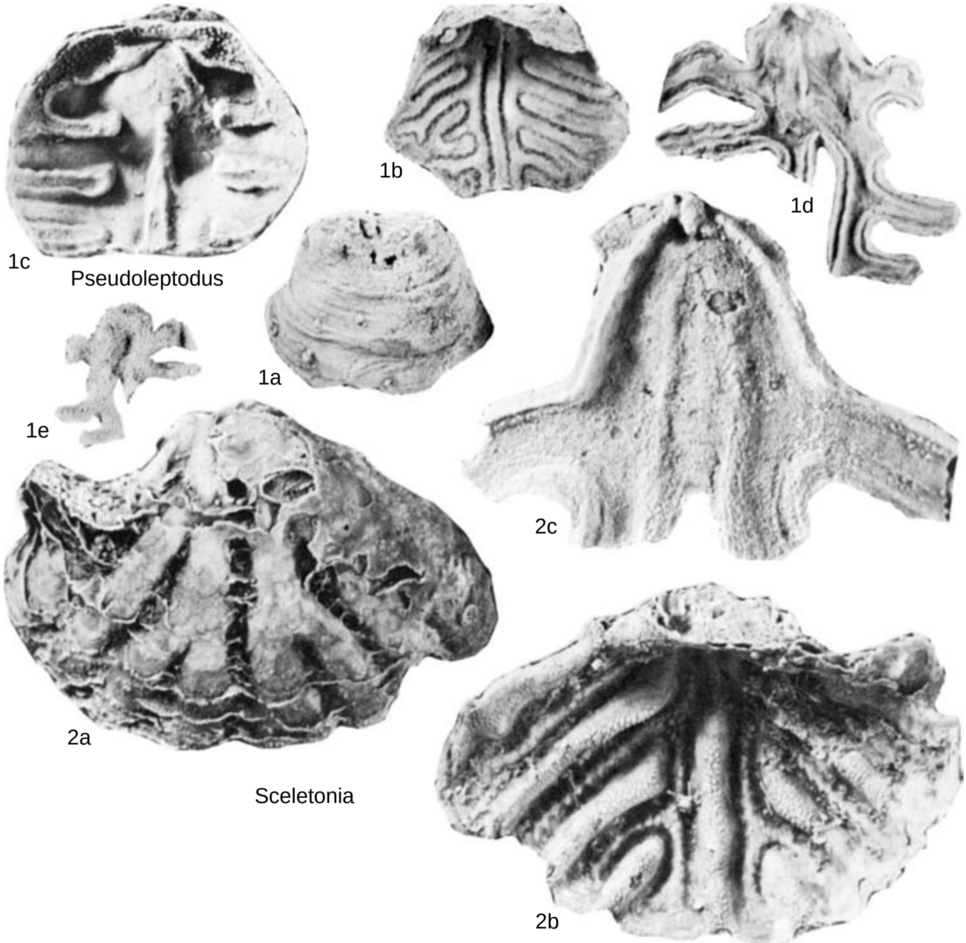


FIG. 460. Lyttoniidae (p. 637–638).

getawayensis, Lower Permian, Cherry Canyon Formation, Texas; *a,b,* external, internal views of ventral valve, ×1; *c,* ventral interior, ×2; *d,* interior of dorsal valve, ×2; *e,* exterior of dorsal valve, ×1 (Cooper & Grant, 1974).

Sceletonia COOPER & GRANT, 1974, p. 405 [**S. crassa;* OD]. Ventral valve cup shaped and deeply grooved externally corresponding to radially disposed, wide ridges internally; cardinal process asymmetrically bilobed. *Lower Permian:* USA (Texas), China (Guangxi Province).——FIG. 460,*2a–c.* **S. crassa,* Lower Permian, Skinner Ranch Formation, Texas; *a,b,* exterior and interior of ventral valve, ×2; *c,* dorsal interior, ×4 (Cooper & Grant, 1974).

Family RIGBYELLIDAE new family

[Rigbyellidae WILLIAMS, HARPER, & GRANT, herein]

Small, transversely oval shells, ventral valve cuplike with longer medioanterior sector (trail) arising more or less vertically from attachment area of beak and, to a lesser extent, from an everted posterior flap; up to 6 or 7 septa subparallel to median axis of shell with correspondingly disposed lobes of dorsal valve; ventral muscle scars symmetrical; cardinal process bilobed. *Lower Permian.*

Rigbyella STEHLI, 1956, p. 310 [**Paralyttonia girtyi* WANNER & SIEVERTS, 1935, p. 209; OD]. Ventral valve thick, margin scalloped and exterior coarsely costal in reflection of internal septa; septa normally uneven in number with median septum slightly higher than others, crests of septa rounded or sharp; ventral muscle scars small, impressed on low pad, bisected and bounded by low myophragms; dorsal valve lobate, smooth inside and outside except for weak growth bands. *Lower Permian:* USA (Texas), southern Thailand.——FIG. 461,*1a–d.* **R. girtyi,* Lower Permian, Bell Canyon Formation, Texas; *a–c,* ventral, lateral, dorsal views of ventral valve, ×3 (Cooper & Grant, 1974); *d,* dorsal view of partly conjoined valves, ×3 (Stehli, 1956).

Paralyttonia Wanner in Wanner & Sieverts, 1935, p. 207 [**P. permica;* OD]. Shell thin with conspicuous trail; ventral septa irregular in number and occasionally branching or bent, crests flat or concave; muscle scars large, distinctly impressed on pads; exterior of dorsal valve reported as smooth and finely tuberculate; cardinal process minute, dorsal adductor scars on low pads. *Lower Permian:* Austria, Japan, Thailand, Timor.——Fig. 461,*2a,b. P. tenax* Grant, Lower Permian, Thailand; *a,* interior of ventral valve attached to small linoproductidine, ×3; *b,* posterior view of ventral interior, ×3 (Grant, 1976).

Superfamily PERMIANELLOIDEA He & Zhu, 1979

[*nom. transl.* Williams, Harper, & Grant, herein, *ex* Permianellida He & Zhu, 1979, p. 136]

Concavoconvex, elongately bilobate, variably emarginate lyttoniidines with finely tuberculate exteriors; ventral valve attached to substrate mainly by hornlike projections of unreflexed, everted posterior flap; flange variably developed, marginal to low vallum; ventral interior with raised dental areas and well-defined median muscle platform; dorsal valve bounded by marginal ridge hinge line, narrow extending laterally as ears; dorsal interior with fused bilobed cardinal process ankylosed to divergent ridges defining sockets, adductor scars variably impressed on either side of median ridge corresponding to external sulcus; pair of low ridges also disposed medianly along valve lobes. *Permian.*

Family PERMIANELLIDAE He & Zhu, 1979

[Permianellidae He & Zhu, 1979, p. 132]

Characters as for superfamily. *Permian.*

Permianella He & Zhu, 1979, p. 137 [**P. typica;* OD]. Gently concavoconvex, with a deep median incision in emarginate margin separating 2 elongate, subparallel lobes of shell; ventral flange developed as narrow fringe. *Upper Permian:* southern China.——Fig. 462,*1a–c.* **P. typica,* Upper Permian, southern China; *a,* internal mold of dorsal valve with adherent shell, ×2.75; *b,* external mold of dorsal valve, ×2.75; *c,* ventral valve, ×1.5 (He & Zhu, 1979).

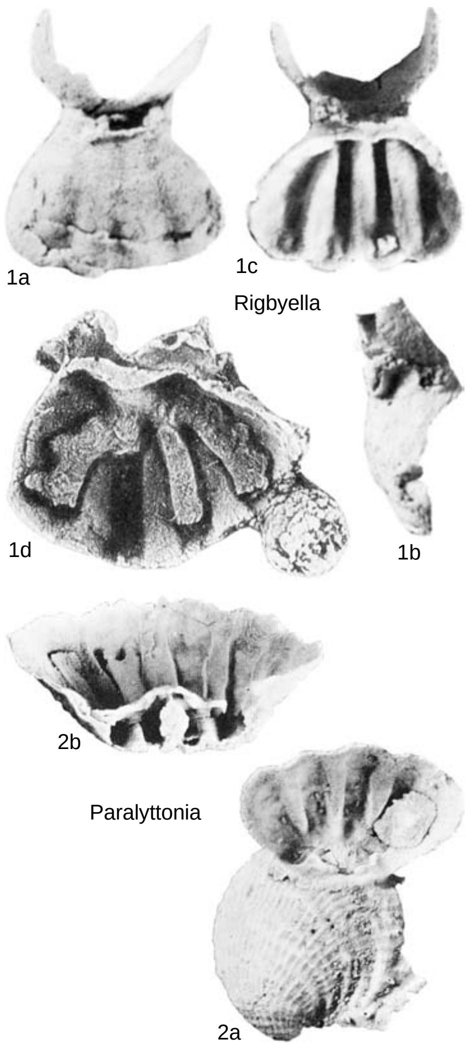


Fig. 461. Rigbyellidae (p. 638–639).

Dicystoconcha Termier & Termier in Termier & others, 1974, p. 122 [**D. lapparenti;* OD] [=*Dipunctella* Liang in Wang & others, 1982, p. 228 (type, *D. stenosulcata*); *Guangjiayanella* Yang De-li, 1984, p. 212[333] (type, *G. guangjiayanensis*); *Guangdongina* Mou & Liu, 1989, p. 458 (type, *G. xiamaoensis*); *Paritisteges* Liang, 1990, p. 488 (type, *P. latesculcata*); *Fabulasteges* Liang, 1990, p. 489 (type, *F. planata;* OD)]. Small shells with only shallow indentation in anterior zone of emarginate margin and with negligible ventral flange. [The genus was founded on a poorly preserved dorsal valve and is better understood through the review of permianellids by Wang and Jin (1991), which is the source of illustrations featuring specimens identified as conspecific with the type species. The genera placed in synonymy were erected for shells with trivial variations in shape]. *Lower Permian:*

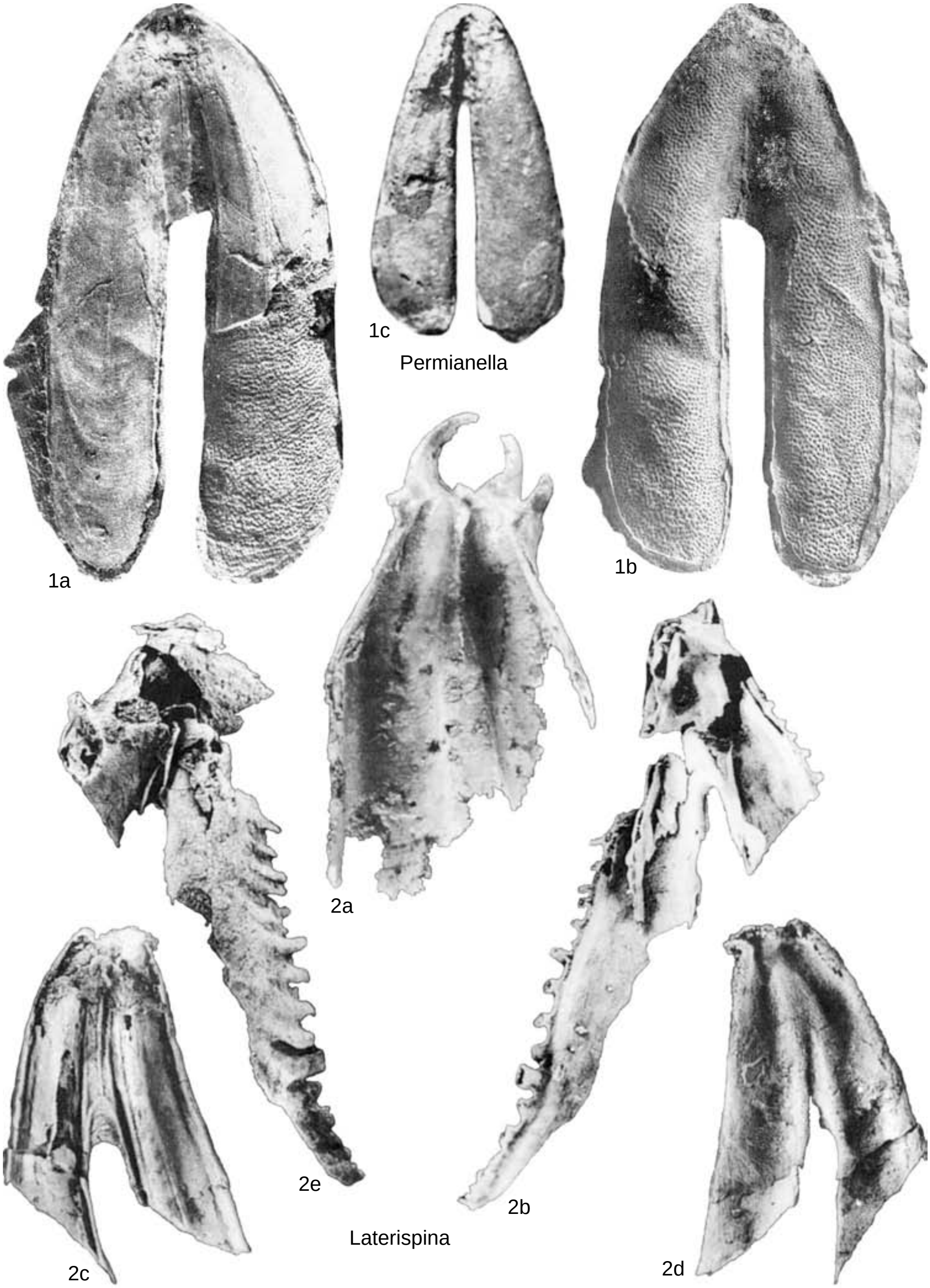


FIG. 462. Permianellidae (p. 639–641).

Afghanistan, southern China, Thailand.——FIG. 463,*3a,b.* **D. lapparenti,* Lower Permian, southern China; *a,* external mold of ventral valve, ×3; *b,* cluster ventral valves, ×2 (Wang & Jin, 1991).

Laterispina WANG & JIN, 1991, p. 496[500] [**L. liaoi;* OD]. Similar to *Permianella* but with more divergent lobes and with ventral flange prolonged laterally into spines. *Upper Permian:* southern China.

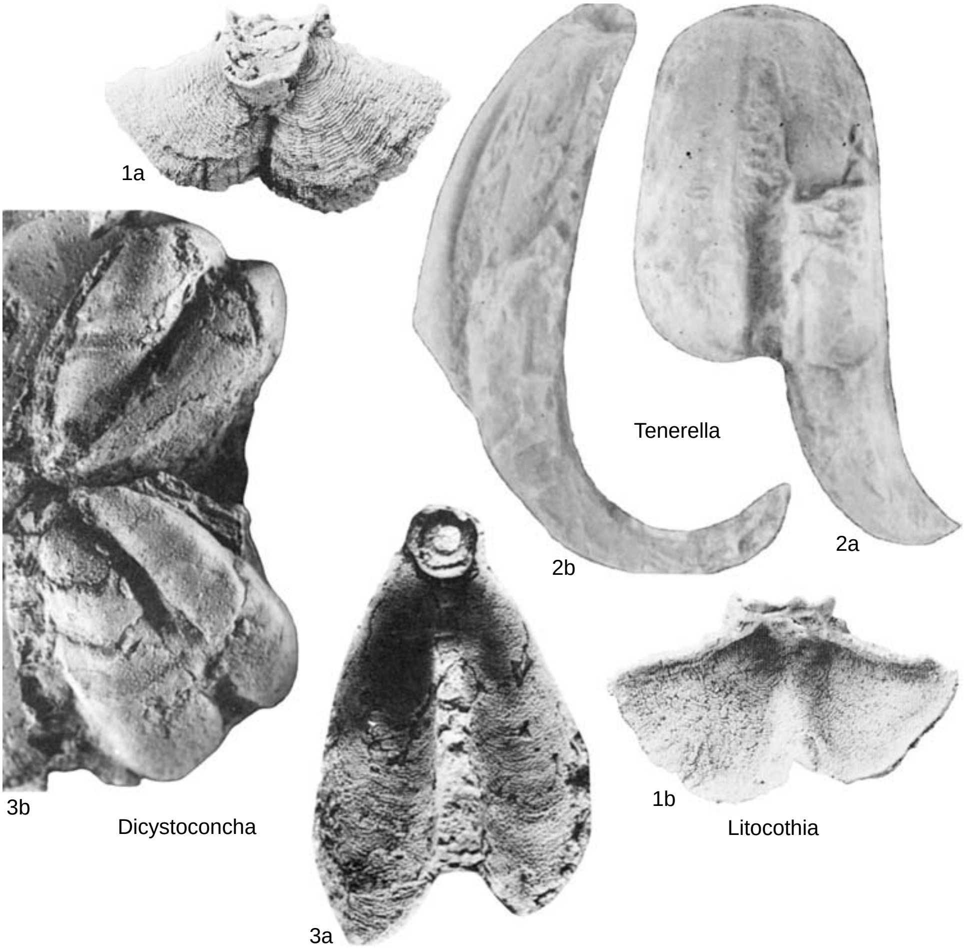


Fig. 463. Permianellidae and Uncertain (p. 639–642).

——Fig. 462,*2a–e.* **L. liaoi,* Upper Permian, southern China; *a,* ventral interior with attachment ring, ×3; *b,* ventral interior showing spines, ×1.5; *c,* dorsal interior, ×1.5; *d,* dorsal exterior, ×1.5; *e,* ventral exterior showing spines, ×1.5 (Wang & Jin, 1991).

Tenerella Liang, 1990, p. 511 [**T. usualisa;* OD] [=*Obliqunsteges* Liang, 1990, p. 511 (type, *O. distortus*); *Sicyusella* Liang, 1990, p. 512 (type, *S. regularis*)]. Similar to *Permianella* but strongly concavoconvex and with curved, divergent lobes; nature of ventral flange unknown. [One of several generic names given to these concavoconvex shells has been provisionally accepted on the assumption that the ventral flange, which is neither described nor revealed in the illustration of the type species, is negligible as in *Dicystoconcha.* Two genera erected at the same time as *Tenerella* have been distinguished in minor changes in shell shape that are likely to reflect nothing more than specific variability.] *Middle Permian–Upper Permian:* southern China.——Fig. 463,*2a,b.* **T. usualisa,* Upper Permian, southern China; ventral, lateral views of ventral valve, ×2 (Liang, 1990).

Family UNCERTAIN

Subfamily LOCZYELLINAE Licharew, 1937

[Loczyellinae Licharew, 1937, p. 83]

Shells ornamented by growth lines, shovel shaped to triangular with rounded anterior margin and sides converging acutely to umbones; ventral valve gently convex, medianly sulcate with flanks almost at right angles to venter; dorsal valve correspondingly concave with low median fold; internal features unknown. [The uncertain taxonomic position of this group is opportunely discussed in the description of *Caninella* LIANG.] *Permian.*

Loczyella FRECH, 1901, p. 503 [**L. nankingensis;* OD]. Characters of the subfamily; no ears developed at hinge line of dorsal valve. *Permian:* China, Caucasus.

Caninella LIANG, 1990, p. 216 [**C. zhinanensis;* OD]. Concavoconvex, uniplicate shells, trigonal in outline, anterior margin truncated, with small ears at narrow hinge line; ventral interior with pair of long lateral septa; dorsal interior with thin median septum and small cardinal process. [*Loczyella* and *Caninella* have been provisionally assigned to the same subfamily as they are evidently strophomenates, probably related to each other and possibly permianelloid in affinity. The genera, however, have been founded on poorly preserved specimens and study of better topotypic material may lead to changes in their taxonomic status.

The type material of *Loczyella* is so poorly preserved that descriptions of the genus have been based on the comments by LIKHAREV (1930) on two specimens from the Permian of northern Caucasus, described as ?*Loczyella parvula* LIKHAREV. JIN Yu-Gan (personal communication to R. E. GRANT, 1991) has examined these specimens in the Institute of Geology, St. Petersburg, and identified them as permianellids as they are bilobate in outline and attached to a crinoid stem by the umbo. It remains to be seen whether topotypic *Loczyella* is congeneric with the specimens from Caucasus.

Caninella is not much better served, as it has been founded on three poorly preserved specimens, one of which, the holotype, is a subconical ventral valve with the umbo broken off and no dorsal valve attached. The relationship between *Caninella* and *Loczyella* is, therefore, not securely established nor is their taxonomic position within the Strophomenata.] *Upper Permian:* China (Zhejian).

Litocothia GRANT, 1976, p. 166 [**L. cateora;* OD]. Small, transverse, bilobate ventral valve with deep, long median sulcus, ornamented by closely spaced fila, attached by beak; small everted posterior flap forming reflexed region dorsal of hinge; ventral interior featureless except for median raised zone corresponding to sulcus. [This ventral valve has a lyttonioid apical region and even its bilobation is reminiscent of juvenile lyttonioids. There is, however, no sign of a vallum within the valve, while the concentric ornamentation and the reflexed, posterior flap are presently unknown among the permianellids. For the time being the genus remains unattributed among the lyttoniidines.] *Lower Permian:* Thailand.——FIG. 463,*1a,b.* **L. cateora,* Lower Permian, Thailand; exterior, interior of ventral valve, ×4 (Grant, 1976).

UNCERTAIN

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Suborder UNCERTAIN

?Chonopectella SARYTCHEVA, 1966, p. 135, *nom. nov. pro Chonopectoides, non* CRICKMAY, 1963 [**Chonopectoides permicus* SARYTCHEVA in SARYTCHEVA & SOKOLSKAYA, 1965, p. 232; OD]. Poorly represented and known; small with weakly convex ventral valve, teeth; spines at hinge; intersecting fine, oblique rugae and single submedian rib. *Upper Permian (Capitanian):* Transcaucasia.——FIG. 464,*2a,b.* **C. permica* (SARYTCHEVA), Dzhulfinsky Formation, Ogbin; holotype, PIN 2071/52; *a,* ventral valve exterior, ×1; *b,* detail of ornamentation, ×5 (Sarytcheva & Sokolskaya, 1965).

Ploughsharella LIANG WEN-PING in WANG & others, 1982, p. 227 [**P. putaoshanensis;* OD]. Poorly known; medium width, outline subtrigonal with extended ventral umbo and trigonal interarea; profile strongly ventribiconvex; seemingly lacking ribbing and spines, but with prominent growth lines; anterior commissure widely unisulcate; interiors unknown. [LIANG placed as an unknown family in the Productidina, but even a productide assignment is in question.] *Upper Permian:* eastern China.z——FIG. 464,*1a–d.* **P. putaoshanensis,* Upper Permian, eastern China; shell viewed posteriorly, anteroventrally, anteriorly, laterally, ×1.3 (Wang & others, 1982).

?Punctoproductus LIANG WEN-PING, 1990, p. 368[481] [**P. eximus;* OD]. LIANG placed in his new order, the Punctoproductida, with endopunctae but no pseudopunctae, along with the Dipunctellidina [=*Dicystoconcha* (Permianellidae)]. Further defined as lacking spines, concavoconvex, and coarsely ribbed. [The claim for endopunctation in the Productida has not been supported, and the genus may not belong here]. *upper Upper Permian:* China.——FIG. 464,*3a–c.* **P. eximus,* upper Upper Permian, Lengwu Formation, Zhejiang; anterior, lateral, posterior views of shell, ×2 (Liang, 1990).

NOMINA NUDA

Achunoproductus USTRITSKY, 1971, p. 21. No diagnosis provided, but possibly related to *Shrenkiella* in the Monticuliferidae. *Upper Carboniferous, ?Lower Permian:* Russia (Urals).

Chaoina CHING YU-GAN in CHING YU-GAN, LIAO ZHAO-TING, & HOU HONG-FEI, 1974, p. 308 [**C. reticulatia;* OD]. Small, subquadrate, widest at hinge; dorsal valve sharply geniculate, but with shallow corpus cavity; ribbing strong, almost entirely costate; rugae on disks; spines in rows separating ears and scattered on ventral valve; cardinal process small, sessile; cardinal ridge thin; adductor scars elevated anteriorly; brachial ridges obscure. [Genus and species not defined, possibly

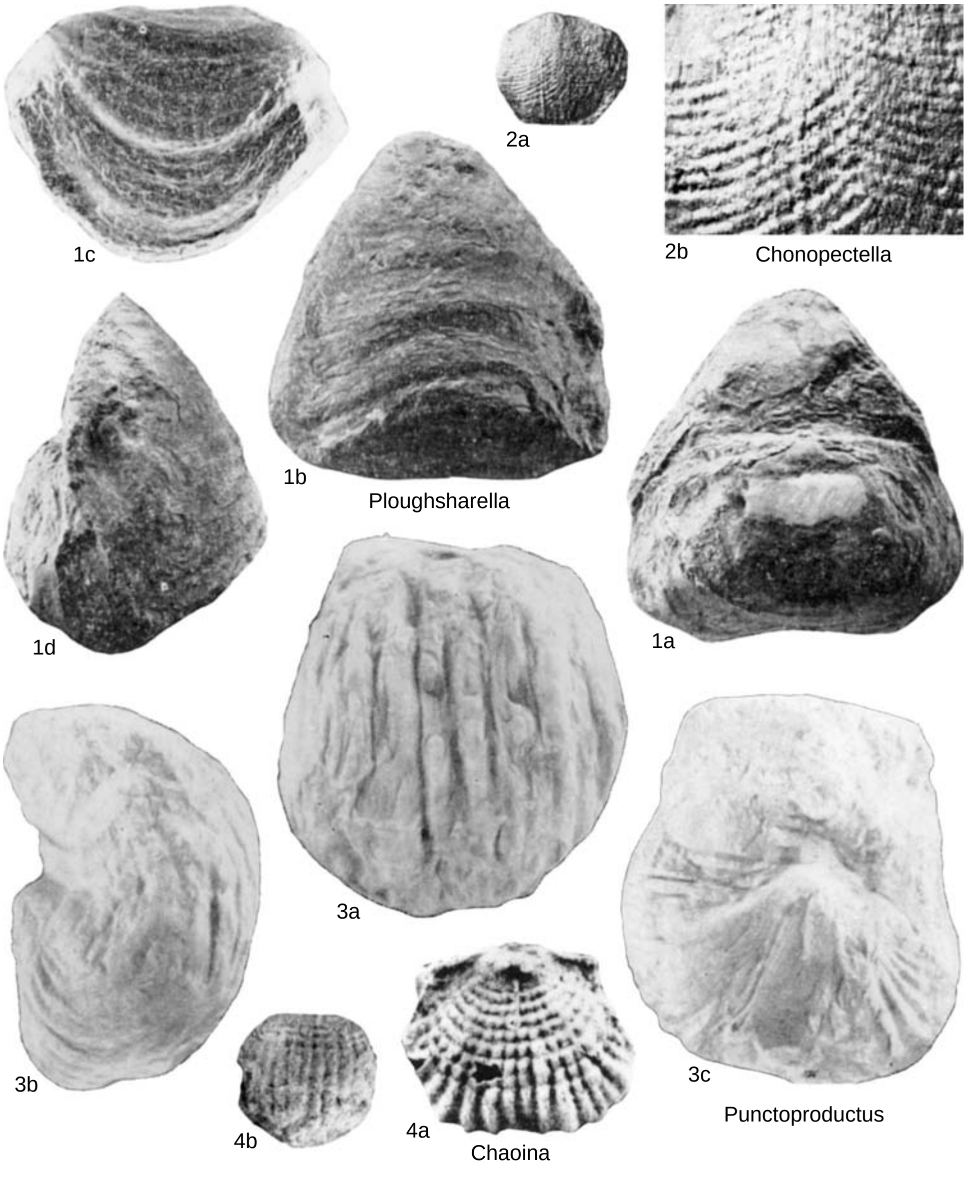

FIG. 464. Uncertain (p. 642–643).

belonging to the Productinae.] *Lower Permian (Kungurian):* southwestern China.——FIG. 464,*4a,b.* **C. reticulata,* Chihsian Formation, Sichuan; *a,* dorsal valve interior with much of shell missing, ×2; *b,* ventral valve viewed anteroventrally, ×1 (new).

Choanoproductus TERMIER & TERMIER, 1970, p. 459 [**C. guberi;* OD] [=*Choanoproductus* TERMIER & TERMIER, 1966, p. 609, *nom. nud.*]. No diagnostic descriptions for genus or species, or relationship provided. Illustrations of muscle scars only, possibly representing a strophalosiidine. *Upper Permian (Capitanian):* Cambodia.

Parapulchratia CHAN in HOU HONG-FEI, ZHAN LI-PEI, & CHEN BIN-WEI, 1979, p. 87 [**Productus pustulosus palliatus* KAYSER, 1883, p. 186; OD]. No diagnosis provided for genus or type specimen. KAYSER's specimens possibly representing several genera. *Upper Permian (?Changhsingian):* China.

Uraloproductus USTRITSKY, 1971, p. 21 [**Productus stuckenbergensis* KROTOW, 1885, p. 72; OD]. No description or diagnosis of genus provided. *Lower Permian:* Asian Arctic.

ORTHOTETIDA

Alwyn Williams,[1] C. Howard C. Brunton,[2] and A. D. Wright[3]
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Order ORTHOTETIDA Waagen, 1884

[*nom. transl.* Williams & Brunton, herein, *ex* Orthotetinae Waagen, 1884, p. 576]

Strophic, commonly biconvex strophomenates; ventral interarea well developed, with pseudodeltidium; dorsal interarea short to obsolete, chilidium variably present; teeth deltidiodont, commonly supported by dental plates; cardinal process bilobed to forked; laminar shell pseudopunctate, less commonly impunctate or extropunctate. *Lower Ordovician (Llanvirn)–Upper Permian.*

Both suborders recognized as comprising the order Orthotetida were first associated by Schuchert (1913a, p. 387) as subfamilies of the family Strophomenidae. The triplesioids with their impunctate shell and biconvex profile did not, however, sit comfortably with the pseudopunctate concavoconvex strophomenides and were cited by Williams (1956, p. 284) as a superfamily, which did not easily fall into place in his six groupings; he suggested that they may belong to either his *Orthis* or *Pentamerus* groups. The triplesioids were regarded as an aberrant group of orthoids by Wright (1963a, 1965b). Through electron microscopy, Williams (1968a) was able to demonstrate that, along with other stocks, the triplesioids and orthotetoids possess a laminar secondary shell. He later suggested (Williams, 1970) that the two groups were closely related, having diverged from the billingselloid stock, probably in Late Cambrian times. The rare occurrence of pseudopunctae in triplesioids (Wright, 1970) supports this interpretation, as does the morphology of the pseudodeltidia and chilidia of the two groups (Wright, 1971, p. 350).

ORTHOTETIDINA

Alwyn Williams and C. Howard C. Brunton
[The University of Glasgow; and formerly of the Natural History Museum, London]

Suborder ORTHOTETIDINA Waagen, 1884

[*nom. transl.* Cooper & Grant, 1974, p. 256, *ex* Orthotetinae Waagen, 1884, p. 576]

Shells of variable size, strophic but commonly semicircular to subrounded in outline, profile variable, weakly concavoconvex to biconvex and ventrally subconical; functional pedicle present only in earliest known species; ventral valve usually cemented by umbo or greater part of shell surface to substrate, dorsal valve invariably convex in young growth stages; radial ornamentation normally well developed, essentially finely costellate by branching or intercalation; ventral interarea commonly with well-defined perideltidium; pseudodeltidium commonly forming complete cover to delthyrium; dorsal interarea becoming short but wide, chilidium well developed to obsolescent; teeth commonly supported by dental plates occasionally converging to form spondylium supporting entire ventral muscle field or septal chamber for adductor scars only; cardinal process bilobed, in many forms greatly extended ventrally with single proximal shaft, ankylosed with variably disposed socket ridges, socket plates, and variably developed brachiophores; shell typically pseudopunctate or, less commonly, extropunctate, impunctate in older stocks. *Upper Ordovician–Upper Permian.*

The orthotetidine brachiopods have always been the subject of taxonomic confusion. The distinctiveness shared by long-established genera, like *Orthotetes* Fischer de Waldheim, 1850, *Hipparionix* Vanuxem, 1842, and *Stroptorhynchus* King, 1850, has never been in doubt; but their precise affinities with other brachiopod groups have repeatedly given free rein to broadly divergent taxonomic practices, well documented by Manankov (1979).

The first authoritative grouping of the orthotetoids within the Brachiopoda as a whole was that presented by Schuchert (in Schuchert & LeVene, 1929, p. 16), who accepted the Orthotetinae of Waagen (1884) as a strophomenoid subfamilial repository, not only for all orthotetoid genera then known but also for an orthoid (*Orthidium*) with a vaguely orthotetoid cardinal process, as well as all resupinate strophomenides.

In the 1950s, when the superfamily Orthotetacea was first proposed (Williams, 1953b, p. 9), a number of families were erected by various students of the group so that, by the end of the decade, seven such taxa were recognized (Williams, 1953b; Stehli, 1954; G. A. Thomas, 1958; Boucot, 1959). These new taxa largely clarified the definitive orthotetoid character states although further complications arose with the assignment to the superfamily by Williams (1953b) of the Davidsoniidae, Gemmellaroiidae, Scacchinellidae, and the Thecospiridae for no better reason than that they were cemented strophic stocks allegedly without spines but with pseudopunctate shells.

By 1965, when the first edition of the brachiopod volumes of the *Treatise on Invertebrate Paleontology* was published (Moore, 1965), the superfamily had acquired the name of Davidsoniacea in place of Orthotetacea in accordance with nomenclatorial rules of priority. Both the Gemmellaroiidae and Scacchinellidae had been found to be spinose and had been removed to the Productidina (Muir-Wood & Cooper, 1960, p. 66); and, although the Triassic spire-bearing Thecospiridae had been retained in the superfamily, the orthotetoids formed a reasonably well-defined group.

Since the 1965 *Treatise* study of the davidsoniaceans (Williams, 1965e, p. 405–412) the number of genera assigned to the group has more than doubled to 104. Only Cooper and Grant (1974), who at the time were dealing mainly with Permian taxa, and Manankov (1979), however, have offered a comprehensive revision of the classification to cope with this generic proliferation. The most important steps taken by Cooper and Grant were to transfer to the Strophomenidina all impunctate genera that were assembled within an amended Davidsoniacea into two families, the Davidsoniidae and Fardeniidae (a junior synonym of the Chilidiopsidae); and to erect a new suborder, Orthotetidina, for all pseudopunctate genera that were grouped into two superfamilies, the Orthotetacea and Derbyiacea, containing seven families and seven subfamilies. Manankov (1979), on the other hand, retained both impunctate and pseudopunctate taxa within an amended Davidsoniacea that embraced four families and ten subfamilies after the removal of the Thecospiridae and its promotion to the rank of superfamily with the Strophomenida. Previously, however, Brunton (1972) and Brunton and MacKinnon (1972) had transferred *Thecospira* to the Koninckinidae within the Spiriferida on the evidence of shell structure, pedicle foramen characteristics, and spiralium.

These two classifications differed fundamentally. Manankov's (1979) approach was essentially phylogenetic and prompted him to identify several recurrent trends, especially changes in shell shape and in the elaboration of dental plates and cardinalia. In contrast, Cooper and Grant (1974) paid less attention to taxonomic complications that could have arisen from the recurrence of parallel trends, particularly in the development of the cardinalia; their approach was largely monothetic, leading, for example, to their transfer of all impunctate species from their Orthotetidina (Cooper & Grant, 1974, p. 256) to the Strophomenidina despite the fact that the latter suborder is essentially pseudopunctate. Prior to the study by Williams and Brunton (1993) three very different, flawed

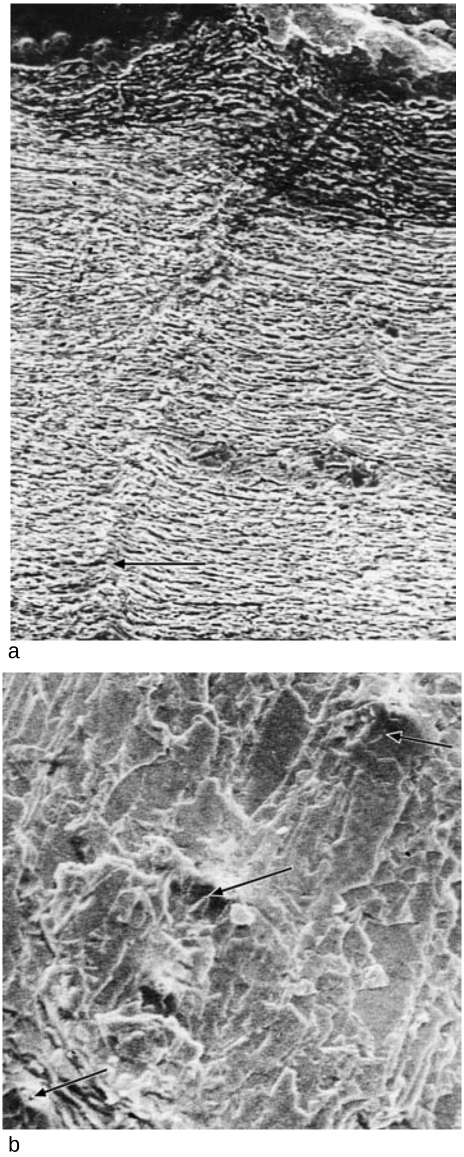

FIG. 465. Extropunctae of *Schuchertella lens* (WHITE) from uppermost Famennian, Louisiana Limestone, Missouri; *a,* polished and etched section with costellate exterior to top, SEM, ×130; *b,* external view of exfoliated surface within cross-bladed laminar succession, SEM, ×440; *arrows* point to extropunctae (new).

classifications were being used in systematic studies of orthotetidines and davidsoniaceans, as the case may be. Their deficiencies were brought into sharp focus during the updating of the taxonomy of the revision of the orthotetoids. Thus the oldest classification currently in use drawn up for the first edition of the *Treatise* is not only incapable of accommodating all valid genera erected since 1965 but also flawed in the way it used shell structure for taxonomic purposes. In particular, the classification did not take into account the discovery by G. A. THOMAS (1958, p. 36) that in *Streptorhynchus* and allied genera, microscopic conical flexuring of the laminar shell points outwardly (extropunctae of WILLIAMS & BRUNTON, 1993, p. 946), not inwardly as in the true pseudopunctate condition. In addition the studies of shell structure and morphology by WILLIAMS and BRUNTON (1993) and their use of phylogenetic analysis to assess the merits of the two other commonly used classifications by COOPER and GRANT (1974) and MANANKOV (1979) revealed that they are also deficient in one way or another.

A feature considered significant in the recognition of all orthotetoids by GRANT (1980) is the condition in which koskinoid perforations are concentrated around ventral umbos. WILLIAMS and BRUNTON (1993) investigated these perforations and concluded that they could not have developed as part of the brachiopod's growth and in consequence have no taxonomic value. Partly because *Gemmellaroia* and allied genera have koskinoid perforations, GRANT (1993a) transferred the Gemmellaroiidae from the Productida to the Orthotetidina. The recognition, however, that *Gemmellaroia* is spinose places it, as well as one other genus, within the richthofenioids. *Loczyella* is probably a permianellid, leaving *Cydalia* questionably placed within the Richthofenioidea.

The orthotetidines constitute one of the few suborders of the Brachiopoda characterized by several basic differences in the ultrastructure of their shells. All true orthotetids have a secondary shell of cross-bladed laminae bearing closely distributed pseudopunctae composed of microscopic conical deflections of the laminae that are directed inwardly. They evolved from the laminar-shelled chilidiopsoids that are impunctate except for a few specimens of Upper Ordovician *Fardenia,* which bear sporadically occurring, impersistent pseudopunctae. The pseudopunctate orthotetoids were in turn ancestral to the laminar-shelled schuchertellids (including the Streptorhynchinae), which are extropunctate with radially distributed microscopic conical deflections of the laminae pointing outwardly, tending to leave dimpled inner surfaces (Fig. 465).

The typical orthotetoid shell is ultrastructurally indistinguishable from that of the strophomenids although the pseudopunctate condition (Fig. 466) arose earlier in the latter group. So far as is known, the extropunctate condition is unique to the orthotetidines, while pseudopunctae with taleolae, so characteristic of the leptaenids, stropheodontids, chonetidines, productidines, and related aberrant Permian forms, have yet to be positively identified in orthotetidines.

The orthotetidines were also closely related to the other strophomenides in many basic morphological features (Fig. 467.2, 467.3). The presence, in Ordovician and lower Silurian species of both groups, of a pseudodeltidium with a supra-apical foramen is indicative of the existence of a ventral body wall in the living state (WILLIAMS, 1956, p. 258), which was absent from other articulated brachiopods except for some orthides. The sealing of the foramen in all later Paleozoic strophomenidines and orthotetidines confirms that atrophy of the pedicle had taken place throughout these groups by Carboniferous times. Subsequently, many strophomenides (including the orthotetidines) acquired a cementing habit; and, since the davidsoniids were also cemented to the substrate and appeared to have a pseudodeltidium, they were widely accepted as orthotetidines and, indeed, gave their name to the suborder. Yet, as JOHNSON illustrated (1982, pl. 1, fig. 11, 14), the so-called pseudodeltidium is a deltidium and, with the discovery (WILLIAMS & BRUNTON, 1993) that the shell is fibrous not laminar, *Davidsonia* and other related, cementing, middle-Paleozoic brachiopods with calcareous spiralia have been transferred to the atrypides.

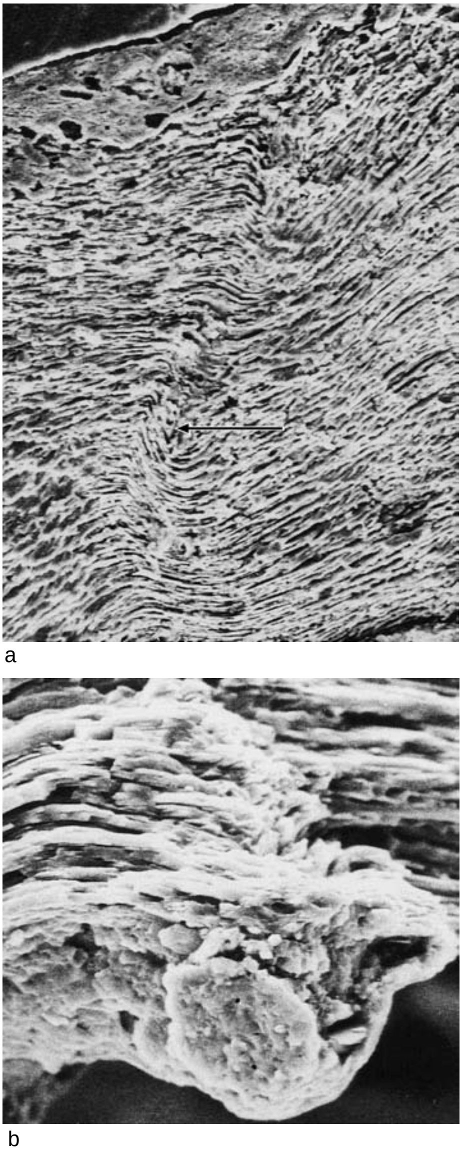

FIG. 466. Pseudopunctae of *Apsocalymma shiellsi* MCINTOSH from Lower Carboniferous, Lower Limestone Group, Scotland; *a,* polished and etched section with weathered exterior to top and *arrow* pointing to trace of pseudopuncta, SEM, ×210; *b,* fractured section of interior showing flexured laminae in relation to tubercle at internal surface, SEM, ×860 (new).

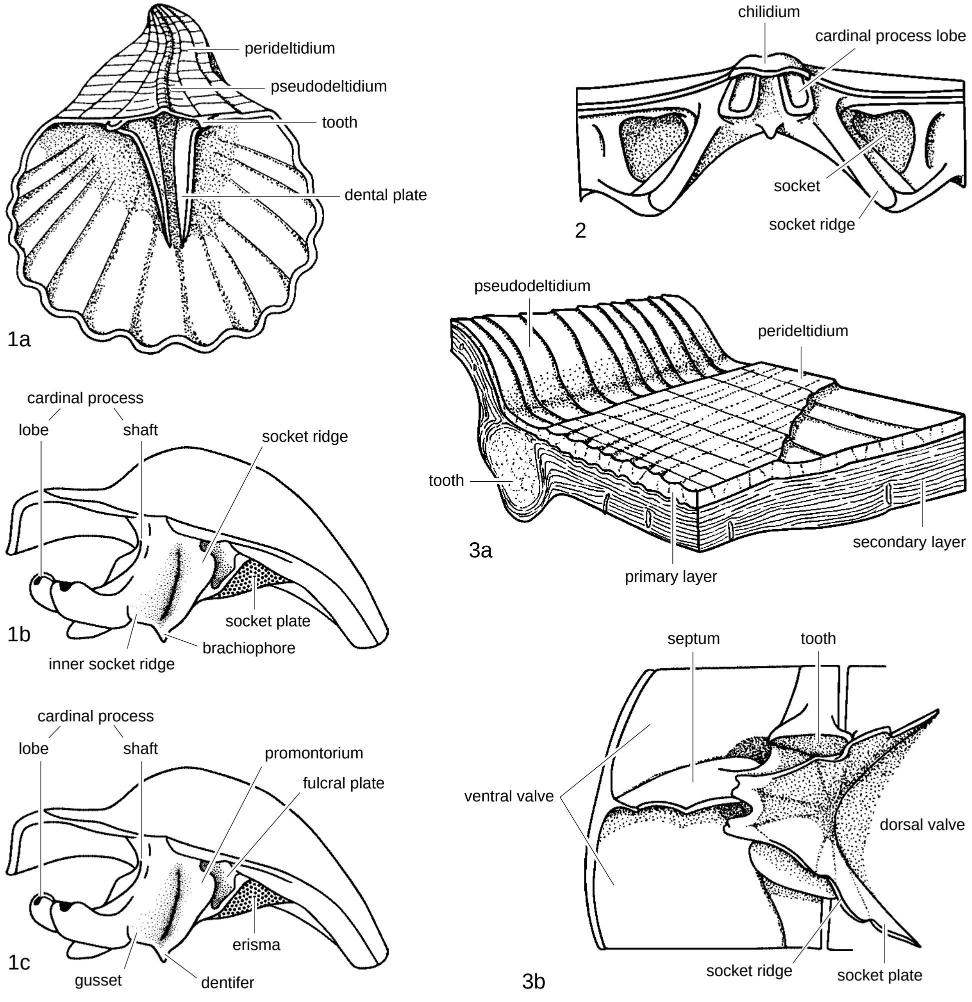

FIG. 467. Morphological features of orthotetidines; *1a–c, Meekella; 1a,* ventral valve interior (Williams, 1965d); *1b,c,* oblique lateral views showing structures in cardinalia, *1b,* terms used herein and *1c,* terms used by COOPER and GRANT, 1974; *2, Schuchertella,* chilidium and adjacent structures of dorsal valve; *3a,b, Derbyia; 3a,* oblique three-dimensional diagram showing structure of part of interarea; *3b,* view of inside of shell looking posteriorly (Williams, 1965d).

The widespread acquisition by many orthotetidines of a cementing habit led repeatedly to the elevation of their shells above the substrate by excessive conical deepening of the attached ventral valves. This conical deepening was accompanied by complementary extensions of skeletal articulatory devices. The morphological effects were quite dramatic, especially with regard to variations in the proportional development of various ridges and plates supporting the teeth, the bilobed cardinal process accommodating the dorsal diductor bases, and other associated parts of the cardinalia defining the dental sockets. These exaggerated structures, exemplified by *Meekella* (Fig. 467.1), were given specific terms by COOPER and GRANT (1974) in order to draw attention to their development within a few subfamilies. Many of these terms, however, are synonyms of others that were already widely used throughout the phylum for homologous structures (Fig.

467.1b–467.1c) and have not been used herein in taxonomic descriptions (see the chapter on morphology, p. 371 in Kaesler, 1997). Not surprisingly, these repeated trends gave rise to similar spectacular structures in several independent stocks. In Late Devonian to Early Carboniferous times elongate cardinal processes, taking with them other elements of the cardinalia, developed in the Adectorhynchinae, Streptorhynchinae, Derbyiinae, and Meekellinae and became very elongated with the conical deepening of ventral valves in Permian species of the last two subfamilies. The trends were broadly synchronous within a readily identifiable phylogeny that was evidently compatible with the stratigraphic ranges of constituent taxa (Fig. 468). As a result, previous classifications were dominated by the preferential weighting of one kind of feature, for example dental plates or socket plates, at the expense of others. In effect, homoplasy has played a more important role than homology in determining the structure of previous orthotetidine classifications.

These homoplastic trends can be disentangled by paying due regard to morphology as a whole through phylogenetic analysis and especially to the more stable changes attending the evolution of shell structure. The present classification attempts to meet these conditions. Even so, it is provisional on getting further information not only on the many poorly described genera currently in circulation but also on such taxa as *Diplanus* and *Hypopsia,* whose exquisitely silicified morphology could well be at variance with their original shell structure, which remains unknown.

Superfamily ORTHOTETOIDEA Waagen, 1884

[*nom. transl.* Williams, 1953b, p. 9, *ex* Orthotetinae Waagen, 1884, p. 576]

Ventral valve lacking supra-apical foramen, cemented or secondarily free with deformed conical shape characteristic of later groups; almost invariably finely costellate with secondary costation and impersistent rugation rarely developing later; pseudodeltidium well developed, normally convex or becoming flat with monticulus in later taxa, chilidium variably developed; dental ridges unsupported in some stocks, discrete or tending to converge to form apical chamber; dental plates, when present, converging to form spondylia or narrow medial chambers; myophragm variably developed in both valves; socket ridges recurved, becoming large, divergent, and ankylosed but with proximal single shaft of cardinal process lobes and with exaggerated brachiophores in independently derived later groups; shell structure pseudopunctate or more rarely extropunctate. *Middle Devonian–Upper Permian.*

Family ORTHOTETIDAE Waagen, 1884

[*nom. transl.* McEwan, 1939, p. 619, *ex* Orthotetinae Waagen, 1884, p. 576] [=Derbyoidinae Thomas, 1958, p. 21]

Large, subquadrate, ventribiconvex to resupinate, normally rectimarginate, finely costellate; ventral beak typically symmetrical, interarea apsacline with well-developed perideltidium and convex pseudodeltidium, dorsal interarea usually short, anacline with small chilidium occasionally grooved; dental ridges normally convergent on median ridge or septum, unsupported by dental plates; socket ridges commonly recurved, not ankylosed to low, discrete cardinal process lobes; ventral muscle scar flabellate, usually impressed; dorsal adductor scars rarely impressed, dorsal myophragm variably developed. *Lower Carboniferous–middle Permian.*

Orthotetes Fischer de Waldheim, 1829, p. 375 [**O. radiata* Fischer de Waldheim, 1850, p. 491; SD Girty, 1909, p. 192] [=*Pseudoorthotetes* Sokolskaya in Sarytcheva & others, 1963, p. 96 (type, *P. borodencovensis*); *Orthotetoides* Lazarev, 1984, p. 65 (type, *Orthotetes socialis* Fischer de Waldheim, 1850)]. Biconvex, rectimarginate, finely costellate by branching; usually with symmetrical ventral beak, convex pseudodeltidium, dorsal interarea linear to vestigial, chilidium small, grooved, dental ridges strong, convergent on high ventral median septum to define small delthyrial chamber commonly filled with secondary shell, less commonly extending anteromedianly for entire length of ventral interarea; socket ridges recurved; ventral muscle scar impressed, large, flabellate, dorsal myophragm

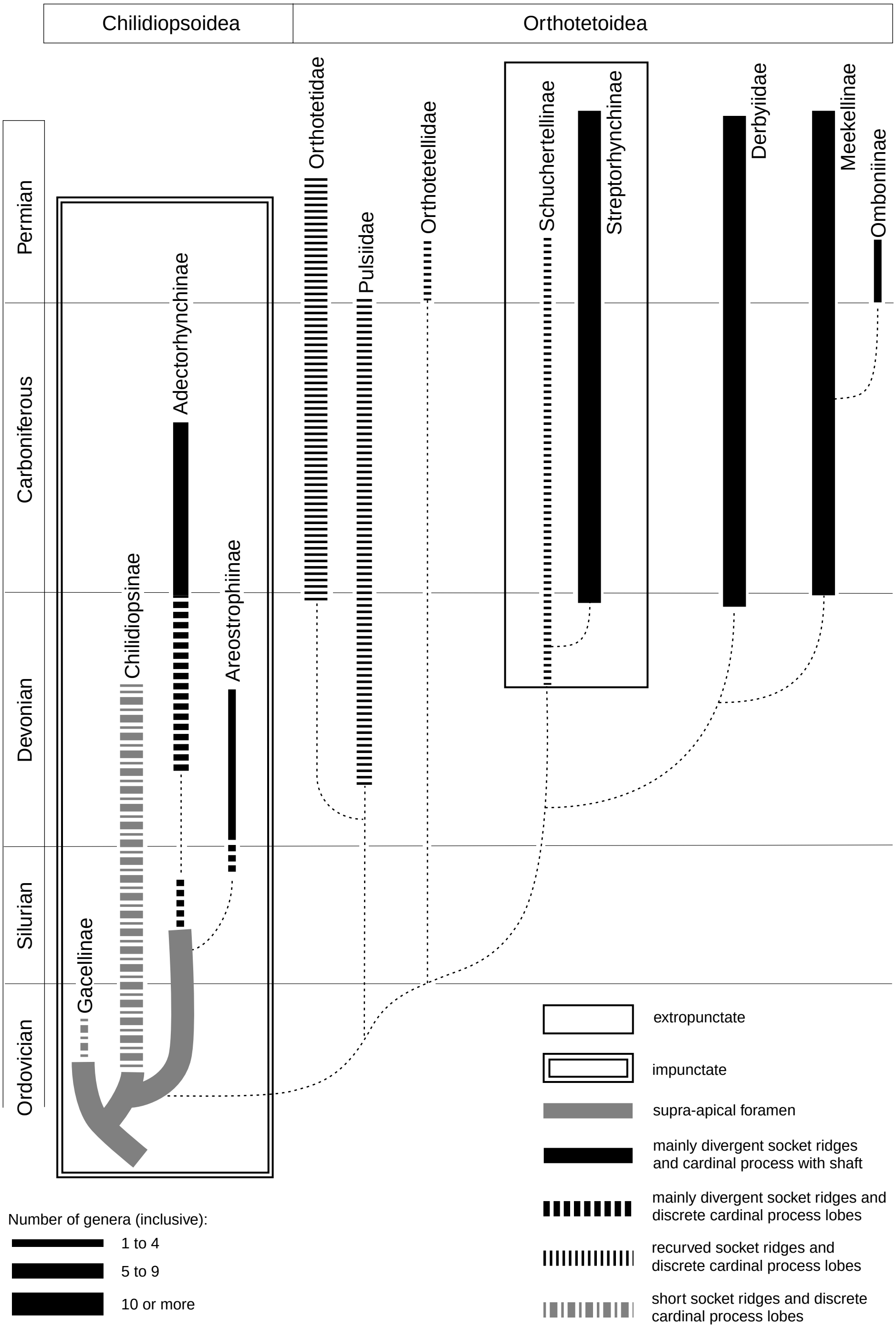

FIG. 468. Chronostratigraphy of orthotetidine phylogeny showing main trends in evolution of pedicle foramen, shell structure, and cardinalia; all taxa outside two designated boxes are pseudopunctate (new).

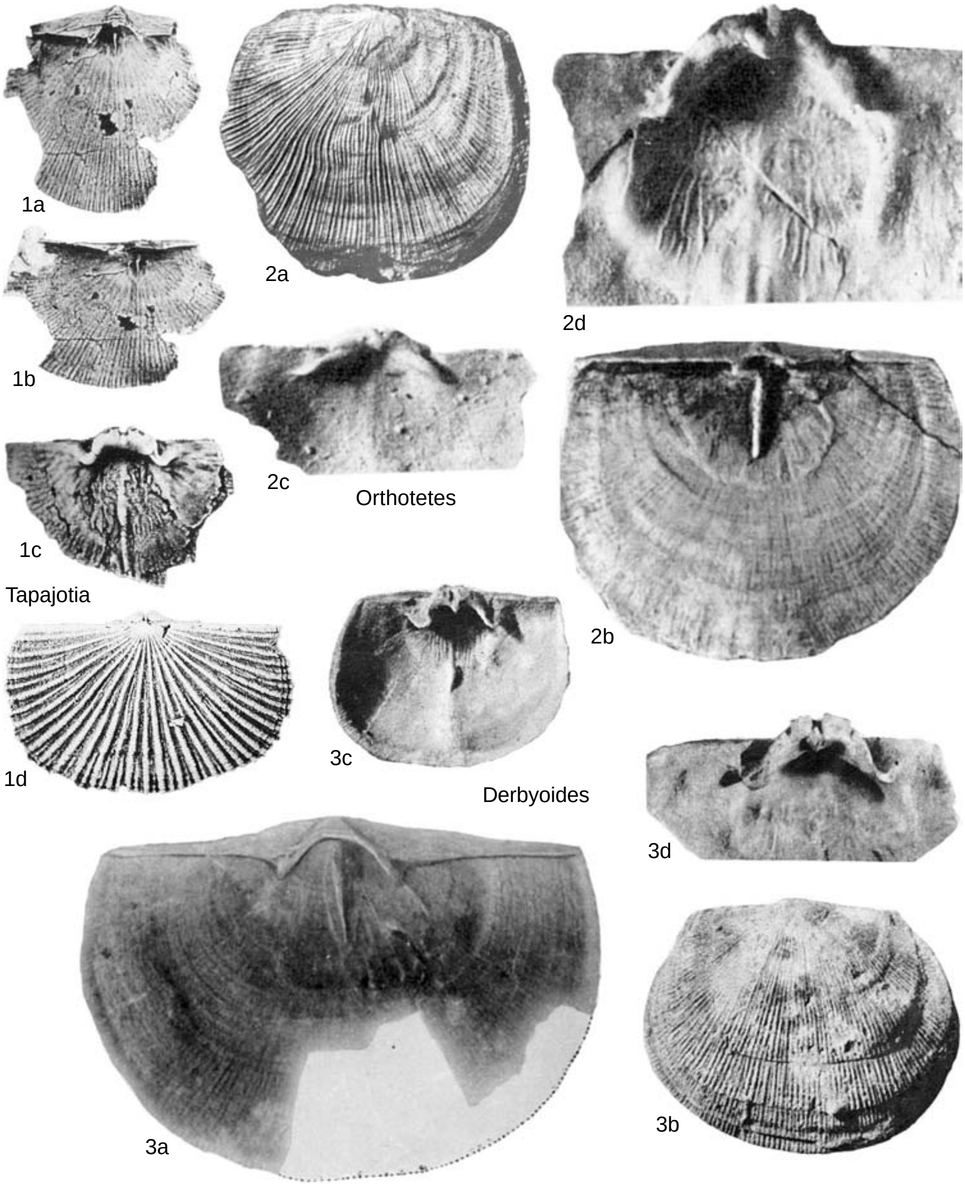

FIG. 469. Orthotetidae (p. 649–652).

broad, low. [*Pseudoorthotetes* was erected for species with longer delthyrial chambers and cardinal processes, *Orthotetoides* for species with medianly grooved chilidium and without dorsal myophragm. Until these differences are shown to be specifically constant, these genera are best treated as junior synonyms of *Orthotetes.*] *Lower Carboniferous–Lower Permian:* Eurasia.——FIG. 469,*2a–d.* **O. radiata* FISCHER DE WALDHEIM, Moscovian, Russia; *a,* ventral valve exterior, ×1 (Sokolskaya, 1954); *b,c,* ventral valve interior, dorsal valve interior, ×1; *d,* dorsal valve interior, ×2 (Manankov, 1973).

Apsocalymma McIntosh, 1974, p. 213 [*A. shiellsi; OD]. Similar to *Brochocarina* but with vestigial pseudodeltidium complementing large, medianly grooved chilidium and strong, dorsal myophragm continuous with base of cardinal process. *Lower Carboniferous (upper Viséan):* Scotland.——Fig. 470,*2a–d.* *A. shiellsi, Lower Limestone Group, Ayrshire; *a,b,* ventral valve, dorsal valve interiors, ×1; *c,* posterior view of dorsal cardinalia and chilidium, ×4; *d,* dorsal valve exterior, ×0.66 (McIntosh, 1974).

Brochocarina Brunton, 1968, p. 31 [**Schuchertella wexfordensis* Smyth, 1930, p. 555; OD]. Similar to *Orthotetes* but essentially planoconvex, finely parvicostellate by intercalation, intersected by fine concentric fila, with anacline dorsal interarea and arched chilidium; dental ridges convergent posteriorly on trifid ridge forming posterior boundary of faintly impressed ventral muscle scar with low myophragm. *Lower Carboniferous:* Ireland, ?Australia.——Fig. 470,*1a–e.* **B. wexfordensis* (Smyth), Asbian, County Fermanagh, Ireland; *a,* posterodorsal view of incomplete shell, ×1.5; *b,c,* ventral valve interior, exterior, ×0.8; *d,* detail of external ornamentation, ×3; *e,* dorsal valve interior, ×0.8 (Brunton, 1968).

Derbyoides Dunbar & Condra, 1932, p. 114 [**D. nebrascensis;* OD]. Similar to *Orthotetes* but more variable in shape with anterior commissure occasionally undulating; pseudodeltidium convex with median groove; dental ridges not cemented to low ventral myophragm; median node at base of cardinal process; dorsal adductor scars impressed, bilobate about low myophragm. *Upper Carboniferous–Lower Permian:* North America.——Fig. 469,*3a–d.* **D. nebrascensis,* Kasimovian, Nebraska; *a,* ventral valve interior, ×1 (Dunbar & Condra, 1932); *b,c,* exterior, interior views of dorsal valve, ×1; *d,* dorsal cardinalia, part of adductor scars, ×1.5 (Dunbar & Condra, 1932).

Liberella Liang, 1990, p. 104[456] [**L. cassidula;* OD]. Small to medium, commonly strongly uniplicate, finely costellate by branching, finely lamellose; pseudodeltidium and chilidium undescribed; dental ridges discrete of strong ventral myophragm ankylosed to internal surface of pseudodeltidium and bisecting faint, flabellate ventral muscle scar; short cardinal process with lobes fused medially into trifid structure; socket ridges recurved. *middle Permian:* China (Zhejiang Province).——Fig. 470,*3a–c.* **L. cassidula,* middle Permian, Zhejiang; *a,b,* dorsal valve, ventral valve exteriors, ×2; *c,* posterior view of internal mold, ×2 (Liang, 1990).

Tapajotia Dresser, 1954, p. 33 [**Streptorhynchus tapajotensis* Derby, 1874, p. 37; OD]. Similar to *Derbyoides* but with weak myophragm in ventral valve and nearly planar dorsal valve with more delicate cardinalia and without impressed dorsal adductor scars or myophragm. *Upper Carboniferous–Lower Permian:* Brazil.——Fig. 469,*1a–d.* **T. tapajotensis* (Derby), Itaituba, Bashkirian, Rio Tapajos; *a,b,* dorsal, anterodorsal views of incomplete ventral valve interiors, ×1; *c,* interior view of dorsal valve, ×1.5; *d,* exterior view of dorsal valve, ×2.1 (Brunton, 1968).

Tethorotes Manankov, 1979, p. 50 [**Ombonia grandis* Sokolskaya, 1968, p. 60; OD]. Similar to *Orthotetes* but more dorsibiconvex to resupinate and broadly unisulcate with impersistent concentric rugae; dorsal interarea anacline, chilidium with median groove; delthyrial chamber asymmetrical; median septal node at base of cardinal process; muscle scars faint. *Lower Carboniferous–Lower Permian:* Kazakhstan.——Fig. 471,*1a–c.* **T. grandis* (Sokolskaya), Serpukhovian, northern Pribalkhash; ventral valve internal mold, dorsal valve internal mold, latex replica of previous specimen showing cardinalia, ×1 (Manankov, 1979).

Werriea Campbell, 1957, p. 44 [**W. australis;* OD] [=*Permorthotetes* G. A. Thomas, 1958, p. 82 (type, *P. callytharensis*)]. Similar to *Orthotetes* but more variable in shape, mainly resupinate with some asymmetry to ventral beak, finely parvicostellate by intercalation, impersistently rugate; dorsal interarea short, anacline, cardinal process with median groove, as in *Permorthotetes;* small median node at base of cardinal process; brachiophores present as sharp, distal edges of recurved socket ridges. *Lower Carboniferous–Lower Permian:* Australia, North America.——Fig. 471,*2a–c.* **W. australis,* lower Viséan, New South Wales; *a,* holotype, internal mold of ventral valve, ×1; *b,* external mold of ventral valve, ×1; *c,* imperfect cast of cardinal process, ×1 (Campbell, 1957).——Fig. 471,*2d.* *W. callytherrensis* (Thomas), Permian, Australia; ventral valve interior, ×1 (Thomas, 1958).

Family PULSIIDAE
Cooper & Grant, 1974

[*nom. transl.* Williams & Brunton, herein, *ex* Pulsiinae Cooper & Grant, 1974, p. 256]

Mostly large, subquadrate, dorsibiconvex, mainly finely parvicostellate by intercalation, intersected by concentric fila; ventral interarea short, apsacline, perideltidium present, beak usually symmetrical; dorsal interarea short, anacline; pseudodeltidium and small chilidium convex; dental plates variable in disposition, strong but not reaching into anterior half of valve; socket ridges recurved; cardinal process lobes discrete, low, usually with grooved myophores; ventral muscle scars variable in size and in insertion on valve floor, myophragm rarely developed; dorsal myophragm present, but low. *Middle Devonian–Upper Carboniferous.*

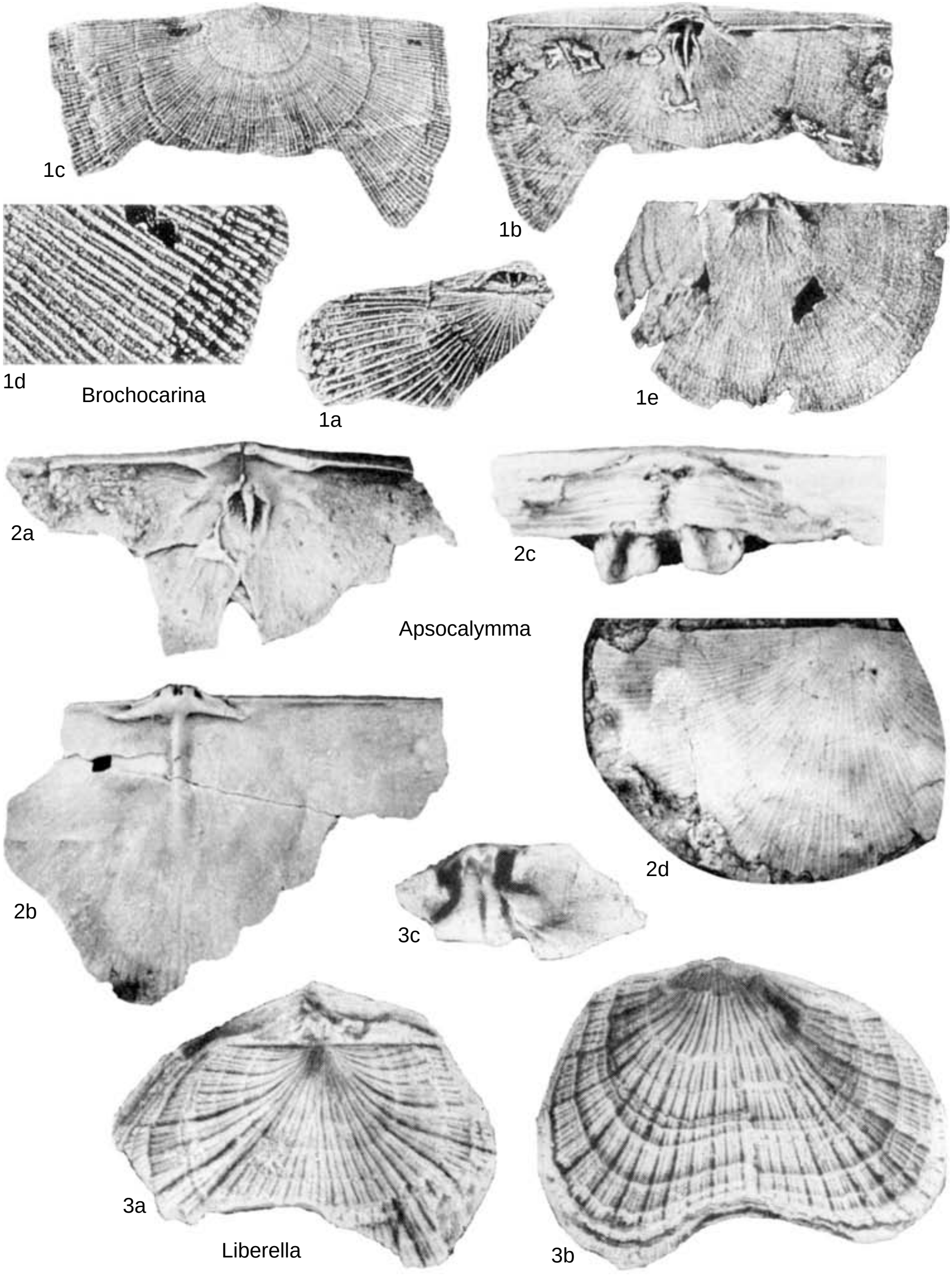

FIG. 470. Orthotetidae (p. 652).

Pulsia IVANOV, 1925, p. 113 [**P. mosquensis;* OD]. Commissure rectimarginate, concentric fila not reported within interspaces or on crests of parvicostellae; dental plates parallel, enclosing callus of secondary shell like pseudospondylium but ventral muscle scars indistinctly impressed; socket ridges well developed, recurved. *Carboniferous:* Russia. ——FIG. 472,*1a–c*. **P. mosquensis,* Kasimovian,

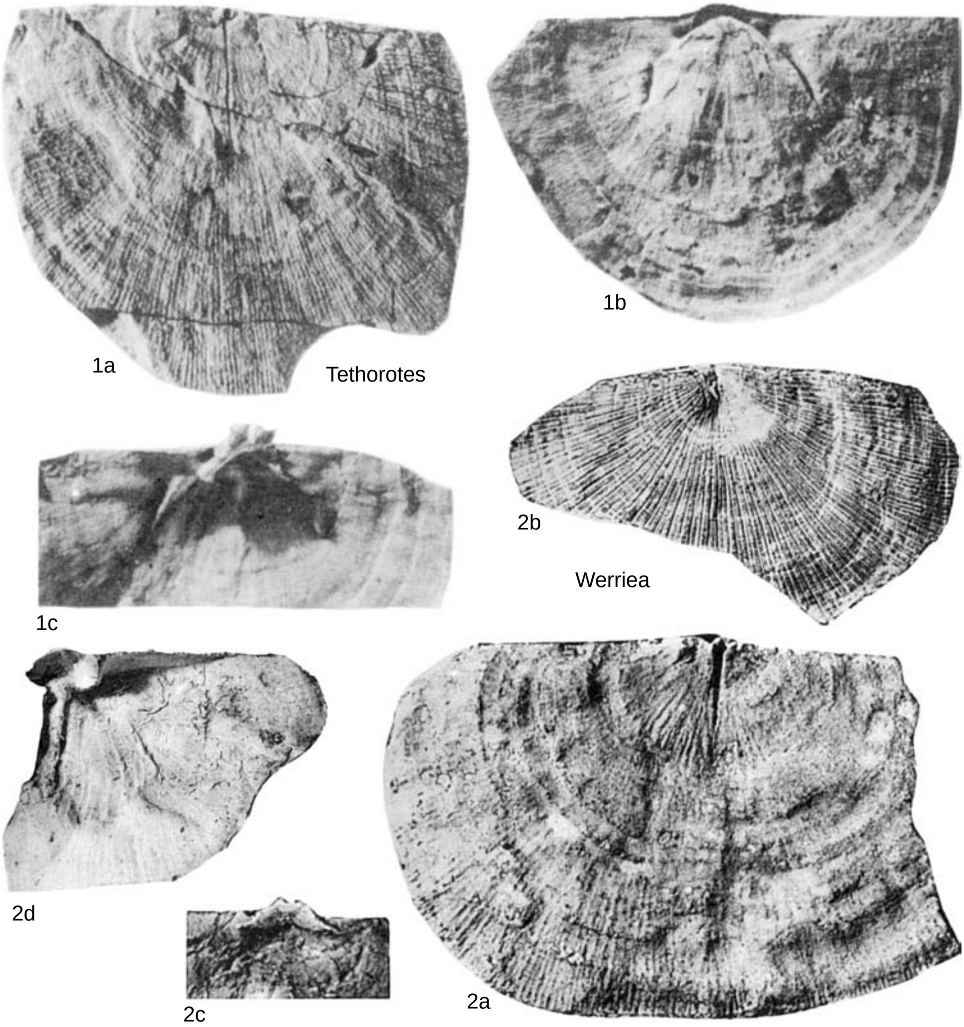

FIG. 471. Orthotetidae (p. 652).

Moscow District; *a,* ventral valve interior, ×0.5 (Sokolskaya, 1954); *b,c,* dorsal valve exterior, ventral valve exterior, ×1 (Orlov, 1960).

Schellwienella I. THOMAS, 1910, p. 92 [**Spirifera crenistria* PHILLIPS, 1836, pl. 216; OD] [=*Carlopsina* REED, 1954, p. 183 (type, *Spirifera radialis* PHILLIPS, 1836)]. Similar to *Pulsia* but commonly gently uniplicate with concentric fila forming serrations along crests of parvicostellae; dental plates short, divergent posteriorly, containing impressed, flabellate ventral muscle scars divided by low myophragm; socket ridges short, recurved. [*Carlopsina* was erected for those species with a short dorsal interarea. Dorsal valves of the type species that are better preserved than the crushed specimen figured by REED have linear or obsolescent interareas similar to those of *Schellwienella s.s.*] *Middle Devonian–Lower Carboniferous:* cosmopolitan.——FIG. 472,*2a–c.* **S. crenistria* (PHILLIPS), Viséan, Lancashire, England, lectotype, BMNH B19675; dorsal, ventral, posterior views of shell, ×1 (new).——FIG. 472,*2d,e. S. radialis* (PHILLIPS), Asbian, Fermanagh, Ireland; dorsal valve posterior, dorsal valve interior, ×1.3 (Brunton, 1968).

Family ORTHOTETELLIDAE
Cooper & Grant, 1974

[Orthotetellidae COOPER & GRANT, 1974, p. 285] [=Hypopsiinae COOPER & GRANT, 1974, p. 256]

Variable profile but asymmetrical ventral valve frequently conical, with apsacline to

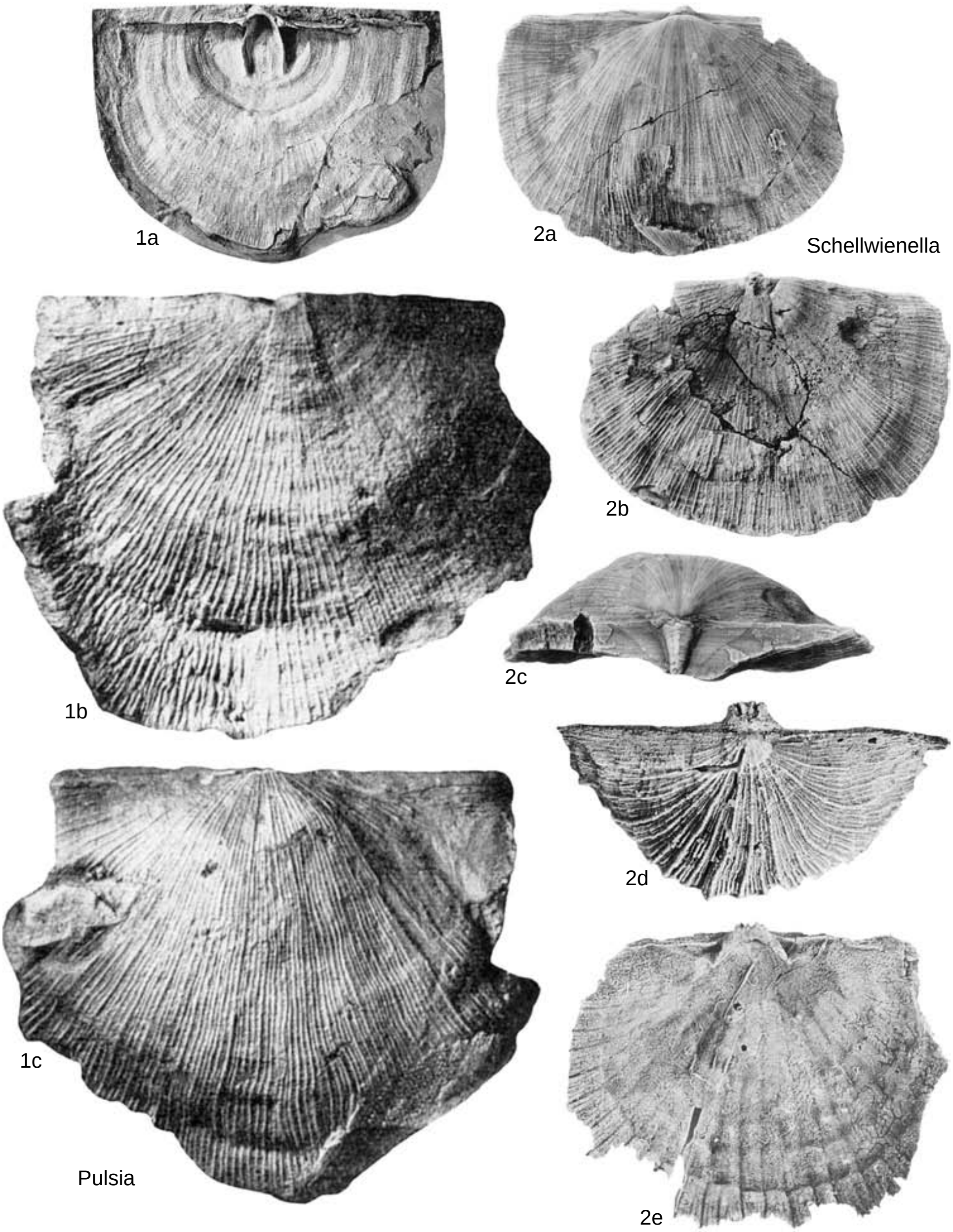

FIG. 472. Pulsiidae (p. 653–654).

procline interarea of variable length, finely costellate by branching or intercalation crossed by concentric fila; dental plates convergent to form spondylium supported by median septum or free, containing ill-defined ventral muscle scar; cardinal process with basal median node, lobes low, discrete; socket ridges recurved or divergent, brachiophores blunt, divergent. *Lower Permian.*

Orthotetella R. E. KING, 1931, p. 51 [**O. wolfcampensis;* OD]. Large, finely parvicostellate by branching; spondylium supported by median

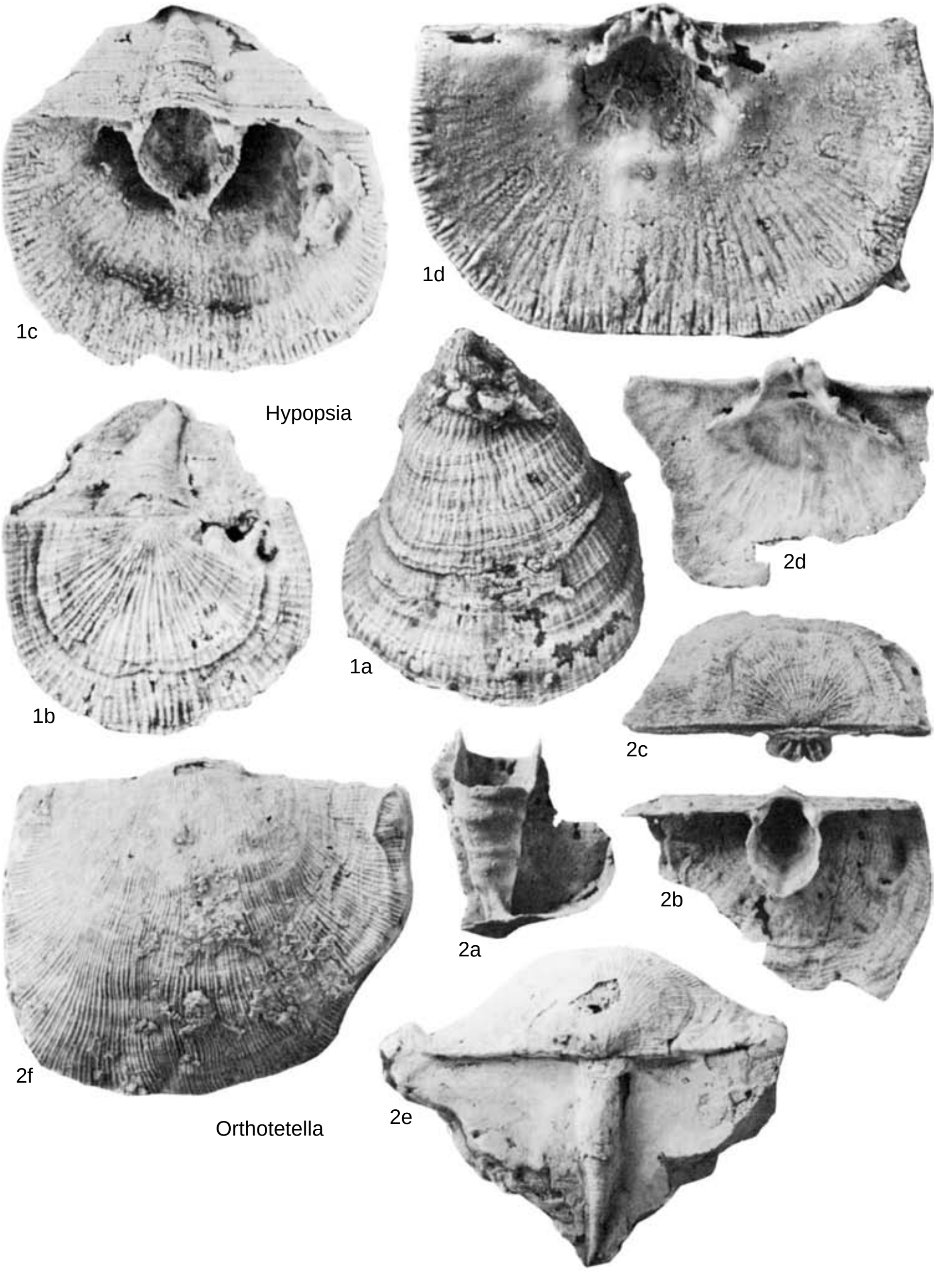

FIG. 473. Orthotetellidae (p. 655–657).

septum in young valves, becoming free in adult valves to form cone with convex pseudodeltidium, containing striate ventral muscle scars; socket ridges ankylosed to cardinal process lobes with slits on posteriorly directed myophores; dorsal adductor scars bilobed, lightly impressed about low myophragm. *Lower Permian:* western USA.——FIG. 473,*2a–f.* **O. wolfcampensis,* Wolfcampian, Texas; *a,* internal view of ventral valve showing tubular spondylium, ×1; *b,* ventral valve interior, ×1; *c,d,* posterior, interior views of dorsal valve, ×1; *e,f,* posterior, dorsal views of shell, ×1 (Cooper & Grant, 1974).

Hypopsia Cooper & Grant, 1974, p. 272 [**H. versuta;* OD]. Medium sized, finely parvicostellate by intercalation; spondylium initially supported by median septum but adnate on floor of adult valves; socket ridges not ankylosed to cardinal process, brachiophores long, divergent, dorsal adductor scars impressed, bilobed about low myophragm. *Lower Permian:* western USA.——Fig. 473,*1a–d.* **H. versuta,* Leonardian, Texas; *a,b,* holotype, ventral, dorsal views of shell, ×3; *c,d,* paratype, ventral valve interior, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Family DERBYIIDAE Stehli, 1954

[*nom. transl.* Cooper & Grant, 1974, p. 256, *ex* Derbyiinae Stehli, 1954, p. 303] [=Diplaninae Cooper & Grant, 1974, p. 256; Dorsoscyphinae Roberts, 1971, p. 49]

Variable in size, outline, and disposition of anterior commissure, normally ventribiconvex, cemented with asymmetrical, high ventral beak, costellation variable in texture, crossed by concentric fila; ventral interarea variably disposed, perideltidium usually well developed, pseudodeltidium broadly convex or flat with narrow monticulus; dorsal interarea linear, chilidium complete, convex, or vestigial; dental ridges discrete, median septum normally strong, ankylosed to internal surface of pseudodeltidium; cardinal process lobes fused proximally, normally high with myophore slits, divergent socket ridges fused with cardinal process, brachiophores normally developed, ventral muscle scars large, flabellate, dorsal muscle scar impressed about myophragm. *Lower Carboniferous–Upper Permian.*

Derbyia Waagen, 1884, p. 576 [**D. regularis;* SD Hall & Clarke, 1892, p. 262] [=*Derbyaeconcha* Licharew, 1934b, p. 507 (type, *Derbya anomata* Licharew, 1932, p. 20); *Grabauellina* Licharew, 1934b, p. 507 (type, *Derbya (?Derbyina) mongolica* Grabau, 1931, p. 259), *nom. nov. pro Derbyina* Grabau, 1931, p. 259, *non* Clarke, 1913; *Magniderbyia* Ting, 1965, p. 265 (type, *Derbya magnifica* Licharew, 1939, p. 80), *nom. nov. pro Licharewiella* Sokolskaya, 1960, p. 219, *non* Ustritsky, 1960; *Pseudoderbyia* Licharew, 1934a, p. 211 (type, *P. netschajewi*); *Plicatoderbya* H. D. Thomas, 1937, p. 14 (type, *Orthotetes magnus* Branson, 1930, p. 26); *Wardakia* Termier & others, 1974, p. 94 (type, *Derbyia grandis* Waagen, 1884, p. 597); *Paraderbyia* Sun, 1983, p. 120 (type, *P. duomaensis*)]. Large, normally distorted in shape and uniplicate, finely costellate by branching and intercalation; pseudodeltidium flat with monticulus, chilidium small, occasionally with median groove, vestigial in later, larger species; dental ridges frequently convergent apically on high ventral median septum ankylosed to internal surface of pseudodeltidium; flabellate ventral muscle scar usually deeply impressed, occasionally with raised boundary; ridgelike brachiophores arising from massive socket plates and ridges fused with cardinal process of variable length; subcircular dorsal adductor scars variably impressed about low myophragm; commonly with interrupted rugation like low plication. [Genera cited as junior synonyms of the cosmopolitan, long-ranging *Derbyia* have been erected on morphological differences that were subject to specific variation in large samples of well-preserved specimens similar to those described by Cooper and Grant (1974, p. 292–318). Thus, such variation affected the persistence of rugation, the development of a raised anterior boundary to the ventral muscle scar, and the strength of the dorsal myophragm, the diagnostic features of *Plicatoderbyia, Magniderbyia,* and *Paraderbyia* respectively, and the relative strength of the dorsal and ventral myophragms and the development of a pseudodeltidial monticulus, which characterize *Wardakia.*] *Upper Carboniferous–Upper Permian:* cosmopolitan.——Fig. 474,*2a–c.* **D. regularis,* Amb Formation, Lower Permian, Salt Range, Pakistan; dorsal, ventral, posterior views of shell, ×1 (new).——Fig. 474,*2d,e. D. profunda* Cooper & Grant, Wolfcampian, Texas; *d,* paratype, broken specimen showing cardinalia and dental ridges, ×1; *e,* paratype, posterior view of dorsal valve, ×1 (Cooper & Grant, 1974).——Fig. 474,*2f. D. filosa* Cooper & Grant, Wordian, Texas; holotype, posteriorly tilted ventral valve interior, ×1 (Cooper & Grant, 1974).

Diplanus Stehli, 1954, p. 299 [**Streptorhynchus lamellatum* R. E. King, 1931, p. 49; OD]. Small, subconical, variable anterior commissure, costellate by branching, strongly lamellose; ventral interarea of variable length, pseudodeltidium convex; dorsal interarea abnormally anacline, chilidium with median groove; dental ridges discrete with large teeth, ventral muscle scar obscure; cardinal process of medium height with slitlike myophores; dorsal adductor scars impressed, bilobed frequently with raised margin, bisected by low myophragm. [Cooper & Grant (1974, p. 256) assigned this genus to the Schuchertellidae; but until the shell structure of unsilicified specimens has been determined, *Diplanus* is, on balance, provisionally identified as a derbyiid despite the absence of a median septum ankylosed to the pseudodeltidium.] *Lower Permian:* western USA.——Fig. 475,*1a–d.* **D. lamellatus* (King), Leonardian, Texas; *a,* ventral valve interior, ×2; *b,c,* posterior, interior views of dorsal valve showing cardinal process and sockets, ×4; *d,* holotype, posterior view of complete specimen, ×2 (Cooper & Grant, 1974).

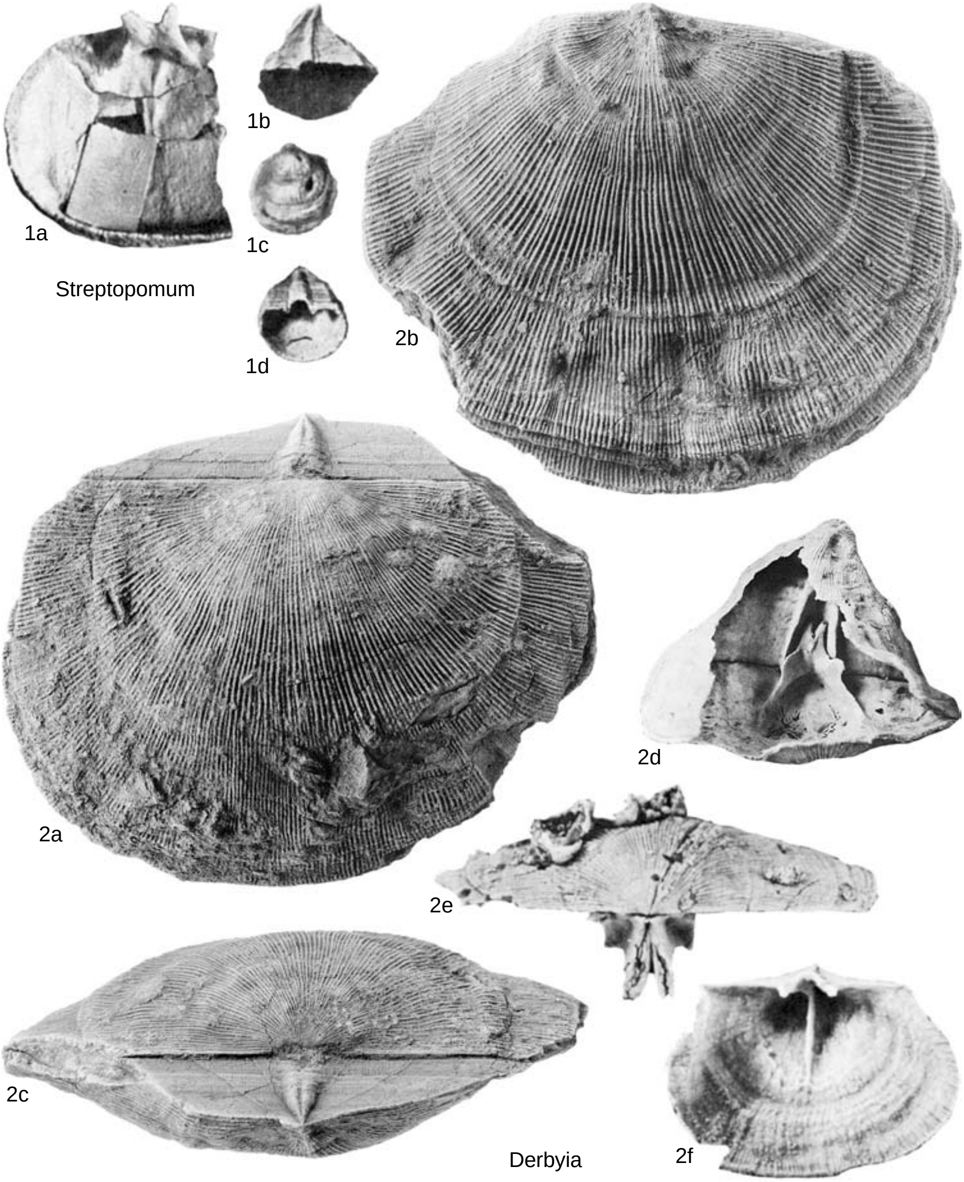

FIG. 474. Derbyiidae (p. 657–660).

Dorsoscyphus ROBERTS, 1971, p. 50 [**D. spinulosus;* OD]. Similar to *Derbyia* but small, ventribiconvex with subconical ventral valve, gently unisulcate, costellate by intercalation, lamellose; ventral interarea high, pseudodeltidium convex, chilidium reduced; cardinal process relatively low with basal median node and grooved myophores; socket ridges divergent, continuous with cuplike platform containing deeply impressed adductor scars about a strong dorsal myophragm; shell free of rugation. *Lower Carboniferous:* Western Australia.——FIG. 475,*3a–d.* **D. spinulosus,* Viséan, Bonaparte Gulf Basin; *a,b,* holotype, interior, exterior views of dorsal valve, CPC 10821, ×6; *c,d,* interior, exterior views of ventral valve, ×6 (Roberts, 1971).

Nothopindax COOPER & GRANT, 1974, p. 318 [**N. egregius;* OD]. Similar to *Derbyia* but normally ventribiconvex with subconical ventral valve,

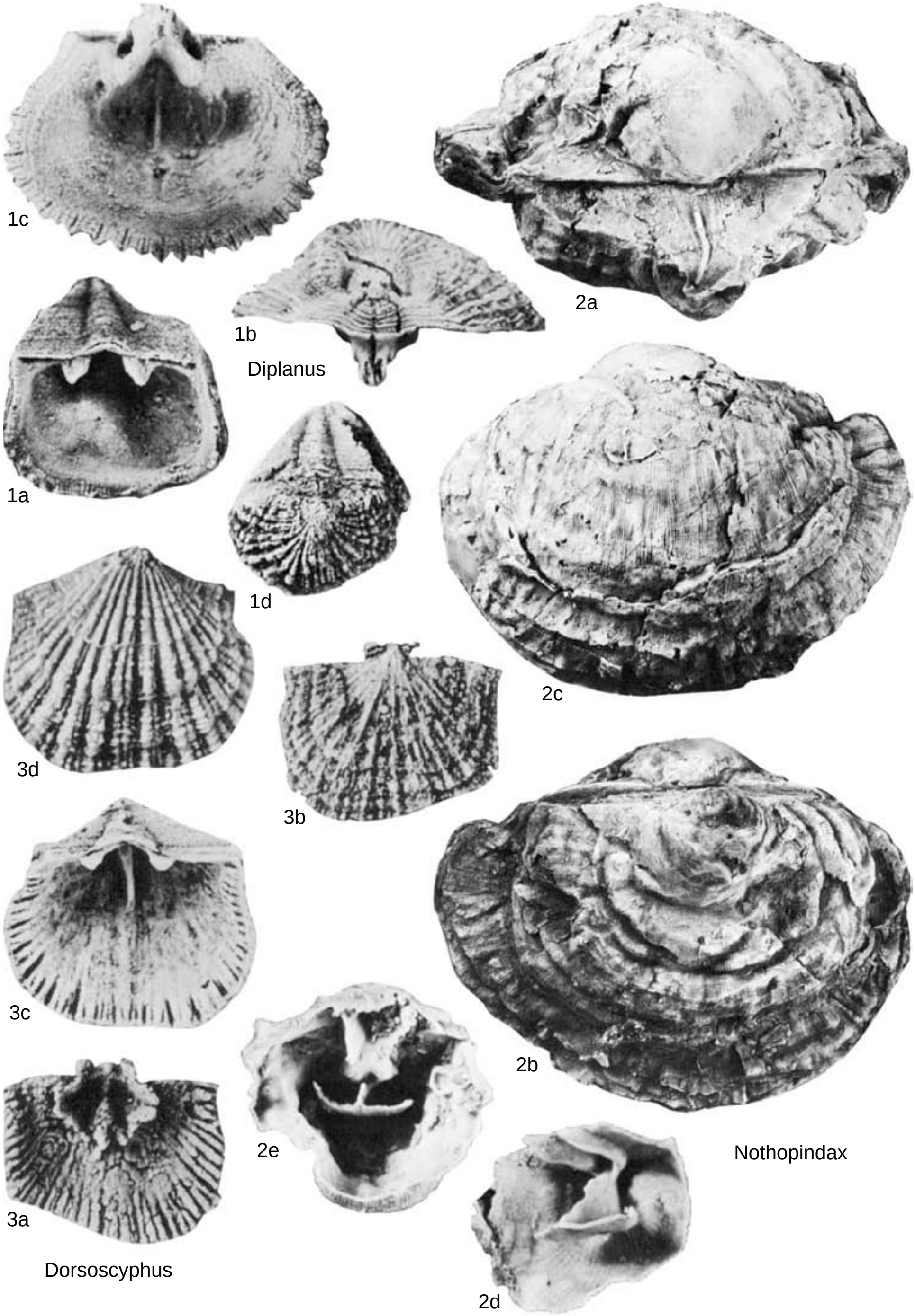

FIG. 475. Derbyiidae (p. 657–660).

rectimarginate, finely costellate by branching; ventral median septum anteriorly ankylosed to transverse, spatulate platform representing raised anterior boundary of ventral muscle scar; dorsal adductor scars ill defined, myophragm not developed. *Lower Permian:* western USA.——Fig. 475,*2a–e.*N. egregius,* Leonardian, Texas; *a–c,* paratype, posterior, dorsal, ventral views of shell, ×0.75; *d,* paratype, lateral view of ventral valve showing elevated muscle platform, ×2; *e,* holotype, posterior view of incomplete shell with cardinal process and median septum, USNM 151225c, ×1 (Cooper & Grant, 1974).

Streptopomum Havlíček, 1967, p. 207 [**Streptorhynchus mjatschkowensis* Sokolskaya in Sarytcheva & Sokolskaya, 1952, p. 54; OD] [=*Miniplanus* Waterhouse & Piyasin, 1970, p. 101 (type, *M. minuta*)]. Similar to *Diplanus* but lacking concentric lamellae and dorsal interarea. [*Streptopomum* is morphologically close to *Diplanus* but its assignment to the Derbyiidae is also provisional on ascertaining its shell structure, which is presently unknown. *Miniplanus* from the middle Permian of Thailand is considered to be a junior synonym of *Streptopomum* despite the fact that it was mistakenly described by its authors as having a deltidium, crural plates, and a cardinal process with "4 to 6 low tubercles along the upper edge."] *Upper Carboniferous:* Russia.——Fig. 474,*1a–d.* **S. mjatschkowensis* (Sokolskaya), Moscovian, Moscow basin; dorsal valve interior, ventral valve posterior, exterior, dorsoposterior views of ventral valve, ×1 (Sarytcheva & Sokolskaya, 1954).

Family MEEKELLIDAE Stehli, 1954

[*nom. transl.* Williams, 1965e, p. 405, *ex* Meekellinae Stehli, 1954, p. 303]

Medium to large, mostly rectimarginate, finely costellate mainly by branching, commonly secondarily costate or costellate; ventribiconvex; beak of subconical ventral valve generally not greatly distorted, interarea variable in height, procline to apsacline, perideltidium well developed, pseudodeltidium usually flat with monticulus, dorsal interarea linear, chilidium commonly reduced to boss; dental ridges discrete, supported by dental plates converging on median septum or on valve floor, flanked by flabellate diductor scars when muscle bases impressed, presumably with adductor attachment between dental plates; cardinal process lobes fused proximally into single shaft and bearing slitlike myophores distally; inner socket ridges divergent, ankylosed to cardinal process, brachiophores well developed, bladelike; dorsal adductor scars and myophragm variably developed. *Lower Carboniferous–Upper Permian.*

Subfamily MEEKELLINAE Stehli, 1954

[Meekellinae Stehli, 1954, p. 303]

Rectimarginate, secondary costae and branching costellae normally fully developed in mature shell; ventral interarea high with flat pseudodeltidium and monticulus accommodating chilidium reduced to boss on posterior surface of shaft of long cardinal process curving posteroventrally; sockets delineated laterally by fulcral plates, brachiophores becoming pointed. *Lower Carboniferous–Upper Permian.*

Meekella White & St. John, 1867, p. 120 [**Plicatula striatocostata* Cox, 1857, p. 568; OD] [=*Gegenella* Li & Gu, 1976, p. 236 (type, *G. gegenensis*)]. Medium sized, finely costellate by branching, ventral interarea high, procline to mainly apsacline; dental plates convergent onto floor of ventral valve and medial of rarely impressed, flabellate diductor scars; cardinal process usually moderately long; dorsal adductor scars variably impressed within distal ends of socket ridges, bilobed about low myophragm. [*Gegenella* from the Lower Permian of Inner Mongolia was erected for species that differed from *Meekella* in having dental plates well separated by a broad median septum. In fact, the degree of convergence of the dental plates of *Meekella* is quite variable and they frequently ankylose on the floor of the ventral valve with a callus of secondary shell that is comparable with the median septum of *Gegenella.*] *Carboniferous–Upper Permian:* cosmopolitan.——Fig. 476,*2a–e.* **M. striatocostata* (Cox), Moscovian, Iowa; *a–c,* dorsal, ventral, lateral views of shell, ×1; *d,* detail of shell ornament, ×5; *e,* posterior view of ventral valve, ×2 (new).——Fig. 476,*2f,g. M. attenuata* (Girty), Leonardian, Texas; *f,* oblique lateral view of cardinalia, ×4; *g,* ventral valve interior, ×1.5 (Cooper & Grant, 1974).

Alatorthotetina He Xi-lin & Zhu Mei-li, 1985, p. 200[203] [**A. sichuanensis;* OD]. Similar to O*rthothetina* but usually planoconvex with mucronate hinge line, finely costellate by branching, ventral diductor scars impressed lateral of short, parallel dental plates. *Upper Permian:* southwestern China.——Fig. 476,*1a–c.* **A. sichuanensis,* Upper Permian, Sichuan; *a,* dorsal valve exterior, ×1; *b,* paratype, ventral valve exterior, ×1; *c,* paratype, ventral valve internal mold, ×1 (He & Zhu, 1985).

Asiomeekella Liang, 1990, p. 120[458] [**A. isoconvexa;* OD]. Similar to *Meekella* in general appearance but with catacline ventral interarea, convex pseudodeltidium, less convergent dental plates bounding a pair of low submedial septa, and short cardinal process. [The assignment of this genus to the Meekellidae is provisional on a more compre-

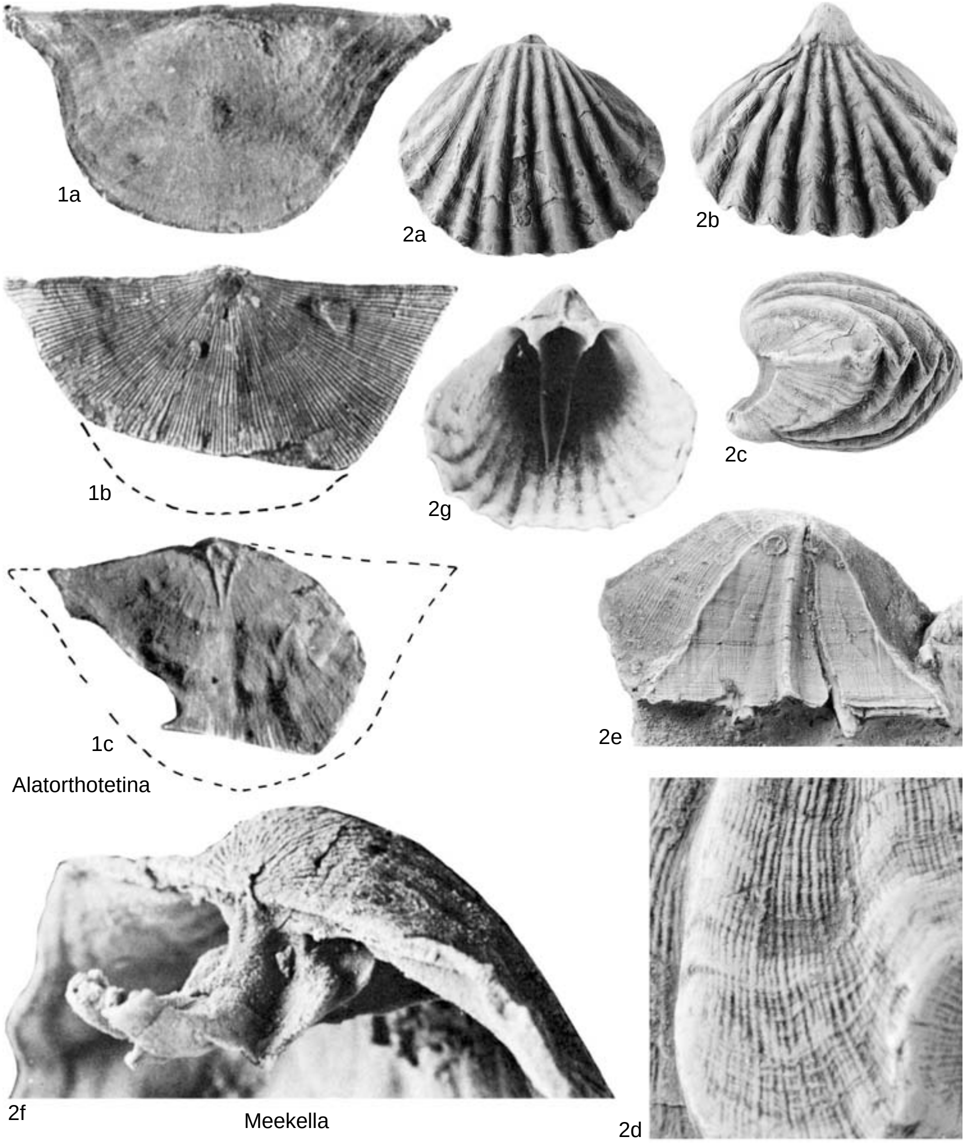

FIG. 476. Meekellidae (p. 660).

hensive description of the type species, based on better material. The submedial ridges between the dental plates on the floor of the ventral valve may be nothing more than radial striations that are commonly associated with muscle scars, while nothing is known about the cardinalia other than the fact that the cardinal process is large, stout but short.] *Carboniferous–Permian:* China.

Geyerella SCHELLWIEN, 1900, p. 12 [**G. gemmellaroi;* OD] [=*Turriculum* DE GREGORIO, 1930, p. 26 (type, *T. imperans*)]. Similar to *Meekella* but variable in size, finely costellate mainly by intercalation, secondary costation variable in amplitude and disposition, occasionally complicated by impersistent rugation; dental plates convering on high median septum, dorsal myophragm variably developed. *Upper Carboniferous–Permian:* cosmopolitan.——FIG. 477,*4a,b.* **G. gemmellaroi,* ?Kazanian, Valle de Sosio, Sicily; *a,* posterior view of shell, ×1; *b,* detail of shell, ×2 (new).——FIG. 477,*4c,d. G. hessi* COOPER & GRANT, Wolfcampian, Texas; paratype, interior of ventral valve showing spondylium, posteriorly tilted view of dorsal valve, ×1 (Cooper & Grant, 1974).

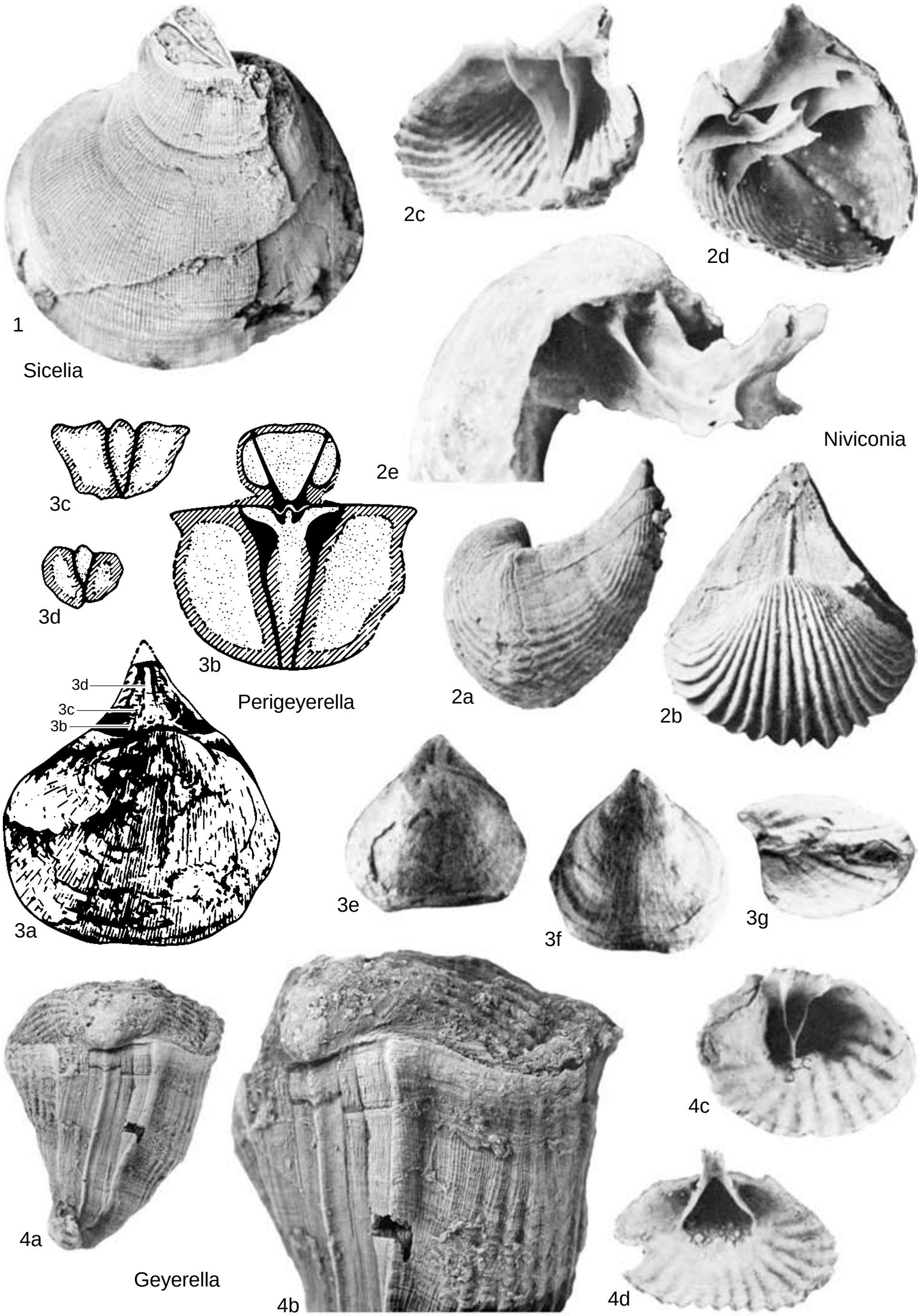

FIG. 477. Meekellidae (p. 661–664).

Niviconia COOPER & GRANT, 1974, p. 373 [**Meekella globosa* R. E. KING, 1931, p. 54; OD]. Similar to *Meekella* but generally large, strongly ventribiconvex with high conical ventral valve; low, even secondary costae; cardinal process high. *Permian (Artinskian–Kungurian):* western USA.——FIG. 477,*2a–e.* **N.*

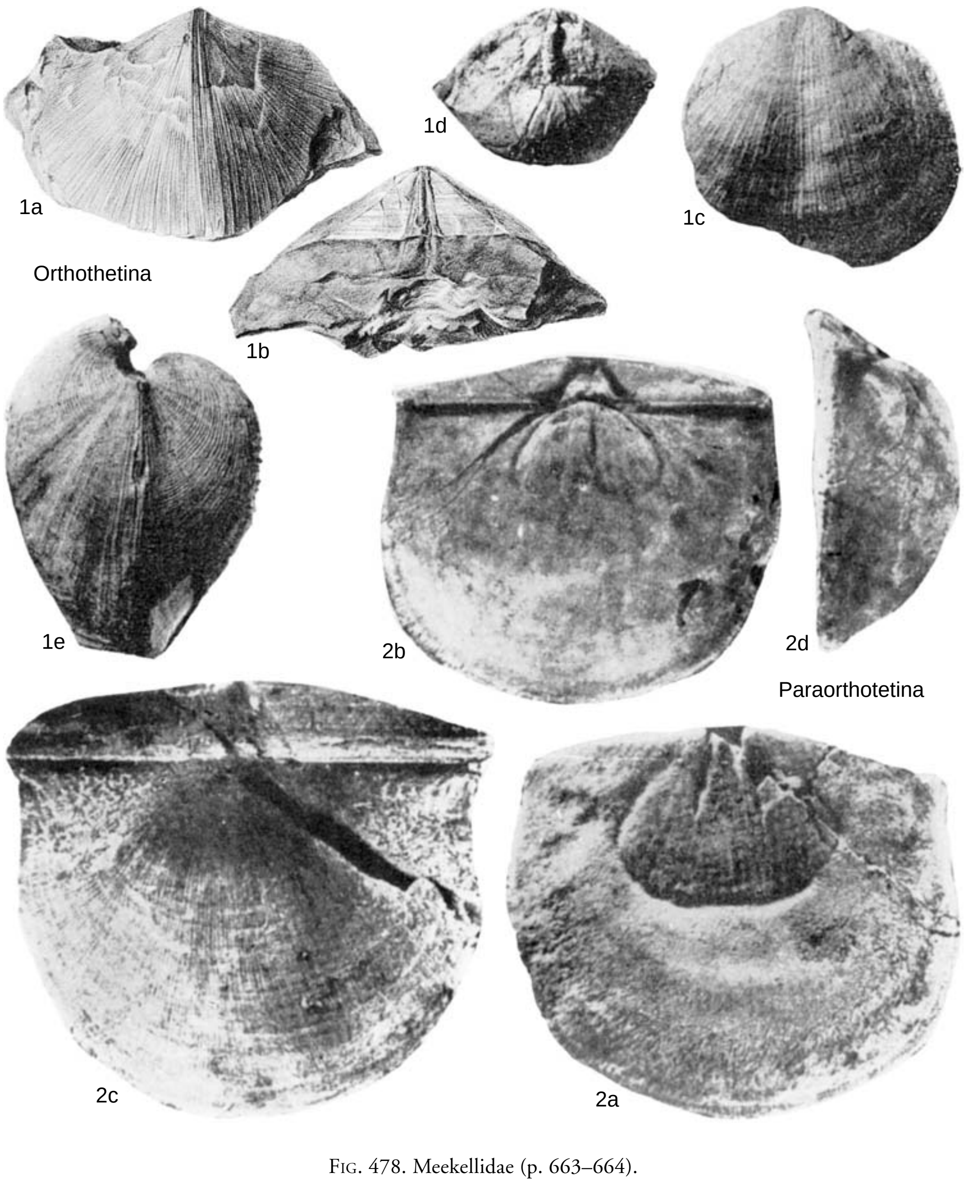

FIG. 478. Meekellidae (p. 663–664).

globosa (KING), Leonardian, Texas; *a,b,* lateral, dorsal views of shell, ×1; *c,* oblique view of ventral valve interior, ×1; *d,* posterolateral internal view of articulated valves, ×1; *e,* lateral view of cardinalia, ×2 (Cooper & Grant, 1974).

Orthothetina SCHELLWIEN, 1900, p. 8 [**Orthothetes persicus;* SD SCHUCHERT in SCHUCHERT & LEVENE, 1929, p. 91] [=*Lopingia* CHAN, 1979, p. 64 (type, *Orthotetes ruber* FRECH, 1911, p. 124)]. Similar to *Meekella* including strong monticulus in flat pseudodeltidium, dental plates converging separately onto floor of ventral valve, and fine costellation mainly by branching but without radial plicae of secondary costation. [*Lopingia* from the Permian of southern China appears to differ from *Orthothetina* only in the less convex to resupinate ventral valve.] *Carboniferous–Permian:* cosmopolitan.——FIG. 478,*1a–c.* **O. persicus* (SCHELLWIEN); *a,b,* exterior, posterior views of ventral valve, Kazanian, Persia, Iran, ×1 (Schellwien, 1900); *c,* dorsal valve exterior, Dzulfian, Transcaucasia, ×1 (Sarytcheva & Sokolskaya, 1965).——FIG. 478,*1d. O. iljinae* (SOKOLSKAYA), Guadalupian, Transcaucasia; holotype, posterior view of dorsal valve, ×1 (Sarytcheva & Sokolskaya, 1965).——FIG. 478,*1e. O. peregrina* (ABICH), Dzhulfian, Transcaucasia; lateral view, ×1 (Sarytcheva & Sokolskaya, 1965).

Paraorthotetina He Xi-lin & Zhu Mei-li, 1985, p. 198[203] [*_Orthotetina provecta_ Liao, 1980, p. 254; OD] [=*Parameekella* He & Zhu, 1985, p. 198[203] (type, *P. hauyinshanensis*)]. Similar to *Orthothetina* but with greatest width at hinge line and deeply impressed ventral muscle scars, including flabellate diductor insertions on either side of parallel dental plates containing impressions of elongate adductor bases; dorsal adductor scars also deeply impressed about strong median septum. [*Parameekella* was erected for contemporaneous orthotetoids which differed from species assigned to *Paraorthotetina* only in being ornamented by impersistent wrinkles which may be radially arranged. This is an infraspecific feature in other Permian orthotetoids, similar to many *Derbyia* species of Texas (Cooper & Grant, 1974); and there is no evidence as yet that rugation in the Chinese forms was any less variable.] *Upper Permian:* southwestern China.——Fig. 478,*2a–d.* *_P. provecta_ (Liao), Upper Permian, western Guizhou; ventral valve internal mold, dorsal valve internal mold, dorsal exterior, lateral view of internal mold, ×1 (He & Zhu, 1985).

Perigeyerella Wang, 1955a, p. 101[1955b, p. 346] [*_P. costellata;_ OD]. Similar to *Geyerella* but without secondary costation and rounded in outline, usually with less conical ventral valve with sharply pointed beak, broadly unisulcate, finely costellate mainly by branching cancellated by strong, concentric fila; dental plates becoming less convergent with growth so that narrow chamber with supporting median septum is characteristic of young ventral valve and sessile septal chamber or discrete dental plates typical of adult valve. *Upper Permian:* China.——Fig. 477,*3a–g.* *_P. costellata,_ Upper Permian, northern Guizhou; *a,* dorsal view of complete shell, ×1; *b–d,* serial sections at intervals shown on *a,* ×2 (Wang, 1955); *e–g,* dorsal, ventral, lateral views of shell, ×1 (Yang & others, 1977).

Sicelia Gortani & Merla, 1934, p. 284, *nom. nov. pro Canavaria* Merla, 1928, p. 70, *non* Oppenheim, 1899, *nec* Gemmellaro, 1886 [*_Canavaria acropedion_ Merla, 1928, p. 70; OD] [=*Gemmellaria* Fabiani & Ruiz, 1933, p. 7 (footnote), *non* Munier-Chalmas, 1873; *Parageyerella* He & Zhu, 1985, p. 203 (type, *P. daijiagouensis*); *Hamletella* Hayasaka, 1953, p. 92 (type, ?*Streptorhynchus altus* Hamlet, 1928)]. Similar to *Meekella* but without secondary costation, finely parvicostellate mainly by intercalation. [*Hamletella,* from the Permian of Timor, with its parvicostellate and impersistently rugate exterior, flat pseudodeltidium with monticulus, convergent, subparallel dental plates and divergent socket ridges, was summarized by its author as a *Meekella* without secondary costation or plication and with a more elongate ventral valve. These are the features distinguishing *Sicelia* from *Meekella.*] *Permian:* Eurasia.——Fig. 477,*1.* *_S. acropedion_ (Merla), Upper Permian, Valle de Sosio, Sicily; ventral valve exterior, broken umbonal section, ×2 (Williams, 1965e).

Subfamily OMBONIINAE
Sokolskaya, 1960

[Omboniinae Sokolskaya, 1960, p. 218]

Finely costellate by branching without secondary radial ornamentation; ventral beak distorted, interarea high with convex pseudodeltidium, dorsal interarea linear, chilidium usually small with median groove; cardinal process relatively low, socket ridges reduced, socket plates delicate, divergent containing lightly impressed bilobed dorsal adductor scars. *Permian.*

Ombonia Caneva, 1906, p. 54 [*_O. canevai_ Merla, 1931, p. 80; SD Merla, 1931, p. 80]. Medium sized, broadly uniplicate, lacking regularly developed concentric ornamentation; ventral interarea commonly apsacline; dental plates converging on strong, high median septum; ventral muscle scars obscure, dorsal myophragm variably developed. *Permian:* Eurasia, North America.——Fig. 479*a,b.* *_O. canevai_ Merla, Upper Permian, Dolomites, Italy; *a,* ventral valve internal mold; *b,* schematic diagram of dorsal valve interior, ×1 (Merla, 1931).——Fig. 479*c,d. O. dieneri* Licharew, Lower Permian, North Caucasus; *c,d,* dorsal, lateral views of shell, ×1 (Orlov, 1960).——Fig. 479*e–g. O. guadalupensis* (Girty), Guadalupian, Texas; ventral valve interior, exterior, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Family SCHUCHERTELLIDAE
Williams, 1953

[*nom. transl.* Stehli, 1954, p. 298, *ex* Schuchertellinae Williams, 1953b, p. 9]

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 ridges and teeth unsupported by 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 brachiopores; shell extropunctate. *Middle Devonian–Permian.*

Subfamily SCHUCHERTELLINAE
Williams, 1953

[Schuchertellinae Williams, 1953b, p. 9]

Normally subconical, rectimarginate, costellate with concentric ornamentation; ventral interarea variably disposed, pseudo-

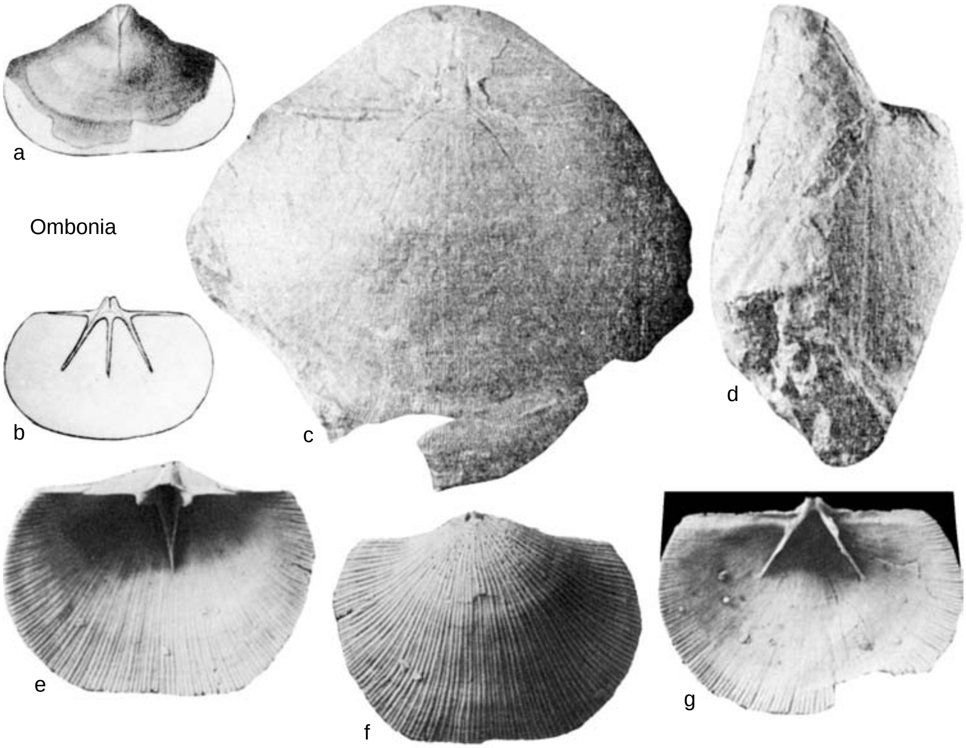

FIG. 479. Meekellidae (p. 664).

deltidium convex, dorsal interarea linear, chilidium normally present; ventral muscle scars usually faintly impressed without myophragm; low, discrete cardinal process lobes with myophore grooves, not ankylosed to recurved socket ridges, brachiophore bases usually prolonged as processes, dorsal muscle scars usually impressed about variably developed myophragm. *Middle Devonian–Lower Permian.*

Schuchertella GIRTY, 1904, p. 734 [**Streptorhynchus lens* WHITE, 1862, p. 28; OD]. Variable in size and in texture of costellae; ventral interarea usually anacline, chilidium convex; flabellate ventral muscle scars and impressed dorsal adductor scars, each set divided by low myophragm; extropunctae better developed in the dorsal valve. [Many middle and Upper Paleozoic schuchertelloid species, morphologically resembling *S. lens* (WHITE) from the Louisiana Limestone of Missouri, have been identified as *Schuchertella.* Some of these are now known to be impunctate; others of those that have been described as pseudopunctate are extropunctate like the type species. Until the shell structure of all such assigned species has been checked, the true stratigraphic and geographic range of *Schuchertella* is in doubt.] *Upper Devonian–Upper Carboniferous, ?Lower Permian:* ?cosmopolitan.——FIG. 480,*1a–f.* **S. lens* (WHITE), upper Famennian, Missouri; *a,b,* dorsal, ventral views of shell, ×1.5; *c,* posterior view of shell, ×2; *d,e,* ventral valve, dorsal valve interiors, ×1.5; *f,* close up of previous specimen showing cardinalia, ×4 (new).

Goniarina COOPER & GRANT, 1969, p. 2 [**G. pyelodes;* OD]. Similar to *Schuchertella* but small, more strongly subconical, secondarily free, relatively coarsely costellate; faintly impressed ventral muscle scar lacking myophragm and strongly impressed dorsal adductor scars on incipient, tuberculate platform with myophragm attaining maximum height anteriorly. *Lower Permian:* USA (Texas).——FIG. 480,*3a–f.* **G. pyelodes,* Wolfcampian, Texas; *a–d,* holotype, dorsal, lateral, ventral, posterior views of shell, USNM 150411g; *e–f,* paratypes, dorsal valve interior, ventral valve interior, ×4 (Cooper & Grant, 1974).

Serratocrista BRUNTON, 1968, p. 39 [**S. fistulosa;* OD]. Similar to *Schuchertella,* small and with more evenly developed costellae bearing arrays of short, pointed spines along crests; ventral interarea variably

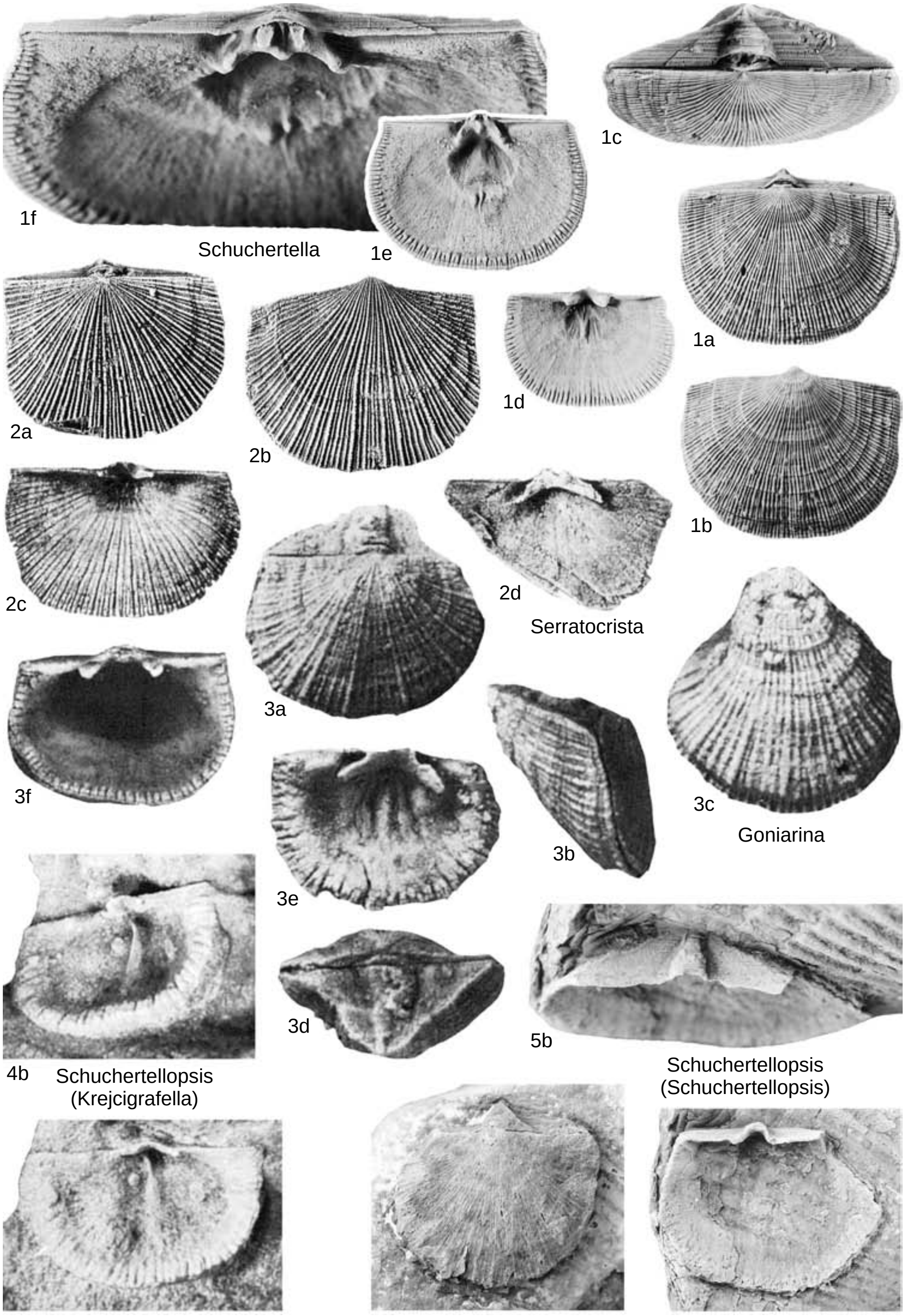

FIG. 480. Schuchertellidae (p. 665–667).

disposed, dorsal interarea and chilidium vestigial; muscle scars faint, lacking myophragms; socket ridges weak. *Lower Carboniferous (upper Viséan):* Ireland, northwestern Australia, ?North America.——FIG. 480,*2a–d.* **S. fistulosa,* Asbian, Fermanagh, Ireland; *a,b,* holotype, dorsal, ventral views of shell, ×1.8; *c,* ventral valve interior, ×1.6; *d,* incomplete dorsal valve interiors, ×1.7 (Brunton, 1968).

Schuchertellopsis MAILLIEUX, 1939, p. 5 [**S. durbutensis;* OD]. Small (10 to 12 mm wide), irregularly shaped shells with ventral valves 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 valves poorly known. [The assignment of this genus and its subgenera is uncertain, but it probably belongs here. It will be fully described and figured in the appendix of Volume 5 of this *Treatise* revision of the Brachiopoda following evaluation of its shell structure.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* western Europe, ?southern North America.

S. (Schuchertellopsis). *Schuchertellopsis* lacking ventral median septum; inner socket ridges extend at shallow angle from hinge, muscle fields indistinct. *Upper Devonian (upper Frasnian):* Belgium, ?southern North America (New Mexico).——FIG. 480,*5a–c.* **S. (S.) durbutensis,* attached to cyrtospiriferid shells, upper Frasnian, Belgium; *a,* syntype, ventral valve viewed dorsally, IRScNB a 1140, ×2; *b,* syntype, ventral valve viewed posteriorly, IRScNB a 1140, ×3; *c,* syntype, complete shell viewed dorsally, IRScNB a 1142, ×2 (new).

S. (Krejcigrafella) STRUVE, 1978, p. 97 [**S. (K.) krejcigrafi;* OD]. Resembles *S. (Schuchertellopsis),* but with ventral median septum from below pseudodeltidium to ridged marginal thickening. [Known only from ventral valves attached to stromatoporoids.] *Middle Devonian (lower Eifelian):* Germany (Eifel region).——FIG. 480,*4a,b.* **S. (K.) krejcigrafi,* lower Eifelian, Germany; holotype, ventral valve interior viewed dorsally and obliquely, SMF 31801, ×3 (Struve, 1978).

Subfamily STREPTORHYNCHINAE Stehli, 1954

[Streptorhynchinae STEHLI, 1954, p. 299] [=Tropidelasminae WATERHOUSE, 1983a, p. 117]

Normally medium sized with variably disposed commissure and fine, branched costellae, secondary costation rare, concentric ornamentation variable; ventral interarea high, usually apsacline with convex pseudodeltidium rarely folded into monticulus, perideltidium rarely absent, dorsal interarea usually linear with chilidium; ventral muscle scars normally flabellate without myophragm; cardinal process lobes long, with myophore slots, fused proximally into single shaft, ankylosed to enlarged socket ridges (erismata), socket ridges usually well developed and prolonged as processes; dorsal muscle scars usually impressed, with low myophragm. *Carboniferous–Permian.*

Streptorhynchus KING, 1850, p. 107 [**Terebratulites pelargonatus* VON SCHLOTHEIM, 1816, p. 28; OD] [=*Lespius* DE GREGORIO, 1930, p. 24 (type, *L. favoritus*); *Mammosum* DE GREGORIO, 1930, p. 24 (type, *M. ipsium*)]. Small to medium sized, subconical, ventribiconvex, relatively coarsely costellate with concentric fila; ventral interarea apsacline, pseudodeltidium with monticulus, chilidium small, grooved medianly; ventral muscle scar flabellate, dorsal muscle scar faintly impressed; cardinal process high, occasionally with short median ridge or node at base. *Carboniferous–Permian:* cosmopolitan.——FIG. 481,*4a–f.* **S. pelargonatus* (VON SCHLOTHEIM), Kazanian, Gera, Germany; *a–c,* ventral, anterior, lateral views of shell, ×1.5; *d,* posterodorsal view of shell, ×3; *e,* dorsal valve interior showing cardinalia; *f,* latex mold of dorsal valve interior showing articulation, ×2 (new).

Arctitreta WHITFIELD, 1908, p. 57 [**A. pearyi;* OD] [=*Grumantia* USTRITSKY in USTRITSKY & TSCHERNJAK, 1963, p. 70 (type, *Streptorhynchus kempei* (ANDERSSON) in WIMAN, 1914)]. Medium to large sized, subpentagonal, ventribiconvex, rectimarginate, finely costellate, concentric ornamentation unknown; apsacline ventral interarea with convex pseudodeltidium and monticulus, vestigial dorsal interarea and chilidium; ventral muscle scar flabellate, dorsal scars faintly impressed about low myophragm; cardinal process high. *Permian:* Arctic North America, Greenland, Spitzbergen, Arctic Russia.——FIG. 481,*2a–d. A. kempei* (ANDERSSON), Seladersk series, Upper Permian, Spitzbergen; *a,* ventral valve exterior, ×0.7; *b,* dorsal valve internal mold, ×1; *c,* ventral valve internal mold, ×0.67; *d,* juvenile dorsal valve interior, ×1 (Manankov, 1979).

Bothrostegium COOPER & GRANT, 1974, p. 330 [**B. derbyoideum;* OD]. Similar to *Streptorhynchus* but small and more finely costellate, with variably disposed high interarea, grooved pseudodeltidium, conspicuous perideltidium, grooved chilidium; relatively low cardinal process; ventral muscle scar faint, dorsal muscle scar subcircular with low myophragm. *Lower Permian:* USA (Texas).——FIG. 481,*1a–f.* **B. derbyoideum,* Roadian, Texas; *a–d,* anterior, dorsal, posterior, lateral views of shell, ×3; *e,* paratype, dorsal valve interior, ×4; *f,* paratype, posterior view of cardinalia, ×3 (Cooper & Grant, 1974).

Chelononia COOPER & GRANT, 1974, p. 327 [**C. neali;* OD]. Similar to *Streptorhynchus* but elongately pyramidal, variably biconvex, unisulcate and

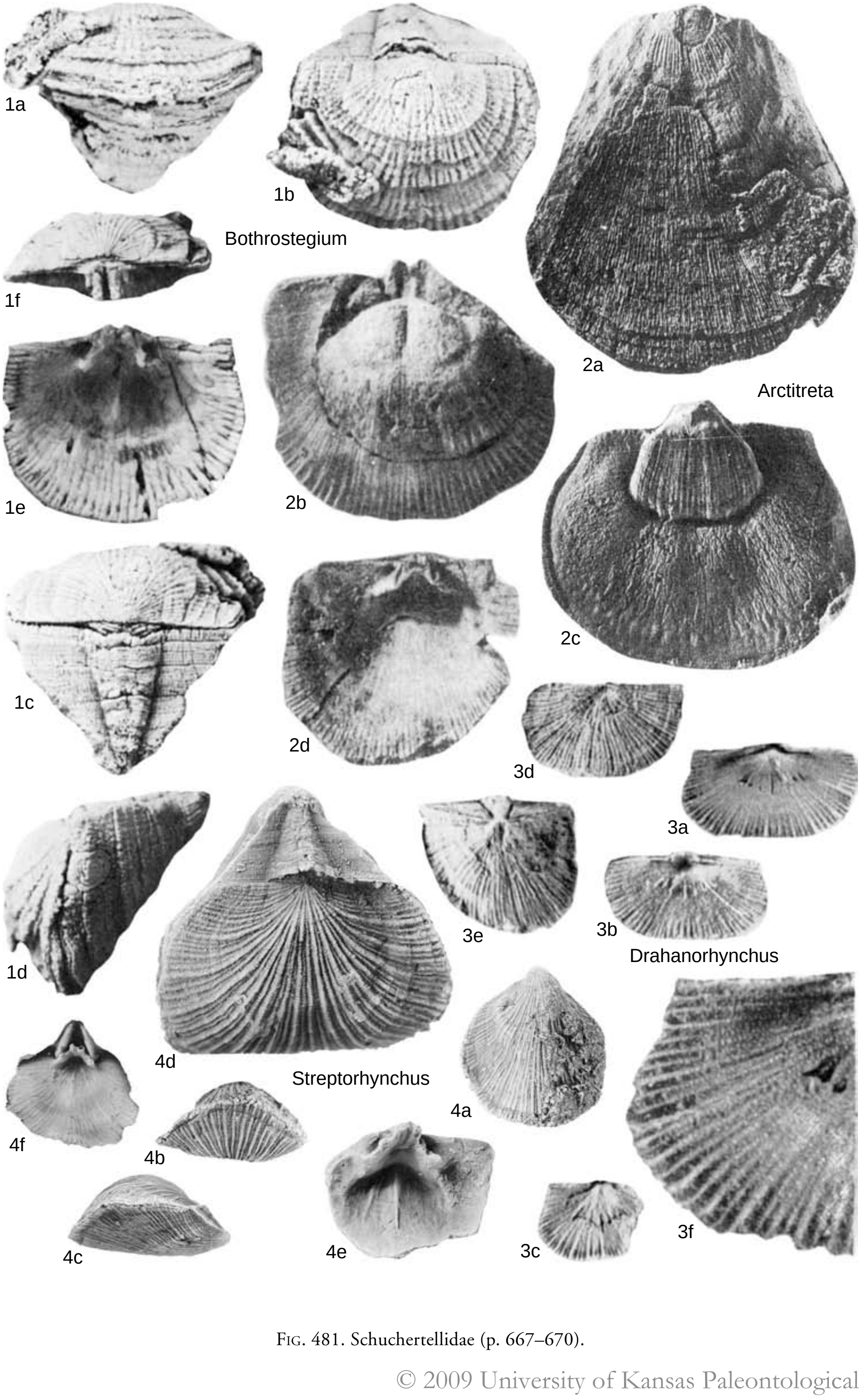

FIG. 481. Schuchertellidae (p. 667–670).

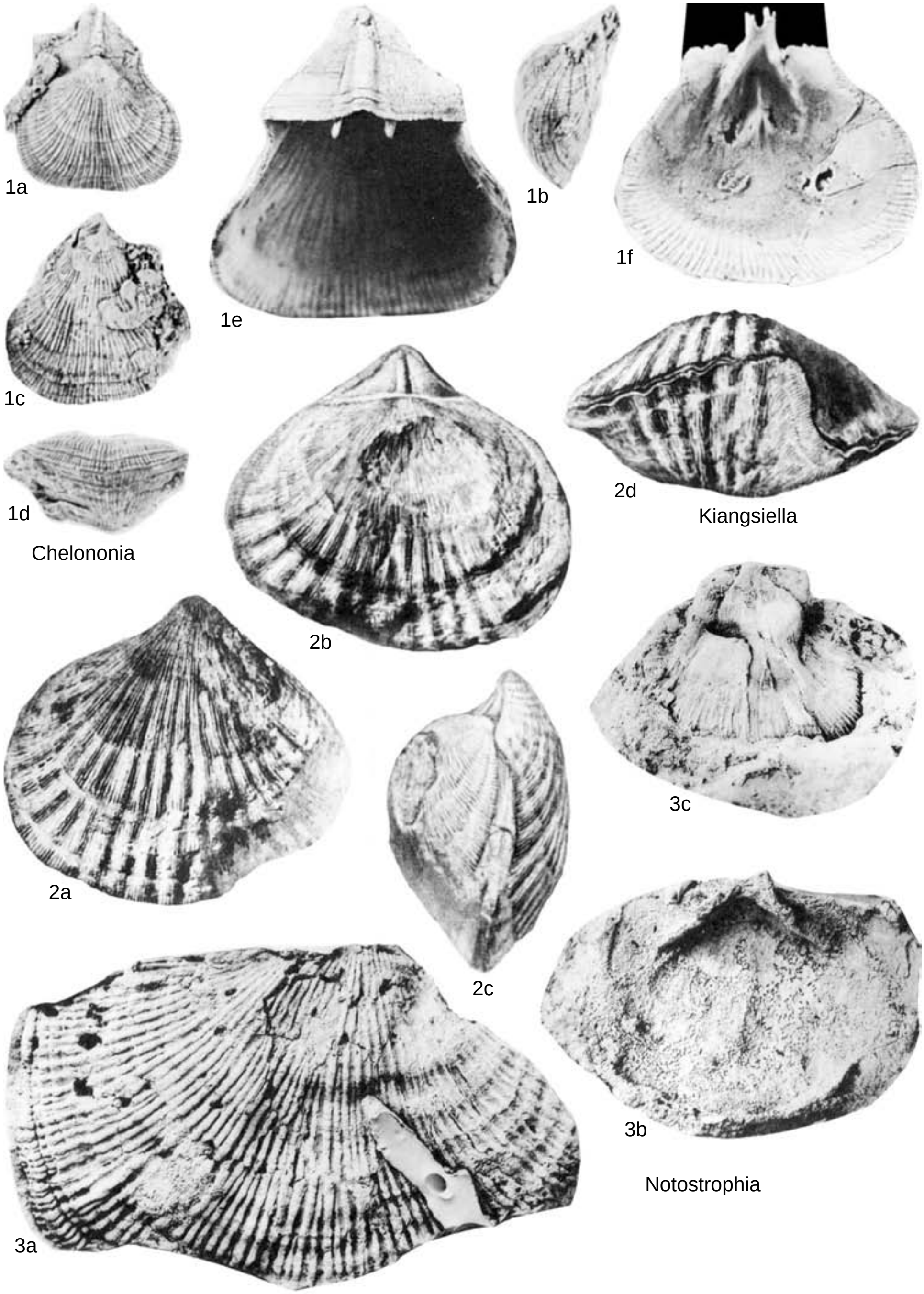

FIG. 482. Schuchertellidae (p. 667–670).

more finely costellate with concentric fila, evenly convex pseudodeltidium; impressed dorsal adductor scar and thick, low myophragm. *Lower Permian:* USA (Texas).——FIG. 482,*1a–f.* **C. neali,* Wolfcampian, Texas; *a–d,* holotype, dorsal, lateral, ventral, anterior views of shell, USNM 152646f,

×1; *e,f,* ventral valve of paratype, dorsal valve interior, ×2 (Cooper & Grant, 1974).

Drahanorhynchus Havlíček, 1967, p. 203 [**D. drahanicus;* OD]. Small, semioval, semiconical ventral valve, concave to plane dorsal valve, finely costellate with microscopic spines along crests; ventral interarea catacline to procline, pseudodeltidium convex, dorsal interarea and chilidium vestigial; dental plates and ventral median septum absent; socket ridges parallel with hinge line, fused with low cardinal process lobes with median process at base, dorsal adductor scar associated with myophragm flanked by 2 or 4 pairs of small radiating septa; shell extropunctate. [This genus is provisionally placed in the Schuchertellidae on the basis of its overall orthotetoid morphology, its lack of dental plates, and especially evidence from well-preserved molds that internal surfaces were indented by "closely crowded pits" (Havlíček, 1967, p. 204). The septal arrangement on the floor of a dorsal valve that is plane to concave in profile is anomalous, however, and the species requires further confirmatory investigation.] *Lower Carboniferous:* Czech Republic.——Fig. 481,*3a–f.* **D. drahanicus,* lower Viséan, Moravia; *a,b,* holotype, internal mold of dorsal valve, latex replica of same specimen, ×3; *c,d,* internal mold of incomplete dorsal valve, external mold of dorsal valve, ×3; *e,* internal mold of ventral valve, ×3; *f,* internal mold of dorsal valve showing small pits in radial arrangement, ×9 (Havlíček, 1967).

Kiangsiella Grabau in Chao, 1927a, p. 103 [**Orthotetes tingi* Grabau, 1924, p. 359; OD]. Similar to *Streptorhynchus* but with strong, secondary costation and with well-developed median ridge at base of cardinal process; dorsal adductor scar impressed about low myophragm. *Upper Carboniferous–Permian:* Asia, Australia.——Fig. 482,*2a–d.* **K. tingi* (Grabau), Lower Permian, southern Kiangsi, China; holotype, ventral, dorsal, lateral, anterior views of shell, ×1 (Chao, 1927a).

Notostrophia Waterhouse, 1973, p. 35 [**N. homeri;* OD]. Large, ventribiconvex with recurved margin to dorsal valve; ventral valve and recurved margin of dorsal valve finely costellate, rest of dorsal valve coarsely costate, rarely rugate; pseudodeltidium undescribed, chilidium platelike; teeth with low dental ridges (also referred to as plates), ventral muscle scar flabellate about low myophragm; cardinal process lobes low, grooved, with median node at base; socket ridges recurved; dorsal adductor scars impressed about short myophragm. [This genus has been assigned by its author to the Schuchertellidae and has been closely compared with the streptorhynchids *Arctitreta, Grumantia,* and an Australian species of *Streptorhynchus.* The author, however, who is given to an idiosyncratic usage of terminology in his systematic descriptions, has also reported the genus as being "pseudopunctate, 2 per mm." Until this and other features of the shell can be checked, no familial assignment of the genus can presently be made with any confidence.] *Lower Permian:* New Zealand.——Fig. 482,*3a–c.* **N. homeri,* Artinskian, Lower Permian, Southland; *a,* external latex cast of dorsal valve; *b,* latex cast of dorsal interior; *c,* internal mold of ventral valve, ×2 (Waterhouse, 1982c).

Taimyropsis Ustritsky in Ustritsky & Tschernjak, 1963, p. 69 [**T. monstrosus;* OD]. This genus was erected for one incomplete asymmetrical, gently convex, rounded ventral valve ornamented by fine costellae and impersistent concentric rugae and with 2 subparallel, shallow grooves traced from the beak for about one-third the length of the valve. These grooves have been interpreted as incipient dental ridges and have been cited as distinguishing the specimen from *Orthothetina* and *Streptorhynchus.* In fact, the grooves could also represent striations associated with muscle scars; more specimens of both valves will have to be examined and described to assess the merits of this genus. *Permian:* Taimyr, Turuzovks Series.

Tropidelasma Cooper & Grant, 1969, p. 3 [**T. culmenatum;* OD] [=*Erismatina* Waterhouse, 1983a, p. 117 (type, *E. cooperi*)]. Similar to *Streptorhynchus* but more finely costellate with flattish pseudodeltidium folded into narrow monticulus, short dorsal interarea, vestigial chilidium; fulcral plates confining sockets, faintly impressed ventral muscle scar, dorsal adductor scars impressed about slender myophragm. *Lower Permian:* USA (Texas), Thailand, ?Western Australia.——Fig. 483*a–e.* **T. culmenatum,* Wolfcampian, Lower Permian, Texas; *a,* holotype, posterior view of shell, USNM 147829b, ×1; *b,* paratype, lateral view of shell, ×1; *c,d,* paratypes, posterior view of ventral valve, posterior view of dorsal valve, ×1; *e,* paratype, internal view of cardinalia, ×3 (Cooper & Grant, 1974).

Superfamily CHILIDIOPSOIDEA
Boucot, 1959

[*nom. transl.* Williams & Brunton, herein, *ex* Chilidiopsidae Boucot, 1959, p. 25] [=Fardeniacea Johnson, 1982, p. 973, *nom. transl. ex* Fardeniinae Williams, 1965e, p. 407]

Normally uncemented, rarely with functional pedicle in adult shell; commonly bilaterally symmetrical, rectimarginate; interareas commonly low, pseudodeltidium variable very rarely with monticulus, chilidium usually developed; dental ridges discrete, unsupported by dental plates in some younger stocks; socket ridges commonly short, recurved, rarely fused with cardinal process lobes, commonly low, discrete; brachiophores usually undeveloped; shell impunctate. *Upper Ordovician–Lower Carboniferous (lower Serpukhovian).*

Family CHILIDIOPSIDAE Boucot, 1959

[Chilidiopsidae BOUCOT, 1959, p. 25]

Uncemented with supra-apical foramen in ventral larval or adult valve; variably sized, symmetrical, semioval to subrounded, normally finely costellate with concentric fila; perideltidium present, occasionally obscure; dental plates short, mostly divergent; ventral muscle scar normally impressed occasionally about myophragm; socket ridges short and low, recurved laterally, not incorporating bases of discrete cardinal process lobes; dorsal muscle scar variably impressed, dorsal myophragm occasionally developed. *Upper Ordovician–Middle Devonian.*

Subfamily GACELLINAE new subfamily

[Gacellinae WILLIAMS & BRUNTON, herein]

Biconvex, uniplicate, supra-apical foramen present in adult ventral valve; interareas well developed, ventral apsacline to procline, dorsal anacline, perideltidium weakly defined, pseudodeltidium and chilidium well developed, convex; dental plates long, subparallel, flanking ventral muscle scar of elongated diductors and median, lanceolate adductors; socket ridges parallel with hinge line, dorsal adductor scars quadripartite about pair of divergent septa flanking low median ridge. *Upper Ordovician (Caradoc).*

Gacella WILLIAMS, 1962, p. 222 [**G. insolita;* OD]. Small, semioval, parvicostellate by intercalation, concentric fila well developed. *Upper Ordovician (Caradoc):* Scotland, southeastern USA.——FIG. 484*a–d.* **G. insolita,* Caradoc, Girvan, Scotland; *a,b,* dorsal, ventral views of shell; *c,d,* internal mold of ventral valve, dorsal valve interior, ×2.25 (Williams, 1965e).

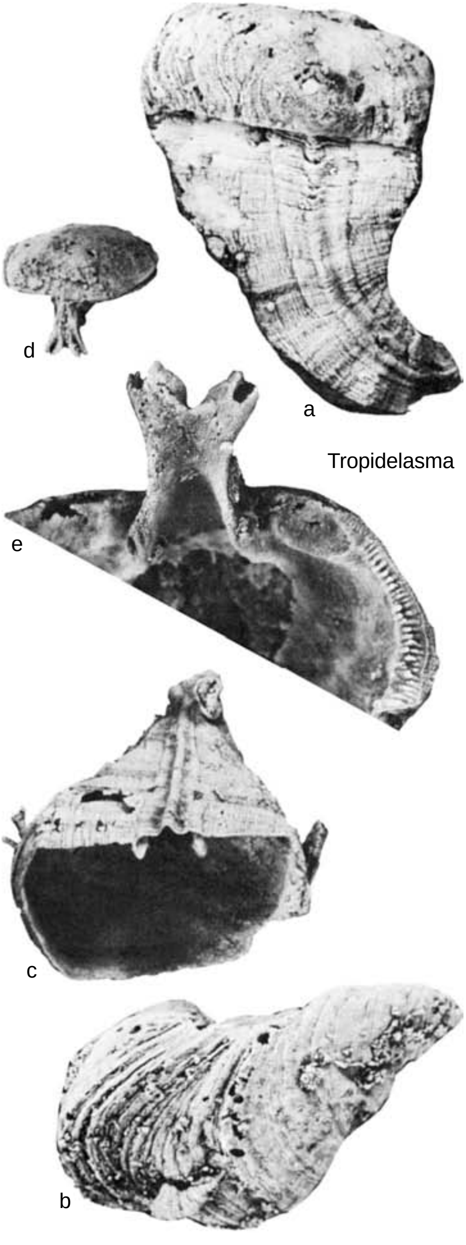

FIG. 483. Schuchertellidae (p. 670).

Subfamily CHILIDIOPSINAE Boucot, 1959

[*nom. transl.* WILLIAMS & BRUNTON, herein, *ex* Chilidiopsidae BOUCOT, 1959, p. 25]

Mainly subquadrate, resupinate and rectimarginate with well-defined perideltidium, pseudodeltidium convex or occasionally vestigial; dental plates short, apical to divergent; short socket ridges mainly recurved, small, blunt brachiophores usually developed, ventral muscle scar usually large, flabellate. *Upper Ordovician–Middle Devonian.*

Coolinia BANCROFT, 1949, p. 7 [*?*Orthis applanata* SALTER, 1846, p. 72; OD] [=*Chilidiopsis* BOUCOT,

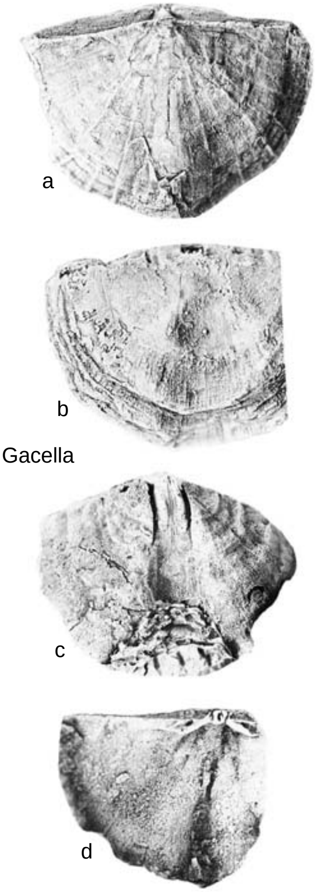

Fig. 484. Chilidiopsidae (p. 671).

1959, p. 25 (type, *Fardenia reedsi* Amsden, 1951, p. 84); *Krizistrophia* Havlíček, 1992, p. 176 (type, *K. micropoma*)]. Semioval to mucronate, biconvex, parvicostellate mainly by intercalation, fine concentric fila in interspaces, sporadically rugate; pedicle foramen not persisting in adult shell; pseudodeltidium apical; chilidium large; median basal node commonly developed between low cardinal process lobes, socket ridges recurved; ventral muscle scar flabellate, dorsal muscle scar divided by low myophore. [*Krizistrophia* Havlíček from middle Silurian limestones of Czech Republic is described as minute and as having strongly reduced cardinal process lobes. It is evidently a juvenile form of *Coolinia.*] *Silurian:* cosmopolitan.——Fig. 485,*2a–f.* **C. applanata* (Salter), upper Llandovery, Mayo, Ireland; *a,b,* ventral valve internal mold, latex replica of ventral interior, ×2; *c,* dorsal valve internal mold, ×2; *d,* latex replica of dorsal interior, ×4; *e,* ventral valve external mold; *f,* latex replica of ventral exterior, ×2 (new).

Fardenia Lamont, 1935, p. 310 [**F. scotica;* OD] [=*Saughina* Bancroft, 1949, p. 7 (type, *Strophomena pertinax* Reed, 1917, p. 907)]. Subquadrate, biconvex, relatively coarsely costellate mainly by branching, pedicle foramen usually persisting in adult shell, pseudodeltidium short, chilidium small, varying from pair of plates to complete cover; socket ridges recurved; muscle scars faint. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* Europe.——Fig. 486*a–f.* **F. scotica,* Ashgill, Girvan, Scotland; *a,b,* exterior mold of dorsal valve, latex replica of same specimen, ×3.5; *c,* interior mold of dorsal valve; *d,* latex replica of same specimen, ×3.75; *e,f,* interior mold of ventral valve, latex replica of same specimen, ×3.5 (new).

Hipparionix Vanuxem, 1842, p. 124 [**H. proximus;* SD Hall & Clarke, 1892, p. 258] [=*Hipparionyx* King, 1846, p. 37]. Large, semioval, resupinate, rectimarginate, finely costellate (concentric ornamentation not preserved); pseudodeltidium large, convex; chilidium vestigial, dorsal interarea linear; dental plates divergent, posteriorly enclosing large, impressed, flabellate ventral muscle scar divided by low myophragm; cardinal process with high, discrete lobes, socket ridges recurved, dorsal muscle scars faint, divided by low myophragm. [*Iridistrophia* is presently distinguishable from *Hipparionix* by its parvicostellation arising by intercalation, interspacial concentric fila, and the median node between the cardinal process lobes. These differences, however, may be refuted when comparisons can be made between well-preserved specimens of both type species.] *Lower Devonian:* North America.——Fig. 485,*1a,b.* **H. proximus,* Lower Devonian, New York; dorsal valve interior, ventral valve interior mold, ×1 (Shimer & Shrock, 1944).

Iridistrophia Havlíček, 1965b, p. 292 [**Orthis umbella* Barrande, 1848, p. 206; OD] [=*Hinganella* Su, 1980, p. 285 (type, *Aesopomum chinensis* Hamada, 1971); *Magicostrophia* Zhu, 1985, p. 51 (type, *M. hingganensis;* OD)]. Large, semioval, resupinate, parvicostellate with fila in interspaces; pseudodeltidium convex, chilidium reduced or vestigal, dorsal interarea rudimentary; dental plates, long, divergent; basal median node between well-developed cardinal process lobes, concave socket ridges parallel with hinge line; muscle scars indistinct. [*Hinganella* Su from the Lower Devonian of northeastern China is now known to be impunctate and appears to differ from *Iridistrophia* only in the weak development of fila that could be ascribed to the state of preservation of the type specimens and in being sporadically unisulcate. *Magicostrophia* Zhu is inadequately described and poorly illustrated. According to known characters, including the disposition of socket ridges, it is a subjective synonym of *Iridistrophia,* but the pseudodeltidium and chilidium have still to be studied.] *Upper Ordovician, upper Silurian (Ludlow)–Lower Devonian (Emsian):* Europe, China, Argentina, *upper Silurian (Ludlow)–Lower Devonian (Emsian);* China, *Upper Ordovician.*——Fig. 485,*3a–d.* **I. umbella* (Barrande), Emsian, Bohemia; *a,* ventral valve exterior,

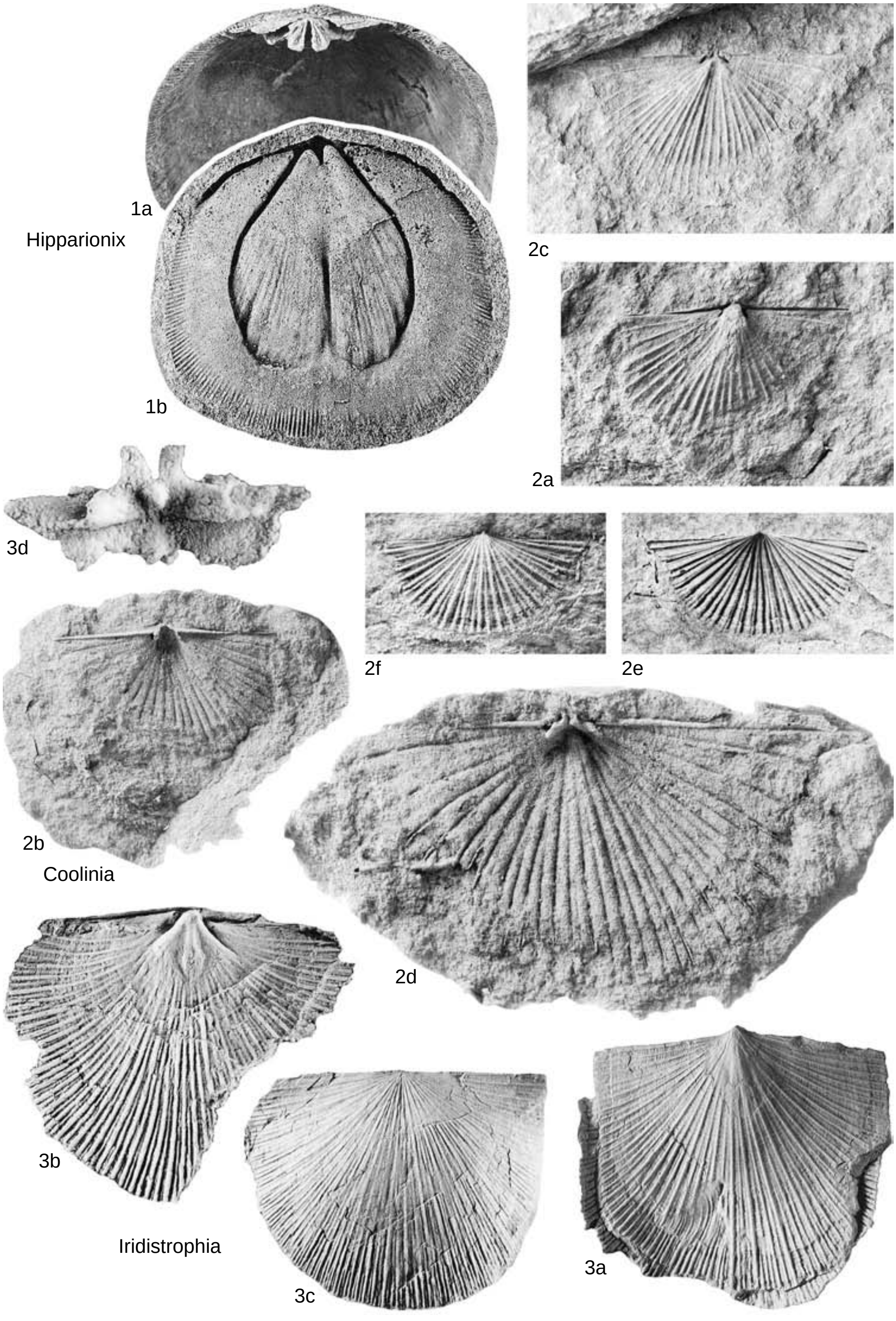

FIG. 485. Chilidiopsidae (p. 671–674).

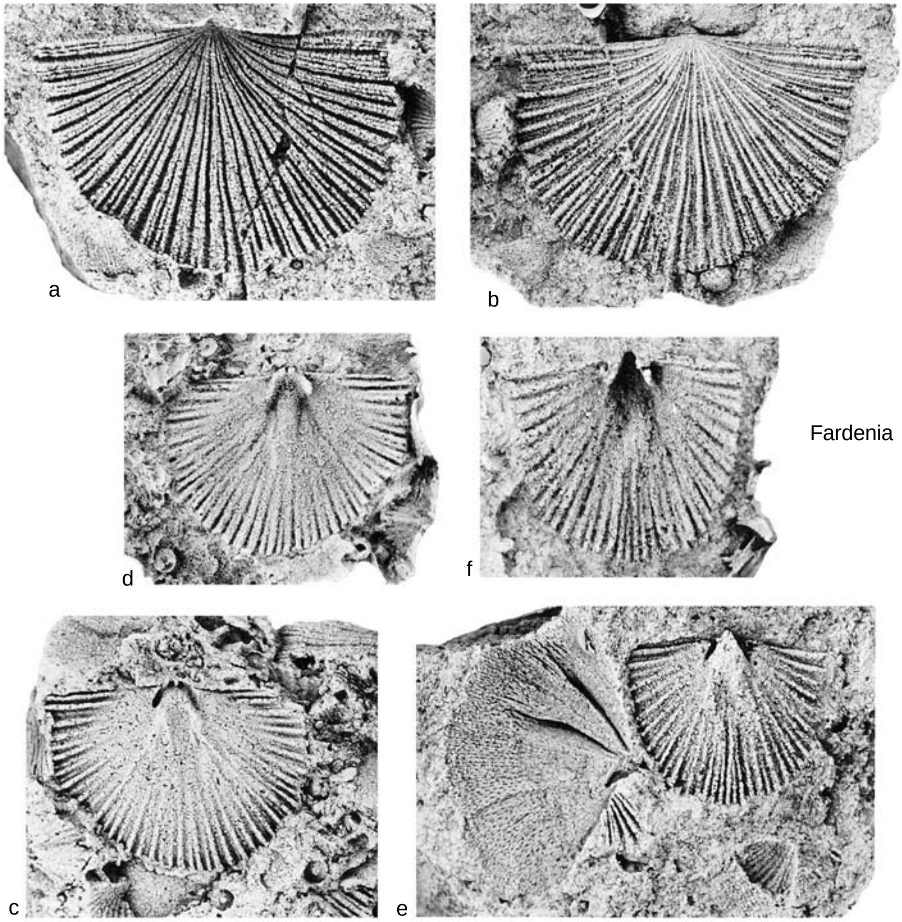

FIG. 486. Chilidiopsidae (p. 672).

×1.8; *b,c,* internal mold of ventral valve, dorsal valve exterior, ×1.5; *d,* internal view of cardinalia, ×4 (Havlíček, 1967).

Morinorhynchus HAVLÍČEK, 1965b, p. 291 [**M. dalmanelliformis;* OD]. Similar to *Fardenia* but subcircular and variably unisulcate; radial ornament tending to be finely fascicostellate, pseudodeltidium convex, chilidium of discrete plates; short socket ridges recurved parallel with hinge line; muscle scars faint with rhombic ventral impressions and lemniscate dorsal mantle canals. *upper Silurian (Ludlow):* Europe.——FIG. 487,*1a–c.* **M. dalmanelliformis,* Ludlow, Bohemia; holotype, ventral valve exterior, internal mold of ventral valve, internal mold of dorsal valve, ×2 (Havlíček, 1967).——FIG. 487,*1d–f. M. crispus* (LINDSTROM), Ludlow, Gotland, Sweden; *d,* syntype, ventral valve interior; *e,f,* lectotype, interior, exterior of dorsal valve, ×3 (Bassett & Cocks, 1974).

Pseudostrophomena RÕÕMUSOKS, 1963, p. 237 [* *P. reclinis;* OD]. Similar to *Coolinia* but small, subquadrate, and resupinate; median basal node between cardinal process lobes unknown; myophragm dividing ventral muscle scar, dorsal adductor scars faint. *Upper Ordovician:* Baltic region.——FIG. 488,*1a–f.* **P. reclinis,* upper Caradoc, Estonia; *a–c,* holotype, dorsal, ventral, lateral views of shell, ×1.7; *d,* holotype, posterior view of shell, ×2.4 (Rõõmusoks, 1963); *e,f,* dorsal interior, ventral interior, ×2 (new). [Note added in proof: but pseudopunctate, see p. 224.]

Valdaria BASSETT & COCKS, 1974, p. 18 [**V. testudo;* OD]. Similar to *Iridistrophia* but subcircular, gently resupinate, and uniplicate; parvicostellate interspaces without fila; chilidium small but entire; dental plates short, teeth weak; flabellate ventral muscle scar faintly impressed, dorsal muscle scar unknown. *lower Silurian–middle Silurian (Wenlock):* Sweden.

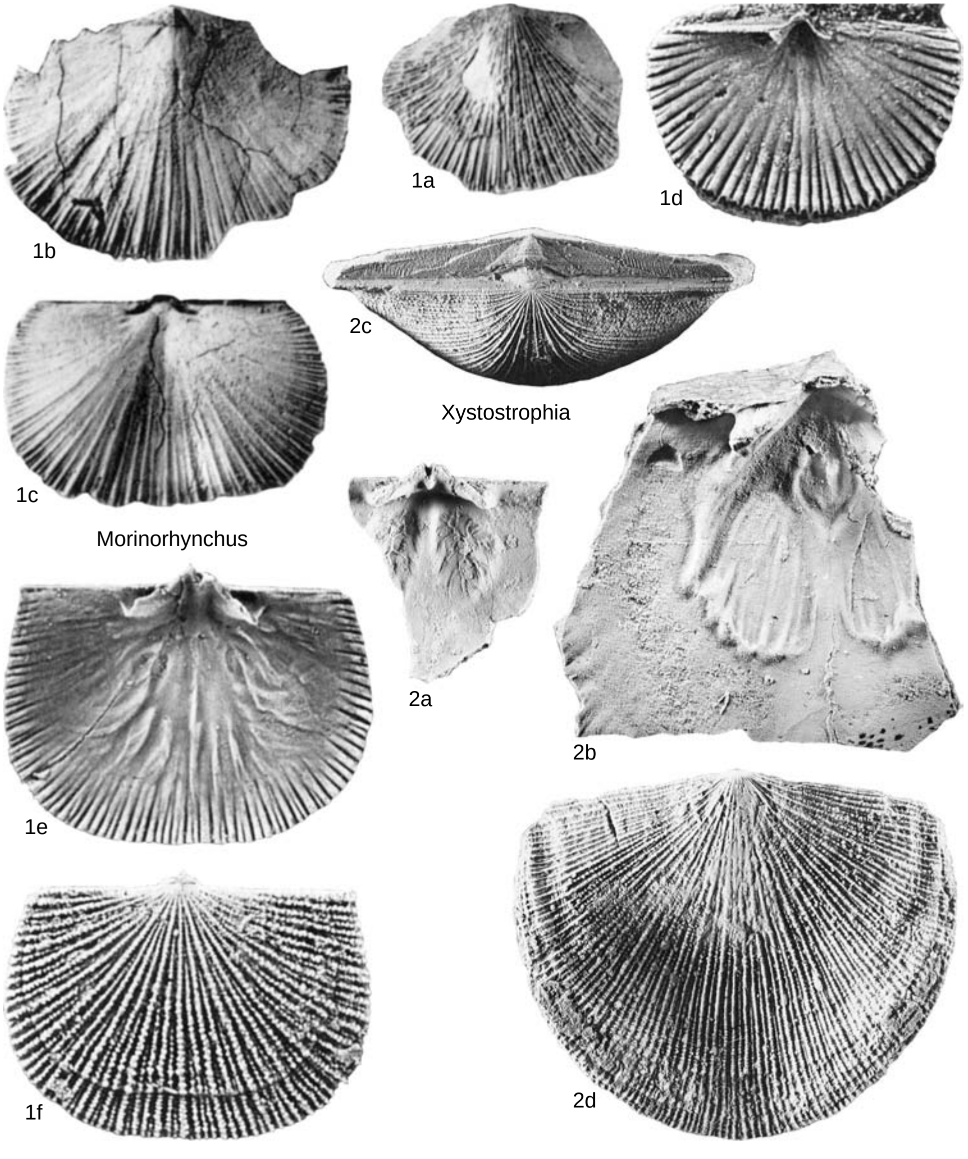

FIG. 487. Chilidiopsidae (p. 674–676).

——FIG. 488,*2a–c*. **V. testudo,* lower Wenlock, Gotland, Sweden; *a,* holotype, enlargement of interarea, ×2.25; *b,c,* ventral valve interior, ventral valve external mold, ×1.25 (Bassett & Cocks, 1974).

Xystostrophia HAVLÍČEK, 1965b, p. 292 [**Terebratulites umbraculum* SCHLOTHEIM, 1820, p. 256; OD] [=*Apicilirella* SU, 1976, p. 179 (type, *A. vulgaris*)]. Similar to *Coolinia* but larger, subquadrate, more resupinate with high convex pseudodeltidium and low chilidium; fila commonly extending as short spines along fine costellae; dorsal muscle scar divided by myophragm. [*Apicilirella* SU has been described by its author as unique among chilidiopsids in having a median ridge developed within the ventral muscle scar, which is not so. In other characteristics a close affinity with *Xystostrophia* was noted except for a stronger median elevation between the bases of the cardinal process lobes.] *Middle*

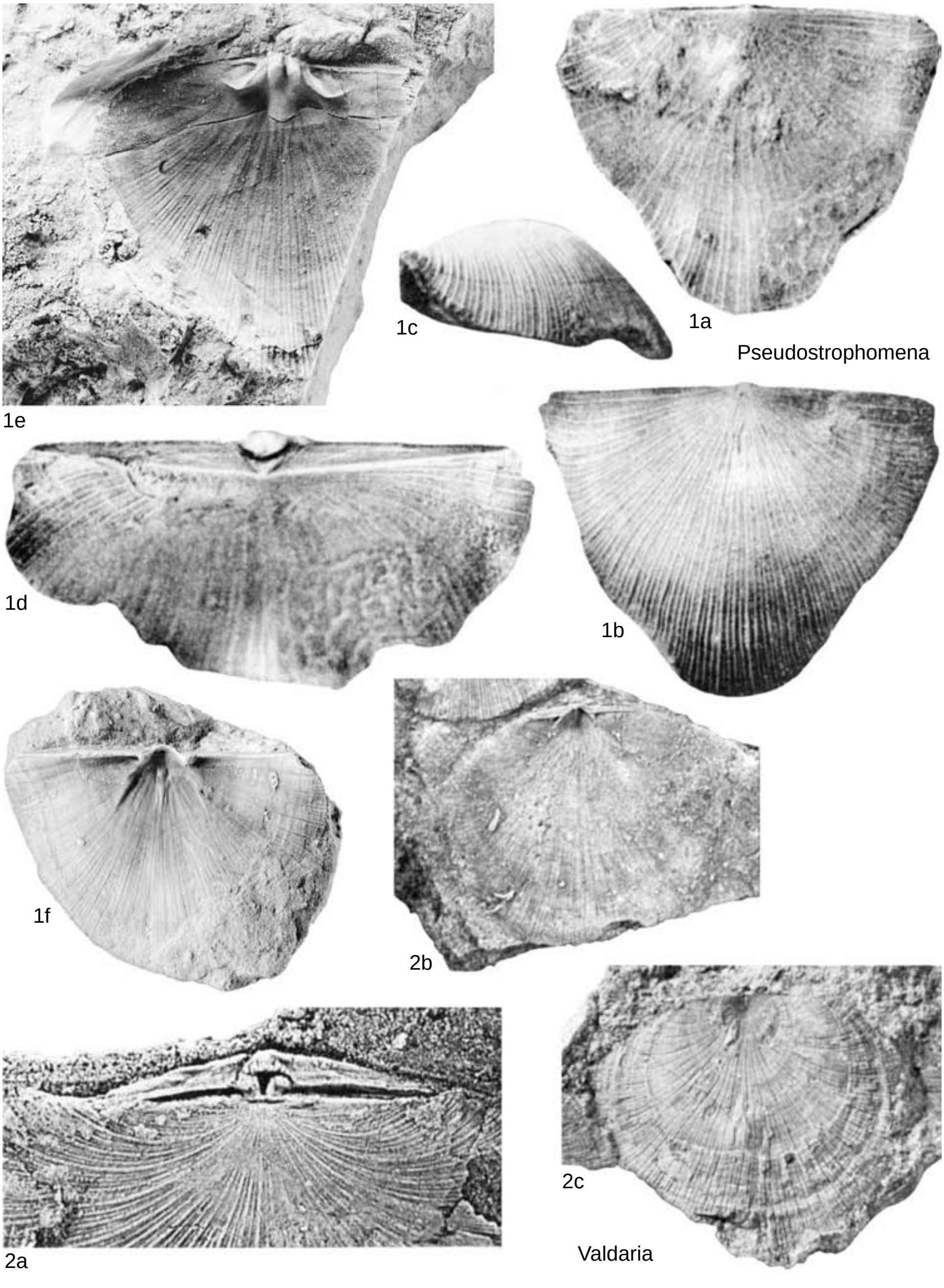

FIG. 488. Chilidiopsidae (p. 674–675).

Devonian: Europe.——FIG. 487,*2a–d.* **X. umbraculum* (SCHLOTHEIM), Givetian; *a,* incomplete dorsal valve, Holy Cross Mountains, Poland, ×1.5; *b,* ventral valve interior, Holy Cross Mountains, Poland, ×2; *c,d,* posterior, ventral views of shell, Rhineland, Germany, ×1.1 (Havlíček, 1967).

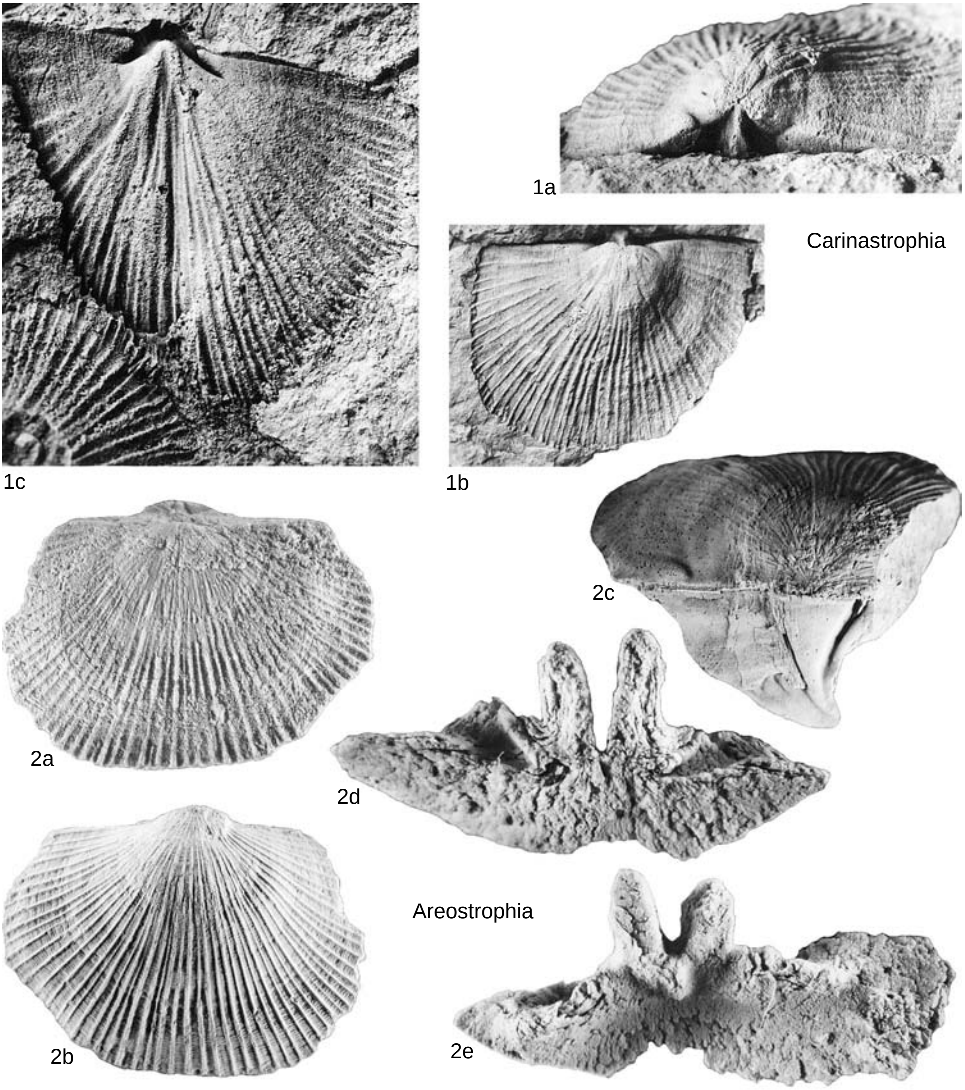

Fig. 489. Areostrophiidae (p. 678–679).

Family AREOSTROPHIIDAE
Manankov, 1979

[*nom. transl.* Williams & Brunton, herein, *ex* Areostrophinae Manankov, 1979, p. 59]

Usually cemented by deformed ventral valve without trace of supra-apical foramen; variably sized, semioval to subconical, rectimarginate, variably costellate and concentrically ornamented; perideltidium present, occasionally obscure; dental ridges discrete, unsupported by dental plates, ventral muscle scar mostly faint, rarely associated with myophragm. *middle Silurian (Wenlock)–Lower Carboniferous (lower Serpukhovian).*

Subfamily AREOSTROPHIINAE
Manankov, 1979

[Areostrophiinae Manankov, 1979, p. 59]

Medium to large, biconvex to resupinate; ventral interarea usually high but variable disposition, pseudodeltidium large, convex,

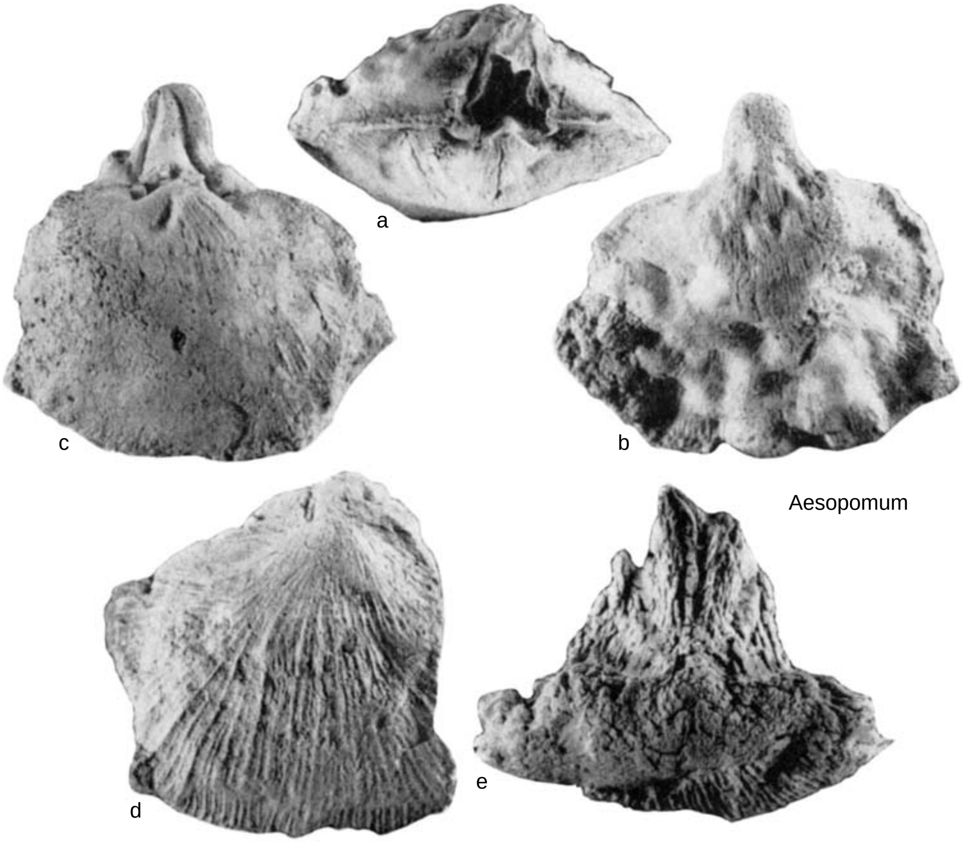

FIG. 490. Areostrophiidae (p. 678).

dorsal interarea lacking or short, anacline, chilidium not developed in adult valves; cardinal process lobes elongated, discrete or fused into proximal shaft, flanked by variably divergent socket ridges; dorsal adductor scars faint without myophragm. *upper Silurian–Middle Devonian (lower Eifelian).*

Areostrophia HAVLÍČEK, 1965b, p. 293 [*?*Orthis distorta* BARRANDE, 1879, p. 163; OD]. Large, biconvex, subrounded, parvicostellate by intercalation with fila in interspaces; ventral interarea commonly high, apsacline, dorsal interarea lacking; cardinal process lobes discrete, with myophore slits directed posteroventrally and united with strong inner socket ridges by divergent concave socket ridges. *upper Silurian–Lower Devonian:* Czech Republic, Siberia. ——FIG. 489,*2a–e.* **A. distorta* (BARRANDE), Pragian, Bohemia; *a,b,* dorsal, ventral valve exteriors, ×1.5; *c,* posterodorsal view of internal mold, ×1.5; *d,e,* external, internal views of cardinalia, ×3.5 (Havlíček, 1967).

Aesopomum HAVLÍČEK, 1965b, p. 293 [**Strophomena aesopea* BARRANDE, 1879, pl. 92, fig. 4, pl. 133, fig. 2; OD]. Similar to *Areostrophia* but subconical and irregular in shape with very high ventral interarea, dorsal interarea short, anacline; cardinal process lobes fused into single shaft, with myophore slits on posterior faces, ankylosed with divergent brachiophore bases and conspicuous, flanking socket ridges to form thick, concave socket plates (erismata); ventral muscle scar small, lightly impressed, without myophragm. *upper Silurian–Lower Devonian (Emsian):* Czech Republic, southern China.——FIG. 490*a–e.* **A. aesopeum* (BARRANDE), Bohemia; *a–c,* posterior, ventral, dorsal views of internal molds, Pragian, ×1.5; *d,* dorsal valve exterior, Pragian, ×1.5; *e,* posterior view of cardinalia, Emsian, ×2 (Havlíček, 1967).

Carinastrophia GRATSIANOVA, 1975, p. 64 [**Areostrophia elinovi;* OD] [=*Xenizostrophia* SU, 1976, p. 181 (type, *X. spinosa*)]. Similar to *Areostrophia* but smaller with fine costellae slightly spinose at intersections with concentric fila; inwardly thickened dental ridges; median node between bases of cardinal process lobes. [*Xenizostrophia* SU from

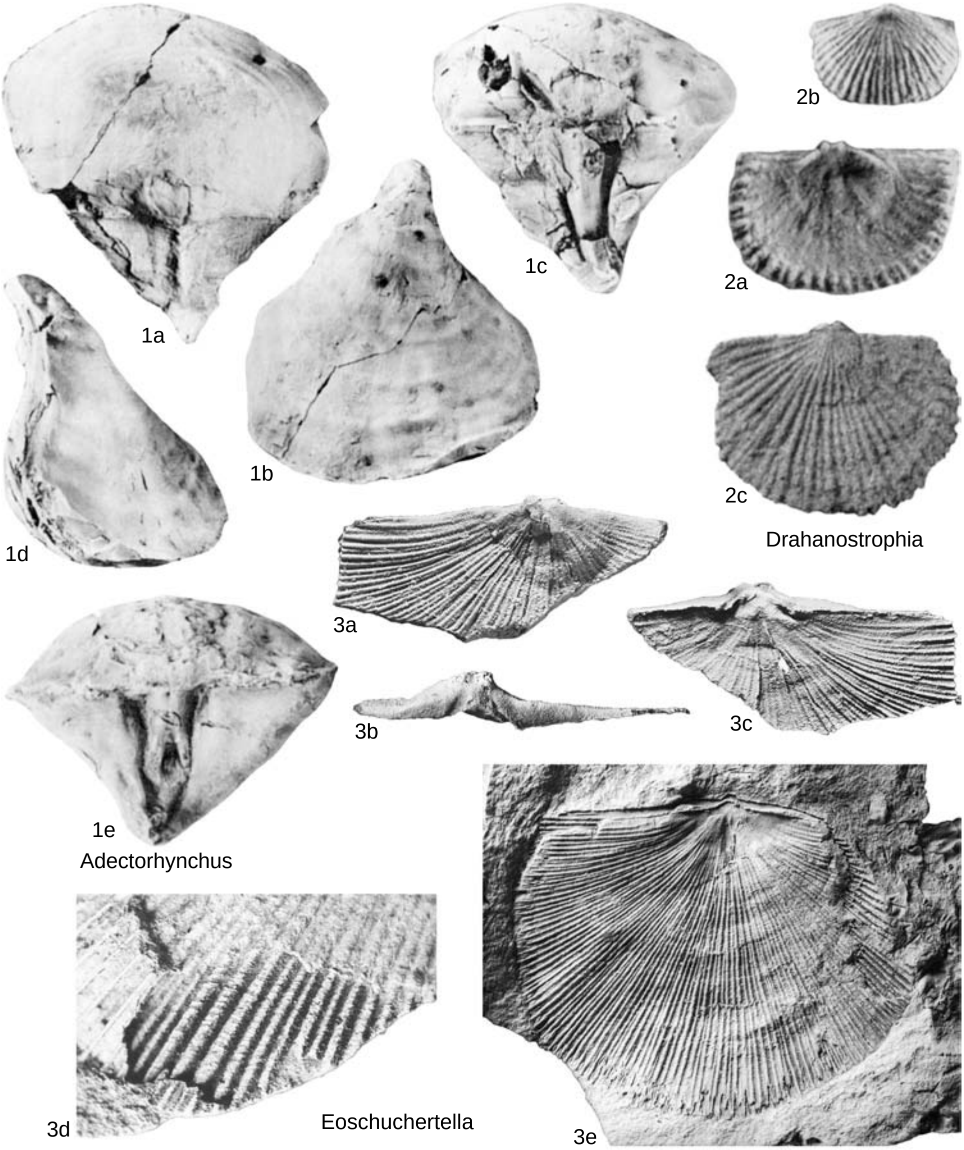

FIG. 491. Areostrophiidae (p. 680–681).

the Lower Devonian of Inner Mongolia is indistinguishable from *Carinastrophia* except for the more variable profile of the shell that, in the type species of the former, varies from planoconvex to ventribiconvex.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Russia (Gorno-Altai).——FIG. 489,*1a–c.* **C. elinovi* (GRATSIANOVA), upper Emsian, Gorno-Altai, southwestern Siberia; *a,* posterior view of ventral valve internal mold, ×3; *b,* holotype, ventral valve internal mold, ×2; *c,* dorsal valve internal mold, ×3 (Gratsianova, 1975).

Subfamily ADECTORHYNCHINAE Henry & Gordon, 1985

[Adectorhynchinae HENRY & GORDON, 1985, p. 36]

Small to medium sized, mostly subrounded, ventribiconvex to resupinate, coarsely to finely costellate; ventral interarea variable in height and disposition, pseudodeltidium normally convex, dorsal interarea short, mainly anacline, chilidium present,

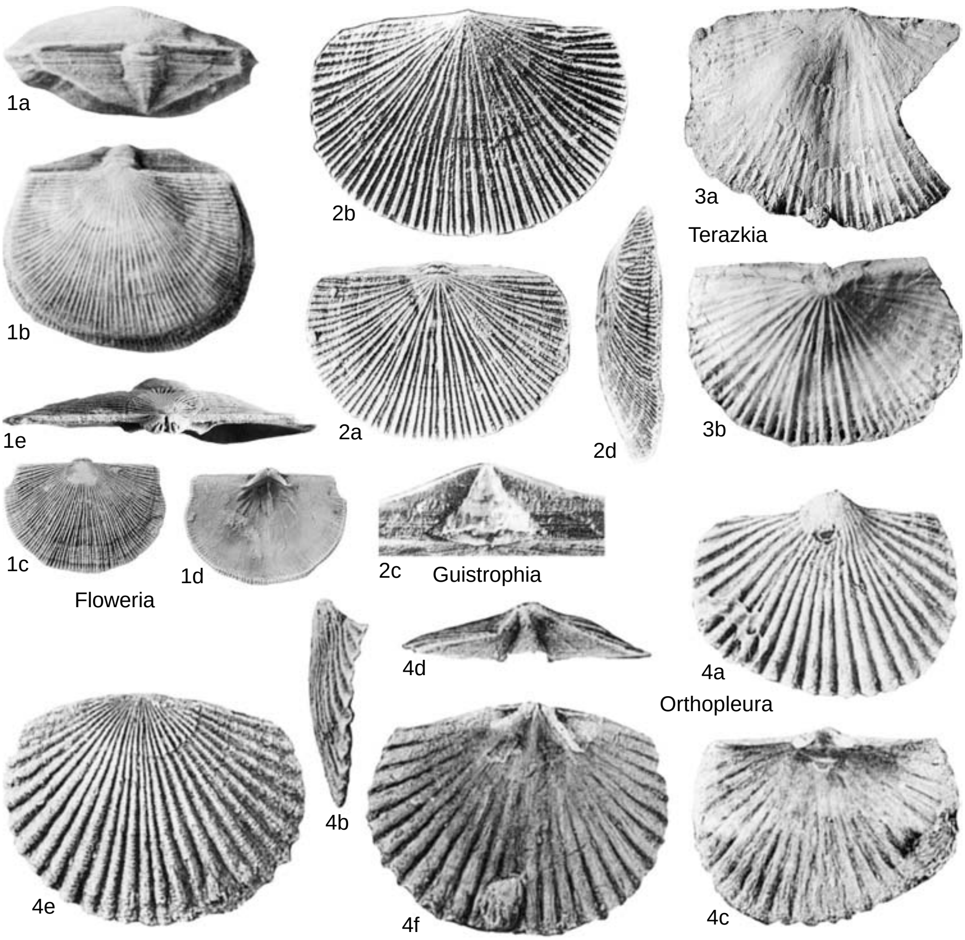

FIG. 492. Areostrophiidae (p. 681).

normally grooved medianly; socket ridges recurved to divergent, cardinal process lobes discrete or fused, rarely high with myophore slits. *middle Silurian (Wenlock)–Lower Carboniferous (lower Serpukhovian).*

Adectorhynchus HENRY & GORDON, 1985, p. 36 [**Streptorhynchus suspectum* GIRTY, 1929, p. 136; OD]. Ventribiconvex, normally subconical with high ventral interarea, flat to slightly convex pseudodeltidium with monticulus and linear dorsal interarea with short, medianly notched chilidium; finely parvicostellate with concentric fila; cardinal process lobes long with myophore slits, fused proximally into single shaft, united with socket ridges into thick socket plates (erisma) extending laterally; ventral muscle scar ill defined, myophragm low, dorsal muscle scar impressed about low myophragm. *Lower Carboniferous (lower Serpukhovian):* North America.——FIG. 491,*1a–e.* **A. suspectum* (GIRTY), upper Chesterian, Arkansas; *a,* posterodorsal view of shell, ×1; *b–d,* ventral, posterior, lateral views of internal mold, ×1; *e,* paralectotype, posterior face of cardinal process, ×3 (Henry & Gordon, 1985).

Drahanostrophia HAVLÍČEK, 1967, p. 202 [**D. ficneri;* OD]. Small, subquadrate, strongly ventribiconvex, costellate by branching; ventral interarea apsacline to catacline with convex pseudodeltidium, dorsal interarea linear with small chilidium either as single piece or pair of plates; cardinal process lobes small, bases ankylosed to widely divergent socket ridges extended laterally as small processes; ventral muscle scar indistinct, dorsal muscle scar broadly oval with low myophragm. [This genus is assigned to the Adectorhynchinae on a balance of features including the presence of a chilidium. It is, however, a rare chilidiopsoid and further study of some of the obscure characters may confirm a closer affinity with the Areostrophiinae, to which it is also cladistically linked.] *Middle Devonian (Givetian):* Czech Republic.——FIG. 491,*2a–c.* **D. ficneri,* Givetian, Moravia; *a,* dorsal valve interior, ×3.5; *b,* ventral valve exterior, ×2.8; *c,* dorsal valve exterior, ×3.8 (Havlíček, 1967).

Eoschuchertella GRATSIANOVA, 1974, p. 83 [**E. popovi;* OD]. Similar to *Floweria* but strongly ventribiconvex, finely costellate by bifurcation with concentric fila in interspaces; socket ridges divergent at about 100°, tips extending ventrolaterally; muscle scars ill defined with occasional weak dorsal myophragm. *upper Lower Devonian–Middle Devonian (Eifelian):* Russia (Gorno-Altai).——FIG. 491,*3a–e.* **E. popovi,* upper Emsian, Gorno-Altai, southwestern Siberia; *a–c,* holotype, cast of ventral valve, interarea, dorsal valve, ×2; *d,* mold of concentric growth lines in intercostal spaces, ×5; *e,* internal mold of dorsal valve, ×1.5 (Gratsianova, 1974).

Floweria COOPER & DUTRO, 1982, p. 53 [**Orthis prava* HALL in HALL & WHITNEY, 1858, p. 490; OD]. Planoconvex to unequally biconvex, subquadrate; finely costellate by intercalation; pseudodeltidium convex; discrete cardinal process lobes low, grooved, with median node at base; socket ridges recurved; muscle scars normally impressed, dorsal adductor scars usually divided by low myophragm. *Upper Devonian:* North America.——FIG. 492,*1a–e.* **F. prava* (HALL), Frasnian, Iowa; *a,b,* posterior, dorsal views of shell, ×2 (Cooper & Dutro, 1982); *c,d,* exterior, interior views of dorsal valve, ×1; *e,* posterior view of dorsal valve, ×2 (new).

Guistrophia WANG & RONG, 1986, p. 110[261] [**G. modesta;* OD]. Similar to *Floweria* but resupinate, parvicostellate, with short, weakly developed socket ridges; muscle scars unknown. *Lower Devonian (Emsian):* Guangxi, southern China.——FIG. 492,*2a–d.* **G. modesta,* lower Emsian, southern Guangxi, paratype; *a,* dorsal view of shell, ×2.5; *b,* ventral view of shell, ×3; *c,* posterior view of shell, ×8; *d,* lateral view of shell, ×1.5 (Wang & Rong, 1986).

Orthopleura IMBRIE, 1959, p. 391 [**O. rhipis;* OD]. Small, subcircular, gently biconvex to planoconvex, costate to coarsely costellate with fine concentric fila; pseudodeltidium large, chilidium short, convex, perideltidium well developed; cardinal process lobes low, myophores directed posteriorly, socket ridges short, divergent; ventral muscle scar unknown, dorsal adductor scar lightly impressed about short myophragm. [This genus was described as being pseudopunctate, but no such structures were found in a recent SEM examination of a shell fragment.] *Middle Devonian:* North America.——FIG. 492,*4a–f.* **O. rhipis,* Traverse Group, Middle Devonian, Michigan; *a–d,* holotype, ventral valve exterior, lateral, interior, posterior views, ×3; *e,f,* dorsal exterior, interior, ×3 (Imbrie, 1959).

Terazkia HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 94 [**Orthis expandens* BARRANDE, 1879, pl. 68, case VIII]. Subquadrate, convexiconcave, coarsely costellate by branching and intercalation, with concentric fila; ventral interarea low, catacline, with open delthyrium, dorsal interarea linear, chilidium not established because of poor preservation; cardinal process lobes discrete, low, socket ridges short, divergent, extending laterally. [This genus is poorly known and, pending further information on the nature of its chilidium and its internal morphology, is assigned to the Areostrophiidae solely on the judgment of its authors.] *middle Silurian (Wenlock):* Czech Republic.——FIG. 492,*3a,b.* **T. expandens* (BARRANDE), Wenlock, Bohemia; dorsal valve, ventral valve exteriors, ×2.2 (Havlíček & Štorch, 1990).

TRIPLESIIDINA

A. D. WRIGHT
[Queen's University, Belfast]

Suborder TRIPLESIIDINA Moore, 1952

[*nom. correct.* WRIGHT, 1965b, p. 355, *pro* suborder Triplesioidea MUIR-WOOD, 1955, p. 89, *nom. transl. ex* order Triplesiida MOORE, 1952, p. 221]

Biconvex to markedly dorsibiconvex strophic and deltidiodont shells. Ventral valve with pseudodeltidium flush with interarea, typically arched medianly into monticulus; foramen apical. Dorsal valve interarea obsolete; internally with long, forked, posteroventrally recurved cardinal process and strong brachiophores. Secondary shell laminar, rarely with pseudopunctae. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

The Triplesiidina form a distinctive and closely knit group among the articulated brachiopods. The external appearance is quite variable and, before the internal structures were fully known, the various species and genera were assigned to such stocks as *Atrypa, Orthis, Productus,* and *Spirifer.* The discovery of the unusual and consistent cardinalia in the then known genera led SCHUCHERT (1913a) to unite them into a single subfamily within the Strophomenidae.

Subsequently the distinctive characters of the subfamily caused it to be elevated progressively to familial (Öpik, 1932), superfamilial (Cooper, 1944), and ordinal rank (Moore, 1952); Muir-Wood (1955) reduced it to the subordinal status. The suborder contains but a single family; attempts to divide this into subfamilies (Amsden, 1968) or to establish additional family groups under the superfamily (Havlíček in Havlíček & Štorch, 1990) have not so far been acceptable due to the plasticity of the morphological characters within the plexus (Wright, 1971, 1993b). The variability is accentuated by asymmetrical growth, which affects shape, ribbing, and the anterior commissure widely within the group, and not simply a few well-known species of *Streptis.*

The discovery of the laminar nature of the secondary shell, coupled with morphology, enabled Williams (1968a, 1970) to identify a close relationship between the triplesioids and the davidsonioids (orthotetidines) and to suggest that both diverged from the billingselloid stock probably in Late Cambrian times. As yet the earliest known triplesioid is *Onychoplecia* from the lower Llanvirn Table Point Formation of Newfoundland (Ross & James, 1987), with *Triplesia* and *Oxoplecia* present in Wales by the later Llanvirn (Lockley & Williams, 1981). The group continued throughout the Ordovician and into the Silurian, being fairly widespread but rarely abundant. Although seven and possibly even nine genera were still present in the Wenlock, only one (*Plectotreta*) has so far been recorded from the Ludlow (Bassett & Cocks, 1974).

The triplesiidine shell varies greatly in outline from the wide-hinged, transverse *Bicuspina* to rounded *Cliftonia,* tear-shaped *Onychoplecia,* and elongate, clawlike *Onychotreta;* in profile the shell is less variable, from biconvex to markedly dorsibiconvex. A strong dorsal fold and ventral sulcus producing a uniplicate anterior commissure is typical; the reverse situation, with ventral fold and dorsal sulcus and a unisulcate commissure, is taken as a diagnostic generic character for the genera *Brachymimulus* and *Paraonychoplecia.* Variations of these basic commissural types are seen in some species of noncostate genera, sulciplicate in *Triplesia* and *Grammoplecia,* and plicosulcate and paraplicate in *Paraonychoplecia.* A sinusoidal anterior commissure produced by a relative twisting of either half of the shell characterizes *Amphiplecia,* many species of *Streptis,* and occasional specimens in populations of other genera. Surface ornament is lacking, for example, in the smooth *Triplesia;* other forms show fine concentric filae (*Caeroplecia*), elevated growth lines (*Oxoplecia*), stronger lamellae (*Cliftonia*), or frills (*Plectotreta*), commonly in combination with radial capillae, costellae, costae, or plications.

The ventral valve has a small apical or supra-apical foramen and a well-developed interarea that reaches exceptional lengths in *Onychotreta.* The delthyrium is closed by a pseudodeltidium flush with the interarea, characteristically with a narrow median fold (monticulus). The development of this structure may vary within a species, but in some later forms its absence is consistent enough to be useful as a generic character, as in *Brachymimulus, Placotriplesia,* and *Placocliftonia.* From the foramen, the pedicle may pass to the interior through thick umbonal calcite (pedicle passage) or may extend to the valve floor through a more or less tubular calcareous sheath (pedicle tube). The teeth are normally supported by dental plates. Muscle scars are known for only a few genera, where they consist of flabellate diductor scars surrounding and all but enclosing cordate or lanceolate adductor scars (see Fig. 495,*2d*). The meager evidence of the mantle canals indicates a saccate or lemniscate pattern.

Although the dorsal valve typically lacks an interarea, with the strongly convex umbo abutting on to the hinge line, a short yet distinct anacline area is known from some species of *Triplesia* including *T. ortoni* (Wright, 1971). In these cases the notothyrium is closed by a chilidium with a marked median fold. Internally the valve possesses a long, forked cardinal process that curves backward from its base on the hinge line to extend

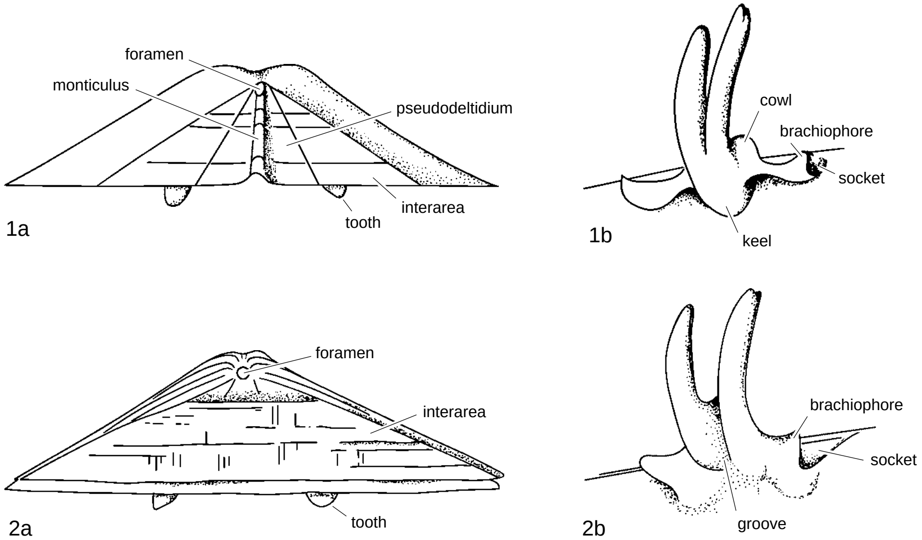

FIG. 493. Commonly associated triplesiid structures; *1a,* ventral valve with monticulate pseudodeltidium and *1b,* dorsal valve cardinalia with keeled cardinal process, cowl, and discrete brachiophores, as in *Triplesia; 2a,* pseudodeltidium lacking monticulus and *2b,* cardinalia with grooved process, each lobe closely fused to adjacent brachiophore, lacking cowl, as in *Ogmoplecia* (new).

posteriorly into the umbo of the ventral valve (see Fig. 494,*1f*). The myophores are located at the distal extremity of each prong, usually as deep grooves in the dorsal surface. At the proximal end, the process is covered by the chilidium if present; in some genera (e.g., *Triplesia,* Fig. 494,*1g*) a proximally directed cowl (hood of WRIGHT, 1963a) arches over the shaft, closing any gap at the front of the pseudodeltidium when the valves are closed; these structures tend to be associated with a well-formed monticulus (Fig. 493). The forked cardinal process ranges from being cleaved from its proximal end, with each prong fused more to its adjacent brachiophore and forming a grooved process as in *Ogmoplecia* (see Fig. 496,*4d*), to the two prongs being fused proximally to form a keeled process as in *Triplesia* (see Fig. 494,*1f*). The pair of calcareous processes that define the anteromedian margins of the sockets differ from typical orthoid brachiophores in having their distal points directed posterolaterally. The adult lophophore is interpreted as being a dorsally directed spirolophe. Where specimens show muscle scars and mantle canal impressions, the dorsal muscle field has a subcentral anterior adductor pair and a broader posterior pair, which are flanked by saccate gonocoels (WRIGHT & JAANUSSON, 1993).

Superfamily TRIPLESIOIDEA Schuchert, 1913

[*nom. transl.* WRIGHT, herein, *ex* superfamily Triplesiacea COOPER, 1944, p. 307, *nom. transl. ex* Triplesiinae SCHUCHERT, 1929, p. 16, *nom. correct. pro* Tripleciinae SCHUCHERT, 1913a, p. 387]

Characters as for suborder. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

Family TRIPLESIIDAE Schuchert, 1913

[*nom. transl.* ÖPIK, 1932, p. 69, *ex* Triplesiinae SCHUCHERT, 1929, p. 16, *nom. correct. pro* Tripleciinae SCHUCHERT, 1913a, p. 387] [=Placotriplesiinae AMSDEN, 1968, p. 39, *partim;* Oxopleciidae HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 60, *partim;* Onychotretidae HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 62, *partim*]

Smooth to strongly ornamented shells of transverse to elongate outline, with fold and sulcus normally producing prominent undulation in anterior commissure; long forked cardinal process with cowl commonly developed on posterior side of base, anterior side keeled or grooved; inner boundaries of sockets defined by posterolaterally directed brachiophores. *Lower Ordovician (Llanvirn)–upper Silurian (lower Ludlow).*

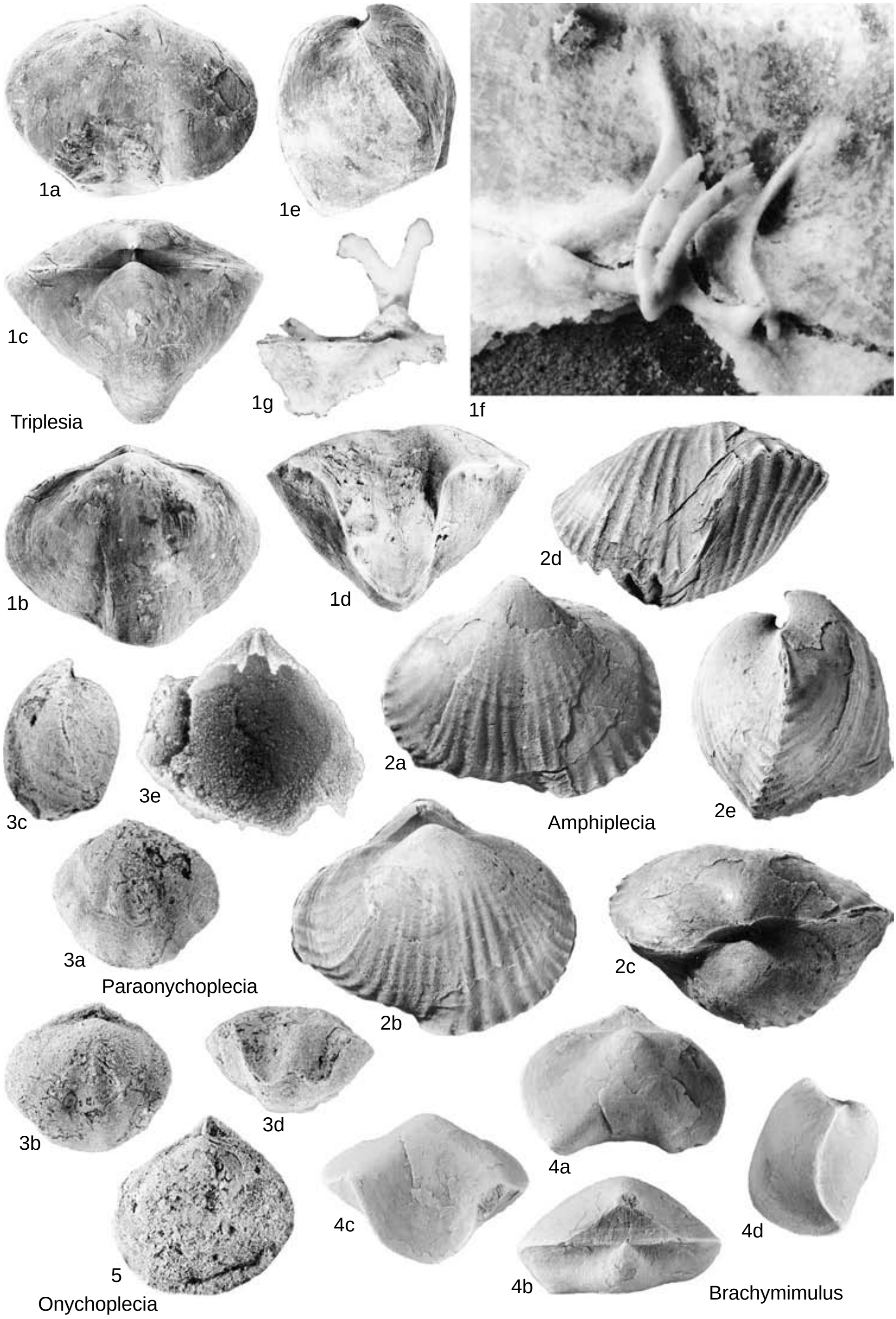

FIG. 494. Triplesiidae (p. 685–688).

Triplesia Hall, 1859b, p. 44 [**Atrypa extans* Emmons, 1842, p. 395; SD Hall & Clarke, 1892, p. 270] [=*Triplecia* Hall & Clarke, 1892, obj.; *Dicraniscus* Meek, 1872b, p. 279 (type, *D. ortoni*)]. Strongly trilobate with pronounced dorsal fold and ventral sulcus; surface smooth, with only faint growth lines; cardinal process keeled, cowl present. *Lower Ordovician (upper Llanvirn)–lower Silurian (upper Llandovery):* widespread in North America, Eurasia; Morocco.——Fig. 494,*1a–e*. **T. extans* (Emmons), Caradoc, Trenton, New York; ventral, dorsal, posterior, anterior, lateral views of complete shell, ×1.5 (Wright, 1965b).——Fig. 494,*1f,g*. *T.* sp., Ashgill, Norway; anterolateral, posterodorsal views of silicified hinge regions, ×8 (new).

Amphiplecia Wright & Jaanusson, 1993, p. 99 [**A. tardicostata;* OD]. Transverse shells twisted about midline, commissure sinusoidal; umbonally smooth, developing coarse ribs with fine growth lamellae; monticulus commonly developed; cardinal process grooved, lacking cowl. *Upper Ordovician (Caradoc–Ashgill):* Sweden, Norway, Siberia.——Fig. 494,*2a–e*. **A. tardicostata,* Ashgill, Sweden; holotype, ventral, dorsal, posterior, anterior, lateral views, ×2 (Wright & Jaanusson, 1993).

Bicuspina Havlíček, 1950, p. 18 [**Orthis cava* Barrande, 1848, p. 209; OD]. Transverse shells with wide hinge, multicostellate, uniplicate; monticulate with long pedicle tube; low keeled cardinal process commonly cowled, brachiophores ponderous. *Ordovician (Llandeilo–Caradoc):* Europe, Morocco, Kazakhstan, China, Argentina.——Fig. 495,*2a–c*. **B. cava* (Barrande), Caradoc, Harnagian, Bohemia; *a,* ventral valve internal mold; *b,c,* dorsal, posterior views of dorsal valve internal mold, ×1.5 (Turek & Horný, new).——Fig. 495,*2d. B. spiriferoides* (M'Coy), Caradoc, Soudleyan, Wales; ventral valve internal mold, ×1.3 (Wright, 1963a).

Brachymimulus Cockerell, 1929, p. 105, *nom. nov. pro Mimulus* Barrande, 1879, p. 109, *non* Stimpson, 1860 [**Mimulus perversus* Barrande, 1879, p. 109; OD]. Smooth with strong ventral fold and dorsal sulcus; hinge moderately wide, outline transverse; monticulus absent. *Silurian (Wenlock):* Bohemia.——Fig. 494,*4a–d*. **B. perversus* (Barrande); holotype, dorsal, posterior, anterior, lateral views, ×3 (Turek & Horný, new).

Caeroplecia Williams, 1974, p. 121 [**C. plicata;* OD]. Similar to *Oxoplecia* but with concentric ornament of fila, not lamellae, delayed rib development and short pedicle tube; cardinalia small, delicate, cardinal process keeled. *Ordovician (Caradoc):* England, Wales, Northern Ireland, USA (Tennessee, Virginia, Alabama).——Fig. 495,*3a–c*. **C. plicata,* Caradoc, Soudleyan, England; *a,* cast of ventral exterior, ×3; *b,* detail of ornament, ×15; *c,* cast of dorsal interior, ×3 (new).

Cliftonia Foerste, 1909a, p. 81 [**C. striata;* OD]. Strongly lamellose and costellate, subcircular, uniplicate shells; monticulate, but cowl lacking on keeled cardinal process; pedicle tube present. *Ordovician (upper Caradoc)–Silurian (Llandovery, ?Wenlock):* Morocco, France, *upper Caradoc;* widespread North America, Eurasia, Argentina, *Ashgill (Hirnantian);* North America, *Llandovery–?Wenlock.*——Fig. 495,*1a*. **C. striata,* Telychian, Tennessee; posteroventral view of asymmetrical ventral internal mold, ×2.5 (new).——Fig. 495,*1b. C. tubulistriata* (Savage), Ashgill, Missouri; dorsal valve exterior, ×2 (Ulrich & Cooper, 1936a).

Craigella Reed, 1935, p. 354 [**Triplesia grayiae* Davidson, 1869, p. 198; OD] [=*Epacroplecia* Williams, 1962, obj.; *Nucleorhynchia* Liang in Liu, Xu, & Liang, 1983, p. 272 (type, *N. hengtangensis*)]. Trigonal form with narrow hinge; dorsal valve highly convex, trilobate, ventral valve shallow with geniculate median tongue; ornament capillate or smooth; cardinal process low keeled, brachiophores bladelike, bases subparallel. *Upper Ordovician (Caradoc–Ashgill):* Scotland, Mongolia, eastern China.——Fig. 496,*1a–e*. **C. grayiae* (Davidson), upper Caradoc, Scotland; *a–c,* lectotype, dorsal, anterior, lateral views, ×2.5; *d,* dorsal valve exterior, ×2.5; *e,* interior of dorsal valve, ×2.5 (new).

Grammoplecia Wright & Jaanusson, 1993, p. 104 [**G. triplesioides;* OD]. Trilobate to transverse shells, strongly uniplicate to sulciplicate, with capillate radial ornament; monticulus present or absent; keeled cardinal process. *Lower Ordovician (Llandeilo)–Upper Ordovician (Ashgill):* Sweden, Urals, Siberia, Kazakhstan, China, ?Scotland, ?USA (Alabama).——Fig. 495,*4a–f*. **G. triplesioides,* Ashgill, Sweden; *a–e,* holotype, ventral, dorsal, posterior, anterior, lateral views, ×2; *f,* detail of shell surface, ×15 (Wright & Jaanusson, 1993).

Ogmoplecia Wright & Jaanusson, 1993, p. 94 [**Triplecia plicata* Wiman, 1907, p. 12; OD]. Coarsely ribbed uniplicate triplesiid with pseudodeltidium typically smooth, without monticulus; cardinal process grooved, lacking cowl. *Upper Ordovician (?Caradoc, Ashgill):* Baltic, British Isles, Belgium, Quebec, Siberia, ?British Columbia (Trenton), *?Caradoc.*——Fig. 496,*4a–e*. **O. plicata* (Wiman), Ashgill, Öland; *a–c,* lectotype, ventral, posterodorsal, anterior views, ×1.3; *d,* latex cast of cardinalia, ×4; *e,* interarea of fragmentary ventral valve, ×8 (Wright & Jaanusson, 1993).

Onychoplecia Cooper, 1956, p. 529 [**O. brevirostris;* OD]. Small shells with tear-shaped outline, elongate beak, and narrow hinge; profile narrowly lenticular, uniplicate, smooth or rarely with costellae; monticulate; cowl on keeled cardinal process. *Ordovician (lower Llanvirn, ?upper Ashgill):* eastern North America, *lower Llanvirn–lower Caradoc;* ?England, ?China, *?upper Ashgill.*——Fig. 494,*5*. **O. brevirostris,* Tennessee; dorsal view of complete shell, ×2.5 (Wright, 1965b).

Onychotreta Ulrich & Cooper, 1936a, p. 339 [**O. mesleri;* OD] [=*Eilotreta* Amsden, 1968, p. 36 (type, *Rhynchotreta lenta* Thomas, 1926); =*Lissotreta* Amsden, 1968, p. 37 (type, *Onychotreta plicata* Ulrich & Cooper, 1936a)]. Outline clawlike, with

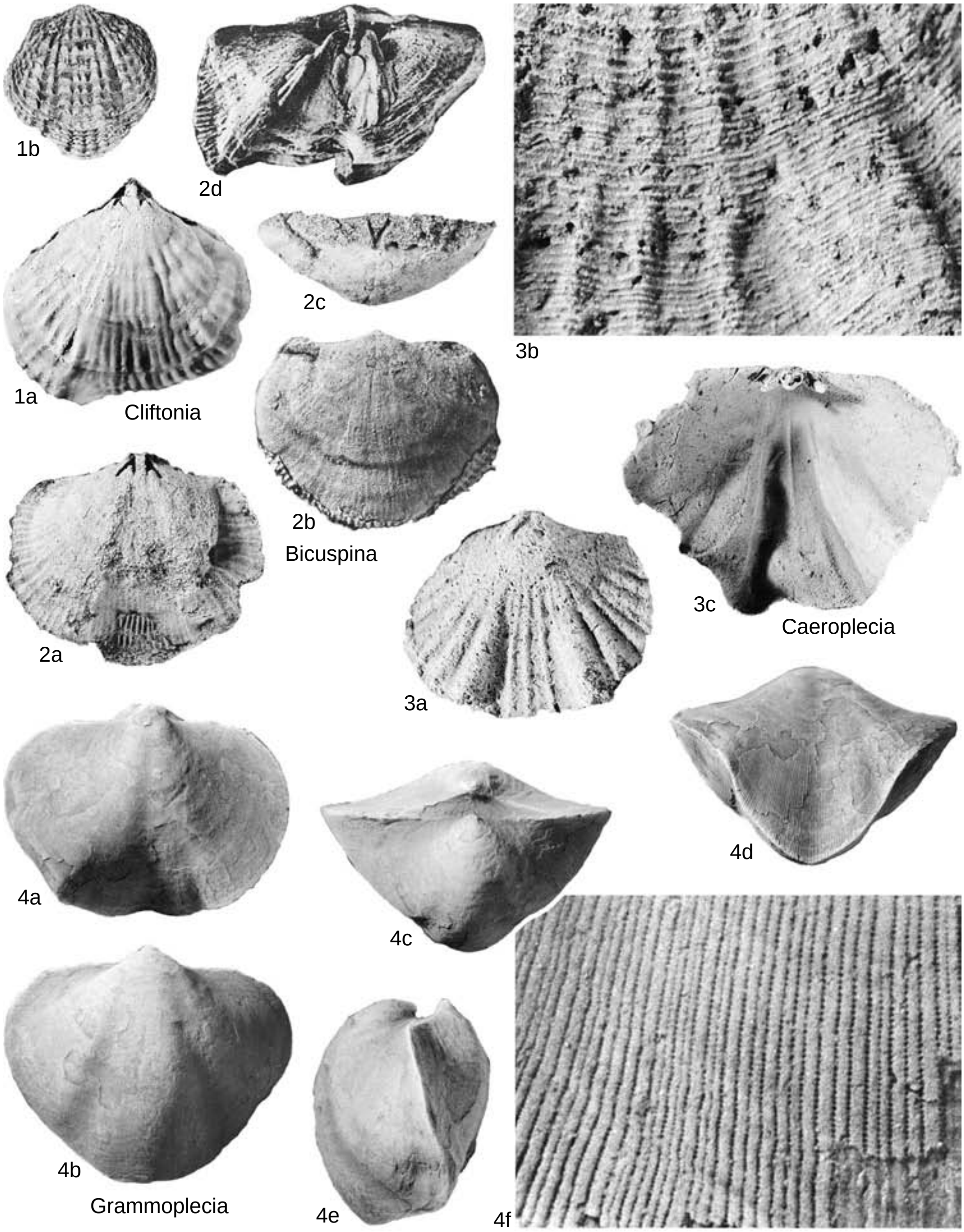

FIG. 495. Triplesiidae (p. 685).

ventral beak and monticulate pseudodeltidium extremely elongate; dorsal valve short; form and ornament variable, costellate to paucicostate or smooth, with asymmetry; fold and sulcus variably defined. *Silurian (Wenlock):* USA (Arkansas, Oklahoma), Bohemia.——FIG. 496,*2a–d.* **O. mesleri,* Wenlock, Arkansas; *a,b,* dorsal view of complete shell, ventral valve exterior, ×2; *c,d,* dorsal valve, exterior, posterior views, ×2 (Wright, 1965b).

Oxoplecia WILSON, 1913, p. 81 [**O. calhouni;* OD] [=*California* BASSLER, 1915, p. 1294]. Roundedly elliptical to transverse shells, costellate with distinc-

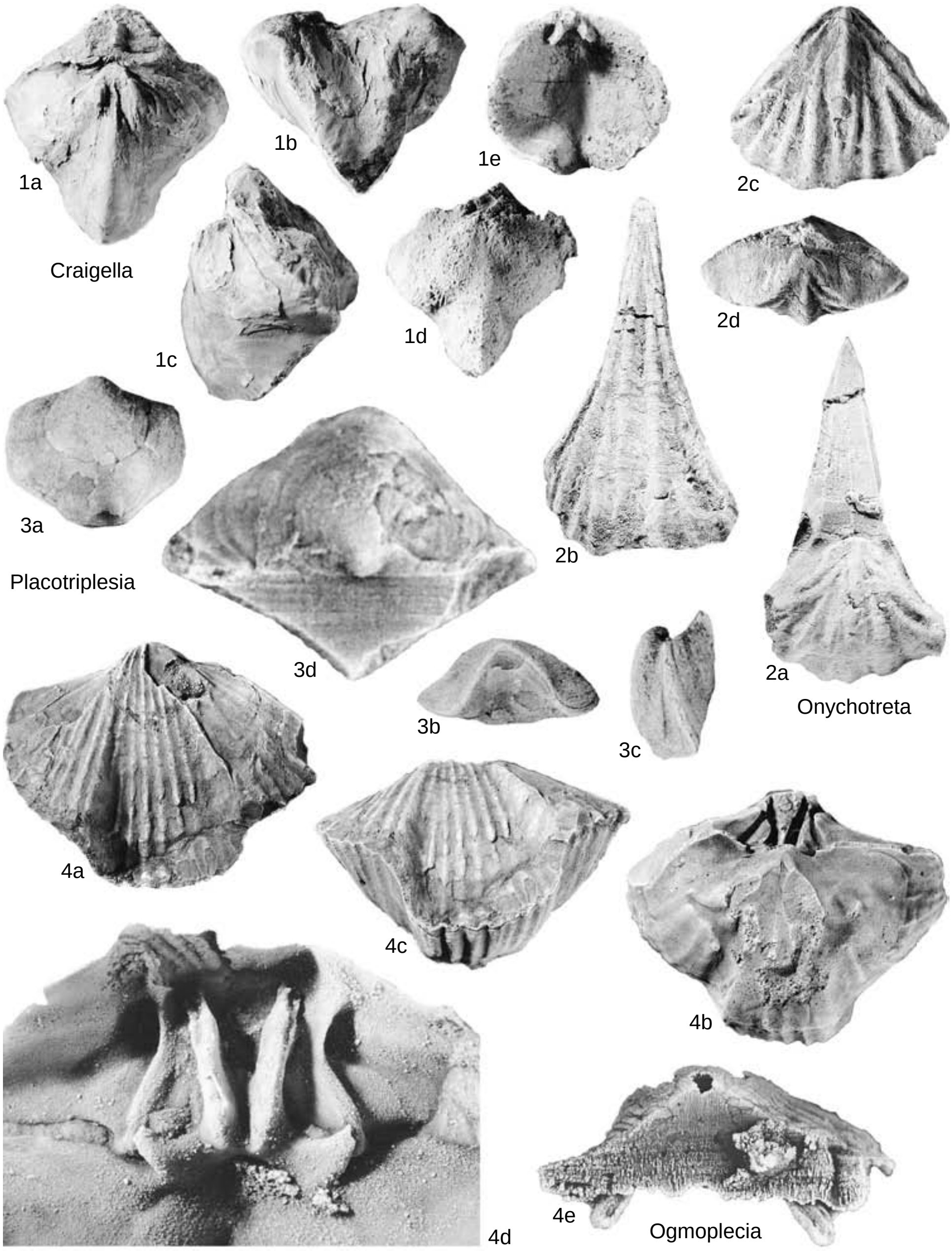

FIG. 496. Triplesiidae (p. 685–689).

tive fine, elevated, concentric growth lines; uniplicate. Monticulus may be lost anteriorly; pedicle tube not developed; cardinal process keeled, cowl lacking. *Ordovician (upper Llanvirn–Caradoc; ?Ashgill), Silurian (?Wenlock):* widespread North America, Eurasia.——FIG. 497,*4a,b.* **O. calhouni,* Caradoc, Ontario; holotype, dorsal, anterior views, ×1.5 (Wright, 1965b).——FIG. 497,*4c. O. gouldi* ULRICH & COOPER, Caradoc, Oklahoma; detail of ornament on dorsal valve, ×15 (new).

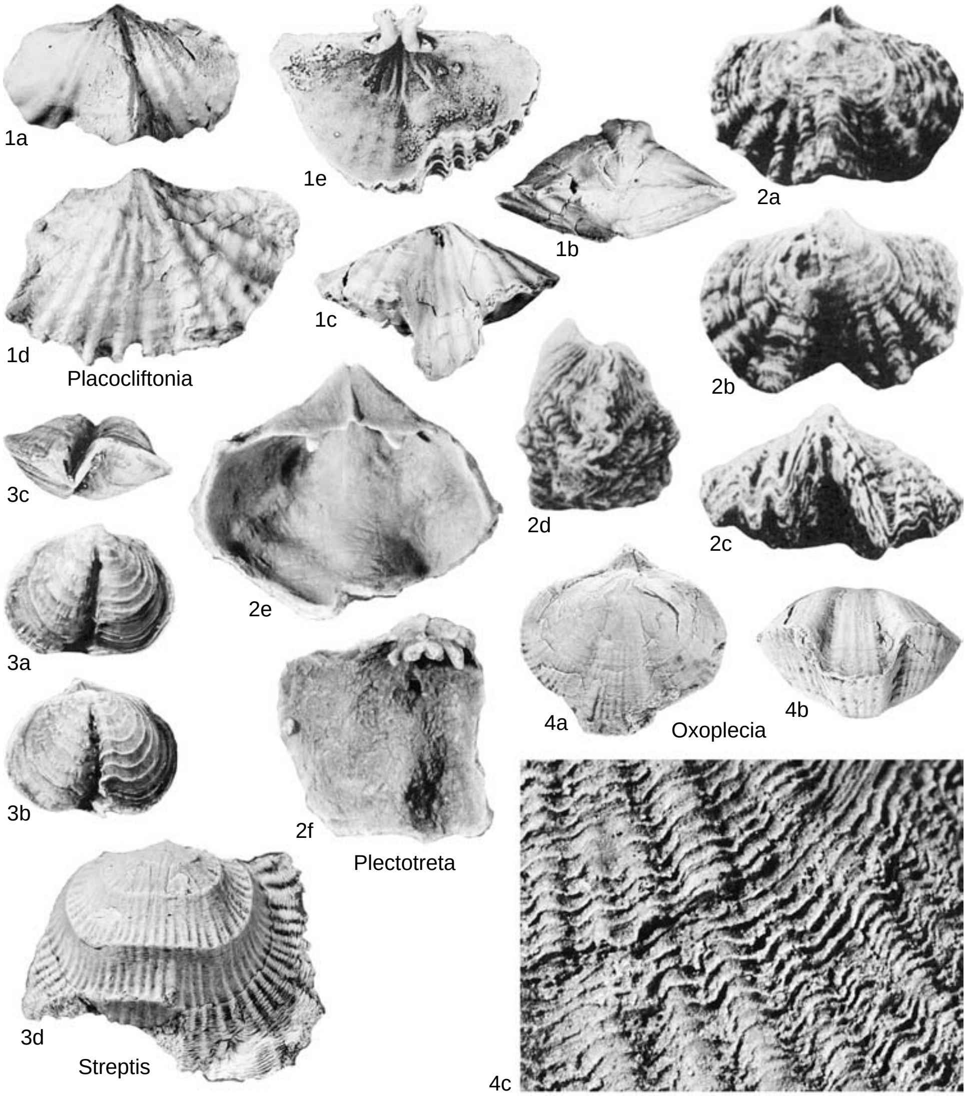

FIG. 497. Triplesiidae (p. 686–689).

Paraonychoplecia PERCIVAL, 1991, p. 133 [**P. inversa;* OD]. Smooth triplesiid with ventral fold and dorsal sulcus; hinge narrow, outline roundedly subtriangular to elongate, developing long, pointed ventral beak; monticulus present; cardinal process keeled. *Upper Ordovician (Caradoc)–Silurian (Wenlock):* Australia, Quebec, British Isles, USA (Arkansas, Oklahoma).——FIG. 494,*3a–e.***P. inversa,* Caradoc, New South Wales; *a–d,* ventral, dorsal, lateral, anterior views of complete shell, ×3; *e,* ventral valve interior and hinge region, ×12 (Percival, 1991).

Placocliftonia HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 60 [**Spirifer colibri* BARRANDE, 1848, p. 173; OD]. Transverse, variably asymmetrical shells, commissure uniplicate or sinusoidal; ribbing accentuated by strong concentric lamellae. Short pedicle tube, but monticulus obsolete; cardinal process grooved, lacking cowl. *Silurian (Wenlock):* Bohemia, USA (Wisconsin), Arctic Canada.——FIG. 497,*1a–d.* **P. colibri* (BARRANDE), Wenlock, Bohemia; *a–c,* holotype, dorsal, posterior, anterior views, ×2.1; *d,* ventral valve exterior, ×3.3 (Havlíček & Štorch, 1990).——FIG. 497,*1e. P. contorta* (ZHANG), Wenlock, Arctic Canada; dorsal valve interior, ×3.3 (Zhang, 1989b).

Placotriplesia Amsden, 1968, p. 40 [**Triplesia praecipta* Ulrich & Cooper, 1936a, p. 346; OD]. Smooth uniplicate shells resembling *Triplesia* but lacking monticulus and cowl on grooved cardinal process. *Silurian (Wenlock):* USA (Arkansas, Oklahoma, Tennessee), Bohemia, England, Estonia.——Fig. 496,*3a–d.* **P. praecipta* (Ulrich & Cooper), Wenlock, Arkansas, Oklahoma; *a–c,* ventral, anterior, lateral views of complete shell, ×4 (Amsden, 1968); *d,* posterior view of shell showing ventral interarea, ×7 (Amsden, 1973).

Plectotreta Ulrich & Cooper, 1936a, p. 339 [**P. lindstroemi;* OD]. Outline subcircular, becoming transversely elliptical, lamellose with strong radial plications; monticulate; cardinal process grooved with small cowl. *Silurian (lower Wenlock–lower Ludlow):* northwestern Europe (Gotland, England).——Fig. 497,*2a–f.* **P. lindstroemi,* Wenlock; *a–d,* dorsal, ventral, anterior, lateral views of complete shell, England, ×3.5 (Bassett, 1972); *e,* ventral valve, Gotland, ×4; *f,* damaged dorsal valve, Gotland, ×5 (Wright, 1993b).

Streptis Davidson, 1881, p. 150 [**Terebratula grayii* Davidson, 1848, p. 331; OD]. Small, commonly twisted shells, commissure uniplicate or sinusoidal; strong concentric lamellae, developing into frills; radial ribbing variable; monticulus present; cardinal process with cowl, keeled, becoming grooved by Wenlock. *Upper Ordovician (Cautleyan)–Silurian (Homerian):* Europe, Kazakhstan, North America, Greenland.——Fig. 497,*3a–c.* **S. grayii* (Davidson), Wenlock, England; *a–c,* ventral, dorsal, anterior views of complete shell, ×3 (Wright, 1965b).——Fig. 497,*3d. S. undifera* (Schmidt), Ashgill, Estonia; dorsal valve with incomplete fourth frill, ×3.3 (Hints, 1986).

BILLINGSELLIDA

Alwyn Williams and David A. T. Harper
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Order BILLINGSELLIDA Schuchert, 1893

[*nom. transl.* Williams & Harper, herein, *ex* Billingsellidae Schuchert, 1893, p. 152]

Concavoconvex to biconvex strophomenates with a long ventral interarea and a convex pseudodeltidium complementary to a chilidium, foramen apical; teeth transverse to deltidiodont, supported by variably disposed dental plates; muscle scars normally well defined but without evidence of adjustor bases; inner socket ridges more or less parallel with the hinge line; notothyrial platform well developed, normally with a ridgelike cardinal process; mantle canal systems saccate to pinnate; secondary layer of shell laminar or fibrous, impunctate, rarely pseudopunctate. *Middle Cambrian–Upper Ordovician (upper Ashgill).*

The grouping of the billingselloids and clitambonitidines into a new order is prompted by the phylogenetic analyses of Williams and others (1996) but is provisional on further studies of shell structure and the closure of the delthyrium. The secondary shell of clitambonitidines and billingselloids are respectively fibrous and laminar, which difference is also characteristic of the plectambonitoids and strophomenoids. The laths of billingselloid laminae, however, are not cross bladed but subparallel (Williams, 1970, p. 312) and may have evolved from flattened fibers. As for the delthyrial covers, Wright and Rubel (1996) have concluded that those of clitambonitidines are essentially deltidia rather than pseudodeltidia. The cover of the billingselloid delthyrium has always been described as a pseudodeltidium, although this has never been confirmed by an explicit study of young shells.

Notwithstanding these contradictions, the presence of mantle canal imprints along the ventral interareas of clitambonitidines (Wright, 1994b) suggests that this group, at least, had a posterior body wall as postulated for strophomenates as a whole, while the muscle systems of both the billingselloids and clitambonitidines appear not to have included pedicle adjustors.

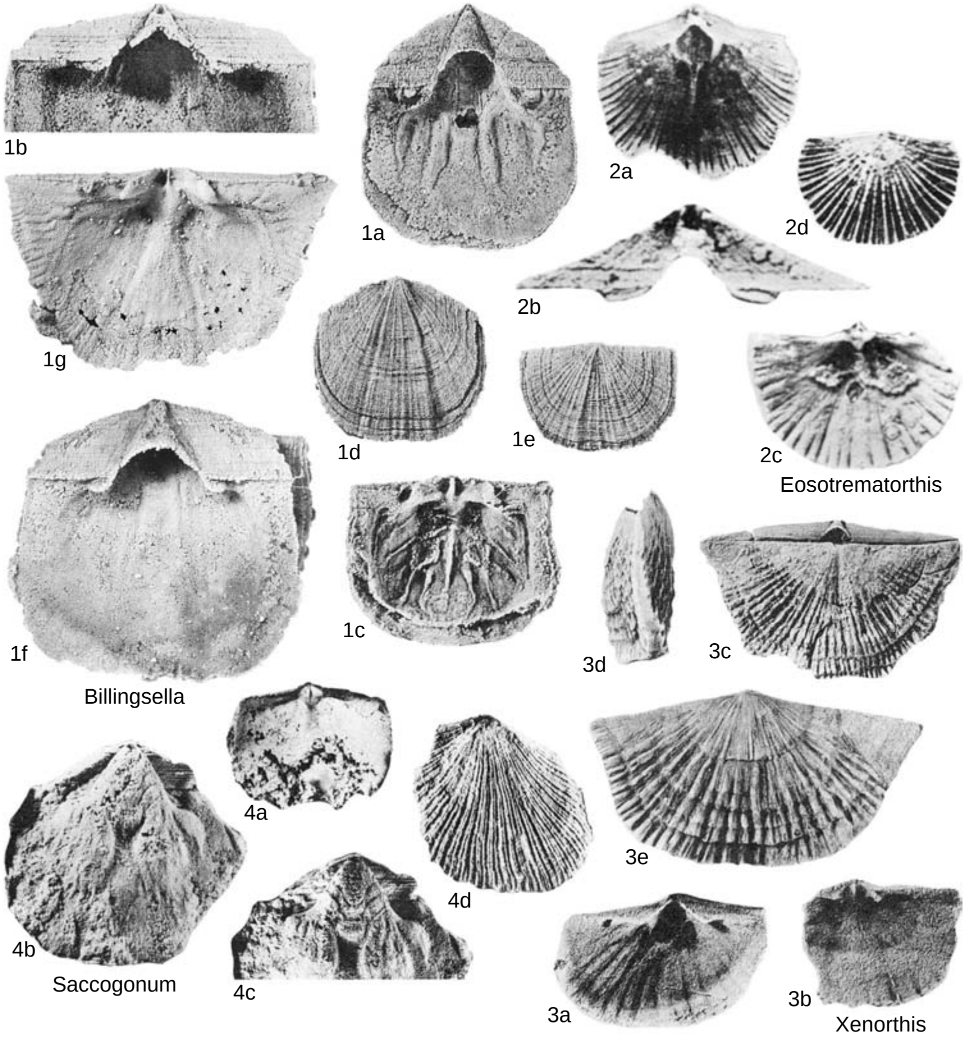

FIG. 498. Billingsellidae (p. 692).

Suborder BILLINGSELLIDINA Schuchert, 1893

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Billingsellidae SCHUCHERT, 1893, p. 152]

Variable size, normally subquadrate, biconvex, unisulcate, costellate strophomenates with strong pseudodeltidium normally complemented by chilidium, foramen apical or vestigial; ventral interarea flat, very much longer than anacline dorsal interarea; teeth commonly large, transverse, occasionally with shallow crural fossettes, variably supported by dental plates; ventral muscle scar variable in shape and size, sockets defined by widely splayed rods or plates more or less parallel with hinge line; notothyrial platform well developed, prolonged anteriorly as median ridge and supporting simple cardinal process; dorsal adductor field subequally quadripartite; ventral and dorsal mantle canal systems basically saccate and digitate respectively; secondary layer of shell laminar, impunctate. *Middle Cambrian–Lower Ordovician (Arenig).*

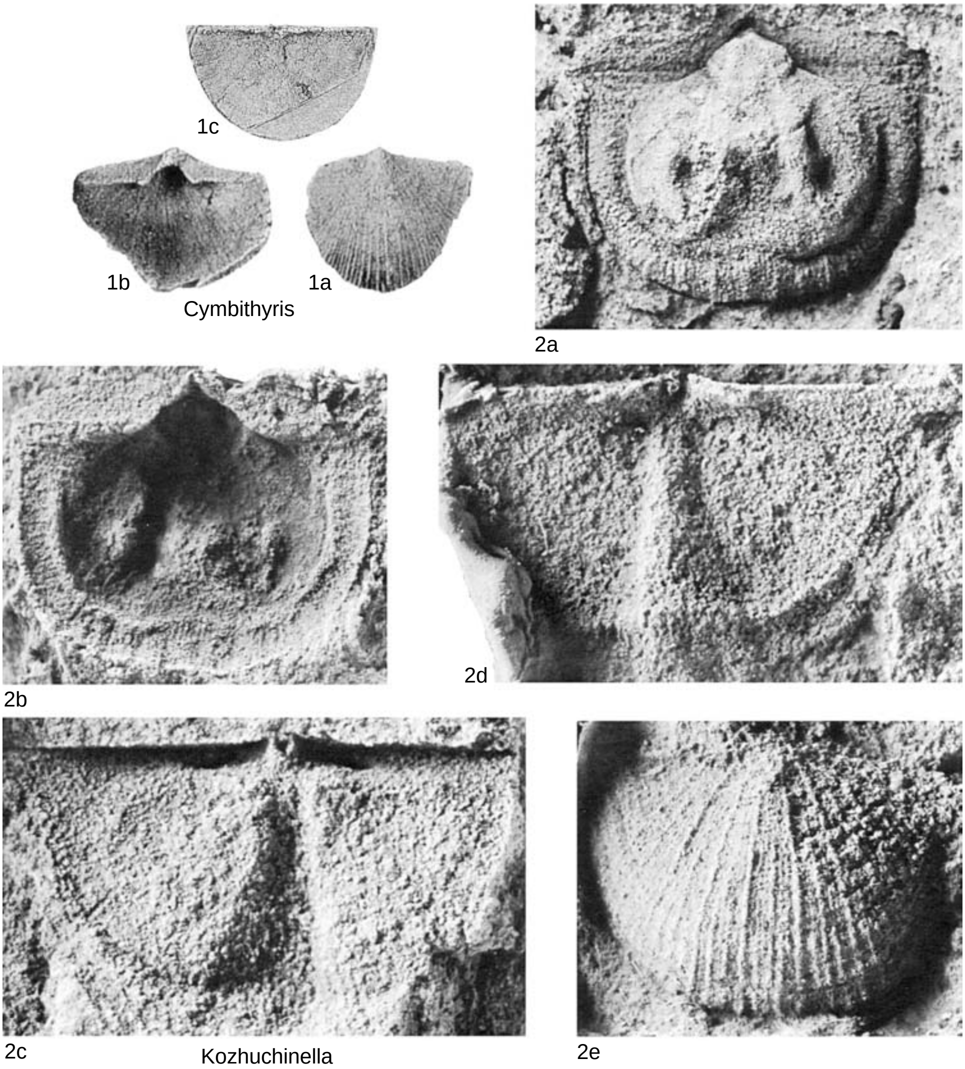

FIG. 499. Billingsellidae (p. 692).

The billingselloids have many features in common with the early Orthida and until recently have been assigned to that order. Yet the presence of a pseudodeltidium and chilidium, the development of transverse teeth and flat-lying socket plates, and especially the discovery that the secondary shell layer of *Billingsella* is composed of cross-bladed laminae in the manner of most strophomenates (WILLIAMS, 1970) recently prompted a reassignment of the superfamily to the Strophomenida (WILLIAMS & others, 1996) and now to the order Billingsellida (WILLIAMS & HARPER, herein).

Superfamily BILLINGSELLOIDEA Schuchert, 1893

[*nom. transl.* WILLIAMS, 1965a, p. 305, *ex* Billingsellidae SCHUCHERT, 1893, p. 152]

Characters as for suborder. *Middle Cambrian–Lower Ordovician (Arenig).*

Family BILLINGSELLIDAE Schuchert, 1893

[Billingsellidae Schuchert, 1893, p. 152]

Characters as for superfamily. *Middle Cambrian–Lower Ordovician (Arenig).*

Billingsella Hall & Clarke, 1892, p. 230 [**Orthis pepina* Hall, 1863c, p. 134; OD]. Ventribiconvex to planoconvex, multicostellate with variably developed cardinal extremities, apical pedicle foramen, convex chilidium, and orthocline to apsacline ventral interarea; dental plates divergent, ventral muscle field with long, divergent diductor scars usually deeply impressed on tonguelike callus extending anteriorly; subperipheral rim occasionally developed. *Middle Cambrian–Lower Ordovician (Tremadoc):* cosmopolitan.——Fig. 498,*1a–f. B. perfecta* Ulrich & Cooper, Upper Cambrian; *a,* ventral interior, Idaho-Wyoming border, ×3; *b,* details of ventral interarea, Idaho-Wyoming border, ×4; *c,* dorsal interior, Idaho-Wyoming border, ×3; *d,e,* ventral exterior, dorsal exterior, Idaho-Wyoming border, ×2 (Ulrich & Cooper, 1938); *f,* ventral interior, Wyoming, ×2.5 (Cocks, new).——Fig. 498,*1g. B. corrugata* Ulrich & Cooper, Upper Cambrian, Oklahoma; dorsal interior, ×2.5 (Cocks, new).

Cymbithyris Cooper, 1952b, p. 5 [**C. hami;* OD]. Similar to *Billingsella* but concavoconvex with mucronate hinge line and lacking dental plates. *Lower Ordovician (Tremadoc):* central USA.——Fig. 499,*1a–c.* **C. hami,* Tremadoc, Oklahoma; ventral exterior, ventral interior, dorsal interior, ×2 (Cooper, 1952b).

Eosotrematorthis Wang, 1955a, p. 93 [**E. sinensis;* OD]. Similar to *Billingsella* but ramicostellate with apsacline ventral interarea, recessive dental plates, rodlike socket ridges, small, subcordate ventral muscle field with lanceolate adductor track not enclosed by larger subtriangular diductor scars, and low median ridge in ventral valve. *Lower Ordovician (Arenig):* southern China.——Fig. 498,*2a–d.* **E. sinensis,* Arenig, southern China; *a,* ventral interior, ×2; *b,* posterior view of ventral valve showing details of interarea, ×4; *c,* dorsal interior, ×3; *d,* dorsal exterior, ×2 (Wang, 1955a).

Kozhuchinella Severinga, 1967, p. 132 [**K. mariinica;* OD]. Similar to *Billingsella* but more concavoconvex and unequally parvicostellate; ventral muscle field suboval with broad undifferentiated adductor scar; cardinal process relatively strong; subperipheral rims well developed. *Lower Ordovician (Tremadoc):* Siberia (Kusnetz-Altai).——Fig. 499,*2a–e.* **K. mariinica,* Tremadoc, Siberia; *a,b,* internal mold, rubber replica of ventral valve, ×9; *c,d,* internal mold, rubber replica of dorsal valve, ×10; *e,* rubber replica of ventral exterior, ×7 (Cocks & Rong, 1989).

Saccogonum Havlíček, 1971a, p. 27 [**S. saccatum;* OD]. Similar to *Billingsella* but strongly dorsibiconvex with obtuse cardinal extremities, vestigial pedicle foramen and apsacline ventral interarea; lacking chilidium and dental plates; undifferentiated ventral muscle scar suboval with short posteromedian ridge; ventral gonocoels distended to occupy *vascula media* and *vascula myaria. Upper Cambrian:* Morocco.——Fig. 498,*4a–d.* **S. saccatum,* Upper Cambrian, Morocco; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×2; *c,* posterior part of internal mold of ventral valve, ×2; *d,* rubber replica of ventral exterior, ×2 (Havlíček, 1971a).

Xenorthis Ulrich & Cooper, 1936b, p. 620 [**Strophomena stosei* Bassler, 1919, p. 250; OD]. Transversely semioval with acute cardinal extremities, subequally biconvex, uniplicate, ramicostellate; foramen vestigial, ventral interarea apsacline; dental plates vestigial, ventral muscle scar subcordate with wide adductor track gently elevated anteriorly; cardinal process simple, ridgelike; dorsal mantle canal digitate. *Upper Cambrian–Lower Ordovician (Tremadoc):* eastern USA.——Fig. 498,*3a–e.* **X. stosei* (Bassler), Upper Cambrian, Maryland; *a,* ventral interior, ×3; *b,* dorsal interior, ×4; *c,d,* dorsal, lateral views of conjoined valves, ×2; *e,* ventral exterior, ×2 (Ulrich & Cooper, 1938).

CLITAMBONITIDINA

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Suborder CLITAMBONITIDINA Öpik, 1934

[*nom. correct.* Williams, 1965c, p. 346, *pro* suborder Clitambonoidea Öpik, 1934, p. 75]

Concavoconvex to convexoconcave strophic, deltidiodont shells with overwhelmingly costellate ribbing and smooth or filose to imbricate concentric ornament; ventral valve commonly with long procline to apsacline ventral interarea and arched deltidium enclosing apical pedicle foramen; teeth simple, rarely supplemented by denticles; dental plates commonly uniting to form spondylium simplex or triplex, less commonly extending directly to valve floor, may have pseudospondylium; cardinal process normally simple ridge fused with strong chilidium, set on strong transverse notothyrial platform bearing widely divergent socket ridges; dorsal adductor field quadripartite to subflabellate; mantle canal system pinnate, more rarely saccate; secondary shell fibrous, impunctate or pseudopunctate. *Lower Ordovician (Tremadoc)–Upper Ordovician (upper Ashgill).*

The clitambonitidines form a distinctive group of brachiopods that are not known from rocks other than of Ordovician age and, although they attained widespread distribution in the shallow seas of the time, are particularly associated with the Baltic faunas of Estonia and western Russia (Ingria). Like other groups developing in the Early Ordovician, there is considerable intraspecific variation of characters, which later become stable elements both in clitambonitidine genera and in other articulated brachiopods. This variability means that definitive ancestral stocks are still being sought. The PAUP analyses of WILLIAMS and others (1996) suggest an origin from somewhere within the billingselloid plexus, but the clitambonitidine position in the strophomenates is uncertain, and a possible origin from Late Cambrian fibrous orthide stocks with open delthyria and dental plates (WRIGHT, 1996) cannot be ruled out. The oldest known clitambonitidine is the Tremadoc *Protambonites* from Bohemia, while the long-ranging and widespread *Vellamo* is one that persists into the latest Hirnantian age of the Ashgill.

Vellamo (Fig. 500) may be regarded as having a fully developed clitambonitidine morphology with its wide hinge, ventribiconvex profile and costellate exterior; a ventral valve with a long interarea, convex deltidium perforated by a large foramen and strong spondylium; and a dorsal valve with a well-developed chilidium, simple, ridgelike cardinal process, and laterally directed socket ridges. Its fibrous shell substance is standard, but the impunctate nature is not, with that of the gonambonitids being strongly pseudopunctate. Shell such as this is commonly associated with the plectambonitoids, with many features of shell morphology also reflecting divergences away from the standard assemblage of characters toward those more closely associated with other brachiopod groupings.

Such divergencies in the external form include a resupinate profile (*Antigonambonites*), a radial ornament that may be fine enough (*Raunites*) to mimic a strophomenoid, a concentric ornament of regular or irregular fila, and/or lamellae or imbrications (*Clitambonites*). With strong ribbing, a reticulate pattern may develop (*Lacunarites*), with the possibility of spines (*Gonambonites*) and tubulose ribs (*Estlandia*). Aditicules are the most common form of perforation of the ribs and may pass through to the interior behind the margin (*Kullervo*); arrugiae (WRIGHT, 1981) developing into spines are known from *Acanthotoechia.* Both interareas are always developed although the length varies; the delthyrium may uncommonly be open (*Oslogonites*) or with small deltidial plates (*Apomatella*); the large foramen of the deltidium may develop a distorted, collarlike extension (*Kullervo*), or become sealed as in many stocks (*Clitambonites, Clinambon, Estlandia*); no pseudodeltidium has yet been confirmed. There is evidence that the shell of high, semicircular chilidia as in *Clitambonites* is laid down beneath the deltidium internally (WRIGHT & RUBEL, 1996). The notothyrium may alternatively have a smaller triangular chilidium (*Estlandia*), a pair of chilidial plates (*Tritoechia*), or remain open (*Oslogonites*).

Internally, the dominating feature of the ventral valve is the spondylium (Fig. 501), which in *Vellamo* is a spondylium simplex but in the gonambonitids is a spondylium triplex that may be free standing (*Estlandia*) or sessile in those forms with closely opposed valves (*Antigonambonites*). The three plates supporting the free-standing spondylium triplex commonly reach the valve floor only close to the umbo; anteriorly they lose contact and are seen simply as longitudinal ridges along the undersurface of the spondylium. The spondylium triplex is mimicked in *Polytoechia* in which the dental plates pass directly to the valve floor rather than uniting above it (WILLIAMS, 1965c). Pseudospondylia are typical of the Polytoechioidea, although

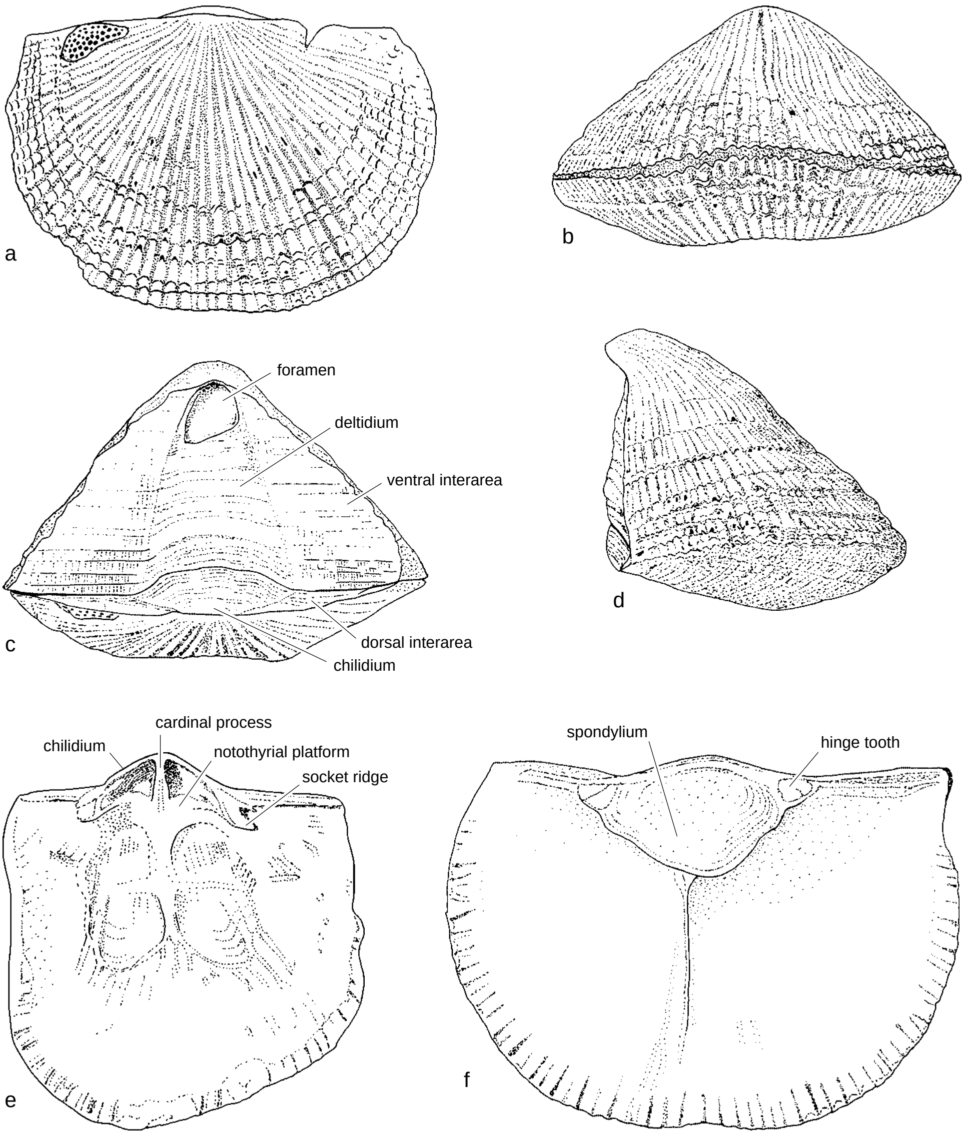

FIG. 500. Basic clitambonitidine morphology, based on specimens of *Vellamo oandoensis* ÖPIK; *a–d,* dorsal, anterior, posterior, lateral views of conjoined valves; *e,* dorsal valve interior with quadripartite adductor scars and some vascular markings preserved; *f,* ventral valve interior (adapted from Wright & Rubel, 1996).

any such structure may be lacking altogether (*Protambonites, Platytoechia*). Two important modifications are seen on the surface of the spondylium. That of *Clinambon* has a pair of sharply crested ridges defining the adductor scars laterally, while in *Kullervo* a pair of medianly directed plates almost isolate a lower central chamber (hemisyrinx).

In the dorsal valve, the notothyrial platform may possess ancillary ridges additional to the commonly strong cardinal process, but their variability from strong development to complete absence within species casts considerable doubt on their continued use as generic characters. Variation in the adductor muscle scar pattern is from subquadrate

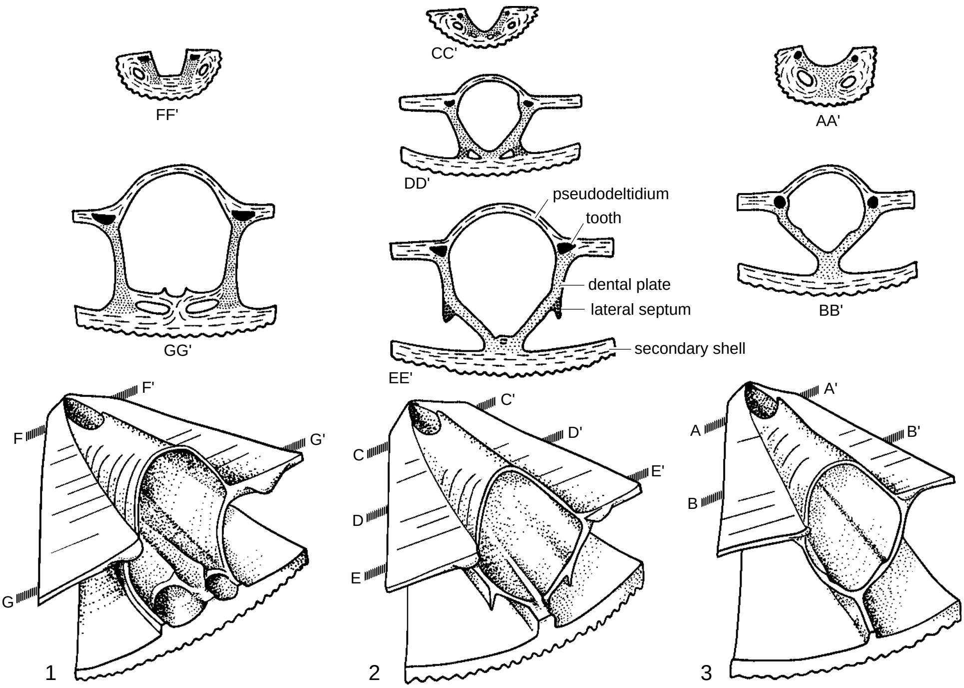

FIG. 501. Parts of three different clitambonitidine ventral valves illustrating spondylia, with sections showing attitudes of dental plates; *1,* polytoechiid; *2,* gonambonitid; *3,* clitambonitid (adapted from Williams & Wright, 1965).

(*Clitambonites*) to radial (*Polytoechia*) or even subpetalloid (*Kullervo*). Relative length of the anterior and posterior pairs may be consistent within a genus or may not (*Vellamo*). Subperipheral rims occur widely in either valve.

The mantle canals of both valves were considered to have a pinnate pattern (WILLIAMS, 1965c) but in *Atelelasma, Apomatella, Neumania,* and *Hemipronites,* at least the ventral valves differ in displaying a saccate pattern (WRIGHT & RUBEL, 1996). This suggests retention of the ancestral condition in these stocks. Mantle canals are also now known to occur on the ventral interareas (WRIGHT, 1994b).

WILLIAMS (1965c) divided the suborder into two superfamilies, based primarily on the impunctate nature of the shell in the clitambonitaceans and the pseudopunctate shell of the gonambonitaceans. Resulting from a cladistic analysis of 38 morphological characters, along with stratigraphic appearance, in a PAUP program, the 32 accepted genera are herein recast into the superfamilial groupings of polytoechioids and clitambonitoids. The latter is spondylial bearing and contains the pseudopunctate gonambonitids in addition to the sister family of impunctate clitambonitids.

Superfamily CLITAMBONITOIDEA Winchell & Schuchert, 1893

[*nom. transl.* RUBEL & WRIGHT, herein, *ex* Clitambonitacea COOPER, 1956, p. 511, *nom. correct. pro* superfamily Clitambonacea SCHUCHERT, 1929, p. 15, *nom. transl. ex* Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377; *emend.,* RUBEL & WRIGHT, herein]

Dental plates form spondylium; shell substance impunctate or pseudopunctate. *Ordovician (lower Arenig–upper Ashgill).*

Family CLITAMBONITIDAE Winchell & Schuchert, 1893

[Clitambonitidae WINCHELL & SCHUCHERT, 1893, p. 377]

Well-developed deltidium or rarely deltidial plates; dental plates united to form spondylium simplex; dorsal adductor scars

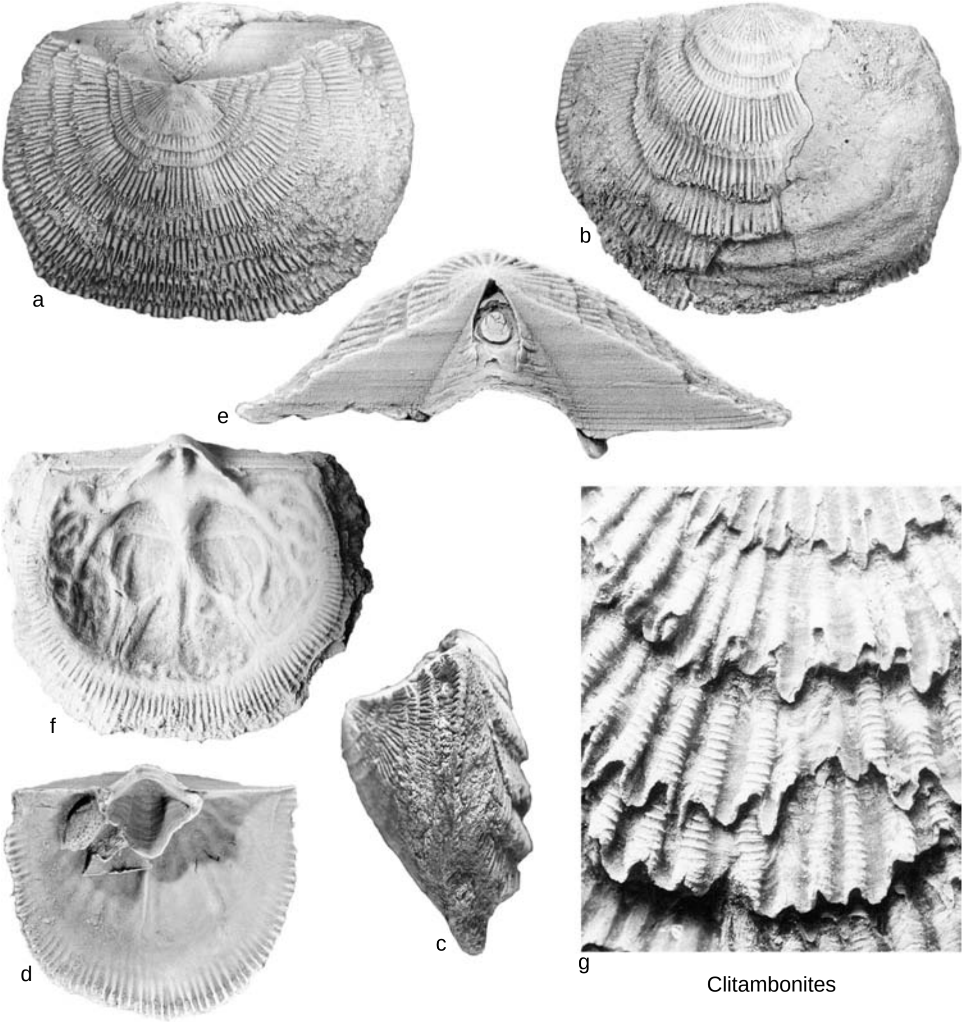

FIG. 502. Clitambonitidae (p. 696).

quadrate; aditicules common. *Ordovician (Arenig–upper Ashgill).*

Clitambonites PANDER, 1830, p. 70, *nom. correct.* AGASSIZ, 1846, p. 90 [**Pronites adscendens* PANDER, 1830, p. 71; SD HALL & CLARKE, 1892, p. 234] [=*Klitambonites* PANDER, 1830, p. 70, *nom. neg.; Pronites* PANDER, 1830, p. 71, obj.; *Prionites* FISCHER DE WALDHEIM, 1834, p. 288, invalid intentional spelling of previously published name; *Orthisina* D'ORBIGNY, 1847, p. 267, obj.]. Planoconvex to ventribiconvex shells with apsacline to procline ventral interareas, coarse costellae, and strong, concentric imbrications. *Ordovician (Arenig–lower Caradoc):* Estonia, Russia, Norway, Sweden, China.——FIG. 502*a–c.* **C. adscendens* (PANDER), Llanvirn, Ingria; ventral, dorsal, lateral views of conjoined valves, ×2 (Williams, 1965c).——FIG. 502*d,e. C. squamatus* (PAHLEN), Llandeilo, Estonia; *d,* ventral valve interior, ×2; *e,* interarea, ×4 (Wright & Rubel, 1996).——FIG. 502*f,g. C. schmidti* (PAHLEN) *epigonus* ÖPIK, lower Caradoc, Estonia; *f,* dorsal valve interior, ×1.5; *g,* ornament, ×6 (Öpik, 1934).

Apomatella SCHUCHERT & COOPER, 1931, p. 245 [**Orthisina ingrica* PAHLEN, 1877, p. 48; OD]. Transverse, subconical ventral valve with procline interarea and small deltidial plates; aditicules lacking; spondylium shorter than in *Neumania. Lower Ordovician (upper Arenig, ?lower Llanvirn):* Norway, Estonia, western Russia (Ingria).——FIG. 503,*1a–e.* **A. ingrica* (PAHLEN), Arenig, Ingria; *a–c,* exterior, interior, lateral views of ventral valve, ×4 (Wright,

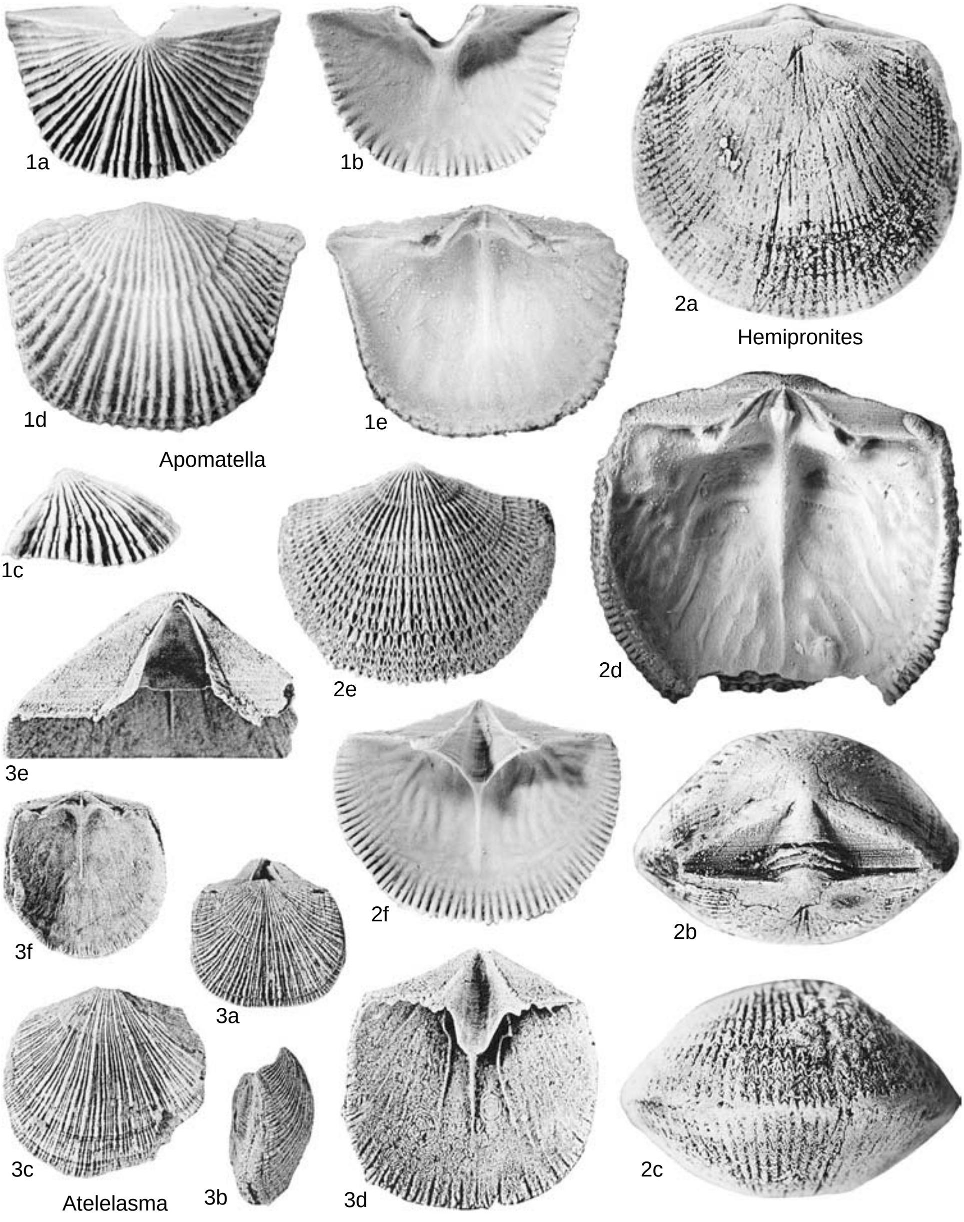

FIG. 503. Clitambonitidae (p. 696–701).

1994b); *d,e,* exterior, interior views of dorsal valve, ×4 (Rubel & Popov, 1994).

Atelelasma COOPER, 1956, p. 517 [**A. perfectum;* OD]. Planoconvex to ventribiconvex subquadrate to subcircular shells; ventral interarea apsacline to procline, laterally disposed deltidial plates only; costellae with aditicules. *Ordovician (Llandeilo–lower Caradoc):* USA (Virginia, Tennessee, Oklahoma, Alabama, Wisconsin, ?New York, ?Vermont), Wales, Siberia, Mongolia.——FIG. 503,*3a–f.* **A. perfectum,* Llandeilo, Tennessee; *a,b,* dorsal, lateral views of conjoined valves, ×1; *c,* ventral valve exterior, ×1; *d,e,* ventral valve interior, ventral interarea, ×2; *f,* dorsal valve interior, ×1 (Cooper, 1956).

Clinambon SCHUCHERT & COOPER, 1932, p. 115 [**Anomites anomala* SCHLOTHEIM, 1822, p. 65; OD]. Hemipyramidal ventral valve with strongly procline ventral interarea, dorsal valve with long interarea

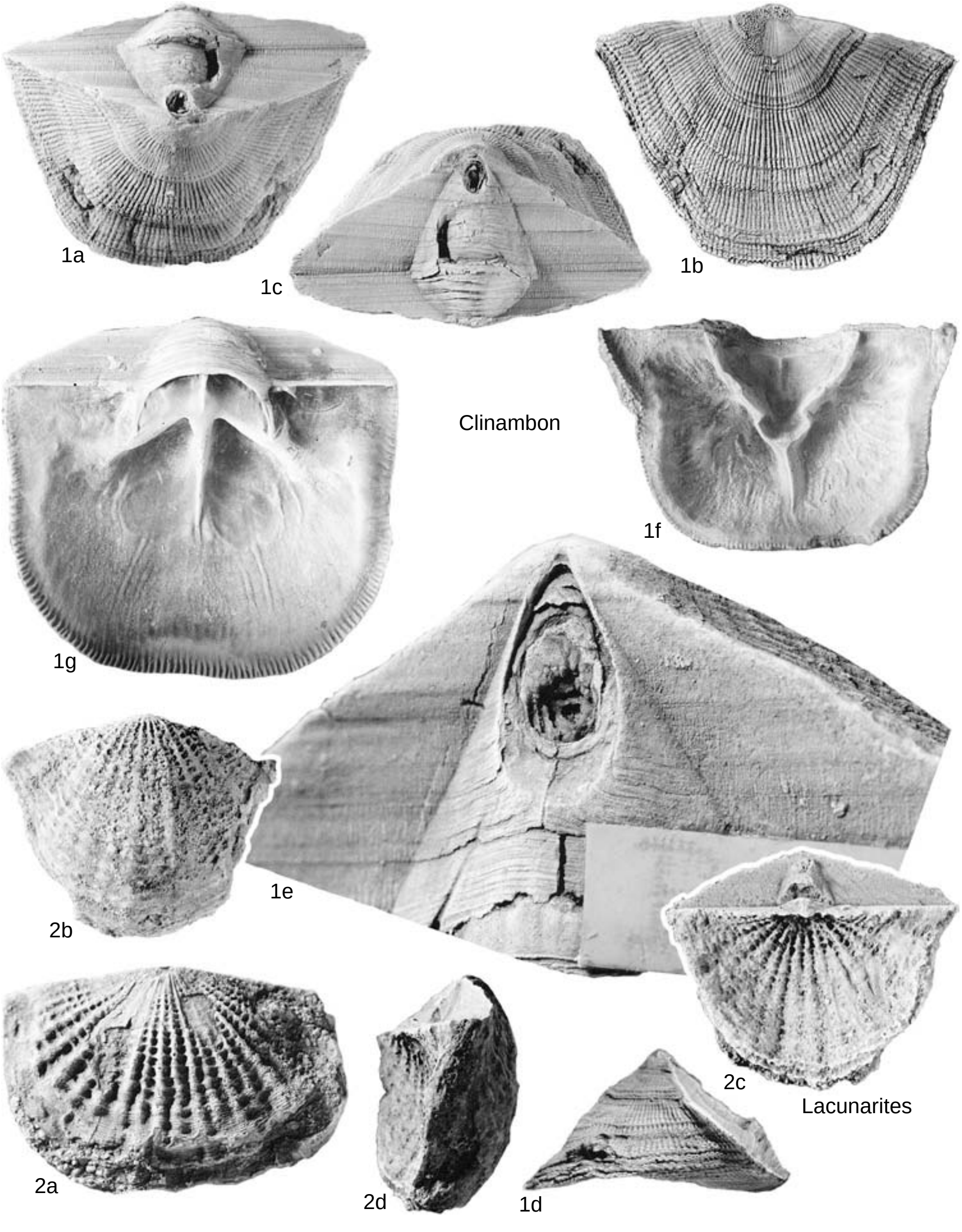

FIG. 504. Clitambonitidae (p. 697–702).

and very strong chilidium; finely costellate, without strong imbrication; ventral adductors on markedly constricted anteromedian portion of spondylium. *Ordovician (Caradoc):* Estonia, western Russia (Ingria).——FIG. 504,*1a–f.* **C. anomalus anomalus* (SCHLOTHEIM), Caradoc, Estonia; *a–d,* ventral, dorsal, posterior, lateral views of conjoined valves, ×1.3; *e,* detail of deltidium with sealed foramen, ×6 (new); *f,* ventral valve interior, ×1 (Öpik, 1934). ——FIG. 504,*1g.* **C. anomalus postumus* ÖPIK, Caradoc, Estonia; dorsal valve interior, ×1.5 (Öpik, 1934).

Fistulogonites NEUMAN, 1971, p. 116 [**F. novaterrensis;* OD]. Ventribiconvex, with pitted, even costellae; notothyrium open; sessile spondylium without median septum; cardinal process absent; pseudopunctate. *Ordovician (Llanvirn):* Newfoundland, China.——FIG. 505,*3a–d.* **F. novaterrensis,* Llanvirn, Newfoundland; *a,b,* holotype, external, internal molds of dorsal valve, ×4; *c,d,* internal

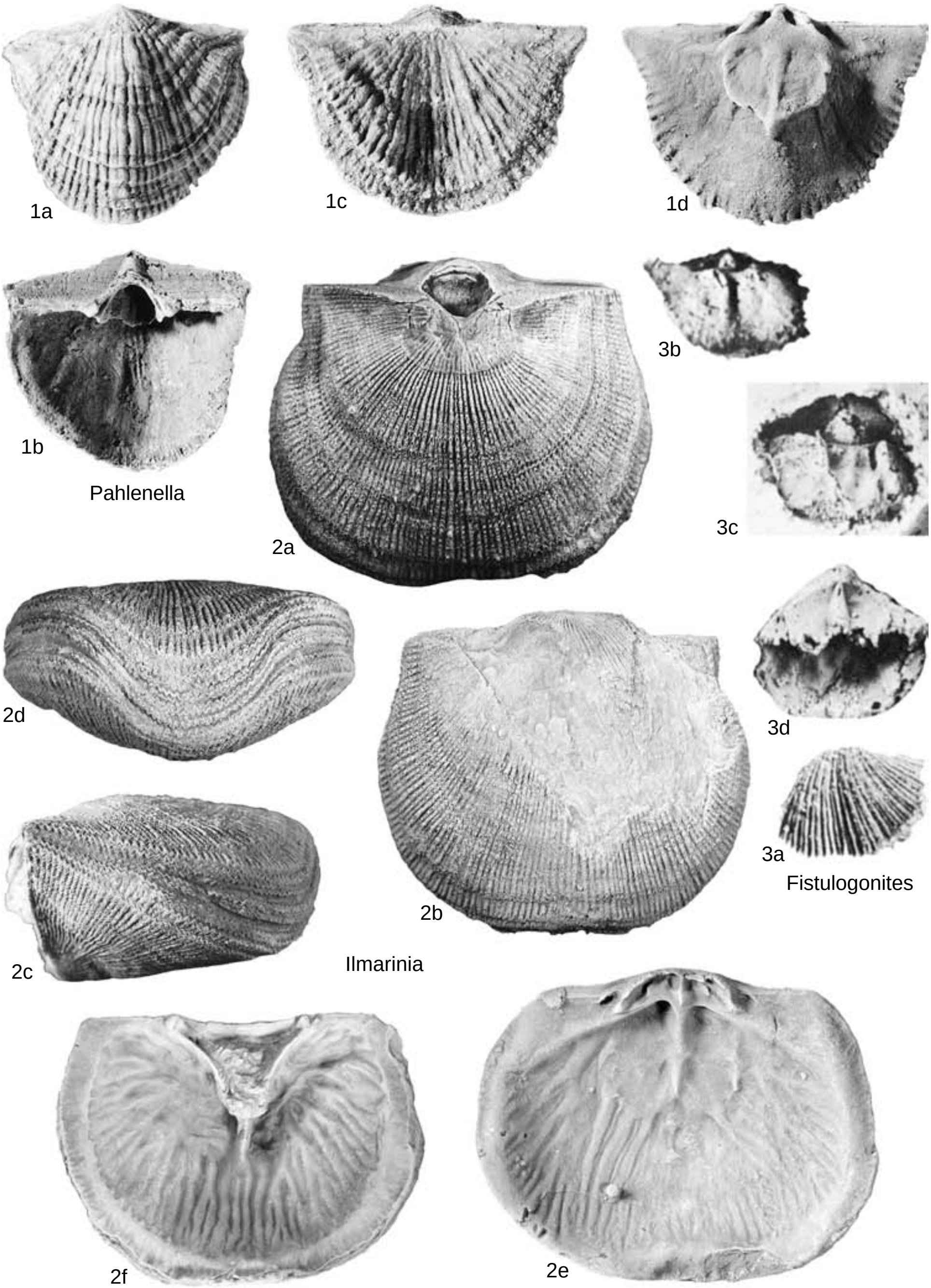

Fig. 505. Clitambonitidae (p. 698–704).

mold, latex cast of ventral valve, ×4 (Neuman, 1971).

Hemipronites Pander, 1830, p. 74 [*H. tumida; SD Dall, 1877, p. 31] [=*Ladogiella* Öpik, 1934, p. 93 (type, *L. imbricata* Öpik, 1934, p. 93)]. Similar to *Clitambonites* but strongly biconvex, with apsacline to catacline ventral interareas and finer costellae. *Ordovician (upper Arenig–Llanvirn):* Estonia, western Russia (Ingria), Norway.——Fig. 503,*2a–c*. **H. tumida,* Llanvirn, Ingria; *a–c,* dorsal, posterior,

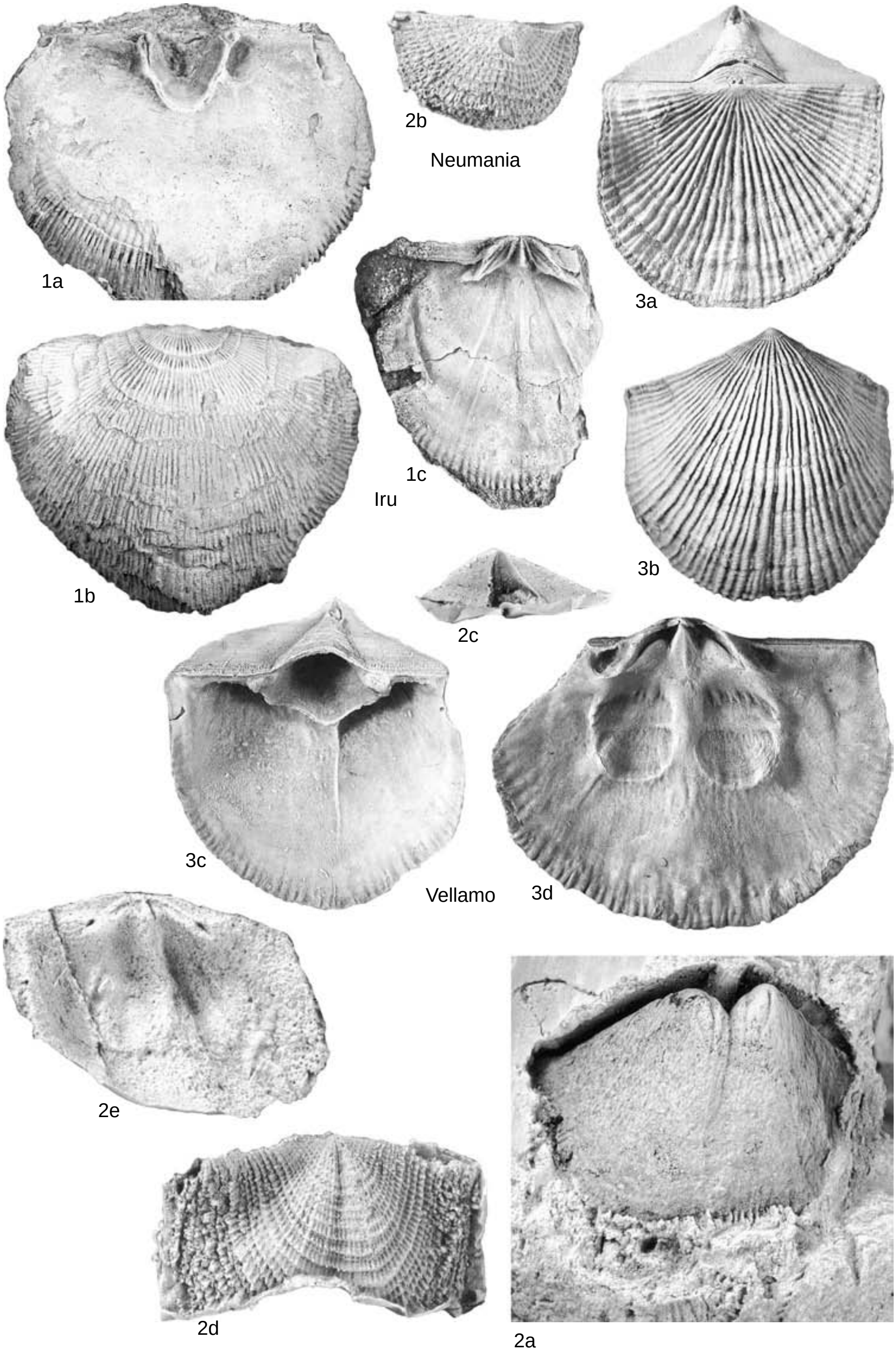

FIG. 506. Clitambonitidae (p. 701–704).

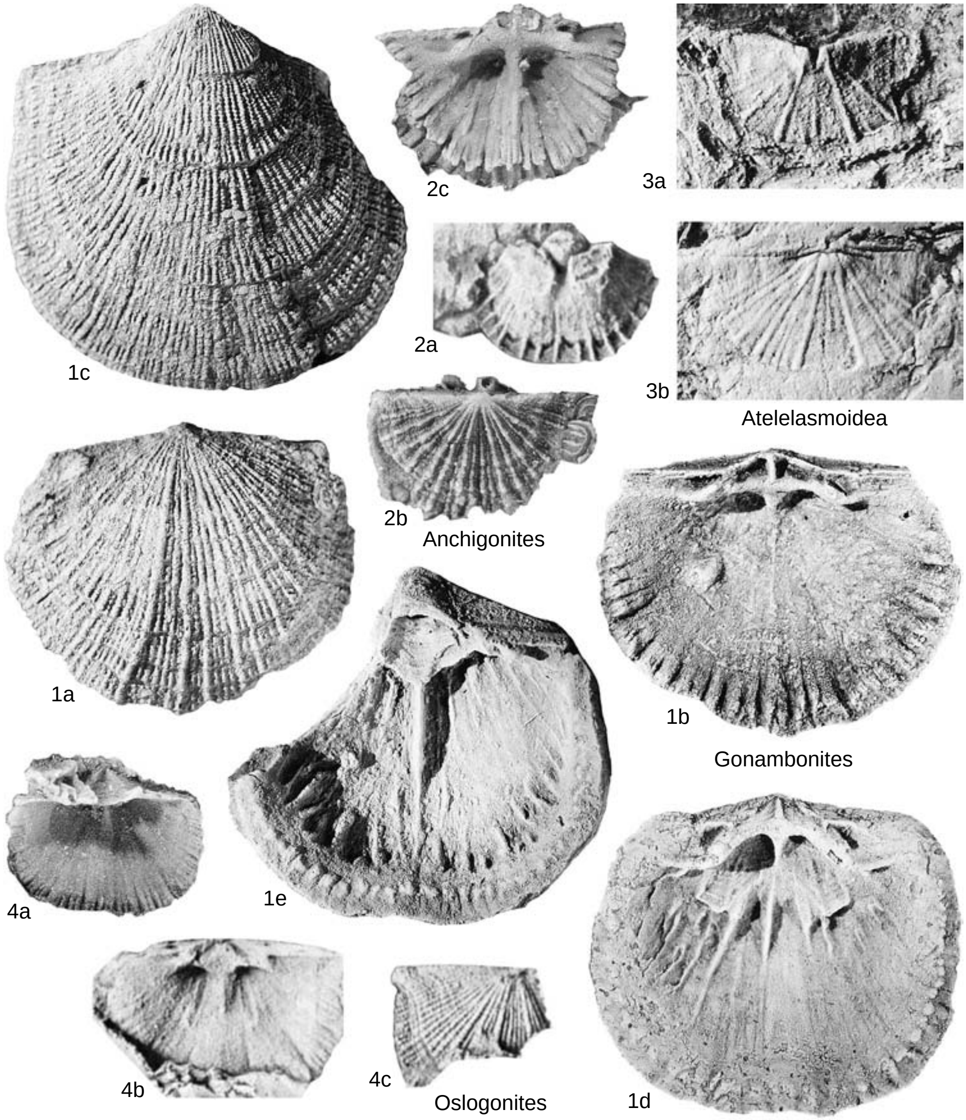

FIG. 507. Gonambonitidae (p. 704).

anterior views of conjoined valves, ×4.5 (Williams, 1965c).——FIG. 503,*2d–f. H. imbricata* (ÖPIK), Llanvirn, Ingria; *d,* dorsal valve interior, ×3 (Öpik, 1934); *e,f,* ventral valve exterior, interior, ×3 (Wright, 1994b).

Ilmarinia ÖPIK, 1934, p. 125 [**Orthisina sinuata* PAHLEN, 1877, p. 44; OD]. Similar to *Clinambon* but with ventral sulcus and dorsal fold, larger foramen, reduced dorsal interarea and chilidium, and spondylial constriction only weakly developed. *Upper Ordovician (upper Caradoc–upper Ashgill):* Estonia, Russia.——FIG. 505,*2a–d.* **I. sinuata* (PAHLEN), Ashgill, Estonia; ventral, dorsal, lateral, anterior views of conjoined valves, ×1.5 (Williams, 1965c).——FIG. 505,*2e,f. I. dimorpha* ÖPIK, upper Caradoc, Estonia; *e,* dorsal valve interior, ×1.5 (Wright & Rubel, 1996); *f,* ventral valve interior, ×1.5 (Wright, 1994b).

Iru ÖPIK, 1934, p. 89 [**Orthisina concava* PAHLEN, 1877, p. 17; OD]. Convexoconcave, strongly imbricate and filose; weakly developed deltidial cover, and chilidial plates only; spondylium sessile. *Ordovician (Arenig–lower Llanvirn):* Estonia, western Russia (Ingria).——FIG. 506,*1a–c.* **I. concava* (PAHLEN),

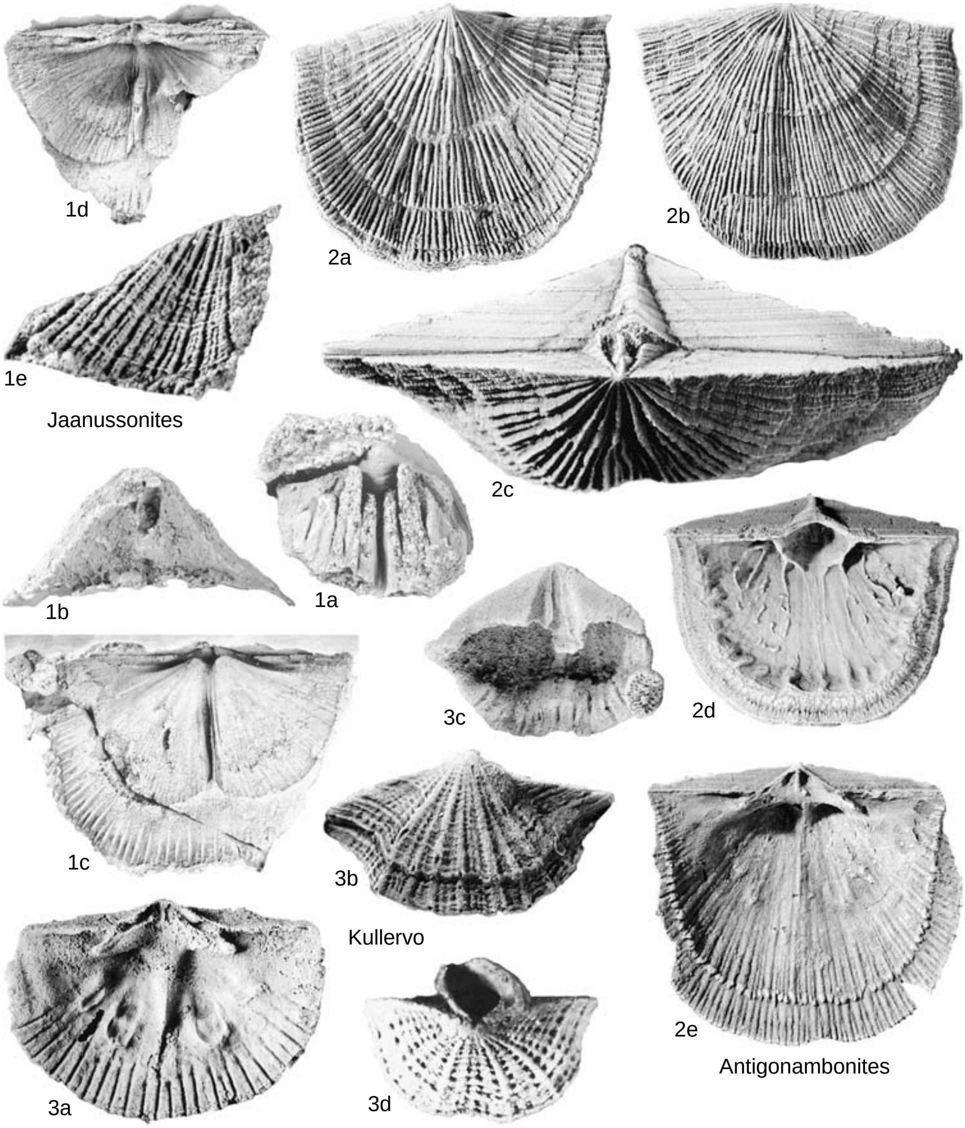

Fig. 508. Gonambonitidae (p. 704).

lower Llanvirn, Estonia; *a,b,* ventral valve interior, dorsal valve exterior, ×1.5; *c,* dorsal valve interior, ×2 (Williams, 1965c).

Lacunarites Öpik, 1934, p. 175 [**L. ilmatar;* OD]. Strongly concavoconvex; combined concentric ridges and coarse, spaced costellae producing pits in intercostal spaces; spondylium sessile. *Ordovician (Llanvirn):* Estonia, western Russia (Ingria).——Fig. 504,*2a–d.* **L. ilmatar,* lower Llanvirn, Estonia; *a,* ventral valve exterior, ×3; *b–d,* holotype, ventral, dorsal, oblique lateral views, ×2 (new).

Neumania Harper in Bruton & Harper, 1981, p. 162 [**Atelelasma atlanticus* Neuman, 1976, p. 24; OD]. Similar to *Apomatella* but with imbricated, transverse shells. *Ordovician (lower Arenig–lower Llanvirn):* Newfoundland, Wales, Norway, Estonia, western Russia (Ingria).——Fig. 506,*2a–e.* **N. atlanticus* (Neuman), upper Arenig, Newfoundland; *a,* ventral valve internal mold, ×3; *b,c,* ventral, posterior views of latex cast of ventral exterior, ×3; *d,* latex cast of dorsal exterior; *e,* latex cast of dorsal interior, ×3 (Neuman, 1976).

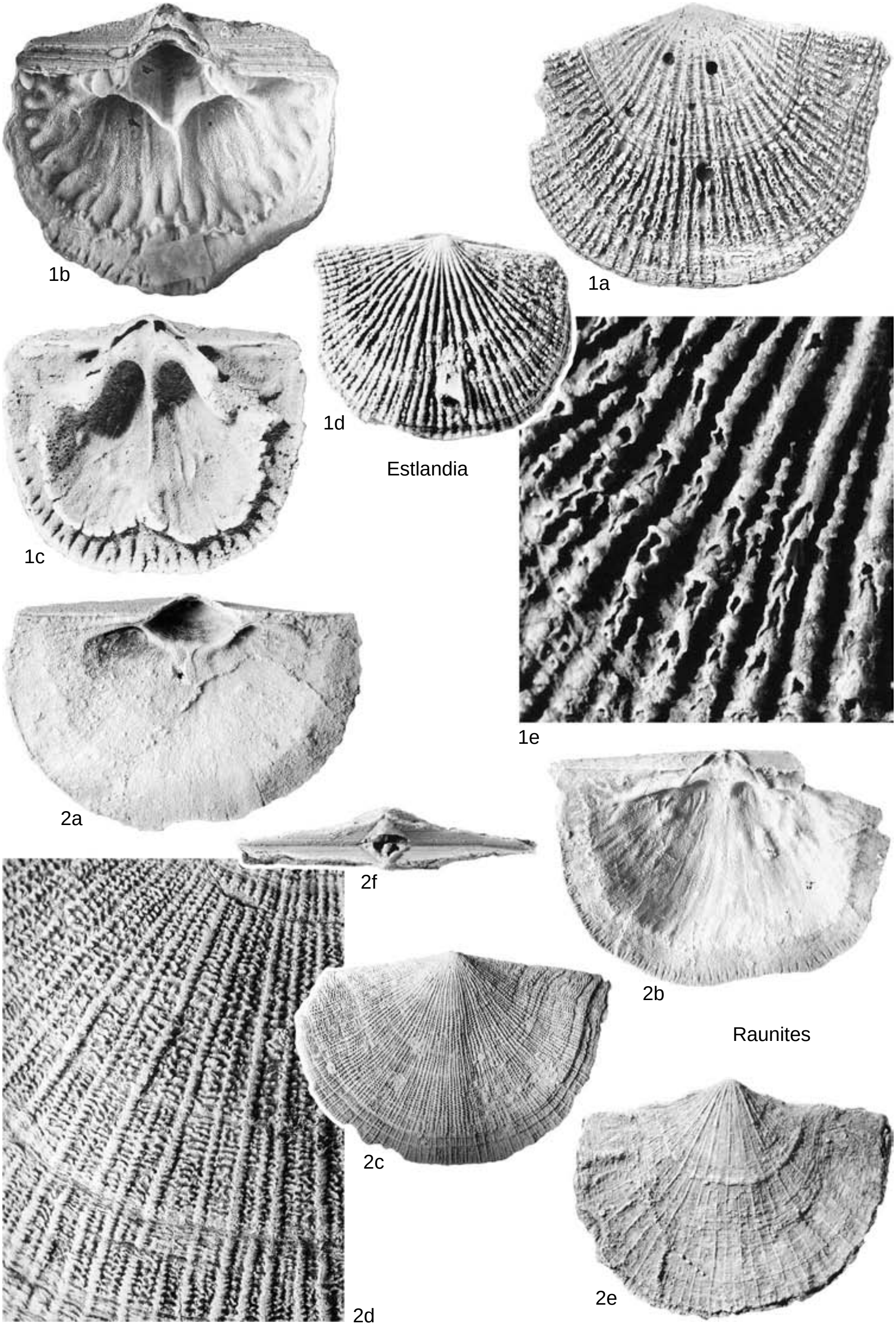

FIG. 509. Gonambonitidae (p. 704–706).

Pahlenella Schuchert & Cooper, 1931, p. 245 [**Orthis trigonula* von Eichwald, 1840, p. 148; OD]. Strongly concavoconvex shells with close, branching coarse costellae; dorsal adductor muscles on elevated platform. *Ordovician (lower Llanvirn):* western Russia (Ingria), Estonia.——Fig. 505,*1a–d.* **P. trigonula* (von Eichwald), lower Llanvirn, Ingria; *a,b,* ventral valve exterior, interior, ×3; *c,d,* lectotype, dorsal valve exterior, interior, ×3 (new).

Vellamo Öpik, 1930, p. 212 [**Orthis verneuili* von Eichwald, 1842, p. 51]. High subpyramidal ventral and flat to gently convex dorsal valves without strong imbrications, commonly asymmetrical. *Ordovician (Llandeilo–upper Ashgill):* Eurasia, North America, North Africa, Tasmania.——Fig. 506,*3a–d.* **V. verneuili* (von Eichwald), Ashgill, Estonia; *a,b,* dorsal, ventral views of conjoined valves, ×1.5; *c,d,* interiors of ventral, dorsal valves, ×2 (Williams, 1965c).

Family GONAMBONITIDAE Schuchert & Cooper, 1931

[*nom. transl.* Rubel, 1963, p. 92, *ex* Gonambonitinae Schuchert & Cooper, 1931, p. 245] [=Estlandiidae Öpik, 1934, p. 76]

Dental plates form spondylium triplex; dorsal adductor scars mostly radiating; shell substance pseudopunctate. *Ordovician (lower Arenig–middle Ashgill).*

Gonambonites Pander, 1830, p. 77 [**G. latus;* SD Schuchert & LeVene, 1929, p. 63] [=*Progonambonites* Öpik, 1934, p. 138 (type, *P. estonus*)]. Unequally biconvex to convexoconcave with medium-sized foramen, commonly sealed; differentiated costellae; dorsal adductor scars strongly impressed. *Ordovician (upper Arenig–lower Llanvirn):* Estonia, western Russia (Ingria), China.——Fig. 507,*1a,b.* **G. latus,* Llanvirn, Ingria; *a,b,* dorsal valve exterior, interior, ×3 (Rubel, 1963).——Fig. 507,*1c–e. G. parallelus* Pander, Llanvirn, Ingria; *c,* ventral valve exterior, ×2; *d,* dorsal valve interior, ×2.5 (Rubel, 1963); *e,* ventral valve interior, ×2 (new).

Anchigonites Öpik, 1939, p. 136 [**A. conulus;* OD]. Concavoconvex to planoconvex; chilidial plates present. *Lower Ordovician (Arenig, ?lower Llanvirn):* Norway, Estonia, western Russia (Ingria), China. ——Fig. 507,*2a–c.* **A. conulus,* upper Arenig, Norway; *a,* ventral valve internal mold, ×4 (Öpik, 1939); *b,* anteriorly tilted view of latex cast of dorsal valve exterior, ×4; *c,* latex cast of dorsal valve interior, ×4 (new).

Antigonambonites Öpik, 1934, p. 147 [**Gonambonites plana* Pander, 1830, p. 78; OD]. Convexoplane to resupinate, deltidium with minute, sealed foramen; costellae undifferentiated; spondylium triplex sessile. *Lower Ordovician (lower Arenig–lower Llanvirn):* Norway, Estonia, western Russia (Ingria), Poland, Newfoundland, China.——Fig. 508,*2a–e.* **A. planus* (Pander), Arenig, Ingria; *a,b,* ventral, dorsal views of conjoined valves, ×1.5 (new); *c,* posterior view of conjoined valves, ×3; *d,* dorsal view of ventral interior, ×1.5 (Wright & Rubel, 1996); *e,* dorsal valve interior, ×2 (new).

Atelelasmoidea Zeng, 1987, p. 225[531] [**A. typica;* OD]. Micromorphic ventribiconvex shells, ventral interarea apsacline to procline with open delthyrium and notothyrium; cardinal process absent; similar to *Oslogonites. Lower Ordovician (Arenig):* central and southwestern China.——Fig. 507,*3a,b.* **A. typica,* Arenig, Hubei; ventral valve, dorsal valve internal molds, ×9 (Zeng, 1987).

Estlandia Schuchert & Cooper, 1931, p. 245 [**Orthisina marginata* Pahlen, 1877, p. 33; OD]. Dorsibiconvex to convexoplane shells similar to *Gonambonites* but with distinctive tubulose costellae and stronger subperipheral rims. *Ordovician (?lower Llanvirn, upper Llanvirn–middle Caradoc):* Estonia, western Russia (Ingria).——Fig. 509,*1a–e.* **E. marginata* (Pahlen), Llandeilo, Estonia; *a,* ventral valve exterior, ×2 (Williams, 1965c); *b,* ventral valve interior, ×2 (Öpik, 1934); *c,* dorsal valve interior, ×3; *d,* dorsal valve exterior, ×2; *e,* detail of ornament, ×10 (Wright & Rubel, 1996).

Jaanussonites Neuman, 1976, p. 26 [**J. hornei;* OD]. Concavoconvex to ventribiconvex; intercostal spaces with fine spines, costellae with aditicules; dorsal subperipheral rim bilobed with long median ridge. *Lower Ordovician (upper Arenig):* eastern North America (Newfoundland, Maine).——Fig. 508,*1a–e.* **J. hornei,* upper Arenig, Newfoundland; *a,* ventral valve internal mold, ×2; *b,* posterior view of latex cast of ventral valve, ×2; *c,d,* dorsal valve internal mold, latex cast, ×1.5; *e,* incomplete dorsal valve external mold, ×4 (Neuman, 1976).

Kullervo Öpik, 1932, p. 70 [**Gonambonites panderi* Öpik, 1930, p. 234; OD]. Planoconvex with subpyramidal ventral valve; strong radial and concentric ornament producing reticulation; aditicules well developed; foramen commonly large, with high, irregular lip; hemisyrinx present; dorsal adductor scars strongly impressed. *Ordovician (upper Llanvirn–middle Ashgill):* Eurasia, North America.——Fig. 508,*3a,b.* **K. panderi* (Öpik), Llandeilo–lower Caradoc, Estonia; *a,* dorsal valve interior, ×3 (Öpik, 1934); *b,* ventral valve exterior, ×3 (Wright & Rubel, 1996).——Fig. 508,*3c. K. lacunata* Öpik, lower Caradoc, Estonia; ventral valve interior, ×3 (Wright & Rubel, 1996).——Fig. 508,*3d. K. complectens* (Wiman), middle Ashgill, Sweden; ventral valve exterior showing exaggerated lip to foramen, ×6 (Harper, new).

Oslogonites Öpik, 1939, p. 133 [**O. costellatus;* OD]. Planoconvex to ventribiconvex; ventral interarea apsacline to catacline, delthyrium and notothyrium open; cardinal process absent. *Ordovician (Arenig–lower Llanvirn):* Norway, Estonia, ?England.——Fig. 507,*4a–c.* **O. costellatus,* upper Arenig, Norway; *a,* latex cast of ventral valve interior, ×4 (new); *b,c,* casts of interior, exterior of dorsal valve, ×4 (Öpik, 1939).

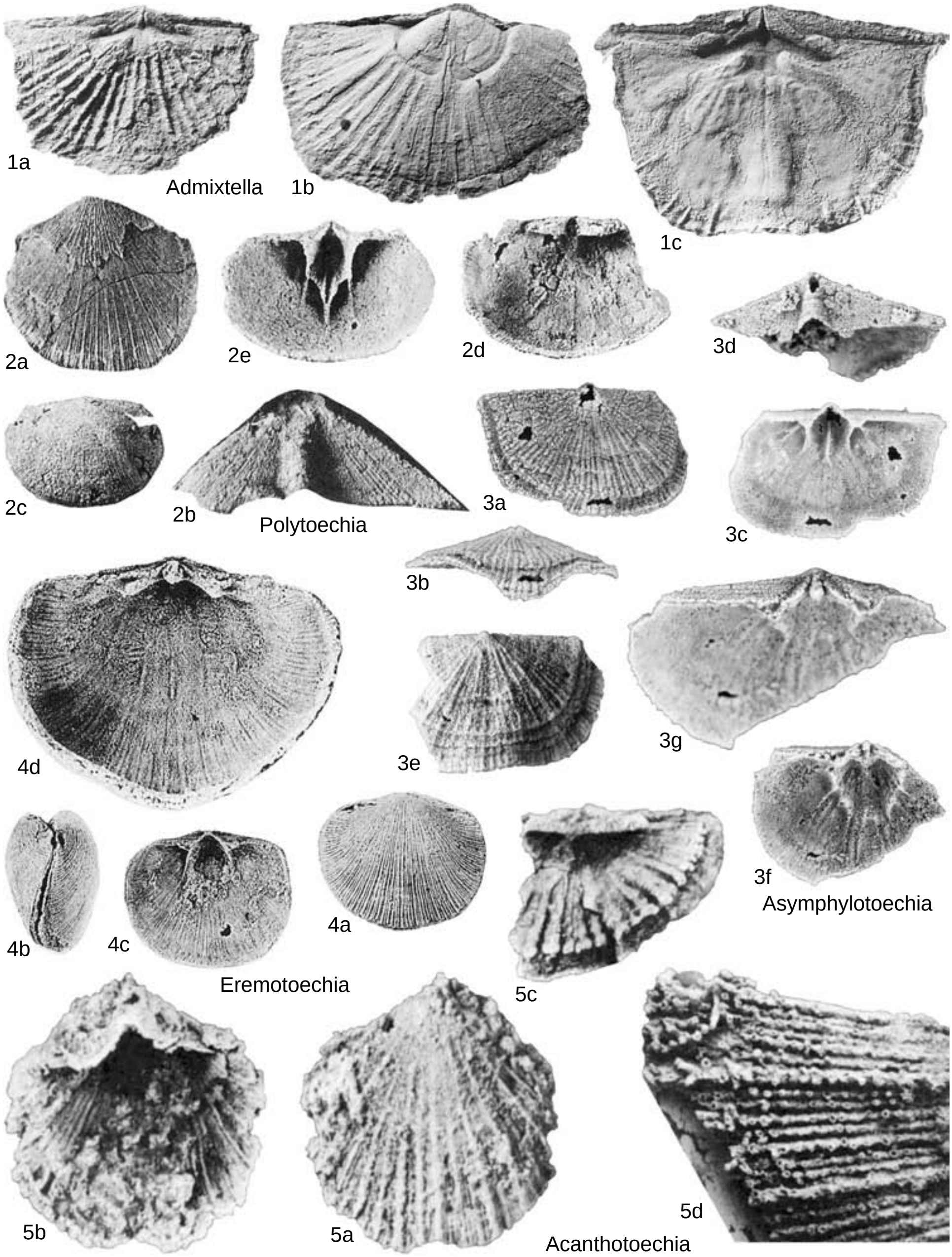

FIG. 510. Polytoechiidae (p. 707–708).

Raunites ÖPIK, 1939, p. 135, *nom. nov. pro Rauna* ÖPIK, 1932, p. 70, *non* MÜNSTER, 1839] [**Orthisina janischewskyi* LESNIKOVA, 1924, p. 153; OD]. Resupinate shells with unequal costellae and well-developed concentric fila. *Lower Ordovician (Arenig–lower Llanvirn):* Estonia, western Russia (Ingria).——FIG. 509,*2a,b*. **R. janischewskyi* (LESNIKOVA), Arenig, Ingria; ventral, dorsal interiors,

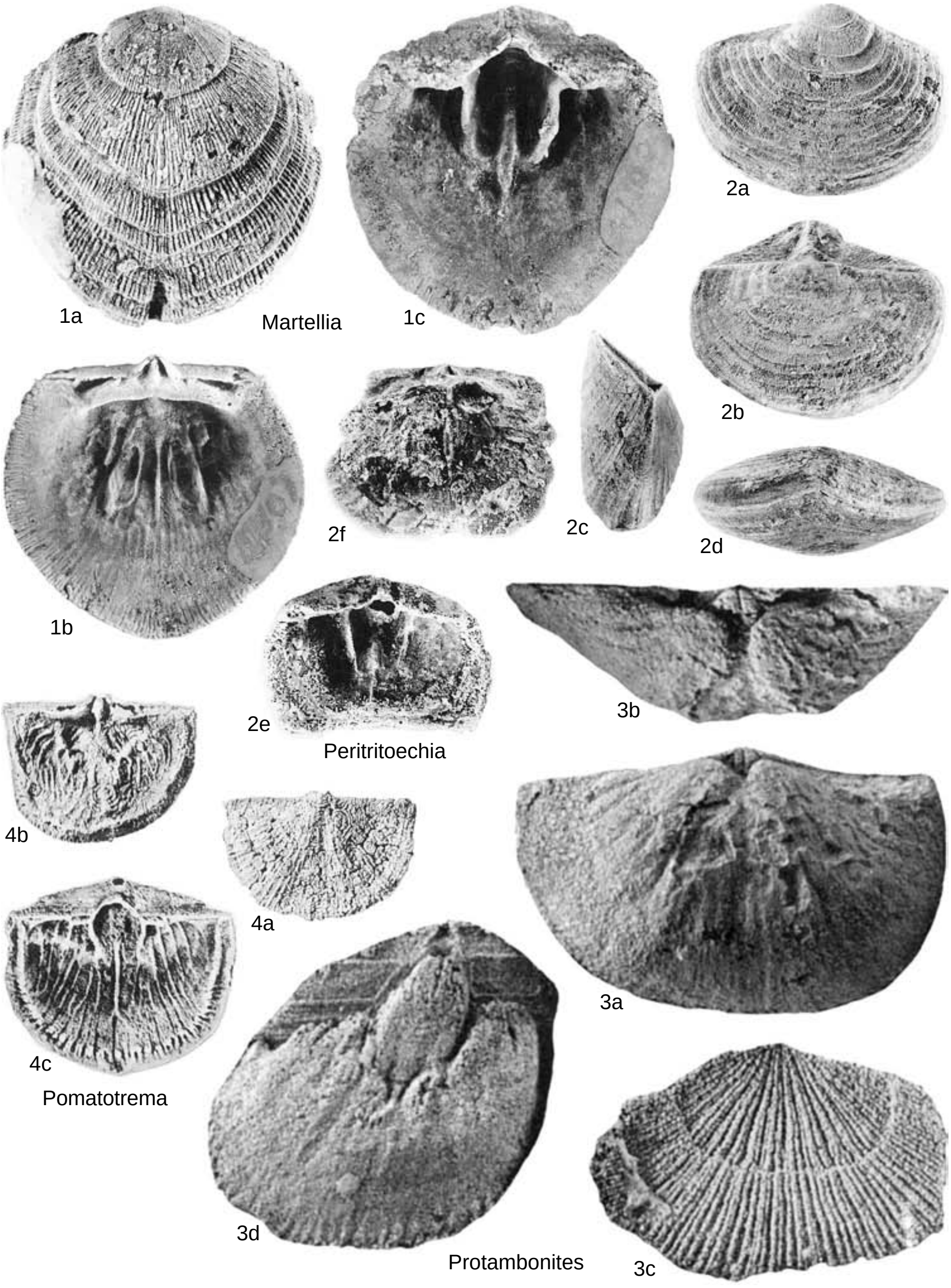

FIG. 511. Polytoechiidae (p. 708).

×1.5 (Öpik, 1934).——FIG. 509,*2c. R. wolchowiana* (ÖPIK); ventral valve exterior, ×2 (Öpik, 1934).——FIG. 509,*2d. R. venusta* (ÖPIK), Arenig, Ingria; detail of ornament, ×5 (Öpik, 1934).——FIG. 509,*2e,f. R. strophomenoides* (ÖPIK), lower Llanvirn, Estonia; ventral, posterior views of conjoined valves, ×1.5 (new).

Superfamily POLYTOECHIOIDEA Öpik, 1934

[*nom. transl.* Rubel & Wright, herein, *ex* Polytoechiinae Öpik, 1934, p. 76] [=Tritoechiidae Ulrich & Cooper, 1936b, p. 624]

Dental plates reach valve floor to form pseudospondylium; shell substance impunctate. *Ordovician (Tremadoc–lower Caradoc).*

Family POLYTOECHIIDAE Öpik, 1934

[*nom. transl.* Cloud, 1948b, p. 461, *ex* Polytoechiinae Öpik, 1934, p. 76] [=Tritoechiidae Ulrich & Cooper, 1936b, p. 624]

Characters as for superfamily. *Ordovician (Tremadoc–lower Caradoc).*

Polytoechia Hall & Clarke, 1892, p. 239 [**Hemipronites apicalis* Whitfield, 1886, p. 300; OD] [=*Deltatreta* Ulrich in Butts, 1926, p. 100 (type, *D. fillistriata* Butts, 1926; SD Schuchert & Cooper, 1932, p. 108); *Deltorthis* Ulrich in Poulsen, 1927, p. 297, *nom. nov. pro Waagenia* Hall, 1889, p. 390, *non* von Kriechbaumer, 1874, obj.]. Unequally biconvex; pseudospondylium with differentiated adductor scars, and with forwardly extending dental plates and median septum. *Lower Ordovician (Arenig):* USA (Alabama, Arkansas, Oklahoma, Texas, Vermont), Greenland, China (Manchuria).——Fig. 510,*2a,b*. **P. apicalis* (Whitfield), Arenig, Vermont; *a,* ventral valve exterior, ×3; *b,* ventral valve interarea, ×4 (Ulrich & Cooper, 1938).——Fig. 510,*2c–e*. *P. subcircularis* Cooper, Arenig, Oklahoma; *c,* dorsal valve exterior, ×3; *d,* dorsal valve interior, ×3; *e,* anterodorsal view of ventral interior, ×3 (Cooper, 1952b).

Acanthotoechia Williams & Curry, 1985, p. 244 [**A. hibernica;* OD]. Concavoconvex; costellae bearing rows of fine spines peripherally; dorsal interior with subperipheral rim. *Lower Ordovician (upper Arenig):* Ireland.——Fig. 510,*5a–d*. **A. hibernica,* Arenig, Ireland; *a,b,* holotype, exterior, interior of ventral valve, ×4; *c,* interior of damaged dorsal valve, ×8; *d,* detail of ornament on fragment, ×17 (Williams & Curry, 1985).

Admixtella Rozman, 1978, p. 84 [**A. orientalis;* OD]. Planoconvex, with narrow dorsal fold and ventral sulcus; delthyrium cover unknown; notothyrium open. *Ordovician (lower Caradoc):* Tien Shan Mountains, Asia.——Fig. 510,*1a–c*. **A. orientalis,* lower Caradoc, Tien Shan Mountains; *a,* ornament on dorsal valve, partly exfoliated umbonally, revealing mold of cardinalia, ×3; *b,* ventral valve internal mold, ×3; *c,* dorsal valve internal mold, ×3 (Rozman, 1978).

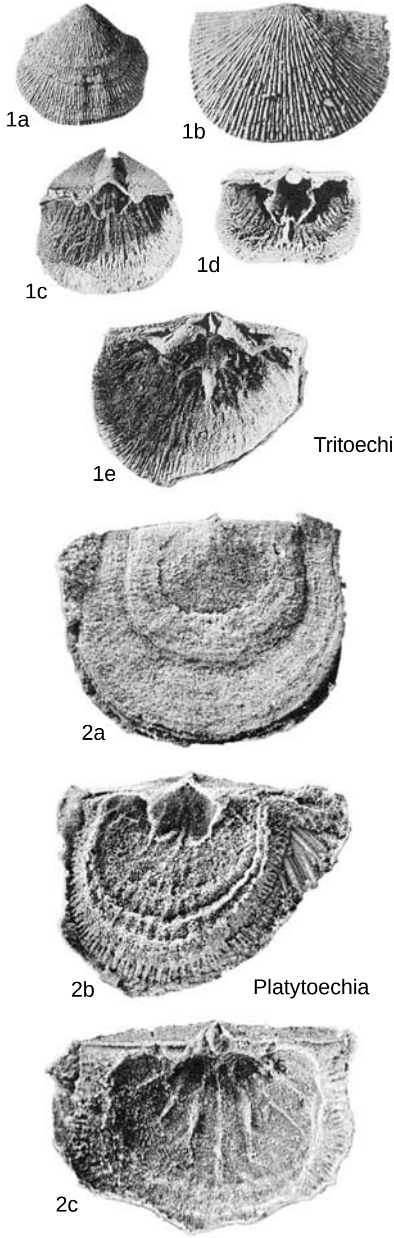

Fig. 512. Polytoechiidae (p. 708).

Asymphylotoechia Ross, 1970, p. 60 [**A. nolani;* OD]. Biconvex, with dorsal fold and ventral sulcus; chilidium present, cardinal process swollen. *Lower Ordovician (upper Llanvirn):* USA (Nevada).——Fig. 510,*3a–g*. **A. nolani,* upper Llanvirn, Nevada; *a–c,* exterior, anterior, interior views of ventral valve, ×3; *d,* ventral interarea, ×3; *e,* dorsal valve exterior, ×3; *f,* dorsal valve interior, ×3; *g,* detail of hinge viewed posteroventrally, ×5 (Ross, 1970).

Eremotoechia Cooper, 1956, p. 513 [**E. cloudi;* OD]. Dorsibiconvex; chilidial plates, prominent trilobed cardinal process. *Ordovician (Llanvirn–Llandeilo):*

USA (Tennessee, Alabama), Scotland, Kazakhstan, Argentina, southwestern China.——FIG. 510,*4a–d.* **E. cloudi,* Llandeilo, Tennessee; *a,b,* dorsal, lateral views of conjoined valves, ×1; *c,* ventral valve interior, ×1; *d,* dorsal valve interior, ×2 (Cooper, 1956).

Martellia WIRTH, 1936, p. 300 [**Orthisina giraldii* MARTELLI, 1901, p. 305; OD]. Planoconvex to ventribiconvex; median ridge extending in front of ventral muscle field; chilidium and cardinal process present, strong dorsal median septum. *Ordovician (upper Arenig–Llanvirn):* central and southwestern China, Argentina.——FIG. 511,*1a–c. M. ichangensis* WANG, upper Arenig, Hubei, China; *a,b,* exterior, interior views of dorsal valve, ×3; *c,* ventral valve interior, ×3 (new).

Peritritoechia XU, RONG, & LIU, 1974, p. 151 [**P. imbricatia;* OD]. Ventribiconvex shell with imbrications and very fine costellae of equal size; dorsal valve with chilidium and strong, trilobed cardinal process. *Ordovician (upper Llanvirn–lower Caradoc):* southwestern China.——FIG. 511,*2a–f.* **P. imbricatia,* lower Caradoc, Guizhou, southwestern China; *a–d,* holotype, ventral, dorsal, lateral, anterior views, ×1.5; *e,* ventral valve interior, ×1.5; *f,* dorsal valve interior, ×1.5 (Xu, Rong, & Liu, 1974).

Platytoechia NEUMAN, 1964, p. E19 [**P. boucoti;* OD]. Convexoplane to convexoconcave; dorsal interior with strong cardinal process and subperipheral rim. *Lower Ordovician (upper Arenig):* USA (Maine).——FIG. 512,*2a–c.* **P. boucoti,* upper Arenig, Maine; *a,* holotype, latex cast of ventral valve exterior, ×2; *b,c,* latex casts of ventral, dorsal interiors, ×2 (Neuman, 1964).

Pomatotrema ULRICH & COOPER in SCHUCHERT & COOPER, 1932, p. 109 [**P. muralis;* OD]. Planoconvex; chilidial plates and prominent cardinal process; subperipheral rim in each valve. *Ordovician (Arenig):* USA (Oklahoma, Vermont), Canada (Alberta, Quebec), Greenland, Ireland, China, Korea.——FIG. 511,*4a–c.* **P. murale,* Arenig, Oklahoma; *a,* dorsal valve exterior, ×2; *b,* dorsal valve interior, ×2; *c,* ventral valve interior, ×2 (Ulrich & Cooper, 1938).

Protambonites HAVLÍČEK in HAVLÍČEK & JOSOPAIT, 1972, p. 348 [**Tritoechia kolihai* HAVLÍČEK, 1949a, p. 113; OD]. Dorsibiconvex to resupinate; notothyrium open, cardinal process weak. *Lower Ordovician (Tremadoc–Arenig):* Bohemia, Spain, China, Urals.——FIG. 511,*3a,b.* **P. kolihai* (HAVLÍČEK), Tremadoc, Bohemia; dorsal, posterior views of dorsal valve internal mold, ×2 (Havlíček, 1977a).——FIG. 511,*3c,d. P. soror* (BARRANDE), Tremadoc, Bohemia; external, internal molds of ventral valves, ×2.5 (Havlíček, 1977a).

Tritoechia ULRICH & COOPER, 1936b, p. 624 [**Deltatreta typica* SCHUCHERT & COOPER, 1932, p. 206; OD]. Ventribiconvex, with pronounced aditicules; prominent median ridge extending in front of ventral muscle field; chilidial plates present, cardinal process swollen. *Ordovician (Tremadoc–Arenig):* widespread.——FIG. 512,*1a–e.* **T. typica* (SCHUCHERT & COOPER), Arenig, Oklahoma; *a,* ventral valve exterior, ×1; *b,* dorsal valve exterior, ×2; *c,d,* dorsal, anterodorsal views of ventral interior, ×1; *e,* dorsal valve interior, ×2 (Ulrich & Cooper, 1938).

RHYNCHONELLATA

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Class RHYNCHONELLATA Williams & others, 1996

[Rhynchonellata WILLIAMS & others, 1996, p. 1193]

Rhynchonelliform brachiopods with fibrous, impunctate, punctate, or endopunctate, biconvex, strophic or astrophic shells, articulated by deltidiodont or cyrtomatodont teeth and sockets buttressed by brachiophores or supported by parallel socket or hinge plates repeatedly converging to form septalium or cruralium; pedicle opening as delthyrium or rounded foramen; interareas and notothyrium commonly vestigial or absent, well developed in some derived groups; ventral muscle scars with posteromedial adductors flanked or enclosed by diductors and laterally placed adjustors; dental plates less commonly converging to form spondylium; dorsal adductor scars petaloid or grouped and quadripartite; crura present in later groups and commonly extended as spiralia or loops; mantle canal systems variable as saccate, digitate, pinnate, or lemniscate impressions. *Lower Cambrian–Holocene.*

The Rhynchonellata is the largest class of brachiopods. It is composed of about 3,000 genera assigned to 75 superfamilies and grouped into 10 orders. The diagnostic synapomorphy is a pedicle developed from a rudiment. In such extinct groups as the orthides and syntrophiidines, the presence of such a pedicle is indicated by the imprint of adjustor scars on the shell interior. A pedicle such as this was variably developed throughout the class, being vestigial in some free-lying groups (pentameridines). But in the thecideides and some atrypides the pedicle rudiment developed into an adhesive pad attended by cementation of the ventral valve, a homoplasy that has caused great difficulties in past classifications of the brachiopods.

The rhynchonellides and related spire-bearing and loop-bearing orders are further characterized by the reversal of the mantle rudiment during larval development. This transformation is indicated on the shells by a forward shift of the attachment area of the ventral muscle field to make way for the pedicle capsule. It is, therefore, well documented in extinct groups.

Other synapomorphies evident in the shell and used in classification at the ordinal level are transformations of articulatory devices. In particular, the development of cyrtomatodont teeth and the elaboration of cardinalia, giving rise to crura supporting the mouth segment of the lophophore, characterize the rhynchonellides and all derived ordinal groups. Such orders, in turn, are well founded on the nature and disposition of spiralia and loops extending from the crura in support of the variously oriented brachia of the lophophore.

Among other features used in the suprafamilial classification of the Rhynchonellata, the strophic shells of spiriferides (*s.l.*), thecideides, and some terebratulides were derived from astrophic stem groups and, therefore, separable taxonomically from those of orthides and protorthides. Punctation is also homoplastic; but putative homologues of the endopunctae characterizing terebratulides and thecideides occur in Jurassic species of spiriferides (*s.l.*).

PROTORTHIDA

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Order PROTORTHIDA Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Small, strophic rhynchonelliforms with wide, open delthyrium and notothyrium; apsacline ventral interarea normally long and flat, anacline dorsal interarea short to vestigial; rudimentary or simple, deltidiodont teeth with dental ridges, slightly lateral of delthyrial edges, uniting with free spondylium; ventral mantle canal system rarely impressed, saccate; secondary layer of shell presumably fibrous as in skenidioids, impunctate. *Lower Cambrian–Upper Devonian (Frasnian).*

The taxa herein assigned to the Protorthida are characterized by a free spondylium (apical plate of COOPER, 1976, p. 286), which accommodated the ventral muscle bases. The protorthides are further characterized by brachiophore plates that converge to form a transverse plate underlying the notothyrial margin. The ontogeny of this plate is not known, but it could have been the same as the early stages in the development of the cardinalia of *Protoskenidioides* prior to the medial fusion of the converging brachiophore plates into a simple cardinal process. For this reason, the Skenidioidea is placed within the Protorthida with the Protorthoidea despite the fact that neither superfamily has yet been found in Upper Cambrian rocks.

The assignment of *Leioria* and *Arctohedra* (with *Loperia*) to the Protorthida is less secure taxonomically as the flat brachiophores of the former genus and the notothyrial platform of the latter are more typically orthide. The variability of these structures among early orthides, however, suggests that they, rather than the free spondylium, are more likely to be homoplastic.

Superfamily PROTORTHOIDEA Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Protorthides with notothyrium underlain by short, transverse plate without cardinal process; dorsal adductor scars probably linear; ventral mantle canal system saccate with divergent *vascula media. Lower Cambrian–Middle Cambrian.*

Family PROTORTHIDAE Schuchert & Cooper, 1931

[Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Generally transversely semioval, uniplicate protorthoids with acute to mucronate cardinal extremities; brachiophores as widely divergent rudimentary brachiophore nubs defining small, shallow sockets. *Lower Cambrian–Middle Cambrian.*

Protorthis HALL & CLARKE, 1892, p. 231 [**Orthis billingsi* HARTT in DAWSON, 1868, p. 644; OD]. Cardinal extremities variable, shells biconvex, rectimarginate, multicostellate; brachiophores subparallel with hinge line; dorsal median ridge absent. *Middle Cambrian:* eastern North America.——FIG. 513,*1a–e.* **P. billingsi* (HARTT), Middle Cambrian, New Brunswick; *a,* ventral exterior, ×2; *b,* ventral interior, ×2.7 (Schuchert & Cooper, 1932); *c,* dorsal interior, ×2; *d,* ventral exterior, ×2; *e,* tilted ventral exterior, ×3 (Hall & Clarke, 1892).

Glyptoria COOPER, 1976, p. 281 [**G. glypta;* OD]. Similar to *Protorthis* but dorsibiconvex, uniplicate, with acute cardinal extremities, coarsely costate and imbricate; small teeth fitting lateral to brachiophore nubs. *Lower Cambrian:* Dead Sea region.——FIG. 513,*2a–e.* **G. glypta,* Lower Cambrian, Dead Sea region; *a,* dorsal interior, ×2; *b,* ventral interior, ×2; *c,* ventral exterior, ×2; *d,e,* lateral, anterior view of dorsal exterior, ×1 (Cooper, 1976).

Israelaria COOPER, 1976, p. 281 [**I. parnesi;* OD]. Similar to *Glyptoria* but ventribiconvex and with impersistent, irregularly developed costae. *Lower Cambrian:* Dead Sea region, Morocco.——FIG. 513,*4a–d.* **I. parnesi,* Lower Cambrian, Dead Sea region; *a,* ventral interior, ×2; *b,* view of hinge area of dorsal valve, ×2; *c,* dorsal interior, ×3; *d,* ventral exterior, ×2 (Cooper, 1976).

Jamesella WALCOTT, 1905, p. 252 [**Orthis perpasta* POMPECKJ, 1896, p. 515; OD]. Similar to *Israelaria* but subquadrate with slightly mucronate cardinal extremities, uniplicate, coarsely costellate, with concentric lamellae. *Middle Cambrian:* Bohemia, Spain.——FIG. 513,*5a–e.* **J. perpasta* (POMPECKJ), Middle Cambrian, Bohemia; *a,b,* normal, tilted views of rubber replica of ventral interior, ×1.7; *c,d,* internal mold, rubber replica of dorsal valve, ×2.5; *e,* rubber replica of dorsal exterior, ×1.6 (Havlíček, 1977a).

Psiloria COOPER, 1976, p. 282 [**P. pauperata;* OD]. Similar to *Glyptoria* but with slightly mucronate cardinal extremities and smooth or faintly costellate exterior. *Lower Cambrian:* Dead Sea region.——FIG. 513,*3a–c.* **P. pauperata,* Lower Cambrian, Dead Sea region; ventral interior, dorsal interior, ventral exterior, ×2 (Cooper, 1976).

Family ARCTOHEDRIDAE new family

[Arctohedridae WILLIAMS & HARPER, herein]

Costellate, unisulcate protorthoids with subpyramidal ventral valve having curved apsacline to catacline interarea; teeth simple, ventral muscle field with relatively broad, subtriangular adductor track flanked by linear diductor scars, rarely impressed on free spondylium; 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 scar; ventral mantle canal system probably saccate with divergent *vascula media.* [The Arctohedridae is provisionally assigned to the Protorthoidea on the assumption that the presence of a free spondylium is more likely to be an apomorphy of taxonomic significance than the development of a notothyrial platform. Indeed, the presence of this feature and of the orthidine-like brachiophores of the Leioriidae suggests the protorthidine genotype had many features that were later to characterize the orthide shell.] *Middle Cambrian.*

Arctohedra COOPER, 1936, p. 210 [**A. minima;* OD]. Transversely semioval with acute cardinal extremities, ventribiconvex to planoconvex, coarsely costellate to ramicostellate. [COOPER (1936, p. 210) described the cardinalia of silicified dorsal valves of the type species of *Arctohedra* as including a well-developed cardinal process and notothyrial platform. ROBERTS and JELL (1990, p. 281), studying their better preserved species *A. alata,* concluded that the notothyrium was occupied by a narrow plate (inappropriately identified as a cardinal plate) ankylosed to a medial plug continuous with the high dorsal median ridge. The latter structure is closer to the protorthoid cardinalia and is assumed to be typical of the arctohedrids as a whole.] *Middle Cambrian:* North America (Alaska), Australia (New South Wales), central Asia (Turkestan, Tyan

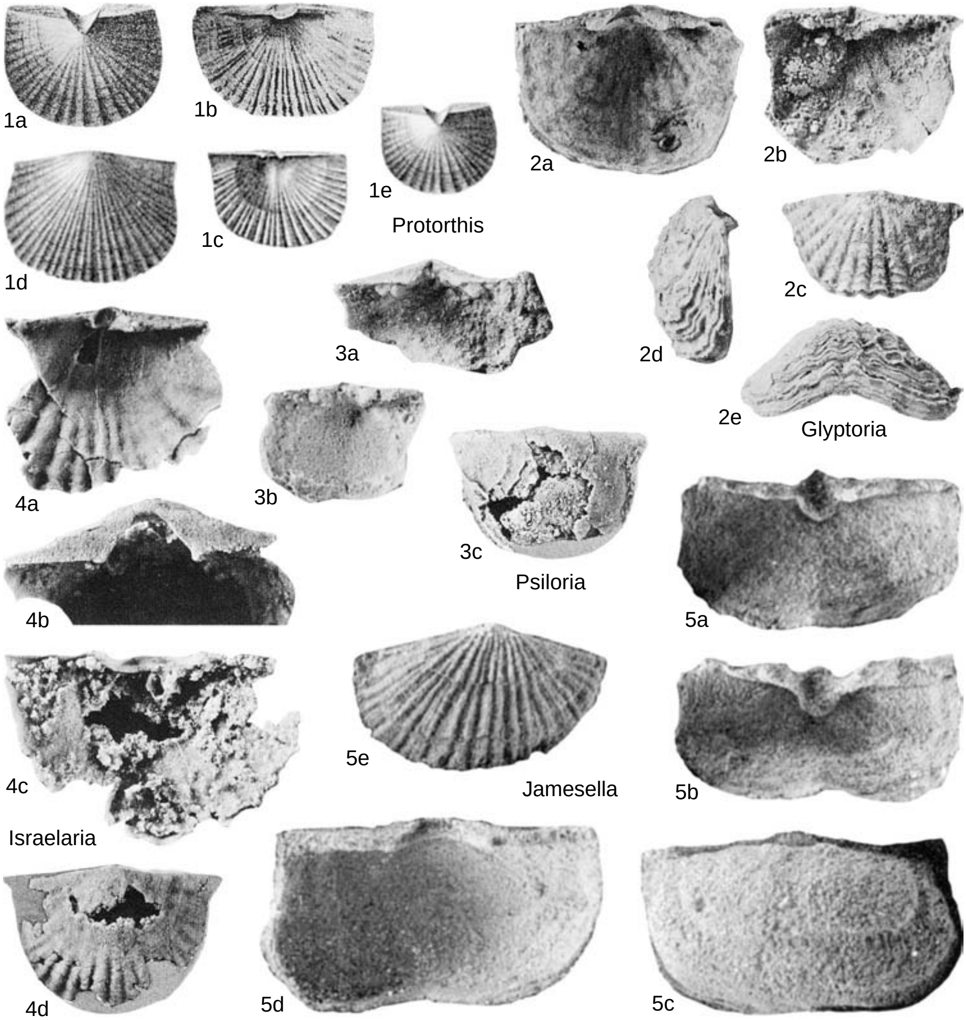

FIG. 513. Protorthidae (p. 710).

Shan).——FIG. 514,*1a–d*. **A. minima,* Middle Cambrian, Alaska; *a,* dorsal exterior, ×10; *b,* ventral exterior, ×6; *c,* ventral interior, ×6; *d,* dorsal interior, ×10 (Cooper, 1936).

Loperia WALCOTT, 1905, p. 287 [**Protorthis (Loperia) dougaldensis;* OD]. Subquadrate with obtuse cardinal extremities, resupinate, multicostellate; delthyrium and notothyrium open, wide; apsacline ventral interarea flat, long; catacline dorsal interarea short; small teeth; socket ridges divergent, bladelike; simple, ridgelike cardinal process supported by small notothyrial platform. [This genus is provisionally included in the Arctohedridae due to its free spondylium and notothyrial platform. In general, however, it differs significantly from arctohedrids in being resupinate and especially in having a well-defined cardinal process.] *Middle Cambrian:* eastern Canada.——FIG. 514,*2a–c*. **L. dougaldensis* (WALCOTT), Middle Cambrian, Cape Breton; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×2; *c,* fragment of valve exterior, ×2 (Walcott, 1912).

Family LEIORIIDAE Cooper, 1976

[Leioriidae COOPER, 1976, p. 284]

Ventribiconvex, rectimarginate protorthoids with blunt, bladelike brachiophores erect, narrowly divergent, delineating elongate sockets; dorsal adductor field consisting of 4 elongate, radiating scars separated by low ridges. *Lower Cambrian.*

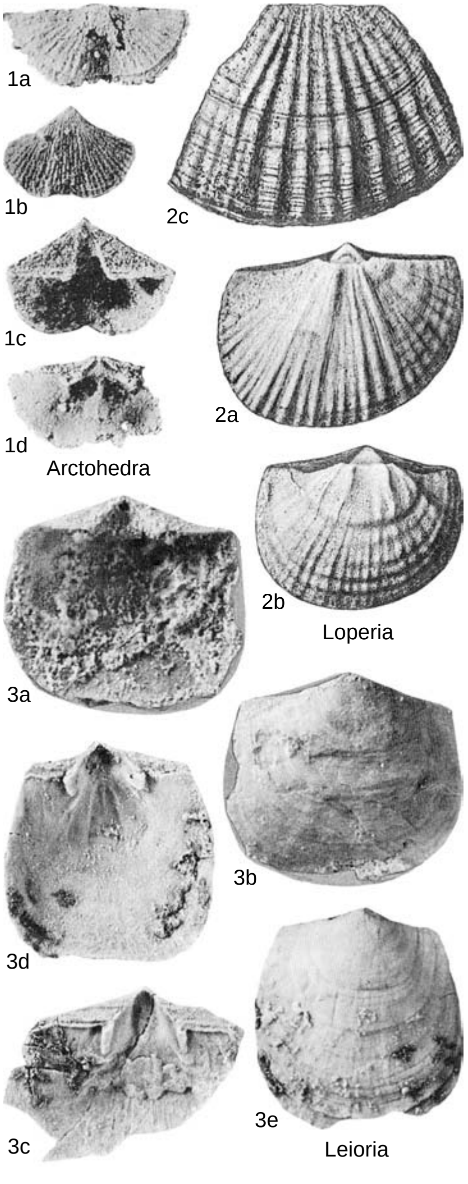

Fig. 514. Arctohedridae and Leioriidae (p. 710–712).

Leioria Cooper, 1976, p. 284 [**L. bentori;* OD]. Small, subquadrate with obtuse cardinal extremities, ornamented only by concentric banding and lines of growth. *Lower Cambrian:* Israel, Jordan.——Fig. 514,*3a–c.* **L. bentori,* Lower Cambrian, Dead Sea region; *a,b,* interior, exterior of ventral valve, ×2; *c,* dorsal interior, ×2 (Cooper, 1976).——Fig. 514,*3d,e. L. elongata* Cooper, Lower Cambrian, Dead Sea region; interior, exterior of dorsal valve, ×2 (Cooper, 1976).

Superfamily SKENIDIOIDEA Kozłowski, 1929

[*nom. transl.* Williams & Harper, herein, *ex* Skenidiidae Kozłowski, 1929, p. 46]

Protorthides with teeth ridges continuous with sides of free spondylium normally supported apically by short ridge; rodlike, divergent brachiophores joined to hinge line by fulcral plates defining elongate sockets and supported by basal plates converging onto high median septum to form septalium; cardinal process normally ridgelike, commonly fused with dorsal median septum; impressions of muscle fields and mantle canals mostly indistinct, ventral mantle canal system probably saccate with convergent *vascula media,* dorsal adductor scar quadripartite. *Lower Ordovician (Arenig)–Upper Devonian (Frasnian).*

Family SKENIDIIDAE Kozłowski, 1929

[*nom. correct.* Schuchert & Cooper, 1931, p. 243, *pro* Scenidiidae Kozłowski, 1929, p. 46]

Ventribiconvex to planoconvex skenidioids with subpyramidal ventral valve and strongly sulcate dorsal valve normally transversely semioval with acute cardinal extremities. *Lower Ordovician (Arenig)–Upper Devonian (Frasnian).*

Skenidium Hall, 1860a, p. 70 [**Orthis insignis* Hall, 1859a, p. 173; SD Hall & Clarke, 1892, p. 241]. Coarsely costate to dichotomously costellate; ventral interarea usually procline, dorsal interarea vestigial; fulcral plates very wide, flat to concave, defining elongate sockets restricted to concave zones adjacent to hinge line; cardinal process ridgelike, apparently formed of upturned posteromedial edges of brachiophore plates, not continuous with dorsal median septum. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian):* cosmopolitan.——Fig. 515,*1a–d.* **S. insignis* (Hall), Lochkovian, Albany; *a,* dorsal interior, ×6; *b,* ventral interior, ×6; *c,* posterior view of conjoined valves, ×6; *d,* dorsal exterior, ×6 (Schuchert & Cooper, 1932).

Crossiskenidium Williams & Curry, 1985, p. 237 [**C. spinosum;* OD]. Ventribiconvex, multicostellate, lamellose, lamellae fringed with flat spines especially on sides of shell; cardinal process vestigial, dorsal median partition more ridgelike, flanked by elongately oval adductor tracks with raised lateral boundaries. *Lower Ordovician (Arenig):* Ireland.——Fig. 515,*6a–c.* **C. spinosum,* Arenig, western Ireland; *a,* dorsal interior, ×14; *b,* ventral interior, ×12; *c,* dorsal view of conjoined valves, ×13 (Williams & Curry, 1985).

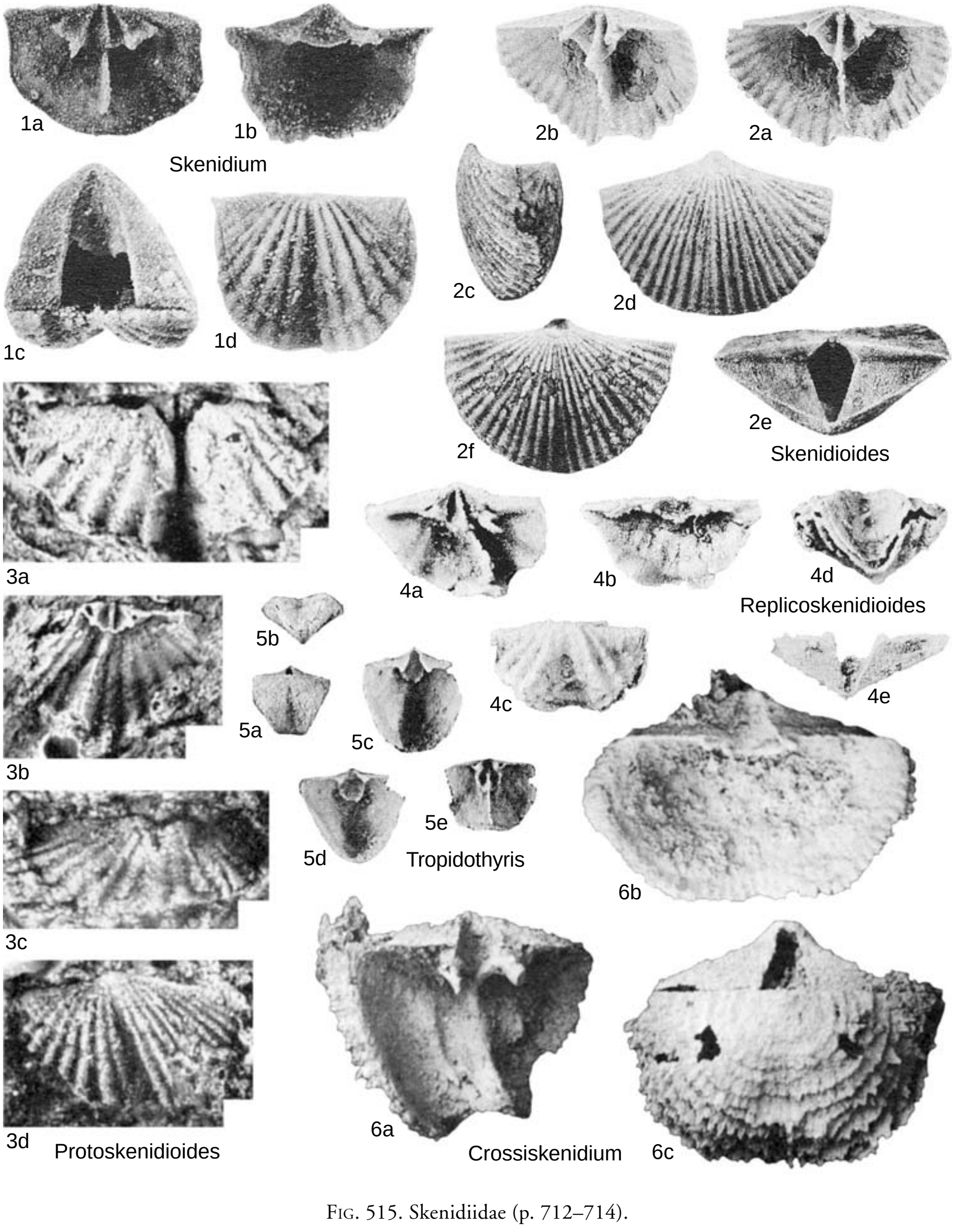

FIG. 515. Skenidiidae (p. 712–714).

Protoskenidioides WILLIAMS, 1974, p. 83 [**P. revelata;* OD]. Usually planoconvex, mucronate, sharply unisulcate, costate; dorsal interarea short, planar; cardinal process ridgelike, formed by coalescence of posteromedial edges of brachiophore plates during early stages of growth; dorsal adductor field bounded laterally by curved ridges, divided by median septum into 2 elongated oval impressions. *Lower Ordovician (Arenig):* Great Britain, eastern China, Ireland.——FIG. 515,*3a–d*. **P. revelata,* Arenig, Shelve; *a,* internal mold of dorsal valve, ×12.4; *b,* rubber replica of dorsal interior, ×9; *c,* internal mold of ventral interior, ×15; *d,* rubber replica of dorsal exterior, ×12.5 (Williams, 1974).

Replicoskenidioides POTTER, 1990b, p. 11 [**R. rodneygreggi;* OD]. Similar to *Skenidioides* but ventribiconvex, ramicostellate; brachiophore plates parallel or divergent. *Upper Ordovician (Ashgill):* western North America.——FIG. 515,*4a–e*. **R. rodneygreggi,* Ashgill, western North America; *a,* dorsal interior, ×7; *b,* ventral interior, ×7; *c,d,* normal, anterior views of dorsal exterior, ×8; *e,* posterior view of ventral valve, ×7 (Potter, 1990b).

Skenidioides SCHUCHERT & COOPER, 1931, p. 243 [**S. billingsi;* OD]. Usually planoconvex, coarsely costellate; ventral interarea apsacline to catacline; cardinal process commonly differentiated into shaft and compressed myophore and continuous with median septum that bisects sporadically impressed, subequal quadripartite dorsal adductor scars. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian):* cosmopolitan.——FIG. 515,*2a–f.* **S. billingsi,* Caradoc, Quebec; *a,b,* normal, oblique views of dorsal interior, ×4; *c,d,* lateral, ventral views of conjoined valves, ×4; *e,f,* posterior, dorsal views of conjoined valves, ×4 (Schuchert & Cooper, 1932).

Tropidothyris COOPER, 1956, p. 507 [**T. pentagona;* OD]. Subpentagonal, ventribiconvex with a tonguelike anterior commissure of deeply sulcate dorsal valve, smooth to variably plicate; dorsal interarea vestigial; cardinal process long, platelike, strongly elevated and continuous with median septum; brachiophore plates subparallel, attaching to floor of valve on either side of median septum that divides elongately oval adductor field, with anterior pair of scars larger than posterior. *Upper Ordovician (Caradoc):* eastern United States.——FIG. 515,*5a–e.* **T. pentagona,* Caradoc, Alabama; *a,b,* dorsal, anterior views of conjoined valves, ×5; *c,d,* normal, tilted views of ventral interior, ×8; *e,* dorsal interior, ×8 (Cooper, 1956).

ORTHIDA

ALWYN WILLIAMS and DAVID A. T. HARPER
[The University of Glasgow; and University of Copenhagen]

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 & HARPER, herein]

Strophic, subquadrate, unisulcate, biconvex, radially ornamented rhynchonellates with open delthyria and notothyria, apsacline ventral and anacline dorsal interareas normally short, curved; teeth simple to mainly deltidiodont with crural fossettes and normally supported by dental plates; ventral muscle field variable, impressed on valve floor, pedicle callist well developed in later stocks; elongate sockets may be delineated by fulcral plates, divergent brachiophores, as blades or rods, may be supported by variably disposed plates or accretions of secondary shell, notothyrial platform vestigial to well developed, cardinal process ridgelike becoming differentiated into myophore and shaft; ventral canal system typically saccate with divergent *vascula media,* dorsal canal system saccate, digitate, or lemniscate. *Lower Cambrian–Upper Permian (Tatarian).*

The Orthida, as here delineated by the 42 sets of character states listed in Table 17 (see p. 720), are an assemblage of extinct Paleozoic stocks that include the oldest known rhynchonellate brachiopods. They were especially prolific during the Cambrian and Ordovician and became so diversified as to anticipate many of the morphological characteristics of other rhynchonellates. Many of these orthide stocks, however, were short-lived deviations from a small number of persistent lineages that typify the 4 superfamilies of the order. Moreover, the differences between the orthoid *Orthambonites* (Fig. 516) and the dalmanelloid *Howellites* (Fig. 517), which display the most commonly occurring characteristics of their respective superfamilies, involve a minority of features so that a representative orthide can be defined.

The exterior of a typical member of the Orthida is quite distinctive. The shell is biconvex and subquadrate in outline with a maximum width anterior of a well-developed hinge line and a curved apsacline ventral interarea that is longer than the anacline dorsal interarea. A strong, median dorsal sulcus is normally present and the shell surface is usually costellate. Variations include the convexoconcave profile of many plaesiomyids, the bilobed outline of *Dicoelosia,* the reduced or mucronate hinge lines respectively of *Angusticardinia* and *Platystrophia,* the obsolescent interareas of *Productorthis,* the dorsal median fold of both *Platystrophia* and *Enteletes,* the latter with its additional superimposed radial plications, and the occurrence of hollow ribs (aditicules) among dalmanellidines and plectorthoids. The most important external distinctions, however, are the strophic hinge line and the open delthyrium and notothyrium. Chilidial-like structures are known in some hesperonomiids, productorthids, and plaesiomyids; and deltidial plates were variably developed in a few independent stocks such as *Trematorthis, Barbarorthis,* and *Phragmophora;* but the latter structures are not homologous with the strophomenate pseudodeltidium.

Basic similarities are also evident in the impressions of muscle attachment areas and mantle canals. The orthide ventral muscle impressions are normally subtriangular to bilobed in outline and confined to the posterior half of the ventral valve (Fig. 516–517). The umbonal chamber never accommodated the base of the pedicle as in other, later rhynchonellates. It was occupied solely by the muscle system up to a variably developed pedicle callist, by which the cuticle of a flat-based pedicle was evidently attached to the ventral valve. The median adductor scars were normally not enclosed anteriorly and the adjustors and lateral diductor lobes were inserted on the inner surfaces of the dental plates (Fig. 517). There is, however, great variation in the outline of the ventral muscle scars reflecting their differential development, especially the relationship between the adductor and adjacent diductor components. Moreover, outlines can vary with the age as well as the curvature of the valve (Williams & Wright, 1963, p. 18). Even so, there are several kinds of outlines that are stable and distinctive enough to be used to discriminate genera (Fig. 518).

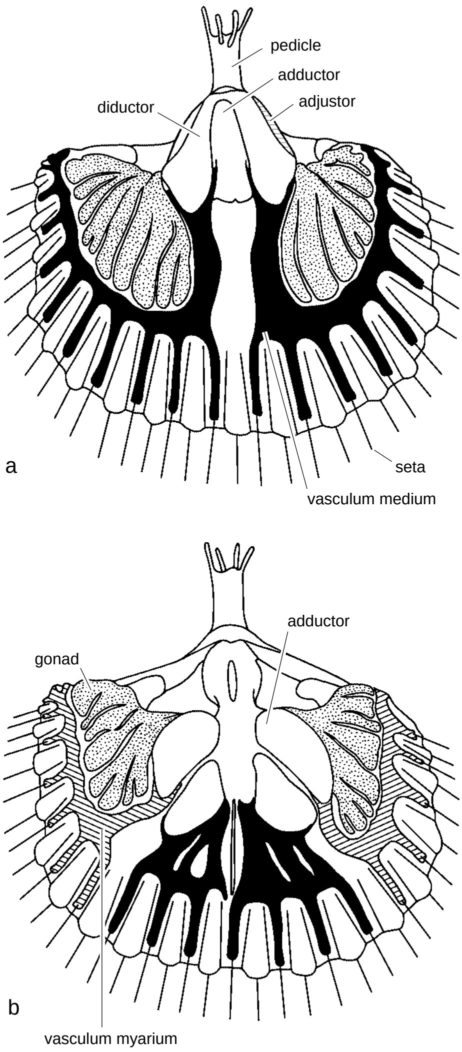

Fig. 516. *Orthambonites;* stylized reconstruction of inferred morphology of soft parts viewed from *a,* ventral and *b,* dorsal exteriors (adapted from Williams & Wright, 1965).

The adductor impressions on the floors of the orthide dorsal valves are also variable in outline although they are essentially quadripartite and consist of a pair of posterior and anterior scars on either side of a variably developed median ridge. The ridge was built up as a low anterior extension of the notothyrial platform or convergent brachiophore plates. Sporadically it culminated in a high median septum, as in the phragmorthids, cremnorthids, and kayserellids. In such stocks as these, the median septum effectively divided the mantle cavity into two compartments, each of which presumably contained a brachium. Irrespective of the nature of the median partition the overall outline of the dorsal

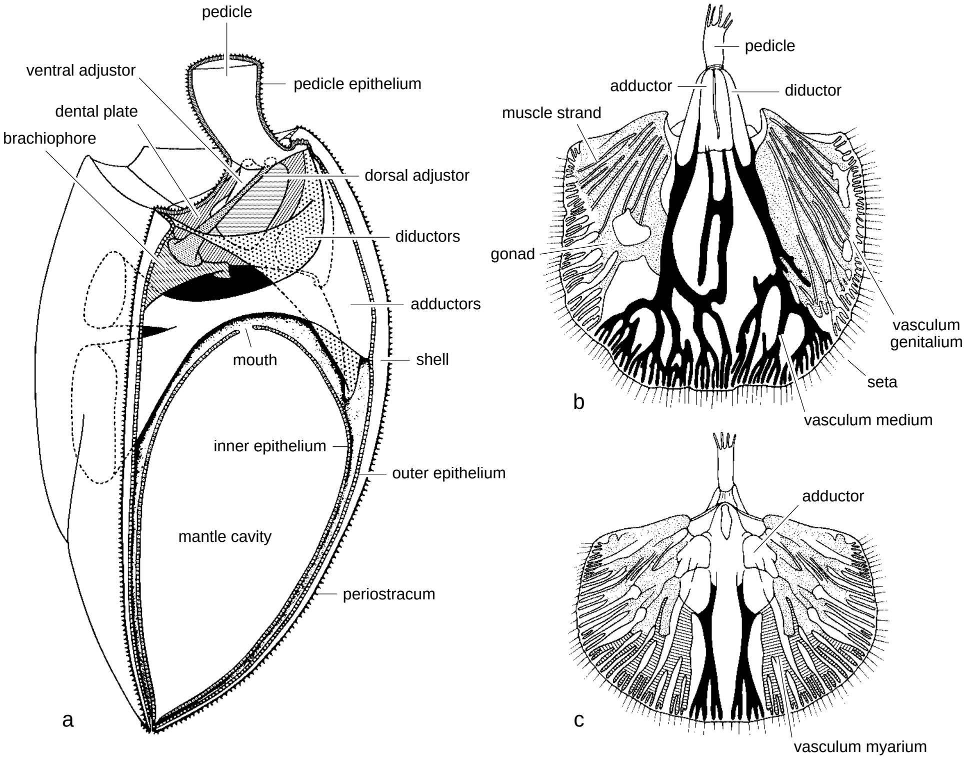

Fig. 517. *Howellites; a,* stylized reconstruction of musculature; inferred morphology of soft parts viewed from *b,* ventral and *c,* dorsal exteriors (Williams & Wright, 1963).

adductor field can vary significantly; especially in the relative sizes of individual scars, and the main changes are used to discriminate genera.

Despite the variation that is known to have occurred in the mantle canal systems of the Orthida, one of the least specialized patterns, comprising saccate and digitate distributions in the ventral and dorsal valves respectively, is the most common among early orthoids (Fig. 516). A lemniscate arrangement in both valves, on the other hand, is prevalent among the dalmanelloids and enteletoids (Fig. 517). Yet these differences between superfamilies are not mutually exclusive. The ventral and dorsal patterns of the dalmanelloid paurorthids, for example, are saccate and digitate like most orthoids, while those of the finkelnburgiids (digitate and digitate) and some plectorthids (saccate and digitate but with the gonads pervading the entire mantles) approach the enteletoid condition.

The most important changes affecting internal morphology were those that led to the diversification of the articulatory devices involving the ventral teeth and dorsal cardinalia. The teeth of Cambrian orthides are typically deltidiodont but are grooved by crural fossettes in later stocks. The brachiophores defining the sockets may be rods or blades proximally encased in a notothyrial platform as in most orthoids, or supported by plates reaching to the floor of the dorsal valve as in plectorthoids and most punctate groups. The brachiophore plates together with fulcral plates define sockets that are distally elevated above the floor of the dorsal valve. The disposition of the brachiophore plates can vary greatly even within a series of such closely related genera as those assigned to the Dalmanellidae. Using members of this

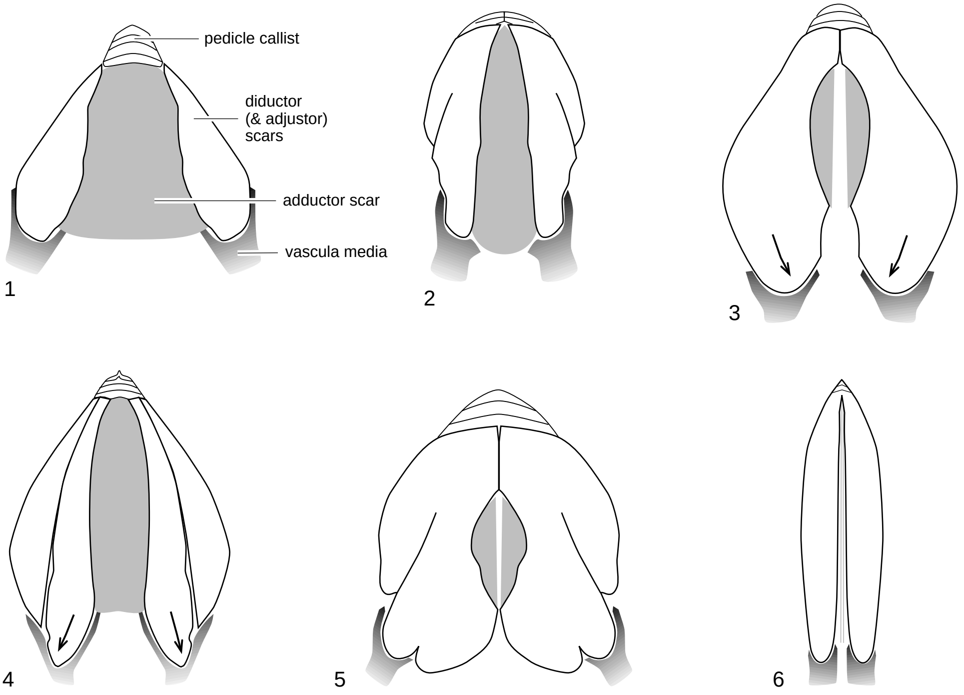

FIG. 518. Outline of orthide ventral muscle scars; *1,* subtriangular as in *Cremnorthis*; *2,* suboval (*Glyptorthis*); *3,* cordate (*Hesperorthis)*; *4,* bilobed (*Dalmanella*), which may be expanded anteriorly as extended lobes; *5,* subquadrate to flabellate (*Plaesiomys*); *6,* linear (*Enteletes*) (new).

family, it is possible to demonstrate a continuous gradient of change between arrangements in which the angle subtended by the brachiophore bases is significantly less or greater than that subtended by the tops of the brachiophores. Hence, although *Bancroftina, Dalmanella,* and *Howellites* are each characterized by a distinctive attitude, the last two genera together include species showing every conceivable variation in the disposition of the bases relative to the top of the brachiophores (Fig. 519). Generally, however, their attitude tends to be consistent in different stocks, so that they may converge onto a median septum to form a septalium, as in *Linoporella,* or be widely divergent, as in *Enteletes.*

The brachiophores may be prolonged distally as processes in attitudes suggesting their having supported the mouth segment of the lophophore. These elaborations are rare and are well exemplified by the brachiophore extensions of *Enteletes* and *Phragmorthis,* which evolved independently of one another and of the crura of later rhynchonellates.

There are important differences in the origin and function of the diverse structures, collectively referred to as the cardinal process, that project posteriorly from the notothyrial platform. The lack of such outgrowths is relatively rare and presumably represents the ancestral condition. Yet it is characteristic of species of the Ordovician punctate *Paurorthis,* while well-developed processes are found in such Cambrian stocks as the eoorthid *Jivinella* and the orthoid bohemiellids. In most orthoids, the most common type of cardinal process consists of a median partition that effectively divides the posterior surface of the notothyrial platform into two halves, each of which received the dorsal ends of the diductor muscles. In a few stocks (e.g., *Dolerorthis* and *Hesperonomia*), the notothyrial areas flanking the median partitions developed into ridges for reception of the diductor bases, and in the orthidiellids these grew high and became fused with the median partition to form a trilobed process. In most plectorthoids, however, further modification involved the migration of the diductor bases onto the posterolateral surfaces of the median partition which, in consequence, is either indented by muscle impressions, as in some plectorthids, or, more commonly, is differentiated into a bulbous crenulated myophore surmounting a thickened shaft, as in many plaesiomyids. This latter arrangement is prevalent among punctate orthides with the myophore mostly fashioned in a bilobed or trilobed manner, thereby separating the diductor bases from each other.

The orthide shell succession appears to have been homologous with that of living rhynchonellides with a banded, calcitic primary layer (normally recrystallized) and a secondary layer composed of orthodoxly stacked fibers ensheathed in glycoproteinaceous membranes. In post-Cambrian times, however, orthides with punctate shells appeared and were the sole representatives of the order in the Late Paleozoic. Orthide punctae with their subconical distal ends are structurally similar to the endopunctae of the later rhynchonellates except that no perforated calcitic canopies to the canals have yet been found. Until the inferred homology of all punctation has been ultrastructurally investigated it still seems better to assume that the punctation of the orthide shell was a single transformation.

Indeed, preliminary study indicates that there is no significant difference in the punctation of the Early Ordovician dalmanelloid *Paurorthis* and the Early Carboniferous dalmanelloid *Rhipidomella* (Fig. 520). The

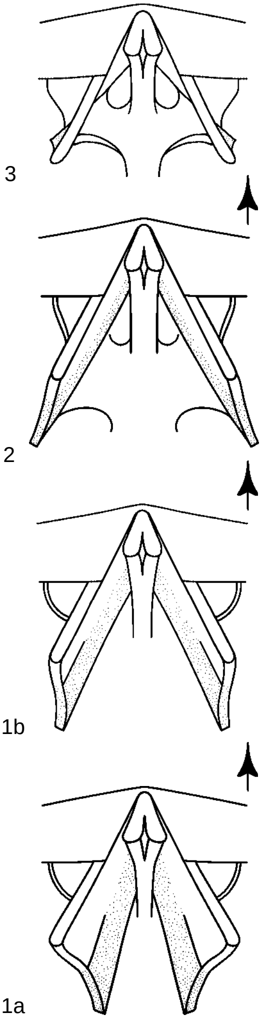

FIG. 519. Evolution of dalmanelloid cardinalia involving lateral migration of brachiophore plates (*shaded*) from *1a, Dalmanella,* subtending an angle significantly less than that between tops of brachiophores to *1b,* a not significantly smaller angle, to *2, Howellites,* a not significantly greater angle, and to *3, Bancroftina,* a significantly greater angle (adapted from Williams & Wright, 1963).

FIG. 520. *1a–c,* Punctae in the fibrous secondary shell, *Paurorthis parva* (PANDER), Lower Ordovician, Volkovian Stage, St. Petersburg, Russia; *1a,b,* internal, sectional fracture surfaces showing punctae, ×560, ×940; *1c,* fracture section of costa showing calcitic infills of aditicular hollows, ×240; *2a,b, Rhipidomella* sp., Lower Carboniferous, Lower Limestone Group, near Glasgow, Scotland; internal, sectional fracture surfaces showing punctal infills and punctal hollow in relation to fibers, ×700, ×1700; *3a–c, Schizophoria resupinata* (MARTIN), Lower Carboniferous, Lower Limestone Group, Ayrshire, Scotland; *3a,* external surface showing recrystallized primary layer and infill tops of punctae, ×380; *3b,* punctal infill partly covered by fibers, ×700; *3c,* punctal hollow bounded by outwardly deflected fibers, ×900 (new).

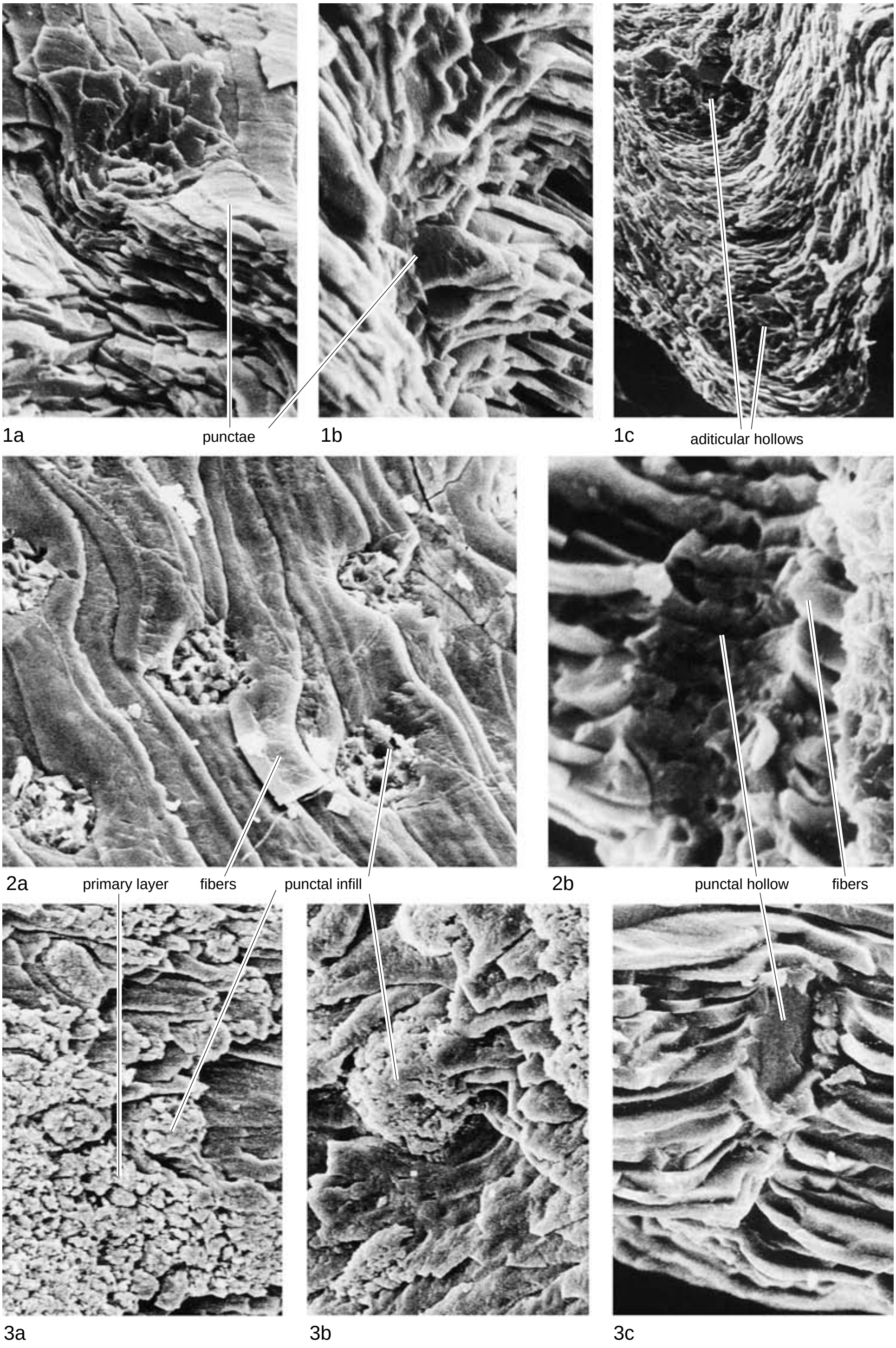

Fig. 520. *For explanation, see facing page.*

TABLE 17. States of 42 characters used in analyses of order Orthida (new).

SHELL STRUCTURE

1. secondary layer: fibrous (0); cross-bladed laminar (1); foliated (2).
2. punctation: impunctate (0); endopunctate (1).
3. aditicules: absent (0); present (1).

SHELL SHAPE

4. outline: subcircular (0); subquadrate (1); transversely semioval (2); elongately semioval (3); variable (4); rostrate (5); cordate (6); bilobed (7).
5. cardinal extremities: variable (0); rectangular to obtuse (1); acute (2); mucronate (3).
6. shell size: small (0); variable (1); large (2).
7. profile (long.): biconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); concavoconvex (4); convexiconcave (5); resupinate (6); geniculate (7); variable (8).
8. profile (trans.): rectimarginate (0); unisulcate (1); sharply unisulcate (2); uniplicate (3); sharply uniplicate (4); multiplicate (5); strangulate (6); variable (7).

ORNAMENTATION

9. radial: smooth (0); costate (1); coarsely costellate (2); ramicostellate (3); fascicostellate (4); multicostellate (5); parvicostellate (6).
10. capillae: absent (0); sporadically present (1); present (2).
11. concentric: growth lines (0); imbricate (1); lamellose (2); spiny lamellose (3); nodular lamellose (4); filate (5); cancellate (6).
12. superficial: absent (0); honeycomb (1); pustulose (2); radiating pits (3).

DELTHYRIUM AND NOTOTHYRIUM

13. delthyrial angle: absent (0); vestigial (1); widely divergent (2); subparallel to narrowly divergent (3).
14. delthyrial cover: open (0); apical deltidium (1); deltidial plates (2); deltidium (3); pseudodeltidium (4).
15. foramen: delthyrial (0); apical (1); supra-apical (2); ventral (3); vestigial (4).
16. pedicle callist: absent (0); present, adnate (1); present as apical plate (2).
17. notothyrial angle: absent (0); vestigial (1); widely divergent (2); subparallel to narrowly divergent (3).
18. notothyrial cover: open (0); antigydium (1); chilidial plates (2); chilidium (3); grooved plates (4).

CARDINAL AREAS

19. ventral: absent (0); vestigial (1); short, curved (2); long, curved (3); short, straight (4); long, straight (5); ginglymus (6); variable (7); subpyramidal (8).
20. inclination (ventral): absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6).
21. dorsal: absent (0); vestigial (1); short, curved (2); long, curved (3); short, straight (4); long, straight (5).
22. inclination (dorsal): absent (0); anacline (1); orthocline (2); apsacline (3); catacline (4); procline (5); hypercline (6).

ARTICULATION

23. teeth: absent or rudimentary (0); deltidiodont (1); deltidiodont with crural fossettes (2); transverse (3); cyrtomatodont (4).
24. dental plates: absent or rudimentary (0); recessive (1); projecting (2); parallel (3); convergent (4); divergent (5); present or absent (6); replaced by free spondylium (7).
25. sockets: absent (0); present (1); rounded (2); elongate (3); parallel to hinge line (4); with hinge plate (5).
26. socket buttresses: absent (0); socket ridges as rods (1); socket ridges as blades (2); brachiophores as nubs (3); brachiophores as rods (4); brachiophores as blades (5); brachiophores with bases (6); brachiophores with fulcral plates (7); brachiophores with bases and fulcral plates (8).
27. brachiophores: absent (0); socket blades or rods (1); parallel or slightly divergent rods (2); widely divergent rods (3); parallel or slightly divergent blades (4); widely divergent blades (5); parallel, long blades (6); hooked to sigmoidal plates (7).
28. brachiophore plates: absent (0); parallel (1); convergent (2); as septalium (3); divergent (4); convergent, recessive (5).
29. fulcral plates: absent (0); present (1).

MUSCULATURE

30. ventral scars: umbonal (0); suboval to subtriangular (1); cordate (2); bilobed (3); extended (4); quadrate to flabellate (5); linear (6); on spondylium (7).
31. ventral muscle supports: unsupported (0); on spondylia, simplex, duplex, or triplex (1); on cella (2); on free spondylium (3).
32. median ridge: absent (0); present (1); grooved (2); double ridge (3); tonguelike (4); forked (5); septum (6).
33. raised ventral scars: impressed on valve floor (0); on callus or pseudospondylium (1); on raised structure (2).

TABLE 17. *(Continued).*

34. dorsal adductor scars: quadripartite (0); linear as in *Nisusia* (1); petaloid with anterior pair inserted between posterior pair as in *Finkelnburgia* (2); dispersed as in the widely separated adductor scars of *Wimanella* (3).
35. quadripartite scars: not quadripartite (0); quadripartite subequal (1); posterior pair larger than anterior (2); anterior pair larger than posterior (3); bilobed anterior pair larger than posterior (4).
36. notothyrial platform: absent or rudimentary (0); transverse plate (1); platform (2); platform with notothyrial ridges (3).
37. cardinal process: absent or rudimentary (0); median ridge (1); shaft or shaft with myophore (2); bilobed (3); trilobed (4); fused with notothyrial ridges (5); not fused with notothyrial ridges (6); variable (7); composed of convergent brachiophore plates (8).
38. myophore of cardinal process: undifferentiated (0); differentiated (1); cleft (2); swollen (3); crenulated (4).
39. median partition: absent or indistinct (0); ridge (1); septum (2); partition (3).
40. subperipheral rim: absent (0); present (1).

MANTLE CANALS

41. ventral systems: saccate with convergent *vascula media* (0); saccate with divergent *vascula media* (1); digitate (2); lemniscate (3); pinnate (4).
42. dorsal systems: saccate (0); digitate (1); lemniscate (2); pinnate (3); apocapate (4).

fibrous walls of punctae in the secondary shell of *Paurorthis* appear to be more steeply inclined externally than those of *Rhipidomella.* This difference, however, could be related to the more lathlike fibers of the Ordovician genus because the canals of both are more or less equispaced at about 50 µm and range between 9 and 14 µm in diameter. As shown in *Paurorthis* (Fig. 520.1a–c), punctae are immediately distinguishable from the larger, horizontally disposed aditicules.

Punctation of the enteletoid *Schizophoria* (Fig. 520.3a–c) appears to be homologous with that of the dalmanelloids (Fig. 520.2a,b). The Carboniferous specimens studied were well enough preserved to retain a recrystallized patina on the exterior of the shells underlain by fibrous secondary layer. The patina is assumed to be recrystallized primary layer, through which the distal ends of punctal infills penetrate (Fig. 520.3a). This relationships suggests that, in life, the punctae were not covered by canopies of primary shell, only by an organic plug, possibly little more than the periostracum. In some specimens, the distal ends of fibers partly cover punctal infills (Fig. 520.3b). It is, however, doubtful whether this arrangement is indicative of the closure of some punctae within the fibrous secondary layer. The outward deflection of fibers delineating punctae (Fig. 520.3c) could simulate partial closure in transverse sections.

The erection of the 300 or so orthide genera currently in circulation has involved the diagnostic use of almost every aspect of shell morphology and structure. In the classification adopted here, 42 character sets have been phylogenetically analyzed to establish an intraordinal hierarchy for all recognized genera (Table 17). This was done in stages. First, each traditional family grouping of genera was analyzed to determine their phylogenetic homogeneity. Excluded genera were then repeatedly analyzed with other families in order to identify the suprageneric taxa, with which they have closest morphological affinities. Finally, all such suprageneric taxa, represented by their internal nodes, were assembled into two cladograms that became the basis of the present infraordinal classification (Fig. 521–522).

All impunctate suprageneric units, including the Protorthidae and Skenidiidae, were analyzed using the nisusiids as the outgroup. Three clades resulted: one representing the Protorthida and the other two a dichotomy of the orthidines (Fig. 521). This is more or less consistent with a division of the orthidines into orthids and plectorthids, in the wide sense, groups that have long been distinguishable especially in the relative

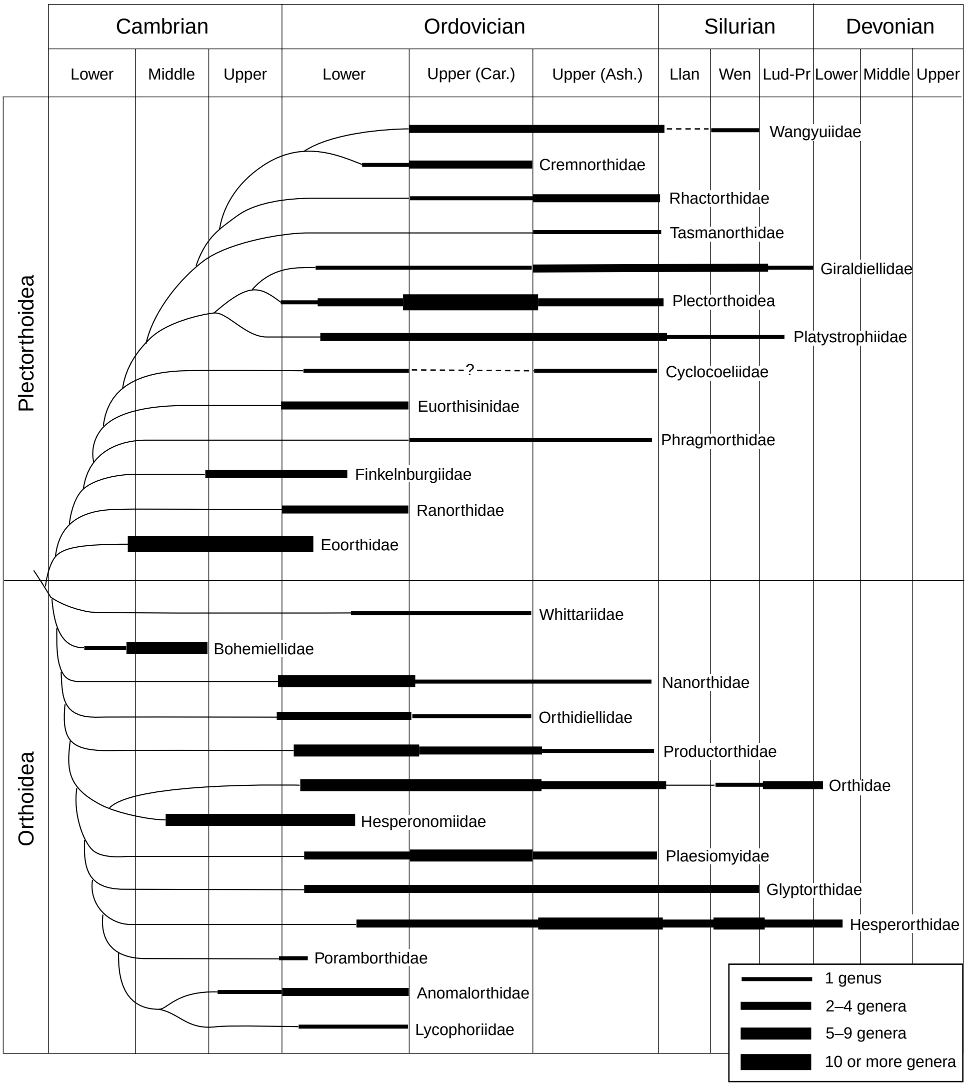

FIG. 521. Cladogram adapted to show chronostratigraphic distribution of constituent orthidine families; the Caradoc (*Car.*) and Ashgill (*Ash.*) series of the Upper Ordovician have been distinguished; the Silurian has been divided into its series: *Llan,* Llandovery; *Wen,* Wenlock; *Lud–Pr,* Ludlow–Přídolí (new).

complexity of the plectorthid cardinalia. Such a grouping can be accommodated within a widely recognized hierarchy consisting of the suborder Orthidina (first proposed by SCHUCHERT & COOPER, 1932, p. 43) and two constituent superfamilies, the Orthoidea (first proposed as Orthacea by WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147) and the Plectorthoidea (first proposed by HAVLÍČEK, 1977a, p. 75).

All punctate suprageneric units were analyzed using the plectorthid node as the outgroup (Fig. 522). On morphological grounds, this was an appropriate choice; indeed, HAVLÍČEK (1977a, p. 54) identified the nanorthids as ancestral to the dalmanellids. Two well-defined clades emerged, with the paurorthids forming a possible sister group. The clades aggregate around the dalmanellids and the draboviids. The latter are distin-

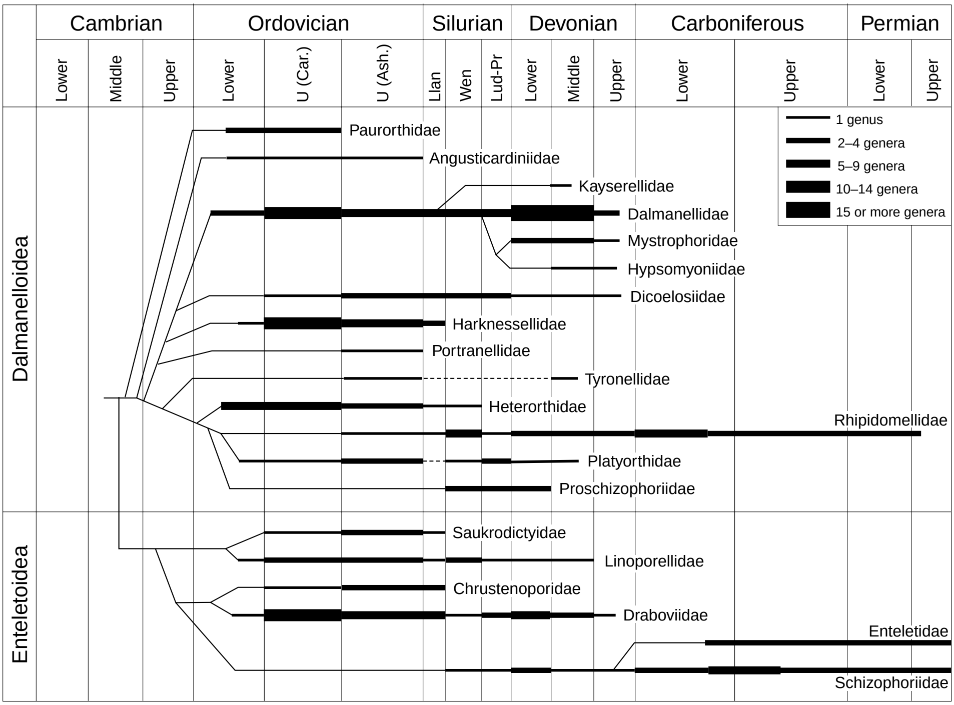

FIG. 522. Cladogram adapted to show chronostratigraphic distribution of constituent dalmanellidine families (new).

guished by their poorly developed notothyrial platform, convergent brachiophore plates, and a relatively simple cardinal process. This grouping is compatible with a hierarchy within the suborder, Dalmanellidina (first proposed by MOORE in MOORE, LALICKER, & FISCHER, 1952), which is composed of the two superfamilies, Dalmanelloidea (first proposed by SCHUCHERT & COOPER, 1931, p. 245) and Enteletoidea (first proposed by ALICHOVA, 1960, p. 193).

The relationship among the orthide superfamilial units was assessed by comparing the nodal codes for the four superfamilies with the nisusiids and protorthides as outgroups. The impunctate and punctate orthides formed two distinct clades, which validated the assignment of these superfamilies to suborders.

This classification is not truly phylogenetic as it has not been possible to identify and allow for all the homoplasy that must have contributed to the evolution of the orthide shell. The repeated lengthening of the ventral muscle scars is an obvious example of a convergence that cannot easily be categorized for phylogenetic analysis. It is also noteworthy that the sudden appearance of mature stocks in the geological record, as it is presently known, occurred during periods of active plate tectonics. Thus difficulties in assigning, for example, the portranellids and tyronellids within the dalmanelloid clade are more likely to reflect their cryptic appearance in the Late Ordovician than a close common ancestry; while the linoporellids and saukrodictyids were also probably enteletoid latecomers with articulatory devices and cardinalia that have been modified by the abnormal growth of the cardinal areas in the former and the development of spike-like brachiophores and a septalium in the latter. Notwithstanding the complications such factors impose on attempts to trace orthide phylogeny, familial groupings have been improved by these analyses, which have also eliminated some of the more contrived aspects of previous classifications.

Suborder ORTHIDINA Schuchert & Cooper, 1932

[*nom. correct.* WILLIAMS & WRIGHT, 1965, p. 300, *pro* Orthoidea SCHUCHERT & COOPER, 1932, p. 43; *emend.,* WILLIAMS & HARPER, herein]

Essentially same range and variability of characters as for Orthida but having impunctate shell with fibrous secondary layer. *Lower Cambrian–Lower Devonian (Emsian).*

Superfamily ORTHOIDEA Woodward, 1852

[*nom. correct.* herein *pro* Orthoidea, *nom. transl.* WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147, *ex* Orthidae WOODWARD, 1852, p. 229]

Typically medium-sized, unisulcate, radially ornamented, and filate orthides with wide, open delthyrium and notothyrium and curved apsacline ventral and anacline dorsal interareas; teeth variable but commonly deltidiodont with crural fossettes, supported by dental plates, normally recessive; ventral muscle scar variable in outline rarely impressed on pseudospondylium, pedicle callist normally preserved; notothyrial platform commonly strongly developed, supporting typically ridgelike cardinal process and variably disposed rodlike or bladelike brachiophores to form elongate sockets and extending anteriorly as dorsal median ridge bisecting dorsal adductor field that is essentially subequally quadripartite; ventral and dorsal mantle canal systems normally saccate and digitate respectively. *Lower Cambrian–Lower Devonian (Emsian).*

Family ORTHIDAE Woodward, 1852

[Orthidae WOODWARD, 1852, p. 229]

Variable size, generally subquadrate with obtuse cardinal extremities, ventribiconvex orthoids, apsacline ventral interarea mainly short and curved, anacline dorsal interarea, shorter but more variable; dental plates recessive, ventral muscle field varying from suboval with broad, poorly differentiated adductor track at least as long as flanking diductor scars to subcordate with elongate diductor scars extending anteriorly beyond relatively narrow adductor track impressed on valve floor about low median ridge; cardinal process ridgelike; brachiophores normally short, rodlike, moderately divergent; dorsal adductor scar quadripartite, variably impressed on either side of low median ridge and normally with larger anterior pair; ventral mantle canal system saccate, *vascula media* normally divergent; dorsal mantle canal system normally digitate. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian).*

Orthis DALMAN, 1828, p. 93 [**O. callactis* DALMAN, 1828, p. 112; SD DAVIDSON, 1853, p. 101]. Large, planoconvex to weakly concavoconvex, rectimarginate, costate, and capillate; ventral muscle scar suboval, brachiophores widely divergent rods; ventral *vascula media* parallel proximally. *Lower Ordovician (Arenig–Llanvirn):* Baltoscandia.——FIG. 523,*3a–g.* **O. callactis* DALMAN, Arenig–Llanvirn, Sweden; *a,* dorsal exterior, ×2.5; *b,* dorsal interior, ×2; *c–e,* dorsal, ventral, lateral views of conjoined valves, ×2; *f,* ventral interior, ×1; *g,* details of capillate ornament, ×10 (Jaanusson & Bassett, 1993).

Diochthofera POTTER, 1990a, p. 58 [**D. conspicua;* OD]. Small, ventribiconvex, strangulate with sulci in both valves, fascicostellate; ventral muscle field suboval, adductor track wide, elevated on medial region of callus extending forward as low ridge; cardinal process commonly bulbous, divergent brachiophores platelike; dorsal adductor field bounded laterally by strong ridges breached by channels for *vascula media* and *myaria,* posterior pair of scars larger, deeply impressed; dorsal median ridge sporadically culminating in low crest; dorsal mantle canal system pinnate. *Upper Ordovician (Ashgill):* western USA.——FIG. 523,*2a–f.* **D. conspicua,* Ashgill, western USA; *a,b,* ventral exterior, interior, ×4; *c,d,* dorsal exterior, interior, ×5; *e,f,* dorsal exterior, interior, ×4 (Potter, 1990a).

Orthambonites PANDER, 1830, p. 80 [**Orthis calligramma* DALMAN, 1828, p. 114; SD JAANUSSON & BASSETT, 1993, p. 24–26; =*Orthambonites rotunda* PANDER, 1830, p. 82]. Similar to *Orthis* but subcircular, ventribiconvex, strongly filate, less divergent brachiophores, and lacking ventral median ridge; pedicle callist preserved. *Lower Ordovician (Arenig–Llanvirn):* Baltoscandia, Russia.——FIG. 524,*1a–f.* **O. calligramma* (DALMAN), Arenig–Llanvirn; *a–c,* dorsal, ventral, lateral views of conjoined valves, Russia, ×2; *d,* details of capillate ornament, Sweden, ×8; *e,* ventral interior, Sweden, ×2; *f,* dorsal interior, Russia, ×2 (Jaanusson & Bassett, 1993).

Orthokopis BAARLI, 1995, p. 9 [**O. idunnae;* OD]. Small, unisulcate, elongately semioval valves with costellate ornament; ventral muscle scar short, oval to subpentagonal and impressed on callus; dorsal interior with widely divergent bladelike brachiophores. *lower Silurian (Llandovery):* Norway (Oslo Region).——FIG. 523,*1a–f.* **O. idunnae,* Llandovery, Oslo Region; *a,b,* internal mold, rubber

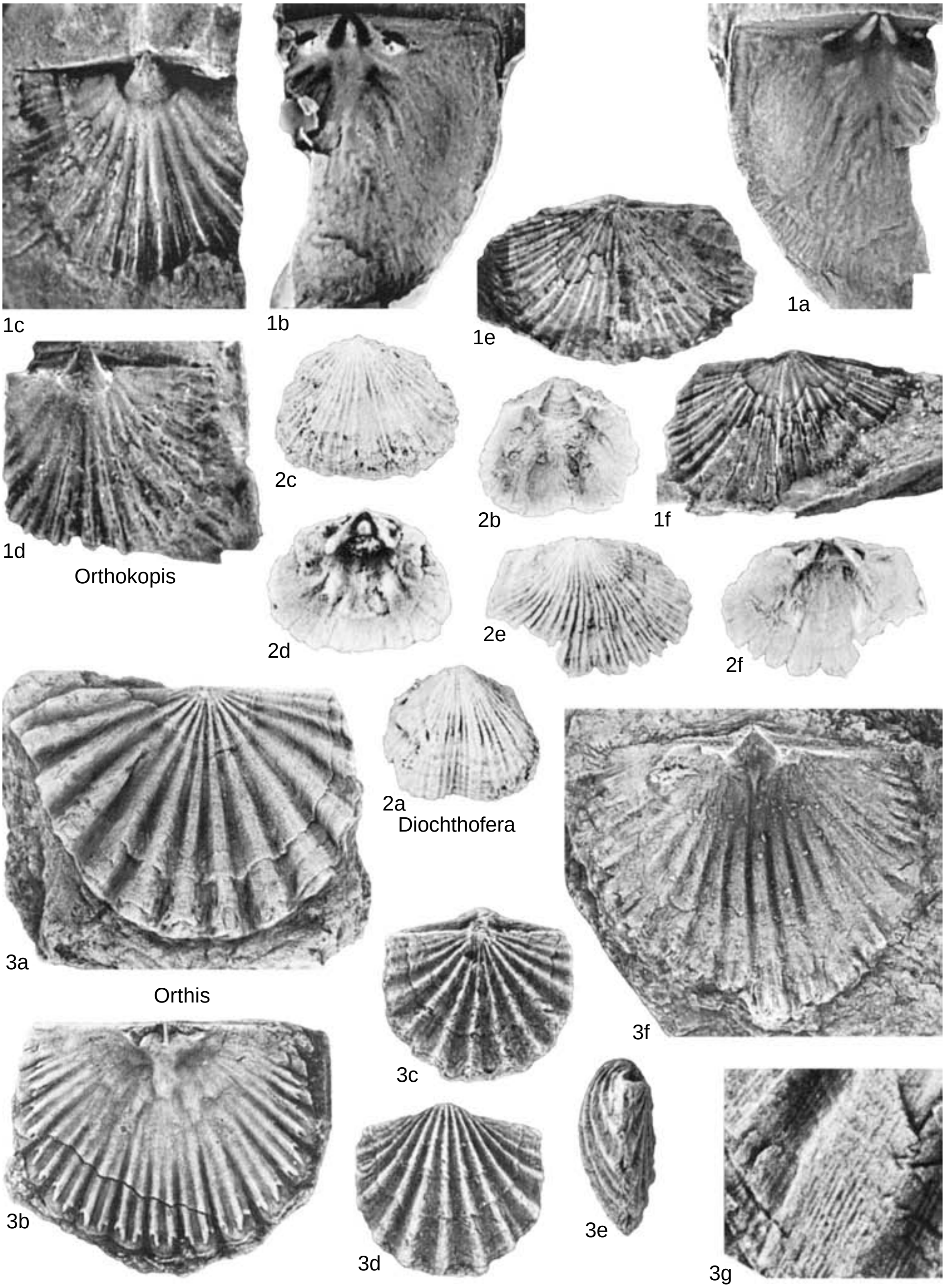

FIG. 523. Orthidae (p. 724–725).

replica of dorsal valve, ×3; *c,d,* internal mold, rubber replica of ventral valve, ×4; *e,f,* dorsal, ventral views of conjoined valves, ×3 (Baarli, 1995).

Orthostrophella AMSDEN, 1968, p. 23 [**Orthostrophia dartae* SCHUCHERT & COOPER, 1932, p. 71; OD]. Similar to *Orthostrophia* but uniplicate with

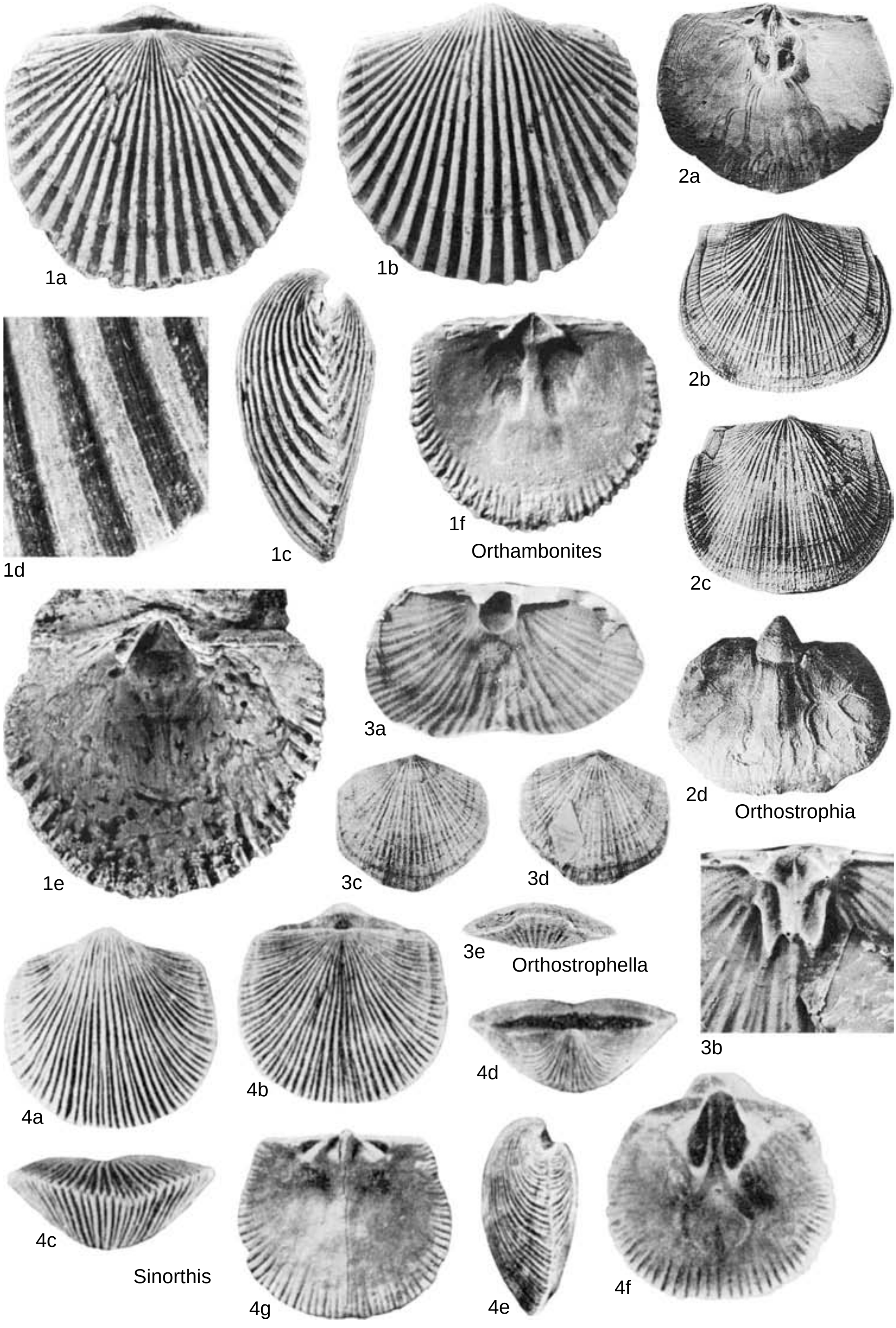

FIG. 524. Orthidae (p. 724–727).

anteriorly sulcate adult ventral valve. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian):* North America (USA, eastern Canada), Bohemia, Great Britain.——FIG. 524,*3a–e.* **O. dartae* (SCHUCHERT & COOPER), Wenlock, Quebec; *a,* rubber replica of ventral interior, ×3; *b,* rubber replica of dorsal interior, ×3; *c–e,* ventral, dorsal, anterior views of conjoined valves, ×1 (Amsden, 1968).

Orthostrophia HALL, 1883, pl. 36, fig. 32–34 [**Orthis strophomenoides* HALL, 1857, p. 46; OD]. Medium sized to large, dorsibiconvex to resupinate, unisulcate, ramicostellate; ventral muscle scar subtriangular with broadly triangular, undifferentiated adductor track; cardinal process ridgelike, occasionally flanked by pair of low notothyrial ridges; mantle canal systems of both valves normally impressed, saccate with ventral *vascula media* curving posterolaterally toward posterior part of valve and branching repeatedly toward anterior margin. [A plectorthid subfamily, the Orthostrophiinae, was erected by SCHUCHERT & COOPER (1932, p. 70) because, although the ventral musculature and cardinalia are like those of *Orthis* and *Hesperorthis,* the mantle canal systems resemble those of *Mimella.* Mantle canal systems, however, are less reliable than cardinalia in establishing stock affinities. Consequently, the subfamily was later discarded and *Orthostrophia* was assigned to the Orthinae (WILLIAMS, 1965b, p. 313). The subfamily was then rescusitated by HAVLÍČEK (1977a, p. 76) on the grounds that the cardinalia are plectorthid. That is not so for *Orthostrophia;* its relatively restricted notothyrial platform is an expression of the strong convexity of the dorsal valve.] *upper Silurian (Přídolí)–Lower Devonian (Lochkovian):* North America, Bohemia, Australia, South America (Argentina), northern China.——FIG. 524,*2a–c.* **O. strophomenoides* (HALL) Lochkovian; *a,* rubber replica of dorsal interior, New York, ×2; *b,c,* ventral, dorsal exteriors, Tennessee, ×1 (Schuchert & Cooper, 1932).——FIG. 524,*2d. O.* sp. aff. *O. strophomenoides,* Přídolí, Oklahoma; internal mold of ventral valve, ×1.5 (Schuchert & Cooper, 1932).

Paralenorthis HAVLÍČEK & BRANISA, 1980, p. 15 [**P. immitatrix;* OD]. Costate, capillate without fila; suboval ventral muscle scar lacking median ridge; brachiophores short, blunt, divergent. *Lower Ordovician (Arenig–Llanvirn):* cosmopolitan.——FIG. 525,*3a–e.* **P. immitatrix,* Arenig–Llanvirn, Bolivia; *a,* internal mold of ventral valve, ×2.3; *b,* internal mold of dorsal valve, ×4.5; *c,* internal mold of dorsal valve, ×2.3; *d,* rubber replica of dorsal exterior, ×2.3; *e,* rubber replica of ventral exterior, ×2.3 (Havlíček & Branisa, 1980).

Sinorthis WANG, 1955b, p. 327 [**S. typica;* OD] [=*Yichangorthis* ZENG, 1987, p. 214 (type, *Y. elegans*)]. Ramicostellate; dental plates narrowly divergent, flanking elongate bilobed ventral muscle scar; brachiophores widely divergent. [*Yichangorthis* ZENG, from the same stratigraphic horizon and locality as *Sinorthis,* differs only in having less well-developed brachiophores and cardinal process.] *Lower Ordovician (Arenig):* southern China, France.——FIG. 524,*4a–g.* **S. typica,* Arenig, southern China; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×3; *f,* ventral interior, ×3; *g,* dorsal interior, ×3 (Wang, 1955b).

Sivorthis JAANUSSON & BASSETT, 1993, p. 45 [**S. filistera;* OD]. Costellate and capillate with strong fila, long ventral interarea; ventral muscle scar subcordate with shallow median groove; brachiophores short; quadripartite adductor scar with larger posterior pair; ventral *vascula media* parallel proximally. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* North America, Europe.——FIG. 525,*1a–g.* **S. filistera,* Caradoc, Sweden; *a–c,* dorsal, ventral, lateral views of conjoined valves, ×3; *d,* details of ornament, ×8; *e,* ventral interior, ×3; *f,g,* dorsal interior, exterior, ×3 (Jaanusson & Bassett, 1993).

Sulcatorthis ZENG, 1987, p. 216 [**S. sulcata;* OD]. Small, subcircular, sharply unisulcate, coarsely costellate; dental plates not developed; muscle scars in both valves obscure. [This genus is based on young individuals from the Arenig. On balance the specimens have the strongest affinities with immature orthid shells rather than those of others within the orthidines.] *Lower Ordovician (Arenig):* southern China.——FIG. 525,*2a,b.* **S. sulcata,* Arenig, southern China; internal mold of ventral valve, internal mold of dorsal valve, ×10 (Zeng, 1987).

Sulevorthis JAANUSSON & BASSETT, 1993, p. 37 [**Orthis lyckholmiensis* WYSOGÓRSKI, 1900, p. 231; OD]. Small, transversely semioval with variable cardinal extremities, costate with strong fila; short, flat interareas; cardinal process differentiated into shaft and crenulated crest, divergent brachiophores bladelike, sockets deep and rounded, delineated anterolaterally by raised ridges simulating fulcral plates; ventral *vascula media* divergent, dorsal mantle canal system apocapate; radially arranged exopunctae along sides of costae. *Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill):* North America, Europe.——FIG. 526,*1a–e.* **S. lyckholmiensis* (WYSOGÓRSKI), Ashgill, Estonia; *a–c,* dorsal, ventral, lateral views of conjoined valves, ×3; *d,* details of ornament, ×12; *e,* ventral interior, ×3 (Jaanusson & Bassett, 1993).——FIG. 526,*1f. S.* sp. cf. *S. lyckholmiensis,* Ashgill, Sweden; dorsal interior, ×5 (Jaanusson & Bassett, 1993).

Taphrorthis COOPER, 1956, p. 326 [**T. emarginata;* OD]. Ramicostellate with strong fila; ventral muscle scar subcordate with low median ridge; brachiophores short, rodlike, widely divergent; quadripartite adductor muscle scars with larger anterior pair; ventral *vascula media* apparently subparallel proximally. *Upper Ordovician (Caradoc):* North America, Scotland, Ireland, Estonia, China.——FIG. 526,*2a–h.* **T. emarginata,* Caradoc; *a,b,* dorsal interior, ventral interior, Tennessee, ×2; *c–g,* posterior, anterior, lateral, ventral, dorsal views of conjoined valves, Alabama, ×1; *h,* enlarged dorsal view of conjoined valves, ×2 (Cooper, 1956).

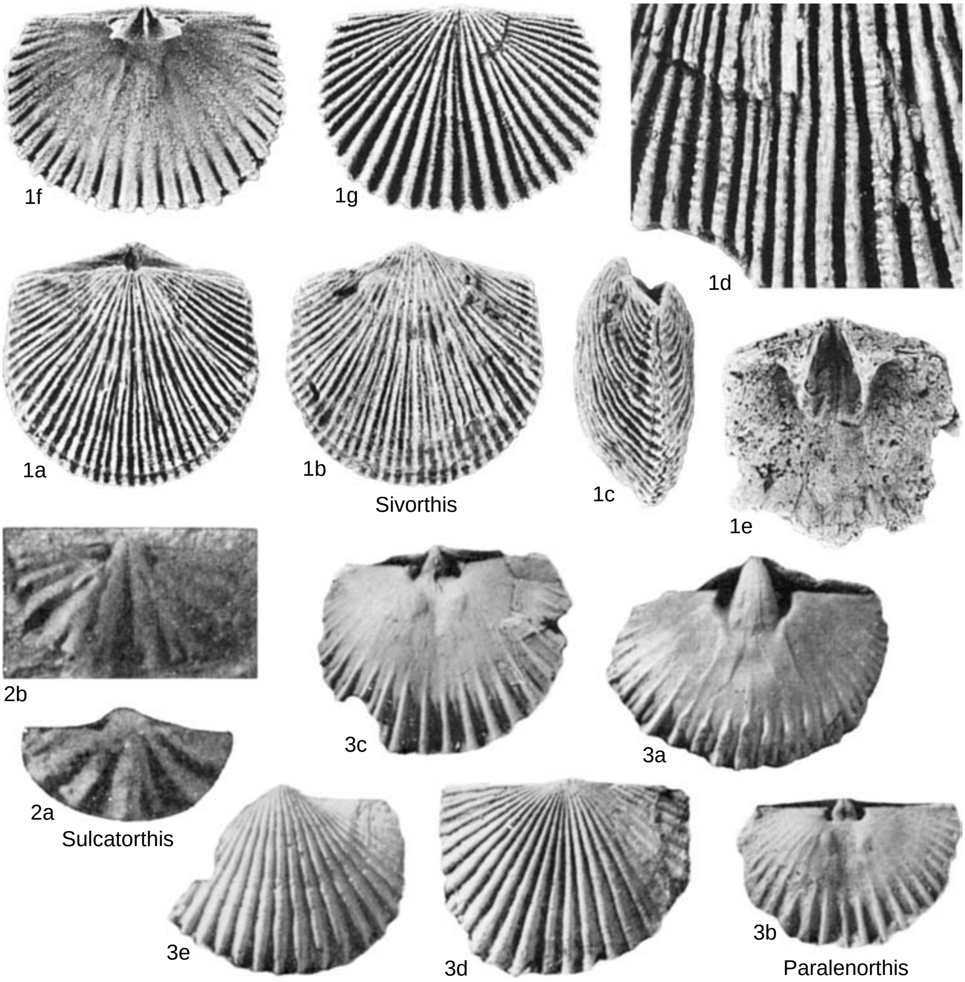

FIG. 525. Orthidae (p. 727).

Trondorthis NEUMAN in NEUMAN & BRUTON, 1974, p. 77 [**Orthambonites bifurcatus* COOPER, 1956, p. 297; OD] [=*Ocorthis* MÉLOU, 1982, p. 25 (type, *O. occitanensis*)]. Similar to *Taphrorthis* but elongately oval and without fila; ventral muscle scar suboval, without ventral median ridge. [According to the diagnoses at hand, *Ocorthis,* based on specimens from the Lower Ordovician of France (Montagne Noire), differs from *Trondorthis* only in its more subquadrate outline.] *Lower Ordovician (Arenig–Llanvirn):* North America, Baltoscandia, France, central Asia.——FIG. 526,*3a–f.* **T. bifurcatus* (COOPER), Arenig–Llanvirn, Toquima Range; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves, ×1.5; *e,* dorsal interior, ×1.5; *f,* ventral interior, ×1.5 (Neuman & Bruton, 1974).

Family ANOMALORTHIDAE Ulrich & Cooper, 1936

[Anomalorthidae ULRICH & COOPER, 1936b, p. 622] [=Alimbellidae ANDREEVA, 1960, p. 291]

Dorsibiconvex, strongly uniplicate, subquadrate orthoids with obtuse cardinal extremities; simple teeth normally without dental plates, ventral muscle scar suboval, impressed on pseudospondylium with fine median ridge, pedicle callist not developed; bladelike cardinal process and strong, outwardly curving brachiophores supported by thick notothyrial platform; quadripartite

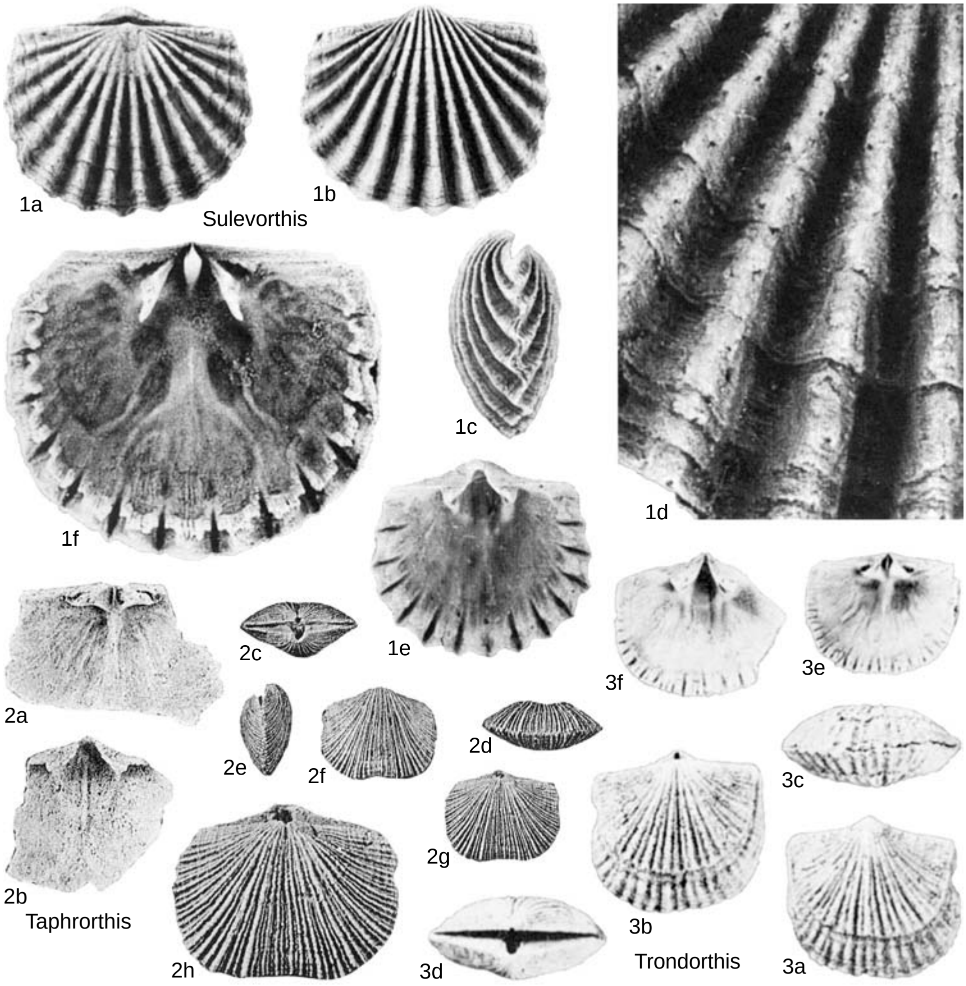

FIG. 526. Orthidae (p. 727–728).

dorsal adductor scar large, deeply impressed, commonly on elevated callus; ventral mantle canal system less commonly impressed, digitate. *Upper Cambrian–Lower Ordovician (Llanvirn).*

Anomalorthis ULRICH & COOPER, 1936b, p. 622 [**A. utahensis;* OD]. Unequally biconvex to convexoconcave, weakly uniplicate, multicostellate valves with long ventral interarea; delthyrium open with small apical plate; ventral interior with muscle scars impressed on raised callus; dorsal interior with simple ridgelike cardinal process. *Lower Ordovician (Arenig–Llanvirn):* USA (Utah, Nevada, Oklahoma, Vermont).——FIG. 527,*1a–e.* **A. utahensis,* Arenig–Llanvirn, Utah; *a–c,* exterior together with normal and tilted views of ventral interior, ×2; *d,* dorsal interior, ×2; *e,* internal mold of dorsal valve, ×2 (Ulrich & Cooper, 1938).

Alimbella ANDREEVA, 1960, p. 292 [**A. armata;* OD]. Large, smooth with some impersistent radial markings; teeth large, small rhomboidal depression anteromedianly of ventral muscle field with narrow adductor scars; brachiophores massive, encased in secondary shell defining rounded sockets; posterior pair of dorsal adductor scars larger than anterior pair. *Lower Ordovician (Tremadoc):* Russia (Urals).——FIG. 527,*2a–c.* **A. armata,* Tremadoc, Urals; *a,* ventral exterior, ×1; *b,* internal mold of ventral valve, ×1; *c,* dorsal interior, ×3 (Andreeva, 1960).

Astraborthis WILLIAMS, 1974, p. 68 [**A. uniplicata;* OD]. Medium size, subcircular with coarse, angular

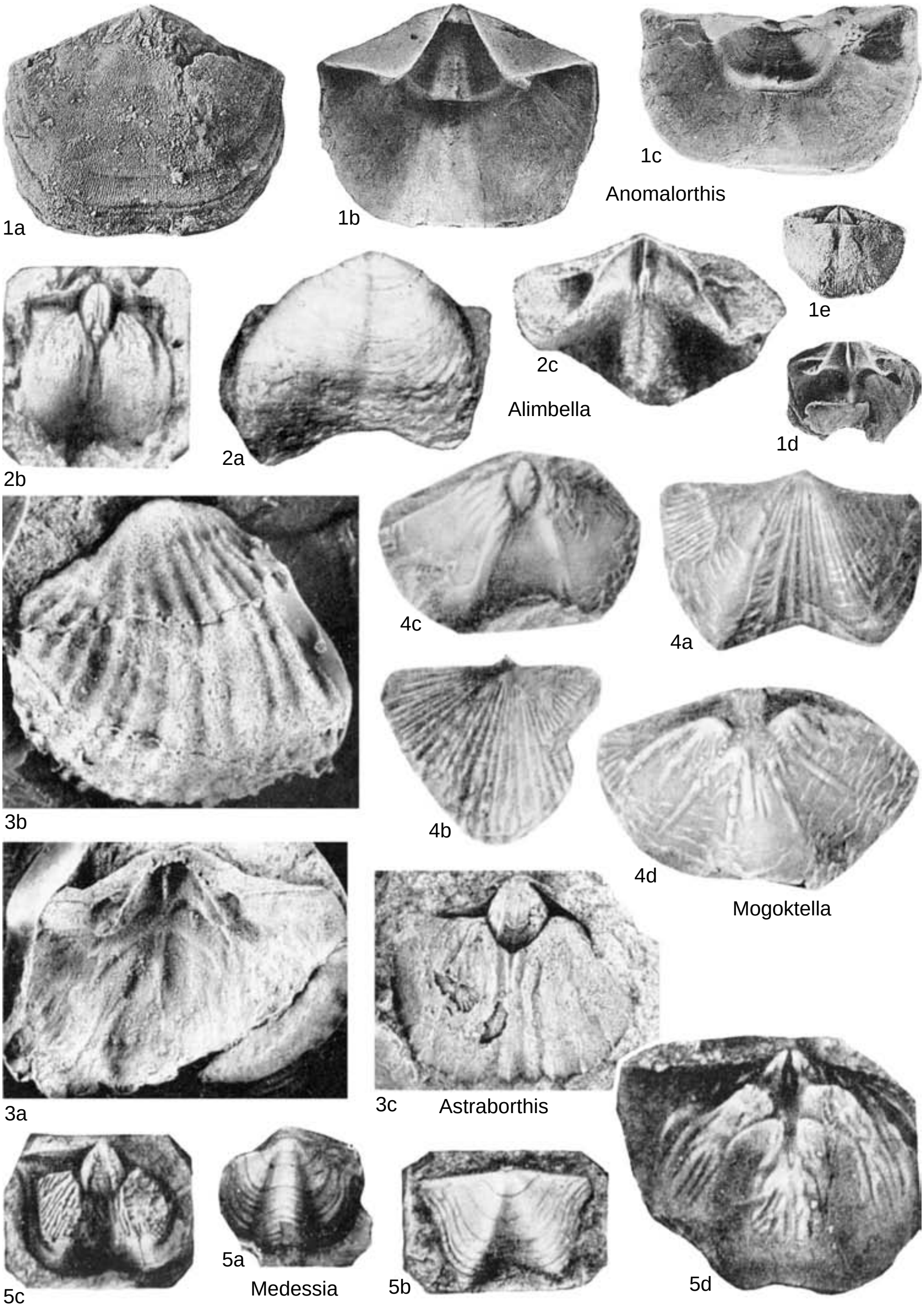

FIG. 527. Anomalorthidae (p. 729–731).

costellae; ventral muscle field with relatively broad, medially divided adductor scars; bilobed anterior pair of dorsal adductor scars larger than posterior pair. *Lower Ordovician (Arenig):* Great Britain.——FIG. 527,*3a–c.* **A. uniplicata,* Arenig, Shelve; *a,* rubber replica of dorsal interior, ×4; *b,* rubber replica of dorsal exterior, ×4.7; *c,* internal mold of ventral valve, ×2.8 (Williams, 1974).

Medessia Andreeva, 1960, p. 295 [**M. uralica;* OD]. Similar to *Alimbella* but medium size, capillate, and with subequal dorsal adductor scars. *Lower Ordovician (Tremadoc):* Russia (Urals).——Fig. 527,*5a–d.* **M. uralica,* Tremadoc, Urals; *a,* dorsal exterior, ×1; *b,* ventral exterior, ×1; *c,* internal mold of ventral valve, ×1.5; *d,* internal mold of dorsal valve, ×3 (Andreeva, 1960).

Mogoktella Andreeva, 1968, p. 82 [**M. islendica;* OD]. Medium size, ramicostellate with variable interspacing of costellae, ventral interarea relatively short; recessive dental plates present; cardinal process ridgelike, dorsal adductor scar quadripartite and splayed with smaller anterior pair inserted submedianly between posterior pair and separated by low median ridge; dorsal mantle canal system digitate (equidistributate). *Upper Cambrian:* northwestern central Siberia.——Fig. 527,*4a–d.* **M. islendica,* Upper Cambrian, northwestern central Siberia; *a,* replica of ventral exterior, ×3; *b,* replica of dorsal exterior, ×3; *c,* internal mold of ventral valve, ×3; *d,* internal mold of dorsal valve, ×3 (Andreeva, 1968).

Family BOHEMIELLIDAE Havlíček, 1977

[Bohemiellidae Havlíček, 1977a, p. 28; *emend.,* Williams & Harper, herein]

Mainly biconvex, subquadrate orthoids with obtuse cardinal extremities; apsacline ventral interarea usually long and curved, anacline dorsal interarea short and flat; teeth transverse and ridgelike, dental plates very rarely developed; ventral muscle scar subtriangular, mainly restricted to delthyrial cavity, notothyrial platform flat, normally with simple cardinal process; brachiophores short, ridgelike, widely divergent, quadripartite adductor scar relatively widely dispersed about low, broad median ridge; ventral mantle canal system saccate with divergent *vascula media,* dorsal system saccate to digitate. *Lower Cambrian–Middle Cambrian.*

Bohemiella Schuchert & Cooper, 1931, p. 242 [**Orthis romingeri* Barrande, 1879, p. 203; OD] [=*Shiragia* Kobayashi, 1935b, p. 70 (type, *S. bilobia*)]. Planoconvex with variable cardinal extremities and multicostellate ornamentation; ventral adductor scar separated from flanking diductor scars by low, slightly divergent ridges, transverse teeth ridges with fine denticles; rounded sockets subtended by short, ridgelike brachiophores and passing laterally into denticulate ridges immediately below hinge line; larger anterior dorsal adductor scars separated from posterior pair by fine oblique ridges. *Middle Cambrian:* Bohemia, New Zealand.——Fig. 528,*3a–c.* **B. romingeri* (Barrande), Middle Cambrian, Bohemia; *a,* internal mold of ventral valve, ×3.9; *b,* internal mold of dorsal valve, ×5; *c,* rubber replica of dorsal exterior, ×2.8 (Havlíček, 1977a).

Chilidorthis Havlíček & Josopait, 1972, p. 342 [**C. tecta;* OD]. Medium sized, planoconvex with weakly developed multicostellae; teeth unknown; lacking dental plates, ventral muscle scar obscure but associated with divergent *vascula media;* ridgelike cardinal process and wide, low, dorsal muscle field; mantle canal system unknown. [This genus is doubtfully assigned to the Bohemiellidae. It is based on poorly preserved molds, scarcely distinguishable below familial rank; but it has been identified as a bohemiellid by its authors notwithstanding the presence of a chilidium (or chilidial plates).] *Middle Cambrian:* Spain.——Fig. 529,*2a–c.* **C. tecta,* Middle Cambrian, northern Spain; *a,* internal mold of ventral valve, ×2.4; *b,* internal mold of dorsal valve, ×2.7; *c,* external mold of dorsal valve, ×3 (Havlíček & Josopait, 1972).

Cymbricia Roberts & Jell, 1990, p. 272 [**C. spinicostata;* OD]. Ventribiconvex, rectimarginate with variable cardinal extremities, multicostellate, cancellate; ventral interarea planar, dorsal one curved; ventral muscle field subcordate with adductor track inserted anteromedianly in heart-shaped pit and not enclosed by elongate diductor scars; cardinal process ridgelike, not always developed. *Middle Cambrian:* Australia (New South Wales).——Fig. 528,*2a–f.* **C. spinicostata,* Middle Cambrian, New South Wales; *a,* ventral exterior, ×1.5; *b,c,* interior, posterior views of ventral valve, ×3; *d,* ventral interior, ×3; *e,* dorsal interior, ×6; *f,* details of ornament, ×3 (Roberts & Jell, 1990).

Diraphora Bell, 1941, p. 243 [**Eoorthis bellicostata* Walcott, 1924, p. 505; OD]. Similar to *Wimanella* but unisulcate with subdued multicostellae and filae. *Middle Cambrian:* North America, Iran, Siberia, Australia.——Fig. 528,*1a.* **D. bellicostata* (Walcott), Middle Cambrian, British Columbia; dorsal interior, ×3 (Walcott, 1924).——Fig. 528,*1b–d. D. striata* (Walcott), Middle Cambrian, Montana; *b,* dorsal exterior, ×3; *c,* ventral exterior, ×3; *d,* mold of ventral interior, ×2 (Bell, 1941).

Murrinyinella Kruse, 1990, p. 39 [**M. garradin;* OD]. Similar to *Wimanella* but transversely to elongately semioval, unisulcate in young growth stages; teeth apices placed more or less medially in transverse teeth ridges, ventral muscle scar unknown; cardinal process simple. *Middle Cambrian:* northern Western Australia.——Fig. 529,*1a–e.* **M. garradin,* Middle Cambrian, Northern Territory; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×5; *d,* dorsal interior, ×5; *e,* broken ventral interior, ×5 (Kruse, 1990).

Oligomys Schuchert & Cooper, 1931, p. 243 [**Orthis exporrecta* Linnarsson, 1876, p. 12; OD]. Transversely semioval, variably planoconvex, costellate, capillate; small wide teeth with rudimentary dental plates, ventral adductor track linear, expanding anteriorly and extending beyond flanking diductor scars; simple cardinal process, short, widely

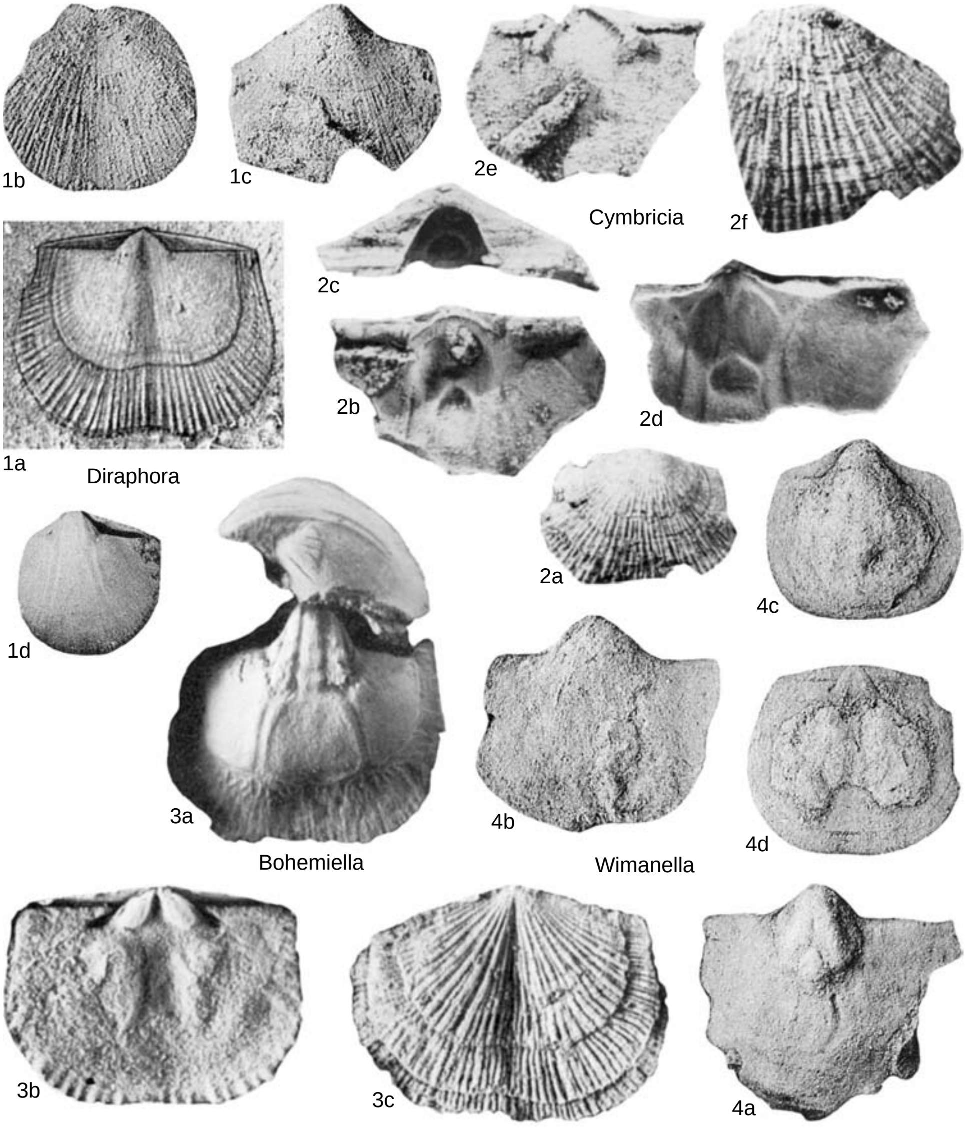

FIG. 528. Bohemiellidae (p. 731–732).

divergent brachiophores. *Middle Cambrian:* Europe.——FIG. 529,*3a,b.* **O. exporrectus* (LINNARSSON), Middle Cambrian, Sweden; *a,* internal mold of ventral valve, ×2.5; *b,* dorsal interior, ×2.5 (Schuchert & Cooper, 1932).

Wimanella WALCOTT, 1908, p. 98 [**W. simplex;* OD]. Subquadrate with variable cardinal extremities, biconvex, unisulcate to rectimarginate, smooth except for concentric growth lines and sporadic, low radial ridges but finely striate on internal margins; teeth apices near delthyrial boundary of transverse teeth ridges; ventral diductor scars elongate, separated posteriorly by low median ridge that bifurcates anteriorly to contain medial adductor scar; cardinal process absent or rudimentary. *Lower Cambrian–Middle Cambrian:* North America, Australia, Siberian Platform, eastern China.——FIG. 528,*4a–d.* **W. simplex,* Middle Cambrian, Montana; *a,* internal mold of ventral valve, ×2; *b,* ventral exterior, ×3; *c,* internal mold of ventral valve, ×3; *d,* internal mold of dorsal valve, ×2 (Bell, 1941).

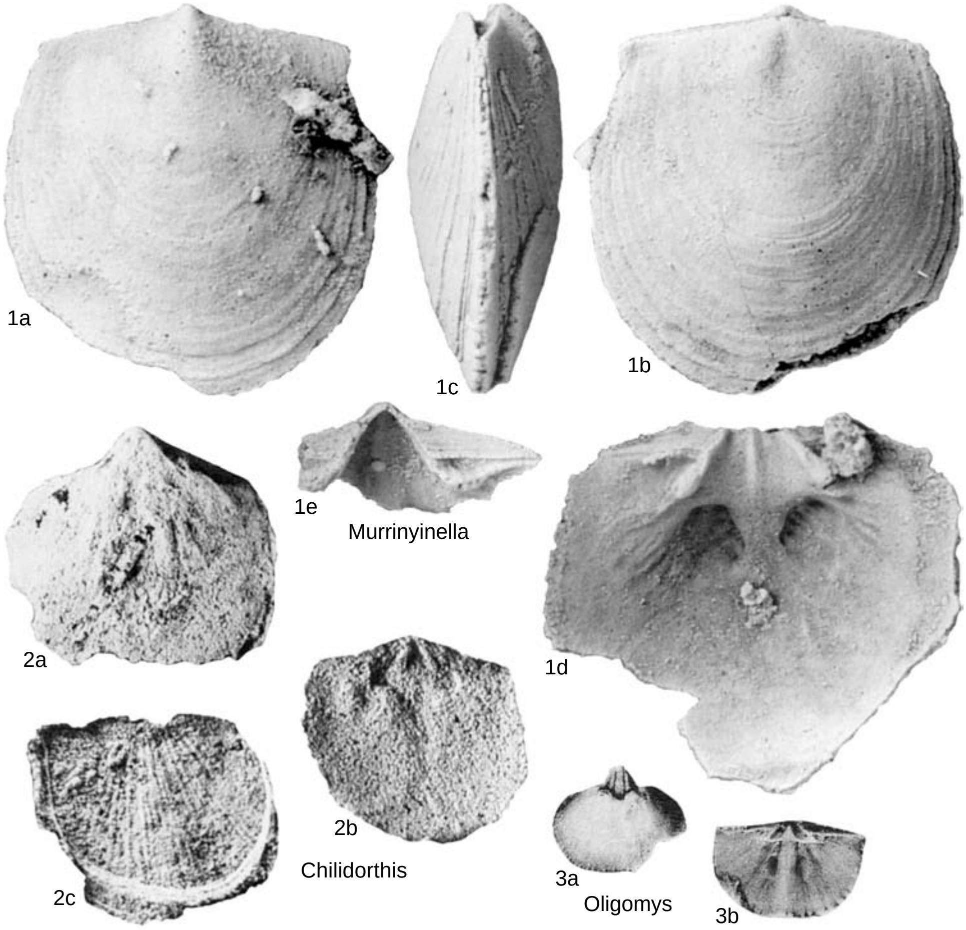

FIG. 529. Bohemiellidae (p. 731–732).

Family GLYPTORTHIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Glyptorthinae SCHUCHERT & COOPER, 1931, p. 243]

Medium to large, subquadrate usually with obtuse cardinal extremities, costate to costellate with strong concentric ornamentation developed as lamellose frills or even drawn out as spines; delthyrium and notothyrium varying in width, exceptionally covered, short dorsal interarea variably orientated; dental plates normally present, recessive, ventral muscle scar variable, with relatively broad adductor track rarely shorter than diductor scars, pedicle callist usually well developed; brachiophores variably structured and disposed, well-developed notothyrial platform normally supporting simple cardinal process and invariably prolonged anteriorly as median ridge; quadripartite dorsal scars commonly with anterior pair larger than posterior pair; sporadically impressed mantle canals with saccate ventral and digitate dorsal systems. *Lower Ordovician (Arenig)–middle Silurian (Wenlock).*

Glyptorthis FOERSTE, 1914, p. 257 [**Orthis insculpta* HALL, 1847, p. 125; OD]. Variable in size and in cardinal extremities, subequally biconvex, ramicostellate, strongly lamellose, ventral interarea of varying length, dorsal interarea short, curved; ventral muscle scars subcordate with adductors

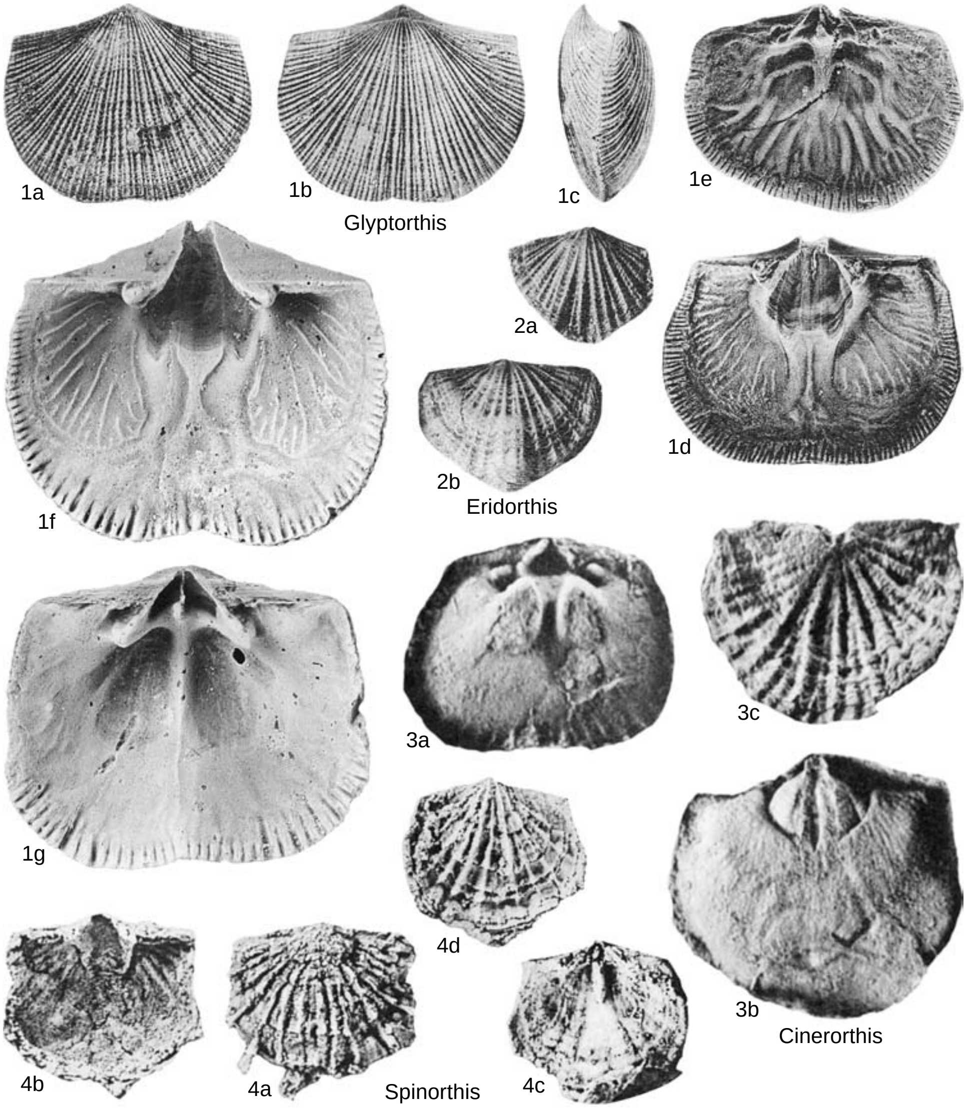

FIG. 530. Glyptorthidae (p. 733–736).

commonly raised on median callist extending forward as tongue of secondary shell; brachiophores divergent, rodlike. _Lower Ordovician (Llanvirn)–middle Silurian (Wenlock):_ Northern Hemisphere.——FIG. 530,_1a–e._ *_G. insculpta_ (HALL), Ashgill, Ohio; _a–c,_ ventral, dorsal, lateral views of conjoined valves, ×1.5; _d,_ ventral interior, ×1.5; _e,_ dorsal interior, ×1.5 (Schuchert & Cooper, 1932).——FIG. 530,_1f,g. G. pulchra,_ Ashgill, Iowa; ventral interior, dorsal interior, ×2 (Cocks, new).

Cinerorthis HAVLÍČEK, 1974, p. 167 [*_C. cineraria;_ OD]. Dorsibiconvex to resupinate, uniplicate, coarsely costellate, delthyrium with convex deltidium commonly perforate apically; interareas short, flat; ventral muscle scar subpentagonal, impressed on callus, adductor track divided by median ridge; undifferentiated cardinal process thick, occupying much of notothyrial platform, divergent brachiophores bladelike. _middle Silurian (Wenlock):_ Bohemia.——FIG. 530,_3a–c._ *_C. cineraria,_ Wenlock, Bohemia; _a,_ internal mold of dorsal valve, ×2.8; _b,_ internal mold of ventral valve, ×1.7; _c,_ rubber replica of ventral exterior, ×3 (Havlíček, 1977a).

Eridorthis FOERSTE, 1909b, p. 223 [*_Plectorthis (Eridorthis) nicklesi;_ OD]. Similar to _Glyptorthis_ but uniplicate with dorsal median sulcus replaced by

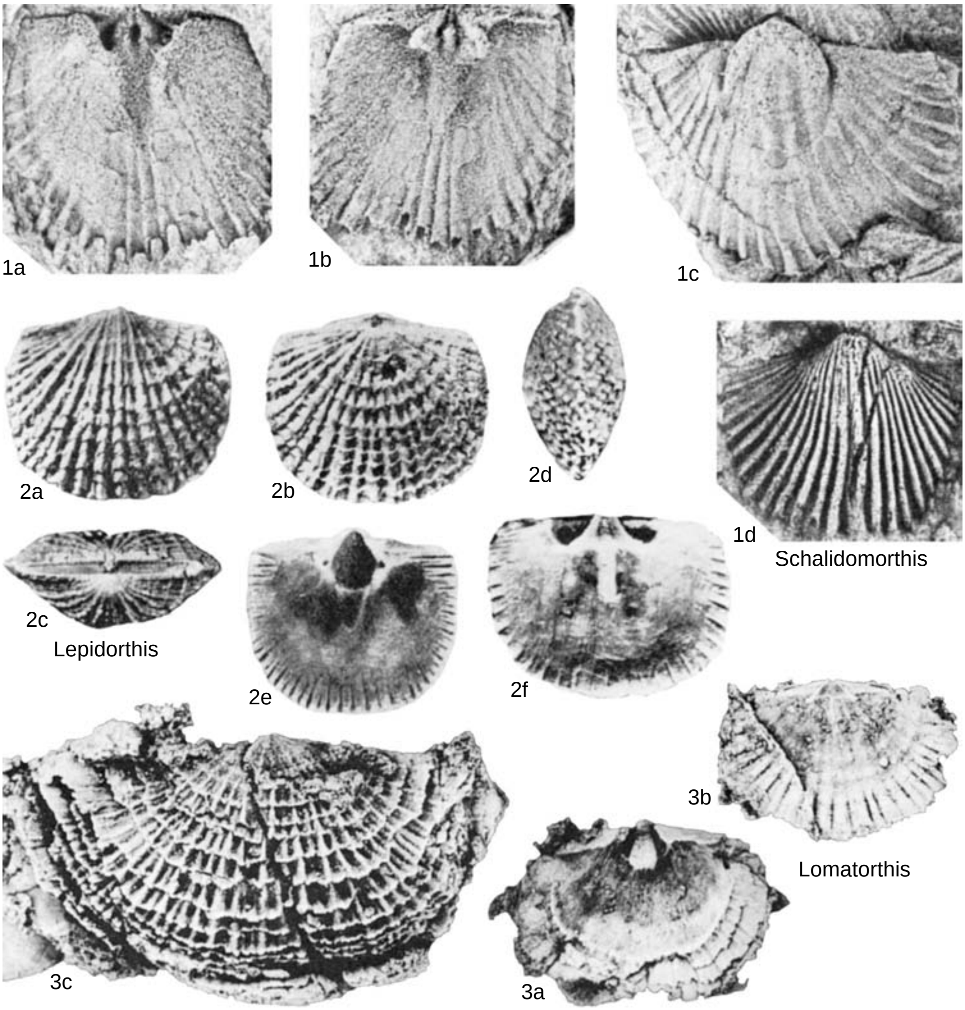

FIG. 531. Glyptorthidae (p. 735–736).

fold in adult shells, obtuse cardinal extremities, long curved ventral interarea and apsacline dorsal interarea, ventral muscle scar supported by callus, adductor track relatively narrow, expanding anteriorly. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock):* North America, Europe, Siberia, central Asia, North Africa, Australia, China.——FIG. 530,*2a.* **E. nicklesi* (FOERSTE), Caradoc, Kentucky; ventral exterior, ×1.5 (Schuchert & Cooper, 1932).——FIG. 530,*2b. E. rogerensis* FOERSTE, Caradoc, Kentucky; dorsal exterior, ×1.5 (Schuchert & Cooper, 1932).

Lepidorthis WANG, 1955b, p. 330 [**L. typicalis;* OD]. Ventribiconvex with relatively narrow delthyrium and notothyrium, curved ventral interarea moderately long; ventral muscle scar suboval with median ridge; cardinal process absent, sockets defined laterally by fulcral plates. *Lower Ordovician (Arenig):* southern China.——FIG. 531,*2a–f.* **L. typicalis,* Arenig, southern China; *a–d,* ventral, dorsal, posterior, lateral views of conjoined valves, ×3.5; *e,* ventral interior, ×3.5; *f,* dorsal interior, ×3.5 (Wang, 1955b).

Lomatorthis WILLIAMS & CURRY, 1985, p. 230 [**L. mimula;* OD]. Subequally biconvex with flattened or gently resupinate margins, rectimarginate, ramicostellate, interareas short, curved; teeth simple, deltidiodont; ventral muscle field elongate with broad adductor components impressed on elevated tonguelike platform, no apical callist seen; cardinal process absent, divergent brachiophores short, bladelike; quadripartite dorsal adductor scar with subequal parts; subperipheral rim developed in adult ventral valves. *Lower Ordovician (Arenig):*

Ireland.——FIG. 531,*3a–c.* **L. mimula,* Arenig, western Ireland; *a,* ventral interior, ×2; *b,* dorsal interior, ×3; *c,* dorsal exterior, ×3 (Williams & Curry, 1985).

Schalidomorthis BASSETT, 1981, p. 650 [**S. stubblefieldi;* OD]. Similar to *Lepidorthis* but costate and lacking concentric lamellae, interareas plane with wide delthyrium and notothyrium. *Lower Ordovician (Llanvirn):* southwestern England.——FIG. 531,*1a–d.* **S. stubblefieldi,* Llanvirn, southwestern England; *a,b,* internal mold, rubber replica of dorsal valve, ×2.5; *c,* internal mold of ventral valve, ×2.5; *d,* rubber replica of ventral exterior, ×2.5 (Bassett, 1981).

Spinorthis WRIGHT, 1964, p. 184 [**S. geniculata;* OD]. Similar to *Glyptorthis* but with adult shell geniculate dorsally and lamellae prolonged into suberect spines along coarser costellae, cardinal extremities obtuse, dorsal interarea vestigial; ventral muscle scar without elevations of secondary shell; brachiophores widely divergent. *Upper Ordovician (Ashgill):* Ireland, Belgium, Wales.——FIG. 530,*4a–d.* **S. geniculata,* Ashgill, eastern Ireland; *a,b,* exterior, interior of ventral valve, ×2.1; *c,d,* interior, exterior of dorsal valve, ×2.1 (Wright, 1964).

Family HESPERONOMIIDAE Ulrich & Cooper, 1936

[Hesperonomiidae ULRICH & COOPER, 1936b, p. 621]

Unequally parvicostellate orthoids with variable outline, cardinal extremities normally acute; variably oriented ventral interarea normally short, flat, anacline; dorsal interarea very short, flat; teeth normally simple with variably developed dental plates; ventral muscle field variable, impressed directly on valve floor; notothyrial platform supporting variably developed cardinal process, normally extending forward as median ridge, quadripartite dorsal adductor scars rarely impressed; mantle canal systems rarely impressed, ventral saccate with divergent *vascula media,* dorsal digitate. *Middle Cambrian–Lower Ordovician (Llanvirn).*

Hesperonomia ULRICH & COOPER, 1936b, p. 621 [**H. planidorsalis;* OD]. Elongately semioval with acute cardinal extremities, concavoconvex; apsacline ventral interarea short, flat; deltidiodont teeth with recessive dental plates; ventral muscle field subcordate with undifferentiated adductor muscle track not enclosed by diductor scars; notothyrial platform bearing notothyrial ridges fused with simple cardinal process and extending anteriorly as median ridge, divergent brachiophores rodlike; dorsal adductor muscle scar vaguely impressed. *Lower Ordovician (Tremadoc–Arenig):* North America, Siberia, Great Britain, South America (Argentina), France, central Asia, China.——FIG. 532,*1a–d.* **H. planidorsalis,* Tremadoc, Alberta; *a,* ventral interior, ×2; *b,* dorsal interior, ×2; *c,* details of cardinalia, ×4; *d,* dorsal exterior, ×2 (Ulrich & Cooper, 1938).

Hesperonomiella ULRICH & COOPER, 1936b, p. 622 [**Protorthis porcias* WALCOTT, 1924, p. 504; OD] [=*Engenella* ANDREEVA, 1987, p. 36 (type, *E. sibirica*)]. Subquadrate with obtuse cardinal extremities, narrowly biconvex; teeth with crural fossettes supported by recessive dental plates; ventral muscle field suboval with a broad adductor track as long as diductor scars; notothyrial platform with simple cardinal process, divergent brachiophores rodlike; quadripartite dorsal adductor scar impressed on either side of low median ridge with posterior pair larger than anterior pair; mantle canal systems impressed, ventral saccate with divergent *vascula media,* dorsal digitate. [According to the brief descriptions and illustrations of the specimens from the *Middle Cambrian* of the Siberian Platform, on which *Engenella* was established, the stock differs from *Hesperonomiella* only in being more strongly biconvex.] *Middle Cambrian–Lower Ordovician (Arenig):* North America, Wales, Ireland, Bohemia, Afghanistan, central Asia, Australia (Tasmania), China, Russia.——FIG. 532,*2a–d.* **H. porcias* (WALCOTT), Tremadoc, Alberta; *a,* internal mold of ventral valve, ×1.5; *b,c,* internal mold, replica of dorsal valve, ×2; *d,* replica of ventral exterior, ×2 (Ulrich & Cooper, 1938).

Monorthis BATES, 1968, p. 144 [**M. typis;* OD]. Subquadrate with acute cardinal extremities, narrowly biconvex, catacline ventral interarea, short, curved; teeth unknown, dental plates recessive, ventral muscle scar unknown; notothyrial platform with simple cardinal process and extending anteriorly as low median ridge; divergent brachiophores bladelike, defining elongate sockets; dorsal adductor muscle scar unknown. *Lower Ordovician (Arenig–Llanvirn):* Wales, Argentina.——FIG. 532,*3a–d.* **M. typis,* Llanvirn, northern Wales; *a,b,* internal mold, rubber replica of dorsal valve, ×3.4; *c,* internal mold of ventral valve, ×3.2; *d,* rubber replica of ventral exterior, ×3.2 (Bates, 1968).

Murjukiana SEVERGINA, 1967, p. 134 [**M. ilovata;* OD]. Similar to *Hesperonomia* but with suboval ventral muscle field having broadly triangular adductor track together with simple, bulbous cardinal process and well-developed dorsal subperipheral rim. *Lower Ordovician (Llanvirn):* Siberia (Kuznetz Altai, Altai-Sayan).——FIG. 533,*2a–d.* **M. ilovata,* Llanvirn, Kuznetz Altai; *a,* internal mold of ventral valve, ×3; *b,c,* internal mold, rubber replica of dorsal valve, ×2.25; *d,* rubber replica of dorsal exterior, ×2.25 (Cocks & Rong, 1989).

Protohesperonomia WILLIAMS & CURRY, 1985, p. 218 [**P. resupinata;* OD]. Transversely semioval with acute cardinal extremities, concavoconvex to weakly resupinate, rectimarginate, ventral interarea catacline; simple deltidiodont teeth with divergent dental plates; ventral muscle field strongly bilobed presumably with short adductor field limited to median, tapering ridge; notothyrial platform poorly

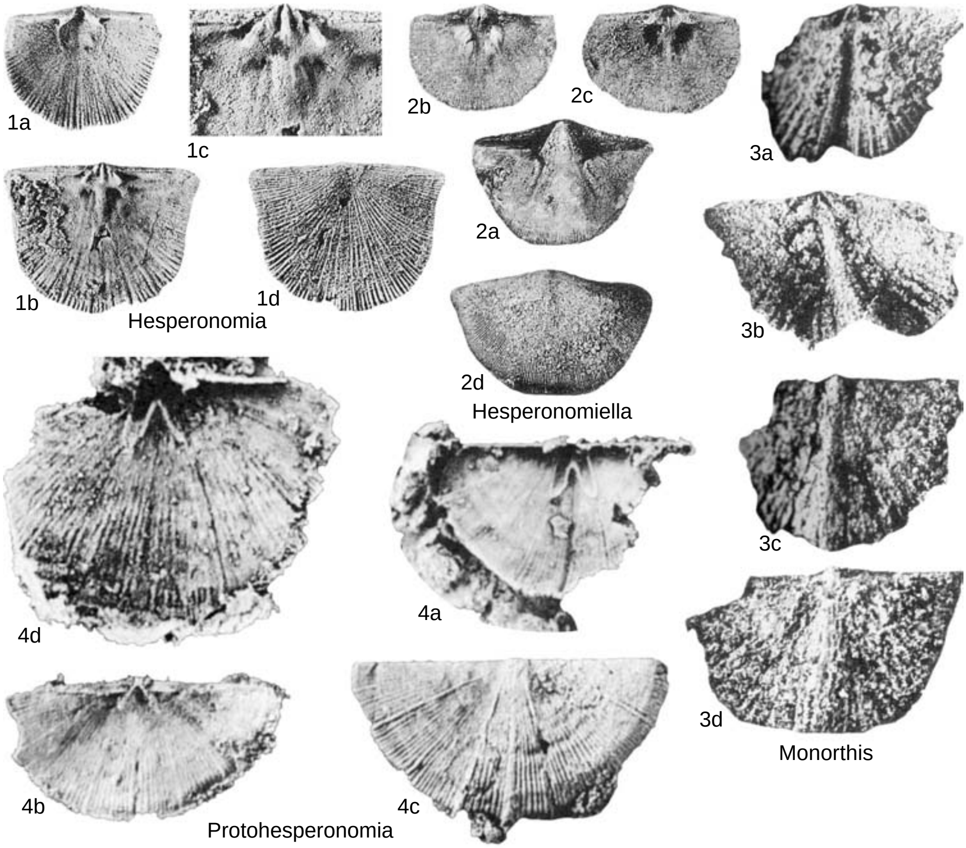

FIG. 532. Hesperonomiidae (p. 736–737).

developed but extending anteriorly as low median ridge; cardinal process absent, divergent brachiophores bladelike, defining elongate sockets. *Lower Ordovician (Arenig):* Ireland, Bohemia.——FIG. 532,*4a–d.* **P. resupinata,* Arenig, western Ireland; *a,* ventral interior, ×6; *b,* dorsal interior, ×5; *c,* ventral exterior, ×5; *d,* ventral interior, ×6 (Williams & Curry, 1985).

Treioria NEUMAN & BATES, 1978, p. 584 [**T. chaulioda;* OD]. Transversely semioval with acute cardinal extremities, narrowly concavoconvex becoming gently resupinate rectimarginate, ventral interarea catacline; large teeth with short, divergent dental plates; ventral muscle field widely subtriangular with slightly elevated, broad, triangular adductor track; notothyrial platform wide with simple cardinal process, not extending anteromedianly, widely divergent, short brachiophores bladelike. *Lower Ordovician (Arenig–Llanvirn):* Wales, Ireland.——FIG. 533,*1a–d.* **T. chaulioda,* Llanvirn, northern Wales; *a,b,* internal mold, rubber replica of ventral valve, ×2; *c,* rubber replica of dorsal interior, ×2; *d,* external mold of ventral valve, ×2 (Neuman & Bates, 1978).

Family HESPERORTHIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Hesperorthinae SCHUCHERT & COOPER, 1931, p. 243]

More elongately than transversely semioval, costate to fascicostellate, variably capillate orthoids almost invariably lacking lamellae; delthyrium and notothyrium commonly narrow with variably developed covers; ventral interarea normally long and flat, dorsal interarea almost invariably anacline, of variable length and curvature; dental plates recessive, cordate ventral muscle scar impressed on valve floor, adductor track typically differentiated, narrow, parallel-sided to lanceolate,

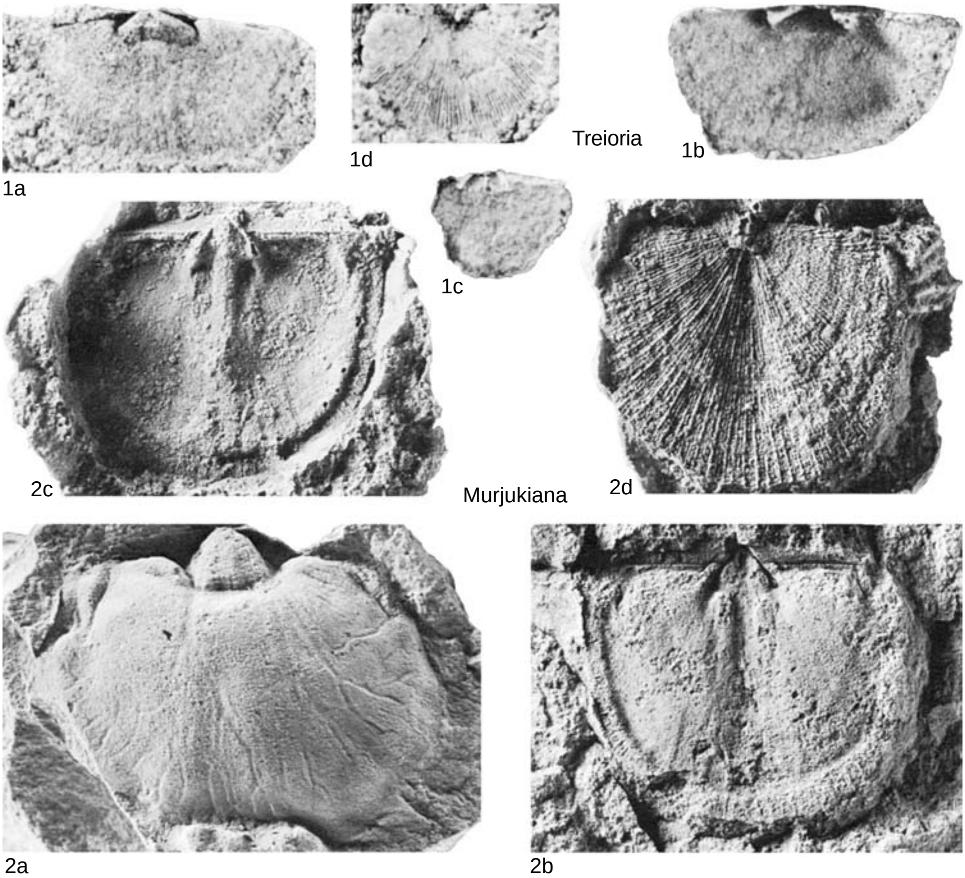

FIG. 533. Hesperonomiidae (p. 736–737).

normally shorter than flanking diductor scars and generally lacking median ridge; notothyrial platform weak to rudimentary but with broad median ridge extending anteriorly, cardinal process almost invariably simple, ridgelike, brachiophores divergent, bladelike; quadripartite dorsal adductor scars generally lightly impressed, variable; ventral mantle canal system saccate with subparallel *vascula media,* dorsal system less well preserved, mainly digitate. *Lower Ordovician (Arenig)–Lower Devonian (Emsian).*

Hesperorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis tricenaria* CONRAD, 1843, p. 333; OD]. Medium to large, elongately semioval with variable cardinal extremities, planoconvex, rectimarginate, costate, capillate; delthyrium with apical plate, notothyrium with antigydium; interareas relatively long and flat; posterior pair of dorsal adductor scars larger than anterior. *Lower Ordovician (Llanvirn)–middle Silurian (Wenlock):* cosmopolitan.——FIG. 534,*1a–f.* **H. tricenaria* (CONRAD), Caradoc, eastern USA; *a,* ventral interior, ×2; *b,* dorsal interior, ×2; *c–e,* ventral, dorsal, posterior views of conjoined valves, ×1.5; *f,* detail of ventral interarea, ×1.5 (Schuchert & Cooper, 1932).

Barbarorthis ÖPIK, 1934, p. 183 [**B. foraminifera;* OD]. Similar to *Hesperorthis* but coarsely costellate, without surface capillae; delthyrium partly closed by delthyrial plates. *Upper Ordovician (Ashgill):* Baltoscandia.——FIG. 534,*2a–d.* **B. foraminifera,* Ashgill, Estonia; *a,* dorsal interior, ×4.5; *b–d,* dorsal, ventral, posterior views of conjoined valves, ×5 (Öpik, 1934).

Boreadorthis ÖPIK, 1934, p. 184 [**B. crassa;* OD]. Similar to *Hesperorthis* but with a strongly and uniformly convex brachial valve. *Upper Ordovician (Ashgill):* Baltoscandia, central Asia, Siberia, Ukraine, Belgium.——FIG. 534,*3a–d.* **B. crassa,* Ashgill, Estonia; *a,* dorsal interior, ×2; *b,* ventral

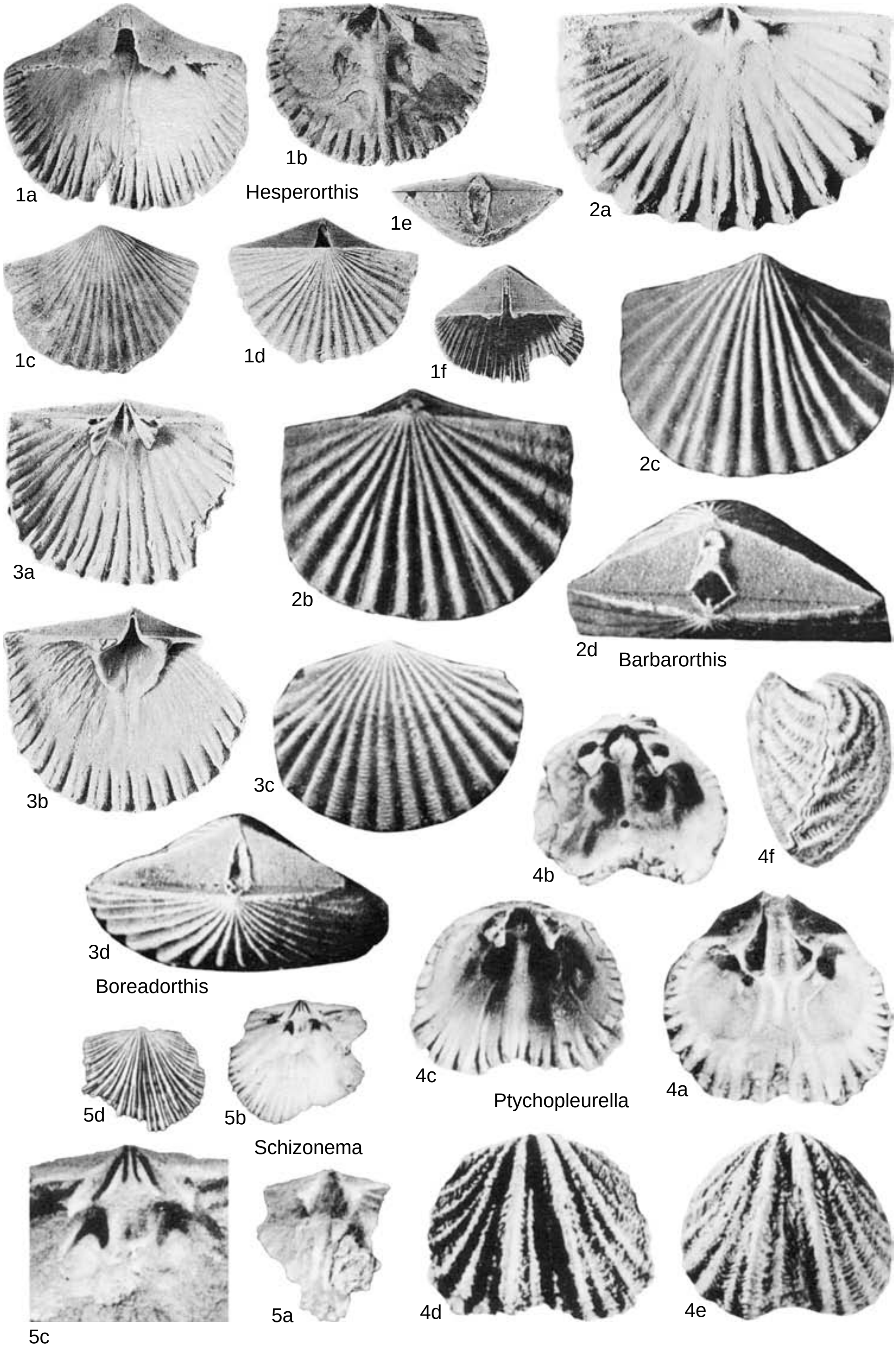

FIG. 534. Hesperorthidae (p. 738–740).

interior, ×2; *c,d,* dorsal, posterior views of conjoined valves, ×5 (Öpik, 1934).

Dolerorthis Schuchert & Cooper, 1931, p. 244 [**Orthis interplicata;* OD] [=*Altaeorthis* Severgina, 1967, p. 124 (type, *A. uskutchevi*); *Munhella* Neuman, 1971, p. 117 (type, *M. cummingi*)]. Transversely semioval, cardinal extremities variable, biconvex to convexoconcave, uniplicate, coarsely costellate without capillae; delthyrium and notothyrium wide; interareas relatively long, curved; ventral muscle scar with median ridge, pedicle callist not developed; posterior pair of dorsal adductor scars lying posterolaterally of anterior pair and separated by strong, divergent *vascula myaria;* dorsal mantle canal system apocapate. [*Altaeorthis* was proposed for specimens from the Middle Ordovician of Siberia (Altai Mountains) that are similar to *Dolerorthis* except for the greater convexity of the ventral valve. The relative convexity of European *Dolerorthis,* however, is also variable; and, since ventribiconvexity is likely to have developed independently in several stocks, it is phylogenetically undesirable to found a genus exclusively on this feature. *Munhella* was erected for deformed brachiopod molds from the Arenig of Newfoundland on the assumption that it was close to the orthid *Glossorthis* except for the dorsibiconvexity of the valves and the lack of a raised callus of secondary shell for the ventral muscle field. These features, like others described and illustrated, are characteristic of *Dolerorthis.*] *Upper Ordovician (Arenig)–Lower Devonian (Emsian):* cosmopolitan.——Fig. 535,*1a.* **D. interplicata* (Schuchert & Cooper), Wenlock, Indiana; dorsal interior, ×1.5 (Schuchert & Cooper, 1932).——Fig. 535,*1b,c. D. flabellites* (Foerste), Wenlock, Indiana; *b,* ventral interior, ×1.5; *c,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).——Fig. 535,*1d–g. D. rustica* (J. de C. Sowerby); *d–f,* ventral, dorsal, lateral views of conjoined valves, Wenlock, Sweden, ×1.5; *g,* dorsal interior, Wenlock, England, ×1.5 (Schuchert & Cooper, 1932).——Fig. 535,*1h–k. D. rigida* (Davidson), Wenlock, Shropshire; *h,* dorsal interior, ×1.5; *i–k,* dorsal, ventral, lateral views of conjoined valves, ×1 (Bassett, 1970).

Flabellitesia Zhang, 1989a, p. 56 [**Hesperorthis kessei* Boucot, Johnson, & Zhang, 1988, p. 107; OD]. Similar to *Hesperorthis* but dorsibiconvex to resupinate, shallowly unisulcate, sporadically developed capillae; delthyrium open; dorsal interarea narrow. *middle Silurian (Wenlock):* North America, Europe.——Fig. 535,*4a–d.* **F. kessei* (Boucot, Johnson, & Zhang), Wenlock, Baillie Hamilton Island; *a,b,* interior, exterior of ventral valve, ×2; *c,d,* interior, exterior of dorsal valve, ×2 (Zhang, 1989a).

Lordorthis Ross, 1959, p. 446 [**L. variabilis;* OD]. Similar to *Hesperorthis* but resupinate and coarsely costellate (capillae not reported). *Upper Ordovician (Ashgill):* western North America.——Fig. 535,*2a–f.* **L. variabilis,* Ashgill, Lemhi Range; *a–d,* ventral, dorsal, posterior, lateral views of conjoined valves, ×1; *e,* ventral interior, ×1; *f,* dorsal interior, ×1 (Ross, 1959).

Paradolerorthis Zeng, 1987, p. 218 [**D. (P.) calla;* OD]. Similar to *Dolerorthis* but more subquadrate with obtuse cardinal extremities, biconvex, ramicostellate; delthyrial opening relatively narrow in shorter ventral interarea; notothyrial platform better developed. *Lower Ordovician (Llanvirn):* southern China.——Fig. 535,*3a–c.* **P. calla,* Llanvirn, southern China; ventral interior, ventral exterior, internal mold of dorsal valve, ×3 (Zeng, 1987).

Ptychopleurella Schuchert & Cooper, 1931, p. 244 [**Orthis bouchardi* Davidson, 1847, p. 64; OD]. Small, transversely semioval with obtuse cardinal extremities, biconvex with subpyramidal ventral valve, strangulate, rectimarginate to gently unisulcate, coarsely costellate without capillae, lamellose; delthyrium and notothyrium narrowly divergent, open; dorsal interarea short, curved, orthocline; ventral muscle scar suboval to subpentagonal with adductor component usually impressed on flat ridge, pedicle callist unknown; rudimentary notothyrial platform with cardinal process, rarely absent, usually thick in maturity; anterior pair of quadripartite dorsal adductor scars larger than posterior. [This genus has long been regarded as a close relative of *Glyptorthis* mainly because of its ornamentation. Other morphological features, however, including the nature of the delthyrium and notothyrium and the longitudinal profile of the ventral valve, are more suggestive of the hesperorthids, with which family it is presently associated cladistically.] *Lower Ordovician (Llanvirn)–Lower Devonian (Emsian):* cosmopolitan.——Fig. 534,*4a–f.* **P. bouchardi* (Davidson), Wenlock, Welsh Borderlands; *a,* ventral interior, ×3; *b,* dorsal interior, ×3; *c,d,* dorsal interior, exterior, ×3; *e,f,* ventral, lateral views of conjoined valves, ×3 (Bassett, 1972).

Schizonema Foerste, 1909a, p. 76 [**Hebertella (Schizonema) fissistriata;* OD] [=*Schizoramma* Foerste, 1912, p. 139 (type *H. (Schizonema) fissistriata)*]. Similar to *Dolerorthis* but with obtuse cardinal extremities, subequally biconvex to slightly dorsibiconvex with shallow, impersistent dorsal sulcus, fascicostellate, well-developed pedicle callist and low notothyrial ridges flanking simple cardinal process. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* cosmopolitan.——Fig. 534,*5a–d.* **S. fissistriata* (Foerste), Wenlock, Indiana; *a,* ventral interior, ×1; *b,* dorsal interior, ×1; *c,* details of cardinalia, ×3; *d,* dorsal exterior, ×1 (Bassett, 1972).

Family LYCOPHORIIDAE
Schuchert & Cooper, 1931

[Lycophoriidae Schuchert & Cooper, 1931, p. 245]

Globular with obtuse cardinal extremities, dorsibiconvex, multicostellate; delthyrium and notothyrium open, narrow, apsacline

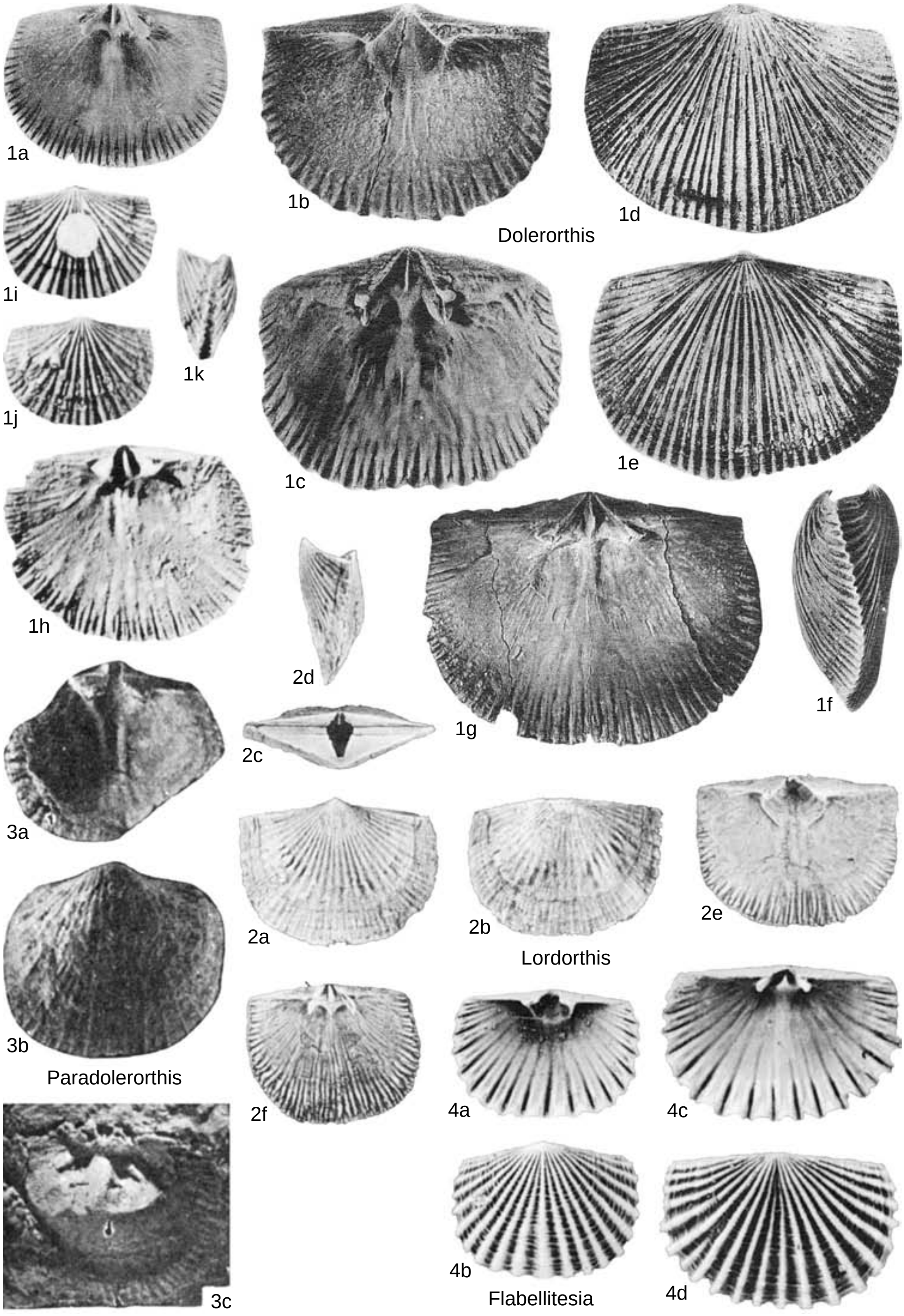

FIG. 535. Hesperorthidae (p. 740).

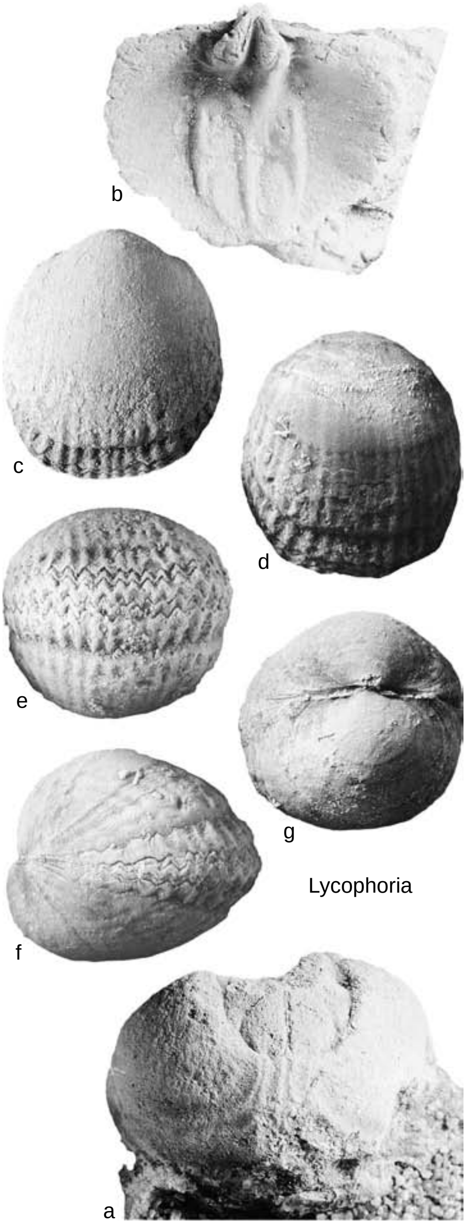

FIG. 536. Lycophoriidae (p. 742).

ventral interarea short, curved, dorsal interarea obsolete; teeth with crural fossettes supported by subparallel dental plates, ventral muscle scar long, bilobed with subcircular adductor track enclosed by elongate diductor scars that are separated anteriorly by median ridge, pedicle callist developed; cardinal process long, curved, bifurcating distally with chilidial plate (hood) on its dorsal surface; brachiophores small, rodlike, emerging from thick notothyrial platform excavated laterally as deep sockets; elongate dorsal adductor field with thickened margins, quadripartite with bilobed anterior pair larger than posterior pair; ventral mantle canal system probably saccate. *Lower Ordovician (Arenig–Llanvirn).*

Lycophoria LAHUSEN, 1886, p. 221 [**Atrypa nucella* DALMAN, 1828, p. 130; OD]. Medium to large in size, variably uniplicate at anterior margin. *Lower Ordovician (Arenig–Llanvirn):* Baltoscandia, Poland.——FIG. 536*a–g*. **L. nucella* (DALMAN), Arenig, Estonia; *a,* internal mold of ventral valve, ×3; *b,* dorsal interior, ×2.5; *c–g,* ventral, dorsal, anterior, lateral, posterior views of conjoined valves, ×2.5 (Rubel, 1961a).

Family NANORTHIDAE Havlíček, 1977

[Nanorthidae HAVLÍČEK, 1977a, p. 59]

Generally small, ventribiconvex costellate orthoids with very short, curved interareas; 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, not shorter than flanking diductor scars; pedicle callist well developed in some species; notothyrial platform normally present with usually simple cardinal process; variably disposed brachiophores typically short, bladelike, dorsal adductor scars quadripartite, variably impressed on either side of median ridge with posteromedian parts of anterior 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).*

Nanorthis ULRICH & COOPER, 1936b, p. 621 [**Orthis hamburgensis* WALCOTT, 1884, p. 73; OD] [=*Evenkinorthis* YADRENKINA, 1977, p. 27 (type, *E. dualis*)]. Subcircular with obtuse cardinal extremities, ramicostellate; short, bladelike brachiophores, notothyrial platform rudimentary, lacking cardinal process. [*Evenkinorthis* has been erected for inadequately described and illustrated specimens from the Ordovician of Siberia. With regard to such features as are unambiguously determinable, the genus is indistinguishable from *Nanorthis.*] *Lower Ordovi-*

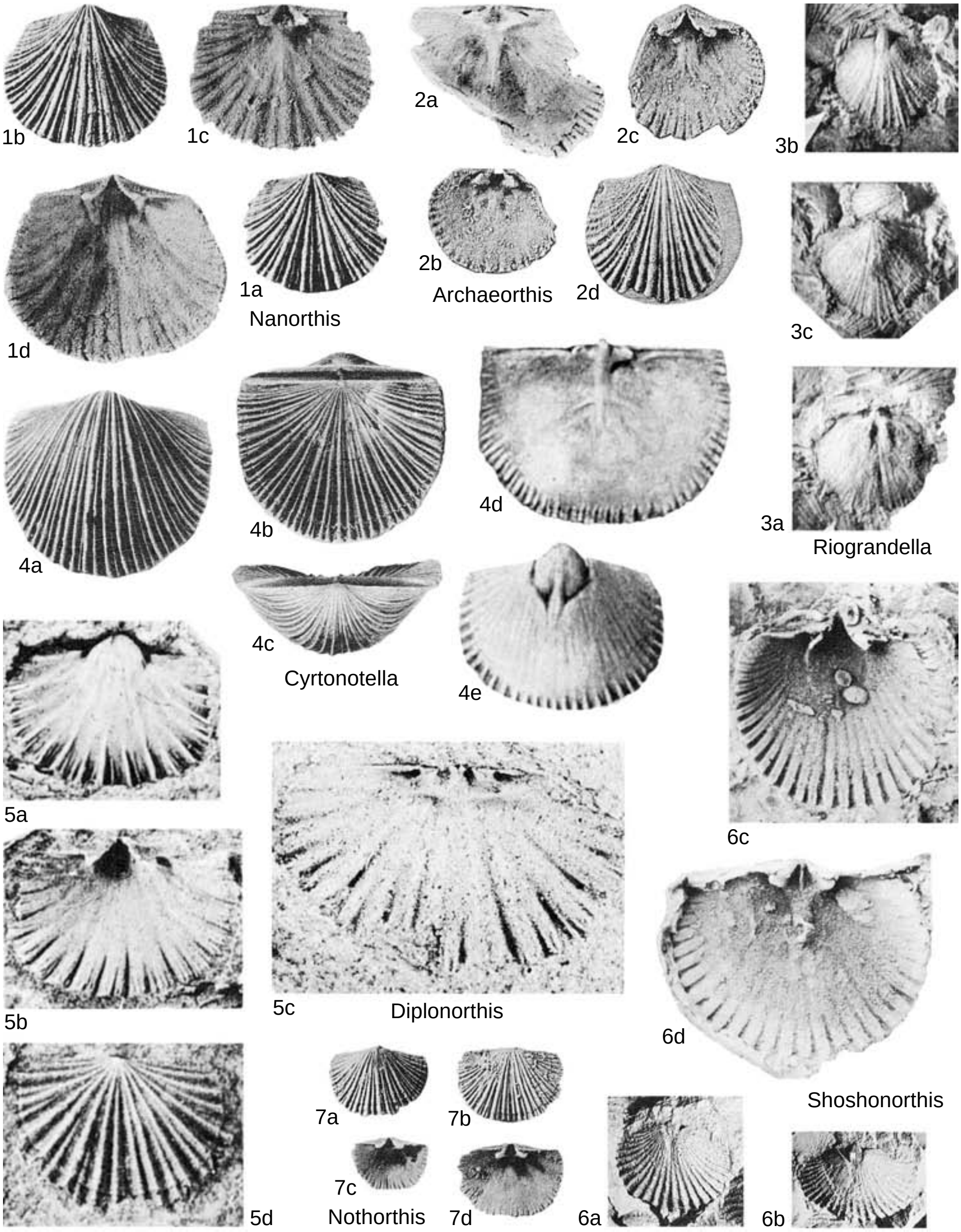

FIG. 537. Nanorthidae (p. 742–745).

cian (Tremadoc): cosmopolitan.——FIG. 537,*1a–d.* **N. hamburgensis* (WALCOTT), Tremadoc, western USA; *a,* dorsal exterior, ×3; *b,* ventral exterior, ×3; *c,* dorsal interior, ×4; *d,* ventral interior, ×4 (Ulrich & Cooper, 1938).

Archaeorthis SCHUCHERT & COOPER, 1931, p. 243 [**Orthis electra* BILLINGS, 1865 in 1861–1865, p. 79; OD]. Medium size, subcircular with obtuse cardinal extremities, multicostellate; elongately oval ventral muscle scar impressed on callosity prolonged forward of scar as wide, median ridge; cardinal process absent. *Lower Ordovician (Tremadoc–Arenig):* North America, Europe, South America, Asia.——FIG. 537,*2a.* **A. electra* (BILLINGS), Tremadoc, Quebec; dorsal interior, ×4 (Schuchert & Cooper, 1932).——FIG. 537,*2b–d. A. biconvexa,* Tremadoc, Oklahoma; *b,* dorsal interior, ×3; *c,* ventral interior, ×3; *d,* ventral interior, ×3 (Cooper, 1956).

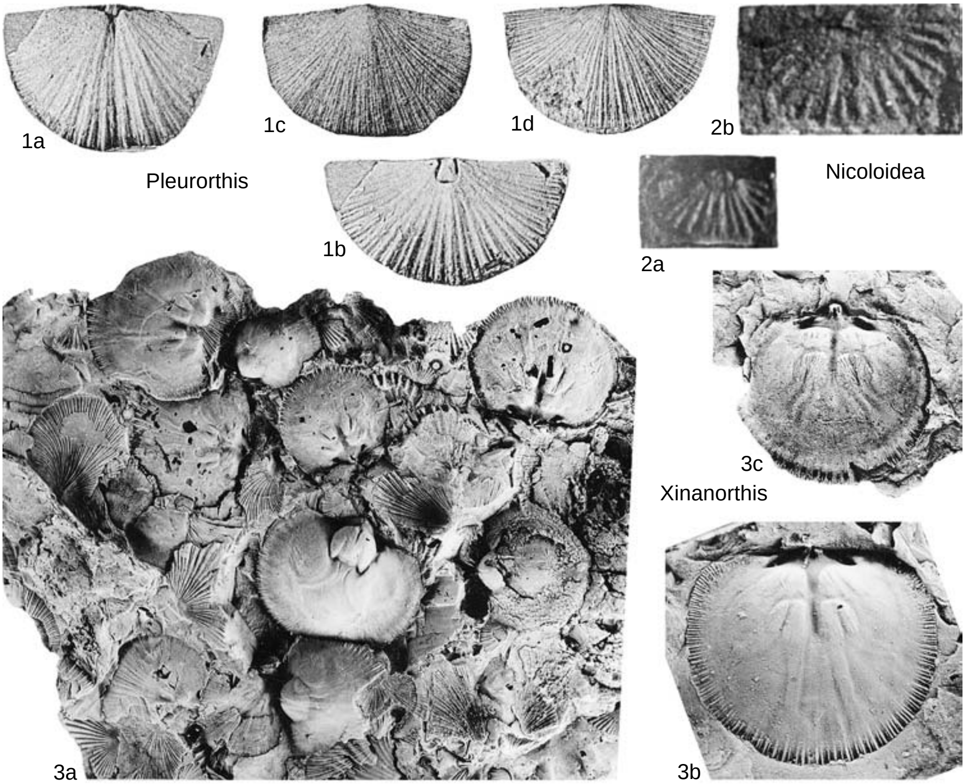

Fig. 538. Nanorthidae (p. 744–745).

Cyrtonotella Schuchert & Cooper, 1931, p. 243 [**Orthis semicircularis* von Eichwald, 1829, p. 276; OD]. Medium size, transversely semioval with acute cardinal extremities, plano- to concavo-convex, rectimarginate, coarsely costellate and filate, ventral interarea anacline; divergent dental plates; short, divergent, bladelike brachiophores. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Northern Hemisphere.——Fig. 537,*4a–c*. **C. semicircularis* (von Eichwald), middle Ordovician, Russia; ventral, dorsal, posterior views of conjoined valves, ×5 (Schuchert & Cooper, 1932).——Fig. 537,*4d,e. C. kukersiana* (Wysogórski), middle Ordovician, Russia; *d,* dorsal interior, ×2.25; *e,* internal mold of ventral valve, ×1 (Sarytcheva, 1960).

Diplonorthis Mitchell, 1977, p. 30 [**D. portlocki;* OD]. Subquadrate with obtuse cardinal extremities, coarsely costellate; ventral muscle field short, subtriangular with broad adductor tract, well-developed pedicle callist; widely divergent brachiophores, cardinal process consisting of shaft and bilobed crest. *Upper Ordovician (Ashgill):* Ireland, Wales.——Fig. 537,*5a–d*. **D. portlocki,* Ashgill, northern Ireland; *a,b,* internal mold, rubber replica of ventral valve, ×3.6; *c,* rubber replica of dorsal interior, ×6; *d,* rubber replica of dorsal exterior, ×9 (Mitchell, 1977).

Nicoloidea Zeng, 1987, p. 215 [**N. mina;* OD]. Similar to *Cyrtonotella* but small with recessive dental plates and lacking cardinal process and dorsal median ridge. *Lower Ordovician (Tremadoc):* southern China.——Fig. 538,*2a,b*. **N. mina,* Tremadoc, southern China; *a,* internal mold of ventral valve, ×9; *b,* internal mold of dorsal valve, ×9 (Zeng, 1987).

Nothorthis Ulrich & Cooper, 1938, p. 106 [**N. delicatula;* OD]. Subquadrate with obtuse cardinal extremities, ramicostellate; teeth deltidiodont (crural fossettes not recorded), suboval ventral muscle scar impressed on callosity; short, divergent brachiophores. *Lower Ordovician (Tremadoc):* eastern North America.——Fig. 537,*7a–d*. **N. delicatula,* Tremadoc, eastern North America; *a,* ventral exterior, ×3; *b,* dorsal exterior, ×3; *c,* ventral interior, ×3; *d,* dorsal interior, ×3 (Ulrich & Cooper, 1938). [Note added in proof: wrong family, see p. 777.]

Pleurorthis Cooper, 1956, p. 329 [**P. fascicostellata;* OD] [=*Ambardella* Andreeva, 1987, p. 37 (type, *A. anabarensis*)]. Medium size, subquadrate with variable cardinal extremities, dorsibiconvex with dorsal posteromedian sulcus passing into fold in adult shell, fascicostellate; weakly developed, platelike, notothyrial platform and cardinal process with short median ridge, divergent, short, bladelike brachiophores. [*Ambardella* was proposed for *Upper Cambrian* brachiopods from Siberia (central Techenie), which were typified as flattened costellate shells without capillae. The description and illustrations of other features, however, confirm only that the specimens are orthoid and, provisionally, better assigned to *Pleurorthis*.] *Lower Ordovician (Tremadoc–Arenig):* eastern North America, Siberia, South America (Argentina).——FIG. 538,*1a–d.* **P. fascicostellata,* Tremadoc, Quebec; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×2; *c,* replica of ventral exterior, ×1; *d,* dorsal exterior, ×1 (Cooper, 1956).

Riograndella KOBAYASHI, 1937, p. 422 [**R. subcircus;* OD]. A typical nanorthin but multicostellate and with shallow, weakly developed notothyrial platform. *Lower Ordovician (Tremadoc):* Bolivia.——FIG. 537,*3a–c.* **R. subcircus,* Tremadoc, Bolivia; *a,* internal mold of dorsal valve, ×1.5; *b,* internal mold of ventral valve, ×1.5; *c,* ventral exterior, ×1.5 (Kobayashi, 1937).

Shoshonorthis JAANUSSON & BASSETT, 1993, p. 51 [**Orthis michaelis* CLARK, 1935, p. 242; OD]. Medium size, subquadrate with obtuse cardinal extremities, rectimarginate, costate and capillate; relatively long, subparallel dental plates flanking elongate, bilobed ventral muscle scar; brachiophores divergent, rodlike; dorsal adductor scars with posterior pair larger than anterior pair. *Lower Ordovician (Arenig–Llanvirn):* North America, China, northern Africa.——FIG. 537,*6a–d.* **S. michaelis* (CLARK), Llanvirn, Utah; *a,* dorsal interior, ×1; *b,* dorsal interior, ×1 (Clark, 1935); *c,* rubber replica of ventral interior, ×2; *d,* rubber replica of dorsal interior, ×2 (Ross, 1967).

Xinanorthis XU, RONG, & LIU, 1974, p. 145 [**X. striata;* OD]. Similar to *Archaeorthis* but lacking wide median ridge extending anteriorly of ventral muscle scar and with low, ridgelike cardinal process on relatively well-developed notothyrial platform; bilobed anterior pair of quadripartite dorsal adductor scar larger than posterior pair; fila not reported. *Lower Ordovician (Arenig):* China.——FIG. 538,*3a–c.* **X. striata,* Arenig, China; *a,* internal molds of ventral valve (center) together with internal molds of dorsal valves (top), ×1; *b,* internal mold of dorsal valve, ×3; *c,* internal mold of dorsal valve, ×1 (Rong, new).

Family ORTHIDIELLIDAE
Ulrich & Cooper, 1936

[Orthidiellidae ULRICH & COOPER, 1936b, p. 621]

Medium size, variably unisulcate, costellate, normally ventribiconvex orthoids with delthyrium and notothyrium rarely constricted by covers, interareas normally short and curved; dental plates recessive, ventral muscle scar variably developed but with broad adductor track not encircled by narrower diductor scars; notothyrial platform supporting high, ridgelike cardinal process ankylosed to pair of notothyrial ridges to simulate trilobed myophore and joined to rodlike brachiophores; variably impressed dorsal adductor scars with posterior pair lying posterolaterally to anterior pair on either side of variably developed dorsal median ridge; saccate ventral mantle canal system sporadically impressed, dorsal mantle canal system poorly impressed, probably digitate. *Lower Ordovician (Tremadoc)–Upper Ordovician (Caradoc).*

Orthidiella ULRICH & COOPER, 1936b, p. 621 [**O. longwelli;* OD]. Subquadrate with obtuse cardinal extremities, sharply unisulcate, ramicostellate with delthyrial apical plate; ventral muscle scar bilobed with elongate diductor and wide adductor impressions; brachiophore rods divergent. *Lower Ordovician (Arenig–Llanvirn):* North America, Estonia, Siberia, South America (Argentina).——FIG. 539,*1a–e.* **O. longwelli,* Llanvirn, Nevada; *a,* ventral interior, ×2; *b,* dorsal interior, ×4; *c,* details of cardinalia, ×12; *d,e,* ventral, dorsal views of conjoined valves, ×4 (Ulrich & Cooper, 1938).

Eostrophomena WALCOTT, 1905, p. 256 [**Strophomena (Eostrophomena) elegantula;* OD]. Transversely semioval with acute cardinal extremities, concavo-convex, parvicostellate and imbricate; delthyrium open, notothyrium partly closed by chilidium, ventral muscle scar subcordate; brachiophore rods widely divergent; subperipheral rims present in both valves. [The assignment of this genus to the Orthidiellidae rests mainly on cardinal process ankylosed to high notothyrial ridges, open delthyrium, and allegedly impunctate shell. Other features are plectambonitoid and even the cardinal process could be interpreted as being trilobed by association with chilidial plates dependent on whether they arise lateral to the posteromedian ends of the brachiophores.] *Lower Ordovician (Tremadoc):* Sweden, eastern Baltic.——FIG. 539,*2a–c.* **E. elegantula* (WALCOTT), Tremadoc, Västergötland; *a,* dorsal interior, ×2; *b,* ventral interior, ×2; *c,* partly exfoliated ventral exterior, ×2 (Williams, 1965b).

Orthidium HALL & CLARKE, 1892, p. 244 [**Orthis gemmicula* BILLINGS, 1862 in 1861–1865, p. 75; OD]. Similar to *Orthidiella* but more strongly ventribiconvex with variable cardinal extremities and long, curved ventral interarea, strongly imbricate. *Lower Ordovician (Tremadoc–Llanvirn):* North America, western Ireland, Scotland, northwestern China, South America (Argentina).——FIG. 539,*5a–d.* **O. gemmicula* (BILLINGS), Tremadoc, Quebec; *a,* ventral interior, ×6; *b,* dorsal interior, ×6; *c,* dorsal exterior, ×4; *d,* ventral exterior, ×4 (Ulrich & Cooper, 1938).——FIG. 539,*5e–g. O. bellullum,* Llanvirn, Nevada; dorsal, ventral, anterior views, ×4 (Cooper, 1956).

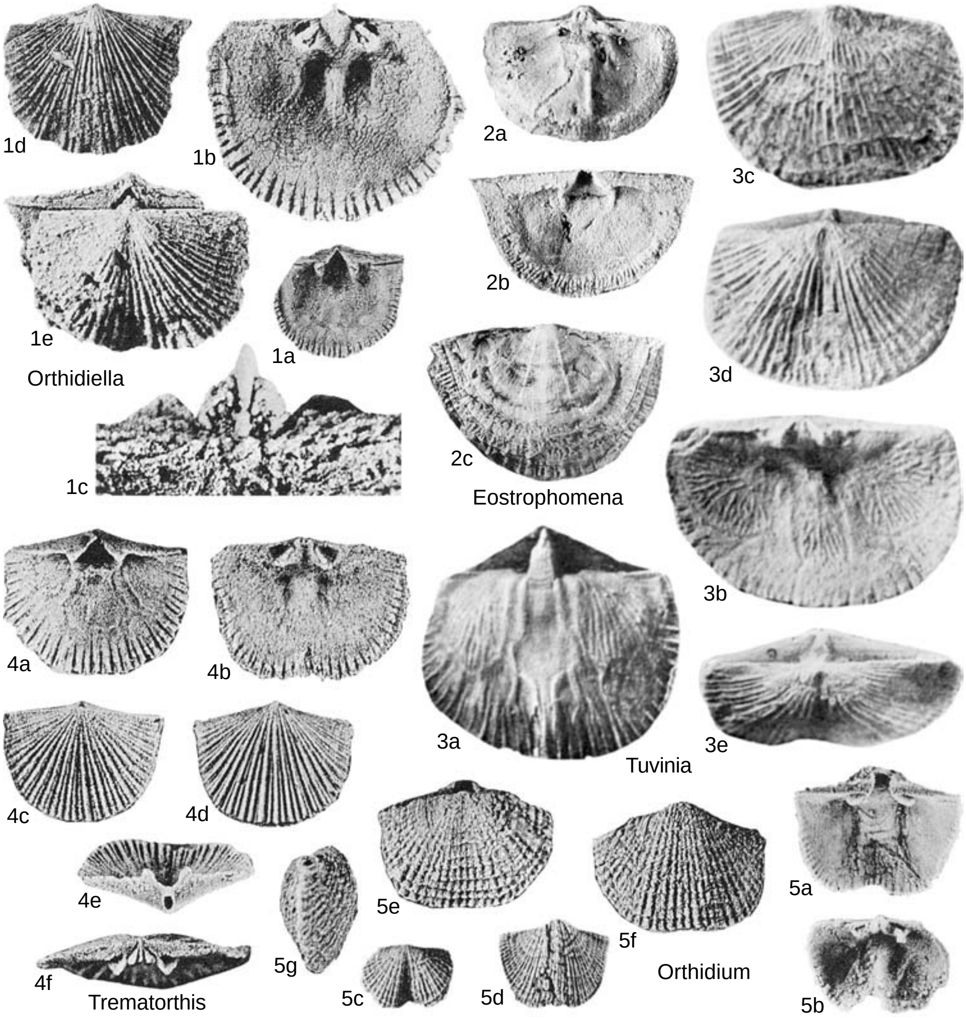

Fig. 539. Orthidiellidae (p. 745–746).

Trematorthis Ulrich & Cooper, 1938, p. 112 [**T. masoni;* OD]. Subquadrate with variable cardinal extremities, ramicostellate, delthyrium partly covered by deltidium with apical foramen, notothyrium open, ventral interarea relatively long, curved; ventral muscle scar suboval. *Lower Ordovician (Arenig–Llanvirn):* North America, South America (Argentina).——Fig. 539,*4a–f.* **T. masoni,* Llanvirn, Nevada; *a,* ventral interior, ×3; *b,* dorsal interior, ×3; *c,d,* dorsal, ventral views of conjoined valves, ×3; *e,* posterior views of ventral valve, ×3; *f,* posterior view of dorsal valve, ×4 (Cooper, 1956).

Tuvinia Andreeva, 1982, p. 53 [**T. radiata;* OD]. Subquadrate with variably angled cardinal extremities, unisulcate, ramicostellate; well-developed deltidium with apical foramen; ventral muscle scar subtriangular; cardinal process consisting of median plate flanked by pair of notothyrial ridges, quadripartite adductor scars subequal; ventral mantle canal system saccate with widely parallel *vascula media* dividing toward anterior margin, dorsal system saccate with gonadal pouches developed between widely spaced *vascula media.* [The illustrations of this genus suggest that the cardinal process is not solely a simple plate, as indicated in the diagnosis, but a trifid structure involving lateral notothyrial ridges. There is also an interesting similarity between the mantle canal systems of *Tuvinia* and *Orthostrophia.*] *Upper Ordovician (Caradoc):* central Asia.——Fig. 539,*3a–e. T. radiata,* Upper Ordovician, central Asia; *a,* internal mold of ventral valve, ×4; *b,* rubber replica of dorsal interior, ×4; *c–e,* ventral, dorsal, posterior views of conjoined valves, ×4 (Andreeva, 1982).

Family PLAESIOMYIDAE
Schuchert, 1913

[*nom. transl. et correct.* WILLIAMS, 1965b, p. 319, *ex* Plaesiomiinae SCHUCHERT, 1913b, p. 382] [=Dinorthidae SCHUCHERT & COOPER, 1931, p. 244]

Costellate orthoids with receding or subparallel dental plates, ventral muscle scar subquadrate to bilobate, with variable enclosure by elongate diductor scars of lanceolate to oval adductor track; notothyrial platform supporting large cardinal process and divergent brachiophores; saccate ventral mantle canal system with divergent *vascula media,* dorsal system sporadically preserved, variable. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Subfamily PLAESIOMYINAE
Schuchert, 1913

[*nom. correct.* WILLIAMS, 1965b, p. 319, *pro* Plaesiominae SCHUCHERT, 1913b, p. 382]

Large, usually transversely semioval with variable cardinal extremities, subequally biconvex to convexoconcave, normally rectimarginate; costellae exceptionally with aditicules; apsacline ventral interarea varying in length and curvature, dorsal interarea extremely variable; ventral muscle scar normally with median ridge, pedicle callist reported in some genera; notothyrial platform strong with low, discrete ridges flanking cardinal process differentiated into myophore and shaft, divergent brachiophores rodlike, sockets obliquely elongate, quadripartite dorsal muscle scar poorly impressed; dorsal system not well known, normally lemniscate. *Ordovician (Llanvirn–Ashgill).*

Plaesiomys HALL & CLARKE, 1892, p. 196 [**Orthis subquadrata* HALL, 1847, p. 126; OD]. Cardinal extremities obtuse, convexoconcave, broadly unisulcate, multicostellate, sporadically lamellose; ventral interarea short, curved, anacline dorsal interarea vestigial; ventral muscle scar without median ridge; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Caradoc–Ashgill):* Northern Hemisphere.——FIG. 540,*1a–d.* **P. subquadrata* (HALL), Ashgill, Indiana; *a,b,* ventral, dorsal exteriors of conjoined pair, ×1; *c,* ventral interior, ×1.5; *d,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).

Austinella FOERSTE, 1909b, p. 224 [**Orthis kankakensis* MCCHESNEY, 1861, p. 77; SD BASSLER, 1915, p. 1002]. Subequally biconvex, unisulcate, ramicostellate with sporadic aditicules, strongly filate; ventral interarea long, curved, anacline dorsal interarea short, plane; ventral muscle scar with thickened margin; dorsal adductor scar subequally quadripartite. *Upper Ordovician (Ashgill):* North America, Europe, Siberia, Kazakhstan, northeastern and northwestern China.——FIG. 540,*3a–d. A. whitfieldi* (WINCHELL), Ashgill, Minnesota; *a,* internal mold of ventral valve, ×1.5; *b,* dorsal interior, ×1.5; *c,d,* ventral, dorsal exteriors, ×1.5 (Schuchert & Cooper, 1932).

Campylorthis ULRICH & COOPER, 1942, p. 621 [**Strophomena deflecta* CONRAD, 1843, p. 332; OD]. Dorsibiconvex to convexoconcave, rectimarginate to uniplicate, multicostellate, apically perforated deltidium and well-developed chilidium; ventral interarea long, plane, dorsal interarea orthocline to anacline. *Upper Ordovician (Caradoc):* United States, Scotland, Ireland.——FIG. 540,*2a–d.* **C. deflecta* (CONRAD), Caradoc, Wisconsin; ventral, dorsal, lateral, posterior views of conjoined valves, ×1 (Cooper, 1956).

Chaulistomella COOPER, 1956, p. 432 [**C. inequistriata;* OD]. Subquadrate with acute cardinal extremities, convexoconcave to convexoplane, generally rectimarginate but varying from slightly uniplicate to unisulcate, multicostellate, strongly filate; ventral interarea long, curved, dorsal interarea relatively long, orthocline to apsacline; pedicle callist well developed; posterior pair of quadripartite dorsal adductor scars larger than anterior; dorsal mantle canal system lemniscate. *Upper Ordovician (Caradoc):* eastern North America, Scotland, Siberia, Kirghizia.——FIG. 541,*4a–e.* **C. inequistriata,* Caradoc, Virginia; *a–c,* ventral, dorsal, posterior views of conjoined valves, ×1; *d,* ventral interior, ×1; *e,* dorsal interior, ×2 (Cooper, 1956).

Dinorthis HALL & CLARKE, 1892, p. 195 [**Orthis pectinella* EMMONS, 1842, p. 394; OD] [=*Diorthis* KOBAYASHI, 1937, p. 12, *nom. nud.*]. Cardinal extremities obtuse, convexoconcave, costate; ventral interarea short, curved, apsacline; dorsal interarea short, curved; dental plates projecting anteriorly, subparallel. *Upper Ordovician (Caradoc):* Northern Hemisphere.——FIG. 541,*1a,b.* **D. pectinella* (EMMONS), Caradoc, eastern United States; *a,* ventral exterior, ×0.75; *b,* ventral interior, ×1 (Schuchert & Cooper, 1932).——FIG. 541,*1c–f. D. holdeni* (WILLARD), Caradoc, eastern United States; *c,* dorsal interior, ×2; *d,* details of cardinalia, ×3; *e,* ventral interior, ×2; *f,* ventral exterior, ×2 (Cooper, 1956).

Multicostella SCHUCHERT & COOPER, 1931, p. 244 [**Orthis saffordi* HALL & CLARKE, 1892, p. 217; OD]. Subquadrate with acute or obtuse cardinal extremities, subequally biconvex, rectimarginate to unisulcate, multicostellate, strongly filate; ventral interarea long, curved, orthocline dorsal interarea relatively short, curved; ventral muscle scar without median ridge, pedicle callist well developed; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Caradoc):*

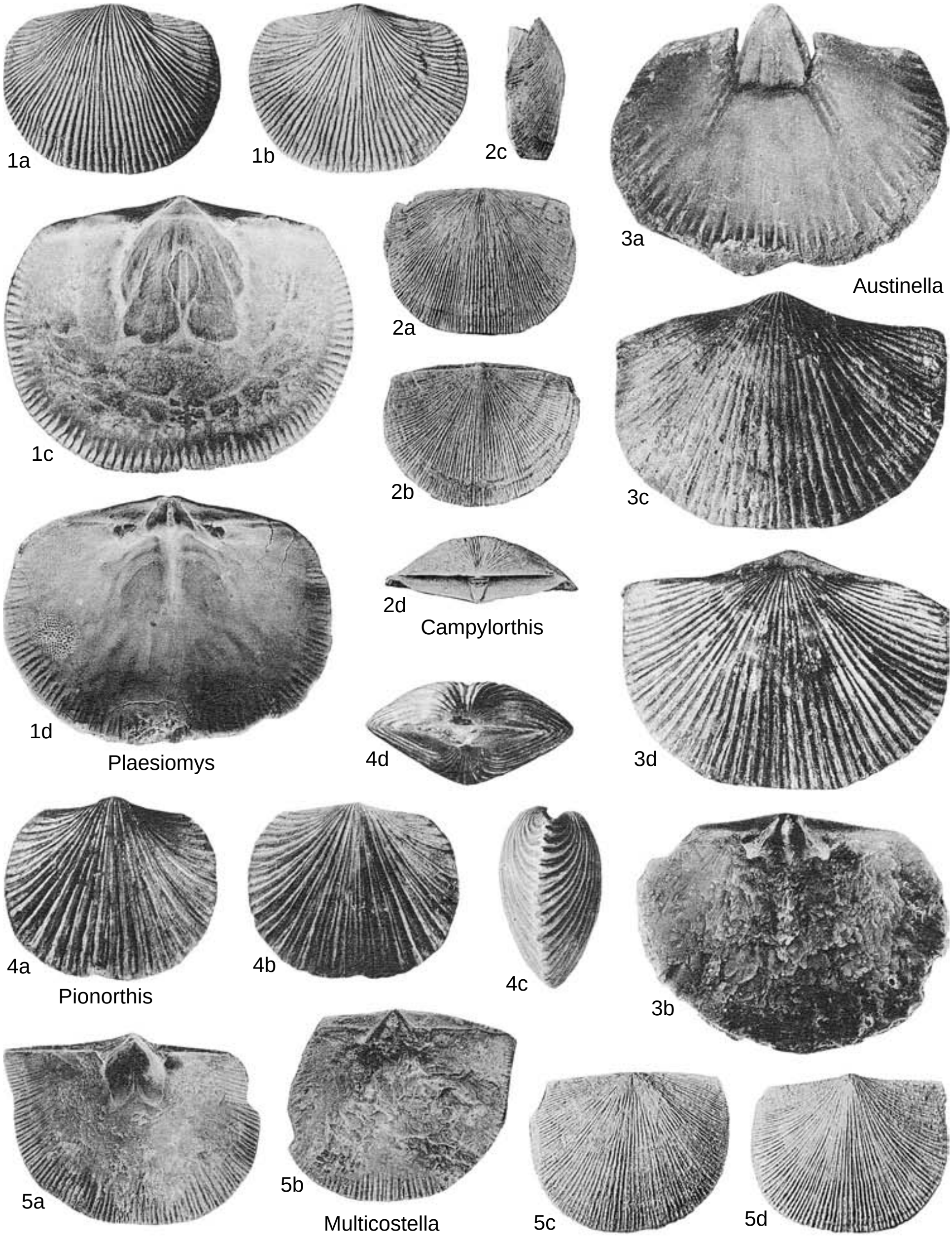

FIG. 540. Plaesiomyidae (p. 747–749).

Northern Hemisphere.——FIG. 540,*5a,b*. **M. saffordi* (HALL & CLARKE), Caradoc, Tennessee; *a,* ventral interior, ×1.5; *b,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).——FIG. 540,*5c,d. M. gerontica* (COOPER), Caradoc, Tennessee; *c,* dorsal exterior, ×1; *d,* ventral exterior, ×1 (Cooper, 1956).

Pionorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis sola* BILLINGS, 1866, p. 12; OD]. Similar to *Plaesiomys* but subequally biconvex and coarsely costellate; apsacline dorsal interarea short curved; ventral muscle scar with low median ridge. *Upper Ordovician (Ashgill):* North America, northwestern

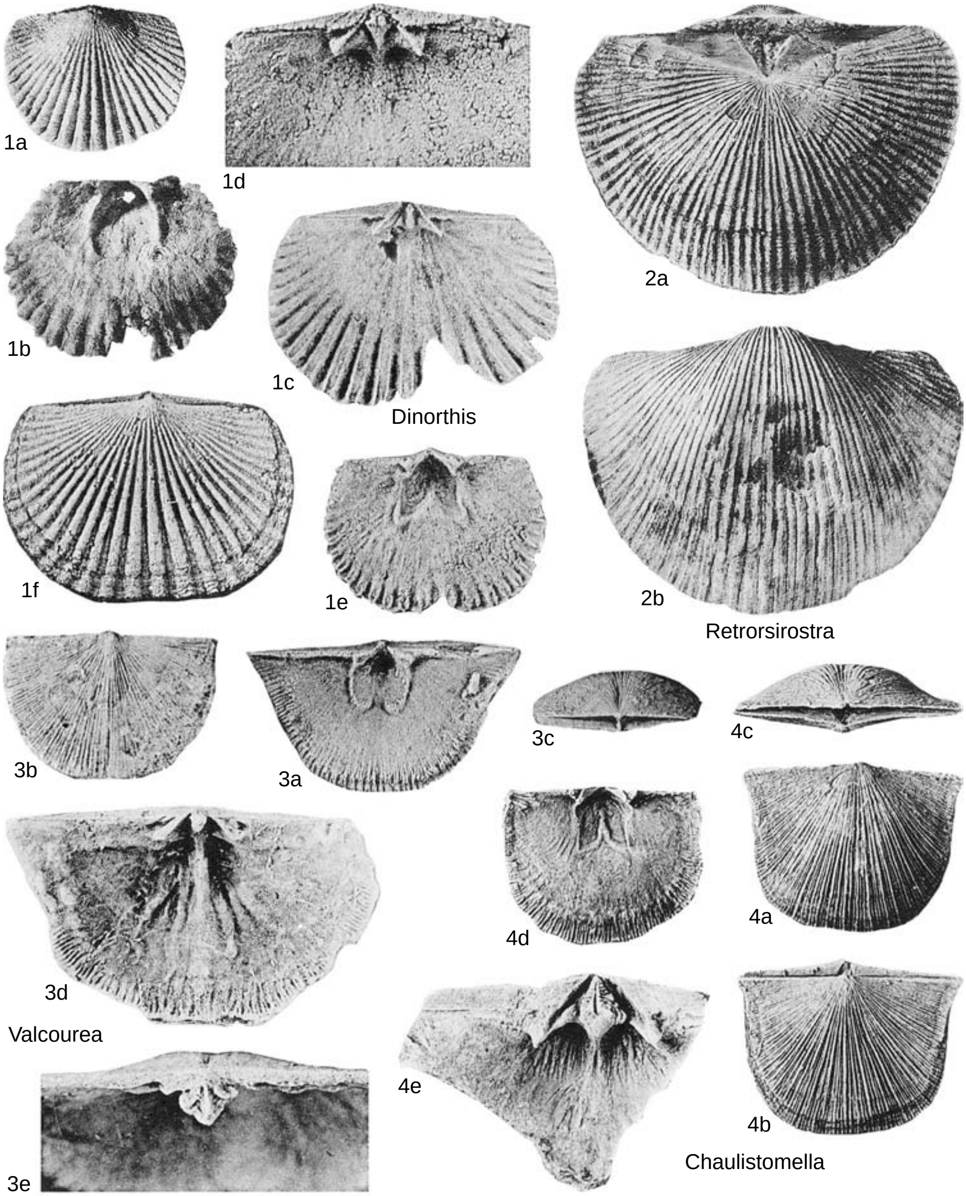

FIG. 541. Plaesiomyidae (p. 747–750).

China.——FIG. 540,*4a–d.* **P. sola* (BILLINGS), Ashgill, Anticosti; ventral, dorsal, lateral, posterior views of conjoined valves, ×1.5 (Schuchert & Cooper, 1932).

Retrorsirostra SCHUCHERT & COOPER, 1931, p. 244 [**Orthis carleyi* HALL, 1847, p. 120; OD]. Similar to *Plaesiomys* but rectimarginate, coarsely costellate, and filate; procline ventral interarea long, planar, orthocline dorsal interarea short, curved; dental plates projecting subparallel, ventral muscle scar impressed on low callus with median ridge. *Upper Ordovician (Ashgill):* Northern Hemisphere.——FIG. 541,*2a,b.* **R. carleyi* (HALL), Ashgill, Indiana; ventral, dorsal exteriors, ×1.5 (Schuchert & Cooper, 1932).

Valcourea RAYMOND, 1911, p. 239 [**Plaesiomys strophomenoides* RAYMOND, 1905, p. 370; OD]. Cardinal extremities acute, convexoconcave, sharply unisulcate umbonally with sulcus becoming fainter toward margin of adult valves, multicostellate to unequally parvicostellate, strongly filate with aditicules; imperforate deltidium and strong chilidium; ventral interarea relatively long planar, dorsal interarea shorter, orthocline to apsacline; dental plates projecting subparallel, ventral muscle scar quadrate, tending to become bilobed anteriorly with diductor enclosing adductor impressions, pedicle callist well developed; subperipheral rim in ventral valve; dorsal mantle canal system pinnate. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* North America, Scotland, Norway, northeastern China, central Asia, South America (Argentina).——FIG. 541,*3a–c.* **V. strophomenoides* (RAYMOND), Caradoc, New York; *a,* ventral interior, ×3; *b,* ventral exterior, ×2; *c,* posterior view of dorsal valve, ×2 (Cooper, 1956).——FIG. 541,*3d,e. V. deckeri* (COOPER), Caradoc, Oklahoma; *d,* dorsal interior, ×2; *e,* details of cardinalia, ×3 (Cooper, 1956).

Subfamily EVENKININAE Williams, 1965

[Evenkininae WILLIAMS, 1965b, p. 321]

Planoconvex or rarely dorsibiconvex, strongly unisulcate; interareas short, curved; ventral muscle scar subquadrate with diductor scars enclosing median ridge probably bearing adductor track; brachiophores platelike, ankylosed to valve floor, cardinal process undifferentiated or with traces of posterior bilobation. *Upper Ordovician (Caradoc).*

Evenkina ANDREEVA in NIKIFOROVA & ANDREEVA, 1961, p. 96 [**E. anarbensis;* OD]. Small, subquadrate with variable cardinal extremities, ramicostellate; quadripartite dorsal adductor scars subequal. *Upper Ordovician (Caradoc):* Siberia.——FIG. 542,*1a–d.* **E. anarbensis,* Caradoc, Siberia; *a,* dorsal exterior, ×3; *b,* ventral interior, ×4; *c,* dorsal interior, ×2; *d,* posterior view of dorsal interior, ×4 (Nikiforova & Andreeva, 1961).

Subfamily METORTHINAE Williams, 1965

[Metorthinae WILLIAMS, 1965b, p. 322]

Planoconvex, unisulcate; notothyrial edges elevated; interareas relatively short, planar; ventral muscle scar elongately bilobed not entirely surrounding lanceolate adductor track; brachiophores rodlike, pointed and embedded in strong notothyrial platform with excavated elongate sockets, cardinal process undifferentiated, dorsal mantle canal system digitate. *Lower Ordovician (Arenig).*

Metorthis WANG, 1955b, p. 333 [**M. alata;* OD]. Subquadrate with variable cardinal extremities, ramicostellate; quadripartite dorsal adductor scars subequal. *Lower Ordovician (Arenig):* China.——FIG. 542,*2a–d.* **M. alata,* Arenig, southern China; *a,b,* dorsal, posterior views of conjoined valves, ×2.5; *c,* ventral interior, ×2.5; *d,* dorsal interior, ×2.5 (Wang, 1955b).

Family PORAMBORTHIDAE Havlíček, 1950

[Poramborthidae HAVLÍČEK, 1950, p. 58]

Subcircular, biconvex, rectimarginate orthoids with dichotomizing capillae cancellated by imbricae; interareas relatively short, curved; dental plates subparallel to narrowly divergent, flanking suboval ventral muscle scar with short ridge posteromedian of elongate adductor track; notothyrial platform rudimentary to low, bearing linear diductor scars on either side of ridgelike cardinal process, divergent brachiophores bladelike, dorsal median ridge absent; adductor scars narrow with posterior pair larger than anterior pair; ventral mantle canal system pinnate with divergent *vascula media,* dorsal system probably pinnate. *Lower Ordovician (Tremadoc).*

Poramborthis HAVLÍČEK, 1949a, p. 107 [**P. klouceki;* OD]. Medium to large size, cardinal extremities obtuse, ventral muscle scar commonly elongate in adult shells. *Lower Ordovician (Tremadoc):* Bohemia, Bavaria, Spain.——FIG. 542,*3a–d.* **P. klouceki,* Tremadoc, Bohemia; *a,* internal mold of ventral valve, ×4.3; *b,* internal mold of ventral valve, ×4.4; *c,* internal mold of dorsal valve, ×4.7; *d,* external mold, ×6.6 (Havlíček, 1977a).

Family PRODUCTORTHIDAE Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Productorthinae SCHUCHERT & COOPER, 1931, p. 241]

Subquadrate, costellate orthoids lacking capillae; teeth normally supported by divergent dental plates, ventral muscle field suboval to subcordate with broad, subtriangular or parallel-sided adductor track commonly undifferentiated and rarely shorter than flanking diductor scars, usually associated with well-developed pedicle callist, less com-

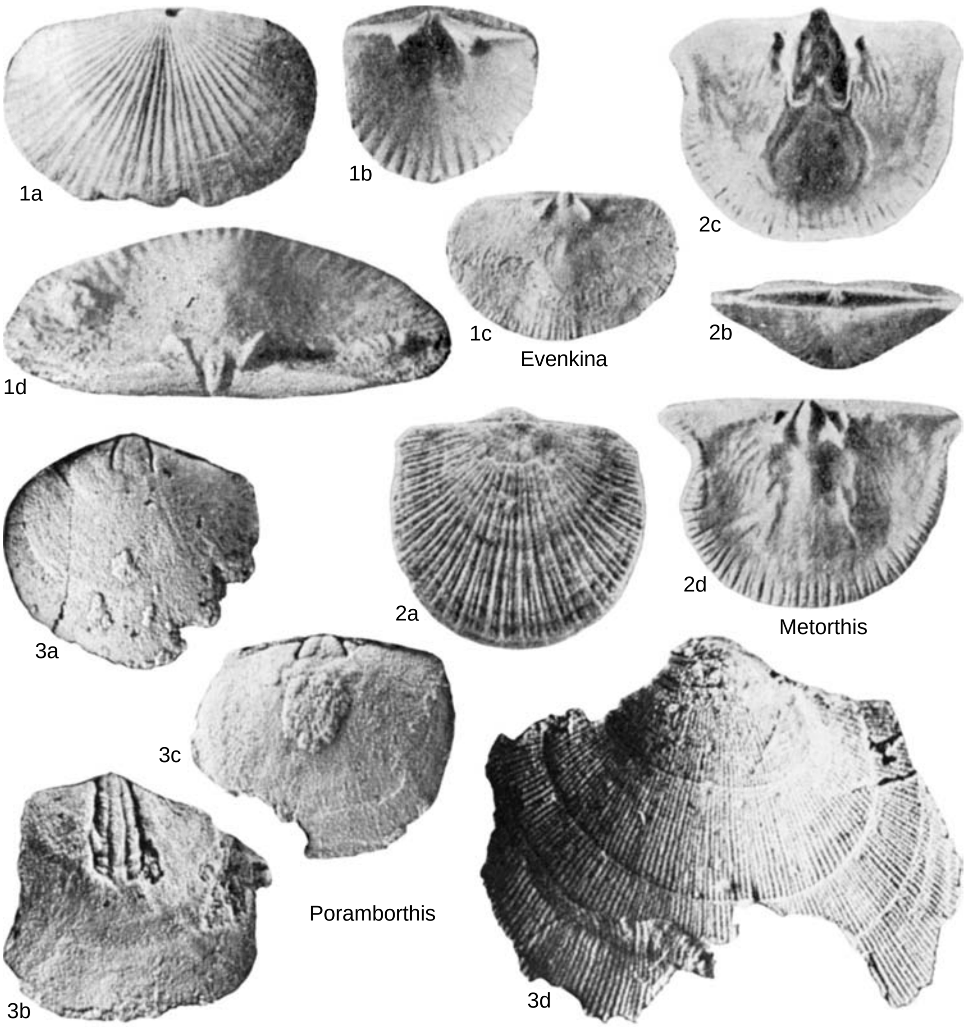

FIG. 542. Plaesiomyidae and Poramborthidae (p. 750).

monly impressed on pseudospondylium; notothyrial platform with cardinal process, typically simple ridge of variable strength; dorsal adductor scars quadripartite with each of larger anterior pair divided into larger inner and smaller outer lobe. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Subfamily PRODUCTORTHINAE Schuchert & Cooper, 1931

[Productorthinae SCHUCHERT & COOPER, 1931, p. 243]

Generally medium-size, planoconvex, gently unisulcate, coarsely costellate productorthids commonly with acute cardinal extremities, short to vestigial interareas; pseudospondylium or callist commonly developed but rarely prolonged anteromedianly as ridge; notothyrial platform extending anteriorly as median ridge, cardinal process of variable complexity; divergent brachiophores rodlike; saccate ventral mantle canal system normally with divergent *vascula media,* dorsal system digitate or less commonly lemniscate. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Productorthis Kozłowski, 1927, p. 9 [**Productus obtusus* Pander, 1830, p. 87; OD]. Rectimarginate to broadly unisulcate, lamellose, ventral beak curved, usually resorbed presumably as pedicle passage, dorsal beak vestigial; interareas vestigial with ventral posterior margin grooved (ginglymoid joint) to accommodate linear, dorsal posterior margin; apical pedicle foramen; ventral muscle scar elongately suboval impressed on thick callist; cardinal process differentiated into thick shaft and carinate myophore, commonly bearing small circular supposed chilidium; saccate ventral mental canal system with subparallel *vascula media* greatly divided anteriorly, dorsal mantle canal system poorly known. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc):* cosmopolitan.——Fig. 543,*1a–e. P. parallela* (Pander), Arenig, Russia; *a,* dorsal interior, ×3; *b,* ventral interior, ×3; *c,d,* ventral, dorsal exteriors of conjoined valves, ×3; *e,* dorsal exterior, ×3 (Schuchert & Cooper, 1932).

Ferrax Havlíček, 1975, p. 231 [**Prantlina oolitica* Havlíček, 1949b, p. 251; OD]. Ventribiconvex with nearly flat dorsal valve, cardinal extremities variable, rectimarginate, sporadically lamellose, apsacline ventral and shorter anacline dorsal interareas flat; ventral muscle scar subtriangular, impressed on low callist bounded by anterior, transverse ridge; cardinal process thick, trilobed; ventral mantle canal system saccate with divergent *vascula media,* dorsal system digitate. *Lower Ordovician (Arenig):* Bohemia.——Fig. 543,*2a–c.* **F. oolitica,* Arenig, Bohemia; *a,* internal mold of ventral valve, ×3.8; *b,* internal mold of dorsal valve, ×4; *c,* external mold of dorsal valve, ×3.3 (Havlíček, 1977a).

Nicolella Reed, 1917, p. 860 [**Orthis actoniae* J. de C. Sowerby, 1839, p. 639; OD]. Rectimarginate, lamellose, notothyrium closed by chilidial plates flanking simple, erect cardinal process; orthocline ventral interarea short, curved, anacline dorsal interarea very short; dental plates widely divergent, ventral muscle field subcordate, impressed on weak callist, diductor scars not enclosing adductor track; anterior dorsal adductor scars probably quadripartite, obscured by impressions of digitate to lemniscate mantle canal system; ventral mantle canal system saccate, slightly divergent *vascula media* divided anteriorly. *Upper Ordovician (Caradoc–Ashgill):* Europe, North America, northern Africa, Asia.——Fig. 544,*1a–d.* **N. actoniae* (Sowerby), Caradoc, Shropshire, England; *a,b,* internal mold, rubber replica of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×1.5; *d,* rubber replica of dorsal exterior, ×1.5 (Cocks, new).

Panderina Schuchert & Cooper, 1931, p. 243 [**Productus abscissus* Pander, 1830, p. 86; OD]. Ramicostellate, filate, vestigial interareas, ventral beak usually resorbed; ventral muscle scar suboval, impressed on pseudospondylium extending anteriorly as low median ridge; cardinal process simple, thick. *Lower Ordovician (Arenig):* Baltic Region, China.——Fig. 544,*3a,b.* **P. abscissus* (Pander), Arenig, Russia; dorsal, ventral views of conjoined valves, ×2.25 (Schuchert & Cooper, 1932).——Fig. 544,*3c,d. P. tetragonum* (Pander), Arenig, Russia; *c,* dorsal interior, ×1.5; *d,* ventral interior, ×1.5 (Schuchert & Cooper, 1932).

Saucrorthis Xu, Rong, & Liu, 1974, p. 150 [**S. minor;* OD]. Similar to *Nicolella* but small, costate, finely pustulose, and lacking chilidial plates. *Lower Ordovician (Llanvirn):* southern China.——Fig. 544,*2a–c.* **S. minor,* Llanvirn, southwestern China; *a,* internal mold of ventral valve, ×8; *b,* internal mold of ventral valve, ×8; *c,* internal mold of dorsal valve, ×8 (Rong, new).

Styxorthis Mergl, 1991, p. 7 [**S. tuffogena;* OD]. Ramicostellate, apsacline ventral interarea short, curved, dorsal interarea vestigial; ventral muscle scar suboval, impressed on valve floor; trilobed cardinal process with high median ridge; ventral mantle canal system saccate, dorsal mantle canal system digitate. *Lower Ordovician (Arenig):* Bohemia.——Fig. 543,*3a–e.* **S. tuffogena,* Arenig, Bohemia; *a,* internal mold of ventral valve, ×3; *b,c,* internal mold, rubber replica of dorsal valve, ×3; *d,e,* normal, anterior view of ventral exterior, ×3 (Mergl, 1991).

Subfamily GLOSSORTHINAE new subfamily

[Glossorthinae Williams & Harper, herein]

Large productorthids normally ramicostellate with variable cardinal extremities, rectimarginate; ventral interarea normally apsacline, short, and curved, dorsal interarea very short, curved or flat; brachiophores normally bladelike, subparallel to divergent; suboval ventral muscle scar normally impressed on pseudospondylium, prolonged anteriorly as median ridge, cardinal process normally simple, notothyrial platform usually extending anteriorly as median ridge; mantle canal systems rarely impressed, ventral digitate, dorsal saccate. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc).*

Glossorthis Öpik, 1930, p. 82 [**G. tacens;* OD]. Ventribiconvex, coarsely costellate, orthocline ventral interarea short, curved, anacline dorsal interarea, very short, flat; dental plates subparallel, pseudospondylium well developed and prolonged anteromedianly as tonguelike projection, pedicle callist not recorded; brachiophores moderately divergent, bladelike. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc):* Europe, northern Africa.——Fig. 545,*1a–d.* **G. tacens,* Caradoc, Estonia; *a,b,* ventral interior, exterior, ×1.5; *c,d,* dorsal interior, exterior, ×1.5 (Schuchert & Cooper, 1932).

Krattorthis Jaanusson & Bassett, 1993, p. 56 [**Glossorthis verneuili* Rubel, 1961a, p. 184]. Similar to *Glossorthis* but ramicostellate with more convex dorsal valve, very short curved dorsal interarea and vestigial dorsal median ridge. *Lower Ordovician*

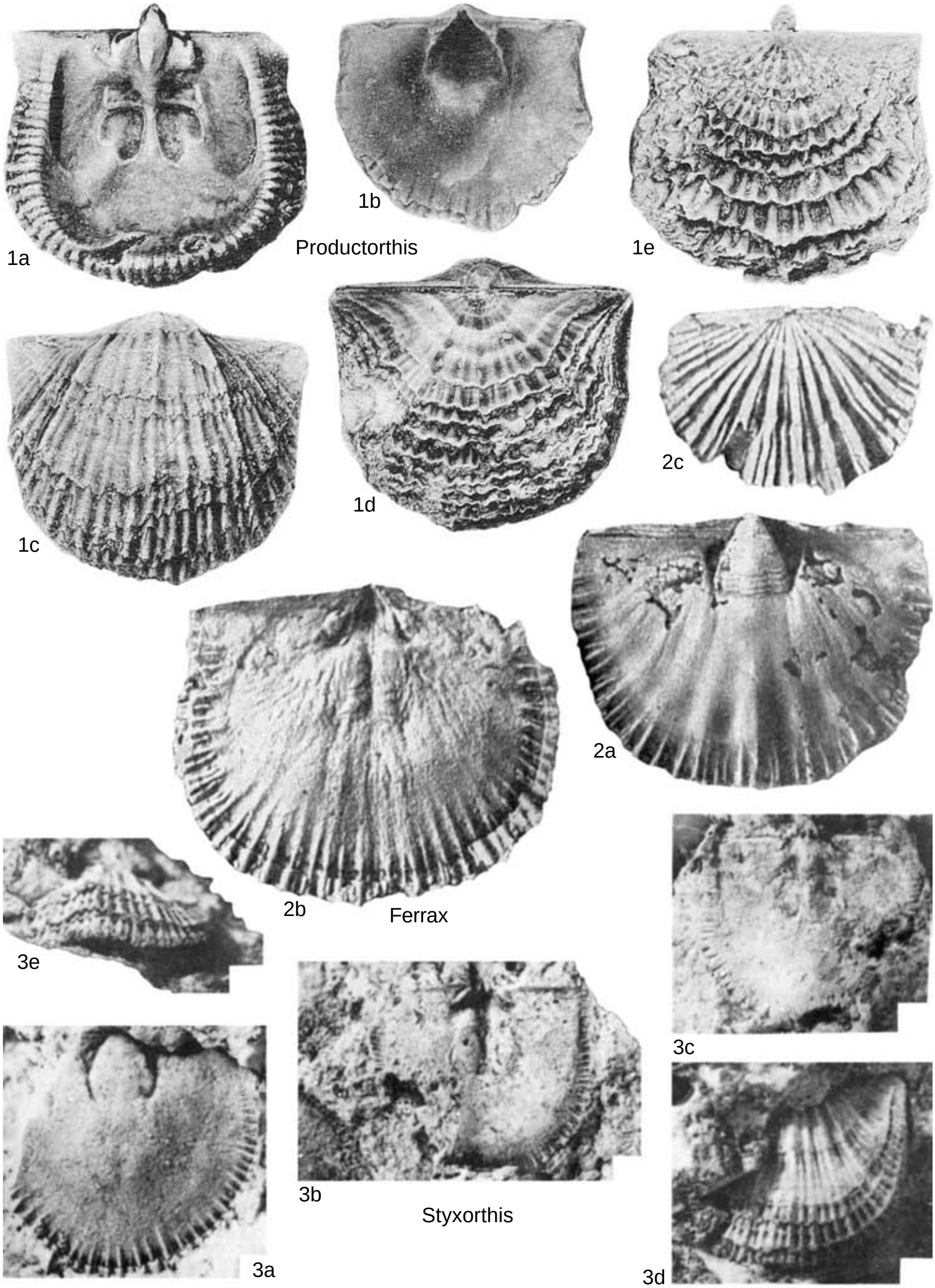

FIG. 543. Productorthidae (p. 752).

(Llanvirn): Baltic Region.——FIG. 545,*3a–e.* **K. verneuili* (RUBEL), Llanvirn, eastern Baltic; *a,b,* ventral, lateral views of conjoined valves, ×2; *c,* details of ornament, ×5; *d,e,* internal molds of ventral, dorsal valves of conjoined pair, ×2 (Jaanusson & Bassett, 1993).

Nicolorthis HAVLÍČEK, 1981, p. 7 [**N. instanta;* OD]. Medium size, planoconvex to gently ventribiconvex,

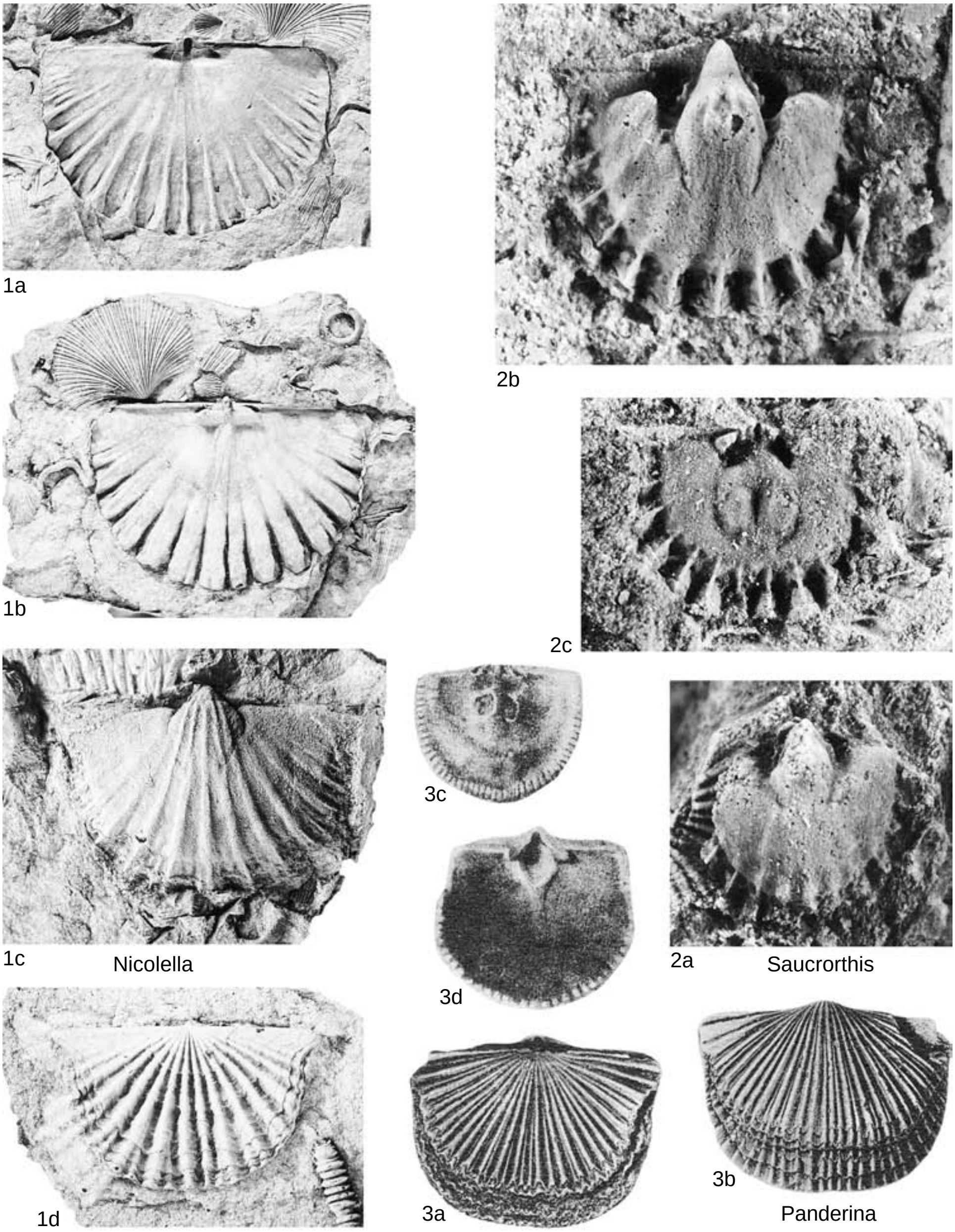

FIG. 544. Productorthidae (p. 752).

unisulcate, ramicostellate and lacking fila, orthocline ventral interarea short, curved, anacline dorsal interarea vestigial; ventral interior unknown; brachiophores narrowly divergent, bladelike, cardinal process thick with trilobed posterior face. *Upper Ordovician (Caradoc):* France (Montagne Noire). ——FIG. 546*a–d*. **N. instanta,* Caradoc, Montagne Noire; *a,b,* dorsal, ventral views of conjoined valves, ×1.3; *c,* dorsal interior, ×1.5; *d,* internal mold of dorsal valve, ×1.6 (Havlíček, 1981).

Prantlina HAVLÍČEK, 1949b, p. 250 [**Orthis desiderata* BARRANDE, 1848, pl. 18, fig. 6; OD]. Gently ventribiconvex, unisulcate, ramicostellate, filate, apsacline ventral interarea short, flat; anacline dor-

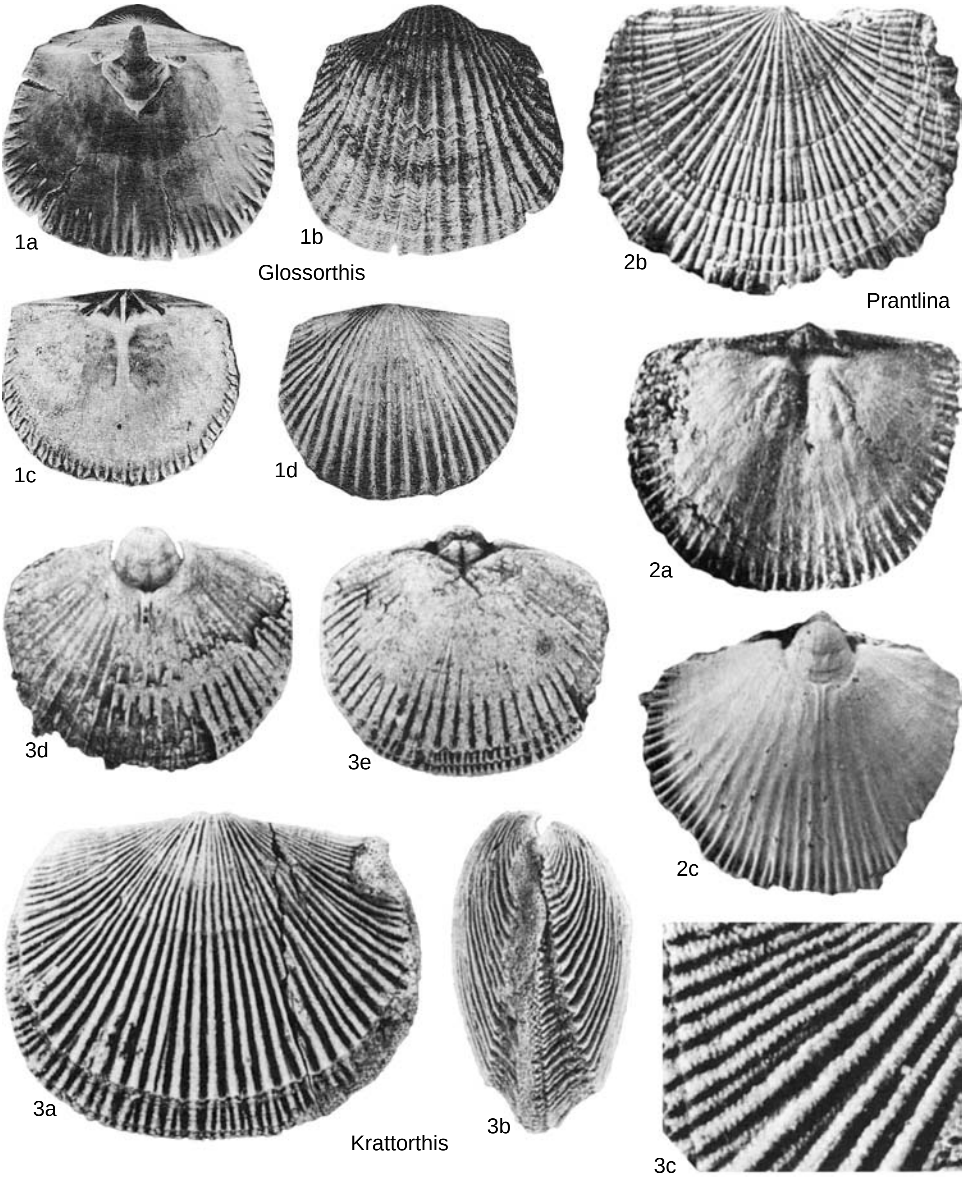

Fig. 545. Productorthidae (p. 752–755).

sal interarea very short, flat; dental plates widely divergent, pseudospondylium absent, pedicle callist well developed; widely divergent brachiophores rodlike; ventral mantle canal system digitate. *Lower Ordovician (Arenig–Llanvirn):* Bohemia, Estonia, France (Montagne Noire).——Fig. 545,*2a–c.* **P. desiderata* (Barrande), Arenig, Bohemia; *a,* internal mold of dorsal valve, ×2; *b,* external mold of dorsal valve, ×2; *c,* internal mold of ventral valve, ×1.7 (Havlíček, 1977a).

Family WHITTARDIIDAE Williams, 1974

[*nom. transl.* Williams & Harper, herein, *ex* Whittardiinae Williams, 1974, p. 60]

Subquadrate, plano- to concavoconvex, disharmonically costellate orthoids; simple oblique teeth, dental plates recessive and subparallel, ventral muscle field short,

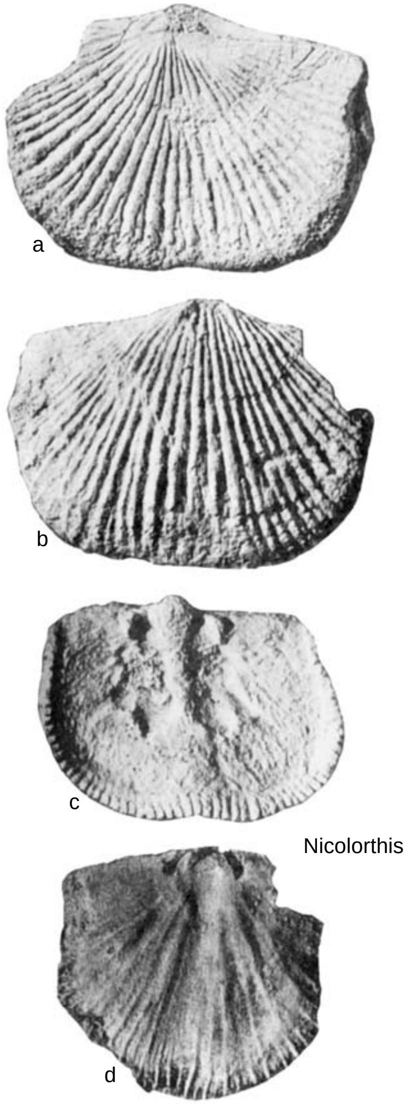

FIG. 546. Productorthidae (p. 753–754).

bilobed with undifferentiated adductor muscle track; notothyrial platform shallow, extending forward as short median ridge, cardinal process ridgelike, widely divergent; short brachiophores ridgelike; narrow, quadripartite dorsal adductor field with smaller posterior pair deeply inserted, dorsal subperipheral rim variably developed with dorsally directed geniculation; ventral mantle canal system probably saccate with *vascula media* branching early, dorsal system lemniscate or pinnate. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc).*

Whittardia WILLIAMS, 1974, p. 62 [**W. paradoxica;* OD]. Medium size with multicostellate and filate ornamentation on both valves but with dorsal umbonal region bearing only 6, strong, symmetrically disposed costae becoming subdued anteriorly; ventral interarea curved catacline to procline with mesothyridid foramen, dorsal interarea anacline, very short; ventral interior with 3 or 4 pairs of low ridges radiating from muscle field and fading away peripherally. *Upper Ordovician (Caradoc):* Great Britain.——FIG. 547,*1a–e.* **W. paradoxica,* Caradoc, England; *a,* internal mold of dorsal valve, ×3.6; *b,* internal mold of ventral valve, ×5; *c,* rubber replica of ventral exterior, ×5; *d,* detail of ornament, ×12.5; *e,* rubber replica of dorsal exterior, ×4.8 (Williams, 1974).

Marginorthis LIU, ZHU, & XUE, 1985, p. 40 [**M. crassocostata;* OD]. Small, multicostellate to fascicostellate; ventral interarea apsacline. [The disharmony of the ribbing and the subperipheral rims with a dorsal deflection of the dorsal margin suggest at least a morphological comparison with *Whittardia; Marginorthis* is included provisionally in this family.] *Lower Ordovician (Llanvirn):* northeastern China.——FIG. 547,*2a–e.* **M. crassocostata,* Llanvirn, northeastern China; *a,* internal mold of dorsal valve, ×3; *b,* internal mold of ventral valve, ×3 (Liu, Zhu, & Xue, 1985); *c,* internal mold of dorsal valve, ×8; *d,* internal mold of dorsal valve, ×4; *e,* external mold of dorsal valve, ×4 (Rong, new).

Superfamily
PLECTORTHOIDEA
Schuchert & LeVene, 1929

[*nom. transl.* HAVLÍČEK, 1977a, p. 75, *ex* Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14]

Costate to costellate orthides with delthyrium and notothyrium open, normally wide; apsacline ventral and almost invariably anacline dorsal interareas variable in length and curvature; teeth normally with crural fossettes, usually supported by divergent dental plates; ventral muscle field variable, impressed on floor of valve; pedicle callist normally well developed; divergent brachiophores usually bladelike, normally joined to hinge line by concave fulcral plates defining elongate sockets and supported by basal plates converging to form notothyrial septalium containing variably developed cardinal process; notothyrial platform variably developed, usually with short subdued dorsal median ridge more rarely culminating in high,

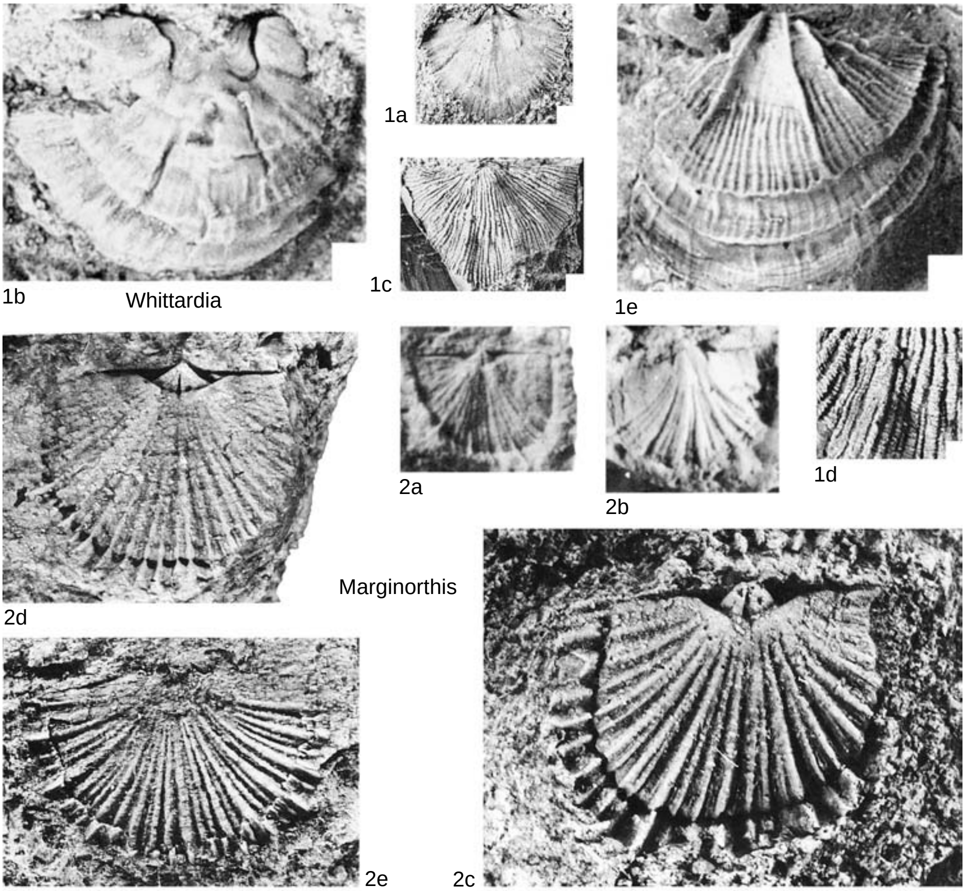

FIG. 547. Whittardiidae (p. 756).

bladelike septum; dorsal adductor field quadripartite; ventral mantle canal system saccate normally with parallel *vascula media;* dorsal system saccate to lemniscate. *Middle Cambrian–upper Silurian (Ludlow).*

Family PLECTORTHIDAE
Schuchert & LeVene, 1929

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 243, *ex* Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14]

Subcircular to transversely semioval plectorthoids commonly with obtuse cardinal extremities, apical plate rarely developed in delthyrium; ventral interarea curved, dorsal interarea variable in length and disposition; teeth with crural fossettes supported by variably disposed plates, ventral muscle field variably cordate but without diductor scars enclosing adductor tracks; brachiophores divergent, bladelike, joined to hinge line by concave fulcral plates and supported by plates convergent on to valve floor, extending forward as variably developed median ridge and containing cardinal process of variable complexity with negligible notothyrial platform; dorsal adductor scars quadripartite, normally with posterior pair larger than anterior. *Lower Ordovician (Tremadoc)–Upper Ordovician (Ashgill).*

Plectorthis HALL & CLARKE, 1892, p. 194 [**Orthis plicatella* HALL, 1847, p. 122; OD]. Transversely semioval, subequally gently biconvex with faintly sulcate to uniplicate anterior commissure, costate to coarsely costellate, filate; ventral interarea short, shorter dorsal interarea orthocline to faintly

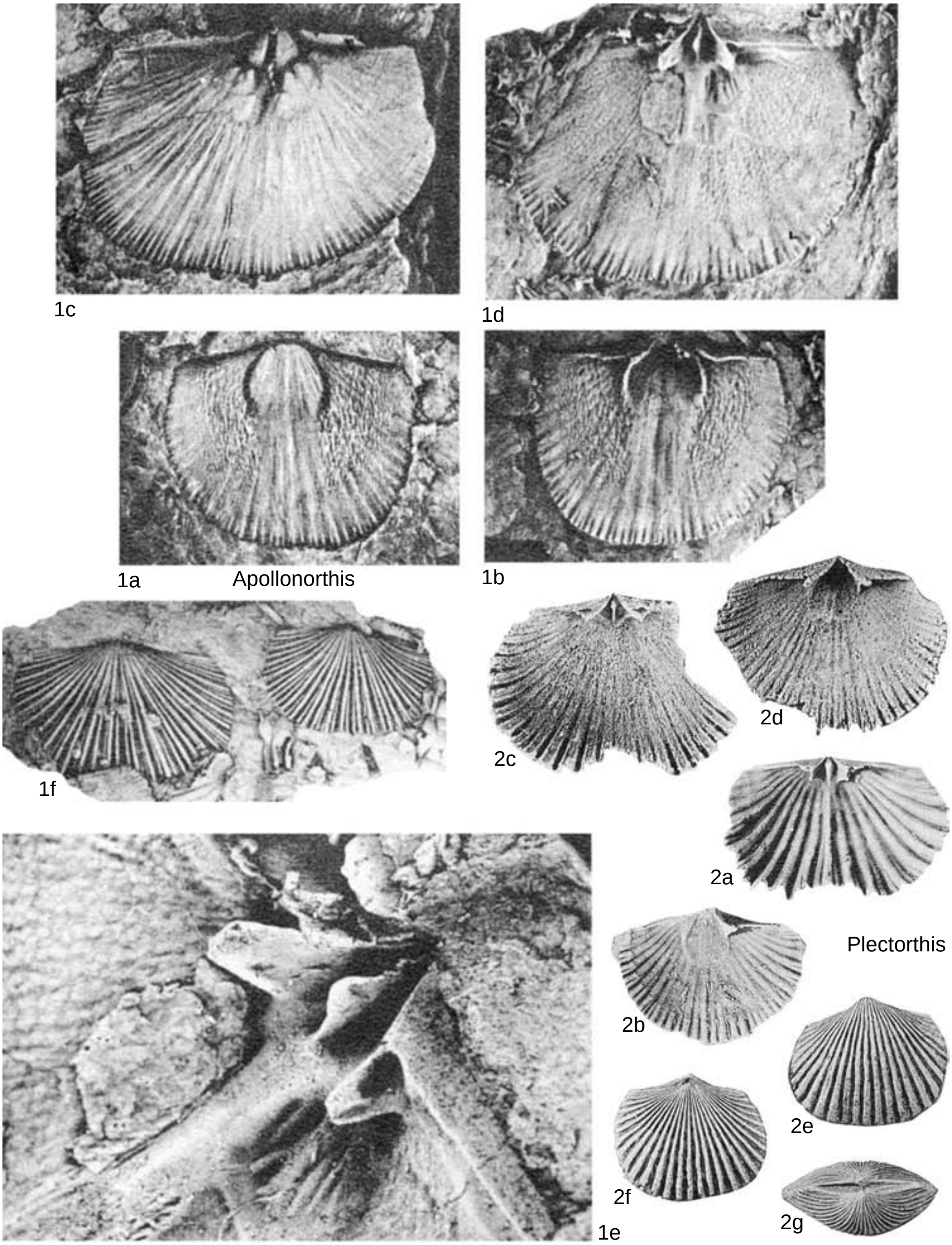

FIG. 548. Plectorthidae (p. 757–759).

anacline; dental plates divergent, ventral muscle field subcordate with linear adductor track contained by subcrescentic diductor scars separated anteriorly by low median ridge; pedicle callist not reported; cardinal process a thick, rounded ridge and crenulated myophore; exopunctate with radially distributed aditicules in some species. *Upper Ordovician (Caradoc–Ashgill):* cosmopolitan.——FIG. 548,*2a,b.* **P. plicatella* (HALL), Ashgill, Ohio; *a,* dorsal interior, ×1.5; *b,* ventral interior, ×1.5 (Schuchert & Cooper, 1932).——FIG. 548,*2c,d. P. compacta,* Caradoc, Tennessee; *c,* dorsal interior, ×2;

d, ventral interior, ×2 (Cooper, 1956).——FIG. 548,*2e–g. P. ponderosa,* Caradoc, Virginia; ventral, dorsal, posterior views of conjoined valves, ×1 (Cooper, 1956).

Apollonorthis MITCHELL, 1974, p. 392 [**A. lusitanica;* OD; =*Orthis bussacensis* SHARPE in RIBEIRO, 1853, p. 152]. Subquadrate, ventribiconvex, gently unisulcate, ramicostellate with aditicules, filate; interareas planar; dental plates divergent, ventral muscle field subcordate, bounded by thickened ridges, with broad adductor track not enclosed anteriorly by diductor scars; undifferentiated cardinal process platelike; posterior pair of quadripartite dorsal adductor scars larger than anterior pair. [This genus has also been assigned to the Hesperorthidae (MÉLOU, 1976, p. 694) because of its undifferentiated cardinal process. In fact, differentiation of the cardinal process took place among plectorthoids after the development of their highly distinctive cardinalia.] *Lower Ordovician (Llanvirn):* western Europe (Portugal, France).——FIG. 548,*1a–f.* **A. bussacensis* (SHARPE), Llanvirn, northwestern France; *a,b,* internal mold, rubber replica of ventral valve, ×2; *c,d,* internal mold, rubber replica of dorsal valve, ×2; *e,* details of cardinalia, ×6; *f,* rubber replica of dorsal exteriors, ×2 (Mélou, 1976).

Atlantida HAVLÍČEK, 1971a, p. 37 [**A. atlantis;* OD]. Large, transversely subquadrate, strongly biconvex to resupinate, ramicostellate (aditicules not reported); subcordate tending to flabellate ventral muscle field with diductor scars enclosing suboval adductor tracks; simple cardinal process. *Lower Ordovician (Llanvirn):* northern Africa.——FIG. 549,*3a–c.* **A. atlantis,* Llanvirn, northern Africa; *a,* internal mold of ventral valve, ×1.5; *b,* internal mold of dorsal valve, ×1.5; *c,* external mold of dorsal valve, ×1.7 (Havlíček, 1971a).

Corineorthis STUBBLEFIELD, 1939, p. 67 [**C. decipiens;* OD]. Subcircular, convexoconcave to resupinate, rectimarginate but with impersistent dorsal sulcus, multicostellate, with aditicules and strong fila simulating exopunctae in intercostellate grooves; open delthyrium and notothyrium relatively narrow; ventral interarea short, shorter dorsal interarea planar, anacline; dental plates short, parallel or narrowly divergent, ventral muscle field cordate with diductor scars not enclosing median adductor tracks that are divided by shallow groove; cardinal process with thick shaft and bulbous myophore, low median ridge bisecting subequally quadripartite adductor muscle scars. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Great Britain, France, southwestern China.——FIG. 549,*2a–f. C. cornubensis,* Llanvirn, southwestern England; *a,b,* internal mold, rubber replica of dorsal valve, ×2; *c,d,* internal mold, rubber replica of ventral valve, ×2; *e,f,* external mold, rubber replica of ventral valve, ×2 (Bassett, 1981).

Desmorthis ULRICH & COOPER, 1936b, p. 624 [**D. nevadensis;* OD]. Similar to *Plectorthis* but more subcircular with rectangular to obtuse cardinal extremities, ventribiconvex; delthyrium with apical plate, dorsal interarea anacline; dental plates narrowly divergent, ventral muscle field quadrate with adductor ridge extending forward; cardinal process simple, platelike. *Lower Ordovician (Llanvirn):* North America, England, Bolivia, southwestern China.——FIG. 549,*1a–d.* **D. nevadensis,* Llanvirn, Nevada; *a,* ventral exterior, ×2; *b,* details of ornament, ×4; *c,* ventral interior, ×3; *d,* dorsal interior, ×3 (Ulrich & Cooper, 1938).

Doleroides COOPER, 1930, p. 375 [**Orthis gibbosa* BILLINGS, 1857, p. 296; OD]. Transversely subelliptical to subquadrate, subequally biconvex, sharply uniplicate, multicostellate with aditicules; both interareas relatively long and curved, dorsal anacline; ventral muscle field quadrate with elliptical adductor track divided by median ridge and not enclosed by diductor scars; cardinal process varying from thin plate to shaft with expanded myophore; ventral mantle canal system lemniscate. *Upper Ordovician (Caradoc–Ashgill):* North America, Scotland, northern Ireland, Kazakhstan, Australia, western China (including Tibet).——FIG. 549,*5a–d.* **D. gibbosa* (BILLINGS), Caradoc, Minnesota; *a–c,* ventral, dorsal, anterior views of conjoined valves, ×1; *d,* ventral interior, ×2 (Cooper, 1956).——FIG. 549,*5e,f. D. tennesseensis* (COOPER), Caradoc, Tennessee; dorsal interior, normal and tilted views, ×1 (Cooper, 1956).

Hebertella HALL & CLARKE, 1892, p. 198 [**Orthis sinuata* HALL, 1847, p. 128; OD]. Mainly large, subquadrate with variable angled cardinal extremities, convexoconcave, uniplicate, multicostellate with aditicules, filate; both interareas relatively long, dorsal apsacline; dental plates divergent, ventral muscle scar subcordate, bounded by ridge, with elongately oval adductor scars impressed on double ridge, not enclosed by diductor tracks; adult cardinal process thick ridge with compressed myophore, brachiophore plates convergent, recessive; posterior pair of quadripartite adductor muscle scars larger than anterior pair. *Upper Ordovician (Caradoc–Ashgill):* North America, Ireland, Kazakhstan, Estonia, Australia.——FIG. 550,*1a–f.* **H. sinuata* (HALL), Ashgill, Ohio; *a–d,* dorsal, ventral, lateral, posterior views of conjoined valves, ×1.5; *e,* ventral interior, ×2; *f,* dorsal interior, ×2 (Schuchert & Cooper, 1932).

Irhirea HAVLÍČEK, 1971a, p. 44 [**Corineorthis gigantea* TERMIER & TERMIER, 1950, p. 41; OD]. Large, subcircular, variably convexoplane, rectimarginate, multicostellate (aditicules not reported); ventral interarea relatively short, not much longer than apsacline dorsal interarea; elongately bilobed ventral muscle field bounded by ridge with ovoid adductor tracks divided by median ridge, not completely enclosed by diductor scars; cardinal process simple plate, convergent brachiophore plates forming small septalium. *Upper Ordovician (Caradoc):* north Africa.——FIG. 551,*1a–d.* **I. gigantea* (TERMIER & TERMIER), Caradoc, northern Africa; *a,* internal mold of ventral valve, ×1.5; *b,* internal mold of ventral valve, ×1.4; *c,* internal mold of dorsal valve, ×1.5; *d,* anterior view of conjoined valves, ×1.5 (Havlíček, 1971a).

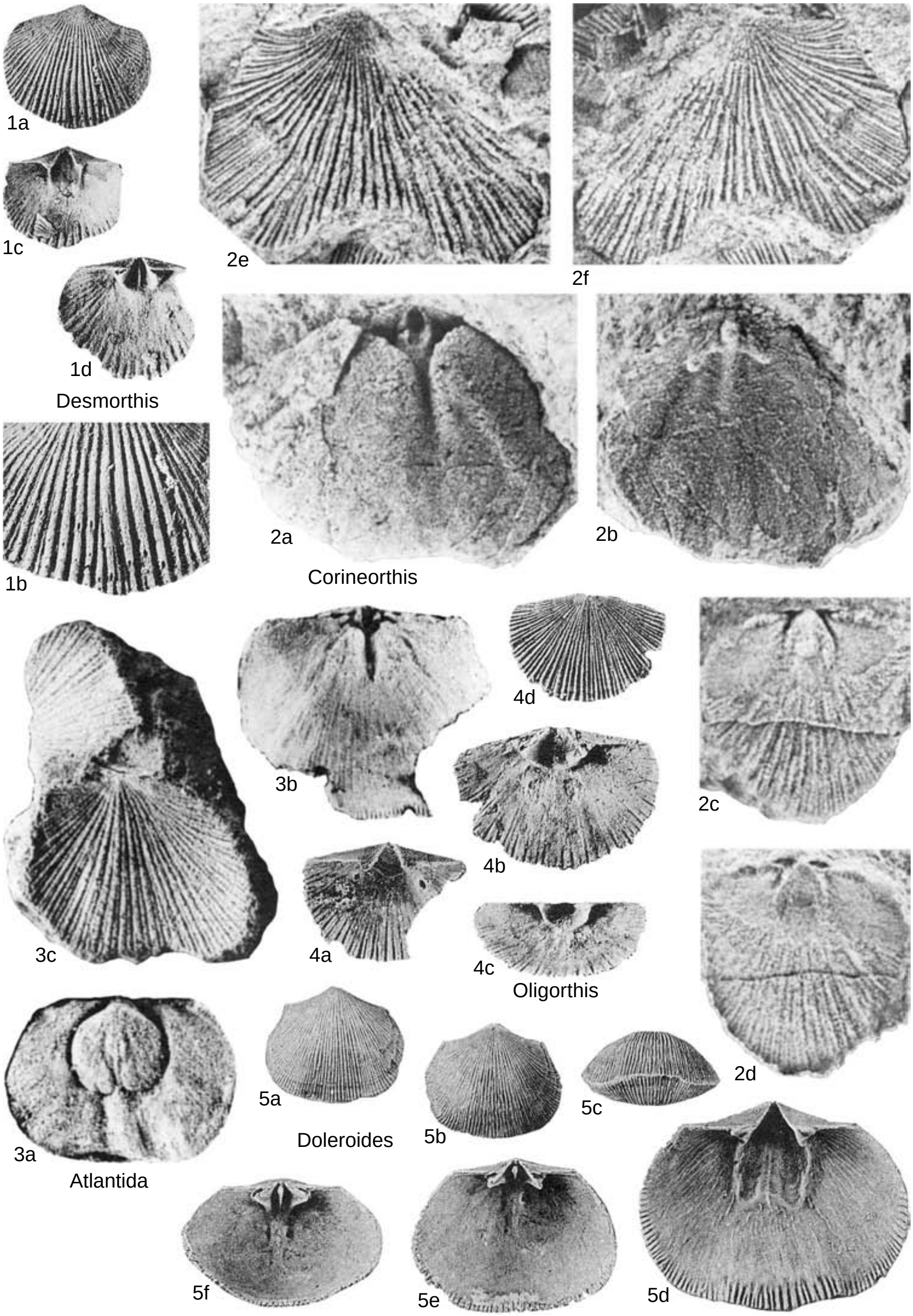

FIG. 549. Plectorthidae (p. 759–762).

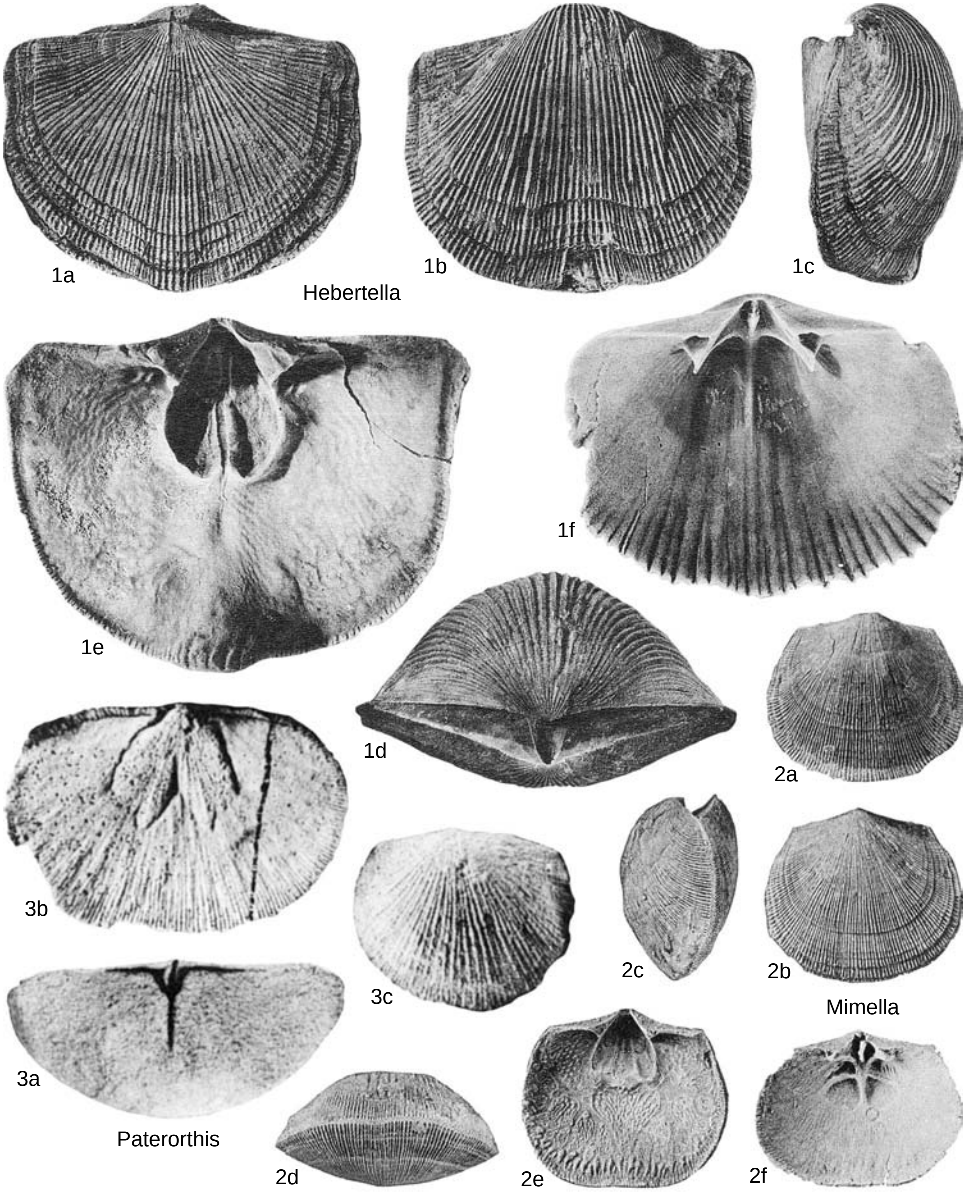

FIG. 550. Plectorthidae (p. 759–762).

Mimella COOPER, 1930, p. 375 [**Pionodema globosa* WILLARD, 1928, p. 274; OD] [=*Sonculina* MISIUS, 1986, p. 111 (type, *S. prima*)]. Similar to *Hebertella* but dorsibiconvex with obtuse cardinal extremities and without fila; dental plates recessive, bilobed ventral muscle scar consisting of long, subparallel impressed diductor scars not enclosing long, anteriorly expanding, elevated adductor track; cardinal process simple, platelike, brachiophore plates convergent to form small septalium; quadripartite dorsal adductor scars with subequal tracks; mantle canal systems well preserved, ventral saccate, dorsal variably digitate. [*Sonculina,* based on shells from the *middle Ordovician* of Khirgiz, has been distinguished by its author (Misius, 1986, p. 113) from *Mimella* in having a fibrous shell and a saccate mantle canal system. These features are, in fact, typical of *Mimella* as are such other characters as were described and illustrated (Misius, 1986).] *Upper Ordovician (Caradoc):* Northern Hemisphere.——Fig. 550,*2a–f.* **M. globosa* (Willard), Caradoc; *a–d,* dorsal, ventral, lateral, anterior views of conjoined valves, Tennessee, ×1; *e,* ventral interior, Tennessee, ×1; *f,* dorsal interior, Virginia, ×1 (Cooper, 1956).

Oligorthis Ulrich & Cooper, 1936b, p. 624 [**O. arbucklensis;* OD]. Similar to *Desmorthis* but more transversely semioval with variably angled cardinal extremities, unisulcate, more finely costellate and without apical plate in delthyrium, cardinal process also lacking. *Lower Ordovician (Tremadoc–Arenig):* North America, southwestern China, Scotland.——Fig. 549,*4a–d.* **O. arbucklensis,* Tremadoc, Oklahoma; *a,* ventral interior, ×3; *b,c,* normal, tilted views of dorsal interior, ×4; *d,* dorsal exterior, ×3 (Ulrich & Cooper, 1938).

Paterorthis Havlíček, 1971a, p. 45 [**P. paterina;* OD]. Large, subcircular, convexoconcave with hemispherical dorsal valve, gently uniplicate, multicostellate (aditicules not reported); ventral interarea catacline, dorsal interarea vestigial; ventral muscle field large, bilobed to flabellate with lanceolate adductor track, pedicle callist well developed; cardinal process simple, bladelike; brachiophore plates converging to form small posteromedian septalium. *Lower Ordovician (Llanvirn):* northern Africa.——Fig. 550,*3a–c.* **P. paterina,* Llanvirn, northern Africa; *a,* posterior view of internal mold of dorsal valve, ×1.6; *b,* internal mold of ventral valve, ×1.5; *c,* rubber replica of exterior, ×1.5 (Havlíček, 1971a).

Pseudomimella Xu & Liu, 1984, p. 179 [**Mimella formosa* Wang, 1955c, p. 125; OD]. Large, subquadrate, dorsibiconvex, rectimarginate, multicostellate; interareas relatively short; dental plates recessive, ventral muscle field suboval with wide undifferentiated adductor track as long as lateral diductor scars; cardinal process platelike; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system saccate with long, subparallel *vascula media,* dorsal system probably saccate. *Lower Ordovician (Arenig):* southwestern China.——Fig. 551,*2a–f.* **P. formosa* (Wang), Arenig, southwestern China; *a,* internal mold of dorsal valve, ×1; *b,* rubber replica of dorsal interior, ×1; *c,* internal mold of ventral valve, ×1; *d–f,* ventral, lateral, anterior views of conjoined valves, ×1.5 (Xu & Lui, 1984).

Schizophorella Reed, 1917, p. 858 [**Orthis fallax* Salter, 1846, p. 72; OD]. Transversely semioval to subquadrate, dorsibiconvex with strong median fold in dorsal valve, uniplicate, multicostellate (no aditicules reported); interareas short, dorsal anacline; dental plates subparallel continuous with ridges flanking elongately bilobed ventral muscle field with diductor scars enclosing lanceolate adductor track divided by low median ridge extending anteriorly beyond muscle field; cardinal process ridgelike with crenulated myophore; posterior pair of quadripartite dorsal adductor scars larger than anterior. *Upper Ordovician (Ashgill):* Great Britain, Ireland, Kazakhstan, northwestern China, Spain, central Asia, Norway.——Fig. 552*a–f.* *S. fallax alta* Harper, Ashgill, southwestern Scotland; *a,* ventral view of conjoined internal molds, ×4; *b,* dorsal view of conjoined internal molds, ×3; *c,d,* internal mold, rubber replica of dorsal valve, ×5; *e,* external mold of ventral exterior, ×3; *f,* rubber replica of ventral exterior, ×4 (Harper, 1984).

Severginella Rozman, 1981, p. 122 [**Pionodema(?) altaica* Severgina, 1960, p. 405; OD]. Similar to *Pseudomimella* but uniplicate, ventral adductor track variable in width, cardinal process wide, differentiated into myophore and shaft; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Upper Ordovician (Caradoc–Ashgill):* central Asia (Altai Mountains, Mongolia, Tuva).——Fig. 551,*3a,b.* **S. altaica* (Severgina), Caradoc, Altai Mountains; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×2 (Rozman, 1981).

Family CREMNORTHIDAE
Williams, 1963

[Cremnorthidae Williams, 1963, p. 377]

Elongately oval unisulcate mainly fascicostellate plectorthoids; delthyrium and notothyrium normally narrow; apsacline ventral interarea curved, anacline dorsal interarea short, curved teeth with crural fossettes, usually without dental plates; ventral muscle scar short, subtriangular with wide undifferentiated adductor scar; cardinal process massive with well-differentiated myophore; brachiophores widely divergent, supporting plates curving laterally and defining sockets; quadripartite dorsal adductor scars with anterior pair larger than posterior, normally divided by high, bladelike median septum; ventral mantle canal system saccate, dorsal system usually indistinct. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc).*

Cremnorthis Williams, 1963, p. 378 [**C. parva;* OD]. Sharply unisulcate with acute cardinal extremities; massive cardinal process having trilobate myophore with high median crest. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Wales, Estonia, Ireland.——Fig. 553,*1a–f.* **C. parva,* Caradoc, Wales; *a,b,* internal mold, rubber replica of ventral valve, ×6.5; *c,* internal mold of dorsal valve, ×8.5; *d,* rubber replica of dorsal valve, ×9.5; *e,* internal mold of dorsal valve, ×7; *f,* rubber replica of dorsal exterior of conjoined valves, ×6 (Williams, 1963).

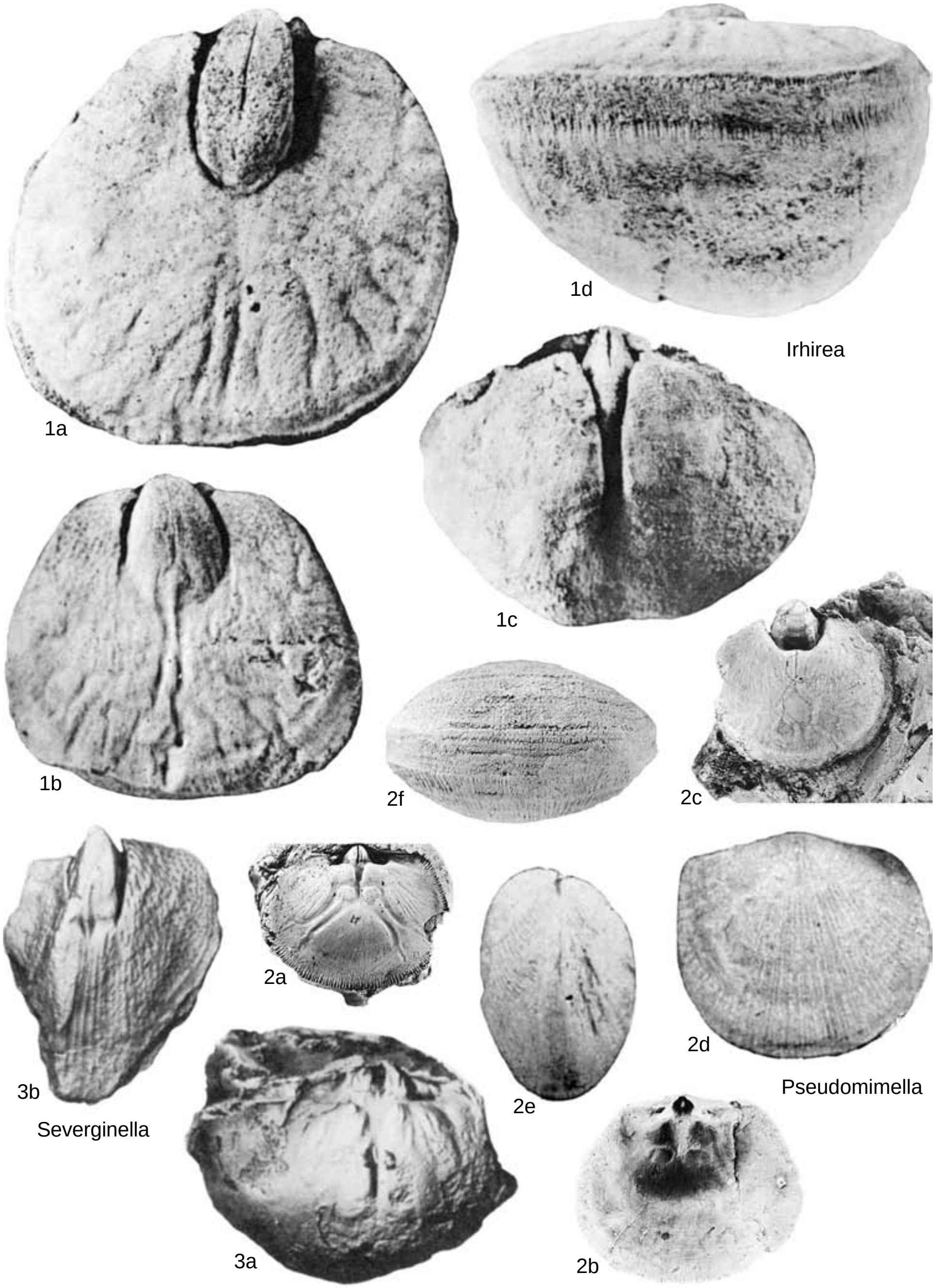

FIG. 551. Plectorthidae (p. 759–762).

Brandysia HAVLÍČEK, 1975, p. 231 [**B. benigna;* OD]. Subquadrate with obtuse cardinal extremities; delthyrium and notothyrium wide; dorsal interarea vestigial; teeth supported by short, recessive dental plates; cardinal process with bilobate myophore. *Lower Ordovician (Llanvirn):* Bohemia, northeastern China.——FIG. 553,*2a–d.* **B. benigna,* Llanvirn, Bohemia; *a,* internal mold of ventral valve, ×11.2;

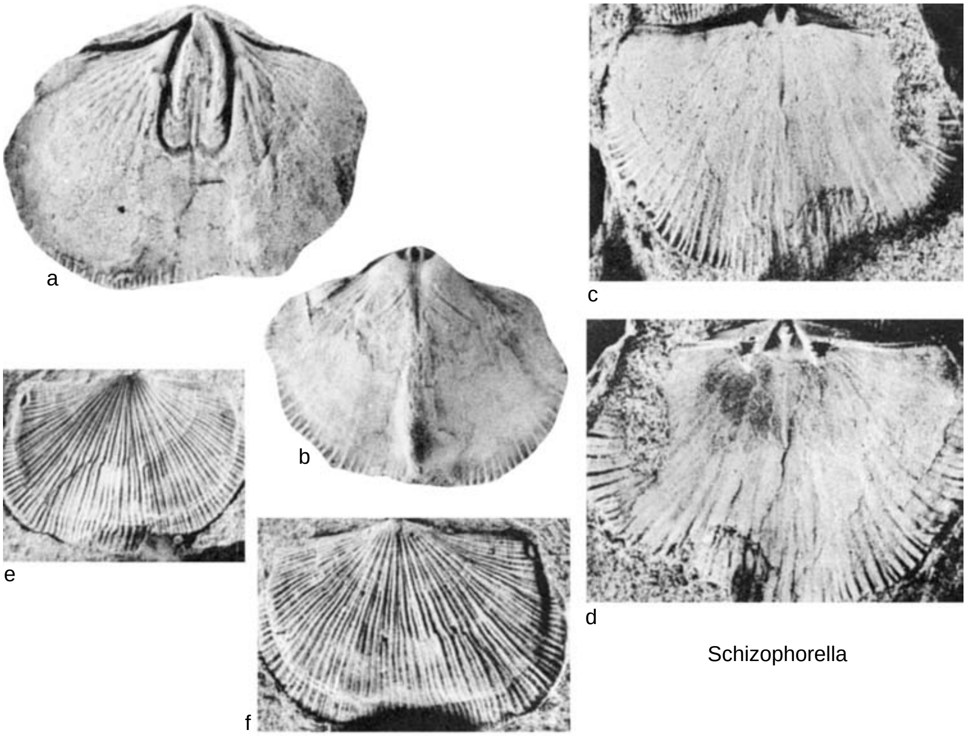

FIG. 552. Plectorthidae (p. 762).

b, internal mold of dorsal valve, ×10; *c,* internal mold of dorsal valve, ×10.5; *d,* rubber replica of ventral exterior, ×10 (Havlíček, 1977a).

Septorthis HINTS, 1973, p. 251 [**S. engurensis;* OD]. Ramicostellate, with obtuse cardinal extremities; cardinal process undifferentiated or with bilobate myophore; quadripartite dorsal adductor field bisected by median septum, consisting of broad, posterior scars with inner lobes impressed on raised platforms, separated from anterior scars by curved, transverse ridges. *Upper Ordovician (Caradoc):* Latvia, Sweden.——FIG. 553,*3a–f.* **S. engurensis,* Caradoc, Latvia; *a–c,* ventral, dorsal, anterior views of conjoined valves, ×7.6; *d,e,* normal, tilted views of dorsal interior, ×7.6; *f,* ventral interior, ×7.7 (Hints, 1973).

Family CYCLOCOELIIDAE
Schuchert & Cooper, 1931

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Cyclocoeliinae SCHUCHERT & COOPER, 1931, p. 243]

Rostrate, biconvex, costate plectorthoids with very narrow hinge lines. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Cyclocoelia FOERSTE, 1909b, p. 227 [**Atrypa sordida* HALL, 1847, p. 148; OD] [=*Encuclodema* FOERSTE, 1912, p. 139, obj.]. Small, rhynchonelliform to subcircular, rectimarginate to gently uniplicate; apsacline ventral interarea short curved, apsacline dorsal interarea very short; strong teeth supported by divergent dental plates; brachiophores supported by convergent plates, cardinal process faint, median ridge long; muscle and mantle canal impressions unknown. *Upper Ordovician (Ashgill):* USA (Ohio), central Asia, eastern Canada, northwestern China.——FIG. 554,*1a–d.* **C. sordida* (HALL), Ashgill, Ohio; *a,b,* ventral, dorsal exteriors, ×2; *c,* internal mold of ventral valve, ×2; *d,* internal mold of dorsal valve, ×2 (Schuchert & Cooper, 1932).

Rhynchorthis BATES, 1968, p. 160 [**R. rotundus;* OD]. Medium size, dorsibiconvex, uniplicate, filate, strongly apsacline interareas relatively short, curved; strong teeth supported by recessive dental plates; ventral muscle scar, impressed on callus, elongately oval with wide adductor track; pedicle callist well defined; bladelike brachiophores with fulcral plates and recessive convergent supporting plates, bladelike cardinal process flanked by low, notothyrial ridges; bilobed anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral mantle canal system saccate, dorsal lemniscate. *Lower Ordovician (Arenig–Llanvirn):* Wales, southeastern Ireland.——FIG. 554,*2a–f.* **R. rotundus,* Arenig, northern Wales; *a,b,* internal mold, rubber replica of ventral valve, ×2; *c,d,* internal mold, rub-

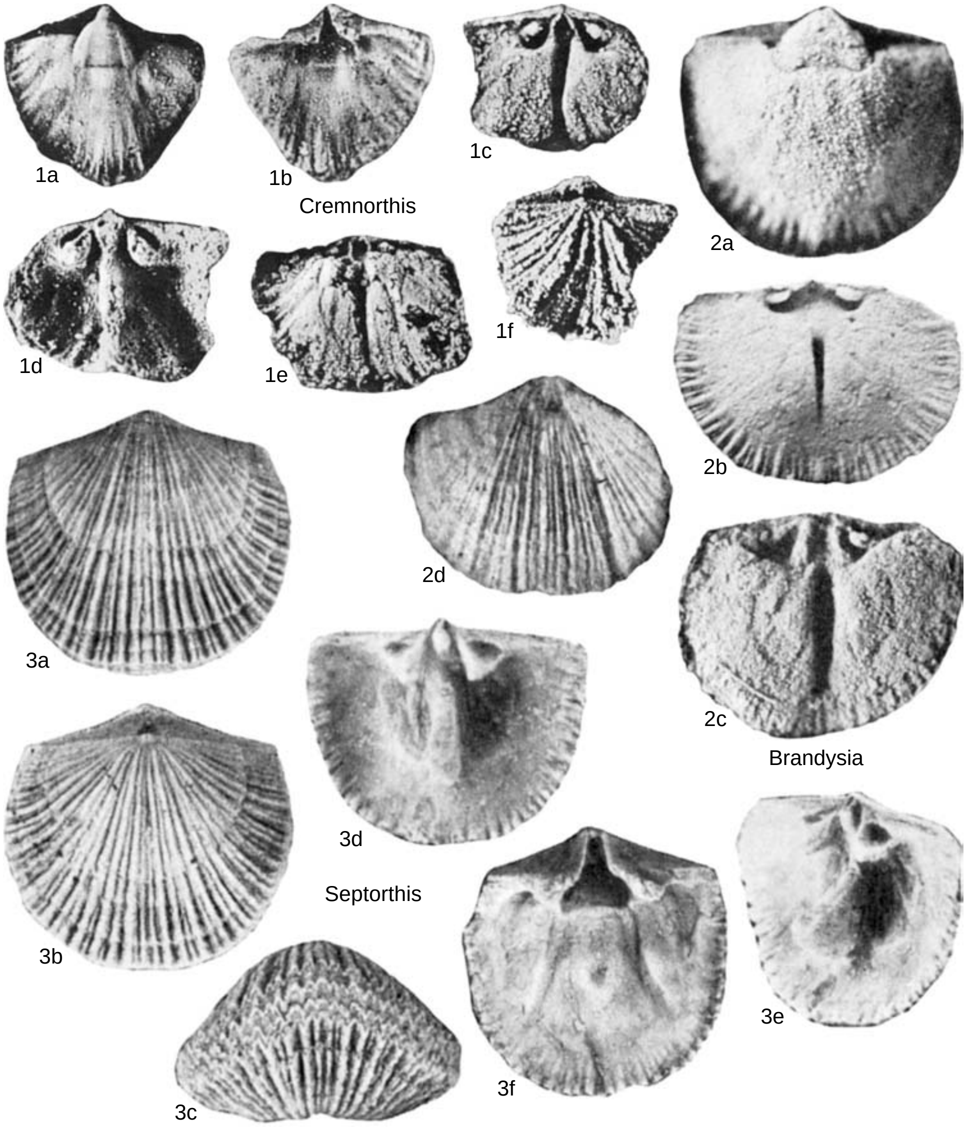

FIG. 553. Cremnorthidae (p. 762–764).

ber replica of dorsal interior, ×2; *e,f,* external mold, rubber replica of dorsal valve, ×2 (Neuman & Bates, 1978).

Family EOORTHIDAE Walcott, 1908

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 242, *ex* Eoorthinae WALCOTT, 1908, p. 148]

Normally subquadrate, biconvex, unisulcate, and variably costellate with curved ventral apsacline and dorsal anacline interareas; delthyrium and notothyrium open; deltidiodont teeth variably supported; ventral muscle field impressed on callus, suboval to subtriangular, commonly with broad, elongate undifferentiated adductor track not enclosed by diductor scars; notothyrial platform and cardinal process variably developed; divergent brachiophores short, bladelike, defining elongate sockets; adductor scars quadripartite with subtriangular anterior pair inserted posteromedianly

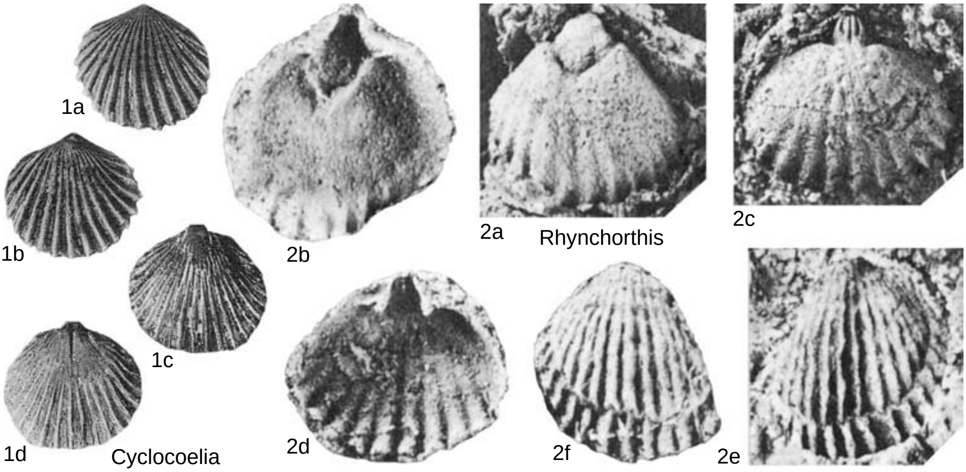

FIG. 554. Cyclocoeliidae (p. 764–765).

between subtriangular posterior pair; ventral mantle canal system saccate, dorsal system obscure but with divergent *vascula media.* [This family clusters with the plectorthoids as the Lower Cambrian stem group with a morphology that differs significantly from that of other, older plectorthoids, finkelnburgiids, and ranorthids only in the lack of development of brachiophore supporting plates or fulcral plates. The eoorthids, however, also have strong affinities with early orthoids and are presently best accepted as representing the link group(s) between the plectorthoids and orthoids.] *Middle Cambrian–Lower Ordovician (Tremadoc).*

Eoorthis WALCOTT, 1908, p. 102 [**Orthis remnicha* WINCHELL, 1885, p. 317; OD]. Radial ornamentation of coarse costellae with superimposed capillae, dental plates receding, ventral muscle scar enclosed by a low ridge; cardinal process simple, dorsal median ridge wide. *Upper Cambrian–Lower Ordovician (Tremadoc):* cosmopolitan.——FIG. 555,*1a–e.* **E. remnicha* (WINCHELL), Upper Cambrian, Montana; *a,b,* interior, exterior of dorsal valve, ×2; *c,d,* internal mold, rubber replica of ventral valve, ×3 (Bell, 1941); *e,* dorsal interior, ×2 (Schuchert & Cooper, 1932).

Apheoorthina HAVLÍČEK, 1949a, p. 99 [**A. ferrigena;* OD]. Similar to *Apheoorthis* but filate with elongately cordate ventral muscle field with diductor scars enclosing lanceolate adductor track and stronger notothyrial platform with ridgelike cardinal process. *Lower Ordovician (Tremadoc):* Bohemia, Baltic.——FIG. 555,*5a–c.* **A. ferrigena,* Tremadoc, Bohemia; *a,* internal mold of dorsal valve, ×3.3; *b,* internal mold of ventral valve, ×2.9; *c,* dorsal exterior, ×3.6 (Havlíček, 1977a).

Apheoorthis ULRICH & COOPER, 1936b, p. 620 [**Eoorthis lineocosta* WALCOTT, 1924, p. 508; OD]. Fascicostellate, dorsal valve strongly sulcate, dental plates well developed on either side of pseudospondylium; notothyrial platform and ridgelike cardinal process rudimentary. *Upper Cambrian–Ordovician (Tremadoc):* North America, Kazakhastan, Siberian Platform, Colombia, Sweden, Baltic, Ireland, eastern, northern, and northeastern China, Australia (Tasmania), Afghanistan.——FIG. 555,*3a–e.* **A. lineocosta* (WALCOTT), Upper Cambrian, Colorado; *a,b,* interior, exterior of ventral valve, ×2; *c,* details of posteromedian part of ventral interior, ×4; *d,e,* interior, exterior of dorsal valve, ×2 (Ulrich & Cooper, 1938).

Austrohedra ROBERTS & JELL, 1990, p. 276 [**A. mimica;* OD]. Ventribiconvex, with long, flat, catacline to slightly apsacline ventral interarea, ramicostellate; dental plates well developed; cardinal process rudimentary. *Middle Cambrian:* Australia (New South Wales).——FIG. 555,*2a–d.* **A. mimica,* Middle Cambrian, New South Wales; *a,b,* interior, exterior of dorsal valve, ×6; *c,d,* interior, posterior views of ventral valve, ×4 (Roberts & Jell, 1990).

Brahimorthis HAVLÍČEK, 1971a, p. 29 [**B. antiqua;* OD]. Ramicostellate and filate, lacking dental plates and cardinal process; small bilobed adductor muscle scars impressed on transverse ridge enclosing delthyrial cavity of ventral valve, with anterior tips of diductor scars possibly enclosing oval adductor track. *Middle Cambrian:* Europe, northern Africa.——FIG. 555,*4a–c.* **B. antiqua,* Middle Cambrian, northern Africa; *a,* dorsal interior, ×1.7; *b,* internal mold of ventral valve, ×2; *c,* dorsal exterior, ×1.5 (Havlíček, 1971a).

Glaphyrorthis ROBERTS & JELL, 1990, p. 278 [**G. fastigiata;* OD]. Small, mucronate, transversely semioval, sharply unisulcate, smooth shells with

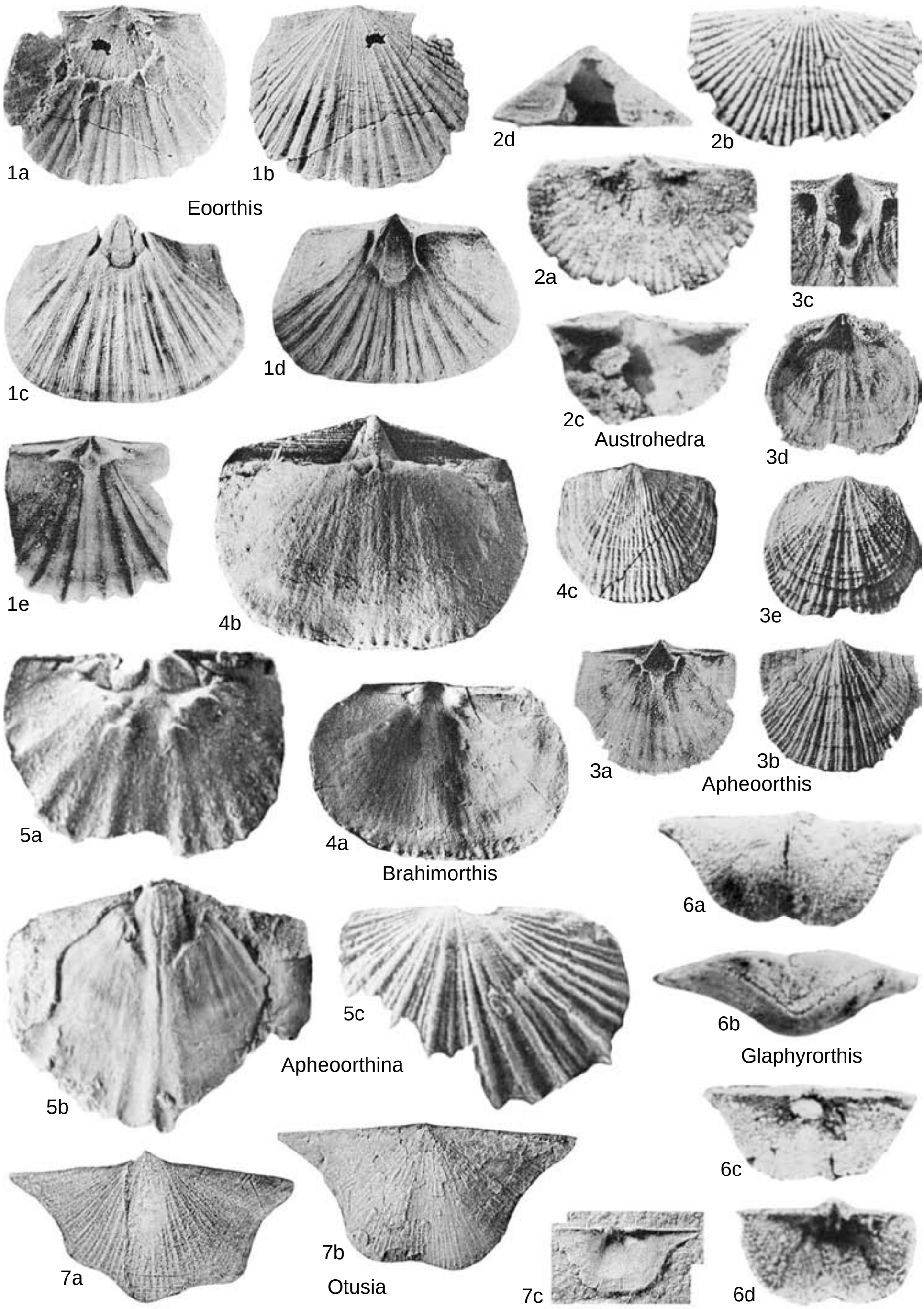

FIG. 555. Eoorthidae (p. 766–769).

well-developed dental plates and a pseudodeltidium; cardinal process not seen. [The inclusion of this genus within the Eoorthidae is provisional based on further information about the cardinalia and the external surfaces of the type species that are presently known only in the silicified state.] *Middle*

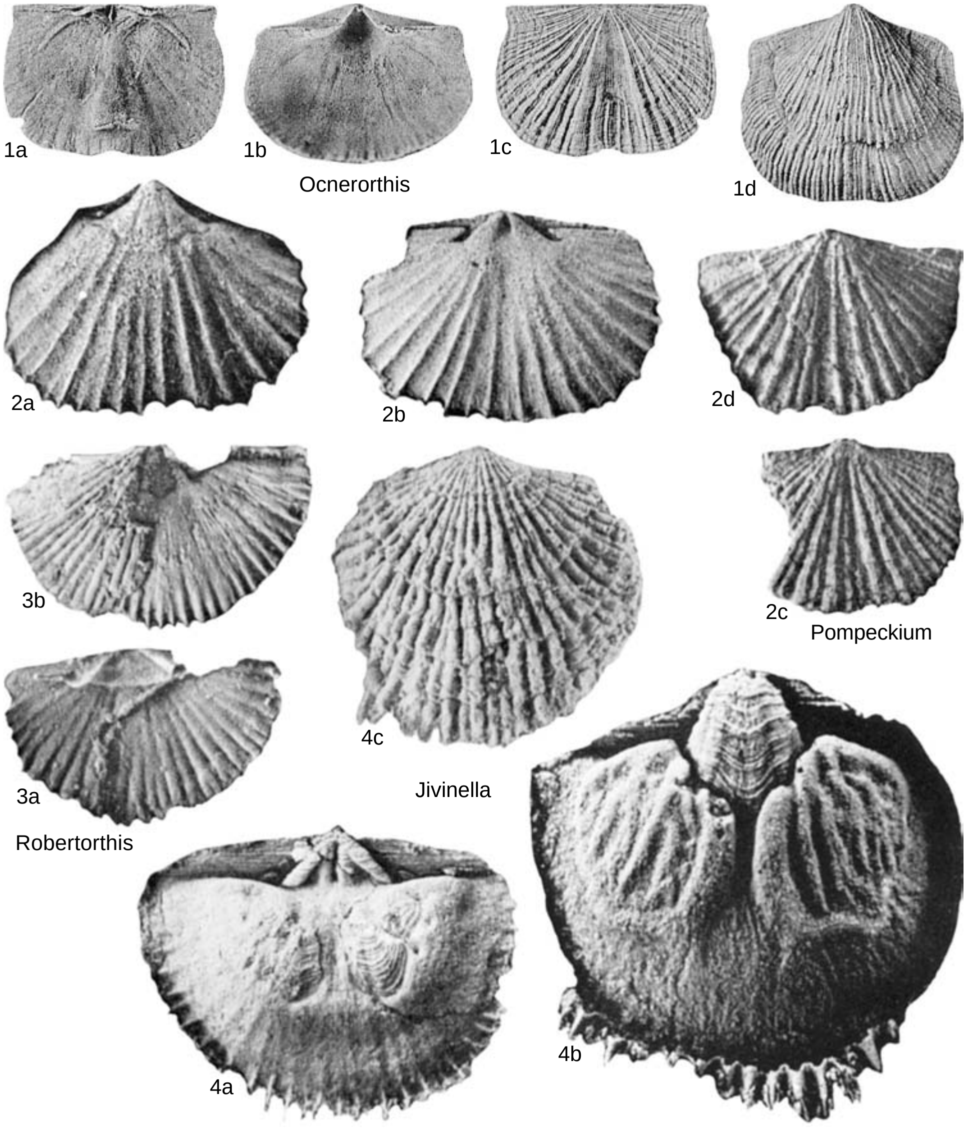

Fig. 556. Eoorthidae (p. 768–769).

Cambrian: Australia (New South Wales).——Fig. 555,*6a–d.* **G. fastigiata,* Middle Cambrian, New South Wales; *a,b,* dorsal, anterior views of conjoined valves, ×8; *c,* dorsal interior, ×8; *d,* ventral interior, ×8 (Roberts & Jell, 1990).

Jivinella Havlíček, 1949a, p. 94 [**Orthis incola* Barrande, 1879, pl. 126, fig. IV; OD] [=*Jevinellina* Liu in Liu, Xu, & Liang, 1983, p. 262 (type, *J. involuta*)]. Ventribiconvex, rectimarginate, interareas strongly developed, fascicostellate and finely capillate in interspaces, imbricate; dental plates recessive, pedicle collar obtusely triangular, transverse ventral muscle scar impressed on pseudospondylium with anterior median ridge; simple cardinal process flanked by discrete notothyrial ridges, and rodlike brachiophores widely divergent. [According to Liu (in Liu, Xu, & Liang, 1983, p. 262), the type species of *Jevinellina* from the Lower Ordovician of southern China differs from European species of *Jivinella* only in being dorsibiconvex and in the development of a short median ridge in the dorsal valve. Liu doubted whether these variably developed features were sufficient to erect a new genus and we agree.] *Lower Ordovician (Tremadoc):* Bohemia, Spain, southern China, Germany.——Fig. 556,*4a–c. J. involuta,* Tremadoc, Bohemia; *a,* internal mold of dorsal valve, ×3.5; *b,* internal mold of ventral valve, ×5.2; *c,* rubber replica of ventral exterior, ×3.5 (Havlíček, 1977a).

Ocnerorthis Bell, 1941, p. 251 [**O. cooperi;* OD]. Unequally biconvex to planoconvex, fascicostellate, strongly apsacline to nearly orthocline ventral interarea; dental plates variably present, ventral muscle scar suboval with anteromedian callosity; brachiophores widely divergent, sockets associated with laterally curving ridges; ventral mantle canal system possibly digitate with narrowly divergent *vascula media. Upper Cambrian–Lower Ordovician (Tremadoc):* North America, Bohemia, Novaya Zemlya.——Fig. 556,*1a–d.* **O. cooperi,* Upper Cambrian, Wyoming; *a,* dorsal interior, ×3; *b,* ventral interior, ×3; *c,* dorsal exterior, ×3; *d,* ventral exterior, ×3 (Bell, 1941).

Otusia Walcott, 1905, p. 246 [**Orthis sandbergi* Winchell, 1885, p. 318; OD]. Small, mucronate, transversely semioval, ventribiconvex, strongly unisulcate, multicostellate; dental plates divergent with suboval ventral muscle scar impressed on valve floor; cardinal process rudimentary, brachiophores short, divergent. *Upper Cambrian:* North America, Argentina.——Fig. 555,*7a–c.* **O. sandbergi* (Winchell), Upper Cambrian, Montana; *a,* ventral exterior, ×4; *b,* dorsal exterior, ×3 (Bell, 1941); *c,* dorsal interior, ×2.5 (Grant, 1965).

Pompeckium Havlíček, 1970b, p. 290 [**Orthis kuthani* Pompeckj, 1896, p. 514]. Gently unisulcate, coarsely costellate, filate, ventral interarea long and curved; dental plates absent, suboval ventral muscle field with broad, triangular adductor track impressed directly on valve floor; simple cardinal process, short, divergent rodlike brachiophores; ventral mantle canal system digitate. *Middle Cambrian:* Bohemia, central USA.——Fig. 556,*2a–d.* **P. kuthani* (Pompeckj), Middle Cambrian, Bohemia; *a,* internal mold of ventral interior, ×3; *b,* internal mold of dorsal interior, ×3; *c,d,* rubber replicas of dorsal exteriors, ×3.3 (Havlíček, 1977a).

Robertorthis Havlíček, 1977a, p. 51 [**R. holoubkovensis;* OD]. Similar to *Eoorthis* but coarsely costellate without fila and with transverse, well-developed notothyrial platform. *Lower Ordovician (Tremadoc):* Bohemia.——Fig. 556,*3a,b.* **R. holoubkovensis,* Tremadoc, Bohemia; *a,* dorsal interior, ×4.9; *b,* broken ventral interior, ×3.1 (Havlíček, 1977a).

Family EUORTHISINIDAE Havlíček, 1977

[Euorthisinidae Havlíček, 1977a, p. 293]

Medium size, transversely suboval with variable cardinal extremities, rectimarginate, coarsely costellate, filate plectorthoids; wide delthyrium and notothyrium; strongly apsacline to orthocline ventral and anacline dorsal interareas short, curved; simple teeth supported by projecting subparallel to divergent dental plates; platelike bases of rodlike brachiophores converging to form small, posteromedian septalium, cardinal process not developed, muscle and mantle impressions unknown. [*Euorthisina* was first assigned by its author (Havlíček, 1950, p. 16) to the syntrophiidines. This attribution was rejected by Biernat in the first edition of the *Treatise on Invertebrate Paleontology* on the Brachiopoda (1965, p. 523–536) because of the development of wide interareas in *Euorthisina* that also lacked a dorsal fold and ventral sulcus. In 1977, Havlíček (1977a, p. 293) created a family based on *Euorthisina,* which he assigned to the plectorthoids. The family does, in fact, share features with both the plectorthoids and the syntrophiidines but on balance is best retained within the plectorthoids. *Lower Ordovician (Tremadoc–Llanvirn).*

Euorthisina Havlíček, 1950, p. 16 [**Orthisina moesta* Barrande, 1879, pl. 57, case I]. Dental plates subparallel; septalium resting on thin dorsal median septum. *Ordovician (Arenig–Llanvirn):* Europe, northern Africa, Bolivia, southwestern, northwestern, and eastern China.——Fig. 557,*1a–c.* **E. moesta* (Barrande), Llanvirn, Bohemia; *a,* internal mold of ventral valve, ×2.4; *b,* internal mold of dorsal valve, ×2.5; *c,* dorsal view of internal mold of conjoined valves, ×1.8 (Williams, 1974).

Notorthisina Havlíček & Branisa, 1980, p. 28 [**N. notoconcha;* OD]. Dental plates divergent; septalium resting on floor of dorsal valve. *Ordovician (Tremadoc):* Bolivia.——Fig. 557,*2a–c.* **N. notoconcha,* Tremadoc, Bolivia; *a,* internal mold of dorsal valve, ×8.4; *b,* internal mold of ventral valve, ×9.3; *c,* rubber replicas of exteriors, ×7.6 (Havlíček & Branisa, 1980).

Family FINKELNBURGIIDAE Schuchert & Cooper, 1931

[*nom. transl.* Schuchert & Cooper, 1932, p. 54, *ex* Finkelburgiinae Schuchert & Cooper, 1931, p. 243]

Generally medium size, biconvex, rectimarginate, costellate plectorthoids with an apsacline, short, curved ventral interarea and an anacline, very short dorsal interarea; teeth supported by variably developed dental plates, ventral muscle field subtriangular to suboval impressed on pseudospondylium, adductor track normally wide and elevated

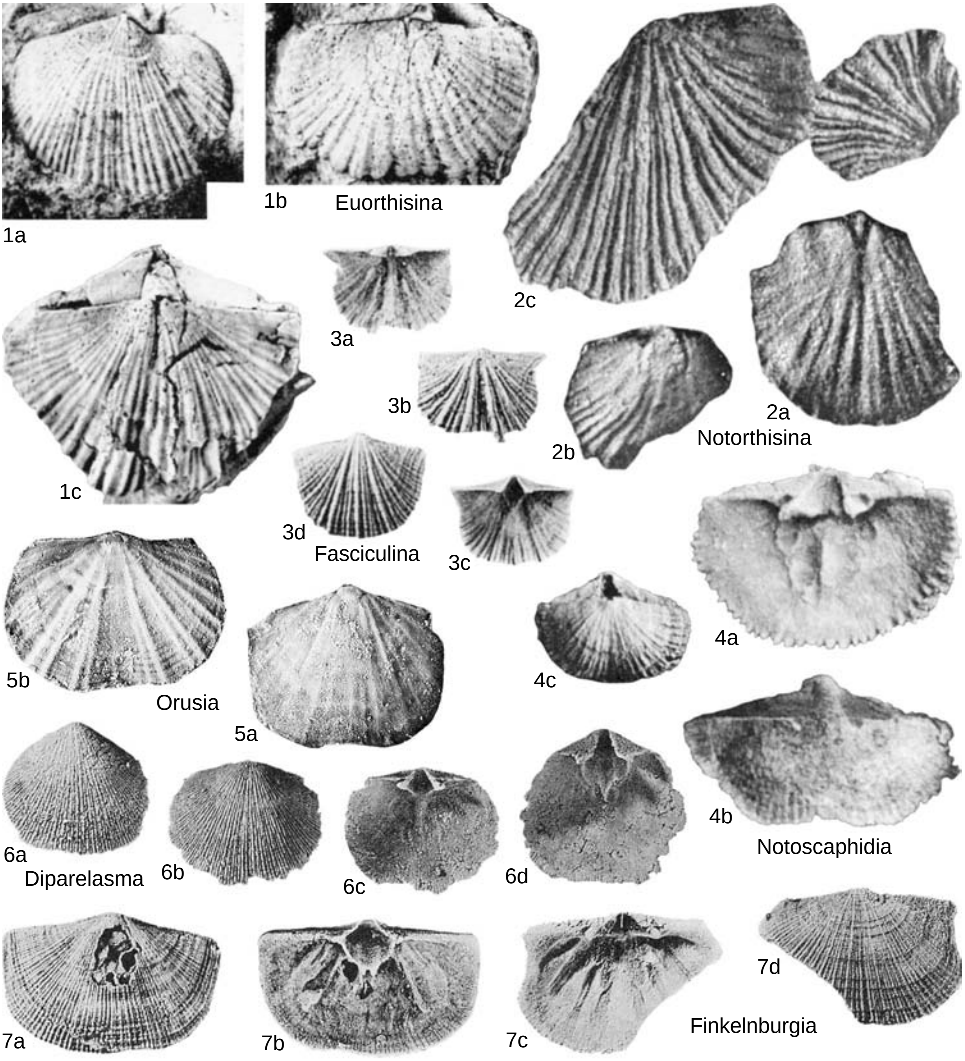

FIG. 557. Euorthisinidae and Finkelnburgiidae (p. 769–771).

and at least as long as flanking diductor scars; notothyrial platform and cardinal process absent or rudimentary; brachiophores variably developed; supported by convergent platelike bases; sockets delineated by small fulcral plates; dorsal median ridge normally developed; quadripartite dorsal adductor scars impressed on low callosites with anterior pair inserted posteromedianly between the posterior pair; mantle canal systems of both valves digitate, variably preserved. *Middle Cambrian–Lower Ordovician (Arenig).*

Finkelnburgia WALCOTT, 1905, p. 277 [**F. finkelnburgi;* OD] [=*Marcharella* ANDREEVA, 1968, p. 75 (type, *M. marchensis*)]. Transversely semioval with variably shaped cardinal extremities, multicostellate; dental plates recessive, pseudospondylium prolonged forward as median ridge; brachiophores blunt, divergent, rudimentary cardinal process rarely developed. [*Marcharella* ANDREEVA from the upper Cambrian of the northeastern Siberian Platform differs from *Finkelnburgia* only in its subquadrate outline.] *Upper Cambrian–Lower Or-*

dovician (Tremadoc): Northern Hemisphere.——Fig. 557,*7a–d. F. buttsi,* Upper Cambrian, Virginia; *a,b,* exterior, interior of ventral valve, ×2; *c,d,* interior, exterior of dorsal valve, ×2 (Ulrich & Cooper, 1938).

Diparelasma Ulrich & Cooper, 1936b, p. 623 [*D. typicum;* OD]. Subcircular with obtuse cardinal extremities, finely multicostellate; pedicle callist present; dental plates parallel; cardinal process not developed. *Lower Ordovician (Tremadoc–Arenig):* North America, Great Britain, eastern and northeastern China.——Fig. 557,*6a–d.* **D. typicum,* Arenig, Oklahoma; *a,b,* ventral, dorsal exteriors of conjoined valves, ×2; *c,* dorsal interior, ×2; *d,* ventral interior, ×2 (Ulrich & Cooper, 1938).

Fasciculina Cooper, 1952b, p. 7 [**Orthis desmopleura* Meek, 1871b, p. 295; OD]. Transversely semioval with mucronate cardinal extremities, unisulcate, fascicostellate; ventral median ridge accentuating pseudospondylium; dorsal median ridge formed by internal crest of sulcus. *Lower Ordovician (Tremadoc–Arenig):* North America, Scotland.——Fig. 557,*3a–d. F. fasciculata,* Tremadoc, Oklahoma; *a,b,* interior, exterior of dorsal valve, ×2; *c,* ventral interior, ×2; *d,* ventral exterior, ×2 (Cooper, 1952b).

Notoscaphidia Williams & Curry, 1985, p. 233 [*N. revelata;* OD]. Small, transversely semioval, variable cardinal extremities, ventribiconvex, unisulcate, coarsely costellate; ventral interarea long, curved. *Lower Ordovician (Arenig):* Ireland.——Fig. 557,*4a–c.* **N. relevata,* Arenig, western Ireland; *a,* dorsal interior, ×8; *b,* ventral interior, ×8; *c,* dorsal view of conjoined valves, ×4 (Williams & Curry, 1985).

Orusia Walcott, 1905, p. 273 [**Anomites lenticularis* Wahlenberg, 1821, p. 66; OD]. Small, subcircular with obtuse cardinal extremities, subequally biconvex, gently unisulcate to rectimarginate, coarsely costellate and filate; pseudospondylium weakly developed; dental plates divergent; brachiophores long, sharp, dorsal median ridge rudimentary. *Middle Cambrian–Lower Ordovician (Tremadoc):* North eastern North America, Baltoscandia, Wales, Argentina, northeastern China.——Fig. 557,*5a,b.* **O. lenticularis* (Wahlenberg), Middle Cambrian, Sweden; *a,* partly exfoliated ventral valve, ×5; *b,* partly exfoliated dorsal valve, ×5 (Williams, 1965b).

Family GIRALDIELLIDAE new family

[Giraldiellidae Williams & Harper, herein]

Costellate plectorthoids, commonly medium size, unisulcate and subcircular to subquadrate with obtuse cardinal extremities; ventral muscle field normally small, triangular to subpentagonal, with wide, triangular, poorly differentiated adductor track flanked by short diductor scars, pedicle callist not always deeply impressed; cardinalia small, commonly delicate with concave fulcral plates, narrowly divergent brachiophores supported by converging plates to form notothyrial chamber or septalium, cardinal process normally simple and bladelike, notothyrial platform not developed; mantle canal systems rarely impressed, ventral probably saccate, dorsal tending to be lemniscate; aditicules not reported. *Lower Ordovician (Arenig)–upper Silurian (Ludlow).*

Giraldiella Bancroft, 1949, p. 5 [**Orthis protensa* J. de C. Sowerby, 1839, p. 638; OD]. Transversely semioval with variable cardinal extremities, dorsibiconvex, multicostellate, filate; short, planar interareas; dental plates parallel to narrowly divergent. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* Wales, Sweden, central Asia (Altai Mountains, Altai Syan, Tyan Shan).——Fig. 558,*3a–c.* **G. protensa* (Sowerby), Llandovery, Wales; *a,* internal mold of ventral valve, ×2; *b,* rubber replica of dorsal interior, ×2; *c,* rubber replica of dorsal exterior, ×2 (Williams, 1965b).

Comatopoma Havlíček, 1950, p. 54 [**C. barrandei;* OD]. Large, subcircular, ventribiconvex, multicostellate; ventral interarea short, curved; dorsal vestigial; ventral muscle scar umbonal with broadly triangular adductor track; brachiophore plates subparallel, dorsal median septum not developed. *Upper Ordovician (Ashgill):* Bohemia, northern Africa.——Fig. 558,*2a–e.* **C. barrandei,* Ashgill, Bohemia; *a–c,* ventral, dorsal, anterior views of conjoined valves, ×2; *d,* internal mold of ventral valve, ×3.4; *e,* internal mold of dorsal valve, ×3 (Havlíček, 1977a).

Famatinorthis Levy & Nullo, 1973, p. 146 [**F. turneri;* OD]. Large, subcircular, dorsibiconvex to convexoplane, multicostellate, ventral interarea relatively long and curved; dental plates divergent, ventral muscle scar suboval, impressed on callist with widely triangular adductor track; simple, bladelike cardinal process. *Lower Ordovician (Arenig):* Argentina, northeastern China, eastern North America.——Fig. 558,*1a–d.* **F. turneri,* Arenig, Argentina; *a,* internal mold of ventral valve, ×1.5; *b,* internal mold of dorsal valve, ×2; *c,* rubber replica of dorsal interior, ×3.5; *d,* rubber replica of dorsal exterior, ×1.5 (Benedetto, 1994).

Gelidorthina Havlíček, 1974, p. 168 [**O. sanctoivanensis* Barrande, 1879, pl. 66, case I; OD]. Medium size, subcircular, strongly biconvex, rectimarginate, multicostellate, interareas relatively short, planar; ventral muscle field small, limited to delthyrial cavity with broadly triangular adductor track impressed on low callosity; simple, bladelike cardinal process; ventral mantle canal system probably saccate with subparallel *vascula media. lower Silurian (Llandovery)–upper Silurian (Ludlow):* Bohemia.——Fig. 558,*4a–c.* **G. sanctoivanensis* (Barrande),

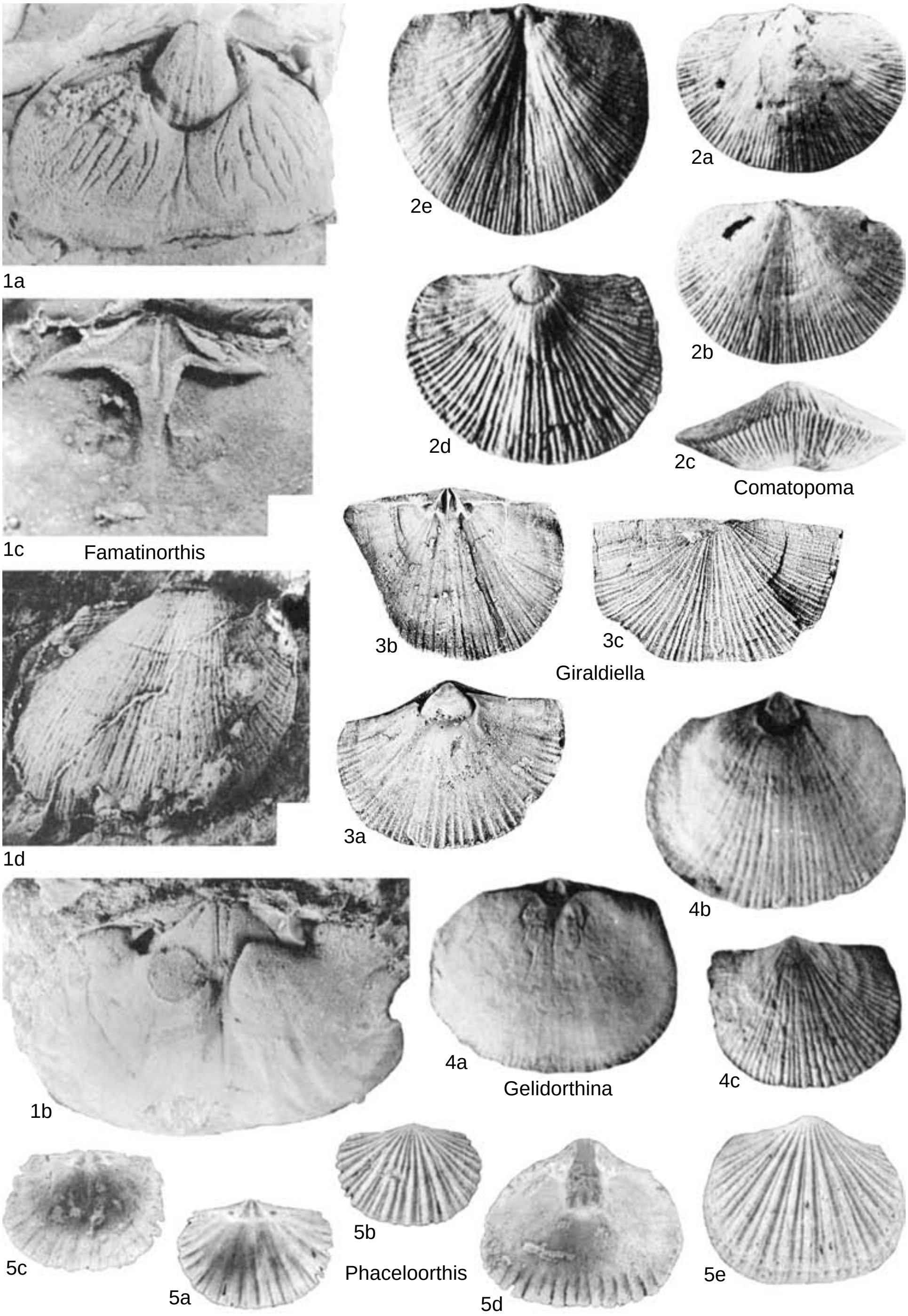

Fig. 558. Giraldiellidae (p. 771–774).

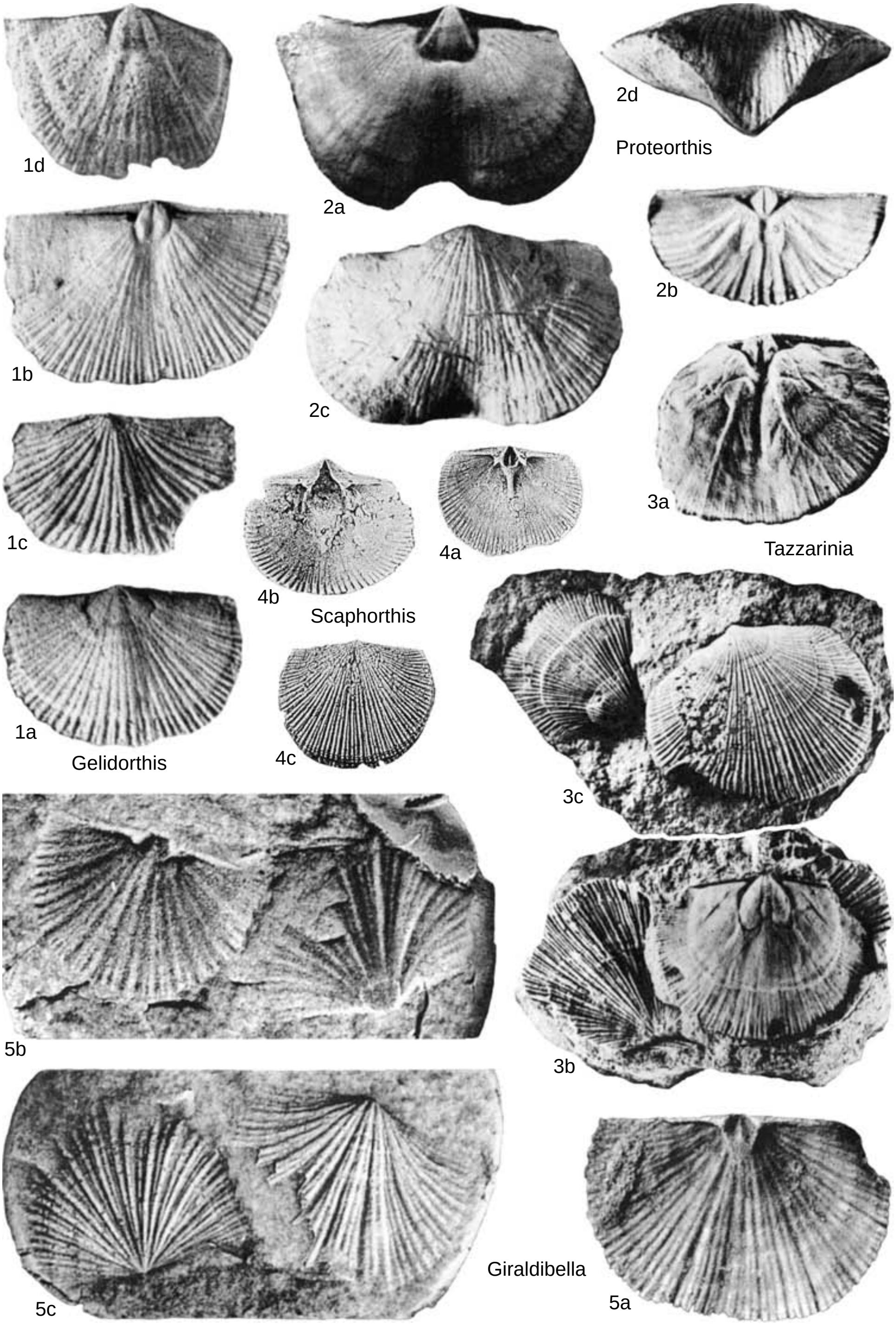

FIG. 559. Giraldiellidae (p. 774).

Wenlock, Bohemia; *a,* internal mold of dorsal valve, ×3; *b,* internal mold of ventral valve, ×3; *c,* ventral exterior, ×3 (Havlíček, 1974).

Gelidorthis HAVLÍČEK, 1968, p. 125 [**Orthis partita* BARRANDE, 1879, pl. 63, case II; OD]. Medium size, subquadrate with acute cardinal extremities, unisulcate, ventribiconvex, ramicostellate; ventral interarea short, planar, dorsal interarea vestigial; ventral muscle scar subpentagonal with broadly triangular adductor track and pair of low median ridges, pedicle callist well developed; adult cardinal process ridgelike with raised bilobate myophore; ventral mantle canal system probably saccate with divergent *vascula media. Upper Ordovician (Caradoc):* Europe, northern Africa.——FIG. 559,*1a–d.* **G. partita* (BARRANDE), Caradoc, Bohemia; *a,* internal mold of ventral valve, ×2.9; *b,* internal mold of dorsal valve, ×3.1; *c,* rubber replica of ventral exterior, ×4.2 (Havlíček, 1977a); *d,* internal mold of ventral valve, ×3.3 (Havlíček, 1968).

Giraldibella HAVLÍČEK, 1977a, p. 87 [**Giraldiella bella* BERGSTRÖM, 1968, p. 8; OD]. Similar to *Gelidorthis* but fascicostellate with obtuse cardinal extremities, short planar dorsal interarea, proportionately smaller ventral muscle scar, and simple, bladelike cardinal process. *Upper Ordovician (Ashgill)–middle Silurian (Wenlock):* Europe, Kazakhstan, Siberia, northeastern China, central Asia (Altai Mountains).——FIG. 559,*5a–c.* **G. bella* (BERGSTRÖM), Ashgill, Sweden; *a,* rubber replica of dorsal interior, ×3 ; *b,c,* rubber replicas of two ventral interiors and exteriors, ×3 (Bergström, 1968).

Phaceloorthis PERCIVAL, 1991, p. 129 [**P. decoris;* OD] [=*Boonderella* PERCIVAL, 1991, p. 130 (type, *B. fasciculata*)]. Transversely subquadrate, ventribiconvex, unisulcate, fascicostellate, filate; ventral interarea short, curved dorsal interarea very short, planar, orthocline; ventral muscle scar quadrate suboval with broad adductor track slightly elevated anteriorly; cardinal process differentiated into thickened shaft and crenulated myophore, sockets rounded; mantle canal systems in both valves probably saccate with subparallel *vascula media.* [*Boonderella* is based on three silicified valves, each from a different locality, which have been distinguished from penecontemporaneous *Phaceloorthis* shells only in having a ridgelike cardinal process and a more elevated ventral muscle field. Immature *Phaceloorthis,* however, have ridgelike cardinal processes, and the shell thickening is variable, judging from illustration. *Phaceloorthis* is only provisionally assigned to the Giraldiellidae as it is cladistically more closely related to the stem group of both the Giraldiellidae and Plectorthidae.] *Upper Ordovician (Caradoc):* Australia (New South Wales).——FIG. 558,*5a–e.* **P. decoris,* Caradoc, New South Wales; *a,b,* interior, exterior of dorsal valve, ×2; *c,* dorsal interior, ×2; *d,* ventral interior, ×2; *e,* ventral exterior, ×2 (Percival, 1991).

Proteorthis HAVLÍČEK, 1974, p. 168 [**Orthis tardissima* BARRANDE, 1879, pl. 108, case VI; OD]. Large, transversely subquadrate, dorsibiconvex, strongly uniplicate, coarsely costellate, filate; apsacline ventral and orthocline dorsal interareas short, curved; ventral muscle field impressed on callus; cardinal process simple, bladelike; anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral mantle canal system pinnate. *middle Silurian (Wenlock):* Bohemia.——FIG. 559,*2a–d.* **P. tardissima* (BARRANDE), Wenlock, Bohemia; *a,* internal mold of ventral valve, ×3.4; *b,* posterodorsal view of internal mold of dorsal valve, ×1.7; *c,d,* ventral, anterior views of conjoined pair, ×1.7 (Havlíček, 1977a).

Scaphorthis COOPER, 1956, p. 502 [**S. virginiensis;* OD]. Subcircular, ventribiconvex, rectimarginate to unisulcate, multicostellate; interareas relatively short, curved; ventral muscle scar subcordate with wide, triangular adductor track impressed on low callosity anteriorly; cardinal process with narrow shaft and thin, bladelike myophore; anterior pair of quadripartite dorsal adductor scars larger than posterior pair; ventral and dorsal muscle canal systems saccate with parallel *vascula media* and lemniscate respectively. *Upper Ordovician (Caradoc–Ashgill):* North America, Scotland, Ireland, Australia (New South Wales), central Asia, Kazakhstan.——FIG. 559,*4a–c.* **S. virginiensis,* Caradoc, Virginia; *a,* dorsal interior, ×2; *b,* ventral interior, ×2; *c,* ventral exterior, ×2 (Cooper, 1956).

Tazzarinia HAVLÍČEK, 1971a, p. 39 [**T. drotae;* OD]. Subquadrate, ventribiconvex, unisulcate, multicostellate, filate; ventral interarea short, planar, dorsal vestigial; ventral muscle scar short, bilobed with wide adductor track, pedicle callist well developed; cardinal process differentiated into thick shaft and bilobed myophore; quadripartite adductor muscle scars subequal; ventral and dorsal mantle canal systems saccate (with divergent *vascula media*) and lemniscate respectively. *Upper Ordovician (Caradoc):* northern Africa, England, Bohemia.——FIG. 559,*3a–c.* **T. drotae,* Caradoc, Morocco; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×1.9; *c,* rubber replicas of two ventral exteriors, ×1.9 (Havlíček, 1971a).

Family PHRAGMORTHIDAE Williams, 1965

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Phragmorthinae WILLIAMS, 1965b, p. 327]

Multicostellate, delthyrial and notothyrial openings narrow: apsacline ventral interarea long, curved, anacline dorsal interarea, short, curved; simple teeth supported by recessive dental plates uniting with thickened anterior boundary to short suboval ventral muscle field; pedicle callist not reported; brachiophores long with supporting plates converging posteromedianly onto median septum to form septalium containing low, ridgelike cardinal process; socket plates normally encased in secondary shell and defining deep sockets; dorsal muscle field quadripartite with anterior pair of scars larger than posterior; ventral mantle canal system saccate with convergent *vascula media. Upper Ordovician (Caradoc–Ashgill).*

Phragmorthis Cooper, 1956, p. 508 [**P. buttsi;* OD]. Subquadrate, unisulcate, costellae sporadically swollen. *Upper Ordovician (Caradoc–Ashgill):* North America, Scotland, Kazakhstan, Ireland, Argentina, southwestern China.——Fig. 560*a–f.* **P. buttsi,* Caradoc, Virginia; *a–c,* ventral, dorsal, posterior views of conjoined valves, ×2; *d,e,* normal, tilted views of dorsal interior, ×4; *f,* ventral interior, ×4 (Cooper, 1956).

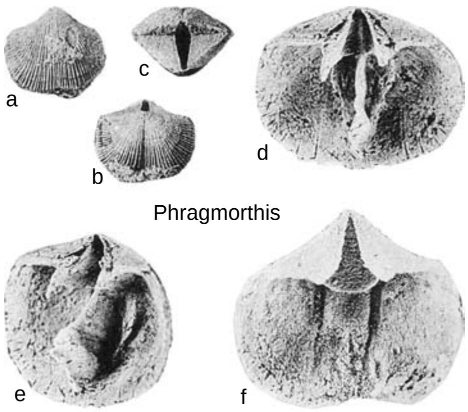

Fig. 560. Phragmorthidae (p. 775).

Family PLATYSTROPHIIDAE
Schuchert & LeVene, 1929

[*nom. transl.* Williams & Harper, herein, *ex* Platystrophiinae Schuchert & LeVene, 1929, p. 14]

Transversely subquadrate to semioval, dorsibiconvex, normally strongly uniplicate, medium-sized plectorthoids; interareas proportionately long and curved; teeth normally with crural fossettes supported by subparallel dental plates flanking poorly differentiated, elongately oval ventral muscle scar with broad adductor track impressed on thick callist, pedicle callist rarely preserved; divergent, bladelike brachiophores joined to hinge line by concave fulcral plates and supported by plates converging posteromedianly to form small septalium, cardinal process bladelike; scars of quadripartite dorsal adductor field variable in size, bisected by median ridge, mantle canal systems rarely impressed. *Lower Ordovician (Arenig)–middle Silurian (Wenlock).*

Platystrophia King, 1850, p. 106 [**Terebratulites biforatus* von Schlotheim, 1820, p. 265; OD]. Normally large, spiriferoid in outline with acute to mucronate cardinal extremities, strongly biconvex, costate and finely granulose, variably lamellose, ventral beak commonly resorbed with apical foramen; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system digitate. *Lower Ordovician (Arenig)–middle Silurian (Wenlock):* cosmopolitan.——Fig. 561,*1a.* **P. biforata,* Caradoc, Cincinnati; dorsal exterior, ×2 (Cocks, new).——Fig. 561,*1b–e. P. ponderosa* Foerste, Ashgill, eastern North America; ventral, dorsal, posterior, anterior views of conjoined valves, ×1 (Shimer & Shrock, 1944).——Fig. 561,*1f,g. P. laticosta* (Meek), Ashgill, Ohio; *f,* ventral interior, ×1.5; *g,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).

Acanthorthis Neuman, 1976, p. 22 [**A. terreneuvensis;* OD]. Subquadrate with obtuse cardinal extremities, multicostellate with spinose lamellae; simple teeth supported by divergent dental plates; brachiophores rodlike; widely divergent; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Lower Ordovician (Arenig):* eastern Canada.——Fig. 561,*3a–c.* **A. terreneuvensis,* Arenig, central Newfoundland; *a,* internal mold of dorsal valve, ×1.5; *b,* internal mold of ventral valve, ×1.5; *c,* external mold of ventral valve, ×1.5 (Neuman, 1976).

Ffynnonia Neuman & Bates, 1978, p. 592 [**Pleurorthis costatus* Bates, 1968, p. 149; OD]. Subquadrate with acute cardinal extremities, coarsely costellate; curved interareas relatively short; dental plates recessive; anterior pair of quadripartite dorsal adductor scars larger than posterior pair. *Lower Ordovician (Arenig–Llanvirn):* Wales, Ireland.——Fig. 562,*1a–e.* **F. costatus* (Bates), Llanvirn, Anglesey; *a,b,* internal mold, rubber replica of dorsal valve, ×2; *c,d,* internal mold, rubber replica of ventral valve, ×2; *e,* rubber replica of ventral exterior, ×2 (Neuman & Bates, 1978).

Mcewanella Foerste, 1920, p. 197 [**Platystrophia fernvalensis* McEwan, 1919, p. 428; OD; =*Hebertella lineolata* Savage, 1917, p. 267]. Similar to *Platystrophia* but with a fine costellate ornamentation commonly superimposed on coarsely costate arrangement of *Platystrophia. Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill):* USA, Great Britain, Ireland, Norway, central Asia (Altai, Kunlou, and Altai Mountains), Spain, France, northwestern China.——Fig. 561,*2a,b.* **M. lineolata* (Savage), Ashgill, Missouri; *a,* ventral interior, ×1; *b,* ventral exterior, ×1(McEwan, 1919).——Fig. 561,*2c–f. M. raymondi* Foerste, Ashgill, Missouri; *c,* ventral exterior, ×1; *d,* dorsal view of con-

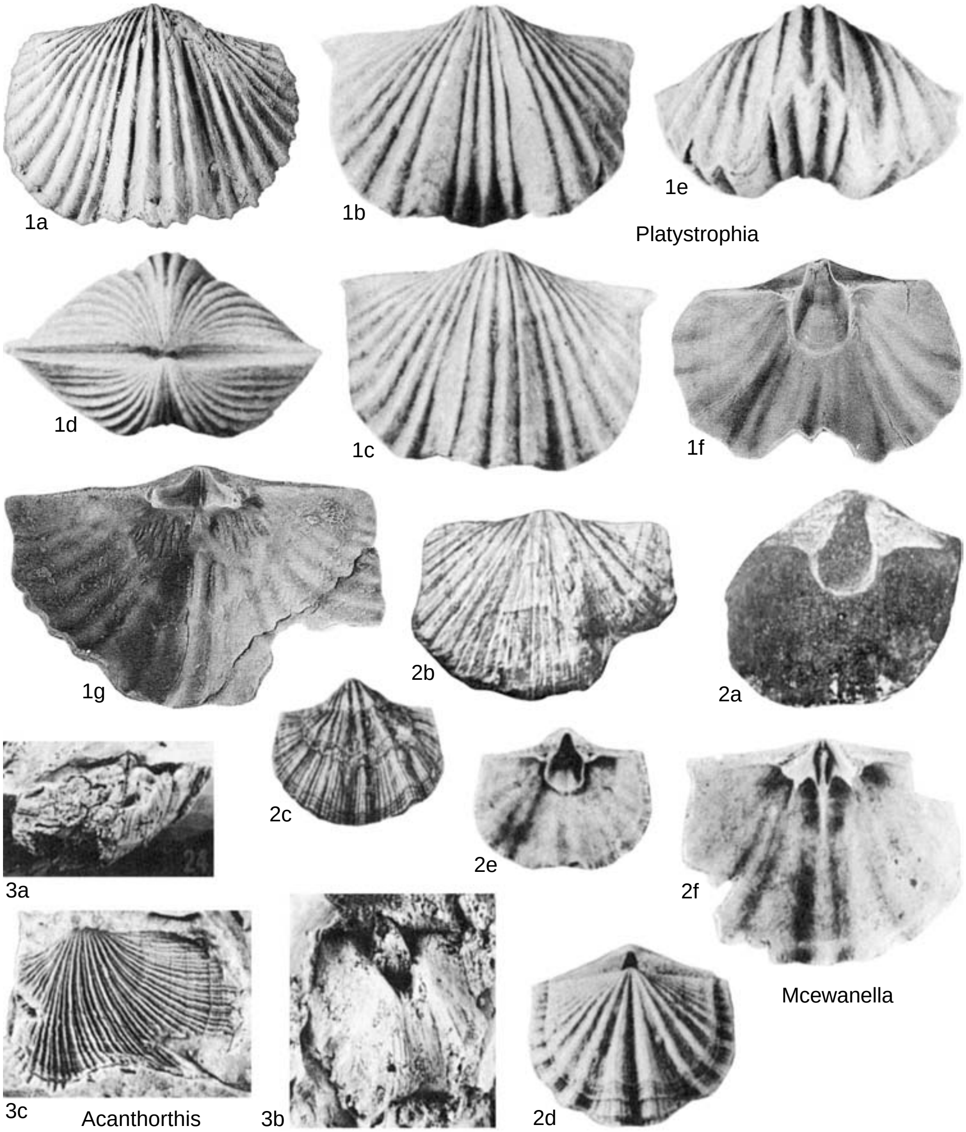

FIG. 561. Platystrophiidae (p. 775–776).

joined valves, ×2; *e,* ventral interior, ×1; *f,* dorsal interior, ×2 (Shimer & Shrock, 1944).

Salacorthis WILLIAMS, 1974, p. 79 [**S. costellata;* OD]. Subquadrate with obtuse cardinal extremities, costate to sporadically costellate with densely distributed, coarse exopunctae quincuncially arranged; ventral muscle scar impressed directly on valve floor, pedicle callist well developed; dorsal adductor scars subequal. *Upper Ordovician (Caradoc–Ashgill):* England, Wales.——FIG. 562,*2a–e.* **S. costellata,* Caradoc, Shelve; *a,* internal mold of dorsal valve, ×7.6; *b,* rubber replica of dorsal valve, ×4.9; *c,* external mold of dorsal valve, ×7.6; *d,* internal mold of ventral valve, ×3.1; *e,* rubber replica of partial dorsal exterior (Williams, 1974).

Family RANORTHIDAE Havlíček, 1949

[Ranorthidae HAVLÍČEK, 1949b, p. 252]

Unisulcate, ramicostellate plectorthoids with apsacline ventral interarea short, curved, shorter anacline dorsal interarea more variable; deltidiodont teeth supported by recessive dental plates, ventral muscle field suboval with broad, subtriangular adductor

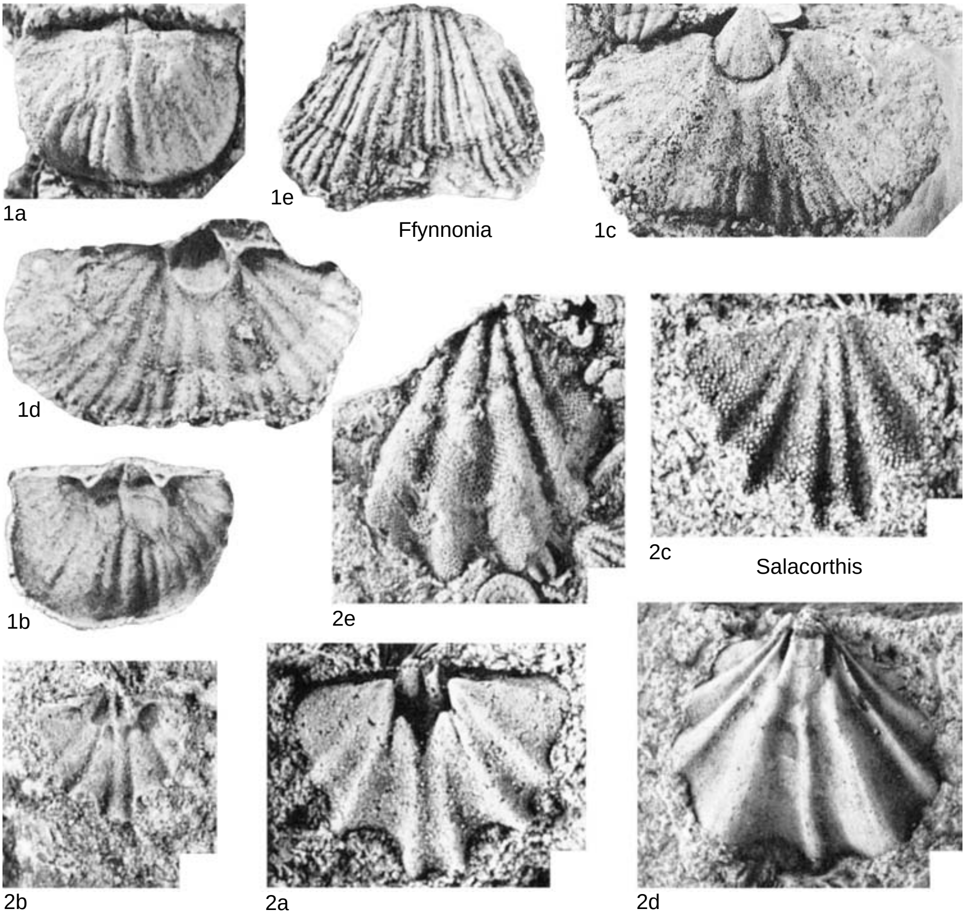

FIG. 562. Platystrophiidae (p. 775–776).

track as long as flanking diductor scars; notothyrial platform usually well developed, prolonged anteriorly as median ridge; cardinal process variable, divergent brachiophores bladelike, lacking supporting plates but joined to hinge line by fulcral plates; narrowly diverging *vascula myaria* forming oblique boundaries separating posterior pair of quadripartite dorsal adductor field from larger anterior pair; ventral mantle canal system saccate with divergent *vascula media,* sporadically impressed dorsal system digitate. *Lower Ordovician (Tremadoc–Arenig).*

Ranorthis ÖPIK, 1939, p. 119 [**R. norvegica;* OD]. Small, subcarinate, elongately semioval with rectangular to obtuse cardinal extremities, dorsal interarea curved, cardinal process rudimentary to ridgelike. *Lower Ordovician (Tremadoc–Arenig):* Europe, northern Africa.——FIG. 563,*1a–d.* **R. norvegica,* Arenig, Oslo Region; *a,* internal mold of dorsal valve, ×3.8; *b,* internal mold of ventral valve, ×8.2; *c,* ventral exterior, ×3.8; *d,* external mold of dorsal valve, ×3.8 (Öpik, 1939).

Eodalmanella HAVLÍČEK, 1950, p. 24 [**Orthis socialis* BARRANDE, 1879, p. 63]. Medium sized, elongately subquadrate with variable cardinal extremities, dorsal interarea planar, cardinal process differentiated into shaft and bilobed myophore. *Lower Ordovician (Llanvirn):* Bohemia, eastern North America, Kazakhstan, central Asia (Altai Mountains).——FIG. 563,*2a–e.* **E. socialis* (BARRANDE), Llanvirn, Bohemia; *a,* internal mold of ventral valve, ×4.9; *b,c,* internal molds of dorsal valves, ×3; *d,* rubber replica of ventral exterior, ×5.2; *e,* rubber replica of dorsal exterior, ×4.1 (Havlíček, 1977a).

Nothorthis ULRICH & COOPER, 1938, p. 106 [**N. delicatula;* OD] [=*Altorthis* ANDREEVA, 1960, p. 288 (type, *A. kinderlensis*)]. Transversely semioval with

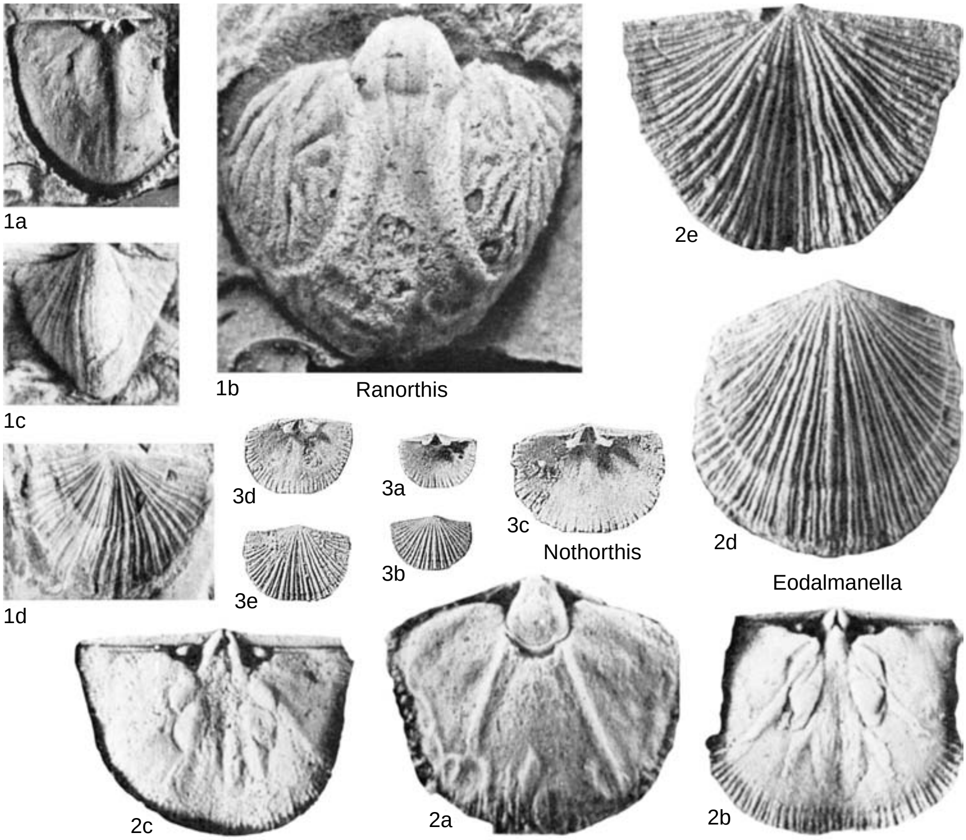

FIG. 563. Ranorthidae (p. 777–778).

obtuse cardinal extremities, ramicostellate; suboval ventral muscle scar impressed on callosity; short, rodlike, divergent brachiophores, notothyrial platform rudimentary, cardinal process absent or rudimentary. *Lower Ordovician (Tremadoc–Llanvirn):* eastern North America, Baltic, Siberia, Scotland, Bohemia, eastern China, central Asia (Altai Mountains).——FIG. 563,*3a–e.* **N. delicatula,* Tremadoc, Quebec; *a,b,* interior, exterior of ventral valve, ×3; *c,* dorsal interior, ×4.5; *d,e,* interior, exterior of dorsal valve, ×3 (Cooper, 1956). [Note added in proof: with fulcral plates; see Fig. 563,*3c.*]

Family RHACTORTHIDAE Williams, 1963

[*nom. transl.* WILLIAMS & HARPER, herein, *ex* Rhactorthinae WILLIAMS, 1963, p. 371]

Medium size, ventribiconvex plectorthoids normally subquadrate with obtuse cardinal extremities, costellate with aditicules; interareas normally planar; ventral muscle field subtriangular to weakly bilobed with wide, triangular, poorly differentiated adductor track normally impressed on elevated median callus; brachiophores widely divergent without basal plates, supported by concave fulcral plates joined to hinge line and defining elongate sockets; cardinal process well differentiated into shaft and myophore; quadripartite dorsal adductor scars indistinct. *Upper Ordovician (Caradoc–Ashgill).*

Rhactorthis WILLIAMS, 1963, p. 371 [**R. crassa;* OD]. Sharply unisulcate, multicostellate, interareas proportionately long; dental plates recessive, ventral adductor track not much elevated, pedicle callist well developed; brachiophores rodlike, cardinal process thickened with crenulated myophore, continuous with median ridge; ventral mantle canal system possibly saccate with subparallel *vascula media,* dorsal system also possibly saccate but with divergent *vascula media. Upper Ordovician (Caradoc–Ashgill):* Great Britain, Ireland, Estonia, Norway, Bohemia.——FIG. 564,*2a–d.* **R. crassa,* Caradoc, Wales; *a,* internal mold of dorsal valve, ×6.6; *b,* internal mold of ventral valve, ×3.5; *c,* rubber replica of ventral exterior, ×3.1; *d,* rubber replica of dorsal exterior, ×3.2 (Williams, 1963).

Aberia Mélou, 1990, p. 549 [**A. havlíceki;* OD]. Subcircular, rectimarginate, ramicostellate, interareas planar, relatively long; ventral muscle scar weakly bilobed; cardinal process thickened with bilobed myophore; dorsal median ridge vestigial. *Upper Ordovician (Ashgill):* France.——Fig. 564,*1a–d.* **A. havliceki,* Ashgill, Brittany; *a,* rubber replica of dorsal interior, ×2; *b,* rubber replica of ventral interior, ×2; *c,* internal mold of ventral valve, ×2; *d,* rubber replica of dorsal exterior, ×2 (Mélou, 1990).

Eripnifera Potter, 1990a, p. 108 [**E. praecipitis;* OD]. Strongly unisulcate, fascicostellate (aditicules not observed), interareas proportionately long, curved; ventral muscle scar subtriangular with anteromedian elevated callus; brachiophores bladelike, supported by fulcral plates and subparallel ancillary struts that are not typical brachiophore plates; cardinal process rodlike, continuous with the median ridge and with bulbous myophore, flanked by low notothyrial thickenings in some valves; quadripartite dorsal adductor field petaloid, bounded by ridge and divided into posterior and anterior components by narrowly divergent *vascula myaria;* mantle canal systems in both valves digitate. *Upper Ordovician (Ashgill):* USA (California, Alaska).——Fig. 564,*3a–e.* **E. praecipitis,* Ashgill, California; *a,b,* interior, exterior of ventral valve, ×2; *c,d,* interior, exterior of dorsal valve, ×3.5; *e,* dorsal interior, ×4 (Potter, 1990a).

Family TASMANORTHIDAE Laurie, 1991

[*nom. transl.* Williams & Harper, herein, *ex* Tasmanorthinae Laurie, 1991, p. 41]

Subequally biconvex, rectimarginate, costate to coarsely costellate, capillate, pustulose plectorthoids; interareas relatively long, curved; simple teeth supported by divergent dental plates, ventral muscle scar elongately quadrate, adductor track broad, triangular, divided by low median ridge; cardinal process differentiated into short shaft and bilobed myophore; brachiophores bladelike with divergent bases, fulcral plates variably developed, defining elongate sockets; notothyrial platform vestigial, dorsal median ridge low; posterior pair of quadripartite dorsal adductor scars larger than anterior pair; ventral mantle canal system probably saccate with divergent *vascula media,* dorsal system unknown. *Upper Ordovician (Caradoc).*

Tasmanorthis Laurie, 1991, p. 41 [**T. costata;* OD]. Medium size, subquadrate with obtuse cardinal extremities. *Upper Ordovician (Caradoc):* Australia (Tasmania).——Fig. 565,*1a–f.* **T. costata,* Caradoc, Tasmania; *a–c,* interior, exterior, posterior view of ventral valve, ×2; *d,e,* interior, exterior of dorsal valve, ×2; *f,* details of ornament, ×8 (Laurie, 1991).

Family WANGYUIIDAE Zhang, 1989

[Wangyuiidae Zhang, 1989a, p. 58] [=Sigmelasmidae Potter, 1990b, p. 23]

Subquadrate to transversely semioval with variable cardinal extremities, ventribiconvex with ventral valve commonly subpyramidal, unisulcate, costellate plectorthoids; delthyrium and notothyrium open, narrow; apsacline ventral interarea long, curved, anacline dorsal interarea short, curved; teeth with recessive dental plates, ventral muscle field subtriangular to bilobate with elongate adductor scars commonly elevated on median ridge; brachiophores long, narrowly divergent with plates S-shaped in section, free of valve floor except posteromedianly, fulcral plates variably developed; cardinal process simple ridge, rarely with bilobed myophore; dorsal median partition ridgelike or absent, dorsal muscle field and mantle canal systems indistinctly impressed. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock).*

Wangyuia Zhang, 1989a, p. 58 [**W. thorsteinssoni;* OD]. Transversely semioval with variable cardinal extremities, coarsely costellate, weakly lamellose; subpyramidal ventral interarea steeply apsacline to procline; ventral muscle field bilobed, cardinal process rodlike, occasionally capped with bilobed myophore; dorsal adductor field elongately quadripartite with anterior pair of scars larger than posterior pair, dorsal median ridge low. *middle Silurian (Wenlock):* Arctic Canada.——Fig. 565,*4a–e.* **W. thorsteinssoni,* Wenlock, Arctic Canada; *a,b,* interior, exterior of ventral valve, ×8; *c,d,* interior, exterior of dorsal valve, ×8; *e,* interior of dorsal valve, ×8 (Zhang, 1989a).

Bowanorthis Percival, 1991, p. 123 [**B. fragilis;* OD]. Subquadrate, delthyrium with apical plate; catacline ventral interarea long, curved, anacline to catacline dorsal interarea shorter, planar; vestigial notothyrial platform continuous with long dorsal median ridge; dorsal adductor field sills equally quadripartite; ventral mantle canal system probably saccate with subparallel *vascula media. Upper Ordovician (Caradoc):* Australia (New South Wales).——Fig. 565,*5a–f.* **B. fragilis,* Caradoc, New South Wales; *a–c,* dorsal, posterior, anterior views of conjoined valves, ×5; *d,e,* interior, exterior of dorsal valve, ×5; *f,* ventral interior, ×5 (Percival, 1991).

Sigmelasma Potter, 1990b, p. 23 [**S. pantherae;* OD]. Subquadrate, strongly apsacline ventral interarea planar, of variable length, anacline dorsal interarea shorter; notothyrial platform and dorsal median

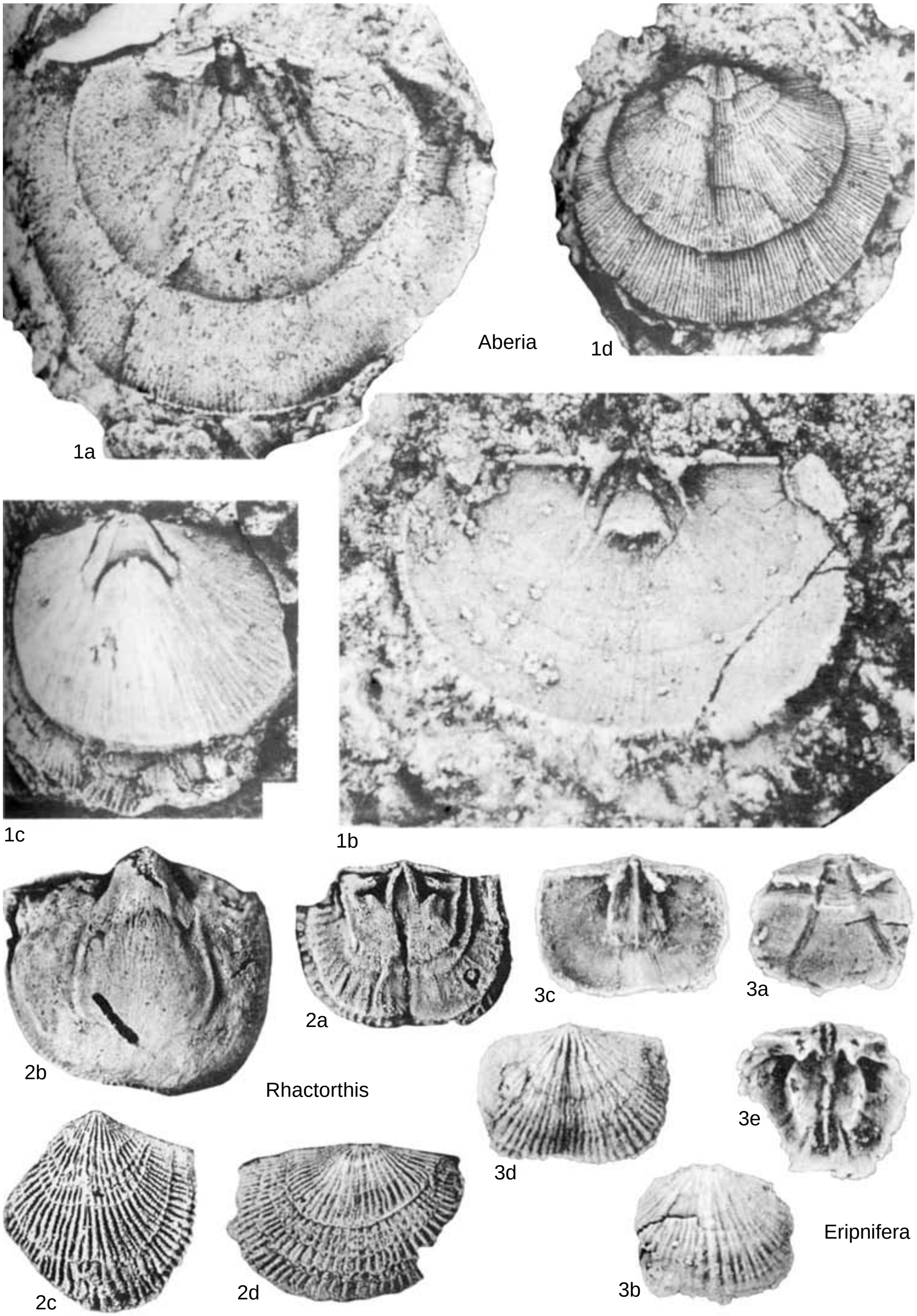

FIG. 564. Rhactorthidae (p. 778–779).

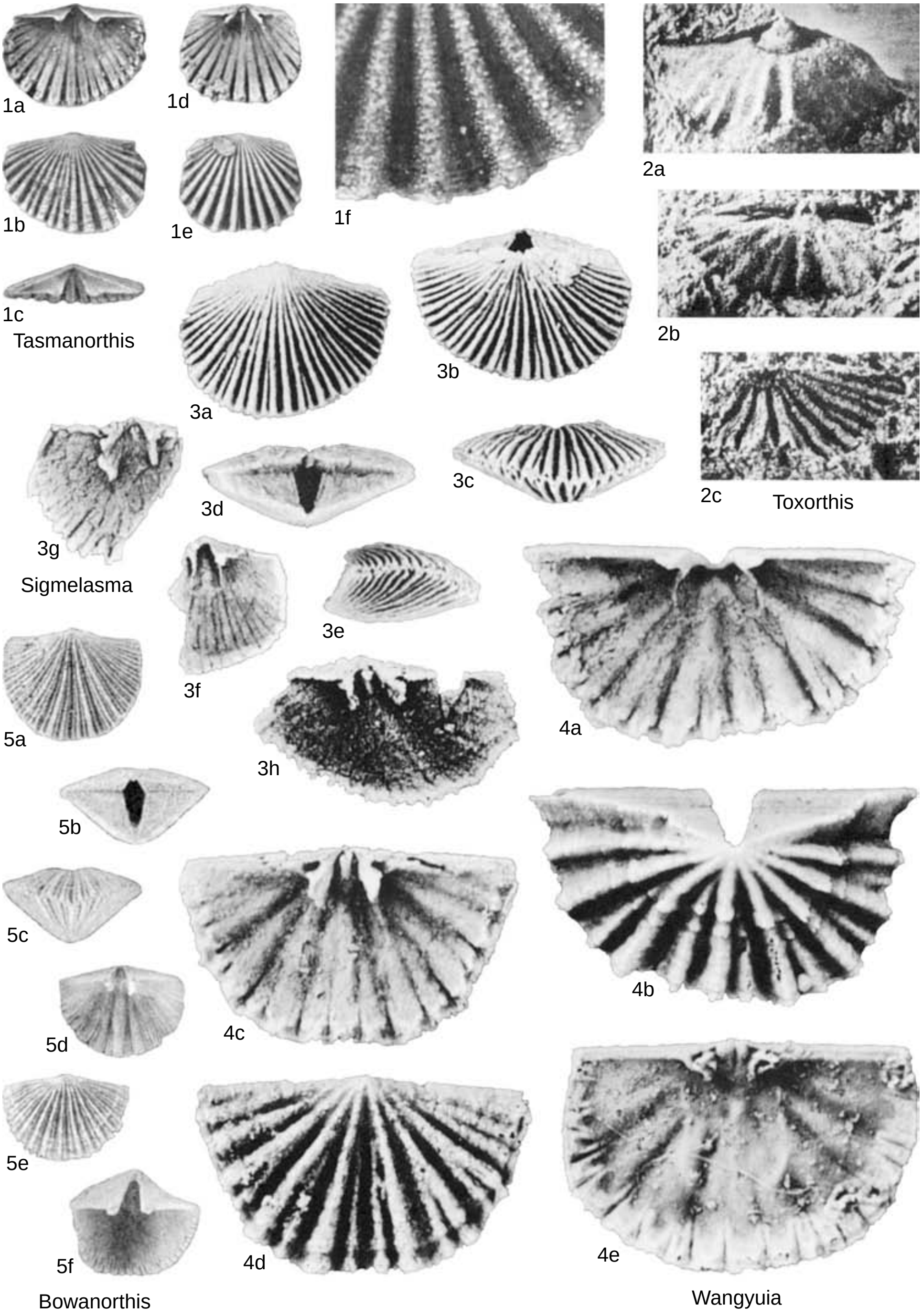

FIG. 565. Tasmanorthidae and Wangyuiidae (p. 779–782).

septum absent. *Upper Ordovician (Caradoc):* western United States.——FIG. 565,*3a–h*. **S. pantherae,* Caradoc, California; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×6; *f,* broken ventral interior, ×6; *g,* broken dorsal interior, ×6; *h,* dorsal interior, ×6 (Potter, 1990b).

Toxorthis TEMPLE, 1968, p. 20 [**T. proteus;* OD]. Transversely semioval with acute cardinal extremities, strongly unisulcate, coarsely costellate; interareas relatively short; teeth usually as elongate ridges, ventral muscle field subtriangular, undifferentiated; cardinal process absent, simple or as a low, bilobed myophore; platelike brachiophores supported at ends of elongate fulcral plates. [The family Toxorthidae RONG, 1984 has already been erected for this genus and, in fact, predates the Wangyuiidae. There is some doubt, however, regarding the relationship between *Toxorthis* and *Wangyuia.* The most distinctive familial feature of the latter (and *Bowanorthis*) are the large S-curved brachiophores. Only the proximal parts of the brachiophores of *Toxorthis* are known as all species assigned to the genus are based exclusively on molds. If further study confirms brachiophore similarity, then the Wangyuiidae will become a junior synonym of Toxorthidae.] *Upper Ordovician (Ashgill):* Great Britain, central China (western Hubei).——FIG. 565,*2a–c*. **T. proteus,* Ashgill, northwestern England; *a,* internal mold of ventral valve, ×10; *b,* internal mold of dorsal valve, ×10; *c,* external mold of dorsal valve, ×10 (Temple, 1968).

DALMANELLIDINA

DAVID A. T. HARPER
[University of Copenhagen]

Suborder DALMANELLIDINA Moore, 1952

[*nom. correct.* HARPER, herein, *pro* Dalmanelloidea MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220; *emend.,* HARPER, herein]

Delthyrium and notothyrium normally open; deltidiodont teeth commonly with dental fossettes, supported by variably developed and disposed dental plates; ventral muscle scar normally suboval to cordate and impressed on valve floor, rarely associated with raised structures; cardinalia usually with bilobed, trilobed, or lobate cardinal process and shaft, occasionally modified, rarely simple, ridgelike, or absent, situated on variably developed notothyrial platform; brachiophores as blades, rods, or spikes with convergent or divergent plates onto valve floor, together with fulcral plates, where present, define variably developed sockets; dorsal septa, partitions, and platforms rarely developed, mainly in later taxa; ventral mantle canal system normally lemniscate, rarely saccate; dorsal mantle canal system lemniscate to digitate and pinnate; shell with fibrous secondary layer, punctate (possibly endopunctate). *Lower Ordovician (Arenig)–Upper Permian (Tatarian).*

The punctate orthides were first accorded superfamilial status as the Dalmanellacea by SCHUCHERT and COOPER (1931, p. 245) on the basis of their endopunctate shell structure. The majority of subsequent authors have accepted variants on this term to describe the group. MOORE (in MOORE, LALICKER, & FISCHER, 1952) first raised the taxon to subordinal status. Alternatively, WRIGHT (1965a, p. 328) argued for a single superfamily to contain the punctate orthide genera, to be named the Enteletacea on grounds of priority (*ex* Enteletinae WAAGEN, 1884, p. 548; *contra* Dalmanellinae SCHUCHERT, 1913b, p. 382). He recognized, however, that a term associated with the widespread, more generalized, earlier, and probably better-known *Dalmanella* would be more appropriate for the group than one based on the later, aberrant *Enteletes.*

Two superfamilies are recognized cladistically, mainly on the features of the cardinalia. The Dalmanelloidea has a well-developed notothyrial platform, reduced in later taxa, with a cardinal process evolving complex and modified, bilobed, trilobed, and generally lobate morphologies; brachiophores are generally rodlike or bladelike, with variably inclined plates and variably developed fulcral plates usually in earlier taxa. The dorsal adductor muscle scars are normally quadripartite. The Enteletoidea lacks a well-developed notothyrial platform and has a relatively simple crenulated cardinal process, expanded in some later taxa; high tusklike brachiophores, especially in later genera; well-developed fulcral plates; and convergent brachiophore plates, mainly in earlier forms. The dorsal adductor muscle scars are commonly petaloid. Dorsal septa, partitions, and platforms are variably developed across both superfamilies, mainly in later taxa.

Both superfamilies are well defined and distinct by their first appearances in the Arenig (see Fig. 522). Although cladistic analysis based on morphological data has helped clarify superfamilial groupings herein, it has not resolved the origin of the punctate orthides. Direct ancestral candidates within the plectorthoids have been suggested (Havlíček, 1977a), but the dalmanellidines and plectorthoids may have shared a common ancester in the Middle to Upper Cambrian.

Superfamily DALMANELLOIDEA Schuchert, 1913

[*nom. transl.* Schuchert & Cooper, 1931, p. 245, *ex* Dalmanellinae Schuchert, 1913b, p. 382] [=Rhipidomellacea Alichova, 1960, p. 190]

Normally subequally to unequally biconvex dalmanellidines; costellate ornament usually lacking aditicules except in later taxa; notothyrial platform well developed, reduced in later taxa; cardinalia normally with complex cardinal process having lobate, bilobed, or trilobed myophore, commonly modified as cleft or differentiated; shaft variably developed; brachiophores as thickened rods or blades with plates, when present, convergent or divergent onto valve floor; fulcral plates commonly developed; dorsal muscle scar quadripartite. *Lower Ordovician (Arenig)–Upper Permian (Tatarian).*

Family DALMANELLIDAE Schuchert, 1913

[*nom. transl.* Schuchert & LeVene, 1929, p. 15, *ex* Dalmanellinae Schuchert, 1913b, p. 382] [=Wattsellidae Schuchert & Cooper, 1931, p. 246; Onniellidae Öpik, 1933b, p. 14]

Normally subcircular, ventribiconvex, unisulcate, fascicostellate dalmanelloids with short, straight or curved ventral and dorsal interareas; ventral interior normally with suboval, subtriangular to cordate muscle scars, with adductors rarely enclosed by diductors, and divergent dental plates; dorsal interior with variably lobate cardinal process and shaft; brachiophores commonly as simple blades, variably disposed with variably inclined brachiophore plates; fulcral plates common, mainly in earlier taxa; median ridges, septa, partitions, and platforms sporadically developed in dorsal valves; ventral and dorsal mantle canal systems commonly lemniscate. *Lower Ordovician (Arenig)–Upper Devonian (Frasnian).*

Subfamily DALMANELLINAE Schuchert, 1913

[Dalmanellinae Schuchert, 1913b, p. 382; *emend.,* Harper, herein]

Normally subcircular to subquadrate, usually ventribiconvex dalmanellids with short ventral and dorsal interareas; delthyrium and notothyrium open; internally lacking well-developed median ridges, septa, partitions, and platforms in dorsal valves. *Lower Ordovician (Arenig)–upper Silurian (Ludlow).*

Dalmanella Hall & Clarke, 1892, p. 205 [**Orthis testudinaria* Dalman, 1828, p. 115; OD] [=*Wattsella* Bancroft, 1928a, p. 55 (type, *W. wattsi*)]. Subcircular, variably biconvex to ventribiconvex valves; ventral interior with dental fossettes, cordate muscle scar, and divergent dental plates; dorsal interior with brachiophore plates convergent onto median ridge; fulcral plates normally present. *Lower Ordovician (Arenig)–lower Silurian (Llandovery):* cosmopolitan.——Fig. 566,*2a–f.* **D. testudinaria* (Dalman), Ashgill, Sweden; *a–e,* ventral, dorsal, posterior, anterior, lateral views of conjoined valves, ×2.3; *f,* rubber replica of dorsal interior, ×4 (Williams & Wright, 1963).——Fig. 566,*2g,h. D. testudinaria ripae* Mitchell, Ashgill, Girvan, Scotland; *g,* internal mold of dorsal valve, ×4; *h,* internal mold of ventral valve, ×4 (Harper, 1989).——Fig. 566,*2i. D. multiplicata,* Caradoc, Shropshire; internal mold of dorsal valve, ×1.5 (Cocks, new).

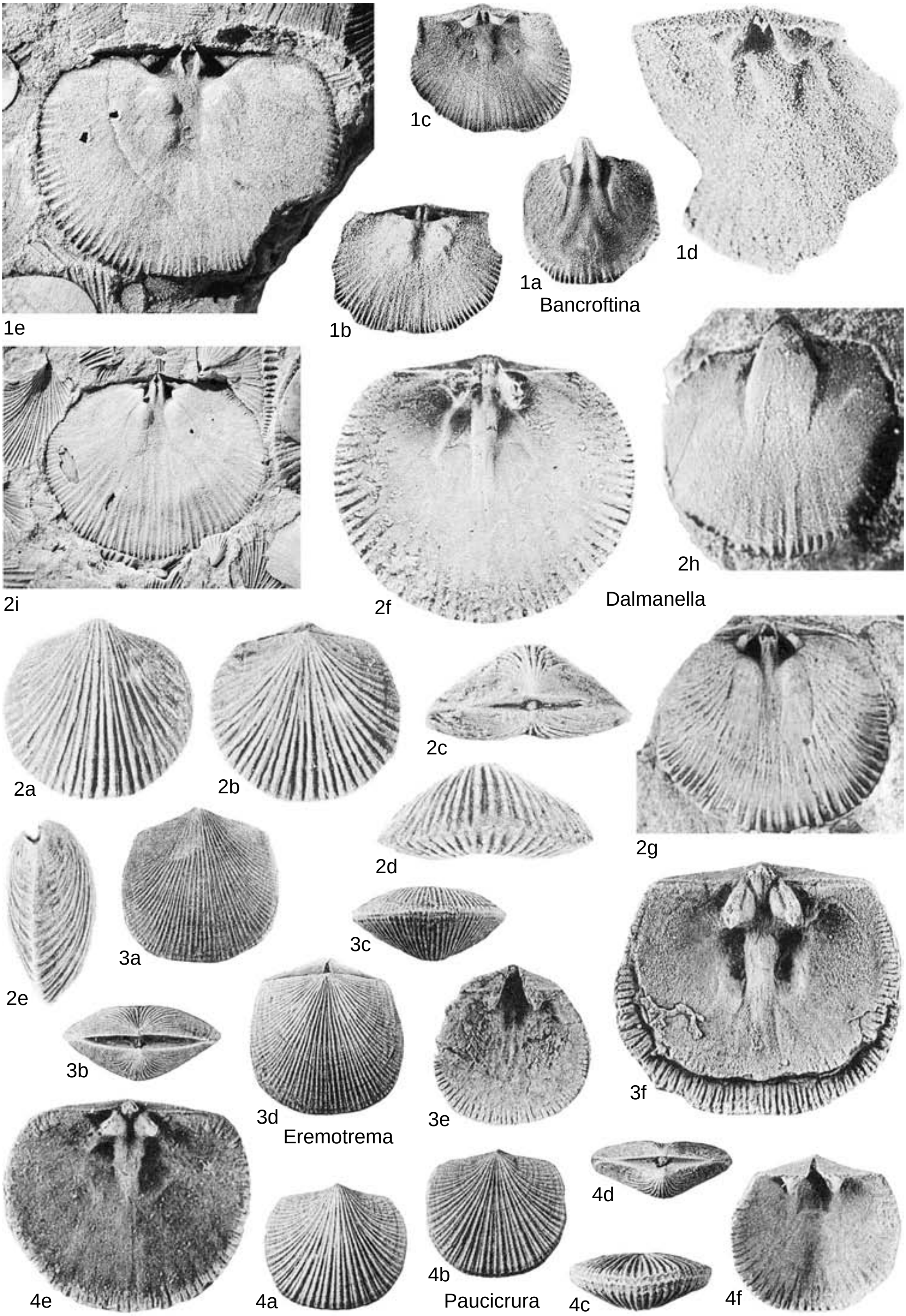

FIG. 566. Dalmanellidae (p. 783–786).

Bancroftina Sinclair, 1946, p. 295, *nom. nov. pro Raymondella* Whittington, 1938, p. 249, *non* Reed, 1935] [**Raymondella typa* Whittington, 1938, p. 249; OD; =*R. typa* Bancroft, 1933, p. 3, *nom. nud.*]. Subquadrate, unequally biconvex to ventribiconvex, nearly rectimarginate valves; ventral interior with bilobed to linear muscle scar and recessive dental plates; dorsal interior with undifferentiated trilobed cardinal process, brachiophores and plates subparallel to hinge line, supported by ancillary struts extending anteriorly from notothyrial platform; fulcral plates rare. *Upper Ordovician (Caradoc):* Britain, Ireland.——Fig. 566,*1a–d.* **B. typa* (Whittington), Caradoc, Shropshire; *a,* internal mold of ventral valve, ×1.5; *b,c,* internal mold, rubber replica of dorsal valve, ×1.5 (Wright, 1965a); *d,* rubber replica of dorsal interior, ×4 (Williams & Wright, 1963).——Fig. 566,*1e. B. robusta* (Bancroft), Caradoc, Shropshire; internal mold of dorsal valve, ×2.5 (Cocks, new).

Cryptothyris Bancroft, 1945, p. 223 [**Resserella paracyclica* Bancroft, 1928a, p. 56; OD]. Subcircular, markedly ventribiconvex, mainly rectimarginate valves; ventral muscle scar subtriangular to cordate with short diductor scars; dorsal interior with massive brachiophores, plates slightly divergent ventrally; bilobed cardinal process undifferentiated; fulcral plates rare. *Upper Ordovician (Caradoc):* Britain.——Fig. 567,*1a–e.* **C. paracyclica* (Bancroft), Caradoc, Shropshire; *a,* internal mold of ventral valve, ×1.5 (Hurst, 1979); *b,* internal mold of dorsal valve, ×2.5; *c,* ventral exterior, ×2.5 (Cocks, new); *d,* rubber replica of dorsal exterior, ×3; *e,* internal mold of dorsal valve, ×3 (Williams & Wright, 1963).

Eremotrema Cooper, 1956, p. 959 [**E. biconvexum;* OD]. Elongately semioval, ventribiconvex valves; ventral interior with bilobed muscle scar and divergent dental plates; dorsal interior with fissured, trilobed cardinal process and brachiophore plates variably divergent ventrally; fulcral plates rare. *Upper Ordovician (Caradoc):* eastern North America, Scotland.——Fig. 566,*3a–f.* **E. biconvexum,* Caradoc, Virginia; *a–d,* ventral, posterior, anterior, dorsal views of conjoined valves, ×2; *e,* ventral interior, ×2; *f,* dorsal interior, ×3 (Cooper, 1956).

Howellites Bancroft, 1945, p. 203 [**Resserella (Howellites) striata;* OD] [=*Mesodalmanella* Havlíček, 1950, p. 26 (type, *M. flava*)]. Subcircular, ventribiconvex valves; ventral interior with bilobed muscle scar and divergent dental plates; dorsal interior with brachiophore plates variably divergent ventrally and rare fulcral plates. *Upper Ordovician (Caradoc):* Europe, Morocco.——Fig. 568,*2a–e.* **H. striatus* (Bancroft), Caradoc, Wales; *a,* rubber replica of ventral exterior, ×2.5; *b,* rubber replica of dorsal exterior, ×2.5; *c,* internal mold of ventral valve, ×3; *d,* internal mold of dorsal valve, ×3.5; *e,* rubber replica of dorsal interior, ×4 (Williams, 1963).

Mirorthis Zeng in Wang & others, 1983, p. 116 [**M. mira;* OD]. Subcircular, small, ventribiconvex valves; ventral interior with divergent dental plates and suboval muscle scar; dorsal interior with bilobed cardinal process, widely divergent brachiophore plates associated with ancillary struts and crural pits; fulcral plates well developed. *Upper Ordovician (Ashgill):* Europe, Morocco, China.——Fig. 567,*2a–g.* **M. mira,* Ashgill; *a,* internal mold of ventral valve of conjoined internal molds, southern China, ×3; *b,* enlargement of posterior part of conjoined internal molds, southern China, ×10; *c,* internal mold of dorsal valve of conjoined internal molds, southern China, ×3; *d,* enlargement of posterior part of conjoined internal molds, southern China, ×10; *e,* external mold of ventral valve of same specimen, southern China, ×3 (Rong, 1984); *f,* internal mold of dorsal valve, Poland, ×6.6; *g,* internal mold of ventral valve, Poland, ×6.6 (Temple, 1965).

Onniella Bancroft, 1928a, p. 55 [**O. broeggeri;* OD] [=*Soudleyella* Bancroft, 1945, p. 209 (type, *S. soudleyella*); *Bagnorthis* Levy & Nullo, 1974, p. 183 (type, *B. garrigoui*)]. Subquadrate, ventribiconvex valves; ventral interior with widely cordate ventral muscle scar and recessive dental plates; dorsal interior with undifferentiated, swollen, bilobed cardinal process; brachiophore plates widely divergent ventrally. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery):* cosmopolitan.——Fig. 569,*1a–d.* **O. broeggeri,* Caradoc, Shropshire; *a,b,* ventral, dorsal views of conjoined valves, ×1.5; *c,* internal mold of ventral valve, ×1.5 (Cocks, new); *d,* internal mold of dorsal valve, ×2.5 (Hurst, 1979).——Fig. 569,*1e–g. O. reuschi,* Caradoc, Shropshire; *e,* internal mold of ventral valve, ×2; *f,* internal mold of dorsal valve, ×3 (Cocks, new); *g,* rubber replica of dorsal interior, ×1.5 (Wright, 1965a).

Onnizetina Havlíček, 1974, p. 168 [**O. mellita;* OD; =*Orthis trubinensis* Barrande, 1879, pl. 112, case II, fig. 1–3]. Subquadrate, small, biconvex valves with variably inclined dorsal interarea; ventral muscle scar subtriangular; dorsal interior with undifferentiated bilobed cardinal process, high, short bladelike brachiophores, and brachiophore plates slightly divergent ventrally; fulcral plates absent. *Upper Ordovician (Caradoc):* Bohemia.——Fig. 568,*3a–e.* **O. trubinensis* (Barrande), Caradoc, Bohemia; *a,b,* internal mold, rubber replica of dorsal valve, ×5.2; *c,* internal mold of ventral valve, ×7.4; *d,e,* external mold, rubber replica of dorsal valve, ×5.2 (Havlíček, 1977a).

Paucicrura Cooper, 1956, p. 956 [**Orthis rogata* Sardeson, 1892, p. 331; OD] [=*Cristiferina* Cooper, 1956, p. 961 (type, *C. cristata*); *Sigopallus* Liu & Liu, 1985, p. 232 (type, *S. vicarius*)]. Subquadrate, ventribiconvex, fascicostellate valves; ventral interior with divergent dental plates and bilobed muscle scar; dorsal interior with differentially trilobed cardinal process with median lobe expanded as crest. *Upper Ordovician (Caradoc–Ashgill):* Britain, North America.——Fig. 566,*4a–e.* **P. rogata* (Sardeson), Caradoc, Minnesota; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves,

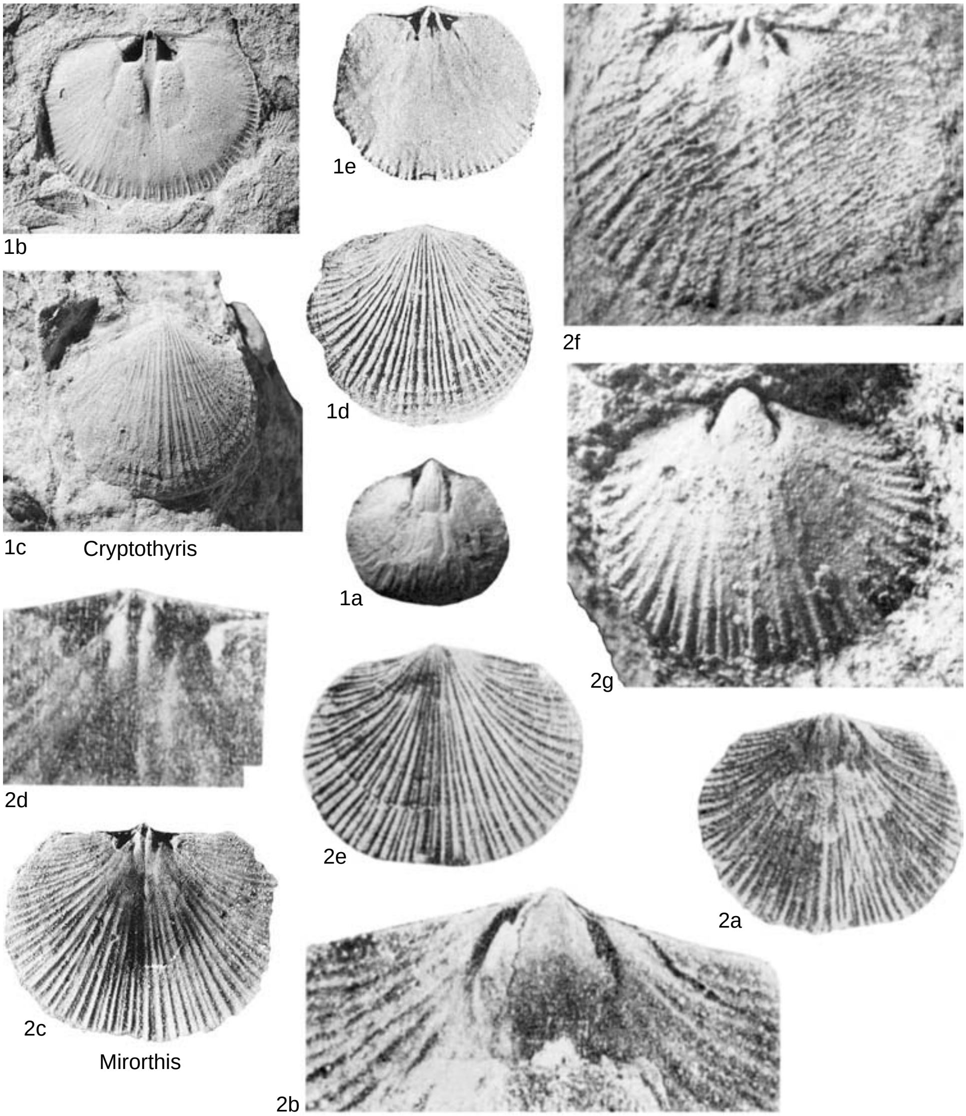

FIG. 567. Dalmanellidae (p. 785).

×2; *e,* dorsal interior, ×3 (Cooper, 1956).——FIG. 566,*4f. P. virginica* COOPER, Caradoc, Virginia; ventral interior, ×3 (Cooper, 1956).

Ravozetina HAVLÍČEK, 1974, p. 169 [**Orthis honorata* BARRANDE, 1879, pl. 68, case III, fig. 1,2]. Subquadrate, small, ventribiconvex, coarsely costellate valves with angular ribs; ventral interior with subtriangular muscle scar on callus; dental plates subparallel, pedicle callist well developed; dorsal interior with cardinal process normally as blade or ridge; fulcral plates absent. *Upper Ordovician (Ashgill)–upper Silurian (Ludlow):* Europe.——FIG. 569,*2a–c.* **R. honorata* (BARRANDE), Ashgill, Bohemia; *a,* internal mold of dorsal valve, ×8; *b,* dorsal exterior, ×10.5; *c,* internal mold of ventral valve, ×8.4 (Havlíček, 1977a).

Trucizetina HAVLÍČEK, 1974, p. 169 [**T. subrotundata;* OD]. Subcircular, ventribiconvex to nearly planoconvex, fascicostellate valves; ventral interior with subtriangular muscle scar and divergent dental plates; dorsal interior with ridgelike or bilobed cardinal process; muscle scar bisected by median ridge and confined posterolaterally by pair of divergent ridges extending forward from brachiophore plates; fulcral plates absent. *Upper Ordovician (Ashgill):* Bohemia.——FIG. 569,*3a–d.* **T. subrotundata,*

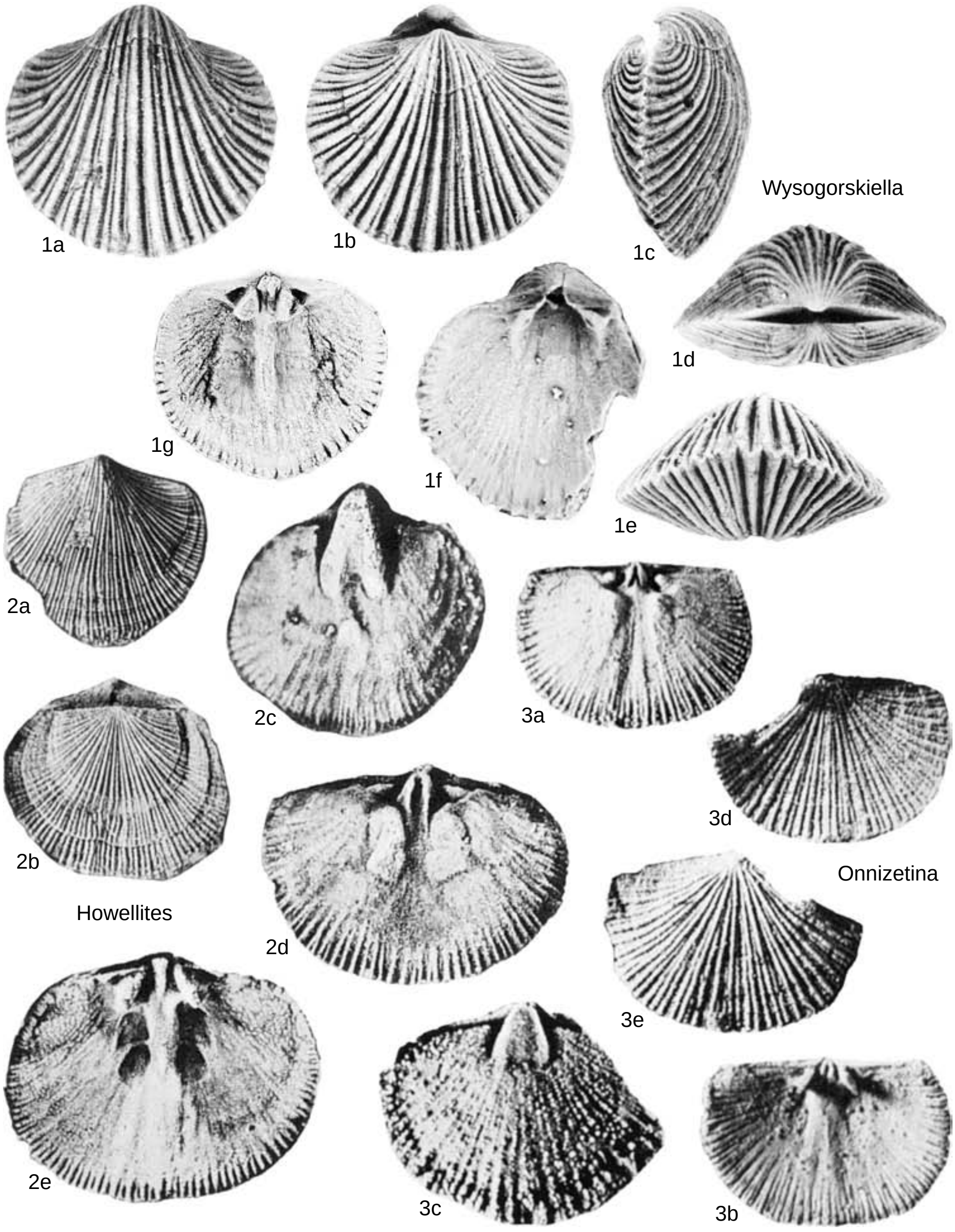

FIG. 568. Dalmanellidae (p. 785–788).

Ashgill, Bohemia; *a,* internal mold of dorsal valve, ×2.7; *b,* rubber replica of dorsal interior, ×3.5; *c,* internal mold of ventral valve, ×3; *d,* dorsal exterior, ×4.3 (Havlíček, 1977a).

Wysogorskiella HINTS, 1975, p. 61 [**W. litviensis;* OD]. Subcircular, ventribiconvex valves; ventral interior with massive teeth, dental fossettes, and divergent dental plates; muscle scar short and cordate; dorsal interior with trilobed cardinal process, massive, erect brachiophores, and fulcral plates; dorsal adductor scars elongate, bisected by well-developed median ridge. *Upper Ordovician (Caradoc–Ashgill):* eastern Baltic.——FIG. 568,*1a–g. W. litviensis,* Caradoc, eastern Baltic; *a–e,* ventral, dorsal, lateral,

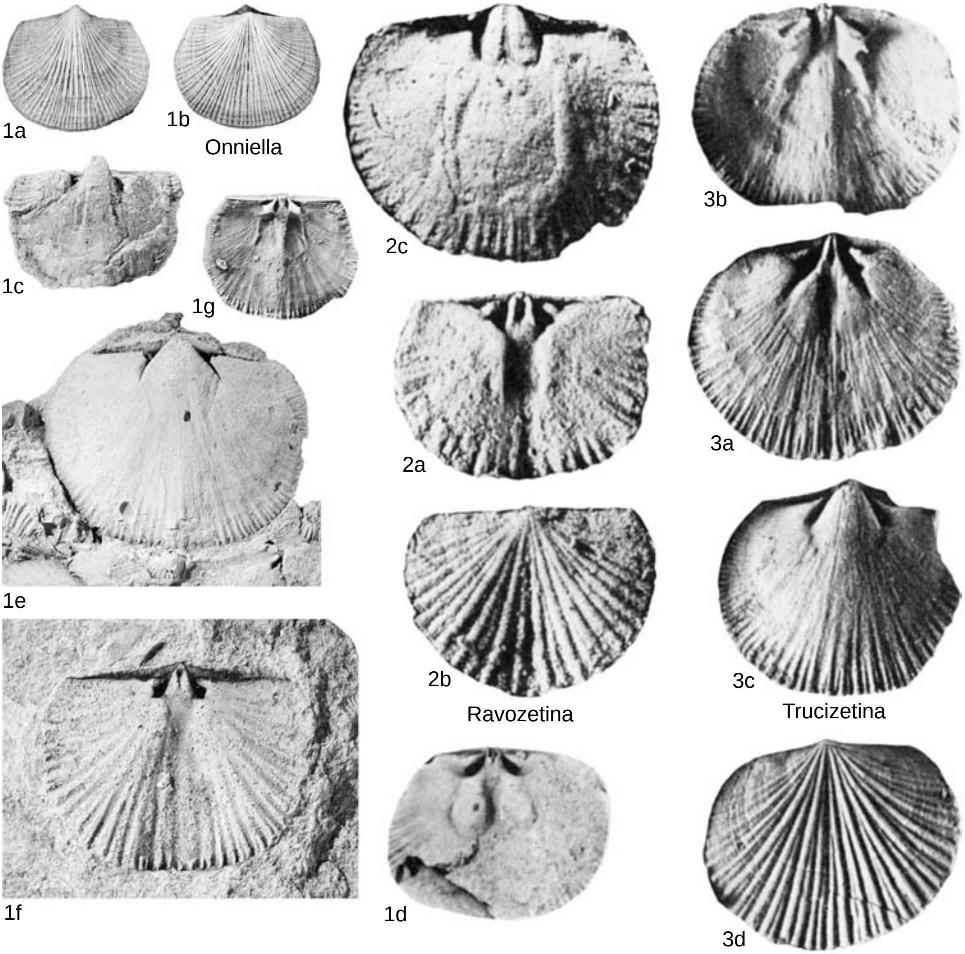

FIG. 569. Dalmanellidae (p. 785–787).

posterior, anterior views of conjoined valves, ×7.5; *f,* ventral interior, ×7.7; *g,* dorsal interior, ×7.5 (Hints, 1975).

Subfamily CORTEZORTHINAE Johnson & Talent, 1967

[Cortezorthinae JOHNSON & TALENT, 1967a, p. 143]

Dalmanellids with ventral interior having linear to quadrate muscle scars; adductor scars fixed in position between surrounding diductors; adductor scars unfacetted and bisected by variably developed median ridge; dorsal interior with well-developed median ridge or septum and widely divergent brachiophores; fulcral plates normally absent. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Cortezorthis JOHNSON & TALENT, 1967a, p. 143 [**C. maclareni;* OD]. Transversely semioval, ventribiconvex, sharply unisulcate valves; ventral interior with dental fossettes and recessive dental plates; muscle scar cordate; dorsal interior with petaloid muscle scar situated on platform, bisected by long, low median septum, triangular in lateral view, extended forward to near anterior margin; radial ridges well developed on anteromedian areas of both interiors. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* North America, Europe.——FIG. 570,*1a–e.* **C. maclareni,* Emsian or Eifelian, Ellesmere Island, Arctic Canada; *a,* dorsal interior, ×3; *b,* incomplete dorsal interior, ×3; *c,* ventral interior, ×2; *d,e,* dorsal, ventral views of conjoined pair, ×2 (Johnson & Talent, 1967a).

Cariniferella SCHUCHERT & COOPER, 1931, p. 246 [**Orthis carinata* HALL, 1843b, p. 267; OD]. Transversely semioval, dorsibiconvex, sharply unisulcate valves; ventral and dorsal interareas catacline and orthocline respectively; ventral interior with bilobed muscle scar; dorsal interior with small, trilobed cardinal process; muscle scar petaloid. *Upper Devonian (Frasnian):* cosmopolitan.——FIG. 570,*3a–f.* **C. carinata* (HALL), Frasnian, New York; *a,b,* internal mold, rubber replica of dorsal valve, ×3; *c–f,* anterior, posterior, dorsal, ventral views of conjoined pair, ×1.25 (Johnson & Talent, 1967a).——FIG. 570,*3g,h. C. tioga* (HALL), Frasnian, New York; internal mold, rubber replica of ventral valve, ×1 (Johnson & Talent, 1967a).

Reeftonia ALLAN, 1947, p. 436 [**R. marwicki;* OD]. Transversely semioval, biconvex, unisulcate valves; ventral interior with recessive dental plates and cordate muscle scar; dorsal interior with small myophore and short shaft. *Middle Devonian (Emsian):* Australia, New Zealand.——FIG. 570,*2a–d.* **R. marwicki,* Emsian, New Zealand; *a,b,* internal mold, rubber replica of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×2; *d,* internal mold of ventral valve, ×1.5 (Johnson & Talent, 1967a).

Subfamily ISORTHINAE
Schuchert & Cooper, 1931

[Isorthinae SCHUCHERT & COOPER, 1931, p. 247; *emend.,* WALMSLEY & BOUCOT, 1975, p. 50]

Ventribiconvex, multicostellate dalmanellids with symmetrically branched median ribs; ventral interior having linear or quadrate muscle field bisected by median ridge; dorsal muscle field, usually long and narrow, confined by raised margins and divided by well-developed median ridge; brachiophores moderately divergent. *lower Silurian (Llandovery)–Middle Devonian (Givetian).*

Isorthis KOZŁOWSKI, 1929, p. 29 [**Dalmanella (Isorthis) szajnochai;* OD]. Subcircular, subequally biconvex, rectimarginate to weakly unisulcate valves; ventral interior with dental fossettes; dorsal interior with variably lobate cardinal process and brachiophore plates divergent ventrally. *lower Silurian (Llandovery)–Middle Devonian (Givetian):* cosmopolitan.

I. (**Isorthis**) KOZŁOWSKI, 1929, p. 29 [**Dalmanella (Isorthis) szajnochai;* OD]. Ventribiconvex to near equally biconvex valves; dorsal interior with small, lobate cardinal process; fulcral plates commonly developed. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian):* cosmopolitan. ——FIG. 571,*1a–h.* **I. (I.) szajnochai* (KOZŁOWSKI), Lochkovian, Podolia; *a–e,* ventral, dorsal, lateral, posterior, anterior views of conjoined valves, ×1 (Walmsley & Boucot, 1975); *f,* ventral interior, ×2; *g,h,* normal, posterior views of dorsal interior, ×2 (Nikiforova, Modzalevskaja, & Bassett, 1985).

I. (**Arcualla**) WALMSLEY & BOUCOT, 1975, p. 79 [**Orthis arcuaria* HALL & CLARKE, 1892, p. 224; OD]. Differs from *I. (Isorthis)* in having more elongate and indistinct quadripartite dorsal muscle scar; ventral interior with wide median ridge dividing muscle field. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian):* North America, Sweden, Podolia, central Asia. ——FIG. 571,*2a–h.* **I. (A.) arcuaria* (HALL & CLARKE), Ludlow, Tennessee; *a–e,* ventral, dorsal, posterior, lateral, anterior views of conjoined valves, ×1; *f,* ventral interior, ×3; *g,* dorsal interior, ×1; *h,* anterior detail of dorsal interior, ×5 (Walmsley & Boucot, 1975).

I. (**Ovalella**) WALMSLEY & BOUCOT, 1975, p. 75 [**Platystrophia ovalis* PASKEVICIUS, 1962, p. 33; OD]. Differs from *I. (Isorthis)* in having elongate, suboval, and indistinct quadripartite muscle scar; ventral interior with short, narrow median ridge. *lower Silurian (Llandovery)–upper Silurian (Přídolí):* eastern North America, eastern Baltic, Britain.——FIG. 571,*3a,b. I. (O.) mackenziei* WALMSLEY, Llandovery, Welsh Borderlands; *a,* internal mold of ventral valve, ×3.2; *b,* internal mold of dorsal valve, ×3.2 (Walmsley & Boucot, 1975).——FIG. 571,*3c–g. I. (O.) scuteformis* WALMSLEY, Ludlow, England; ventral, dorsal, lateral, posterior, anterior views of conjoined valves, ×1 (Walmsley & Boucot, 1975).

Costisorthis HAVLÍČEK, 1974, p. 170 [**Orthis occlusa* BARRANDE, 1848, pl. 19, fig. 2; OD]. Similar to *Isorthis* but multiplicate. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Europe.——FIG. 572,*1a–c.* **C. occlusa* (BARRANDE), Pragian, Bohemia; ventral, dorsal, anterior views of conjoined pairs, ×2 (Havlíček, 1977a).

Levenea SCHUCHERT & COOPER, 1931, p. 246 [**Orthis subcarinata* HALL, 1857, p. 43; OD]. Subcircular, ventribiconvex valves; ventral interior with short subpentagonal muscle field bisected by wide median ridge; dorsal interior with swollen, lobate myophore lacking well-developed shaft and brachiophores expanded medianly; deep sockets excavated into valve floor; fulcral plates rare. *lower Silurian (Llandovery)–Middle Devonian (Eifelian):* cosmopolitan.——FIG. 571,*4a–c.* **L. subcarinata* (HALL), Lochkovian, Tennessee; *a,* ventral interior, ×1.5; *b,* dorsal interior, ×1.5; *c,* enlargement of posterior region, ×3.5 (Schuchert & Cooper, 1932).——FIG. 571,*4d–f. L.* sp. cf. *L. subcarinata,* Lochkovian, Tennessee; ventral, dorsal, posterior views of conjoined valves, ×1.5 (Schuchert & Cooper, 1932).

Peleicostella HAVLÍČEK, 1971b, p. 230 [**Spirifer peleus* BARRANDE, 1879, pl. 74, case IV, fig. 1–3]. Subcircular, fascicostellate, multiplicate valves with capillae; ventral interior with divergent dental plates. *Lower Devonian (Pragian)–Middle Devonian (Emsian):* Bohemia.——FIG. 572,*2a–d.* **P. peleus* (BARRANDE), Pragian, Bohemia; *a,b,* ventral, dorsal views of conjoined pair, ×2.7; *c,* dorsal exterior, ×2.1; *d,* dorsal interior, ×4.4 (Havlíček, 1977a).

Protocortezorthis JOHNSON & TALENT, 1967a, p. 154 [**Orthis fornicatimcurvata* FUCHS, 1919, p. 58; OD]. Subcircular, ventribiconvex valves; ventral interior with linear muscle scar, bisected by median ridge, and recessive dental plates. Dorsal muscle scar petaloid; fulcral plates variably developed. *middle Silurian (Wenlock)–Lower Devonian (Pragian):*

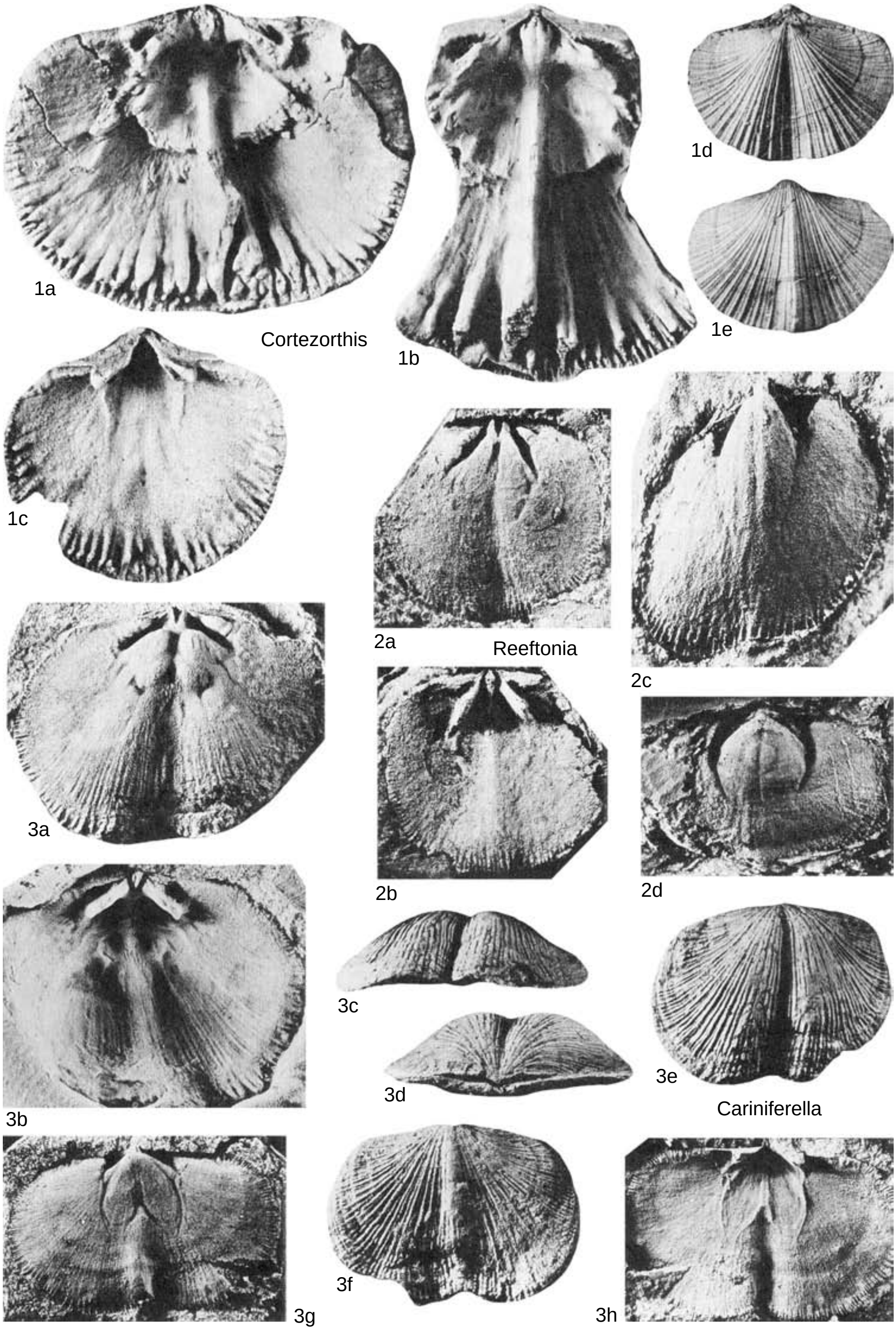

FIG. 570. Dalmanellidae (p. 788–789).

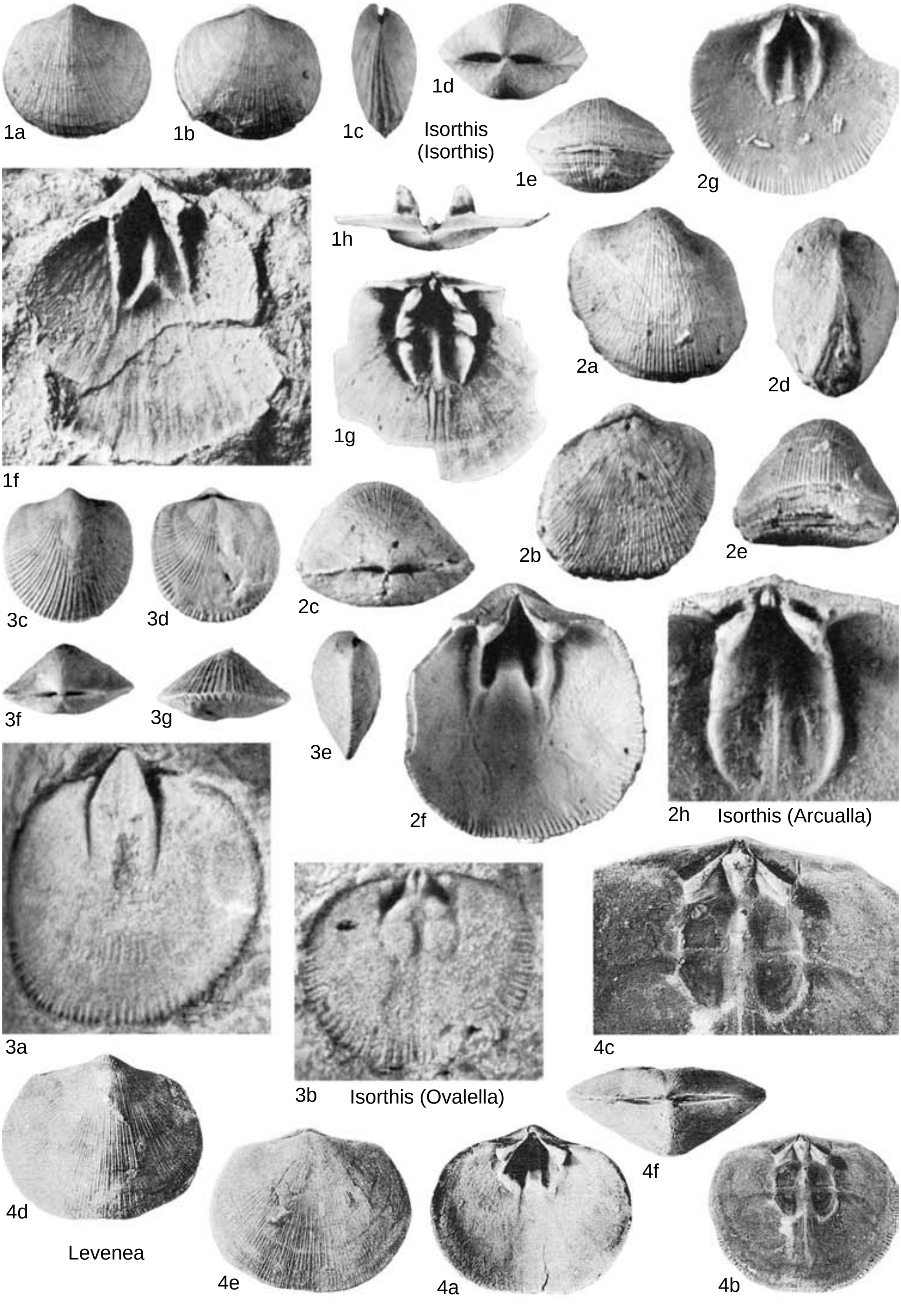

FIG. 571. Dalmanellidae (p. 789).

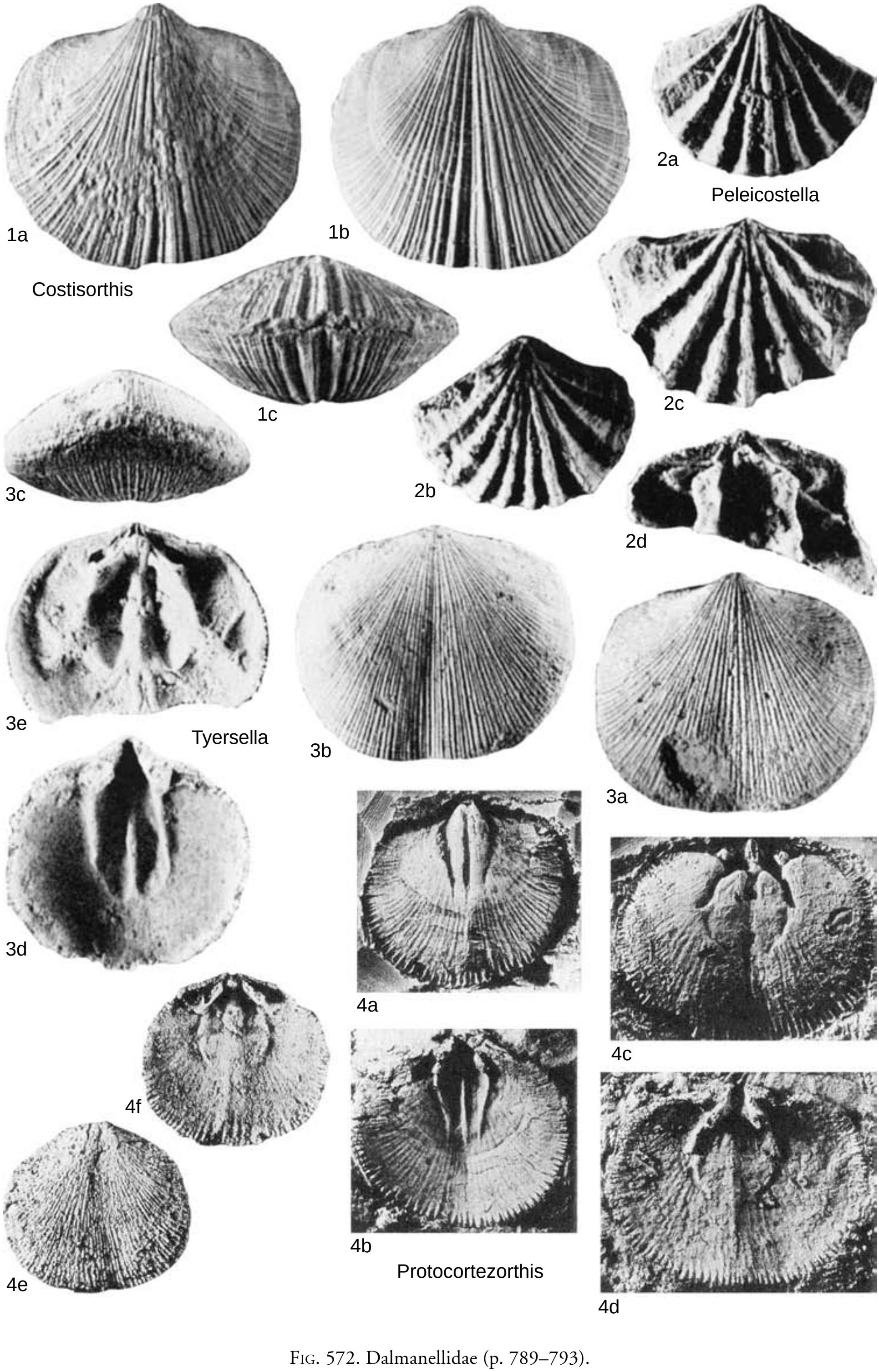

FIG. 572. Dalmanellidae (p. 789–793).

cosmopolitan.——FIG. 572,*4a–d.* **P. fornicatimcurvata* (FUCHS), Lochkovian, Germany; *a,b,* internal mold, rubber replica of ventral valve, ×2; *c,d,* internal mold, rubber replica of dorsal valve, ×2 (Johnson & Talent, 1967a).——FIG. 572,*4e,f. P. windmillensis* JOHNSON & TALENT, Pragian, central Nevada; exterior, interior of dorsal valve, ×1.5 (Johnson & Talent, 1967a).

Tyersella PHILIP, 1962, p. 197 [**T. typica;* OD]. Subcircular, ventribiconvex valves; ventral interior with divergent dental plates and median ridge; dorsal interior with petaloid muscle scar having elevated margins; deep sockets excavated into valve floor; fulcral plates absent. *middle Silurian (Wenlock)–Middle Devonian (Givetian):* cosmopolitan.——FIG. 572,*3a–e. T. snajdri* (HAVLÍČEK), Emsian, Bohemia; *a,* ventral view of conjoined valves, ×2.1; *b,* dorsal view of conjoined valves, ×1.8; *c,* anterior view of conjoined valves, ×2.1; *d,* ventral interior, ×2; *e,* dorsal interior, ×2.2 (Havlíček, 1977a).

Subfamily PROKOPIINAE Wright, 1965

[Prokopiinae WRIGHT, 1965a, p. 338; *emend.,* HARPER, herein]

Subcircular, normally small dalmanellids with long ventral interarea, delthyrium open or variably covered; dorsal interior with bilobed cardinal process and shaft, suberect brachiophore plates and dorsal median partition; fulcral plates variably developed. *Lower Devonian (Pragian)–Middle Devonian (Givetian).*

Prokopia HAVLÍČEK, 1953, p. 6 [**P. bouskai;* OD]. Subcircular valves with delthyrium containing flat apical plate; ventral interarea long, straight; ventral interior with recessive dental plates; dorsal interior lacking fulcral plates. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Bohemia, Germany, Morocco, USA (Nevada).——FIG. 573,*2a–h.* **P. bouskai,* Pragian, Bohemia; *a–d,* ventral, dorsal, anterior, lateral views of conjoined valves, ×10.6; *e–g,* normal, posterior, oblique views of dorsal interior, ×11.2; *h,* ventral interior, ×11.1 (Havlíček, 1977a).

Eosophragmophora WANG in WANG, YU, & WU, 1974, p. 36 [**E. sinensis;* OD]. Subcircular, medium-sized valves with open delthyrium; dorsal interior lacking fulcral plates. *Lower Devonian (Emsian):* southern China, Australia (New South Wales).——FIG. 573,*1a–f.* **E. sinensis,* Emsian, southern China; *a–c,* ventral, dorsal, posterior views of conjoined valves, ×2.5; *d,* ventral interior, ×3; *e,f,* normal, tilted views of dorsal interior, ×3 (Wang & Rong, 1986).

Miniprokopia HAVLÍČEK, 1971b, p. 229 [**M. miniconcha;* OD]. Subcircular, coarsely paucicostellate valves with long, curved ventral interarea; ventral interior with rudimentary dental plates and muscle field on well-developed callus; dorsal interior with subperipheral rim. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Bohemia.——FIG. 573,*3a–f.* **M. miniconcha,* Pragian, Bohemia; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×12.4; *d,e,* normal, oblique views of dorsal interior, ×9.5; *f,* ventral interior, ×13.5 (Havlíček, 1977a).

Phragmophora COOPER, 1955, p. 50 [**P. schnuri;* OD]. Subquadrate, medium-sized, unisulcate to rectimarginate valves with long, straight ventral interarea; delthyrium covered by variably developed notodeltidium with minute apical foramen; cardinal process bilobed, expanded, and medially cleft; fulcral plates developed in adult shells. *Middle Devonian (Eifelian–Givetian):* Europe.——FIG. 574,*1a–i.* **P. schnuri; a–d,* ventral, dorsal, anterior, lateral views of conjoined valves, Eifelian, Germany, ×1; *e,* internal mold of ventral valve, Eifelian, Germany, ×2; *f,g,* normal, tilted views of dorsal interior, ×2 (Cooper, 1955); *h,* ventral interior, Givetian, Poland, ×5; *i,* dorsal interior, Givetian, Poland, ×5 (Biernat, 1959).

Protophragmapora ALEKSEEVA, 1967, p. 7 [**P. chotchalensis;* OD]. Similar to *Phragmophora* but with open delthyrium and simple cardinal process. *Lower Devonian:* northeastern Russia, Australia.——FIG. 574,*2a–e.* **P. chotchalensis,* Lower Devonian, northeastern Russia; *a–c,* ventral, dorsal, posterior views of conjoined valves, ×1; *d,* internal mold of ventral valve, ×2; *e,* internal mold of dorsal valve, ×1.5 (Alekseeva, 1967)

Subfamily RESSERELLINAE Walmsley & Boucot, 1971

[Resserellinae WALMSLEY & BOUCOT, 1971, p. 488]

Planoconvex to ventribiconvex, transversely semioval or shield-shaped, multicostellate dalmanellids with asymmetrically branched median ribs and prominent ventral umbo; ventral interior having compact suboval, subtriangular or cordate muscle field; dorsal muscle field confined by variably developed ridges and divided by median ridge; brachiophores and plates widely divergent, cardinal process bilobed; fulcral plates commonly developed. *lower Silurian (Llandovery)–Middle Devonian (Eifelian).*

Resserella BANCROFT, 1928a, p. 54 [**Orthis canalis* J. DE C. SOWERBY, 1839, p. 630, pl. 13, fig. 12a; OD] [=*Parmorthis* SCHUCHERT & COOPER, 1931, p. 246 (type, *Orthis elegantula* DALMAN, 1828, p. 117)]. Subcircular valves with recessive dental plates and suboval ventral muscle scar. *lower Silurian (Llandovery)–Lower Devonian (Emsian):* cosmopolitan. ——FIG. 575,*1a–g.* **R. canalis* (J. DE C. SOWERBY), Wenlock–Ludlow, Gotland, Sweden; *a,* ventral interior, ×3; *b,* dorsal interior, ×3; *c–g,* anterior, posterior, lateral, dorsal, ventral views of conjoined pair, ×3 (Walmsley & Boucot, 1971).

Dedzetina HAVLÍČEK, 1950, p. 33 [**Parmorthis (Dedzetina) macrostomoides;* OD]. Subcircular,

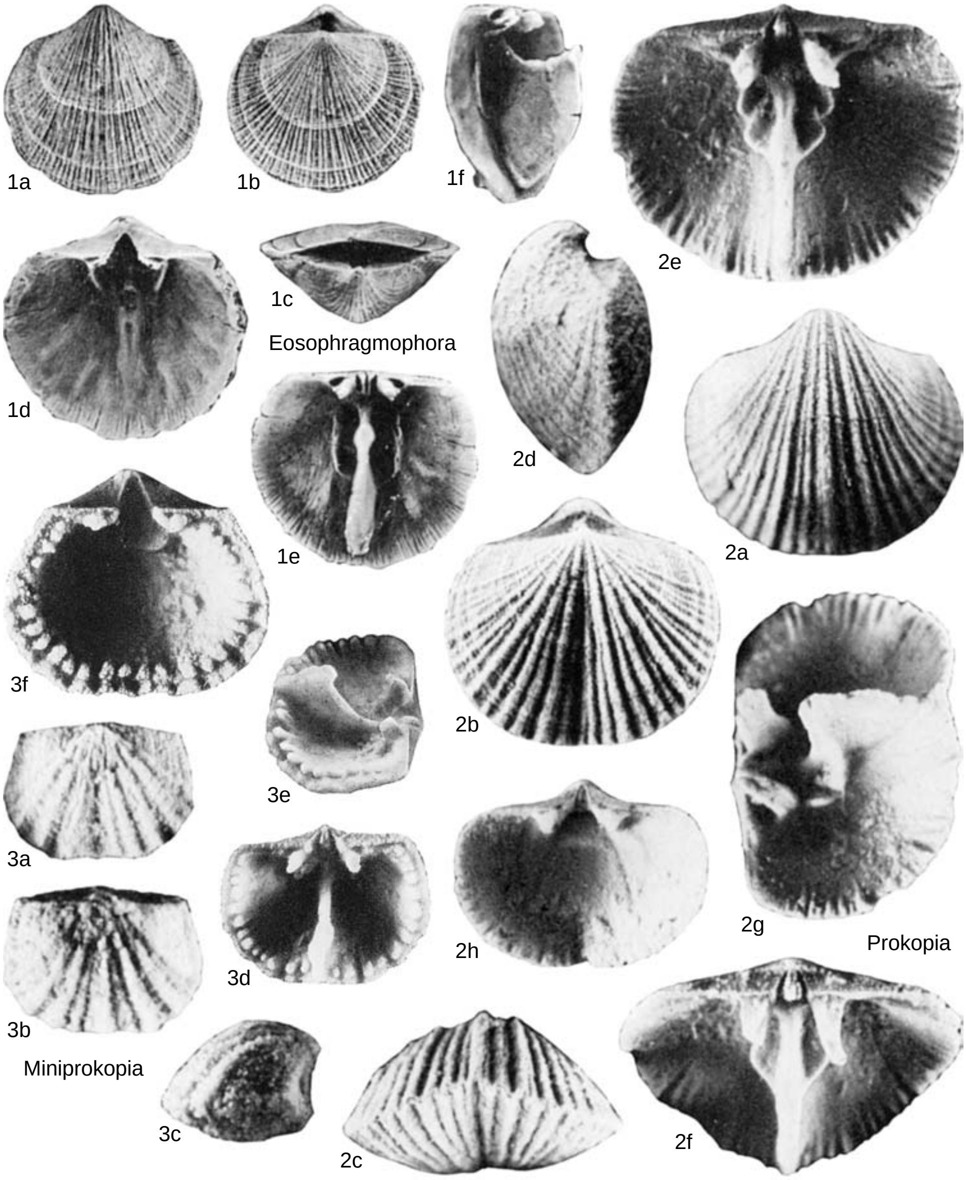

Fig. 573. Dalmanellidae (p. 793).

ventribiconvex, coarsely costellate valves with apical deltidium and hypercline dorsal interarea; ventral interior with recessive dental plates, cordate muscle scar, and well-developed pedicle callist. *Upper Ordovician (Caradoc–Ashgill):* cosmopolitan.——Fig. 576,*1a–c*. **D. macrostomoides* (Havlíček), Ashgill, Bohemia; *a,* internal mold of ventral valve, ×3.2; *b,* internal mold of dorsal valve, ×3.4; *c,* external mold of dorsal valve, ×3.8 (Havlíček, 1977a).

Fascicostella Schuchert & Cooper, 1931, p. 246 [**Strophomenes gervilii* Defrance, 1828, p. 152; OD]. Subcircular, coarsely fascicostellate valves; ventral interior with recessive dental plates and suboval muscle scar. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Europe, Algeria.——Fig. 576,*3a,b*. **F. gervilii* (Defrance), Pragian, Bohemia; ventral, dorsal exteriors of conjoined pair, ×1.5 (Schuchert & Cooper, 1932).——Fig. 576,*3c–f*. *F. undulata* Walmsley & Boucot, Lower

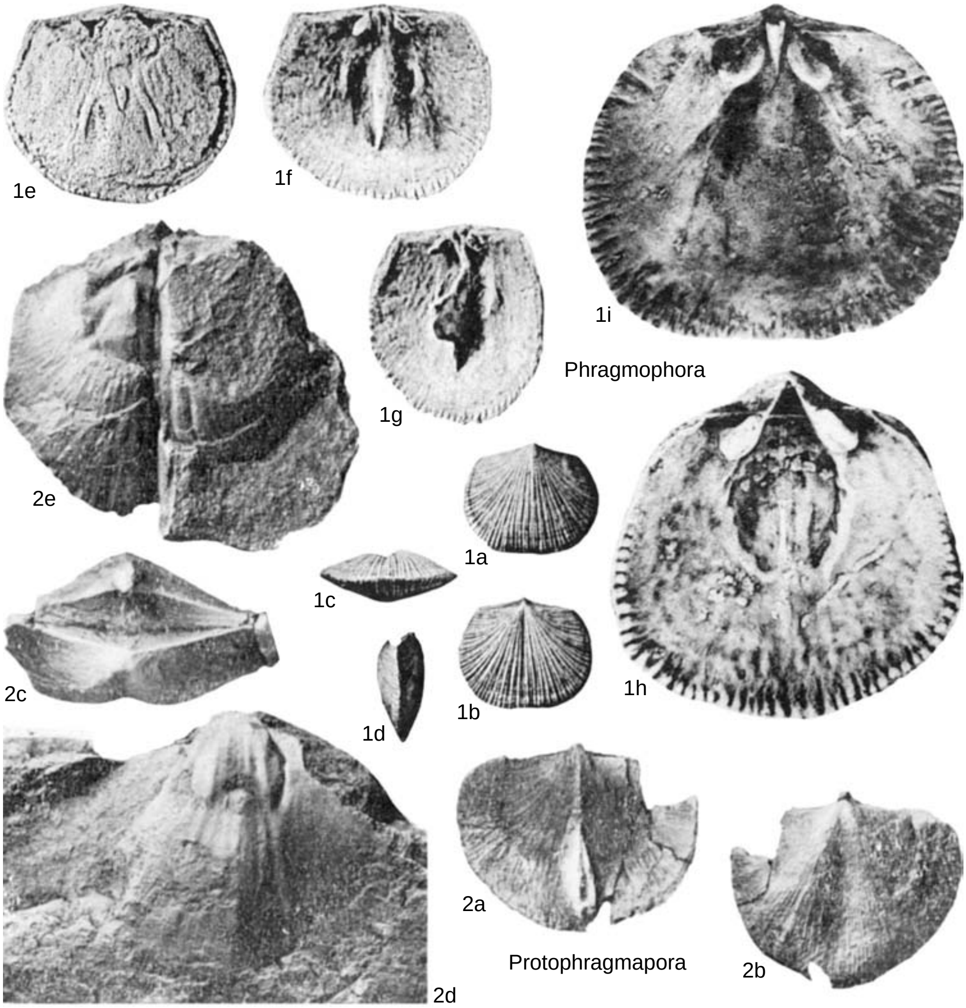

Fig. 574. Dalmanellidae (p. 793).

Devonian, France; *c,d,* internal, external views of dorsal valve, ×3; *e,f,* internal molds of dorsal, ventral valves of conjoined pair, ×2 (Walmsley & Boucot, 1971).

Fascizetina Havlíček, 1975, p. 232 [**Orthis gervilli konieprusensis* Oehlert, 1886, p. 46; OD]. Transversely semioval, fascicostellate, multiplicate valves; ventral interior with divergent dental plates. *Lower Devonian (Lochkovian–Emsian):* Europe, northern Africa.——Fig. 576,*2a–d.* **F. konieprusensis* (Oehlert), Pragian, Bohemia; dorsal, ventral, anterior, posterior views of conjoined pair, ×2.1 (Havlíček, 1977a).

Karlicium Havlíček, 1974, p. 169 [**K. karlicum;* OD]. Subquadrate, small, coarsely costellate valves; dorsal interarea catacline; ventral interior with recessive dental plates and cordate muscle scar; cardinalia lacking fulcral plates. *Upper Ordovician (Caradoc–Ashgill):* Bohemia.——Fig. 576,*4a–c.* **K. karlicum,* Ashgill, Bohemia; *a,* internal mold of ventral valve, ×7.8; *b,* internal mold of dorsal valve, ×9.2; *c,* external mold of dorsal valve, ×10.5 (Havlíček, 1977a).

Molongella Savage, 1974, p. 13 [**M. talenti;* OD] [=*Bouskia* Havlíček, 1975, p. 233]. Transversely semioval, small, ventribiconvex, sharply unisulcate, coarsely costellate valves; ventral interior with divergent dental plates and bilobed muscle scar on callus. *upper Silurian (Přídolí)–Lower Devonian (Pragian):* Bohemia, Australia.——Fig. 577,*1a–c.* **M. talenti,* Pragian, Australia; *a,* internal mold of dorsal valve, ×5; *b,* internal mold of ventral valve, ×5; *c,* rubber replica of ventral exterior, ×5 (Savage, 1974).——Fig. 577,*1d–g. M. lineata* (Havlíček), Lochkovian,

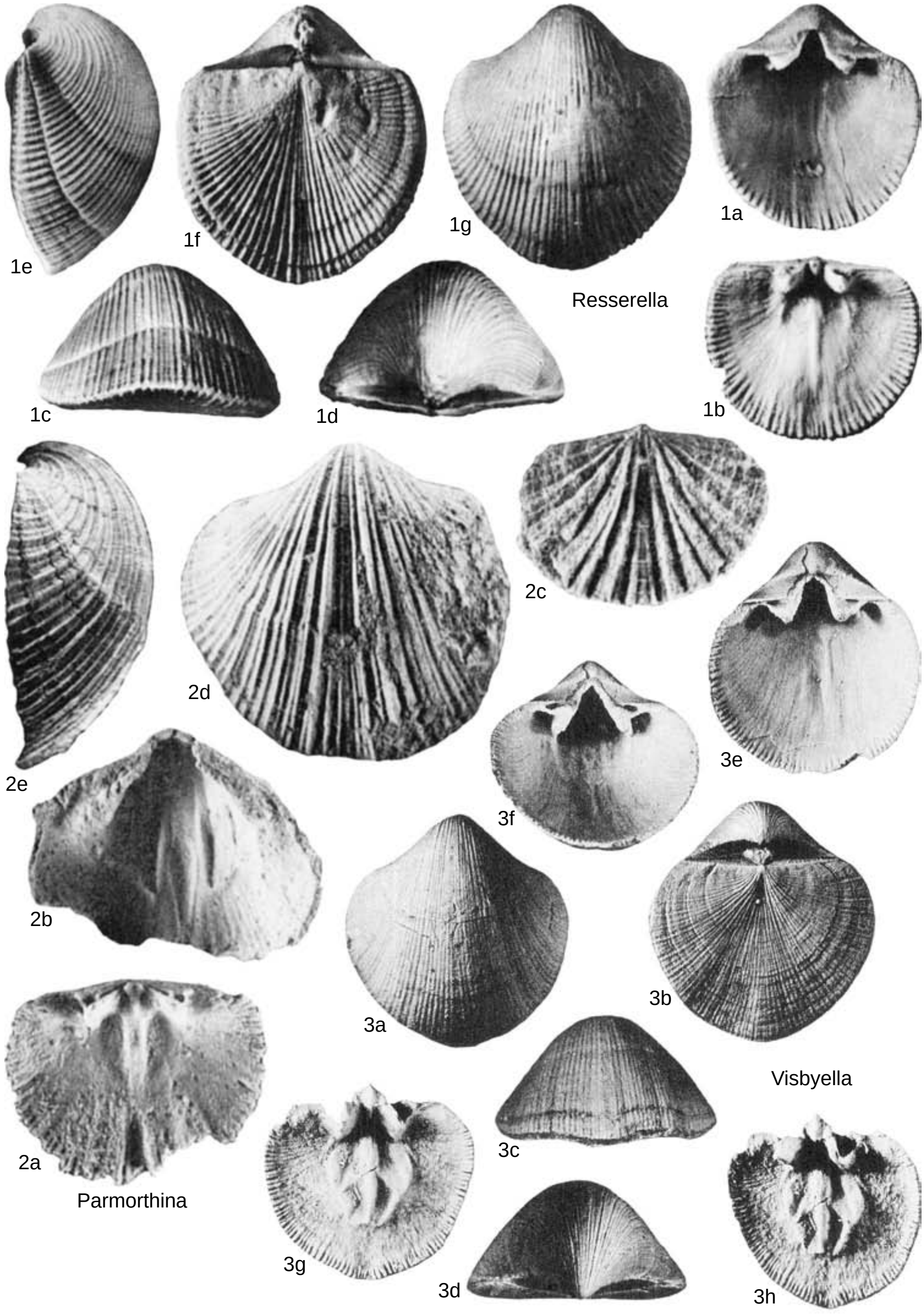

FIG. 575. Dalmanellidae (p. 793–798).

Bohemia; *d,* ventral exterior, ×7.1; *e,* dorsal exterior, ×6.8; *f,* ventral interior, ×6; *g,* dorsal interior, ×7.6 (Havlíček, 1977a).

Parmorthina HAVLÍČEK, 1975, p. 232 [**Parmorthis pragensis* HAVLÍČEK, 1956, p. 539; OD]. Subcircular, fascicostellate, unisulcate to weakly strangulate

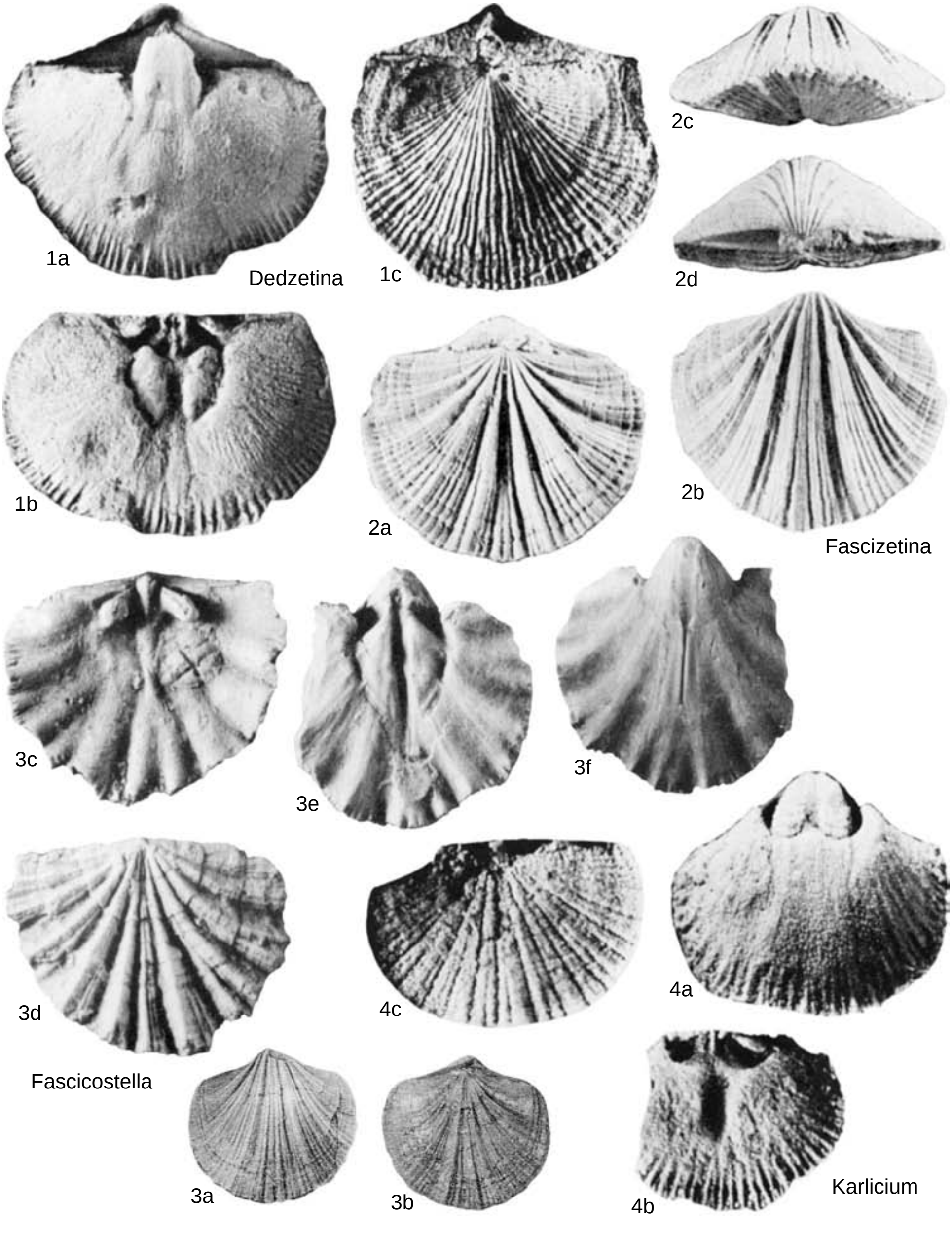

FIG. 576. Dalmanellidae (p. 793–795).

valves; ventral interior with recessive dental plates and cordate muscle scar; cardinalia lacking fulcral plates. *middle Silurian (Wenlock)–Lower Devonian (Emsian):* Europe, North America.——FIG. 575, *2a–e.* **P. pragenesis* (HAVLÍČEK), Emsian, Bohemia; *a,* dorsal interior, ×2; *b,* ventral interior, ×2; *c,* dorsal exterior, ×4.6; *d,e,* ventral, lateral views of ventral exterior, ×1.8 (Havlíček, 1977a).

Visbyella WALMSLEY & others, 1968, p. 306 [**Orthis visbyensis* LINDSTRÖM, 1861, p. 366; OD]. Subcircular, small valves with apical deltidium and hypercline dorsal interarea; ventral interior with recessive dental plates and cordate muscle scar; dorsal interior with trilobed, dorsally facing cardinal process and median septum. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* widespread.——

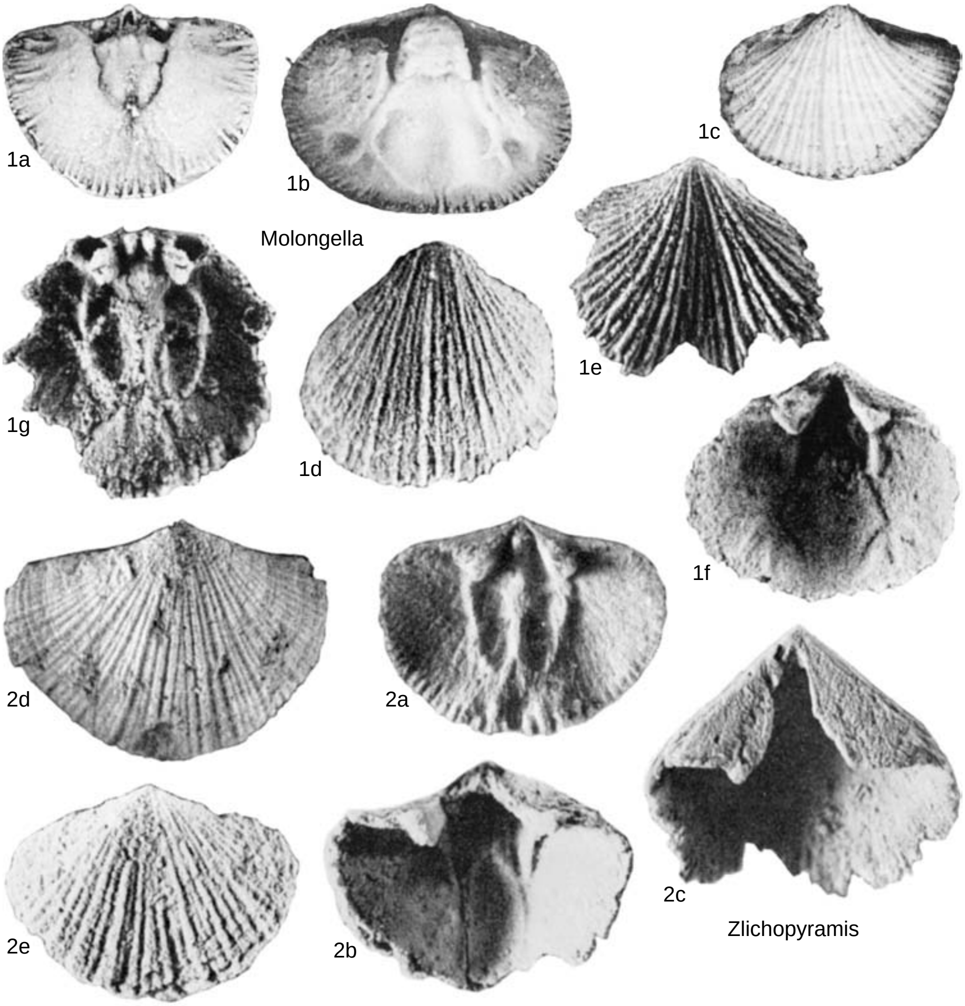

FIG. 577. Dalmanellidae (p. 795–798).

FIG. 575,*3a–h.* **V. visbyensis* (LINDSTRÖM), Llandovery, Gotland; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves, ×3; *e,f,* normal, tilted views of ventral interior, ×3; *g,h,* normal, tilted views of dorsal interior, ×3 (Walmsley & others, 1968).

Zlichopyramis HAVLÍČEK, 1975, p. 233 [**Z. tibicen;* OD]. Transversely semioval, ventribiconvex valves, unisulcate and imbricate; ventral interarea subpyramidal with apical deltidium; ventral interior with recessive dental plates and cordate muscle scar; dorsal interior with anterior adductor scars larger than posterior pair. *Lower Devonian (Emsian):* Bohemia.——FIG. 577,*2a–e.* **Z. tibicen,* Emsian, Bohemia; *a,* dorsal interior, ×4.1; *b,* ventral interior, ×5.7; *c,* posterior view of ventral valve showing interarea, ×4.2; *d,* ventral exterior, ×4; *e,* dorsal exterior, ×4.1 (Havlíček, 1977a).

Subfamily TEMPLEELLINAE new subfamily

[Templeellinae HARPER, herein]

Subcircular dalmanellids with long ventral interarea; ventral muscle field cordate; dorsal interior with short, anteriorly vaulted cruralium; strong median septum bisects and extends forward from cruralium; cardinal process bilobed or trilobed. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery).*

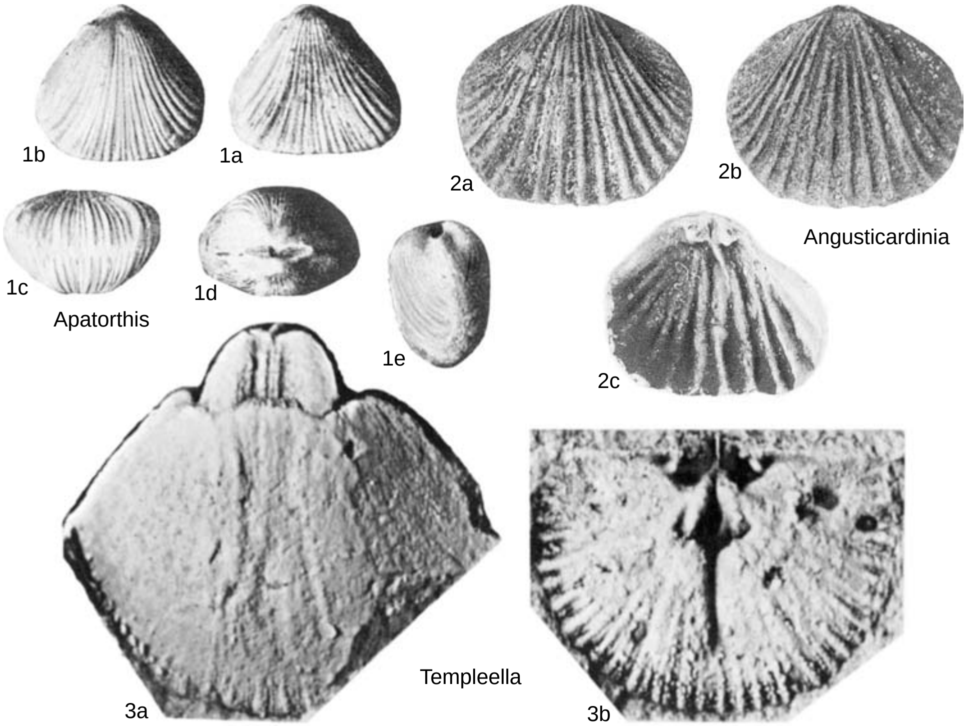

FIG. 578. Dalmanellidae and Angusticardiniidae (p. 799).

Templeella ROZMAN & RONG, 1993, p. 36 [**T. gobiensis;* OD]. Subcircular, concavoconvex valves with hypercline dorsal interarea; dorsal interior with strongly divergent brachiophores. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* Britain, Mongolia.——FIG. 578,*3a,b. *T. gobiensis,* Llandovery, southwestern Mongolia; *a,* internal mold of ventral valve, ×10; *b,* internal mold of dorsal valve, ×12 (Rozman & Rong, 1993).

Family ANGUSTICARDINIIDAE Schuchert & Cooper, 1931

[*nom. transl.* WRIGHT, 1965a, p. 343, *ex* Angusticardiniinae SCHUCHERT & COOPER, 1931, p. 243] [=Apatorthidae ÖPIK, 1933b, p. 5]

Normally biconvex, uniplicate, coarsely costellate dalmanelloids with short hinge lines; both interareas short and curved, ventral apsacline, dorsal anacline; delthyrium and notothyrium open; ventral interior with small teeth and strong dental plates; dorsal interior with brachiophore plates convergent onto median septum; cardinal process ridgelike or absent. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Angusticardinia SCHUCHERT & COOPER, 1931, p. 244 [**Porambonites recta* PANDER, 1830, p. 97; OD]. Subcircular, weakly uniplicate valves occasionally with small alae; dorsal interior with simple, ridgelike cardinal process, short brachiophores, and well-developed median septum bisecting small, quadripartite adductor scar. *Lower Ordovician (Arenig):* Russia.——FIG. 578,*2a–c. *A. recta* (PANDER), Arenig, Russia; *a,b,* ventral, dorsal views of conjoined pair, ×3; *c,* dorsal interior, ×3 (Schuchert & Cooper, 1932).

Apatorthis ÖPIK, 1933b, p. 5 [**A. punctata;* OD]. Subtriangular to rostrate, uniplicate valves with small, well-developed alae; shell surface granular; dorsal interior lacking cardinal process. *Ordovician (Llanvirn–Ashgill):* eastern Baltic.——FIG. 578,*1a–e. *A. punctata,* Caradoc, eastern Baltic; ventral, dorsal, anterior, posterior, lateral views of conjoined pair, ×1.3 (Öpik, 1933b).

Family DICOELOSIIDAE Cloud, 1948

[*nom. correct.* ROGER, 1952, p. 82, *pro* Dicaelosiidae CLOUD, 1948a, p. 374] [=Bilobitidae SCHUCHERT & COOPER, 1931, p. 246]

Small strangulate valves with variably ventribiconvex to concavoconvex longitudinal profiles and costellate radial ornament;

brachiophores long, bladelike, often hooked proximally. *Upper Ordovician (Caradoc)–Upper Devonian (Frasnian).*

Dicoelosia King, 1850, p. 106 [**Anomia biloba* Linné, 1767, p. 1154; OD] [=*Dicaelosia* King, 1850, p. 106; =*Bilobites* Quenstedt, 1869, p. 550, obj., *non* Rafinesque, 1831, *nec* d'Orbigny, 1839, *nec* Bronn, 1848]. Bilobed, multicostellate valves with long, curved ventral interarea; ventral muscle scar cordate; cardinalia with lobate process and shaft; fulcral plates absent. *Upper Ordovician (Caradoc)–Lower Devonian (Emsian):* cosmopolitan.——Fig. 579,*1a–h.* **D. biloba* (Linné), Wenlock, Gotland, Sweden; *a–e,* ventral, dorsal, posterior, anterior, lateral views of conjoined valves, ×5; *f,g,* interior, exterior of ventral valve, ×7.5; *h,* dorsal interior, ×6 (Wright, 1968a).

Epitomyonia Wright, 1968b, p. 128 [**E. glypha;* OD]. Bilobed, multicostellate valves with long, curved ventral interarea; ventral muscle scar cordate; cardinalia with lobate myophore and shaft continuous with high dorsal median septum extending almost to anterior margin, bisecting dorsal platform; fulcral plates absent. *Upper Ordovician (Ashgill)–upper Silurian (Ludlow):* Baltic, Bohemia, Britain, Italy, North America, Spain, Scandinavia, central Asia.——Fig. 579,*2a–g.* **E. glypha; a–e,* posterior, anterior, dorsal, lateral, ventral views of conjoined pair, ×6; *f,g,* normal, oblique views of dorsal interior, ×6 (Wright, 1968b).

Teichertina Veevers, 1959, p. 37 [**T. fitzroyensis;* OD]. Cordate, fascicostellate, imbricate valves with subpyramidal ventral interarea and narrowly divergent notothyrium; wide hinge line with acute cardinal extremities; ventral muscle scar oval; cardinalia with bilobed cardinal process and shaft continuous with dorsal median ridge; fulcral plates present. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* Bohemia, Moravia, USA (Nevada), Western Australia, China.——Fig. 579,*3a–h.* **T. fitzroyensis,* Frasnian, Fitzroy basin, Western Australia; *a–e,* ventral, dorsal, lateral, anterior, posterior views of conjoined valves, ×5; *f,g,* anterior, posterior views of ventral interior, ×5; *h,* dorsal interior, ×5 (Johnson, 1972).

Family HARKNESSELLIDAE
Bancroft, 1928

[*nom transl.* Alichova, 1960, p. 192, *ex* Harknessellinae Bancroft, 1928b, p. 173; *emend.,* Wright, 1965a, p. 339] [=Wulongellidae Zhu, 1985, p. 36]

Usually subquadrate, biconvex, and unisulcate with mucronate hinge line and angular costellae; ventral interarea apsacline, dorsal interarea anacline to orthocline; ventral interior with suboval to cordate muscle scars; dorsal interior with rudimentary notothyrial platform containing deep diductor pits and lobate myophore and shaft; brachiophores variably disposed, fulcral plates normally present. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery).*

Harknessella Reed, 1917, p. 862 [**Orthis vespertilio* J. de C. Sowerby, 1839, p. 640; OD]. Biconvex, medium-sized, unisulcate valves with acute cardinal extremities and fascicostellate ornament; dorsal interior with parallel to divergent bladelike brachiophores and divergent plates; brachiophore plates variably attached to fulcral plates. *Upper Ordovician (Caradoc):* Europe.——Fig. 580,*1a–e.* **H. vespertilio* (Sowerby), Caradoc, England; *a,* rubber replica of ventral exterior, ×1; *b,c,* internal mold of dorsal valve, rubber replica, ×1 (Wright, 1965a); *d,* internal mold of ventral valve, ×2; *e,* internal mold of dorsal valve, ×2 (Bancroft, 1945).

Horderleyella Bancroft, 1928b, p. 178 [**H. plicata;* OD]. Dorsibiconvex, small, sharply unisulcate valves with obtuse cardinal extremities and coarsely fascicostellate ornament; ventral interior with small suboval to rhomboidal muscle field; dorsal interior with parallel to divergent brachiophore blades; cardinal process small and lobate, crural pits and fulcral plates well developed. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Europe, China, Morocco, Sweden, eastern Baltic.——Fig. 580,*3a–e.* **H. plicata,* Caradoc, England; *a,* rubber replica of ventral exterior, ×1; *b,* rubber replica of dorsal exterior, ×1; *c,* internal mold of ventral interior, ×1; *d,e,* internal mold, rubber replica of dorsal valve, ×1 (Wright, 1965a).

Kampella Baarli, 1988, p. 1116 [**K. guttula;* OD]. Biconvex, small, multicostellate, weakly unisulcate to rectimarginate valves with obtuse cardinal extremities and short hinge line; ventral interior with projecting dental plates and short cordate to bilobed muscle scar; dorsal interior with widely divergent brachiophore blades, swollen semioval cardinal process, and fulcral plates. [Baarli (1988) assigned her new genus to the Heterorthidae but compared it with both *Heterorthina* and *Onniella.* The cardinalia and ventral muscle scars are, however, more typical of the Harknessellidae than those of the heterorthids where it is now provisionally placed.] *lower Silurian (Llandovery):* Norway.——Fig. 581,*1a–d.* **K. guttula,* Llandovery, Oslo Region; *a,* internal mold of ventral valve, ×2.5; *b,c,* internal mold, rubber replica of dorsal valve, ×3; *d,* external mold of ventral valve, ×3 (Baarli, 1988).

Reuschella Bancroft, 1928b, p. 180 [**R. semiglobata;* OD]. Dorsibiconvex, large, sharply unisulcate valves with acute cardinal extremities and coarsely costellate ornament; dorsal interior with widely divergent brachiophore blades. *Upper Ordovician (Caradoc–Ashgill):* Europe, eastern Baltic, Argentina, eastern USA, central Asia.——Fig. 580,*2a–e.* **R. semiglobata,* Caradoc, England; *a,* internal mold of ventral valve, ×1.5 (Cocks, new); *b,c,* internal mold, rubber replica of dorsal valve, ×1; *d,* detail of posterior region of replica of dorsal interior, ×2.5; *e,* rubber replica of dorsal exterior, ×1 (Wright, 1965a).——Fig. 580,*2f. R. horderlyensis* Bancroft,

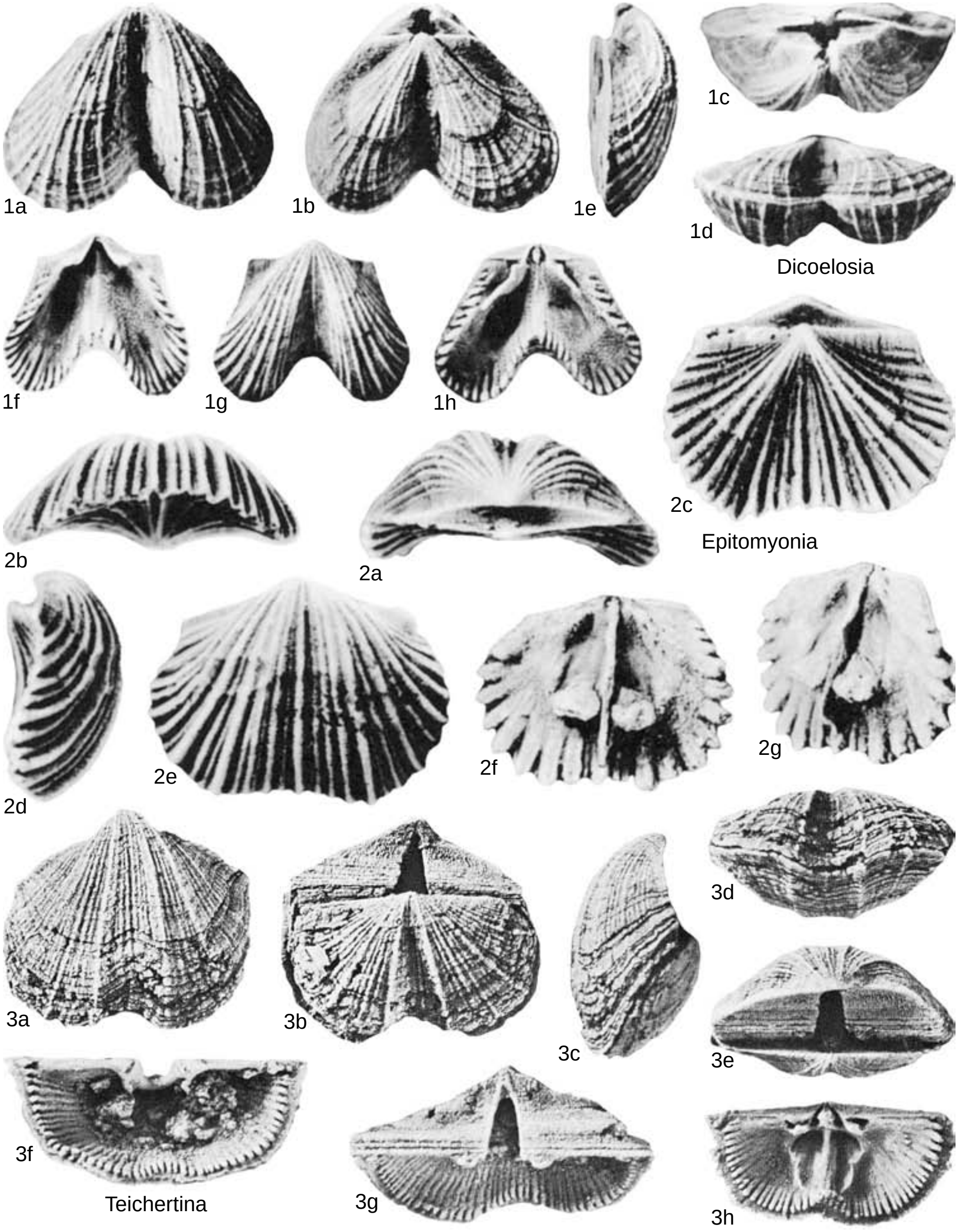

FIG. 579. Dicoelosiidae (p. 800).

Caradoc, England; internal mold of dorsal valve, ×1.5 (Cocks, new).

Smeathenella BANCROFT, 1928b, p. 177 [**S. harnagensis;* OD]. Dorsibiconvex, medium sized, sharply unisulcate valves with flattened profiles and multicostellate ornament; dorsal interior with parallel to divergent brachiophore blades, lacking fulcral plates. *Upper Ordovician (Caradoc):* Welsh Borderlands.——FIG. 581,*2a,b. *S. harnagensis,* Caradoc, England; *a,* internal mold of ventral valve, ×1; *b,* internal mold of dorsal valve, ×1 (Wright, 1965a).——FIG. 581,*2c. S. strophomenoides* BANCROFT, Caradoc, England; rubber replica of ventral exterior, ×2 (Bancroft, 1945).

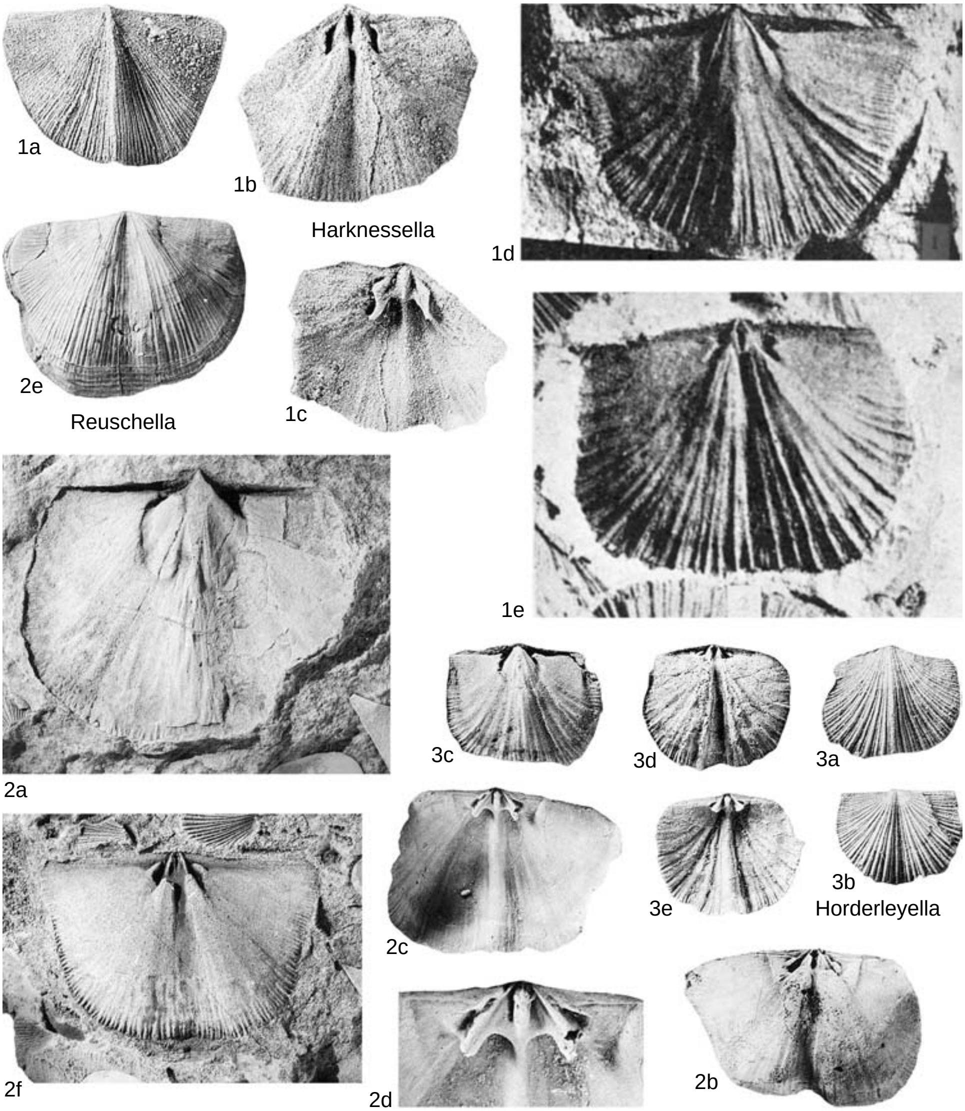

FIG. 580. Harknessellidae (p. 800–801).

Wulongella ZHU, 1985, p. 36 [**W. convexiplanus;* OD]. Convexoconcave, medium sized, rectimarginate valves with obtuse cardinal extremities and parvicostellate ornament; ventral interior with short divergent dental plates and subtriangular muscle field; dorsal interior with widely divergent brachiophores and bases together with cleft cardinal process; muscle field bisected by median ridge; subperipheral rims developed in both ventral and dorsal interiors. [This genus, previously associated with both *Dolerorthis* and *Eostrophomena* (ZHU, 1985), is provisionally included within the Harknessellidae; under this arrangement the Wulongellidae ZHU, 1985 is a junior synonym of the Harknessellidae.] *Upper Ordovician (Caradoc–Ashgill):* northeastern China.——FIG. 581,*3a–d.* **W. convexiplanus,* upper Caradoc–lower Ashgill, Hinggang Ling, northeastern China; *a,c,* ventral and dorsal internal molds together with rubber replicas of *b,d,* dorsal and ventral valves, ×2.5 (Rong, new).

Family HETERORTHIDAE Schuchert & Cooper, 1931

[Heterorthidae SCHUCHERT & COOPER, 1931, p. 246; *emend.,* HARPER, herein]

Normally transversely semioval to subquadrate, large, rectimarginate dalmanel-

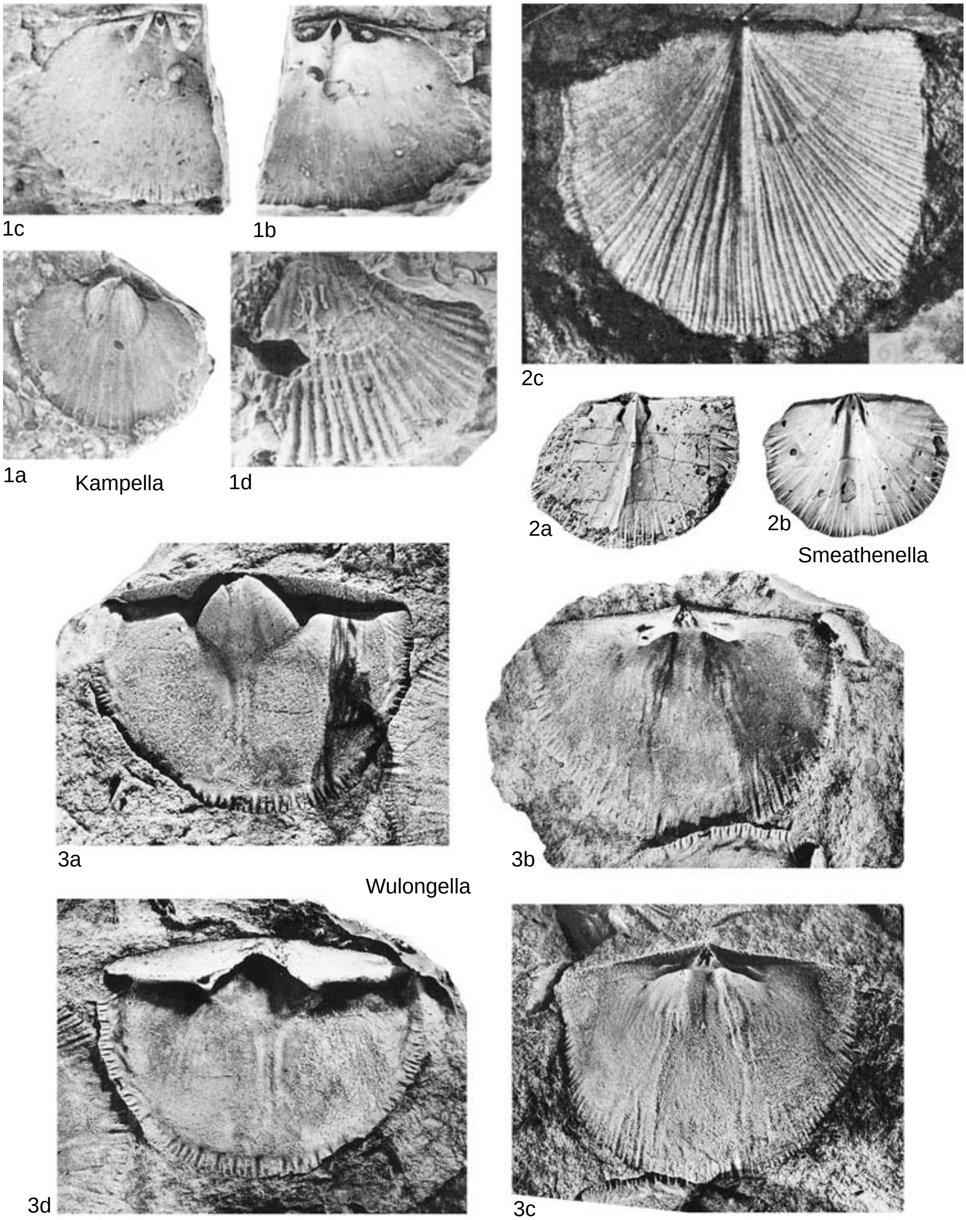

FIG. 581. Harknessellidae (p. 800–802).

loids with aditicules variably developed; ventral interior with extended, flabellate diductor muscle scar, anterior ends commonly widely splayed, not enclosing adductor scar; dorsal interior usually with lobate, commonly modified cardinal process, brachiophores as thickened rods, lacking plates; fulcral plates absent; dorsal mantle canal system normally lemniscate, ventral system probably lemniscate. *Lower Ordovician (Arenig)–middle Silurian (Wenlock).*

Heterorthis HALL & CLARKE, 1892, p. 202 [**Orthis clytie* HALL, 1861b, p. 90; OD]. Subquadrate, large, rectimarginate, concavoconvex to planoconvex, multicostellate valves; notothyrium partly covered by well-developed chilidium; ventral interior with projecting dental plates and extended, flabellate muscle scars; dorsal interior with lobate cardinal process, tripartite on posteroventral surface; subperipheral rim developed in adults. *Upper Ordovician (Caradoc):* Europe, North America.——Fig. 582,*1a–d.* **H. clytie* (Hall), Caradoc, Kentucky; *a,b,* ventral, dorsal views of conjoined valves, ×1.5; *c,* ventral interior, ×1.5; *d,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).——Fig. 582,*1e–g. H. alternata* (J. de C. Sowerby), Caradoc, Shropshire; *e,* internal mold of ventral valve, ×1.5; *f,* internal mold of dorsal valve, ×1.5; *g,* rubber replica of dorsal exterior, ×1.5 (Williams, 1963).

Arenorthis Havlíček, 1970a, p. 29 [**A. arenaria;* OD]. Large, ventribiconvex valves, unisulcate, fascicostellate; ventral interior with projecting dental plates; dorsal interior with lobate cardinal process, posteroventral face tripartite. *Upper Ordovician (Ashgill):* Morocco.——Fig. 582,*2a–d.* **A. arenaria,* Ashgill, Morocco; *a,b,* internal mold, rubber replica of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×1.5; *d,* rubber replicas of ventral and dorsal exteriors, ×1.5 (Havlíček, 1970a).

Cacemia Mitchell, 1974, p. 394 [**Orthis ribeiroi* Sharpe in Ribeiro, 1853, p. 152; OD]. Small, transversely semioval, mucronate valves with acute to extended cardinal extremities; ventral interior with divergent dental plates; dorsal interior with widely divergent brachiophores; lobate cardinal process, medially cleft. *Lower Ordovician (Llanvirn):* Portugal, France.——Fig. 583,*1a–c.* **C. ribeiroi* (Sharpe), Llanvirn, Portugal; internal mold, rubber replica of ventral valve, rubber replica of ventral exterior, ×2 (Mitchell, 1974).——Fig. 583,*1d,e. C.* sp. aff. *C. ribeiroi,* Llanvirn, Portugal; internal mold, rubber replica of dorsal valve, ×4 (Mitchell, 1974).

Cilinella Havlíček, 1970a, p. 16 [**Svobodaina svobodai* Havlíček, 1950, p. 41; OD]. Dorsibiconvex, transversely semioval, rectimarginate, fascicostellate valves; ventral interior with divergent dental plates and bilobed muscle scar, semiflabellate; dorsal interior with high, bladelike brachiophores. *Upper Ordovician (Caradoc):* Bohemia.——Fig. 584,*1a–c.* **C. svobodai* (Havlíček), Caradoc, Bohemia; *a,* internal mold of ventral valve, ×2; *b,c,* internal mold, rubber replica of dorsal valve, ×2 (Havlíček, 1970a).

Heterorthella Harper, Boucot, & Walmsley, 1969, p. 79 [**H. maehli;* OD]. Planoconvex to concavoconvex valves; dorsal interior with high, simple, bladelike cardinal process. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* Canada (Nova Scotia), Bolivia, Brazil.——Fig. 583,*2a–e.* **H. maehli,* Wenlock, Nova Scotia; *a,b,* internal mold, rubber replica of dorsal valve, ×1.5; *c,* internal mold of ventral valve, ×1.5; *d,* rubber replica of ventral interior, ×1.5; *e,* rubber replica of dorsal exterior, ×1.5 (Harper, Boucot, & Walmsley, 1969).

Heterorthina Bancroft, 1928a, p. 59, *nom. nov. pro Bekkerella* Rosenstein, 1943, p. 471, *non* Reed, 1935 (type, *Bekkerella bekkeri* Rosenstein, 1943) [**H. praeculta;* OD]. Transverse, planoconvex, unisulcate, fascicostellate valves; ventral interior with cordate to bilobed muscle scar; dorsal interior with lobate, medially cleft, cardinal process and widely divergent brachiophores. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* Europe.——Fig. 584,*3a,b.* **H. praeculta,* Caradoc, Shropshire; *a,* internal mold of ventral valve, ×1.5; *b,* rubber replica of dorsal interior, ×1.5 (Wright, 1965a).

Incorthis Havlíček & Branisa, 1980, p. 18 [**I. boliviana;* OD]. Subcircular, subequally biconvex, unisulcate valves; ventral interior with subtriangular to bilobed muscle scar; dorsal interior with simple ridgelike cardinal process on low notothyrial platform and divergent bladelike brachiophores; fulcral plates incipient. [Havlíček and Branisa (1980) tentatively assigned *Incorthis* to the Orthidae. Although no details of the shell structure are known, *Incorthis* bears similarities to the early heterorthid *Tissintia* and accordingly is provisionally included within that family.] *Lower Ordovician (Arenig):* Bolivia.——Fig. 583,*3a–d.* **I. boliviana,* Arenig, Bolivia; *a,* internal molds of dorsal (above) and ventral (below) valves, ×2; *b,* rubber replicas of two valve exteriors, ×1.4; *c,* internal mold of dorsal interior, ×3.4; *d,* rubber replicas of dorsal interior (above) and valve exterior (below), ×2.6 (Havlíček & Branisa, 1980).

Marionites Cooper & Muir-Wood, 1951, p. 195, *nom. nov. pro Marionella* Bancroft, 1928b, p. 181, *non* Cobb, 1922 [**Marionella typa* Bancroft, 1928b, p. 181; OD]. Transversely semioval, convexiplane to convexoconcave, resupinate, unisulcate valves; ventral interior with divergent dental plates and quadrate to linear muscle scar; dorsal interior with simple, slightly swollen cardinal process. *Upper Ordovician (Caradoc):* Britain, Bohemia.——Fig. 585,*1a–d.* **M. typa* (Bancroft), Caradoc, Shropshire; *a,* rubber replica of ventral interior, ×1; *b,c,* internal mold, rubber replica of dorsal interior, ×1; *d,* rubber replica of ventral exterior, ×1 (Williams, 1965b).

Svobodaina Havlíček, 1950, p. 38 [**Orthis ellipsoides* Barrande, 1848, p. 204; SD Havlíček, 1977a, p. 122; =*Orthis inclyta* Barrande, 1879, pl. 67, case I] [=*Svobodiana* Alichova, 1960, p. 192; *Planoharknessella* Havlíček, 1950, p. 42 (type, *P. planidorsa*)]. Transversely semioval, large, dorsibiconvex, unisulcate, fascicostellate valves; ventral interior with divergent dental plates; dorsal interior with complex multifid cardinal process in adults. *Upper Ordovician (Caradoc):* Europe.——Fig. 584,*2a–d.* **S. ellipsoides,* Caradoc, Bohemia; *a,* internal mold of ventral valve, ×1.5; *b,c,* internal mold, rubber replica of dorsal valve, ×1.5; *d,* external mold of dorsal valve, ×1.5 (Havlíček, 1977a).

Tafilaltia Havlíček, 1970a, p. 17 [**T. occidentalis;* OD]. Similar to *Heterorthis* but with subcircular, ventribiconvex valves lacking chilidium. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Bohemia, France, Morocco.——Fig. 584,*4a–d.* **T. occidentalis,* Caradoc, Morocco; *a,b,* internal mold, rubber replica of dorsal valve, ×2.3; *c,* external mold of dorsal valve, ×2.4; *d,* internal molds of ventral (upper) and dorsal valve (lower), ×2.4 (Havlíček, 1970a).

Tarfaya Havlíček, 1971a, p. 32 [**T. marocana;* OD]. Subcircular, ventribiconvex valves; ventral interior

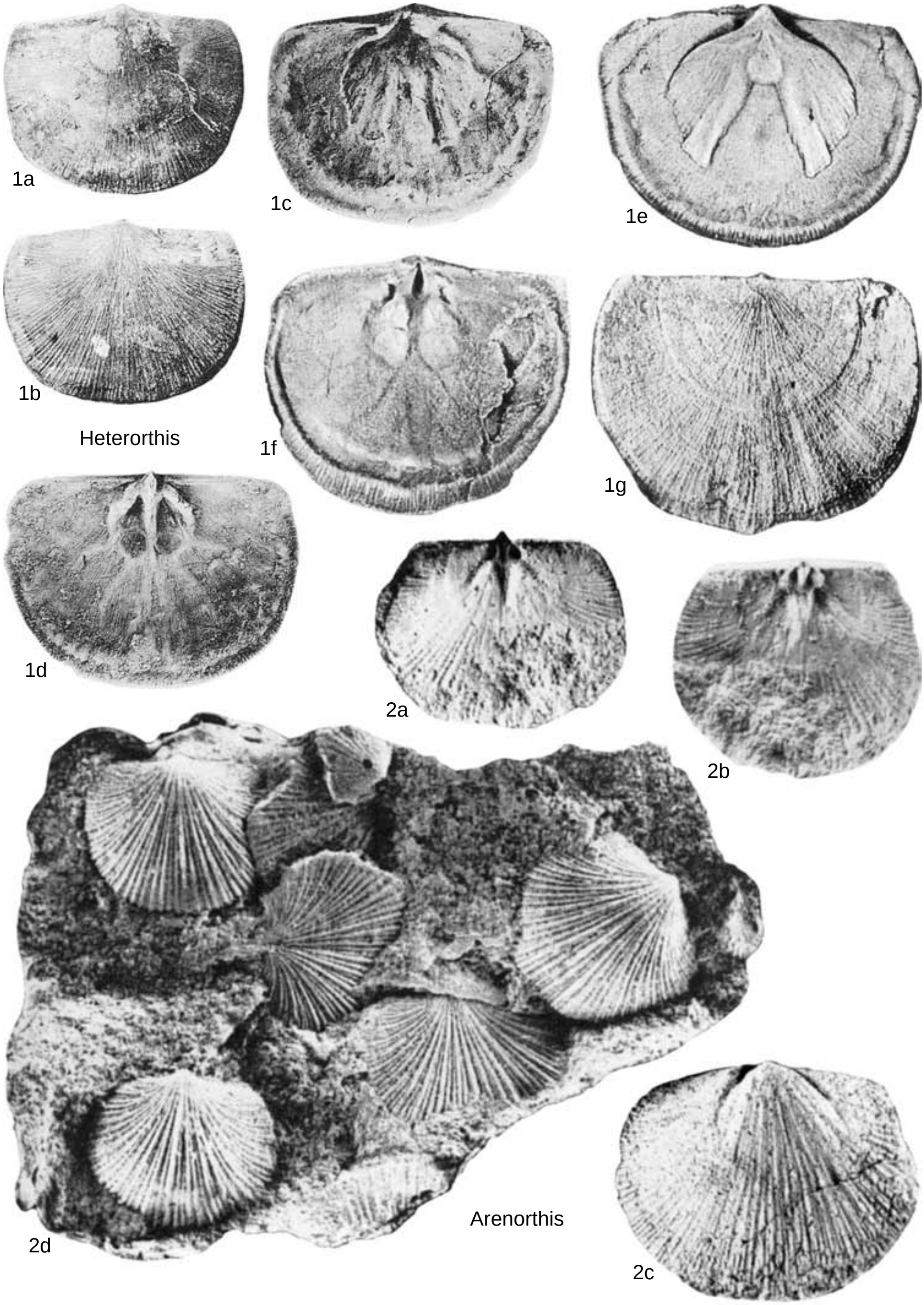

FIG. 582. Heterorthidae (p. 803–804).

with short subtriangular to suboval muscle scar; dorsal interior with simple, ridgelike cardinal process, continuous with short median septum; mantle canal systems saccate. *Lower Ordovician (Arenig):* Morocco.——FIG. 585,*2a–d.* **T. marocana,* Arenig, Morocco; *a,* internal mold of ventral valve, ×2.5; *b,*

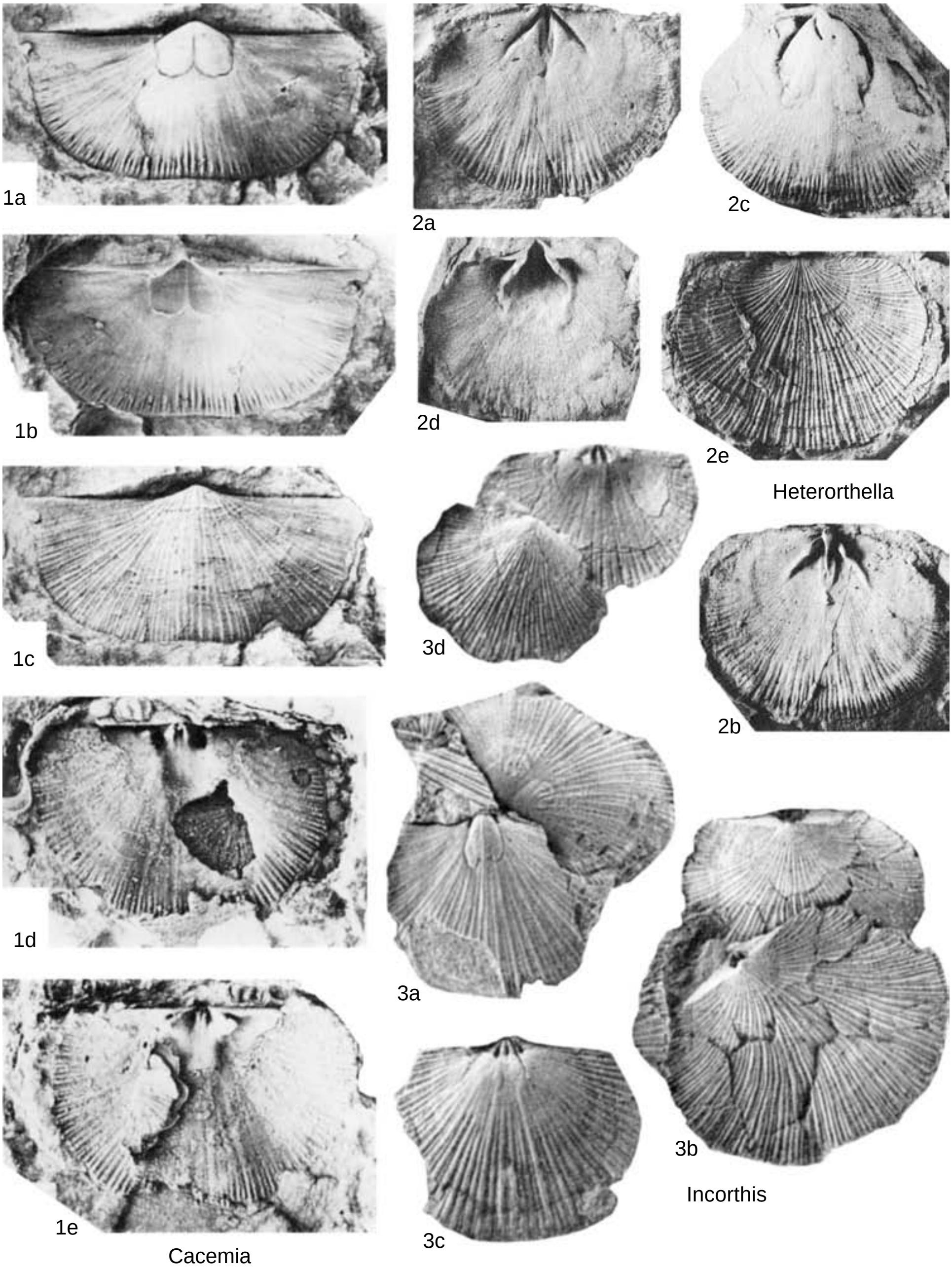

FIG. 583. Heterorthidae (p. 804).

internal mold of dorsal valve, ×1.5; *c,* rubber replica of ventral exterior, ×2; *d,* rubber replica of dorsal exterior, ×1.9 (Havlíček, 1971a).

Tissintia HAVLÍČEK, 1970a, p. 14 [**T. convergens;* OD]. Subcircular, commonly small, ventribiconvex, fascicostellate valves; dorsal interior with bilobed, medially cleft, cardinal process and brachiophores convergent onto valve floor and extended forward as ridges; dorsal muscle scar bisected by median ridge. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Morocco, Bolivia, Wales.——FIG. 584,*5a–c.* **T. convergens,* Llanvirn, Morocco; *a,* in-

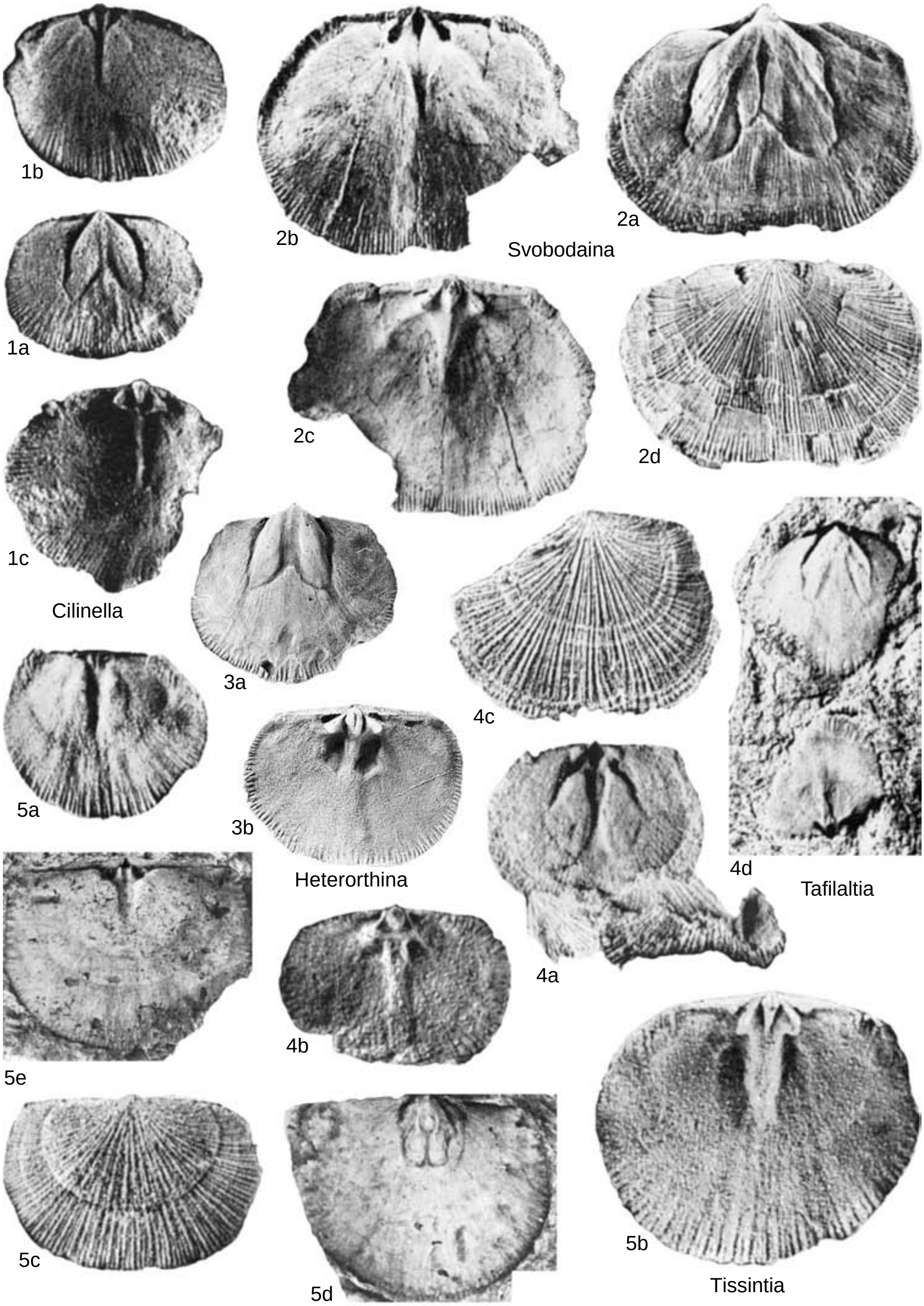

FIG. 584. Heterorthidae (p. 804–807).

ternal mold of dorsal valve, ×2; *b,* rubber replica of dorsal interior, ×3.3; *c,* rubber replica of dorsal exterior, ×4.1 (Havlíček, 1970a).——FIG. 584,*5d,e.* *T. plana* (WILLIAMS), Llanvirn, Wales; *d,* internal mold of ventral valve, ×1.5; *e,* internal mold of dorsal valve, ×1.5 (Lockley & Williams, 1981).

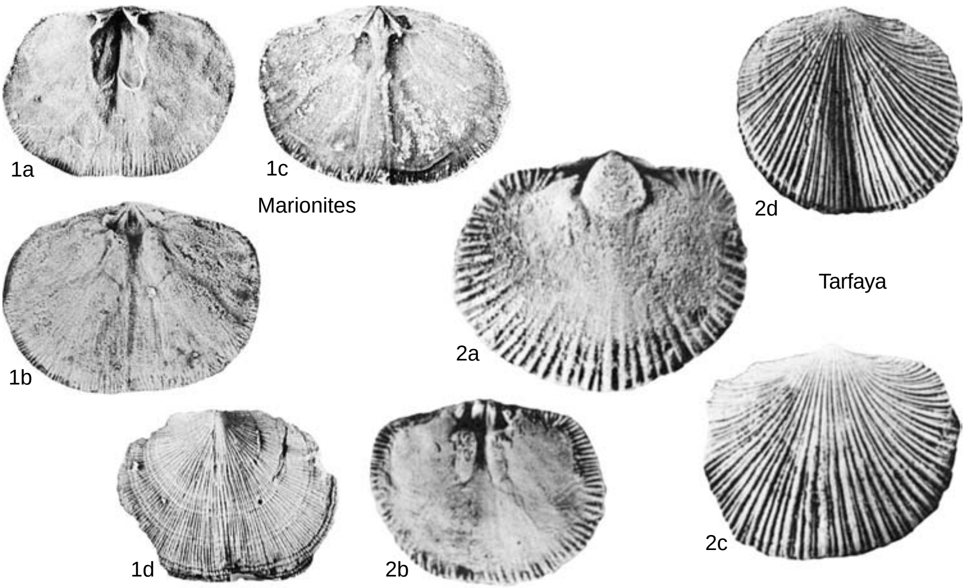

FIG. 585. Heterorthidae (p. 804–806).

Family HYPSOMYONIIDAE Wright, 1965

[Hypsomyoniidae WRIGHT, 1965a, p. 339]

Ventribiconvex dalmanelloids with open delthyrium and notothyrium; ventral interior with receding dental plates; dorsal interior with bilobed cardinal process and shaft, widely divergent rodlike brachiophores with plates subparallel to hinge and lacking fulcral plates; cruralium develops from valve floor, in front of brachiophores, supported on high septum. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian).*

Hypsomyonia COOPER, 1955, p. 52 [**H. stainbrooki;* OD]. Transversely semioval, small, unisulcate valves with long curved ventral interarea. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* North America, Europe, Western Australia.——FIG. 586,*1a–g.* **H. stainbrooki,* Frasnian, Iowa; *a–e,* ventral, dorsal, posterior, anterior, lateral views of conjoined valves, ×5; *f,g,* normal, tilted views of dorsal interior, ×7.5 (Cooper, 1955).

Family KAYSERELLIDAE Wright, 1965

[Kayserellidae WRIGHT, 1965a, p. 336]

Ventribiconvex dalmanelloids with long, curved ventral interarea and open delthyrium; ventral interior with short, widely cordate muscle field; dorsal interior with bilobed cardinal process and long, slender shaft continuous with median septum extending forward to near anterior margin; brachiophore plates convergent onto septum to form short, narrow septalium. *Middle Devonian (Eifelian).*

Kayserella HALL & CLARKE, 1892, p. 259 [**Orthis lepida* SCHNUR, 1854, p. 218; OD]. Subcircular, fascicostellate valves; ventral interior with recessive dental plates and well-developed pedicle callist; dorsal interior with fulcral plates. *Middle Devonian (Eifelian):* Germany, Moravia, USA (New York). ——FIG. 586,*2a–e.* **K. lepida* (SCHNUR), Eifelian, Germany; ventral, dorsal, posterior, anterior, lateral views of conjoined valves, ×2 (Cooper, 1955).——FIG. 586,*2f–i. K. americana* COOPER, Eifelian, New York; *f,* internal mold of ventral valve, ×3; *g,* rubber replica of dorsal exterior, ×3; *h,i,* internal mold, rubber replica of dorsal valve, ×3 (Cooper, 1955).

Family MYSTROPHORIDAE Schuchert & Cooper, 1931

[Mystrophoridae SCHUCHERT & COOPER, 1931, p. 246]

Medium-sized dalmanelloids normally with long, straight apsacline ventral interarea; delthyrium and notothyrium usually open; ventral interior with bilobed ventral muscle scar and well-developed pedicle callist; dorsal interior normally with bilobed

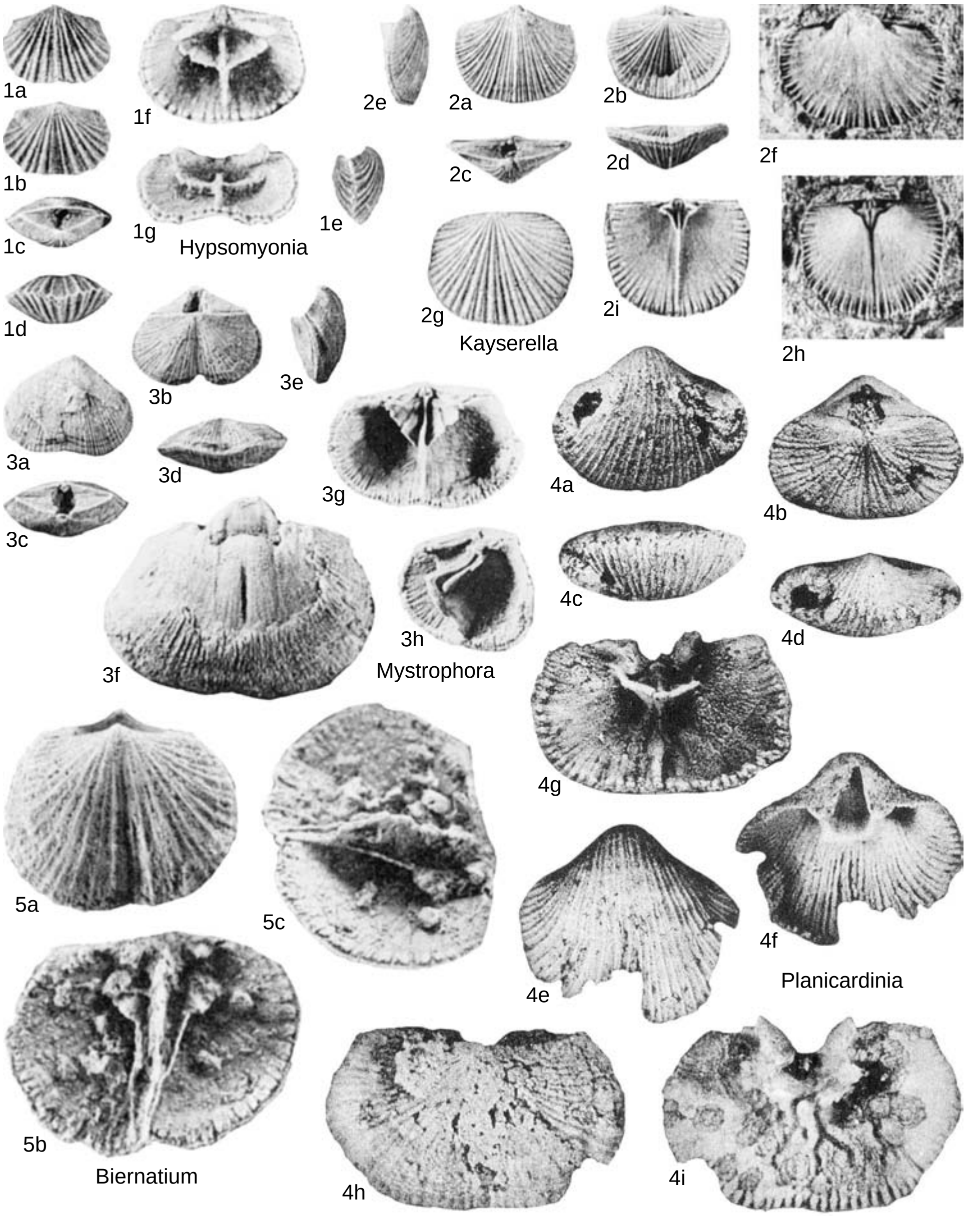

FIG. 586. Hypsomyoniidae, Kayserellidae, and Mystrophoridae (p. 808–810).

cardinal process and shaft continuous with median partition supporting variably inclined cruralium, probably containing quadripartite dorsal muscle scar. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Mystrophora KAYSER, 1871, p. 612 [**Orthis areola* QUENSTEDT, 1871, p. 589; SD WILLIAMS & BREGER, 1916, p. 61]. Transversely semioval, unisulcate valves with ventral median ridge; dorsal interior with complex cruralium comprising 4 fused plates; fulcral plates present. *Middle Devonian (Eifelian):* Germany, Burma.——FIG. 586,*3a–h*. **M. areola*

(QUENSTEDT), Eifelian, Germany; *a–e,* ventral, dorsal, posterior, anterior, lateral views of conjoined valves, ×1; *f,* partly exfoliated internal mold of ventral valve, ×2; *g,h,* normal, tilted views of dorsal interior, ×2 (Cooper, 1955).

Biernatium HAVLÍČEK, 1975, p. 234 [**Skenidium fallax* GÜRICH, 1896, p. 235; OD]. Transversely semioval, coarsely costellate valves with narrowly divergent delthyrium variably open or closed by apical plate; ventral interarea subpyramidal, apsacline to catacline; ventral interior with recessive dental plates; dorsal interior with ridgelike cardinal process and long rodlike brachiophores; cruralium long, narrowing anteriorly; fulcral plates absent. *Lower Devonian (Pragian)–Upper Devonian (Frasnian):* Europe, Burma, Western Australia.——FIG. 586,*5a–c.* **B. fallax* (GÜRICH), Givetian, Moravia; *a,* dorsal view of conjoined valves, ×4.4; *b,c,* normal, tilted views of dorsal interior, ×4.2 (Havlíček, 1977a).

Planicardinia SAVAGE, 1968, p. 628 [**P. carroli;* OD]. Transversely semioval valves with long, curved, anacline ventral interarea; dorsal interarea hypercline; dorsal interior with cruralium perpendicular to valve floor. *Lower Devonian (Pragian):* southeastern Australia.——FIG. 586,*4a–i.* **P. carroli,* Pragian, New South Wales; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves, ×6.5; *e,f,* ventral exterior, interior, ×6.5; *g,* dorsal interior, ×6.5; *h,i,* dorsal exterior, interior, ×6.5 (Savage, 1968).

Family PAURORTHIDAE Öpik, 1933

[Paurorthidae ÖPIK, 1933b, p. 11]

Normally small, ventribiconvex dalmanelloids with curved, apsacline ventral interarea and shorter anacline dorsal interarea; delthyrium usually open, rarely constricted by lateral plates; notothyrium open; ventral interior with subtriangular muscle scar normally on callus extended forward as low, broad median ridge; dorsal interior with simple, variably divergent brachiophores; cardinal process ridgelike or absent on low notothyrial platform; fulcral plates usually absent; ventral mantle canal system saccate, dorsal system lemniscate to digitate. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc).*

Paurorthis SCHUCHERT & COOPER, 1931, p. 243 [**Orthambonites parva* PANDER, 1830, p. 83; OD] [=*Paurorthina* RUBEL, 1961a, p. 187 (type, *P. resima*)]. Subcircular, weakly unisulcate with fascicostellate radial ornament; quadripartite dorsal muscle scars with bilobed anterior scars larger than posterior pair. *Lower Ordovician (Arenig)–Upper Ordovician (Caradoc):* cosmopolitan.——FIG. 587,*1a–d.* **P. parva* (PANDER), upper Arenig–lower Llanvirn, Russia; *a,b,* ventral, dorsal views of conjoined valves, ×3; *c,* ventral interior, ×3; *d,* dorsal interior, ×3 (Schuchert & Cooper, 1932).——FIG. 587,*1e. P.* sp. cf. *P. inflata* RUBEL, upper Arenig–lower Llanvirn, eastern Baltic; ventral interior, ×5.8 (Hints, 1975).——FIG. 587,*1f. P. savalensis* HINTS, Caradoc, Estonia; dorsal interior, ×9 (Hints, 1975).

Cyclomyonia COOPER, 1956, p. 974 [**C. peculiaris;* OD]. Differs from *Paurorthis* in having fine multicostellate ornament, and petaloid dorsal muscle scars. *Upper Ordovician (Caradoc):* eastern USA.——FIG. 587,*2a–e.* **C. peculiaris,* Caradoc, Alabama; *a,* ventral exterior, ×2; *b,* ventral interior, ×3; *c,d,* exterior, interior views of dorsal valve, ×4; *e,* broken dorsal interior showing cardinalia, ×4 (Cooper, 1956).

Nereidella WANG, 1955b, p. 338 [**N. typa;* OD]. Differs from *Paurorthis* in having transversely semioval outline and brachiophores, extended, widely divergent, and parallel to hinge line. *Lower Ordovician (Arenig–Llanvirn):* southern China, Bohemia.——FIG. 587,*3a–f.* **N. typa,* Arenig, southern China; *a–d,* ventral, dorsal, posterior, and lateral views of conjoined valves, ×3; *e,* ventral interior, ×2.5; *f,* dorsal interior, ×3.5 (Wang, 1955a).

Family PLATYORTHIDAE
Harper, Boucot, & Walmsley, 1969

[*nom. transl.* HARPER, herein, *ex* Platyorthinae HARPER, BOUCOT, & WALMSLEY, 1969, p. 81]

Medium-sized, usually rectimarginate, planoconvex to biconvex and multicostellate, variably aditiculate dalmanelloids commonly with short hinge line; ventral interior with large diductor scars usually enclosing adductors; dorsal interior normally with complex, trilobed cardinal process; fulcral plates usually absent. *Lower Ordovician (Llanvirn)–Middle Devonian (Eifelian).*

Platyorthis SCHUCHERT & COOPER, 1931, p. 246 [**Orthis planoconvexa* HALL, 1859a, p. 168; OD]. Subcircular, biconvex valves with aditicules; ventral interarea long, curved, and orthocline, dorsal interarea vestigial; ventral interior with quadrate muscle scar and median ridge; dorsal interior with brachiophores as spikelike rods with divergent plates; muscle scar with anterior scars larger than posterior pair. *upper Silurian (Přídolí)–Middle Devonian (Eifelian):* cosmopolitan.——FIG. 588,*1a–e.* **P. planoconvexa* (HALL), Emsian, eastern North America; *a–c,* dorsal, ventral, lateral views of conjoined valves, ×1; *d,* ventral interior, ×1.5; *e,* dorsal interior, ×1.5 (Schuchert & Cooper, 1932).

Crozonorthis MÉLOU, 1976, p. 700 [**C. musculosa;* OD]. Subquadrate, dorsibiconvex valves with wide hinge line and obtuse cardinal extremities; ventral interior with quadrate muscle scar with scalloped

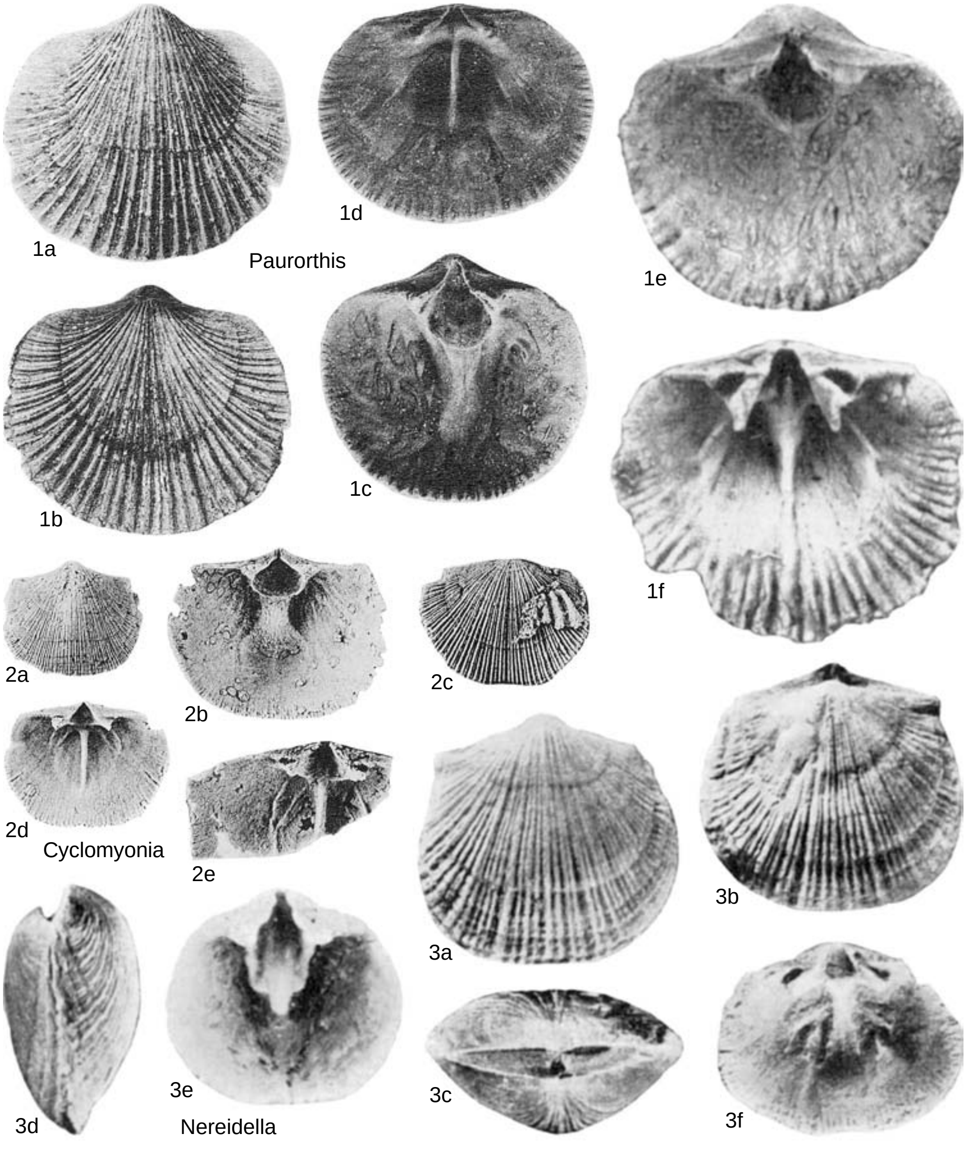

FIG. 587. Paurorthidae (p. 810).

margins on thickened callus bisected by median ridge; dorsal interior with brachiophores as parallel to divergent rods; posterior scars larger than anterior pair. *Lower Ordovician (Llanvirn):* France, Iberia. ——FIG. 588,*2a–e.* *_C. musculosa,_ Llanvirn; *a,b,* internal mold, rubber replica of ventral valve, Brittany, ×4; *c,* rubber replica of ventral exterior, Brittany, ×4; *d,e,* internal mold, rubber replica of dorsal valve, La Alameda, ×4 (Mélou, 1976).

Diceromyonia WANG, 1949, p. 35 [*_Orthis tersa_ SARDESON, 1892, p. 331; OD]. Subcircular, unisulcate valves with short, straight, anacline ventral interarea and vestigial dorsal interarea; dorsal interior with brachiophores as widely divergent rods, lacking plates; anterior muscle scars larger than posterior pair. *Upper Ordovician (Ashgill):* North America.——FIG. 588,*3a–c.* *_D. tersa_ (SARDESON), Ashgill, Iowa; dorsal, ventral, lateral views of conjoined valves, ×1.5 (Harper, Boucot, & Walmsley, 1969).——FIG. 588,*3d. D.* sp. cf. *D. ignota* (SARDESON), Ashgill, Wyoming; ventral interior, ×1.5 (Harper, Boucot, & Walmsley, 1969).——FIG.

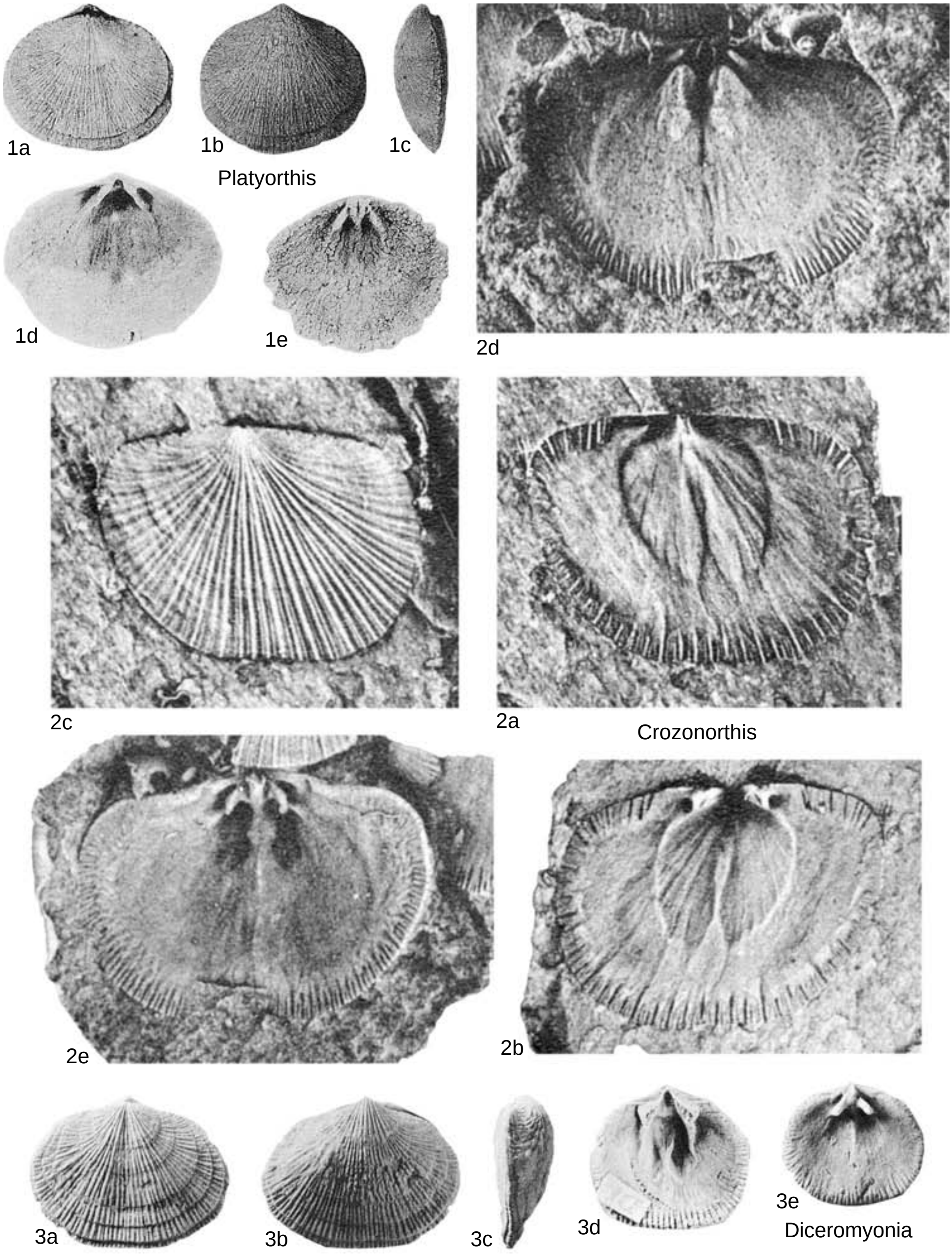

Fig. 588. Platyorthidae (p. 810–812).

588,*3e. D.* sp. cf. *D. tersa,* Ashgill, Illinois; dorsal interior, ×1.5 (Harper, Boucot, & Walmsley, 1969).

Elsaella Alichova, 1960, p. 192 [**Bekkerella bekkeri* Rosenstein, 1943, p. 474; OD]. Subcircular, biconvex, coarsely costellate, imbricate valves with aditicules; ventral interarea short and curved, dorsal interarea short, curved, and orthocline; ventral interior with extended muscle scar; dorsal interior with brachiophores as parallel to divergent rods with divergent plates; muscle scars having larger anterior

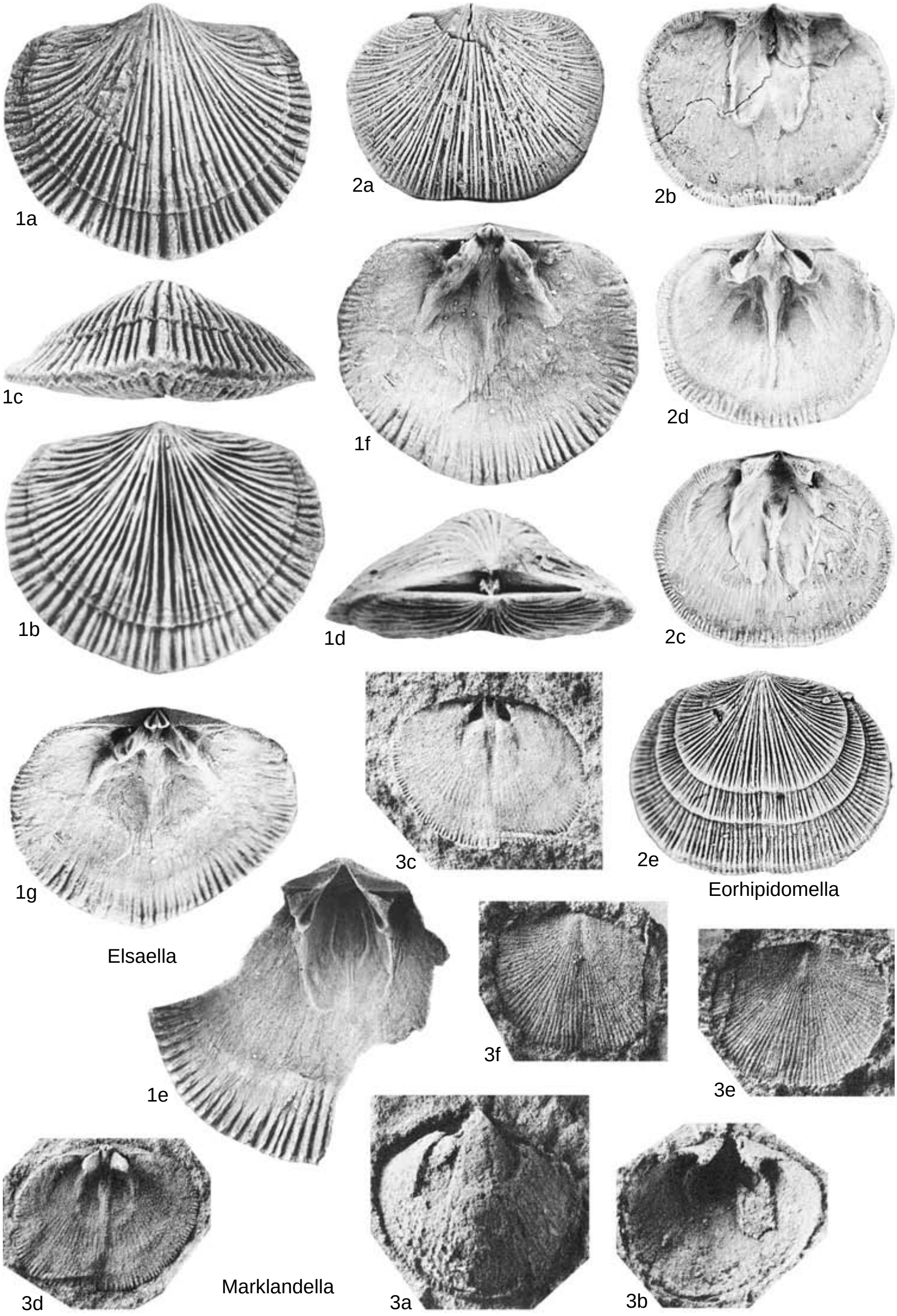

FIG. 589. Platyorthidae (p. 812–814).

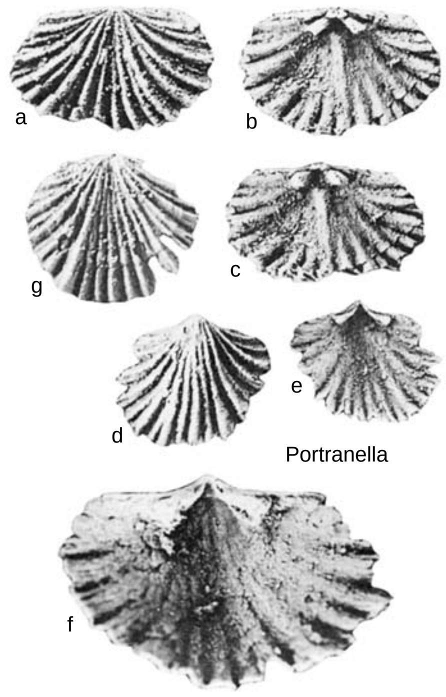

FIG. 590. Portranellidae (p. 814).

pair and bisected by low, short median ridge. *Upper Ordovician (Ashgill):* eastern Baltic, Russia.——FIG. 589,*1a–e.* **E. bekkeri* (ROSENSTEIN), Ashgill, northern Estonia; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves, ×4.7; *e,* ventral interior, ×4.6 (Hints, 1975).——FIG. 589,*1f,g. E.* sp. cf. *E. bekkeri,* Ashgill, eastern Baltic; normal, tilted views of dorsal interior, ×3.2 (Hints, 1975).

Eorhipidomella HINTS, 1971, p. 267 [**E. ovalis;* OD]. Subquadrate, dorsibiconvex, imbricate valves with short, curved, orthocline ventral interarea and vestigial dorsal interarea; ventral interior with linear muscle scar on thickened callus bisected by median ridge; dorsal interior with brachiophores as parallel to divergent rods with divergent plates; anterior muscle scars larger than posterior pair bisected by median ridge. *Upper Ordovician (Caradoc):* Russia.——FIG. 589,*2a–e.* **E. ovalis,* Caradoc, Russia; *a,b,* external, internal views of ventral valve, ×3.3; *c,* ventral interior, ×3.3; *d,* dorsal interior, ×3.3; *e,* dorsal exterior, ×3.3 (Hints, 1975).

Marklandella HARPER, BOUCOT, & WALMSLEY, 1969, p. 82 [**M. giraldi;* OD]. Transversely semioval valves with aditicules; ventral interarea short and curved, dorsal interarea short, curved, and anacline; ventral interior with parallel dental plates and cordate muscle scar; dorsal interior with brachiophores as widely divergent rods lacking plates; anterior and posterior muscle scars subequal. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Canada (Nova Scotia), Wales.——FIG. 589,*3a–f.* **M. giraldi,* Wenlock–Ludlow, southern Wales; *a,b,* internal mold, rubber replica of ventral valve, ×1.5; *c,d,* internal mold, rubber replica of dorsal valve, ×1.5; *e,f,* external mold, rubber replica of dorsal valve, ×1.5 (Harper, Boucot, & Walmsley, 1969).

Family PORTRANELLIDAE new family

[Portranellidae HARPER, herein]

Coarsely costellate dalmanelloids with reduced notothyrial platform and lateral lobes of trilobed cardinal process extending over posteromedian surfaces of rodlike, divergent brachiophores; plates divergent; fulcral plates absent. *Upper Ordovician (Ashgill).*

Portranella WRIGHT, 1964, p. 167 [**P. angulocostellata;* OD]. Subcircular with obtuse cardinal angles; ventral interior with suboval muscle scar impressed on callus. *Upper Ordovician (Ashgill):* Ireland, Wales, Belgium, Spain.——FIG. 590*a–g. P. angulocostellata,* Ashgill, eastern Ireland; *a–c,* exterior, normal, tilted views of dorsal interior, ×2.7; *d,e,* exterior, interior of ventral valve, ×2.5; *f,* tilted view of ventral interior, ×5.3; *g,* dorsal exterior, ×1.9 (Wright, 1964).

Family PROSCHIZOPHORIIDAE
Boucot, Gauri, & Johnson, 1966

[*nom. transl.* HARPER, herein, *ex* Proschizophoriinae BOUCOT, GAURI, & JOHNSON, 1966, p. 158]

Normally transversely semioval, unisulcate dalmanelloids with long, curved ventral interarea; ventral interior normally with large cordate muscle scar and divergent dental plates; dorsal interior with complex, lobate cardinal process; fulcral plates commonly absent. *middle Silurian (Wenlock)–Lower Devonian (Emsian).*

Proschizophoria MAILLIEUX, 1912, p. 177 [**Orthis personata* ZEILER, 1857, p. 48; OD]. Transversely semioval, large, convexoconcave, unisulcate valves; ventral muscle scar suboval to subtriangular; dorsal interior with massive lobate cardinal process, lacking fulcral plates; posterior adductor scars larger than anterior pair. *Lower Devonian (Lochkovian–Pragian):* Europe, Altai Mountains, Canada (Nova Scotia), Kazakhstan, Morocco, New Zealand, China, Turkey.——FIG. 591,*1a–f.* **P. personata* (ZEILER), Pragian, Siegerland, Germany; *a,b,* internal mold, rubber replica of ventral valve, ×1; *c–e,* normal, posterior views of internal mold, rubber replica of dorsal valve, ×1; *f,* external mold of ventral valve, ×1 (Boucot, Gauri, & Johnson, 1966).

Baturria CARLS, 1974, p. 167 [**Orthis edgelliana* DAVIDSON, 1869, p. 228; OD]. Subcircular, medium-sized, dorsibiconvex, rectimarginate valves;

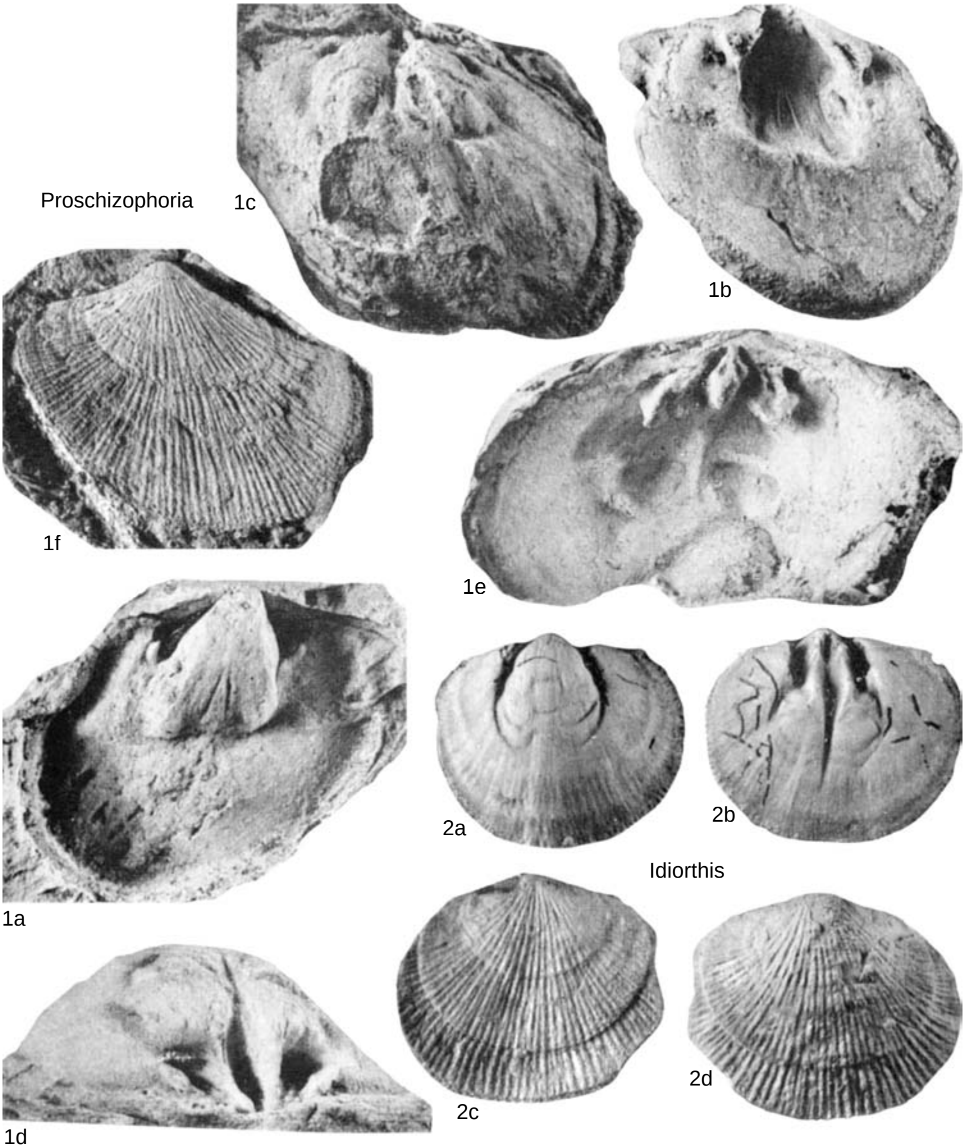

FIG. 591. Proschizophoriidae (p. 814–817).

ventral interior with pseudospondylium and cordate muscle scar; dorsal interior with bilobed cardinal process; posterior adductor scars larger than anterior pair. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian):* Bohemia, Britain, Mexico, Morocco, Spain, Venezuela.——FIG. 592,*2a–g.* **B. edgelliana* (DAVIDSON), Wenlock, Wales; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×1.5; *f,* ventral interior, ×1.5; *g,* dorsal interior, ×1.5 (Bassett, 1972).

Cordatomyonia BOUCOT, GAURI, & JOHNSON, 1966, p. 164 [**C. shupei;* OD]. Transversely semioval, medium-sized, ventribiconvex, weakly unisulcate valves; ventral interior with pseudospondylium, well-developed pedicle callist and cordate muscle scar; dorsal interior with bilobed cardinal process; anterior adductor scars larger than posterior pair. *Lower Devonian (Lochkovian):* USA (Maryland). ——FIG. 592,*1a–g.* **C. shupei,* Lochkovian, Maryland; *a–d,* ventral, dorsal, anterior, lateral views of

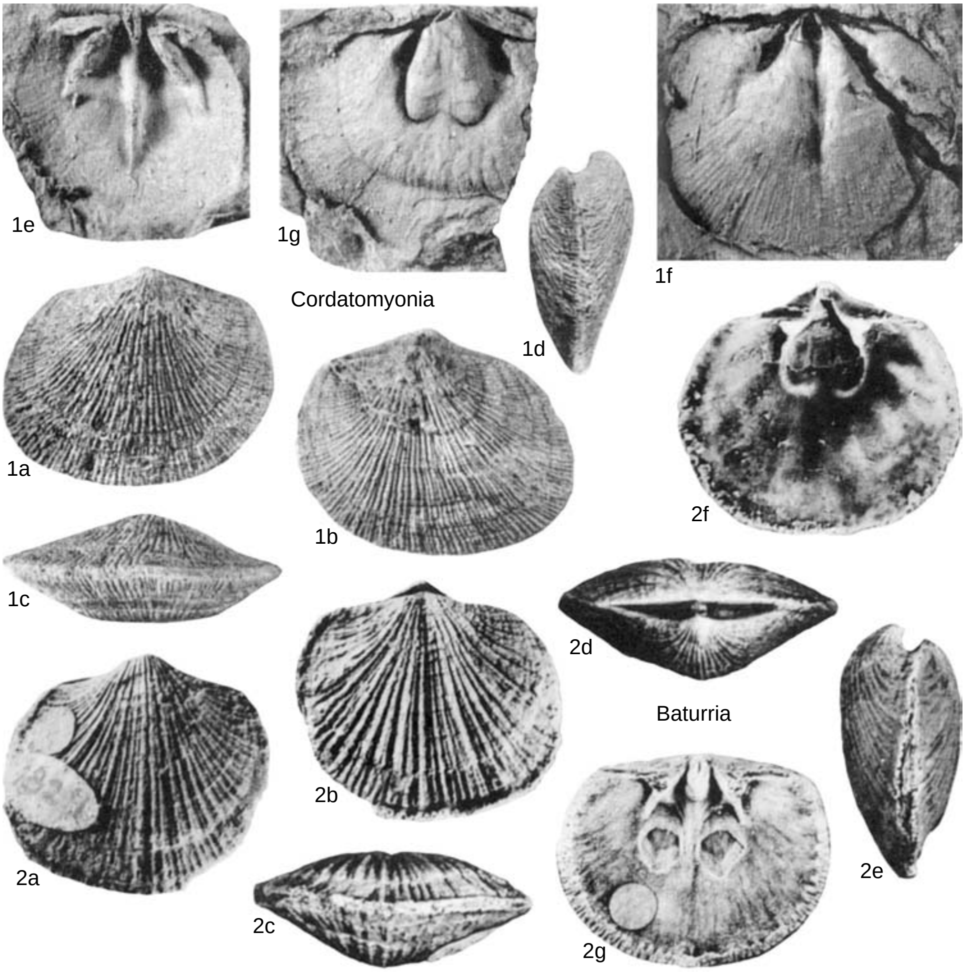

FIG. 592. Proschizophoriidae (p. 814–816).

conjoined valves, ×1.5; *e,* rubber replica of dorsal interior, ×1.5; *f,* internal mold of dorsal valve, ×1.5; *g,* internal mold of ventral valve, ×1.5 (Boucot, Gauri, & Johnson, 1966).

Elegesta VLADIMIRSKAYA in KULKOV, VLADIMIRSKAYA, & RYBKINA, 1985, p. 66 [**E. nikiforovae;* OD]. Medium-sized, rectimarginate, dorsibiconvex valves; dorsal interior with simple cardinal process, swollen posteriorly; brachiophore plates widely divergent; ventral interior with rounded subtriangular to subcordate muscle scar. *middle Silurian (Wenlock):* Tuva.——FIG. 593,*2a–f.* **E. nikiforovae,* Wenlock, Tuva; *a–d,* ventral, dorsal, anterior, lateral views of conjoined internal molds, ×2; *e,* ventral exterior, ×2; *f,* dorsal exterior, ×2 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Fulcriphoria CARLS, 1974, p. 176 [**F. navarrae;* OD]. Subcircular, large, dorsibiconvex, rectimarginate valves; dorsal interior with bilobed cardinal process; posterior adductor scars larger than anterior pair; ventral interior with pseudospondylium, well-developed pedicle callist, and cordate muscle scar. *Lower Devonian (Lochkovian–Emsian):* Belgium, France, Spain.——FIG. 593,*1a–e.* **F. navarrae,* Emsian; *a–c,* lateral, dorsal, posterior views of internal mold of dorsal valve, Iberian Chains, ×1.3; *d,* internal mold of dorsal valve, Pyrenees, ×1.3; *e,* internal mold of ventral valve, Pyrenees, ×1.3 (Carls, 1974).

Idiorthis MCLEARN, 1924, p. 56 [**I. matura;* OD]. Transversely semioval, medium-sized, planoconvex, unisulcate valves; ventral muscle scar cordate; dorsal interior with trilobed cardinal process on well-developed notothyrial platform; anterior adductor scars larger than posterior pair. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Canada (Nova

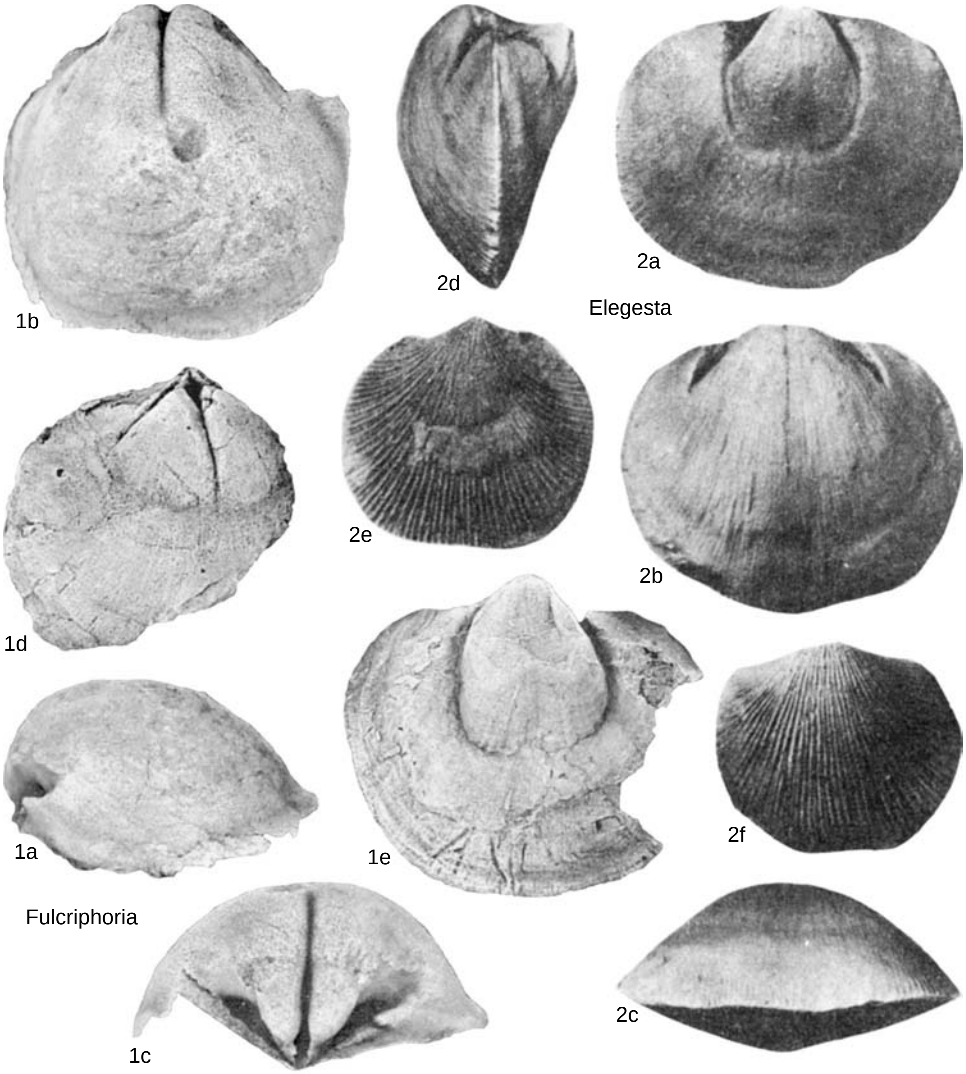

FIG. 593. Proschizophoriidae (p. 816).

Scotia).——FIG. 591,*2a–d*. **I. matura,* Wenlock–Ludlow, Arisaig, Nova Scotia; *a,* internal mold of ventral valve, ×1.5; *b,* internal mold of dorsal valve, ×1.5; *c,d,* dorsal, ventral views of conjoined pair, ×1.5 (Boucot, Gauri, & Johnson, 1966).

Family RHIPIDOMELLIDAE Schuchert, 1913

[Rhipidomellidae SCHUCHERT, 1913b, p. 382]

Normally subcircular, large, unisulcate dalmanelloids with aditicules; ventral interarea, usually long and curved; dorsal interarea vestigial; ventral interior with recessive dental plates, median ridge and extended to quadrate diductor scars with scalloped margins, normally enclosing adductors scars; dorsal interior with variably lobate cardinal process, short brachiophores, extended in later taxa, with erect plates; notothyrial platform reduced; fulcral plates absent; ventral and dorsal mantle canal systems lemniscate. *Upper Ordovician (Ashgill)–Upper Permian (Tatarian).*

Subfamily RHIPIDOMELLINAE Schuchert, 1913

[*nom. transl.* HARPER, herein, *ex* Rhipidomellidae SCHUCHERT, 1913b, p. 382]

Normally subcircular, large, rhipidomellids with well-developed hinge line; ventral interarea, usually long and curved; dorsal interarea vestigial; ventral interior with recessive dental plates associated with strong subtriangular teeth. *Upper Ordovician (Ashgill)–Upper Permian (Tatarian).*

Rhipidomella OEHLERT, 1890, p. 366, *nom. nov. pro Rhipidomys* OEHLERT, 1887b, p. 1288, *non* WAGNER, 1844 [**Terebratula michelini* LÉVEILLÉ, 1835, p. 39; OD] [=*Blairella* MILLER & GURLEY, 1897, p. 6, *nom. nud.*]. Dorsibiconvex, rectimarginate to weakly unisulcate valves; notothyrium covered by chilidial plates in later species; ventral interior with extended, flabellate muscle scars, bisected in front of adductor scar by short median ridge; dorsal interior with brachiophores supported by adventitious shell. *Middle Devonian (Eifelian)–Upper Permian (Tatarian):* cosmopolitan.——FIG. 594,*2a–f.* **R. michelini* (LÉVEILLÉ), Viséan, Belgium; *a–d,* ventral, dorsal, posterior, lateral views of conjoined valves, ×1; *e,* ventral interior, ×1; *f,* dorsal interior, ×1 (Wright, 1965a).

Ambonorthella BASSETT, 1972, p. 66 [**A. hancocki;* OD]. Elongately semioval, biconvex, rectimarginate valves with short, curved ventral interarea; ventral interior with divergent dental plates; dorsal interior with widely divergent brachiophores and subperipheral rim. *middle Silurian (Wenlock):* Britain.——FIG. 594,*1a–e.* **A. hancocki,* Wenlock, southern Wales; *a,b,* internal mold, rubber replica of ventral valve, ×1.5; *c,d,* internal mold, rubber replica of dorsal valve, ×1.5; *e,* rubber replica of dorsal exterior, ×1.5 (Bassett, 1972).

Aulacella SCHUCHERT & COOPER, 1931, p. 246 [**Orthis eifelensis* SCHNUR, 1854, p. 213; OD]. Dorsibiconvex, unisulcate valves; ventral interior with bilobed muscle scar and median ridge, bifurcate anteriorly in front of muscle field; dorsal interior with trilobed cardinal process on low notothyrial platform. *Middle Devonian (Eifelian)–Lower Carboniferous (Tournaisian):* Europe.——FIG. 594,*3a–d.* **A. eifelensis* (SCHNUR), Eifelian; *a,b,* ventral, dorsal views of conjoined valves, Germany, ×1.5 (Schuchert & Cooper, 1932); *c,* dorsal interior, Poland, ×1; *d,* ventral interior, Poland, ×2.5 (Biernat, 1959).

Clavodalejina HAVLÍČEK, 1977a, p. 227 [**C. clavigera;* OD]. Ventribiconvex, rectimarginate valves; ventral interarea long and narrow, apsacline; ventral interior with divergent dental plates, suboval to subtriangular muscle scar, lacking median ridge; dorsal interior with large muscle scar, elevated peripherally and bisected by wide median ridge expanded in front of muscle field to form peglike swelling. *Lower Devonian (Emsian):* Bohemia.——FIG. 594,*4a–e.* **C. clavigera,* Emsian, Bohemia; *a,* ventral exterior, ×4.4; *b,* detail of ventral interarea, ×4.3; *c,d,* normal, oblique views of dorsal interior, ×4.4; *e,* dorsal interior, ×5.8 (Havlíček, 1977a).

Dalejina HAVLÍČEK, 1953, p. 5 [**D. hanusi;* OD] [=*Rhipidomelloides* BOUCOT & AMSDEN, 1958, p. 165 (type, *Rhipidomella henryhousensis* AMSDEN, 1951, p. 74)]. Dorsibiconvex, unisulcate valves with short, curved ventral interarea; ventral interior with rudimentary dental plates and extended, often flabellate, muscle scars; median ridge absent. *middle Silurian (Wenlock)–Lower Devonian (Emsian):* cosmopolitan.——FIG. 595,*1a–e.* **D. hanusi,* Pragian, Bohemia; *a–c,* ventral, dorsal, anterior views of conjoined valves, ×7.1; *d,* ventral interior, ×6.8; *e,* dorsal interior, ×5.9 (Havlíček, 1977a).

Discomyorthis JOHNSON, 1970a, p. 84 [**Orthis musculosa* HALL, 1857, p. 46; OD]. Convexiplane, resupinate, large valves internally similar to *Dalejina* but ventral interior with very large, pentagonal diductor scars with scalloped margins. *Lower Devonian (Pragian):* western USA.——FIG. 595,*5a–d.* **D. musculosa* (HALL), Pragian, Nevada; posterior, lateral, external, internal views of ventral valve, ×1 (Johnson, 1970a).

Mendacella COOPER, 1930, p. 380 [**Orthis uberis* BILLINGS, 1866, p. 42; OD]. Ventribiconvex, rectimarginate valves; ventral interior with short, widely divergent dental plates; dorsal interior with brachiophores widely divergent relative to brachiophore plates; fulcral plates present. *Upper Ordovician (Ashgill)–middle Silurian (Wenlock):* cosmopolitan.——FIG. 596,*4a–e.* **M. uberis* (BILLINGS), Ashgill, Anticosti Island; *a–c,* ventral, dorsal, anterior views of conjoined valves, ×2 (Wright, 1965a); *d,* ventral interior, ×2; *e,* dorsal interior, ×2 (Schuchert & Cooper, 1932).

Peridalejina HAVLÍČEK, 1973, p. 337 [**Dalejina periens* HAVLÍČEK, 1956, p. 542]. Small, biconvex valves with variable transverse profile; ventral interarea short, straight; ventral interior with rudimentary dental plates and cordate muscle scar. *Middle Devonian (Eifelian):* Bohemia.——FIG. 595,*3a–f.* **P. periens* (HAVLÍČEK), Eifelian, Bohemia; *a–d,* ventral, dorsal, posterior, anterior views of conjoined valves, ×7.2; *e,* ventral interior, ×8.4; *f,* dorsal interior, ×9 (Havlíček, 1977a).

Pseudodicoelosia BOUCOT & AMSDEN, 1958, p. 162 [**Rhipidomella oklahomensis* AMSDEN, 1951, p. 76; OD]. Bilobed, small, ventribiconvex, unisulcate valves with extended, flabellate ventral muscle scar. *middle Silurian (Wenlock):* USA (Oklahoma, Tennessee).——FIG. 595,*2a–g.* **P. oklahomensis* (AMSDEN), Wenlock, south central Oklahoma; *a–e,* ventral, dorsal, lateral, posterior, anterior views of conjoined valves, ×3; *f,* ventral interior, ×5; *g,* dorsal interior, ×5 (Amsden, 1951).

Pseudomendacella ZHANG, 1989a, p. 69 [**P. boucoti;* OD]. Dorsibiconvex, circular, uniplicate valves with bilobed to linear ventral muscle scar and small, nonlobate cardinal process. *middle Silurian (Wenlock):* Canadian Arctic, United States (California), Venezuela.——FIG. 596,*3a–f.* **P. boucoti,* Wenlock,

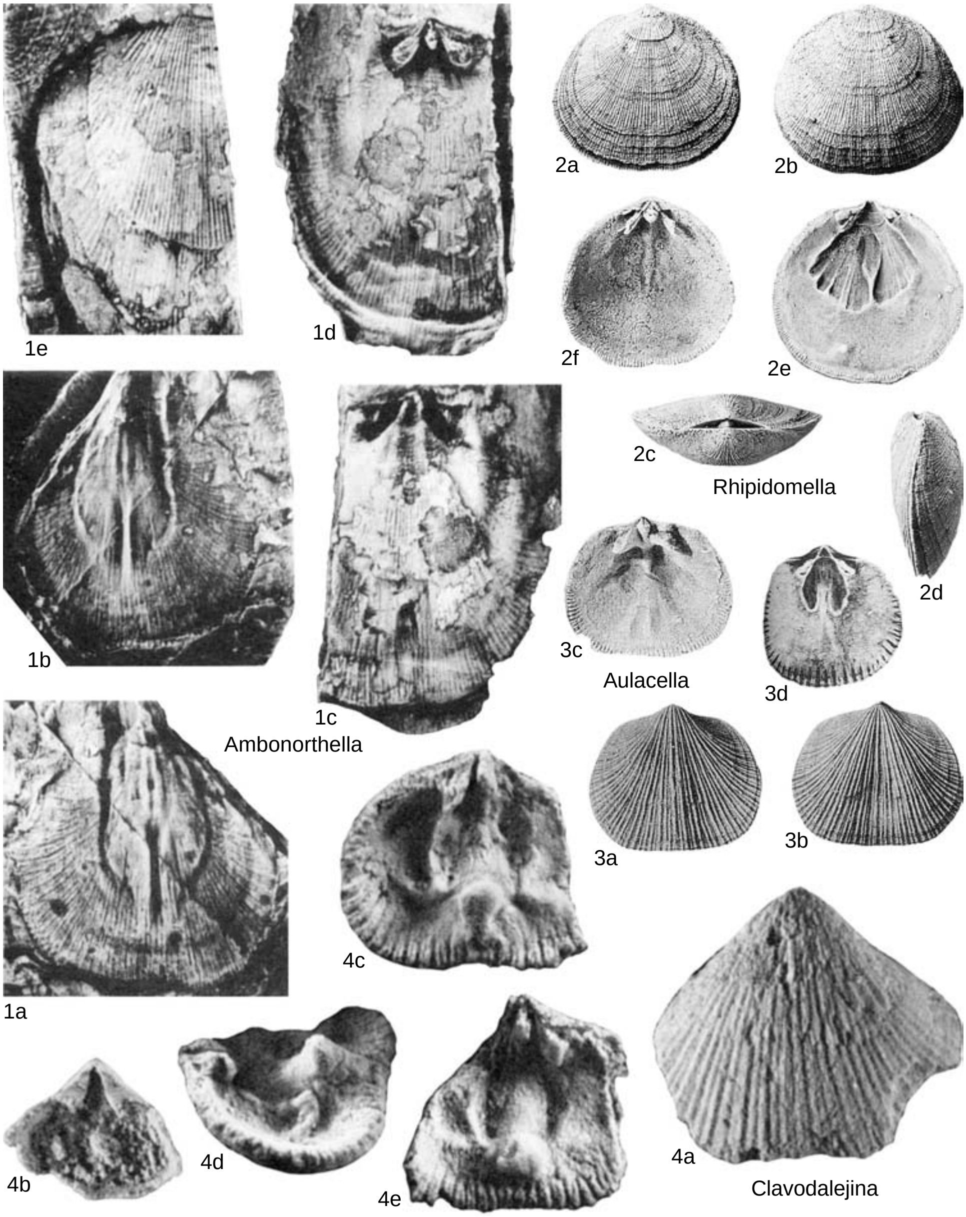

FIG. 594. Rhipidomellidae (p. 818).

Arctic Canada; *a,b,* ventral exterior, interior, ×2; *c,d,* dorsal exterior, interior, ×2; *e,* detail of cardinalia, muscle field, ×5; *f,* ventral interior, ×1 (Zhang, 1989a).

Stainbrookia COOPER & DUTRO, 1982, p. 39 [**Orthis infera* CALVIN, 1878, p. 728; OD]. Subquadrate, biconvex, small valves modified from unisulcate to uniplicate during ontogeny; ventral interior with quadrate to linear muscle scar, well-developed median ridge, bifurcate anteriorly in front of muscle field; dorsal interior with trilobate cardinal process, widely divergent brachiophores, muscle scars confined and supported by ridges; median ridge well developed. *Upper Devonian (Frasnian):* USA (Iowa, New Mexico).——FIG. 596,*1a–g.* **S. infera* (CALVIN), Frasnian, Iowa; *a–e,* ventral, dorsal,

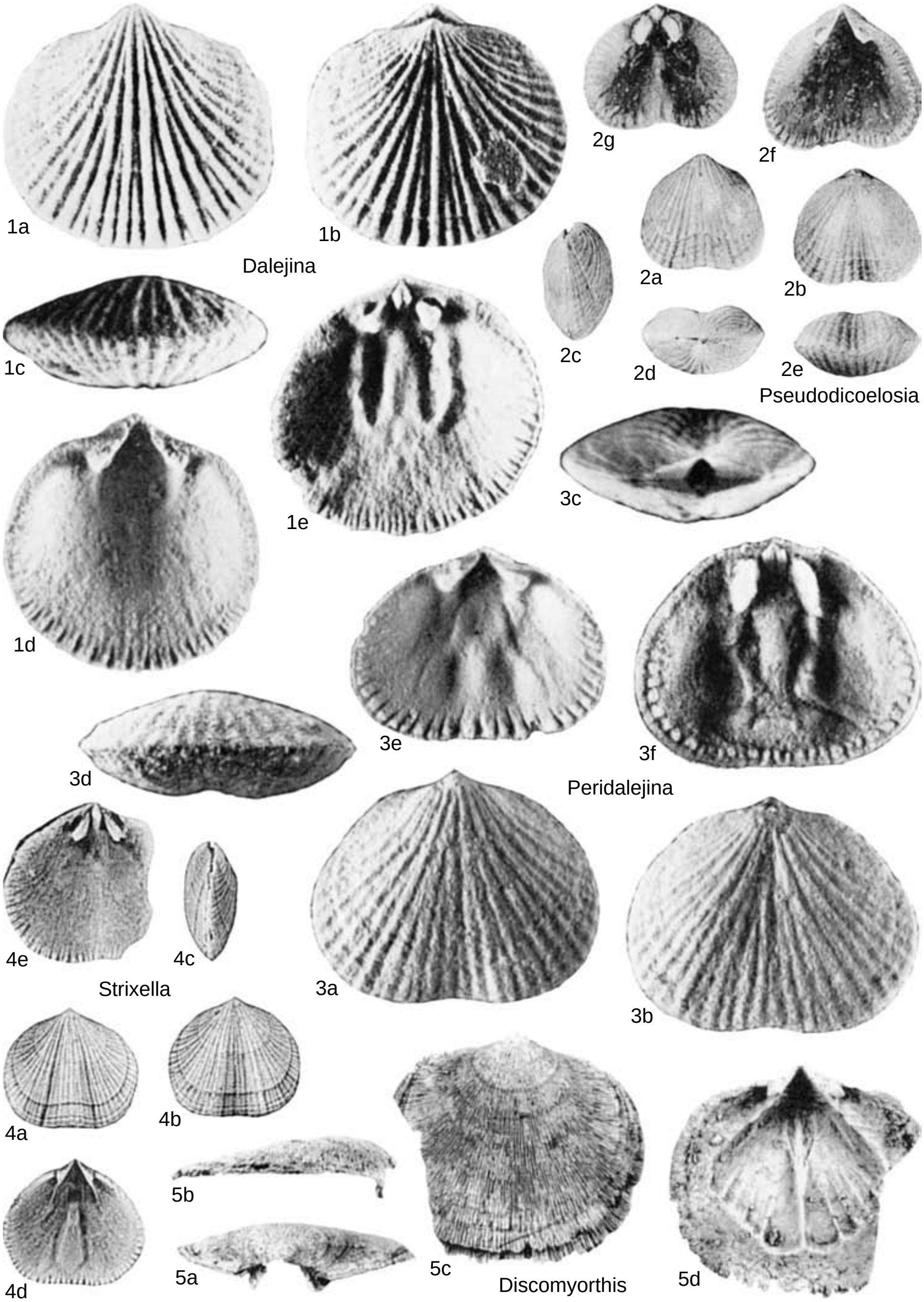

FIG. 595. Rhipidomellidae (p. 818–821).

anterior, posterior, lateral views of conjoined valves, ×2; *f,* dorsal interior, ×2; *g,* ventral interior, ×2 (Cooper & Dutro, 1982).

Strixella BOUCOT & AMSDEN, 1958, p. 170 [**Rhipidomella acutisulcata* AMSDEN, 1951, p. 75; OD]. Subquadrate, biconvex, sharply unisulcate, imbri-

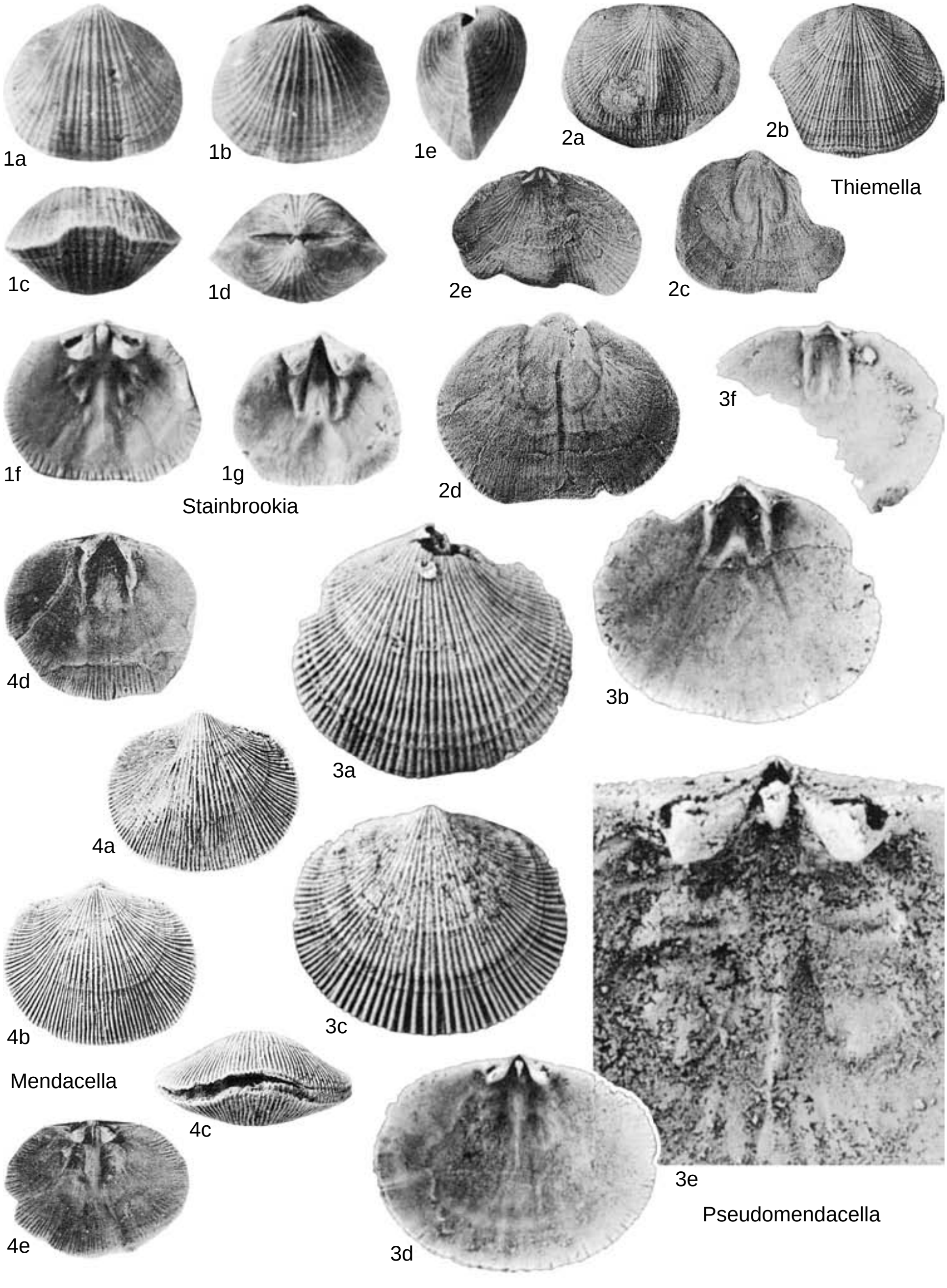

FIG. 596. Rhipidomellidae (p. 818–822).

cate valves with divergent ventral adductor scars and lacking dorsal median ridge. *middle Silurian (Wenlock):* eastern and central USA.——FIG. 595,*4a–e.* **S. acutisulcata* (AMSDEN), Wenlock, south central Oklahoma; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×2; *d,* ventral interior, ×2; *e,* dorsal interior, ×3 (Boucot & Amsden, 1958).

Thiemella WILLIAMS, 1908, p. 59 [**T. villenovia;* OD]. Dorsibiconvex, sharply unisulcate valves; ventral

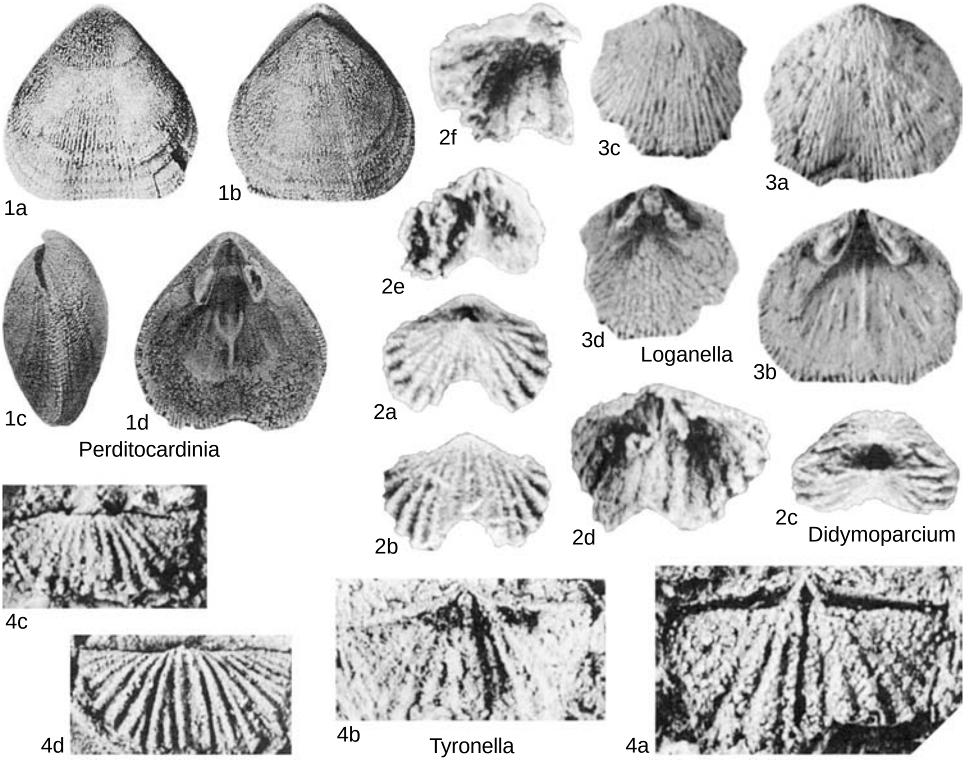

FIG. 597. Rhipidomellidae and Tyronellidae (p. 822–823).

interior with convergent dental plates, subcordate muscle scar and long median ridge; dorsal interior with delicate cardinalia including small myophore and shaft and thin brachiophores; anterior scars larger than posterior pair. *Upper Devonian (Frasnian)–Lower Carboniferous:* eastern USA, Germany.——FIG. 596,*2a–e.* **T. villenovia,* Frasnian, New York; *a,* rubber replica of ventral exterior, ×1.5; *b,* rubber replica of dorsal exterior, ×1.5; *c,* internal mold of ventral valve, ×1.5; *d,* internal mold of ventral valve, ×2; *e,* rubber replica of dorsal interior, ×1.5 (Schuchert & Cooper, 1932).

Subfamily PERDITOCARDINIINAE new subfamily

[Perditocardiniinae HARPER, herein]

Rostrate rhipidomellids lacking both interareas; ventral interior with massive teeth and dental fossettes; muscle scar flabellate; dorsal interior with deep sockets. *Lower Devonian (Pragian)–Lower Permian.*

Perditocardinia SCHUCHERT & COOPER, 1931, p. 246 [**Orthis dubia* HALL, 1858b, p. 12; OD]. Dorsibiconvex, uniplicate valves with short hinge line; ventral interior with massive, elongate teeth and dental fossettes, extending anteriorly; muscle scar extended and flabellate. *Lower Carboniferous (Viséan)–Lower Permian:* cosmopolitan.——FIG. 597,*1a–d.* **P. dubia* (HALL), Viséan, Indiana; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×1; *d,* ventral interior, ×1 (Schuchert & Cooper, 1932).

Loganella BOUCOT & AMSDEN, 1958, p. 164 [**Rhipidomella lehuquetiana* CLARKE, 1905, p. 144; OD]. Biconvex, unisulcate valves; ventral interior with massive teeth and dental fossettes; muscle scar flabellate; dorsal interior with deep sockets; lobate cardinal process fused to brachiophores. *Lower Devonian (Pragian):* eastern Canada.——FIG. 597,*3a–d.* **L. lehuquetiana* (CLARKE), Pragian, Gaspé; *a,b,* ventral exterior, interior, ×2; *c,d,* dorsal exterior, interior, ×2 (Boucot & Amsden, 1958).

Family TYRONELLIDAE Mitchell, 1977

[Tyronellidae MITCHELL, 1977, p. 64]

Small, transversely semioval, coarsely costellate dalmanelloids; ventral interior with free spondylium confined to delthyrial chamber; cardinalia with lobate myophore and shaft continuous with median septum extending forward from rudimentary notothyrial platform. *Upper Ordovician (Ashgill)–Lower Devonian (Emsian).*

Tyronella MITCHELL, 1977, p. 64 [**T. killeyensis;* OD]. Small, biconvex, tranversely semioval valves with acute cardinal extremities and coarsely costellate ornament. *Upper Ordovician (Ashgill):* Northern Ireland, eastern Canada.——FIG. 597,*4a–d.* **T. killeyensis,* Ashgill, Northern Ireland; *a,* internal mold of dorsal valve, ×11.5; *b,* rubber replica of dorsal valve, ×10; *c,* internal mold of ventral valve, ×10; *d,* rubber replica of dorsal exterior, ×10 (Mitchell, 1977).

Didymoparcium LENZ, 1977, p. 62 [**D. costata;* OD]. Small, ventribiconvex, strangulate valves with obtuse cardinal extremities and coarsely costellate ornament. [This genus has been tentatively assigned to the Dicoelosiidae on the basis of its bilobed and emarginate outline (LENZ, 1977). It differs markedly, however, from contemporary dicoelosiids, kayserellids, and mystrophorids in having a free spondylium. Here it is tentatively associated with *Tyronella* on the basis of the internal similarities between both genera.] *Lower Devonian (Emsian):* Arctic Canada.——FIG. 597,*2a–f.* **D. costata,* Emsian, Canadian Arctic; *a–c,* dorsal, ventral, posterior views of conjoined valves, ×10; *d,* dorsal interior, ×10; *e,* dorsal interior, ×10; *f,* ventral interior, ×10 (Lenz, 1977).

Superfamily ENTELETOIDEA Waagen, 1884

[*nom. transl.* ALICHOVA, 1960, p. 193, *ex* Enteletinae WAAGEN, 1884, p. 548; *emend.,* HARPER, herein]

Commonly subequally biconvex dalmanellidines; costellate ornament commonly with aditicules; notothyrial platform reduced or absent, developed as variable cavity; cardinalia normally with simple, rarely lobate, crenulated myophore and shaft; brachiophores high and long, commonly tusklike with plates usually convergent in earlier taxa; fulcral plates normally present. *Lower Ordovician (Arenig)–Upper Permian (Tatarian).*

Family ENTELETIDAE Waagen, 1884

[*nom. transl.* LICHAREV & ALICHOVA in ALICHOVA, 1960, p. 194, *ex* Enteletinae WAAGEN, 1884, p. 548; *emend.,* HARPER, herein]

Normally large, dorsibiconvex, plicate, imbricate enteletoids with long, curved ventral interarea; ventral interior with strong, subparallel to convergent dental plates and extended muscle scar bisected by median ridge or septum; pedicle callist reduced or absent; dorsal interior with well-developed median septum. *Carboniferous (Namurian)–Upper Permian (Tatarian).*

Enteletes FISCHER DE WALDHEIM, 1825, p. 6 [**Enteletes glabra* FISCHER DE WALDHEIM, 1830, pl. 26, fig. 6, 7; SM] [=*Anteletes* D'ORBIGNY, 1847–1849, p. 348; *Syntrilasma* MEEK & WORTHEN, 1866, p. 277 (type, *Spirifer hemiplicatus* HALL, 1852); *Syntrielasma* MEEK & WORTHEN, 1866, p. 321]. Sharply uniplicate, capillate valves; ventral interior with high, flat, subparallel to slightly convergent dental plates, bisected by high, thin median septum; dorsal interior with well-developed tusklike brachiophores defining deep, tubular sockets; cardinal process variably expanded. *Carboniferous (Namurian)–Upper Permian (Tatarian):* widespread.——FIG. 598,*1a–c. E. lamarcki* (FISCHER DE WALDHEIM), Namurian, Russia; ventral, dorsal, lateral views of conjoined valves, ×1 (Schuchert & Cooper, 1932).——FIG. 598,*1d–m. E. wordensis* (R. E. KING), Kazanian, western Texas; *d–g,* ventral, lateral, posterior, anterior views of conjoined valves, ×1; *h–j,* normal, tilted, lateral views of ventral interior, ×1; *k–m,* normal, tilted, lateral views of dorsal interior, ×1 (Cooper & Grant, 1976).

Enteletella LICHAREV, 1926, p. 719 [**E. nikschitchi;* OD]. Sharply uniplicate valves, similar to *Enteletes* but with convergent dental plates onto median ridge forming spondylium simplex. *Lower Permian:* Russia (Caucasus).——FIG. 599,*4.* **E. nikschitchi,* Lower Permian, Caucasus; lateral view of conjoined valves, ×1 (Schuchert & Cooper, 1932).

Enteletina SCHUCHERT & COOPER, 1931, p. 247 [**Enteletes latesinuatus* WAAGEN, 1884, p. 559; OD]. Sharply unisulcate valves with convergent dental plates. *Upper Permian:* central Asia.——FIG. 599,*1a–c.* **E. latesinuatus* (WAAGEN), Permian, Salt Ranges; *a,* ventral interior, ×1; *b,* dorsal exterior, ×1; *c,* dorsal interior, ×1 (Schuchert & Cooper, 1932).

Mapingtichia LI in LI, YANG, & FENG, 1986, p. 217 [**M. longliensis;* OD]. Sharply unisulcate valves with divergent anterior parts of dental plates and widely divergent brachiophore plates. *Lower Permian:* China.——FIG. 599,*3a–c.* **M. longliensis,* Lower Permian, southern China; *a,b,* internal, anterior views of ventral valve, ×1; *c,* dorsal view of valve, ×1 (Li, Yang, & Feng, 1986).

Parenteletes KING, 1931, p. 48 [**P. cooperi;* OD]. Sharply unisulcate valves, similar to *Enteletina* but with divergent dental plates and cella under anterior extension of ventral median septum; sockets elongate. *Carboniferous (Namurian)–Upper Permian (Tatarian):* Europe, central Asia, North America.——FIG. 598,*2a–h.* **P. cooperi,* Asselian, western Texas; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×1; *f,g,* normal, tilted views of ventral interior, ×1; *h,* oblique view of dorsal interior, ×1 (Cooper & Grant, 1976).

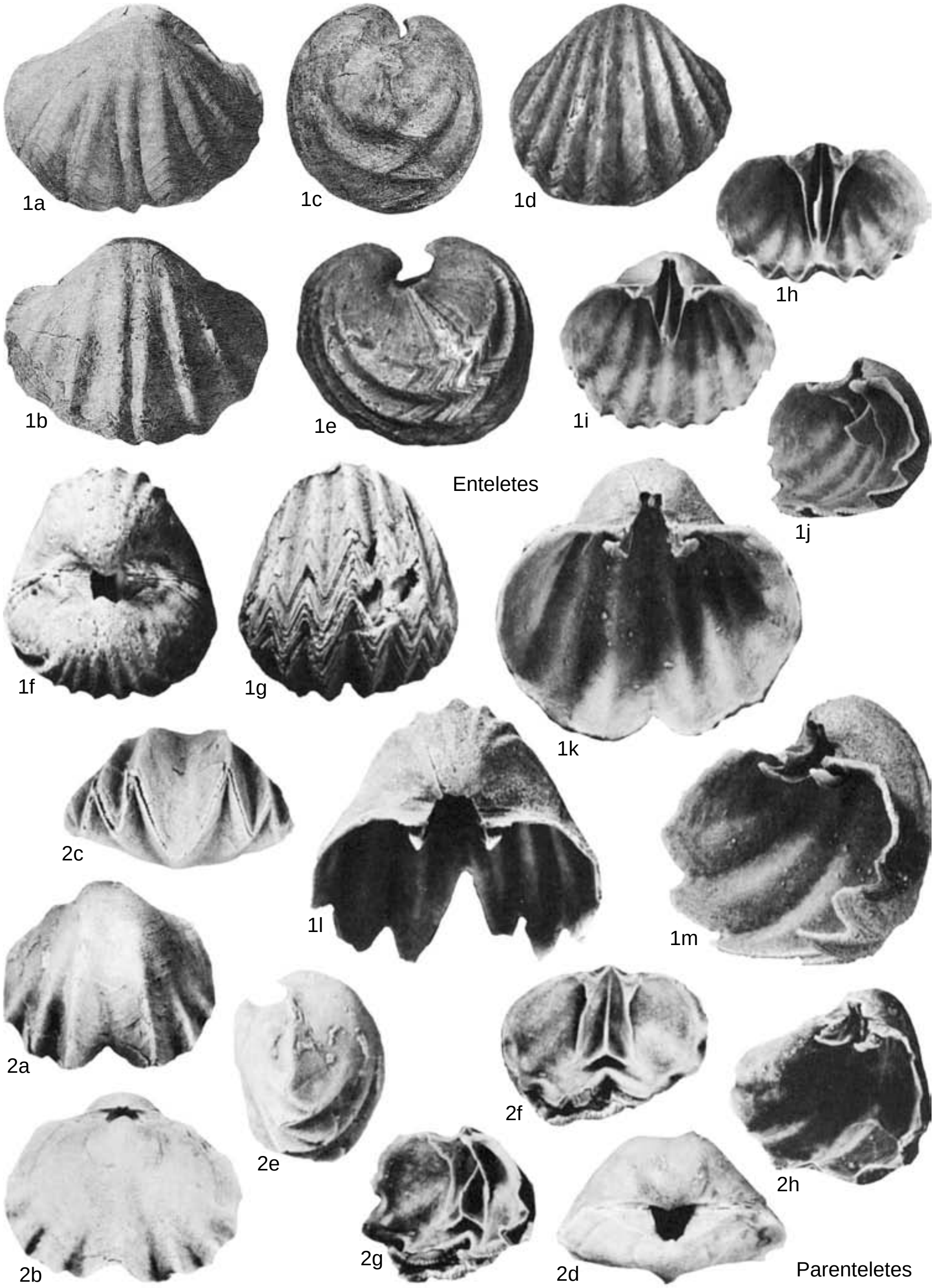

FIG. 598. Enteletidae (p. 823).

Peltichia JIN & LIAO in JIN & SUN, 1981, p. 129 [_*Parenteletes sinensis zigzag_ HUANG, 1933, p. 13; OD]. Unisulcate, medium-sized valves with parallel dental plates and well-developed median septum. _Upper Permian (Tatarian):_ southern China, Tibet.——FIG. 599,_2a–e_. _*P. zigzag_ (HUANG), Tatarian, southern China; _a–e,_ ventral, dorsal, lateral, posterior, anterior views of conjoined pair, ×1 (Shen, Tazawa, & Shi, 1999).——FIG. 599,_2f,g_. _P. transversus_ (HUANG), Tatarian, southern China; _f,_ internal

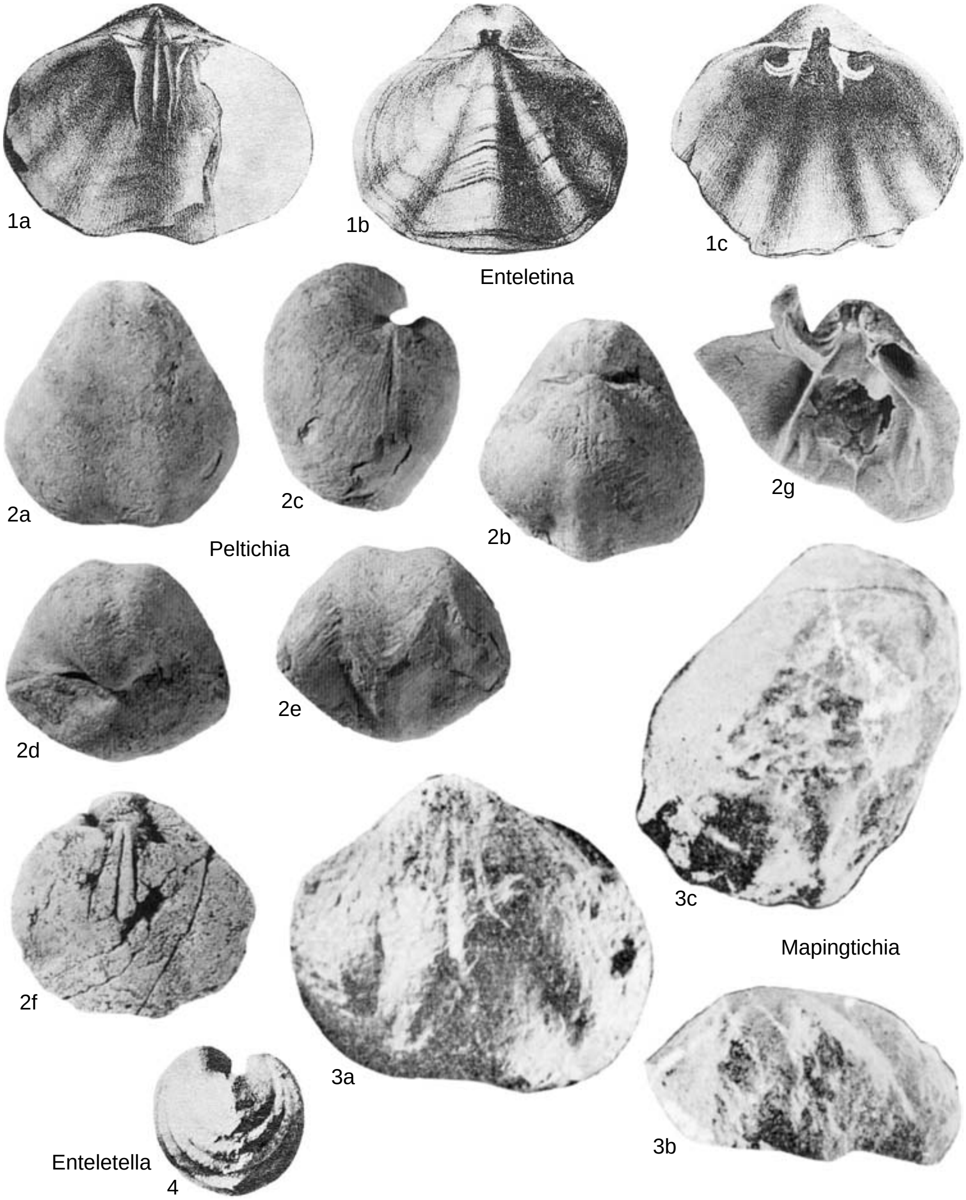

FIG. 599. Enteletidae (p. 823–825).

mold of ventral valve; *g,* dorsal interior, ×1 (Shen, Tazawa, & Shi, 1999).

Family DRABOVIIDAE Havlíček, 1950

[*nom. transl.* ALICHOVA, 1960, p. 193, *ex* Draboviinae HAVLÍČEK, 1950, p. 45; *emend.,* HARPER, herein]

Normally ventribiconvex, rectimarginate, multicostellate enteletoids with aditicules; ventral and dorsal interareas apsacline and anacline, respectively; ventral muscle scar suboval to subtriangular; dental plates divergent; dorsal interior with extensions of brachiophore plates commonly convergent forward onto median ridge; anterior muscle scars usually larger than posterior pair; fulcral plates present. *Lower Ordovician (Arenig)–Upper Devonian (Frasnian).*

Subfamily DRABOVIINAE
Havlíček, 1950

[Draboviinae HAVLÍČEK, 1950, p. 45; *emend.,* HARPER, herein]

Draboviids lacking well-developed dorsal median septum or partition. *Lower Ordovician (Arenig)–Upper Devonian (Frasnian).*

Drabovia HAVLÍČEK, 1950, p. 45 [**Orthis redux* BARRANDE, 1848, pl. 18, fig. 7; OD] [=*Crassiorina* HAVLÍČEK, 1950, p. 36 (type, *Orthis notata crassior* BARRANDE, 1879)]. Subquadrate, biconvex, coarsely costellate valves with long straight ventral interarea; ventral interior with well-developed pedicle callist. *Upper Ordovician (Caradoc–Ashgill):* Europe, northern Africa.——FIG. 600,*4a–e.* **D. redux* (BARRANDE), Caradoc, Bohemia; *a,* internal mold of dorsal valve, ×1.8; *b,* internal mold of ventral valve, ×2.1; *c,* internal mold of ventral valve, ×1.8; *d,* rubber replica of dorsal exterior, ×2.5 (Havlíček, 1977a); *e,* internal molds of two dorsal valves, ×1.5 (Cocks, new).

Boticium HAVLÍČEK & MERGL, 1982, p. 43 [**B. boticense;* OD]. Similar to *Pionodema* but subcircular, small valves with short hinge line and short, deeply impressed subtriangular to bilobed muscle scar, confined laterally by long subparallel dental plates with adductor field impressed on callus; brachiophore plates subparallel and median ridge variably developed. *Upper Ordovician (Ashgill):* Bohemia.——FIG. 600,*3a–d.* **B. boticense,* Ashgill, Bohemia; *a,b,* normal, tilted views of internal mold of ventral valve, ×3.6; *c,* internal mold of dorsal interior, ×3.6; *d,* external mold of ventral valve, ×4 (Havlíček & Mergl, 1982).

Dalmanellopsis KHALFIN, 1948, p. 208 [**D. septiger;* OD]. Similar to *Salopina,* transversely semioval valves with short curved ventral interarea, parallel to divergent rodlike brachiophores and ventral median ridge; but with dorsal median septum extending forward from muscle scar to near anterior commissure. *Lower Devonian:* Altai Mountains.——FIG. 600,*1a,b.* **D. septiger,* Lower Devonian, Altai Mountains; internal mold, rubber replica of dorsal valve, ×3 (Boucot, Gauri, & Johnson, 1966).

Destombesium HAVLÍČEK, 1971a, p. 58 [**D. pectiniferum;* OD]. Transversely semioval, dorsibiconvex valves similar to *Pionodema* with large bilobed ventral diductor scar and lobate cardinal process, but commonly with several pairs of small, parallel plates arising from floor of apical part of notothyrial cavity. *Upper Ordovician (Caradoc–Ashgill):* northern Africa.——FIG. 601,*2a–d.* **D. pectiniferum,* Caradoc, Morocco; *a,* internal molds of two ventral valves (top left and top right), one external mold of dorsal valve (bottom left) and internal mold of dorsal valve (bottom right), ×1.5; *b,* internal mold of dorsal valve, ×3; *c,* posterior view of internal mold of dorsal valve, ×1.5; *d,* posterior views of internal mold of two dorsal valves, ×1.5 (Havlíček, 1971a).

Diorthelasma COOPER, 1956, p. 997 [**D. parvum;* OD]. Transversely semioval, small, sharply unisulcate valves lacking aditicules; ventral interarea long, straight; ventral interarea with wide, cordate muscle scar and median ridge; dorsal interior with convergent brachiophore plates and petaloid muscle scar; cardinal process with uncrenulated myophore. *Upper Ordovician (Caradoc):* USA, Scotland.——FIG. 601,*3a–e.* **D. parvum,* Caradoc, Alabama; *a,b,* ventral, dorsal views of conjoined valves, ×4; *c,d,* normal, tilted views of dorsal interior, ×4; *e,* ventral interior, ×4 (Cooper, 1956).

Drabovinella HAVLÍČEK, 1950, p. 50 [**Orthis draboviensis* BARRANDE, 1879, pl. 61, case V; OD]. Transversely semioval, large, biconvex, rectimarginate, coarsely costellate valves; ventral interarea long, straight; ventral interior with subtriangular to bilobed, narrow muscle scar; dorsal interior with petaloid muscle scar and cardinal process with uncrenulated myophore and parallel brachiophore plates. *Upper Ordovician (Caradoc):* Bohemia, northern Africa.——FIG. 602,*1a–f.* **D. draboviensis* (BARRANDE), Caradoc, Bohemia; *a,b,* dorsal, posterior views of conjoined internal molds, ×2.2; *c,* ventral view of conjoined internal molds, ×1.8; *d,* internal mold of dorsal valve, ×1.7; *e,* internal mold of dorsal valve, ×2; *f,* partly exfoliated dorsal valve, ×1.3 (Havlíček, 1977a).

Eodiorthelasma XU & LIU, 1984, p. 188 [**Diorthelasma striata* XU in XU, RONG, & LIU, 1974, p. 148; OD]. Small, ventribiconvex, unisulcate, fascicostellate or multicostellate valves; ventral interior with small subtriangular muscle field with long diductor and short adductor scars and short dental plates; dorsal interior with small cardinal process, narrow posteriorly, expanded anteriorly where continuous with median ridge; muscle field petaloid with elongate adductor scars. *Lower Ordovician (Arenig):* southwestern China.——FIG. 600,*2a–d.* **E. striata* (XU), Arenig, southwestern China; *a,* internal mold of ventral valve, ×5; *b,* internal mold of dorsal valve, ×5; *c,* internal mold of dorsal valve, ×5; *d,* external mold of dorsal valve, ×5 (Xu & Liu, 1984).

Fascifera ULRICH & COOPER, 1942, p. 620 [**F. subcarinata;* OD]. Transversely semioval, biconvex, unisulcate, fascicostellate valves; ventral interarea short, curved; dorsal interarea orthocline; ventral interarea with well-developed dental fossettes; muscle scar extended and bisected by median ridge; dorsal interior with lobate cardinal process and brachiophore plates normally convergent onto median ridge. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* North America.——FIG. 603,*2a–g.* **F. subcarinata,* Caradoc, Tennessee; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×2; *f,* ventral interior, ×2; *g,* dorsal interior, ×2 (Cooper, 1956).——FIG. 603,*2h,i. F. stonensis* (SAFFORD), Caradoc, Tennessee; normal, tilted views of dorsal interior, ×2 (Cooper, 1956).

Hirnantia LAMONT, 1935, p. 313 [**Orthis sagittifera* M'COY, 1851, p. 398; OD] [=*Villicundella* LEVY &

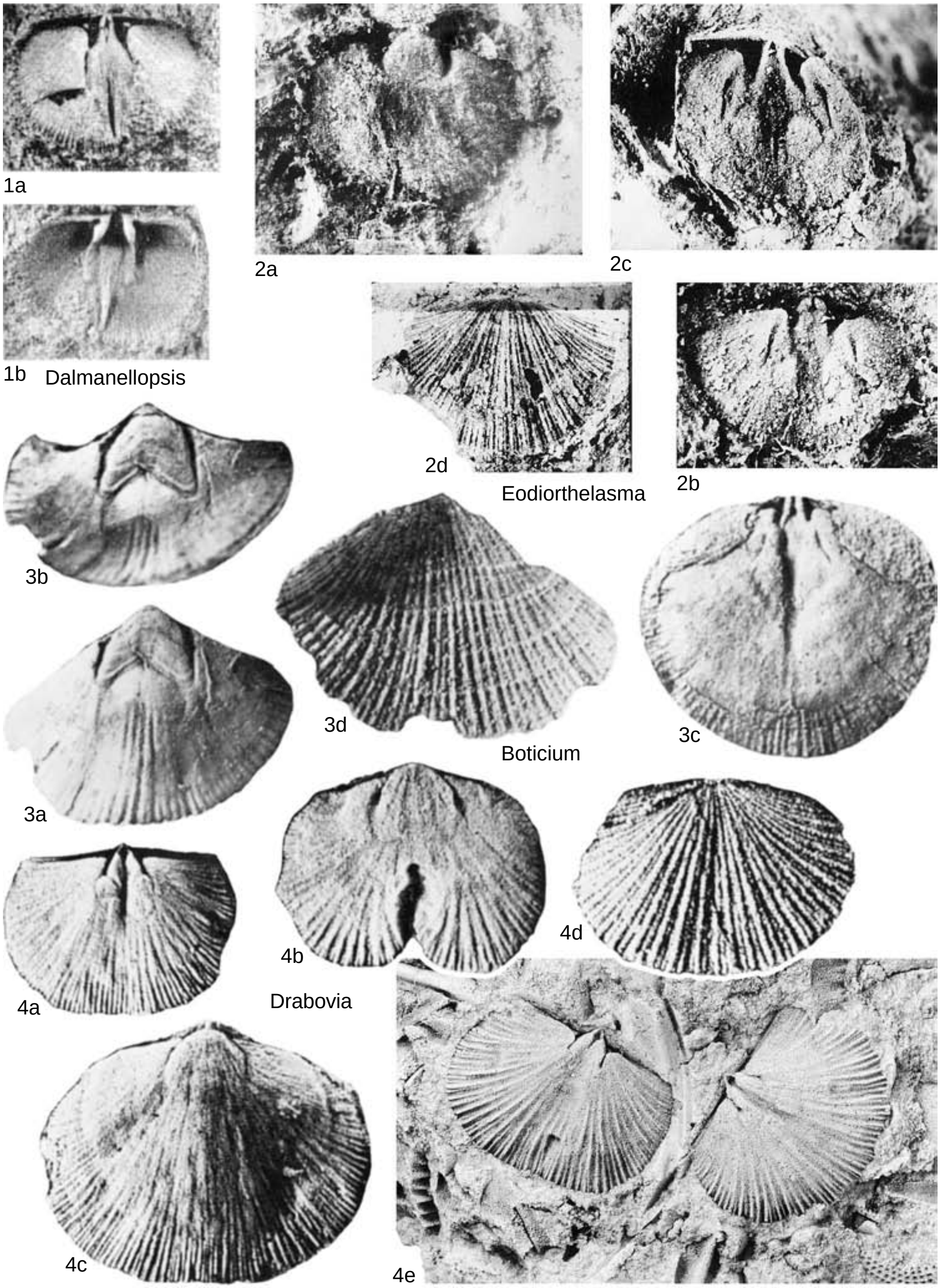

FIG. 600. Draboviidae (p. 826).

NULLO, 1974, p. 178]. Subcircular, dorsibiconvex, rectimarginate to weakly unisulcate valves with long straight ventral interarea; ventral interior with subtriangular to suboval muscle scar; dorsal interior with small myophore and long shaft. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):*

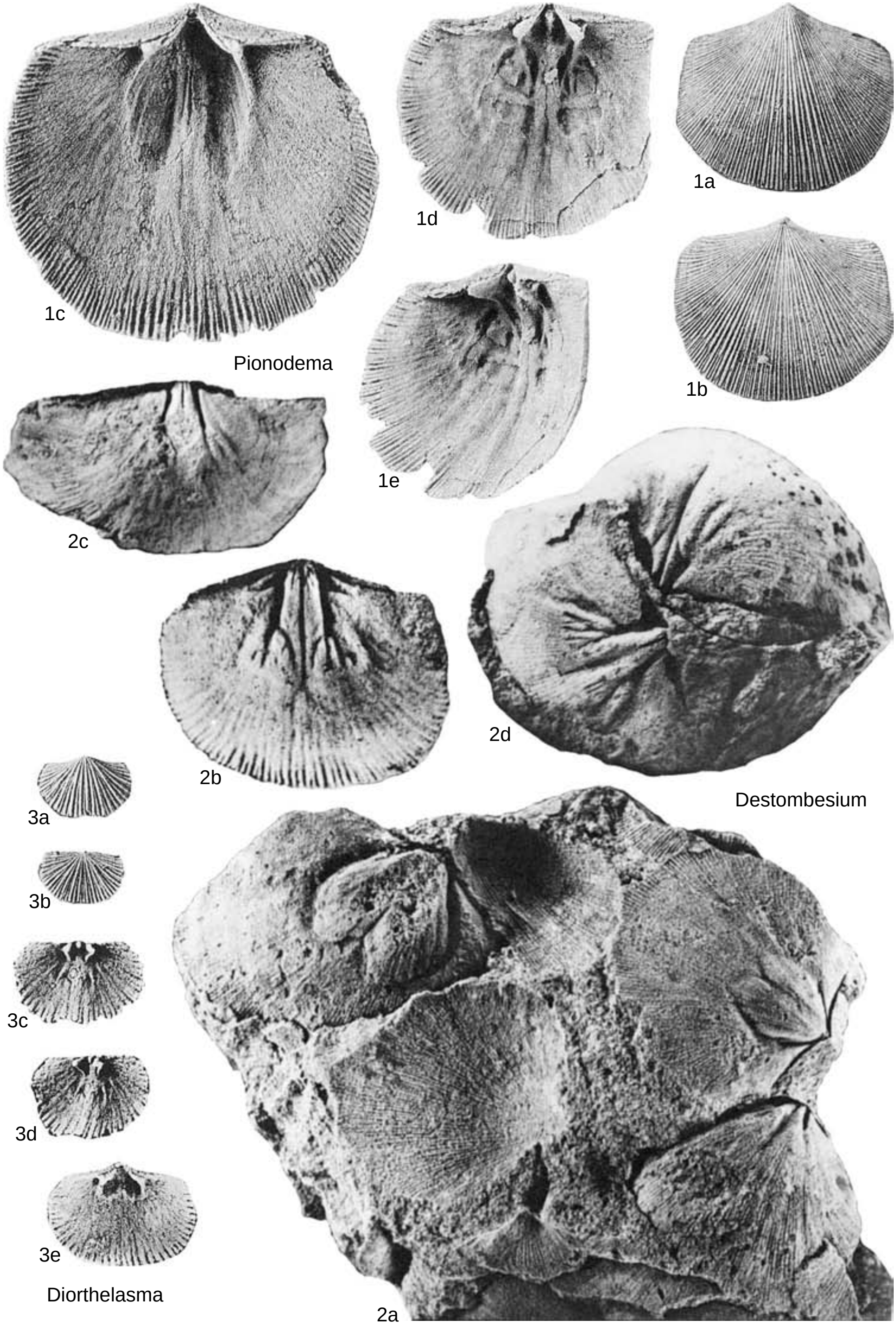

FIG. 601. Draboviidae (p. 826–831).

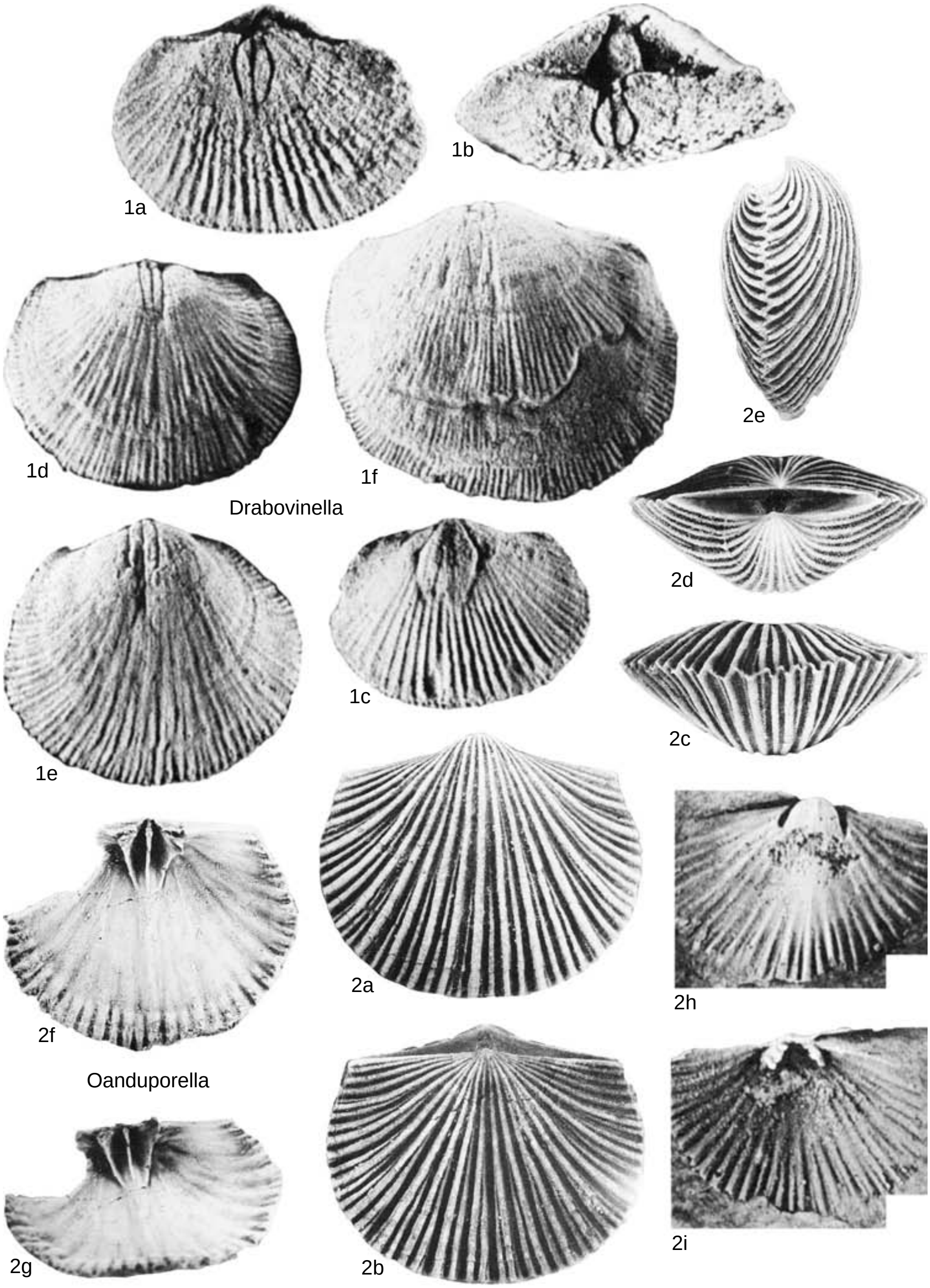

FIG. 602. Draboviidae (p. 826–831).

cosmopolitan.——FIG. 603,*1a–g*. **H. sagittifera* (M'COY), Ashgill; *a,b,* normal, posterior views of internal mold of dorsal valve, Scotland, ×2; *c,* rubber replica of dorsal exterior, Scotland, ×2 (Harper, 1989); *d,* internal mold of ventral valve, Bohemia, ×1.5; *e,* internal mold of dorsal valve, Bohemia,

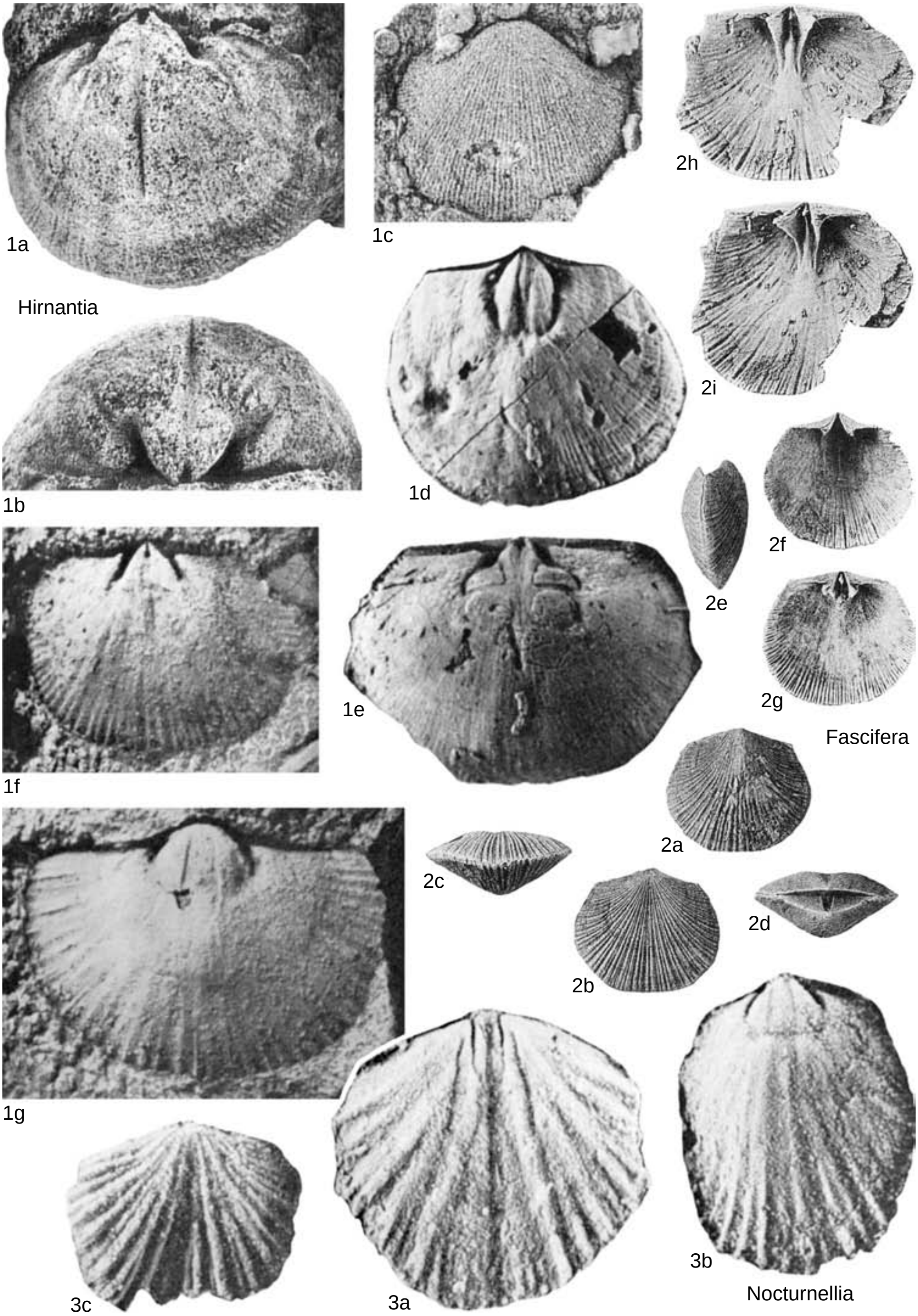

FIG. 603. Draboviidae (p. 826–831).

×1.7 (Havlíček, 1977a); *f,* internal mold of dorsal valve, Poland, ×3.3; *g,* internal mold of ventral valve, Poland, ×6.6 (Temple, 1965).

Kinnella BERGSTRÖM, 1968, p. 11 [**Hirnantia? kielanae* TEMPLE, 1965, p. 401; OD]. Subcircular, small, dorsibiconvex, rectimarginate valves; ventral interarea subpyramidal, apsacline to procline; ventral interior with suboval muscle scar; dorsal interior with bilobed, crenulated cardinal process. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* cosmopolitan.——FIG. 604,*1a–f.* **K. kielanae* (TEMPLE), Ashgill, Poland; *a,* internal mold of ventral valve, ×6.6; *b,* internal mold of dorsal valve, ×6.6; *c–e,* normal, lateral, posterior views of rubber replica of ventral exterior, ×6.6 (Temple, 1965); *f,* rubber replica of dorsal interior with attached ventral exterior, Sweden, ×1 (Bergström, 1968).

Megasalopina BOUCOT, GAURI, & JOHNSON, 1966, p. 166 [**Dalmanella (Mystrophora) elevata* WILLIAMS & BREGER, 1916, p. 62; OD]. Subcircular, large valves with well-developed ventral median ridge and swollen cardinal process. *Lower Devonian (Lochkovian):* USA.——FIG. 604,*2a–e.* **M. elevata* (WILLIAMS & BREGER), Lochkovian, Maine; *a,b,* internal mold, rubber replica of dorsal valve, ×1.5; *c,d,* internal mold, rubber replica of ventral valve, ×1.5; *e,* rubber replica of dorsal exterior, ×1.5 (Boucot, Gauri, & Johnson, 1966).

Nocturnellia HAVLÍČEK, 1950, p. 53 [**Orthis nocturna* BARRANDE, 1879, pl. 152, case IV]. Subcircular, small, unisulcate, fascicostellate valves, lacking aditicules; ventral interarea short, straight; dorsal interior with petaloid muscle scar contained by subparallel ridges; cardinal process ridgelike, uncrenulated. *Lower Ordovician (Arenig):* Bohemia.——FIG. 603,*3a–c.* **N. nocturna* (BARRANDE), Arenig, Bohemia; *a,* internal mold of dorsal valve, ×8.3; *b,* internal mold of ventral valve, ×7.7; *c,* rubber replica of dorsal exterior, ×8.7 (Havlíček, 1977a).

Oanduporella HINTS, 1975, p. 19 [**O. reticulata;* OD]. Subquadrate, rectimarginate valves with honeycomb-like array of pits; ventral interarea short, straight; ventral interior with cordate muscle scar; dorsal interior with small, crenulated myophore and long shaft; adductor scar petaloid and elongate. *Upper Ordovician (Caradoc):* eastern Baltic, Ireland.——FIG. 602,*2a–i.* **O. reticulata,* Caradoc; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, eastern Baltic, ×5; *f,g,* normal, tilted views of dorsal interior, eastern Baltic, ×5.5 (Hints, 1975); *h,i,* internal mold, rubber replica of ventral interior, eastern Ireland, ×5 (Harper & others, 1985).

Orthiella LJASCHENKO, 1985, p. 11 [**O. devoniana;* OD]. Transversely oval, biconvex, uniplicate, small, coarsely costellate valves. *Upper Devonian (Frasnian):* Siberia (Timan).——FIG. 604,*3a–c.* **O. devoniana,* Frasnian, Timan; *a,b,* exterior, interior of ventral valve, ×5; *c,* exterior of dorsal valve, ×5 (Ljaschenko, 1985).

Pionodema FOERSTE, 1912, p. 139, *nom. nov. pro Bathycoelia* FOERSTE, 1909b, p. 221, *non* AMYOT & SERVILLE, 1843 [**Orthis subaequata* CONRAD, 1843, p. 333; OD]. Transversely semioval, dorsibiconvex valves with short, curved ventral interarea and orthocline dorsal interarea; ventral interior with extended muscle scar bisected by median ridge; dorsal interior with small, lobate cardinal process and thin shaft on low notothyrial platform; brachiophore plates converge anteriorly onto median ridge. *Upper Ordovician (Caradoc–Ashgill):* North America, Europe.——FIG. 601,*1a–e.* **P. subaequata* (CONRAD), Caradoc, Missouri; *a,b,* ventral, dorsal views of conjoined valves, ×2; *c,* ventral interior, ×2; *d,e,* normal, tilted views of dorsal interior, ×2 (Cooper, 1956).

Protomendacella HAVLÍČEK, 1970a, p. 31 [**P. eos;* OD]. Dorsibiconvex valves; ventral interior with extended muscle scar having narrow, linear adductor field and long, narrowly divergent dental plates; dorsal interior with bilobed myophore and strong shaft commonly extended forward as short septum; high brachiophores with short plates convergent onto valve floor extend anteriorly as ridges laterally confining posterior areas of adductor muscle scar. [In the absence of well-preserved exteriors, HAVLÍČEK (1970a) tentatively included *Protomendacella* within the Rhipidomellidae on the basis of internal similarities with *Mendacella.* But he also noted similarities with the draboviid *Hirnantia.* The ventral and dorsal muscle fields together with the cardinalia suggest placement within the Draboviidae.] *Upper Ordovician (Caradoc):* Morocco.——FIG. 605,*1a,b.* **P. eos,* Caradoc, Morocco; *a,* internal mold of ventral valve, ×2; *b,* internal mold of dorsal valve, ×2.1 (Havlíček, 1970a).

Salopina BOUCOT, 1960a, p. 3 [**Orthis lunata* J. DE C. SOWERBY, 1839, p. 611; OD] [=*Salopinella* YANG & RONG, 1982, p. 433 (type, *S. minuta*)]. Transversely semioval valves with short, curved ventral interarea; ventral interior with cordate muscle scar bisected by variably developed median ridge. *Upper Ordovician (Ashgill)–Middle Devonian (Eifelian):* cosmopolitan.——FIG. 605,*4a–f.* **S. lunata* (SOWERBY), Ludlow, England; *a,b,* internal mold, rubber replica of ventral valve, ×3; *c,d,* internal mold, rubber replica of dorsal valve, ×3; *e,f,* rubber replicas of dorsal, ventral exteriors of conjoined valves, ×2 (Walmsley, Boucot, & Harper, 1969).

Sphenophragmus IMBRIE, 1959, p. 365 [**S. nanus;* OD]. Subcircular, planoconvex valves with short, curved ventral and dorsal interareas; ventral interarea with cordate muscle scar and well-developed dental fossettes; dorsal interior with elongate sockets and lobate myophore. *Middle Devonian (Givetian):* North America.——FIG. 605,*3a–f.* **S. nanus,* Givetian, Michigan; *a–c,* ventral, dorsal,

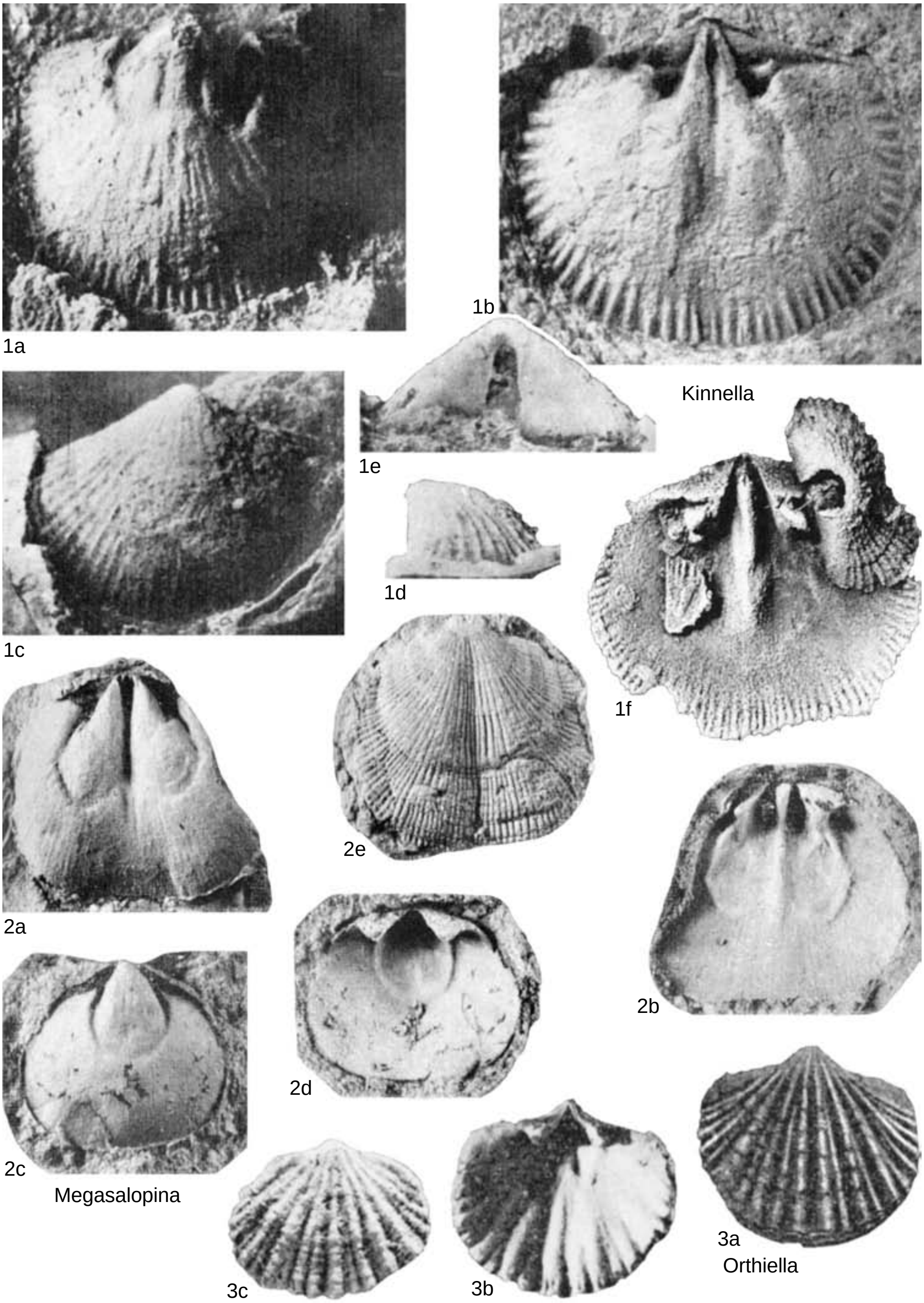

FIG. 604. Draboviidae (p. 831).

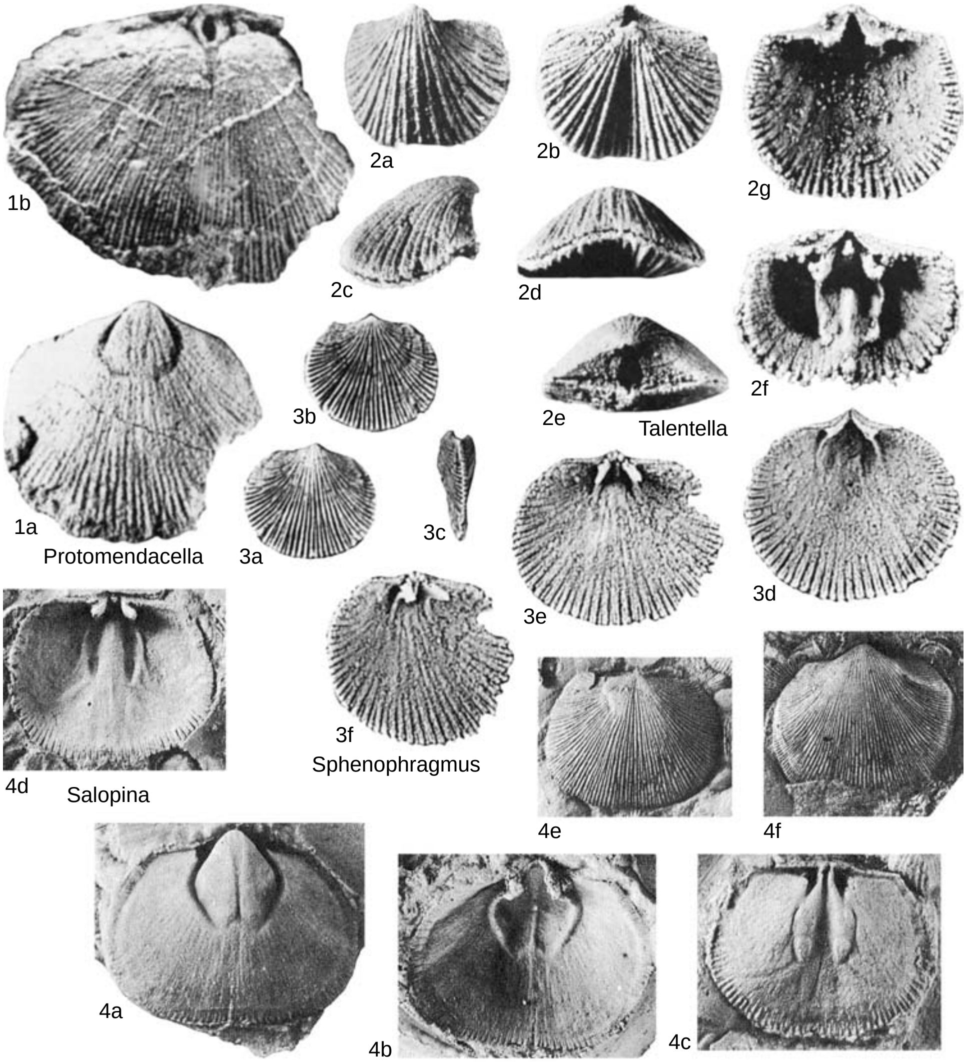

FIG. 605. Draboviidae (p. 831–833).

lateral views of conjoined pair, ×2; *d,* ventral interior, ×4; *e,f,* normal, oblique views of dorsal interior, ×4 (Imbrie, 1959).

Talentella JOHNSON, 1990, p. 489 [**Salopina submurifer* JOHNSON, BOUCOT, & MURPHY, 1973, p. 26; OD]. Small valves similar to *Salopina* but with short undivided ventral muscle scar and narrow elongate dorsal diductor scars bisected by long median ridge. *upper Silurian (Přídolí)–Lower Devonian (Pragian):* USA (Maine, Nevada), Arctic and northwestern Canada, eastern Australia, Podolia.——FIG. 605,*2a–g.* **T. submurifer* (JOHNSON, BOUCOT, & MURPHY), Lochkovian, Nevada; *a–e,* ventral, dorsal, lateral, anterior, posterior views of conjoined valves, ×5; *f,* dorsal interior, ×7; *g,* ventral interior, ×5 (Johnson, Boucot, & Murphy, 1973).

Subfamily MONELASMINIINAE new subfamily

[Monelasminiinae HARPER, herein]

Small draboviids with well-developed dorsal median septum or partition. *Lower*

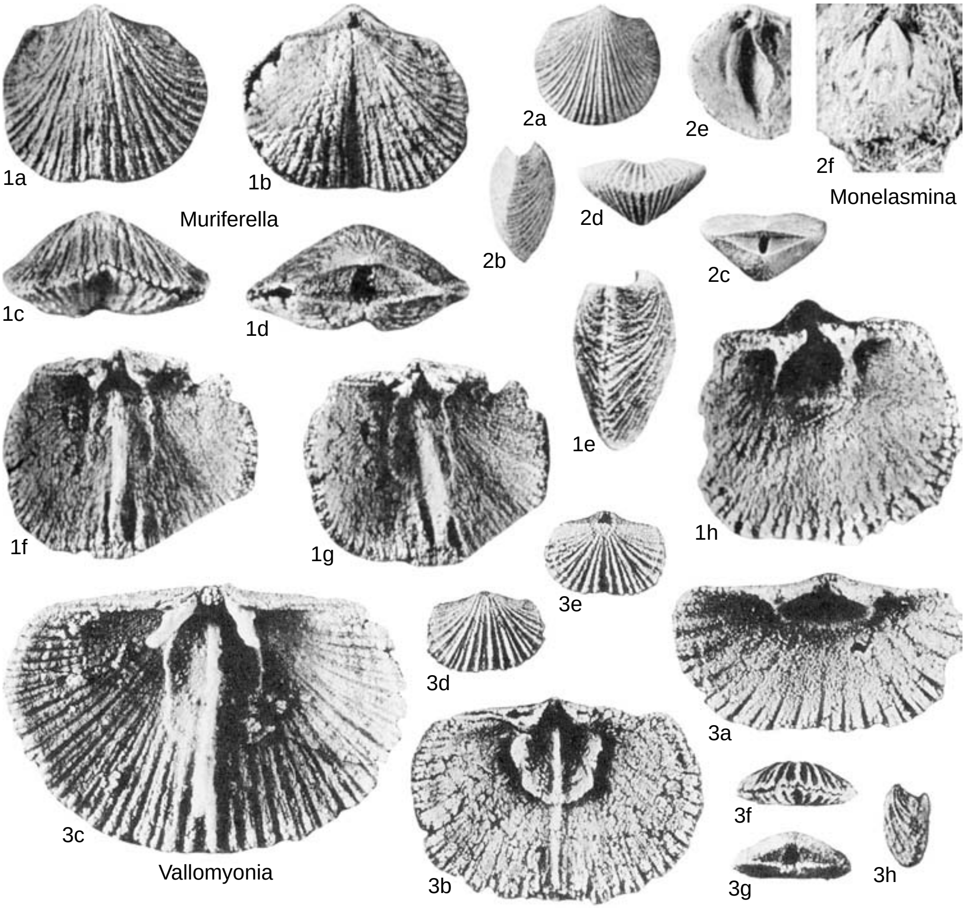

FIG. 606. Draboviidae (p. 834).

Devonian (Pragian)–Upper Devonian (Frasnian).

Monelasmina COOPER, 1955, p. 53 [**Orthis deshayesi* RIGAUX, 1873, p. 50; OD]. Subcircular, small, sharply unisulcate valves with long straight ventral interarea; ventral interior with well-developed dental fossettes and recessive dental plates; dorsal interior with bilobed cardinal process, deep sockets and median partition. *Upper Devonian (Frasnian):* Canada, Europe.——FIG. 606,*2a–f*. **M. deshayesi* (RIGAUX), Frasnian, France; *a–d,* ventral, lateral, posterior, anterior views of conjoined pair, ×3; *e,* oblique view of dorsal interior, ×4; *f,* internal mold of ventral valve, ×3 (Cooper, 1955).

Muriferella JOHNSON & TALENT, 1967b, p. 44 [**M. masurskyi;* OD]. Transversely semioval, small valves, similar to *Salopina;* ventral interarea short, straight; dorsal interior with well-developed median septum and uncrenulated cardinal process. *Lower Devonian (Pragian–Emsian):* USA (Nevada), Australia (Victoria), Bohemia.——FIG. 606,*1a–h*. **M. masurskyi,* Emsian, Nevada; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined pair, ×4; *f,g,* normal, oblique views of dorsal interior, ×6; *h,* ventral interior, ×7 (Johnson & Talent, 1967b).

Vallomyonia JOHNSON, 1966a, p. 158 [**Skenidium devonicum* WALCOTT, 1884, p. 116; OD]. Similar to *Muriferella* but with smaller dental plates, dorsal partition, and strong ridges confining dorsal adductor muscle field. *Middle Devonian (Eifelian–Givetian):* USA (Nevada).——FIG. 606,*3a–h*. **V. devonicum* (WALCOTT), Eifelian, Nevada; *a,* ventral interior, ×6; *b,* dorsal interior, ×4; *c,* interior of dorsal valve, ×8; *d–h,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×5 (Johnson, 1966a).

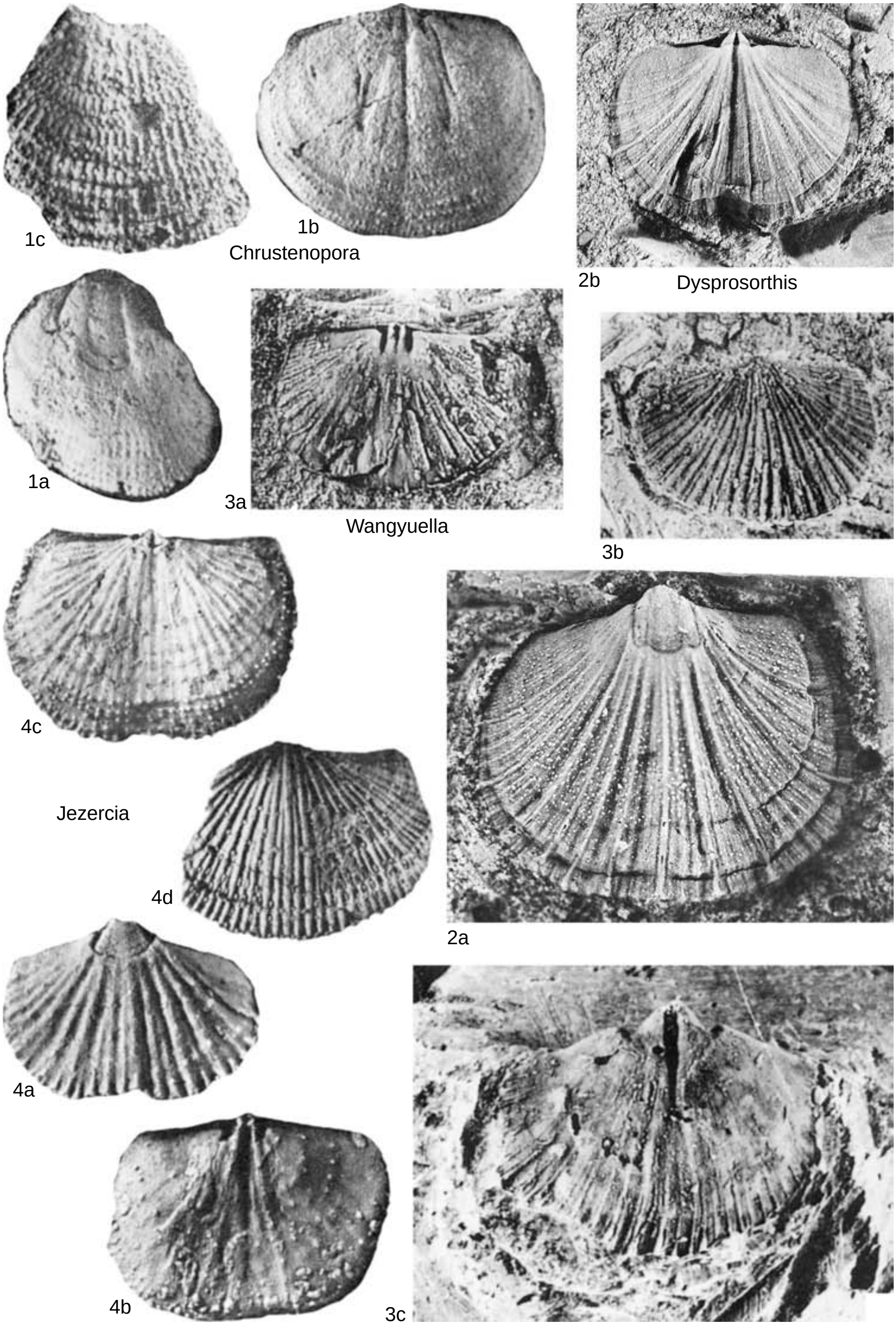

FIG. 607. Chrustenoporidae (p. 836).

Family CHRUSTENOPORIDAE Havlíček & Mergl, 1982

[*nom. transl.* BAARLI, 1988, p. 1124, *ex* Chrustenoporinae HAVLÍČEK & MERGL, 1982, p. 39]

Normally unequally biconvex, rectimarginate, fascicostellate to multicostellate enteletoids commonly with aditicules; ventral and dorsal interareas both short and apsacline and anacline, respectively; ventral muscle scar suboval to subtriangular; dental plates divergent; dorsal interior with short cardinalia comprising crenulated cardinal process and widely divergent brachiophores having short, subparallel plates; anterior muscle scars usually larger than posterior pair and separated by oblique transverse ridges; fulcral plates commonly present. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery).*

Chrustenopora HAVLÍČEK, 1968, p. 123 [**C. imbricata;* OD]. Subcircular, biconvex valves with multicostellate and imbricate radial and concentric ornaments; ventral interior with median groove; dorsal muscle scar linear. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* Bohemia, southern Norway. ——FIG. 607,*1a–c.* **C. imbricata,* Caradoc, Bohemia; *a,* internal mold of ventral valve, ×3; *b,* internal mold of dorsal valve, ×2.1; *c,* external mold of dorsal valve, ×3.5 (Havlíček, 1977a).

Dysprosorthis RONG, 1984, p. 133 [**D. sinensis;* OD]. Small, biconvex, fascicostellate valves; ventral interarea short, curved; ventral interior with subtriangular to suboval muscle scar and rudimentary teeth and dental plates; dorsal interior with short cardinalia including small cardinal process and very widely divergent brachiophores; muscle scar petaloid. *Upper Ordovician (Ashgill):* England, Ireland, Morocco, China.——FIG. 607,*2a,b.* **D. sinensis,* Ashgill, southwestern China; *a,* internal mold of ventral valve, ×8; *b,* internal mold of dorsal valve, ×6 (Rong, new).

Jezercia HAVLÍČEK & MERGL, 1982, p. 40 [**J. ostiaria;* OD]. Transversely semioval, biconvex to dorsibiconvex valves with coarse, fascicostellate ornament; ventral interior with subtriangular muscle scar; dorsal interior with crenulated, ridgelike cardinal process continuous with median ridge; dorsal muscle scar petaloid. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* Bohemia, southern Norway, Podolia, Sardinia, Spain, Ukraine.——FIG. 607,*4a–d.* **J. ostiaria,* Ashgill, Bohemia; *a,* internal mold of ventral valve, ×6; *b,* internal mold of dorsal valve, ×5; *c,d,* internal, external molds of dorsal valve, ×4 (Havlíček & Mergl, 1982).

Wangyuella ZHAN & RONG, 1995, p. 551 [**W. ventribiconvexa;* OD]. Transverse, small valves with long, apsacline ventral interarea; ventral interior with short dental plates and small subtriangular muscle scar; dorsal interior with short cardinalia having bilobed, crenulated myophore and subparallel brachiophore plates. *Upper Ordovician (Ashgill):* eastern China.——FIG. 607,*3a–c.* **W. ventribiconvexa,* Ashgill, eastern China; *a,b,* internal, external molds of dorsal valve, ×8; *c,* internal mold of ventral valve, ×5 (Zhan & Rong, 1995).

Family LINOPORELLIDAE Schuchert & Cooper, 1931

[Linoporellidae SCHUCHERT & COOPER, 1931, p. 247]

Normally subcircular, medium-sized, multicostellate enteletoids with variably developed aditicules; ventral interarea normally short, curved, and apsacline, dorsal interarea shorter, curved, and anacline; ventral interior with raised, variably cordate muscle scar and pedicle callist; dorsal interior with brachiophore plates convergent onto median ridge to form septalium; cardinal process usually simple; dorsal adductors with posterior scars larger than anterior pair; fulcral plates present; ventral mantle canal system probably saccate, dorsal lemniscate. *Lower Ordovician (Llanvirn)–Lower Devonian (Emsian).*

Linoporella SCHUCHERT & COOPER, 1931, p. 247 [**Orthis punctata* DE VERNEUIL, 1848a, p. 343; OD]. Biconvex, unisulcate valves with radial rows of intercostellate pits; ventral interior with projecting dental plates and median ridge bisecting elongate muscle scar; cardinalia with swollen myophore and shaft, adductor scar elongately oval. *lower Silurian (Llandovery)–upper Silurian (Ludlow):* Europe, eastern North America.——FIG. 608,*1a–g.* **L. punctata* (DE VERNEUIL), Wenlock, Gotland; *a,b,* dorsal, lateral views of conjoined valves, ×2 (Wright, 1965a); *c,d,* external, internal views of ventral valve, ×1.5; *e,* posterior part of dorsal interior showing cardinalia, ×2 (Schuchert & Cooper, 1932); *f,* normal view of dorsal valve of conjoined pair, ×2; *g,* enlarged view of dorsal valve of conjoined pair, ×5 (Amsden, 1974).

Cycladigera HAVLÍČEK, 1971b, p. 230 [**Orthis palliata* BARRANDE, 1848, pl. 19, fig. 6; OD]. Large, biconvex, rectimarginate valves lacking aditicules; ventral interior with long, divergent dental plates, confining large, oval diductor muscle scar bisected by median ridge; adductor scar long and narrow; dorsal interior with simple, ridgelike cardinal process, located in deep notothyrial cavity and continuous anteriorly with prominent median septum. *Lower Devonian (Pragian–Emsian):* Europe.——FIG. 608,*3a–e.* **C.*

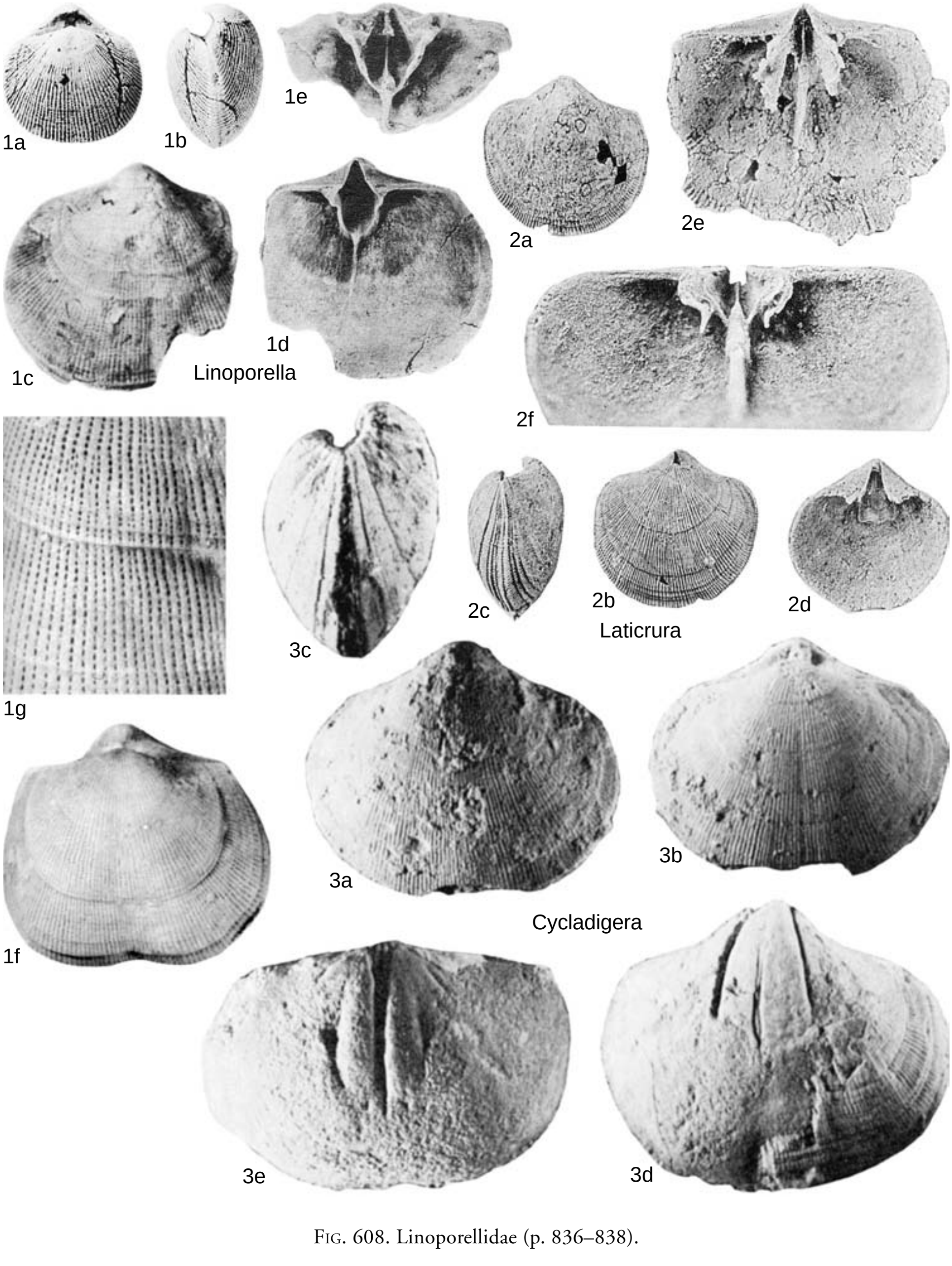

FIG. 608. Linoporellidae (p. 836–838).

palliata (BARRANDE), Pragian, Bohemia; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×1.5; *d,* internal mold of ventral valve, ×1.4; *e,* internal mold of dorsal valve, ×1.5 (Havlíček, 1977a).

Elasmothyris COOPER, 1956, p. 983 [**E. concinnula;* OD]. Small, transversely semioval valves with aditicules; profiles ventribiconvex and unisulcate; ventral muscle scar on raised plate adjacent to divergent dental plates; cardinalia with expanded myophore and shaft and widely divergent brachiophores. *Upper Ordovician (Caradoc):* eastern USA.——FIG. 609,*2a–f.* **E. concinnula,* Caradoc,

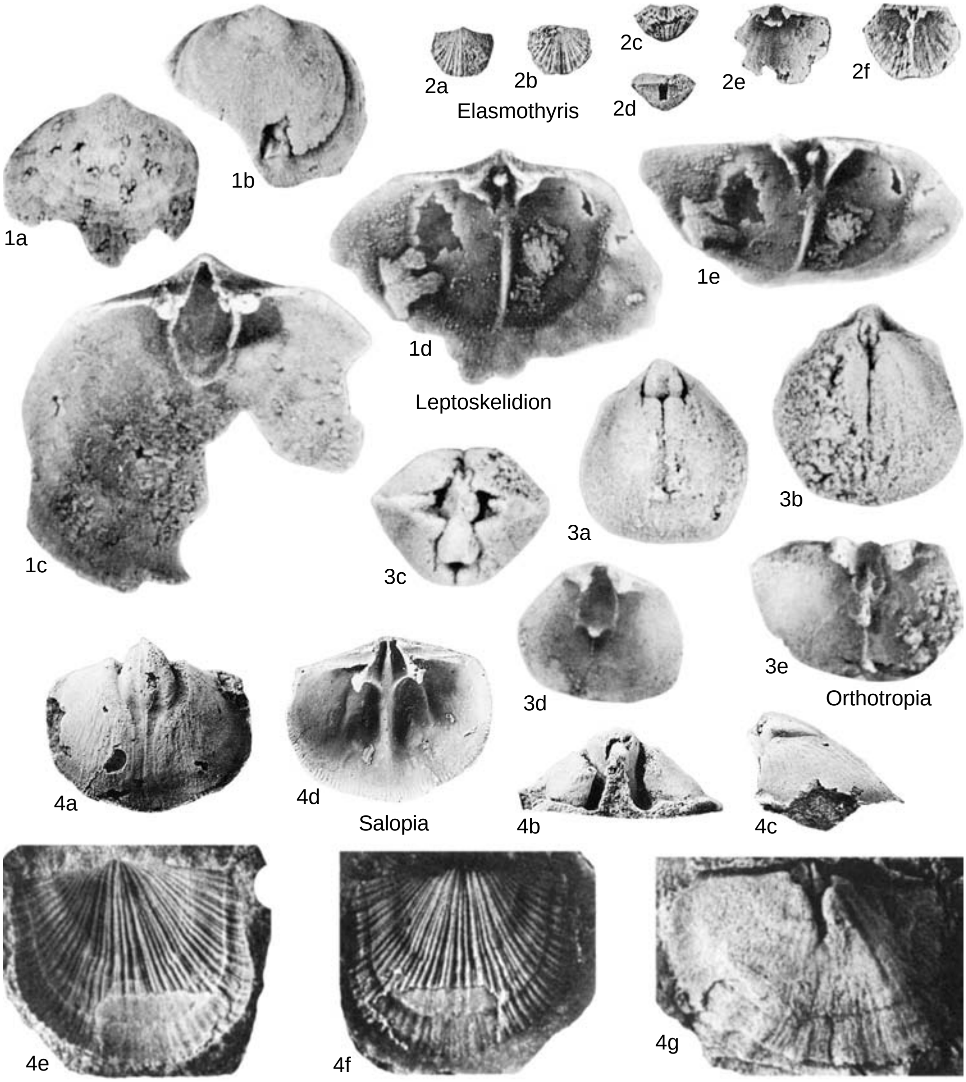

FIG. 609. Linoporellidae (p. 837–839).

Alabama; *a–d,* ventral, dorsal, anterior, posterior views of conjoined valves, ×5; *e,* ventral interior, ×8; *f,* dorsal interior, ×8 (Cooper, 1956).

Laticrura Cooper, 1956, p. 979 [**L. pionodema;* OD]. Ventribiconvex, rectimarginate valves with occasional aditicules; ventral interior with convergent dental plates; dorsal interior with simple, ridgelike cardinal process and large brachiophores, sigmoidal in section. *Upper Ordovician (Caradoc–Ashgill):* eastern North America, Scotland, Ireland.——Fig. 608,*2a–f.* **L. pionodema,* Caradoc, Virginia; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×2; *d,* ventral interior, ×2; *e,* dorsal interior, ×4; *f,* posterior part of dorsal interior showing cardinalia, ×6 (Cooper, 1956).

Leptoskelidion Amsden, 1974, p. 47 [**L. septulosum;* OD]. Biconvex, rectimarginate valves with aditicules; valve exterior imbricate, lacking well-defined radial ornament; ventral interior with convergent dental plates confining oval muscle field; cardinalia with swollen myophore and shaft. *Upper Ordovician (Ashgill):* eastern North America, Scandinavia, Russia.——Fig. 609,*1a–e.* **L. septulosum,* Ashgill, Missouri; *a,* ventral exterior, ×3; *b,* dorsal exterior, ×3; *c,* ventral interior, ×5; *d,e,* normal, tilted views of dorsal interior, ×5 (Amsden, 1974).

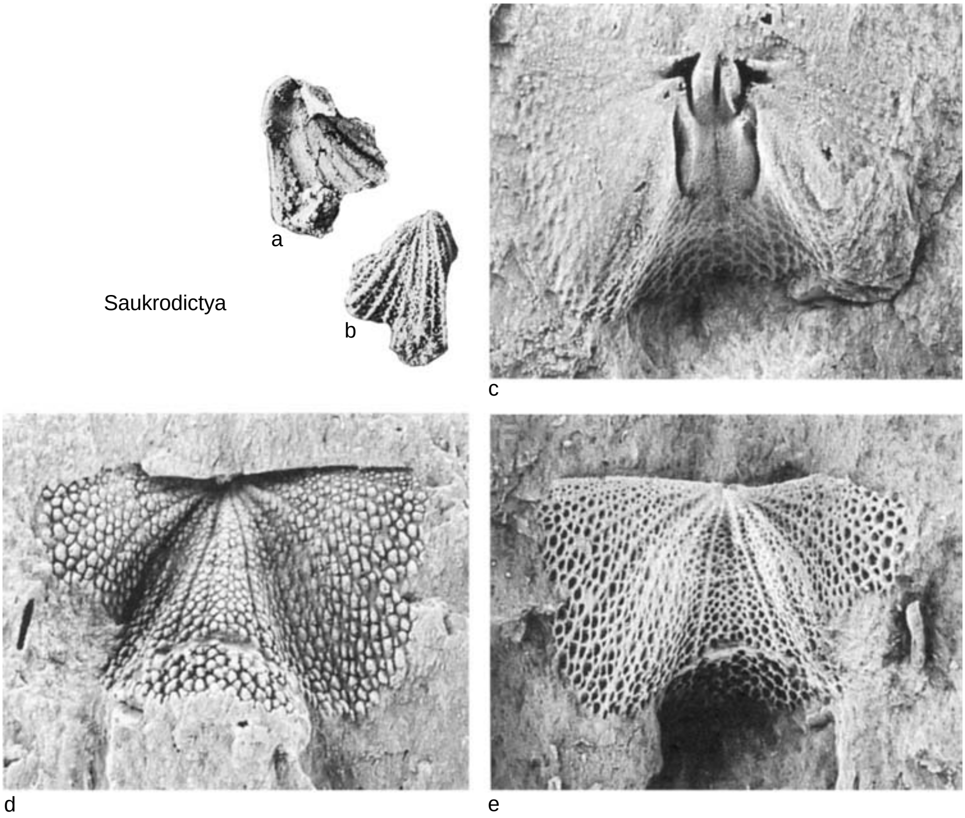

FIG. 610. Saukrodictyidae (p. 839–840).

Orthotropia HALL & CLARKE, 1894b, p. 943 [**O. dolomitica;* M]. Ventribiconvex, unisulcate valves; ventral interior with projecting dental plates and median ridge; cardinal process simple, ridgelike. *middle Silurian (Wenlock):* USA (Wisconsin).——FIG. 609,*3a–e.* **O. dolomitica,* Wenlock, Wisconsin; *a–c,* ventral, dorsal, posterior views of conjoined internal molds, ×2; *d,e,* rubber replicas of same ventral, dorsal interiors, ×2 (Amsden, 1974).

Salopia WILLIAMS in WHITTINGTON & WILLIAMS, 1955, p. 409 [**Orthis salteri* DAVIDSON, 1871, p. 255; OD]. Biconvex, rectimarginate valves with high, nearly catacline ventral interarea; ventral interior with convergent dental plates; cardinalia with simple, ridgelike cardinal process. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* Britain.——FIG. 609,*4a–d.* **S. salteri* (DAVIDSON), Caradoc, England; *a–c,* ventral, posterior, lateral views of internal mold of ventral valve, ×2; *d,* rubber replica of dorsal interior, ×2 (Wright, 1965a).——FIG. 609,*4e–g. S. abbreviata* HARPER & BRENCHLEY, Caradoc, northern Wales; *e,f,* external mold, rubber replica of ventral valve, ×2; *g,* internal mold of dorsal valve, ×2 (Harper & Brenchley, 1993).

Family SAUKRODICTYIDAE Wright, 1964

[Saukrodictyidae WRIGHT, 1964, p. 218; *emend.,* HARPER, herein]

Small, normally ventribiconvex and multicostellate enteletoids with honeycomb-like array of intercostal pits; long, curved ventral interarea; cardinalia with weak myophore and shaft and spikelike brachiophores; notothyrial floor extended forward as septalium; fulcral plates present. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery).*

Saukrodictya WRIGHT, 1964, p. 218 [**S. hibernica;* OD]. Transversely semioval, unisulcate valves with short septalium. *Upper Ordovician (Caradoc)–lower Silurian (Llandovery):* Britain, Ireland, Belgium, Baltic states, Bohemia, Sardinia, Spain, Siberia.——FIG. 610*a,b.* **S. hibernica,* Ashgill, Ireland; interior, exterior of broken ventral valve, ×5 (Wright,

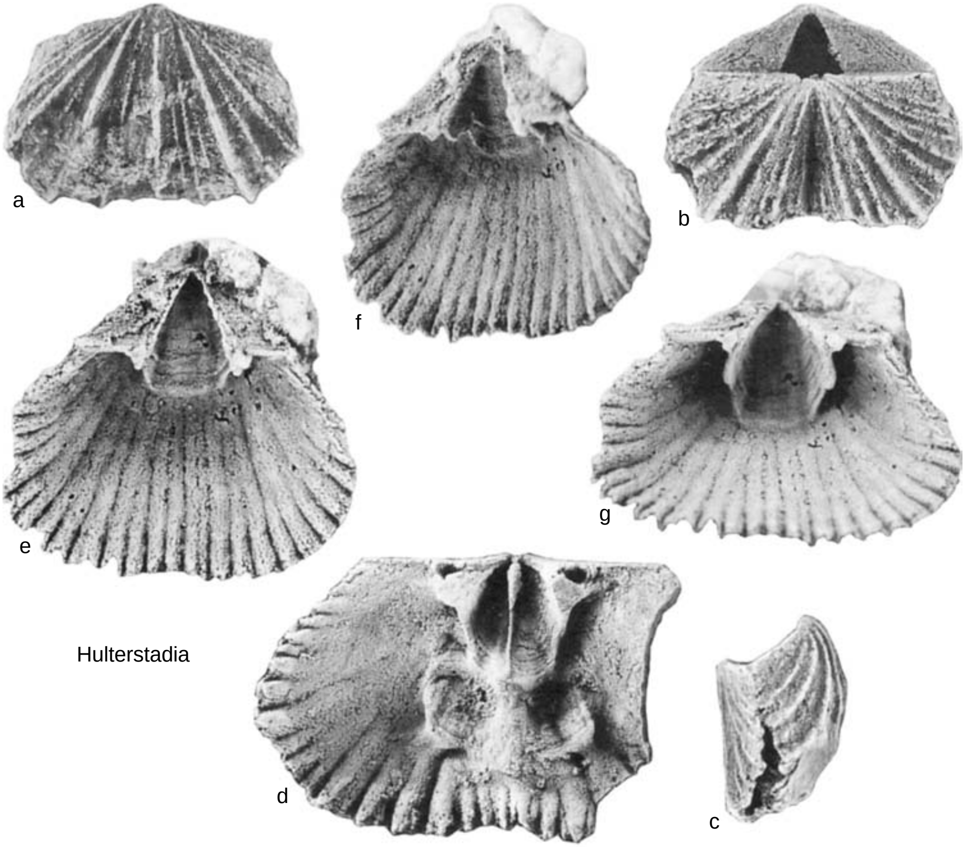

FIG. 611. Saukrodictyidae (p. 840).

1964).——FIG. 610*c–e*. *S. phillipi* (DAVIDSON), Ashgill, Wales; internal mold, external mold, rubber replica of dorsal valve, ×8 (Wright, 1993a).

Hulterstadia WRIGHT, 1993a, p. 73 [**Orthis cor* WIMAN, 1907, p. 9; OD]. Cordate, strangulate valves with long septalium. *Upper Ordovician (Ashgill):* Sweden.——FIG. 611*a–g*. **H. cor* (WIMAN), Ashgill, Sweden; *a–c,* ventral, dorsal, lateral views of conjoined valves, ×8; *d,* dorsal interior, ×8; *e–g,* normal and tilted views of ventral interior, ×8 (Wright, 1993a).

Family SCHIZOPHORIIDAE
Schuchert & LeVene, 1929

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 139, *ex* Schizophoriinae SCHUCHERT & LEVENE, 1929, p. 15]

Normally large, dorsibiconvex, multicostellate enteletoids; ventral interior with variably developed median septum, bisecting bilobed to cordate muscle scar; pedicle callist present; dorsal interior with petaloid adductor field confined posterolaterally by brachiophore plates. *middle Silurian (Wenlock)–Upper Permian (Tatarian).*

Schizophoria KING, 1850, p. 106 [**Conchyliolithus (Anomites) resupinatus* MARTIN, 1809, pl. 49, fig. 13–14; OD]. Normally transversely semioval, weakly uniplicate valves; ventral interior with strong teeth and dental plates extending forward as ridges laterally confining ventral muscle field; dorsal interior with prominent, crenulated cardinal process. *Lower Devonian (Lochkovian)–Lower Carboniferous (Viséan):* cosmopolitan.

S. (**Schizophoria**) KING, 1850, p. 106 [**Conchyliolithus (Anomites) resupinatus* MARTIN, 1809, pl. 49, fig. 13–14; OD]. Dorsibiconvex *Schizophoria* with divergent dental plates confining bilobed to widely cordate ventral muscle field; dorsal

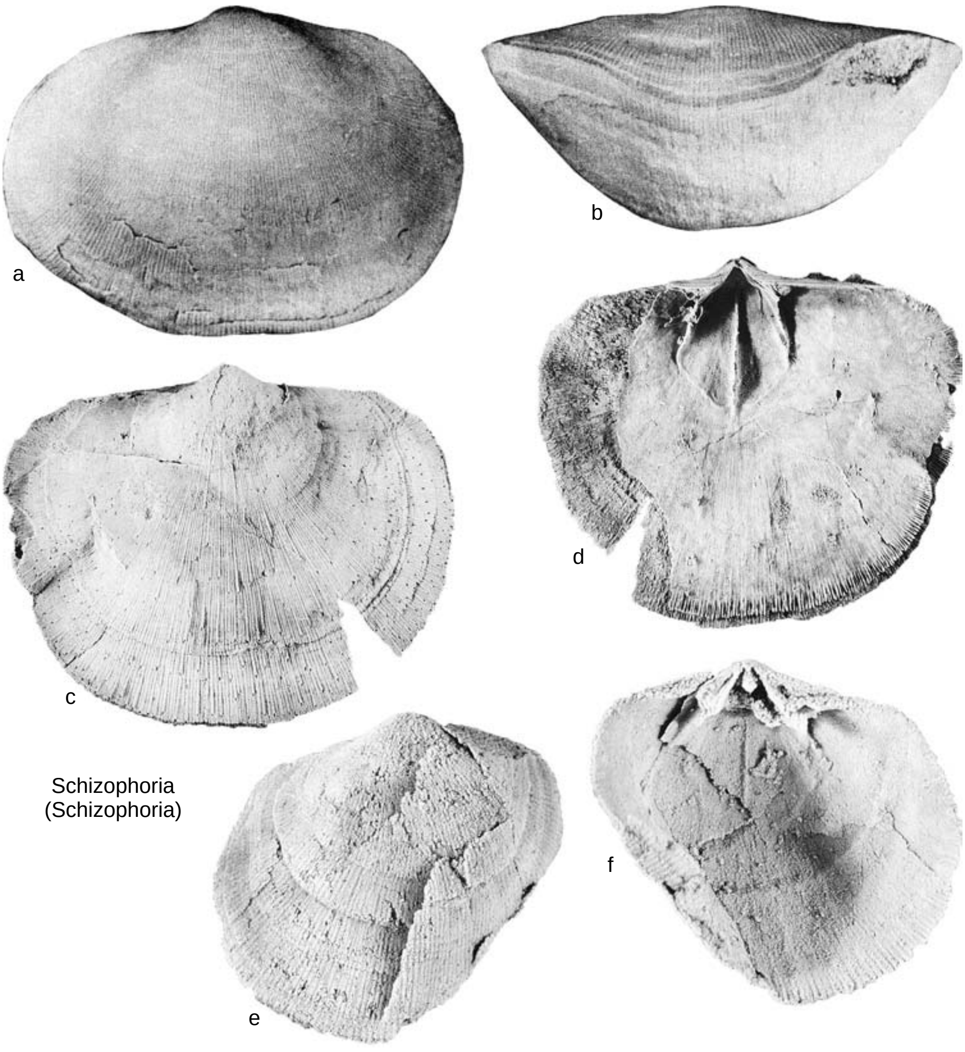

FIG. 612. Schizophoriidae (p. 840–841).

diductor scar petaloid and equidimensional. [LAZAREV (1976) established two subgenera for this widespread and common mid-Paleozoic genus; *Paraschizophoria* is based on the *S. woodi* BOND and *S. antiqua* SOLLE group and *Pocockia* on the *S. gibbera* (PORTLOCK), *S. linguata* (QUENSTEDT), and *S. annectans* POCOCK group, established by POCOCK (1968). As many of the diagnostic features of each subgenus are manifest in the main *Schizophoria* lineage, their use is restricted.] *Lower Devonian (Lochkovian)–Lower Carboniferous (Viséan):* cosmopolitan.——FIG. 612*a,b.* **S. (S.) resupinata* (MARTIN), Viséan, Isle of Man; dorsal, anterior views of conjoined valves, ×1.5 (Pocock, 1968).——FIG. 612*c–f. S. (S.) resupinata lata* DEMANET, Viséan, western Ireland; *c,d,* exterior, interior of ventral valve, ×0.85; *e,f,* exterior, interior of dorsal valve, ×2 (Jeffrey, new).

S. (Paraschizophoria) LAZAREV, 1976, p. 110 [**Schizophoria woodi;* OD]. Similar to *S. (Schizophoria)* but imbricate with narrow ventral and dorsal muscle fields. *Lower Devonian (Lochkovian)–Lower Carboniferous (Viséan):*

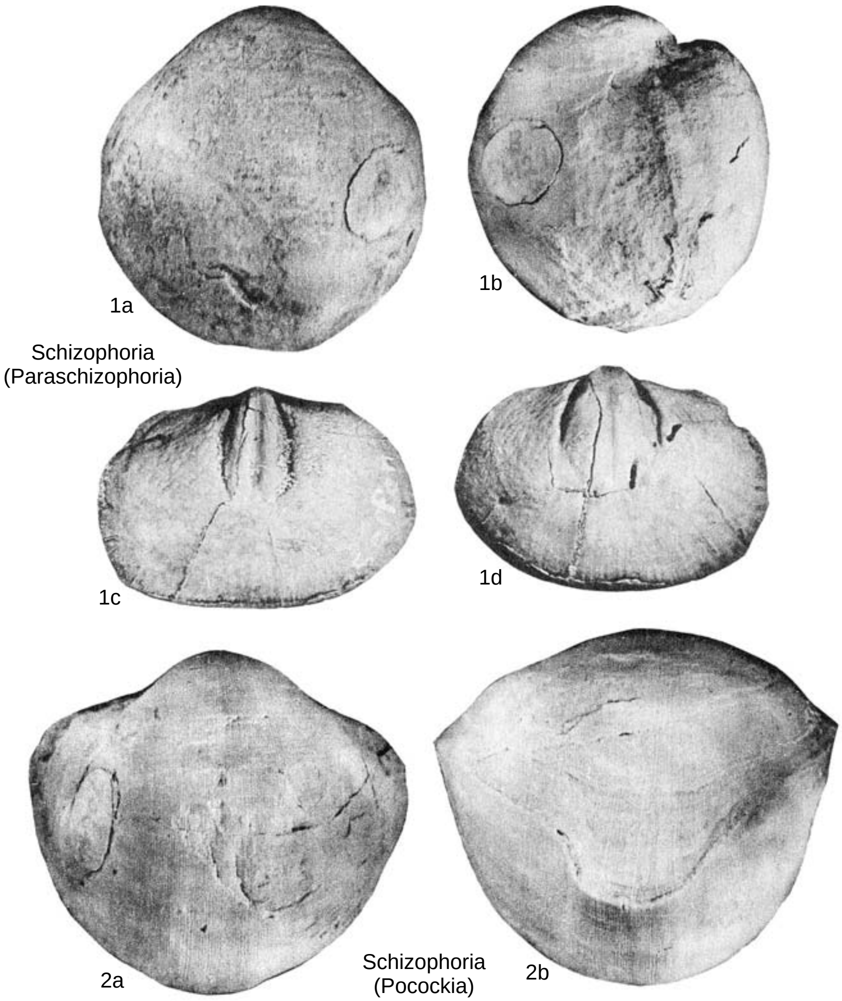

FIG. 613. Schizophoriidae (p. 841–842).

Europe.——FIG. 613,*1a,b.* **S (P.) woodi,* Viséan, Isle of Man; dorsal, lateral views of conjoined pair, ×1.5 (Pocock, 1968).——FIG. 613,*1c,d. S (P.) antiqua* SOLLE, Emsian, Germany; ventral, dorsal views of conjoined internal molds, ×1.5 (Pocock, 1966).

S. (**Pocockia**) LAZAREV, 1976, p. 112 [**Atrypa (Porambonites) gibbera* PORTLOCK, 1843, p. 460; OD]. Similar to *S. (Schizophoria)* but with geniculate ventral valve and narrow, linear ventral muscle field confined by parallel dental plates; dorsal diductor scar elongate. *Lower Carboniferous (Tournaisian–Viséan):* Europe.——FIG. 613,*2a,b. *S. (Pocockia) gibbera* (PORTLOCK), Viséan, northern Ireland; dorsal, anterior views of conjoined valves, ×1.5 (Pocock, 1968).

Acosarina COOPER & GRANT, 1969, p. 2 [**A. dorsisulcata;* OD]. Transversely semioval, medium-sized, biconvex valves; ventral interior with small teeth, large fossettes, and short dental plates; dorsal interior with widely divergent brachiophore plates and deep sockets. *Upper Carboniferous–Upper Permian:* USA (Texas, New Mexico), China, Thailand, Venezuela.——FIG. 614,*1a–i. *A. dorsisulcata,* middle Permian, Texas; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×1; *f,* ventral interior, ×2; *g,h,* normal, tilted views of dorsal interior, ×2; *i,* dorsal interior, ×2 (Cooper & Grant, 1976).

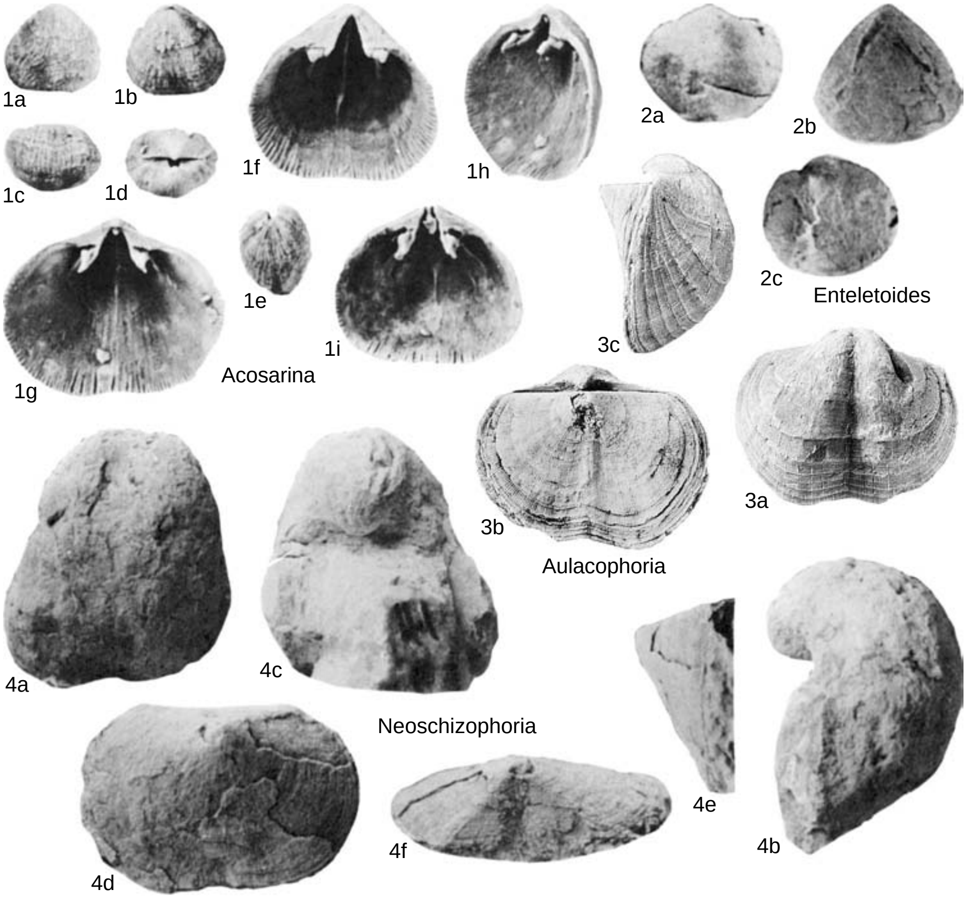

FIG. 614. Schizophoriidae (p. 842–843).

Aulacophoria Schuchert & Cooper, 1931, p. 247 [**Orthis keyserlingia* de Koninck, 1843, p. 230; OD]. Similar to *Schizophoria* but planoconvex, sharply unisulcate with commonly flat, catacline ventral interarea. *Lower Carboniferous–Upper Carboniferous:* Europe, Urals.——Fig. 614,*3a–c*. **A. keyserlingia* (de Koninck), lower Carboniferous, England; ventral, dorsal, lateral views of conjoined valves, ×1 (Wright, 1965a).

Enteletoides Stuckenberg, 1905, p. 59 [**E. rossicus;* OD]. Similar to *Schizophoria* but small with extravagantly developed dental plates and ventral median septum. *Carboniferous:* Russia, central Asia, China. ——Fig. 614,*2a–c*. *E. shuichengensis,* Upper Carboniferous, southern China; dorsal, ventral, lateral views of conjoined valves, ×1 (Ching & Liao, 1974).

Eoschizophoria Rong & Yang, 1980, p. 286 [**Schizophoria hesta* Rong & Yang in Rong, Xu, & Yang, 1974, p. 202; OD]. Small, biconvex valves; ventral interior with long, thin median ridge bisecting muscle scar; dorsal interior with delicate cardinalia, brachiophores narrowly divergent. *upper Silurian (Ludlow)–Lower Devonian (Pragian):* China, Canada, central Asia, Podolia, USA.——Fig. 615,*1a–c*. **E. hesta* (Rong & Yang), Ludlow, southern China; ventral, dorsal, lateral views of conjoined pair, ×1 (Rong, new).

Neoschizophoria Yanagida, 1983, p. 103 [**N. otai;* OD]. Similar to *Schizophoria* but unisulcate with flat, procline ventral interarea and modified cardinal process. *Lower Carboniferous (Viséan)–Upper Carboniferous (Namurian):* southwestern Japan.——Fig. 614,*4a–f*. **N. otai,* Viséan–Namurian, southwestern Japan; *a–c,* dorsal, lateral, ventral views of dorsal exterior, ×1; *d–f,* ventral, lateral, posterior views of ventral exterior, ×2 (Yanagida, 1983).

Orthotichia Hall & Clarke, 1892, p. 213 [**Orthis? morganiana* Derby, 1874, p. 29; OD]

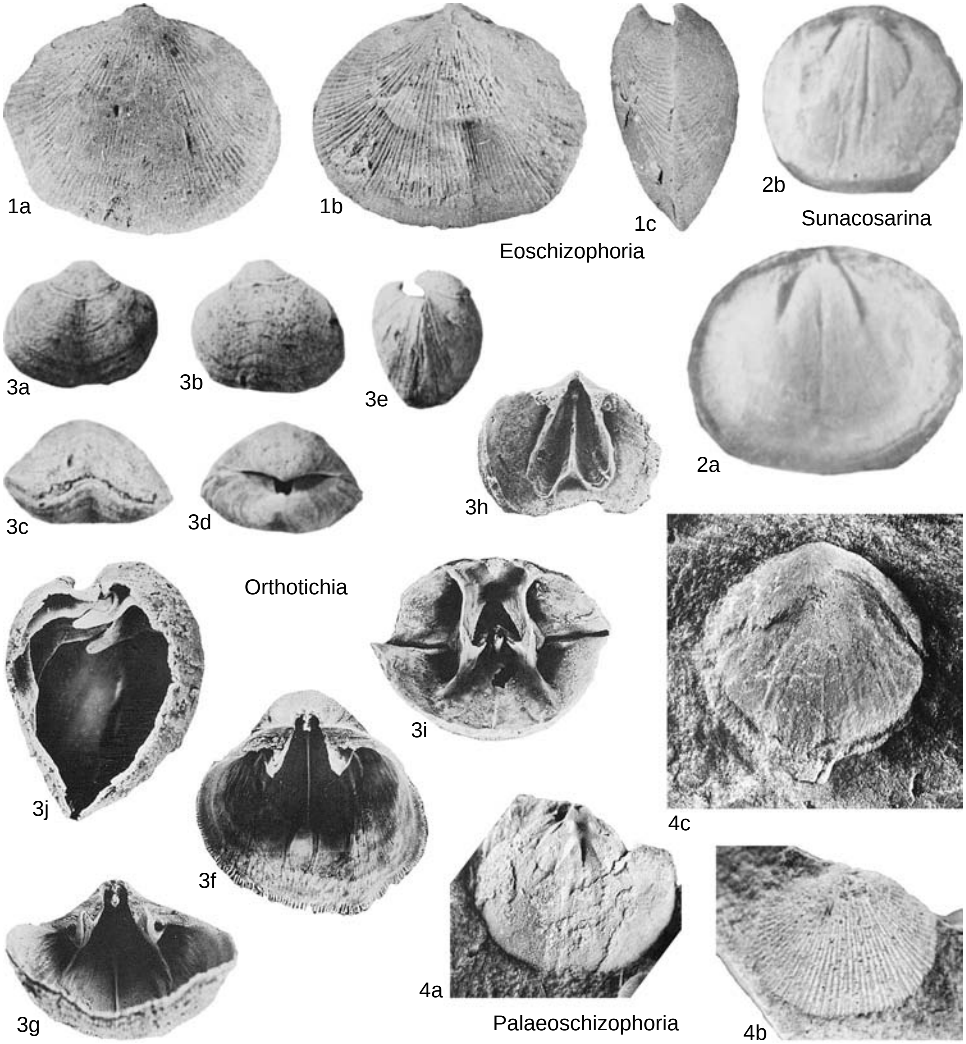

FIG. 615. Schizophoriidae (p. 843–844).

[=*Orthotichina* CHERNYSCHEV, 1914, pl. VII, fig. 1]. Similar to *Schizophoria* but more finely costellate with strong dental plates extending forward, as high ridges, to in front of muscle field together with well-developed ventral median septum. *Upper Carboniferous (Namurian)–Upper Permian (Tatarian):* widespread.——FIG. 615,*3a–j. O. kozlowskii* KING, middle Permian, Texas; *a–e,* ventral, dorsal, anterior, posterior, lateral views of conjoined valves, ×1; *f,g,* normal, tilted views of dorsal interior, ×2; *h,* ventral interior, ×2; *i,* posterior view of conjoined valves, ×2; *j,* lateral view of conjoined valves, ×2 (Cooper & Grant, 1976).

Palaeoschizophoria FU, 1982, p. 108 [**P. latisepta;* OD]. Transversely semioval, weakly uniplicate valves; ventral interior with short dental plates; dorsal interior with short, ridgelike cardinal process and short brachiophore plates. *middle Silurian (Wenlock):* northwestern China, western USA (California).——FIG. 615,*4a–c.* **P. latisepta,* Wenlock, northwestern China; *a,* internal mold of dorsal interior, ×1; *b,* latex replica of ventral exterior, ×1; *c,* partly exfoliated ventral valve, ×1 (Rong, new).

Sunacosarina LIANG, 1990, p. 355 [**S. campana;* OD]. Circular, small, convexiplane valves; ventral interior with short, widely divergent dental plates and short high median ridge extending forward to front of muscle field; dorsal interior with delicate, ridgelike cardinal process. *Lower Permian:* China.——FIG. 615,*2a,b.* **S. campana,* Lower Permian, China; *a,* internal mold of dorsal valve, ×2; *b,* internal mold of ventral valve, ×2 (Liang, 1990).

UNCERTAIN

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Suborder UNCERTAIN

Apatoskenidioides LIU, ZHU, & XUE, 1985, p. 22 [**A. rara;* OD]. Small, subquadrate with subrectangular cardinal extremities, ventribiconvex, costellate, sharply unisulcate; thin dental plates; cardinal process ridgelike, brachiophore bases convergent. [The specimens on which this genus was founded and which have no skenidiid affinities are too generalized in their morphology to permit more than their tentative identification as plectorthoids. They could be young shells.] *Lower Ordovician (Llanvirn):* northeastern China.

Bajanorthis ANDREEVA, 1968, p. 73 [**B. tukolandica;* OD]. Small, biconvex, subcircular, fascicostellate, capillate, and filate shells with subtriangular ventral muscle scar and small teeth supported by recessive dental plates; dorsal interior unknown. [It is presently not possible to check the validity of this poorly known genus except to concur that it is an orthoid, probably an orthid or eoorthid.] *Upper Cambrian:* Siberia.——FIG. 616,*1a–c. B. tukolandica,* Upper Cambrian, northwestern Siberia; ventral, dorsal, lateral views of conjoined valves, ×2 (Andreeva, 1968).

Humaella ZHU, 1982, p. 53 [**H. huangbanjiensis;* OD]. Small, subcircular with acute cardinal extremities, biconvex, unisulcate, multicostellate; apsacline ventral and anacline dorsal interareas moderately long; teeth undescribed, dental plates recessive, ventral muscle scar short, subovoid with pedicle callist; cardinal process wide, undifferentiated, brachiophores divergent, dorsal median septum long, high; posterior pair of quadripartite dorsal adductor scars larger than anterior pair. [The description of this genus is too generalized to permit a more precise identification of the specimens than orthoid. The mold of an apparently high dorsal septum, however, suggests some affinity with such stocks as the cremnorthids, although *Humaella* is older than other genera assigned to the family. The genus is also listed by L. R. M. COCKS and RONG Jia-yu, herein, as a junior synonym of *?Akelina* SEVERGINA, 1967. This ambiguity should be resolved when the shell structure of one or preferably both genera is known.] *Lower Ordovician:* China (Da Hingan Ling).——FIG. 616,*2a,b.* **H. huangbanjiensis,* Tremadoc, Da Hingang Ling; *a,* internal mold of ventral valve, ×4; *b,* internal mold of dorsal valve, ×4 (Zhu, 1982).

Lebediorthis SEVERGINA, 1984, p. 46 [**L. rarus;* OD]. *Lebediorthis,* erected for specimens from the *Lower Ordovician* of Siberia (Gorno Altai), was assigned by its author to the Cremnorthidae notwithstanding the absence of a differentiated cardinal process and a high dorsal median septum, which are diagnostic of that family. In fact, these small shells could be either ranorthids or nanorthids dependent on their cardinalia, which are inadequately described and illustrated. *Lower Ordovician (Arenig):* Gorno Altai.——FIG. 616,*4a,b.* **L. rarus,* Arenig, Gorno Altai; *a,* internal mold of ventral valve, ×4; *b,* internal mold of dorsal valve, ×4 (Severgina, 1984).

Malinella ANDREEVA, 1982, p. 55 [**M. tavelensis;* OD]. Biconvex, subquadrate, multicostellate shells with pseudodeltidium; ventral muscle scar narrowly triangular, teeth (undescribed) supported by dental plates; cardinal process simple, brachiophores massive; dorsal adductor scars quadripartite with anterior pair slightly elongate; mantle canal system in both valves saccate, with subparallel *vascula media.* [The species on which this genus was founded is too generally described and too poorly illustrated to warrant a more precise identification than orthoid. ANDREEVA (1982, p. 55) compared the internal features with those of *Ranorthis,* which, however, is characterized by divergent *vascula media* in the ventral valve. There is also the possibility that the ventral valve with the pseudodeltidium does not belong with the other figured specimens.] *Upper Ordovician (Caradoc):* Siberia (Tuva).——FIG. 616,*5a–d.* **M. tavelensis,* Caradoc, Tuva; *a,* internal mold of ventral valve, ×3; *b,* internal mold of dorsal valve, ×3; *c,* ventral exterior, ×3; *d,* view of ventral interarea, ×4 (Andreeva, 1982).

Nugnecella LEVY & NULLO, 1975, p. 28 [**N. rafaelensis;* OD]. Small, subequally biconvex, subquadrate ramicostellate; pseudodeltidium reported; teeth small, subtriangular, supported by divergent dental plates, ventral muscle field subtriangular; cardinal process ridgelike, brachiophores strongly divergent, sockets elongate with two(?) radiating ridges. [*Nugnecella* was identified by its authors as a billingselloid presumably on the basis of a reported pseudodeltidium. Other described (and illustrated) features, however, are more typically orthoid; and there is a possibility that the type specimens include representatives of more than one stock.] *Upper Ordovician (Ashgill):* Argentina.

Ottadalenites HARPER in BRUTON & HARPER, 1981, p. 165 [**O. incertus;* OD]. Large, transversely semioval with acute cardinal extremities, convexiplane, rectimarginate; anacline dorsal interarea short, planar, notothyrium with small chilidium; notothyrial platform shallow with ridgelike cardinal process and short, widely divergent brachiophores; dorsal musculature, mantle canal system, ventral interior unknown. [Despite the obscurity of much of its interior, this unusual genus is more likely to be an orthoid than a plectambonitoid, although it has some similarities to the orthoidlike taffiids. The size and profile of the specimens may be diagnostic of an early plectorthid or plaesiomyid notwithstanding the chilidium; ventral interiors are required to confirm this.] *Lower Ordovician (Arenig–Llanvirn):* Norway.——FIG. 616,*6a–d.* **O. incertus,* Arenig–

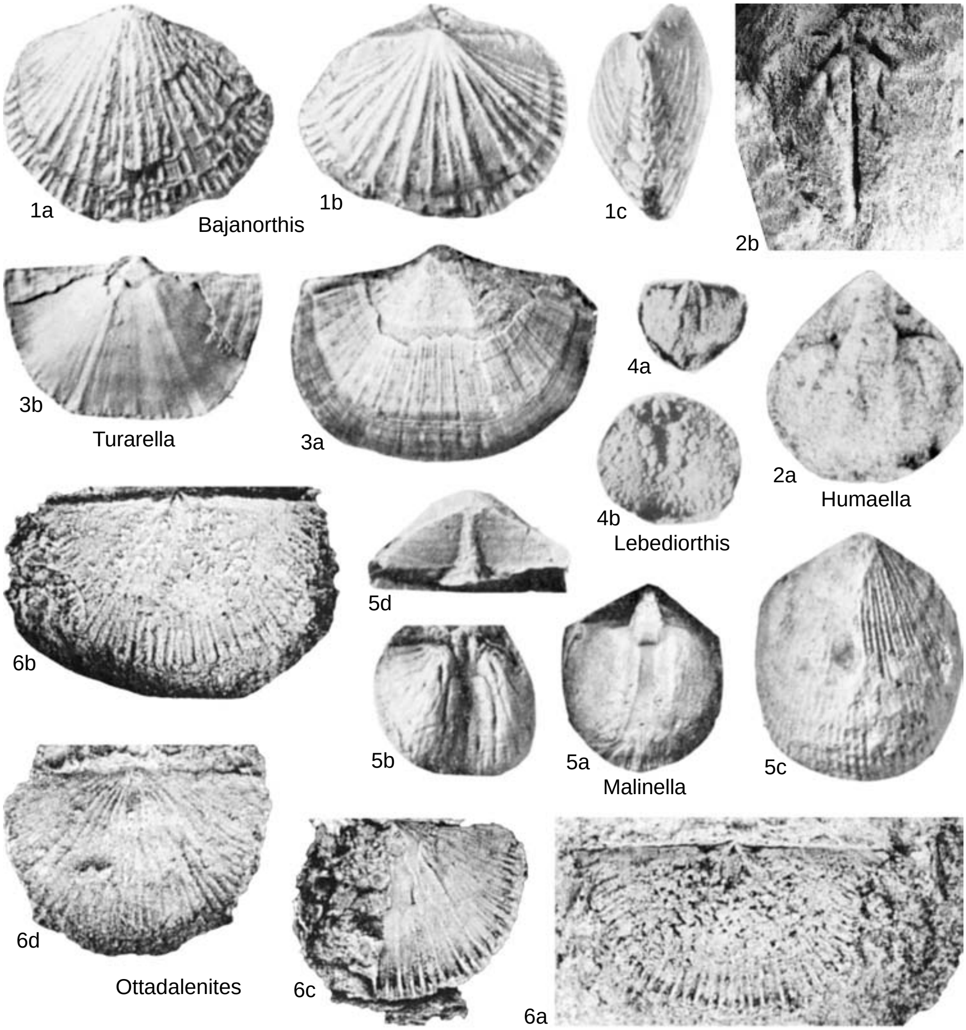

FIG. 616. Uncertain (p. 845–846).

Llanvirn, south central Norway; *a,b,* internal mold, rubber replica of dorsal valve, ×1; *c,* partly exfoliated ventral valve, ×1; *d,* rubber replica of dorsal exterior, ×1 (Bruton & Harper, 1981).

Turarella ANDREEVA, 1987, p. 34 [**T. alleri;* OD]. Transversely semioval, dorsibiconvex, multicostellate; ventral muscle field small, suboval with wide, undifferentiated adductor track longer than flanking diductor scars and divergent *vascula media;* dorsal interior unknown. [In the absence of any information on the dorsal interior including the articulatory apparatus, these specimens could be allocated to several orthoid families, having some similarity, for example, with such unrelated genera as *Bohemiella* and *Pleurorthis.* Indeed, the genus should be suppressed until dorsal interiors confirm that it is not a synonym of one of these or some other, better-described taxon.] *Upper Cambrian:* Siberia.——FIG. 616,*3a,b.* **T. alleri,* Upper Cambrian, Siberia; *a,* partly exfoliated ventral exterior, ×4; *b,* internal mold of ventral valve, ×4 (Andreeva, 1987).

Zhejiangorthis LIANG in LIU, XU, & LIANG, 1983, p. 268 [**Z. zhejiangensis;* OD]. Medium size, subcircular, planoconvex, coarsely costellate, ventral interarea nearly catacline, dorsal interarea orthocline; delthyrium and notothyrium open; teeth supported by dental plates, ventral adductor track not enclosed by longer, diductor scars; cardinal process differentiated into shaft and myophore, brachiophores subparallel. [The specimens on which this genus was founded may be dinorthid, but the diagnosis is presently too ambiguous to be useful, especially in the absence of internal details.] *Upper Ordovician:* China (Zhejiang Province).

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