Treatise on Invertebrate Paleontology

Part H

Brachiopoda

Revised

Volume 4:
Rhynchonelliformea (part)

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PART H, Revised

BRACHIOPODA

VOLUME 4:
Rhynchonelliformea (part)

ALWYN WILLIAMS, C. H. C. BRUNTON, S. J. CARLSON, FERNANDO ALVAREZ, R. B. BLODGETT, A. J. BOUCOT, PAUL COPPER, A. S. DAGYS, R. E. GRANT, JIN YU-GAN, D. I. MACKINNON, M. O. MANCEÑIDO, E. F. OWEN, RONG JIA-YU, N. M. SAVAGE, and SUN DONG-LI

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

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

Part C. Protista 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), Volumes 1 and 2, xxxi + 900 p., 653 fig., 1964.

Part D. Protista 3 (Protozoa: Chiefly Radiolaria, Tintinnina), xii + 195 p., 92 fig., 1954.

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EDITORIAL PREFACE

Roger L. Kaesler
[The University of Kansas]

From the outset the aim of the *Treatise on Invertebrate Paleontology* has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early *Treatise* volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new *Treatise* volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part H, Revised, Brachiopoda, Volume 4, has 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 this volume are discussed near the end of this editorial preface.

ZOOLOGICAL NAMES

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

The Commission, ever aware of the changing needs of systematists, revised the *Code* in 1999 to enhance further nomenclatorial stability, specifying that the revised *Code* should take effect at the start of 2000. Among other requirements, the revised *Code* is clear in Chapter 14 that the type genus of family-level taxa must be specified. In this volume we have continued the practice that has characterized most previous volumes of the *Treatise*, namely that the type genus of all family-level taxa is the first listed and diagnosed. In spite of the revisions, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the *Code* to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise,* especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a family-group. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are not regulated by the *Code.* It is both natural and convenient to discuss nomenclatorial matters in general terms first and then to consider each of these three, recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

FORMS OF NAMES

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

ORIGINAL SPELLINGS

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

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

Incorrect original spellings are any that fail to satisfy requirements of the *Code,* represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names. They call for correction. For example, a name originally published with a diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary purpose of zoological nomenclature as an information retrieval system. One looks forward with hope to further revisions of the *Code* wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

SUBSEQUENT SPELLINGS

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

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If "demonstrably intentional" (*Code,* Article 33), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable.

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

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

AVAILABLE AND UNAVAILABLE NAMES

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

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code,* Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code,* Article 13.1), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code,* Article 13.2). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

VALID AND INVALID NAMES

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

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

NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES

SPECIES-GROUP NAMES

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

GENUS-GROUP NAMES

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

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

FAMILY-GROUP NAMES

Family-Group Names: Authorship and Date

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

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

Family-Group Names: Use of *nomen translatum*

The *Code* (Article 29.2) specifies the suffixes for tribe (-ini), subfamily (-inae), family (-idea) and superfamily (-oidea), the formerly widely used ending (-acea) for superfamily having been disallowed. All these family-group categories are defined as coordinate (*Code*, Article 36.1): "A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at other ranks in the family group; all these taxa have the same type genus, and their names are formed from the stemof the name of the type genus (Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank." Such changes of rank and concomitant changes of endings as elevation of a subfamily to family rank or of a family to superfamily rank, if introduced subsequent to designation of the original taxon or based on the same nominotypical genus, are *nomina translata*. In the *Treatise* it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term *nomen translatum,* abbreviated to *nom. transl.* Similarly for clarity, authors should record the author, date, and page of the alteration, as in the following example.

Family HEXAGENITIDAE
Lameere, 1917

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

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

Superfamily AGNOSTOIDEA M'Coy, 1849

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

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

Family-Group Names: Use of *nomen correctum*

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

Family STREPTELASMATIDAE
Nicholson, 1889

[*nom. correct.* Wedekind, 1927, p. 7, *pro* Streptelasmidae Nicholson in Nicholson & Lydekker, 1889, p. 297]

Family PALAEOSCORPIDAE
Lehmann, 1944

[*nom. correct.* Petrunkevitch, 1955, p. 73, *pro* Palaeoscorpionidae Lehmann, 1944, p. 177]

Family-Group Names: Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for all family-group categories, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (*Code,* Article 39), in which case ". . . it must be replaced either by the next oldest available name from among its synonyms [Art. 23.3.5], including the names of its subordinate family-group taxa, or, if there is no such synonym, by a new name based on the valid name . . . of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the *Code,* however, specifies that for subsequent application of the rule of priority, the family-group name "... should be cited with its original author and date (see Recommendation 22A.2.2), followed by the date of its priority as determined by this Article; the date of priority should be enclosed in parentheses." Many family-group names that have been in use for a long time are *nomina nuda,* since they fail to satisfy criteria of availability (*Code,* Article 11.7). These demand replacement by valid names.

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

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

SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

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

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

The considerations just stated do not prevent the editors of the *Treatise* from making rules for dealing with suprafamilial groups of animals described and illustrated in this publication. Some uniformity is needed, especially for the guidance of *Treatise* authors. This policy should accord with recognized general practice among zoologists; but where general practice is indeterminate or nonexistent, our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa that, on taxonomic grounds, are changed from their originally assigned rank. Accordingly, a few rules expressing *Treatise* policy are given here, some with examples of their application.

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

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (*e.g.,* Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (*e.g.,* Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (*e.g.,* Yuania); none of these, however, can end in -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (*e.g.,* order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus *Chonetoidea* JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that, respectively, are named from the same type genus, since one is not considered to be transferable to the other (*e.g.,* suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontacea MCCOY, 1851 or family Bellerophontidae MCCOY, 1851).

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

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

Order CORYNEXOCHIDA
Kobayashi, 1935

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

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

Order DISPARIDA
Moore & Laudon, 1943

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

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

Order HYBOCRINIDA
Jaekel, 1918

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

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

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

Subclass ENDOCERATOIDEA Teichert, 1933

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

Order ENDOCERIDA Teichert, 1933

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

TAXONOMIC EMENDATION

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

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

Order ORTHIDA Schuchert & Cooper, 1932

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

Subfamily ROVEACRININAE Peck, 1943

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

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

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

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

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

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

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

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

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

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication except that diacritical marks have been removed. Where other mandatory changes are required, these are introduced later in the text, typically in the description of a figure.

Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code,* may be fixed in various ways in the original publication; or it may be fixed subsequently in ways specified by the *Code* (Article 68) and described in the next section. Type species fixed in the original publication include (1) *original designation* (in the *Treatise* indicated by OD) when the type species is explicitly stated or (before 1931) indicated by n. gen., n. sp. (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as M), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

Fixation of Type Species Subsequently

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

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

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

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

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

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

HOMONYMS

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

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

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

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

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

Synonymous Homonyms

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

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

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

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

SYNONYMS

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

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

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

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

OTHER EDITORIAL MATTERS

BIOGEOGRAPHY

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

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

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

NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

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

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

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

MATTERS SPECIFIC TO THIS VOLUME

Some languages, in this volume most notably the Polish and Czech languages, are enriched with the use of diacritical marks that provide enhanced alphabetical diversity. While celebrating diversity, we have nevertheless elected to omit such marks from Polish and Czech geographical terms used in the *Treatise*. We continue to insert diacritical marks in authors' names 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, consistency, and information retrieval.

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

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

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

ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Jill Hardesty, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task of moving this volume through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team including Jack Keim with photography and computer graphics, Mike Cormack with his outstanding computer skills, and Jean Burgess with general support. Jill Krebs, the remaining member of the Paleontological Institute editorial staff, is involved with preparation of PaleoBank, the paleontological database for future *Treatise* volumes, and has not been closely involved with 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
July 1, 2002

STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well established throughout the world, but minor divisions (*e.g.,* subseries, stages, and substages) are more likely to be provincial in application. The stratigraphical units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to the revision of Part H. They are adapted from the International Union of Geological Sciences 1989 Global Stratigraphic Chart, compiled by J. W. Cowie and M. G. Bassett. An updated time scale was published by the IUGS and UNESCO in 2000.

Cenozoic Erathem
- **Quaternary System**
  - Holocene Series
  - Pleistocene Series
- **Neogene System**
  - Pliocene Series
  - Miocene Series
- **Paleogene System**
  - Oligocene Series
  - Eocene Series
  - Paleocene Series

Mesozoic Erathem
- **Cretaceous System**
  - Upper Cretaceous Series
  - Lower Cretaceous Series
- **Jurassic System**
  - Upper Jurassic Series
  - Middle Jurassic Series
  - Lower Jurassic Series
- **Triassic System**
  - Upper Triassic Series
  - Middle Triassic Series
  - Lower Triassic Series

Paleozoic Erathem
- **Permian System**
  - Upper Permian Series
  - Lower Permian Series

Carboniferous System
- Upper Carboniferous Subsystem
  - Stephanian Series
  - Westphalian Series
  - Namurian Series (part)
- Lower Carboniferous Subsystem
  - Namurian Series (part)
  - Viséan Series
  - Tournaisian Series

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

Silurian System
  - 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]

The 1,170 or so genera described in volume 4 of *Treatise Part H (Revised, Brachiopoda)* belong to four rhynchonellate orders that make up the ancestral mainstream of all articulated brachiopods living today. Their relative modernity is reflected in two ways. First, although the orders as a whole span the Phanerozoic geological record, their peaks of generic diversity are post-Ordovician, unlike those of linguliforms, craniiforms, and primitive rhychonelliforms (except for the productides), described in volumes 2 and 3. The greatest generic diversities of the Pentamerida and Atrypida were attained during the Silurian (Wenlock) and Middle Devonian, respectively. The geological distribution of athyridide genera is bimodal with a peak in the Middle Devonian and a strong, subsidiary one in the Upper Triassic. The rhynchonellide distribution is polymodal with peaks in the Upper Devonian, Lower Carboniferous, and Upper Jurassic. The extent and separateness of these peaks, especially those of rhynchonellides, may be exaggerated by investigative practices referred to below.

The orders also share many basic morphological and anatomical characters that distinguish living rhychonelliforms. Devices precursory to the crural supports for the lophophore arose within the Pentamerida. The interlocking, cyrtomatodont teeth and sockets and the curved, astrophic hinge line are synapomorphies of the Rhynchonellida, Atrypida, and Athyridida; and, judging from the disposition of muscle scars relative to pedicle collars, the lobation and mantle reversal of living rhynchonelliform larvae were also ontogenetic features of extinct species of all three orders. Yet, despite well-documented geological records and demonstrably close affinities, infraordinal classifications have been difficult to erect and are more subjective in structure than originally anticipated. The resultant compromises are due mainly to the limitations of morphological data in characterizing suprageneric taxa. All four ordinal classifications, however, have also been affected to a varying degree by the way subtle changes in the microscopic features of the shell have been revealed and interpreted.

The complementary intergrowth of cyrtomatodont teeth and their sockets has always caused valves of later rhynchonelliforms to be interlocked and to remain so even after death and autolysis. Consequently, most samples, especially of fossil rhynchonellides and athyridides, include complete shells within which the cardinalia and calcified lophophore supports are commonly perfectly preserved. For most of the last century these features that play so important a role in rhynchonelliform systematics have been studied by preparing serial sections of shells. Unfortunately, much data obtained in this way can be misleading. It is seldom possible to prepare serial sections of shells of different species so that exposed surfaces being compared for taxonomic purposes bear the same relationship to, say, a constant medial vector of growth. Moreover, very few studies have taken into account microstructural evidence of the way features grew. Nothwithstanding these shortcomings, serial sections have been (and still are) used to erect genera based on micromorphological differences in internal skeletal pieces that have been viewed in two dimensions only.

The limitations of such practices were recognized nearly seventy years ago by ST. JOSEPH. In a series of pioneering reconstructions of spiriferides (1935a), pentamerides (1935b, 1941), and rhynchonellides (1937), ST. JOSEPH used camera lucida enlargements of serial sections to build scale models in wax of cardinalia and spiralia. Had this procedure been universally adopted, there would now be less concern about the validity of some genera and a much wider appreciation of how differences in internal features need reflect nothing more than variations in rates of shell secretion. Of course, computer programs are now available to generate digitized, three-dimensional models from sets of serial sections. It is hoped that this volume will inspire computerized reappraisals based on serial sections of those features that have been used for systematic purposes.

Preparing for the *Treatise* systematic descriptions of genera founded on serial sections inevitably raised a conflict of interests with no set battle line. On the one hand, it would have been editorially and scientifically unacceptable to publish copies of every section used to illustrate original generic diagnoses. Apart from excessively high publication costs and the scientific dubiety of some of the data, even specialist readers would have found the full array indigestible. On the other hand, there were options either to publish serial sections separately on compact disk or for *Treatise* authors to undertake a selective cull of up to thirty percent of serial-section sets figured in the original description of genera. All *Treatise* authors were consulted on which procedure should be adopted. The great majority decided that they themselves should select the sections illustrating the diagnoses that they had written. This responsibility fell heaviest on the authors of the chapters on the rhynchonellides and athyridides, and we are indebted to them for having carried out such painstaking culls after they had submitted their contributions.

Another problem facing authors of this volume was the need to standardize terminology for use not only between but even within orders. The terms now adopted to describe pentameride cardinalia have been brought in line with those used for homologous structures (Williams, Brunton, & MacKinnon, 1997, p. 369) in other rhynchonelliform groups. The intention is to signal that the synapomorphies concerned with late rhynchonellate articulation and lophophore support had their origins in the Pentamerida. The change to a new terminology has been accepted with varying reluctance (p. 928 herein) because the early ontogeny of pentamerides is too poorly known to confirm (or refute) the postulated homologies. Terminology has even suffered the effects of the Permian mass extinction! The unprecedented collaboration among authors of the rhynchonellides uncovered terminological and other differences of approach (p. 1027 herein) between brachiopodologists describing Paleozoic species and those restricting their attention to samples from younger stocks.

The four orders described in this volume have been classified in different ways ranging from the intuitive to the cladistic. The orders themselves are clearly defined and probably more or less compatible with the genealogy of their constituent taxa. Infraordinal groupings, however, are much less secure, as they are generally based on relative minor changes in shell morphology that are prone to homoplasy.

This complication determined the way the rhynchonellides were eventually classified. The morphology of the rhynchonellide shell has always been relatively simple. Yet the number of genera has increased threefold since 1965 (p. 1027 herein), many of them founded on subtle changes of internal parts as seen in serial sections. As a result, initial attempts at cladistic analysis of the order were thwarted by repeated convergence that has affected virtually every feature of the rhynchonellide shell in the course of its long geological history. Eventually, the authors had to content themselves with ensuring that the sixty-five families of the order are well-founded morphological units.

The authors describing the other three orders have had the systematic advantage of classifying groups with shorter geological records and generally more elaborate shells, which reduced the potential for obfuscation by repeated homoplasy. The pentameride syntrophiidines, with their well-differentiated internal markings and varied devices serving as muscle bases, have been cladistically analyzed and are shown to be the paraphyletic link between older rhynchonelliforms (Orthida) and the rhynchonellate crown group (Rhynchonellida). In contrast, genera belonging to the other pentameride suborder, the pentameridines, have been assembled hierarchically by classical comparative methods. In fact, however, the absence of internal markings and the relative simplicity of shell apophyses limit the efficacy of cladistic analysis in classifying pentameridines, at least until more is known about the fine structure and growth of spondylia and cardinalia.

The classifications of the Atrypida and Athyridida are most likely to accord, at least broadly, with their genealogies because additional apophyses (spiralia) characterizing both orders underwent elaborate transformations that have been taxonomically exploited to the full. The atrypides have been classified by traditional methods. They are, however, the shortest lived of all rhynchonellate ordinal stocks and have been so comprehensively studied that a phylogeny differing significantly from the classification presented here is difficult to visualize. The same assertion can be made about the athyridide classification, which is based on the cladistic analysis of a group characterized by the most elaborate brachidia ever to have evolved within the phylum. Admittedly the distinction between the atrypides and athyridides is only unambiguous because four families classified as Uncertain (p. 1604 herein) have been excluded from either order as presently defined. This group is noteworthy not only because further study of its genera might cast light on the phylogenetic relationships between the athyridides and atrypides. It was also prepared jointly as a priority by Fernando Alvarez and Paul Copper, the senior and sole authors, respectively, of the athyridides and atrypides. Such collaboration is the hallmark of *Treatise* teamwork, which augurs well for brachiopod research in the twenty-first century.

In summary, the classifications used as frameworks for the systematic descriptions of the later rhynchonellates are more traditional than cladistic in construction. Even so, they are likely to be, at least, broad reflections of the genealogies of the orders described. This assumption can be tested for the rhynchonellides, which, as the most morphologically conservative order with the longest geological history of all other rhynchonellates, would have been most prone to homoplasy. Four rhynchonellide superfamilies, erected exclusively on morphological differences, are represented by living species. Two superfamilies, the Dimerelloidea and Pugnacoidea, date back to the Devonian, the other two (the Norelloidea and Hemithiridoidea) to the Triassic. It is noteworthy that, in a recent molecular study involving living brachiopods (COHEN, 2000), a rhynchonellide clade shows the pugnacoid *Eohemithiris* as a sister group of the hemithiridoid *Notosaria* and the norelloid *Neorhynchia.* The test of concordance between traditional and molecular methods of classifying rhynchonellides, however, will come when living representatives of the fourth superfamily, the Dimerelloidea, are studied genetically. Living dimerelloids, like *Cryptopora* (see HELMCKE, 1940), have one pair of metanephridia as do all other brachiopods and not two pairs as in other extant rhynchonellides. Presumably, the dimerelloids belong to a group that is ancestral to the other three superfamilies as the current classification suggests (Miguel MANCEÑIDO, personal communication, August 2001). Whether this will be confirmed by molecular studies remains to be seen. Meanwhile, for the rhynchonellates at least, the classical paleontological methods of constructing phylogenetic-taxonomic hierarchies by morphological comparison have not yet had their day.

It is saddening to end this Introduction with notices of the deaths of four distinguished scientists who contributed so much to our understanding of the Brachiopoda. Two were authors of the revised *Treatise.* Alan Ansell, who died on 18 July, 1999, was a marine biologist of great versatility. He was a key contributor to the ground-breaking chapter on brachiopod physiology in Volume 1 (PECK & others, 1997) and, up to the time of his death, was actively engaged in preparing materials for the last volume of the revision of *Treatise Part H,* the Supplement. Algirdas Dagys of the Lithuanian Academy of Science died on 7 January, 2000. He was an internationally acclaimed palaeontologist whose perceptive studies of brachiopod cardinalia, loops, and spires have been pivotal to the revisions of the Rhynchonellida, Terebratulida, and Athyridida. His coauthored contributions are published in this volume and will also appear in the Supplement.

Introductions to previous volumes have always acknowledged the indebtedness of many authors for advice and access to private materials, so freely given by two giants of twentieth century Paleontology. Their wise counsels, alas, are no longer available. G. Arthur Cooper, formerly of the United States National Museum, died on 17 October, 2000. His beautifully illustrated monographs on brachiopods from the Appalachians, western Texas, the Caribbean Sea, and Indian Ocean will long continue to serve not only as standard references but also as models for the presentation of meticulously prepared data. Vladimír Havlíček, formerly of the Czechoslovakian Geological Survey, died on 10 September, 1999. His splendid monographs were concerned primarily with Bohemian brachiopods, but he also described southern European and North African assemblages with equal authority. Arthur Cooper and Vladimír Havlíček were truly the James Hall and Joachim Barrande of their day!

ACKNOWLEDGMENTS

This volume could not have been published without the help received by all authors during the preparation of their contributions. Collation of data, of course, has been going on for many years and has entailed the study of collections in institutions throughout the world. These repositories are exhaustively listed below and we all greatly appreciate the range of facilities placed at our disposal whenever our needs were made known. Special mention should be noted of Dr. Sarah Long, Curator at the Natural History Museum, London, who not only made collections immediately available *in situ* or by loan but also retrieved, at short notice, vital information about, or from, the most obscure references. The systematic descriptions of most authors have benefitted from gifts of photographs as well as the loan of specimens. The sources of those that have been used for illustration are acknowledged in the appropriate figure captions in the text.

Finally, some authors have received previously unreported grants in support of their *Treatise* work and wish to thank the funding bodies. The grants include those from The University of Kansas Paleontological Institute and the University of La Plata for M. O. Manceñido; the Natural Science Foundation of China and the Laboratory of Palaeontology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Academia Sinica for Rong Jia-yu; and The University of Kansas Paleontological Institute and the University of Glasgow for secretarial assistance for A. Williams.

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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

D, EM, ENSM, FSI, FSL, SSL, TA: Université Claude Bernard, Lyon I, Villeurbanne, France

DNGM: Servicio Nacional Minero Geológico, Buenos Aires, Argentina

DP, DPO: Departamento de Geología, Oviedo University, Oviedo, Spain

DPO: see DP

DPUCM: Departamento de Paleontologia, Universidad Complutense, Madrid, Spain

EM: see D

ENSM: see D

FD: Geological College of Eastern China, Fuzhou, China

FSI: see D

FSL: see D

GB: Xian Institute of Geology and Mineral Resources, Xian, China

GBA: Geologisches Bundesanstalt Museum, Vienna, Austria

GIB: Geological Institute, Bonn, Germany

GIBAS: Geological Institute, Bulgarian Academy of Sciences, Sofia, Bulgaria

GIN KAZ: Institute of Geology, Kazakh Academy of Sciences, Alma-Ata, Kazakhstan

GIN TAD: Institute of Geology, Dushanbe, Tadzhikistan

GIN UZ: Institute of Geology, Uzbek Academy of Sciences, Tashkent, Uzbekistan

GLAHM: Hunterian Museum, Glasgow University, Scotland, United Kingdom

GMC, IV: Geological Museum of China, Beijing, China

GMUT: see TUG

GM YaRGTS: Geological Museum of the Regional Geological Centre, Yakutsk, Yakutia

GPIBo: Palaontological Institute, Bonn, Germany

GPIT: Geological and Palaeontological Institute, University of Tübingen, Germany (Geologisch-Paläontologisches Institut, Tübingen Universität)

GPZ: Department of Geology and Palaeontology, Zagreb, Croatia

GSC: Geological Survey of Canada, Ottawa, Ontario, Canada
GSE: see IGS GSE
GSI: Geological Survey of India, Calcutta, India
GSM: see BGS
GSQ: Geological Survey, Queensland, Australia
GSV: Geological Survey of Victoria, Australia
GS YA: see CGS
HB: Bureau of Geology and Mineral Resources of Hunan Province, Hunan, China
HGI: Hungarian Geological Institut, Budapest, Hungary
HIGS: Hangzhou Institute for Geological Science, Hangzhou, China
HM: see GLAHM
HNHMB: Hungarian Natural History Museum, Budapest, Hungary
HUB: see MB
I: New York State Geological Survey, Albany, New York, USA
IGAS: Institute of Geology, Chinese Academy of Sciences, Beijing, China
IGiG: Institute of Geology and Geophysics, Siberian Branch, Academy of Sciences, Akademgorodok, Russia
IGM: Instituto de Geología, Universidad Autónoma de México, Ciudad Univesitaria, México City, Mexico
IGN: Institute of Geological Sciences, Kiev, Ukraine
IGR: Institute of Geology, University of Rennes, Rennes, France
IGS GSE: Institute of Geological Sciences, Edinburgh, United Kingdom
IGS GSM: see BGS
IMGPT: Geological-Paleontological Institute and Museum of Tübingen University, Germany
Inst. Geol.: Geological Institute, Bishkek, Kyrgyzstan
IO: P. P. Shirshov Institute of Oceanology, Moscow, Russia
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
L: National Museum, Prague, Czech Republic, Barrande specimens
LGE: St. Petersburg State University, St. Petersburg, Russia
LGI: Leningrad Geological Institute, Leningrad, Russia
LM: see LO
LMT: Loodus Museum, Tallinn, Estonia
LO (formerly LM): Lund University Museum, Sweden
LPB: Laboratoire de Paléontologie, Université de Bretagne Occidentale, Brest, France
LS: Linnean Society of London, United Kingdom
MANK: see KAS
MB (formerly HUB): Humboldt University, Berlin, Germany
M.Ch: Museum Chabarovsk, Verkhoyan, eastern Siberia, Russia
MCMB: Department of Geology, University of Beijing, Beijing, China
MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
MDSGF: Museo del Dipartimento di Scienze Geolgiche dell'Università di Ferrara, Ferrara, Italy
MFLV: Museo dei Fossili della Lessinia, Verona, Italy
MFMGB: Museum of the Faculty of Mining and Geology, Belgrade University, Belgrade, Yugoslavia
MG: Institute of Geology, Ashkhabad, Turkmenistan
MGBW: Museum of the Geologische Bundesanstalt of Wien, Austria
MGRI: Moscow Geological Prospecting Institute, Moscow, Russia
MGSB: Museo Geológico del Seminario de Barcelona, Barcelona, Spain
MGU: Moscow State University, Russia
MGUP: Museum of Geology, University of Palermo, Sicily, Italy
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
MNB: see MB
MNHN: Muséum National d'Histoire Naturelle, Paris, France
MONZ: see NMNZ
MPUM: Museo di Paleontologia del Dipartimento di Scienze della Terra dell'Università degli Studi di Milano, Italy
MUGT: see GIN TAD
Muz IG: Geological Museum of the Geological Institute, Warsaw, Poland
MV: see NMVP
NHMB: Natural History Museum, Basel, Switzerland (Naturhistorisches Museum Basel)
NIGP: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China
NM: National Museum, Prague, Czech Republic
NMING: National Museum of Ireland, Dublin, Ireland
NMNZ: Te Papa, Museum of New Zealand, Wellington, New Zealand
NMVP: Victoria Museum, Melbourne, Victoria, Australia
NMW: National Museum of Wales, Cardiff, United Kingdom
NS: Northeastern Institute of Geology, Inner Mongolia
NUF: Department of Geology, University of Newcastle, New South Wales, Australia
NYSM: New York State Museum, Albany, USA
NZGS: New Zealand Geological Survey, Lower Hutt, New Zealand (presently called Institute of Geological and Nuclear Sciences)

NZOI: New Zealand Oceanographic Institute, National Institute of Water and Atmospheric Research, Wellington, New Zealand
OKGS: Oklahoma Geological Survey, Norman, Oklahoma, USA
OMR: District Museum, Rokycany, Czech Republic
OMR VH: see OMR
OSU: Orton Geological Museum, Ohio State University, Columbus, Ohio, USA
OU: University of Oklahoma, Norman, USA
OUM: Oxford University Museum, United Kingdom
OU NZ: Geology Department, Otago University, Dunedin, New Zealand
PAN: see PIN
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
PMU: see PM
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
RX: Rowley Collection, University of Illinois, Urbana, Illinois, USA
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
SNM: Slovakian National Museum, Bratislava, Slovakia (Slovenské Narodné Múzeum, Bratislava)
SSL: see D
SUI: University of Iowa, Department of Geology, Iowa City, USA
SUP: University of Sydney, New South Wales, Australia
T: Paleontological Museum, University of Naples, Naples, Italy
TA: see D
TAGI BR: Geological Museum, Institute of Geology, Tallinn Technical University, Tallinn, Estonia
TBR: see TF
TF: Geological Survey Division, Department of Mineral Resources, Bangkok, Thailand
TsGM: see CNIGR
TsNIGRA: see CNIGR
TUG: Museum of Geology, University of Tartu, Tartu, Estonia
UA: Geology Department, University of Alberta, Edmonton, Canada
UC: Field Museum of Natural History, Chicago, Illinois, USA
UCF: The University, Calgary, Canada
UCM: University of Canterbury, Christchurch, New Zealand
UCMP: University of California, Museum of Paleontology, USA
UD: University of Dijon, Dijon, France
UHR: Hokkaido University, Sapporo, Japan
UI: University of Illinois, Urbana, Illinois, USA
UL: Department of Geology and Palaeontology, University of Ljubljana, Slovenia
UM: Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA
UMC (formerly UMO): University of Missouri, Columbia, Missouri, USA
UMMF: Department of Geology, University of Montpellier, Montpellier, France
UMUT: University Museum of the University of Tokyo, Tokyo, Japan
UND: University of Notre Dame, Indiana, USA
UPS: Université de Paris-Sud, France
UQF: University of Queensland, Department of Geology, Brisbane, Australia
USNM: United States National Museum, Washington, D.C., USA
UT: Department of Geology, University of Texas, Austin, Texas, USA
UTC: Department of Geology, University of Toronto, Toronto, Canada
UTGD: University of Tasmania Geology Department, Hobart, Tasmania, Australia
U.W.A.: University of Western Australia, Nedlands, Western Australia
VH: see OMR
VSEGEI: Russian Geology Institute, St. Petersburg, Russia
XAGM: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China
XIGMR: Xi'an Institute of Geology and Mineral Resources, Shaanxi, China
YaTGU: Geological Museum, Yakutsk, Yakutia
YIGM: Yichang Institute of Geology and Mineral Resources, Yichang, China
YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA
ZI: Zhejiang Institute of Geology and Mineralogy, Zhejiang, China
ZPAL Br: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland

OUTLINE OF SUPRAFAMILIAL CLASSIFICATION AND AUTHORSHIP

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The following outline of the classification of the Brachiopoda is an amended version of that published at the beginning of Volume 2 of the *Treatise on Invertebrate Paleontology, Part H (Revised), Brachiopoda,* edited by R. L. Kaesler (2000, p. 22–27). It lists all suprafamilial taxa recognized and described in the three systematic volumes already published and those in preparation. The main changes are the inclusion of suprafamilial taxa of uncertain order or class. The thirty-four contributors identified in the list were responsible for authorship of diagnoses for the listed taxa. In the case of orders, suborders, and superfamilies, the authors were also responsible for all lower ranking taxa down to genera and subgenera.

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
Matutelloidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Dictyonellida. Upper Ordovician–Lower Permian.
L. E. Holmer
Eichwaldioidea. Upper Ordovician–Lower Permian.
L. E. Holmer
Obolellata. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Obolellida. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Obolelloidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Uncertain.
L. E. Popov & L. E. Holmer
Naukatida. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Naukatoidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & L. E. Holmer
Kutorginata. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Kutorginida. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Kutorginoidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Nisusioidea. Lower Cambrian–Middle Cambrian.
L. E. Popov & Alwyn Williams
Strophomenata. Middle Cambrian–Upper Permian, ?Lower 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 Ordovician–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, & R. E. Grant
Chonetidina. Upper Ordovician–Upper Permian, ?Lower Triassic.
P. R. Racheboeuf
Chonetoidea. Upper Ordovician–Upper Permian, ?Lower Triassic.
P. R. Racheboeuf
Productidina. Lower Devonian–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Productoidea. Lower Devonian–Upper Permian, ?Lower Triassic.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Echinoconchoidea. Middle Devonian–Upper Permian.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Linoproductoidea. Lower Devonian–Upper Permian.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan
Uncertain.
C. H. C. Brunton, S. S. Lazarev, R. E. Grant, & Jin Yu-gan

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

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

Anazygoidea. Ordovician–Silurian.
Paul Copper
Davidsoniidina. Silurian–Middle Devonian.
Paul Copper
Davidsonioidea. Silurian–Middle Devonian.
Paul Copper
Palaferelloidea. Silurian–Middle Devonian.
Paul Copper
Lissatrypidina. Ordovician–Upper Devonian.
Paul Copper
Lissatrypoidea. Ordovician–Middle Devonian.
Paul Copper
Glassioidea. Silurian–Upper Devonian.
Paul Copper
Protozygoidea. Ordovician–Silurian.
Paul Copper
Athyridida. Upper Ordovician–Lower Jurassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Athyrididina. Upper Ordovician–Upper Triassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Athyridoidea. ?Upper Ordovician–Upper Triassic, ?Upper Jurassic.
Fernando Alvarez & Rong Jia-yu
Meristelloidea. Upper Ordovician–Upper Carboniferous.
Fernando Alvarez & Rong Jia-yu
Nucleospiroidea. Silurian–Lower Permian.
Fernando Alvarez & Rong Jia-yu
Retzielloidea. Silurian–Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Uncertain.
Fernando Alvarez & Rong Jia-yu
Retziidina. Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Retzioidea. Silurian–Upper Triassic.
Fernando Alvarez & Rong Jia-yu
Mongolospiroidea. Lower Devonian.
Fernando Alvarez & Rong Jia-yu
Rhynchospirinoidea. Silurian–Upper Devonian.
Fernando Alvarez & Rong Jia-yu
Koninckinidina. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Koninckinoidea. Middle Triassic–Lower Jurassic.
D. I. MacKinnon
Uncertain.
Fernando Alvarez & Paul Copper
Dayioidea. Silurian–Lower Devonian.
Fernando Alvarez & Paul Copper
Anoplothecoidea. Silurian–Middle Devonian.
Fernando Alvarez & Paul Copper
Uncitoidea. Middle Devonian.
Fernando Alvarez & Paul Copper
Uncertain.
Fernando Alvarez & Rong Jia-yu
Spiriferida. Upper Ordovician–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–Permian.
J. G. Johnson, J. L. Carter, & Hou Hong-Fei
Martinioidea. Silurian–Upper Permian.
J. L. Carter & Rémy Gourvennec
Spiriferoidea. Upper Devonian–Upper Permian.
J. L. Carter
Paekelmanelloidea. Upper Devonian–Upper Permian.
J. L. Carter
Brachythyridoidea. 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
Uncertain.
P. R. Racheboeuf
Spiriferinida. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinidina. Lower Devonian–Lower Jurassic.
J. L. Carter & J. G. Johnson
Cyrtinoidea. Lower Devonian–Lower Carboniferous.
J. G. Johnson
Suessioidea. Lower Carboniferous–Lower Jurassic.
J. L. Carter
Spondylospiroidea. Middle Triassic–Upper Triassic.
J. L. Carter
Syringothyridoidea. Upper Devonian–Upper Permian.
J. L. Carter
Pennospiriferinoidea. Upper Devonian–Lower Jurassic.
J. L. Carter
Spiriferinoidea. Middle Triassic–Lower Jurassic.
J. L. Carter
Thecideida. Upper Triassic–Holocene.
P. G. Baker
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, & D. E. Lee
Stringocephaloidea. Lower Devonian–Upper Devonian.
A. J. Boucot, Jin Yu-gan, & D. E. Lee
Terebratulidina. Lower Devonian–Holocene.
D. E. Lee, A. J. Boucot, A. S. Dagys, T. N. Smirnova, Sun Dong-li, & Jin Yu-gan
Cryptonelloidea. Lower Devonian–Upper Triassic.
A. J. Boucot, Jin Yu-gan, & D. E. Lee
Dielasmatoidea. Lower Devonian–Lower Jurassic.
D. E. Lee, Jin Yu-gan, A. J. Boucot, Sun Dong-li, & A. S. Dagys

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
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
Uncertain.
Plicanoplitoidea. Upper Silurian-Middle Devonian.
P. R. Racheboeuf
Cadomelloidea. Lower Jurassic.
D. I. Mackinnon

PENTAMERIDA

Sandra J. Carlson,[1] A. J. Boucot,[2] Rong Jia-yu,[3] and Robert B. Blodgett[2]
[[1]University of California, Davis; [2]Oregon State University, Corvallis; and [3]Nanjing Institute of Geology and Palaeontology]

Order PENTAMERIDA Schuchert & Cooper, 1931

[*nom. transl.* Moore in Moore, Lalicker, & Fischer, 1952, p. 220, *ex* suborder Pentameroidea Schuchert & Cooper, 1931, p. 247]

[Diagnosis prepared by S. J. Carlson and A. J. Boucot]

Small to very large articulated brachiopods, subquadrate to subpentameral to elongate-oval in outline; commonly strongly biconvex; commissure uniplicate, less commonly rectimarginate or unisulcate; hinge line either strophic with well-developed interareas or astrophic; exterior smooth, costate, or costellate, rarely pitted, granulose, or rugose. Delthyrium open, rarely partly closed by deltidial plates; teeth deltidiodont, rarely cyrtomatodont; dental plates well developed, commonly forming spondylium, rarely pseudospondylium or remaining discrete and subparallel; spondylium commonly supported by median ridge or septum, rarely absent; ventral muscle field, when visible, commonly restricted to spondylium; ventral mantle canals, when visible, commonly digitate, rarely saccate. Notothyrium, when present, open; cardinal process commonly absent, rarely as low vertical ridge on floor of valve or on callosity or narrow shelf at valve posterior; inner socket ridges short and blunt; socket plates commonly convergent, may unite with low median septum to form septalium, or remain discrete, subparallel, and continue anteriorly into extensions of varying length, rarely forming cruralium, rarely divergent; crura absent in early taxa, occur as rodlike or bladelike processes in later taxa; lophophore configuration unknown; adductor muscle field commonly well developed, oval or petaloid, rarely elevated on low callosities; dorsal mantle canal systems commonly poorly developed, digitate. Secondary shell structure fibrous, becoming dominantly prismatic in many later groups, impunctate. [The first stratigraphic occurrence of Pentamerida in the Toyonian is somewhat questionable. *Tcharella* (tentatively assigned to Syntrophopsinae, see p. 941) occurs in the Toyonian, but is so poorly known that its assignment to Pentamerida is questionable. *Cambrotrophia* is the first unquestionable pentameride genus; it first appears in the Middle Cambrian (Amgaian).] *Lower Cambrian (Toyonian)–Upper Devonian (Frasnian).*

Pentamerides comprise a relatively small but significant group (approximately 170 genera) of early and middle Paleozoic articulated brachiopods. The crown-group rhynchonellates—including the extant rhynchonellides, terebratulides, and thecideides, and the extinct atrypides, athyridides, spiriferides, and spiriferinides—together trace their closest common ancestry to the extinct pentamerides (see chapter on Brachiopod Classification, Williams, Carlson, & Brunton, 2000, p. 1–27). For this reason, pentamerides play a particularly important role in our understanding of articulated brachiopod evolution and phylogeny.

Evolution in the Pentamerida is characterized primarily by changes in hinge line width and the degree and nature of development of dental plates in the ventral valve (commonly converging to form a spondylium) and socket plates in the dorsal valve, which may converge to form a septalium. Four stages of morphological innovation can be recognized: the origin of the pentameride clade itself and of the rhynchonellide clade, the camerelloid clade, and the pentameridine clade, three successively more derived subclades within Pentamerida (Fig. 617).

Pentamerides can be distinguished from their orthide ancestors by several distinctive features that necessarily also characterize the Porambonitoidea. Convexity of adult valves evolved from weak to moderate or quite

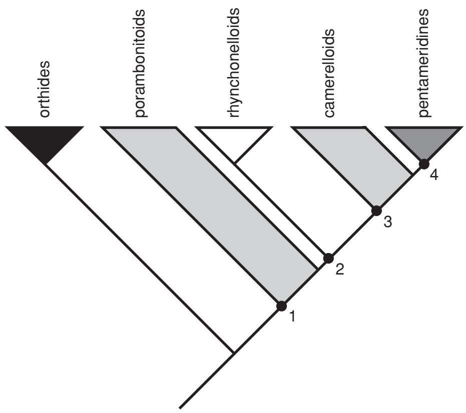

FIG. 617. Generalized cladogram adapted from CARLSON (1996, fig. 1), simplified to show the orthides (*black*) as a sister group to the pentamerides (*shaded*); the paraphyletic porambonitoids and camerelloids (*light shading*); and monophyletic rhynchonelloids (*white*) and pentameridines (*dark shading*). Numbered nodes mark four stages of morphological innovation within the order, as discussed in text (adapted from Carlson, 1996).

strong and from equibiconvex to pronounced dorsibiconvexity. The commissure changed from rectimarginate to strongly uniplicate as a deep dorsal fold and ventral sulcus developed. The hinge line commonly decreased from wide to medium width and the interareas were reduced, particularly in the dorsal valve. Dental plates became quite distinct and their orientation changed from divergent to convergent, most commonly forming a spondylium in the ventral valve. The cardinal process was generally lost, although a few primitive syntrophiidines retained a rudimentary process and a few pentameridines evolved a cardinal process secondarily. Adductor muscle attachment areas in the dorsal valve evolved from quadrilobate to elongate oval within the syntrophiidines. Muscle scars are seldom expressed on pentameridine valves.

Within the order Pentamerida, two suborders are recognized: the more primitive, paraphyletic Syntrophiidina, with highest diversity in the Ordovician, and the derived, monophyletic Pentameridina, with highest diversity in the Silurian (Fig. 617–618). Syntrophiidina includes two superfamilies—Porambonitoidea and Camerelloidea—that may be distinguished primarily by the presence or absence of a wide hinge line and interareas, the nature of the ventral spondylial structure, and presence or absence of crura and associated dorsal cardinalia. The more representative of these are illustrated in Figures 619–620. Pentameridina includes four superfamilies—Stricklandioidea, Pentameroidea, Clorindoidea, and Gypiduloidea—that may be distinguished primarily by variation in their dorsal interiors. In particular, the disposition of the hinge plates, relative to rodlike or bladelike crura, gave rise to a number of differently styled cardinalia. The more representative of these are illustrated in Figures 619–621. Stricklandioid shell structure is distinctly different from the other pentameridines, but syntrophiidine shell structure is too poorly known to allow generalizations about the evolution of shell structure across the entire order.

Differing opinions exist among the authors of this chapter regarding the ancestry of the Pentameridina. One of us (S. J. C.) holds that the pentameridines comprise a distinctive, derived group whose ancestry is shared with the camerelloids (Fig. 617), most likely the parastrophinids, despite the fact that they possess alate plates (a unique derived feature), or possibly the parallelelasmatids, with which pentameridines share a spondylium duplex, lengthening of the cardinalia, and bladelike crura.

The other authors (A. J. B., R. J.-Y., and R. B. B.) share a somewhat different view, outlined below. In the pre-Ashgill, the Llanvirn and Caradoc in particular, there are a handful of relatively provincial genera with low abundance that may include the precursors of the undoubted pentameroids. Included here are the Parallelelasmatidae and *Vaga,* from the uppermost Caradoc of Kazakhstan, that possess hinge plates similar to those of the Pentameridina rather than of the varied taxa within the Syntrophiidina. For none of these genera, however, may one be certain of the details of the hinge plates

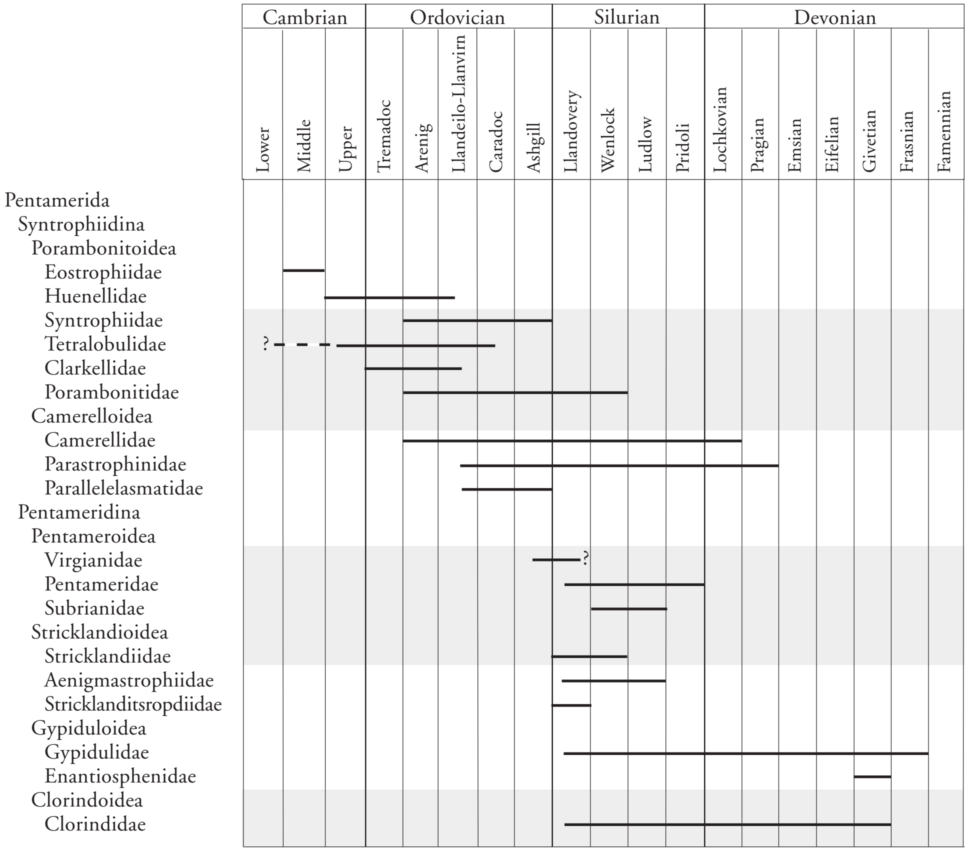

FIG. 618. Stratigraphic ranges of pentameride families; not to absolute time scale; all epochs or stages shown as equal in length (new).

(using traditional pentameroid terminology), and for none of them are there useful data about shell structure. In a general sort of way one is more inclined to see the origins of the Pentameridina within the pre-Ashgill or possibly pre-Caradoc Syntrophiidina owing to overall external and internal similarities. When the genera within the varied syntrophiidine families are considered, however, it is currently unclear just where such origins might be. The alate plates of the parastrophinids rule them out, while the relatively simple camerellid cardinalia similarly make them unlikely ancestors. The very specialized cardinalia of *Brevicamera* rule it out. The very specialized ventral interior of the Xenelasmatinae rules them out as potential ancestors, as does the spondylium simplex of the Syntrophiidae. There are probably no better prospects in terms of potential ancestors for the other families.

PENTAMERIDE MORPHOLOGY

Overall Size and Shape

Size varies considerably, but the largest pentamerides (*Zdimir, Supertrilobus,* and *Kirkidium*) are very large indeed (up to 20 cm long), are among the most derived in the order, and appear relatively late stratigraphically within their respective families. Biconvexity increased over time, expressed as dorsibiconvexity in the syntrophiidines and most commonly ventribiconvexity in the pentameridines (Fig. 622). Very generally, valve outline transformed from wider than long to longer than wide (although several

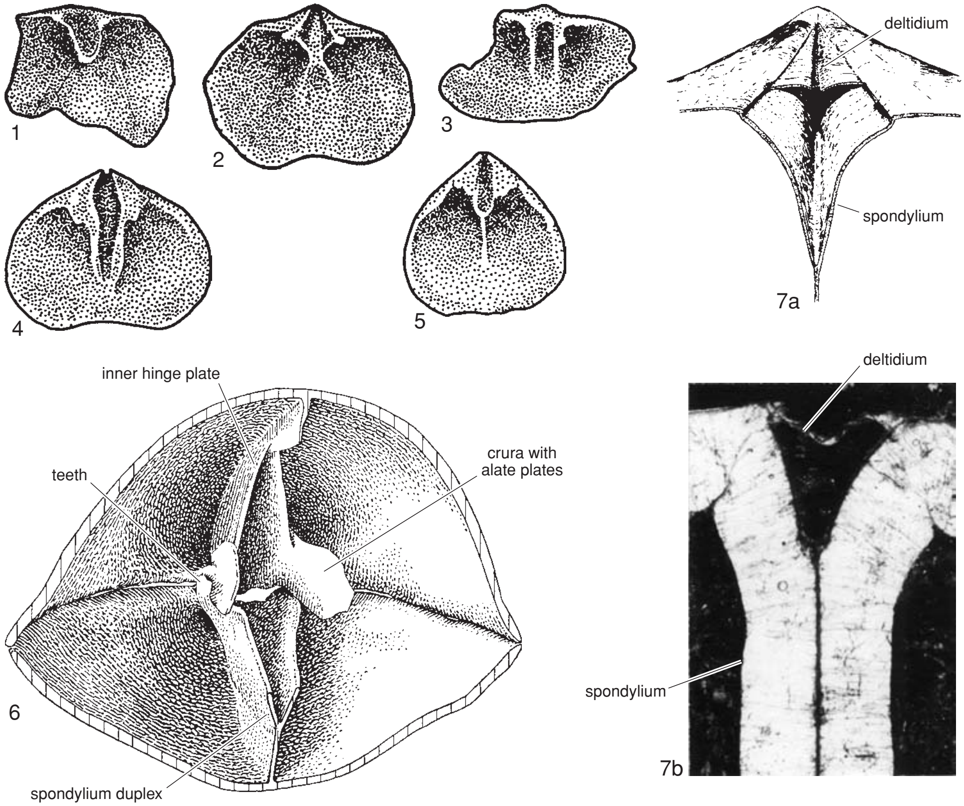

FIG. 619. Features of the ventral interior; *1, Huenella texana,* pseudospondylium lacking a median ridge or septum; *2, Tetralobula delicatula,* sessile spondylium supported anteriorly only by broad ridge; *3, Xenelasma syntrophioides,* parallel dental plates; *4, Porambonites schmidti,* long, parallel dental plates that converge anteriorly; *5, Camerella bella,* spondylium simplex on high median septum (new); *6, Parastrophina hemiplicata,* ×6 (St. Joseph, 1941); *7, Pentamerus* sp. cf. *P. oblongus* SOWERBY, Silurian, Reynales Formation, New York; *7a,* drawing of silicified specimen (×3) showing deltidium and spondylium duplex; *7b,* photomicrograph of part of section through ventral valve posterior showing deltidium and spondylium, ×10 (Amsden, 1965).

exceptions exist, e.g., *Aliconchidium*); and from subquadrate in wide-hinged forms (*Glyptotrophia*); to subpentameral in narrow-hinged forms (*Syntrophopsis*); to subtriangular, round, or elongate oval in astrophic forms (*Idiostrophia, Liricamera, Virgiana*). Derived pentamerides (*Conchidium*) are much more rostrate than primitive pentamerides (*Huenella*).

Ornament

Ornament varies considerably among pentamerides. Every family exhibits nearly the full complement of ornament types, from smooth (*Palaeostrophia*) to various types of radial ribs (*Anastrophia, Mesonomia*) to a range of more unusual kinds of ornament—concentric lamellae (*Imbricatia*), radial grooves (*Geniculogypa*), spines (*Acanthoglypha*), nodules or granules (*Calliglypha, Devonogypa*), or pits (*Punctolira, Porambonites, Wyella*).

Fold and Sulcus

Most of the earliest and more primitive pentamerides possess a strongly uniplicate commissure (*Plectotrophia*), which persisted through much of the evolutionary history of the group (including the clorindoids). Many pentameridines are rectimarginate

(*Rhipidium*); the unisulcate condition has evolved independently at least once, if not more (*Gypidula*).

Hinge and Dentition

A clear transformation from wide, strophic hinge lines (*Huenella*) to successively narrower strophic hinge lines (*Clarkella*) to astrophic hinge lines (*Pentamerus*) is apparent, although wide hinge lines reappeared in more derived pentamerides (most stricklandioids, *Aliconchidium, Gypidulella*). While width of the hinge line varies within species, it usually varies within a small, predictable range. Predominantly astrophic species may include individuals with very narrow, strophic hinge lines, but predominantly strophic species only rarely include astrophic individuals. Most pentamerides have deltidiodont dentitions; a few porambonitids (*Porambonites*) and camerelloids (*Camerella, Idiostrophia*) appear to have cyrtomatodont dentitions.

Ventral Interior

Dental plates extend from below the teeth to the floor of the valve and may diverge anteriorly, remain parallel, or converge. The dental plates were transformed during pentameride evolution from small, insignificant features (*Cambrotrophia*) to larger, convergent plates that may form a pseudospondylium or one of three different types of true spondylia. The transformation order predicted in a purely structural sense (successive enlarging, converging, and raising of the dental plates above the valve floor) is reflected in the phylogenetic pattern as well. A pseudospondylium lacks a median septum but possesses a low, curved ridge that connects the anterior ends of the dental plates and surrounds the thickened callus of the ventral muscle field (*Huenella, Mesonomia;* Fig. 619.1). A sessile spondylium is characterized by a low, median ridge or septum that supports and raises only the anterior portion of a spoon- or trough-shaped spondylium formed by the convergence of the dental plates (*Tetralobula, Stichotrophia;* Fig. 619.2). The posterior portion of a sessile spondylium remains confluent with the valve floor. A single, narrow median septum supports the entire length of a simplex spondylium (*Camerella, Clarkella;* Fig. 619.5), while a duplex spondylium is supported by a duplex septum, apparently most commonly formed from the extension and fusion of the anterior portion of the dental plates themselves (*Pentamerus, Liostrophia;* Fig. 619.6–619.7), although the septum itself, distinct from the dental plates, can appear to be divided in two by a thin layer of prismatic shell (*Parastrophinella;* see Fig. 619.7b). Although they are commonly assumed to be homologous, the homology of a simplex and duplex spondylium or even all duplex spondylia has not yet been clearly established. At least three different times in pentameride evolution, the median septum (and thus spondylium) was lost, and the dental plates returned to a subparallel orientation (*Xenelasma, Stenocamara, Rhabdostrophia;* Fig. 619.3–619.4). Accessory plates that appear to support the spondylium at approximately right angles to the dental plates may be present (*Yangtzeella*) but are not common.

Ventral muscle attachment sites are present but not particularly well developed in the spondylia of most pentamerides. Some pentameridines (some species of *Stricklandiella, Chiastodoca, Proconchidium, Pleurodium, Plicidium, Pentamerus,* and *Clorinda*), however, possess well-developed muscle-attachment areas on the anterior margin of the dorsal surface of the spondylium.

Dorsal Interior

Evolution in elements of the dorsal interior is perhaps the most complex and distinctive aspect of pentameride evolution. Confusion about terminology and homology of features of the pentameride dorsal interior is common in the literature; ontogenetic development of the pentameride cardinalia is very poorly known. Features that are likely homologues on the basis of positional similarity may have several different terms applied to

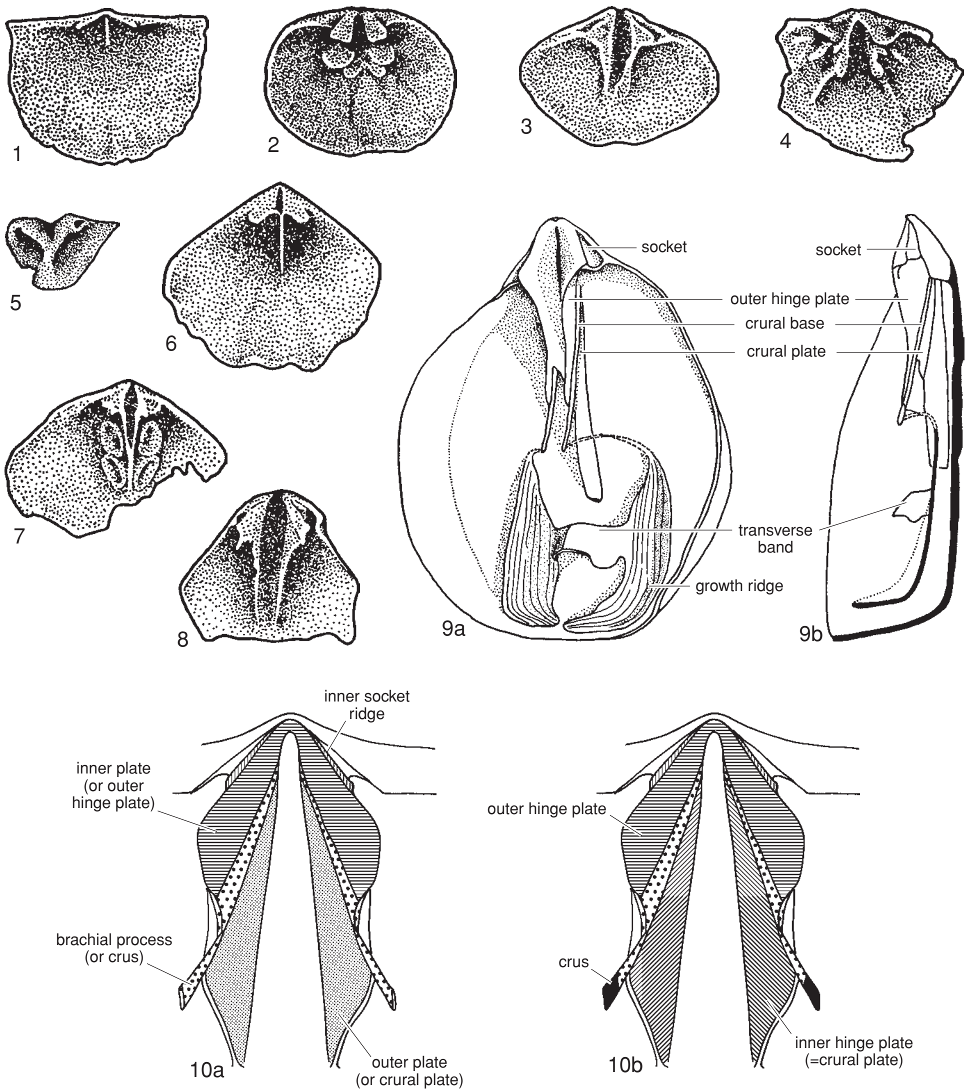

FIG. 620. Features of the dorsal interior; *1, Mesonomia magna,* cardinal process, simple socket plates; *2, Tetralobula delicatula,* petaloid socket plates, raised muscle platforms; *3, Porambonites schmidti,* long socket plates with long extensions; *4, Clarkella* sp., socket plates with short extensions and accessory septa; *5, Xenelasma syntrophioides,* wide, short septalium; *6, Camerella bella,* narrow septalium; *7, Perimecocoelia semicostata,* outer and inner hinge plates, septalium (not cruralium) with adductor muscle scars anterolateral; *8, Metacamarella pentagonum,* crura, long parallel inner hinge plates (new); *9a–b, Enantiosphen vicaryi* (DAVIDSON), dorsal valve in oblique ventral and lateral views, showing loop, Middle Devonian, England (adapted from Williams & Wright, 1961); *10, Gypidula* sp., comparison of *10a,* former terminology (now obsolete) of dorsal cardinalia (Williams & Rowell, 1965), and *10b,* current terminology of dorsal cardinalia (Williams, Brunton, & MacKinnon, 1997).

them, while a single term may be applied to several features of questionable homology. For this reason, we explain below what terms we use, why we use them, and how they compare to previously used terms.

A separate terminology evolved with respect to pentameridine cardinalia (also referred to as the brachial apparatus or brachial plates). The terms used were inner plate (or inner lamellae), brachial process (or brachial

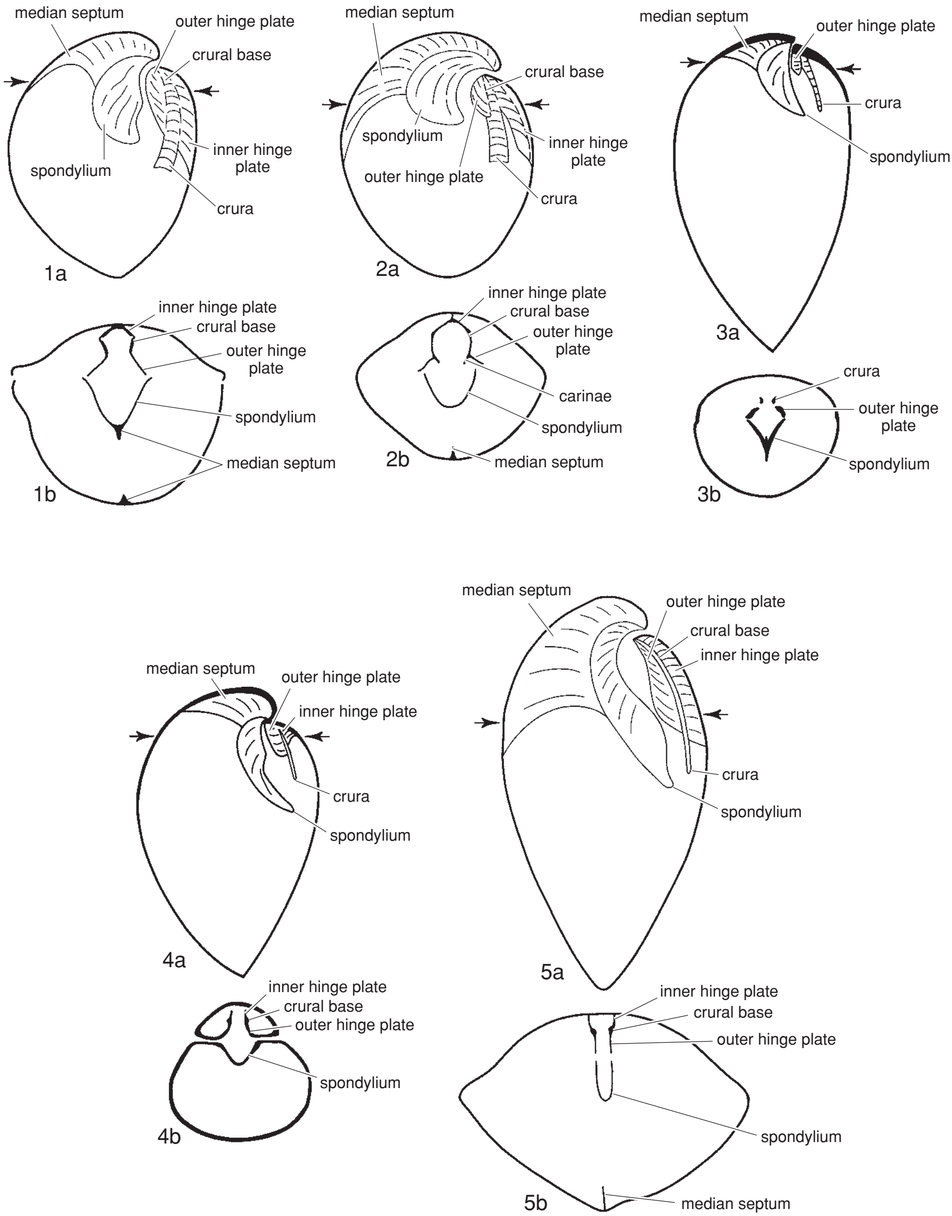

FIG. 621. *1a–b, Amsdenina roemeri,* gypiduloid; *2a–b, Clorindella areyi,* clorindoid; *3a–b, Costistricklandia gaspeensis,* stricklandioid; *4a–b, Virgiana barrandei,* virgianid; and *5a–b, Pentamerus* sp. cf. *P. oblongus,* pentamerid; longitudinal sections (above, ventral valve at left) and transverse sections (below, ventral valve below) showing internal structure, *arrows* on longitudinal sections show position of transverse sections (adapted from Amsden, 1965).

lamellae), and outer plate (or outer lamellae) (Fig. 620.10a), largely following SCHUCHERT and COOPER (1932) and AMSDEN (1953, 1964). These features appear to be homologous with the outer hinge plate, crus (crura), and inner hinge plate, respectively, of other rhynchonellates (CARLSON, 1993). Although now entrenched in the literature, the unique pentameride terminology obscures these apparent homologies, and their use is no longer recommended (Brunton, Alvarez, & MacKinnon, 1996). All four authors of this pentameride chapter accept, with varying reluctance, the new terminology. Until early ontogenies have been studied within at least a few pentameridines, however, there is still the possibility that outer and inner hinge plates are not homologues of inner and outer lamellae or crura of brachial processes (A. J. B.).

Plate terminology differs depending on the presence or absence of crura. Outer and inner hinge plates lie on the posterolateral and anteromedian sides of the crus respectively. In keeping with terminology applied to the ventral valve (e.g., dental plates), in taxa lacking crura we use the more generalized term socket plate for the plate that extends from the inner socket ridge to the floor of the valve. Socket plates can vary from short and subparallel to recumbent (*Mesonomia;* Fig. 620.1) to convergent (*Tetralobula, Syntrophopsis;* Fig. 620.2) or divergent (*Clarkella, Acanthoglypha;* Fig. 620.4). Socket plates that remain discrete may possess long, anterior extensions that are narrower and longer than the plates themselves (*Porambonites, Clarkella;* Fig. 620.3–620.4) and may be homologous to inner hinge plates in taxa possessing crura. Elongate and subparallel inner hinge plates exist in *Metacamarella* (Fig. 620.8) and *Pentamerus* (Fig. 621.5).

Accessory plates that appear to support the socket plates at approximately right angles may be present; their terminology and homology (in, for example, Clarkellidae) are unclear and confusing in the literature (*Stichotrophia*). Alate plates, characteristic of the Parastrophinidae, diverge anterolaterally from the outer side of the inner hinge plates and appear to be dorsal extensions of bladelike crura (Fig. 619.6). Boucot, Rong, and Blodgett employ herein the term carina for a small keel or ridge along the crural base to describe the form of the dorsal interiors of their genera, as has been customary for these taxa. This use of the term is additional to the definition used in Part H, Revised, Volume 1 (Kaesler, 1997), where the term carina is restricted to an external feature. There should be no confusion here since one usage is purely for an external feature and the other for an internal feature.

A true septalium, in which the socket plates (or inner and outer hinge plates) converge and unite to form a duplex septum that forms a raised triangular structure posteriorly, evolved at least twice in the pentamerides (in the Syntrophiidae, *Xenelasma,* Fig. 620.5, and Camerellidae, *Camerella, Perimecocoelia,* Fig. 620.6–620.7). A sessile septalium is formed by socket plates that converge and meet on the valve floor, lacking a septal elevation (*Brevicamera*). A cruralium is defined as a structure that houses the adductor muscles, while the septalium houses only the diductor and pedicle adjustor muscles and specifically excludes the adductor muscles, which may be located more anteriorly (Kaesler, 1997, p. 437). The relationship between septalium and cruralium is commonly unclear, however, particularly in pentamerides for which muscle scars are indistinct. When direct evidence of adductor muscle scars is lacking, the term cruralium is avoided.

SYNTROPHIIDINA

Sandra. J. Carlson

[University of California, Davis]

Suborder SYNTROPHIIDINA Ulrich & Cooper, 1936

[*nom. correct.* Biernat, 1965, p. 526, *pro* suborder Syntrophioidea Ulrich & Cooper, 1936, p. 627, *nom. transl. et emend. ex* superfamily Syntrophiacea Schuchert & Cooper, 1931, p. 247]

Commonly small to medium size (less than 2 cm), rarely larger; most wider than long, outline varies from subquadrate to subelliptical to oval as hinge line width varies; strong dorsibiconvexity, not commonly rostrate; uniplicate, rarely rectimarginate; delthyrium open; inner hinge plates (or socket plate extensions), if present, never enclose adductor muscle field. *Lower Cambrian (Toyonian)–Lower Devonian (Pragian).*

The Syntrophiidina is divided into the older, primitive Porambonitoidea and the younger, more derived Camerelloidea, both of which are paraphyletic (Fig. 617). Mosaic and iterative evolution among the porambonitoids make it somewhat difficult to define unambiguously the families within the group. Although most taxa in each family share common character states (presence or absence of a cardinal process; pseudospondylium, sessile or simplex spondylium, or parallel dental plates; septalium or discrete socket plates), different states are developed in at least a few taxa in each family. Families within the derived taxa—camerelloids and pentameridines—are more easily discerned, largely by features of the cardinalia.

In general, Syntrophiidina transformed from primitive orthidelike morphologies (for example, *Mesonomia* or *Glyptotrophia*) with wide hinge line and subquadrate outline, poorly developed fold and sulcus, small but distinct cardinal process, pseudospondylium or no spondylium at all, and no septalium, to derived, rhynchonellide-like morphologies (for example, *Camerella, Plectocamara,* or *Parastrophina*) with an astrophic hinge line, costate ornament, presence of crura, nature of the socket plates, and occasional presence of a septalium (Fig. 619–622). Rhynchonellida (and descendants from the rhynchonellides; see chapter on Classification, Kaesler, 2000, p. 1) originated from within the Syntrophiidina, as a sister group to the clade of Camerelloidea plus Pentameridina (Fig. 617). Rhynchonellides share a number of primitive characters with the derived porambonitoids (dorsibiconvexity, uniplicate commissure, and some features of the dorsal interior) and share numerous derived characters (listed above) with the camerelloids.

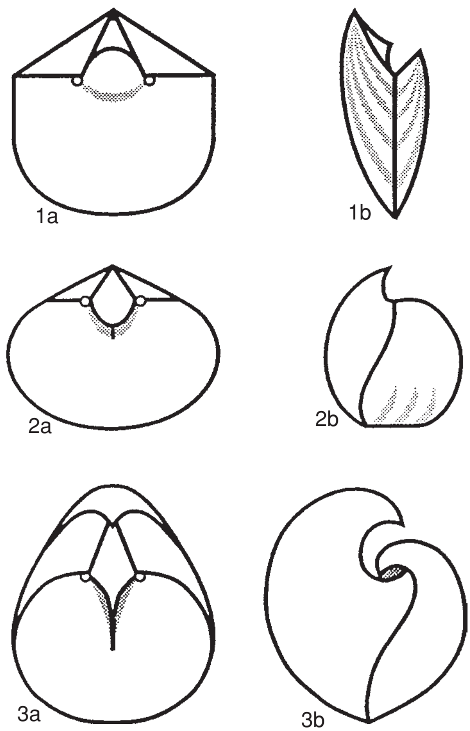

Fig. 622. Generalized drawings of overall shape; *1,* orthide; *2,* syntrophiidine; *3,* pentameridine; on left, ventral valve interior; on right, lateral view of articulated valves, ventral valve on left (adapted from Carlson, 1993).

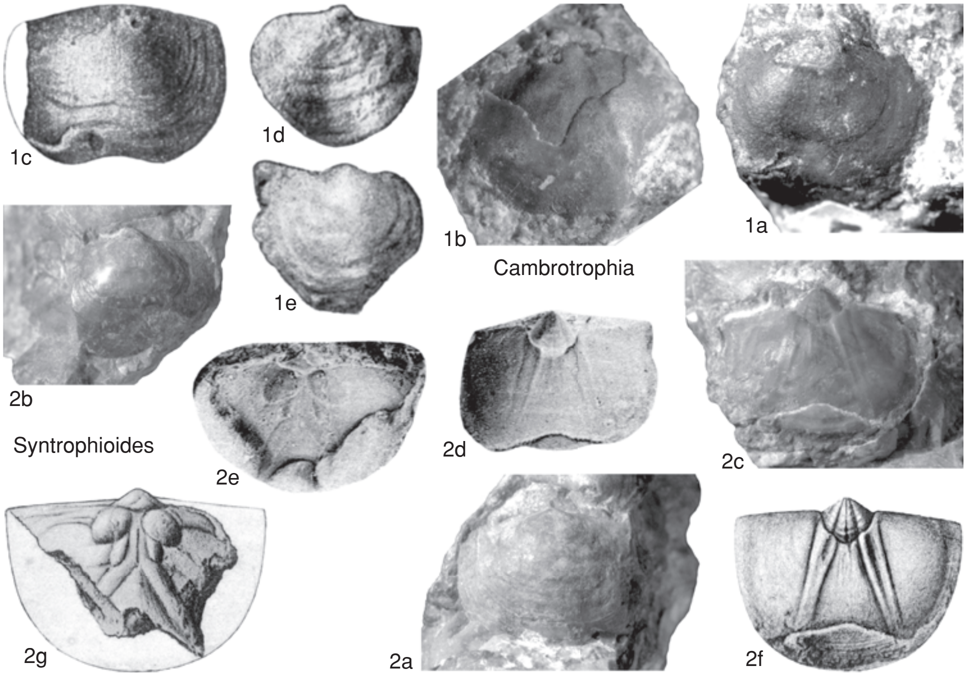

FIG. 623. Eostrophiidae (p. 930–931).

Superfamily PORAMBONITOIDEA Davidson, 1853

[*nom. correct.* CARLSON, herein, *pro* Porambonitacea BIERNAT, 1965, p. 526, *nom. transl. ex* Porambonitidae DAVIDSON, 1853b, p. 99]

Exterior smooth, costate, costellate, or with radial rows of subcircular pits; hinge line strophic, varying in width; interareas well developed to obsolete, ventral areas commonly wider than dorsal; dental plates converge to form sessile, rarely simplex, spondylium, less commonly form pseudospondylium or remain discrete and subparallel; cardinal process absent, rarely present as low vertical ridge on floor of valve or on callosity or narrow shelf at valve posterior; short socket plates commonly discrete and convergent, may unite with low median septum to form simplex septalium, or remain subparallel and rarely extend anteriorly, rarely divergent; crura absent. *Lower Cambrian (Toyonian)–lower Silurian (Wenlock).*

Family EOSTROPHIIDAE Ulrich & Cooper, 1936

[Eostrophiidae ULRICH & COOPER, 1936, p. 627]

Smooth shells; outline commonly subquadrate; moderate biconvexity; weakly uniplicate; wide hinge line; spondylium commonly absent; ventral mantle canals digitate; cardinal process absent; socket plates poorly developed. *Middle Cambrian.*

Cambrotrophia ULRICH & COOPER, 1937, p. 78, *nom. nov. pro Eostrophia* ULRICH & COOPER, 1936, p. 627, *non* DALL, 1890 [**Syntrophia cambria* WALCOTT, 1908, p. 106; OD]. Small to medium in size, hinge line nearly as wide as widest part of shell, poorly developed interareas. *Middle Cambrian (Amgaian):* USA (Utah), Canada (Quebec), Siberia, Kazakhstan, ?Australia.——FIG. 623,*1a–e*. **C. cambria* (WALCOTT); *a,* ventral valve exterior, Ute Formation, Utah; *b,* hypotype, partly exfoliated ventral valve, Ute Formation, Utah, USNM 52477, ×3 (new); *c,* dorsal valve exterior, Ute Formation, Utah, ×3 (Walcott, 1908); *d,* ventral valve exterior, Kazakhstan; *e,* dorsal valve exterior, Kazakhstan, ×1 (Nikiforova, 1960d).

Syntrophioides Schuchert & Cooper, 1931, p. 247 [**Billingsella harlanensis* Walcott, 1905, p. 236; OD]. Hinge line as wide or wider than widest part of shell, interareas relatively wide, pseudospondylium poorly developed; inner socket ridges short, supported by short, convergent but discrete socket plates; dorsal adductor muscle field well developed with weak callosities. *Middle Cambrian (Mayaian):* Russia (Urals), southern USA.——Fig. 623,*2a–g*. **S. harlanensis* (Walcott), Rogersville Shale, Tennessee, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* hypotype, ventral valve interior mold, USNM 52252, ×2 (new); *d,* cast of ventral valve interior mold; *e,* cast of dorsal valve interior mold, ×2 (Schuchert & Cooper, 1932); *f,* drawing of ventral valve interior mold; *g,* drawing of dorsal valve interior mold, ×2 (Walcott, 1912).

Family HUENELLIDAE Schuchert & Cooper, 1931

[Huenellidae Schuchert & Cooper, 1931, p. 247]

Costate or costellate, rarely smooth; subquadrate in outline; strongly uniplicate; wide hinge line, rarely narrow, with well-developed interareas; teeth strong; dental plates converge slightly to form pseudospondylium, rarely sessile spondylium, or remain parallel; cardinal process present as low vertical ridge, less commonly absent; socket plates short, small, discrete, commonly convergent, may be recumbent; dorsal adductor muscle field commonly well developed with weak callosities, elongate oval in outline. *Upper Cambrian (Dresbachian)–Lower Ordovician (lower Llanvirn).*

Subfamily HUENELLINAE Schuchert & Cooper, 1931

[*nom. transl.* Shaw, 1953, p. 143, *ex* Huenellidae Schuchert & Cooper, 1931, p. 247] [=Rectotrophiinae Bates, 1968, p. 176]

Costate, rarely smooth; pseudospondylium present, rarely with parallel dental plates; socket plates subparallel to convergent, rarely unite with median septum to form septalium. *Upper Cambrian (Dresbachian)–Lower Ordovician (lower Llanvirn).*

Huenella Walcott, 1908, p. 109 [**Syntrophia texana* Walcott, 1905, p. 294; OD]. Type species costate; pseudospondylium tending toward sessile spondylium in some, with anterior edge supported by broad, low ridge that widens anteriorly; cardinal process present in type species, lacking in some others. *Upper Cambrian (Dresbachian)–Lower Ordovician (Tremadoc):* USA, Canada, Siberia, China.——Fig. 624,*1a–f*. **H. texana* (Walcott), Upper Cambrian, USA; *a,* ventral valve exterior, Packsaddle Mountain, Texas; *b,* ventral valve exterior, Packsaddle Mountain, Texas; *c,* ventral sulcus, anterior view, Packsaddle Mountain, Texas; *d,* dorsal valve exterior, Packsaddle Mountain, Texas; *e,* hypotype, dorsal valve, lateral view, Packsaddle Mountain, Texas, USNM 52494, ×4 (new; photographs courtesy of Michael Bassett); *f,* ventral valve interior, pseudospondylium, Gallatin Valley, Wyoming, ×3 (Ulrich & Cooper, 1938).——Fig. 624,*1g*. *H. abnormis* (Walcott), ?Upper Cambrian, Yellowstone National Park, Wyoming, USA; drawing of dorsal valve interior, ×2 (Walcott, 1912).

Bondarevia Carlson, herein, p. 1616, *nom. nov. pro Triseptata* Bondarev in Bondarev & others, 1965, p. 34, *non* Hoshide, 1958 [**Triseptata nelidovi* Bondarev in Bondarev & others, 1965, p. 34; M]. Large costellate shells, subelliptical in outline; commissure rectimarginate; pseudospondylium supported by two short accessory septa; cardinal process a relatively high ridge on narrow shelf at posterior of notothyrial cavity; short, narrow socket plates converge and unite with long median septum to form deep septalium, supported by 2 long accessory septa; dorsal adductor muscle field slightly elevated. [This genus, known from only 1 species, is highly distinctive in its morphology and, as it becomes better known, may warrant subfamily status within the Huenellidae, suggested tentatively by Bondarev in Bondarev and others (1965, p. 35). It has an unusual combination of characters including the pseudospondylium and cardinal process of Huenellidae, accessory septa, notothyrial platform, and elevated dorsal adductor muscle field of Clarkellidae, and septalium of Syntrophiidae, in addition to its large size and rectimarginate commissure.] *Lower Ordovician (lower Arenig):* Novaya Zemlya. ——Fig. 625,*3a–n*. **B. nelidovi* (Bondarev), Nelidovsk beds; *a,* ventral valve exterior; *b,* articulated valves, ventral valve on right, ×1 (Bondarev, 1968); *c–e,* serial sections of ventral valve showing pseudospondylium and accessory septa, ×4; *f–j,* serial sections of dorsal valve showing cardinal process and notothyrial platform, ×4 (Bondarev & others, 1965); *k,* ventral valve interior, in section; *l,* dorsal valve mold, posterior view; *m,* dorsal valve interior mold; *n,* cast of *m,* ×1 (Bondarev, 1968).

Eosyntrophopsis Yadrenkina, 1989, p. 77 [**E. njuicus;* OD]. Small smooth shells, rectimarginate; hinge line wide, but interareas reduced; low, wide median ridge extending anterior to pseudospondylium; cardinal process absent. *Lower Ordovician (Tremadoc):* southeastern Siberia.——Fig. 624,*3a–d*. **E. njuicus,* Loparsk beds, Njuya River; *a,* ventral valve exterior; *b,* ventral valve interior mold; *c,* ventral valve interior; *d,* dorsal valve interior mold, ×3 (Yadrenkina, 1989).

Huenellina Schuchert & Cooper, 1931, p. 247 [**Huenella triplicata* Walcott, 1924, p. 526; OD].

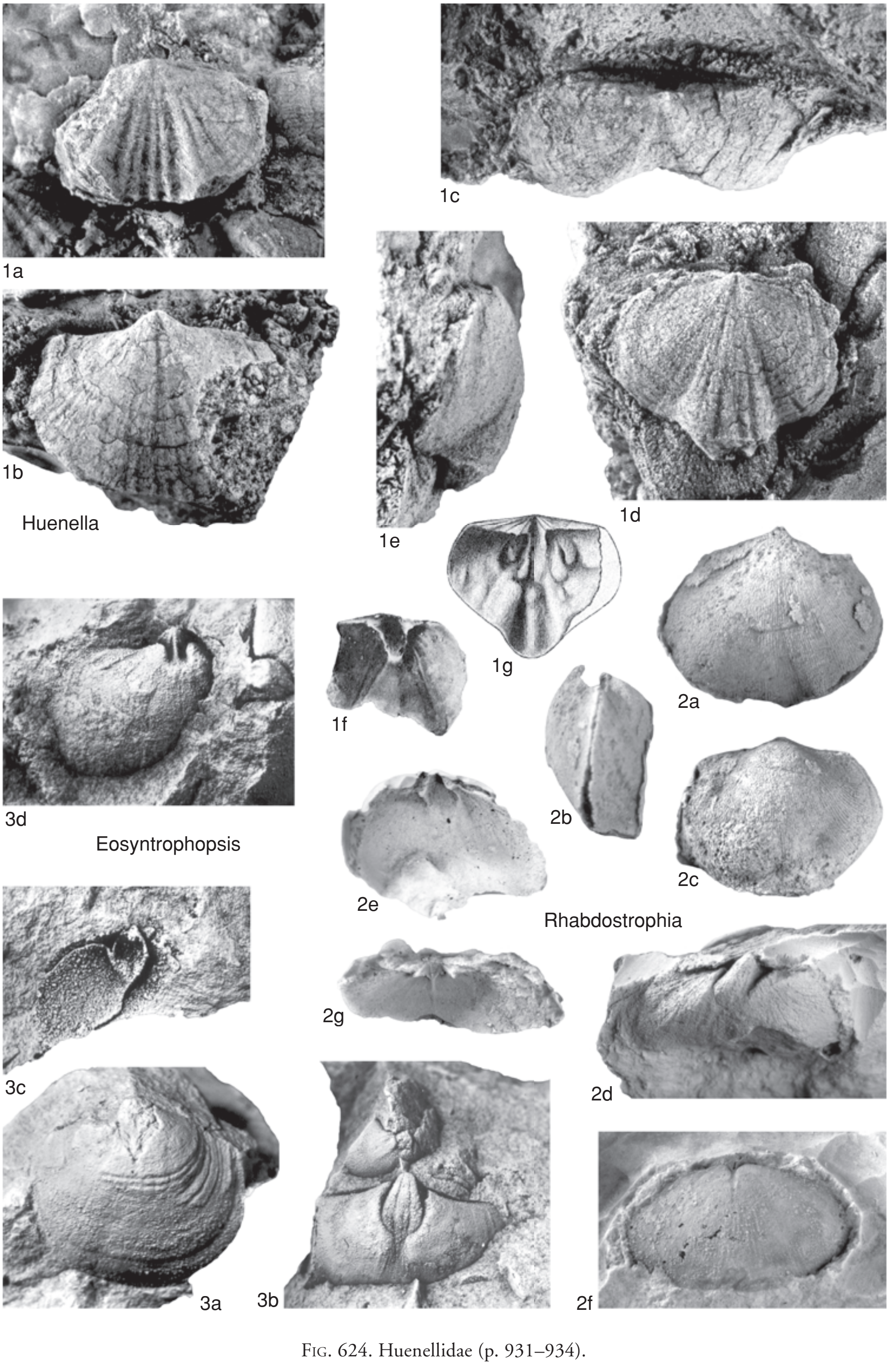

FIG. 624. Huenellidae (p. 931–934).

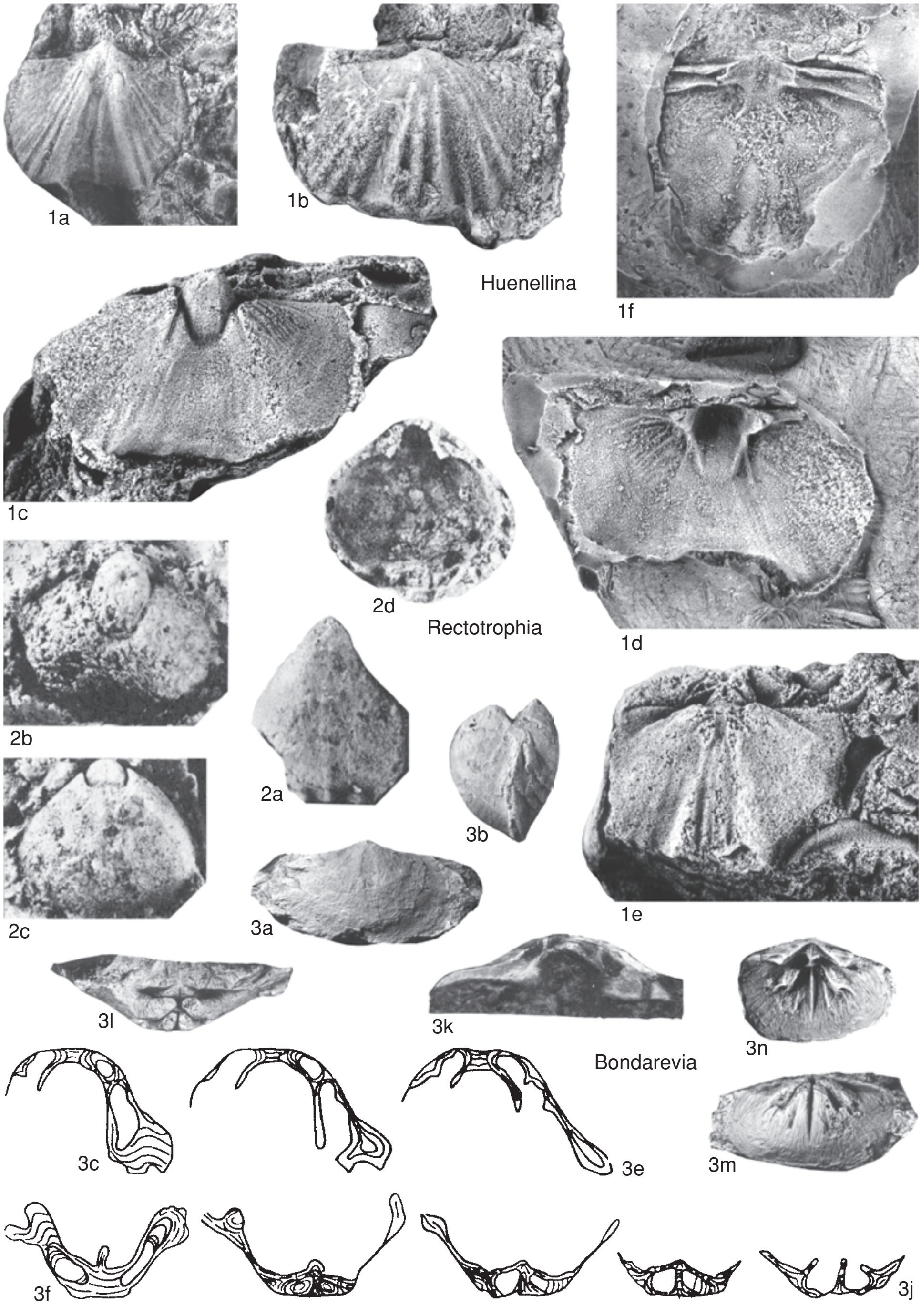

FIG. 625. Huenellidae (p. 931–934).

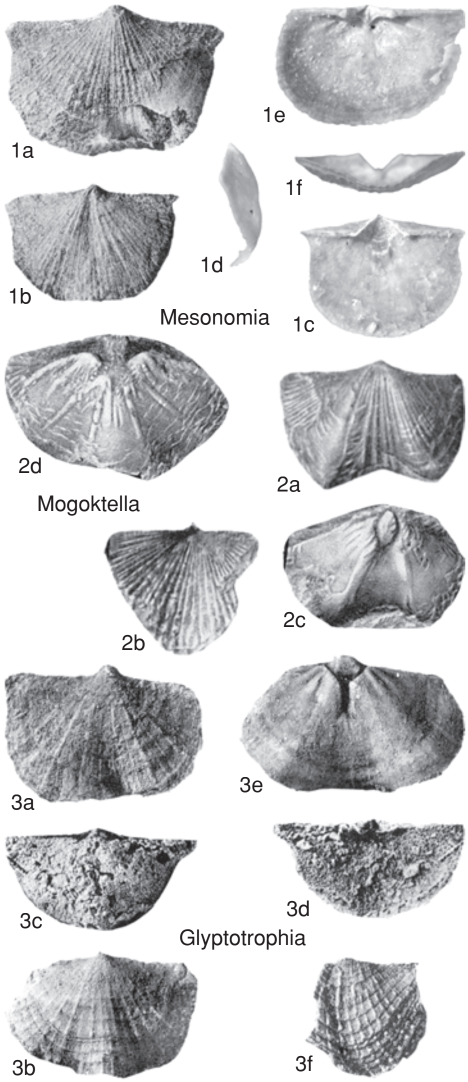

FIG. 626. Huenellidae (p. 934–935).

Similar to *Huenella,* but with 2 long lateral septa that emerge at low angle to hinge line and do not support the wide, short socket plates; cardinal process absent. *Upper Cambrian (Franconian–Trempealeauan):* Novaya Zemlya.——FIG. 625,*1a–f.* **H. triplicata* (WALCOTT), hypotype; *a,* ventral valve exterior, PMO A3293; *b,* dorsal valve exterior, PMO A3350; *c,* ventral valve interior mold, PMO A3352; *d,* latex cast of *c,* ×3; *e,* dorsal valve interior mold, PMO A3348; *f,* latex cast of *e,* ×4 (new; photographs courtesy of Michael Bassett).

Rectotrophia BATES, 1968, p. 176 [**R. globularis;* OD]. Small smooth shells, weakly uniplicate to bisulcate; hinge line narrow, less than half widest part of shell, interareas reduced; pseudospondylium long and wide; cardinal process on slightly thickened notothyrial platform. *Lower Ordovician (Arenig):* Wales, northeastern China.——FIG. 625,*2a–d.* **R. globularis,* Treiorwerth Formation, Wales; *a,* ventral valve exterior; *b,* ventral valve interior mold; *c,* dorsal valve interior mold; *d,* cast of *c,* ×3 (Neuman & Bates, 1978).

Rhabdostrophia NEUMAN, 1989, p. 68 [**R. striatisculpta;* OD]. Finely ramicostellate; biconvexity moderate; relatively weakly uniplicate; strong dental plates discrete, subparallel; cardinal process may be present on low, rhomboidal notothyrial platform formed by convergent socket plates. *Lower Ordovician (Arenig–lower Llanvirn):* Norway.——FIG. 624,*2a–g.* **R. striatisculpta,* Hølonda Limestone; *a,* ventral valve exterior; *b,* articulated valves, ventral on left; *c,* dorsal valve exterior; *d,* ventral valve interior mold; *e,* cast of ventral valve interior; *f,* dorsal valve interior mold; *g,* cast of dorsal valve interior, ×2 (Neuman, 1989).

Subfamily MESONOMIINAE Ulrich & Cooper, 1936

[Mesonomiinae ULRICH & COOPER, 1936, p. 627]

Costellate; hinge line commonly widest part of shell; pseudospondylium, rarely sessile spondylium, present; cardinal process present; socket plates subparallel to recumbent. [Some genera in this subfamily are very orthidelike in their overall morphology and may be more appropriately classified in the Orthida.] *Upper Cambrian (Dresbachian)–Lower Ordovician (Tremadoc).*

Mesonomia ULRICH & COOPER, 1936, p. 627 [**Eoorthis iophon* WALCOTT, 1924, p. 507; OD]. Fine but distinct costellae; biconvexity weak to moderate; weakly uniplicate, dorsal sulcus reverts to fold early in growth. *Upper Cambrian (Dresbachian)–Lower Ordovician (Tremadoc):* USA, Canada, ?Kazakhstan, ?eastern China.——FIG. 626,*1a–b.* **M. iophon* (WALCOTT), Tremadoc, Mons Formation, Alberta, Canada; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×2 (Ulrich & Cooper, 1938).——FIG. 626,*1c–f. M. magna* COOPER, Fort Sill Formation, Oklahoma, USA; *c,* ventral valve interior; *d,* ventral valve, lateral view; *e,* dorsal valve interior; *f,* dorsal valve, anterior view, USNM 116694, ×1.66 (new).

Glyptotrophia ULRICH & COOPER, 1936, p. 627 [**G. imbricata;* OD]. Small shells with fine costellae and strong concentric lamellae; biconvexity moderate; shallow sessile spondylium supported anteriorly only by low, wide median ridge. *Upper Cambrian (Trempealeauan)–Lower Ordovician (Tremadoc):* USA, Canada, eastern China, ?Kazakhstan.——FIG. 626,*3a–d.* **G. imbricata,* Tremadoc, Mons Formation, Alberta, Canada; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* dorsal valve interior mold; *d,* cast of *c,* ×3 (Ulrich & Cooper, 1938).——Fig. 626,*3e–f. G. jasperensis* (Kindle), Tremadoc, Mons Formation, Alberta, Canada; *e,* ventral valve interior mold; *f,* ornament, dorsal valve, ×3 (Ulrich & Cooper, 1938).

Mogoktella Andreeva, 1968, p. 82 [**M. islendica;* OD]. Parvicostellate; biconvexity strong; teeth weak; cardinal process a well-developed ridge on raised notothyrial platform; socket plates very rudimentary. *Upper Cambrian (Franconian):* northwestern Siberia.——Fig. 626,*2a–d.* **M. islendica,* Chopko River; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Andreeva, 1968).

Family SYNTROPHIIDAE Schuchert, 1896

[Syntrophiidae Schuchert, 1896, p. 320]

Costate or smooth shells; outline rounded quadrate to wide elliptical; weakly uniplicate; narrow to medium hinge line, rarely wide; interareas reduced or obsolete, rarely wide and well developed; dental plates commonly discrete and subparallel, rarely converge to form spondylium simplex; cardinal process absent; narrow socket plates may converge and unite with long median septum to form septalium, or may remain discrete. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Subfamily SYNTROPHIINAE Schuchert, 1896

[*nom. transl.* Ulrich & Cooper, 1936, p. 631, *ex* Syntrophiidae Schuchert, 1896, p. 320]

Smooth shells with wide hinge line and well-developed interareas; spondylium simplex and septalium present. *Lower Ordovician (Arenig).*

Syntrophia Hall & Clarke, 1893, p. 216 [**Triplesia lateralis* Whitfield, 1886, p. 303; OD] [=*Syntrophia* Hall & Clarke, 1892, p. 270, *nom. nud.*]. Type species relatively large; biconvexity moderate; uniplication developed only near commissure; spondylium simplex supported only in the posteriormost portion by high median septum, spondylium nearly free in some species; long, deep socket plates converge and unite with long median septum to form long, broad, shallow septalium. *Lower Ordovician (Arenig):* USA, Canada, Europe, Greenland, Russia, Siberia, China.——Fig. 627,*1a–b.* **S. lateralis* (Whitfield), Cassin Formation, Vermont, USA; *a,* dorsal valve exterior, ×1.5; *b,* posterior view of complete but exfoliated specimen showing spondylium and septalium (as molds), ×2 (Ulrich & Cooper, 1938).——Fig. 627,*1c–i. S. torynifera* (Ulrich & Cooper), Smithville Formation, Arkansas, USA; *c,* ventral valve exterior; *d,* articulated valves, ventral valve on right; *e,* dorsal valve exterior, open delthyrium and well-developed interareas; *f,* ventral valve interior, spondylium nearly free; *g,* ventral valve interior, anterior view; *h,* ventral valve interior, oblique lateral view; *i,* dorsal valve interior, septalium, ×2 (Ulrich & Cooper, 1938).

Subfamily XENELASMATINAE Ulrich & Cooper, 1936

[*nom. correct.* Biernat, 1965, p. 534, *pro* Xenelasminae Ulrich & Cooper, 1936, p. 631]

Costate or costellate shells, rarely smooth, with narrow to medium hinge line; dental plates discrete and subparallel, spondylium absent. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill).*

Xenelasma Ulrich & Cooper, 1936, p. 631 [**X. syntrophioides;* OD]. Small smooth shells; biconvexity moderate; relatively strong uniplication commencing anterior to umbo; narrow hinge line, less than half widest part of shell; dental plates long, nearly half valve length, and closely spaced; ventral adductor muscle field anterior to and commonly separated from diductors by very low ridge; narrow, very short septalium simplex supported by median septum commonly extending anterior to septalium, less commonly sessile septalium lacking median septum; elongate oval dorsal adductor muscle field well developed. *Lower Ordovician (Arenig):* USA, Russia (Urals).——Fig. 627,*2a–i.* **X. syntrophioides,* USA; *a,* ventral valve exterior, Gorman Formation, Texas; *b,* articulated valves, ventral on right, Gorman Formation, Texas; *c,* dorsal valve exterior, Gorman Formation, Texas; *d,* articulated valves, anterior view, ventral valve below, Gorman Formation, Texas; *e,* ventral valve interior, Gorman Formation, Texas; *f,* hypotype, dorsal valve interior, Gorman Formation, Texas, USNM 328688, ×3 (new); *g,* ventral valve interior, Rockdale Run Formation, Maryland, ×4; *h,* dorsal valve interior, Rockdale Run Formation, Maryland, ×6 (Sando, 1957); *i,* cast of ventral valve interior mold, Longview Formation, Virginia, ×3 (Ulrich & Cooper, 1938).

Rhyselasma Yadrenkina, 1972, p. 177 [**R. akitiense;* OD]. Small costate shells; hinge line narrow, less than half widest part of shell; socket plates discrete and subparallel, median septum and septalium absent. [Interiors generally poorly known.] *Lower Ordovician (Arenig):* Siberia.——Fig. 627,*3a–d.* **R. akitiense; a,* ventral valve exterior, Ugorian beds, Kulumba River; *b,* dorsal valve exterior, Ugorian beds, Kulumba River, ×4 (Yadrenkina, 1982); *c,* ventral valve interior, drawing from etched exteriors, Chunski stage, Khantaika River; *d,* dorsal

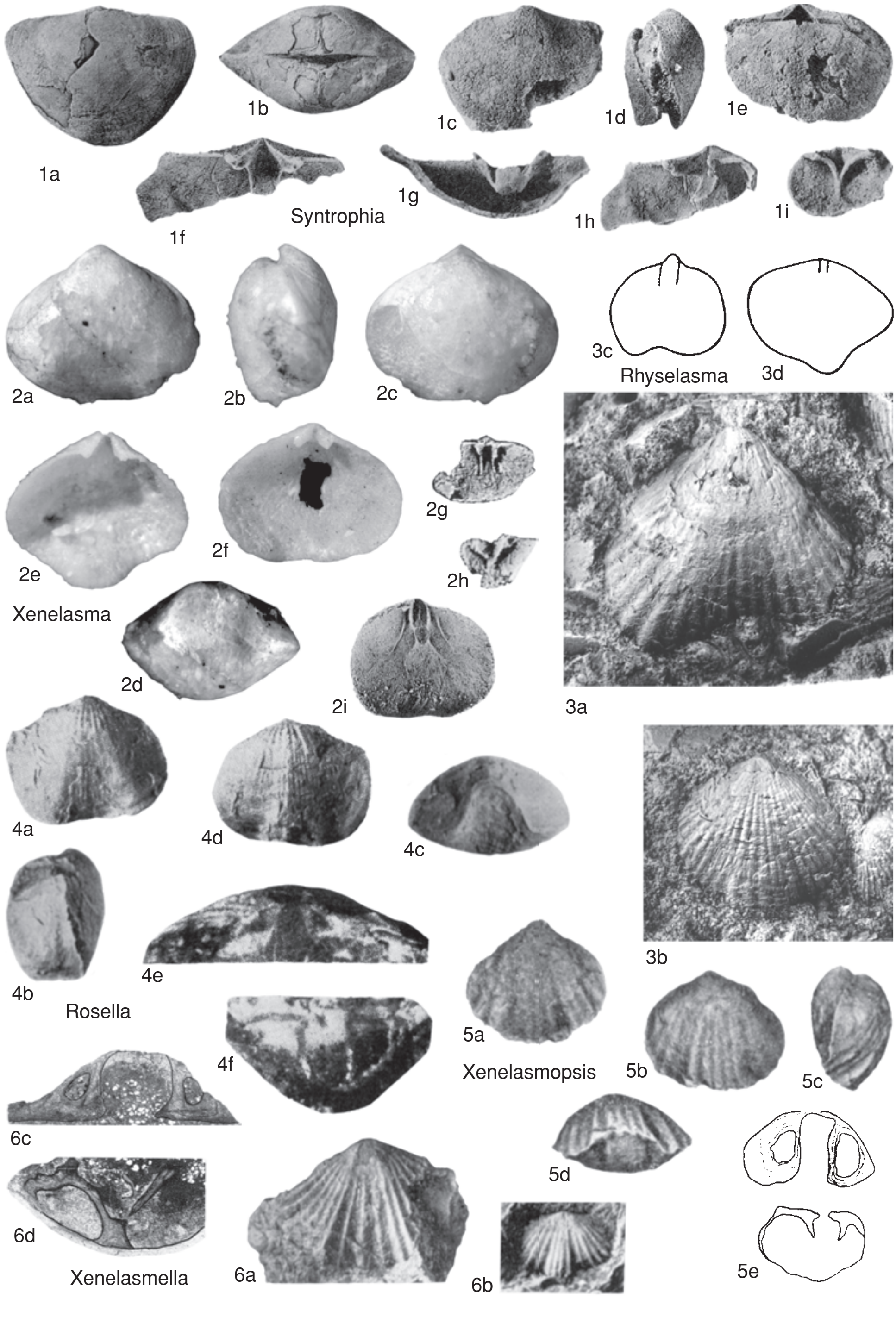

FIG. 627. Syntrophiidae (p. 935–937).

valve interior, drawing from etched exteriors, Chunski stage, Khantaika River, ×3 (Yadrenkina, 1972).

Rosella Andreeva, 1972, p. 52 [**R. karakulensis;* OD]. Large, strongly parvicostellate shells with weak but distinct growth lines; biconvexity strong; hinge line wide but narrower than widest part of shell; teeth weak; dental plates long, subparallel, widely spaced; socket plates discrete and subparallel, median septum and septalium absent. *Lower Ordovician (Arenig):* Russia (Urals).——Fig. 627,*4a–f.* **R. karakulensis,* Kuragan Suite, southern Urals; *a,* ventral valve exterior; *b,* articulated valves, ventral on right; *c,* articulated valves, anterior view; *d,* dorsal valve exterior, ×1; *e,* ventral valve, ground section near beak; *f,* dorsal valve, ground section near beak, ×2 (Andreeva, 1972).

Xenelasmella Rozman, 1964b, p. 137 [**X. graciosa;* OD]. Costate shells; biconvexity strong; strong and angular uniplication; hinge line wide, but narrower than widest part of shell; teeth strong; septalium wider than in *Xenelasma.* [Interiors generally poorly known.] *Lower Ordovician (lower Llanvirn–upper Llanvirn):* Siberia, northwestern China.——Fig. 627,*6a–d.* **X. graciosa,* Sienskii beds, Kalychan stream, Siberia; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×2; *c,* ventral valve section, ×4; *d,* dorsal valve section, ×6 (Rozman, 1964b).

Xenelasmopsis Rozman, 1968, p. 56 [**X. selennjahia;* OD]. Costae on anterior half of valve only; biconvexity strong; hinge line astrophic or extremely narrow; teeth weak; socket plates discrete and subparallel, median septum and septalium absent. *Upper Ordovician (Ashgill):* Siberia.——Fig. 627,*5a–e.* **X. selennjahia,* Sakyndzhinskaya Suite, Selenniakhsk Range; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, ventral valve on left; *d,* articulated valves, anterior view, ×2 (Rozman, 1968); *e,* articulated valves, section, ventral valve above, ×4 (Rozman, 1970).

Family TETRALOBULIDAE Ulrich & Cooper, 1936

[Tetralobulidae Ulrich & Cooper, 1936, p. 627] [=Syntrophopsidae Ulrich & Cooper, 1936, p. 630]

Smooth to finely costellate, may also have strong concentric lamellae that may intersect to form radial rows of subcircular pits; outline rounded quadrate to wide elliptical; dental plates converge to form sessile spondylium supported anteriorly only by low, wide median ridge or septum, rarely as pseudospondylium or spondylium simplex or duplex; cardinal process absent, only rarely present; socket plates commonly long, robust, convergent but discrete, rarely forming sessile septalium. *Lower Cambrian (Toyonian), Upper Cambrian (Franconian)–Upper Ordovician (lower Caradoc).*

Subfamily TETRALOBULINAE Ulrich & Cooper, 1936

[*nom. transl.* Sapelnikov, 1980, p. 10, *ex* Tetralobulidae Ulrich & Cooper, 1936, p. 627; *emend.,* Carlson, herein]

Costellate, commonly with weak to strong concentric lamellae; moderately biconvex; weak uniplication commencing anterior to umbo; wide to medium hinge line with well-developed interareas; sessile spondylium present, rarely as pseudospondylium or spondylium simplex or duplex, 2 long accessory septa may be present; long, petaloid socket plates converge but remain discrete, rarely with accessory septa or forming sessile septalium; dorsal adductor muscle field commonly well developed, may be slightly elevated, with strong callosities. *Lower Ordovician (Tremadoc–Arenig).*

Tetralobula Ulrich & Cooper, 1936, p. 628 [**T. delicatula;* OD]. Finely costellate, with weak but distinct concentric growth lines; teeth strong; sessile spondylium supported anteriorly by low, wide ridge that widens further as it extends slightly anterior to spondylium; 2 long accessory septa may be prolonged in front of spondylium; dorsal adductor muscle field elevated on callosities, petaloid in shape, posterior scars commonly larger than anterior. *Lower Ordovician (Tremadoc–Arenig):* USA, Canada, Siberia, ?Kazakhstan, China.——Fig. 628,*1a–f.* **T. delicatula,* Chepultepec Formation, Virginia, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior; *d,* dorsal valve interior, ×3 (Ulrich & Cooper, 1938); *e,* ventral valve, posterior view, teeth, sulcus; *f,* ventral valve, lateral view, USNM Biologic Collection, ×3 (new).

Disepta Zeng, 1987, p. 237 [**Tetralobula*? *yichangensis* Zeng, 1977, p. 50; OD] [=*Disepta* Zeng, 1983, p. 48, *nom. nud.*]. Costellate without concentric lamellae; biconvexity strong; strongly uniplicate; teeth small; sessile spondylium supported anteriorly by relatively high duplex septum and 2 short accessory septa, not prolonged in front of spondylium; socket plates converge to form short, weak sessile septalium supported by 2 short accessory septa. *Lower Ordovician (Tremadoc):* southern China.——Fig. 628,*2a–f.* **D. yichangensis* (Zeng), lower Nantsinkuan Formation, Hubei; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* dorsal valve, anterior view; *d,* ventral valve interior, ×2; *e,* ventral valve interior, anterior view, ×3; *f,* dorsal valve interior, ×2 (Zeng, 1983).

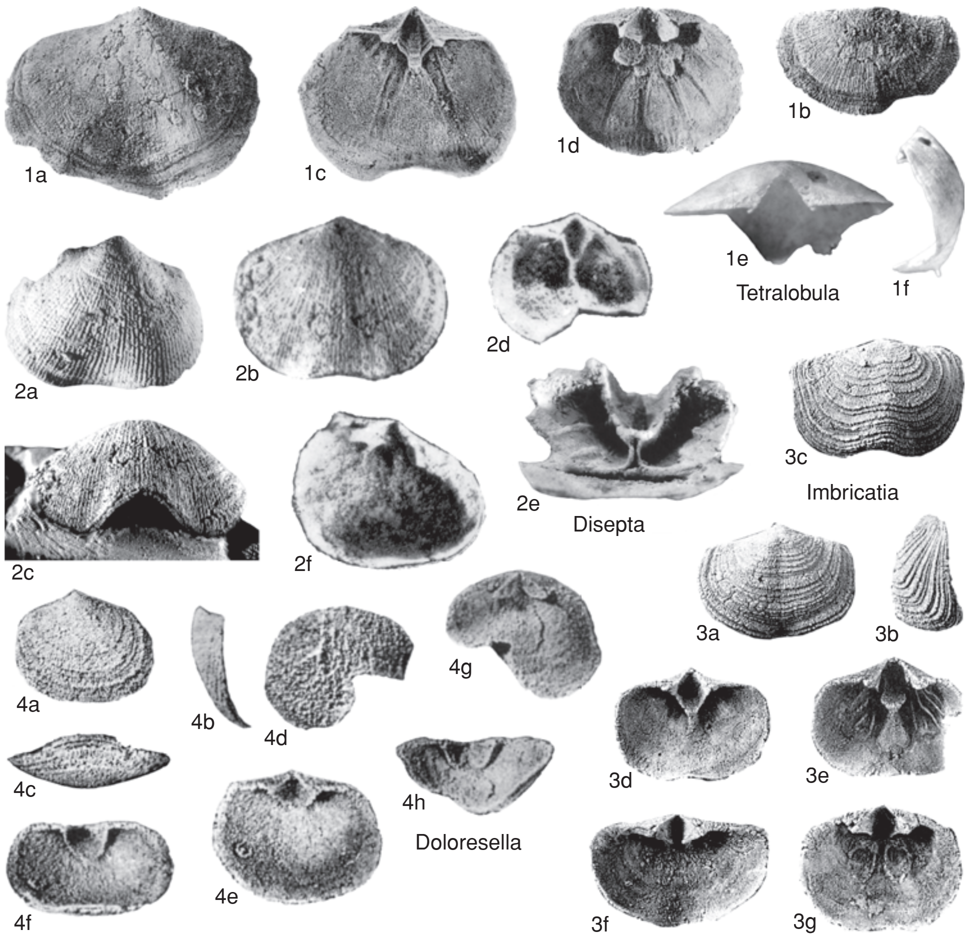

FIG. 628. Tetralobulidae (p. 937–938).

Doloresella SANDO, 1957, p. 122 [**D. concentrica;* OD]. Ornament similar to *Tetralobula;* uniplication near anterior margin only; teeth small; pseudospondylium present but poorly developed; median ridge absent; accessory septa absent; dorsal adductor muscle field poorly developed, not elevated on callosities. *Lower Ordovician (Arenig):* USA (Maryland), Russia, China.——FIG. 628,*4a–h.* **D. concentrica,* Rockdale Run Formation, Maryland, USA; *a,* ventral valve exterior; *b,* ventral valve lateral view; *c,* ventral valve anterior view; *d,* dorsal valve exterior; *e,* ventral valve interior; *f,* ventral valve interior, oblique; *g,* dorsal valve interior; *h,* dorsal valve interior, oblique, ×2 (Sando, 1957).

Imbricatia COOPER, 1952, p. 21 [**I. lamellata;* OD] [=*Thaumatrophia* WANG, 1955, p. 342 (type, *T. sinensis*); *Thaumotrophia* BIERNAT, 1965, p. 531, *nom. null.*]. Finely costellate with strong, sharp, concentric lamellae; teeth small; spondylial structure quite variable, type species with sessile spondylium supported anteriorly by low, wide ridge, others with spondylium simplex supported by high, wide median septum; accessory septa absent; dorsal adductor muscle field not elevated, but weak callosities are present. [*Thaumatrophia* has strong teeth and is strongly uniplicate but is otherwise very similar to *Imbricatia*.] *Lower Ordovician (Tremadoc):* USA, Canada, Kazakhstan, Novaya Zemlya, China, ?Argentina.——FIG. 628,*3a–g.* **I. lamellata,* Cool Creek Formation, Oklahoma, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* dorsal valve lateral view; *d,* ventral valve interior; *e,* ventral valve interior, gerontic individual; *f,* dorsal valve interior; *g,* dorsal valve interior, gerontic individual, ×2 (Cooper, 1952).

Subfamily SYNTROPHOPSINAE Ulrich & Cooper, 1936

[*nom. transl.* ANDREEVA, 1982, p. 58, *ex* Syntrophopsidae ULRICH & COOPER, 1936, p. 630; *emend.,* CARLSON, herein] [=Palaeostrophiinae ULRICH & COOPER, 1936, p. 627; Rhysostrophiinae SAPELNIKOV, 1980, p. 11]

Smooth or costellate, rarely costate; strongly biconvex; strongly uniplicate; narrow hinge line with well-developed to reduced interareas; sessile spondylium present, accessory septa rare; socket plates commonly long, convergent but discrete, rarely forming sessile septalium. *Lower Cambrian (Toyonian), Upper Cambrian (Franconian)–Upper Ordovician (lower Caradoc).*

Syntrophopsis ULRICH & COOPER, 1936, p. 630 [**S. magna;* OD]. Type species large, others commonly small to moderate in size; smooth; uniplication present only on anterior half; teeth relatively small; long, sessile spondylium supported at anterior only by low, wide ridge that widens to broad, slightly elevated triangular area anterior to spondylium between digitate mantle canals, median ridge absent in some species; long socket plates discrete and closely spaced; fulcral plates present under sockets; very weak callosities mark dorsal adductor muscle field. *Lower Ordovician (Tremadoc–Arenig):* USA, Scotland, southern China, north-central Russia, Siberia, Tasmania, ?Argentina.——FIG. 629,*1a–g.* **S. magna,* Odenville Formation, Alabama, USA; *a,* ventral valve exterior; *b,* articulated valves, ventral valve on left; *c,* dorsal valve exterior; *d,* articulated valves, posterior view; *e,* articulated valves, anterior view; *f,* ventral valve interior; *g,* dorsal valve interior, ×1.5 (Ulrich & Cooper, 1938).

Altunella LIU, ZHANG, & DI, 1984, p. 160 [**A. typica;* OD]. Costate shells, length and width nearly equal; very strongly biconvex; uniplication present on entire valve; interareas narrow; sessile spondylium supported by 2 accessory septa; weak, narrow sessile septalium supported by short median septum. [Interiors poorly known.] *Upper Ordovician (lower Caradoc):* northwestern China.——FIG. 629,*2a–d.* **A. typica,* Maleziji Group, Xinjiang; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve below, ×1.5 (Liu, Zhang, & Di, 1984).

Bobinella ANDREEVA, 1968, p. 80 [**B. kulumbensis;* OD]. Similar to *Syntrophopsis,* but parvicostellate; weakly uniplicate; interareas narrow to obsolete. *Upper Cambrian (Franconian):* northwestern Siberia.——FIG. 629,*4a–d.* **B. kulumbensis,* Kulumba River; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior mold; *d,* dorsal valve interior mold, ×3 (Andreeva, 1968).

Hesperotrophia ULRICH & COOPER, 1936, p. 630 [**H. obscura;* OD]. Similar to *Syntrophopsis,* but finely costellate; weak, narrow uniplication. [Interiors poorly known.] *Lower Ordovician (Arenig):* Canada (Alberta).——FIG. 629,*3a–d.* **H. obscura,* Sarbach Formation; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×2; *c,* fine costellae, ×4; *d,* dorsal valve interior mold, ×2 (Ulrich & Cooper, 1938).

Palaeostrophia ULRICH & COOPER, 1936, p. 627 [**Syntrophia orthia* WALCOTT, 1906, p. 11; OD]. Smooth, moderately biconvex shells; uniplication very deep and rounded, reverts from gentle unisulcation early in ontogeny in some individuals; type species with medium hinge line, others narrow to medium in width; teeth strong; sessile spondylium narrow, supported at anterior only by short, low, wide median ridge not prolonged anterior to spondylium; shallow notothyrial cavity; socket plates narrow, very short, delicate, may have thickened callus of shell in between; dorsal adductor muscle field elongate oval in outline. *Upper Cambrian (Franconian)–Lower Ordovician (lower Llanvirn):* USA, Canada, Norway, Russia, Kazakhstan, China, South Korea.——FIG. 629,*5a–b.* **P. orthia* (WALCOTT), upper Franconian–lower Trempealeauan, Chaumitien Limestone, Tsinan, China; *a,* dorsal valve exterior, ×2; *b,* dorsal valve interior, ×3 (Ulrich & Cooper, 1938).——FIG. 629,*5c–j. P.* sp., upper Franconian–lower Trempealeauan, Wilburns Formation, Texas, USA; *c,* ventral valve exterior; *d,* ventral valve exterior, lateral view; *e,* ventral valve, posterior view; *f,* dorsal valve exterior; *g,* dorsal valve exterior, lateral view; *h,* dorsal valve exterior, posterior view; *i,* ventral valve interior; *j,* dorsal valve interior, USNM Biologic Collection, ×2 (new).

Plectotrophia ULRICH & COOPER, 1936, p. 627 [**P. bridgei;* OD]. Similar to *Palaeostrophia,* but with fine, widely spaced costellae, some nearly smooth; uniplication strong and angular; hinge line wide, may be widest part of shell; socket plates narrow, short, convergent but discrete, rarely unite to form short sessile septalium duplex; dorsal adductor muscle field not well developed. *Upper Cambrian (Franconian):* USA, Canada (Alberta).——FIG. 630,*1a–h.* **P. bridgei,* Wilberns Formation, Texas, USA; *a,* ventral valve exterior; *b,* ventral valve exterior, lateral view; *c,* dorsal valve exterior; *d,* dorsal valve exterior, lateral view; *e,* ventral valve interior; *f,* dorsal valve interior, ×2; *g,* dorsal valve interior, socket plates discrete; *h,* dorsal valve interior, socket plates nearly united, ×3 (Ulrich & Cooper, 1938).

Rhysostrophia ULRICH & COOPER, 1936, p. 630 [**R. nevadensis;* OD]. Similar to *Syntrophopsis,* but with strong costae; moderately biconvex; hinge line width varies considerably, narrow in type species, with narrow interareas; teeth strong; short spondylial structure commonly sessile and supported at anterior only by short, wide median septum, but may be simplex and supported for entire length; socket plates discrete but approach a sessile septalium in some individuals. *Lower Ordovician (Arenig–lower Llanvirn):* USA, Canada, Europe, Siberia, ?New Zealand.——FIG. 630,*2a–f.* **R. nevadensis,*

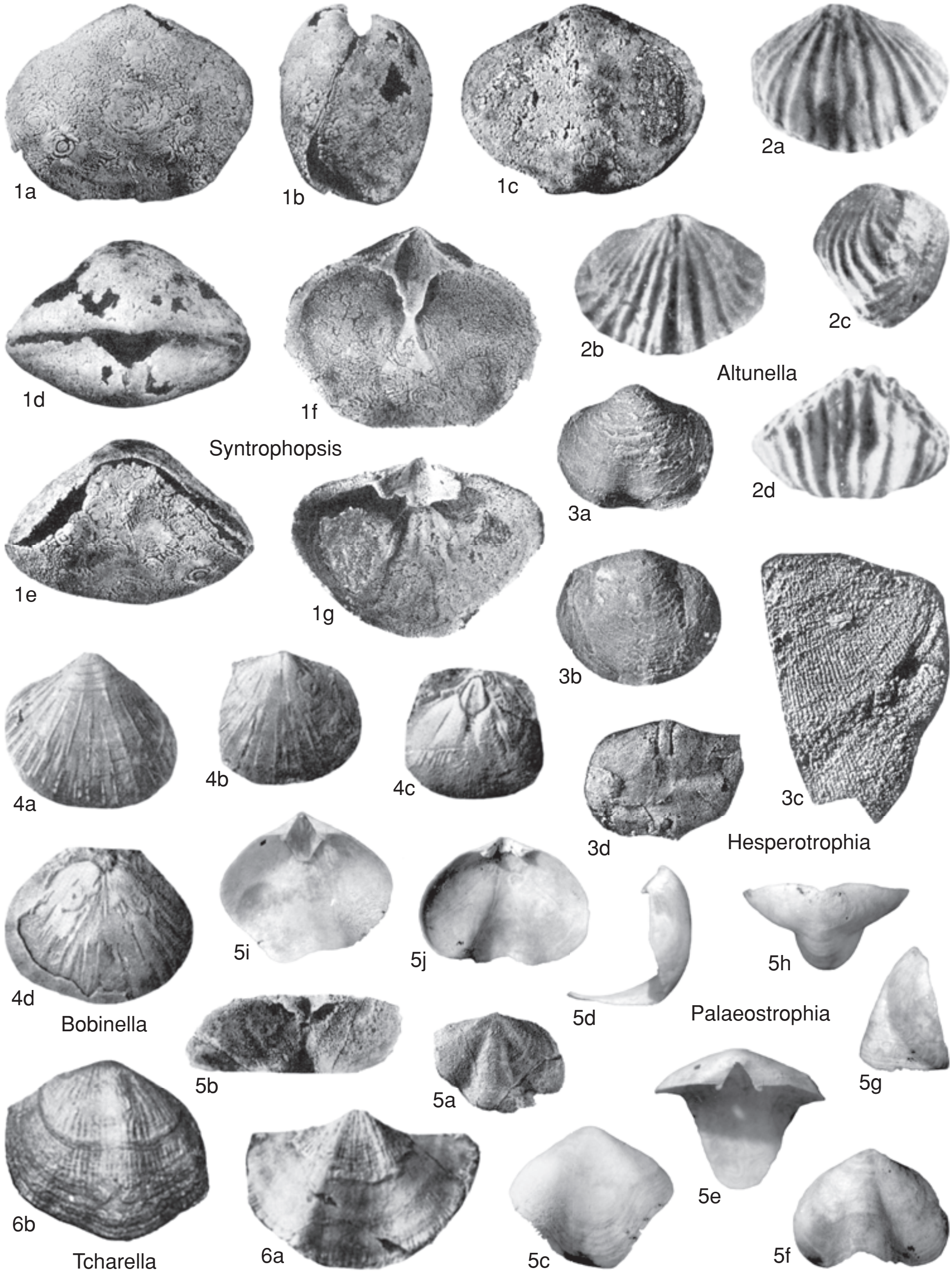

FIG. 629. Tetralobulidae (p. 939–941).

upper Pogonip Formation, Nevada, USA; *a,* ventral valve exterior; *b,* articulated valves, ventral valve on left; *c,* dorsal valve exterior, ×1; *d,* articulated valves, anterior view; *e,* dorsal valve interior mold, ×1.5; *f,* dorsal valve interior, oblique mold, ×2 (Ulrich & Cooper, 1938).——FIG. 630,*2g. R. vagans* (REED), Hølonda Limestone, Norway; ventral valve interior, ×2 (Neuman, 1989).

?Tcharella Andreeva, 1987, p. 38 [**T. amgensis;* OD]. Costellate; subquadrate in outline; moderately biconvex; uniplication narrow, present on entire valve; hinge line wide, as wide as widest part of shell; interareas very narrow; inner socket ridges short, socket plates appear to be absent. [Ventral interior unknown. *Tcharella* (tentatively assigned here to Syntrophopsinae) occurs unquestionably in the Toyonian; the genus is so poorly known that its assignment to Pentamerida is questionable.] *Lower Cambrian (Toyonian):* Siberia.——Fig. 629,*6a–b.* **T. amgensis, Kooteniella* zone, Amga River; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×1.5 (Andreeva, 1987).

Subfamily PUNCTOLIRINAE Andreeva, 1982

[Punctolirinae Andreeva, 1982, p. 58; *emend.,* Carlson, herein]

Fine costellae and concentric lamellae intersect and merge to form distinctive radial rows of subcircular pits; wide to medium hinge line with well-developed interareas; teeth strong; sessile spondylium (rarely pseudospondylium) present, accessory septa uncommon; ventral mantle canal systems saccate; cardinal process only rarely present; socket plates convergent but discrete, septalium absent. *Lower Ordovician (Tremadoc–lower Llanvirn).*

Punctolira Ulrich & Cooper, 1936, p. 628 [**P. punctolira;* OD]. Type species medium size, others may be quite large; strongly biconvex; uniplication strong and angular, reverts from gentle unisulcation early in ontogeny in some individuals; cardinal process very rarely present as low ridge; dorsal adductor muscle field well developed, petaloid, with strong callosities. *Lower Ordovician (Tremadoc–Arenig):* USA, Canada, Argentina, China, Russia. ——Fig. 631,*1a–e.* **P. punctolira,* Tremadoc; *a,* ventral valve exterior, Mons Formation, Alberta, Canada; *b,* ventral valve, anterior view, Mons Formation, Alberta, Canada (Ulrich & Cooper, 1938); *c,* dorsal valve exterior, Goodwin Formation, Nevada, USA; *d,* dorsal valve, anterior view, Goodwin Formation, Nevada, USA, ×2; *e,* ornament, Goodwin Formation, Nevada, USA, ×10 (Ulrich & Cooper, 1938).——Fig. 631,*1f–g. P. orientalis* Wang & Xu, Arenig, Lunshan limestone, Tangshan, China; *f,* ventral valve interior; *g,* dorsal valve interior, ×2 (Wang & Xu, 1966).

Cuparius Ross, 1971, p. 125 [**C. cardilatus;* OD]. Moderate to large size; moderately biconvex; uniplication strong and broad, present only on anterior half; narrow median septum does not extend anterior to spondylium; notothyrial cavity shallow; socket plates long, deep, subparallel, and uniting with valve in short, slightly divergent, anterior extensions, not petaloid as in *Tetralobula;* fulcral plates present under sockets; dorsal adductor muscle field poorly developed. [Neuman and Bates (1978) synonymized *Cuparius* with *Rugostrophia,* and Xu and Liu (1984) synonymized *Cuparius* with *Punctolira,* but differences in ventral and dorsal interiors warrant recognition of all 3 genera.] *Lower Ordovician (lower Llanvirn):* USA, Canada, Siberia.——Fig. 631,*2a–f.* **C. cardilatus,* Antelope Valley Limestone, Nevada, USA; *a,* ventral valve exterior; *b,* articulated valves, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view; *e,* ventral valve interior; *f,* dorsal valve interior, ×2 (Ross, 1971).

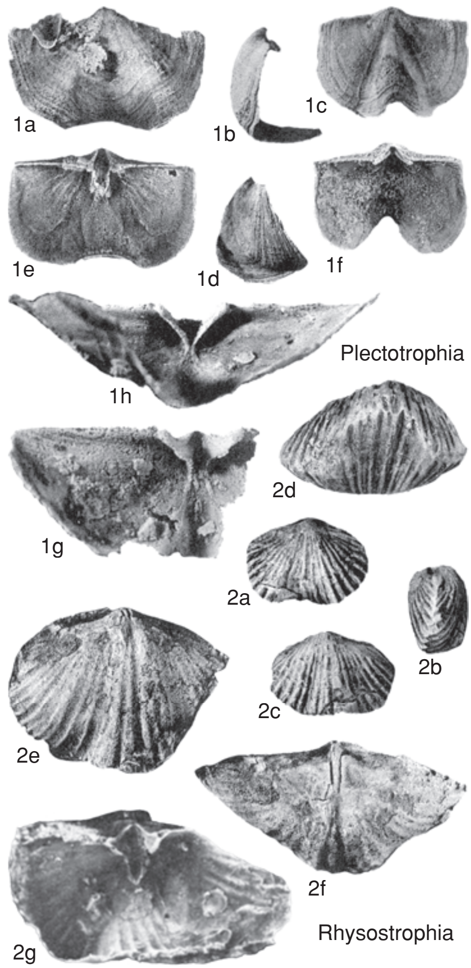

Fig. 630. Tetralobulidae (p. 939–940).

Pseudoporambonites Zeng, 1977, p. 51 [**P. yichangensis;* OD] [=*Porambonitoides* Xu in Xu, Wan, & Chen, 1978, p. 315 (type, *P. hupeihensis*)]. Large to very large in size; length and width nearly equal; dorsal and ventral valve convexity nearly equal; weak uniplication present only on anterior half;

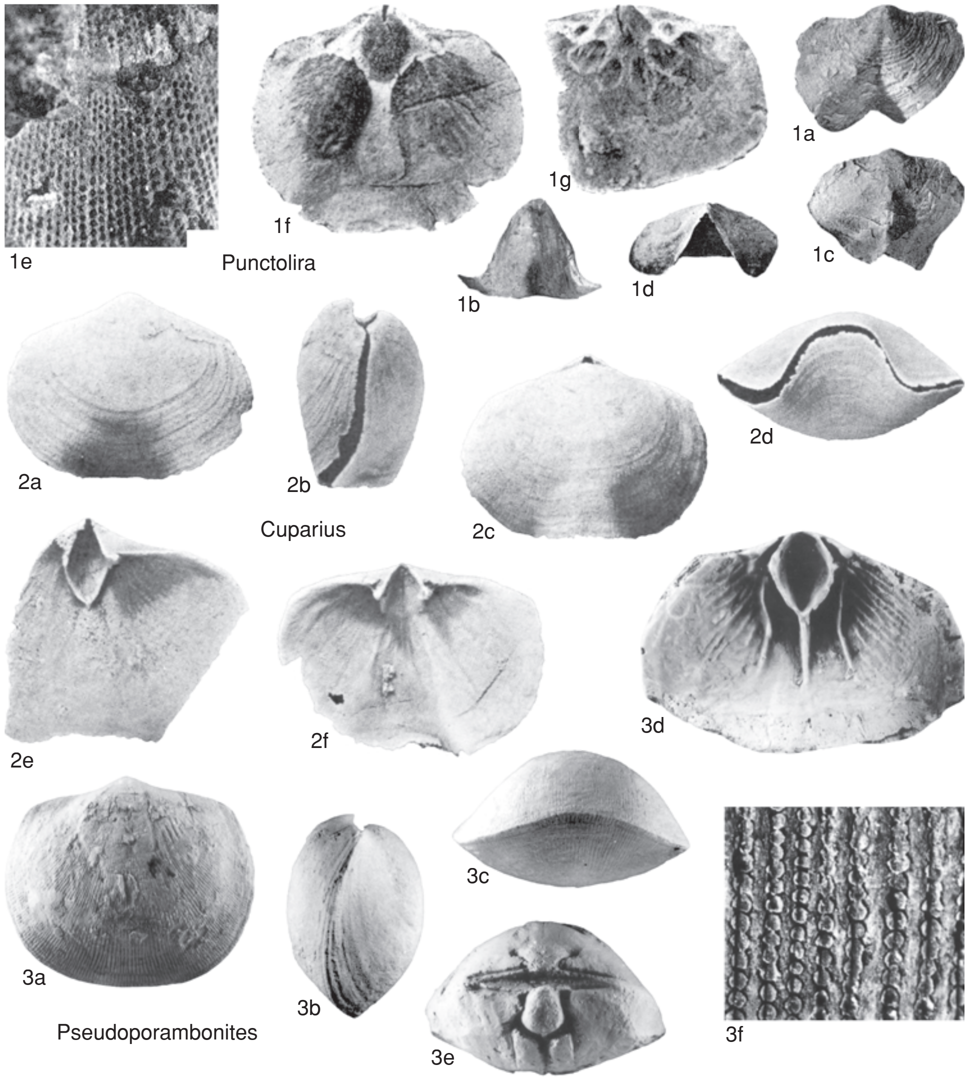

FIG. 631. Tetralobulidae (p. 941–942).

sessile spondylium supported by relatively high, narrow median septum; 2 long accessory septa present, prolonged in front of spondylium; dorsal adductor muscle field poorly developed. [*Porambonitoides* lacks uniplication and has smaller hinge teeth but appears to be well within the variability of *Pseudoporambonites*.] *Lower Ordovician (Arenig):* southwestern China. ——FIG. 631,*3a–f.* **P. yichangensis,* Dawan Formation, Hubei, China; *a,* ventral valve exterior; *b,* articulated valves, ventral on left; *c,* articulated valves, anterior view, ventral below; *d,* ventral valve interior; *e,* mold of articulated valves, posterior view, ventral below, ×1; *f,* ornament, ×10 (Zeng, 1977).

Rugostrophia NEUMAN, 1971, p. 118; *emend.,* NEUMAN, 1976, p. 40; NEUMAN & BATES, 1978, p. 607 [**R. silvestris;* OD]. Large shells; strongly biconvex; concentric lamellae distinct and strong; strong uniplication present on entire valve; long pseudospondylium present; socket plates short and narrow; fulcral plates present under sockets; dorsal adductor muscle field well developed, petaloid, with weak callosities. *Lower Ordovician (upper Arenig–lower Llanvirn):* USA, Canada, Argentina.——FIG. 632,*1a–d.* **R. silvestris,* New Brunswick, Canada; *a,* ventral valve interior mold; *b,* cast of *a; c,* dorsal valve interior mold, post-depositional elongation in anterior-posterior direction; *d,* cast of dorsal valve

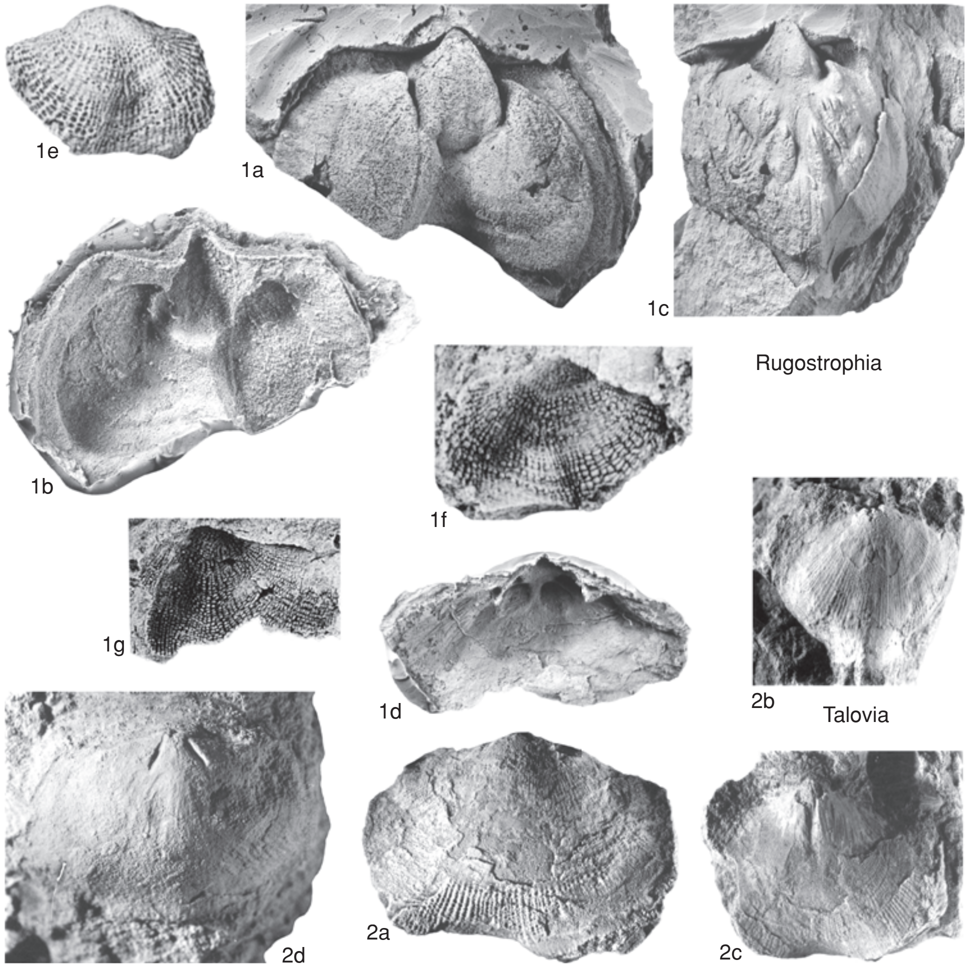

FIG. 632. Tetralobulidae (p. 942–943).

interior mold, ×1.5 (Neuman, 1971).——FIG. 632,*1e–g. R. latireticulata* NEUMAN, Newfoundland, Canada; *e,* ventral valve exterior mold; *f,* cast of *e,* ×1.5; *g,* dorsal valve exterior mold, ×1 (Neuman, 1976).

Talovia SEVERGINA, 1975, p. 62 [**T. reticulata;* OD]. Small shells; moderately biconvex; weak uniplication present near anterior margin only; sessile spondylium short, narrow, and shallow; 2 short accessory septa present; long inner socket ridges supported by wide, deep, slightly divergent socket plates; dorsal adductor muscle field poorly developed. *Lower Ordovician (lower Llanvirn):* Russia (Gorno-Altay).——FIG. 632,*2a–d.* **T. reticulata,* Rudnikovo Formation; *a,* ventral valve exterior, ×3; *b,* dorsal valve exterior, ×1.5; *c,* ventral valve interior mold, ×2; *d,* dorsal valve interior mold, ×3 (Severgina, 1975).

Family CLARKELLIDAE Schuchert & Cooper, 1931

[Clarkellidae SCHUCHERT & COOPER, 1931, p. 247] [=Yangtzeellidae ZENG, 1986, p. 79]

Commonly smooth, may be costellate or with strong concentric lamellae, rarely with spines or nodules; outline subpentameral to subelliptical; strongly uniplicate; hinge line varies from wide to narrow with well-developed to reduced interareas; spondylium simplex, less commonly sessile spondylium, rarely duplex spondylium, or absent entirely, two short accessory septa may be present; cardinal process rare, diductor muscles attach on callosity or narrow shelf at posterior of notothyrial cavity; socket plates subparallel to divergent, commonly continue anteriorly into short divergent extensions, rarely with 2 or 4 long accessory septa, or forming a kind of septalium simplex; adductor muscle field commonly well developed, rarely slightly elevated, with weak callosities. *Lower Ordovician (Tremadoc–lower Llanvirn).*

Clarkella Walcott, 1908, p. 110 [**Polytoechia? montanensis* Walcott, 1905, p. 295; OD]. Small to medium shells; smooth; strongly biconvex; uniplication strong and quite angular in some species, present on anterior half only; hinge line narrow, less than half widest part of shell; interareas narrow; teeth small; spondylium simplex supported along entire length by high median septum that extends anterior to spondylium; 2 or more short accessory septa present rarely in some species; socket plates fairly long, shallow; 4, less commonly 2, long accessory septa support socket plates. *Lower Ordovician (Tremadoc–Arenig):* USA, Canada, southwestern China, Korea, Russia, Siberia, Kazakhstan.——Fig. 633,*1a–b.* **C. montanensis* (Walcott), Montana, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×1.5 (Ulrich & Cooper, 1938).——Fig. 633,*1c–d. C. mcgerriglei* Ulrich & Cooper, Hastings Creek Formation, Quebec, Canada; *c,* paratype, ventral valve exterior; *d,* paratype, dorsal valve exterior, USNM 91477, ×2.5 (new).——Fig. 633,*1e–g. C.* sp.; *e,* ventral valve interior, Hastings Creek Formation, Quebec, Canada, ×3 (Schuchert & Cooper, 1932); *f,* dorsal valve interior, Upper Cool Creek Formation, Oklahoma, USA; *g,* anterior view of *f,* Upper Cool Creek Formation, Oklahoma, USA, USNM 116750, ×2.5 (new).

Acanthoglypha Williams & Curry, 1985, p. 257 [**Streptis affinis* Reed in Gardiner & Reynolds, 1909, p. 151; OD]. Parvicostellate with strong concentric lamellae bearing hollow, bifurcating spines; moderately ventribiconvex; subquadrate in outline; weakly uniplicate; hinge line wide, but narrower than widest part of shell; interareas reduced; teeth weak; sessile spondylium supported anteriorly only by low, wide median ridge that does not extend anterior to spondylium; accessory septa absent; socket plates widely divergent, lacking anterior extensions; dorsal adductor muscle field elongate oval, strongly elevated, and marked by strong callosities. [Cocks (1978) reexamined the lectotype of *Streptis affinis* and placed the species in *Calliglypha;* differences in ornament and dorsal muscle field warrant separate generic status for *Acanthoglypha* and *Calliglypha.*] *Lower Ordovician (Arenig):* Ireland. ——Fig. 633,*2a–g.* **A. affinis* (Reed), Tourmakeady Limestone; *a,* dorsal valve exterior mold, ×3; *b,* bifurcating spines, ×14; *c,* dorsal valve exterior, anterior view, ×3; *d,* ventral valve exterior, anterior view; *e,* ventral valve interior, ×5; *f,* dorsal valve interior; *g,* dorsal valve interior, ×4 (Williams & Curry, 1985).

Calliglypha Cloud, 1948, p. 468 [**C. miseri;* OD]. Small shells; fine costellae and strong concentric lamellae intersect to form nodular ornament; strongly biconvex; subquadrate outline; weakly uniplicate; hinge line wide, often widest part of shell; interareas relatively wide; teeth strong; narrow spondylium simplex; accessory septa absent; socket plates short, shallow, divergent, lacking anterior extensions. *Lower Ordovician (Arenig):* USA, Britain, Russia, ?Argentina.——Fig. 633,*4a–g.* **C. miseri,* El Paso Formation, Texas, USA; *a,* ventral valve exterior; *b,* ventral valve exterior, anterior view, ×2; *c,* dorsal valve exterior, ×3; *d,* ventral valve interior, ×2; *e,* ventral valve interior, oblique view; *f,* dorsal valve interior; *g,* dorsal valve interior, oblique view, ×3 (Cloud, 1948).

Diaphelasma Ulrich & Cooper, 1936, p. 629 [**D. pennsylvanicum;* OD]. Smooth shells; very strongly biconvex; commonly broadly uniplicate, but width and depth varies; hinge line narrow; teeth strong; spondylium simplex supported along entire length by high median septum that extends anterior to spondylium for considerable distance, in some individuals most extreme posterior of spondylium may be sessile; accessory septa absent; minute cardinal process may be present as low ridge on callosity at valve posterior, rarely on short notothyrial platform; short, shallow, widely divergent socket plates, supported in some species by 2 short accessory septa; elongate oval dorsal adductor muscle field poorly developed. *Lower Ordovician (Arenig):* USA, Canada, Argentina, Britain, Russia.——Fig. 633,*3a–i.* **D. pennsylvanicum,* Longview Limestone, Pennsylvania, USA; *a,* ventral valve exterior; *b,* ventral valve exterior, lateral view; *c,* ventral valve exterior, anterior view; *d,* dorsal valve exterior; *e,* dorsal valve exterior, lateral view; *f,* dorsal valve exterior, anterior view, ×1.5; *g,* ventral valve interior, ×3; *h,* dorsal valve interior; *i,* dorsal valve interior, oblique view, ×1.5 (Ulrich & Cooper, 1938).

Fenxiangella Wang, 1978, p. 224 [**F. deltoides;* OD]. Small smooth shells, length and width subequal; moderately biconvex; subtriangular outline; weakly uniplicate near anterior margin only; hinge line narrow; dental plates subparallel, spondylium, median septum, and accessory septa absent; deep, divergent socket plates, lacking anterior extensions; accessory septa absent; dorsal adductor muscle field poorly known. [Genus rather poorly known.] *Lower Ordovician (Arenig):* southwestern China.——Fig. 634,*1a–d.* **F. deltoides,* Dawan Formation, Hubei; *a,* dorsal valve exterior; *b,* articulated valves, ventral on left; *c,* anterior view, ventral below; *d,* posterior view, ventral below, ×4 (Wang, 1978).

Stichotrophia Cooper, 1948, p. 473 [**S. lamellata;* OD]. Finely costellate with strong concentric lamellae; subquadrate to subelliptical in outline;

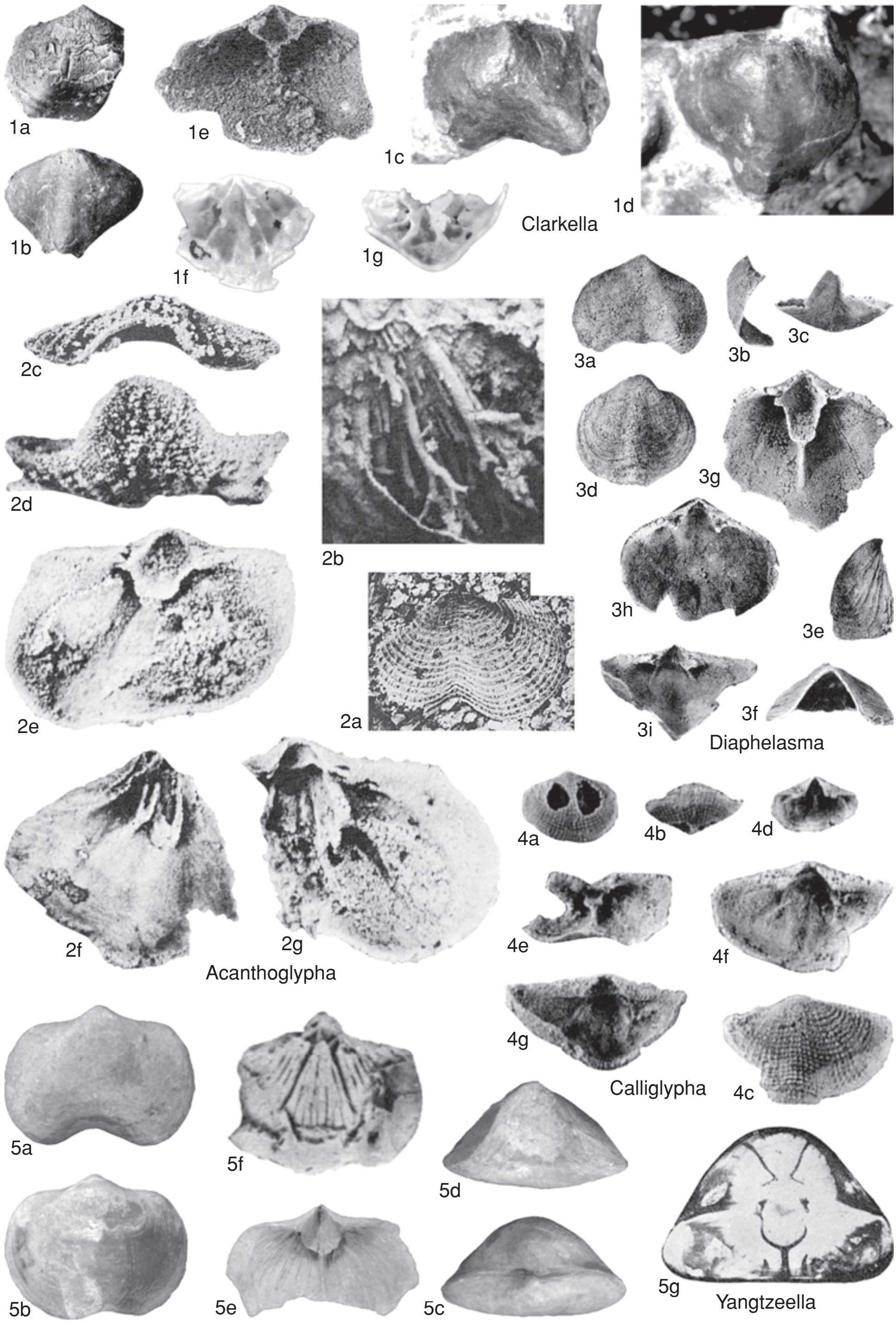

FIG. 633. Clarkellidae (p. 944–947).

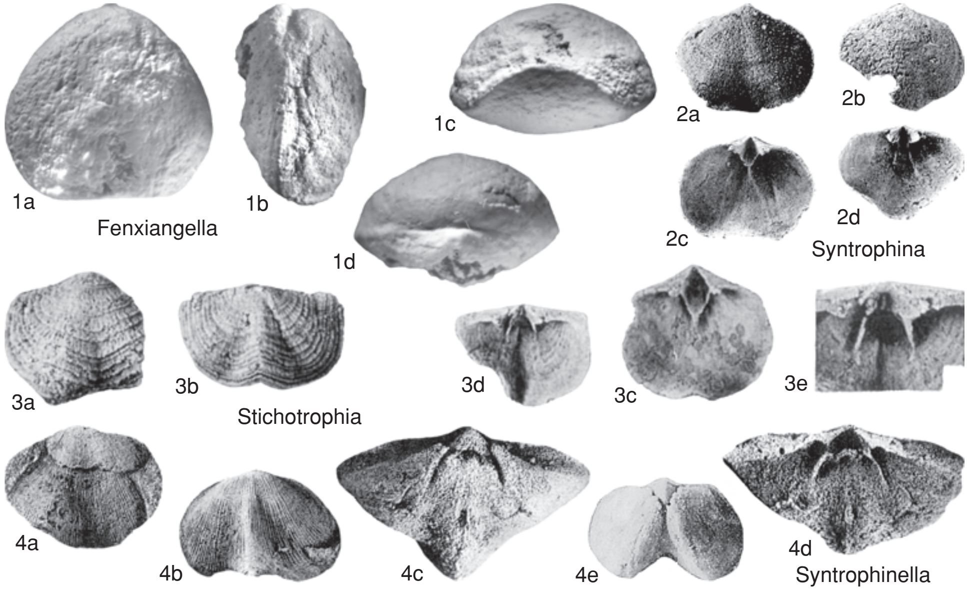

FIG. 634. Clarkellidae (p. 944–946).

hinge line wide, but narrower than widest part of shell; interareas relatively wide; teeth strong; sessile spondylium, supported at anterior only by low, narrow median septum that does not extend anterior to spondylium; accessory septa absent; cardinal process may be present as low ridge on callosity at valve posterior; subparallel socket plates continue anteriorly into short, receding, divergent extensions [these extensions have been referred to in the literature as accessory septa, but they are coplanar with the socket plates and do not support them]; dorsal adductor muscle field not well developed. *Lower Ordovician (Arenig):* USA, southern China, ?Russia.——FIG. 634,*3a–e.* **S. lamellata,* Longview Limestone, Virginia, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior; *d,* dorsal valve interior, ×2; *e,* close up of *d,* ×4 (Cooper, 1948).

Syntrophina SCHUCHERT & COOPER, 1931, p. 247 [**Syntrophia campbelli* WALCOTT, 1908, p. 107; OD] [=*Syntrophina* ULRICH in WELLER & ST. CLAIR, 1928, p. 74, *nom. nud.*]. Smooth shells, with strong concentric lamellae in some species [not visible on type species]; uniplication variably developed; hinge line narrow; teeth strong; spondylium simplex relatively short and narrow, may be sessile at extreme posterior of valve; 2 short accessory septa present rarely in some species; deep petaloid socket plates continue anteriorly into short, divergent extensions, similar to *Stichotrophia. Lower Ordovician (Tremadoc):* USA, Canada, Argentina, Ireland, Kazakhstan, Novaya Zemlya, China, India.——FIG. 634,*2a–d.* **S. campbelli* (WALCOTT), McKenzie Hill Formation, Oklahoma, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Cooper, 1952).

Syntrophinella ULRICH & COOPER in KOBAYASHI, 1934, p. 164 [**S. typica;* OD] [=*Syntrophinella* SCHUCHERT & COOPER, 1932, p. 224, *nom. nud.*]. Finely costellate; entire valve strongly uniplicate, may be quite angular; hinge line narrow; sessile spondylium, supported at anterior only by low, narrow median septum that extends anterior to spondylium; 2 very short accessory septa may be present near the spondylium posterior; subparallel socket plates continue anteriorly into short, widely divergent extensions, similar to *Stichotrophia. Lower Ordovician (Tremadoc):* USA, Canada, China, North Korea, Kazakhstan.——FIG. 634,*4a–e.* **S. typica,* Longview Limestone; *a,* ventral valve exterior, wax replica of mold, Virginia, USA; *b,* dorsal valve exterior, wax replica of mold, Virginia, USA, ×2; *c,* dorsal valve interior mold, Virginia, USA; *d,* wax replica of mold in *c,* Virginia, USA, ×3 (Ulrich & Cooper, 1938); *e,* ventral valve interior mold, Alabama, USA, ×2 (Kobayashi, 1934).

Yangtzeella KOLAROVA, 1925, p. 219 [**Schizophoria poloi* MARTELLI, 1901, p. 302; OD]. Large smooth shells; moderately biconvex; weakly uniplicate; hinge line wide, but narrower than widest part of shell; large, knoblike teeth and sockets may interlock in some individuals; wide spondylium appears to be supported along entire length by low, wide, long duplex median septum; from 2 to 6 short accessory septa commonly present, not prolonged in front of spondylium; socket plates converge to form short, deep septalium-like structure supported by 2 widely spaced, divergent septa that extend anteriorly of so-called septalium for some distance; from 2 to 4 short accessory septa present posteriorly; it is unclear whether short crura may be present; dorsal adductor muscle field poorly developed. [MARTELLI (1901) named the type specimens *Schizophoria poloi.* WELLER (1913) subsequently and erroneously referred these specimens to *Triplecia poloi,* as have many others including KOLAROVA (1925; while reassigning them to *Yangtzeella*), causing some confusion in the literature.] *Lower Ordovician (Tremadoc–lower Llanvirn):* China, ?Kazakhstan.——FIG. 633,*5a–f.* **Y. poloi* (MARTELLI), Arenig, Dawan Formation; *a,* ventral valve exterior, Hubei; *b,* dorsal valve exterior, Hubei; *c,* articulated valves, posterior view, ventral valve below, Hubei; *d,* articulated valves, anterior view, ventral valve below, Hubei; *e,* ventral valve interior, USNM 339345, Hubei, ×1 (new); *f,* dorsal valve interior mold, Guizhou, ×1 (Xian & Jiang, 1978).——FIG. 633,*5g. Y. yichangensis* ZENG; section through articulated valves, ventral valve below, showing duplex spondylium and divergent dorsal septa, ×2 (Zeng, 1986).

Family PORAMBONITIDAE Davidson, 1853

[Porambonitidae DAVIDSON, 1853b, p. 99]

Large shells (greater than 2 cm) with fine costellae and concentric lamellae that intersect to form radial rows of subcircular pits; outline highly variable; strongly uniplicate; hinge line varies in width, interareas reduced; teeth strong and knoblike, possibly cyrtomatodont; very long dental plates vary in orientation from subparallel to convergent, forming long sessile spondylium supported at anteriormost edge by low, wide median ridge; cardinal process commonly absent, rarely present as low ridge on narrow shelf at posterior of notothyrial cavity; long, subparallel to convergent socket plates commonly continue anteriorly into long, subparallel extensions that may converge at anteriormost end, appearing to form long sessile septalium; adductor muscle field commonly well developed with weak callosities. *Lower Ordovician (Arenig)–lower Silurian (Wenlock).*

Porambonites PANDER, 1830, p. 95 [**P. intermedia;* SD HALL & CLARKE, 1893, p. 225]. Biconvexity very strong; uniplication commences on anterior half; dental plates commonly remain parallel for most of their considerable length, converging only at their anteriormost ends to join with median ridge; ventral adductor muscle field anterior to and commonly separated from diductors by very low ridge; very long socket plates and extensions commonly remain subparallel for entire length, may converge only at their anteriormost ends to join with median ridge; internal features in both valves commonly thicken and coalesce in older individuals. [Loss of the type specimens of *P. intermedia,* the legally established type species, has caused some systematists to recognize *P. reticulatus* informally instead, in agreement with more than a century of usage. See BIERNAT, 1965, p. 532 for further discussion on designation of type species of this genus.] *Lower Ordovician (Arenig)–lower Silurian (Wenlock):* Canada, Argentina, Russia, Europe, Himalayas, India, China, Australia, South Africa.

P. (Porambonites). Subelliptical to circular in outline, valve proportions may be quite variable; hinge line distinct but narrow, less than half widest part of shell; cardinal process commonly absent, rarely present as low ridge. *Lower Ordovician (Arenig)–Upper Ordovician (Ashgill):* Russia, Estonia, Europe, Britain, Himalayas, China, Australia, ?South Africa.——FIG. 635,*1a–e. P. (P.) planus* PANDER, Arenig, Glauconite limestone, Estonia; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve on right; *c,* dorsal valve exterior; *d,* posterior view, ventral valve above; *e,* anterior view, ventral valve above, USNM 81599, ×1 (new).——FIG. 635,*1f–g. P. (P.) intercedens* PANDER, Upper Ordovician, Hohenholm, Estonia; *f,* dorsal valve exterior; *g,* posterior view, ventral valve above, beaks ground off showing dental and socket plates, USNM 26897, ×1 (new).——FIG. 635,*1h–i. P. (P.) schmidti* NOETLING, lower Llanvirn, Estonia; *h,* ventral valve interior; *i,* dorsal valve interior, ×1 (Schuchert & Cooper, 1932).

P. (Equirostra) COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Isorhynchus* KING, 1850, p. 112, *non* SCHOENHERR, 1833 [**Terebratulites aequirostris* VON SCHLOTHEIM, 1820 in 1820–1823, p. 282; OD]. Subtriangular in outline, longer than wide; hinge line extremely narrow, astrophic in some individuals. *Lower Ordovician (lower Llanvirn)–Upper Ordovician (Caradoc):* Russia, Estonia, Europe, Canada.——FIG. 635,*3a–e.* **P. (E.) aequirostris* (VON SCHLOTHEIM), Vaginaten Limestone, Russia; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve on right; *c,* dorsal valve exterior; *d,* posterior view, ventral valve above; *e,* anterior view, ventral valve above, USNM 26898, ×1 (new).——FIG. 635,*3f–g. P. (E.) baueri* (NOETLING), middle Ordovician, Estonia; *f,* ventral valve interior; *g,* dorsal valve interior, USNM 85369A, ×1 (new).

P. (Noetlingia) HALL & CLARKE, 1893, p. 229 [**Spirifer tcheffkini* DE VERNEUIL, 1845, p. 129; M]. Moderate to large size; subquadrate to subelliptical in outline; hinge line wide, but narrower than widest part of shell; cardinal process present as low ridge on narrow shelf in notothyrial cavity; long socket plates converge and

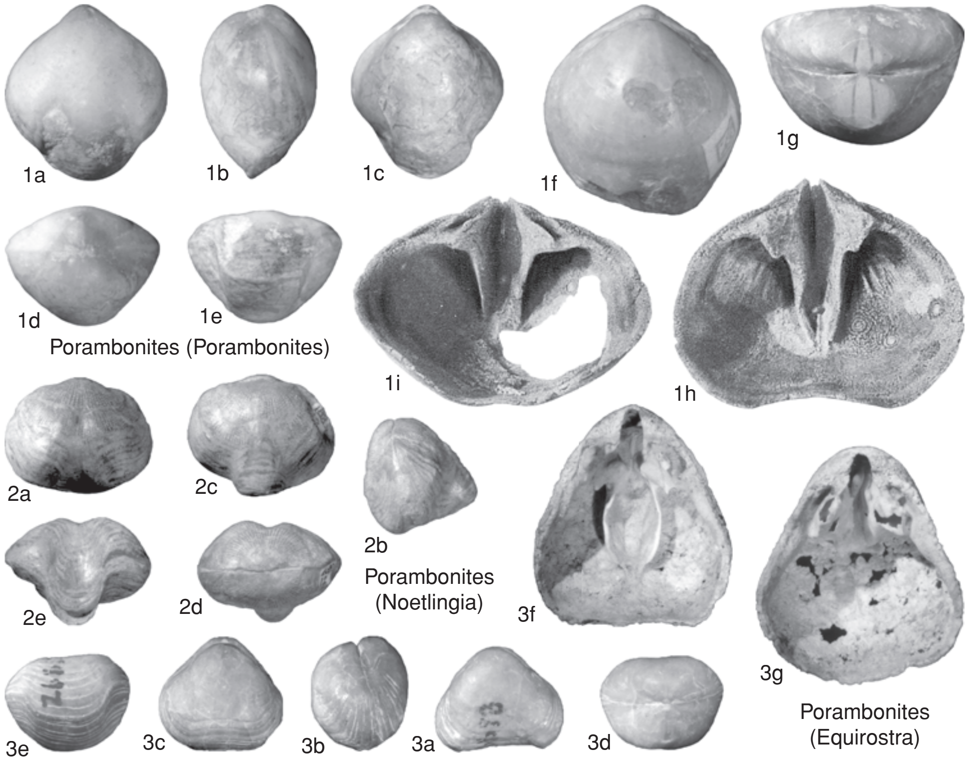

FIG. 635. Porambonitidae (p. 947–948).

unite anteriorly only with short median septum to form long sessile septalium. *lower Silurian (Llandovery–Wenlock):* Russia.——FIG. 635,*2a–e*. **P. (N.) tcheffkini* (DE VERNEUIL), Pulkovka River; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve on left; *c,* dorsal valve exterior; *d,* posterior view, ventral valve above; *e,* anterior view, ventral valve above, USNM 346824, ×1 (new).

Superfamily CAMERELLOIDEA Hall & Clarke, 1895

[*nom. correct. et emend.* CARLSON, herein, *pro* Camerellacea NIKIFOROVA, 1960d, p. 201, *nom. transl. et correct. ex* Camarellidae HALL & CLARKE, 1895, p. 355]

Commonly costate or paucicostate, rarely costellate or smooth; outline subtriangular to subcircular, less commonly subelliptical; hinge line astrophic, rarely narrow and strophic; interareas commonly obsolete; dental plates converge to form simplex or duplex spondylium, rarely sessile spondylium; accessory septa absent; ventral mantle canals unknown; cardinal process absent; outer hinge plates converge and either remain discrete, subparallel and commonly continue anteriorly into long, subparallel inner hinge plates, or may converge to form simplex, duplex, or less commonly sessile, septalium; short, rodlike or bladelike crura present. *Lower Ordovician (Arenig)–Lower Devonian (Pragian).*

Family CAMERELLIDAE Hall & Clarke, 1895

[*nom. correct.* SCHUCHERT & COOPER, 1931, p. 248, *pro* Camarellidae HALL & CLARKE, 1895, p. 355; *emend.,* ULRICH & COOPER, 1938, p. 248] [=Brevicameridae COOPER, 1956a, p. 560; Karakulinidae ANDREEVA, 1972, p. 55]

Small shells; paucicostate, costate, or smooth; commonly strongly uniplicate, may be rectimarginate; spondylium simplex supported by high median septum that commonly extends anterior to spondylium, rarely sessile or duplex spondylium, less commonly subparallel dental plates; narrow, relatively long hinge plates commonly converge on long median septum to form deep, narrow septalium simplex or duplex, rarely sessile or absent; alate plates absent; crura, when present, rodlike. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian).*

Subfamily CAMERELLINAE Hall & Clarke, 1895

[*nom. transl. et correct.* BIERNAT, 1965, p. 535, *ex* Camarellidae HALL & CLARKE, 1895, p. 355]

Spondylium simplex supported by high, narrow median septum, rarely as sessile or duplex spondylium. *Lower Ordovician (Arenig)–Lower Devonian (Lochkovian).*

Camerella BILLINGS, 1859b, p. 301 [**C. volborthi;* SD HALL & CLARKE, 1893, p. 219] [=*Camarella* DALL, 1877, p. 18, *nom. null.; Rhynchocamara* SCHUCHERT & COOPER, 1931, p. 248 (type, *R. plicata*)]. Most species small, some moderate in size; type species and most others paucicostate, some species with strong costae on entire valve, few species with tiny granules or bumps over surface; uniplication commonly present on anterior third of valve only; teeth small; relatively long spondylium simplex, rarely duplex; short, deep outer hinge plates, nearly horizontal in some species; long, narrow inner hinge plates converge and unite with long median septum to form short, deep, narrow septalium duplex; short, rodlike crura visible in some species, not type species; dorsal adductor muscle field weakly developed. [*Rhynchocamara* was named for rectimarginate forms; uniplication varies sufficiently to warrant synonymy.] *Lower Ordovician (upper Llanvirn)–Silurian (Wenlock):* Canada, USA, Britain, northern Europe, Russia, Siberia, Kazakhstan, China, Mongolia, ?India, ?Bolivia.——FIG. 636,*1a–d.* **C. volborthi,* upper Llanvirn, Rockland Formation, Ontario, Canada; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve right; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral below, ×2 (Cooper, 1956a).——FIG. 636,*1e–f. C. bella* FENTON; upper Llanvirn, Macy Formation, Missouri, USA; *e,* ventral valve interior; *f,* dorsal valve interior, ×2 (Cooper, 1956a).

Bleshidium HAVLÍČEK, 1982b, p. 371 [**Atrypa patellina* BARRANDE, 1879b, pl. 147; OD] [=*Bleshidimerus* HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 101 (type, *Rhynchonella irregularis* BARRANDE, 1879b, pl. 4)]. Nearly circular outline; moderately biconvex; costae present on fold and sulcus only, concentric lamellae present as gentle rugae; uniplication highly variable, may be absent; hinge line narrow, less than half widest part of valve; spondylium simplex supported by very high, narrow median septum; socket plates short, deep, convergent; anterior extensions [comparable to inner hinge plates] absent; crura unknown; median septum may be absent or present and short; septalium absent. [*Bleshidimerus* is very strongly uniplicate with angular, bifurcating costae; appears to be within variability of *Bleshidium.*] *Silurian (Wenlock–Přídolí):* Czech Republic.——FIG. 636,*2a–e.* **B. patellinum* (BARRANDE), lower Ludlow, upper Kopanina Formation, Prague basin, Bohemia; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, anterior view, ventral above, ×6.2 (Havlíček & Štorch, 1990); *d–e,* transverse sections, ventral valve above, ×15 (Havlíček, 1982b).——FIG. 636,*2f. B.* sp. cf. *B. papalas* HAVLÍČEK & ŠTORCH, Motol Formation; ventral valve interior mold, ×3 (Havlíček & Štorch, 1990).

?Branconia GAGEL, 1890, p. 62 [**B. borussica;* M]. Large smooth shell; subelliptical outline, wider than long; very strongly ventribiconvex; strongly rostrate; strongly unisulcate; ventral and dorsal interiors unknown, except for long median septum present in both valves. [Only 1 poorly known specimen exists; it may not be a syntrophiidine.] *Upper Ordovician (Caradoc):* ?Poland (Prussia).——FIG. 637,*1a–d.* **B. borussica; a,* drawings of ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, lateral view, ventral on left; *d,* articulated valves, posterior view, ventral above, ×1 (Gagel, 1890).

Brevicamera COOPER, 1956a, p. 560 [**B. camerata;* OD]. Small, paucicostate shells; subelliptical outline, wider than long; biconvexity strong; uniplication broad and strong, present only on anterior half of valves; very short spondylium simplex supported posteriorly by narrow, commonly low, median septum; short, deep, convergent outer hinge plates; short, rodlike crura present; inner hinge plates converge slightly but join floor of valve in widely separated, subparallel lines to form a broad, long sessile septalium; long, low median septum extending anterior to, and does not support, septalium; dorsal adductor muscle field well developed with weak callosities. *Lower Ordovician (upper Llanvirn):* southern USA.——FIG. 637,*3a–g.* **B. camerata,* Pratt Ferry Formation, Alabama; *a,* ventral valve exterior; *b,* ventral valve, lateral view; *c,* ventral valve, anterior view; *d,* dorsal valve exterior; *e,* dorsal valve, lateral view; *f,* ventral valve interior, ×2; *g,* dorsal valve interior, ×4 (Cooper, 1956a).

Idiostrophia ULRICH & COOPER, 1936, p. 631 [**I. perfecta;* OD] [=*Trigonotrophia* ANDREEVA, 1972, p. 54 (type, *Idiostrophia paucicostata* COOPER, 1956a, p. 588)]. Type species small, others may be very small; distinctly triangular outline, sides of both valves do not taper gently to commissure, but flex sharply to meet in a plane perpendicular to commissural plane; paucicostate; rectimarginate, but single, narrow radial groove runs down center of each valve; socket plates short, deep, convergent; anterior extensions [comparable to inner hinge plates] absent; crura unknown; septalium rather long. [*Trigonotrophia* lacks the distinctive strangulate grooves and possesses only 3 to 4 costae on anterior margin; is otherwise indistinguishable from *Idiostrophia.*] *Lower Ordovician (Arenig–upper Llanvirn):* Canada, USA, Argentina, Britain, Europe, northern Russia, Siberia.——FIG. 637,*6a–e.*

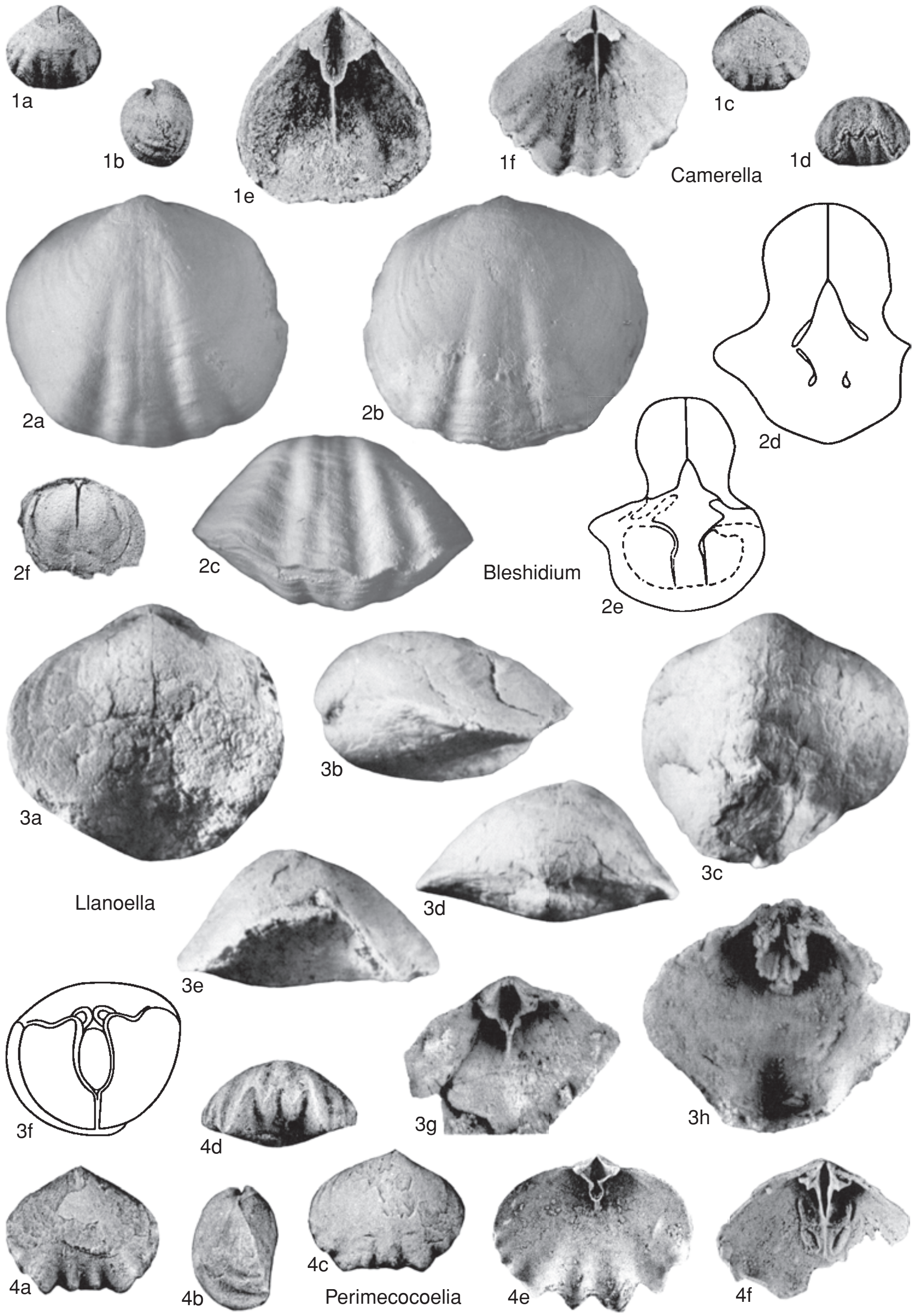

FIG. 636. Camerellidae (p. 949–952).

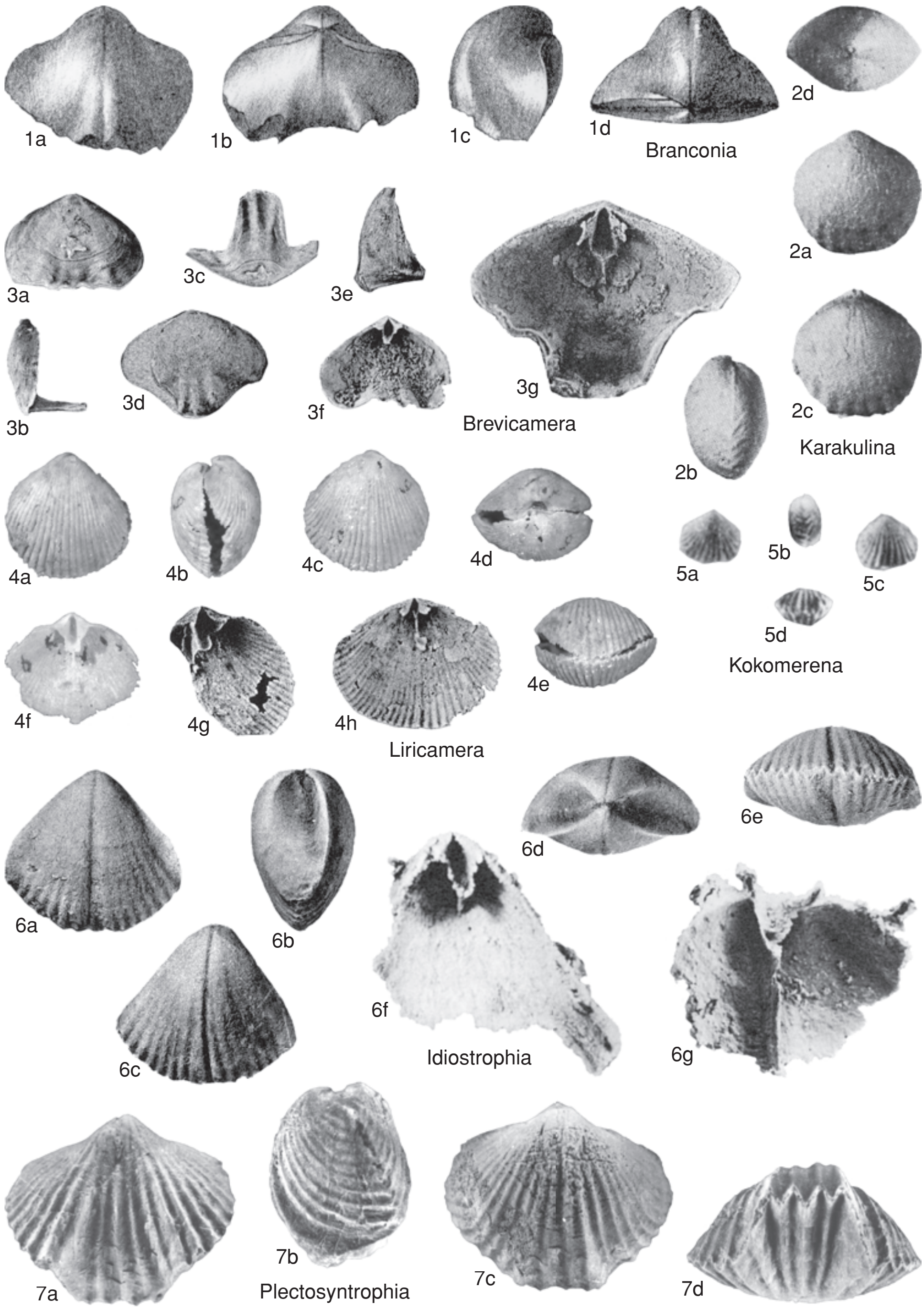

FIG. 637. Camerellidae (p. 949–953).

**I. perfecta,* upper Llanvirn, Mystic conglomerate, Quebec, Canada; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral below; *e,* articulated valves, anterior view, ventral below, ×1.5 (Ulrich & Cooper, 1938).——Fig. 637,*6f–g. I. costata* Ulrich & Cooper, upper Arenig, Tourmakeady Limestone, Ireland; *f,* ventral valve interior, ×5; *g,* dorsal valve interior, oblique anterior view, ×11 (Williams & Curry, 1985).

Karakulina Andreeva, 1972, p. 55 [**K. nana;* OD]. Elongate oval in outline; paucicostate; rectimarginate; dorsal median septum and septalium absent. [Valve interiors rather poorly known.] *Lower Ordovician (Arenig):* northern Russia (Urals).——Fig. 637,*2a–d.* **K. nana,* Kuragan Suite, Kinderlya River; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral above, ×4 (Andreeva, 1972).

Kokomerena Misius, 1986, p. 182 [**K. prima;* OD]. Subtriangular to subelliptical in outline, wider than long; entire valve costate; moderately biconvex; weak uniplication, present near anterior margin only; teeth strong; sessile spondylium may be supported at anterior only by low, wide median ridge, which may be absent; fairly long, wide, sessile septalium present; dorsal median septum absent. *Upper Ordovician (lower Caradoc):* Kirgizia.——Fig. 637,*5a–d.* **K. prima,* Tabylgat River; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral above, ×1 (Misius, 1986).

Liricamera Cooper, 1956a, p. 592 [**L. nevadensis;* OD]. Nearly circular in outline; entire valve finely costellate; moderately biconvex; commonly rectimarginate, may be very weakly uniplicate; hinge line narrow, less than half widest part of shell; interareas narrow; teeth strong; deep spondylium simplex of medium length; crura very short, rodlike; dorsal interior otherwise similar to *Camerella. Lower Ordovician (lower Llanvirn–upper Llanvirn):* western USA, northwestern Tibet.——Fig. 637,*4a–h.* **L. nevadensis,* lower Llanvirn, Pogonip Group, Nevada, USA; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral above; *e,* articulated valves, anterior view, ventral above; *f,* ventral valve interior, USNM 117174, ×1.6 (new); *g,* ventral valve interior, oblique view; *h,* dorsal valve interior, ×2 (Cooper, 1956a).

Llanoella Boucot, 1975a, p. 351 [**L. stephensi;* OD]. Medium to large shells; outline subelliptical, wider than long; commonly smooth, larger individuals with costae at anterior margin only; moderately biconvex; strong uniplication, present on entire valve; teeth relatively strong; spondylium simplex much like *Camerella;* outer hinge plates convergent; long inner hinge plates converge both dorsally and ventrally to form long cylindrical septalium with ventral edge of each plate terminating in an unusual tubular structure; cruralium housing dorsal adductor muscle field present anterior to septalium. *Lower Devonian (Lochkovian):* southern and western USA.——Fig. 636,*3a–f.* **L. stephensi,* Pillar Bluff Limestone, Texas; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral below; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral below; *e,* articulated valves, anterior view, ventral below, ×1.5; *f,* drawing of transverse section, dorsal valve, ×3 (Boucot, 1975a).——Fig. 636,*3g–h. L.* sp., Rabbit Hill Limestone, Nevada; *g,* ventral valve interior, ×3; *h,* dorsal valve interior, ×4 (Johnson, 1970b).

Neostrophia Ulrich & Cooper, 1936, p. 631 [**N. subcostata;* OD]. Smooth with very short, weak costae near anterior margin only, present only on fold and sulcus; moderately biconvex; uniplication commonly broad and strong, may be weak, only on anterior third of valves; hinge line extremely narrow, but discernible; interiors similar to *Camerella. Lower Ordovician (upper Llanvirn):* Canada, USA.——Fig. 638,*2a–e.* **N. subcostata,* Mystic conglomerate, Quebec, Canada; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral below; *e,* posterior section through articulated valves, ventral below, ×2 (Ulrich & Cooper, 1938).

Perimecocoelia Cooper, 1956a, p. 593 [**P. semicostata;* OD]. Most species moderate in size, some small; subelliptical in outline, wider than long; paucicostate, with short broad costae present only on anterior third of valves; moderately biconvex; spondylium simplex of variable length that narrows anteriorly, in some individuals nearly divided into anterior-posterior chambers by pinching inward of dental plates near midlength; supported by relatively low, wide median septum; outer hinge plates convergent, receding; long inner hinge plates converge to form long septalium supported by short median septum; crura unknown, but crural bases commonly visible on hinge plates; dorsal adductor muscle field well developed, marked by weak callosities. *Lower Ordovician (upper Llanvirn):* USA, Kazakhstan.——Fig. 636,*4a–f.* **P. semicostata,* USA; *a,* ventral valve exterior, Effna Formation, Virginia; *b,* articulated valves, lateral view, ventral right, Effna Formation, Virginia; *c,* dorsal valve exterior, Effna Formation, Virginia; *d,* articulated valves, anterior view, ventral below, Effna Formation, Virginia; *e,* ventral valve interior, Pratt Ferry Formation, Alabama; *f,* dorsal valve interior, Pratt Ferry Formation, Alabama, ×2 (Cooper, 1956a).

Plectocamara Cooper, 1956a, p. 596 [**P. costata;* OD]. Very small size; outline quite variable; strong, angular costae on entire valve; uniplication broad and strong, on entire valve; narrow sessile spondylium, commonly decreases in width on anterior half, supported at anterior only by short, low, narrow median septum; petaloid socket plates convergent, nearly horizontal, join floor of valve to form short,

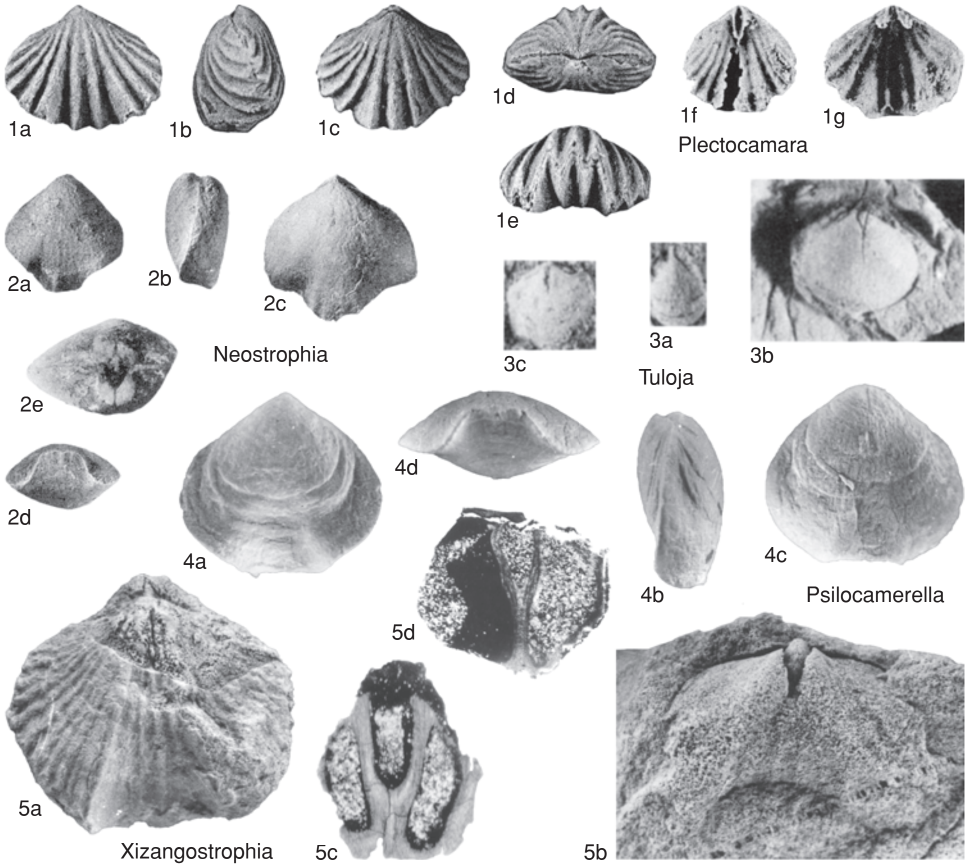

FIG. 638. Camerellidae (p. 952–954).

shallow, sessile septalium; dorsal median septum variable in length or absent; crura unknown, but crural bases visible. *Lower Ordovician (upper Llanvirn)–Upper Ordovician, ?Silurian:* USA, Alaska, Siberia, western China.——FIG. 638,*1a–g.* **P. costata,* upper Llanvirn, Lincolnshire Formation, Tennessee, USA; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral right; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral below; *e,* articulated valves, anterior view, ventral below; *f,* ventral valve interior; *g,* dorsal valve interior, ×3 (Cooper, 1956a).

Plectosyntrophia FU, 1982, p. 129 [**P. qilianshanensis;* OD]. Shells medium in size; subpentagonal in outline, wider than long; strong costae on entire valve; teeth strong; sessile spondylium supported at anterior only by short, low, wide median ridge; septalium duplex long, wide, supported by high median septum; crura unknown. *Lower Ordovician (lower Llanvirn):* northwestern China.——FIG. 637,*7a–d.* **P. qilianshanensis,* Yingou Formation, Gansu; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral below, ×2 (Fu, 1982).

Psilocamerella FU, 1982, p. 128 [**P. planosulcata;* OD] [=*Psilocamerella* FU, 1980, p. 2, *nom. nud.*]. Shells small; subpentagonal in outline, wider than long; smooth, but gentle concentric rugae may be present; moderately biconvex; uniplication may be absent or broad and weak, near anterior margin only; spondylium simplex supported by low, narrow median septum; septalium supported by short median septum; dorsal adductor muscle field unknown. [Dorsal interior poorly known.] *Upper Ordovician (Caradoc):* northwestern China.——FIG. 638,*4a–d.* **P. planosulcata,* Jinghe Formation, Shaanxi; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral below, ×3 (Fu, 1982).

Tuloja SEVERGINA in ROZMAN & SEVERGINA, 1983, p. 24 [**T. karasuensis;* OD]. Very small size; nearly circular outline; smooth, with weak concentric

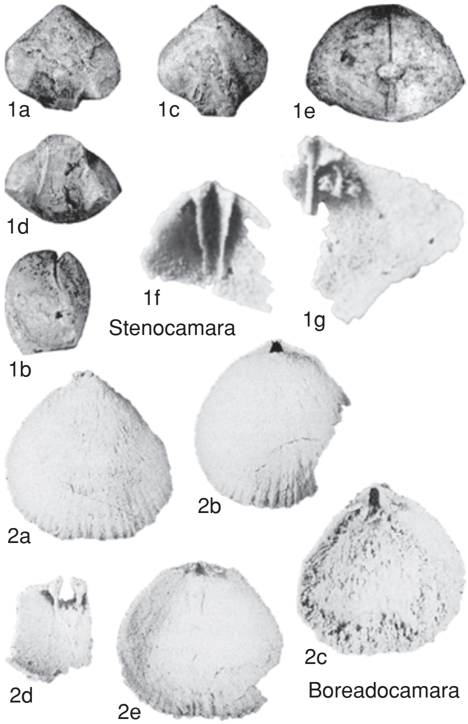

FIG. 639. Camerellidae (p. 954).

lamellae; moderately ventribiconvex; rectimarginate; spondylium simplex supported by long, narrow median septum. [Valve interiors poorly known; may be juvenile of another species.] *Lower Ordovician (upper Llanvirn):* south-central Russia, Mongolia.——FIG. 638,*3a–c.* **T. karasuensis,* Bugryshikhinsk beds, northeastern Gorno-Altay; *a,* ventral valve exterior; *b,* ventral valve interior mold, ×5; *c,* dorsal valve interior mold, ×4 (Rozman & Severgina, 1983).

Xizangostrophia RONG, 1976, p. 150 [**X. sinensis;* OD]. Subpentagonal outline, wider than long; costae on entire valve; moderately biconvex; uniplication broad, strong, on entire valve; spondylium duplex supported by low, wide median septum; cruralium duplex may be present anterior to narrow septalium. [Taxon very poorly known.] *Lower Ordovician (Arenig–lower Llanvirn):* southern Tibet.——FIG. 638,*5a–d.* **X. sinensis,* lower Llanvirn, lower Chiatsun Formation, Nyalam; *a,* dorsal valve exterior; *b,* ventral valve interior mold, ×2; *c,* section through ventral valve showing spondylium duplex; *d,* section through dorsal valve showing septalium or cruralium, ×8 (Rong, 1976).

Subfamily STENOCAMARINAE Cooper, 1956

[Stenocamarinae COOPER, 1956a, p. 602]

Discrete, subparallel dental plates, spondylium lacking. *Lower Ordovician (Arenig–upper Llanvirn), ?Upper Ordovician (Ashgill).*

Stenocamara COOPER, 1956a, p. 602 [**S. perplexa;* OD]. Small to medium in size; outline similar to *Camerella;* type species smooth, other species may be paucicostate, but only on fold and sulcus near anterior margin; uniplication broad, strong, angular, present only on anterior half of valves; teeth small; discrete dental plates long, very closely spaced; median septum absent; short, shallow socket plates converge and unite with very long, high median septum to form short, deep, wide septalium; crura unknown; dorsal adductor muscle field not well known. *Lower Ordovician (Arenig–upper Llanvirn), ?Upper Ordovician (Ashgill):* USA, Norway, Estonia, north-central Russia.——FIG. 639,*1a–e.* **S. perplexa,* upper Llanvirn, Mosheim Formation, Tennessee, Alabama, USA; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral below, ×1; *e,* articulated valves, posterior view, ventral below, ×2 (Cooper, 1956a).——FIG. 639,*1f–g. S.*? sp., lower Llanvirn, Antelope Valley Limestone, Nevada, USA; *f,* ventral valve interior; *g,* dorsal valve interior, ×5 (Ross, 1967).

Boreadocamara CURRY & WILLIAMS, 1984, p. 308 [**B. fragilis;* OD]. Small size; nearly circular in outline; weak costae present on entire valve, stronger near anterior margin only; moderately biconvex; rectimarginate; hinge line narrow, less than half widest part of shell; discrete dental plates very short; short socket plates discrete, septalium absent; elongate dorsal adductor muscle field well developed. *Lower Ordovician (Arenig):* Scotland.——FIG. 639,*2a–e.* **B. fragilis,* Ben Suardal Limestone, Isle of Skye; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* ventral valve interior; *d,* ventral valve interior, oblique view; *e,* dorsal valve interior, ×4 (Curry & Williams, 1984).

Family PARASTROPHINIDAE Schuchert & LeVene, 1929

[*nom. transl.* ULRICH & COOPER, 1938, p. 248, *ex* Parastrophininae SCHUCHERT & LEVENE, 1929b, p. 121; *emend.*, ST. JOSEPH, 1941, p. 371] [=Anastrophiidae NIKIFOROVA, 1960d, p. 202]

Commonly costate, may be costellate, rarely smooth; weakly to strongly uniplicate; spondylium duplex supported by low median septum, less commonly as sessile duplex spondylium; outer hinge plates short, inner hinge plates long and parallel or converge to form simplex or duplex septalium, rarely sessile septalium; 2 relatively large alate plates present, diverge anterolaterally from outer side of hinge plates, as dorsal extensions of bladelike crura. *Lower Ordovician (upper Llanvirn)–Lower Devonian (Pragian).*

Parastrophina SCHUCHERT & LEVENE, 1929b, p. 121, *nom. nov. pro Parastrophia* HALL & CLARKE, 1893, p. 221, *non* FOLIN, 1875 [**Atrypa hemiplicata* HALL, 1847, p. 144; OD]. Small to medium in size; subelliptical in outline, wider than long; strong, angular costae present near anterior margin only, valves otherwise smooth; dorsibiconvexity strong; dorsal umbo commonly more pronounced than ventral, may make valves appear falsely unisulcate; uniplication broad and strong, commences anterior to umbo; teeth strong; narrow spondylium duplex supported for entire length by low, narrow median septum that extends anterior to spondylium; short, shallow outer hinge plates, nearly horizontal in some species, extend into long inner hinge plates that converge and unite with long median septum to form long, narrow septalium duplex; long, bladelike crura; dorsal adductor muscle field well developed, elongate oval in outline. *Lower Ordovician (upper Llanvirn)–Upper Ordovician (Ashgill):* USA, eastern Canada, Britain, northern Europe, Ukraine, Russia, Kazakhstan, Siberia, China.——FIG. 640,*1a–e.* **P. hemiplicata* (HALL), upper Llanvirn, Martinsburg Formation, USA; *a,* ventral valve exterior, Virginia; *b,* articulated valves, lateral view, ventral on right, Virginia, ×2; *c,* dorsal valve exterior, Virginia; *d,* articulated valves, anterior view, ventral valve below, Virginia, ×1; *e,* section through articulated valves 9.5 mm from posterior end, dorsal valve above, showing alate plates, New York, ×4 (St. Joseph, 1941).——FIG. 640,*1f–g. P. bilobata* COOPER, upper Llanvirn, Pratt Ferry Formation, Alabama, USA; *f,* ventral valve interior, ×3; *g,* dorsal valve interior, ×4 (Cooper, 1956a).——FIG. 640,*1h. P. rotundiformis* (WILLARD), Caradoc, Prosser Formation, Iowa, USA; articulated valves, interior view of valve posteriors, ventral below, ×3 (Cooper, 1956a).

Anastrophia HALL, 1867a, p. 162–163, *nom. nov. pro Brachymerus* SHALER, 1865, p. 69, *non* DE JEAN, 1834 [**Pentamerus verneuili* HALL, 1857a, p. 104; OD] [=*Savageina* BOUCOT, 1975a, p. 355 (type, *Terebratula deflexa* J. de C. SOWERBY in MURCHISON, 1839, p. 625)]. Strong costae cover entire valve surface, minimal bifurcation anteriorly; exaggerated dorsibiconvexity; uniplication broad and strong; hinge line astrophic, less commonly strophic, of variable width; teeth strong; wide, long sessile spondylium duplex supported anteriorly only by low, narrow median septum that extends anterior to spondylium, less commonly supported along entire length by relatively high duplex median septum; short outer hinge plates, slightly splayed out, that extend into long, subparallel inner hinge plates anterior to long, bladelike crura; median septum and septalium absent; internal features often thickened in older individuals, anterior ends of hinge plates may converge, simulating sessile septalium, not unlike *Porambonites;* alate plates vary in length; adductor muscle field quadrilobate, may have weak callosities. [*Savageina* was distinguished as being about one-half the size of *Anastrophia* and much wider than long, but appears to be within the variability of *Anastrophia;* synonymy follows HAVLÍČEK & ŠTORCH, 1990.] *Silurian (Wenlock)–Lower Devonian (Pragian):* USA, Canada, Britain, Europe, Ukraine, Russia, Kazakhstan, China, Mongolia, Indochina, Australia, Venezuela.

A. (**Anastrophia**). Medium to large size, less commonly small; subelliptical to subtriangular in outline; costae relatively fine; hinge line astrophic or less commonly narrow, strophic. *Silurian (Wenlock)–Lower Devonian (Pragian):* USA, Canada, Britain, Europe, Ukraine, Russia, Kazakhstan, China, Mongolia, Indochina, Australia, Venezuela.——FIG. 640,*2a–f.* **A. (A.) verneuili* (HALL), Lochkovian, lower Helderberg Group, New York, USA; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×1 (Shimer & Shrock, 1944); *c,* ventral valve interior; *d,* dorsal valve interior; *e,* articulated valves, interior view of valve posteriors, ventral below, ×1.5 (Schuchert & Cooper, 1932); *f,* section through articulated valves, dorsal valve below, showing alate plates, ×2 (St. Joseph, 1941).

A. (**Grayina**) BOUCOT, 1975a, p. 354 [**A. magnifica* KOZLOWSKI, 1929, p. 140; OD]. Size variable; outline subquadrate; costae very coarse and angular, with pronounced bifurcation near margins of fold and sulcus; hinge line wide and strophic, may be as wide as widest part of valve; ventral interarea present, varies from reduced to extensive. *Silurian (Wenlock)–Lower Devonian (Pragian):* USA, Canada, Europe, Russia, Kazakhstan, Australia.——FIG. 640,*3a–e.* **A. (G.) magnifica* KOZLOWSKI, Lochkovian, Roberts Mountain Formation, Nevada, USA; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on right; *c,* articulated valves, anterior view, ventral valve below; *d,* ventral valve interior, ×2.5; *e,* dorsal valve interior, ×2 (Johnson, Boucot, & Murphy, 1973).

Eoanastrophia NIKIFOROVA & SAPELNIKOV, 1973, p. 65 [**E. antiquata;* OD]. Similar to *Anastrophia* externally but uniplication broad and shallow, present on entire valve; teeth weak; deep, narrow spondylium duplex supported along entire length by low median septum that does not extend anterior to spondylium; socket plates converge to form deep, narrow septalium simplex supported on long, low

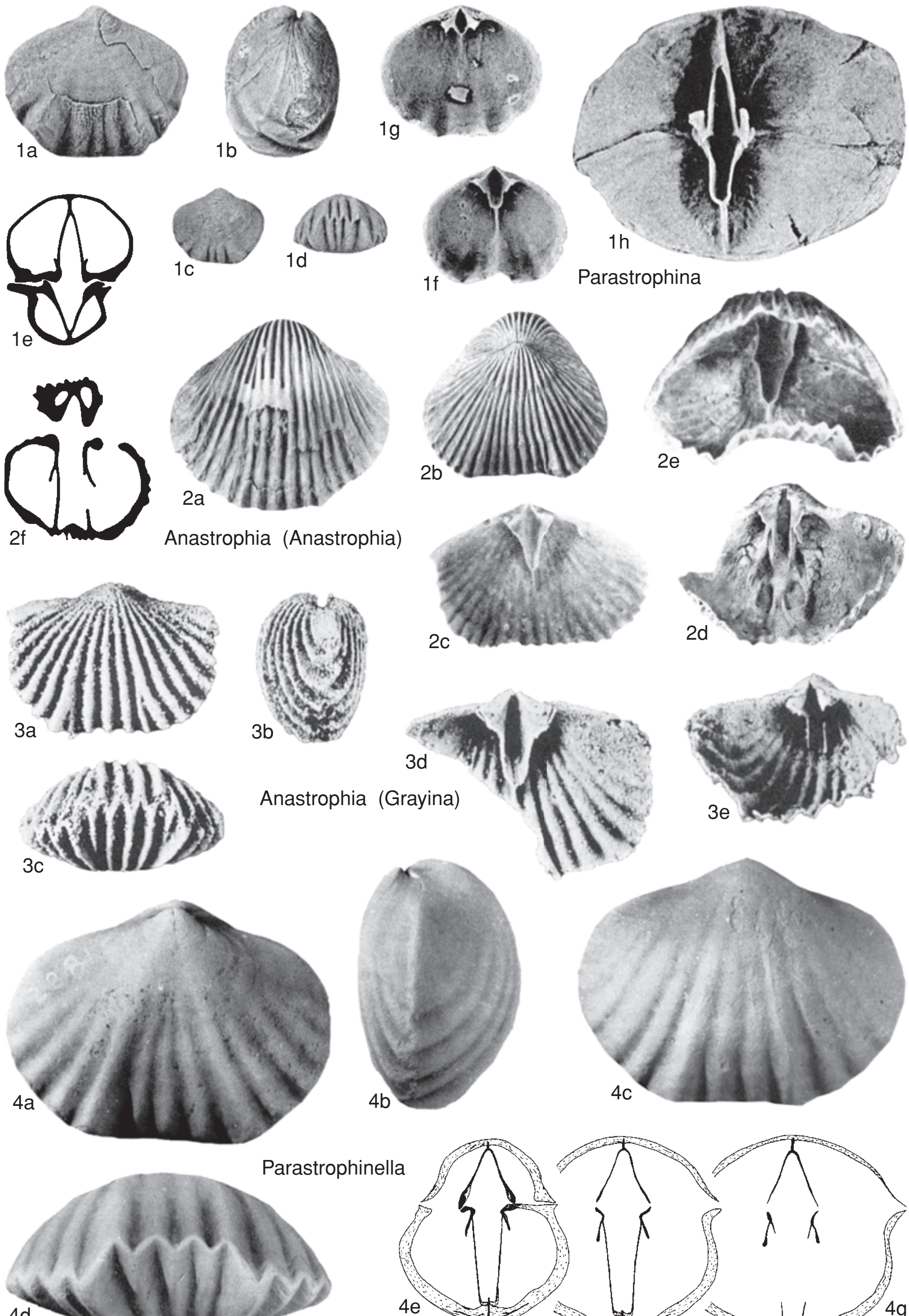

FIG. 640. Parastrophinidae (p. 955–958).

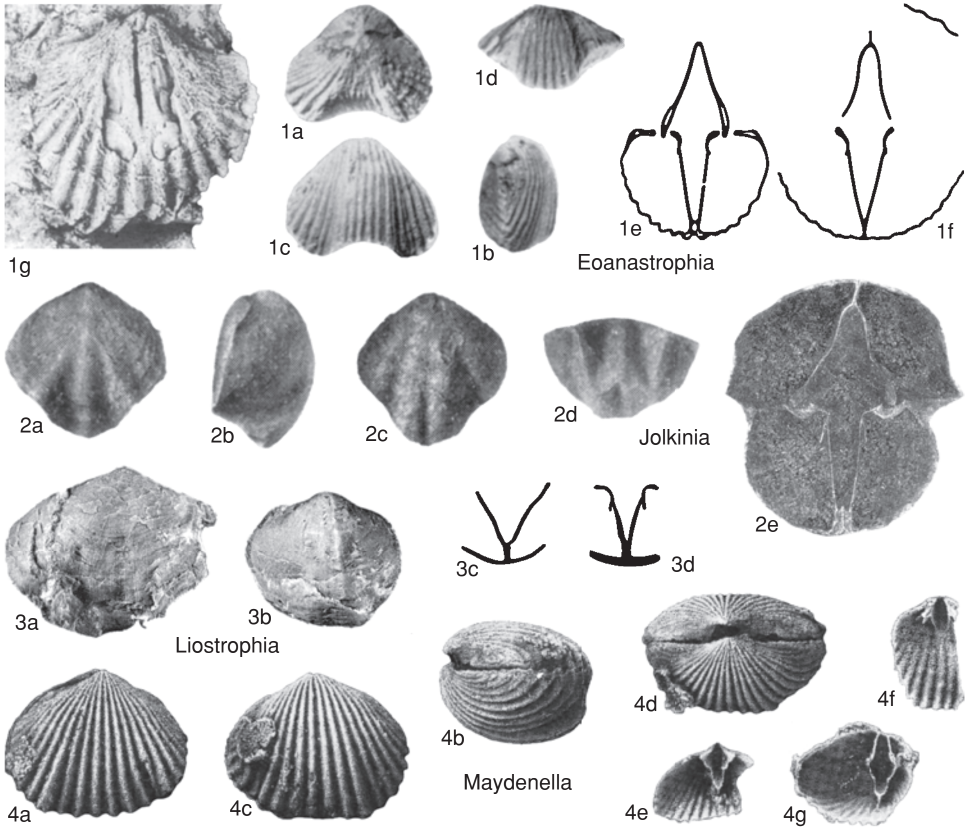

FIG. 641. Parastrophinidae (p. 955–958).

median septum; alate plates may be weakly developed or rarely absent. *Upper Ordovician (Caradoc–Ashgill):* Russia, Kirgizia, Kazakhstan, Europe.——FIG. 641,*1a–f.* **E. antiquata,* Caradoc or Ashgill, Zeravshan Range, Tadzhikistan; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral valve above, ×1; *e–f,* serial sections 0.6 and 0.9 mm from posterior end of specimen, ventral valve above, ×3.5 (Nikiforova & Sapelnikov, 1973).——FIG. 641,*1g. E. pentamera* (MENEGHINI), Ashgill, Rosan Formation, Armorican Massif, France; dorsal valve interior mold, ×2 (Melou, 1990).

Jolkinia BREIVEL & BREIVEL, 1988, p. 36 [**Camarella turjensis* KHODALEVICH, 1939, p. 8; OD]. Similar to *Parastrophina* but strongly plicate on anterior half only, with up to 3 plicae on fold and sulcus; hinge line narrow, less than half width of valves; spondylium wide. *Silurian (Wenlock):* Russia (Urals).——FIG. 641,*2a–e.* **J. turjensis* (KHODALEVICH), Elkinsk beds, eastern Urals; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral valve above, ×1; *e,* section through articulated valves, ventral valve above, ×3.5 (Breivel & Breivel, 1988).

Liostrophia COOPER & KINDLE, 1936, p. 355 [**L. glabra;* OD]. Similar to *Parastrophina,* but smooth, not costate; medium to large size; uniplication broad and shallow; spondylium wide; septalium relatively wide. [Genus rather poorly known.] *Upper Ordovician (Ashgill):* eastern Canada, ?Ireland, Kazakhstan, ?northwestern China.——FIG. 641,*3a–d.* **L. glabra,* Whitehead Formation, Quebec; *a,* ventral valve exterior; *b,* dorsal valve exterior, ×1; *c,* section through ventral valve beak; *d,* section through dorsal valve, 3 mm from beak, ×3 (Cooper & Kindle, 1936).

Maydenella LAURIE, 1991, p. 85 [**M. asymmetrica;* OD]. Small to medium in size; strong costae present on entire valve; uniplication strong and deep; hinge line strophic, narrow, less than half width of valve; teeth strong; ventral interarea reduced, dorsal interarea obsolete; wide sessile spondylium supported anteriorly by short, low median septum that may or may not extend anterior to spondylium; short, subparallel to convergent outer hinge plates that extend into long, subparallel inner hinge plates, anterior to short, bladelike crura, forming long, shallow, flat-bottomed, sessile septalium; alate plates short. *Lower Ordovician (upper Llanvirn):* Tasmania.——FIG. 641,*4a–g.* **M. asymmetrica,* upper Cashions Creek Limestone; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral above; *c,* dorsal valve exterior; *d,* articulated valves, posterior view, ventral valve above; *e,* ventral valve interior; *f,* dorsal valve interior; *g,* articulated valves, interior view of valve posteriors, ventral below, ×2 (Laurie, 1991).

Parastrophinella SCHUCHERT & COOPER, 1931, p. 248 [**Pentamerus reversus* BILLINGS, 1857, p. 295; OD]. Medium to large size; strong costae present on anterior half of valves; exaggerated dorsibiconvexity; dorsal umbo more pronounced than ventral, making valves appear falsely unisulcate; uniplication broad and relatively shallow; teeth small; narrow spondylium duplex, sessile only at extreme posterior, supported in anterior by low, narrow median septum that extends anterior to spondylium; short, subparallel to convergent outer hinge plates that extend into long, closely spaced inner hinge plates, anterior to long, bladelike crura, that converge only near valve floor and unite with short, low median septum at anteriormost edge to form long, very narrow sessile septalium or very low septalium simplex. *Lower Ordovician (upper Llanvirn)–Silurian (Wenlock):* USA, eastern Canada, Britain, northern Europe, Ukraine, Estonia, Russia, Siberia, China, Mongolia, India.——FIG. 640,*4a–g.* **P. reversa* (BILLINGS), Ashgill, Ellis Bay Formation, Anticosti Island, Canada; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral on left; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral valve below, ×2.5; *e–g,* serial sections 2.2, 2.8, and 3.2 mm from posterior end of specimen 20.5 mm long, ventral valve above (Jin & Copper, 1997).

Family PARALLELELASMATIDAE Cooper, 1956

[Parallelelasmatidae COOPER, 1956a, p. 611] [=Saloniidae SAPELNIKOV, 1972, p. 39; Vagidae SAPELNIKOV, 1973, p. 40]

Smooth or costate, may have strong concentric lamellae; weakly to strongly uniplicate; spondylium duplex or simplex supported by high median septum, rarely sessile; short outer hinge plates converge and remain discrete, subparallel, and continue anteriorly into long, subparallel inner hinge plates; median septum and septalium absent; alate plates absent; bladelike crura present. *Lower Ordovician (upper Llanvirn)–Upper Ordovician (Ashgill).*

Metacamarella REED, 1917, p. 934; *emend.,* WILLIAMS, 1962, p. 231 [**Stricklandinia? balcletchiensis* DAVIDSON, 1883, p. 166; OD] [=*Metacamerella* SCHUCHERT & COOPER, 1931, p. 248, *nom. null.; Parallelelasma* COOPER, 1956a, p. 611 (type, *P. pentagonum*)]. Medium to large size; subtriangular in outline, longer than wide; costae wide, present only on anterior half, valves otherwise smooth; broad and shallow uniplication near anterior margin only, may be absent; teeth long and slender; very wide, short spondylium duplex commonly decreases in width on anterior half, supported for entire length by median septum of variable height that extends anterior to spondylium, some spondylia nearly free anteriorly; outer hinge plates very short, convergent to nearly horizontal, and extend into long, subparallel inner hinge plates that extend anteriorly well beyond long, recurved bladelike crura; adductor muscle field elongate oval. [*Parallelelasma* appears to differ from *Metacamarella* only in having a higher ventral median septum supporting the spondylium, and shorter and straighter crura, features that can vary widely among individuals.] *Lower Ordovician (upper Llanvirn)–Upper Ordovician (Caradoc):* southeastern USA, Britain, Norway, Estonia.——FIG. 642,*6a–b.* **M. balcletchiensis* (DAVIDSON), Caradoc, Balclatchie Conglomerate, Scotland; *a,* dorsal valve exterior; *b,* dorsal valve interior, ×1 (Williams, 1962).——FIG. 642,*6c–f. M. pentagonum* COOPER, upper Llanvirn, Pratt Ferry Formation, Alabama, USA; *c,* ventral valve exterior, ×2; *d,* articulated valve fragments, lateral view, ventral valve on right, ×3; *e,* ventral valve interior; *f,* dorsal valve interior, ×8 (Cooper, 1956a).

Didymelasma COOPER, 1956a, p. 615 [**D. longicrurum;* OD]. Small to very small size; length and width approximately equal; appears elongate oval in outline; dorsal and ventral valves equal and moderate in convexity; valves smooth, but weak costae may be present anteriorly only in broad, shallow, distinct fold and sulcus; short, narrow spondylium simplex or duplex; dorsal interior appears similar to *Metacamarella* with long, subparallel inner hinge plates, but valve interiors rather poorly known; crura long and straight, not curved. *Upper Ordovician (Caradoc–Ashgill):* USA, Canada, Australia, China, Russia, Kazakhstan, Siberia.——FIG. 642,*2a–e.* **D. longicrurum,* Ashgill, Lebanon Formation, Tennessee, USA; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve on right; *c,* dorsal valve exterior; *d,* articulated valves, anterior view, ventral valve below; *e,* slab showing valve exteriors and dorsal and ventral valve interiors, ×3 (Cooper, 1956a).

Limstrophina FU, 1982, p. 132 [**L. ptychorete;* OD] [=*Limstrophia* FU, 1980, p. 2, *nom. null.*]. Small size; wider than long; subelliptical to subpentagonal in outline; weak costae and concentric rugae present on entire valve; valves equally and strongly biconvex; uniplication broad and very shallow, covers entire valve; hinge line appears to be narrow, strophic; valve interiors poorly known but appear to

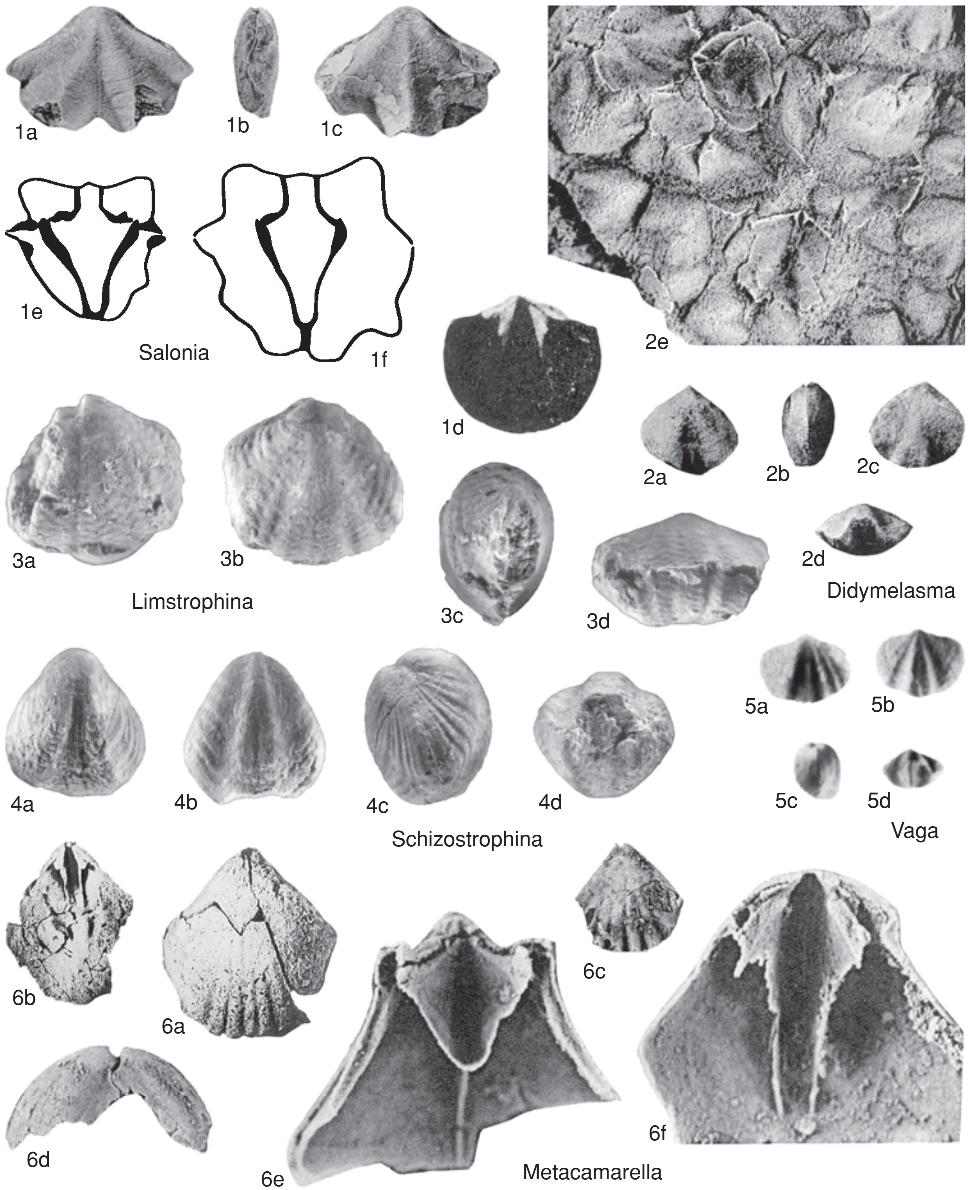

FIG. 642. Parallelelasmatidae (p. 958–960).

contain spondylium supported by median septum, and narrow, discrete, parallel socket plates. [*Limstrophina* known from only a single specimen.] *Upper Ordovician (Caradoc):* northwestern China.——FIG. 642,*3a–d*. **L. ptychorete,* Jinhe Formation, Shaanxi Province, Liquan; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, ventral on left; *d,* articulated valves, anterior view, ventral below, ×3 (Fu, 1982).

Salonia COOPER & WHITCOMB, 1933, p. 500 [**S. magnaplicata;* OD]. Small to medium size; valve proportions vary; subtriangular, trilobate, or subelliptical in outline; valve form dominated by 3 to 4 smooth, angular costae or plicae present on entire valve; ventribiconvexity moderate, umbo strongly rostrate; uniplication strong, angular; dorsal sulcus appears to revert to fold during growth; very short, sessile spondylium supported anteriorly by low, short median septum that does not extend anterior to spondylium; short, narrow outer hinge plates extend into relatively short inner hinge plates that converge but remain discrete anterior to very long, curved crura. *Upper Ordovician (lower Caradoc):* northeastern USA.——FIG. 642,*1a–f*. **S. magnaplicata,* Salona Formation, Pennsylvania; *a,* ventral valve exterior; *b,* articulated valves, lateral view, ventral valve on right; *c,* dorsal valve exterior, ×2; *d,* close up of posterior of dorsal interior [semicircular lower outline is artificial and does not reflect shape of dorsal valve outline], ×6 (Cooper, 1956a); *e–f,* sections through articulated specimen, ventral valve below, 0.5 and 0.8 mm from beak, ×5 (Cooper & Whitcomb, 1933).

Schizostrophina FU, 1982, p. 132 [**S. margarita;* OD] [=*Schizostrophia* FU, 1980, p. 2, *nom. null.*]. Small size; valves smooth, rarely with few, coarse plicae; ventribiconvexity very strong; uniplication broad and strong, covers entire valve; valve interiors poorly known but appear to contain spondylium supported by median septum, and narrow, divergent socket plates. *Upper Ordovician (Caradoc):* northwestern China.——FIG. 642,*4a–d*. **S. margarita,* Jinhe Formation, Shaanxi Province, Liquan; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, ventral on right; *d,* articulated valves, anterior view, ventral below, ×3 (Fu, 1982).

Vaga SAPELNIKOV & RUKAVISHNIKOVA, 1973, p. 33 [**V. sinualis;* OD]. Small size; wider than long, subelliptical in outline; angular plicae present primarily on fold and sulcus, valves otherwise smooth; valves equally and strongly biconvex; uniplication broad, strong, angular, covers entire valve; short, narrow, shallow spondylium simplex supported by high, short median septum; very short, narrow outer hinge plates extend into very short inner hinge plates that converge but remain discrete anterior to robust, bladelike crura. *Upper Ordovician (upper Caradoc):* Kazakhstan.——FIG. 642,*5a–d*. **V. sinualis,* Chu-Ili Mountains; *a,* ventral valve exterior; *b,* dorsal valve exterior; *c,* articulated valves, ventral on left; *d,* articulated valves, ventral valve below, ×1 (Sapelnikov & Rukavishnikova, 1973).

PENTAMERIDINA

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Suborder PENTAMERIDINA Schuchert & Cooper, 1931

[*nom. correct.* AMSDEN, 1965, p. 541, *pro* Pentameroidea SCHUCHERT & COOPER, 1931, p. 247]

Shells ranging from small to large, with very large examples known from the three superfamilies but few very small examples known. The key subordinal character a spondylium commonly, but not invariably supported by a median septum. Tripartite cardinalia involving inner and outer hinge plates separated by crura. Ornamentation and shell convexity highly variable. *Upper Ordovician (middle Ashgill)–Upper Devonian (Frasnian).*

Although the origins of the pentameroid brachiopods are veiled in uncertainty, they first occurred with any certainty and in some taxonomic as well as numerical abundance in the mid-Ashgill with the appearance of the Virgianidae. The virgianids are typical thick-shelled pentameroids, many reaching a large size (10 cm in length) and commonly occurring in monospecific aggregations that can extend laterally for kilometers or more, as is typical of the younger Silurian and Devonian pentameroids as well. The pentameroids are typically a benthic assemblage 3, inner shelf, photic zone group (BOUCOT, 1975a).

In the pre-Ashgill, the Llanvirn and Caradoc in particular, there is a handful of numerically uncommon, relatively provincial genera that may include the precursors of the undoubted pentameroids. Included here are COOPER's (1956a) Parallelelasmatidae and SAPELNIKOV and RUKAVISHNIKOVA's (1973) not too well understood *Vaga* from the upper Caradoc of Kazakhstan. The five parallelelasmids plus *Vaga,* whose familial position is possibly virgianid, possess hinge plates like those of the Pentameridina rather than of the varied taxa within the Syntrophiidina. For none of the six genera involved here (five parallelelasmids plus *Vaga*) may one be certain of the details of the hinge plates, however, and for none of them are there useful data about shell structure that could be compared with profit to that available for the Pentameridina. There is also lack of information on the shell structure of the Syntrophiidina. (Traditional pentameroid terminology for the inner and outer hinge plates, plus the crura, has been inner and outer brachial lamellae, plus the brachial processes. We defer to the decision made by the editors in replacing the older terminology (see Fig. 620.10). Until early ontogenies have been studied within at least a few pentameroids, however, there is still the possibility that hinge plates are not homologs of brachial lamellae or crura of brachial processes.)

In a general sort of way one is more inclined to see the origins of the Pentameridina within the pre-Ashgill or possibly pre-Caradoc Syntrophiidina owing to overall external and internal similarities. When the genera within the varied syntrophiid families are considered, however, it is currently unclear just where such origins might be. The alate plates of the parastrophinids rule them out, while the relatively simple camerellid cardinalia similarly make them unlikely ancestors. The very specialized cardinalia of *Brevicamera* rule it out. The very specialized ventral interior of the Xenelasmatinae makes it too specialized to serve as an ideal ancestor, as does the spondylium simplex of the Syntrophiidae. There are probably no better prospects for the other families.

The relationships within the Pentameridina are complicated by repeated instances of homeomorphy, convergence, and parallelism. It is almost as though the basic pentameroid genome held within itself the capacity for some permutations and combinations that were variably expressed time after time. For example, the relatively large, strongly costate, thick-shelled *Conchidium*-type shell has been repeated in the virgianids with *Pleurodium,* in the subrianids with *Conchidium,* in the Pentameridae with *Kirkidium,* and in the Gypiduloidea with *Zdimir* (=*Conchidiella*); no clorindid *Conchidium* type has yet been seen, but it would not be all that extraordinary if one were to be uncovered ultimately. A review of the fossil record is given below.

The Virgianidae of the mid-Ashgill to middle Llandovery include varied external morphologies. Mention has already been made about how similar *Pleurodium* is externally to the large, ribbed shells, all of which were formerly placed into *Conchidium.* The bulk of the virgianids were extinct well before the end of the Ashgill, however, with only the aspondylose, smooth form *Holorhynchus* and the clorindiform *Brevilamnulella* bridging the Ordovician-Silurian boundary. Neither of these genera is morphologically gradational into the Llandovery virgianids. The well-defined Llandovery virgianids (*Virgiana* [Fig. 621.4], *Virgianella, Borealis, Pseudoconchidium, Mariannaella, Pleurodium, Plicidium*) include varied external forms. All of them, however, were gone by the end of the Aeronian (mid-Llandovery) or possibly Telychian (late Llandovery). *Borealis* can easily be thought of as a precursor to *Pentamerus* (Fig. 621.5) of the later Llandovery. *Pentamerus,* in turn, can easily serve as the precursor of the costate and smooth younger Silurian Pentameridae (BOUCOT & JOHNSON, 1979).

The Subrianidae, ranging from the later Wenlock to the Ludlow, pose problems since there are no truly transitional forms between them and their most logical precursors, the

Pentameridae. The Subrianidae, however, may have been neotenically derived from the Pentameridae by a process of reduction in length of the hinge plates, plus the addition of medially projecting crura.

The gypiduloids (see Fig. 621.1) seem likely to have evolved from the mid-Ashgillian *Galeatellina,* whereas the clorindoids (see Fig. 621.2) probably evolved from the mid-Llandovery *Brevilamnulella.*

We place the Pentamerellinae into the Clorindoidea owing to their clorindid external form. *Pentamerella,* however, lacks carinae in the dorsal valve, as do most gypidulinids. We place *Levigatella* (Levigatellinae) into the Gypidulidae despite the presence of carinae in the dorsal valve because of its gypidulid external form.

The Stricklandioidea clearly have a pre-Silurian origin relatively independent of the Virgianidae, as is shown both by their unique internal features in both valves, particularly the cardinalia (see Fig. 621.3), and by the presence of prismatic shell on the medial faces of the hinge plates rather than on the lateral faces as is true of the Virgianidae and their potential descendants discussed above. Despite the characteristic form of their cardinalia, however, the stricklandiids possess the long, rodlike crura so characteristic of the Ashgill and younger Virgianidae and Pentameridae that make it clear that the origins of the two groups cannot be too remote from each other. We divide the Stricklandiidae into two subfamilies, Stricklandiinae and a new subfamily Kulumbellinae. The earliest kulumbellid is probably *Microcardinalia mullochensis* (Reed, 1917). The Aenigmastrophiidae probably evolved from the Kulumbellinae, since their specialized morphologies are closer to that subfamily than that of the Stricklandiinae.

The affinities of the Aenigmastrophiidae were previously considered to be very uncertain (Boucot & Rong, 1994). We now conclude that they have more in common with the stricklandiids than with any other group since the cardinalia and ventral interior of aenigmastrophiids are similar to those in *Kulumbella* s.l. *transversa* (Grabau) (see Rong & Yang, 1981) and other stricklandiids lacking outer hinge plates. Notable is the distinctive, later diversification of the Aenigmastrophiidae, with their unique cardinalia and external forms.

The affinities of the internally poorly known Stricklandistrophiidae are also uncertain but fit most comfortably within the stricklandioids.

The Enantiosphenidae are most reasonably viewed as gypiduloids with unusual external form plus the presence of a loop (see Fig. 620.9), the latter being a convergently developed feature that has no relationship to the terebratuloid loop.

The suborder is divided into the superfamilies Pentameroidea, Stricklandioidea, Gypiduloidea, and Clorindoidea.

Superfamily PENTAMEROIDEA M'Coy, 1844

[*nom. transl.* Schuchert, 1896, p. 320, *ex* Pentameridae M'Coy, 1844, p. 103]

[Materials prepared by A. J. Boucot, Rong Jia-yu, & Robert B. Blodgett]

Shells tend to be large; moderately to strongly ventribiconvex; exterior smooth, costellate, costate, or diagonally rugose; interareas absent except in some Subrianinae; ventral interior with well-developed spondylium formed from medially fused plates and commonly supported by a median septum formed from the basal and anterior continuation of those plates; hinge teeth well developed; inner hinge plates may be conjunct to form a cruralium; hinge plates may be laminar or curved in cross section, long or short, and may be tripartite; crura may protrude medially; ventral valve with outer lamellar layer and inner prismatic layer, dorsal valve with lamellar layer and with or without prismatic layer; prismatic layer on hinge plates of Virgianidae and Pentameridae invariably situated on lateral faces of plates. *Upper Ordovician (middle Ashgill)–Silurian (Přídolí).*

Family VIRGIANIDAE Boucot & Amsden, 1963

[Virgianidae BOUCOT & AMSDEN, 1963, p. 296]

Median septum in ventral valve relatively short, less commonly long or absent; hinge plates relatively short, extending short distance anterior of inner socket ridges; outer hinge plates parallel to each other for only a short distance. *Upper Ordovician (middle Ashgill)–Silurian (lower Wenlock).*

Subfamily VIRGIANINAE Boucot & Amsden, 1963

[*nom transl.* BOUCOT, RONG, & BLODGETT, herein, *ex* Virgianidae BOUCOT & AMSDEN, 1963, p. 296] [=Tcherskidiinae SAPELNIKOV, 1972, p. 35; Holorhynchiinae SAPELNIKOV, 1973, p. 40; Holorhynchusinae SAPELNIKOV, 1985a, p. 19]

Small to large; smooth or costate; ventral median septum of variable length, present in some; hinge plates commonly short and crura short; prismatic and lamellar shell in investigated genera; commonly no fold or sulcus. *Upper Ordovician (middle Ashgill)–Silurian (lower Wenlock).*

Virgiana TWENHOFEL, 1914, p. 27 [**Pentamerus barrandei* BILLINGS, 1857, p. 296; OD]. Small to medium; ventribiconvex, subcircular to elongate; weak to strong costae to costellate; spondylium short with median septum short. *Silurian (lower Llandovery–middle Llandovery):* North America, Asia.

V. (Virgiana). Medium; strongly ventribiconvex; prominent ventral beak; umbo may be smooth. *Silurian (lower Llandovery–middle Llandovery):* North America, Asia.——FIG. 643,*1a–g.* **V. (V.) barrandei* (BILLINGS), Anticosti, Quebec, Canada; *a–d,* lateral, ventral, dorsal, and posterior views of articulated specimen, Becscie River Formation, ×1 (Schuchert & Cooper, 1932); *e,* anterior view of articulated specimen, Becscie River Formation, ×1 (Amsden, 1965); *f–g,* ventral and lateral of articulated specimen, Gun River Formation, ×1 (Boucot, Johnson, & Rubel, 1971).——FIG. 643,*1h–j. V. (V.) mayvillensis,* Mayville Dolomite, Mayville, Wisconsin, USA; *h–i,* dorsal and posterior views of articulated specimens, ×1; *j,* dorsal interior, ×2 (Boucot, Johnson, & Rubel, 1971).

V. (Platymerella) FOERSTE, 1909a, p. 70 [**P. manniensis;* OD]. Small to medium; ventral beak weak; gently biconvex with valves subequally sized. *Silurian (middle Llandovery):* midcontinent North America.——FIG. 643,*2a–j.* **V. (P.) manniensis,* USA; *a–c,* dorsal, posterior, ventral, Tennessee, no formation given, ×1 (Amsden, 1965); *d–g,* ventral, lateral, anterior, and posterior of articulated specimen, Brassfield Formation, Ohio, ×1.5; *h,* posterior view of ventral interior, Brassfield Formation, Ohio, ×3; *i,* posterior view of interior, Brassfield Formation, Ohio, ×2; *j,* posterior view of dorsal interior, Brassfield Formation, Ohio, ×3 (Boucot, Johnson, & Rubel, 1971).

Borealis BOUCOT, JOHNSON, & RUBEL, 1971, p. 274 [**Gypidia borealis* EICHWALD, 1843, p. 74; OD]. Medium; smooth; ventribiconvex; elongate; short, broad spondylium supported by well-developed median septum. *Silurian (lower Llandovery):* Baltic region, South China, Russia (Kolyma, Siberia).——FIG. 644,*1a–g.* **B. borealis* (EICHWALD), Juuru Stage, Estonia; *a–d,* lateral, ventral, dorsal, and lateral views of articulated specimens, ×1.3; *e,* dorsal view of interior mold, ×1.4; *f,* interior of ventral valve, ×1.5; *g,* dorsal view of dorsal interior mold, ×2 (Boucot, Johnson, & Rubel, 1971).

Holorhynchus KIAER, 1902, p. 68 [**H. giganteus;* OD]. Smooth; strongly ventribiconvex; spondylium unsupported by median septum. *Upper Ordovician (middle Ashgill)–Silurian (middle Llandovery):* Eurasia, North America (including Alaska).

H. (Holorhynchus). Large; subcircular to variable outline; short, low median ridge may be present in dorsal valve. *Upper Ordovician (middle Ashgill), Silurian (?lower Llandovery):* Eurasia, USA (Alaska).——FIG. 645*a–g.* **H. (H.) giganteus,* Sandvik, Oslo region, Stage 5; *a–d,* ventral, dorsal, lateral, posterior views of articulated specimen, ×1; *e–f,* dorsal and posterior views of dorsal mold, ×1; *g,* dorsal view of dorsal interior mold, ×1.5 (Boucot, Johnson, & Rubel, 1971).

H. (Nondia) BOUCOT & CHIANG, 1974, p. 66 [**N. canadensis;* OD]. Medium; moderately biconvex; subrhomboidally shaped outline; median ridge in dorsal valve. *Silurian (lower Llandovery–middle Llandovery):* western Canada.——FIG. 646*a–e.* **H. (N.) canadensis,* Nonda Formation, British Columbia; ventral, anterior, dorsal, posterior views of articulated specimen, lateral view, ×1.5 (Boucot & Chiang, 1974).

Proconchidium SAPELNIKOV in NIKOLAEV & SAPELNIKOV, 1969, p. 15 [**Conchidium munsteri* ST. JOSEPH, 1938, p. 301; OD] [=*Norgium* BREIVEL & BREIVEL in ANTSIGIN & others, 1970, p. 7, obj.]. Medium; subcircular to elongate; costellate; ventral median septum extending almost to anterior margin and longer than spondylium; long outer hinge plates; inner hinge plates shorter than outer; cardinal process may be present. *Upper Ordovician (middle Ashgill):* Urals, Central Asia [Sredni Azii], Kazakhstan, Norway, Arctic Canada, northern Greenland.——FIG. 644,*3a–g.* **P. munsteri* (ST. JOSEPH), Norway, Stage 5b; *a–d,* ventral of internal mold, ventral of internal mold, dorsal view of internal mold, dorsal view of internal mold, Skien

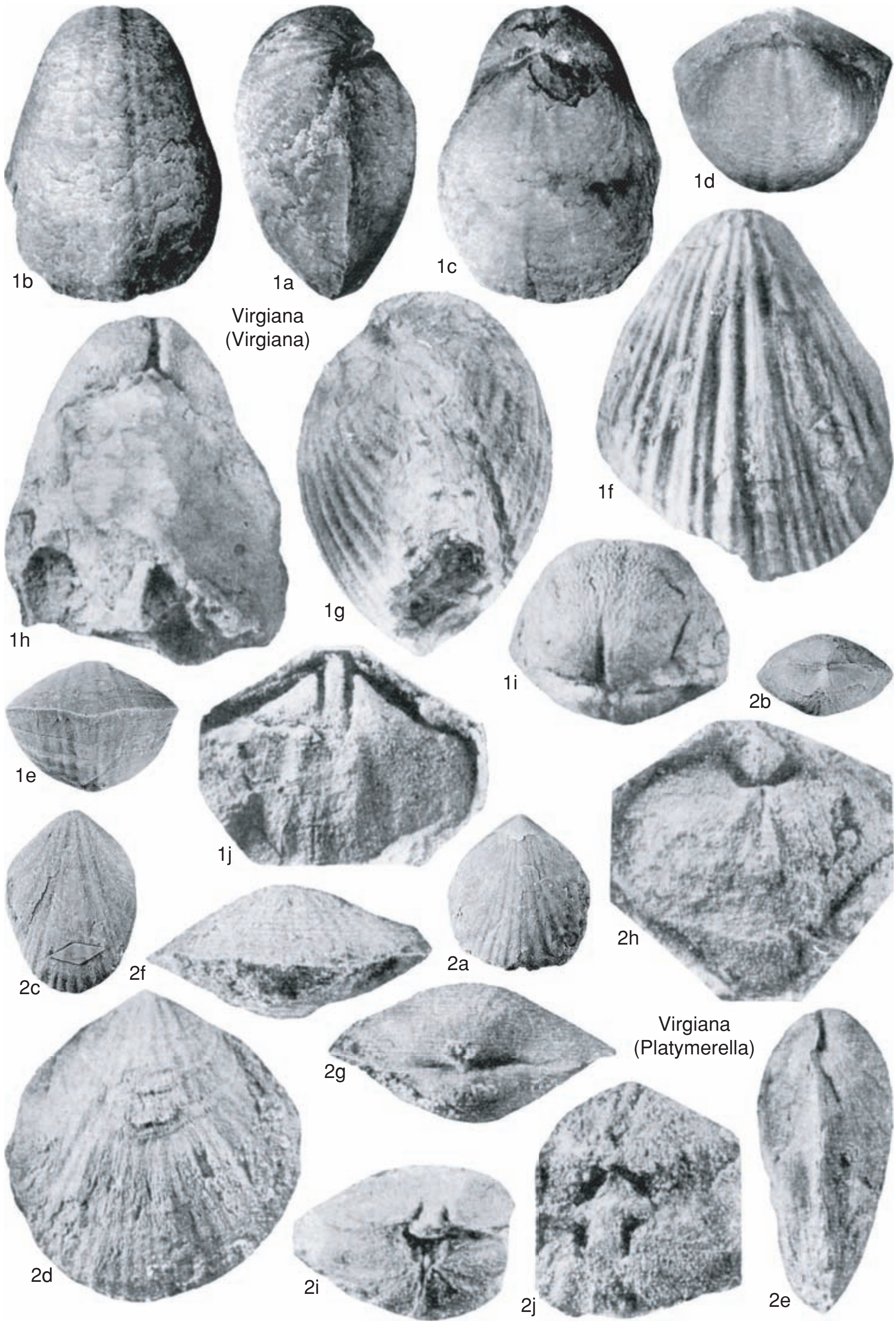

FIG. 643. Virgianidae (p. 963).

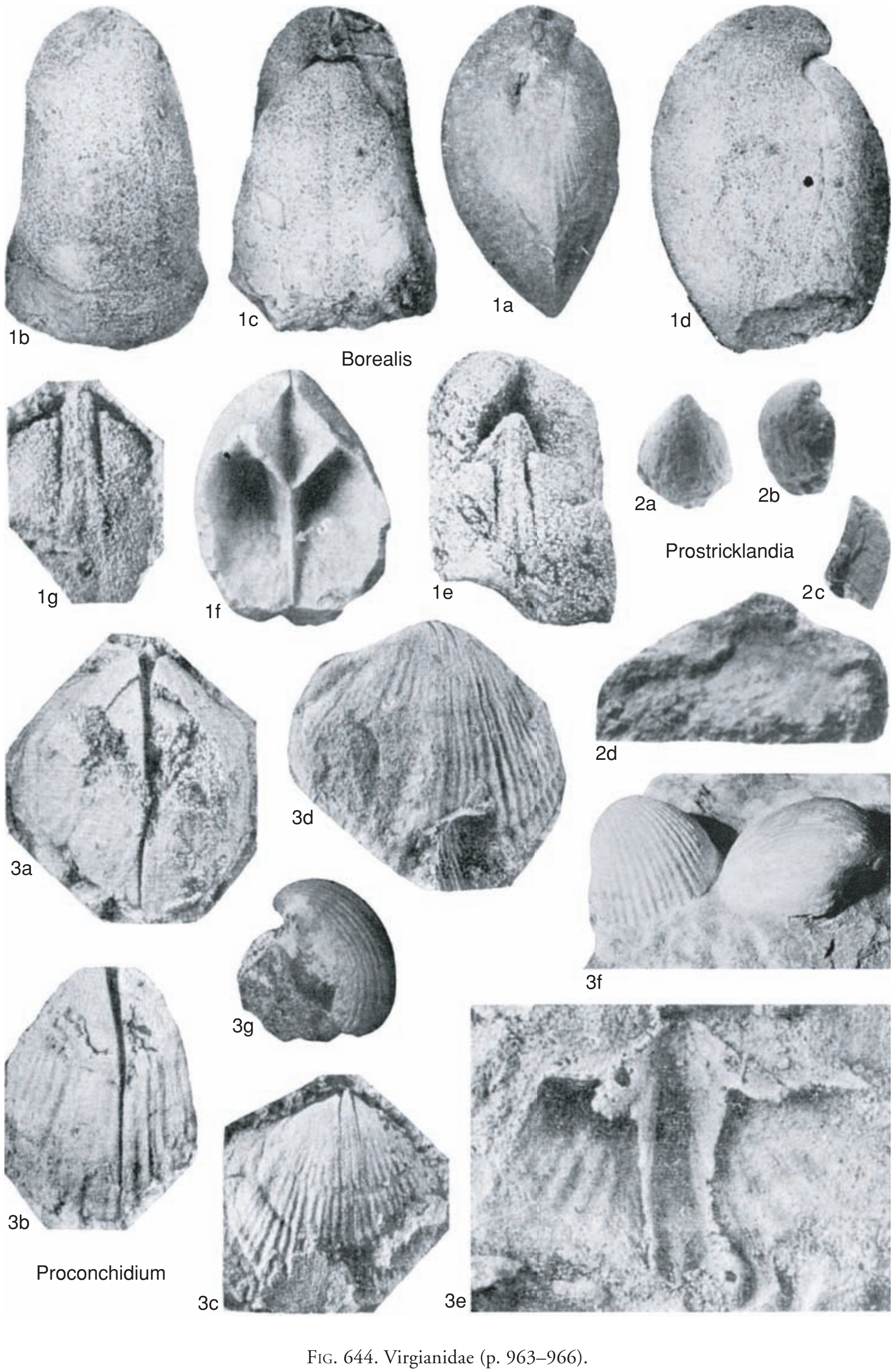

FIG. 644. Virgianidae (p. 963–966).

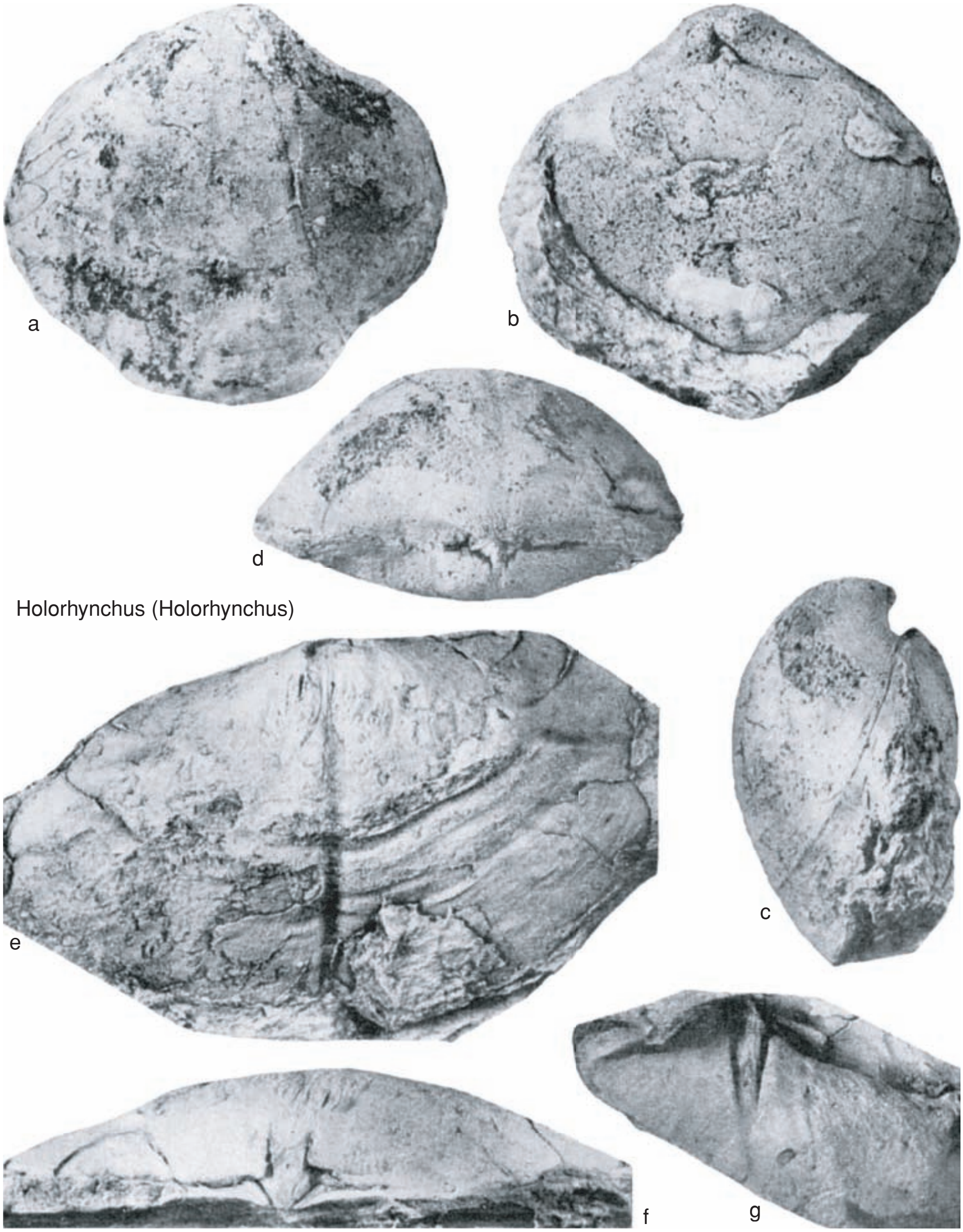

FIG. 645. Virgianidae (p. 963).

region, Oslo, ×1.5; *e,* rubber replica of dorsal interior, Ringerike area, Oslo region, ×4 (Boucot, Johnson, & Rubel, 1971); *f–g,* ventral plus side, and lateral, ×1 (St. Joseph, 1938).

Prostricklandia RUKAVISHNIKOVA & SAPELNIKOV, 1973, p. 106 [**P. prisca;* OD]. Small; smooth; moderately ventribiconvex; possibly with relatively straight hinge line and possibly well-developed interarea; long ventral median septum supporting short spondylium; short hinge plates. *Upper Ordovician (middle Ashgill):* Kazakhstan.——FIG. 644,*2a–d.* **P. prisca,* Ulkuntass Stage [Gorizont], Chu'ilii Mountains, Pribalkhash, southeastern Kazakhstan; *a–b,* ventral and lateral views, ×1; *c,* dorsal interarea, ×3; *d,* lateral view showing median septum, ×1 (Rukavishnikova & Sapelnikov, 1973).

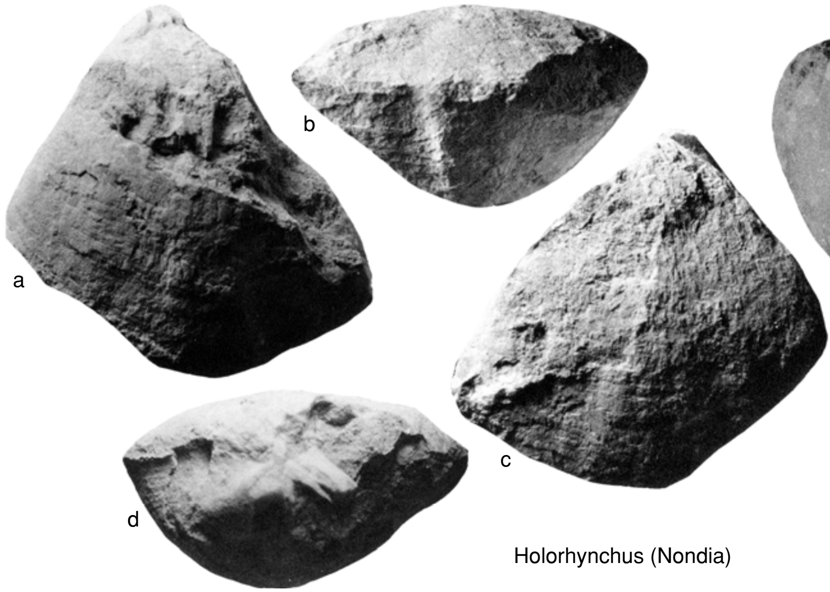

FIG. 646. Virgianidae (p. 963).

Pseudoconchidium NIKIFOROVA & SAPELNIKOV, 1971, p. 52 [**P. kozhimicum* NIKIFOROVA in NIKIFOROVA & SAPELNIKOV, 1971, p. 53; OD] [=*Paraconchidium* RONG & YANG in RONG, XU, & YANG, 1974, p. 198 (type, *P. shiqianensis,* OD)]. Large; variably sized costae anteriorly, irregularly bifurcating to costellate; ventribiconvex; aseptate to variably developed ventral median septum; long spondylium; basally convergent inner hinge plates, outer hinge plates, and crura. *Silurian (middle Aeronian, ?lower Telychian):* USA (Alaska), South China, Arctic Urals, Russia (Kolyma, Vaygach).——FIG. 647,*2a–d.* **P. kozhimicum* (NIKIFOROVA), upper Llandovery–lower Wenlock, Pechora region, Russia; *a,* posterior view of internal impression, ×1; *b–d,* ventral, lateral, and dorsal views, ×1 (Nikiforova & Sapelnikov, 1971).

Tcherskidium NIKOLAEV & SAPELNIKOV, 1969, p. 12 [**Conchidium*? *unicum* NIKOLAEV, 1968, p. 47; OD]. Large; costellate; strongly ventribiconvex; elongate; spondylium supported by moderately long median septum; relatively short inner hinge plates; laterally inclined; outer hinge plates about twice as long as inner; crura well developed. *Upper Ordovician (middle Ashgill):* Russia (Kolyma, Taymyr), northern Greenland, USA (Alaska), South China, ?Kazakhstan.——FIG. 648*a–d.* **T. unicum* (NIKOLAEV), Iryudinsk Stage [Gorizont], Ina River, Omulevsk Mountains, Russia; ventral, dorsal, lateral, dorsal views, ×1 (Nikolaev & Sapelnikov, 1969).

Virgianella NIKIFOROVA & SAPELNIKOV, 1971, p. 49 [**V. vaigatschensis* NIKIFOROVA in NIKIFOROVA & SAPELNIKOV, 1971, p. 49; OD]. Large; smooth; ventribiconvex; very short ventral median septum supporting spondylium. *Silurian (middle Llandovery–lower Wenlock):* Arctic Urals, Central Asia [Sredni Azii], northern Greenland, South China, Russia (Kolyma, Vaygach).——FIG. 647,*1a–c.* **V. vaigatschensis* (NIKIFOROVA), upper Llandovery–lower Wenlock, Pechora River, Arctic Urals, Russia; dorsal, ventral, lateral views, ×1 (Nikiforova & Sapelnikov, 1971).

Subfamily MARIANNAELLINAE Sapelnikov & Rukavishnikova, 1975

[Mariannaellinae SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71]

Medium; transverse; smooth to plicate; fold and sulcus commonly well developed; very short median septum, if present, supporting spondylium; inner hinge plates absent or very short; prismatic shell commonly present. *Upper Ordovician (middle Ashgill)–Silurian (Llandovery):* Asia, Europe, North America.

Mariannaella SAPELNIKOV & RUKAVISHNIKOVA, 1975b, p. 7 [**M. koksengirensis;* OD]. Small to medium; costate; ventral fold and dorsal sulcus well developed; median septum absent or short, supporting short spondylium; short hinge plates, inner hinge plates very short or absent, outer hinge plates massive, short, free. *Silurian (Llandovery):* Kazakhstan.——FIG. 649,*1a–c.* **M. koksengirensis,* Alpeisk Stage [Gorizont], Chingiz Range; ventral, ventral, dorsal views, ×1 (Sapelnikov & Rukavishnikova, 1975a).——FIG. 649,*1d. M. levisulcata,* Alpeisk

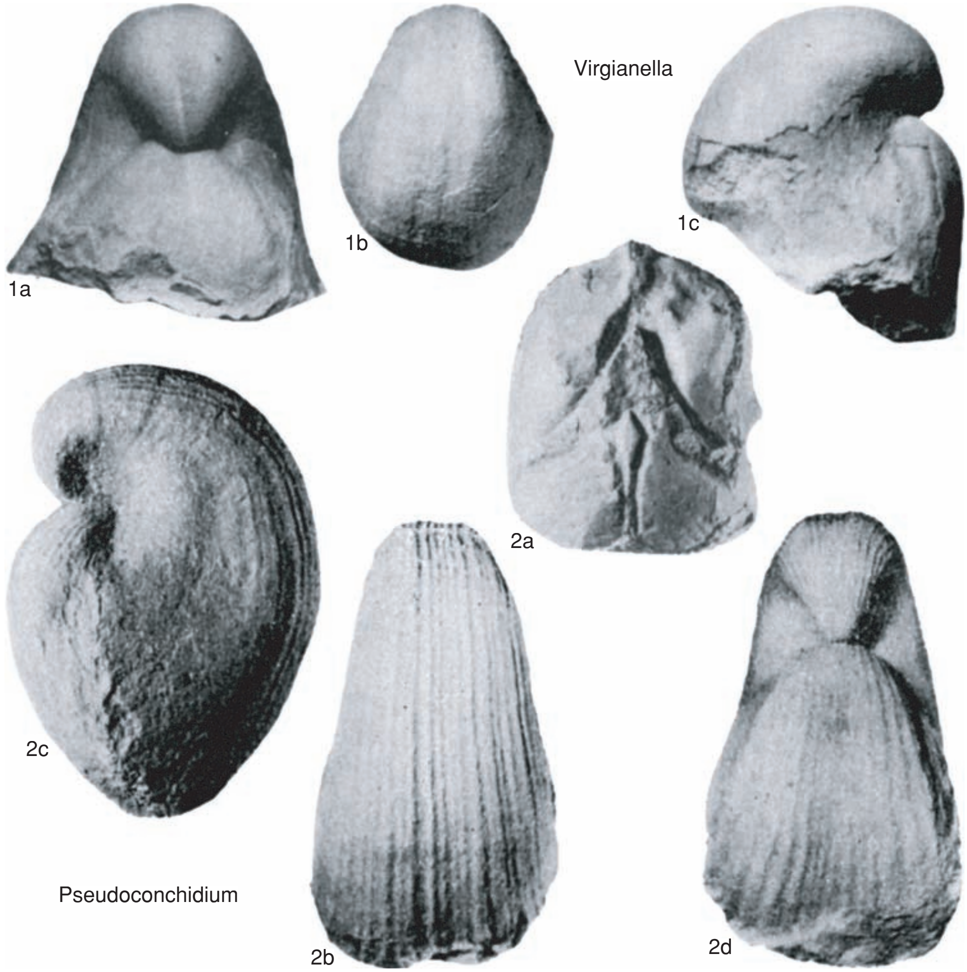

FIG. 647. Virgianidae (p. 967).

Stage [Gorizont], western Pribalkhash, southeastern Kazakhstan; lateral view, ×1 (Sapelnikov & Rukavishnikova, 1975a).

Brevilamnulella AMSDEN, 1974, p. 62 [**Clorinda*? *thebesensis* SAVAGE, 1913a, p. 125; OD] [=*Antigaleatella* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 74 (type, *A. laevis,* OD); *Brevilamula* BOUCOT & CHIANG, 1974, p. 72, *nom. null.*]. Small; smooth to weakly costate anteriorly; ventral sulcus and dorsal fold; uniplicate anterior commissure; small spondylium and short median septum; very short inner hinge plates, thicker outer hinge plates, with noncarinate crura. *Upper Ordovician (middle Ashgill)–Silurian (middle Llandovery):* North America, Europe, Asia.——FIG. 649,*4a–i.* **B. thebesensis* (SAVAGE), Leemon Formation, Cape Girardeau County, Missouri, USA; *a–e,* ventral, lateral view of ventral valve, dorsal view of exterior, anterior view of ventral valve, lateral view of dorsal valve, ×2; *f–g,* oblique view of dorsal cardinalia, dorsal interior; *h,* oblique posterior of ventral valve, ×5; *i,* oblique view of ventral valve interior, ×3 (Amsden, 1974).

Disulcatella FU, 1982, p. 134 [**D. didyma;* OD]. Small; smooth; subcircular to transverse; ventribiconvex; bisulcate; short median septum supporting short spondylium; short hinge plates. *Silurian (upper Rhuddanian–lower Aeronian):* North China.——FIG. 649,*5a–e.* **D. didyma,* Zhaohuajing Formation, Zhaohuajing, Tongxin County, Ningxia Province; ventral, dorsal, lateral, anterior, posterior of articulated specimen, ×3 (Fu, 1982).

Eoconchidium ROZMAN, 1967, p. 62 [**E. indigiricum;* OD]. Small to medium; transverse; costate; ventribiconvex; short median septum, no more than one-

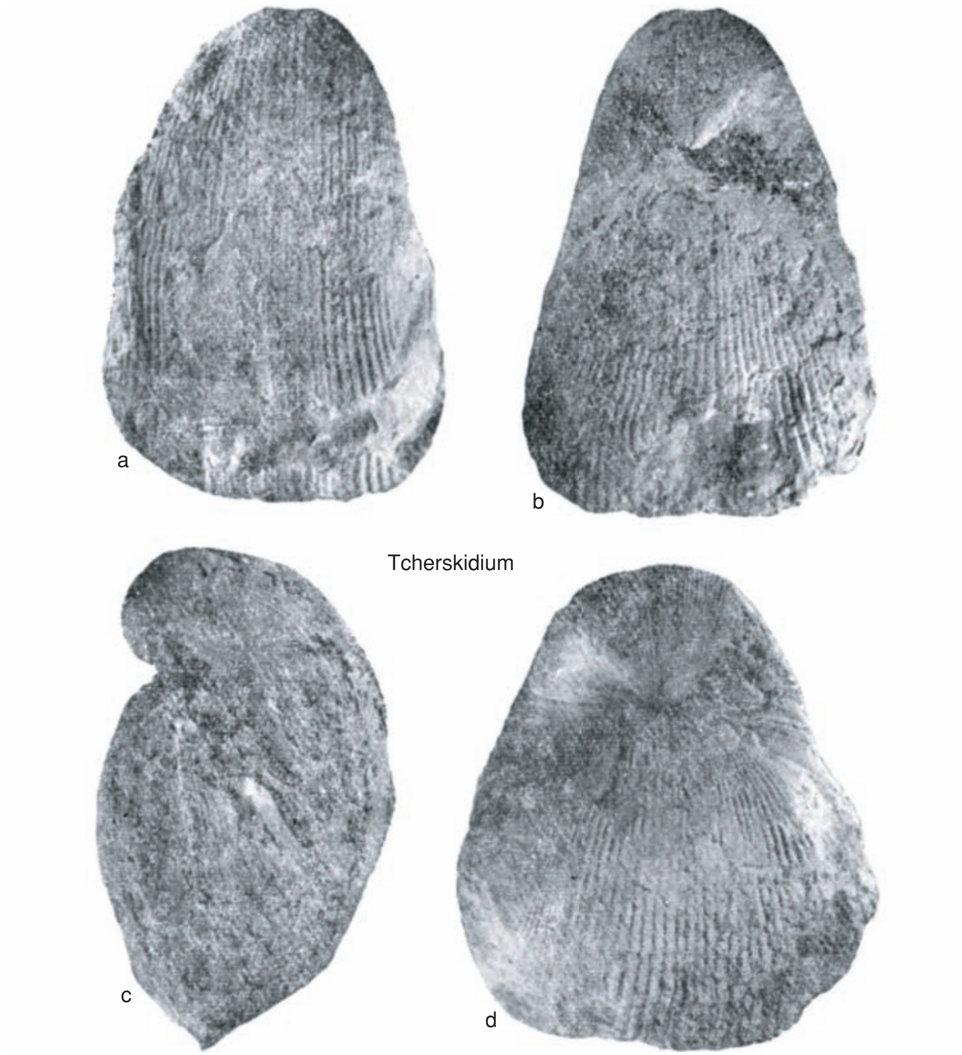

FIG. 648. Virgianidae (p. 967).

third shell length, supporting longer spondylium; short hinge plates. *Upper Ordovician (middle Ashgill):* Russia (Kolyma), Kazakhstan, USA (Alaska).——FIG. 649,*2a–d*. **E. indigiricum,* Selennyakh Ridge, northeastern Russia; ventral, dorsal, lateral, anterior, ×2 (Rozman, 1967).

Galeatellina SAPELNIKOV & RUKAVISHNIKOVA, 1976, p. 122 [**Galeatella kajnarensis* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71; OD] [=*Galeatella* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 71, *non* MUIR-WOOD & COOPER, 1960, p. 173]. Small; biconvex; smooth; ventribiconvex; dorsal sulcus and ventral fold similar to *Gypidula;* short median septum supporting short spondylium; short hinge plates. *Upper Ordovician (middle Ashgill):* Kazakhstan.——FIG. 649,*3a–d*. **G. kajnarensis* (SAPELNIKOV & RUKAVISHNIKOVA), Tolensk superhorizon, Chingiz Range, southeastern Kazakhstan; ventral, dorsal, lateral, anterior views, ×1 (Sapelnikov & Rukavishnikova, 1975a).

Subfamily PLEURODIINAE Rong & Yang, 1977

[Pleurodiinae RONG & YANG, 1977, p. 75]

Medium to large; transverse; evenly costate to plicate; commonly no fold or sulcus; long spondylium supported by short median septum; outer and inner hinge plates short; long crura; prismatic layer absent. *Silurian*

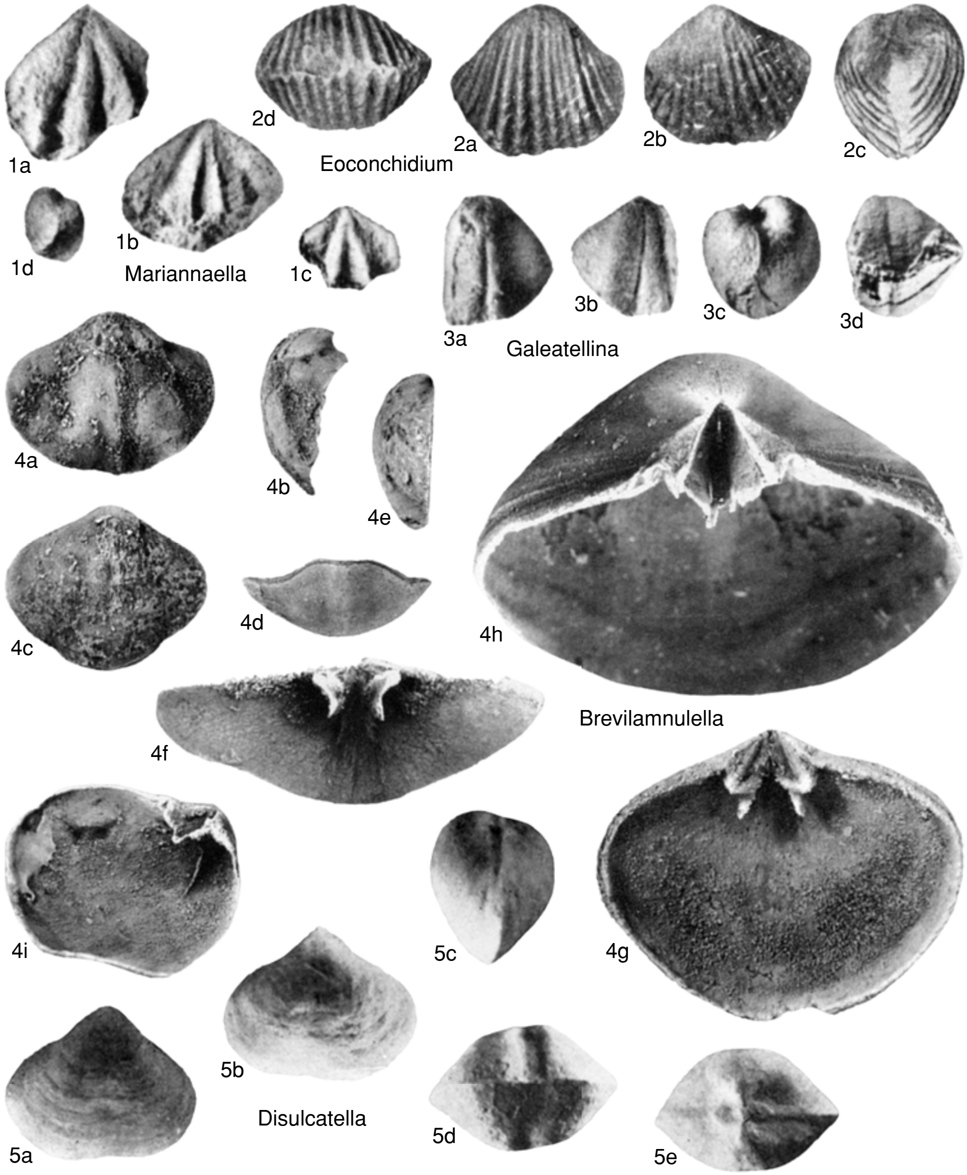

FIG. 649. Virgianidae (p. 967–969).

(middle Aeronian–upper Aeronian): South China.

Pleurodium WANG, 1955, p. 111 [**Conchidium tenuiplicatus* GRABAU, 1925, p. 80; OD]. Medium to large; transverse, evenly costate. *Silurian (upper Aeronian):* South China.——FIG. 650,*1a–f.* **P. tenuiplicatus* (GRABAU), upper part of Lopoping Formation, Dazhongba, Fenxiang, western Hubei; *a–e,* ventral, dorsal, posterior, anterior, lateral views, ×1 (Wang, 1955); *f,* impression of dorsal interior, ×1 (Rong & Yang, 1981).

Plicidium RONG & YANG, 1981, p. 203 [**Virgiana*? *sinanensis* RONG & YANG in RONG, XU, & YANG, 1974, p. 197; OD]. Medium; subcircular; coarsely costate; anteriorly bifurcating costae; similar internally to *Pleurodium* but differs in its coarse ornamentation. *Silurian (middle Aeronian):* South China.——FIG. 650,*2a–e.* **P. sinanensis* (RONG & YANG), Xiangshuyuan Formation, northeastern

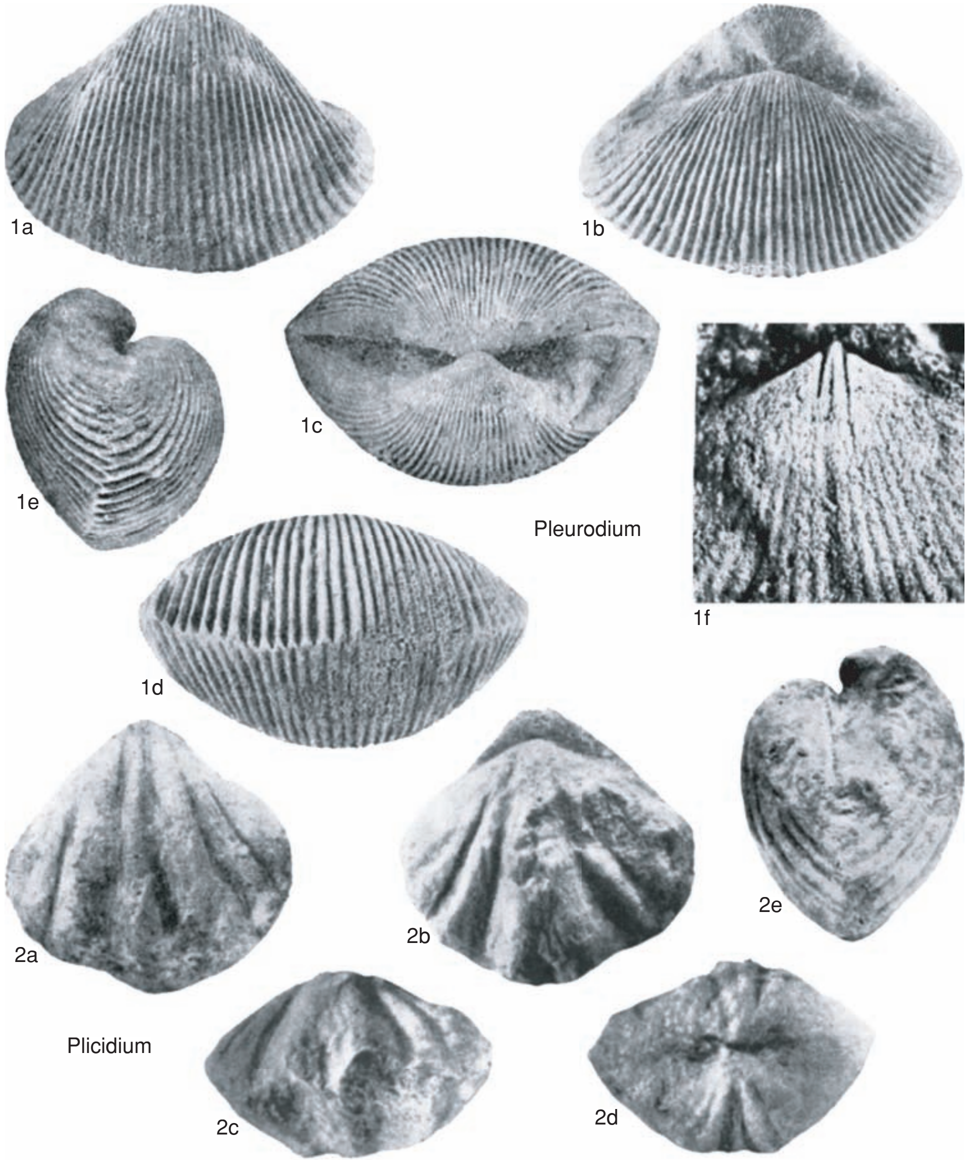

FIG. 650. Virgianidae (p. 970–971).

Guizhou; *a–d,* ventral, dorsal, anterior, posterior views, ×1; *e,* lateral view, ×2 (Rong & Yang, 1981).

Family PENTAMERIDAE M'Coy, 1844

[Pentameridae M'COY, 1844, p. 103] [=Pentameroidinae AMSDEN, 1953, p. 144; Brooksininae SAPELNIKOV, 1973, p. 40; Conchidiidae SAPELNIKOV, 1973, p. 40, *pars*]

Ventral valve median septum and spondylium variable in length; deltidium not always preserved; relatively long hinge plates commonly subparallel, and sometimes fused medially, laminar in cross section; cardinal process or striated area for diductor attachment may be present. [*Nanukidium* does possess carinae supporting the posterior extensions of the crura, a feature otherwise restricted to the Subrianinae but interpreted by

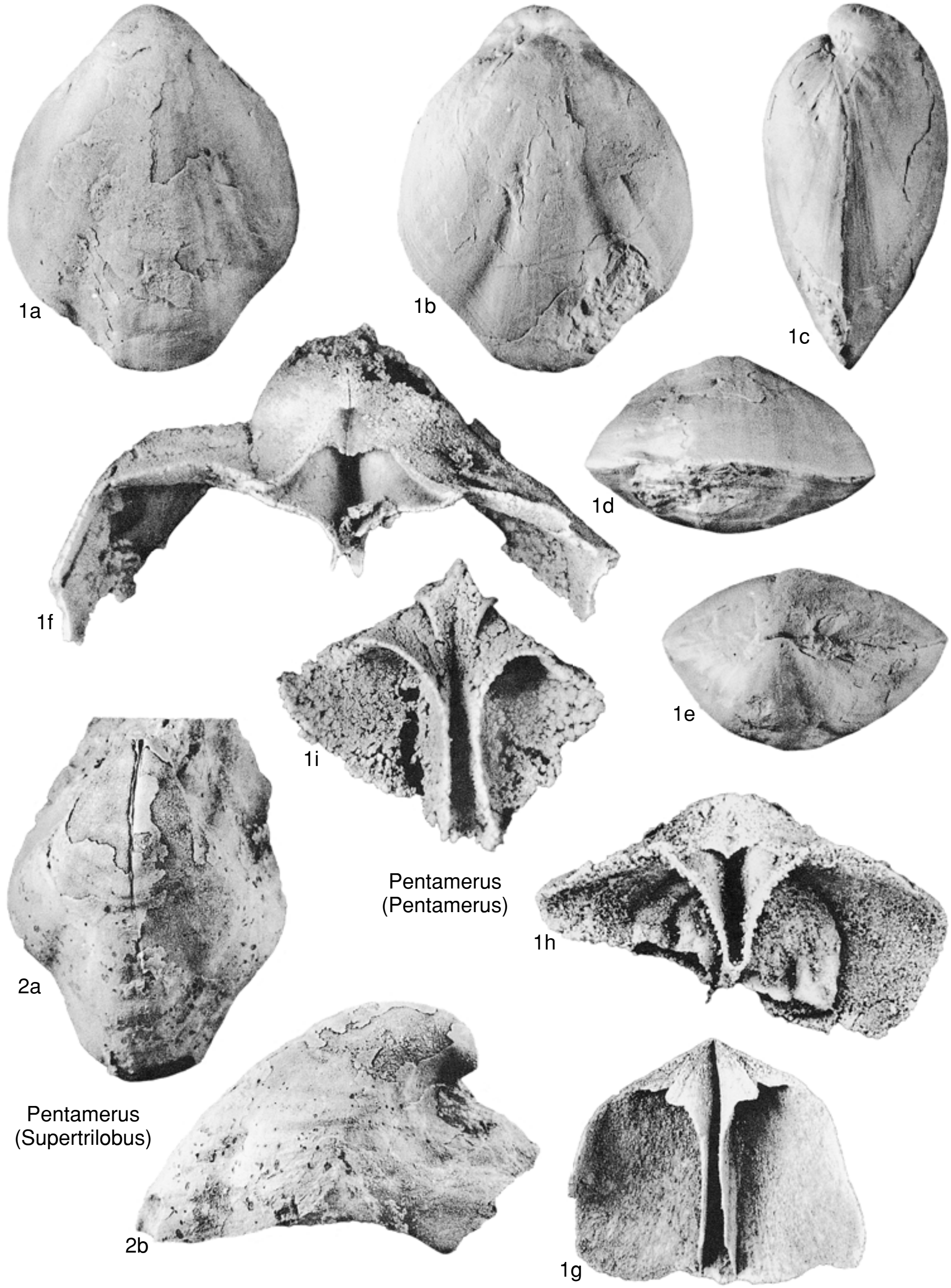

FIG. 651. Pentameridae (p. 973).

us as an example of convergence, since it is otherwise a homeomorph of *Kirkidium* in all regards; i.e., ours is the most parsimonious explanation.] *Silurian (middle Aeronian–Přídolí):* North America, Europe, Asia, Australia.

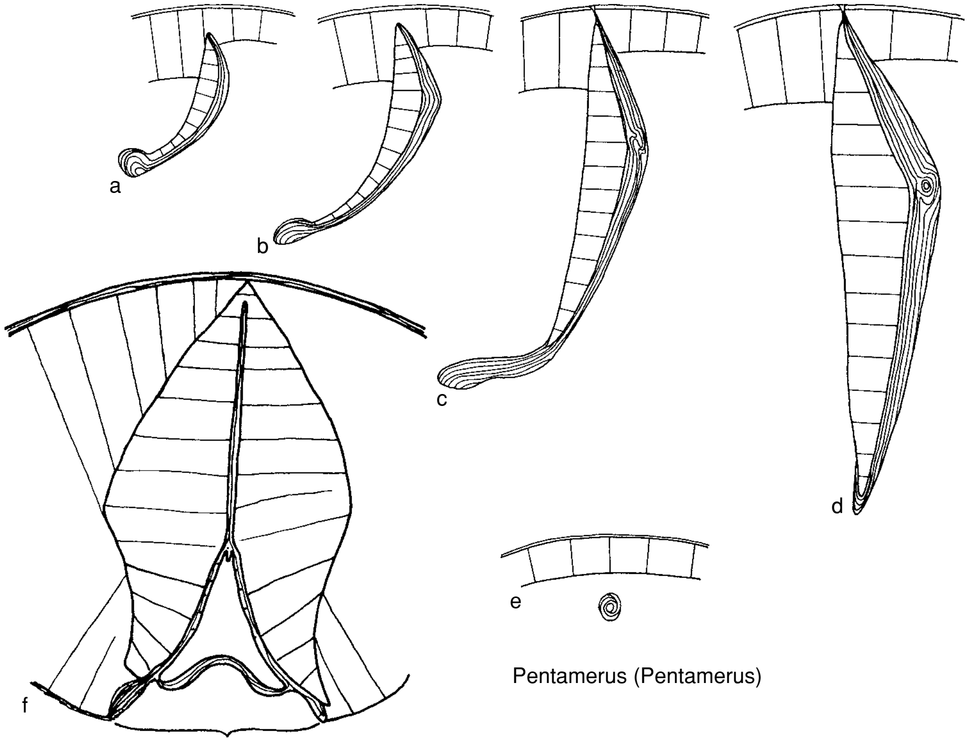

FIG. 652. Pentameridae (p. 973).

Pentamerus J. SOWERBY, 1813 in 1812–1815, p. 73 [**P. oblongus* J. de C. SOWERBY, 1839, p. 641; ICZN, 1954, Opinion 297; Opinion 297 placed *Pentamerus* J. SOWERBY, 1813 in 1812–1815, on the Official List of Generic Names in Zoology; *Pentamerus oblongus* J. de C. SOWERBY, 1839, was designated the type species and added to the Official List of Specific Names in Zoology. The following names were placed on the Official List of Rejected and Invalid Generic Names in Zoology: *Gypidia* DALMAN, 1828; *Trimurus* CALDWELL, 1934; *Miopentamerus* ALEXANDER (née CALDWELL), 1936; *Miopentamerus* WOODS, 1937. *Pentamerus laevis* J. SOWERBY, 1813 in 1812–1815, was placed in the Official Index of Rejected and Invalid Names in Zoology]. Medium to large; smooth; subequally biconvex; Ziegler's blisters present in small percentage; trilobate, with fold on each valve; ventral median septum about one-half valve length, hinge plates discrete, subparallel, and long. [Ziegler's blisters (see BOUCOT in BOUCOT & MCCUTCHEON, 1986) are calcitic partitions present in the posterior portion of one or both umbonal chambers; they are anterior of a space that may be filled either with clear calcite or sediment, and are interpreted as a teratological condition; their presence in samples of both *Pentamerus* and *Pentameroides* is considered to have phylogenetic value.] *Silurian (upper Aeronian–Ludlow):* North America, Europe, Asia, Australia.

P. (**Pentamerus**). Moderately biconvex. *Silurian (upper Aeronian–Wenlock):* North America, Europe, Asia, Australia.——FIG. 651,*1a–e.* **P. (P.) oblongus;* ventral, dorsal, lateral, anterior, posterior views, Jupiter Formation, Anticosti Island, Quebec, Canada, ×1 (Boucot & Johnson, 1979).——FIG. 652*a–f.* **P. (P.) oblongus;* sections showing hinge plate and crural development and spondylium, Wallington Limestone, central New York, USA, ×2 (Gauri & Boucot, 1968).——FIG. 651,*1f–i. Pentamerus* sp., USA; *f,* interior of ventral, Wallington Limestone, central New York, ×2; *g,* interior of dorsal, Wallington Limestone, central New York, ×1; *h,* interior of ventral, Wallington Limestone, central New York, ×2, *i,* interior of dorsal, Louisville Limestone, Louisville, Kentucky, ×3 (Boucot & Johnson, 1979).

P. (**Supertrilobus**) BOUCOT & JOHNSON, 1979, p. 100 [**S. hawthornensis;* OD]. Large; ventral fold very large and prominent, strongly biconvex. *Silurian (upper Wenlock–Ludlow):* central North America.——FIG. 651,*2a–b.* **P. (S.) hawthornensis,* Racine Dolomite, Cook County, Illinois, USA; interior of ventral, side view, ×1 (Boucot & Johnson, 1979).

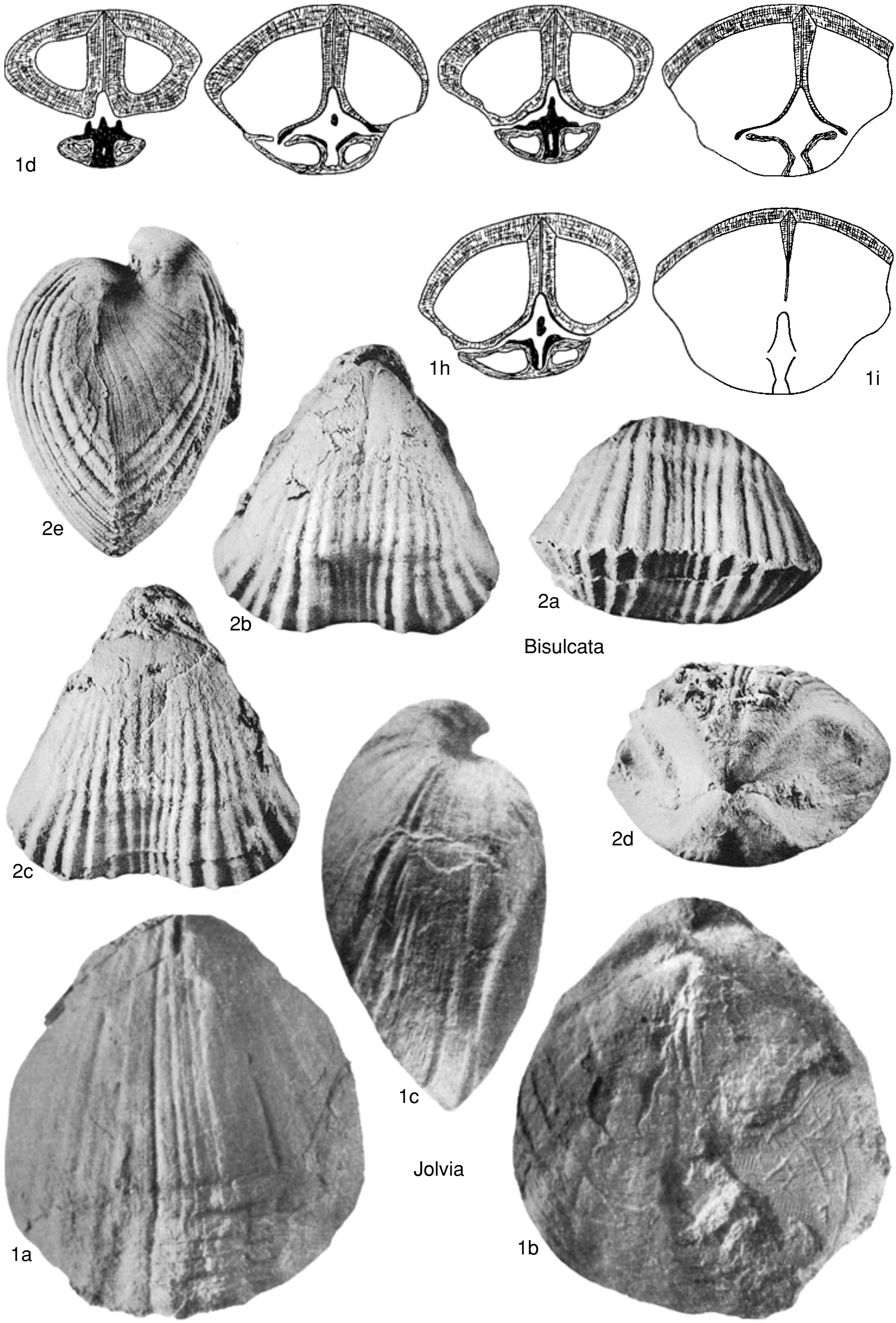

FIG. 653. Pentameridae (p. 975–976).

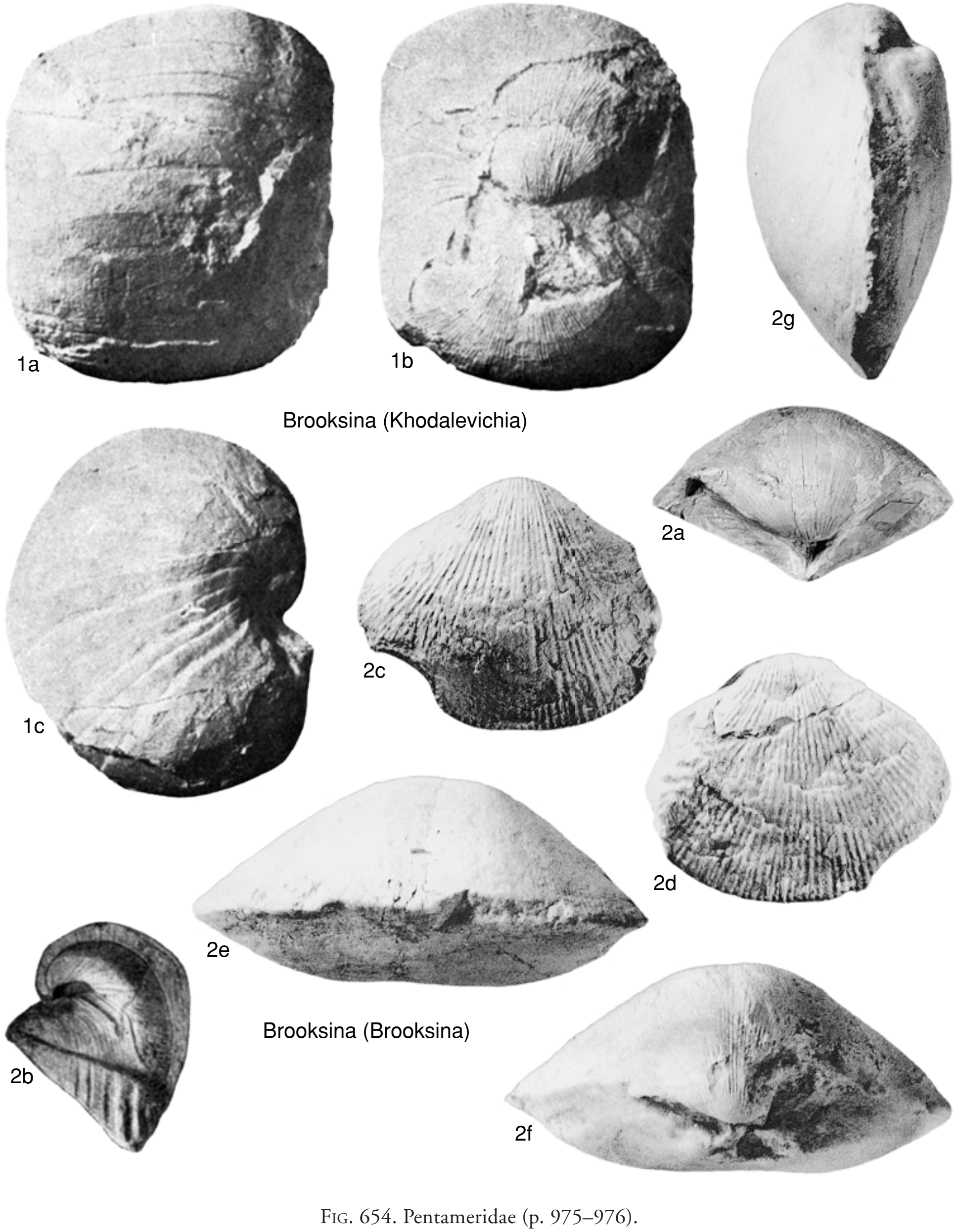

FIG. 654. Pentameridae (p. 975–976).

Bisulcata BOUCOT & JOHNSON, 1979, p. 117 [**B. indianensis;* OD]. Medium; moderately biconvex; costate; shallow sulcus on each valve, moderately long ventral median septum and longer spondylium, hinge plates as in *Kirkidium. Silurian (upper Wenlock–Přídolí):* midcontinent North America, Urals.——FIG. 653,*2a–e.* **B. indianensis,* Kenneth Limestone, Logansport, Indiana, USA; *a–c,* anterior, ventral, dorsal views, ×2; *d–e,* posterior, lateral views, ×1.25 (Boucot & Johnson, 1979).

Brooksina KIRK, 1922, p. 2 [**B. alaskensis;* OD]. Medium; costate; dorsibiconvex with dorsal valve beak strongly curved, extending posteriorly beyond ventral beak, ventral median septum very long, discrete hinge plates. *Silurian (upper Wenlock–Ludlow):* western North America, Urals, Central Asia [Sredni Azii], Kazakhstan, Altai Mountains.

B. (Brooksina). Medium; moderately biconvex. *Silurian (upper Wenlock–Ludlow):* western North America, Urals, Central Asia [Sredni Azii], Kazakhstan, Altai Mountains.——Fig. 654,*2a–b.* **B. (B.) alaskensis,* Heceta Limestone, Prince of Wales Island, southeastern Alaska, USA; *a,* posterior view, ×1 (Amsden, 1965); *b,* lateral view of interior, ×1 (Kirk, 1922).——Fig. 654, *2c–g. B. (B.) striata,* Striatus Stage [Gorizont], eastern slope of northern Urals, Russia; *c–d,* dorsal, ventral views, ×2; *e–g,* anterior, posterior, lateral views, ×1.5 (Boucot & Johnson, 1979).

B. (Khodalevichia) Boucot & Johnson, 1979, p. 116 [**Brooksina*(?) *crassa* Khodalevich, 1939, p. 35; OD]. Very inflated, almost hemispherical valves, ventribiconvex. *Silurian (Ludlow):* Urals.——Fig. 654,*1a–c.* **B. (K.) crassa* (Khodalevich), Striatus Stage [Gorizont], Isovsk Region, eastern Urals; anterior, posterior, lateral views, ×1 (Khodalevich, 1939).

Capelliniella Strand, 1928, p. 38, *nom. nov. pro Capellinia* Hall & Clarke, 1893, p. 249, *non* Trichese, 1874 [**Capellinia mira* Hall & Clarke, 1893, p. 249; OD]. Smooth; dorsibiconvex; not markedly trilobate; very long ventral median septum, hinge plates as in *Pentamerus. Silurian (upper Wenlock–Ludlow):* North America, Urals, Central Asia [Sredni Azii], Malaysia.——Fig. 655,*1a–d.* **C. mira* (Hall & Clarke), Racine Formation, Racine, Wisconsin, USA; dorsal, ventral, posterior, lateral views, ×1 (Boucot & Johnson, 1979).

Eokirkidium Khodalevich & Sapelnikov, 1970, p. 196 [**E. jachteljaensis;* OD]. Strongly biconvex; finely costate; no ventral median septum, dorsal interior as in *Kirkidium. Silurian (upper Wenlock–Ludlow):* Urals, Altai Mountains, Central Asia [Sredni Azii], Kazakhstan.——Fig. 655,*2a–e.* **E. jachteljaensis,* Striatus Stage [Gorizont], Ivdel region, eastern slope of northern Urals; ventral, ventral, lateral, anterior, dorsal views, ×1 (Khodalevich & Sapelnikov, 1970).

Harpidium Kirk, 1925, p. 1 [**H. insignis;* OD]. Smooth; nontrilobate; strongly ventribiconvex; dorsal interior as in *Pentamerus. Silurian (middle Aeronian–Ludlow):* North America, Europe, Asia.

H. (Harpidium). Ventral median septum very short; long spondylium. *Silurian (upper Aeronian–Ludlow):* North America, Urals, Asia.——Fig. 656,*1a–f.* **H. (H.) insignis,* Heceta Limestone, Prince of Wales Island, Alaska, USA; side view of interior, ventral, lateral, lateral, posterior, anterior views, ×1 (Kirk, 1925).

H. (Isovella) Breivel & Breivel in Antsigin & others, 1970, p. 52 [**I. regina;* OD] [=*Carmanella* Boucot in Berry & Boucot, 1970, p. 30, *nom. nud.; Apopentamerus* Boucot & Johnson, 1979, p. 104 (type, *A. racinensis;* OD)]. Large; marked umbonal thickenings in ventral posterior region; ventral median septum moderately long. *Silurian (upper Aeronian–Ludlow):* midcontinent North America, Urals, China. ——Fig. 657*a–d.* **H. (I.) regina,* Wenlock, Isovsk region, eastern slope of central Urals; ventral, posterior, lateral, ventral views, ×1 (Antsigin & others, 1970).——Fig. 657*e–g. H. (I.) maquoketa,* Hopkinton Dolomite, Jones County, Iowa, USA; ventral view of interior, lateral view of internal mold, posterior view of internal mold, ×1 (Boucot & Johnson, 1979).

H. (Sulcipentamerus) Zeng, 1987, p. 240 [**S. sulcus;* OD]. Large; elongate; unevenly biconvex with dorsal valve gently convex to weakly concave, sulcate anteriorly in some specimens, ventral valve deep; ventral fold; unisulcate anterior margin; short ventral median septum. *Silurian (middle Aeronian–upper Aeronian):* Yangtze Gorge region.——Fig. 656,*2a–d.* **H. (S.) sulcus,* central China; anterior, lateral, ventral, dorsal views, ×1 (Zeng, 1987).

Jolvia Sapelnikov, 1960b, p. 56 [**J. multiplexa* Sapelnikov, 1960b, p. 58; OD]. Low, broad costae variably present; long median septum, ventribiconvex; variably developed ventral fold and dorsal sulcus, massive cardinal process commonly developed. *Silurian (upper Llandovery–lower Wenlock):* eastern slope Urals.——Fig. 653,*1a–i.* **J. multiplexa,* basal Wenlock, Novo-Lialinsk region; *a–c,* ventral, dorsal, lateral views, ×1; *d–i,* serial sections, ×0.875 (Sapelnikov, 1960b).

Kirkidium Amsden, Boucot, & Johnson, 1967, p. 865 [**Pentamerus knighti* J. Sowerby, 1813 in 1812–1815, p. 73; OD] [=*Praekirkidium* Breivel & Breivel, 1988, p. 54 (type, *P. uncinus,* OD)]. Coarsely costate; unequally biconvex with ventral valve deeper; nontrilobate, long ventral median septum, hinge plates as in *Pentamerus,* crura very prominent. *Silurian (upper Wenlock–Přídolí):* North America, Europe, Asia, Australia.

K. (Kirkidium). Strongly biconvex. *Silurian (upper Wenlock–Přídolí):* North America, Europe, Asia, Australia.——Fig. 658,*2a–c.* **K. (K.) knighti,* Aymestry Limestone, England; *a–b,* lateral, lateral view of interior, ×.67; *c,* posterior view, ×1 (Murchison, 1839).

K. (Bateridium) Su, Rong, & Li, 1985, p. 84 [**B. bateroboensis;* OD]. Large; biconvex; nonlobate *Kirkidium* with fine costae; thin, long median septum reaching almost to anterior margin and supporting somewhat short, narrow spondylium; inner hinge plates parallel, extending anteriorly about two-thirds length of dorsal valve; median flangelike ridges on lateral faces of hinge plates. *Silurian (Wenlock–Ludlow):* North China, central Urals.——Fig. 659*a–f.* **K. (B.) bateroboensis,* Bateaobao Formation, Bateaobao, Inner Mongolia; posterior view of internal mold, lateral view of interior, lateral view of interior, lateral, ventral view of internal mold, dorsal view of internal mold, ×1 (Su, Rong, & Li, 1985).

K. (Pinguaella) Boucot & Johnson, 1979, p. 114 [**Rhipidium pingue* Amsden, 1949a, p. 47; OD]. Medium to large; moderately biconvex. *Silurian (upper Wenlock–Přídolí):* North America, Europe, Asia, Australia.——Fig. 658,*1a–i.* **K. (P.) pingue* (Amsden), Brownsport Formation, western Tennessee, USA; *a–e,* ventral, dorsal, ventral,

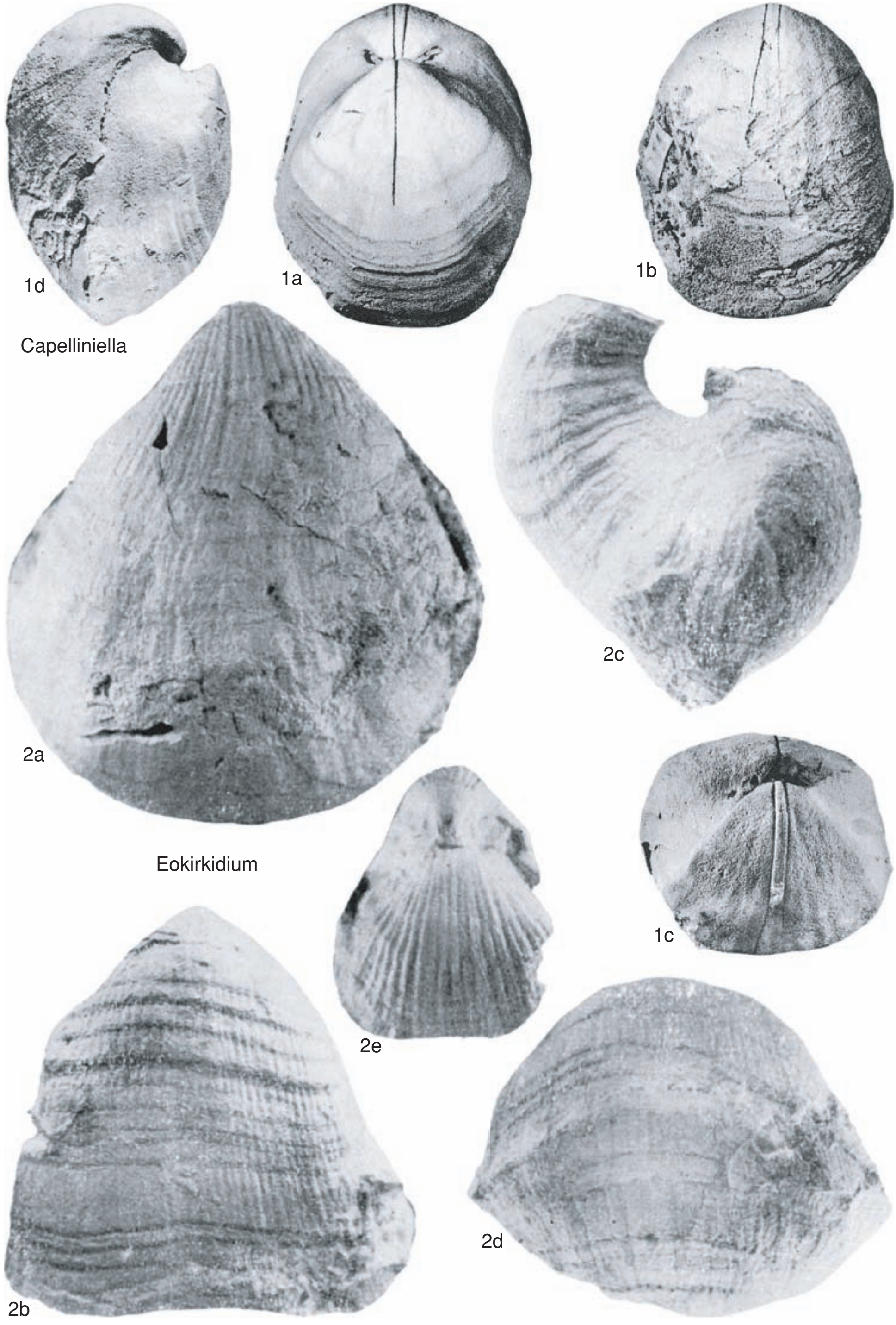

FIG. 655. Pentameridae (p. 976).

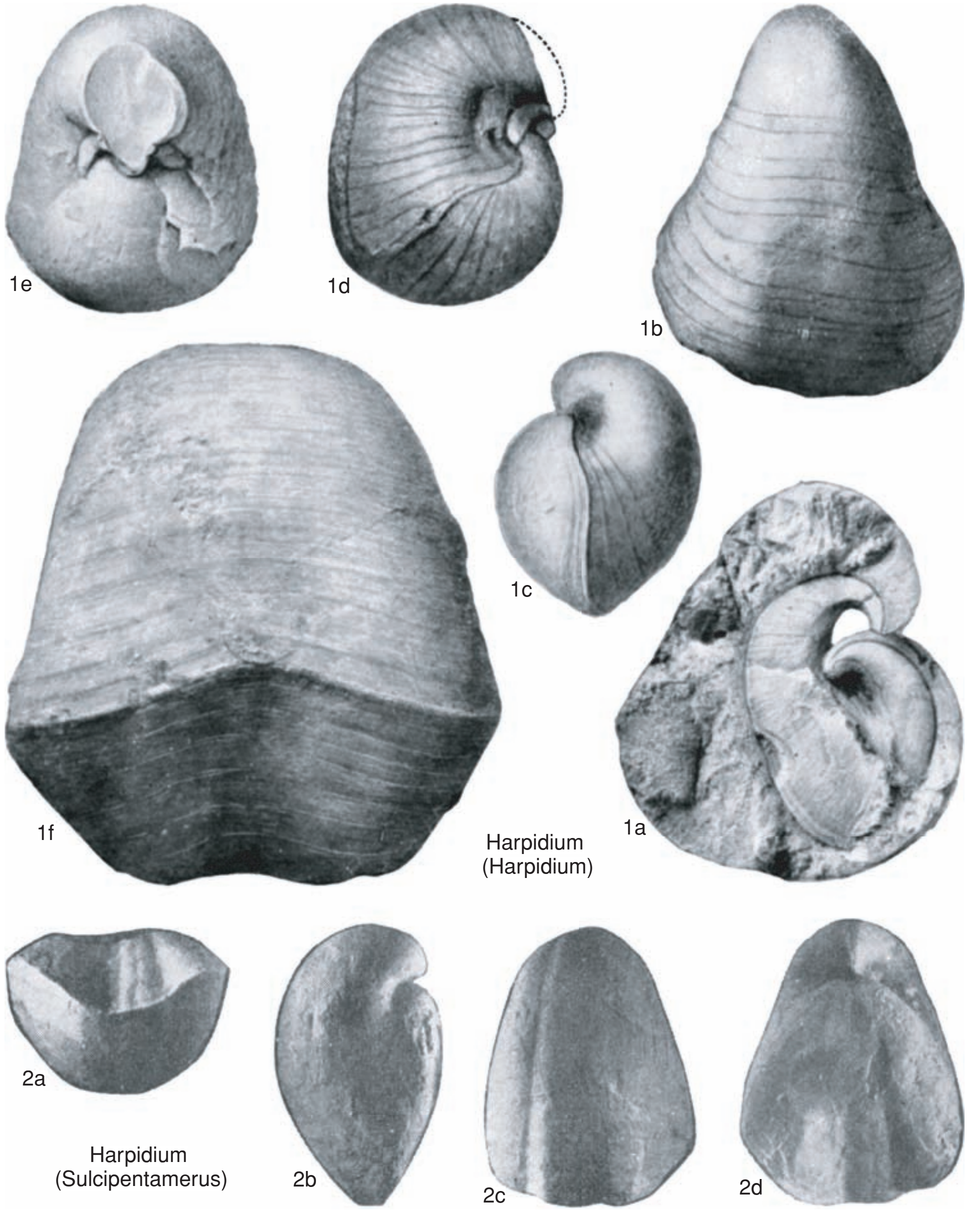

FIG. 656. Pentameridae (p. 976).

posterior, anterior views, ×2; *f–g,* posterior, lateral views, ×1.5; *h,* ventral view, ×1; *i,* impression of dorsal interior, ×1 (Boucot & Johnson, 1979).

Lissocoelina SCHUCHERT & COOPER, 1931, p. 248 [**Pentamerus pergibbosus* HALL & WHITFIELD, 1875, p. 139; OD]. Medium to large; very deep ventral valve; radial costellae poorly developed anteriorly, very long ventral median septum. *Silurian (upper Wenlock–Ludlow):* midcontinent North America. ——FIG. 660*a–h.* **L. pergibbosa* (HALL & WHITFIELD), Racine Dolomite, Hawthorne, Illinois, USA; *a–e,* dorsal, ventral, anterior, lateral, lateral views, ×1 (Boucot & Johnson, 1966b); *f–h,*

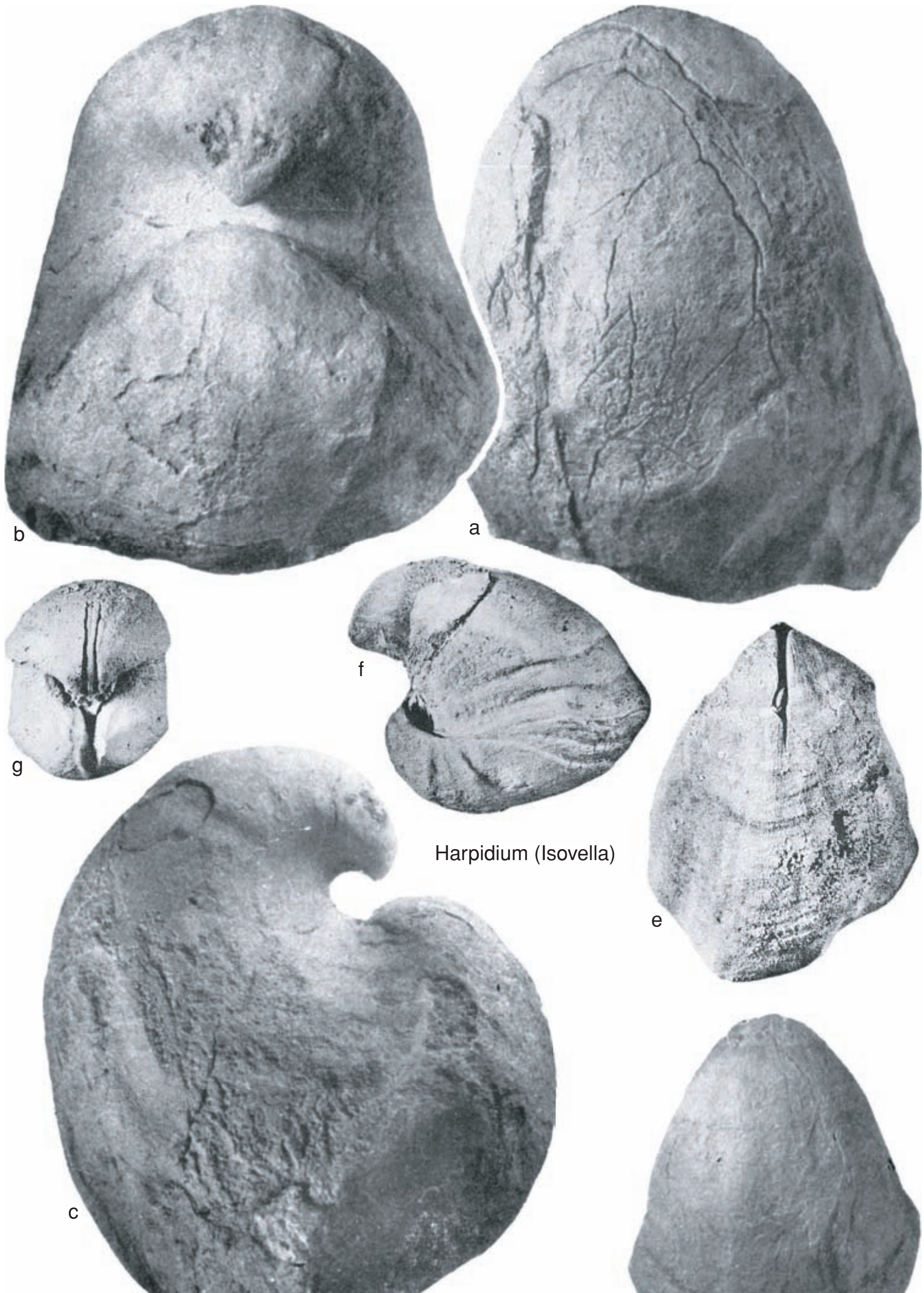

FIG. 657. Pentameridae (p. 976).

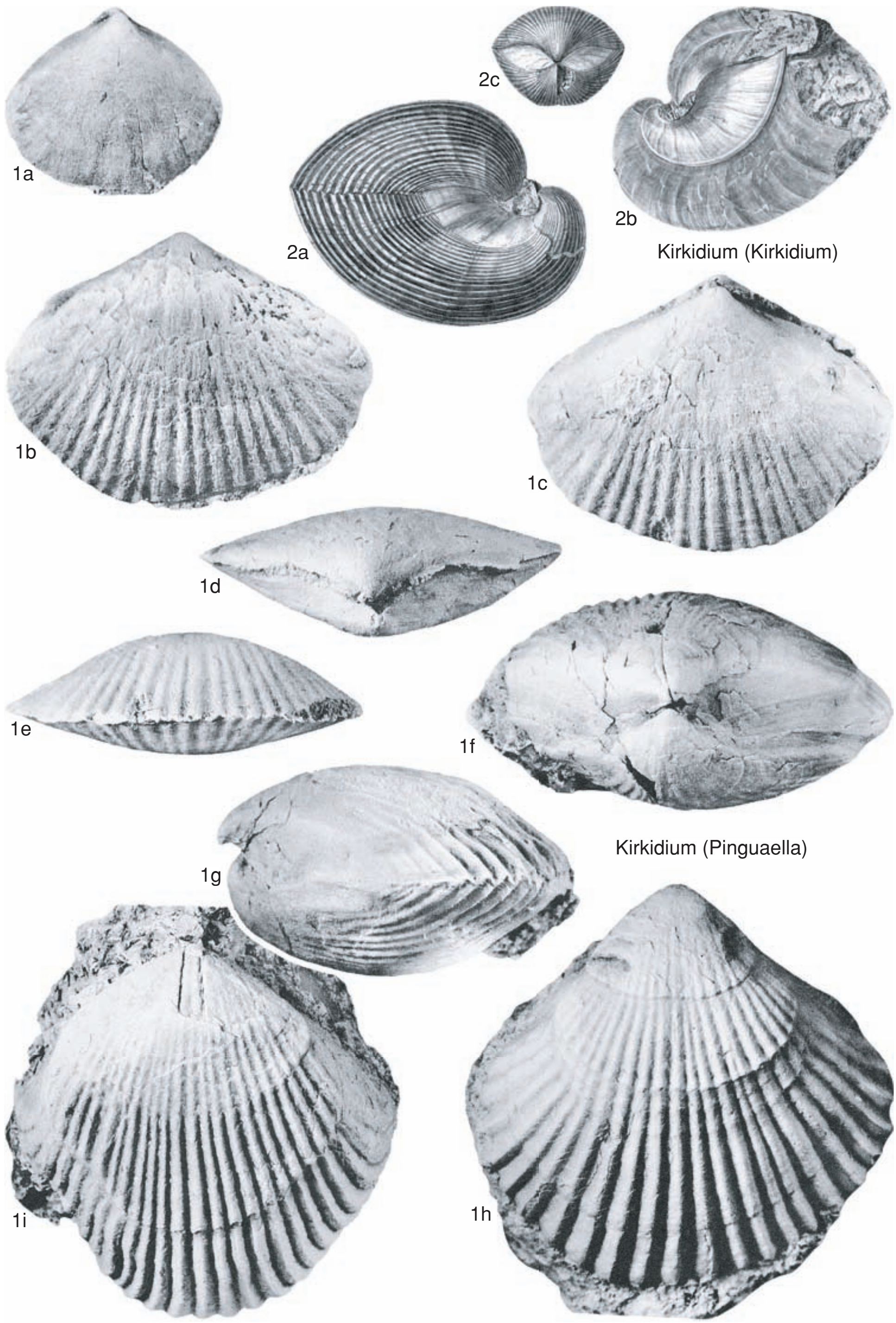

FIG. 658. Pentameridae (p. 976–979).

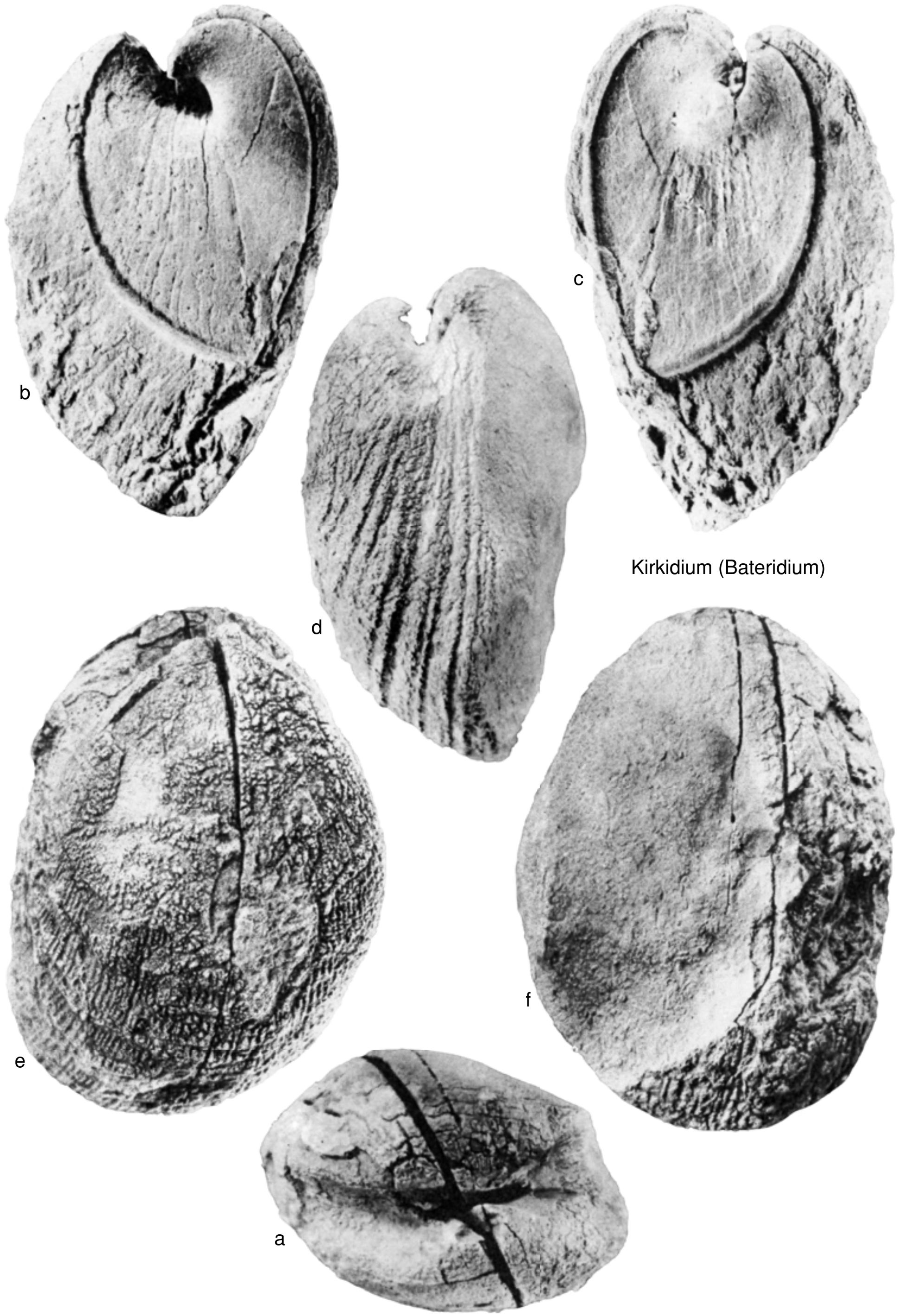

FIG. 659. Pentameridae (p. 976).

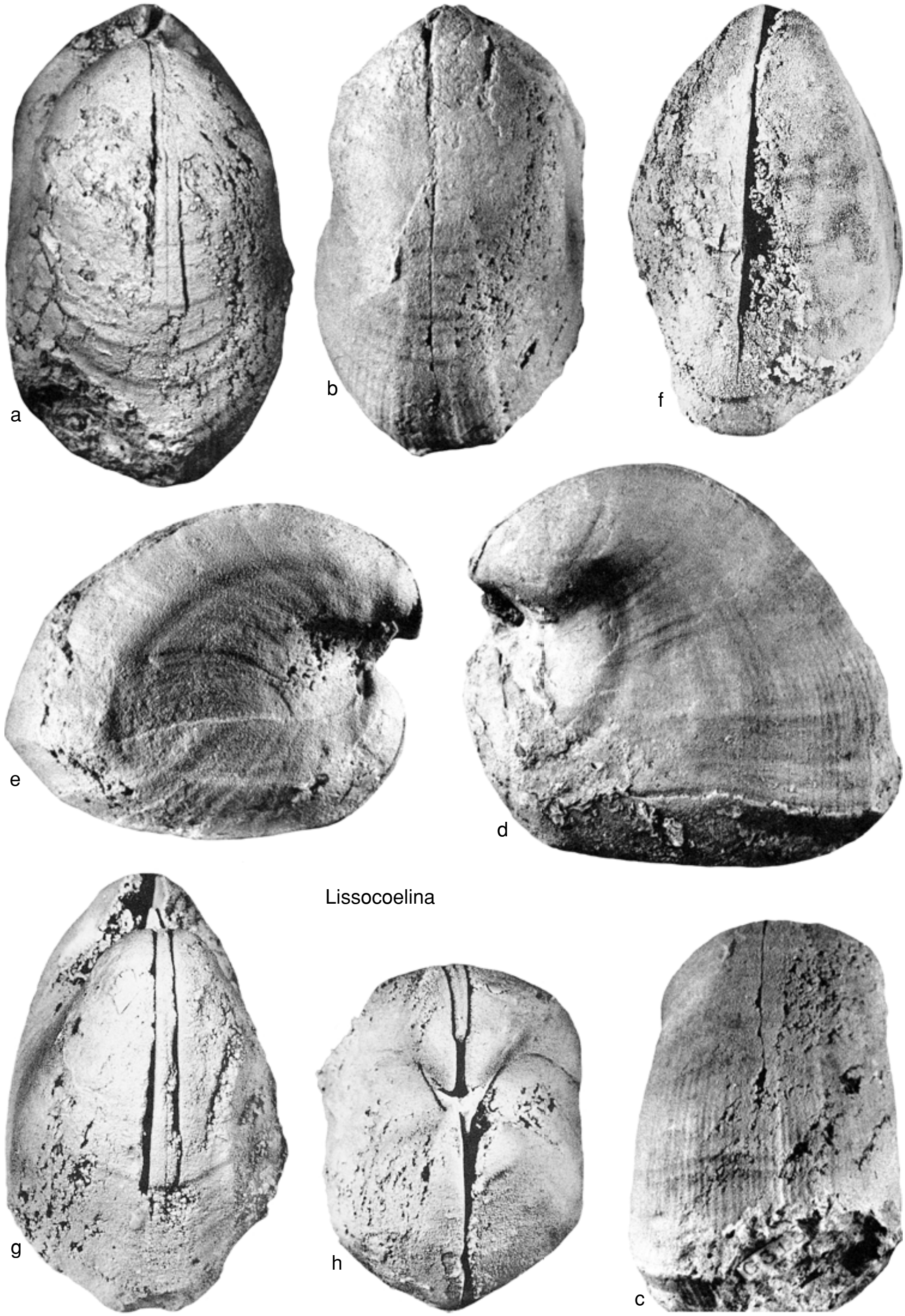

FIG. 660. Pentameridae (p. 978–983).

impression of ventral interior, impression of dorsal interior, impression of posterior interior, ×1 (Boucot & Johnson, 1979).

Nanukidium Jones, 1979, p. 1261 [**Rossella arctica* Jones, 1978, p. 547; OD; *non Rossella* Carter, 1872]. Medially directed carinae support inner extensions of crura; otherwise similar to *Kirkidium,* ventral median septum very long. *Silurian (Ludlow–lower Přídolí):* Canadian Arctic, USA (southeastern Alaska).——Fig. 661,*2a–d.* **N. arctica* (Jones), Read Bay Formation, Somerset Island, Arctic Canada; *a–c,* ventral, dorsal, lateral views; *d,* serial section, ×1 (Jones, 1978).

Pentamerifera Khodalevich, 1939, p. 22 [**Pentamerus taltiensis* Chernyshev, 1893, p. 183; OD]. Smooth; ventral median septum very long, almost extending to anterior margin; nontrilobate, ventribiconvex, dorsal interior as in *Pentamerus. Silurian (Ludlow):* USA (Nevada), Urals, Central Asia [Sredni Azii], northwestern China.——Fig. 661,*1a–d.* **P. taltiensis* (Chernyshev), Striatus Stage [Gorizont], Ivdel region, eastern slope Urals; ventral, dorsal, lateral, lateral of interior, ×1 (Khodalevich, 1939).

Pentameroides Schuchert & Cooper, 1931, p. 248 [**Pentamerus subrectus* Hall & Clarke, 1893, p. 238; OD]. Smooth to chevronlike ornamentation, inner hinge plates fused to form a cruralium supported by a median septum. *Silurian (upper Llandovery–upper Wenlock).*

P. (**Pentameroides**). Smooth; lenticular; trilobate; external homeomorph of *Pentamerus.* [Type material unsuitable for illustration.] *Silurian (upper Llandovery–upper Wenlock):* North America, Europe.——Fig. 662*a–f. P. (P.)* sp.; *a–e,* ventral, dorsal, lateral, posterior, anterior views of internal impression, Schoolcraft Dolomite?, Calumet County, Wisconsin, USA, ×1 (Boucot & Johnson, 1979); *f,* serial section, Meritton Limestone, Thorold, Ontario, Canada (Gauri & Boucot, 1968).

P. (**Callipentamerus**) Boucot, 1964a, p. 887 [**Pentamerus corrugatus* Weller & Davidson, 1896, p. 173; OD]. Variably ornamented with chevronlike corrugations; otherwise similar to *Pentameroides. Silurian (upper Llandovery–lower Wenlock):* midcontinent North America.——Fig. 663,*2a–f.* **P. (C.) corrugatus* (Weller & Davidson), Hopkinton Dolomite, Monticello, Iowa, USA; dorsal, posterior, ventral, lateral, dorsal, ventral views, ×1 (Boucot, 1964a).

P. (**Reveroides**) Sapelnikov, 1976, p. 32 [**P. jolvensis* Sapelnikov, 1961a, p. 103; OD] [=*Sapelnikovia* Boucot & Johnson, 1979, p. 118, homonym]. Smooth; bisulcate; anteriorly or posteriorly conjunct inner hinge plates, inner hinge plates separate posteriorly, becoming conjunct anteriorly; spondylium and median septum of equal length. *Silurian (upper Llandovery–Wenlock):* Ontario, northern Greenland, Urals, Altai Mountains, Canadian Arctic.——Fig. 663,*1a–c.* **P. (R.) jolvensis* Sapelnikov, basal Wenlock, Novo-Lialinsk region, eastern slope of central Urals; ventral internal mold, dorsal internal mold, lateral view, ×1 (Sapelnikov, 1961a).

Rhipidium Schuchert & Cooper, 1931, p. 249 [**Pentamerus knappi* Hall & Whitfield, 1872, p. 184; OD]. Finely to coarsely costate; faintly to very trilobate, discrete inner hinge plates, median septum about half valve length. *Silurian (Wenlock–Ludlow):* North America, Europe.

R. (**Rhipidium**). Coarsely costate; moderately biconvex; faintly trilobate to nontrilobate. *Silurian (upper Wenlock):* midcontinent North America.——Fig. 664*a–e.* **R. (R.) knappi* (Hall & Whitfield), Louisville Formation, Kentucky, USA; ventral, dorsal, lateral, posterior, anterior views, ×1 (Boucot & Johnson, 1979).

R. (**Ectorhipidium**) Boucot & Johnson, 1979, p. 102 [**Conchidium trilobatum* Kindle & Breger in Kindle, 1904, p. 436; OD]. Very large, costate, anteriorly bifurcating; elongate, lenticular; very strongly trilobate. *Silurian (Ludlow):* midcontinent North America.——Fig. 665*a–c.* **R. (E.) trilobatum* (Kindle & Breger), Wabash Formation, Huntington, Indiana, USA; ventral, anterior, and lateral views of internal impressions, ×1 (Boucot & Johnson, 1979).——Fig. 666*a–c.* **R. (E.) trilobatum* (Kindle & Breger), Wabash Formation, Huntington, Indiana, USA; posterior, posterior, and ventral views of internal impressions, ×1 (Boucot & Johnson, 1979).

R. (**Pararhipidium**) Boucot & Johnson, 1979, p. 101 [**Pentamerus tenuistriatus* Lindström in Angelin & Lindström, 1880, p. 24; OD]. Finely costate; elongate-pyriform, lenticular; faintly trilobate to nontrilobate. *Silurian (upper Wenlock–Ludlow):* North America, Sweden, Urals, Kazakhstan, Malaysia.——Fig. 667*a–d.* **R. (P.) tenuistriatum* (Lindström), Gotland, Sweden; *a–c,* lateral, dorsal, ventral views, Slite beds, Färo, ×1 (Boucot & Johnson, 1979); *d,* serial section, Slite Group, Eskelhem, ×30 (Gauri & Boucot, 1968).

Stenopentamerus Boucot & Johnson, 1979, p. 111 [**Pentamerus oblongus* var. *compressa* Kindle & Breger in Kindle, 1904, p. 437; OD]. Smooth, strongly biconvex and very laterally compressed, very long ventral median septum. *Silurian (upper Wenlock–Ludlow):* midcontinent North America, Kazakhstan.——Fig. 668,*1a–e.* **S. compressa* (Kindle & Breger), Racine Dolomite, Cook County, Illinois, USA; lateral view of ventral, lateral, posterior, ventral posterior, dorsal interior view, ×1 (Boucot & Johnson, 1979).

Twenhofelia Boucot & Smith, 1978, p. 271 [**Stricklandia exploitensis* Shrock & Twenhofel, 1939, p. 260, *pars;* OD]. Subcircular; costellate, with some costae anteriorly bifurcating; ventribiconvex; conjunct inner hinge plates form base of cruralium. *upper Silurian:* Canada (Newfoundland).——Fig. 668,*2a–e.* **T. exploitensis* (Shrock & Twenhofel), Upper Black Island Marble, Bay of Exploits region, northern Newfoundland; *a,* ventral view, ×1.5; *b,* ventral view, ×1; *c,* dorsal view, ×1; *d,* ventral

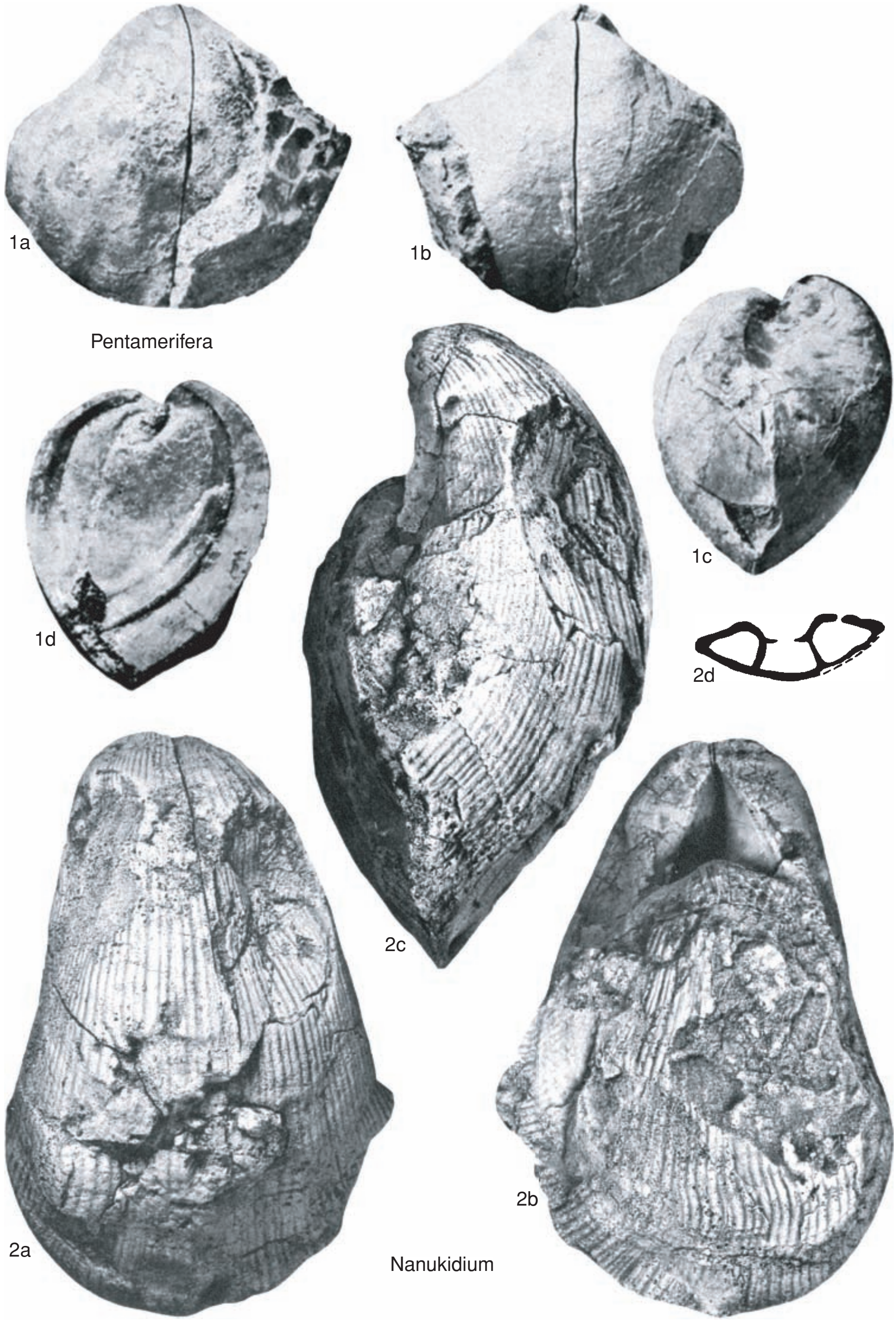

FIG. 661. Pentameridae (p. 983).

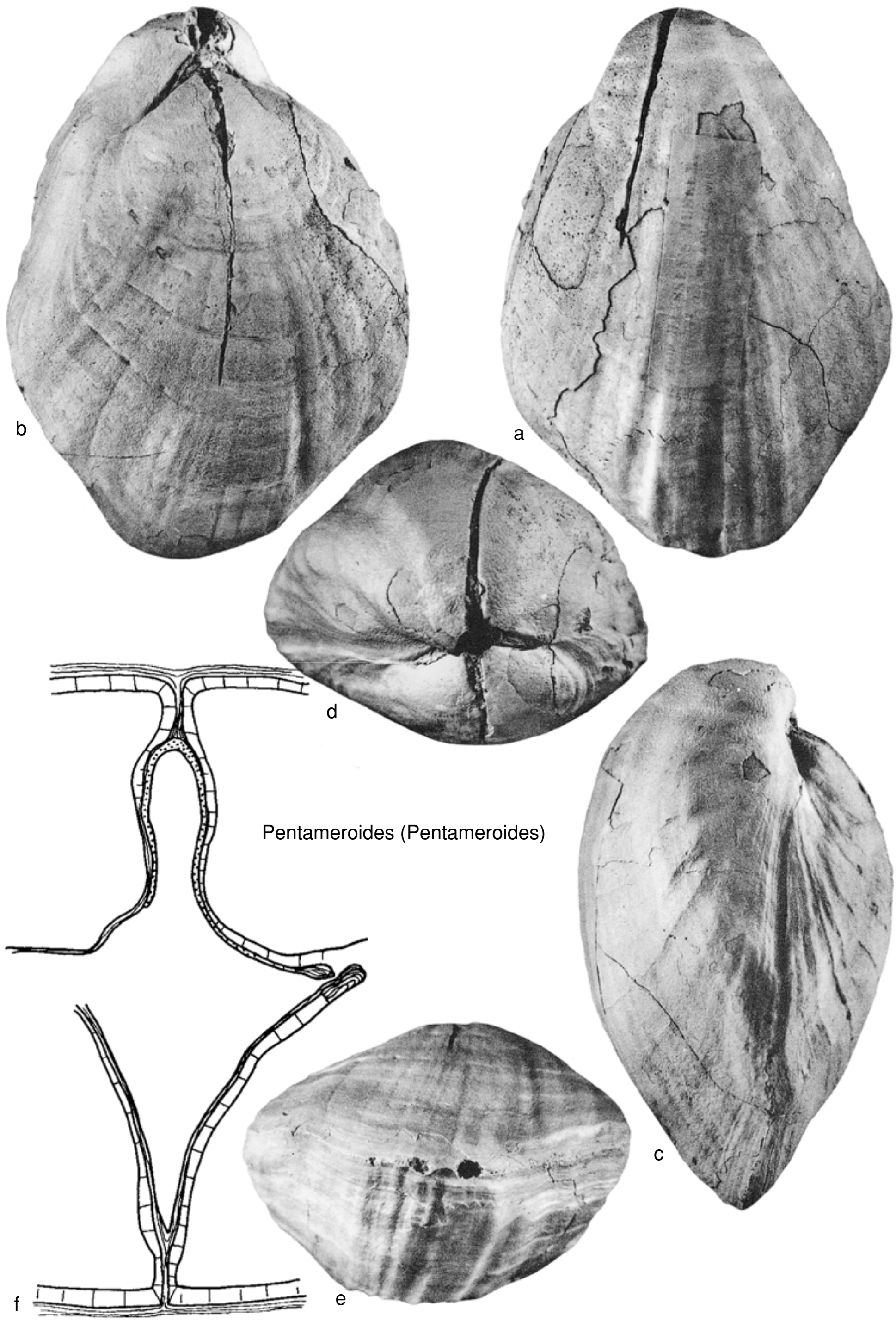

FIG. 662. Pentameridae (p. 983).

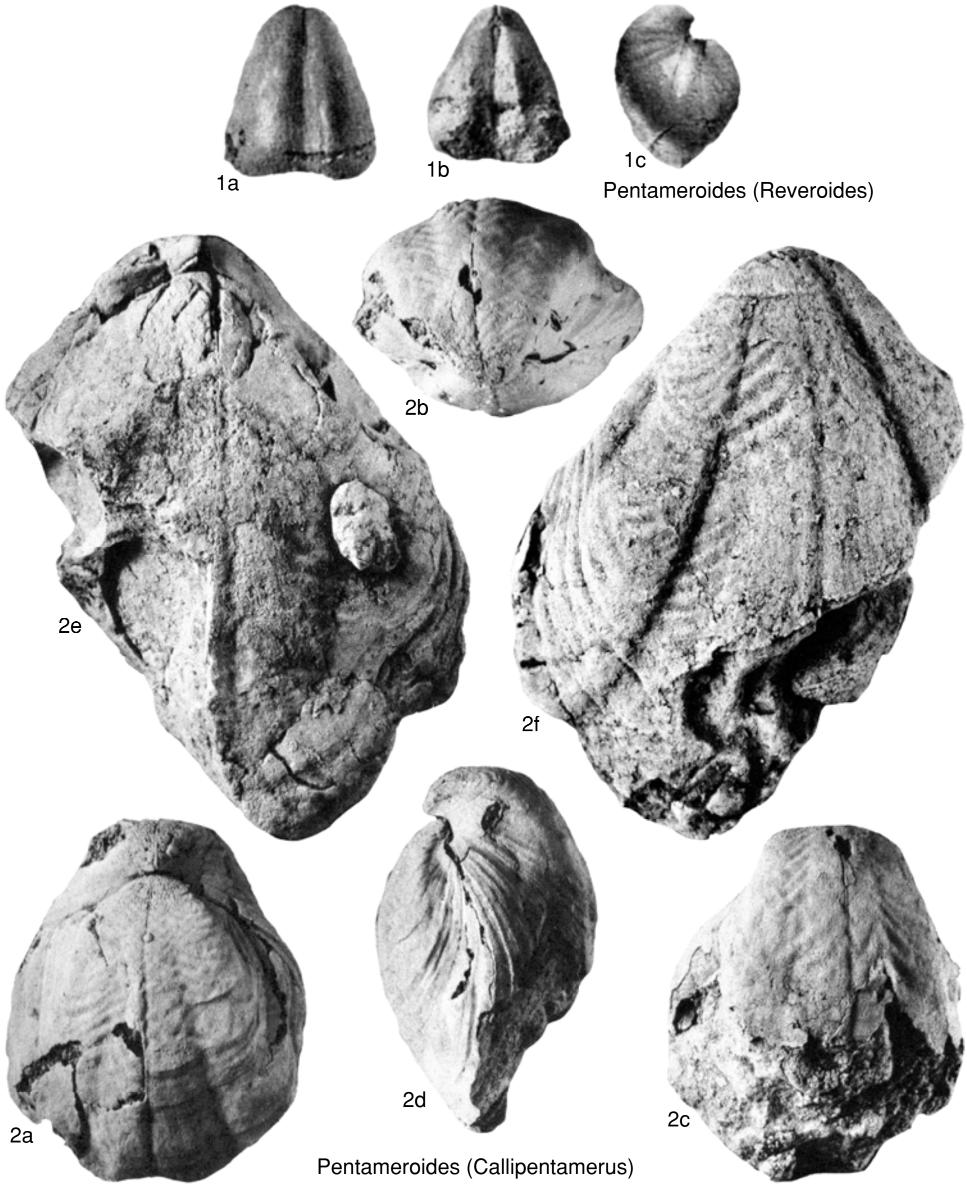

FIG. 663. Pentameridae (p. 983).

posterior, ×2; *e,* dorsal view, ×1.1 (Boucot & Smith, 1978).

Family SUBRIANIDAE Sapelnikov, 1963

[*nom. transl.* BOUCOT, RONG, & BLODGETT, herein, *ex* Subrianinae SAPELNIKOV, 1963a, p. 65]

Hinge plates relatively short, usually one-third or much less than dorsal valve length; prominent, medially projecting, subcylindrical, crural bases converge in dorsal direction toward plane of symmetry; inner hinge plates laterally inclined basally; outer hinge plates laterally inclined distally; deltidium and cardinal process may be present; ventral median septum. *Silurian (Wenlock–Ludlow):* Eurasia, North America, Australia.

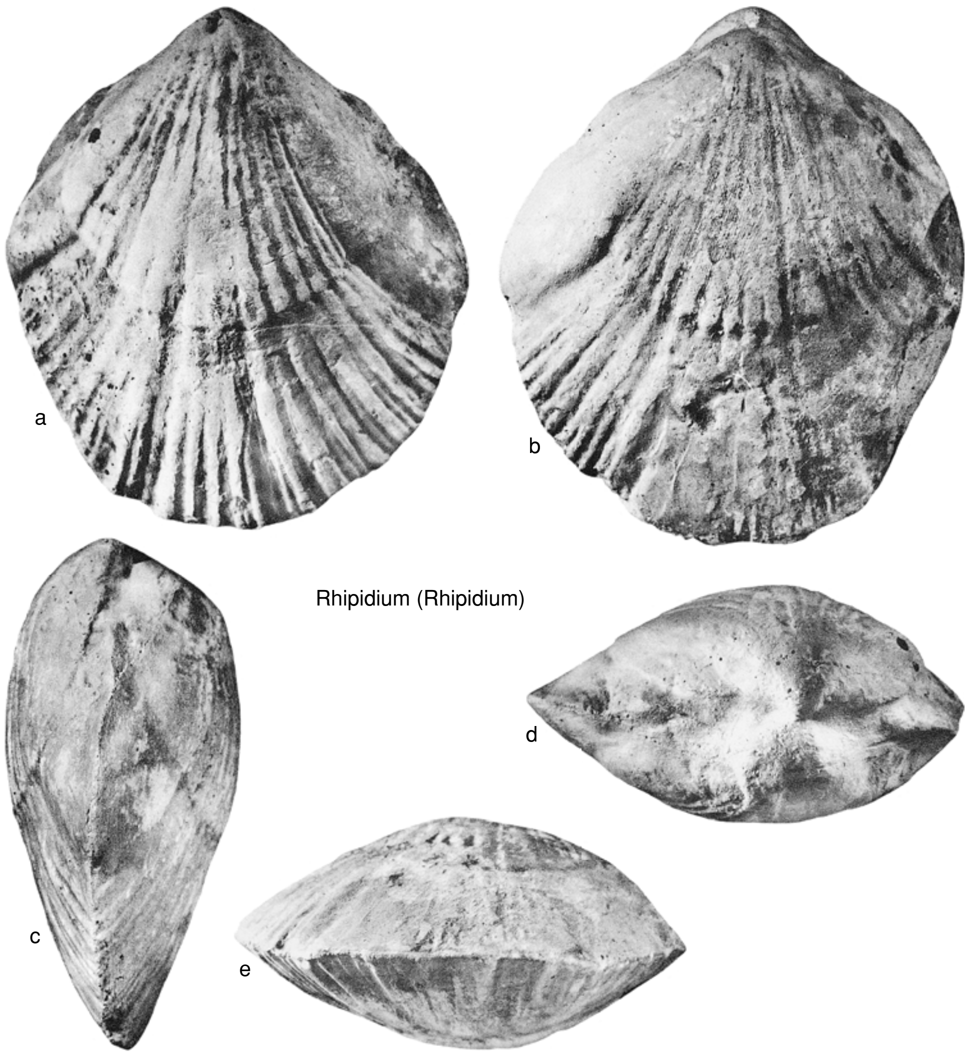

FIG. 664. Pentameridae (p. 983).

Subfamily SUBRIANINAE Sapelnikov, 1963

[Subrianinae SAPELNIKOV, 1963a, p. 65]

Cardinalia very short, inner hinge plates submerged in secondary shell material, outer hinge plates very short. *Silurian (Wenlock–Ludlow):* Urals.

Subriana SAPELNIKOV, 1960a, p. 111 [**S. subrini;* OD]. Medium, transverse; few, angular, coarse plicae; biconvex with ventral valve deeper; free spondylium; strongly unisulcate; outer hinge plates projecting anteriorly beyond very short inner hinge plates submerged in secondary tissue; crura present. *Silurian (lower Ludlow):* Urals.——FIG. 669,*1a–d.* **S. subrini,* upper Wenlock, Istok River, eastern Urals; ventral, dorsal, lateral, anterior views, ×1 (Sapelnikov, 1960a).

Vagranella SAPELNIKOV, 1960a, p. 116 [**V. diversoplicata;* OD]. Small to medium; costate to costellate; short, free spondylium and no median septum; cardinalia and ventral interior similar to *Subriana. Silurian (Wenlock–Ludlow):* Urals.——FIG. 669,*2a–m.* **V. diversoplicata,* Isovsk Stage [Gorizont], Istok River, eastern slope of Urals; *a–c,* ventral, lateral, dorsal views, ×1 (Sapelnikov, 1972); *d–m,* serial sections (Sapelnikov, 1985a).

FIG. 665. Pentameridae (p. 983).

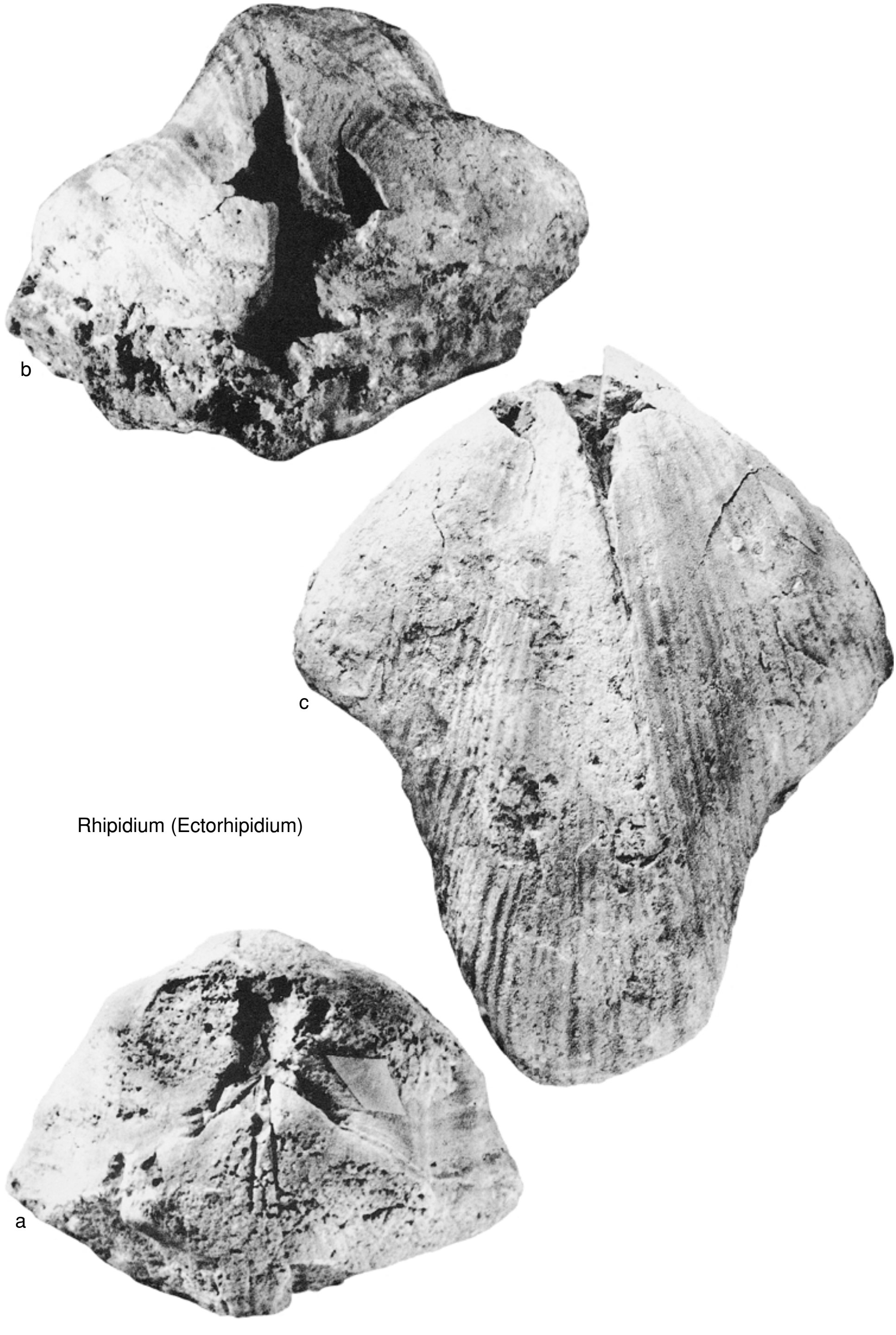

FIG. 666. Pentameridae (p. 983).

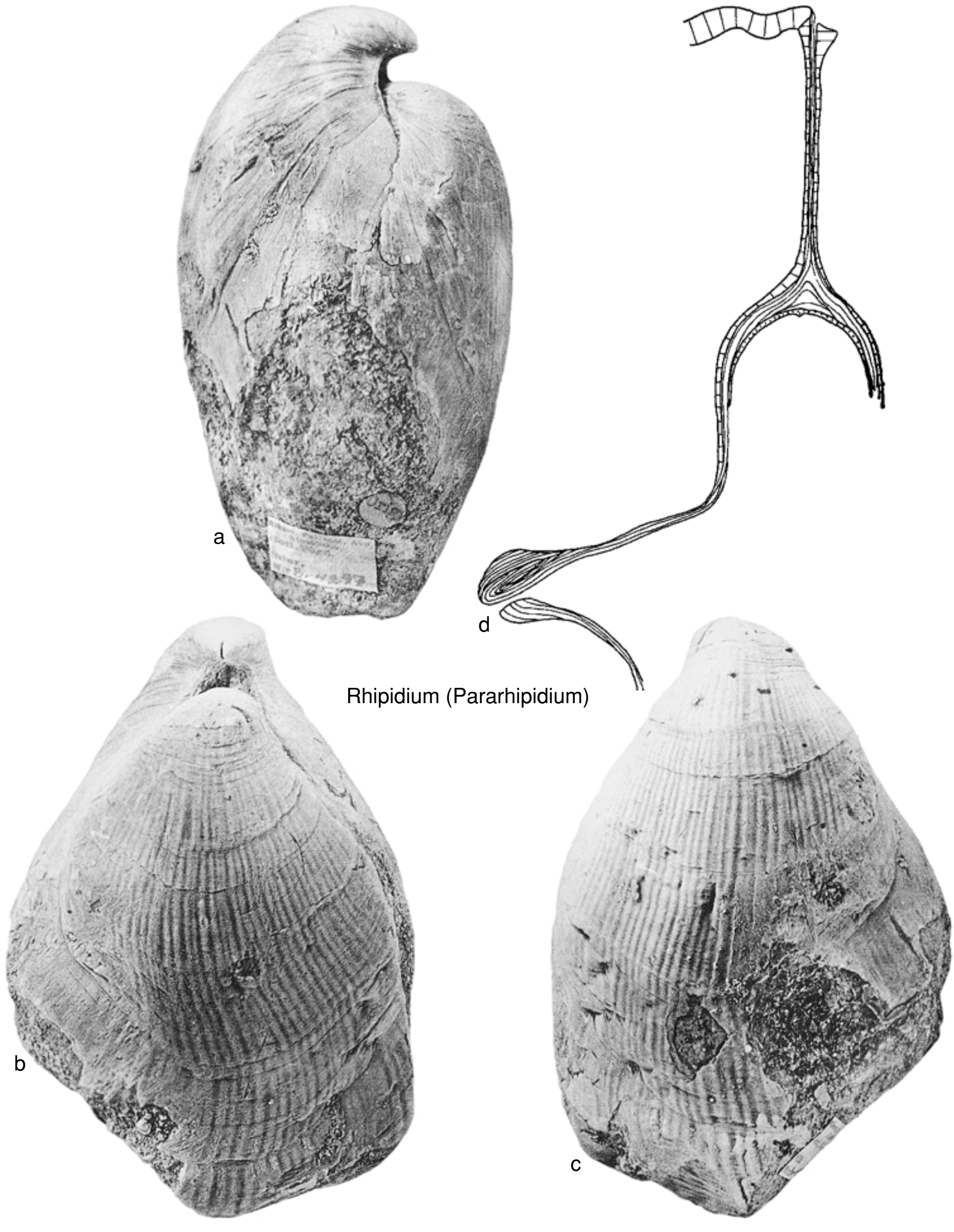

FIG. 667. Pentameridae (p. 983).

Subfamily CONCHIDIINAE Sapelnikov, 1973

[Conchidiinae SAPELNIKOV, 1973, p. 40]

Relatively short, laterally concave hinge plates unsubmerged by secondary shell material. *Silurian (Wenlock–Ludlow):* Eurasia, North America, Australia.

Conchidium OEHLERT, 1887a, p. 1311 [**Anomia bilocularis* HISINGER, 1799, p. 285; OD]. Medium; subcircular to elongate; costellate, commonly anteriorly bifurcating; unequally biconvex with ventral

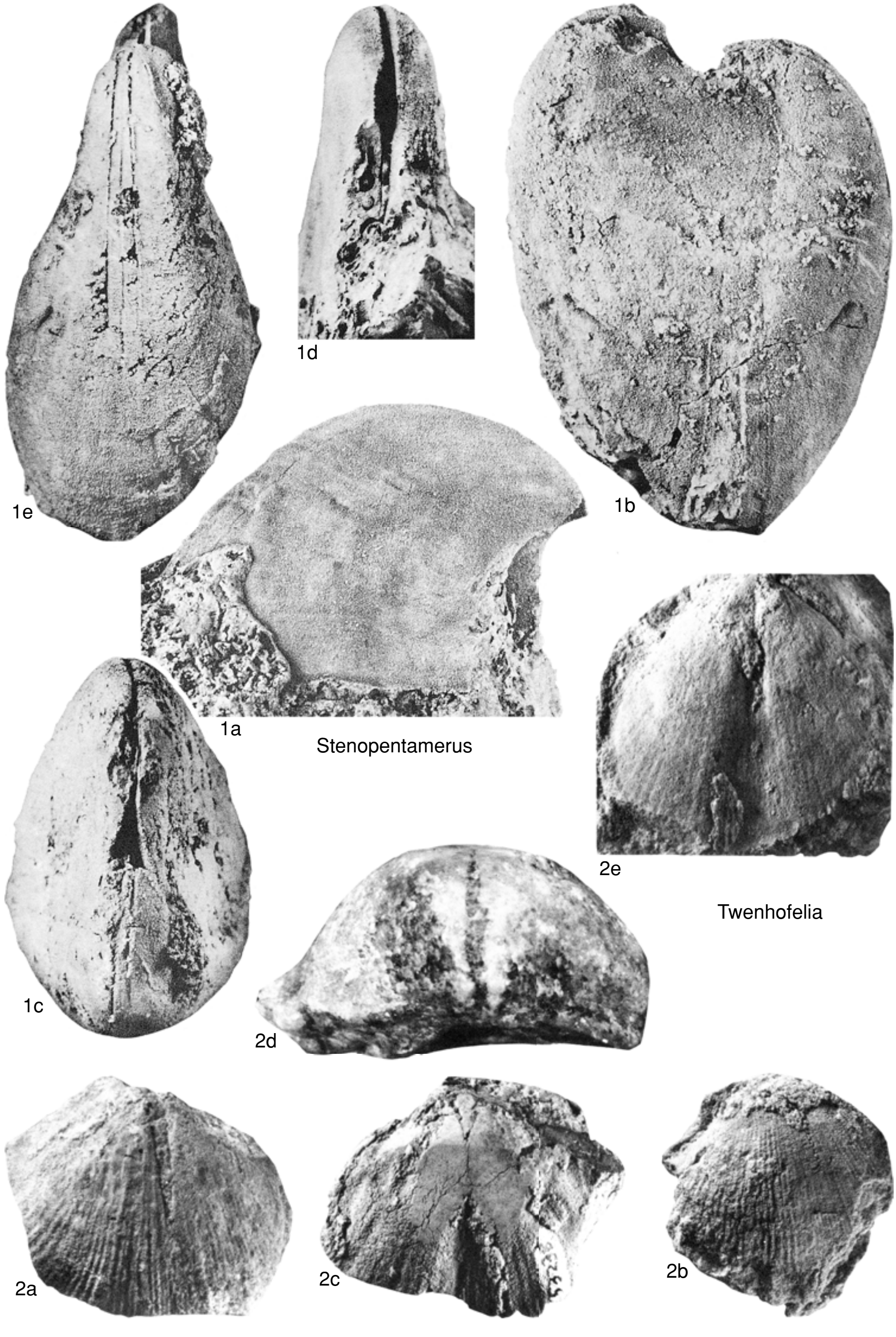

FIG. 668. Pentameridae (p. 983–986).

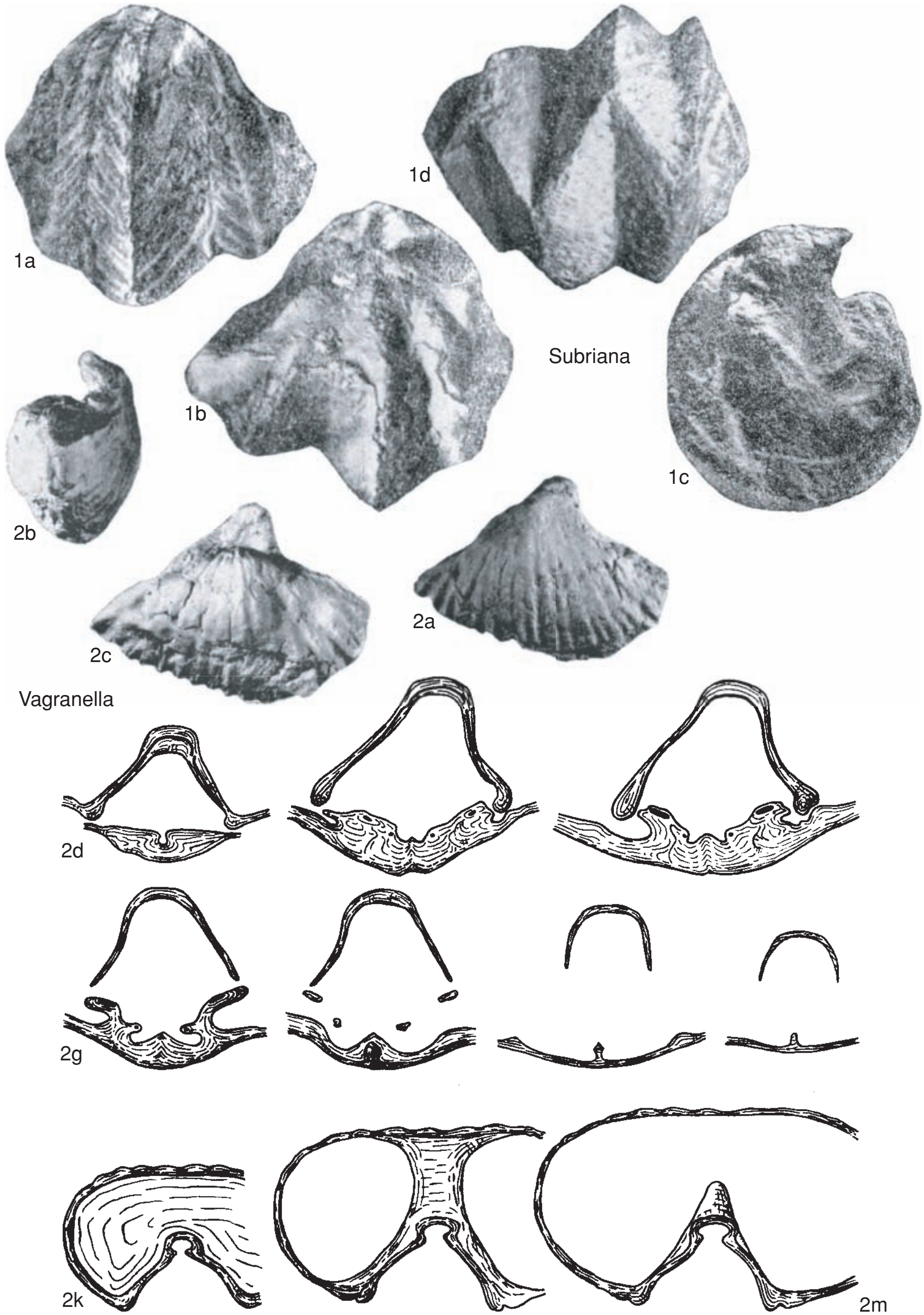

FIG. 669. Subrianidae (p. 987).

valve deeper; well-developed median septum and spondylium; outer hinge plates laterally inclined basally, inner hinge plates laterally inclined distally; crural bases variably projecting medially. *Silurian (upper Wenlock–Ludlow):* Eurasia, North America.——FIG. 670,*1a–g.* **C. bilocularis* (HISINGER), Klinteberg Group, Klinteberget, Gotland, Sweden; *a–b,* dorsal, posterior views, ×1; *c,* ventral interior, ×1.5 (Schuchert & Cooper, 1932); *d–e,* lateral, ventral views, ×1 (Amsden, 1965); *f,* dorsal interior, ×2; *g,* cross section of dorsal shell, ×6 (Amsden, Boucot, & Johnson, 1967).

Aliconchidium ST. JOSEPH, 1942, p. 247 [**A. yassi;* OD]. Medium to large; elongate to transverse; large, strongly developed ventral interarea; sulcate to nonsulcate ventral valve; costellate; very twisted beak common; hinge line long to short; internally as in *Conchidium. Silurian (Ludlow):* eastern Australia.——FIG. 671,*1a–f.* **A. yassi,* Bowsping Limestone, Yass area, New South Wales; *a–b,* ventral, ventrolateral views; *c–d,* ventral interiors, ×1; *e,* dorsal interior, ×2; *f,* dorsal interior, ×1 (Boucot, Johnson, & Link, 1969).

Cymbidium KIRK, 1926, p. 2 [**C. acutum;* OD]. Small; subcircular; plicate to costate ornament that may bifurcate; no median septum in ventral valve; unsupported spondylium; cardinalia shorter than in *Conchidium,* otherwise similar. [Type material unsuitable for illustration.] *Silurian (Wenlock–Ludlow):* USA (Alaska, Nevada), Arctic Canada. ——FIG. 672,*1a–f. C. imitor,* Roberts Mountains Formation, Birch Creek area, Eureka County, Nevada; *a,* ventral interior, ×3; *b–d,* ventral exterior, ventral posterior, ventral anterior, ×1.5; *e,* ventral interior, ×2; *f,* dorsal interior, ×2 (Johnson, Boucot, & Murphy, 1976).——FIG. 672,*1g. C.* sp., Cape Phillips Formation, Baillie Hamilton Island, Arctic Canada; dorsal interior, ×3.3 (Zhang Ning, 1989a).

Lamelliconchidium KULKOV, 1968, p. 38 [**L. tchergense;* OD]. Medium; subcircular to elongate; concentric, lamellose ornamentation; fine costellae may bifurcate anteriorly; cardinalia as in *Conchidium;* medium septum almost reaching anterior margin, supporting spondylium. [Type material unsuitable for illustration.] *Silurian (Ludlow):* Altai Mountains (Russia), USA (Nevada).——FIG. 670,*2a–h. L. micropleura,* Roberts Mountains Formation, Eureka County, Nevada; dorsal posterior, dorsal anterior, dorsal interior, ventral exterior, ventral interior, ventrolateral, anteroventral, dorsal interior, ×1.5 (Johnson, Boucot, & Murphy, 1976).

Lissidium LENZ, 1989, p. 1223 [**L. erugatus;* OD]. Smooth; short spondylium free or supported by very short median septum; cardinalia as in *Conchidium. Silurian (Wenlock–Ludlow):* USA (Nevada), Canada (Northwest Territories).——FIG. 671,*2a–d.* **L. erugatus,* Whittaker Formation, southern Mackenzie Mountains, Northwest Territories; ventral interior, ventral exterior, oblique ventral interior, dorsal interior, ×2.3 (Lenz, 1989).——FIG. 671,*2e–g. L. lissa,* Roberts Mountains Formation, Eureka County, Nevada; *e–f,* ventral interior, ventral exterior, ×3; *g,* ventral interior, ×4 (Johnson, Boucot, & Murphy, 1976).

?Plicocoelina BOUCOT & JOHNSON, 1966b, p. 1038 [**Pentamerus occidentalis* HALL, 1852, p. 341; OD]. Small to medium; posteriorly smooth, costellae bifurcating anteriorly; cap-shaped dorsal valve and very deep ventral valve; cardinalia similar to *Conchidium;* ventral median septum of variable length. *Silurian (Ludlow):* midcontinent North America.——FIG. 672,*3a–g.* **P. occidentalis* (HALL), Greenfield Dolomite, Wood County, Ohio, USA; *a–b,* dorsal internal mold, rubber replica of dorsal interior, ×2; *c–e,* lateral, ventral, posterior views, ×1; *f–g,* ventral interiors, ×2 (Boucot & Johnson, 1966b).

Raridium SAPELNIKOV & MIZENS in SAPELNIKOV, MIZENS, & SHATROV, 1987, p. 56 [**Eoconchidium*? *rarum* SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 67; OD]. Small; subcircular; ventral sulcus and dorsal fold; ventribiconvex; costate; short median septum supporting short spondylium; short hinge plates, with medially directed carinae. *Silurian (Ludlow):* Pribalkhash, Kazakhstan.——FIG. 673,*1a–e.* **R. rarum* (SAPELNIKOV & RUKAVISHNIKOVA), Akkansk Stage [Gorizont], southeastern Kazakhstan; ventral, dorsal, lateral, anterior, ventral views, ×1 (Sapelnikov & Rukavishnikova, 1975a).

Severella SAPELNIKOV, 1963b, p. 15 [**Brooksina (S.) magnificaformis;* OD]. Small; coarsely costate to costellate; costellae may bifurcate anteriorly; fold or sulcus present alternatively on either valve in separate species; short spondylium and median septum shorter than spondylium; cardinalia as in *Conchidium.* [Type material unsuitable for illustration.] *Silurian (Wenlock–Ludlow):* Urals, USA (Nevada). ——FIG. 673,*2a–f. S. munda,* Roberts Mountains Formation, Eureka County, Nevada; *a–c,* ventral interior, ventral posterior, ventral exterior, ×2; *d,* dorsal exterior, ×1.25; *e,* dorsal interior, ×2; *f,* dorsal interior, ×5 (Johnson, Boucot, & Murphy, 1976).

Spondylopyxis JOHNSON, BOUCOT, & MURPHY, 1976, p. 47 [**S. ignotus;* OD]. Smooth; undulating, irregular, rugose concentric markings; subcircular; spondylium supported by median septum, short in small specimens, long in large specimens; lenticular lateral profile; cardinalia as in *Conchidium. Silurian (Ludlow):* USA (Nevada), Arctic Canada.——FIG. 672,*2a–f.* **S. ignotus,* Roberts Mountains Formation, Eureka County, Nevada; *a,* ventral exterior, ×3; *b–d,* posterior, ventral exterior, dorsal exterior, ×6; *e,* dorsal interior, ×8; *f,* ventral interior, ×4 (Johnson, Boucot, & Murphy, 1976).

Vosmiverstum BREIVEL & BREIVEL in ANTSIGIN & others, 1970, p. 54 [**Conchidium triquetrum* SAPELNIKOV, 1961b, p. 47; OD]. Similar to *Conchidium* except for its relatively short spondylium and

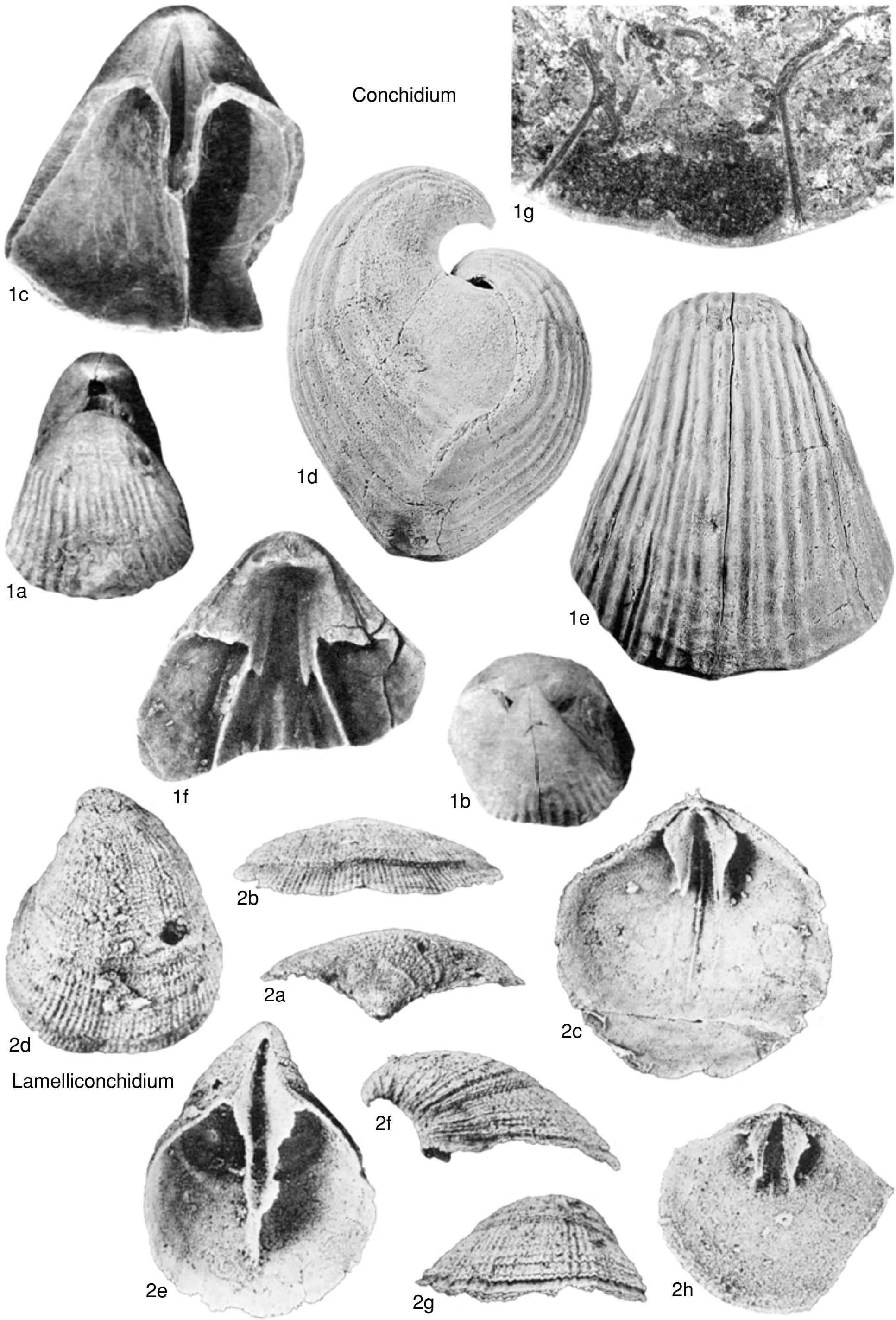

FIG. 670. Subrianidae (p. 990–993).

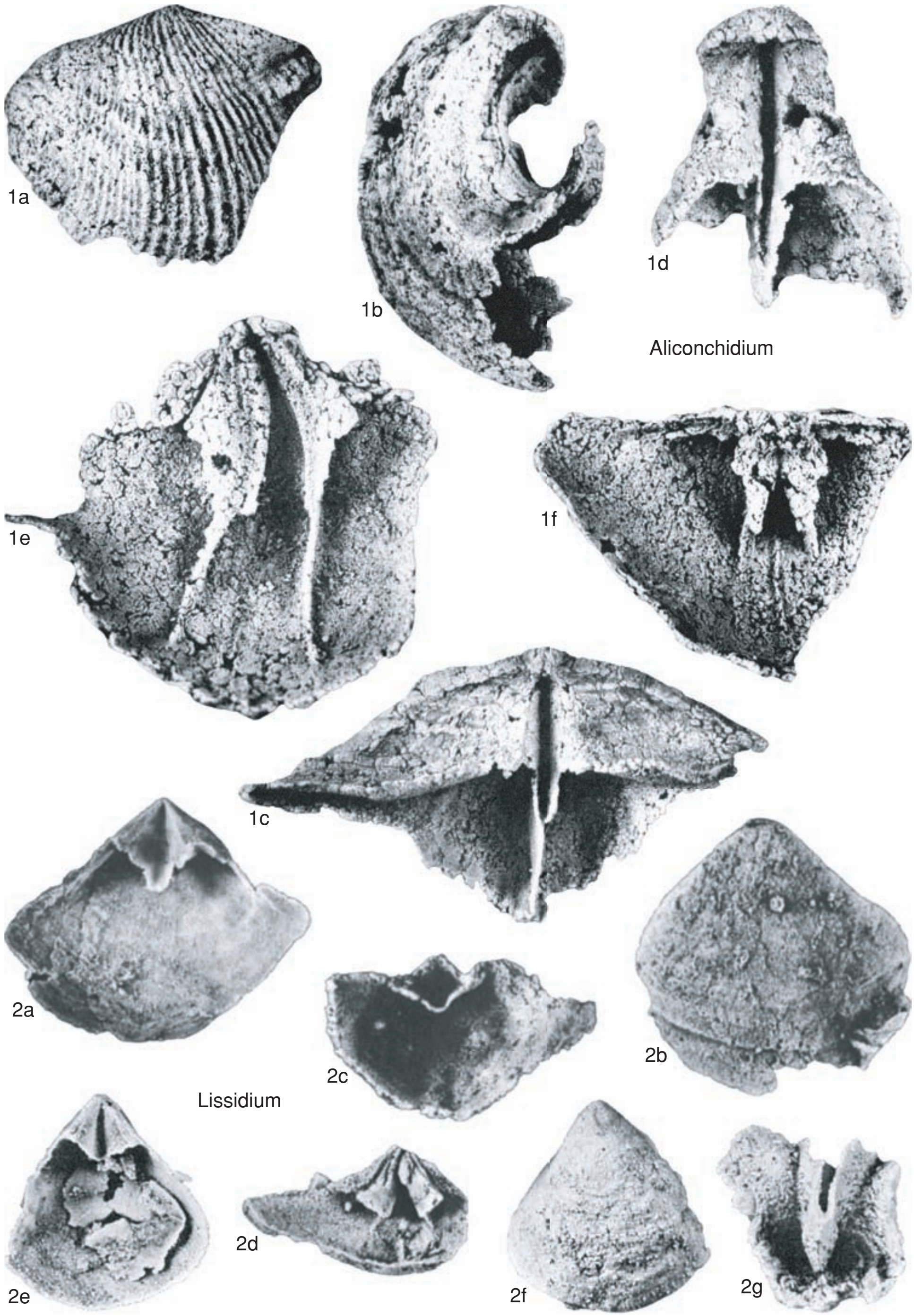

FIG. 671. Subrianidae (p. 993).

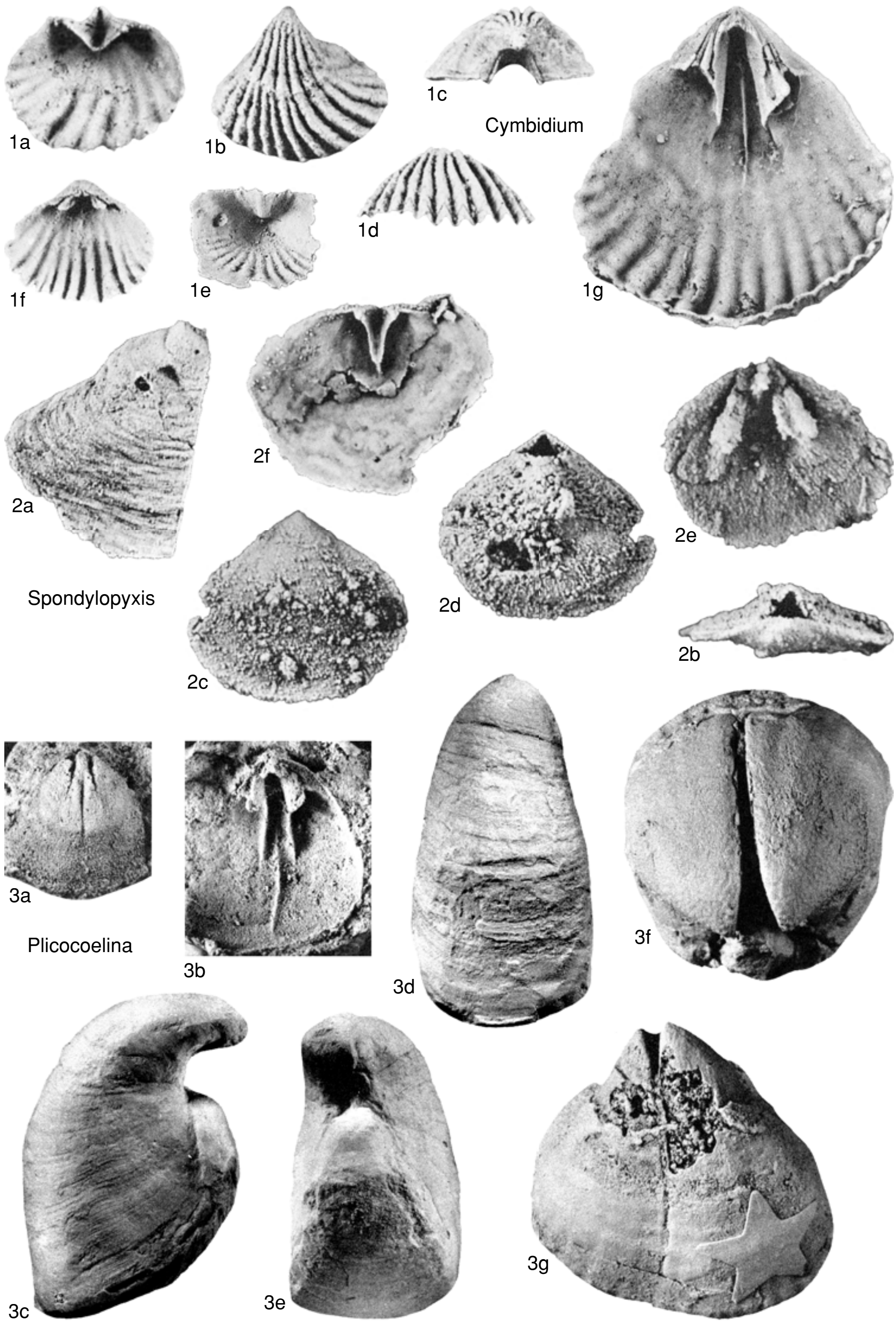

FIG. 672. Subrianidae (p. 993).

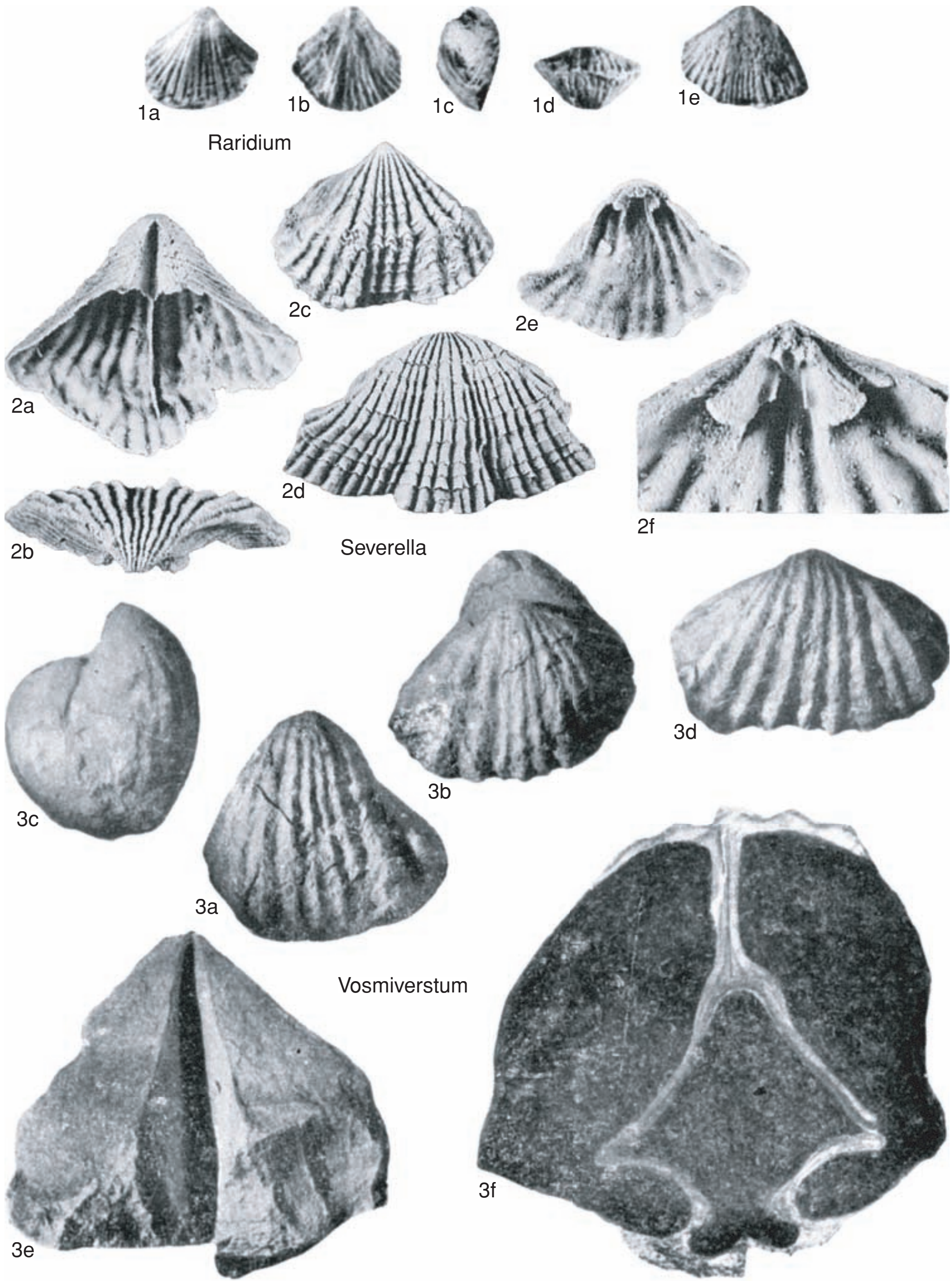

FIG. 673. Subrianidae (p. 993–997).

supporting median septum, which is much shorter than spondylium; cardinalia as in *Conchidium. Silurian (upper Wenlock–Ludlow):* Urals, USA (Nevada, California), Canadian Arctic.——FIG. 673,*3a–f.* **V. triquetrum* (SAPELNIKOV), Wenlock, Novo-Lialinsk region, eastern Urals; *a–e,* ventral, dorsal, lateral, dorsal, ventral interarea, ×1; *f,* serial section, ×3 (Antsigin & others, 1970).

Superfamily STRICKLANDIOIDEA Schuchert & Cooper, 1931

[*nom. transl.* BOUCOT, RONG, & BLODGETT, herein, *pro* Stricklandiidae SCHUCHERT & COOPER, 1931, p. 248]

[Materials prepared by A. J. BOUCOT, RONG JIA-YU, & ROBERT B. BLODGETT]

Small to very large; smooth, costate, or diagonally rugose; moderately biconvex to convexoconcave; long to short, well-developed interareas and hinge lines; ventral valve median septum short or absent; short spondylium; brachial apparatus relatively short; inner hinge plates in earlier forms of Stricklandiinae; rodlike crura present; outer hinge plates long or short. *Silurian (lower Llandovery–Ludlow).*

Family STRICKLANDIIDAE Schuchert & Cooper, 1931

[Stricklandiidae SCHUCHERT & COOPER, 1931, p. 248] [=Stricklandiniidae HALL & CLARKE, 1895, p. 355; Stricklandidae AMSDEN, 1953, p. 146; Stricklandiacea SAPELNIKOV, 1973, p. 40, *pars*]

Ventral median septum well developed; dental sockets relatively short; inner hinge plates present in earlier forms, lost in younger forms; short spondylium supported by short median septum. *Silurian (lower Llandovery–upper Wenlock).*

Subfamily STRICKLANDIINAE Schuchert & Cooper, 1931

[Stricklandiinae SCHUCHERT & COOPER, 1931, p. 248]

Prismatic layer present on medial faces of hinge plates of investigated genera. *Silurian (lower Llandovery–lower Wenlock).*

Stricklandia BILLINGS, 1859a, p. 132 [**Atrypa lens* J. SOWERBY in MURCHISON, 1839, p. 637; SD OEHLERT, 1887a, p. 1310] [=*Stricklandinia* BILLINGS, 1863a, p. 370, obj.]. Medium to large; smooth to anteriorly weakly plicate; subcircular to elongate; interareas relatively wide in older forms to narrower in younger forms; moderately ventribiconvex, rodlike crura; outer hinge plates enlarged in younger forms. *lower Silurian:* North America, Eurasia.——FIG. 674,*1a–e*. **S. lens* (SOWERBY), 70.8 meters, Sulustvere borehole, Llandovery, Adavere Stage [Gorizont], Estonia; ventral, dorsal, posterior, anterior, lateral views, ×1.5 (Rubel, 1970).——FIG. 674,*1f–g*. *S. lens progressa,* C_1 beds, Sefin footbridge, Llandovery, Wales; mold of dorsal cardinalia, internal mold of posterior, ×1 (Williams, 1951).

?Aenigmastricklandia ZIEGLER, 1966a, p. 347 [**A. contorta;* OD]. Small; subcircular; unequally ventribiconvex; coarse, irregularly branching costae; prominent growth lines; high dorsal fold and corresponding ventral sulcus; straight hinge line; small outer hinge plates. *Silurian (upper Aeronian):* Wales.——FIG. 674,*3a–d*. **A. contorta,* south of Presteigne; internal dorsal mold, posterior view of rubber replica of exterior of ventral valve, internal mold of ventral valve, anterior view of internal mold of ventral valve, ×2 (Ziegler, 1966a).

Costistricklandia AMSDEN, 1953, p. 143 [**Stricklandia gaspeensis* BILLINGS, 1859a, p. 134; OD]. Large to very large; subcircular to elongate; similar to youngest form of *Stricklandia* but with costae that bifurcate anteriorly; moderately ventribiconvex; relatively large outer hinge plates and crura. *Silurian (upper Telychian–lower Wenlock):* eastern North America, Europe, Novaya Zemlya.——FIG. 674,*2a–c*. **C. gaspeensis* (BILLINGS), La Vieille Formation, Québec; *a,* dorsal interior showing brachial processes, La Vieille Cove, east of Gascons, ×2; *b,* posterior of ventral valve exterior, Port Daniel, ×1 (Schuchert & Cooper, 1932); *c,* dorsal valve exterior, ×1 (Amsden, 1965).

Ehlersella BOUCOT & JOHNSON, 1966a, p. 569 [**Stricklandinia davidsoni* BILLINGS, 1868, p. 59; OD]. Medium to large; subcircular to elongate; crisscross concentric and chevronlike plications; unequally ventribiconvex; short hinge line; inner and outer hinge plates. *Silurian (upper Aeronian–lower Telychian):* Canada (Quebec), USA (Alabama).——FIG. 675*a–e*. **E. davidsoni* (BILLINGS), Jupiter Formation, Pavillion River, Anticosti Island, Quebec; dorsal, ventral, anterior, posterior, lateral exteriors, ×1 (Boucot & Johnson, 1966a).——FIG. 675*f–i*. *E. norwoodi,* Red Mountain Formation, Tuscaloosa County, Alabama; *f,* dorsal internal mold, ×4; *g,* rubber replica of dorsal interior, ×2; *h,* ventral internal mold, ×1.5; *i,* dorsal internal mold, ×1 (Boucot & Johnson, 1966a).

Subfamily KULUMBELLINAE new subfamily

[Kulumbellinae BOUCOT, RONG, & BLODGETT, herein]

Small to medium; smooth to costate, or crisscross ornament; subcircular to elongate; interarea relatively narrow to wide; gently biconvex to concavoconvex; inner hinge plates in earlier forms, lost in younger forms. *Silurian (lower Llandovery–upper Wenlock).*

Kulumbella NIKIFOROVA, 1960c, p. 61 [**K. kulumbensis;* OD]. Large; subcircular to transverse; gently concavoconvex with ventral valve slightly deeper; long, narrow interarea; crisscross ornamentation; short outer hinge plates and crura. *Silurian (middle Llandovery):* Siberia, eastern Canada (Anticosti Island).——FIG. 676,*1a–e*. **K. kulumbensis,* Kulumbe River, Siberia; ventral exterior, dorsal exterior, external lateral, internal ventroposterior, ventral exterior impression, ×1 (Nikiforova, 1960c).

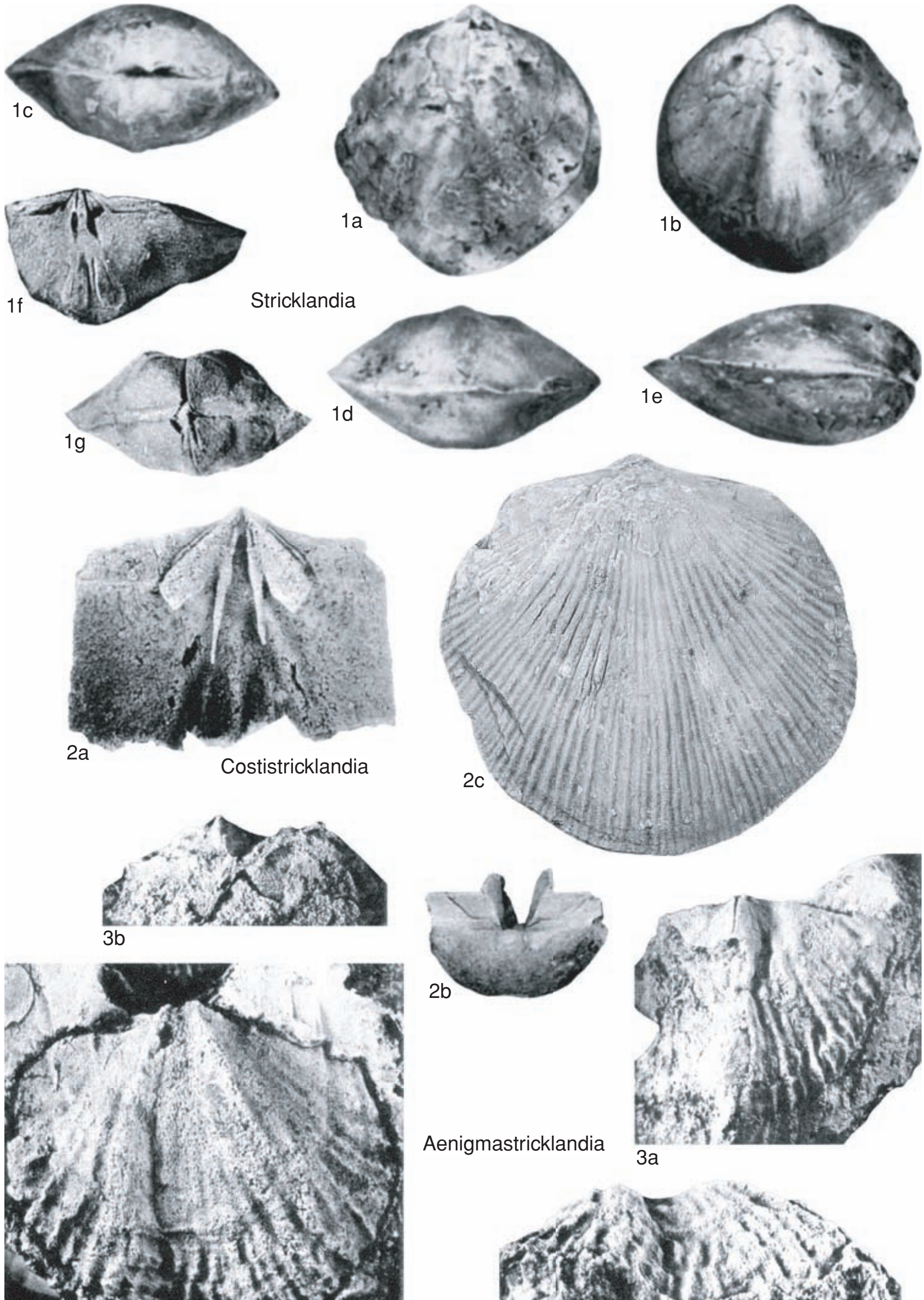

FIG. 674. Stricklandiidae (p. 998).

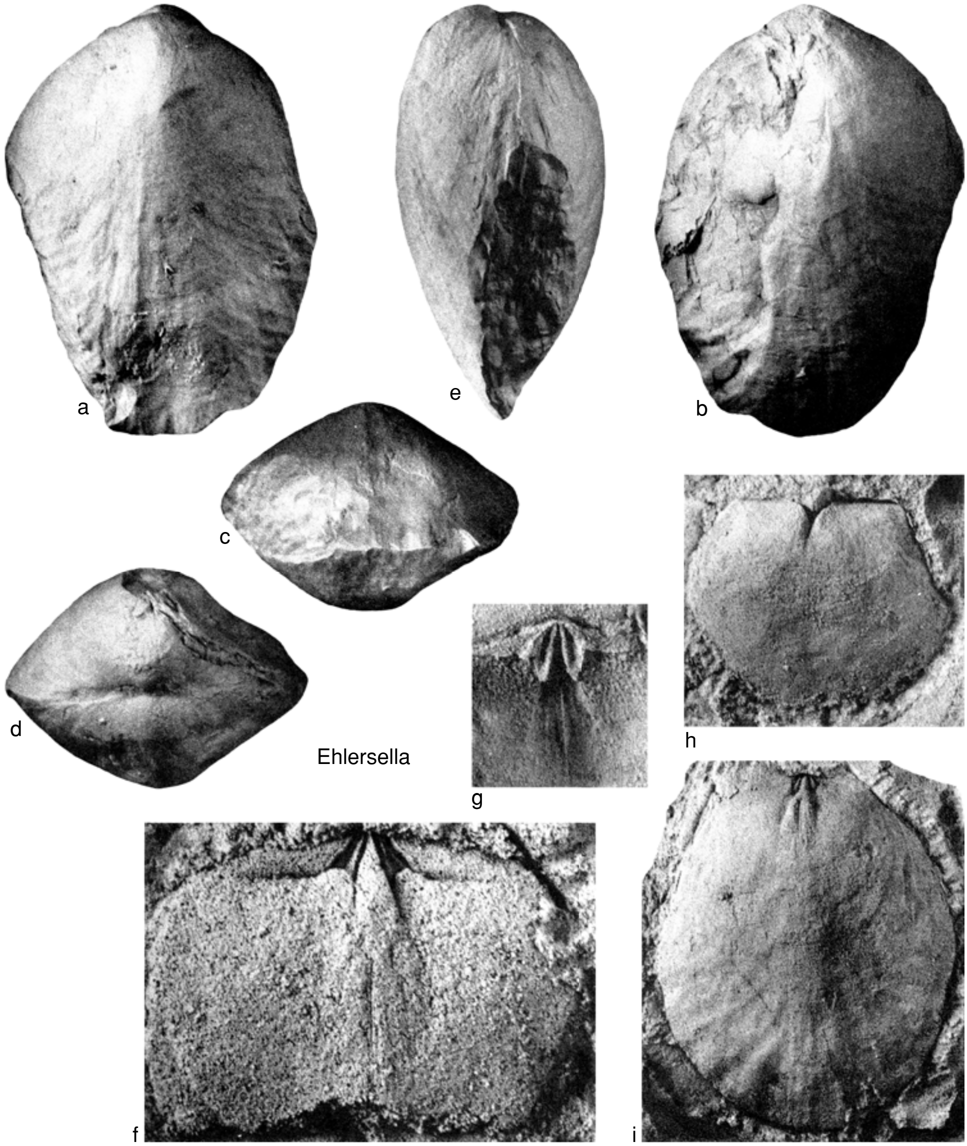

FIG. 675. Stricklandiidae (p. 998).

Chiastodoca JIN & COPPER, 1998, p. 451 [**Stricklandia salteri* BILLINGS, 1868, p. 61; OD]. Medium to large; subcircular to subelliptical, weakly biconvex, with long, straight hinge line, narrow ventral and dorsal interarea, divaricate ribs, short, low ventral median septum supporting broad, U-shaped spondylium, no inner hinge plates. *Silurian (upper Aeronian–lower Telychian):* eastern North America, South China, Kazakhstan, Estonia, Norway, Siberia, northern Greenland.——FIG. 676,*2a–b*. **C. salteri* (BILLINGS), Ferrum Member, Jupiter Formation, Anticosti Island, Quebec; ventral exterior, dorsal exterior, ×2 (Jin & Copper, 1998).

Microcardinalia BOUCOT & EHLERS, 1963, p. 51 [**Stricklandinia triplesiana* FOERSTE, 1890, p. 323; OD]. Medium; smooth to anteriorly weakly plicate; subcircular to very elongate; ventribiconvex; inner hinge plates in older forms, lost in younger forms;

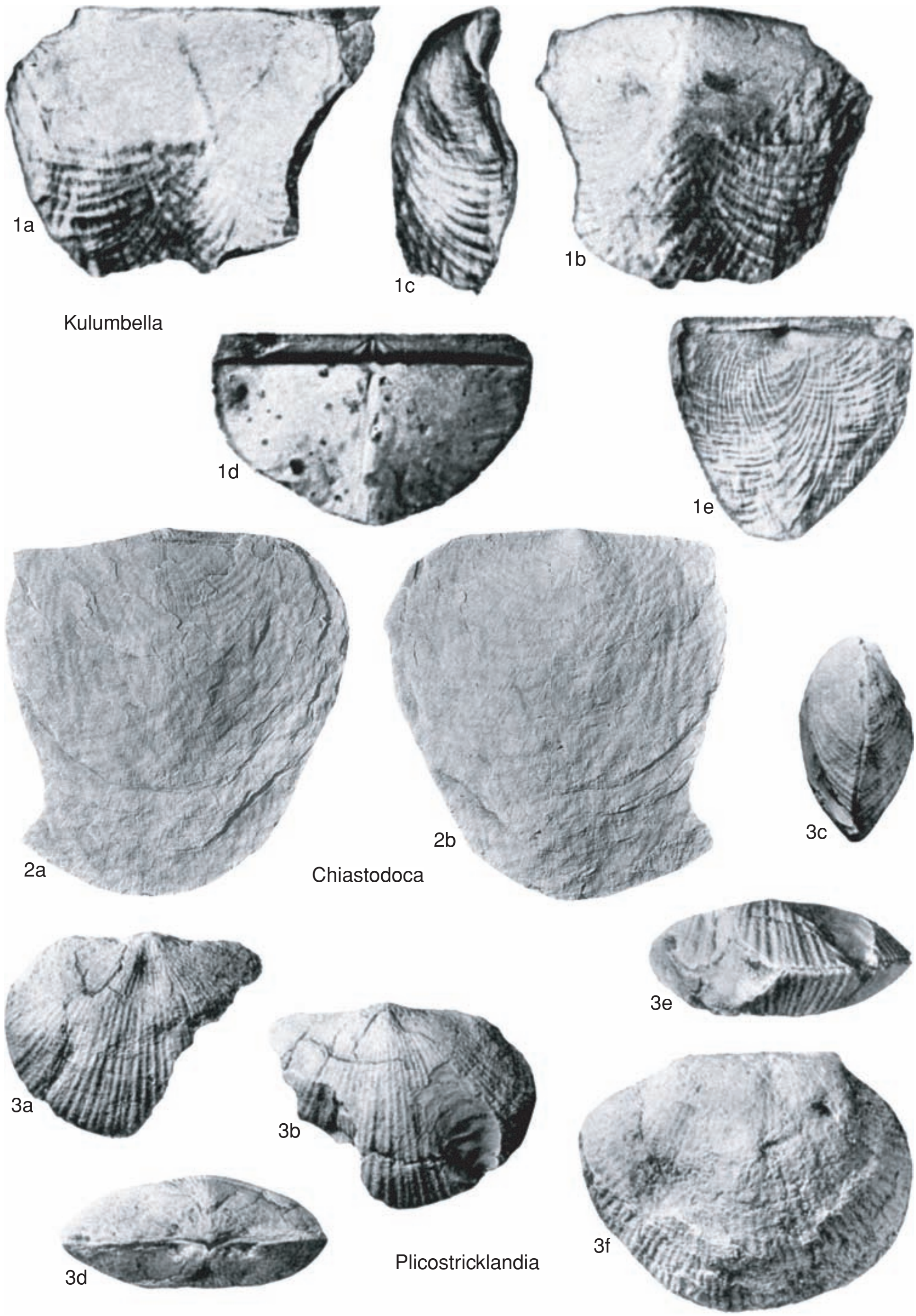

FIG. 676. Stricklandiidae (p. 998–1002).

small outer hinge plates. Equivalently aged forms similar to *Stricklandia* except smaller and possessing smaller outer hinge plates. *Silurian (middle Llandovery–upper Llandovery):* midcontinent North America, Scotland.——FIG. 677,*2a–d*. **M. triplesiana* (FOERSTE), Brassfield Limestone, Dayton, Ohio, USA; dorsal, ventral, lateral, and posterior exteriors, ×1 (Amsden, 1966).——FIG. 677,*2e–f. M. raberensis,* basal Cordell Dolomite, Chippewa County, Michigan, USA; *e,* dorsal interior, ×2; *f,* enlargement of preceding, ×4 (Boucot & Ehlers, 1963).——FIG. 677,*2g–j. M. protriplesiana,* Blackgum Formation, Cherokee County, Oklahoma, USA; *g–h,* lateral and posterior views of spondylium, ×2; *i,* dorsal interior from side, ×8; *j,* dorsal interior from above, ×2 (Amsden, 1966).

Plicostricklandia BOUCOT & EHLERS, 1963, p. 55 [**Stricklandinia multilirata* WHITFIELD, 1878, p. 81; OD]. Medium; subcircular to transverse; costae bifurcating anteriorly; moderately ventribiconvex; straight hinge line; small outer hinge plates. Similar to *Costistricklandia* except for smaller size and smaller outer hinge plates. *Silurian (upper Telychian–Wenlock):* midcontinent North America.——FIG. 676,*3a–f*. **P. multilirata* (WHITFIELD); *a–e,* ventral, dorsal, lateral, posterior, anterior exteriors, Hopkinton Dolomite, Delhi, Iowa, USA, ×1; *f,* dorsal exterior, Engadine Dolomite, Drummond Island, Michigan, USA, ×1 (Boucot & Ehlers, 1963).

Stricklandiella SAPELNIKOV & RUKAVISHNIKOVA, 1973, p. 36 [**S. aseptata;* OD]. Smooth; large; laterally elongate; long hinge line; moderately ventribiconvex; narrow interareas; dorsal fold and ventral sulcus; uniplicate commissure; no median septum under short spondylium; short outer hinge plates, submerged in secondary material, laterally directed. *Silurian (Llandovery):* Kazakhstan.——FIG. 677,*1a–d*. **S. aseptata,* Salamatsk Suite, Koizharilgan Mountains, southern Kazakhstan; dorsal internal mold, ventral internal mold, ventral posterior internal mold, mold of ventral exterior, ×1 (Sapelnikov & Rukavishnikova, 1973).

Family AENIGMASTROPHIIDAE Boucot & Rong, 1994

[Aenigmastrophiidae BOUCOT & RONG, 1994, p. 405]

Small to medium; transverse; long, straight hinge line; long, well-defined, narrow interareas; profile weakly to moderately biconvex to weakly concavoconvex; spondylium short, wide, shallow, sessile or supported by low, short median septum; crura widely divergent, rodlike; short outer hinge plates only, bordered posteriorly by narrow, lengthy hinge grooves; ventral median septum short, posterior, low, septum possibly present in dorsal valve. Prismatic layer lacking in some taxa, unrecognized overall. [If *Stricklandistrophia* belongs to this group, SAPELNIKOV and KULKOV's (1976) family name Stricklandistrophiidae has precedence.] *Silurian (Wenlock–Ludlow):* USA (Nevada, California), Canada (Northwest Territories).

Aenigmastrophia BOUCOT, 1971, p. 156 [**A. cooperi;* OD]. Small to large; gently concavoconvex; ventral interarea long and narrow, apsacline; much narrower, anacline dorsal interarea; smooth; transverse; short, sessile spondylium; rodlike crura laterally directed at a very high angle, very short outer hinge plates. *Silurian (Ludlow):* USA (Nevada, California).——FIG. 678,*1a–e*. **A. cooperi,* Roberts Mountains Formation, Eureka County, Nevada; *a–c,* interior, posterior, lateral views of dorsal valve, ×4; *d–e,* dorsal interior, exterior views, ×5 (Johnson, Boucot, & Murphy, 1976).——FIG. 678,*1f. A. greggi,* Ludlow age sandstone, Siskiyou County, California; rubber replica of dorsal interior, ×1 (Boucot, 1971).

Rugolepyros LENZ, 1989, p. 1224 [**R. latispondylus;* OD]. Medium; hemicircular outline; weakly biconvex; moderately strong, discontinuous, irregular, concentric rugae; apsacline, long ventral interarea and short, anacline dorsal interarea; large, wide, shallow, spatulate, posteriorly sessile spondylium; rodlike crura cemented to valve floor; short, laterally directed outer hinge plates. *Silurian (Wenlock):* Canada (Northwest Territories).——FIG. 678,*2a–f*. **R. latispondylus,* Whittaker Formation, southern Mackenzie Mountains; *a,* ventral exterior, ×2.4; *b,* ventral interior; *c,* ventral interior; *d,* ventral exterior, ×4.4; *e,* ventral interior, ×8; *f,* dorsal interior, ×4.2 (Lenz, 1989).

Vadimia BOUCOT & RONG, 1994, p. 407 [**V. nevadensis;* OD]. Dorsal valve gently sulcate; costae coarse; laterally elongate; spondylium short, wide, shallow, supported by short median septum; short rodlike crura cemented to valve floor; very short outer hinge plates. *Silurian (Ludlow):* USA (Nevada).——FIG. 679*a–e*. **V. nevadensis,* Roberts Mountains Formation, Eureka County; *a–b,* ventral interior and exterior; *c,* anterior view of ventral interior, ×3; *d–e,* interior and exterior of dorsal valve, ×5 (Johnson, Boucot, & Murphy, 1976).

?Family STRICKLANDISTROPHIIDAE Sapelnikov & Kulkov, 1976

[Stricklandistrophiidae SAPELNIKOV & KULKOV, 1976, p. 113]

Internal structures not well known. Spondylium well developed, with or without median septum. Brachial interior with no inner hinge plates. Similar to the Aenigmastrophiidae in having a very long, straight

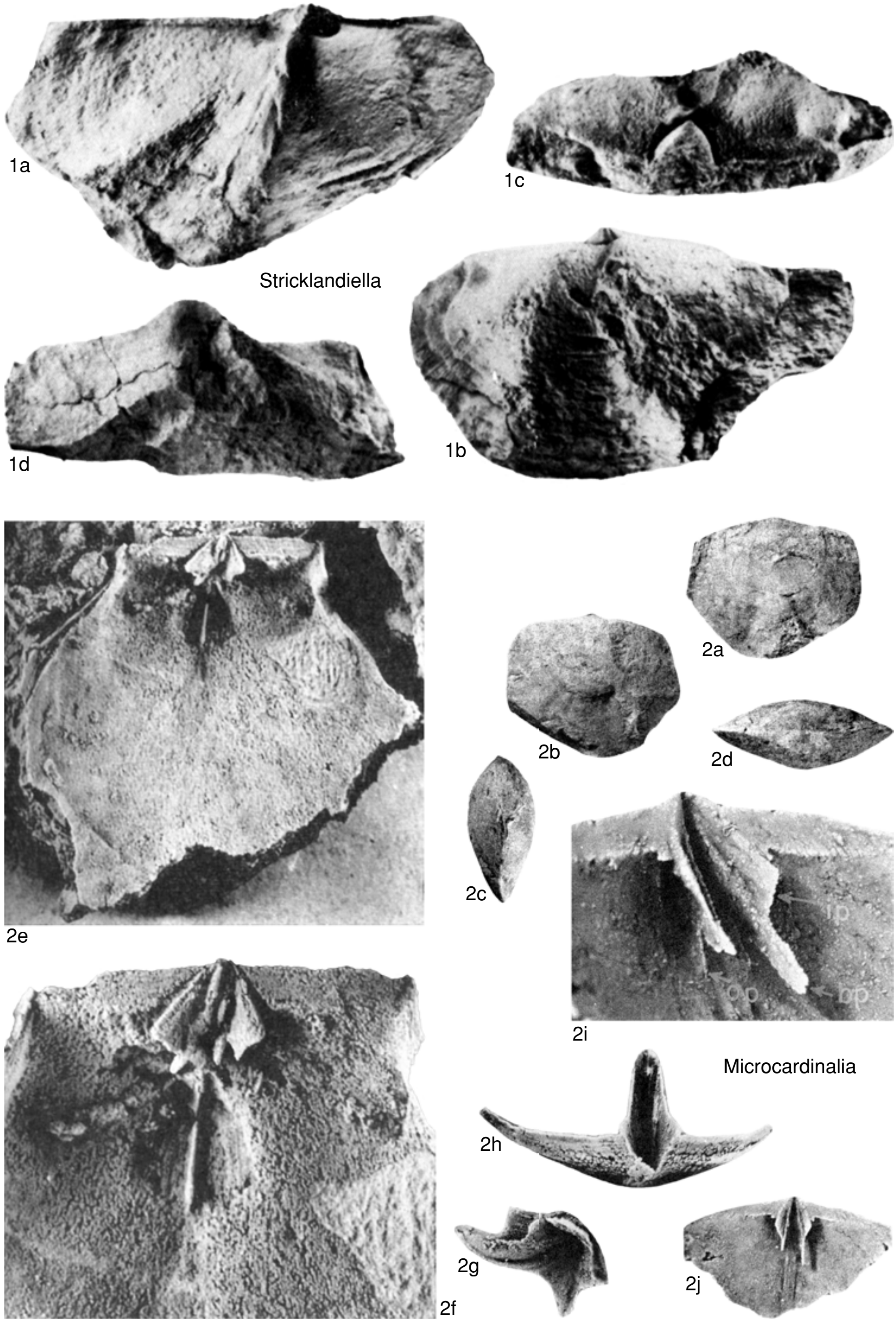

FIG. 677. Stricklandiidae (p. 1000–1002).

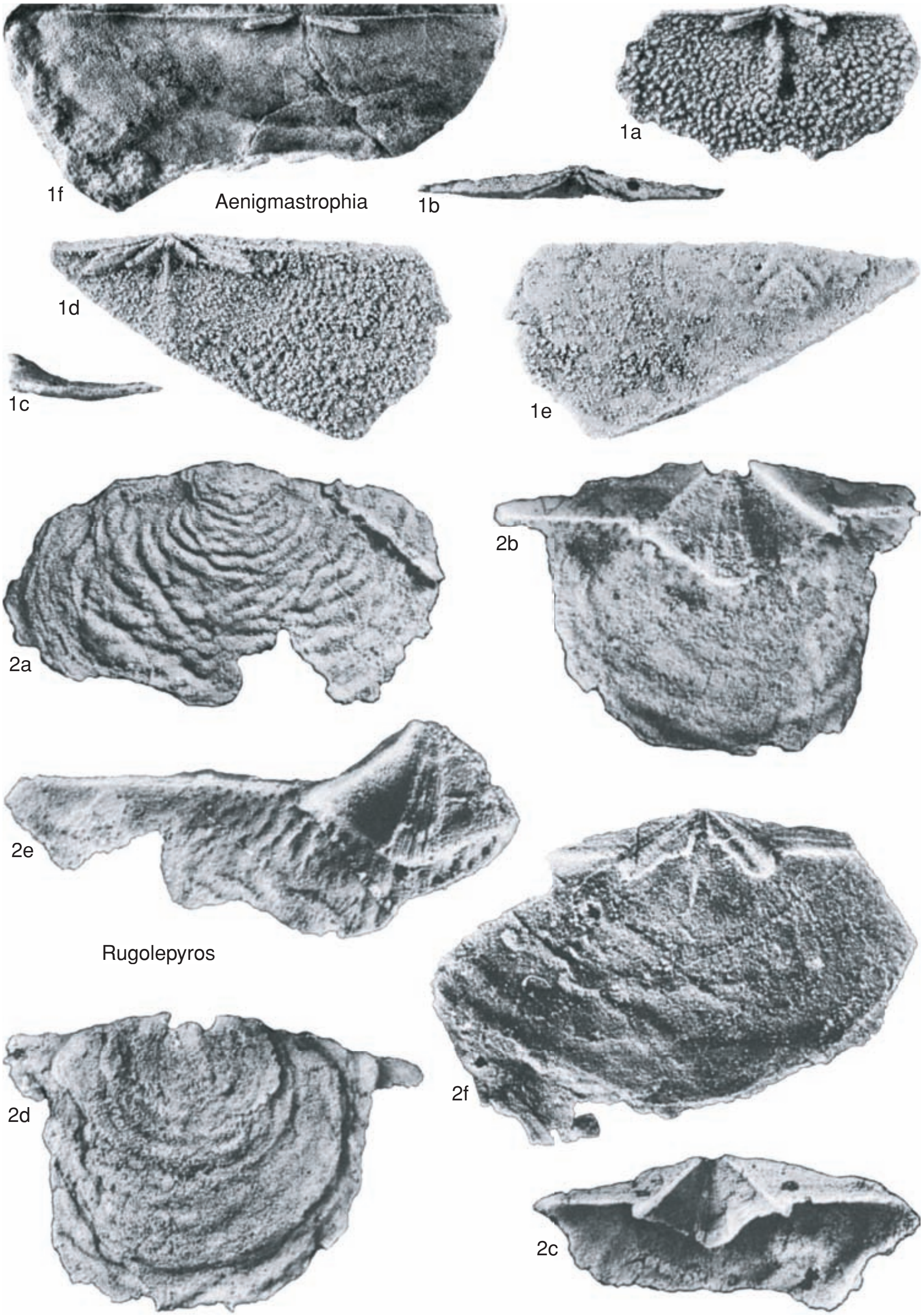

FIG. 678. Aenigmastrophiidae (p. 1002).

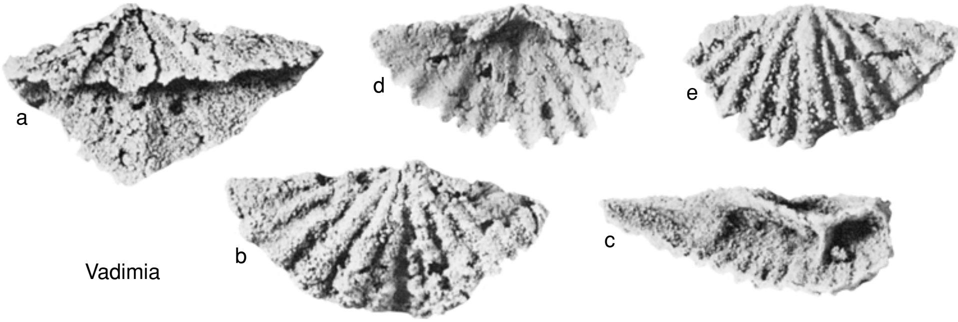

FIG. 679. Aenigmastrophiidae (p. 1002).

hinge line and well-developed interareas. Moderately biconvex as contrasted with the flattish aenigmastrophiids. Uniplicate commissure. [Whether the 2 genera within this family are stricklandids remains uncertain owing to ignorance of their internal structures adequate to confirm such an assignment.] *Silurian (Llandovery):* Altai Mountains, Kazakhstan.

Stricklandistrophia SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 96 [**S. lata;* OD]. Small to medium; alate, suboval, ventral sulcus, dorsal fold, long hinge line; costellae that bifurcate anteriorly; dorsal interarea linear; central interarea, low, wide; short ventral median septum supporting short spondylium; massive, very short outer, laterally inclined hinge plates, crura. *Silurian (Llandovery):* Kazakhstan.——FIG. 680,*1a–f.* **S. lata,* Alpeisk Stage [Gorizont], Dzhungar Alatai; ventral exterior, dorsal exterior, ventral exterior, dorsal exterior, lateral view, dorsal exterior, ×1 (Sapelnikov & Rukavishnikova, 1975a).

Spondylostrophia KULKOV, 1967, p. 33 [**S. lata;* OD]. Small; alate; hinge line long, straight; interareas well developed; dorsal sulcus and ventral sulcus; costae that may bifurcate anteriorly; spondylium short, U-shaped; ventral median septum absent; outer hinge plates thin, relatively short, laterally directed. *Silurian (upper Llandovery):* Altai Mountains.——FIG. 680,*2a–e.* **S. lata,* Chagirsk? Suite; ventral exterior, dorsal exterior, anterior external, ventral exterior, dorsal exterior, ×2 (Kulkov, 1967).

Superfamily GYPIDULOIDEA Schuchert & LeVene, 1929

[*nom. transl.* SAPELNIKOV in SAPELNIKOV & RUKAVISHNIKOVA, 1975a, p. 127, *ex* Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15]

[Materials prepared by ROBERT B. BLODGETT, A. J. BOUCOT, & RONG JIA-YU]

Pentameridines typically unisulcate, smooth or costate to costellate; hinge plates lyre shaped or laterally concave in cross section; inner hinge plates discrete or coalesced to form cruralium; crura bladelike. *Silurian*

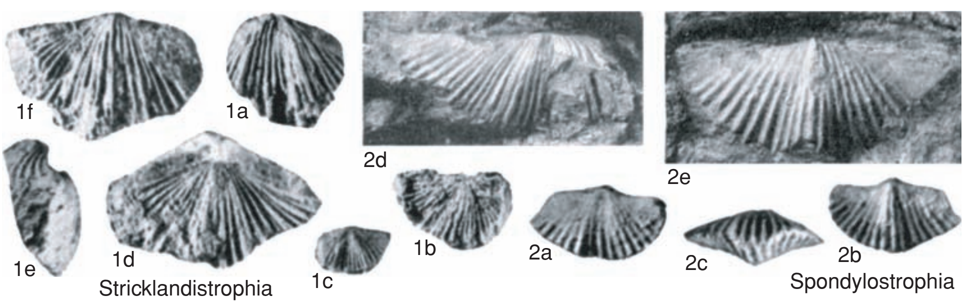

FIG. 680. Stricklandistrophiidae (p. 1005).

(upper Llandovery)–Upper Devonian (Frasnian).

Family GYPIDULIDAE Schuchert & LeVene, 1929

[*nom. transl.* RZHONSNITSKAIA, 1961, p. 47 *ex* Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15]

Gypiduloids usually with well-developed dorsal sulcus and ventral fold, rarely absent; shell surface costate, plicate, or smooth; hinge plates lyre shaped in cross section; some have inner hinge plates that diverge basolaterally. *Silurian (Telychian)–Upper Devonian (Frasnian).*

Subfamily GYPIDULINAE Schuchert & LeVene, 1929

[Gypidulinae SCHUCHERT & LEVENE, 1929a, p. 15] [=Sieberellinae SAPELNIKOV, 1973, p. 41]

Galeatiform gypidulids; shell surface smooth, costate, or plicate; costae or plicae when present not split at anterior commissure; microornament generally lacking, without tubercles, pits, or concentric lines; crura arched in cross section; inner hinge plates discrete or united into cruralium. *Silurian (Telychian)–Upper Devonian (Frasnian).*

Gypidula HALL, 1867b, p. 163 [**Gypidula typicalis* AMSDEN, 1953, p. 140, *nom. nov. pro Pentamerus occidentalis* HALL, 1858a, p. 514, *non* HALL, 1852; OD HALL, 1867b, p. 380] [=*Metabolipa* GODEFROID, 1974, p. 5 (type, *Pentamerus greindli* MAILLIEUX, 1909, p. 230, OD); *Neometabolipa* GODEFROID, 1974, p. 23 (type, *N. duponti* GODEFROID, 1974, p. 24, OD)]. Size variable, shell oval to subcircular in outline; strongly ventribiconvex, ventral beak arched over dorsal; variably costate or plicate anteriorly; inner hinge plates discrete. [HALL (1867b, p. 380) designated *Pentamerus occidentalis* HALL, 1858a, as the type species of his new genus *Gypidula. Pentamerus occidentalis* HALL, 1858a, is a homonym of *Pentamerus occidentalis* HALL, 1852, the latter being a species of *Plicocoelina.* AMSDEN, 1953, p. 140, replaced *Pentamerus occidentalis* HALL, 1858a (not *Pentamerus occidentalis* HALL, 1852) with *Gypidula typicalis.*] *Silurian (Telychian)–Upper Devonian (Frasnian):* widespread in Europe, Asia, North America, North Africa, Australia.——FIG. 681,*2a–d.* **G. typicalis* (AMSDEN), Cedar Valley Group, Iowa, USA; *a–c,* dorsal, anterior, lateral views, ×1 (Amsden, 1965); *d,* serial section at 5.0 mm from tip of ventral umbo (Godefroid, 1979).

Amsdenina BOUCOT, 1975a, p. 357 [**Sieberella roemeri* HALL & CLARKE, 1892, p. 247; OD]. Similar to *Sieberella,* but differs in having rounded costae separated by rounded interspaces; umbo smooth; short median septum and spondylium; inner hinge plates wedged into shell dorsally, almost conjunct posteriorly, becoming discrete anteriorly. *Silurian (Wenlock–Přídolí):* Canadian Arctic Islands, *Wenlock;* midcontinent North America (Tennessee, Oklahoma), northern Appalachians (Maine, Quebec, New Brunswick), *Ludlow–Přídolí.*——FIG. 681,*1a–d.* **A. roemeri* (HALL & CLARKE), Brownsport Formation, Tennessee; *a–c,* ventral, dorsal, lateral views, ×1; *d,* polished section, ×2 (Amsden, 1949a).

Ascanigypa HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 113 [**Pentamerus ascanius* BARRANDE, 1879b, pl. 80, fig. III; OD]. Smooth shells similar to *Gashaomiaoia,* but differs in having low ventral fold and dorsal sulcus; externally similar to *Gypidula,* but differs in lack of costae; fold low, well developed in anterior part of shell; sulcus shallow; anterior commissure rectimarginate in juveniles, becoming unisulcate in adults; microornament not observed; ventral median septum short; inner hinge plates converge medially, less commonly diverging anteriorly. *Silurian (upper Wenlock):* Czech Republic.——FIG. 681,*3a–d.* **A. ascania* (BARRANDE), Motol Formation, Prague region; lateral, ventral, anterior, dorsal views, ×1.7 (Havlíček & Štorch, 1990).

Breviseptum SAPELNIKOV, 1960b, p. 109 [**Conchidium (Breviseptum) oriens;* OD]. Medium-sized shells, suboval outline, usually more transverse; similar to *Sieberella,* but lacking well-developed fold and sulcus; ventribiconvex, evenly convex in width or with weak fold, coarsely costate, costae irregular, simple or dividing near anterior margin into 2 to 3 branches; anterior commissure convex dorsally; inner hinge plates short, discrete; thin, very short ventral median septum. *Silurian (lower Ludlow):* Urals.——FIG. 681,*4a–d.* **B. oriens,* Isovsk Stage [Gorizont], Istok River, eastern Urals; ventral, dorsal, lateral, anterior views, ×1 (Sapelnikov, 1985a).

Cadudium HAVLÍČEK, 1985b, p. 296 [**Pentamerus caducus* BARRANDE, 1847, p. 469; OD]. Globose shells with unisulcate commissure; ventral fold low, commonly with pair of low, rounded plications anteriorly, sometimes obscure; dorsal sulcus shallow, flanked by rounded rib on either side, sulcus smooth or bearing median plication; lateral sides of both valves smooth or with short, weak plications; inner hinge plates short, discrete. *Silurian (Ludlow)–Lower Devonian (Lochkovian):* Czech Republic, Urals, *Ludlow–Přídolí;* Urals, Tian Shan, *Lochkovian.*——FIG. 681,*5a–c.* **C. caducum* (BARRANDE), Přídolí Formation, Prague region; anterior, posterior, dorsal views, ×2.6 (Havlíček & Štorch, 1990).

Carinagypa JOHNSON & LUDVIGSEN, 1972, p. 128 [**Gypidula loweryi* MERRIAM, 1940, p. 81; OD]. Large, smooth to faintly medioplicate; ventral fold and dorsal sulcus weakly developed; ventral median septum present or absent; hinge plates discrete,

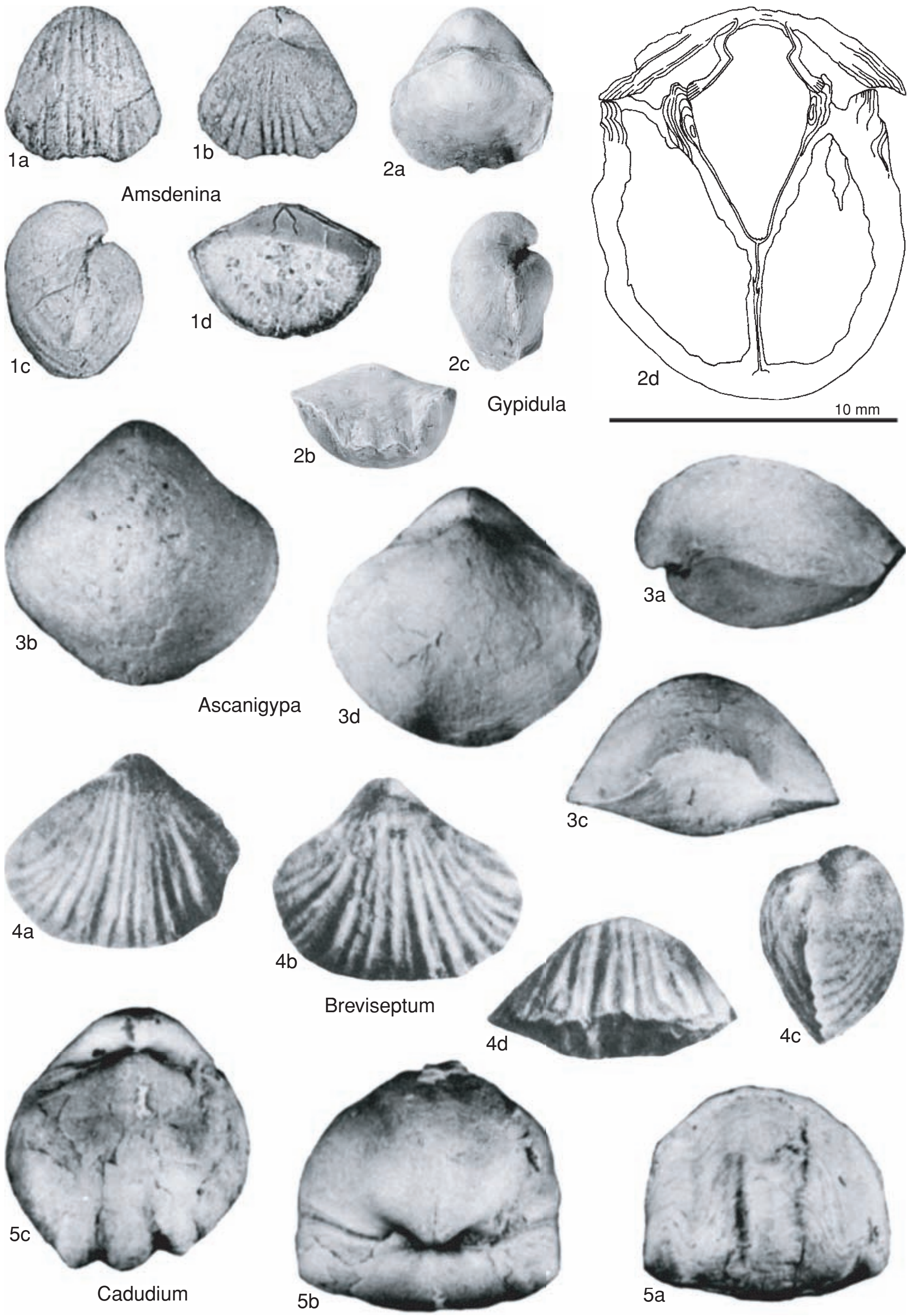

FIG. 681. Gypidulidae (p. 1006).

with single pair of ventrally directed carinae. *Lower Devonian (upper Lochkovian)–Middle Devonian (Eifelian):* Czech Republic, Canadian Arctic, *upper Lochkovian;* USA (Nevada, Alaska), Yukon Territory, Arctic Canada, *Emsian–Eifelian.*

C. (**Carinagypa**). Ventral medium septum present. *Lower Devonian (upper Lochkovian)–Middle Devonian (Eifelian):* Canadian Arctic Islands, Czech Republic, *upper Lochkovian;* USA (Nevada, Alaska), Yukon Territory, Arctic Canada, *Emsian–Eifelian.*——FIG. 682,*3a–h.* **C. (C.) loweryi* (MERRIAM); *a–e,* ventral, dorsal, lateral, posterior, anterior views, McColley Canyon Formation, Eureka County, Nevada, ×1 (Johnson, 1970b); *f–h,* dorsal serial sections, Michelle Formation, Yukon Territory, Canada, ×6 (Johnson & Ludvigsen, 1972).

C. (**Aseptagypa**) BRICE, 1982, p. 26 [**C. (A.) maclareni;* OD]. Similar to *C. (Carinagypa),* but differs in lacking ventral septum, resulting in completely free spondylium. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Canadian Arctic Islands, USA (east-central Alaska, Nevada), Yukon Territory.——FIG. 682,*2a–e.* **C. (A.) maclareni,* Blue Fiord Formation, Eifelian, Ellesmere Island, Canadian Arctic Islands; *a–d,* dorsal, ventral, anterior, lateral views of articulated specimen, ×1; *e,* serial section at 11.1 mm from ventral umbo, ×2.1 (Brice, 1982).

Caryogyps JOHNSON, BOUCOT, & MURPHY, 1976, p. 53 [**C. plicata* JOHNSON, BOUCOT, & MURPHY, 1976, p. 54; OD]. Small; angularly plicate with short ventral beak; wide ventral fold and dorsal sulcus; inner hinge plates discrete. *Silurian (Ludlow):* USA (Nevada, Idaho).——FIG. 683,*4a–e.* **C. plicata,* Roberts Mountains Formation, Eureka County, Nevada; anterior, dorsal, ventral, posterior, lateral views, ×5 (Johnson, Boucot, & Murphy, 1976).

Galeatagypa SAPELNIKOV, 1981, p. 11 [**Pentamerus pelagicus* BARRANDE, 1847, p. 469; OD]. Similar to *Gypidula* internally; relatively angular dorsal sulcus margins and correspondingly angular ventral fold margins; ranging from no costa in dorsal sulcus to a prominent dorsomedian costa, if present extending almost to beak region and having corresponding ventral groove. [This genus was established as a subgenus of *Gypidula* by SAPELNIKOV, 1981.] *upper Silurian–Middle Devonian (Eifelian):* Europe, Asia, western and Arctic North America.——FIG. 684,*2a–e.* **G. pelagica* (BARRANDE), Lochkov Formation, Prague region, Czech Republic; ventral, lateral, dorsal, anterior, posterior views, ×1 (Barrande, 1879b).

Gashaomiaoia RONG, SU, & LI, 1985 (July), p. 34 [**Gypidula (Gashaomiaoia) glabera;* OD] [=*Lysidium* HAVLÍČEK, 1985b (October), p. 299 (type, *Pentamerus integer* BARRANDE, 1847, p. 464; *Rectigypidula* ZHANG Yan, 1987, p. 108 (type, *Gypidula parva* BIERNAT, 1966, p. 30)]. Similar to *Gypidula* internally but differs in being totally smooth and in lacking dorsal sulcus and ventral fold; anterior commissure rectimarginate or weakly curved ventrally. *Silurian (Přídolí)–Lower Devonian (Pragian), Middle Devonian:* Neimonggol, Czech Republic, Austria (Carnic Alps), *Přídolí–Pragian;* Poland, China, *Middle Devonian.*——FIG. 683,*2a–d.* **G. glabera* (RONG, SU, & LI), Xibiehe Formation, Darhan Mumingan Joint Banner, Inner Mongolia, China; lateral, ventral, dorsal, anterior views, ×2 (Rong, Su, & Li, 1985).

Gypidulina RZHONSNITSKAIA, 1956b, p. 49 [**Pentamerus optatus* BARRANDE, 1847, p. 471; OD] [=*Sieberina* ANDRONOV, 1961, p. 88, obj.]. Essentially smooth shells with sharply defined ventral fold and dorsal sulcus, both of which may sometimes bear low, obscure costae; ventral median septum thin, short; inner hinge plates closely drawn together or united to form cruralium; internally similar to *Gypidula. Lower Devonian:* Novaya Zemlya, Urals, Tian Shan, Salair, Altai Mountains, Czech Republic, ?North America (Gaspé).——FIG. 684,*4a–d.* **G. optata* (BARRANDE), Koneprusy Limestone, Prague region, Czech Republic; ventral, lateral, posterior, anterior views, ×1 (Barrande, 1879b).

Gypiduloides SAVAGE in SAVAGE & BAXTER, 1995, p. 1035 [**G. craigensis;* OD]. Small, transversely pentagonal, ventribiconvex; nongaleatiform, pauciplicate; plications well developed, rounded, with pronounced low profile in posterior and anterior view; fold and sulcus wide; anterior commissure intraplicate. *Upper Devonian (Frasnian):* USA (southeastern Alaska).——FIG. 684,*3a–e.* **G. craigensis,* Wadleigh Limestone; dorsal, ventral, anterior, posterior, lateral views, ×4.5 (Savage & Baxter, 1995).

Levigypa SAPELNIKOV, 1985b, p. 9 [**Gypidula substricta* MALYGINA & SAPELNIKOV, 1973, p. 75; OD]. Medium, smooth, fold and sulcus very weak to absent; longitudinally elongate with thin, elongate ventral beak; ventral fold weakly developed or absent; massive, short ventral median septum; inner hinge plates widely separated, subparallel, fused with inner shell layer. *Lower Devonian (Emsian):* southern Tian Shan, Kyrgyzstan.——FIG. 684,*1a–c.* **L. substricta* (MALYGINA & SAPELNIKOV), Manaksk Stage [Gorizont], Isfara River region, Kyrgyzstan; *a–b,* ventral, lateral views, ×1; *c,* serial section of ventral valve, ×10 (Malygina & Sapelnikov, 1973).

Lysigypa HAVLÍČEK in HAVLÍČEK & KUKAL, 1990, p. 139 [**L. morosoides;* OD]. Similar to *Gashaomiaoia,* but inner hinge plates converge basally to form cruralium. Smooth, unisulcate; anterior commissure rectimarginate or weakly curved ventrally or dorsally; large spondylium, supported by very short ventral median septum. *Lower Devonian (Pragian–Emsian):* Czech Republic.——FIG. 683,*1a–c.* **L. morosoides,* Suchomasty Limestone, Prague region; ventral, dorsal, anterior views, ×2.1 (Havlíček & Kukal, 1990).

Multicosta KHODALEVICH & BREIVEL in BREIVEL & BREIVEL, 1977, p. 71 [**Gypidula osturalica* KHODALEVICH & BREIVEL, 1959, p. 22; OD]. Coarsely costate shells, costae generally simple, sharp, covering most of shell but not found near either beak; gently ventribiconvex; fold and sulcus absent or weakly

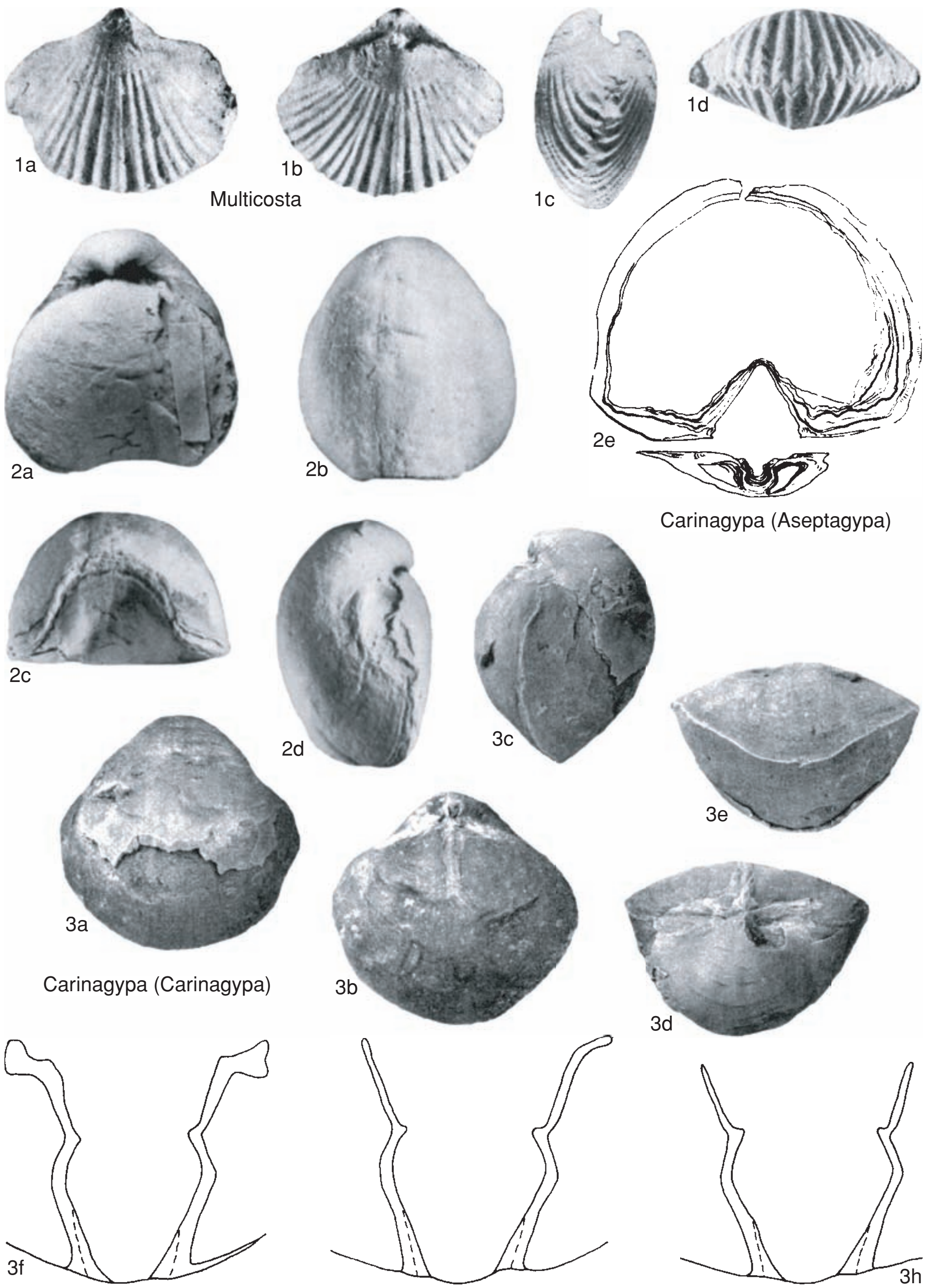

FIG. 682. Gypidulidae (p. 1006–1009).

developed anteriorly. *Lower Devonian–Middle Devonian (lower Eifelian):* Urals, ?Tian Shan.——FIG. 682,*1a–d*. **M. osturalica* (KHODALEVICH & BREIVEL), Emsian–earliest Eifel, Ivdel region, eastern slope of Urals; ventral, dorsal, lateral, anterior views, ×1 (Khodalevich & Breivel, 1959).

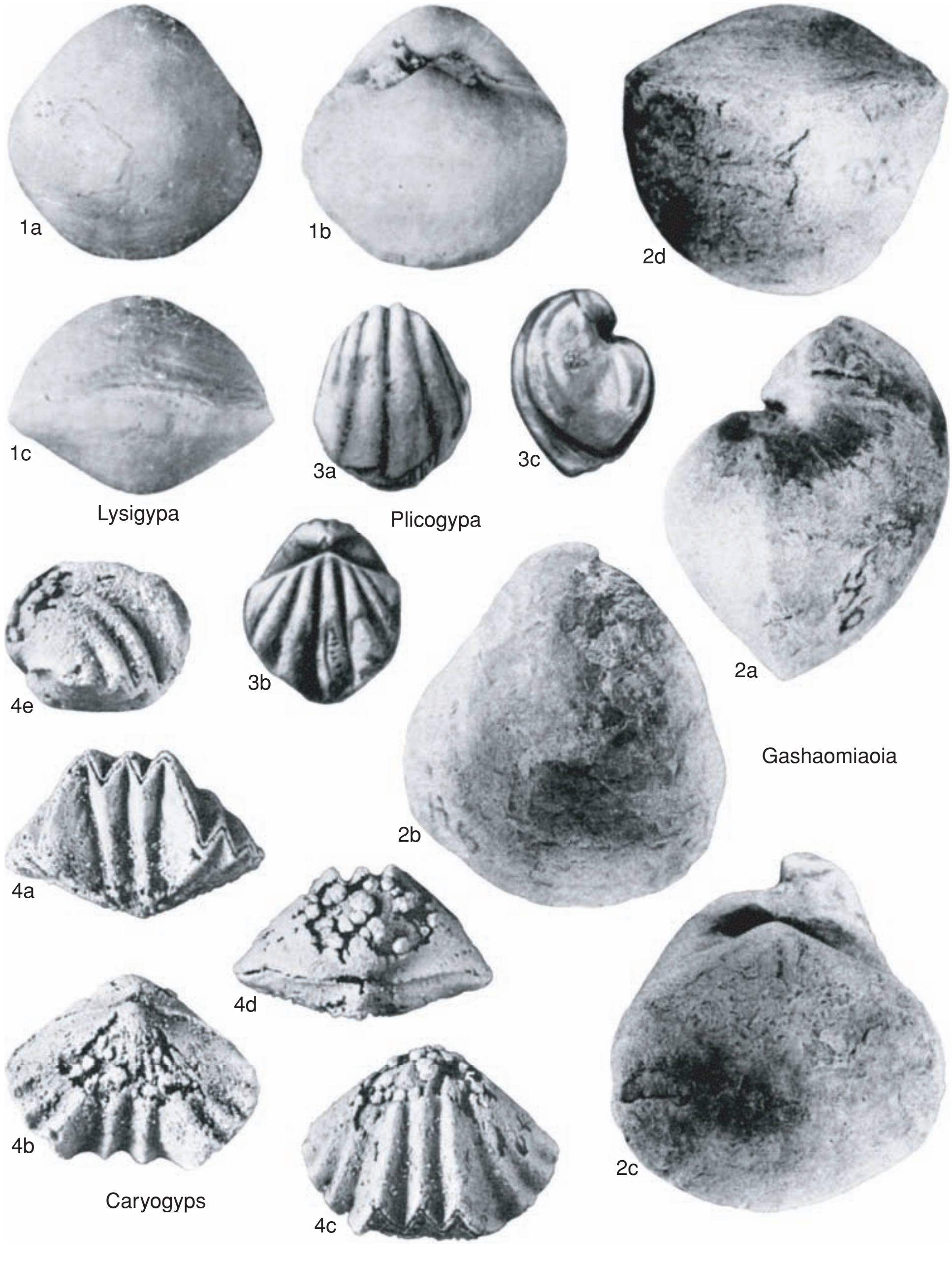

FIG. 683. Gypidulidae (p. 1008–1013).

Novozemelia CHERKESOVA, 1973, p. 28 [**N. olgae;* OD]. Medium; elongate-oval; weak anterior costae; weak fold and sulcus; short ventral median septum with long spondylium; ventral mantle canals well developed. [May be a synonym of *Carinagypa* if carinae can be demonstrated.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Novaya Zemlya.——FIG.685,*2a–e.* **N. olgae,* Kabanin Stage [Gorizont], South Island, Novaya Zemlya; *a–c,* ventral, dorsal, anterior views, ×1; *d,*

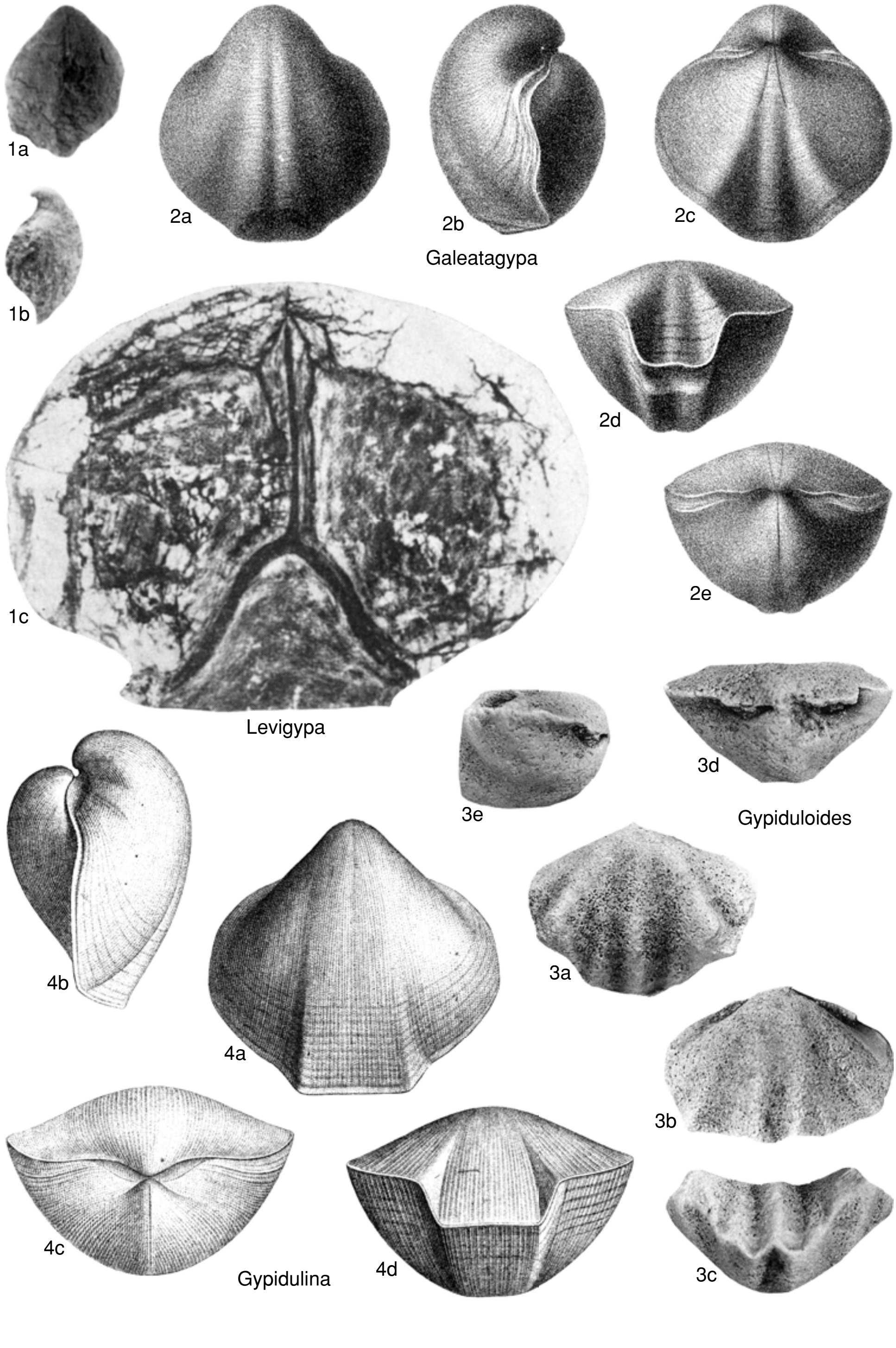

FIG. 684. Gypidulidae (p. 1008).

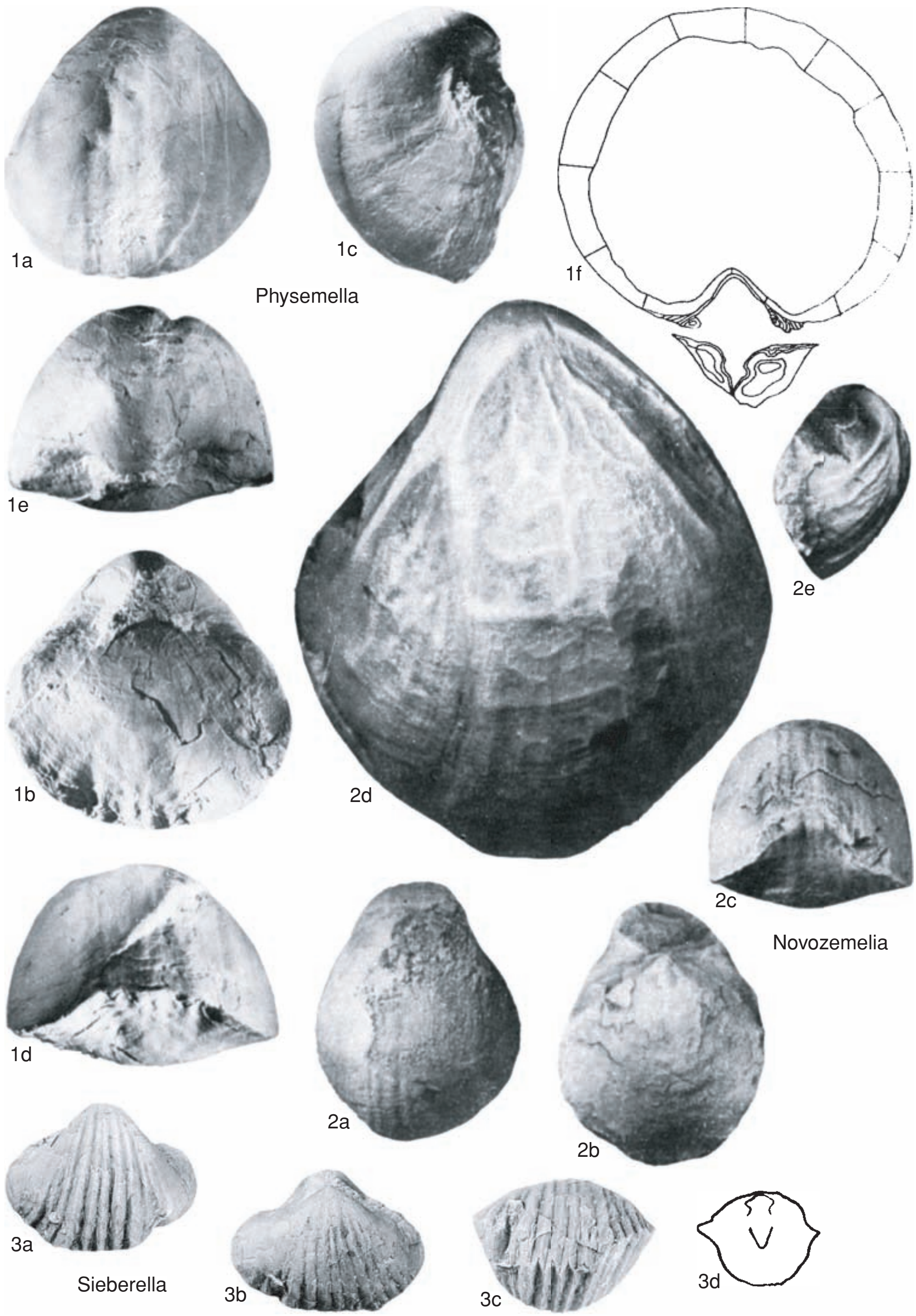

FIG. 685. Gypidulidae (p. 1010–1013).

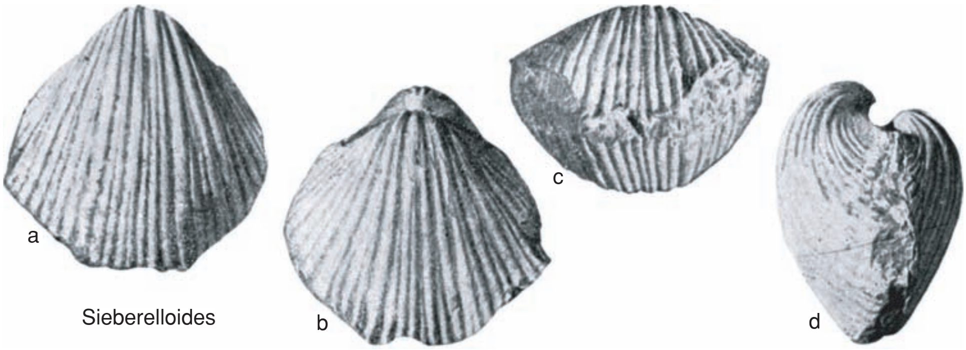

FIG. 686. Gypidulidae (p. 1013).

ventral view showing vascular marks, ×3; *e,* side view showing vascular marks, ×1 (Cherkesova, 1973).

Physemella GODEFROID, 1974, p. 49 [**P. maillieuxi* GODEFROID, 1974, p. 52; OD]. Similar to *Gypidula* externally, but ventral valve median septum absent or very short, hinge plates basally conjunct to form cruralium supported by median septum. *Upper Devonian (Frasnian):* Belgium.——FIG. 685,*1a–f.* **P. maillieuxi,* middle Frasnian, Couvin; *a–e,* ventral, dorsal, lateral, anterior, posterior views, ×1; *f,* serial section at 6.0 mm from ventral umbo, ×3 (Godefroid, 1974).

Plicogypa RZHONSNITSKAIA, 1975, p. 27 [**Pentamerus kayseri* VON PEETZ, 1901, p. 165; OD]. Similar to *Gypidula* but more coarsely ribbed, plicae extending anteriorly from beak, simple to bifurcate; inner hinge plates relatively high, parallel to one another, intersecting dorsal valve floor at nearly right angle. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Russia (Kuznetsk basin, Taymyr), Altai Mountains, USA (southwestern Alaska), Canadian Arctic Islands, Germany (Harz Mountains).——FIG. 683,*3a–c.* **P. kayseri* (VON PEETZ), Krekov Stage [Gorizont], Kuznetsk basin; ventral, dorsal, lateral views, ×1 (Rzhonsnitskaia, 1975).

Sieberella OEHLERT, 1887a, p. 1311 [**Pentamerus sieberi* VON BUCH in BARRANDE, 1847, p. 465; OD]. Medium size, ventribiconvex; costate shells; outline typically transverse, subellipsoidal, less commonly rounded; costae simple, strongly angular in cross section, covering entire shell or restricted to anterior half; V-shaped interspaces separating costae; inner hinge plates variably united to form cruralium or even low median septum; ventral median septum absent or low. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian):* widespread in Europe, North America, North Africa, Kazakhstan, Tian Shan, Salair, Urals, Vietnam.——FIG. 685,*3a–d.* **S. sieberi* (VON BUCH), Koneprusy Limestone, Prague region, Czech Republic; *a–c,* ventral, dorsal, anterior views, ×1; *d,* serial section at 7.9 mm from ventral valve beak, ×2 (Amsden, 1965).

Sieberelloides SAPELNIKOV, 1985a, p. 107 [**Sieberella weberi* KHODALEVICH, 1951, p. 38; OD]. Finely costate, suboval shells; costae extending anteriorly from beak, increasing by bifurcation; ventral fold absent or weakly developed, dorsal sulcus indistinct, developed only anteriorly; hinge plates converge basally to form sessile cruralium; short ventral median septum. [The generic name *Sieberelloides* was used by RZHONSNITSKAIA (1975, p. 20) as a text citation without diagnosis or comparison but with the designation of *Sieberella weberi* KHODALEVICH as the type species. The status of *nomen nudum* applies to her usage of the name; hence, SAPELNIKOV's 1985a description stands as the first legal usage, since it fulfills the ICZN rules for the establishment of a new generic name.] *Lower Devonian (Emsian)–Middle Devonian (lower Eifelian):* Urals.——FIG. 686*a–d.* **S. weberi* (KHODALEVICH), Emsian–lower Eifelian horizon, Serov region, eastern Urals; ventral, dorsal, anterior, lateral views, ×1 (Khodalevich, 1951).

Subfamily IVDELINIINAE Sapelnikov, 1985

[Ivdeliniinae SAPELNIKOV, 1985a, p. 118] [=Ivdelininae SAPELNIKOV, 1973, p. 41, original spelling]

Strongly ventribiconvex, costate to plicate, usually with median furrows on ribs at anterior margin; unisulcation well expressed; crura crescentic in cross section. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian).*

Ivdelinia ANDRONOV, 1961, p. 45 [**Gypidula ivdelensis* KHODALEVICH, 1951, p. 22; OD] [=*Procerulina* ANDRONOV, 1961, p. 76 (type, *Pentamerus acutolobatus procerulus* BARRANDE, 1879b, p. 60)]. Medium to large sized, galeatiform; costate to plicate, costae distinctly bifurcating anteriorly, crossed by fine concentric ridges; with or without ventral median septum; outer hinge plates discrete or rarely united into cruralium. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Europe, Urals, Central Asia [Sredni Azii], Siberia, USA (Alaska), *Lochkovian–Emsian;* Europe, Urals, Russia (Kolyma, Salair), Canadian Arctic Islands, *Eifelian.*

I. (Ivdelinia). With strongly raised costae or plicae, with median septum. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Europe, Urals, Central Asia [Sredni Azii], Siberia, USA (Alaska), *Lochkovian–Emsian;* Europe, Urals, Russia (Kolyma, Salair), Canadian Arctic Islands, *Eifelian.*——FIG. 687,*1a–d.* **I. (I.) ivdelensis* (KHODALEVICH), upper Emsian–lower Eifelian, Ivdel region, eastern slope Urals; ventral, dorsal, anterior, lateral views, ×1 (Khodalevich, 1951).——FIG. 687,*1e–f. I. procerulus,* Koneprusy Limestone, Prague region, Czech Republic; dorsal, ventral views, ×1 (Andronov, 1961).

I. (Ivdelinella) BRICE, 1982, p. 34 [**I. (I.) ellesmerensis* BRICE, 1982, p. 36; OD]. Similar to *I. (Ivdelinia),* but differs in lacking a ventral median septum and having very low costae. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Canadian Arctic Islands.——FIG. 687,*2a–e.* **I. (I.) ellesmerensis,* Blue Fiord Formation, Ellesmere Island; *a–c,* dorsal, ventral, posterior views of articulated specimen, ×1; *d,* anterior view of another articulated specimen, ×1; *e,* serial section at 5.25 mm from ventral beak, ×2.6 (Brice, 1982).

Ivdeliniella KIM, 1981, p. 36 [**I. trilobata* KIM, 1981, p. 37; OD]. Medium, outline subrhombohedral; high median fold and deep sulcus, lateral plications poorly developed, present only on large specimens; inner hinge plates united into low septum. *Lower Devonian (Lochkovian–Pragian):* USA (southwestern Alaska), *Lochkovian;* Tian Shan, *Pragian.*——FIG. 687,*3a–d.* **I. trilobata,* Manak Stage [Gorizont], Nuratau Range, southern Tian Shan; ventral, dorsal, lateral, anterior views, ×1 (Kim, 1981).

Subfamily LEVIGATELLINAE Rzhonsnitskaia, 1975

[Levigatellinae RZHONSNITSKAIA, 1975, p. 20]

Smooth with microsculpture of thin concentric growth lines; carinae well developed; inner hinge plates widely spaced and strongly inclined away from one another basally. *Silurian (upper Llandovery)–Lower Devonian (Lochkovian).*

Levigatella ANDRONOV, 1961, p. 38 [**Gypidula olga* KHODALEVICH, 1939, p. 15; OD]. Small to medium sized, transverse, ventribiconvex; unisulcation well developed and wide, short ventral median septum; inner hinge plates basolaterally directed, well-developed carinae. *Silurian (upper Llandovery)–Lower Devonian (Lochkovian):* Altai Mountains, *upper Llandovery;* northeastern Siberia, *Wenlock;* Urals, Tian Shan, *Ludlow–Lochkovian.*——FIG. 687,*4a–f.* **L. olga* (KHODALEVICH); *a–d,* ventral, dorsal, lateral, anterior views, Severouralsk Stage [Gorizont], eastern slope northern Urals, ×1; *e,* external ornamentation, Severouralsk Stage [Gorizont], eastern slope northern Urals, ×6; *f,* serial section of dorsal valve, Isovsk Stage [Gorizont], eastern slope central Urals, ×6 (Sapelnikov, 1985a).

Subfamily DEVONOGYPINAE Breivel & Breivel, 1977

[Devonogypinae BREIVEL & BREIVEL, 1977, p. 70]

Tuberculate microsculpture; weakly developed fold and sulcus; smooth umbonal region. *Silurian (Ludlow)–Middle Devonian (Givetian).*

Devonogypa HAVLÍČEK, 1951, p. 5 [**Gypidula (Devonogypa) spinulosa;* OD] [=*Devonogypa (Glabrigalites)* STRUVE, 1992, p. 547 (type, *D. (G.) glabrigal* STRUVE, 1992, p. 548)]. Medium to large, smooth, strongly ventribiconvex with microsculpture of granules or fine spines arranged in oblique or horizontal rows; ventral fold absent or weakly developed, dorsal sulcus absent or shallow; inner hinge plates widely discrete. *Middle Devonian (Eifelian–Givetian):* Czech Republic, Poland, Germany, Caucasus.——FIG. 688,*2a–f.* **D. spinulosa; a,* dorsal view, Celechovice, Czech Republic, ×1 (Havlíček, 1951); *b–e,* ventral, lateral, dorsal, anterior views, Skaly beds, Holy Cross Mountains, Poland, ×1; *f,* external ornament, Skaly beds, Holy Cross Mountains, Poland, ×8 (Biernat, 1966).

Gypidulella KHODALEVICH & BREIVEL, 1959, p. 26 [**G. pennatula;* OD]. Medium, wide, gently biconvex, finely costate; long, straight hinge line; dorsal sulcus and ventral fold wide and flat, developed anteriorly; exterior shell surface tuberculate; hinge plates adjoin each other basally. *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Urals.——FIG. 688,*1a–f.* **G. pennatula,* upper Emsian–lower Eifelian, Taltiisk Stage [Gorizont], eastern slope northern Urals; *a–d,* ventral, dorsal, lateral, anterior views, ×1; *e,* external ornamentation, ×3; *f,* serial section, ×4 (Khodalevich & Breivel, 1959).

Pseudosieberella GODEFROID, 1972, p. 3 [**P. corrugata* GODEFROID, 1972, p. 6; OD]. Externally similar to *Sieberella* but differs in having small tubercles; discrete inner hinge plates. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Czech Republic, *Emsian;* Belgium, Germany, *Eifelian.*——FIG. 689,*1a–f.* **P. corrugata,* Couvinian Stage

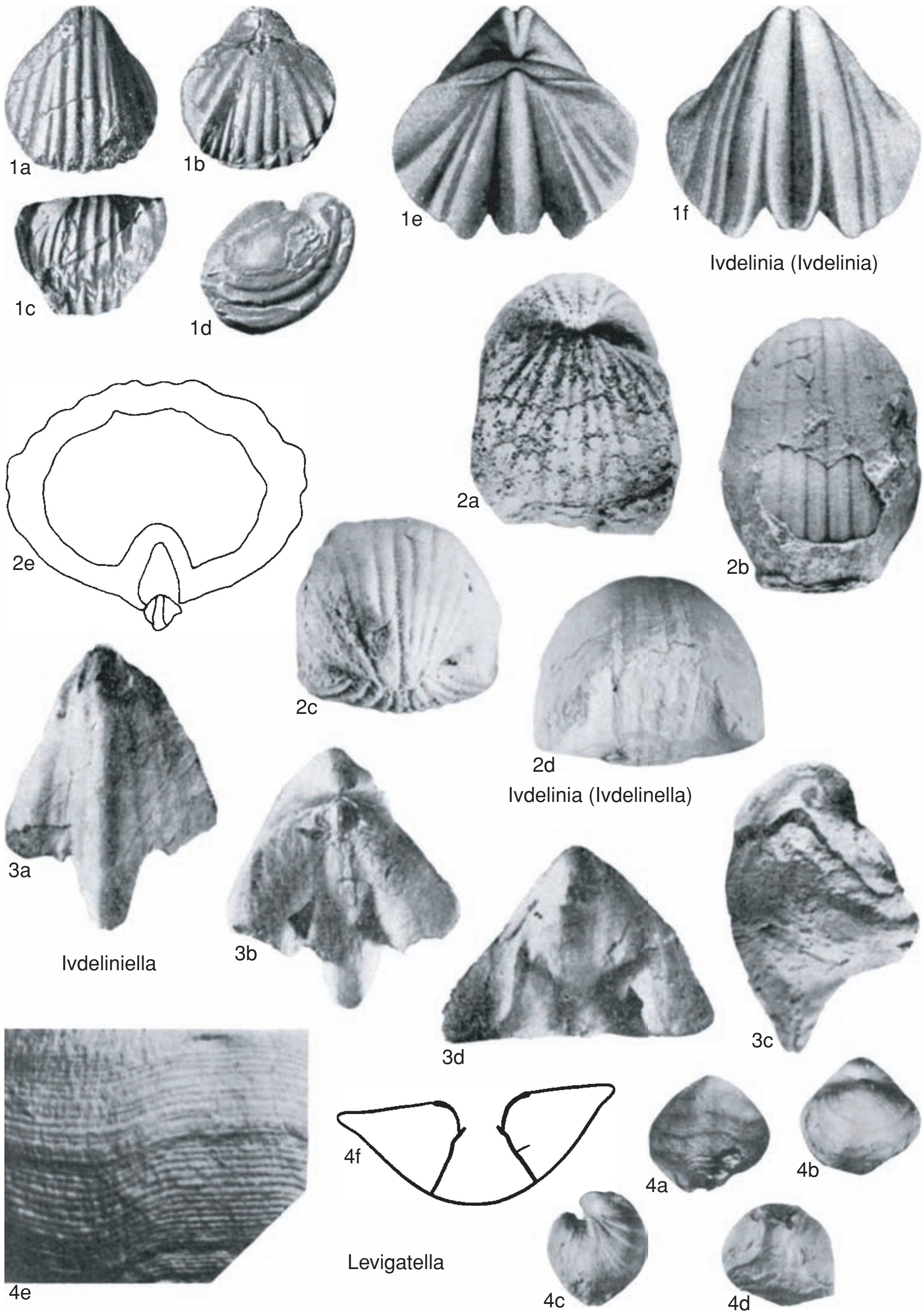

FIG. 687. Gypidulidae (p. 1013–1014).

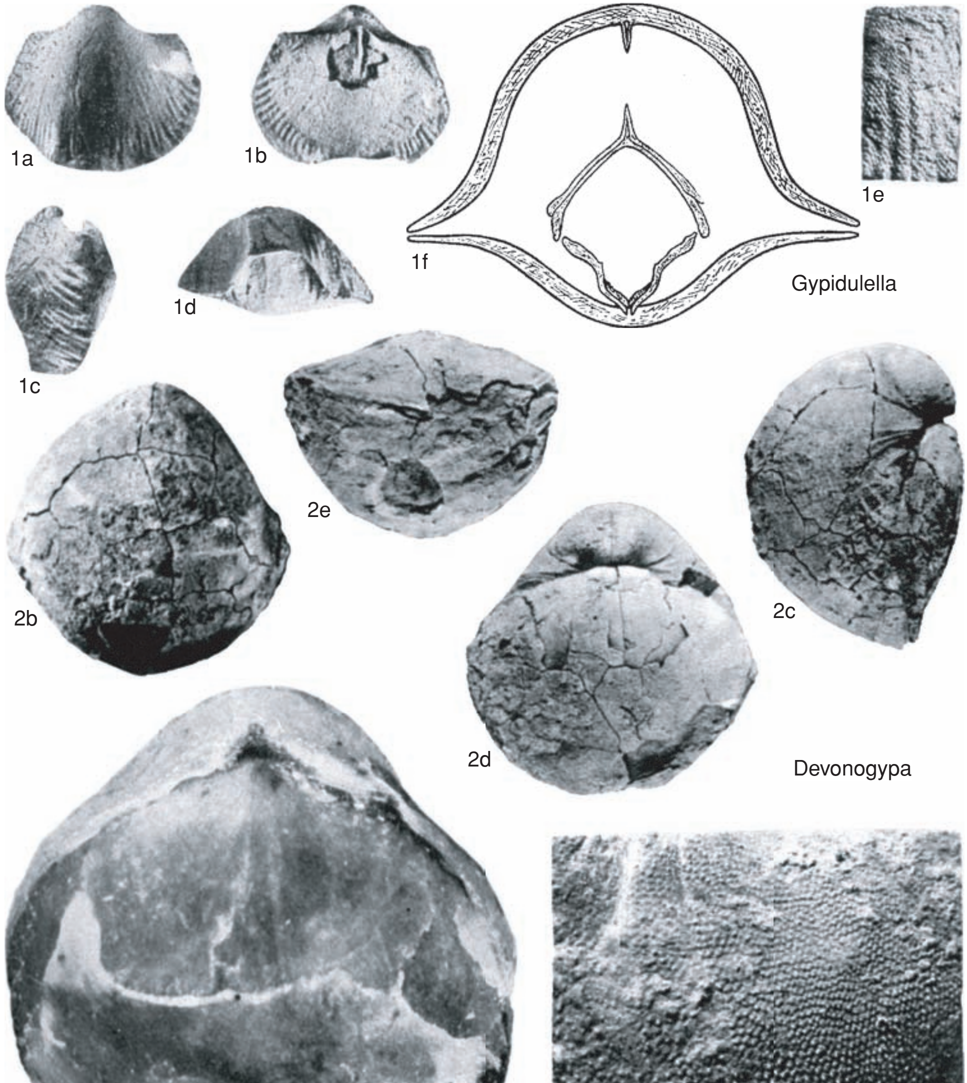

FIG. 688. Gypidulidae (p. 1014).

[Gorizont], Couvin, Belgium; *a–e,* ventral, dorsal, lateral, anterior, posterior views, ×1.5; *f,* serial section at 8.0 mm from ventral umbo, ×2.5 (Godefroid, 1972).

?**Wyella** KHODALEVICH, 1939, p. 21 [**Eichwaldia uralica* CHERNYSHEV, 1893, p. 179; OD]. Medium; smooth to plicate with honeycomb-like pitted exterior; fold and sulcus variably developed; inner hinge plates discrete. *Silurian (Ludlow)–Middle Devonian (upper Eifelian):* Urals, Central Asia [Sredni Azii], Kazakhstan, *Ludlow–Přídolí;* Urals, *Pragian–upper Eifelian.*——FIG. 689,*2a–e.* **W. uralica* (CHERNYSHEV), Isovsk Stage [Gorizont], Vagran River, eastern Urals; *a–d,* ventral, dorsal, lateral, anterior views, ×1; *e,* external ornamentation, ×8 (Sapelnikov, 1985a).

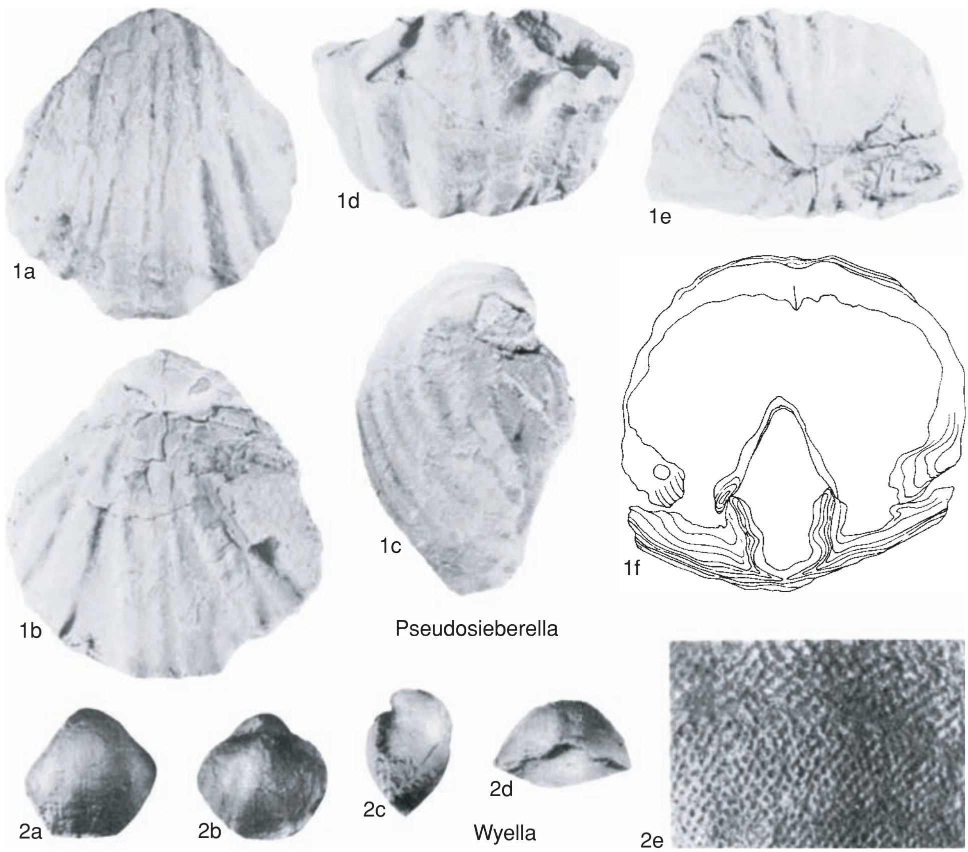

FIG. 689. Gypidulidae (p. 1014–1016).

Subfamily CONCHIDIELLINAE Rzhonsnitskaia, 1961

[Conchidiellinae RZHONSNITSKAIA, 1961, p. 47]

Medium to large sized, elongate, shells externally similar to *Kirkidium,* usually costate, rarely smooth; fold and sulcus absent or poorly developed. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Zdimir BARRANDE, 1881, p. 171 [**Z. solus;* OD; =*Porambonites*? *robustus* BARRANDE, 1879b, p. 97] [=*Conchidiella* KHODALEVICH, 1939, p. 32 (type, *Pentamerus pseudobaschkiricus* CHERNYSHEV, 1885, p. 55)]. Shell large, inner hinge plates discrete, hinge plates lyre shaped. [Type material unsuitable for illustration.] *Lower Devonian (upper Emsian)–Middle Devonian (Givetian):* Czech Republic, Germany, Belgium, Carnic Alps, Urals, Russia (Novaya Zemlya, Salair, northeastern Siberia), Tian Shan, Transcaucasus, South China, Japan.——FIG. 690,*1a–c. Z. pseudobaschkiricus sibiricus,* Shandinsk Stage [Gorizont], Gurevsk region, Siberia; ventral, dorsal, lateral views, ×1 (Rzhonsnitskaia, 1975).

Biseptum KHODALEVICH & BREIVEL, 1959, p. 39 [**B. rectecostatum;* OD]. Costate, costae commonly nonbifurcating; consists of fused inner hinge plates so that short median septum supports cruralium. *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Urals.——FIG. 691,*1a–d. *B. rectecostatum,* Taltiisk Stage [Gorizont], Ivdel region, eastern Urals; *a–c,* ventral, dorsal, lateral views, ×1; *d,* serial section, ×2 (Khodalevich & Breivel, 1959).

?Glyptogypa STRUVE, 1992, p. 549 [**Pentamerus galaeatus* var. *multiplicata* [C.] F. ROEMER, 1854 in 1852–1854, p. 352; OD]. Similar to *Zdimirella,* but differs in having costellae that commonly bifurcate and in having inner hinge plates that unite to form cruralium. *Middle Devonian (Eifelian):* Germany, France, Poland.——FIG. 690,*2a–e. *G.* sp. cf. *G. multiplicata* (ROEMER), Skaly beds, Holy

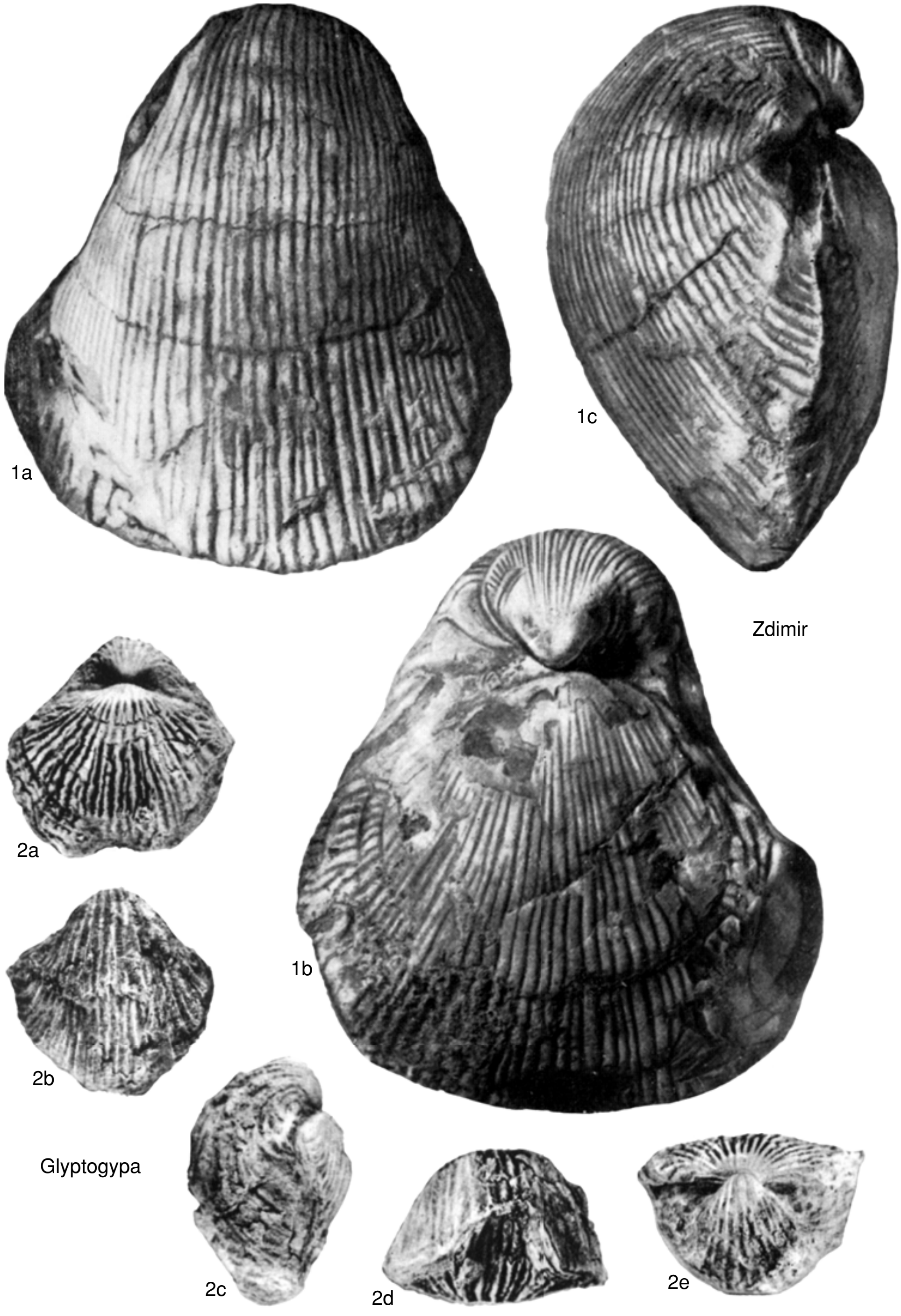

FIG. 690. Gypidulidae (p. 1017–1020).

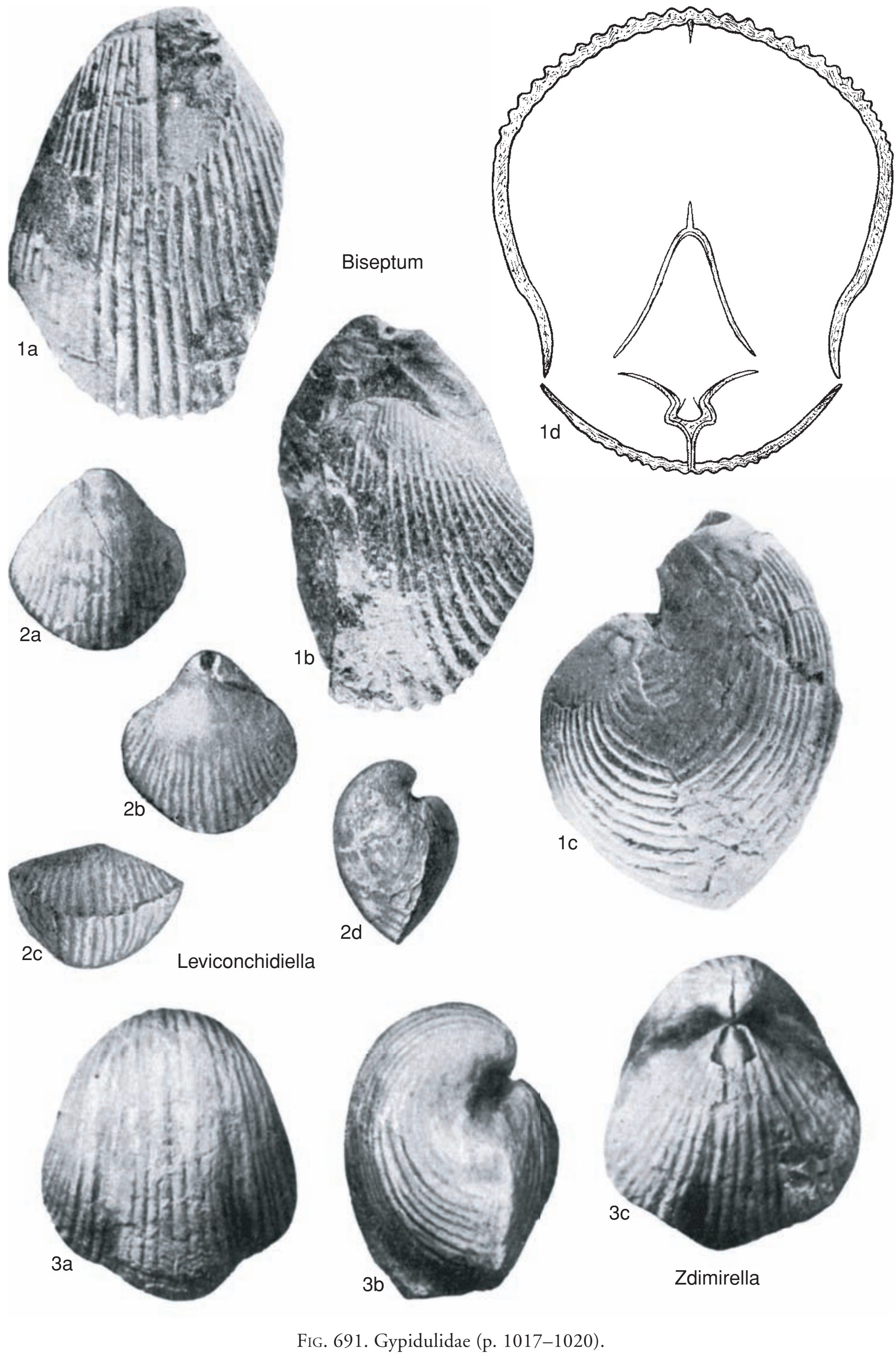

FIG. 691. Gypidulidae (p. 1017–1020).

Cross Mountains, Poland; dorsal, ventral, lateral, anterior, posterior views, ×1 (Biernat, 1966).

Leviconchidiella Rzhonsnitskaia, 1960c, p. 301 [**Sieberella*? *vagranica* Khodalevich, 1951, p. 39; OD]. Subcircular to transverse, anteriorly costate, entirely lacking or with weakly developed ventral fold and dorsal sulcus; costae simple, flatly rounded; anterior commissure rectimarginate or weakly deflected ventrally; inner hinge plates discrete. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Urals, Tian Shan, Kuznetsk basin.——Fig. 691,*2a–d*. **L. vagranica* (Khodalevich), Karpinsk Stage [Gorizont], Serov region, eastern Urals; ventral, dorsal, anterior, lateral views, ×1 (Khodalevich, 1951).

?Zdimirella Cherkesova, 1973, p. 32 [**Z. kuzmini;* OD]. Large, strongly ventribiconvex; costellate, costellae extending from umbo; ventral fold and dorsal sulcus well expressed in anterior half of shell; inner hinge plates disjunct; ventral median septum high and long. *Middle Devonian (lower Givetian):* Novaya Zemlya, western Canada.——Fig. 691,*3a–c*. **Z. kuzmini,* basal Givetian, South Island, Novaya Zemlya; ventral, lateral, dorsal views, ×1 (Cherkesova, 1973).

Subfamily GENICULIGYPINAE Blodgett & Boucot, 1998

[Geniculigypinae Blodgett & Boucot, 1998, p. 454]

Prominent geniculation developed in both valves; microornament composed of fine radial grooves. *Middle Devonian (Givetian).*

Geniculigypa Blodgett & Boucot, 1998, p. 454 [**Sieberella newtonensis* Imbrie, 1959, p. 369; OD]. Medium, ventribiconvex shells; anterior commissure nearly rectimarginate; smooth with microornament of fine radial grooves; inner hinge plates united to form cruralium supported by median septum. *Middle Devonian (Givetian):* USA (Michigan).——Fig. 692*a–f*. **G. newtonensis* (Imbrie), Newton Creek Limestone; *a–e,* posterior, anterior, ventral, dorsal, lateral views, ×3; *f,* oblique ventral, ×6 (Blodgett & Boucot, 1998).

NOMEN NUDUM

Schegultania Andronov, 1961, p. 108 [no type species designated]. In same work Andronov assigned to the genus three species: *S. karpinskii* Andronov, 1961, *S. archangelskii* Andronov, 1961, and *S.* sp. Andronov, 1961. Sapelnikov (1985a, p. 134–135) redescribed the genus, and restricted to it only *S. karpinskii* [from the *Zdimir* Zone of northern Urals (upper Emsian–lower Eifelian)]. The other two species of Andronov he indicated belong to unrelated, nonpentamerid brachiopods. Sapelnikov did not formally designate *S. karpinskii* as the type species of *Schegultania.*

GENERA REJECTED FROM THE GYPIDULIDAE

Levibiseptum Xian, 1975, p. 31, placed in Rhynchospiriferinae by Carter & others (1994, p. 337).

Family ENANTIOSPHENIDAE Torley, 1934

[Enantiosphenidae Torley, 1934, p. 93]

Specialized forms with crura terminating in loop; supporting plates consisting of outer hinge plate, crura, inner hinge plate; hinge plates unite to form median septum. *Middle Devonian (Givetian).*

Enantiosphen Whidborne, 1893, p. 97 [**Meganteris*? *vicaryi* Davidson, 1882, p. 20; SD Holzapfel, 1908, p. 123]. Large, smooth, biconvex, transversely elliptical to subtriangular shells; lateral and anterior margins of both valves strongly geniculate; spondylium supported on high median septum; crura extending forward and expanding to form broad plates connected to one another by transverse plate supported in center by median septum. *Middle Devonian (Givetian):* England, Germany, Urals.——Fig. 693*a–d*. **E. vicaryi* (Davidson), Massenkalk, Bilveringsen, Germany; *a–b,* dorsal, lateral views, ×1 (Holzapfel, 1908); *c–d,* dorsal median septum and large part of loop, reconstruction of brachial loop and apparatus, ×1 (Leidhold, 1928).——Fig. 694*a–d*. **E. vicaryi* (Davidson); *a,* cross section, Massenkalk, Bilveringsen, Germany, ×1 (Torley, 1934); *b–d,* dorsal, lateral views of brachial apparatus, ventral interior, no horizon or locality provided, ×1 (Williams & Wright, 1961).——Fig. 693*e*. *E. torleyi;* posterior view, ×1 (Holzapfel, 1908).

Enantiosphenella Johnson, 1974, p. 67 [**E. cybele* Johnson, 1974, p. 68; OD]. Similar to *Enantiosphen* but differs in its lack of median septa in both valves, resulting in discrete, long dental plates in ventral valve that enclose sessile spondylium, and in closely spaced, discrete, long, subparallel inner hinge plates in dorsal valve. *Middle Devonian (Givetian):* USA (Nevada).——Fig. 695*a–f*. **E. cybele,* Denay Limestone, western Roberts Mountains; *a–c,* tilted view of ventral interior, ventral interior, posterior view of ventral exterior; *d,* ventral exterior; *e–f,* tilted view of dorsal interior, dorsal interior, ×2 (Johnson, 1974).

Superfamily CLORINDOIDEA Rzhonsnitskaia, 1956

[*nom. transl.* Blodgett, Boucot, & Rong, herein, *ex* Clorindinae Rzhonsnitskaia, 1956b, p. 49]

[Materials prepared by Robert B. Blodgett, A. J. Boucot, & Rong Jia-yu]

Small to medium-sized, galeatiform, uniplicate shells; smooth or costate; brachial

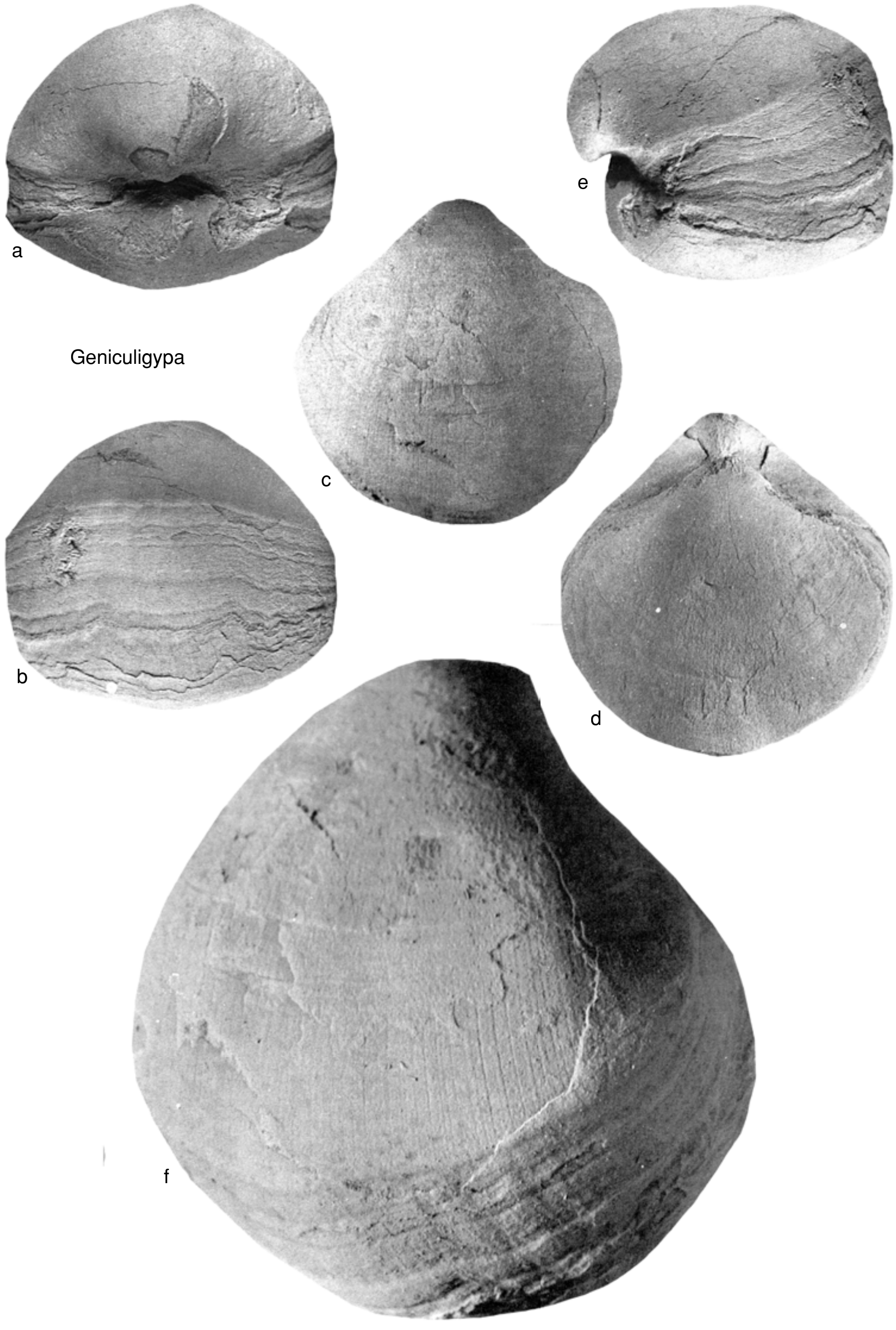

FIG. 692. Gypidulidae (p. 1020).

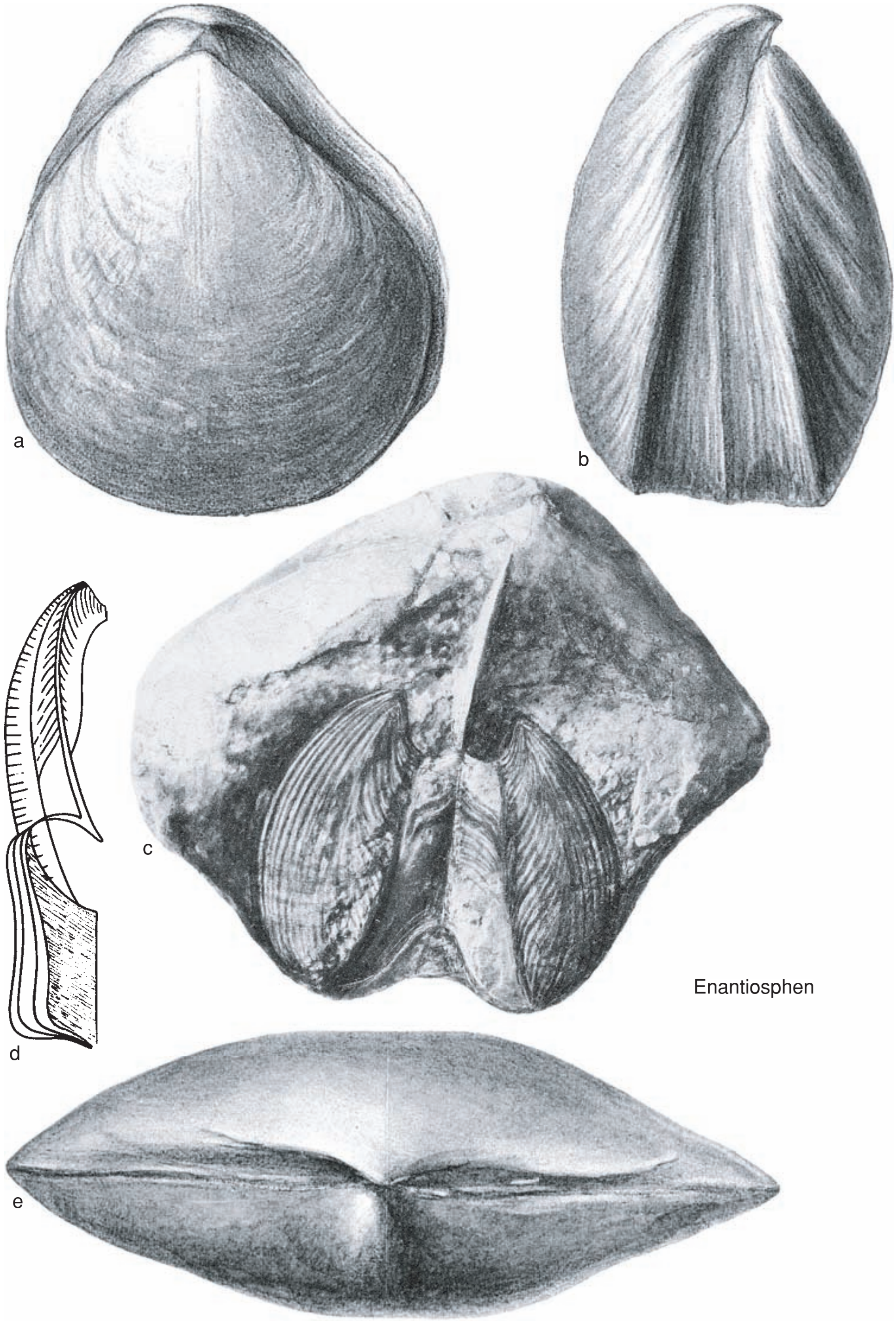

FIG. 693. Enantiosphenidae (p. 1020).

apparatus well developed with exceedingly short inner hinge plates that are discrete or united to form cruralium; hinge plates may be lyre shaped or straight in cross section; crura bladelike in cross section; carinae commonly developed. *lower Silurian (Rhuddanian)–Middle Devonian (Givetian).*

Family CLORINDIDAE Rzhonsnitskaia, 1956

[*nom. transl.* Rzhonsnitskaia, 1961, p. 47, *ex* Clorindinae Rzhonsnitskaia, 1956b, p. 49] [=Barrandellinae Andronov, 1961, p. 34; Antirhynchonellidae Nikiforova, 1960d, p. 205]

Description as for superfamily. *lower Silurian (Rhuddanian)–Middle Devonian (Givetian).*

Subfamily CLORINDINAE Rzhonsnitskaia, 1956

[Clorindinae Rzhonsnitskaia, 1956b, p. 49]

Smooth. *Silurian (Rhuddanian)–Middle Devonian (Givetian).*

Clorinda Barrande, 1879b, p. 109 [**C. armata;* OD]. Small to medium, smooth, ventribiconvex; dorsal fold and ventral sulcus well developed anteriorly, inner hinge plates discrete, widely spaced apart; hinge plates not lyre shaped in cross section; carinae present. *Silurian (Rhuddanian)–Middle Devonian (Givetian):* widespread in Europe, Asia, North America, Greenland, Australia, North Africa.——Fig. 696,*1a–c.* **C. armata,* Hlubocepy Limestone, Prague region, Czech Republic; lateral, dorsal, posterior views, ×1 (Barrande, 1879b).——Fig. 696,*1d–f.* *C. tumidula,* Gun River Formation, Anticosti, Québec, Canada; ventral, anterior, dorsal views, ×1 (Schuchert & Cooper, 1932).

Antirhynchonella Oehlert, 1887a, p. 1311 [**Atrypa linguifera* J. de C. Sowerby in Murchison, 1839, p. 629; OD] [=*Barrandella* Hall & Clarke, 1893, p. 241, obj.; in 1955, ICZN (Opinion 374) placed *Antirhynchonella* (type, *Atrypa linguifera* J. de C. Sowerby in Murchison, 1839, p. 629) on The Official List of Generic Names; *Antirhynchonella* Quenstedt, 1871 in 1868–1871, *nom. nud.,* and *Barrandella* Hall & Clarke, 1893, were added to The Index of Rejected and Invalid Generic Names in Zoology]. Medium, smooth, strongly ventribiconvex shell; dorsal fold rounded; inner hinge plates united to form cruralium that may or may not be supported by median septum; lyre-shaped cross section; carinae present. *Silurian (Aeronian)–Middle Devonian (Givetian):* Europe, Siberia, Turkestan, South China, North America, Venezuela, *Aeronian–Přídolí;* Urals, Czech Republic, *Lochkovian–Emsian;* Poland, South China, *Givetian.*——Fig. 696,*3a–g.* **A. linguifera* (J. de C.

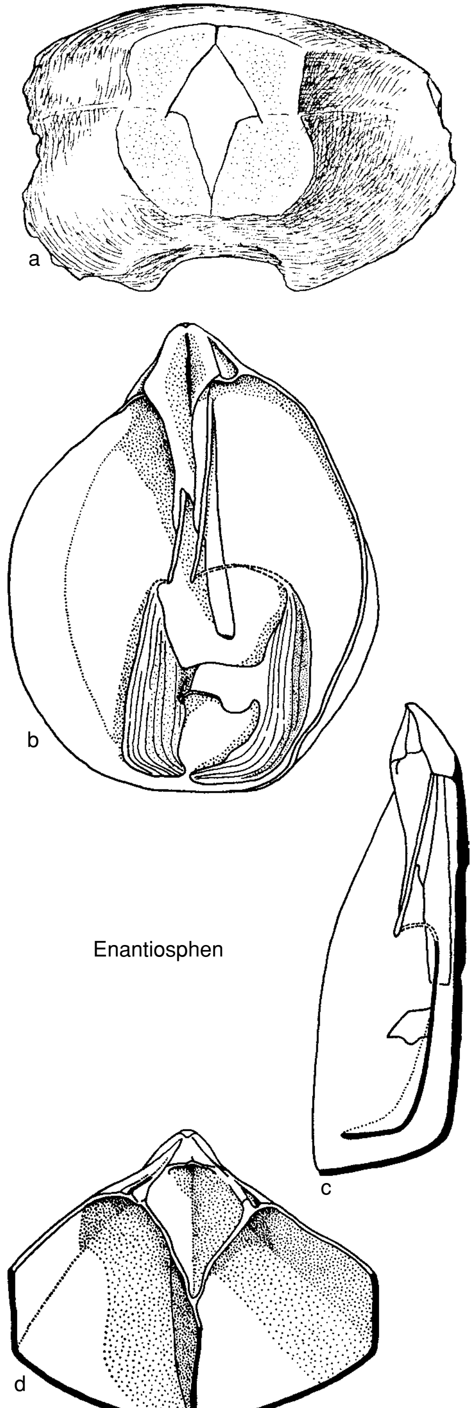

Fig. 694. Enantiosphenidae (p. 1020).

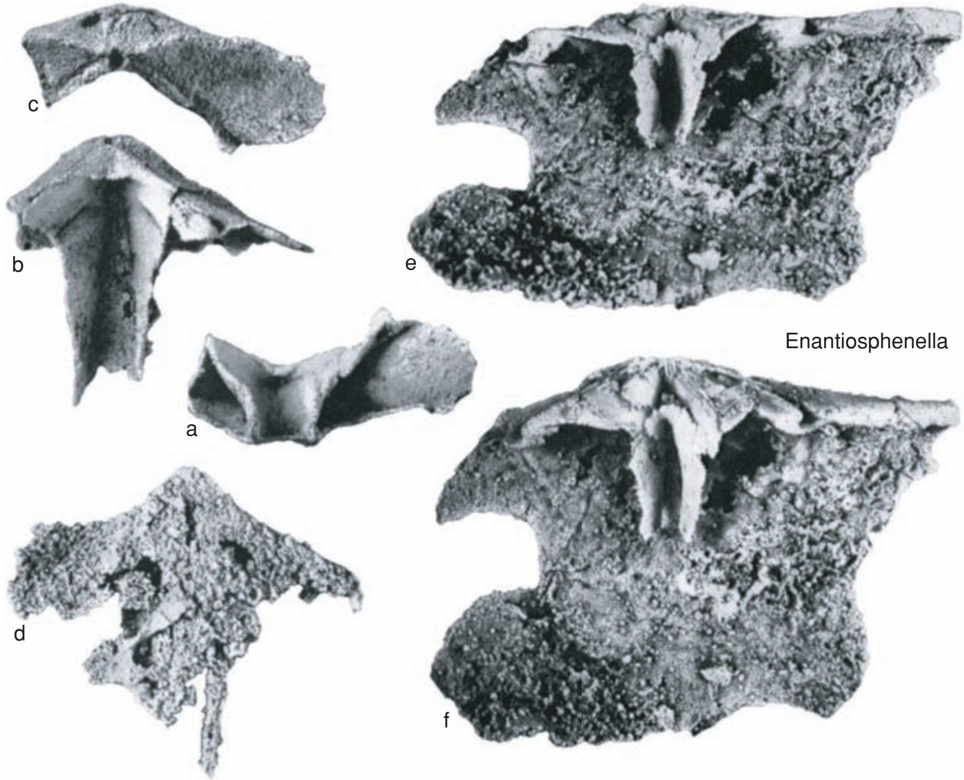

FIG. 695. Enantiosphenidae (p. 1020).

SOWERBY), Wenlock Limestone, Dudley, England; *a–c,* lateral, dorsal, anterior views, ×1; *d–g,* serial sections, ×2 (Amsden, 1965).

Barrandina BOOKER, 1926, p. 131 [**Pentamerus linguifera* var. *wilkinsoni* ETHERIDGE, 1892, p. 52; OD]. Medium, smooth, outline suboval, generally transverse; ventral umbo large, highly arched and strongly thickened; dorsal fold and ventral sulcus well developed; inner hinge plates discrete; hinge plates with lyre-shaped cross section; carinae small or absent. *upper Silurian:* Australia (New South Wales), Czech Republic, Urals.——FIG. 696,*2a–d.* **B. wilkinsoni* (ETHERIDGE), Barrandella Shales, Yass, New South Wales; dorsal, ventral, lateral, anterior views, ×1 (Booker, 1926).

Boucotides AMSDEN, 1968, p. 44 [**B. barrandei* AMSDEN, 1968, p. 45; OD]. Medium, smooth clorindinid with inner hinge plates uniting to form cruralium or even low median septum; hinge plates with lyre-shaped cross section, lacking carinae; similar to *Antirhynchonella* but differs in having a deep V-shaped sulcus and corresponding ridgelike fold. *Silurian (Wenlock):* USA (Arkansas), Czech Republic.——FIG. 696,*5a–d.* **B. barrandei,* St. Clair Limestone, Batesville district, Arkansas; *a,* dorsal view, ×2; *b–c,* ventral, anterior views, ×1; *d,* ventral view, ×2 (Amsden, 1968).

Indaclor HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 119 [**I. sellarius* HAVLÍČEK & ŠTORCH, 1990, p. 120; OD]. Small, externally similar to *Clorinda* with low, rounded fold on dorsal valve; anterior commissure uniplicate; ventral sulcus absent or weakly developed; inner hinge plates lacking; no carinae or lyre-shaped cross section. *Silurian (upper Wenlock–Ludlow):* Czech Republic.——FIG. 696,*4a–d.* **I. sellarius* HAVLÍČEK & ŠTORCH, Motol Formation, Prague region; anterior, ventral, dorsal, lateral views, ×2.5 (Havlíček & Štorch, 1990).

Subfamily PENTAMERELLINAE Sapelnikov, 1973

[Pentamerellinae SAPELNIKOV, 1973, p. 40]

Exterior surface costate. *Silurian (Telychian)–Middle Devonian (Givetian).*

Pentamerella HALL, 1867b, p. 373 [**Atrypa arata* CONRAD, 1841, p. 55; OD]. Variable size, ventribiconvex; inner hinge plates united to form

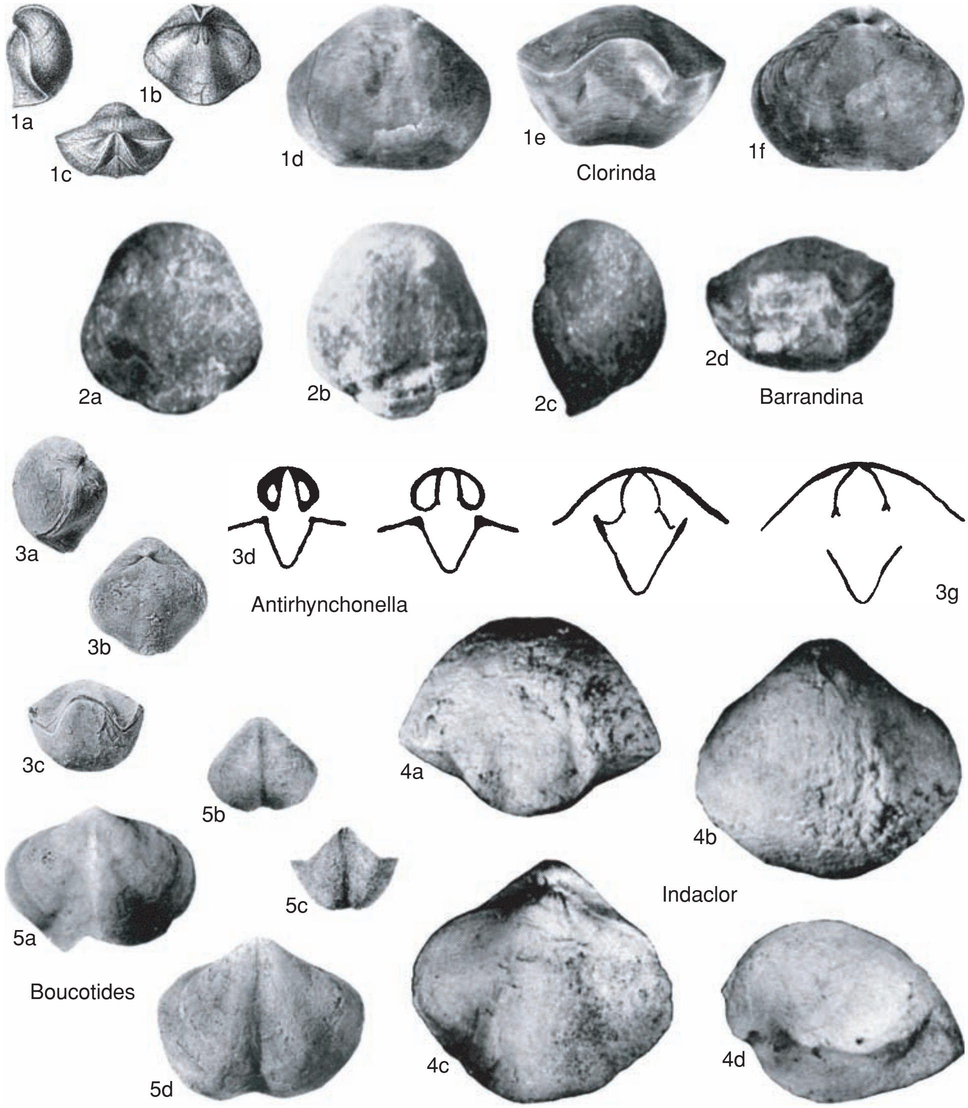

FIG. 696. Clorindidae (p. 1023–1024).

cruralium, sometimes supported by median septum; hinge plates with lyre-shaped cross section; noncarinate. *Lower Devonian (Emsian)–Middle Devonian (Givetian):* North America, Europe, Siberia.——FIG. 697,*3a–c.* **P. arata* (CONRAD), Schoharie Formation, Albany County, New York, USA; anterior, dorsal, lateral views, ×1 (Schuchert & Cooper, 1932).

Clorindella AMSDEN, 1964, p. 236 [**Barrandella areyi* HALL & CLARKE, 1893, p. 368; OD]. Small, paucicostate shell; costae coarse, subangular, undivided anteriorly; outer hinge plates and crura join with upper (ventral) edge of processes projecting as carinae; inner hinge plates unite above dorsal valve floor to form cruralium; hinge plates with lyre-shaped cross section; carinae present. *Silurian (Telychian):* USA (New York).——FIG. 697,*4a–h.* **C. areyi* (HALL & CLARKE), Clinton Group; *a–e,* posterior, ventral, anterior, lateral, dorsal views, Rochester, ×2 (Amsden, 1964); *f–h,* transverse serial sections at 2.5, 3.1, and 4.0 mm from tip of ventral valve beak, ×3 (Amsden, 1965).

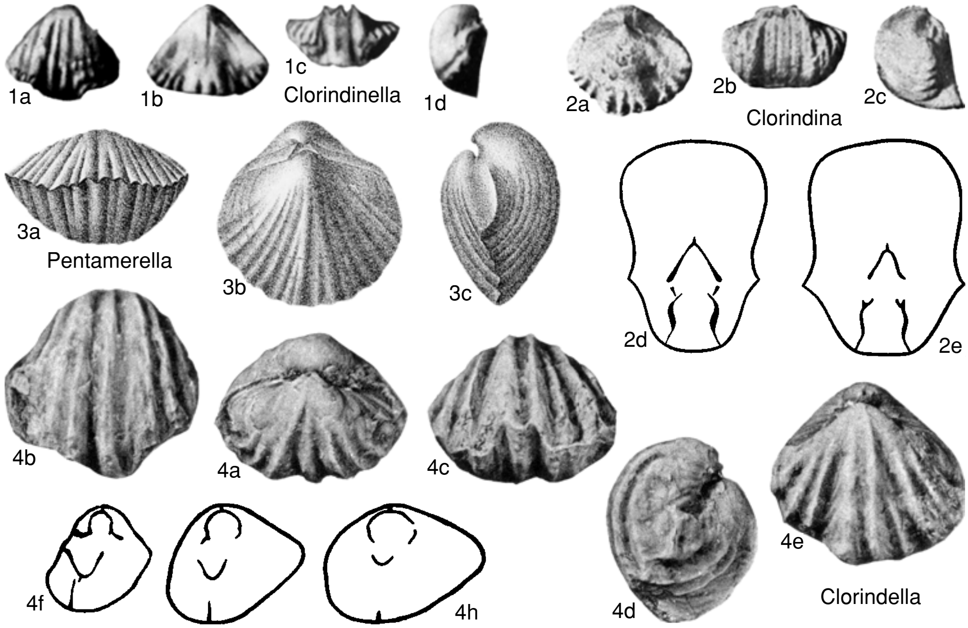

FIG. 697. Clorindidae (p. 1024–1026).

Clorindina KHODALEVICH, 1939, p. 11 [**C. uralica;* OD]. Medium, strongly to moderately inflated, ventribiconvex; uniplication developed anteriorly; costae divided by longitudinal furrows anteriorly; longitudinal furrows at anterior margin; inner hinge plates discrete; hinge plates weakly lyre shaped; carinae may or may not be present. *Lower Devonian–Middle Devonian (Eifelian):* Russia (Novaya Zemlya, Kolyma), Altai Mountains, Urals, Salair, Tian Shan, *Lower Devonian;* Germany, *Eifelian.* ——FIG. 697,*2a–c. *C. uralica,* Saumsk Stage [Gorizont], Nadezhdin region, eastern Urals; dorsal, anterior, lateral views, ×2 (Khodalevich, 1939).——FIG. 697,*2d–e. C. arataeformis,* Solobykhin beds, Altai Mountains; serial sections, ×3.7 (Sapelnikov, 1985a).

Clorindinella RZHONSNITSKAIA, 1975, p. 61 [**C. alaica;* OD; =*Clorindina alaica* NIKIFOROVA, 1960d, pl. 25, fig. 4a–d, *nom. nud.*]. Small, with sharp-edged lateral and anterior commissure; ventral sulcus wide with trapezoidal or arched tongue; costae rounded, with longitudinal furrows at anterior margin; ventral septum and spondylium short; hinge plates discrete; lyre-shaped cross section; carinae may or may not be present. [The type species was given by RZHONSNITSKAIA (1975, p. 61) as *Clorindina alaica* NIKIFOROVA, 1960d, which appeared only as an illustration (pl. 25, fig. 4a–d) in the brachiopod volume of the *Osnovy Paleontologii* (T. G. SARYCHEVA, ed., 1960). Because it lacks a written description or diagnosis, the usage by NIKIFOROVA in 1960d stands as a *nomen nudum.* RZHONSNITSKAIA in 1975 gave a description of the species, and under ICZN rules this usage is accepted as the first legal usage of the species name.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Urals, Kuznetsk Basin, Tian Shan, ?western Europe.——FIG. 697,*1a–d. *C. alaica,* Baskuskan Limestone, Gurevsk, Siberia; ventral, dorsal, anterior, lateral views, ×1 (Rzhonsnitskaia, 1975).

RHYNCHONELLIDA

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Order RHYNCHONELLIDA Kuhn, 1949

[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 221, *pro* order Rhynchonellacea KUHN, 1949, p. 104]

[Diagnosis and Introduction prepared by NORMAN M. SAVAGE, MIGUEL O. MANCEÑIDO, & ELLIS F. OWEN]

Rostrate articulated brachiopods with biconvex shell that usually has dorsal fold and ventral sulcus; interareas typically low and limited to ventral valve. Shell commonly with coarse costae, sometimes fine; mostly impunctate. Ventral interior typically with dental plates; spondylium normally absent. Dorsal interior commonly with medium septum supporting septalium or hinge plates; outer parts of hinge plates form bases for crura that in recent genera are attached to spirolophous lophophore. *Lower Ordovician (Llanvirn)–Holocene.*

INTRODUCTION

The Rhynchonellida comprise a group distinctive in external morphology, with genera typically rostrate, markedly biconvex, astrophic, strongly ribbed, and with a zigzag anterior commissure. The teeth and sockets are almost always interlocked so that the valves are preserved conjoined and difficult to separate. The ventral valve's internal structures preserved in fossilized material include teeth, often supported by dental plates, and the dorsal valve's internal structures include cardinalia, sometimes supported by a median septum, with anteriorly directed crura. Other important features include muscle attachment scars in both valves.

Many kinds of external and internal structures appear to have evolved several times. Some are variably developed within single species. Muscle scars may be of more taxonomic importance than some of the other internal features but are commonly poorly known because of the limitations of clarity of serial sections. Classification has been hindered by the various approaches to description and illustration related to differences in preservation. Comparing silicified interiors with internal molds or serial sections impedes accurate differentiation, and workers have sometimes assigned taxonomic significance to features seen in one type of preservation that are rarely visible in other material. Some of these same problems were discussed in the introduction to the rhynchonellide section in the 1965 *Treatise* (MOORE, 1965).

Since the publication of the introductory discussions of SCHMIDT and MCLAREN (1965) on the Paleozoic Rhynchonellida and of AGER (1965) on the Mesozoic and Cenozoic Rhynchonellida in the 1965 *Treatise,* the number of genera has almost tripled, but the approaches and taxonomic procedures adopted by workers describing rhynchonellide genera have changed little, principally because of the limitations imposed by the material. Additional faunas have been collected, and effort has been expended in preparing and illustrating what appear in most instances to be distinctive new taxa. Relatively few comparative taxonomic studies of rhynchonellides on a global scale have been attempted, perhaps because the pace of influx of new taxa has made such studies seem premature. The uneven morphological information made available, particularly with regard to the form of the crura and details of the shell microstructure, may explain why quantitative or cladistic approaches have been rare.

We have attempted to reduce the artificial separation of Paleozoic from Mesozoic and Cenozoic rhynchonellides in our taxonomic treatment, but it remains the case that few workers truly bridge the Paleozoic-Mesozoic boundary and the associated mass extinction and that there have been resultant terminological and other differences of approach.

GENERIC CHARACTERS OF RHYNCHONELLIDA

As noted above, the number of proposed genera within the Rhynchonellida has expanded rapidly during the past 35 years. Many of the new genera are from newly explored regions. Others reflect the precise discrimination of specialists who become expert in a few families from a relatively small part of the column. In discussing brachiopods in general, COOPER (1970) expressed his view that family characters are found mainly in the interior of the dorsal valve and generic characters on the exterior and in minor details of the interior of both valves but more particularly in the ventral valve. He commented that recent rhynchonellides illustrate the point clearly but that the cardinalia of older rhynchonellides were not sufficiently well known to support the principle. We shall attempt to assess these observations and to examine the relative significance of features used to characterize rhynchonellide genera. Other noteworthy surveys of rhynchonellide features are those of WESTBROEK (1968), whose study is largely confined to the Uncinulidae but with valuable observations on rhynchonellides in general; GRANT (1965a) on Devonian-Permian families; LAURIN (1984) on mid-Jurassic families; JIN (1989) on several Late Ordovician to early Silurian families; and SHI and GRANT (1993) on most Jurassic families.

EXTERNAL FEATURES

Size is significant in a general way. Such genera as *Dorytreta* and *Cryptopora* are always small; others, such as *Ladogia* and *Grandirhynchia,* are consistently large; and most others, such as *Pugnax* and *Tetrarhynchia,* are variable in size. A few extinct giants, like *Septirhynchia* and *Peregrinella,* rivaled in size the largest brachiopods in other orders. Thus size should not be dismissed from generic diagnoses although care should be taken to allow for the effect of environment, especially temperature and factors causing faunal stunting.

Shape is an important generic feature, notwithstanding the frequency of homeomorphs. The genera *Pleurocornu, Hypothyridina, Lessinirhynchia,* and many others have a sufficiently distinctive shape that initial diagnosis is unlikely to be reversed by investigation of interior features, although such investigation is always necessary. Outline is rarely diagnostic in itself, but elongation as in *Sphenotreta,* triangularity as in *Oligorhynchia* and *Sphenorhynchia,* circularity as in *Peregrinelloidea,* and transversity as in *Calvinaria* are meaningful diagnostic characters at the genus level. Outline does not, however, appear to be of much familial significance. Other common outline types include subpentagonal, subrhomboidal, securiform, and cordiform. Profile is not as variable or generically diagnostic in the rhynchonellides as in some other brachiopod orders. No genera are resupinate or geniculate in lateral profile, although the terms are often appropriate for describing parts of individual valves, as with the broadly sulcate ventral valve of *Paurorhyncha* and the opposed anterior geniculations of both valves of *Uncinulus.* Although lenticular equibiconvex profiles are common in juveniles, the characteristic lateral profile of rhynchonellides is dorsibiconvex, with varying amounts of dorsal valve inflation. The inflation can become extreme and distinctive, as in *Parapugnax* and *Gibbirhynchia,* but in its less extreme condition is too general to be diagnostically valuable at the genus level. Degree of curvature of the beaks is a profile feature and has been recorded for most genera, yet it usually increases with age and should be used with caution as a generic character. Strength of fold and sulcus in rhynchonellides is often sufficient to be part of the general shape, as with *Pugnax, Rhynchonella,* and *Ladogia.* Sometimes the strength, height, and depth of the fold and sulcus are maintained throughout the range of a genus, as exemplified in *Goniorhynchia* and *Rhactorhynchia.*

Further external features that have significance in generic diagnosis include commissure, ornament, presence of marginal spines, development of interareas (rare in Paleozoic rhynchonellides), nature of deltidial plates, and the condition of the foramen. The anterior commissure is of importance as it is variously folded to allow the flow of water into and from the shell. Most rhynchonellides have a strongly uniplicate anterior commissure, although a few genera, such as *Paranorella, Camarophorina,* and *Neorhynchia,* have unisulcate commissures. The latter condition, though rare, appears to be more likely to occur in smooth genera. Rhynchonellides usually have costae or stronger plicae superimposed on the fold and sulcus, resulting in a zigzag margin. The extent of the commissural deflection is often great enough to be termed a tongue or linguiform extension. This may be rectangular, as in *Uncinulus* and *Cirpa,* or more rounded, as in *Leiorhynchus* and *Aetheia.* These conditions of the anterior commissure may have generic diagnostic value when they depart from the norm but are otherwise almost routinely present in one of the states described above in any particular family. Although the shape and extent of the anterior commissure is largely determined by the type of fold and sulcus, this is by no means always so. The sulcus of a high-folded species may be shallow with extensive linguiform extension, which might be subquadrate to trapezoidal in general outline. The commissure itself might vary from straight to asymmetrical, as in *Cyclothyris,* or maintain the asymmetry, as in *Torquirhynchia.* In analyzing the posterior part of the lateral commissure one must designate specific features. Beyond the suppression point (Fig. 698.1) of the zigzag deflection (*sensu* RUDWICK, 1970), the commissure is commonly undeflected. A short but pronounced arc, however, sometimes occurs resulting from a semicircular extension of one valve over an underlapping embayment of the other. Paleozoic workers have called such structures squama and glotta (WESTBROEK, 1968). In the Paleozoic genera *Uncinulus* and its allies the arc is ventrally convex (Fig. 698.1), whereas in *Plectorhyncha* and *Trigonirhynchia* it is ventrally concave. In post-Paleozoic genera only the ventrally concave condition has been observed (MANCEÑIDO & OWEN, 1996). The stolidium is a thin, marginal extension of one or both valves that forms a frill protruding at an angle to the main commissural plane of the shell. It is common in genera of the Stenoscismatoidea and exemplified by *Stenoscisma.*

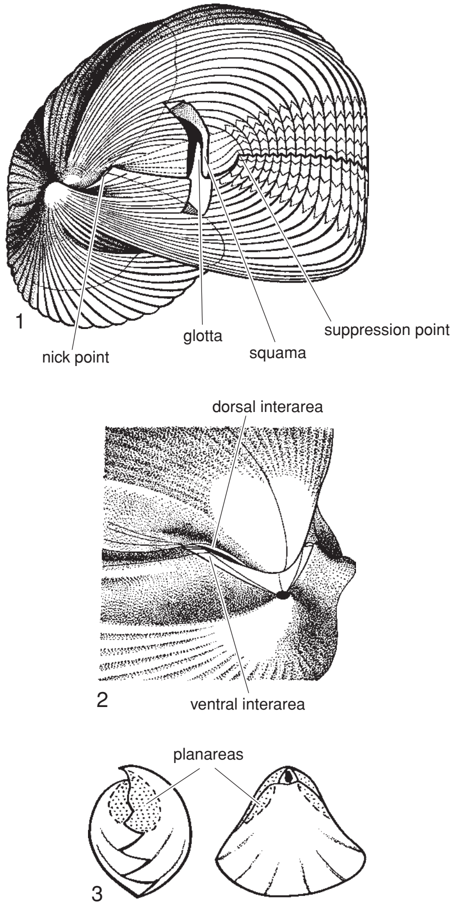

FIG. 698.*1,* Posterolateral view of *Uncinulus orbignyanus* showing lateral commissure; *2,* hinge of *Glossinotoechia* showing interareas (adapted from Westbroek, 1968); *3,* posterior morphology of rhynchonellide with well-developed planareas, based on *Lokutella* (new).

Radial ornament is present in the earliest known rhynchonellides. Smooth forms do not occur until later, becoming increasingly frequent but never prevalent. The details of ornament are usually of generic value, and the point at which changes occur during the growth of an individual can be diagnostic, such as the change from smooth initially to costate at midlength and then the development of a fold and flanking plicae more anteriorly. Such changes clearly relate to the aspect of the gape at the commissure during successive growth stages. The ratio of body size and water inflow requirement to commissure length increases disproportionately as growth proceeds. The possible need to restrict access to harmful predators or extraneous particles may have influenced the development of the zigzag margin and other flexures. Costae and plicae also increase shell strength. The various combinations of costae, fold and sulcus, and flanking plicae, occasionally with superimposed fine striae, are all of importance in diagnoses. The attention paid by many workers to angularity of costae may be misplaced except for genera where angularity or roundness is especially marked. Usually the angularity is variable within a genus and often within a species. Such genera as *Rhynchotrema* and *Flabellirhynchia* have simple costae continuous from beak to anterior and lateral margins; others such as *Fenestrirostra* and *Sedenticellula* have costae that increase by bifurcation and intercalation, with a tendency toward infrageneric and infraspecific variation. A few genera have distinctive radial striae superimposed on coarser costae, as in *Yunnanella, Porostictia,* and *Paraphorhynchus.* Others have fine costae that merge anteriorly to form coarse costae or plicae (antidichotomous ribbing), as in *Schnurella* and *Nayunnella.* Although superimposed striae are distinctive at the genus level, it may be debated whether they have arisen only once and justify the inclusion of these disparate genera in a single family. *Porostictia* is particularly unusual among rhynchonellides in having the fine radial striae separated by rows of fine pits or exopunctae. Some genera develop short spines that tend to follow the radial ornament, although they are truly extensions of the lamellae.

Concentric ornament in rhynchonellides consists of fine growth lines and lamellae and has limited diagnostic value. In a few genera, such as *Lepidocyclus,* the concentric growth features are strongly lamellose and may have taxonomic significance, although whether at the subfamily level, as has been used for the Lepidocyclinae, may be questioned. *Protegulorhynchia* and *Tegulorhynchia* have spinelike extensions of the lamellae. Some specimens of *Acanthothiris* have radial spines of this kind that are several centimeters long.

Marginal spines have been discussed in detail by WESTBROEK (1968) and RUDWICK (1970). These spines grew as an enrollment of shelly extensions from the margin and commonly display a suture along their commissural side. They are elongate in representatives of the Uncinulidae, where genera frequently have geniculate dorsal and ventral anterior and lateral valve margins, so that the spines are vertically disposed and fit into notches or grooves in the opposing valve. In *Kransia* the valve margins are straight, but the spines are long and fit into appropriate grooves on the inside of the opposite valve to form a grille that probably restricted access to intruders or extraneous particles, although WESTBROEK (1968) contended that they should be viewed more as a sensory warning system rather than a physical barrier to access. One might reason that they served both functions, initially resulting in the closing of the valves, but eventually permitting sufficient gape for some feeding and respiration. In *Uncinulus* the valve margins are moderately serrated and the spines less elongate but in combination form an effective grille that presumably performed the same service as in *Kransia.* Shorter spines that occur in the genera *Glossinulus* and *Eoglossinulus* arise at the tips of more strongly serrated valve margins, and even shorter spines in *Sphaerirhynchia* arise from the tips of zigzag valve margins and fit into grooves on the inside of the opposite valve.

The rostrate and astrophic nature of most rhynchonellides means that interareas are often absent. The narrow hinge and incurved nature of the dorsal beak into the ventral delthyrium obscures the interareas even in those genera where they are developed (Fig. 698.2). Interareas have been described in a few thin forms where the umbones are not pronounced, generally from such early Paleozoic genera as *Drepanorhyncha* and *Oligorhynchia.* Mesozoic and Cenozoic genera more commonly have marked interareas that are of diagnostic value. These include *Cardinirhynchia* and *Flabellirhynchia* from the Jurassic and *Cyclothyris* from the Cretaceous. A number of Paleozoic and Mesozoic genera, including all Rhynchotetradoidea and Septirhynchiidae, have flat to concave planareas on either side of the posterior part of one or both valves (Fig. 698.3).

The delthyrium and deltidial plates are of uncertain taxonomic value. Many early rhynchonellides, such as *Ancistrorhyncha, Drepanorhyncha,* and *Orthorhynchula,* have an open delthyrium or very narrow marginal thickening that leaves the delthyrium of the ventral valve essentially open. Others, such as *Fenestrirostra,* have narrow elongate deltidial plates that do not meet. Most rhynchonellides, however, have well-developed deltidial plates. Although these are used commonly in generic diagnoses, some variation may occur even within a population of a single species. Conditions include disjunct, as in *Cupularostrum* and *Hemithiris,* conjunct, as in *Hypsiptycha* and *Basiliola,* and duplex, as in *Rhynchotrema* and *Cirpa* (see Cooper, 1970, pl. 2, fig. 12, 15, 17–19). A rounded foramen to accommodate the pedicle is usually present posteriorly near the apex of the valve so that even when the deltidial plates are conjunct they often lack their apical tips, as in *Hypsiptycha.* Occasionally the deltidial plates are alate, as in *Grammetaria* and *Ptilotorhynchus,* but this condition may not be a generic character, sometimes varying within a genus from extreme, as in *Cryptopora rectimarginata* Cooper, to barely evident, as in *Cryptopora gnomon* (Jeffreys). The position of the foramen relative to the apex of the delthyrium has often been used as a generic character when it departs significantly from the usual submesothyrid condition, as in *Neorhynchia,* which has a hypothyrid foramen. Other types of foramen position, such as epithyrid and permesothyrid, and other types of delthyrial covers, such as a notodeltidium or a pseudodeltidium, do not seem to occur in rhynchonellides.

INTERNAL FEATURES

Internal features in the ventral valve variously used in generic diagnosis of rhynchonellides include details of the dental plates and associated lateral umbonal chambers, teeth, and platforms (Fig. 699.1b). Those in the dorsal valve include the details of the hinge plates, cardinal process, median septum, and crura (Fig. 699.1a).

Immediately inside the foramen a pedicle collar may be present, but this is of doubtful value as a taxonomic feature, despite the weight accorded it for younger genera by some workers. Muscle scars are inadequately known for most genera and often have not been included in our diagnoses. This is because they are indistinct in serial sections except in such families as the Leiorhynchidae, where the muscle attachment areas are deeply impressed. When internal features are readily visible, as in molds, calcined, or silicified shells, the muscle scars may have considerable generic and familial value. In the ventral valve the adductor scars are commonly small and enclosed by the diductor scars, which are long and lacriform. In the dorsal valve the adductor scars usually form a quadrate pattern mostly confined to the posterior half of the valve, with the posterior adductors slightly smaller than the anterior adductors. The details of the arrangement are of generic importance, but the variable information about most genera hinders comparison.

Dental plates are present in most rhynchonellides and vary enough to have been used widely in generic diagnosis. They are reasonably constant within a genus and are easily observed except where they are very close to the shell wall or where the associated

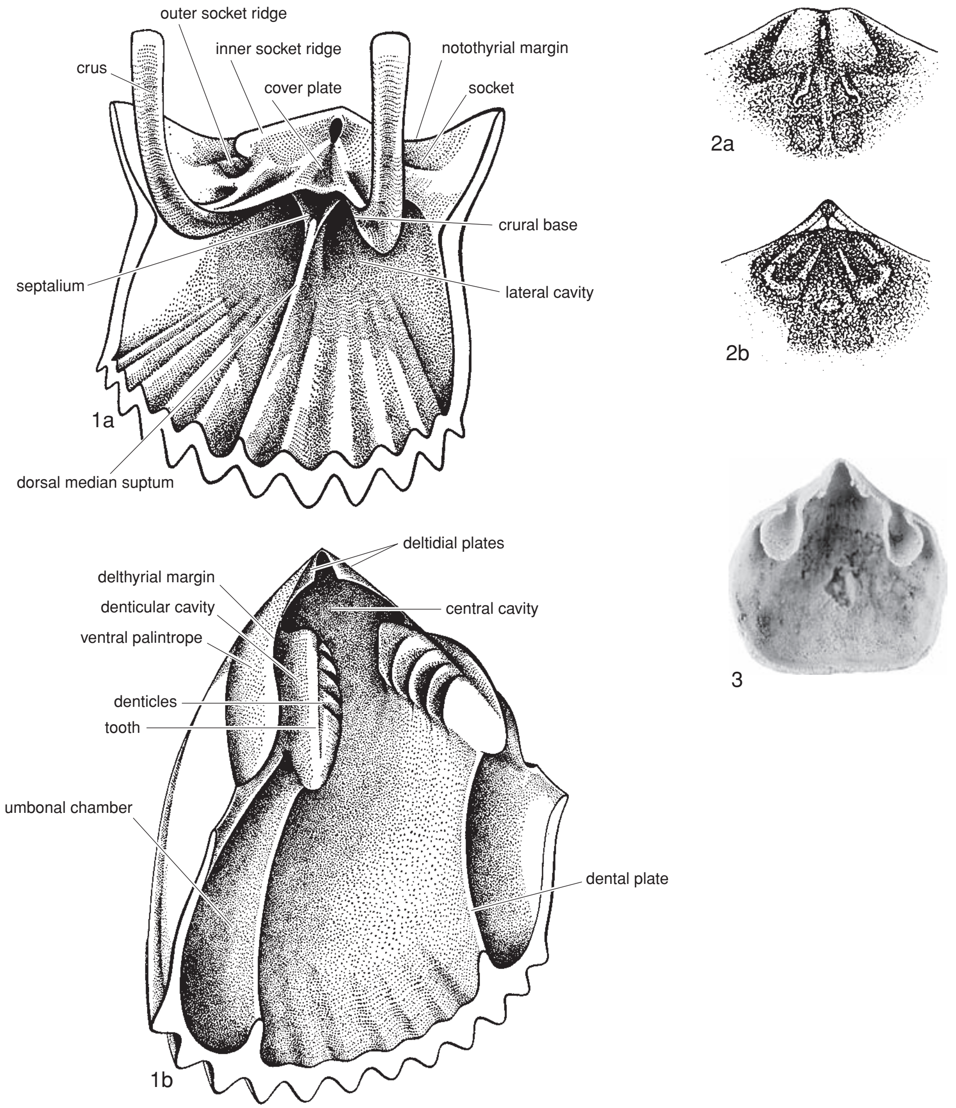

FIG. 699.*1,* Internal morphology of posterior of *Trigonirhynchia pareti, a,* dorsal valve, *b,* ventral valve (adapted from Westbroek, 1968)*; 2,* internal morphology of posterior of *Australirhynchia,* showing *a,* inflated inner socket ridges in dorsal valve, and *b,* long, deeply grooved teeth in ventral valve (adapted from Savage, 1968); *3,* internal morphology of ventral valve of *Amphipella,* showing pouchlike apricatria (Cooper & Grant, 1976).

lateral umbonal cavities are filled with callus, as in *Uncinulus,* or where the plates are short and only clearly present in younger individuals, as in *Ellesmerhynchia.* The dental plates may be vertical, as in *Petasmaria;* medially convex, as in *Ladogia;* medially concave, as in *Stegorhynchella;* divergent toward the valve floor, as in *Trigonirhynchia;* convergent toward the floor, as in *Prionorhynchia;* convergent to form a spondylium, as in *Rhynchotetra;* or may otherwise display a consistently distinctive form that may be useful in generic and even familial diagnosis. Associated with the dental plates are the lateral umbonal cavities between the plates and the valve wall. The shape and size of the cavities are dependent on the configuration of the plates relative to the contours of the shell wall. The various shapes of the cavities have not been used much in generic diagnosis, and the feature is probably too dependent on infraspecific variation, age of individuals, and degree of callus infilling to be of much value.

Teeth of rhynchonellides are sometimes elongate and transversely corrugated in heavy, thick-shelled genera with sturdy dental plates, as in *Trigonirhynchia* (Fig. 699.1b), or may be small and smooth in genera with short dental plates or more delicate shells, as in *Orthorhynchula.* Crenulated teeth are sometimes present in thin-shelled genera, such as *Basiliola* and *Neorhynchia.* A fossette may be developed on the inner side of the tooth where it presses against the inner socket ridge (Fig. 699.2b). This may add to the rigidity of the articulation, and in extreme cases the fit of the inner socket ridges into the fossettes may become as important in holding the valves together as the fit of the teeth into the sockets. The shape of teeth can vary from a simple deltidiodont condition to a more hooked condition that may help lock the valves together. In general the shape and surface of the teeth have not been given much taxonomic significance by workers, perhaps because they are difficult to describe from sections or because they vary with shell thickness and other age factors.

Muscle platforms are unusual yet of considerable value in generic and familial diagnoses. They help characterize the Stenoscismatoidea, which have a camarophorium in the dorsal valve and usually a spondylium in the ventral valve, and a few other Paleozoic groups, such as the Camerophorinidae, which have a spondylium, and the Tetracameridae and Rhynchotetradidae, which have a low or sometimes sessile spondylium.

The hinge plates form an important part of the rhynchonellide dorsal valve and include all the cardinalia except for the cardinal process, thus comprising the sockets and socket ridges, the outer and inner hinge plates, the crural bases and, if present, the crural plates and septalium (Fig. 699.1a). The hinge plates as a whole perform two important unrelated functions in rhynchonellides: they provide support for the sockets and provide attachments for the crura. The outermost parts of the hinge plates are connected to the valve walls and are often coincident with the outer socket ridges. Medially from the outer socket ridges lie the sockets and the inner socket ridges. The outer hinge plates then extend medially from the inner socket ridges to the crural bases, and the inner hinge plates or sometimes the crural plates extend medially from the crural bases. The term inner hinge plates is used for plates that are horizontal or subhorizontal, as in *Glossinotoechia* and *Frieleia.* If the plates medial of the crural bases are inclined to meet the valve floor or form a V-shaped septalium supported by a median septum that joins the valve floor, they are generally termed crural plates. Often the crural bases can be seen as discrete structures, distinct from the outer hinge plates laterally and the inner hinge plates or crural plates medially. Occasionally, as in *Trigonirhynchia,* a cover plate caps the septalium for part or all its length. This terminology differs from that of Westbroek (1968) and Johnson and Westbroek (1971), who considered the cover plate over a septalium to be formed by the inner hinge plates. Williams and Rowell (1965a) considered that in some rhynchonellides the inner hinge plates and the septalial (crural) plates are two distinct sets of plates that lie successively medial of the crural bases. Jin (1989) defined a septalium as a trough-shaped chamber encompassed by a pair of hinge plates, crural bases, and septalial plates and did not limit the composition of the septalium to any specific pair of these plates. If these features occurred only in rhynchonellides, had a distinctive microstructure, or developed at very different growth periods in individuals, the terminological discrepancies described above would be easier to settle. Hinge plates, however, are present in several different orders, and the component features are variously developed in these orders. The component features are also variously developed within the rhynchonellides so that more terms are needed to describe the relatively complex hinge plate of *Trigonirhynchia,* with its outer hinge plates, crural bases, septalium, and cover plate (Fig. 699.1a), than that of *Australirhynchia* SAVAGE (1968), where the swollen inner socket ridges almost meet and the crura appear to arise directly from these ridges (Fig. 699.2a). These various structures and their numerous combinations have been assigned great importance by most workers in their generic diagnoses of rhynchonellides.

Outer socket ridges may have considerable taxonomic utility. Those genera that have a relatively wide ventral valve at the hinge line, such as *Glossinulus* and *Eucharitina,* usually have the teeth directed inwardly so that the outer socket ridge may be low. In those with a comparatively narrow ventral valve at the hinge line, such as *Stegerhynchus* and *Lepidocyclus,* outer socket ridges tend to be much larger. The socket floor may be smooth, as in *Glossinulus,* or crenulate, as in *Trigonirhynchia,* and this is used as a generic characteristic where it has been recognized. The length and orientation of the sockets is often dependent on whether the shell is strophic, in which case the sockets are usually short, relatively transverse, and parallel to the hinge line, as in *Sphaerirhynchia,* or astrophic, which is normal in rhynchonellides and causes the teeth and sockets to be more anteriorly directed and relatively locked in position. As these structures really do not articulate to any significant extent, they can become quite elongate, as in *Australirhynchia,* where the sockets are smooth, and in *Trigonirhynchia,* where the sockets are crenulate. Inner socket ridges vary greatly in size and may be small in more strophic shells, such as *Porostictia,* or very large in astrophic shells such as *Australirhynchia,* particularly when these are mature or gerontic specimens (Fig. 699.2a). Medially from the inner socket ridges there is not much outer hinge plate present in many of the earlier rhynchonellides, such as *Rhynchotrema,* but by about Middle Devonian time hinge plates were often broader and more complex so that in *Uncinulus, Parapugnax,* and *Porostictia* there are distinct horizontal outer hinge plates between the inner socket ridges and the crural bases. The width, inclination, and outline of these have been afforded considerable generic importance by rhynchonellide workers.

Crural bases are usually distinct in the shell interior and in serial sections so that they form a valuable reference point in describing the hinge plates. Individually they form a rodlike or bladelike dense structure along the medial edge of the outer hinge plate. Their distal extensions are generically distinctive and will be discussed below under the section on crura. Inward from the crural bases the hinge plates are often divided, as in *Orthorhynchula* and *Callipleura,* and the outer hinge plates and crural bases may then be supported by crural plates that can extend down to the valve floor, as in *Callipleura* and *Septocrurella.* Alternatively, the crural plates may unite to form a septalium supported by a median septum, with a cover plate, as in *Trigonirhynchia,* or without a cover plate, as in *Hebetoechia* and *Piarorhynchia.* In addition, the subhorizontal inner hinge plates may be divided, as in *Hispanirhynchia,* or variably united, as in *Frieleia* and *Aetheia.*

Repeatedly referred to above, the septalium is a feature deserving special attention because, since its proposal by LEIDHOLD (1921), it has been sometimes misused or variously given other names. Essentially the same structure is also named in Mesozoic specimens a muscle trough by PEARSON (1977) and in Paleozoic specimens a crural cavity by WELLER (1910) and a cruralium by COOPER (1970). Even the noncommittally named apical V-shaped chamber of COOPER (1959), used for some Cenozoic forms, was subsequently regarded as a septalium by DAGYS (1968). When it occurs, it is a V-shaped or U-shaped structure, restricted in length to the vicinity of the hinge line, and apparently functioning to spread the support from the median septum to the outer hinge plates and thus buttress the sockets (Fig. 699.1a). As employed herein the usage of the term is consistent with CHILDS (1969), JOHNSON and WESTBROEK (1971), DELANCE and LAURIN (1973), JIN (1989), and BRUNTON, ALVAREZ, and MACKINNON (1996). Genera without such a structure usually have alternative support for the sockets, as with the crural plates of *Callipleura* and *Machaeraria* or the separate oblique septal buttresses directly attached to the valve floor, as in *Crurirhynchia.* The sockets may rest directly on the valve floor or wall, as in *Lepidorhynchia* and *Sulcatina,* or be supported by thick shell material below the hinge plate, as in *Pegmarhynchia.* Thus in one way or another the pressure that the teeth exert on the sockets is spread, and the whole rigid articulation structure that characterizes the rhynchonellides is strengthened. Usually a genus is characterized by a single one of these structures, but JIN (1989) has shown that in *Fenestrirostra* several different structures evolved in successive early Llandoverian species on Anticosti Island, commencing with thick shell material below the hinge plate in *Fenestrirostra primaeva,* followed by a fairly typical septalium supported on a median septum in *Fenestrirostra glacialis* and then by hinge plates supported by oblique buttresses from the valve walls in *Fenestrirostra pyrrha.* In each of the species there is some development of a septalium posteriorly, but its importance as a support at the point of articulation differs considerably. If this lineage is a guide, giving too much generic significance to the size of the septalium seems unwise. SHI and GRANT (1993) suggested that in both the ontogeny and phylogeny of some evolutionary lineages the septalium may be a structure that became gradually obsolete.

The dorsal median septum is part of the buttressing structure for the articulation, and, as with the plates of the septalium that it commonly supports, it is variably developed and not always a reliable family character. Some median septa appear not to be supportive of any cardinal structure but seem merely to divide the lophophore or muscles. In many families, such as the Ancistrorhynchidae, Allorhynchidae, Petasmatheridae, Amphipellidae, Pontisiidae, and Basiliolidae, a dorsal median septum is rare or absent, usually because the sockets are small and supported by the valve walls. In other families, such as the Uncinulidae, the presence of a median septum is variable, but usually the hinge plates are close to the valve floor and often supported by crural plates or callus. In families where the median septum is present, as in the Rhynchonellidae, Rhynchotetradidae, and Tetrarhynchiidae, the details of its size and other features are useful generic characters. Much rarer is the development of a ventral median septum, usually supporting a spondylium, as in *Camerophorina, Nantanella,* and all Stenoscismatoidea, or exceptionally free, as in *Septirhynchia.*

A cardinal process increased the area of diductor muscle attachment or otherwise made the attachment more secure, varying with the plan of the particular taxon and its stage of growth. It also allowed the diductor attachment surface to protrude into the ventral valve to permit specific valve articulation relationships and muscle arrangements as discussed by RUDWICK (1970) and CARLSON (1989). A cardinal process is more frequent in Paleozoic genera than in post-Paleozoic genera, although absent from such earlier rhynchonellide families as the Ancistrorhynchidae, Oligorhynchiidae, Trigonirhynchiidae, and Leiorhynchidae. In families where it occurs it is variable but usually regarded as having generic significance. In the Rhynchotrematidae the cardinal process is normally septiform, as in *Rhynchotrema.* This seems to be a primitive condition. In the Orthorhynchulidae a cardinal process is generally present, but in this family the shape varies from septiform, as in *Zlichorhynchus,* to branched, as in *Orthorhynchyllion.* In the Uncinulidae several genera have a tonguelike cardinal process that protrudes well into the ventral valve, as in *Glossinulus* and *Markitoechia;* but others have a broader multilobed process, as in *Glossinotoechia,* or a bulbous process, as in *Uncinulus.* In the Eatoniidae the cardinal process is bilobate, trilobate, or quadrilobate; and in *Eatonia* and *Eucharitina* it is massive, bilobed, and deeply excavated, forming a structure that occupies much of the hinge plate. Thus, although the cardinal process is not developed at all in several families, it can be complex and have considerable familial and generic diagnostic value when it is present.

The crura of living rhynchonellide genera are paired processes extending from the hinge plates and associated with the proximal ends of the soft lophophore spires. The crural bases enclose an angle within which the food particles are directed from the food grooves of the lophophore and into the mouth. The crura of fossil rhynchonellides are varied, and although several crural types have been recognized, those of most genera are poorly known. This is partly because of difficulty finding delicately preserved specimens that can be sectioned to the distal tips of the crura (SAVAGE, 1996). The lack of knowledge is unfortunate since details of the crura appear to be of considerable taxonomic value. AGER (1965) considered the three most common types of rhynchonellide crura to be those described by ROTHPLETZ (1886) as raduliform, falciform, and septiform. A further 14 types that have been listed or proposed by later workers are discussed and illustrated herein. 1. Arcuiform crura (Fig. 700.1) were first described by WISNIEWSKA (1932, p. 6) based on the genus *Monticlarella.* Later discussion and illustrations of AGER (1965, p. 599, fig. 478,*4*), SMIRNOVA (1965), and DAGYS (1968, 1974) show that these crura are widely divergent. Each is short and laterally compressed with its distal end flared dorsoventrally. 2. Spinuliform crura (Fig. 700.2) were described by COOPER (1959, p. 9) and also discussed and illustrated by AGER (1965, p. 600, fig. 478,*7*) and DAGYS (1968, 1974). These crura are also widely divergent. Each is short, narrow, and relatively straight although inclined slightly toward the ventral valve. AGER stated that these could be viewed as laterally compressed variants of the radulifer type with ancestors back in early rhynchonellide stock. 3. Flared arcuiform crura (Fig. 700.3) as in *Tethyrhynchia.* These were called lunifer in LOGAN and ZIBROWIUS, 1994. Each has its distal end extremely flared dorsoventrally. 4. Falciform crura (Fig. 700.4) were first described by ROTHPLETZ (1886, p. 86). The type has been further discussed and illustrated by COOPER (1959), AGER (1965, p. 598, fig. 478,*2*), and DAGYS (1968, p. 34, fig. 27b, 28b). These crura arise on the dorsal side of the hinge plates and project more into the dorsal than the ventral valve. The broad subvertical blades are sickle shaped or sigmoidal in section. Falciform crura are associated with divided hinge plates and a reduced median septum. They have been recorded mostly in Mesozoic and Cenozoic genera. 5. Subfalciform crura (Fig. 700.5) resemble falciform crura but have a crescentic (instead of falcoid) cross section and may be serrated distally, as in *Acanthobasiliola.* 6. Hamiform (=prefalciform) crura (Fig. 700.6) of PEARSON (1977), replacing the term prefalcifer of AGER (1962). Each is short, straight, and slightly compressed, as in *Pseudogibbirhynchia.* 7. Septiform crura (Fig. 701.1) were first described by ROTHPLETZ (1886, p. 86) and further discussed and illustrated by AGER (1965, p. 598, fig. 478,*3*). There is some discrepancy of interpretation, which was emphasized by DAGYS (1968, p. 37). Septiform crura are subparallel. Each is wide proximally with its inner edge descending to meet the valve floor, as in *Septocrurella.* 8. Lyrate septiform crura (Fig. 701.2) are septiform crura that are more divergent and have a lyrate cross section distally, as in *Pygmaella.* 9. Raduliform crura (Fig. 701.3) were first described by ROTHPLETZ (1886, p. 86) and further discussed by COOPER (1959), AGER (1965), and DAGYS (1968). These crura are common and simple. They are relatively long, rodlike projections that curve uniformly forward into the ventral valve and may show considerable variation in cross section (subtriangular, compressed, squarish, elliptical) and in distal ends (barbed, hooked). They are generally accompanied by a more or less well-developed dorsal median septum. They are interpreted here to include the hamuliform type of JIN (1989) that has small, incurved distal hooks on the crura. Raduliform crura are commonly

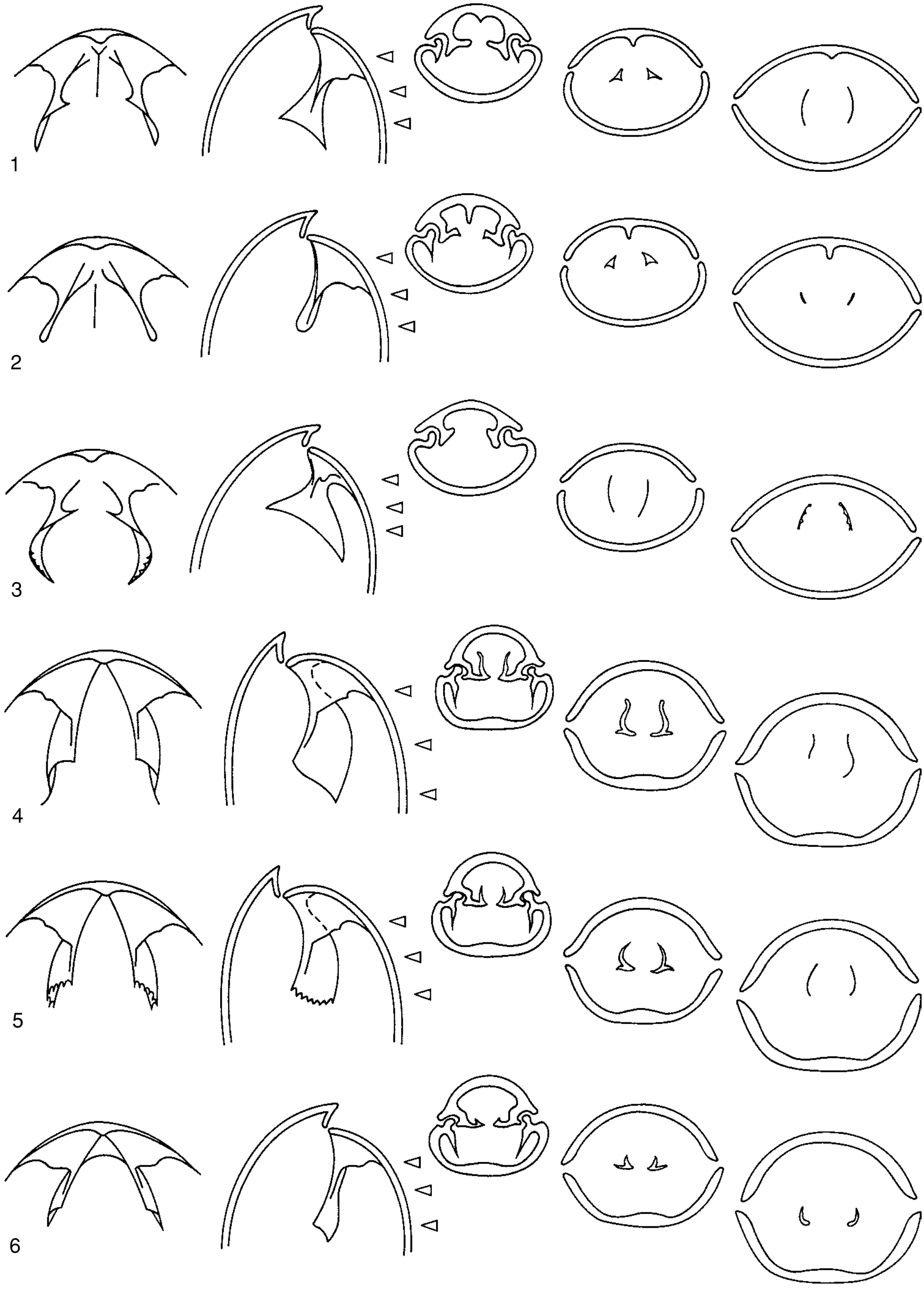

FIG. 700. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; *1,* arcuiform crura, based on *Monticlarella; 2,* spinuliform crura, based on *Frieleia; 3,* flared arcuiform crura, based on *Tethyrhynchia; 4,* falciform crura, based on *Lacunosella; 5,* subfalciform crura, based on *Acanthobasiliola; 6,* hamiform (=prefalciform) crura, based on *Pseudogibbirhynchia* (new).

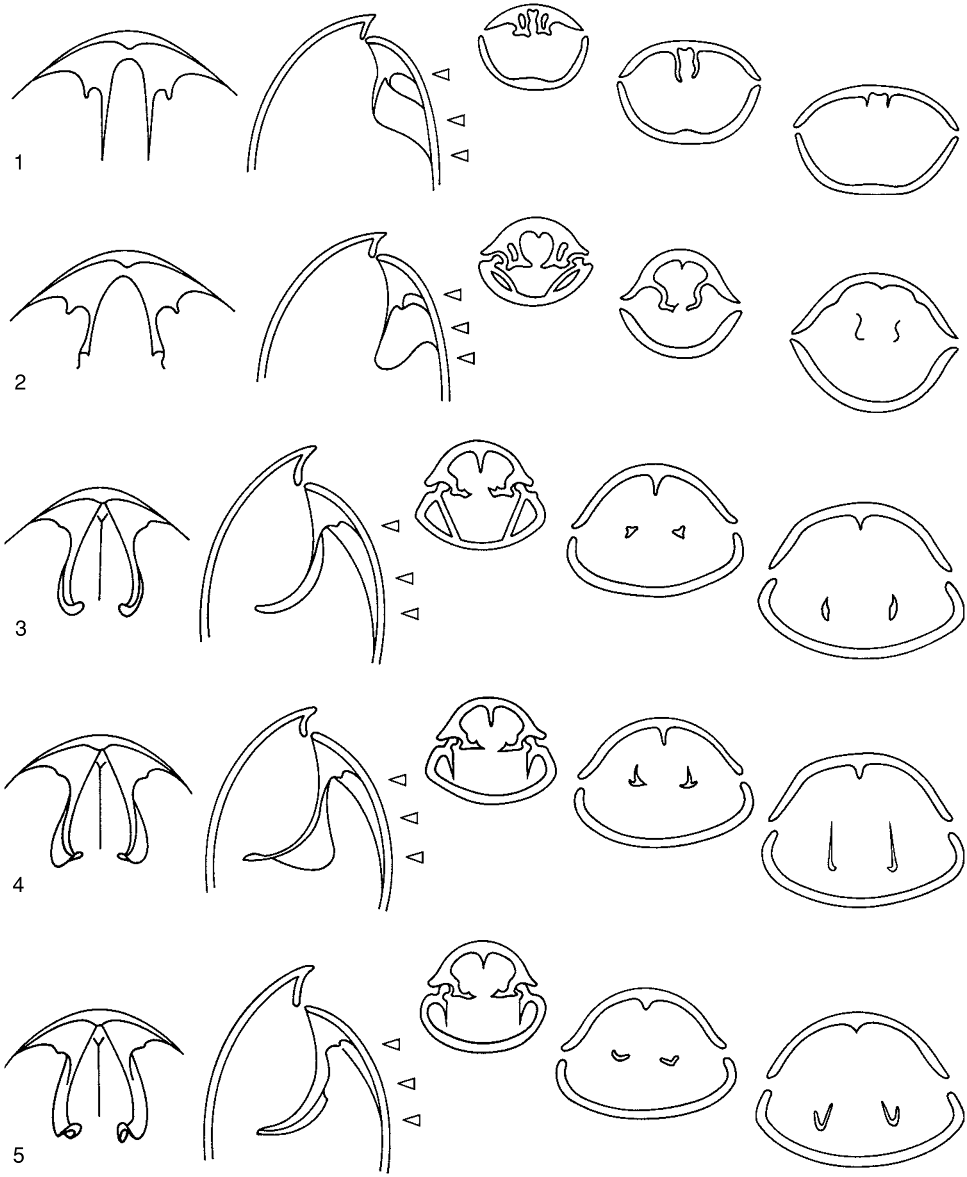

FIG. 701. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; *1,* septiform crura, based on *Septocrurella; 2,* lyrate septiform crura, based on *Pygmaella; 3,* raduliform crura, based on *Rhynchonella; 4,* calcariform crura, based on *Rhynchonelloidella; 5,* canaliform crura, based on *Cyclothyris* (new).

FIG. 702. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; *1,* mergiform crura, based on *Peregrinella; 2,* submergiform (=terebratuliform) crura, based on *Peregrinelloidea; 3,* ensiform crura, based on *Rhynchonellina; 4,* maniculiform crura, based on *Cryptopora; 5,* ciliform crura, based on *Halorella; 6,* clivuliform crura, based on *Ochotorhynchia* (new).

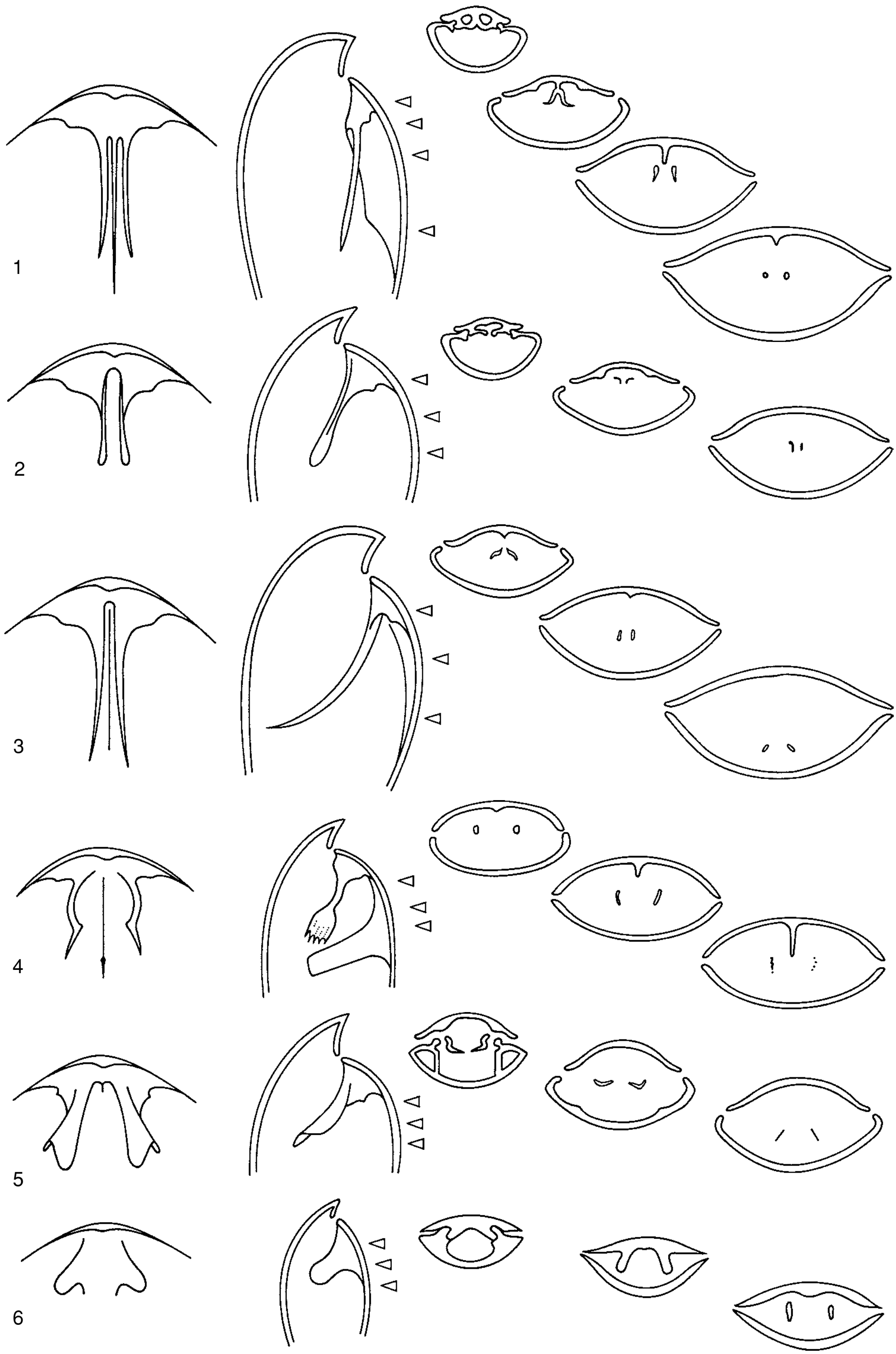

FIG. 702. *For explanation, see facing page.*

considered the basic type from which others evolved. 10. Calcariform crura (Fig. 701.4) were named by MUIR-WOOD (1934, p. 525) based on crura in the genus *Kallirhynchia.* Later she believed the same type of crura were exemplified in the genus *Rhynchonelloidella.* Modern authors have agreed that these crura are well exemplified in species of *Rhynchonelloidella* and *Thurmannella* (CHILDS, 1969, p. 18; LAURIN, 1984, p. 76). Calcariform crura are initially horizontal but twist to the vertical plane and become directed ventrally. The distal tips are variable. 11. Canaliform crura (Fig. 701.5) were described by AGER (1965, p. 600) but were not illustrated by him or by DAGYS, who discussed the type briefly (1968, p. 34). These are a variation of raduliform crura that are strongly concave dorsally and are characteristic of the Cyclothyridinae. 12. Mergiform crura (Fig. 702.1) were described by AGER (1965, p. 600), based on *Peregrinella.* They are long, very close together, parallel, and arise from the thickened upper edge of a high median septum. DAGYS (1968, p. 39, fig. 31b, 32a) commented that they differ significantly from the raduliform type in being relatively straight and not curved ventrally. 13. Submergiform (=terebratuliform) crura (Fig. 702.2) were described and illustrated by DAGYS (1968, p. 39, fig. 31a, 32b) based on the crura in *Peregrinelloidea.* These subparallel crura are short, narrow, and laterally compressed. They arise from the ventral surface of the hinge plates. Unlike the mergiform crura, they are not associated with a median septum. 14. Ensiform crura (Fig. 702.3) are subparallel, laterally compressed, long, ventrally curved, saberlike blades. 15. Maniculiform crura (Fig. 702.4) were described by COOPER (1959, p. 9) and further discussed and illustrated by AGER (1965, p. 600, fig. 478,*6*) and DAGYS (1968, p. 39). In these crura the distal extremities are flattened vertically and bear grooves that suggest small fingers on a hand, as in *Cryptopora.* 16. Ciliform crura (Fig. 702.5) were described by AGER (1965, p. 600, fig. 480), based on genera of the Halorellinae and further discussed and illustrated by DAGYS (1968, p. 35, fig. 28b, 30i) based on the genus *Halorella.* These crura are proximally flattened in the horizontal plane but distally have their outer edges geniculated vertically. 17. Clivuliform crura (Fig. 702.6) were described and illustrated by DAGYS (1968, p. 40, fig. 31b) based on *Ochotorhynchia.* These crura are massive, fused with the inner socket ridges, strongly divergent, and extend almost to the floor of the ventral valve.

This list of crural types is strongly slanted toward post-Paleozoic crura, mostly because of lack of work on Paleozoic genera, as discussed above. This was also true when the 1965 *Treatise* (MOORE, 1965) was published. Many of the Paleozoic genera have crura that have been classified by their describers as raduliform. This term is probably appropriate in its general sense, but several modifications of raduliform crura probably evolved during Silurian and Devonian times. Further work should lead to the recognition of additional types of Paleozoic crura that may have taxonomic value.

Pouchlike structures were developed in the posterior region of some groups. These are symmetrical cavities close to the hinge line with participation of both valves or entirely within the ventral valve. Paleozoic examples include the conspicuous apricatrium of Permian Amphipellidae (Fig. 699.3) and the parathyridium of Carboniferous Lambdarinidae. In the Mesozoic, striking bubblelike ventral pouches occur in the Bilaminellinae, and elongate, pouchlike gutters occur along the cardinal margins in Cardinirhynchiinae.

Endopunctuation in rhynchonellides is extremely rare, and the few Paleozoic genera that have this feature do not appear to be closely related, though they are provisionally maintained here in the superfamily Rhynchoporoidea. The nature and significance of endopunctae in such rhynchonellides as *Rhynchopora* and *Tretorhynchia* require additional investigation. The poorly known genus *Rariella* is regarded as a *nomen dubium* awaiting further material and information.

ANCISTRORHYNCHOIDEA

NORMAN M. SAVAGE
[University of Oregon]

Superfamily ANCISTRORHYNCHOIDEA Cooper, 1956

[*nom. transl.* SAVAGE, 1996, p. 251, *ex* Ancistrorhynchinae COOPER, 1956a, p. 618]

Rhynchonellida with subcircular, transverse, or elongate outline; dorsal fold usual but occasionally dorsal sulcus present; ventral interarea low; delthyrium open or with small deltidial plates anteriorly; costae fine to coarse, extending from beaks. Dental plates usually well developed but occasionally absent. Hinge plates divided; dorsal median septum and cardinal process usually absent; crura long, raduliform. *Lower Ordovician (Llanvirn)–Lower Devonian (Pragian).*

Family ANCISTRORHYNCHIDAE Cooper, 1956

[*nom. transl.* SCHMIDT, 1965b, p. 553, *ex* Ancistrorhynchinae COOPER, 1956a, p. 618]

Ancistrorhynchoidea with subcircular outline; dorsal fold and ventral sulcus; costae fine to medium; delthyrium open. Dental plates usually short. Hinge plates divided; dorsal median septum and cardinal process absent. *Lower Ordovician (Llanvirn)–Lower Devonian (Pragian).*

Ancistrorhyncha ULRICH & COOPER, 1942, p. 624 [**A. costata;* OD]. Shell small with subcircular outline and subequibiconvex, lenticular profile. Small ventral interarea; ventral beak erect; delthyrium open. Fold and sulcus weak; anterior commissure uniplicate, rounded. Costae fine and numerous, simple, arising at beaks. Dental plates short, strong; ventral muscle impressions weak. Hinge plates divided; sockets deep, partly overhung by inner socket ridges; crura long, curved anteroventrally. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* North America, Baltic, Kazakhstan, central Asia, eastern Siberia, China.——FIG. 703,*1a–j*. **A. costata,* lower Caradoc, Bromide Formation, Oklahoma, USA; *a–e,* hypotype, dorsal, ventral, lateral, anterior, and posterior views, ×2 (Cooper, 1956a); *f–j,* serial sections, ×6 (Schmidt, 1965b).

Drepanorhyncha COOPER, 1956a, p. 627 [**Porambonites ottawaensis* BILLINGS, 1862, p. 140; OD]. Shell small with elongate subtriangular outline and subequibiconvex profile; anterior and lateral margins not steep; interareas narrow; delthyrium open; ventral beak erect. Fold and sulcus weak, narrow, arising at midlength; anterior commissure weakly uniplicate, serrate. Costae few but strong, rounded, arising at umbones. Dental plates long and closely set, slightly convergent ventrally; teeth large; ventral musculature indistinct. Hinge plates concave, divided; crural bases arising from underside of notothyrial cavity; crura very long and slender. *Lower Ordovician (middle Llanvirn)–Upper Ordovician (upper Caradoc):* North America, Europe, Kirghizia, central Asia.——FIG. 703,*2a–g*. **D. ottawaensis* (BILLINGS), Caradoc, Rocklandian, Rockland Formation, Paquette Rapids, Ontario, Canada; *a–c,* lectotype, dorsal, ventral, anterior views; *d,* hypotype, lateral view, ×1; *e,* dorsal valve interior, ×3; *f,* ventral valve interior; *g,* longitudinal section showing crura, ×2 (Cooper, 1956a).

Kholbotchonia BARANOV, 1988, p. 40 [**Machaeraria pygmaea* ALEKSEEVA, 1967, p. 34; OD]. Small with subcircular outline and subequibiconvex profile; anterior and lateral margins not steep; ventral beak suberect; delthyrium open. Fold and sulcus moderately well developed, arising at umbones; anterior commissure uniplicate, serrate. Costae medium strength, simple, rounded in section. Dental plates short, thin, divergent ventrally. Hinge plates divided; crura bases subtriangular; crura strongly curved ventrally. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 703,*3a–i*. **K. pygmaea* (ALEKSEEVA), Sette-Daban subformation, Sette-Daban Range; *a–c,* hypotype, dorsal, anterior, and lateral views, ×5; *d–i,* serial sections 1.5, 1.7, 1.9, 2.1, 2.4, 2.8 mm from posterior margin, ×6 (Baranov, 1988).

Nikolaevirhynchus BARANOV, 1988, p. 38 [**N. boldymbensis;* OD]. Small with transversely subcircular outline and subequibiconvex profile; anterior and lateral margins acute. Ventral beak short, suberect; delthyrium open. Fold and sulcus weak; anterior commissure broad, rounded, uniplicate. Costae medium strength, simple, rounded, arising at beaks. Dental plates thick, vertical. Hinge plates divided, thick, subhorizontal; crura stout, ventrally curved. *middle Silurian (Wenlock):* eastern Siberia.——FIG. 704,*1a–j*. **N. boldymbensis,* Ryabina Formation, Tas-Khayakhtakh Range; *a–d,* holotype, dorsal, ventral, anterior, lateral views, ×5; *e–j,* serial sections, ×6 (Baranov, 1988).

Obscurella BARANOV, 1991, p. 36 [**O. costata*; OD]. Small with subcircular outline and dorsibiconvex profile; lateral and anterior margins steep; ventral beak straight to suberect. Fold and sulcus distinct, arising at umbones; anterior commissure uniplicate, serrate; tongue high, trapezoid. Costae medium

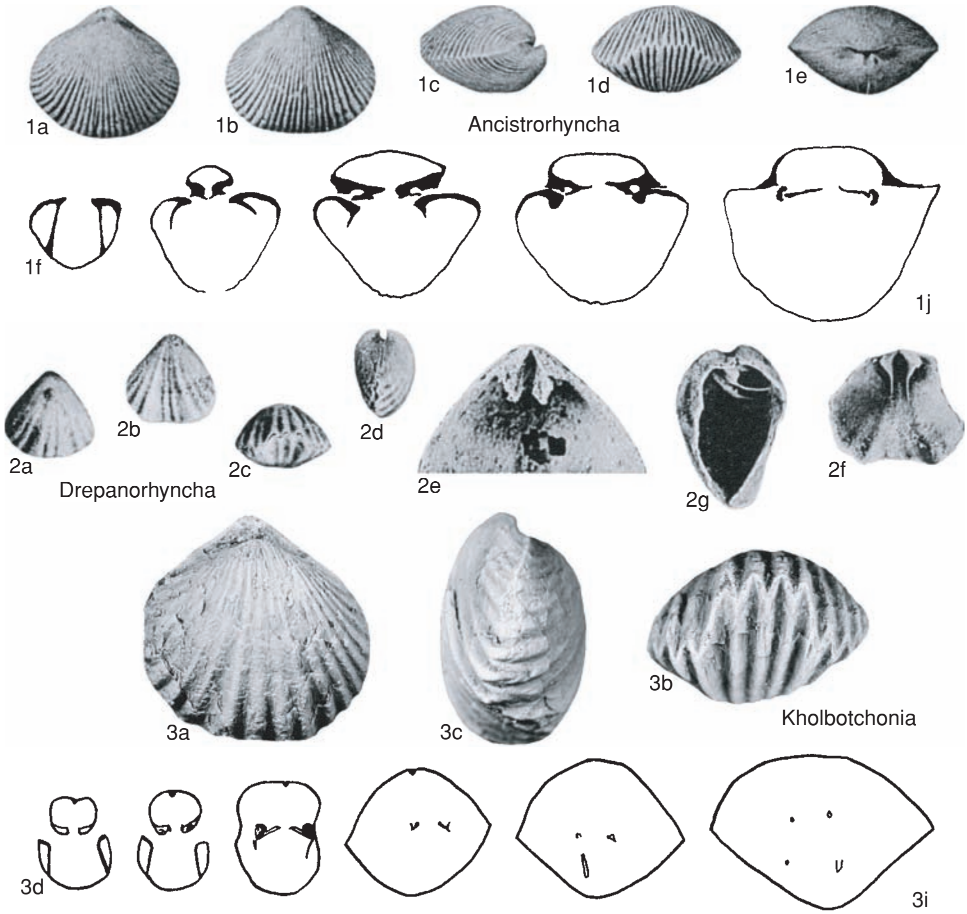

FIG. 703. Ancistrorhynchidae (p. 1041).

strength, subangular, simple, arising at beaks. Dental plates short, thin, vertical. Hinge plates horizontal, may be united; crural bases triangular in section. *Lower Devonian (Pragian):* eastern Siberia.——FIG. 704,*2a–i.* **O. costata,* lower Pragian, lower Sagyrskaya Formation, Selennyakhskiy Kryazh, Talyndzhi River, Gon Creek; *a–d,* holotype, dorsal, ventral, anterior, lateral views, with posterior part removed by sectioning, ×2; *e–i,* holotype, serial sections, ×6 (Baranov, 1991).

Tyryrhynchus BARANOV, 1988, p. 39 [**T. tyryensis;* OD]. Small with subcircular to subpentagonal outline and biconvex, lenticular profile; lateral and anterior margins acute; ventral beak straight. Fold and sulcus low; anterior commissure weakly uniplicate. Costae fine, arising at beaks, rounded in section. Dental plates short; teeth stout. Hinge plates rest on valve floor; inner socket ridges high; crura narrow, curved ventrally. *lower Silurian (Llandovery):* eastern Siberia.——FIG. 704,*3a–h.* **T. tyryensis,* Tayakh Formation, Sette-Daban Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–h,* topotype, serial sections, ×2.5 (Baranov, 1988).

Family SPHENOTRETIDAE Savage, 1996

[Sphenotretidae SAVAGE, 1996, p. 251]

Small and elongate Ancistrorhynchoidea; weak dorsal sulcus and ventral fold; low ventral interarea; costae fine; foramen with small deltidial plates. Dental plates short. Hinge plates small and divided; cardinal process absent. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc).*

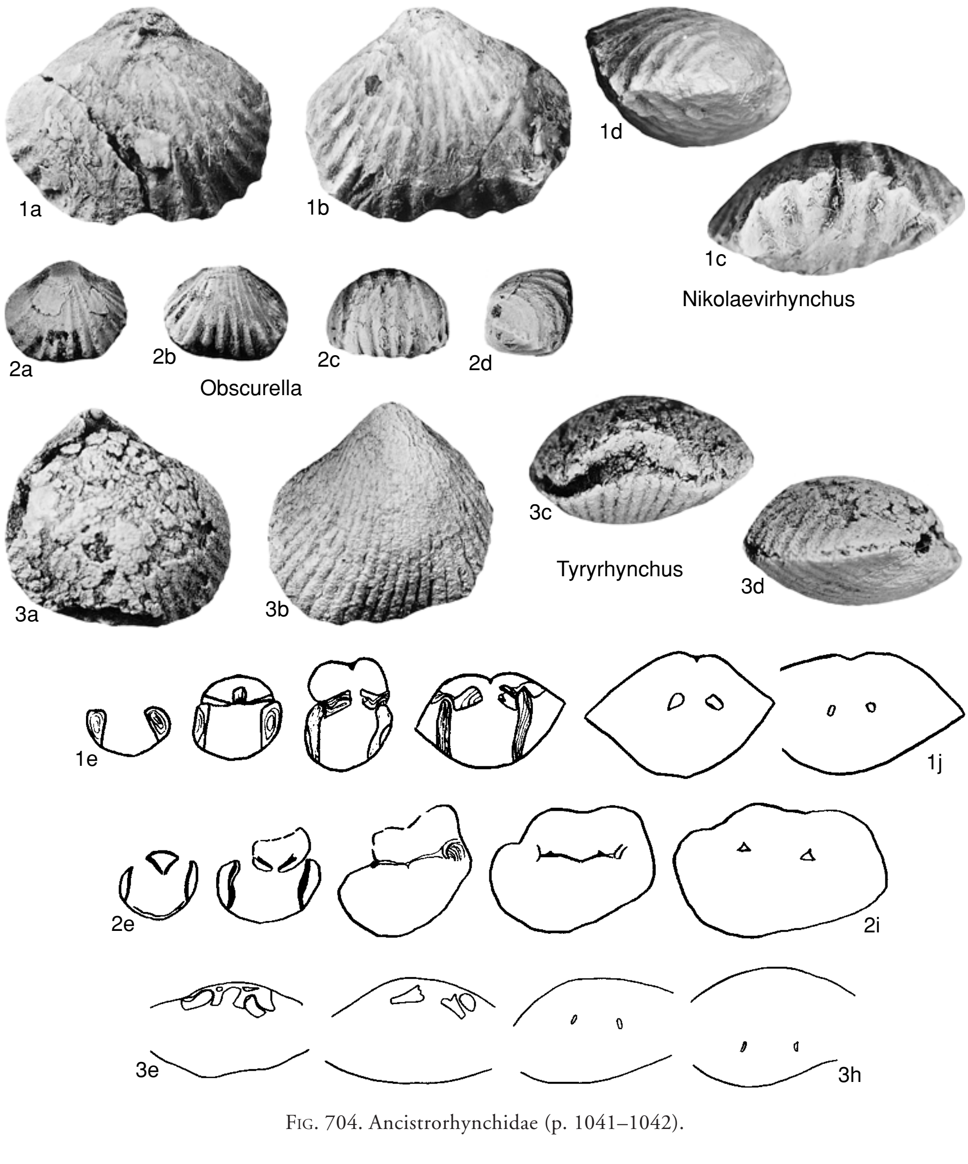

FIG. 704. Ancistrorhynchidae (p. 1041–1042).

Sphenotreta COOPER, 1956a, p. 663 [**S. cuneata;* OD]. Small with elongate subelliptical outline and weakly biconvex profile; beak straight; foramen elongate oval; deltidial plates small, triangular, disjunct. Distinct ventral fold and dorsal sulcus; anterior commissure unisulcate. Costae fine, simple, arising at beaks, narrowly rounded in section. Dental plates short, ventrally divergent. Hinge plate divided; crural bases triangular; crura long, slender, curved ventrally. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc):* North America, eastern and central Siberia, China.——FIG. 705,*3a–d. *S. cuneata,* lower Caradoc, Sevier Formation, Athens, Tennessee, USA; holotype, dorsal, ventral, lateral, and anterior views, ×4 (Cooper, 1956a).

Dorytreta COOPER, 1956a, p. 666 [**D. bella;* OD]. Small with elongate subelliptical outline but less elongate than *Sphenotreta;* biconvex profile; lateral and anterior margins rounded; beak straight; foramen elongate; deltidial plates small, triangular, disjunct. Weak dorsal sulcus and ventral fold; anterior commissure almost rectimarginate. Costae numerous but less fine than in *Sphenotreta,* simple, arising at beaks. Dental plates short, divergent ventrally.

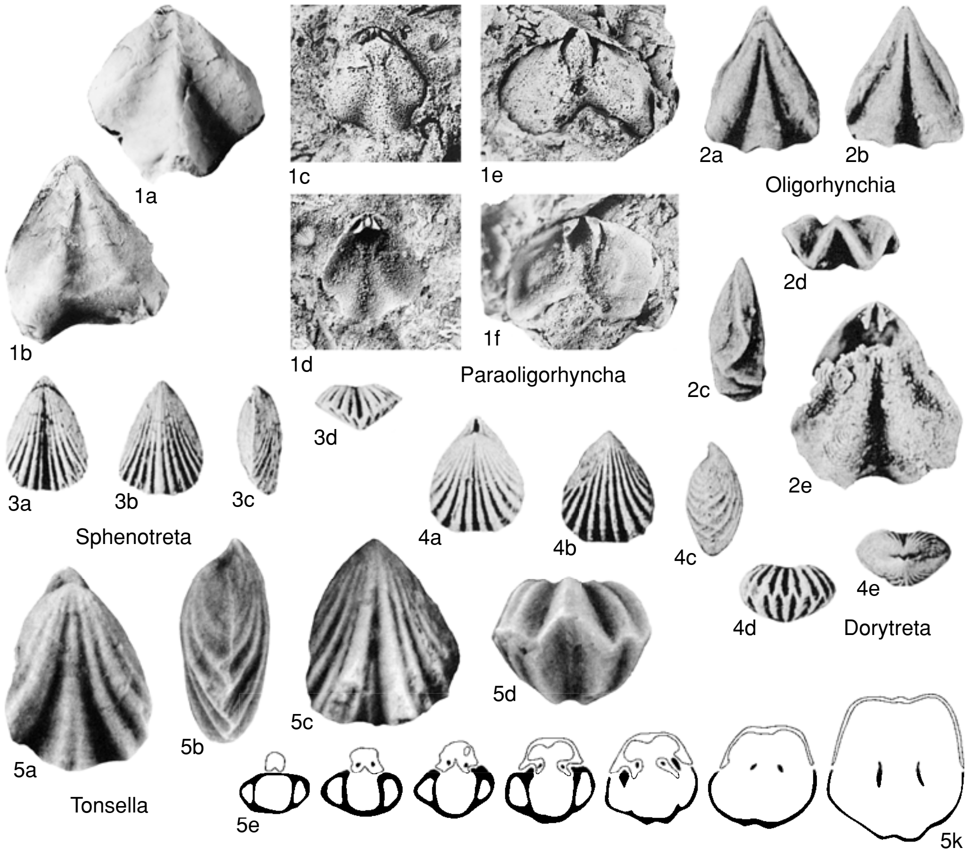

FIG. 705. Sphenotretidae and Oligorhynchiidae (p. 1043–1046).

Hinge plates divided, supported by swelling of median sulcus; crura short, bent abruptly ventrally. *Lower Ordovician (Llanvirn):* North America, eastern Siberia, Kazakhstan.——FIG. 705,*4a–e.* **D. bella,* upper McLish Formation, Pontotoc County, Oklahoma, USA; holotype, dorsal, ventral, lateral, anterior, and posterior views, ×4 (Cooper, 1956a).

Family OLIGORHYNCHIIDAE Cooper, 1956

[Oligorhynchiidae COOPER, 1956a, p. 658]

Ancistrorhynchoidea with elongate subtriangular outline; beak suberect; plicae coarse and few; weak dorsal fold masked by coarse plicae; delthyrium with small deltidial plates anteriorly. Dental plates distinct and vertical. Hinge plates divided; dorsal median septum absent, cardinal process usually absent. *Upper Ordovician (Caradoc–Ashgill).*

Oligorhynchia COOPER, 1935, p. 49 [**O. subplana;* OD]. Small with elongate subtriangular outline and low biconvex profile; ventral beak suberect to straight; foramen elongate-oval; deltidial plates small, triangular. Fold and sulcus weak and masked by 3 angular dorsal plicae and 2 to 4 ventral plicae. Dental plates strong, vertical; teeth long. Divided hinge plates supported by swelling of median anterior sulcus; cardinal process absent; crura long and straight or curved slightly ventrally. *Upper Ordovician (Caradoc–Ashgill):* North America, Europe, Novaya Zemlya, northern Urals, Kazakhstan.——FIG. 705,*2a–e.* **O. subplana,* lower Caradoc, Lincolnshire Formation, Hogskin Member, Tennessee, USA; *a–d,* hypotype, dorsal, ventral, lateral, anterior views, ×4; *e,* hypotype, view into dorsal interior showing hinge plates, ×6 (Cooper, 1956a).

Paraoligorhyncha POPOV, 1981, p. 65 [**P. reducta;* OD]. Small with elongate subtriangular outline and dorsibiconvex profile; lateral margins acute. Ventral beak suberect; delthyrium open. Dorsal fold and ventral sulcus masked by very coarse rounded plicae, with 3 dorsal plicae and 2 to 4 ventral plicae;

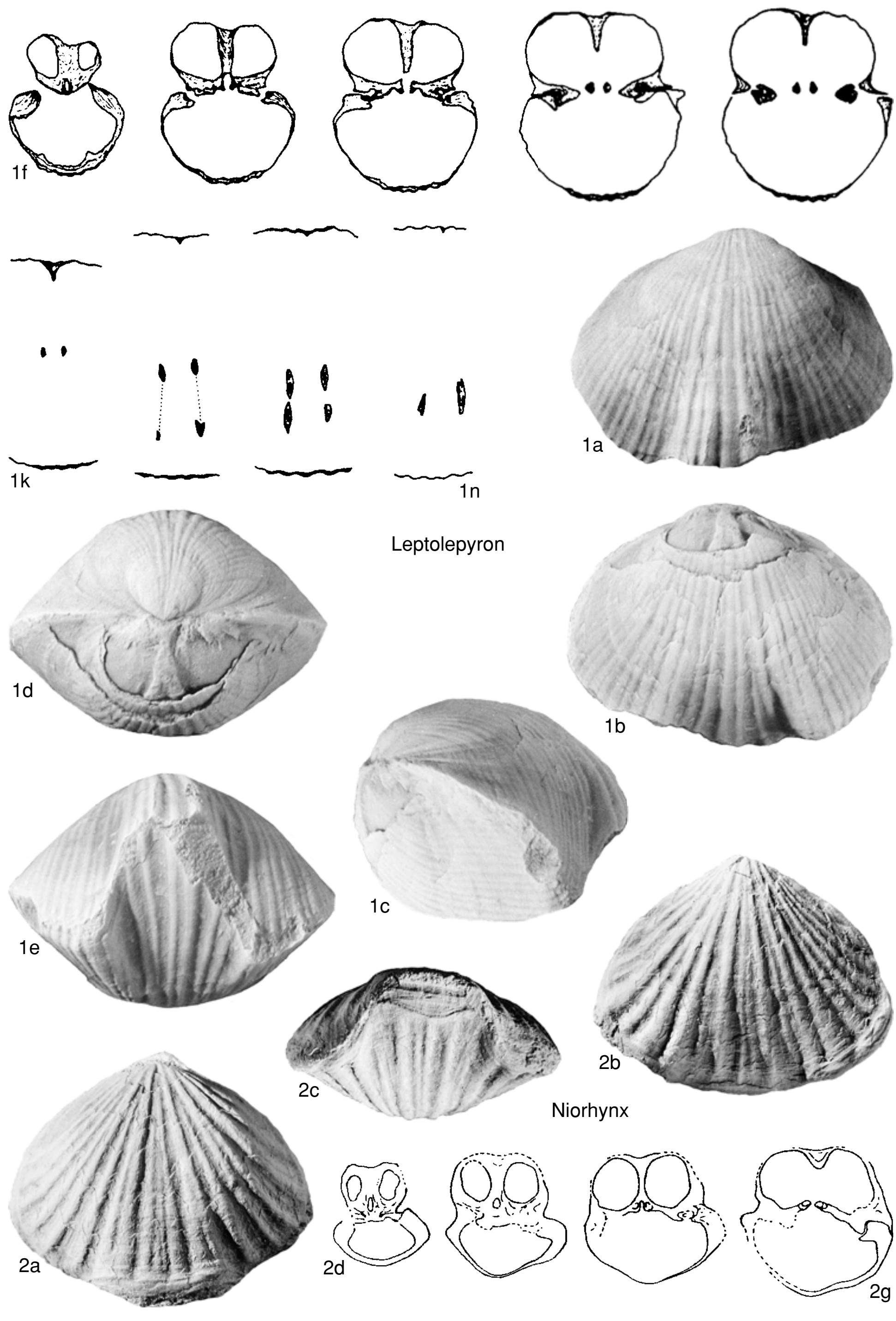

FIG. 706. Niorhynicidae (p. 1046).

anterior commissure parasulcate. Dental plates long, parallel anteriorly, and diverging ventrally; teeth stout. Hinge plate divided; bulbous cardinal process; crural bases triangular in section. *Upper Ordovician (Ashgill):* central Asia, Kazakhstan.——FIG. 705,*1a–f.* **P. reducta,* Dulankara horizon, Chu-Ili Range, Dulankara, Kazakhstan; *a,* topotype, dorsal view; *b,* ventral view of another topotype; *c–d,* holotype, dorsal internal mold and impression; *e–f,* ventral internal mold and impression, ×5 (Nikiforova & Popov, 1981).

Tonsella AMSDEN, 1988, p. 21 [**T. parva;* OD]. Small with elongate triangular outline and equibiconvex profile; lateral and anterior margins acute; ventral beak suberect. Plicae coarse, with median dorsal plication emulating fold and median ventral interplical space emulating sulcus; narrow dorsal sinus on median dorsal plication and corresponding narrow ridge in ventral sulcus; anterior commissure parasulcate. Dental plates distinct, vertical. Hinge plates divided; cardinal process absent; crura straight and rodlike but laterally flattened distally. *Upper Ordovician (Ashgill):* North America.——FIG. 705,*5a–k.* **T. parva,* upper Cincinnatian, Hirnantian, Cason Oolite, St. Clair Springs, Arkansas, USA; *a–b,* holotype, dorsal and lateral views; *c–d,* topotype, ventral view, anterior view, ×5; *e–k,* topotype, serial sections, ×4.5 (Amsden, 1988).

Family NIORHYNICIDAE Savage, 1996

[Niorhynicidae SAVAGE, 1996, p. 251]

Ancistrorhynchoidea with subcircular outline; low dorsal fold and ventral sulcus; costae coarse; delthyrium with small deltidial plates. Dental plates absent. Dorsal median septum short; septalium short and with or without cover plate; cardinal process absent. *lower Silurian (Llandovery)–middle Silurian (Wenlock).*

Niorhynx HAVLÍČEK, 1982b, p. 368 [**Terebratula niobe* BARRANDE, 1847, p. 78; OD]. Subcircular outline and biconvex, lenticular profile with acute lateral margins; beak suberect; delthyrium open except for small disjunct deltidial plates. Low fold and sulcus; anterior commissure uniplicate; tongue low, trapezoid, occasionally with incipient trail. Costae low, rounded, with some intercalation, arising at beaks. Dental plates absent; teeth stout, arising from valve margins. Hinge plates united; narrow septalium supported on short septum and covered by convex plate; septalium flanked by rodlike crural bases. *middle Silurian (Wenlock):* Bohemia.——FIG. 706,*2a–g.* **N. niobe* (BARRANDE), Motol Formation; *a–c,* hypotype, dorsal, ventral, and anterior views, ×4; *d–g,* serial sections, ×12 (Havlíček, 1982b).

Leptolepyron JIN, 1989, p. 113 [**Rhynchonella? argentea* BILLINGS, 1866, p. 43; OD]. Small to medium with transversely ovate outline and equibiconvex profile; nonprecipitous lateral slopes; beak incurved; delthyrium open, deltidial plates rudimentary. Fold and sulcus shallow to medium; costae fine to medium, arising at beaks, some intercalation and bifurcation. Dental plates absent; teeth stout, arising from valve margins; ventral muscle field well impressed. Hinge plates divided; septalium short, narrow, open; dorsal median septum long, high; crura long, slender, strongly curved ventrally. *lower Silurian (Llandovery):* Canada.——FIG. 706,*1a–n.* **L. argenteum* (BILLINGS), Jupiter Formation, Anticosti Island; *a–e,* lectotype, dorsal, ventral, lateral, posterior, and anterior views, ×3; *f–n,* hypotype, serial sections 1.0, 1.3, 1.4, 1.6, 1.7, 2.0, 3.1, 3.2, 3.3 mm from posterior, ×3 (Jin, 1989).

RHYNCHOTREMATOIDEA

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Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913

[*nom. transl.* SAVAGE, 1996, p. 252, *ex* Rhynchotrematinae SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *nom. correct. pro* Rhynchotreminae SCHUCHERT, 1913, p. 396]

Rhynchonellida with subpentagonal outline; dorsal fold and ventral sulcus; costae medium to coarse, usually extending from beaks; delthyrium open or with deltidial plates variously developed. Dental plates present or fused to valve walls. Dorsal median septum usually long, occasionally short or absent; hinge plates thick; septalium variably developed; cardinal process septiform to unilobed, rarely absent; crura long, commonly raduliform. *Lower Ordovician (Llanvirn)–Lower Carboniferous (Viséan).*

Family RHYNCHOTREMATIDAE Schuchert, 1913

[*nom. transl.* COOPER, 1956a, p. 628, *ex* Rhynchotrematinae SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *nom. correct. pro* Rhynchotreminae SCHUCHERT, 1913, p. 396]

Early Rhynchotrematoidea with strong dorsal median septum; hinge plates short, thick; cardinal process septiform. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow).*

Subfamily RHYNCHOTREMATINAE Schuchert, 1913

[*nom. correct.* SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *pro* Rhynchotreminae SCHUCHERT, 1913, p. 396]

Rhynchotrematidae with strong, simple costae. Delthyrium usually open or with disjunct deltidial plates. Dental plates short. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow).*

Rhynchotrema HALL, 1860a, p. 68 [**Atrypa increbescens* HALL, 1860a, p. 68; OD]. Shell small to large with subtriangular to subpentagonal outline and equibiconvex profile; lateral and anterior margins generally steep. Beak suberect to incurved; delthyrium partly closed by marginal deltidial plates. Dorsal fold and ventral sulcus arising at umbones; anterior commissure uniplicate; tongue trapezoid, dentate. Costae subangular, simple, arising at beaks. Dental plates short, almost vertical; teeth stout, with large fossettes; ventral muscle field flabellate. Septalium with distinct septalial plates; dorsal median septum low, thick, extending to midlength; crural bases arising from septal plates; crura long, ventrally curved; cardinal process septiform. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock):* North America, Europe, northern Africa, Urals, Siberia, Kazakhstan, Kirgizia, China, Australia.——FIG. 707,*1a–l.* **R. increbescens* (HALL), Caradoc, upper Trentonian, Sherman Falls Formation, Lakefield, Ontario, Canada; *a–d,* hypotype, dorsal, lateral, posterior, and anterior views, ×2; *e–l,* serial sections 1.6, 1.75, 1.95, 2.15, 2.3, 2.75, 3.45, 3.75 mm from posterior, ×4 (new).

Hiscobeccus AMSDEN, 1983a, p. 37 [**Atrypa capax* CONRAD, 1842, p. 264; OD]. Subcircular outline and dorsibiconvex profile; lateral and anterior margins generally steep. Beak erect to incurved; delthyrium wide, deltidial plates absent or incipient. Fold and sulcus strong; anterior commissure uniplicate; tongue distinct, trapezoid, dentate. Costae strong, simple, angular, arising at beaks. Dental plates rudimentary or fused to valve walls; ventral muscle field deeply impressed. Hinge plates thick; dorsal median septum long; cardinal process septiform. *Upper Ordovician (Ashgill):* North America.——FIG. 707,*2a–h.* **H. capax* (CONRAD), Richmondian, USA; *a–b,* hypotype, dorsal and ventral views, Dismukes, Tennessee, ×1.5; *c–e,* posterior, anterior, and lateral views; *f,* hypotype, dorsal valve interior, Fernvale Formation, Tennessee, ×2 (Howe, 1969); *g,* hypotype, dorsal view showing open delthyrium, Welling Formation, Cherokee County, Illinois; *h,* neotype, ventral interior, Richmond, Indiana, ×2 (Amsden, 1983a).

Otarorhyncha NIKIFOROVA & POPOV, 1981, p. 62 [**Rhynchotrema otarica* RUKAVISCHNIKOVA, 1956, p. 156; OD]. Transversely subpentagonal outline and dorsibiconvex profile; low, apsacline ventral interarea; delthyrium open. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue pronounced, trapezoid, serrate. Costae arising at beaks, moderately strong, rounded, some bifurcation. Dental plates very short, hardly distinct from shell wall; ventral muscle field well impressed. Septalium and dorsal median septum very short; small septate cardinal process. *Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill):* Anderken-Dulankara horizons, Kazakhstan, central Asia.——FIG. 707,*3a–i.* **O. otarica* (RUKAVISCHNIKOVA), Upper Ordovician, Dulankara Formation, Dulankara Mountain, Chu-Ili Range, Kazakhstan; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×2; *e–i,* serial sections at 1, 2, 2.5, 3, 3.5 mm from posterior (Rukavischnikova, 1956).

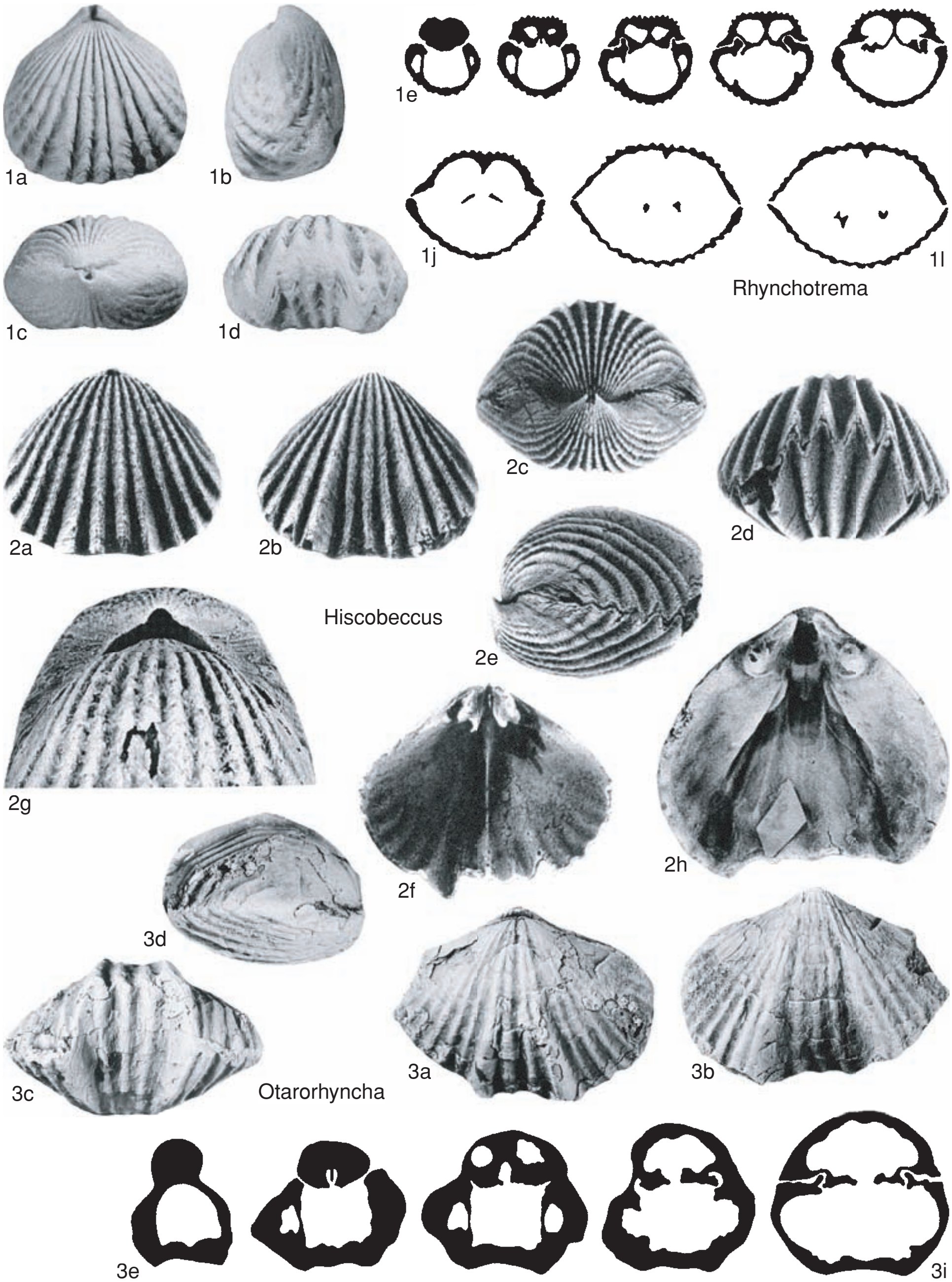

FIG. 707. Rhynchotrematidae (p. 1047).

Pleurocornu HAVLÍČEK, 1961, p. 46 [**Rhynchonella amissa* BARRANDE, 1879b, pl. 38, fig. 4; OD]. Small to medium size; distinctive securiform outline with emarginate posterolateral edges; dorsibiconvex profile. Ventral beak narrow, protracted. Dorsal fold and ventral sulcus evident but masked by strong plicae, with 3 plicae on fold and 2 strong plicae bordering the splayed sulcus; anterior commissure strongly uniplicate, denticulate. Dental plates short, scarcely distinct from thick valve walls; teeth stout;

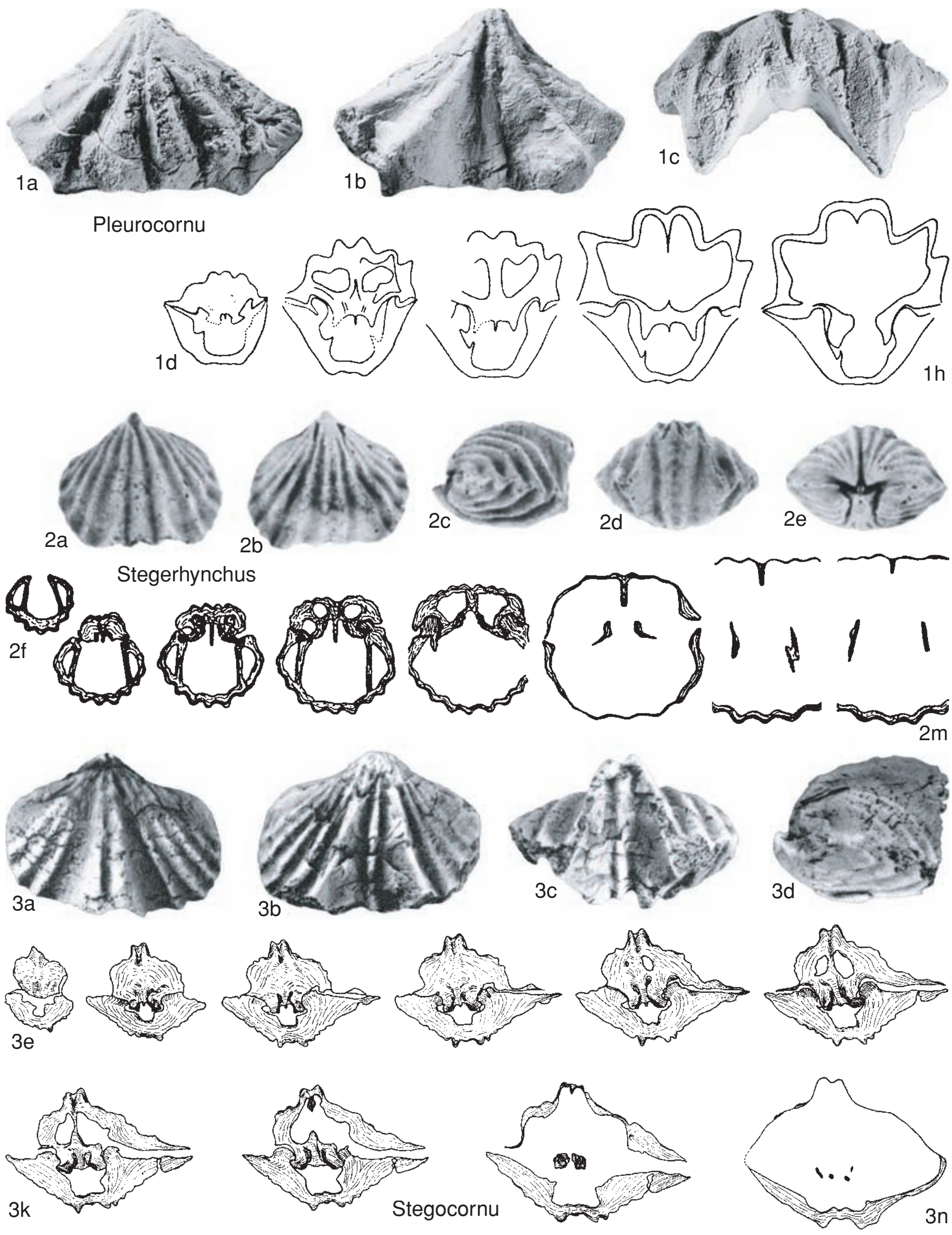

FIG. 708. Rhynchotrematidae (p. 1047–1050).

ventral muscle field well impressed. Hinge plate undivided; notothyrial cavity with septiform cardinal process; dorsal median septum short, thick. *middle Silurian (Wenlock):* Bohemia.——FIG. 708,*1a–h*. **P. amissum* (BARRANDE), Lodenice; *a–c,* lectotype, dorsal, ventral, and anterior views, ×2.7 (new); *d–h,* serial sections of hypotype at 8.5, 7.8, 7.3, 6.3, 6.0 from anterior, ×3 (Havlíček, 1961).

Stegerhynchus FOERSTE, 1909a, p. 96 [**Rhynchonella (Stegerhynchus) whitii-praecursor* FOERSTE, 1909a, p. 96*;* OD; =*Stegerhynchus praecursor* FOERSTE, 1909a, p. 96] [=*Stegorhynchella* RZHONSNITSKAIA, 1959, p. 27 (type, *Stegerhynchus decimplicata angaciensis* CHERNYSHEV, 1937, p. 29); *Tungussotoechia* LOPUSHINSKAYA, 1976, p. 60 (type, *Stegorhynchella tungussensis* LOPUSHINSKAYA, 1972, p. 186);

Stegerhynchops AMSDEN, 1978, p. 27 (type, *S. marblensis*)]. Subtriangular to subpentagonal outline and dorsibiconvex profile. Beak erect to suberect; delthyrium open or with rudimentary deltidial plates. Fold and sulcus narrow, strong, from umbones; anterior commissure uniplicate, trapezoid, serrate. Costae simple, subangular, from beaks. Dental plates short, subvertical, sometimes obscured by callus. Hinge plates thick, short; septalium small, with short septalial plates; dorsal median septum thick, long; cardinal process septiform; crural bases arising from septalial plates; crura laterally flattened, ventrally curved. *lower Silurian (Llandovery)–upper Silurian (Ludlow):* North America, Europe, Siberia, Altai, Mongolia, Australia.——FIG. 708,*2a–m.* **S. praecursor* (FOERSTE)*; a–e,* topotype, dorsal, ventral, lateral, anterior, and posterior views, lower Silurian, Clinton Beds, Clifton, Tennessee, USA, collected by FOERSTE, ×2.4 (Jones, 1981); *f–m,* hypotype, serial sections 0.3, 0.6, 0.7, 0.9, 1.0, 1.3, 1.9, 2.0 mm from posterior, lower Silurian, Bescie Formation, Anticosti Island, Canada, ×7 (Jin, 1989).

Stegocornu DÜRKOOP, 1970, p. 185 [**S. procerum;* OD] [=*Xerxespirifer* COCKS, 1979, p. 40 (type, *X. iranicus,* OD)]. Transversely ovate outline and dorsibiconvex profile; anterior margin particularly high. Beak erect to incurved; delthyrium with narrow opening. Fold and sulcus narrow, strong, arising near beaks; anterior commissure high, tapering dorsally, sulciplicate. Costae coarse, subangular, arising at beaks, typically 2 on fold and 1 in sulcus. Dental plates lacking or fused to valve walls; ventral muscle field deeply impressed. Hinge plates massive, united; cardinal process septiform; dorsal median septum very short, thick; inner socket ridges massive; crural bases stout, arising from inner socket ridges; crura radulifer. *lower Silurian (Llandovery):* Afghanistan, Iran.——FIG. 708,*3a–n.* **S. procerum,* upper Llandovery, Dascht-e-Nawar/East, eastern Afghanistan; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–n,* serial sections 1.3, 1.7, 1.9, 2.0, 2.1, 2.3, 2.5, 2.6, 3.2, 4.6 mm from posterior, ×1.75 (Dürkoop, 1970).

Subfamily LEPIDOCYCLINAE Cooper, 1956

[*nom. transl.* AMSDEN, 1978, p. 26, *ex* Lepidocyclidae COOPER, 1956a, p. 657]

Rhynchotrematidae with subcircular to elongate oval outline; strongly biconvex. Costae coarse, crossed by imbricating growth lamellae. Delthyrium usually with conjunct deltidial plates. Dental plates fused to thick shell walls or obscured by callus. *Upper Ordovician (Ashgill)–upper Silurian (lower Ludlow).*

Lepidocyclus WANG, 1949, p. 12 [**L. laddi;* OD]. Medium to large with elongate subcircular to subcircular outline and strongly biconvex profile. Beak erect to incurved; deltidial plates conjunct to disjunct. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue trapezoid, tapering dorsally, dentate. Costae strong, angular to subangular, simple, from beaks, with lamellose growth lines. Dental plates reduced or fused to valve walls; ventral muscle field deeply impressed. Dorsal median septum extending to valve midlength; septalium small; cardinal process thin, septiform; hinge plates thick; crural bases horizontal; crura rodlike proximally, becoming laterally flattened distally, ventrolaterally curved. *Upper Ordovician (Ashgill):* North America, Kazakhstan.——FIG. 709,*2a–f.* **L. laddi,* upper Cincinnatian, Maquoketa Formation, Elgin Member, Winneshiek County, Orleans township, Iowa, USA; *a–d,* holotype, dorsal, ventral, lateral, and anterior view; *e–f,* paratype, dorsal valve interior, ventral valve interior, ×1 (Wang, 1949).——FIG. 709,*2g–m. L. gigas* WANG, upper Cincinnatian, Vaureal Formation, Anticosti Island, Canada; serial sections 1.6, 1.8, 2.0, 2.8, 3.6, 4.3, 5.0 mm from posterior, ×2 (Jin, 1989).

Hypsiptycha WANG, 1949, p. 17 [**H. hybrida;* OD]. Elongate-subtriangular outline and strongly dorsibiconvex profile; lateral and anterior margins steep. Beak erect to suberect; delthyrium with conjunct deltidial plates. Fold and sulcus strong, narrow; anterior commissure uniplicate; tongue generally high, trapezoid, dentate. Costae strong, subangular, simple, from beaks, with strongly lamellose growth lines. Dental plates partly fused to shell walls; teeth large, arising from valve margins; ventral muscle field well impressed. Septalium short; cardinal process septiform; dorsal septum short; crura long, strongly curved ventrally. *Upper Ordovician (Ashgill):* North America.——FIG. 709,*3a–f.* **H. hybrida,* upper Cincinnatian, Maquoketa Formation, Brainard Member, Jackson County, Fairfield, Iowa, USA; *a–d,* holotype, dorsal, ventral, anterior, and lateral views; *e,* ventral valve interior, ×2; *f,* dorsal valve beak interior, ×4 (Wang, 1949).——FIG. 709,*3g–n. H. anticostiensis* (BILLINGS), upper Cincinnatian, Ellis Bay Formation, Anticosti Island, Canada; serial sections 1.3, 1.6, 1.7, 1.9, 2.3, 3.6, 4.4, and 4.5 mm from posterior, ×3 (Jin, 1989).

Rhytidorhachis JIN & CALDWELL, 1990, p. 32 [**R. hudsonensis;* OD]. Subpentagonal to subtriangular outline and moderately biconvex profile. Beak erect to suberect; delthyrium with conjunct deltidial plates and submesothyrid foramen. Fold and sulcus extending from umbones. Costae strong, from beaks, some bifurcation and intercalation anteriorly. Dental plates short and mostly fused to shell walls; teeth short and thick; ventral muscle field well impressed. Dorsal median septum short to absent; hinge plates short, thick, divided anteriorly; cardinal process septiform; crural bases triangular; crura laterally flattened. *lower Silurian (upper Llandovery)–upper Silurian (lower Ludlow):* North America, Europe.——FIG. 709,*1a–k.* **R.*

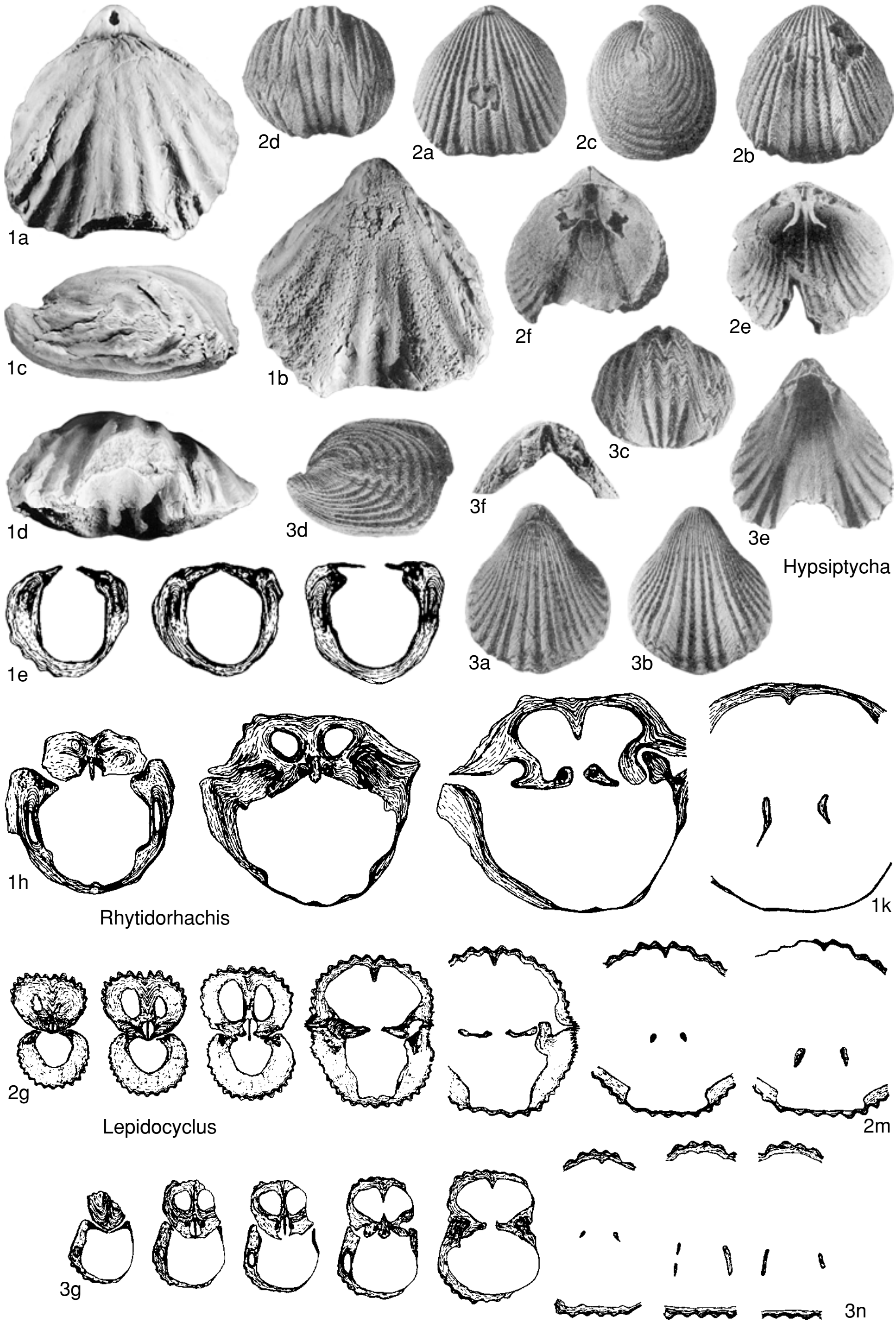

FIG. 709. Rhynchotrematidae (p. 1050–1052).

hudsonensis, upper Llandovery, Ekwan River Formation, Little Current River, Hudson Bay Lowlands, Canada; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×3; *e–k,* serial sections 0.8, 0.9, 1.3, 1.6, 2.2, 2.6, 3.2 mm from posterior, ×8 (Jin & Caldwell, 1990).

Family TRIGONIRHYNCHIIDAE Schmidt, 1965

[Trigonirhynchiidae SCHMIDT, 1965a, p. 2]

Rhynchotrematoidea with subtriangular outline; dorsal fold and ventral sulcus variable; costae often extending from beaks but umbones commonly smooth; delthyrium open or with disjunct to conjunct deltidial plates; anterior commissure often dentate, sometimes spinose. Dental plates and dorsal medium septum present. Septalium with or without cover plate; cardinal process absent. *Lower Ordovician (Llanvirn)–Lower Carboniferous (Viséan).*

Subfamily TRIGONIRHYNCHIINAE Schmidt, 1965

[*nom. transl.* SAVAGE, 1996, p. 252, *ex* Trigonirhynchiidae SCHMIDT, 1965a, p. 2]

Trigonirhynchiidae with covered septalium. *lower Silurian (Llandovery)–Lower Carboniferous (Viséan).*

Trigonirhynchia COOPER, 1942, p. 228, *non Trigonirhynchia* DAGYS, 1961, p. 94 [**Uncinulina fallaciosa* BAYLE, 1878, pl. 13, fig. 13–16; OD] [=*Uncinulina* BAYLE, 1878, pl. 13, fig. 13–16, *non* TERQUEM, 1862, Holothuroidea]. Shell small to medium; subtrigonal to subpentagonal outline; strongly biconvex. Beak erect to suberect; delthyrium open, bordered by disjunct deltidial plates. Dorsal fold and ventral sulcus distinct but low, with gentle margins; anterior commissure uniplicate; tongue high, trapezoid, serrate. Costae strong, simple, rounded, from beaks. Dental plates distinct but short; teeth elongate, crenulate. Dorsal septum low, thin, long; septalium well developed, with cover plate; cardinal process absent; crural bases horizontal; crura curved ventrally, ventromedian surfaces concave in section. *middle Silurian (lower Wenlock)–Middle Devonian (lower Eifelian):* Europe, North America, Siberia, China, Mongolia.——FIG. 710,*1a–n.* **T. fallaciosa* (BAYLE), Lower Devonian, Néhou, France; *a–d,* hypotype, dorsal, ventral, lateral, and anterior views, ×1.2; *e–n,* hypotype, serial sections 21.3, 21.2, 21.1, 21.0, 20.8, 20.7, 20.4, 20.0, 19.7, 19.3 mm from anterior, ×1.6 (Schmidt, 1965a).

Agarhyncha HAVLÍČEK, 1982b, p. 369 [**Terebratula famula* BARRANDE, 1847, p. 87; OD]. Subpentagonal to subcircular outline; biconvex to globose profile. Beak suberect to erect; foramen with minute deltidial plates. Fold and sulcus well defined, broad, anterior commissure uniplicate; tongue rectangular, serrate. Costae coarse, rounded, simple, but umbones smooth. Dental plates very short. Dorsal median septum thin; septalium with cover plate anteriorly; crura close to septum posteriorly. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian):* Bohemia, Germany, Carnic Alps. ——FIG. 710,*2a–l.* **A. famula* (BARRANDE), lower Ludlow, Kopanina Formation, Bohemia; *a–e,* hypotype, dorsal, ventral, anterior, posterior, and lateral views, ×4.6; *f–l,* serial sections 7.15, 7.05, 7.03, 6.85, 6.65, 6.60, 6.45 from anterior, ×12 (Havlíček, 1982b).

Ancillotoechia HAVLÍČEK, 1959, p. 78 [**Rhynchonella ancillans* BARRANDE, 1879b, pl. 36; OD] [=*Trigonirhynchioides* FU, 1982, p. 144, subj. (type, *T. qinlingensis*, OD)]. Small with subcircular to elongate outline; dorsibiconvex profile. Beak suberect; delthyrium open or with disjunct deltidial plates. Fold and sulcus narrow; anterior commissure uniplicate; tongue high, serrate. Costae strong, simple, from beaks. Dental plates short, thin, vertical. Septalium with cover; dorsal median septum low; cardinal process absent. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian):* cosmopolitan.——FIG. 711,*1a–h.* **A. ancillans* (BARRANDE), upper Silurian, Kopanina Limestone, Bohemia; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, Kopanina Limestone, basal Budnany, V Kozle, near Beroun, ×3.5 (new); *e–h,* serial sections 7.55, 7.50, 7.45, 7.40 mm from anterior, ×10 (Havlíček, 1961).

Aratoechia HAVLÍČEK, 1982b, p. 368 [**Terebratula minerva* BARRANDE, 1847, p. 69; OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak suberect; foramen with conjunct deltidial plates. Fold and sulcus wide; anterior commissure with wide, rounded tongue, sharply dentate. Costae numerous, angular; some bifurcation. Dental plates distinct, slightly convergent ventrally. Septalium with cover; dorsal median septum high, long; cardinal process absent; crural bases horizontal. *middle Silurian (Wenlock):* Bohemia.——FIG. 711,*2a–h.* **A. minerva* (BARRANDE), Motol Formation; *a–c,* hypotype, dorsal, ventral, and anterior views, ×1.9 (new); *d–h,* serial sections 13.7, 13.4, 13.3, 12.9, 12.8 mm from anterior, ×3.6 (Havlíček, 1961).

Astua HAVLÍČEK, 1992, p. 85 [**Rhynchonella astuta* BARRANDE, 1879b, pl. 18, case 5, fig. 2a–e; OD]. Shell medium to large with subpentagonal outline and emarginate anterior; strongly biconvex, inflated anteriorly. Beak erect to incurved. Dorsal fold and ventral sulcus strong with distinct margins; tongue high; rectangular, serrate. Costae strong, simple, subangular, weak on umbones, numerous on flanks. Dental plates distinct; vertical, divergent anteriorly. Well-developed septalium without cover; dorsal median septum present; cardinal process absent; crura unknown. *Lower Devonian (Lochkovian):* Bohemia, central Asia.——FIG. 712,*1a–h.* **A.*

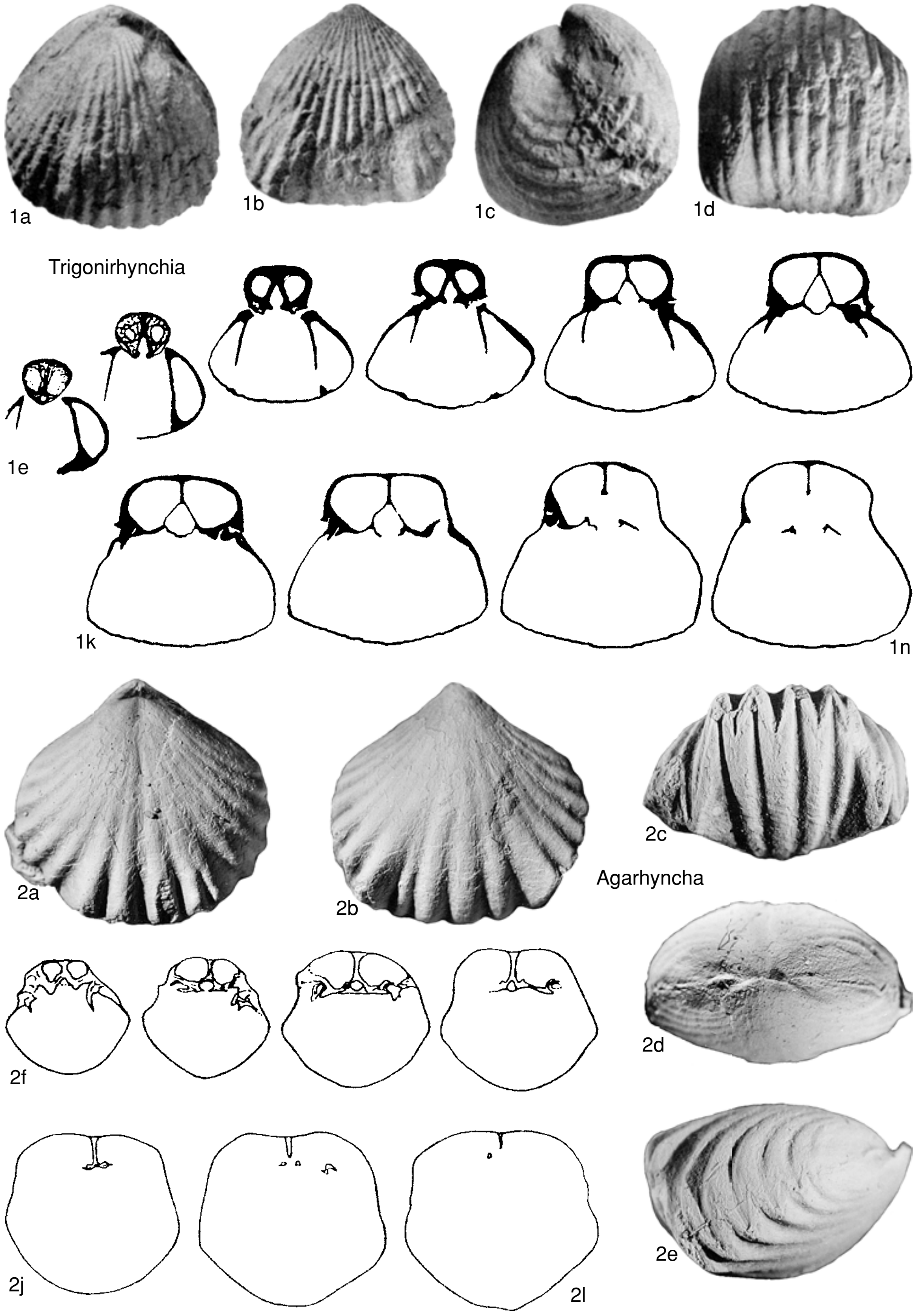

FIG. 710. Trigonirhynchiidae (p. 1052).

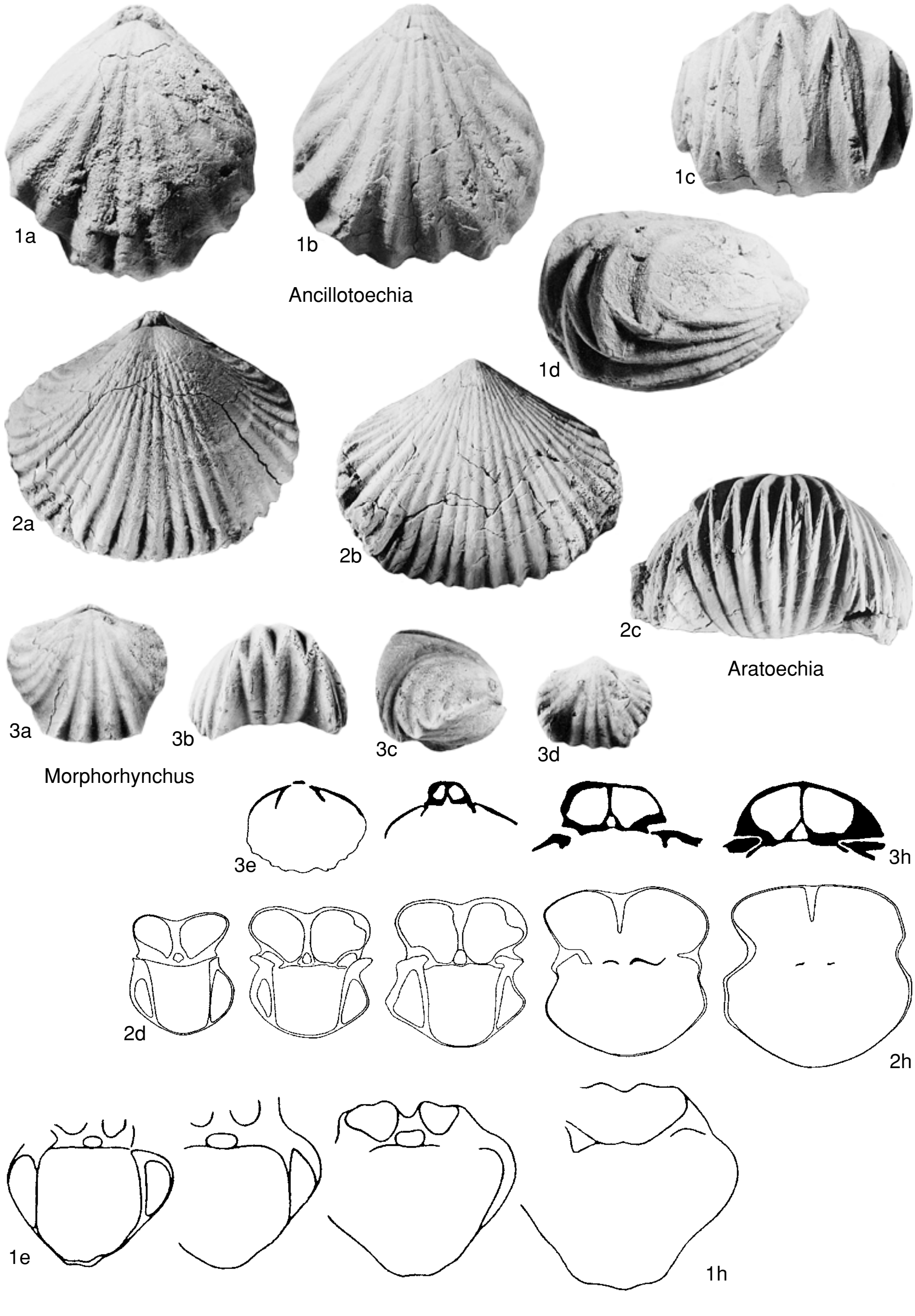

FIG. 711. Trigonirhynchiidae (p. 1052–1059).

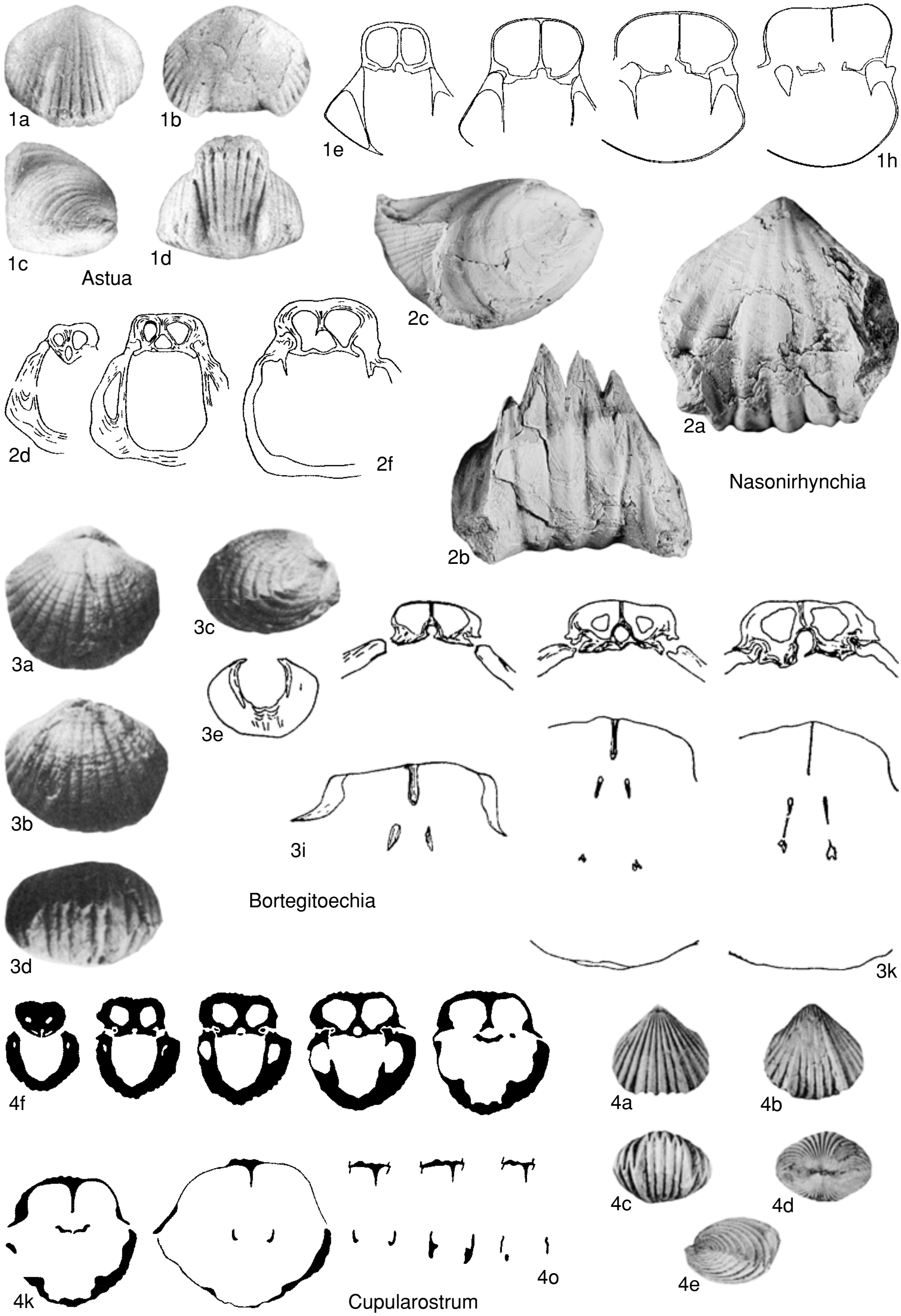

FIG. 712. Trigonirhynchiidae (p. 1052–1059).

astuta (Barrande), Kotys Limestone, Svaty Jan pod Skalou, Bohemia; *a–d,* lectotype, dorsal, ventral, lateral, and anterior views, ×1; *e–h,* serial sections 13.6, 13.3, 12.7, 12.6 mm from anterior, ×2.5 (Havlíček, 1961).

Bortegitoechia Erlanger, 1994, p. 94 [**B. tsogtella;* OD]. Transversely subcircular outline and dorsibiconvex profile. Beak incurved; foramen unrecorded. Fold and sulcus weak, arising anteriorly; anterior commissure uniplicate; tongue low, trapezoid, serrate. Costae rounded, arising at beaks; some bifurcation; concentric growth lines distinct. Dental plates very short, obscured by callus. Dorsal median septum low, long; septalium short, open posteriorly and anteriorly but with cover plate at midlength; hinge plates divided anterior of septalium; crural bases and crura closely set, laterally flattened. *Lower Devonian (Lochkovian):* Mongolia.——Fig. 712,*3a–k.* **B. tsogtella,* Bortegsk Series, eastern Gobi, Bortegst Massif, Tsogt-Obo; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1.5; *e–k,* serial sections 2.65, 3.15, 3.35, 3.65, 4.15, 4.35, 5.05 mm from posterior, ×2.5 (Erlanger, 1994).

Cupularostrum Sartenaer, 1961d, p. 2 [**C. recticostatum;* OD]. Subcircular outline; strongly biconvex. Beak suberect; delthyrium with small foramen, deltidial plates disjunct. Fold and sulcus arising from umbones; anterior commissure uniplicate with trapezoid tongue; serrate. Costae strong, straight, simple, subangular, from beaks. Dental plates distinct, umbonal cavities may be set in thick shell walls; ventral muscle area deeply impressed. Dorsal median septum low, long; well-developed septalium with arched cover plate anteriorly; crura laterally flattened, concave medially. *Lower Devonian (Emsian)–Upper Devonian (Frasnian):* cosmopolitan.——Fig. 712,*4a–o.* **C. recticostatum,* Givetian, Skaneateles Formation, Hamilton, New York, USA; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f–o,* serial sections 1.3, 1.7, 2.0, 2.2, 2.4, 2.55, 3.2, 3.3, 3.5, 3.7 mm from posterior, ×3 (Sartenaer, 1961d).

Hercotrema Jin, 1989, p. 87 [**H. bulbicostatum;* OD]. Small to medium with transversely subcircular outline and biconvex profile. Beak small, incurved; delthyrium open to partly covered by rudimentary deltidial plates. Fold and sulcus with few large costae; anterior commissure sulciplicate. Costae very coarse, rounded, extending from beaks. Dental plates high, thin; teeth small, arising from valve margins. Septalium small, lacking cover plate but with opening restricted by lateral extensions of hinge plates; cardinal process absent; crural bases horizontal; crura laterally flattened, digitose distally. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian):* North America, Bohemia.——Fig. 713,*1a–o.* **H. bulbicostatum,* Llandovery, Jupiter Formation, Bai du Naufrage, Anticosti Island, Canada; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×3; *f–o,* paratype, serial sections 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 1.9, 2.2, 2.3 mm from posterior, ×4 (Jin, 1989).

Iberirhynchia Drot & Westbroek, 1966, p. 165 [**I. santaluciensis;* OD]. Shell small with trigonal to subpentagonal outline and dorsibiconvex profile, anteriorly inflated; apical angle acute to right angular. Beak erect; large delthyrium with incipient disjunct deltidial plates. Fold and sulcus weak; anterior commissure uniplicate with low, rectangular tongue, dentate. Costae simple, subangular; extending from beaks. Dental plates distinct, long, vertical; teeth large. Dorsal median septum long; septalium with cover plate; cardinal process absent; crura laterally flattened. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Spain, Bohemia.——Fig. 713,*2a–n.* **I. santaluciensis,* Emsian-Eifelian boundary, upper Santa Lucia Formation, Pic Aguasalio, Leon Province, Spain; *a–d,* dorsal, ventral, lateral, and anterior views, ×2; *e–l,* topotype, serial sections; *m–n,* topotype, anterior and anterolateral views of plastic model based on serial sections (Drot & Westbroek, 1966).

Lissopleura Whitfield, 1896, p. 232 [**Rhynchonella aequivalvis* Hall, 1857a, p. 66; OD]. Small with subtriangular outline and biconvex profile. Beak small, suberect. Foramen not recorded. Fold and sulcus weak; anterior commissure uniplicate; tongue low on holotype but moderately high and rectangular on most specimens. Umbones smooth. Costae fine, rounded to somewhat flattened. Dental plates short, ventrally convergent; ventral muscle field well impressed. Dorsal median septum strong, long; septalium deep, short, with cover plate anteriorly; hinge plates united, extend slightly anterior of septalium; crural bases triangular; crura with V-shaped cross section, open dorsally. *Lower Devonian (Lochkovian):* North America.——Fig. 714,*1a–p.* **L. aequivalvis* (Hall), lower Helderberg, Albany County, New York, USA; *a–d,* holotype, dorsal, ventral, lateral, and anterior views of cast; *e–h,* hypotype, dorsal, ventral, anterior, and lateral views, ×1.5; *i–p,* serial sections 1.0, 1.45, 1.75, 2.35, 2.55, 3.35, 4.2, 4.65 mm from posterior, ×2.2 (new).

Macropotamorhynchus Sartenaer, 1970a, p. 24 [**Camarotoechia mitcheldeanensis* Vaughan, 1905, p. 302; OD]. Small with subtrigonal to subpentagonal outline and dorsibiconvex profile. Beak suberect to erect; foramen small, ovate; delthyrium with conjunct deltidial plates. Fold and sulcus weak, arising at umbones; anterior commissure uniplicate; tongue moderately high, dentate. Costae angular, strong, simple, arising at beaks. Dental plates short, vertical. Dorsal median septum low, long, extending to about half valve length; septalium short, generally with cover plate; hinge plates divided immediately anterior of septalium; crural bases triangular; crura laterally flattened. *Lower*

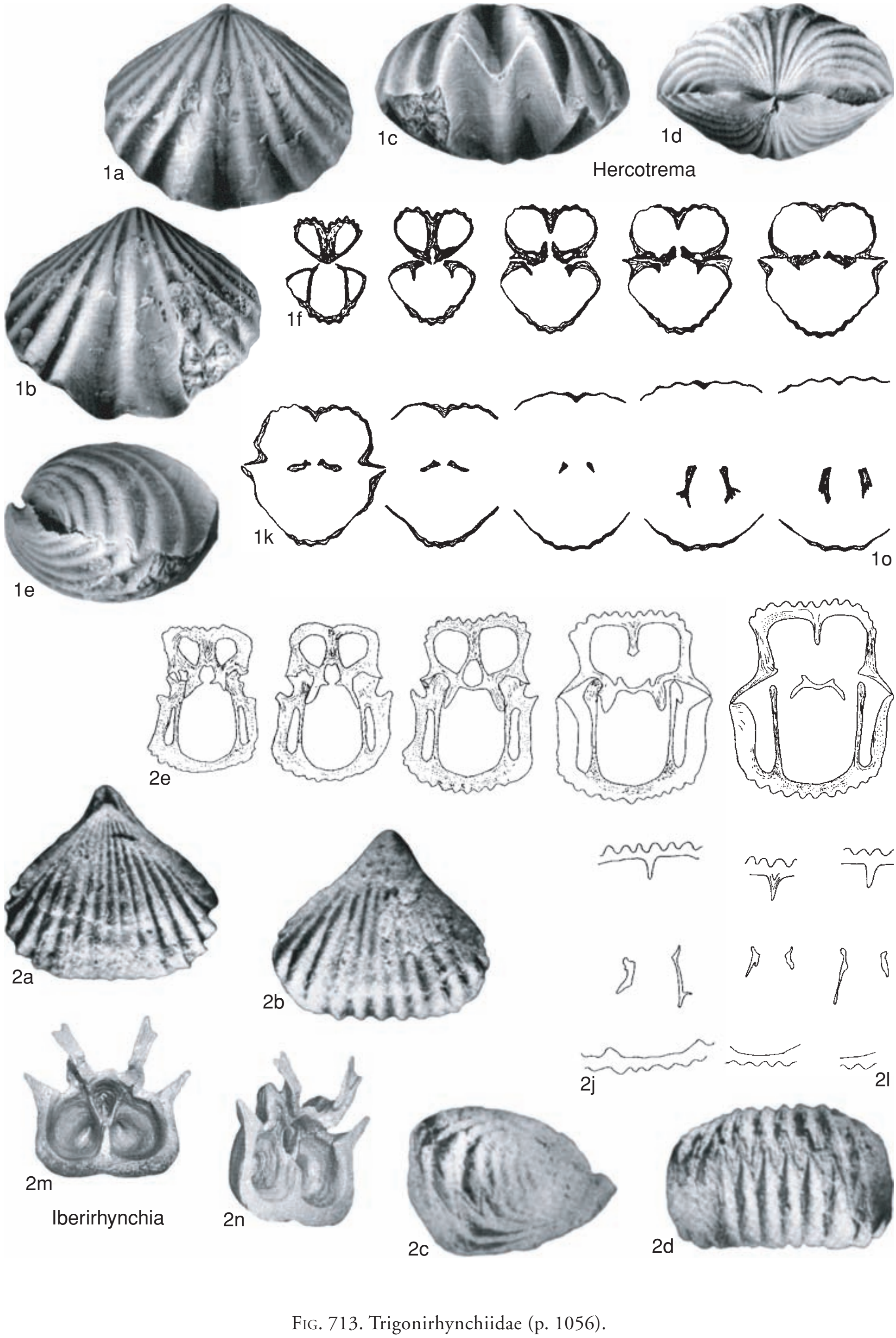

FIG. 713. Trigonirhynchiidae (p. 1056).

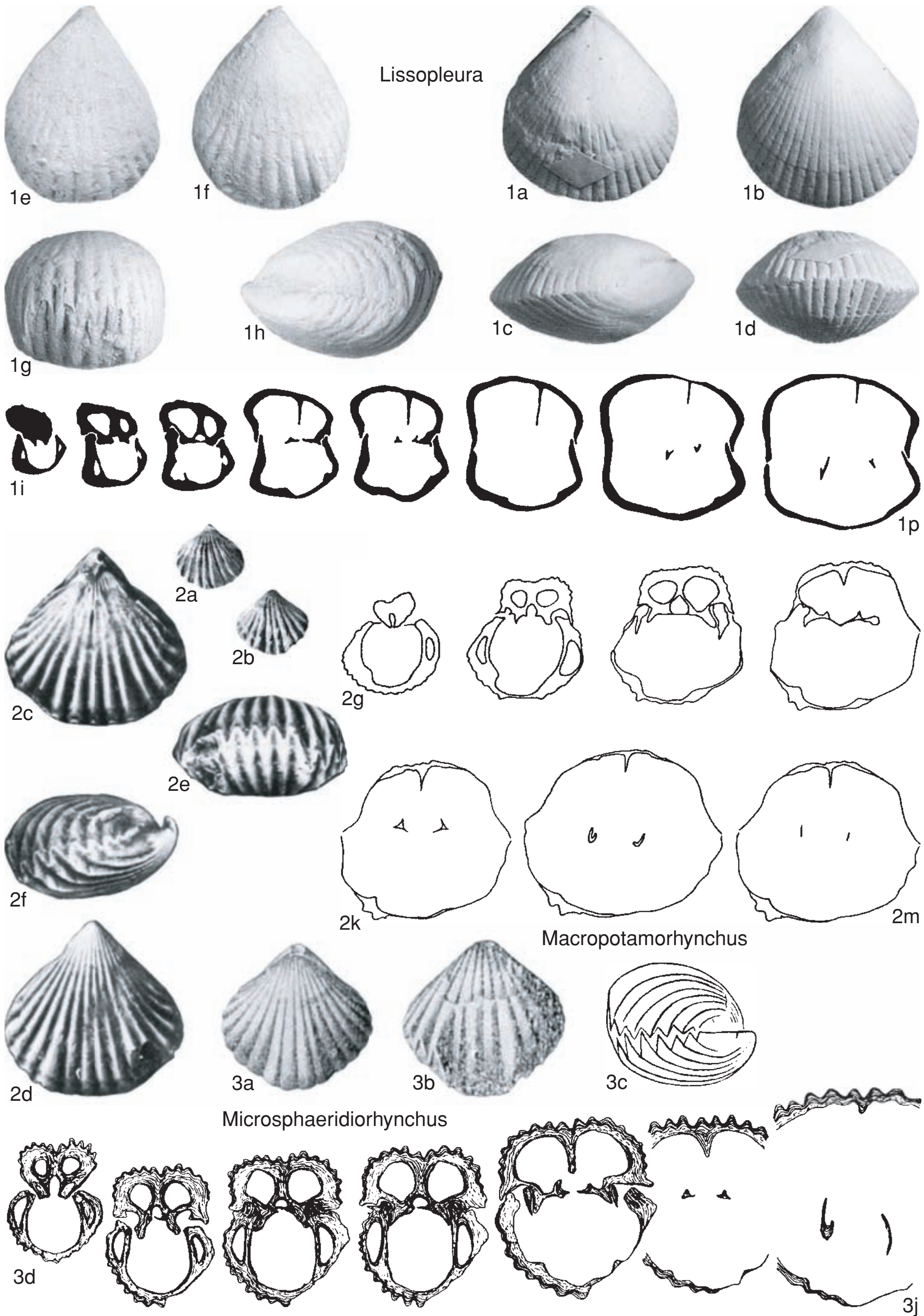

FIG. 714. Trigonirhynchiidae (p. 1056–1059).

Carboniferous (lower Tournaisian): western and eastern Europe, Asia, North America, Australia.——FIG. 714,*2a–b.* **M. mitcheldeanensis* (VAUGHAN), Carboniferous Limestone, Gloucestershire, Mitcheldean, England; holotype, dorsal and ventral views, ×1 (Vaughan, 1905).——FIG. 714,*2c–m. M. curiosus,* Banff Formation, Alberta, Forbidden Creek, Canada; *c–f,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *g–m,* serial sections 1.4, 1.7, 2.0, 2.3, 2.6, 3.0, 3.8 mm from posterior, ×4.5 (Carter, 1987).

Microsphaeridiorhynchus SARTENAER, 1970a, p. 27 [**Rhynchonella (?) litchfieldensis* SCHUCHERT, 1903, p. 167; OD]. Rounded trigonal outline and strongly biconvex profile. Ventral beak incurved; delthyrium bordered by narrow disjunct deltidial plates. Fold and sulcus strong, from umbones; anterior commissure uniplicate, dentate. Costae strong, simple, angular, from beaks. Dental plates distinct but short; vertical. Dorsal median septum thick, long; well-developed septalium with cover plate; cardinal process absent; crura laterally flattened, concave dorsomedially. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian):* North America, Europe, China.——FIG. 714,*3a–c.* **M. litchfieldensis* (SCHUCHERT), Přídolí, Coblestone Limestone, Litchfield, New York, USA; lectotype, dorsal, ventral, and lateral views, ×1 (Schuchert, 1903).——FIG. 714,*3d–j. M. nucula* (SOWERBY), hypotype, serial sections 0.7, 0.9, 1.0, 1.1, 1.4, 1.5, 2.3 mm from posterior from Eke Beds, Ludlow, Lau Backar, Gotland, ×5 (Jin, Caldwell, & Norford, 1993).

Moorefieldella GIRTY, 1911, p. 62 [**Rhynchonella eurekensis* WALCOTT, 1884, p. 223; OD]. Subtrigonal to ovate outline and biconvex profile. Beak erect to suberect; foramen partly closed by narrow disjunct deltidial plates. Fold and sulcus low, flat, developed anteriorly; tongue low, trapezoid. Costae fine, arising at about one-third shell length; concentric growth lines commonly visible anteriorly. Dental plates short, ventrally divergent; subtriangular ventral muscle field weakly impressed. Dorsal median septum high in type species but may be low in others; septalium very short, partly covered in type species by fused inner hinge plates; crura short, closely set and dorsally concave in type species. *Lower Carboniferous (Tournaisian–Viséan):* North America.——FIG. 715,*2a–e.* **M. eurekensis* (WALCOTT), Meramecian, Spring Creek Limestone, Moorefield, White River Junction, Arkansas, USA; dorsal, ventral, lateral, anterior, and posterior views of specimen illustrated by COOPER, 1942, ×1.5 (new).——FIG. 715,*2f–n. M. prisca* CARTER, Kinderhookian, Banff Formation, Jasper Park region, Alberta, Canada; serial sections at 1.4, 1.5, 1.7, 2.0, 2.2, 2.4, 2.6, 2.9, 3.1 mm from posterior, ×1.5 (Carter, 1987).

Morphorhynchus COOPER & DUTRO, 1982, p. 71 [**M. varicostatum;* OD]. Subrectangular outline and strongly dorsibiconvex profile; inflated anteriorly. Beak incurved; foramen small, deltidial plates disjunct. Fold and sulcus strong; anterior commissure uniplicate; tongue high, with subrounded margins. Costae strong and subangular, arising from umbones. Dental plates diverging ventrally toward valve floor. Dorsal median septum long; septalium with cover plate anteriorly; inner socket ridges high, thin; crura long, flattened distally. *Middle Devonian (upper Givetian):* western North America.——FIG. 711,*3a–h.* **M. varicostatum,* Orñate Formation; *a–c,* holotype, dorsal, anterior, lateral views, ×2; *d,* ventral view, ×1.5; *e–h,* paratype, serial sections 0.9, 1.2, 1.3, 1.6 mm from posterior, ×3 (Cooper & Dutro, 1982).

Myrmirhynx HAVLÍČEK, 1982b, p. 366 [**Rhynchonella myrmex* BARRANDE, 1879b, pl. 28, case 3, fig. 1–15; OD]. Shell small; subtriangular outline; moderately biconvex with shape dominated by strong plicae. Ventral beak erect to incurved; foramen with disjunct deltidial plates. Dorsal fold and ventral sulcus low but with distinct margins. Plicae increasing by bifurcation and intercalation; anterior commissure sulciplicate. Dental plates short, converging ventrally toward valve floor. Short septalium with cover; cardinal process absent. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Bohemia.——FIG. 715,*1a–h.* **M. myrmex* (BARRANDE), Ludlow, *Cromus beaumonti* layer, Kopanina Formation, Zadni Kopanina; *a–c,* hypotype, dorsal, ventral, and anterior views, ×5; *d–h,* hypotype, serial sections 7.95, 7.80, 7.65, 7.60, 7.50 mm from anterior, ×12 (Havlíček, 1982b).

Nasonirhynchia HAVLÍČEK, 1992, p. 83 [**N. naso;* OD]. Subpentagonal outline with emarginate anterior; strongly biconvex, inflated anteriorly. Beak erect to incurved, deltidial plates unknown. Dorsal fold and ventral sulcus strong with steep margins, arising at umbones: tongue high, dentate. Plicae strong, simple, angular, weak on umbones and flanks. Dental plates distinct but short; subvertical. Well-developed septalium with cover plate; dorsal median septum low; cardinal process absent; crura unknown. *Lower Devonian (Pragian):* Bohemia.——FIG. 712,*2a–f.* **N. naso,* Koneprusy Limestone, Zlaty kun Hill; *a–c,* holotype, ventral, anterior, and lateral views, ×2; *d–f,* topotype, serial sections 14.25, 13.25, 13.0 mm from anterior, ×3.8 (Havlíček, 1992).

Nekhoroshevia BUBLICHENKO, 1956, p. 101 [**N. altaica;* OD]. Subpentagonal outline; strongly dorsibiconvex to inflated. Beak incurved. Fold and sulcus very wide with rounded margins, arising at umbones. Costae rounded to flattened, from beaks. Dental plates vertical; dorsal median septum high, slender; septalium deep, with convex cover; crura unknown. *Upper Devonian (lower Famennian)–Lower Carboniferous (upper Tournaisian):* Altai, Kazakhstan, Verkhoyan.——FIG. 716,*2a–e.* **N. altaica; a–d,* holotype, dorsal, ventral, anterior, and

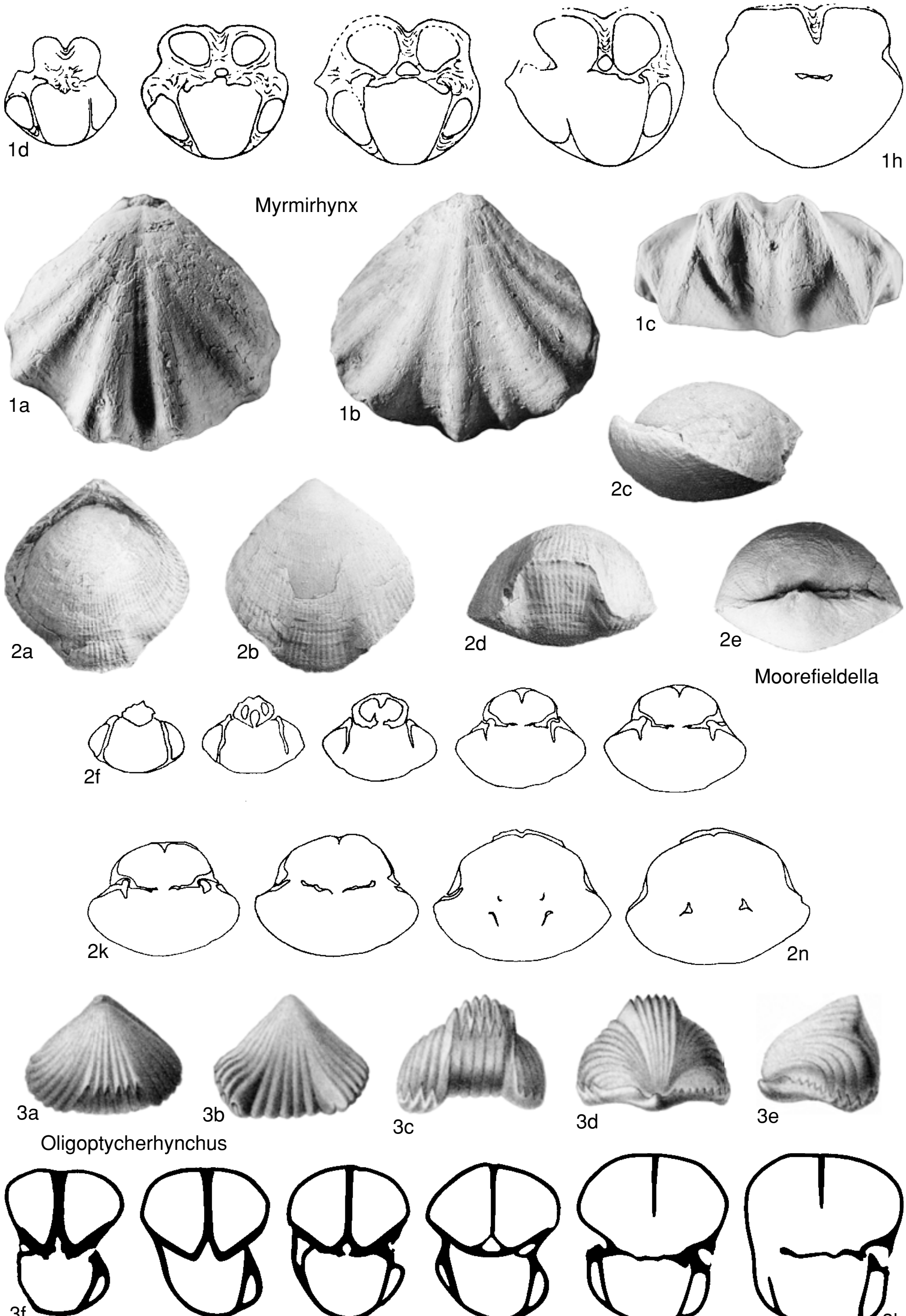

FIG. 715. Trigonirhynchiidae (p. 1059–1062).

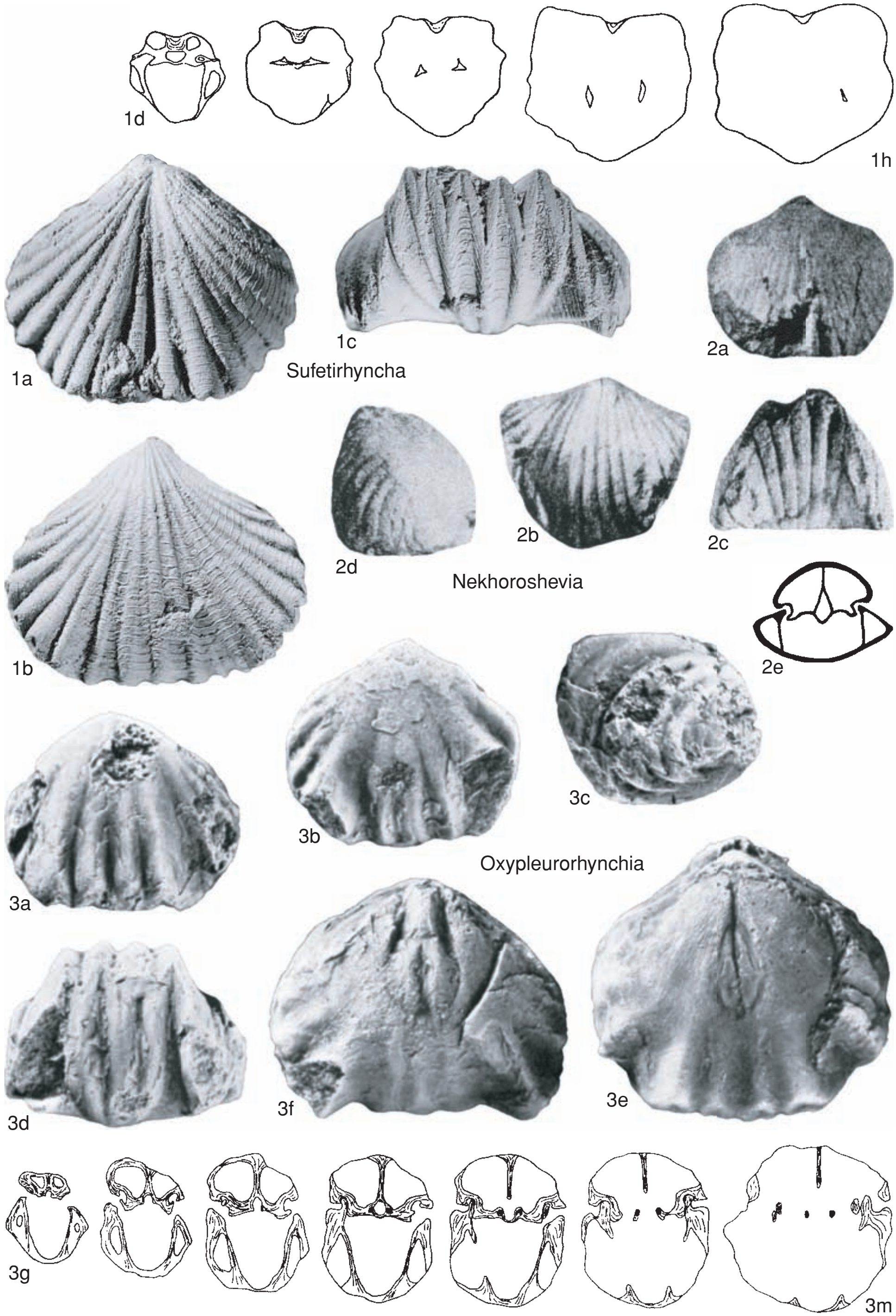

FIG. 716. Trigonirhynchiidae (p. 1059–1062).

lateral views, ×1; *e,* serial section near posterior, ×2 (Bublichenko, 1974).

Oligoptycherhynchus Sartenaer, 1970a, p. 20 [**Terebratula hexatoma* Schnur, 1851, p. 3; OD]. Subtrigonal to subpentagonal outline; strongly dorsibiconvex; beak suberect to erect. Fold and sulcus strong; arising at umbones; anterior commissure uniplicate; tongue high, rectangular, dentate. Costae strong, simple, angular, from beaks. Dental plates distinct, ventrally convergent. Dorsal median septum long, high; septalium with cover anteriorly; crura unknown. *Lower Devonian (lower Emsian)–Middle Devonian (upper Eifelian):* Europe, Morocco, Canada.——Fig. 715,*3a–k.* **O. hexatomus* (Schnur), lower Eifelian, Gondelsheimer Formation, Geeser bed, Uxheim, Eifel, Germany; *a–e,* dorsal, ventral, anterior, posterior, and lateral views of original figured specimen, ×2.6 (Schnur, 1853); *f–k,* serial sections of specimen from same formation, ×4 (Schmidt, 1941a).

Oxypleurorhynchia Plodowski, 1973, p. 85 [**O. acutiplicata;* OD]. Subtrigonal to subpentagonal outline and dorsibiconvex profile. Beak erect to incurved; foramen small. Fold and sulcus pronounced, from umbones; tongue high in mature specimens. Costae coarse, rounded, simple, arising at umbones. Dental plates well developed, ventrally convergent; ventral muscle field narrow, bilobed, with marginal rim. Dorsal median septum prominent, extending to valve midlength; septalium long, with cover for part of length; crura closely set, rodlike proximally. *upper Silurian (Přídoli):* Austria (Carnic Alps).——Fig. 716,*3a–m.* **O. acutiplicata,* lower Přídolí, upper "eosteinhornensis" Zone, Lawinenrinne am E-Hang des Cellon, Carnic Alps; *a–d,* paratype, dorsal, ventral, lateral, and anterior views, ×2; *e,* holotype, dorsal surface of internal mold; *f,* holotype, ventral surface of internal mold, ×3; *g–m,* serial sections 0.7, 0.8, 1.3, 1.4, 1.6, 1.8, 2.2 mm from posterior, ×3.5 (Plodowski, 1973).

Sinotectirostrum Sartenaer, 1961c, p. 3 [**S. medicinale;* OD]. Equidimensional to elongate subpentagonal outline; dorsibiconvex. Beak erect to incurved; foramen small, epithyrid. Fold and sulcus low; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, from beaks. Dental plates short, slender, vertical; teeth arising from valve margins; ventral muscle field moderately impressed. Hinge plates united; septalium with cover plate anteriorly; crural bases horizontal; crura with gutterlike surface directed dorsomedially. *Upper Devonian (Famennian):* Canada, ?Belorussia.——Fig. 717,*2a–o.* **S. medicinale,* Alexo Formation, Medicine Lake, Alberta, Canada; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–o,* paratype, serial sections 1.60, 1.95, 2.3, 2.6, 2.8, 3.0, 3.35, 3.8, 4.4, 4.75 mm from posterior, ×3 (Sartenaer, 1969).

Stenorhynchia Brice, 1981b, p. 195 [**Terebratula nympha* Barrande, 1847, p. 66; OD] [=*Stenorhynchites* Havlíček in Havlíček & Štorch, 1990, p. 145 (type, *Rhynchonella infelix* Barrande, 1879b, pl. 28, case 1, fig. 3–4)]. Subpentagonal outline and strongly dorsibiconvex, inflated, profile; lateral and anterior shell margins precipitous. Fold and sulcus strong, wide, from umbones, with high anterior tongue. Beak erect to incurved. Costae strong, simple, from beaks; interspaces extended into spines at anterior commissure. Dental plates distinct, well separated from valve walls. Dorsal median septum long; septalium perforate posteriorly but covered anteriorly; cardinal process absent; crural bases arising from septalium cover plates; crura ventrally curved, convex ventrolaterally in cross section. *upper Silurian (Ludlow)–Lower Devonian (Emsian):* Europe, northern Africa, Urals, Tadzhikistan, Mongolia.——Fig. 717,*1a–p.* **S. nympha* (Barrande), Lower Devonian; *a–d,* neotype, dorsal, ventral, anterior, and lateral views, Koneprusy Limestone, Koneprusy, Bohemia, ×1; *e–h,* hypotype, serial sections 10.5, 10.3, 10.2, 10.1 mm from anterior, Koneprusy Limestone, Koneprusy, Bohemia, ×2.5 (Havlíček, 1961); *i–p,* hypotype, serial sections 1.0, 1.1, 1.2, 1.7, 2.0, 2.6, 2.9, 3.2 mm from posterior, upper Emsian, Marettes Formation, Brittany, France, ×3 (Brice, 1981b).

Sufetirhyncha Havlíček, 1982b, p. 367 [**Ancillotoechia radvani* Havlíček, 1961, p. 62; OD]. Small to medium with subpentagonal outline and dorsibiconvex profile. Beak straight to suberect. Dorsal fold and ventral sulcus low but distinct, wide anteriorly; fold with median depression, sulcus with corresponding low rise; anterior commissure sulciplicate; tongue low, broad, dentate. Costae strong, increasing by bifurcation and intercalation, from beaks; crossed by concentric rugae. Dental plates very short, converging toward valve floor. Dorsal median septum short; septalium low, with cover plate; crural bases triangular; crura laterally compressed. *upper Silurian (Ludlow):* Bohemia.——Fig. 716,*1a–h.* **S. radvani* (Havlíček), Kopanina Formation, Velka Morina; *a–c,* hypotype, dorsal, ventral, and anterior views, ×3.8; *d–h,* hypotype, serial sections 5.3, 5.15, 4.85, 4.55, 4.4 mm from anterior, ×9 (Havlíček, 1982b).

Tetratomia Schmidt, 1941a, p. 13 [**Terebratula tetratoma* Schnur, 1851, p. 4; OD]. Small with elongate subtriangular to subpentagonal outline and biconvex profile. Beak erect to incurved. Fold and sulcus strong, narrow, from umbones; anterior commissure uniplicate, strongly serrate. Costae strong, simple, from beaks. Dental plates short, vertical, may be obscured by callus. Dorsal median septum short; hinge plates united by convex plate; septalium absent; cardinal process absent; crura laterally compressed. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Europe, Morocco.——Fig. 718,*1a–j.* **T. tetratoma* (Schnur), lower Eifelian, Eifel, Germany; *a–c,* ventral, lateral, and anterior views, ×2 (Schmidt, 1941a); *d–j,* serial sections, ×5.3 (McLaren, 1965).

Wilsoniella Khalfin, 1939, p. 83, *non Wilsonella* Nikiforova, 1937a [**W. prima;* OD] [=*Ussovia* Khalfin, 1955, p. 239, obj.]. Large with elongate-

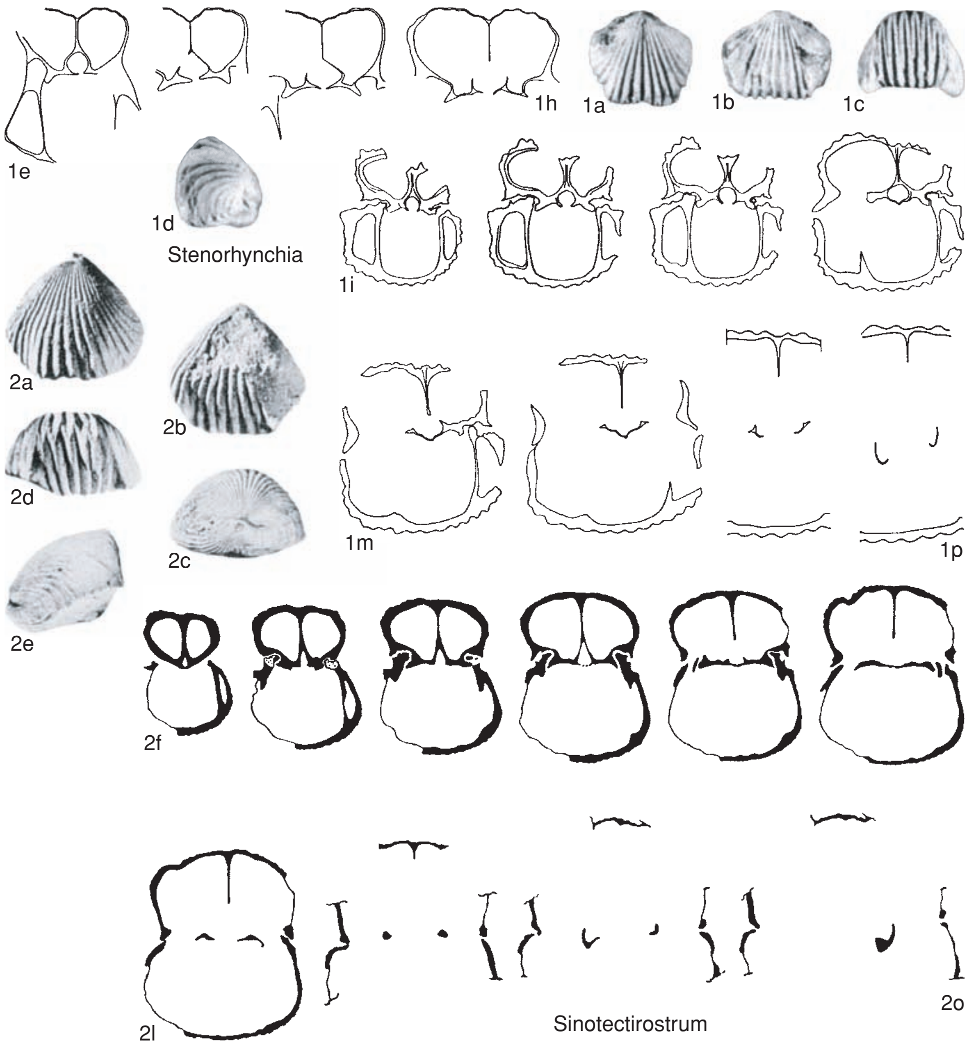

FIG. 717. Trigonirhynchiidae (p. 1062).

oval to subtrigonal outline and inflated dorsibiconvex profile. Beak incurved; foramen small. Fold and sulcus developed anteriorly; anterior commissure uniplicate; tongue high, trapezoid. Costae numerous, simple, arising at beaks, rounded in profile with narrow interspaces, flattened anteriorly. Dental plates convex medially. Hinge plates united posteriorly; dorsal median septum low, long; septalium covered posteriorly but open, large, and wide anteriorly where supported on median septum; crural bases arising from vertical walls of septalium, crura laterally flattened. *Lower Devonian (Pragian–Emsian):* Altay, Mongolia.——FIG. 718,*2a–d.* **W. prima,* Pragian, northwestern Mongolia; dorsal and lateral, ventral and lateral views, ×1 (Erlanger, 1994).——FIG. 718,*2e–m. W. prisca* ERLANGER, Pragian, northwestern Mongolia; serial sections 3.3, 3.85, 4.2, 4.7, 5.3, 5.7, 5.85, 7.1, 8.25 mm from posterior, ×1.75 (Erlanger, 1994).

Subfamily ROSTRICELLULINAE Rozman, 1969

[Rostricellulinae ROZMAN, 1969, p. 94]

Early Trigonirhynchiidae with uncovered septalium and costae crossed by distinct concentric lamellae; delthyrium open or with

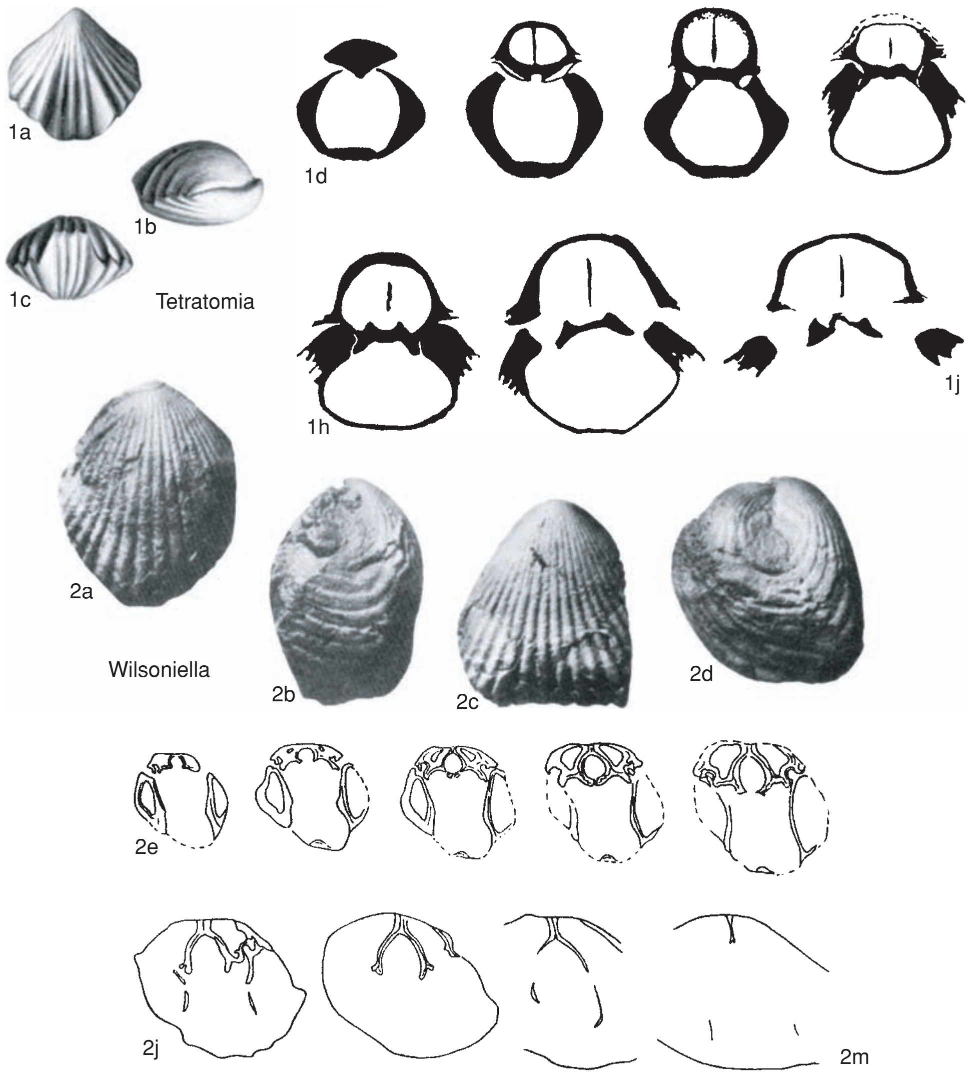

FIG. 718. Trigonirhynchiidae (p. 1062–1063).

incipient deltidial plates; dorsal median septum short. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery).*

Rostricellula ULRICH & COOPER, 1942, p. 625 [**R. rostrata;* OD] [=*Longxianirhynchia* FU, 1982, p. 143 (type, *L. transversa,* OD)]. Subtrigonal to subpentagonal outline; moderately biconvex. Beak erect to incurved; delthyrium open to partly closed by incipient deltidial plates. Fold and sulcus distinct with rounded margins; anterior commissure uniplicate; tongue low, serrate. Costae fine to medium, simple, extending from umbones; crossed by concentric growth lamellae. Dental plates distinct but short. Dorsal median septum to midlength; septalium short, without cover; hinge plates divided anterior of septalium; crural bases subhorizontal; crura distally slender, ventrally curved. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery):* North America, Europe, Asia.——FIG. 719,*1a–h.* **R. rostrata,* Lebanon Formation, Middle Ordovician, Clinton, Tennessee, USA; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f,* paratype, ventral valve interior, ×2; *g–h,* paratypes, dorsal valve interiors showing cardinalia and crura, ×4 (Ulrich & Cooper, 1942).

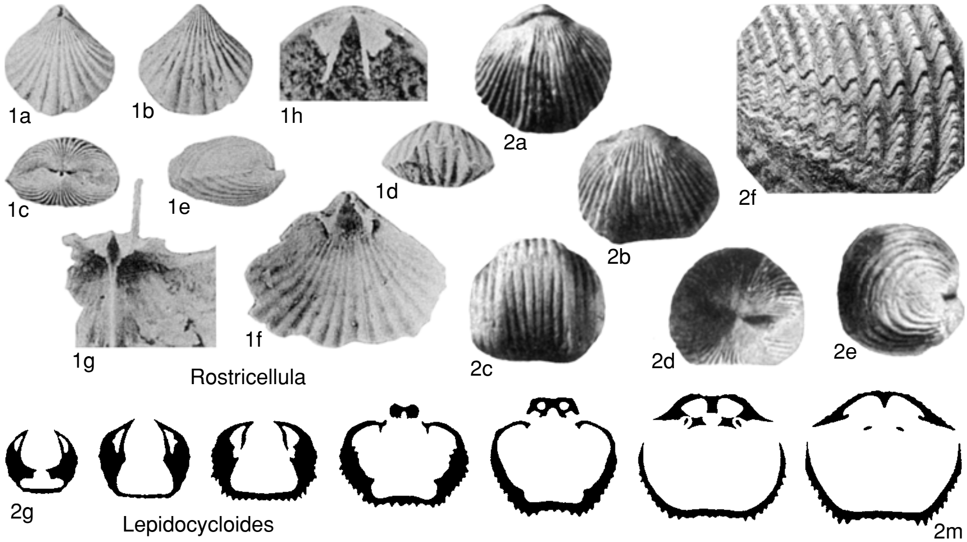

FIG. 719. Trigonirhynchiidae (p. 1064–1065).

Azamella LAURIE, 1991, p. 93 [**A. rotunda;* OD]. Transversely ovate outline; strongly biconvex. Beak erect to incurved; delthyrium open. Fold and ventral sulcus with rounded margins; anterior commissure weakly uniplicate; costae strong, simple, extending from umbones, crossed by lamellose concentric growth lines. Dental plates distinct but short; ventral muscle field well impressed. Hinge plates divided anterior of short septalium, without cover; dorsal median septum long, to midlength; crura ventrally curved. *Lower Ordovician (upper Llanvirn):* southeastern Australia (Tasmania).——FIG. 720,*2a–h. *A. rotunda,* Benjamin Limestone, lower Limestone Member, Florentine Valley; *a–d,* holotype, dorsal, ventral, anterior, and lateral views; *e–f,* paratype, interior views of ventral valve; *g,* paratype, interior of dorsal valve; *h,* paratype, interior of dorsal valve showing crura, ×3.25 (Laurie, 1991).

Evenkorhynchia ROZMAN, 1969, p. 102 [**Rostricellula dichotomians* ROZMAN, 1968, p. 71; OD]. Subcircular to subpentagonal outline and biconvex to dorsibiconvex profile. Beak suberect to erect; delthyrium open with narrow rudimentary deltidial plates. Fold and sulcus flattened, distinct anteriorly; anterior commissure uniplicate; tongue prominent, trapezoid. Costae strong, rounded, from beaks, some intercalation and bifurcation, crossed by fine tuberculate growth lamellae. Dental plates short, vertical. Dorsal median septum short, thick; septalium short, open; crural bases horizontal; crura distally slender, ventrally curved. *Upper Ordovician (upper Caradoc–Ashgill):* northeastern Siberia.——FIG. 720,*3a–i. *E. dichotomians* (ROZMAN), Ashgill, Nirundinian, Selennyakh Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–i,* serial sections 0.8, 1.0, 1.2, 1.4, 2.3 mm from posterior, ×6 (Rozman, 1970).

Lepidocycloides NIKIFOROVA, 1961, p. 212 [**L. baikiticus;* OD]. Medium to large size; globular. Beak incurved; foramen mesothyrid, delthyrium open, deltidial plates absent. Fold and sulcus distinct, arising at umbones; tongue high, rectangular to subrounded. Costae fine, simple, or with rare bifurcations, arising at beaks; crossed by distinct concentric lamellae. Dental plates short, vertical to ventrally divergent; ventral muscle area deeply impressed. Septalium short, open, wide; dorsal medium septum low, short. *Upper Ordovician (Caradoc–Ashgill):* central Siberia, Altai, China.——FIG. 719,*2a–m. *L. baikiticus,* Dolborsky Stage, lower Chunku River, Baikit; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* enlargement of costae showing lamellae, ×4; *g–m,* serial sections 14.1, 13.8, 13.5, 12.8, 12.1, 11.6, 11.3 mm from anterior, ×1.5 (Nikiforova, 1961).

Plectothyrella TEMPLE, 1965, p. 412 [**P. platystrophoides;* OD; =*P. crassicosta* (DALMAN), 1828, p. 131]. Subcircular to subtrigonal; strongly biconvex. Beak suberect; delthyrium open. Dorsal fold and ventral sulcus from umbones but faint ventral fold and dorsal sulcus posteriorly. Costae strong, subangular, from beaks; some intercalation. Growth lamellae closely spaced; strongest anteriorly. Dental plates convergent ventrally; teeth small, cyrtomatodont; ventral muscle field deeply impressed. Dorsal median septum low, thick; septalium short, without cover; hinge plates divided; inner socket ridges massive; sockets thin; crural bases thick; crura long, thick. *Upper Ordovician (Ashgill):* Europe, eastern North America, northern Africa, South Africa, South America, Siberia, China.——FIG. 720,*1a–e.*

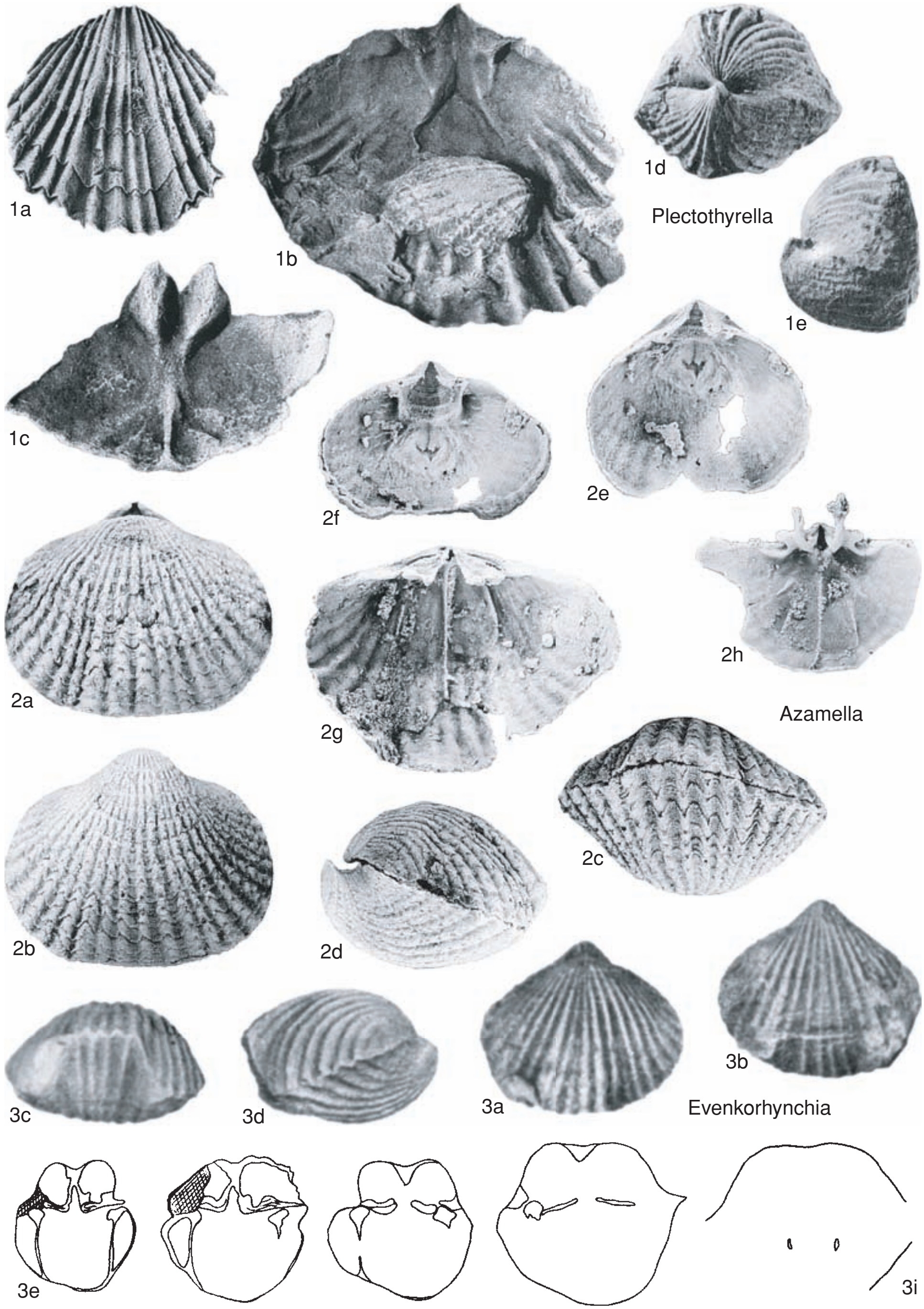

FIG. 720. Trigonirhynchiidae (p. 1065–1067).

**P. crassicosta* (DALMAN), upper Ashgill, Hirnantian; *a,* ventral valve exterior, Bestorp, Sweden, ×1.2; *b,* interior of same, Bestorp, Sweden, ×2; *c,* interior of dorsal valve posterior, Bestorp, Sweden, ×2.6 (Bergström, 1968); *d–e,* posterior and lateral of broken conjoined shell, Quebec, Percé, Canada, ×1.5 (Lespérance & Sheehan, 1976).

Subfamily HEMITOECHIINAE Savage, 1996

[Hemitoechiinae SAVAGE, 1996, p. 252]

Trigonirhynchiidae with uncovered septalium. *Lower Ordovician (Llanvirn)–Lower Carboniferous (Tournaisian).*

Hemitoechia NIKIFOROVA, 1970, p. 103 [**H. distincta;* OD] [=*Linterella* AMSDEN, 1988, p. 20 (type, *Camarotoechia perryvillensis* AMSDEN, 1949a, p. 56, OD); *Undulorhyncha* AMSDEN, 1988, p. 21 (type, *"Camarotoechia" hollandi,* OD); *Pseudocamarotoechia* KULKOV, 1974, p. 53 (type, *P. nuculaeformis,* OD); *Tichirhynchus* BARANOV, 1989, p. 42 (type, *T. settedabanicus,* OD)]. Subcircular to subpentagonal outline; biconvex. Beak suberect; small foramen, deltidial plates not recorded. Fold and sulcus moderately strong, with gentle margins; anterior commissure uniplicate; tongue trapezoid, serrate. Costae medium, simple, rounded, from umbones. Dental plates distinct, slightly concave medially. Dorsal median septum long but low; septalium without cover; cardinal process absent; crural bases subtriangular; crura strongly curved ventrally. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian):* cosmopolitan.——FIG. 721,*1a–m.* **H. distincta,* upper Silurian, Chatanzeisky horizon, Vaigatch Island, Belushja Bay, Arctic Russia; *a–b,* holotype, dorsal and ventral views; *c–f,* paratype, dorsal, ventral, lateral, and anterior views, ×1; *g–m,* serial sections of posterior of another paratype (Nikiforova, 1970).

Alorostrum SAVITSKII, 1992, p. 107 [**A. elegans;* OD]. Transversely subpentagonal in outline and subequibiconvex profile. Beak suberect to erect. Fold and sulcus moderately strong, arising near umbones; anterior commissure uniplicate; tongue wide, trapezoid, dentate. Costae numerous, angular, arising at beaks and covering entire surface. Dental plates distinct, vertical to slightly convergent ventrally, extending past hinge line, well separated from valve walls. Dorsal median septum absent but with wide median ridge; hinge plates divided, horizontal; crural bases triangular in section; crura with crescentic section, concave medially. *Lower Devonian (upper Emsian):* Tian Shan.——FIG. 721,*2a–j.* **A. elegans,* Liaglian Horizon, Alaisk Range, Liaglian River, southern Tian Shan; *a–b,* holotype, dorsal and anterior views; *c,* hypotype, lateral view, ×1; *d–j,* serial sections 1.1, 1.3, 1.8, 2.2, 2.6, 2.9, 3.8 mm from posterior, ×4 (Savitskii, 1992).

Bathyrhyncha FUCHS, 1923, p. 854 [**B. sinuosa;* OD]. Medium to large size with dorsibiconvex, inflated profile. Fold and sulcus distinct, arising at umbones; anterior commissure uniplicate; tongue pronounced, trapezoid. Costae arising at or near beaks. Dental plates long; ventral muscle field well impressed, elongate. Dorsal median septum long; septalium seemingly without cover. Other external and internal features poorly known. *Lower Devonian (Lochkovian):* Belgium, Germany.——FIG. 722,*2a–c.* **B. sinuosa,* upper Gedinnian, Schistes de Weismes, Malmedy, Gdoudmont, Belgium; *a,* holotype, ventral internal mold, ×1 (Dahmer, 1942); *b–c,* anterior and posterior views of internal mold, ×2 (Boucot, 1960).

Browneella CHATTERTON, 1973, p. 117 [**B. browneae;* OD]. Small to medium size with subpentagonal outline and dorsibiconvex profile. Beak erect to suberect; delthyrium open; deltidial plates narrow, disjunct. Fold and sulcus developed anteriorly; anterior commissure uniplicate; tongue trapezoid. Costae strong, arising at beaks, some multiplication. Dental plates short. Dorsal median septum weak; septalium small, without cover; hinge plates divided anterior of septalium; crura radulifer; cardinal process unknown. *Lower Devonian (Emsian):* southeastern Australia.——FIG. 721,*3a–g.* **B. browneae,* upper Emsian, "*Receptaculites*" Limestone, Yass, New South Wales; *a,* holotype, dorsal view, ×3.7; *b,* holotype, ventral view, ×2.75; *c,* holotype, lateral view, ×3.7; *d,* paratype, anterior view, ×2.5; *e,* ventral valve interior; *f,* interior of dorsal valve posterior, ×5; *g,* reconstruction of posterior of dorsal valve interior (Chatterton, 1973).

Centrorhynchus SARTENAER, 1970a, p. 11 [**Camarotoechia baitalensis* REED, 1922, p. 94; OD]. Medium to large with subpentagonal outline and dorsibiconvex profile. Beak suberect; foramen circular, mesothyrid; deltidial plates disjunct to conjunct. Fold and sulcus arising at umbones, prominent anteriorly; anterior commissure uniplicate; tongue high, trapezoid, triplicate to quadruplicate. Costae strong, simple, subangular, from beaks. Shell thick. Dental plates short, convergent ventrally; teeth short, strong, crenulated; ventral muscle field flabellate, deeply impressed. Dorsal median septum thick, long, fairly high; septalium moderately wide and long, usually with posterior cover plate; hinge plates divided immediately anterior of septalium, horizontal; sockets large and crenulated; dorsal muscle field distinct; crura closely set, ventrally curved, distal part with gutterlike section open dorsally. *Upper Devonian (Famennian):* Iran, Afghanistan, Turkey, Pamir, China, western Europe, Russia, North America, Australia.——FIG. 721,*4a–c.* **C. baitalensis* (REED), Ak Baital, Pamir; *a–b,* lectotype, dorsal and ventral views; *c,* anterior view of different specimen, ×1.5 (Reed, 1922).——FIG. 721,*4d–l. C. charakensis* (BRICE), Afghanistan, Ghouk; serial sections 0.7, 1.0, 1.6, 1.9, 2.0, 2.5, 3.3, 3.7, 4.1 mm from posterior, ×2 (Brice, 1970).

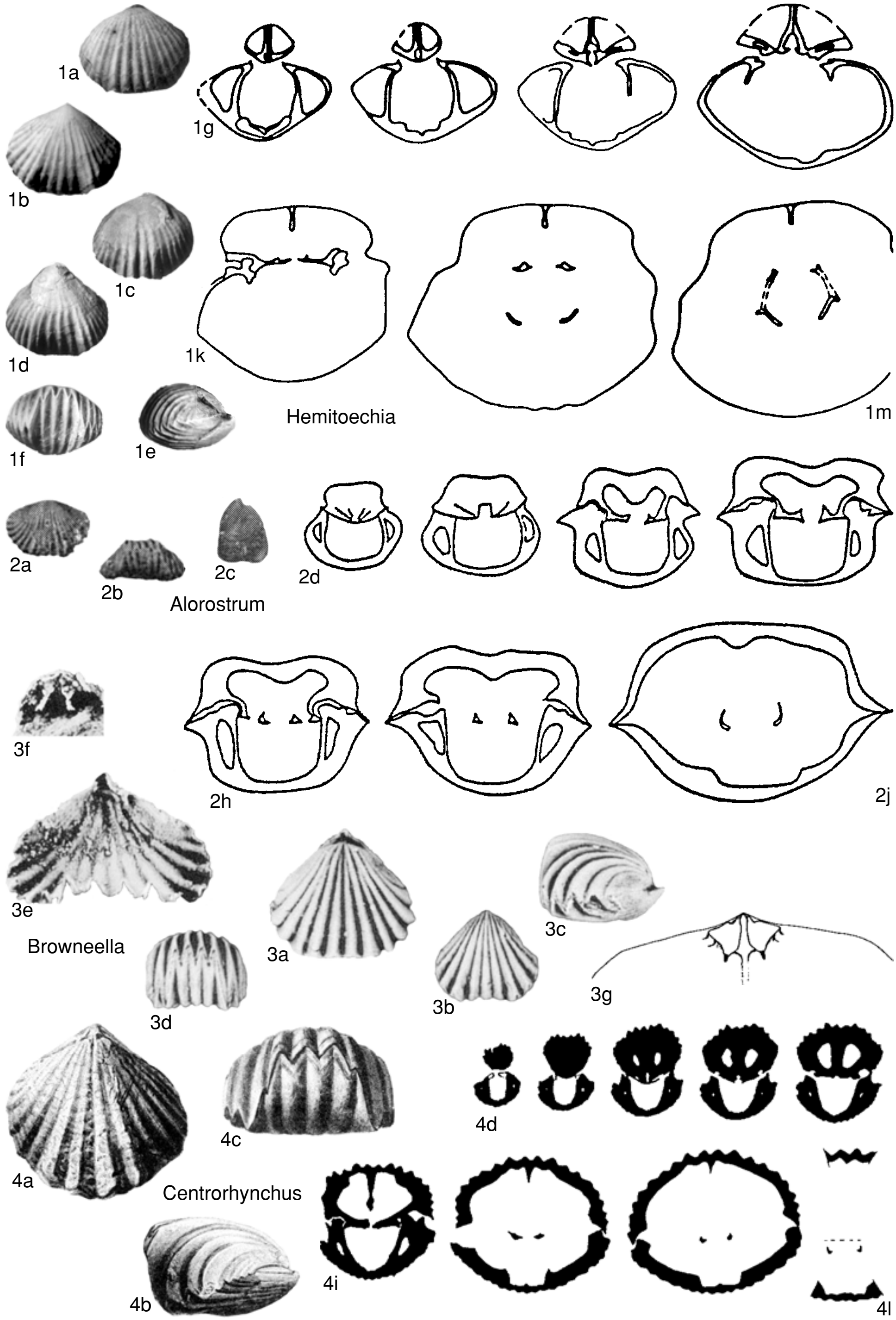

FIG. 721. Trigonirhynchiidae (p. 1067).

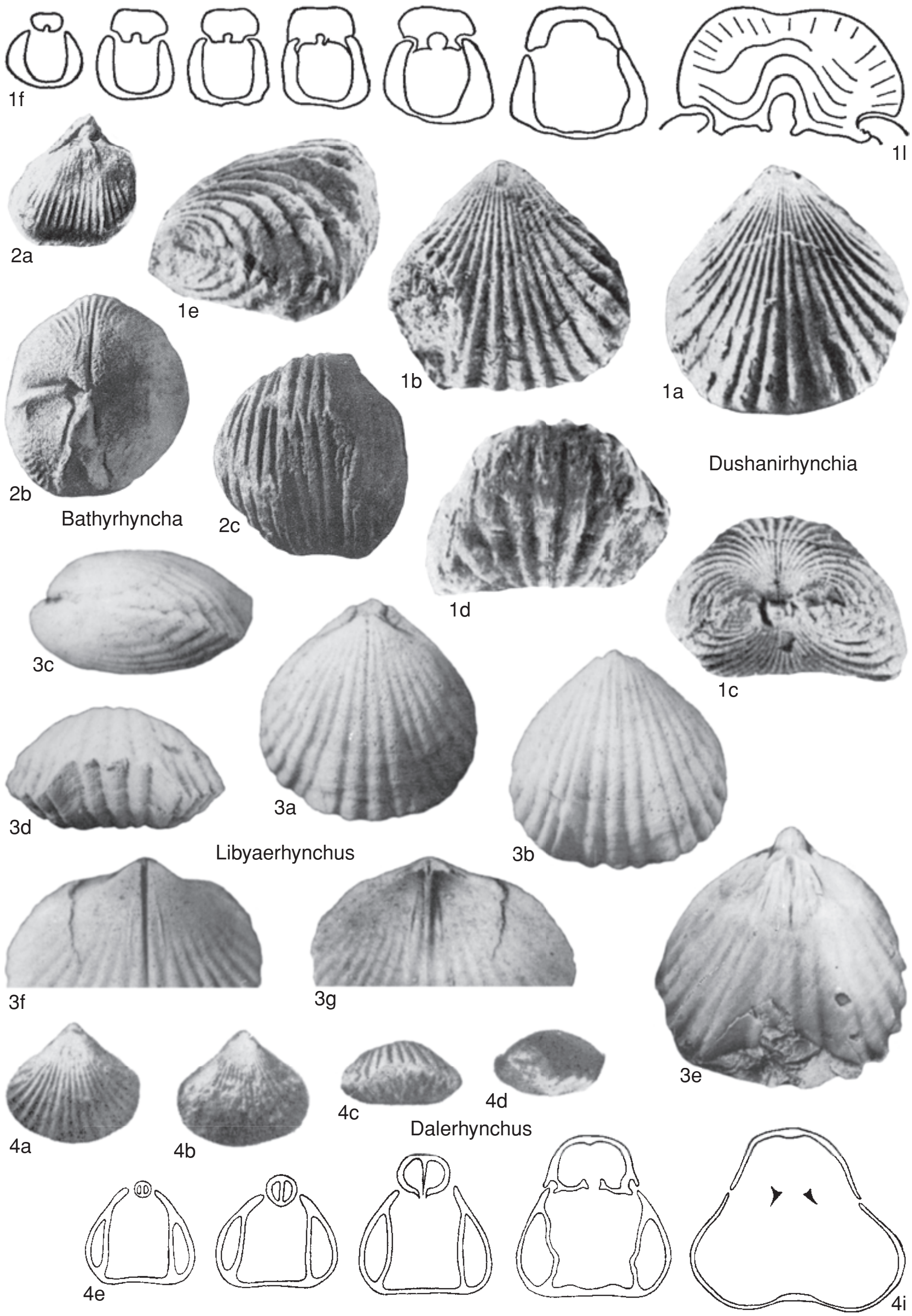

FIG. 722. Trigonirhynchiidae (p. 1067–1070).

Dalerhynchus Bai, 1978, p. 51 [**D. dingshanlingensis;* OD]. Transversely subpentagonal outline and moderately biconvex profile. Beak erect to suberect; large foramen at apex. Fold and sulcus very weak; anterior commissure weakly uniplicate. Costae numerous, simple, subangular, arising at beaks. Dental plates convex medially. Dorsal median septum short, low; septalium and cardinal process absent; crural bases triangular in section; crura strongly curved ventrally. *Lower Devonian (Emsian):* China.——Fig. 722,*4a–i.* **D. dingshanlingensis,* Dale Formation, Xiangzhou County, Dale, Guangxi; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i,* serial sections, interval and scale not given (Bai, 1978).

Dushanirhynchia Wang & Zhu, 1979, p. 42 [**D. inflata;* OD]. Subpentagonal in outline and strongly biconvex profile. Beak erect to incurved; foramen not observed. Fold and sulcus strong, from umbones; tongue high. Numerous strong, angular, simple costae extending from beak. Shell wall thick. Dental plates weak or obscured in thick callus of shell wall. Divided hinge plates resting on thick callus. Dorsal median septum and septalium absent. *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* southern China.——Fig. 722,*1a–l.* **D. inflata,* Eifelian, Longdongshui Formation, Guizhou, Houershan; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×2; *f–k,* serial sections at 0.95, 1.50, 1.55, 1.9, 2.1, 2.4 mm from posterior, ×2.5; *l,* serial section of dorsal valve at 1.75 from posterior, ×5 (Wang & Zhu, 1979).

Lenatoechia Nikiforova, 1970, p. 106 [**Camarotoechia elegans* Nikiforova, 1961, p. 205; OD]. Small to medium; subcircular to transversely ovate in outline; biconvex with gentle lateral and anterior slopes. Beak erect to suberect; delthyrium open apically, deltidial plates poorly known but may be disjunct. Fold and sulcus moderate, from midlength; anterior commissure uniplicate with low rounded tongue. Costae fine, numerous, simple, evenly covering fold, sulcus, and flanks. Dental plates long, concave medially. Dorsal median septum low, long, thick; septalium wide, long, without cover; cardinal process absent; crura poorly known. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow):* northern Siberian platform, Novaya Zemlya, northern Urals.——Fig. 723,*3a–h.* **L. elegans* (Nikiforova), Llandovery, northern Siberian platform, Morkoka River, Lena River Basin; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×2; *e–h,* paratype, serial sections 13.8, 13.7, 13.3, 12.7 mm from anterior, ×6 (Nikiforova, 1961).

Libyaerhynchus Mergl & Massa, 1992, p. 65 [**L. fragosus;* OD]. Subcircular to elongate oval in outline and subequibiconvex profile. Beak suberect to erect. Fold and sulcus low, arising at umbones, fold with flat crest; anterior commissure uniplicate; tongue low, trapezoid. Costae strong, simple, subangular, from umbones. Dental plates short, convergent ventrally; teeth large; ventral muscle field gently impressed, subovate. Dorsal median septum thick, long, fairly high; septalium small, narrow, open; hinge plates small, horizontal; sockets narrow, widely divergent; dorsal muscle field weakly impressed, elongate; no cardinal process; crural bases short, widely divergent. *Upper Devonian (lower Frasnian–upper Famennian):* Libya.——Fig. 722,*3a–g.* **L. fragosus,* lower Frasnian, Aouinet Ouenine II Formation, Ghadamis Basin, Awaynat Wanin type section; *a–d,* dorsal, ventral, lateral, and anterior views of steinkern, ×2; *e,* holotype, ventral valve internal mold, ×1.4; *f–g,* dorsal valve, internal mold and latex cast, ×2 (Mergl & Massa, 1992).

Losvia Breivel & Breivel, 1976, p. 116 [**Pugnoides(?) operosa* Khodalevich, 1951, p. 53; OD]. Medium to large with subtriangular to flabellate outline; dorsibiconvex profile with precipitous lateral and anterior margins and concave posterolateral margins. Beak erect; foramen and deltidial plates not recorded. Fold and sulcus weak, extending from midlength; anterior commissure weakly uniplicate, dentate; tongue low to absent. Costae strong, angular, simple, almost straight, extending from beaks. Dental plates thin, vertical, very close to walls. Dorsal median septum long, high; septalium very short, without cover plate; cardinal process absent; crural bases triangular; crura closely set. *Lower Devonian (Emsian):* Urals.——Fig. 723,*1a–i.* **L. operosa* (Khodalevich), Emsian, Vizhaisk layer, Vizhai River; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1.3 (Khodalevich, 1951); *e–i,* serial sections of posterior, distances not given, ×4 (Breivel & Breivel, 1977).

Luterella Amsden, 1988, p. 20 [**Camarotoechia altisulcata* Amsden, 1951, p. 86; OD]. Transversely subpentagonal in outline and with dorsibiconvex profile. Beak suberect; foramen mesothyrid. Fold and sulcus strong, wide, from umbones; tongue high, trapezoid. Costae prominent, angular, simple, arising at beaks; anterior commissure strongly dentate. Dental plates vertical; ventral muscle field weakly impressed. Dorsal median septum short, low, supporting short, wide, uncovered septalium. *Silurian (Ludlow–Přídolí):* USA.——Fig. 723,*4a–d.* **L. altisulcata* (Amsden), Henryhouse Formation, Arbuckle Mountains, Oklahoma; *a–c,* holotype, dorsal, ventral, and anterior views, ×1; *d,* interior of posterior of dorsal valve, ×3 (Amsden, 1951).——Fig. 723,*4e–j.* *L. carmelensis* (Amsden), Brownsport Formation, Cedar Grove Church, western Tennessee; *e–g,* holotype, dorsal, lateral, and anterior views, ×1; *h,* interior of posterior of dorsal valve, ×5; *i–j,* transverse sections 1.5, 2.5 mm from posterior of different specimens, ×4 (Amsden, 1949a).

Nymphorhynchia Rzhonsnitskaia, 1956c, p. 53 [**N. bischofioides;* OD] [=*Wenxianirhynchus* Zhang Yan, 1983a, p. 316 (type, *W. platiformis,* OD)]. Subtrigonal to subpentagonal outline; delthyrium open. Fold and sulcus wide, low; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, from beaks. Dental plates very close to vertical valve walls; dorsal median septum high; septalium without cover; crura unrecorded. *upper Silurian (Přídolí)–Middle Devonian (Givetian):* Kuznetsk, Urals, Altai, Mongolia,

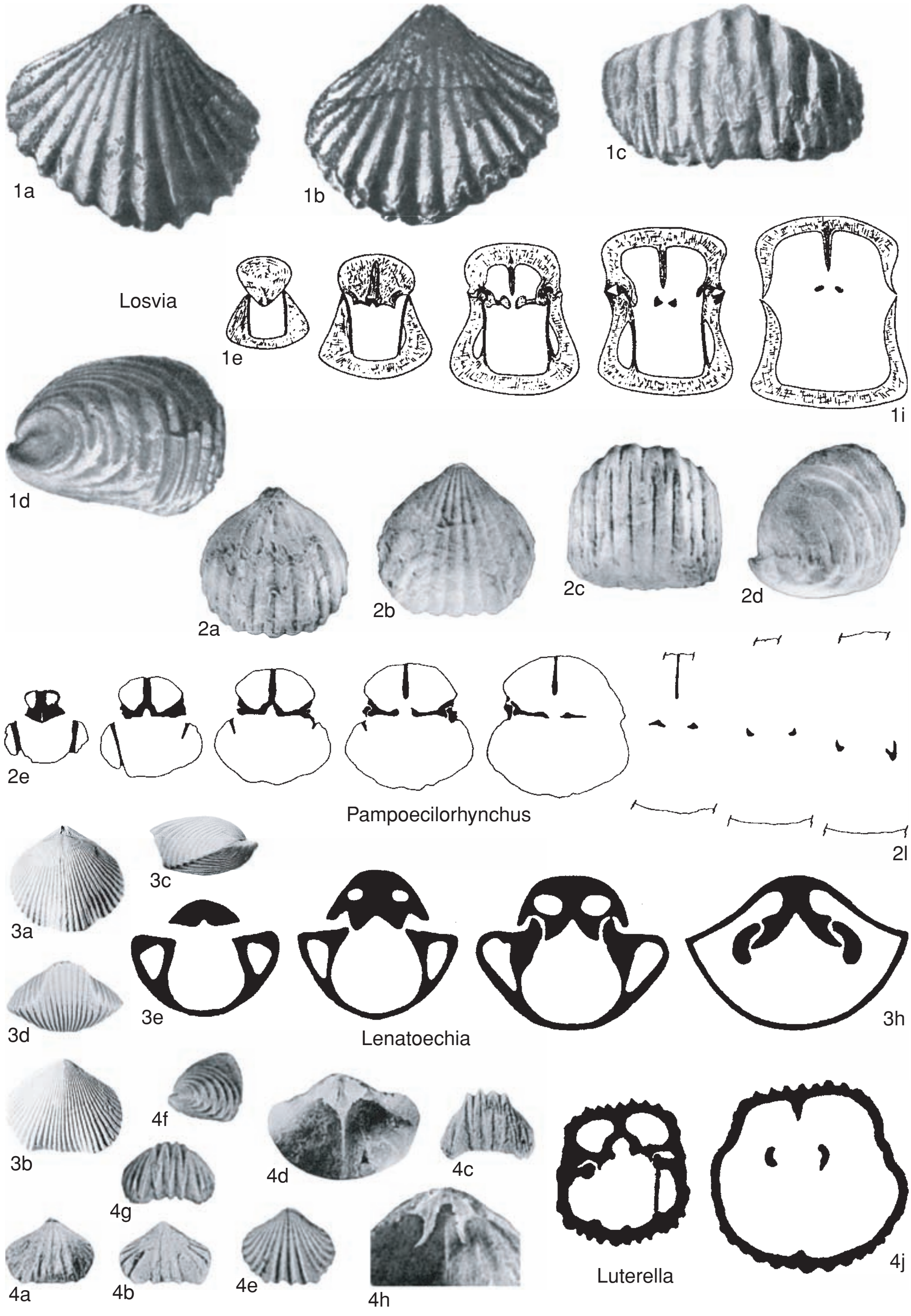

FIG. 723. Trigonirhynchiidae (p. 1070–1073).

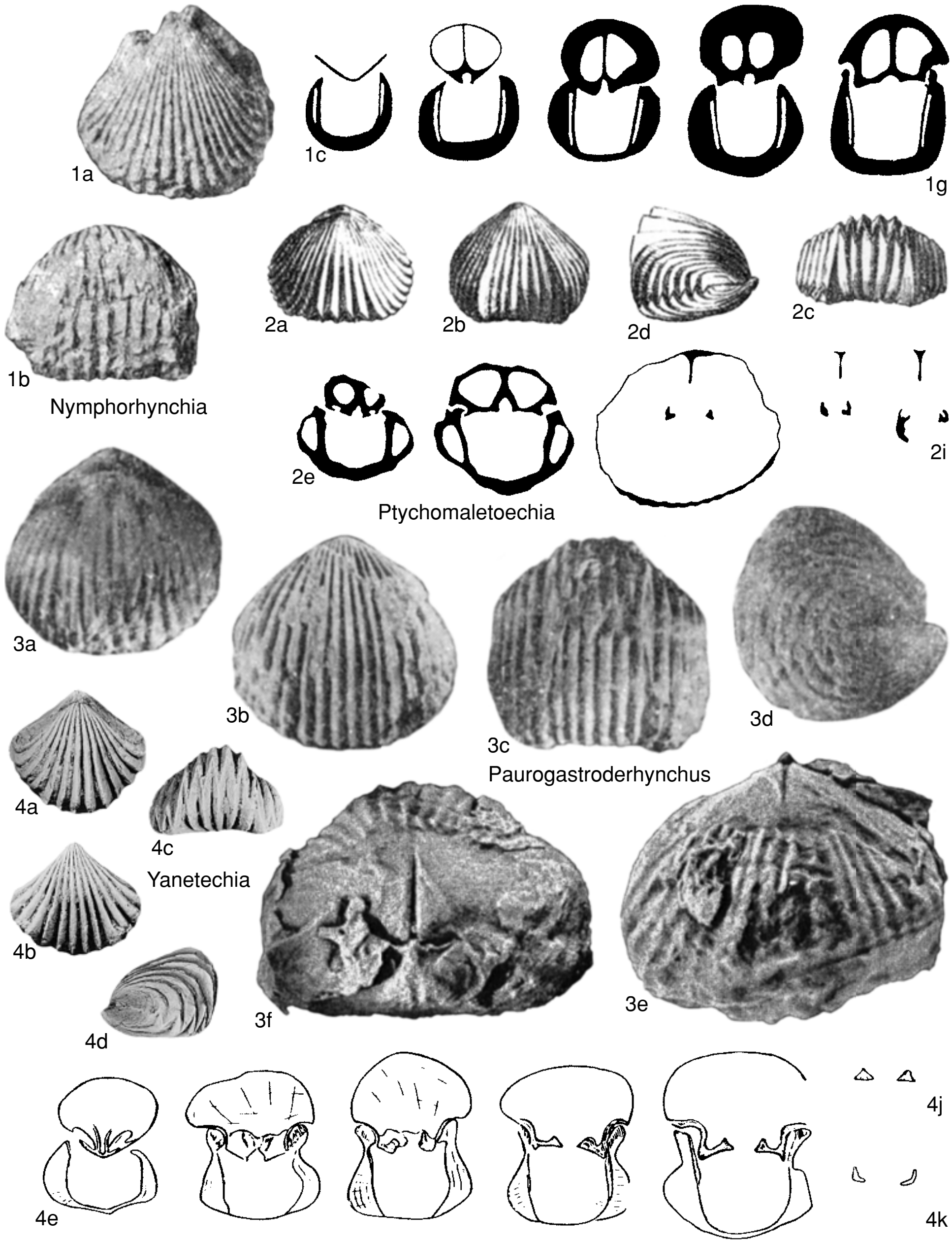

FIG. 724. Trigonirhynchiidae (p. 1070–1074).

China, Bohemia, Canada.——FIG. 724,*1a–g*. **N. bischofioides,* Kuznetsk, Eifelian; *a–b,* holotype, dorsal and anterior views, ×1.5; *c–g,* serial sections of posterior, ×3 (Rzhonsnitskaia, 1956c).

Pampoecilorhynchus SARTENAER, 1968d, p. 3 [**Rhynchonella nux* GOSSELET, 1887, p. 210; OD]. Medium to large with subpentagonal outline and dorsibiconvex globular profile. Beak erect; foramen small with disjunct deltidial plates. Fold and sulcus obscured by shell inflation; anterior commissure uniplicate; tongue high, often rounded, denticulate. Costae strong, simple, from beaks. Dental plates short, slightly convergent ventrally; ventral muscle field flabellate, not strongly impressed. Dorsal

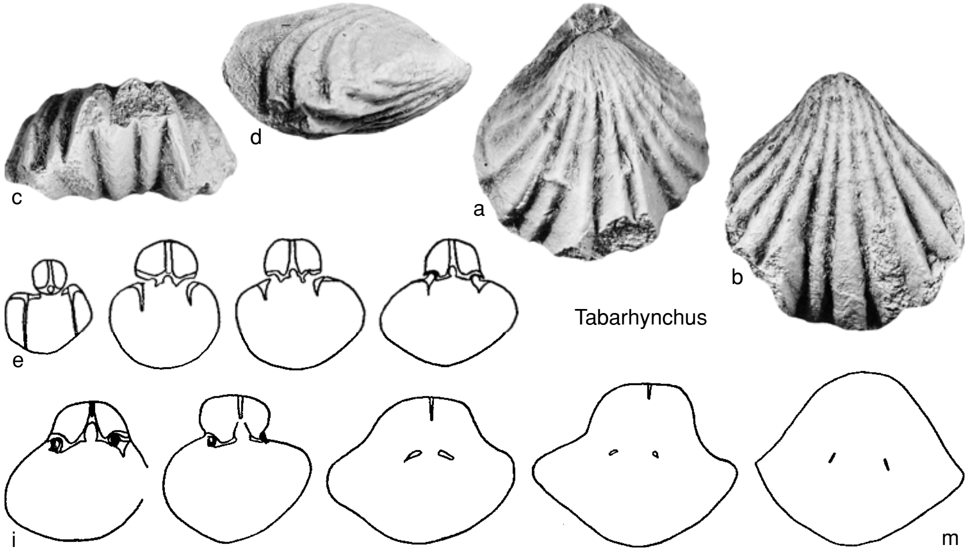

FIG. 725. Trigonirhynchiidae (p. 1073).

median septum thin, moderately high; septalium wide, long, V-shaped; hinge plates divided immediately anterior of septalium, horizontal; dorsal muscle field weak; crura short, only slightly ventrally curved, tips with phrygian cap section open dorsally. *Upper Devonian (lower Famennian):* Europe, Morocco, Iran, Afghanistan.——FIG. 723,*2a–l*. **P. nux* (GOSSELET), Belgium; *a–d,* dorsal, ventral, anterior, and lateral views, ×1 (Sartenaer, 1958); *e–l,* serial sections 0.95, 1.65, 1.85, 2.05, 2.65, 3.45, 4.8, 5.15 mm from posterior, ×2 (Sartenaer, 1968d).

Paurogastroderhynchus SARTENAER, 1970a, p. 25 [**Camarotoechia(?) nalivkini* ABRAMIAN, 1957, p. 48; OD]. Medium to large with subcircular outline and globular, biconvex profile. Beak erect to incurved. Fold and sulcus weak; anterior commissure uniplicate, tongue high. Costae strong, simple, straight, evenly developed over fold, sulcus, and flanks. Dental plates long. Dorsal median septum short, thick; septalium short; hinge plates divided anterior of septalium; crura with crescentic distal cross section. *Upper Devonian (upper Famennian):* Armenia, Iran, Afghanistan, Algeria.——FIG. 724,*3a–d*. **P. nalivkini* (ABRAMIAN), Armenia; dorsal, ventral, anterior, and lateral views, ×1 (Abramian, 1957).——FIG. 724,*3e–f*. *P.* sp., Algeria; dorsal and posterior views of internal mold, ×1 (Sartenaer, 1975a).

Ptychomaletoechia SARTENAER, 1961c, p. 7 [**Rhynchonella Omaliusi* GOSSELET, 1877b, p. 314; OD]. Transversely subpentagonal outline; strongly dorsibiconvex with steep lateral margins. Beak erect to suberect; foramen circular, with deltidial plates disjunct to conjunct. Fold and sulcus distinct, from umbones; tongue high, rectangular, dentate. Costae strong, angular, simple, arising at beaks. Dental plates slightly convergent ventrally. Dorsal median septum low, long; septalium deep, without cover; crural bases triangular; crura closely placed, concave dorsomedially in section. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* Europe, Afghanistan, Altai, China, North America.——FIG. 724,*2a–i*. **P. omaliusi* (GOSSELET), Famennian, Senzeilles beds, Senzeilles, Belgium; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, ×1 (Gosselet, 1877b); *e–f,* topotype, serial sections 0.85, 1.15 mm from posterior, ×3.4; *g–i,* serial sections 2.93, 3.08, 3.18 mm from posterior of another topotype, ×2.7 (Sartenaer, 1961c).

Tabarhynchus BARANOV, 1989, p. 45 [**T. mirandus;* OD]. Subtrigonal to subpentagonal in outline; moderately biconvex. Beak suberect; fold and sulcus weak to moderate, from umbones; anterior commissure uniplicate; tongue low, serrate. Costae coarse, rounded, simple, arising at beaks. Dental plates very short. Dorsal median septum long, thin; septalium without cover; crural bases subhorizontal; crura thin, laterally flattened. *Upper Devonian (Frasnian):* eastern Siberia.——FIG. 725*a–m*. **T. mirandus,* Mauchanskaya Formation, Sette-Daban Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2.5; *e–m,* topotype, serial sections 7.7, 7.8, 7.85, 7.95, 8.05, 8.45, 8.65, 9.15, 9.45 mm from posterior, ×3.5 (Baranov, 1989).

Yanetechia BARANOV, 1980, p. 85 [**Y. excelsa;* OD]. Subtriangular to subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak erect to incurved; delthyrium open, narrow deltidial plates disjunct. Fold and sulcus moderately strong, extending from umbones; anterior commissure uniplicate; tongue high, arcuate, dentate. Costae strong, angular, simple, extending from beaks. Dental plates vertical, mostly fused to valve walls.

Dorsal median septum absent; septalium very short, open; hinge plates divided; crural bases triangular; crura ventrally curved, concave dorsomedially in section. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* eastern Siberia, Salair.——FIG. 724,*4a–k*. **Y. excelsa,* Seymchan Formation, Yakutskaya, Ulakhan-Sis Range, eastern Siberia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k,* serial sections, ×4.5 (Baranov, 1980).

Subfamily VIRGINIATINAE Amsden, 1974

[*nom. correct.* SAVAGE, 1996, p. 252, *pro* Virginiatiinae AMSDEN, 1974, p. 68]

Trigonirhynchiidae with elongate subtriangular outline; apical angle acute; equibiconvex lateral profile; fold and sulcus weak to absent; anterior commissure rectimarginate to moderately unisulcate or uniplicate; costae coarse, straight, simple, arising at beaks or on umbones; ventral beak straight to erect; delthyrium with disjunct or conjunct deltidial plates. Dental plates well developed, close to valve walls, vertical. Dorsal median septum short, low, thick; septalium open or with partial cover plate. *Upper Ordovician (Ashgill)–upper Silurian (Ludlow).*

Virginiata AMSDEN, 1968, p. 56 [**Camarotoechia arkansana* THOMAS, 1926, p. 388; OD]. Small size; elongate subtrigonal outline; subequally weakly biconvex. Beak erect to incurved; delthyrium open to partly closed by rudimentary deltidial plates. Fold and sulcus lacking; anterior commissure rectimarginate, serrate. Costae low, from umbones; mostly simple but some umbonal bifurcation. Dental plates distinct but short; vertical. Small septalium covered posteriorly; dorsal median septum short. *Silurian (Llandovery–Ludlow):* North America, Siberia, China.——FIG. 726,*1a–i*. **V. arkansana* (THOMAS), Wenlock, Arkansas, Batesville district, USA; *a–d,* hypotype, dorsal, ventral, lateral, and anterior views, St. Clair Limestone, ×3; *e,* lectotype, dorsal view, St. Clair Limestone, ×2; *f–i,* serial sections 0.4, 0.6, 0.8, 1.0 mm from posterior, ×7.5 (Amsden, 1968).

Hostimex HAVLÍČEK, 1982b, p. 370 [**H. hostimensis;* OD]. Shell small; elongate subtriangular in outline; weakly biconvex profile. Beak suberect. Fold and sulcus weak; anterior commissure uniplicate; tongue low, wide. Costae arising at umbones, numerous, simple, or with minor bifurcation. Dental plates long, umbonal cavities distinct; ventral muscle area weakly impressed. Dorsal median septum low, extending to one-third valve length; septalium small, with cover plate; cardinal process absent. *Silurian (upper Wenlock–Ludlow):* Bohemia.——FIG. 726,*3a–f*. **H. hostimensis,* upper Wenlock, Motol Formation, V Kozle Rock, between Beroun and Hostim; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×4.6; *e,* internal mold of ventral valve, ×6.2; *f,* internal mold, posterior view, ×7.8 (Havlíček, 1982b).

Rhynchotreta HALL, 1879, p. 166 [**Terebratula cuneata* DALMAN, 1828, p. 141; OD] [=*Bailongjiangella* FU, 1982, p. 139 (type, *B. astuta,* OD)]. Small; elongate triangular outline; apical angle acute; biconvex. Beak straight to suberect; ventral interarea long, delthyrium long with circular foramen bounded anteriorly by conjunct to disjunct deltidial plates. Fold and sulcus weak; anterior commissure uniplicate, serrate. Costae strong, rounded, simple, usually from beaks. Dental plates well developed, close to valve walls, vertical; teeth stout. Dorsal median septum short, low, thick; septalium without cover; cardinal process absent; crural bases subtriangular; crura long, laterally compressed, concave medially in section. *lower Silurian (Llandovery)–upper Silurian (Ludlow):* Europe, Urals, Altai, China, North America.——FIG. 727*a–o*. **R. cuneata* (DALMAN), upper Wenlock–lower Ludlow; *a–c,* lectotype, dorsal, ventral, and anterior views, Klinteberg Beds, Klinteberg, Gotland, ×3 (Bassett & Cocks, 1974); *d–h,* hypotype, dorsal, ventral, posterior, anterior, and lateral views, Klinteberg Beds, Bryten, near Klinte, Gotland, ×2.5; *i,* enlargement of delthyrial area showing deltidial plates, ×8.3; *j–o,* hypotype, serial sections 1.6, 1.8, 2.2, 2.9, 3.4, 3.5 mm from posterior, Klinteberg Beds, Bryten, near Klinte, Gotland, ×8.3 (Jin & Caldwell, 1990).

Thebesia AMSDEN, 1974, p. 69 [**Rhynchotreta thebesensis* FOERSTE, 1909a, p. 94; OD]. Small with elongate subtrigonal outline; apical angle acute and posterolateral margins slightly concave; profile biconvex. Beak straight to suberect; delthyrium open to partly closed by rudimentary deltidial plates. Fold and sulcus absent; anterior commissure rectimarginate, serrate. Costae strong, simple, subangular, slightly curved outward. Dental plates distinct. Small open septalium; dorsal median septum short; crura not recorded. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* North America, Europe, Asia.——FIG. 726,*2a–h*. **T. thebesensis* (FOERSTE), Ashgill, Edgewood Group, USA; *a–e,* lectotype, dorsal, ventral, anterior, posterior, and lateral views from the Leeman Formation, near Thebes, Illinois, ×2; *f–h,* hypotype, serial sections at 0.5, 0.8, 0.9 mm from posterior, ×12 (Amsden, 1974).

Subfamily RIPIDIORHYNCHINAE Savage, 1996

[Ripidiorhynchinae SAVAGE, 1996, p. 252]

Late Trigonirhynchiidae with strong fold and sulcus; anterior tongue conspicuous; delthyrium with deltidial plates usually conjunct; costae numerous, straight, arising

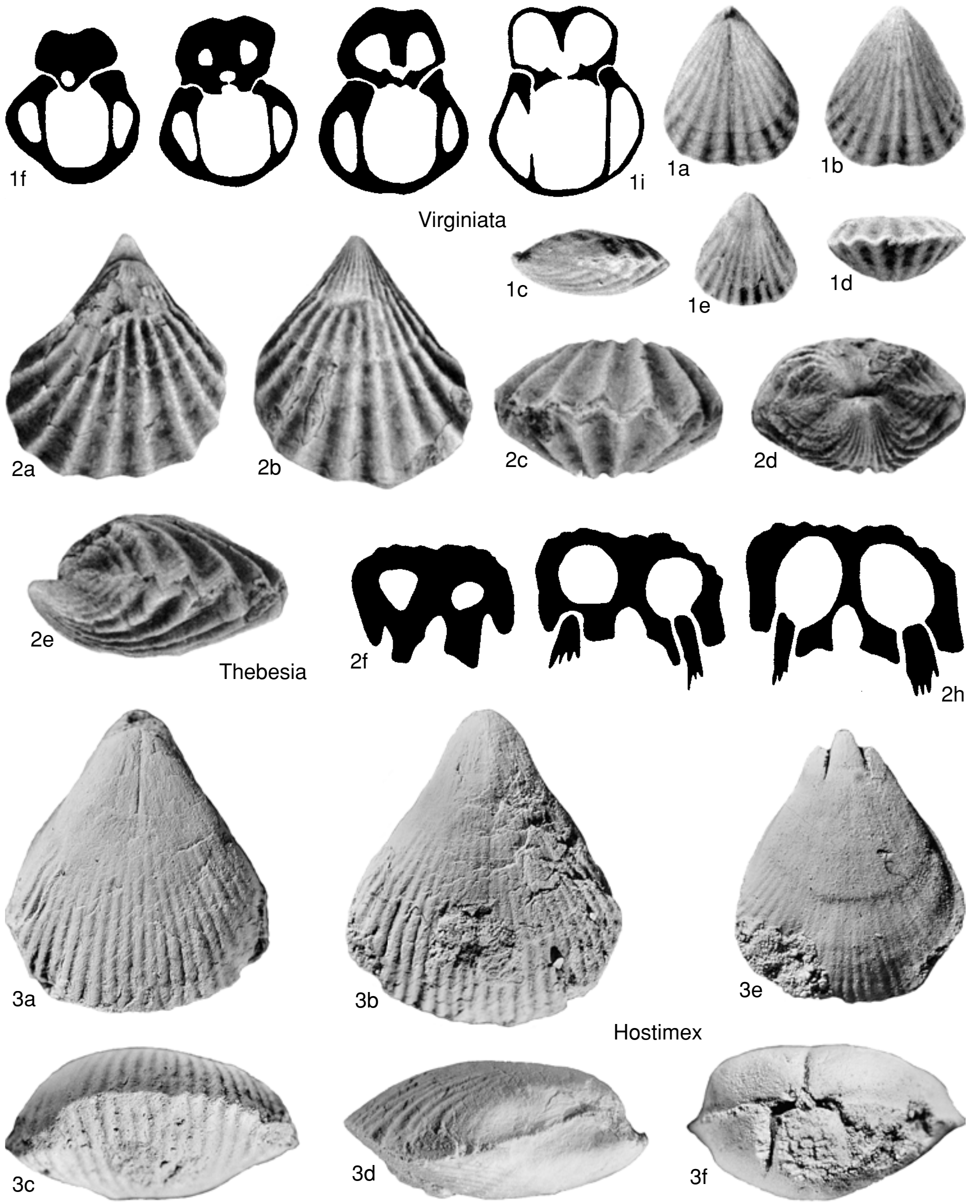

FIG. 726. Trigonirhynchiidae (p. 1074).

from beaks. Dental plates long. Dorsal median septum short; septalium may have cover plate anteriorly. *Middle Devonian (upper Givetian)–Lower Carboniferous (Tournaisian).*

Ripidiorhynchus SARTENAER, 1966b, p. 2 [**Terebratula livonica* VON BUCH, 1834, p. 57; OD]. Subpentagonal to transversely ovate in outline, often emarginate anteriorly; strongly biconvex to inflated. Beak erect to incurved; delthyrium with wide base, circular foramen, deltidial plates almost meeting. Fold and sulcus strong, narrow, extending from umbones; anterior commissure uniplicate; tongue high, rounded to acuminate. Costae medium, rounded, simple, from beaks. Dental plates long, almost straight, strongly convergent ventrally.

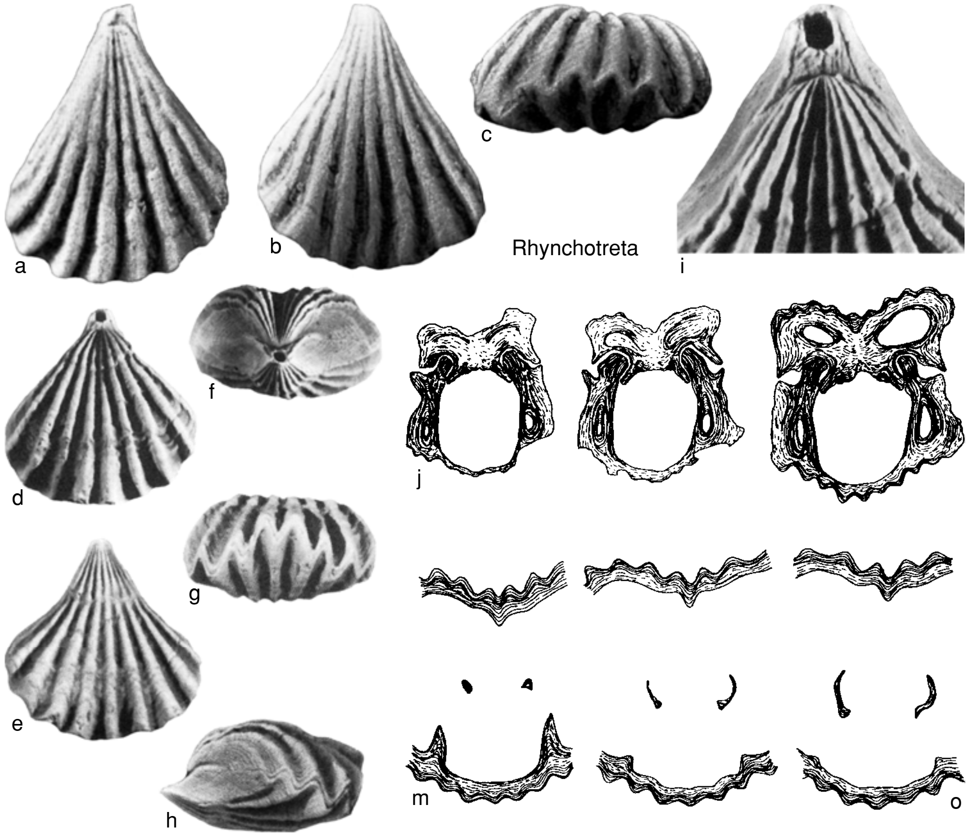

FIG. 727. Trigonirhynchiidae (p. 1074).

Dorsal median septum short; septalium with cover plate anteriorly; crura with cross section concave dorsomedially. *Middle Devonian (upper Givetian)–Upper Devonian (lower Famennian):* Europe, Asia, northern Africa, North America.——FIG. 728,*3a–n*. **R. livonicus* (VON BUCH), Frasnian, lectotype and paralectotypes earlier thought to come from Adsel, Latvia but because of preservation now considered by SARTENAER (1985a, p. 324) to come from Izborsk, near Pskov; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–n,* paralectotype, serial sections 0.7, 0.79, 0.94, 1.12, 1.35, 1.5, 1.75, 2.45, 2.85 mm from posterior, ×4.5 (Sartenaer, 1966b).

Cyphoterorhynchus SARTENAER, 1965c, p. 51 [**Uncinulus (Uncinulina) koraghensis* REED, 1922, p. 40; OD]. Subcircular in outline and strongly biconvex profile. Beak suberect to erect; foramen minute. Fold and sulcus weak, developed only anteriorly; anterior commissure uniplicate; tongue high, rounded. Costae fine, numerous, simple, rounded, covering all of shell. Dental plates close to shell walls, not convergent ventrally; ventral muscle field moderately impressed. Dorsal median septum short, thin, moderately high; septalium V-shaped, with cover plate anteriorly; hinge plates united anterior of septalium; crura short, with V-shaped tips open dorsally. *Upper Devonian (middle Frasnian–upper Frasnian):* Pakistan, Iran, Afghanistan, Armenia, Spain, Libya.——FIG. 728,*1a–n*. **C. koraghensis* (REED), middle or upper Frasnian, Chitral, Koragh Ridge, northwestern Pakistan; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×1; *e–n,* serial sections 1.1, 1.65, 2.0, 2.2, 2.4, 2.6, 2.85, 3.3, 4.0, 4.25 mm from posterior, ×1.6 (Sartenaer, 1965c).

Hemiplethorhynchus VON PEETZ, 1898, p. 178 [**H. fallax;* OD] [=*Greenockia* BROWN, 1952, p. 91 (type, *G. snaringensis,* OD)]. Subcircular to subpentagonal in outline; moderately biconvex. Beak small, erect to incurved; delthyrium with deltidial plates. Fold and sulcus rather weak, but distinct anterior tongue present. Costae fine to medium, simple, angular, from beaks. Dental plates concave medially and slightly convergent ventrally. Dorsal median septum long, low; septalium with-

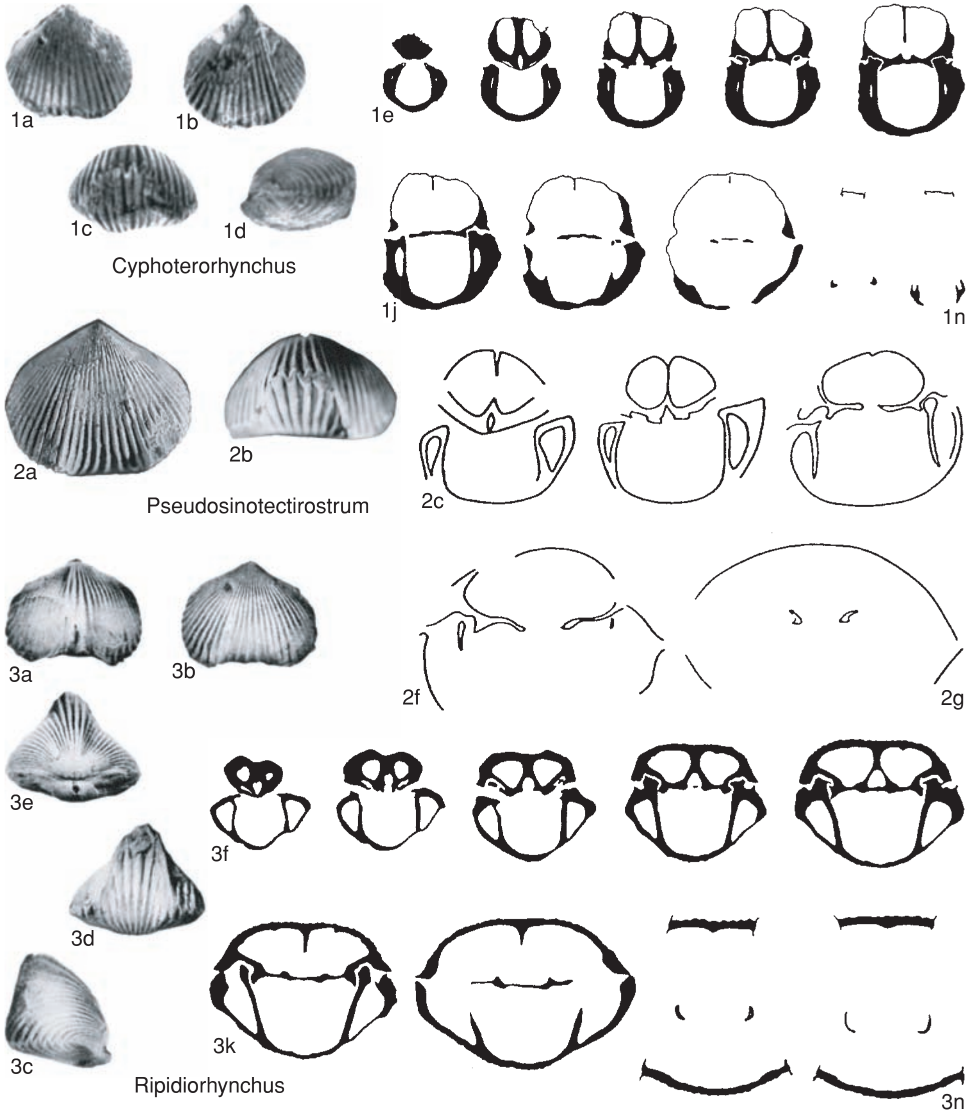

FIG. 728. Trigonirhynchiidae (p. 1075–1077).

out cover but anteriorly from septalium, crural bases meet medially; distal parts of crura with V-shaped cross section, open dorsally. *Lower Carboniferous (Tournaisian):* Altai, Europe, China, North America.——FIG. 729*a–l*. **H. fallax,* upper Tournaisian; *a–d,* dorsal, ventral, anterior, and lateral views, Altai, ×1 (Sarytcheva & others, 1963); *e–l,* hypotype, serial sections 1.6, 2.5, 2.85, 3.35, 3.5, 3.7, 4.35, 4.9 mm from posterior, Kuznetzk basin, ×3 (Sartenaer, 1965a).

Pseudosinotectirostrum YUDINA, 1991, p. 45 [**P. arcticum;* OD]. Subcircular to subpentagonal in outline; moderately biconvex; foramen with deltidial plates. Dorsal fold and ventral sulcus distinct but with rounded margins. Costae fine, numerous, simple, extending from beaks. Dental plates short, vertical. Dorsal median septum low, short; septalium short, without cover plate. *Upper Devonian (Famennian):* Russia (Timan, Pechora). ——FIG. 728,*2a–g*. **P. arcticum,* middle Famennian, Ust'-Pechora Horizon, northern Timan, Pechora Province; *a–b,* holotype, ventral and anterior views, ×1.3; *c–g,* topotype, serial sections 0.8, 1.1, 1.4, 2.0, 2.2 mm from posterior, ×4 (Yudina, 1991).

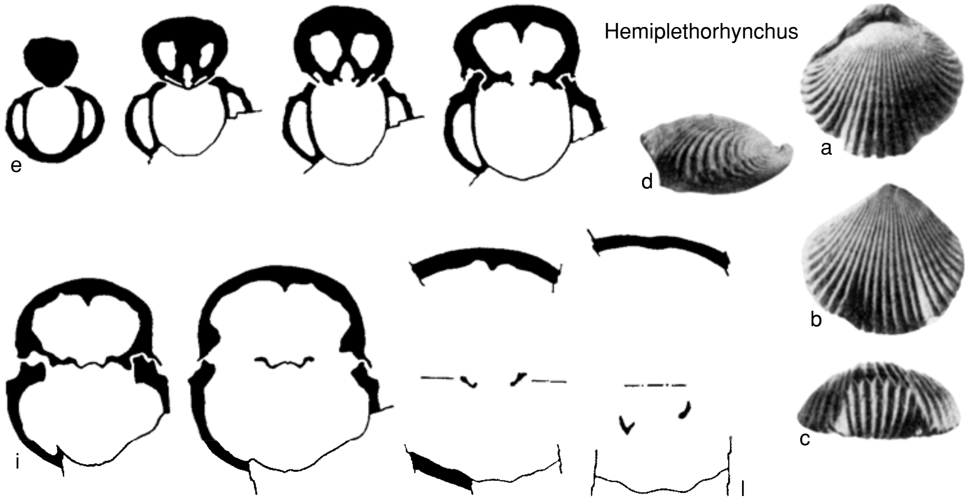

FIG. 729. Trigonirhynchiidae (p. 1076–1077).

Family ORTHORHYNCHULIDAE Cooper, 1956

[Orthorhynchulidae COOPER, 1956a, p. 669]

Rhynchotrematoidea with delthyrium open or with incipient deltidial plates; ventral interarea commonly present; dental plates reduced; hinge plates slope medially to join septalium that is sessile or supported on low median septum; cardinal process septiform, lobed, or branching. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock).*

Orthorhynchula HALL & CLARKE, 1893, p. 181 [**Orthis? linneyi* JAMES, 1881, p. 41; OD]. Transversely ovate to subcircular outline and dorsibiconvex profile. Beak suberect; ventral interarea prominent; delthyrium open. Fold and sulcus moderate, from umbones; anterior commissure uniplicate; tongue low, serrate. Costae rounded, simple, from beaks. Dental plates fused to valve walls; ventral muscle field quadrate. Very short septalium supported on median ridge; hinge plates divided, prolonged anteriorly, concave ventrally; cardinal process septiform to lobate; crural bases subhorizontal. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery):* North America, ?western Europe.——FIG. 730,*1a–m*. **O. linneyi* (JAMES), Ashgill, Maysvillian, Kentucky, USA; *a–e,* hypotype, dorsal, ventral, anterior, lateral, and posterior views, ×1.5; *f–g,* hypotypes, dorsal valve interior and ventral valve interior, Brannon Formation, Devils Hollow, Coletown, ×1.5 (new); *h–m,* serial sections 13.2, 13.0, 12.8, 12.5, 12.3, 12.0 mm from anterior margin, ×3.75 (Schmidt, 1965b).

Orthorhynchuloides WILLIAMS, 1962, p. 240 [**Hemithyris nasuta* MCCOY, 1852, p. 203; OD]. Elongate-oval outline and dorsibiconvex profile. Ventral beak incurved; delthyrium open with only traces of deltidial plates. Fold and sulcus pronounced anteriorly; tongue pronounced. Costae numerous, weak posteriorly. Dental plates long, ventrally convergent; ventral muscle field well impressed. Sessile septalium merges anteriorly into median septum extending to midlength; cardinal process absent; crura unknown. *Upper Ordovician (Caradoc):* Scotland.——FIG. 730,*2a–e*. **O. nasuta* (MCCOY), lower Caradoc, Craighead Limestones, Girvan; *a–c,* lectotype, dorsal, ventral, and anterior views, ×1.3; *d,* dorsal internal mold, ×2; e, ventral internal mold, ×1.5 (Williams, 1962).

Orthorhynchyllion JIN, 1989, p. 72 [**Rhynchotrema prinstanum* TWENHOFEL, 1928, p. 208; OD]. Subpentagonal to subtriangular outline with dorsibiconvex profile. Ventral beak small, incurved; triangular interareas on both valves; delthyrium open. Fold and sulcus broad, low, developed anteriorly. Costae numerous, from beaks, simple, rounded. Dental plates short, subvertical. Dorsal median septum thin, long; hinge plates wide, inclined dorsally; septalium large with strong septalial plates; cardinal process septiform with branched crest; crura laterally flattened. *Upper Ordovician (Ashgill):* Canada.——FIG. 731,*2a–m*. **O. prinstanum* (TWENHOFEL), upper Ashgill, Hirnantian, Ellis Bay Formation, Anticosti Island; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3 (new); *f–m,* hypotype, serial section 0.7, 0.8, 1.0, 1.3, 1.4, 1.9, 2.8, 3.1 mm from posterior, ×4 (Jin, 1989).

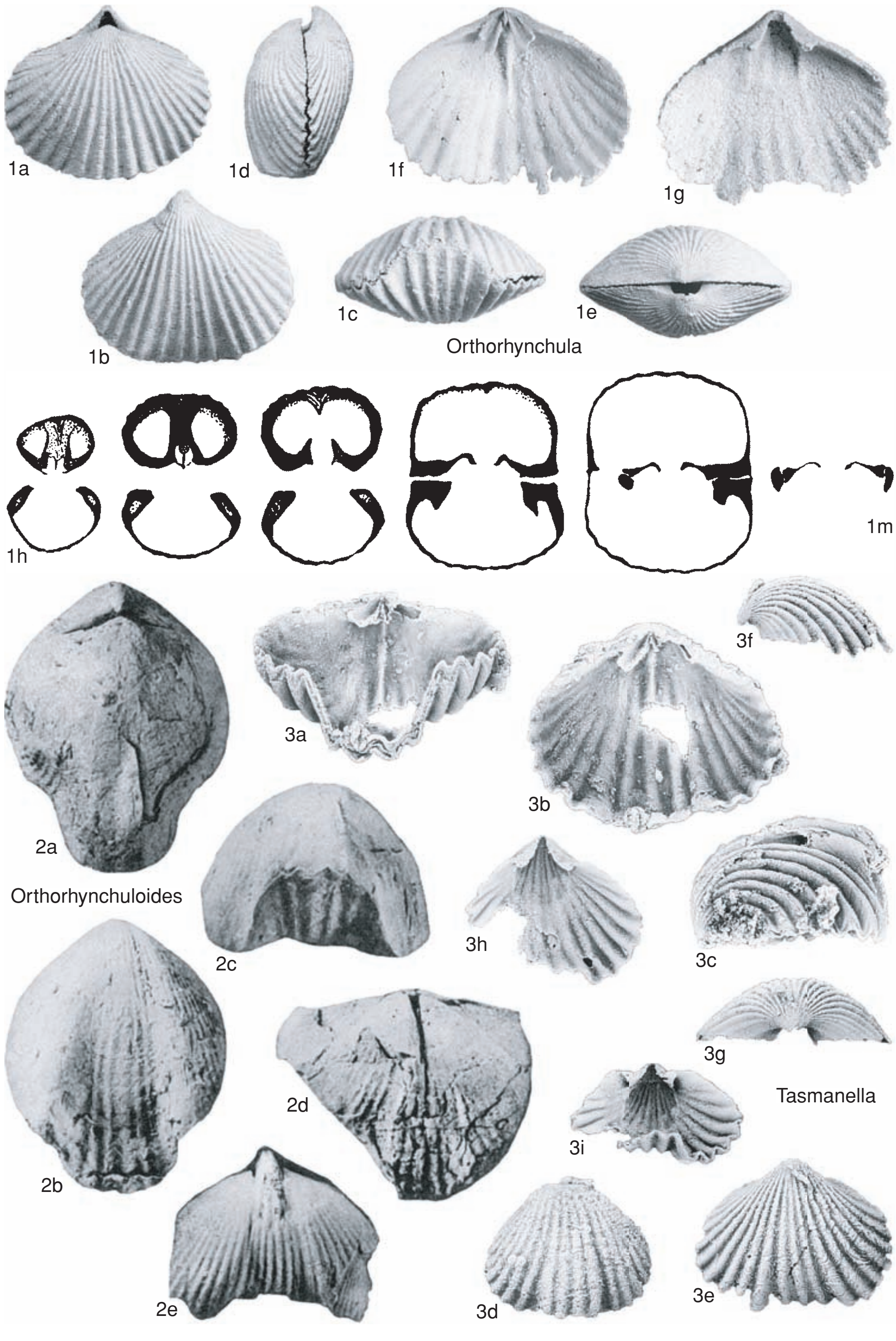

FIG. 730. Orthorhynchulidae (p. 1078–1081).

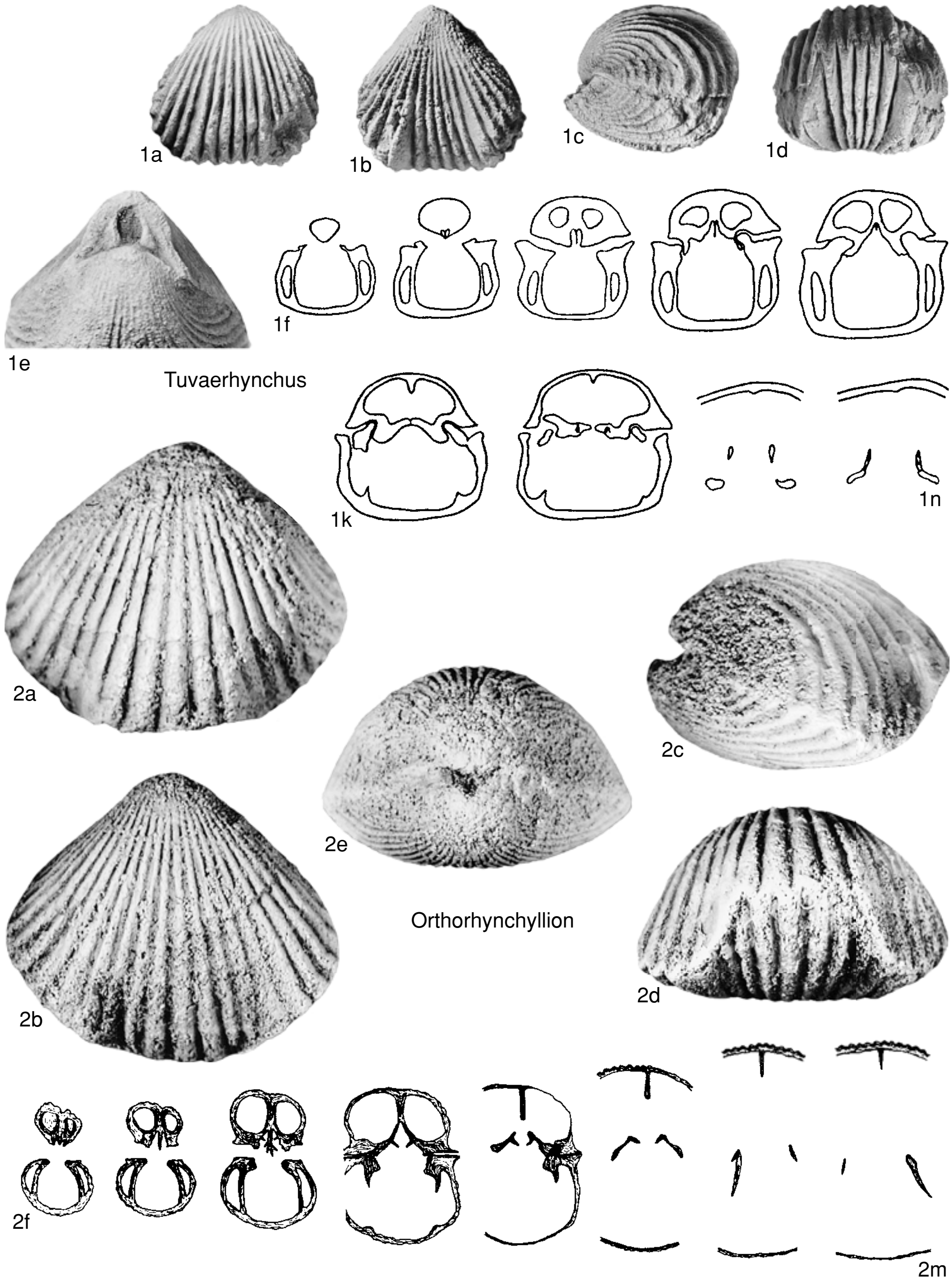

FIG. 731. Orthorhynchulidae (p. 1078–1081).

Tasmanella LAURIE, 1991, p. 96 [**T. nova;* OD]. Transversely subcircular outline and dorsibiconvex profile. Ventral beak erect; ventral interarea prominent; delthyrium open. Fold and sulcus well developed, from umbones; anterior commissure uniplicate; tongue trapezoid. Costae strong and angular, simple, from beaks. Dental plates fused to shell walls; ventral muscle field well impressed. Hinge plates anteriorly extended, concave; dorsal median septum short, high; septalium narrow, short, elevated; cardinal process septiform; crura unknown. *Upper Ordovician (Caradoc):* southeastern Australia (Tasmania).——FIG. 730,*3a–i.* **T. nova,* lower Caradoc, Benjamin Limestone, Florentine Valley; *a–c,* holotype, interior and lateral views of dorsal valve; *d,* dorsal view of dorsal valve; *e–g,* paratype, ventral, lateral, and posterior views of ventral valve; *h–i,* interior and inclined interior views of ventral valve, ×2 (Laurie, 1991).

Tuvaerhynchus KULKOV, 1985, p. 123 [**T. khalfini;* OD]. Small with subpentagonal to subtriangular outline and dorsibiconvex profile. Beak suberect; delthyrium with disjunct deltidial plates. Fold and sulcus strong, narrow, well defined, from umbones; anterior commissure uniplicate; tongue high, trapezoid, dentate. Costae numerous, simple, angular. Dental plates short, vertical, close to valve wall. Septalium short, wide; hinge plates concave, slope medially; cardinal process septiform, thin; crura short, curved sharply ventrally. *lower Silurian (Llandovery)–middle Silurian (Wenlock):* Tuva.——FIG. 731,*1a–n.* **T. khalfini,* Wenlock, Dashtygoisk Beds; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e,* topotype, delthyrium, ×3; *f–n,* topotype, serial sections 0.6, 0.8, 1.0, 1.3, 1.7, 2.0, 2.1, 2.7, 3.0 mm from posterior (Kulkov, 1985).

Family LEPTOCOELIIDAE Boucot & Gill, 1956

[Leptocoeliidae BOUCOT & GILL, 1956, p. 1174]

Rhynchotrematoidea with subcircular to subpentagonal outline; lateral profile planoconvex to biconvex; valves meet at acute angle laterally; fold and sulcus weak; costae simple, strong, extending from beaks; delthyrium open or with disjunct deltidial plates. Dental plates usually absent. Dorsal median septum weak or absent; hinge plates sessile; cardinal process large to absent. *lower Silurian (Llandovery)–Middle Devonian (upper Eifelian).*

Leptocoelia HALL, 1857a, p. 107 [**L. propria;* SD OEHLERT, 1887a, p. 1324; =*Atrypa flabellites* CONRAD, 1841, p. 55; *Leptocoelia propria* HALL, 1857a, p. 108]. Small to medium with subcircular to subpentagonal outline and subequally biconvex to planoconvex profile. Beak erect to incurved; deltidial plates disjunct; foramen small, circular. Weak, narrow dorsal fold and ventral sulcus developed anteriorly in larger specimens; anterior commissure weakly uniplicate to rectimarginate. Costae simple, strong, rounded, extending from beaks. Dental plates absent; stout crenulate teeth fused directly to valve walls; ventral diductor field flabellate, enclosing small, oval adductor impressions. Cardinal process large, bulbous, base attached to large inner socket plates and thick median ridge that extends to about valve midlength; sockets crenulate; anterior adductor impressions larger than posterior adductors. *Lower Devonian (upper Lochkovian)–Middle Devonian (middle Eifelian):* North America, South America, Asia.——FIG. 732,*1a–d.* **L. flabellites* (CONRAD), Oriskanian, Glenerie Limestone, Glenerie, New York, USA; *a,* exterior of dorsal valve, ×1; *b,* interior of dorsal valve, ×2; *c–d,* exterior and interior of ventral valve, ×1 (Boucot & Gill, 1956).

Anabaia CLARKE, 1893, p. 141, fig. 124–127 [**A. Paraia;* OD] [=*Harringtonina* BOUCOT, 1972, p. 10 (type, *H. australis,* OD; =*Leptocoelia acutiplicata* KAYSER, 1897, p. 295, *non* CONRAD, 1841, p. 54, *sensu* DE MELO & BOUCOT, 1990, p. 365)]. Subcircular outline and biconvex profile. Dorsal fold with median groove; anterior commissure sulciplicate. Costae coarse, simple, straight, rounded, extending from beaks. Short dental plates; stubby teeth; flabellate diductor impressions surrounding small oval adductors. Dorsal interior with stout myophragm to midlength; small crural plates; cardinal process not evident. *lower Silurian (lower Llandovery)–upper Silurian (Přídolí):* South America.——FIG. 732,*2a–b.* **A. paraia,* Llandovery, Trombetas Formation, Pitinga Member, Pará, Trombetas River, Viramundo Rapids, Brazil; paralectotypes, dorsal and ventral internal molds, ×2.5 (de Melo & Boucot, 1990).

Australocoelia BOUCOT & GILL, 1956, p. 1174 [**Atrypa palmata* MORRIS & SHARPE, 1846, p. 276; OD; =*Australocoelia tourteloti* BOUCOT & GILL, 1956, p. 1175]. Small to medium with subcircular outline and ventribiconvex profile. Beak suberect. Dorsal sulcus and ventral fold low; anterior commissure weakly sulcate. Costae strong, simple, rounded, arising at beaks. Dental plates absent; teeth stout, attached to posterior valve walls; deeply impressed pedicle scar; elongate diductor and smaller adductor impressions well impressed. Pronounced notothyrial platform with stout median ridge supporting large cardinal process; adductor field ovate, well impressed. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* South America, South Africa, Falkland Islands, Australia.——FIG. 732,*3a–g.* **A. palmata* (MORRIS & SHARPE), Emsian, Argentina, Bolivia, Falkland Islands; *a–b,* dorsal and ventral external views, San Juan, Lomas de los Piojos, Argentina, ×1 (Boucot & Gill, 1956); *c,* posterior of a dorsal valve showing cardinal process, San Juan, Lomas de los Piojos, Argentina, ×4 (Amos & Boucot, 1963); *d,* dorsal internal mold, San Juan, Quebrada de Talacasto, Argentina, ×2; *e,* ventral internal mold, Santa Cruz, Comorapa-Tunal region, Bolivia, ×2; *f–g,* latex casts of dorsal and ventral valve interiors of figured material of MORRIS and SHARPE, 1846, Falkland Islands, ×1 (Boucot & Gill, 1956).

Eocoelia NIKIFOROVA, 1961, p. 252 [**Atrypa hemisphaerica* J. DE C. SOWERBY, 1839, p. 637; OD]. Subcircular to transversely elliptical outline with subbiconvex to planoconvex profile. Delthyrium open. Weak ventral fold and dorsal sulcus often evident, or merely weak narrow trough on dorsal valve; anterior commissure rectimarginate. Costae

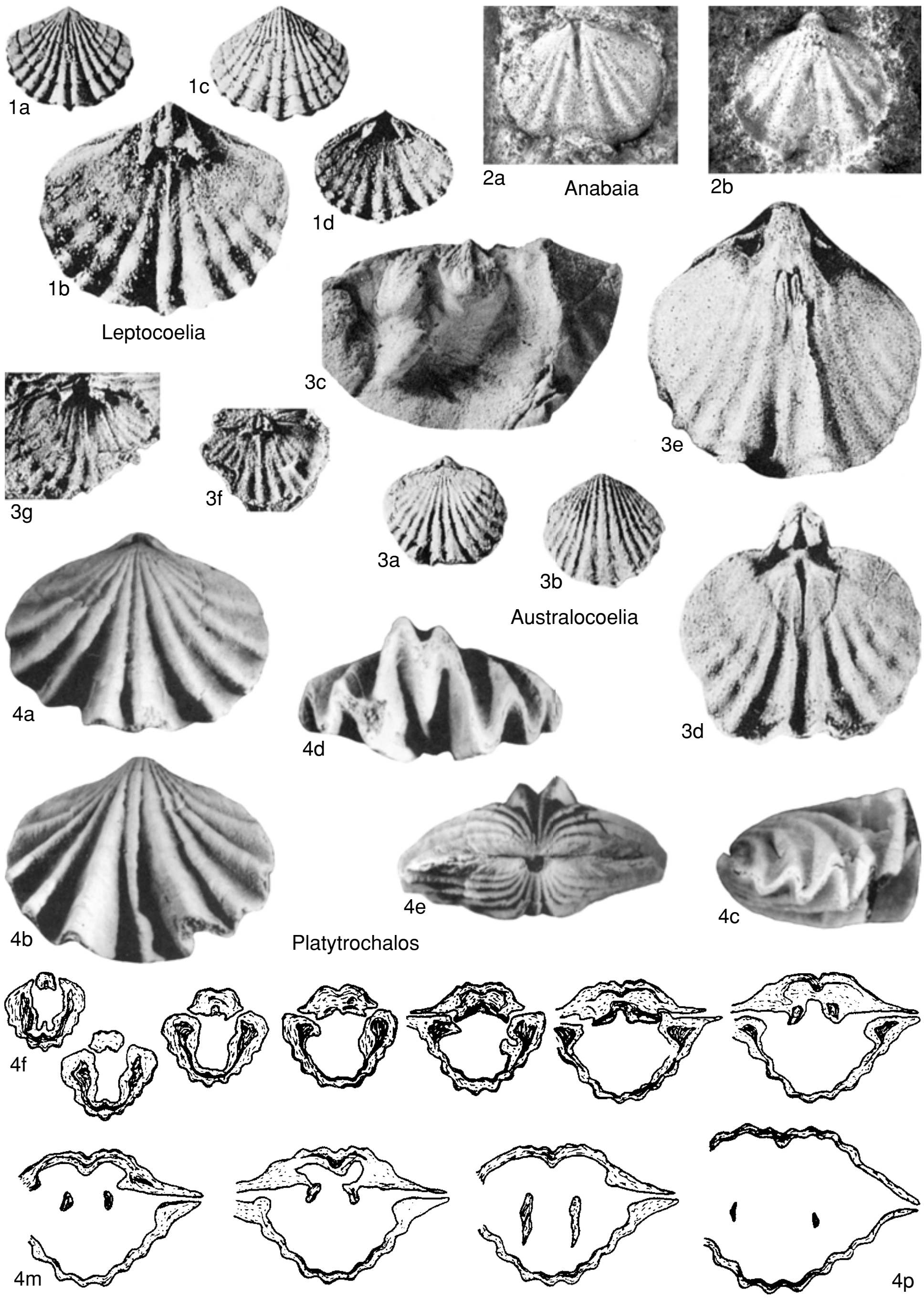

FIG. 732. Leptocoeliidae (p. 1081–1083).

simple, strong, rounded, extending from beaks. Dental plates short to absent; teeth arising from posterior valve walls and bear fossettes on median face; muscle scars not impressed. Dorsal valve with short, robust socket plates bounding deep, divergent sockets; broad, low median ridge reflecting exterior trough; muscle field not impressed; costae strongly reflected internally; cardinal process rare to absent. *lower Silurian (lower Llandovery)–middle Silurian (upper Wenlock):* Europe, Asia, North America, South America, Australia.——FIG. 733,*3a–g.* **E. hemisphaerica* (SOWERBY), upper Llandovery, Cowleigh Park Beds, Worcestershire, Ankerdine Hill, England; *a,* original illustration of SOWERBY (1839), ×1; *b,* lectotype, ventral external mold of *a,* ×2 (Murchison, 1839); *c,* dorsal external mold; *d–e,* ventral internal mold and latex cast; *f–g,* dorsal internal mold and latex cast, ×4 (Ziegler, 1966b).

Leptocoelina JOHNSON, 1970b, p. 170 [**L. squamosa;* OD]. Subpentagonal outline and biconvex profile. Beak suberect with apical foramen. Pronounced dorsal fold and ventral sulcus; anterior commissure sulciplicate. Costae few, coarse, low, rounded, arising at beaks; numerous imbricate growth lamellae. Dental plates absent; teeth attached to posterior valve margin, with fossettes present medially; diductor field elongate, triangular, well impressed; adductor field distinct within diductor field. Dorsal interior with knoblike cardinal process and prominent inner socket plates; short, wide, median ridge present posteriorly; adductor field elongate oval. *Lower Devonian (lower Pragian–upper Emsian):* USA (Nevada).——FIG. 733,*1a–g.* **L. squamosa,* lower Pragian, Coal Canyon; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×2; *f,* interior of dorsal valve, ×3; *g,* interior of ventral valve, ×2 (Johnson, 1970b).

Pacificocoelia BOUCOT, 1975a, p. 361 [**Leptocoelia murphyi* JOHNSON, 1970b, p. 165; OD]. Medium to large with subovate to subpentagonal outline and biconvex profile. Beak erect to incurved with small apical foramen; delthyrium absent. Anteriorly flaring low dorsal fold and ventral sulcus; anterior commissure sulciplicate. Costae extending from beaks, strong, rounded, simple, flaring anteriorly; growth lamellae few, pronounced. Dental plates short to absent; teeth stout, elongate; diductor field bilobed, strongly impressed but often with bounding ridges; adductor field small and situated within diductor field. Dorsal interior with prominent, bilobed cardinal process on thick notothyrial platform; short, thick median ridge present; sockets deep, short; dorsal adductor field ovate, tapering anteriorly; crura thin, ventrally curved. *Lower Devonian (middle Lochkovian)–Middle Devonian (upper Eifelian):* North America, South America.——FIG. 733,*2a–g.* **P. murphyi* (JOHNSON), middle Pragian, Sulphur Spring Range, Nevada, USA; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1.5; *f,* paratype, posterior of ventral valve interior, ×3; *g,* interior of dorsal valve, ×2 (Johnson, 1970b).

Platytrochalos JIN, 1989, p. 106 [**P. crudicostatus;* OD]. Small to medium with subcircular outline and weakly biconvex profile, but with high anterior fold. Beak erect to incurved; delthyium open; foramen small, mesothyrid. Dorsal fold and ventral sulcus narrow, strong anteriorly; anterior commissure sulciplicate. Costae strong, simple, rounded, arising at beaks. Dental plates fused to shell walls; teeth small; short, low ventral median ridge developed posteriorly; ventral muscle field weakly impressed. Hinge plates sessile; cardinal process and dorsal median septum absent; crural bases stout, arising from sessile hinge plates at hinge line; crural bases triangular in section; crura thick and laterally flattened, tapering distally. *lower Silurian (Llandovery):* eastern Canada.——FIG. 732,*4a–p.* **P. crudicostatus,* Jupiter Formation, Richardson Member, Anticosti Island; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3.75; *f–p,* serial sections 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3, 1.5, 1.6, 2.0 mm from posterior, ×6 (Jin, 1989).

Family MACHAERARIIDAE Savage, 1996

[Machaerariidae SAVAGE, 1996, p. 252]

Rhynchotrematoidea with subpentagonal to triangular outline; dorsal fold and ventral sulcus strong; costae medium to coarse, extending from beaks; delthyrium with deltidial plates disjunct to conjunct. Dental plates short or fused with valve walls; teeth elongate and swollen. Dorsal median septum and septalium incipient to absent; hinge plates undivided and sessile; inner socket ridges prominent to massive; cardinal process septiform or unilobed. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian).*

Machaeraria COOPER, 1955, p. 55 [**Rhynchonella formosa* HALL, 1857a, p. 76; OD] [=*Qinlingotoechia* FU, 1983a, p. 331 (type, *Q. simplex,* OD)]. Subpentagonal to subcircular outline and dorsibiconvex profile; lateral margins usually acute. Beak suberect; delthyrium partly closed by disjunct deltidial plates. Fold and sulcus sharply defined; anterior commissure uniplicate; tongue trapezoid, narrowing dorsally. Dental plates short and thin; teeth with small fossettes. Dorsal median septum absent; crural plates meeting valve floor; cardinal process with thin shaft and crinkled myophore; crura with pronounced ventral curvature, crescentic in section. *Lower Devonian (Lochkovian):* cosmopolitan.——FIG. 734,*1a–h.* **M. formosa* (HALL),

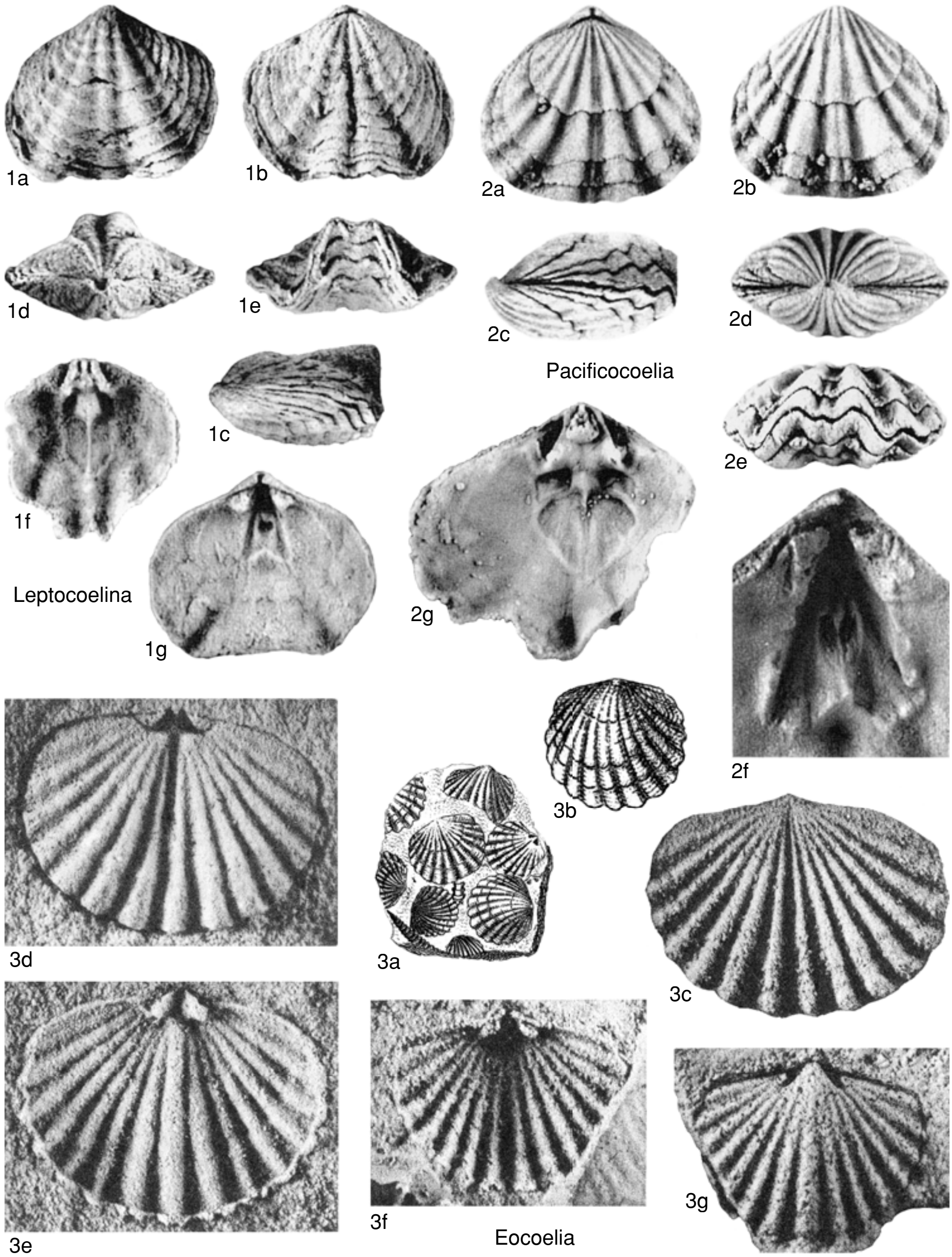

FIG. 733. Leptocoeliidae (p. 1081–1083).

New York, USA; *a–e,* hypotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* hypotype, posterior showing dental plates and cardinalia; *g,* hypotype, part of dorsal interior showing cardinalia, ×4; *h,* hypotype, ventral interior, ×3 (Cooper, 1955).

Australirhynchia SAVAGE, 1968, p. 731 [**A. cudalensis;* OD]. Small to medium with transversely subpentagonal outline and dorsibiconvex profile; lateral margins steep. Beak straight to suberect; delthyrium small, with circular foramen, deltidial plates almost meeting. Fold and sulcus pronounced, from

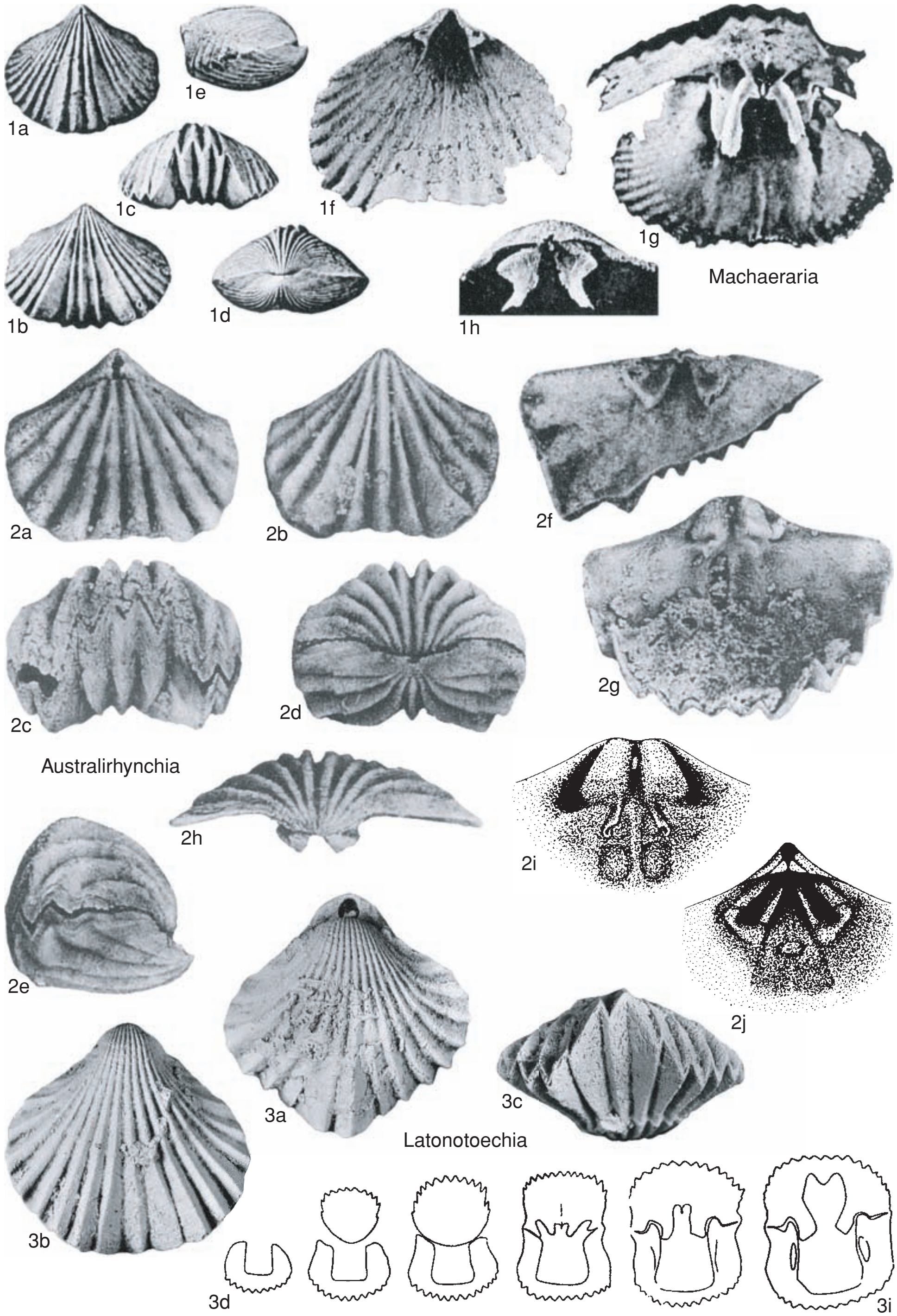

FIG. 734. Machaerariidae (p. 1083–1086).

umbones; anterior commissure uniplicate; tongue trapezoid, dentate. Costae strong, angular, from beaks, bifurcating on fold, intercalating in sulcus. Dental plates absent or fused to valve walls; teeth long, thick, grooved to fit inner socket ridges; adductor muscle field small, rounded, set within elongate diductor field. Dorsal median septum absent; hinge plates fused to valve floor; inner socket ridges large, inflated; cardinal process small, bosslike; crura crescentic in section. *Lower Devonian (Lochkovian):* eastern Australia, Altai.——FIG. 734,*2a–j.* **A. cudalensis,* Mandagery Park Formation, Manildra, New South Wales, eastern Australia; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views; *f,* topotype, interior view of ventral valve; *g–h,* topotype, interior and posterior views of dorsal valve, ×6; *i–j,* drawings of interiors of dorsal and ventral valves, ×8 (Savage, 1968).

Callipleura COOPER, 1942, p. 228 [**Rhynchospira nobilis* HALL, 1860b, p. 83; OD] [=*Cyclorhina* HALL & CLARKE, 1893, p. 206, *non* PETERS, 1871]. Medium to large with transversely subpentagonal outline and lenticular dorsibiconvex profile; lateral margins acute. Beak with large, circular foramen; deltidial plates disjunct to barely conjunct. Fold and sulcus from umbones, well defined anteriorly; anterior commissure uniplicate; tongue low, dentate. Costae strong, angular, numerous, simple, arising at beaks. Dental plates distinct but partly fused to valve wall, anteriorly divergent; ventral muscle field raised, extending almost to valve midlength. Crural plates resting on valve floor; cardinal process septiform and very delicate; crura sharply curved ventrally. *Middle Devonian (Givetian):* North America.——FIG. 735,*2a–g.* **C. nobilis* (HALL); *a–e,* hypotype, dorsal, ventral, posterior, anterior, and lateral views, New York, USA, ×1.3 (new); *f–g,* interiors of dorsal and ventral valves, upper Givetian, Traverse Group, Thunder Bay Formation, Thunder Bay Quarry, Ann Arbor, Michigan, USA, ×1.3 (new).

Cherubicornea HAVLÍČEK, 1992, p. 70 [**Terebratula amalthea* BARRANDE, 1847, pl. 19, fig. 6; OD]. Subtriangular outline and alate cardinal margins; convexoplane profile with acute lateral margins. Beak straight to suberect; delthyrium with circular, permesothyrid foramen, deltidial plates conjunct. Fold and sulcus well developed, from umbones; anterior commissure uniplicate; tongue narrow, low, distinct, dentate. Costae strong, angular, from beak, with some bifurcation; growth lamellae crowded. Dental plates thin, close to shell walls. Hinge plate steeply sloping to valve floor, underlain by callus; septalium not developed; bladelike cardinal process deeply recessed in notothyrial cavity; crura unknown. *Lower Devonian (Pragian–upper Emsian):* Bohemia, France.——FIG. 735,*3a–c.* **C. amalthea* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; hypotype, dorsal, ventral, and anterior views, ×1.8 (Havlíček, 1992).

Ferganella NIKIFOROVA, 1937a, p. 39 [**F. turkestanica;* OD]. Subpentagonal to rounded outline and biconvex profile. Beak suberect; delthyrium open but small deltidial plates may be present. Fold and sulcus low; anterior commissure uniplicate; tongue broad, low, dentate. Costae strong, angular, from beaks, rare bifurcation. Dental plates short, vertical. Septalium with cover, septalial plates long; hinge plates conjunct posteriorly; cardinal process septiform, within septalium, merges with dorsal medium septum that extends to midvalve. *Lower Devonian (Lochkovian):* Fergana.——FIG. 736,*3a–f.* **F. turkestanica,* lower Lochkovian, Manak Beds; *a–d,* dorsal, ventral, lateral, and anterior views, ×1 (Nikiforova, 1937a); *e,* serial section, ×2.5; *f,* serial section, ×3.5 (Jones, 1981).

Latonotoechia HAVLÍČEK, 1960, p. 244 [**Terebratula latona* BARRANDE, 1847, p. 89; OD]. Medium to large with elongate to subpentagonal outline and biconvex profile; lateral margins acute. Beak suberect; foramen hypothyrid, bounded anteriorly by large, disjunct deltidial plates. Fold and sulcus narrow, often asymmetrical; anterior commissure uniplicate; tongue tapering dorsally, dentate. Costae strong, simple, sharply angular, from beaks. Dental plates close to valve wall or cavities filled with callus; teeth stout. Hinge plates underlain by callus; inner socket ridges thick, sessile; dorsal septum absent; cardinal process septiform; crura unknown. *Lower Devonian (Pragian):* Europe, North America, Urals, Altai, Salair, Tadzikhistan, China.——FIG. 734,*3a–i.* **L. latona* (BARRANDE), Koneprusy Limestone, Zlaty kun Hill, Bohemia; *a–c,* hypotype, dorsal, ventral, and anterior views, ×1.5 (Havlíček, 1992); *d–i,* serial sections 17.7, 17.0, 16.3, 16.0, 15.3, 14.8 mm from anterior, ×2 (Havlíček, 1961).

Machaeratoechia HAVLÍČEK, 1992, p. 63 [**M. marsyas;* OD]. Elongate to subtriangular outline; moderately biconvex; lateral margins acute. Beak suberect; foramen hypothyrid to submesothyrid, bounded anteriorly by conjunct deltidial plates. Fold and sulcus distinct but low; anterior commissure weakly uniplicate; tongue low, broad, serrate. Costae strong, simple, rounded, from beaks. Dental plates absent; teeth stout, arising from valve margins; ventral muscle field deeply impressed. Hinge plates triangular, sloping medially to valve floor, attached to valve floor by curved crural plates; dorsal median septum absent; cardinal process weak, septiform; crura unknown. *Lower Devonian (Pragian–upper Emsian):* Bohemia.——FIG. 735,*1a–f.* **M. marsyas,* Emsian, Zlichov Limestone, Hlubocepy quarry; *a–c,* hypotype, dorsal, ventral, and anterior views, ×2.4; *d,* hypotype, dorsal view showing deltidial plates, ×1.5; *e,* hypotype, ventral valve interior, ×2.8; *f,* holotype, dorsal valve interior, ×3.7 (Havlíček, 1992).

Sicorhyncha HAVLÍČEK, 1961, p. 28 [**Stegerhynchus trinacrius* HAVLÍČEK, 1956, p. 571; OD]. Small to medium with elongate trigonal outline; posterolateral margins emarginate; weakly biconvex profile with lateral margins low, rounded. Beak short, straight; delthyrium small with deltidial plates conjunct, foramen permesothyrid to epithyrid. Fold and sulcus weak; anterior commissure weakly uniplicate; tongue low, dentate. Costae fine,

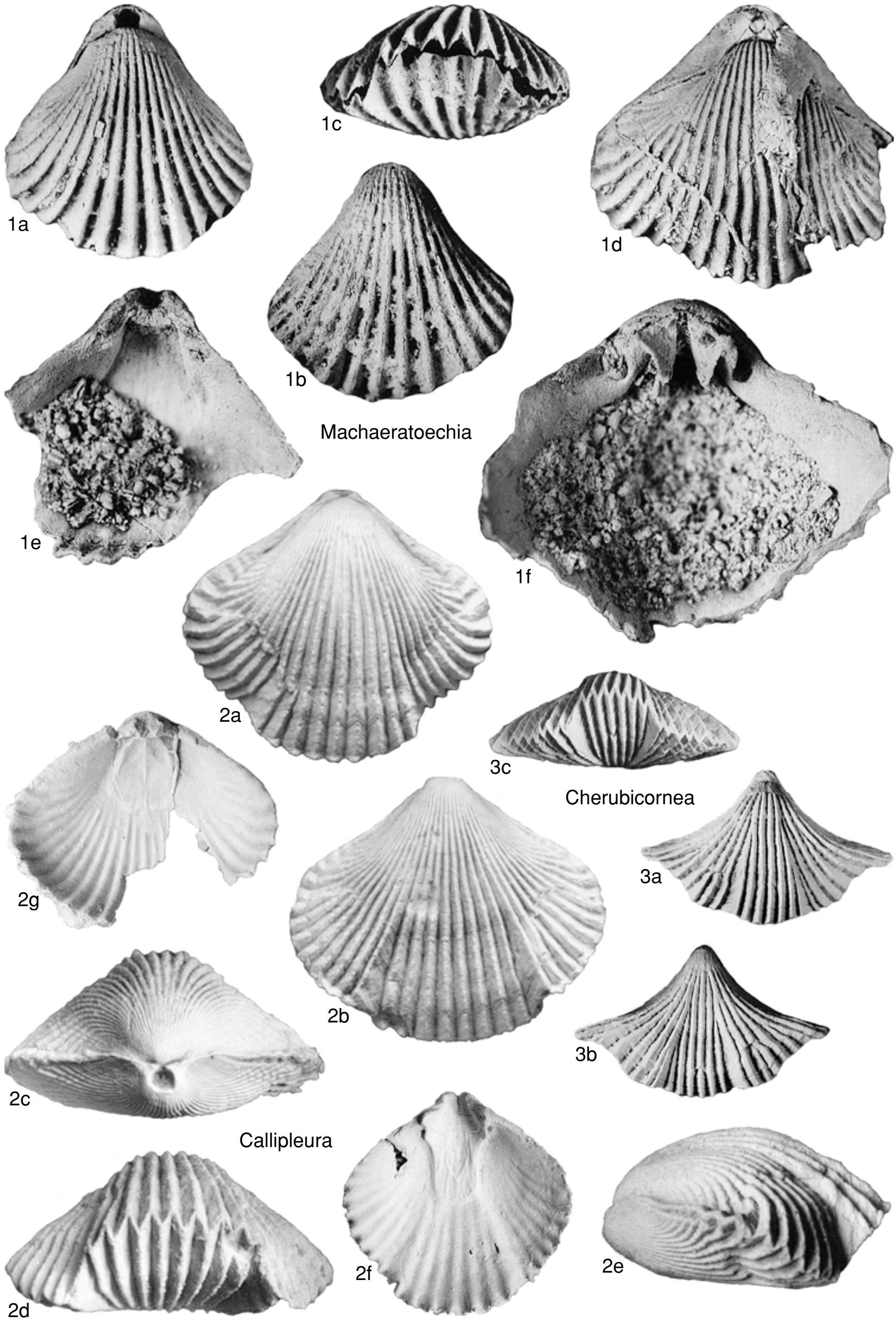

FIG. 735. Machaerariidae (p. 1086).

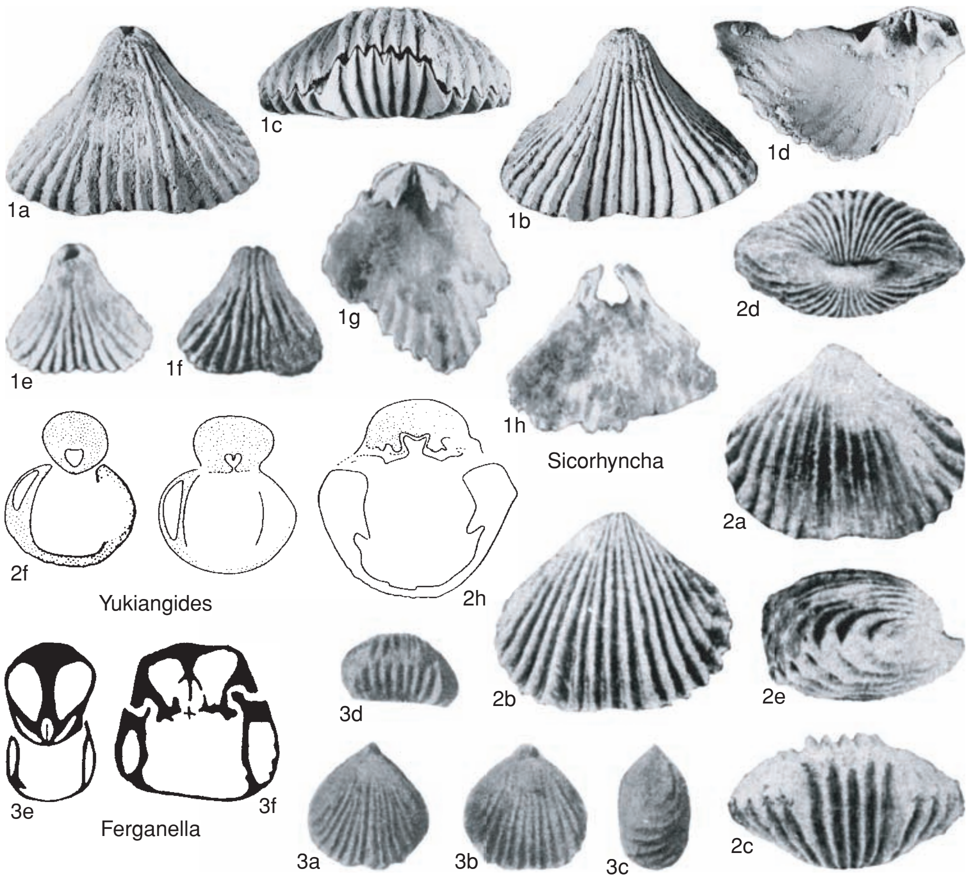

FIG. 736. Machaerariidae (p. 1086–1089).

angular, from beaks; some bifurcation and intercalation. Dental plates largely fused to valve walls. Hinge plates small, triangular, posteriorly sessile; dorsal median septum absent; cardinal process septiform; crura strongly curved, laterally flattened. *Lower Devonian (Pragian–Emsian):* Europe, Morocco, Urals, Salair, Tadzhikistan.——FIG. 736,*1a–h*. **S. trinacria* (HAVLÍČEK), Emsian, Zlichov Limestone, Hlubocepy, Bohemia; *a–c,* hypotype, dorsal, ventral, and anterior views, ×2.3; *d,* hypotype, dorsal valve interior, ×3.9 (Havlíček, 1992); *e–f,* holotype, dorsal and ventral views, ×2.5; *g,* dorsal valve interior; *h,* ventral valve interior, ×2.8 (Havlíček, 1956).

Thliborhynchia LENZ, 1967, p. 1188 [**T. julli;* OD] [=*Franklinella* LENZ, 1973, p. 1405 (type, *F. pedderi* LENZ, 1973, p. 1407), *non* STEWART & HENDRIX, 1945, Ostracoda]. Subtriangular outline; posterolateral margins emarginate; profile convexoplane. Beak erect to suberect; delthyrium with oval foramen, deltidial plates disjunct. Fold and sulcus low, from midlength; anterior commissure weakly uniplicate, dentate. Costae strong, simple, from beaks, angular. Dental plates thin, close to shell walls. Hinge plates concave, sessile; septalium not developed; dorsal median septum absent but low myophragm present posteriorly; inner socket ridges massive; cardinal process septiform; crura strongly curved ventrally, laterally compressed proximally, then twisted to horizontal distally. *Lower Devonian (Lochkovian–Pragian):* North America.——FIG. 737,*1a–g*. **T. julli,* Royal Creek, Yukon, Canada; *a–c,* holotype, dorsal, lateral, and posterior views; *d–e,* hypotype, ventral and anterior views, ×1; *f,* hypotype, ventral valve interior, ×2; *g,* hypotype, dorsal valve interior, ×3 (Lenz, 1967).

Yukiangides HAVLÍČEK, 1992, p. 61 [**Camarotoechia parasappho* WANG, 1956, p. 141; OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak straight to suberect; foramen hypothyrid with conjunct deltidial plates. Fold and sulcus low but distinct anteriorly; anterior commissure uniplicate. Costae mostly simple, from beaks, subangular. Dental plates short with umbonal cavities mostly filled with callus; teeth stout, arising from valve margins. Hinge plates massive, sessile; cardinal

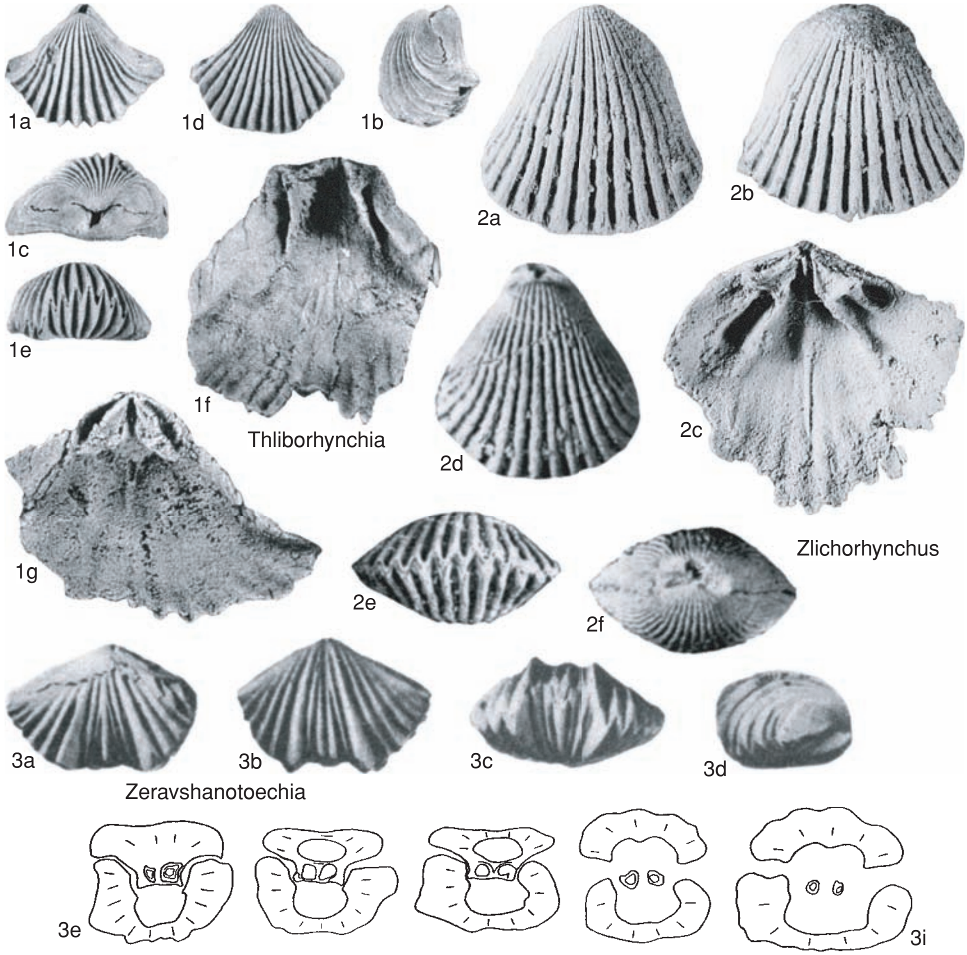

FIG. 737. Machaerariidae (p. 1088–1091).

process septiform; crura short, curved ventrally. *Lower Devonian (Lochkovian–Emsian):* China, Altai, Urals, Bohemia.——FIG. 736,*2a–e.* **Y. parasappho* (WANG), Pragian–Emsian, Yukiang Formation, central Guangxi, southern China; holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1.5 (Wang, 1956).——FIG. 736,*2f–h. Y. vesta* (BARRANDE), Lochkovian, Lochkov Formation, Bohemia; *f–g,* hypotype, serial sections 10.2, 10.0 mm from anterior, ×3.8; *h,* serial section of another specimen, ×2.6 (Havlíček, 1961).

Zeravshanotoechia RZHONSNITSKAIA, 1977, p. 127 [**Z. zeravshanica;* OD]. Small to medium with angular subpentagonal outline, tending toward alate; dorsibiconvex profile. Dorsal fold bearing sulcuslike depression, and sulcus with marked medial rib; anterior commissure sulciplicate, denticulate. Costae of varying size, fasciculate, most pronounced bordering fold and sulcus. Shell wall very thick. Dental plates absent; teeth massive, arising from valve margin. Hinge plates undivided, sessile posteriorly; septalium not developed; dorsal median septum absent; cardinal process septiform, with notothyrial cavity roofed by cover plate; crura long, rather straight. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Tadzhikistan, Urals.——FIG. 737,*3a–i.* **Z. zeravshanica; a–d,* holotype, dorsal, ventral, anterior, and lateral views, Zlichovian, Zeravshansk Range, Tadzhikistan, ×2; *e–i,* serial sections 1.0, 1.7, 2.1, 2.4, 2.7 mm from posterior, ×2.5 (Rzhonsnitskaia, 1977).

Zlichorhynchus HAVLÍČEK, 1963, p. 403 [**Z. hiatus;* OD]. Small with rounded subtriangular elongate outline, widest at about three-quarter length; biconvex profile. Beak straight; foramen large mesothyrid, flanked by thin disjunct deltidial plates. Fold and sulcus absent; anterior commissure rectimarginate. Costae straight, narrow, rounded,

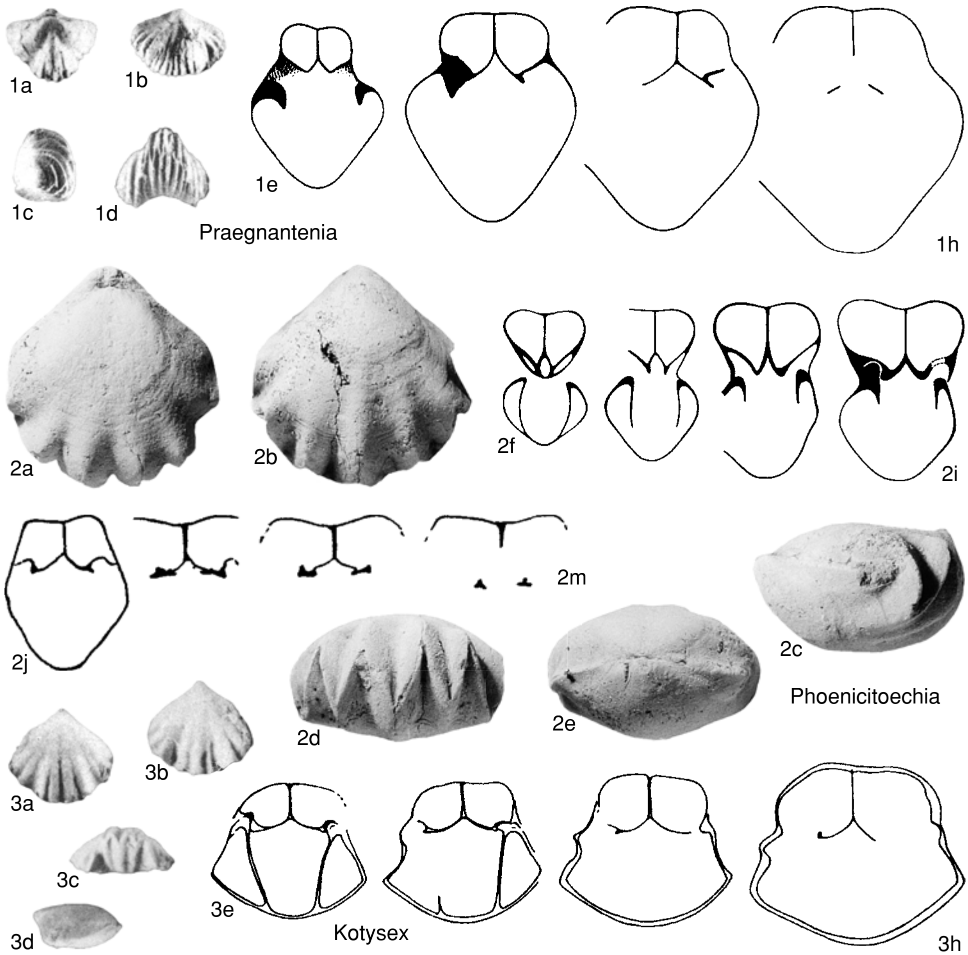

FIG. 738. Phoenicitoechiidae (p. 1091).

never bifurcating. Dental plates short, commonly fused with valve walls. Hinge plates triangular, concave, inner edges extending anteriorly as long crural plates that bound muscle field; dorsal median septum absent; cardinal process septiform, within deep notothyrial cavity; crura unknown. *Lower Devonian (Pragian–Emsian):* Bohemia, China, Australia.——FIG. 737,*2a–f.* **Z. hiatus,* Emsian, Zlichov Limestone, Hlubocepy, Bohemia; *a–b,* holotype, dorsal and ventral views; *c,* hypotype, dorsal valve interior, ×3.1; *d–f,* hypotype, dorsal, anterior, and posterior views, ×2.8 (Havlíček, 1992).

Family PHOENICITOECHIIDAE Havlíček, 1990

[Phoenicitoechiidae HAVLÍČEK, 1990b, p. 216]

Rhynchotrematoidea with subcircular to subtrigonal outline; fold and ventral sulcus moderate to strong; costae strong, simple or sometimes arising by bifurcation and intercalation; umbones generally smooth; delthyrium with disjunct to conjunct deltidial plates. Dental plates short, thin. Hinge plates form wide, open, ventrally convex septalium; cardinal process absent. *Lower Devonian (Lochkovian–Emsian).*

Phoenicitoechia HAVLÍČEK, 1960, p. 242 [**Terebratula phoenix* BARRANDE, 1847, p. 75; OD]. Subtriangular to transversely ovate outline; equibiconvex, lateral and anterior margins precipitous. Beak erect; foramen open; deltidial plates disjunct to conjunct. Fold and sulcus weak, from midlength; anterior commissure weakly uniplicate, denticulate. Costae few, strong, subangular, restricted to lateral and anterior margins. Dental plates short, slender. Dorsal median septum high, long; septalium long, wide, without cover plate; crural bases subtriangular. *Lower Devonian (lower Pragian–lower Emsian):* Europe, Urals, China.——FIG. 738,*2a–m.* **P. phoenix* (BARRANDE), Pragian, Koneprusy Limestone, Bohemia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, Koneprusy, ×3.5 (new); *f–i,* hypotype, serial sections 8.6, 8.55, 8.5, 8.4 mm from anterior, ×3 (Havlíček, 1961); *j–m,* hypotype, serial sections showing crural bases, ×7.5 (Schmidt, 1965b).

Kotysex HAVLÍČEK, 1990b, p. 218 [**Rhynchonella simulans* BARRANDE, 1879b, pl. 147, case 7, fig. 1a–d; OD]. Subcircular to subpentagonal in outline; equibiconvex, lenticular, not inflated anteriorly, never truncated at lateral and anterior margins. Beak suberect to erect; foramen open; deltidial plates disjunct to conjunct. Fold and sulcus weak, from umbones; anterior commissure uniplicate; tongue broad, low, serrate. Costae few, subangular, arising anterior of smooth umbones, with some bifurcation. Dental plates thin, short, slightly convergent ventrally. Septalium large, wide, long; median septum thin, high; crura unknown. *Lower Devonian (Lochkovian–Pragian):* Bohemia, Carnic Alps.——FIG. 738,*3a–h.* **K. simulans* (BARRANDE); *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, Vinarice Limestone, Menany, Bohemia, ×1 (Havlíček, 1961); *e–h,* hypotype, serial sections, ×5.25 (Havlíček, 1990b).

Praegnantenia HAVLÍČEK, 1961, p. 99 [**Terebratula praegnans* BARRANDE, 1847, p. 72; OD]. Subpentagonal outline; dorsibiconvex, strongly inflated anteriorly. Beak small, incurved; delthyrium open posteriorly to leave small foramen; deltidial plates disjunct to conjunct. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue high, rounded, dentate. Costae low, angular, present on fold, sulcus, and flanks, some bifurcation; umbones smooth. Dental plates thin, short. Septalium large, wide, supported by high, long dorsal median septum. *Lower Devonian (lower Pragian–lower Emsian):* Bohemia, southern Urals.——FIG. 738,*1a–h.* **P. praegnans* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; *a–d,* lectotype, dorsal, ventral, lateral, and anterior views, ×1; *e–h,* hypotype, serial sections 7.2, 7.0, 6.85, 6.75 mm from anterior, ×5 (Havlíček, 1961).

UNCINULOIDEA

NORMAN M. SAVAGE
[University of Oregon]

Superfamily UNCINULOIDEA Rzhonsnitskaia, 1956

[*nom. transl.* SAVAGE, 1996, p. 252, *ex* Uncinulidae RZHONSNITSKAIA, 1956a, p. 125]

Rhynchonellida with globular, cuboid, or lenticular shape; dorsal fold and ventral sulcus weak; tongue high; costae numerous, flattened anteriorly on *paries geniculatus;* anterior and lateral margin spines usually present; foramen small, commonly with conjunct to disjunct deltidial plates anteriorly; squamae and glottae often developed. Dental plates weak or infilled with callus. Dorsal median septum, septalium, and cardinal process generally present; crura commonly raduliform. *lower Silurian (Llandovery)–Upper Devonian (upper Famennian).*

Family UNCINULIDAE Rzhonsnitskaia, 1956

[Uncinulidae RZHONSNITSKAIA, 1956a, p. 125]

Uncinuloidea with thick shell; anterior marginal spines long. Dental plates short or obscured by umbonal callus. Dorsal median septum present; septalium usually infilled by callus; cardinal process wide, multilobed. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian).*

Uncinulus BAYLE, 1878, pl. 11, fig. 11, 12, 15, 16 expl. [**Hemithyris subwilsoni* d'ORBIGNY, 1850 in 1849–1852, p. 92; SD OEHLERT, 1884, p. 423] [=*Tridensilis* SU, 1976, p. 193 (type, *T. gibbosa,* OD); *Uncina* KAPLUN, 1991, p. 125 (type, *U. bublitschenkoi,* OD)]. Medium to large size; subcircular to subpentagonal outline; hinge line strophic; articulation with squamae and glottae; strongly biconvex to globular profile; anterior margin and flanks vertical. Beak erect to incurved; foramen absent or minute. Dorsal fold and ventral sulcus weak but rectangular to subrectangular anterior tongue distinct. Costae fine, from beaks, some bifurcation and intercalation, grooved at commissure to accommodate marginal spines. Dental plates well developed, convex medially, umbonal cavities commonly filled with callus; ventral muscle area deeply impressed, divided by thin septum. Septalium small, usually filled with callus; dorsal median septum buried in callus; cardinal process wide, multilobed, filling posterior of septalial cavity. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* cosmopolitan.——FIG. 739,*2a–p.* **U. subwilsoni* (D'ORBIGNY), Lower Devonian, northwestern France; *a–d,* dorsal, ventral, anterior, and lateral views; *e,* interior of ventral valve, ×.95; *f,* interior of dorsal valve, enlarged (Bayle, 1878); *g–p,* serial sections 13.0, 12.8, 12.6, 12.3, 11.8, 11.7, 11.6, 11.5, 11.2, 10.2 mm from anterior, ×2 (Schmidt, 1965b).——FIG. 739,*2q–s. Uncinulus,* marginal spines (schematic); *q,* both valves connected, slightly opened; *r,* dorsal valve; *s,* ventral valve, approximately ×1.5 (Schmidt, 1937).

Bulgania ERLANGER, 1994, p. 109 [**B. mongolica;* OD]. Subovate to subcircular outline; lateral profile strongly biconvex and anteriorly inflated but ventral valve slightly resupinate; anterior and lateral margins vertical. Beak erect; foramen submesothyrid; tongue high, rectangular. Fold and sulcus weak. Costae fine, arising at umbones, flattened and bearing grooves anteriorly on *paries geniculatus;* intercostal furrows extending as marginal spines. Dental plates very short to absent, obscured by thick callus; ventral muscle field deeply impressed, divided by low ridge. Dorsal interior with massive, linguiform, trilobed cardinal process filling short, low septalium; dorsal median septum high, long; crura long, closely set. *Upper Devonian (Frasnian):* Mongolia.——FIG. 739,*1a–l.* **B. mongolica,* Bulgan area, 2 km northeast of Mt. Zagin-Khar-Ula, southwestern Mongolia; *a–e,* holotype, dorsal, ventral, posterior, lateral, and anterior views, ×1; *f–l,* serial sections 1.1, 1.95, 2.8, 3.1, 3.2, 3.9, 3.95 mm from posterior, ×2.5 (Erlanger, 1994).

Eucharitina SCHMIDT, 1955, p. 121 [**Terebratula eucharis* BARRANDE, 1847, p. 68; OD]. Medium to large size; subcircular outline; dorsibiconvex to convexoconcave lateral profile; lateral and anterior margins steep to vertical. Beak erect to incurved; foramen absent. Fold and sulcus low, from midlength; anterior commissure uniplicate; tongue low, wide. Costae flattened, with longitudinal grooves on lateral and anterior shell margins; commissure denticulate with marginal spines that taper uniformly to point, extending under costae of opposite valve. Dental plates very short; ventral muscle field deeply impressed, divided by small septum. Septalium small, filled by large cardinal process that is multilobed posteriorly but massively bilobed anteriorly; crura long, slender, closely set. *Lower Devonian (Pragian):* Europe, northern Africa.——FIG.

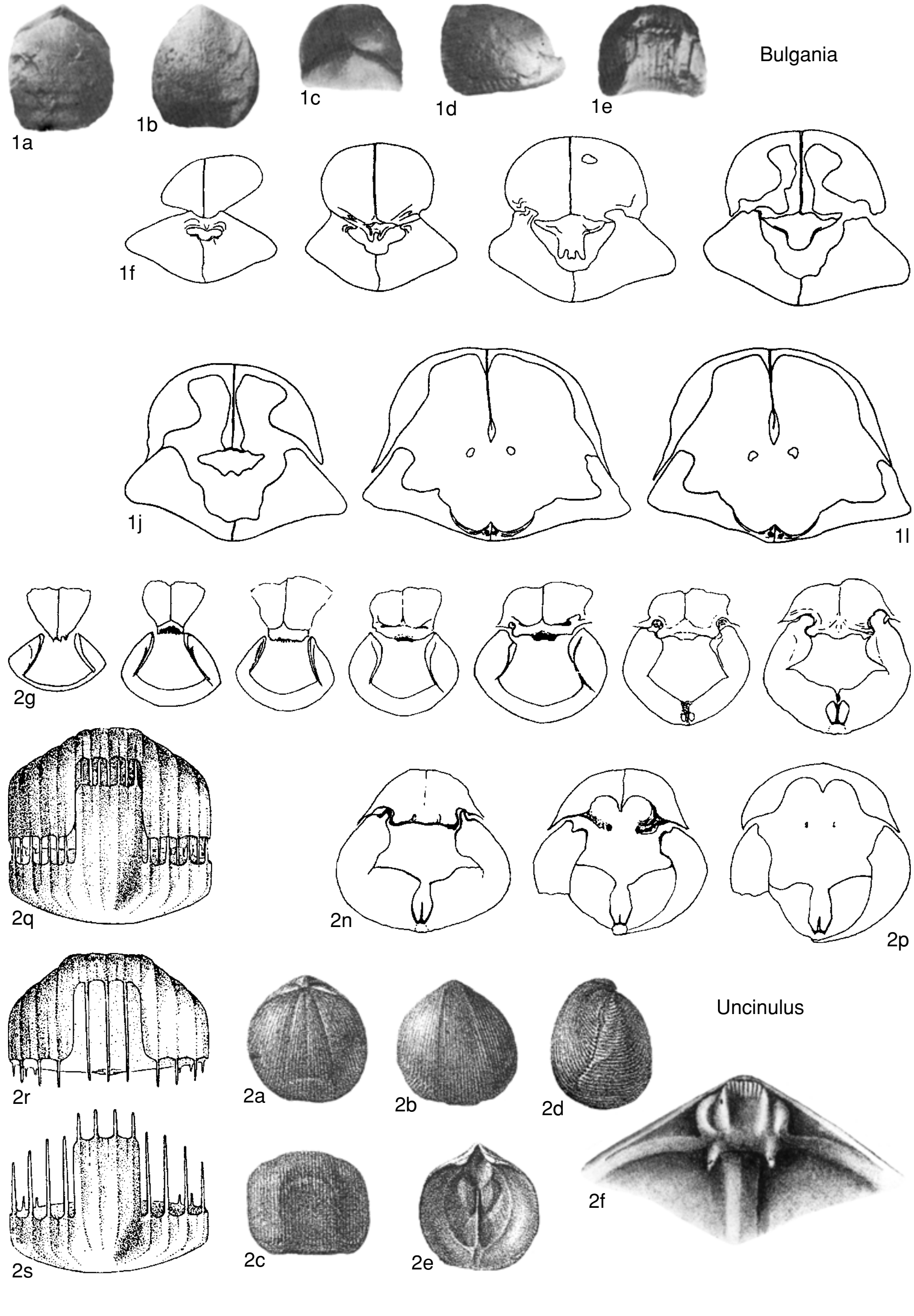

FIG. 739. Uncinulidae (p. 1092).

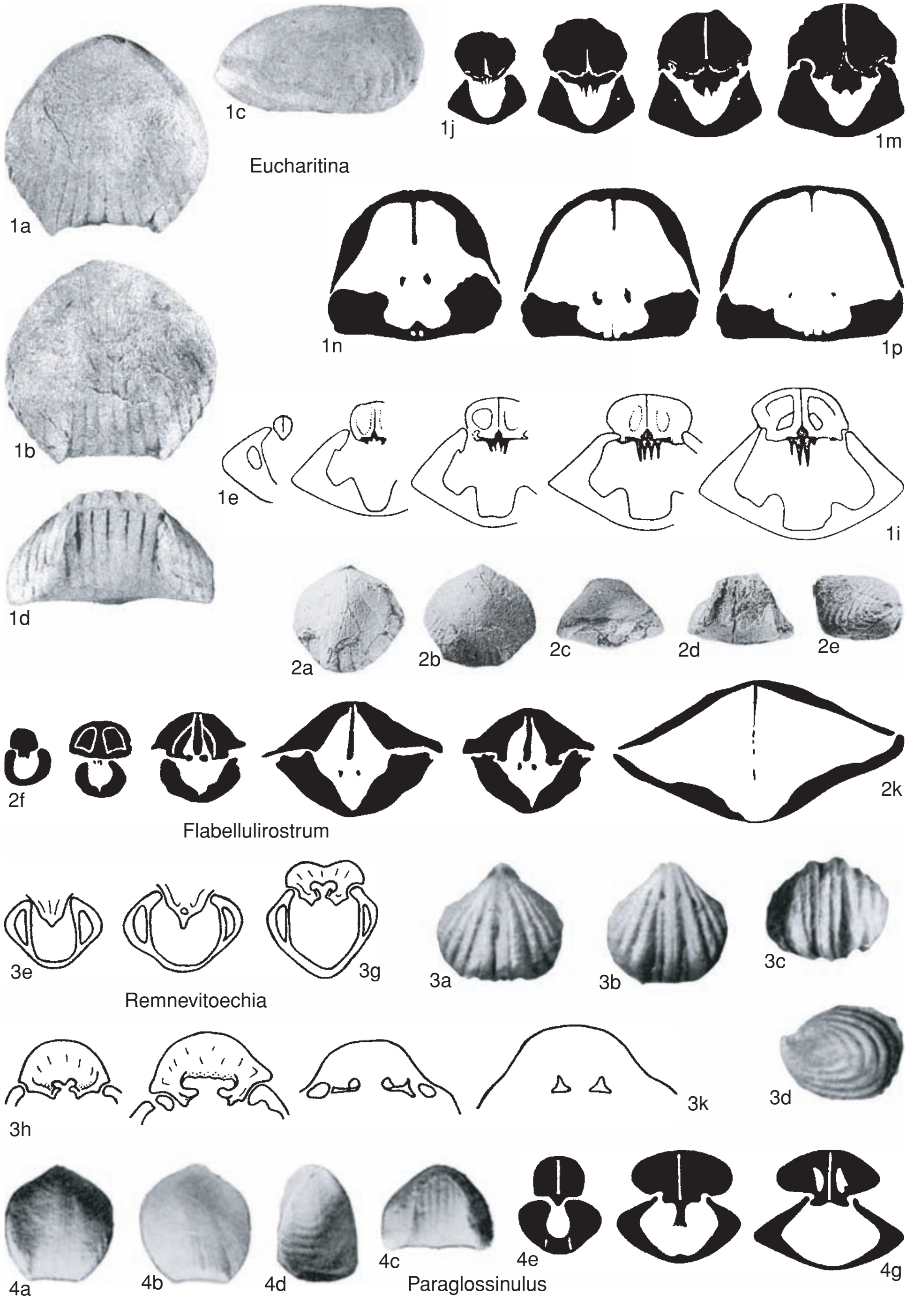

FIG. 740. Uncinulidae (p. 1092–1097).

740,*1a–i.* **E. eucharis* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e–i,* hypotype, serial sections 29.1, 29.0, 28.9, 28.7, 28.6 mm from anterior (Havlíček, 1961). ——FIG. 740,*1j–p. E. oehlerti* (BAYLE), Pragian, Saint-Cenéré section, northwestern France; *j–m,* hypotype, serial sections 1.1, 2.0, 2.6, 2.9 mm from posterior, ×1.8; *n–p,* serial sections 6.4, 7.2, 8.7 mm from posterior of another hypotype, ×1.3 (Brice, 1991).

Fitzroyella VEEVERS, 1959a, p. 104 [**F. primula;* OD]. Medium to small with subpentagonal outline and biconvex profile. Beak suberect; foramen small, circular, bounded by conjunct deltidial plates. Costae coarse, uneven, multiplying by intercalation and bifurcation; costae flattened and grooved anteriorly and anterolaterally; short marginal spines present. Dental plates well developed, ventrally divergent; ventral muscle field bilobed; socket holes for spines prominent around anterior internal margin. Dorsal median septum short, low; septalium very short; hinge plates anterior of septalium divided, horizontal; cardinal process small, low. *Middle Devonian (middle Givetian)–Upper Devonian (middle Frasnian):* Western Australia, Germany, England, Poland.——FIG. 741,*1a–m.* **F. primula,* lower Frasnian, Sadler Formation, Fitzroy basin, Sadler Ridge, Western Australia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×4; *e,* interior of ventral valve showing marginal spine socket holes, ×6; *f–m,* serial sections 0.65, 0.80, 0.85, 0.90, 0.95, 1.10, 1.15, 1.70 mm from posterior, ×4 (Veevers, 1959a).——FIG. 741,*1n–p. F. alata* BIERNAT, lower Frasnian, Holy Cross Mountains, Kielce, Poland; dorsal, lateral, and anterior views, ×3.6 (Biernat, 1969).——FIG. 741,*1q. F. juxi,* lower Frasnian, Refrath Formation, Bergisches Land, Germany; transverse section showing cardinal process, ×10 (Struve, 1978).

Flabellulirostrum SARTENAER, 1971a, p. 5 [**Uncinulus wolmericus* VEEVERS, 1959a, p. 96; OD]. Medium size with subcircular to transversely ovate outline and dorsibiconvex profile. Beak erect to incurved; foramen mesothyrid. Fold and sulcus arising near umbones; anterior commissure uniplicate; tongue medium to high, trapezoid, projecting. Costae simple, strong on fold and in sulcus, weaker on flanks, separated by narrow grooves; short marginal spines present. Dental plates short to absent; ventral muscle field narrow, in thick callus. Hinge plates short, breaking up early; cardinal process large with longitudinal lobes; dorsal median septum long, high; dorsal muscle field narrow, in thick callus; crura closely set, ventrally curved. *Middle Devonian (upper Givetian)–Upper Devonian (middle Frasnian):* Western Australia, Europe, northern Africa.——FIG. 740,*2a–k.* **F. wolmericus* (VEEVERS), lower Frasnian, Sadler Formation, Fitzroy basin, Sadler Ridge, Western Australia; *a–b,* holotype, dorsal and ventral views; *c–e,* hypotype, posterior, anterior, and lateral views, ×1; *f–k,* serial sections 0.4, 0.6, 1.0, 1.35, 1.8, 3.5 mm from posterior, ×3.2 (Veevers, 1959a).

Markitoechia HAVLÍČEK, 1959, p. 81 [**Uncinulus (U.) marki* HAVLÍČEK, 1956, p. 568; OD]. Shell small; subcircular to subpentagonal outline; biconvex with truncated anterior and lateral margins. Beak suberect; foramen mesothyrid, bounded by conjunct deltidial plates. Fold and sulcus weak; tongue high, rounded to rectangular. Most of valves smooth; costae arising close to anterior and lateral margins, flattened and grooved on *paries geniculatus;* spines at commissure. Dental plates thin, close to valve walls; ventral muscle field well impressed. Dorsal median septum low, long; septalium small, with arched cover plate anteriorly and filled posteriorly with very high, rodlike cardinal process. *Lower Devonian (Emsian):* Europe, northern Africa.——FIG. 741,*2a–i.* **M. marki* (HAVLÍČEK), Zlichov Limestone, Hlubocepy, Bohemia; *a–b,* holotype, dorsal and ventral views; *c,* anterior view, ×2.4 (Havlíček, 1956); *d–e,* serial sections, ×7 (Havlíček, 1961); *f–i,* hypotype, dorsal, ventral, lateral, and anterior views, ×4.5 (Havlíček, 1992).

Paraglossinulus MARTYNOVA, 1988, p. 41 [**P. parvus;* OD]. Shell small; subtriangular to subcircular; anteriorly inflated but ventral valve slightly resupinate; anterior and lateral margins vertical. Fold and sulcus strong, arising from umbones; anterior commissure uniplicate; tongue high, rounded. Costae arising at umbones, flattened and bearing grooves anteriorly. Dental plates and septalium very short; dorsal median septum reaching valve midlength; cardinal process high, linguiform. *Upper Devonian (Frasnian):* Kazakhstan.——FIG. 740,*4a–g.* **P. parvus,* Maya bed, Cischingiz, Koryk River, central Kazakhstan; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–g,* serial sections, ×3.6 (Martynova, 1988).

Plethorhyncha HALL & CLARKE, 1893, p. 191 [**Rhynchonella speciosa* HALL, 1857a, p. 81; SD SCHUCHERT & LEVENE, 1929a, p. 99]. Medium to large with elongate oval outline; inflated, lateral and anterior margins vertical. Beak incurved; foramen absent; squamae and glottae prominent. Fold and sulcus weak, tongue low; anterior commissure weakly uniplicate, zigzag denticulation. Costae arising at beaks, simple, flattened anteriorly where they bear grooves that accommodate marginal spines. Dental plates absent or obscured by callus; teeth attached to valve walls; ventral muscle field elongate, deeply impressed. Dorsal median septum extending to valve midlength; septalium small, open; large bilobed cardinal process; crura short, straight. *Lower Devonian (Emsian):* North America, ?Europe.——FIG. 742,*1a–h.* **P. speciosa* (HALL), Oriskanian, Cumberland, Maryland, USA; *a–c,* posterior, anterior, and lateral views, ×0.8; *d,* interior of ventral valve; *e,* interior of young dorsal valve, ×1; *f,* interior of mature dorsal valve, ×0.8 (Hall & Clarke, 1895); *g,* interior of silicified dorsal

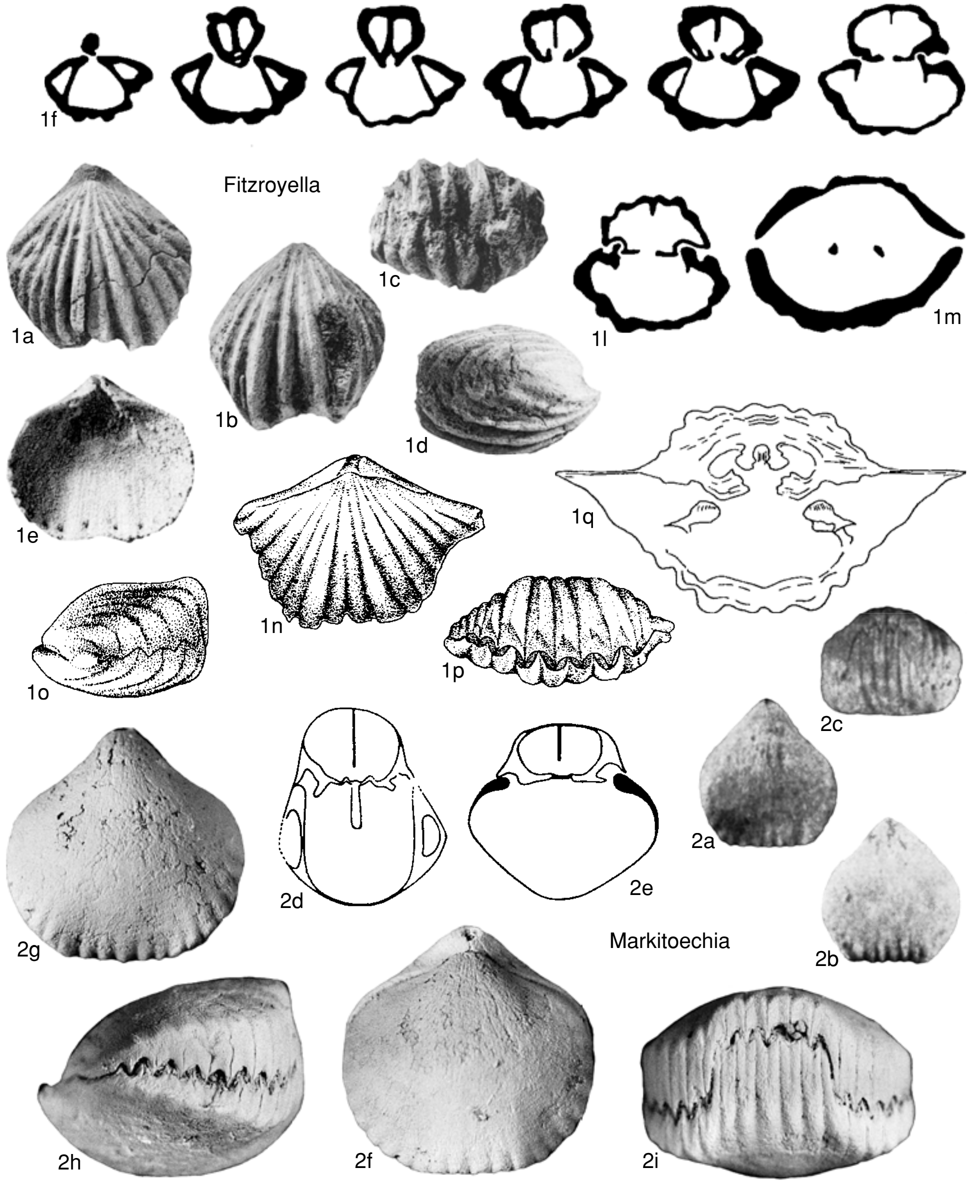

FIG. 741. Uncinulidae (p. 1095).

fragment showing cardinalia, ×1.6; *h,* interior of silicified ventral fragment showing teeth and muscle field, ×1.3 (new).

Remnevitoechia GRATSIANOVA, 1970, p. 97 [**R. pseudogurjevskensis;* OD]. Small size with subpentagonal outline and strongly biconvex profile. Beak erect to incurved; foramen small, mesothyrid. Fold and sulcus well defined, from umbones; tongue high, rectangular. Costae coarse, uneven, from beaks, some splitting and intercalation, flattened and bearing grooves at *paries geniculatus,* marginal spines developed. Dental plates distinct, vertical. Cardinal process massive, single lobed. Dorsal median septum and septalium absent. Hinge plates supported on thick callus, divided. Crura long, sharply curved ventrally, triangular in cross section. *Lower Devonian (Lochkovian):* Salair, Altai.——FIG. 740,*3a–k.* **R. pseudogurjevskensis,* Tom'chumyshskie Beds, northeastern Salair Gurevsk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–g,*

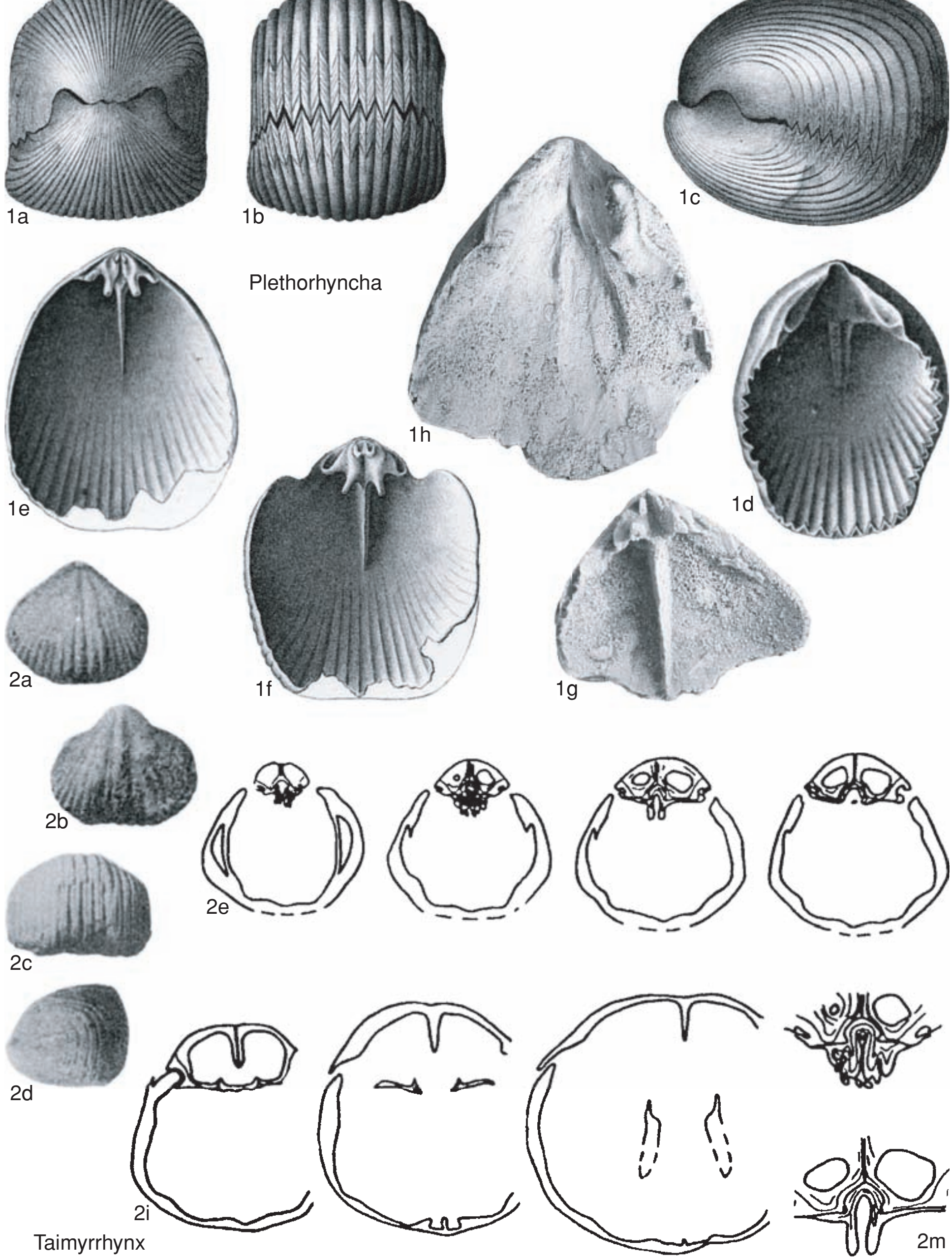

FIG. 742. Uncinulidae (p. 1095–1098).

serial sections 0.3, 0.5, 0.7 mm from posterior; *h–k,* serial sections 0.6, 0.8, 1.0, 1.2 mm from posterior of different specimen, approximately ×6 (Gratsianova, 1970).

Taimyrrhynx HAVLÍČEK, 1983, p. 154 [**Uncinulus irbitensis taimyricus* NIKIFOROVA, 1960b, p. 365; OD]. Subpentagonal outline; strongly biconvex to globular profile. Beak erect to incurved; foramen small, with minute conjunct deltidial plates. Fold and sulcus weak; tongue rectangular. Costae from beaks, some bifurcation and intercalation, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short, close to valve walls; ventral muscle field divided by thin septum. Septalium small, filled posteriorly with large cardinal process that is multilobed posteriorly but high and bilobed anteriorly; septalium with cover anteriorly; dorsal median septum low, long. *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Urals, Bohemia.——FIG. 742,*2a–m.* **T. taimyricus taimyricus* (NIKIFOROVA), upper Emsian, central Taimyr; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k,* serial sections, ×5; *l–m,* enlargements of cardinal process sections in *f* and *g,* ×10 (Tcherkesova, 1968).

Family EATONIIDAE Schmidt, 1965

[Eatoniidae SCHMIDT, 1965b, p. 570]

Uncinuloidea with subcircular to elongate outline; costae usually extending from beaks, often with superimposed striae; dorsal fold and ventral sulcus strong but narrow; lateral margins of valves generally meet at acute angle, never truncated; foramen with conjunct deltidial plates anteriorly; anterior and lateral valve margins commonly with stubby spines that project into notches in opposite valve. Dental plates absent or infilled with callus; ventral muscle field large with strong border and distinct myophragm; large diductor scars enclose small adductor scars, also with strong border and myophragm. Dorsal median septum usually weak or absent; cardinal process very large, linguiform, bilobed to quadrilobed; hinge plates usually united by cardinal process; crural bases stout; crura short, laterally compressed. *lower Silurian (Llandovery)–Lower Devonian (upper Pragian).*

Eatonia HALL, 1857a, p. 90 [**Atrypa medialis* VANUXEM, 1842, p. 120; SD HALL & CLARKE, 1893, p. 205] [=*Pareatonia* MCLEARN, 1918, p. 137, obj.]. Large with subcircular to transversely ovate outline and dorsibiconvex profile; lateral margins not steep. Beak erect to incurved; foramen small, deltidial plates large, conjunct. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, serrate. Costae strong, simple, extending from beak; fine radial striae superimposed on costae; at anterior and lateral valve margins stubby spines project into notches in opposite valves. Dental plates cemented to valve walls; ventral muscle field deeply impressed, bounded by marked border; diductor muscle field bilobed, large, ovate, divided by myophragm; adductor field small, enclosed by diductors, also divided by distinct myophragm, covered posteriorly. Cardinal process large, very high, trilobed, merging with and dominating hinge plates; sockets deep, short; low median septum extending two-thirds valve length; adductor muscle field large, ovate, divided by myophragm; crural bases stout, rounded, arising from beneath cardinal process; crura fairly straight with tips laterally compressed. *Lower Devonian (Lochkovian):* North America, Australia, China.——FIG. 743,*1a–g.* **E. medialis* (VANUXEM), upper Helderbergian, upper Helderberg Group, Maryland, USA; *a–e,* hypotype, dorsal, ventral, posterior, anterior, and lateral views, Iron Mountain, Cumberland, ×1; *f,* interior of ventral valve, Licking Creek, Indian Springs, ×1.5; *g,* latex impression of dorsal valve, Licking Creek, Indian Springs, ×1.2 (new).

Aratanea SCHMIDT, 1967, p. 92 [**A. monodi;* OD]. Elongate oval outline and equibiconvex profile. Beak erect to incurved. Fold and sulcus distinct but low; anterior commissure uniplicate; tongue low, wide, serrate. Costae medium to coarse, variable, some bifurcation, rounded, arising at beaks. Dental plates short, thick, ventrally divergent, usually cemented to valve walls or obscured by callus; ventral muscle field weakly impressed. Cardinal process small to lacking; median myophragm extending to about midlength; adductor field large, elongate, quadripartite; hinge plates united, comprising stout crural bases directed anteriorly and thick inner socket ridges directed anterolaterally. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Mauritania.——FIG. 743,*2a–h.* **A. monodi,* Grès á Brachiopodes, Majâbat al-Koubrâ; *a–e,* holotype, dorsal, ventral, anterior, lateral, and posterior views of internal mold, ×1.3; *f,* paratype, interior of latex cast showing dental plates and cardinalia; *g,* paratype, interior of latex cast of dorsal valve mold showing cardinalia; *h,* paratype, interior of latex cast of dorsal valve mold showing cardinalia and muscle field, ×2 (Schmidt, 1967).

Boucotella BOWEN, 1966, p. 186 [**Camarotoechia gigantea* MAYNARD, 1913, p. 354; OD]. Large with subcircular to subtriangular outline and dorsibiconvex profile. Beak erect to incurved; small permesothyrid to mesothyrid foramen; deltidial plates conjunct. Fold and sulcus strong anteriorly, narrow; tongue high, tapering dorsally. Costae medium size, rounded. Dental plates short, close to valve walls or obscured by callus; ventral muscle field deeply impressed, cardiform with medial myophragm. Cardinal process very large, bilobed, high, tonguelike, excavated ventrally and anteriorly, extending almost to ventral valve floor and filling space between dental plates. *upper Silurian (Přídolí):* eastern USA.——FIG. 744,*2a–j.* **B. gigantea* (MAYNARD), upper Přídolí, middle Keyser Limestone, Virginia; *a–e,* hypotype, dorsal (beak broken, not perforate), ventral, posterior, anterior,

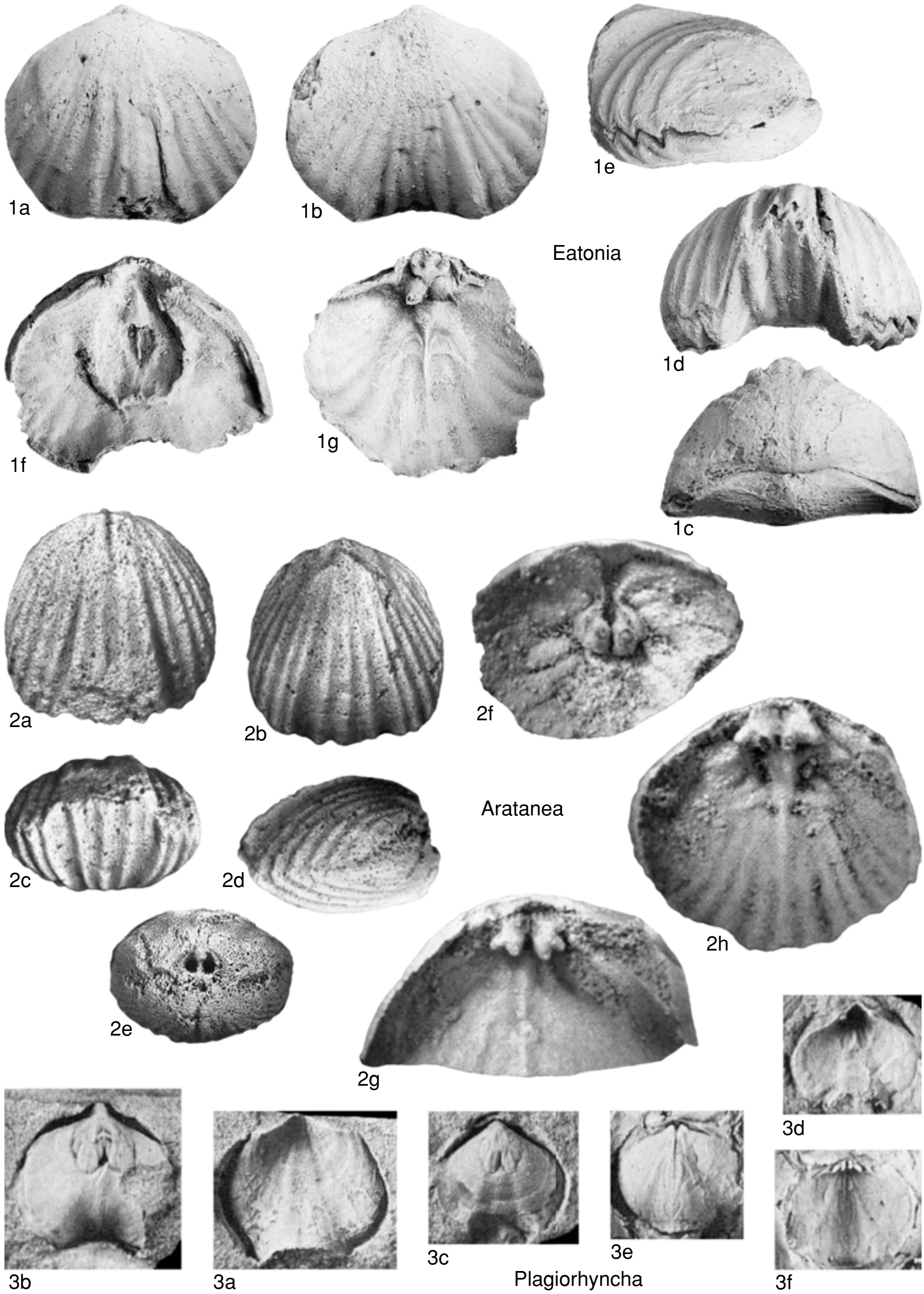

FIG. 743. Eatoniidae (p. 1098–1104).

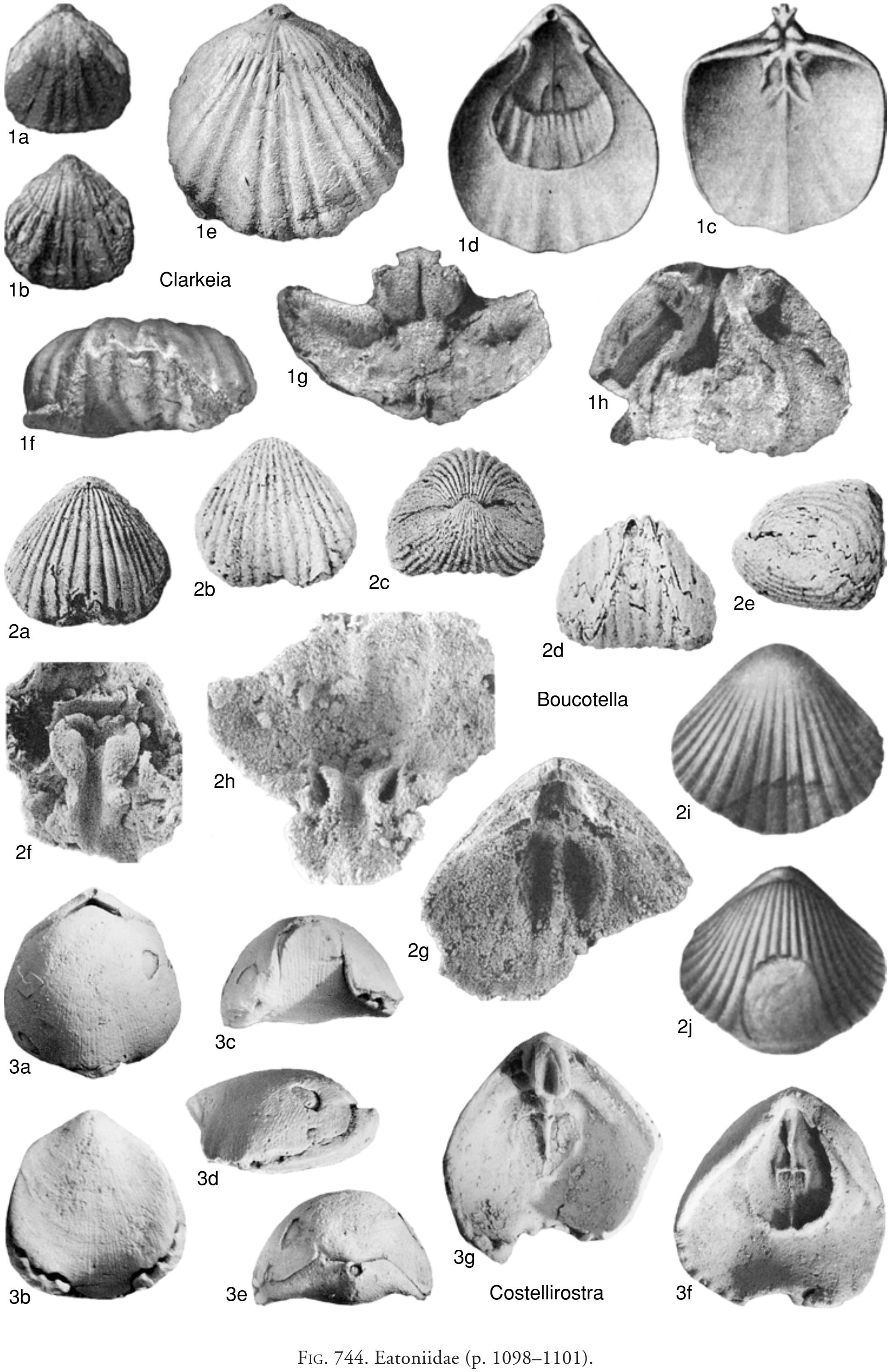

FIG. 744. Eatoniidae (p. 1098–1101).

and lateral views, Warm Springs, ×1; *f,* cardinal process of dorsal valve articulated with broken ventral valve showing dental plates, Lantz Mountain; *g,* hypotype, interior of broken ventral valve, Lantz Mountain; *h,* interior of broken conjoined valves, Lantz Mountain, ×2 (Bowen, 1966); *i–j,* holotype, dorsal and ventral views, Devil's Backbone, ×1 (Maynard, 1913).

Clarkeia Kozlowski, 1923, p. 86 [**Terebratula antisiensis* d'Orbigny, 1847 in 1847–1849, p. 36; OD]. Subcircular outline and moderately biconvex profile. Beak erect to incurved; foramen small, dorsal beak filling remainder of delthyrium. Fold and sulcus distinct, low, arising at umbones; anterior commissure uniplicate, wide, trapezoid to rounded, serrate. Costae coarse, variable in width, rounded, arising at beaks. Dental plates short, thick, ventrally divergent, usually evident but may be obscured by callus; ventral muscle area well impressed, bisected by low myophragm; diductor scars ovate to flabellate, large; adductor scars surrounded by diductor scars. Cardinal process large, tonguelike, bilobed, trilobed, or tetralobed; median myophragm extending to about midlength; adductor field large, elongate, quadripartite with oblique ridges between posterior and anterior adductors; crural bases stout, merging with cardinal process dorsolaterally, crura short, tapering, ventrally curved. *lower Silurian (Llandovery)–upper Silurian (Přídolí):* South America, western Africa, Europe.——Fig. 744,*1a–h*. **C. antisiensis* (d'Orbigny), Wenlock, South America; *a–b,* hypotype, dorsal and ventral views, Bolivia, ×1; *c–d,* dorsal and ventral valve interior, Bolivia, ×2 (Kozlowski, 1923); *e–f,* dorsal and anterior views, San Juan Province, Argentina, ×2; *g,* latex cast of dorsal valve internal mold showing cardinal process and crural bases, San Juan Province, Argentina, ×3; *h,* latex cast of ventral valve internal mold showing dental plates and muscle field, San Juan Province, Argentina, ×3 (Cocks, 1972).

Costellirostra Cooper, 1942, p. 231 [**Atrypa peculiaris* Conrad, 1841, p. 56; OD]. Elongate oval to subtriangular outline and dorsibiconvex profile; lateral margins sloping. Beak erect to incurved, rounded foramen at apex, deltidial plates conjunct. Fold and sulcus weak, evident only anteriorly; anterior commissure uniplicate; tongue high, rounded. Costellae fine, numerous, bifurcating. Narrow, gutterlike groove extending around anterior and lateral valve margins from which stubby spines project into notches in opposite valve. Dental plates cemented to valve walls; ventral muscle field ovate, deeply impressed, with high border; diductor field bilobed, divided by myophragm; adductor field small, surrounded by diductors, divided by myophragm, partly covered posteriorly. Cardinal process very large and high with 2 large outer lobes and 2 small inner lobes; crura short, stout. *Lower Devonian (Pragian):* North America, USA, Canada, Mexico.——Fig. 744,*3a–g*. **C. peculiaris* (Conrad), Oriskanian, Glenerie Limestone, Glenerie, New York, USA; *a–e,* paralectotype, dorsal, ventral, anterior, lateral, and posterior views; *f–g,* paralectotype, interior of ventral valve, interior of dorsal valve, ×1.5 (new).

Diabolirhynchia Drot, 1964a, p. 111 [**D. hollardi;* OD]. Small to medium with elongate oval outline and biconvex profile. Beak suberect to erect; delthyrium with short rectangular deltidial plates. Sulcate fold and plicate sulcus; 2 large costae on fold, 1 large costa in sulcus, costae on flanks smaller and more numerous, arising near beaks. Dental plates long, vertical or slightly convergent ventrally. Hinge plates undivided; cardinal process very large, high, trilobed; septalium absent; dorsal median septum long, thick, low; crural bases triangular in section; crura long, ventrally curved, concave dorsomedially. *upper Silurian (Ludlow):* Morocco, Mauritania.——Fig. 745,*1a–k*. **D. hollardi,* Ludlow Series, Morocco; *a–c,* holotype, dorsal, lateral, and anterior views, ×1; *d–k,* serial sections 0.2, 1.0, 1.2, 1.4, 1.7, 2.2, 2.5, 3.5 mm from posterior (Drot, 1964a).

Eatonioides McLearn, 1918, p. 137 [**E. lamellornatus;* OD]. Large with subcircular to transversely ovate outline and dorsibiconvex profile; lateral margins not steep. Beak erect to incurved. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, serrate. Costae strong, simple, extending from beak, separated by angular interspaces; crossed by widely spaced, imbricated growth lamellae. Dental plates cemented to valve walls; teeth stout, rounded; ventral muscle field deeply impressed, circular to oval, bounded by marked border; diductor muscle field divided by myophragm; adductor field small, elongate, enclosed by diductors, also divided by myophragm. Cardinalia consist of hinge plates supported medially by septalium; cardinal process may be merged with hinge plates posteriorly; sockets deep, short; low median septum extending to one-third valve length; crural bases originating from anteromedian edge of hinge plates; adductor muscle field not impressed. *upper Silurian (Ludlow):* eastern North America.——Fig. 746,*1a–i*. **E. lamellornatus*, lower Ludlow, Arisaig Group, Moydart Formation, Lower Member, Nova Scotia, Arisaig, Canada; *a–b,* internal mold and latex impression of ventral valve; *c–d,* internal mold and latex impression of dorsal valve; *e–h,* holotype, dorsal, ventral, anterior, and lateral views; *i,* ventral valve external mold, ×1.2 (Harper, 1973).

Pegmarhynchia Cooper, 1955, p. 58 [**P. zimmi;* OD]. Medium size with subcircular outline and dorsibiconvex profile. Beak erect to incurved; foramen triangular, deltidial plates absent. Fold and sulcus weak posteriorly, strong and narrow anteriorly; anterior commissure uniplicate; tongue high, narrow, rounded, typically biserrate. Costae simple, rounded, arising at beaks, covering entire shell. Dental plates absent, ventral muscle area large, flabellate, well impressed, commonly divided by low myophragm. Hinge plates united to form prominent bilobed cardinal plate that probably incorporated

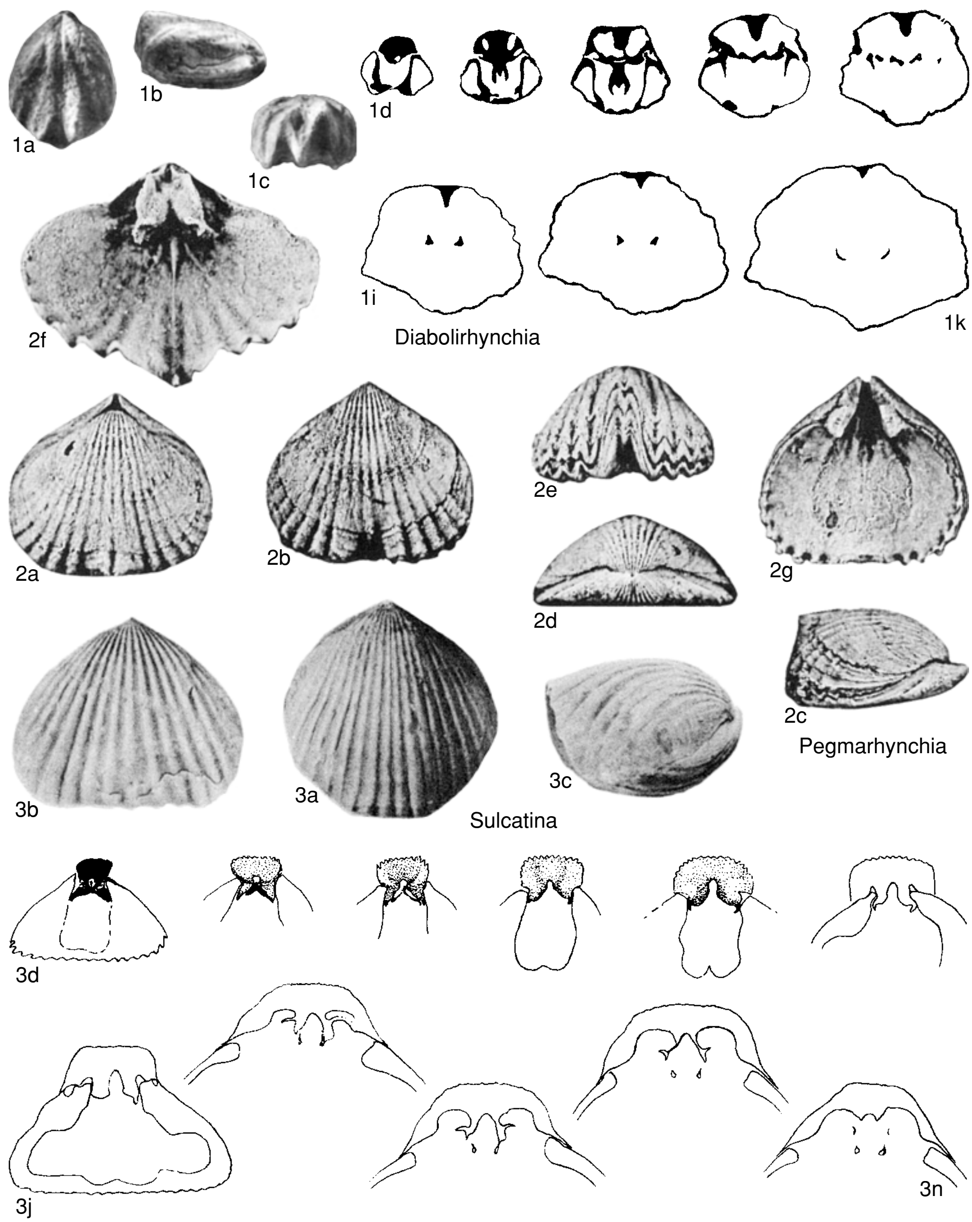

FIG. 745. Eatoniidae (p. 1101–1104).

cardinal process posteriorly; crescentic crural bases arising from cardinal plate anteriorly. *Lower Devonian (upper Pragian):* USA (New York, Maryland).——FIG. 745,*2a–g.* **P. zimmi,* Oriskanian, Glenerie Limestone, Glenerie, New York; *a–d,* holotype, dorsal, ventral, lateral, and posterior views; *e,* paratype, anterior view; *f,* dorsal valve interior; *g,* paratype, ventral valve interior, ×2 (Cooper, 1955).

Plagiorhyncha MCLEARN, 1918, p. 138 [**Rhynchonella glassii* DAVIDSON, 1883, p. 155; OD; =*Atrypa depressa* J. DE C. SOWERBY, 1839, p. 629, subj.]. Small to medium with subcircular outline; lateral

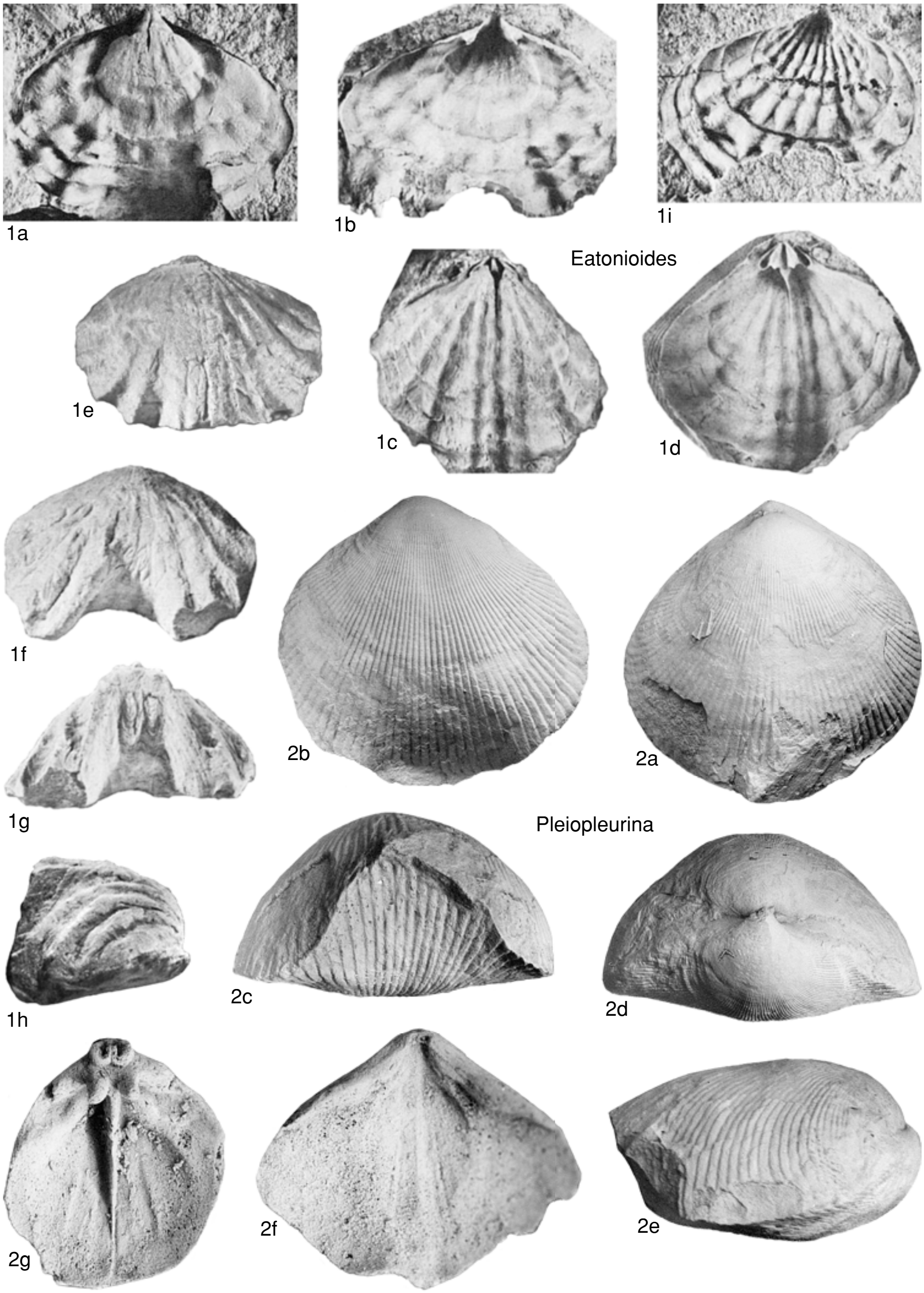

FIG. 746. Eatoniidae (p. 1101–1104).

margins flat or recurved ventrally; posterior margin of some dorsal valves recurved to be concave dorsally. Delthyrium triangular; open. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, undulate. Costae weak, broad, extending from umbones; fine costellae usually present. Dental plates cemented to valve walls; teeth small, rounded; ventral muscle field large, deeply impressed, scalloped outline, bounded by marked border; diductor muscle field divided by myophragm; adductor field small, elongate oval, enclosed by diductors. Hinge plates merge posteriorly with bilobed cardinal process; sockets distinct, bounded by socket ridges laterally; low median septum extending one-half valve length; adductor muscle field with small oval posterior adductors and larger elongate anterior adductors. *lower Silurian (Llandovery)–upper Silurian (Ludlow):* Europe, eastern North America.——FIG. 743,*3a–f.* **P. glassii* (DAVIDSON), upper Llandovery, Ross Brook Formation, Middle Member, Nova Scotia, Pictou County, Arisaig, Canada; *a–b,* external and internal mold of ventral valve, ×2; *c–d,* internal mold and latex impression of ventral valve; *e–f,* internal mold and latex impression of dorsal valve, ×1.5 (Harper, 1973).

Pleiopleurina SCHMIDT, 1964, p. 506 [**Atrypa pleiopleura* CONRAD, 1841, p. 55; OD]. Very large with subcircular outline and dorsibiconvex profile; lateral margins not steep; ventral valve shallow. Beak small, incurved. Dorsal fold and ventral sulcus prominent anteriorly, arising at about midlength; anterior commissure uniplicate; tongue rounded to acuminate, dentate. Costae strong, angular, simple, straight, arising at beaks. Dental plates obscured by callus; ventral muscle field deeply impressed, ovate, divided by low ridge. Cardinal process very large, high, bilobed, with each lobe excavated; dorsal median septum long, thick, low; hinge plates thick, sessile; crural bases stout; dorsal adductor field large, well impressed, flabellate. *Lower Devonian (upper Pragian):* USA, Canada.——FIG. 746,*2a–g.* **P. pleiopleura* (CONRAD); *a–e,* dorsal, ventral, anterior, posterior, and lateral views, Oriskanian, Gaspé Limestone, Cape Gaspé, Shiphead, Quebec, ×0.9 (new); *f,* ventral valve interior, Oriskanian, Glenerie Limestone, Glenerie, New York, ×1.5; *g,* dorsal valve interior, Oriskanian, Glenerie Limestone, Glenerie, New York, ×2 (new).

Sulcatina SCHMIDT, 1964, p. 506 [**Trigonirhynchia sulcata* COOPER, 1942, p. 234; OD]. Large with subtriangular outline and dorsibiconvex profile; lateral margins not steep; ventral valve shallow. Beak small, incurved. Dorsal fold and ventral sulcus low, wide, arising at about midlength; anterior commissure uniplicate, rounded. Costae strong, simple, straight, arising at beaks. Dental plates obscured by callus; ventral muscle field deeply impressed, bilobed. Cardinal process very large, high, bilobed, ventrally and anteriorly excavated, extending anteriorly to merge with hinge plate and crural bases. *middle Silurian (Wenlock):* North America.——FIG. 745,*3a–n.* **S. sulcata* (COOPER), upper Wenlock, Waldron Shale, Waldron, Indiana, USA; *a–c,* holotype, dorsal, ventral, and lateral views, ×1 (Cooper, 1944); *d–n,* serial sections 26.2, 26.1, 26.0, 25.7, 25.2, 24.8, 24.6, 23.6, 23.2, 22.9, 22.8 mm from posterior, ×1.7 (Schmidt, 1965a).

Family HEBETOECHIIDAE Havlíček, 1960

[Hebetoechiidae HAVLÍČEK, 1960, p. 243]

Uncinuloidea that are strongly biconvex to globular with fold and sulcus weak; lateral and anterior margins vertical in mature specimens; tongue high; costae numerous, flattened and grooved on *paries geniculatus;* marginal spines developed; small foramen with disjunct to conjunct deltidial plates usually present; squamae and glottae frequently developed. Dental plates vertical to ventrally convergent. Dorsal median septum distinct; septalium deep, without cover plate, often infilled with callus; cardinal process usually absent or incipient in early genera, larger and commonly multilobed or longitudinally striated in later genera. *middle Silurian (Wenlock)–Middle Devonian (Givetian).*

Subfamily HEBETOECHIINAE Havlíček, 1960

[*nom. transl.* SCHMIDT, 1965b, p. 566, *ex* Hebetoechiidae HAVLÍČEK, 1960, p. 243]

Hebetoechiidae with few, relatively coarse costae; umbones smooth; marginal spines short. Dental plates short; dorsal median septum distinct. Septalium present; low, calluslike cardinal process usually developed. *upper Silurian (Přídolí)–Lower Devonian (Emsian).*

Hebetoechia HAVLÍČEK, 1959, p. 79 [**Terebratula hebe* BARRANDE, 1847, p. 86; OD]. Subcircular to subpentagonal outline; dorsibiconvex to subglobular. Beak erect to incurved; squamae and glottae absent; foramen small, deltidial plates conjunct. Fold and sulcus low, from umbones; high rectangular tongue, dentate. Costae arising on umbones, rounded, simple, flattened and grooved on *paries geniculatus;* marginal spines short. Dental plates converging slightly ventrally. Dorsal median septum short, low; calluslike cardinal process sometimes present in posterior part of septalium, may be bilobed anteriorly, but cardinal process absent in some species; crural bases subhorizontal. *upper*

Silurian (Přídolí)–Lower Devonian (Lochkovian): Europe, northern Africa, Asia, North America, Australia.——FIG. 747,*1a–m*. **H. hebe* (BARRANDE), upper Silurian, Přídolí Limestone, Dlouha Hora, Bohemia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×2.7 (new); *f–i,* hypotype, serial sections 9.9, 9.7, 9.5, 9.4 mm from anterior, ×3 (Havlíček, 1961); *j–m,* serial sections 10.35, 10.1, 9.95, 9.5 mm from anterior of different hypotype (Havlíček, 1983).

Gerrhynx BARANOV, 1991, p. 40 [**G. vescus;* OD]. Small to medium size; subpentagonal outline; strongly biconvex. Fold and sulcus low, from umbones; tongue distinct, subrectangular. Costae medium to coarse, rounded, arising at midlength, leaving umbones smooth, bifurcating on fold to form 2 clusters; costae at anterior margin flat and grooved. Dental plates thin, ventrally convergent. Dorsal septum long; septalium short, filled with bilobed to quadrilobed cardinal process; hinge plates united anterior of septalium. *Lower Devonian (Pragian):* eastern Siberia.——FIG. 748,*3a–m*. **G. vescus,* Pragian, Khobochalinskaya Formation, Tas-Khayakhtakh Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–m,* topotype, serial sections 0.3, 0.5, 0.7, 0.9, 1.2, 1.3, 1.4, 1.5, 1.6 mm from posterior, ×7 (Baranov, 1991).

Lanceomyonia HAVLÍČEK, 1960, p. 243 [**Terebratula tarda* BARRANDE, 1847, p. 85; OD] [=*Cratorhynchonella* TONG, 1982, p. 333 (type, *C. biconvexa,* OD)]. Medium to large size; subcircular to subpentagonal outline. Beak incurved; foramen absent. Fold and sulcus developed anteriorly; umbones smooth; tongue strong, rectangular. Costae broad, low, longitudinally grooved at *paries geniculatus;* marginal spines present. Dental plates short, ventrally convergent; ventral muscle field well impressed. Dorsal median septum high, long; septalium open. *upper Silurian (Přídolí)–Lower Devonian (Lochkovian):* Europe, northern Africa, Asia, North America, Australia.——FIG. 748,*1a–g*. **L. tarda* (BARRANDE), Přídolí, Přídolí Limestone, Dvorce, Bohemia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–g,* hypotype, serial sections 20.7, 20.0, 19.8 mm from anterior, ×3 (Havlíček, 1961).

Lapradella BARANOV, 1989, p. 49 [**L. definita;* OD]. Trigonal to subpentagonal outline; dorsibiconvex profile. Beak suberect to erect; foramen permesothyrid, deltidial plates conjunct. Fold and sulcus developed anteriorly; tongue high, rectangular; umbones smooth. Costae coarse, rounded, simple, flattened and grooved on *paries geniculatus;* short marginal spines present. Dental plates short, close to shell walls; ventral muscle field well impressed. Dorsal median septum thick, short; hinge plates united; septalium wide; cardinal process small; crural bases horizontal; crura closely set. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 748,*2a–o*. **L. definita,* upper Lochkovian, base of Sagyrshaya Formation, Selennyakhskiy Kryazh, Serp Creek on right bank Sakyndzha River, eastern Siberia; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e–o,* serial sections of shell posterior and crura 0.5, 1.4, 1.8, 2.1, 2.3, 2.6, 2.8, 3.2, 3.3, 3.6, 5.2 mm from posterior, ×4 (Baranov, 1989).

Mongolorhynx ERLANGER, 1992, p. 54 [**M. drosdovae;* OD]. Small to medium size; subpentagonal outline; strongly biconvex. Fold and sulcus low, developed anteriorly; tongue distinct, subrectangular to trapezoid. Costae medium, rounded, arising at midlength leaving umbones smooth; costae at anterior margin grooved. Dental plates thin, ventrally convergent; dorsal septum low, short; septalium short, filled with multilobed cardinal process; hinge plates united anterior of septalium. *Lower Devonian (Emsian):* western Mongolia.——FIG. 747,*2a–h*. **M. drosdovae,* upper Emsian, Tsagankhalginsk layer, northern shore of Lake Khara-Us-Nur; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×2; *f–h,* paratypes, serial sections, ×15 (Erlanger, 1994).

Voskopitoechia HAVLÍČEK, 1992, p. 105 [**V. orbona;* OD]. Small size; subpentagonal outline; biconvex. Fold and sulcus short, arising at midlength; tongue high; umbones smooth. Costae restricted to margins, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short; ventral muscle field well impressed. Dorsal median septum thin; septalium short, wide, filled with large, calluslike, bilobed cardinal process; hinge plates undivided, horizontal; crural bases vertical, becoming horizontal anteriorly. *Lower Devonian (Pragian–Emsian):* Bohemia.——FIG. 747,*3a–f*. **V. orbona,* Pragian, Koneprusy Limestone, Na Voskope Hill; *a–b,* holotype, ventral, and anterior views, ×5; *c–f,* serial sections 5.7, 5.55, 5.4, 5.25 mm from anterior, ×9.5 (Havlíček, 1992).

Subfamily SPHAERIRHYNCHIINAE Savage, 1996

[Sphaerirhynchiinae SAVAGE, 1996, p. 253]

Globular Hebetoechiidae with weak fold, high tongue, and fine, distally grooved costae. Dental plates convergent ventrally. Dorsal median septum well developed; cardinal process absent or calluslike. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian).*

Sphaerirhynchia COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Wilsonella* NIKIFOROVA, 1937a, p. 35, *non* CARTER, 1885 [**Terebratula wilsoni* SOWERBY, 1816 in 1815–1818, p. 38; OD]. Medium to large size; globular. Beak suberect to incurved; foramen in younger specimens mesothyrid, circular, deltidial plates incipient; in older specimens foramen obscured by curvature of beak; squamae and glottae absent. Fold and sulcus very weak; tongue high, rectangular. Costae arising at beaks, fine, rarely splitting, grooved distally; marginal

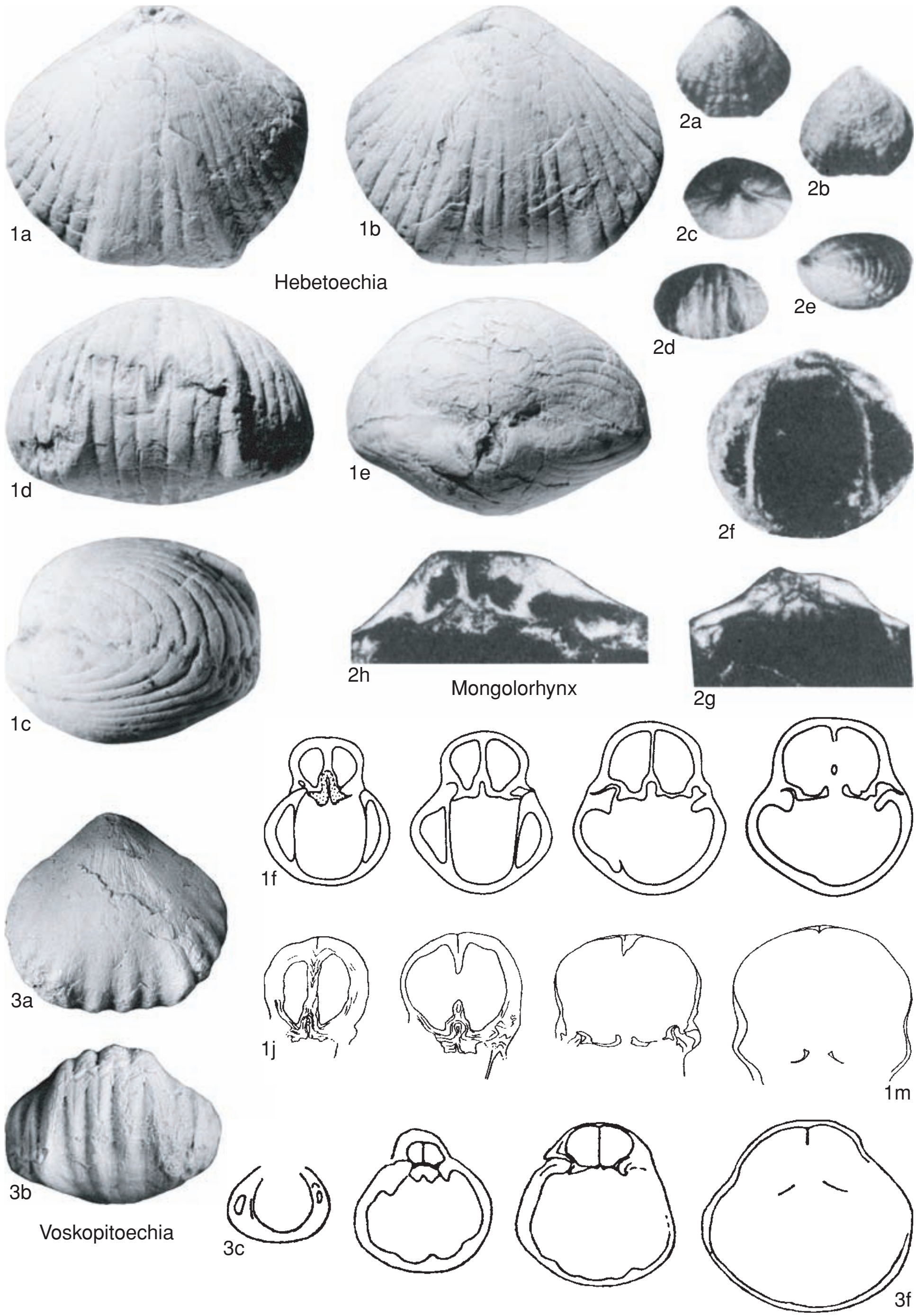

FIG. 747. Hebetoechiidae (p. 1104–1106).

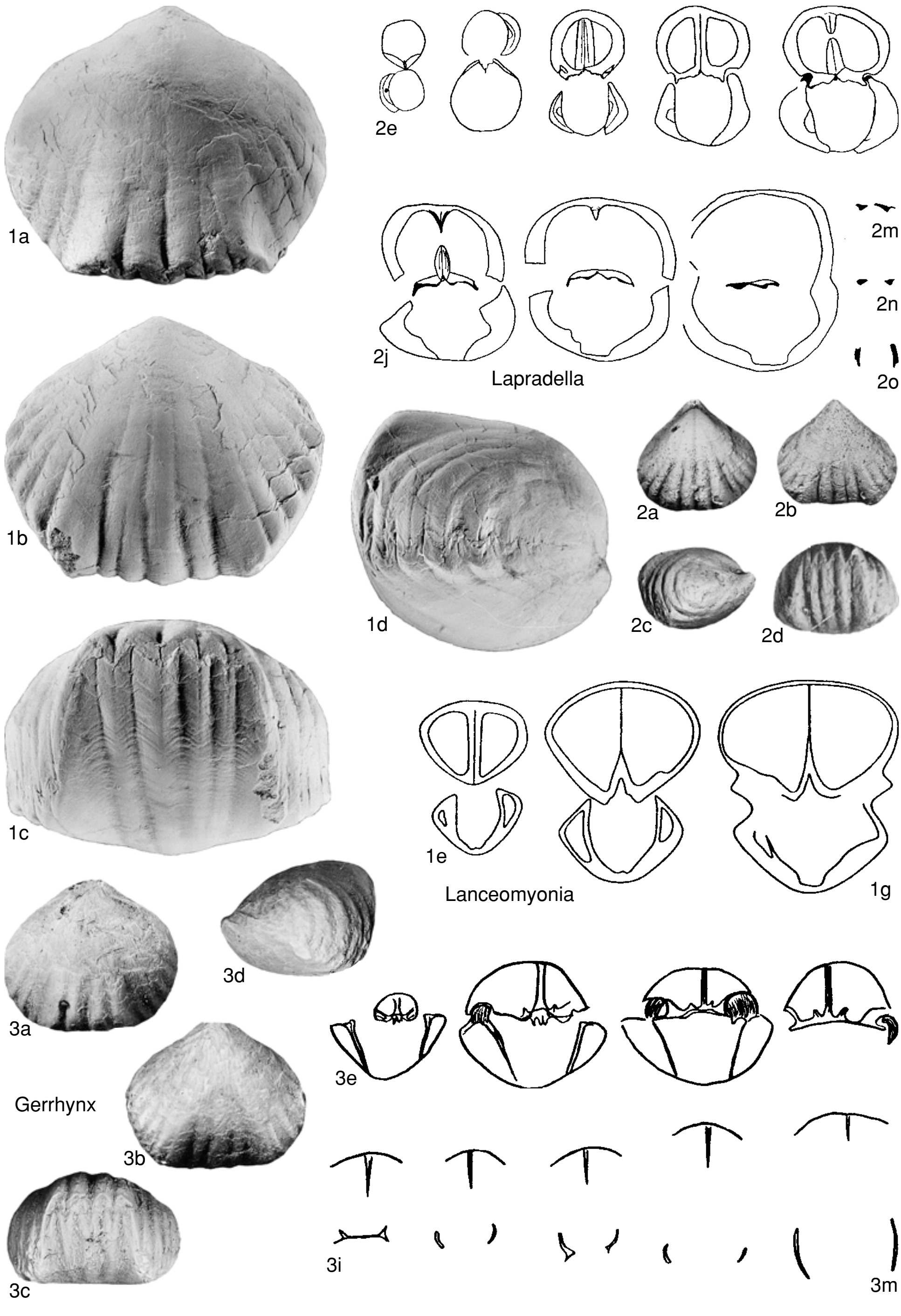

FIG. 748. Hebetoechiidae (p. 1105).

spines present. Dental plates short, convergent ventrally; ventral muscle field deeply impressed. Dorsal median septum long; septalium short, lacking cover; cardinal process absent; crura long, thin. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian):* Europe, Urals, Salair, Altai, China, Australia, North America.——FIG. 749,*1a–n.* **S. wilsoni* (SOWERBY), Wenlock Series, Shropshire, England; *a–c,* dorsal, lateral, anterior views, ×1 (Davidson, 1869); *d–m,* serial sections 1.2, 1.4, 1.6, 1.8, 2.0, 2.4, 2.6, 2.8, 3.0, 3.9 mm from posterior, ×2.2 (new); *n,* sketch of part of the *paries geniculatus* and marginal spines, based on serial sections, approximately ×2.5 (Westbroek, 1968).

Estonirhynchia SCHMIDT, 1954, p. 236 [**Sphaerirhynchia (E.) estonica;* OD]. Globular; beak erect to incurved; foramen not observed. Fold and sulcus very weak; tongue high, rectangular. Umbones smooth; costae simple, lacking anterior grooves or spines; anterior commissure zigzag. Dental plates short, convergent ventrally; ventral muscle field weakly impressed. Dorsal median septum thick, long; septalium short, without cover plate; cardinal process absent; crura unknown. *middle Silurian (Wenlock)–upper Silurian (Ludlow):* Baltic.——FIG. 749,*2a–f.* **E. estonica* (SCHMIDT), upper Wenlock, Oesel Group, Oesel, Estonia; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×3; *e–f,* sections of posterior of different specimens, ×4 (Schmidt, 1954).

Notoconchidium GILL, 1951, p. 187 [**N. thomasi* GILL, 1951, p. 188; OD; *N. thomasi* GILL, 1950, p. 243, *nom. nud.,* no description or illustration given] [=*Notoconchidium* GILL, 1950, p. 242, *nom. nud.,* no type species given]. Large size; elongate subtrigonal outline; strongly inflated to globular. Fold and sulcus weak; tongue high, rectangular to trapezoid. Costae simple or with rare bifurcation, rounded, flattened and grooved on *paries geniculatus;* umbones smooth. Dental plates long, ventrally and anteriorly convergent; ventral muscle field long, narrow, deeply impressed. Dorsal median septum long; septalium distinct; cardinal process absent or poorly developed. *upper Silurian (Přídolí):* Australia, New Zealand.——FIG. 750*a–e.* **N. thomasi,* Mount Ida Formation, Victoria, Heathcote, Australia; *a,* holotype, ventral view of ventral valve internal mold, ×2 (Wright & Garratt, 1991); *b–c,* plaster replica and rubber impression of dorsal internal mold, ×1.5; *d–e,* plaster replica and rubber impression of ventral internal mold, ×1.5 (Boucot, Johnson, & Staton, 1964).——FIG. 750*f–h.* *N. tasmaniensis* (ETHERIDGE), Florence Sandstone, Silver Bell, near Zeehan, Tasmania; lateral, anterior, and posterior views of internal mold of conjoined shell, ×1.5 (Wright & Garratt, 1991).

Tadschikia NIKIFOROVA, 1937a, p. 35 [**Wilsonella (T.) wilsoniaformis;* OD]. Medium to large size; subcircular outline; globular profile. Beak suberect to erect; foramen small, circular. Fold and sulcus weak; tongue high. Costae medium, simple, flattened and grooved on *paries geniculatus.* Dental plates long, convergent ventrally. Dorsal median septum long; septalium with low, calluslike cardinal process posteriorly and with cover plate anteriorly. *middle Silurian (Wenlock):* Turkestan, China.——FIG. 749,*3a–g.* **T. wilsoniaformis* (NIKIFOROVA), Turkestan; *a–d,* dorsal, ventral, lateral, and anterior views, ×1; *e,* serial section at articulation area, ×2 (Nikiforova, 1937a); *f–g,* sections through septalium, ×2 (Havlíček, 1961).

Subfamily AMSDENELLINAE new subfamily

[Amsdenellinae SAVAGE, herein]

Hebetoechiidae with rounded lateral margins; numerous fine costae arising at beaks; marginal spines short. Dental plates lacking; ventral muscle field deeply impressed. Hinge plates sessile; cardinal process large, bilobed. *Lower Devonian (Lochkovian).*

Amsdenella TILLMAN, 1967, p. 1251 [**Rhynchonella abrupta* HALL, 1857a, p. 68; OD]. Medium to large with subcircular to subpentagonal outline and dorsibiconvex profile with rounded lateral margins. Beak erect to incurved; foramen mesothyrid. Fold and sulcus prominent but with gentle margins; tongue high, often rounded. Costae numerous, simple, rounded, arising at beaks; costae flattened and grooved on *paries geniculatus* of mature specimens, and taper uniformly into points. Dental plates lacking; ventral muscle field ovate, deeply impressed, with large, flabellate diductor field enclosing small adductor field; adductor field divided by low median septum and partly covered by a thin ridge posteriorly. Cardinal process large, high, bilobed, with each lobe excavated; dorsal median septum long, low; hinge plates sessile; crural bases stout, rounded, arising from beneath cardinal process; dorsal muscle scars weakly defined. *Lower Devonian (Lochkovian):* eastern USA.——FIG. 751*a–g.* **A. abrupta* (HALL), Helderbergian, New Scotland Formation, West Virginia; *a–c,* hypotype, dorsal, lateral, and anterior views, near Franklin, ×2; *d,* ventral view of ventral valve, near Mustoe; *e,* lateral view of dorsal valve, near Mustoe, ×1.8; *f,* ventral valve interior, near Mustoe, ×2; *g,* dorsal view of cardinal process, Bullpasture Mountain, ×4 (Tillman, 1967).

Subfamily GLOSSINULININAE Savage, 1996

[Glossinulininae SAVAGE, 1996, p. 253]

Transversely subpentagonal Hebetoechiidae with sharply delineated fold and sulcus, rectangular tongue, fine costae that are flattened and grooved on *paries geniculatus,* and well-developed marginal spines. Dental

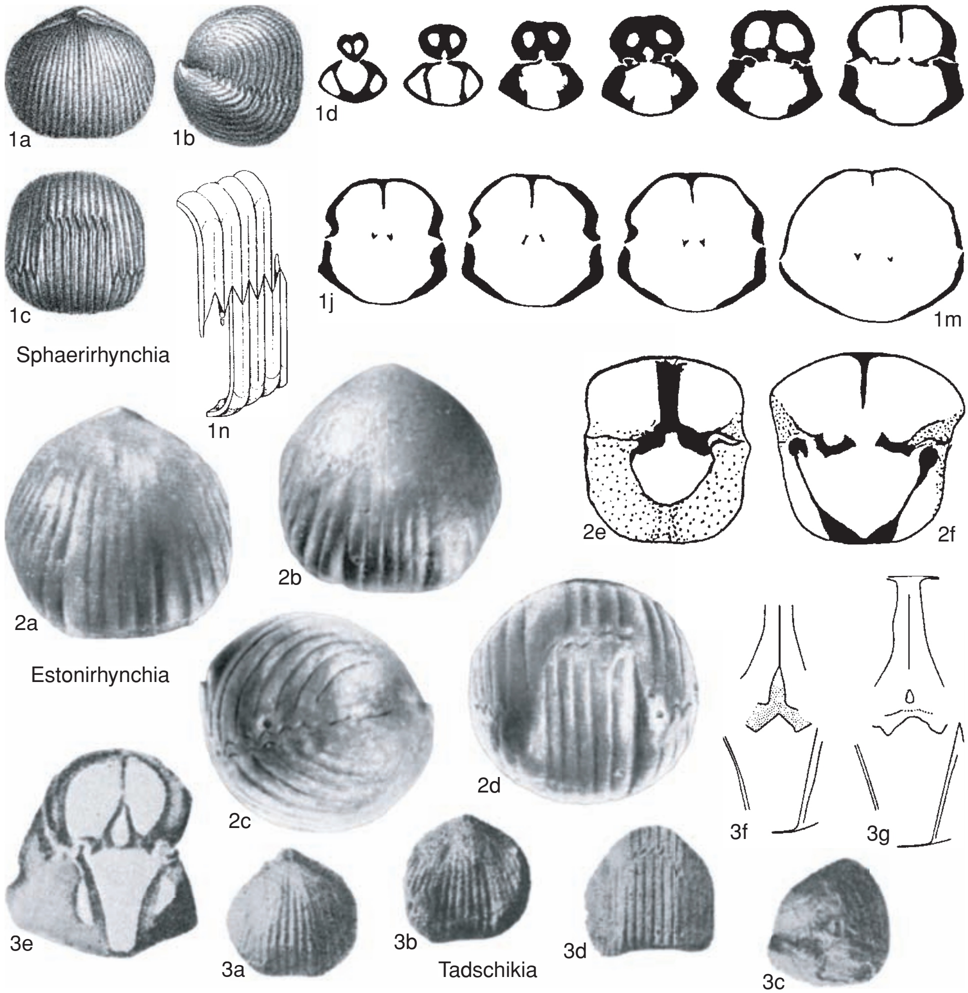

FIG. 749. Hebetoechiidae (p. 1105–1108).

plates short or obscured by callus. Septalium reduced; cardinal process small to absent. *Lower Devonian (Pragian–Emsian).*

Glossinulina JOHNSON, 1975, p. 958 [**G. khodalevichi;* OD]. Transversely subpentagonal outline; dorsal valve strongly convex, ventral weakly convex. Beak erect to incurved; foramen unknown. Fold and sulcus wide, strong, well delineated; median groove on fold, median ridge in sulcus; tongue high, rectangular. Umbones smooth; costae medium, simple, flattened and grooved on *paries geniculatus;* commissure with spines. Dental plates short, ventrally convergent. Dorsal median septum high, thin, long; septalium short, shallow; cardinal process small, with ridges. *Lower Devonian (Emsian):* Arctic Canada.——FIG. 752,*1a–n.* **G. khodalevichi,* Disappointment Bay Formation, Lowther Island; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×2; *f–n,* serial sections 8.0, 7.8, 7.7, 7.6, 7.5, 7.4, 7.3, 7.2, 7.1 mm from anterior, ×4 (Johnson, 1975).

Glossinulinirhynchia BARANOV, 1991, p. 41 [**G. venusta;* OD]. Small to medium size; thick shell; subpentagonal outline; strongly biconvex; beak suberect. Fold and sulcus wide, strong; tongue high, rectangular. Costae rounded in section but on *paries geniculatus* flattened and grooved; umbones smooth; costae on fold gathered into 2 clusters with gentle sinus between, those in sulcus raised along medial part. Dental plates absent or umbonal cavities infilled; ventral muscle field deeply impressed. Dorsal median septum short, low; septalium

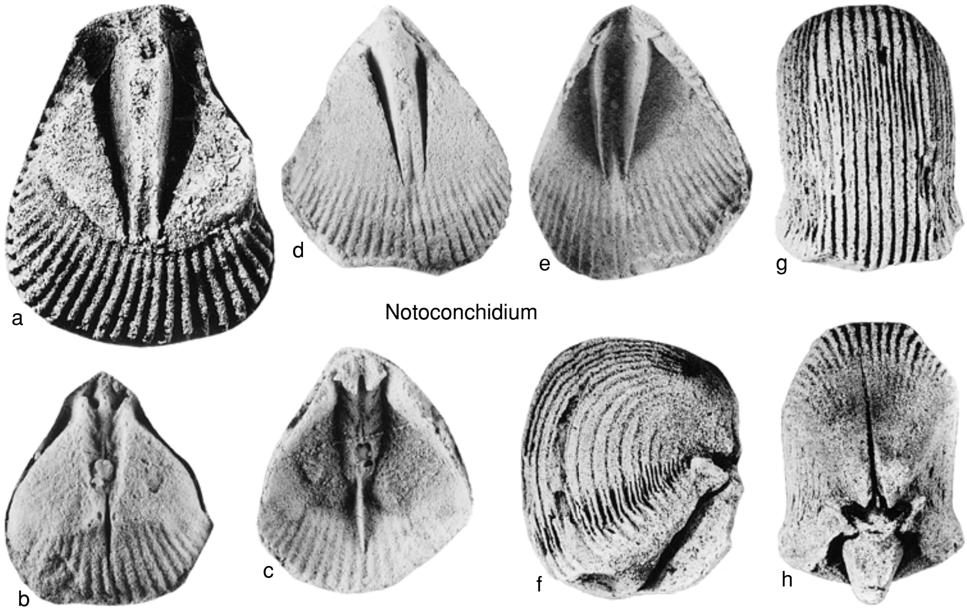

FIG. 750. Hebetoechiidae (p. 1108).

reduced; hinge plates anterior of septalium divided, horizontal; cardinal process short, with ridges; crura long, closely set. *Lower Devonian (Pragian):* eastern Siberia.——FIG. 752,*2a–l.* **G. venusta,* Nelichenskaya Formation, Selennyakhskiy Kryazh; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e–l,* successive serial sections through posterior, intervals not given, ×3 (Baranov, 1991).

Nordotoechia TCHERKESOVA, 1965, p. 80 [**N. tumida;* OD]. Large with transversely oval outline; biconvex profile, dorsal valve inflated; lateral and anterior margins vertical; beak incurved. Fold and sulcus distinct; tongue high, rectangular. Costae dichotomizing, flattened and grooved on *paries geniculatus;* arising at beaks; marginal spines present. Dental plates thin, short; ventral muscle area deeply impressed. Septalium and dorsal median septum very short; cardinal process absent; crura arising from edges of septalium, long, closely set. *Lower Devonian (Emsian):* Novaya Zemlya.——FIG. 753,*2a–q.* **N. tumida,* Val'nevsk layer, mouth of Sakhanin River; *a–d,* holotype, ventral, lateral, anterior, and posterior, ×1; *e,* enlargement of left anterior margin, ×5; *f–k,* serial sections 1.1, 1.55, 1.85, 2.1, 2.15, 2.35 mm from posterior, ×1.4; *l–q,* serial sections 2.6, 2.8, 2.96, 3.05, 3.2, 3.35 mm from posterior of different specimen, ×1.4 (Tcherkesova, 1965).

Pseudoglossinotoechia TCHERKESOVA, 1967, p. 9 [**P. atalanta;* OD] [=*Tainotoechia* TCHERKESOVA, 1967, p. 5 (type, *Sphaerirhynchia (?) subarmoricana* NIKIFOROVA, 1960a, p. 347, OD)]. Medium to large size; subpentagonal outline; strongly inflated, almost cuboidal. Beak incurved; delthyrium with small slitlike foramen almost closed by deltidial plates. Fold and sulcus low but distinct, with median groove on fold; tongue prominent, rectangular. Costae fine, bifurcating, arising at beaks, flattened and grooved anteriorly where internal marginal spines developed. Dental plates close to shell walls; ventral muscle field deeply impressed and divided anteriorly by low median ridge. Dorsal median septum long, low; septalium short, open or filled by cardinal-process-like callus in gerontic specimens; crura closely set. *Lower Devonian (Emsian):* Novaya Zemlya, Urals.——FIG. 753,*1a–q.* **P. atalanta,* Val'nevsk horizon, South Island, Novaya Zemlya; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f,* hypotype, enlargement of commissure and spine traces, ×2; *g–q,* serial sections 1.45, 2.65, 2.8, 2.9, 3.0, 3.2, 3.5, 3.95, 4.05, 4.3, 5.75 mm from posterior, approximately ×1.5 (Tcherkesova, 1967).

Subfamily BETTERBERGIINAE Savage, 1996

[Betterbergiinae SAVAGE, 1996, p. 253]

Thick-shelled, rounded Hebetoechiidae with low fold, fine costae that are flattened and grooved anteriorly, and long marginal spines. Dental plates short or obscured by

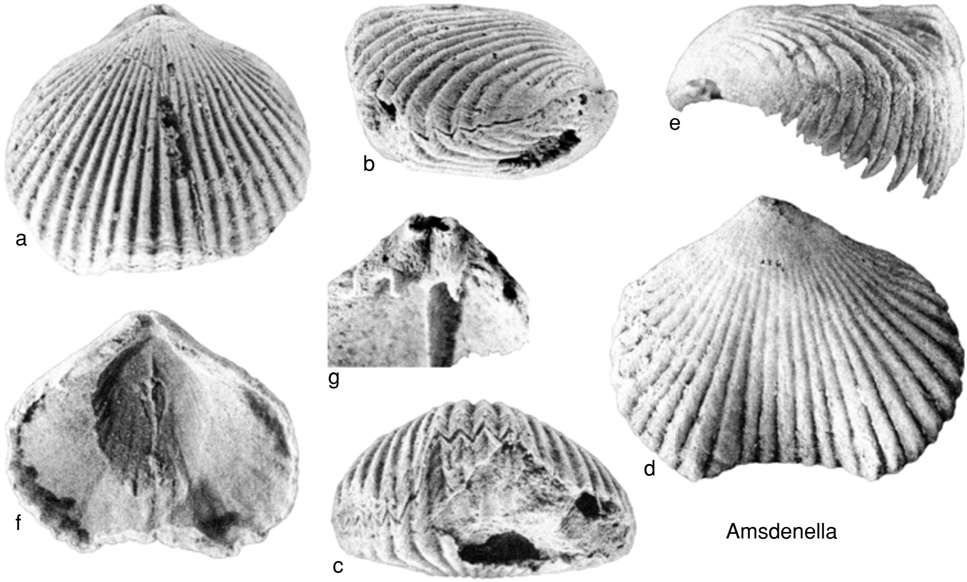

FIG. 751. Hebetoechiidae (p. 1108).

callus. Dorsal median septum and septalium short; cardinal process commonly present. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Betterbergia SCHMIDT, 1981, p. 218 [**Camarotoechia betterbergiana* SCHMIDT, 1950, p. 79; OD]. Medium to large size with subtriangular outline and biconvex profile; lateral and anterior margins steep. Beak incurved; foramen small. Fold and sulcus moderate, extending from midlength; anterior commissure uniplicate; tongue broad, low. Costae fine, simple, numerous, from umbones, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short, subvertical, commonly buried in callus; ventral muscle field well impressed. Dorsal median septum and septalium short; hinge plates divided anteriorly; cardinal process absent; crura with V-shaped cross section, open dorsomedially. *Middle Devonian (Eifelian):* Germany.——FIG. 754,*1a–k*. **B. betterbergiana* (SCHMIDT), middle Eifelian, Ahrdorf Formation, Flesten Member, Hillesheimer Mulde, Dollendorf, Eifel; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–k,* serial sections, ×3 (Schmidt, 1981).

Kransia WESTBROEK, 1968, p. 81 [**Terebratula parallelepipeda* BRONN, 1837, p. 71; OD]. Subpentagonal outline; strongly biconvex profile. Beak erect; well-developed mesothyrid foramen with small, conjunct deltidial plates; squamae and glottae present. Fold and sulcus weak; high, rounded tongue. Costae simple, arising on umbones, flattened anteriorly and grooved to accommodate long marginal spines. Dental plates short, subparallel, close to valve walls; ventral muscle scars deeply impressed in thick shell. Dorsal median septum low, long; septalium short; cardinal process bearing several longitudinal ridges; hinge plates united anterior of septalium. *Lower Devonian (Emsian)–Middle Devonian (Givetian):* Europe, northern Africa, Urals, Afghanistan, China.——FIG. 754,*2a–m*. **K. parallelepipeda* (BRONN), Givetian; *a,* hypotype, dorsal view, ×3; *b,* hypotype, anterior view; *c,* lateral view of another hypotype, ×3; *d–k,* hypotype, serial sections 0.4, 0.5, 0.6, 0.7, 0.9, 1.2, 1.4, 1.7 mm from posterior, upper Givetian, northwestern France, ×4 (Brice & Morzadec, 1983); *l,* reconstruction of apical interior, based on serial sections; *m,* reconstruction of marginal spines, based on serial sections (Westbroek, 1968).

Nalivkinaria RZHONSNITSKAIA, 1968c, p. 117 [**N. lacunata;* OD]. Subpentagonal outline; hinge line wide; profile strongly dorsibiconvex. Beak small, incurved; mesothyrid foramen, disjunct deltidial plates. Fold and sulcus strong, arising near umbones; tongue high, rectangular. Costae numerous, rounded, rarely dividing, arising at beak, flattened anteriorly and grooved. Dental plates very short, close to valve walls or obscured by callus, converging ventrally; teeth small; ventral muscle scars deeply impressed in thick shell. Dorsal median septum high, thick, long; septalium short; cardinal process massive, typically with 2, high lateral lobes; hinge plates divided. *Middle Devonian (Eifelian–Givetian):* Kuznets, Spain.——FIG. 755,*2a–j*. **N.*

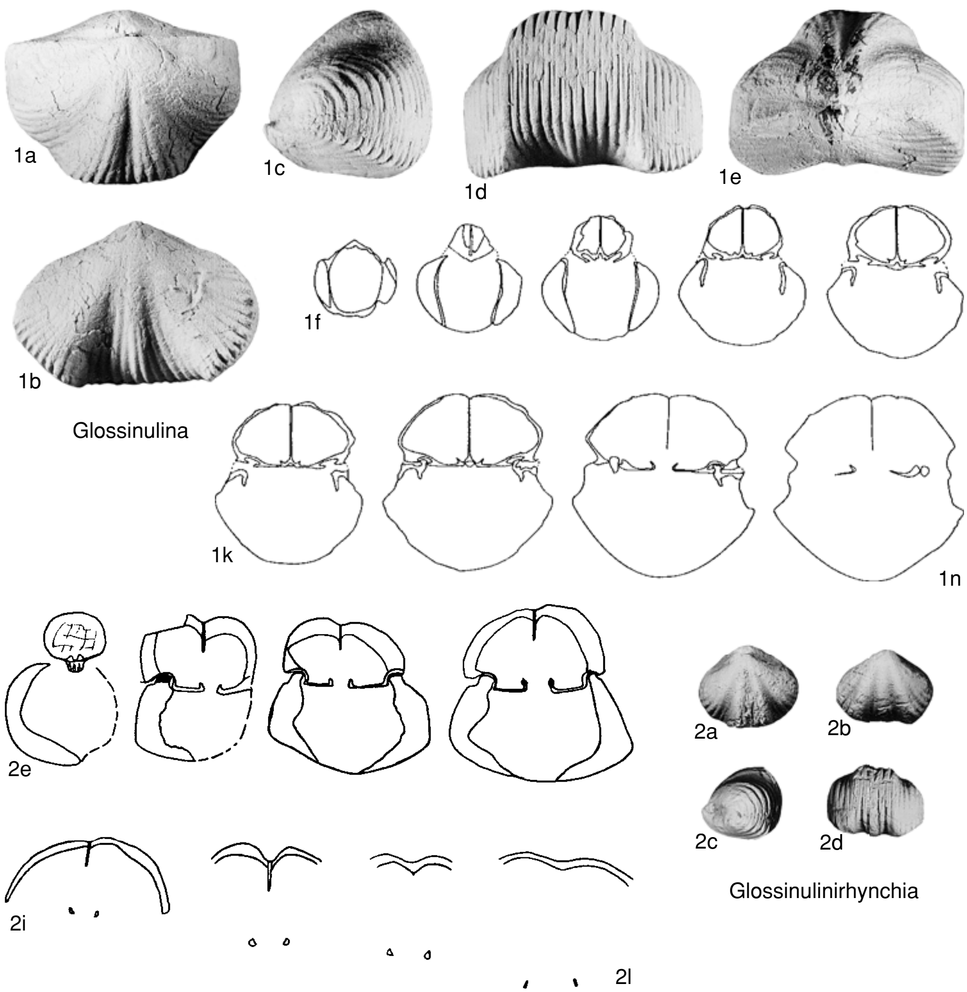

FIG. 752. Hebetoechiidae (p. 1109–1110).

lacunata, Eifelian, Kuznets basin; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–j,* transverse serial sections across shell posterior, approximately ×2.5 (Rzhonsnitskaia, 1968c).

Primipilaria STRUVE, 1992, p. 549 [**Terebratula primipilaris* VON BUCH, 1834, p. 88; OD]. Medium to large size; subcircular outline; biconvex profile, inflated anteriorly. Beak erect; mesothyrid foramen with conjunct deltidial plates. Fold and sulcus medium size; anterior commissure with high, rounded tongue; articulation with squamae and glottae well developed. Costae fine, arising at beaks, multiplying, flattened anteriorly and grooved; long marginal spines; commissure without zigzag deflections. Dental plates short, subparallel, close to valve walls; ventral muscle scars deeply impressed in thick shell, separated by median myophragm. Dorsal median septum thick, low, extending to valve midlength; septalium short, filled by cardinal process bearing longitudinal ridges; hinge plates united anterior of septalium. *Middle Devonian (Eifelian–Givetian):* Europe.——FIG. 755,*1a–g.* **P. primipilaris* (VON BUCH), Givetian, Skaly Beds, Holy Cross Mountains, Poland; *a,* hypotype, dorsal view, ×2.7; b, hypotype, lateral view, ×2.1; *c,* anterior view of another hypotype; *d,* ventral view of another hypotype; *e,* dorsal interior; *f,* ventral interior, ×2.5 (Biernat, 1966); *g,* reconstruction of *paries geniculatus* and marginal spines, based on serial sections, approximately ×2.5 (Westbroek, 1968).

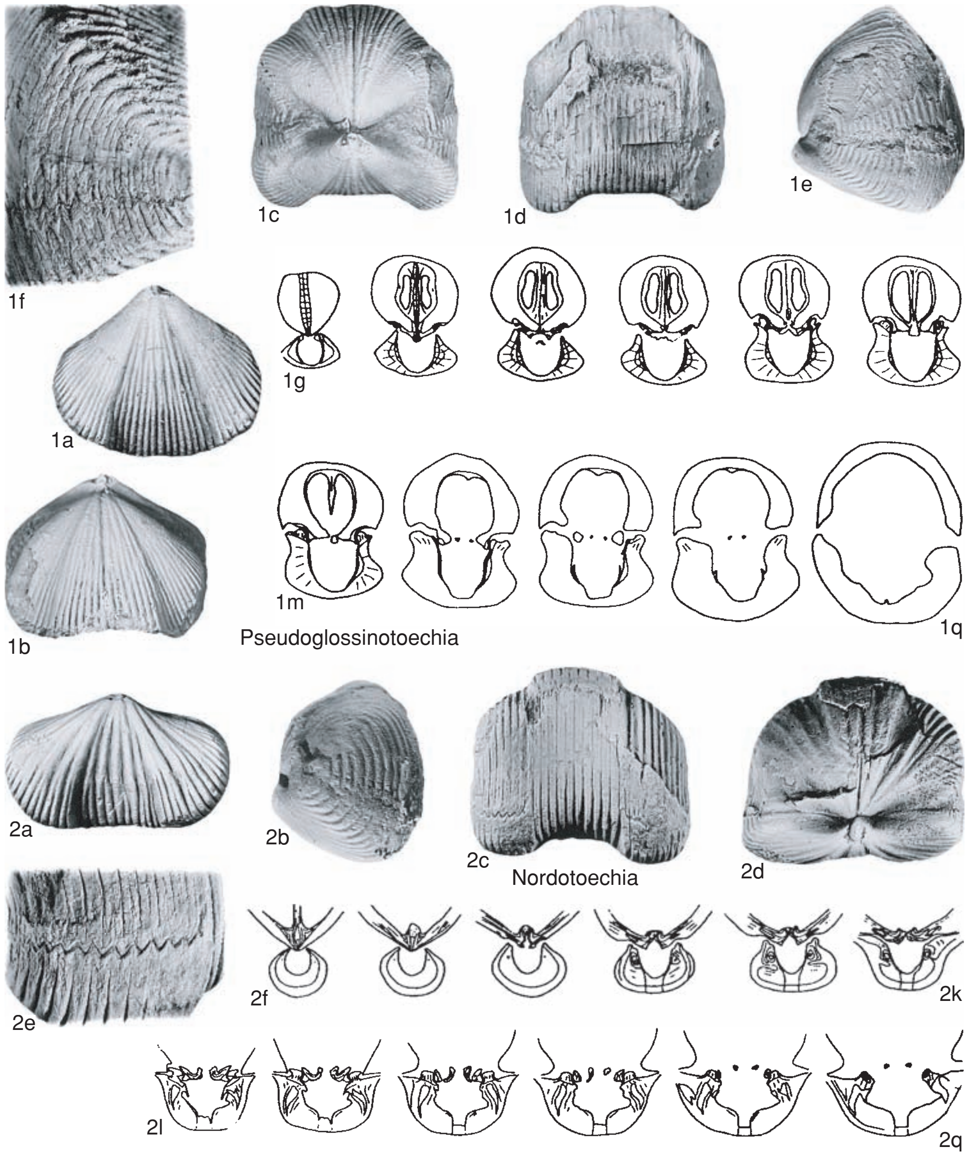

FIG. 753. Hebetoechiidae (p. 1110).

Subfamily BECKMANNIINAE Savage, 1996

[Beckmanniinae SAVAGE, 1996, p. 253]

Subcircular Hebetoechiidae with broad fold, smooth umbones, rounded exterior features; marginal spines weakly developed. Dental plates short. Dorsal median septum may be prominent; calluslike cardinal process generally present. *Middle Devonian (Givetian).*

Beckmannia MOHANTI, 1972, p. 166 [**Uncinulus minor beckmanni* SCHMIDT, 1951, p. 89; OD]. Shell small; subcircular to subpentagonal outline; lenticular biconvex profile; flanks generally rounded, not truncated. Beak erect to incurved; foramen

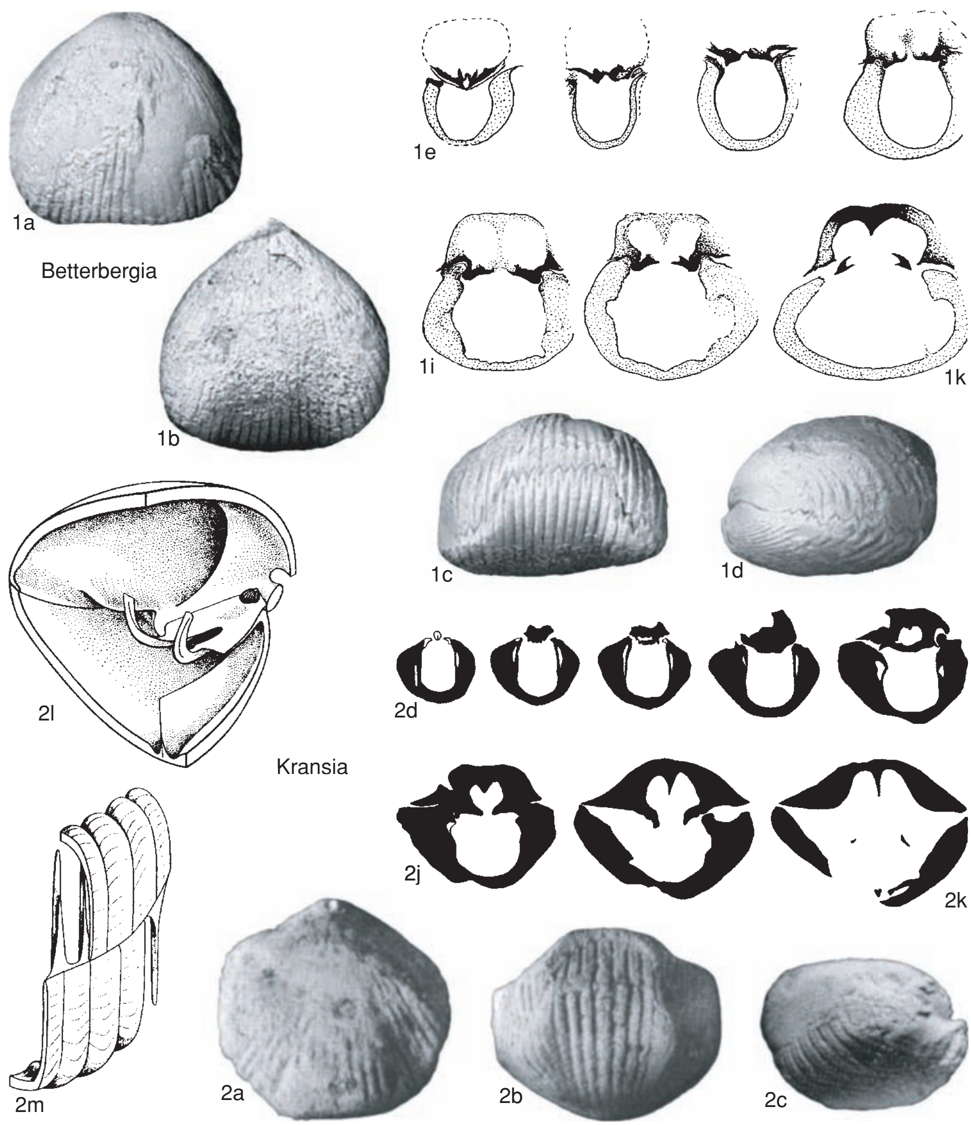

FIG. 754. Hebetoechiidae (p. 1111).

mesothyrid, deltidial plates conjunct. Fold and sulcus weak; anterior commissure weakly uniplicate. Costae coarse, rounded in section; marginal spines short. Dental plates short, ventrally divergent; ventral muscle field well impressed. Dorsal median septum short, thin; septalium absent; calluslike cardinal process may join hinge plates posteriorly; hinge plates divided anteriorly. *Middle Devonian (Givetian):* Europe, Urals, Tadzhikistan.——FIG. 756,*1a–l*. **B. minor beckmanni* (SCHMIDT), lowest Givetian; *a–b,* holotype, dorsal, anterior views, Letmathe, near Dortmund, Germany, ×3.3; *c–d,* holotype, ventral and lateral views, Letmathe, near Dortmund, Germany, ×3 (Schmidt, 1951); *e–h,* topotype, serial sections, intervals not given, Letmathe, near Dortmund, Germany, ×7.2 (Mohanti, 1972); *i–l,* dorsal, ventral, lateral, and anterior views, basal Member B, Portillo Formation, Los Barrios de Luna near Leon, northwestern Spain, ×4.3 (Mohanti, 1972).

Cassidirostrum MCLAREN, 1961, p. 2 [**C. pedderi;* OD]. Subcircular to subpentagonal in outline, and profile dorsibiconvex. Beak erect to incurved; small foramen at apex of delthyrium bounded by small

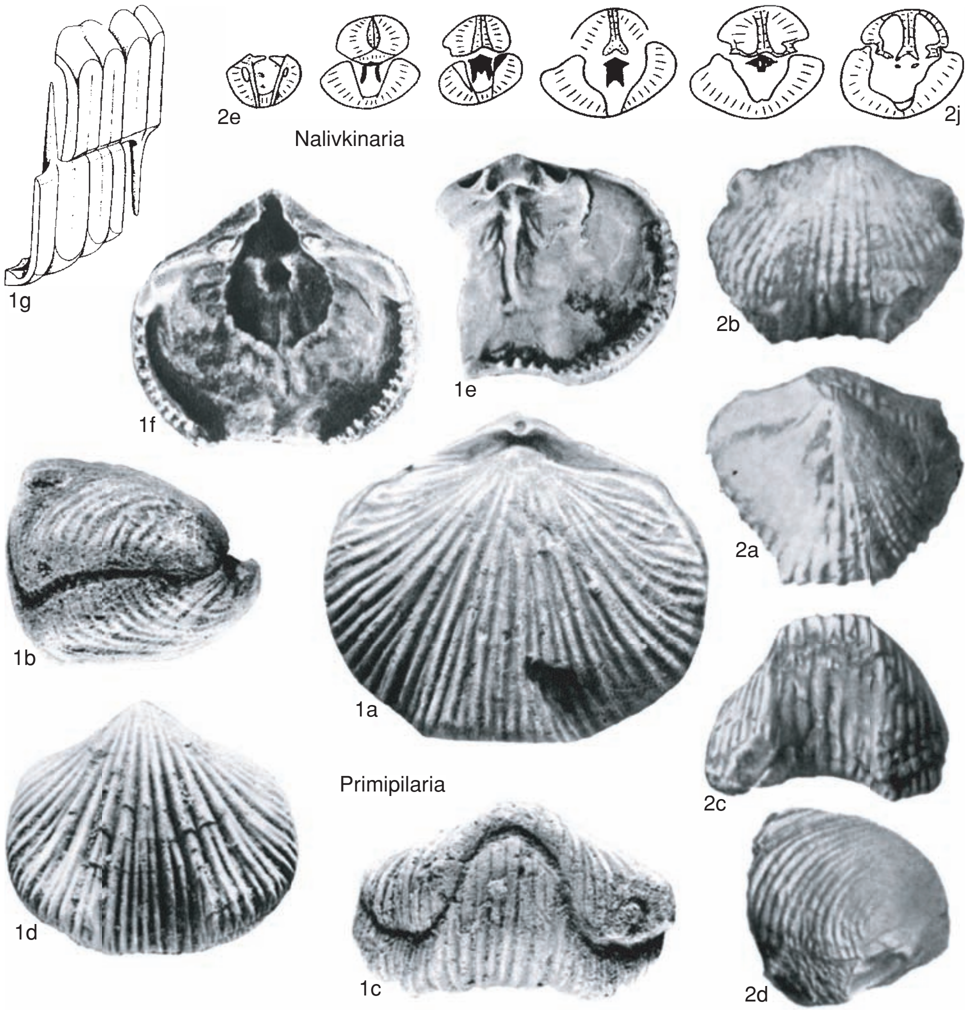

FIG. 755. Hebetoechiidae (p. 1111–1112).

triangular deltidial plates. Fold and sulcus distinct, from midlength; anterior commissure uniplicate; tongue, broad, rounded, dentate. Costae numerous, angular, simple, arising at umbones, covering all surface; some specimens have marginal spines. Dental plates converging ventrally; ventral muscle field well impressed. Dorsal median septum long, high; septalium short, commonly filled with callus, which may be developed into bilobed cardinal process; hinge plates divided anteriorly; dorsal muscle field long, narrow, well impressed; crura ventrally curved, gutterlike anteriorly with open side directed dorsally, tips laterally compressed. *Middle Devonian (lower Givetian):* western North America, Spain, Libya.——FIG. 756,*3a–m.* **C. pedderi,* Hare Indian Formation, Anderson River, Northwest Territories; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–m,* serial sections 2.2, 2.8, 3.0, 3.3, 3.6, 5.9, 6.3, 6.35 mm from posterior, ×1.5 (McLaren, 1962).

Homeocardiorhynchus SARTENAER, 1985b, p. 220 [**H. pityinus;* OD]. Transversely oval outline; moderately biconvex, with lateral and anterior margins not steep. Beak suberect to erect; foramen small, circular, mesothyrid, deltidial plates present. Fold and sulcus weak; tongue low. Umbones smooth; costae few, rounded, simple, flattened and grooved at anterior margin. Dental plates converging ventrally. Dorsal median septum thick, extending to one-third valve length; septalium wide, deep, open; small cardinal process present; crura arising from inner edges of septalium, closely set. *Middle*

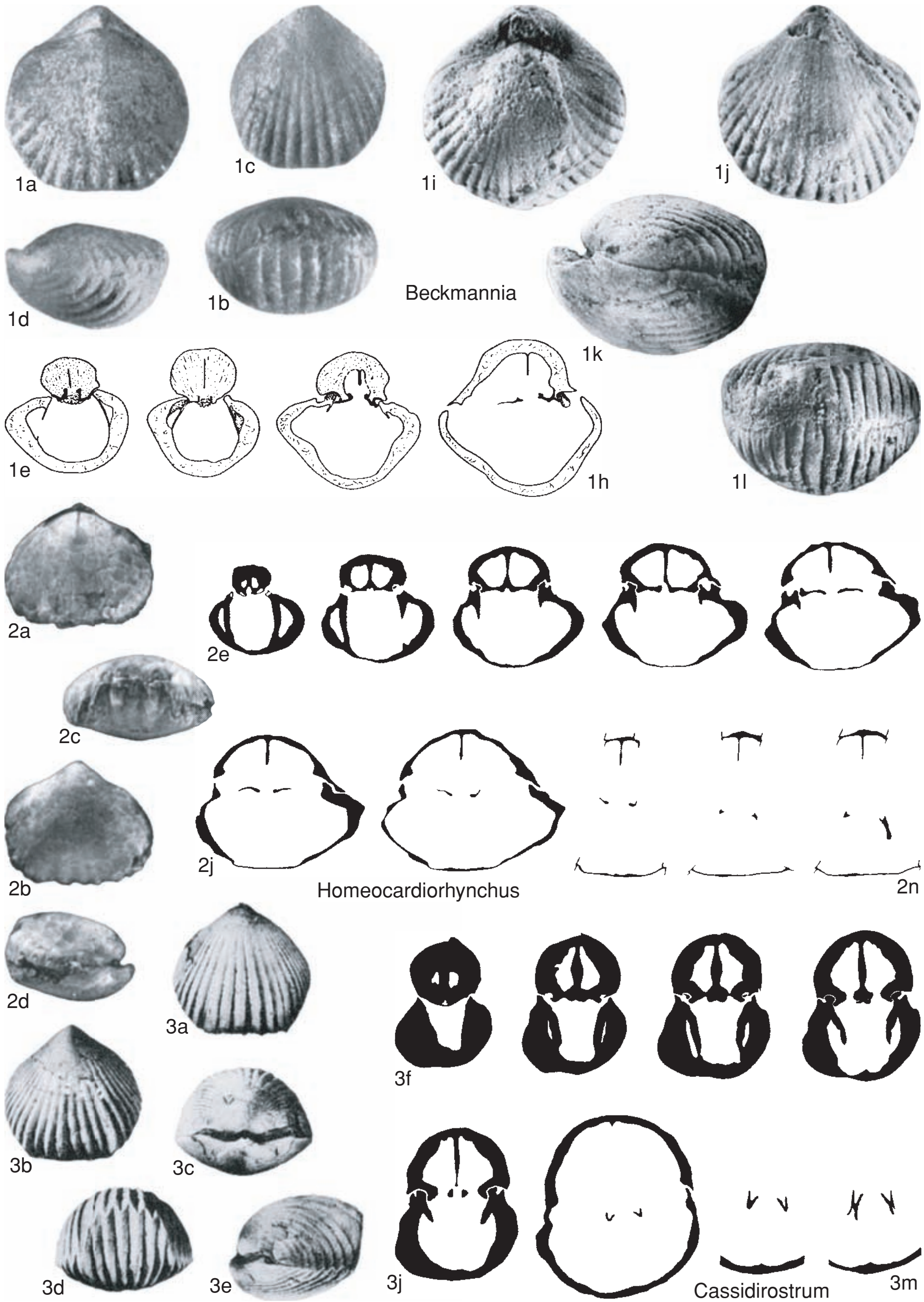

FIG. 756. Hebetoechiidae (p. 1113–1117).

Devonian (Givetian): western Canada.——FIG. 756,*2a–n.* **H. pityinus,* middle Givetian, Pine Point Formation, Great Slave Lake; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–n,* paratype, serial sections 2.2, 2.6, 3.0, 3.45, 3.8, 4.15, 4.4, 4.6, 5.25, 5.45 mm from posterior, ×2.8 (Sartenaer, 1985b).

Family OBTURAMENTELLIDAE Savage, 1996

[Obturamentellidae SAVAGE, 1996, p. 253]

Uncinuloidea with very thick shell; costae coarse; marginal spines short. Dental plates rudimentary, mostly infilled with callus. Teeth massive, longitudinally grooved, arising from shell walls; ventral muscle field deeply impressed. Dorsal median septum low, thick, long; septalium filled posteriorly with massive, linguiform, bilobed cardinal process. *upper Silurian (lower Ludlow)–Lower Devonian (Pragian).*

Obturamentella AMSDEN, 1958, p. 99 [**Wilsonia wadei* DUNBAR, 1919, p. 53; OD]. Small to medium; subcircular outline; biconvex profile. Beak suberect; delthyrium with well-developed foramen and deltidial plates. Fold and sulcus from about midlength; tongue high, narrow, rectangular. Costae coarse, rounded in section, arising at umbones; marginal spines short. Dental plates not distinguishable in thick shell material; teeth supported by shell wall; ventral muscle field deeply impressed and divided by long, low ventral median myophragm. Dorsal median septum low, short; septalium rudimentary, filled with callus that forms bilobed or variable cardinal process posteriorly. *Lower Devonian (Lochkovian–Pragian):* North America, Europe.——FIG. 757,*2a–j.* **O. wadei* (DUNBAR), Lochkovian, Oklahoma, Tennessee, USA; *a–c,* hypotype, dorsal, ventral, and lateral views, Oklahoma, ×2; *d–e,* lectotype, anterior and ventral views, Ross Limestone, Grandview, Tennessee, ×2; *f,* hypotype, ventral interior, ×3; *g–i,* serial sections at 0.5, 1.0, 1.3 mm from posterior, ×4; *j,* enlarged view of dorsal part of *h,* showing shell structure, ×12 (Amsden, 1958).

Pectorhyncha MCLEARN, 1918, p. 137 [**Atrypa obtusiplicata* HALL, 1852, p. 279; OD]. Small to medium; subtriangular to subovate outline; biconvex to gibbous profile; lateral margins not vertical; beak erect. Fold and sulcus arising at umbones; anterior commissure uniplicate, trapezoid, serrate. Costae coarse, simple, rounded in section, from beaks. Shell thick. Dental plates mostly obscured by infilling of umbonal cavities; ventral muscle field deeply impressed. Dorsal median septum thick, low; septalium long, wide, filled posteriorly with large, calluslike, bilobed to multilobed cardinal process; crura long, convex laterally. *Silurian (lower Ludlow):* eastern North America.——FIG. 757,*1a–r.* **P. obtusiplicata* (HALL), Niagaran, Lockportian, Lockport, New York, USA; *a–e,* hypotype, dorsal, ventral, lateral, anterior, and posterior views from type area, ×2; *f–r,* hypotype, serial sections 0.85, 0.95, 1.05, 1.25, 1.65, 2.15, 2.6, 2.8, 3.0, 3.2, 3.6, 3.8, 4.1 mm from posterior of another hypotype from type area, ×2 (new).

Family INNAECHIIDAE Baranov, 1980

[Innaechiidae BARANOV, 1980, p. 78]

Uncinuloidea lacking septalium and cardinal process. *upper Silurian (Ludlow)–Middle Devonian (Eifelian).*

Subfamily INNAECHIINAE Baranov, 1980

[*nom. transl.* SAVAGE, 1996, p. 253, *ex* Innaechiidae BARANOV, 1980, p. 78]

Innaechiidae with median septum; dental plates very short. *Lower Devonian (Lochkovian).*

Innaechia BARANOV, 1980, p. 78 [**I. retracta;* OD]. Medium to large with transversely subpentagonal outline; dorsibiconvex; anteriorly inflated. Beak erect; delthyrium closed by deltidial plates. Fold and sulcus developed anteriorly; tongue high, rectangular. Costae medium, simple, developed laterally and anteriorly only, flattened and grooved on *paries geniculatus;* marginal spines present. Dental plates short, close to shell walls. Dorsal median septum slender, long; hinge plates divided, horizontal. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 758,*1a–l.* **I. retracta,* lower Sagyr Formation, Selennyakh ridge, Talyndzha River; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–j,* serial sections of shell 1.0, 1.2, 1.4, 1.6, 2.0, 2.1 mm from posterior; *k–l,* sections of crura 2.3, 3.7 mm from posterior of shell, ×3 (Baranov, 1980).

Subfamily CORVINOPUGNACINAE Savage, 1996

[Corvinopugnacinae SAVAGE, 1996, p. 253]

Innaechiidae with fold and sulcus low, wide; costae numerous; short dental plates present. *upper Silurian (Ludlow)–Middle Devonian (Eifelian).*

Corvinopugnax HAVLÍČEK, 1961, p. 36 [**Rhynchonella corvina* BARRANDE, 1847, p. 70; OD]. Transversely subpentagonal outline; subcuboid with steep lateral and anterior margins. Beak incurved. Fold and

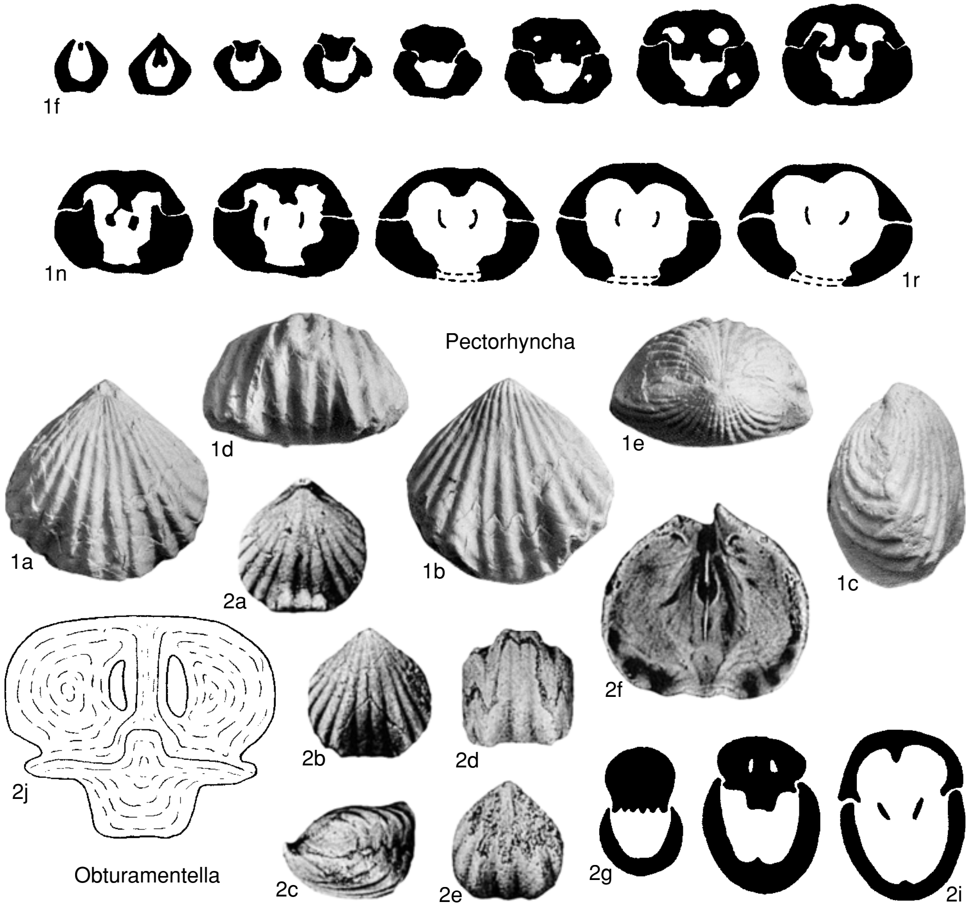

FIG. 757. Obturamentellidae (p. 1117).

sulcus distinct, from midlength; tongue wide, rectangular. Costae strong, simple, restricted to anterior third of shell, rounded in profile except on *paries geniculatus* where flattened and grooved; marginal spines well developed. Dental plates short, convergent ventrally. Dorsal median ridge short and low; hinge plates divided; septalium, median septum, and cardinal process absent. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Europe, northern Africa, Urals, Siberia, China.——FIG. 759*a–i.* **C. corvinus* (BARRANDE), upper Emsian, Suchomasty Limestone, Koneprusy, Bohemia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×2 (new); *f–i,* serial sections, ×3 (Havlíček, 1961).——FIG. 759*j–p. C. crassus* (LE MAITRE), lower Eifelian, Morocco; serial sections 1.15, 1.55, 1.8, 2.1, 2.5, 2.8, 3.1 mm from posterior, ×8 (Drot, 1980).

Aseptalium HOU & XIAN, 1975, p. 37 [**Uncinulus guangxiense* WANG, 1965, p. 72; OD]. Medium to large with transversely subpentagonal outline and dorsibiconvex profile. Fold and sulcus well defined; tongue wide, rectangular. Costae numerous, strong, simple, from beaks, flattened and grooved on *paries geniculatus;* marginal spines pronounced. Dental plates short, convergent ventrally; ventral muscle field deeply impressed. Dorsal interior with very short crural plates posteriorly, sometimes meeting on valve floor; outer hinge plates horizontal, divided; median ridge short and low; crura long, rodlike; septalium, dorsal median septum, and cardinal process absent. *Lower Devonian (Pragian–Emsian):* China.——FIG. 760,*1a–k.* **A. guangxiense* (WANG), upper Pragian–lower Emsian, Nagaoling Formation, Guangxi, Henxian County, Liujing, southern China; *a–d,* dorsal, ventral, anterior, and lateral views, ×2.2 (Hou & Xian, 1975); *e–k,* serial sections, ×3.3 (new).

Decoropugnax HAVLÍČEK, 1960, p. 244 [**Terebratula berenice* BARRANDE, 1847, p. 77; OD]. Transversely

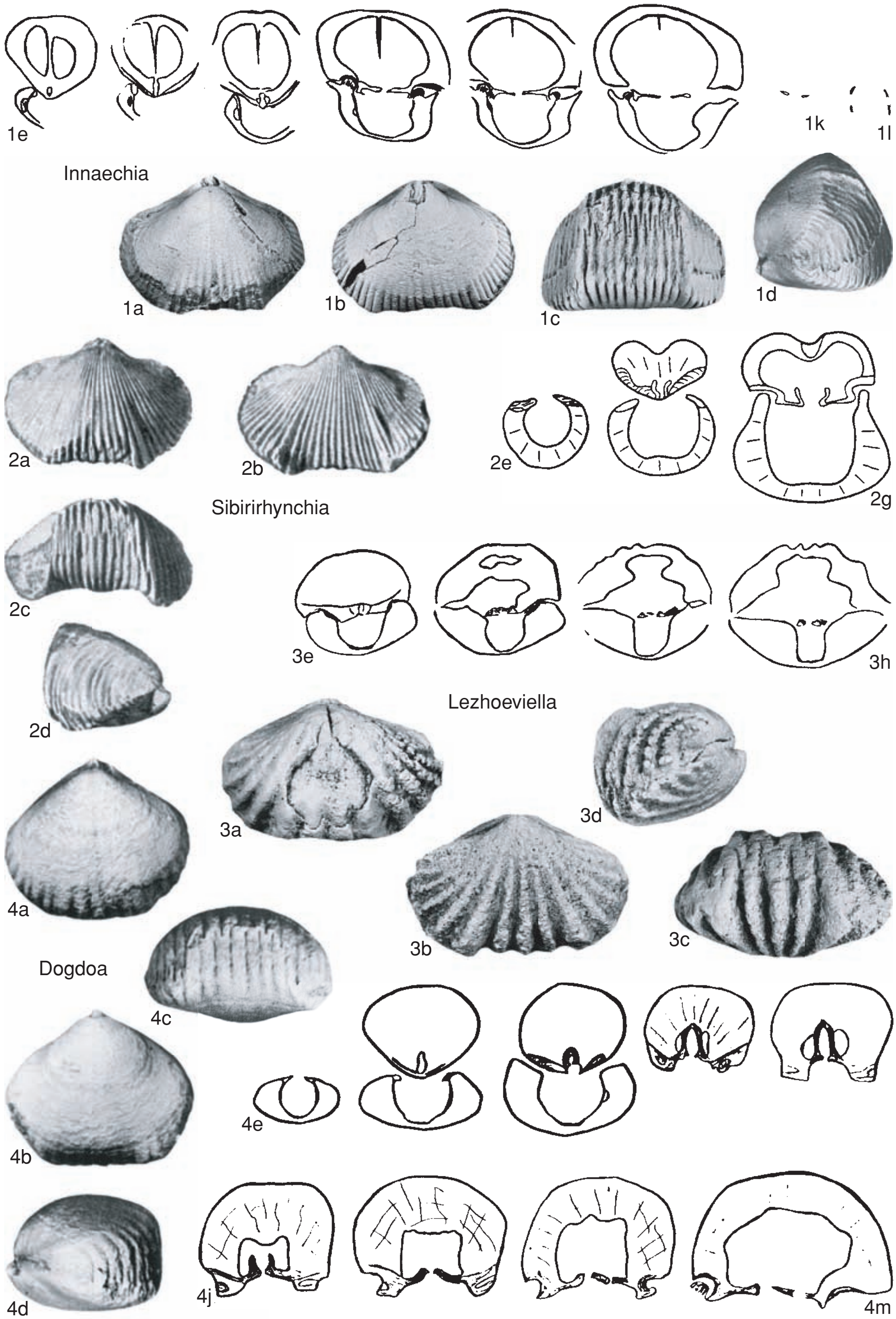

FIG. 758. Innaechiidae (p. 1117–1122).

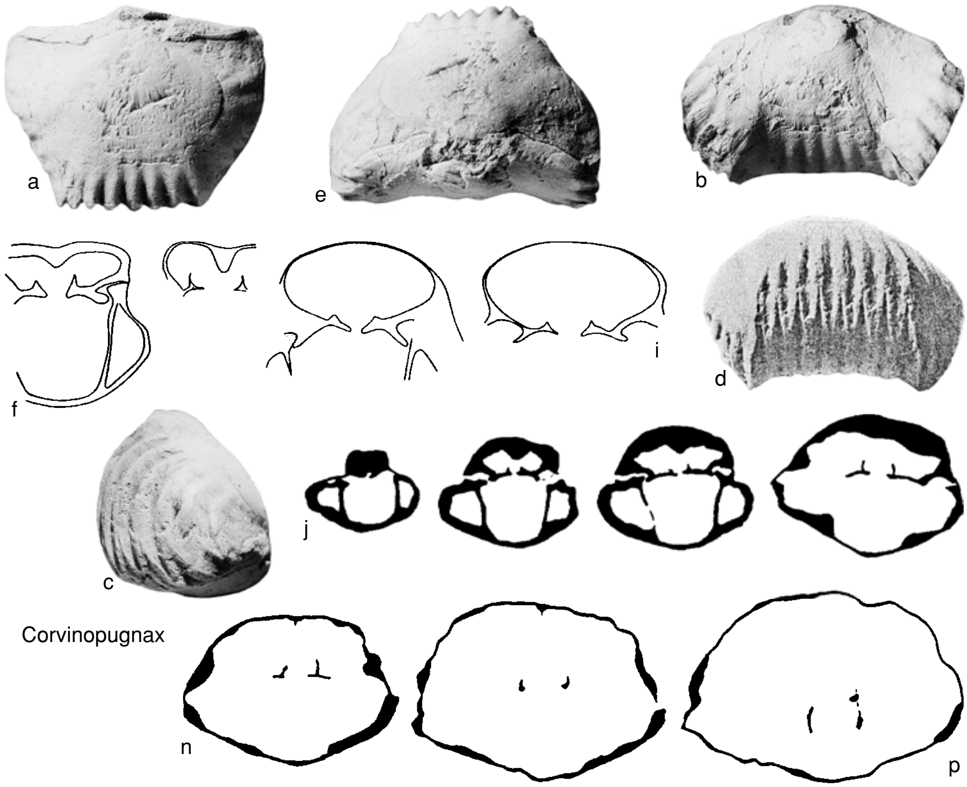

FIG. 759. Innaechiidae (p. 1117–1118).

trigonal outline; moderately biconvex to tabular profile. Beak erect; delthyrium triangular, open, deltidial plates incipient to absent. Fold and sulcus weak, broad; tongue wide, low, rectangular. Costae fine, simple, restricted to anterior third of shell; costae rounded in profile except on *paries geniculatus* where flattened and grooved; marginal spines pronounced. Dental plates short, vertical. Dorsal median septum, septalium, and cardinal process lacking. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian):* Bohemia, Urals, Altai, Yakutsk, Tadzhikistan, northwestwern Canada. ——FIG. 760,*2a–e*. **D. berenice* (BARRANDE), Ludlow, Dlouha Hora, Bohemia; *a–c,* dorsal, ventral, and anterior views, ×3.7 (new); *d–e,* serial sections, ×6 (Havlíček, 1961).

Xeniopugnax HAVLÍČEK, 1982a, p. 111 [**Terebratula modica* BARRANDE, 1847, p. 76; OD]. Subtriangular outline; moderately biconvex profile; beak incurved. Fold and sulcus wide, low, restricted to anterior half of valves; tongue low, very wide, dentate. Costae coarse, rounded, only present anteriorly, flattened and grooved on low *paries geniculatus.* Dental plates thin, short, convergent toward valve floor. Hinge plates divided, thin, horizontal; dorsal median septum and septalium absent. *upper Silurian (Ludlow):* Bohemia.——FIG. 760,*3a–f.* **X. modicus* (BARRANDE), Kopanina Formation, *Cromus beaumonti* horizon, Dlouha hora; *a–d,* dorsal, ventral, lateral, and anterior views, ×3.2; *e–f,* serial sections 8.75, 8.55 mm from anterior, ×10 (Havlíček, 1982a).

Subfamily DOGDOINAE Baranov, 1982

[Dogdoinae BARANOV, 1982, p. 42]

Innaechiidae lacking dental plates and dorsal median septum. *Lower Devonian (Lochkovian–Emsian).*

Dogdoa BARANOV, 1982, p. 42 [**D. chalimensis;* OD]. Subpentagonal outline; biconvex profile. Beak erect; delthyrium with small foramen and narrow deltidial plates. Fold and sulcus weak; tongue distinct, rectangular. Valves smooth posteriorly but with rounded costae anteriorly; costae becoming flattened and grooved on *paries geniculatus;* marginal spines short. Dental plates absent or buried in

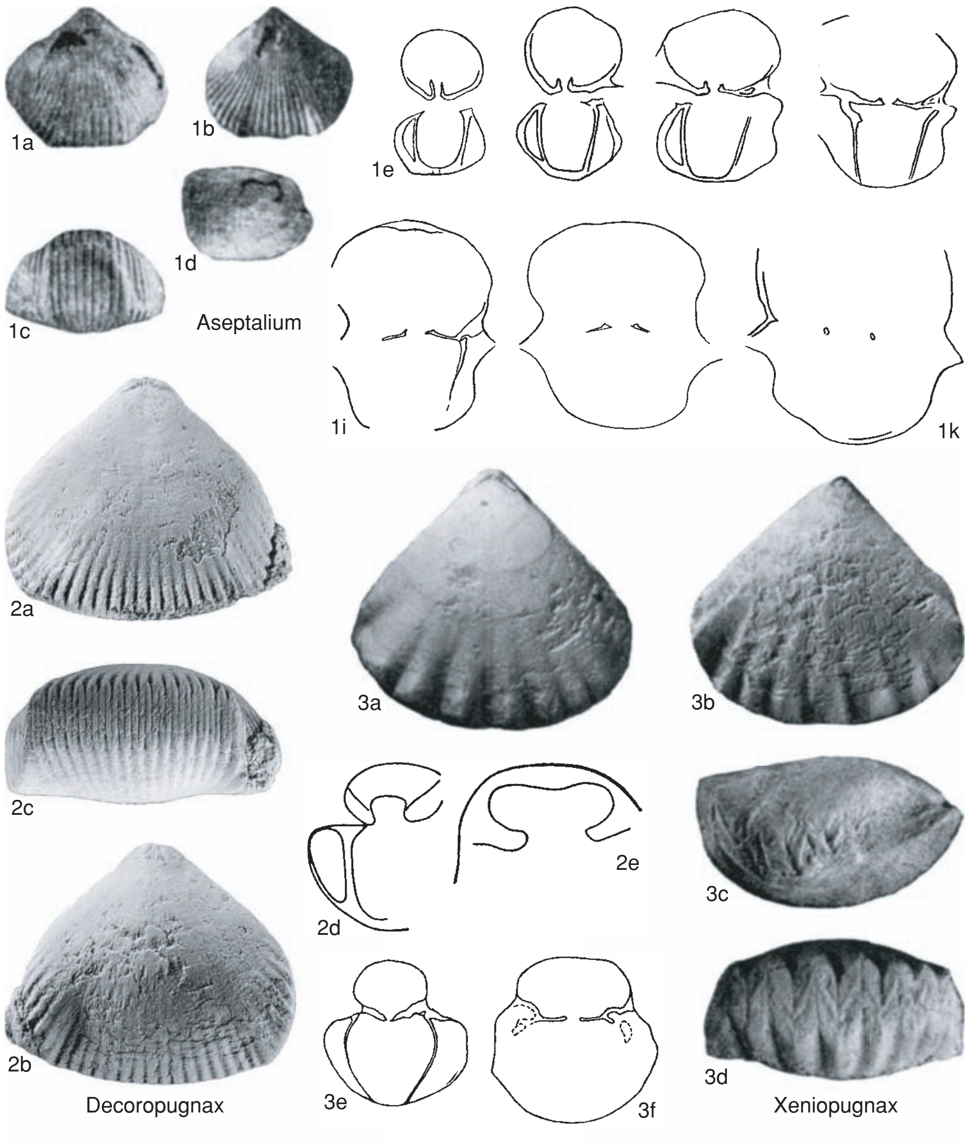

FIG. 760. Innaechiidae (p. 1118–1120).

callus. Hinge plates divided, horizontal; septalium, dorsal septum, and cardinal process absent; crural plates meeting valve floor, forming cruralium. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 758,*4a–m.* **D. chalimensis,* upper Datninskaya Formation, eastern Yakutia, Tas-Khayakhtakh Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–g,* serial sections through conjoined valves; *h–m,* serial sections through dorsal valve 0.5, 0.6, 0.7, 0.8, 0.9, 1.0 mm from posterior, ×7 (Baranov, 1982).

Lezhoeviella BARANOV, 1978, p. 48 [**L. protensa;* OD]. Transversely subpentagonal outline; dorsibiconvex profile. Fold and sulcus arising at umbones, strong anteriorly; tongue distinct, trapezoid. Costae coarse, extending from umbones, rounded in profile except on *paries geniculatus* where flattened and grooved. Dental plates absent; ventral and dorsal muscle areas deeply impressed. Hinge plates divided; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Emsian):* eastern Siberia.——FIG. 758,*3a–h.* **L. protensa,* lower Emsian, Nelichensk Series, Yakutia, Selenniakhsk Ridge; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h,* serial sections 0.2, 0.7, 0.9, 1.1 mm from posterior, ×4.5 (Baranov, 1978).

Sibirirhynchia RZHONSNITSKAIA, 1978, p. 182 [**Hypothyridina alata* KHODALEVICH, 1951, p. 50; OD] [=*Sibirirhynchia* RZHONSNITSKAIA, 1968a, p. 41, *nom. nud.,* no description, illustration, or type species given]. Transversely ovate outline; strongly biconvex profile. Beak suberect; foramen with marginal deltidial plates. Fold and sulcus wide with distinct lateral margins; tongue high, rectangular. Costae numerous, fine, simple, from beak, flattened and grooved on *paries geniculatus.* Dental plates absent. Divided hinge plates horizontal; septalium, dorsal septum, and cardinal process absent. *Lower Devonian (upper Emsian):* Kuznetsk, Urals, eastern Siberia, Tadzhikistan.——FIG. 758,*2a–d.* **S. alata* (KHODALEVICH), Sverdlovsk, eastern Urals; holotype, dorsal, ventral, anterior, and lateral views, ×1 (Khodalevich, 1951).——FIG. 758,*2e–g. S. alata fainecostata* (TORBAKOVA), northeastern slope of Urals; serial sections, ×7 (Sapelnikov, Mizens, & Shatrov, 1987).

Subfamily VLADIMIRIRHYNCHINAE Baranov, 1982

[Vladimirirhynchinae BARANOV, 1982, p. 44]

Innaechiidae with short dental plates; median furrow dividing fold, corresponding ridge dividing sulcus; dorsal median septum commonly absent. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian).*

Vladimirirhynchus BARANOV, 1982, p. 44 [**V. lezhoevi;* OD]. Small size; subcircular to subpentagonal outline; biconvex profile. Beak erect to incurved; foramen permesothyrid. Fold strong with weak median sinus, sulcus with corresponding ridge; tongue high; trapezoid to tapering. Costae coarse, rounded in section, bifurcating on fold and in sulcus; costae on *paries geniculatus* bear grooves. Dental plates short. Hinge plates divided, dorsally inclined; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 761,*1a–l.* **V. lezhoevi,* lower Sagyr Formation, Yakutia, Ulakhan-Sis Range; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d–l,* serial sections 0.4, 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 1.3, 1.6 mm from posterior, ×3.5 (Baranov, 1982).

Alekseevaella BARANOV, 1980, p. 80 [**A. sulcata;* OD]. Small size; elongate subpentagonal outline; dorsal valve inflated. Beak erect to incurved; foramen permesothyrid, deltidial plates conjunct. Fold divided by groove, sulcus with corresponding ridge. Costae bundled on fold and sulcus, flattened and grooved on *paries geniculatus.* Dental plates short. Dorsal median septum thin; septalium lacking; hinge plates divided, horizontal; cardinal process absent; crura ventrally curved, narrow. *Middle Devonian (Eifelian):* eastern Siberia.——FIG. 761,*2a–n.* **A. sulcata,* lower Seymchan Formation, Ulakhan-Sis Range, Pravyy Naanchan River; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l,* serial sections of shell 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 mm from posterior; *m–n,* sections of crura, intervals not given, ×3.5 (Baranov, 1980).

Selennjachia BARANOV, 1982, p. 45 [**S. abaimovae;* OD]. Small size; subpentagonal outline; moderately biconvex profile. Beak suberect; foramen mesothyrid. Fold and sulcus low, fold divided by sinus, sulcus divided by weak ridge; umbones smooth. Costae rounded in profile, flattened and grooved anteriorly. Dental plates very short or obscured by callus. Hinge plates divided, subhorizontal; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* eastern Siberia.——FIG. 761,*4a–k.* **S. abaimovae,* Zlichovian–Eifelian, Seymchan Formation, Selennyakh Range, eastern Yakutia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–k,* serial sections 0.2, 0.25, 0.35, 0.45, 0.65, 0.95, 1.05 mm from posterior, ×3.5 (Baranov, 1982).

Sulcicostula BARANOV, 1989, p. 47 [**Corvinopugnax tichiensis* ALEKSEEVA, 1967, p. 65; OD]. Small size; subpentagonal outline; biconvex profile. Beak erect; foramen permesothyrid; umbones smooth. Fold divided by weak sinus, sulcus divided by low ridge. Costae rounded in section but flattened and grooved on *paries geniculatus.* Dental plates short; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Lochkovian):* eastern Siberia.——FIG. 761,*3a–k.* **S. tichiensis* (ALEKSEEVA); *a–d,* holotype, dorsal, ventral, anterior, and lateral views, upper Lochkovian, middle Sette-Daban Formation, Sette-Daban Range, ×2.5; *e–g,* serial sections, upper Lochkovian, middle Sette-Daban Formation, Sette-Daban Range, ×6 (Alekseeva, 1967); *h–k,* hypotype, dorsal, ventral, anterior, and lateral views, base of Sagyrskaya Formation, ×2 (Baranov, 1989).

Tatjania BARANOV, 1982, p. 47 [**T. trigona;* OD]. Small size; subpentagonal outline; highly inflated dorsal valve. Beak erect. Fold divided by weak sinus; sulcus divided by low ridge; tongue high. Most of valves smooth, with costae restricted to anterior third; costae flattened and grooved on *paries geniculatus.* Dental plates convergent ventrally; ventral muscle field deeply impressed. Hinge plates divided; dorsal median septum, septalium, and cardinal process absent; crura close set anteriorly. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* eastern Siberia.——FIG. 762,*1a–m.* **T. trigona,* lower Eifelian, Seymchan Formation, Ulakhan-Sis Range, eastern Yakutia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–m,* serial sections 0.9, 1.2, 1.4, 1.5, 1.7, 1.9, 2.1, 2.2, 2.3 mm from posterior, ×2.5 (Baranov, 1982).

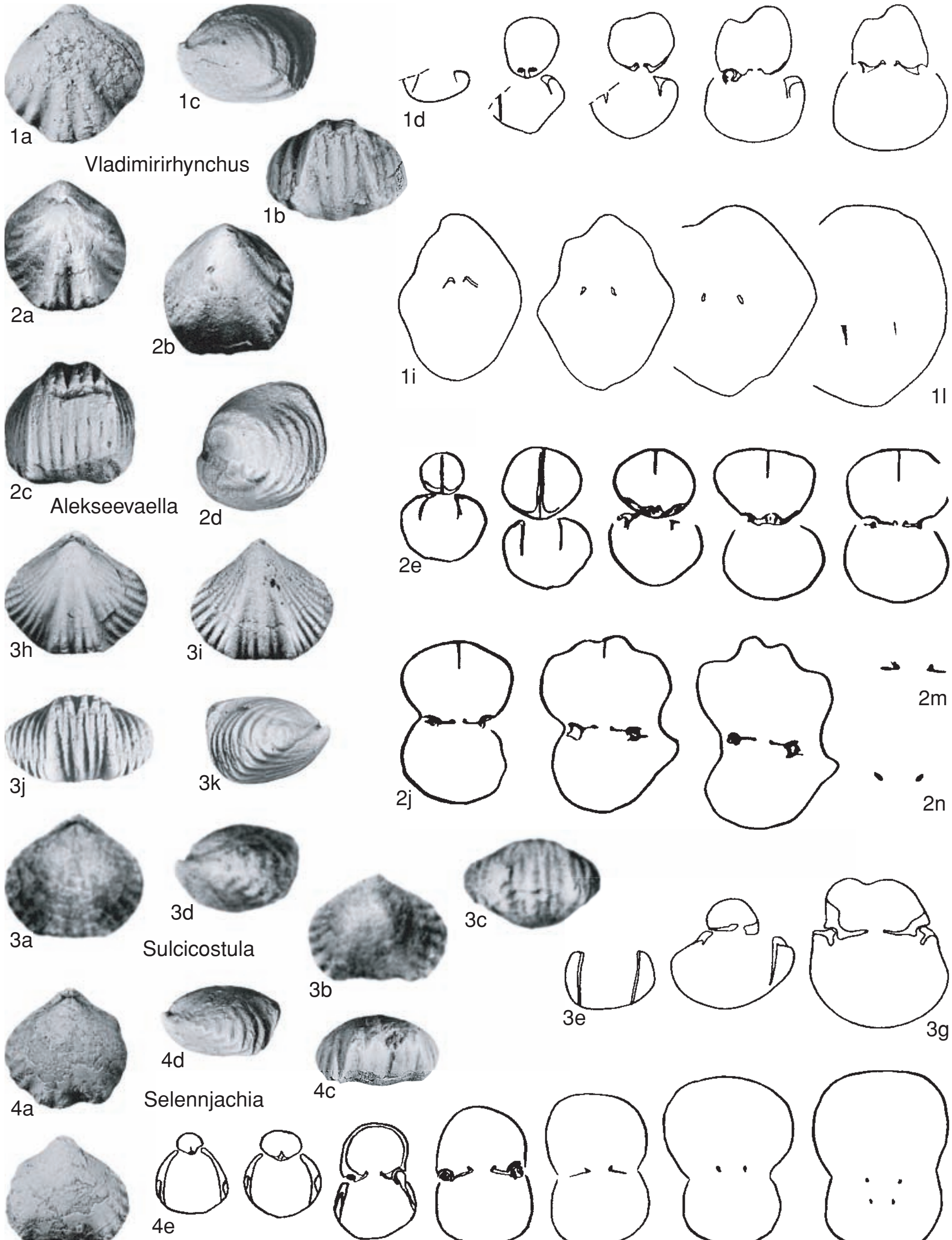

FIG. 761. Innaechiidae (p. 1122).

Yakutijaella BARANOV, 1977, p. 77 [**Y. dubatolovi;* OD]. Subpentagonal to transversely ovate outline and moderately biconvex profile. Beak erect; foramen small, rounded. Fold and sulcus weak, from umbones, with groove on fold, plication in sulcus; tongue low, denticulate; umbones smooth. Costae weak, subangular, arising near umbones. Dental plates absent. Dorsal median septum and septalium absent; hinge plates united, thick; crural bases large, concave dorsolaterally, developing on dorsal side of

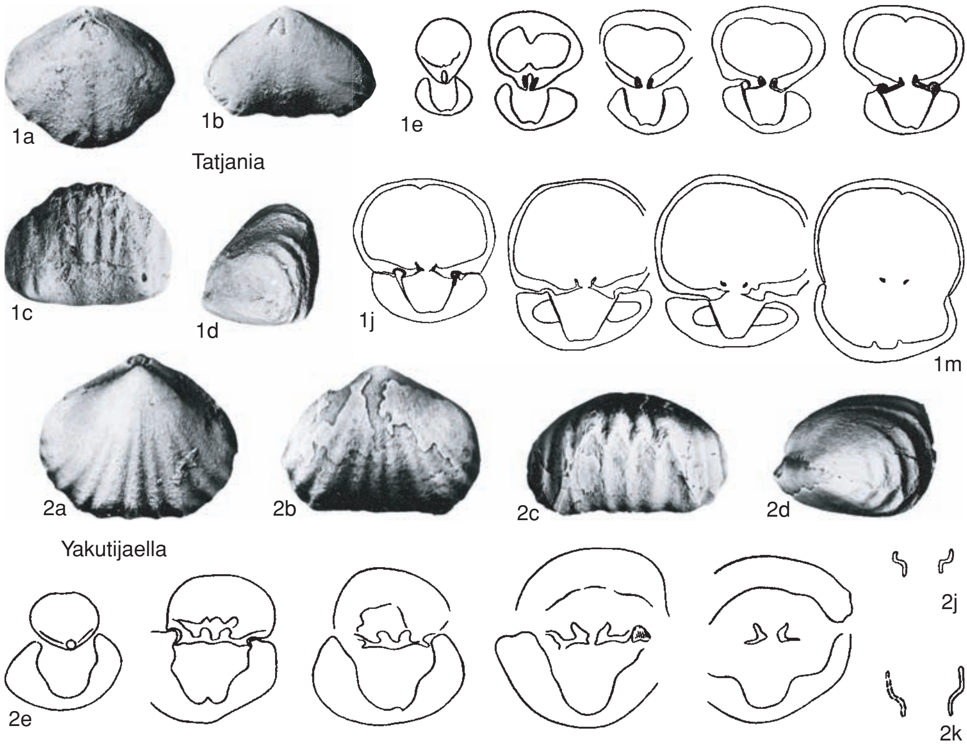

FIG. 762. Innaechiidae (p. 1122–1124).

hinge plates as prominent ridges; crura long, laterally compressed, sigmoidal in section. *Lower Devonian (lower Emsian):* northeastern Siberia.——FIG. 762,*2a–k*. **Y. dubatolovi,* Nelichenian suite, Yakutsk, Selennyakh Ridge; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–k,* serial sections at 1.7, 2.2, 2.4, 2.7, 2.8, 4.1, 4.4 mm from posterior, ×3.7 (Baranov, 1977).

Family GLOSSINOTOECHIIDAE Havlíček, 1992

[Glossinotoechiidae HAVLÍČEK, 1992, p. 92]

Uncinuloidea with cordiform to subtriangular outline, acuminate posteriorly; tongue distinct; costae numerous, flattened anteriorly; marginal spines developed; foramen mesothyrid with conjunct deltidial plates. Dental plates short, close to valve walls. Septalium usually with cover plate; cardinal process high, linguiform, often striated. *upper Silurian (Ludlow)–Middle Devonian (Eifelian).*

Glossinotoechia HAVLÍČEK, 1959, p. 79 [**Terebratula henrici* BARRANDE, 1847, p. 84; OD]. Subtriangular outline with acuminate posterior angle; ventral valve flat to concave, dorsal valve highly inflated; anterior and lateral margins sharply truncated in adults. Beak straight; mesothyrid foramen with conjunct deltidial plates. Fold and sulcus weak to absent but tongue high and rectangular; squamae and glottae poorly developed. Costae arising at beaks, rounded in profile but flattened and grooved anteriorly. Dental plates distinct but close to shell walls. Dorsal median septum long, low, thick; septalium completely filled with callus; large multilobed to linguiform cardinal process. *Lower Devonian (Pragian)–Middle Devonian (lower Eifelian):* Europe, northern Africa, Urals, Siberia, China.——FIG. 763,*1a–k*. **G. henrici* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, ×2; *e–k,* serial sections 13.4, 13.2, 13.0, 12.8, 12.6, 12.2, 12.0 mm from anterior, ×2 (Havlíček, 1961).

Chlupacitoechia HAVLÍČEK, 1992, p. 100 [**Uncinulus (Glossinotoechia) chlupaci* HAVLÍČEK, 1956, p. 569; OD]. Subtriangular with emarginate posterolateral and anterior margins; dorsibiconvex profile but

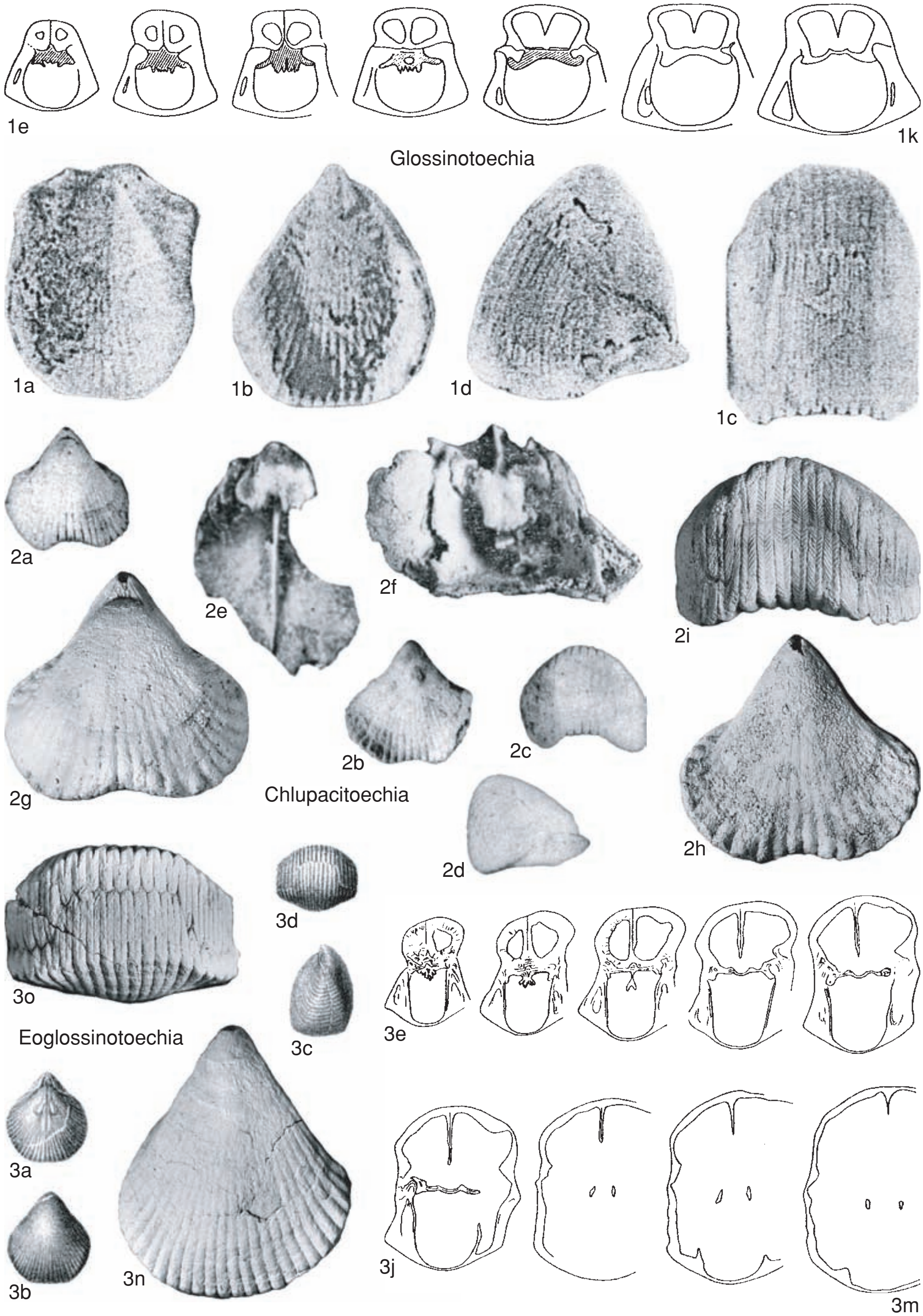

FIG. 763. Glossinotoechiidae (p. 1124–1126).

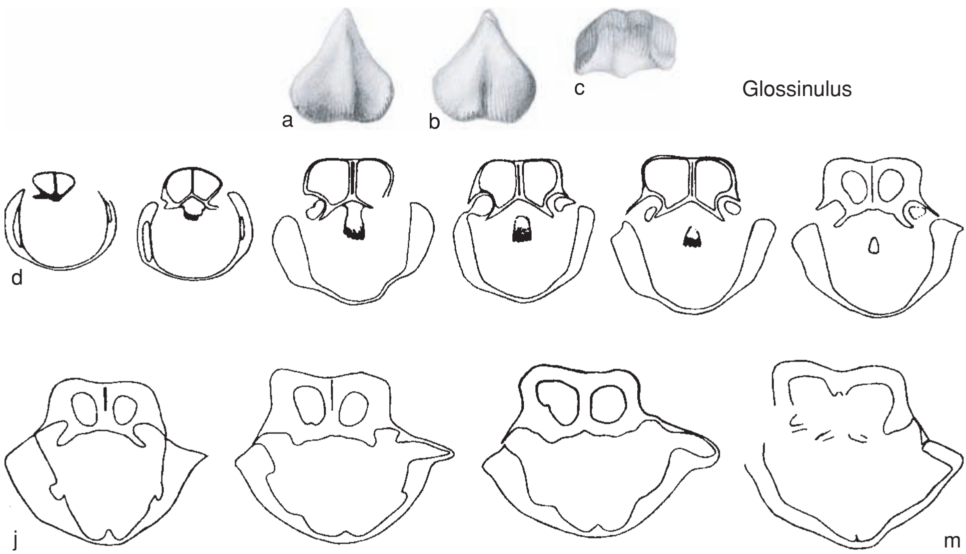

FIG. 764. Glossinotoechiidae (p. 1126).

with concavity on ventral valve; anterior margin and flanks vertical to truncated. Beak straight to suberect; foramen small, circular, mesothyrid, deltidial plates conjunct. Dorsal fold and ventral sulcus weak; anterior tongue distinct, high, rectangular. Costae fine, grooved at commissure to accommodate marginal spines. Dental plates well developed, strongly divergent anteriorly, close to valve margins; septalium large, commonly filled with callus. Dorsal median septum high, extending to valve midlength; cardinal process wide, high, posteriorly striated. *Lower Devonian (Pragian)–Middle Devonian (lower Eifelian):* Bohemia, Spain, France.——FIG. 763,*2a–i*. **C. chlupaci* (HAVLÍČEK), Emsian, Zlichov Limestone, Hlubocepy, Bohemia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1 (Havlíček, 1961); *e,* dorsal interior, ×3.8; *f,* articulated umbonal interior showing dental plates, septalium, and cardinal process, ×5; *g–i,* hypotype, dorsal, ventral, and anterior views, ×2.4 (Havlíček, 1992).

Eoglossinotoechia HAVLÍČEK, 1959, p. 81 [**E. cacuminata;* OD]. Small size; subtriangular acuminate outline; biconvex with truncated anterior and lateral margins. Beak suberect; foramen small, deltidial plates large, conjunct. Fold and sulcus weak to absent; tongue distinct, rectangular. Costae fine, rounded in section, arising at beaks, becoming flattened and grooved on *paries geniculatus;* marginal spines short. Dental plates distinct, subparallel; ventral muscle field deeply impressed. Dorsal median septum high, long; septalium small, filled with cardinal process; hinge plates united; cardinal process multilobed posteriorly, linguiform, and bilobed or trilobed anteriorly. *upper Silurian (Ludlow)–Lower Devonian (Emsian):* cosmopolitan.——FIG. 763,*3a–o*. **E. cacuminata,* Pragian, Slivenec Limestone, Dvorce, Bohemia; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Barrande, 1879b); *e–m,* serial sections 11.35, 11.2, 11.05, 10.9, 10.7, 10.55, 10.2, 10.05, 9.65 mm from anterior, ×4; *n–o,* holotype, ventral and anterior views, ×3.2 (Havlíček, 1992).

Glossinulus SCHMIDT, 1942, p. 394 [**Rhynchonella adolfi mimica* BARRANDE, 1879b, p. 178; OD; =*Glossinulus mimicus* (BARRANDE), 1879b, p. 178]. Triangular outline, posteriorly acuminate; tabular profile, flattened to concave ventral valve with low median fold, flattened to slightly convex dorsal valve with gentle median sulcus; truncated anterior and lateral margins; tongue high, rectangular. Beak suberect; foramen small, circular, mesothyrid, deltidial plates conjunct. Costae fine, arising on umbones, flattened and grooved on *paries geniculatus;* spines at anterior and lateral margins. Dental plates very short, close to shell wall; ventral muscle field deeply impressed; low ventral median myophragm. Dorsal median septum low; septalium wide, filled posteriorly with high, linguiform cardinal process bearing fine longitudinal ridges; inner socket ridges prominent. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Europe, northern Africa, Siberia, China.——FIG. 764*a–m*. **G. mimicus* (BARRANDE), Emsian, Eifel, Germany; *a–c,* dorsal, ventral, and anterior views, ×1 (Schmidt, 1965b); *d–m,* serial sections 6.9, 6.6, 6.4, 6.3, 6.2, 6.1, 6.0, 5.9, 5.8, 5.7 mm from anterior, ×4 (Havlíček, 1961).

Family HYPOTHYRIDINIDAE Rzhonsnitskaia, 1956

[Hypothyridinidae RZHONSNITSKAIA, 1956a, p. 125]

Uncinuloidea with dorsal median septum and septalium weak or lacking. Cardinal process usually wide, with myophore consisting of numerous vertical ridges, but cardinal process sometimes poorly developed or absent. *Lower Devonian (Emsian)–Upper Devonian (upper Famennian).*

Hypothyridina BUCKMAN, 1906, p. 324, *nom. nov. pro Hypothyris* PHILLIPS, 1841, p. 55, *non* HÜBNER, 1821 [**Atrypa cuboides* SOWERBY, 1840a, pl. 56, fig. 24; SD KING, 1846, p. 28]. Medium to large with subcircular to subrectangular outline; strongly biconvex to inflated; lateral and anterior margins very steep. Beak suberect to erect; foramen small, circular, usually obscured by inflated dorsal umbo. Fold and sulcus weak; tongue very high, rectangular to rounded. Costae numerous, evenly developed, simple, flattened on *paries geniculatus;* marginal spines present. Dental plates short, subvertical to vertical. Dorsal median septum and septalium weak to absent; hinge plates short, horizontal, divided, or sometimes united by cardinal process; cardinal process usually short, with several lobes. *Middle Devonian (Eifelian)–Upper Devonian (Famennian):* cosmopolitan.——FIG. 765,*1a–e*. **H. cuboides* (SOWERBY); *a–b,* dorsal and anterior views, Givetian, Plymouth Limestone, Plymouth, England, ×1 (Sowerby, 1840a); *c–e,* dorsal, anterior, and lateral views, Frasnian, Philippeville, Belgium, specimen 67298, Smithsonian, ×1 (new).——FIG. 765,*1f–g*. *H.* sp. cf. *H. impleta* (SOWERBY), Upper Devonian, Langennaubach, Germany; transverse sections of different young specimens, ×7 (Schmidt, 1965b).

Glosshypothyridina RZHONSNITSKAIA, 1978, p. 180 [**Rhynchonella procuboides* KAYSER, 1871, p. 513; OD]. Transversely subpentagonal outline and dorsibiconvex profile; dorsal valve very inflated, ventral valve almost flat. Beak erect. Fold and sulcus pronounced, from umbones; tongue rectangular. Costae fine, numerous, flattened and grooved on *paries geniculatus.* Dental plates very short, ventrally convergent. Septalium and dorsal median septum absent; cardinal process low, bilobed; hinge plates horizontal, divided anterior of cardinal process. *Middle Devonian (Eifelian):* Germany, Belgium, European Russia, Urals.——FIG. 766,*1a–j*. **G. procuboides* (KAYSER), Eifel, Germany; *a–b,* holotype, anterior and lateral views, lower Eifelian, Gondelsheimer Formation, ×1 (Kayser, 1871); *c–f,* serial sections, lower Eifelian, Gondelsheimer Formation, ×2.5 (Schmidt, 1941a); *g–j,* serial sections 16.9, 16.7, 16.5, 16.4 mm from anterior, ×5 (Schmidt, 1965b).

Lorangerella CRICKMAY, 1963, p. 10 [**L. phaulomorpha;* OD]. Small size with subcircular outline and lenticular to subglobose profile. Beak erect to incurved; foramen minute. Fold and sulcus weak but subrectangular tongue distinct. Valves mostly smooth, with low, rounded costae developed only at anterior margin; costae grooved at commissure. Dental plates very short, divergent ventrally. Cardinal process small, multilobed, close to posterior apex, supported by short median ridge. Hinge plates short, divided; septalium absent; crura curved sharply ventrally. *Upper Devonian (Frasnian):* North America, Europe.——FIG. 765,*2a–m*. **L. phaulomorpha,* lower Frasnian, Waterways Formation, Alberta, Canada; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2.3 (Crickmay, 1963); *f–m,* serial sections 0.2, 0.6, 0.8, 0.9, 1.0, 1.2, 1.6, 1.9 mm from posterior, ×5 (McLaren, 1965).

Pseudouncinulus RZHONSNITSKAIA, 1968b, p. 111 [**P. mamontovensis;* OD]. Small to medium with subtrigonal outline. Beak erect. Fold and sulcus weak; tongue rectangular. Costae arising at umbones, rounded in section, rarely bifurcating, flattened and grooved on *paries geniculatus.* Dental plates very short, close to shell walls. Septalium and dorsal median septum absent; cardinal process wide, with several longitudinal ridges; hinge plates anterior of cardinal process horizontal, united by dorsally concave plate. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Salair, Kuznetz, Urals, Yakutskaya.——FIG. 766,*3a–h*. **P. mamontovensis,* southwestern Kuznetz basin; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h,* serial sections, intervals and scale not given (Rzhonsnitskaia, 1968b).——FIG. 766,*3i–u*. *P. pusillis* BARANOV, Seymchan Formation, Yakutskaya, Ulakhan-Sis Range, eastern Siberia; *i–k,* holotype, ventral, anterior, and lateral views, ×2; *l–u,* serial sections at 0.2, 0.4, 0.6, 0.8, 1.0, 1.1, 1.2, 1.3, 1.4, 1.9 mm from posterior, ×8 (Baranov, 1980).

Uchtella LJASCHENKO, 1973, p. 50 [**Hypothyridina praesemilukiana* LJASCHENKO, 1958, p. 130; OD]. Subcircular to subpentagonal outline and strongly dorsibiconvex to subglobose profile; lateral and anterior margins steep to vertical. Beak small, incurved. Fold and sulcus weak posteriorly but distinct anteriorly; anterior commissure uniplicate; tongue wide, high, subrectangular to rounded. Valves smooth posteriorly but with low, rounded costae developed from about midlength; costae flattened and grooved anteriorly and especially on *paries geniculatus.* Dental plates very short. Hinge plates short, divided. Dorsal median septum absent. Cardinal process not recorded. *Upper Devonian (Frasnian):* European Russia, Urals.——FIG. 766,*2a–e*. **U. praesemilukiana* (LJASCHENKO), upper Timanski bed, southern Timan, Ukhtinsk region, European Russia; *a–c,* holotype, dorsal, anterior, and lateral views, ×1; *d–e,* transverse sections near posterior, approximately ×6 (Ljaschenko, 1973).

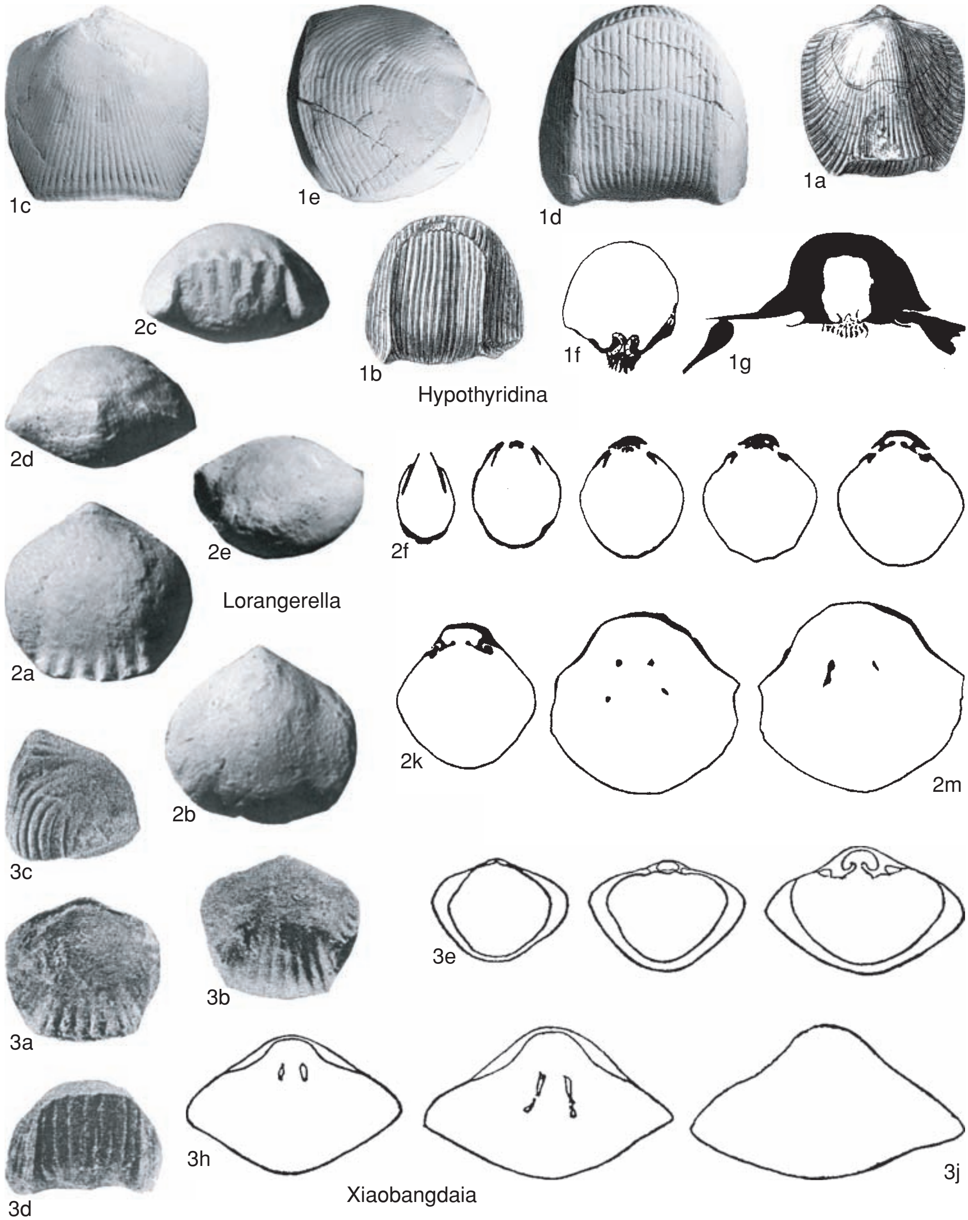

FIG. 765. Hypothyridinidae (p. 1127–1129).

Xiaobangdaia WANG, 1985, p. 200 [**X. zhuogedongensis;* OD]. Subcircular to subpentagonal outline and strongly anteriorly inflated, biconvex profile. Beak erect. Fold and sulcus distinct anteriorly; tongue high, rounded to subquadrate. Costae broad and low, restricted to anterior third of shell; flattened and grooved on *paries geniculatus;* marginal spines well developed, insert in line of holes just inside interior margin of opposite valve. Dental plates absent. Hinge plates short, united posteriorly but divided anteriorly. Dorsal median septum absent; cardinal process not recorded; crura short, strongly curved ventrally. *Upper Devonian (upper Famennian):* Tibet.——FIG. 765,*3a–j*. **X.*

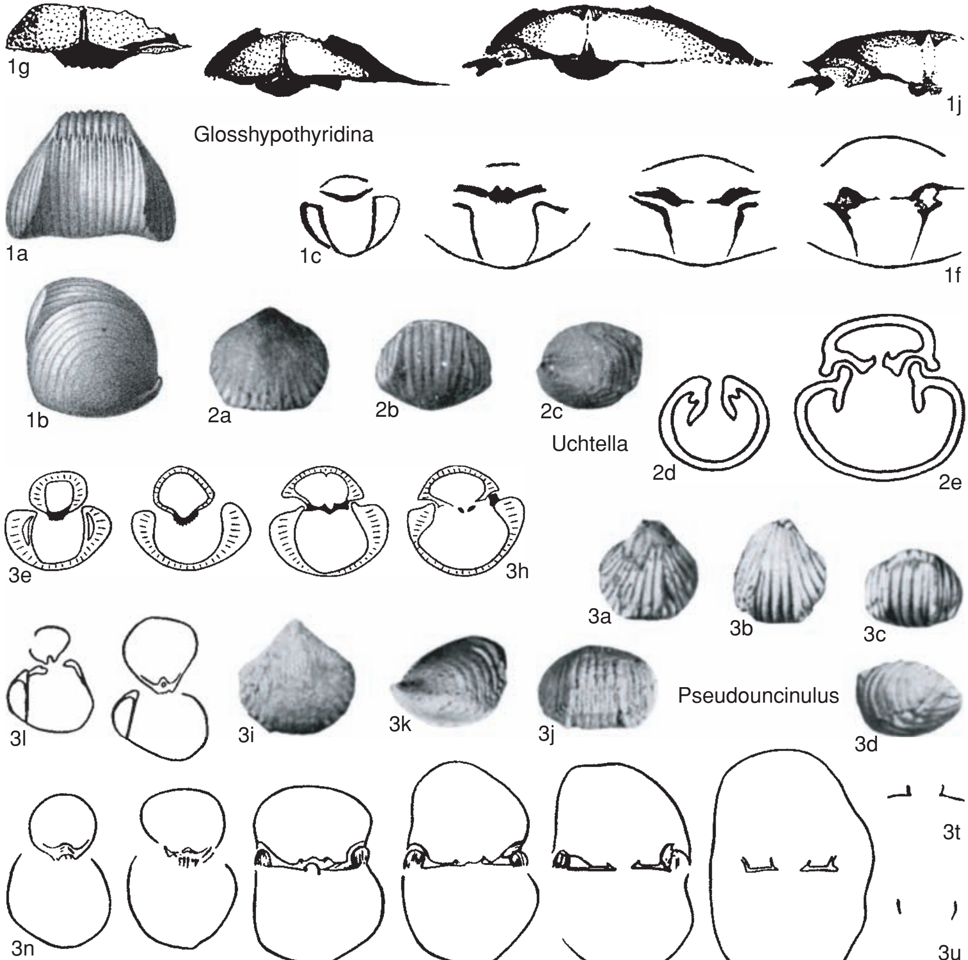

FIG. 766. Hypothyridinidae (p. 1127).

zhuogedongensis, upper Famennian, Zhougedong Formation, Markham County, Xiaobangda; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×2; *e–j,* serial sections 1.0, 1.2, 1.4, 1.7, 2.0, 2.3 mm from posterior, ×3.2 (Wang, 1985).

Family HADRORHYNCHIIDAE McLaren, 1965

[*nom. transl.* SAVAGE, 1996, p. 253, *ex* Hadrorhynchiinae MCLAREN, 1965, p. 569]

Uncinuloidea with coarse costae; commissure acutely denticulate with marginal grooves; fold and sulcus developed anteriorly; tongue high, rectangular to acute. Small septalium; hinge plates horizontal, divided; bilobed calluslike cardinal process may be present. *Middle Devonian (Eifelian–Givetian).*

Hadrorhynchia MCLAREN, 1961, p. 3 [**Pugnoides sandersoni* WARREN, 1944, p. 115; OD]. Medium to large with subpentagonal outline; dorsibiconvex; lateral and anterior margins steep. Beak erect; foramen elliptical, submesothyrid, with disjunct to conjunct deltidial plates. Fold and sulcus prominent anteriorly; tongue high, rectangular to acute. Much of valves smooth, with coarse, rounded costae developed only near lateral and anterior margins; superimposed fine, radial capillae commonly

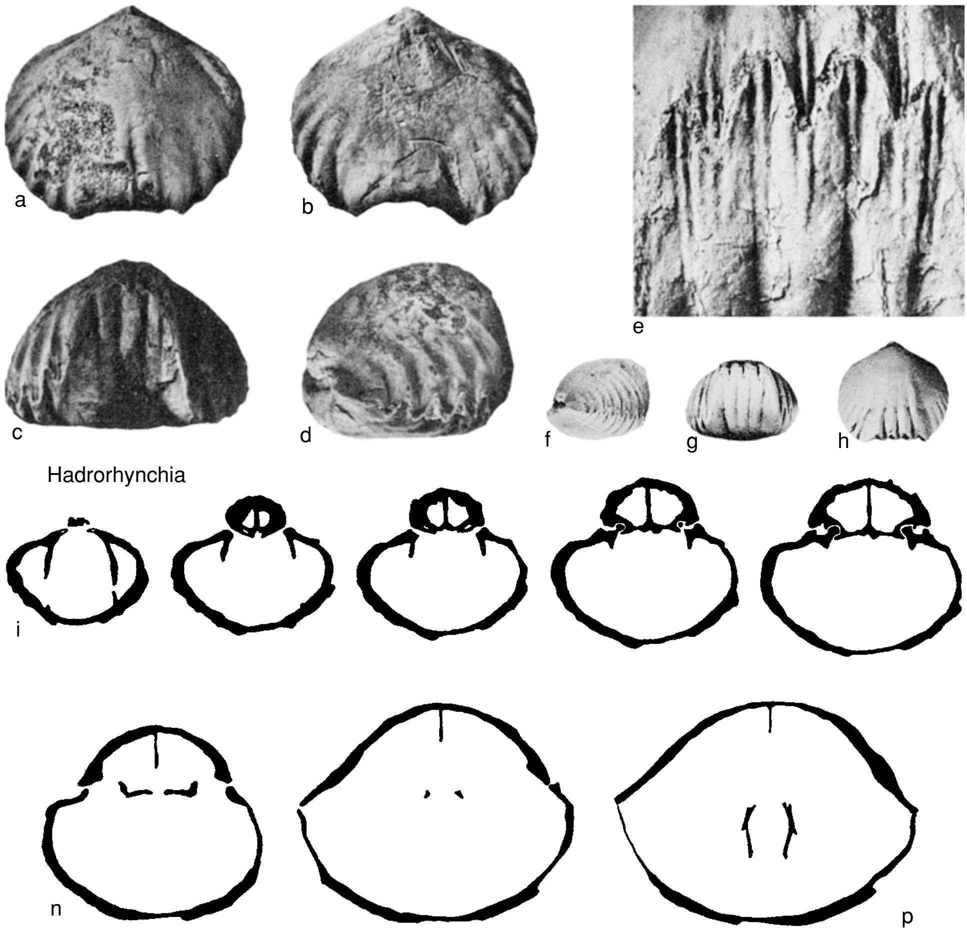

FIG. 767. Hadrorhynchiidae (p. 1129–1130).

developed; commissure denticulate with marginal grooves; marginal spines present. Dental plates short, subvertical. Dorsal median septum long, thin; small septalium; bilobed calluslike cardinal process. *Middle Devonian (Givetian):* western North America, Siberia, China.——FIG. 767*a–p*. **H. sandersoni* (WARREN), Givetian, Mackenzie District, western Canada; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, ×1; *e,* hypotype, spines at commissure, ×3; *f–h,* hypotype, lateral, anterior, and dorsal views, ×1; *i–p,* serial sections 1.2, 1.65, 1.75, 2.15, 2.35, 2.65, 3.35, 3.9 from posterior, ×3 (McLaren, 1962).

Droharhynchia SARTENAER, 1985b, p. 218 [**Hadrorhynchia intermissa* CRICKMAY, 1963, p. 2; OD]. Transversely subpentagonal outline; dorsibiconvex; anteriorly inflated. Beak suberect; foramen large, oval, submesothyrid, small deltidial plates disjunct. Fold and sulcus broad, arising at umbones; tongue strong, trapezoid, dentate. Umbones smooth; costae

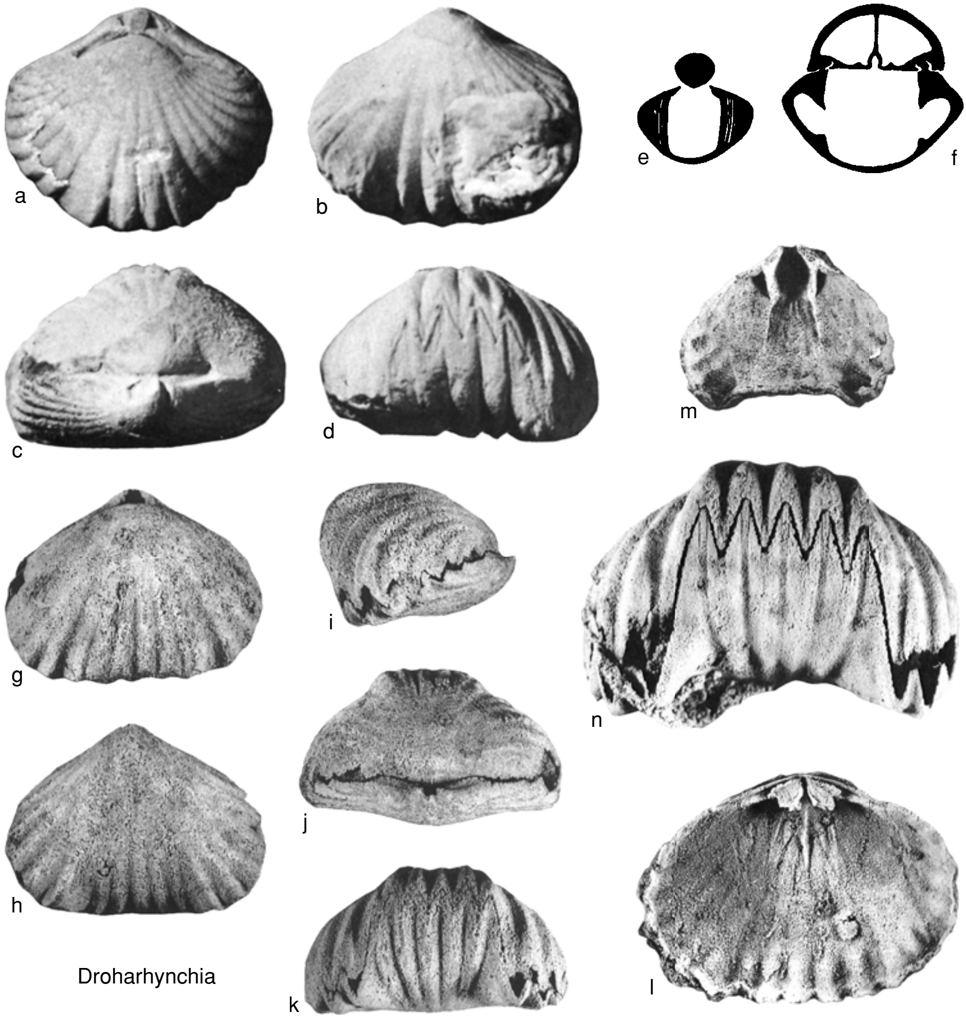

FIG. 768. Hadrorhynchiidae (p. 1130–1131).

coarse, low, rounded, simple, flattened and grooved on *paries geniculatus.* Dental plates distinct, ventrally convergent; ventral muscle field well impressed. Dorsal median septum thin, septalium distinct, open; dorsal median septum high, thin; cardinal process absent. *Middle Devonian (Eifelian–Givetian):* western Canada, USA (Alaska).——FIG. 768*a–f.* **D. intermissa* (CRICKMAY), middle Givetian, Pine Point Formation, Great Slave Lake, District of Mackenzie, western Canada; *a–d,* holotype, dorsal, ventral, posterior, and anterior views, ×2; *e–f,* serial sections 1.5, 2.5 from posterior, ×3 (Crickmay, 1963).——FIG. 768*g–n. D. rzhonsnitskayae* BAXTER & BLODGETT, lower Eifelian, west-central Alaska; *g–k,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×2; *l,* dorsal interior, ×2.6; *m,* ventral interior, ×2; *n,* paratype, anterior, ×2.8 (Baxter & Blodgett, 1994).

CAMAROTOECHIOIDEA

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Superfamily CAMAROTOECHIOIDEA Schuchert, 1929

[*nom. transl.* Savage, 1996, p. 254, *ex* Camarotoechiidae Schuchert in Schuchert & LeVene, 1929a, p. 18]

Rhynchonellida with subcircular to transversely ovate outline; dorsal fold and ventral sulcus weak to moderate; tongue low to high; costae weak to strong, simple to bifurcating, more pronounced anteriorly so that umbones often smooth; foramen small with conjunct deltidial plates anteriorly. Dental plates strong, usually convergent ventrally, occasionally infilled with callus. Dorsal median septum long; septalium short, usually without cover plate; hinge plates divided anterior of septalium; cardinal process absent; crura long, commonly raduliform. Shell often thick and muscle fields deeply impressed. *lower Silurian (Llandovery)–Lower Carboniferous (Tournaisian).*

Family CAMAROTOECHIIDAE Schuchert, 1929

[Camarotoechiidae Schuchert in Schuchert & LeVene, 1929a, p. 18]

Camarotoechioidea with short dental plates and low dorsal median septum. *lower Silurian (upper Llandovery)–Middle Devonian (Givetian).*

Subfamily CAMAROTOECHIINAE Schuchert, 1929

[Camarotoechiinae Schuchert in Schuchert & LeVene, 1929a, p. 18]

Moderately biconvex Camarotoechiidae with costae that show some bifurcation. Dental plates nearly vertical. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Camarotoechia Hall & Clarke, 1893, p. 189 [**Atrypa congregata* Conrad, 1841, p. 55; OD]. Subcircular to transversely ovate with moderately biconvex profile; maximum thickness at umbones, sides and anterior not steep. Fold and sulcus low, commencing at umbones; anterior commissure uniplicate, broad, gentle. Costae low, rounded, present on flanks as well as fold and sinus, bifurcating and intercalating. Dental plates short, strong. Hinge plates divided anteriorly; dorsal median septum long but low; septalium short; dorsal muscle field long, narrow. *Middle Devonian (Givetian):* North America.——Fig. 769,*1a–b*. **C. congregata* (Conrad), Skaneateles Formation, Butternut Shale, Onondaga County, Conklin's Falls, New York, USA; *a,* two dorsal valve internal molds, ×1.5; *b,* ventral valve internal mold, ×1 (Sartenaer, 1961b).

Ellesmerhynchia Brice, 1990, p. 717 [**Camarotoechia* s.l. *pseudomedea* Brice, 1982, p. 51; OD]. Elongate subtriangular to rounded outline and subequally biconvex profile; sides and anterior not truncated. Beak erect. Fold and sulcus low; anterior commissure uniplicate; tongue low, broad, gentle. Costae fine, numerous. Dental plates short, close to valve walls. Septalium short, shallow; hinge plates divided; dorsal median septum low; crura closely set, ventrally curved. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Canada, Podolia.——Fig. 769,*2a–l*. **E. pseudomedea* (Brice), upper Emsian, Blue Fiord Formation, southwestern Ellesmere Island, Ontario, Arctic Canada; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–l,* serial sections 1.8, 1.9, 2.2, 2.3, 2.6, 2.8, 2.9, 4.5 mm from posterior, ×2.5 (Brice, 1990).

Subfamily LINGUOPUGNOIDINAE Savage, 1996

[Linguopugnoidinae Savage, 1996, p. 254]

Early Camarotoechiidae with broad fold and sulcus; tongue high; costae strong, simple; dental plates weak. *lower Silurian (upper Llandovery)–Lower Devonian (Emsian).*

Linguopugnoides Havlíček, 1960, p. 242 [**Rhynchonella nympha* var. *carens* Barrande, 1879b, pl. 122; OD]. Subcircular to subpentagonal outline and dorsibiconvex profile; lateral and anterior margins steep. Beak incurved; delthyrium open; foramen may migrate to mesothyrid position in mature specimens. Fold and sulcus distinct, extending from umbones; anterior commissure uniplicate; tongue broad, high, dentate. Costae coarse, low, simple, subangular, from midlength, weak on flanks. Dental plates well developed, high, thin, convergent ventrally; ventral muscle field not deeply impressed. Dorsal median septum short, thin; septalium short, deep, narrow; hinge plates dividing immediately anterior of septalium; crura slender, ventrally curved, tips laterally flattened. *lower Silurian (upper Llandovery)–Lower Devonian (upper Emsian):* cosmopolitan.——Fig. 770,*1a–i*. **L. carens* (Barrande), Lochkovian, Lochkov Limestone, Prague,

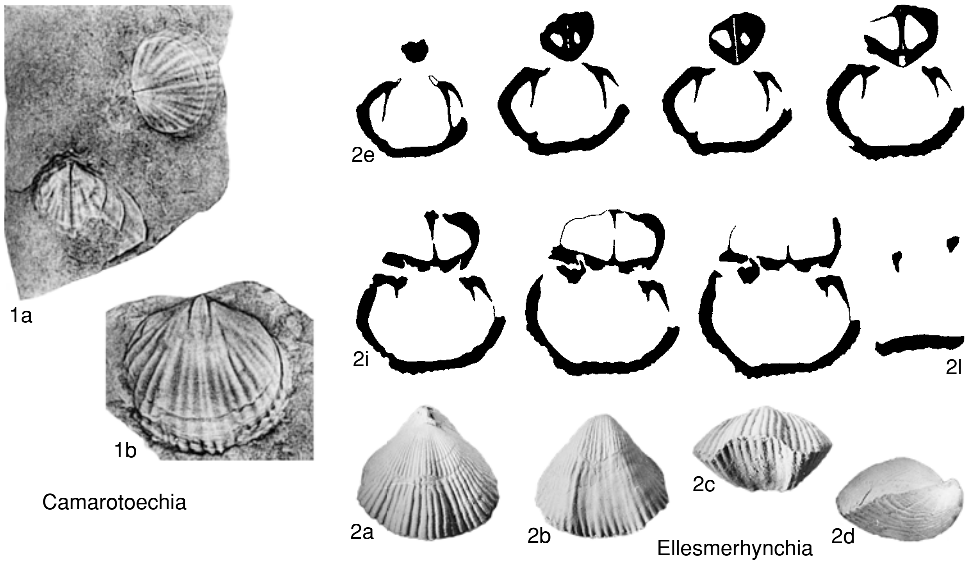

FIG. 769. Camarotoechiidae (p. 1132).

Svaty Jan, Bohemia; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, ×1.75 (new); *f–i,* serial sections 12.35, 12.15, 11.8, 11.6 mm from anterior, ×3.3 (Havlíček, 1961).

Astutorhyncha HAVLÍČEK, 1961, p. 105 [**Rhynchonella proserpina* BARRANDE, 1847, p. 64; OD]. Subcircular to subpentagonal outline; strongly biconvex profile, anteriorly inflated, sides and anterior nearly vertical. Beak incurved. Fold and sulcus strong, extending from umbones; anterior commissure uniplicate; tongue high, subrectangular, serrate. Costae strong, simple, subangular, arising just anterior of umbones, present in sulcus and on fold and flanks. Dental plates short, subvertical; ventral muscle field weakly impressed. Dorsal median septum slender, low; septalium broad, shallow; hinge plates dividing anterior of septalium. *Lower Devonian (Lochkovian–Emsian):* Bohemia, central Asia, China.——FIG. 770,*2a–j*. **A. proserpina* (BARRANDE), upper Emsian, Suchomasty Limestone, Koneprusy, Bohemia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1.5; *f–j,* serial sections 19.4, 19.3, 18.8, 18.7, 18.5 mm from anterior, ×2.5 (Havlíček, 1961).

Family LEIORHYNCHIDAE Stainbrook, 1945

[*nom. transl.* CRICKMAY, 1952b, p. 1, *ex* Leiorhynchinae STAINBROOK, 1945, p. 43]

Camarotoechioidea with dental plates convergent ventrally, and dorsal median septum long and high. Profile strongly biconvex. Shell commonly thick with ventral muscle field deeply impressed. *lower Silurian (Llandovery)–Lower Carboniferous (Tournaisian).*

Subfamily LEIORHYNCHINAE Stainbrook, 1945

[Leiorhynchinae STAINBROOK, 1945, p. 43]

Leiorhynchidae with smooth umbones. *Lower Devonian (Lochkovian)–Lower Carboniferous (Tournaisian).*

Leiorhynchus HALL, 1860a, p. 75 [**Orthis quadracostata* VANUXEM, 1842, p. 168; SD OEHLERT, 1887a, p. 1308] [=*Liorhynchus* OEHLERT, 1887a, p. 1308, obj., *non* RUDOLPHI, 1801; *Nudirostra* COOPER & MUIR-WOOD, 1951, p. 195, obj.]. Subcircular to transversely ovate outline and biconvex profile. Beak incurved; foramen small, permesothyrid. Fold and sulcus low; arising at midlength; anterior commissure gently uniplicate. Costae low, simple, most pronounced on fold and sulcus, weak on flanks; umbones smooth. Dental plates strongly convergent ventrally and almost meeting; occasionally forming spondylium duplex; ventral muscle field often in thick callus or deeply impressed. Dorsal median septum long, high; supporting short septalium; hinge plates divided anteriorly; dorsal muscle field narrow, usually with marginal thickening; crura long, thin, slightly curved ventrally, with narrow trough opening ventrally. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* North America, eastern Europe, Urals, Altai, Siberia,

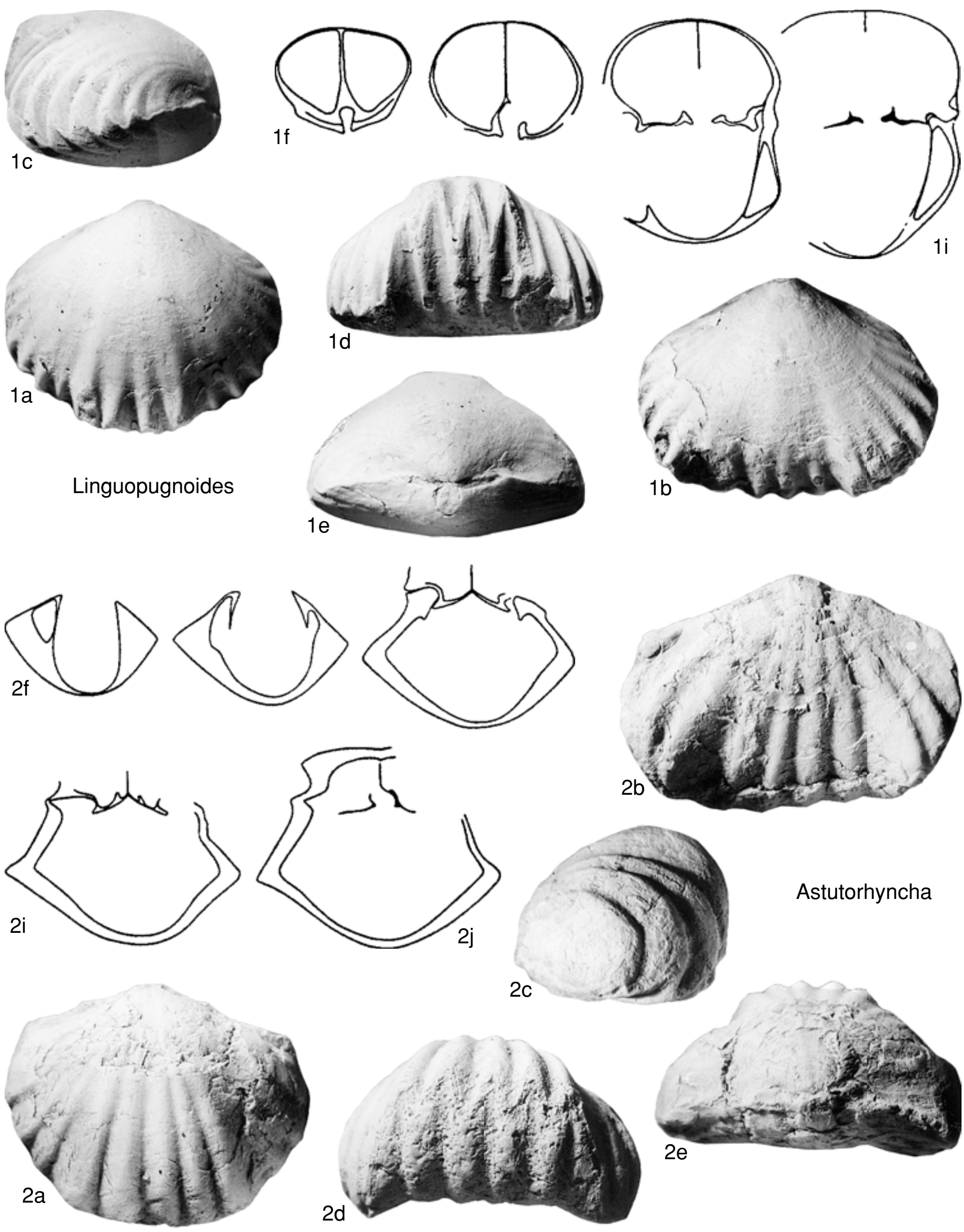

FIG. 770. Camarotoechiidae (p. 1132–1133).

China.——FIG. 771,*1a–o*. **L. quadracostata* (VANUXEM), uppermost Givetian, Sherburne Flagstone, Sheldrake, New York, USA; *a–e,* dorsal, ventral, posterior, anterior, and lateral views of internal mold, Cornell specimen no. 40605, listed by SARTENAER, 1961f, p. 969, ×1.5 (new); *f–o,* serial sections 0.45, 0.8, 0.85, 0.95, 1.0, 1.05, 1.1, 1.5, 1.8, 3.03 mm from posterior, ×3.2 (Sartenaer, 1961f).

Caryorhynchus CRICKMAY, 1952b, p. 1 [**Leiorhynchus carya* CRICKMAY, 1952a, p. 599; OD]. Subcircular outline and strongly dorsibiconvex to globular profile. Beak incurved; foramen small, semicircular, epithyridid. Fold and sulcus moderately developed, arising at umbones; anterior commissure broad; tongue moderately high, trapezoid, serrated. Fold with 2 pairs of costae separated by a sinus; sulcus with 3 costae, the median one wider than others;

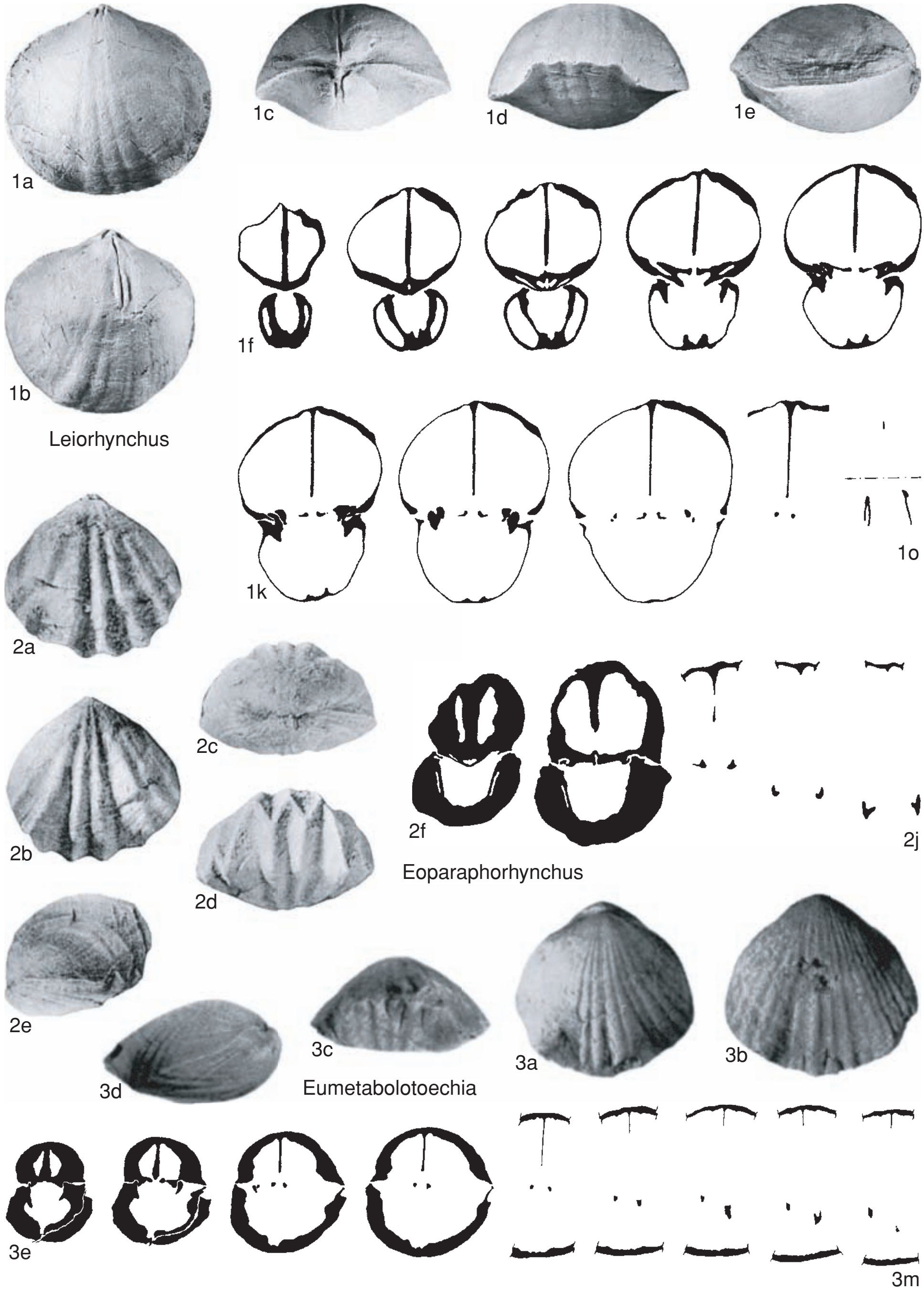

FIG. 771. Leiorhynchidae (p. 1133–1136).

flanks almost smooth. Dental plates short, converging ventrally, usually obscured by thick callus; ventral muscle field narrow, well impressed. Hinge plates short, divided; dorsal median septum high, long; dorsal muscle field narrow, well impressed; crura closely set, ventrally curved, laterally flattened distally. *Upper Devonian (middle Frasnian–upper Frasnian):* North America, Europe, Morocco.——

FIG. 772,*1a–q*. **C. carya* (CRICKMAY), middle Frasnian, Perdix Formation, Alberta, Canada; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1.3; *e–h,* hypotype, dorsal, posterior, anterior, and lateral views, ×1; *i,* enlargement of posterior, ×3; *j–m,* hypotype, serial sections, ×2.2 (Crickmay, 1952b); *n–q,* serial sections 1.0, 1.5, 2.1, 4.2 mm from posterior, ×1.5 (McLaren, 1962).

Eliorhynchus SARTENAER, 1987c, p. 142 [**Rhynchonella castanea* MEEK, 1868, p. 93; OD]. Subcircular to longitudinally ovate outline and strongly dorsibiconvex to globular profile. Ventral beak erect to incurved, sometimes pierced by small foramen; ventral beak overlapped by dorsal beak in holotype. Fold and sulcus low, most evident anteriorly; anterior commissure uniplicate; tongue high in mature shells, weakly serrate. Costae low, from midlength, with some bifurcation, mostly confined to fold and sulcus but may be weakly developed on flanks. Dental plates converging ventrally to meet at valve floor; ventral muscle field long, narrow, pointed posteriorly, rounded anteriorly. Dorsal median septum long, high; septalium very short; hinge plates short, breaking up early; dorsal muscle field narrow, well impressed, extending to midlength; crura long, ventrally curved, with distinct distal trough opening dorsally. *Middle Devonian (Givetian):* western North America.——FIG. 773,*1a–l*. **E. castanea* (MEEK), lower Givetian, Hare Indian Formation, Northwest Territories, Canada; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views [only specimen figured by MEEK], Carnwath River [given as Lockhart River by MEEK], USNM 5890, ×1.5 (Johnson, 1974); *f–l,* hypotype, serial sections 1.6, 2.1, 2.25, 2.5, 3.1, 4.4, 6.7 mm from posterior, Anderson River, ×2 (McLaren, 1962).

Eoparaphorhynchus SARTENAER, 1961c, p. 2 [**E. maclareni;* OD]. Subtriangular to ovate outline and dorsibiconvex profile. Beak suberect; foramen small, circular. Fold and sulcus strong, from beaks; anterior commissure uniplicate; tongue high, serrate. Costae angular, strong on fold and sulcus, weaker on flanks. Surface with fine radial striae. Dental plates short, close to walls, convergent ventrally; ventral muscle field impressed, flabellate, to midlength, with stout myophragm. Septalium short, narrow, deep; hinge plates divided, horizontal; dorsal median septum high, stout, extending to one-third valve length; dorsal muscle field transversely ovate, divided by septum; crura short, curved ventrally, V-shaped cross section open dorsally. *Upper Devonian (lower Famennian):* western North America, Europe, Kazakhstan, Pamir, China.——FIG. 771,*2a–j*. **E. maclareni,* Northwest Territories, Root River, Canada; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–j,* serial sections 1.65, 2.2, 3.6, 5.2, 5.8 mm from posterior, ×2 (Sartenaer, 1961c).

Eumetabolotoechia SARTENAER, 1975b, p. 2 [**Rhynchonella(?) laura* BILLINGS, 1860, p. 273; OD]. Subcircular to longitudinally ovate outline and biconvex profile; sides and anterior not precipitous. Beak incurved. Fold and sulcus low, arising at umbones; anterior commissure gently uniplicate; tongue low. Costae weak, increasing by bifurcation and intercalation, on flanks as well as fold and sulcus. Dental plates short, converging ventrally, obscured by thick callus; ventral muscle field narrow, well impressed. Dorsal median septum long, high; septalium short; hinge plates short, breaking up early; dorsal muscle field narrow, well impressed; crura long, ventrally curved, tip V-shaped in cross section, open dorsally. *Middle Devonian (Givetian):* eastern North America, Libya.——FIG. 771,*3a–m*. **E. laura* (BILLINGS), middle Givetian, Hamilton Group, Bosanquet, Ontario, Canada; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–m,* serial sections 0.8, 1.4, 1.8, 1.9, 3.4, 4.4, 4.7, 4.9, 4.95 mm from posterior, ×2 (Sartenaer, 1975b).

Evanescirostrum SARTENAER, 1965b, p. 8 [**Nudirostra gibbosa seversoni* MCLAREN, 1954, p. 180; OD]. Subpentagonal to transversely ovate outline and dorsibiconvex profile. Beak suberect, pierced by small foramen. Fold and sulcus strong, arising near umbones; anterior commissure uniplicate; tongue high, broad, serrate. Costae strong, angular, simple, weak on flanks. Dental plates short, near walls, convergent ventrally; ventral muscle field well impressed. Septalium short, well developed; hinge plates divided; dorsal median septum long, high; crura long, ventrally curved, tip with trough-shaped cross section open dorsally. *Upper Devonian (Famennian):* western North America, Europe, Afghanistan, Iran.——FIG. 772,*3a–l*. **E. seversoni* (MCLAREN), lower Famennian, Palliser Formation, Alberta, Banff Park, western Canada; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f–l,* serial sections 1.4, 1.6, 2.05, 2.3, 2.7, 3.75, 4.1 mm from posterior, ×2.3 (Sartenaer, 1969).

Hadrotatorhynchus SARTENAER, 1986a, p. 138 [**Leiorhynchus Halli* FLAMAND, 1911, p. 820; OD]. Subcircular to transversely ovate outline and biconvex profile; sides not steep. Beak erect to incurved. Fold and sulcus distinct, arising at umbones; anterior commissure uniplicate; tongue low, broad. Costae low, simple, weak on fold and in sulcus, very weak on flanks. Dental plates very short; ventral muscle field deeply impressed. Dorsal median septum high, thin, extending to midlength; hinge plates short; septalium very short to absent, crural bases delicate; crura closely set, fine, laterally compressed at tips. *Middle Devonian (upper Givetian)–Upper Devonian (lower Frasnian):* northern Africa, Poland.——FIG. 773,*3a–h*. **H. halli* (FLAMAND), uppermost Givetian, Mouydir, Algeria; *a–b,* lectotype, dorsal and anterior views, ×1 (Flamand, 1911); *c–h,* serial sections 1.3, 1.5, 1.9, 2.9, 4.4, 5.1 mm from posterior, ×1.4 (Drot, 1964b).——FIG. 773,*3i–q*. *L. laskowaesis* SARTENAER & RACKI, uppermost Givetian, Szydlwek Beds, Holy Cross Mountains, Kostomloty, Poland; serial sections 0.95, 1.05, 1.75, 2.0, 2.1, 2.6, 3.05, 3.2, 4.1 mm from posterior, ×1.7 (Sartenaer & Racki, 1992).

Havlicekella AMSDEN, 1985, p. 6 [**H. miticonvexa;* OD]. Subcircular to subpentagonal outline and dorsibiconvex profile. Beak erect. Fold and sulcus

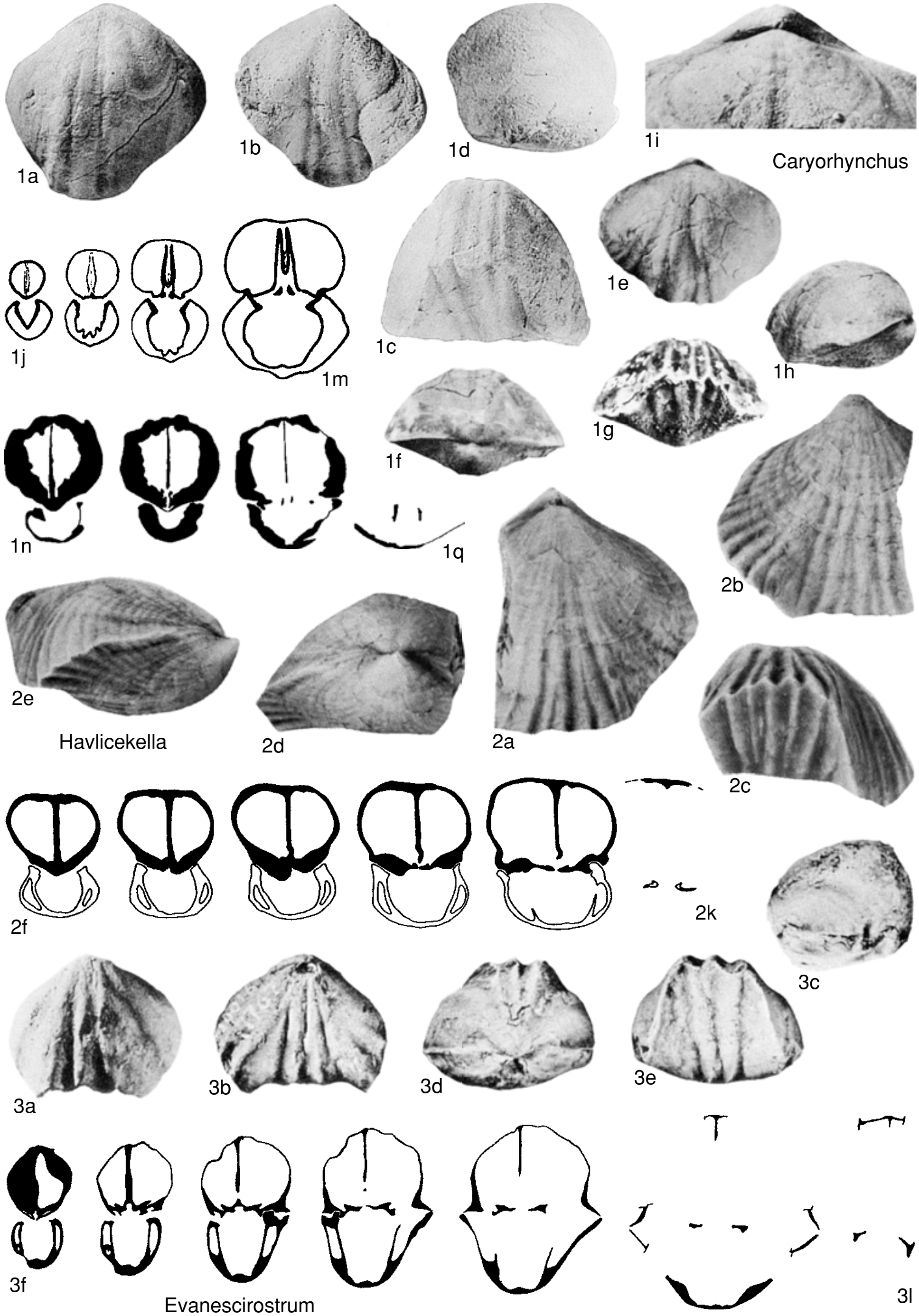

FIG. 772. Leiorhynchidae (p. 1134–1139).

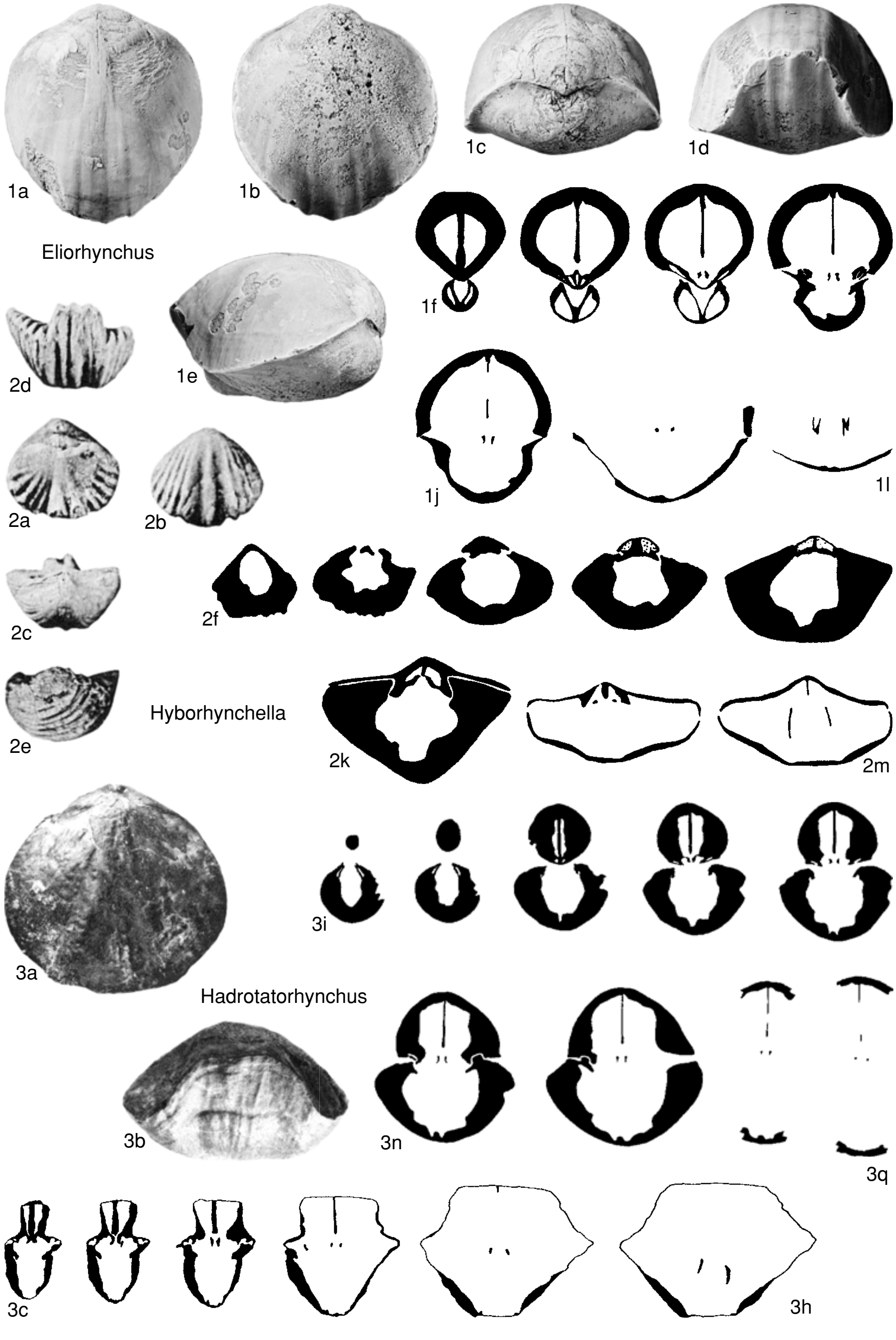

FIG. 773. Leiorhynchidae (p. 1136–1139).

from midlength; anterior commissure uniplicate, broad; tongue high, rounded in large specimens. Costae low, arising near beaks, bifurcating on fold, intercalating in sulcus; distinct posteriorly and on flanks. Dental plates short, converging ventrally; muscle field not strongly impressed. Dorsal median septum long, high; septalium short to absent; hinge plates dividing early. *Lower Devonian (Pragian):* USA.——FIG. 772,*2a–k*. **H. miticonvexa,* Turkey Creek Limestone, Turkey Creek, Oklahoma; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f–k,* serial sections 1.2, 1.3, 1.4, 1.5, 1.8, 2.2 mm from posterior, ×4.5 (Amsden, 1985).

Hyborhynchella COOPER, 1955, p. 59 [**H. bransoni;* OD]. Small size with subcircular outline and planoconvex profile. Beak incurved; delthyrium plugged by dorsal beak; foramen small, posterior of beak. Fold and sulcus strong, narrow, extending from umbones. Costae rounded, particularly large on fold and in sulcus, arising at umbones; smaller costae on flanks. Dental plates absent; ventral muscle field narrow, deeply impressed. Dorsal median septum thick, low, long, extending to midlength; hinge plates short, flattened posterior of wide septalium, then dividing anterior of septalium; crura long, slender, laterally compressed distally. *Upper Devonian (Frasnian):* western North America.——FIG. 773,*2a–m*. **H. bransoni,* upper Frasnian, Sly Gap Formation, Alamogordo, Indian Wells Canyon, New Mexico, USA; *a–c,* holotype, dorsal, ventral, posterior views; *d–e,* paratype, anterior and lateral views, ×2; *f–k,* paratype, serial sections, sections 0.35, 0.5, 0.65, 0.8, 1.0, 1.15 from posterior, ×3; *l–m,* sections of another paratype 0.16 mm apart, showing crura, approximately ×3 (Cooper, 1955).

Iloerhynchus BALINSKI, 1995a, p. 47 [**I. mesoplicatus;* OD]. Subcircular outline and dorsibiconvex profile; lateral and anterior slopes gentle. Beak incurved. Fold and sulcus strong, arising at umbones; tongue of moderate strength, trapezoid, only rarely becoming vertical. Costae few, subangular, most prominent anteriorly; strong on fold and sulcus with generally 3 on fold and 2 in sulcus, weak or absent on flanks; anterior commissure typically triserrate. Dental plates absent or obscured by callus; ventral muscle field deeply impressed; teeth supported by short oblique ridges. Dorsal median septum thin, low, extending to one-third valve length; hinge plates and septalium very short; crura strongly curved ventrally. *Upper Devonian (lower Famennian):* Poland.——FIG. 774,*1a–l*. **I. mesoplicatus, Palmatolepis triangularis* Zone, Debnik, southern Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×2; *f–l,* serial sections 1.1, 1.5, 1.8, 2.0, 2.3, 2.5, 2.7 mm from posterior, ×3.3 (Balinski, 1995a).

Ilopsyrhynchus SARTENAER, 1988, p. 59 [**I. iteinus;* OD]. Large with subcircular outline and dorsibiconvex profile; with sides and anterior not precipitous. Beak erect to incurved; foramen small, semicircular, mesothyrid. Fold and sulcus weak, from midlength; anterior commissure uniplicate; tongue low, broad, angular, trapezoid. Costae weak, restricted to fold and sulcus, arising at about midlength. Dental plates very short, meeting ventrally in thick callus to form short spondylium; ventral muscle field long, narrow, well impressed. Dorsal muscle field narrow, in thick callus; septalium long, narrow; hinge plates short, breaking up early; crura long, closely set, slightly curved ventrally. *Middle Devonian (lower Givetian):* western North America.——FIG. 774,*2a–m*. **I. iteinus,* Denay Limestone, Roberts Mountains, Willow Creek, Nevada, USA; *a–e,* holotype, dorsal, ventral, posterior, lateral, anterior views, ×1 (Johnson, 1974); *f–m,* serial sections 2.75, 3.05, 3.25, 3.45, 4.05, 4.35, 5.35, 8.25 mm from posterior, ×2.5 (Sartenaer, 1988).

Katuniella KULKOV in SAVAGE, herein, p. 1615, *nom. nov. pro Katunia* KULKOV, 1963, p. 54, *non* ROMANENKO & ROMANENKO, 1962, p. 25, Trilobita [**Katunia subtrigonata* KULKOV, 1963, p. 54*;* OD]. Subtrigonal outline and dorsibiconvex profile. Beak suberect to erect; foramen small. Fold and sulcus wide; anterior commissure uniplicate; tongue trapezoid in mature specimens. Costae weak, subangular, arising at midlength; Dental plates absent or obscured by callus. Dorsal median septum low, short, supporting very short septalium; crural bases triangular. *Lower Devonian (Lochkovian):* Gorno-Altai, China, North America.——FIG. 774,*3a–m*. **K. subtrigonata,* Solovikha Limestone, Gorno-Altai; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e–i,* topotype, serial sections of posterior, ×4 (Kulkov, 1963); *j–m,* topotype, new serial sections of dorsal valve showing median septum, intervals unknown, approximately ×4 (new; courtesy of N. P. Kulkov).

Leptocaryorhynchus SARTENAER, 1970a, p. 14 [*"*Camarotoechia" jamensis* BRICE, 1967, p. 100; OD]. Subpentagonal outline and dorsibiconvex profile. Beak prominent, erect to incurved; foramen small, circular. Fold and sulcus pronounced anteriorly; tongue high, trapezoid, serrate. Costae strong, rounded, extending from umbones. Dental plates short, partly obscured by thick callus that also accentuates ventral muscle impression. Dorsal median septum thick, low; septalium partly overhung by hinge plates and obscured by callus; crura curved ventrally, tips with V-shaped cross section, open dorsomedially. *Upper Devonian (Famennian):* Afghanistan.——FIG. 775,*1a–m*. **L. jamensis* (BRICE), Ghor, Ghouk Pass; *a–e,* holotype, dorsal, ventral, posterior, lateral, and anterior views, ×1; *f–m,* serial sections 1.4, 1.6, 1.7, 1.9, 2.3, 2.5, 2.6, 3.6 from posterior, ×3 (Brice, 1967).

Mononusphaericorhynchus SARTENAER, 1996, p. 247 [**Leiorhynchus (Leiorhynchus) sartenaeri* JOHNSON, 1974, p. 56; OD]. Small to medium size for subfamily; subcircular to longitudinally ovate outline and strongly dorsibiconvex to globular profile. Ventral beak erect to incurved, pierced by small foramen. Fold and sulcus low, most evident anteriorly; anterior commissure uniplicate; tongue high in

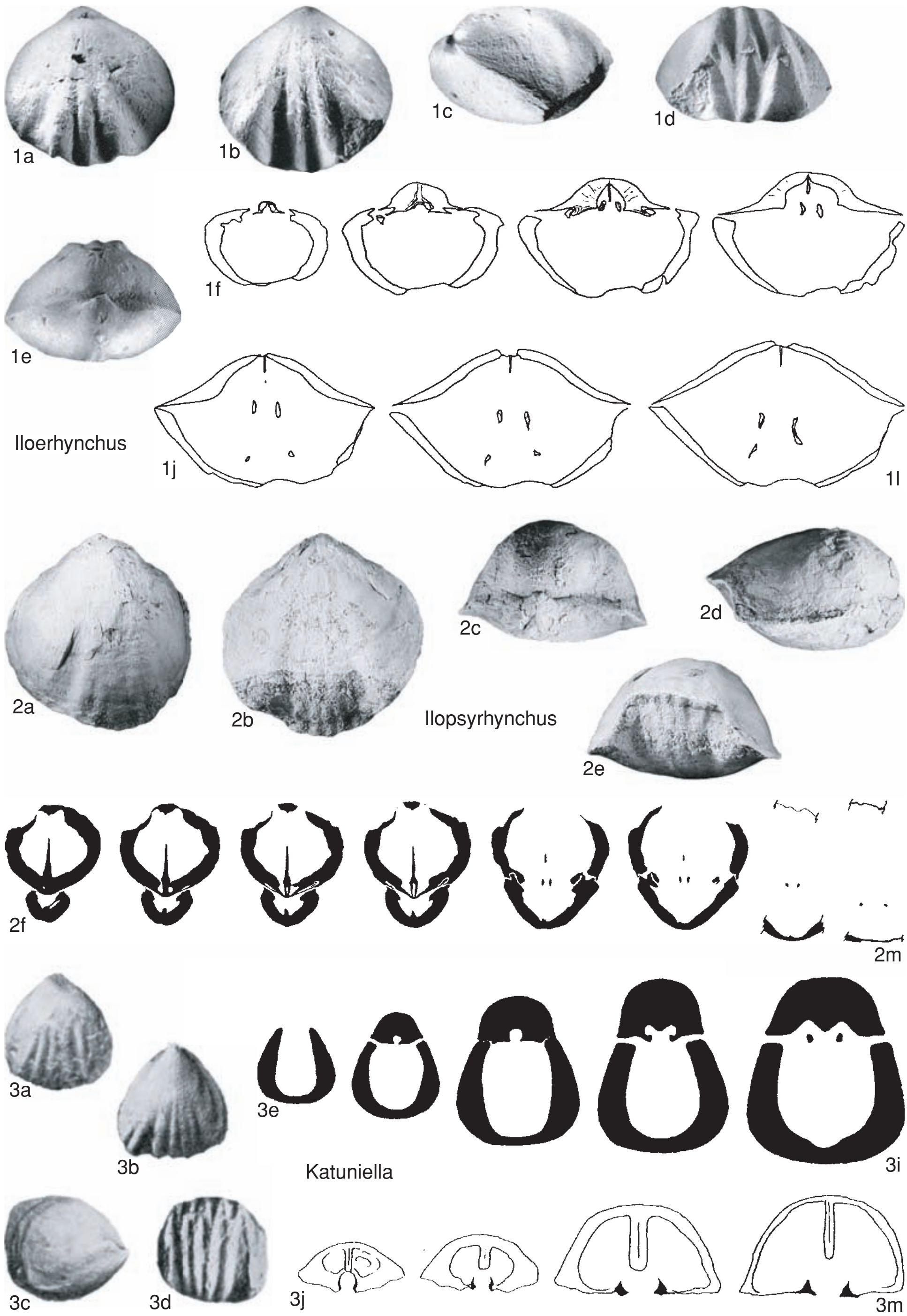

FIG. 774. Leiorhynchidae (p. 1139).

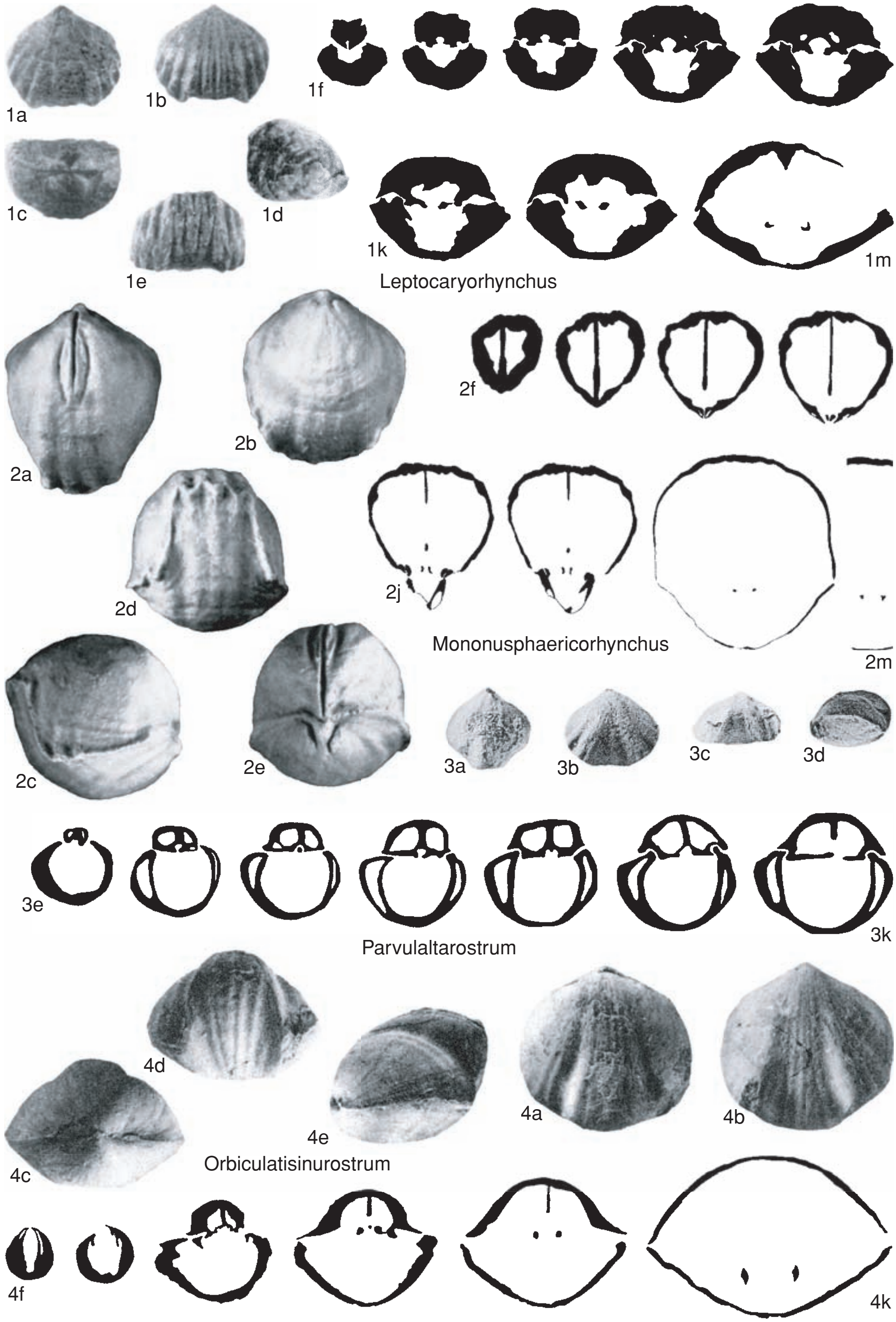

FIG. 775. Leiorhynchidae (p. 1139–1142).

mature shells, weakly serrate. Costae low, from midlength, mostly confined to fold and sulcus but may be weakly developed on flanks. Dental plates short, converge ventrally to meet at valve floor; teeth small, stout; ventral muscle field weakly impressed. Dorsal median septum thin, extending almost to valve midlength; hinge plates and septalium very short or not developed; dorsal muscle field narrow, well-impressed, extending to midlength, spindle shaped; crura long, almost touching, ventrally curved. *Middle Devonian (Givetian):* western North America.——FIG. 775,*2a–m.* **M. sartenaeri* (JOHNSON), lower Givetian, Woodpecker Limestone, Sulphur Spring Range, Nevada, USA; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1.5 (Johnson, 1974); *f–m,* serial sections 0.95, 1.2, 1.7, 2.0, 2.35, 2.65, 5.6, 6.25 mm from posterior of topotype, ×1.7 (Sartenaer, 1996).

Orbiculatisinurostrum SARTENAER, 1984b, p. 2 [**Leiorhynchus laevis* GURICH, 1903, p. 150; OD]. Subcircular to subpentagonal outline and biconvex profile; lateral and anterior slopes gentle. Beak erect to incurved. Fold and sulcus strong, extending from umbones; anterior commissure uniplicate; tongue wide, trapezoid, high; Costae low, bifurcate and intercalate, arising at umbones, weak on flanks. Dental plates very short, close to walls, ventrally convergent. Dorsal median septum thin, long; septalium short; hinge plates short, divided, breaking up early; crura ventrally curved. *Upper Devonian (upper Frasnian):* Poland.——FIG. 775,*4a–k.* **O. laevis* (GURICH), uppermost Frasnian, Cracow, near Debnik, southern Poland; *a–e,* neotype, dorsal, ventral, posterior, anterior, and lateral views, ×1.5; *f–k,* serial sections 0.3, 0.4, 1.0, 1.4, 1.7, 2.8 mm from posterior, ×1.5 (Balinski, 1979).

Parvulaltarostrum SARTENAER, 1979b, p. 2 [**P. veeversi;* OD]. Small with subcircular to transversely ovate outline and equibiconvex, lenticular profile. Beak suberect; delthyrium narrow, open. Fold and sulcus strong, arising just anterior of umbones; anterior commissure uniplicate, tongue high, rounded, tapering apically. Costae few, low, very weak on flanks. Dental plates long, close to walls, concave medially. Hinge plates divided; dorsal median septum long; septalium short. *Upper Devonian (Frasnian):* northwestern Australia.——FIG. 775,*3a–k.* **P. veeversi,* Napier Formation, Fitzroy basin, Napier Range, south of Van Emmerick Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k,* serial sections 1.1, 1.3, 1.4, 1.5, 1.6, 1.8, 2.0 mm from posterior, ×3 (Veevers, 1959a).

Paurorhyncha COOPER, 1942, p. 231 [**Rhynchonella endlichi* MEEK, 1875, p. 46; OD]. Large with subtriangular outline and dorsibiconvex profile; convexoconcave form of large specimens resulting from strong, wide fold and sulcus. Beak small, erect; foramen minute. Fold and sulcus very wide; anterior commissure broad, uniplicate; tongue high, arched. Costae numerous, extending from beaks, with minor bifurcation and intercalation. Dental plates short, thin; ventral muscle field lachrymal, impressed, anteriorly expanded. Dorsal median septum short, high; septalium short, wide; hinge plates short, united by septalium, breaking up early. *Upper Devonian (Famennian):* western North America.——FIG. 776,*1a–b.* **P. endlichi* (MEEK), upper Famennian, Ouray Limestone, Mount Eolus, Colorado, USA; dorsal and ventral views, ×0.6 (Kindle, 1909).——FIG. 776,*1c–h. P. cooperi* STAINBROOK, upper Famennian, Percha Shale, New Mexico, USA; *c–f,* dorsal, ventral, posterior, and lateral views of internal mold, ×0.9 (Cooper, 1942); *g,* interior of conjoined valves, ×2; *h,* transverse section, ×1.3 (Cooper & Dutro, 1982).

Properotundirostrum SARTENAER, 1986b, p. 490 [**Leiorhynchus miriam* JOHNSON, 1971, p. 315; OD]. Subcircular to subpentagonal outline and equibiconvex lenticular profile; gentle lateral and anterior slopes. Beak erect; foramen small, circular. Fold and sulcus low, extending from umbones; anterior commissure uniplicate, broad, low, serrate. Costae simple, arising at umbones, low on fold and sulcus; very weak on flanks. Dental plates thin, short, strongly convergent ventrally to almost meeting; ventral muscle field very faint, flabellate, extending almost to midlength. Dorsal median septum short, thin, high; septalium short; hinge plates divided; dorsal muscle field very faint. *Middle Devonian (Eifelian):* western North America.——FIG. 776,*2a–g.* **P. miriam* (JOHNSON), upper Eifelian, Roberts Mountains, Lone Mountain, Nevada, USA; *a–e,* paratype, dorsal, ventral, posterior, lateral, anterior views, ×1.5; *f,* interior of ventral valve, ×3; *g,* interior of articulated valves, ×4 (Johnson, 1971).

Rossirhynchus GAETANI, 1964, p. 637 [**R. adamantinus;* OD] [=*Septemirostellum* ROBERTS, 1971, p. 132 (type, *Camarotoechia septima* VEEVERS, 1959b, p. 12, OD)]. Subpentagonal outline and dorsibiconvex profile; flanks steeply rounded. Beak incurved. Fold and sulcus moderately strong, from umbones; anterior commissure uniplicate, broad, rounded, denticulate. Costae strong, angular, simple, present on fold, sulcus, flanks. Dental plates moderately long, ventrally convergent, close to walls; ventral muscle field narrow, well impressed. Dorsal median septum long, high, thick; septalium deep, long, with cover; hinge plates united; dorsal muscle field narrow, well impressed; crura long, dorsally grooved, ventrally curved, with tips laterally compressed. *Lower Carboniferous (Tournaisian):* Iran, Australia, Argentina, Chile.——FIG. 776,*3a–k.* **R. adamantinus,* Geirud Formation, central Elburz, Zaigun Valley, Iran; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–k,* serial sections 2.1, 2.4, 3.05, 3.55, 5.35, 5.55 mm from posterior, ×1.5 (Gaetani, 1964).

Ryocarhynchus SARTENAER, 1984b, p. 7 [**Camarophoria tumida* KAYSER, 1872, p. 695; OD]. Subcircular outline and strongly dorsibiconvex to globular profile. Beak incurved; foramen small, semicircular, epithyrid. Fold and sulcus moderate to strong, arising at umbones; anterior commissure broad; tongue moderately high, trapezoid. Fold

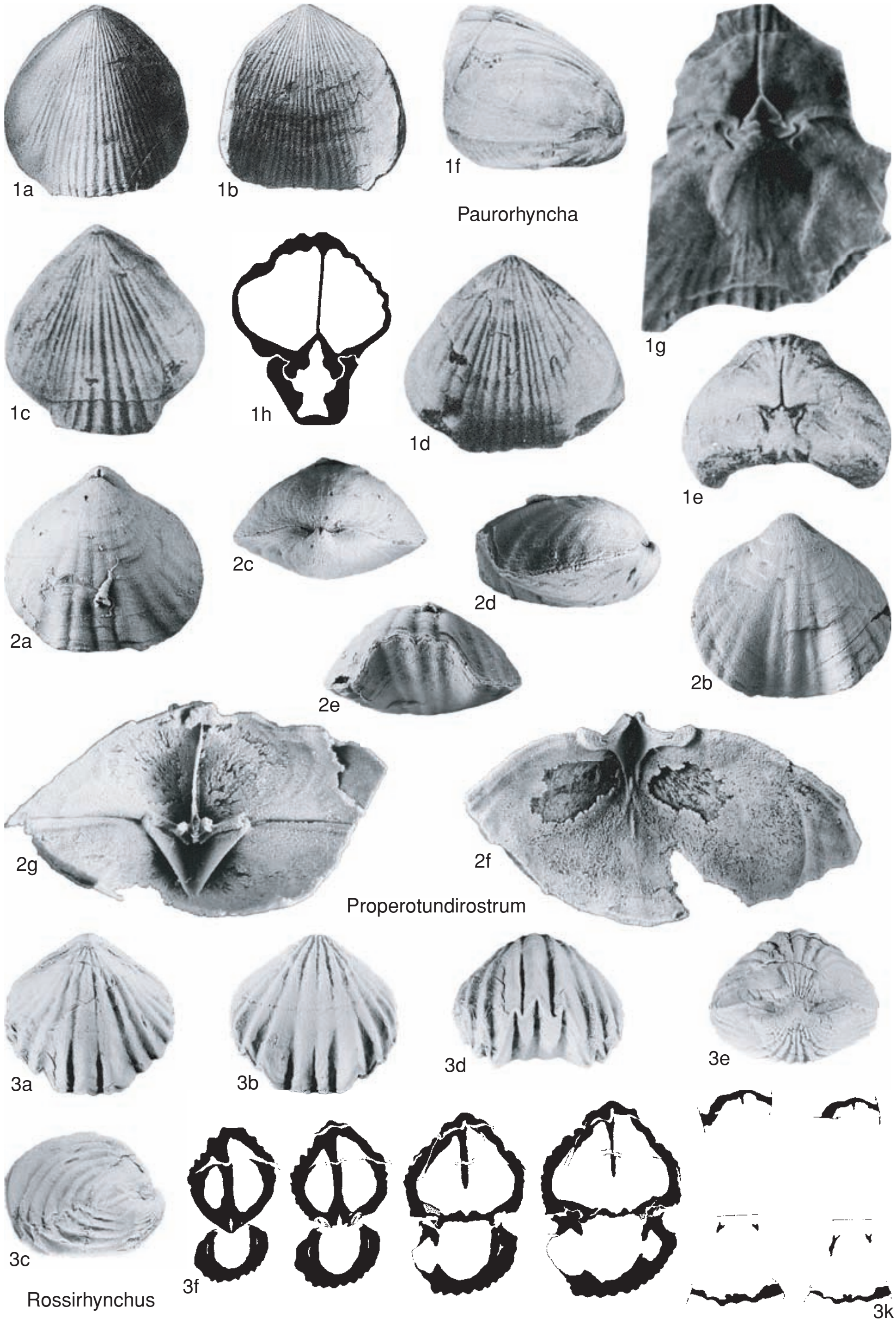

FIG. 776. Leiorhynchidae (p. 1142).

typically with pair of wide costae separated by sinus; sulcus with single costa; flanks almost smooth. Shell walls very thick. Dental plates absent; ventral muscle field narrow, deeply impressed. Dorsal median septum high, long, very thick posteriorly and along its ventral edge, thin anteriorly; septalium wide, short; hinge plates divided anterior of septalium; dorsal muscle field narrow, divided by low ridge; crura closely set, thin, ventrally curved. *Upper Devonian (upper Frasnian):* Europe, Morocco.——FIG. 777,*1a–j.* **R. tumidus* (KAYSER), "Matagne" Shales, Fragnes, Belgium; *a–d,* paralectotype, dorsal, ventral, anterior, and lateral views, ×1; *e–j,* serial sections 2.0, 2.1, 2.45, 2.6, 2.9, 3.1 mm from posterior, ×1.4 (Sartenaer, 1968b).

Stenoglossariorhynchus SARTENAER, 1970a, p. 6 [**Leiorhynchus awokanak* MCLAREN, 1962, p. 91; OD]. Subcircular to transversely ovate outline and equibiconvex profile. Beak incurved; foramen small, submesothyrid. Fold and sulcus low, from midlength; anterior commissure uniplicate; tongue wide, moderately high, trapezoid, serrate. Umbones smooth. Costae low, narrow, extending from near umbones, on fold, sulcus, flanks. Dental plates short, almost meeting ventrally in thick callus; ventral muscle field narrow. Dorsal median septum long, high, thick; septalium short, narrow; hinge plates divided immediately anterior of septalium; dorsal muscle field narrow; crura long, deep, ventrally curved, tips laterally compressed. *Middle Devonian (Givetian):* western Canada.——FIG. 777,*2a–m.* **S. awokanak* (MCLAREN), lower Givetian, Pine Point Formation, Great Slave Lake, Pine Point; *a–e,* holotype, dorsal, ventral, posterior, lateral, and anterior views, ×1; *f–m,* serial sections 2.0, 2.4, 3.0, 3.4, 3.7, 4.2, 5.3, 5.6 mm from posterior, ×2 (McLaren, 1962).

Striatorhynchus PUSHKIN, 1986, p. 91 [**S. komarovichensis;* OD]. Subpentagonal outline and dorsibiconvex profile. Beak small, erect to incurved. Fold and sulcus weak except at anterior margin; anterior commissure uniplicate; tongue wide, high, serrate. Costae coarse, rounded, weak, restricted to anterior margin. Outer layer of shell bearing fine radial striae in which are dotlike exopunctae. Dental plates short, vertical. Dorsal median septum long, high; septalium long, deep; hinge plates horizontal, divided anterior of septalium. *Upper Devonian (Famennian):* Belorussia.——FIG. 777,*3a–k.* **S. komarovichensis,* Zadonsk Horizon, Gomelsk; *a–e,* holotype, dorsal, ventral, lateral, posterior, anterior views, ×1; *f,* enlargement of surface showing striae, exopunctae, ×9; *g–k,* serial sections 0.8, 1.5, 1.7, 2.1, 2.4 mm from posterior, ×2 (Pushkin, 1986).

Tenuisinurostrum SARTENAER, 1967, p. 2 [**Camarophoria crenulata* GOSSELET, 1877b, p. 316; OD]. Transversely ovate outline; moderately biconvex profile. Beak erect to incurved; foramen small, mesothyrid. Fold and sulcus moderate; anterior commissure uniplicate, tongue rounded to rectimarginate. Costae few, weak; flanks almost smooth. Dental plates absent; ventral muscle field well impressed. Hinge plates divided anterior of short septalium; dorsal median septum short and thin; crura laterally compressed; closely set. *Upper Devonian (lower Famennian):* Europe, northern Africa.——FIG. 778,*1a–n.* **T. crenulatum* (GOSSELET), Senzeilles section, upper *Palmatolepis triangularis* Zone, railway cutting northwest of Senzeilles tunnel, Belgium; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, ×1; *e–n,* serial sections 0.85, 1.05, 1.15, 1.4, 1.7, 2.1, 3.0, 3.15, 3.35, 3.4 mm from posterior, ×2 (Sartenaer, 1967).

Werneckeella LENZ, 1971, p. 844 [**W. hartensis;* OD] [=*Irgislella* TJAZHEVA, 1972, p. 90 (type, *I. indecora,* OD)]. Subtriangular to subpentagonal outline and dorsibiconvex profile. Beak small, suberect; foramen circular, delthyrium with conjunct deltidial plates. Fold and sulcus pronounced, extending from umbones; anterior commissure uniplicate; tongue high, broad, dentate. Costae moderately strong, simple, distinct on fold and in sulcus, weak on flanks. Dental plates thin, concave medially, converging ventrally; ventral muscle field narrow, anteriorly expanded, slightly impressed, reaching about one-third shell length. Dorsal median septum high, about one-third shell length; septalium short, narrow, deep; hinge plates divided; dorsal muscle field elongate oval; crura long, strongly curved ventrally, L-shaped in cross section. *Lower Devonian (Pragian):* North America, Russia (western Urals), Australia, China.——FIG. 777,*4a–l.* **W. hartensis,* Prongs Creek Formation, Yukon, Wernecke Mountains, Canada; *a–c,* holotype, dorsal, ventral, and anterior views, ×1.5; *d,* hypotype, lateral view, ×1.25; *e,* dorsal valve interior, ×2.5; *f,* ventral valve interior, ×1.7; *g–l,* serial sections 0.4, 0.6, 0.75, 0.9, 1.15, 1.2 mm from posterior, approximately ×10 (Lenz, 1971).

Yocrarhynchus SARTENAER, 1995, p. 117 [**Leiorhynchus orientalis* CHEN, 1978a, p. 326; OD]. Subpentagonal to subrounded outline and dorsibiconvex profile. Beak suberect, with small foramen; deltidial plates evident in sections. Fold and sulcus strong, arising near umbones; anterior commissure uniplicate; tongue low to moderate, serrate. Costae strong, rounded to subangular, simple, weak on flanks. Dental plates short, near walls, convergent ventrally, occasionally meeting near valve floor to form low ventral median septum that may continue anteriorly to hinge area as low median ridge; ventral muscle field weakly impressed. Teeth simple, short, thick. Hinge plates short, horizontal; septalium barely developed; dorsal median septum high posteriorly, thinning anteriorly and extending to about one-third valve length, bordered by well-impressed muscle field; crura short, thin, ventrally curved, tip V-shaped in cross section, open dorsally. *Upper Devonian (Frasnian):* China, northeastern Europe.——FIG. 778,*2a–o.* **Y. orientalis* (CHEN), lower Frasnian, Tuqiaozi Formation, Tuqiaozi,

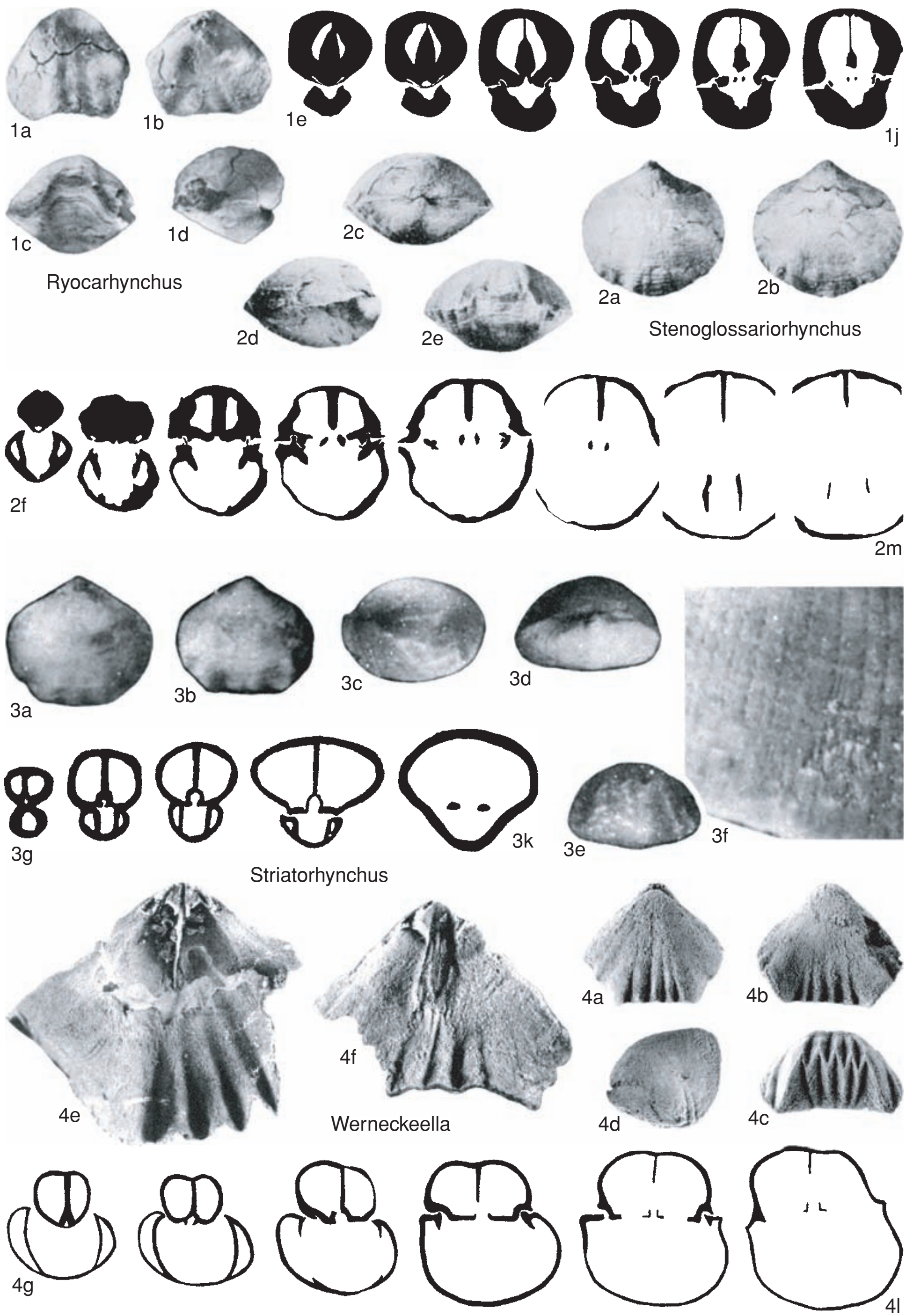

FIG. 777. Leiorhynchidae (p. 1142–1144).

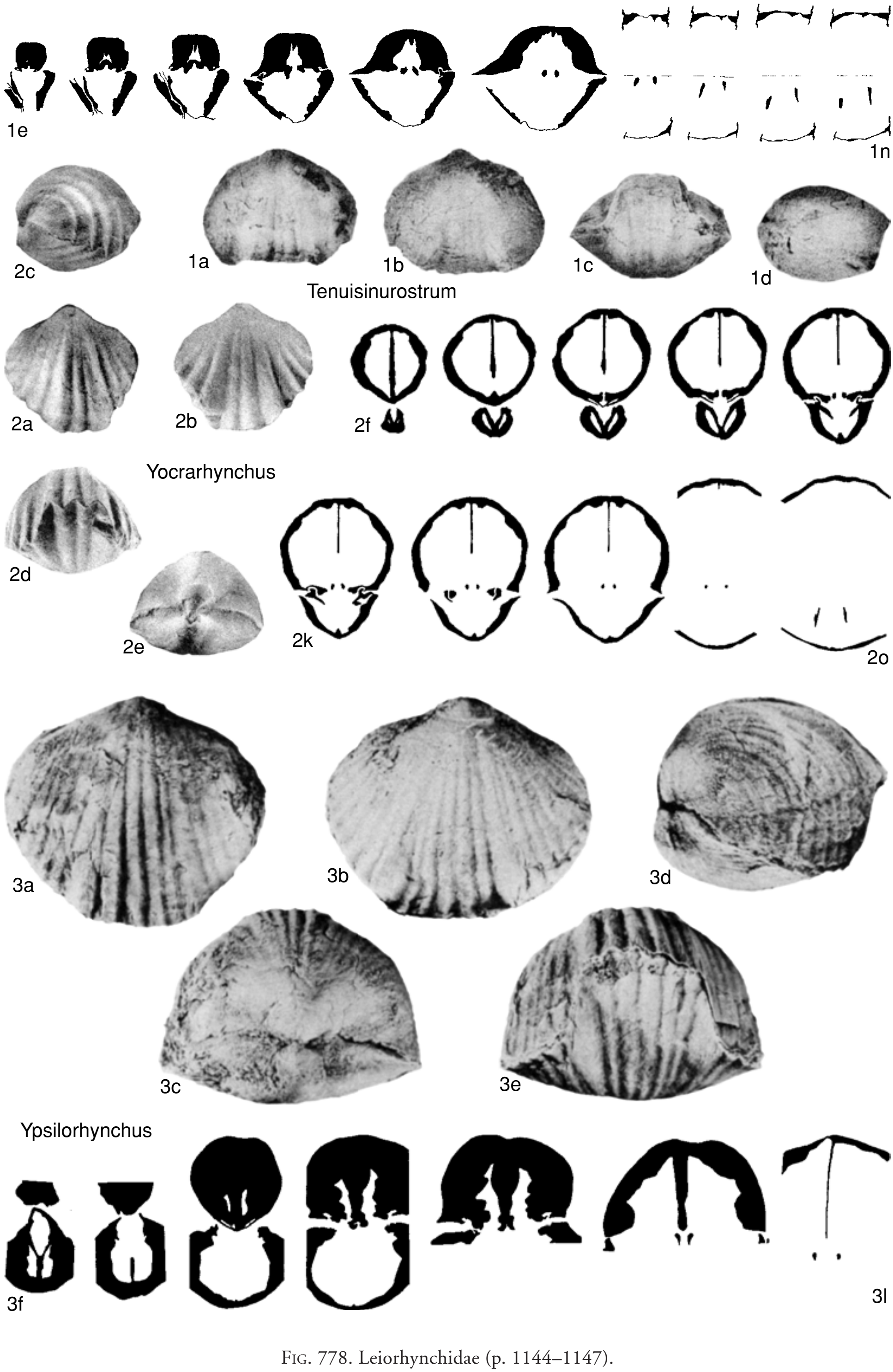

FIG. 778. Leiorhynchidae (p. 1144–1147).

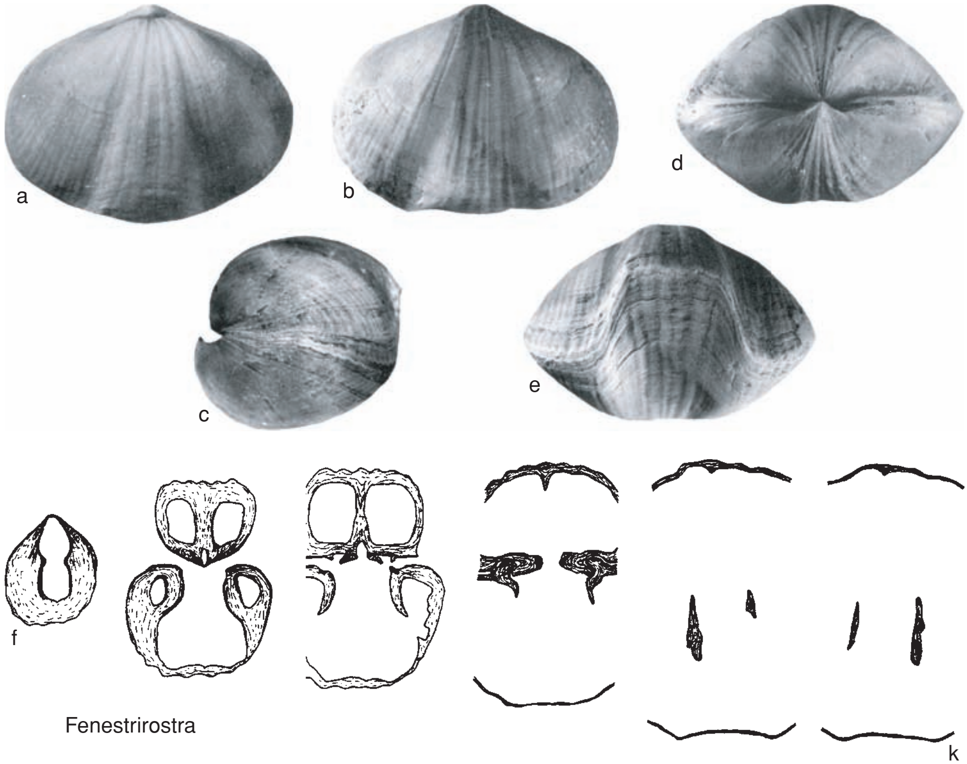

FIG. 779. Leiorhynchidae (p. 1147–1148).

Beichuan County, Sichuan Province, China; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1 (Chen, 1984); *f–o,* serial sections of topotype 1.7, 2.3, 2.55, 2.75, 3.0, 3.2, 3.5, 3.7, 5.8, 7.6 mm from dorsal umbo, ×1.5 (Sartenaer, 1995).

Ypsilorhynchus SARTENAER, 1970a, p. 9 [**Leiorhynchus manetoe* MCLAREN, 1962, p. 79; OD]. Subcircular to transversely ovate outline and dorsibiconvex to galeate profile. Beak incurved. Fold and sulcus broad, low, extending from umbones; anterior commissure uniplicate; tongue broad, low, serrate. Costae moderately strong on fold and sulcus, weak on flanks, with some bifurcation. Dental plates short, meeting ventrally where supported by septum to form spondylium; ventral muscle field elongate, narrow posteriorly, expanding anteriorly, well impressed. Dorsal median septum high, thick posteriorly, thin anteriorly, extending to midlength, well impressed; septalium very short; hinge plates very short, breaking up immediately anterior of septalium; crura close together, long, slender, strongly curved ventrally. *Middle Devonian (Eifelian–Givetian):* western North America, China.——FIG. 778,*3a–l.* **Y. manetoe* (MCLAREN), upper Eifelian, Headless Formation, Northwest Territories, southern Manetoe Range, western Canada; *a–e,* holotype, dorsal, ventral, posterior, lateral, and anterior views, ×1; *f–l,* serial sections 2.4, 2.8, 4.1, 4.8, 5.3, 6.8, 9.9 mm from posterior, ×1.5 (McLaren, 1962).

Subfamily FENESTRIROSTRINAE Savage, 1996

[Fenestrirostrinae SAVAGE, 1996, p. 254]

Early Leiorhynchidae with low costae, dental plates short to absent. *lower Silurian (Llandovery)–Lower Devonian (Pragian).*

Fenestrirostra COOPER, 1955, p. 56 [**Rhynchonella glacialis* BILLINGS, 1862, p. 143; OD]. Transversely ovate outline and subequally biconvex profile. Beak incurved; delthyrium open apically. Fold and sulcus arising at beak; anterior commissure uniplicate; tongue moderately high, trapezoid. Costae rounded, uneven, on fold, in sulcus, and on flanks, increasing by bifurcation and intercalation. Dental plates low, short, ventrally divergent, enclosing small circular umbonal cavities; ventral muscle field deeply impressed. Dorsal median septum low,

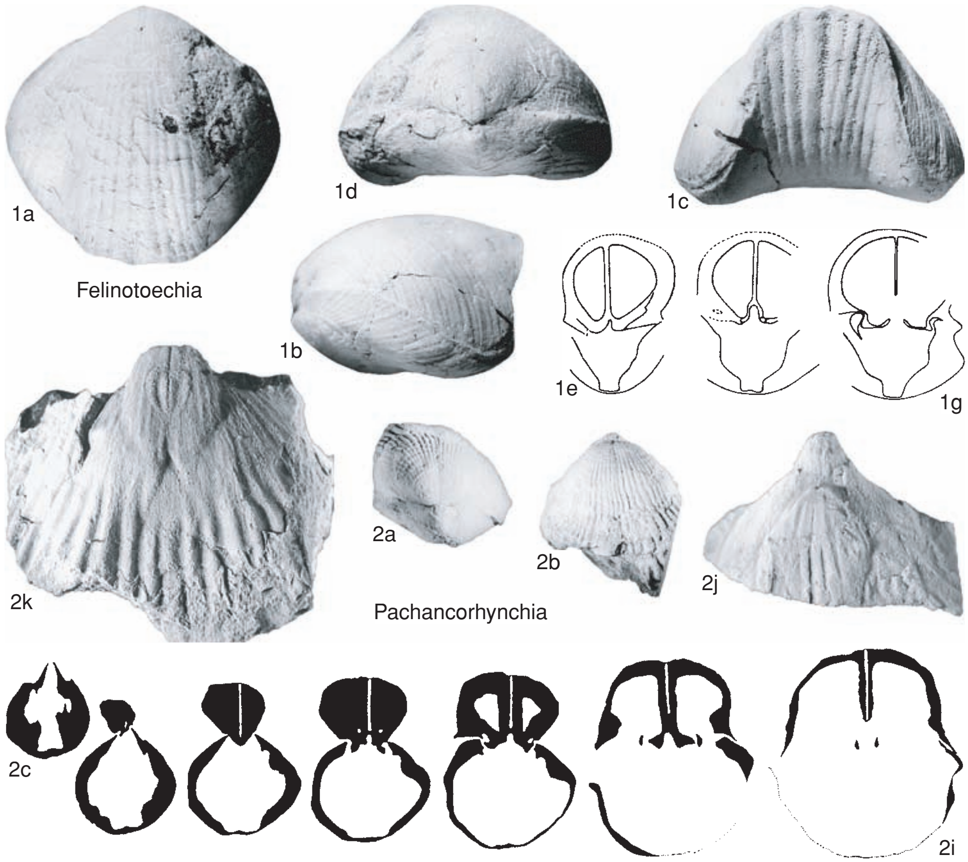

FIG. 780. Leiorhynchidae (p. 1148–1149).

short; septalium small, short; hinge plates divided immediately anterior of septalium; crura long, ventrally curved, tips laterally compressed. *lower Silurian (Llandovery):* eastern Canada (Quebec).——FIG. 779*a–k*. **F. glacialis* (BILLINGS), lower Llandovery, Merrimack Formation, Anticosti Island, Baie Innommée; *a–e,* lectotype, dorsal, ventral, lateral, posterior, and anterior views, ×1.6; *f–k,* serial sections 1.1, 2.0, 2.5, 3.0, 3.3, 3.5 mm from posterior, ×4 (Jin, 1989).

Felinotoechia HAVLÍČEK, 1961, p. 73 [**Atrypa astuta* BARRANDE var. *felina* BARRANDE, 1879b, pl. 18; OD]. Subpentagonal to transversely ovate outline and dorsibiconvex profile; dorsal valve strongly inflated. Beak incurved. Fold and sulcus pronounced from umbones; anterior commissure uniplicate; tongue very high, broad, rounded. Costae low, numerous on fold and in sulcus, weak on flanks and umbones. Dental plates absent or obscured by callus; ventral muscle field narrow, deeply impressed. Dorsal median septum long, high; septalium short, deep, narrow; hinge plates divided immediately anterior of septalium. *upper Silurian (Přídolí)–Lower Devonian (Pragian):* Bohemia.——FIG. 780,*1a–g*. **F. felina* (BARRANDE), Přídolí Limestone, Prague, Slivenec; *a–d,* lectotype, dorsal, lateral, anterior, and posterior views, ×1.7 (new); *e–g,* serial sections at 0.1 mm intervals, ×2.2 (Havlíček, 1961).

Pachancorhynchia BRICE, 1986, p. 121 [**P. leviniensis;* OD]. Subpentagonal to transversely ovate outline and dorsibiconvex profile; dorsal valve strongly inflated. Beak incurved. Fold and sulcus weak; anterior commissure uniplicate; tongue low. Costae numerous; weak on umbones. Dental plates very short, partly obscured by callus; ventral muscle field narrow, deeply impressed. Dorsal median septum long, high, thick; septalium long, deep; hinge plates united, narrow; crura closely set. *Lower Devonian (Lochkovian):* Europe.——FIG. 780,*2a–k*. **P. leviniensis,* Noulette Formation, Artois, Liévin, France; *a–b,* holotype, posterior and dorsal views,

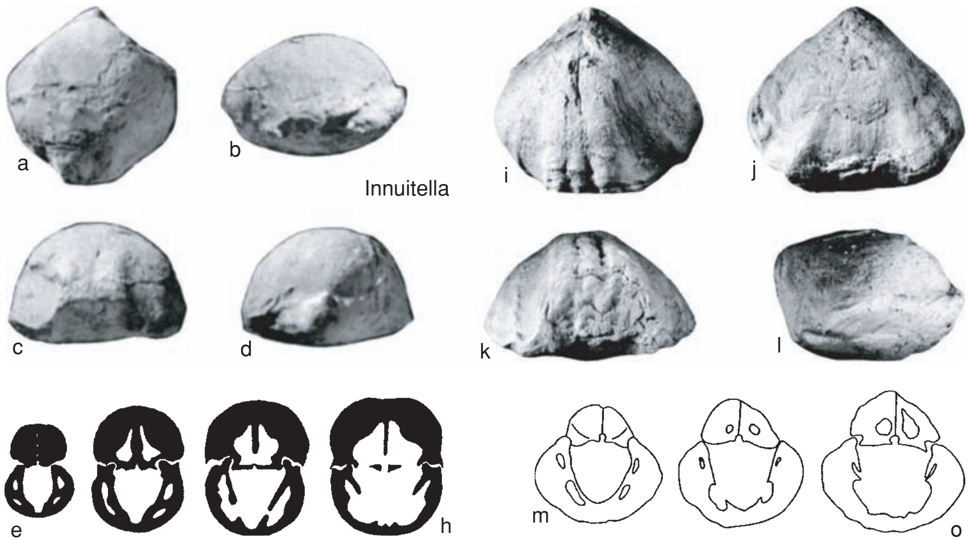

FIG. 781. Leiorhynchidae (p. 1149).

×1; *c–i,* serial sections 0.8, 1.5, 1.9, 2.5, 2.9, 3.9, 5.2 mm from posterior, ×1.7 (Brice, 1986); *j–k,* ventral valve internal molds showing muscle field, ×2 (Barrois, Pruvost, & Dubois, 1922).

Subfamily INNUITELLINAE Crickmay, 1968

[*nom. transl.* SAVAGE, 1996, p. 254, *ex* Innuitellidae CRICKMAY, 1968, p. 5]

Leiorhynchidae with dental plates supported by buttresses; dorsal valve inflated; fold and costae weak. *Lower Devonian (Emsian).*

Innuitella CRICKMAY, 1968, p. 5 [**I. innuitana;* OD]. Subcircular to subpentagonal outline and dorsibiconvex profile. Beak erect; foramen small, submesothyrid. Fold and sulcus weak; anterior commissure uniplicate; tongue low, weakly serrate. Costae low on fold and sulcus; weak to absent on flanks. Dental plates almost meeting ventrally, having lateral buttresses across umbonal cavities; ventral muscle field very narrow. Dorsal median septum long, high; septalium short; hinge plates united past hinge line; crura long, ventrally curved, triangular section. *Lower Devonian (Emsian):* western North America.——FIG. 781*a–h.* **I. innuitana,* upper Emsian, Inuvik, Arctic Canada; *a–d,* holotype, dorsal, lateral, anterior, and posterior views, ×1; *e–h,* paratype, serial sections across posterior, ×1.5 (Crickmay, 1968).——FIG. 781*i–o. I.* aff. *I. innuitana,* upper Emsian, McColley Canyon Formation, Lone Mountain, Nevada, USA; *i–l,* dorsal, ventral, anterior, and lateral views, ×1.5; *m–o,* serial sections 9.2, 9.0, 8.6 mm from anterior, ×0.7 (Johnson, 1973a).

Subfamily GIGANTORHYNCHINAE Savage, 1996

[Gigantorhynchinae SAVAGE, 1996, p. 254]

Large Leiorhynchidae, smooth apart from low fold and sulcus, often with fine striae; thick hinge plates divided or undivided; dental plates and septalium short or absent. *Middle Devonian (Givetian)–Upper Devonian (Famennian).*

Gigantorhynchus SAPELNIKOV & MALYGINA, 1977, p. 62 [**G. dubius;* OD]. Very large with rounded subtriangular outline and biconvex profile. Beak incurved; delthyrium open apically; deltidial plates disjunct. Fold and sulcus low, flat, wide, arising at umbones; anterior commissure uniplicate, tongue low. Costae very weak to absent. Shell thick. Dental plates absent or obscured by callus; ventral muscle field narrow. Dorsal median septum short, thick; septalium absent; hinge plates united; cardinal process narrow, linguiform, unilobed to trilobed; crural bases stout; crura long, oblique in section. *Middle Devonian (Givetian):* Tian Shan.——FIG. 782,*1a–k.* **G. dubius,* eastern Altai, Archaltur Range; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×0.5; *e–k,* serial sections

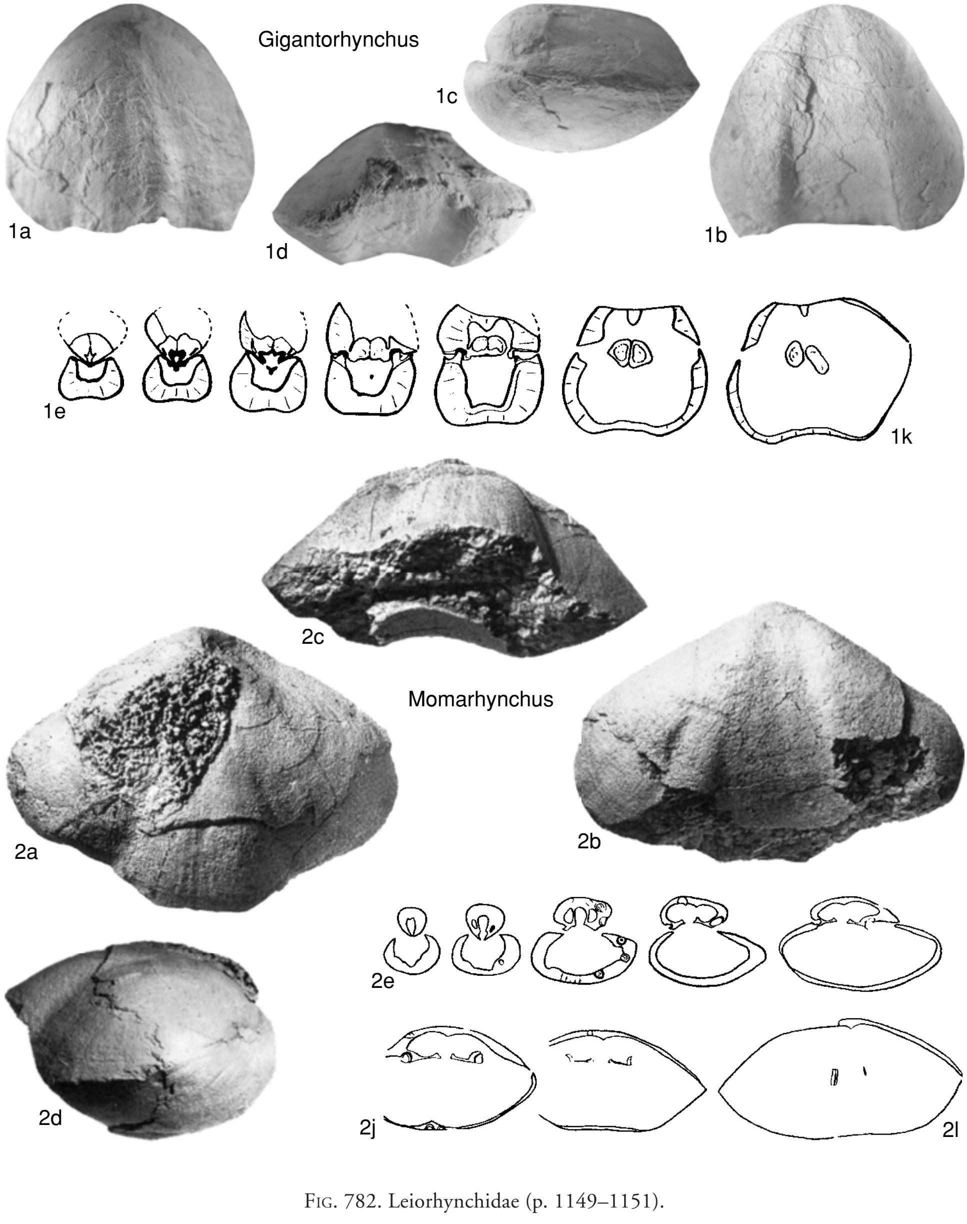

FIG. 782. Leiorhynchidae (p. 1149–1151).

30.0, 29.5, 29.0, 28.0, 27.0, 24.0, 20.0 mm from anterior, ×0.6 (Sapelnikov & Malygina, 1977).

Momarhynchus BARANOV & SARTENAER, 1996, p. 39 [**M. indigirkaensis;* OD]. Very large with transversely subpentagonal outline and biconvex profile. Ventral beak small, incurved; delthyrium open. Fold and sulcus wide, fold gently convex, sulcus gently concave; anterior commissure uniplicate, tongue low, slightly arched. Flanks of both valves gently convex. Costae very weak to absent; fine radial striae sometimes preserved. Shell thick posteriorly. Dental plates absent; teeth stout and short; ventral muscle field poorly defined. Dorsal median ridge long, low; hinge plates divided, subhorizontal, with short sockets and low inner socket ridges; crural bases stout, horizontal; crura subtriangular in cross section, distal parts curve ventrally. *Upper Devonian (Famennian):* Russia (Yakutia).——FIG. 782,*2a–l.* **M. indigirkaensis,* lower Famennian, upper half of Moma Suite, Moma River, Moma

Range; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–l,* serial sections 1.5, 1.8, 2.2, 2.4, 3.1, 3.6, 4.2, 6.2 mm from posterior, ×1 (Baranov & Sartenaer, 1996).

Subfamily CALVINARIINAE Sartenaer, 1994

[*nom. transl.* Savage, 1996, p. 254, *ex* Calvinariidae Sartenaer, 1994, p. 97]

Leiorhynchidae with transverse outline, smooth umbones, high tongue, few coarse costae, and strongly convergent dental plates. *Upper Devonian (Frasnian).*

Calvinaria Stainbrook, 1945, p. 43 [**Rhynchonella ambigua* Calvin, 1878, p. 729; OD]. Large with markedly transversely ovate outline. Biconvex profile with lateral and anterior slopes low. Beak incurved; foramen oval. Fold and sulcus strong, arising at umbones; anterior commissure broadly uniplicate; tongue high, trapezoid, serrate. Costae broad, arising near umbones; present on fold, sulcus, and flanks. Dental plates convergent ventrally, often obscured by thick callus; ventral muscle field deeply impressed. Dorsal median septum long, thin, high; septalium short, narrow; hinge plates divided anterior of septalium; crura long, ventrally curved. *Upper Devonian (Frasnian):* North America, Europe, northern Africa, China.——Fig. 783,*1a–j.* **C. ambigua* (Calvin), upper Frasnian, Iowa, USA; *a–b,* hypotype, dorsal and posterior views, Amana Beds, Amana, ×1.2; *c,* holotype, ventral view, Independence Shale, Independence; *d,* hypotype, anterior view, Independence Shale, Brandon, ×1 (Stainbrook, 1945); *e–j,* serial sections 2.6, 2.7, 2.95, 3.3, 3.5, 3.8 mm from posterior, ×2 (Sartenaer, 1955).

Canavirilia Sartenaer, 1994, p. 97 [**C. atrousensis;* OD]. Large with transversely ovate, anteriorly emarginate outline; dorsibiconvex profile; lateral margins moderately steep but not truncated; dorsal valve inflated posteriorly and anteriorly. Beak incurved; foramen with deltidial plates. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, trapezoid, subacuminate. Costae very broad, arising at umbones, mostly on fold and sulcus, rare on flanks. Dental plates short, strongly convergent ventrally; ventral muscle field well impressed. Dorsal median septum long, high, thin; septalium short; hinge plates dividing early; crura closely set, long, rodlike for much of length. *Upper Devonian (middle Frasnian):* Morocco, Europe, Urals, North America.——Fig. 783,*2a–l.* **C. atrousensis,* Tafilalt, Morocco; *a–d,* holotype, ventral, posterior, anterior, and lateral views, ×1; *e–l,* serial sections 0.6, 1.0, 1.1, 1.2, 1.45, 1.55, 1.8, 2.3 mm from posterior, ×2.3 (Sartenaer, 1994).

Lateralatirostrum Sartenaer, 1979a, p. 539 [**Leiorhynchus athabascense* Kindle, 1924, p. 217; OD]. Large, with transversely ovate outline and dorsibiconvex profile; lateral slopes gentle. Beak erect, truncated by small foramen. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue very high, broad, rounded. Costae low, most evident on fold and in sulcus, weak on flanks. Dental plates short, converging ventrally; ventral muscle field weakly impressed. Dorsal median septum long, thin, high; septalium short; hinge plates breaking up early; crura long, ventrally curved. *Upper Devonian (lower Frasnian):* western North America, Russian Platform, Volga-Urals, central Timan.——Fig. 784,*1a–l.* **L. athabascense* (Kindle), Flume Formation, Jasper Park, Alberta, Canada; *a–d,* hypotype, ventral, lateral, posterior, and anterior views, ×1; *e–l,* serial sections 0.55, 1.1, 1.3, 1.4, 1.9, 2.2, 3.2, 5.5 mm from posterior, ×2 (McLaren, 1962).

Navalicria Sartenaer, 1989, p. 66 [**N. compacta;* OD]. Transversely ovate, anteriorly emarginate outline; dorsibiconvex profile, anteriorly inflated, flanks not steep. Beak slightly incurved; foramen small, deltidial plates narrow. Fold and sulcus strong, from umbones; anterior commissure uniplicate to biplicate; tongue high, trapezoid. Costae low, simple, rounded, arising anterior of umbones; approximately 2 costae on fold, 1 in sulcus; flanks smooth. Dental plates incipient, convergent ventrally; ventral muscle field narrow, deeply impressed. Septalium short, small; hinge plates divided; dorsal septum long, high, thin; dorsal muscle field narrow; crura long, thin, slightly curved ventrally, closely set. *Upper Devonian (Frasnian):* western Europe, western Canada, China.——Fig. 783,*3a–m.* **N. compacta,* middle Frasnian–upper Frasnian, Schistes gris with *Reticularia pachyrhyncha,* Ardennes, near Frasnes, Belgium; *a–e,* holotype, ventral, dorsal, lateral, posterior, and anterior views, ×1; *f–m,* serial sections 0.55, 0.95, 1.15, 1.3, 1.7, 2.0, 2.2, 3.7 mm from posterior, ×3.2 (Sartenaer, 1989).

Plionoptycherhynchus Sartenaer, 1979a, p. 537 [**P. exformosus;* OD]. Large, with transversely ovate outline and dorsibiconvex profile; gentle lateral slopes. Beak erect; foramen obscured by dorsal umbo. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, trapezoid, serrate. Costae distinct, subangular, simple, extending from umbones, present on fold, sulcus, and flanks. Dental plates absent; ventral muscle field narrow, deeply impressed in thick shell material. Dorsal median septum long, high, thick; septalium short; hinge plates divided immediately anterior of septalium; crura curved ventrally, tips laterally flattened. *Upper Devonian (lower Frasnian):* Europe, western Canada.——Fig. 784,*2a–j.* **P. exformosus,* upper lower Frasnian, Givet, Chapel of Notre Dame de Walcourt, northeastern France; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1 (Sartenaer, 1979a); *e–j,* serial sections 1.8, 2.05, 2.3, 2.45, 3.15, 4.10 mm from posterior, ×2 (Sartenaer, 1955).

Tomestenoporhynchus Sartenaer, 1993, p. 13 [**Leiorhynchus rudkini* Ljaschenko, 1959, p. 151; OD]. Large; subpentagonal, transversely ovate outline;

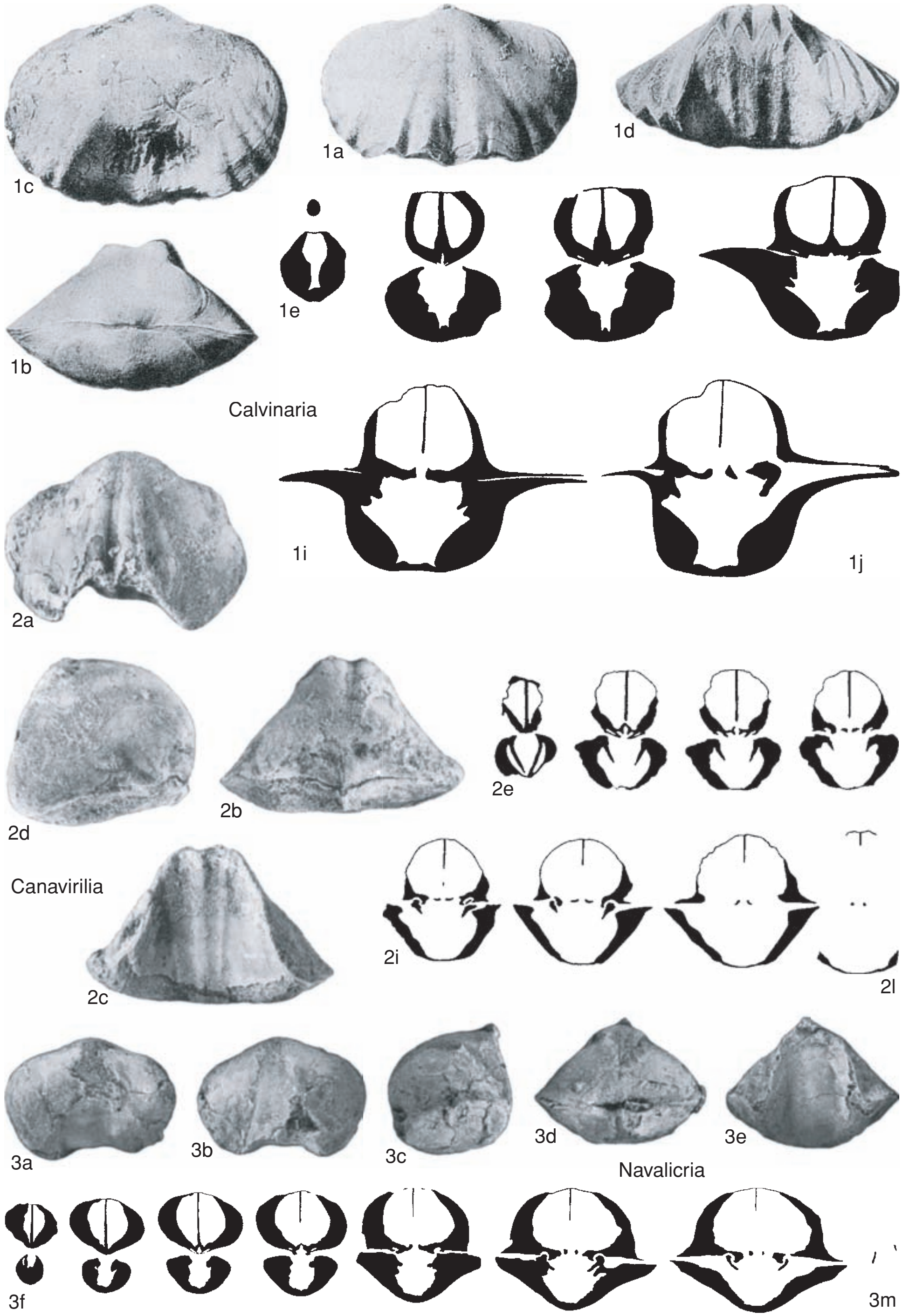

FIG. 783. Leiorhynchidae (p. 1151).

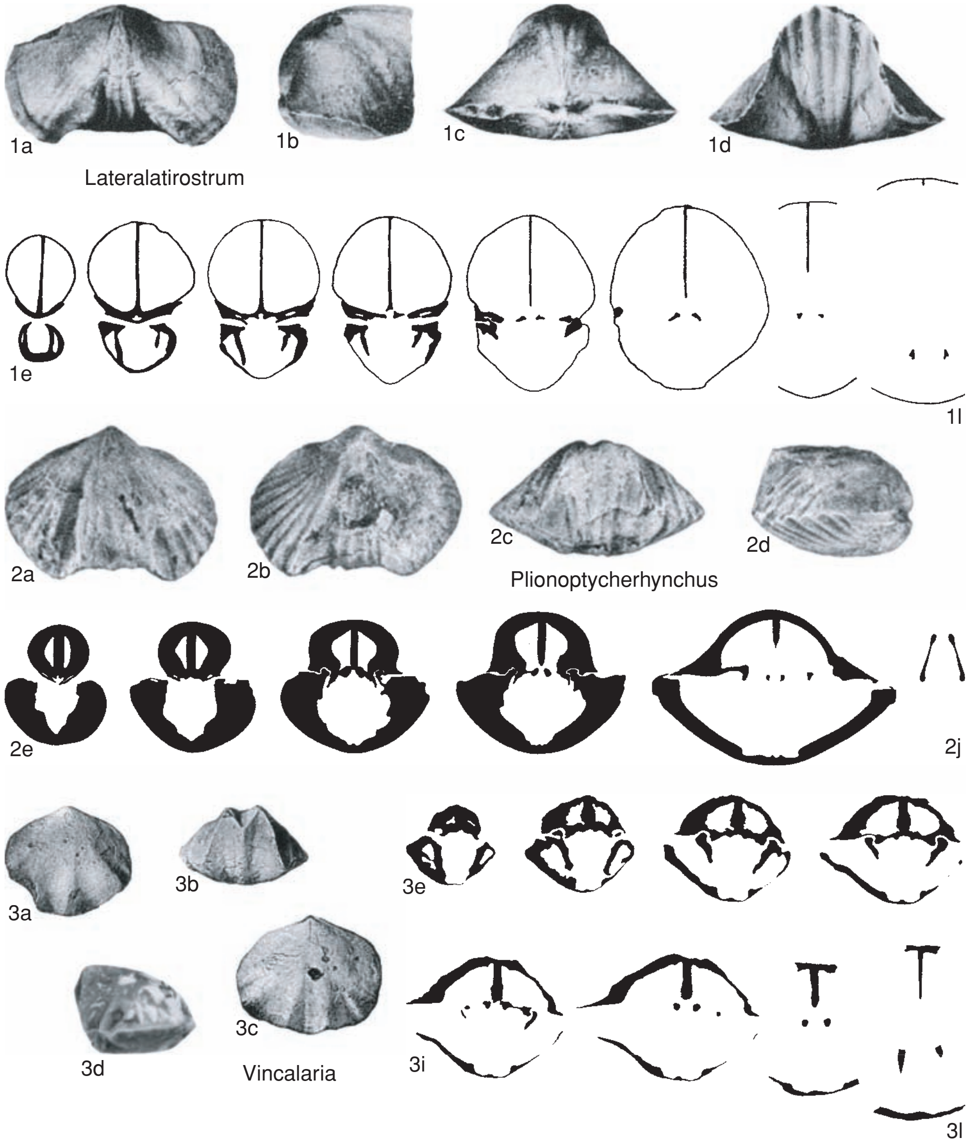

FIG. 784. Leiorhynchidae (p. 1151–1154).

dorsibiconvex profile with sides sloping steeply but not truncated; dorsal valve inflated posteriorly and anteriorly. Beak incurved; foramen small, semicircular; deltidial plates delicate. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue high, subacuminate, dentate. Costae coarse, arising at umbones; angular; most prominent on fold and sulcus, weak on flanks. Dental plates short, strongly convergent ventrally; teeth small, delicate. Dorsal median septum long, high, thin; septalium short to absent; hinge plates very short; crura closely set, long, slender, ventrally curved at tips. *Upper Devonian (lower Frasnian):* European Russia.——FIG. 785*a–n*. **T. rudkini* (LJASCHENKO), Rudkino horizon, Russian Platform, River Don, Rudkino; *a–d,* holotype, dorsal, ventral, posterior, and anterior views, ×1; *e,* topotype, lateral view, ×1; *f–n,* serial sections 2.2, 2.25, 2.45, 2.55, 3.05, 3.2, 3.4, 5.9, 6.7 mm from posterior, ×3.25 (Sartenaer, 1993).

Vincalaria SARTENAER, 1989, p. 61 [**Calvinaria bransoni* STAINBROOK, 1948, p. 774; OD]. Transversely ovate outline and dorsibiconvex profile; lateral slopes moderate. Beak erect to incurved; foramen

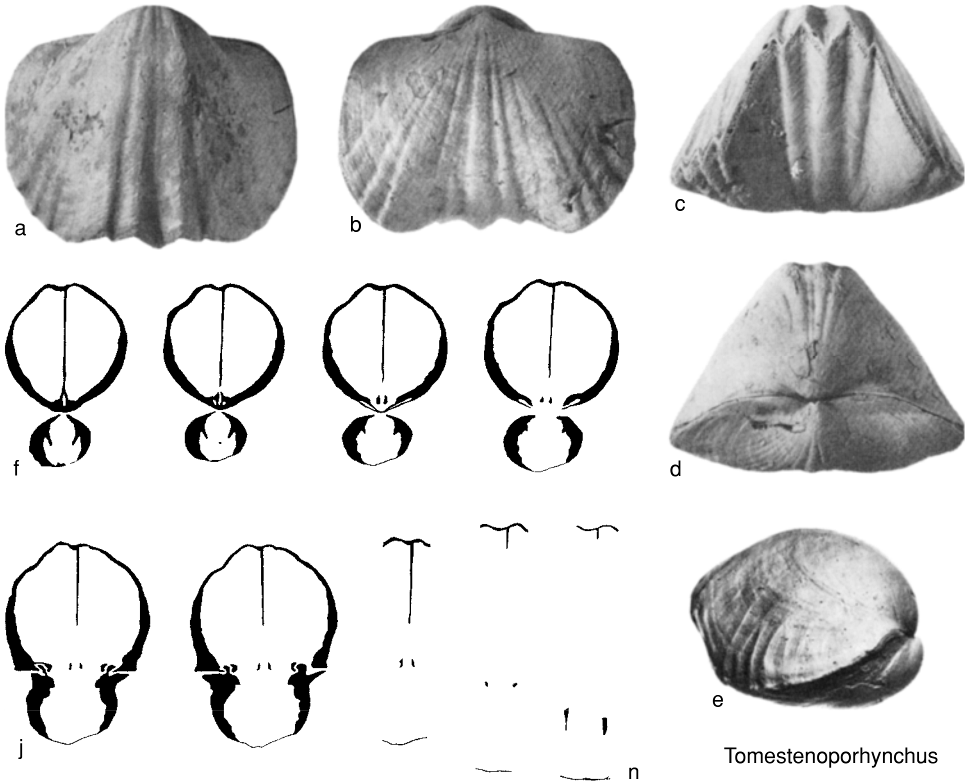

FIG. 785. Leiorhynchidae (p. 1151–1153).

small, oval. Fold and sulcus strong, arising at umbones; tongue pronounced, broadly biplicate to triplicate. Costae strong, broad, from umbones, usually 2 to 4 on fold, 1 to 3 in sulcus, weak on flanks. Dental plates strongly convergent ventrally, often obscured by thick callus; ventral muscle field well impressed. Septalium short; hinge plates divided anterior of septalium; dorsal median septum long, low, thick; crura closely set. *Upper Devonian (Frasnian):* Europe, western North America, China.——FIG. 784,*3a–l*. **V. bransoni* (STAINBROOK), middle Frasnian–upper Frasnian, Sly Gap Formation, Alamogordo, New Mexico, USA; *a–b,* holotype, ventral and anterior views; *c,* paratype, dorsal view, ×1 (Stainbrook, 1948); *d,* hypotype, lateral view, ×1 (Cooper & Dutro, 1982); *e–l,* serial sections 0.65, 0.9, 1.1, 1.3, 1.45, 1.55, 2.0, 3.2 mm from posterior, ×2.7 (Sartenaer, 1989).

Subfamily PLATYTERORHYNCHINAE Savage, 1996

[Platyterorhynchinae SAVAGE, 1996, p. 254]

Leiorhynchidae with lenticular profile and low fold; costae weak and uneven; dental plates short, almost meeting ventrally. *Middle Devonian (upper Givetian)–Upper Devonian (lower Famennian).*

Platyterorhynchus SARTENAER, 1970a, p. 5 [**Leiorhynchus russelli* MCLAREN, 1962, p. 95; OD]. Subcircular to transversely ovate outline and equibiconvex, lenticular profile. Beak incurved; delthyrium with vestigial deltidial plates, foramen mesothyrid. Fold and sulcus broad, low, from midlength; anterior commissure uniplicate; tongue low, wide. Costae weak and uneven on fold and sulcus, very weak on flanks. Dental plates short, converging ventrally; ventral muscle field narrow, moderately impressed. Dorsal median septum long, high, thin; septalium very short, shallow; hinge plates dividing immediately anterior of septalium; dorsal muscle field long, narrow; crura long, slender, ventrally curved, tips laterally flattened. *Middle Devonian (upper Givetian)–Upper Devonian (lower Frasnian):* western and eastern North America, western Europe, Morocco, Turkey, Russian Platform, Volga-Urals, Timan, China.——FIG. 786,*4a–l*. **P. russelli* (MCLAREN), uppermost Givetian, lowermost *Asymmetricus* Zone, Waterways Formation,

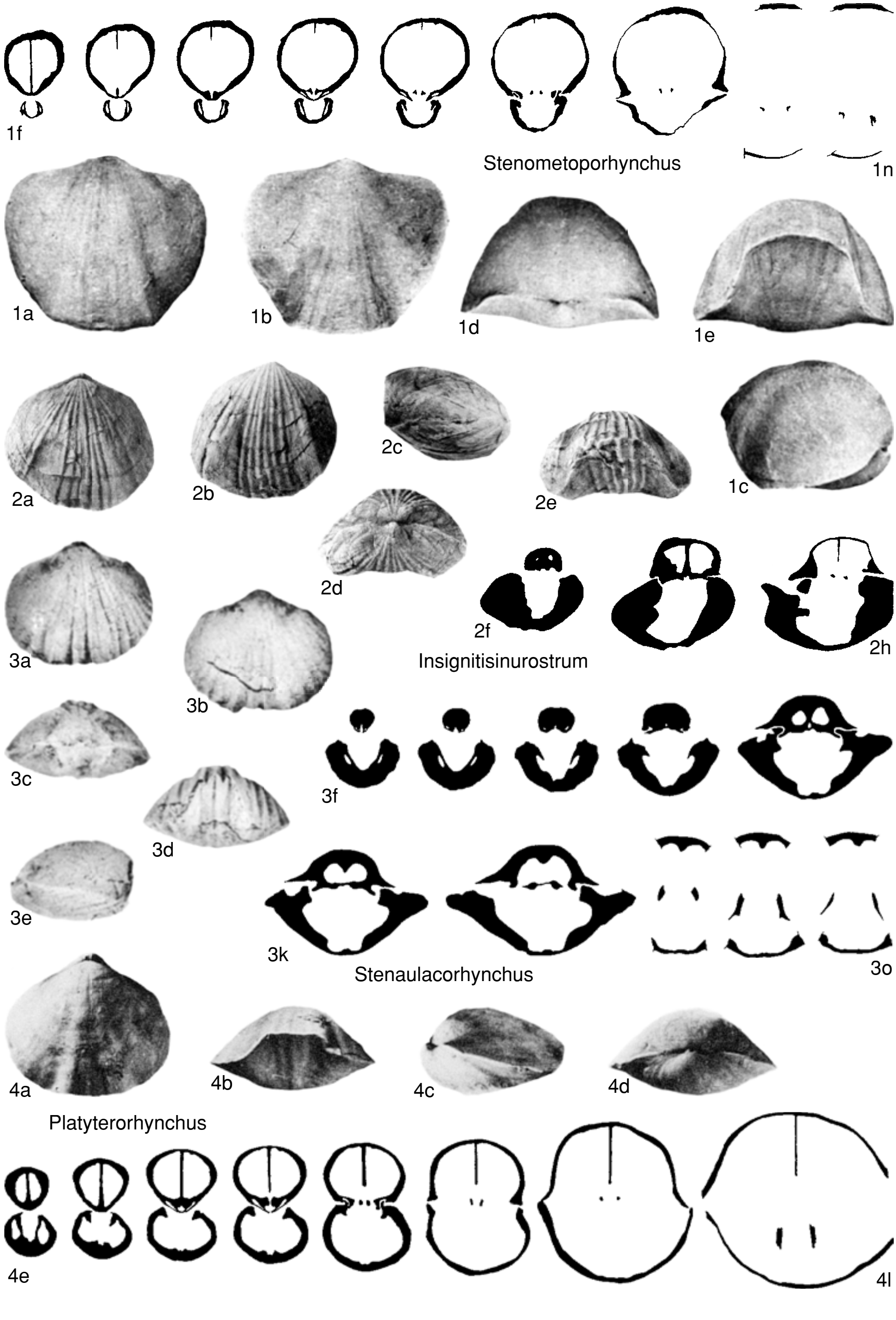

FIG. 786. Leiorhynchidae (p. 1154–1156).

Peace River, Boyer Rapids, Alberta, Canada; *a–d,* holotype, dorsal, anterior, lateral, and posterior views, ×1; *e–l,* serial sections 1.0, 1.3, 1.7, 1.8, 2.1, 2.7, 3.7, 5.5 mm from posterior, ×1.5 (McLaren, 1962).

Insignitisinurostrum Sartenaer, 1987b, p. 85 [**Camarotoechia latisinuata* Cooper & Dutro, 1982, p. 79; OD]. Subcircular to transversely ovate outline and dorsibiconvex profile; lateral slopes rounded. Beak erect to suberect; foramen subovate. Fold and sulcus low, from umbones; anterior commissure broadly uniplicate; tongue low, broad, serrate. Costae narrow, rounded, arising at beaks, increasing by bifurcation and intercalation, present on fold, sulcus, and flanks. Dental plates absent or buried in thick callus; ventral muscle field deeply impressed. Dorsal median septum short, thin; septalium very short, with crural bases arising from sides; hinge plates also very short, dividing immediately anterior of septalium; crura closely set, long, thin, distally ovate in cross section. *Upper Devonian (lower Famennian):* western USA.——Fig. 786,*2a–h.* **I. latisinuatum* (Cooper & Dutro), upper lower Famennian, basal Thoroughgood Formation, Sheep Mountain, New Mexico; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f–h,* serial sections 1.9, 2.4, 2.9 mm from posterior, ×2 (Cooper & Dutro, 1982).

Stenaulacorhynchus Sartenaer, 1968a, p. 3 [**S. cheshmehshirensis;* OD]. Transversely ovate outline and dorsibiconvex profile; gentle lateral and anterior slopes. Beak erect; foramen small, circular. Fold and sulcus moderate, extending from umbones; anterior commissure uniplicate; tongue low, rounded, serrate. Costae extending from umbones but most evident at anterior and lateral margins. Dental plates short, strongly convergent ventrally; ventral muscle field narrow, well impressed in thick shell material. Dorsal median septum very short, thick, low; septalium very short, wide, with cover plate anteriorly; hinge plates united anterior of septalium; dorsal muscle field narrow, well impressed; crura curve ventrally, tips laterally flattened. *Upper Devonian (lower Famennian):* northern Iran, Spain.——Fig. 786,*3a–o.* **S. cheshmehshirensis,* Ozbak-Kuh, Cheshmeh Shir, northern Iran; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–o,* serial sections 1.37, 1.45, 1.6, 1.85, 2.35, 2.5, 2.7, 3.2, 3.4, 3.6 mm from posterior, ×2.2 (Sartenaer, 1968a).

Subfamily STENOMETOPORHYNCHINAE Savage, 1996

[Stenometoporhynchinae Savage, 1996, p. 254]

Leiorhynchidae with ventral valve flattened to concave and dorsal valve highly inflated; dental plates, dorsal median septum, and hinge plates very short; septalium absent. *Upper Devonian (lower Frasnian).*

Stenometoporhynchus Sartenaer, 1987d, p. 126 [**Liorhynchus pavlovi* Nalivkin, 1930b, p. 72; OD; *non Liorhynchus pavlovi* Mufke, *nomem manuscriptum* (see Nalivkin, 1930b, p. 73[88], and Sartenaer, 1987d, p. 126)]. Subpentagonal to scutiform outline and dorsibiconvex, galeate profile; dorsal valve inflated. Beak incurved; foramen small, apical. Fold and sulcus wide, low; anterior commissure uniplicate; tongue wide, rounded; Costae weak on fold and sulcus, very weak on flanks. Dental plates short, close to shell walls, ventrally convergent; ventral muscle field weakly impressed. Dorsal median septum short, thin; septalium absent; hinge plates very short, divided; dorsal muscle field narrow, weakly impressed; crura long, slender, closely set, ventrally curved, V-shaped distally with open side directed ventrally. *Upper Devonian (lower Frasnian):* European Russia, China.——Fig. 786,*1a–n.* **S. pavlovi* (Nalivkin), Semiluki beds, Voronezh, Semiluki, European Russia; *a–e,* lectotype, dorsal, ventral, lateral, posterior, and anterior views, ×1 (Nalivkin, 1930b); *f–n,* serial sections 1.05, 1.3, 1.5, 1.7, 1.8, 2.1, 2.75, 4.65, 4.9 mm from posterior, ×1.7 (Sartenaer, 1987d).

Subfamily BASILICORHYNCHINAE Savage, 1996

[Basilicorhynchinae Savage, 1996, p. 254]

Leiorhynchidae with subcircular outline; high tongue; strong costae. Dental plates and dorsal median septum distinct. *Upper Devonian (Famennian).*

Basilicorhynchus Crickmay, 1952b, p. 1 [**Leiorhynchus basilicum* Crickmay, 1952a, p. 600; OD]. Subcircular outline and strongly dorsibiconvex profile; flanks and anterior very steep. Beak incurved; foramen mesohypothyrid. Fold and sulcus restricted to extreme anterior; anterior commissure uniplicate; tongue high, trapezoid to rectangular, serrate. Costae few, strong, subangular, developed only anteriorly. Dental plates long, ventrally convergent; ventral muscle field well impressed. Dorsal median septum long; septalium deep, V-shaped; hinge plates horizontal, divided anterior of septalium; crura short, slender, gutterlike distally with dorsal side open. *Upper Devonian (lower Famennian):* western and northern Canada, Europe, Siberia.——Fig. 787,*1a–k.* **B. basilicus* (Crickmay), upper lower Famennian, Mackenzie River, Root River, Northwest Territories; *a–c,* holotype, dorsal, ventral, and anterior views; *d,* paratype, lateral view, ×1; *e–k,* serial sections 0.4, 0.5, 0.8, 1.1, 1.3, 1.4, 2.0 mm from posterior, ×5 (Sartenaer, 1969).

Gastrodetoechia Sartenaer, 1965b, p. 2 [**Leiorhynchus utahensis* Kindle, 1908, p. 105; OD]. Large; subpentagonal to transversely ovate outline; dorsibiconvex profile. Beak erect; foramen small, circular. Fold and sulcus strong, extending from umbones; anterior commissure uniplicate; tongue

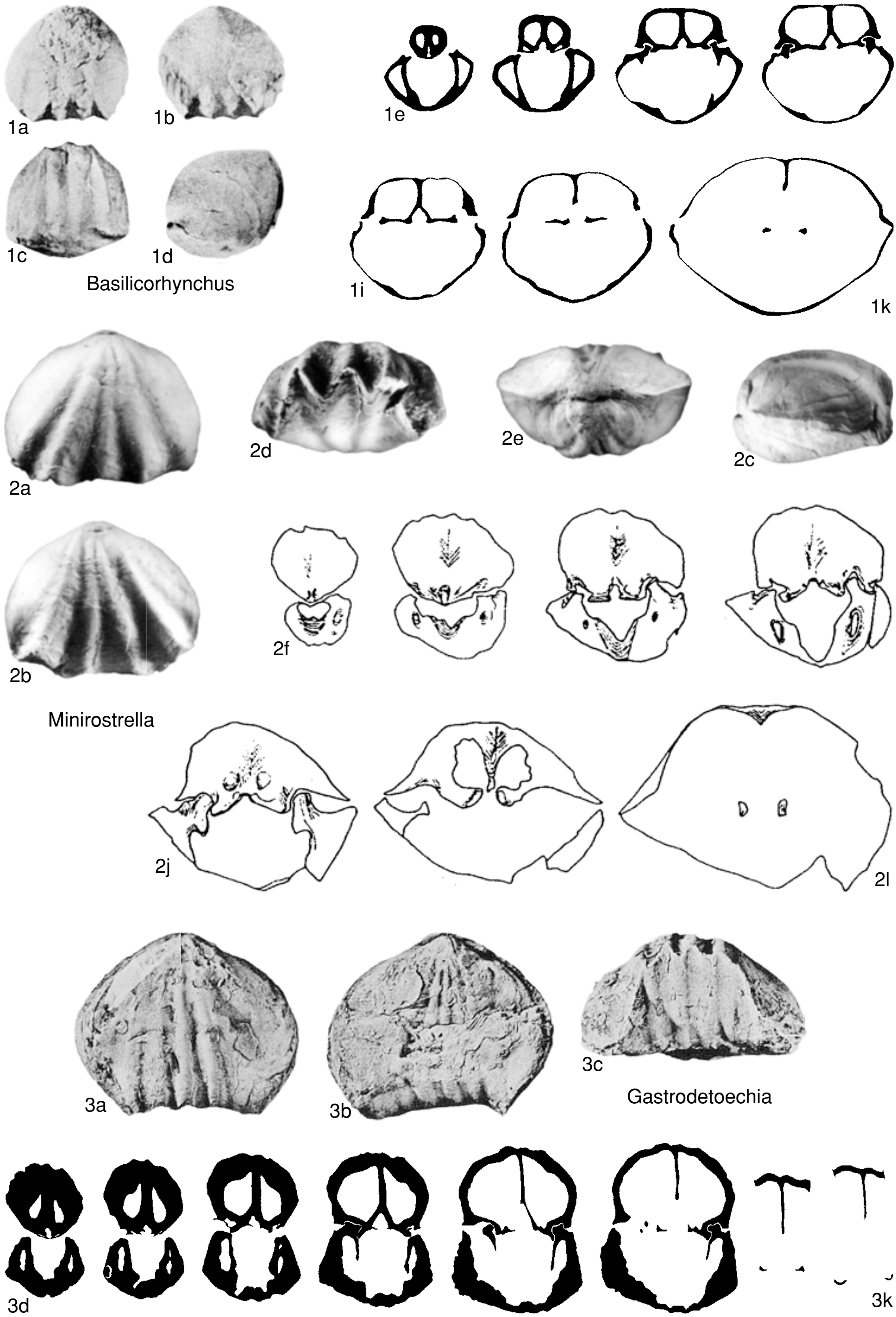

FIG. 787. Leiorhynchidae (p. 1156–1158).

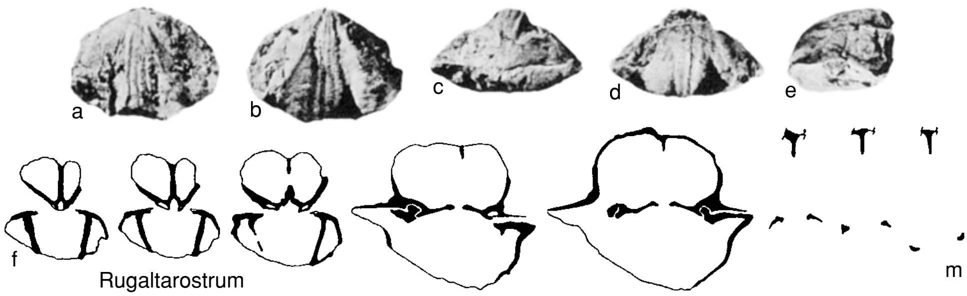

FIG. 788. Leiorhynchidae (p. 1158).

high, angular, serrate. Costae arising on umbones; subangular; strong on fold and in sulcus, weak on flanks. Dental plates long, near valve walls, convergent ventrally; ventral muscle field narrow, well impressed. Dorsal median septum long, high; septalium large, deep, long, V-shaped, with fragile cover; hinge plates joined by septalium; dorsal muscle field narrow, well impressed; crura curved ventrally, concave dorsally. *Upper Devonian (Famennian):* western North America, Europe, Iran, Armenia, Afghanistan, Algeria.——FIG. 787,*3a–k.* **G. utahensis* (KINDLE), lower upper Famennian; *a–c,* hypotype, dorsal, ventral, and anterior views, Three Forks Formation, Montana, USA, ×0.8; *d–k,* hypotype, serial sections 1.85, 1.95, 2.1, 2.85, 3.5, 3.8, 4.1, 5.3 mm from posterior, Palliser Formation, Mount Coleman, Banff Park, Alberta, Canada, ×1.5 (Sartenaer, 1969).

Minirostrella BALINSKI, 1995a, p. 50 [**M. rara;* OD]. Transversely ovate outline and dorsibicovex profile; flanks with low lateral slopes. Beak erect to incurved. Fold and sulcus of medium strength, extending from beaks; tongue wide, high, typically triplicate. Costae broad, subangular, arising at umbones, strong on fold and sulcus, weak on flanks. Dental plates very short, convergent ventrally; ventral muscle field deeply impressed. Dorsal median septum short, low, thick; septalium wide, short; hinge plates inclined dorsally, divided anterior of septalium; crura long, closely set, ventrally curved. *Upper Devonian (lower Famennian):* Poland.——FIG. 787,*2a–l.* **M. rara, Palmatolepis triangularis* Zone, Debnik, southern Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×2; *f–l,* serial sections 0.35, 0.65, 0.7, 0.85, 1.1, 1.4, 2.3 mm from posterior, ×4.4 (Balinski, 1995a).

Rugaltarostrum SARTENAER, 1961c, p. 6 [**Leiorhynchus madisonense* HAYNES, 1916, p. 39; OD]. Transversely ovate outline and dorsibicovex profile; flanks with low lateral slopes. Beak erect to incurved; foramen minute. Fold and sulcus strong, extending from beaks; anterior commissure uniplicate; tongue wide, high, serrate. Costae broad, arising at umbones, strong on fold and sulcus, weak on flanks. Dental plates long, convergent ventrally. Dorsal median septum long, high; septalium deep, short; hinge plates slightly inclined dorsally, divided anterior of septalium; crura long, ventrally curved, surfaces concave dorsally. *Upper Devonian (Famennian):* western North America, Western Australia, central Asia.——FIG. 788*a–m.* **R. madisonense* (HAYNES), lower upper Famennian, Three Forks Formation, Logan, Montana, USA; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–m,* serial sections 0.57, 0.62, 0.7, 1.0, 1.1, 1.4, 1.55, 1.7 mm from posterior, ×6 (Sartenaer, 1969).

Family SEPTALARIIDAE Havlíček, 1960

[Septalariidae HAVLÍČEK, 1960, p. 241]

Camarotoechioidea with tongue generally extended into trail; hinge plates united; dorsal median septum high; cardinal process commonly developed. *Lower Devonian (Pragian)–Upper Devonian (middle Frasnian).*

Septalaria LEIDHOLD, 1928, p. 35 [**Terebratula ascendens* STEININGER, 1853, p. 61; SD TORLEY, 1934, p. 74]. Subpentagonal outline and dorsibiconvex profile; anteriorly inflated. Beak sharp, incurved; foramen permesothyrid. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue broad, high, rectangular, serrate, often projecting anterodorsally as trail. Costae low, simple, extending from umbones, weak on flanks; short marginal spines commonly developed. Dental plates very short, close to walls; ventral muscle field weakly impressed. Dorsal median septum short, high; pointed at about midlength in lateral view, with acute angle directed ventrally; septalium short, wide, partly filled by large, ridged cardinal process; hinge plates undivided for short distance anterior of septalium; crural bases arising from dorsal edge of hinge plates; crura long, straight, closely set, rodlike. *Lower Devonian (upper Emsian)–Middle Devonian (upper Givetian):* Europe, Urals, Altai, China, Australia.——FIG. 789,*1a–e.* **S. ascendens* (STEININGER), Eifelian, Nohn Beds, Prüm, Hauenborn, Germany; neotype, dorsal, ventral, posterior, lateral, and anterior views, ×2 (Schmidt, 1975).——Fig. 789,*1f–p. S. subtetragona* (Schnur), Eifelian, Nohn Beds, Prüm, Germany; *f–i,* serial sections 15.2, 15.0, 14.9, 14.8 mm from anterior; *j–k,* serial sections 11.2, 11.1 mm from anterior, ×3.3 (Schmidt, 1965b); *l–p,* serial sections 10.25, 10.1, 10.0, 9.8, 9.6 mm from posterior, ×3 (Havlíček, 1961).

Amissopecten Havlíček, 1960, p. 243 [**Terebratula velox* Barrande, 1847, p. 74; OD]. Subpentagonal outline and dorsibiconvex profile; anteriorly inflated and with prominent trail. Beak suberect to incurved; foramen permesothyrid. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue broad, very high, often splayed, serrate, projecting anterodorsally as trail. Costae of 2 sizes, fine costae from beaks to midlength merge to form coarse costae extending to anterior margin. Dental plates absent; ventral muscle field weakly impressed. Dorsal median septum high; septalium short, wide; cardinal process absent; hinge plates horizontal, divided anterior of septalium. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Bohemia, Germany.——Fig. 789,*2a–i. *A. velox* (Barrande), upper Emsian, Suchomasty Limestone, Koneprusy, Bohemia; *a–e,* neotype, dorsal, ventral, lateral, anterior, and posterior views, ×2 (new); *f–i,* serial sections 16.3, 16.1, 15.9, 15.7 mm from anterior, ×5 (Havlíček, 1961).

Athyrhynchus Johnson, 1973a, p. 467 [**A. susanae;* OD]. Large; subpentagonal to subtriangular outline and dorsibiconvex profile; sides not truncated. Beak incurved. Fold and sulcus weak, arising at midlength; anterior commissure uniplicate; tongue broad, high, trapezoid. Costae few, weak, restricted mainly to fold and sulcus, arising near midlength. Dental plates short, close to walls; ventral muscle field elongate oval. Dorsal median septum long, high; septalium short; hinge plates undivided; sockets large, with recurved inner socket ridges; dorsal muscle field located near midlength, raised, rhombohedral outline; large bilobed cardinal process. *Lower Devonian (upper Emsian):* USA (Nevada), Arctic Canada.——Fig. 790,*1a–f. *A. susanae,* Disappointment Bay Formation, Lowther Island, Arctic Canada; *a–d,* dorsal, ventral, anterior, and lateral views, ×1.5; *e,* interior of dorsal valve, ×3; *f,* interior of ventral valve, ×3 (Johnson, 1973a).

Bergalaria Schmidt, 1975, p. 101 [**B. bergica;* OD]. Subpentagonal outline and dorsibiconvex profile. Beak erect to incurved; foramen small, with deltidial plates. Fold and sulcus strong, arising anterior of umbones; tongue broad, medium height, trapezoid, projecting anterodorsally as trail with commissure at leading edge. Costae developed on anterior third, numerous, rounded, weak on flanks, arising from radial capillae that are present posterior of costae. Dental plates short, convergent ventrally. Dorsal median septum short, high; in lateral profile with acute point directed ventrally at about one-third septum length; hinge plates horizontal, undivided; septalium absent; cardinal process large, ridged, rounded posteriorly but dividing into 2 splayed lobes anteriorly. *Upper Devonian (lower Frasnian–middle Frasnian):* Europe.——Fig. 790,*2a–j. *B. bergica,* lower Frasnian, Herzkamper Mulde, Bergisches Land, Elberfeld, Germany; *a–e,* holotype, dorsal, ventral, posterior, lateral, and anterior views, ×2; *f,* paratype, surface showing capillae, ×3; *g–h,* serial sections showing cardinal process, ×5; *i,* transverse section showing median septum and dental plates, ×4.2; *j,* longitudinal section showing acute angle on median septum, ×3 (Schmidt, 1975).

Monadotoechia Havlíček, 1960, p. 243 [**Terebratula monas* Barrande, 1847, p. 88; OD]. Small with elongate-oval outline and biconvex profile. Beak incurved. Fold and sulcus moderately strong, arising at umbones; anterior commissure uniplicate; tongue rounded to trapezoid, serrate, trail not developed. Costae few, subangular, extending from umbones. Dental plates small to absent. Hinge plates united, horizontal; cardinal process and septalium absent; dorsal median septum short, thin, high; crura closely set, delicate, tips laterally compressed. *Lower Devonian (Pragian–Emsian):* Bohemia, Morocco, southern Urals, Taimir.——Fig. 791,*1a–j. *M. monas* (Barrande), Koneprusy, Bohemia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, Pragian, Vinarice Limestone, ×5 (new); *e–i,* serial sections 5.65, 5.55, 5.4, 5.32, 5.2 mm from posterior, Emsian, Suchomasty Limestone, ×6; *j,* transverse section of another specimen, Emsian, Suchomasty Limestone, ×8 (Havlíček & Kukal, 1990).

Nemesa Schmidt, 1941a, p. 41 [**N. nemesana;* OD]. Transversely subpentagonal outline and dorsibiconvex profile; anteriorly inflated. Beak incurved; foramen permesothyrid. Fold and sulcus weak, from about midlength; tongue broad, low, sulciplicate to serrate. Surface smooth or with weak, broad costae developed anteriorly. Dental plates very short, close to walls. Dorsal median septum short; small cardinal process and septalium. *Middle Devonian (Eifelian):* Europe.——Fig. 789,*3a–c. *N. nemesana,* Rommersheimer Beds, Goldelsheim, Germany; holotype, ventral, anterior, and lateral views, ×1.5 (Schmidt, 1941a).——Fig. 789,*3d–f. N. hertae* Havlíček, Hlubocepy Limestone, Hlubocepy, Bohemia; serial sections 9.55, 9.1, 8.9 mm from anterior, ×2.5 (Havlíček, 1961).

Onugorhynchia Havlíček, 1992, p. 87 [**Terebratula matercula* Barrande, 1847, p. 65; OD]. Subpentagonal outline and dorsibiconvex profile; anteriorly inflated with very pronounced anterodorsal trail. Beak sharp, straight to suberect; foramen circular, mesothyrid; deltidial plates small, conjunct. Fold and sulcus strong anteriorly, weak posteriorly; tongue broad, very high, rectangular, projecting anterodorsally as prominent trail. In some specimens anterior trail and equivalent extensions of lateral margins unbroken but usually these thin flanges broken off, leaving introverted truncated edge. Costae low, simple, extending from

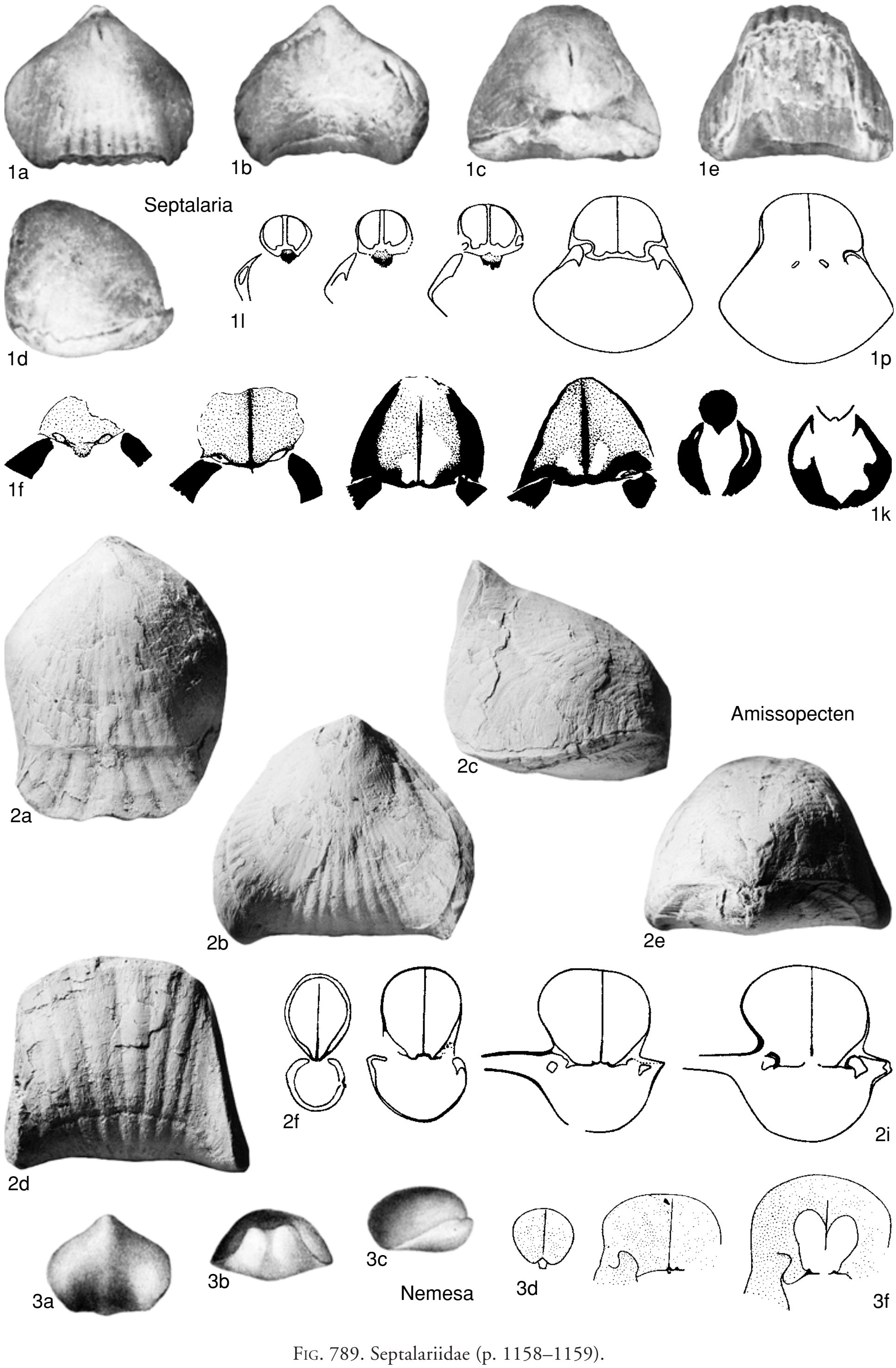

FIG. 789. Septalariidae (p. 1158–1159).

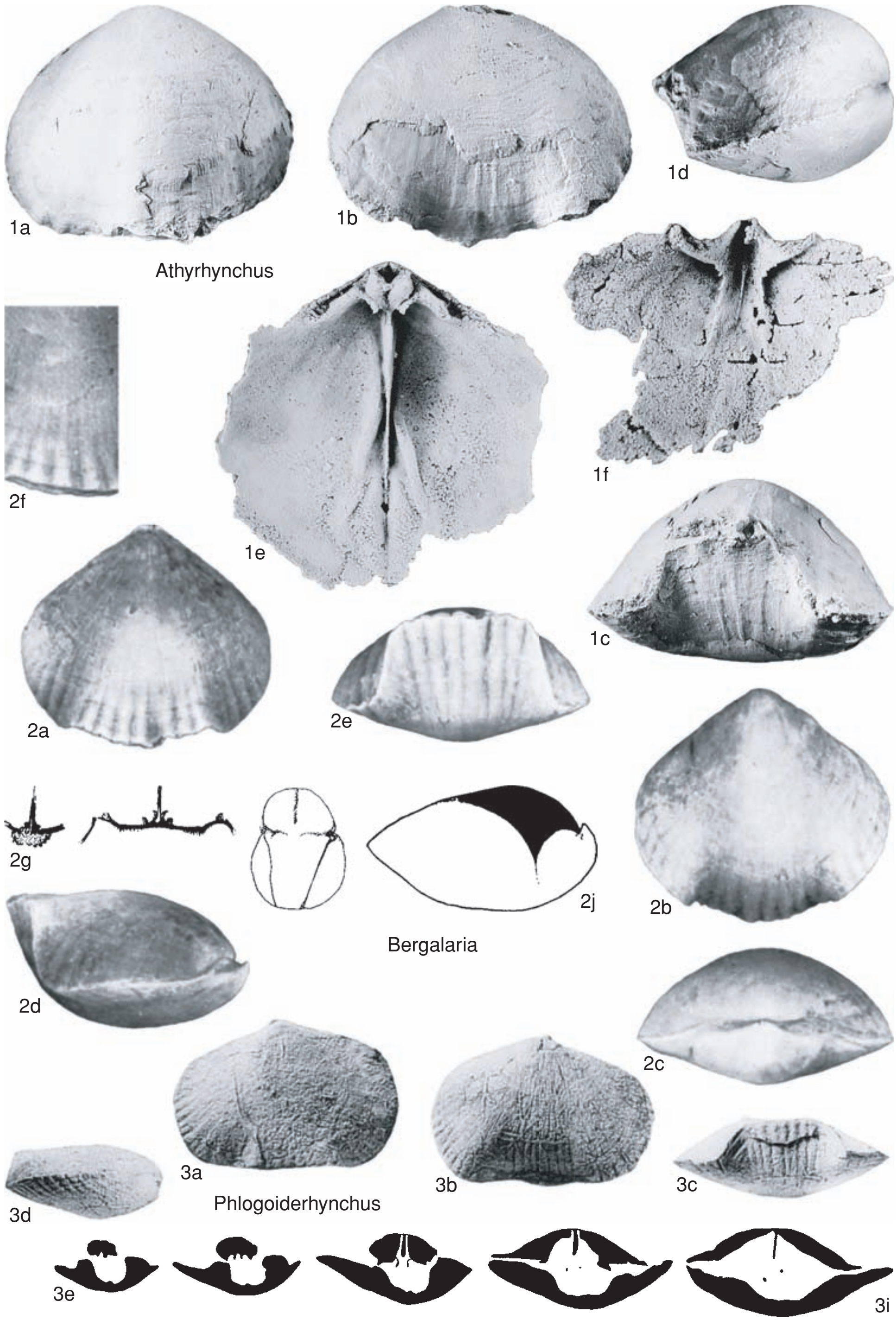

FIG. 790. Septalariidae (p. 1159–1164).

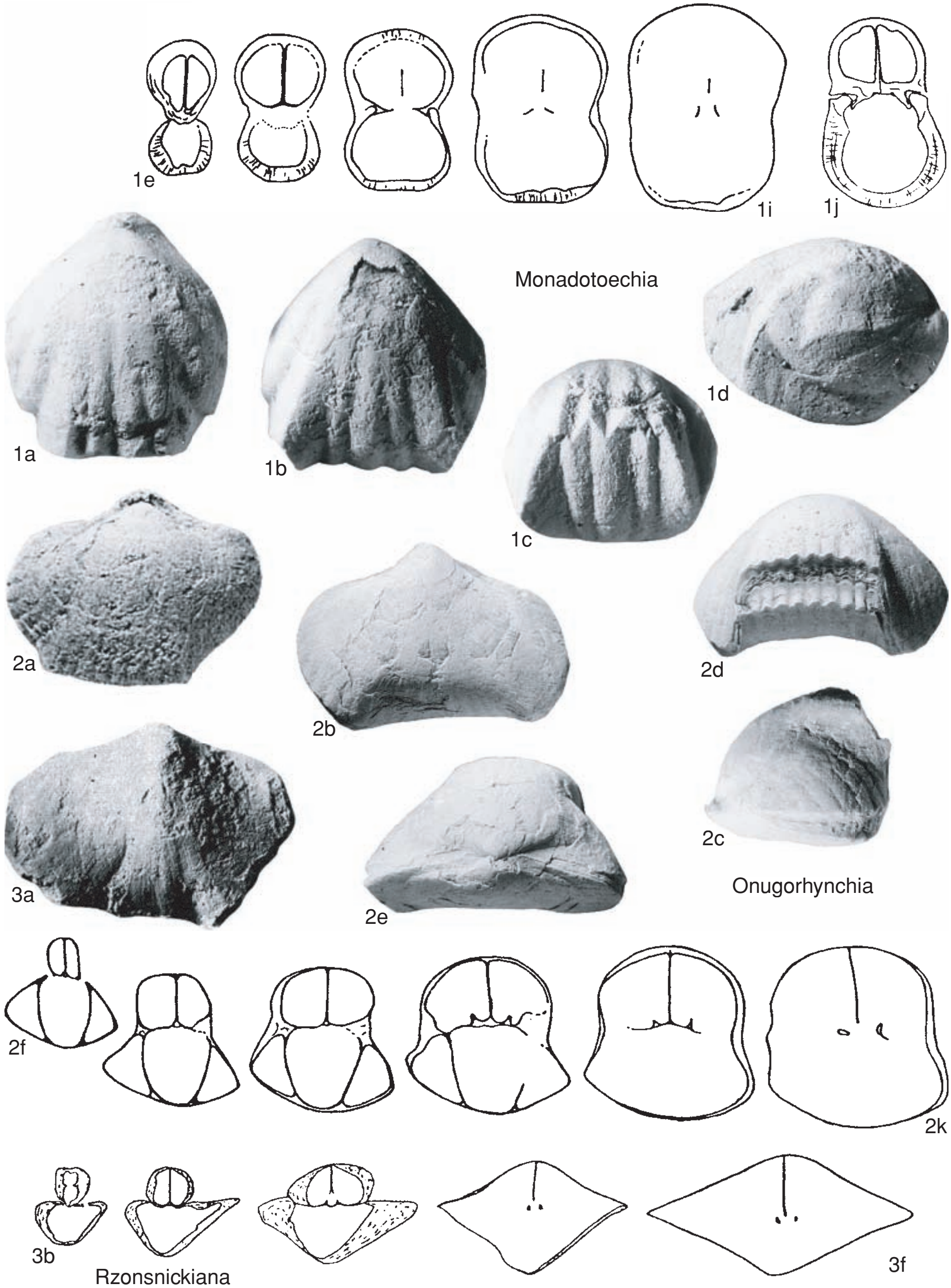

FIG. 791. Septalariidae (p. 1159–1164).

midlength, weak on umbones and flanks; costae changing into grooves on *paries geniculatus.* Short triangular marginal spines commonly developed. Dental plates short, convergent ventrally; ventral muscle field weakly impressed. Dorsal median septum short, high; septalium absent; hinge plates undivided, without median groove; cardinal process small to absent. *Lower Devonian (Pragian–Emsian):*

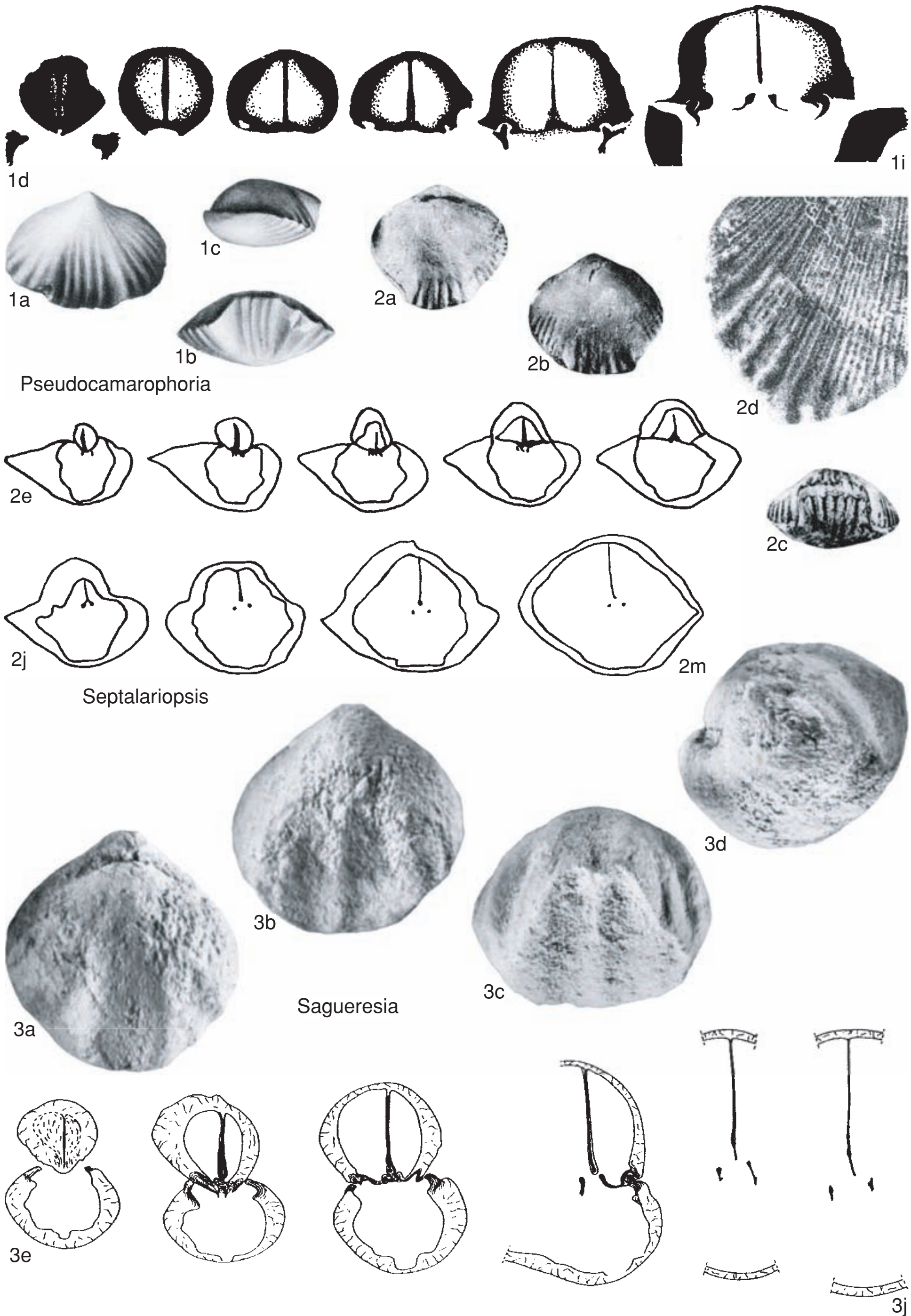

FIG. 792. Septalariidae (p. 1164).

Bohemia.——FIG. 791,*2a–k.* **O. matercula* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Prague; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, ×2.75 (new); *f–k,* serial sections 5.7, 5.5, 5.45, 5.35, 5.25, 5.15 mm from anterior, ×10 (Havlíček, 1992).

Phlogoiderhynchus SARTENAER, 1970a, p. 18 [**Uncinulus artefactus* VEEVERS, 1959a, p. 99; OD]. Transversely ovate outline and biconvex profile; gentle lateral slopes. Beak erect; foramen minute, circular. Fold and sulcus broad, extending from midlength; anterior commissure uniplicate; tongue variable, trapezoid to rounded, generally highest part of shell. Dental plates absent; teeth large, widely separated; ventral muscle field deeply impressed. Dorsal median septum long, high; septalium not developed; hinge plates incipient; crura long, slender, arising very early at extreme posterior of valve, thin and delicate, ventrally curved. *Middle Devonian (upper Givetian)–Upper Devonian (lower Frasnian):* Western Australia, Europe, China, Morocco.——FIG. 790,*3a–i.* **P. artefactus* (VEEVERS), lower Frasnian, Sadler Formation, Fitzroy Basin, Sadler Ridge, Western Australia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i,* serial sections 0.7, 0.85, 1.25, 1.95, 2.5 mm from posterior, ×1 (Veevers, 1959a).

Pseudocamarophoria WEDEKIND, 1926, p. 197 [**Terebratula microrhyncha* ROEMER, 1844, p. 65; OD]. Transversely ovate to equidimensional subpentagonal outline and biconvex, lenticular profile. Beak sharp, erect to incurved. Fold and sulcus moderately strong, from umbones; anterior commissure uniplicate; tongue wide, trapezoid, serrate. Costae from umbones, simple, subangular. Dental plates short, umbonal cavities commonly filled with callus. Dorsal median septum high, pointed ventrally in lateral profile, as in *Septalaria,* extending to about one-third valve length; septalium short, wide; cardinal process absent; crura closely set, thin, straight for much of length, arising from dorsal edge of undivided hinge plates. *Lower Devonian (Emsian)–Middle Devonian (Givetian):* Europe, China.——FIG. 792,*1a–i.* **P. microrhyncha* (ROEMER), lower Eifelian, Gondelsheimer Formation, Geeser bed, Eifel, Schönecken, Germany; *a–c,* ventral, anterior, and lateral views, ×1; *d–i,* serial sections 15.3, 15.0, 14.8, 14.6, 14.4, 14.0 mm from anterior, ×4 (Schmidt, 1965b).

Rzonsnickiana MAMEDOV, 1976, p. 121 [**R. sadarakensis;* OD]. Transversely ovate outline and moderately biconvex profile; gentle lateral slopes. Fold and sulcus broad, weak, extending from midlength; anterior commissure uniplicate; tongue low. Costae weak, broad, restricted to anterior margin; radial striae present. Dental plates absent. Dorsal median septum long, high; septalium short, with cover; crura closely set. *Middle Devonian (Eifelian):* Azerbaijan.——FIG. 791,*3a–f.* **R. sadarakensis,* Nakhichevan, Sadarak; *a,* holotype, ventral view, ×2.25; *b–f,* serial sections 1.0, 1.3, 1.4, 1.9, 2.34 mm from posterior, ×3.5 (Mamedov, 1976).

Sagueresia MOHANTI, 1972, p. 172 [**S. saguerana;* OD]. Subpentagonal outline and biconvex, globular profile. Beak incurved. Fold and sulcus moderate, from umbones; anterior commissure sulciplicate. Costae few, large, simple, rounded, arising at midlength. Dental plates absent or obscured by callus; ventral muscle field well impressed. Dorsal median septum high, thin; septalium short to absent; hinge plates undivided; cardinal process absent; crura long, almost straight, closely set, laterally compressed. *Middle Devonian (Eifelian–Givetian):* Spain.——FIG. 792,*3a–j.* **S. saguerana,* Eifelian–Givetian boundary, Portilla Formation, Cantabrian Mountains, Saguera; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–j,* serial sections, ×5.6 (Mohanti, 1972).

Septalariopsis CHEN, 1978a, p. 331 [**S. zhonghuanensis;* OD]. Subcircular to transversely ovate outline and dorsibiconvex profile; moderate lateral slopes. Beak erect to incurved; foramen small, circular. Fold and sulcus strong, from umbones; anterior commissure uniplicate, tongue wide, rectangular; broken anterior commissure in several specimens suggests projecting trail. Costae of 2 sizes, fine costae from beaks to near margins merging to form coarse costae at anterior and lateral margins. Dental plates absent or obscured by thick callus; ventral muscle field well impressed, narrow in thick callus. Dorsal median septum thin, high, long; septalium short; hinge plates divided anterior of septalium; cardinal process large, with longitudinal ridges; dorsal muscle field narrow, well impressed; crura long, slender, almost straight, closely placed. *Upper Devonian (lower Frasnian):* China (Sichuan).——FIG. 792,*2a–m.* **S. zhonghuanensis,* Tuqiaozi Member, Longmenshan; *a–c,* holotype, dorsal, ventral, and anterior views, ×1; *d,* holotype, costae at margin, ×6; *e–m,* serial sections 1.85, 2.1, 2.3, 2.5, 2.85, 2.95, 3.15, 3.85, 4.15 mm from posterior, ×3 (Chen, 1984).

PUGNACOIDEA

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Superfamily PUGNACOIDEA Rzhonsnitskaia, 1956

[*nom. transl.* SAVAGE, 1996, p. 253, *ex* Pugnacidae SCHMIDT, 1965b, p. 572, *nom. correct. pro* Pugnaxinae RZHONSNITSKAIA, 1956a, p. 125] [contains superfamily Basilioloidea COOPER, *nom. transl.* MAKRIDIN, 1964, p. 198, *ex* Basiliolidae COOPER, 1959, p. 15]

[Diagnosis prepared by N. M. SAVAGE, M. O. MANCEÑIDO, E. F. OWEN, and A. S. DAGYS]

Rhynchonellida with transversely ovate to subtriangular outline; strongly inflated anteriorly. Dorsal fold and ventral sulcus distinct; tongue high; plicae or costae few, simple, most pronounced anteriorly; umbones usually smooth; superimposed radial striae or costellae occasionally present; foramen generally present, usually with conjunct deltidial plates. Dental plates short to absent, or rarely long. Dorsal median septum short to absent; hinge plates commonly divided, often sloping dorsally to merge with crural plates; septalium absent to rare, short when present; cardinal process absent; crura commonly calciform or septiform. *Lower Devonian (Lochkovian)–Holocene.*

Family PUGNACIDAE Rzhonsnitskaia, 1956

[*nom. transl. et correct.* SCHMIDT, 1965b, p. 572, *ex* Pugnaxinae RZHONSNITSKAIA, 1956a, p. 125]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea with high fold and tongue; umbones usually smooth; costae few; superimposed radial striae common; foramen generally present, with conjunct deltidial plates. Dental plates variable, occasionally absent. Dorsal median septum short to absent; hinge plates divided; crural plates inclined dorsally; septalium absent. *Lower Devonian (Pragian)–Upper Permian (Tatarian).*

Pugnax HALL & CLARKE, 1893, p. 202 [**Terebratula acuminata* SOWERBY, 1822 in 1821–1822, p. 23; SD ICZN Opinion 420, 1956, p. 134] [=*Physetorhyncha* SARTENAER & ROZMAN, 1968, p. 137 (type, *Pugnax biloba* ROZMAN, 1960, p. 386, OD); *Striatopugnax* CHEN, 1978a, p. 322 (type, *S. triplica,* OD)]. Commonly large size; subtriangular to transversely ovate outline; tetrahedral shape with tongue very high, forming pointed arch, dorsal valve strongly inflated, ventral valve relatively flat or concave posteriorly. Beak incurved; foramen small. Fold and sulcus very strong and narrow anteriorly. Costae weak to absent, when present few, simple, most pronounced anteriorly where may be angular; fine radial striae commonly present. Dental plates short, vertical, or ventrally divergent. Septalium and dorsal median septum absent; hinge plates divided; crural plates inclined dorsally, almost meeting valve floor; crura laterally flattened, subparallel, variable. *Middle Devonian (Givetian)–Upper Permian (Tatarian):* cosmopolitan.——FIG. 793,*1a–t.* **P. acuminatus* (SOWERBY); *a–e,* hypotype, dorsal, ventral, lateral, anterior, and posterior views, Lower Carboniferous, Viséan subzone D2, Derbyshire, Thorpe Cloud, England, ×1 (new); *f–t,* hypotype, serial sections, Lower Carboniferous, Dublin, Eire, ×2.8 (Schmidt, 1965a).

Aikarhyncha HAVLÍČEK, 1990b, p. 212 [**Rhynchonella praecox* BARRANDE, 1879b, pl. 29, case 1, fig. 1a–e; OD]. Shell small; subpentagonal outline; dorsibiconvex profile with dorsal valve strongly inflated anteriorly. Beak suberect; delthyrium open. Fold and sulcus strong, from midlength. Costae very strong, angular, arising at about one-third shell length; anterior commissure uniplicate and coarsely dentate, tongue high. Dental plates short, converging toward valve floor. Hinge plates divided; dorsal median septum and septalium absent. *Lower Devonian (Pragian):* Bohemia, Salair.——FIG. 793,*2a–i.* **A. praecox* (BARRANDE), Koneprusy Limestone, Koneprusy, Bohemia; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×4 (new); *f,* serial section, ventral valve, ×6; *g–i,* serial sections, dorsal valve at 7.1, 6.95, 6.7 from anterior, ×6 (Havlíček, 1990b).

Allorhynchoides SAVAGE, EBERLEIN, & CHURKIN, 1978, p. 392 [**A. kirki;* OD]. Small, subcircular to longitudinally ovate, with few, strong plications on fold and in sulcus. Umbones smooth. Fold with median sinus and sulcus with median plication. Dental plates short, ventrally convergent; large elongate teeth inclined dorsally. Hinge plates divided, subhorizontal. Dorsal median septum and septalium absent. *Upper Devonian (Famennian):* southeastern Alaska.——FIG. 794,*3a–l.* **A. kirki,* upper

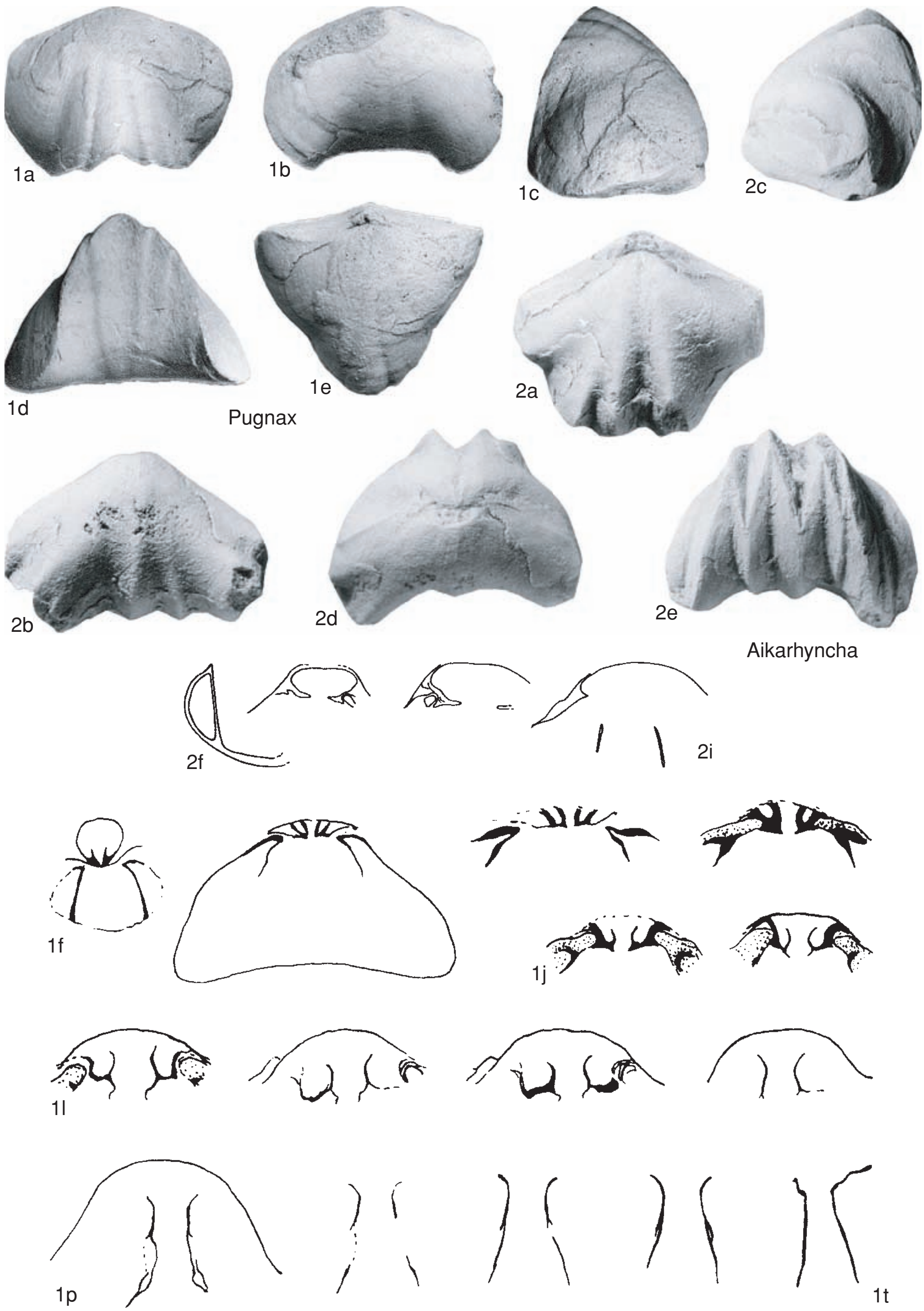

FIG. 793. Pugnacidae (p. 1165).

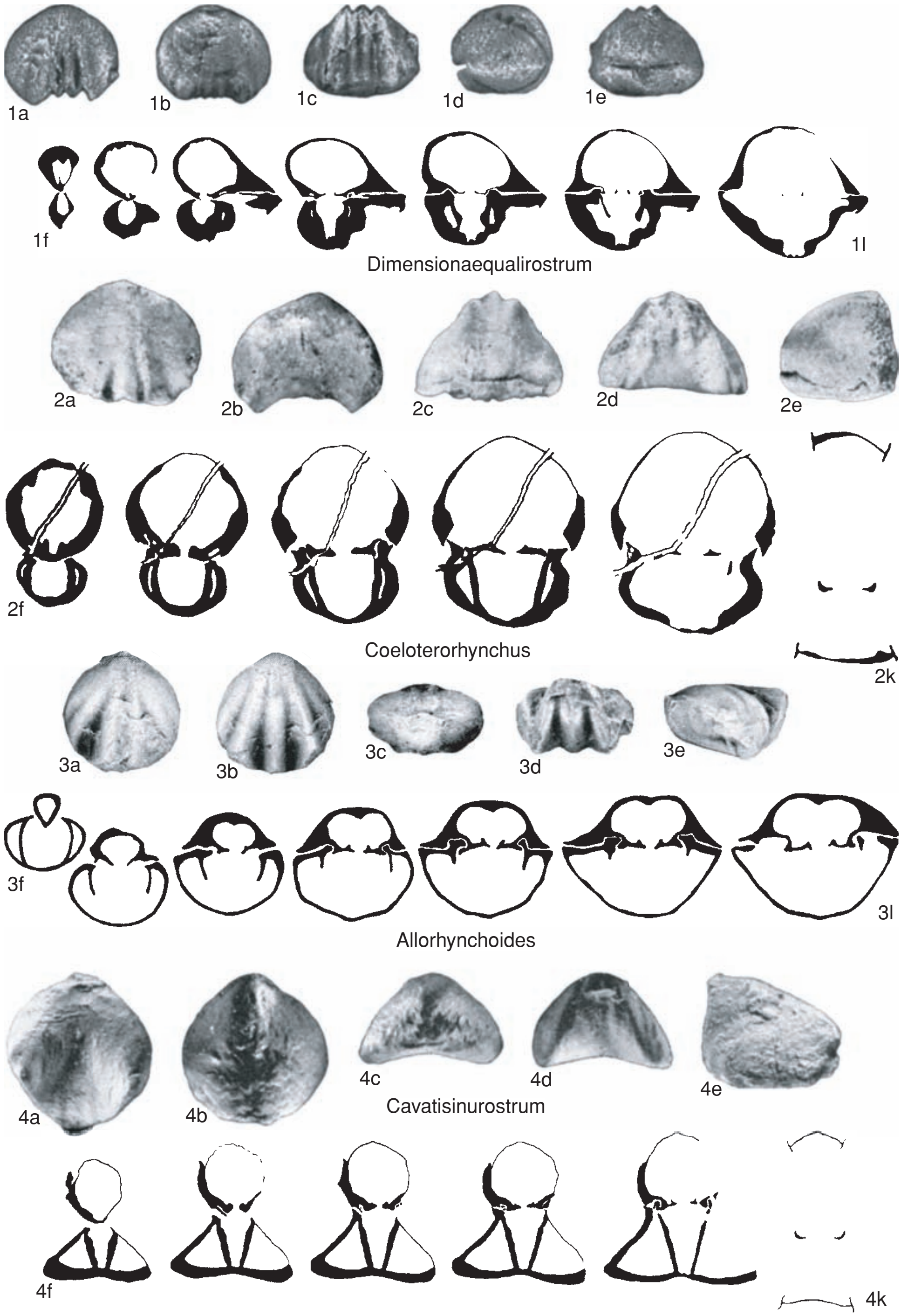

FIG. 794. Pugnacidae (p. 1165–1168).

Famennian, Port Refugio Formation, Suemez Island, Port Refugio; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×3; *f–l,* serial sections 0.6, 0.7, 0.8, 0.9, 1.1, 1.2, 1.3 mm from posterior, ×4 (Savage, Eberlein, & Churkin, 1978).

Cavatisinurostrum SARTENAER, 1972, p. 2 [**C. faniae;* OD]. Large; subcircular to subtriangular; strongly convexiconcave, dorsal valve inflated anteriorly, ventral valve flat to concave; anterior commissure uniplicate to acuminate. Costae weak, rounded, restricted to extreme anterior of fold and sulcus; fine radial striae present. Dental plates long, converging almost to meet ventrally. Hinge plates divided, small; dorsal septum absent; crura long, thin, convex ventrolaterally. *Upper Devonian (Famennian):* western Europe, Western Australia.——FIG. 794,*4a–k.* **C. faniae,* lower Famennian, Heure, Belgium; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–k,* serial sections 1.9, 2.35, 2.5, 2.9, 3.5, 6.1 mm from posterior, ×2 (Sartenaer, 1972).

Chapinella SAVAGE, EBERLEIN, & CHURKIN, 1978, p. 388 [**C. bucareliensis;* OD]. Small; transversely ovate outline and dorsibiconvex profile. Fold and sulcus distinct anteriorly; shell mostly smooth but costae strong and subangular in anterior third; tongue strongly plicated. Dental plates short, ventrally convergent. Dorsal median septum and septalium absent; hinge plates divided, inner edges flexed dorsally. *Upper Devonian (Famennian):* southeastern Alaska.——FIG. 795,*1a–l.* **C. bucareliensis,* upper Famennian, Port Refugio Formation, Suemez Island, Port Refugio; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–l,* serial sections 0.4, 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 2.1 mm from posterior, ×4 (Savage, Eberlein, & Churkin, 1978).

Coeloterorhynchus SARTENAER, 1966a, p. 41 [**C. tabasensis;* OD]. Subtriangular to transversely ovate; dorsal valve inflated, ventral flat to concave. Beak incurved; foramen small, with small deltidial plates. Fold and sulcus wide; tongue high, serrated to acute. Costae few, rounded, from about midlength, with striae in some specimens. Dental plates distinct, ventrally convergent; ventral muscle field well impressed. Hinge plates divided; dorsal median septum and septalium absent. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Iran, Afghanistan, Europe, northern Africa, China.——FIG. 794,*2a–k.* **C. tabasensis,* Frasnian, Shishtu Formation, Niaz, Sardar Valley, Iran; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–k,* serial sections 1.0, 1.45, 1.75, 2.1, 2.3, 3.35 mm from posterior, ×3 (Sartenaer, 1966a).

Colophragma COOPER & DUTRO, 1982, p. 77 [**C. ellipticum;* OD]. Transversely subpentagonal outline; strongly biconvex, dorsal valve inflated. Beak erect; foramen small, mesothyridid, deltidial plates conjunct. Fold and sulcus pronounced anteriorly; tongue high, serrate; umbones smooth. Costae weak and rounded at midlength, strong and angular anteriorly. Dental plates long, ventrally convergent. Hinge plates divided, horizontal; septalium and dorsal median septum very short. *Upper Devonian (Frasnian–Famennian):* USA (New Mexico).——FIG. 796,*1a–j.* **C. ellipticum,* upper Frasnian, Contadero Formation, San Andres Mountains; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–j,* serial sections 0.3, 0.5, 0.6, 1.1, 1.7 mm from posterior, ×2 (Cooper & Dutro, 1982).

Dimensionaequalirostrum SARTENAER, 1980, p. 2 [**D. pileum;* OD]. Subcircular outline and strongly biconvex profile. Beak erect; foramen small and circular. Fold and sulcus wide, commencing at midlength; tongue high. Costae strong and subangular anteriorly. Dental plates short, ventrally convergent; ventral muscle field deeply impressed. Hinge plates divided; dorsal median septum weak to absent; crura delicate, tips curved ventrally and in form of inverted gutter. *Upper Devonian (Famennian):* Belgium, Moravia, ?Bashkirskaya.——FIG. 794,*1a–l.* **D. pileum,* lower Famennian, Senzeilles section, railway cutting southeast of Senzeilles tunnel, Belgium; *a–e,* holotype, dorsal, ventral, anterior, lateral, and posterior views, ×1; *f–l,* serial sections 0.7, 1.3, 1.6, 2.2, 2.6, 3.0, 3.4 mm from posterior, ×2.4 (Sartenaer, 1980).

Eopugnax BARANOV, 1991, p. 37 [**E. gonensis;* OD]. Small; subtriangular to subpentagonal outline; dorsibiconvex. Fold and sulcus weak, wide; shell mostly smooth. Costae few, rounded, arising at two-thirds shell length, with 2 wide costae on fold, 1 in sulcus; tongue high; anterior commissure sulciplicate. Dental plates absent. Hinge plates divided, inclined dorsally; dorsal median ridge present; septum and septalium absent. *Lower Devonian (Emsian):* eastern Siberia.——FIG. 796,*2a–i.* **E. gonensis,* middle Krivoy Ruchey Formation, Selennyakhskiy Kryazh, Gon Creek; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–i,* serial sections, intervals not given, ×7 (Baranov, 1991).

Evanidisinurostrum SARTENAER, 1987a, p. 135 [**Pseudoleiorhynchus (?) zemoulensis* DROT, 1964b, p. 172; OD]. Subtriangular outline; moderately biconvex profile. Beak suberect; foramen small. Fold and sulcus weak but arising at umbones; most of shell smooth, with costae developed anteriorly. Costae coarse, rounded, with 2 costae on fold, single costa in sulcus; tongue low, rounded; anterior commissure sulciplicate. Dental plates absent; ventral muscle field moderately impressed. Hinge plates divided, sloping slightly dorsally; dorsal median septum and septalium absent; crura rodlike, subparallel, with distal ends sharply flexed ventrally. *Upper Devonian (Famennian):* Morocco.——FIG. 795,*3a–k.* **E. zemoulensis* (DROT), lower Famennian, plains of Drah-el-Kelba; *a–c,* holotype, dorsal, anterior, and lateral views, ×1; *d–k,* serial sections 1.1, 1.3, 1.5, 1.7, 1.9, 2.1, 2.6, 3.0 mm from posterior, ×3.6 (Drot, 1964b).

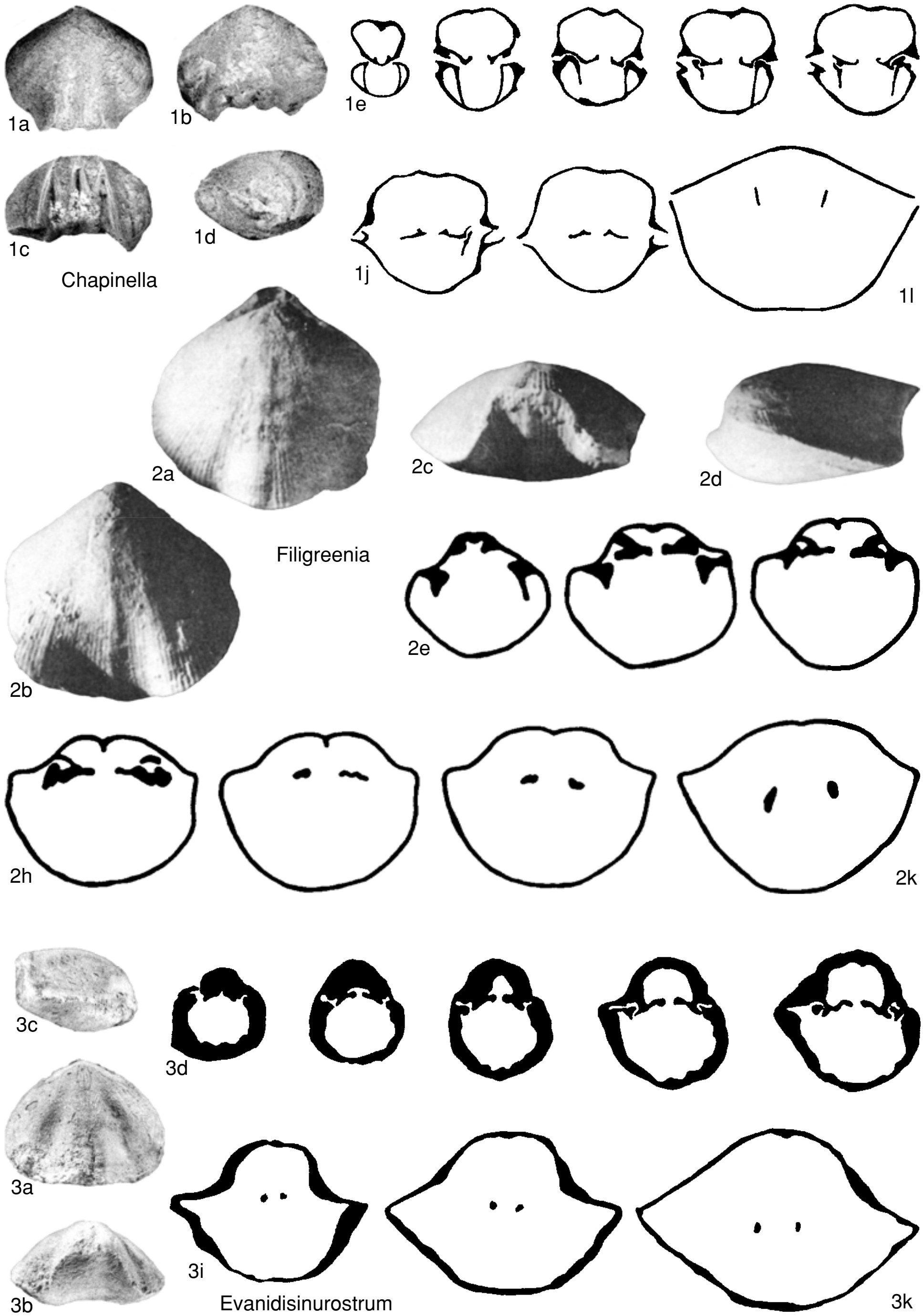

FIG. 795. Pugnacidae (p. 1168–1171).

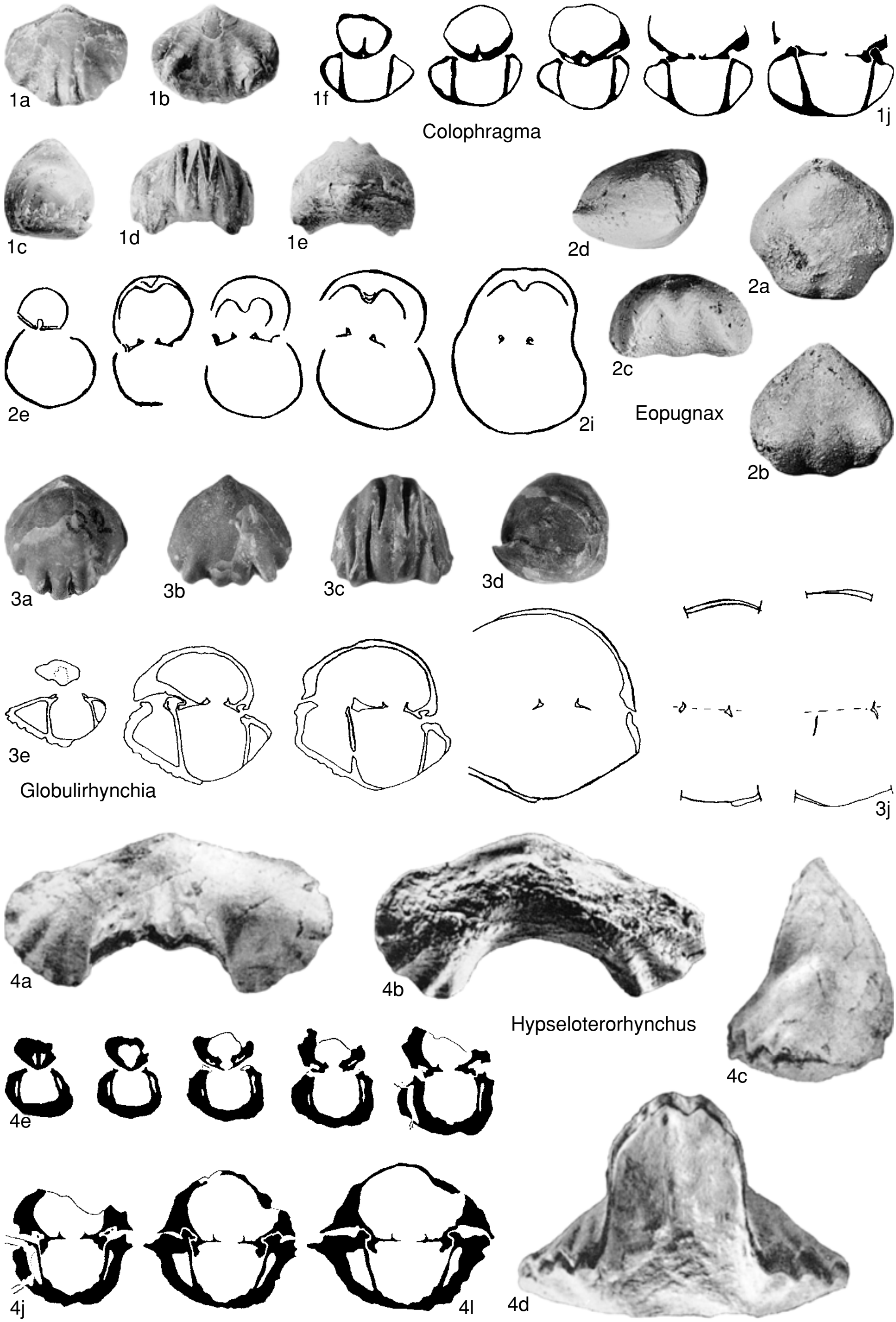

FIG. 796. Pugnacidae (p. 1168–1171).

Filigreenia SOJA, 1988, p. 156 [**F. circularis;* OD]. Outline subcircular; profile dorsibiconvex. Beak suberect; foramen hypothyrid. Fold and sulcus rounded, arising near umbones; faint sinus on fold, ridge in sulcus; anterior commissure uniplicate. Fine costellae present and most evident anteriorly. Dental plates short and ventrally divergent. Hinge plates divided; dorsal median ridge extending to about hinge line; crural bases horizontal; crura becoming laterally compressed distally. *Lower Devonian (Emsian):* USA (southeastern Alaska).——FIG. 795,*2a–k.* **F. circularis,* middle Emsian, Kasaan Island; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2.5; *e–k,* serial sections 1.3, 1.55, 1.65, 1.75, 1.85, 1.95, 2.20 mm from posterior, ×6 (Soja, 1988).

Globulirhynchia BRICE, 1981a, p. 149 [**Rhynchonella le mesli* RIGAUX, 1892, p. 103; OD]. Subtriangular outline; strongly inflated dorsal valve. Beak suberect; foramen small, mesothyridid. Fold and sulcus strong anteriorly; tongue high. Costae coarse, few, rounded, developed only anteriorly. Dental plates well developed, slightly convergent ventrally. Hinge plates divided; dorsal median septum and septalium absent. *Upper Devonian (lower Frasnian):* western Europe.——FIG. 796,*3a–j.* **G. lemesli* (RIGAUX), Beaulieu Formation, Boulonnais, Ferques, northeastern France; *a–d,* dorsal, ventral, anterior, and lateral views, ×1; *e–j,* serial sections 0.7, 1.1, 1.2, 1.7, 2.0, 2.4 mm from posterior, ×8 (Brice, 1981a).

Hypseloterorhynchus SARTENAER, 1971a, p. 2 [**H. pennatus;* OD]. Large; transversely ovate, with emarginate anterior; inflated profile, tongue very high. Beak incurved. Fold and sulcus very strong anteriorly. Costae few, low, developed anteriorly only. Dental plates long, ventrally convergent. Hinge plates divided; septalium absent; dorsal median septum rudimentary. *Upper Devonian (Famennian):* Western Australia.——FIG. 796,*4a–l.* **H. pennatus,* Virgin Hills Formation, Mount Pierre, Casey Falls; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1; *e–l,* paratype, serial sections 0.85, 0.95, 1.20, 1.35, 1.55, 1.75, 2.05, 2.25 mm from posterior, ×3 (Sartenaer, 1971a).

Kwangsirhynchus HOU & XIAN, 1975, p. 38 [**K. liujingensis;* OD]. Small with subtriangular to subpentagonal outline and dorsibiconvex profile, strongly inflated anteriorly. Beak suberect. Fold and sulcus from umbones; anterior commissure uniplicate with high tongue trapezoid to acuminate. Costae subangular, simple, from beak, present on entire surface. Dental plates short, thin, vertical. Hinge plates divided, horizontal; crural plates not meeting valve floor; dorsal septum and septalium absent. *Lower Devonian (Pragian–Emsian):* southern China, Vietnam.——FIG. 797,*2a–i.* **K. liujingensis,* Pragian–lower Emsian, Nagaoling Formation, Guangxi, Hengxian County, Liujing, southern China; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Hou & Xian, 1975); *e–i,* serial sections 1.0, 3.8, 4.0, 4.2, 5.5 mm from posterior, ×3 (new).

Longdongshuia HOU & XIAN, 1975, p. 39 [**L. subaequata;* OD]. Small to medium with subcircular to subpentagonal outline and dorsibiconvex profile. Beak erect. Fold and sulcus strong but obscured by shell convexity; anterior commissure uniplicate; tongue high, rounded, dentate. Costae strong, simple, interspaces narrow, subangular, from beaks, covering entire surface. Dental plates short, vertical. Dorsal median septum, septalium, cardinal process absent; hinge plates united by convex plate, supported by pair of short crural plates posteriorly; crura short, strongly curved ventrally. *Middle Devonian (Eifelian):* China.——FIG. 798,*2a–n.* **L. subaequata,* Beiliuan, Longdongshui Formation, Guizhou, Dushan County, Houershan; *a–c,* holotype, ventral, lateral, and anterior views, ×1 (Hou & Xian, 1975); *d–g,* hypotype, dorsal, ventral, anterior, and lateral views, ×2; *h–n,* serial sections 0.9, 1.0, 1.4, 1.8, 1.9, 2.4, 2.5 mm from posterior, ×2.5 (Wang & Zhu, 1979).

Ningbingella ROBERTS, 1971, p. 152 [**N. flexuosa;* OD]. Large; outline transversely subpentagonal with emarginate anterior margin. Beak small, erect to incurved, pierced by small foramen. Fold and sulcus strong anteriorly; tongue high. Costae few, subangular, most pronounced anteriorly; radial striae present. Dental plates short, convergent ventrally, concave medially; uncovered septalium short, wide, supported by low dorsal median septum for one-third valve length; crura laterally compressed, with medially directed flange on distal ventral edge. *Lower Carboniferous (Tournaisian):* Western Australia, western Canada.——FIG. 799,*2a–l.* **N. flexuosa,* Ningbing Limestone, Bonaparte Gulf, Ningbing Range, northwestern Australia; *a–d,* holotype, ventral, anterior, posterior, and lateral views, ×1; *e–l,* serial sections 1.8, 2.0, 2.2, 2.8, 3.0, 3.2, 3.5, 3.9 mm from posterior, ×3.6 (Roberts, 1971).

Pammegetherhynchus SARTENAER, 1977, p. 68 [**P. merodae;* OD]. Transversely ovate with emarginate anterior; strongly dorsibiconvex with inflated anterior. Beak erect to incurved. Fold and sulcus very strong; anterior commissure strongly uniplicate; tongue high, rounded. Costae very weak to absent; radial striae present. Dental plates short, convergent ventrally. Hinge plates short, divided; dorsal median septum and septalium absent; long thin crura, concave dorsally. *Upper Devonian (Frasnian):* France, Poland.——FIG. 797,*1a–k.* **P. merodae,* upper Frasnian, Trélon, France; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–k,* serial sections 1.5, 1.65, 2.1, 2.8, 4.1, 4.2 mm from posterior, ×2.5 (Sartenaer, 1977).

Parapugnax SCHMIDT, 1964, p. 505 [**Pugnax pugnus brecciae* SCHMIDT, 1941b, p. 278; OD]. Large; transversely subovate outline with emarginate anterior; strongly inflated, especially anteriorly. Fold and sulcus pronounced; tongue very high. Costae few, developed anteriorly. Dental plates very short. Hinge plates slope dorsally to form septalium-like structure supported by weak median septum; hinge plates divided anterior of septalium; crura laterally

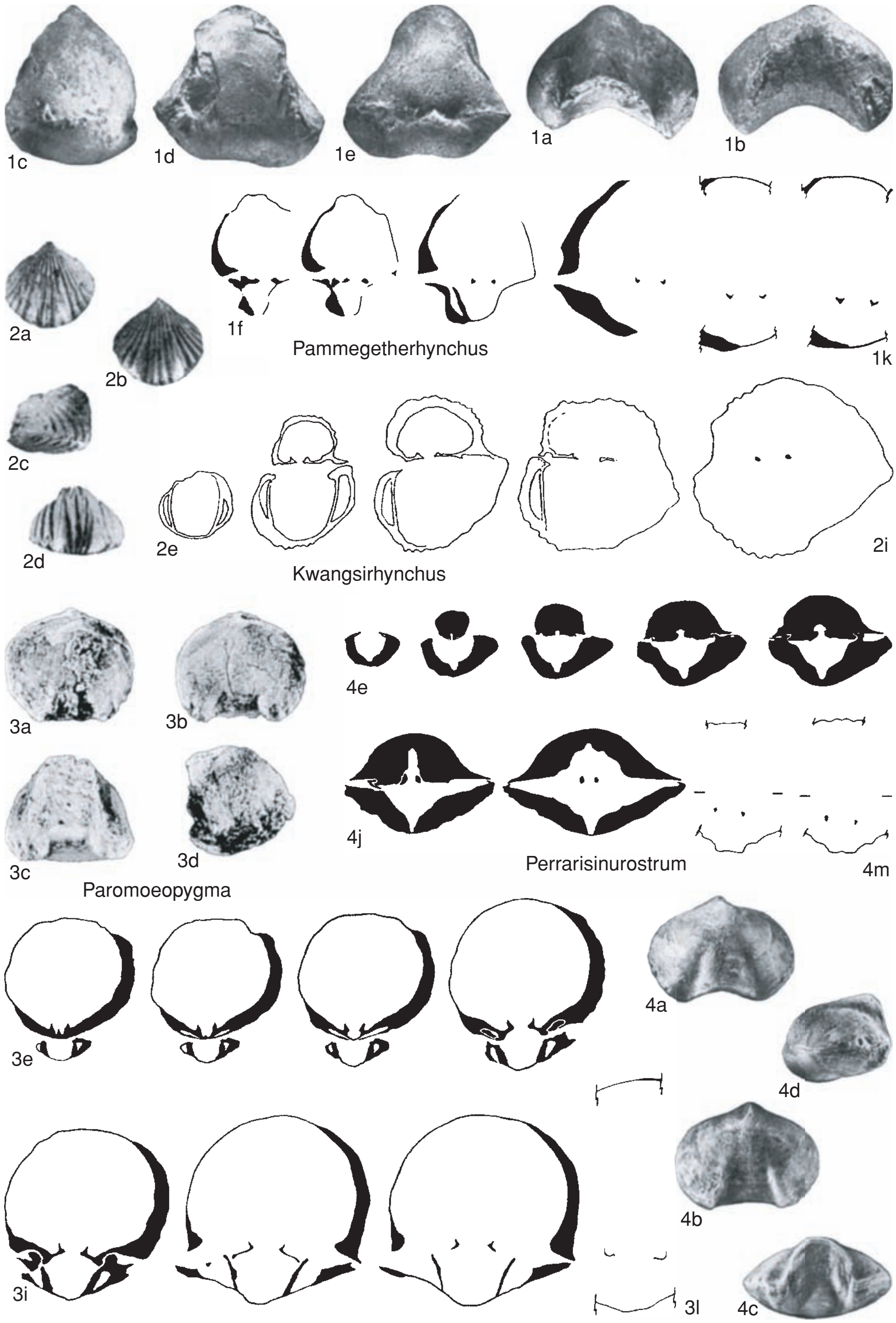

FIG. 797. Pugnacidae (p. 1171–1174).

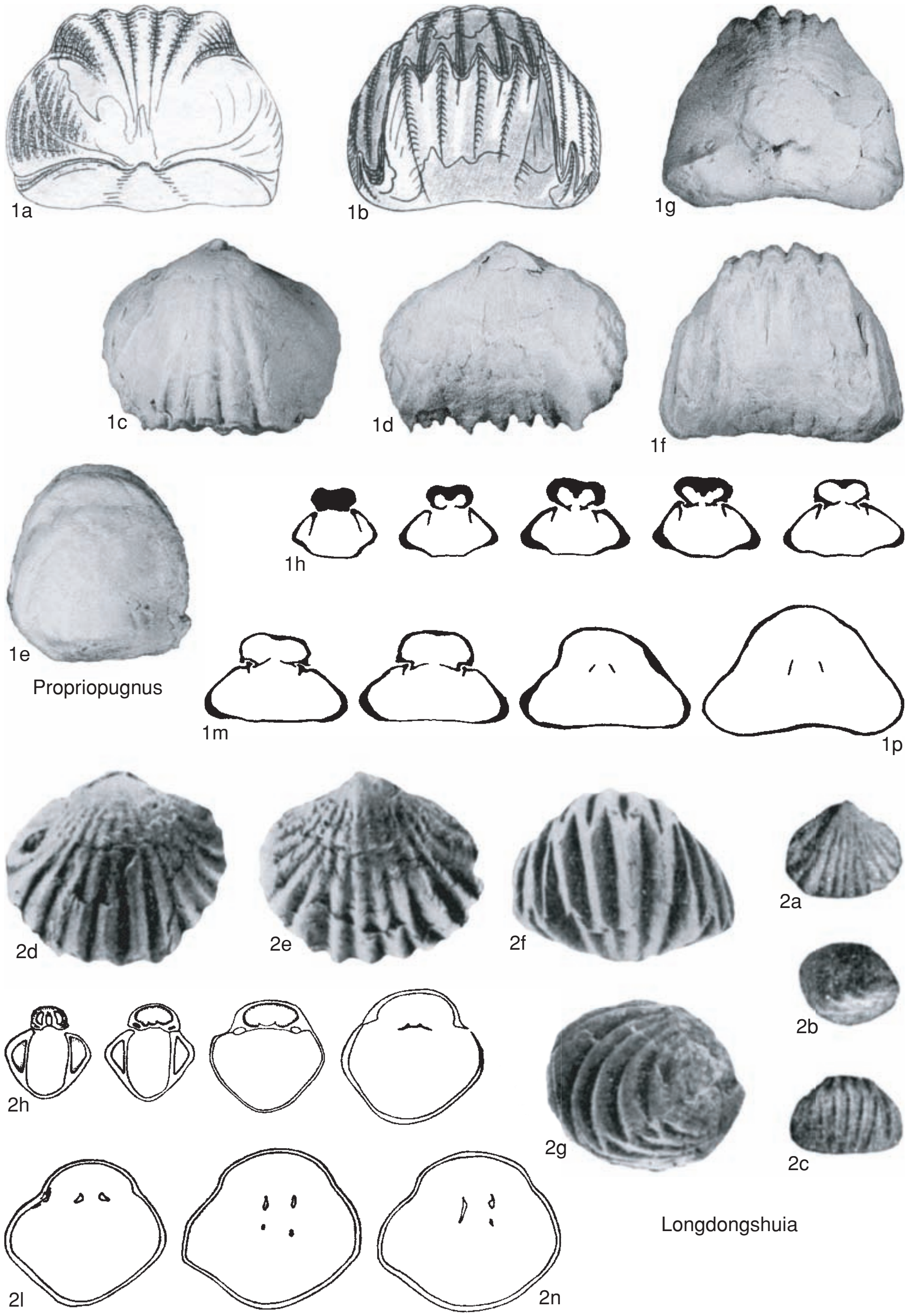

FIG. 798. Pugnacidae (p. 1171–1174).

compressed, with small, medially directed flange on distal ventral edge. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* cosmopolitan.——FIG. 799,*1a–m.* **P. brecciae* (SCHMIDT), Upper Devonian, Iberger Limestone, Dill syncline, Langenaubach, Germany; *a–c,* holotype, posterior, anterior, and lateral views, ×1 (Schmidt, 1941b); *d–i,* serial sections 15.3, 15.1, 15.0, 14.9, 14.7, 14.6 mm from anterior, ×3; *j–m,* serial sections 22.2, 21.8, 21.3, 21.0 mm from anterior, ×2.3 (Schmidt, 1965a).

Paromoeopygma SARTENAER, 1968c, p. 3 [**P. bellicastellana;* OD]. Medium to large with subcircular to transversely ovate outline and dorsibiconvex, anteriorly inflated profile. Beak suberect to erect; foramen small, deltidial plates present. Fold and sulcus most evident anteriorly; tongue high, serrate, may be rounded. Costae weak, coarse, rounded, only distinct anteriorly; umbones smooth; fine radial striations present. Dental plates low, short, ventrally convergent. Hinge plates divided; inner hinge plates inclined dorsally; dorsal median septum and septalium absent; crural bases small, crescentic in section, concave laterally; crura thin, concave dorsally. *Upper Devonian (Famennian):* Europe.——FIG. 797,*3a–l.* **P. bellicastellana,* lower Famennian, railway cutting southeast of Senzeilles tunnel, Belgium; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–l,* serial sections 0.9, 0.95, 1.05, 1.25, 1.35, 1.75, 1.85, 3.25 mm from posterior, ×3 (Sartenaer, 1968c).

Perrarisinurostrum SARTENAER, 1984a, p. 4 [**P. bensbergicum;* OD]. Transversely ovate outline; strongly biconvex, inflated anteriorly. Beak incurved; foramen small, deltidial plates present. Fold and sulcus strong; tongue rounded. Costae very weak, few, flanks smooth. Dental plates absent; hinge plates divided; dorsal median septum and septalium absent; crura long, thin, closely placed, slightly curved ventrally. *Upper Devonian (Famennian):* Germany, Morocco.——FIG. 797,*4a–m.* **P. bensbergicum,* lower Famennian, Knoppenbiessener Beds, Bergischland, Bensberg, Germany; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–m,* serial sections 0.65, 1.15, 1.35, 1.55, 1.7, 1.85, 2.3, 4.2, 4.45 mm from posterior, ×2.1 (Sartenaer, 1984a).

Pleuropugnoides FERGUSON, 1966, p. 354 [**Terebratula pleurodon* PHILLIPS, 1836, p. 222; OD]. Subpentagonal to transversely ovate outline and dorsibiconvex profile, inflated anteriorly. Beak straight to suberect; deltidial plates conjunct, foramen circular to oval. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue wide, high, trapezoid to rounded; margins zigzag. Costae strong, simple, rounded, extending from beaks. Dental plates short, vertical. Septalium very short to absent; hinge plates divided; dorsal median septum very short; crura ventrally curved with V-shaped section, open ventrally, and tips laterally flattened. *Carboniferous (lower Viséan–lower Westphalian):* Europe, Libya, China, Australia.——FIG. 800,*1a–k.* **P. pleurodon* (PHILLIPS); *a–c,* lectotype, dorsal, anterior, and lateral views, ×1; *d–k,* serial sections 0.7, 0.8, 1.0, 1.2, 1.6, 1.8, 2.2, 3.4 mm from posterior, ×4.5 (Ferguson, 1966).

Propriopugnus BRUNTON, 1984, p. 32 [**Conchyliolithus Anomites (Pugnus)* MARTIN, 1809, pl. 22, fig. 4–5; OD]. Large with subtriangular to subpentagonal outline and strongly biconvex profile; inflated anteriorly. Beak incurved; foramen mesothyrid. Fold and sulcus distinct, arising at umbones; tongue high, wide, trapezoid. Costae arising at umbones, coarse, most pronounced anteriorly, 4 or 5 on fold and in sulcus, fewer and weaker on flanks; radial striae not evident. Dental plates short. Dorsal median septum very short, low, thick; small septalium; hinge plates divided, thin, subhorizontal or inclined slightly dorsally; crura thin, becoming steeply oblique distally, laterally compressed. *Lower Carboniferous (Viséan):* western Europe.——FIG. 798,*1a–p.* **P. pugnus* (MARTIN), Carboniferous Limestone, England; *a–b,* holotype, posterior and anterior views, Derbyshire, ×1 (Martin, 1809); *c–g,* hypotype, dorsal, ventral, lateral, anterior, and posterior views, Staffordshire, Wetton, ×1.5; *h–p,* serial sections 1.1, 1.2, 1.3, 1.4, 1.5, 1.9, 2.4, 3.0, 4.3 mm from posterior, Staffordshire, Wetton, ×1.3 (new).

Solidipontirostrum SARTENAER, 1970a, p. 21 [**Terebratula pugnoides* SCHNUR, 1851, p. 3; OD]. Triangular to subpentagonal outline; very inflated dorsally. Beak erect to incurved. Fold and sulcus strong anteriorly; uniplicate with prominent tongue. Costae few, most prominent anteriorly. Dental plates short, vertical. Hinge plates united anterior of small septalium; dorsal median septum short. *Middle Devonian (Eifelian–Givetian):* Europe, western Siberia.——FIG. 800,*4a–i.* **S. pugnoides* (SCHNUR), upper Eifelian, Gondelsheimer Beds, Geeser bed, Germany; *a–c,* ventral, lateral, and anterior views, ×1.33; *d–i,* serial sections across posterior, intervals not given, ×3 (Schmidt, 1941a).

Trifidorostellum SARTENAER, 1961c, p. 5 [**Leiorhynchus dunbarense* HAYNES, 1916, p. 38; OD] [=*Pseudoleiorhynchus* ROZMAN, 1962, p. 122 (type, *Leiorhynchus uralicus* NALIVKIN, 1947, p. 90, OD)]. Transversely ovate outline; strongly biconvex, anteriorly inflated. Beak erect to incurved; foramen small, hypothyrid. Fold and sulcus strong, extending from umbones; anterior commissure uniplicate; tongue high, rounded. Strong costae arising at umbones, present in sulcus and on fold and flanks. Dental plates very short, close to walls. Hinge plates divided; dorsal median septum and septalium absent; crural plates short; crura concave dorsolaterally. *Upper Devonian (Famennian):* western North America, China, Kazakhstan.——FIG. 800,*2a–i.* **T. dunbarense* (HAYNES), middle Famennian, Three Forks Shale, Three Forks, Montana, USA; *a–e,* holotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f–i,* serial sections 0.8, 1.0, 1.1, 1.3 mm from posterior, ×2.9 (Sartenaer, 1961c).

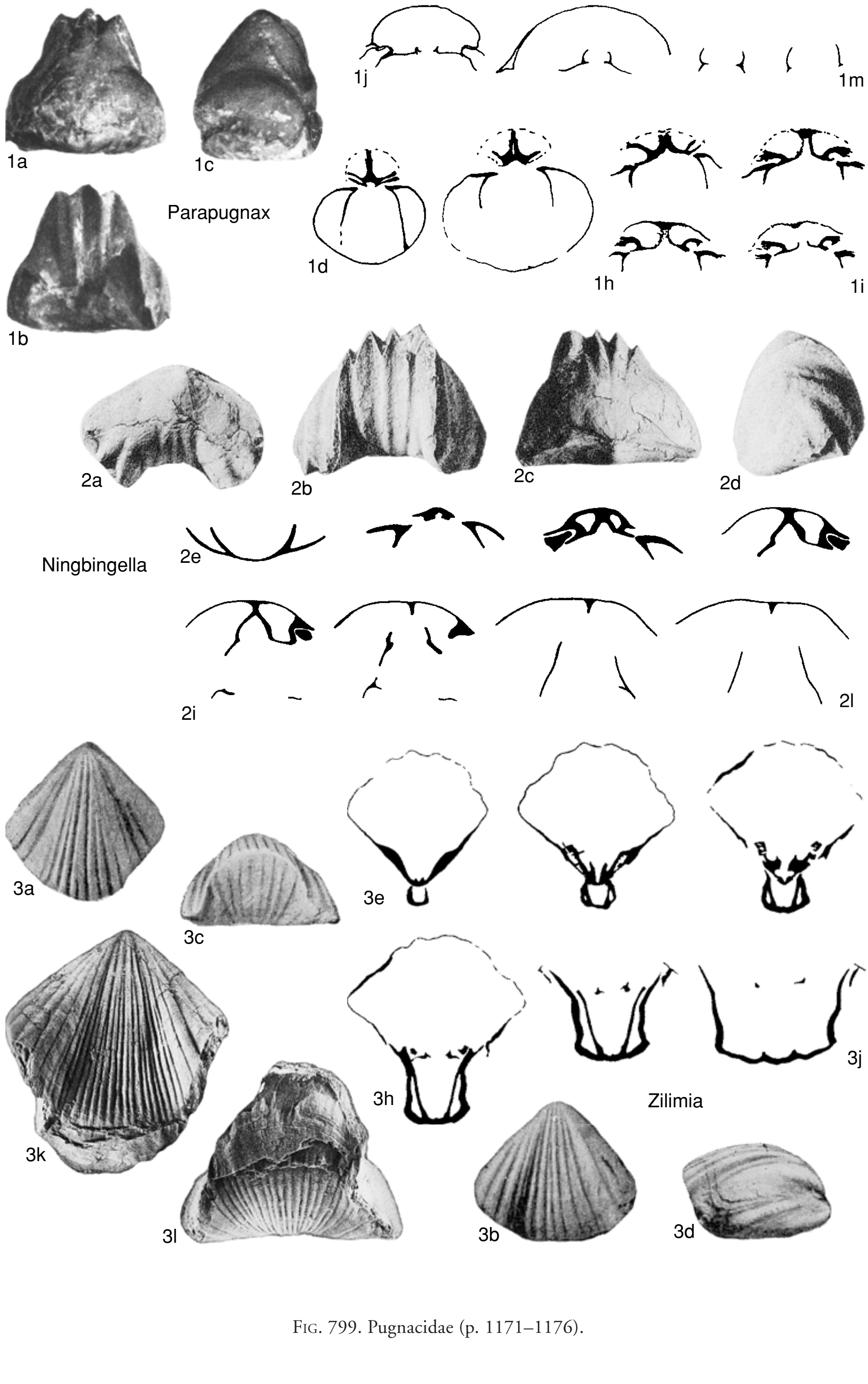

FIG. 799. Pugnacidae (p. 1171–1176).

Ujandinella Baranov, 1977, p. 75 [**U. remissiformis;* OD]. Small; subtriangular outline; moderately biconvex. Beak erect; fold and sulcus developed anteriorly; uniplicate with moderate tongue; smooth except for anterior costae; costae coarse, few, subangular. Dental plates short, thin. Hinge plates divided; dorsal septum and septalium absent. *Lower Devonian (Pragian):* eastern Siberia.——Fig. 800,*3a–k.* **U. remissiformis,* lower Pragian, Sagyrian suite, Selennyakhskiy Kryazh; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–k,* serial sections 0.6, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3 mm from posterior, ×4.5 (Baranov, 1977).

Zilimia Nalivkin, 1947, p. 93 [**Rhynchonella polonica* Gürich, 1896, p. 291; OD]. Large with subtriangular to subpentagonal outline and dorsibiconvex profile; ventral valve concave anteriorly because of strong, wide sulcus. Beak straight to suberect; foramen ovate. Fold and sulcus strong, wide, rounded; anterior commissure uniplicate, arched. Costae moderately strong, arising at beak, multiplying by bifurcation, variable in size. Dental plates long, converging and almost meeting toward valve floor. Hinge plates divided, small; dorsal septum absent; crural bases triangular in section; crura long, thin, convex ventrolaterally in section. *Upper Devonian (lower Famennian):* Poland, Urals, Kazakhstan, Tian Shan.——Fig. 799,*3a–l.* **Z. polonica* (Gurich); *a–d,* dorsal, ventral, anterior, and lateral views, southern Urals, ×1 (Rzhonsnitskaia, Likharev, & Makridin, 1960); *e–j,* serial sections 3.0, 3.4, 4.0, 4.95, 5.5, 7.7 mm from posterior, southern Urals, ×1.7 (Sartenaer, 1972); *k–l,* neotype, ventral and anterior views, Holy Cross Mountains, Gora Cmentarna, Poland, ×1.3 (Biernat & Szulczewski, 1993).

Family PLECTORHYNCHELLIDAE Rzhonsnitskaia, 1958

[Plectorhynchellidae Rzhonsnitskaia, 1958, p. 117]

[Materials prepared by Norman M. Savage]

Small Pugnacoidea with dorsal sulcus and ventral fold, longitudinally ovate outline, anterior commissure plicosulcate, smooth or with weak costae on fold and in sulcus. Dental plates short. Dorsal median septum absent or very short; hinge plates divided. *Lower Devonian (Lochkovian)–Upper Devonian (upper Famennian).*

Subfamily PLECTORHYNCHELLINAE Rzhonsnitskaia, 1958

[*nom. transl.* Savage, 1996, p. 254, *ex* Plectorhynchellidae Rzhonsnitskaia, 1958, p. 117]

Plectorhynchellidae with crura long, closely set. *Middle Devonian (lower Eifelian)–Upper Devonian (upper Famennian).*

Plectorhynchella Cooper & Muir-Wood, 1951, p. 195, *nom. nov. pro Monticola* Nalivkin, 1930b, p. 86, *non* Boie, 1822 [**Athyris collinensis* Frech, 1902, p. 99; OD]. Small; longitudinally ovate outline; ventribiconvex. Beak straight to erect; foramen rounded, hypothyrid. Dorsal sulcus and ventral fold low, wide; anterior commissure plicosulcate; umbones smooth. Costae subrounded, irregular, most pronounced in sulcus and on fold. Dental plates short, convergent to divergent ventrally; teeth short, convergent dorsally. Dorsal median septum short, thin, abruptly truncated; hinge plates divided; septalium absent; crura long, closely set. *Upper Devonian (Famennian):* Europe, Urals, northern Africa, central Asia, western North America.——Fig. 801,*1a–k.* **P. collinensis* (Frech), middle Famennian, Pizzo Collina Formation, Carnic Alps, Pizzo Collina, northern Italy; *a–d,* neotype, dorsal, ventral, anterior, and lateral views, ×1.5; *e–k,* serial sections 0.7, 0.8, 0.9, 1.0, 1.15, 1.3, 1.4 mm from posterior, ×7 (Ferrari & Vai, 1973).

Ipherron Havlíček, 1982a, p. 113 [**I. iphis;* OD]. Small; longitudinally ovate to cordiform with emarginate anterior; dorsal valve broadly sulcate, ventral valve broadly convex; anterior commissure unisulcate. Beak straight to suberect; foramen rounded and hypothyrid. Costae absent. Dental plates short, thin, vertical to ventrally convergent. Hinge plates united to form single flat plate supported by thin median septum that increases in height toward valve midlength. *Middle Devonian (lower Eifelian):* Bohemia.——Fig. 801,*2a–j.* **I. iphis,* upper Eifelian, Chotec Formation, Holyne, Prastav Quarry, Prague; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–j,* serial sections 6.55, 6.43, 6.33, 6.20, 6.05, 5.70 mm from anterior, ×7.5 (Havlíček, 1982a).

Kindleina Savage, Eberlein, & Churkin, 1978, p. 390 [**K. suemezensis;* OD]. Small; longitudinally ovate to subpentagonal outline; equibiconvex to ventribiconvex profile. Beak suberect; foramen circular, small, mesothyrid. Wide ventral fold extending most of valve length, bearing strong median groove; correspondingly wide dorsal sulcus bearing median ridge; anterior commissure plicosulcate. Costae weak, low, restricted to anterior of fold and sulcus; shell flanks smooth. Dental plates short, ventrally convergent; ventral muscle scars weakly impressed. Hinge plates divided, subhorizontal; crural plates, dorsal median septum, and septalium absent. *Upper Devonian (Famennian):* USA (southeastern Alaska).——Fig. 801,*3a–n.* **K. suemezensis,* upper Famennian, Port Refugio Formation, Suemez Island, Port Refugio; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f–n,* serial sections 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.9 mm from posterior, ×4.5 (Savage, Eberlein, & Churkin, 1978).

Nyege Veevers, 1959a, p. 113 [**N. scopimus;* OD]. Small; longitudinally subpentagonal outline; equibiconvex to ventribiconvex profile. Beak suberect; delthyrium open; dorsal sulcus with median

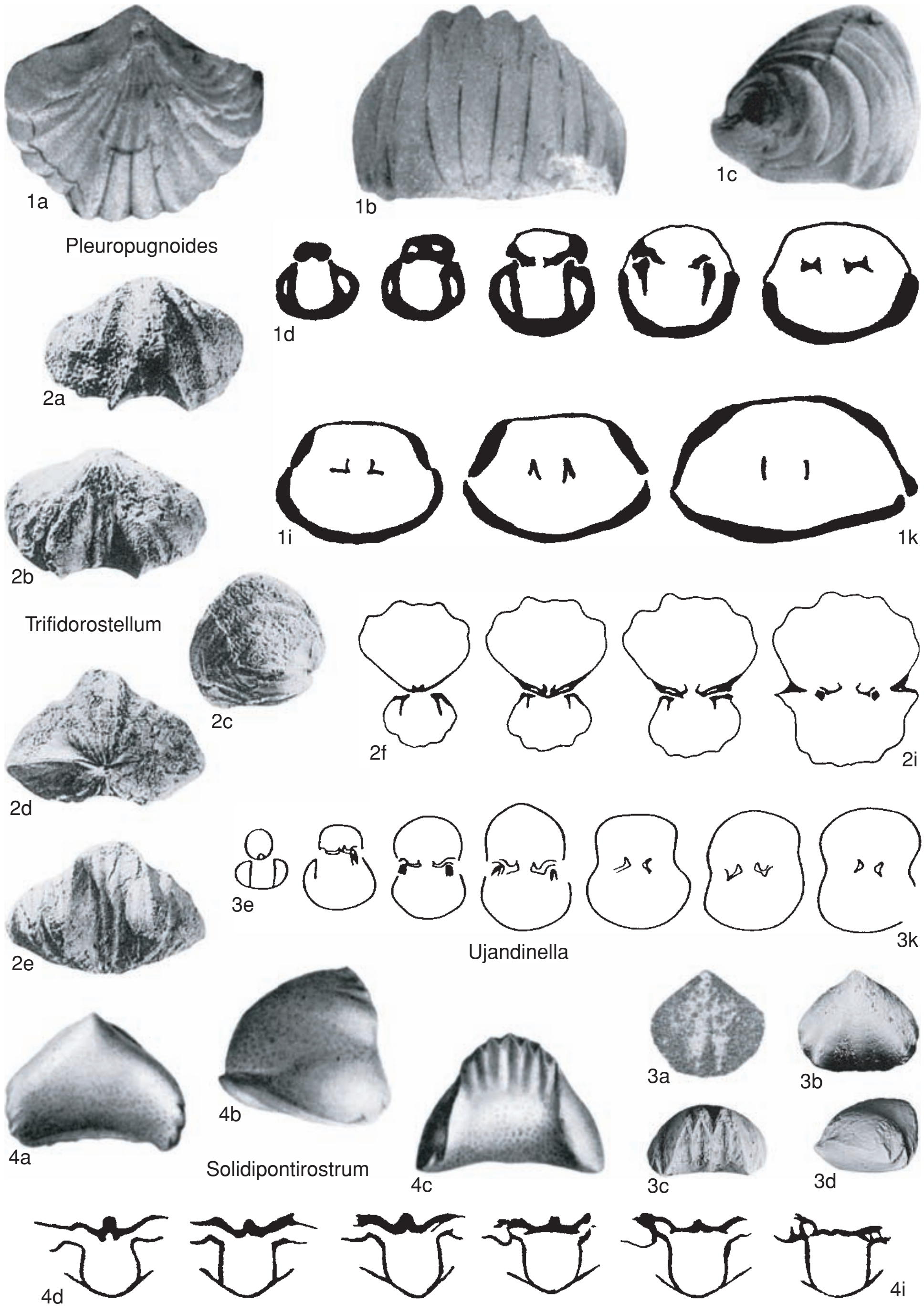

FIG. 800. Pugnacidae (p. 1174–1176).

fold and ventral fold with median sinus; anterior commissure plicosulcate. Costae arising at umbones, increasing by intercalation and bifurcation, present on flanks, fold, and sulcus. Dental plates short, vertical. Hinge plates divided, subhorizontal; crural plates, dorsal median septum, and septalium absent; cardinal process probably absent; crura long, parallel. *Upper Devonian (Famennian):* Western Australia.——FIG. 801,*5a–k.* **N. scopimus,* Bugle Gap Limestone, Fitzroy basin, Bugle Gap; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1.5; *f–k,* serial sections 0.7, 0.9, 0.95, 1.05, 1.15, 1.35 mm from posterior, ×4.5 (Veevers, 1959a).

Pseudoyunnanella CHEN, 1978a, p. 336 [**P. sichuanensis;* OD]. Small size with subcircular to subpentagonal outline and ventribiconvex profile. Beak straight to suberect. Dorsal sulcus with median fold and ventral fold with median sinus; anterior commissure plicosulcate. Fine costae arising at umbones, often coalescing to form coarse costae anteriorly. Dental plates short, vertical. Dorsal median septum short to absent; hinge plates divided, subhorizontal; cardinal process probably absent; crura long, parallel. *Upper Devonian (upper Famennian):* China.——FIG. 801,*4a–k.* **P. sichuanensis,* Maoba Formation, Sichuan, Chongin, Changheba; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–k,* serial sections 0.35, 0.5, 0.6, 0.9, 1.1, 1.85, 2.0 mm from posterior, ×4 (Chen, 1978a).

Subfamily PYGMAELLINAE Baranov, 1977

[*nom. transl.* SAVAGE, 1996, p. 254, *ex* Pygmaellidae BARANOV, 1977, p. 79]

Early Plectorhynchellidae with lyre-shaped crura in cross section. *Lower Devonian (Lochkovian–Emsian).*

Pygmaella BARANOV, 1977, p. 80 [**P. pygmaea;* OD]. Small; longitudinally ovate outline; ventribiconvex. Beak suberect to erect; delthyrium with narrow deltidial plates; foramen permesothyrid. Dorsal sulcus with low median ridge and ventral fold with low median groove; anterior commissure plicosulcate. Costae few, strong; umbones smooth. Dental plates short, slender. Hinge plates divided; crural plates resting on valve floor; dorsal median septum and septalium absent; crura long, straight, bearing small distal plates with lyre-shaped section. *Lower Devonian (Pragian):* eastern Siberia.——FIG. 802,*1a–m.* **P. pygmaea,* lower Pragian, Sagyrian beds, Selennyakh Range, Yakutsk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–m,* serial sections 0.3, 0.4, 0.5, 0.7, 1.0, 1.1, 1.3, 1.5, 1.6 mm from posterior, ×6 (Baranov, 1977).

Sibiritoechia ALEKSEEVA, 1966, p. 1147 [**S. convexa;* OD]. Small with longitudinally ovate outline and ventribiconvex profile. Beak suberect to erect. Dorsal valve with slight sulcus; ventral valve with weak fold; anterior commissure bisulcate. Costae few, strong, arising just anterior of umbones. Dental plates very short. Hinge plates divided; crural plates resting on valve floor; dorsal median septum and septalium absent; crural bases ovate, oblique; crura poorly known. *Lower Devonian (Lochkovian–Emsian):* eastern Siberia.——FIG. 802,*2a–e.* **S. convexa,* Emsian, southern Verkhoyansk Range, Sette-Daban Ridge, Krutoy Creek, northeastern Siberia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2.4; *e,* topotype, transverse section across posterior, ×7 (Alekseeva, 1966).——FIG. 802,*2f–l. S. oblongata* ALEKSEEVA, Lochkovian, southern Verkhoyansk Range, Sette-Daban Ridge, Tikhiy Creek, northeastern Siberia; topotype, serial sections, ×5 (Alekseeva, 1966).

Family LADOGIIDAE Ljaschenko, 1973

[Ladogiidae LJASCHENKO, 1973, p. 52]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea with high, rounded to acuminate tongue and fine, evenly spaced costae arising at beaks. Dental plates and dorsal median septum distinct; septalium short, often with cover plate. *Lower Devonian (Pragian)–Upper Devonian (Famennian).*

Ladogia NALIVKIN, 1941, p. 165 [**Terebratula meyendorfii* DE VERNEUIL, 1845, p. 74; OD]. Large with longitudinally ovate to rhomboid outline; strongly convex, acuminate dorsal valve and concave, sulcate ventral valve. Beak small, pointed, incurved; foramen hypothyrid. Fold and sulcus strong, wide to include most of shell width, extending from umbones. Anterior commissure uniplicate, acuminate. Flattened costellae cover shell surface. Dental plates long, convex medially; ventral muscle field well impressed, divided by low median ridges. Dorsal median septum strong, long; septalium wide, long; hinge plates concave, divided anteriorly; crura long, ventrally curved, distal parts concave dorsally. *Upper Devonian (Frasnian):* Baltic, European Russia, Urals, Siberia, Pamirs.——FIG. 803,*2a–o.* **L. meyendorfii* (DE VERNEUIL), lower Frasnian, Pskov Beds, Pskov, Baltic Russia; *a–c,* holotype, posterior, anterior, and lateral views, ×1 (de Verneuil, 1845); *d–h,* hypotype, dorsal, ventral, posterior, and anterior views, ×1; *i,* part of *e* showing costellae, ×3; *j–o,* hypotype, serial sections 1.8, 2.6, 3.1, 3.8, 4.9, 6.5 mm from posterior, ×2.4 (McLaren, 1962).

Camarothyridina LINNIK, 1966, p. 129 [**C. furssenkoi;* OD]. Medium size with subtriangular to subpentagonal outline and dorsibiconvex profile. Beak suberect; delthyrium open. Fold and sulcus arising at umbones; anterior commissure uniplicate, high, rounded. Costae fine, simple, numerous, covering entire surface. Dental plates short, vertical. Septalium short; hinge plates divided; dorsal median

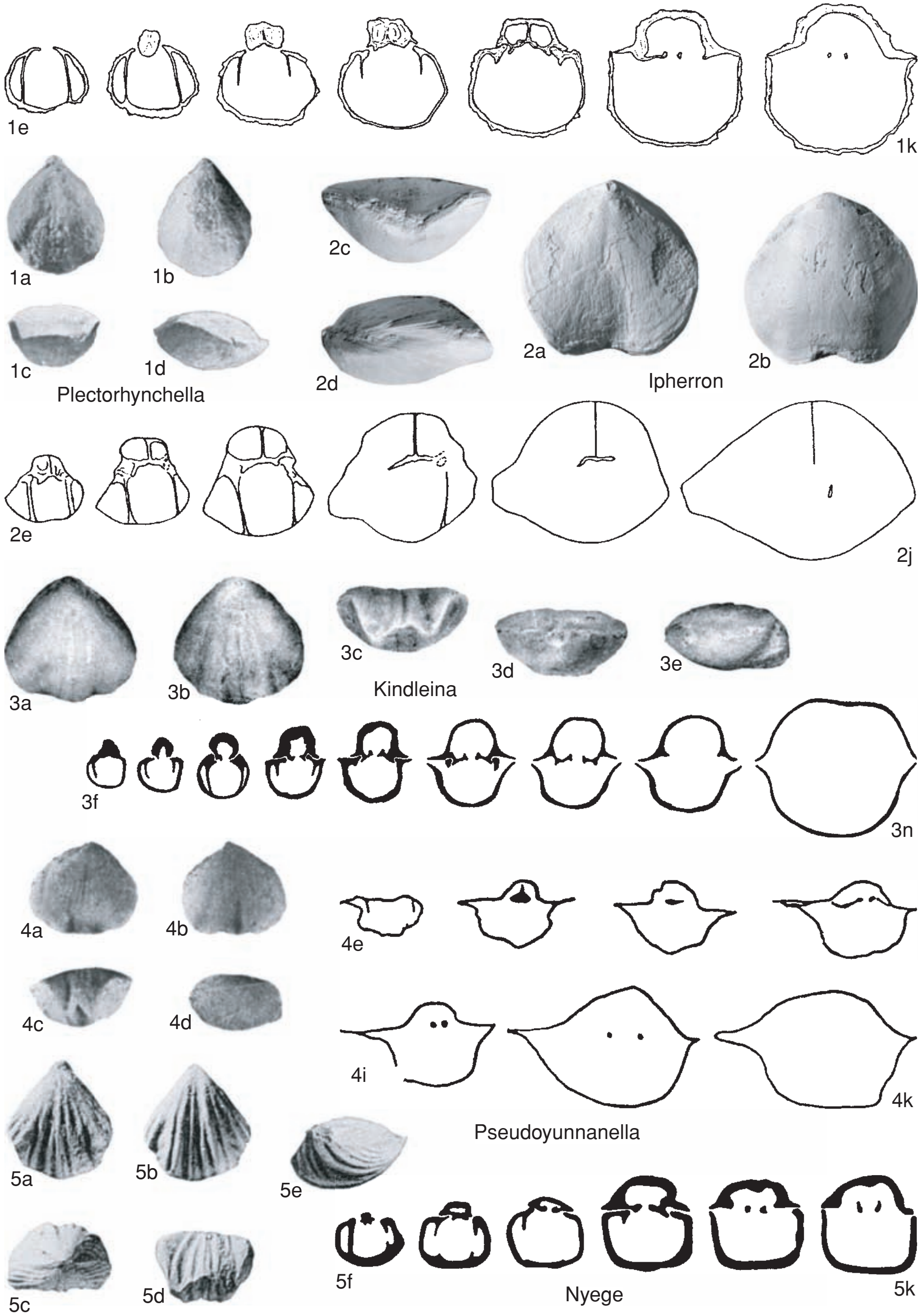

FIG. 801. Plectorhynchellidae (p. 1176–1178).

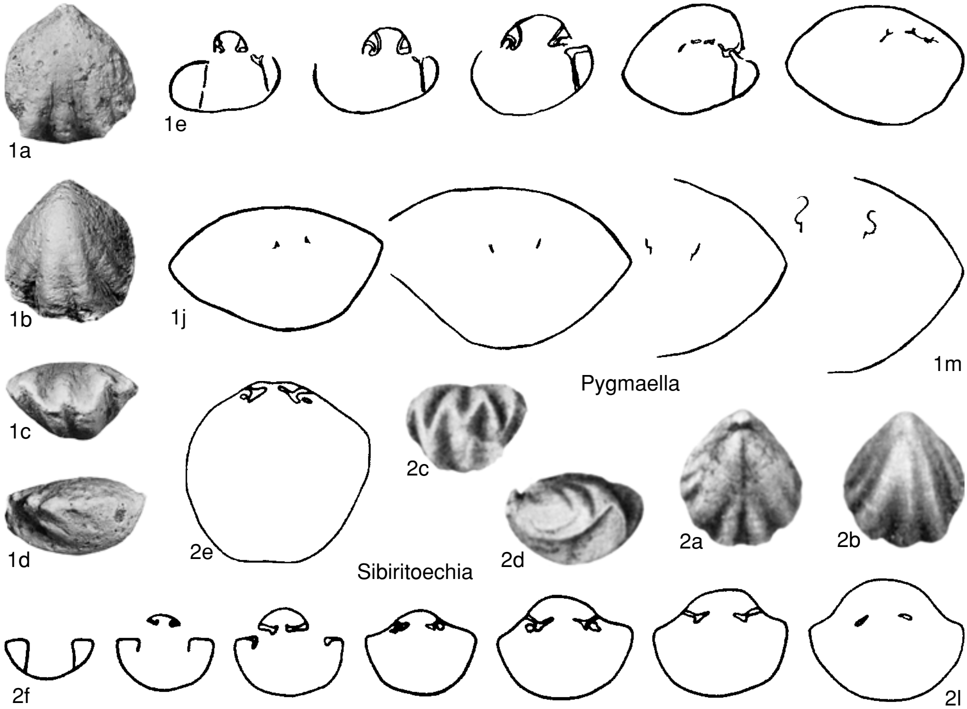

FIG. 802. Plectorhynchellidae (p. 1178).

septum long, low. Crura long, concave dorsomedially. *Upper Devonian (Famennian):* Belorussia (Pripet depression).——FIG. 804,*4a–g*. **C. furssenkoi,* lower Famennian, Zadonsk horizon, Minsk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e,* serial section, ×1.7; *f,* serial section, ×1.2; *g,* serial section, ×1.5 (Linnik, 1966).

Comiotoechia LJASCHENKO, 1973, p. 37 [**Camarotoechia galinae* LJASCHENKO, 1958, p. 124; OD]. Small size with transversely ovate outline and moderately biconvex profile. Beak large, posteriorly protruding, suberect. Fold and sulcus with rounded margins, expressed anteriorly as evenly rounded, flared tongue. Costae fine, simple, rounded, extending from umbones to commissure. Dental plates stout, short. Dorsal median septum short; septalium open posteriorly but with ridged cover plate anteriorly. *Upper Devonian (lower Frasnian):* Timan, Urals, central Russian Platform.——FIG. 804,*1a–g*. **C. galinae* (LJASCHENKO), Ust-Iaregisk beds, southern Timan, mouth of Yaregi River; *a–e,* dorsal, ventral, anterior, posterior, and lateral views, ×2; *f–g,* serial sections, ×2 (Ljaschenko, 1973).

Gracilotoechia BARANOV, 1977, p. 78 [**G. sinuata;* OD]. Subpentagonal to subcircular outline and biconvex, lenticular profile. Beak straight; delthyrium open. Fold and sulcus weak, from midlength; anterior commissure gently uniplicate. Surface costellate. Dental plates short, vertical. Dorsal median septum short, low; septalium wide, short; hinge plates divided anterior of septalium. *Lower Devonian (Pragian):* eastern Siberia.——FIG. 803,*1a–m*. **G. sinuata,* lower Pragian, Sagyrian suite, Selennyakh Ridge; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–h,* hypotype, dorsal, ventral, anterior, and lateral views, ×2; *i–m,* serial sections 0.5, 1.4, 2.1, 2.3, 2.4 mm from posterior, ×5 (Baranov, 1977).

Ladogifornix SCHMIDT, 1964, p. 505 [**Terebratula fornicata* SCHNUR, 1853, p. 175; OD]. Subtetrahedral shape; ventral valve flat to concave, dorsal valve convex and inflated anteriorly. Beak suberect. Fold and sulcus broad, rounded; anterior commissure uniplicate; tongue wide, high, rounded. Costae fine, from umbones, with some bifurcation. Dental plates vertical, long; umbonal cavities wide. Dorsal median septum high, extending to midlength; septalium long, wide, V-shaped, partly covered by inner hinge plates; hinge plates undivided; crura long, ventrally curved. *Middle Devonian (Eifelian):* Germany.——FIG. 804,*6a–j*. **L. fornicatus* (SCHNUR), Eifel; *a–d,* dorsal, ventral, anterior, and lateral views, Gerolsteiner Kalk, ×1 (Schnur, 1853); *e–j,* serial sections 16.5, 16.0, 15.4, 15.2, 15.0, 14.3 mm from anterior, Nohner Beds, ×5 (Schmidt, 1965a).

Ladogilina LJASCHENKO, 1973, p. 58 [**L. rossica;* OD] [=*Ladogilinella* LJASCHENKO, 1973, p. 61 (type, *L.*

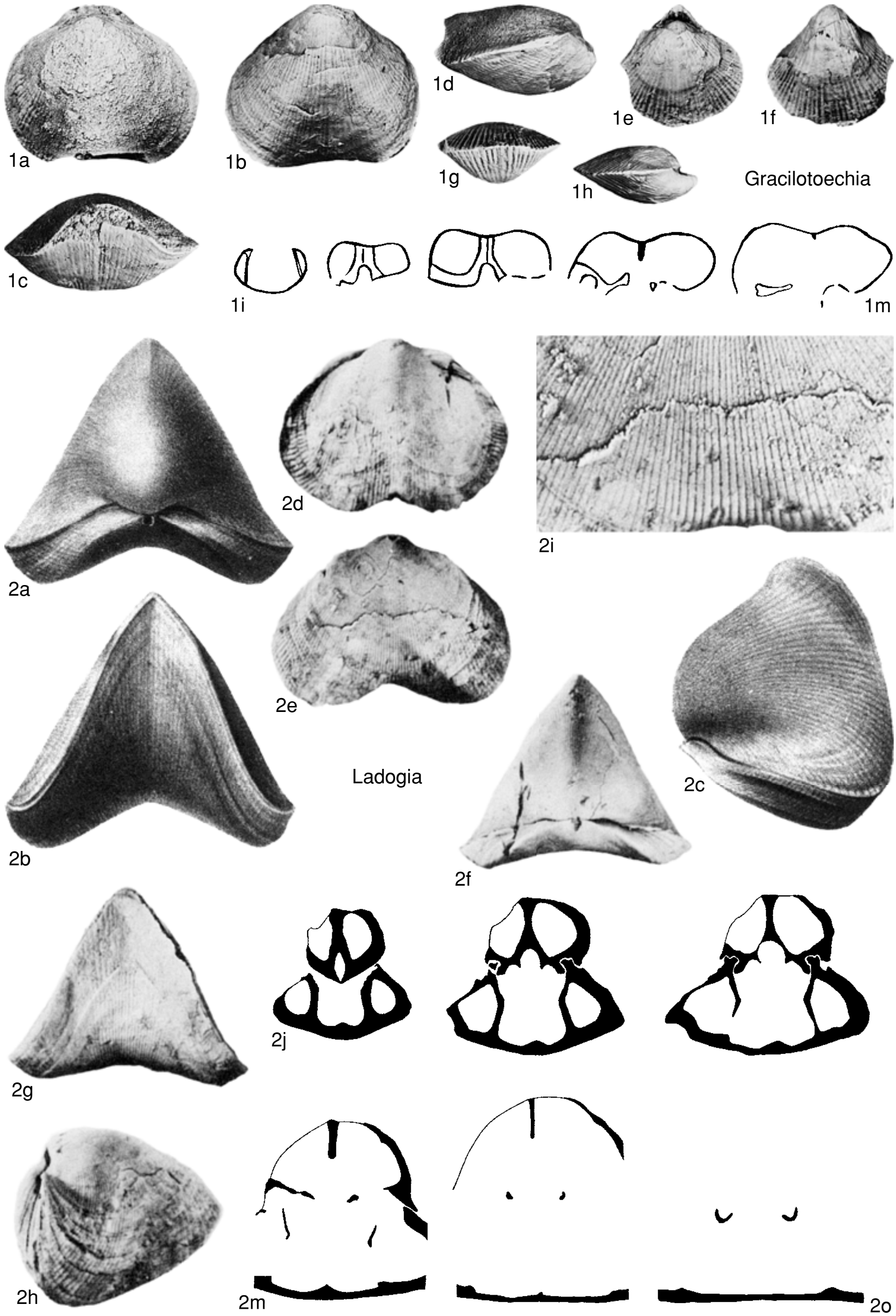

FIG. 803. Ladogiidae (p. 1178–1180).

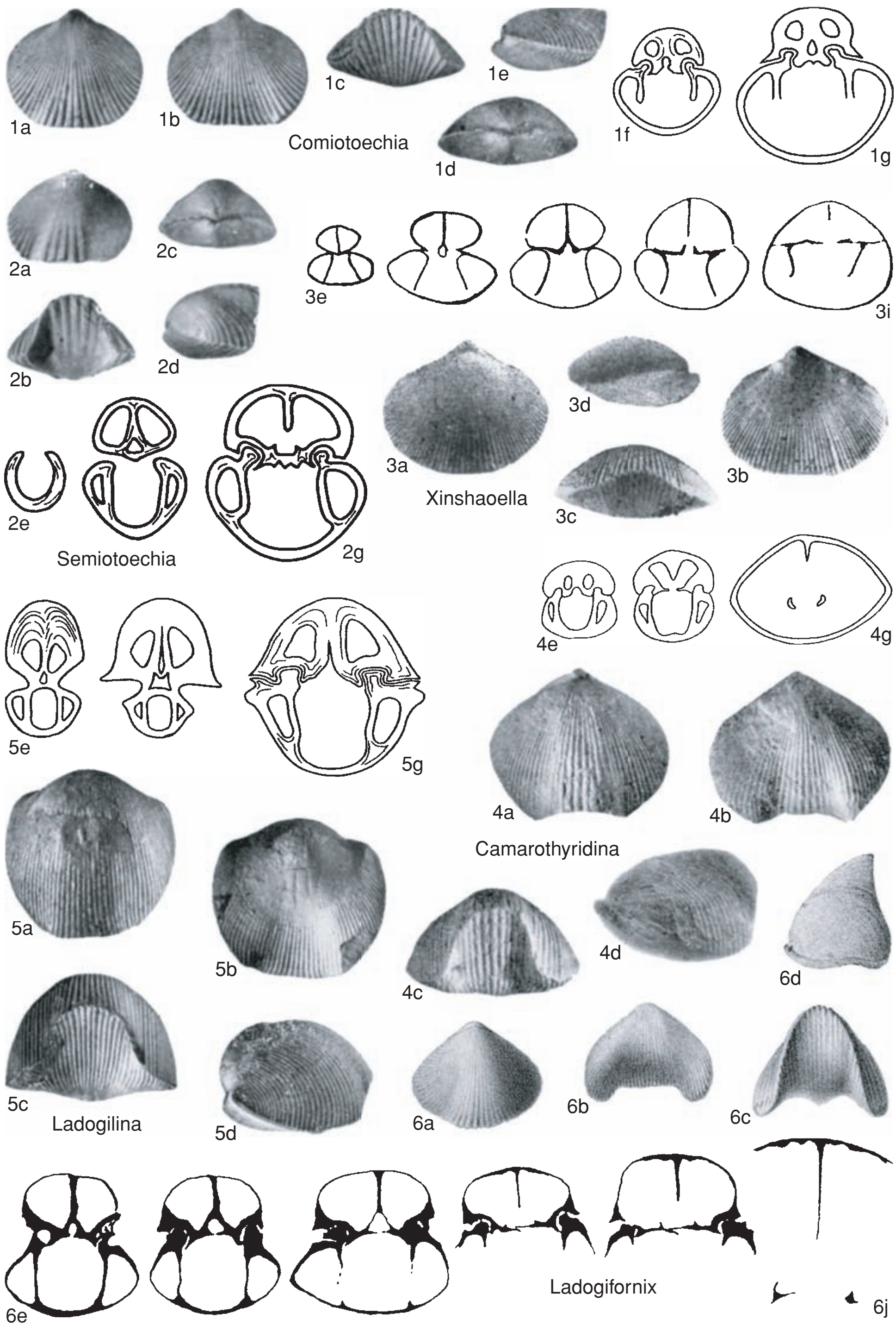

FIG. 804. Ladogiidae (p. 1178–1183).

mutabilis, OD)]. Subcircular to subovate outline and strongly dorsibiconvex profile. Beak erect to incurved. Fold and sulcus with gentle lateral margins, arising at about one-third valve length. Tongue high, flared, and rounded. Costae fine, even, simple, rounded, arising at beaks. Dental plates distinct, vertical. Dorsal interior with strong median septum; septalium with posterior cover plate. *Upper Devonian (lower Frasnian):* Volga-Urals, Timan. ——Fig. 804,*5a–d.* **L. rossica,* Sargaevsk Beds, Perm, Veslianka, Volga-Urals; holotype, dorsal, ventral, anterior, and lateral views, ×1.5 (Ljaschenko, 1973).——Fig. 804,*5e–g. L. simensis* (Ellern, Ivanov, & Kurbanov), lower Ust-Iaregsk Beds, Ukhta River, southern Timan; serial sections (Ljaschenko, 1973).

Semiotoechia Ljaschenko, 1973, p. 44 [**Camarotoechia polita* Ljaschenko, 1960, p. 9; OD]. Small with subpentagonal to transversely ovate outline and dorsibiconvex profile; anterior high because of strong fold; lateral flanks gently sloping. Beak erect. Fold and sulcus strong, extending from umbones; anterior commissure uniplicate; tongue wide, high, rounded, commonly forming highest part of shell. Costae extending from umbones, weak and rounded on umbones and flanks, becoming moderately strong and subangular anteriorly on fold and sulcus. Dental plates short, vertical. Dorsal median septum low, short; septalium short, with cover plate; hinge plates undivided anterior of septalium. *Middle Devonian (upper Givetian)–Upper Devonian (lower Frasnian):* Timan, Volga-Urals.——Fig. 804,*2a–g.* **S. polita* (Ljaschenko), lower Frasnian, between Kynovsk and Ust-Iaregsk beds, Ukhta River, mouth of the Yarega River, southern Timan; *a–d,* holotype, dorsal, anterior, posterior, and lateral views, ×1; *e–g,* serial sections (Ljaschenko, 1973).

Xinshaoella Zhao, 1977, p. 391 [**X. huaqiaoensis;* OD]. Transversely ovate outline and biconvex, lenticular profile. Beak suberect. Fold and sulcus very weak, restricted to anterior fifth of shell; anterior commissure gently uniplicate, rounded. Costae fine, numerous, rounded, from beaks. Dental plates short, ventrally divergent posteriorly, becoming convergent anteriorly. Dorsal median septum long; septalium short; hinge plates undivided, horizontal. *Upper Devonian (Famennian):* southern China.——Fig. 804,*3a–i.* **X. huaqiaoensis,* Hsikuangshan Formation, Hunan, Xinshau, Huaqiao; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i,* serial sections, ×2 (Zhao, 1977).

Family ROZMANARIIDAE Havlíček, 1982

[*nom. transl.* Havlíček, 1990b, p. 214, *ex* Rozmanariinae Havlíček, 1982a, p. 112]

[Materials prepared by Norman M. Savage]

Pugnacoidea with transversely ovate to subcircular outline; fold and sulcus sometimes low, generally fold in dorsal valve but may be in ventral valve; costae weak to absent; foramen with conjunct deltidial plates anteriorly. Dental plates short to absent. Dorsal median septum low or lacking; hinge plates divided; cardinal process absent. *Lower Devonian (Pragian)–Upper Devonian (Famennian).*

Rozmanaria Weyer, 1972, p. 85 [**Liorhynchus? equitans* Schmidt, 1924, p. 145; OD]. Transversely ovate outline, emarginate anterior, and ventribiconvex profile. Beak erect to incurved; foramen small; deltidial plates conjunct. Dorsal sulcus and ventral fold very strong anteriorly, resulting in unisulcate anterior commissure. Costae absent. Ventrally directed tongue pronounced, rounded. Dental plates absent. Hinge plates divided and curved dorsally, almost reaching valve floor; dorsal median septum and septalium absent; crura laterally compressed, ventrally divergent. *Upper Devonian (upper Famennian):* Germany, Bohemia, Poland, Urals.——Fig. 805,*1a–n.* **R. equitans* (Schmidt), Dasberg Beds, Sauerland, Oberroedinghausen, Germany; *a–e,* hypotype, dorsal, ventral, lateral, posterior, and anterior views, ×2; *f–n,* serial sections, ×8 (Weyer, 1972).

Errhynx Havlíček, 1982a, p. 112 [**E. erron;* OD]. Transversely ovate to cordiform outline; moderately ventribiconvex profile; emarginate anterior margin. Beak erect to incurved; foramen small; deltidial plates conjunct. Dorsal sulcus and ventral fold narrow, arising at umbones, becoming strong anteriorly; tongue rounded to rectangular, ventrally directed. Costae absent. Dental plates very short. Hinge plates divided, delicate, slightly inclined dorsally; dorsal median septum and septalium absent. *Middle Devonian (Eifelian):* Bohemia.——Fig. 805,*2a–g.* **E. erron,* upper Eifelian, Chotec Formation, Prague, Holyne; *a–d,* holotype, dorsal, ventral, posterior, and anterior views, ×3; *e–g,* serial sections 9.2, 8.8, 8.35 mm from anterior, ×5.5 (Havlíček, 1982a).

Hadyrhyncha Havlíček, 1979, p. 98 [**H. hadyensis;* OD]. Transversely ovate outline and weakly biconvex, lenticular profile. Beak small, incurved. Dorsal sulcus and ventral fold low, arising at midlength; anterior commissure gently unisulcate. Costae weak, rounded, developed on fold, in sulcus, and on flanks. Dental plates short to absent. Hinge plates divided, small, resting on valve floor; dorsal median septum and septalium absent. *Upper Devonian (Famennian):* Moravia.——Fig. 805,*3a–d.* **H. hadyensis,* upper Famennian, Hady Limestone, Brno, Hady Hill; *a–c,* holotype, dorsal, ventral, and anterior views, ×2; *d,* transverse section showing crural bases, scale not given (Havlíček, 1979).

Levipugnax Pushkin, 1986, p. 78 [**L. malynskensis;* OD]. Small; subcircular outline; evenly biconvex to lenticular. Beak suberect to erect; fold and sulcus wide, weak; anterior commissure weakly uniplicate. Costae faint to absent. Dental plates short, vertical. Hinge plates divided; septalium and dorsal median septum absent. *Upper Devonian (Famennian):*

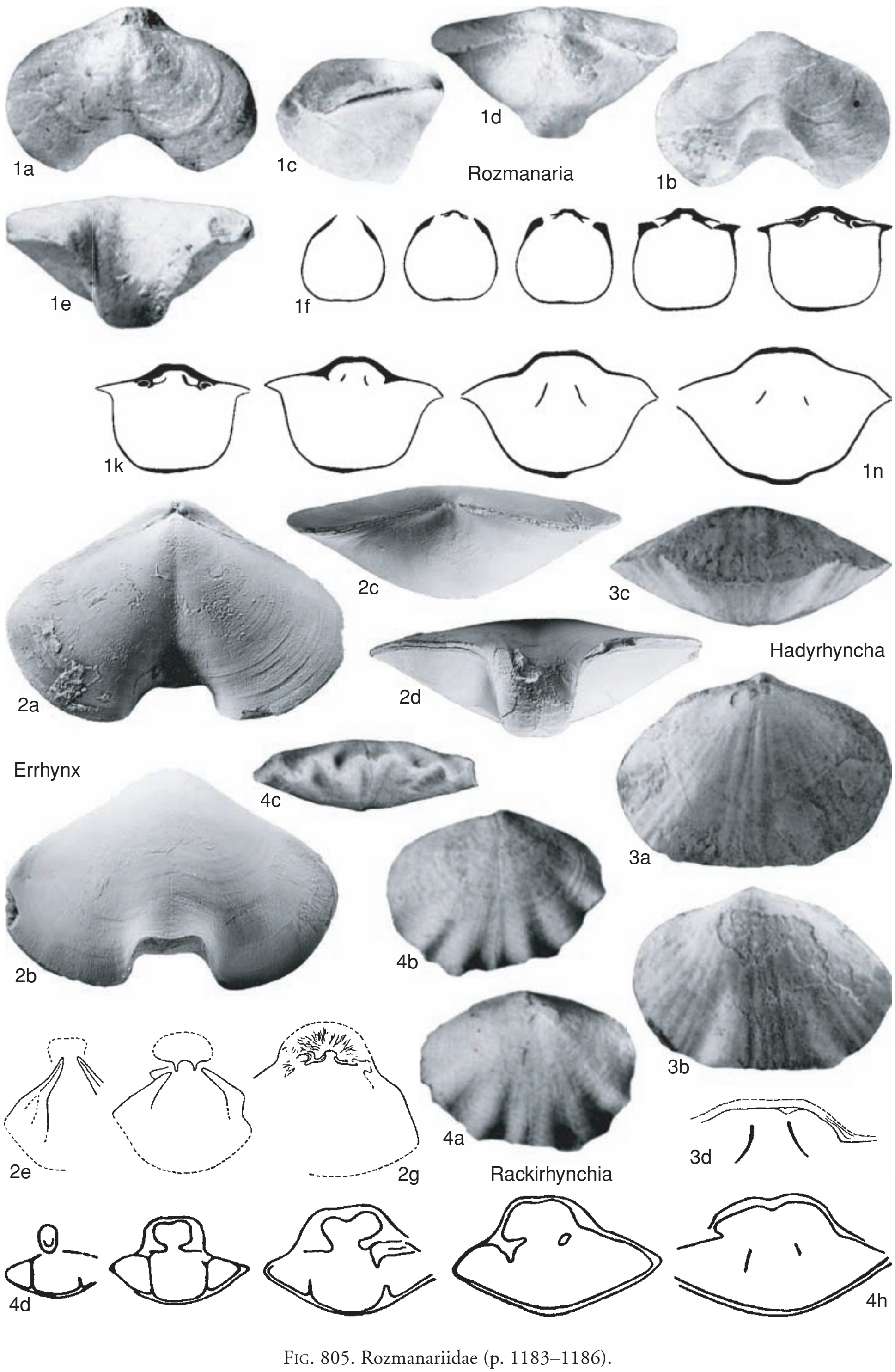

FIG. 805. Rozmanariidae (p. 1183–1186).

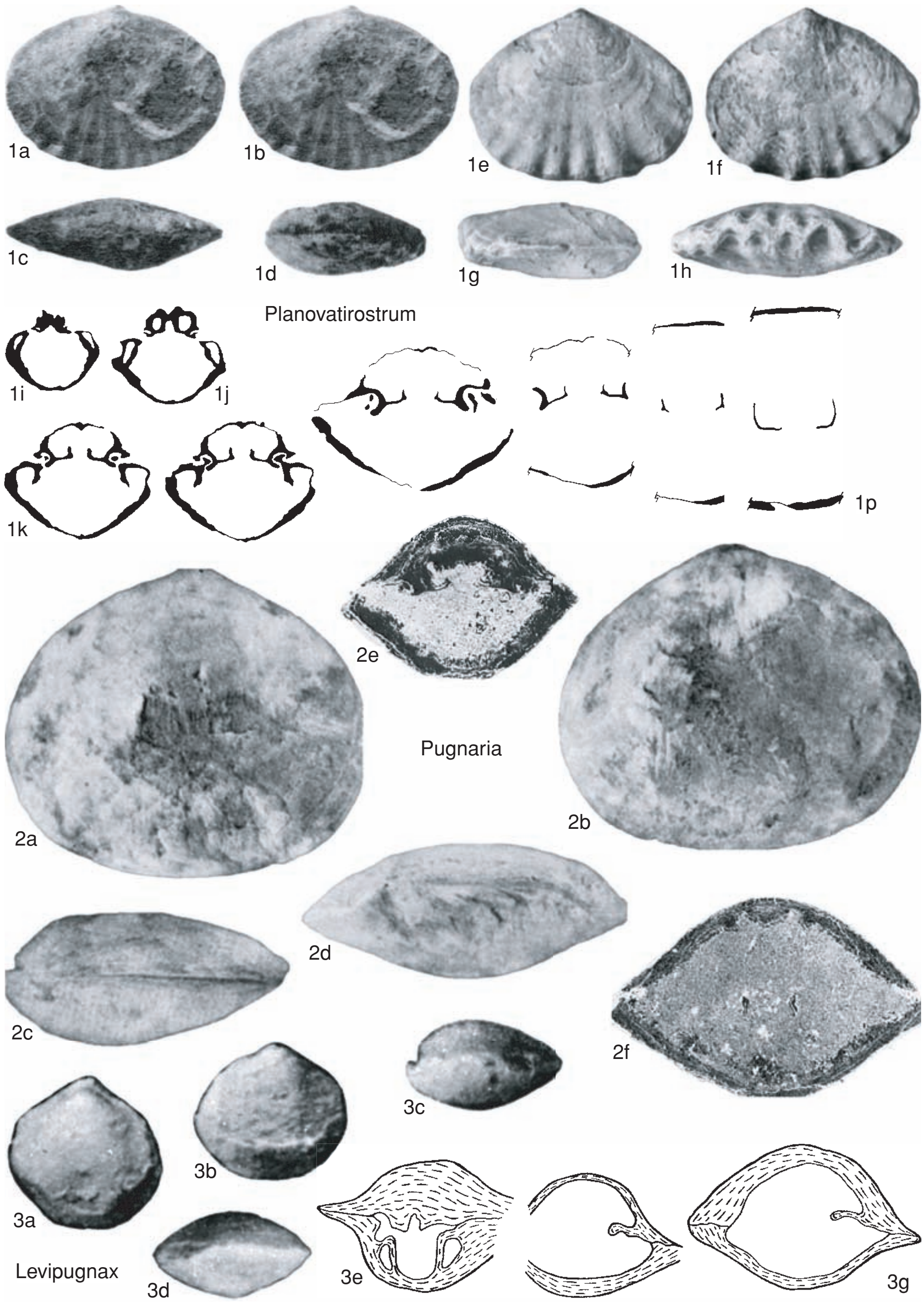

FIG. 806. Rozmanariidae (p. 1183–1186).

Belorussia (Gomel).——FIG. 806,*3a–g*. **L. malynskensis,* Petrikovsk Horizon, Malynsk borehole; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×3; *e–g,* serial sections 0.5, 0.7, 0.9 mm from posterior, ×7.5 (Pushkin, 1986).

Planovatirostrum SARTENAER, 1970a, p. 16 [**Liorhynchus plano-ovalis* NALIVKIN, 1937, p. 76; OD]. Transversely ovate outline; flattened to weakly biconvex. Beak suberect to incurved; foramen small. Fold and sulcus low, wide. Costae low, rounded, from about midlength. Dental plates short; ventral muscle field moderately impressed; teeth long, thick. Hinge plates divided; dorsal median septum and septalium absent; crura plates present; crura long, convex ventrolaterally. *Upper Devonian (Famennian):* Kazakhstan, China, Poland, Moravia, Germany, northern Africa.——FIG. 806,*1a–p*. **P. planoovale* (NALIVKIN), upper Famennian; *a–d,* holotype, dorsal, ventral, anterior, and lateral views from *sulcifer* beds, Ulenty district, Mount Alchagyr, northeastern Kazakhstan, ×1 (Nalivkin, 1937); *e–h,* hypotype, dorsal, ventral, lateral, and anterior views, Hongguleleng Formation, Xinjiang, China, ×1; *i–p,* serial sections 0.9, 1.1, 1.5, 1.6, 2.0, 2.2, 3.2, 4.15 mm from posterior, ×3.2 (Sartenaer & Xu, 1989).

Pugnaria BIERNAT & RACKI, 1986, p. 95 [**P. plana;* OD]. Circular outline; weakly biconvex profile. Fold and sulcus very low; anterior commissure uniplicate; tongue low, wide; valves smooth. Dental plates, dorsal median septum, septalium absent. Hinge plates horizontal, divided; crura long, thin. *Upper Devonian (Famennian):* Poland.——FIG. 806,*2a–f*. **P. plana,* upper Famennian, Holy Cross Mountains, Kowala, Wola Quarry; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×2; *e–f,* serial sections, ×3.5 (Biernat & Racki, 1986).

Rackirhynchia HAVLÍČEK, 1990b, p. 214 [**Atrypa lacerata* BARRANDE, 1879b, pl. 87, case 1, fig. 1a–e; OD]. Transversely ovate outline and equibiconvex, lenticular profile. Beak small, straight to suberect. Fold and sulcus absent; anterior commissure rectimarginate to undulate. Costae few, broad, gentle to weak, arising at shell midlength. Dental plates short, thin, vertical. Hinge plates divided; septalium and dorsal median septum absent; crura laterally compressed. *Lower Devonian (Pragian):* Bohemia.——FIG. 805,*4a–h*. **R. lacerata* (BARRANDE), Koneprusy Limestone, Koneprusy; *a–c,* dorsal, ventral, and anterior views, ×2.7; *d–h,* serial sections 8.3, 8.2, 8.1, 8.05, 8.0 mm from anterior, ×8 (Havlíček, 1990b).

Family ASEPTIRHYNCHIIDAE Savage, 1996

[Aseptirhynchiidae SAVAGE, 1996, p. 254]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea lacking dental plates, dorsal median septum, and septalium. Fold and sulcus developed anteriorly. *Lower Devonian (Pragian)–Upper Devonian (Famennian).*

Aseptirhynchia SOJA, 1988, p. 153 [**A. glabrata;* OD]. Subtriangular outline and dorsibiconvex profile. Beak erect to incurved; foramen small, hypothyrid. Fold and sulcus weak to moderate, arising at umbones; anterior commissure uniplicate; tongue low, typically coarsely serrate but rounded in immature specimens. Costae weak, few, stronger in mature shells, flanks smooth. Dental plates short, close to walls. Hinge plates short, divided; dorsal median septum absent; crural bases crescentic in section, concave laterally; crura long, thin. *Lower Devonian (middle Emsian):* USA (Alaska).——FIG. 807,*1a–m*. **A. glabrata,* Kasaan Island, southeastern Alaska; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×2.7; *e–g,* hypotype, dorsal, ventral, and anterior views, ×2.8; *h–m,* serial sections 0.9, 1.4, 1.6, 1.7, 1.9, 2.2 mm from posterior, ×6 (Soja, 1988).

Brunnirhyncha HAVLÍČEK, 1979, p. 97 [**B. brunniensis;* OD]. Subcircular outline and dorsibiconvex profile. Beak suberect to erect; foramen small. Fold and sulcus wide, flattened. Most of shell smooth; weak costae developed anteriorly, very low and broad. Dental plates absent, teeth arising from valve wall; ventral muscle field well impressed. Hinge plates thick, divided, sloping dorsally and resting on thick callus; dorsal median septum and septalium absent; crura laterally flattened distally. *Upper Devonian (Famennian):* Moravia.——FIG. 807,*2a–j*. **B. brunniensis,* lower Famennian, Krtiny Limestone, Brno, Hady Hill; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1.5; *e–j,* serial sections 0.08, 0.43, 0.53, 0.68, 1.18, 1.43 mm from posterior (Havlíček, 1979).

Carolirhynchia HAVLÍČEK, 1992, p. 73 [**C. carolina;* OD]. Subpentagonal subtrigonal outline and dorsibiconvex profile, inflated anteriorly. Beak suberect to erect; foramen small. Fold and sulcus wide, tongue high. Most of shell smooth; costae weak, developed anteriorly. Shell walls thick; dental plates absent. Hinge plates divided, horizontal, resting on secondary shell material; dorsal median septum absent but weak ridge developed; crura flattened laterally. *Lower Devonian (Pragian–Emsian):* Bohemia.——FIG. 808,*1a–h*. **C. carolina,* Emsian, Zlichov Limestone, Karlstejn; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2.2; *e–h,* serial sections 10.0, 9.3, 9.15, 8.8 mm from anterior, ×3 (Havlíček, 1992).

Chalimia BARANOV, 1978, p. 45 [**C. gracilis;* OD]. Transversely subpentagonal outline and moderately dorsibiconvex profile. Beak erect to incurved and fold and sulcus distinct but not strong. Costae weak to absent. Dental plates short, vertical. Hinge plates divided; septalium, dorsal median septum, and cardinal process absent. *Middle Devonian (Eifelian):* eastern Siberia.——FIG. 808,*2a–l*. **C. gracilis,* Geremgandzhinsk series, Tas-Khaiakhtakh Mountains, Khalim River; *a–c,* holotype, dorsal, ventral,

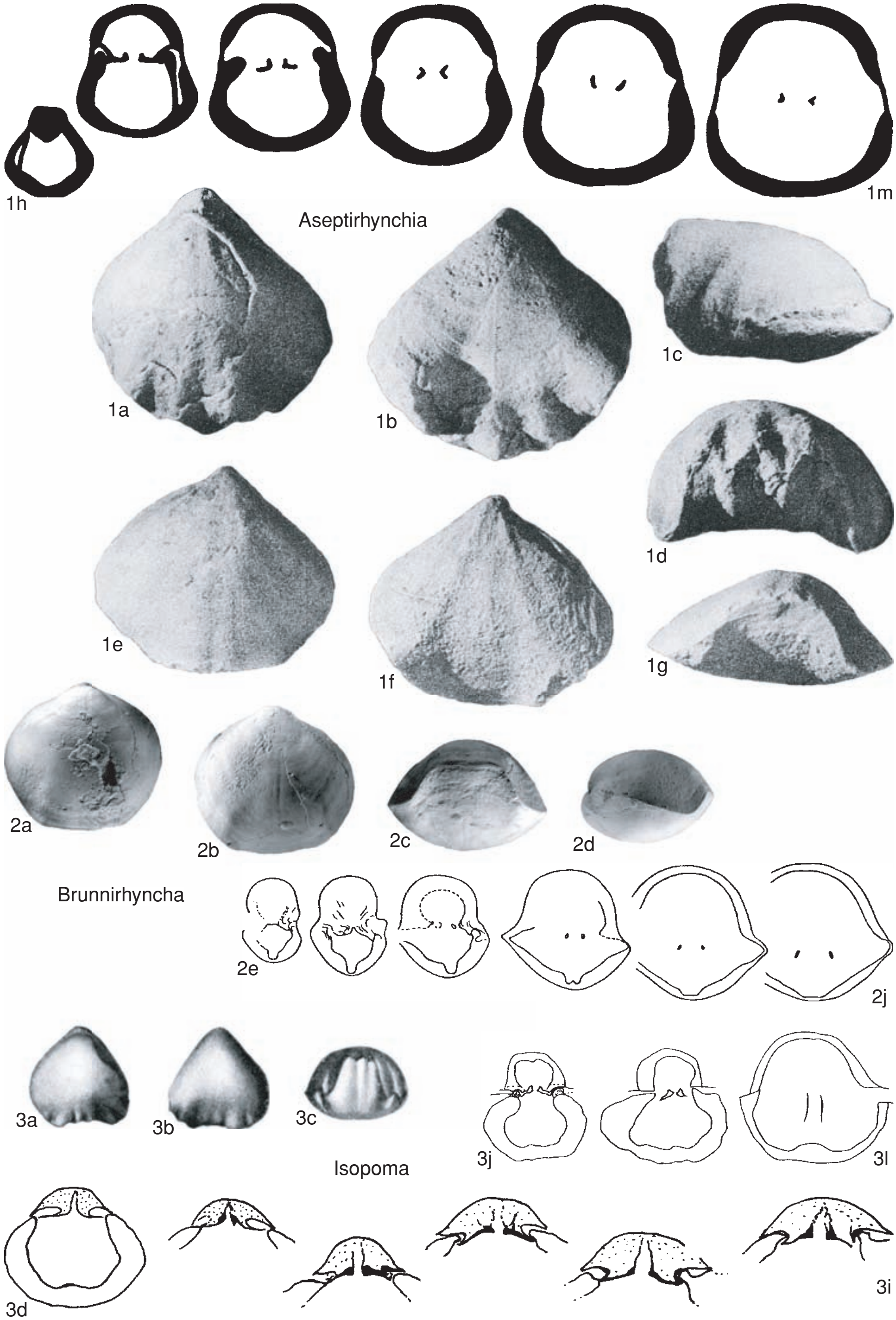

FIG. 807. Aseptirhynchiidae (p. 1186–1189).

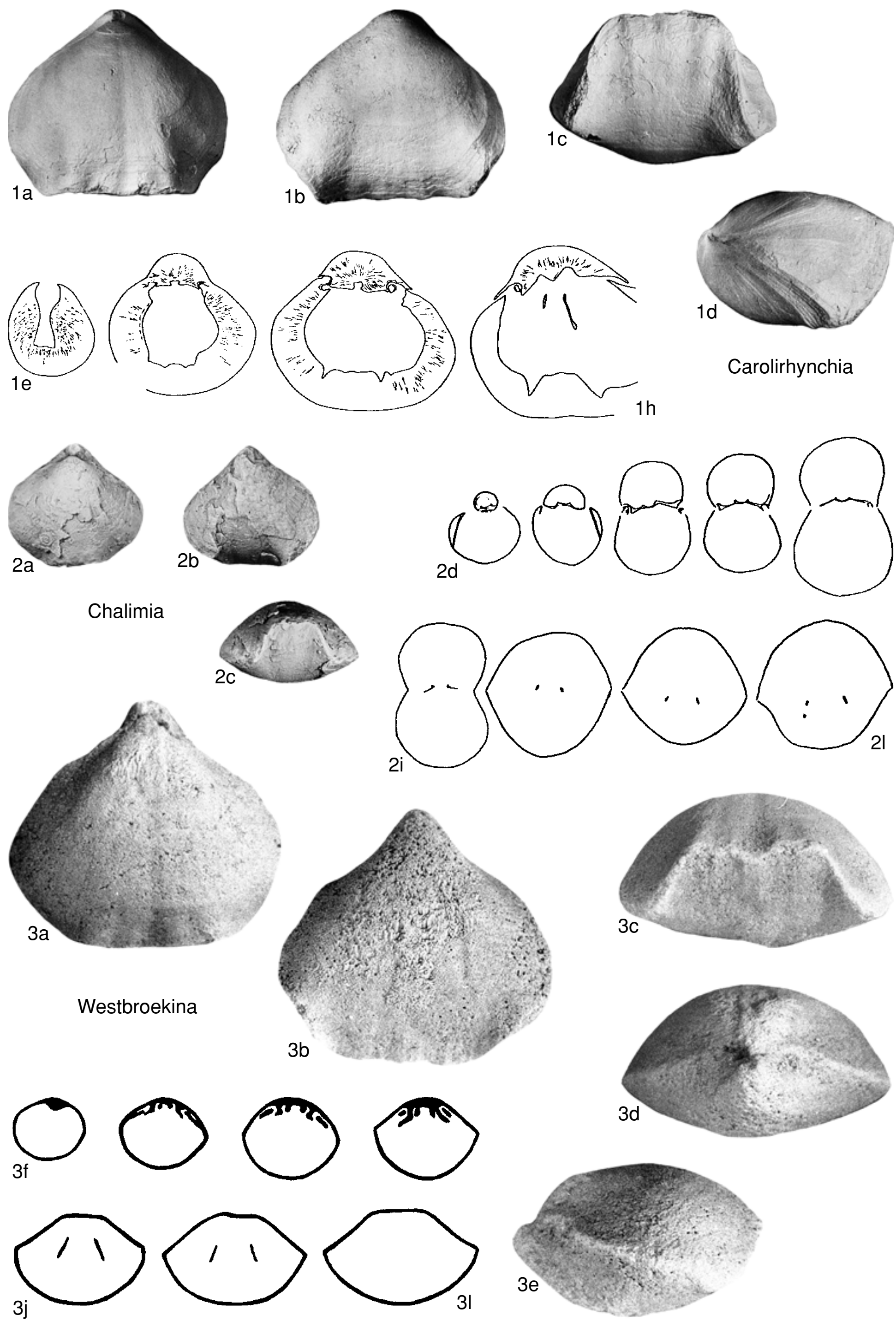

FIG. 808. Aseptirhynchiidae (p. 1186–1189).

and anterior views, ×2 (Baranov, 1978); *d–l,* serial sections, ×3.5 (new).

Isopoma TORLEY, 1934, p. 81 [**Terebratula brachyptycta* SCHNUR, 1853, p. 178; OD]. Small to medium size with subtriangular to subcircular outline and equibiconvex profile. Beak erect, foramen small. Fold and sulcus weak; tongue high. Costae coarse and only developed anteriorly. Dental plates weak to absent. Low median ridge in ventral valve. Hinge plates divided; septalium and dorsal median septum absent; crura thin, short, parallel. *Middle Devonian (Givetian):* Europe, Urals, Altai, China. ——FIG. 807,*3a–l.* **I. brachyptycta* (SCHNUR); *a–c,* hypotype, dorsal, ventral, and anterior views, middle Eifelian, Gonelsheimer Beds, Geeser Horizon, Eifel, Ahrdorf, Germany, ×1.5 (Schmidt, 1941a); *d–i,* serial sections 8.0, 7.9, 7.8, 7.7, 7.6, 7.5 mm from anterior, upper Givetian, Bergische Land, Schneppruthe, ×5 (Schmidt, 1965a); *j–l,* serial sections 8.6, 8.5, 7.7 mm from anterior, upper Eifelian, Skaly Beds, Holy Cross Mountains, Poland, ×3 (Biernat, 1966).

Westbroekina SAVAGE, 1995, p. 1037 [**W. chaconensis;* OD]. Transversely ovate to subpentagonal outline with weakly biconvex lateral profile; dorsal valve inflated anteriorly. Beaks suberect; foramen small. Weak dorsal fold with broad medial depression and ventral sulcus with broad medial fold; gently paraplicate anterior commissure. Costae absent or very faint. Dental plates absent. Hinge plates divided, with outer edges curved ventrolaterally. Crural bases long, rodlike, expanding into oblique and laterally flattened crura that terminate at about one-third valve length. Cardinal process absent. Muscle scars not impressed. *Upper Devonian (Frasnian):* USA (Alaska).——FIG. 808,*3a–l.* **W. chaconensis,* upper Frasnian, Wadleigh Limestone, islet near Wadleigh Island, southeastern Alaska; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×6.5; *f–l,* paratype, serial sections 0.75, 0.95, 1.25, 2.45, 2.85, 2.95, 3.05 mm from posterior, ×5 (Savage & Baxter, 1995).

Family PETASMARIIDAE Savage, 1996

[Petasmariidae SAVAGE, 1996, p. 254]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea with strong dental plates; hinge plates divided and horizontal. Dorsal median septum short but distinct; septalium short to absent. Fine striae present on surface with rows of pits observed in well-preserved specimens of some genera. *Middle Devonian (Eifelian)–Upper Permian (Capitanian).*

Petasmaria COOPER & DUTRO, 1982, p. 83 [**P. patens;* OD]. Subpentagonal outline and dorsibiconvex, anteriorly inflated profile. Beak incurved; foramen mesothyrid; deltidial plates disjunct. Fold and sulcus very strong, from umbones; anterior commissure uniplicate; tongue high, rounded, dentate. Costae angular, from umbones, infrequent increase by bifurcation and intercalation; fine radial striae present anteriorly. Dental plates strong, long, vertical; ventral muscle field weakly impressed. Dorsal median septum long, high; septalium narrow, deep; hinge plates divided, horizontal; crura subtriangular to dorsally concave in section. *Upper Devonian (upper Famennian):* USA (New Mexico).——FIG. 809,*1a–m.* **P. patens,* Percha Formation, Box Member, Alamogordo; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f,* paratype, part of dorsal valve, showing surface striae, ×3; *g–m,* serial sections 1.5, 1.8, 2.8, 2.9, 3.2, 3.3, >3.3 mm from posterior, ×2.3 (Cooper & Dutro, 1982).

Athabaschia CRICKMAY, 1963, p. 9 [**A. asmenista;* OD]. Subpentagonal outline and moderately biconvex profile. Beak erect to incurved; foramen hypothyrid; deltidial plates large. Fold and sulcus pronounced anteriorly; tongue wide, typically triplicate. Costae few, arising at midlength. Dental plates short, vertical. Septalium very short; dorsal median septum strong, extending to about one-third valve length; hinge plates divided, inner hinge plates elevated ventrally. *Upper Devonian (lower Frasnian):* western Canada.——FIG. 809,*4a–i.* **A. asmenista,* Waterways Formation, Athabasca River, Alberta; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×2; *f–i,* serial sections 1.0, 1.8, 2.5, 3.0 mm from posterior, ×4 (Crickmay, 1963).

Bryorhynchus COOPER & GRANT, 1969, p. 11 [**Camarophoria(?) bisulcata* SHUMARD, 1860a, p. 296; OD]. Subcircular to longitudinally ovate outline and biconvex profile with sides and anterior not truncated. Beak erect; foramen triangular, deltidial plates small, conjunct. Fold and sulcus weak, developed anteriorly; anterior commissure broadly uniplicate. Costae weak, present only anteriorly, usually restricted to fold and sulcus. Dental plates convergent ventrally, often fused to valve walls; ventral muscle field narrow, triangular, expanding anteriorly. Dorsal median ridge low, long, extending almost to midlength; septalium short; hinge plates divided anteriorly; sockets crenulated; dorsal muscle field long, narrow, diverging anteriorly; crura curved ventrally, obliquely flattened in section. *Upper Permian (Capitanian):* USA (Texas).——FIG. 810,*1a–i.* **B. bisulcata* (SHUMARD), Bell Canyon Formation, Guadalupe Mountains; *a–e,* hypotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f,* dorsal view of posterior showing deltidial plates, ×5; *g,* interior of conjoined shell, ×4; *h,* dorsal interior showing socket plates and crura, ×3; *i,* ventral interior, ×2 (Cooper & Grant, 1976a).

Eurycolporhynchus SARTENAER, 1968e, p. 566 [**Pugnax pugnus torleyi* SCHMIDT, 1941b, p. 279; OD]. Subcircular to subpentagonal in outline; strongly dorsibiconvex in profile with inflated dorsal valve, lateral and anterior margins precipitous. Beak erect to incurved; small circular foramen. Fold and sulcus strong, arising at about one-third shell

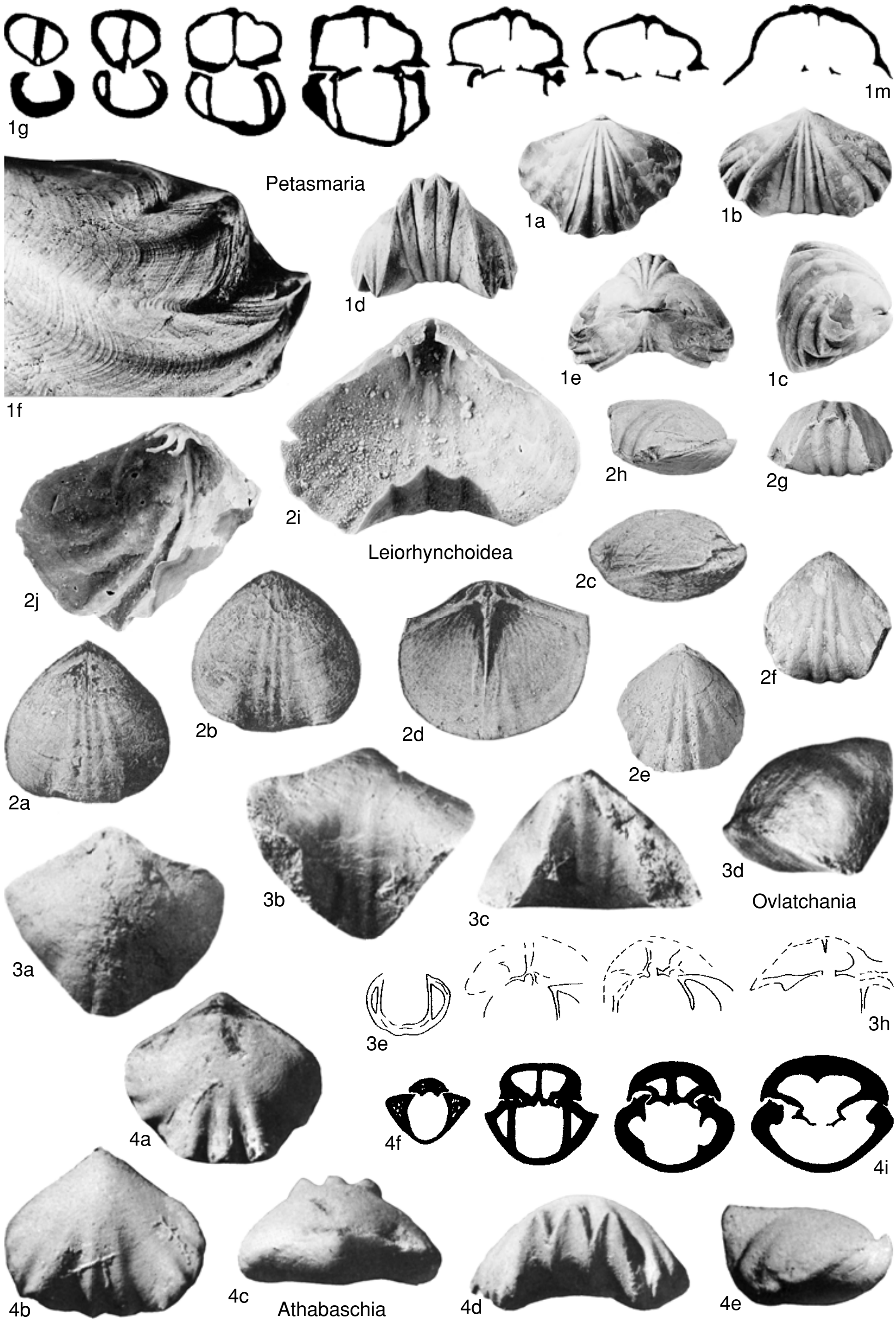

FIG. 809. Petasmariidae (p. 1189–1192).

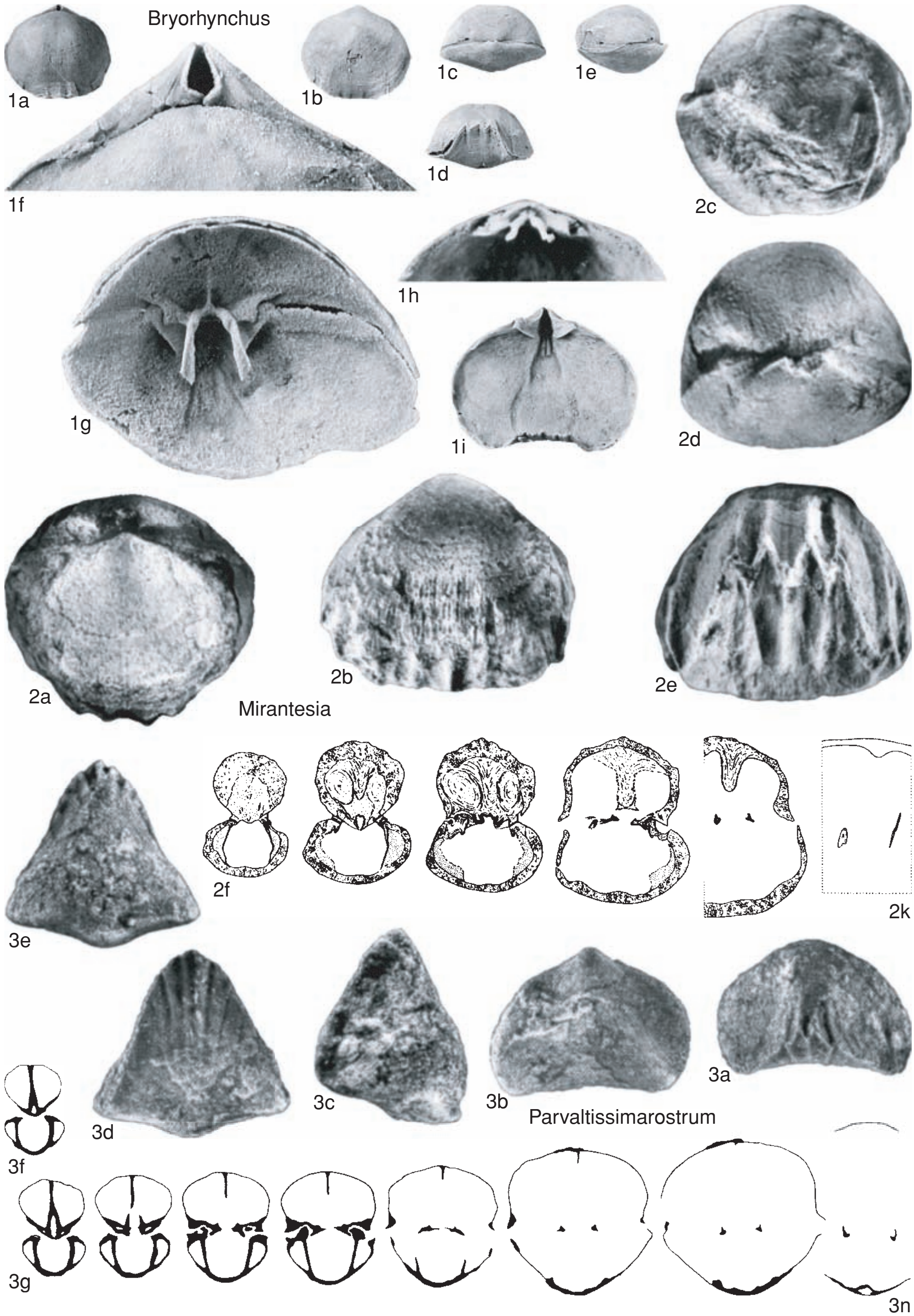

FIG. 810. Petasmariidae (p. 1189–1192).

length; anterior commissure uniplicate, tongue high, broad, and rectangular. Costae low, simple, strongest on fold and in sulcus, weak on flanks. Dental plates short, convergent ventrally. Septalium absent or incipient; hinge plates divided, horizontal; dorsal median septum short, low; crura long, straight, triangular in cross section. *Middle Devonian (Givetian):* Germany, France, Urals.——FIG. 811,*2a–j*. **E. torleyi* (SCHMIDT), upper Givetian, Massenkalk, Sauerland, Bilveringsen, Germany; *a–c,* holotype, posterior, anterior, and lateral views, ×1 (Schmidt, 1941b); *d–j,* serial sections 0.45, 0.55, 0.85, 0.95, 1.45, 1.65, 1.95 mm from posterior, ×2.3 (Sartenaer, 1968e).

Leiorhynchoidea CLOUD, 1944, p. 57 [**L. schucherti;* OD]. Large; subcircular to elongate oval; biconvex profile; gentle lateral and anterior slopes. Beak erect; delthyrium open apically, conjunct deltidial plates. Fold and sulcus weak, from umbones; anterior commissure uniplicate, tongue low, serrate. Costae low, few, rounded; weak on fold and in sulcus, very weak on flanks. Dental plates short, slightly convergent ventrally; ventral muscle field an elongate triangle expanding anteriorly. Dorsal median septum moderately strong, long; septalium short; dorsal muscle field narrow; crura long, ventrally curved, tips horizontally flattened. *Lower Carboniferous (lower Namurian)–Upper Permian (Wordian):* North America, eastern Siberia.——FIG. 809,*2a–d*. **L. schucherti,* Wordian, southwestern Coahuila, Las Delicias, Mexico; *a–c,* holotype, dorsal, ventral, and lateral views, ×1; *d,* Plasticine cast of dorsal interior mold, ×2 (Cloud, 1944).——FIG. 809,*2e–j*. *L. amygdaloidea* COOPER & GRANT, Guadalupian, Word Formation, Glass Mountains, Texas, USA; *e–h,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *i,* paratype, ventral valve interior, ×2; *j,* paratype, oblique view of dorsal valve interior, ×2.6 (Cooper & Grant, 1976a).

Megalopterorhynchus SARTENAER, 1965b, p. 5 [**M. haynesi;* OD]. Subpentagonal to transversely ovate outline; biconvex profile, anteriorly inflated. Beak small, erect; foramen absent. Fold and sulcus strong, extending almost from beak; anterior commissure uniplicate with high rounded tongue. Costae originate near beak, pronounced on fold and in sulcus, weak on flanks; radial striae cover surface. Dental plates slightly convergent ventrally, umbonal cavities wide; septalium wide and deep; hinge plates divided anterior of septalium; dorsal median septum long and thin; crura long, straight, slightly incurved. *Upper Devonian (Famennian):* western North America, Iran, Afghanistan, northern Africa, Spain.——FIG. 811,*3a–k*. **M. haynesi,* upper Famennian, Palliser Formation, Banff National Park, Alberta, Canada; *a–e,* paratype, dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–k,* serial sections 1.9, 2.8, 3.05, 3.9, 6.9, 8.1 mm from posterior, ×2 (Sartenaer, 1969).

Mirantesia MOHANTI, 1972, p. 176 [**M. mirantana;* OD]. Subcircular outline and strongly biconvex profile. Beak erect, foramen small, submesothyrid. Fold and sulcus weak but tongue high, subrectangular. Umbones smooth. Angular costae arising anteriorly in mature specimens, young specimens wholly smooth. Dental plates short, slightly convergent ventrally. Dorsal median septum short; very short septalium buried in posterior callus; hinge plates divided; crura triangular in cross section, curved ventrally, becoming laterally flattened distally. *Middle Devonian (Eifelian):* Spain.——FIG. 810,*2a–k*. **M. mirantana,* middle Eifelian, lower Member A of Portillo Formation, Leon, Mirantes; *a–d,* holotype, dorsal, ventral, lateral, and posterior views, ×3.5; *e,* holotype, anterior view, ×3.2; *f–k,* serial sections, ×4.5 (Mohanti, 1972).

Ovlatchania ABRAMOV & GRIGORJEWA, 1986, p. 113 [**Leiorhynchus ovlatchanensis* ABRAMOV, 1970, p. 129; OD]. Large; subpentagonal to transversely ovate; dorsibiconvex, inflated, tetrahedral. Beak erect; delthyrium with small apical opening. Fold and sulcus very strong, extending from umbones; anterior commissure uniplicate, tongue high, acute; few low costae in sulcus, few low grooves on fold, flanks smooth. Dental plates vertical. Septalium short; hinge plates divided; dorsal median septum short, low. *Lower Carboniferous (Tournaisian–Viséan):* eastern Siberia.——FIG. 809,*3a–h*. **O. ovlatchanensis* (ABRAMOV), Ovlatchansk Series, southern Verkhoyansk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×0.8; *e–h,* serial sections 0.3, 0.8, 0.9, 1.4 mm from posterior, ×3.3 (Abramov & Grigorjewa, 1986).

Parvaltissimarostrum SARTENAER & XU, 1991, p. 127 [**P. minimum;* OD]. Small with tetrahedral shape; outline transversely ovate and lateral profile subtrigonal with very high anterior margin. Beak suberect; foramen large, rounded; deltidial plates narrow, disjunct. Fold and sulcus very strong; anterior commissure uniplicate; tongue very high and broad but tapering dorsally, rounded at crest. Commissure flared and sharp where valves meet anteriorly. Costae few, low, flattened; only present anteriorly; weak to absent on flanks. Dental plates short, convergent ventrally. Dorsal median septum short, low; septalium narrow, deep; hinge plates divided; crural bases flattened, becoming triangular and then crescentic in section distally. *Upper Devonian (Frasnian):* China.——FIG. 810,*3a–n*. **P. minimum,* middle Frasnian–upper Frasnian, Shetienchiao Formation, Xiangxiang County, Hunan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3; *f–n,* serial sections 0.625, 0.675, 0.775, 0.825, 0.95, 1.15, 1.25, 1.325, 1.55 mm from posterior, ×4.8 (Sartenaer & Xu, 1991).

Porostictia COOPER, 1955, p. 62 [**Paraphorhynchus perchaensis* STAINBROOK, 1947, p. 316; OD]. Subpentagonal outline and dorsibiconvex, anteriorly inflated profile. Beak suberect; deltidial plates disjunct or just meeting anteriorly, foramen large. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue broad, high, dentate. Costae strong, angular, from umbones, weak on flanks. In well-preserved specimens surface with radial striae separated by rows of fine pits. Dental plates short, ventrally convergent. Dorsal median

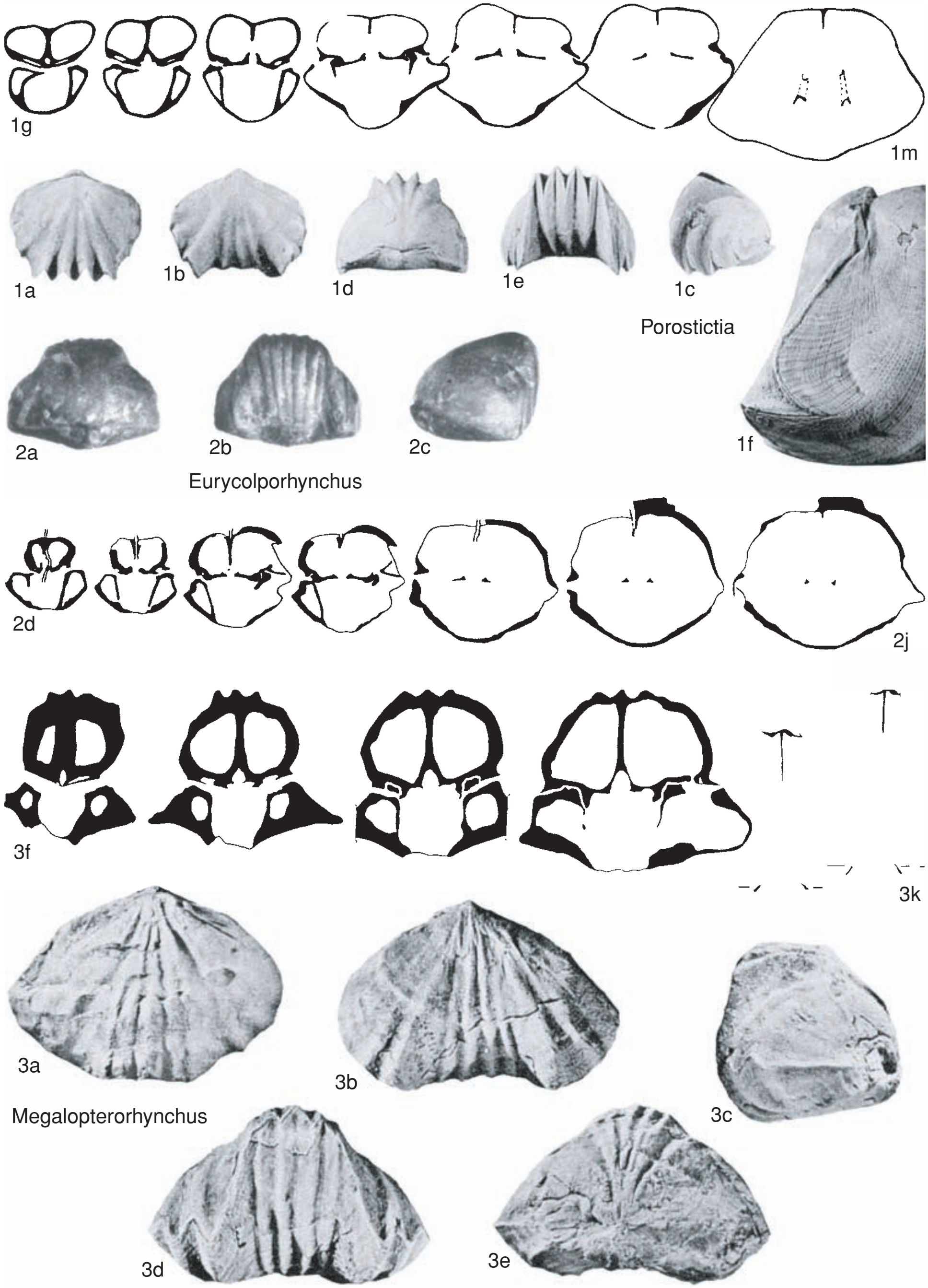

FIG. 811. Petasmariidae (p. 1189–1194).

septum long, low, slender; septalium short, V-shaped; hinge plates divided, horizontal; crura long, ventrally curved, horizontal posteriorly, tips compressed laterally. *Upper Devonian (upper Famennian):* USA (New Mexico).——FIG. 811,*1a–m*. **P. perchaensis* (STAINBROOK), Percha Formation, Box Member, Hillsboro; *a–e,* hypotype, dorsal, ventral, lateral, posterior, and anterior views, ×1; *f,*

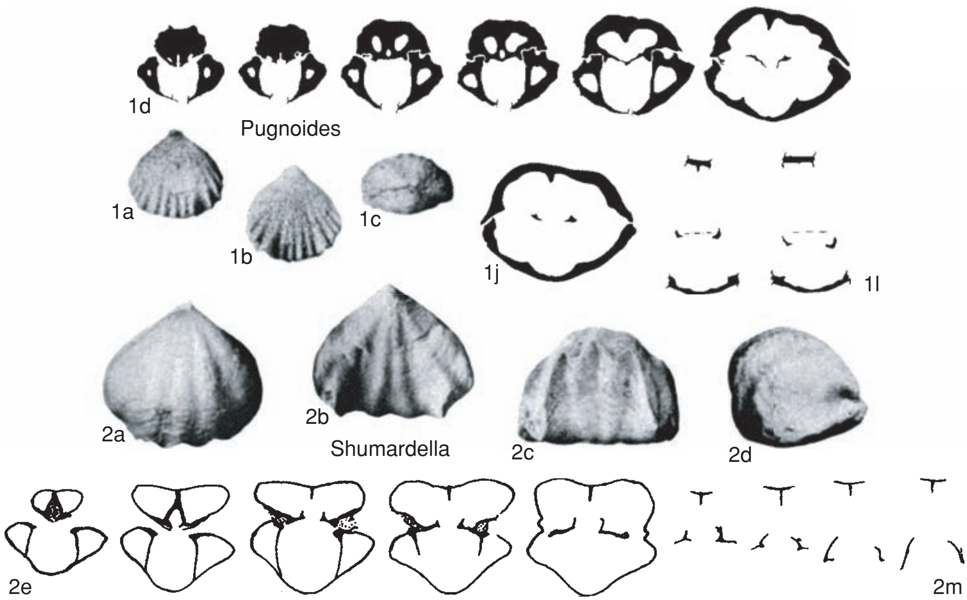

FIG. 812. Petasmariidae (p. 1194).

paratype, side view, showing striae and pits, ×2; *g–m,* serial sections 1.5, 2.2, 2.6, 3.0, 3.2, 3.4, 3.7 mm from posterior, ×3.5 (Cooper, 1955).

Pugnoides WELLER, 1910, p. 512 [**Rhynchonella ottumwa* WHITE, 1865, p. 23; OD]. Small to medium; subcircular to subtriangular; strongly biconvex. Beak incurved; large oval foramen. Fold and sulcus arising at midlength; anterior commissure uniplicate; tongue moderate. Costae arising at one-third shell length. Dental plates well developed, vertical, umbonal cavities large. Septalium distinct, with cover posteriorly; hinge plates divided, horizontal; dorsal median septum short and thick; crura long, concave dorsomedially, curving slightly ventrally. *Lower Carboniferous (Viséan):* North America, Europe, Asia, Western Australia.——FIG. 812,*1a–l.* **P. ottumwa* (WHITE), Mississippian, Meramecian, Ottumwa, Iowa, USA; *a–c,* dorsal, ventral, and posterior views, ×1 (Cooper, 1944); *d–l,* serial sections 1.15, 1.25, 1.4, 1.45, 1.6, 1.95, 2.15, 2.50, 2.85 mm from posterior, ×3.5 (Sartenaer, 1964).

Shumardella WELLER, 1910, p. 512 [**Rhynchonella missouriensis* SHUMARD, 1855, p. 204; OD]. Subtriangular to subpentagonal outline; dorsibiconvex profile, inflated anteriorly. Beak suberect to incurved. Fold and sulcus strong; tongue high. Costae coarse, few, subangular, arising on umbones. Dental plates vertical to ventrally convergent. Dorsal median septum low, long; hinge plates subhorizontal, divided anterior of short septalium; crura laterally compressed. *Lower Carboniferous (Tournaisian):* North America, Asia.——FIG. 812,*2a–m.* **S. missouriensis* (SHUMARD), Mississippian, Kinderhookian, Chouteau Limestone, Missouri, USA; *a–d,* dorsal, ventral, anterior, and lateral views, ×1 (Cooper, 1944); *e–m,* serial sections 12.05, 12.0, 11.9, 11.8, 11.6, 11.2, 11.0, 10.8, 10.7 mm from posterior, ×4 (Schmidt, 1965a).

Family CAMEROPHORINIDAE Rzhonsnitskaia, 1958

[*nom. correct.* RZHONSNITSKAIA, 1958, p. 115 *pro* Camarophorinidae RZHONSNITSKAIA, 1956a, p. 126]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea with dental plates joined to form spondylium. Dorsal median septum and septalium absent; hinge plates undivided. *Middle Devonian (Eifelian–Givetian).*

Camerophorina SCHMIDT, 1941a, p. 43 [**Terebratula pachyderma* QUENSTEDT, 1871 in 1868–1871, p. 200; OD]. Transversely ovate outline and dorsibiconvex profile. Beak erect to incurved. Fold and sulcus low; anterior commissure uniplicate, tongue moderately high, triserrate. Costae low, rounded, restricted to fold and sulcus, umbones and flanks smooth. Dental plates meet ventrally with septum to form spondylium. Hinge plates undivided; dorsal septum and septalium absent. *Middle Devonian (Eifelian–Givetian):* Germany, Spain, Moravia, Urals.——FIG. 813*a–f.* **C. pachyderma* (QUENSTEDT), Givetian, Rommersheimer Beds, Heiligenstein, Eifel; *a–d,* dorsal, ventral, anterior, and lateral views, ×1; *e–f,* serial sections, ×2.5 (Schmidt, 1941a).

Family YUNNANELLIDAE Rzhonsnitskaia, 1959

[*nom. transl.* McLaren, 1965, p. 585, *ex* Yunnanellinae Rzhonsnitskaia, 1959, p. 28]

[Materials prepared by Norman M. Savage]

Pugnacoidea with fine costae posteriorly merging into coarse costae anteriorly. Dental plates usually present. Dorsal median septum supporting short septalium. *Middle Devonian (Givetian)–Upper Devonian (Famennian).*

Yunnanella Grabau, 1923 in 1923–1924, p. 195 [**Rhynchonella Hanburii* Davidson, 1853a, p. 356; OD]. Subpentagonal outline and dorsibiconvex profile; anteriorly inflated. Beak suberect to erect; foramen small, semicircular, bounded by deltidial plates. Fold and sulcus strong from umbones and particularly pronounced anteriorly; anterior commissure uniplicate; tongue high, typically tridentate. Costae angular, originating at about midlength; entire surface bearing radial striae. Dental plates strong, ventrally convergent. Dorsal median septum strong, short; septalium narrow, short, V-shaped, open; hinge plates dividing immediately anterior of septalium, horizontal; crura long, slender, tips concave ventrally in cross section. *Upper Devonian (Famennian):* China.——Fig. 814*a–n.* **Y. hanburii* (Davidson), Kwangsi; *a–d,* lectotype, dorsal, ventral, anterior, and lateral views, ×1.5; *e,* paralectotype, dorsal view showing striae, ×2; *f–n,* serial sections 0.95, 1.1, 1.25, 1.4, 1.5, 2.0, 2.25, 3.3, 3.65 mm from posterior, ×2 (Sartenaer, 1971b).

Ladogioides McLaren, 1961, p. 4 [**L. pax;* OD]. Subcircular outline and strongly dorsibiconvex, anteriorly inflated profile. Beak erect; foramen large, hypothyrid to submesothyrid; deltidial plates small, disjunct. Fold and sulcus pronounced anteriorly; anterior commissure uniplicate, tongue acuminate. Costae few, weak, restricted to anterior; radial striae over whole shell. Dental plates close to walls, ventrally convergent. Septalium deep, narrow, short; hinge plates divided, horizontal; dorsal median septum short, high, thin. Crura short, slender, dorsally grooved. *Middle Devonian (upper Givetian)–Upper Devonian (lower Frasnian):* western North America, western Europe, Siberia, China.——Fig. 815,*3a–i.* **L. pax,* lower Frasnian, Waterways Formation, Alberta, Gypsum Cliffs, Canada; *a–c,* holotype, dorsal, lateral, and anterior views, ×1; *d,* surface showing radial striae, ×3; *e–i,* serial sections 1.0, 1.4, 1.7, 2.1, 2.6 mm from posterior, ×3 (McLaren, 1961).

Nayunnella Sartenaer, 1961a, p. 2, *nom. nov. pro Yunnanella* Grabau, 1931b, p. 141, *non* Grabau, 1923 in 1923–1924 [**Yunnanella synplicata* Grabau, 1931b, p. 141; OD]. Subpentagonal outline and dorsibiconvex profile; anterior and lateral margins truncated. Beak suberect; delthyrium with disjunct deltidial plates leaving elongate foramen. Fold and sulcus moderately strong, from midlength; anterior commissure uniplicate; tongue serrate, moderately high, broad. Costae large, rounded, developed only anteriorly; radial costellae extending from umbones, superimposed on costae. Dental plates short, convex medially. Dorsal median septum low, short; hinge plates divided anterior of short septalium. *Upper Devonian (Famennian):* China, Kazakhstan, Australia.——Fig. 815,*1a–e.* **N. synplicata* (Grabau), Yaoso Group, eastern Yunnan, China; *a–c,* holotype, dorsal, anterior, and lateral views, ×2 (Grabau, 1931b); *d–e,* transverse sections, enlarged (Grabau, 1932a).——Fig. 815,*1f–k. N. tugida* Roberts, Ningbing Limestone, Bonaparte Gulf basin, Ningbing Range, northwestern Australia; serial sections 1.6, 1.8, 2.0, 2.8, 3.4, 3.6 mm from posterior, ×2 (Roberts, 1971).

Schnurella Schmidt, 1964, p. 505 [**Terebratula schnurii* de Verneuil, 1840, p. 261; OD]. Subtriangular to longitudinally ovate outline and dorsibiconvex, anteriorly inflated profile; anterior and lateral margins truncated. Beak erect to incurved. Fold and sulcus weak, obscured by convexity of shell; anterior commissure uniplicate; tongue low. Costae low, restricted to anterior margin; costellae present from midlength, superimposed on costae anteriorly. Dental plates short, close to walls. Dorsal median septum short, obscured by callus; septalium U-shaped; hinge plates undivided. *Middle Devonian (Givetian):* Europe, Kuznetsk basin, Armenia, Urals.——Fig. 815,*2a–i.* **S. schnuri* (de Verneuil), lower Givetian, Gerolstein, Eifel; *a–c,* ventral, anterior, and lateral views, ×1 (Schmidt, 1941b); *d–i,* serial sections 13.1, 13.0, 12.8, 12.6, 12.3, 12.0 mm from anterior, ×2 (Schmidt, 1965a).

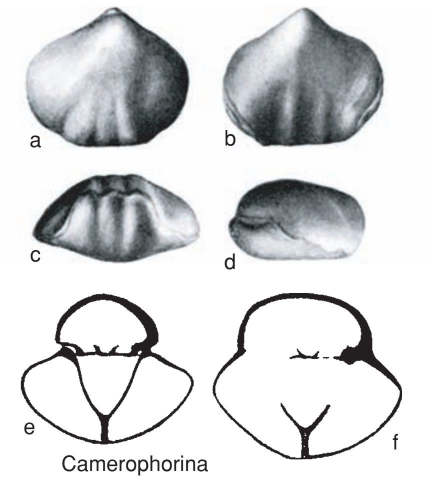

Fig. 813. Camerophorinidae (p. 1194).

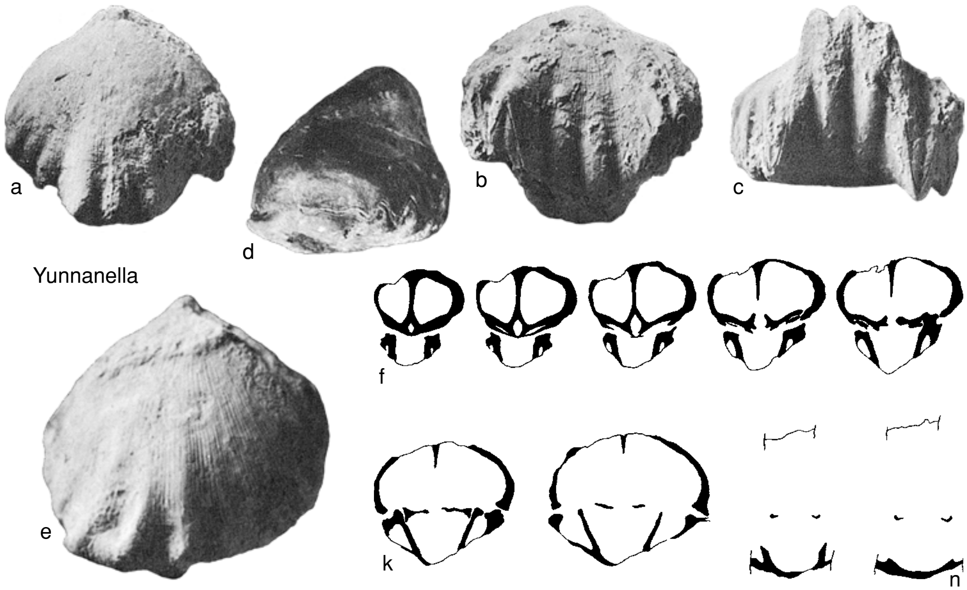

FIG. 814. Yunnanellidae (p. 1195).

Family PARANORELLIDAE Cooper & Grant, 1976

[*nom. transl.* SAVAGE, 1996, p. 254, *ex* Paranorellinae COOPER & GRANT, 1976a, p. 2073]

[Materials prepared by NORMAN M. SAVAGE]

Pugnacoidea with subcircular to elongate outline; fold and sulcus weak, commonly ventral fold, dorsal sulcus; costae weak to absent. Hinge plates divided. Dental plates and dorsal median septum short. *Lower Carboniferous (Tournaisian)–Upper Permian (Kazanian).*

Subfamily PARANORELLINAE Cooper & Grant, 1976

[Paranorellinae COOPER & GRANT, 1976a, p. 2073]

Subcircular Paranorellidae with dorsal sulcus. *Lower Carboniferous (Tournaisian)–Upper Permian (Kazanian).*

Paranorella CLOUD, 1944, p. 59 [**P. imperialis;* OD]. Subcircular outline and ventribiconvex profile. Beak incurved. Ventral fold and dorsal sulcus weak, extending from midlength. Surface smooth. Dental plates short; ventral muscle field elliptical, with bounding ridge. Socket ridges strongly recurved. Hinge plates undivided but deeply notched, short. Crural bases stout, with keels that unite with low median septum to form narrow septalium. Dorsal muscle field elliptical, divided by median ridge. *Permian (Asselian–Kazanian):* Mexico, USA.——FIG. 816,*1a–e.* **P. imperialis,* Wordian, *Waagenoceras* Shale, southwestern Coahuila, Mexico; *a–c,* holotype, dorsal, ventral, and lateral views, ×1 (Cloud, 1944); *d–e,* hypotype, dorsal and anterior view, ×1 (Cooper & Grant, 1976a).——FIG. 816,*1f–g. Paranorella* sp., Wordian, Word Formation, western Texas, USA; *f,* ventral interior, ×1.5; *g,* dorsal interior, ×3 (Cooper & Grant, 1976a).

Boloria GRUNT, 1973, p. 119 [**B. garmoensis;* OD]. Subcircular to subpentagonal outline and ventribiconvex profile. Beak long, suberect; foramen small and circular. Ventral fold and dorsal sulcus arising at umbones, deep, wide, with gentle margins. Costae absent. Tongue pronounced, subtrapezoid. Dental plates short, vertical. Hinge plates divided; dorsal median septum absent but with low, short ridge. *Lower Permian (Asselian–Sakmarian):* Pamir.——FIG. 816,*2a–g.* **B. garmoensis,* Darvaz Stage, Mamazair, southeastern Pamir; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–g,* serial sections 0.2, 0.5, 0.7 mm from posterior, ×2.8 (Grunt, 1973).

Sanjuania AMOS, 1958, p. 841 [**S. dorsisulcata;* OD]. Subcircular to subpentagonal outline and ventriconvex profile. Beak slightly incurved; foramen submesothyridid, circular. Fold and sulcus weak; anterior commissure weakly unisulcate. Costae absent. Dental plates short, vertical. Hinge plates divided; dorsal median septum and septalium absent. *Lower Carboniferous (Tournaisian):* Argentina.——FIG. 816,*3a–g.* **S. dorsisulcata,* Volcan Formation, Guandacol; *a–d,* holotype, dorsal, ventral, anterior,

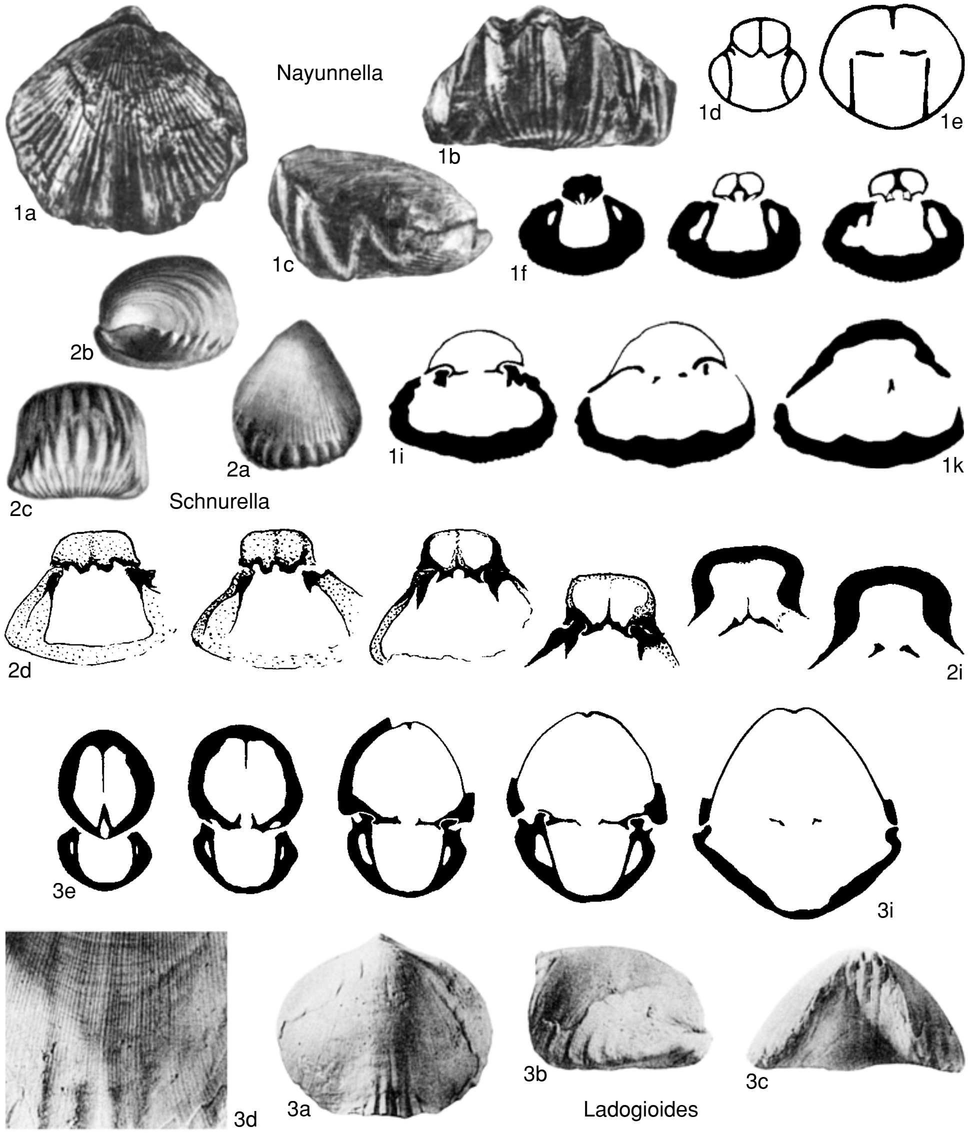

FIG. 815. Yunnanellidae (p. 1195).

and lateral views, ×1.3; *e–g,* serial sections 1.15, 2.0, 2.2 mm from posterior, ×1.8 (Amos, 1958).

Subfamily IOWARHYNCHINAE Savage, 1996

[Iowarhynchinae SAVAGE, 1996, p. 254]

Small, smooth Paranorellidae with elongate oval outline; weak dorsal fold; mesothyrid foramen. Dental plates short. Dorsal median septum and septalium absent; hinge plates divided. *Lower Carboniferous (Tournaisian).*

Iowarhynchus CARTER, 1983, p. 66 [**I. mirandum;* OD]. Small with elongate cordate outline and equibiconvex profile. Beak suberect; delthyrium narrow, joining rounded foramen. Dorsal fold very low to absent, dorsal sulcus rare; ventral sulcus very low; anterior commissure weakly uniplicate to rectimarginate. Costae absent. Dental plates short,

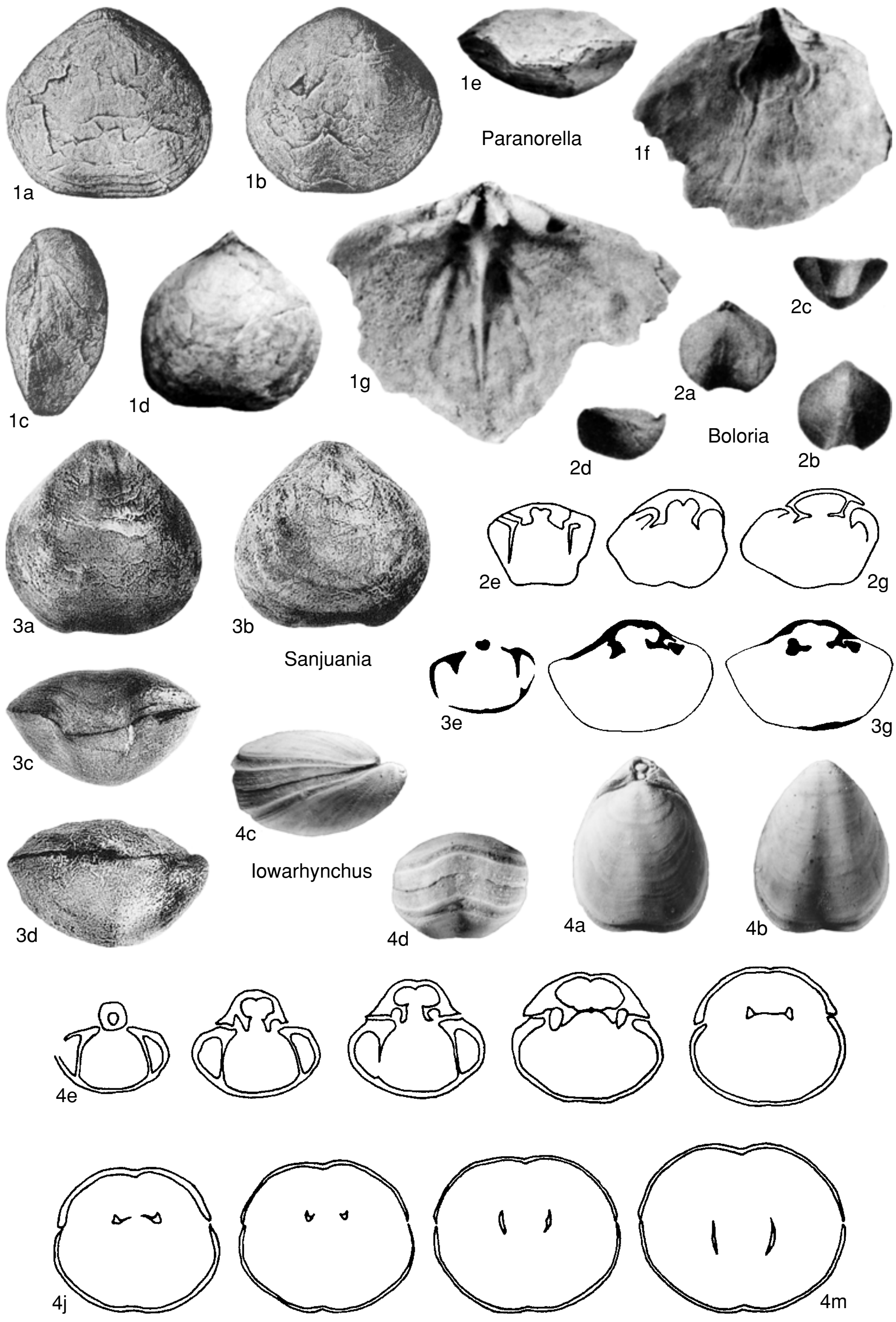

FIG. 816. Paranorellidae (p. 1196–1199).

diverging toward valve floor; hinge plates divided; inner socket ridges overhanging sockets; dorsal median septum absent, myophragm low; crura ventrally curved, becoming flattened laterally. *Lower Carboniferous (Tournaisian):* USA.——FIG. 816,*4a–m*. **I. mirandum,* Gilmore City Limestone, Humboldt County, Hodge's Quarry, Iowa; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×6; *e–m,* serial sections 0.12, 0.16, 0.20, 0.24, 0.28, 0.30, 0.34, 0.38, 0.44 mm from posterior, ×12 (Carter, 1983).

Family BASILIOLIDAE Cooper, 1959

[Basiliolidae COOPER, 1959, p. 15]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Smooth or radially costate Pugnacoidea with deltidial plates conjunct and foramen small and auriculate; pedicle collar well developed; squama and glotta absent; crura broad, falciform (or modification thereof) supported by outer hinge plates or socket ridges; dorsal median septum reduced to ridge or absent; conoidal spirolophe bearing several whorls. *Upper Triassic (Carnian)–Holocene.*

Subfamily BASILIOLINAE Cooper, 1959

[Basiliolinae COOPER, 1959, p. 15]

Smooth or marginally costate Basiliolidae; commissure broadly to acutely uniplicate, occasionally asymmetrical. Dorsal valve with hamiform to falciform crura attached to broad outer hinge plates; median septum and spines absent. *Lower Jurassic (?Sinemurian, Pliensbachian)–Holocene.*

Basiliola DALL, 1908, p. 442 [**Hemithyris beecheri* DALL, 1895, p. 717; OD] [=*Basiola* THOMSON, 1915, p. 390, *nom. null.; Neohemithyris* YABE & HATAI, 1934, p. 587 (type, *Rhynchonella lucida* GOULD, 1861, p. 323, OD)]. Smooth, elongate-pentagonal to rounded-subpentagonal; widest at about midvalve; dorsibiconvex, dorsal valve acutely convex, ventral valve moderately convex; uniplicate, dorsal fold almost imperceptible; ventral sulcus broad, shallow, arcuate; beak small, suberect; foramen small, circular, submesothyrid; deltidial plates small, conjunct, auriculate. Crura often distally serrate, bases not thickened; pedicle collar strong, elaborate. [Living species mainly bathyal, ranging from abyssal to sublittoral.] *Upper Cretaceous (Turonian)–Holocene:* Donetz basin, Turkmenistan, ?Denmark, *Turonian–Maastrichtian;* western Pacific (Okinawa, Ryukyu, Fiji, Vanuatu), *Miocene–Pleistocene;* Indo-Pacific (Madagascar to Japan and Hawaii), *Holocene.*——FIG. 817,*1a–e*. **B. beecheri* (DALL), Holocene, off Hawaii; *a,* dorsal view, ×2; *b,* lateral view, ×1; *c,* anterior view, USNM 334678, ×1; *d,* ventral valve interior, ×4; *e,* oblique view of crura, USNM 334679, ×4 (Cooper, 1959).——FIG. 817,*1f–t*. *B. lucida* (GOULD), Holocene, Bonin Islands; transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.6, 1.0, 1.5, 2.0, 2.3, 2.6, 2.8, 3.0, 3.3, 3.5, 3.7, 3.9, 4.1 (Zezina & Smirnova, 1977).

?Almorhynchia OVCHARENKO, 1983, p. 45 [**Rhynchonella urtabusensis* MOISEEV, 1935, p. 128; OD] [=*Shroshaerhynchia* OVCHARENKO, 1977, p. 38, *nom. nud.*]. Small, posteriorly smooth, with 11 to 21 rounded costae or plicae anteriorly (4 to 6 on feebly defined fold); beak small. Pedicle collar well developed; dental plates long, ventrally convergent proximally to subparallel; hinge plates broad, crura hamiform, dorsoventrally oriented; septal pillar broad, long. *Lower Jurassic (Toarcian)–Middle Jurassic (lower Aalenian):* southeastern Pamirs.——FIG. 817,*2a–u*. **A. urtabusensis* (MOISEEV), Toarcian; *a–c,* dorsal, lateral, anterior views, MUGT 93/1266, ×1; *d–u,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.5, 0.7, 0.9, 1.1, 1.2, 1.4, 1.5, 1.9, 2.1, 2.2, 2.3, 2.6, 2.7, 3.1, 3.4, 3.6, 3.9, MUGT 94/1266 (Ovcharenko, 1983).

Apringia DE GREGORIO, 1886, p. 22 [**A. giuppa;* OD]. Small to medium size, subcircular, globose equibiconvex; uniplication wide, rectangular (possibly asymmetrical), and fold scarcely raised; faint irregular costae anteriorly (up to 3 on fold), otherwise smooth; beak small, erect, with minute foramen. Delicate pedicle collar; dental plates subvertical; hinge plates narrow, without septalium, nor dorsal median septum; crura hamiform. *Lower Jurassic (?Sinemurian, Pliensbachian)–Middle Jurassic (Bathonian):* Italy, Sicily, Austria, Hungary, ?Greenland, Morocco.——FIG. 817,*3a–c*. **A. giuppa,* Toarcian, Italy; dorsal, lateral, anterior views, ×1 (de Gregorio, 1886).——FIG. 817,*3d–m*. *A.* sp., Toarcian, eastern High Atlas, Morocco; transverse serial sections through umbo (Rousselle, 1975).

Basiliolella D'HONDT, 1987, p. 39 [**B. ferox;* OD]. Small, subtriangular, smooth but for few, obscure marginal plicae; uniplication flattopped, paucidentate; beak ridges submesothyrid; foramen small, slightly auriculate. Median septum reduced to a ridge or low keel; distal ends of crura broad and truncated or serrated; crural bases thickened, increasingly swollen to medially coalescent. [Living species inhabit upper bathyal zone.] *Holocene:* New Caledonia, Fiji, Australia.——FIG. 818,*1a–e*. **B. ferox,* Chesterfield Bank, New Caledonia; *a–d,* dorsal, ventral, lateral, anterior views, ×1.5; *e,* cardinalia and crura, ×25 (d'Hondt, 1987).

Eohemithiris HERTLEIN & GRANT, 1944, p. 55 [**E. alexi;* OD] [=*Eohemithyris* COOPER, 1959, p. 30, unjust. emend.]. Similar to *Basiliola* but flatter, almost equibiconvex, with broader, lower

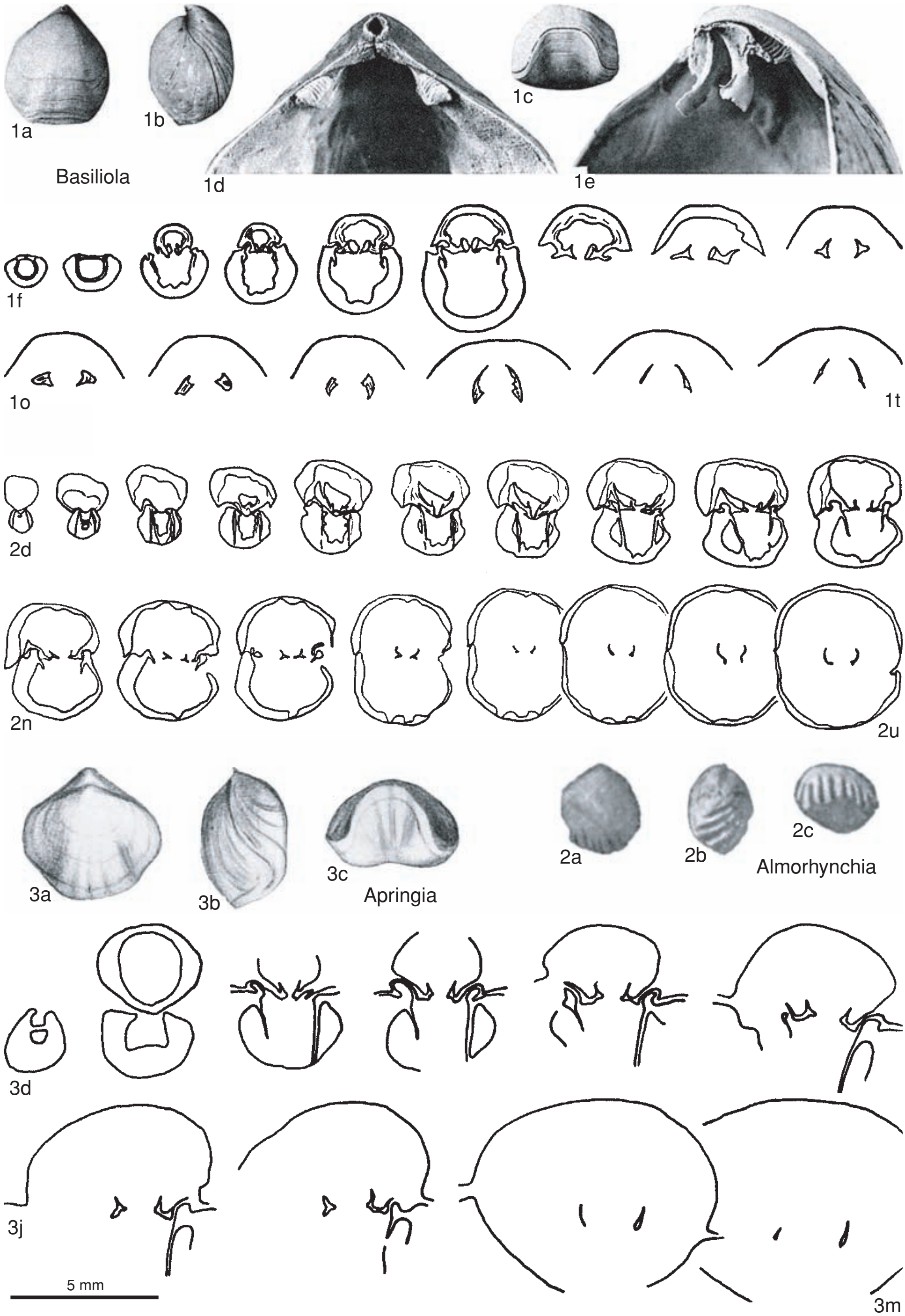

FIG. 817. Basiliolidae (p. 1199).

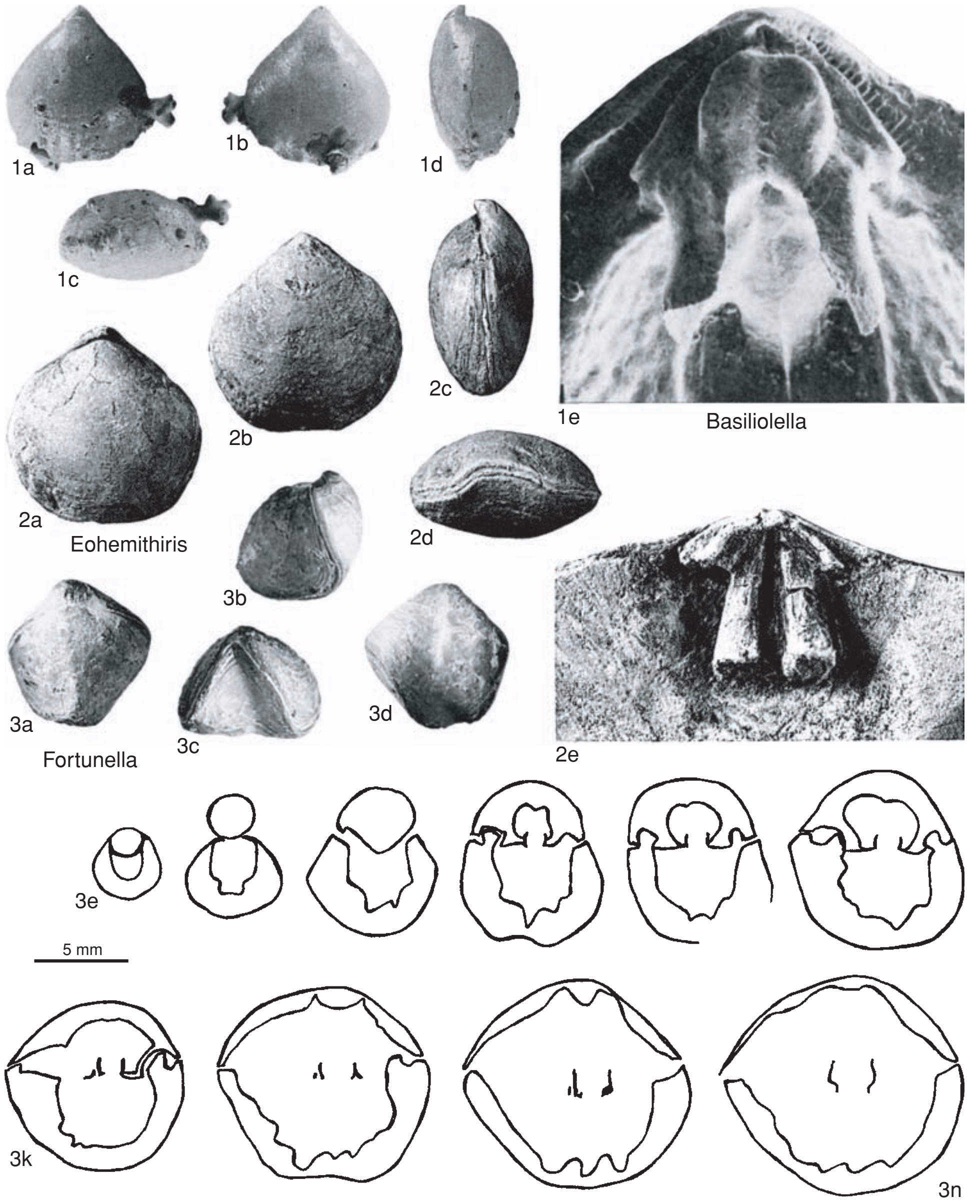

FIG. 818. Basiliolidae (p. 1199–1202).

uniplication and shallow ventral sulcus; surface smooth; deltidial plates conjunct, rimmed. Very broad subfalciform crura; no pedicle collar. *Paleogene (Eocene)–Neogene (Miocene):* western USA (California, Washington).——FIG. 818,*2a–e.* **E. alexi,* Eocene, California; *a–d,* dorsal, ventral, lateral, anterior views, UCMP 15524, ×2; *e,* dorsal interior showing cardinalia and crura, UCMP 15545, ×6 (Cooper, 1959).

Fortunella CALZADA, 1985, p. 78 [**F. fortunae;* OD]. Small to medium, smooth but faintly capillate in early stages; uniplicate with high, shallow, acutely arcuate ventral sulcus and extensive triangular linguiform extension. Pedicle collar present; dental plates usually fused to shell wall; hinge plates narrow, long falciform crura. [Closely related to *Rionirhynchia* KAMYSHAN & KVAKHADZE, 1980, p. 72, possibly even a junior subjective synonym.] *Upper Jurassic (lower Oxfordian)–Lower Cretaceous (upper Aptian):* southeastern Spain, Alps, Poland, Moravia, Slovakia, Russian platform, Caucasus, Azerbaijan, ?Hungary, ?Greenland, Algeria.——FIG. 818,*3a–n.* **F. fortunae,* lower Hauterivian, Sierra del Lugar, southeastern Spain; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MGSB 32491-13, ×1; *e–n,* transverse serial sections, distances in mm from ventral umbo, 1.1, 1.5, 1.9, 2.2, 2.4, 2.7, 3.0, 3.4, 3.7, 4.1, MGSB 32491-L4 (Calzada, 1985).

Probolarina COOPER, 1959, p. 37 [**Rhynchonella holmesii* DALL, 1903, p. 1536; OD]. Small, subpentagonal, uniplicate, anteriorly costate; beak long, pointed, nearly straight; foramen hypothyrid to submesothyrid; deltidial plates auriculate, conjunct. Strong pedicle collar and dental plates; crura long, scimitar-like. *Upper Cretaceous–Paleogene (Eocene):* ?central Asia, *Upper Cretaceous;* eastern USA, Jamaica, New Zealand (Chatham Islands), *Paleocene–Eocene.*——FIG. 819,*1a–e.* **P. holmesii* (DALL), Eocene, North Carolina, USA; *a–d,* dorsal, ventral, lateral, anterior views, USNM 549359a, ×2; *e,* oblique view of crura, USNM 549359g, ×6 (Cooper, 1959).

Rhytirhynchia COOPER, 1957b, p. 8 [**Hemithyris sladeni* DALL, 1910, p. 440; OD]. Similar to *Basiliola* but paucicostate anteriorly and with much reduced dental plates; deltidial plates auriculate, conjunct; anterior commissure sulciplicate, i.e., dorsal fold not differentiated, but bidentate, trapezoidal linguiform extension well developed. Crural bases incipiently thickened. [Living species inhabit upper bathyal zone.] *Neogene (Pliocene)–Holocene:* Pacific, Indian Ocean.——FIG. 819,*2a–e.* **R. sladeni* (DALL), Holocene, Saya de Malha Banks, western Indian Ocean; *a–c,* dorsal, lateral, anterior views, ×1; *d,* ventral interior showing foramen and teeth, ×3; *e,* lectotype, dorsal interior showing crura, USNM 111086, ×4 (Cooper, 1959).

Rionirhynchia KAMYSHAN & KVAKHADZE, 1980, p. 72 [**R. tsessiensis;* OD]. Small, equibiconvex, broadly oval; smooth or with few marginal costae; beak short, suberect, foramen small. Uniplicate, ventral valve with shallow sulcus and subtriangular linguiform extension; dorsal fold poorly developed. Shell thickened; dental plates fused to shell wall; hinge plates short, subquadrate with concave inner surfaces; crura moderately long. *Lower Cretaceous (Hauterivian–Barremian):* western Georgia (Caucasus).——FIG. 819,*5a–j.* **R. tsessiensis,* lower Hauterivian, Georgia; *a–d,* dorsal, lateral, anterior, ventral views, GMG 327/120, ×1; *e–j,* transverse serial sections, distances in mm from ventral umbo, 2.0, 2.7, 3.4, 3.9, 4.7, 5.3 (Kamyshan & Kvakhadze, 1980).

?Soaresirhynchia ALMÉRAS, 1994, p. 26 [**Rhynchonella bouchardi* DAVIDSON, 1852b, p. 82; OD]. Small to medium size, subcircular to transversely oval, equibiconvex to dorsibiconvex; smooth stage extended at least to midvalve; costae few, simple, rounded anteriorly (2 to 7 on scarcely raised dorsal fold); uniplication generally symmetrical; beak delicate, suberect to slightly incurved, foramen circular to oval, deltidial plates mostly disjunct, otherwise conjunct. Dental plates subparallel to ventrally convergent, often fused to shell wall; hinge plates divided; cardinal process and septalium absent; dorsal median septum absent or reduced to a ridge; crura hamiform to subfalciform; pedicle collar reduced to absent. [May be a subjective synonym of *Almorhynchia* OVCHARENKO, 1983, p. 45.] *Lower Jurassic (Toarcian):* England, ?Scotland, Germany, France, Spain, Portugal, Italy, Dinarids, Morocco, Algeria.——FIG. 819,*4a–t.* **S. bouchardi* (DAVIDSON), lower Toarcian; *a–c,* dorsal, lateral, anterior views, Somerset, England, SM J.36787, ×2 (Ager, 1962); *d–t,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.5, 0.8, 2.2, 2.35, 2.5, 2.65, 2.8, 2.95, 3.1, 3.25, 3.45, 3.7, 3.8, 4.0, 4.2, 4.4, Portugal, FSL 307406 (Alméras, 1994).

Streptaria COOPER, 1959, p. 38 [**Terebratula de Buchii* MICHELOTTI, 1839, p. 122; OD]. Pentagonal, almost planoconvex with acutely uniplicate asymmetrical commissure; possible faint striation anteriorly; beak short, foramen auriculate. Dental plates reduced; pedicle collar poorly developed. [Probably a subgenus of *Basiliola* DALL, 1908, p. 442.] *Paleogene (Eocene)–Neogene (Miocene):* southern Europe, northern Africa, Cuba, Arabia, western Kazhakhstan, ?New Zealand, Antarctica.——FIG. 819,*3a–d.* **S. debuchii* (MICHELOTTI), middle Miocene, Messina, Sicily; *a–c,* dorsal, lateral, anterior views, USNM 549352a, ×2; *d,* internal view of dorsal umbo showing strong socket ridges, wide outer hinge plates and crura, USNM 549352b, ×6 (Cooper, 1959).

Subfamily PAMIRORHYNCHIINAE Ovcharenko, 1983

[Pamirorhynchiinae OVCHARENKO, 1983, p. 50; *emend.,* MANCEÑIDO & OWEN, herein]

Medium to small Basiliolidae, subspherical to somewhat depressed, compact, equibiconvex shells; fully costate with round-crested but sharply incised costae, typically acute and simple, sometimes bifurcating or intercalated, never spinose; uniplication of anterior commissure gently to strongly arcuate, but not disrupting overall shell outline. Dental plates relatively thin, subparallel, or slightly ventrally convergent; dorsal median septum absent or extremely reduced (confined apically); outer hinge

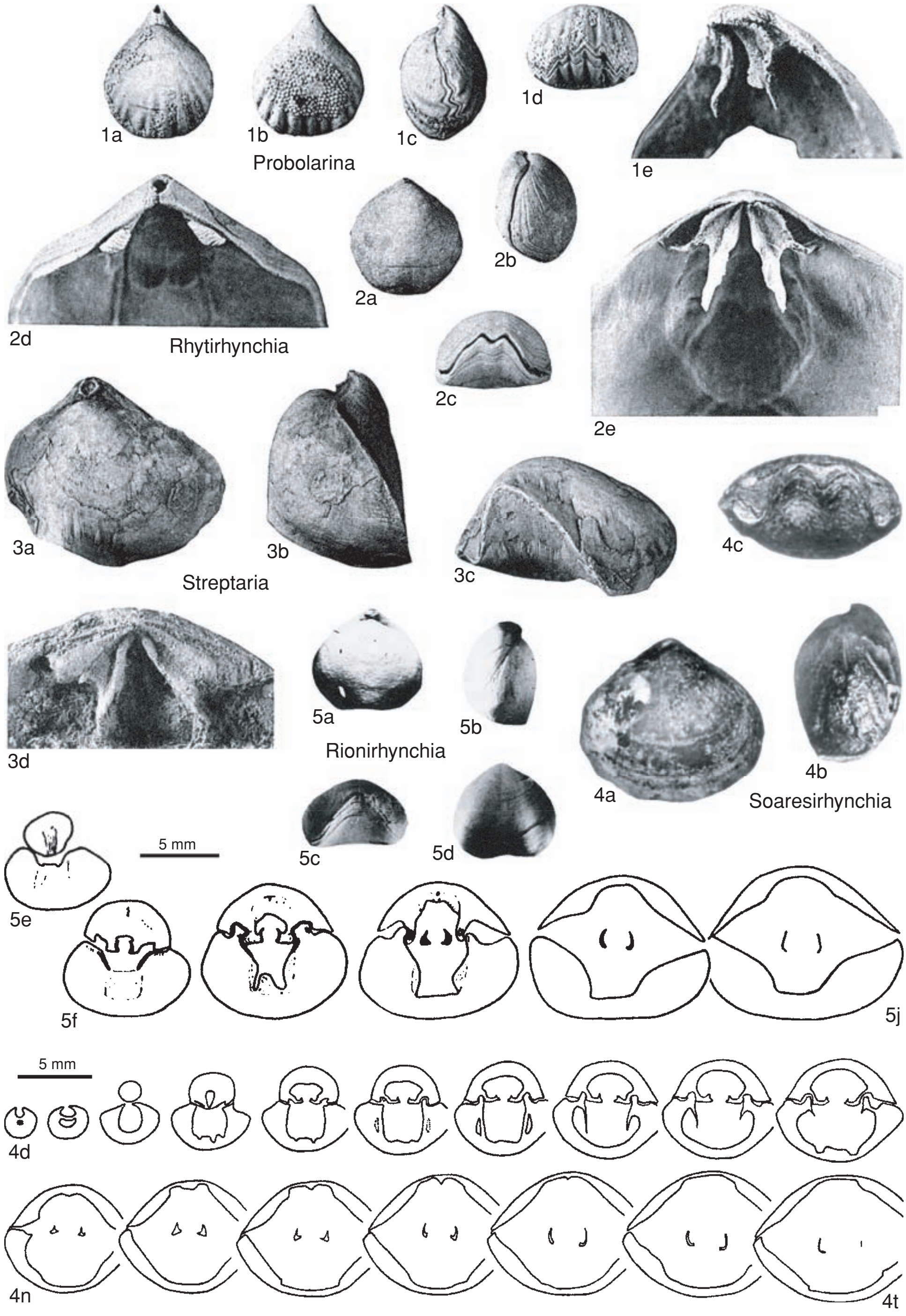

FIG. 819. Basiliolidae (p. 1202).

plates ventrally convex; crura falciform or modification thereof (may be hamiform in young stages). [Other special crural types named by OVCHARENKO seem superfluous; name herein redefined to include demoted Pamirorhynchiidae OVCHARENKO, 1983, p. 49 and part of Dzhangirhynchiinae OVCHARENKO, 1983, p. 70, *emend.* SHI & GRANT, 1993, p. 20 (*partim* excluding type genus *Dzhangirhynchia*).] *Upper Triassic (Carnian)–Paleogene (Paleocene, ?Eocene).*

Pamirorhynchia OVCHARENKO, 1983, p. 51 [**Rhynchonella pamirensis* MOISEEV, 1937, p. 7; OD] [=*Pamirorhynchia* OVCHARENKO, 1977, p. 38, *nom. nud.; Aidynkulirhynchia* OVCHARENKO, 1983, p. 59–60 (type, *A. aidynkulensis,* OD); *Aidynkulirhynchia* OVCHARENKO, 1977, p. 38, *nom. nud.; Aldynkulirhynchia* DOESCHER, 1981, p. 3, *nom. nud.*]. Medium to large, with costae rather thick, not numerous, seldom dichotomizing. Dental plates long, subparallel, converging ventrally or diverging; young shells with small septalium, septum not distinct; adult shells with massive distinct septum; outer hinge plates ventrally convex; crura hamiform in young shells to subfalciform in adults. *Middle Jurassic (upper Aalenian–upper Bajocian):* southeastern Pamirs.——FIG. 820,*2a–l.* **P. pamirensis* (MOISEEV); *a–d,* dorsal, lateral, anterior, ventral views, MUGT 104/1266, ×1; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.55, 1.7, 2.3, 2.85, 3.25, 3.8, 4.6, 5.0, MUGT 106/1266 (Ovcharenko, 1983).——FIG. 820,*2m–v. P. aidynkulensis* (OVCHARENKO), lower Bajocian; *m–o,* holotype, dorsal, lateral, anterior views, MUGT 125/1266, ×1; *p–v,* transverse serial sections, distances in mm from ventral umbo, 3.65, 4.55, 4.8, 5.35, 6.15, 7.15, 9.1, MUGT 124/1266 (Ovcharenko, 1983).

Gagriella MOISEEV, 1939, p. 193[205] [**G. abbhasiaensis;* OD]. Globose, compact, covered with numerous sharp costae, usually simple, but possibly showing bifurcations. Otherwise like *Orbirhynchia* in its internal structures. [This genus is revalidated herein.] *Upper Jurassic (Tithonian), Lower Cretaceous (?Hauterivian, Barremian):* Georgia, Stramberk. ——FIG. 821,*3a–q.* **G. abhasiaensis,* Barremian, Georgia; *a–d,* dorsal, lateral, anterior, ventral views, ×1 (Moiseev, 1939); *e–q,* transverse serial sections, distances in mm from ventral umbo, 0.8, 2.3, 3.1, 3.4, 4.1, 4.4, 4.7, 5.0, 5.3, 5.9, 6.3, 7.1, 7.4, LGE 10/181 (new; courtesy of S. V. Lobacheva).

?Kvesanirhynchia KVAKHADZE, 1976, p. 505 [**K. tenuicostata;* OD]. Small, rounded-pentagonal, broader than long; dorsibiconvex; costae numerous, simple, angular; beak slender, low, slightly incurved to suberect, foramen mesothyrid; anterior commissure with broad, shallow sulcus meeting low, weakly developed dorsal median fold. Umbonal chambers small; outer hinge plates narrow; crural bases thick; dorsal ridge or low septum persisting to middle part of valve. [Closely related to *Gagriella* MOISEEV, 1939, p. 193, possibly even a junior subjective synonym.] *Lower Cretaceous (Berriasian):* Georgia.——FIG. 822,*1a–s.* **K. tenuicostata,* Berriasian, Abhazia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, GMG 334/3, ×1; *e–s,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.4, 0.5, 0.7, 0.9, 1.1, 1.3, 1.6, 1.8, 2.2, 2.3, 2.4, 2.7, 2.8 (Kvakhadze, 1976).

Orbirhynchia PETTITT, 1954, p. 29 [**O. orbignyi* PETTITT, 1954, p. 45; OD]. Small, biconvex, orbicular with uniplication low, arcuate or ventral sulcus shallow; dorsal fold poorly developed; anterior commissure rarely asymmetrical; numerous finely rounded costae, shell smooth posteriorly; beak small, foramen circular, beak ridges indistinct. Dental plates slender, often close to wall; dorsal septum absent. *Cretaceous (Albian–lower Maastrichtian):* England, France, Germany, Switzerland, Spain, Italy, Slovakia, Poland, Bulgaria, Ukraine, Caucasus, Turkmenistan, western Kazakhstan, Tibet.——FIG. 822,*2a–r.* **O. orbignyi,* lower Cenomanian, Holy Cross Mountains, Poland; *a–c,* dorsal, lateral, anterior views, MZ VIII Bra-997, ×2; *d–r,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.6, 0.8, 1.0, 1.2, 1.3, 1.5, 1.6, 1.8, 2.1, 2.3, 2.5, 2.8, 3.3, MZ VIII Bra-997/a1 (Popiel-Barczyk, 1977).

?Parthirhynchia TITOVA, 1980, p. 77 [**P. unguiseformis;* OD] [=*Partirhynchia* IASIUKEVICH, 1974, p. 108, *nom. nud.*]. Small, costate or semicostate without dichotomy or bifurcation; elongate-oval; anterior commissure broad, arcuate with dorsal fold poorly developed and ventral sulcus shallow. Dental plates weakly ventrally divergent; dorsal valve with median ridge low, poorly developed or very low septum. [Though shell shape of type species is unusual, evidence from other assigned species tends to support this subfamily allocation, being similar to *Orbirhynchia* but with longer smooth stage.] *Upper Cretaceous (Turonian–Maastrichtian):* Turkmenistan, Bulgaria.——FIG. 821,*1a–n.* **P. unguiseformis,* upper Maastrichtian, Kopet Dag, Turkmenistan; *a–c,* holotype, dorsal, lateral, anterior views, CNIGR 148/10445, ×1.5; *d–n,* transverse serial sections, distances in mm from ventral umbo, 2.05, 2.45, 2.55, 2.7, 2.95, 3.25, 3.4, 3.7, 4.35, 4.8, 4.95, CNIGR 134/10445, approximately ×2 (Titova, 1980).

Pseudogibbirhynchia AGER, 1962, p. 108 [**Rhynchonella Moorei* DAVIDSON, 1852b, p. 82; OD]. Small, globose, subcircular, equibiconvex, dorsal valve flattened posteriorly; uniplication low, but dorsal fold absent, multicostate throughout; beak small, incurved. Median septum very short, strengthened deltidial plates, hamiform crura. *Lower Jurassic (Sinemurian)–Middle Jurassic (lower Bajocian):* England, France, Portugal, Spain, Germany, Switzerland, Italy, Slovakia, Dinarids, Hungary, Greece, Morocco, Algeria, Madagascar, Thailand,

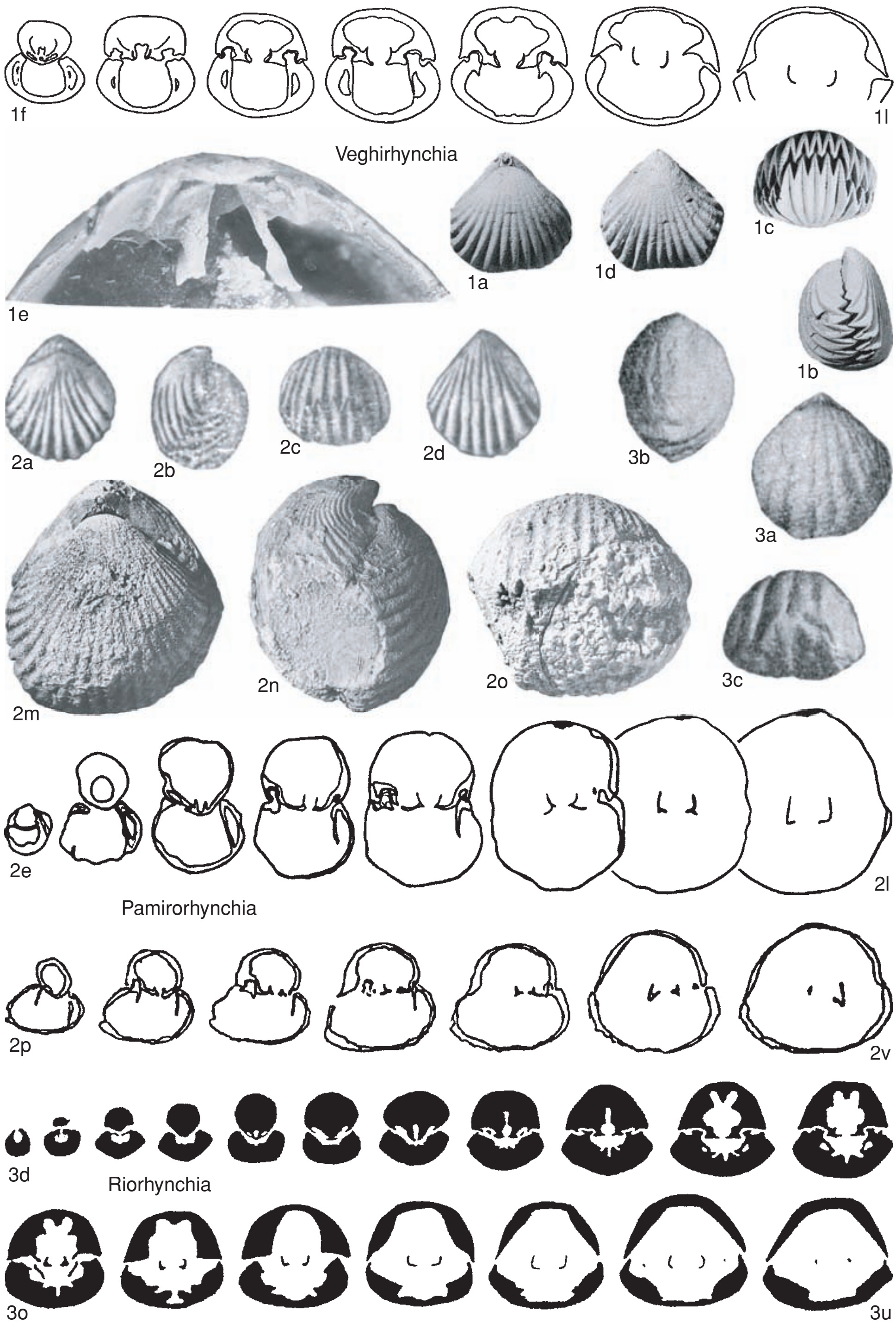

FIG. 820. Basiliolidae (p. 1204–1208).

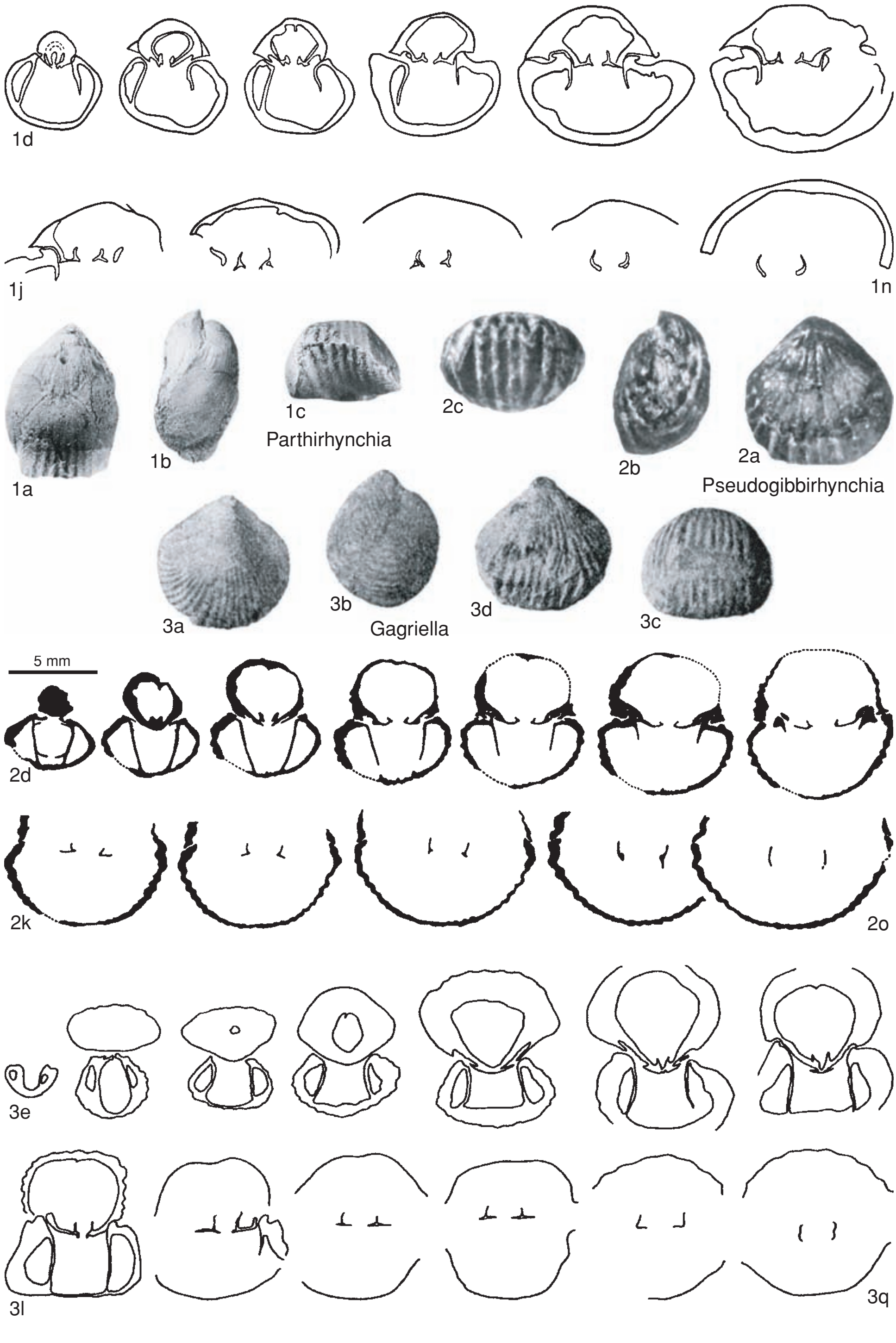

FIG. 821. Basiliolidae (p. 1204–1208).

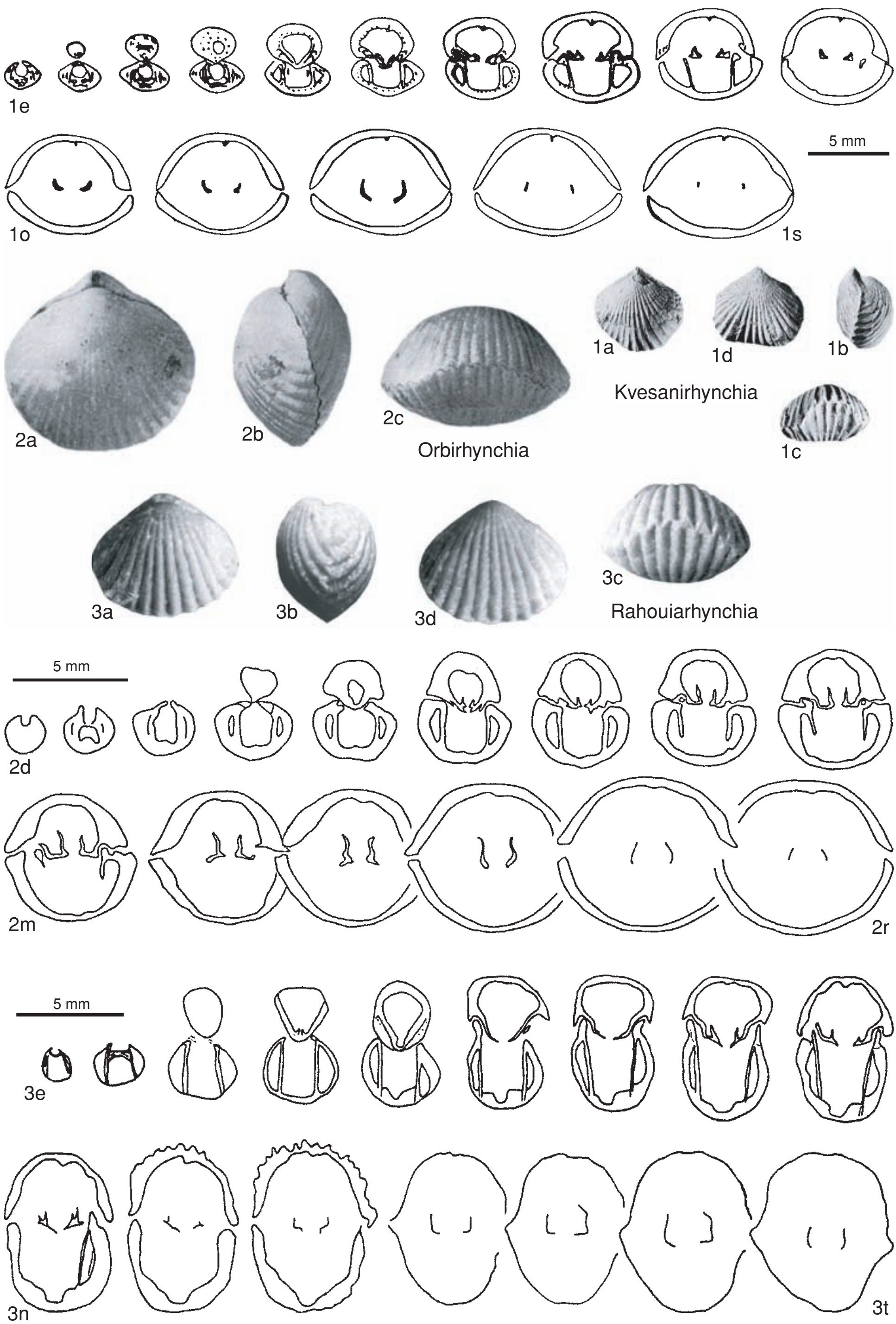

FIG. 822. Basiliolidae (p. 1204–1208).

?Indonesia, western USA (Oregon), *Sinemurian–Toarcian;* Italy, Austria, Yugoslavia, Caucasus, Transcaucasus, *Aalenian–lower Bajocian.*——FIG. 821,*2a–o.* **P. moorei* (DAVIDSON), lower Toarcian, England; *a–c,* lectotype, dorsal, lateral, anterior views, Somerset, BMNH B.12230, ×2; *d–o,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.1, 1.3, 1.5, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 3.0, 3.2, Dorset, MKH D.134 (Ager, 1962).

Rahouiarhynchia TCHOUMATCHENKO, 1987, p. 53 [**R. zidarovi;* OD]. Medium to small size, dorsibiconvex; costae numerous (13 to 17), subangular, running from umbo to front commissure; uniplicate sinus wide and low, fold not raised from shell surface. Dorsal median septum and septalium absent; crura subfalciform to hamiform. *Upper Jurassic (upper Oxfordian–lower Kimmeridgian):* Algeria, ?China (Qinghai).——FIG. 822,*3a–t.* **R. zidarovi,* Algeria; *a–d,* holotype, dorsal, lateral, anterior, ventral views, ×1.5; *e–t,* transverse serial sections, distances in mm from ventral umbo, 0.17, 0.44, 0.8, 1.0, 1.17, 1.4, 1.6, 1.82, 1.97, 2.14, 2.3, 2.49, 2.8, 2.97, 3.22, 3.47 (Tchoumatchenko, 1987).

?Riorhynchia IASIUKEVICH, 1974, p. 108, footnote [**R. nechrikovae;* OD]. Rounded-pentagonal, with more or less strong radial ribs in anterior part; short, curved beak; short pedicle collar; small ventral sulcus. Thick dental plates often almost fused to shell walls; outer hinge plates narrow and very thick, sometimes almost vestigial; crura hamiform; all elements of cardinalia massive, thickened. [Serial sections from type species unknown.] *Paleogene (Paleocene, ?Eocene):* Caucasus, Ukraine (Crimea), Turkmenistan, western Kazakhstan, ?Italy.——FIG. 820,*3a–u. R. rionensis* (ANTHULA), Paleocene, Danian, Kopet Dagh, Turkmenistan; *a–c,* dorsal, lateral, anterior views, MG 35/1915, ×1; *d–u,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.8, 1.1, 1.4, 1.9, 2.1, 2.3, 2.5, 2.9, 3.3, 3.6, 3.9, 4.3, 4.8, 5.6, 6.0, 6.6, 6.9 (Vanchurov & Kalugin, 1966).

Veghirhynchia DAGYS, 1974, p. 84 [**Rhynchonella arpadica* BITTNER, 1890, p. 160; OD] [=*Veghirhynchia* DETRE, 1972, p. 88, *nom. nud.; Veghjirhynchia* XU, 1990, p. 68, *nom. null.; Vegirhynchia* SULSER, 1993, p. 157, *nom. null.*]. Small, subpentagonal, moderately dorsibiconvex, uniplicate; multicostate, similar in general outline to *Orbirhynchia;* ventral sulcus broad, shallow, and trapezoidal linguiform extension meeting a poorly developed dorsal fold; beak short, suberect, beak ridges distinct, deltidial plates conjunct. Dental plates long, subparallel; hinge teeth subquadrate; hinge plates short, distally concave; crura long, subfalciform. *Upper Triassic (Carnian):* southern Alps, Carpathians, ?northwestern Caucasus.——FIG. 820,*1a–l.* **V. arpadica* (BITTNER), Hungary; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/199, ×2; *e,* detail of crura, IGiG 394/200, ×7; *f–l,* transverse serial sections, distances in mm from first section, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.1, IGiG 394/202 (Dagys, 1974).

Subfamily LACUNOSELLINAE Smirnova, 1963

[Lacunosellinae SMIRNOVA, 1963, p. 15] [Includes Dzhangirhynchiinae OVCHARENKO, 1983, p. 70, with its original scope, *partim* Dzhangirhynchiinae OVCHARENKO, *emend.,* SHI & GRANT, 1993, p. 20 (i.e., only the type genus)]

Medium to large Basiliolidae, multicostate to partly smooth, trilobate, with central dorsal fold usually well detached from lateral slopes; costae sharp, simple, commonly bifurcating, occasionally antidichotomous; anterior commissure typically uniplicate, sometimes asymmetrical; spines absent; characterized mainly by absence or very slight development of dorsal median septum and septalium and by presence of falciform crura. *Middle Jurassic (Aalenian)–Lower Cretaceous (Barremian).*

Lacunosella WISNIEWSKA, 1932, p. 30 [**Rhynchonella arolica* OPPEL in OPPEL & WAAGEN, 1866, p. 294; OD] [=*Kolhidaella* MOISEEV, 1939, p. 189 (type, *K. kolhidaensis,* OD); *Kolchidaella* MAKRIDIN in SARYCHEVA, 1960, p. 334, *nom. null.; Lagunosella* KAMYSHAN & KVAKHADZE, 1980, p. 74, *nom. null.*]. Medium to large, equibiconvex to dorsibiconvex, subtriangular to subpentagonal; trilobate, uniplicate, rarely asymmetrical; with few strong costae commonly bifurcating; dorsal fold little raised; beak small, conjunct deltidial plates. Hinge teeth strong, dental plates reduced; hinge plates long, almost horizontal; crura falciform; dorsal septum and septalium absent. *Middle Jurassic (Bathonian)–Lower Cretaceous (Barremian):* Europe, Africa, Asia, ?Mexico, ?Argentina.

L. (**Lacunosella**). Costae simple, subangular, starting near umbo and often showing normal dichotomous branching. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Barremian):* France, Greenland, Switzerland, Germany, Carpathians, Poland, Bulgaria, Crimea, Caucasus, Turkmenistan, Tunisia, southwestern China, ?India, ?Mexico, ?Argentina.——FIG. 823,*2a–o.* **L. (L.) arolica* (OPPEL), Upper Jurassic, France; *a–c,* dorsal, lateral, anterior views, BMNH B.12037, ×1; *d–o,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.8, 2.0, 2.3, 2.7, 3.1, 3.6, 4.3, 4.7, 5.2, 5.6, 6.3, ×2 (Childs, 1969).——FIG. 823,*2p–z. L. (L.) kolhidaensis* (MOISEEV), Barremian, Caucasus, Georgia; *p–s,* holotype, dorsal, lateral, anterior, ventral views, approximately ×1 (Moiseev, 1939); *t–z,* transverse serial sections, distances in mm from ventral umbo, 1.7, 4.2, 5.25, 5.65, 6.0, 7.1, 8.0, LGE 3/181 (new; courtesy of S. V. Lobacheva).

L. (**Dichotomosella**) TCHOUMATCHENKO, 1987, p. 51 [**L. (D.) bourheddouensis;* OD]. Ornament of antidichotomous costae fused into few, short, coarse, marginal plicae anteriorly. *Middle Jurassic*

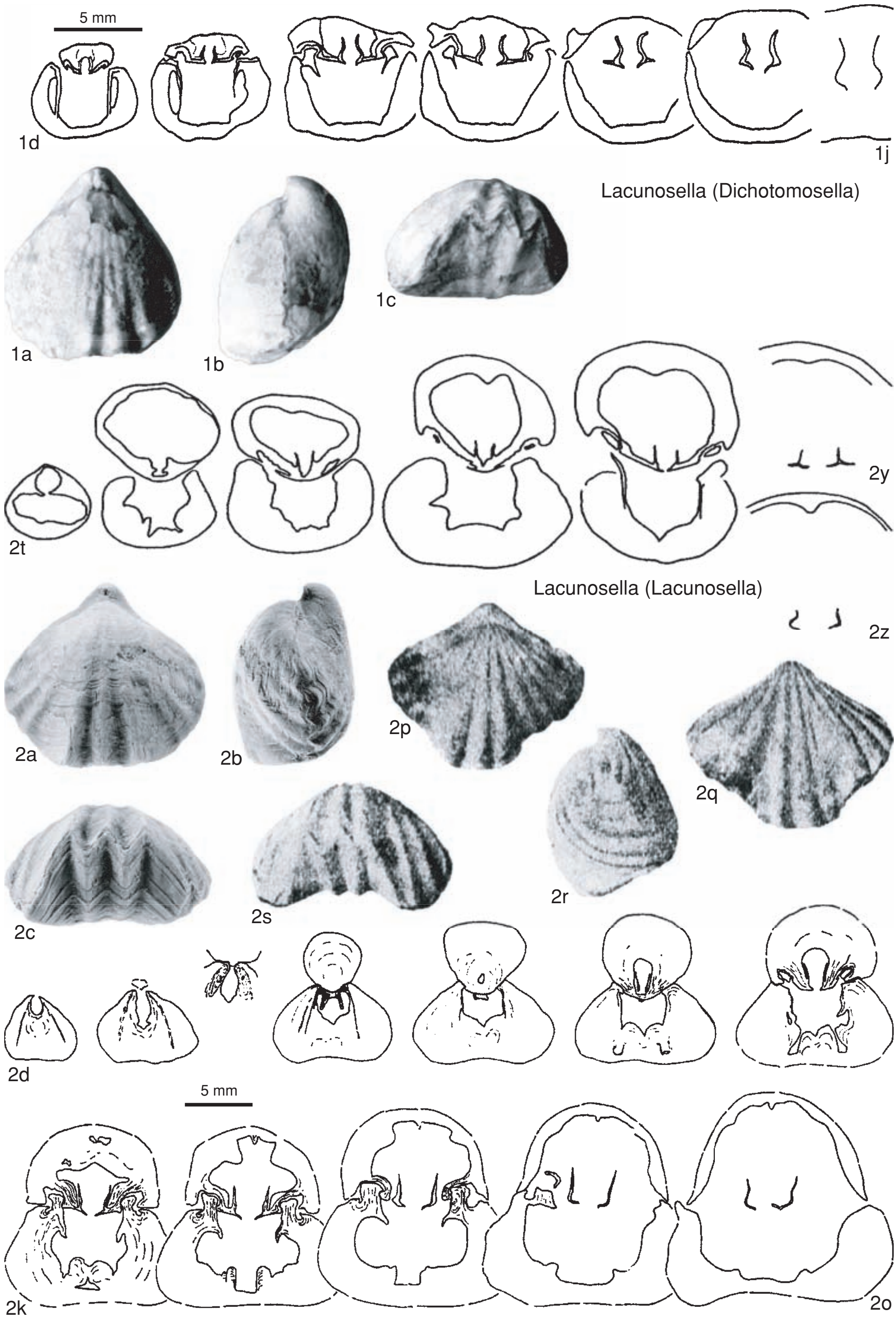

FIG. 823. Basiliolidae (p. 1208–1210).

(Bathonian)–Upper Jurassic (Kimmeridgian): Algeria, Hungary.——FIG. 823,*1a–j*. **L. (D.) bourheddouensis,* upper Kimmeridgian, north of Tiaret, Algeria; *a–c,* holotype, dorsal, lateral, anterior views, ×1.5; *d–j,* transverse serial sections, distances in mm from first section, 1.6, 1.98, 2.35, 2.75, 2.95, 3.18, 3.43 (Tchoumatchenko, 1987).

Stolmorhynchia BUCKMAN, 1918, p. 46 [**S. stolidota;* OD] [=*Stolmorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Dzhangirhynchia* OVCHARENKO, 1983, p. 71 (type, *D. dzhangiensis,* OD)]. Small to medium, subtrigonal to subpentagonal, uniplicate; dorsal fold usually well developed, sometimes asymmetrical; few (12 to 16) strong, fairly angular costae; posterior smooth area absent; beak small, strong, suberect. Dental plates strong, subparallel; dorsal median septum absent or barely detectable; no septalium; muscle scars impressed; crura falciform. *Middle Jurassic (Aalenian–Callovian):* Europe, northern Africa, Asia.

S. (**Stolmorhynchia**). Dorsibiconvex, globose posteriorly; anterior commissure often asymmetrical; costae typically simple. Hinge plates strong and slightly convergent ventrally. *Middle Jurassic (Aalenian–Bathonian):* England, France, Spain, Italy, Austria, Hungary, Ukraine, Caucasus, Morocco, southeastern Pamirs, ?India.——FIG. 824,*2a–r*. **S. stolidota,* upper Bajocian, Dorset, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH B.70762, ×1 (new); *d–r,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.5, 1.6, 2.0, 2.2, 2.4, 2.8, 3.2, 3.4, 3.9, 4.3, 4.6, 4.9, 5.3, 5.6, 5.8, BMNH B. 71933 (Prosser, 1993).

S. (**Praelacunosella**) WISNIEWSKA-ZELICHOWSKA, 1978, p. 109[148] [**P. substephani;* OD] [=*Praelacunesella* WISNIEWSKA-ZELICHOWSKA, 1978, p. 65, alternative original spelling]. Subequibiconvex, tapering, and somewhat depressed posteriorly, may be highest at front; uniplication gentle, arcuate but indistinct dorsal fold, tendency to asymmetry slight; only densely ribbed shells may show dichotomy. Hinge plates subhorizontal, dental plates relatively thinner. *Middle Jurassic (upper Bajocian–Callovian):* Poland, Carpatho-Balkanids, Crimea, southeastern Pamirs, ?southwestern China.——FIG. 824,*1a–v*. **S. (P.) substephani,* lower Callovian, Czestochowa area, Poland; *a–e,* paratype, dorsal, lateral, anterior, ventral, posterior views, Muz IG 1352.II.144, ×1; *f,* detail of apical region, Muz IG 1352.II.140, ×3; *g–v,* transverse serial sections, distances in mm from first section, 0.0, 0.5, 0.7, 1.3, 1.7, 2.0, 2.2, 2.5, 2.6, 2.9, 3.1, 3.6, 4.3, 4.4, 5.0, 5.3, Muz IG 1352.II.147 (Wisniewska-Zelichowska, 1978).——FIG. 824,*1w–ll*. *S. (?P.) dzhangiensis* (OVCHARENKO), upper Bajocian, southeastern Pamirs; *w–y,* dorsal, lateral, anterior views, MUGT 137/1266, ×1; *z–gg,* transverse serial sections, distances in mm, 0.6, 1.55, 2.25, 2.7, 3.15, 3.6, 3.8, 4.1; *hh–ll,* transverse serial sections, distances in mm, 1.55, 1.85, 2.05, 2.7, 3.15, MUGT 138/1266 (Ovcharenko, 1983).

Subfamily AETHEIINAE Cooper, 1959

[Aetheiinae COOPER, 1959, p. 15]

Smooth Basiliolidae, without spines; foramen minute, deltidial plates concave. Dental plates reduced to obsolete, inner hinge plates thick. *Paleogene (?lower Eocene, middle Eocene)–Neogene (lower Miocene).*

Aetheia THOMSON, 1915, p. 389 [**Waldheimia(?) sinuata* HUTTON, 1873, p. 36; OD; =*?Terebratula gualteri* MORRIS in MANTELL, 1850, p. 329] [=*Thomsonica* COSSMANN, 1920, p. 137, obj.]. Medium, elongate oval to triangular, dorsibiconvex, smooth; broadly uniplicate, but inconspicuous dorsal fold; beak small, erect, submesothyrid, with concave, conjunct deltidial plates. Hinge teeth thick, buttressed directly against shell wall; dental plates absent; dorsal median septum short, stout; swollen inner hinge plates filling intercrural space; cardinal process small; subfalciform crura, crescentic in section. *Paleogene (?lower Eocene, middle Eocene)–Neogene (lower Miocene):* New Zealand.——FIG. 825,*2a–e*. **A. gualteri* (MORRIS), upper Oligocene, Duntroonian, Otago; *a–c,* dorsal, lateral, anterior views, USNM 89828a, ×1; *d,* ventral interior, USNM 369298a, ×2; *e,* dorsal interior, detail of cardinalia, USNM 89828b, ×4 (Cooper, 1959).

Subfamily APHELESIINAE Cooper, 1959

[Aphelesiinae COOPER, 1959, p. 15]

Smooth or marginally costate Basiliolidae, without spines. Crura attached directly to side of socket ridge; dorsal valve with thick median ridge (myophragm). *Paleogene (Eocene)–Neogene (Pliocene).*

Aphelesia COOPER, 1959, p. 41 [**Anomia bipartita* BROCCHI, 1814, p. 469; OD]. Subtrigonal to subpentagonal, uniplicate, smooth with faint or incipient costae developing anteriorly; beak elongated, hypothyrid, foramen small, auriculate. Dental plates slightly convergent, teeth subquadrate; hinge plates short, distally concave; dorsal septum absent, septalial plates not developed; crura broad with acutely concave dorsal surfaces. *Paleogene (Eocene)–Neogene (Pliocene):* Italy (northern Apennines to Sicily), Malta, Hungary, Spain, ?Germany.——FIG. 826,*3a–e*. **A. bipartita* (BROCCHI); *a–c,* dorsal, lateral, anterior views, Pliocene, Sicily, USNM 549349a, ×1; *d,* oblique view of crura, USNM 549380, ×3; *e,* detail of ventral umbo showing teeth and auriculate foramen, Pliocene,

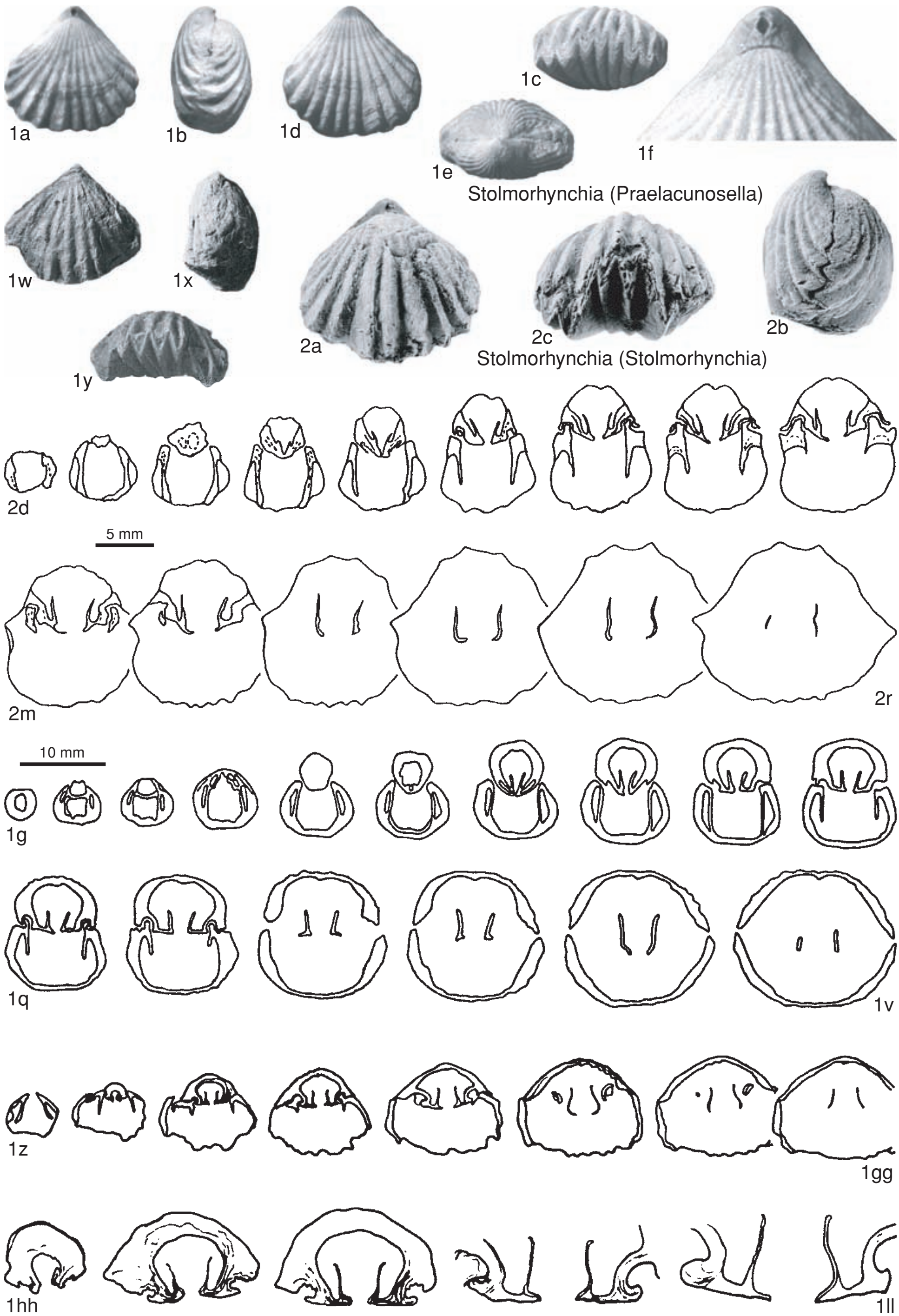

FIG. 824. Basiliolidae (p. 1210).

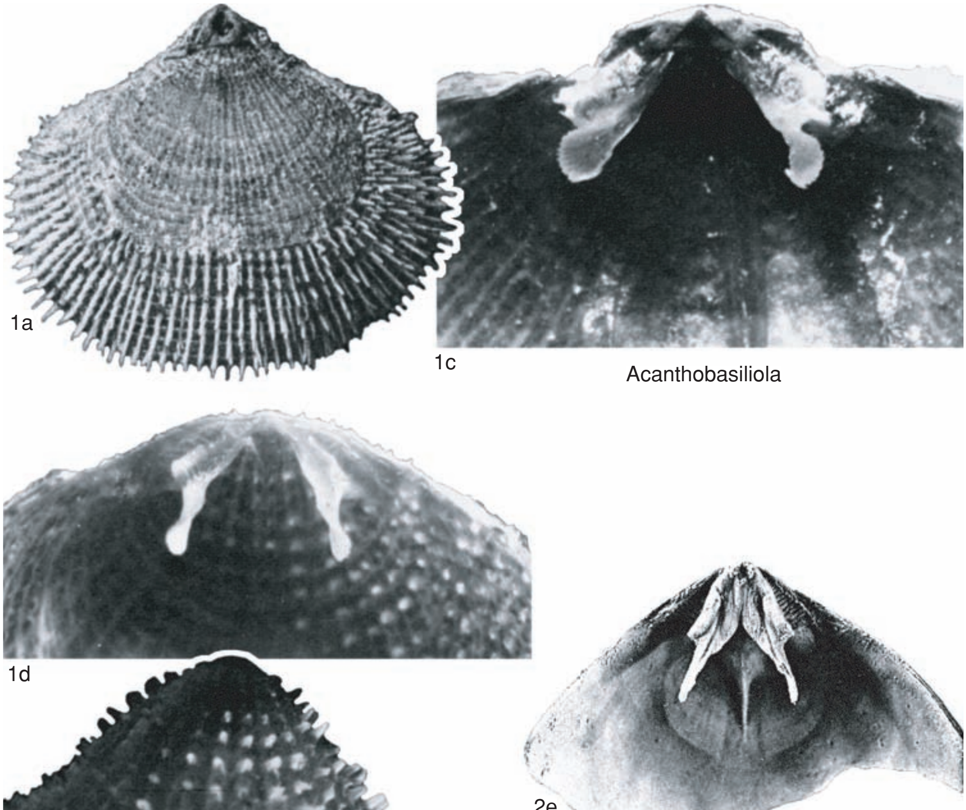

FIG. 825. Basiliolidae (p. 1210–1214).

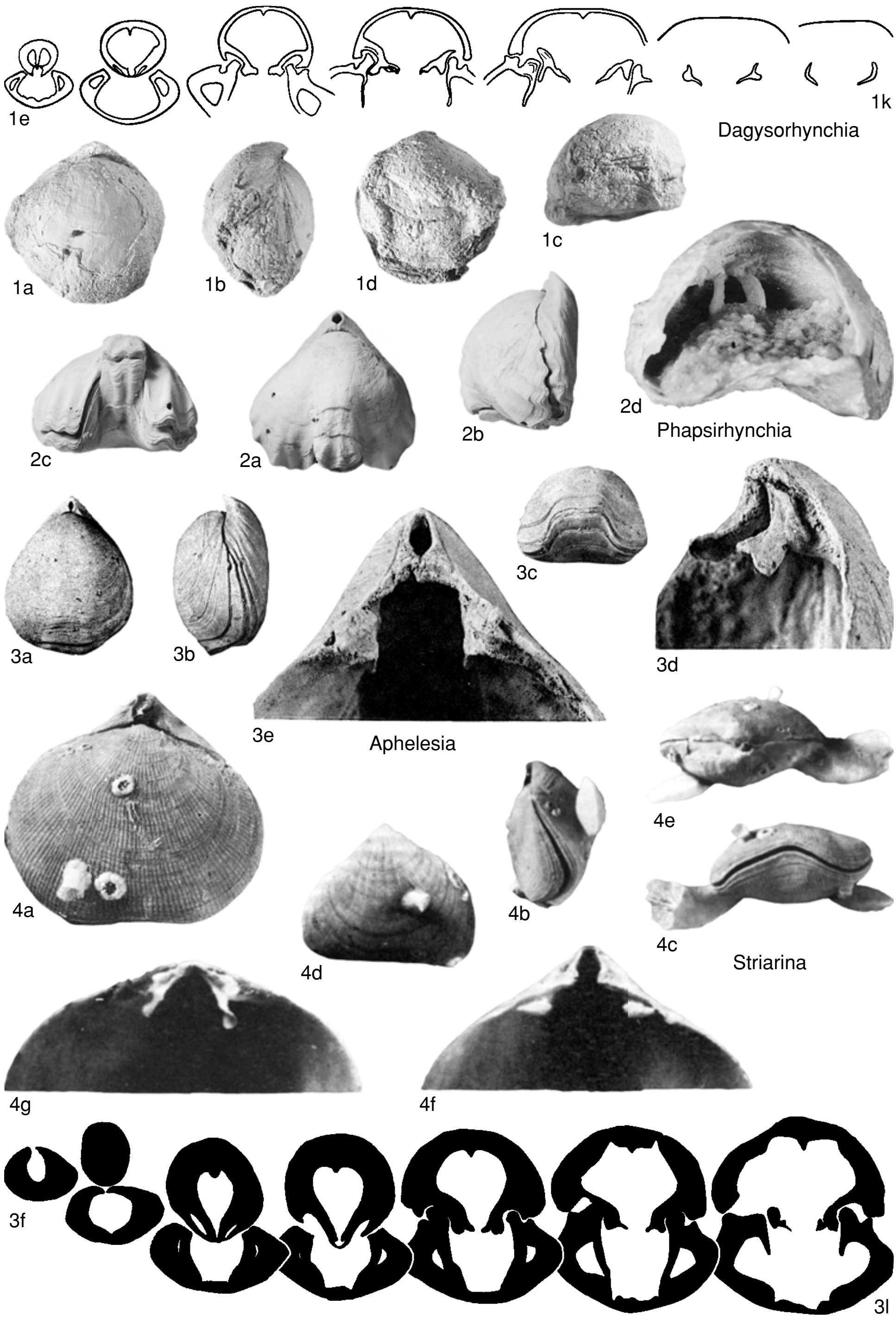

FIG. 826. Basiliolidae (p. 1210–1214).

Sicily, USNM 549349b, ×4; *f–l,* transverse serial sections, distances in mm from ventral umbo, 1.0, 2.0, 2.6, 2.8, 3.2, 3.6, 4.0, Miocene, Tuscany, BMNH unnumbered, ×2 (Cooper, 1959).

Phapsirhynchia Pájaud, 1976, p. 102 [**P. sanctapaulensis;* OD]. Medium to large, globose, almost planoconvex with acutely concave ventral valve developed anteriorly; few strong marginal costae; foramen relatively small, subapical. Large, dorsally concave subfalciform crura deflected ventrally. [Regarded as a junior subjective synonym of *Aphelesia* by Llompart & Calzada, 1983, and Gaetani & Saccà, 1985.] *Neogene (Pliocene):* southern Spain.——Fig. 826,*2a–d.* **P. sanctapaulensis,* Alicante; *a–c,* dorsal, lateral, anterior views, ×1; *d,* anterior view showing crura, ×1.5 (Pájaud, 1976).

Subfamily ACANTHOBASILIOLINAE Zezina, 1981

[Acanthobasiliolinae Zezina, 1981, p. 11]

Basiliolidae with outer surface of shell covered by spines; densely costate. Crura attached to narrow outer hinge plates; dorsal valve with thick median ridge. *Neogene (Miocene)–Holocene.*

Acanthobasiliola Zezina, 1981, p. 11 [**Rhynchonella doederleini* Davidson, 1886a, p. 1; OD]. Medium, transversely oval, inflated, uniplicate. Resembles *Basiliola* in outline but differs in having shell surface covered with short spines; beak small, erect with complete foramen, strong pedicle collar; dental plates weak or not well developed. Hinge plates narrow; dorsal valve with thin median ridge or weak septum; crura short, with additional festoons at distal ends. [Differs from *Tegulorhynchia* Chapman & Crespin, 1923, p. 175, in general morphology, type of crura, and spinose shell ornament.] *Neogene (Miocene)–Holocene:* Borneo to Japan, bathyal.——Fig. 825,*1a–d.* **A. doederleini* (Davidson), Holocene; *a,* dorsal view, BMNH ZB3999, Banda Sea, ×3 (Brunton & Alvarez, 1989); *b,* detail of spinose ornament, Java Sea, ×5; *c,* dorsal interior showing crura and weak septal ridge, Java Sea, ×5; *d,* cardinalia of juvenile, Java Sea, ×6 (Zezina, 1981).

Subfamily UNCERTAIN

?Dagysorhynchia Smirnova, 1994, p. 34 [**D. compacta;* OD]. Medium, equibiconvex, rounded-pentagonal, almost as wide as long; umbo broad, massive; shell smooth or with fine, indistinct costellation. Pedicle collar sometimes developed; dental plates ventrally divergent; hinge plates narrow, dorsal surfaces concave, acutely dorsally inclined with well-developed inner and outer socket ridges; crura hamiform; dorsal median septum apically confined. *Lower Cretaceous (Hauterivian–Barremian):* Russia (northwestern Kamchatka). ——Fig. 826,*1a–k.* **D. compacta; a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 138/515, ×1; *e–k,* transverse serial sections, distances in mm from first section, 1.6, 2.5, 3.0, 3.2, 3.7, 4.5, 5.3, MGU 138/517 (Smirnova, 1994).

?Striarina Cooper, 1973, p. 7 [**Rhynchonella valdiviae* Helmcke, 1940, p. 290; OD]. Small, transversely triangular to subpentagonal, dorsibiconvex; broadly, irregularly uniplicate, finely costellate; beak small, nearly straight, with fairly large hypothyrid foramen and disjunct deltidial plates. Pedicle collar short; teeth strong, triangular, with flaring dental plates; sockets broad, deep, corrugated; outer hinge plates narrow, concave, inner hinge plates absent; crura short, subfalciform with rounded extremities; slender dorsal median ridge. [Living species is bathyal.] *Holocene:* southern Indian Ocean.——Fig. 826,*4a–g.* **S. valdiviae* (Helmcke), St. Paul Island; *a,* dorsal view, ×3; *b–e,* lateral, anterior, ventral, posterior views, ×2; *f,* detail of ventral umbo, ×4; *g,* hypotype, detail of cardinalia, dorsal interior, USNM 549729a–b, ×4 (Cooper, 1973).

Family ERYMNARIIDAE Cooper, 1959

[Erymnariidae Cooper, 1959, p. 17]

[Materials prepared by Miguel O. Manceñido & Ellis F. Owen]

Pugnacoidea with septiform crura or variation thereof (sometimes with lyre-shaped cross section distally), variously folded, smooth to partially or fully costate. Trend to reduction or loss of dental plates, dorsal median septum, and septalium; squama and glotta absent, cardinal process exceptionally present. *Upper Triassic (Carnian)–Paleogene (Eocene).*

Subfamily ERYMNARIINAE Cooper, 1959

[*nom. transl.* Ager, Childs, & Pearson, 1972, p. 217, *ex* Erymnariidae Cooper, 1959, p. 17]

Erymnariidae with full septiform crura; uniplicate or asymmetrical; smooth to irregularly costate around margins, occasionally finely and densely costate. Dental plates weak; median septum, septalium, and cardinal process absent. *Upper Cretaceous (Cenomanian)–Paleogene (Eocene).*

Erymnaria Cooper, 1959, p. 64 [**Terebratula polymorpha* Massalongo, 1850, p. 18; OD]. Subtrigonal to subpentagonal, dorsibiconvex; uniplication broadly arcuate, commissure sometimes asymmetrical; smooth or irregularly costate anteriorly; beak short, foramen hypothyrid, deltidial plates conjunct, planareas absent. Crural plates ventrally convergent, somewhat sigmoidal, or lyrate anteriorly.

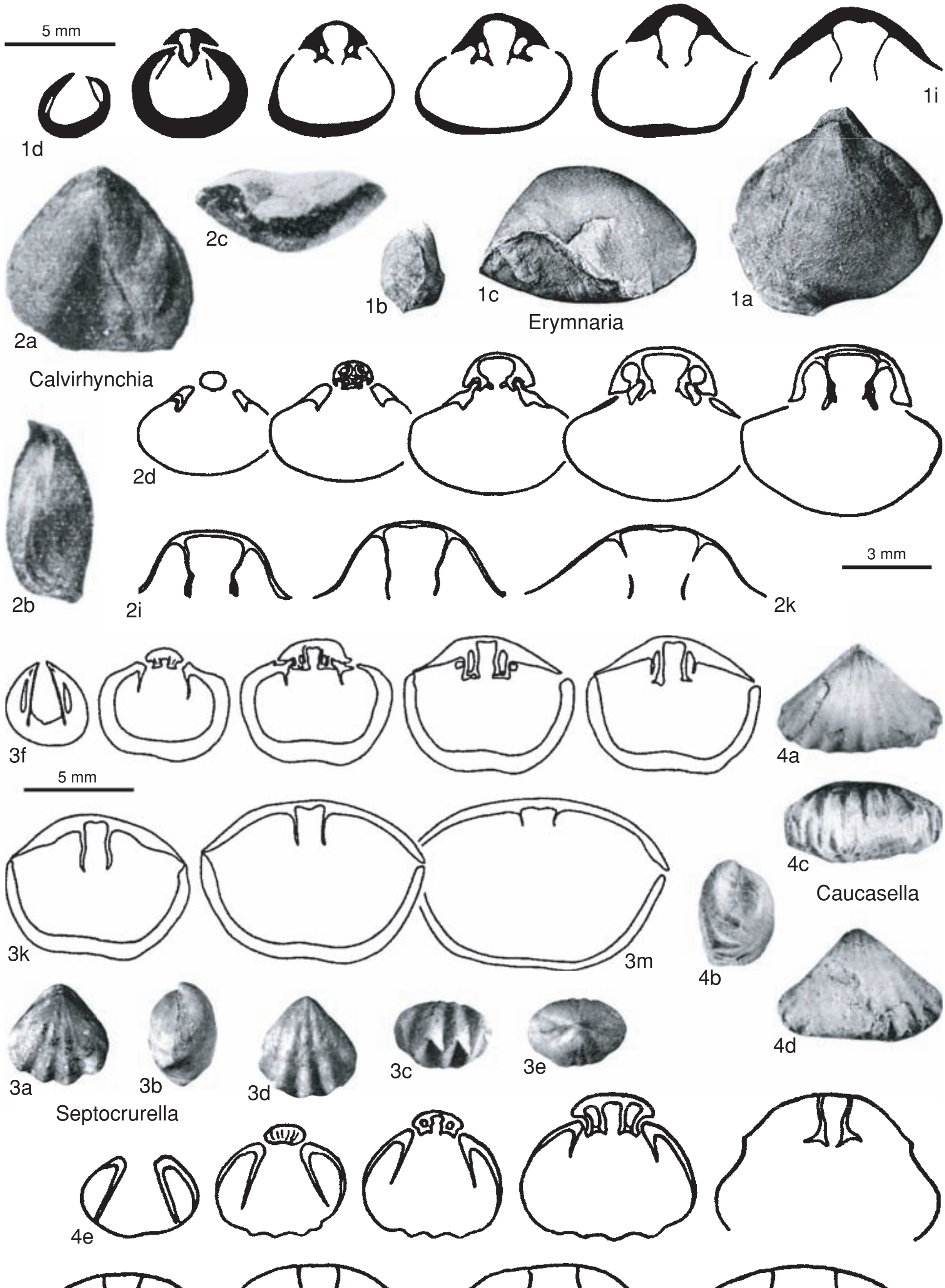

FIG. 827. Erymnariidae (p. 1214–1218).

Upper Cretaceous (Cenomanian)–Paleogene (Eocene): Caucasus, Ukraine, Austria, Italy, Turkmenistan, Kazakhstan, *Cenomanian–Danian;* Mediterranean, Hungary, Cuba, western Kazakhstan, *Eocene.*——FIG. 827,*1a–i.* **E. polymorpha* (MASSALONGO), Eocene, Verona, Italy; *a,* dorsal view, USNM 75888a, ×2; *b,* lateral view, USNM 549384a, ×1; *c,* anterior view, USNM 75888a, ×2; *d–i,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.7, 1.95, 2.25, 2.6, 4.0, USNM 549384e (Cooper, 1959).

Subfamily CRYPTORHYNCHIINAE Shi & Grant, 1990

[Cryptorhynchiinae SHI & GRANT in SHI, 1990, p. 313]

Erymnariidae bearing septiform crura, with lateral septa totally or partially fused to socket fulcral plates; fully and sharply multicostate to densely costellate, no smooth areas; uniplication variable, scarcely to well developed. Septalium rudimentary, confined to early stages, dorsal median septum variably developed; subparallel dental plates; crural plates ventrally convergent and typically detached from dorsal floor distally. *Upper Triassic (Carnian)–Middle Jurassic (Callovian), Upper Jurassic (?Kimmeridgian).*

Cryptorhynchia BUCKMAN, 1918, p. 66 [**Rhynchonella pulcherrima* KITCHIN, 1897, p. 33; OD] [=*Cryptorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Small, dorsibiconvex, uniplicate, transversely oval; dorsal fold moderate; reticulate ornament, with costae sharp and growth lamellae foliaceous; beak sharp, suberect. Teeth and sockets projecting well into dorsal valve, fulcral plates fused to lateral septa; septalium absent. *Middle Jurassic (Aalenian–Callovian), ?Upper Jurassic (?Kimmeridgian):* Alps, Pamirs, India, ?China, ?North America.——FIG. 828,*1a–o.* **C. pulcherrima* (KITCHIN), Callovian, Kutch, India; *a–c,* topotype, dorsal, lateral, anterior, USNM 76009a, ×1.8; *d,* topotype, dorsal, USNM 429605, ×2; *e–o,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.3, 0.5, 0.6, 0.9, 1.2, 1.5, 1.9, 2.2, 2.4, 2.5, 2.8, USNM 76009b (Shi & Grant, 1993).

Aethirhynchia SHI, 1990, p. 314 [**A. lenticulata;* OD]. Medium size, elongate-oval to cuneiform, gently equibiconvex; nearly rectimarginate, fully covered with numerous fine costellae; beak slightly incurved. Dorsal median septum stout, septalial plates pendant, lateral septa short, incompletely fused with fulcral plates. *Middle Jurassic (middle Callovian–upper Callovian):* China (Qinghai).——FIG. 828,*3a–v.* **A. lenticulata,* Geladangdong, southern Qinghai; *a,* dorsal view, MCMB G14751, ×1 (Shi, 1992); *b–i,* holotype, transverse serial sections, distances in mm from ventral umbo, 2.6, 3.0, 4.6, 5.3, 5.7, 6.0, 6.3, 7.0, MCMB Y14750 (Shi, 1990).

Crurirhynchia DAGYS, 1961, p. 96 [**C. kiparisovae;* OD]. Small to medium size, rounded-subpentagonal, gently dorsibiconvex; weakly uniplicate, sharply multicostate throughout; beak low, suberect, with hypothyrid foramen and conjunct deltidial plates. Pedicle collar fused to dental plates; dorsal median septum low; septalium rudimentary or absent; crura long, arising from oblique septa, more or less fused with socket fulcral plates. *Upper Triassic (Norian–Rhaetian):* Balkans, Crimea, northwestern Caucasus, Pamirs, China.——FIG. 828,*2a–v.* **C. kiparisovae,* Norian, northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 91/600, ×1; *e–v,* transverse serial sections, distances in mm from first section, 0.1, 0.3, 0.4, 0.6, 0.8, 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.7, 1.8, 2.0, 2.2, 2.4, 2.5, 2.9, IGiG 394/203 (Dagys, 1974).

Dierisma CHING, SUN, & YE in CHING & others, 1979, p. 133 [**D. furcatum;* OD]. Medium size, transverse-oval; depressed lenticular, almost equibiconvex; dorsal fold gentle and flattopped, ventral sulcus wide and shallow; slight, low arch, uniplication, costae narrow, subangular, and sometimes bifurcated anteriorly. Dental plates short; crural plates issued vertically from inner edge of outer hinge plates to floor of dorsal valve and extending to one-third dorsal valve length. [May be a subgenus of *Crurirhynchia* or a synonym.] *Upper Triassic (Carnian–Norian):* China (Qinghai, Tibet).——FIG. 828,*4a–k.* **D. furcatum,* Upper Triassic, Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42813, ×1; *e–k,* holotype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.65, 1.0, 1.6, 2.0, 2.2, 3.8, NIGP 42813 (Ching & others, 1979).

Subfamily SEPTOCRURELLINAE Ager, Childs, & Pearson, 1972

[Septocrurellinae AGER, CHILDS, & PEARSON, 1972, p. 217]

Erymnariidae with full septiform crura; broadly unisulcate to rectimarginate and fairly sharply paucicostate (mostly anteriorly). Dental plates weak, ventrally divergent; median septum ridgelike to absent; crural plates vertical; cardinal process absent. *Lower Jurassic (?Sinemurian, Pliensbachian)–Upper Jurassic (Kimmeridgian, ?Tithonian).*

Septocrurella WISNIEWSKA, 1932, p. 63 [**Rhynchonella Sanctae Clarae* ROEMER, 1870, p. 247; OD]. Small, ventribiconvex, dorsally sulcate, with few rounded

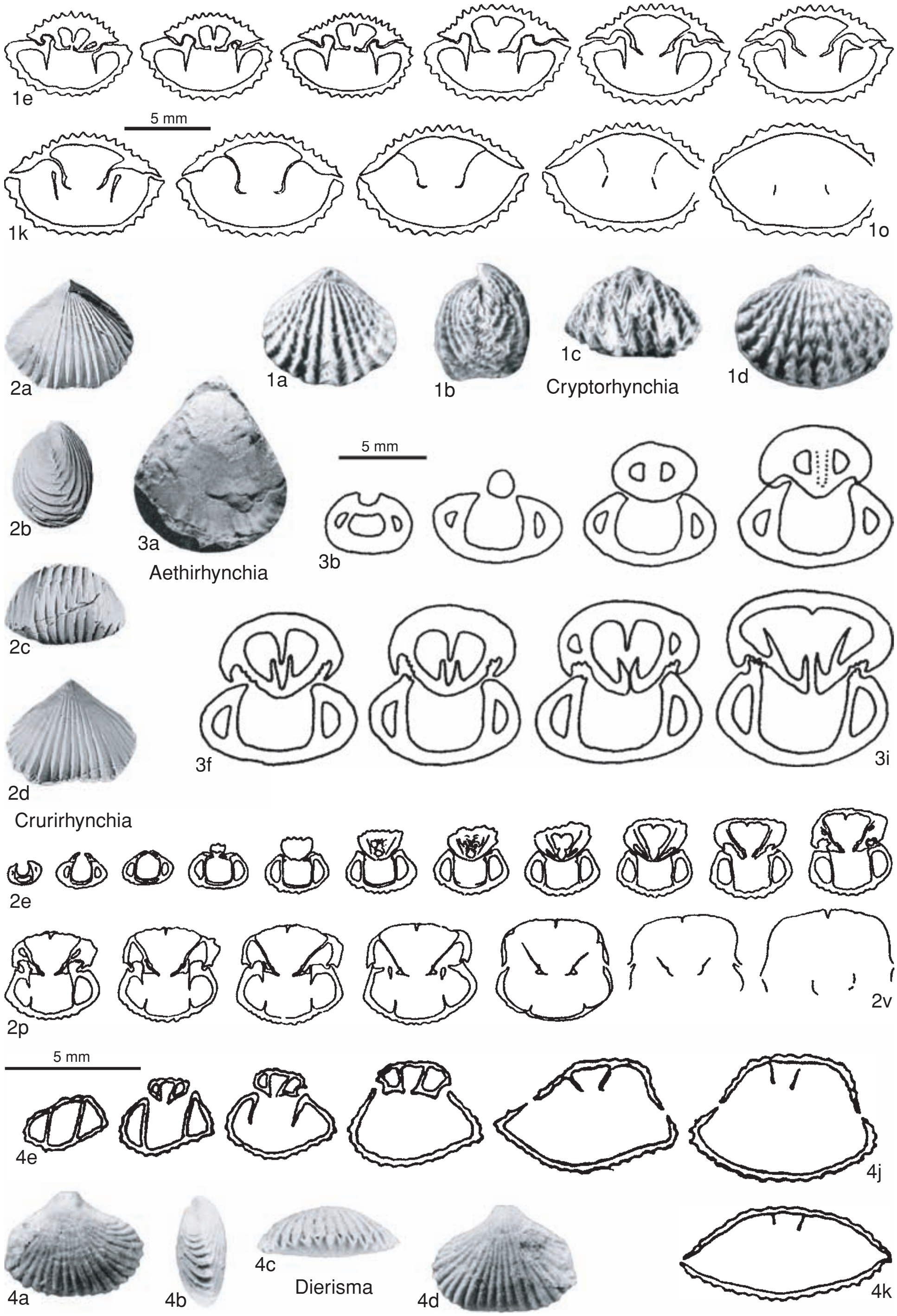

FIG. 828. Erymnariidae (p. 1216).

costae; beak small, upright, without planareas, foramen hypo- to submesothyrid. Crura short, supported by subparallel crural plates extending to one-third dorsal valve length; dorsal septum absent to vestigial. *Lower Jurassic (?Sinemurian, Pliensbachian)–Upper Jurassic (Kimmeridgian, ?Tithonian):* southern and eastern Europe.——FIG. 827,*3a–m.* **S. sanctaeclarae* (ROEMER); *a–e,* dorsal, lateral, anterior, ventral, posterior views, Oxfordian, Jasna Góra, Poland, ×1 (Wisniewska, 1932); *f–m,* transverse serial sections, distances in mm from ventral umbo, 1.4, 2.4, 2.8, 3.3, 3.4, 3.6, 4.5, 5.2, Aiglun, France (Laurin, 1979).

Caucasella MOISEEV, 1934, p. 83[187] *non* HACOBJAN in AKOPYAN & others, 1969, Gastropoda, *nec* LONGORIA, 1974, Foraminiferida [**Rhynchonella trigonella* ROTHPLETZ, 1886, p. 154; OD]. Small, trigonal to securiform, depressed equibiconvex, wide and flat anteriorly; sharply costate, with evenly serrate commissure but no fold or sulcus; beak small, gently incurved, with planareas. Short dental plates, no dorsal median septum, crural plates closely subparallel. *Middle Jurassic (upper Bajocian–Callovian), Upper Jurassic (?Kimmeridgian):* France, Switzerland, Germany, Austria, Italy, Slovakia, Romania, Bulgaria, Ukraine, Yugoslavia, Tisia River (Hungary), Caucasus, Crimea.——FIG. 827,*4a–m.* **C. trigonella* (ROTHPLETZ), Callovian, Greben, Yugoslavia; *a–d,* dorsal, lateral, anterior, ventral views, 4/45, ×1 (Radulovic & Rabrenovic, 1993); *e–m,* transverse serial sections, distances in mm from ventral umbo, 0.5, 1.1, 1.3, 1.8, 2.0, 2.1, 2.6, 4.3, 4.9, Theodosia, Crimea, KHGU 3298/8 (Kamyshan & Babanova, 1973).

Subfamily CALVIRHYNCHIINAE Kamyshan, 1967

[*nom. transl.* MANCEÑIDO & OWEN, herein, *ex* Calvirhynchiidae KAMYSHAN, 1967a, p. 56]

Erymnariidae with septiform crura, broadly unisulcate and smooth or only faintly undulate anteriorly. Dental plates reduced, ventrally divergent or concave; median septum ridgelike to absent; crural plates variably fused to socket fulcral plates, remaining joined to dorsal floor; sometimes with cardinal process (or possible callus-infilled septalium); outer hinge plates absent. *Lower Jurassic (?Sinemurian, ?Pliensbachian), Middle Jurassic (Aalenian–Callovian).*

Calvirhynchia KAMYSHAN, 1967a, p. 56 [**C. kubanensis;* OD]. Small to medium size, smooth, rounded subtrigonal, ventribiconvex; well-defined median dorsal sulcus and ventral fold; beak small, suberect, planareas absent. Pedicle collar absent. *Lower Jurassic (?Sinemurian, ?Pliensbachian), Middle Jurassic (Aalenian–Callovian):* southern Europe, Caucasus, central Asia.——FIG. 827,*2a–k.* **C. kubanensis,* upper Bajocian, Kuban River, Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, KHGU 6/2135, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.1, 1.3, 1.7, 2.1, 2.3, 2.8, 3.3, 4.0, KHGU 6/2140 (Kamyshan, 1967a).

STENOSCISMATOIDEA

S. J. CARLSON and R. E. GRANT

[University of California, Davis; and deceased]

Superfamily STENOSCISMATOIDEA Oehlert, 1887 (1883)

[*nom. correct.* CARLSON, herein, *pro* Stenoscismatacea MUIR-WOOD, 1955, p. 69, *nom. correct. pro* Stenoscismacea SHROCK & TWENHOFEL, 1953, p. 317, *nom. transl. et correct. ex* Stenoschismatinae OEHLERT, 1887a, p. 1304] [=Camerophoriacea WAAGEN, 1883, p. 435, *nom. transl.* GRABAU, 1936, p. 70, *ex* Camerophoriinae WAAGEN, 1883, p. 435]

Small to medium sized, rarely large; outline commonly subpentagonal, may be triangular, oval, or round; valves moderately to strongly dorsibiconvex; strong uniplication with flat, rarely rounded, fold and sulcus, rarely unisulcate; stolidium present uncommonly in well-preserved individuals of a few species; slit-shaped to oval foramen present; ventral spondylium present, commonly elevated on low duplex septum, less commonly sessile; dorsal camarophorium present, commonly robust, strongly curved, on high median septum; hinge plates undivided, rarely divided in some forms lacking intercamarophorial plate; cardinal process absent, weak, or robust; intercamarophorial plate may be present or absent; crura raduliform. [Regarding the two dates of publication listed for OEHLERT, GRANT (1965a) states [comments in square brackets by SJC]:

"ICZN (Article 40) requires the retention of family-group names that are based on junior synonyms [as is *Camerophoria* King, 1846; see for example Parallelelasmatidae, p. 958, herein], unless the synonymy was discovered before 1961, in which case the family-group name is changed, and the change generally accepted. As Schmidt (1964, p. 132) has pointed out, the family-group names based on Stenoscismatinae Oehlert (1887) [as a correction of Stenoschismatinae Oehlert (1887)] were in general use prior to 1961, and should be retained in the interest of stability. [Stenoscismatinae was placed on the Official List of Family-Group Names in Zoology (Opinion 770, 1966) by the ICZN.] The rules require, however, that the pertinent date in this case is the first recognition of the family group, and this is the date of Waagen's (1883) establishment of Camerophoriinae." Thus Oehlert, 1887 (1883) is recognized as the publication date for Stenoscismatoidea.] *Lower Devonian (Pragian)–Upper Permian (Changhsingian).*

Stenoscismatoids are rhynchonellides distinguished by a dorsal camarophorium and a ventral spondylium and are commonly strongly dorsibiconvex and strongly uniplicate with undivided hinge plates. The classification of the Stenoscismatoidea (Grant, 1965a, 1965b) has been emended here because of several difficulties, acknowledged by Grant himself, including the erratic preservation of some characters deemed to be diagnostic, and the unreliable presence of supposedly diagnostic features in named higher taxa because of the frequency of homoplasy. Grant's classification (1965a) was erected explicitly as a key to the identification of taxa rather than as a statement of phylogenetic relationships, making these difficulties particularly vexing. The revised classification herein is based on a morphologic and stratigraphic analysis of the phylogenetic affinities of the stenoscismatoids (Carlson, 1998) and is, interestingly, more in agreement with Grant's informal assessment of relationships (1965a; unpublished notes, 1994) than his classification (1965a, 1965b).

Family STENOSCISMATIDAE Oehlert, 1887 (1883)

[*nom. transl. et correct.* Muir-Wood, 1955, p. 91, *ex* Stenoschismatinae Oehlert, 1887a, p. 1304; *emend.,* Carlson, herein] [=Camerophoriidae Waagen, 1883, p. 435, *nom. transl.* Grabau, 1936, p. 70, *ex* Camerophoriinae Waagen, 1883, p. 435]

Costae commonly strong, sharp, simple, present on anterior half only, may be absent entirely, rarely on entire valve; valve edges commonly overlapping slightly to strongly, rarely not overlapping; beak straight, erect, rarely gently incurved; delthyrium commonly unconstricted by dorsal beak; deltidial plates present, disjunct or conjunct, rarely absent; spondylium elevated on low duplex septum, rarely sessile. *Lower Devonian (Pragian)–Upper Permian (Kazanian, ?Tatarian).*

Subfamily STENOSCISMATINAE Oehlert, 1887 (1883)

[*nom. correct.* Muir-Wood, 1955, p. 91, *pro* Stenoschismatinae Oehlert, 1887a, p. 1304; *emend.,* Carlson, herein] [=Camerophoriinae Waagen, 1883, p. 435]

Geniculation rarely present; beak may be short or elongate; stolidium narrow to broad, present in some species; broad hinge plates; cardinal process robust; intercamarophorial plate strong, thick. *Middle Devonian (Eifelian)–Upper Permian (Kazanian, ?Tatarian).*

Stenoscisma Conrad, 1839, p. 59, *non Stenocisma* Hall, 1847, p. 142, *nec Stenocisma* Conrad-Hall in Hall, 1867b, p. 334–335, *nec Stenoschisma* Hall & Clarke, 1893, p. 187, *nec Stenochisma* Schuchert, 1897, p. 413, *nec Stenochisma* Grabau & Shimer, 1907, p. 288 [**Terebratula schlottheimii* von Buch, 1834, p. 59–60; OD] [=*Camerophoria* King, 1844, p. 312, *nom. nud.; Camerophoria* King, Aug. 1846, p. 89–91, obj.; *Camarophoria* Herrmannsen, Dec. 1846, p. 161, obj.; *Stenocisma* Dall, 1877, p. 65, obj.; *Stenoschisma* Oehlert, 1887a, p. 1309, obj.]. Valves of medium size, may be large; costae rounded or sharp, on fold, flanks, or both, beginning near beaks or far in front of them; broad stolidium around anterior margins of adults; posterolateral edges of ventral valve flattened, strongly overlapped by edges of dorsal valve; beak long, varying from nearly straight to tightly incurved; deltidial plates conjunct or disjunct; foramen oval, open or completely closed; weak muscle marks in spondylium with adductors narrow, medial and diductors large, surrounding adductors; adjustors undifferentiated in apical part of spondylium; *vascula genitalia* deep, transverse, beginning at anterior edge of median septum; *vascula media* beginning as mesial pair near origin of gonocoels, bifurcating toward margins, extending onto stolidium; large, low, finely striated cardinal process; weak muscle marks in camarophorium with anterior adductors small, paired, medial and posterior adductors larger, lateral; mantle canals as in ventral valve. [Several variations of this generic name exist. Some have been applied to specimens appropriately included within *Stenoscisma schlottheimii,* others not, as indicated above. Several variations of the specific name exist also. VON BUCH (1834) clearly refers to *Terebratula schlottheimii,* the spelling used here. CONRAD (1839), when first referring these specimens to *Stenoscisma,* refers to *Terebratula schlotheimii;* most others afterward refer to *schlotheimi.* It seems that SCHLOTTHEIM allowed his name to appear in print in several different spellings, contributing to the confusion.] *Lower Carboniferous–Upper Permian (Kazanian, ?Tatarian):* cosmopolitan.——FIG. 829,*1a–n.* **S. schlottheimii* (VON BUCH), middle Upper Permian, Germany; *a,* dorsal valve exterior; *b,* lateral view, ventral valve on right; *c,* anterior view, ventral valve below; *d,* posterior view, ventral valve below; *e,* lateral interior, ventral valve on right, ×2 (Grant, 1965b); *f–n,* serial transverse sections, ventral valve below, ×2.5 (Weller, 1914).——FIG. 829,*1o–t. S. venustum* (GIRTY), lower Permian, Leonard Formation, Texas, USA; *o,* dorsal valve exterior; *p,* ventral valve exterior; *q,* lateral interior, ventral valve below, ×1.5; *r,* dorsal valve interior, oblique; *s,* dorsal valve interior; *t,* ventral valve interior, ×2 (Grant, 1965a).

Atribonium GRANT, 1965a, p. 37 [**A. simatum;* OD]. Valves small; outline subtrigonal; costae weak, rounded; valve edges overlapping slightly along posterior slopes, geniculate at anterior margin; stolidium absent; small conjunct or nearly conjunct deltidial plates present; spondylium sessile near apex in most species, elevated on low median septum duplex anteriorly; cardinal process low; camarophorium short, relatively flat, braced to underside of hinge plate by short, thick intercamarophorial plate. *Middle Devonian (Eifelian)–Lower Carboniferous (Tournaisian):* USA, Canada, Russia (Urals).——FIG. 830,*1a–k.* **A. simatum,* Middle Devonian, Newton Creek Limestone, Michigan, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below; *e,* dorsal valve interior, oblique, ×2; *f–k,* serial transverse sections, ventral valve below, 0.6, 0.8, 1.0, 1.2, 1.5, 1.6 mm from ventral valve beak, ×4 (Grant, 1965b).——FIG. 830,*1l–o. A. ? cooperorum* GRANT, Middle Devonian, Ferron Point Formation, Michigan, USA; *l,* dorsal valve exterior; *m,* ventral valve exterior; *n,* lateral view, ventral valve on left; *o,* anterior view, ventral valve below, ×2 (Grant, 1965b).——FIG. 830,*1p–v. A. cooperorum* GRANT, Middle Devonian, Bell Shale, Michigan, USA; serial transverse sections, ventral valve below, 0.3, 0.5, 0.8, 1.1, 1.4, 2.1, 2.9, ×4 (Grant, 1965b).

Camerisma GRANT, 1965a, p. 63 [**C. prava;* OD] [=*Laevicamera* GRABAU, 1936, p. 87, *nom. nud., non Levicamera* GRABAU, 1934, p. 18; see *Psilocamara,* p. 1224, herein]. Valves of medium size; outline oval or subpentagonal, type species commonly asymmetrical; shell walls commonly thick; costae absent or very weak, confined to anterior fold and sulcus; strong, angular uniplication; valve edges overlapping strongly; stolidium absent; beak thick, blunt, tightly curved against dorsal umbo in some species, constricting delthyrium and foramen. *Lower Carboniferous (Serpukhovian)–Lower Permian (Artinskian):* USA, Europe, Russia, China.——FIG. 829,*2a–h.* **C. prava,* Serpukhovian, Alaska, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e–h,* serial transverse sections, ventral valve below, 2.0, 2.6, 2.7, 3.0 mm from ventral valve beak, ×2.7 (Grant, 1965b).

Coledium GRANT, 1965a, p. 95 [**C. erugatum;* OD]. Valves commonly small, only rarely large; costae absent or few, rounded, weak, on anterior half only; stolidium narrow and sporadic or absent; beak short, suberect to incurved; deltidial plates small and disjunct or absent; spondylium on low median septum duplex, rarely sessile posteriorly. *Middle Devonian (Givetian)–Lower Permian (Sakmarian):* USA, Britain, Timor, ?Australia.——FIG. 830,*2a–n.* **C. erugatum,* Viséan, Moorefield Formation, Oklahoma, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×2; *e–n,* serial transverse sections, ventral valve below, 1.2, 1.5, 2.1, 2.6, 2.9, 3.0, 3.4, 4.0, 4.2, 4.7 mm from ventral valve beak; *f,* low spondylium duplex; *g,* cardinal process large, distinct; *h,* hinge plates broad, undivided; *i,* camarophorium on high septum with intercamarophorial plate clear, ×4 (Grant, 1965b).——FIG. 830,*2o–q. C. bowsheri* (COOPER), Upper Carboniferous, Magdalena Group, New Mexico, USA; *o,* dorsal valve interior; *p,* anterior view of interior of articulated valves, ventral valve above, ×3; *q,* lateral interior view, ventral valve on right, ×4 (Grant, 1965a).

Sedenticellula COOPER, 1942, p. 231 [**Camarophoria hamburgensis* WELLER, 1910, p. 500; OD]. Valves of medium size, elongate or transverse oval in outline, of moderate dorsibiconvexity; costae low, narrow, rounded, beginning at or very near beaks, simple, bifurcating or intercalating; uniplication weak, rounded; valve edges not overlapping; stolidium absent; beak short, suberect; delthyrium constricted by dorsal beak; deltidial plates absent; spondylium sessile or duplex on low median septum; camarophorium weakly curved, on low median septum; cardinal process not well known. *Lower Carboniferous (Tournaisian):* USA, France.——FIG. 831*a–r.* **S. hamburgensis* (WELLER), Hamburg Oolite, Illinois, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* anterior view, ventral valve below, ×2 (Grant, 1965b); *d–l,* dorsal valve, serial transverse sections; *m–r,* ventral valve, serial transverse

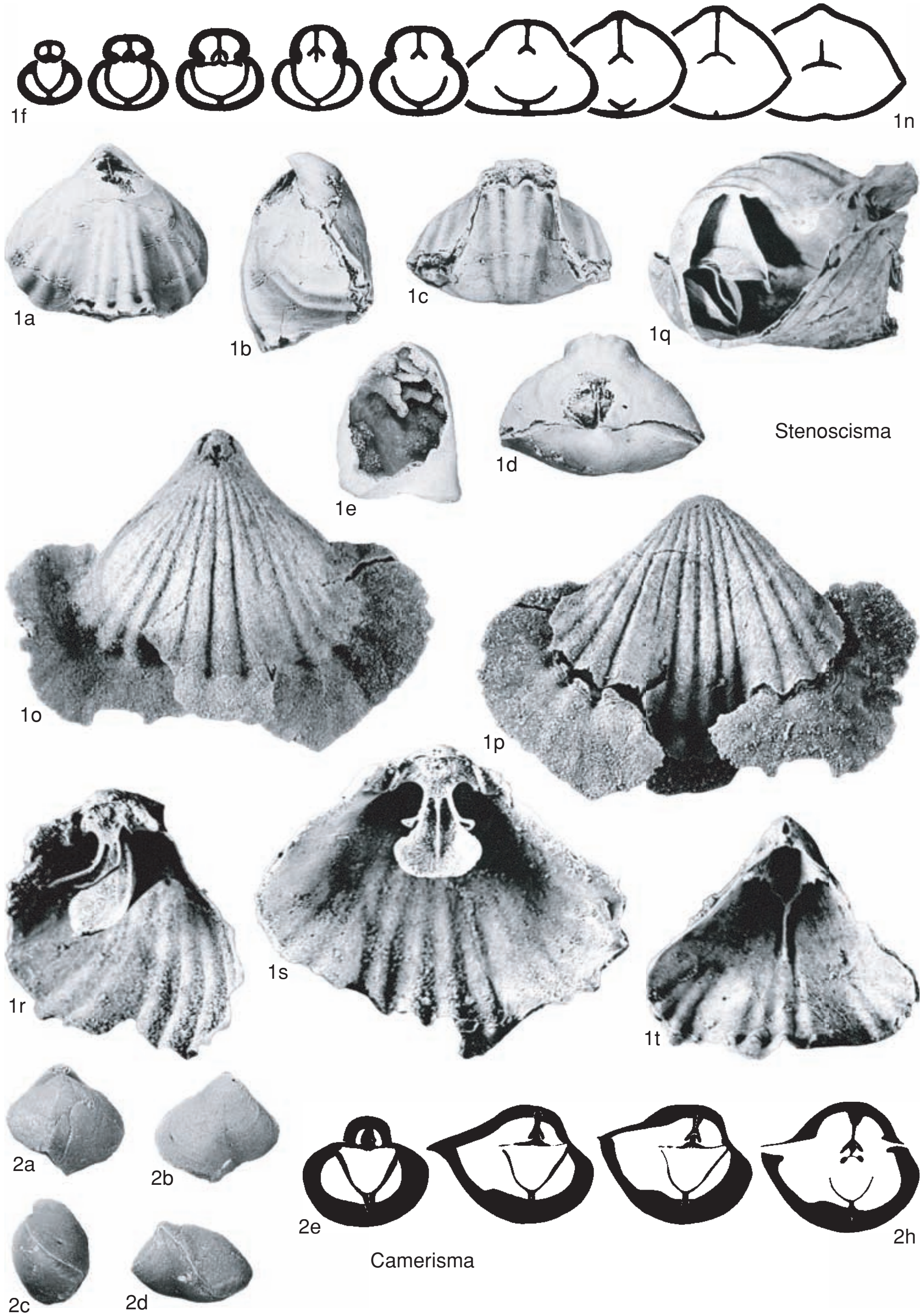

FIG. 829. Stenoscismatidae (p. 1219–1220).

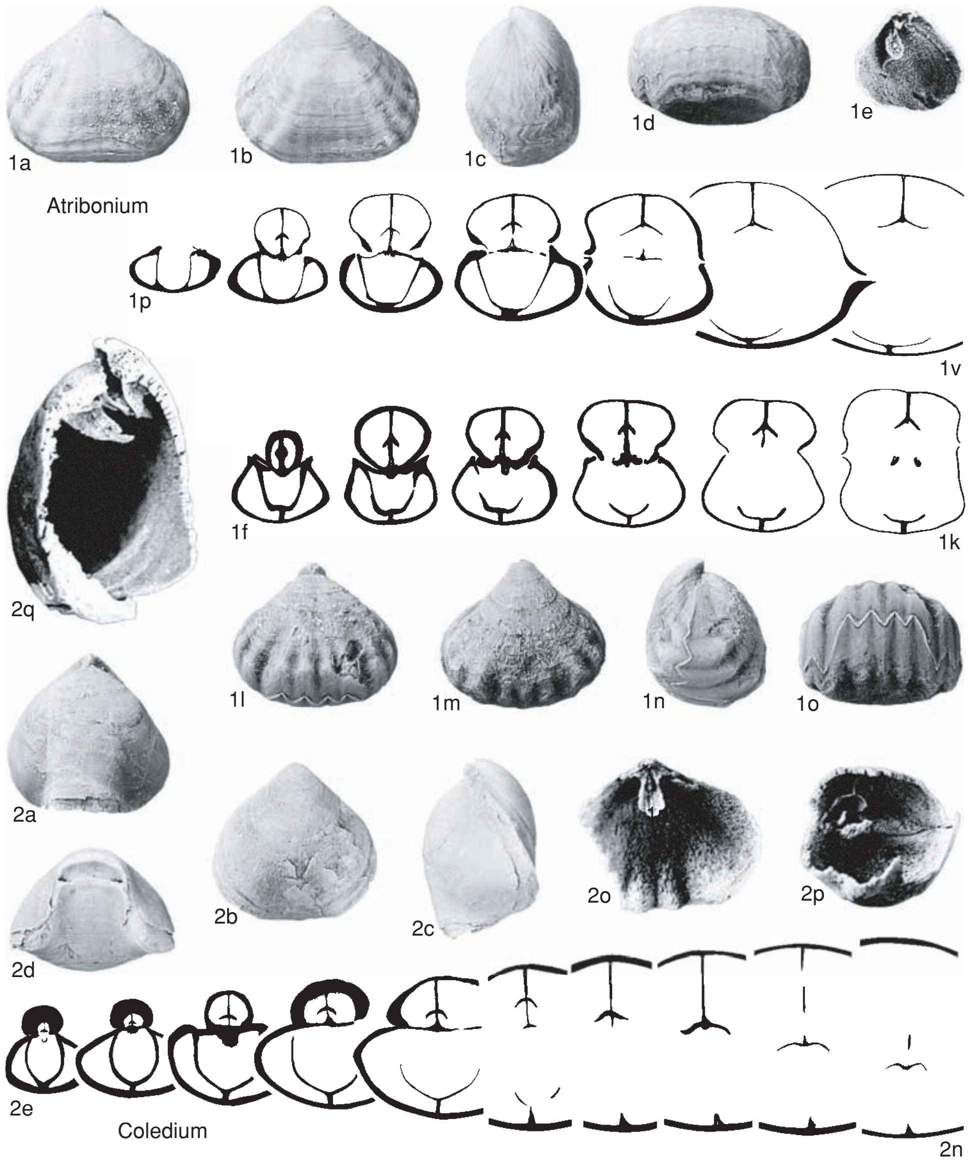

FIG. 830. Stenoscismatidae (p. 1220).

sections, intersection distances unknown, ×2.5 (Weller, 1914).——FIG. 831*s–w. S. sacra* GRANT, Chappel Limestone, Texas, USA; *s,* dorsal valve exterior; *t,* ventral valve exterior; *u,* lateral view, ventral valve on right; *v,* anterior view, ventral valve below; *w,* posterior view, ventral valve below, ×2 (Grant, 1965b).

Torynechus COOPER & GRANT, 1962, p. 1128 [**T. caelatus;* OD]. Valves medium to large, rounded subtrigonal in outline; costae fine, sharp, numerous, beginning at beaks, intercalating and bifurcating; fold and sulcus low, broad; valve edges overlapping slightly, sharply geniculate at anterior margin; stolidium absent or indicated as slight protrusion along anterior margins; beak long; deltidial plates small; foramen small, oval; muscle marks and mantle canals as in *Stenoscisma. Lower Permian (Artinskian):* USA (Texas).——FIG. 832*a–g.* **T. caelatus,* Leonard Formation, Glass Mountains; *a,* dorsal valve exterior; *b,* lateral view, ventral valve on

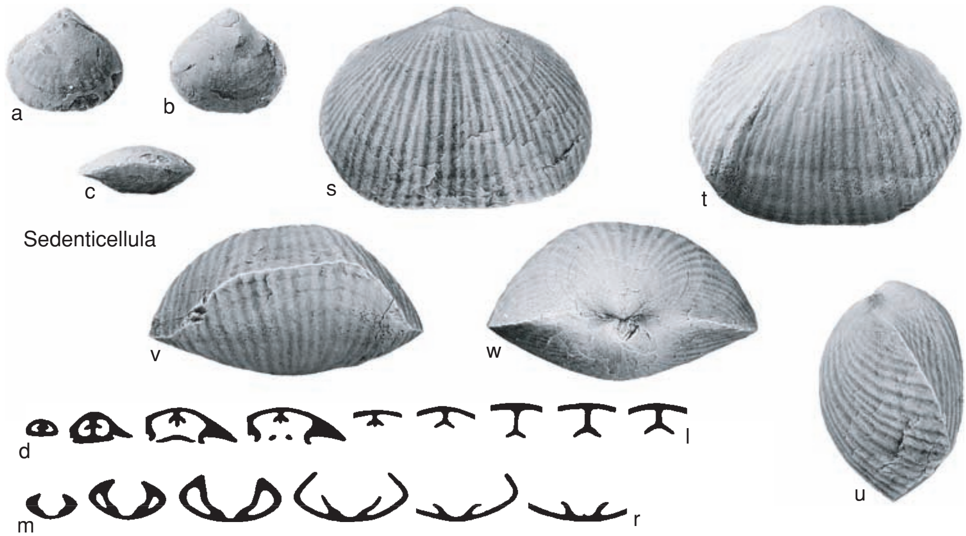

FIG. 831. Stenoscismatidae (p. 1220–1222).

right; *c,* anterior view, ventral valve below; *d,* dorsal valve interior; *e,* ventral valve interior; *f,* lateral interior, ventral valve on right, ×1; *g,* posterior interior, ventral valve below, ×2 (Grant, 1965a).

Subfamily PROATRIBONIINAE Gratsianova, 1967

[Proatriboniinae GRATSIANOVA, 1967, p. 91; *emend.,* CARLSON, herein]

Valves small, rarely of medium size; stolidium absent; beak short; hinge plates narrow, divided, rarely broad, undivided; cardinal process absent; intercamarophorial plate absent. *Lower Devonian (Pragian)–upper Middle Devonian (Givetian).*

Proatribonium GRATSIANOVA, 1967, p. 92 [**P. altaicum;* OD]. Valves subtrigonal in outline; costae weak, on anterior half only; valve edges overlap slightly along sides; hinge plates thick; camarophorium robust, on low median septum. *Lower Devonian (Pragian):* Russia (Altai Range).——FIG. 833,*3a–g.* **P. altaicum,* Iakushinskie beds, *kindlei* zone; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve above, ×1.5; *e–g,* serial transverse sections, ventral valve above, 0.9, 1.1, 1.4 mm from ventral valve beak, ×9 (Gratsianova, 1967).

?Beichuanella CHEN in XU, WAN, & CHEN, 1978, p. 338 [**B. uniplicata;* OD]. Valves paucicostate with 1 to 3 strong, sharp costae near anterior margin only; valve edges not overlapping; spondylium sessile, elevated on low median septum anteriorly; hinge plates undivided. [With further study, *Beichuanella* may well be more appropriately assigned to a superfamily other than Stenoscismatoidea within the Rhynchonellida. See also p. 1372 herein.] *upper Middle Devonian (Givetian):* China (Sichuan).——FIG. 833,*1a–h.* **B. uniplicata,* Guanwushan Formation, Guangxi; *a,* dorsal valve

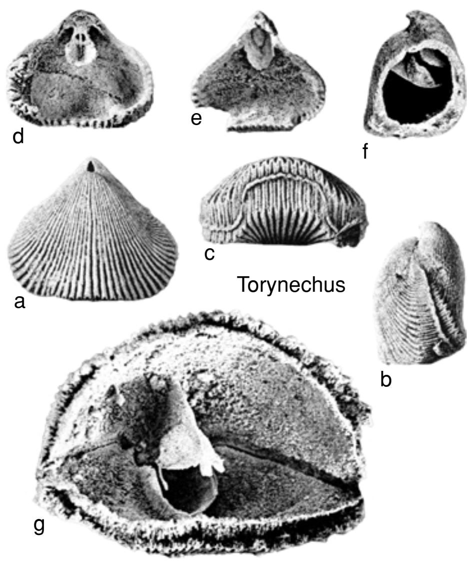

FIG. 832. Stenoscismatidae (p. 1222–1223).

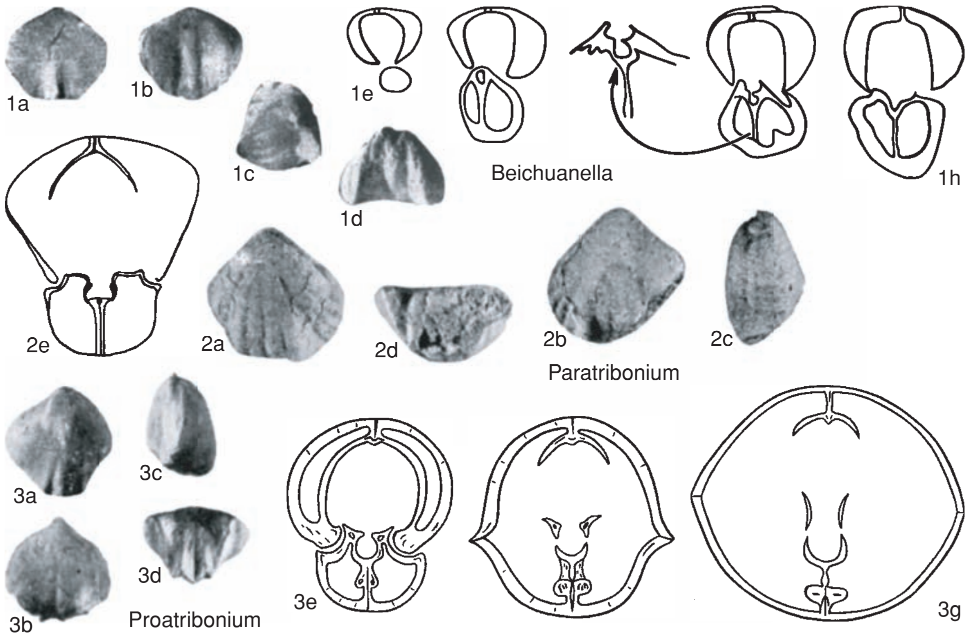

FIG. 833. Stenoscismatidae (p. 1223–1224).

exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral below, ×1; *e–h,* serial transverse sections, ventral valve above, 0.10, 0.45, 0.55, 0.90 mm from ventral valve beak, ×6.6, enlarged drawing of camarophorium, on left, is at ×16 (Xu, Wan, & Chen, 1978).

Paratribonium SAPELNIKOV & MIZENS, 1991, p. 107 [**P. rhomboidalis;* OD]. Valves of medium size, rounded rhombic in outline; nature of deltidium and foramen unknown; camarophorium delicate, gently curved; hinge plates broad, thick. *Lower Devonian (Pragian):* Russia (Urals).——FIG. 833,*2a–e.* **P. rhomboidalis,* Tyutyulen bed, Chelyabinsk Oblast; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve above, ×1; *e,* transverse section, ventral valve above, ×6 (Sapelnikov & Mizens, 1991).

Family PSILOCAMARIDAE Grant, 1965

[*nom. transl.* KOCZYRKEVICZ, 1969, p. 11, *ex* Psilocamarinae GRANT, 1965a, p. 29; *emend.,* CARLSON, herein]

Costae absent entirely, or strong, sharp, simple, and commonly present on entire valve, rarely present on fold and sulcus only; valve edges commonly not overlapping, rarely overlapping slightly or strongly; beak erect, gently, or strongly incurved, short, rarely elongate; deltidial plates absent, rarely present and disjunct; spondylium either sessile or elevated on low duplex septum; hinge plates narrow. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian).*

Subfamily PSILOCAMARINAE Grant, 1965

[Psilocamarinae GRANT, 1965a, p. 29; *emend.,* CARLSON, herein]

Costae present on entire valve, rarely absent or present on fold and sulcus only; valve edges not overlapping; stolidium absent; beak gently incurved, less commonly erect; delthyrium commonly unconstricted; spondylium duplex; cardinal process weak or robust, very rarely absent; intercamarophorial plate absent, rarely present but weak. *middle Upper Carboniferous (Moscovian)–Upper Permian (Changhsingian).*

Psilocamara COOPER, 1956b, p. 523 [**P. renfroarum;* OD] [=*Levicamera* GRABAU, 1934, p. 18, *nom. nud., non Laevicamera* GRABAU, 1936, p. 87; see *Camerisma,* p. 1220, herein]. Valves small, of moderate ventribiconvexity; smooth with strong, angular uniplication; beak gently to strongly incurved; delthyrium constricted by dorsal beak; deltidial plates present, disjunct; delicate, gently curved camarophorium; cardinal process apparently lacking in type species, broad, striated, and comblike in

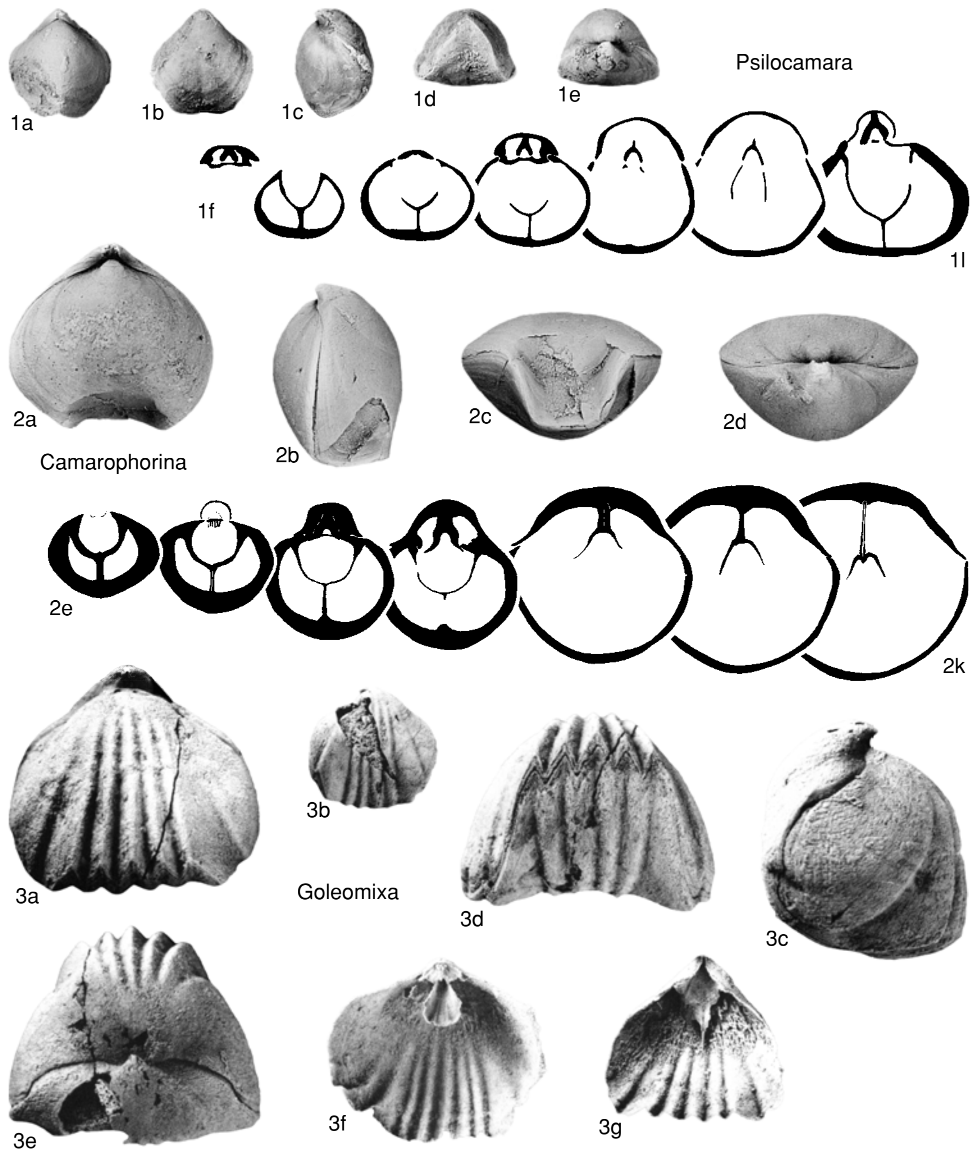

FIG. 834. Stenoscismatidae (p. 1224–1227).

other species. *middle Upper Carboniferous (Moscovian)–Lower Permian (Sakmarian):* USA (Texas, Missouri), China (Nantan, Yunnan), New Zealand.——FIG. 834,*1a–l.* **P. renfroarum,* Moscovian, Mineral Wells Formation, Texas, USA; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, dorsal valve above; *e,* posterior view, dorsal valve above, ×2; *f,* serial transverse section, ventral valve below, ×4.5; *g–k,* ventral valve below, serial transverse sections, 0.3, 0.65, 0.77, 1.0, 1.2 mm from ventral valve beak, ×4 (Cooper, 1956b); *l,* serial transverse section, ventral valve below, 1.0 mm from ventral valve beak, ×5 (Grant, 1965b).

Camarophorina LIKHAREV, 1934, p. 213 [**Camarophoria antisella* BROILI, 1916, p. 58; OD]. Valves small to medium sized, of moderate equibiconvexity, shell walls commonly thick; smooth, or with very weak costae; unisulcation (not uniplication) strong, with flat fold and sulcus; beak suberect; delthyrium constricted by dorsal beak; spondylium on high median septum; cardinal process robust. *Upper Permian (Kazanian–Tatarian):* Timor.——FIG. 834,*2a–k.* **C. antisella* (BROILI), Basleo; *a,*

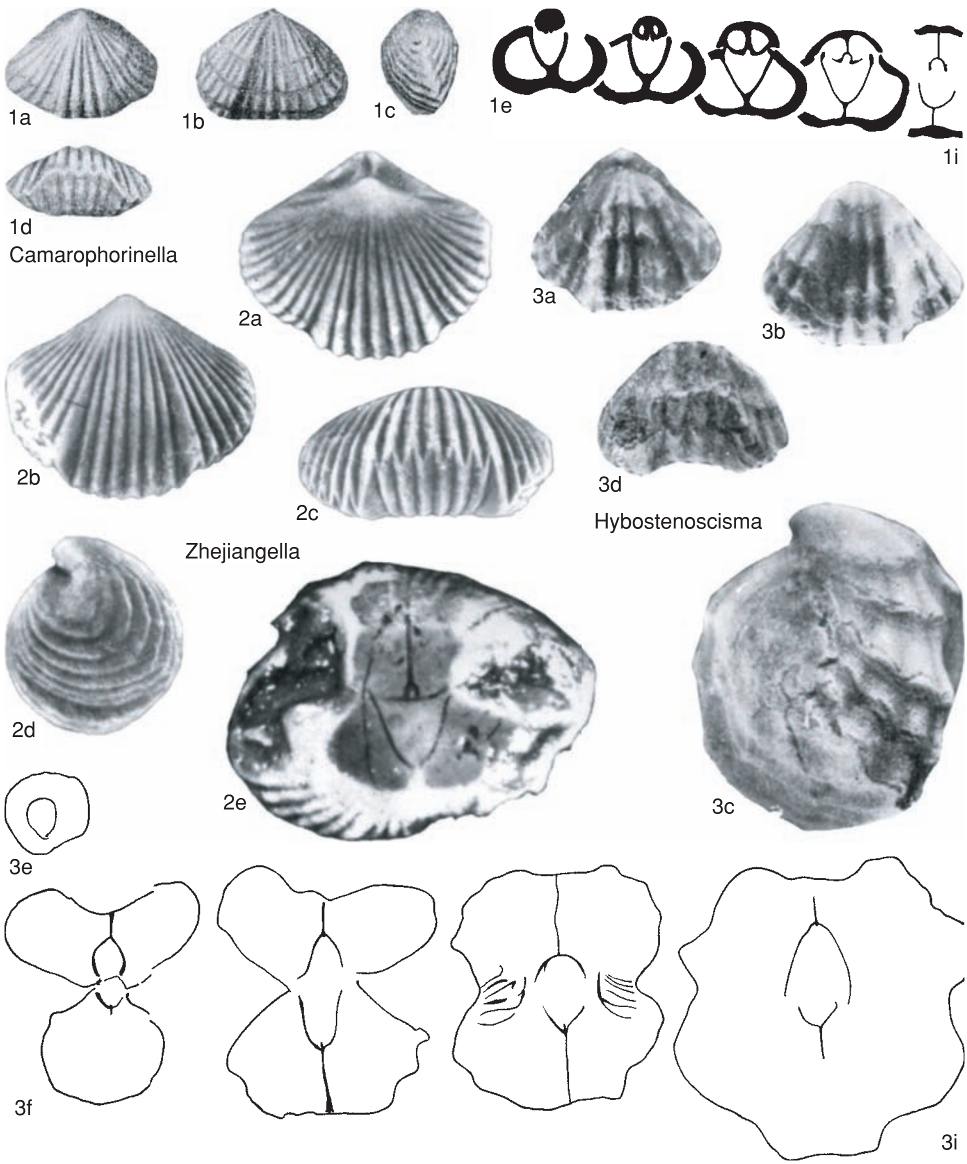

FIG. 835. Stenoscismatidae (p. 1226–1227).

dorsal valve exterior; *b,* lateral view, ventral valve on right; *c,* anterior view, dorsal valve above; *d,* posterior view, dorsal valve above, ×2; *e–k,* serial transverse sections, ventral valve below, 0.8, 1.2, 1.6, 1.8, 2.6, 3.0, 3.4 mm from ventral valve beak, ×3.3 (Grant, 1965b).

Camarophorinella LIKHAREV, 1936, p. 63 [**C. caucasica;* OD]. Valves of medium size, shell walls commonly thick; costae simple, bifurcating, or intercalating; delthyrium, deltidial plates, and foramen unknown; edges of camarophorium attached to sides of hinge plates; hinge plates divided; cardinal process weak. *Upper Permian (Kazanian–Changhsingian):* southern Russia (northern Caucasus), southern China.——FIG. 835,*1a–i.* **C. caucasica,* formation unknown, northern Caucasus; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e–i,* serial transverse sections, ventral valve below, intersection distances unknown, ×2 (Grant, 1965b).

Goleomixa GRANT, 1976, p. 180 [**G. acymata;* OD]. Valves small, strongly ventribiconvex; valve flanks smooth, 5 to 7 strong costae present only on anterior half of fold and sulcus; beak erect, elongate; deltidial plates present, disjunct; cardinal process present as small plate or low, minutely serrated knob. *Lower Permian (Kungurian):* southern Thailand.——FIG. 834,*3a–g.* **G. acymata,* Rat Buri Limestone, Ko Muk; *a,* dorsal valve exterior, ×2; *b,* ventral valve exterior, ×1; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral below; *e,* posterior view, ventral below; *f,* dorsal valve interior; *g,* ventral valve interior, ×2 (Grant, 1976).

Hybostenoscisma LIAO & MENG, 1986, p. 83 [**H. bambusoides;* OD]. Valves small, subtrigonal in outline; strong, bamboo-jointed costae on entire valve; beak gently incurved; spondylium on high median septum; hinge plates and cardinal process unknown; thin, low intercamarophorial plate present. *Upper Permian (Changhsingian):* China (southern Hunan).——FIG. 835,*3a–i.* **H. bambusoides,* Changhsing Formation, Huatang; *a,* dorsal valve exterior; *b,* ventral valve exterior, ×2; *c,* lateral view, ventral valve on right, ×4; *d,* anterior view, ventral valve below, ×2; *e–i,* serial transverse sections, ventral valve above, 0.1, 0.3, 0.4, 0.7, 0.9 mm from ventral valve beak, ×4 (Liao & Meng, 1986).

Zhejiangella LIANG in WANG & others, 1982, p. 236 [**Z. sexplicata;* OD]. Valves large, transversely oval in outline, strongly dorsibiconvex; costae commence slightly anterior to beak; beak suberect; cardinal process robust. *Upper Permian (Capitanian):* eastern China (Zhejiang).——FIG. 835,*2a–e.* **Z. sexplicata,* Lengwu Formation, Tonglu; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below, ×1; *e,* section through beaks of articulated valves, ventral valve below, ×3 (Liang, 1990).

Zhejiangellina LIANG, 1990, p. 257 [**Z. wangi;* OD]. Valves of medium size, subpentagonal in outline, moderately equibiconvex; costae commence at beak; fold and sulcus and interior of both valves identical to *Zhejiangella.* [*Zhejiangellina* may well be synonymous with *Zhejiangella.*] *Upper Permian (Capitanian):* eastern China (Zhejiang).——FIG. 836*a–e.* **Z. wangi,* Lengwu Formation, Tonglu; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve below, ×2; *e,* beaks of articulated valves broken, revealing internal casts, ventral valve below, ×4 (Liang, 1990).

Subfamily CYROLEXINAE new subfamily

[Cyrolexinae CARLSON, herein]

Rounded outline common; costae absent or present on anterior half only; beak strongly incurved; narrow stolidium rarely present; delthyrium constricted by dorsal beak; spondylium sessile; cardinal process robust; intercamarophorial plate present, rarely absent. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian).*

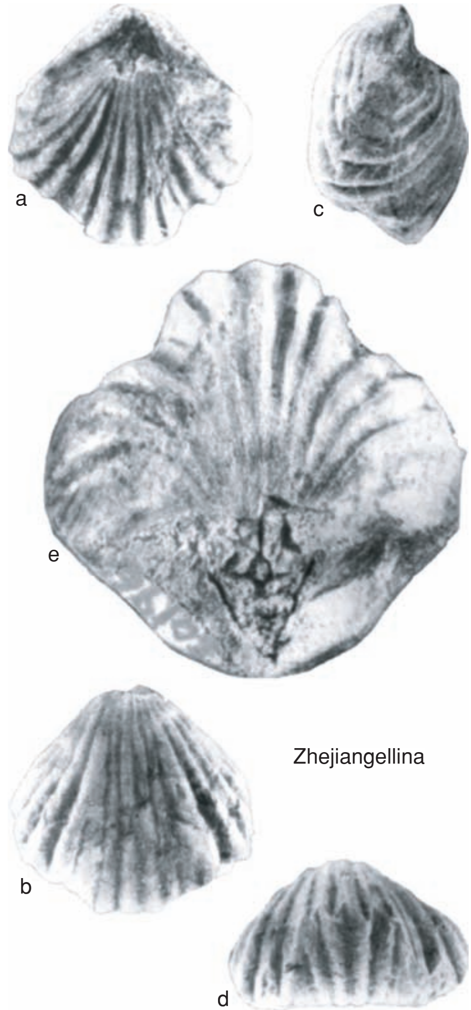

FIG. 836. Stenoscismatidae (p. 1227).

Cyrolexis GRANT, 1965a, p. 88 [**C. haquei;* OD]. Valves of medium size; strong equibiconvexity; weak, rounded costae on anterior half only; valve edges overlapping broadly on posterior slopes; beak short; nature of deltidium and foramen unknown; camarophorium curved strongly ventrally, posterior edges touching underside of hinge plates; intercamarophorial plate weak or absent. *Upper Carboniferous (Bashkirian)–Upper Permian (Changhsingian):* Spain, Russia (Urals, eastern Siberia), Pakistan (Salt Range), southern China, western Japan.——FIG. 837,*2a–m.* **C. haquei,* Lower Permian, lower *Productus* Limestone, Rukhla, Pakistan; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, dorsal valve above; *e,* posterior view, dorsal valve above, ×2; *f,* articulated valves in lateral view, ventral valve on left, broken along sagittal plane,

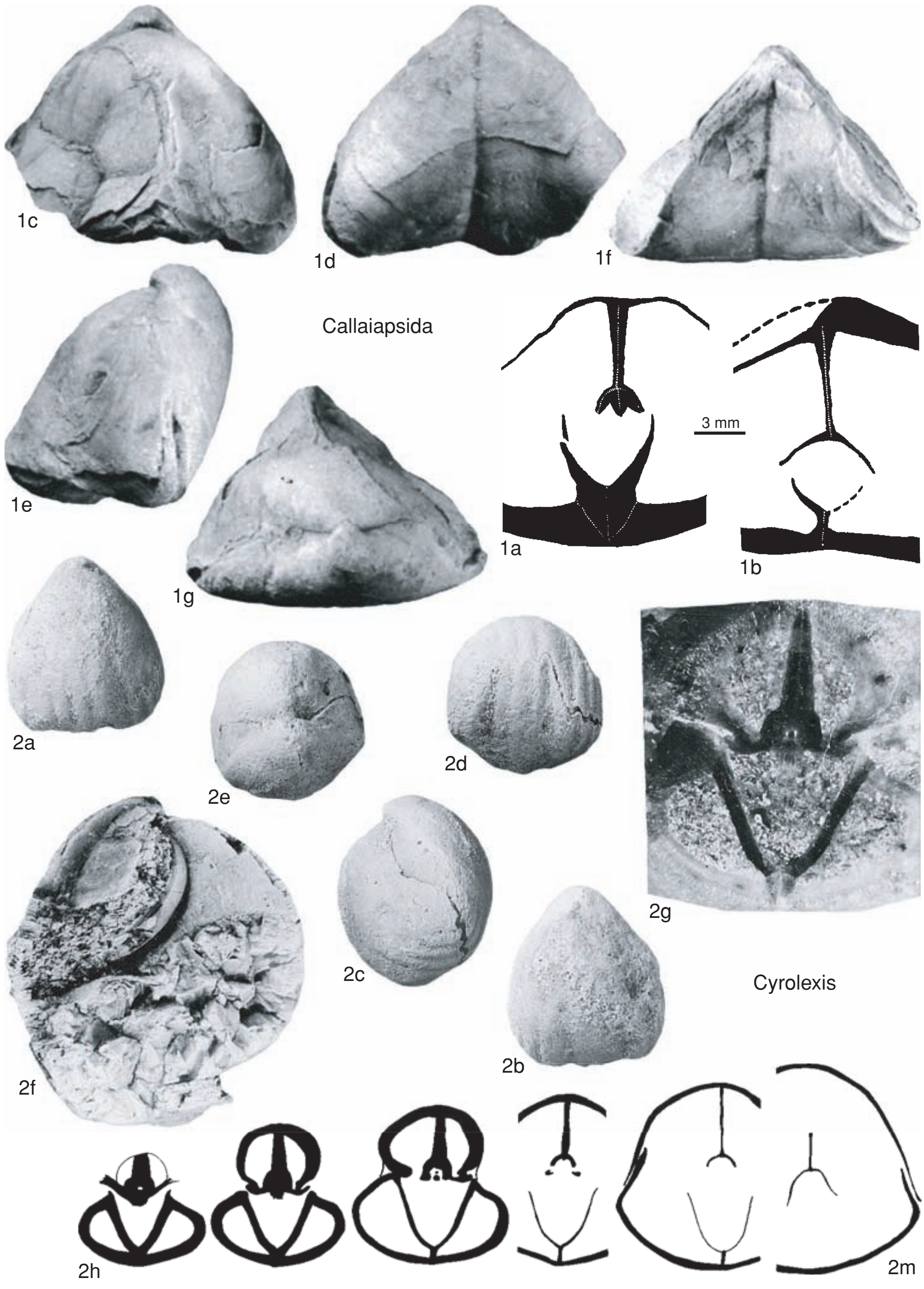

FIG. 837. Stenoscismatidae (p. 1227–1229).

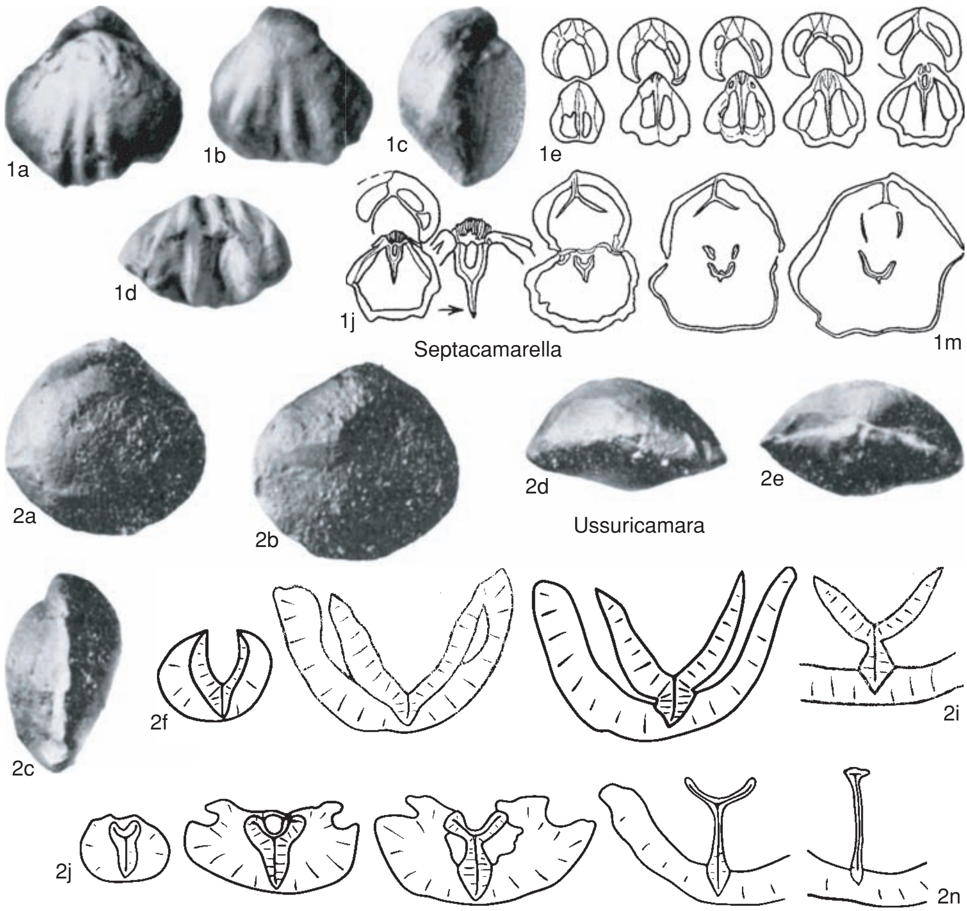

FIG. 838. Stenoscismatidae (p. 1229–1230).

showing profile of camarophorium and spondylium; *g,* cross section of articulated valves, ventral valve below, 0.5 mm from ventral valve beak, ×6; *h–m,* serial transverse sections, ventral valve below, 0.9, 1.1, 1.3, 1.8, 2.4, 3.5 mm from ventral valve beak, ×2.7 (Grant, 1965b).

Callaiapsida GRANT, 1971, p. 323 [**Camerisma (Callaiapsida) kekuensis;* OD]. Valves large, strongly ventribiconvex; outline subtrigonal; costae absent; uniplication very strong and angular; median groove present exteriorly along trough of sulcus; valve posterior flanks broadly flanged, with dorsal flange overlapping ventral flange; beak elongate; deltidial plates and foramen unknown; shell commonly thickened at posterior; camarophorium delicate; hinge plates and cardinal process unknown. *Upper Carboniferous (Bashkirian)–Lower Permian (Kungurian):* USA (Alaska), Spain, Svalbard, Russia, Novaya Zemlya, Mongolia.——FIG. 837,*1a–b.* **C. kekuensis,* Halleck Formation, Kuiu Island, Alaska, USGS loc. 3683; *a,* section 10 mm anterior to ventral beak, confirming presence of intercamarophorial plate, USNM 163658; *b,* section of fragmentary specimen, about 12 mm anterior to ventral beak, USNM 163659, ×0.75 (Grant, 1971).——FIG. 837,*1c–g. C. arctica,* Lower Permian, unnamed formation, Alaska, USA; *c,* dorsal valve exterior; *d,* ventral valve exterior; *e,* lateral view, ventral valve on right; *f,* anterior view, ventral valve below; *g,* posterior view, ventral valve below, ×1 (Grant, 1971).

Septacamarella GLUSHENKO, 1975, p. 101 [**S. nonnulla;* OD]. Valves small, rotund to subpentagonal, slightly transverse; strong costae present on anterior half of valves; valve edges not overlapping; deltidial plates and foramen unknown; 2 subspondylial (accessory) plates supporting spondylium; long camarophorium on low septum; cardinal process wide, heavy, three-lobed with traces of muscle attachment. *Lower Permian:* Ukraine (Slaviansk Series, northwestern Donets ridge).——FIG. 838,*1a–m.* **S. nonnulla,* limestone S_3; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on left; *d,* anterior view, ventral valve below, ×3; *e–m,* serial transverse sections, ventral valve above, 0.1, 0.2, 0.25, 0.3, 0.5, 0.6, 0.9, 1.4, 2.25 mm from ventral valve beak, ×4 (Glushenko, 1975).

Ussuricamara Koczyrkevicz, 1969, p. 11 [**U. majchensis;* OD]. Valves small, globular, of moderate dorsibiconvexity; shell walls commonly thick; costae absent; uniplication very weak, rounded; valve edges overlap slightly; narrow stolidium present; foramen absent; camarophorium delicate; hinge plate divided anteriorly; cardinal process poorly known; intercamarophorial plate absent. *Upper Permian:* eastern Russia (southern Primor).——Fig. 838,*2a–n.* **U. majchensis,* Ussuri region; *a,* dorsal valve exterior; *b,* ventral valve exterior; *c,* lateral view, ventral valve on right; *d,* anterior view, ventral valve below; *e,* posterior view, ventral valve below, ×3; *f–i,* serial transverse sections, ventral valve, 0.32, 2.25, 2.65, 3.1 mm from ventral valve beak, *j–n,* serial transverse sections, dorsal valve, 0.35, 1.0, 1.32, 2.1, 3.15 mm from ventral valve beak, ×7 (Koczyrkevicz, 1969).

LAMBDARINOIDEA

Norman M. Savage
[University of Oregon]

Superfamily LAMBDARINOIDEA Brunton & Champion, 1974

[*nom. transl.* Savage, 1996, p. 255, *ex* Lambdarininae Brunton & Champion, 1974, p. 819]

Very small Rhynchonellida with outline bilobed to cordiform; surface smooth; commonly with dorsal and ventral sulci and emarginate anterior; delthyrium with symphytium or conjunct deltidial plates or open; ventral median septum may be present anteriorly; dorsal median septum absent posteriorly but may occur anteriorly; hinge plates short; cardinal process absent. *Upper Devonian (lower Famennian)–Upper Carboniferous (Stephanian).*

Family LAMBDARINIDAE Brunton & Champion, 1974

[*nom. transl.* Savage, 1996, p. 255, *ex* Lambdarininae Brunton & Champion, 1974, p. 819]

Lambdarinoidea with outline bilobed to cordiform; symphytium present or absent; ventral interarea long; foramen circular or delthyrium open; dental plates short or absent; ventral and dorsal median septa absent or present anteriorly. *Upper Devonian (lower Famennian)–Upper Carboniferous (Stephanian).*

Subfamily LAMBDARININAE Brunton & Champion, 1974

[Lambdarininae Brunton & Champion, 1974, p. 819]

Lambdarinidae with symphytium. Ventral interarea long; foramen circular; dental plates short; ventral and dorsal median septa absent. *Lower Carboniferous (upper Tournaisian–upper Viséan).*

Lambdarina Brunton & Champion, 1974, p. 819 [**L. manifoldensis;* OD]. Very small with outline strongly bilobed; each lobe almost as large as rest of shell; lateral profile planoconvex to biconvex, ventral umbone slightly upcurved. Beak straight, elongate; foramen subcircular, apical; symphytium flat, elongate. Bisulcate, dorsal sulcus strong, ventral sulcus weak with median ridge; anterior commissure rectimarginate to sulcate. Surface smooth, impunctate. Dental plates thin, short, developed only in vicinity of teeth; teeth narrow, curved anteromedially. Hinge plates undivided; notothyrial platform thickened; sockets ovoid, weakly excavated into shell wall; inner sockets ridges prominent; cardinal process absent. *Lower Carboniferous (upper Tournaisian–upper Viséan):* Europe, eastern Australia.——Fig. 839,*1a–e.* **L. manifoldensis,* lower Viséan, Carboniferous Limestone, Staffordshire, Wetton, England; *a–b,* holotype, dorsal and ventral views, ×15; *c,* interior of ventral valve posterior, ×22; *d,* interior of dorsal valve posterior, ×42; *e,* drawing of interior of ventral valve showing foramen, symphytium, dental plates, and teeth, ×18 (Brunton & Champion, 1974).

Hampsia Morris, 1994, p. 271 [**H. cooperi;* OD]. Very small with outline bilobed and profile arched. Beak elongate and resupinate, projecting ventrally

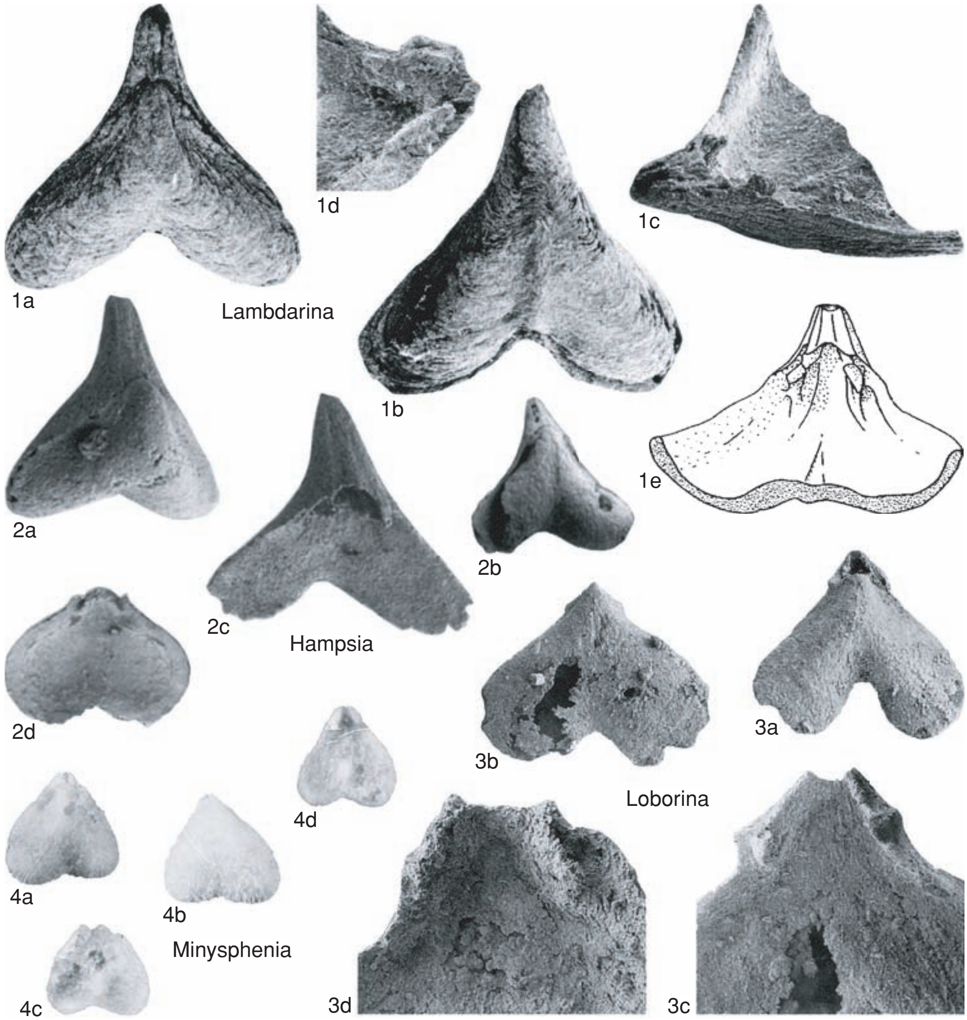

FIG. 839. Lambdarinidae (p. 1230–1232).

away from plane of commissure; foramen minute, rounded, and apical; symphytium long, narrow, closed by single deltidial plate. Dorsal valve markedly convex, ventral valve less so; each valve sulcate anteriorly with anterior shell margin deeply indented; anterior commissure weakly unisulcate. Surface smooth. Dental plates unknown but may be present below symphytium. Teeth project anteriorly from anterior edge of symphytium; ventral muscle field unknown. Hinge plates undivided; notothyrial platform thick; inner and outer socket ridges low; sockets rounded, short; crura unknown; dorsal muscle field short, rounded. *Lower Carboniferous (Viséan):* England.——FIG. 839,*2a–d.* **H. cooperi,* Milldale Limestone, Staffordshire, Waterhouses, Brownend Quarry; *a,* holotype, dorsolateral view, ×22; *b,* hypotype, dorsolateral view, ×20; *c,* dorsolateral view of ventral valve interior, ×22; *d,* interior of dorsal valve, ×20 (Morris, 1994).

Subfamily LOBORININAE Savage, 1996

[Loborininae SAVAGE, 1996, p. 255]

Lambdarinidae lacking symphytium. Delthyrium elongate, open; dental plates fused to valve walls; teeth massive; hinge plates poorly developed; ventral and dorsal median septa absent. *Upper Devonian (lower Famennian).*

Loborina BALINSKI, 1982, p. 130 [**L. lobata;* OD]. Very small with outline strongly bilobed; lobes diverging at 45 degrees; profile weakly biconvex.

Bisulcate, with strong dorsal sulcus, weak ventral sulcus; anterior commissure rectimarginate to sulcate. Surface smooth. Beak straight, elongate; foramen ovate, large, apical; delthyrium open. Symphytium absent. Dental plates arising from valve walls, supporting long massive teeth. Hinge plates and notothyrial platform poorly developed; sockets long, bounded by strong inner and outer socket ridges. *Upper Devonian (lower Fammenian):* Poland.——FIG. 839,*3a–d*. **L. lobata,* Cracow; *a,* holotype, dorsal view; *b,* hypotype, ventral view, approximately ×15; *c,* interior of ventral valve posterior; *d,* interior of dorsal valve posterior, ×50 (Balinski, 1982).

Subfamily MINYSPHENIINAE Savage, 1996

[*nom. correct.* SAVAGE, herein, *pro* Minispheniinae SAVAGE, 1996, p. 256]

Lambdarinidae lacking symphytium and dental plates, but with dorsal and ventral median septa present anteriorly; teeth directed anteromedially. *Upper Carboniferous (Stephanian).*

Minysphenia GRANT, 1988, p. 126 [**M. conopia;* OD]. Very small with outline subtriangular to cordiform and profile biconvex. Beak straight, short; foramen circular, apical; symphytium absent, small conjunct deltidial plates present anterior of foramen. Sulcus weak in both valves; anterior commissure rectimarginate to sulcate. Surface smooth. Dental plates not evident; teeth very small, cyrtomatodont; rounded swelling present at about two-thirds valve length. Incipient cardinal process or swollen notothyrial platform present. *Upper Carboniferous (Stephanian):* USA (New Mexico). ——FIG. 839,*4a–d*. **M. conopia,* upper Magdalena Formation, Sacramento Mountains, Grapevine Canyon; *a–b,* holotype, dorsal and ventral views; *c–d,* dorsal and ventral interiors, ×8 (Grant, 1988).

RHYNCHOPOROIDEA

NORMAN M. SAVAGE
[University of Oregon]

Superfamily RHYNCHOPOROIDEA Muir-Wood, 1955

[*nom. transl.* ERLANGER, 1993, p. 120, *ex* Rhynchoporidae MUIR-WOOD, 1955, p. 91]

Rhynchonellida with shell endopunctate; costal interspaces may be developed into marginal spines. *Upper Devonian (lower Famennian)–Upper Permian (Tatarian).*

Family RHYNCHOPORIDAE Muir-Wood, 1955

[Rhynchoporidae MUIR-WOOD, 1955, p. 91]

Rhynchoporoidea with endopunctae simple or merging. Fold and sulcus variously developed or absent. *Upper Devonian (lower Famennian)–Upper Permian (Tatarian).*

Subfamily RHYNCHOPORINAE Muir-Wood, 1955

[*nom. transl.* SAVAGE, herein, *ex* Rhynchoporidae MUIR-WOOD, 1955, p. 91]

Rhynchoporidae with simple endopunctae. Dorsal fold and ventral sulcus strong; anterior commissure uniplicate, rectangular. Costae simple, extending from beaks, flattened and grooved anteriorly, extending as sharp spines. *Lower Carboniferous (upper Tournaisian)–Upper Permian (Tatarian).*

Rhynchopora KING, 1865, p. 124 [**Terebratula geinitziana* DE VERNEUIL, 1845, p. 83; OD] [=*Rhynchoporina* OEHLERT, 1887a, p. 1305, obj.]. Outline transversely subpentagonal and profile dorsibiconvex. Beak straight to suberect; delthyrium oval; deltidial plates disjunct, rarely conjunct. Fold and sulcus becoming prominent anteriorly; tongue distinct, rectangular. Costae numerous, simple, rounded, from beaks; flattened and grooved anteriorly; intertroughs narrow, extending as sharp spines. Shell finely endopunctate. Dental plates short, thin, convergent ventrally; teeth cyrtomatodont. Dorsal median septum short, low; hinge plates united; septalium with cover plate that is often perforated posteriorly; inner socket ridges overhanging sockets; crural bases horizontal; crura ventrally curved, concave dorsomedially in section. Ventral and dorsal muscle fields poorly impressed. Small cardinal process occasionally present. *Lower Carboniferous (upper Tournaisian)–Upper Permian (Tatarian):* cosmopolitan.——FIG. 840,*1a–f*. **R. geinitziana* (DE VERNEUIL), lower Kazanian, North Dvina River Basin, Shidrovo, northern European Russia; *a–b,* holotype, dorsal and lateral views, ×1 (de Verneuil, 1845); *c–e,* ventral, anterior, and lateral views, ×2; *f,* punctae on ground surface 10 mm from beak, ×19 (Erlanger, 1981).——FIG. 840,*1g–n. R. parambula* COOPER & GRANT, lower Guadalupian, Word Formation, Glass Mountains, Hess Canyon, Texas, USA; *g–j,* holotype, dorsal, posterior, lateral, and anterior views, ×1; *k,* holotype, apical view, ×3; *l,* paratype, interior of dorsal valve, ×2; *m,* anterior of another paratype showing spines, ×1.5; *n,* paratype, interior of ventral valve, ×2 (Cooper & Grant, 1976b).——FIG. 840,*1o–s. R. sansabensis* CARTER, upper Kinderhookian–lower Osagian, Chappel Limestone, central Texas, USA; paratype, serial sections 1.0, 1.4, 2.0, 2.4, 3.2 mm from posterior, ×2 (Carter, 1967).

Subfamily GREIRINAE Erlanger, 1993

[*nom. transl.* SAVAGE, herein, *ex* Greiridae ERLANGER, 1993, p. 120]

Rhynchoporidae with two-layered shell and merging endopunctae in fibrous layer. Costae angular, numerous, arising at beaks; anterior commissure uniplicate. Dental plates short. Dorsal median septum well developed. *Upper Devonian (lower Famennian).*

Greira ERLANGER, 1993, p. 120 [**G. transcaucasica;* OD]. Shell small to medium with subrounded to subpentagonal outline and biconvex profile. Beak straight, narrow; delthyrium open. Dorsal fold and ventral sulcus well developed, arising at umbones; anterior commissure uniplicate, rounded. Costae numerous, straight, simple, angular, from beaks. Shell finely punctate with punctae present only in fibrous layer, randomly disposed in umbonal region but arranged in lines parallel to commissure anteriorly; punctae sometimes merging, present on costae and interspaces. Dental plates very short; teeth small and elongate. Dorsal median septum low and thin but extending one-quarter valve length; septalium short, with cover plate bearing medial ridge; sockets small and shallow; inner socket ridges slightly overhanging sockets; crural bases triangular in section; crura long, laterally flattened, slightly oblique, divergent, curved ventrally. Muscle fields poorly impressed. Cardinal process absent. *Upper Devonian (lower Famennian):* Azerbaijan (Nakhichevan Republic).——FIG. 840,*2a-o.* **G. transcaucasica, Mesoplica meisteri* Zone, left bank of Arpa River between Geran-Kalasy and Kabakhyal Mountains, Nakhichevan; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* punctae on broken surface of sulcus in ventral valve of topotype, ×100; *g,* transverse section through puncta in dorsal valve of topotype, ×300; *h–o,* serial sections 1.3, 1.4, 1.5, 1.7, 2.1, 2.4, 2.5, 2.75 mm from posterior of topotype, ×3 (Erlanger, 1993).

Subfamily ARARATELLINAE Erlanger, 1986

[*nom. transl.* SAVAGE, herein, *ex* Araratellidae ERLANGER, 1986, p. 54]

Rhynchoporidae with three-layered shell and merging endopunctae in fibrous layer. Costae coarse, rounded, arising at umbones, anterior commissure uniplicate. Dental plates short. Dorsal median septum well developed. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian).*

Araratella ABRAMIAN, PLODOWSKI, & SARTENAER, 1975, p. 5 [**Liorhynchus dichotomians* ABRAMIAN, 1954, p. 66; OD]. Elongate subpentagonal outline and biconvex profile; flanks and anterior not truncated. Beak erect to incurved; foramen small and circular. Fold and sulcus well developed, arising near umbones. Anterior commissure uniplicate; tongue distinct, subrectangular, serrated. Costae coarse, rounded, originating near beaks, strong on fold and in sulcus, weak on flanks. Dental plates short, slightly convergent ventrally; ventral muscle field narrow, well impressed. Dorsal median septum thick, long; septalium long, wide; crural bases closely set; crura short, ventrally curved, V-shaped in section, open dorsally. Fine endopunctae present in fibrous shell layer. *Upper Devonian (upper Famennian)–Lower Carboniferous (lower Tournaisian):* Armenia, Germany, Spain, Urals, Kazakhstan, Iran, Afghanistan.——FIG. 841,*1a–l.* **A. dichotomians* (ABRAMIAN), high in upper Famennian, Nakhichevan, Biralichay River, Armenia; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×1; *e–l,* serial sections 0.5, 0.6, 0.8, 1.0, 1.6, 2.4, 2.55, 2.95 mm from posterior, ×4 (Erlanger, 1986).

Subfamily TRETORHYNCHINAE new subfamily

[Tretorhynchinae SAVAGE, herein]

Rhynchoporidae with subtriangular outline; anterior commissure rectimarginate; endopunctae in fibrous secondary shell layer. *Lower Carboniferous (middle Viséan–upper Viséan).*

Tretorhynchia BRUNTON, 1971, p. 98 [**Terebratula trilatera* DE KONINCK, 1843 in 1841–1844, p. 292; OD]. Outline elongate subtriangular and profile biconvex. Beak straight; delthyrium open; deltidial plates incipient. Both valves sulcate posteriorly but lacking fold or sulcus anteriorly; anterior commissure rectimarginate. Costae numerous, straight, simple, angular, from beaks. Shell finely

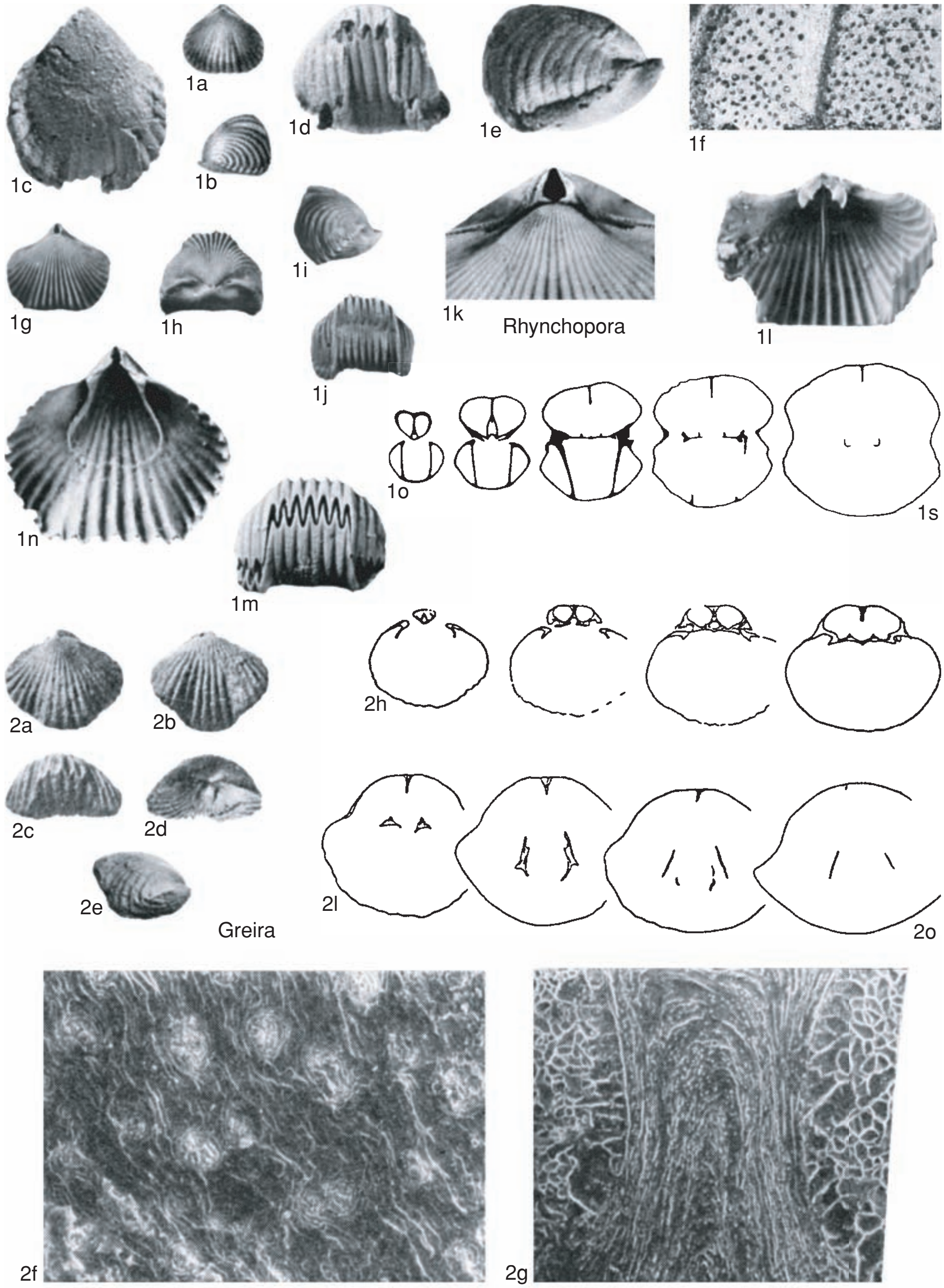

FIG. 840. Rhynchoporidae (p. 1232–1233).

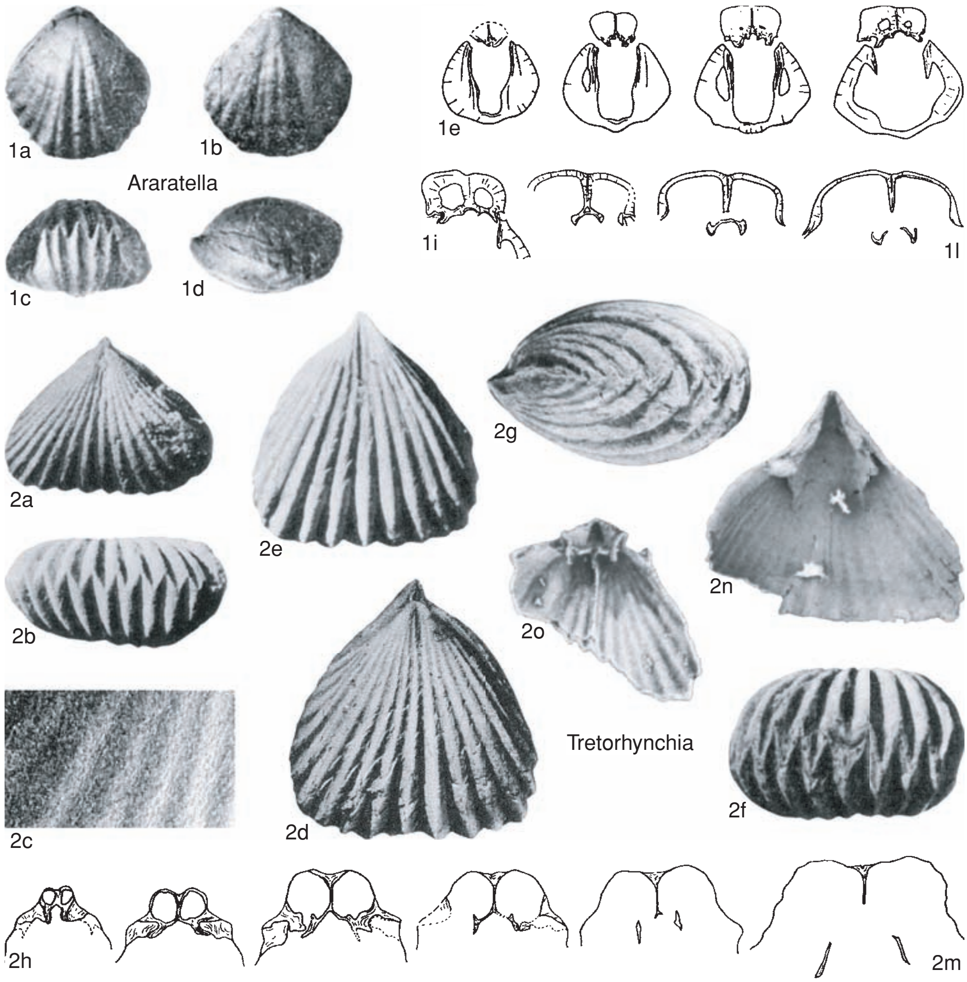

FIG. 841. Rhynchoporidae (p. 1233–1235).

endopunctate. Dental plates short, thin, slightly convergent ventrally; teeth cyrtomatodont. Dorsal median septum short, low; septalium wide; inner socket ridges overhang sockets; crural bases oblique; crura flattened, vertical to slightly oblique, ventrally curved. Ventral and dorsal muscle fields poorly impressed. Cardinal process absent. *Lower Carboniferous (middle Viséan–upper Viséan):* western Europe.——FIG. 841,*2a–o.* **T. trilatera* (DE KONINCK); *a–b,* neotype, dorsal and anterior views, Carboniferous Limestone, Visé, Belgium, ×2.6; *c,* enlargement of surface showing punctae, middle Viséan, Llanfair, Anglesey, Wales, ×22; *d,* dorsal view, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×3; *e–f,* ventral and anterior views, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×2.7; *g,* lateral view, middle Viséan, Carboniferous Limestone, Staffordshire, Wetton, England, ×3; *h–m,* serial sections 0.07, 0.11, 0.39, 0.44, 0.54, 1.04 mm from posterior, middle Viséan, Carboniferous Limestone, Derbyshire, Treak Cliff, England, ×8 (Brunton, 1971); *n,* ventral valve interior, Asbian, Dartry Group, County Fermanagh, Ireland, ×5.6; *o,* dorsal valve interior, Asbian, Dartry Group, County Fermanagh, Ireland, ×6 (Brunton, 1984).

DIMERELLOIDEA

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and A. S. DAGYS[4]

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Superfamily DIMERELLOIDEA Buckman, 1918

[*nom. transl.* SAVAGE, 1996, p. 257, *ex* Dimerellidae BUCKMAN, 1918, p. 72]

Rhynchonellida with shells ventribiconvex to equibiconvex, mostly subcircular; tendency to dorsal sulcation; surface smooth or radially ribbed; deltidial plates reduced or absent. Dorsal median septum variable; cardinal process may be present; crura mainly mergiform, submergiform, or ensiform. *Upper Devonian (Famennian)–Holocene.*

Family DIMERELLIDAE Buckman, 1918

[Dimerellidae BUCKMAN, 1918, p. 72]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Usually sulcate dimerelloids, commonly with reduced deltidial plates. Dental plates rudimentary, fused to wall or absent; primarily ensiform bladed crura; dorsal septum may be prominent. *Upper Triassic (Norian)–Upper Jurassic (Tithonian).*

Subfamily DIMERELLINAE Buckman, 1918

[*nom. transl.* AGER, 1959b, p. 330, *ex* Dimerellidae BUCKMAN, 1918, p. 72]

Small dimerellids with dorsal median septum very strong and anteriorly rising; crura precursor of ensiform variant. *Upper Triassic (Norian).*

Dimerella VON ZITTEL, 1870, p. 220 [**D. gümbeli;* M]. Small, depressed, ventribiconvex; transverse oval to heart shaped with wide, straight hinge line and shallow dorsal sulcus; densely costellate throughout; beak high, suberect; delthyrium wide open and beak ridges sharp. Distant teeth stout but dental plates poorly developed; crura long, bladelike, moderately bent ventrally, attaining one-third dorsal valve length; dorsal median septum low posteriorly, rising very high anteriorly, almost up to ventral valve. [Other interior details not well known.] *Upper Triassic (Norian):* Austria, Dinarids.——FIG. 842,*2a–c*. **D. guembeli,* Steiermark, Austria; *a–b,* dorsal, lateral views, ×2; *c,* longitudinal section, ×2 (von Zittel, 1870).

Subfamily RHYNCHONELLININAE Ager, 1959

[Rhynchonellininae AGER, 1959b, p. 330]

Mostly ventribiconvex dimerellids with little or no dorsal median septum and crura extremely long, ensiform (sagittally bladelike or somewhat rodlike); cardinalia strong, crura direct prolongations of narrow hinge plates; muscle fields lanceolate, elongate, about two-thirds to three-quarters shell length. *Upper Triassic (Norian)–Upper Jurassic (Tithonian).*

Rhynchonellina GEMMELLARO, 1871, p. 100[29] [**R. suessi* GEMMELLARO, 1871, p. 102[31]; SD HALL & CLARKE, 1894, p. 1027] [=*Terebratulopsis* DE GREGORIO, 1930b, p. 5, obj., SD AGER, 1960, p. 161; *Rhynconellina* DE GREGORIO, 1930b, p. 12, *nom. null.*]. Medium size, equibiconvex to ventribiconvex, subcircular to ovoid, globose; rectimarginate to sulcate, incipiently ligate, ventral median sulcus possibly indenting front margin; smooth but for feeblest capillation; beak strong suberect to nearly straight, with well-developed palintrope, wide delthyrium, and rudimentary deltidial plates (sometimes conjunct). Dental plates rudimentary; hinge plates divided, cardinal process thick; variable dorsal median septum, often apically confined; crura very long (over one-half valve length), closely parallel, with tips almost touching ventral valve, reportedly with short crural processes proximally. [Alleged Toarcian and younger records unconfirmed.] *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian):* Italy (Sicily), Austria, Switzerland, Dalmatia, Hungary, ?Crimea, Morocco, Algeria.——FIG. 842,*1a–q*. **R. suessi suessi,* Hettangian–Sinemurian, Sicily; *a–e,* dorsal, lateral, anterior, ventral, posterior views, MGUP, ×1; *f–q,* transverse serial sections, distances in mm from ventral umbo, 1.55, 2.5, 2.85, 3.25, 3.4, 3.6, 3.75, 4.2, 4.7, 5.1, 5.75, 7.45, MGUP (Cicardi & Gaetani, 1974).——FIG. 842,*1r–s*. *R. suessi orobica* CICARDI & GAETANI, upper Hettangian–lower Sinemurian, Lombardia, Italy; *r,* internal mold showing dorsal muscle scars, G507/169; *s,* internal mold showing ventral muscle scars, G507/221, ×1 (Cicardi & Gaetani, 1974).

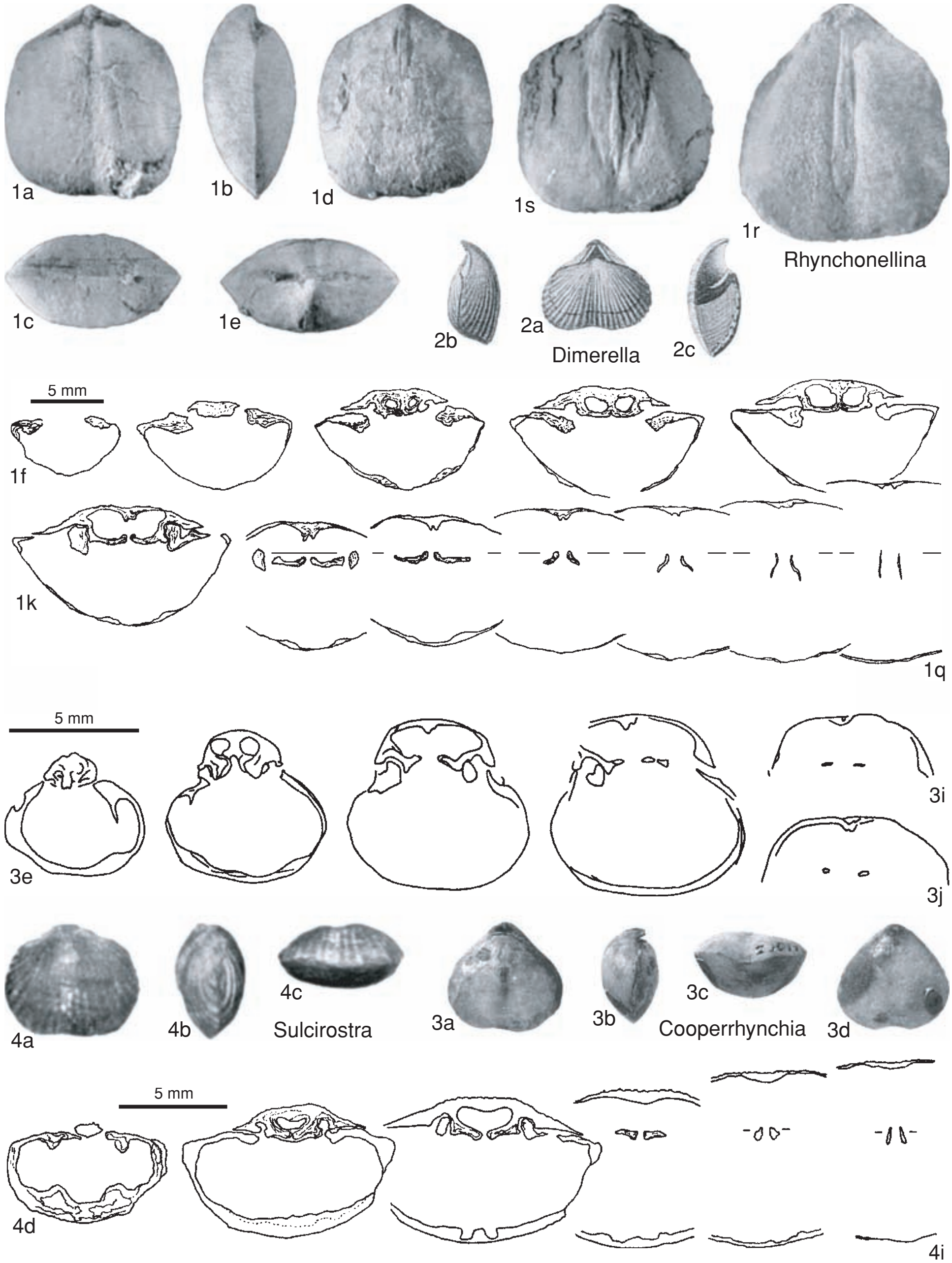

FIG. 842. Dimerellidae (p. 1236–1238).

Cooperrhynchia SANDY & CAMPBELL, 1994, p. 1245 [**Rhynchonella schucherti* STANTON, 1895, p. 31; OD] [=*Bothrorhynchia* COOPER in SANDY & CAMPBELL, 1994, p. 1250, obj.]. Small to medium size, subtriangular, gently ventribiconvex; smooth, sulcate; shallow median sulcus on both valves producing weak anterior margin indentation; beak erect to incurved, deltidial plates conjunct. Dental plates short, weak; long, low dorsal median septum; short septalium; crura closely parallel, less than midvalve in length. *Upper Jurassic (Tithonian):* USA (California).——FIG. 842,*3a–j.* **C. schucherti* (STANTON); *a–d,* lectotype, dorsal, lateral, anterior, ventral views, USNM 23017a, ×1; *e–j,* transverse serial sections, distances in mm from ventral umbo, 1.8, 2.2, 2.7, 3.1, 3.4, 3.7, USNM 23189j (Sandy & Campbell, 1994).

Sulcirostra COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Rhynchonellopsis* DE GREGORIO, 1930b, p. 5, *non* VINCENT, 1893, Terebratulida, *nec* BÖSE, 1894, Rhynchonellida [**Rhynchonellina seguenzae* GEMMELLARO, 1871, p. 106[34] (although originally spelled *R. sequenzae,* prevailing usage is preserved under Article 33.3.1 of ICZN, 1999); M]. Small to medium size, equibiconvex to ventribiconvex; dorsal sulcation sometimes indenting front margin; ornament finely and densely costellate, usually also cancellate; delthyrium wide, triangular; deltidial plates rudimentary. Dental plates weak, short; septalium absent; dorsal median septum apically confined or absent; lateral septa, partly fused to fulcral plates, supporting massive hinge plates; crura closely parallel, long, reaching beyond midvalve. [Record from USA (Oregon) requires further research.] *Upper Triassic (Norian)–Lower Jurassic (Pliensbachian), Middle Jurassic (?Aalenian):* Italy (Sicily), Austria, Dalmatia, Slovenia, Hungary, Morocco, Algeria, Turkey.——FIG. 842,*4a–c.* **S. seguenzae* (GEMMELLARO), Hettangian–Sinemurian, Sicily; dorsal, lateral, anterior views, approximately ×1 (Giovannoni, 1983).——FIG. 842,*4d–i. S. paronai* (BOESE), Pliensbachian, Bergamo, Italy; topotype, transverse serial sections, distances in mm from ventral umbo, 4.3, 5.6, 6.7, 7.95, 9.1, 11.85, G 509/14 (Cicardi & Gaetani, 1974).

Family PEREGRINELLIDAE Ager, 1965

[*nom. transl.* SAVAGE, 1996, p. 257, *ex* Peregrinellinae AGER, 1965, p. 605]

Medium to large, coarsely costate Dimerelloidea with shells ventribiconvex to equibiconvex, discoidal to subglobose; commissure rectimarginate or almost rectimarginate, serrate; dental plates reduced or absent; teeth small. Dorsal median septum present or absent; crura mergiform or submergiform. *Upper Devonian (Famennian)–Lower Cretaceous (Hauterivian).*

Subfamily PEREGRINELLINAE Ager, 1965

[Peregrinellinae AGER, 1965, p. 605]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Very large, fully costate to capillate Peregrinellidae, mostly ventribiconvex; faint, broad sulcation often perceivable in juveniles, otherwise rectimarginate throughout. Dental plates much reduced and wide apart; hinge plates flat to gently convex, with inner edge strongly deflected inward dorsally and swollen; true mergiform crura arising directly from this point, initially in contact with dorsal median septum, always present. *Upper Triassic (?Norian, Rhaetian)–Lower Cretaceous (Hauterivian).*

Peregrinella OEHLERT, 1887a, p. 1305 [**Terebratula peregrina* VON BUCH, 1834, p. 73; OD; =*Terebratula multicarinata* LAMARCK, 1819, p. 253, *non* SCHLOTHEIM, 1813]. Large, circular, equibiconvex to ventribiconvex, rectimarginate; costae numerous, deeply incised, sharp; beak massive, incurved. Hinge plates wide, flat; dental plates short, acutely divergent ventrally; teeth small, peglike; crura long, subparallel, laterally concave; septum low, long. *Lower Cretaceous (Berriasian–Hauterivian):* Europe (mainly southern), North America, Asia.

P. (Peregrinella). Costae simple, angular, or sometimes subquadrate. *Lower Cretaceous (Berriasian–Hauterivian):* Crimea, *Berriasian;* France, Alps, Italy, Romania, Carpathians, Caucasus, USA (California, Alaska), ?Mexico, Tibet, northern Siberia, *Valanginian–Hauterivian.*——FIG. 843*a–n.* **P. (P.) multicarinata* (LAMARCK), Hauterivian, France; *a–c,* dorsal, lateral, anterior views, ×1 (new); *d–n,* transverse serial sections, distances in mm from ventral umbo, 2.5, 3.2, 3.7, 4.1, 4.9, 5.2, 5.6, 5.9, 6.2, 7.4, 12.6, approximately ×2 (Ager, 1968).

P. (Peregrinellina) HOU & WANG, 1984, p. 211 [**P. (P.) xizangensis;* OD]. Similar to *P. (Peregrinella)* but costae dense, subangular, increasing by frequent bifurcation. *Lower Cretaceous (Valanginian–Hauterivian):* northern Tibet, Silesia.——FIG. 844*a–l.* **P. (P.) xizangensis,* lower Hauterivian; *a–b,* dorsal, lateral views, GMC IV 83908, ×1; *c,* ventral view, GMC IV 83905, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 5.0, 5.7, 6.1, 6.6, 6.8, 7.6, 8.1, 8.6, 10.7 (Hou & Wang, 1984).

?Carapezzia TOMLIN, 1930, p. 24, *nom. nov. pro Geyeria* CARAPEZZA & SCHOPEN, 1897, p. 248, *non* BUCHECKER, 1876, Insecta, *nec* BUCKMAN, 1899, Cephalopoda, *nec* FUCINI, 1901, Cephalopoda, *nec* WAGNER, 1914, Gastropoda [**Rhynchonellina (Geyeria) globosa* CARAPEZZA & SCHOPEN, 1897, p. 248; OD]. Large to very large, round to ovoid, strongly globose and massive, ventribiconvex; without median sulcus or fold, rectimarginate or slightly planoplicate; ornament of fine capillae (on well-preserved specimens, otherwise smooth); stout, pointed beak, suberect to strongly incurved when adult; broad palintrope with sharp beak ridges; wide delthyrium and triangular conjunct deltidial plates. Dental plates ventrally divergent and distant

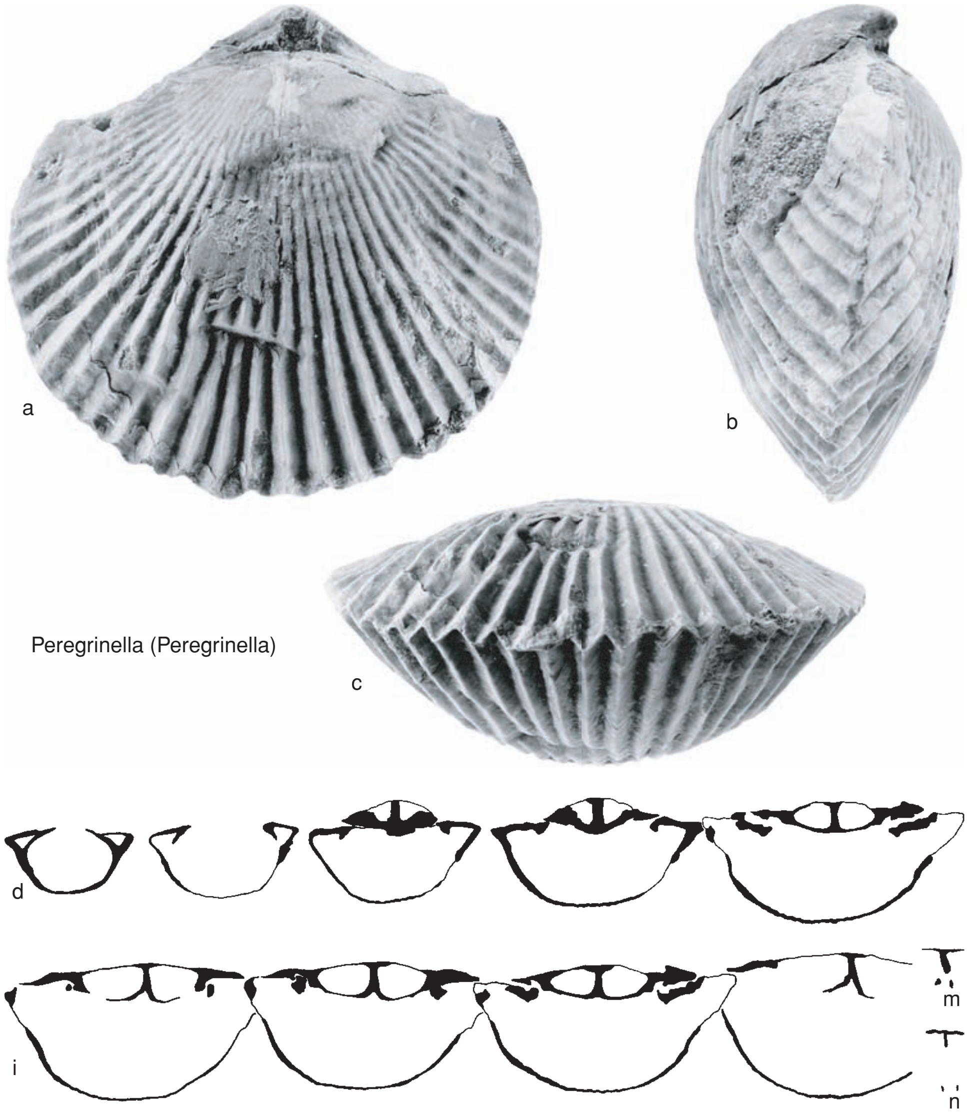

FIG. 843. Peregrinellidae (p. 1238).

or absent; dorsal median septum extending at least one-quarter valve length; crura long, over half shell length, fused apically to divide valve, with short crural processes on ventral side of crura. [Serial sections from type species unknown.] *Upper Triassic (?Norian, Rhaetian)–Lower Jurassic:* Austria, Italy (Sicily), Turkey, Algeria, ?Morocco, ?Crimea.——FIG. 845*a–n. C. geyeri* (BITTNER), Rhaetian, Gailtaler Alps, Austria; *a–c,* lectotype, dorsal, lateral, anterior views, GBA 1898/1, ×1 (Siblík, 1988); *d–n,* transverse serial sections through umbo, approximately ×1.15 (Bittner, 1898).

Subfamily DZIEDUSZYCKIINAE Savage, 1996

[Dzieduszyckiinae SAVAGE, 1996, p. 257]

[Materials prepared by NORMAN M. SAVAGE]

Large, transversely ovate Peregrinellidae with costae strong, simple, full; both valves sulcate; dental plates short, vertical; dorsal median septum short; crura long, thin, closely set. *Upper Devonian (Famennian).*

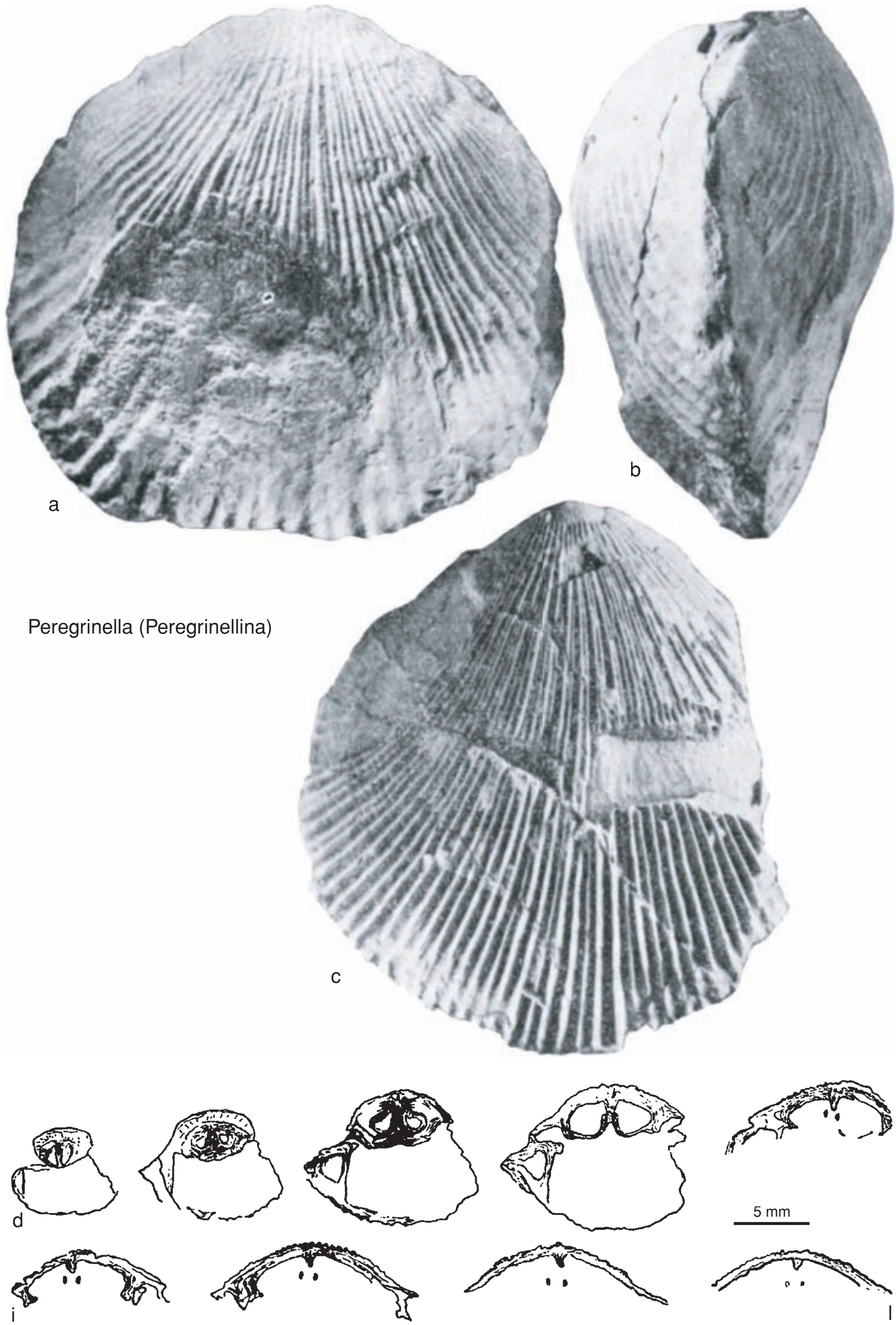

FIG. 844. Peregrinellidae (p. 1238).

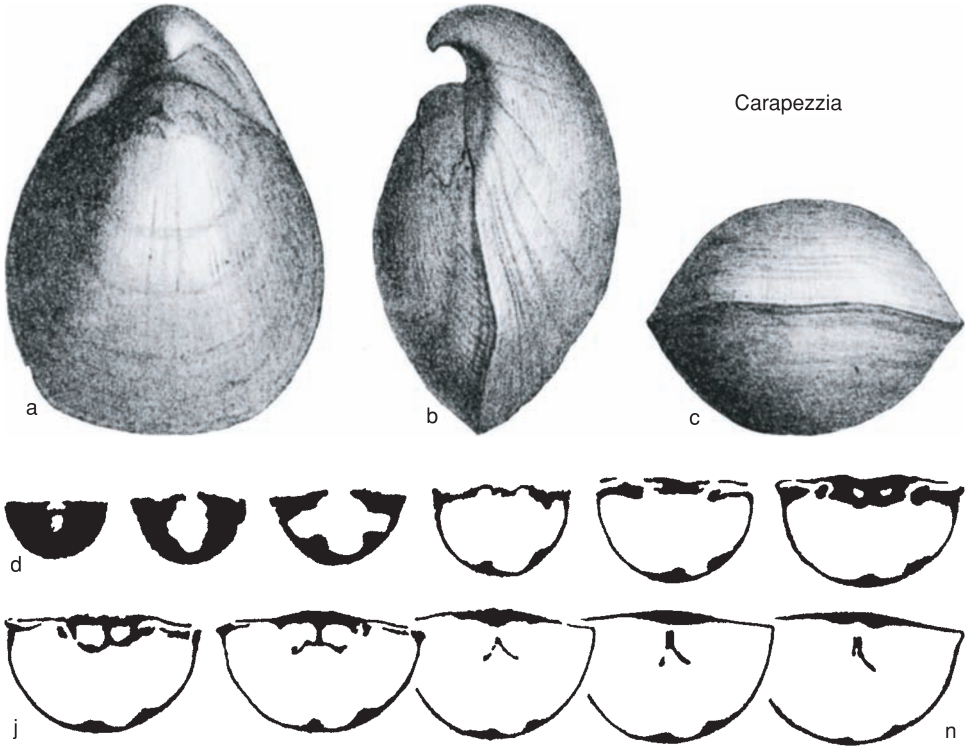

FIG. 845. Peregrinellidae (p. 1238–1239).

Dzieduszyckia SIEMIRADZKI, 1909, p. 768 [**Terebratula (?) kielcensis* ROEMER, 1866, p. 671; OD] [=*Eoperegrinella* AGER, 1968, p. 61 (type, *Halorella crassicostata* TERMIER & TERMIER, 1948, p. 51, fig. 4–5)]. Large with outline transversely ovate and profile biconvex. Beak prominent. Bisulcate with ventral sulcus usually more marked; anterior commissure weakly uniplicate to rectimarginate; serrate. Shells commonly asymmetrical, possibly resulting from crowding in monospecific groups. Costae numerous, rounded, arising at beaks, simple or sometimes dichotomous. Dental plates distinct, vertical to slightly convergent ventrally, well separated from valve walls, leaving large lateral umbonal cavities; teeth small; ventral muscle field only weakly impressed. Dorsal median septum long, low; septalium distinct, small; crura long, thin, closely set. *Upper Devonian (Famennian):* Poland, Morocco, Urals, Kazakhstan, USA.——FIG. 846,*1a–h*. **D. kielcensis* (ROEMER), upper Famennian, Holy Cross Mountains, Kielce, Kadzielnia Quarry, Poland; *a–d,* neotype, dorsal, ventral, anterior, and posterior views, ×1; *e–h,* serial sections 23.3, 22.8, 22.5, 21.5 mm from anterior, ×6 (Biernat, 1967).

Subfamily PEREGRINELLOIDEINAE Dagys, 1968

[*nom. transl.* MANCEÑIDO & OWEN, herein, *ex* Peregrinelloideidae DAGYS, 1968, p. 42]

[Materials prepared by MIGUEL O. MANCEÑIDO, ELLIS F. OWEN, & A. S. DAGYS]

Medium to large, fully costate Peregrinellidae, mostly equibiconvex, discoidal, and rectimarginate. Dental plates and dorsal median septum absent; flat, wide, subhorizontal hinge plates with inner edge deflected inward ventrally, giving rise to submergiform crura. *Lower Jurassic, ?Middle Jurassic.*

Peregrinelloidea DAGYS, 1968, p. 43 [**P. malkovi;* OD]. Large, laterally oval, thin, equibiconvex, shallow sulcus in posterior of dorsal valve, anterior commissure rectimarginate; surface with distinct, branching costae; beak suberect, ridges distinct,

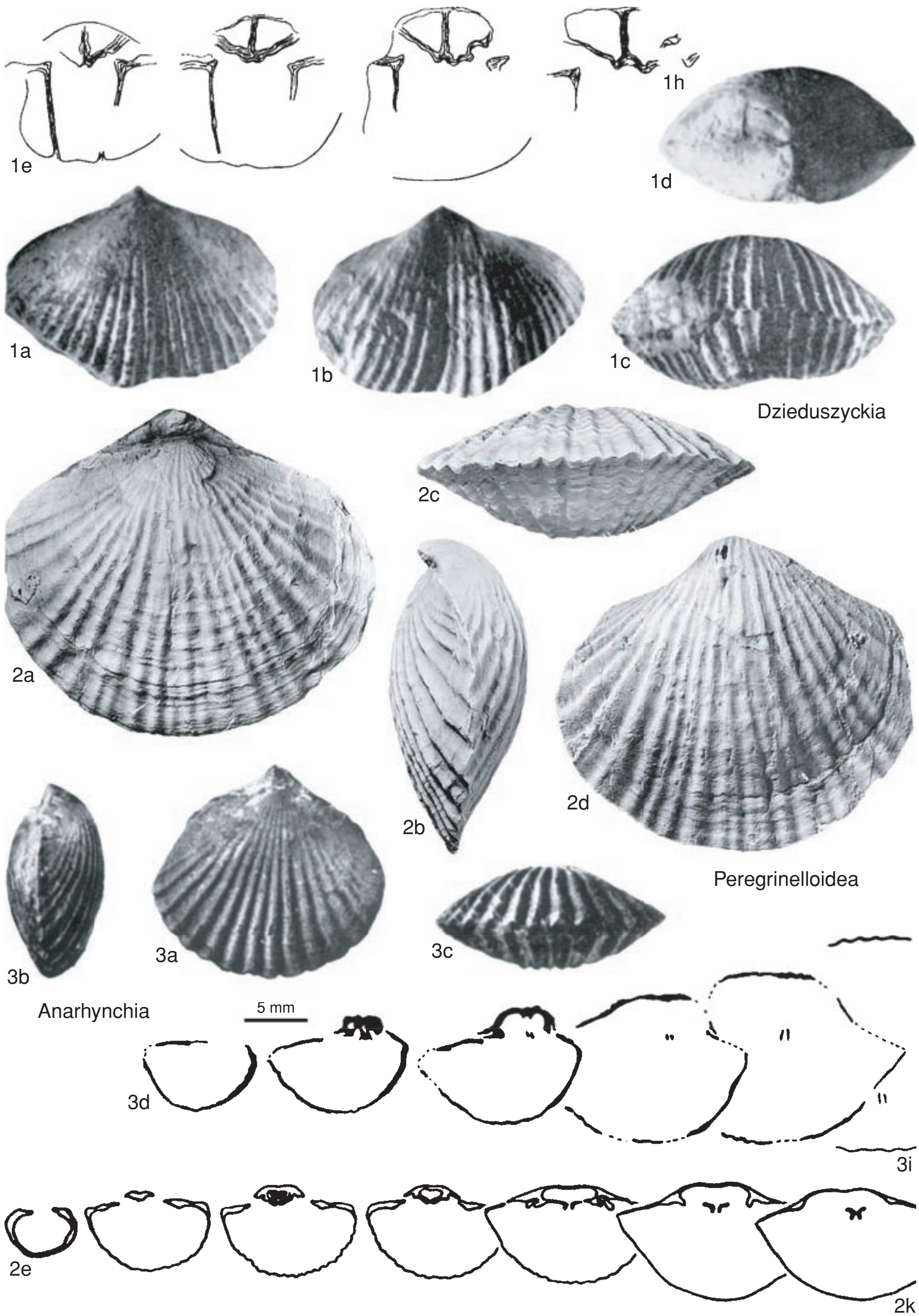

FIG. 846. Peregrinellidae (p. 1241–1243).

foramen hypothyrid, deltidial plates disjunct. Dental plates, pedicle collar, and median septum absent; outer hinge plates broad, incipiently concave in section, crural bases directed only ventrally; crura long, parallel, situated along commissural plane. *Lower Jurassic (Pliensbachian):* northeastern Siberia, ?Argentina.——FIG. 846,*2a–k.* **P. malkovi,* northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 215/78, ×1; *e–k,* transverse serial sections, distances in mm from first section, 0.7, 2.6, 3.2, 3.6, 4.3, 5.1, 5.7 (Dagys, 1968).

Anarhynchia AGER, 1968, p. 63 [**A. gabbi;* OD]. Large, subcircular to transverse elliptical; dorsal valve almost equibiconvex, somewhat flattened posteriorly; both valves fully costate; costae numerous, strong, blunt, attenuated on either side; rectimarginate, serrate; beak prominent, upright to suberect, with large, mesothyrid foramen. No dental plates, teeth small, arising from valve wall; hinge plates fused, no septalium; crura long, closely set, bladelike, extended along commissural plane, distally gently curved. *Lower Jurassic, ?Middle Jurassic:* western USA (California, ?Oregon), ?Argentina.——FIG. 846,*3a–i.* **A. gabbi,* ?Callovian, California; *a–c,* dorsal, lateral, anterior views, personal collection, Derek Ager, J.1223, ×1; *d–i,* transverse serial sections, distances in mm from ventral umbo, 3.4, 4.2, 4.8, 6.6, 8.6, 17.5, USNM M899 (Ager, 1968).

?Family HALORELLIDAE Ager, 1965

[*nom. transl.* DAGYS, 1974, p. 85, *ex* Halorellinae AGER, 1965, p. 605]

[Materials prepared by MIGUEL O. MANCEÑIDO, ELLIS F. OWEN, & A. S. DAGYS]

Large rhynchonellide shells, with wide, straight hinge line, rectimarginate or nearly so, commonly with opposite sulci, may be asymmetrical; beak high, hypothyrid. Dental plates widely spaced, septum very small or absent; crura direct prolongations of hinge plates, flattened in plane of commissure (ciliform type). [A distinctive group tentatively retained within this superfamily following AGER, CHILDS, and PEARSON (1972), although DAGYS (1974) placed it within the basiliolids.] *Upper Triassic (?upper Carnian, Norian).*

Halorella BITTNER, 1884, p. 107 [**Rhynchonella amphitoma* BRONN, 1832, p. 162; SD HALL & CLARKE, 1894, p. 832] [=*Harorella* CHING, SUN, & YE in CHING & others, 1979, p. 166, *nom. null.; Halorelella* GUPTA, 1984, p. 105–106, *nom. null.*]. Medium size to large, transverse oval to subpentagonal with sharp costae beginning from umbo; sulci on both valves or uniplicate; beak suberect, ridges sharp, foramen oval, hypothyrid, deltidial plates conjunct. Dental plates distinct, ventrally divergent, pedicle collar present; septum weak or absent, long ciliform crura. *Upper Triassic (?upper Carnian, Norian):* Alps, Carpathians, Turkey, Pamirs, northeastern Siberia, China, Indonesia, western USA, New Zealand.——FIG. 847,*1a–r.* **H. amphitoma* (BRONN), Norian, Pamirs; *a–c,* dorsal, ventral, anterior views, IGiG 200/6, ×1; *d–r,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.6, 1.2, 1.8, 2.4, 2.7, 3.1, 3.3, 3.6, 4.1, 4.6, 5.3, 5.9, 6.7 (Dagys, 1963).

Halorelloidea AGER, 1960, p. 159 [**Halorella rectifrons* BITTNER, 1884, p. 107; OD]. Similar to *Halorella* but smooth or with low, rounded costae. Dental plates subparallel, pedicle collar present; septum and septalium absent; crura long, curved ventrally, ciliform. *Upper Triassic (Norian):* eastern Alps, Carpathians, Italy (Sicily), Pamirs, Himalayas, Indonesia (Seran), Primorye.——FIG. 847,*2a–p.* **H. rectifrons* (BITTNER), Pamirs; *a–b,* dorsal, anterior views, IGiG 200/32, ×1; *c–p,* transverse serial sections, distances in mm, 0.3, 0.8, 1.3, 1.6, 2.0, 2.3, 2.5, 2.9, 3.2, 3.5, 3.9, 4.3, 4.6, 4.9 (Dagys, 1963).

?Family CRYPTOPORIDAE Muir-Wood, 1955

[Cryptoporidae MUIR-WOOD, 1955, p. 76]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Small, smooth rhynchonellide shells, with large deltoid foramen slightly restricted by elongate, triangular, auriculate deltidial plates, distant from each other; beak ridges sharp. Dental plates variably developed to absent; crura moderately long, maniculiform, continuous with socket ridges; dorsal median septum usually elevated anteriorly; cardinal process a bilobate thickening between socket ridges; single pair of metanephridia, 2 pairs of adductor muscles and circinate spirolophe. [A seemingly primitive and controversial group that is tentatively included in this superfamily in spite of a considerable Cretaceous gap; alternatively, possible relationships with norelloids may not be totally ruled out.] *Upper Cretaceous (upper Campanian)–Holocene.*

Cryptopora JEFFREYS, 1869, p. 136 [**C. gnomon;* M; =*Atretia gnomon* JEFFREYS, 1876, p. 251] [=*Atretia* JEFFREYS in CARPENTER, JEFFREYS, & THOMSON, 1870, p. 421 (type, *A. gnomon* JEFFREYS, 1876, p. 251); *Neatretia* FISCHER & OEHLERT, 1891, p. 122, obj.; *Crytopora* COOPER, 1959, p. 22, *nom. null.; Mannia* DAVIDSON, 1874a, p. 156 (type, *M. nysti,*

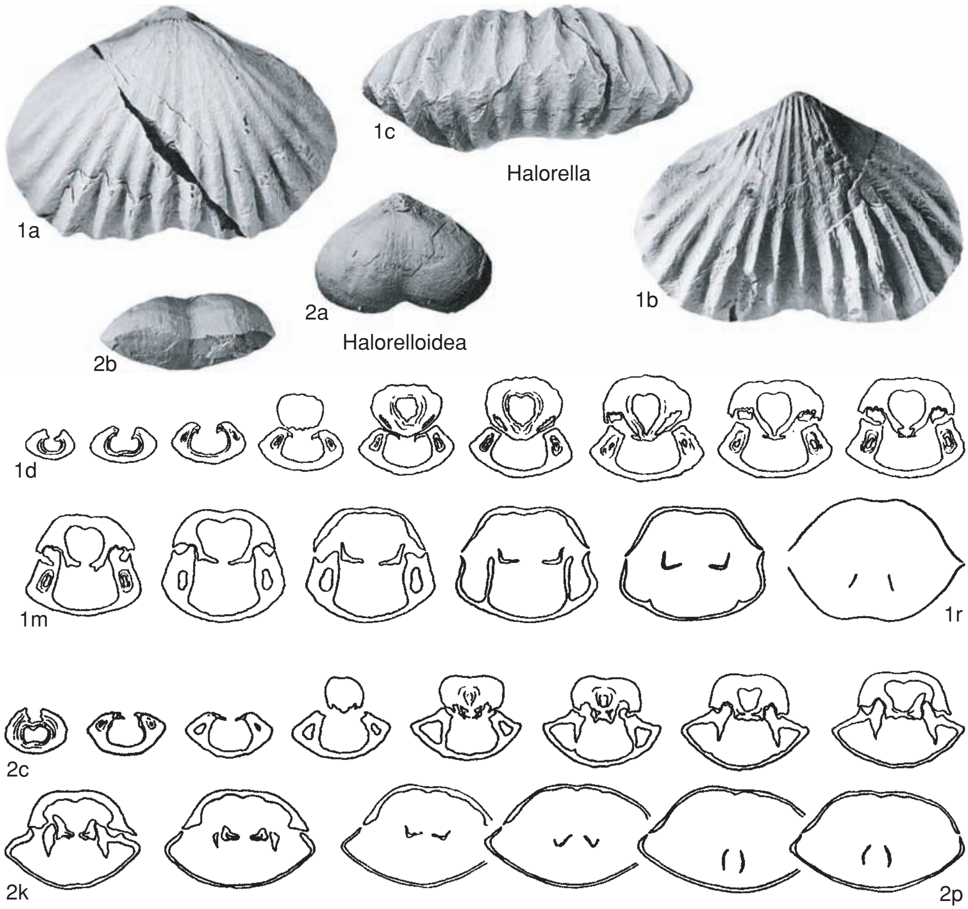

FIG. 847. Halorellidae (p. 1243).

M); *Mannia* DEWALQUE, 1868, p. 432, *nom. nud.*]. Small, translucent, subtrigonal to ovoid-lenticular, almost equibiconvex; rectimarginate to broadly sulcate, smooth; beak moderately long, pointed, nearly straight; foramen large, incomplete; deltidial plates auriculate, rudimentary, disjunct. Dental plates distinct, subvertical; cardinal process small and transverse; dorsal median septum high; crura digitate distally. [Living species range from abyssal to sublittoral.] *Paleogene (lower Danian)–Neogene (Pliocene), Holocene:* Denmark, Belgium, Spain, Austria, Italy, Sardinia, Poland, Hungary, Ukraine, USA (Alabama), Cuba, Venezuela, Fiji, Antarctica, *lower Danian–Pliocene;* North Atlantic (Massachusetts), South Atlantic, Africa, Indopacific, *Holocene.*——FIG. 848,*1a–d.* **C. gnomon* (JEFFREYS), Holocene, Massachusetts, off eastern USA; *a–b,* ventral, lateral views, USNM 44911a, ×6; *c,* anterior view, USNM 44911c, ×6; *d,* interior of dorsal valve with maniculiform crura, USNM 44911d, ×8 (Cooper, 1959).——FIG. 848,*1e. C. nysti* (DAVIDSON), dorsal view showing auriculate deltidial plates and incomplete foramen, upper Miocene, Antwerp, Belgium, USNM 549422a, ×20 (Cooper, 1959).

Aulites RICHARDSON, 1987, p. 45 [**Atretia brazieri* CRANE, 1886, p. 183; OD]. Similar to *Cryptopora* but without dental plates, rectimarginate to gently uniplicate; foramen large with narrow marginal deltidial plates bordering delthyrium. Crura nondigitate maniculiform and inwardly curving; hinge plates well developed; cardinal process as paired semicircular thickenings. *Paleogene (upper Oligocene)–Holocene:* Australia (neritic to bathyal).——FIG. 848,*2a–h.* **A. brazieri* (CRANE), Holocene, southeastern Australia; *a–f,* dorsal view, ventral view, ventral valve interior, dorsal valve interior, lateral view, anterior view, ×10; *g,* interior of dorsal umbo showing cardinalia, ×30; *h,* interior of dorsal valve showing maniculiform crura, ×30 (Richardson, 1987).

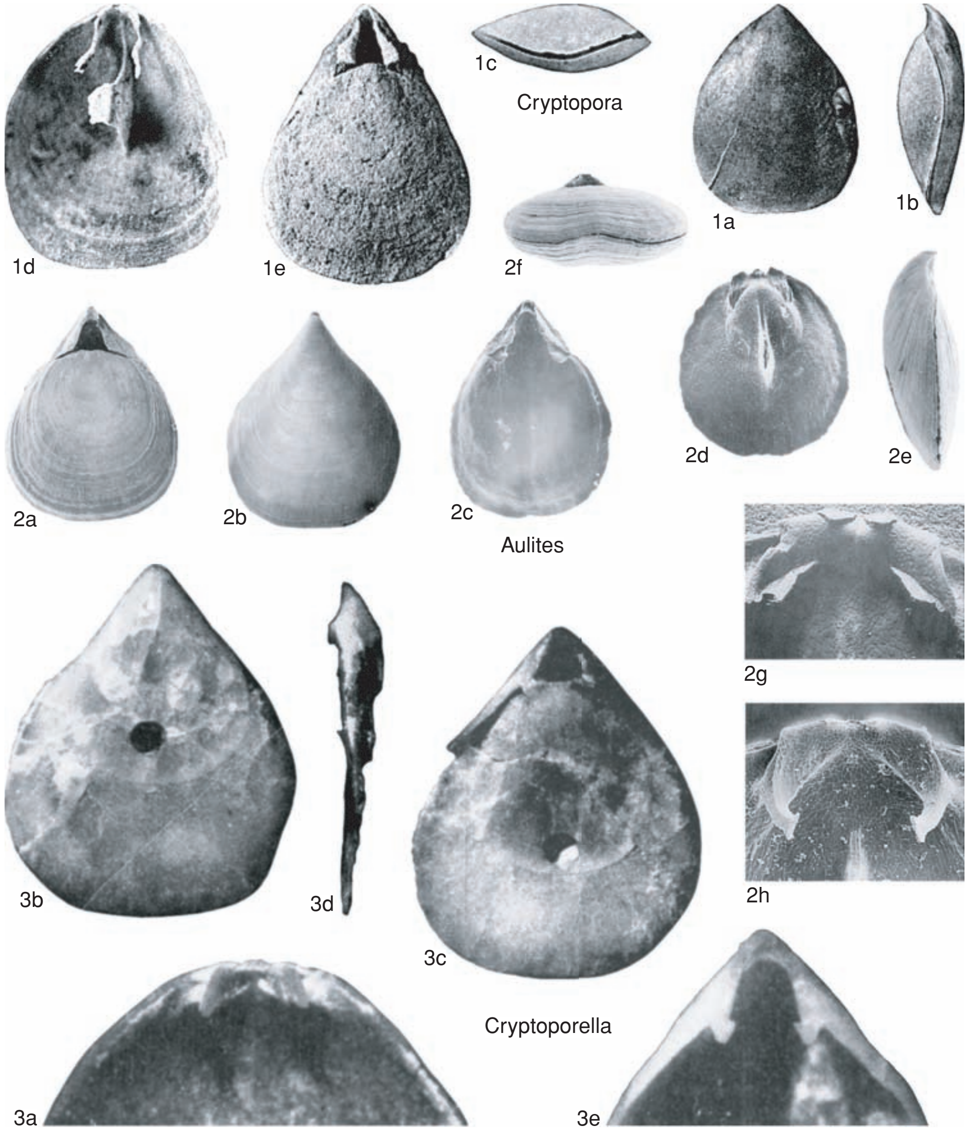

FIG. 848. Cryptoporidae (p. 1243–1245).

?Cryptoporella BITNER & PISERA, 1979, p. 71 [**C. antiqua;* OD]. Small, smooth, subtrigonal; externally similar to *Cryptopora,* rectimarginate, greatest width anterior to midvalve; moderately biconvex; beak sharp, fairly long, foramen large, triangular. Hinge teeth long, inwardly curved, and deeply inserted, supported by parallel dental plates; crura very short and wide; median septum absent. [Lack of dorsal septum unusual; family allocation requires revision.] *Upper Cretaceous (upper Campanian–lower Maastrichtian):* eastern Poland. ——FIG. 848,*3a–e.* **C. antiqua,* lower Maastrichtian, Mielnik; *a,* dorsal valve interior, ×20; *b–d,* ventral valve, dorsal valve, lateral view of ventral valve, ×15; *e,* pedicle valve, inner view, ×20 (Bitner & Pisera, 1979).

RHYNCHOTETRADOIDEA

NORMAN M. SAVAGE,[1] MIGUEL O. MANCEÑIDO,[2] ELLIS F. OWEN,[3]
and A. S. DAGYS[4]

[[1]University of Oregon; [2]La Plata Natural Sciences Museum, Argentina; [3]formerly of The Natural History Museum; and [4]deceased]

Superfamily RHYNCHOTETRADOIDEA Licharew, 1956

[*nom. transl.* SAVAGE, 1996, p. 254, *ex* Rhynchotetradidae MCLAREN, 1965, p. 589, *nom. correct. pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

Rhynchonellida with elongate oval outline; apical angle acute; dorsal fold and ventral sulcus weak; planareas distinct, often concave; costae coarse to very coarse, often with superimposed striae anteriorly; foramen with conjunct deltidial plates. Dental plates converge ventrally to form sessile spondylium or spondylium duplex; spondylium with or without lateral buttresses, atrophied and lost in all Mesozoic genera. Dorsal median septum strong; septalium present without cover plate; cardinal process absent; crural bases usually triangular in cross section. *Upper Devonian (Famennian)–Middle Jurassic (Callovian).*

Family RHYNCHOTETRADIDAE Licharew, 1956

[*nom. correct.* MCLAREN, 1965, p. 589, *pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

[Materials prepared by NORMAN M. SAVAGE]

Rhynchotetradoidea without lateral buttresses in ventral valve; shell surface with radial striae. *Upper Devonian (Famennian)–Upper Carboniferous (lower Bashkirian).*

Subfamily RHYNCHOTETRADINAE Licharew, 1956

[*nom. transl.* SAVAGE, 1996, p. 255, *ex* Rhynchotetradidae MCLAREN, 1965, p. 589, *nom. correct. pro* Rhynchotetraidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

Rhynchotetradidae with sessile spondylium or spondylium duplex in ventral valve. *Lower Carboniferous (Tournaisian)–Upper Carboniferous (lower Bashkirian).*

Rhynchotetra WELLER, 1910, p. 506 [**Rhynchonella caput testudinis* WHITE, 1865, p. 23; OD]. Subtriangular to elongate outline and biconvex profile; anterior and lateral margins subvertical; posterolateral margins concave. Beak erect. Fold and sulcus weak; anterior commissure uniplicate; tongue distinct, serrate. Costae rounded, some bifurcation and intercalation; shell surface with fine radial striae. Dental plates meet as sessile or supported spondylium. Dorsal median septum strong, extending to midlength; septalium narrow, deep, long, open but with medially projecting edges; crural bases triangular in section. *Lower Carboniferous (Tournaisian):* North America, Russia.——FIG. 849,*1a–c.* **R. caputtestudinis* (WHITE), Kinderhookian, Burlington Limestone, Burlington, Iowa, USA; dorsal, lateral, and anterior views, ×1 (Weller, 1914).——FIG. 849,*1d–k. R. missouriensis,* Kinderhookian, Burlington Limestone, Missouri; *d–g,* dorsal, ventral, anterior, and lateral views, ×1; *h–k,* serial sections, ×2.5 (Weller, 1914).

Goniophoria JANISCHEWSKY, 1910, p. 80 [**G. monstrosa;* SD SCHUCHERT & LEVENE, 1929a, p. 63]. Large with elongate subpentagonal outline and biconvex profile; anterior and lateral margins truncated. Beak erect. Dorsal fold and ventral sulcus obscured by plicae; anterior commissure sulciplicate. Plicae strong, arising at umbones, typically 4 on dorsal valve with 2 on fold, and 5 on ventral valve with 1 in sulcus. Spondylium in ventral valve supported by strong median septum. Dorsal median septum protruding into large U-shaped septalium. *Carboniferous (Tournaisian–Namurian):* Urals, Donetz basin, Siberia, China.——FIG. 849,*2a–c.* **G. monstrosa,* Lower Carboniferous, Khabar, southern Urals; holotype, dorsal, lateral, and anterior views, ×1 (Licharew, 1957).——FIG. 849,*2d. G. carinata* JANISCHEWSKY, Lower Carboniferous, southern Urals; transverse section near posterior, ×2 (Licharew, 1957).

Nepasitoechia HAVLÍČEK, 1979, p. 91 [**N. sartenaeri;* OD]. Elongate triangular outline and thin, biconvex profile. Beak straight; foramen not recorded. Fold and sulcus very weak to absent; anterior commissure rectimarginate. Costae numerous, some bifurcation and intercalation; fine striae occasionally preserved. Dental plates strong, slightly convergent ventrally. Dorsal median septum short, low, thick; septalium deep, U-shaped, partly restricted by projecting inner edges of hinge plates; hinge plates divided anterior of septalium. *Lower Carboniferous (lower Tournaisian):* Bohemia.——FIG. 850*a–j.* **N. sartenaeri,* 4 m above *Clymenia* Zone, Nepasice borehole, Hradec Kralove; *a,* holotype, dorsal view; *b–d,* topotype, dorsal, ventral, and lateral views; *e,* anterior view of another topotype, ×2.8; *f–j,* serial sections 0.1, 0.2, 0.4, 0.7, 1.3 mm from posterior, approximately ×5 (Havlíček, 1979).

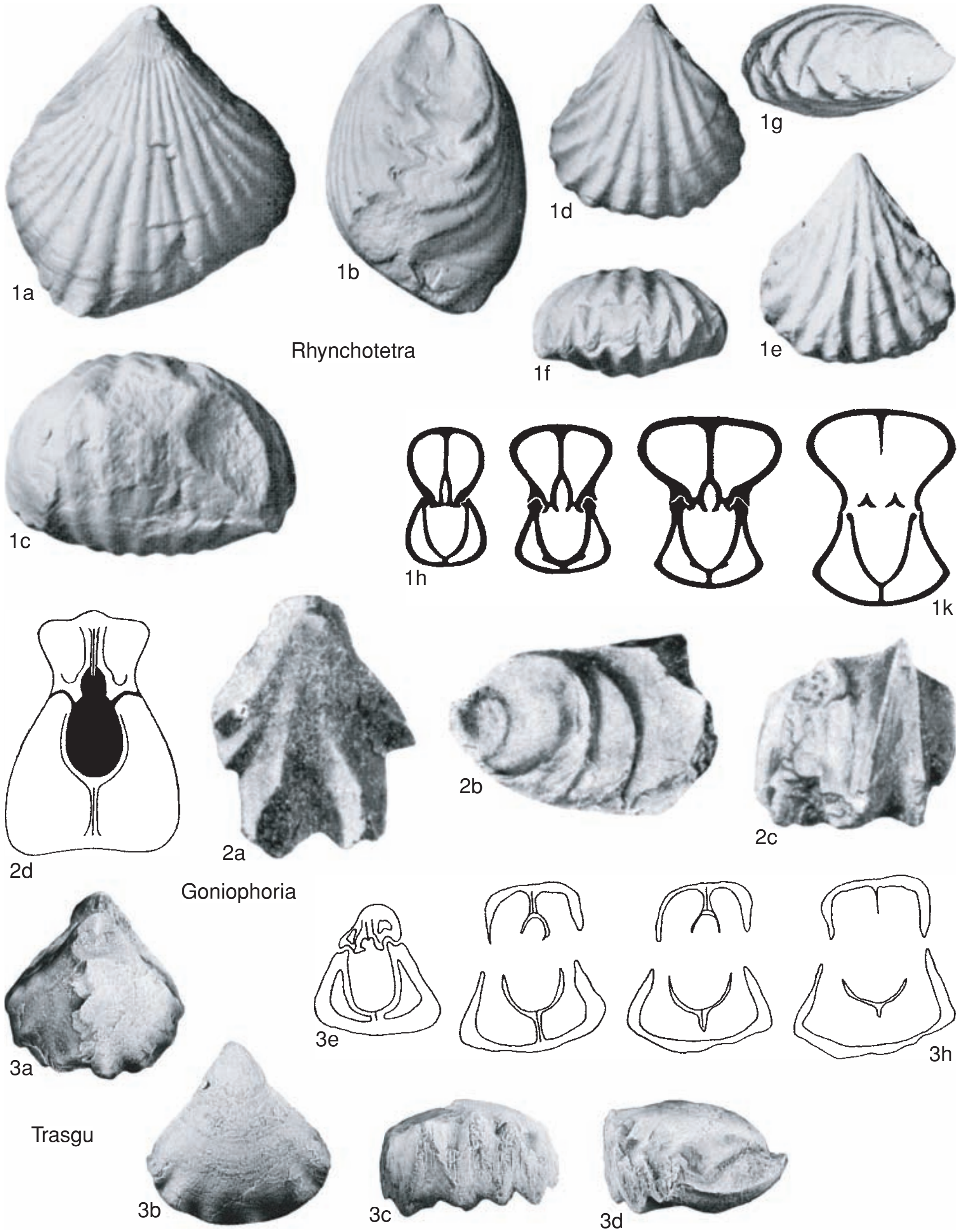

FIG. 849. Rhynchotetradidae (p. 1246–1248).

Trasgu MARTÍNEZ-CHACÓN, 1979, p. 251 [**T. minor;* OD]. Small with subtriangular outline and dorsibiconvex, anteriorly inflated profile; anterior margin subvertical; posterolateral margins concave. Beak erect. Fold and sulcus very weak to absent; anterior commissure uniplicate; tongue low, coarsely denticulate. Costae very coarse, mostly restricted to anterior margin. Dental plates and ventral median septum forming large U-shaped spondylium. Dorsal median septum wide, low, supporting septalium; septalium long, U-shaped, with median septum projecting slightly into septalium; crura laterally flattened. *Upper Carboniferous (lower Bashkirian):* Spain (Cantabrian Mountains).——FIG. 849,*3a–h.*

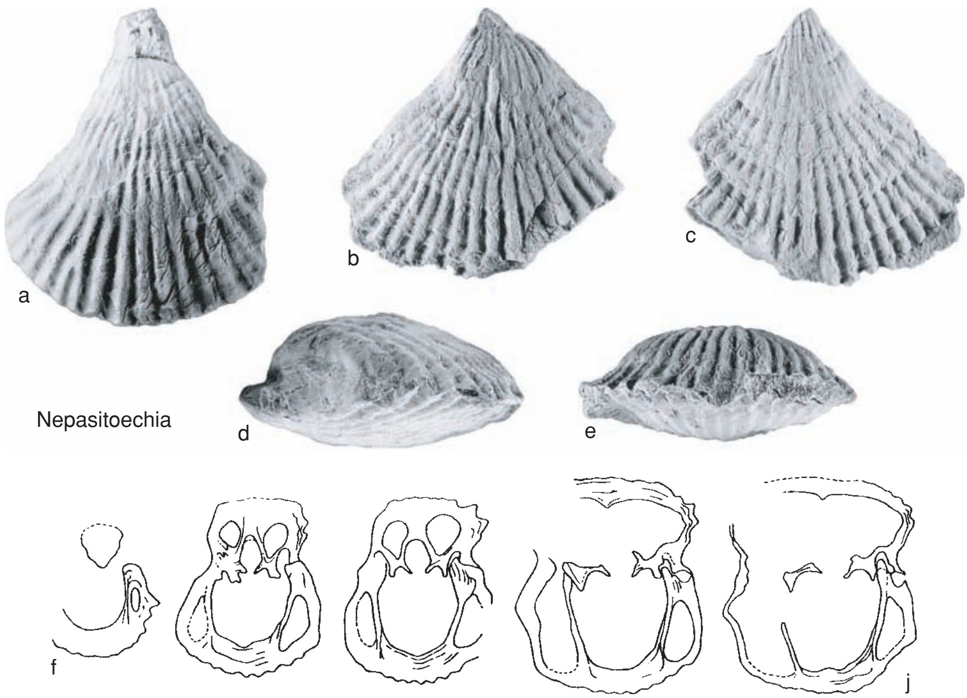

FIG. 850. Rhynchotetradidae (p. 1246).

T. minor, upper Valdeteja Formation, Oviedo; *a–d,* holotype, dorsal, ventral, anterior, lateral views, ×2.5; *e–h,* serial sections 1.2, 2.2, 2.3, 2.6 mm from posterior, ×4.5 (Martínez-Chacón, 1979).

Subfamily AXIODEANEIINAE Savage, 1996

[Axiodeaneiinae SAVAGE, 1996, p. 255]

Rhynchotetradidae with sessile spondylium; elongate outline; costae very coarse. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian).*

Axiodeaneia CLARK, 1917, p. 374 [**A. platypleura;* OD]. Narrowly elongate outline and biconvex profile; anterior and lateral margins subvertical. Beak erect; foramen present apically. Fold and sulcus weak; anterior commissure uniplicate; tongue low, typically tridentate. Costae very coarse, angular; shell surface with fine radial striae. Dental plates converging ventrally but not meeting, extending one-quarter valve length. Dorsal median septum strong, long, reaching one-third valve length; septalium wide, V-shaped; hinge plates ending with septalium; crural bases large, ventrally concave; crura with triangular cross section. *Lower Carboniferous (Tournaisian):* North America.——FIG. 851,*1a–f.* **A. platypleura,* Lodgepole Formation, Bridger Mountains, Montana, USA; *a–d,* dorsal, ventral, anterior, and lateral views, ×1.25; *e–f,* interiors of dorsal and ventral valves, ×3 (new).——FIG. 851,*1g–o. A. usheri* (BROWN), Banff Formation, Jasper Park, western Alberta, Canada; serial sections 2.0, 2.6, 3.0, 3.2, 3.6, 4.2, 5.2, 5.4, 6.2 mm from posterior, ×2 (Carter, 1987).

Paraphorhynchus WELLER, 1905, p. 260 [**P. elongatum;* OD]. Elongate oval to subtriangular outline and biconvex profile; subvertical anterior and lateral margins. Beak erect; foramen elongate. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue high, broad, serrate. Costae rounded, arising at umbones, weak on flanks; shell surface with fine radial striae. Dental plates long, almost meeting ventrally; narrow ventral muscle field between dental plates. Dorsal median septum strong, short; septalium large, open; hinge plates divided anterior of septalium. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America, Europe, Urals, Novaya Zemlya, Kazakhstan.——FIG. 851,*2a–j.* **P. elongatum,* lower Mississippian, Kinderhookian, Knox County, Missouri, USA; *a–e,* dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–j,* serial sections, ×2 (Weller, 1914).

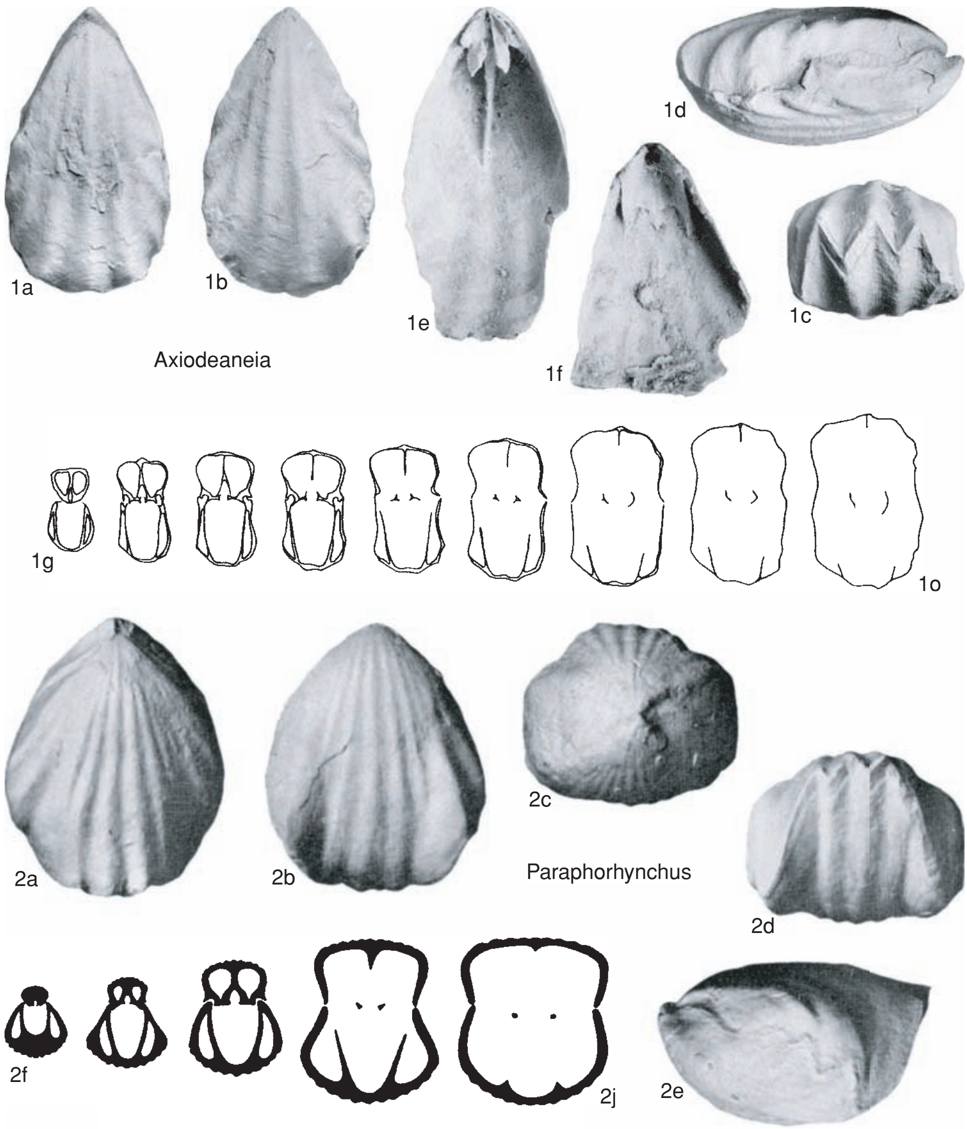

FIG. 851. Rhynchotetradidae (p. 1248).

Family TETRACAMERIDAE Licharew, 1956

[*nom. transl.* RZHONSNITSKAIA, 1958, p. 115, *ex* Tetracamerinae LICHAREW in RZHONSNITSKAIA, 1956a, p. 126]

[Materials prepared by NORMAN M. SAVAGE]

Rhynchotetradoidea with lateral buttresses in ventral valve; shell surface without radial striae. *Lower Carboniferous (lower Tournaisian–upper Tournaisian).*

Tetracamera WELLER, 1910, p. 503 [**Rhynchonella subcuneata* HALL, 1858b, p. 11; OD]. Outline subtriangular and biconvex, profile subrectangular; anterior and lateral margins vertical. Beak small, erect; delthyrium with small foramen apically. Fold and sulcus very low; anterior commissure weakly uniplicate to rectimarginate; dentate. Costae angular, simple, from beaks. Shell surface with fine radial striae. Dental plates converging as sessile spondylium with a lateral buttress plate across each umbonal cavity. Dorsal median septum strong, extending almost to midlength; septalium narrow,

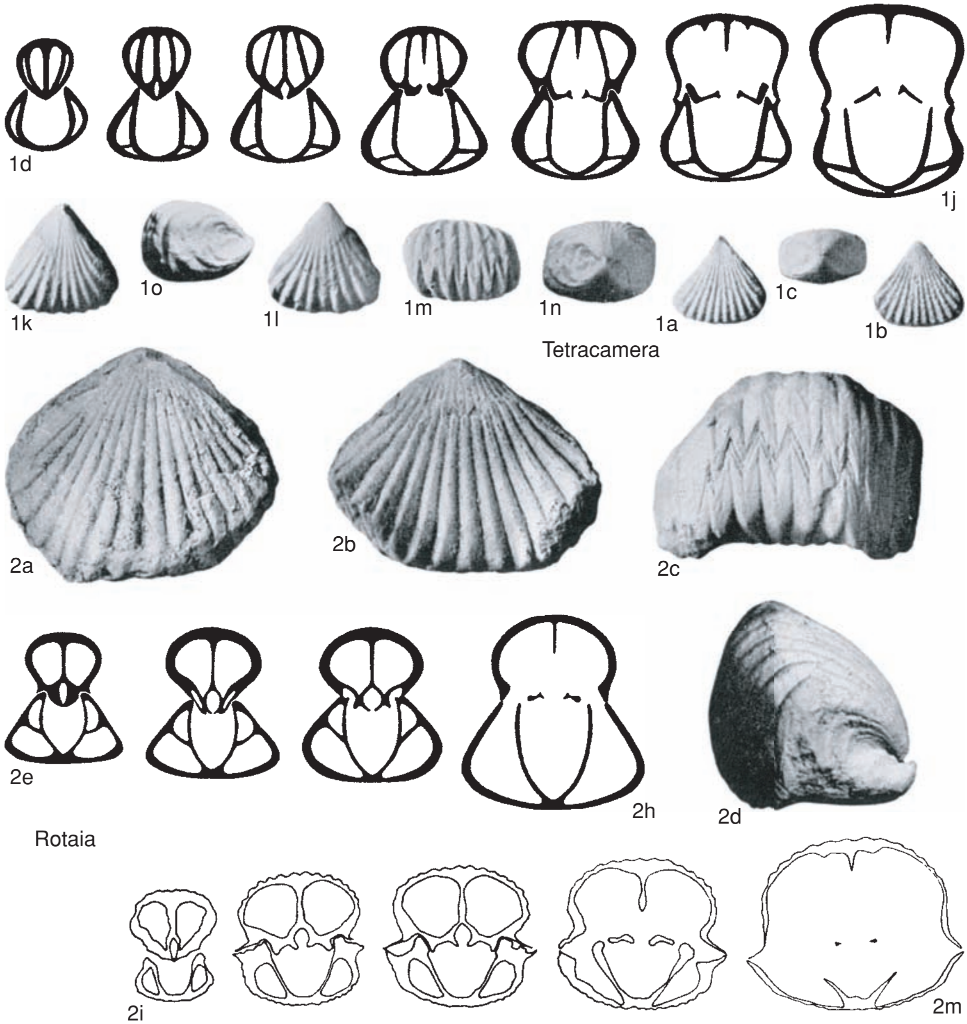

FIG. 852. Tetracameridae (p. 1249–1251).

short, open; hinge plates dividing immediately anterior of septalium, supported by subvertical plates extending to valve floor; crural bases inclined ventrolaterally. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* North America, Kazakhstan, Urals, Australia.——FIG. 852,*1a–j.* **T. subcuneata* (HALL), Mississippian, Osagean, Salem Limestone, Salem, Indiana, USA; *a–c,* dorsal, ventral, and posterior views, ×1; *d–j,* serial sections, ×2.5 (Weller, 1914).——FIG. 852,*1k–o. T. arctirostrata* (SWALLOW), Mississippian, Osagean, Salem Limestone, Alton, Illinois, USA; dorsal, ventral, anterior, posterior, and lateral views, ×1 (Weller, 1914).

Rotaia RZHONSNITSKAIA, 1959, p. 30, *nom. nov. pro Welleria* ROTAI, 1941, p. 107, *non* ULRICH & BASSLER, 1923 [**Rhynchonella subtrigona* MEEK & WORTHEN, 1860, p. 451; OD]. Large with subpentagonal to transversely subtrigonal outline and biconvex profile; vertical anterior and lateral margins truncated. Beak erect. Fold and sulcus broad, from umbones; anterior commissure uniplicate, low, dentate. Dental plates meeting as sessile spondylium, with high buttress plates. Septalium long, deep, wide, partly covered by inner hinge plates; hinge plates divided, without lateral supporting plates; dorsal median septum strong, to midlength, crural bases transversely ovate; crura short, straight, delicate, triangular in section. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* North America, European Russia, Altai, Siberia, China. ——FIG. 852,*2a–h.* **R. subtrigona* (MEEK & WORTHEN), Mississippian, Osagean, Keokuk Lime-

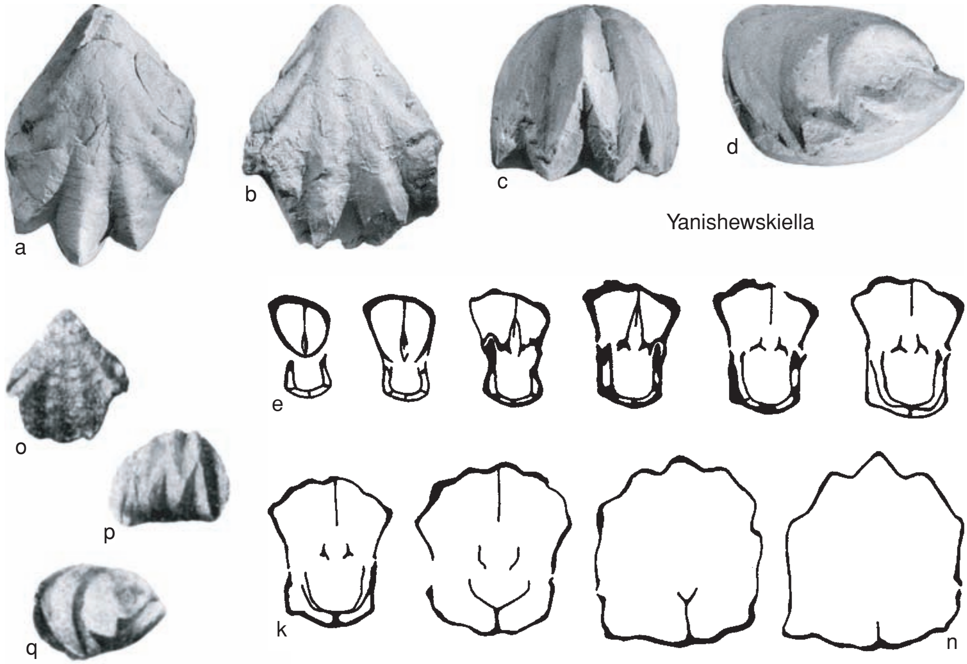

FIG. 853. Tetracameridae (p. 1251).

stone, Warsaw, Illinois, USA; *a–d,* hypotype, dorsal, ventral, anterior, and lateral views, ×1; *e–h,* serial sections, ×1.25 (Weller, 1914).——FIG. 852,*2i–m. Rotaia* sp., Mississippian, Chappel Limestone, Texas, USA; serial sections 1.8, 2.8, 3.0, 3.4, 4.6 mm from posterior, ×1.5 (Carter, 1967).

Yanishewskiella LICHAREW, 1957, p. 139 [**Anomia angulata* LINNAEUS, 1758, p. 703; OD]. Subpentagonal outline and dorsibiconvex profile; vertical anterior and lateral margins; concave posterolateral margins. Beak suberect; delthyrium with foramen apically. Fold and sulcus weak; anterior commissure gently uniplicate but strongly dentate. Plicae angular, simple, from umbones. Shell surface with fine radial striae. Dental plates converge as spondylium supported by low median septum and short lateral buttresses; septalium extending to one-third valve length, ventral median septum to half valve length. Dorsal median septum strong, long; septalium narrow, deep; median septum projecting ventrally well into septalium; hinge plates divided immediately anterior of septalium; crural bases triangular in section, long; crura laterally flattened, slightly sigmoidal. *Lower Carboniferous (lower Tournaisian–upper Tournaisian):* Uzbekistan, Urals, Europe, Japan. ——FIG. 853*a–q.* **Y. angulata* (LINNAEUS); *a–d,* dorsal, ventral, anterior, and lateral views, Lancashire, England, ×1.5 (new); *e–n,* serial sections 1.6, 2.0, 2.2, 2.6, 3.0, 3.4, 4.2, 6.0, 7.8, 9.4 mm from anterior, Lancashire, England, ×1.8 (new); *o–q,* lectotype, ventral, anterior, and lateral views, Fergana, Uzbekistan, ×1 (Licharew, 1957).

?Family AUSTRIRHYNCHIIDAE Ager, 1959

[Austrirhynchiidae AGER, 1959b, p. 331]

[Materials prepared by MIGUEL O. MANCEÑIDO, ELLIS F. OWEN, & A. S. DAGYS]

Rhynchonellida with shells triangular to extremely expanded laterally; planareas flat to concave. Dental plates subparallel to ventrally divergent, close to wall; dorsal median septum short and weak; crura distally compressed or concave; alleged cardinal process spurious; spondylium undeveloped. [Formerly thought to be related to cyclothyridines (AGER, CHILDS, & PEARSON, 1972) and even regarded as a subfamily only (DAGYS, 1974, p. 109; PEARSON, 1977, p. 53), this peculiar group is here tentatively retained as a family and reallocated among dominantly cuneiform rhynchotetradoids.] *Middle Triassic–Upper Triassic.*

Austrirhynchia AGER, 1959b, p. 325 [**Terebratula cornigera* SCHAFHÄUTL, 1851, p. 407; OD]. Small, triangular, with anterolateral wings, moderately equibiconvex, both valves flattened, multicostate, except for smooth lateral sides, which are curved at right angles to plane of commissure; anterior commissure rectimarginate or weakly uniplicate; beak short, incurved, ridges distinct, foramen large, elliptical, deltidial plates conjunct. Dental plates subparallel, pedicle collar long, fused to dental plates; septum weak, outer hinge plates narrow, indistinct, fused to socket ridges, crura raduliform. *Upper Triassic (Rhaetian):* northern Alps, Carpathians, northwestern Caucasus, Turkey, Iran.——FIG. 854,*4a–u.* **A. cornigera* (SCHAFHÄUTL), northern Alps; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/231, ×1; *e–u,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.5, 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.7, 1.9, 2.1, 2.3, 2.6, 2.8, 3.0, 3.2, IGiG 394/232, approximately ×2 (Dagys, 1974).

Decurtella GAETANI, 1966, p. 344 [**Terebratula decurtata* GIRARD, 1843, p. 474; OD]. Small, triangular, moderately and equally biconvex, weakly uniplicate; both valves flattened, distinctly costate, lateral sides smooth, curved at right angle to commissural plane, forming structures similar to planareas, which never continue into wings; beak suberect, ridges distinct, foramen oval, hypothyrid, deltidial plates disjunct. Dental plates subparallel, diverging anteriorly; umbonal chambers small, partly filled by callus, no pedicle collar; septalium shallow, supported by short septum only in posterior part, crura raduliform. *Middle Triassic (Anisian–Ladinian):* Alps, Balkans, Carpathians, Transdanubian range, northwestern Caucasus.——FIG. 854,*2a–n.* **D. decurtata* (GIRARD), Anisian; *a–e,* dorsal, lateral, anterior, ventral, posterior views, Lombardia, northern Italy, ×2; *f,* detail of apical region, Lombardia, northern Italy, G 4/1, ×15 (Gaetani, 1966); *g–n,* transverse serial sections, distances in mm from ventral umbo, 0.6, 0.9, 1.05, 1.15, 1.3, 1.4, 1.75, 2.1, Balaton area, Hungary (Pálfy, 1988).

Excavatorhynchia CHING & FENG, 1977, p. 44 [**Rhynchonella raxana* BITTNER, 1892, p. 31; OD]. Small, cuneiform, nearly equibiconvex; umbo flattened; lateral and anterior margin abruptly geniculated; large, concave planareas posterolaterally; commissure slightly uniplicate or nearly rectimarginate; dorsal fold low, flat, developed only at anterior half; shallow ventral sulcus bent dorsally into low, truncate linguiform extension; costation variable, usually attenuated or evanescent posteriorly; beak incurved; foramen mesothyrid. Dental plates short, thin, close to lateral wall; low, thick septum supporting very small septalium; crura possibly raduliform, distally subvertical, bladelike. *Middle Triassic–Upper Triassic:* Alps, China.——FIG. 854,*3a–m.* **E. raxana* (BITTNER), Carnian, Yunnan, China; *a–e,* dorsal, lateral, anterior, ventral, posterior views, NIGP 26829, ×1.5 (new); *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.6, 0.7, 1.0, 1.2, 1.5, 1.9, 2.5, NIGP 26829 (Ching & Feng, 1977).

?Trigonirhynchella DAGYS, 1963, p. 41, *nom. nov. pro Trigonirhynchia* DAGYS, 1961, p. 94, *non* COOPER, 1942, Rhynchonellida [**Trigonirhynchia trigona* DAGYS, 1961, p. 95; OD]. Small, trigonal, medially flattened, moderately biconvex, smooth posteriorly, with few rounded costae anteriorly; sulci possibly present on both valves; commissure unisulcate to uniplicate; beak small, suberect, ridges rounded. No pedicle collar, dental plates short, divergent, almost fused to lateral walls; weak dorsal median septum confined apically, supporting septalium; crura distally subvertical, bladelike. [Alternatively may be related to *Prelissorhynchia,* according to XU, 1990, p. 77.] *Upper Triassic (Norian):* ?Alps, Carpathians, Hungary, northwestern Caucasus, Pamirs, Vietnam.——FIG. 854,*1a–k.* **T. trigona* (DAGYS), Norian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, IGiG 179/20, ×1; *d–k,* transverse serial sections, distances in mm from first section, 1.0, 1.4, 1.6, 1.9, 2.2, 2.3, 2.8, 3.6 (Dagys, 1961).

Family PRIONORHYNCHIIDAE new family

[Prionorhynchiidae MANCEÑIDO & OWEN, herein]

[Materials prepared by MIGUEL O. MANCEÑIDO & ELLIS F. OWEN]

Medium to large Rhynchotetradoidea, subtriangular to subpentagonal, cuneiform, or securiform; planareas mostly concave, or flat; beak narrow, suberect to scarcely incurved, with small hypothyrid foramen. Ventrally convergent to subparallel dental plates; dorsal median septum and septalium present, though variably developed; crura raduliform to distally flattened and somewhat flared or crescentic; triangular crural bases; spondylium undeveloped. *?Middle Triassic, Upper Triassic–Middle Jurassic (Callovian).*

Prionorhynchia BUCKMAN, 1918, p. 62 [**Terebratula serrata* J. de C. SOWERBY, 1825 in 1823–1825, p. 168; OD] [=*Prionorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, subtrigonal to subpentagonal, depressed equibiconvex to globose dorsibiconvex; without interarea but planareas well developed; rectimarginate or uniplicate; costae strong, sharp; beak very small, somewhat incurved; deltidial plates narrow, thick. Dental plates thin, ventrally convergent to subparallel, often with low apical ventral median ridge in between; dorsal median septum very short; septalium small, pitlike;

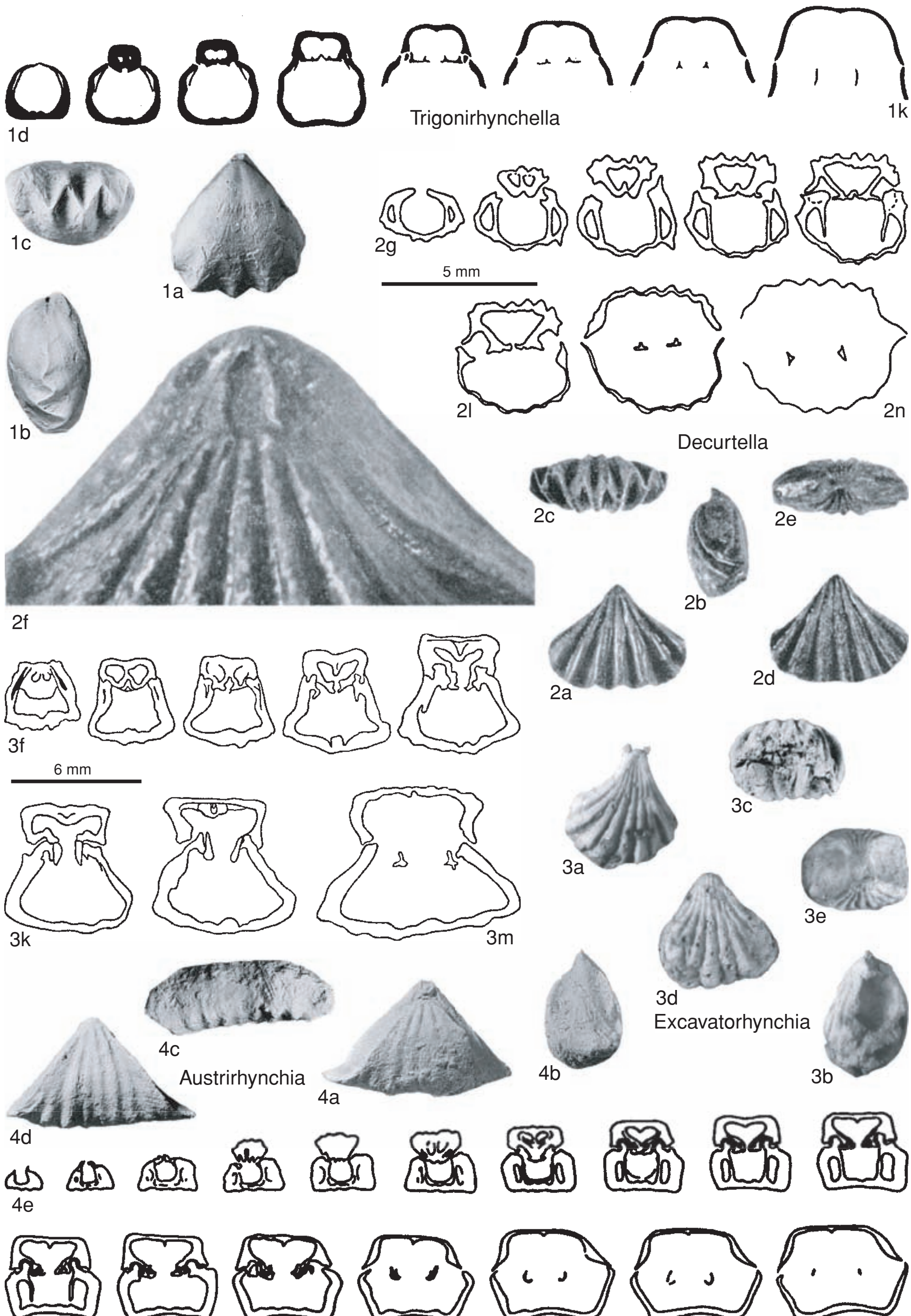

FIG. 854. Austrirhynchiidae (p. 1252).

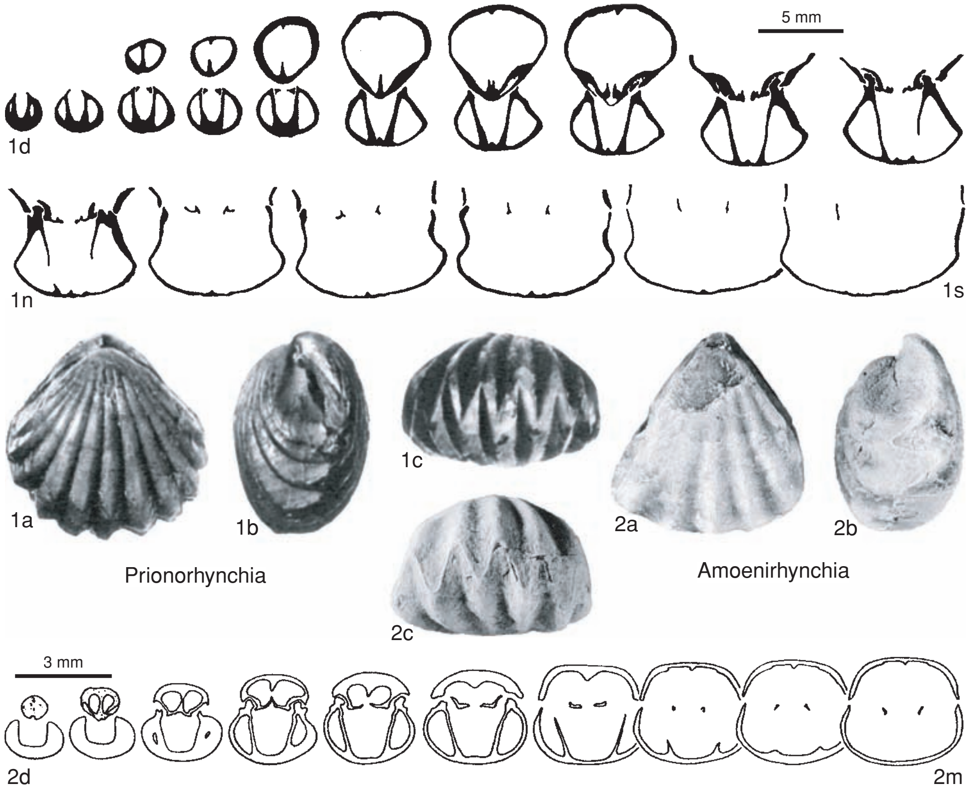

FIG. 855. Prionorhynchiidae (p. 1252–1253).

hinge teeth may be crenulated; crura raduliform to possibly incipiently canaliform. *Lower Jurassic (?Hettangian, Sinemurian)–Middle Jurassic (Aalenian):* England, France, Germany, Austria, Italy, Spain, Switzerland, Slovakia, Hungary, Yugoslavia, Greece, Bulgaria, Morocco, Algeria, Anatolia, Caucasus, Thailand, Indonesia (Seran, ?Timor), Argentina, ?New Zealand.——FIG. 855,*1a–s.* **P. serrata* (J. de C. SOWERBY), upper Pliensbachian, Dorset, England; *a–c,* holotype, dorsal, lateral, anterior views, BMNH B.61517, ×1; *d–s,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.9, 1.0, 1.1, 1.6, 1.8, 2.0, 2.3, 2.6, 2.9, 3.5, 4.1, 4.3, 4.7, 5.3, BMNH B.33333 (Ager, 1956).

Amoenirhynchia SIBLÍK, 1986, p. 23 [**Rhynchonella seydelii* BITTNER, 1891, p. 56; OD]. Small, triangular, moderately equibiconvex, costae low, rounded, developed only anteriorly, no distinct sulcus and fold, anterior commissure rectimarginate or incipiently uniplicate; beak suberect, ridges distinct, planareas well developed. Dental plates long, subparallel to ventrally convergent, pedicle collar absent; septum low, septalium short, present only posteriorly; hinge teeth without crenulation; crura raduliform to incipiently flared. *?Middle Triassic, Upper Triassic:* Alps, Carpathians.——FIG. 855,*2a–m.* **A. seydelii* (BITTNER), Carnian, Slovakia; *a–c,* dorsal, lateral, anterior views, SNM Z 19428, ×3; *d–m,* transverse serial sections, distances in mm from ventral umbo, 0.15, 0.45, 0.95, 1.55, 2.3, 3.8, 4.85, 6.0, 7.3, 8.7 (Siblík, 1986).

Lokutella VÖRÖS, 1983, p. 6 [**Rhynchonella palmaeformis* HAAS, 1912, p. 232; OD]. Small to medium size, trigonal to securiform; nearly equibiconvex; fold and sulcus absent; anterior commissure straight but forming wide sinus; planareas well developed, generally concave; costae few, usually strong, after variable posterior smooth stage; beak small, erect to slightly incurved. Strong subparallel dental plates and crenulated teeth; dorsal median septum long but low; hinge plates fused, forming septalium; crura distally crescentic and outwardly convex. *Lower Jurassic (upper Sinemurian–Pliensbachian):* Sicily, Apennines, southern Alps, Hungary, ?Greece.——FIG. 856,*1a–l.* **L. palmaeformis* (HAAS), Pliensbachian, Kericser, Hungary; *a–e,* dorsal, lateral, anterior, ventral, posterior views, HNHMB M.98.3, ×1.5 (new); *f–l,* transverse serial sections, distances in mm from ventral umbo, 0.3, 1.0, 1.3, 1.8, 2.4, 2.8, 3.1, HGI J.9185 (Vörös, 1983).

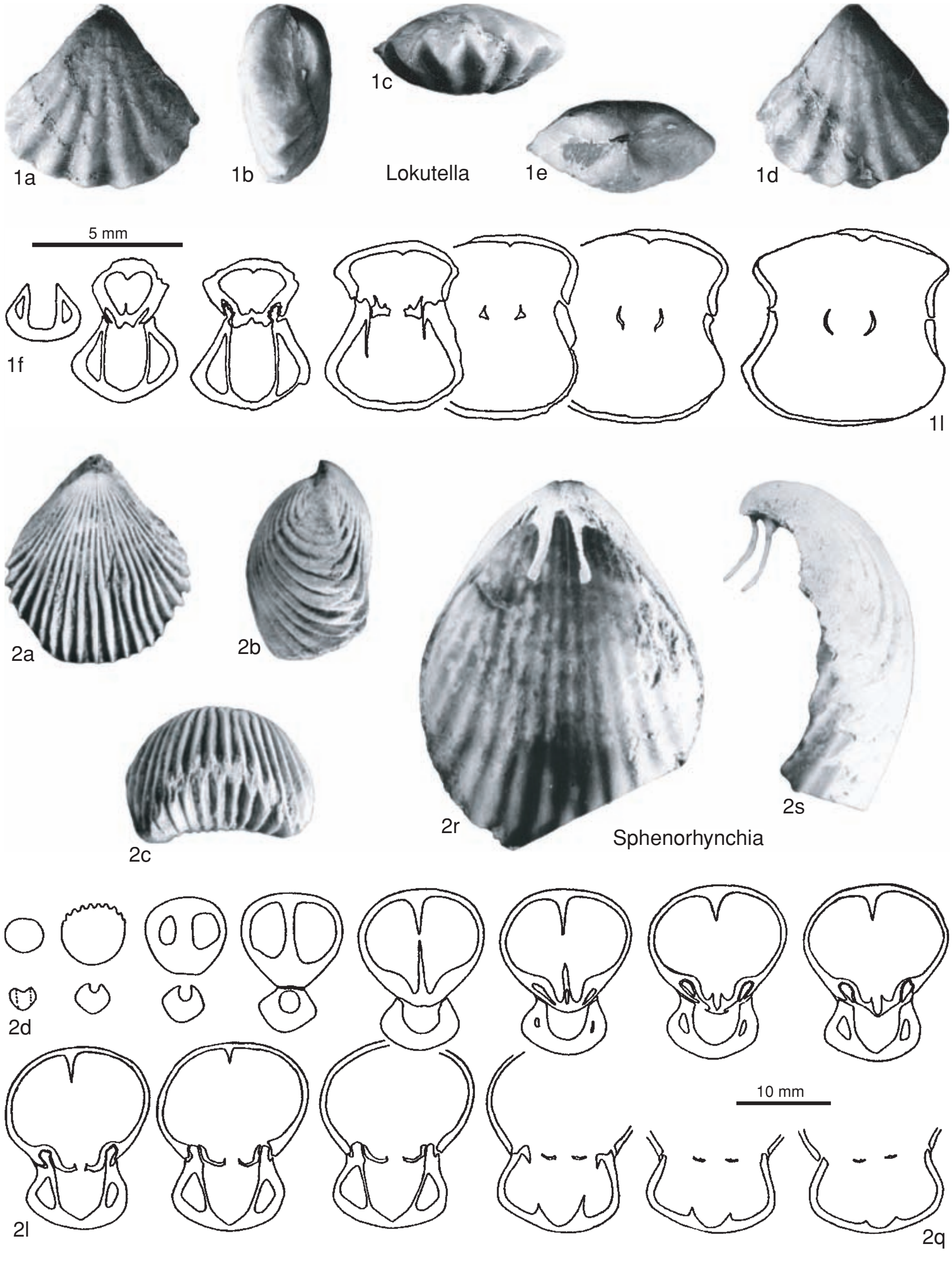

FIG. 856. Prionorhynchiidae (p. 1254–1256).

?Sphenorhynchia BUCKMAN, 1918, p. 30 [**Terebratula plicatella* J. de C. SOWERBY, 1825 in 1823–1825, p. 167; OD] [=*Sphenorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, globose, equibiconvex to dorsibiconvex; elongate oval to subtrigonal; wedge shaped due to well-developed, concave planareas; squama and glotta junction dorsoconvex; uniplication arcuate, but dorsal fold rarely or not at all raised; flattish ventral valve may bear ill-defined, shallow, wide sulcus anteriorly; costae numerous, prominent, narrow, sharp, and sometimes dichotomous; beak small, massive, suberect to erect, rarely incurved; conjunct deltidial plates. Dental plates ventrally convergent to subparallel, teeth massive, crenulated; oblique hinge plates; dorsal median septum strong, septalium narrow; raduliform crura, becoming dorsally concave distally. *Middle Jurassic (Bajocian–Callovian):* England, France, Germany, Switzerland, Austria, Poland, Romania, Bulgaria, Crimea, Caucasus, ?Arabia, ?Afghanistan, China, Morocco, Algeria, ?Madagascar.——FIG. 856,*2a–q.* **S. plicatella* (J. de C. SOWERBY), upper Bajocian; *a–c,* dorsal, lateral, anterior, Dorset, England, USNM 88733a, ×1 (Shi & Grant, 1993); *d–q,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.9, 1.3, 1.9, 2.8, 3.1, 3.5, 3.7, 3.9, 4.3, 4.5, 5.0, 5.2, 5.5, Calvados, France, FSL 49413 (Alméras, 1980).——FIG. 856,*2r–s. S. matisconensis* (LISSAJOUS), upper Bajocian, Monsard, France; *r,* dorsal interior showing variant of raduliform crura; *s,* same, oblique lateral view, USNM 429399, ×1.8 (Shi & Grant, 1993).

WELLERELLOIDEA

NORMAN M. SAVAGE,[1] MIGUEL O. MANCEÑIDO,[2] ELLIS F. OWEN,[3] A. S. DAGYS,[4] and SUN DONG-LI[5]

[[1]University of Oregon; [2]La Plata Natural Sciences Museum, Argentina; [3]formerly of The Natural History Museum; [4]deceased; and [5]Nanjing Institute of Geology and Palaeontology]

Superfamily WELLERELLOIDEA Licharew, 1956

[*nom. correct.* SAVAGE, 1996, p. 255, *pro* Wellerellacea XU & LIU, 1983, p. 73, *nom. transl. ex* Wellerellidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 125]

Rhynchonellida with subcircular to subpentagonal outline; dorsal fold and ventral sulcus strong to weak; costae usually simple; umbones commonly smooth; delthyrium with or without deltidial plates. Dental plates and dorsal median septum variously developed; hinge plates undivided, notched, or totally divided; septalium occasionally present in Mesozoic genera; cardinal process absent; crura falciform in Paleozoic genera, may be hamiform in Mesozoic genera. *Lower Carboniferous (Tournaisian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Family WELLERELLIDAE Licharew, 1956

[Wellerellidae LICHAREW in RZHONSNITSKAIA, 1956a, p. 125]

[Materials prepared by NORMAN M. SAVAGE & MIGUEL O. MANCEÑIDO]

Wellerelloidea with mostly subpentagonal outline; costae usually coarse. Dental plates often short and vertical, occasionally convergent ventrally, rarely absent. *Upper Carboniferous (Westphalian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Subfamily WELLERELLINAE Licharew, 1956

[Wellerellinae LICHAREW in RZHONSNITSKAIA, 1956a, p. 125]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with short dental plates and costae arising anterior of beaks. Delthyrium with conjunct deltidial plates; dorsal median septum present; hinge plates usually undivided. *Upper Carboniferous (Westphalian)–Upper Permian (Kazanian).*

Wellerella DUNBAR & CONDRA, 1932, p. 286 [**W. tetrahedra;* OD] [=*Changyangrhynchus* YANG, 1984, p. 229 (type, *C. nantanelloides,* OD)]. Small; subcircular to subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak straight to suberect; deltidial plates conjunct anteriorly, leaving small oval submesothyrid foramen. Fold and sulcus strong; commissure uniplicate anteriorly; tongue high, wide, usually triserrate. Costae coarse, from midlength; umbones smooth. Dental plates short, vertical; ventral muscle field elongate oval, extending to one-third valve length. Hinge plates undivided; dorsal median septum short, low; dorsal muscle field small, subcircular, with median myophragm; crura laterally flattened, twisted, dorsally carinate. *Upper Carboniferous (Stephanian)–Upper Permian (Kazanian):* cosmopolitan.——FIG. 857,*1a–e.* **W. tetrahedra,* middle Pennsylvanian, Marmaton Group, Missouri, USA; *a–b,* anterior and posterior views of different paratypes, ×2; *c–e,* paratype, serial sections of posterior (Dunbar & Condra, 1932).——FIG. 857,*1f–i. W. girtyi girtyi* COOPER & GRANT, Guadalupian, Word Formation, Glass Mountains, Texas, USA; *f–*

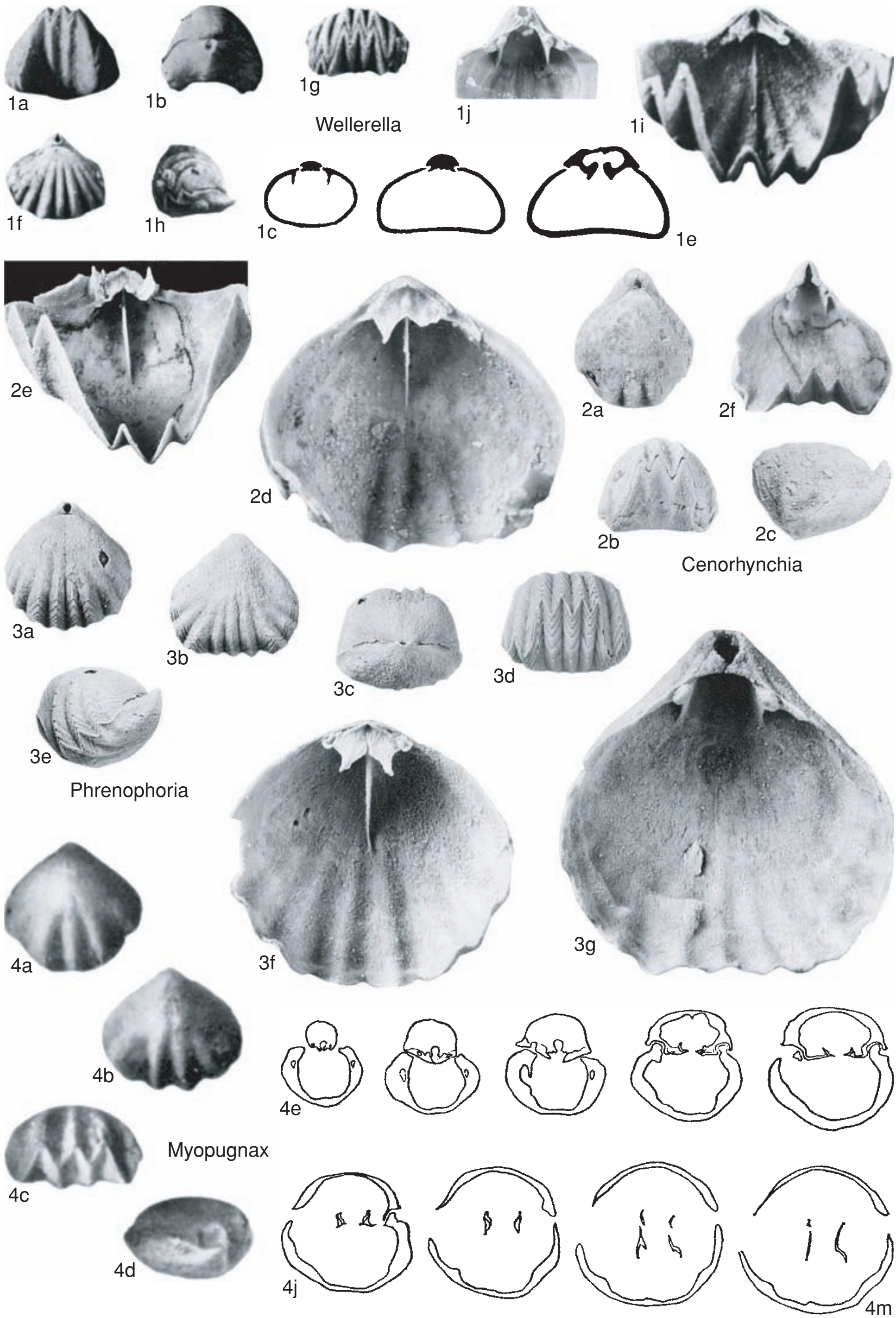

FIG. 857. Wellerellidae (p. 1256–1258).

h, paratype, dorsal, anterior, and lateral views, ×1; *i,* paratype, interior view of tilted dorsal valve, ×3 (Cooper & Grant, 1976a).——Fig. 857,*1j. W. girtyi seorsa* Cooper & Grant, Guadalupian, Cherry Canyon Formation, Guadalupe Mountains, Texas, USA; interior of ventral valve posterior, ×3 (Cooper & Grant, 1976a).

Cenorhynchia Cooper & Grant, 1976a, p. 1986 [**C. fracida;* OD]. Small; elongate subpentagonal outline and dorsibiconvex profile. Beak erect; delthyrium ovate; deltidial plates incipient. Fold and sulcus weak to moderate, from midlength; anterior commissure uniplicate; tongue high, biserrate to triserrate. Costae coarse, restricted to anterior margin and fold and sulcus. Dental plates short, vertical. Dorsal median septum high, long, extending to one-third valve length and supporting undivided hinge plates posteriorly; dorsal muscle field suboval, divided by myophragm; crura laterally flattened, concave medially, dorsally carinate. *Lower Permian (Sakmarian–Kungurian):* USA.——Fig. 857,*2a–f.* **C. fracida,* lower Guadalupian, Wordian, Word Formation, Glass Mountains, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* paratype, ventral view of dorsal valve interior; *e,* paratype, anterior view of dorsal valve interior, ×4; *f,* paratype, dorsal view of ventral valve interior, ×1.5 (Cooper & Grant, 1976a).

Lissella Campbell, 1961, p. 452 [**L. booralensis;* OD]. Small; subcircular to elongate oval outline; biconvex profile. Foramen large, circular; deltidial plates narrow, short. Fold and sulcus weak, from midlength; anterior commissure uniplicate. Plicae rounded, from one-third valve length, 2 to 4 on fold, 1 to 3 in sulcus, weakly developed on flanks. Dental plates thin, concave medially. Dorsal median septum long, thick, high; appearing not to support hinge plates. Hinge plates undivided, with low median ridge on upper surface; dorsal muscle field elongate oval; crural bases triangular in section. *Upper Carboniferous (Westphalian):* Australia (New South Wales). ——Fig. 858,*3a–g.* **L. booralensis,* middle Westphalian, Booral Formation, Newcastle, Booral; *a,* holotype, dorsal internal mold, ×2; *b,* posterior view of steinkern, ×2; *c–g,* serial transverse sections, ×3 (Campbell, 1961).

Myopugnax Glushenko, 1975, p. 96 [**M. priva;* OD]. Small; subcircular to subpentagonal outline; biconvex profile. Beak suberect to erect; foramen small. Fold and sulcus low, wide, from midlength; anterior commissure uniplicate, typically triserrate. Dental plates short, buried in callus; ventral muscle field well impressed. Dorsal median septum and septalium absent; hinge plates divided; crural bases triangular in section; crura laterally flattened, strongly curved ventrally, tips bearing V-shaped grooves. *Lower Permian (Sakmarian–Artinskian):* Russia (Donetz basin).——Fig. 857,*4a–m.* **M. priva,* Slaviansk Series, Iziumsk; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×3; *e–m,* serial sections 0.45, 0.55, 0.70, 1.00, 1.15, 1.4, 1.7, 2.0, 2.05 mm from posterior, ×6 (Glushenko, 1975).

Phrenophoria Cooper & Grant, 1969, p. 12 [**P. subcarinata;* OD]. Subcircular to subpentagonal outline and dorsibiconvex, anteriorly inflated profile; anterior and lateral margins steep. Beak straight to erect; deltidial plates conjunct anteriorly, foramen small, oval, submesothyrid to mesothyrid. Fold and sulcus poorly defined; anterior commissure uniplicate; tongue wide, trapezoid, serrate. Costae angular, from midlength, umbones smooth. Dental plates short, vertical; ventral muscle field cordate. Dorsal median septum high posteriorly, low anteriorly, supporting undivided hinge plates; dorsal muscle field elongate oval, divided by septum; crura ventrally curved, anteriorly divergent, with dorsal carina. *Lower Permian (Sakmarian–Kungurian):* USA.——Fig. 857,*3a–g.* **P. subcarinata,* lower Guadalupian, Wordian, Word Formation, Glass Mountains, Texas; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×1; *f–g,* paratype, ventral view of dorsal valve interior, dorsal view of ventral valve interior, ×3 (Cooper & Grant, 1976a).

Plekonella Campbell, 1953, p. 17 [**P. acuta;* OD]. Subpentagonal to transversely oval outline and biconvex profile. Beak suberect. Fold and sulcus moderately strong, from umbones; anterior commissure uniplicate; tongue low, rounded, serrate. Costae coarse, simple, from beaks, on fold, sulcus, flanks. Dental plates short, vertical. Hinge plates undivided, bearing low median ridge; dorsal median septum low, stout, extending to midlength. *Upper Carboniferous (Stephanian)–Lower Permian (Kungurian):* eastern Australia, New Zealand.——Fig. 858,*2a–i.* **P. acuta,* Artinskian–Kungurian, Ingelara Formation, Queensland, eastern Australia; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×1; *e–i,* serial sections from several specimens (Campbell, 1953).

Tautosia Cooper & Grant, 1969, p. 14 [**T. fastigiata;* OD]. Transversely triangular outline and dorsibiconvex profile; apical angle acute; lateral slopes gentle. Beak straight; deltidial plates conjunct; foramen elongate, mesothyrid. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue wide, low, trapezoid, dentate. Costae strong, from one-third valve length, simple; umbones smooth. Dental plates short, vertical; ventral muscle field elongate oval. Hinge plates undivided; dorsal median septum high, supporting hinge plates; dorsal muscle field subcircular, extending to midlength; crura twisted, dorsally carinate, curved ventrally. *Permian (Sakmarian–Kungurian):* USA.——Fig. 858,*1a–h.* **T. fastigiata,* Leonardian, Cathedral Mountain Formation, Glass Mountains, Cathedral Mountain, Texas; *a–d,* holotype, dorsal, ventral, anterior, and posterior views; *e,* paratype, lateral view, ×1; *f,* anterior view of interior, ×2; *g,* interior of ventral valve, ×1.5; *h,* view of foramen, ×3 (Cooper & Grant, 1976a).

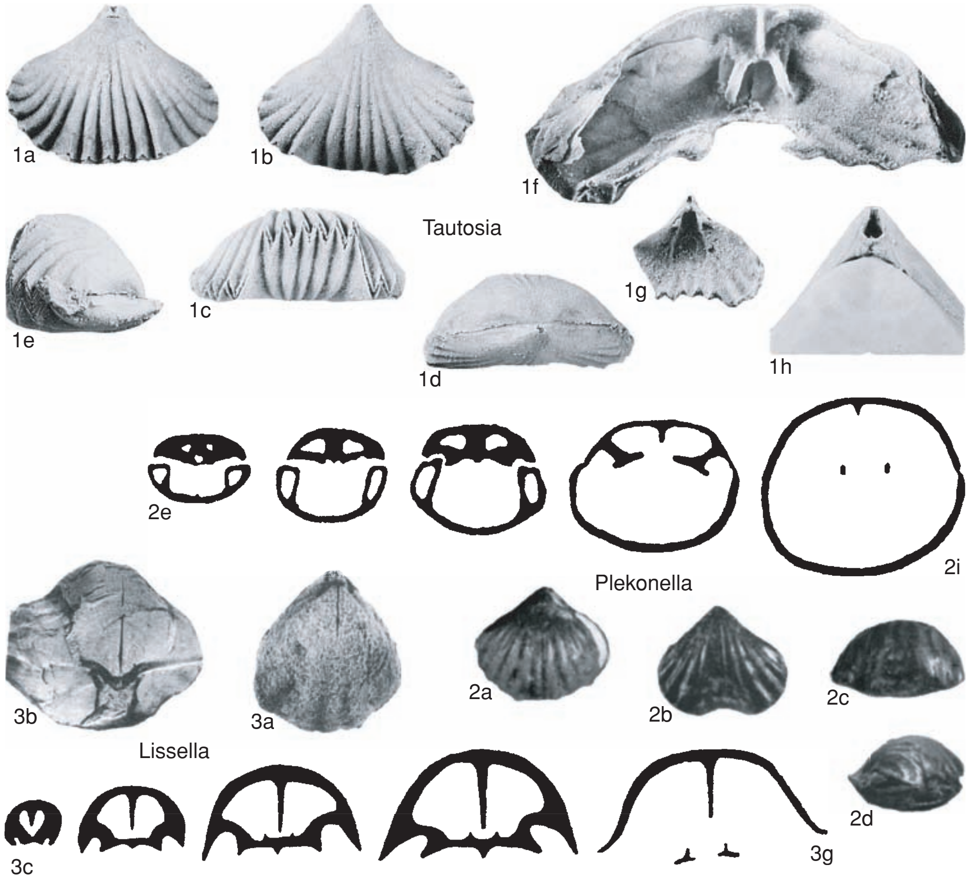

FIG. 858. Wellerellidae (p. 1258).

Subfamily TRICORIINAE Cooper & Grant, 1976

[Tricoriinae COOPER & GRANT, 1976a, p. 2077]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with completely costate shells, rectimarginate anterior commissure, obsolete dental plates, and high dorsal median septum. *Lower Permian (Asselian).*

Tricoria COOPER & GRANT, 1976a, p. 1945 [**T. hirpex;* OD]. Small; outline transverse and subpentagonal; profile subequally biconvex. Beak erect to incurved; delthyrium open, without deltidial plates. Fold and sulcus weak to absent; anterior commissure rectimarginate. Costae fine, simple, arising at beaks. Dental plates weak to obsolete; ventral muscle field triangular. Dorsal median septum high; septalium short; crura laterally compressed; sharply curved ventrally. *Lower Permian (Asselian):* USA (Texas). ——FIG. 859,*1a–f.* **T. hirpex,* Skinner Ranch Formation, Glass Mountains; *a–d,* holotype, dorsal, anterior, posterior, and lateral views, ×1; *e,* ventral interior; *f,* dorsal interior, ×4 (Cooper & Grant, 1976a).

Subfamily NIPPONIRHYNCHIINAE Savage, 1996

[Nipponirhynchiinae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with costae flattened anteriorly; marginal spines developed from intertroughs. Dorsal median septum high; septalium well developed. *Lower Permian (Sakmarian).*

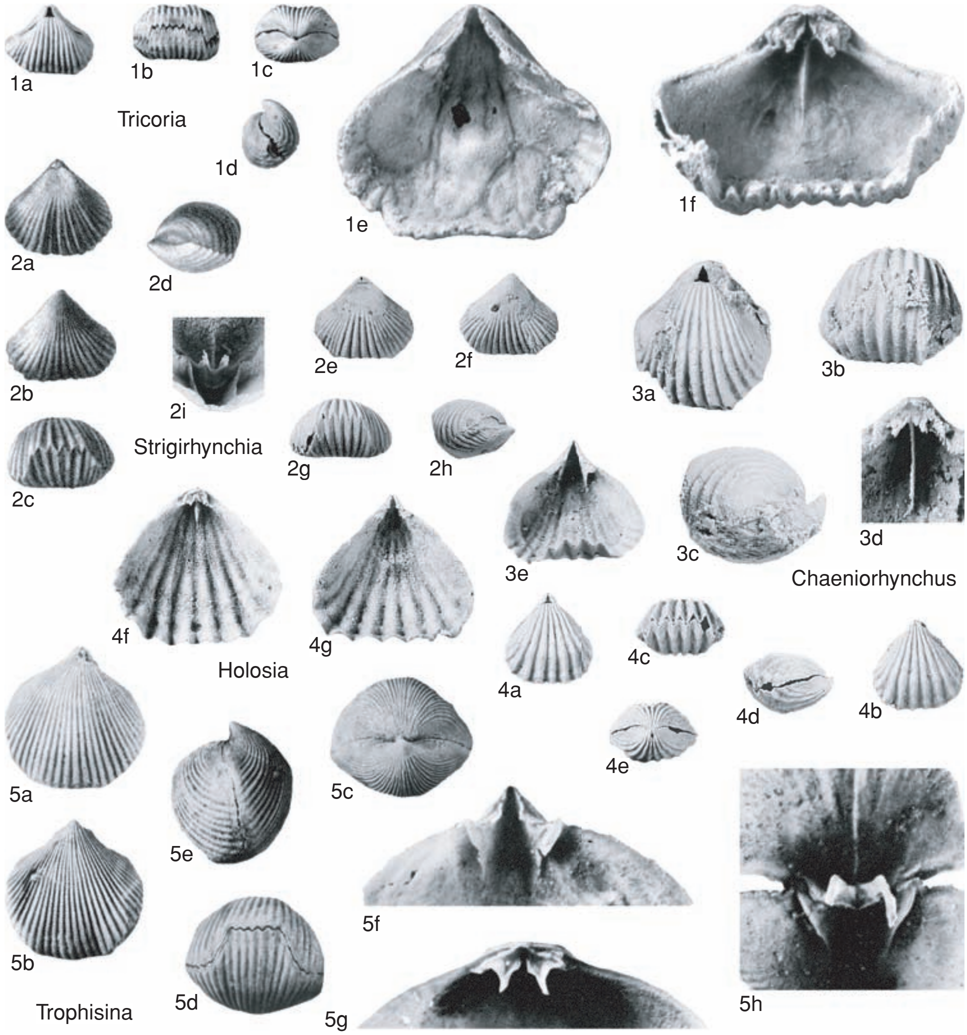

FIG. 859. Wellerellidae (p. 1259–1263).

Nipponirhynchia YANAGIDA & NISHIKAWA, 1984, p. 163 [**N. shutoi;* OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak suberect. Fold and sulcus wide, rounded, from umbones; tongue broad, rounded. Costae numerous, simple, subangular, arising at beaks, with deep intertroughs; costal crests flattened and grooved on *paries geniculatus;* intertroughs extended into marginal spines. Dental plates prominent, ventrally convergent. Dorsal median septum thick, long; septalium deep, wide; hinge plates divided anterior of septalium; crural bases triangular in section. *Lower Permian (Sakmarian):* Japan.——FIG. 860,*1a–h.* **N. shutoi,* holotype, Yaikian, Kawai Limestone, Hiroshima, Kawai, Joge; *a–d,* dorsal, ventral, anterior, and lateral views, ×1.5; *e–k,* serial sections, ×2.3 (Yanagida & Nishikawa, 1984).

Subfamily UNCINUNELLININAE Savage, 1996

[Uncinunellininae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with costae flattened anteriorly and marginal spines developed from intertroughs. Median septum low to absent; septalium absent. *Permian (Sakmarian–Tatarian).*

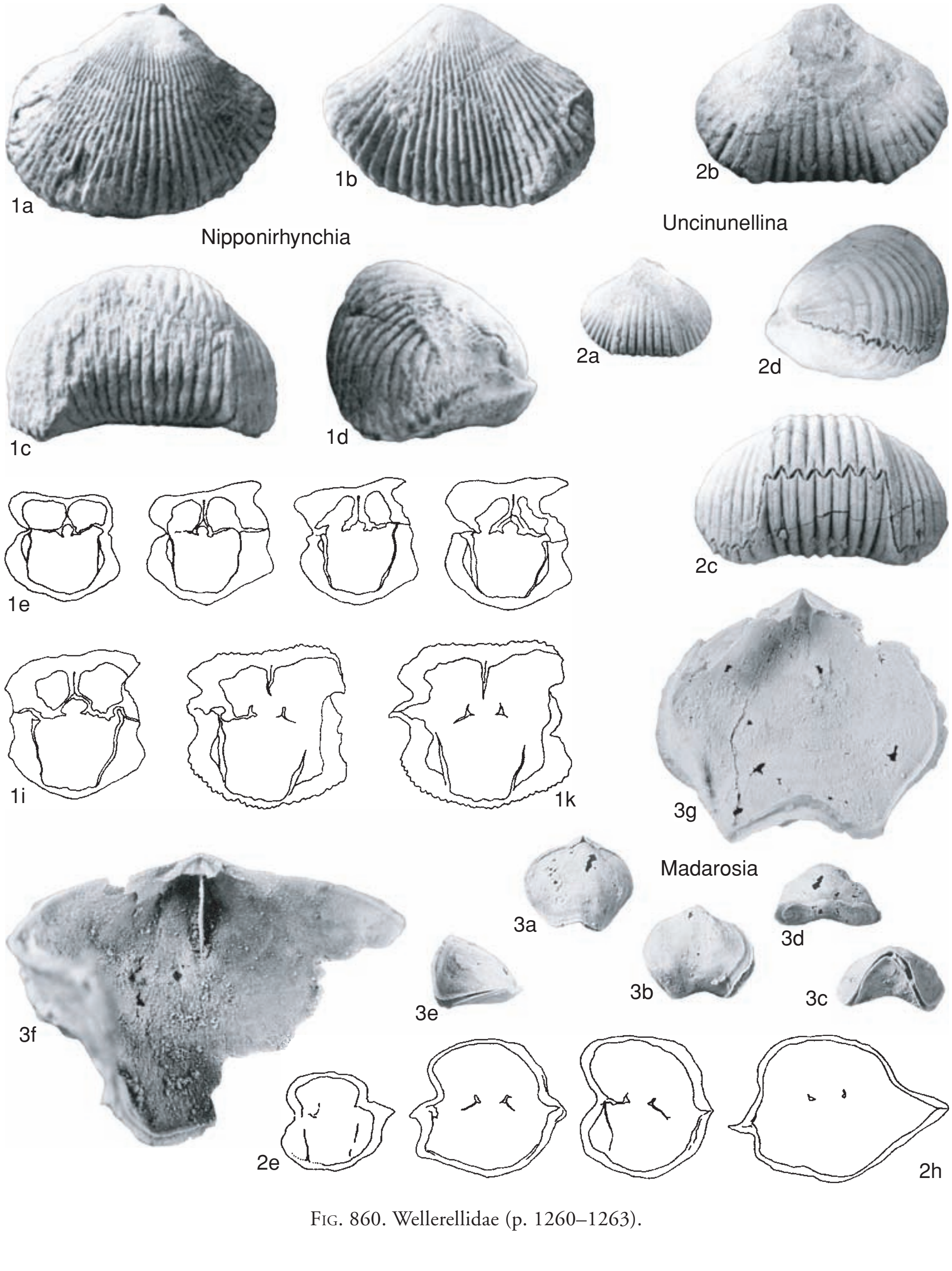

FIG. 860. Wellerellidae (p. 1260–1263).

Uncinunellina GRABAU, 1932a, p. 100 [**Uncinulus theobaldi* WAAGEN, 1883, p. 425; OD]. Transversely ovate outline and dorsibiconvex profile. Beak sharp, straight to suberect; foramen small; deltidial plates small, disjunct. Fold and sulcus low, wide, flat, arising at midlength; tongue wide, trapezoid. Umbones generally smooth. Costae low, simple, rounded, with narrow intertroughs, crests flattened and grooved on *paries geniculatus;* intertroughs extended at anterior and lateral margins to form spines that insert into holes near margin of opposite valve. Dental plates short, vertical to ventrally convergent; ventral muscle field weakly impressed. Dorsal median ridge low to absent; hinge plates thin, divided; crura ventrally curved. *Permian (Sakmarian–Tatarian):* Pakistan, India, Thailand, China, Mongolia, Japan, Iran, Fergana, Pamir, Urals, Ukraine, Mexico.——FIG. 860,*2a–d.* **U. theobaldi* (WAAGEN), Kungurian, Wargal Limestone, Kalabagh Member, Salt Range, Pakistan; *a,* topotype, dorsal view, ×1; *b–d,* topotype, ventral, anterior, and lateral views, ×1.8 (Grant, 1976). ——FIG. 860,*2e–h. U. hayasakai* YANAGIDA & NISHIKAWA, Sakmarian, Yaikian, Kawai Limestone, Hiroshima, Kawai, Joge, Japan; paratype, serial sections, ×3 (Yanagida & Nishikawa, 1984).

Subfamily TROPHISININAE Cooper & Grant, 1976

[Trophisininae COOPER & GRANT, 1976a, p. 2077]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with finely costate shells and strongly convergent dental plates. *Lower Permian (Artinskian).*

Trophisina COOPER & GRANT, 1976a, p. 2078 [**T. fenaria;* OD]. Subcircular outline and strongly biconvex to globose profile. Beak suberect; foramen large, ovate; delthyrium with disjunct deltidial plates. Fold and sulcus weak; anterior commissure low, trapezoid. Costae numerous, simple, arising at beaks. Dental plates short, ventrally convergent. Hinge plates undivided; dorsal septum short; septalium wide; crura slender, ventrally curved, concave medially. *Lower Permian (Artinskian):* USA (Texas).——FIG. 859,*5a–h.* **T. fenaria,* lower Cathedral Mountain Formation, Glass Mountains, Split Tank; *a–e,* holotype, dorsal, ventral, posterior, anterior, and lateral views, ×2; *f,* paratype, interior of ventral valve posterior, ×5; *g–h,* paratype, interior of dorsal valve posterior, interior of conjoined valves, ×6 (Cooper & Grant, 1976a).

Subfamily STRIGIRHYNCHIINAE Cooper & Grant, 1976

[Strigirhynchiinae COOPER & GRANT, 1976a, p. 1996]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with costae arising at beaks; dental plates short; dorsal median septum high; hinge plates usually undivided. *Permian (Artinskian–Kazanian).*

Strigirhynchia COOPER & GRANT, 1969, p. 14 [**Rhynchonella? indentata* SHUMARD, 1860b, p. 393; OD]. Outline subtriangular to subpentagonal and profile equibiconvex. Beak straight to suberect; deltidial plates conjunct anteriorly, foramen small, oval. Fold and sulcus weak, dorsal umbone flattened or concave; anterior commissure uniplicate; tongue low, trapezoid. Costae simple, extending from beaks. Dental plates short, vertical; ventral muscle field elongate-oval. Dorsal median septum high, bisecting posterior half of muscle field and supporting undivided hinge plates; dorsal muscle field elongate-oval; crura diverging anteriorly and curving ventrally, each with dorsal carina. *Upper Permian (Kungurian–Kazanian):* USA.——FIG. 859,*2a–i.* **S. indentata* (SHUMARD), Capitan Group, Guadalupe Mountains, Texas; *a–d,* dorsal, ventral, anterior, and lateral views, ×1 (Girty, 1909); *e–h,* dorsal, ventral, anterior, and lateral views, ×1; *i,* interior of conjunct specimen showing cardinalia and dental plates, ×3 (Cooper & Grant, 1976a).

Chaeniorhynchus COOPER & GRANT, 1976a, p. 1999 [**C. inauris;* OD]. Small; outline subtriangular to subpentagonal; profile dorsibiconvex; greatest thickness at midlength. Beak suberect to erect; delthyrium open, no deltidial plates. Fold and sulcus weak to moderate; anterior commissure uniplicate; tongue moderate, trapezoid, serrate. Costae fine to medium, extending from beaks. Dental plates strong, vertical to slightly convergent ventrally; ventral muscle field elongate oval. Dorsal median septum high, supporting undivided hinge plates; dorsal muscle field small, oval, expanding anteriorly; crura divergent anteriorly and ventrally, dorsally carinate. *Lower Permian (Artinskian):* USA.——FIG. 859,*3a–d.* **C. inauris,* Cathedral Mountain Formation, Glass Mountains, Split Tank, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* interior of posterior of dorsal valve, ×4 (Cooper & Grant, 1976a).——FIG. 859,*3e. C. salutare* COOPER & GRANT, upper Leonardian, Road Canyon Formation, Glass Mountains, Texas; interior of ventral valve, ×2 (Cooper & Grant, 1976a).

Holosia COOPER & GRANT, 1976a, p. 1971 [**H. regularis;* OD]. Small; subtriangular outline and equibiconvex profile; anterior and lateral margins subvertical. Beak straight; deltidial plates conjunct anteriorly, foramen oval mesothyrid to submesothyrid. Fold and sulcus weak; anterior commissure weakly uniplicate; tongue low, wide, serrate. Costae medium to fine, simple, rounded, arising at beaks. Dental plates short, vertical, close to walls; ventral muscle field small, ovate. Hinge plates small, undivided; dorsal median septum high posteriorly where it supports hinge plate. *Upper Permian (Kungurian–Kazanian):* USA.——FIG. 859,*4a–g.* **H. regularis,* holotype, upper Guadalupian, Bell Canyon Formation, Guadalupe Mountains, Texas; *a–e,* dorsal, ventral, anterior, lateral, and posterior views, ×1; *f,* interior of dorsal valve; *g,* interior of ventral valve, ×2 (Cooper & Grant, 1976a).

Subfamily MADAROSIINAE Savage, 1996

[Madarosiinae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Wellerellidae with surface smooth, anterior emarginate, dorsal median septum high, and delthyrium open. *Upper Permian (Kungurian–Kazanian).*

Madarosia Cooper & Grant, 1976a, p. 2002 [**M. anterolamellata;* OD]. Transversely ovate to subpentagonal outline with emarginate anterior and anterolateral borders; convexiplane to convexiconcave form, inflated anteriorly. Beak suberect; delthyrium open, deltidial plates absent or incipient. Fold and sulcus weak posteriorly, strong anteriorly; anterior commissure strongly uniplicate, rounded. Surface smooth apart from concentric lamellae. Dental plates short, confining narrow delthyrial chamber; ventral muscle field elongate oval. Dorsal median septum high, supporting small undivided hinge plates; crura laterally compressed, diverging anteriorly and ventrally, dorsally carinate. *Upper Permian (Kungurian–Kazanian):* USA.——Fig. 860,*3a–g.* **M. anterolamellata,* upper Guadalupian, Bell Canyon Formation, Guadalupe Mountains, Texas; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* paratype, interior of dorsal valve, ×4; *g,* paratype, interior of ventral valve, ×3 (Cooper & Grant, 1976a).

Subfamily CIRPINAE Ager, 1965

[Cirpinae Ager, 1965, p. 605] [=Cipridae Ovcharenko, 1983, p. 50, *nom. nud.*]

[Materials prepared by Miguel O. Manceñido, Ellis F. Owen, & A. S. Dagys]

Multicostate Wellerellidae, hinge plates fused; dorsal median septum usually very much reduced; beak generally small and incurved, with well-developed planareas and small foramen. Double deltidial plates thick and distinctive; crura hamiform where known; septalium usually absent. *Middle Triassic (?Anisian), Upper Triassic (Carnian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Cirpa de Gregorio, 1930a, p. 40 [**Rhynchonella (C.) primitiva;* OD; =*R. briseis* Gemmellaro, 1874, p. 97, subj.] [=*Cipra* Makridin in Sarycheva, 1960, p. 255, *nom. null.*]. Medium size, subtriangular to subpentagonal, depressed dorsibiconvex, rectangular and flattened anteriorly; with low fold, flattopped uniplication, and a few strong, sharp costae; beak small, flattened planareas with diffuse boundaries. Hinge plates flat, fused; dorsal median septum very short; crenulated teeth; crura hamiform. *Lower Jurassic (Sinemurian–Pliensbachian, ?Toarcian):* England, France, Germany, Austria, Italy, Greece, Switzerland, Slovakia, Dinarids, Hungary, Algeria, Turkey (Anatolia), ?Himalayas, Indonesia (Seram), ?New Zealand, Argentina.——Fig. 861,*1a–m.* **C. briseis* (Gemmellaro), middle Lias, Sicily, Italy; *a–e,* dorsal, lateral, anterior, ventral, posterior views, ×1.5 (Benigni, 1978); *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.2, 1.4, 1.8, 2.0, 2.4, 3.0, 3.4, BMNH B.167748 (Ager, 1959a).

Apertirhynchella Siblík, 1986, p. 26 [**A. triplex;* OD]. Small to medium size, subpentagonal, sulcus and fold distinct although low, anterior commissure uniplicate, blunt costae only in fold and sinus, lateral parts of valves smooth; beak short, suberect, ridges well developed. Dental plates very short, fused to lateral walls, pedicle collar absent; no septum, outer hinge plates broad, horizontal in section, inner hinge plate very short; crura hamiform. *Middle Triassic (?Anisian), Upper Triassic:* Dinarids, Transdanubian ranges (Carnian), Alps, Carpathians, Germany.——Fig. 861,*3a–k.* **A. triplex,* Carnian, southeastern Slovakia; *a–c,* holotype, dorsal, lateral, anterior views, SNM Z19430, ×2; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.3, 0.75, 1.2, 1.4, 1.7, 2.4, 2.8 (Siblík, 1986).

Calcirhynchia Buckman, 1918, p. 30 [**C. calcaria;* OD] [=*Calcirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, subtrigonal to subpentagonal or pyriform, globose to depressed subequibiconvex; with wide, flattopped uniplication, low fold and many sharp costae (2 to 7 on fold), no posterior smooth stage; beak small, incurved. Dental plates thin and subparallel, small crenulated teeth; dorsal median septum very short; crura hamiform. *Upper Triassic (Norian)–Lower Jurassic (Sinemurian, ?Pliensbachian):* Germany, Austria, Slovakia, Hungary, Romania, *Norian–Rhaetian;* England, France, Luxemburg, Spain, Germany, Switzerland, Austria, Italy, Sicily, Dinarids, Hungary, Greece, ?Algeria, Turkey, ?Iran, *Hettangian–Sinemurian, ?Pliensbachian.*——Fig. 862,*3a–k.* **C. calcaria,* Hettangian–Sinemurian, England; *a–c,* holotype, dorsal, lateral, anterior, GSM 31947, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 0.8, 0.9, 1.2, 1.35, 1.7, 2.3, personal collection, Derek Ager, J.107/1 (Ager, 1962).

Euxinella Moiseev, 1936, p. 41, *non* Drensky, 1938, Arachnida, *nec* Nordsieck, 1973, Gastropoda [**E. iatirgvantaensis, error pro E. iatirgvartaensis;* OD]. Small, rounded or rounded-pentagonal, globose, multicostate, strong uniplication, distinct fold absent; beak short, incurved, ridges rounded, foramen hypothyrid; deltidial plates double, conjunct. Dental plates subparallel, pedicle collar feeble; septum low, short, outer hinge plates broad, equal to inner hinge plate, horizontal in section, crura hamiform. [The species was originally described and illustrated (Moiseev, 1936, p. 42–43) as *iatirgvartaensis,* but on page 41, which fixing the species, the name was recorded as “genotip *Euxinella iatirgvantaensis* nov. sp.” Subsequent usage is *iatirgvartaensis,* as in the Caucasian locality Iatirgvarta.] *Upper Triassic (Norian–Rhaetian):* Alps, Carpathians, Balkans, Romania, Crimea, northwestern Caucasus, Anatolia, Pamirs, Tibet.——Fig. 862,*4a–r.* **E. iatirgvartaensis,* Rhaetian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, TsGM 1/4801, ×1; *d–r,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.4, 0.6, 0.9,

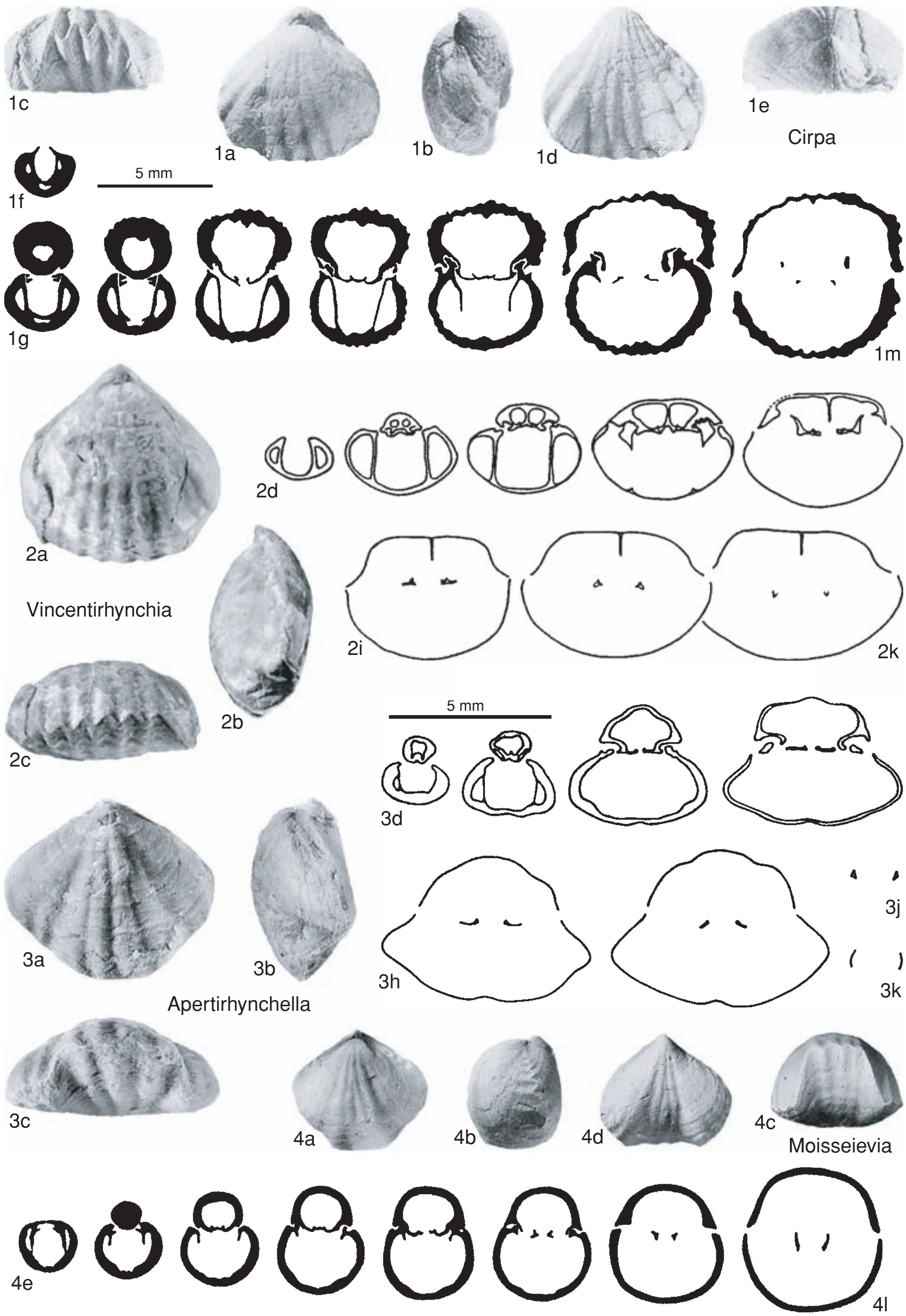

FIG. 861. Wellerellidae (p. 1263–1266).

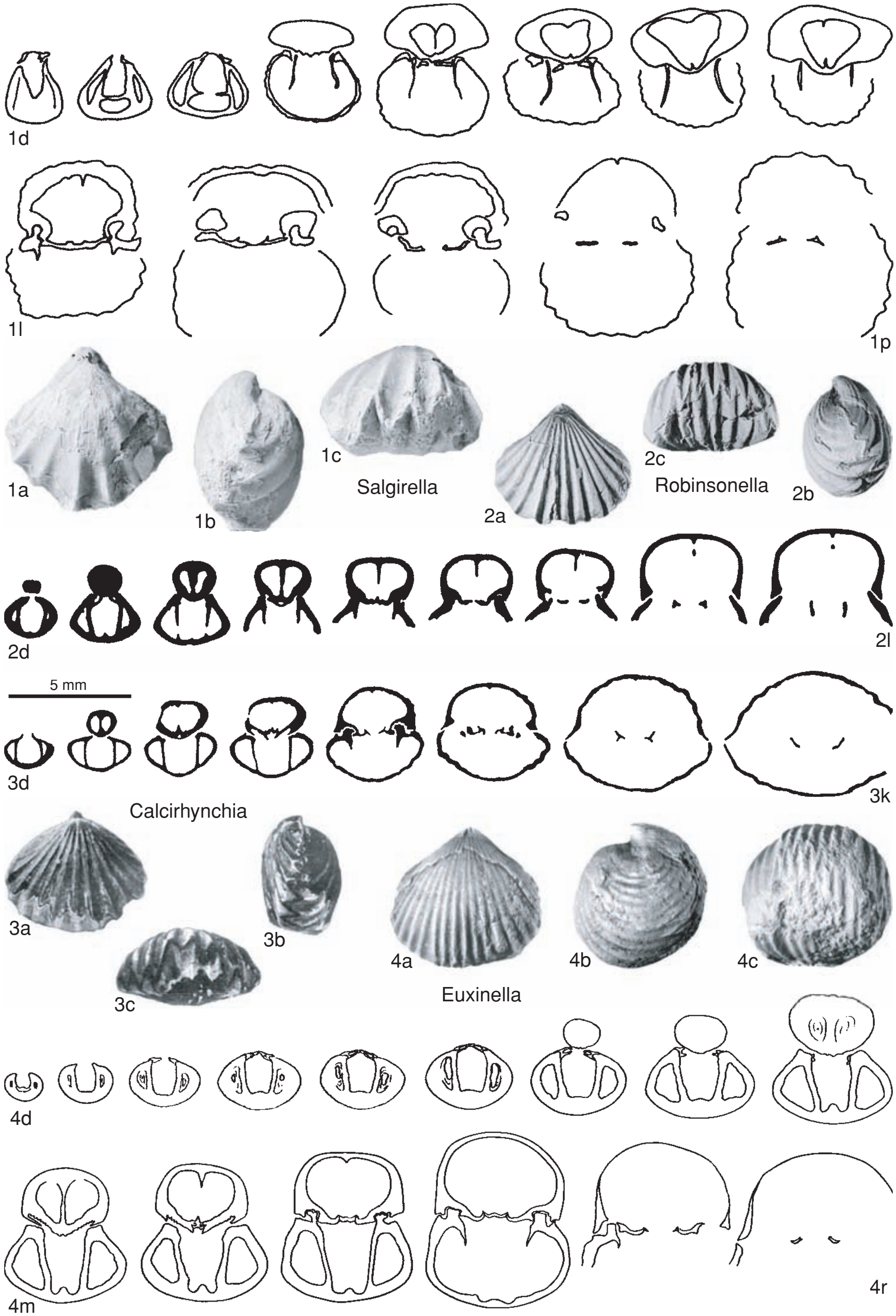

FIG. 862. Wellerellidae (p. 1263–1266).

1.1, 1.5, 1.7, 2.1, 2.5, 2.8, 3.2, 3.5, 3.9, 4.2 (Dagys, 1963).

Moisseievia Dagys, 1963, p. 46 [**M. moisseievi;* OD]. Small, subpentagonal, with distinct fold and sulcus; low, rounded costae in sulcus and on fold; indistinct costae only in anterior part on lateral sides; beak short, ridges rounded, foramen hypothyrid, deltidial plates double, conjunct. Dental plates short, parallel, pedicle collar fused to dental plates; median septum absent, hinge plate thin, horizontal in section, crura hamiform. *Upper Triassic (Norian):* Balkans, Carpathians, Crimea, northwestern Caucasus, Pamirs, China.——Fig. 861,*4a–l.* **M. moisseievi,* northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 91/640, ×1; *e–l,* transverse serial sections, distances in mm from first section, 0.6, 0.8, 1.2, 1.6, 1.7, 1.9, 2.3, 2.9 (Dagys, 1963).

?Robinsonella Moiseev, 1936, p. 45 [**R. mastakanensis;* OD]. Small, subpentagonal, moderately biconvex, strongly costate, with distinct sinus and feeble corresponding fold; beak short, incurved, ridges rounded, foramen hypothyrid, deltidial plates double, conjunct. Dental plates subparallel, no pedicle collar; septum distinct, about one-third valve length, hinge plate horizontal in section, crura allegedly hamiform. [Alternatively, may be related to ivanoviellines (hinted by development of ribbing, dorsal septum, and pitlike septalium); further studies of crura needed.] *Upper Triassic (Norian–Rhaetian):* northwestern Caucasus, India, China, Vietnam, Japan, ?New Guinea.——Fig. 862,*2a–l.* **R. mastakanensis,* Rhaetian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, TsGM 55/4801, ×1; *d–l,* transverse serial sections, distances in mm from first section, 0.6, 1.0, 1.5, 1.8, 2.1, 2.5, 3.0, 3.8, 4.3 (Dagys, 1963).

?Salgirella Moiseev, 1936, p. 48 [**Rhynchonella albertii* Oppel, 1861, p. 546; OD]. Rounded-pentagonal, beak thick, curved, no pseudointerarea; costae acute, coarse, simple, no radial striae, dorsal valve with fold. Dental plates ventrally divergent to subparallel, detached from valve floor anteriorly; pedicle collar present; deltidial plates wavy; dorsal median septum weakly developed, hinge plate flat, entire near beak, distinct anteriorly; septalium not supported by septum; crura slender, ventrally curved. [Very closely related, if not synonymous with *Cirpa* de Gregorio, 1930a, p. 40.] *Lower Jurassic (Hettangian–Pliensbachian):* Crimea, Caucasus, Austria, Hungary, Romania.——Fig. 862,*1a–p.* **S. alberti* (Oppel), Pliensbachian, Salgir river, Crimea; *a–c,* dorsal, lateral, anterior views, CNIGR 512/3808, ×1 (new); *d–p,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.1, 1.6, 2.1, 2.9, 3.3, 3.6, 4.0, 5.0, 5.4, 5.7, 6.15, 6.3, CNIGR N.509/3808 (new; courtesy of S. V. Lobacheva).

?Vincentirhynchia MacFarlan, 1992, p. 145 [**Rhynchonella pomeyroli* Drot, 1953, p. 99; OD]. Moderate size, subtriangular to subpentagonal; equibiconvex, moderately inflated; both valves with broad, flat, central parts and narrow lateral slopes; uniplication broad, shallow, flattopped; costae low, rounded, almost extending back to umbo; beak small, erect, with relatively large submesothyrid foramen. Dental plates subparallel and widely apart; dorsal valve with narrow hinge plates, and septalium supported by thin median septum. [Best restricted to type species, as other assigned species may be referable to *Cirpa* and *Prionorhynchia.*] *Upper Triassic (Rhaetian)–Lower Jurassic (Hettangian, ?Sinemurian):* New Zealand, New Caledonia, ?Siberia.——Fig. 861,*2a–k.* **V. pomeyroli* (Drot); *a–c,* holotype, dorsal, lateral, anterior views, Otapirian, Rhaetian, New Caledonia, MNHN B8395, ×1.5 (MacFarlan, 1992); *d–k,* transverse serial sections, distances in mm from first section, 0.0, 1.0, 1.3, 1.7, 2.3, 2.6, 2.9, 3.3, Hettangian, Siberia (Dagys, 1968).

Family ALLORHYNCHIDAE Cooper & Grant, 1976

[Allorhynchidae Cooper & Grant, 1976a, p. 2003] [=Septaliphorioididae Xu & Liu, 1983, p. 73]

[Materials prepared by Norman M. Savage & Miguel O. Manceñido]

Wellerelloidea with subcircular to subpentagonal outline; narrow costae extending all or most of shell length, bifurcated or intercalated in all Mesozoic and several Permian genera; dorsal fold and ventral sulcus weak to absent; delthyrium with or without deltidial plates. Thin dental plates, often almost fused to wall or absent; dorsal median septum low to absent; hinge plates divided; crura generally falciform, subfalciform, or hamifom. *Lower Carboniferous (Tournaisian)–Upper Triassic (Norian, ?Rhaetian).*

Allorhynchus Weller, 1910, p. 509 [**Rhynchonella heteropis* Winchell, 1865, p. 121; OD]. Subtriangular to subpentagonal outline and dorsibiconvex profile. Beak straight to suberect; delthyrium open, triangular, deltidial plates marginal, narrow. Fold and sulcus weak to moderate; anterior commissure uniplicate; tongue low, trapezoid. Costae of medium size, simple, subangular, extending from beaks, covering entire shell. Dental plates short, vertical; ventral muscle field elongate oval, expanding anteriorly. Hinge plates divided; dorsal median septum absent; dorsal muscle field elongate, posterior adductors elongate, narrow, partly flanking larger anterior adductors; crura diverge anteriorly, curved ventrally, dorsal edges carinate. *Lower Carboniferous (Tournaisian)–Upper Permian (Tatarian):* North America, Donetz Basin, Kazakhstan, China, Japan.——Fig. 863,*1a–i.* **A. heteropis* (Winchell), lower Mississippian, Kinderhookian, Burlington, Iowa, USA; *a–d,* dorsal, ventral, anterior, and lateral views, ×1; *e–i,*

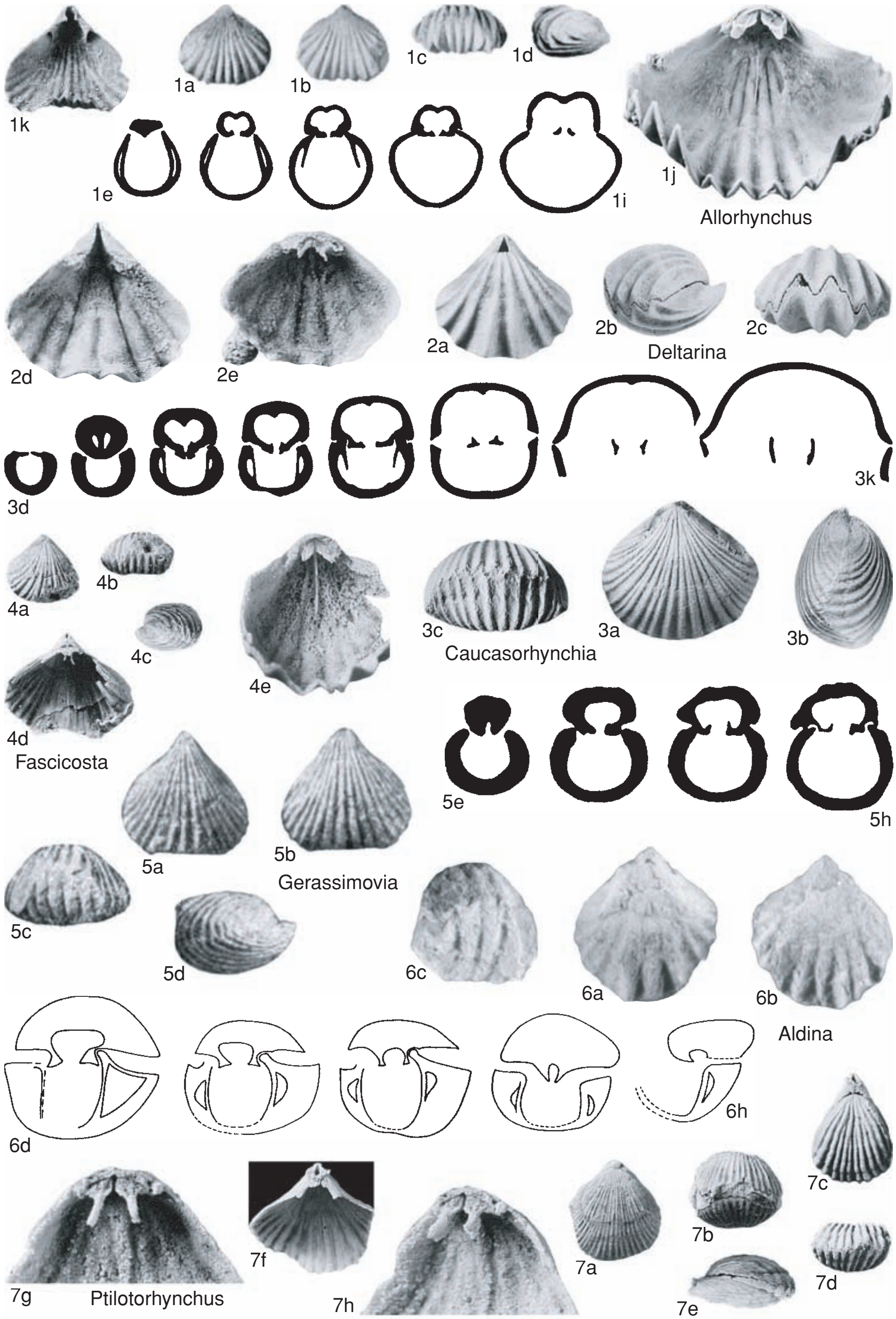

FIG. 863. Allorhynchidae (p. 1266–1270).

serial sections, ×3.8 (Weller, 1914).——FIG. 863,*1j–k. A. permianum permianum* STEHLI; *j,* interior of tilted dorsal valve, ×3; *k,* interior of tilted ventral valve, ×1.5 (Cooper & Grant, 1976a).

Aldina ANGIOLINI, 1995, p. 209 [**A. exilis;* OD]. Small; subtriangular to subpentagonal outline and dorsibiconvex profile, strongly inflated anteriorly. Ventral beak suberect; foramen small, deltidial plates conjunct. Fold and sulcus starting at midlength; anterior commissure uniplicate; tongue high, wide, typically tridentate. Costae strong, simple, angular, arising at midlength. Dental plates short, vertical. Hinge plates divided; dorsal median septum absent. *Lower Permian (Kungurian):* Pakistan.——FIG. 863,*6a–h. *A. exilis,* Bolorian, Lashkargaz Formation, Karakoram Mountains; *a–b,* holotype, dorsal and ventral views, ×3 (Angiolini, 1995); *c,* topotype, anterior view, ×3 (new); *d–h,* serial sections of topotype, 0.9, 1.1, 1.3, 1.6, 1.8 mm from posterior, no scale given (Angiolini, 1995).

Caucasorhynchia DAGYS, 1963, p. 66 [**C. kunensis;* OD]. Small to medium size, rounded-pentagonal, sulcus shallow and fold low or absent, multicostate, costae with intensive branching; beak short, ridges rounded, foramen hypothyrid, deltidial plates conjunct. Dental plates short, weakly diverging, umbonal chambers, pedicle collar absent; dorsal median septum apically confined, ridgelike to absent; septalium absent; outer hinge plates incipiently ventrally convex in section; crura hamiform. *Middle Triassic (?Anisian), Upper Triassic (Carnian–Norian, ?Rhaetian):* Alps, Carpathians, northwestern Caucasus, Pamirs, Turkey, China (Himalayas, Tibet).——FIG. 863,*3a–k. *C. kunensis,* Norian, northwestern Caucasus; *a–c,* dorsal, lateral, anterior views, IGiG 49/5, ×1; *d–k,* transverse serial sections, distances in mm from first section, 0.3, 0.9, 1.2, 1.4, 1.8, 2.2, 2.9, 3.8 (Dagys, 1963).

Deltarina COOPER & GRANT, 1976a, p. 2012 [**D. magnicostata;* OD]. Small; subtriangular outline and equibiconvex profile. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow. Fold and sulcus weak to moderate, anterior commissure sulciplicate. Costae moderate to coarse but usually with 1 large plication in sulcus and 2 on fold. Dental plates short, ventrally convergent; ventral muscle field elongate oval, expanding anteriorly. Hinge plates divided; dorsal median septum absent to low; crura strongly divergent anteriorly, laterally compressed, short. *Upper Permian (Kazanian):* USA.——FIG. 863,*2a–e. *D. magnicostata,* Bell Canyon Formation, Guadalupe Mountains, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d–e,* paratype, ventral valve interior, dorsal valve interior, ×3 (Cooper & Grant, 1976a).

Fascicosta STEHLI, 1955, p. 71 [**Rhynchonella? longaeva* GIRTY, 1909, p. 322; OD]. Small; outline subtriangular to subpentagonal; profile equibiconvex; maximum thickness near midlength. Beak straight to suberect; delthyrium open, triangular, deltidial plates absent. Fold and sulcus very weak; anterior commissure uniplicate, low. Costae fine to moderate, extending from beaks, fasciculate, some bifurcation. Dental plates short, convergent ventrally; ventral muscle field elongate oval, expanded anteriorly. Hinge plates divided; dorsal median septum low, thin, supporting hinge plates posteriorly; dorsal muscle field quadripartite, expanded anteriorly; crura divergent anteriorly, ventrally curved, dorsal surface carinate. *Upper Permian (Kazanian):* USA.——FIG. 863,*4a–e. *F. longaeva* (GIRTY), Guadalupe Mountains, Texas; *a–c,* lectotype, dorsal, anterior, and lateral views, Capitan Limestone, El Capitan Mountain; *d,* ventral valve interior and foramen, Bell Canyon Formation, McKittrick Canyon Draw, ×1; *e,* dorsal valve interior, Bell Canyon Formation, Hegler Ranch, ×3 (Cooper & Grant, 1976a).

Gerassimovia LICHAREW, 1956, p. 59 [**G. gefoensis;* OD]. Small with outline subtriangular to subpentagonal and profile equibiconvex. Beak suberect to erect. Fold and sulcus low. Numerous strong costae extending from beaks, fasciculate, increasing by bifurcation and intercalation. Dental plates absent. Hinge plates divided; dorsal median septum absent. *Permian (Kungurian–Tatarian):* northern Caucasus, Pamir.——FIG. 863,*5a–h. *G. gefoensis,* northern Caucasus; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2; *e–h,* serial sections, ×6 (Licharew, 1956).

Grammorhynchus ROBERTS, 1971, p. 144 [**Camarotoechia eganensis* VEEVERS, 1959a, p. 9; OD]. Outline subcircular to longitudinally ovate; profile strongly biconvex to globular. Beak incurved, truncated by circular, mesothyrid foramen. Fold and sulcus weak, broad; anterior commissure uniplicate; tongue low, serrate. Costae strong, subangular, simple, arising at beaks, present on entire shell. Dental plates long, vertical, may be obscured by callus; ventral muscle field narrow, impressed. Hinge plates divided; dorsal median septum long, low; septalium short, deep; dorsal muscle field narrow, deeply impressed, expanded anteriorly; crural bases with triangular section; crura long, gently curved ventrally. *Lower Carboniferous (Tournaisian):* northwestern Australia.——FIG. 864,*1a–m. *G. eganensis* (VEEVERS), Laurel Formation, Fitzroy basin; *a–d,* holotype, dorsal, ventral, anterior, and lateral views, ×2 (Veevers, 1959a); *e–m,* serial sections 2.2, 3.0, 3.4, 3.6, 3.8, 4.0, 4.2, 4.4, 4.8 mm from posterior, ×2.6 (Roberts, 1971).

Hagabirhynchia JEFFERIES, 1961, p. 5 [**H. arabica;* OD] [=*Magabirhynchia* XU & LIU, 1983, p. 71, *nom. null.*]. Small, rounded-pentagonal, with sulcus shallow and fold low, costae strong and extending from umbo and often forking; beak thick, suberect, deltidial plates conjunct. Dental plates diverging, pedicle collar absent; dorsal median septum low, septalium rudimentary, outer hinge plates narrow, divided; crura hamiform. *Upper Triassic (Norian):* Oman, China, India, ?New Guinea.——FIG. 864,*3a–l. *H. arabica,* Oman; *a–c,* holotype, dorsal, lateral, anterior views, ×2; *d,* holotype, ventral view,

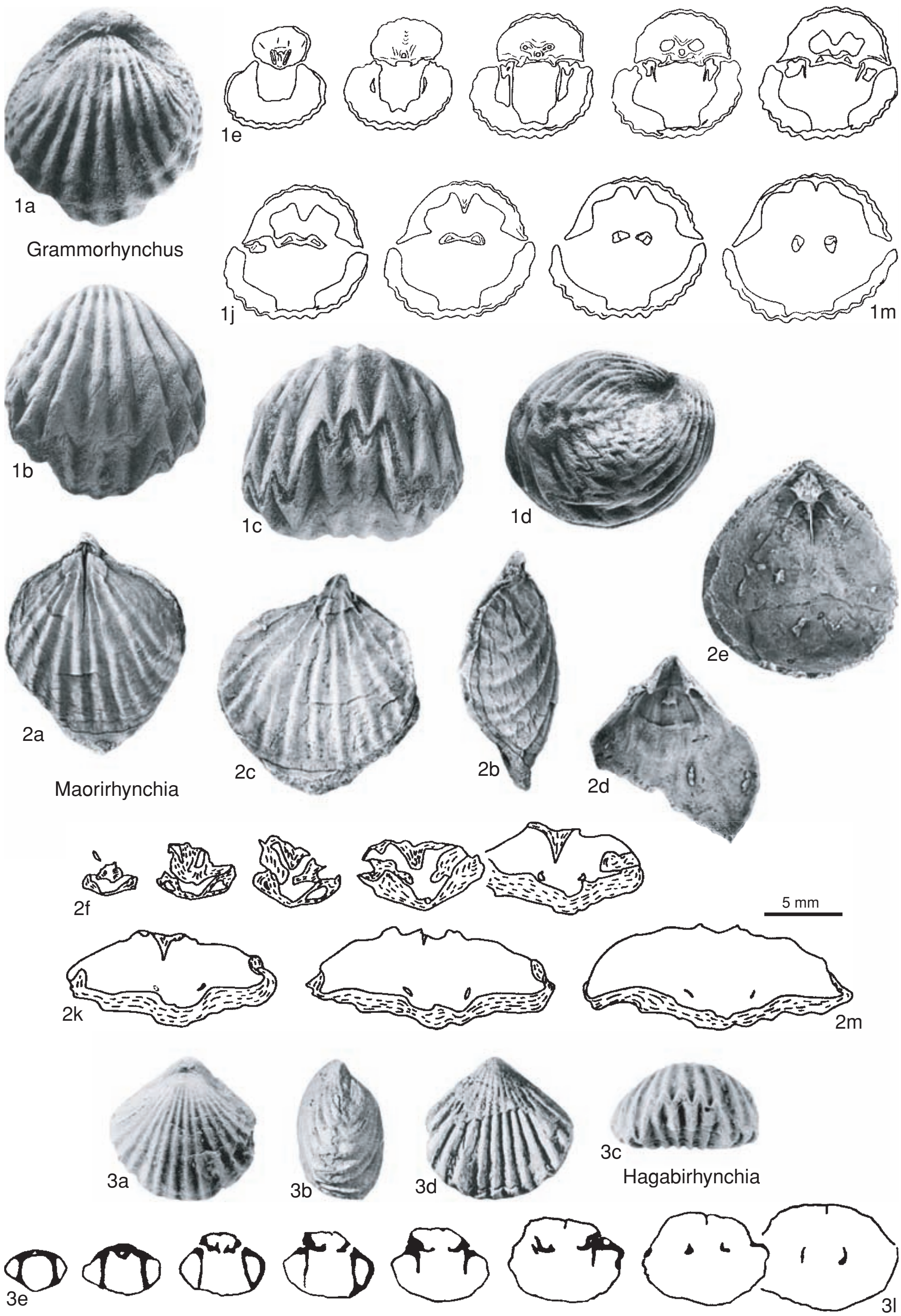

FIG. 864. Allorhynchidae (p. 1268–1270).

BMNH BB.20248, ×2 (new); *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.0, 1.2, 1.3, 1.5, 2.0, 2.3, 2.7, BMNH BB.20249, approximately ×3.2 (Jefferies, 1961).

Hemileurus Cooper & Grant, 1976a, p. 2017 [**H. runcinatus;* OD]. Small; outline subtriangular; profile equibiconvex; maximum thickness just anterior of midlength. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow. Fold and sulcus very weak; anterior commissure uniplicate, low, serrate. Costae moderate, simple, rounded, arising anterior of umbones. Dental plates short, vertical; ventral muscle field forming elongate triangle, expanded anteriorly. Hinge plates divided by deep notch; dorsal median septum absent; dorsal muscle field oval, quadripartite, slightly expanded anteriorly; crura divergent anteriorly, curved ventrally, twisted, dorsal edges carinate. *Lower Permian (Asselian–Sakmarian):* USA.——Fig. 865,*1a–d.* **H. runcinatus,* Neal Ranch Formation, Glass Mountains, Wolf Camp Hills, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×1; *d,* view of broken shell showing cardinalia, ×4 (Cooper & Grant, 1976a).

?Maorirhynchia MacFarlan, 1992, p. 71 [**Rhynchonella nuggetensis* Wilckens, 1927, p. 22; OD]. Moderate to large size, rounded-subtriangular to subcircular or elliptical; equibiconvex, slightly to moderately inflated; costae low, rounded or obsolescent, typically extending back to beak and bifurcating, occasionally dying out near anterior margin; rectimarginate to uniplicate, fold and sulcus usually broad and arcuate; beak small with minute foramen. Dorsal valve with broad horizontal hinge plates and shallow septalium; posterior part of both valves may be greatly thickened internally, dental plates almost fused to wall. *?Lower Triassic, Middle Triassic (Anisian)–Upper Triassic (lower Norian):* New Zealand, New Caledonia.——Fig. 864,*2a–m.* **M. nuggetensis* (Wilckens), Ladinian, Kaihikuan, Southland, New Zealand; *a–c,* dorsal, lateral, ventral views, OU NZ C2455; *d,* latex mold of pedicle valve interior, OU NZ C2969, ×1; *e,* latex mold of brachial valve interior, OU NZ C2952, ×1; *f–m,* transverse serial sections, distances in mm from ventral umbo, 0.7, 1.3, 1.5, 2.1, 3.1, 4.1, 5.1, 5.9, OU NZ 16309 (MacFarlan, 1992).

Neofascicosta Xu, 1978, p. 277 [**N. pulchra;* OD]. Small to medium, roundly trigonal, moderately biconvex to nearly flat; fold and sulcus weakly developed; anterior commissure slightly uniplicate, commonly somewhat ligate; covered with clustered subangular costae increasing anteriorly by bifurcation or intercalation; ornamented with dense, fine concentric growth lines and concentric lamellae marginally; beak small and nearly straight; foramen hypothyrid to mesothyrid; beak ridges angular, planareas narrow. Dental plates well developed; teeth stout; dorsal beak projecting into delthyrial cavity; hinge plates divided and fused with inner socket ridges; septalium shallow and short; septum low and thick, ridgelike anteriorly; crural bases trigonal; crura hamiform to subfalciform. *Upper Triassic:* southwestern and southeastern China (Sichuan, Qinghai).——Fig. 865,*4a–i.* **N. pulchra,* Sichuan; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CIGMR SCSb 6020, ×1; *e–i,* transverse serial sections, distances in mm from first section, 0.0, 0.55, 0.7, 0.8, 1.5 (Xu, 1978).

Pseudowellerella Licharew, 1956, p. 58 [**P. nikchitchi;* OD] [=*Denticuliphoria* Licharew, 1956, p. 57 (type, *D. rara,* OD); *Wairakiella* Waterhouse, 1967, p. 87 (type, *W. rostrata,* OD)]. Small; subtriangular to subpentagonal outline; equibiconvex profile. Beak suberect to erect; foramen small. Fold and sulcus weak, wide; anterior commissure uniplicate, serrate. Costae medium size, numerous, extending from beak. Dental plates poorly developed or absent. Hinge plates united; dorsal median ridge short, low. *Permian (Kungurian–Tatarian):* northern Caucasus, New Zealand.——Fig. 865,*3a–f.* **P. nikchitchi; a–d,* dorsal, ventral, anterior, and lateral views, ×2; *e–f,* transverse sections, ×5.3 (Licharew, 1956).

Ptilotorhynchus Cooper & Grant, 1976a, p. 2010 [**P. delicatum;* OD]. Outline elongate subtriangular with greatest width near anterior; profile weakly dorsibiconvex. Beak straight; delthyrium with large conjunct alate deltidial plates, foramen oval, close to beak. Fold and sulcus weak; anterior commissure uniplicate, low. Costae fine, increasing by bifurcation and intercalation. Dental plates short to absent; ventral muscle field large, rounded. Hinge plates short, divided; dorsal median septum very short, supporting posterior of hinge plates; dorsal muscle field elongate, divided by low myophragm; crura curved ventrally, laterally flattened. *Permian (Kungurian–Kazanian):* USA.——Fig. 863,*7a–h.* **P. delicatum,* Guadalupe Mountains, Texas; *a–b,* holotype, dorsal and anterior views, ×1; *c–e,* paratype, dorsal, anterior, and lateral views of young specimen, ×3; *f,* paratype, posterior of ventral valve showing alate deltidial plates, ×2; *g–h,* interiors of dorsal valve showing cardinalia, ×6 (Cooper & Grant, 1976a).

Septaliphorioidea Yang & Xu, 1966, p. 29[101] [**S. paucicostata;* OD] [=*Septaliphoroidea* Ching, Sun, & Ye in Ching & others, 1979, p. 131–132, *nom. null.*]. Small, roundly triangular to subpentagonal, depressed subequibiconvex, uniplicate; ventral sulcus and dorsal fold well developed, fold flattopped and truncated at front; covered with plicae, bifurcating on dorsal but intercalating on ventral valve; rounded costae, extending from umbo, 2 to 4 on fold, 3 to 4 on lateral slopes; beak straight to slightly incurved; narrow deltidial plates. Dental plates short; hinge plates divided; median ridge weak and low, septalium absent. *Middle Triassic (Anisian):* western China.——Fig. 865,*5a–l.* **S. paucicostata,* paratype, Gheizhou; *a–d,* dorsal, lateral, anterior, ventral views, MCMB DDR3C3, ×2; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.7, 0.9, 1.1, 1.25, 1.4, 1.7, 2.0, MCMB DDR III D3-2 (Yang & Xu, 1966).

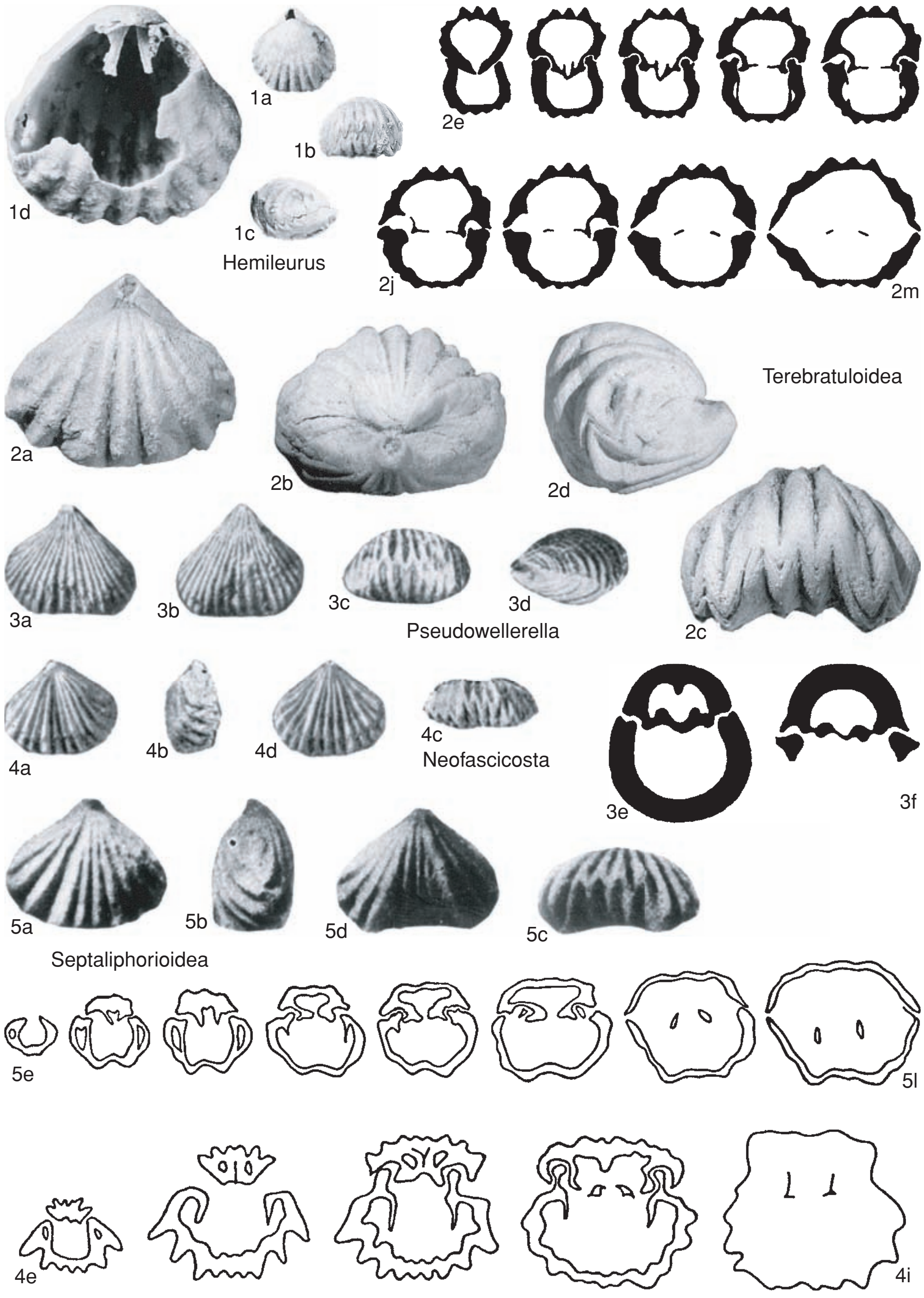

FIG. 865. Allorhynchidae (p. 1270–1272).

Terebratuloidea WAAGEN, 1883, p. 410 [**T. davidsoni;* OD]. Outline transversely subpentagonal and profile dorsibiconvex. Beak suberect and truncated by large circular mesothyrid foramen; delthyrium with conjunct deltidial plates. Fold and sulcus moderately strong, arising at umbones; anterior commissure uniplicate, serrate. Costae coarse, arising at beaks, rounded in profile. Dental plates close to valve walls, may be obscured by callus but distinct in specimen sectioned; teeth large, rounded. Dorsal median septum absent; hinge plates joined posteriorly by convex plate, divided for most of length; crural bases and crura horizontal to slightly oblique. *Lower Carboniferous (Viséan)–Upper Permian (Kazanian):* Pakistan, India, central and southeastern Asia, China, Europe, Urals.——FIG. 865,*2a–m.* **T. davidsoni,* Wordian, Salt Range, Pakistan; *a–d,* dorsal, posterior, anterior, and lateral views, Buri Khel, ×1.3 (new); *e–m,* serial sections 3.6, 3.9, 4.2, 4.4, 4.6, 5.0, 5.2, 5.6, 6.4 mm from posterior, middle *Productus* Limestone, Seminodular band, Dhak Pass Nala, ×1.4 (new).

Family PONTISIIDAE Cooper & Grant, 1976

[Pontisiidae COOPER & GRANT, 1976a, p. 2019] [=Lissorhynchiidae XU, 1990, p. 77]

[Materials prepared by NORMAN M. SAVAGE & MIGUEL O. MANCEÑIDO]

Wellerellidae with dorsal median septum weak to absent. Costae usually coarse. Dental plates commonly distinct; hinge plates undivided but notched anteriorly; dorsal median septum absent. *Upper Carboniferous (Bolsovian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Subfamily PONTISIINAE Cooper & Grant, 1976

[*nom. transl.* SAVAGE, 1996, p. 255, *ex* Pontisiidae COOPER & GRANT, 1976a, p. 2019] [=Lissorhynchiinae XU & LIU, 1983, p. 73]

[Materials prepared by NORMAN M. SAVAGE & MIGUEL O. MANCEÑIDO]

Pontisiidae with coarse costae. *Upper Carboniferous (Bolsovian)–Lower Jurassic (Pliensbachian, ?Toarcian).*

Pontisia COOPER & GRANT, 1969, p. 13 [**P. stehlii;* OD]. Outline subtriangular to subpentagonal and profile dorsibiconvex, strongly inflated anteriorly. Beak suberect; delthyrium triangular, foramen elongate oval, deltidial plates conjunct. Fold and sulcus strong, wide, from umbones; anterior commissure uniplicate; tongue high, wide, typically tridentate. Costae strong, simple, angular, arising at umbones. Dental plates strong, vertical; ventral muscle field transversely subtriangular, expanded anteriorly. Hinge plates undivided; inner socket ridges large, inclined over crenulate sockets; dorsal median septum absent, median ridge low; dorsal muscle field elongate quadripartite, expanded anteriorly; crura with horizontal bases, strongly twisted to become laterally flattened, dorsally carinate, curved ventrally. *Upper Carboniferous (Bolsovian)–Upper Permian (Kazanian):* USA, Guatemala, Venezuela, Thailand, Spain, Kazakhstan.——FIG. 866,*1a–g.* **P. stehlii,* upper Leonardian, Road Canyon Formation, Glass Mountains, Hess Canyon, Texas, USA; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* interior of dorsal valve, ×4.5; *g,* interior of posterior of ventral valve, ×4 (Cooper & Grant, 1976a).

Anteridocus COOPER & GRANT, 1976a, p. 2054 [**A. gongylus;* OD]. Small; subpentagonal outline; dorsibiconvex profile, inflated anteriorly. Beak suberect; delthyrium triangular, deltidial plates disjunct, foramen oval. Fold and sulcus moderate, extending from one-third shell length; anterior commissure uniplicate; tongue moderate to low, typically triserrate. Costae coarse, simple, from one-third shell length. Dental plates strong, ventrally convergent; ventral muscle field cordate, expanded anteriorly. Hinge plates undivided but with deep notch; inner socket ridges narrow; dorsal median septum low, very short; crura laterally compressed, long, dorsally carinate. *Permian (Sakmarian–Kazanian):* USA.——FIG. 866,*3a–e.* **A. gongylus,* Leonardian, Cathedral Mountain Formation, Glass Mountains, Split Tank, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d,* interior of conjoined posterior, showing dental plates and cardinalia, ×4; *e,* interior of dorsal valve, ×6 (Cooper & Grant, 1976a).

Antronaria COOPER & GRANT, 1976a, p. 2036 [**A. speciosa;* OD]. Transversely subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak suberect; delthyrium triangular, deltidial plates just conjunct, foramen oval. Fold and sulcus strong, wide, from umbones; anterior commissure uniplicate; tongue high, wide, typically triserrate. Costae strong, simple, arising at umbones. Dental plates strong, vertical to medially convex; ventral muscle field large, cordate, expanded anteriorly. Hinge plates undivided; dorsal median septum absent, median ridge low, thick; dorsal muscle field elongate oval; crura long, twisted, dorsally carinate, curved ventrally. *Lower Permian (Sakmarian–Artinskian):* USA.——FIG. 866,*5a–g.* **A. speciosa,* upper Wolfcampian, Hess Formation, Glass Mountains, Taylor Ranch, Texas; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views; *f,* paratype, interior of ventral valve, ×1; *g,* paratype, tilted view of dorsal valve interior, ×3 (Cooper & Grant, 1976a).

?Bodrakella MOISEEV, 1936, p. 47 [**Rhynchonella bodrakensis* MOISEEV, 1934, p. 56; OD]. Shell small, oval, beak slightly incurved, thin, sharp, without pseudointerarea, sulcus shallow, fold weakly developed; costae coarse, simple, only near shell margin, growth lines well developed, no radial striae. Pedicle

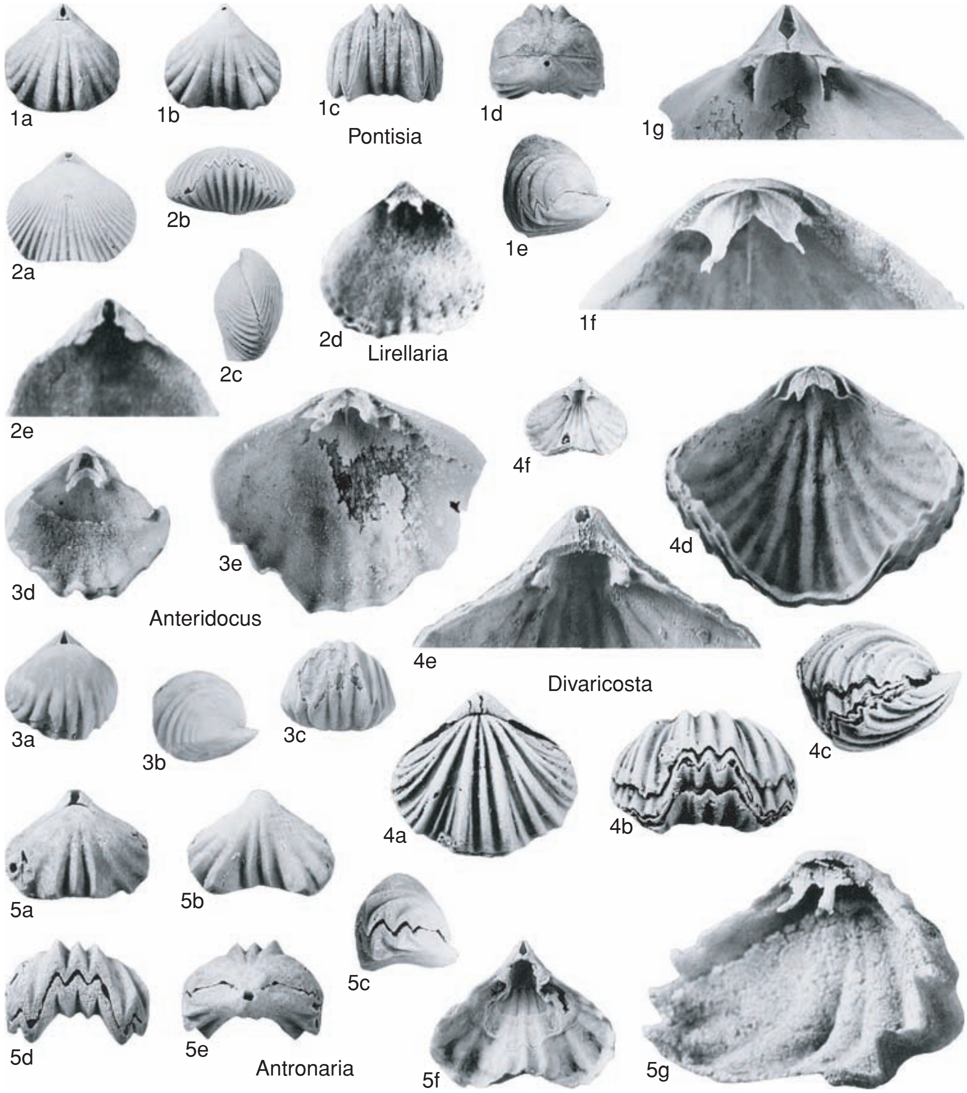

FIG. 866. Pontisiidae (p. 1272–1275).

collar present, dental plates vertical, joined to shell not the whole distance; teeth massive, teeth and sockets crenulated, denticula absent; dorsal median septum weakly developed; hinge plate entire, at level of socket ridges; crura slender, ventrally incurved. *Lower Jurassic (?Sinemurian, Pliensbachian, ?Toarcian):* Crimea, Bulgaria, ?Caucasus. ——FIG. 867,*1a–l.* **B. bodrakensis* (MOISEEV), Pliensbachian, Crimea; *a–d,* dorsal, lateral, anterior, ventral, ×1.5 (new); *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.55, 0.9, 1.35, 1.6, 2.0, 2.2, 2.8, 3.2, CNIGR 601/3808 (new; courtesy of S. V. Lobacheva).

Divaricosta COOPER & GRANT, 1969, p. 11 [**D. squarrosa;* OD]. Small; outline subtriangular to subpentagonal; profile dorsibiconvex, not inflated anteriorly. Beak straight to suberect; delthyrium wide, almost closed by large deltidial plates. Dorsal fold and sulcus low, from midlength; anterior commissure uniplicate; tongue low to moderate, serrate. Costae varied in size, markedly fasciculate, increasing by bifurcation and intercalation. Dental plates strong, vertical, close to walls; ventral muscle field narrowly triangular, expanding anteriorly. Hinge plates large, undivided; inner socket ridges slightly overhanging sockets; dorsal median septum absent,

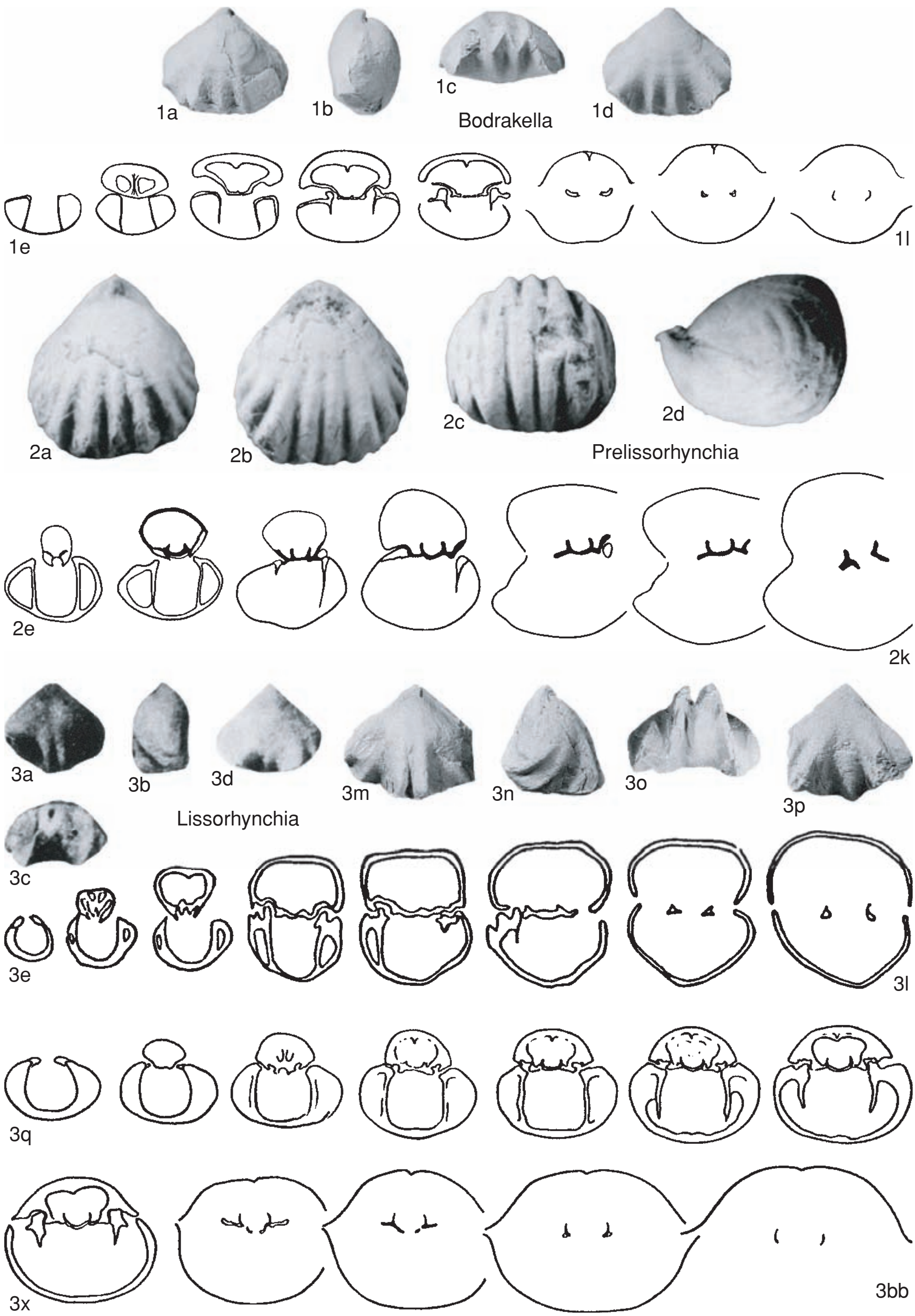

FIG. 867. Pontisiidae (p. 1272–1275).

median ridge moderately low, thick, short; dorsal muscle field elongate, quadripartite, expanded anteriorly; crura laterally compressed, not twisted, curved ventrally. *Lower Permian (Kungurian):* USA.——FIG. 866,*4a–f.* **D. squarrosa,* lower Guadalupian, Cherry Canyon Formation, Getaway Member, Guadalupe Mountains, Guadalupe Pass, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* interior of dorsal valve posterior, ×4; *e,* interior of ventral valve; *f,* interior of tilted ventral valve, ×1 (Cooper & Grant, 1976a).

Lirellaria COOPER & GRANT, 1976a, p. 2031 [**L. costellata;* OD]. Outline subpentagonal to subcircular and profile equibiconvex. Beak suberect to erect; delthyrium triangular, deltidial plates conjunct, foramen oval, submesothyrid. Fold and sulcus weak, arising at about midlength; anterior commissure uniplicate, low, rounded. Costae fine, simple, extending from umbones. Dental plates short, strong. Hinge plates undivided, outer hinge plates small, inner hinge plates coalesced; inner socket ridges strong; dorsal median septum absent; crura ventrally curved, concave medially, laterally compressed. *Permian (Artinskian–Kazanian):* USA.——FIG. 866,*2a–e.* **L. costellata,* upper Guadalupian, Bell Canyon Formation, Lamar Member, Guadalupe Mountains, Texas; *a–c,* holotype, dorsal, anterior, and lateral views, ×2; *d,* dorsal valve interior, ×3; *e,* interior of ventral valve posterior, ×4 (Cooper & Grant, 1976a).

Lissorhynchia YANG & XU, 1966, p. 14[94] [**L. pygmaea;* OD] [=*Neowellerella* DAGYS, 1974, p. 116 (type, *N. vesca,* OD)]. Small, subtrigonal to subpentagonal, dorsibiconvex, with flattened ventral valve; smooth posteriorly, with ventral sulcus and dorsal fold developed anteriorly; commissure uniplicate bidentate; each lateral slope bearing pair of marginal plicae; beak small, slightly incurved; disjunct deltidial plates narrow, foramen small, submesothyrid to hypothyrid. Muscle scars elongate oval, indistinctly differentiated into several pairs; septalium very small, median ridge exceedingly short and crura short and slightly incurved. *Lower Triassic (Scythian)–Middle Triassic:* Caucasus, Russia, *Lower Triassic;* Alps, Himalayas, southwestern China (southern Qilian), *Middle Triassic.*——FIG. 867,*3a–l.* **L. pygmaea,* Anisian, Gheizhou, China; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MCMB DDR VI 1, ×2; *e–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 0.9, 1.1, 1.2, 1.35, 1.4, 1.8, MCMB DDR VI 1-2 (Yang & Xu, 1966).——FIG. 867,*3m–bb. L. vesca* (DAGYS), Induan, Scythian, northwestern Caucasus; *m–p,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/71, ×2; *q–bb,* transverse serial sections, distances in mm from first section, 0.1, 0.2, 0.4, 0.6, 0.66, 0.76, 0.96, 1.16, 1.31, 1.41, 1.51, 1.76, IGiG 394/72 (Dagys, 1974).

Prelissorhynchia XU & GRANT, 1994, p. 36 [**Pugnax pseudoutah* HUANG, 1933, p. 64; OD] [=*Prelissorhynchia* XU, 1990, p. 68, *nom. nud.;* ?*Wellerellina* SHEN, HE, & ZHU, 1992, p. 183 (type, *W. chongqingensis,* OD)]. Small; outline subcircular to ovate; profile inflated dorsibiconvex. Beak straight to suberect; delthyrium open or with small deltidial plates. Fold and sulcus prominent anteriorly; tongue high, trapezoid, typically tridentate. Costae coarse, rounded, simple, from umbones. Dental plates short, vertical. Hinge plates undivided, inner hinge plates arched; crural bases arising from dorsal edges of hinge plates; crura twisted, dorsally carinate. [*Wellerellina* may eventually be shown to be the senior synonym, but present knowledge of interior is insufficient to indicate this.] *Upper Permian (Tatarian)–Lower Triassic (Scythian):* China.——FIG. 867,*2a–k.* **P. pseudoutah* (HUANG), Tatarian, Changxing Formation, Sichuan Province; *a–d,* dorsal, ventral, anterior, and lateral views, ×3; *e–k,* serial sections (Xu & Grant, 1994).

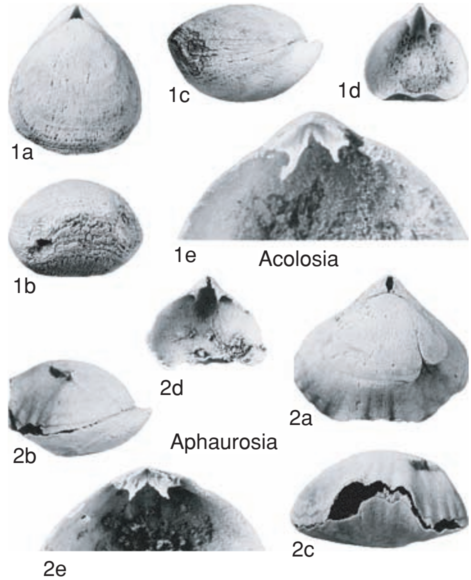

FIG. 868. Pontisiidae (p. 1275–1276).

Subfamily ACOLOSIINAE Savage, 1996

[Acolosiinae SAVAGE, 1996, p. 255]

[Materials prepared by NORMAN M. SAVAGE]

Pontisiidae with surface smooth except for very weak costae anteriorly. *Permian (Sakmarian–Kazanian).*

Acolosia COOPER & GRANT, 1976a, p. 2050 [**A. glabra;* OD]. Small; outline elongate oval; profile equibiconvex. Beak suberect to erect; delthyrium open, triangular; deltidial plates absent. Dorsal fold and ventral sulcus weak, limited to anterior third of shell; anterior commissure weakly uniplicate, rounded. Surface smooth except for 3 very weak costae at anterior of fold and sulcus and 1 very weak costa on each flank. Dental plates strong, vertical. Hinge plates undivided; inner socket ridges stout; dorsal median septum absent, median ridge low; crura short, laterally compressed. *Permian (Sakmarian–Kungurian):* USA.——FIG. 868,*1a–e*. **A. glabra,* lower Guadalupian, Wordian, Word Formation, China Tank Member, Glass Mountains, Hess Canyon, Texas; *a–c,* holotype, dorsal, anterior, and lateral views; *d,* interior of ventral valve, ×2; *e,* interior of dorsal valve posterior, ×6 (Cooper & Grant, 1976a).

Aphaurosia COOPER & GRANT, 1976a, p. 2048 [**A. scutata;* OD]. Outline transversely subpentagonal and profile dorsibiconvex. Beak suberect; delthyrium triangular, deltidial plates disjunct, foramen oval. Fold and sulcus low, wide, developed in anterior third of shell; anterior commissure uniplicate, low to moderate, serrate. Costae weak, low, rounded, developed only anteriorly. Hinge plates triangular, undivided; dorsal median septum absent, median ridge thick, short, low; dorsal muscle field elongate quadripartite, expanded anteriorly; crura long, concave medially. *Upper Permian (Kazanian):* USA.——FIG. 868,*2a–e*. **A. scutata,* upper Guadalupian, Bell Canyon Formation, Lamar Member, Guadalupe Mountains, Pratt Place, Texas; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d,* paratype, interior of ventral valve, ×1; *e,* paratype, interior of dorsal valve, ×3 (Cooper & Grant, 1976a).

Family PETASMATHERIDAE Cooper & Grant, 1976

[Petasmatheridae COOPER & GRANT, 1976a, p. 1928]

[Materials prepared by NORMAN M. SAVAGE]

Small Wellerelloidea with dorsal fold weak to absent; anterior commissure rectimarginate; costae strong, simple, arising at beaks; interarea well developed; delthyrium open, without deltidial plates. Dental plates short; hinge plates divided. *Lower Permian (Sakmarian–Kungurian).*

Petasmatherus COOPER & GRANT, 1969, p. 12 [**P. opulus;* OD]. Small; outline subpentagonal; profile equibiconvex. Beak straight to suberect; delthyrium open, triangular, deltidial plates narrow, disjunct. Dorsal fold and ventral sulcus weak; anterior commissure uniplicate to rectimarginate; serrate. Costae coarse relative to shell size, simple, from beaks. Dental plates short, vertical or slightly convergent ventrally, close to or fused to walls; ventral muscle field elongate oval, expanded anteriorly. Hinge plates divided; dorsal median septum absent but low median ridge may be present; dorsal muscle field quadripartite, expanded anteriorly; crura short, widely divergent, laterally compressed, slightly curved ventrally. *Lower Permian (Sakmarian–Kungurian):* USA (Texas).——FIG. 869,*1a–h*. **P. opulus,* lower Guadalupian, Word Formation, Glass Mountains, Hess Canyon; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×2; *f,* hypotype, interior of conjoined valves showing dental plates and cardinalia; *g,* paratype, interior of dorsal valve, ×6; *h,* hypotype, interior of ventral valve, ×3 (Cooper & Grant, 1976a).

Elassonia COOPER & GRANT, 1976a, p. 1935 [**E. micraria;* OD]. Very small; outline subcircular to subpentagonal; profile equibiconvex. Beak straight; delthyrium open, triangular, deltidial plates absent. Weak ventral fold and dorsal sulcus; anterior commissure weakly sulcate. Costae moderately strong for size of shell, fasciculate, multiplying by bifurcation and intercalation. Dental plates short, vertical, close to valve walls; ventral muscle field elongate oval. Hingle plates deeply divided; dorsal median septum absent, median ridge low; dorsal muscle field elongate, quadripartite, expanded anteriorly; crura long, laterally compressed. *Lower Permian (Sakmarian–upper Artinskian):* USA (Texas).——FIG. 869,*2a–h*. **E. micraria,* upper Leonardian, Road Canyon Formation, Glass Mountains, Old Word Ranch; *a–e,* holotype, dorsal, ventral, anterior, posterior, and lateral views, ×3; *f,* paratype, ventral valve interior; *g,* paratype, dorsal valve interior; *h,* interior of inclined ventral valve, ×12 (Cooper & Grant, 1976a).

Iotina COOPER & GRANT, 1976a, p. 1944 [**I. minuta;* OD]. Small; outline subpentagonal; profile biconvex. Beak straight; delthyrium long, open, triangular, deltidial plates absent. Fold and sulcus strong, narrow, from beaks; anterior commissure sulciplicate, narrow. Costae coarse for size, simple, arising near beaks, typically 2 on fold. Dental plates absent. Hinge plates deeply divided; dorsal median septum absent; crura short, laterally compressed, concave medially. *Lower Permian (Sakmarian):* USA (Texas).——FIG. 869,*3a–e*. **I. minuta,* lower Bone Spring Formation, Sierra Diablo, Black John Canyon; *a–c,* holotype, dorsal, lateral, and anterior views, ×2; *d–e,* paratype, dorsal valve interior, ventral valve interior, ×4 (Cooper & Grant, 1976a).

Ptygmactrum COOPER & GRANT, 1976a, p. 1939 [**P. extensum;* OD]. Small; outline transversely semicircular; profile equibiconvex; cardinal margin very wide, alate. Beak straight; delthyrium narrow, triangular, open, deltidial plates absent. Dorsal fold and ventral sulcus very weak; anterior commissure rectimarginate to weakly uniplicate; serrate. Costae coarse for size, simple, from cardinal margin. Dental plates short, vertical. Hinge plates deeply divided; dorsal median septum absent, median ridge

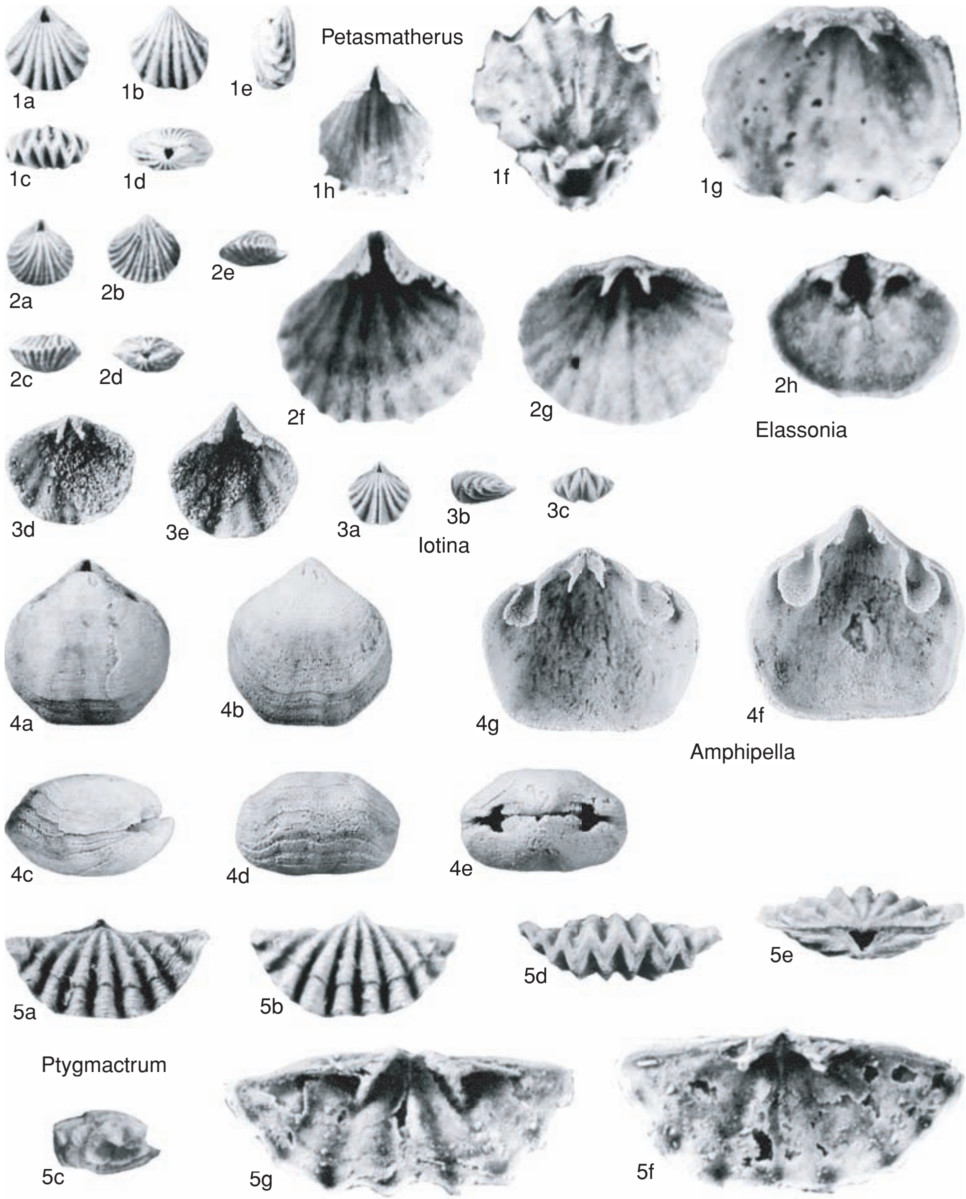

FIG. 869. Petasmatheridae and Amphipellidae (p. 1276–1278).

low; crura short, laterally compressed. *Lower Permian (lower Artinskian–Kungurian):* USA (Texas).——FIG. 869,*5a–g*. **P. extensum,* upper Leonardian, lower Road Canyon Formation, Glass Mountains, Old Word Ranch; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×4; *f–g,* paratype, dorsal valve interior, ventral valve interior, ×9 (Cooper & Grant, 1976a).

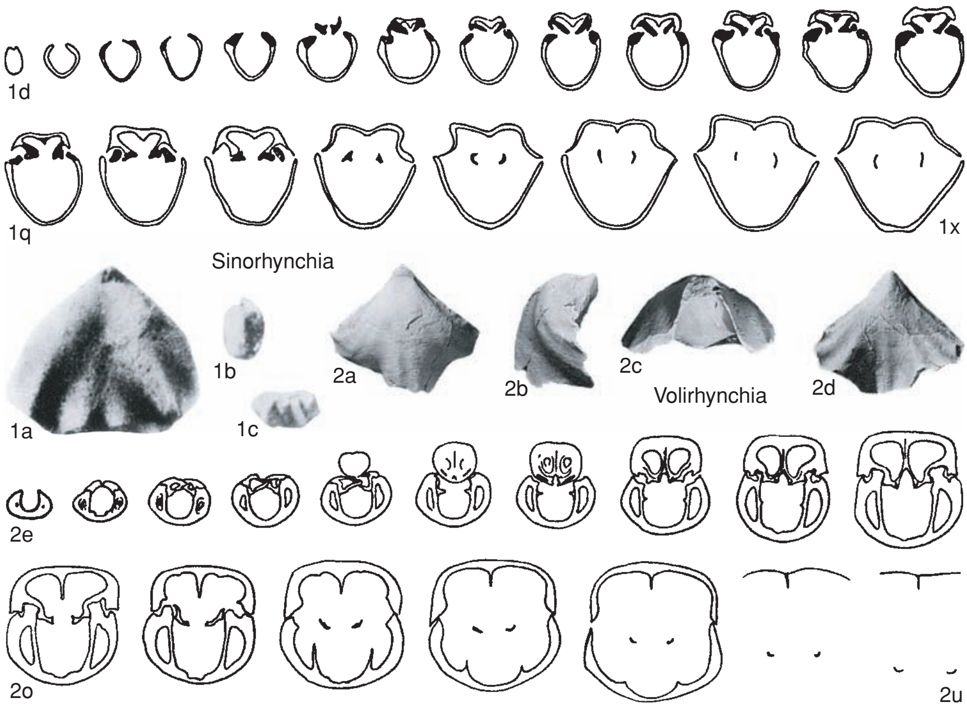

FIG. 870. Sinorhynchiidae (p. 1278–1279).

Family AMPHIPELLIDAE Cooper & Grant, 1976

[Amphipellidae COOPER & GRANT, 1976a, p. 1947]

[Materials prepared by NORMAN M. SAVAGE]

Small Wellerelloidea with outline subcircular, posterolateral pouches (apricatria) in both valves, and dental plates very short. *Lower Permian (Artinskian).*

Amphipella COOPER & GRANT, 1969, p. 11 [**A. arcaria;* OD]. Very small with outline subcircular to subpentagonal and profile equibiconvex. Posterolateral pouches (apricatria of COOPER & GRANT, 1976a, p. 1948) in both dorsal and ventral valves, visible as invaginations along posterolateral margins. Beak suberect to erect; delthyrium open, triangular, deltidial plates absent. Very weak dorsal fold and ventral sulcus; anterior commissure rectimarginate to weakly uniplicate. Surface smooth, growth lines pronounced anteriorly. Dental plates short, slightly convergent ventrally, may be fused to walls; large, narrow-necked apricatrial pouches present each side of delthyrium; ventral muscle field small, heart shaped. Hinge plate divided; dorsal median septum absent, median ridge low; apricatria present flanking cardinalia, similar to apricatria in ventral valve and closing onto them to form globose pouches; dorsal muscle field weakly impressed, wide, multilobed; crura falciform, short, slightly curved ventrally. *Lower Permian (Artinskian):* USA (Texas).——FIG. 869,*4a–g*. **A. arcaria,* lower Leonardian, lower Cathedral Mountain Formation, Glass Mountains, Split Tank; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views; *f,* ventral valve interior; *g,* dorsal valve interior, ×6 (Cooper & Grant, 1976a).

Family SINORHYNCHIIDAE Xu & Liu, 1983

[*nom. correct.* XU, 1990, p. 77, *pro* Sinorhynchidae XU & LIU, 1983, p. 73]

[Materials prepared by MIGUEL O. MANCEÑIDO & SUN DONG-LI]

Subtriangular Wellerelloidea with long smooth stage, few coarse marginal plicae; conspicuous dorsal sulcus starting early and split anteriorly by rising dorsal fold. Hinge plates typically divided; dental plates absent or thin and parallel. *Middle Triassic (Anisian–Ladinian).*

Sinorhynchia YANG & XU, 1966, p. 32[102] [**S. bifaceta;* OD]. Small, roundly triangular, ventribiconvex, thickest slightly posterior to midlength; completely smooth posteriorly, with 5 to 6 rounded, marginal plicae; dorsal sulcus developing from posterior and widening forward, becoming divided by 2 short plications at about midlength; commissure bidentate, flanked by round sulci; beak small, pointed, and strongly incurved; delthyrium small, open, possibly without deltidial plates. Hinge teeth small; dental plates, septalium, and median septum absent, with short median ridge only; hinge plates narrow, divided; crura short, hamiform, concavity facing medially. *Middle Triassic (Anisian):* China (Guizhou), ?Alps.——FIG. 870,*1a–x.* **S. bifaceta,* Guizhou; *a,* holotype, dorsal view, ×3; *b–c,* lateral, anterior views, MCMB DDRc65, ×1; *d–x,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.6, 0.7, 0.8, 0.95, 1.0, 1.07, 1.15, 1.2, 1.25, 1.3, 1.4, 1.5, 1.58, 1.65, 1.8, 1.9, 2.0, 2.1, 2.25, MCMB DDKc65 1-3 (Yang & Xu, 1966).

?Volirhynchia DAGYS, 1974, p. 104 [**Rhynchonella volitans* BITTNER, 1890, p. 47; OD] [=*Uolirhynchia* XU & LIU, 1983, p. 72, *nom. null.*]. Small, subpentagonal, unequally biconvex, ventral valve feebly convex posteriorly and flattened on lateral sides, strongly uniplicate; few, blunt costae only in anterior part, smooth posteriorly; beak suberect, ridges rounded, foramen submesothyrid, deltidial plates double, conjunct. Dental plates long, subparallel, pedicle collar absent; septalium deep, supported by high septum about one-half valve length, crura thin, intermediate between raduliform and hamiform, concavity facing dorsally. [Genus in need of revision; affinities with Rhynchonellinae cannot be discounted.] *Middle Triassic (Anisian–Ladinian):* Alps, Dinarids, Carpathians, northwestern Caucasus, ?India, ?China.——FIG. 870,*2a–u.* **V. volitans* (BITTNER), Anisian, northwestern Caucasus; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/226, ×1; *e–u,* transverse serial sections, distances in mm from first section, 0.0, 0.4, 0.6, 0.8, 0.9, 1.0, 1.1, 1.4, 1.6, 1.9, 2.1, 2.2, 2.4, 2.5, 2.8, 3.2, 3.7, IGiG 394/228 (Dagys, 1974).

RHYNCHONELLOIDEA

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Superfamily RHYNCHONELLOIDEA d'Orbigny, 1847

[*nom. transl.* SCHUCHERT, 1896, p. 323, *ex* Rhynchonellidae GRAY, 1848, p. 438, *recte* D'ORBIGNY, 1847, p. 268 (see MANCEÑIDO, OWEN, & MORRIS, 1993, p. 197)]

Rhynchonellida with shells subtriangular to subpentagonal, partly or fully costate; central uniplication well developed; surface may be also smooth, capillate, or covered with spines. Crura raduliform, calcariform, or variation thereof; dorsal median septum and uncovered septalium present; ventral septum, squama, and glotta absent. *Lower Triassic–Upper Cretaceous (Maastrichtian).*

Family RHYNCHONELLIDAE d'Orbigny, 1847

[Rhynchonellidae D'ORBIGNY, 1847, p. 268] [=Rhinchonellidae [BRONN], 1848, p. 246; Rhynconellidae CARPENTER, 1853 in DAVIDSON, 1853b, p. 35 (see MANCEÑIDO, OWEN, & MORRIS, 1993, p. 197)]

Rhynchonelloidea with anterior commissure rectimarginate or uniplicate, most often with costation superimposed; surface covered with nonlamellose growth lines, spines not developed; dorsal median septum and septalium variably developed; crura comparatively short and bent ventrally, cardinal process absent. *Lower Triassic–Upper Cretaceous (Maastrichtian).*

Subfamily RHYNCHONELLINAE d'Orbigny, 1847

[*nom. transl.* GILL, 1871, p. 25, *ex* Rhynchonellidae DAVIDSON, 1853b, p. 93, *recte* D'ORBIGNY, 1847, p. 268 (see MANCEÑIDO, OWEN, & MORRIS, 1993, p. 197)]

Dorsibiconvex Rhynchonellidae with strong, sharp dorsal fold and paucidentate uniplication, typically cynocephalous; with usually long smooth stage posteriorly and paucicostate anteriorly, seldom fully costate. Crura raduliform, triangular in cross section, somewhat expanded distally; dorsal median septum and septalium well developed; lateral umbonal chambers small, triangular, wide apart. *Lower Triassic–Lower Cretaceous (upper Hauterivian, ?Barremian).*

Rhynchonella Fischer de Waldheim, 1809, p. 35 [**R. loxiae;* OD] [=*Eurhynchonella* Leidhold, 1921, p. 352, obj.; *Rhynchonellis* Keferstein, 1829, p. 50, *nom. null.; Rhyngonella* Fischer de Waldheim, 1843, p. 117, *nom. null.; Rhinchonella* d'Orbigny, 1851 in 1848–1851, p. 343, *nom. null.; Rhynconella* Carpenter in Davidson, 1853b, p. 35, *nom. null.*]. Small to medium, subtriangular, gibbous, nearly convexiplane and cynocephalous; dorsal fold high, ventral sulcus somewhat flattened; smooth stage long, costae few and sharp anteriorly; commissure uniplicate, acuminate to paucidentate; beak small, slightly incurved. Dental plates strong, septalium shallow, dorsal median septum short; crura short, raduliform. *Upper Jurassic (Oxfordian)–Lower Cretaceous (Valanginian, ?Barremian):* Britain, France, Germany, Poland, Russia, Slovakia, Bulgaria, Mexico.——Fig. 871,*1a–v.* **R. loxiae,* upper Volgian, Khoroschevo, near Moscow, Russia; *a–e,* dorsal, lateral, anterior, ventral, posterior, BMNH B.39132, ×1 (new); *f–v,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.6, 1.0, 1.3, 1.5, 1.6, 1.7, 1.8, 1.9, 2.0, 2.3, 2.5, 2.7, 3.1, 3.2, 3.4, 3.6, BMNH B.1325 (Ager, 1957).

?Curtirhynchia Buckman, 1918, p. 36 [**Rhynchonella oolitica* Davidson, 1852b, p. 81; OD] [=*Curtirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, subpentagonal, depressed dorsibiconvex; fold low, dorsal, uniplication tridentate to tetradentate; costae few, blunt anteriorly, smooth posteriorly; beak sharp, suberect, foramen hypothyrid. Dorsal median septum high, septalium small, pitlike, pedicle collar may be present; crura raduliform, distally expanded. *Middle Jurassic (Aalenian):* England, ?France, Morocco.——Fig. 871,*3a–j.* **C. oolitica* (Davidson), Aalenian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, BMNH B.31753, ×1; *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.0, 1.4, 1.6, 1.8, 2.0, 2.6, 3.5, CDP 23, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

?Fusirhynchia Dagys, 1968, p. 68 [**Rhynchonella micropteryx* d'Eichwald, 1865–1868, p. 344; OD]. Medium, subquadrate, acutely dorsibiconvex; coarsely costate with few, deep, angular costae; median dorsal fold well defined, flattopped, bi- to tetradentate; dorsal umbo inflated, posteriorly smooth; ventral sulcus broadly trapezoidal with fairly extensive linguiform extension; umbo short, beak sharp, suberect to almost erect. Dental plates strong, ventrally divergent to subparallel; pedicle collar short, fused to dental plates; hinge plates subhorizontal, inner and outer socket ridges well developed; high median septum supporting deep septalium; crural bases triangular. *Upper Jurassic (lower Volgian)–Lower Cretaceous (Valanginian):* northern Urals, northern Siberia, ?England (Dorset).——Fig. 872,*2a–k.* **F. micropteryx* (d'Eichwald), lower Volgian, northern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, ×1; *e–k,* transverse serial sections, distances in mm from first section, 2.1, 2.6, 3.1, 3.5, 3.7, 4.4, 4.9 (Dagys, 1968).

?Herangirhynchia MacFarlan, 1992, p. 155 [**H. herangiensis;* OD]. Small, subcircular to subpentagonal; equibiconvex to dorsibiconvex, moderately inflated, almost subcynocephalous; dorsal valve possibly bearing faint posterior sulcation; generally with strong narrow sulcus and fold; uniplication fairly high, usually bidentate or acuminate; beak small, broad with small foramen and sharp beak ridges. Dental plates short, thick, slightly ventrally divergent; median septum long, massive; hinge plates dorsally inclined with shallow septalium; crura raduliform; transversely crenulated hinge teeth. *Upper Triassic (Rhaetian)–Lower Jurassic (Toarcian), ?Middle Jurassic (?Aalenian):* New Zealand, New Caledonia.——Fig. 871,*2a–j.* **H. herangiensis,* Toarcian, upper Ururoan, Awakino, New Zealand; *a–d,* dorsal, lateral, anterior, ventral views, OU NZ 16719, ×2; *e–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.4, 1.6, 1.7, 1.9, 2.4, 2.8, OU NZ 17307 (MacFarlan, 1992).

Homoeorhynchia Buckman, 1918, p. 36 [**Terebratula acuta* J. Sowerby, 1816 in 1815–1818, p. 115; OD; *non* J. de C. Sowerby, 1825] [=*Homoeorhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Blochmannella* Leidhold, 1921, p. 356 (type, *Rhynchonella Friereni* Branco, 1879, p. 128, OD, *error pro R. Frireni*), =*Blochmanella* Schuchert & LeVene, 1929a, p. 132, unjustified emend.; *Slovenirhynchia* Siblík, 1967, p. 159 (type, *S. maninensis,* OD)]. Small to medium (seldom large), subtrigonal to subpentagonal, cynocephalous; dorsibiconvex to almost convexoplane, strongly inequivalve and everted with uniplication acuminate to multidentate; dorsal fold high, sharp, and costae few and sharp anteriorly, starting after onset of fold; beak small, incurved. Dorsal median septum short and high; deep septalium; crura fairly long, raduliform. *Upper Triassic (Carnian, Rhaetian), Lower Jurassic (?Sinemurian, Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Alps, *Carnian, Rhaetian;* Europe (mainly southern), Morocco, Algeria, Turkey, southwestern China, Canada, Peru, *?Sinemurian, Pliensbachian–Aalenian, ?Bajocian.*——Fig. 872, *3a–k.* **H. acuta* (J. de C. Sowerby), upper Pliensbachian; *a–c,* dorsal, lateral, anterior views, England, BMNH BM.67719, ×1.6 (new); *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.7, 1.3, 1.7, 1.8, 2.2, 2.6, 3.0, 4.5, Ardeche, France, FSL 49276 (Alméras, 1979).——Fig. 872,*3l–o. H. frireni* (Branco), Aalenian, Lorraine, France; dorsal, lateral, anterior, ventral views, ×1 (Branco, 1879).——Fig. 872,*3p–z. H. maninensis* (Siblík), upper Pliensbachian, Kostelec, Slovakia; *p–r,* holotype, dorsal, lateral, anterior views, CGS MS 167, ×1; *s–z,* transverse serial

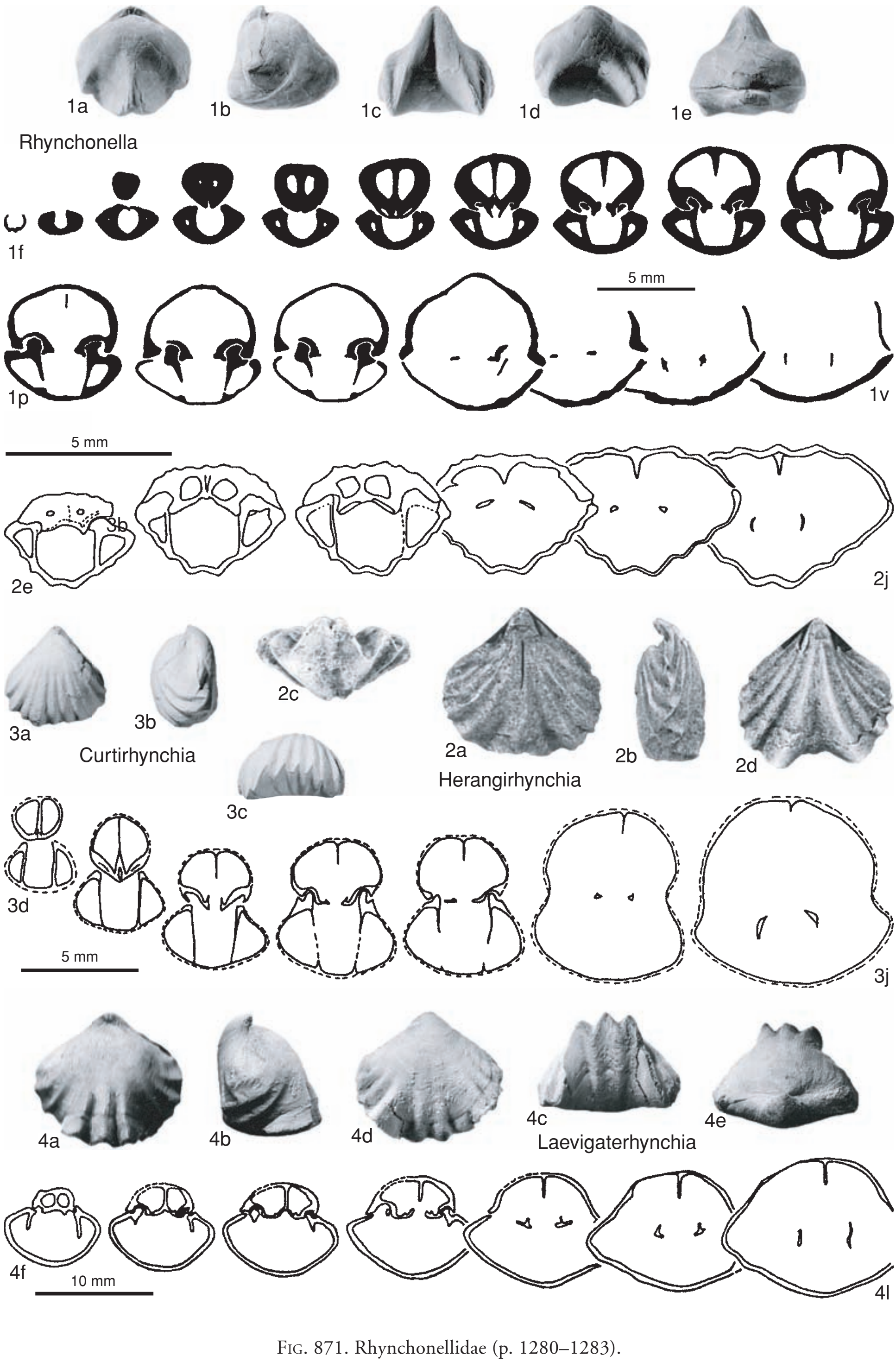

FIG. 871. Rhynchonellidae (p. 1280–1283).

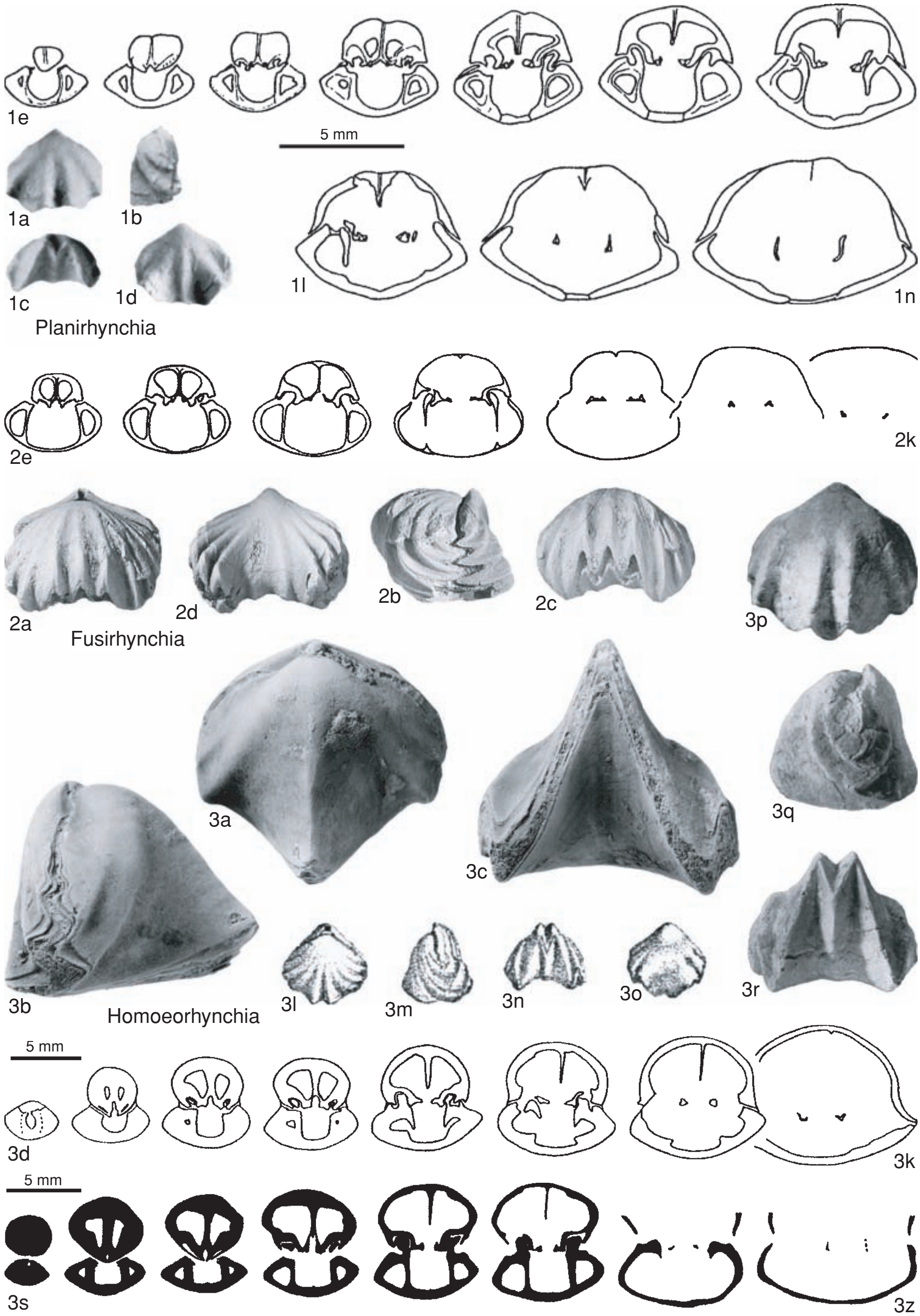

FIG. 872. Rhynchonellidae (p. 1280–1283).

sections, distances in mm from ventral umbo, 0.7, 1.8, 2.1, 2.7, 3.2, 3.8, 4.9, 6.5 (Siblík, 1967).

Kabanoviella Smirnova, 1973, p. 43 [**Rhynchonella obliterata* Lahusen, 1874, p. 54; OD]. Small, dorsibiconvex; costae simple, coarse, originating some distance from umbo; broadly uniplicate, sulcus and fold clearly defined; beak short, erect, pointed; foramen auriculate. Dental plates short, teeth crenulated; dorsal median septum long, reaching midlength, supporting short septalium; hinge plates broad, dorsally concave, indistinctly separated from inner socket ridges; crura ventrally deflected. [Hardly distinguishable from *Rhynchonella s.s.*] *Lower Cretaceous (upper Hauterivian):* Russian Platform.——Fig. 873,*1a–d.* **K. obliterata* (Lahusen), Ulianovsk area; dorsal, ventral, lateral, anterior views, MGU 139/342, ×1 (Smirnova, 1990a).——Fig. 873,*1e–k. K. lahuseni;* transverse serial sections, distances in mm from first section, 0.3, 0.7, 1.0, 1.2, 1.8, 2.5, 3.2, approximately ×2 (Smirnova, 1978).

Laevigaterhynchia Wisniewska-Zelichowska, 1978, p. 112[150] [**Terebratula triplicosa* Quenstedt, 1851–1852, p. 454; OD] [=*Laevigatorhynchia* Wisniewska-Zelichowska, 1978, p. 65 (alternative original spelling)]. Small to medium, dorsibiconvex, usually somewhat longer than wide; fold on dorsal valve and ventral sulcus, both distinct, deflected dorsally in wide, trapeziform, linguiform extension; beak erect or suberect; foramen slightly oval; 8 to 10 subangular costae, beginning closer to anterior part of shell, central fold bidentate to multidentate; surfaces smooth, without capillae. Dorsal median septum high and septalium small; crura allegedly falciform, in fact raduliform, distally expanded. *Middle Jurassic (Callovian):* Germany, Poland, Switzerland, Carpatho-Balkanids, ?Greenland.——Fig. 871,*4a–l.* **L. triplicosa* (Quenstedt), Czestochowa area, Poland; *a–e,* dorsal, lateral, anterior, ventral, posterior views, Muz IG 1352.2.162, ×1 (new); *f–l,* transverse serial sections, distances in mm from first section, 1.5, 2.0, 2.2, 2.4, 2.7, 2.9, 3.6 (Wisniewska-Zelichowska, 1978).

?Lunarhynchia Jin, Manceñido, & Sun, 1997, p. 392, *nom. nov. pro Lunaria* Ching, Sun, & Ye in Ching & others, 1979, p. 155–156, *non* Fabricius, 1823, Mollusca [**Lunaria dorsata* Ching, Sun, & Ye in Ching & others, 1979, p. 155; OD]. Medium to large, pyriform to pentagonal, almost convexoplane; dorsal fold and ventral sulcus well defined, developed anteriorly; linguiform extension subquadrate; lateral slopes smooth or with few, short, coarse plicae; plicae on sulcus and fold usually extending from umbo; ventral beak short and straight; beak ridges angular; foramen submesothyrid; delthyrium covered with symphytium. Dental plates vertical, subparallel, not extending beyond articulation zone; dorsal median septum reaching midvalve; septalium wide and shallow; hinge plates flat, fused with inner socket ridges; raduliform crura projecting horizontally to end ventrally incurved. [Shell shape of type species is unusual; evidence from other assigned species tends to support this subfamily allocation.] *Upper Triassic:* China (Tibet, Qinghai, Sichuan, Yunnan).——Fig. 873,*5a–n.* **L. dorsata* (Ching, Sun, & Ye), Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42838, ×1; *e–n,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 0.9, 1.2, 1.55, 2.1, 2.4, 2.55, 2.95, 4.0, NIGP 42837 (Ching & others, 1979).

?Nudirostralina Yang & Xu, 1966, p. 21[97] [**N. subtrinodosi;* OD] [=*Nudirostrolina* Sun, 1981, p. 196, *nom. null.; Nudirostrlina* Xu & Liu, 1983, p. 72, *nom. null.*]. Medium size, subtrigonal to subpentagonal, dorsibiconvex to gently everted; ventral sulcus and dorsal fold well marked anteriorly; commissure uniplicate, bidentate to multidentate; shell completely smooth posteriorly and with only few short plicae anteriorly and laterally, 2 to 5 on fold, usually 2 on each lateral slope; beak small, slightly incurved; deltidial plates small, covering delthyrium, hypothyrid to submesothyrid. Dental plates ventrally divergent; dorsal median septum short, supporting septalium; crura short, ventrally curved. *Lower Triassic–Upper Triassic:* China (Guizhou, Qinghai, Tibet), ?India.——Fig. 873,*4a–l.* **N. subtrinodosi,* Anisian, Guizhou; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MCMB DDR IA4-2, ×1; *e–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.2, 0.9, 1.3, 1.5, 1.8, 2.05, 2.2, 2.4, MCMB DDR Ia4-4 (Yang & Xu, 1966).

?Planirhynchia Sucic-Protic, 1969, p. 19 [**P. tantilla;* OD]. Medium to small, depressed subpentagonal; smooth in posterior half and covered with few, low, blunt costae in anterior half; commissure uniplicate, bidentate, or tridentate; linguiform extension flattopped, wide, and shallow; beak straight to fairly curved, with round submesothyrid foramen. Septalium wide, dorsal median septum low, long, and massive; crura raduliform, fairly curved. [Tchoumatchenko (1989, p. 18) regarded the type species as a subjective junior synonym of *Homoeorhynchia almaensis* (Moiseev).] *Upper Triassic (Carnian)–Lower Jurassic (Pliensbachian):* Siberia, ?southern Europe, *Carnian–Rhaetian;* Yugoslavia (Carpatho-Balkanids), *Pliensbachian.*——Fig. 872,*1a–n.* **P. tantilla,* middle Lias, Carpatho-Balkanids, Yugoslavia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MFMGB 3/1669, ×1; *e–n,* transverse serial sections, distances in mm from first section, 0.8, 0.9, 1.0, 1.3, 1.4, 1.6, 1.9, 2.2, 2.5, 3.1 (Sucic-Protic, 1969).

Rhynchonelloidea Buckman, 1918, p. 38 [**Rhynchonella ruthenensis* Reynès, 1868, p. 107; OD] [=*Rhynchonelloidea* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small to medium, strongly dorsibiconvex, rounded subpentagonal, more or less everted, dorsal fold pronounced and uniplication bidentate to multidentate; costae few and fairly

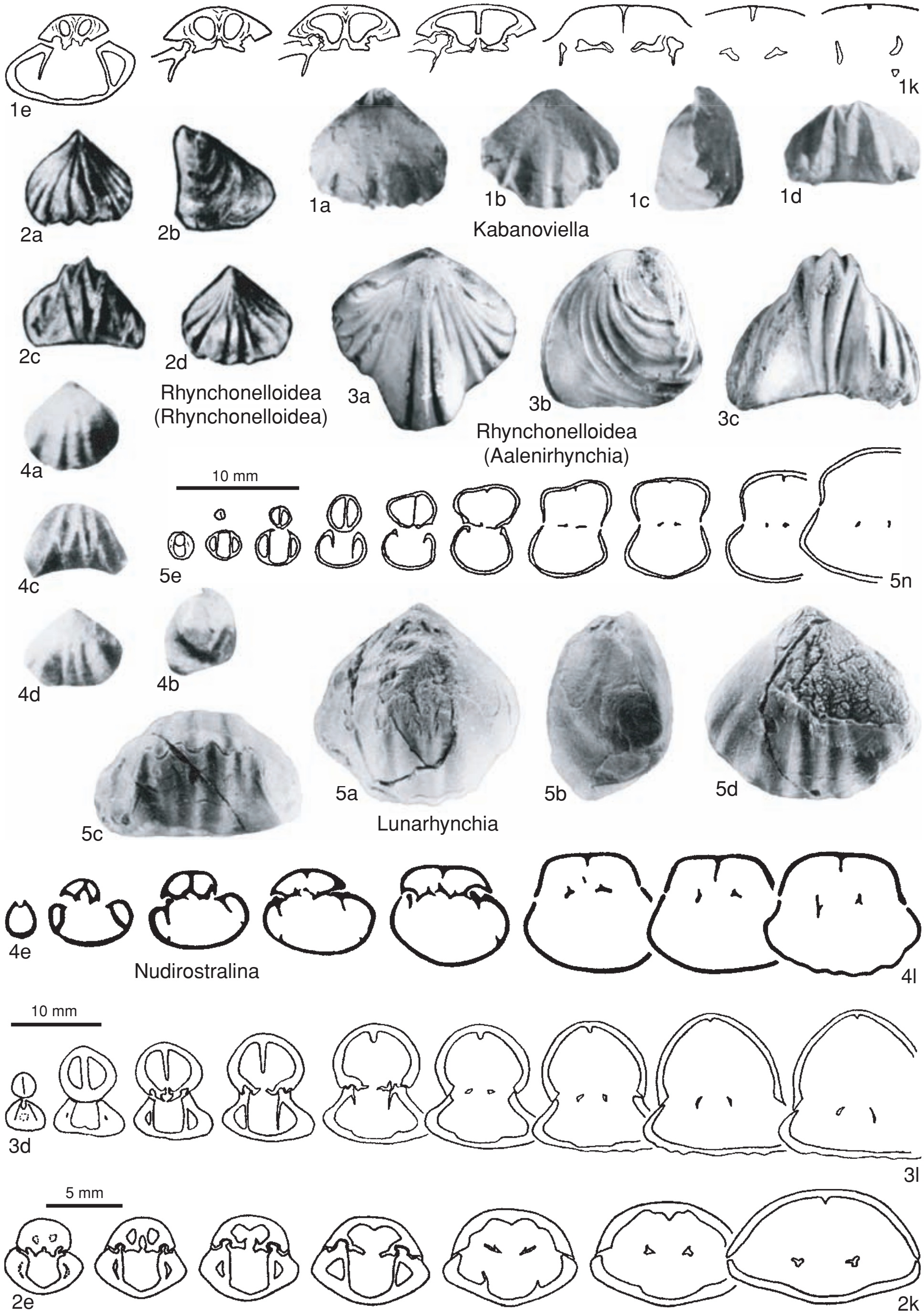

FIG. 873. Rhynchonellidae (p. 1283–1285).

sharp, starting before onset of fold, smooth stage negligible to absent. Dorsal septum strong, short; septalium narrow, pitlike; crura raduliform, may be distally concave. *Upper Triassic (?Rhaetian), Lower Jurassic (Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Europe, northern Africa, Asia, South America.

R. (**Rhynchonelloidea**). Subcynocephalous, costae coarse, simple, flanks of fold and sulcus smooth; beak small, acute and erect; deltidial plates disjunct. *Upper Triassic (?Rhaetian), Lower Jurassic (Pliensbachian)–Middle Jurassic (Aalenian, ?Bajocian):* Great Britain, France, Spain, Switzerland, Austria, Yugoslavia, Romania, Bulgaria, ?Germany, Caucasus, Argentina, Algeria, southwestern China.——FIG. 873,*2a–k.* **R. (R.) ruthenensis* (REYNÈS), lower Aalenian, Aveyron, France; *a–d,* dorsal, lateral, anterior, ventral views, FSL 49254, ×1; *e–k,* transverse serial sections, distances in mm from ventral umbo, 1.5, 1.8, 2.0, 2.4, 2.9, 3.4, 4.4, FSL 49254 (Alméras, 1979).

R. (**Aalenirhynchia**) SHI & GRANT, 1993, p. 57 [**Rhynchonella subdecorata* DAVIDSON, 1855, p. 21; OD]. Cynocephalous, may attain larger size; costae may be finer, denser, with 1 or 2 dying out along flanks of median fold before reaching front; incurved beak may conceal foramen and deltidial plates. *Lower Jurassic (Toarcian)–Middle Jurassic (Aalenian):* England, Spain, Argentina.——FIG. 873,*3a–l.* **R. (A.) subdecorata* (DAVIDSON), Aalenian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.9, 2.3, 2.8, 3.3, 3.5, 4.0, 4.9, 5.5, USNM 123721b (Shi & Grant, 1993).

Subfamily PIARORHYNCHIINAE Shi & Grant, 1993

[Piarorhynchiinae SHI & GRANT, 1993, p. 21]

Small to medium Rhynchonellidae, moderately equibiconvex to subglobose; beak and foramen small; smooth areas well developed posteriorly, with costae few, strong, and rounded anteriorly; rectangular uniplication not well detached from lateral slopes. Crura raduliform; dorsal median septum and septalium conspicuous; dental plates present; lateral umbonal chambers often filled up. *Lower Triassic–Lower Cretaceous (Albian).*

Piarorhynchia BUCKMAN, 1918, p. 34 [**Rhynchonella lineata* var. *radstockiensis* DAVIDSON, 1878, p. 210; OD] [=*Piarorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Tropiorhynchia* BUCKMAN, 1918, p. 33 (type, *Rhynchonella thalia* D'ORBIGNY, 1850 in 1849–1852, p. 239, OD); *Tropiorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, globose to depressed, nearly equibiconvex, uniplicate, dorsal fold low, flattopped; pronounced smooth stage posteriorly, costae rounded anteriorly; beak small, incurved. Dorsal septum massive; crura raduliform; thick horizontal hinge plates. *Upper Triassic (Carnian)–Lower Jurassic (Toarcian):* Alps, Siberia, Japan, western Canada and USA, *Carnian–Rhaetian;* England, France, Portugal, Spain, Sweden, Germany, Switzerland, Austria, Yugoslavia, Hungary, Ukraine, Morocco, Turkey (Anatolia, Taurids), Argentina, ?Chile, western Canada, *Hettangian–Toarcian.*——FIG. 874,*1a–v.* **P. radstockiensis* (DAVIDSON), lower Pliensbachian, Somerset, England; *a–e,* dorsal, lateral, anterior, ventral, posterior views, BMNH BB.33750, ×1.5 (new); *f–v,* transverse serial sections, distances in mm from ventral umbo, 0.4, 1.4, 1.5, 1.7, 2.0, 2.1, 2.2, 2.3, 2.5, 2.7, 2.8, 3.0, 3.2, 3.6, 4.0, 4.5, 4.8, J.197, Derek Ager, personal collection (Ager, 1962).——FIG. 874,*1w–y. P. thalia* (D'ORBIGNY), Pliensbachian, Calvados, France; dorsal, lateral, anterior views, MNHN, ×1.5 (Ager, 1962).

Abrekia DAGYS, 1974, p. 98 [**A. sulcata;* OD]. Small, subpentagonal, moderately depressed, equibiconvex; sulcus on posterior half of dorsal valve and shallow ventral sulcus and low dorsal fold on anterior half; few rounded costae anteriorly, smooth posteriorly; beak suberect, ridges rounded, foramen submesothyrid. Dental plates short, ventrally convergent; septum and septalium distinct; hinge plates subhorizontal; crura raduliform; pedicle collar absent. *Lower Triassic–Middle Triassic:* far eastern Russia, Tibet, Himalayas, Caucasus.——FIG. 875,*3a–k.* **A. sulcata,* Lower Triassic, Induan, Scythian, Primorye, Russia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/40, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.4, 0.6, 0.8, 0.9, 1.35, 1.55, 1.65, IGiG 394/45 (Dagys, 1974).

Aorhynchia MACFARLAN, 1992, p. 173 [**A. ohaiensis;* OD]. Small to moderate size, rounded outline; dorsibiconvex, moderate to great inflation; uniplication narrow, rounded, but fold and sulcus poorly developed; costae low, rounded, usually after a posterior smooth stage; beak large, blunt, erect, with large, round, mesothyrid foramen and long pedicle collar. Hinge plates small, septalium poorly defined, troughlike or pitlike; dorsal median septum short; raduliform crura short, distally bladelike and concave. *Middle Triassic (Anisian):* New Zealand.——FIG. 875,*2a–k.* **A. ohaiensis,* lower Anisian, Malakovian, South Island; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, OU NZ 14667, ×2; *f–k,* transverse serial sections, distances in mm from ventral umbo, 0.7, 0.8, 1.2, 1.5, 1.9, 2.3, OU NZ 177418 (MacFarlan, 1992).

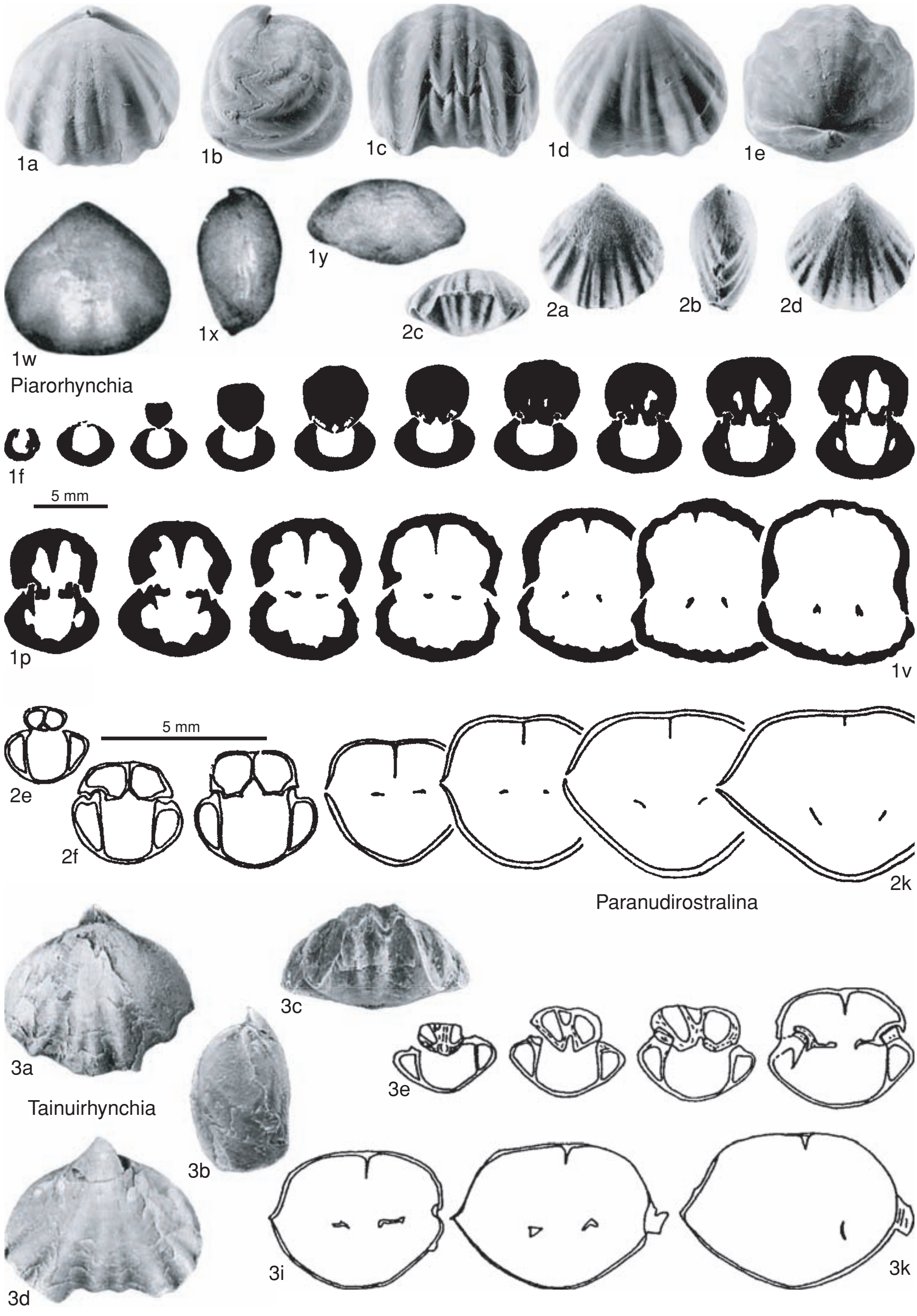

FIG. 874. Rhynchonellidae (p. 1285–1290).

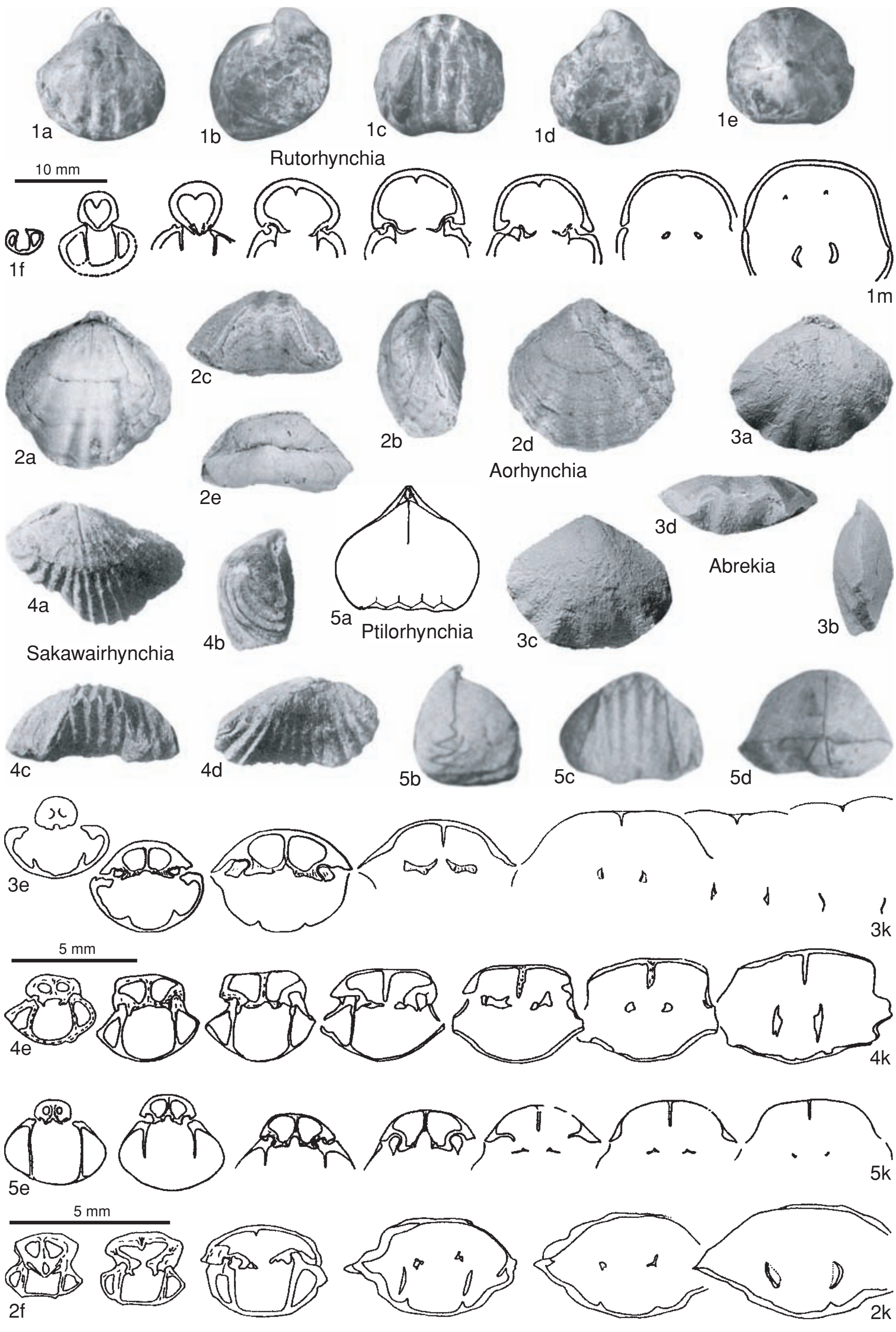

FIG. 875. Rhynchonellidae (p. 1285–1290).

Caledorhynchia MacFarlan, 1992, p. 209 [**C. caledonica;* OD]. Medium size, rounded triangular to subpentagonal; dorsibiconvex, strongly inflated to globose; fold and sulcus well defined, uniplication shallow, flattopped, anterior margin may be geniculate; costae few, strong, rounded or angular, after posterior smooth stage; beak prominent, erect, with hypothyrid foramen and pedicle collar. Massive hinge plates with narrow, deep septalium; dorsal median septum long and high; shell thick, muscle scar may be deeply incised. *Lower Jurassic (Sinemurian)–Middle Jurassic (Callovian):* New Zealand, New Caledonia.——Fig. 876,*2a–n.* **C. caledonica,* middle Temaikan, New Caledonia; *a–e,* dorsal, lateral, anterior, ventral, posterior views of bivalved steinkern, OU NZ 17202, ×1.5; *f–n,* topotype, transverse serial sections, distances in mm from ventral umbo, 2.2, 2.4, 2.6, 2.8, 3.0, 3.2, 3.6, 3.9, 4.7, OU NZ 17491 (MacFarlan, 1992).

Cuneirhynchia Buckman, 1918, p. 35 [**Rhynchonella dalmasi* Dumortier, 1869, p. 331; OD] [=*Cuneirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, depressed subtriangular, convexiplane or convexiconcave; pronounced smooth stage with costae few, blunt anteriorly; uniplicate, but fold slightly developed, if at all; beak small, upright to erect. Dental plates gently convergent ventrally; hinge plates massive; dorsal median septum long and low; crura raduliform. *Lower Jurassic (?Hettangian, Sinemurian–Pliensbachian, ?Toarcian):* England, France, Germany, Switzerland, Austria, Italy, Slovakia, Hungary, Romania, Yugoslavia, Greece, ?Crimea, ?Algeria, Turkey (Anatolia, Taurids), Siberia.——Fig. 876,*1a–i.* **C. dalmasi* (Dumortier), lower Pliensbachian, Somerset, England; *a–c,* dorsal, lateral, anterior views, HM L.2464, ×2; *d–i,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.2, 1.7, 2.0, 2.4, 2.8, J.1202, Derek Ager, personal collection (Ager, 1962).

Paranudirostralina Sun & Ye, 1982, p. 156[169] [**P. bifurcata;* OD]. Small to medium; subtriangular to subpentagonal, equibiconvex, with greatest convexity posteriorly; uniplicate, with ventral sulcus and dorsal fold well defined anteriorly; shell surface smooth posteriorly, but with few subangular plicae anteriorly, increasing by bifurcation or intercalation; beak small, slightly incurved to suberect; foramen small, mesothyrid or permesothyrid; delthyrium open. Dental plates long, subparallel; hinge plates flat, merged with socket ridges; median septum high and stout, septalium deep; crural bases triangular; crura raduliform, strongly curved ventrally. [May be a subgenus of *Abrekia.*] *Middle Triassic (Anisian):* China (Qinghai).——Fig. 874,*2a–k.* **P. bifurcata; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67016, ×1.5; *e–k,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.34, 0.6, 0.78, 0.86, 1.04, 1.34, 1.54, NIGP 67018 (Sun & Ye, 1982).

Ptilorhynchia Crickmay, 1933, p. 877 [**P. plumasensis;* OD] [=*Ptylorhynchia* Smirnova, 1984, p. 77, *nom. null.*]. Medium size, triangular to subpentagonal, subglobose, dorsibiconvex; uniplication marked with strong, short, marginal plicae; anterior commissure rarely asymmetrical; dorsal fold almost imperceptible, ventral sulcus broad, shallow, linguiform extension trapezoidal. Dental plates long, subparallel; hinge plates horizontal to dorsally deflected; dorsal septum high with well-marked septalium. [Inconclusive evidence hints of a possible persistence in Antarctica well into the Upper Cretaceous (Sandy, 1991).] *Middle Jurassic (?Bajocian, Bathonian)–Lower Cretaceous (Aptian):* USA (California), western Canada (British Columbia), northern Siberia, Urals, *?Bajocian, Callovian–Volgian;* northern Siberia, ?Slovakia, Antarctica, Argentina (mainly circum-Pacific), *Berriasian–Aptian.*——Fig. 875,*5a–d.* **P. plumasensis,* Callovian, California; holotype, dorsal, lateral, anterior, posterior views, ×1 (Crickmay, 1933).——Fig. 875,*5e–k. P. anadyrensis* Dagys, Bathonian–Callovian, northeastern Siberia, Anadyr basin; transverse serial sections, distances in mm from first section, 1.7, 2.0, 2.3, 2.7, 3.0, 3.3, 3.8 (Dagys, 1968).

Rutorhynchia Sun, 1981, p. 201 [**R. jieshanensis;* OD] [=*Roturhynchia* Shi & Grant, 1993, p. 18, *nom. null.*]. Medium size; oval to trigonal; globose, equibiconvex; dorsal fold and ventral sinus low and flat with subquadrate linguiform extension; posterior smooth stage variable; few, stout plicae developed marginally; uniplication bidentate to tetradentate; beak sharp, pointed, and incurved; beak ridges angular; foramen small and mesothyrid to hypothyrid, delthyrium covered with symphytium. Dental plates subparallel; outer hinge plates narrow, dorsal septum reduced to low ridge and short; septalium undeveloped, only rudimentary pendant septalial plates; crura strongly bent; pedicle collar absent. *Upper Jurassic:* Tibet.——Fig. 875,*1a–m.* **R. jieshanensis; a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, NIGP 48427, ×1 (new); *f–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.7, 3.3, 3.6, 4.3, 4.7, 5.0, 5.6, 6.4, NIGP 48429 (Sun, 1981).

Sakawairhynchia Tokuyama, 1957, p. 126 [**S. tokomboensis* Kobayashi & Tokuyama in Tokuyama, 1957, p. 127; OD; *Rhynchonella tokomboensis* Kobayashi, 1931, p. 231, *nom. nud.*]. Moderate size, subpentagonal or elliptical; dorsibiconvex, moderately to greatly inflated; strongly uniplicate, with fold flattopped and sulcus moderately deep; variable smooth stage posteriorly, few, blunt costae anteriorly, exceptionally noncostate; beak small erect, with poorly developed beak ridges. Hinge plates broad, subhorizontal, with shallow septalium; dorsal median septum long and high; dental plates well developed; raduliform crura long, sharply bent. *Middle Triassic (Ladinian)–Lower Jurassic (lower Toarcian):* New Zealand, New Caledonia,

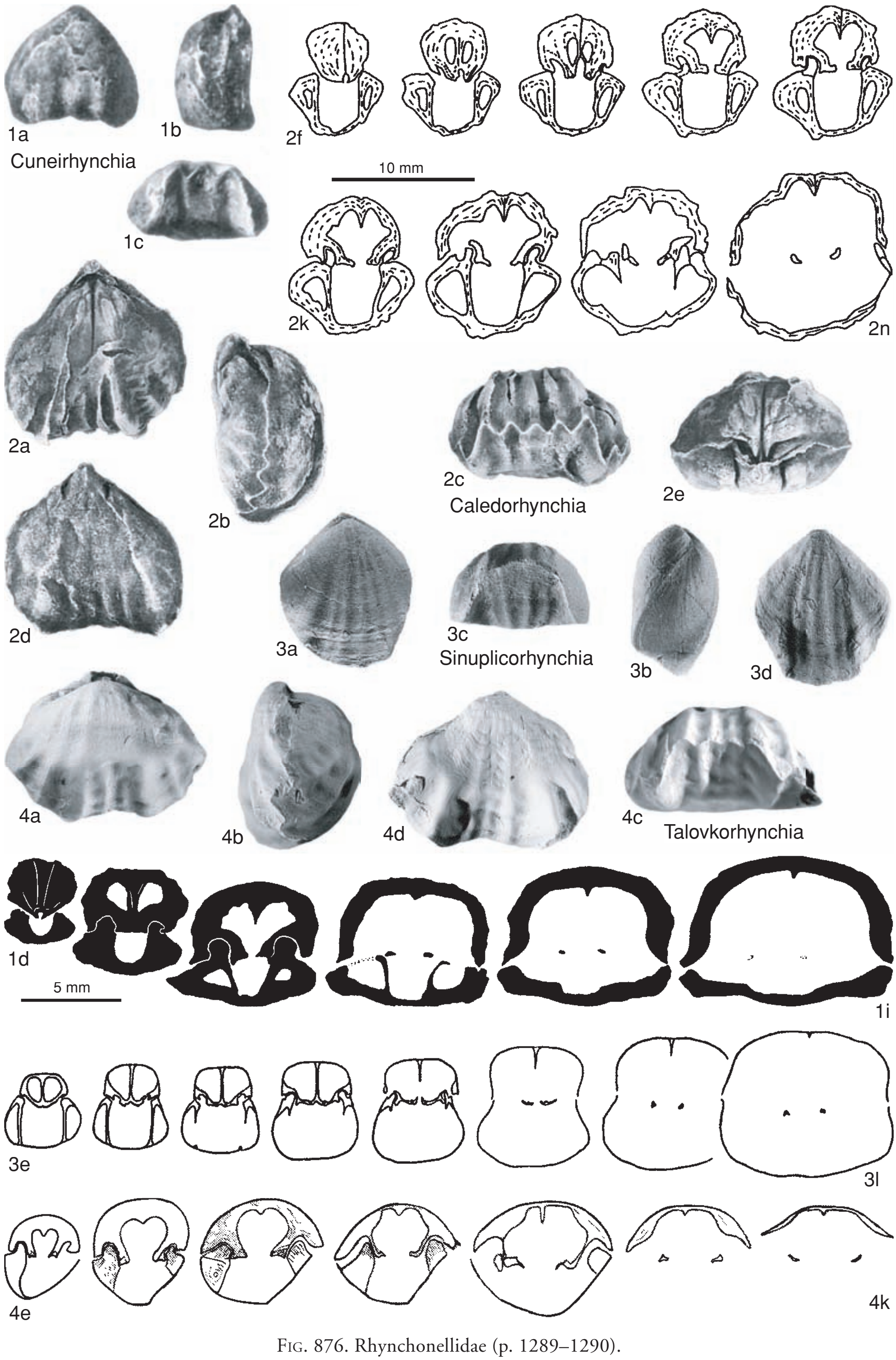

FIG. 876. Rhynchonellidae (p. 1289–1290).

Ladinian–lower Toarcian; Japan, Canada, Siberia, Primorye, Thailand, Hungary, *Carnian.*——FIG. 875,*4a–d.* **S. tokomboensis* KOBAYASHI & TOKUYAMA, Carnian, Kochi, Japan; syntype, dorsal, lateral, anterior, ventral views, ×1.5 (Tokuyama, 1957).——FIG. 875,*4e–k. S. zealandica* (TRECHMANN), Ladinian, Kaihikuan, Hokonui, New Zealand; transverse serial sections, distances in mm from ventral umbo, 1.3, 1.9, 2.2, 2.4, 2.6, 3.0, 3.7, OU NZ 15789 (MacFarlan, 1992).

Sinuplicorhynchia DAGYS, 1965, p. 56 [**S. kegalensis;* OD]. Small to medium size, rounded-pentagonal, distinctly uniplicate but with low fold. Sulcus and fold with low, rounded costae, lateral surfaces smooth; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates conjunct. Dental plates thin, subparallel, pedicle collar absent; dorsal septum long, more than one-half valve length, septalium narrow, distinct, outer hinge plates broad, incipiently ventrally convex, crura raduliform. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* northeastern Siberia, ?China, USA (Alaska).——FIG. 876,*3a–l.* **S. kegalensis,* Ladinian, northeastern Siberia; *a–d,* dorsal, lateral, anterior, ventral views, ×1 (new); *e–l,* transverse serial sections, distances in mm from first section, 0.7, 1.3, 1.7, 2.2, 2.7, 3.2, 3.7, 4.5 (Dagys, 1965).

?Tainuirhynchia MACFARLAN, 1992, p. 233 [**T. tainuii;* OD]. Medium size, subtriangular to subpentagonal; dorsibiconvex; uniplication flattopped, bidentate to pentadentate; fold and sulcus broad and low; posterior part smooth or with faint capillae, anterior with few, strong, round or angular costae; beak prominent, sharp, erect, with small foramen and short pedicle collar. Hinge plates short, thick, with deep, narrow septalium; dorsal median septum long, high; crural bases triangular. *Middle Jurassic (?Bathonian, Callovian)–Upper Jurassic (Tithonian):* New Zealand, ?New Caledonia. ——FIG. 874,*3a–k.* **T. tainuii,* Oxfordian, middle Heterian, Kawhia, New Zealand; *a–d,* holotype, dorsal, lateral, anterior, ventral views, AU B254, ×1.5; *e–k,* transverse serial sections, distances in mm from ventral umbo, 2.0, 2.2, 2.6, 3.0, 3.6, 4.2, 4.6, NZGS BR1791, ×2.8 (MacFarlan, 1992).

Talovkorhynchia SMIRNOVA, 1994, p. 31 [**T. pochialajneni;* OD]. Medium, moderately biconvex with prominent dorsal sulcus, deep ventral sulcus, and extensive trapezoidal linguiform extension; ornamentation of few strong costae with 4 on fold and 3 to 4 in ventral sulcus. Dental plates fused; hinge teeth massive, subquadrate, and slightly inwardly directed; hinge plates short, slender, dorsally concave; dorsal septum reduced to median ridge; crural bases with concave distal ends. *Lower Cretaceous (Albian):* northeastern Russia (Kamchatka). ——FIG. 876,*4a–k.* **T. pochialajneni; a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 138/405, ×1.5; *e–k* transverse serial sections, distances in mm from ventral umbo, 1.4, 2.1, 2.8, 3.4, 3.6, 4.5, 5.3, MGU 138/407, ×1.3 (Smirnova, 1994).

Subfamily URALORHYNCHIINAE new subfamily

[Uralorhynchiinae MANCEÑIDO & OWEN, herein]

Small to medium-sized Rhynchonellidae, moderately dorsibiconvex to subglobose; beak and foramen small; few coarse, rounded costae anteriorly and extensive posterior smooth areas, which may be finely capillate; arcuate uniplication not well detached from lateral slopes. Crura raduliform proximally, very close to strong dorsal median septum; septalium shallow; dental plates almost fused to wall; lateral umbonal chambers mostly filled up. *Middle Triassic (Ladinian)–Upper Triassic (Norian), Upper Jurassic (lower Volgian)–Lower Cretaceous (Berriasian).*

Uralorhynchia DAGYS, 1968, p. 54 [**Terebratula striatissima* D'EICHWALD, 1865–1868, p. 313; OD]. Large to medium size, smooth, strongly dorsibiconvex, oval; with dorsal median fold high, ill defined; ventral valve with broad, shallow extensive sulcus and linguiform extension; uniplicate anterior commissure showing faint marginal plicae. Short hinge plates with inner and outer socket ridges well developed; thickened septalium supported by short median septum; umbonal chambers callus filled. *Upper Jurassic (lower Volgian)–Lower Cretaceous (Berriasian):* northern Urals, Siberia.——FIG. 877,*1a–t.* **U. striatissima* (D'EICHWALD), upper Volgian, northern Siberia; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 256/78, ×1; *e–t,* transverse serial sections, distances in mm from first section, 0.4, 1.1, 1.5, 1.8, 2.0, 2.2, 2.7, 3.0, 3.2, 3.5, 3.8, 4.3, 4.8, 5.2, 5.5, 5.9, approximately ×1.5 (Dagys, 1968).

Omolonella MOISEEV, 1936, p. 39 [**O. omolonensis;* OD]. Medium size, oval, unequally biconvex, ventral valve essentially flattened with wide sulcus, fold low or absent, anterior commissure distinctly uniplicate, smooth, with costae few and faint anteriorly; beak short, incurved, ridges rounded, foramen submesothyrid, deltidial plates conjunct. Dental plates, septum, and septalium distinct in young specimens, in adults umbonal chambers filled with callus, crura thick, raduliform; pedicle collar absent. *Upper Triassic (Norian):* northeastern Siberia, southwestern China.——FIG. 877,*3a–v.* **O. omolonensis,* northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, TsGM 30/4803, ×1 (Moiseev, 1936); *e–v,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.6, 0.9, 1.1, 1.3, 1.6, 1.8, 2.1, 2.5, 2.7, 3.1, 3.3, 3.6, 4.0, 4.2, 4.5, 4.7 (Dagys, 1965).

Sulcorhynchia DAGYS, 1974, p. 103 [**Holcorhynchia borealis* DAGYS, 1965, p. 75; OD]. Small, rounded-pentagonal to oval, moderately equibiconvex;

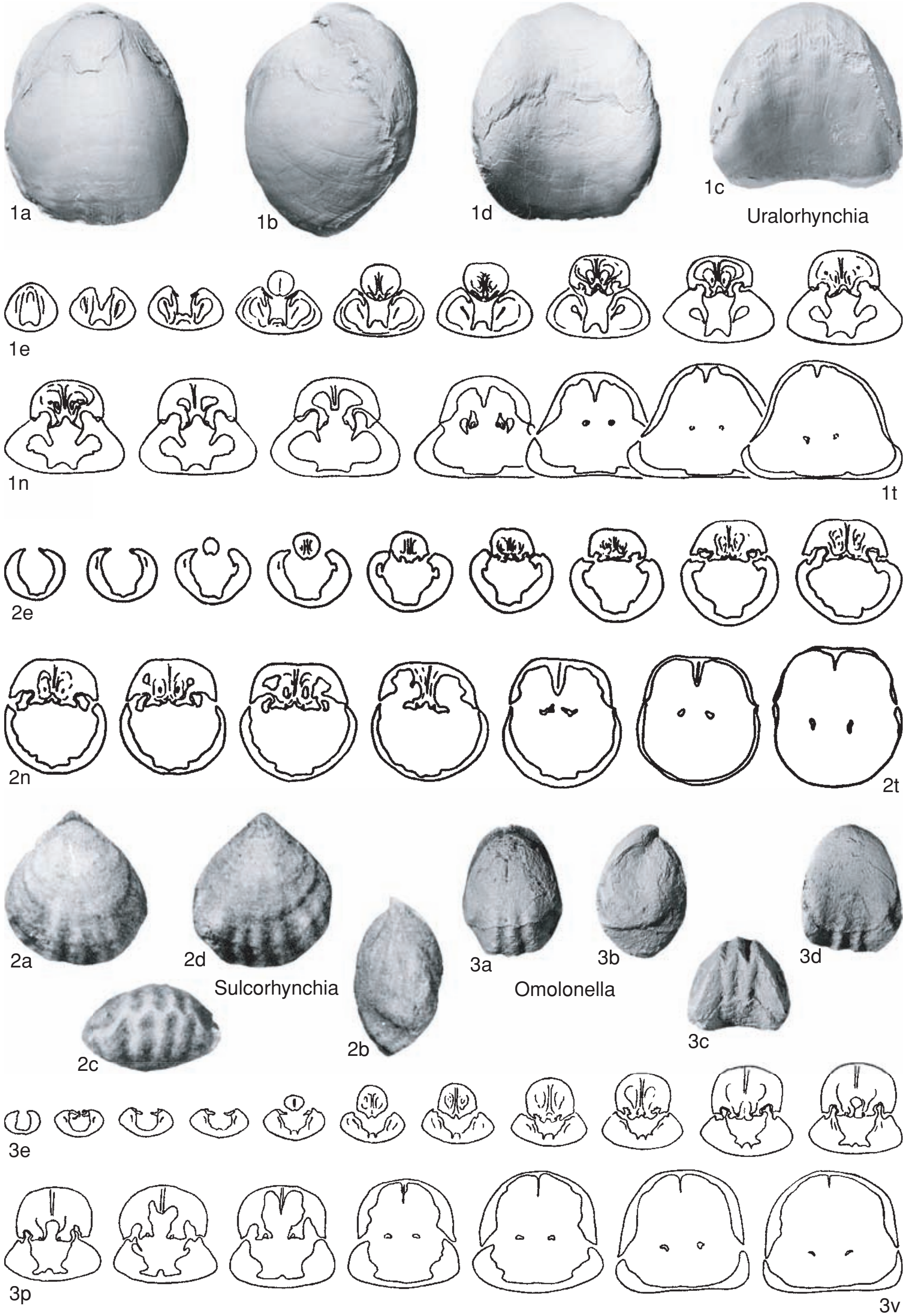

FIG. 877. Rhynchonellidae (p. 1290–1292).

posterior with dorsal sulcus, anterior with low, indistinct dorsal fold and matching shallow ventral sulcus; costae few and rounded in anterior part, posteriorly smooth; beak short, incurved, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Young specimens with distinct diverging dental plates, high septum, supporting deep septalium; adults with massive cardinalia, umbonal chambers filled with callus, crura thin, raduliform. *Middle Triassic (Ladinian)–Upper Triassic (Norian):* northeastern Siberia, Himalayas, Japan.——FIG. 877,*2a–t.* **S. borealis* (DAGYS), Norian, northeastern Siberia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 146/118, ×1.5; *e–t,* transverse serial sections, distances in mm from first section, 0.0, 0.3, 0.7, 0.8, 0.9, 1.0, 1.2, 1.4, 1.5, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, 3.1 (Dagys, 1965).

Subfamily IVANOVIELLINAE Makridin, 1964

[Ivanoviellinae MAKRIDIN, 1964, p. 129] [=Ivanoviellinae KATS, 1962, p. 132, *nom. nud.*]

Small- to medium-sized Rhynchonellidae, with costae strong and subangular to rounded, and posterior smooth area variably developed; uniplication well marked and linguiform extension often well developed; subcynocephalous to cynocephalous. Septalium reduced, sometimes sessile or absent, dorsal median septum variably developed, crura calcariform. *Upper Triassic (Norian)–Upper Cretaceous (Maastrichtian).*

Ivanoviella MAKRIDIN, 1955, p. 83, *non* IVANOVA in ABUSHIK & others, 1960, Ostracoda [**Rhynchonella alemanica sensu* MAKRIDIN, 1955*;* OD; *non* ROLLIER, 1917; =*Ivanoviella gaetanii* ALMÉRAS, BENIGNI, & TINTORI, 1991, p. 431] [=*Jvanoviella* MAKRIDIN, 1955, p. 83 (alternative original spelling, first reviser AGER, 1965, p. 611); *Ivanoviella* MAKRIDIN, 1954, p. 103, *nom. nud.; Ivanowiella* WISNIEWSKA-ZELICHOWSKA, 1978, p. 65, *nom. null.*]. Small, sulcus and fold pronounced in maturity, radial costae numerous, narrow, simple, covering shell, beginning near beak after variable smooth stage; beak slender, short, usually weakly incurved, foramen elliptical, sometimes almost circular, submesothyrid; deltidial plates conjunct. Dental plates thin, wide apart, becoming detached around articulation zone; crura short, bladelike, extending ventrally; dorsal septum thin, united with hinge plate margins; ventral muscle scars rounded-rectangular, dorsal anterior adductors pear shaped, dorsal posterior adductors oval. *Middle Jurassic (Bajocian–Callovian), Upper Jurassic (?Oxfordian):* France, Germany, Switzerland, Russian Platform, Poland, Crimea, Caucasus, central Asia, western Himalayas (India, Nepal), China.——FIG. 878,*3a–l.* **I. gaetanii* ALMÉRAS, BENIGNI, & TINTORI, Middle Callovian, Ryazan region, Russia; *a–c,* dorsal, lateral, anterior views, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.7, 2.05, 2.6, 2.75, 3.0, 3.1, 3.5, 3.7 (Makridin, 1964).

Bihendulirhynchia MUIR-WOOD, 1935, p. 104 [**B. afra;* OD] [=*Bihenidulirhynchia* SHI, 1987a, p. 20, *nom. null.*]. Small, dorsibiconvex, smooth and sulcate posteriorly, uniplicate anteriorly with low fold and about 10 subangular costae (3 to 4 on fold; beak erect, foramen hypothyrid, disjunct deltidial plates. Pedicle collar present; dorsal median septum short and low; septalium shallow, confined to apex; calcariform crura shaped as curved blades. *Middle Jurassic (Bathonian–Callovian), Upper Jurassic (?lower Kimmeridgian):* Somaliland, ?Kenya, ?Iran, ?India, ?China.——FIG. 878,*2a–j.* **B. afra,* ?lower Kimmeridgian, Daghani, Somaliland; *a–c,* holotype, dorsal, lateral, anterior views, BMNH B.85633, ×1; *d–j,* transverse serial sections, BMNH B.89276 (Muir-Wood, 1935).

?Bradfordirhynchia SHI & GRANT, 1993, p. 26 [**Cryptorhynchia bradfordensis* BUCKMAN, 1918, p. 228; OD]. Similar to *Sharpirhynchia,* but dental plates gently ventrally divergent, septalium short, pitlike, or pendant (though allegedly absent), and crura with slightly more extended subvertical blades. [Distinction between these two closely similar genera requires better substantiation.] *Middle Jurassic (upper Bathonian):* England, France.——FIG. 878,*5a–k.* **B. bradfordensis* (BUCKMAN), Bradford-on-Avon, England; *a–c,* topotype, dorsal, lateral, anterior views, USNM 104765b, ×1; *d–k,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.9, 2.2, 2.8, 3.3, 3.7, 3.9, 4.2, 4.6, USNM 104765d (Shi & Grant, 1993).

Grasirhynchia OWEN, 1968, p. 19 [**Rhynchonella grasiana* D'ORBIGNY, 1849 in 1848–1851, p. 38; OD]. Small to medium, transversely oval to subcircular; almost planoconvex, dorsal valve markedly convex with imperceptible median fold; ventral valve less convex with wide shallow sulcus; anterior commissure broadly arcuate; linguiform extension extensive; umbo short, beak suberect with small foramen and auriculate deltidial plates; interarea triangular, poorly exposed; beak ridges hypothyrid. Crura long. *Cretaceous (upper Albian–Cenomanian):* England, France, Germany, Denmark, Belgium, ?Poland, Crimea.——FIG. 879,*1a–k.* **G. grasiana* (D'ORBIGNY), Cenomanian; *a–c,* lectotype, dorsal, lateral, anterior views, MNHN 6497, Le Havre, France, ×2; *d,* detail of apical region showing auriculate deltidial plates, Le Havre, France, BMNH BB.84908, ×6; *e–k,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.1, 1.3, 1.5, 2.1, 2.6, 3.0, BMNH BB.43909, Sussex, England, ×3.5 (Owen, 1968).

?Himalairhynchia CHING & SUN in CHING, SUN, & RONG, 1976, p. 292 [**H. media;* OD]. Small to medium size, roundly pentagonal, equibiconvex, truncated front and sides steeply sloping, fold and sulcus developed only in anterior half and

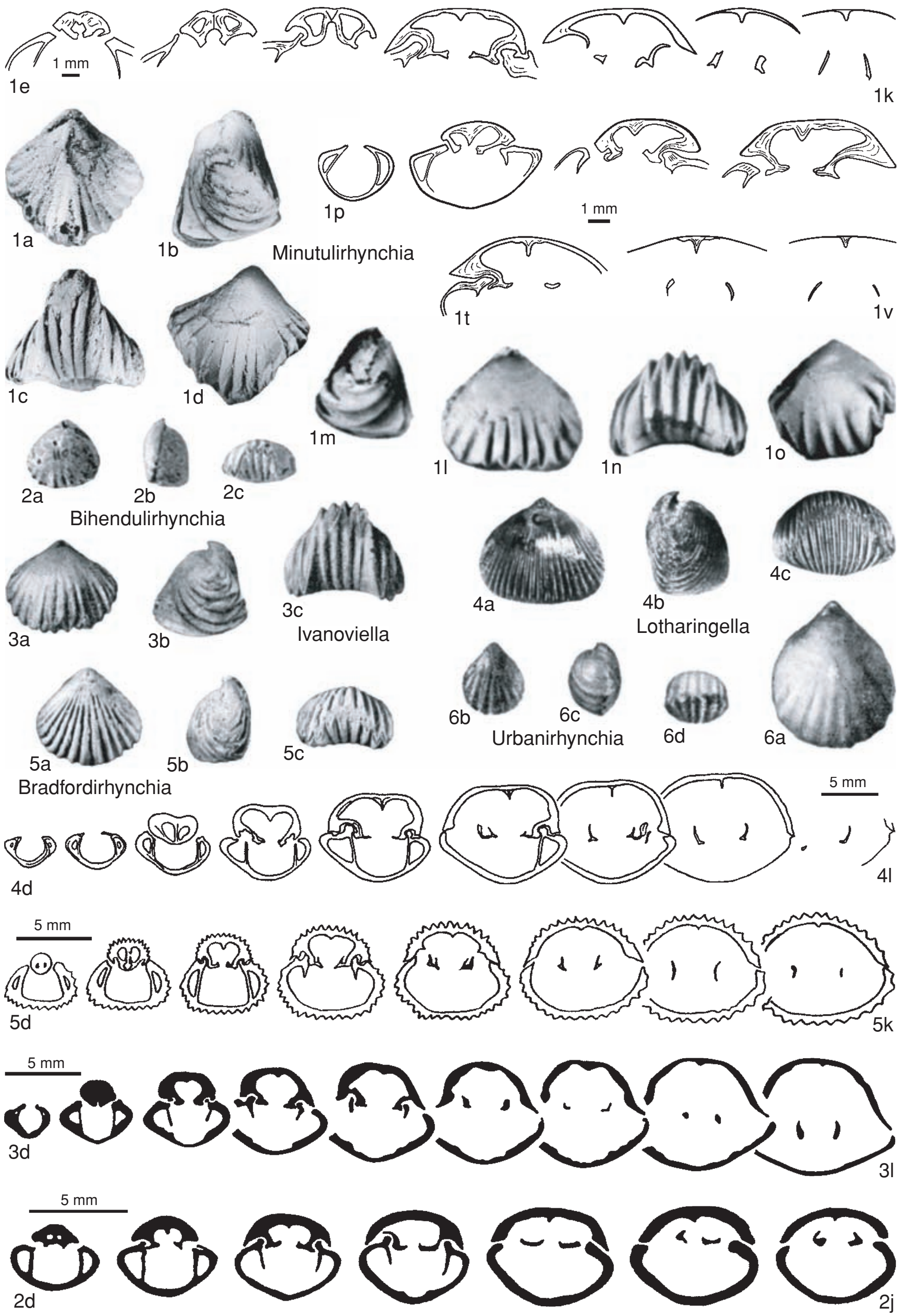

FIG. 878. Rhynchonellidae (p. 1292–1297).

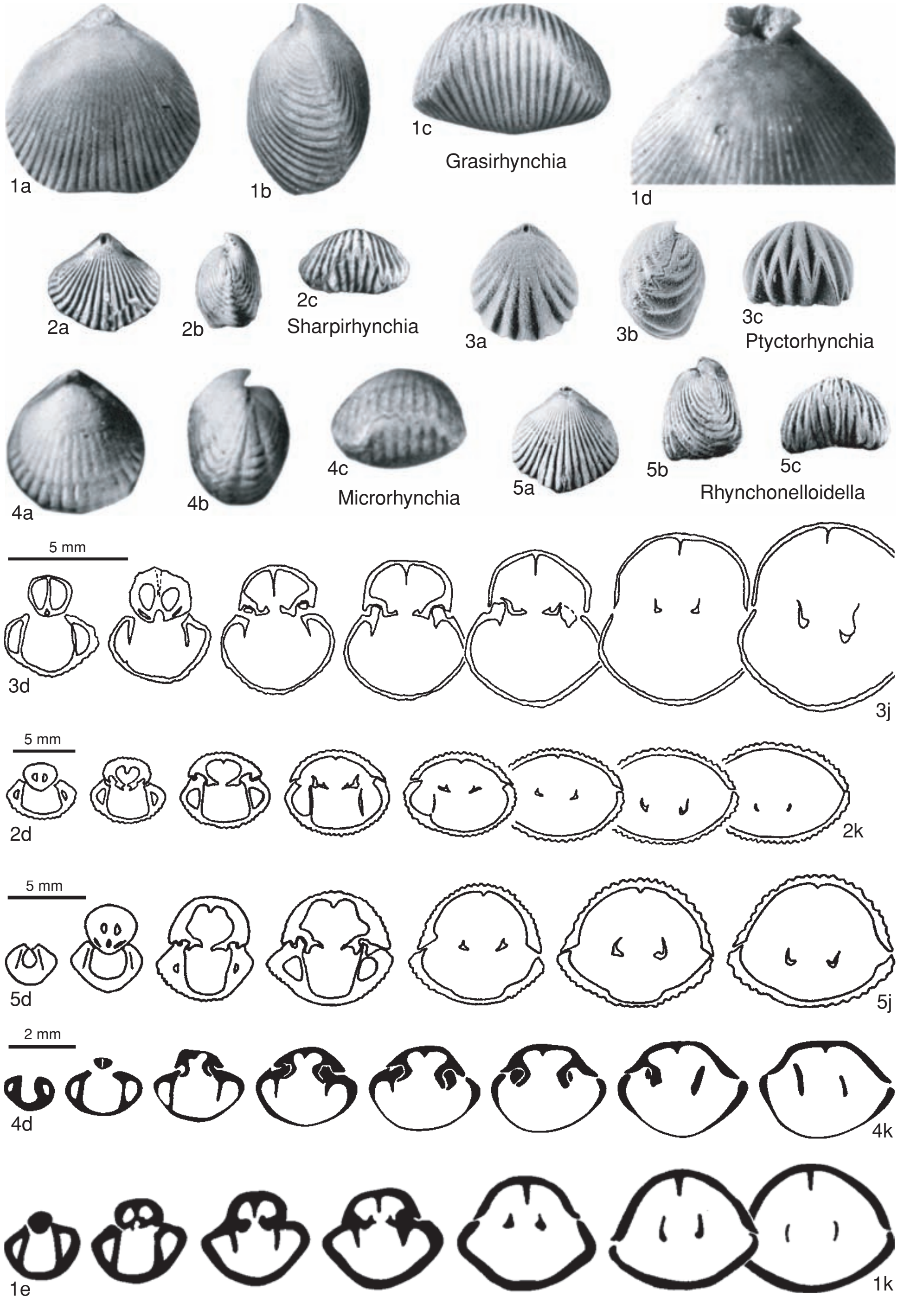

FIG. 879. Rhynchonellidae (p. 1292–1297).

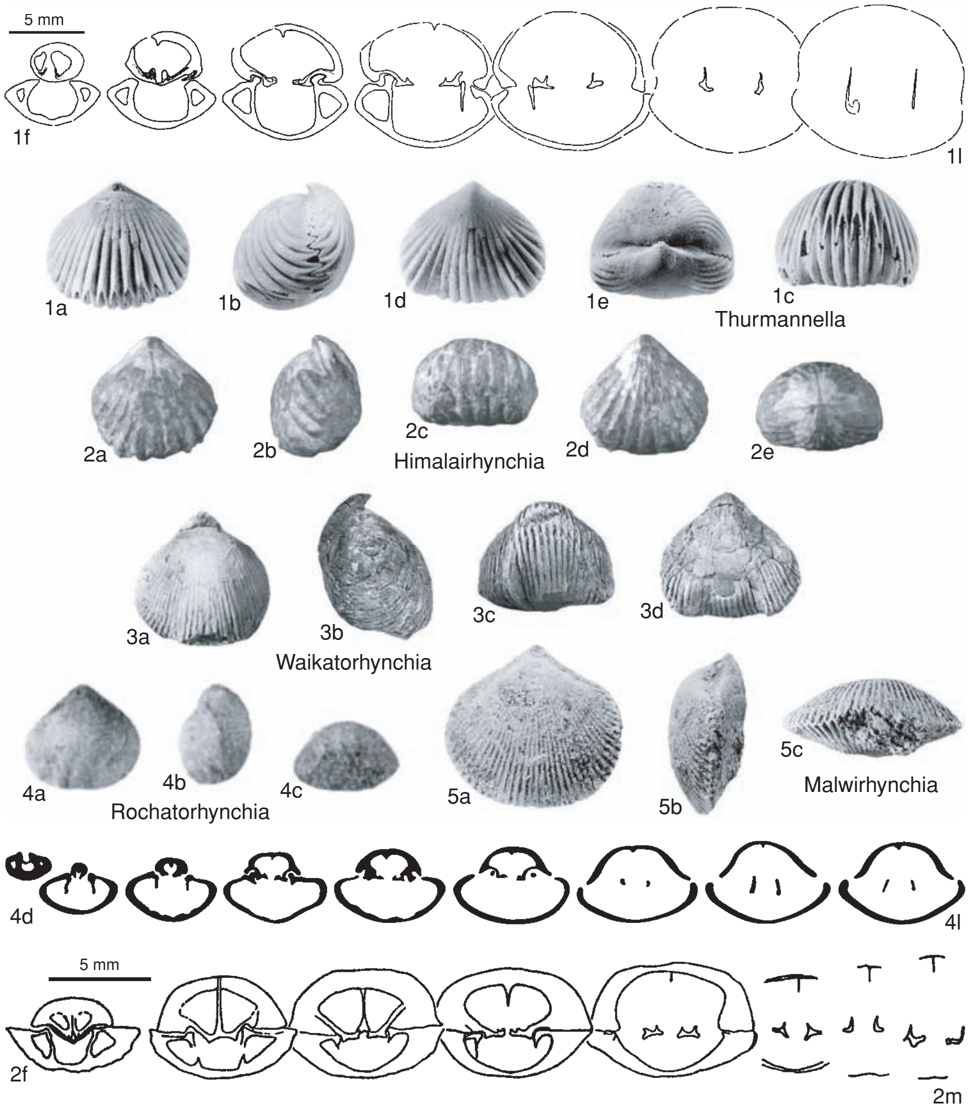

FIG. 880. Rhynchonellidae (p. 1292–1297).

demarcated clearly from sides; linguiform extension subquadrate; subangular costae starting from beak; furrows between costae projecting beyond margin of valves as slender spines and extending under costae of opposite valve; beak short and slightly incurved; beak ridges obtuse, delthyrium covered by symphytium; foramen circular, permesothyrid. Dental plates short, thin and ventrally convergent; hinge plates flat, subhorizontal, median septum supporting septalium; crura calcariform, distally modified. *Upper Triassic (Norian):* China (Qinghai, Tibet), Austria.——FIG. 880,*2a–m.* **H. media,* Tibet; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, NIGP 28746, ×1.5 (new); *f–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.9, 2.3, 2.5, 2.7, 3.0, 3.4, 3.8, 4.3, NIGP 28749 (Ching, Sun, & Rong, 1976).

Lotharingella LAURIN, 1984, p. 368 [**L. woevrica;* OD]. Small to medium size, globose equibiconvex to dorsibiconvex; with arcuate uniplication relatively narrow but without raised fold on dorsal valve; fine costae developing after a rather well-marked sulcate stage (6 to 9 on uniplication); beak small, incurved, with rather sharp beak ridges.

Septalium apparently absent; crura varying its shape during ontogeny, from calcariform to nearly raduliform. *Middle Jurassic (lower Bathonian–lower Callovian):* France, England, China (Qinghai, Tibet).——FIG. 878,*4a–c*. **L. woevrica woevrica,* Bathonian, Lorraine, France; holotype, dorsal, lateral, anterior views, ×1 (Laurin, 1984).——FIG. 878,*4d–l*. *L. woevrica minor* LAURIN, Bathonian, France; transverse serial sections, distances in mm from ventral umbo, 1.9, 2.2, 2.7, 3.1, 3.6, 4.0, 4.3, 4.7 (Laurin, 1984).

Malwirhynchia CHIPLONKER, 1938, p. 306 [**M. transversalis;* OD]. Small, transversely oval, uniplication low, broadly arcuate, and dorsal fold ill defined; costellae numerous and fine, bifurcating anteriorly; umbo short, beak suberect with relatively large foramen; deltidial plates conjunct, auriculate; dorsal umbo planate. Median septum low, up to one-half the length of dorsal valve; crural bases extended dorsally; crura ventrally deflected. *Cretaceous (Albian–Cenomanian):* India, ?Don basin.——FIG. 880,*5a–c*. **M. transversalis,* India; dorsal, lateral, anterior views, BMNH unregistered, ×1.5 (new).

?Microrhynchia MUIR-WOOD, 1952, p. 124 [**M. barnackensis;* OD]. Small, rarely sulcoconvex in early stage, becoming biconvex, everted, median fold and sinus often ill defined; shell smooth to finely costate; beak suberect to slightly incurved, deltidial plates conjunct in adult; hypothyrid to just mesothyrid. Dental plates thin, subparallel; median septum extending almost up to midvalve; crura calcariform; hinge plates almost indistinguishable from inner socket ridges and obliquely inclined relative to low median septum. *Middle Jurassic (?Aalenian, Bajocian):* England, ?France, ?Russia. ——FIG. 879,*4a–k*. **M. barnackensis,* Bajocian, Northamptonshire, England; *a–c,* holotype, dorsal, lateral, anterior views, BMNH BB.9718, ×4; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.6, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3, BMNH B.15856 (Muir-Wood, 1952).

Minutulirhynchia SMIRNOVA, 1992, p. 27 [**M. triangularis;* OD] [=*Sulciphoria* SMIRNOVA, 1992, p. 23 (type, *S. acutimarginata* SMIRNOVA, 1992, p. 24, OD)]. Small, acutely biconvex to cynocephalous, with ventral sulcus deep, and linguiform extension greatly extended; 1 to 2 costae on lateral flanks of sulcus. Dental plates parallel to ventrally divergent; dorsal septum low, ridgelike; septalium almost sessile; crura strongly curved, distally shaped as flat, inclined blades. [Differences between each type species insufficient for generic separation, and clear distinction of both from *Rhynchonelloidella* MUIR-WOOD, 1936b, p. 49 and *Ivanoviella* MAKRIDIN, 1955, p. 83 requires substantiation.] *Middle Jurassic (Callovian)–Upper Jurassic (Oxfordian):* Kazakhstan (Aktyubinsk region).——FIG. 878,*1a–k*. **M. triangularis,* Callovian; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 139/1311, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.7, 1.6, 1.9, 2.2, 2.32, 2.41, 2.53 (Smirnova, 1992).——FIG. 878,*1l–v*. *M. acutimarginata* (SMIRNOVA), Callovian; *l–o,* holotype, dorsal, lateral, anterior, ventral views, MGU 139/1673, ×2; *p–v,* transverse serial sections, distances in mm from first section, 0.2, 1.0, 1.5, 1.73, 2.46, 2.96, 3.56, MGU 139/1701 (Smirnova, 1992).

Ptyctorhynchia BUCKMAN, 1918, p. 47 [**Rhynchonella pentaptycta* BUCKMAN, 1910, p. 103; OD] [=*Ptyctorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Ptychtorhynchia* AGER, CHILDS, & PEARSON, 1972, p. 163, *nom. null.*]. Small, subcircular, globose, subequibiconvex; uniplication low and wide and fold indistinct; smooth stage posteriorly and relatively strong, round, costae developed anteriorly (5 to 7 on fold); beak small, suberect, with hypothyrid, slightly rimmed, foramen. Dorsal median septum well developed; septalium variable; crura deflected ventrally as curved blades. *Lower Jurassic (?upper Toarcian), Middle Jurassic (Aalenian, ?lower Bajocian):* England, ?France, ?Spain, ?Morocco, Tibet.——FIG. 879,*3a–j*. **P. pentaptycta* (BUCKMAN), ?uppermost Toarcian, Aalenian, Dorset, England; *a–c,* dorsal, lateral, anterior views, BMNH B.68376, ×1.5 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.3, 1.5, 1.8, 2.0, 2.2, 2.7, 3.1, CDP 7, C. D. Prosser, personal collection (new; courtesy of C. Prosser).

Rhynchonelloidella MUIR-WOOD, 1936b, p. 49 [**Rhynchonella varians* var. *smithii* DAVIDSON, 1878, p. 213; OD] [=*Phynchonelloidella* SHI, 1987a, p. 20, *nom. null.*]. Medium size, subtrigonal to subpentagonal, dorsibiconvex to cynocephalous; ventral valve often almost flat, dorsal valve everted; strongly uniplicate, dorsal fold variably raised; costae numerous, fine, subangular (3 to 10 on fold); beak small, suberect to incurved. Dental plates long, umbonal chambers small; dorsal median septum low, supporting septalium; crura calcariform or slight variant thereof. *Lower Jurassic (Toarcian), Middle Jurassic (Aalenian–Callovian), Upper Jurassic (?Oxfordian):* England, France, Germany, Switzerland, Poland, Russia, Crimea, Caucasus, ?Armenia, China, Argentina, *Bajocian–Callovian, ?Oxfordian;* Spain, *Aalenian;* Morocco, *Toarcian.*——FIG. 879,*5a–j*. **R. smithii* (DAVIDSON), Bathonian, Bath, Somerset, England; *a–c,* topotype, dorsal, lateral, anterior views, USNM 75628a, ×1; *d–j,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.6, 2.3, 3.1, 3.4, 4.0, 4.3, USNM 75628d (Shi & Grant, 1993).

Rochatorhynchia KATS, 1962, p. 132 [**R. rochatensis;* OD]. Small, smooth, equibiconvex, rounded-pentagonal to broadly oval; maximum breadth and thickness at midvalve; sulcus and fold poorly defined; anterior commissure polyplicate with linguiform extension moderately long; beak short, suberect, beak ridges distinct, foramen small, circular, mesothyrid to permesothyrid. Pedicle collar present; dental plates thin, subparallel; dorsal septum low, short with septalium in early stages; hinge plates divided; crural bases often V-shaped. *Upper Cretaceous (Maastrichtian):* Tadzhikistan.——FIG. 880,*4a–l*. **R. rochatensis,* lower Maastrichtian; *a–c,* dorsal, lateral, anterior views, KHGU 4-787, ×1;

d–l, transverse serial sections, distances in mm from ventral umbo, 0.5, 1.6, 2.2, 3.1, 3.4, 3.7, 4.2, 4.3, 4.5, ×1 (Kats, 1962).

Sharpirhynchia Shi & Grant, 1993, p. 49 [**Kallirhynchia sharpi* Muir-Wood, 1938, p. 74; OD]. Small, depressed to moderately dorsibiconvex, subtrigonal to transverse-oval; uniplicate, with low dorsal fold; fully costate, with numerous fine costae and conspicuous, dense growth lines; beak suberect, with rimmed hypothyrid foramen. Dorsal median septum reduced; septalium absent (but if present, tiny, pitlike); relatively narrow calcariform crura. *Middle Jurassic (?upper Bajocian, lower Bathonian):* England, France.——Fig. 879,*2a–k.* **S. sharpi* (Muir-Wood), lower Bathonian, Kettering, England; *a–c,* dorsal, lateral, anterior views, USNM 429195, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.8, 2.1, 2.8, 3.2, 3.4, 4.0, 4.6, 4.8, USNM 429196 (Shi & Grant, 1993).

Thurmannella Leidhold, 1921, p. 357 [**Terebratula obtrita* Defrance, 1828, p. 161–162; SD Schuchert & LeVene, 1929a, p. 124] [=*Thurmanella* Wisniewska, 1932, p. 3, unjustified emendation]. Small to medium size, subpentagonal, dorsibiconvex to almost convexiplane; with uniplication strong and fold slight; linguiform extension high, trapeziform; posterior smooth area variably developed, with numerous simple, subangular costae (4 to 9 on fold); beak small, sharp, suberect. Dorsal median septum short and thick, septalium poorly developed; crura calcariform, strongly curved and expanded ventrally, with distal points directed toward each other. *Middle Jurassic (middle Callovian)–Upper Jurassic (lower Oxfordian, ?lower Tithonian):* England, France, Switzerland, Russian platform, Crimea, Caucasus, China (?Qinghai), Argentina, ?Indonesia, ?Algeria.——Fig. 880,*1a–l.* **T. obtrita* (Defrance), lower Oxfordian, Lorraine, France; *a–e,* dorsal, lateral, anterior, ventral, posterior views, BMNH BB.44154, ×1 (new); *f–l,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.4, 1.6, 2.0, 2.4, 2.8, 3.2, 3.6 (Childs, 1969).

?Urbanirhynchia Kats, 1974, p. 252 [**U. urbani;* OD]. Small, subcircular, subequibiconvex; paucicostate with some intercalations toward the anterior margin; uniplication broad, arcuate. Septalium narrow and buttressed by euseptum; crura well developed, reported as calcariform. *Upper Cretaceous (Cenomanian–Turonian):* Don basin, Crimea, Caucasus, Russia.——Fig. 878,*6a–d.* **U. urbani,* upper Turonian, Don basin; *a,* dorsal view, ×2; *b–d,* holotype, ventral, lateral, anterior views, ×1 (Kats, 1974).

?Waikatorhynchia MacFarlan, 1992, p. 243 [**W. waikatoensis;* OD]. Medium size, elongate-oval to subcircular outline; equibiconvex to dorsibiconvex, inflation moderate to great; dorsal valve with flat central part posteriorly and strongly convex lateral slopes; rectimarginate or with arcuate uniplication; fold and sulcus poorly developed; costae even and dense throughout; beak sharp, erect to slightly incurved, with sharp beak ridges and short pedicle collar. Hinge plates short, with small septalium; dorsal median septum high, narrow; dental plates wide apart, umbonal chambers narrow; crura unknown. *Upper Jurassic (Kimmeridgian–Tithonian):* New Zealand (North Island).——Fig. 880,*3a–d.* **W. waikatoensis,* Tithonian, Puaroan; holotype, dorsal, lateral, anterior, ventral views, AU B273, ×1 (MacFarlan, 1992).

Subfamily NUCLEUSORHYNCHIINAE Xu, 1990

[*nom. transl.* Owen & Manceñido, herein, *ex* Nucleusorhynchiidae Xu, 1990, p. 77]

Rhynchonellidae with smooth shell and typically rectimarginate commissure; ventral sulcus absent and dorsal fold inconspicuous, broad, and flat if present. Dental plates developed; dorsal median septum and septalium present; crura raduliform. *Middle Triassic (Anisian)–Lower Jurassic (Hettangian, ?Sinemurian).*

Nucleusorhynchia Sun & Ye, 1982, p. 159[170] [**N. typica;* OD]. Small, gently biconvex, lenticular, smooth, rectimarginate; beak short and small; foramen permesothyrid; deltidial plates discrete; beak ridges rounded. Dental plates subparallel; septalium wide and shallow; median septum thick and low; crura rodlike proximally, narrow, bladelike, inclined inward distally, and slightly curved ventrally. *Middle Triassic (Anisian):* China (Qinghai).——Fig. 881,*1a–j.* **N. typica; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67026, ×2; *e–j,* holotype, transverse serial sections, distances in mm from ventral umbo, 0.68, 0.94, 1.12, 1.4, 1.58, 2.22, NIGP 67026 (Sun & Ye, 1982).

?Murihikurhynchia MacFarlan, 1992, p. 131 [**M. malingi;* OD]. Small subtriangular to subpentagonal; equibiconvex, slightly to moderately inflated; lateral slopes of both valves more strongly convex than central part; dorsal valve flat or sulcate posteriorly, with uniplication broad, shallow anteriorly; fold and sulcus low; costae few, low, blunt, after long posterior smooth stage (exceptionally non-costate); beak small, sharp, erect, with rounded beak ridges; deltidial plates disjunct. Hinge plates thick, flat, often with medially ridged shallow septalium; dorsal median septum long, thin, moderately high. *Upper Triassic (upper Carnian)–Lower Jurassic (Hettangian, ?Sinemurian):* New Zealand, New Caledonia.——Fig. 881,*2a–b.* **M. malingi,* lower Norian, Otamitan, Southland syncline, New Zealand; holotype, dorsal, ventral views, OU NZ 16428, ×2 (MacFarlan, 1992).——Fig. 881,*2c–e. M. braxtonensis* MacFarlan, upper Carnian–Norian, Oretian, Southland syncline, New Zealand; holotype, dorsal, lateral, anterior views, OU NZ 16641, ×1 (MacFarlan, 1992).

Uniplicatorhynchia Sun & Ye, 1982, p. 158[169] [**U. trigona;* OD]. Medium size, subtriangular to round pentagonal, equibiconvex, smooth; broad, low ventral sulcus and dorsal fold; commissure uniplicate,

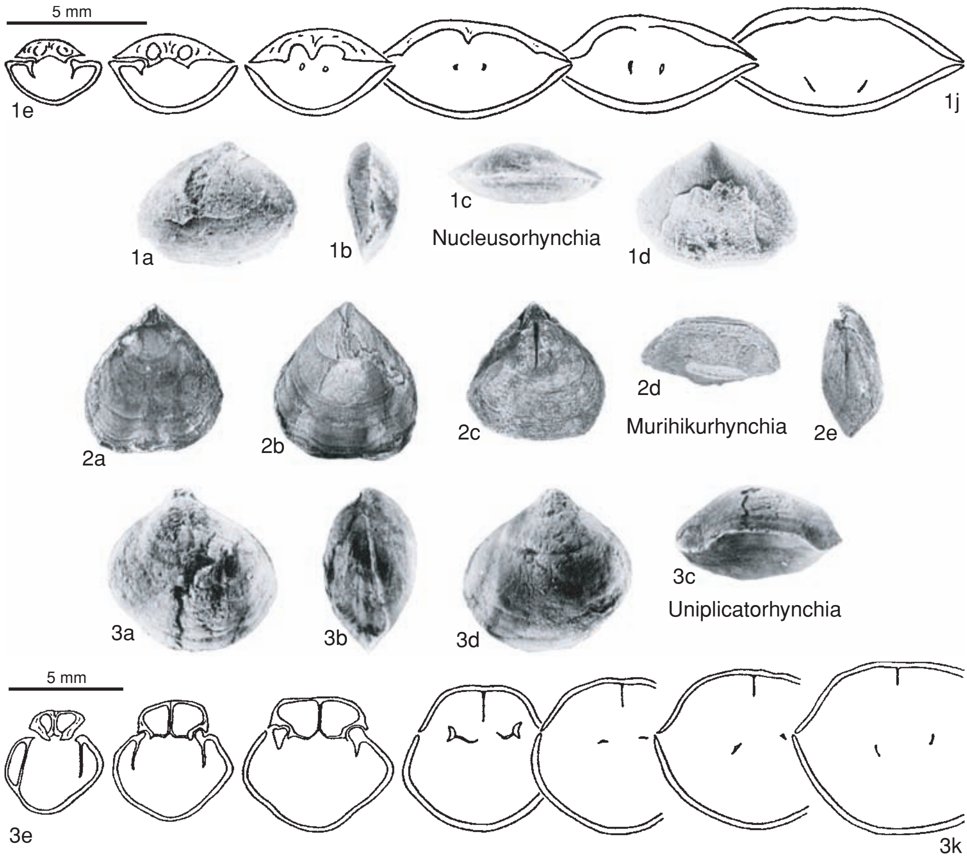

FIG. 881. Rhynchonellidae (p. 1297–1298).

flattopped; ventral beak small, incurved; foramen small, permesothyrid; delthyrium open. Dental plates long and parallel; hinge plates flat, subhorizontal; shallow, V-shaped septalium; median septum thin, high, long; crura raduliform, with trigonal crural bases and narrow bladelike distal ends. *Middle Triassic (Anisian)–Upper Triassic (Carnian):* China (Qinghai), Nepal.——FIG. 881,*3a–k.* **U. trigona,* Anisian, Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 67025, ×1.5; *e–k,* holotype, transverse serial sections, distances in mm from ventral umbo, 1.1, 1.5, 1.75, 2.1, 2.35, 2.7, 3.05, NIGP 67025 (Sun & Ye, 1982).

Subfamily BILAMINELLINAE Babanova, 1964

[*nom. transl.* OWEN & MANCEÑIDO, herein, *ex* Bilaminellini BABANOVA, 1964, p. 66; *emend.,* OWEN & MANCEÑIDO, herein]

Small- to medium-sized Rhynchonellidae, transversely elliptical, almost fully costate, with uniplication wide, flattopped, bearing a fairly dense, delicate, blunt costation superimposed. Ventral valve with pair of ovoid posterolateral hinge pouches that, in cross section, give impression of bifurcate dental plates (alluded to in original diagnosis of tribe); dental plates subparallel, umbonal chambers ample; crura raduliform or variation thereof; septalium present, at least in early ontogeny. *Upper Triassic (Norian)–Middle Jurassic (Callovian), Upper Jurassic (?Oxfordian).*

Bilaminella BABANOVA, 1964, p. 66 [**B. inaequicostata;* OD]. Medium size, subpentagonal, depressed dorsibiconvex, broadly uniplicate; radial costae narrow, simple, rounded. Hinge teeth and denticula well developed; alleged radially bifurcated dental plates due to convergence of pouch structure walls with subparallel dental plates; septalium observed only in early stages of shell; crura calcariform. *Middle Jurassic (Callovian), Upper Jurassic*

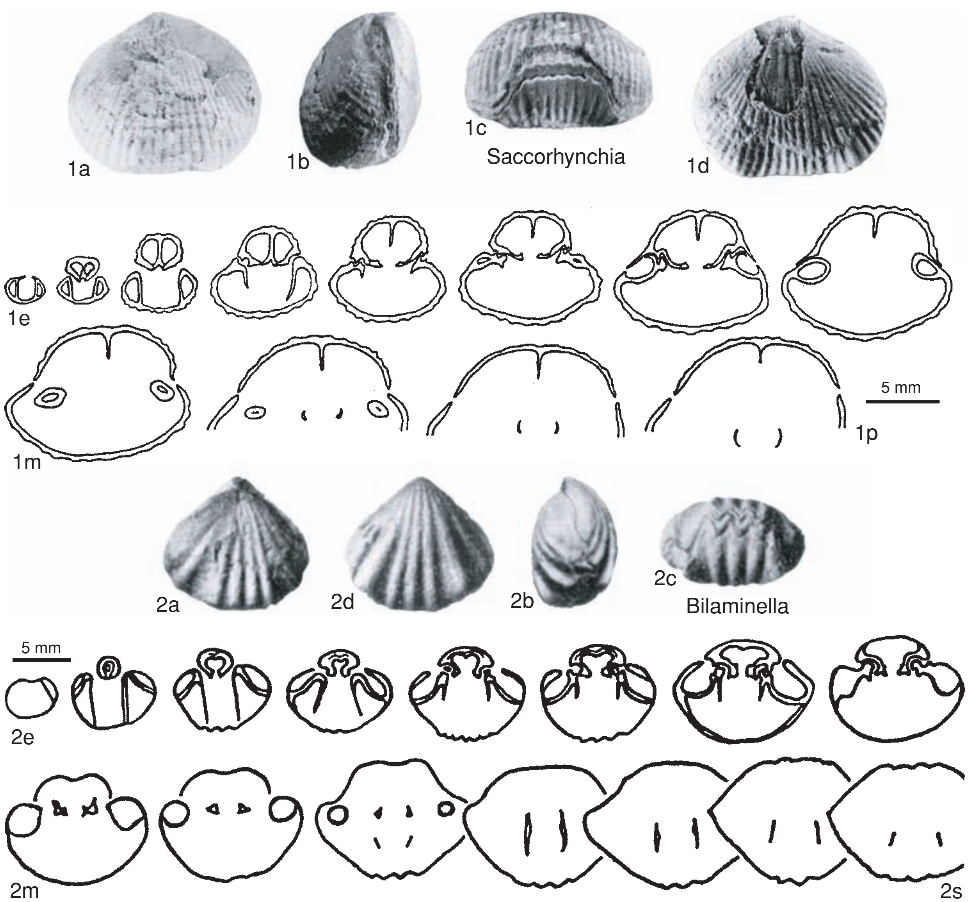

FIG. 882. Rhynchonellidae (p. 1298–1299).

(?Oxfordian): Ukraine (Crimea), central Asia.——FIG. 882,*2a–s*. **B. inaequicostata,* upper Callovian, Crimea; *a–d,* holotype, dorsal, lateral, anterior, ventral views, KHGU 4031/8, ×2 (Babanova, 1964); *e–s,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.4, 0.5, 0.6, 0.9, 1.1, 1.2, 1.3, 1.4, 1.6, 1.8, 1.9, 2.4, 2.8, 3.1, KHGU 2007/8 (Kamyshan & Babanova, 1973).

Saccorhynchia CHING, SUN, & YE in CHING & others, 1979, p. 154 [**S. xiangdaica;* OD]. Large size; roundly pentagonal, dorsibiconvex; fold and sulcus low, developed only anteriorly; linguiform extension roundly arched; costae thin, round, beginning from beak and increasing by intercalation or bifurcation; beak short and nearly straight; foramen submesothyrid; delthyrium covered by raised symphytium. Teeth angular; dental plates short, subparallel; pouch structure present anterolaterally of dental plate; dorsal septum high; septalium short and shallow; crura raduliform. *Upper Triassic (Norian):* China (Qinghai, Xizang).——FIG. 882,*1a–p*. **S. xiangdaica,* Qinghai; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42830, ×1; *e–p,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.65, 1.0, 1.2, 1.3, 1.9, 2.3, 3.25, 3.55, 3.75, 4.3, 4.8, NIGP 42830 (Ching & others, 1979).

Subfamily DAVANIRHYNCHIINAE Ovcharenko, 1983

[Davanirhynchiinae OVCHARENKO, 1983, p. 41]

Small- to medium-sized Rhynchonellidae with complex, antidichotomous costae; thin, ventrally divergent to subparallel dental plates; subhorizontal hinge plates; dorsal median septum and septalium variously developed, and raduliform to calcariform crura. [These are reminiscent of Paleozoic yunnannellids.] *Upper Triassic (Norian)–Lower Cretaceous (Valanginian).*

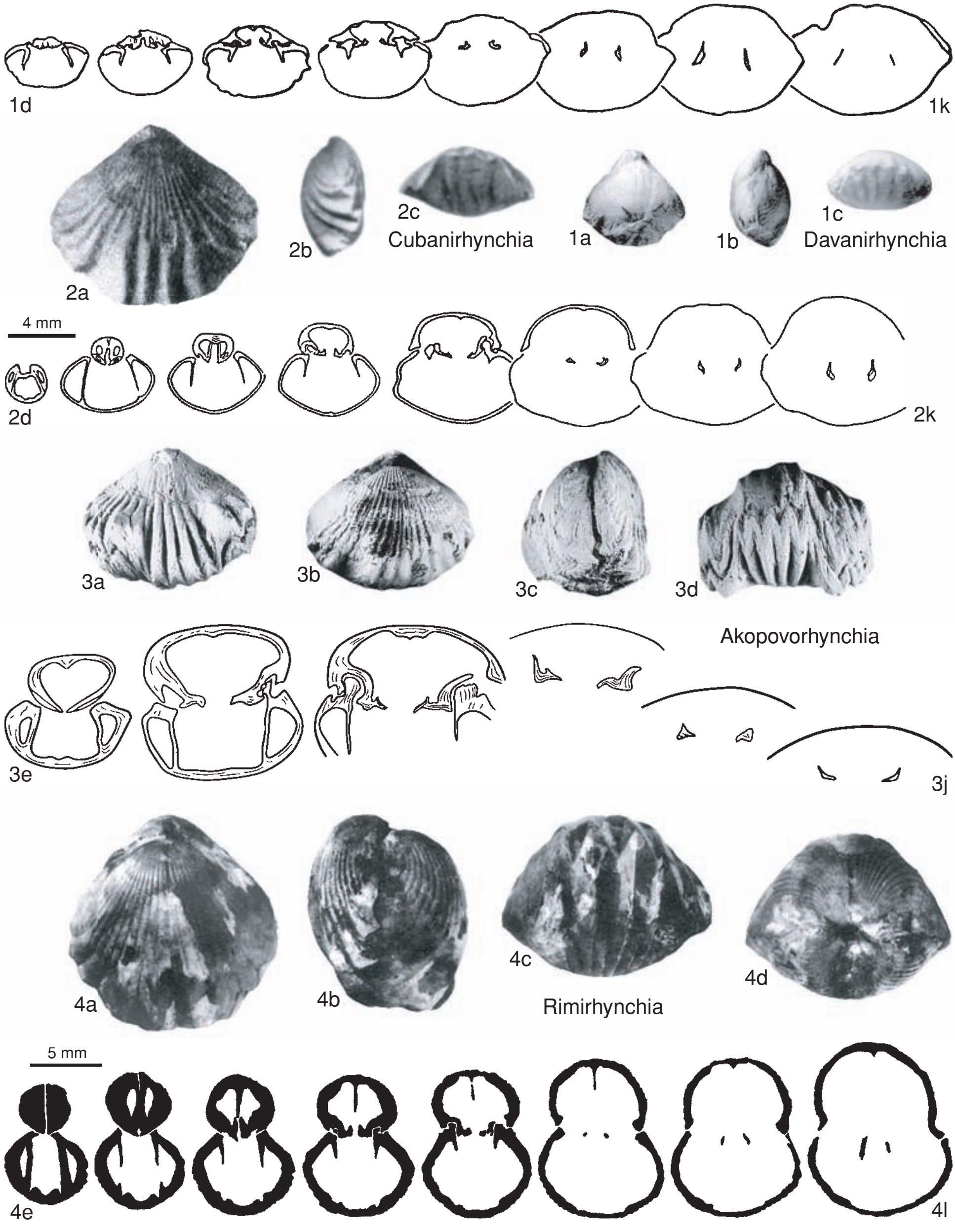

FIG. 883. Rhynchonellidae (p. 1300–1301).

Davanirhynchia OVCHARENKO, 1983, p. 42 [**D. davanensis;* OD]. Small shells, rounded-trigonal, costellae numerous and thin posteriorly, passing into fewer rounded plicae anteriorly. Dental plates short, diverging ventrally, hinge plates broad, convex ventrally, inclined dorsally; dorsal median septum reduced to ridge, barely buttressing a nearly sessile, narrow septalium; crura raduliform approaching to spinuliform. *Middle Jurassic (Bathonian):* southeastern Pamirs.——FIG. 883, *1a–k. *D. davanensis; a–c,* holotype, dorsal, lateral, anterior views, MUGT 92/1266, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.65, 0.9, 1.2, 1.5, 1.8, 2.0, MUGT 91/1266 (Ovcharenko, 1983).

Akopovorhynchia SMIRNOVA, 1990b, p. 47 [**A. akopovi;* OD] [=*Acopovorhynchia* SMIRNOVA, 1994, p. 31, *nom. null.*]. Medium, moderately to strongly dorsibiconvex, with numerous sharp, angular, deeply incised costae; dorsal fold well developed; commissure with fairly extensive trapezoidal linguiform extension; beak massive, incurved. Hinge teeth massive, deeply inserted with lateral secondary denticles; pedicle collar present; dental plates long, subparallel; crura with gently concave distal ends. *Lower Cretaceous (Valanginian):* northwestern Kazakhstan.——FIG. 883,*3a–j.* **A. akopovi; a–d,* dorsal, ventral, lateral, anterior views, ×1; *e–j,* transverse serial sections, distances in mm from first section, 2.2, 3.0, 3.6, 3.95, 5.12, 5.73, approximately ×2.5 (Smirnova, 1990b).

Cubanirhynchia KAMYSHAN, 1968, p. 57 [**C. rostovzevi;* OD]. Marginal plicae formed by fusion of 2 thin radial costellae or by further growth of one of them whereas its companion vanishes. Pedicle collar present, dental plates diverging ventrally; septalial plates distinct, parallel to each other or converging dorsally sometimes, sessile in early stages, hanging free in other species, or joining to weakly developed dorsal median septum in later stages; crura calcariform or similar. [Usage in KAMYSHAN, 1967b, p. 7, of doubtful availability.] *Lower Jurassic (?Toarcian), Middle Jurassic (Aalenian–Bajocian):* Caucasus, Armenia, Alps, Transcarpathia.——FIG. 883,*2a–k.* **C. rostovzevi,* lower Bajocian, northwestern Caucasus; *a,* holotype, dorsal view, ×1.5 (Kamyshan, 1968); *b–c,* holotype, lateral, anterior views, KHGU 6/1485, ×1 (Kamyshan & Babanova, 1973); *d–k,* transverse serial sections, 0.4, 1.7, 1.9, 2.2, 3.0, 3.5, 3.8, 4.0, KHGU 6/1488 (Kamyshan, 1968, text-fig. 3, not 4).

Furcirhynchia BUCKMAN, 1918, p. 59 [**F. furcata;* OD] [=*Furcirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Lineirhynchia* BUCKMAN, 1918, p. 59 (type, *L. cotteswoldiae* UPTON, 1899, p. 129, OD); *Lineirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Small to medium size, transverse-oval to subtrigonal, equibiconvex to dorsibiconvex, depressed to subcynocephalous; sharp uniplication and fold; capillate posteriorly, with few strong, sharp costae anteriorly; beak strong, upright, with large, oval foramen. Dorsal median septum long; hinge plates horizontal, with shallow septalium; crura raduliform. *Lower Jurassic (Hettangian–Toarcian):* England, France, Germany, Slovakia, Italy, Austria, ?Switzerland, western Canada, Siberia, Japan, Indonesia (Seran), New Zealand, New Caledonia, Argentina, ?Chile.——FIG. 884,*2a–k.* **F. furcata,* lower Pliensbachian, Dorset, England; *a–c,* holotype, dorsal, lateral, anterior views, GSM 31871, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 0.9, 2.3, 2.9, 3.1, 3.4, 4.0, 4.6, 4.9, J.1068/2, Derek Ager, personal collection (Ager, 1959a).——FIG. 884,*2l–v. F. cotteswoldiae* (UPTON), Toarcian, Gloucestershire, England; *l–n,* syntype, dorsal, lateral, anterior views, Gloucester Museum, ×1.5; *o–v,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.0, 1.2, 1.3, 1.5, 1.7, 2.1, 2.3, J.1157, personal collection, Derek Ager (Ager, 1962).

Rimirhynchia BUCKMAN, 1918, p. 60 [**R. rimosiformis;* OD; =*Rhynchonella anglica* ROLLIER, 1917, p. 92] [=*Rimirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium to large, globose dorsibiconvex, subcircular; strong obtuse uniplication and fold; both valves bearing many fine capillae posteriorly giving way to few strong costae anteriorly; beak massive, strongly incurved with submesothyrid foramen. Hinge plates horizontal with deep septalium; crura raduliform, distally transitional to calcariform. *Lower Jurassic (upper Sinemurian–Pliensbachian):* England, Scotland, Germany, France, ?Switzerland, ?Crimea, Siberia, northwestern Canada (mainly boreal).——FIG. 883,*4a–l.* **R. anglica* (ROLLIER), lower Pliensbachian, Somerset, England; *a–d,* holotype, dorsal, lateral, anterior, posterior views, BMNH B.12282, ×1.5; *e–l,* transverse serial sections, distances in mm from ventral umbo, 1.9, 2.4, 2.5, 2.8, 3.2, 3.8, 4.1, 4.7, personal collection, Derek Ager (Ager, 1959a).

Rimirhynchopsis DAGYS, 1963, p. 71 [**R. triadicus;* OD]. Medium size, laterally ovate or subpentagonal, with distinct sulcus and low fold, fine capillae posteriorly, rare, strong, rounded costae anteriorly; beak low, suberect, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Dental plates short, almost fused to wall; no pedicle collar; septum and septalium stout, umbonal chambers small, partly filled with callus, gently curved raduliform crura. *Upper Triassic (Norian–Rhaetian):* Alps, northwestern Caucasus, China (Qinghai). ——FIG. 884,*1a–k.* **R. triadica,* Norian, northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 179/160, ×1; *e–k,* transverse serial sections, distances in mm from first section, 1.6, 2.2, 2.4, 2.7, 3.3, 3.7, 4.4 (Dagys, 1963).

Subfamily STRIIRHYNCHIINAE Kamyshan, 1968

[Striirhynchiinae KAMYSHAN, 1968, p. 55]

Rhynchonellidae covered with numerous thin radial costae that may be dichotomous or intercalated, appearing at various distances from beak; small folds (plicae) in anterior part of shell; small, incurved beak; deltidial plates narrow, disjunct. Outer hinge plates well developed; septalial plates variously oriented, sessile in early stages; dorsal

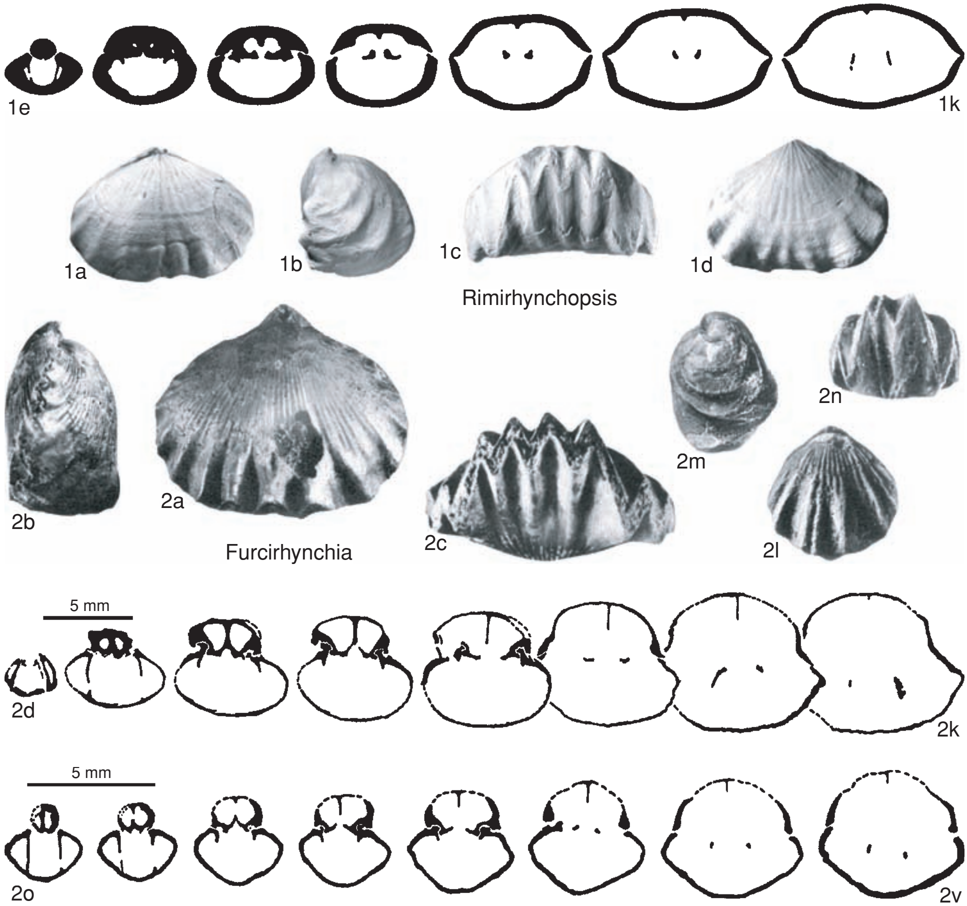

FIG. 884. Rhynchonellidae (p. 1301).

median septum weakly developed; crura calcariform or gently curved raduliform. *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Callovian).*

Striirhynchia BUCKMAN, 1918, p. 68 [**S. dorsetensis;* OD; =*Rhynchonella dorsetiensis* DAVIDSON, 1884, p. 277] [=*Striirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Stiirhynchia* AGER, 1965, p. 619, unjustified emendation]. Small to medium size, depressed, uniplicate, with many fine dichotomizing capillae, costae absent; beak small, sharp. Dental plates short; dorsal septum feeble. *Middle Jurassic (Aalenian–Bathonian):* England, Austria, Hungary, Poland, Slovakia, Sicily, Caspian Basin, Transcarpathia, Caucasus, Armenia, Nakhichevan, Algeria.——FIG. 885,*2a–o.* **S. dorsetiensis* (DAVIDSON), lower Bajocian, Dorset, England; *a–b,* dorsal, anterior views, GSM 3758, ×2; *c–o,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 1.1, 1.3, 1.4, 1.5, 1.6, 1.7, 1.9, 2.1, 2.3, 2.5, 2.7, BMNH B.70673 (new; courtesy of C. D. Prosser).

Capillirhynchia BUCKMAN, 1918, p. 58 [**Rhynchonella wrightii* DAVIDSON, 1852b, p. 69; OD] [=*Capillirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Large, globose, dorsibiconvex, rounded to subpentagonal, broadly uniplicate, with low fold; capillae all over shell, strong, sharp costae anteriorly (3 to 10 on fold); beak strong, suberect. *Middle Jurassic (Aalenian–Callovian):* England, France, Poland, Bulgaria, Yugoslavia, ?Hungary, ?Russian platform, Crimea, Caucasus, western North America.——FIG. 885,*3a–t.* **C. wrightii* (DAVIDSON), Aalenian, Cotswolds, England; *a–c,* topotype, dorsal, lateral, anterior views, GSM 31942, ×1; *d–t,* topotype, transverse serial sections, distances in

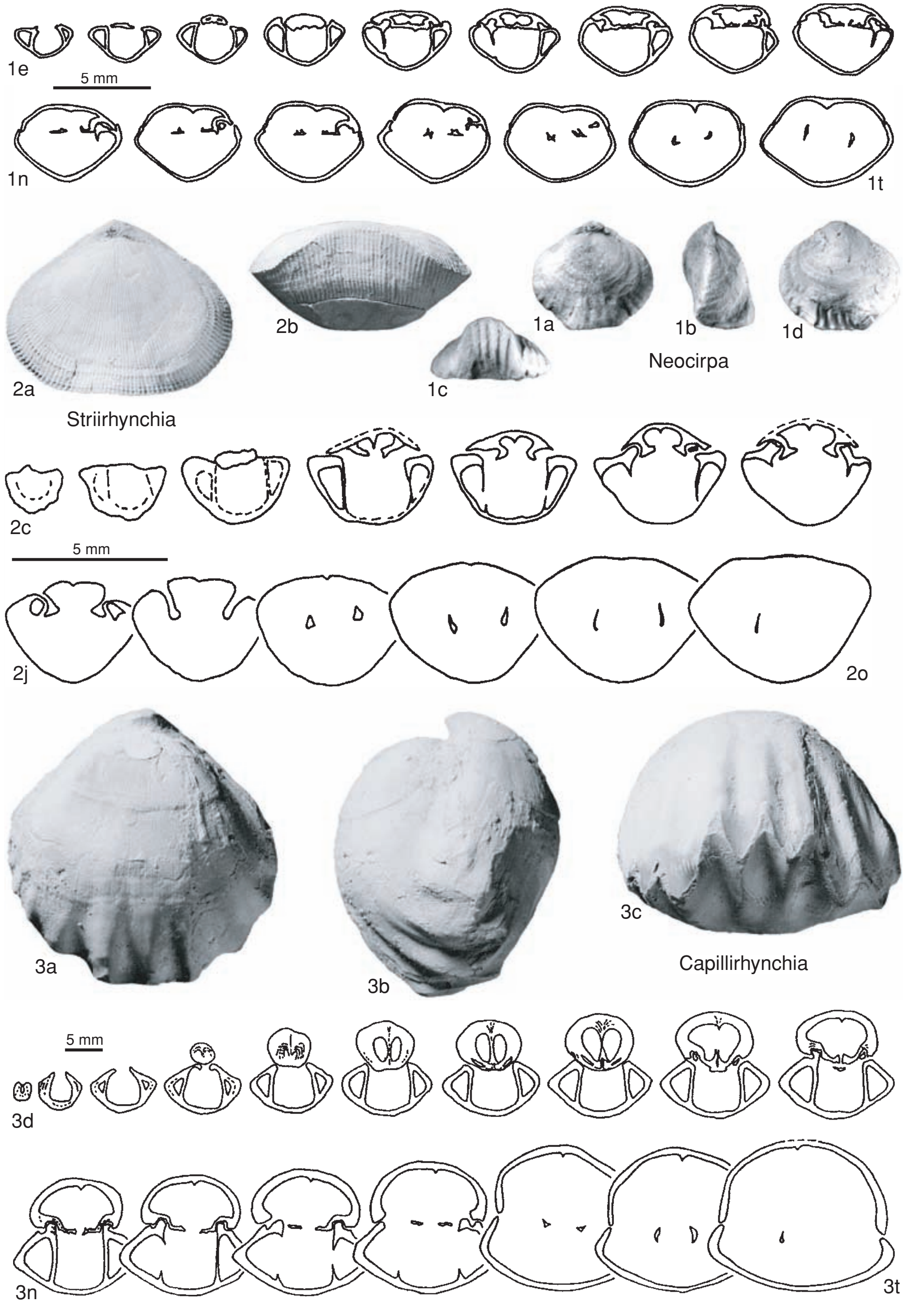

FIG. 885. Rhynchonellidae (p. 1302–1304).

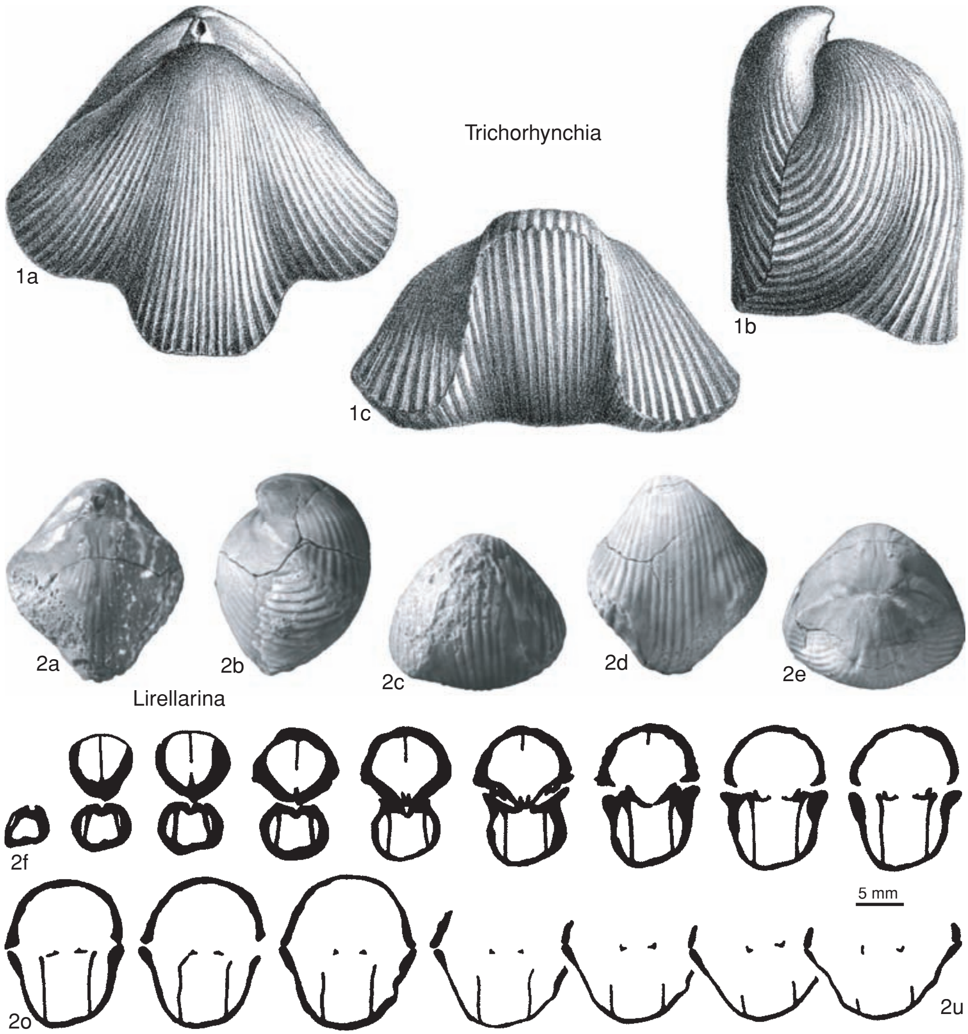

FIG. 886. Rhynchonellidae (p. 1304–1305).

mm from ventral umbo, 0.5, 1.8, 2.7, 3.2, 3.7, 3.9, 4.5, 4.7, 5.0, 5.2, 5.6, 6.0, 6.2, 6.8, 8.4, 8.7, 9.3, CDP 27, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

?Lirellarina COOPER, 1989, p. 49 [**L. costellata;* OD]. Medium size, dorsibiconvex; subpentagonal; strongly uniplicate, narrow, rounded, dorsal fold, strongly raised in anterior third; costellate, with costellae bifurcating on umbones and flanks; beak low, suberect; deltidial plates conjunct; foramen oval, rimmed. Dental plates long, thin, parallel; dorsal median septum long; septalium small; raduliform crura. *Middle Jurassic (Bajocian):* Arabia.——FIG. 886,*2a–u.* **L. costellata,* upper Bajocian, Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380241c, ×1.5; *f–u,* transverse serial sections, distances in mm from ventral umbo, 0.6, 0.9, 1.2, 1.4, 1.7, 2.1, 2.4, 2.6, 2.8, 3.1, 3.4, 3.6, 3.8, 4.3, 4.6, 4.9, USNM 380690 (Cooper, 1989).

?Neocirpa PROZOROVSKAIA, 1985, p. 110 [**N. armenica;* OD]. Small, subpentagonal, very small beak, uniplicate with fold low, arcuate, smooth or striate posteriorly, costate anteriorly. Entire hinge plates rather thin, septum ridgelike; septalium absent; crura raduliform. *Middle Jurassic (Bajocian):* Armenia, Nakhichevan.——FIG. 885,*1a–t.* **N. armenica,* upper Bajocian, Armenia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CNIGR 1166a/12282, ×1; *e–t,* transverse serial sections, distances in mm from ventral umbo, 2.1, 2.4, 2.8, 3.1, 3.7, 3.8, 4.0, 4.2, 4.3, 4.5, 4.7, 4.8, 4.9, 5.0, 5.2, 5.5 (Prozorovskaia, 1985).

?Trichorhynchia Buckman, 1918, p. 58 [**Rhynchonella deslongchampsii* Davidson, 1852a, p. 253; OD] [=*Trichorhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium to large, trilobate, dorsibiconvex; sometimes nasute, with wide uniplication, strong, flattened, high, narrow, dorsal fold; many fine costellae throughout, sometimes dichotomous or intercalated; beak massive. *?Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Bajocian):* England, France, northwestern Caucasus.——Fig. 886,*1a–c*. **T. deslongchampsii* (Davidson), Liassic, ?Pliensbachian, Normandy, France; dorsal, lateral, anterior views, ×1 (Davidson, 1852a).

Family ACANTHOTHIRIDIDAE Schuchert, 1913

[*nom. correct.* Owen & Manceñido, herein, *pro* Acanthothyridae Shi & Grant, 1993, p. 23, *nom. transl. ex* Acanthothyridinae Ager, 1965, p. 611, *nom. correct. pro* Acanthothyrinae Schuchert, 1913, p. 400]

Spinose, subequibiconvex to dorsibiconvex Rhynchonelloidea, crura variable, usually raduliform or its varieties; cardinal process rarely present or absent. [Name based on unjustified emendation of *Acanthothiris,* herein corrected in accordance with ICZN, 1999, Art. 35.4.1.] *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian)–Lower Cretaceous (lower Aptian).*

Subfamily ACANTHOTHIRIDINAE Schuchert, 1913

[*nom. correct.* Owen & Manceñido, herein, *pro* Acanthothyridinae Ager, 1965, p. 611, *nom. correct. pro* Acanthothyrinae Schuchert, 1913, p. 400]

Acanthothirididae with shell ornamented, costae coarse and spines relatively few but strong; beak strongly incurved. Dental plates and dorsal median septum present; septalium generally present; cardinal process absent; crura raduliform or modification thereof; deltidial plates and pedicle collar usually well developed. [Name based on unjustified emendation of *Acanthothiris,* herein corrected in accordance with ICZN, 1999, Art. 35.4.1.] *Middle Jurassic (Aalenian)–Upper Jurassic (Tithonian).*

Acanthothiris d'Orbigny, 1850, p. 323 [**Hemithiris spinosa* d'Orbigny, 1850 in 1849–1852, p. 268; SD Buckman & Walker, 1889, p. 43; =*Anomia spinosa* von Linné, 1767, p. 1154] [=*Acanthothyris* Bronn, 1862, p. 303, obj.]. Medium size, globose, dorsibiconvex to equibiconvex; uniplicate with dorsal fold low, ill defined; fully costate, no smooth stage; with many costae, intercalating, bi- or trifurcating, coarsely spinose throughout; beak small, incurved, pedicle collar may be tubelike. Dorsal median septum low and short; crura raduliform, sometimes with modified distal ends; septalial plates narrow, poorly developed, usually on early growth stages. *Middle Jurassic (Aalenian–Callovian):* England, France, Germany, Switzerland, Poland, Romania, Bulgaria, Slovakia, Crimea, Caucasus, Morocco, Afghanistan, Pamirs.——Fig. 887,*1a–n*. **A. spinosa* (von Linné), Bajocian, England; *a–e,* neotype, dorsal, lateral, anterior, ventral, posterior views, BMNH BB.45400, ×1; *f,* enlargement of dorsal view with spines, BMNH B.10617, ×1.5 (new); *g–n,* transverse serial sections through umbo, ×4 (Ager, 1965).

Kawhiarhynchia MacFarlan, 1992, p. 255 [**Rhynchonella (Cryptorhynchia) kawhiana* Trechmann, 1923, p. 283; OD]. Medium size, rounded to transverse-elliptical outline; equibiconvex to dorsibiconvex, moderately to well inflated; usually with uniplication broad, arcuate but no definite fold; shell covered with rounded or angular costae, foliaceous growth lamellae, and crescentic or tubular spines; beak broad, suberect to erect with large foramen and pedicle collar thick. Ventral median ridge low, possibly occurring posteriorly; dorsal valve with broad hinge plate, long, low median septum; crura short, with vertical terminations. *Middle Jurassic (?Bathonian, Callovian)–Upper Jurassic (Tithonian):* New Zealand.——Fig. 887,*3a–m*. **K. kawhiana* (Trechmann), Oxfordian, middle Heterian, North Island; *a–d,* dorsal, anterior, ventral, posterior views, NZGS BR2296, ×1.5; *e,* latex mold of dorsal exterior showing spine bases, OU NZ 17239, ×1.5; *f,* lateral view, OU NZ 17235, ×1.5; *g–m,* transverse serial sections, distances in mm from ventral umbo, 2.4, 2.8, 3.0, 3.6, 4.2, 4.6, 4.9, OU NZ 17230 (MacFarlan, 1992).

?Paraacanthothyris Kamyshan in Kamyshan & Babanova, 1973, p. 67–68 [**P. paucicostata;* OD] [=*Paraacanthothyris* Kamyshan, 1967b, p. 7, unavailable name; *Paracanthothyris* Kamyshan in Ager, Childs, & Pearson, 1972, p. 163, *nom. nud.*]. Medium size, dorsibiconvex, uniplicate, with coarse, sparsely spinose costae, subdued on periumbonal region (3 to 7 of them on low dorsal fold). Dental plates ventrally divergent or parallel; dorsal median septum long, well developed; septalial plates wide, almost sessile in early stages, joining the median septum later, more rarely arising from it to form a V- or U-shaped septalium; crura calcariform. *Middle Jurassic (Aalenian–Bajocian):* ?France, northwestern Caucasus.——Fig. 887,*2a–j*. **P. paucicostata,* Bajocian, northwestern Caucasus; *a–c,* holotype, dorsal, lateral, anterior views, KHGU 6/1925, ×1.5; *d–j,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.4, 1.7, 1.9, 2.1, 2.4, 3.0 (Kamyshan & Babanova, 1973).

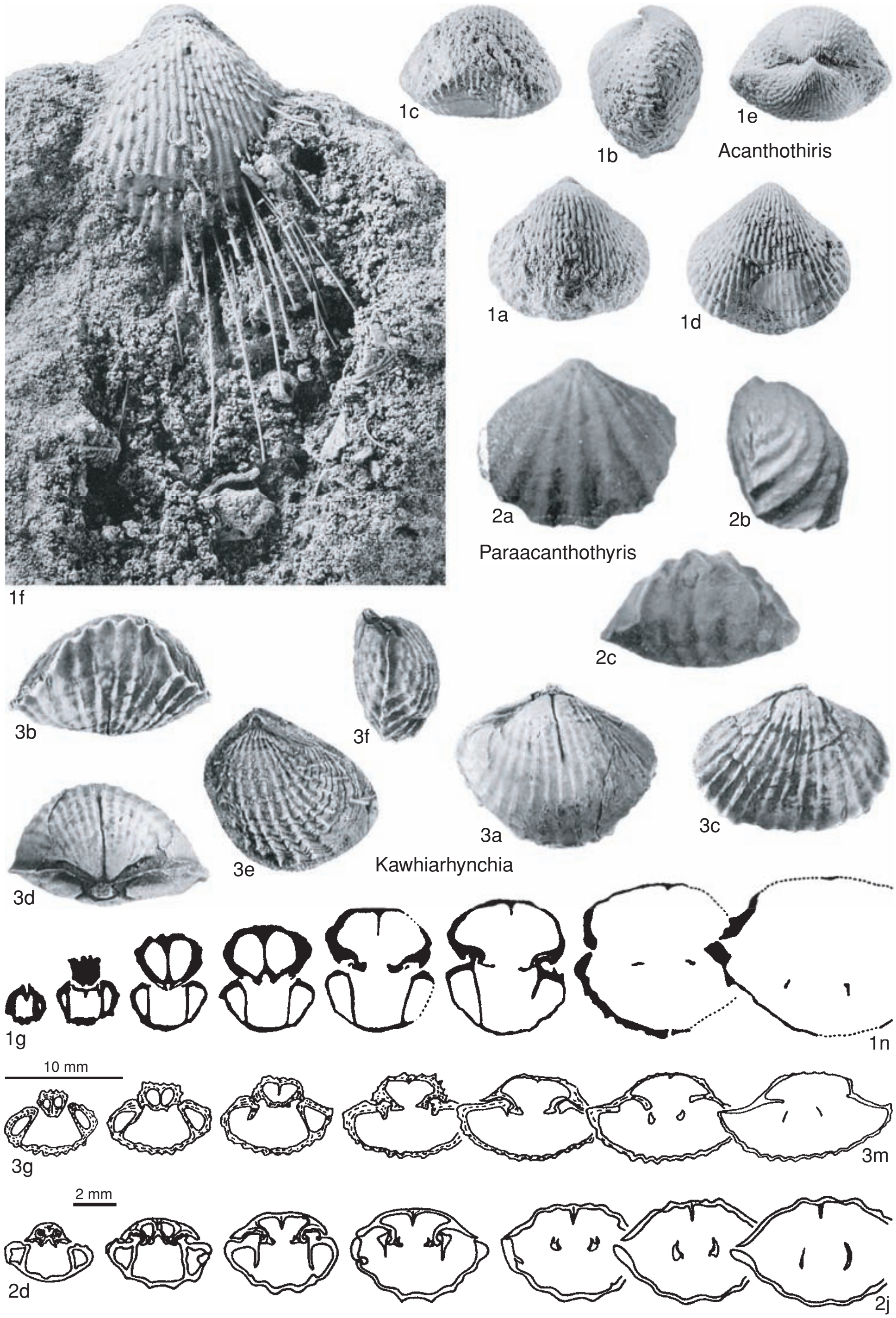

FIG. 887. Acanthothirididae (p. 1305).

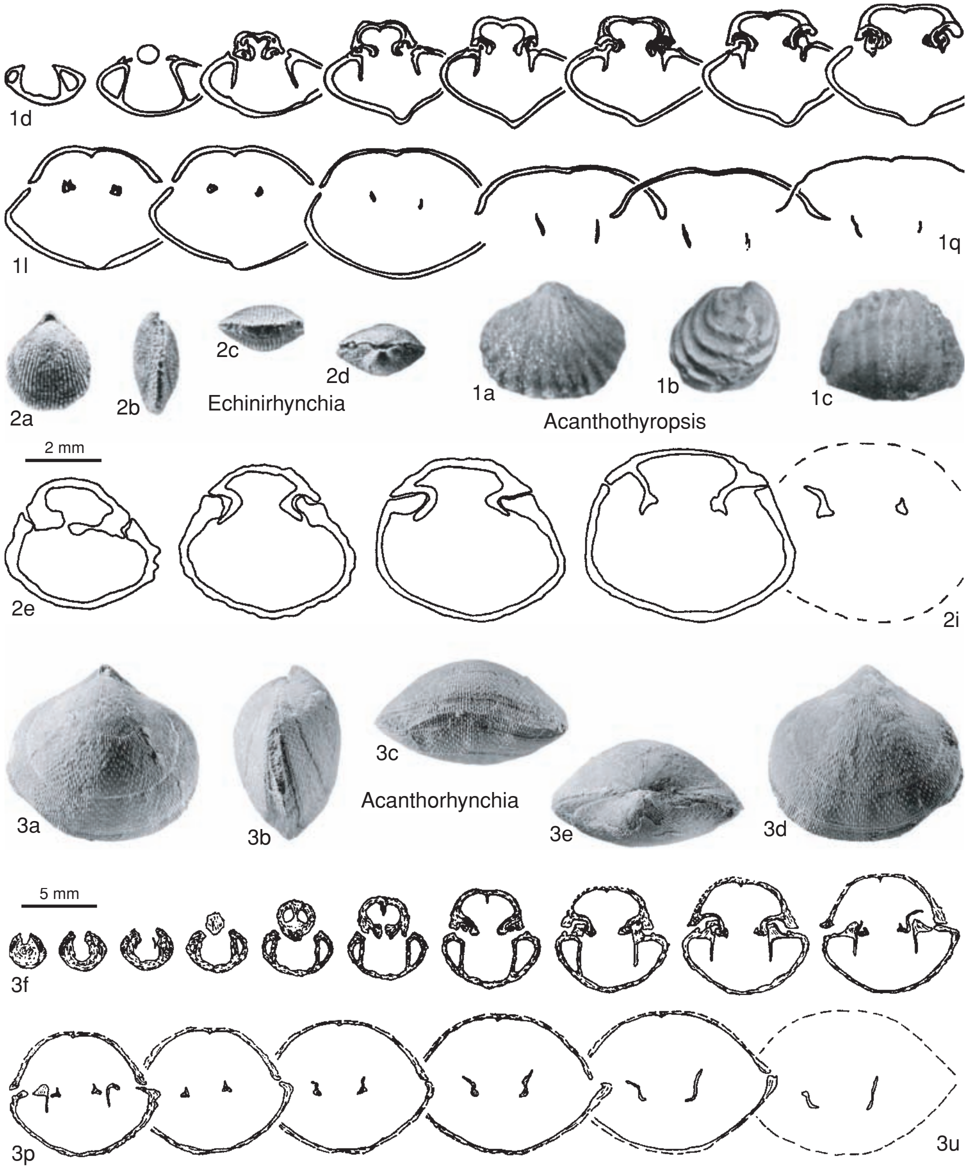

FIG. 888. Acanthothirididae (p. 1307–1308).

Subfamily ACANTHORHYNCHIINAE Shi & Grant, 1993

[Acanthorhynchiinae SHI & GRANT, 1993, p. 24]

Acanthothirididae with shell typically covered with numerous costellae and delicate, fine spines. Dental plates and hinge plates variable, often reduced or absent; septalium and dorsal median septum usually reduced or absent; crura calcariform to possibly subfalciform; cardinal process alleged to occur in some species. *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian)–Lower Cretaceous (lower Aptian).*

Acanthorhynchia BUCKMAN, 1918, p. 69 [**Acanthothyris panacanthina* BUCKMAN & WALKER, 1889, p. 53; OD] [=*Acanthorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium to large size, equibiconvex to dorsibiconvex; transversely oval; very slightly uniplicate, but no proper fold; thin test, very densely and finely costellate, often dichotomously, delicately spinose throughout; beak strong, sharp, suberect to incurved; disjunct deltidial plates. Dorsal median septum feeble, apically confined; crura calcariform or raduliform; cardinal process or small septalium sometimes present; dental plates weak, wide apart. *Middle Jurassic (upper Bajocian)–Lower Cretaceous (Berriasian):* western and eastern Europe, Africa, India.——Fig. 888,*3a–u.* **A. panacanthina* (Buckman & Walker), upper Bajocian, Dorset, England; *a–e,* lectotype, dorsal, lateral, anterior, ventral, posterior views, BMNH B.12082, ×1 (new); *f–u,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.4, 1.0, 1.2, 1.4, 1.7, 1.9, 2.3, 2.6, 2.9, 3.2, 3.4, 3.6, 4.0, 4.3, 4.6, 5.0 (Childs, 1969).

?Acanthothyropsis Kamyshan, 1967b, p. 7 [**Rhynchonella crossi* Walker, 1869, p. 215; OD; virtual monotypy] [=*Acanthotnyropsis* Kamyshan in Kamyshan & Babanova, 1973, p. 64, obj.]. Small, equibiconvex to dorsibiconvex; uniplicate, dorsal fold gentle to well marked, bearing 2 to 8 costae; costae simple, effaced posteriorly to smooth stage and bearing few rows of weak, mostly peripheral, spines; beak suberect to incurved; deltidial plates disjunct. Sessile septalial plates parallel or dorsally divergent, separated from myophragm; hinge plates absent; crura thickly based and sharply bent (allegedly calcariform or spinuliform). *Lower Jurassic (?Pliensbachian), Middle Jurassic (Aalenian–Bajocian):* England, ?Switzerland, ?France, Caucasus, *?Pliensbachian, Aalenian–Bajocian;* ?Argentina, *?Pliensbachian.*——Fig. 888,*1a–q.* **A. crossi* (Walker), Bajocian, northwestern Caucasus; *a–c,* dorsal, lateral, anterior views, ×1.5; *d–q,* transverse serial sections, distances in mm from ventral umbo, 0.5, 0.7, 0.8, 0.9, 0.95, 1.05, 1.15, 1.35, 1.45, 1.65, 1.75, 1.85, 1.95, 2.05 (Kamyshan & Babanova, 1973).

Echinirhynchia Childs, 1969, p. 73 [**Terebratulites senticosus* von Schlotheim, 1820 in 1820–1823, p. 268; OD] [=*Spinulirhynchia* Smirnova, 1972, p. 52, *nom. nud.*]. Similar to *Acanthorhynchia,* but smaller, equibiconvex to ventribiconvex; usually subtriangular, rectimarginate or sulcate. Dental plates and septalium absent. *Upper Jurassic (Oxfordian)–Lower Cretaceous (lower Aptian):* western and eastern Europe, Crimea, Caucasus, Antarctica.——Fig. 888,*2a–i.* **E. senticosa* (von Schlotheim), Kimmeridgian, Franconia, near Erlangen, Germany; *a–d,* dorsal, lateral, anterior, posterior views, ×1; *e–i,* transverse serial sections, distances in mm from ventral umbo, 1.7, 2.0, 2.4, 2.8, 3.1 (Childs, 1969).

NORELLOIDEA

Miguel O. Manceñido,[1] Ellis F. Owen,[2] A. S. Dagys,[3] and Sun Dong-Li[4]

[[1]La Plata Natural Sciences Museum, Argentina; [2]formerly of The Natural History Museum; [3]deceased; and [4]Nanjing Institute of Geology and Palaeontology]

Superfamily NORELLOIDEA Ager, 1959

[*nom. transl.* Manceñido, Owen, Dagys, & Sun, herein, *ex* Norellinae Ager, 1959b, p. 330]

Rhynchonellida with shells smooth to capillate or gently fluted, ovoid to subtriangular, with generally sulcate dorsal valves, minute beak and foramen; squama and glotta absent. Crura arcuiform or a derivation thereof; dorsal median septum variable to absent. *Lower Triassic–Holocene.*

Family NORELLIDAE Ager, 1959

[*nom. transl.* Ager, Childs, & Pearson, 1972, p. 175, *ex* Norellinae Ager, 1959b, p. 330]

Small- to medium-sized Norelloidea, smooth or with plicae blunt, radial, commonly with sulcate dorsal valves (at least in juvenile, often also in adult stage), and often with ventral valves subcarinate. Dorsal median septum absent or present. *Lower Triassic–Upper Cretaceous (Turonian).*

Subfamily NORELLINAE Ager, 1959

[Norellinae Ager, 1959b, p. 330]

Small, mostly smooth Norellidae with small delthyria; dorsally sulcate to rectimarginate, or dorsal fold broad and flat, if present. Crura arcuiform where known; dorsal septum and septalium absent. *Middle Triassic (Anisian)–Middle Jurassic (Bathonian).*

Norella Bittner, 1890, p. 315 [**Rhynchonella refractifrons* Bittner, 1890, p. 39; SD ICZN, 1962, Opinion 633, p. 148]. Small, smooth, unequally biconvex, with dorsal valve flattened, anterior commissure unisulcate to plicosulcate; beak short, incurved, ridges rounded, foramen hypothyrid. Dental plates very short, fused to lateral wall, pedicle collar absent; septum and septalium absent, outer hinge plate narrow, fused with socket ridges; crura short, arcuiform. *Middle Triassic (Anisian)–Upper Triassic (Rhaetian):* Alps, Carpathians, northwestern Caucasus.——FIG. 889,*2a–d.* **N. refractifrons* (BITTNER), Anisian, Alps, Austria; dorsal, lateral, anterior, ventral views, ×1.5 (Bittner, 1890).

?Austriellula STRAND, 1928, p. 37, *nom. nov. pro Austriella* BITTNER, 1890, p. 314, *non* TENISON-WOODS, 1883, Mollusca [**Rhynchonella dilatata* SUESS, 1855, p. 29; OD] [=*Jacobella* PÁTTE, 1926, p. 125, *non* JEANNET, 1908, Cephalopoda, *nec* PASSENDORFER, 1930, Cephalopoda, *nec* MERCIER, 1935, Echinodermata; *Austriellina* SCHUCHERT & LEVENE, 1929b, p. 119, obj.]. Small or medium size, subtrigonal, with anterior commissure rectimarginate or incipiently unisulcate, some species uniplicate; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Internal structures similar to *Norella. ?Middle Triassic, Upper Triassic (Carnian–Norian), ?Lower Jurassic:* Alps, Dinarids, Carpathians, northwestern Caucasus, Indonesia, ?Vietnam, ?Himalayas, *?Middle Triassic, Carnian–Norian;* Greece, *?Lower Jurassic.*——FIG. 889,*5a–j.* **A. dilatata* (SUESS), Norian, northern Alps, Sandling, Austria; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/209, ×1.5 (Dagys, 1974); *e–j,* transverse serial sections, distances in mm from ventral umbo, 0.3, 0.45, 0.6, 1.0, 1.3, 1.8, MB B233.23 (Siblík, 1982).

?Kericserella VÖRÖS, 1983, p. 9 [**Rhynchonella inversaeformis* SCHLOSSER in BÖSE & SCHLOSSER, 1900, p. 199; OD]. Small, outline subtrigonal to rounded; subequibiconvex; broadly sulcate anteriorly; costae few, strong, rounded after short posterior smooth stage; planareas flat, well demarcated by beak ridges; beak small, erect; lateral commissure straight, running in middle of planareas. Dorsal median septum and septalium absent; hinge plates missing, crural bases supported by elevated inner socket ridges; crura reminiscent of falciform but convex toward each other, possibly modified arcuiform; dental plates subparallel. *Lower Jurassic (Pliensbachian):* Apennines, southern Alps, Hungary, ?Greece.——FIG. 889,*4a–k.* **K. inversaeformis* (SCHLOSSER), lower Pliensbachian, Kericser, Hungary; *a–e,* dorsal, lateral, anterior, ventral, posterior views, HNHMB M.98.1, ×2 (new); *f–k,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.5, 0.7, 0.9, 1.15, 1.6, HGI J.9187 (Vörös, 1983).

Pisirhynchia BUCKMAN, 1918, p. 28 [**Rhynchonella pisoides* VON ZITTEL, 1869, p. 129; OD] [=*Pisirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, globose, subequibiconvex; sulcate, ventral fold low, possibly with few rounded plicae after long smooth stage. Umbonal callosities absent. *Lower Jurassic (Sinemurian–Pliensbachian):* Italy, Austria, Slovakia, Hungary, ?southern Spain, Greece.——FIG. 889,*1a–e.* **P. pisoides* (VON ZITTEL), Pliensbachian, Kericser, Hungary; dorsal, lateral, anterior, ventral, posterior views, HNHMB M.98.2, ×2 (new).

Rectirhynchia BUCKMAN, 1918, p. 74 [**Rhynchonella lopensis* MOORE, 1855, p. 114; OD]. Minute, subtrigonal smooth, depressed, gently ventribiconvex; sulcate, with strong ventral fold; short, straight hinge line; beak large, hypothyrid. *Middle Jurassic (Bajocian–Bathonian):* England, Italy.——FIG. 889,*3a–b.* **R. lopensis* (MOORE), England; dorsal, ventral views, ×4 (Davidson, 1878).——FIG. 889,*3c–h. R. camporoverensis* FERRARI, Bajocian–Bathonian, Trentino, Italy; transverse serial sections, distances in mm from first section, 0.0, 0.1, 0.45, 0.55, 0.65, 0.75 (Ferrari, 1962).

Subfamily PARANORELLININAE Xu, 1990

[*nom. transl.* MANCEÑIDO, OWEN, DAGYS, & SUN, herein, *ex* Paranorellinidae XU, 1990, p. 76]

Small, shallow sulcate Norellidae with long smooth stage and variable number of round marginal plicae on anterior part. Septalium shallow and dorsal median septum present; hinge plates gently inclined, often remaining welded to the latter anteriorly from sockets; crura resembling spinuliform, approaching ventral valve floor distally. *Lower Triassic (Scythian)–Middle Triassic (Anisian).*

Paranorellina DAGYS, 1974, p. 100 [**P. parisi;* OD] [=*Paxanorellina* XU & LIU, 1983, p. 72, *nom. null.*]. Minute, thin, equibiconvex, smooth, with distinct sulcus on anterior half of dorsal valve, corresponding ventral fold low, flat, anterior commissure unisulcate; beak suberect, ridges sharp, foramen hypothyrid, deltidial plates disjunct. Dental plates short, diverging, pedicle collar absent; septum long, septalium distinct, crura close to spinuliform, allegedly raduliform. *Lower Triassic (Scythian):* Russia (Far East, Primorye), China (Jiangsu, Zhejiang, Anhui, Tibet).——FIG. 890,*2a–l.* **P. parisi,* Olenekian, Primorye; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/46, ×2; *e–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.2, 1.4, 1.6, 1.8, 1.9, 2.2, 2.8, IGiG 394/50 (Dagys, 1974).

Costinorella DAGYS, 1974, p. 101 [**C. zharnikovae;* OD]. Minute, rounded-triangular, thin, equally biconvex; dorsal sulcus shallow, broad, without corresponding fold; anterior commissure weakly unisulcate, multicostate anteriorly and smooth posteriorly; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates conjunct. Dental plates long, subparallel, pedicle collar absent; septum high, about one-half valve length, septalium shallow, crura spinuliform. *Middle Triassic (Anisian):* Russia (Far East).——FIG. 890,*1a–k.* **C.*

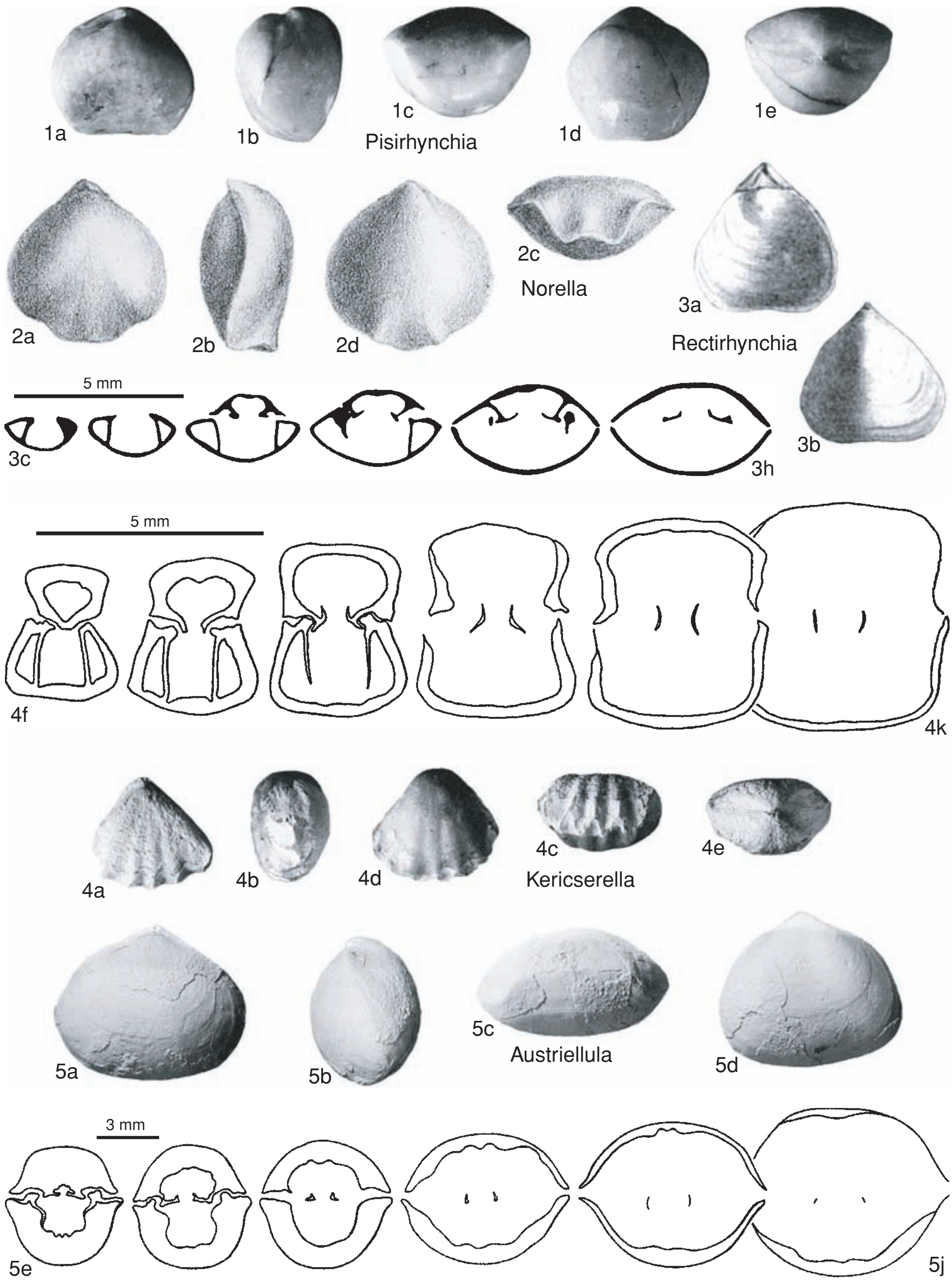

FIG. 889. Norellidae (p. 1308–1309).

zharnikovae, Primorye; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/51, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.8, 1.05, 1.4, 1.5, 1.7, 2.0, 2.2, IGiG 394/53 (Dagys, 1974).

?Qilianoconcha CHING, SUN, & YE in CHING & others, 1979, p. 166 [**Q. corcula;* OD]. Small to medium size, subpentagonal to elongate-elliptical, planoconvex to ventribiconvex; commissure sulcate-antiplicate; surface smooth; ventral valve axially

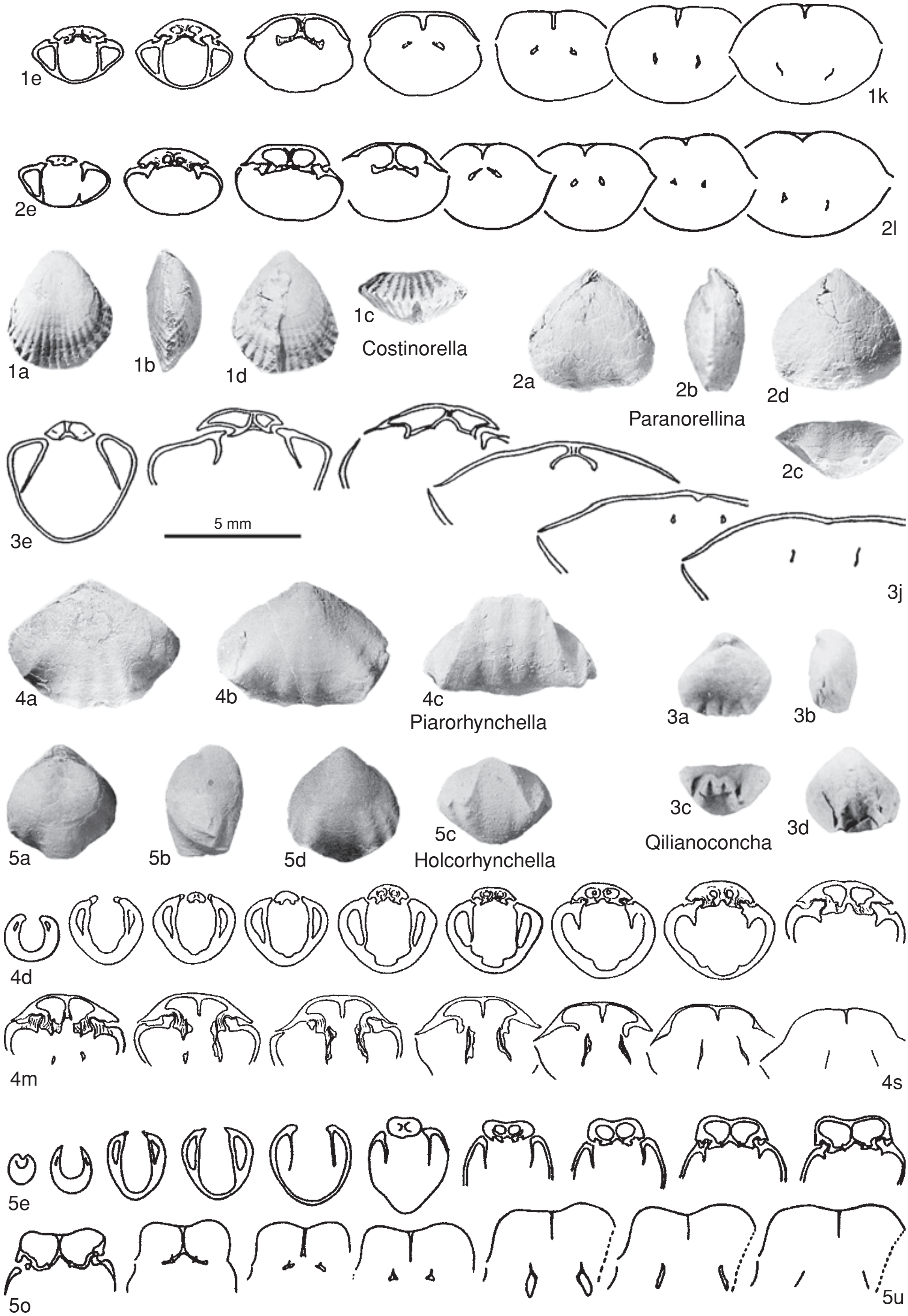

FIG. 890. Norellidae (p. 1309–1312).

carinate or with median groove marked by 1 short plica; dorsal sulcus variously developed, gradually merging into lateral slopes and sometimes with median ridge or 2 short plicae anteriorly; beak small and pointed; beak ridges narrow and rounded; foramen epithyrid; delthyrium closed by symphytium. Pedicle collar may be present; dental plates widely divergent ventrally; umbonal chambers narrow, about one-fourth width of delthyrial chamber; outer hinge plates slightly inclining toward dorsal floor; septalium wide and deep; septum attaining one-third length of dorsal valve; crural bases trigonal; crura allegedly prefalciform, also resemble arcuiform, extending horizontally, thinly ridge shaped in proximal part and upright short blades at distal ends. [Discrimination from co-occurring genera *Eoantiptychia, Parasulcatinella,* and *Paraantiptychia* interpreted as terebratulides by XU & LIU, 1983, is not yet unequivocally resolved.] *Middle Triassic (Anisian):* China (Qinghai).——FIG. 890,*3a–j.* **Q. corcula; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 42868, ×1; *e–j,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.7, 2.1, 2.8, 3.85, 4.05, 4.75, NIGP 42869 (Ching & others, 1979).

Subfamily HOLCORHYNCHELLINAE Dagys, 1974

[Holcorhynchellinae DAGYS, 1974, p. 109]

Small Norellidae with long smooth stage and with round marginal plicae on anterior part; sulcate or depressed in early ontogeny to become uniplicate later. Dental plates, median septum, and septalium present; crura allegedly calcariform, modified arcuiform, distally flaring ventrally. *Lower Triassic (Scythian)–Middle Triassic (Ladinian).*

Holcorhynchella DAGYS, 1974, p. 110 [**Rhynchonella delicatula* BITTNER, 1890, p. 17; OD]. Small, subpentagonal, unisulcate young and uniplicate adult, distinct sulcus in posterior half of dorsal valve, posteriorly smooth, costae few, short in anterior part; beak short, incurved, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Dental plates subparallel, pedicle collar absent; outer hinge plates broad, ventrally convex on section, dorsal median septum high, more than one-half valve length, septalium distinct; crura as for subfamily. *Middle Triassic (Anisian–Ladinian):* Alps, Dinarids, Carpathians, Hungary, northwestern Caucasus, Turkey, Vietnam, ?China.——FIG. 890,*5a–u.* **H. delicatula* (BITTNER), Anisian, northwestern Caucasus; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/234, ×2; *e–u,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.5, 0.7, 0.9, 1.0, 1.1, 1.2, 1.4, 1.5, 1.6, 1.8, 2.0, 2.3, 2.6, 2.8, 3.0, IGiG 394/236 (Dagys, 1974).

Piarorhynchella DAGYS, 1974, p. 110 [**P. mangyshlakensis;* OD] [=*Piarorhyncholla* XU & LIU, 1983, p. 72, *nom. null.*]. Small, rounded-pentagonal, strongly uniplicate, posteriorly smooth, costae few and low anteriorly; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Dental plates subparallel, pedicle collar absent, outer hinge plates horizontal in section, dorsal median septum and septalium distinct, crura curved from cardinalia at right angles. *Lower Triassic–Middle Triassic:* Alps, Balkans, Carpathians, northwestern Caucasus, western Kazakhstan, Primorye, ?China, western USA.——FIG. 890,*4a–s.* **P. mangyshlakensis,* Scythian, Olenekian, Mangyshlak, Kazakhstan; *a–c,* holotype, dorsal, ventral, anterior views, IGiG 394/61, ×2; *d–s,* transverse serial sections, distances in mm from first section, 0.0, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.2, 1.4, 1.5, 1.6, 1.7, 1.8, 2.0, 2.2, IGiG 394/66 (Dagys, 1974).

Subfamily PRAEMONTICLARELLINAE new subfamily

[Praemonticlarellinae MANCEÑIDO & OWEN, herein]

Small, depressed equibiconvex Norellidae; usually narrow at hinge and somewhat truncated anteriorly; smooth stage variable, blunt plicae often peripheral; rectimarginate or weakly uniplicate. With shallow septalium and variable dorsal median septum; hinge plates inclined dorsally. *Lower Triassic–Upper Jurassic (Volgian).*

Praemonticlarella GARCÍA JORAL, 1993, p. 75 [**P. distercica;* OD] [=*Praemonticlarella* GARCÍA JORAL, GOY, & URETA, 1990, p. 58, *nom. nud.*]. Small, round to subpentagonal, depressed equibiconvex; costae numerous, blunt, and radial, attenuated posteriorly; uniplication subrectangular, but fold not raised; beak short and erect, with sharp beak ridges. Hinge plates oblique inclined; dental plates nearly subparallel; septalium shallow; dorsal median septum long, low; crura arcuiform. *Lower Jurassic (Toarcian)–Middle Jurassic (lower Aalenian):* Spain, ?France, ?Italy.——FIG. 891,*5a–j.* **P. distercica,* lower Aalenian, Spain; *a–c,* holotype, dorsal, lateral, anterior views, DPUCM HT.15.2, ×3; *d–j,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.1, 1.4, 1.65, 1.85, 2.1, 2.2, DPUCM FZ.68.17 (García Joral, 1993).

?Aparimarhynchia MACFARLAN, 1992, p. 65 [**A. dunrobinensis* MACFARLAN, 1992, p. 66; OD; *non* p. 16, confirmed by first reviser MACFARLAN, 1995, p. 527]. Small, slightly inflated ventribiconvex, rounded to subtrigonal in outline; rectimarginate or shallowly uniplicate; costae narrow, rounded, sometimes branching, other times with long smooth stage posteriorly; beak large, erect; hypothyrid

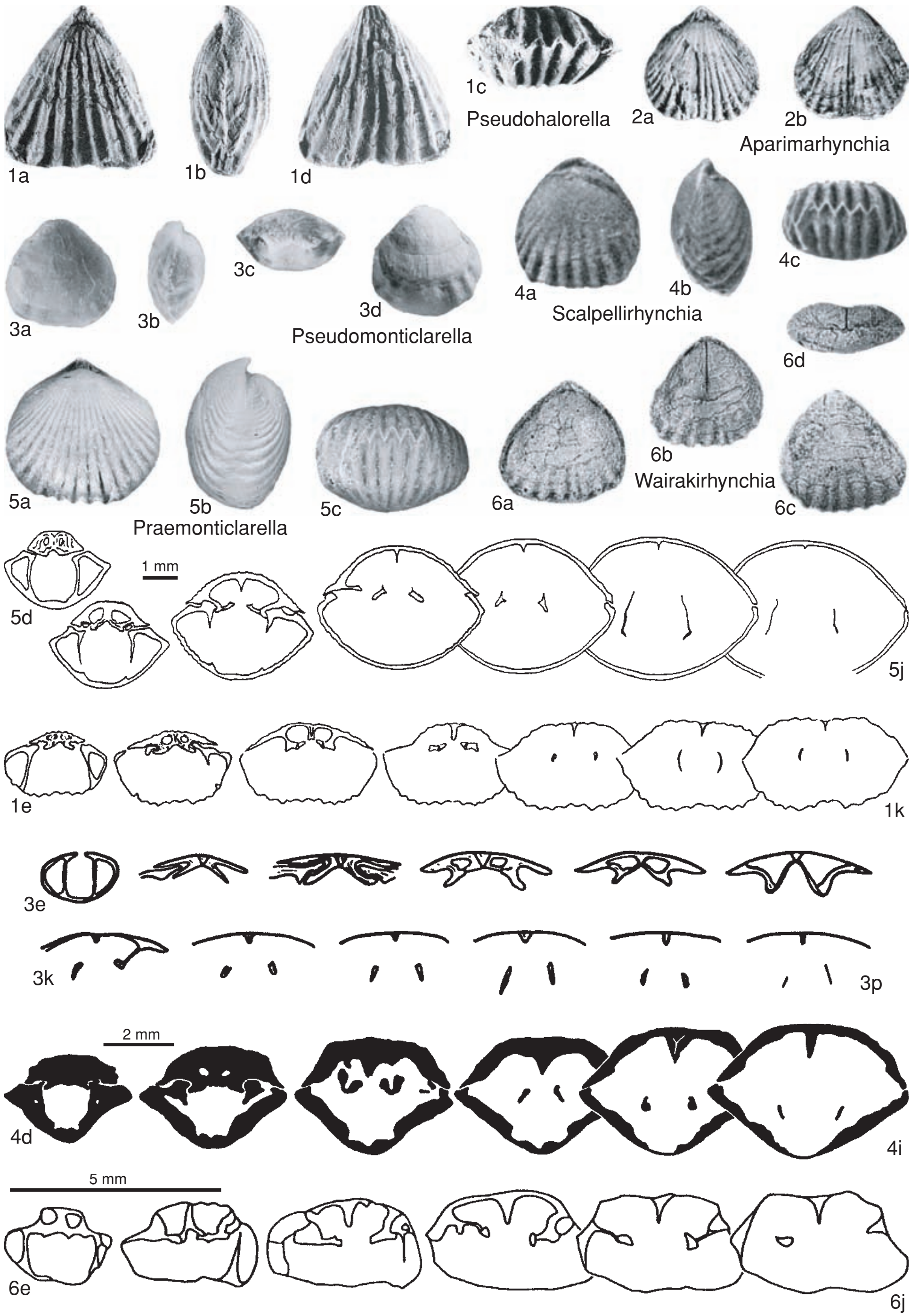

FIG. 891. Norellidae (p. 1312–1314).

elliptical foramen with conjunct deltidial plates. Broad, thick hinge plate; no septalial plates; dorsal median septum long, high. *Lower Triassic–Middle Triassic (Anisian):* New Zealand.——FIG. 891,*2a–b.* **A. dunrobinensis,* Etalian, Southland syncline; holotype, dorsal, ventral views, OU NZ 15533, ×2 (MacFarlan, 1992).

Pseudohalorella DAGYS, 1965, p. 66 [**P. sibirica;* OD]. Minute, trigonal, moderately equibiconvex, both valves medially flattened, with distinct sulci, beginning from umbonal part, anterior commissure rectimarginate, multicostate, costae sharp; beak short, suberect, ridges rounded, foramen hypothyrid, deltidial plates disjunct. Dental plates slightly ventrally divergent, pedicle collar absent; septum and septalium distinct, crura modified spinuliform. *Upper Triassic (Rhaetian):* northeastern Siberia.——FIG. 891,*1a–k.* **P. sibirica; a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 135/118, ×3; *e–k,* transverse serial sections, distances in mm from first section, 1.4, 1.8, 2.3, 2.5, 2.9, 3.8, 4.2 (Dagys, 1965).

Pseudomonticlarella SMIRNOVA, 1987, p. 30 [**P. varia;* OD]. Small, equibiconvex, striate, somewhat ligate; outline variable from rounded-triangular to rounded or pyriform; maximum width at midvalve; 3 to 5 small lateral folds or plicae; anterior commissure with lateral folds resembling *Monticlarella;* ventral sulcus broadly arcuate with trapezoidal linguiform extension; ventral umbo long with pointed and slightly incurved beak; foramen small, hypothyrid. Hinge teeth long, deeply inserted; dental plates subparallel to weakly ventrally divergent; strong socket ridges; elongated hinge plates supported by strong, low septum. *Upper Jurassic (Volgian):* Russian Platform.——FIG. 891,*3a–p.* **P. varia; a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 139/570, ×3; *e–p,* transverse serial sections, distances in mm from first section, 0.13, 0.25, 0.35, 0.48, 0.61, 0.66, 0.76, 0.84, 0.96, 1.0, 1.06, 1.15, MGU 139/584 (Smirnova, 1987).

Scalpellirhynchia MUIR-WOOD, 1936a, p. 477 [**Terebratula scalpellum* QUENSTEDT, 1851 in 1851–1852, p. 453; OD]. Small, depressed equibiconvex, flattened anteriorly; uniplication low, flattopped, with at least 10 to 16 blunt costae anteriorly (3 to 6 of them on indistinct fold); beak short, erect; deltidial plates disjunct to barely touching. Dental plates short, almost fused to wall, teeth crenulated; dorsal median septum long, supporting wide septalium; oblique hinge plates, inclined dorsally; crura bladelike, nearly to arcuiform, allegedly raduliform or calcariform. [Middle Jurassic records from Asia (China, Pamirs) should be verified.] *Lower Jurassic (upper Sinemurian–Pliensbachian):* England, France, Germany, Bulgaria, ?Switzerland, ?Algeria, ?Turkey, ?Argentina.——FIG. 891,*4a–i.* **S. scalpellum* (QUENSTEDT), lower Pliensbachian, Würtenberg, Germany; *a–c,* dorsal, lateral, anterior views, ×2; *d–i,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.1, 1.3, 1.5, 1.8, 2.0, BMNH B.38460 (Ager, 1967).

?Wairakirhynchia MACFARLAN, 1992, p. 55 [**W. etaliana;* OD]. Small to medium size, rounded to subtriangular, usually longer than wide; equibiconvex depressed to moderately inflated; shallow posterior sulcus and strongly convex lateral slopes on brachial dorsal valve; rectimarginate or uniplicate; costae strong, subangular to rounded, usually after posterior smooth stage; beak short, broad, erect. Hinge plate thick, with shallow septalium; dorsal median septum long, high. *Middle Triassic (Anisian, ?Ladinian):* New Zealand (South Island).——FIG. 891,*6a–j.* **W. etaliana,* Anisian, upper Etalian, Southland; *a–d,* holotype, dorsal view, dorsal internal mold, ventral, posterior views, OU NZ 17382, ×2; *e–j,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.0, 1.1, 1.3, 1.4, 1.5, OU NZ 15525 (MacFarlan, 1992).

Subfamily DIHOLKORHYNCHIINAE Xu & Liu, 1983

[Diholkorhynchiinae XU & LIU, 1983, p. 74]

Small to medium-sized Norellidae, subequibiconvex to ventribiconvex; dorsally sulcate, ventrally subcarinate; long smooth stage followed by blunt marginal plicae. Dental plates parallel; dorsal median septum high, steeply inclined hinge plates; septalium not persisting beyond articulation zone; crura modified arcuiform, distal ventral flaring variable. [Raising to family Diholkorhynchiidae (as in XU, 1990, p. 77) is not endorsed herein.] *Middle Triassic–Middle Jurassic (Bajocian, ?Bathonian, ?Callovian).*

Diholkorhynchia YANG & XU, 1966, p. 24[99] [**Rhynchonella sinensis* KOKEN, 1900, p. 206; OD] [=*Dihorhynchia* XU & LIU, 1983, p. 72, *nom. null.*]. Small, triangular to subpentagonal, with short hinge; biconvex; anterior commissure multiplicate; beak small, straight or strongly incurved; pedicle opening small, oval; deltidial plates conjunct; ventral sulcus well developed and limited to anterior half of shell; dorsal valve regularly convex, but with medial depression starting near umbonal area, widening at slightly anterior of middle of dorsal length, and weakening on fold; shell completely smooth posteriorly and marked only anteriorly and laterally with short plicae; costellae absent. Dental plates almost parallel; muscle scars pear shaped; pallial markings bifurcated in ventral interior. Dorsal interior with well-developed hinge plates, septalium, median septum; muscle scars oval, situated at both sides of median septum; pallial markings bifurcated. *Middle Triassic:* southwestern China.——FIG. 892,*2a–q.* **D. sinensis* (KOKEN), Anisian, Gheizhou; *a,* syntype, dorsal view, MCMB DDM4, ×3; *b–d,* syntype, lateral, anterior, ventral views, MCMB DDM4, ×1; *e,* syntype, dorsal view of steinkern

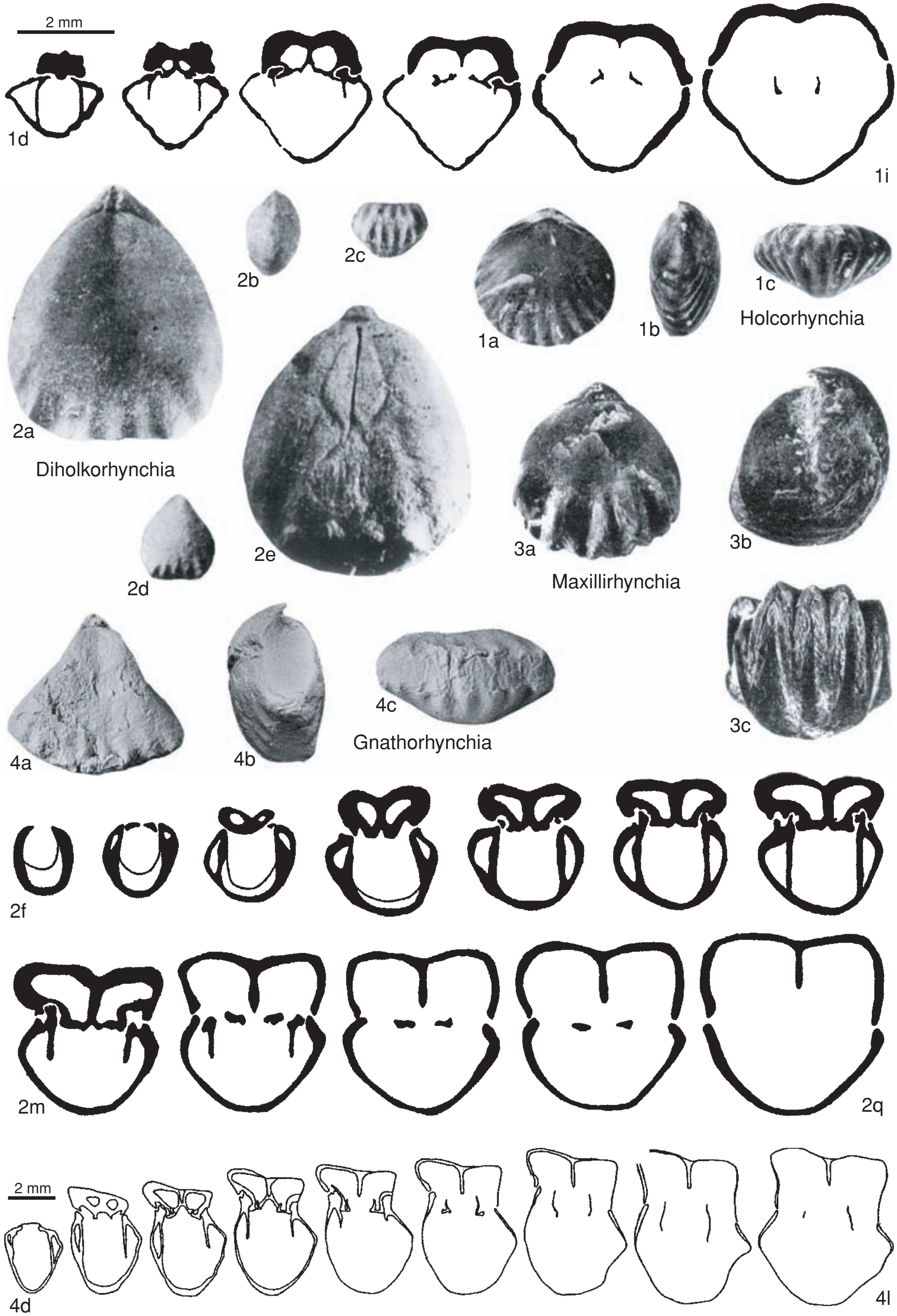

FIG. 892. Norellidae (p. 1314–1316).

with muscle scars, ×3; *f–q,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.8, 1.0, 1.3, 1.5, 1.6, 1.8, 2.0, 2.2, 2.4, 2.6, 2.9, MCMB DDKC 120 *4-2 (Yang & Xu, 1966).

Gnathorhynchia BUCKMAN, 1918, p. 29 [**Rhynchonella liostraca* BUCKMAN, 1886, p. 217; OD] [=*Gnathorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Similar to *Holcorhynchia* but triangular to securiform in outline, depressed equibiconvex to ventribiconvex, wide and flat anteriorly; posteriorly smooth, paucicostate anteriorly, with shallow dorsal sulcus and evenly serrate anterior commissure. Dorsal median septum strong, septalium wide; crura allegedly septiform, but arcuiform rather. *Middle Jurassic (Aalenian–Bajocian, ?Bathonian, ?Callovian):* England, France, Austria, ?Morocco, ?Algeria, USA (?California).——FIG. 892,*4a–l.* **G. liostraca* (BUCKMAN), Aalenian, Vilser Alps, Austria; *a–c,* dorsal, lateral, anterior views, ×2; *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.3, 1.5, 1.8, 2.1, 2.3, 2.6, 3.1, 3.6 (new; courtesy of F. García Joral).

Holcorhynchia BUCKMAN, 1918, p. 28 [**Rhynchonella standishensis* BUCKMAN, 1901, p. 245; OD] [=*Holcorhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Holochorhynchia* TOKUYAMA, 1957, p. 133, *nom. null.*]. Small, subcircular to subtriangular, depressed ventribiconvex; posteriorly sulcate, subcarinate ventrally with costae numerous, fine, blunt anteriorly after long smooth stage; beak small, hypothyrid slightly incurved. Persistent dorsal median septum, septalium deep, hinge plates inclined dorsally; arcuiform crura rather than raduliform. *Lower Jurassic (?Sinemurian, Pliensbachian–Toarcian), Middle Jurassic (?Bathonian):* England, Portugal, Italy, Germany, ?Austria, Anatolia, Algeria, *?Sinemurian, Pliensbachian–Toarcian;* ?Siberia, *?Bathonian.*——FIG. 892,*1a–c.* **H. standishensis* (BUCKMAN), lower Toarcian, Gloucestershire, England; dorsal, lateral, anterior views, GSM 31920, ×2 (Ager, 1967).——FIG. 892,*1d–i. H. yakacikensis* AGER, ?Sinemurian, Pliensbachian, Turkey; transverse serial sections, distances in mm from ventral umbo, 0.5, 0.7, 0.9, 1.0, 1.3, 1.8, J.1076/3, Derek Ager, personal collection (Ager, 1959c).

Maxillirhynchia BUCKMAN, 1918, p. 55 [**M. implicata;* OD] [=*Maxillirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Small, round subpentagonal, equibiconvex to dorsibiconvex; fold and uniplication low, rectangular after short early sulcate stage; capillate throughout, few strong costae anteriorly; beak sharp, incurved, hypothyrid. Dental plates ventrally divergent; septalium pendant; dorsal median septum ill developed; crura weakly flared, pedicle collar absent. *Upper Triassic (Norian), Lower Jurassic (?Pliensbachian, Toarcian), Middle Jurassic (?Aalenian, Bajocian):* ?Siberia, *Norian;* England, *?Pliensbachian, Toarcian;* Caucasus, ?Italy, *?Aalenian, Bajocian.*——FIG. 892,*3a–c.* **M. implicata,* upper Toarcian, Gloucestershire, England; dorsal, lateral, anterior views, GSM 31938, ×2 (Ager, 1967).

Subfamily MONTICLARELLINAE Childs, 1969

[Monticlarellinae CHILDS, 1969, p. 18]

Small to medium-sized Norellidae, ornamented with radial striae but costae variably developed or even absent; beak small and pointed; slightly sulcate, rectimarginate or weakly uniplicate. Crura arcuiform where known; dorsal median septum and septalium much reduced or absent; dental plates may be obsolescent. *Middle Triassic (Ladinian)–Upper Cretaceous (Turonian).*

Monticlarella WISNIEWSKA, 1932, p. 55 [**Rhynchonella czenstochowiensis* ROEMER, 1870, p. 247; OD, *error pro R. czenstochaviensis*]. Small, subtriangular to subpentagonal with maximum width anterior to midvalve; slightly ventribiconvex, posteriorly sulcate, umbonally capillate, becoming costellate anteriorly with some intercalation; anterior commissure polyplicate with characteristic lateral enlarged plicae; small, sharp beak, tiny foramen. Dental plates weak to vestigial; dorsal median septum poorly developed; crura arcuiform. [Species name was originally spelled *Czenstochaviensis,* then WISNIEWSKA (1932, p. 55) adopted the spelling *czenstochowiensis,* attributing it to ROEMER, but this is an unjustified emendation.] *Middle Jurassic (upper Callovian)–Upper Cretaceous (Turonian):* England, France, Switzerland, Germany, western Carpathians, Poland, Bulgaria, Crimea, Caucasus, Algeria, ?China.——FIG. 893,*2a–r.* **M. czenstochaviensis* (ROEMER), Oxfordian, Czestochowa area, Poland; *a–d,* dorsal, lateral, anterior, ventral views, ×1; *e,* detail of apical region showing deltidial plates, ×5 (Wisniewska, 1932); *f–r,* transverse serial sections, distances in mm from ventral umbo, 0.7, 0.8, 1.0, 1.1, 1.2, 1.3, 1.4, 1.6, 1.8, 2.0, 2.1, 2.3, 2.4, J.1219/2, Derek Ager, personal collection (Childs, 1969).

Batangorhynchia SUN & LI, 1990, p. 108[118] [**B. xiaoleica;* OD]. Small to medium size; roundly triangular to roundly pentagonal in outline; almost equibiconvex; anterior commissure sulcate; beak small, incurved; pedicle opening small, rounded, and hypothyrid; surface of shell smooth posteriorly and marked by low, rounded costae anteriorly. Pedicle collar and dental plates absent or fused to wall; teeth thin; hinge plates discrete, narrow, and tapering; inner socket ridges high, merged with outer hinge plates; crural base triangular; crura arcuiform; median septum just a ridge; septalium absent. *Middle Triassic (Ladinian):* China (southern Qinghai).——FIG. 894,*3a–r.* **B. xiaoleica; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP

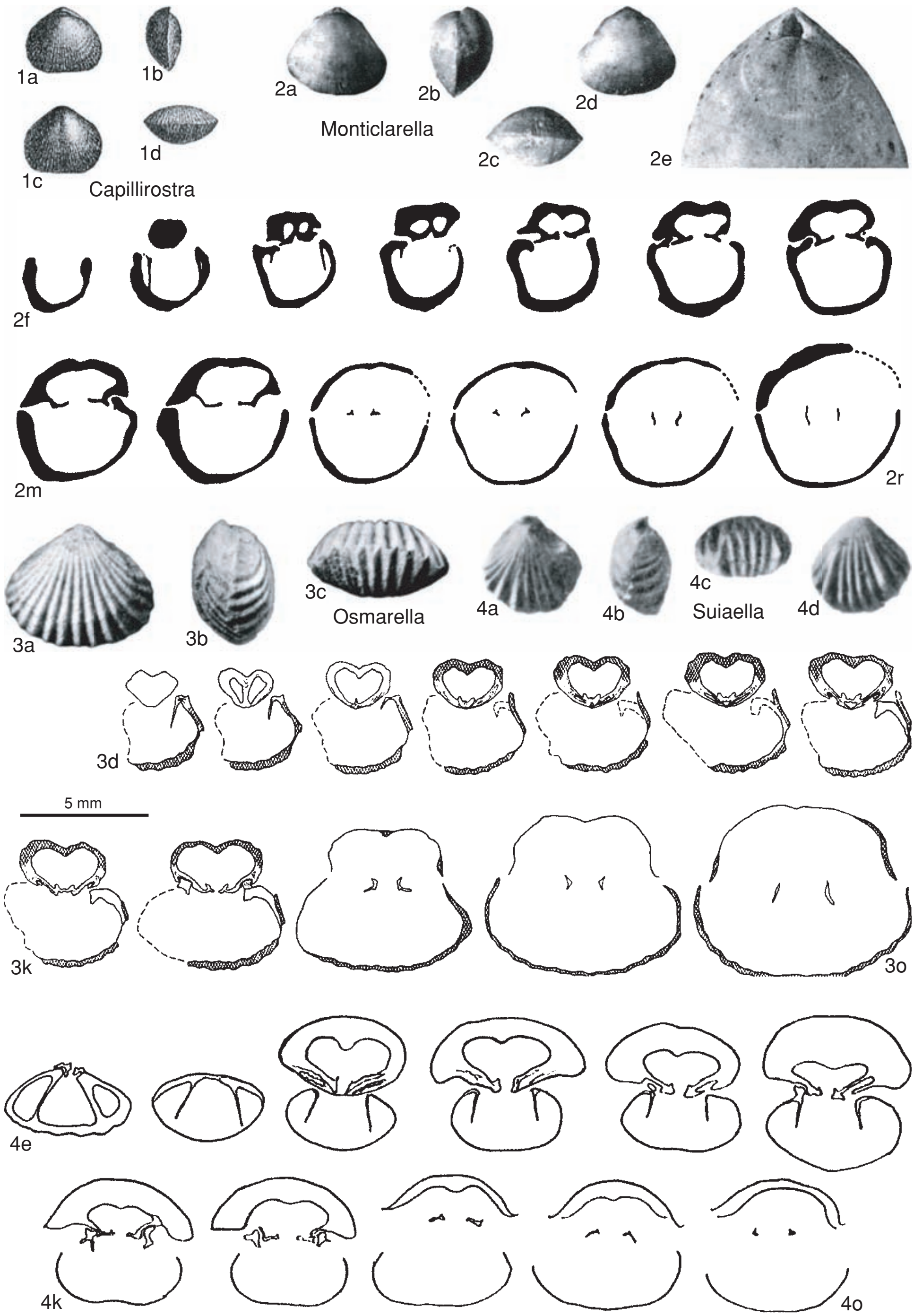

FIG. 893. Norellidae (p. 1316–1319).

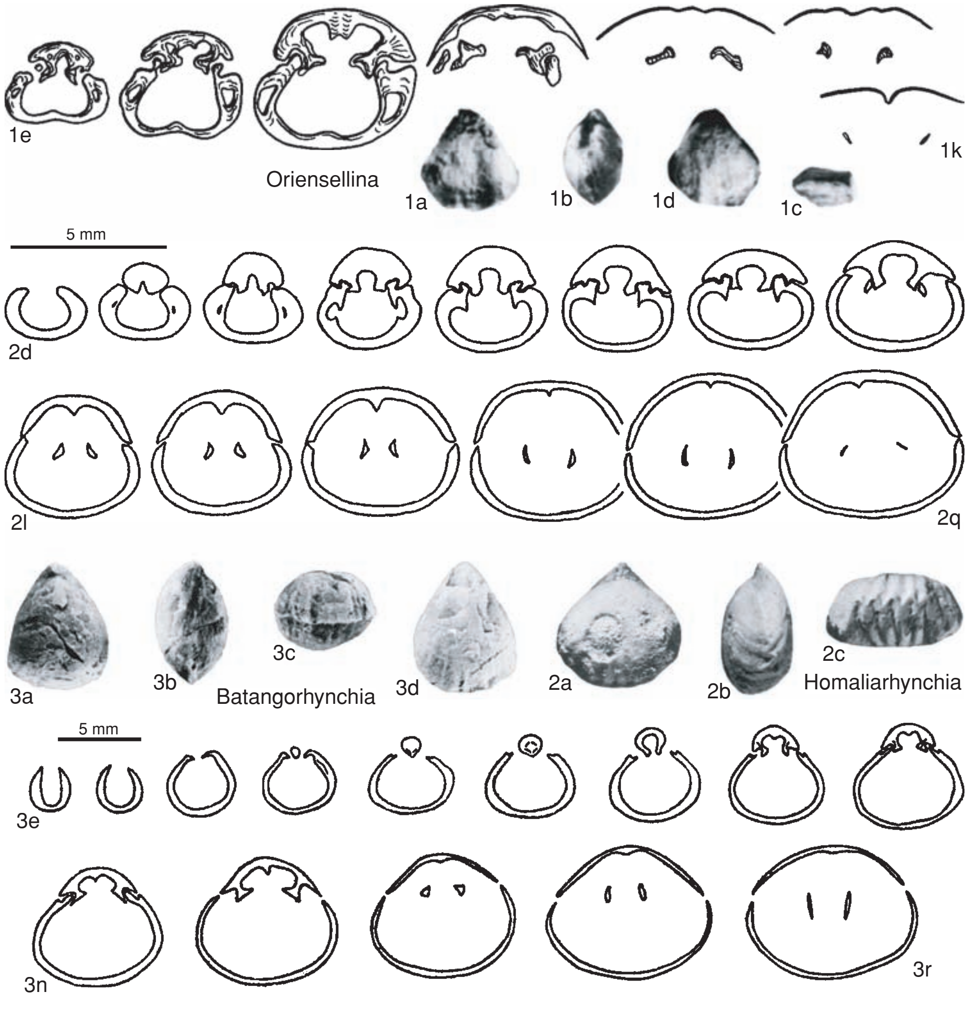

FIG. 894. Norellidae (p. 1316–1319).

97336, ×1; *e–r,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 1.15, 1.4, 1.65, 1.8, 1.9, 2.1, 2.5, 3.1, 3.5, 3.8, 4.6, 4.9, NIGP 97337 (Sun & Li, 1990).

Capillirostra COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Rhynchonellopsis* BÖSE, 1894, p. 78 (footnote), *non* VINCENT, 1893, Terebratulida, *nec* DE GREGORIO, 1930b, also Rhynchonellida [**Rhynchonellina? finkelsteini* BÖSE, 1894, p. 77; SD SCHUCHERT & LEVENE, 1929a, p. 107] [=*Capilirostra* MAKRIDIN in SARYCHEVA, 1960, p. 257, *nom. null.*]. Similar to *Monticlarella* but rectimarginate; small, depressed, ventribiconvex, with grooves delimiting dorsal muscle scars and short crura. [Probably a juvenile form and a subjective synonym of *Monticlarella* WISNIEWSKA, 1932, p. 55; cf. AGER, CHILDS, & PEARSON, 1972, p. 181; SULSER, 1993, p. 32, unless recognizable as subgenus.] *Upper Jurassic (Oxfordian, ?Kimmeridgian):* Germany.——FIG. 893,*1a–d.* **C. finkelsteini* (BÖSE), Oxfordian or ?Kimmeridgian, Swabia, Germany; dorsal, lateral, anterior, ventral views, ×1 (Böse, 1894).

Homaliarhynchia SHI, 1990, p. 306 [**H. minuta;* OD]. Shell minute, gently equibiconvex and uniplicate; costate anteriorly after a long smooth stage, no sulcation in dorsal umbo. Dorsal median septum a vestigial ridge; septalium and septalial plates absent; hinge plates not differentiated; rudimentary dental plates fused to wall; crura arcuiform. *Middle Jurassic (Bathonian):* China (eastern Tibet), England.——FIG. 894,*2a–q.* **H. minuta; a–c,* holotype, dorsal, lateral, anterior views, MCMB

M161761, ×1.5 (Shi, 1992); *d–q,* transverse serial sections, distances in mm from ventral umbo, 0.2, 0.5, 0.6, 0.8, 0.9, 1.0, 1.1, 1.2, 1.4, 1.5, 1.7, 1.9, 2.0, 2.2, MCMB L126172 (Shi, 1990).

?Oriensellina SMIRNOVA in SMIRNOVA & KONOVALOV, 1986, p. 75 [**O. minutalis;* OD] [=*Oriensirhynchia* SMIRNOVA, 1984, p. 116, *nom. nud.; Eastirhynchia* SMIRNOVA, 1984, p. 120, *nom. nud.*]. Small, rounded to triangular or pyriform, equibiconvex, smooth stage occupying half the length of shell; ventral sulcus shallow; dorsal fold moderately developed; beak long, slightly incurved, foramen small. Dental plates parallel to slightly ventrally divergent; sessile septalium developed; hinge plates short, dorsally concave; crura narrow, divergent, approaching spinuliform. *Lower Cretaceous (Berriasian–Valanginian):* Russia (eastern Siberia).——FIG. 894,*1a–k.* **O. minutalis,* Primorye; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 245/141, ×2 (Smirnova, 1990); *e–k,* transverse serial sections, distances in mm from first section, 0.9, 1.1, 1.3, 1.5, 2.1, 2.5, 3.4, MGU 245/145, approximately ×4 (Smirnova & Konovalov, 1986).

?Osmarella PEARSON, 1977, p. 58 [**Rhynchonella Starhembergica* ZUGMAYER, 1880, p. 38; OD]. Small to medium size; ribs numerous, low, rounded; branching occurring posteriorly or may be smooth; beak and area very small; sulcus and fold poorly developed. Dorsal median septum very low and short; hinge plate entire; crural bases bulbous, crura arcuiform. [Alternatively, may be related to Praemonticlarellinae, or, according to DAGYS (1994, personal communication), even to Cirpinae, being similar to *Euxinella.*] *Upper Triassic (Norian)–Lower Jurassic (Hettangian, ?Pliensbachian):* Slovakia, northern Alps.——FIG. 893,*3a–o.* **O. starhembergica* (ZUGMAYER), Rhaetian, Austria; *a–c,* dorsal, lateral, anterior views, ×1.3; *d–o,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.6, 0.7, 0.85, 0.9, 0.95, 1.0, 1.05, 1.1, 1.2, 1.6, 2.0, 2.5, PC.28, personal collection of D. A. B. Pearson, to be placed in the Natural History Museum of Vienna (Pearson, 1977).

Suiaella MOISSEEV in WEBER, 1949, p. 109 [**S. weberi* MOISSEEV in WEBER, 1949, p. 110; M] [=*Suiaella* MOISEEV in RZHONSNITSKAIA & others, 1956, p. 61, obj.]. Small, subtriangular, depressed equibiconvex; rounded costae throughout, with some bifurcation; beak short, suberect, foramen small, hypothyrid; ventral sulcus broad with shallow trapezoidal linguifom extension bounded by marked lateral plicae. Dental plates ventrally divergent, not attached along full length. [Possibly a subjective synonym of *Monticlarella* WISNIEWSKA, 1932, or else a subgenus with sharper costation.] *Lower Cretaceous (Valanginian, Barremian):* Crimea, western Carpathians.——FIG. 893,*4a–o.* **S. weberi,* lower Barremian, Crimea; *a–d,* dorsal, lateral, anterior, ventral views, MGU 522/3, ×2 (Smirnova, 1972); *e–o,* transverse serial sections, distances in mm from ventral umbo, 0.6, 0.9, 1.0, 1.2, 1.25, 1.3, 1.4, 1.7, 1.9, 2.0, 2.4, CNIGR 299/4802 (new; courtesy of S. V. Lobacheva).

Subfamily LAEVIRHYNCHIINAE Dagys, 1974

[*nom. transl.* MANCEÑIDO & OWEN, herein, *ex* Laevirhynchiidae DAGYS, 1974, p. 91]

Very small smooth norellids with neat sinus on ventral valve and round fold on dorsal, usually flanked by radial sulci. Hinge plates divided; dorsal median septum and septalium absent; dental plates much reduced or absent; crura arcuiform or variant. *Upper Triassic (Carnian)–Middle Jurassic (Bajocian).*

Laevirhynchia DAGYS, 1974, p. 91 [**Terebratula tricostata* VON MÜNSTER in WISSMANN & VON MÜNSTER, 1841, p. 57; OD] [=*Levirhynchia* DETRE, 1972, p. 88, *nom. nud.*]. Small, subtriangular, smooth, moderately biconvex; ventral valve with marked sulcation originating from umbo and broadening anteriorly; dorsal valve with matching, arcuate, median fold; umbo massive, beak slightly produced, suberect, foramen small; deltidial plates absent; beak ridges well defined, permesothyrid. Dental plates absent; hinge teeth deeply inserted, outer socket ridges well developed; hinge plates short; crura wide, deflected ventrally, connected by spicules; dorsal septum and septalium absent. *Upper Triassic (Carnian):* southern Alps, Carpathians.——FIG. 895,*1a–x.* **L. tricostata* (VON MÜNSTER), Hungary; *a–d,* dorsal, lateral, anterior, ventral views, IGiG 394/219, ×2; *e–x,* transverse serial sections, distances in mm from first section, 0.0, 0.1, 0.2, 0.3, 0.5, 0.6, 0.7, 0.8, 1.0, 1.1, 1.2, 1.4, 1.5, 1.6, 1.7, 1.8, 1.9, 2.0, 2.05, 2.15, IGiG 394/220 (Dagys, 1974).

Nannirhynchia BUCKMAN, 1918, p. 67 [**N. subpygmaea;* OD] [=*Nannirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Minute, globose equibiconvex; sulcate, with well-marked median uniplication and fold rounded to flattopped; with few rounded costae anteriorly, otherwise smooth; beak small, short, incurved, foramen small, deltidial plates disjunct. Dental plates weak, subparallel to dorsally divergent, often almost fused to wall; dorsal median septum absent; crura arcuiform. *Lower Jurassic (?Pliensbachian, Toarcian)–Middle Jurassic (Bajocian):* England, France, Portugal, ?Slovakia, ?Austria, Morocco, Algeria, Tunisia.——FIG. 895,*2a.* **N. subpygmaea,* upper Bajocian, Somerset, England; holotype, dorsal view, GSM 51308, ×2.5 (Ager, 1967).——FIG. 895,*2b–t.* *N. pygmaea* (MORRIS), Toarcian, Peniche, Portugal; *b–d,* dorsal, lateral, anterior views, FSL 305185, approximately ×2.5; *e–t,* transverse serial sections, distances in mm from ventral umbo, 0.1, 0.2, 0.3, 0.35, 0.4, 0.45, 0.5, 0.55, 0.6, 0.65, 0.7, 0.8, 0.9, 1.0, 1.2, 1.3, FSL 307191 (Alméras & others, 1995).

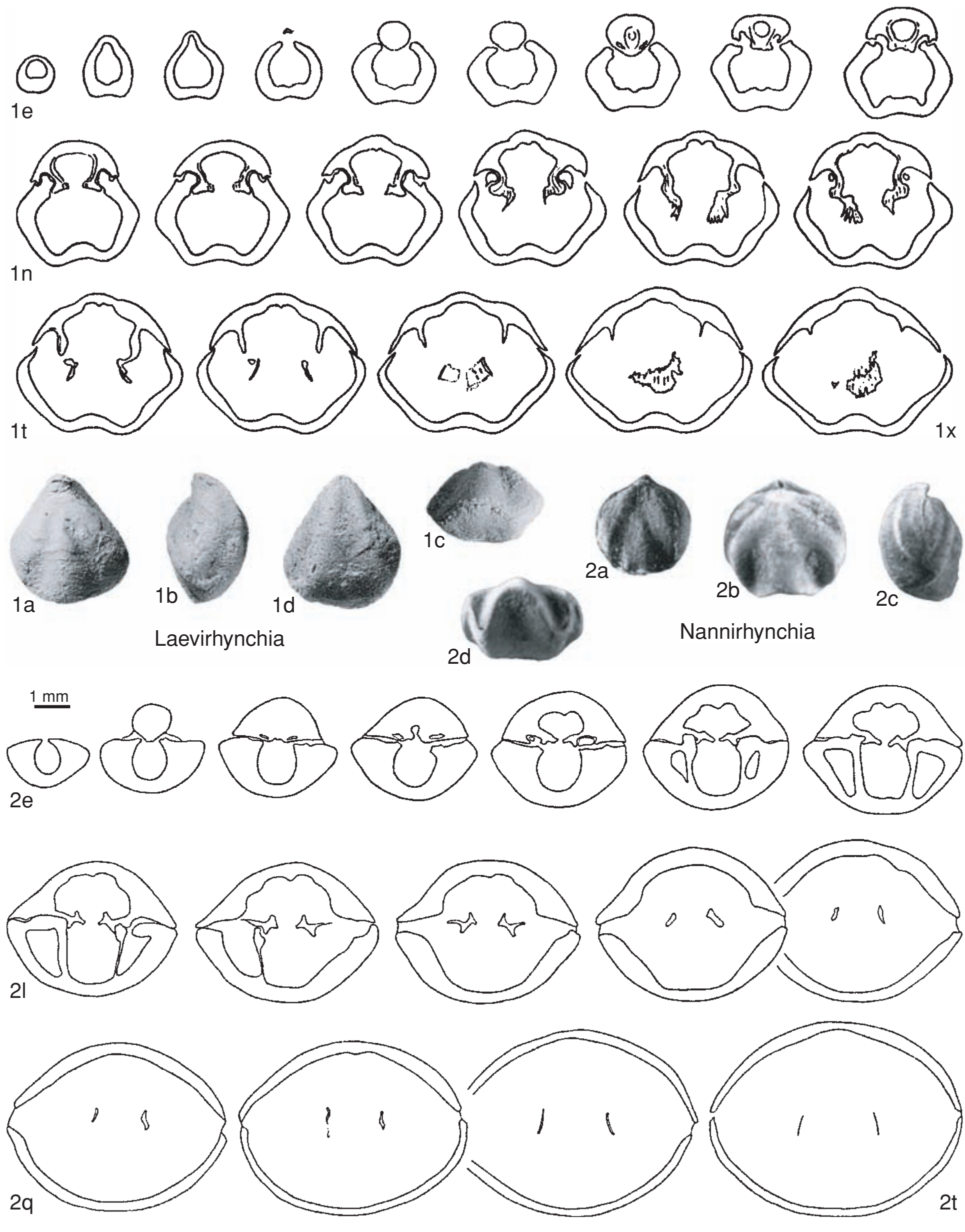

FIG. 895. Norellidae (p. 1319).

?Family OCHOTORHYNCHIIDAE Dagys, 1968

[Ochotorhynchiidae DAGYS, 1968, p. 47]

Small, subequibiconvex to nearly plano-convex shells, with sulcate dorsal valve, straight or slightly curved hinge margin, and round radial costae. Crura arising from inner socket ridges and directed anteroventrally, so-called clivuliform type; dental plates rudimentary to absent; median septum, septalium, and cardinal process undeveloped. [This small group with a discontinuous record, which was proposed among rhynchonelloids, is now tentatively placed closer to sulcate norelloids.] *Lower Jurassic (Sinemurian), Lower Cretaceous (Berriasian).*

Ochotorhynchia Dagys, 1968, p. 47 [**O. omolonensis;* OD]. Minute, thin, planoconvex, with few, low, rounded costae, distinct sulcus on dorsal valve, anterior commissure unisulcate; beak suberect, ridges distinct, foramen hypothyrid, deltidial plates absent. Dental plates and pedicle collar absent; cardinalia massive, fused inner socket ridges and hinge plates similar to brachiophores; crura thick, knoblike, almost reaching ventral valve. *Lower Jurassic (Sinemurian):* northeastern Siberia.——Fig. 896,*1a–r.* **O. omolonensis; a–d,* dorsal, lateral, anterior, ventral views, IGiG 231/78, ×3; *e–r,* transverse serial sections, distances in mm from first section, 0.0, 0.2, 0.3, 0.4, 0.6, 0.8, 1.1, 1.3, 1.4, 1.7, 1.9, 2.1, 2.2, 2.4 (Dagys, 1968).

?Tonasirhynchia Lobacheva & Smirnova, 1994, p. 131 [**T. janini;* OD]. Ventribiconvex, transversely oval in outline with dorsal sulcus and anterior commissure broad, arcuate and ventral fold smooth; umbo low, broad and beak small; valves ornamented by numerous fine plicae developing anteriorly. Pedicle collar present, dental plates undifferentiated; inner socket ridges high; hinge plates strongly inclined toward floor of dorsal valve; crural bases rounded in outline, developing thick, platelike crura fused with socket ridges. *Lower Cretaceous (Berriasian):* Ukraine (Crimea).——Fig. 896,*3a–q.* **T. janini; a–d,* holotype, dorsal, ventral, lateral, anterior views, CNIGR 1/12075, ×2; *e–q,* transverse serial sections, distances in mm from first section, 0.2, 0.3, 0.4, 0.5, 0.6, 0.8, 1.0, 1.2, 1.5, 1.7, 2.0, 2.2, 2.4, CNIGR 5/12810, approximately ×3 (Lobacheva & Smirnova, 1994).

Family FRIELEIIDAE Cooper, 1959

[Frieleiidae Cooper, 1959, p. 16] [=Hispanirhynchiidae Cooper, 1959, p. 16]

Small, thinly shelled Norelloidea, subtriangular to subpentagonal, rectimarginate, sulcate or ligate. Dental plates strong, crura modified from arcuiform, small septalium occurring apically sometimes; dorsal median septum present, ridgelike, or absent; 2 pairs of metanefridia; intestines straight, no terminal expansion; lophophore trocholophe to spirolophe. *Paleogene (?Danian, Eocene)–Holocene.*

Subfamily FRIELEIINAE Cooper, 1959

[*nom. transl.* Manceñido & Owen, herein, *ex* Frieleiidae Cooper, 1959, p. 16]

Subrectimarginate or ligate Frieleiidae, with shell surface capillate to costellate; with septalium supported by variably developed dorsal median septum; with short, straight, nonflaring spinuliform crura. *Paleogene (?Danian), Neogene (Miocene), Holocene.*

Frieleia Dall, 1895, p. 713 [**F. halli* Dall, 1895, p. 714; OD]. Elongate-oval to subtrigonal; rectimarginate to ligate, shell surface smooth to faintly costellate; beak short, nearly straight to suberect, hypothyrid; deltidial plates thick, disjunct. Inner hinge plates strongly developed; median dorsal septum supporting short septalium; crura long and divergent. [Living species range from bathyal to neritic.] *Paleogene (?Danian), Neogene (Miocene), Holocene:* western USA and North Pacific.——Fig. 897,*3a–l.* **F. halli,* Holocene; *a–c,* dorsal, lateral, anterior views, off Kamchatka, North Pacific, USNM 110830a, ×1; *d,* internal view of ventral valve showing dental plates and foramen, off Kamchatka, North Pacific, USNM 110830b, ×2; *e,* internal view of dorsal valve showing crura, off San Diego, California, USA, USNM 549348b, ×4 (Cooper, 1959); *f–l,* transverse serial sections through dorsal umbo (Dagys, 1968).

Compsothyris Jackson, 1918, p. 188 [**Rhynchonella Racovitzae* Joubin, 1901, p. 5; OD]. Uniplication trigonal, broad, gentle, dorsal fold poorly developed; shell surface with fine radial striae; foramen hypothyrid. Median dorsal septum ridgelike, supporting small septalium; crura somewhat spatulate, flat. [Living species have a circumpolar, bathyal range.] *Holocene:* Antarctica.——Fig. 897,*2a–e.* **C. racovitzae* (Joubin), McMurdo Sound; *a,* enlarged dorsal view, ×2; *b–c,* lateral, anterior views, ×1; *d,* ventral umbo showing foramen, deltidial plates, and hinge teeth, ×4; *e,* dorsal umbo showing crura, USNM 549343, ×4 (Cooper, 1959).

Grammetaria Cooper, 1959, p. 58 [**Hemithyris bartschi* Dall, 1920, p. 289; OD]. Elongate-trigonal, rectimarginate; capillate; beak small, suberect; foramen comparatively large, hypothyrid; deltidial plates conjunct, auriculate; crura short; dorsal median ridge or septum stout, supporting wide septalium. [Living species are bathyal.] *Holocene:* Philippines, Molluccas, off Bali, New Caledonia, South Africa.——Fig. 897,*1a–e.* **G. bartschi* (Dall), Mollucca Pass; *a,* enlarged dorsal view, ×2; *b–c,* lateral, anterior view, ×1; *d,* detail of ventral umbo, ×4; *e,* holotype, oblique view of dorsal umbo showing cardinalia and crura, USNM 239269, ×4 (Cooper, 1959).

Subfamily HISPANIRHYNCHIINAE Cooper, 1959

[*nom. transl.* Manceñido & Owen, herein, *ex* Hispanirhynchiidae Cooper, 1959, p. 16]

Rectimarginate to faintly sulcate, with capillate or striate shell surface; with crura short, straight, spinuliform, and with dorsal median ridge reduced to absent and without septalium. *Paleogene (Eocene)–Holocene.*

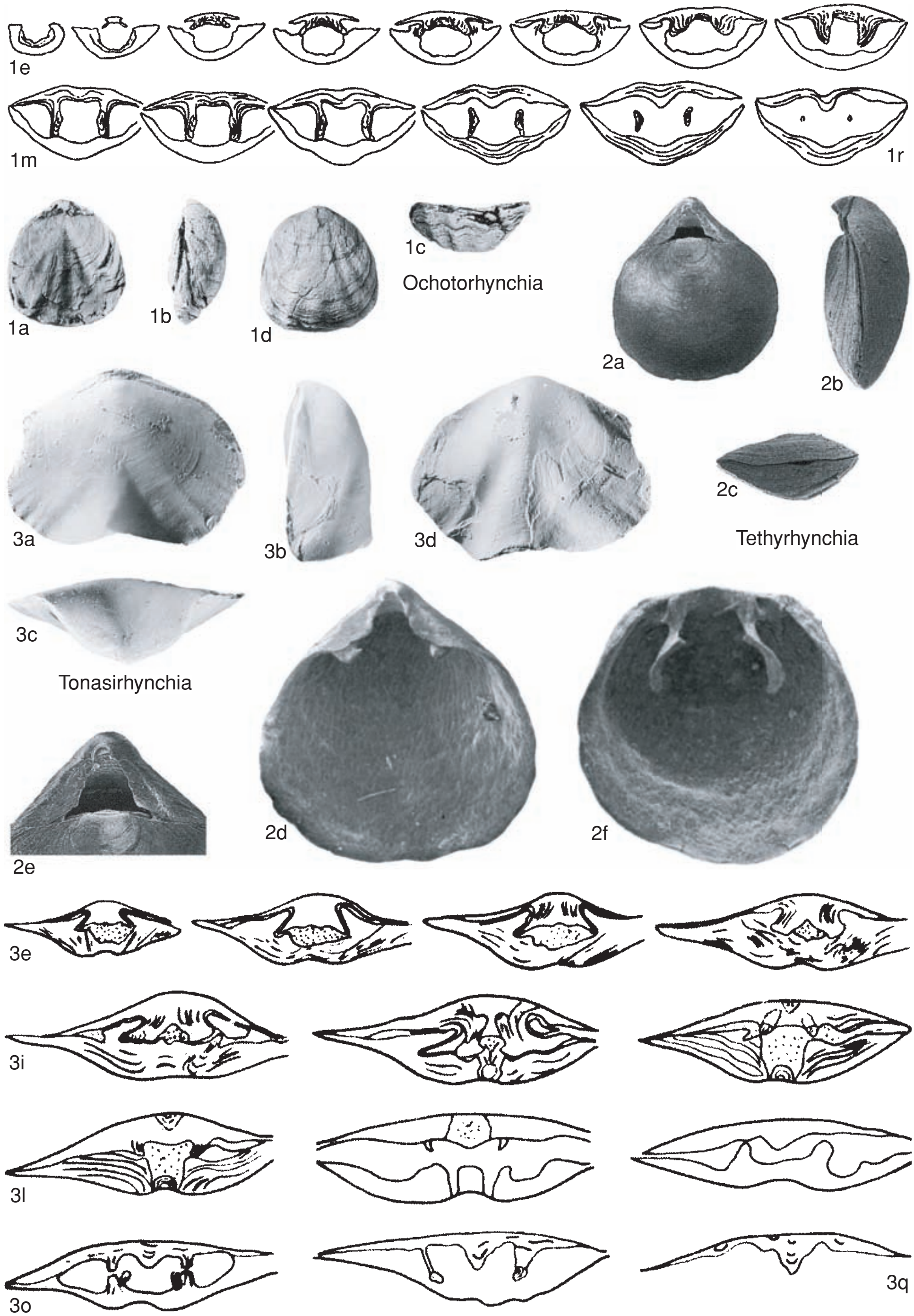

FIG. 896. Ochotorhynchiidae and Tethyrhynchiidae (p. 1321–1325).

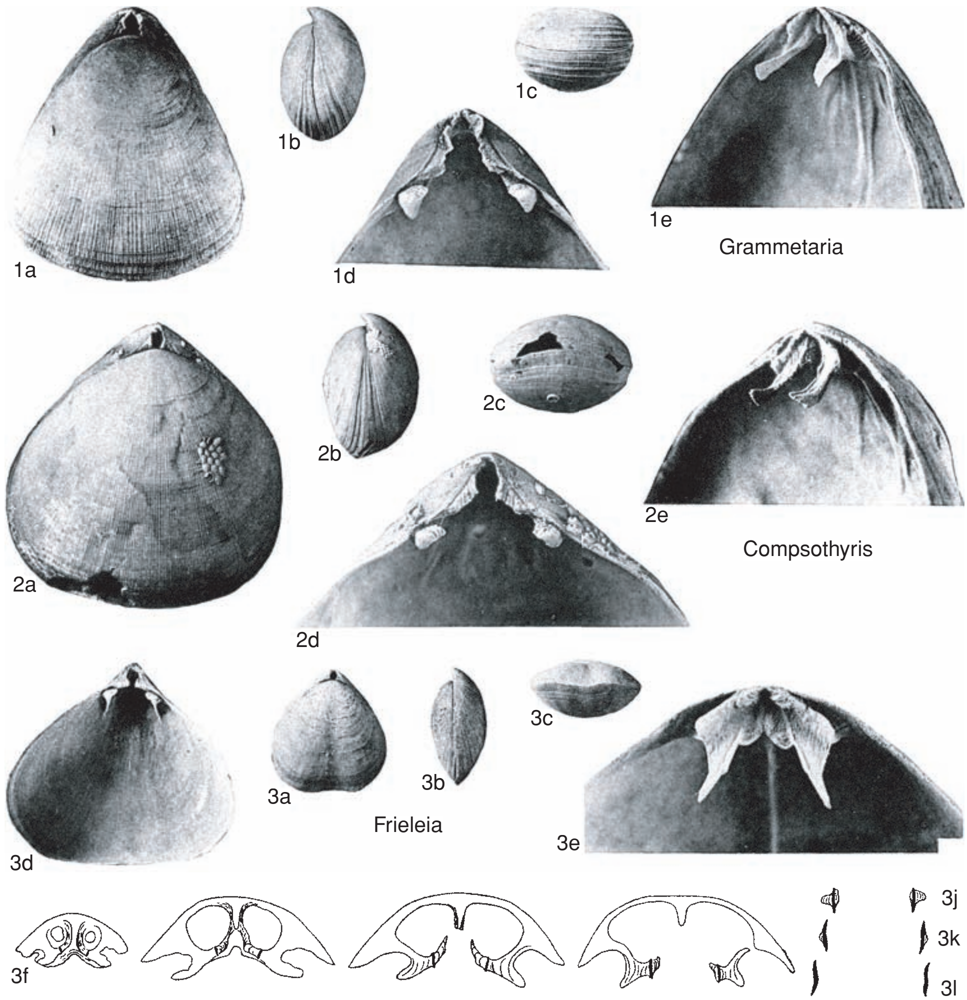

FIG. 897. Frieleiidae (p. 1321).

Hispanirhynchia THOMSON, 1927, p. 159 [**Rhynchonella cornea* FISCHER (MS) in DAVIDSON, 1887, p. 171; OD]. Elongate-triangular with greatest width anterior to midvalve; ventribiconvex; rectimarginate to incipiently uniplicate; beak short, suberect, foramen large, incomplete, hypothyrid; deltidial plates small, disjunct. Ventral valve with well-developed but incomplete pedicle collar and thick teeth supported by short dental plates; dorsal valve with crenulated sockets, small and narrow hinge plates, short bladelike crura and thick median ridge extending to apex of valve. [Living species are largely bathyal.] *Paleogene (Eocene), Holocene:* Cuba, *Eocene;* Morocco, off Sudan and Canary Islands to Cape Finistere, *Holocene.*——FIG. 898,*1a–e.* **H. cornea* (FISCHER), Holocene, off Mogador, Morocco; *a–c,* dorsal, lateral, anterior views, USNM 130327a, ×1; *d,* dorsal interior showing cardinalia and crura, USNM 130327d, ×6; *e,* ventral umbo, USNM 130327c, ×4 (Cooper, 1959).

Abyssorhynchia ZEZINA, 1980, p. 16 [**Hemithyris craneana* DALL, 1895, p. 717; OD]. Medium, translucent, rounded-triangular; rectimarginate to broadly sulcate; ventribiconvex; shell smooth to faintly striate; beak short, suberect, foramen open, large, hypothyrid. Dorsal septum very short and low; crura anteriorly enlarged, forming small, flat, spadelike distal ends. [Living species range from deep-bathyal to abyssal.] *Holocene:* southeastern Pacific Ocean.——FIG. 898,*2a–e.* **A. craneana*

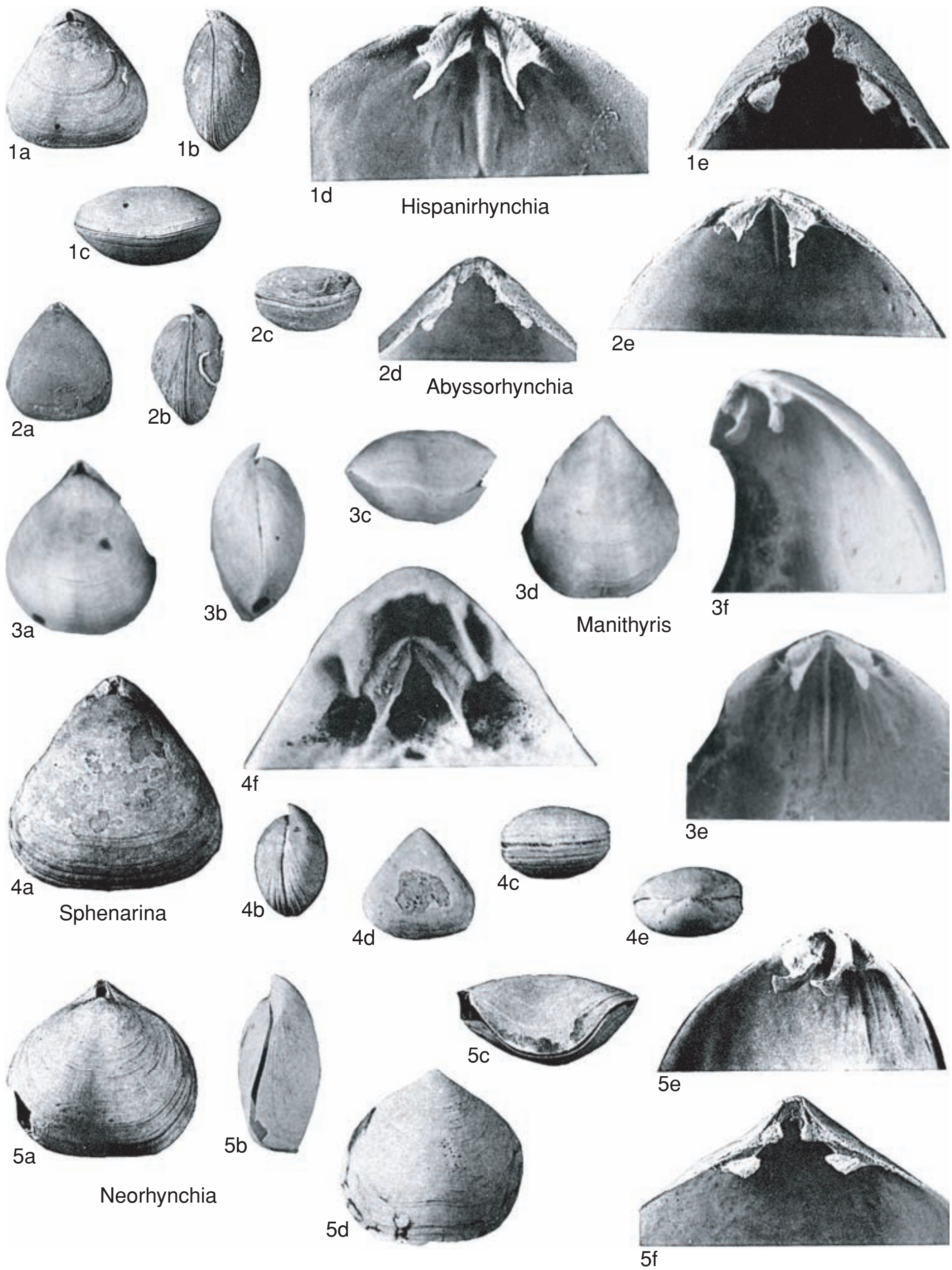

FIG. 898. Frieleiidae (p. 1323–1325).

(DALL), off Cocos Island, Panama; *a–c,* dorsal, lateral, anterior views, ×1; *d,* detail of beak region, ×4; *e,* holotype, cardinalia and crura in dorsal interior, USNM 122861, ×4 (Cooper, 1959).

?Manithyris FOSTER, 1974, p. 55 [**M. rossi;* OD]. Small, subequibiconvex, broadest anterior to midlength; finely capillate shell surface and irregularly ligate anterior commissure. Widely spaced crura spatulate, with outer surfaces strongly convex and inner surfaces concave, transitional between spinuliform and arcuiform; low dorsal median ridge; outer hinge plate narrow, no inner hinge plate. [Living species are abyssal.] *Holocene:* Antarctica (Ross Sea).——FIG. 898,*3a–f.* **M. rossi; a–d,* dorsal, lateral, anterior, ventral views, ×1.5; *e,* dorsal interior, ×5; *f,* holotype, oblique view of cardinalia, USNM 549997, ×5 (Foster, 1974).

Sphenarina COOPER, 1959, p. 62 [**Rhynchonella sicula* SEGUENZA in DAVIDSON, 1870, p. 461; OD]. Triangular in outline with greatest width anterior to midvalve; slightly ventribiconvex; rectimarginate; shell surface with fine radial striae. Similar in general character to *Hispanirhynchia* but without dorsal ridge or low septum. [Living species are bathyal.] *Neogene (Pliocene), Holocene:* Mediterranean region, *Pliocene;* Flores Sea, *Holocene.*——FIG. 898,*4a–f.* **S. sicula* (SEGUENZA), Pliocene, Messina, Sicily; *a,* enlarged dorsal view, ×2; *b–e,* lateral, anterior, ventral, posterior view, USNM 173728s, ×1; *f,* interior of dorsal umbo showing cardinalia and crura, USNM 549318a, ×10 (Cooper, 1959).

Subfamily NEORHYNCHIINAE new subfamily

[Neorhynchiinae MANCEÑIDO & OWEN, herein]

Smooth Frieleiidae, subpentagonal and strongly sulcate to almost rectimarginate. Teeth crenulated, dental plates short; dorsal median ridge present; crura crescentic, arcuiform; septalium absent. *Holocene.*

Neorhynchia THOMSON, 1915, p. 388 [**Hemithyris strebeli* DALL, 1908, p. 441; OD]. Suboval to pentagonal, gently ventribiconvex, typically sulcate, smooth; broad but deep, arcuate anterior commissure; beak short, hypothyrid; foramen moderate, deltidial plates disjunct. Crura short, gently arcuiform. [Living species are largely abyssal, shallower in Antarctica.] *Holocene:* Pacific Ocean.——FIG. 898,*5a–f.* **N. strebeli* (DALL), mid-Pacific; *a–d,* paratype, dorsal, lateral, anterior, ventral views, USNM 110741a, ×2; *e,* oblique view of crura, ×4; *f,* holotype, detail of ventral umbo, USNM 110741, ×4 (Cooper, 1959).

Family TETHYRHYNCHIIDAE Logan, 1994

[Tethyrhynchiidae LOGAN in LOGAN & ZIBROWIUS, 1994, p. 81]

Smooth Norelloidea, rectimarginate, faintly ventribiconvex; teeth not crenulated; dental plates, dorsal median septum, and cardinal process absent; flaring crescentic, so-called luniform crura; bell-shaped trocholophe. *Holocene.*

Tethyrhynchia LOGAN in LOGAN & ZIBROWIUS, 1994, p. 79 [**T. mediterranea;* OD]. Very small, smooth, translucent to transparent; subcircular, rectimarginate; almost equibiconvex with ventral valve barely deeper than dorsal; beak large, produced, slightly incurved; deltidium incomplete, deltidial plates disjunct, foramen comparatively large. *Holocene:* southern France, off Tunisia, Croatia (in submarine caves).——FIG. 896,*2a–f.* **T. mediterranea,* paratype, Marseille region, French coast; *a,* dorsal view, USNM 477119, ×25; *b,* lateral view, USNM 477121, ×25; *c,* anterior view, USNM 477120, ×25; *d,* ventral interior, USNM 477123, ×36; *e,* detail of apical region showing deltidium and foramen, USNM 477119, ×50; *f,* dorsal interior showing flared arcuiform crura, USNM 477125, ×36 (Logan & Zibrowius, 1994).

HEMITHIRIDOIDEA

MIGUEL O. MANCEÑIDO,[1] ELLIS F. OWEN,[2] SUN DONG-LI,[3] and A. S. DAGYS[4]

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Superfamily HEMITHIRIDOIDEA Rzhonsnitskaia, 1956

[*nom. transl. et correct.* MANCEÑIDO, OWEN, SUN, & DAGYS, herein, *ex* Hemithyrinae RZHONSNITSKAIA, 1956a, p. 126]

Rhynchonellida with subtriangular to subpentagonal, often globose, commonly strongly costate shells, sometimes bearing attenuated radial ribbing; moderate to prominent beak; dorsal fold and squama and glotta usually well defined. Dorsal median septum and uncovered septalium present, though variably developed; crura raduliform or variation thereof. *Middle Triassic–Holocene.*

Family HEMITHIRIDIDAE Rzhonsnitskaia, 1956

[*nom. transl. et correct.* AGER, 1965, p. 623, *ex* Hemithyrinae RZHONSNITSKAIA, 1956a, p. 126]

Dorsibiconvex, globose Hemithiridoidea, typically bearing numerous, fine, dense, radial costellae; commissure broadly to narrowly uniplicate, but dorsal fold indistinct; squama and glotta junction dorsally convex. Crura strong, slender, curved raduliform, attached to small outer hinge plates by their posterodorsal face or to thick socket ridges; crura raduliform, distally pointed and horizontally flattened; somewhat sunken biconcave cardinal process. Two pairs of metanefridia; intestines with curved distal end and terminal expansion; conoidal spirolophe bearing up to 5 whorls. [Based on unjustified emendation of *Hemithiris* D'ORBIGNY, 1847, p. 268, herein corrected in accordance with Article 35.4.1 of ICZN, 1999.] *Paleogene (Eocene)–Holocene.*

Hemithiris D'ORBIGNY, 1847, p. 268 [**Anomia psittacea* GMELIN, 1790, p. 3348; SD DAVIDSON, 1852a, p. 252] [=*Hemithyris* [BRONN], 1848, p. 246, obj., unjustified emendation]. Medium, trigonal, uniplicate, finely costellate, finely striate to smooth; beak long, suberect, hypothyrid. Ventral median ridge posteriorly; dorsal median ridge low; crura long, flattened posteriorly, and with moderate concave surfaces dorsally becoming more acute at the distal ends. [Living species range from subtidal to circalittoral, even bathyal.] *Paleogene (Eocene)–Holocene:* England, Belgium, Japan, Alaska, Canada, Sicily, *Pliocene–Pleistocene;* from Alaska to Japan via European Mediterranean and North Atlantic to North Pacific, *Holocene;* Antarctica (Cockburn and Seymour Islands), *Eocene–Oligocene.*——FIG. 899,*2a–f.* **H. psittacea* (GMELIN), Holocene, Alaska; *a–c,* dorsal, lateral, anterior views, USNM 111004a, ×1; *d,* internal view of dorsal valve showing crura and low median ridge, ×2; *e,* ventral interior showing dental plates and teeth, ×2; *f,* dorsal interior showing crura, USNM 111004b, ×3 (Cooper, 1959).

?Patagorhynchia ALLAN, 1938, p. 199 [**Rhynchonella patagonica* VON IHERING, 1903, p. 334; OD]. Subcircular to subpentagonal, uniplicate; finely costate with growth lines prominent anteriorly; dorsal fold well defined; ventral sulcus shallow, broadly trapezoidal. Beak small, nearly straight, foramen submesothyrid. *Paleogene (Eocene):* Argentina, Chile.——FIG. 899,*1a–e.* **P. patagonica* (VON IHERING), Santa Cruz province, Argentina; dorsal, ventral interior, lateral, anterior, dorsal interior showing thickened cardinalia and crura, ×1 (Cooper, 1959).

Pemphixina COOPER, 1981, p. 13–14 [**Rhynchonella nigricans* var. *pyxidata* DAVIDSON, 1880, p. 59; OD]. Small to medium, moderately dorsibiconvex, rounded to globular, strongly uniplicate, but dorsal fold scarcely raised; beak short, erect, foramen hypothyrid, elongate-oval, small; deltidial plates disjunct; shell surface multicostellate, costellae rounded, interrupted by numerous concentric growth lines. Hinge teeth thick, buttressed by short dental plates; crura short, crescentic in cross section, incipiently canaliform; dorsal median septum short but rising to crest just anterior to crura. [Living species range from circalittoral to upper bathyal.] *Holocene:* southern Indian Ocean (Kerguelen and Amsterdam Islands).——FIG. 899,*3a–f.* **P. pyxidata* (DAVIDSON), off Kerguelen Island; *a,* dorsal view, MNHN BRA-78-15d, ×2; *b–c,* lateral, anterior views, MNHN BRA-78-15h, ×1; *d,* oblique view of crura and cardinalium, MNHN BRA-78-15f, ×2; *e,* ventral interior, ×2; *f,* dorsal interior showing septum and cardinalia, MNHN BRA-78-15i, ×2 (Cooper, 1981).

Family CYCLOTHYRIDIDAE Makridin, 1955

[*nom. correct.* SMIRNOVA, 1984, p. 78, *pro* Cyclothyridae MAKRIDIN, 1964, p. 189, *nom. transl. ex* Cyclothyrisinae MAKRIDIN, 1955, p. 82]

Trilobate, sharply costate Hemithiridoidea, with anterior commissure uniplicate

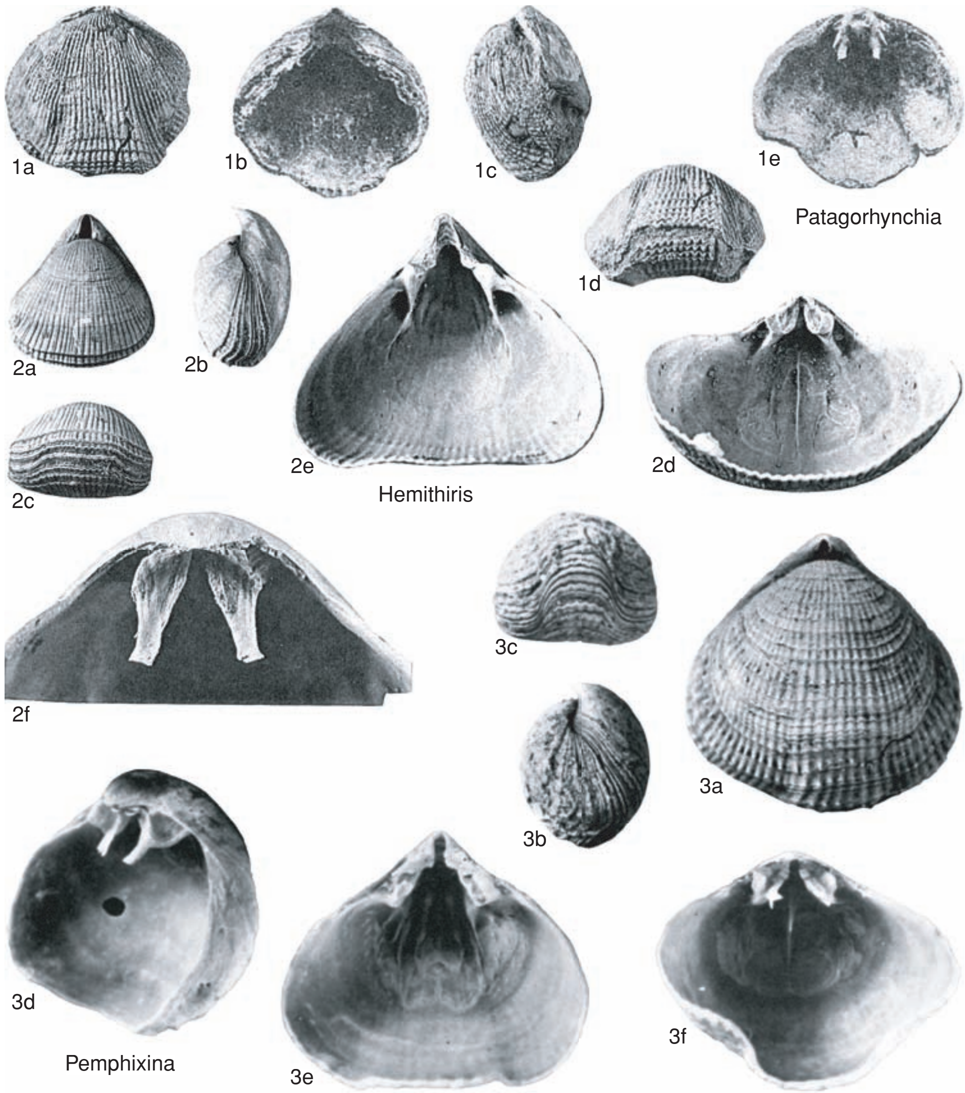

FIG. 899. Hemithirididae (p. 1326).

or sometimes asymmetrical; lamellose ornament frequently developed; squama-glotta obsolescent. *Middle Triassic (Anisian)–Upper Cretaceous (Maastrichtian).*

Subfamily CYCLOTHYRIDINAE Makridin, 1955

[*nom. correct.* AGER, 1965, p. 614, *pro* Cyclothyrisinae MAKRIDIN, 1955, p. 82] [=Praecyclothyrinae MAKRIDIN, 1964, p. 149 *partim* (containing type genus)]

Fully costate Cyclothyrididae, rarely with posterior smooth area; beak massive, with large hypothyrid rimmed foramen (i.e., deltidial plates produced into short tube around pedicle). Dorsal median septum usually very much reduced, septalium reduced or absent; crura canaliform (or at least distally concave modified raduliform). Characteristically strongly and densely costate. [Cyclothyridae, proposed by PHILLIPS, 1841, p. 55 for *Epithyris* and *Hypothyris,* is not an available family group name under Article 11.7.1.1 of the ICZN (1999).] *Middle*

Triassic (Anisian)–Upper Cretaceous (Maastrichtian).

Cyclothyris M'Coy, 1844, p. 103 [**Terebratula latissima* J. de C. Sowerby, 1840 in 1840–1846, index, p. 7; SD Buckman, 1906, p. 326; =*T. lata* J. de C. Sowerby, 1825 in 1823–1825, p. 165, *non* J. Sowerby, 1815] [=*Cyclothiris* d'Orbigny, 1850, p. 323, *nom. null.*]. Medium to large, wide, with uniplication low, arcuate, commonly asymmetrical; costellae numerous, fine posteriorly, given to bifurcation and antidichotomy anteriorly; beak erect, foramen large, auriculate; deltidial plates conjunct, well exposed. Dorsal septum short or absent; hinge plates distally concave; crura long, dorsally concave. *Lower Cretaceous (Aptian)–Upper Cretaceous (Maastrichtian):* England, France, Germany, Switzerland, Belgium, Poland, Romania, Bulgaria, Spain, Slovakia, Yugoslavia, Russia, Morocco, South Africa, Madagascar, ?Pakistan, India, Turkmenistan, USA, Chile.——Fig. 900,*1a–q.* **C. latissima* (J. de C. Sowerby), upper Aptian, Berkshire, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH BB.41494, ×1 (new); *d–q,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.3, 1.7, 2.3, 2.7, 3.2, 3.6, 3.9, 4.1, 4.4, 4.8, 5.1, 5.3, 5.6, 5.8, BMNH BB.5482 (Owen, 1962).——Fig. 900,*1r. C.* aff. *difformis* (Valenciennes in Lamarck), Cenomanian, near Prague, Bohemia; interior showing dorsal septum, canaliform crura, and dental plates, CGS ON16/690, ×3 (Nekvasilová, 1973).

Almerarhynchia Calzada Badia, 1974, p. 94 [**A. virgiliana;* OD]. Medium, equibiconvex, nearly as wide as long; median dorsal fold poorly developed; umbo short, massive, truncated by large foramen; costae rounded, deeply incised (4 to 8 on fold). Dental plates short, subparallel; hinge plates moderately long, ventrally deflected in early stages to horizontal; dorsal myophragm ridgelike to indistinct; crura incurved, distally canaliform. [Possibly a junior synomyn of *Hesperorhynchia.*] *Upper Cretaceous (Campanian–upper Maastrichtian):* Spain, ?eastern Europe.——Fig. 900,*2a–j.* **A. virgiliana,* Maastrichtian, Catalonian pre-Pyrenees, Spain; *a–c,* paratype, dorsal, lateral, anterior views, MGSB 11789, ×1; *d–j,* transverse serial sections, distances in mm from ventral umbo, 2.6, 3.1, 3.5, 3.9, 4.6, 5.8, 6.2 (Calzada Badia, 1974).

Aucklandirhynchia MacFarlan, 1992, p. 217 [**A. aucklandica;* OD]. Small to moderate size, rounded to subpentagonal; dorsibiconvex, well inflated; uniplicate, may be asymmetrical, fold ill defined and sulcus distinct, rounded; costae strong, narrow, subangular to rounded, sometimes with posterior smooth stage; beak large, foramen large, circular and pedicle collar. Dorsal median septum moderately short, usually low; septalium broad; dental plates wide apart, slightly dorsally divergent. *Lower Jurassic (Pliensbachian)–Middle Jurassic (Callovian):* New Zealand.——Fig. 900,*3a–k.* **A. aucklandica,* Temaikan, North Island; *a–d,* holotype, dorsal, lateral, anterior, ventral views, NZGS BR1874, ×2; *e–k,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.2, 1.3, 1.6, 1.9, 2.2, 2.4, 2.6, OU NZ 17309 (MacFarlan, 1992).

Bicepsirhynchia Shi, 1990, p. 310 [**B. asperata;* OD]. Small to medium; suboval to pyriform; fully costate; beak relatively strong; foramen hypothyrid to mesothyrid with deltidial plates conjunct and thickened. Dorsal median septum and septalial plates extremely reduced; no septalium; crura canaliform, incurved abruptly toward ventral valve. *Upper Jurassic (Oxfordian):* China (southern Qinghai), France.——Fig. 900,*4a–j.* **B. asperata,* lower Oxfordian, southern Qinghai; *a–c,* holotype, dorsal, lateral, anterior, MCMB Y154193, ×1 (Shi, 1992); *d–j,* paratype, transverse serial sections, distances in mm from first section, 4.0, 4.2, 4.7, 5.4, 5.8, 6.0, 6.2, MCMB Y154192 (Shi & Grant, 1993).

Costirhynchopsis Dagys, 1977, p. 387[139], *nom. nov. pro Costirhynchia* Dagys, 1974, p. 105, *non* Buckman, 1918, also Rhynchonellida [**Costirhynchia spatiosa* Dagys, 1974, p. 106; OD]. Small to medium size, laterally oval to wide subpentagonal, uniplicate, with fold low or absent; thickest near front; strongly costate throughout; beak suberect, ridges distinct, foramen hypothyrid, deltidial plates disjunct. Dental plates ventrally divergent; septalium short, supported by low septum, crura raduliform; pedicle collar absent. *Middle Triassic (Anisian)–Upper Triassic (Carnian):* Alps, Balkans, central Europe, Carpathians, northwestern Caucasus, Pamirs, northeastern Iran, China, ?New Guinea.——Fig. 901,*1a–k.* **C. spatiosa* (Dagys), Carnian, northwestern Caucasus; *a–d,* holotype, dorsal, lateral, anterior, ventral views, IGiG 394/55, ×2; *e–k,* transverse serial sections, distances in mm from first section, 0.2, 1.1, 1.5, 1.9, 2.2, 2.6, 3.1, IGiG 394/58 (Dagys, 1974).

Fissirhynchia Pearson, 1977, p. 48 [**Rhynchonella fissicostata* Suess, 1854, p. 30; OD]. Small to medium size, laterally oval to subpentagonal; uniplicate, sinus broad, corresponding fold low or absent; fully costate, costae sharp, branching prominently near umbones; beak acuminate, incurved to erect, ridges indistinct; foramen submesothyrid. Dental plates long, subparallel; pedicle collar absent; outer hinge plates arched, septalium deep, supported by high median septum; crura canaliform. *Upper Triassic (?upper Carnian, Norian)–Lower Jurassic (Pliensbachian):* Alps (Austria), Balkans (Bulgaria, Greece), Carpathians (Slovakia), central Italy, Hungary, northwestern Romania, Yugoslavia, Crimea, northwestern Caucasus, Turkey, Iran, New Zealand, New Caledonia, ?Himalayas, ?Peru, *?upper Carnian, Norian–Rhaetian;* northern Alps (Austria, Switzerland), Sicily, Hungary, ?Indonesia, Argentina, *Hettangian–Pliensbachian.*——Fig. 901,*2a–k.* **F. fissicostata*

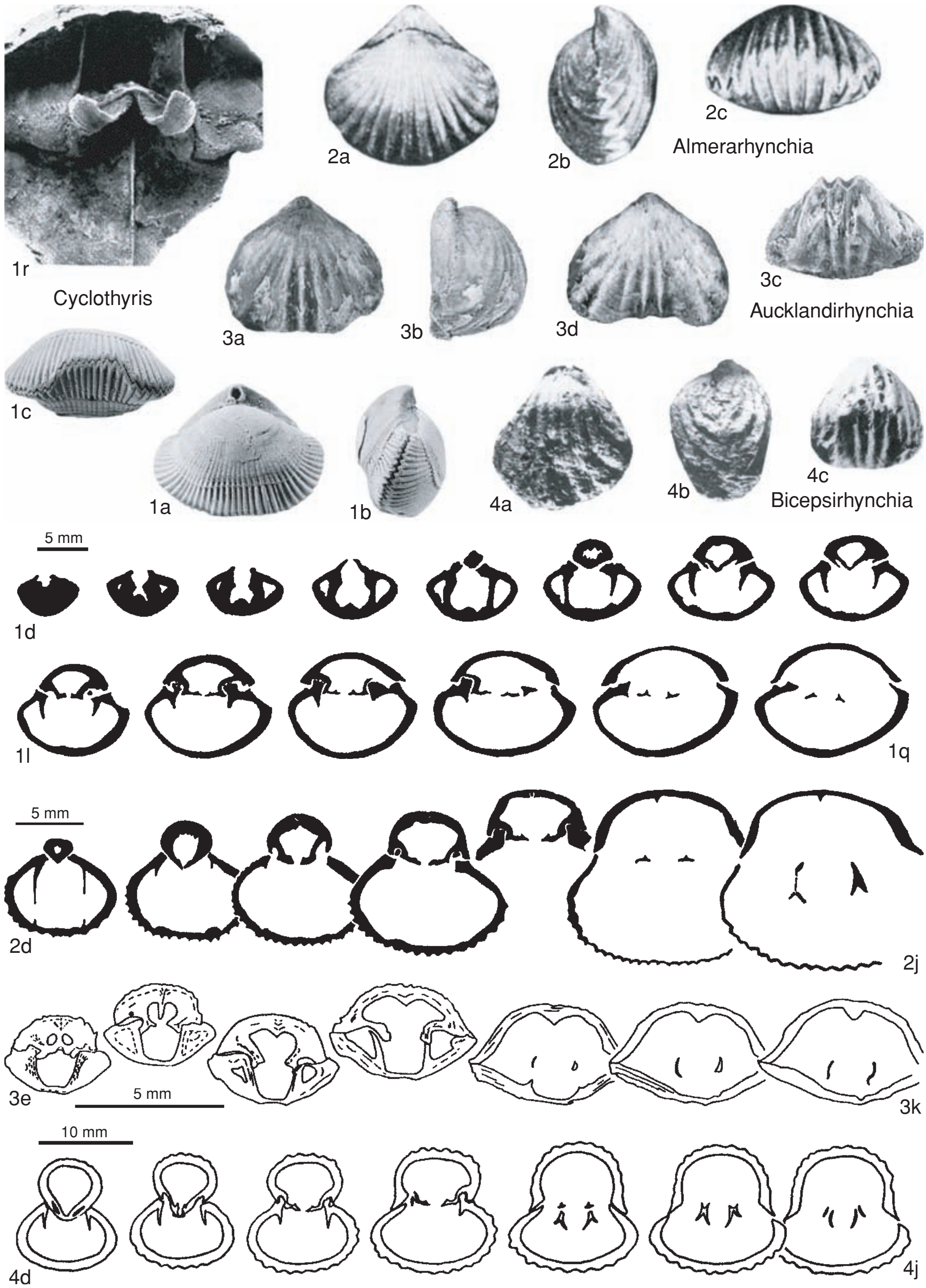

FIG. 900. Cyclothyrididae (p. 1328).

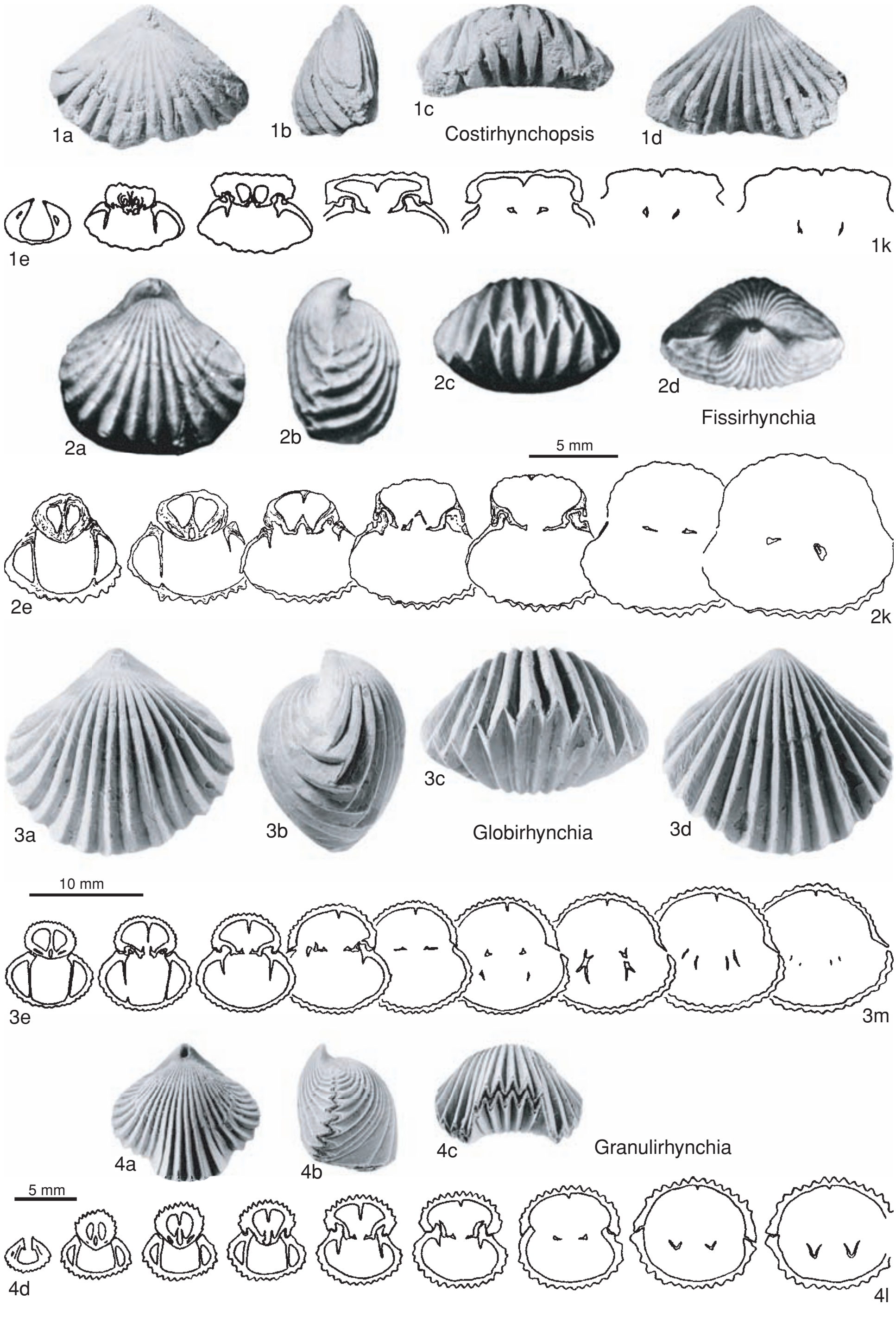

FIG. 901. Cyclothyrididae (p. 1328–1331).

(Suess), Rhaetian, Piesting-Tal, Austria; *a–d,* topotype, dorsal, lateral, anterior, posterior views, ×1.3; *e–k,* transverse serial sections, distances in mm from ventral umbo, 2.7, 3.0, 3.15, 3.65, 4.05, 5.05, 5.75, PC 2, D. A. B. Pearson, personal collection, to be placed in the Natural History Museum of Vienna (Pearson, 1977).

Globirhynchia Buckman, 1918, p. 48 [**Rhynchonella subobsoleta* Davidson, 1852b, p. 91; OD] [=*Globirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small to medium size, globose subequibiconvex; uniplication arcuate and dorsal fold low, indistinct; costae numerous, simple, coarse subangular, no smooth stage; beak massive, suberect, foramen rimmed, hypothyrid. Dorsal septum long and low; septalium variable, may be pitlike to deep V-shaped; hinge plates broad, subhorizontal; canaliform crura strongly incurved ventrally. *Middle Jurassic (Aalenian–Bajocian, ?Bathonian):* England, France, Spain, Austria, Italy, Transcarpathia, northwestern Caucasus, Arabia, Egypt (Sinai), Thailand, USA (?California).——Fig. 901,*3a–m.* **G. subobsoleta* (Davidson), Aalenian, Cotswolds, England; *a–d,* dorsal, lateral, anterior, ventral views, BMNH B.31698, ×1.5 (new); *e–m,* transverse serial sections, distances in mm from ventral umbo, 2.3, 2.5, 2.7, 3.5, 3.8, 4.4, 4.6, 5.0, 5.3, USNM 429428 (Shi & Grant, 1993).

Granulirhynchia Buckman, 1918, p. 64 [**Rhynchonella granulata* Upton, 1905, p. 83; OD] [=*Granulirhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, subtrigonal, wide, depressed, dorsibiconvex; fold low, wide and uniplication strong; costae numerous, complete, simple, sharp, covered with fine granules; beak strong, suberect to nearly straight; foramen large, rimmed, with conjunct deltidial plates. Dorsal median septum strong; hinge plates broad; crura canaliform. *Middle Jurassic (Aalenian):* England, France.——Fig. 901,*4a–l.* **G. granulata* (Upton), Cotswolds, England; *a–c,* dorsal, lateral, anterior views, BMNH B.68633, ×1 (new); *d–l,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.8, 2.9, 3.3, 3.5, 3.7, 4.4, 4.9, 5.7, 5.9, USNM 104770d (Shi & Grant, 1993).

?Halorellina Xu, 1978, p. 276 [**H. zhonghuaensis;* OD]. Small to medium size; pentagonal to transverse elliptical in outline; beak stout, short, and nearly straight; beak ridges angular; palintrope wide and flattened; delthyrium open; sulci commonly developed on both valves; commissure rectimarginate to slightly uniplicate; surface ornamented with angular plicae increasing by bifurcation or intercalation. Dental plates present; teeth strongly developed; dorsal interior with septum high and narrow, septalium very short, and crura short. [Possibly a junior subjective synonym of *Fissirhynchia;* differences, such as special gabled inner hinge plates and chiselled crura, attributable to tilted sectioning.] *Upper Triassic:* southeastern China (Sichuan).——Fig. 902,*4a–i.* **H. zhonghuaensis; a–d,* holotype, dorsal, lateral, anterior, ventral views, ×1; *e,* detail of apical region, CIGMR SCSb 6036, ×4; *f–i,* transverse serial sections, distances in mm from ventral umbo, 1.5, 2.15, 2.65, 3.15 (Xu, 1978).

Hesperorhynchia Warren, 1937, p. 2 [**H. superba;* OD]. Medium, subtriangular to subcircular; semiglobose with uniplication moderate, wide, arcuate, and dorsal fold low, inconspicuous; costae few, strong, subangular (3 to 4 on fold); beak small, incurved. Dorsal septum and septalium reported as absent; dental plates short and weak. [Very similar to *Almerarhynchia.*] *Upper Cretaceous:* Canada, western USA.——Fig. 903,*3a–d.* **H. superba,* upper Senonian, Saskatchewan, Canada; holotype, dorsal, lateral, anterior, ventral views, UA H160 ct809, ×1 (new).

Lacunaerhynchia Alméras, 1966, p. 97 [**L. vergissonensis;* OD] [=*Septulirhynchia* Alméras, 1966, p. 110 (type, *S. davidi,* OD); *Nyalamurhynchia* Ching, Rong, & Sun in Ching, Sun, & Rong, 1976, p. 300 (type, *N. mirifica* Ching, Rong, & Sun in Ching, Sun, & Rong, 1976, p. 301, OD)]. Medium, subtrigonal, subcircular to subpentagonal, depressed equibiconvex; uniplication shallow, arcuate to flattopped, but median fold barely raised; costae numerous, subangular, 5 to 8 on fold; beak short, suberect to incurved; foramen submesothyrid; deltidial plates conjunct to subconjunct. Dental plates thin, subparallel; dorsal median septum well developed and septalium deep; crura raduliform, long. *Middle Jurassic (Bajocian–Bathonian):* France, Poland, Romania, China (Himalayas), Argentina.——Fig. 903,*1a–k.* **L. vergissonensis,* lower Bajocian, Saône-et-Loire, France; *a–c,* holotype, dorsal, anterior, ventral views, FSL 45737, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.5, 2.75, 2.9, 3.55, 4.6, 4.9, 5.8, 6.2, FSL 45736 (Alméras, 1966).——Fig. 903,*1l–u. L. davidi* (Alméras), lower Bajocian, Saône-et-Loire, France; *l–n,* dorsal, anterior, ventral views, FSL 45750, ×1; *o–u,* transverse serial sections, distances in mm from ventral umbo, 1.0, 2.45, 2.55, 2.75, 3.3, 3.5, 4.6, FSL 45745 (Alméras, 1966).——Fig. 903,*1v–gg. L. mirifica* (Ching, Rong, & Sun), Bajocian, Tibet; *v–y,* holotype, dorsal, lateral, anterior, ventral views, NIGP 28762, ×1; *z–gg,* holotype, transverse serial sections, distances in mm from ventral umbo, 1.2, 1.6, 2.0, 2.3, 2.6, 3.3, 3.8, 4.8, NIGP 28762 (Ching, Sun, & Rong, 1976).

Lamellaerhynchia Burri, 1953, p. 274 [**Terebratula rostriformis* Roemer, 1836, p. 40; OD; =*T. multiformis* Roemer, 1839, p. 19, *partim*]. Medium size, multicostate; uniplicate, rectimarginate or asymmetrical; beak strong, suberect; dorsal septum ridgelike, strong, varying in length; crura long, dorsally concave with acutely concave distal ends giving rise to diabolo appearance when serial sectioned. *Lower Cretaceous (?Berriasian, Valanginian–Barremian, ?Aptian, Albian):* England, France, Switzerland, Germany, Italy, Caucasus,

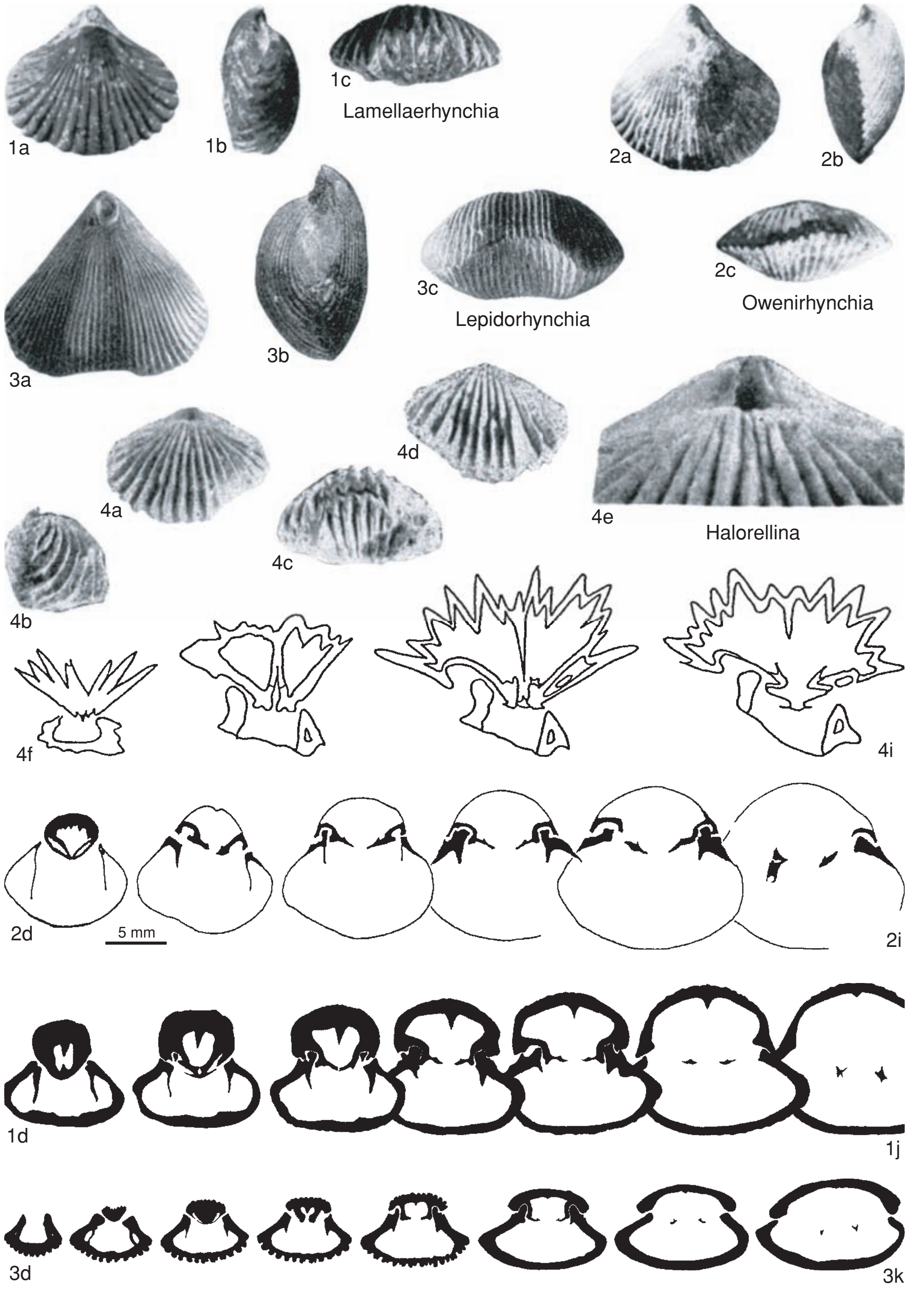

FIG. 902. Cyclothyrididae (p. 1331–1334).

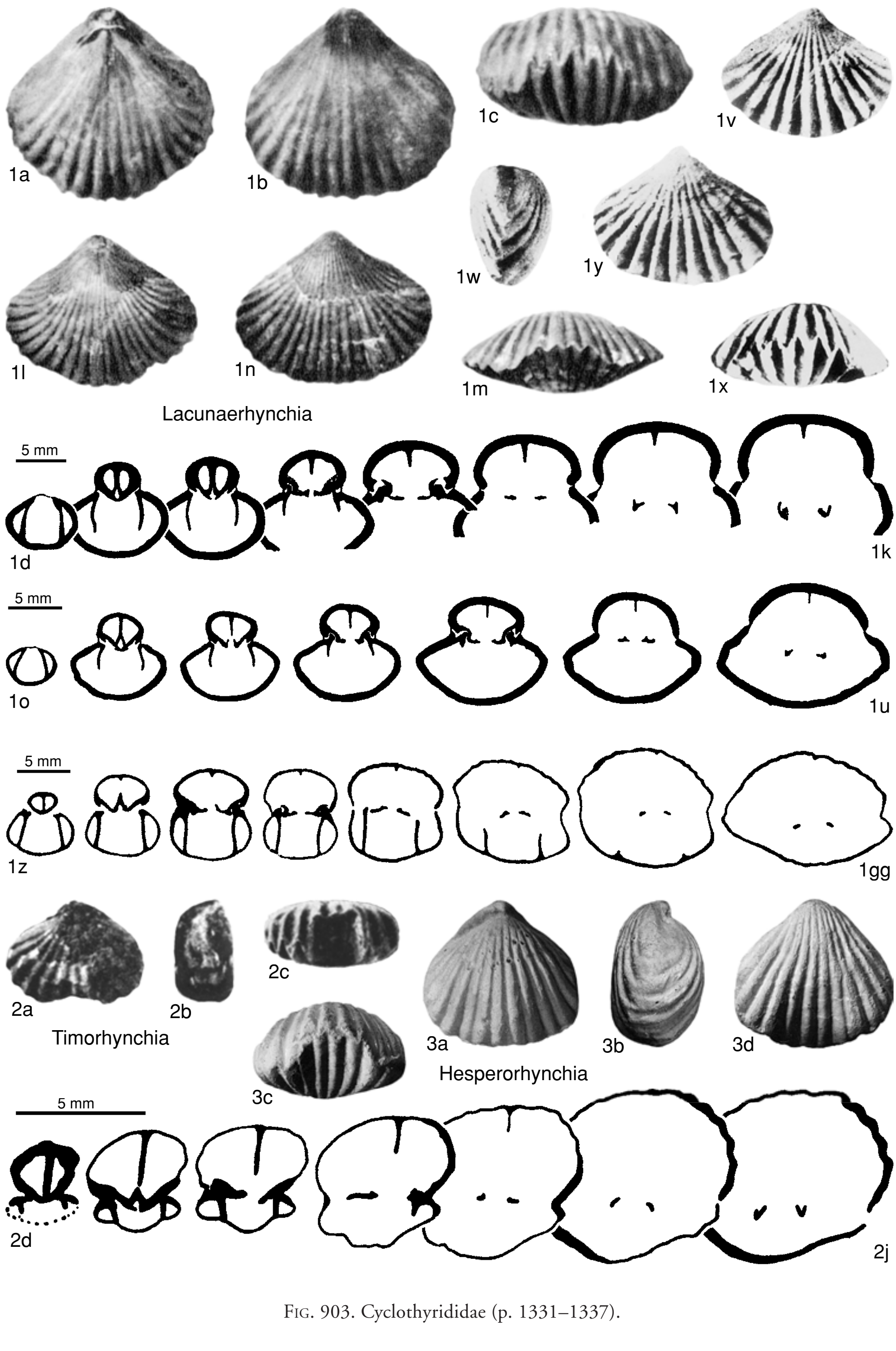

FIG. 903. Cyclothyrididae (p. 1331–1337).

Morocco, USA, Mexico, Turkmenistan, ?Antarctica.——FIG. 902,*1a–j*. **L. rostriformis* (ROEMER); *a–c,* dorsal, lateral, anterior views, lowest Hauterivian, St. Croix, Swiss Jura, NHMB 6, ×1 (Burri, 1953); *d–j,* transverse serial sections of umbo, 3.8, 4.4, 4.8, 5.1, 5.8, 6.4, 6.9, Neocomian, northwestern Germany, BMNH B.35703, approximately ×2 (Owen & Thurrell, 1968).

Lepidorhynchia BURRI, 1957, p. 689 [**L. dichotoma;* OD]. Small to medium, equibiconvex, with numerous, fine, rounded costellae given to marginal dichotomy; rectimarginate, faintly bisulcate; beak long with large circular foramen. Dental plates short; median septum poorly developed or low ridge in dorsal valve; hinge plates horizontal to dorsally deflected; crural bases with concave distal ends. General appearance similar to young *Cyclothyris. Lower Cretaceous (upper Hauterivian–lower Barremian):* France, Switzerland.——FIG. 902,*3a–k*. **L. dichotoma,* lower Barremian, Switzerland; *a–c,* holotype, dorsal, lateral, anterior views, NHMB 25a, ×2; *d–k,* transverse serial sections, cumulative distances in mm from first section, 0.5, 1.2, 1.4, 1.7, 1.9, 2.4, 2.9, 3.3, ×2 (Burri, 1957).

Owenirhynchia CALZADA in CALZADA & POCOVÍ, 1980, p. 14 [**O. rubra;* OD]. Medium, oval-subtriangular, equibiconvex, wider than long, similar to *Cyclothyris,* rather more densely multicostate; anterior commissure broadly arcuate, rectimarginate but given to slight asymmetry. Dental plates subparallel to slightly ventrally divergent, supporting deeply inserted subquadrate hinge teeth; hinge plates long, ventrally deflected, distally concave; inner and outer socket ridges well developed. [Possibly a subgenus or a subjective synonym of *Cyclothyris.*] *Upper Cretaceous (Turonian–upper Campanian):* Spain, ?France, ?Bohemia.——FIG. 902,*2a–i*. **O. rubra,* upper Campanian, Lérida, Spain; *a–c,* holotype, dorsal, lateral, anterior views, MGSB 30294, ×1.3; *d–i,* transverse serial sections, distances in mm from ventral umbo, 3.3, 3.7, 4.3, 4.7, 5.3, 5.9 (Calzada & Pocoví, 1980).

Pararhactorhynchia SHI, 1990, p. 311 [**P. trigona;* OD]. Shell subtrigonal to subpentagonal; uniplicate; strong ribs; inequivalve, weakly subcynocephalous in profile. Dorsal median septum and septalium well developed; crura canaliform, incurved ventrally. *Middle Jurassic (Bajocian):* southern Tibet.——FIG. 904,*4a–l*. **P. trigona; a–d,* holotype, dorsal, lateral, anterior, ventral views, MCMB N124051-1, ×1; *e–l,* holotype, transverse serial sections, 2.6, 3.1, 3.7, 4.3, 4.7, 5.8, 6.4, 6.8, distances in mm from ventral umbo, MCMB N124050-1 (Shi, 1992).

Plicarostrum BURRI, 1953, p. 281 [**P. hauteriviense;* OD]. Medium size, with costae numerous, sharp, or angular, deeply incised; cynocephalous, nearly convexoplane; beak projecting. Thick dental plates almost fused to shell wall; median septum or low ridge rising late; crura distally concave. *Lower Cretaceous (Hauterivian):* Switzerland.——FIG. 904,*1a–j*. **P. hauteriviense; a–c,* holotype, dorsal, lateral, anterior views, NHMB L348, ×1.5; *d–j,* transverse serial sections, distances in mm from first section, 1.5, 1.6, 1.8, 2.4, 3.1, 4.1, 5.3 (Burri, 1957).

Proteorhynchia OWEN, 1981, p. 307 [**Rhynchonella miquihuanensis* IMLAY, 1937, p. 570; OD]. Small, poorly biconvex, broadly oval-subtrigonal, dorsal fold well defined, ventral sulcus shallow, linguiform extension trapezoidal; ornament of strong angular costae; beak slightly incurved, interarea poorly demarcated. Subparallel dental plates support elongate, deeply inserted hinge teeth; dorsal septum high, supporting deep septalium; concave distal ends of hinge plates developing long crura. *Lower Cretaceous (Valanginian–Aptian):* Mexico.——FIG. 904,*2a–l*. **P. miquihuanensis* (IMLAY), Valanginian, Tamaulipas; *a–c,* holotype, dorsal, lateral, anterior views, UM 18738, ×1 (Imlay, 1937); *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.9, 1.6, 2.0, 2.6, 3.0, 3.5, 3.8, 4.4, 4.8, ×2 (Owen, 1981).

?Rudirhynchia BUCKMAN, 1918, p. 44 [**R. rudis;* OD] [=*Rudirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Mediterranirhynchia* SUCIC-PROTIC, 1969, p. 53–54 (type, *M. mediterranea* SUCIC-PROTIC, 1969, p. 54, OD)]. Small to medium size, subtriangular to subpentagonal, depressed dorsibiconvex, uniplicate, dorsal fold low; smooth posteriorly, with costae numerous, strong, fairly sharp (2 to 6 on fold); beak strong, sharp, projecting, upright to slightly incurved, with large elongate rimmed foramen and disjunct deltidial plates. Dental plates thin, becoming subparallel, teeth crenulated; dorsal median septum and septalium well developed; crura raduliform, perhaps developing concave distal ends; pedicle collar usually present. *Lower Jurassic (Pliensbachian, ?lower Toarcian):* England, Scotland, France, Germany, ?Portugal, Slovakia, Yugoslavia, Romania, Italy, ?Bulgaria, Caucasus, Siberia, ?Algeria, Argentina, Chile.——FIG. 905,*3a–k*. **R. rudis,* lower Pliensbachian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, GSM 31867, ×1.5; *d–k,* transverse serial sections, distances in mm from ventral umbo, 2.7, 2.9, 3.1, 3.4, 4.1, 4.7, 5.5, 6.0, J.922/1, Derek Ager, personal collection (Ager, 1959a).——FIG. 905,*3l–v*. *R. mediterranea* (SUCIC-PROTIC), middle Lias, Carpatho-Balkanids, Yugoslavia; *l–n,* holotype, dorsal, lateral, anterior views, MFMGB 1/64, ×1; *o–v,* transverse serial sections, distances in mm from first section, 1.3, 1.6, 2.0, 2.2, 2.4, 3.2, 3.7, 3.95 (Sucic-Protic, 1969).

Septaliphoria LEIDHOLD, 1921, p. 354 [**Rhynchonella arduennensis* OPPEL, 1857 in 1856–1858, p. 608[p. 310 of 2nd part]; OD; =*R. inconstans* D'ORBIGNY, 1850 in 1849–1852, p. 24, *non* SOWERBY, 1821] [=*Praecyclothyris* MAKRIDIN, 1955, p. 84 (type, *Rhynchonella moeschi donetziana* MAKRIDIN, 1952, p. 74, OD); *Septaliaphoria* MACFARLAN, 1992, p. 191, *nom. null.*]. Medium size to large,

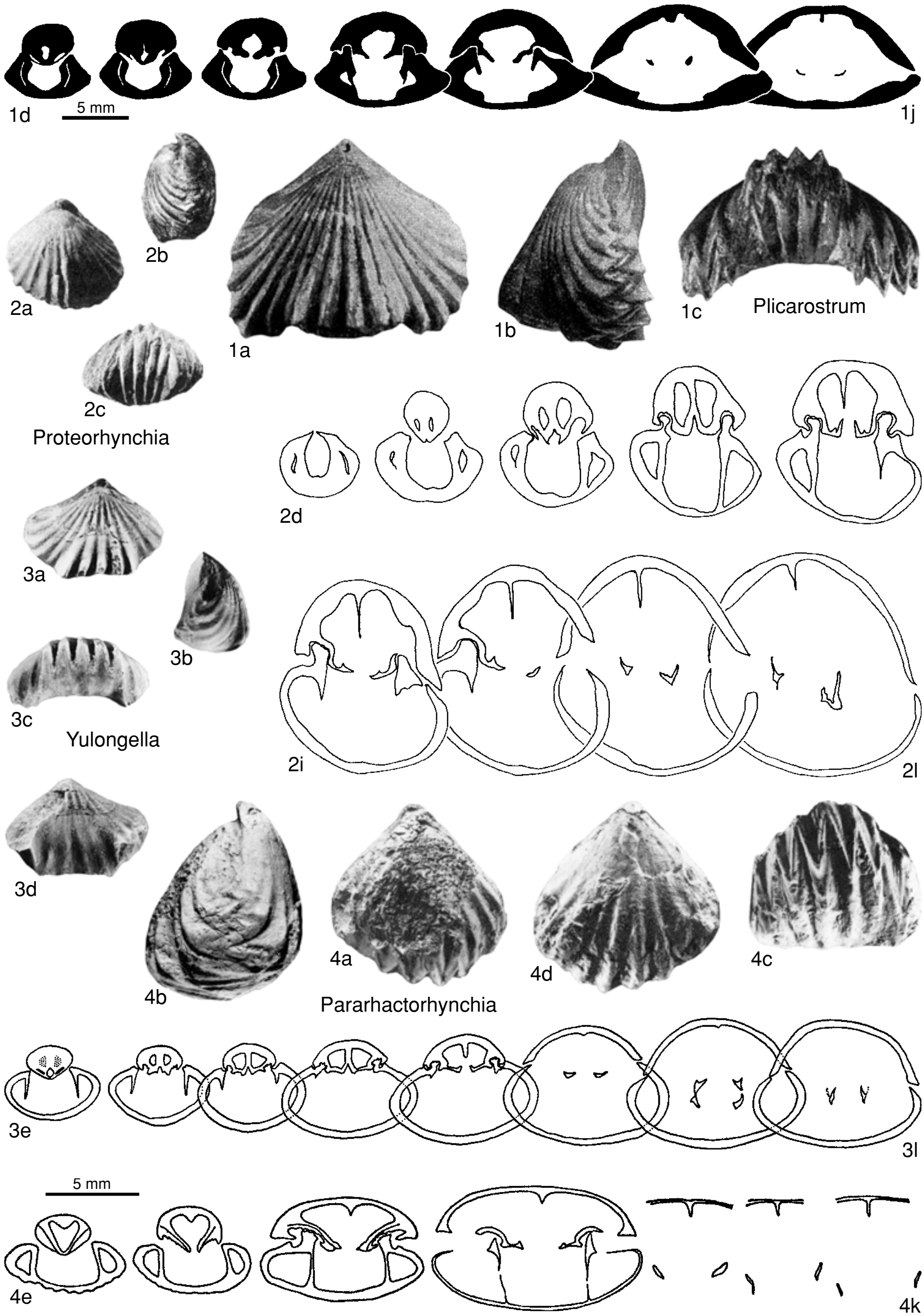

FIG. 904. Cyclothyrididae (p. 1334–1340).

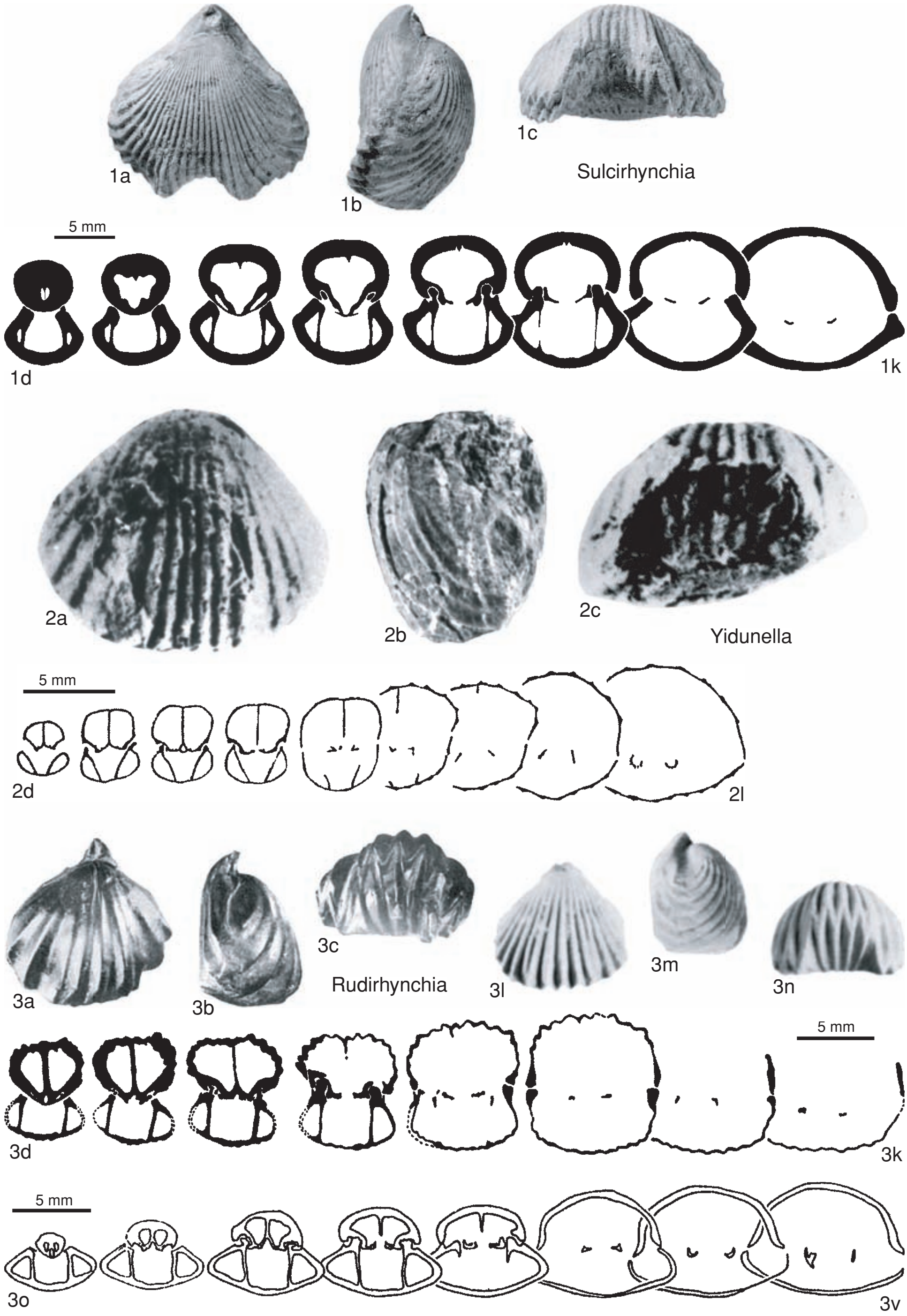

FIG. 905. Cyclothyrididae (p. 1334–1340).

dorsibiconvex, subpentagonal to oval, uniplicate, or slightly asymmetrical; dorsal fold wide, conspicuous to indistinct, posterior smooth area absent, with costae numerous, coarse, simple, subangular (3 to 7 on fold); beak strong, high, with foramen large, rimmed, hypothyrid, deltidial plates usually conjunct. Septalium raised on reduced median septum, or sessile; crura strongly curved, concave dorsally, canaliform. *Middle Jurassic (Callovian)–Lower Cretaceous (Barremian, ?Aptian):* England, Scotland, France, ?Portugal, Switzerland, Germany, Poland, Russia, Ukraine, ?Crimea, Caucasus, Morocco, Algeria, Uzbekistan, Turkmenistan, Turkey, southwestern and eastern China, India, Mexico, ?South America, *Callovian–Volgian;* Russian platform, Caspian basin, Crimea, Caucasus, Slovakia, Germany, Turkmenistan, *Berriasian–Barremian, ?Aptian.*——FIG. 906,*1a–k.* **S. arduennensis* (OPPEL), Oxfordian, Lorraine, France; *a–d,* neotype, dorsal, lateral, anterior, posterior views, BMNH BB.44173, ×1; *e–k,* transverse serial sections, distances in mm from ventral umbo, 3.1, 3.3, 3.6, 4.3, 5.0, 6.1, 6.5 (Childs, 1969).——FIG. 906,*1l–v. S. donetziana* (MAKRIDIN), upper Oxfordian, Russian Platform; *l–n,* holotype, dorsal, lateral, anterior views, KHGU 196/102, ×1; *o–v,* transverse serial sections, distances in mm from ventral umbo, 2.7, 3.1, 3.3, 4.5, 5.4, 6.2, 6.7, 6.8 (Makridin, 1964).

Septocyclothyris XU, 1978, p. 282 [**S. markamensis;* OD]. Small, trigonal to pentagonal; inequibiconvex to convexoplane; beak small and slightly incurved; foramen circular, submesothyrid-hypothyrid with short tubular rim produced by raised deltidial plates; sulcus and fold present; surface marked by simple costae starting from beak. Dental plates well developed and long; teeth stout, hooked, crenulated; dorsal septum well developed; septalium small and short; hinge plates subhorizontal; crural bases triangular. *Upper Triassic:* Tibet.——FIG. 906,*2a–l.* **S. markamensis; a–c,* holotype, dorsal, lateral, ventral views, ×1; *d,* detail of apical region and conjunct deltidial plates, CIGMR SCSb 6039, ×4; *e–l,* transverse serial sections, distances in mm from first section, 0.35, 0.45, 0.9, 1.3, 1.45, 1.55, 1.65, 1.75 (Xu, 1978).

?Squamirhynchia BUCKMAN, 1918, p. 63 [**Terebratula triplicata squamiplex* QUENSTEDT, 1871 in 1868–1871, p. 72; OD] [=*Squamirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, depressed equibiconvex to dorsibiconvex; dorsal valve nearly flat, with uniplication and fold low; costae strong (3 to 6 on central fold) showing early branching and no smooth stage; beak strong, upright, with large foramen. Septum low, persistent, septalium shallow; crura canaliform-like, concave dorsally, or diabolo shaped at distal ends; possibly buttressed deltidial plates. *Lower Jurassic (Sinemurian–Pliensbachian):* England, Germany. ——FIG. 906,*3a–k.* **S. squamiplex* (QUENSTEDT), lower Pliensbachian, Würtenberg, Germany; *a–c,* lectotype, dorsal, lateral, anterior, GPIT, approximately ×2; *d–k,* transverse serial sections, distances in mm from ventral umbo, 2.1, 2.2, 2.3, 2.5, 2.9, 3.6, 3.8, 4.0, BMNH B.38425 (Ager, 1967).

Sulcirhynchia BURRI, 1953, p. 272 [**Rhynchonella valangiensis* DE LORIOL, 1864, p. 442; OD]. Medium size with many sharp or angular costae; slight sulcus in dorsal fold anterior to midvalve; anterior commissure with ventral sulcus deep, trapezoidal, meeting slight sulcus on dorsal valve and developing well-defined ligation; beak strong, sharp, and slightly projecting, suberect. Median septum low, diminishing to low ridge; crura slightly concave distally; dental plates subparallel, supporting strong, subquadrate hinge teeth; hinge plates short, slightly concave dorsally. *Lower Cretaceous (upper Valanginian–Hauterivian, ?lower Aptian):* England, France, Switzerland.——FIG. 905,*1a–k.* **S. valangiensis* (DE LORIOL), upper Valanginian, Switzerland; *a–c,* dorsal, lateral, anterior views, ×1.5 (new); *d–k,* transverse serial sections, distances in mm from first section, 2.25, 2.5, 3.0, 3.2, 3.5, 3.95, 4.7, 7.2 (Burri, 1957).

Timorhynchia AGER, 1968, p. 58 [**Halorella nimassica* KRUMBECK, 1924, p. 10; OD]. Small to medium, subtrigonal to transverse-oval to subpentagonal, equibiconvex to depressed dorsibiconvex; dorsal valve flattened or sulcate posteriorly, with uniplication broad, low, flattopped, but fold scarcely raised; multicostate throughout, costae low posteriorly, may become strong and angular anteriorly; beak small, incurved with submesothyrid foramen. Dental plates diverging; dorsal median septum high, long, supporting short septalium; canaliform crura projecting into ventral valve. *Middle Triassic (Ladinian)–Upper Triassic (Norian):* New Zealand, New Caledonia, *Ladinian–lower Norian;* Timor, China, *?Carnian, Norian.*——FIG. 903,*2a–j.* **T. nimassica* (KRUMBECK), Upper Triassic, Alianbata, eastern Timor; *a–c,* dorsal, lateral, anterior views, Derek Ager, personal collection, ×1.5; *d–j,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.1, 1.2, 1.6, 2.0, 2.6, 2.8, Derek Ager, personal collection (Ager, 1968).

Torquirhynchia CHILDS, 1969, p. 95 [**Terebratula inconstans* J. SOWERBY, 1821 in 1818–1821, p. 137; OD] [=*Serbiorhynchia* RADULOVIC, 1991, p. 16 (type, *S. asymmetrica,* OD)]. Medium to large, equibiconvex to dorsibiconvex, subtriangular to suboval, bilobate, asymmetrical, indiscriminately twisted either side, but uniplication and fold never developed; costae coarse, subangular, simple beginning from umbones; beak suberect to incurved with foramen circular, deltidial plates disjunct or conjunct. Teeth strong, crenulated; dorsal median septum low and relatively long; septalium poorly developed, often reduced to pendant septalial plates; crura basically raduliform, showing channelling and other variations toward distal ends. *Middle Jurassic (?upper Bajocian, Bathonian)–Lower Cretaceous (Valanginian):* Great Britain, France, Germany,

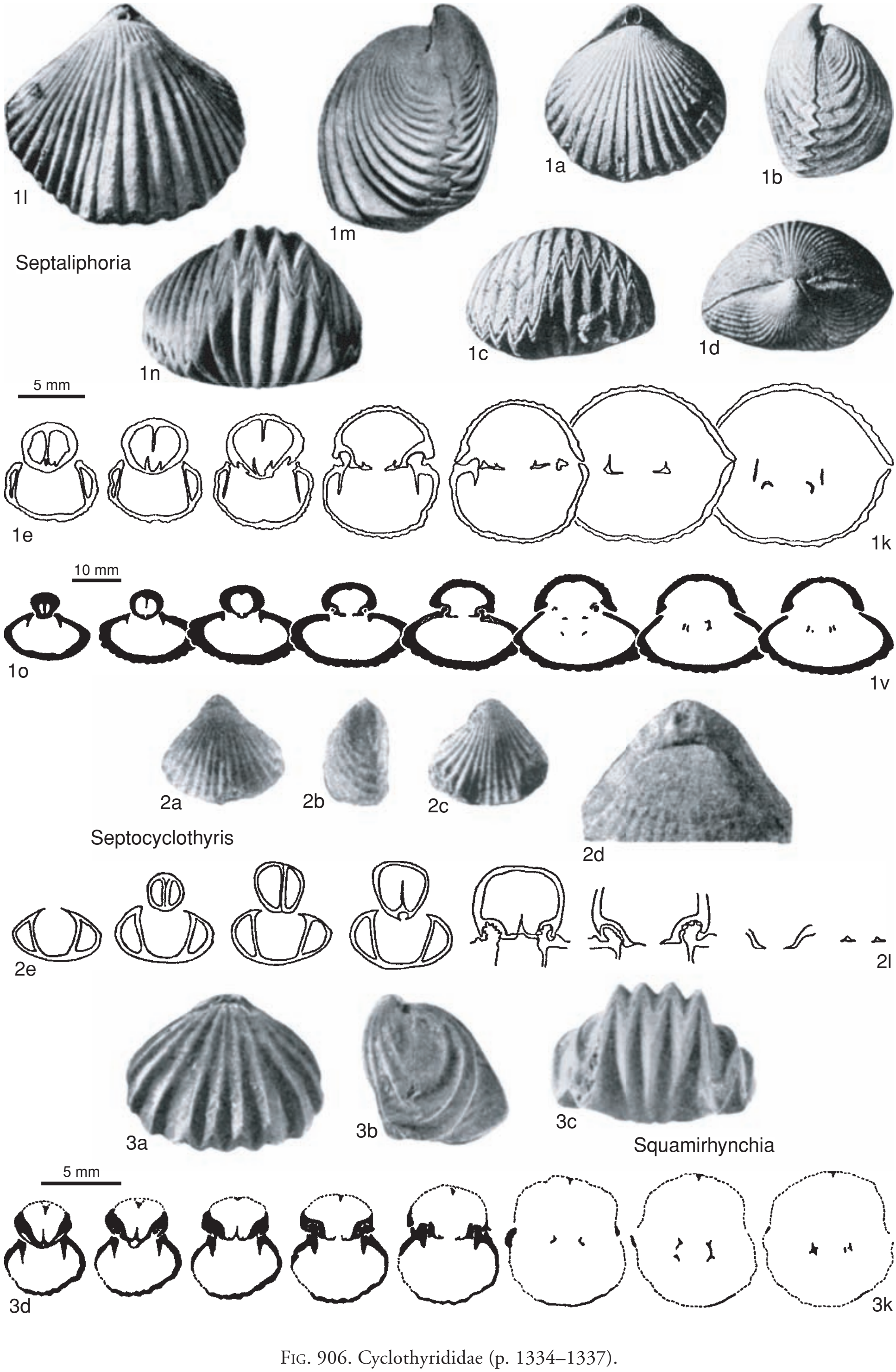

FIG. 906. Cyclothyrididae (p. 1334–1337).

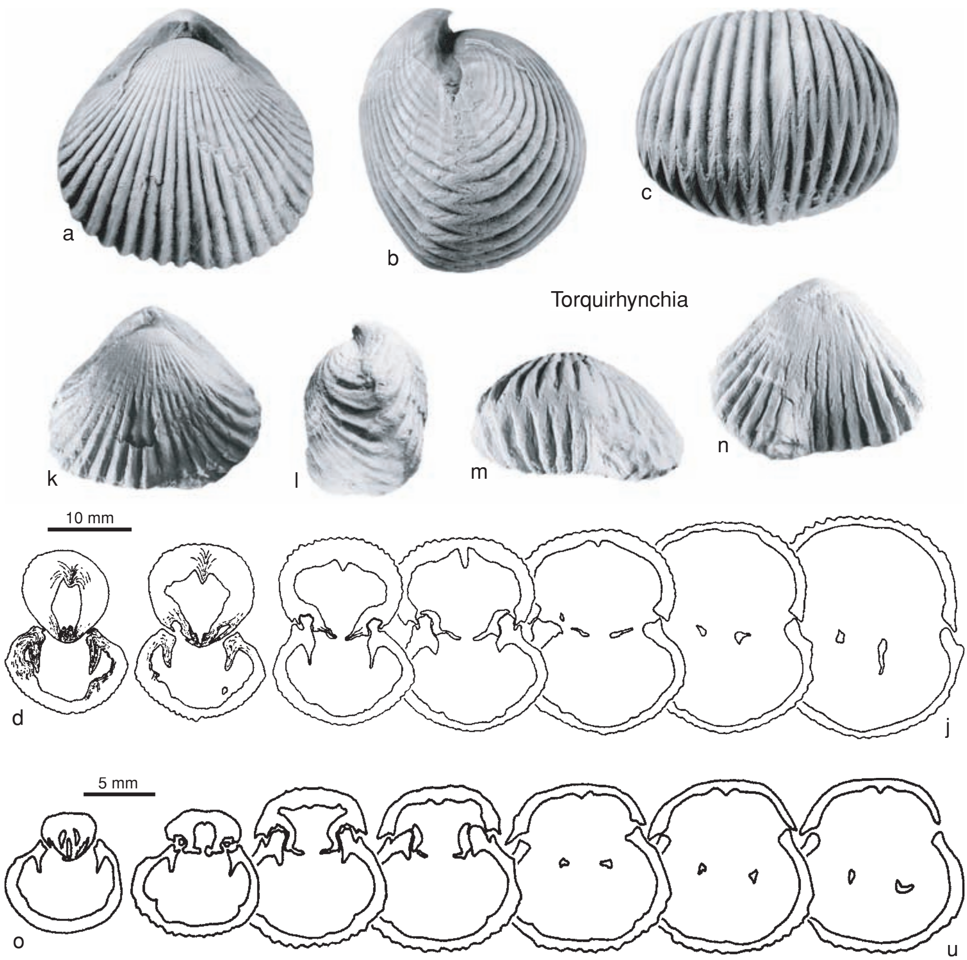

FIG. 907. Cyclothyrididae (p. 1337–1339).

Switzerland, Poland, Slovakia, Yugoslavia, Romania, Russian Platform, ?Crimea, ?Caucasus, Algeria, Somalia, Madagascar, India, China, Iran, Argentina, ?Chile, *?upper Bajocian, Bathonian–Volgian;* France, ?Switzerland, ?Caucasus, Caspian depression, *Berriasian–Valanginian.*——FIG. 907*a–j.* **T. inconstans* (J. SOWERBY), Kimmeridgian, Dorset, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH 67671, ×1 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 5.2, 5.9, 6.8, 7.6, 8.4, 9.4, 10.0 (Childs, 1969).——FIG. 907*k–u. T. asymmetrica* (RADULOVIC), ?upper Bajocian, Bathonian, Carpatho-Balkanids, Yugoslavia; *k–n,* holotype, dorsal, lateral, anterior, ventral, L 1/319, ×1; *o–u,* transverse serial sections, distances in mm from ventral umbo, 3.1, 3.6, 4.8, 5.2, 5.7, 6.0, 6.2, L 1/326 (Radulovic, 1991).

Yidunella CHING, SUN, & YE in CHING & others, 1979, p. 148 [**Y. magna;* OD]. Large, asymmetrical; nearly convexoplane in lateral view; fold and sulcus starting from umbones, but more marked anteriorly; plicae simple, appearing near beak, round-subangular; posterior smooth area obscure or absent; beak short, slightly incurved; beak ridges angular; planarea concave; foramen hypothyrid; delthyrium covered by thickened symphytium. Dental plates subparallel or ventrally convergent; dorsal septum high and long; septalium wide; crura canaliform, extending along plane of commissure, bladelike proximally, passing distally to semicircular canal. *Upper Triassic:* southwestern China (Tibet, Sichuan).——FIG. 905,*2a–l.* **Y. magna,* Sichuan; *a–c,* holotype, dorsal, lateral, anterior views, NIGP 42862, ×1; *d–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.25, 0.85, 0.95, 1.15, 1.25, 1.85, 2.45, 3.25, 3.95, NIGP 42859 (Ching & others, 1979).

?Yulongella SUN, 1981, p. 191 [**Y. bolilaensis;* OD]. Medium size, roundly trigonal and transversely widened; convexoplane to convexoconcave, thickest anteriorly; ventral sulcus wide, deeply concave and dorsally geniculated anteriorly; dorsal fold wide and flattened; linguiform extension transverse rectangular; commissure uniplicate; angular plicae starting from beak, 4 to 5 on fold and 5 to 6 on lateral slopes; ventral beak pointed and nearly straight; foramen circular and permesothyrid; delthyrium open. Dental plates long, slightly ventrally divergent to subparallel; subhorizontal hinge plates narrow, divided; crura with triangular crural bases, and distally forming subvertical short blades; dorsal median ridge low near umbo, elevated anteriorly, and extending to midvalve. [Remarkably similar to *Costirhynchopsis* except for alleged lack of septalium.] *Upper Triassic (Norian):* Tibet.——FIG. 904,*3a–k.* **Y. bolilaensis; a–d,* holotype, dorsal, lateral, anterior, ventral views, NIGP 48396, ×1; *e–k,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.4, 1.8, 2.2, 2.7, 3.4, 3.6, 3.8, NIGP 48541, ×2.5 (Sun, 1981).

Subfamily CARDINIRHYNCHIINAE Makridin, 1964

[*nom. transl.* KAMYSHAN, 1968, p. 59, *ex* Cardinirhynchiidae MAKRIDIN, 1964, p. 192; *emend.,* MANCEÑIDO & OWEN, herein]

Small- to medium-sized Cyclothyridae, transversely expanded, fully covered by subangular radial costae; growth lines often lamellose; palintrope well developed, and beak acute, prominent; deltidial plates disjunct to conjunct; hinge margin long and nearly straight. Crural bases attached to inner socket ridges; dorsal valve with conspicuous median septum and very feebly developed septalium, nearly always filled with shell substance; crura canaliform; fusiform cardinal furrow and commissural groove usually present. *Middle Jurassic (Aalenian)–Upper Jurassic (Oxfordian).*

Cardinirhynchia BUCKMAN, 1918, p. 74 [**Terebratula acuticosta* HEHL, 1832, in VON ZIETEN, 1830–1833, p. 58; OD]. Medium to large size, equibiconvex to dorsibiconvex, flabelliform to semicircular, widest at nearly straight hinge line; sharply multicostate throughout; uniplication incipient to acuminate, central fold variably raised, often high; broad suberect to erect beak with large foramen; deltidial plates narrow, disjunct. Teeth broad, crenulated; hinge plates massive, narrow; dorsal median septum well developed, septalium ill developed; crura canaliform; commissural grooves sometimes present. *Middle Jurassic (Bajocian–Callovian), Upper Jurassic (?lower Oxfordian):* Germany, ?Switzerland, Poland, Romania, Russia, Crimea, ?India, *Bajocian–Callovian;* Russian platform, *?lower Oxfordian.*——FIG. 908,*1a–q.* **C. acuticosta* (HEHL), upper Bajocian, Suabia, Germany; *a–c,* dorsal, lateral, anterior views, ×1.5; *d,* detail of hinge area, BMNH B.38123, ×4 (new); *e–q,* paratype, transverse serial sections through umbo (Seifert, 1963).

Eurysites COOPER, 1989, p. 32 [**E. transversus;* OD]. Small, dorsibiconvex; transversely elliptical to subtriangular; commissure gently uniplicate, but dorsal fold and ventral sulcus mostly indistinct; strong, narrowly rounded costae throughout; beak long, straight to suberect; deltidial plates disjunct; large foramen. Dental plates long; septalium small, dorsal median septum weak; raduliform crura. *Middle Jurassic (Bathonian–Callovian):* Saudi Arabia, ?China, ?Argentina.——FIG. 909,*2a–t.* **E. transversus,* Bathonian, Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380232, ×1.5; *f–t,* transverse serial sections, distances in mm from ventral umbo, 0.3, 1.1, 1.8, 2.2, 2.3, 2.5, 2.9, 3.1, 3.3, 3.5, 3.7, 4.0, 4.3, 4.5, 4.6, USNM 380680 (Cooper, 1989).

Flabellirhynchia BUCKMAN, 1918, p. 65 [**Rhynchonella lycettii* DAVIDSON, 1852b, p. 81; OD] [=*Flabellirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, wide subtrigonal, depressed subequibiconvex, with fold low and costae numerous, strong, sharp; anterior margin thickened; growth lines lamellose; beak strong, upright, with foramen large, rimmed; deltidial plates conjunct to disjunct, thickened. Dorsal median septum feeble; crura canaliform; septalium pitlike. *Middle Jurassic (Aalenian–Bajocian, ?Bathonian):* England, France, USA (California), Argentina, Antarctica.——FIG. 908,*2a–s.* **F. lycettii* (DAVIDSON), Aalenian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, USNM 75591, ×1 (Shi & Grant, 1993); *d,* detail of hinge area, BMNH B.32284, ×3 (new); *e–s,* transverse serial sections, distances in mm from ventral umbo, 0.7, 2.1, 2.5, 2.9, 3.2, 3.4, 3.8, 3.9, 4.2, 4.4, 4.6, 5.0, 5.4, 6.0, 6.6, CDP 28, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

Parvirhynchia BUCKMAN, 1918, p. 56 [**Rhynchonella parvula* EUDES-DESLONGCHAMPS, 1862, p. 276; OD] [=*Parvirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Small, depressed equibiconvex, round subpentagonal, with low fold and uniplication almost flattopped; fully costate, costae few, strong, blunt, widely spaced over whole surface (2 to 6 on fold), bifurcations or intercalations rare; beak small, pointed, erect to straight, deltidial plates disjunct to conjunct, foramen rimmed, submesothyrid, short pedicle collar. Dental plates dorsally divergent; hinge plates subhorizontal; dorsal median septum low, short; crura canaliform, cardinal furrows and commissural grooves present. *Middle Jurassic (Aalenian)–Upper Jurassic (Oxfordian):* England, France, Germany, Switzerland, Poland, Romania,

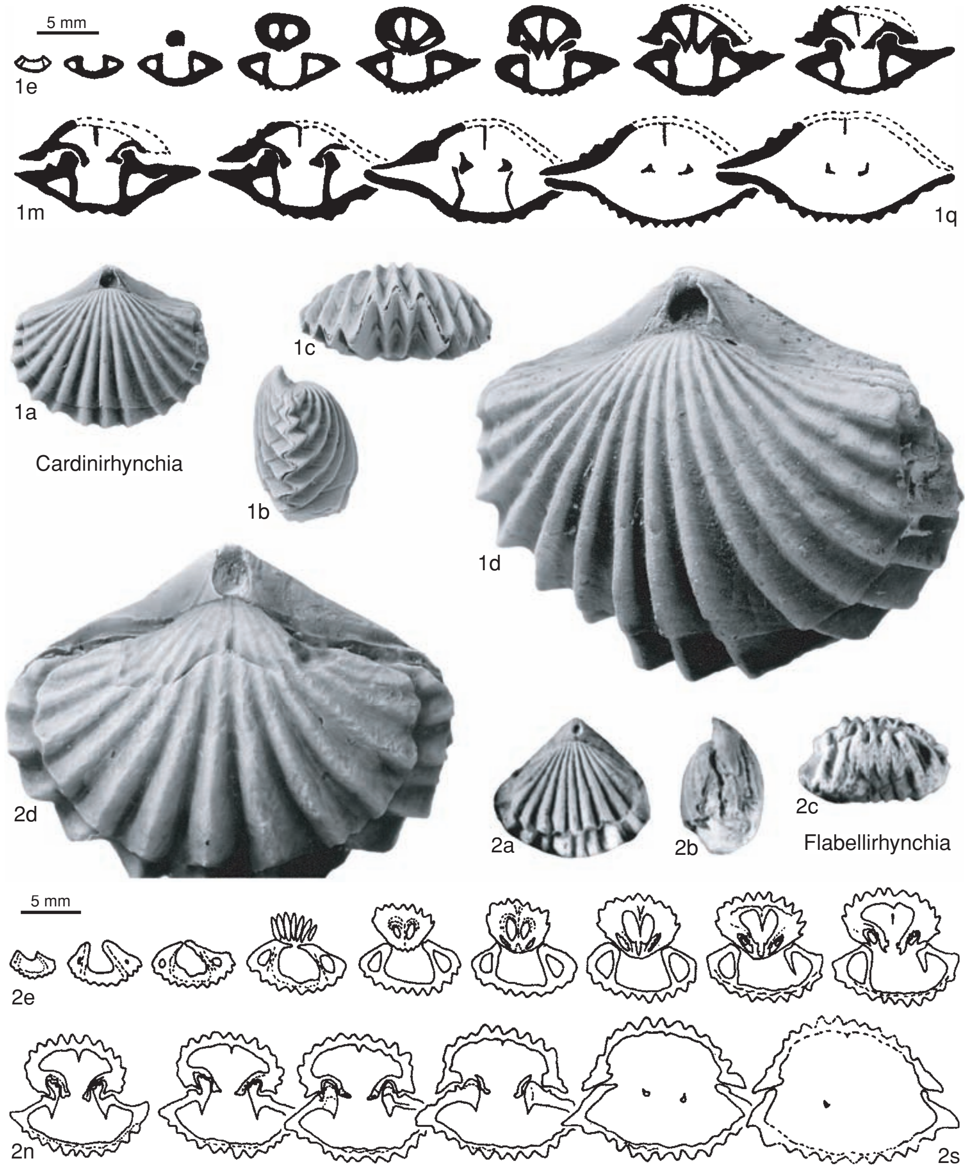

FIG. 908. Cyclothyrididae (p. 1340).

Caucasus, Transcaucasia, Spain, ?Italy, Morocco, Argentina, *Aalenian–Callovian;* France, ?Japan, *Oxfordian.*——FIG. 909,*1a–s.* **P. parvula* (EUDES-DESLONGCHAMPS), lower Bajocian, France; *a–d,* neotype, dorsal, lateral, anterior, ventral views, FSL 305425, ×1; *e,* detail of hinge area of ventral valve, FSL 305456, ×5; *f–s,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.6, 1.1, 1.4, 1.55, 1.7, 1.85, 2.0, 2.15, 2.3, 2.45, 2.6, 2.8, 3.0, FSL 305458 (Alméras & Lathuilière, 1984).

Subfamily INDORHYNCHIINAE Ovcharenko, 1975

[Indorhynchiinae OVCHARENKO, 1975, p. 123–124]

Medium-sized Cyclothyrididae, fully multicostate and uniplicate; dorsal fold and ventral sinus weak, sometimes asymmetrical; costae dense, often dichotomous. Dental

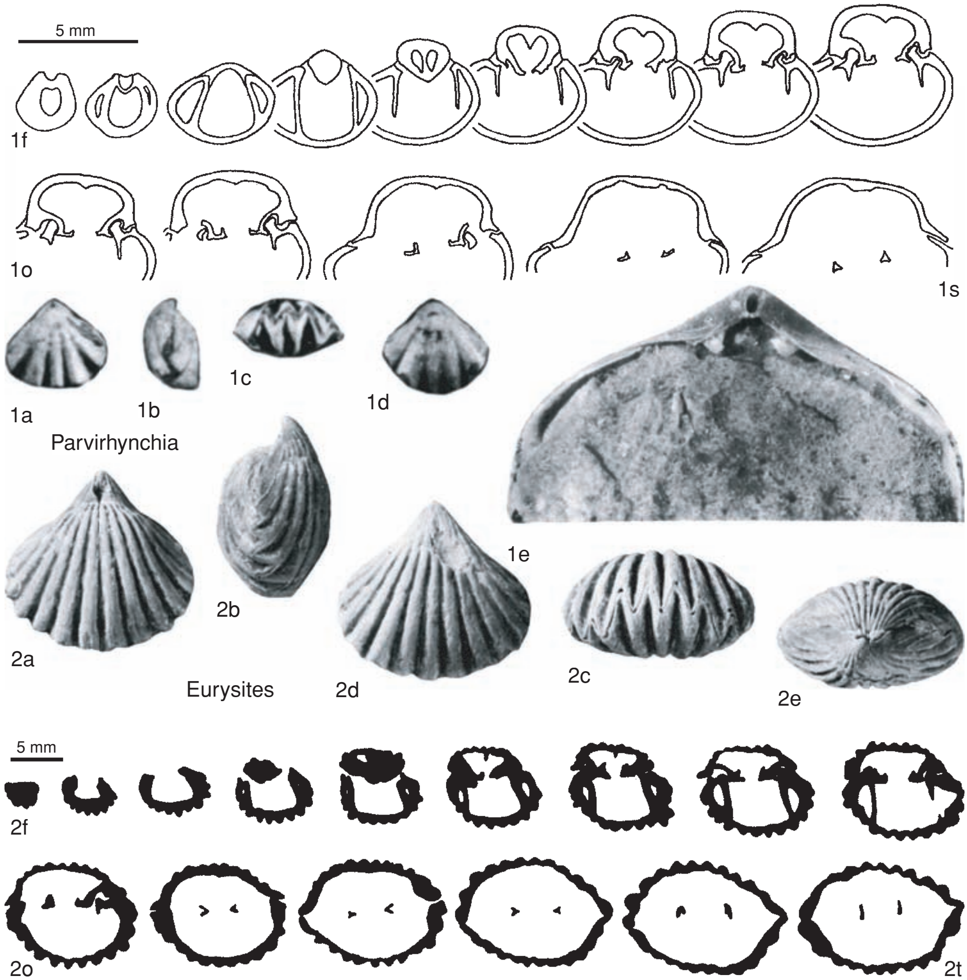

FIG. 909. Cyclothyrididae (p. 1340–1341).

plates thin, subparallel; median septum reduced, septalial plates well developed, typically sessile; crura peculiarly modified raduliform with various canaliform distal ends or transitional to calcariform. *Middle Jurassic (Bajocian–Callovian).*

Indorhynchia OVCHARENKO, 1975, p. 124 [**I. subtrigonalis;* OD]. Medium size, often asymmetrical shells, covered with numerous dichotomizing costae, fold weakly raised. Dental plates thin, rather short, from parallel to ventrally divergent; hinge teeth simple, massive, sometimes with short denticula; hinge plates ventrally convex, septalial plates variously developed, sessile or pendant, oriented dorsoventrally or slightly diverging dorsally; crura short, ventrally deflected, may be flared distally. *Middle Jurassic (?lower Callovian, middle Callovian–upper Callovian):* Tadjikistan, southeastern Pamirs, India, ?Arabia, ?Sinai.——FIG. 910,*4a–n.* **I. subtrigonalis,* middle Callovian, southeastern Pamirs; *a–c,* holotype, dorsal, lateral, anterior views, MUGT 12/1184, ×1; *d–j,* transverse serial sections, distances in mm from first section, 0.0, 0.7, 1.2, 1.8, 2.5, 3.1, 3.4, approximately ×1.25; *k–n,* enlarged details of dorsal umbo, 1.1, 1.2, 1.5, 1.7, MUGT 16/1184, approximately ×5 (Ovcharenko, 1975).

Moquellina CHING, SUN, & YE in CHING & others, 1979, p. 141 [**M. arcuata;* OD]. Medium size, cuneiform-elongate oval, dorsibiconvex, fold and sulcus only anteriorly; commissure subrectimarginate or slightly uniplicate; costae subangular or rounded, developed anteriorly to fully costate; beak nearly straight to suberect; foramen hypothyrid; deltidial plates disjunct, rimmed. Pedicle collar short; dental plates long, subparallel; hinge plates discrete;

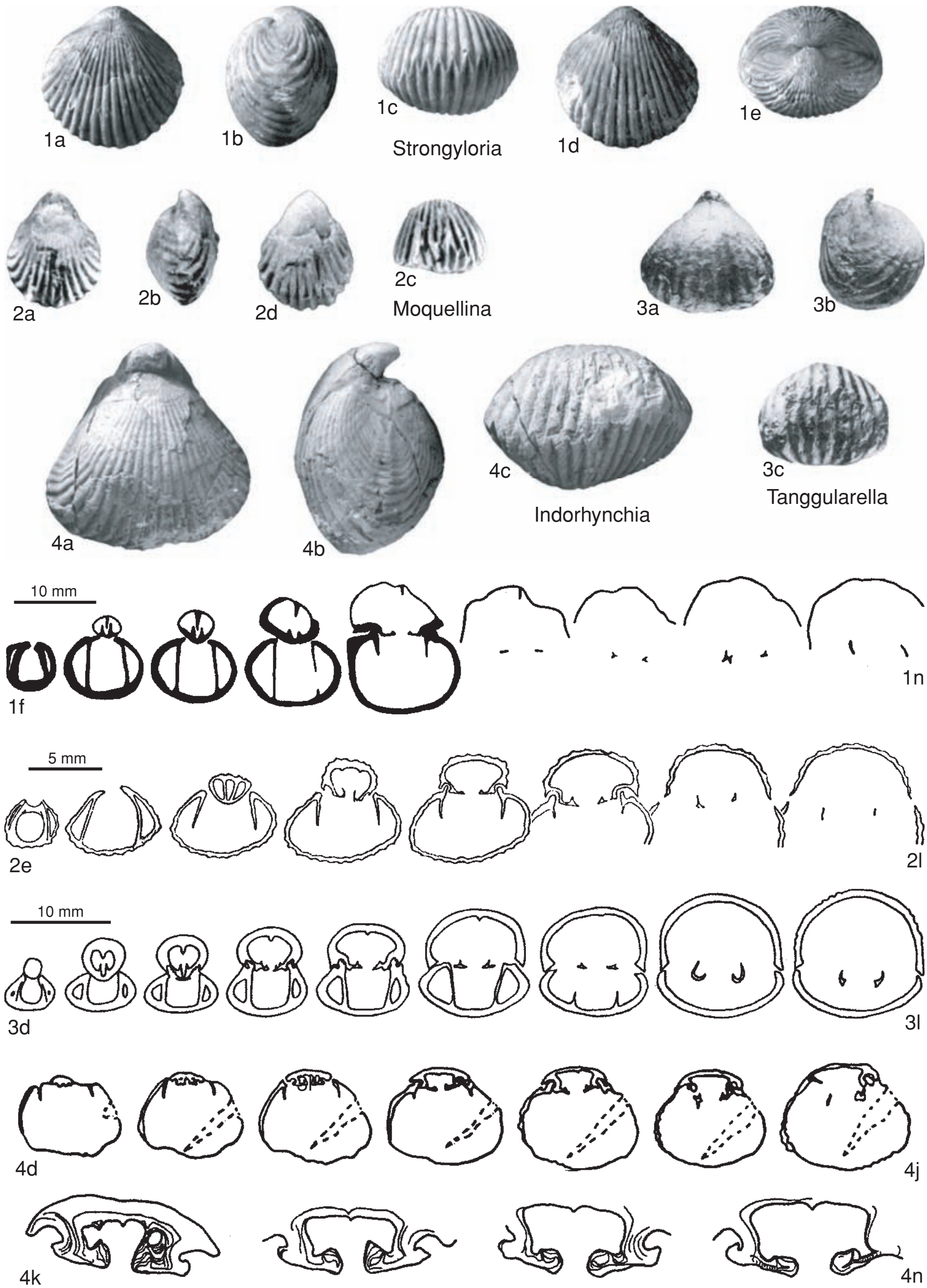

FIG. 910. Cyclothyrididae (p. 1342–1344).

septalial plates descending directly to floor of dorsal valve and extending to articulation zone; crura projecting horizontally, trigonal proximally and vertical bladelike distally; dorsal median septum reduced or absent. *Middle Jurassic (Bathonian–Callovian):* China (Qinghai, Yunnan).——FIG. 910,*2a–l*. **M. arcuata,* upper Bathonian–lower Callovian, Qinghai; *a–d*, holotype, dorsal, lateral, anterior, ventral views, NIGP 42893, ×1; *e–l,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.8, 1.9, 2.4, 2.9, 3.55, 4.4, 4.95, 5.35, NIGP 42894 (Ching & others, 1979).

Strongyloria Cooper, 1989, p. 63 [**S. circularis;* OD]. Medium size, moderately equibiconvex, round, with uniplication gently arcuate; dorsal fold subdued; costae numerous, low, rounded, with intercalation and bifurcation on umbones (7 to 10 on fold); beak low, incurved; deltidial plates disjunct, rimmed; foramen small. Dental plates well developed; dorsal median septum moderate; septalium short, may be pendant; raduliform to canaliform crura. *Middle Jurassic (Bajocian–Bathonian):* Arabia.——Fig. 910,*1a–n.* **S. circularis,* upper Bajocian, Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380200a, ×1; *f–n,* transverse serial sections, distances in mm from ventral umbo, 0.6, 1.4, 1.6, 1.9, 2.5, 3.3, 3.7, 4.0, 4.3, USNM 400917 (Cooper, 1989).

Tanggularella Shi, 1990, p. 308–309 [**T. feraxa;* OD]. Small, rounded subtrigonal to subpentagonal, inequibiconvex; uniplicate and fully multicostate; fold and sulcus generally weak; costae simple. Dorsal median septum very short or reduced; pendant septalial plates; incurved canaliform crura, dorsally concave. *Middle Jurassic (Bathonian, ?lower Callovian):* China (northern Tibet, southern Qinghai).——Fig. 910,*3a–l.* **T. feraxa,* upper Bathonian, southern Qinghai; *a–c,* holotype, dorsal, lateral, anterior views, MCMB Y 152164, ×1 (Shi, 1992); *d–l,* transverse serial sections, distances in mm from ventral umbo, 0.5, 1.5, 1.6, 2.1, 2.5, 3.4, 3.8, 4.9, 5.2, MCMB Y152167 (Shi, 1990).

?Family TRIASORHYNCHIIDAE Xu & Liu, 1983

[Triasorhynchiidae Xu & Liu, 1983, p. 74(90)]

[Materials prepared by Miguel O. Manceñido, E. F. Owen, & Sun Dong-Li]

Hemithiridoidea with completely costate shells, dental plates absent; dorsal fold and ventral sulcus developed; anterior commissure uniplicate; dorsally arched squama-glotta junction. Septalium and median septum present; crura raduliform (triangular-ridge form). [Recognition of this queried family (or subfamily) rests on lack of dental plates; if this were due to any preservational accident, both genera included would fall entirely within the Tetrarhynchiinae.] *Middle Triassic.*

Triasorhynchia Xu & Liu, 1983, p. 90 [**T. subglobulina;* OD]. Small, subcircular, subglobular, dorsibiconvex; uniplication arcuate; ventral sulcus wide and shallow, starting slightly anterior to midlength; dorsal fold low, beginning from slightly posterior to midlength; plicae angular starting from umbonal area; plicae arranged with 3 within sulcus, 4 on fold, 3 or 4 on each side; ventral beak short, pedicle opening relatively large, permesothyrid, delthyrium completely covered by dorsal beak. Dental plates and pedicle collar absent; dorsal hinge plates discrete and narrow, septalium shallow; septum extending over two-fifths of dorsal length; crura triangular-ridge form. *Middle Triassic (Anisian):* China (Qilian Mountains).——Fig. 911,*1a–t.* **T. subglobulina,* Qinghai; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, QIGX DDY010, ×1; *f–t,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.5, 0.8, 1.0, 1.2, 1.3, 1.4, 1.6, 1.7, 1.8, 1.9, 2.1, 2.3, 2.5, 2.7, 2.9, QIGX DDY011 (Xu & Liu, 1983).

Multicorhynchia Chen Yongming, 1983, p. 152 [**M. tulungensis;* OD]. Medium size, roundly triangular to pentagonal in outline; shell length nearly equal to shell width; depressed dorsibiconvex; subrectimarginate commissure, dorsal fold and ventral sulcus subdued and only appearing anteriorly; costae thin and round, 6 to 7 in sulcus, 7 to 8 on fold; 7 to 8 at each lateral region; beak small; foramen circular, submesothyrid. Teeth short; dental plates absent; pedicle collar undeveloped; dorsal septum high and thin; septalium narrow and deep. *Middle Triassic:* China (Tibet, ?southern Qilian Mountains).——Fig. 911,*2a–m.* **M. tulungensis,* Tibet, Tulung; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CIGMR SC22-2, ×1; *e–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.2, 0.4, 0.6, 0.9, 1.3, 1.6, 1.9, 2.3, 2.8, CIGMR SC22-2 (Chen Yongming, 1983).

Family TETRARHYNCHIIDAE Ager, 1965

[*nom. transl.* Manceñido & Owen, herein, *ex* Tetrarhynchiinae Ager, 1965, p. 611]

Globose to trilobate Hemithiridoidea, with dorsally arched squama-glotta junction, though variably developed; dorsal fold always present (moderate to ill defined); radial costae invariably present; surface spines not developed. Crura raduliform or modified; cardinal process absent. *Upper Triassic–Upper Cretaceous (Maastrichtian).*

Subfamily TETRARHYNCHIINAE Ager, 1965

[Tetrarhynchiinae Ager, 1965, p. 611] [Includes Praecyclothyrinae Makridin, 1964, p. 149, *partim* (not containing type genus)]

Dorsibiconvex to convexoplane trilobate Tetrarhynchiidae; multicostate, sometimes with short smooth stage posteriorly; uniplicate, with dorsal fold well defined, moderately to strongly raised, often subcarinate; linguiform extension distinct, trapeziform to subtriangular; beak small, usually suberect to

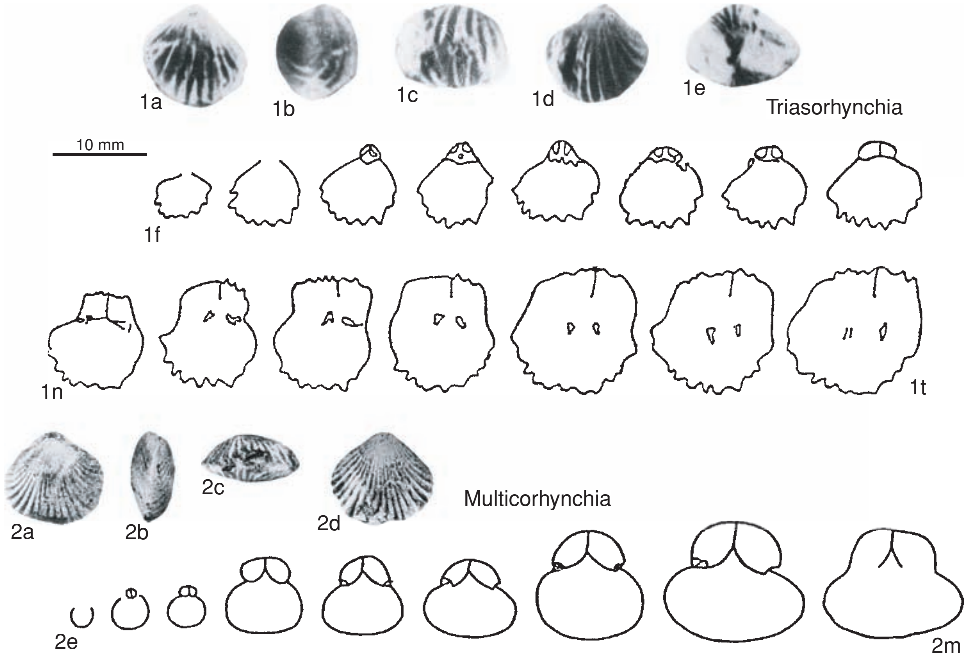

FIG. 911. Triasorhynchiidae (p. 1344).

incurved; delthyrium typically small, foramen usually not rimmed. Hinge plates subhorizontal to convex ventrally; dental plates variable, subparallel, convergent or divergent ventrally; conspicuous septalium, Y-shaped to pitlike; lateral umbonal chambers subtriangular, empty. Crura raduliform, usually in form of simple hooks, occasionally somewhat expanded distally. *Upper Triassic–Lower Cretaceous (Aptian).*

Tetrarhynchia BUCKMAN, 1918, p. 41 [**Terebratula tetraëdra* J. SOWERBY, 1812 in 1812–1815, p. 191; OD; =*Tetrarhynchia tetrahedra* J. SOWERBY, 1812 in 1812–1815, p. 191, *nom. correct.* AGER, 1956, p. 7, prevailing spelling preserved under Article 33.3.1 of ICZN (1999)] [=*Tetrarhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957); *Makridinirhynchia* SUCIC-PROTIC, 1969, p. 81 (type, *M. makridini,* OD)]. Medium size, laterally expanded, rounded subtriangular, dorsibiconvex; arcuate uniplication well developed; costae numerous, fairly sharp, short smooth stage posteriorly; beak small, incurved. Dorsal median septum short, septalium deep; crura raduliform, possibly widening distally; subparallel dental plates separating subrectangular delthyrial cavity from triangular lateral umbonal chambers. *Lower Jurassic, Middle Jurassic (?Bajocian):* Eurasia, northern Africa, North and South America.

T. (**Tetrarhynchia**). Shell becoming gibbous, everted with age; strong dorsal fold with subangular top. [Differences in internal structure attributable to tilted sectioning.] *Lower Jurassic (Sinemurian–Toarcian), Middle Jurassic (?Bajocian):* England, Scotland, France, Portugal, Spain, Germany, Switzerland, Austria, Italy, Slovakia, Yugoslavia, Hungary, Romania, Bulgaria, Morocco, Algeria, Turkey, Siberia, northwestern Canada, Argentina, Chile.——FIG. 912,*1a–k.* **T. (T.) tetrahedra* (J. SOWERBY), upper Pliensbachian, Northamptonshire, England; *a–c,* holotype, dorsal, lateral, anterior views, BMNH B.71566, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.2, 2.2, 2.4, 2.7, 3.3, 3.9, 4.8, 5.2, Warwickshire, J.500/105, Derek Ager, personal collection (Ager, 1956).——FIG. 912,*1l–u. T. (T.) makridini* (SUCIC-PROTIC), middle Lias, Carpatho-Balkanids, Yugoslavia; *l–n,* holotype, dorsal, lateral, anterior views, MFMGB 1/10, ×1; *o–u,* transverse serial sections, distances in mm from first section, 1.2, 1.8, 2.2, 2.5, 2.8, 3.1, 3.3 (Sucic-Protic, 1969).

T. (**Rostrirhynchia**) SUCIC-PROTIC, 1969, p. 47 [**R. rostrata;* OD]. Depressed subtriangular shape persisting in adult; dorsal fold little raised, uniplication broadly arcuate, reduced linguiform extension; costation may be denser. *Lower Jurassic (Sinemurian–Toarcian):* Great Britain, France, Spain, Yugoslavia, Romania, ?Crimea, Algeria, Argentina.——FIG. 912,*2a–k.* **T. (R.) rostrata,* middle Lias, Carpatho-Balkanids,

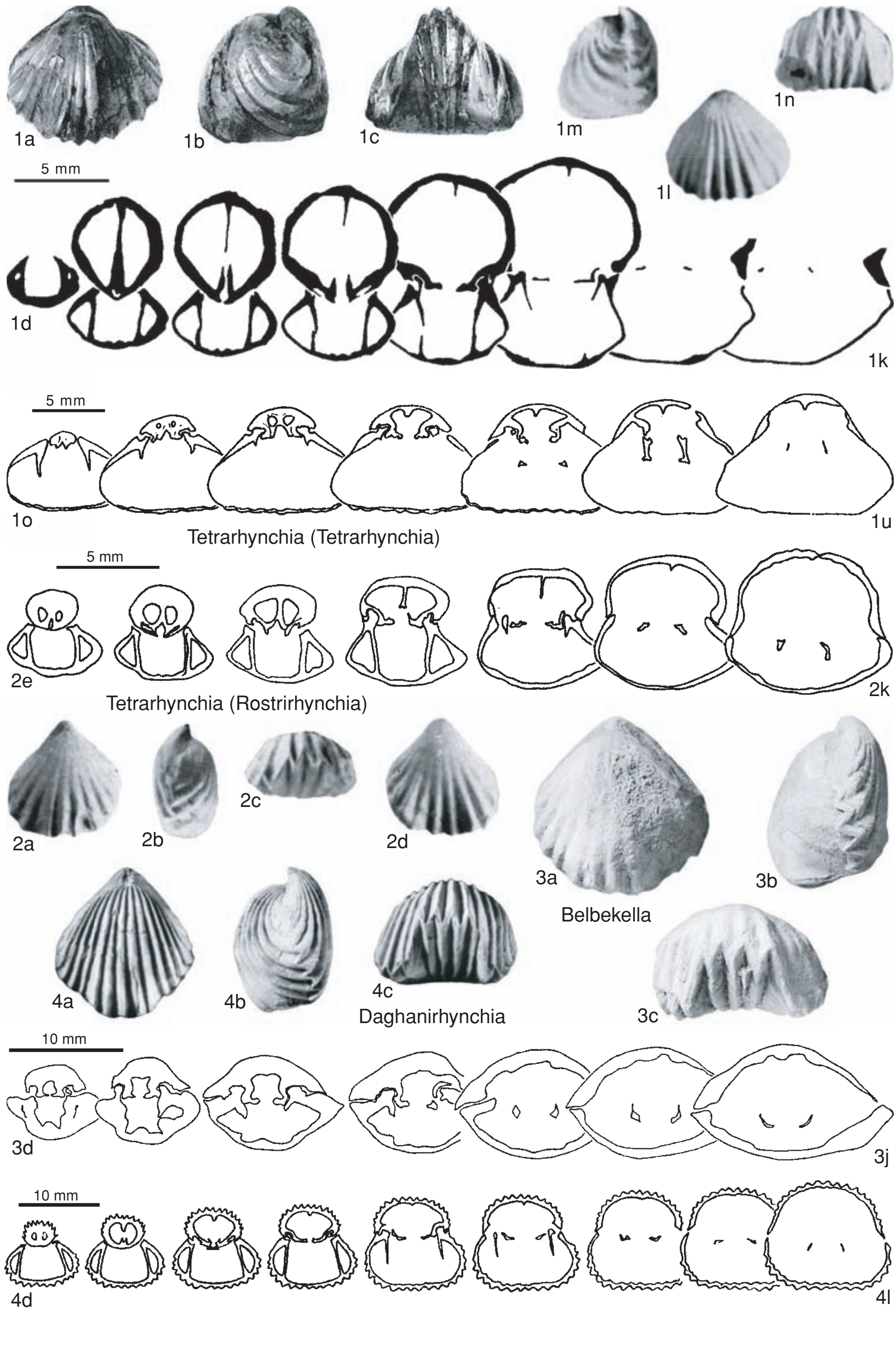

FIG. 912. Tetrarhynchiidae (p. 1345–1347).

Yugoslavia; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MFMGB 1/961, ×1; *e–k,* transverse serial sections, distances in mm from first section, 1.5, 1.8, 2.0, 2.2, 2.7, 3.2, 3.8 (Sucic-Protic, 1969).

Baeorhynchia COOPER, 1989, p. 12 [**B. nucleata;* OD]. Small, dorsibiconvex; subtriangular; narrowly uniplicate, rounded dorsal fold starting anterior to umbo and bearing 3 to 6 costae; completely costate, subangular; beak long, erect to suberect; deltidial plates disjunct to almost conjunct. Dental plates short; dorsal median septum long; septalium small, narrow; crura raduliform. *Middle Jurassic (Bajocian–Bathonian):* Saudi Arabia.——FIG. 913,*1a–n.* **B. nucleata,* Bathonian; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380264a, ×1.5; *f–n,* transverse serial sections, distances in mm from ventral umbo, 1.1, 1.5, 1.8, 2.0, 2.3, 2.5, 2.9, 3.2, 3.7, USNM 380675 (Cooper, 1989).

?Belbekella MOISEEV, 1939, p. 195[205] [**B. airgulensis;* OD] [=*Belbekella* MOISEEV in RZHONSNITSKAIA & others, 1956, p. 62, obj.]. Medium size, subtriangular to subpentagonal, dorsibiconvex, globose, uniplicate; dorsal fold poorly developed, ventral sulcus shallow, trapezoidal; costae sharp, angular, radiating from umbo; beak massive, erect. Dental plates slightly ventrally convergent; teeth subquadrate, strong; dorsal median septum weak to absent; septalium not developed or pitlike; raduliform crura gently concave distally. *Lower Cretaceous (Berriasian–Aptian):* Crimea, Caucasus, Turkmenistan, France, Sardinia, Romania, Russia (Caspian Basin), ?eastern China (Heilongjiang).——FIG. 912,*3a–j.* **B. airgulensis,* Hauterivian, Crimea; *a–c,* dorsal, lateral, anterior views, ×1.5 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.5, 2.4, 3.0, 3.3, 4.1, 4.6, 5.2 (Dieni, Middlemiss, & Owen, 1975).

Cymatorhynchia BUCKMAN, 1918, p. 53 [**Rhynchonella cymatophorina* BUCKMAN, 1910, p. 105; OD; =*R. cymatophora* BUCKMAN, 1895, p. 447, *non* ROTHPLETZ, 1886] [=*Cymatorhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Formosarhynchia* SEIFERT, 1963, p. 177 (type, *F. formosa,* OD)]. Medium size to large, subpentagonal to transverse-oval, depressed equibiconvex to dorsibiconvex, with strong uniplication and dorsal fold broad, gently raised; many (10 to 24) sharp costae (4 to 10 on fold), no smooth stage; beak small, erect to incurved, foramen hypothyrid, conjunct or disjunct deltidial plates. Dorsal median septum strong; septalium deep; straight, subhorizontal hinge plates; crura raduliform, with concave distal ends; crenulated teeth. *Middle Jurassic (Aalenian–lower Bathonian):* England, France, Germany, Switzerland, Poland, Bulgaria, Romania, Spain, ?Caucasus, Morocco, Algeria, Madagascar, Arabia, Israel, ?Jordan, southwestern China (Tibet, Himalayas), Argentina.——FIG. 914,*1a–j.* **C. cymatophorina* (BUCKMAN), Aalenian, Dorset, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH B.11981, ×1 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 3.9, 4.2, 4.7, 5.5, 6.3, 6.8, 7.3, BMNH B.68374 (new; courtesy of C. D. Prosser).——FIG. 914,*1k. C. quadriplicata* (ZIETEN), Bajocian; interior showing raduliform crura and cardinalia of silicified specimen, BMNH B.69919, ×2 (new).——FIG. 914,*1l–u. C. formosa* (SEIFERT), lower Bajocian, Swabian Alb, Germany; *l–n,* holotype, dorsal, lateral, anterior views, GPIT Br 3/38/42, ×1; *o–u,* paratype, transverse serial sections through umbo (Seifert, 1963).

Daghanirhynchia MUIR-WOOD, 1935, p. 82 [**D. daghaniensis;* OD]. Medium size, subtrigonal to subpentagonal, subglobose dorsibiconvex, often nasute; uniplicate, with distinct dorsal fold, costae few (3 to 6 on fold); linguiform extension high, trapezoidal; beak acute, erect to incurved. Dental plates strong, dorsal median septum weak, persistent; divided hinge plates, septalium usually pendant; crura nearly horizontal, raduliform slightly incurved ventrally. *Middle Jurassic (Bathonian–Callovian), Upper Jurassic (?Oxfordian):* ?Morocco, Tunisia, Somalia, Kenya, ?Ethiopia, Egypt (Sinai), Arabia, Israel, Syria, China, India.——FIG. 912,*4a–l.* **D. daghaniensis,* lower Callovian, Daghani, Somalia; *a–c,* topotype, dorsal, lateral, anterior views, USNM 75666b, ×1; *d–l,* transverse serial sections, distances in mm from ventral umbo, 3.1, 3.4, 3.8, 4.0, 4.9, 5.1, 5.5, 5.9, 6.4, USNM 75666a (Shi & Grant, 1993).

Deltarhynchia COOPER, 1989, p. 29 [**D. triangulata;* OD]. Medium to large, inequivalve dorsibiconvex; subtriangular; strongly uniplicate, with dorsal fold conspicuous, narrow, subcarinate; costae thick, angular, 3 to 5 on fold; beak narrow, short, suberect to erect; deltidial plates disjunct, thick; foramen small, hypothyrid. Dental plates very long, divergent; dorsal median septum high, reaching midvalve; teeth and sockets corrugated; septalium fairly large; raduliform crura. [Very similar to *Daghanirhynchia.*] *Middle Jurassic (Bathonian):* Saudi Arabia.——FIG. 913,*2a–n.* **D. triangulata,* lower Bathonian; *a–e,* paratype, dorsal, lateral, anterior, ventral, posterior views, USNM 380217a, ×1; *f–n,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.6, 2.1, 2.3, 2.6, 2.8, 3.5, 4.1, 4.8, USNM 380679 (Cooper, 1989).

Druganirhynchia TCHOUMATCHENKO, 1983, p. 70 [**D. nevelinae;* OD]. Medium to large size, with rounded subpentagonal outline; dorsibiconvex spherical in adult specimens; uniplicate, sinus and fold rather distinct; costae sharp numerous; beak small, of medium height, erect. Hinge plates massive, overgrown ventrally convergent; dorsal median septum short; septalium lacking; crura radulifer; hinge teeth crenulated. *Middle Jurassic (Aalenian):* Bulgaria.——FIG. 915,*1a–k.* **D. nevelinae,* southwestern Bulgaria; *a–c,* holotype, dorsal, lateral, anterior views, GIBAS Br.465/1, ×1; *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.6, 2.45, 3.85, 4.85, 5.3, 6.95, 9.2, 9.9, GIBAS Br.465/9 (Tchoumatchenko, 1983).

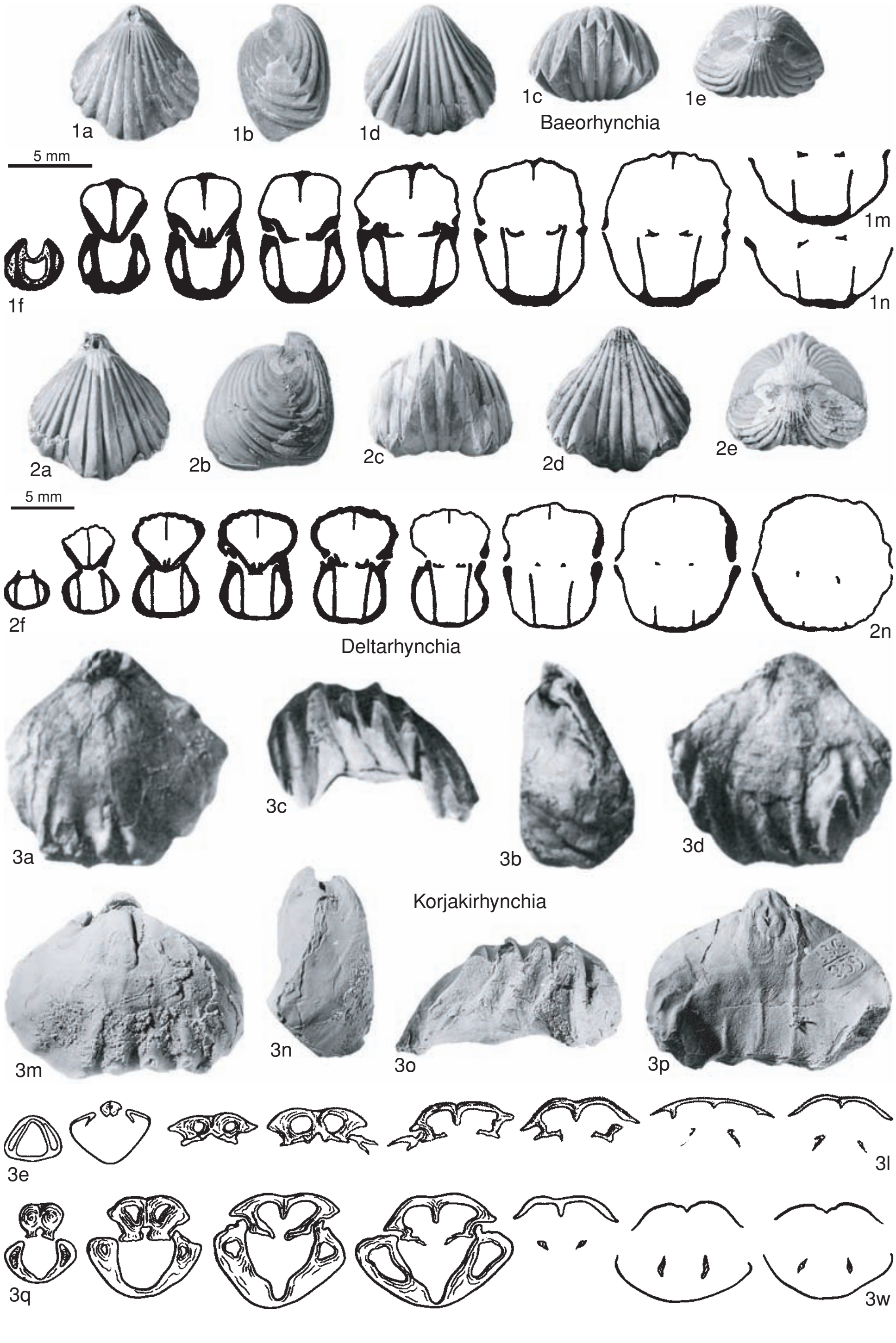

FIG. 913. Tetrarhynchiidae (p. 1347–1351).

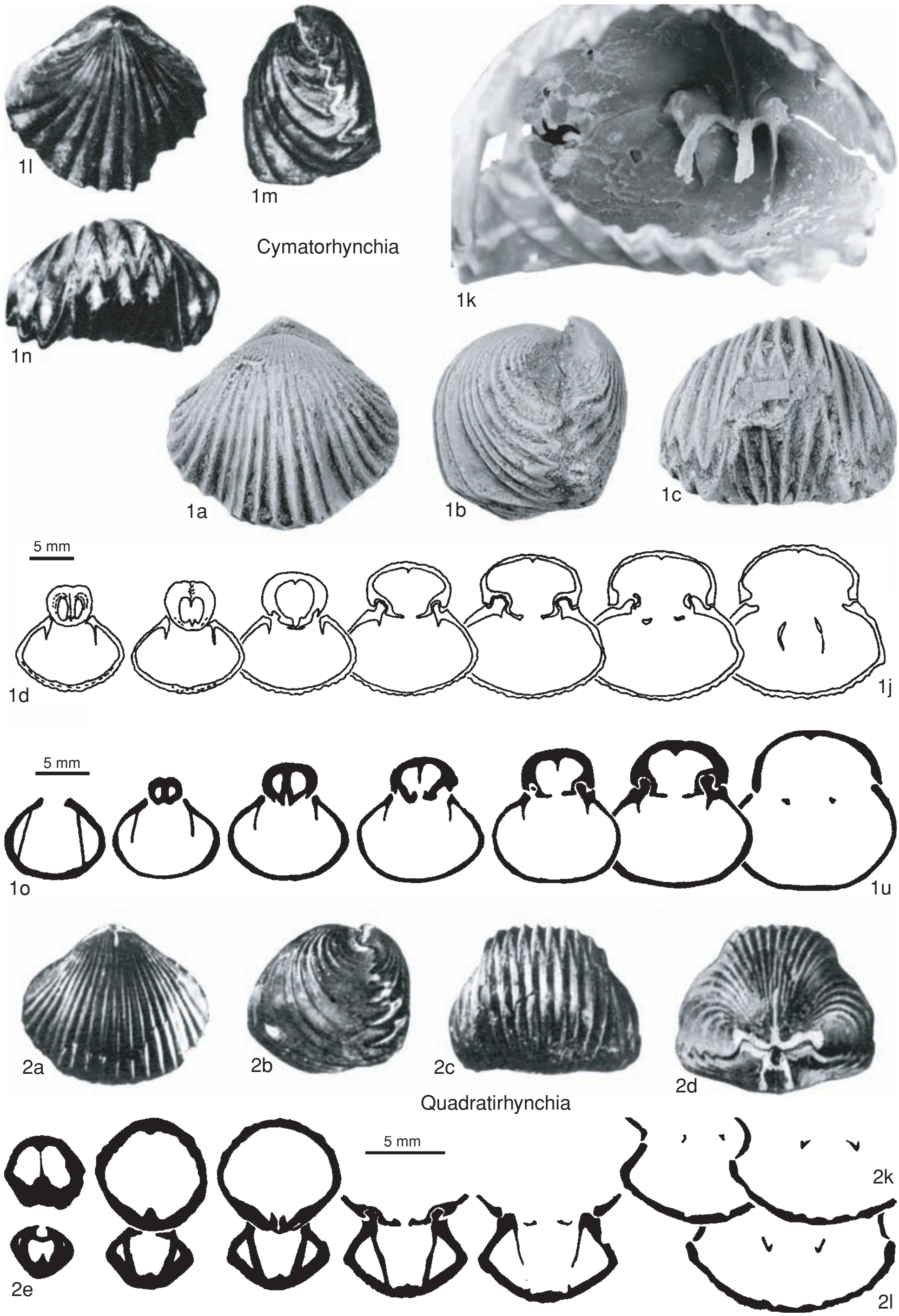

FIG. 914. Tetrarhynchiidae (p. 1347–1354).

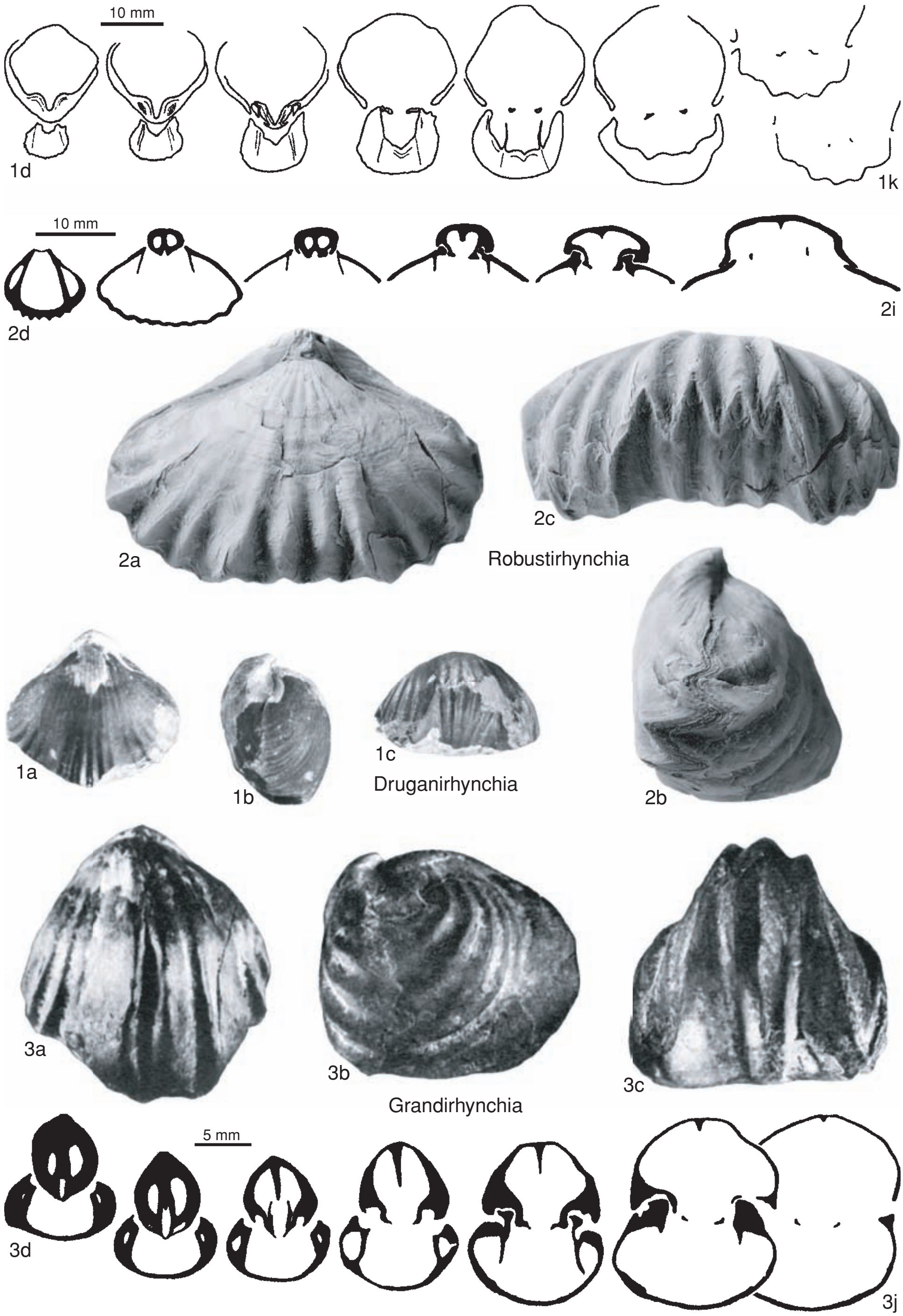

FIG. 915. Tetrarhynchiidae (p. 1347–1354).

Echyrosia Cooper, 1989, p. 30 [**E. costata;* OD]. Medium size, inequivalve dorsibiconvex; subtriangular in outline; uniplicate, dorsal fold narrow, low posteriorly, well elevated in anterior half; costae few, strong, subangular, with 3 to 5 on fold; beak erect; deltidial plates narrow, thick, disjunct; foramen small. Dental plates long; dorsal median septum short; septalium narrow, no cardinal process; crura thin, raduliform. *Middle Jurassic (Bajocian):* Saudi Arabia, ?Israel.——Fig. 916,*1a–l.* **E. costata,* upper Bajocian, Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380195a, ×1; *f–l,* transverse serial sections, distances in mm from ventral umbo, 2.0, 2.8, 3.1, 3.4, 3.9, 4.5, 5.2, USNM 380650 (Cooper, 1989).

Eoseptaliphoria Ching & Sun in Ching, Sun, & Rong, 1976, p. 294 [**E. tulungensis;* OD]. Small to medium, elongate pentagonal or oval, subequibiconvex and subspherical; maximum width slightly anterior to midvalve; uniplication multidentate; linguiform extension prominent, semicircular; with ribs simple, subangular, starting from umbo; beak short, slightly incurved; delthyrium open; foramen permesothyrid. Dental plates short and subparallel; hinge plates disjunct and fused with inner socket ridges; median septum long, thin, high, supporting deep, narrow septalium; crura raduliform. *Upper Triassic:* China (Tibet, Qinghai), ?Alps, ?Caucasus.——Fig. 917,*3a–m.* **E. tulungensis,* Norian, Tibet; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, NIGP 28751, ×1.5 (new); *f–m,* paratype, transverse serial sections, distances in mm from ventral umbo, 0.4, 0.7, 1.0, 1.3, 1.5, 1.7, 1.9, 2.1, NIGP 28752 (Ching, Sun, & Rong, 1976).

Goniorhynchia Buckman, 1918, p. 52 [**G. goniaea;* OD] [=*Goniorhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, wide subtrigonal to transversely subpentagonal; markedly dorsibiconvex; trilobate, with uniplication strong and dorsal fold conspicuous; costae numerous, strong, sharp; not smooth posteriorly; beak short, suberect with small, circular, hypo- to submesothyrid foramen, conjunct deltidial plates. Strong, crenulated teeth; dorsal median septum low, persistent, small, pitlike septalium; crura raduliform; much internal secondary thickening. *Middle Jurassic (Bathonian):* England, France.——Fig. 916,*3a–n.* **G. boueti goniaea,* upper Bathonian, Dorset, England; *a–c,* dorsal, lateral, anterior views, BMNH B.27527, ×1 (new); *d–n,* transverse serial sections, distances in mm from ventral umbo, 0.8, 1.5, 2.2, 3.1, 3.3, 3.5, 4.0, 4.6, 4.8, 5.0, 5.2 (Laurin, 1984).

Grandirhynchia Buckman, 1918, p. 40 [**G. grandis;* OD] [=*Grandirhynchia* Buckman, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Large, oval to subtrigonal, laterally expanded, uniplicate; depressed equibiconvex to gibbous dorsibiconvex; uniplication slight to strongly arcuate; with few (10 to 16) strong blunt costae (3 to 5 on central fold) and pronounced smooth stage posteriorly; beak large, suberect, sharp beak ridges, foramen large. Septalium very deep, median septum long; crura long, raduliform, strongly divergent distally. *Lower Jurassic (Pliensbachian):* Scotland, England, Greenland.——Fig. 915,*3a–j.* **G. grandis,* upper Pliensbachian, Hebrides, Scotland; *a–c,* topotype, dorsal, lateral, anterior views, MKH J44324, ×1; *d–j,* transverse serial sections, distances in mm from ventral umbo, 3.9, 4.1, 4.5, 5.1, 5.8, 7.3, 8.1, MKH R.112 (Ager, 1956).

Korjakirhynchia Smirnova, 1990a, p. 23 [**K. vodopadica;* OD] [=*Korjakirhynchia* Smirnova, 1984, p. 116, *nom. nud.; Snezhnorhynchia* Smirnova, 1990a, p. 26 (type, *S. dvorjankini,* OD); *Snezhnorhynchia* Smirnova, 1984, p. 116, *nom. nud.*]. Medium to large, acutely dorsibiconvex, broad with deep ventral sulcus and trapeziform linguiform extension; smooth posteriorly, with costae few, strong, and angular, developed marginally; beak short, broad, strongly incurved; deltidial plates conjunct, foramen small. Dental plates wide apart, subparallel or divergent; dorsal median septum high, supporting septalium; crura moderately long, elongated ventrally; posterior diductor scars with strongly divergent anterior ends; adductor scars horseshoe shaped. [Synonymized because differences between their nominal type species are insignificant, attributable to deformation and tilted sectioning of the same taxon.] *Lower Cretaceous (Hauterivian):* northeastern Russia (Koryakiya), Slovakia.——Fig. 913,*3a–l.* **K. vodopadica,* Koryakiya; *a–d,* holotype, dorsal, lateral, anterior, ventral views, MGU 138/278, ×1; *e–l,* transverse serial sections, distances in mm from first section, 0.8, 1.4, 2.4, 2.7, 3.0, 3.6, 4.3, 4.6 (Smirnova, 1990a).——Fig. 913,*3m–w. K. dvorjankini* (Smirnova), Koryakiya; *m–p,* dorsal, lateral, anterior, ventral views, MGU 138/276, ×1.5; *q–w,* transverse serial sections, distances in mm from first section, 1.6, 1.8, 2.3, 2.9, 3.3, 4.15, 4.3, ×1 (Smirnova, 1990a).

Orlovirhynchia Dagys, 1968, p. 75 [**Septaliphoria viligaensis* Moiseev, 1947b, p. 90; OD]. Very large, oval to rounded-pentagonal, sulcus broad, corresponding fold low or not developed, anterior commissure uniplicate, costae strong; beak short, incurved, ridges distinct, foramen hypothyrid. Dental plates long, subparallel, pedicle collar absent; septum high and long (about two-fifths valve length), septalium narrow, deep, crura raduliform. *Lower Jurassic (Pliensbachian):* northeastern Siberia.——Fig. 916,*2a–k.* **O. viligaensis* (Moiseev); *a–c,* dorsal, anterior, ventral views, IGiG 318/78, ×1; *d–k,* transverse serial sections, distances in mm from first section, 3.2, 4.1, 4.7, 5.8, 6.8, 7.9, 9.7, 10.9 (Dagys, 1968).

Pontaltorhynchia Owen & Rose, 1997, p. 505 [**Rhynchonella schopeni* Di Stefano, 1887, p. 68; OD]. Medium size, transversely oval, equibiconvex, multicostate; broadly uniplicate with linguiform extension moderate, trapezoidal, and dorsal fold poorly developed; umbo massive; beak short,

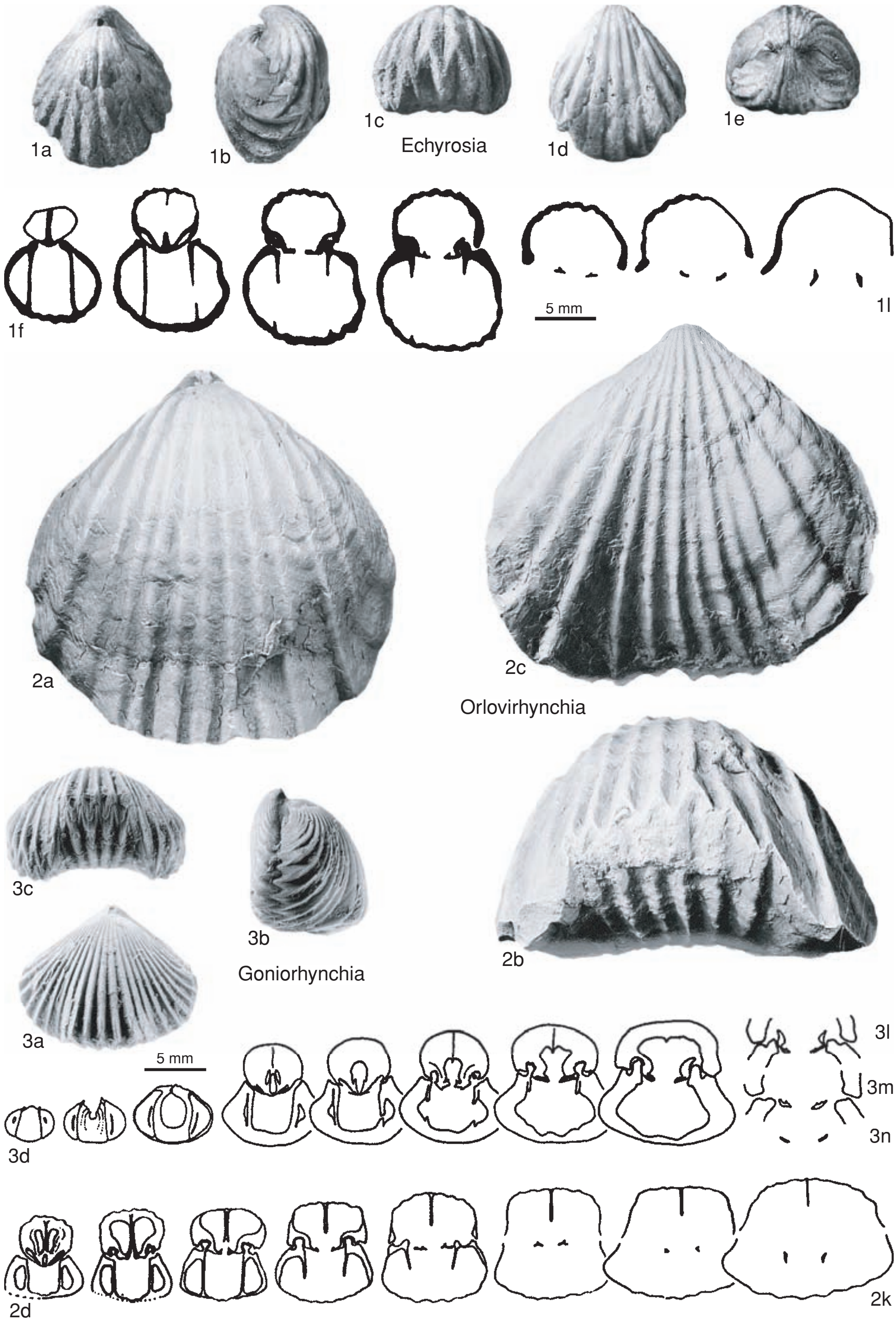

FIG. 916. Tetrarhynchiidae (p. 1351).

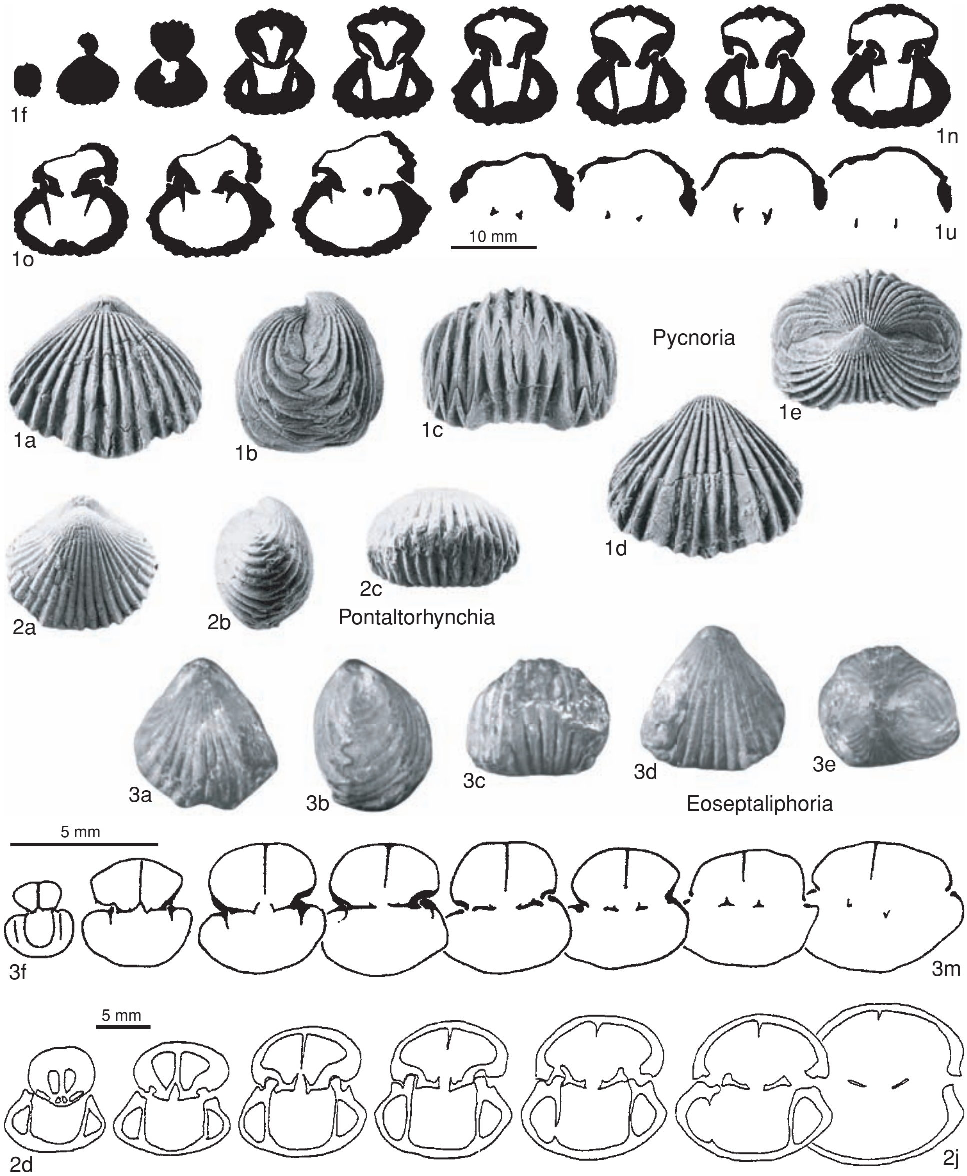

FIG. 917. Tetrarhynchiidae (p. 1351–1354).

suberect, beak ridges rounded, indistinct. Cardinal process bilobed; median dorsal ridge short, low; dental plates subparallel; hinge plates gently convex, dorsal median septum high, and septalium deep. *Lower Jurassic (Sinemurian–Pliensbachian):* Italy (Apennines, Sicily), Gibraltar.——FIG. 917,*2a–j.* **P. schopeni* (DI STEFANO); *a–c,* dorsal, lateral, anterior views, Sinemurian, central Apennines, BMNH B.14969, ×1; *d–j,* transverse serial sections, distances in mm from ventral umbo, 1.6, 2.0, 2.2, 2.4, 2.6, 2.8, 3.4, lower Pliensbachian, Sicily, BMNH BB.20290 (Owen & Rose, 1997).

Pycnoria COOPER, 1989, p. 51 [**P. magna;* OD]. Medium to large, dorsibiconvex; subtriangular to subpentagonal; narrowly uniplicate, dorsal fold gently elevated above steep, rounded lateral slopes; strong, subangular costae (3 to 5 on fold); beak small, low, erect to incurved; deltidial plates conjunct, rimmed; foramen small. Dental plates long, thick; dorsal median ridge low, thick, moderately long; septalium small, raduliform crura; both valves thickened by adventitious shell. *Middle Jurassic (Bathonian):* Saudi Arabia, Sinai, Israel, ?Somalia, ?Tunisia, ?southern France.——FIG. 917,*1a–u.* **P. magna,* Saudi Arabia; *a–e,* paratype, dorsal, lateral, anterior, ventral, posterior views, USNM 380565a, ×1; *f–n,* transverse serial sections, distances in mm from ventral umbo, 1.6, 3.1, 3.4, 3.7, 4.0, 4.3, 4.6, 4.8, 5.1, USNM 380648; *o–u,* distances in mm from first section, 0.0, 0.5, 0.9, 1.2, 1.8, 2.1, 2.6, USNM 380678 (Cooper, 1989).

Quadratirhynchia BUCKMAN, 1918, p. 42–43 [**Q. quadrata;* OD] [=*Quadratirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, oval to subtrigonal, laterally expanded, depressed equibiconvex to gibbous dorsibiconvex, everted; uniplication strong, wide, flattopped, with costae numerous, very sharp (5 to 10 or 15 on fold); no smooth stage; beak small, incurved, foramen small, submesothyrid. Pedicle collar present; dorsal median septum very short, septalial plates short; crura raduliform. Dorsal muscle scars elliptical, separated, equidimensional; ventral muscle scar area U-shaped or elliptical. *Lower Jurassic (upper Sinemurian)–Middle Jurassic (Aalenian):* England, France, Spain, Portugal, ?Germany, Morocco, Algeria, Argentina, USA (Nevada).——FIG. 914,*2a–l.* **Q. quadrata,* upper Pliensbachian, Somerset, England; *a–d,* holotype, dorsal, lateral, anterior, posterior views, GSM 31864, ×1; *e–l,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.6, 1.9, 2.5, 2.9, 3.7, 4.7, 5.0, J.953/1, Derek Ager, personal collection (Ager, 1956).

Robustirhynchia SEIFERT, 1963, p. 174–175 [**Terebratula Ehningensis* QUENSTEDT, 1857 in 1856–1857, p. 497; OD; =*R. kurri* OPPEL, 1857 in 1856–1858, p. 577 (p. 279 in 2nd part), subj.] [=*Robustirhynhia* SULSER, 1993, p. 221, *nom. null.*]. Similar to *Goniorhynchia* but very wide, with uniplication broad, flattopped, and shell thinner. Large, depressed dorsibiconvex, wide subrectangular, transversely elongate; sinus anteriorly flattened and fold strong; costae few (12 to 15), sharp, simple, beginning at apex (4 to 6 on fold); apical region massive, foramen oval to circular; deltidial plates disjunct; apex suberect to weakly incurved. Dental plates thin, strongly divergent; teeth long, tongue shaped, not completely filling wide sockets; dorsal median septum strong but low reaching beyond midvalve; hinge plates straight or slightly concave ventrally; crura not fully preserved. *Middle Jurassic (Callovian):* Germany, Poland (extra-Alpine).——FIG. 915,*2a–i.* **R. ehningensis* (QUENSTEDT), Swabian Alb, Germany; *a–c,* dorsal, lateral, anterior views, BMNH B.12005, ×1.5 (new); *d–i,* paratype, transverse serial sections through umbo (Seifert, 1963).

Somalirhynchia WEIR, 1925, p. 79 [**S. africana;* OD] [=*Somolirhynchia* GACOVIC & TCHOUMATCHENCO, 1994, p. 20, *nom. null.*]. Large, roundly subtrigonal to broadly subpentagonal, trilobate; dorsibiconvex, uniplicate, dorsal fold low, distinct; 20 to 38 multicostate, coarse, simple, subangular costae (5 to 12 on fold); beak strong, suberect to incurved, with small hypothyrid foramen; muscle scars well marked. Dorsal median septum long, septalium strong, pitlike; hinge plates subhorizontal; crura raduliform, enlarged distally; teeth crenulated. [Genus in need of further studies; pre-Callovian records are suspect and thus excluded.] *Middle Jurassic (?Callovian), Upper Jurassic (Oxfordian–Kimmeridgian):* Scotland, France, Spain, Switzerland, Russia, Caucasus, ?Poland, ?Yugoslavia, Morocco, Algeria, Tunisia, Egypt, Somalia, Ethiopia, Kenya, Syria, Jordan, Saudi Arabia, Israel, Nepal, India, ?Pakistan.——FIG. 918*a–q.* **S. africana,* Oxfordian, Bihendula, Somalia; *a–c,* dorsal, lateral, anterior views, USNM 429404, ×1 (Shi & Grant, 1993); *d–q,* transverse serial sections, distances in mm from ventral umbo, 1.1, 1.4, 2.3, 3.8, 4.2, 4.8, 5.1, 5.3, 5.5, 5.9, 6.4, 6.7, 7.0, 7.2, BMNH B.46172, ×1.4 (Muir-Wood, 1935).——FIG. 918*r.* *S. arabica* COOPER, Kimmeridgian, Saudi Arabia; paratype, interior showing septalium and raduliform crus, USNM 380514, ×2 (Cooper, 1989).

Subfamily GIBBIRHYNCHIINAE new subfamily

[Gibbirhynchiinae MANCEÑIDO & OWEN, herein]

Tetrarhynchiidae with densely costate, moderately uniplicate, nearly equibiconvex shells; dorsal and ventral valves both globose, with fold and sulcus ill defined, often merging gradually into convex lateral slopes; linguiform extension typically arcuate and rather low; ventral beak acuminate, erect to incurved. Usually with median septum high and septalium narrow; dental plates subparallel to slightly ventrally divergent; strongly incurved raduliform crura. *Lower Jurassic (Sinemurian), Middle Jurassic (Callovian).*

Gibbirhynchia BUCKMAN, 1918, p. 43 [**G. gibbosa;* OD] [=*Gibbirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, globose, equibiconvex to dorsibiconvex, with uniplication strong, arched topped; multicostate, 11 to 38 costae (3 to 9 on fold); beak small, incurved, with 2 deep, narrow muscle impressions. Crura raduliform short, rodlike. [Middle Jurassic (Bajocian–Bathonian) records of Arabia as in COOPER, 1989, are probably referable to *Nastosia.*] *Lower Jurassic (Sinemurian–Toarcian):* England, Scotland, France, Belgium, Germany, ?Portugal, Spain, Gibraltar, Switzerland, Italy, Yugoslavia, Greece, Slovakia, Hungary, Romania, ?Bulgaria, Morocco, Algeria, Anatolia, Israel, Iran, Argentina, ?Peru, western USA (?Nevada), Canada,

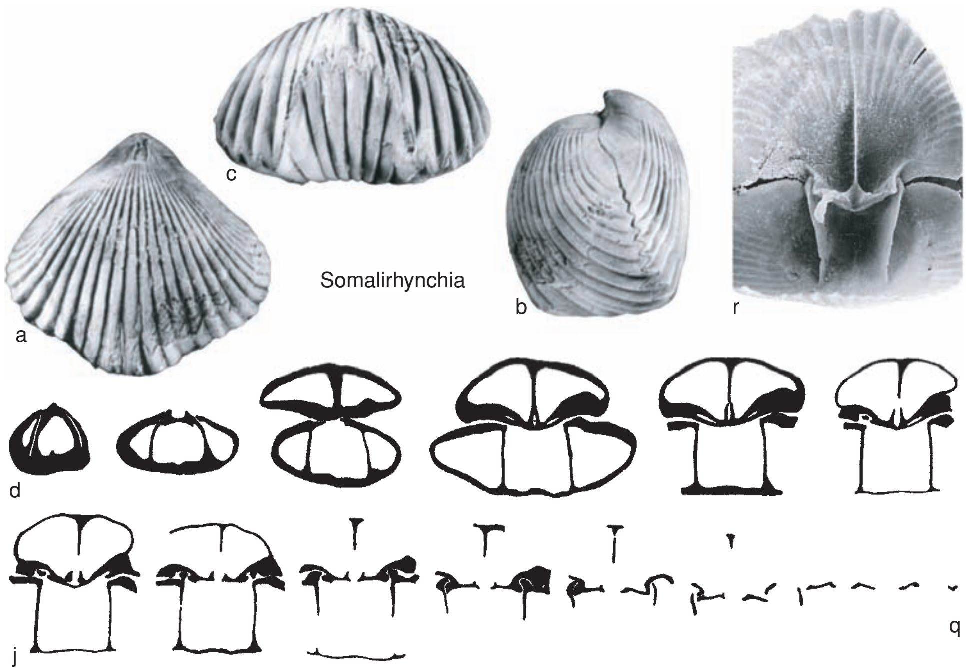

FIG. 918. Tetrarhynchiidae (p. 1354).

?Indonesia.——FIG. 919,*3a–i*. **G. gibbosa,* upper Pliensbachian, Somerset, England; *a–c,* holotype, dorsal, lateral, anterior views, GSM 31866, ×1.5; *d–i,* topotype, transverse serial sections, distances in mm from ventral umbo, 0.5, 0.8, 1.2, 1.5, 1.8, 2.7, BMNH B.64700 (Ager, 1962).

Amydroptychus COOPER, 1989, p. 10 [**A. formosus;* OD]. Medium size, dorsibiconvex to equibiconvex; widely, roundly subtriangular; rectimarginate or with slight, faint arcuate uniplication, but dorsal fold barely perceptible; costae full length, subangular, with occasional intercalations on umbones; long, erect beak with small, tubular, hypothyrid foramen; deltidial plates disjunct rimmed. Dorsal median septum short, supporting small septalium; dental plates short, wide apart; raduliform crura, laterally expanded distally. *Middle Jurassic (Bajocian):* Saudi Arabia, ?Israel.——FIG. 920,*1a–m*. **A. formosus,* Saudi Arabia; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380223c, ×1; *f–m,* transverse serial sections, distances in mm from ventral umbo, 2.8, 3.2, 3.5, 3.7, 4.2, 4.7, 5.1, 5.4, USNM 380683 (Cooper, 1989).

Burmirhynchia BUCKMAN, 1918, p. 49 [**B. gutta;* OD] [=*Burmirhynchia* BUCKMAN, 1915, p. 76, suppressed (ICZN, 1971, Opinion 957)]. Small to medium, globose, equibiconvex to dorsibiconvex, thickest at midvalve, convex anteriorly; uniplication distinct, but dorsal fold indistinct to gently prominent; linguiform extension always neat, deflected dorsally; costae numerous, simple, smooth posterior area not present; beak massive, incurved to suberect, subdued beak ridges; foramen small, hypothyrid, deltidial plates disjunct to barely conjunct. Dental plates ventrally divergent; dorsal median septum strong, septalium variable; crura slender, strongly incurved, raduliform. *Middle Jurassic (?Bajocian, Bathonian–Callovian):* Europe, Africa, Asia, ?Australasia.

B. (**Burmirhynchia**). More subspherical, both valves inflated, dorsal fold undifferentiated, and costae rounder. Dorsal septum and septalium may be reduced; secondary thickenings not noticeable on the interior. *Middle Jurassic (?Bajocian, Bathonian–Callovian):* Europe, Somalia, Middle East, Afghanistan, India, Myanmar (Burma), China, ?Japan, ?New Zealand.——FIG. 919,*1a–k*. **B. (B.) gutta,* Bathonian, northern Shan States, Myanmar; *a–c,* topotype, dorsal, lateral, anterior views, USNM 123602, ×1; *d–k,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.9, 2.2, 2.4, 2.7, 3.0, 3.5, 4.0, 4.7, USNM 123602 (Shi & Grant, 1993).

B. (**Hopkinsirhynchia**) SHI & GRANT, 1993, p. 63 [**Rhynchonella hopkinsi* DAVIDSON, 1852b, p. 97; OD] [=*Hopkinsirhynchia* SHI & YANG, 1992, p. 555, *nom. nud.*]. More dorsibiconvex, and somewhat trilobate; fold and sulcus well developed, linguiform extension high, trapezoidal; costae rather coarser, subangular. Dorsal median septum stout, septalium generally V-shaped; secondary thickenings frequently developed inside both valves. *Middle Jurassic (middle*

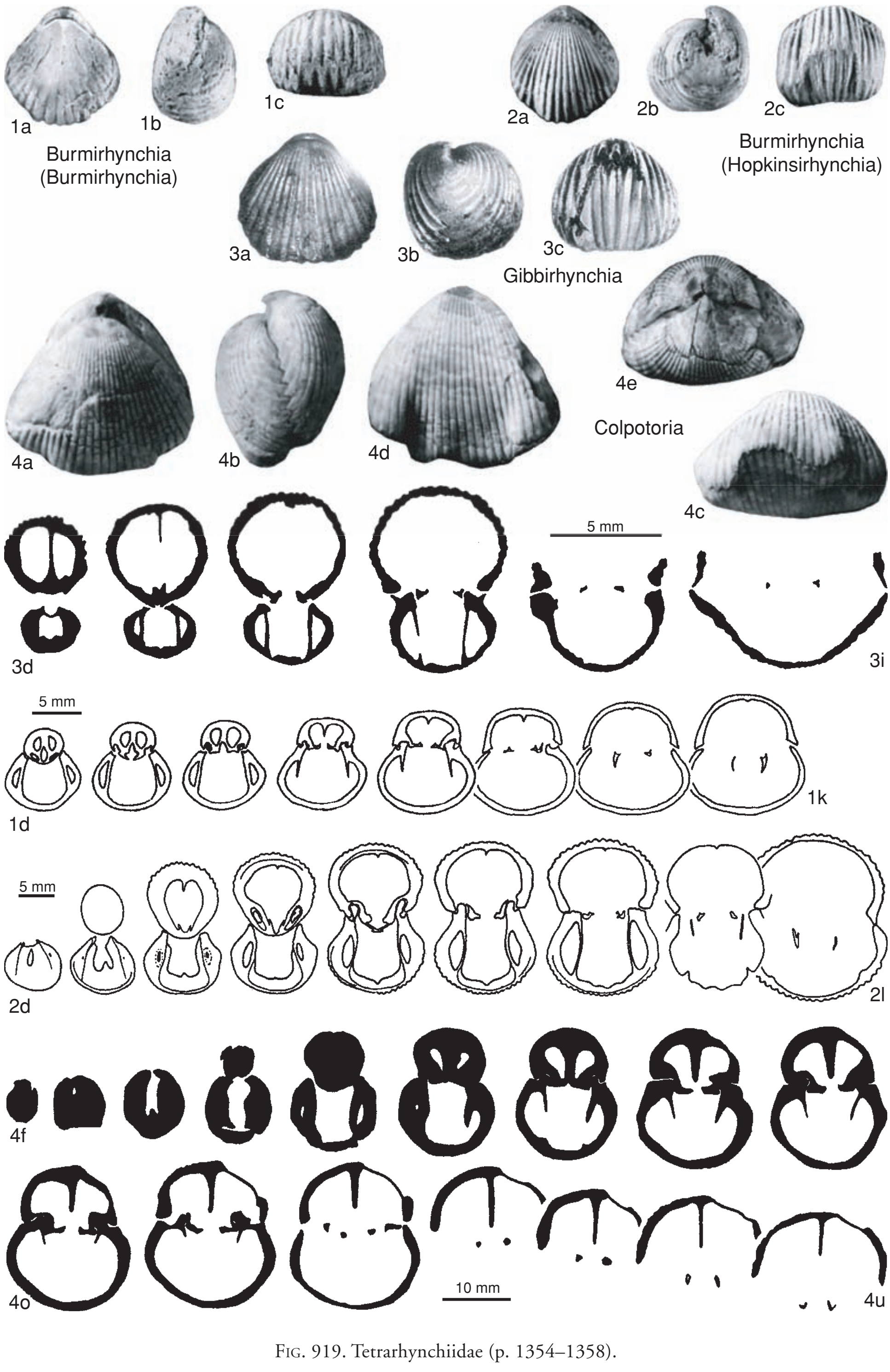

FIG. 919. Tetrarhynchiidae (p. 1354–1358).

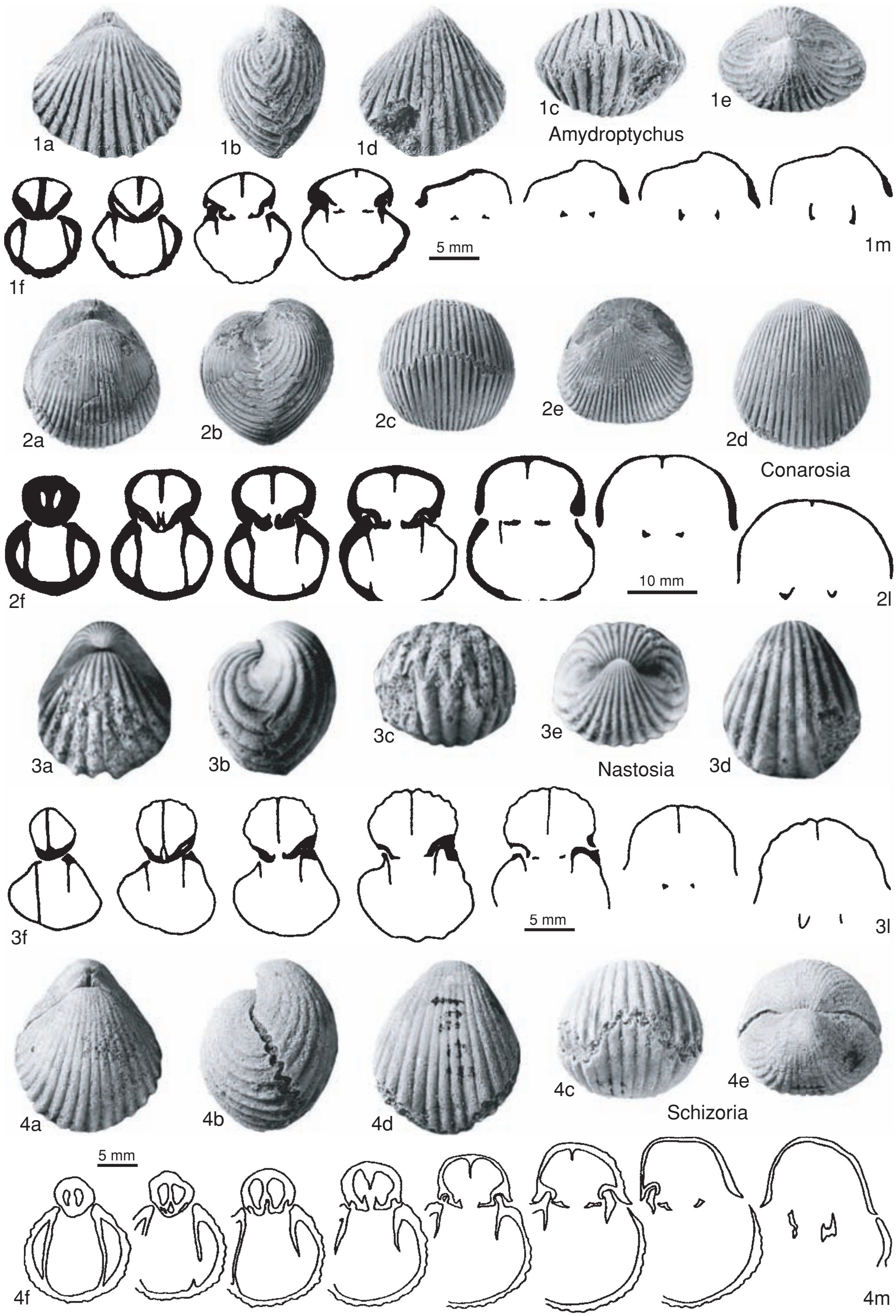

FIG. 920. Tetrarhynchiidae (p. 1355–1358).

Bathonian–lower Callovian): England, France, Germany, Switzerland, Middle East, Africa.——FIG. 919,*2a–l*. **B. (H.) hopkinsi* (DAVIDSON), middle Bathonian, northwestern France; *a–c,* dorsal, lateral, anterior views, USNM 104676a, ×1 (Shi & Grant, 1993); *d–l,* transverse serial sections, distances in mm from ventral umbo, 1.6, 2.2, 3.1, 3.6, 4.1, 4.4, 5.0, 5.7, 6.6 (Laurin, 1984).

?Colpotoria COOPER, 1989, p. 18 [**C. plicatilis;* OD; =*Burmirhynchia nazeri* ALMÉRAS, 1987, p. 177, subj.]. Large, dorsibiconvex; elongate subtriangular; anteriorly quadrilobate, dorsal fold with anterior sulcus; costae numerous, narrow, flattened, crowded, separated by striae narrower than costae; beak narrow pointed, straight to erect; deltidial plates disjunct to conjunct; foramen small, hypothyrid. Dental plates long, divergent; dorsal median septum long, thick; cardinalia thickened; septalium small, shallow; cardinal process absent; crura raduliform, distally concave. [May be an iterative forerunner of Cretaceous Cretirhynchinae or ancestral to them.] *Middle Jurassic (Bathonian–Callovian):* Saudi Arabia.——FIG. 919,*4a–u*. **C. nazeri plicatilis,* Bathonian; *a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, USNM 380208a, ×1; *f–u,* transverse serial sections, distances in mm from ventral umbo, 0.9, 2.1, 2.7, 3.0, 4.0, 4.7, 5.0, 5.4, 5.6, 6.0, 6.4, 6.7, 7.0, 7.3, 7.7, 8.1, USNM 380654 (Cooper, 1989).

Conarosia COOPER, 1989, p. 20 [**C. rotundata;* OD; =*Burmirhynchia moulani* ALMÉRAS, 1987, p. 177, subj.]. Often large, strongly dorsibiconvex; roundly oval in outline and side view; uniplicate, but with indistinct dorsal fold and ventral sulcus; costae numerous, narrow, rounded to flattened, separated by striae narrower than costae; beak massive, rounded, strongly incurved, almost touching umbo of dorsal valve; deltidial plates disjunct to conjunct; foramen small, hypothyrid. Dental plates long; dorsal median septum long; septalium small, cardinal process absent; crura raduliform, widening distally. *Lower Jurassic (Toarcian), Middle Jurassic (Bajocian–Bathonian):* Saudi Arabia.——FIG. 920,*2a–l*. **C. moulani rotundata,* upper Bajocian–Bathonian; *a–e,* paratype, dorsal, lateral, anterior, ventral, posterior views, USNM 380379, ×1; *f–l,* transverse serial sections, distances in mm from ventral umbo, 3.0, 3.7, 4.0, 4.5, 5.0, 6.5, 7.6, USNM 380663 (Cooper, 1989).

Nastosia COOPER, 1989, p. 50 [**N. coangustata;* OD]. Medium to large, nearly equibiconvex; roundly ovate; moderately uniplicate, but dorsal fold and sulcus subdued; strongly costate; beak erect; deltidial plates disjunct, marginally rimmed; foramen a minute, narrow slit. Dental plates long, thin, very closely positioned and nearly parallel; dorsal median septum thin, persistent; septalium thin; raduliform crura. *Middle Jurassic (upper Bajocian):* Arabia.——FIG. 920,*3a–l*. **N. coangustata,* Saudi Arabia; *a–e,* paratype, dorsal, lateral, anterior, ventral, posterior views, USNM 380279, ×1; *f–l,* transverse serial sections, distances in mm from ventral umbo, 3.3, 3.7, 4.0, 4.5, 4.8, 5.7, 6.2, USNM 380656 (Cooper, 1989).

?Schizoria COOPER, 1989, p. 54 [**S. elongata;* OD]. Small to medium, dorsibiconvex; subtriangular, subpentagonal to subcircular, narrowly uniplicate, dorsal fold poorly defined; costae numerous, subangular, bifurcated and intercalated especially on umbones, 3 to 8 on fold; beak suberect to strongly incurved; deltidial plates disjunct; foramen small, narrow, tubular hypothyrid. Dental plates long, subparallel; dorsal median septum long; septalium small, short; crura raduliform. [Also shows affinities with Indorhynchiinae but placed here due to its deep, Y-shaped septalium.] *Middle Jurassic (Bajocian):* Arabia, Sinai.——FIG. 920,*4a–m*. **S. elongata; a–e,* holotype, dorsal, lateral, anterior, ventral, posterior views, Saudi Arabia, USNM 380260b, ×2 (Cooper, 1989); *f–m,* transverse serial sections, distances in mm from ventral umbo, 3.9, 4.2, 4.7, 5.5, 6.5, 7.5, 8.3, 8.8, Sinai, GSI M6823 (Feldman, Owen, & Hirsch, 1991).

Subfamily KALLIRHYNCHIINAE new subfamily

[Kallirhynchiinae MANCEÑIDO & OWEN, herein]

Tetrarhynchiidae with densely costate, trilobate, moderately inequibiconvex shells; dorsal valve with broad, flat, multidentate fold, best defined anteriorly; linguiform extension variably developed, often wide, trapeziform to subquadrate; beak prominent, erect to substraight. Dental plates thin, subparallel to ventrally divergent; dorsal median septum apically confined, supporting narrow or pitlike septalium; incurved raduliform crura strongly deflected ventrally. [Circumstantial evidence suggests likely persistence of members of this subfamily into the Cretaceous.] *Middle Jurassic (?Aalenian, Bajocian–Bathonian, ?Callovian), Upper Jurassic (?Oxfordian).*

Kallirhynchia BUCKMAN, 1918, p. 31 [**Rhynchonella concinna* var. *yaxleyensis* DAVIDSON, 1878, p. 206; OD] [=*Kallirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Medium size, globose, almost convexiplane, thickest anteriorly; subpentagonal, anteriorly flat to gently indented; uniplication prominent, subrectangular, but fold indistinct; linguiform extension shallowly concave, flattopped, strongly bent and rising above midheight; multicostate (24 to 32) after short posterior smooth stage (5 to 8 on fold); beak hypothyrid, suberect, deltidial plates disjunct or barely conjunct. Dorsal septum short, low; septalium almost sessile or pendant; crura long, allegedly calcariform to possibly falciform, in fact raduliform with concave distal ends. *Middle Juras-*

sic (Bajocian–Bathonian, ?Callovian): England, France, ?Germany, ?Switzerland, ?Poland, ?Egypt, Saudi Arabia, ?Jordan, Pamirs, India, China, ?Japan, ?USA, Canada, ?Argentina.——Fig. 921,*2a–j.* **K. yaxleyensis* (Davidson), upper Bathonian; *a–c,* topotype, dorsal, lateral, anterior, Cambridgeshire, England, USNM 429303, ×1 (Shi & Grant, 1993); *d–j,* transverse serial sections, distances in mm from ventral umbo, 2.0, 2.2, 3.4, 4.2, 4.3, 4.4, 4.5, Lorraine, France (Laurin, 1984).

Kutchirhynchia Buckman, 1918, p. 54 [**Rhynchonella concinna* var. *kutchensis* Kitchin, 1897, p. 31; OD] [=*Kutchirhynchia* Buckman, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Karakulirhynchia* Ovcharenko, 1991, p. 18 (type, *K. karakulensis,* OD)]. Medium to large, subglobose, moderately dorsibiconvex, roundly subpentagonal; uniplication broad, strong and dorsal fold little raised; smooth stage absent, costae numerous, simple, sharp; beak short, suberect to erect; foramen large; deltidial plates disjunct or conjunct. Dental plates long, subparallel; teeth massive, expanded, crenulated; dorsal median septum stout but short, low; hinge plates subhorizontal; septalium variable; slender raduliform crura, strongly curved ventrally. [Possibly comprising *Obsoletirhynchia* as synonym or subgenus.] *Middle Jurassic (Bathonian–lower Callovian):* England, France, Romania, ?Morocco, ?Tunisia, ?Somalia, Saudi Arabia, India, Uzbekistan, Pamirs, ?Iran.——Fig. 921,*3a–j.* **K. kutchensis* (Kitchin), upper Bathonian, Kutch, India; *a–c,* topotype, dorsal, lateral, anterior views, USNM 75997, ×1 (Shi & Grant, 1993); *d–j,* transverse serial sections, distances in mm from first section, 5.45, 5.8, 6.0, 7.2, 8.2, 9.0, 9.5, BMNH B.52574, ×1 (new).——Fig. 921,*3k–u. K. karakulensis* (Ovcharenko), lower Callovian, Pamirs; *k–m,* dorsal, lateral, anterior views, ×1; *n–u,* transverse serial sections, distances in mm from first section, 2.6, 3.5, 3.9, 4.2, 4.6, 5.0, 5.5, 6.5 (Ovcharenko, 1991).

Obsoletirhynchia Shi, 1992, p. 143 [**Terebratula obsoleta* J. Sowerby, 1815 in 1812–1815, p. 192; OD] [=*Obsoletirhynchia* Yang & Shi, 1990, p. 18, *nom. nud.*]. Similar to *Kutchirhynchia* but with beak substraight to suberect, foramen rimmed, fold and sulcus less developed, occasionally given to slight asymmetry; septalium rudimentary, pendant. [May be included in *Kutchirhynchia* as synonym or subgenus]. *Middle Jurassic (Bathonian):* England, France, Germany, China.——Fig. 921,*1a–k.* **O. obsoleta* (Sowerby), upper Bathonian; *a–c,* topotype, dorsal, lateral, anterior views, Bradford-on-Avon, England, USNM 31006a, ×1 (Shi & Grant, 1993); *d–k,* transverse serial sections, distances in mm from ventral umbo, 1.67, 2.5, 3.0, 3.7, 4.2, 4.6, 6.0, 8.5, France (Laurin, 1984).

Rhactorhynchia Buckman, 1918, p. 50 [**R. rhacta;* OD; =*Rhynchonella subtetrahedra* Davidson, 1852b, p. 95, subj.] [=*Rhactorhynchia* Buckman, 1914, p. 1, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957); *Rhactarhynchia* Wisniewska-Zelichowska, 1978, p. 65, *nom. null.*]. Medium size to large, dorsibiconvex, oval to round subtrigonal, subglobose to globose; dorsal fold and ventral sulcus generally weak, sometimes asymmetrical; costae numerous, strong, sharp; beak strong, slightly incurved, foramen rimmed, hypothyrid, conjunct deltidial plates. Dorsal median septum strong, septalium brief, pitlike; crura raduliform, transitional to canaliform distally; muscle scars expanded. [Species name was originally spelled *subtetraëdra.* Prevailing spelling adopted by Buckman (1918, p. 226), preserved under Article 33.3.1 of ICZN (1999).] *Middle Jurassic (?Aalenian, Bajocian–Bathonian, ?Callovian), Upper Jurassic (?Oxfordian):* England, France, ?Switzerland, ?Austria, ?Poland, ?Yugoslavia, Russia, Caucasus, ?Morocco, ?Israel, India, China, ?USA, ?Canada, ?Chile.——Fig. 922*a–p.* **R. subtetrahedra* (Davidson), upper Bajocian, Cotswolds, England; *a–c,* dorsal, lateral, anterior views, USNM 88731, ×1 (Shi & Grant, 1993); *d–p,* transverse serial sections, distances in mm from ventral umbo, 1.0, 1.8, 2.5, 3.7, 4.4, 5.2, 5.5, 6.2, 6.7, 7.5, 8.2, 9.1, 9.4, BUM 5029(3) (new; courtesy of C. D. Prosser).

Subfamily ISJUMINELLINAE new subfamily

[Isjuminellinae Manceñido & Owen, herein]

Tetrarhynchiidae with shells paucicostate, uniplicate, strongly inequibiconvex; dorsal valve prominently inflated, with central fold conspicuously raised; linguiform extension high and prominent; ventral beak strongly incurved, often closely appressed to dorsal umbo. Hinge plates very narrow; inner structures thickened, with lateral umbonal chambers often infilled with callus; crura raduliform, short, and slender. *Middle Jurassic (Aalenian)–Upper Jurassic (Volgian).*

Isjuminella Makridin, 1955, p. 85, *pars* [**Rhynchonella decorata* Buch [sic]; OD; =*Terebratulites decoratus* von Schlotheim, 1820 in 1820–1823, p. 264; Drot & Fischer, 1966, p. 53] [=*Sardorhynchia* Taddei-Ruggiero & Ungaro, 1984, p. 228 (type, *S. crassa* Taddei-Ruggiero & Ungaro, 1984, p. 232, OD)]. Large, pentagonal, strongly folded, and highly uniplicate; costae few, very strong, sharp, posterior smooth areas absent; beak massive, incurved; foramen small, hypothyrid, conjunct deltidial plates. Dental plates very short, ill-defined posteriorly; dorsal median septum reduced, thin, bulging in middle; hinge plates narrow, divided, septalium present; crura raduliform, short, incurved ventrally; shell thick, with marked secondary thickenings and callus inside both valves. *Middle Jurassic (Bathonian–Callovian):* western France, Belgium, England, Germany, Portugal, Sardinia, ?Morocco, ?Algeria.——Fig. 923*a–n.* **I. decorata* (von Schlotheim), Bathonian, Ardennes,

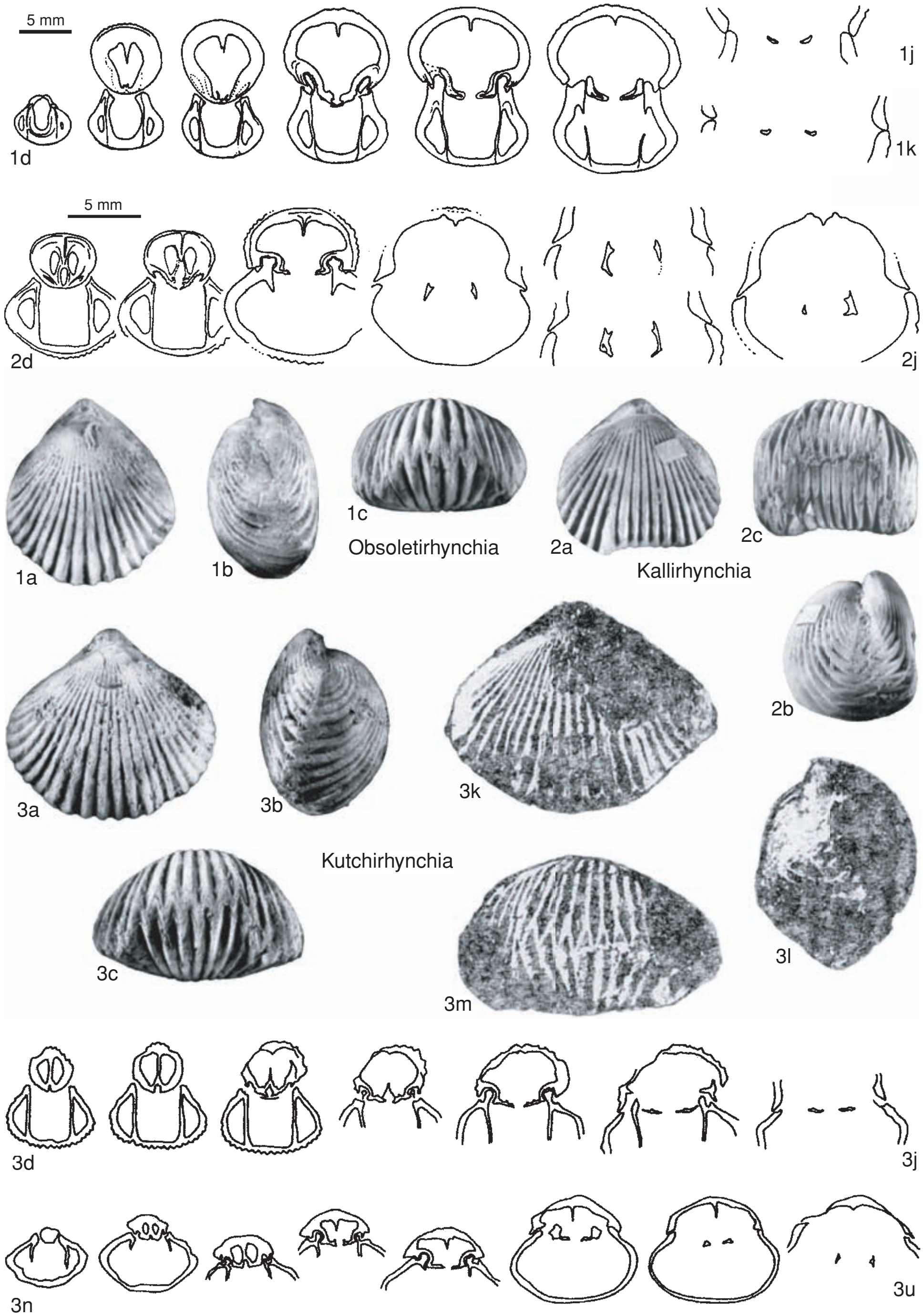

FIG. 921. Tetrarhynchiidae (p. 1358–1359).

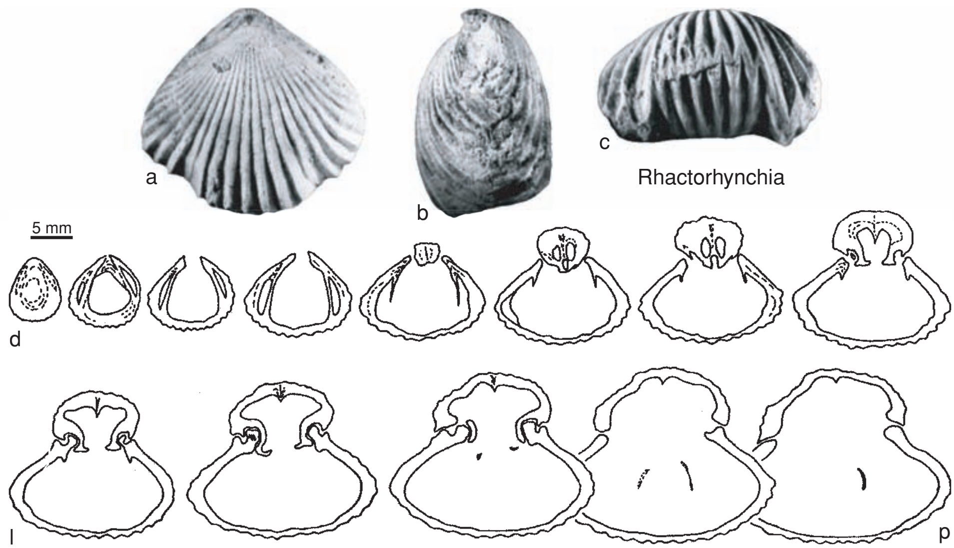

FIG. 922. Tetrarhynchiidae (p. 1359).

France; *a–c,* dorsal, lateral, anterior views, USNM 31331b, ×1 (Shi & Grant, 1993); *d–n,* transverse serial sections, distances in mm from ventral umbo, 2.9, 4.3, 6.5, 6.8, 8.1, 8.6, 9.4, 9.9, 10.5, 11.5, 13.3 (Drot & Fischer, 1966).——FIG. 923*o–cc. I. crassa* (TADDEI-RUGGIERO & UNGARO), upper Bathonian–Callovian, northwestern Sardinia; *o–r,* holotype, lateral, anterior, ventral, posterior views, T187, Paleontological Museum, University of Naples, Naples, Italy, ×1; *s–cc,* transverse serial sections, distances in mm from ventral umbo, 1.5, 3.5, 4.8, 5.4, 5.7, 6.6, 7.3, 7.9, 8.1, 8.4, 8.8, T164, Paleontological Museum, University of Naples, Naples, Italy (Taddei-Ruggiero & Ungaro, 1984).

Costirhynchia BUCKMAN, 1918, p. 39, *non* DAGYS, 1974, also Rhynchonellida [**C. costigera;* OD] [=*Costirhynchia* BUCKMAN, 1914, p. 1, and 1915, p. 76, both suppressed (ICZN, 1971, Opinion 957)]. Small, globose, dorsibiconvex, with fold high, bi- or tridentate and costae few, coarse; dorsal flanking costae often branching at least once quite early; beak small, short, suberect to incurved with foramen slitlike; squama and glotta present. Shell thick; dental plates short, convex; dorsal median septum high and long; hinge plates narrow; septalium pitlike. *Middle Jurassic (Aalenian–Bajocian):* England, Italy, Pamirs.——FIG. 924,*1a–j. *C. costigera,* Aalenian, Cotswolds, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH B.86314, ×1.5 (new); *d–j,* topotype, transverse serial sections, distances in mm from ventral umbo, 1.6, 1.8, 2.2, 2.5, 2.8, 3.4, 4.5, CDP 10, C. D. Prosser, personal collection (new; courtesy of C. D. Prosser).

Mosquella MAKRIDIN, 1955, p. 86 [**Rhynchonella oxyoptycha* FISCHER WALDHEIM (sic), 1843, p. 118; OD; =*Terebratula oxyoptycha* FISCHER DE WALDHEIM, 1843, p. 118, OD] [=*Moscvella* MAKRIDIN, 1954, p. 103, *nom. nud.*]. Large and medium size, oval or rounded-trigonal, covered with costae, simple, coarse, radial (6 to 7 on fold); sulcus and fold wide and well developed. Dorsal septum in young specimens wedge shaped; dental plates crescentic; crura slender, short, bladelike, almost straight; distal end of septum in mature specimens indistinctly overgrown and filling cavity in beak region; septum buttressing disjunct parts of hinge plate, crura gradually becoming hook shaped; ventral muscle scars slender, deep, demarcated with distinct ridges, diverging anteriorly from bases of dental plates; dorsal anterior adductors small, rounded-trigonal near anterior part of septum; adjustors punctae shaped near crural bases. *Upper Jurassic (Volgian):* Russian Platform.——FIG. 924,*2a–m. *M. oxyoptycha* (FISCHER DE WALDHEIM), lower Volgian, Moscow basin; *a–c,* dorsal, lateral, anterior views, ×1; *d–m,* transverse serial sections, distances in mm from first section, 0.0, 0.1, 1.5, 1.8, 2.2, 2.9, 3.6, 4.7, 5.7, 6.5 (Makridin, 1964).

Russirhynchia BUCKMAN, 1918, p. 52 [**Terebratula (Rhynchonella) Fischeri* ROUILLIER, 1847 in ROUILLIER & VOSINSKY, 1847–1848, p. 394; OD] [=*Russirhynchia* BUCKMAN, 1914, p. 2, and 1915, p. 77, both suppressed (ICZN, 1971, Opinion 957)]. Medium size to large, globose, round subpentagonal to subtrigonal, depressed dorsibiconvex to almost convexoplane; uniplication strong, dorsal fold; costae numerous, very strong (3 to 7 on fold); beak short, suberect, foramen round, deltidial plates disjunct. Dental plates subparallel, teeth stout; dorsal septum strong, low; septalium distinct in juveniles, extremely narrow and sessile in adults; crura raduliform; with much internal secondary thickening. *Upper Jurassic (Kimmeridgian–Volgian):* Russia,

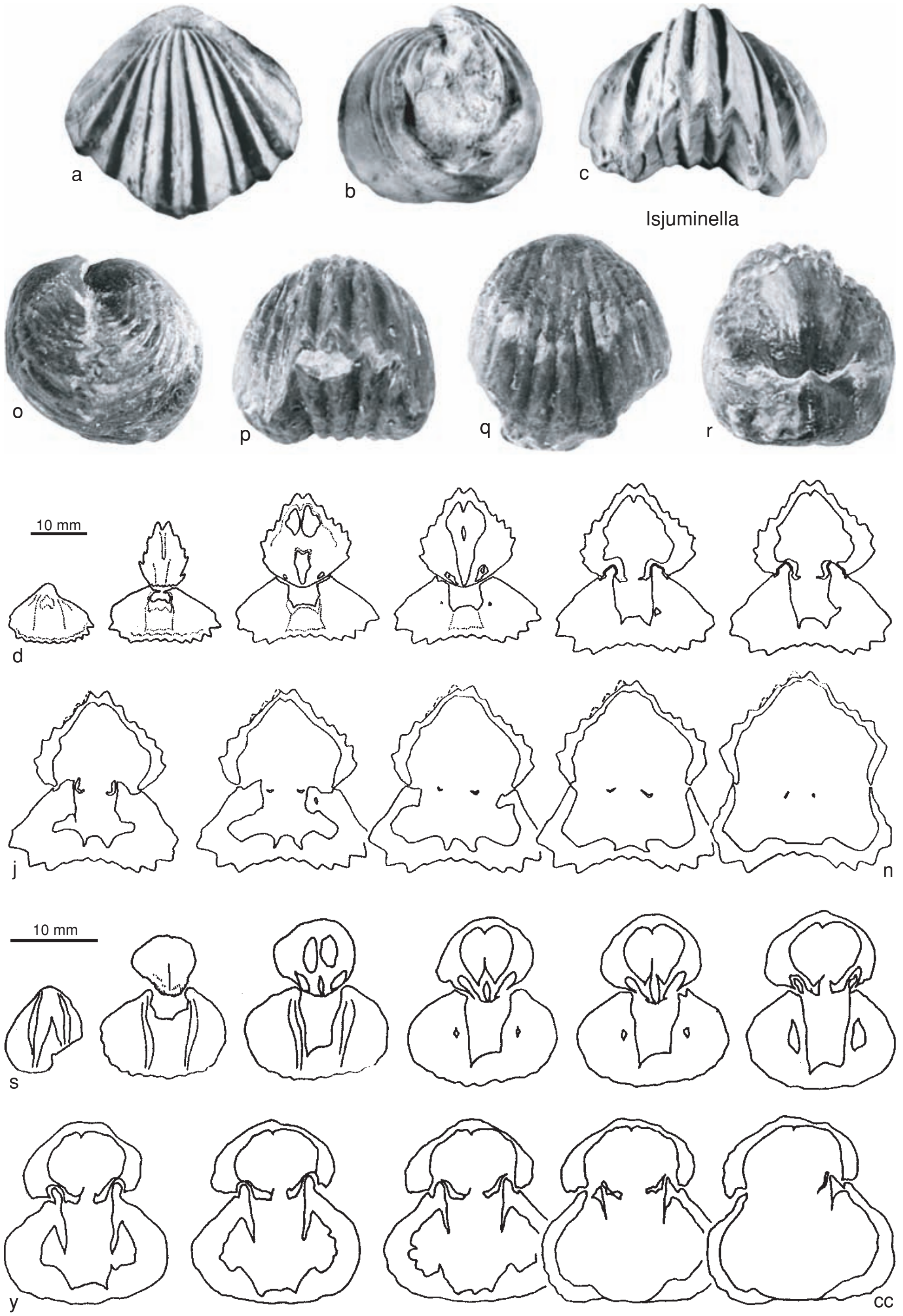

FIG. 923. Tetrarhynchiidae (p. 1359–1361).

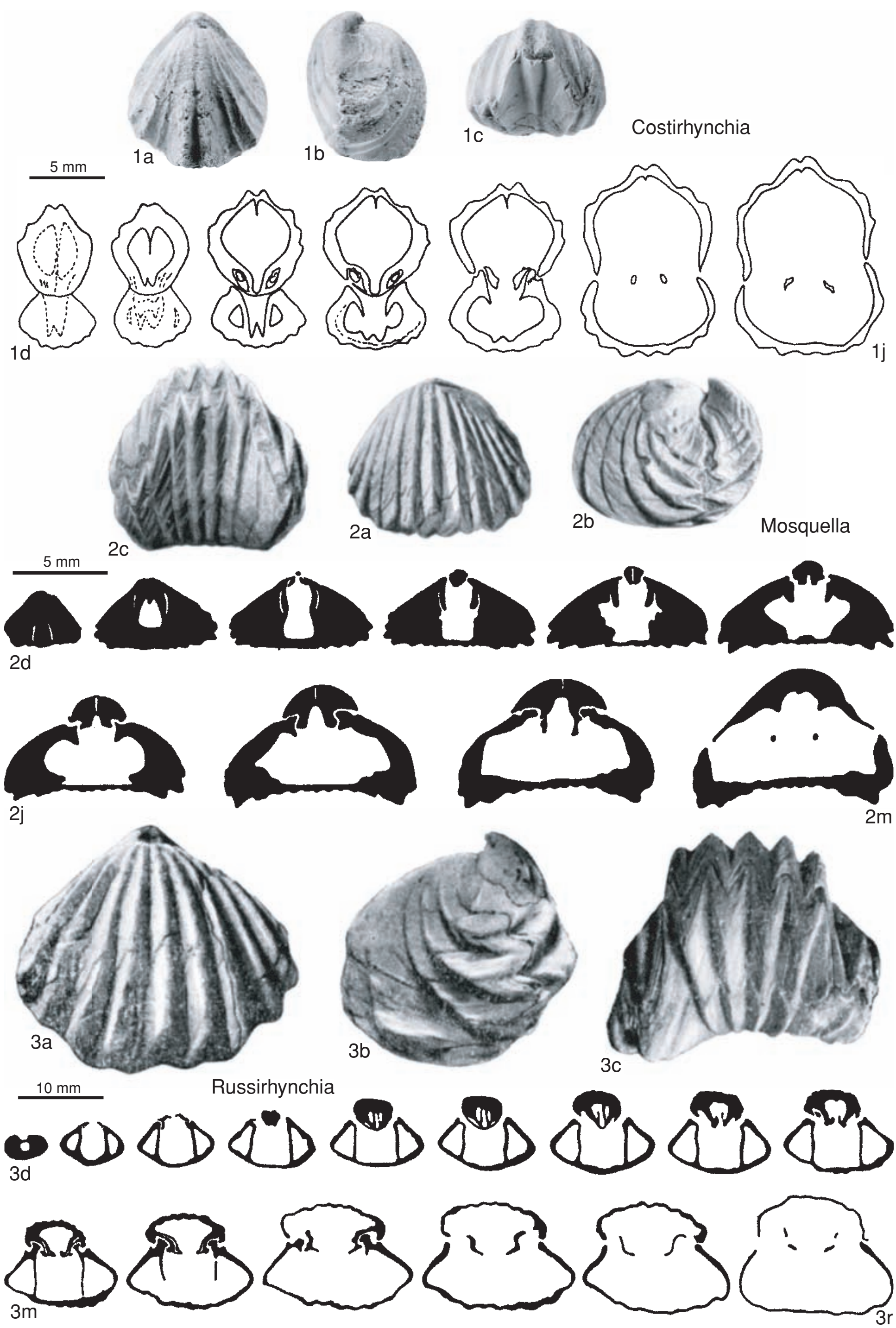

FIG. 924. Tetrarhynchiidae (p. 1361–1364).

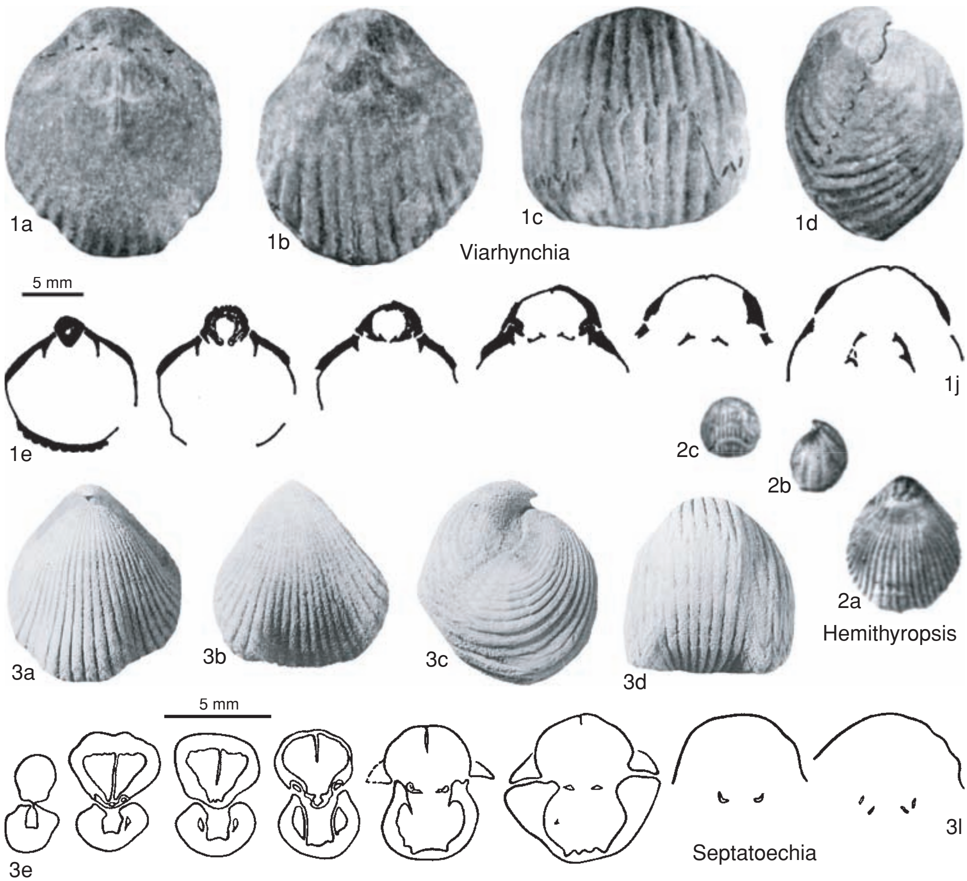

FIG. 925. Tetrarhynchiidae (p. 1364–1365).

western Europe.——FIG. 924,*3a–r.* **R. fischeri fischeri* (ROUILLIER), lower Volgian, Moscow Basin; *a–c,* dorsal, lateral, anterior views, ×1; *d–r,* transverse serial sections, distances in mm from ventral umbo, 3.5, 4.8, 5.7, 6.5, 6.9, 7.1, 7.3, 7.4, 7.6, 7.9, 8.5, 9.4, 9.9, 10.2, 10.3 (Makridin, 1964).

Subfamily VIARHYNCHIINAE new subfamily

[Viarhynchiinae MANCEÑIDO & OWEN, herein]

Nearly equibiconvex, subspherical Tetrarhynchiidae; densely multicostate, broadly uniplicate, with linguiform extension semicircular to subquadrate, but with dorsal fold only gently raised anteriorly; beak prominent, incurved. Crura distally concave, transitional to canaliform. *Lower Cretaceous (Albian)–Upper Cretaceous (Maastrichtian).*

Viarhynchia CALZADA BADIA, 1975, p. 170 [**Rhynchonella cerdanyolae* BATALLER, 1947, p. 195; OD; =*Rhynchonella sardanyolae* BATALLER, 1947, p. 195, prevailing spelling is preserved under Article 33.3.1 of ICZN (1999)]. Large, equibiconvex, globulose; costae numerous, strong, rounded; umbo massive, beak slightly incurved, foramen relatively small; uniplicate with dorsal fold poorly developed; ventral sulcus high, shallow with linguiform extension extensive. Dental plates short, ventrally divergent; hinge plates long, dorsally directed, raduliform crura with concave distal ends. Septum reduced to low, median ridge persistent. *Upper Cretaceous (upper Campanian–lower Maastrichtian):* northeastern Spain.——FIG. 925,*1a–j.* **V. cerdanyolae* (BATALLER), upper Campanian, Catalonian pre-Pyrenees; *a–c,* lectotype, dorsal, ventral, anterior views, MGSB 6605, ×1; *d,* lateral view, ×1; *e–j,* transverse serial sections, distances in mm from ventral umbo, 3.8, 4.4, 4.8, 5.9, 6.6, 7.0 (Calzada Badia, 1975).

Hemithyropsis KATS, 1974, p. 254 [**H. globulosa;* OD]. Shell variable in outline, usually elongate with fold and sulcus weakly developed and beak high, suberect. Hinge plates and socket ridges fused, forming cardinalium; often protruding near cardinal margin, producing muscle platform. *Upper Cretaceous (Cenomanian–Maastrichtian):* north of Don basin, Russia.——FIG. 925,*2a–c.* **H. globulosa,* lower Maastrichtian, Russia; *a,* holotype, dorsal view, ×2; *b–c,* lateral, anterior views, ×1 (Kats, 1974).

Septatoechia LOBACHEVA & TITOVA, 1977, p. 102 [**S. inflata;* OD]. Large, subtrigonal to subcircular, acutely biconvex; fold and sulcus well developed; costae numerous, rounded, originating from umbonal area, becoming more angular anteriorly; umbo short, beak massive, small, slightly incurved, foramen small, epithyrid, sometimes obscured by deltidial plates. Dental plates subparallel to slightly ventrally convergent; hinge plates short, dorsal septum high, long; crural bases ventrally deflected. Anterior commissure with sulcus high, arcuate, and dorsal fold well defined. *Lower Cretaceous (Albian)–Upper Cretaceous (Maastrichtian):* France, Spain, Bulgaria, Crimea, Turkmenistan, western Kazakhstan.——FIG. 925,*3a–l.* **S. inflata,* upper Maastrichtian, Tuarkyr, Turkmenistan; *a–d,* holotype, dorsal, ventral, lateral, anterior views, CNIGR 1/10153, ×1; *e–l,* transverse serial sections, distances in mm from ventral umbo, 2.2, 3.2, 3.4, 3.85, 4.35, 4.7, 5.6, 6.0, ×2.7 (Lobacheva & Titova, 1977).

Subfamily CRETIRHYNCHIINAE Kats, 1974

[*nom. transl.* MANCEÑIDO & OWEN, herein, *ex* Cretirhynchiidae KATS, 1974, p. 250]

Dorsibiconvex Tetrarhynchiidae, surface finely and densely costellate to capillate; uniplication broad, subrectangular to subquadrate, but with dorsal fold scarcely raised, ventral sulcus wide, shallow, and commonly bearing also a shallow dorsal median sulcus anteriorly; beak suberect to incurved, with beak ridges characteristically sharp. Dorsal median septum variably developed; hinge plates relatively narrow; crura raduliform with concave distal ends. *Lower Cretaceous (?Barremian, Aptian)–Upper Cretaceous (Maastrichtian).*

Cretirhynchia PETTITT, 1950, p. 1 [**Terebratula plicatilis* J. SOWERBY, 1816 in 1815–1818, p. 37; OD] [=*Crettirhynchia* MAKRIDIN in SARYCHEVA, 1960, p. 257, *nom. null.*]. Medium, transversely oval to subpentagonal; acutely dorsibiconvex; dorsal fold low, broad, flattened, developed anteriorly; well-marked shallow trapezoidal linguiform extension of ventral sulcus dorsally directed; ornament of rounded costellae; umbo small, beak erect. Hinge teeth subquadrate, deeply inserted; dental plates subparallel to slightly ventrally convergent; hinge plates short, triangular; median septum and septalium developed; crura long. [Danian records based on juveniles from Denmark (BAGGE JOHANSEN, 1987) may refer to early hemithiridids.] *Upper Cretaceous (Cenomanian–upper Maastrichtian):* Europe, northern Africa, ?Kazakhstan, ?Turkey, ?Turkmenistan, ?Antarctica.——FIG. 926,*1a–l.* **C. plicatilis* (J. SOWERBY), upper Chalk, lower Senonian, Northfleet, Kent, England; *a–c,* topotype, dorsal, lateral, anterior views, BMNH B.79814, ×1 (new); *d–l,* transverse serial sections, distances in mm from ventral umbo, 1.7, 2.4, 3.3, 3.5, 3.9, 4.2, 4.4, 6.0, 6.7, ×1 (Pettitt, 1950).

Begiarslania TITOVA, 1992, p. 142 [**Cretirhynchia begiarslanensis* NEKHRIKOVA, 1967, p. 32; OD]. Small to medium, subpentagonal, moderately dorsibiconvex, dorsal valve with slight umbonal inflation and median fold poorly developed, anteriorly sulcate; ventral valve with broad but shallow sulcus and linguiform extension trapezoidal; umbo short, beak slightly incurved. Pedicle collar present; dental plates subparallel to slightly ventrally convergent; teeth subquadrate, inner and outer socket ridges well developed; hinge plates short, horizontal to slightly ventrally deflected, crura distally concave; median septum or septalium absent. *Upper Cretaceous (Maastrichtian):* Turkmenistan, western Kazakhstan.——FIG. 926,*2a–u.* **B. begiarslanensis* (NEKHRIKOVA), upper Maastrichtian, Tuarkyr, Turkmenistan; *a–d,* holotype, dorsal, lateral, anterior, ventral views, CNIGR 34/10445, ×1; *e–u,* transverse serial sections, distances in mm from ventral umbo, 0.75, 1.4, 2.1, 2.5, 2.6, 2.7, 3.2, 3.3, 3.4, 3.5, 3.7, 4.0, 4.2, 4.3, 4.4, 4.5, 5.1, approximately ×1.5 (Titova, 1992).

Bohemirhynchia NEKVASILOVÁ, 1973, p. 78 [**B. soukupi;* OD]. Medium, heart shaped, dorsibiconvex to almost convexoplane; broadly oval to subpentagonal, uniplicate, bisulcate; multicostate with some bifurcation; beak short, suberect, foramen small, submesothyrid; deltidial plates auriculate. Dental plates ventrally convergent, teeth massive, crenulated; median septum low; thick shelled; crura slightly concave dorsally. *Upper Cretaceous (Cenomanian):* Slovakia.——FIG. 926,*4a–k.* **B. soukupi,* upper Cenomanian, Miscovice; *a–c,* holotype, dorsal, lateral, anterior views, CGS ON 12/2, ×1.5; *d–k,* paratype, transverse serial sections, distances in mm from ventral umbo, 1.4, 2.85, 3.25, 3.65, 4.1, 4.7, 5.3, 5.7, CGS ON 12/35, ×1.5 (Nekvasilová, 1973).

Burrirhynchia OWEN, 1962, p. 58 [**Rhynchonella leightonensis* LAMPLUGH & WALKER, 1903, p. 261; OD]. Small to medium, dorsibiconvex, elongate-triangular to subquadrate. Similar to *Cretirhynchia* but deltidial plates disjunct, hinge plates thinner and longer, and dorsal fold almost imperceptible; broadly uniplicate with linguiform extension extensive, trapezoidal; shell ornament fine, costellate. Dental plates subparallel to slightly convergent; median septum variable; crura moderately long. *Lower Cretaceous (?Barremian, Aptian)–Upper Cretaceous (Cenomanian):* England, France, Switzerland, Spain, Germany, Poland, Romania, Caucasus, Morocco, Donets basin, Turkmenistan.——FIG. 926,*3a–j.* **B. leightonensis* (LAMPLUGH & WALKER), lower Albian, Leighton Buzzard, Bedfordshire,

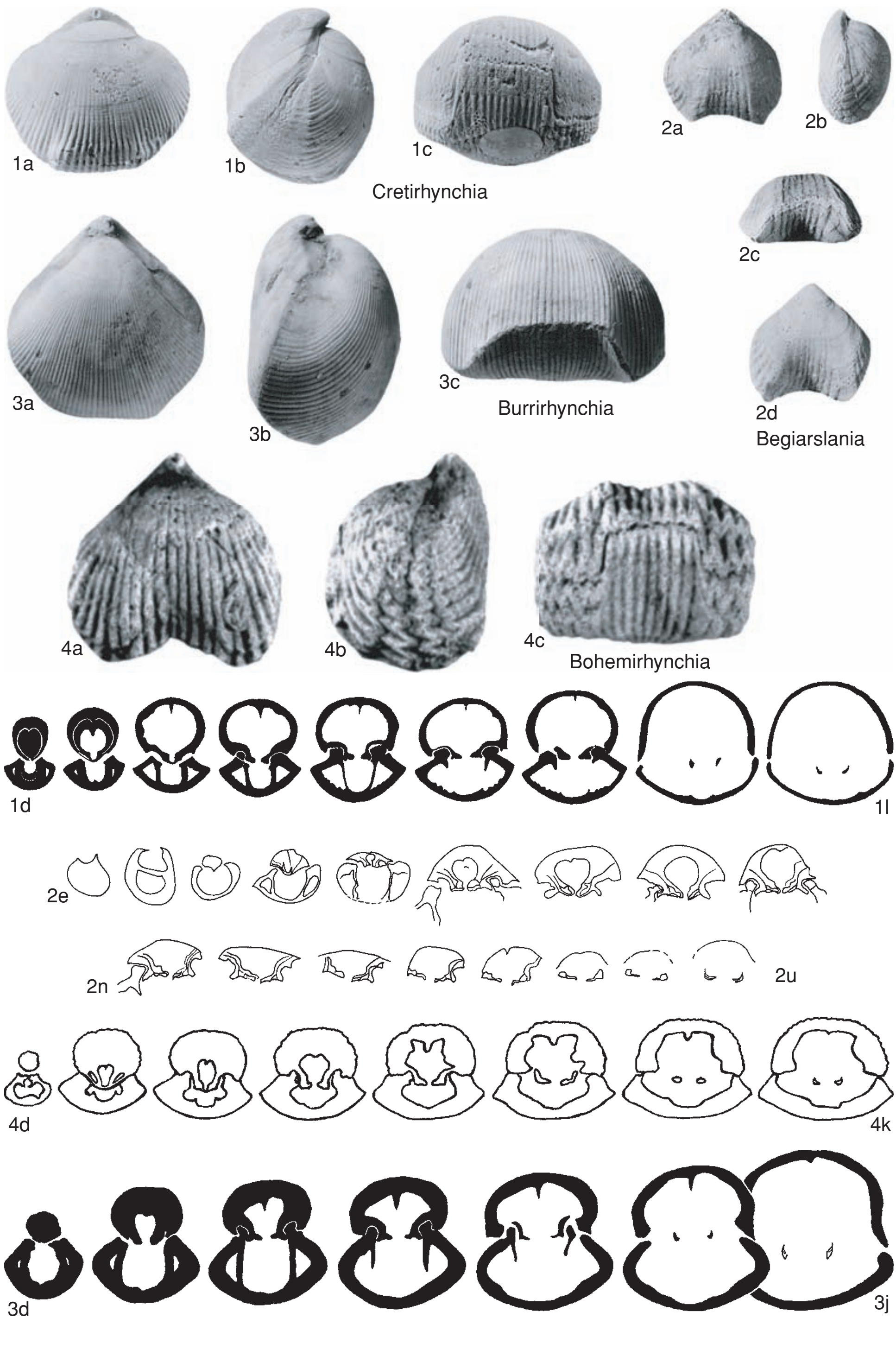

FIG. 926. Tetrarhynchiidae (p. 1365–1367).

United Kingdom; *a,* dorsal view, BMNH B.26573, ×1.5; *b–c,* lateral, anterior views, BMNH B.26573, ×1.65 (new); *d–j,* transverse serial sections, distances in mm from ventral umbo, 1.5, 2.5, 2.9, 3.1, 3.4, 4.0, 4.5, ×1.5 (Owen, 1956).

Family NOTOSARIIDAE new family

[Notosariidae MANCEÑIDO & OWEN, herein]

Trilobate, sharply costate Hemithiridoidea; uniplicate; smooth stage may be variably developed; squama and glotta obsolescent; ornament often lamellose, imbricate, even passing into spinose. Crura curved raduliform, distally flattened to concave; cardinal process overhanging, ledgelike, bilobed biconcave. Two pairs of metanefridia; intestines with curved distal end and terminal expansion; conoidal spirolophe bearing up to 8 whorls. *Upper Cretaceous (Campanian)–Holocene.*

Notosaria COOPER, 1959, p. 48 [**Terebratula nigricans* G. B. SOWERBY, 1846, p. 91; OD]. Subpentagonal, uniplicate, dorsal fold low; costate, growth lines developing anteriorly, beak nearly straight to suberect; large hypothyrid foramen, deltidial plates disjunct. Median dorsal ridge low; cardinal process wide, transversely triangular. [Living species range from intertidal to upper bathyal.] *Paleogene (Eocene)–Holocene:* New Zealand, *lower Oligocene–Holocene;* Poland, *middle Miocene;* Belgium, *Pliocene;* Antarctica (Seymour Island), *Eocene.*——FIG. 927,*4a–e.* **N. nigricans nigricans* (SOWERBY), Holocene, New Zealand; *a–c,* dorsal, lateral, anterior, USNM 111018b, ×1; *d,* ventral interior showing large foramen and massive teeth; *e,* dorsal interior showing bilobed cardinal process and crura, USNM 111018a, ×4 (Cooper, 1959).

?Paraplicirhynchia BITNER, 1996, p. 76 [**P. gazdzickii;* OD]. Medium size, subcircular to broadly oval, nearly equibiconvex, weakly uniplicate; marginal costae, many developing anteriorly after distinctive smooth stage; beak prominent, foramen large, hypothyrid, deltidial plates disjunct. Transverse, bilobed cardinal process; short, low median dorsal ridge; dental plates reduced in adults. *Paleogene (Eocene):* Antarctica (Seymour Island).——FIG. 927,*1a–e.* **P. gazdzickii,* ?lower Eocene, middle Eocene; *a–c,* dorsal, lateral, ventral views, ×1.5; *d,* ventral interior, ×3; *e,* holotype, dorsal interior, ZPAL Bp.XXXVII/107, ×3 (Bitner, 1996).

Plicirhynchia ALLAN, 1947b, p. 493 [**Rhynchonella plicigera* VON IHERING, 1897, p. 270; OD]. Subtrigonal-subpentagonal, dorsibiconvex, uniplicate; striate posteriorly, marginal costae developing anteriorly; beak long, pointed, foramen large, hypothyrid, deltidial plates conjunct. Bilobed cardinal process; short, low median dorsal ridge. *Paleogene (Eocene):* Argentina, ?Antarctica (Seymour and Cockburn Islands).——FIG. 927,*3a–e.* **P. plicigera* (VON IHERING), Argentina; *a–c,* dorsal, lateral, anterior views, ×1; *d,* umbonal detail showing foramen, thick deltidial plates, and faint umbonal striation, USNM 549346a, ×4; *e,* oblique dorsal interior showing crura and bilobed cardinal process, USNM 549346c, ×4 (Cooper, 1959).

?Protegulorhynchia OWEN, 1980, p. 129 [**P. meridionalis;* OD]. Small, subcircular to broadly oval; uniplicate, dorsal fold poorly developed; shell ornament costellate with marked concentric growth lines becoming more lamellose anteriorly; ventral sulcus shallow with narrow but acutely arcuate anterior commissure and poorly defined linguiform extension; beak sharp, short, suberect; beak ridges distinct, foramen small. *Upper Cretaceous (Campanian):* Antarctica, southern India.——FIG. 927,*2a–c.* **P. meridionalis,* lower Campanian, James Ross Island, Antarctica; holotype, dorsal, lateral, anterior views, BMNH BB.76770, ×1.5 (Owen, 1980).

Tegulorhynchia CHAPMAN & CRESPIN, 1923, p. 175 [**Rhynchonella squamosa* HUTTON, 1873, p. 37; OD]. Trigonal to subpentagonal, uniplicate, dorsal fold low; ornament of strong costae that are lamellose and often with hollow spines; beak long, straight; foramen large, hypothyrid; deltidial plates usually conjunct. Crura short; dorsal median septum short, low. *Paleogene (lower Paleocene)–Neogene (Miocene):* Australasia, Antarctica.——FIG. 927,*5a–c.* **T. squamosa* (HUTTON), upper Oligocene, Duntroonian, northern Otago, New Zealand; dorsal, lateral, anterior views, OU NZ DL20, ×2 (Lee, 1980).

?Family SEPTIRHYNCHIIDAE Muir-Wood & Cooper, 1951

[Septirhynchiidae MUIR-WOOD & COOPER, 1951, p. 5]

Usually large, equibiconvex Rhynchonellida, pentameroid in appearance; posterolateral commissure with dorsally convex squama-glotta junction; fully costate to almost smooth (with few gentle radial flutings). With late ontogenetic development of recurved cardinal process in dorsal valve and of median septum in ventral valve; simple raduliform crura, fairly long and high dorsal median septum. [Although its family/subfamily rank has been questioned, this is a highly distinctive group of the mid-Jurassic Ethiopian province.] *Middle Jurassic (upper Bathonian–Callovian).*

Septirhynchia MUIR-WOOD, 1935, p. 106 [**Rhynchonella azaisi* COTTREAU, 1925, p. 581; OD]. Very large, equibiconvex, with low dorsal fold; fully costate, with many coarse unbranching costae; planareas smooth, lateral, increasing at the expense of lateral costae; uniplication broad, multidentate

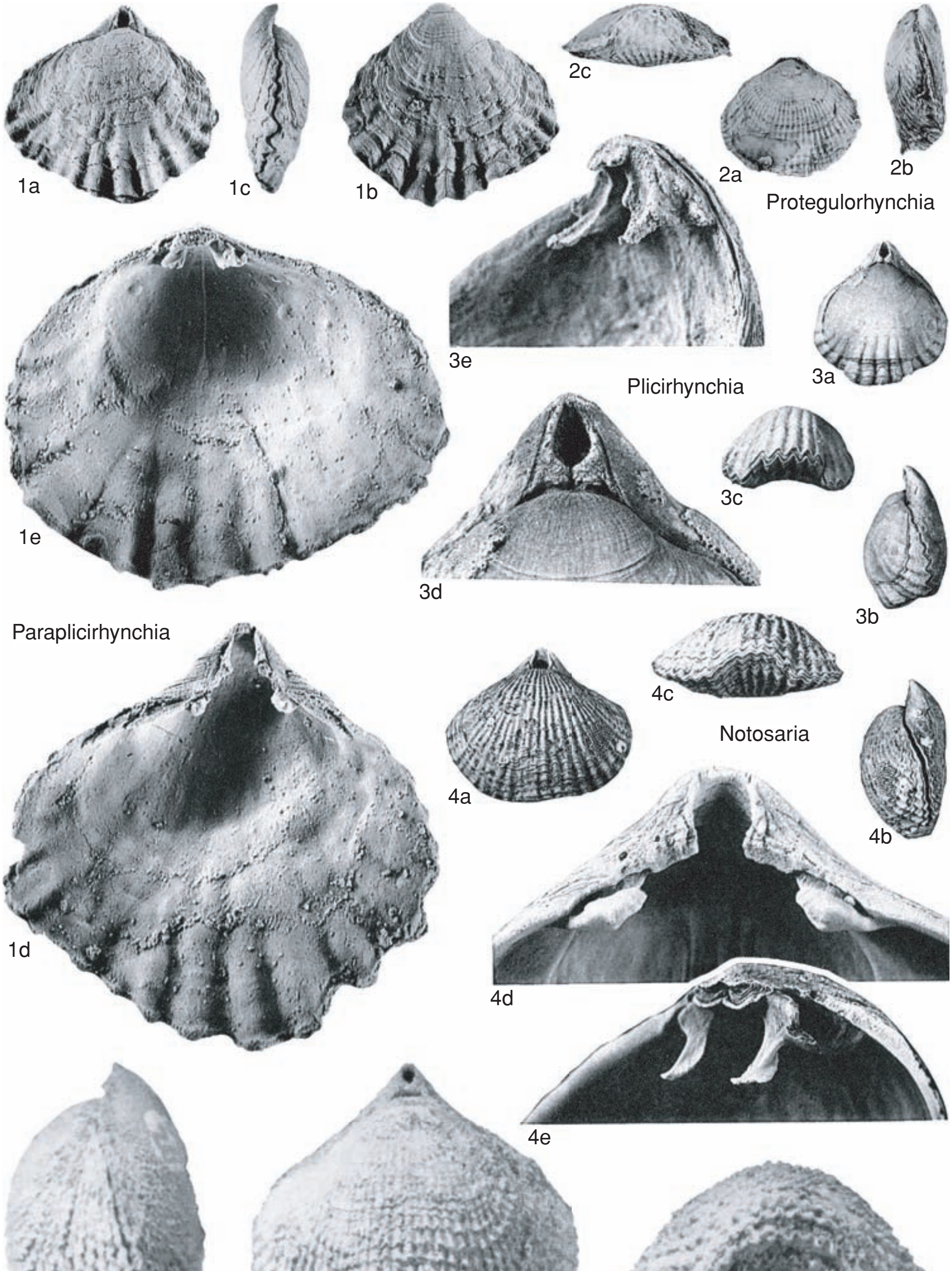

FIG. 927. Notosariidae (p. 1367).

anteriorly; beak prominent, greatly incurved in adult, concealing minute foramen and deltidial plates (disjunct in juvenile, later fused). Strong dental plates; ventral median septum well developed in adult, but absent or low ridge in juvenile; dorsal median septum of similar height and length throughout ontogeny; septalium present in juvenile then overturned and concealed by adult cardinal process, formed by recurved calcite sheets partly enveloping dorsal umbo and septalium; crura simple raduliform, sometimes depressed in cross section; teeth and sockets smooth. *Middle Jurassic (?upper Bathonian, Callovian):* Tunisia, Somalia, Ethiopia, Kenya, Sinai, Syria, Oman, ?Iran, ?Madagascar, ?Lebanon.——FIG. 928*a–b*. **S. azaisi* (COTTREAU), ?Callovian (rather than Kimmeridgian), Somalia; *a,* dorsal view, BMNH B.46235, ×1 (Feldman, 1987); *b,* holotype, sagittal section, Harrar, Ethiopia, MNHN, ×1 (Cottreau, 1925). ——FIG. 928*c–v. S. numidiensis* MANCEÑIDO & WALLEY, Callovian, Tunisia; *c–g,* holotype, dorsal, lateral, anterior, ventral, posterior views, BMNH BB.76530, ×1; *h–m,* paratype, transverse serial sections extending from 0.0 to 3.5 mm from ventral umbo; *n–v,* paratype, distances in mm from ventral umbo, 3.1, 4.7, 7.2, 8.8, 10.2, 11.8, 12.8, 14.2, 15.0 (Manceñido & Walley, 1979).

Heteromychus COOPER, 1989, p. 41–42 [**H. magnificus;* OD]. Large, oval, subequibiconvex, uniplicate, with median sulcus shallow and dorsal fold low, ill-defined; steep, rounded lateral slopes; beak small, closely appressed on dorsal umbo; lateral planareas present; fully costate, with numerous, dense, blunt costae. Long, strong dental plates, ventral median septum not developed, or just a ridge in adult; with dorsal median septum long, septalium small, shallow, and cardinal process large, backward growing. [Sections remarkably similar to those of young *S. numidiensis;* kept as separate genus on COOPER's claim of its being adult but lacking ventral median septum; otherwise it might be a subgenus or immature form of *Septirhynchia.* Family reallocation based on this reinterpretation.] *Middle Jurassic (upper Bathonian–Callovian):* Saudi Arabia, ?Africa.——FIG. 929,*1a–v.* **H. magnificus,* Saudi Arabia; *a–c,* holotype, dorsal, lateral, posterior views, USNM 380576, ×1; *d–v,* transverse serial sections, distances in mm from ventral umbo, 0.4, 1.3, 1.9, 2.1, 2.5, 3.4, 3.7, 4.0, 4.2, 4.4, 4.6, 4.9, 5.3, 5.6, 6.1, 6.5, 7.3, 8.1, 8.4, USNM 380655 (Cooper, 1989).

Lessinirhynchia VÖRÖS, 1995, p. 55, *nom. nov. pro Lessiniella* VÖRÖS, 1993, p. 52, *non* PAVAN, 1941, Insecta [**Lessiniella benettii* VÖRÖS, 1993, p. 53; OD]. Large, equibiconvex, strongly gibbose, pyriform; umbones massive, beaks strongly incurved; dorsal fold and ventral sulcus weak, anterior commissure round uniplicate to parasulcate; planareas well developed; deltidial plates fused. Dental plates and pedicle collar present; cardinal process formed by bladelike extension of dorsal umbo; septalium slightly overturned; dorsal median septum well developed, long; crura raduliform, crural bases emerge dorsally; teeth and sockets crenulated; ventral median septum absent. *Middle Jurassic (Callovian):* southern Alps (northern Italy).——FIG. 929,*2a–o.* **L. benettii* (VÖRÖS), Verona; *a–d,* holotype, dorsal, lateral, posterior, ventral views, MFLV CC100 Cv-B, ×1; *e–o,* paratype, transverse serial sections, distances in mm from ventral umbo, 4.7, 6.4, 7.9, 8.2, 8.8, 9.1, 9.5, 10.8, 11.4, 12.2, 13.2, MFLV CC99 Cv-B (Vörös, 1993).

UNCERTAIN

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Superfamily UNCERTAIN

Barzellinia DE GREGORIO, 1930b, p. 8 [**B. primogenita;* M]. Shell tumid, equilateral, rounded, equibiconvex, terebratuliform; ornamented with very fine, radial, equidistant striae; ventral umbo very small, incurved. [This genus has been regarded as a subjective synonym of *Halorella* BITTNER, 1884, p. 107, yet it seems advisable to stress its uncertain systematic affinities.] ?*Upper Triassic* or *?Lower Jurassic:* Italy (Sicily).——FIG. 930,*5a–d.* **B. primogenita;* dorsal, lateral, anterior, ventral views, ×1 (de Gregorio, 1930b).

Isjuminelina MAKRIDIN in SARYCHEVA, 1960, p. 254 [**Rhynchonella pseudodecorata* ROLLIER, 1917, p. 139, *sensu* MAKRIDIN, 1964, p. 176, *non* ROLLIER, 1917; =*Isjuminella isjumica* MAKRIDIN, 1955, facing p. 86, fig. 4] [=*Isjuminella* MAKRIDIN, 1955, p. 85, *partim*]. Rounded-pentagonal, medium size with costae radial; sulcus and fold not strong. Median dorsal septum high, comparably short, strongly fused with massive crural bases, pseudodeltidium possibly present; crura very short, thick, hook shaped, sometimes with disjunct septalium; hinge teeth large, crenulated, on very short thick dental plates, fused to valve almost along its whole length; teeth sockets deep with strong crenulations, delimited by massive, almost parallel inner socket ridges. Muscle scars occupying about one-third inner surface of dorsal valve; anterior adductors deep, transverse-elongated or semioval, converging to anterior part of septum; ventral muscle scars pear shaped, wide, occupying one-half its inner surface. [Family allocation has been dependent upon dual interpretation of misidentified type species. Preferred action for stability is to fix taxonomic species actually involved in the misidentification under ICZN, 1999, Article 70.30.2. This would allow inclusion among

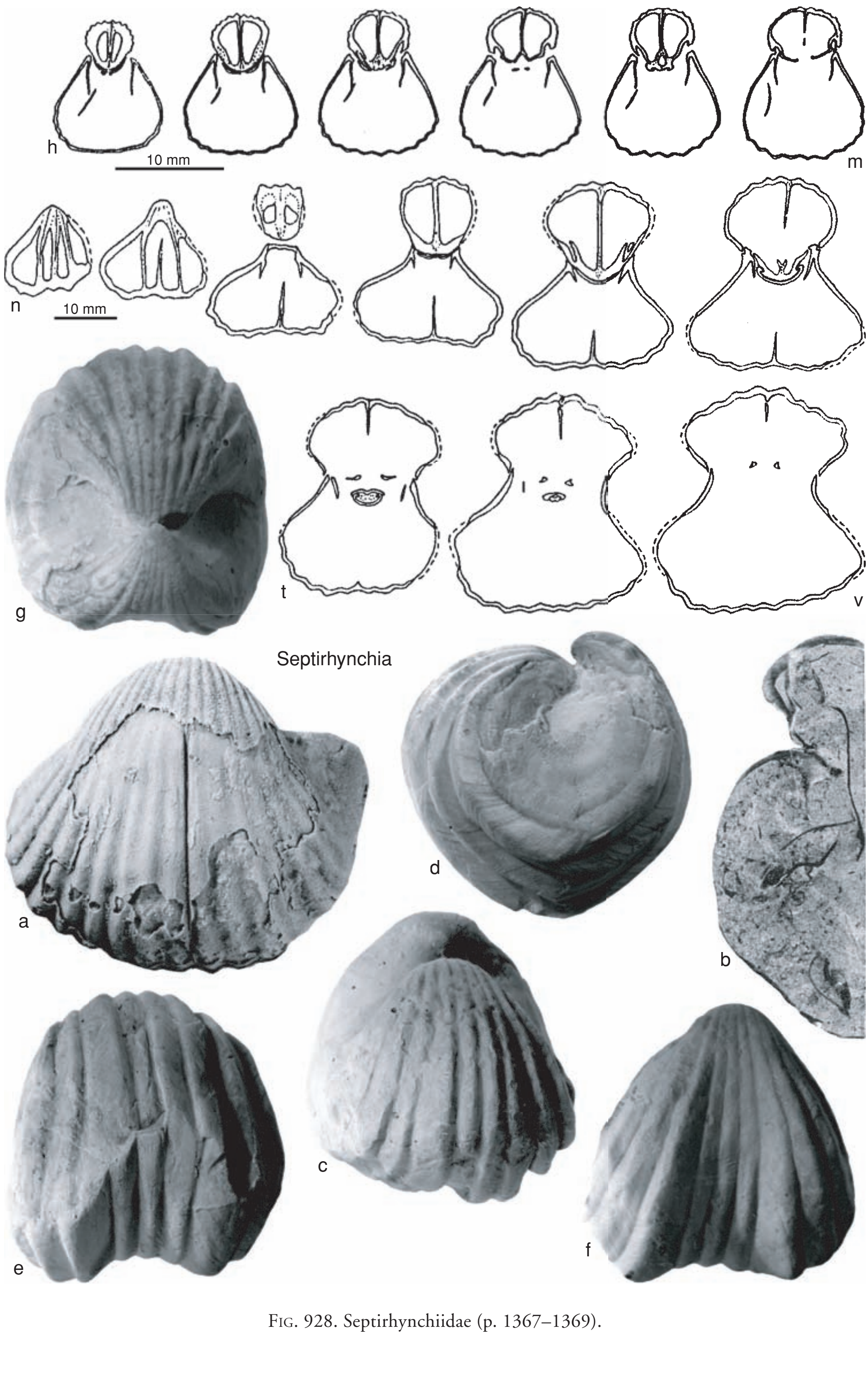

FIG. 928. Septirhynchiidae (p. 1367–1369).

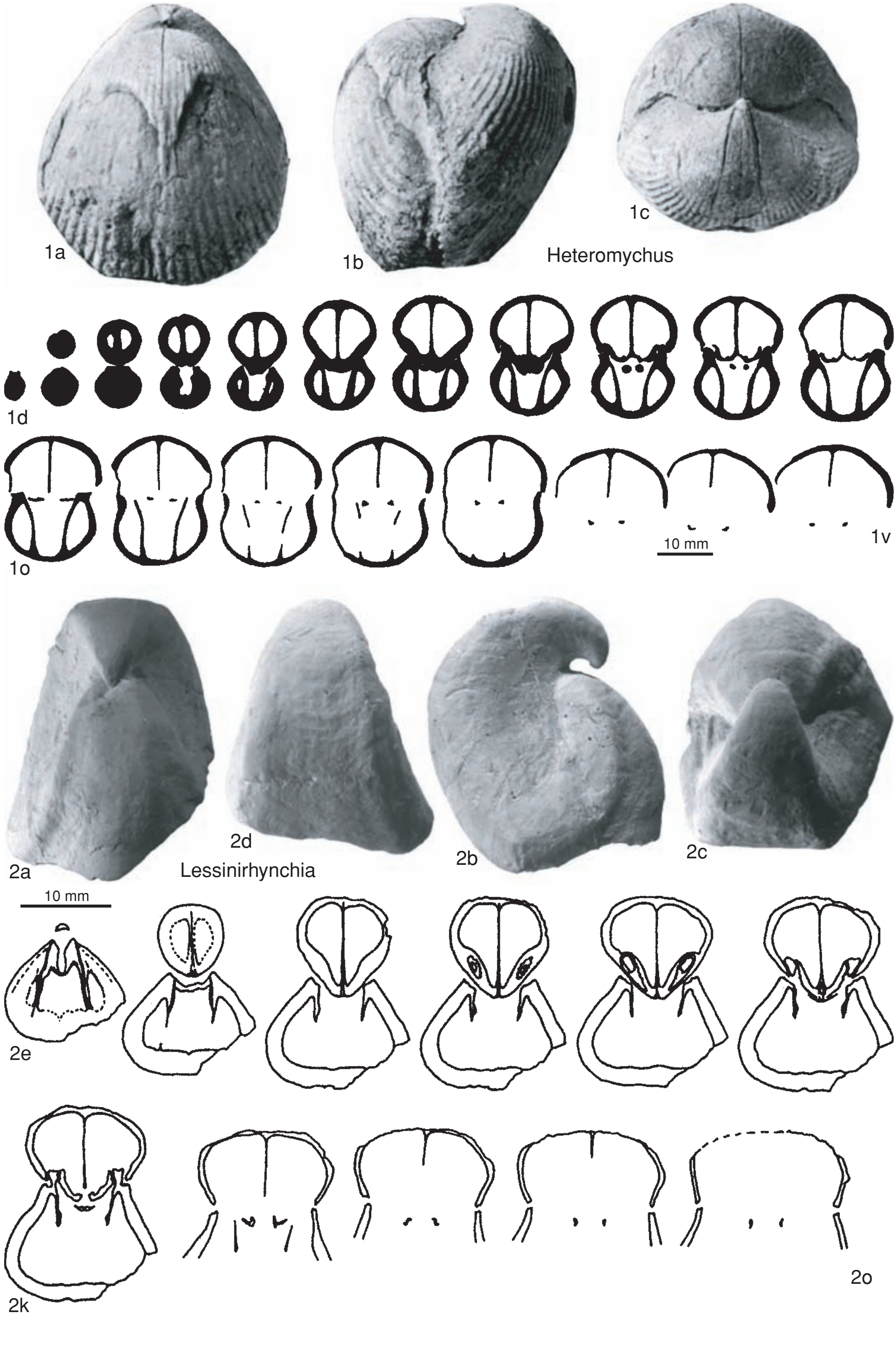

FIG. 929. Septirhynchiidae (p. 1369).

Isjuminellinae.] *Upper Jurassic (Oxfordian):* Europe, Russia (Donetz basin, ?Crimea ?Caucasus).——FIG. 930,*4a–c.* **I. isjumica* (MAKRIDIN), upper Oxfordian, Kharkov, Russia; dorsal, lateral, anterior views, ×1 (Makridin, 1964).

Sacothyropsis CHEN & others, 1986, p. 76 [**S. jiangdaensis;* OD]. Small, elongate, rounded triangular, moderately dorsibiconvex, smooth; thickest just beyond midlength, widest anteriorly; carinate ventral valve; ventral beak small, incurved; foramen permesothyrid; beak ridges angular; anterior commissure plicosulcate; dorsal sulcus shallow, widening anteriorly and split by blunt median fold. Pedicle collar present; hinge plates divided, extending horizontally; dental plates, septum, and septalium absent. [Originally referred to Zeilleriidae, *Sacothyropsis* was regarded by SUN as a *nomen dubium,* with possible affinities to Norellidae.] *Upper Triassic:* Tibet.——FIG. 930,*3a–i.* **S. jiangdaensis; a–d,* holotype, dorsal, lateral, anterior, ventral views, CIGMR SC 248, ×2; *e–i,* transverse serial sections, distances in mm from ventral umbo, 0.4, 0.7, 1.0, 1.7, 2.2 (Chen & others, 1986).

Yunshannella LI & GU, 1982, p. 54 [**Y. triphylla;* OD] [=*Yunshanella* LI & GU, 1982, p. 57, *nom. null.; Yunnshanella* SHI & GRANT, 1993, p. 18, *nom. null.*]. Shell medium size; nearly flabelliform in outline; apical angle about 90°; feebly biconvex in profile; fold low, sulcus shallow; plicae rounded and ornamented with dense, radial, elongate, thin tubercles; other characters as in *Septaliphoria.* [Genus based on inadequate material, thus almost unrecognizable; uncertain if alleged tubercles are indeed diagnostic shell microtexture or an artifact; age originally referred to Callovian–Oxfordian, but now considered as Lower Cretaceous; presently regarded by SUN as a *nomen dubium.*] *Lower Cretaceous:* northeastern China.——FIG. 930,*2a–b.* **Y. triphylla,* Lower Cretaceous (rather than Callovian or Oxfordian), Heilongjiang; *a,* paratype, dorsal view, SIGM MBr 77009, ×2; *b,* holotype, ventral view, SIGM MBr 81009, ×1 (Li & Gu, 1982).

NOMINA DUBIA

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NOMINA DUBIA

The following genera are considered *nomina dubia,* in most instances because the type material is insufficiently well preserved or insufficiently well described to warrant generic status at this time.

Ancorhynchia JIN & YE, 1979, p. 101 [**A. madoensis;* OD]. [Poor description and poor figures. Best considered *nomen dubium* until better data available.] *Upper Permian (Changhsingian):* China.

Areella ERLANGER, 1992, p. 51 [**A. burunica;* OD]. [Poor photographs. Single, very poor interior section. Best considered *nomen dubium* until additional data available.] *Lower Devonian (Emsian):* Mongolia.

Asiarhynchia SU, 1980, p. 294 [**Zlichorhynchus asiaticus* HAMADA, 1971, p. 63; OD]. [Poor material and single schematic section. Best considered *nomen dubium* until additional data available.] *Lower Devonian (Emsian):* northern China.

Beichuanella CHEN, 1978a, p. 338 [**B. uniplicata* CHEN, 1978a, p. 339; OD]. [HOU Hong-fei (unpublished manuscript, 1992) stated that CHEN (1978a) misassigned the type species to Stenoscismatacea, mistaking callus for spondylium and septalium for camarophorium. HOU Hong-fei recommended restudy of type specimens and states that it is a doubtful genus. See also p. 1223 herein.] *Middle Devonian (Eifelian):* China.

Beichuanrhynchus CHEN, 1990, p. 7 [**Kwangsirhynchus beichuanensis* CHEN, 1979, p. 7; OD]. Shell small, subpentagonal, strongly biconvex; strong fold and sulcus anteriorly; pronounced, rounded tongue; costae simple, restricted to anterior half of shell; dental plates short, merge with shell wall; hinge plates divided; median septum, septalium, cardinal process absent; crura unknown. [Poor photographs and poor sections. Best considered *nomem dubium.*] *Lower Devonian:* China.

Borealirhynchia SU, 1976, p. 194 [**B. delerensis;* OD]. Medium to large with outline subtriangular to subpentagonal; moderately biconvex with lateral and anterior margins not vertical; beak suberect; fold and sulcus strong, arising at umbones; anterior commissure uniplicate, high; plicae strong, extending from umbones, covering flanks as well as fold and sulcus; dental plates long, strong; ventral muscle field broad, lachrymal outline; dorsal median septum strong, extending about one-third valve length; septalium absent. [Poor material and sections. Best considered *nomen dubium* at present. Assigned to Uncinulidae by SU, 1976, p. 191, but to Trigonirhynchiidae by SU, 1980, p. 295, and to Camarotoechiidae in translation sent to SAVAGE by SU (1990).] *Lower Devonian (Lochkovian–Emsian):* northern China.

Camarotoechioides RZHONSNITSKAIA, 1978, p. 178 [**Camarotoechia lazutkini* RZHONSNITSKAIA, 1955, p. 246; OD]. [Poor figures. No internal information, no sections. Best considered *nomen dubium.*] *Lower Devonian:* central Asia.

Chivatschella ZAVODOWSKY, 1968, p. 125 [**C. orotchensis;* OD]. [The material is unlikely to be adequate to justify diagnosis of a new genus. Best considered *nomen dubium.* Assigned to Wellerellidae

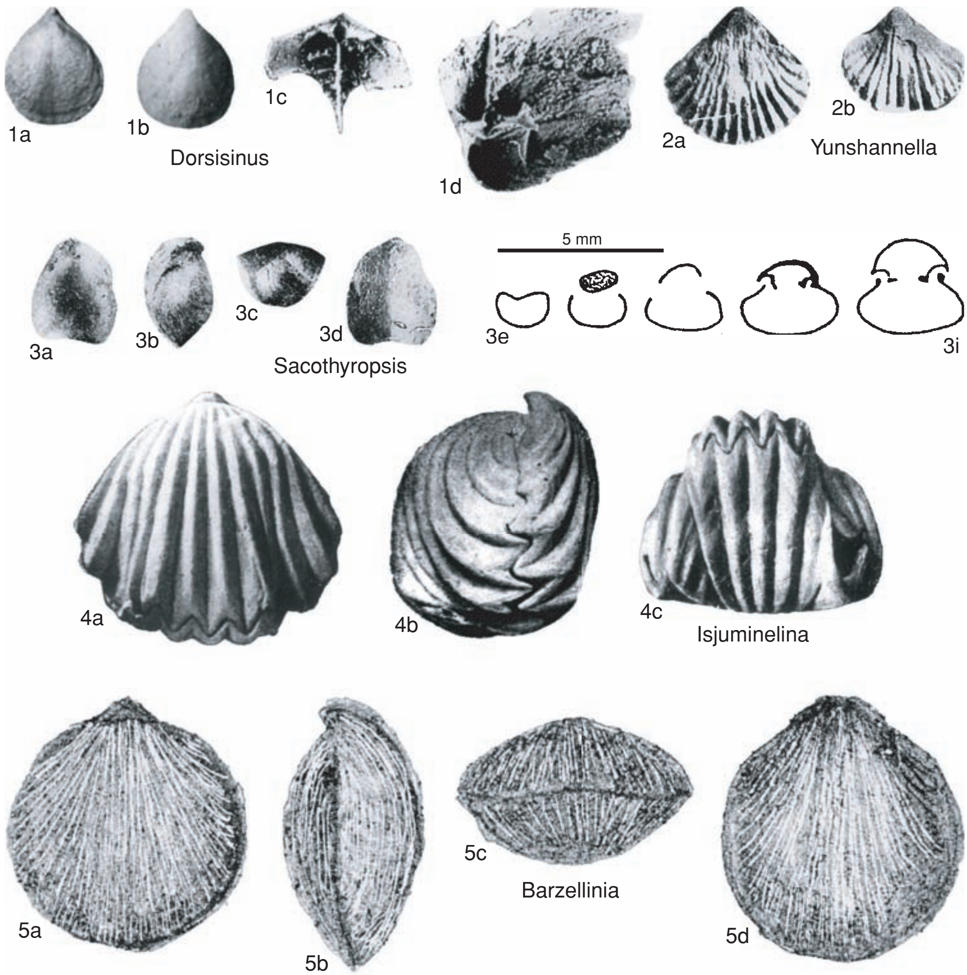

FIG. 930. Uncertain (p. 1369–1373).

by ZAVODOWSKY, 1968, p. 125.] *Upper Permian:* northeastern Asia.

Corrugatimediorostrum SARTENAER, 1970a, p. 23 [**Terebratula rocky-montana* MARCOU, 1858, p. 50; OD]. [Holotype poorly illustrated and interior uncertain, therefore difficult to assign to family or genus. Best considered *nomen dubium.*] *Upper Carboniferous (Westphalian):* North America.

Donella ROTAI, 1931, p. 21 [**D. minima;* OD]. Shell small; outline rounded, elongate oval; dorsibiconvex, dorsal valve slightly inflated anteriorly; beak erect; foramen closed by dorsal beak; fold and sulcus weak, broad, with short sinus in anterior part of fold, otherwise surface smooth. [Based on few specimens. No interior figures or sections. Best considered *nomen dubium.* Assigned to Pugnacidae in 1965 *Treatise.*] *Lower Carboniferous:* central Asia.

Dorsisinus SANDERS, 1958, p. 53 [**Centronella louisianensis* WELLER, 1914, p. 241; OD]. Shell very small with outline elongate oval and profile equibiconvex. Beak straight to suberect; delthyrium triangular, incipient deltidial plates present anteriorly, leaving small foramen. Ventral fold and dorsal sulcus gentle, from umbones, anterior commissure sulcate. Shell surface smooth. Dental plates vertical, moderately long. Septalium short; hinge plates divided; dorsal median septum high, extending to midlength; crura long. [Insufficient material to justify new genus or to determine superfamily. Internal information poor. Best considered *nomen dubium.*] *Lower Carboniferous (Tournaisian):* USA (Mississippi Valley), Mexico.——FIG. 930,*1a–d.* **D. louisianensis* (WELLER); *a–b,* dorsal and ventral views, Kinderhookian, Louisiana Limestone, USA, ×4 (Weller, 1914); *c,* dorsal valve interior, lower Mississippian, Sonora, Mexico, ×3; *d,* interior of conjoined posterior fragment, lower Mississippian, Sonora, Mexico, ×4 (Sanders, 1958).

Ferganotoechia RZHONSNITSKAIA in RZHONSNITSKAIA, KULIKOVA, & PETROSYAN, 1978, p. 68

[**Camerotoechia (?) ferganica* NALIVKIN, 1930b, p. 72; OD]. [Mentioned by RZHONSNITSKAIA as new genus based on *C. (?) ferganica* but not described. Original photographs of NALIVKIN inadequate for type species; also there are no internals or sections. Best considered *nomen dubium.*] *Lower Devonian–Middle Devonian:* central Asia, Urals.

Globidorsum JIN, 1988, p. 215 [*G. basale;* OD]. [No interior figures. Only single specimen figured to show exterior. Best considered *nomen dubium* until additional data available.] *Middle Devonian (Eifelian):* southern China.

Glyptorhynchia SHEN & HE, 1994, p. 452 [**G. lens;* OD]. [Poor figures. Few specimens. May not be rhynchonellid. Best considered *nomen dubium* until adequate description and information about interiors is available.] *Upper Permian (Changhsingian):* southern China.

Hypoleiorhynchus LINNIK, 1976, p. 64 [**Hypothyridina (?) schelonica* NALIVKIN, 1941, p. 163; OD]. [Need topotype material for sectioning because published sections very inadequate. Interiors unknown. Best considered *nomen dubium* until better data available.] *Upper Devonian (Frasnian):* Belorus, European Russia.

Langkawia HAMADA, 1969b, p. 261 [**L. jonesae;* OD]. [Poor mold material comprising only 2 dorsal valves, poorly described and figured. Best considered *nomen dubium* until more data available. Assigned to Camarotoechiidae by HAMADA, 1969b, p. 260.] *Upper Devonian or Lower Carboniferous:* Malay Peninsula.

Laosia MANSUY, 1913, p. 83 [**L. dussaulti;* OD]. [No sections or other internal figures have been published. Best regarded as *nomen dubium.* Assigned to family Uncertain in 1965 *Treatise* (MOORE, 1965).] *Permian:* Indo-China.

Leiorhynchoides DOVGAL, 1953, p. 140 [**L. gratianovae;* OD]. [No sections or other internal figures have been published. Best regarded as *nomen dubium.* Assigned to family Uncertain in 1965 *Treatise* (MOORE, 1965).] *Middle Devonian:* Altai.

Linxiangxiella YANG, 1984, p. 230 [**L. typica;* OD]. [Poor photographs. Only 2 transverse sections. May not be rhynchonellid. Best considered *nomen dubium* until more data available. Assigned to family Uncertain by YANG, 1984, p. 230, but assigned to Hypothyridininae by YANG in English translation sent in letter. Does not seem to be a genus of Uncinulinae or Uncinulidae.] *Upper Devonian (Famennian):* southern China.

Miaohuangrhynchus YANG in YANG & others, 1977, p. 374 [**M. uncinuliformis;* OD]. Small; foramen small, circular; marginal spines not evident; dental plates perhaps close to shell walls; septalium perhaps not present; hinge plate may be divided; dorsal median septum short, possibly stout; cardinal process may be absent. [Poor photographs; only single poor quality transverse section; no reliable information about internal features; best considered *nomen dubium* until more data available;assigned to Rhynchotrematidae by YANG (YANG & others, 1977, p. 374).] *Lower Devonian (Emsian):* southern China.

Mongolirhynchia HOU & ZHAO, 1976, p. 191 [**M. delitescens;* OD]. [Poor photographs. No figures of interior of type species. Descriptions based on interior of different species (*M. simplex*) from different formation and different region (West Qinling, FU, 1983b). Best considered *nomen dubium* until better data available to justify genus status. Assigned to Uncinulidae (HOU & ZHAO, 1976, p. 191).] *Silurian (Ludlow–Přídolí):* Mongolia, northern China.

Nantanella GRABAU, 1936, p. 70 [**N. mapingensis;* OD]. [Poor photographs and section. Assigned to Stenoscismatacea by GRABAU, 1936, and by TONG, 1978. Regard as *nomen dubium* until better data available, otherwise as Stenoscismatoidea. Assigned to family Uncertain in 1965 *Treatise* (MOORE, 1965).] *Lower Permian:* China.

Neimongolella ZHANG Yan, 1981a, p. 385 [**N. paraplicata;* OD]. Shell medium size; weakly biconvex; foramen present; fold and sulcus very weak; anterior commissure almost rectimarginate; straight plications extending from beak to commissure; dental plates straight, vertical, distinct; septalium perhaps absent; hinge plates may be divided; dorsal septum absent; cardinal process may be absent; crura long, laterally flattened. [Photographs and sections quite good but HOU Hong-fei (unpublished manuscript, 1993) stated: "*Neimongolella* is similar to *Kwangsirhynchus* HOU & XIAN, 1975, . . . because specimens of *Neimongolella* are too few and have been poorly preserved, it is not enough that has been established a new genus at condition. Thus, *Neimongolella* should be abandoned and to have assigned in *nomen dubium.*" Because of this it seems best to consider the genus a *nomen dubium* until better data available or (less acceptably) as a synonym of the coeval *Kwangsirhunchus.* Assigned to Pugnacidae by ZHANG Yan, 1981a, p. 385.] *Lower Devonian (Emsian):* northern China.

Paratetratomia YANG in YANG & others, 1977, p. 394 [**P. xiangzhouensis;* OD]. [Poor photographs. Only single poor transverse section. Genus not used. Best considered *nomen dubium* until better data available. Assigned to family Uncertain by YANG in YANG & others, 1977, p. 394.] *Middle Devonian (Givetian):* southern China.

Paryphorhynchopora SIMORIN, 1956, p. 245 [**Pugnoides korsakpaica* NALIVKIN, 1937, p. 77; OD]. Size medium; outline subpentagonal; dorsibiconvex profile with inflated anterior; beak suberect; anterior commissure uniplicate, high, rounded; plicae angular, from umbones; shell surface with radial striae; dental plates present; septalium deep, V-shaped; dorsal median septum short. [Good photographs but no interior figures. Genus name appears to have been ignored. It is not listed in Russian treatise (ORLOV, 1960), nor in 1965 *Treatise* (MOORE, 1965). No references apart from original publication of SIMORIN. Best considered *nomen dubium* until better internal data available.] *Lower Carboniferous (Tournaisian):* Kazakhstan.

Payuella GRABAU, 1934, p. 150 [**P. obscura;* OD]. [Seems that genus name not used except in original publication of GRABAU. Only holotype figured. No description or figures of interior. Best considered a *nomen dubium* until better data available. Assigned to family Uncertain in 1965 *Treatise* (MOORE, 1965).] *Lower Permian:* southern China.

Perakia HAMADA, 1969a, p. 7 [**P. undulata;* OD]. [Type material poorly preserved and insufficient for generic or even superfamily assignment. Best considered *nomen dubium* until better data available.] *Lower Devonian–Middle Devonian (Emsian–Eifelian):* Malaya.

Platyglossariorhynchus SARTENAER, 1970a, p. 8 [**Pugnax proteus* TORLEY, 1934, p. 73; OD]. [Exterior photographs of TORLEY (1934) suitable but interior features unknown. Only reference seems to be original publication of SARTENAER, 1970a, who stated interior imperfectly known and did not provide sections or other figures. Best considered *nomen dubium* until better data available.] *Middle Devonian (middle Givetian–upper Givetian):* Germany, North America.

Plekonina WATERHOUSE, 1986a, p. 65 [**P. spissatella;* OD]. [Material insufficiently figured for genus description. Only 2 views of crushed holotype. Interior unknown. Best considered *nomen dubium* until better data available. Assigned to Wellerellidae by WATERHOUSE, 1986a, p. 64.] *Upper Carboniferous* or *Lower Permian:* Dresden Formation, eastern Australia (Bowen Basin, Queensland).

Protorhyncha HALL & CLARKE, 1893, p. 180 [**Atrypa dubia* HALL, 1947, p. 21; OD]. [Probably not a rhynchonellid (see COOPER, 1956a, p. 618, also 1965 *Treatise* [MOORE, 1965], p. 597). Types lost. Interior unknown. Best considered *nomen dubium* until better data available.] *Ordovician (Cham plainian):* eastern USA (New York).

Pseudopugnax LICHAREW, 1956, p. 56 [**P. planissima;* OD]. [Poor exterior photographs. Poor sections. Surface appears to be weakly costate or even spinose. Cannot be placed into superfamily. Genus name used in original publication in 1956 but no other use since then. Best considered *nomen dubium* until better data available. Assigned to Septalariinae in 1965 *Treatise* (MOORE, 1965) but occurs in Upper Permian, whereas there are no known septalariids after Devonian.] *Upper Permian:* northern Caucasus.

Pugnacina ZUONG & RZHONSNITSKAIA in ZUONG & RZHONSNITSKAIA & others, 1968, p. 43 [**P. baoi;* OD]. [Only single specimen (holotype) figured showing exterior. No interiors figured. No basis for erecting new genus. Best considered *nomen dubium* until additional data available. Assigned to Uncinulidae by ZUONG and RZHONSNITSKAIA, 1968, p. 41.] *?Lower Devonian, ?Middle Devonian (?lower Eifelian):* Vietnam.

Rhynchotretaoides SEVERGINA, 1967, p. 136 [**R. aincus;* OD]. [SEVERGINA (1967, p. 136–137) described and illustrated the exterior of the type species. No illustrations of interior then or subsequently. ROZMAN (1981, p. 158) illustrated interior of species he called *Rhynchotretaoides bairimicus* sp. nov. There is no way to decide whether this is same genus without interior information of type species. Best treated as *nomen dubium* until more information available.] *Upper Ordovician:* central Asia.

Rhynchotretina KHALFIN, 1948, p. 175 [**R. aequivalvis;* OD]. Small, outline subtriangular elongate with angle acute apical; almost equibiconvex; fold or sulcus absent; rectimarginate; beak short, straight; plicae weak, from midlength; dental plates short, convergent ventrally; septalium may be absent; hinge plates may be divided; dorsal median septum long. [Letter from GRATSIANOVA (March 16, 1994) said she is is sure this genus is invalid because of insufficient material—KHALFIN had only 2 conjoined shells, 1 of which was broken posteriorly and what was left of it was used for the few serials sections. The other is the holotype. Regard it as a *nomen dubium.* Assigned to Camarotoechiinae in 1965 *Treatise (*MOORE, 1965).] *Lower Devonian:* Altai.

Rhynoleichus ABRAMOV & GRIGORJEWA, 1983, p. 95 [**R. delenjaensis;* OD]. Medium to large, subpentagonal to transversely ovate; dorsibiconvex with lateral and anterior slopes gentle; beak erect; fold and sulcus very wide; anterior commissure uniplicate, rounded, very wide, resulting in narrow alate flanks; plicae wide, rounded, weak on fold and sulcus, very weak on flanks; dental plates very short, strongly divergent ventrally; septalium short; hinge plates divided; dorsal median septum short, low. [Only 7 specimens total assigned to type species, only 3 poorly preserved specimens from type locality. Serial sections poor. Similar to Leiorhynchoidea, but material too poor to determine features. Best treated as *nomen dubium* at present.] *Upper Carboniferous:* Taimyr, Russia.

Salairotoechia RZHONSNITSKAIA, 1968d, p. 123 [**Nudirostra? pseudocarens* KULKOV, 1960, p. 174; OD]. [No figures of interior of type species. Not enough information to warrant new genus. Best treated as *nomen dubium* at present.] *Middle Devonian (Eifelian):* Kuznets Basin.

Sichuanrhynchus TONG, 1978, p. 243 [**S. sulcatus;* OD]. Shell small to medium; subpentagonal to subcircular; strongly inflated and subtetrahedral; beak incurved; fold and sulcus strong; uniplicate tongue; surface smooth; interior uncertain. [No figures of interiors. Best treated as *nomen dubium* at present.] *Upper Carboniferous:* southern China.

Straelenia MAILLIEUX, 1935, p. 10 [**Rhynchonella Dunensis* DREVERMANN, 1902, p. 108; OD; =*Rhynchonella Dannenbergi* KAYSER *mut. nov. minor* DREVERMANN, 1902, p. 107] [=*Dinapophysia* MAILLIEUX, 1935, p. 5 (type, *Orthis papilio* KRANTZ, 1857, p. 156, OD)]. [Material poorly preserved. Could be genus of Camarotoechioidea. Need fuller description and better topotype specimens. Probably best treated as *nomen dubium* until additional work done.] *Lower Devonian (Emsian):* western Europe, northern Africa.

Tanerhynchia ALLAN, 1947a, p. 442 [**Eatonia parki* ALLAN, 1935, p. 22; OD]. Genus poorly known; size medium, outline transversely subcircular; profile weakly biconvex; dorsal fold and ventral sulcus weak posteriorly, moderately strong anteriorly; costae poorly known, appearing simple and low; dental plates not evident; ventral muscle area weakly impressed, myophragm weak; dorsal median septum short and stout; cardinal process with erect shaft and rugose myophore. [Type material inadequate to base new genus. Probably belongs to Eatoniidae. Best treated as *nomen dubium* until better material described.] *Lower Devonian (Emsian):* New Zealand, Antarctica.

Togaella SEVERGINA, 1960b, p. 409 [**T. grandis;* OD]. [Poor material. Unless better topotype material becomes available, best regarded as a *nomen dubium.* Also see KULKOV & SEVERGINA, 1989, for additional (poor) illustrations of internal and external molds; they assigned the genus to the Rhynchotrematidae.] *Ordovician:* Altai, Mongolia.

Trilobatoechia XIAN, 1990, p. 44 [**T. daxinensis;* OD]. [Poor material, no sections. Unless better topotype material becomes available, best regarded as a *nomen dubium.*] *Lower Devonian (Emsian):* southern China.

Uralotoechia SAPELNIKOV, 1963b, p. 17 [**U. vagranensis;* OD]. [Assigned to Hypothyridinidae by SAPELNIKOV, 1963b, p. 17 but seems an unlikely age for members of that group. Photographs and sections not adequate to warrant new genus. Probably best regarded as *nomen dubium* until new topotype sections available.] *Silurian (upper Ludlow):* Northern Urals.

Wulungguia ZHANG Yan, 1981b, p. 91 [**W. wulungguensis;* OD]. Outline elongate; margins of fold and sulcus sudden; dental plates very short; septalium very short, without cover. [Assigned to Rhynchotrematidae in ZHANG Chuan & ZHANG Zi-Xin, 1981, p. 90, but to Trigonirhynchiidae in an English translation of unknown origin. This genus is poorly described and figured and seems best treated as *nomen dubium* until better topotype material is described.] *Upper Ordovician:* China.

Yanbianella TONG, 1978, p. 238 [**Y. dorsiconvexa;* OD]. Size small; outline transversely subovate; moderately biconvex; ventral beak erect to incurved; costae strong anteriorly, umbones smooth; short septalium without cover. [Assigned to Trigonirhynchiidae by TONG, 1978, p. 239. Photographs and sections of type material very poor.] *Carboniferous:* southern China.

Yarirhynchia JIN & SUN, 1981, p. 147 [**Y. concava;* OD]. Very small; outline subcircular; profile weakly biconvex; fold and sulcus not evident; short septalium without cover. [Assigned to Trigonirhynchiidae by JIN & SUN, 1981, p. 145. Described and figured material seems inadequate as basis for genus. Best treated as *nomen dubium* until additional data available.] *Lower Carboniferous:* Tibet.

Yingtangella BAI & YING in YOH & BAI, 1978, p. 54 [**Y. sulcatilis* (HOU), 1963, p. 417; OD]. [Assigned to Rhynchoporidae by BAI & YING in YANG & others, 1977, p. 397, *nomen nudum.* Poor illustrations. Inadequate information for new genus. Best treated as *nomen dubium* until more data available. May be terebratulid.] *Lower Devonian:* southern China.

UNAVAILABLE GENERA

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[La Plata Natural Sciences Museum, Argentina; and formerly of The Natural History Museum]

UNAVAILABLE GENERA MENTIONED IN PRINT
(manuscript, nomina nuda, etc.)

Almogilabinella GEORGESCU (in press) in GEORGESCU, 1993, p. 43, with type species *A. almogilabini* GEORGESCU (in press). *Middle Jurassic.*

Crurirhynchella XU & LIU, 1983, p. 83, for "*Crurirhynchia*" *subfissicostata* YANG & XU, 1966, p. 27. [Possibly referable to *Caucasorhynchia* DAGYS, 1963, p. 66]. *Middle Triassic.*

Dingleirhynchia GEORGESCU (in press), in GEORGESCU, 1993, p. 43, with type species *D. dinglei* GEORGESCU (in press). *Middle Jurassic.*

Holcothyroides DAGYS, 1974, p. 89, for *Rhynchonella delicatula* BITTNER, 1890, p. 17 and *Rhynchonella deliciosa* BITTNER, 1890, p. 155. [Probably a *lapsus pro Holcorhynchella* DAGYS, 1974, p. 110.] *Middle Triassic.*

Orbignyrhynchia MICHALÍK, 1992, p. 61 [*nom. null.,* personal communication, 1995]. *Paleogene (Danian).*

Postcirpa SMIRNOVA, 1984, p. 54 [further details unknown; might refer to *Neocirpa* PROZOROVSKAIA, 1985, p. 110].

Septalirhynchia XU & LIU, 1980, p. 37, further in XU & LIU, 1983, p. 83, for "*Septaliphoria*" *tienchungensis* YANG & YIN, 1962, p. 93 and "*S.*" *rhomba* YANG & YIN, 1962, p. 95. [Possibly referable to *Costirhynchopsis* or *Eoseptaliphoria*]. *Middle Triassic.*

Septocrurallia MAKRIDIN, 1954, p. 103. [Further details unknown; might refer to *Praecyclothyris* MAKRIDIN, 1955, p. 84.]

Tuwaiqirhynchia NAZER [1970, unpublished manuscript deposited in a library], p. 45, in ALMÉRAS, 1987, p. 177, with type species *T. arabiensis* NAZER [1970, unpublished manuscript deposited in a library]. [Most likely a synonym of *Conarosia* COOPER, 1989, p. 20.] *Middle Jurassic.*

Vindobonella PEARSON [1967, unpublished manuscript deposited in a library], in SIBLÍK, 1988, p. 51, with type species *V. katzeri* PEARSON [1967, unpublished manuscript deposited in a library; SIBLÍK also mentions "museum labels."] *Upper Triassic* [in need of proper validation].

ATRYPIDA

Paul Copper
[Laurentian University, Ontario, Canada]

INTRODUCTION

Atrypida are articulated brachiopods identified by a pair of medially to dorsally directed spiralia, which are in the form of mirror image, logarithmic spiral cones. They include the oldest known spire-bearing brachiopods.

Spiralia arise from crura along the inner socket ridges, then splay as primary lamellae to the sides of the shell, and are finally coiled anterodorsally into ever thinner and narrower lamellae terminating at the apex of the cone. Their spiralial orientation is diametrically opposed to the inside-out direction that characterizes the Spiriferida and Athyridida, which have laterally to ventrally directed spiralia and are thus assumed to have evolved independently from the ancestral spire-bearing stock(s) in Caradoc and Ashgill times. In complex, derived Siluro-Devonian taxa the spiralial whorls of atrypides increased in number and size until they almost filled the shell interior, becoming D-shaped in outline and dorsomedially to dorsally directed. The major evolutionary trends of the Atrypida are defined by the development of these calcified spiral lophophore supports and the jugum or jugal processes connecting them. They normally possess a jugum (primitive forms) or jugal processes (derived forms), which connect or nearly touch in the midlength of the shell, extending from the primary lamellae of the spiralia toward each other (Fig. 931).

Some common characteristics of the lamellae (whorls) of the spiralia follow.

(1) Primitive types of spiralia have whorls coiled in the plane of symmetry and are medially directed; derived spiralia have cones rotated into a mediodorsal to dorsal direction with the spiral lamellae roughly parallel to the commissural plane or partly tilted toward the plane of symmetry.

(2) The basal parts of the spiralium have the widest and thickest calcite lamellae; the apex, in contrast, has thin and delicate lamellae. (The thickness of lamellae varies from side to center, but lamellar width thins apically.)

(3) The spiral lamellae are thickest on the interior of the cones and thin out to very delicate flanges on the lateral sides of the cones. (Spiral lamellae are not evenly thick in cross section: they are convex dorsally, flat to concave ventrally.)

(4) Apical parts of the spiralium or small spiralia are always circular in plan view.

(5) The connection between the crura and primary lamellae of the spiralia is continuous in primitive Ordovician and Silurian taxa, but generally, in derived Siluro-Devonian taxa, the crura end in a zone of loosely disconnected fibers of calcite (feathery crura), or there may be no calcite connection. (The spiralia presumably were always connected by soft tissue.)

(6) Stratigraphically oldest taxa have small spiralia, with few whorls (fewer than 5 to 8), which may occupy only a portion of the shell; advanced forms have many spiralial whorls (up to about 20) that crowd the expanded dorsal valve interior.

(7) The spiralia in small and primitive shells tend to be circular in plan view; in large shells, the basal coils are commonly D-shaped in plan view or outline so as to face the opposing spiralium and to maximize space within the shell cavity.

(8) Some spiral lamellae appear to have possessed an outer fringe of spines, but in others this is absent.

(9) In some atrypides (glassiids) the medially directed spires are barrel shaped, instead of cone shaped, reaching their maximum whorl diameter in the center of the spire.

(10) In the flat-shelled Davidsoniidae and Carinatinidae, the spiralia form low cones

accommodated in grooves on the opposing ventral valve.

The first definitive atrypide spire bearers are known from lower Caradoc strata, but some forms appear to have been already present in late Llandeilo time. These early forms, with limited spiral coils, were very small shells (less than 5 mm wide) with relatively fine ribs or were partly smooth with simple corrugations. The coils of the spiralium were derived from elongated crura that were extended into the first ascending lamella, then coiled parallel to the plane of symmetry into the center of the shell (in a plane at right angles to the commissural plane). Some appear to have had less than one spiral whorl, and the space taken up by the spiral lamellae inside the shell was limited. The crura in these early shells were directed ventroanteriorly and laterally, then geniculated dorsally. Medially directed spiralia were lost in the later, advanced atrypides (e.g., the suborders Atrypidina, Davidsoniidina, and later Lissatrypidina). Dorsally directed spiral lophophores are developed in living rhynchonellides, but these lack a calcified lophophore support.

Secreting the calcite support of the spiral lophophores of Atrypida required the expenditure of metabolic energy, i.e., the constant secretion and resorption of calcite, for which the atrypides must have paid a price. (The group were the first spire-bearers to die out, although this may have had little or nothing to do with the spiralia.) The mechanism of secretion of the calcite lamellae of the spiralia is disputed. One proposed mechanism consists of a corkscrew system (SAMTLEBEN, 1972, 1975) in which the spiralia were generated around and from the ends of the crura at the base of the spiralium, the oldest part of the calcite spiralium being the tip of the spiralium. The other proposed mechanism, called the mushroom system (MACKINNON, 1991), consists of constant growth from the apex of the spiralium toward the crura, with the apex thus representing the youngest secretion of calcite (the whole spiralium, or at least the apex, is the generative zone in this case). Both systems required simultaneous secretion and resorption of calcite, particularly where the spiralia were large, crowded much of the shell interior, and show a noncircular or D-shaped spiral base. The corkscrew system would have been more efficient, it seems, in the sense that resorption was required only in later ontogenetic stages and only toward the plane of symmetry. The mushroom system required constant secretion at one side and resorption at the other, over the complete length of the spiralium.

The oldest, late Llandeilo to early Caradoc spire-bearing taxa possessed medially directed atrypoid spiralia, with or without a jugum. These are assigned either to the Anazygidina or else to the primitive Lissatrypidina, e.g., the Protozyginae. One subfamily of smooth atrypides, the Late Ordovician Idiospirinae, and one early Silurian lissatrypinid (*Cerasina*), are known to have retained a simple jugum, strikingly also in a primitively dorsal position within the shell. One subfamily, the late Caradoc to Ashgill Cyclospirinae, retained the medially directed spiralia and lacked the jugum; whether this was by loss of a partial jugum or whether this group acquired one only later is not clear. For example, the Ashgill to Llandovery genus *Xysila,* with medially directed spiralia, is a homeomorph of *Cyclospira* but developed a jugum probably by acquisition via *Cyclospira* (or derivation from a *Protozyga* stock with a jugum). The earliest type of jugum, as seen in early Caradoc *Manespira,* arose near the anterior commissure from the ascending lamella of the first spiral whorl. This was developed variably among species: sometimes it did not stretch all the way across to meet the opposing jugal branch and thus was incomplete. In early Caradoc *Anazyga* and *Protozyga,* the complete jugum was a broad band located in an anterior and dorsal position (Fig. 931), and the spiralia were medially directed. By late Caradoc time the genus *Zygospira* had a jugum that had migrated into a medial position in the shell, and the spiralia began to be oriented partially toward the dorsal valve. The last survivors of the

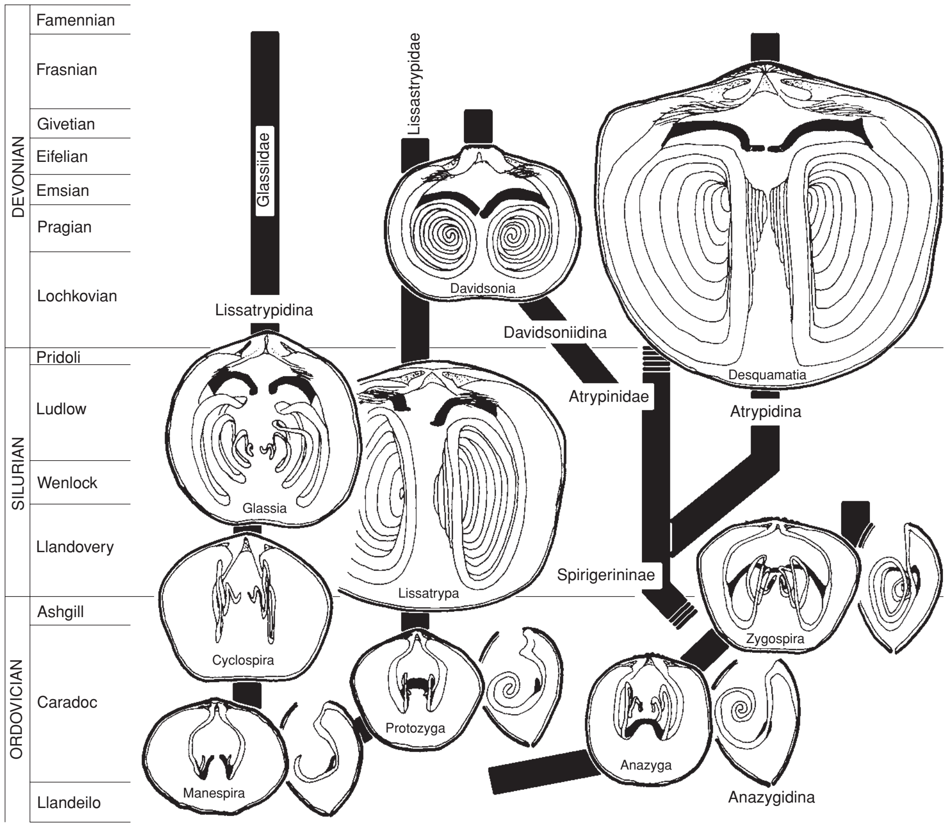

FIG. 931. Generalized evolution of the brachidia in atrypid brachiopods; jugum or jugal processes are shown in *black;* scale variable, approximately ×1.5 to ×4 (new).

anazygines were early Wenlock *Zygatrypa,* in which the jugum had moved almost into a posterior position. The migration of the jugum from an anterodorsal to postero-central position and the eventual loss of a jugum, with replacement by jugal processes, are two key early evolutionary trends. No jugate atrypides are known from the Wenlock onward. Later forms that were said to have had a complete jugum have been inspected and determined to be nonjugate. Even neanic growth stages of large atrypide shells of Siluro-Devonian age have no jugum. Perhaps with enlargement of the spiralia, a complete jugum was liable to breakage in large, adult shells, with separate jugal processes allowing greater flexibility in the spiralia.

The first atrypides to develop separate jugal processes were the subfamily Spirigerininae: these belonged to the Asian and Australian, late Caradoc to Ashgill genus *Sulcatospira,* and related taxa, that evolved jugal processes located in a posterior position more or less in the commissural plane (and which, concomitantly, increased the number of spiral whorls in the spiralia by up to about 50 percent). Such spirigerinid shells are superficially similar to the anazyginids, except that the anterior commissure is plicate instead of sulcate. In Silurian (Wenlock and younger) and Devonian atrypides of the suborders Lissatrypidina, Atrypidina, and Davidsoniidina the jugum was normally split into two separate jugal processes, many of which are curved away from each other in

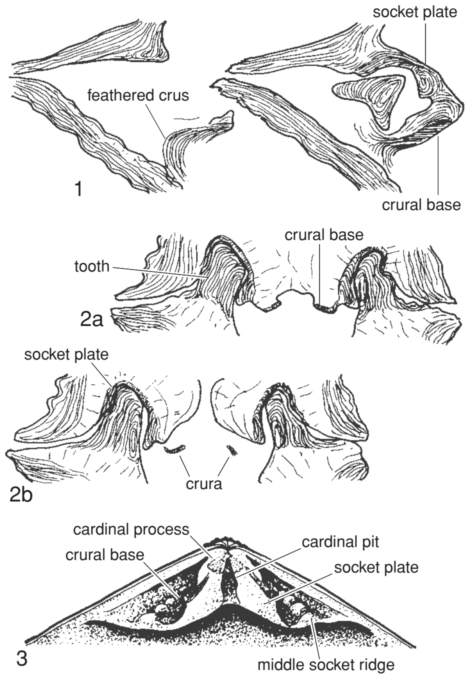

FIG. 932. Crura in Atrypida; *1, Desquamatia (Seratrypa),* variatrypinid; *2a–b, Mimatrypa,* karpinskiinid; *3,* reconstruction of dorsal hinge plate in *Planatrypa* (Eifelian), approximately ×5 (new).

the center of the shell (Fig. 931). The jugal processes, particularly the ends, were the thickest and strongest brachidial structures. In many advanced taxa, the jugal processes terminated in jugal plates consisting of hooklike, half ring, or spoon-shaped structures or a spinose boss. Spines are also a common feature along the jugal processes or the jugal plates in many unrelated Siluro-Devonian genera. The jugal processes were always in a posterior location and either in the commissural plane or toward the ventral valve side. Little is yet known about the details of the jugal processes in many poorly described genera, and new structures are bound to be discovered here.

The jugum and jugal processes of atrypides grew in tandem with the spiralia during ontogeny, suggesting that their growth was coordinated and contained within the same bauplan. The tips of the jugum almost always terminate in the commissural plane (i.e., the plane separating the two valves) and in a central position between the two cones of the spiralia. In advanced forms the position of the jugal processes shifted toward the hinge axis and toward the ventral valve, but this was probably a reflection of the fact that advanced forms often had a more convex dorsal valve to accommodate more spiralial coils. Whether the jugal processes also contained the filaments and cilia of the lophophore is unknown. The lophophorate function of the jugal processes is unclear. Their position within the shell suggests that the jugal ends supported the mouth parts and that food particles were canalized along the spiralial coils toward the base of the spiralium then to the jugum or jugal processes. If so, then the jugal processes or jugum probably were lined with cilia or tentacles, providing an analogue with the lophophorate function of the loop in terebratulides. The terebratulide loop, however, is unlikely to have developed from separated jugal processes that are present in Early Devonian atrypides but may have developed from the complex jugum of Athyridida. Whether the jugal processes also were muscle-attachment sites, permitting some mobility of the spiralia, is equally unclear. Some jugal processes possess spines, but this is a feature also not unknown in the spiral lamellae.

The brachidial apparatus in the Atrypida was connected to the dorsal hinge via the crura. This connection is known as the crural base and was derived from the inner portion of the socket plate, i.e., the inner socket ridges (Fig. 932). The crural bases in early neanic stages are visible and traceable almost from the inner apex of the dorsal valve, even in mature shells where these are buried in later secondary shell fibers. The primary lamellae of the spiralia are continuous from the crural extensions in the earlier atrypide taxa. Commonly there is a groove at the side of the opposing ventral valve to accommodate these lamellae. A typical development in Siluro-Devonian taxa, however, is the distal disintegration of the crura into loose

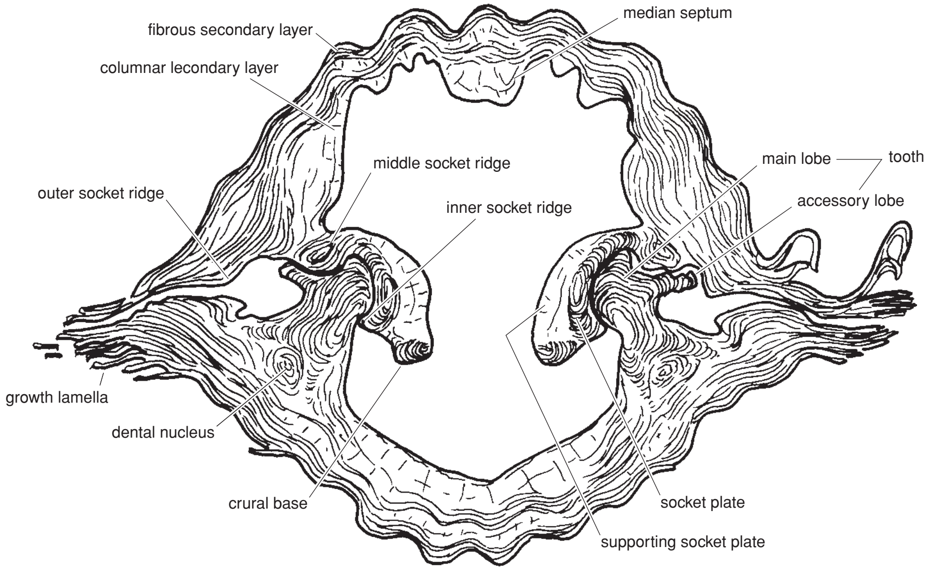

FIG. 933. Serial section view of tooth and socket structures in *Spinatrypa curvirostra* (lower Givetian), demonstrating common features in the Atrypida, approximately ×4 (new).

bunches of calcite fibers with a feathery appearance (COPPER, 1965a). This occurs in the Variatrypinae and Spinatrypinae particularly but also in Silurian Lissatrypinae (COPPER, 1973a). In some atrypides there was therefore no direct or solid connection of the primary lamellae, hence the spiralia, to the socket plate. In fact, in some taxa, the spiralia appear to sit loose in the shell, a feature not recognizably due to breakage. The primary lamellae and jugal processes begin nearly simultaneously as solid, thick structures at the sides of the shell, often with the jugal processes appearing first, a few millimeters away from their initiation in crural fibers. Such features are not known to be present in athyridides or spiriferides, although some Ashgill Hindellinae (Athyridida) also lack any calcite connection between crura and spiralia.

The reasons for the common lack of connection between crura and spiralia in the atrypides are not directly evident. It is possible that this juncture represents the generative zone of the atrypide spiralium. Alternatively, it may represent a structural advantage, providing greater flexibility or maneuverability for large atrypide spiralia and less liability of breakage. It may not be a coincidence that this occurs only in forms that have disconnected jugal processes, possibly indicating that the jugal processes may have been attached to muscles that allowed the spiral lophophores some movement, as in living rhynchonellides. If this is correct, the feathery crura may have evolved simultaneously with splitting of the jugum into two separate processes in the three remaining atrypide suborders. The Anazygidina thus may have become extinct in competition with larger atrypides having more efficient, larger, and flexible lophophores.

The socket plate in atrypides lines the sockets and consists of densely packed fibers of the secondary layer, which acted as a support for the teeth from the opposing valve (Fig. 933). Socket plates may be relatively thin, as in many earlier Ordovician atrypides, in the thin-walled Silurian Septatrypinae, or in some of the Devonian Vagraniininae and Karpinskiinae. In the last two subfamilies the very thin socket plate was supported by the massive, coarsely fibrous secondary layer of the hinge plate. In taxa with thin socket plates the crura were generally also thin and delicate. The middle socket ridge in many later atrypides is composed of a radial row of small knobs that probably constrained the accessory lobes of the teeth; indeed, these seem to be present only in forms that have accessory tooth lobes, which rested on these middle socket ridges. Toward the apex of the shell, the inner socket ridges and the middle part of the cardinal pit were the attachment sites for the diductors. This is evident in the presence of a small cardinal process, which in the atrypides seems to be variably developed, being prominent in gerontic shells but absent in neanic stages. There is little evidence of a cardinal process in the Ordovician Anazygidina, and there is only minimal development of these in many of the Lissatrypidae. The Atrypidina and Davidsoniidina, however, commonly feature a well-developed cardinal process that shows up as a series of striated, often irregular to knoblike or comblike ridges lining the inner socket ridges and cardinal pit. Size of the shell seems to be important: large shells are more likely to have a cardinal process than small shells. Possibly this is related to increasing size and strength of the diductor muscles required in larger shells. As a rule, there is little evidence of secondary shell fibers in the cardinal process; the calcite growths of the cardinal process appear to consist of a granular layer.

Atrypides had an impunctate shell wall with a relatively thin, granular, primary layer underlain by an impunctate secondary layer. No punctate nor pseudopunctate shell wall has been confirmed. One carinatinid subgenus from Novaya Zemlya, *Biconostrophia (Cherkesovaena),* is said to have a pseudopunctate shell (CHERKESOVA, 1980); this needs corroboration. In terms of macroornamentation, Caradoc atrypides had generally small, thin-walled shells that were either finely ribbed or smooth. By Ashgill time, the ribbed atrypides began to develop sharp breaks or growth interruptions in the primary and secondary layers, which ultimately led to growth lamellae freed from the shell surface in Silurian time. As the shell continued to expand in volume, the growth of such lamellae led to expansive frills or spines, especially in Devonian atrypides. The secondary layer consists of bundles of overlapping, flat, bladelike crystals that usually radiate from the shell apex in ribbed shells (Fig. 934). In smooth shells (Lissatrypinae), these radial bundles of secondary fibers tend to be cross layered with bundles that are oblique and nonradiate, especially at the posterolateral shell margins. In *Lissatrypa* the surface calcite fibers may also flex upward, providing the shell surface with concentric layers of fine structures with a spinelike appearance. This is also known in the early Silurian Chinese subgenus *Gracianella (Guangyuania),* where the secondary fibers form curved feathery structures that are evident as concentric ridges on the shell surface. This seems to have reinforced the shell wall and is typical of the smooth forms of atrypides, perhaps with a strengthening function in lieu of the existence of ribs. Early forms of atrypides usually had a thin shell wall, but this was thickened in more advanced taxa and provided additional strength for the shell wall and for muscle attachment.

Atrypides typically lack microornamentation. The shell surface is usually relatively smooth and with scanning magnification (×100 or more) has a granular to pebbly appearance (Fig. 934). Several Silurian and Devonian ribbed atrypide taxa belonging to different subfamilies, however, show highly

FIG. 934. Microornamentation in Atrypida, as seen under SEM; *1,* growth lamellae of upper Llandovery *Gotatrypa hedei* STRUVE, 1966, with only primary layer visible on surface, ×30.6; *2,* growth lamellae of Givetian *Spinatrypa spinosa* (HALL, 1861), showing the granular primary outer layer overlying the fibrous secondary layer, ×151.6; *3,* primary layer of Wenlock *Endrea tubulosa* (BASSETT & COCKS, 1974), showing concentric microfilae, ×22.8; *4,* microfilae and fine radial ornament in primary layer of Ludlow S*pirigerina quinquecostata* (MUNTHE, 1911), ×43; *5a–b,* middle Llandovery *Lissatrypa atheroidea* TWENHOFEL, 1914; *a,* growth interruptions and secondary layer, ×228; *b,* detached fibrous secondary layer at shell margins, ×457 (new).

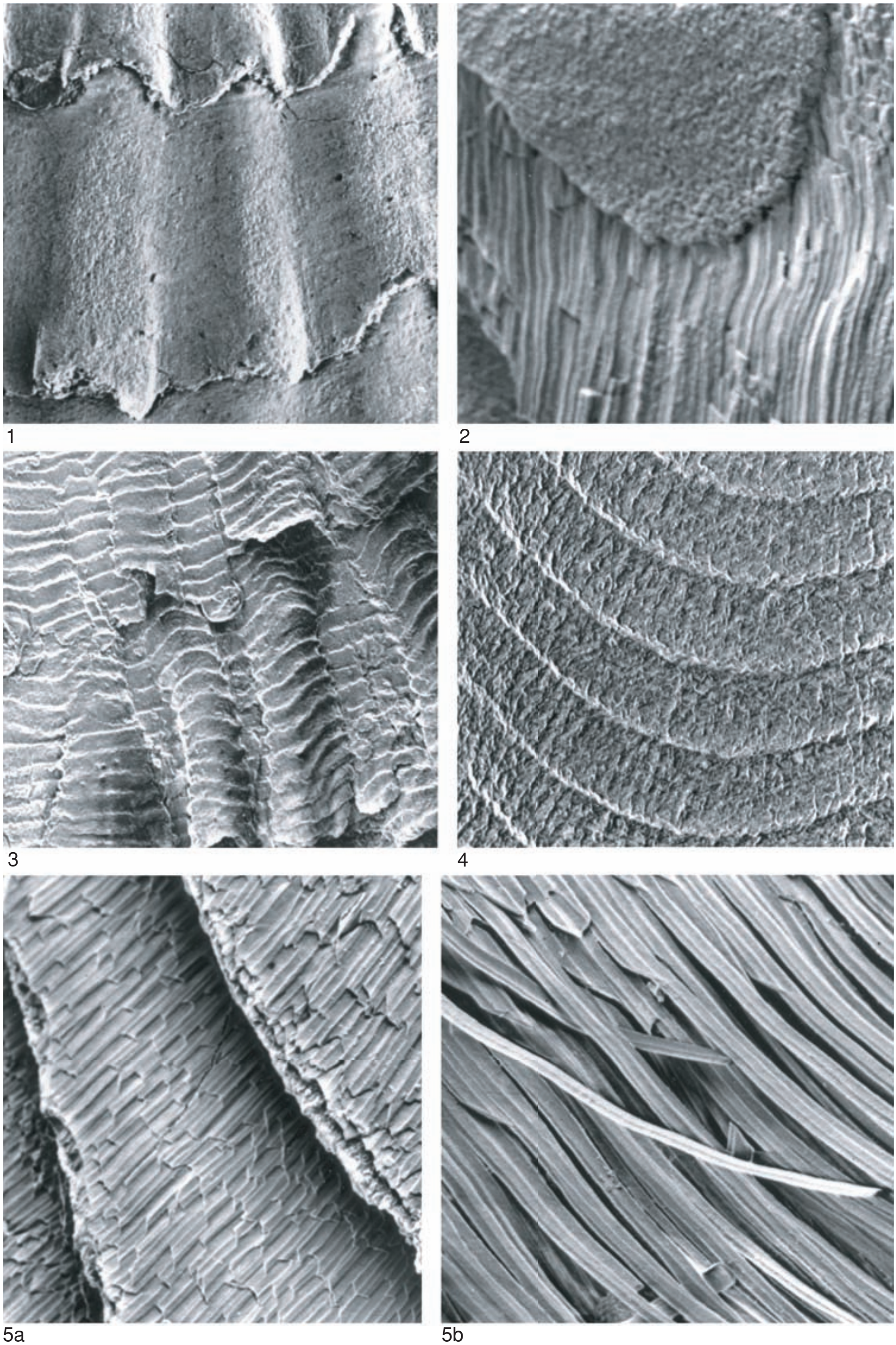

FIG. 934. *For explanation, see facing page.*

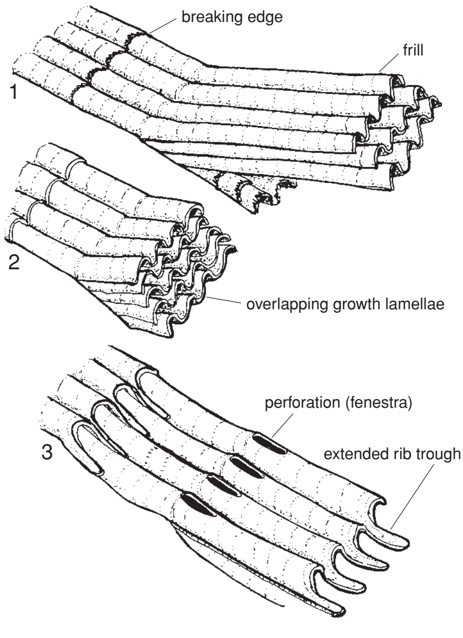

FIG. 935. Idealized growth lamellae and frills in Atrypida; *1, Desquamatia; 2, Gotatrypa; 3, Atrypa,* showing perforations facilitating the detachment of frills, approximately ×10 (new).

regular, very fine filae (concentric growth ridges) that are spaced at a density of 5 to 10 per millimeter. These are more evident in the troughs of ribs, where they have a better chance of preservation. The earliest such filae appear in Llandovery Atrypidae. Other variations of these filae show zigzag microornament and some carinatinids appear to have had a pustulose microornament. Since such microornament is often not preserved, it is difficult to evaluate its taxonomic significance; however, it has sometimes been used as a generic character when well developed.

Early shell forms had ribbed or smooth macroornamentation or a combination of these, and the shell had nearly continuous growth. Although growth interruptions were present, such early shells had no retraction of the mantle edge. Growth lamellae, extensions of secondary and primary layer beyond the normal shell wall, are a common feature of the Atrypidina (Fig. 935.2). The growth lamellae could extend evenly from the shell, irregularly, or more rapidly along the troughs than along rib crests. Later forms of shells in the Atrypidina (especially Atrypinae and Variatrypinae) show considerable growth of the shell beyond the shell wall to produce frills. The first frills evolved in late Llandovery atrypides. Very wide, multiple, overlapping frills could double or triple shell width, with the widest shells of *Desquamatia (Independatrypa)* in the Givetian reaching an overall width of nearly 150 mm without a significant change in internal shell volume. The frills of many atrypides are broken naturally during ontogeny with only the last grown frills serving a function and the earlier frills broken off, demonstrating repair of the surface suture. The frills broke off episodically at the crest of each concentric wave (Fig. 935.1). Spines were the result of extensions of shell wall where the crests of ribs grew more rapidly, then curved together to form a hollow tube, unfused on the underside. Spines were often irregular in their extension and of various lengths over the shell surface (Fig. 936.5). Another sort of spine was formed by sharp protrusion of the rib troughs, as seen in early Silurian Atrypinae.

Some Silurian *Atrypa* possess elongate perforations at regular concentric intervals normally along the rib crests (but also along the rib troughs), very much like perforations in sheets of postage stamps (Fig. 935.3). These perforations undoubtedly facilitated the deliberate breakage of frills during life, with retention of only the last few frills at the commissure. Although these perforations are somewhat comparable to the fenestrae seen in the Punctatrypinae, they do not penetrate the shell interior and are entirely exterior to the shell cavity. (They are absent on the inner shell surface.) The secondary and primary layers of the Punctatrypinae are penetrated by small, elongated or rounded, concentrically aligned pores called fenestrae (about 0.1 to 0.3 mm in diameter), located along the shell commissure. These were successively closed, filled, or plugged posteriorly as the shell grew (Fig. 936.7–936.8). Fenestrae normally developed along rib crests (monofenestrate forms), but more than one fenestra may be present along each rib

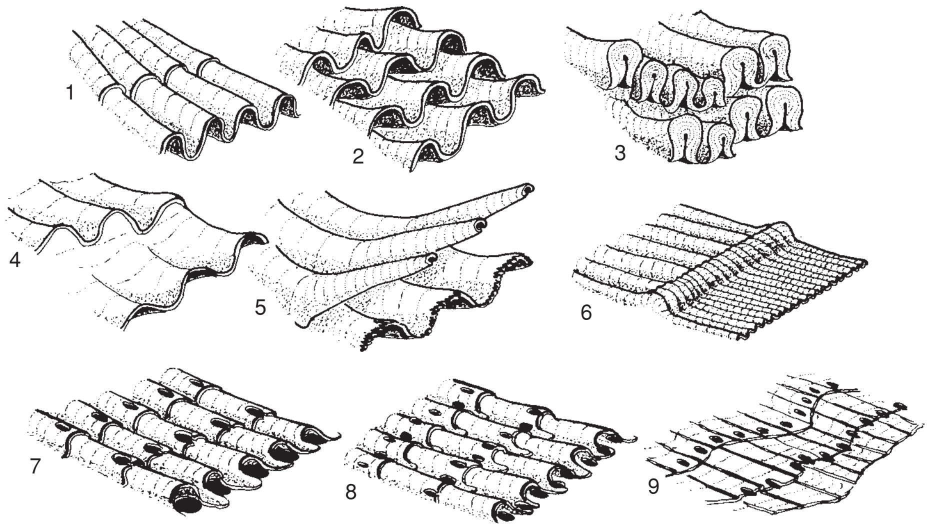

FIG. 936. Macroornamentation in Atrypida, demonstrating various features seen in different groups; *1, Desquamatia,* corrugate; *2, Plectatrypa,* imbricate; *3, Gutnia,* capidulate; *4, Atrypa,* undulose; *5, Spinatrypa,* spinose; *6, Carinatina,* trailed; *7, Punctatrypa,* monofenestrate; *8, Sinopunctatrypa,* multifenestrate; *9, Crassipunctatrypa,* platyfenestrate; approximately ×10 (new).

(multifenestrate forms). In the middle of adult shells and posteriorly, these fenestrae are completely sealed off by calcite overgrowth, a process that began as the mantle retreated from the commissure. The function of these is not known. Since the holes penetrate the shell interior they could not have facilitated detachment of the frills, and are more likely to have had either a sensory or feeding-respiratory function. Moreover, such shells do not normally have frills, except for the short, grooved, flat frills of *Crassipunctatrypa,* which commonly cover the fenestrae during growth (Fig. 936.9). This genus also has narrow radial grooves along its extended growth lamellae.

Atrypides were usually attached by a pedicle that protruded through a pedicle opening located at the apex of the delthyrium and flanked by two triangular deltidial plates. (The ordinal name is therefore somewhat of a misnomer for the Greek *a* and *trypa,* meaning without a hole.) A typical example here is the genus *Spirigerina,* which had two hollow deltidial plates partially surrounding the pedicle opening (Fig. 937.1). Atrypides lacked a dorsal area and possessed neither notothyrium nor chilidium. Some atrypides lost a pedicle opening by progressive incurvature of the beak, placing the area in orthocline through anacline positions until the area was pressed against the dorsal umbo in a position called hypercline. Among other atrypides (particularly those related directly to the type genus *Atrypa*) a pedicle opening is missing, usually, although not invariably, even in the earliest growth stages. The two valves then meet umbo-to-umbo in a position better called adpressed (since the area is not hypercline in this case, and the beak not incurved). The pedicle, however, may still have been squeezed into the remaining gap between the two valves despite the lack of a formal pedicle opening. The pediculate nature of such Atrypinae during life is unsettled. Moreover, the ventral umbo is often pierced or resorbed in such forms (Fig. 937). Loss of the pedicle was often accompanied by modification of the ventral valve into a flat shape (convexoplane) or by growth of spinose or frilly ornamentation, which stabilized the shell on soft substrates. Another method of pedicle loss occurred in

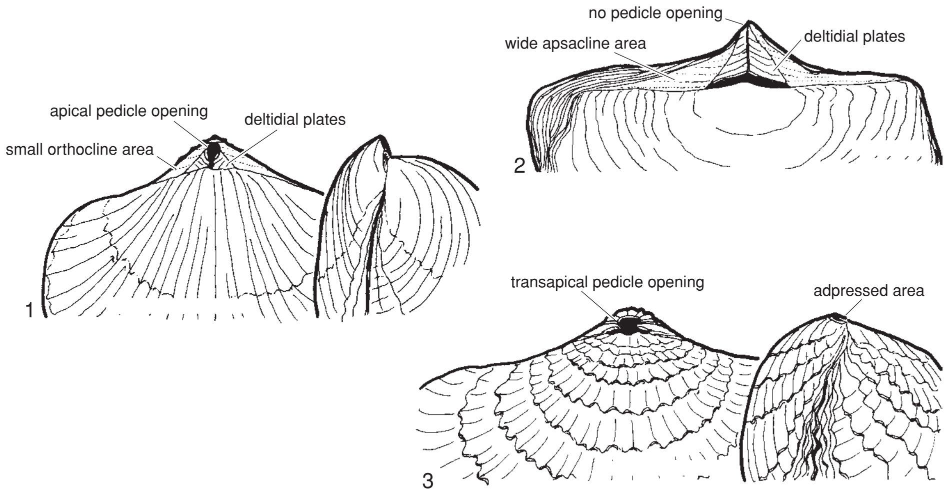

FIG. 937. External view of delthyrial structures in Atrypida; *1, Spirigerina marginalis; 2, Davidsonia; 3, Atrypa reticularis;* from camera lucida drawings, ×3 (new).

fixosessile, cementing atrypides such as the Davidsoniinae. Here the delthyrium is usually completely filled in by two deltidial plates and the foramen is closed (Fig. 937.2). In atrypide shells with a short pedicle muscle or a proportionally large pedicle opening and deltidial plates, the area may be curved backward ventrally into an apsacline to procline position, the most extreme excurvature seen in the atrypides. This suggests that a strong pedicle muscle affected the growth of the beak, pedicle opening, and deltidial plates. Many such shells grew in a skewed fashion, and a number of such affected brachiopods were coral-sponge-thicket or reef dwellers.

Internal delthyrial structures in the Atrypida may be quite complex (Fig. 938). Simplest forms have extremely small, hollow deltidial plates flanking a small pedicle opening or no discernible pedicle callist or deltidial plates. The deltidial plates may retreat from the outer margin of the delthyrium to a position inside the pedicle cavity. The development of a pedicle callist, thick layers of calcite in the pedicle cavity, is especially striking in taxa that have an adpressed or hypercline area with loss or reduction of a pedicle opening. The pedicle callist may almost completely fill the pedicle cavity, be layered, and sometimes also have a structure raised above the shell floor as a pedicle collar. These structures are extremely variably developed even within species from one locality and stratigraphic horizon. A pedicle callist or pedicle collar is common in such diverse taxa as the Lissatrypinae (*Lissatrypa*), Atrypinae (*Atrypa*), Variatrypinae (*Desquamatia*), Vagraniinae (*Vagrania*), and Palaferellinae (*Gruenewaldtia*). In some forms, the pedicle collar is consistently fused with the deltidial plates (Karpinskiidae, Palaferellidae), and in others the deltidial plates were kept separate from the pedicle collar (e.g., in *Iowatrypa, Desquamatia*). The presence of deltidial plates may be of familial importance in taxonomy, but this requires caution in identification; e.g., in *Lissatrypa* perfectly preserved material must be sectioned so that these are visible in peels. In loose valves any trace of deltidial plates is difficult to find. Pedicle callist and pedicle collar are highly variable even within species and thus not very reliable indicators of taxonomic affinity in many groups. The fusion of pedicle collar with deltidial plates, however, is characteristic and consistent within the Karpinskiidae and Palaferellidae and thus of diagnostic value.

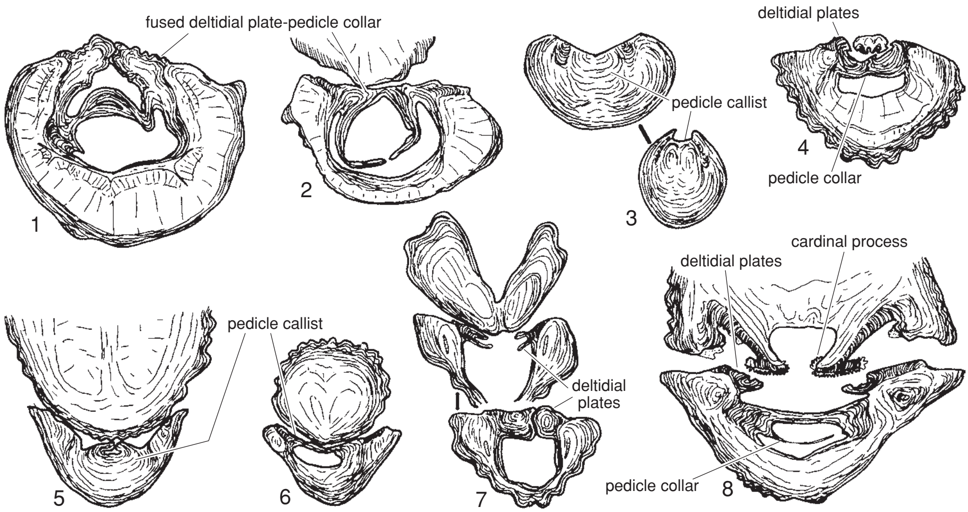

FIG. 938. Internal delthyrial structures in Atrypida as seen in serial section views, showing pedicle callists, pedicle collars, and deltidial plates; *1, Gruenewaldtia; 2, Desatrypa; 3, Lissatrypa; 4, Iowatrypa; 5, Atryparia; 6, Atrypa; 7, Spirigerina; 8, Desquamatia;* approximately ×7 (new).

The typical atrypide shell has a small, orthocline cardinal area, the margins of which may be slightly rounded (palintropelike, astrophic) to almost square edged, as in a true strophic shell. True strophic shells seem to occur only in the Davidsonioidea, but in some Variatrypinae the area widened, the delthyrium enlarged, and the shell approached a nearly strophic condition. Thus atrypide shells straddle the boundary between astrophic and strophic shells, with the latter evolving from the former, since the earliest shells were rhynchonelliform and astrophic.

Atrypides generally have a hinge mechanism composed of tightly fitting cyrtomatodont teeth, normally with accessory lobes. (This means that the teeth needed to be broken to allow valve detachment.) Some but not all of the flat atrypide shells (Davidsoniidae, Carinatininae) had teeth with a more deltidiodont nature; i.e., they appear to have been relatively easily detached and loose fitting at death. The teeth fit into sockets on the dorsal valve that were lined by socket plates, sometimes with accessory middle socket ridges used to constrain the teeth (see Fig. 933). The inner part of the socket plates is defined by inner socket ridges, usually separated in the middle of the shell by a cardinal pit and on the outer side by a weak ridge or a slope leading to the side of the shell. In some taxa a cardinal pit is absent in adult shells and replaced by a low boss (e.g., in *Lissatrypa* and *Tuvaella*). The cardinal pit, which is only a slight depression in some atrypides and a relatively narrow, deep trough in others, is lined by a distinctive, comblike cardinal process in a number of independently derived Siluro-Devonian forms (e.g., Atrypinae, Variatrypinae, Carinatininae, Vagraniinae). This cardinal process may line not only the cardinal pit but spill over onto the inner socket ridges of the socket plates. The cardinal process, however, is relatively insignificant in atrypides and is highly variably developed even within species and during ontogeny: gerontic shells feature well-preserved cardinal processes in a number of Devonian taxa, but this feature is not evident in primitive Ordovician taxa and in relatively few Silurian forms.

Muscle scars consist of three types, including attachment for the pedicle muscle (the pedicle callist), the adductors, and the diductors. These are variably but not consistently developed within different groups. The ventral adductor scars occur in the center of a depression toward the shell apex, are bean shaped and relatively narrow, and are sometimes difficult to discern from the diductor scars, which surround them on both sides. A low median septum rarely separates the ventral adductor scars. The diductors are larger, flabellate, and depressed on the ventral valve but rarely occupy more than one-quarter to one-third of the shell length. The dorsal adductors were modestly developed and attached to rounded depressions, commonly separated by a weak median septum (myophragm). When globose, gerontic dorsal valves are serially sectioned, this myophragm may often show up deceptively as a septalium, but a true septalium of the sort present in rhynchonellides is absent (see, for example, the misnamed genus *Septatrypa,* which lacks a septalium and where in some shells the median dorsal septum is barely detectable). Muscle scars may also be raised from the shell floor; in some globose Silurian and Devonian taxa (e.g., *Joviatrypa, Gotatrypa, Iowatrypa*) the scars have a lip elevated above the shell floor at the anterior margin of the scar. In only one family of atrypides, the Palaferellidae (represented by a single Middle Devonian genus *Gruenewaldtia*), are the dorsal and ventral muscle platforms raised above the shell floor by means of septa. In the earlier Eifelian species of *Gruenewaldtia* these muscle platforms are supported by numerous short septa; by late Eifelian to Givetian time, the supporting septa were reduced to two in each valve.

Raised vascular canals and gonadal pits are evident in thicker or gerontic atrypide shells but are generally not visible in thin-shelled taxa. They are rarely preserved in Ordovician shells, except for the genus *Catazyga.* Vasculae normally consist of curved, mirror-image branches that bifurcate or trifurcate frequently near the shell commissure and are most similar to those of living rhynchonellides. They are stronger on the ventral than the dorsal valve. Vasculae flank the muscle scars laterally and leave a gap between the muscle scars anteriorly. Vascular canals are highly variably developed within species; they are most obvious in gerontic specimens. The taxonomic and evolutionary significance of the vasculae is not yet clearly established in the Atrypida. In the late Silurian-Devonian Vagraniinae and in Devonian Karpinskiinae, very striking raised vascular ridges, almost like irregular septa, are highly characteristic of most genera. In most other groups, however, the vasculae are weakly displayed and require further investigation.

Order ATRYPIDA Rzhonsnitskaia, 1960

[Atrypida RZHONSNITSKAIA, 1960a, p. 257; *emend.,* COPPER, herein] [=Procampyli QUENSTEDT, 1882, p. 723, *nom. oblit.*]

Shell wall impunctate, rarely fenestrate; macroornamentation ranging from smooth to ribbed to divaricate, lamellose, spinose, or fenestrate; microornamentation of primary layer usually absent, or with filae, capillae. Shell usually rounded, biconvex to dorsibiconvex, usually astrophic, less commonly flat, strophic; ventral valve rarely partly or wholly cemented; small, flat or rounded ventral area; foramen apical to transapical, dividing 2 triangular deltidial plates; pedicle callist or collar common, perhaps fused with overlying deltidial plates; ventral diductor muscle field large, usually incised, less commonly raised; ventral adductors small; dorsal adductors rounded, separated by weak median septum; small, bushy cardinal process normally located in cardinal pit; weak to prominent ventral vasculae branched around muscle field, saccate to lemniscate, weaker on dorsal valve; faint to strong gonadal pits flanking all muscle fields; crura arising from inner socket ridges, laterally to dorsovertically directed, merging into primary lamellae at sides of shell, may be feathered; medially to dorsally directed, conical spiralia, arising laterally, connected by simple jugum or jugal processes, rarely ajugate. [RZHONSNITSKAIA (1960a, p. 257) was the first to raise the group to ordinal status, using as criteria that the spiralia were dorsally or medially directed, based on the evolution of these character states in the Atrypida. She also included the planoconvex *Coelospira* and *Dayia* shells, as did the 1965 brachiopod *Treatise* (BOUCOT, JOHNSON, & STATON, 1965; but see suborder Uncertain, p. 1604 herein), based ostensibly on serial sections that appear to demonstrate a dorsal direction for spiralia. When these latter taxa are examined, it is evident that they possess laterally directed spiralia and complex juga with jugal stems, as known only from the order Athyridida, and thus cannot be assigned to the Atrypida. MOORE (1952, p. 221) defined the "suborder Atrypacea" as impunctate shells with a short hinge and the negative character "spiralia not directed toward cardinal extremities." A number of Atrypida have a long strophic hinge and lack cardinal extremities; moreover, *Cyrtia* (Spiriferida) have spiralia not directed to lateral extremities (and would thus have to be accommodated in his definition of the Atrypacea), so that the only character of MOORE's 1952 definition that remains is an impunctate shell. This is impractical, and does not reflect the nature of the Atrypida fossil record. RZHONSNITSKAIA's 1960 definition is thus accepted as the first reasonably accurate description of the order Atrypida, including the Cyclospiridae, Anazygidae, and Atrypidae, as defined by her (but excluding her Coelospiracea and Dayiacea). This attribution has been almost universally adopted in the last 25 years.] *Ordovician (Llandeilo)–Upper Devonian (Frasnian).*

Suborder ATRYPIDINA Moore, 1952

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1965, p. 632, *pro* suborder Atrypoidea MUIR-WOOD, 1955, p. 77, *nom. correct. pro* suborder Atrypacea MOORE, 1952, p. 221; *emend.,* COPPER, herein]

Ribbed, tubular, lamellose, wavy, spinose, fenestrate, or secondarily smooth-shelled atrypoids; generally rectimarginate to plicate commissure; spiralia dorsomedial to dorsal in direction, with up to 25 whorls; separated jugal processes in a posteromedial and ventral position toward hinge. *Ordovician (lower Caradoc)–Upper Devonian (Frasnian).*

Superfamily ATRYPOIDEA Gill, 1871

[*nom. correct.* COPPER, herein, *pro* superfamily Atrypacea SCHUCHERT & LEVENE, 1929a, p. 19, *nom. transl. ex* Atrypidae GILL, 1871, p. 25; *emend.,* COPPER, herein]

Ribbed atrypides, commonly with concentric growth lamellae or frills; spiralia dorsally or dorsomedially directed; jugal processes posteroventrally located. *Ordovician (lower Caradoc)–Upper Devonian (Frasnian).*

Family ATRYPIDAE Gill, 1871

[Atrypidae GILL, 1871, p. 25, *partim; emend.,* COPPER, herein]

Small to very large, ribbed atrypoids, lacking carination; characterized by strong development of extended, concentric growth lamellae, sometimes as expansive frills, skirts, or spines (expanding shell width to more than 150 mm); pedicle callist variably developed; weak to strong, comblike cardinal process developed in cardinal pit; spiralia usually with more than 8 whorls, up to 25 whorls in large shells, jugal processes posteroventral; jugal plates attached to ends of processes. *Silurian (Llandovery)–Upper Devonian (Frasnian).*

Subfamily ATRYPINAE Gill, 1871

[*nom. transl.* COPPER, herein, *ex* Atrypidae GILL, 1871, p. 25; *emend.,* COPPER, herein]

Atrypides with short, concentric, usually wavelike growth lamellae, to very wide overlapping or imbricate lamellae extended as frills; ribs discontinuous, commonly wavelike at frill breakage points; beak small; area varying from small, orthocline (rare) to hypercline (common), to absent; foramen and deltidial plates commonly lost in adult shells; usually small to wide, thick pedicle callist; teeth solid, but dental nucleus or small dental cavity in some taxa; weak to strong cardinal process spilling over cardinal pit; crura delicate to strong; spiralia with many whorls; relatively thick jugal processes terminating in gently curved to spatulate jugal plates. *Silurian (Llandovery)–Upper Devonian (Frasnian).*

Atrypa DALMAN, 1828, p. 127 [**Anomia reticularis* LINNAEUS, 1758, p. 702; OD]. Medium to large,

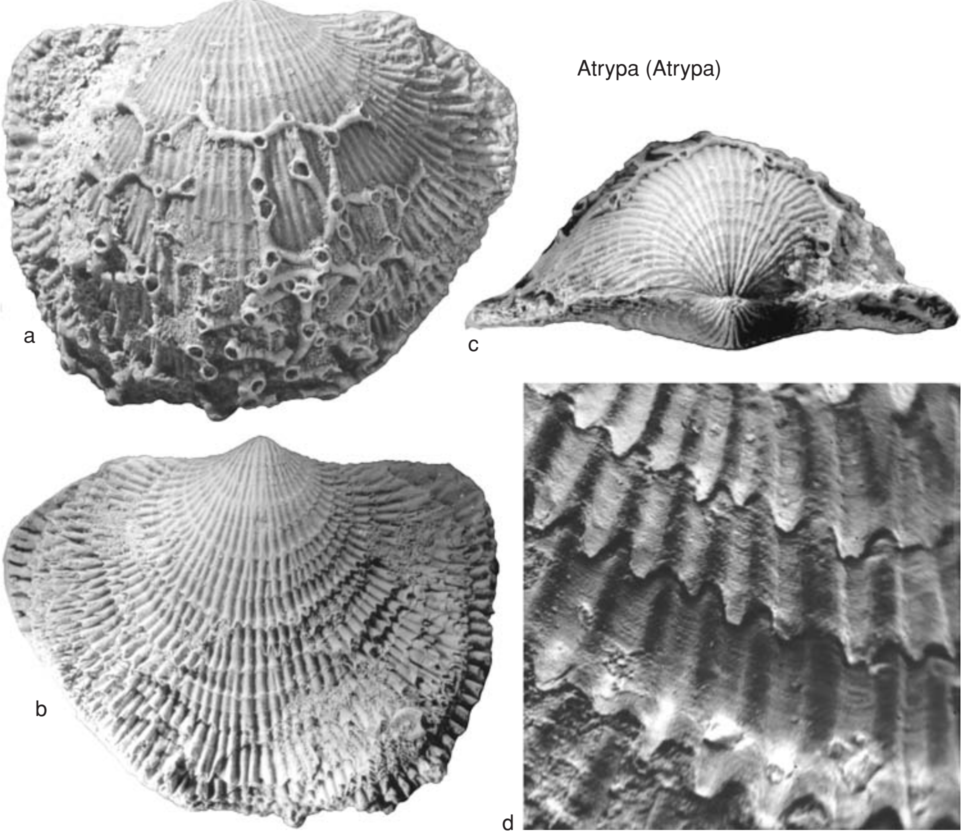

FIG. 939. Atrypidae (p. 1390).

broadly convexoplane to dorsibiconvex adult shell, ventral valve from very weakly convex apically; dorsal valve usually strongly convex; area generally absent; beak adpressed; foramen transapical or obscured; deltidial plates absent; ribs medium to coarse; regular, concentric, undulose to wavelike growth lamellae, usually expanded as prominent, multiple frills; commissure rectimarginate to plicate; thick pedicle callist; teeth massive, with dental nuclei, accessory lobes (dental cavities in neanic shells); muscle field depressed; vascular ridges weakly to strongly developed around muscle areas; hinge socket plates strong; comblike cardinal process lining cardinal pit; sockets with accessory ridges; crural bases large, bulbous; crura commonly feathered; spiralia dorsal, up to 20 whorls in large shells; jugal processes thick, terminating in long, dorsally directed spatulate jugal plates. [Differs from ancestral *Gotatrypa* in convexoplane shell, development of frills; from *Atryparia* in more imbricate ribs, lack of dental nuclei in adult teeth.] *Silurian (upper Llandovery)–Middle Devonian (lower Givetian):* worldwide.

A. (Atrypa). Description as for genus. Medium to large, broadly convexoplane shell, with ventral valve from very weakly convex apically, to planar, to resupinate; area absent or minute; foramen obscured; deltidial plates absent except in earliest growth stages; ribs fine to medium sized; multiple frills sometimes broken during life by seam of perforations; commissure plicate. [Differs from *A. (Planatrypa)* in weakly convex ventral umbo, possessing numerous frills, dental nuclei (and dental cavities in neanic stages).] *Silurian (upper Llandovery)–Lower Devonian (Emsian):* worldwide.——FIG. 939*a–d.* **A. (A.) reticularis* (LINNAEUS), lower Ludlow, Gotland; *a–c,* dorsal, ventral, posterior views, ×2; *d,* SEM detail of macroornament, ×12 (new).——FIG. 940*a–d.* **A. (A.) reticularis* (LINNAEUS), lower Ludlow, Gotland; *a–c,* serial sections, ×4; *d,* reconstruction from serial sections, ×3.5 (new).

A. (Planatrypa) STRUVE, 1966, p. 143 [**A. (P.) collega;* OD] [=*Mikrothyris* QUENSTEDT, 1871 in 1868–1871, p. 30, *nom. oblit.,* no type designated; *Planatrypa* COPPER, 1967a, p. 237 (type,

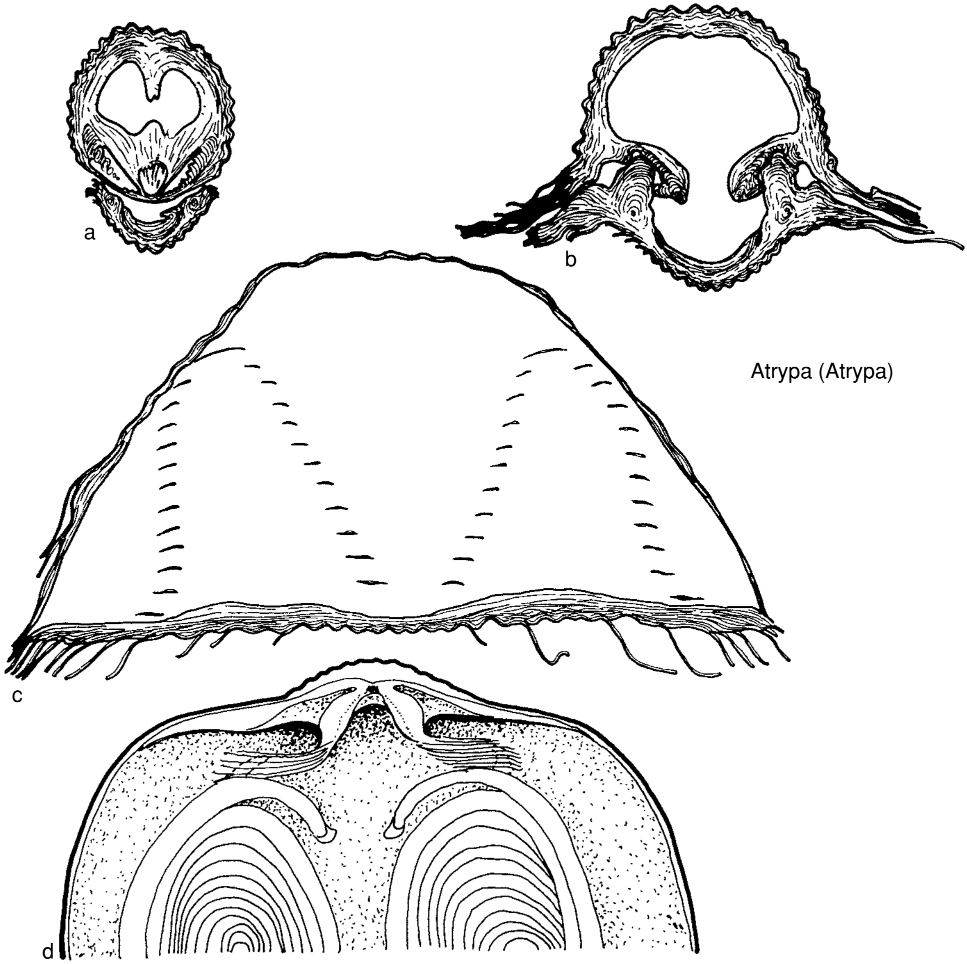

FIG. 940. Atrypidae (p. 1390).

A. (P.) petasa, OD)]. Medium to large, convexoplane; beak adpressed; foramen transapical or obscured; deltidial plates absent; ribs medium size, interrupted by numerous, flat, weakly imbricate growth lamellae; frills absent; anterior commissure rectimarginate to weakly plicate; prominent pedicle callist; cardinal process in cardinal pit; solid large teeth, lacking dental nuclei; hinge, socket plates stout; cardinal pit, inner socket ridges with bushy cardinal process; crura curved, feathery; spiralia with more than 8 whorls; posteroventral jugal processes terminating in curved, short, spatulate jugal plates. [Similar to *A. (Atrypa),* except that in early mature shell, the pedicle valve is flat, anterior fold weakly developed to absent, frills not known to be present, jugal processes more ventrally located. QUENSTEDT stated for *Atrypa,* "und *Atrypa* (besser wäre es *Mikrothyris),*" but no type was designated]. *Middle Devonian (Eifelian–lower Givetian):* worldwide.——FIG. 941*a–h.* **A. (P.) collega*, middle Eifelian, Germany; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×2; *f–h,* serial sections, ×5 (Copper, 1967b).——FIG. 941*i–k. A. (P.) petasa* COPPER, upper Eifelian, Germany; *i,* ventral interior, ×2; *j,* dorsal interior, ×4; *k,* reconstruction of brachidia, ×3 (Copper, 1967b).

Atryparia COPPER, 1966a, p. 982 [**A. instita* COPPER, 1966a, p. 983; OD] [=*Hyponeatrypa* STRUVE, 1966, p. 137 (type, *Atrypa (Hyponeatrypa) aureolata* STRUVE, 1966, p. 140, OD)]. Medium to very large, dorsibiconvex-convexoplane; ventral valve inflated posteriorly, commonly keel-like; very coarse to fading ribs intersected by flat, relatively widely spaced growth lamellae extended into broad, multiple

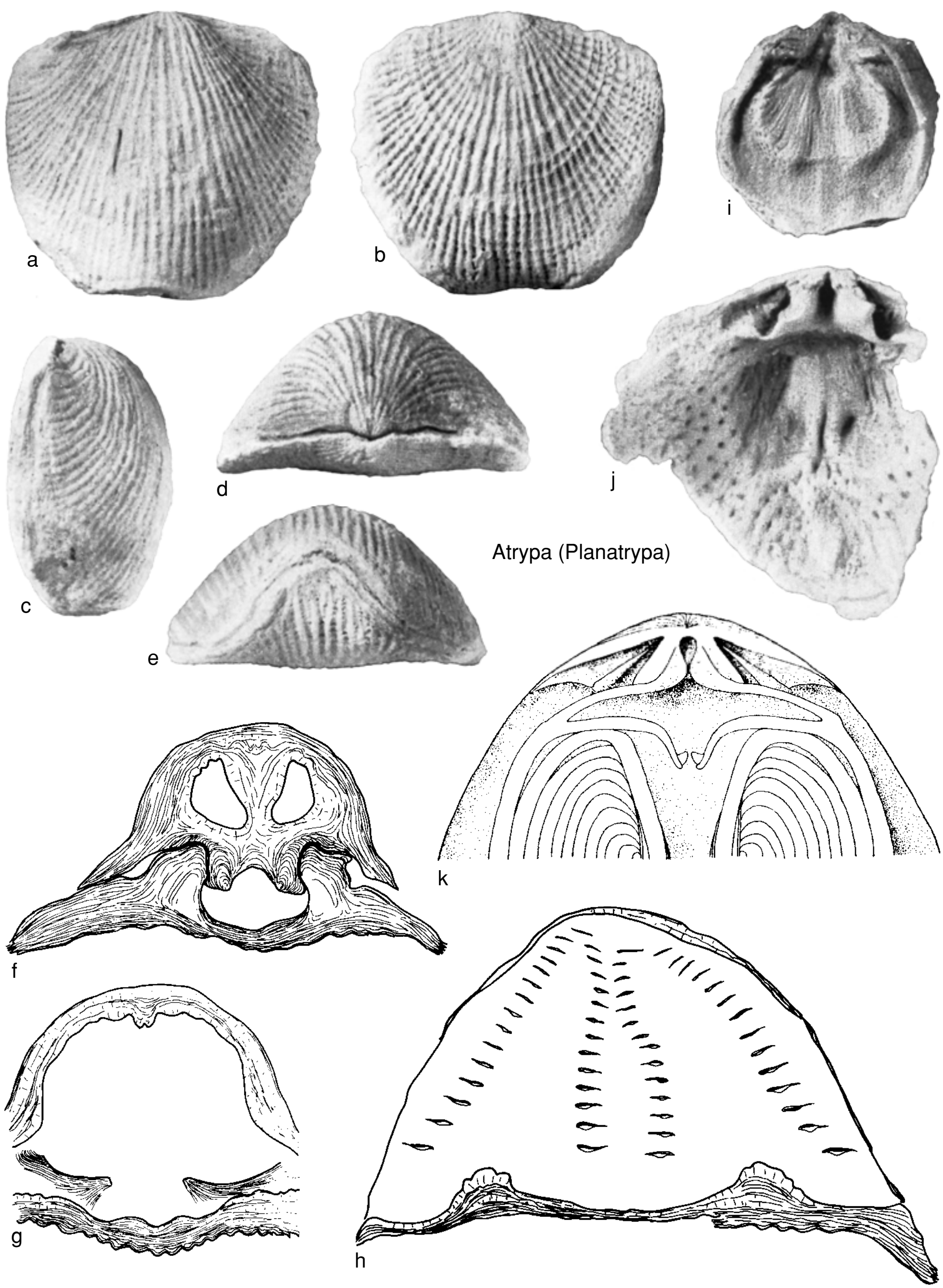

FIG. 941. Atrypidae (p. 1390–1391).

overlapping frills; thick, wide pedicle callist, commonly with narrow central groove; teeth possessing dental nuclei; fewer than 15 relatively widely spaced spiral whorls; jugal processes terminating in long, downturned plates. [Distinguished from *Atrypa* and *Kyrtatrypa* by coarse, flattened ribs and growth lamellae showing smoothed, distally expanding ribs, wide multiple frills, internally in having dental nuclei.] *Lower Devonian (Emsian)–Upper Devonian (Frasnian):* worldwide.

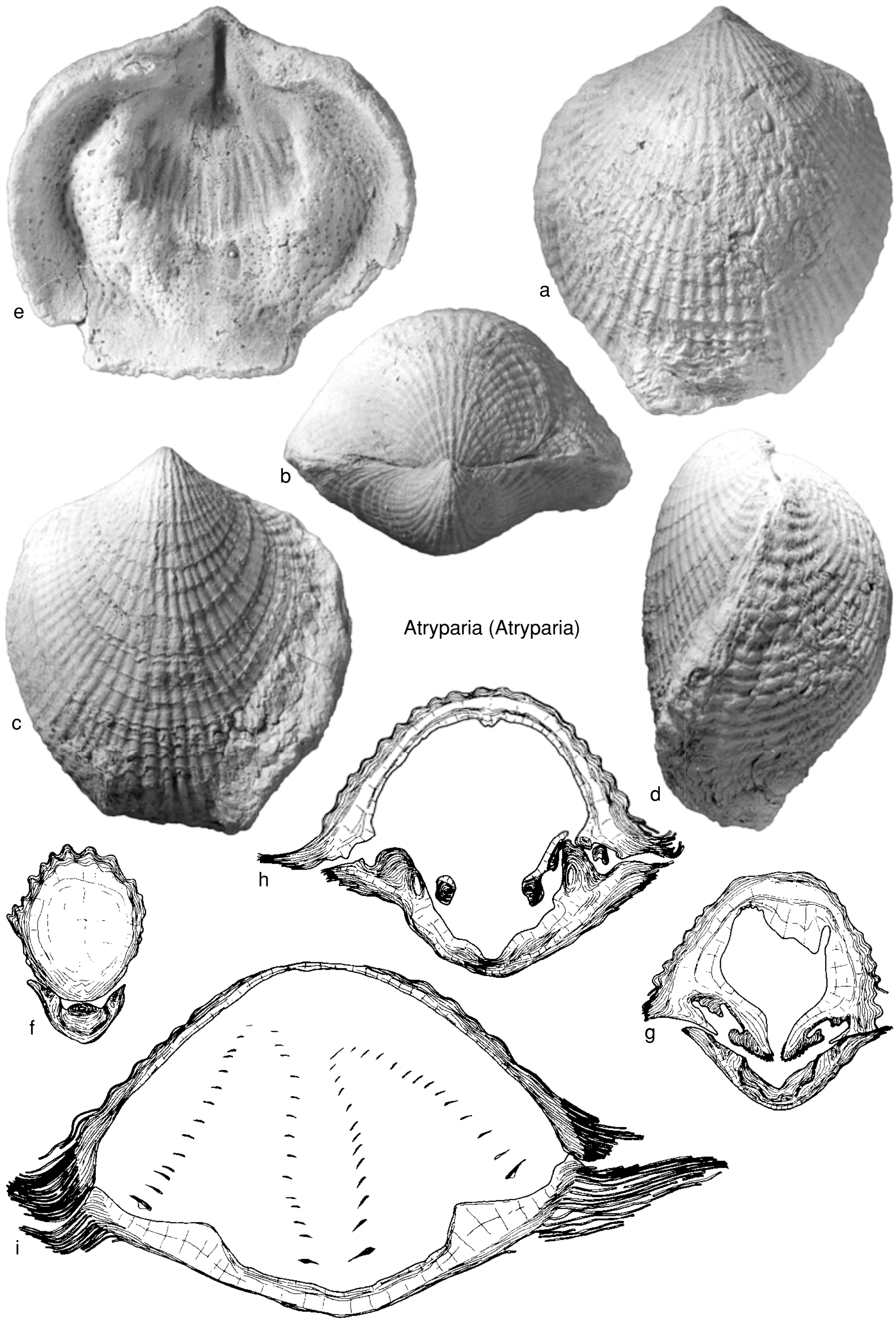

FIG. 942. Atrypidae (p. 1394).

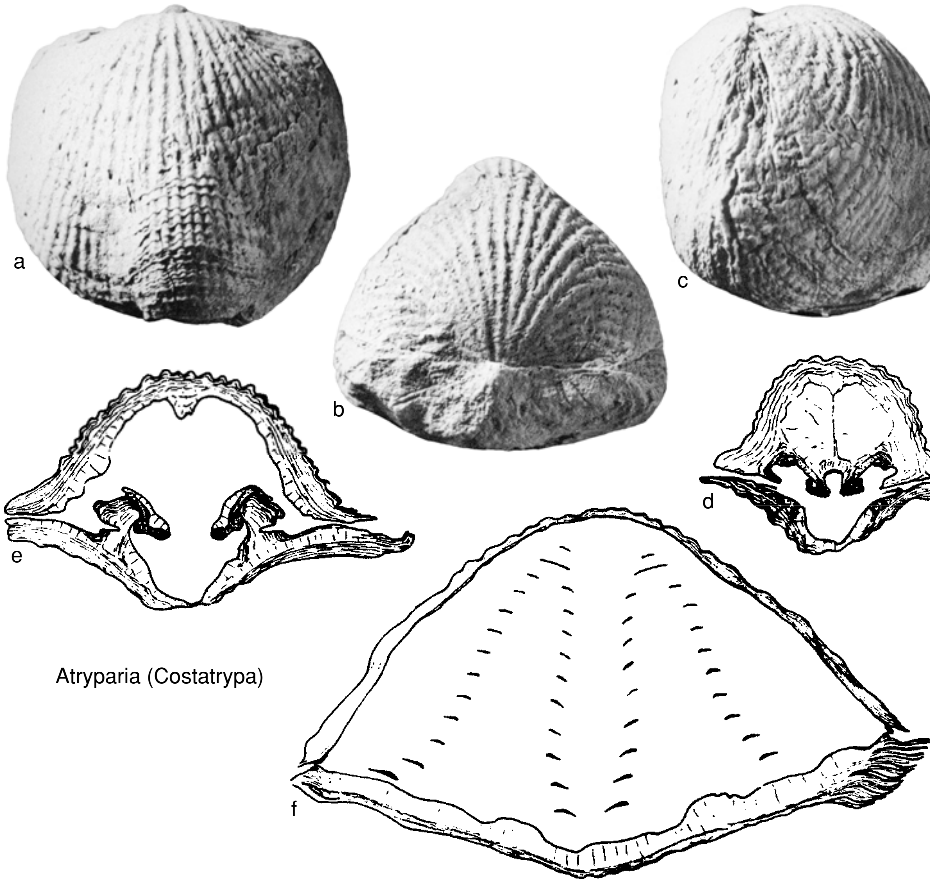

FIG. 943. Atrypidae (p. 1394).

A. (**Atryparia**). Description as for genus, but medium to very large, dorsibiconvex. *Lower Devonian (Emsian)–Middle Devonian (Givetian):* Eurasia, northern Africa, North America.——FIG. 942*a–i*. **A. (A.) instita,* upper Eifelian, Germany; *a–e,* dorsal, posterior, ventral, lateral, interior of ventral valve, ×2; *f–i,* serial sections, ×5 (new).

A. (**Costatrypa**) COPPER, 1973c, p. 494 [**Atrypa varicostata* STAINBROOK, 1945, p. 47; OD]. Medium to large, dorsibiconvex-convexoplane, shield shaped to subquadrate; generally relatively long hinge; adpressed area; small beak, lacking apical foramen; ribs shallow, medium size, coarser ribs on frills; prominent frills up to about 15 mm long; moderate to strongly plicate commissure; moderate pedicle callist; large teeth; minute dental nuclei; crural bases thick, rounded; crura feathered; dorsomedial spiralia with fewer than 15 whorls; curved jugal processes terminating in hook-shaped plates. [Differentiated from *A. (Atryparia)* by more clearly defined ribs, flatter, wider, shield-shaped shell, less prominent frills.] *Upper Devonian (Frasnian):* worldwide.——FIG. 943*a–c*. **A. (C.) varicostata* (STAINBROOK), Iowa, USA; dorsal, posterior, lateral views, ×2 (Copper, 1973c).——FIG. 943*d–f*. *A. (C.) variabilis* GODEFROID, Belgium; serial sections, ×3 (new).

Dihelictera COPPER, 1995, p. 855 [**D. acrolopha;* OD]. Small to medium, planar to weakly biconvex; posterior ventral valve weakly carinate; small, orthocline area; apical foramen flanked by deltidial plates; relatively straight ribs posteriorly; short growth interruptions or lamellae anteriorly; regular concentric filae; rectimarginate to weakly plicate commissure; pedicle callist absent; teeth with moderate dental cavities; small, distinct cardinal pit lined by minute cardinal process; spiralia dorsomedial, fewer than 6 whorls; jugal processes simple, terminating in small, hooklike jugal plates. [Similar externally to *Procarinatina,* but possessing fine, concentric filae, ribs straight to tubular posteriorly, lacking wavelike imbrication; differs from

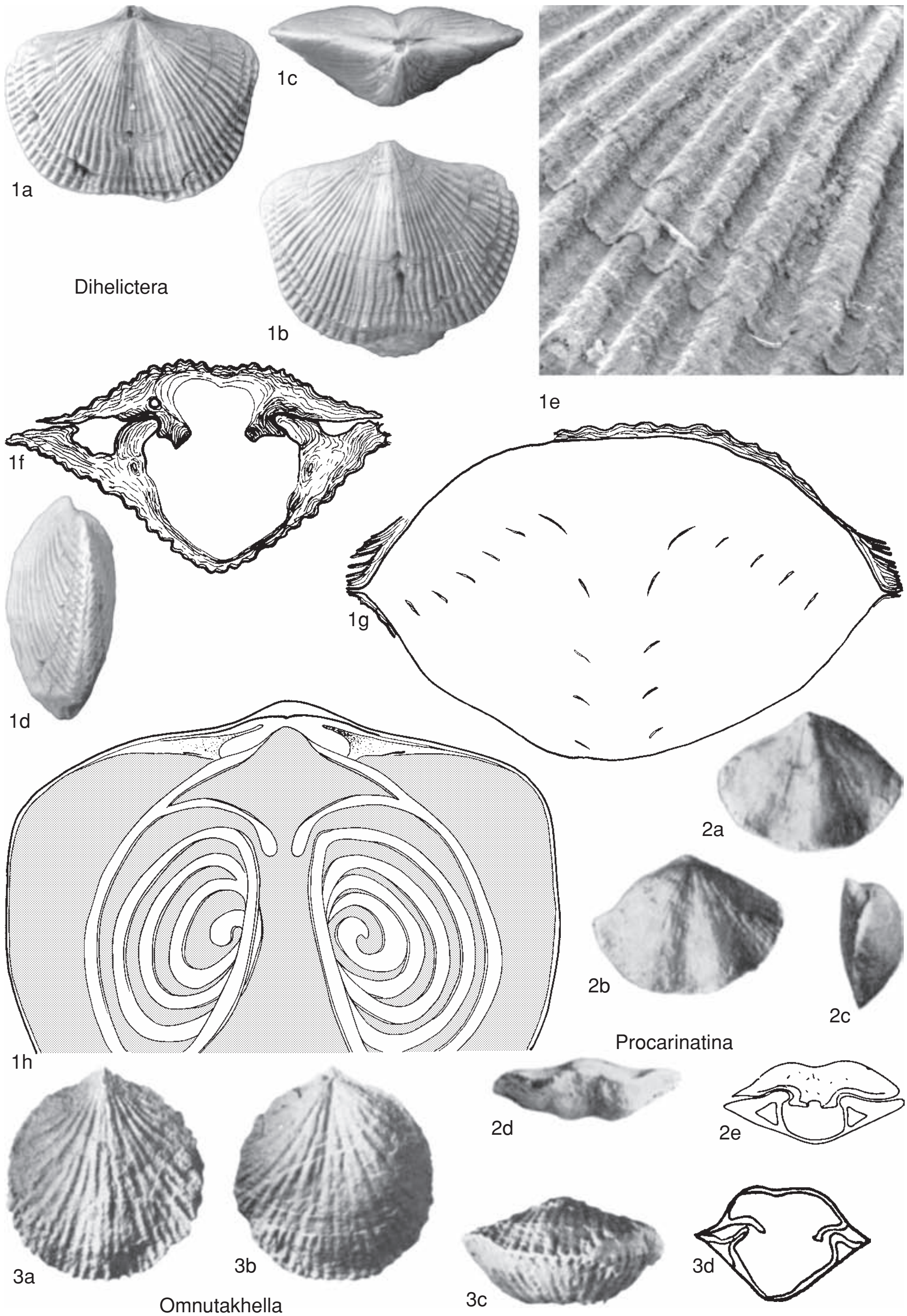

FIG. 944. Atrypidae (p. 1394–1400).

Protatrypa by nature of hinge plate, ornamentation, teeth with dental cavities.] *Silurian (middle Llandovery–upper Llandovery):* North America, Siberia.——FIG. 944,*1a–h.* **D. acrolopha,* Aeronian, Anticosti, Canada; *a–d,* dorsal, ventral, posterior, lateral views, ×3; *e,* SEM detail of ornament, ×13; *f–h,* serial sections and reconstruction of brachidia, ×5 (Copper, 1995).

Endrea COPPER, 1996b, p. 919 [**E. echoica;* OD]. Medium to large, biconvex-dorsibiconvex, rarely convexoplane, shield shaped; small orthocline-anacline area, apical foramen surrounding small deltidial plates even in adult shells; highly arched, tubular-imbricate ribs, short frills or frills lacking, fine concentric filose microornament; commissure weakly to strongly folded; pedicle callist very thin to lacking; teeth with small dental cavities; spiralia with fewer than 10 whorls; jugal processes terminating in small, weakly curved jugal plates. [Distinguished from *Atrypa* by tubular-imbricate ribs, very short frills or no frills, filose microornament (where preserved), small deltidial plates, dental cavities, lack of pedicle callist; rib structure *Spinatrypina*-like, but shells have short frills; *Rugosatrypa* is most similar, but has finer, more *Atrypa*-like, flatter ribs, convexoplane shell.] *Silurian (Wenlock–Ludlow):* western Europe, North America.——FIG. 945,*2a–d.* **E. echoica,* lower Wenlock, Gotland; *a–b,* ventral, lateral views, ×2; *c–d,* serial sections, ×5 (Copper, 1996b).

Gotatrypa STRUVE, 1966, p. 130 [**Atrypa (Gotatrypa) hedei;* OD]. Small to medium, globose, ventribiconvex to biconvex to weakly dorsibiconvex; minute, adpressed area; foramen transapical or obscured; deltidial plates absent, except in neanic stages; fine ribs intersected by closely spaced, weak, wavelike growth lamellae, projected less than 2 to 3 mm, commonly pointed as spines and longer in rib troughs; frills absent; pedicle callist moderate; teeth with dental nuclei; crura thin, rarely bushy; spiralia dorsomedial, fewer than 8 to 12 whorls; short, centroposterior jugal processes with small jugal plates. [Differs from *Atrypa* in convexity, globose shape, closely spaced, overlapping growth lamellae, lack of frills. Distinguished from *Oglupes* by small size, very fine ribs, very short frills.] *Silurian (Aeronian–Telychian, ?Wenlock):* worldwide.——FIG. 945,*1a–g.* **G. hedei,* Telychian, Gotland; *a–d,* dorsal, ventral, posterior, lateral views, ×2; *e–g,* serial sections, ×5 (new).

Joviatrypa COPPER, 1995, p. 858 [**J. brabyla* COPPER, 1995, p. 859; OD]. Medium to large, ovoid, globose, ventribiconvex-biconvex; small, hypercline area; foramen transapical-apical; deltidial plates absent; ribs fine to medium, interrupted by numerous, closely spaced (less than 1 mm), short growth interruptions, projecting growth lamellae; frills lacking; weakly plicate commissure; thick pedicle callist bisected by narrow groove; strong teeth with minute dental nuclei; rounded cardinal pit; weak cardinal process on bulbous inner socket ridges; crura stout, fibrous; dorsomedial spiralia with fewer than 15 whorls; jugal processes terminated in thick, blocky jugal plates. [Differs from *Gotatrypa* and *Atrypa* in lacking growth lamellae and frills, presence of anteriorly raised, ventral muscle platform; resembles *Nalivkinia* externally, but lacks dental cavities, dental plates, has ventral muscle platform.] *Silurian (middle Llandovery–upper Llandovery):* North America, ?Siberia.——FIG. 946*a–i.* **J. brabyla,* Aeronian, Anticosti, Canada; *a–e,* dorsal, posterior, anterior, lateral views, internal of ventral valve, ×2; *f–h,* serial sections, ×3.5; *i,* reconstruction of serial sections, ×2.5 (Copper, 1995).

Kyrtatrypa STRUVE, 1966, p. 133 [**Atrypa (Kyrtatrypa) culminigera* STRUVE, 1966, p. 135; OD] [=*Anulatrypa* HAVLÍČEK, 1987a, p. 73 (type, *A. anulata,* OD)]. Small to large, biconvex to strongly dorsibiconvex, globose; narrow, hypercline to adpressed area; transapical foramen; deltidial plates lacking, except possibly in some neanic specimens; ribs medium size, intersected by numerous overlapping growth lamellae, commonly expanded into long, wide frills; moderately to strongly plicate commissure; thick pedicle callist, with deep central groove; pedicle collar common; prominent, large, solid teeth; hinge plates bulbous; crural bases round, large; spiralia with fewer than 20 whorls, dorsomedially directed; jugal processes tipped by small jugal plates. [Differs from *Atrypa* in strong biconvexity, presence of wide frills over shell surface, plicate commissure; differs from *Atryparia* in finer, rounded, wavelike ribs, absence of ventral keel, thick pedicle callist.] *Lower Devonian (Lochkovian)–Upper Devonian (middle Frasnian, ?upper Frasnian):* worldwide.——FIG. 947*a–g.* **K. culminigera,* middle Eifelian, Germany; *a–d,* dorsal, ventral, lateral, posterior views, ×2; *e–g,* serial sections, ×3 (new).

Oglupes HAVLÍČEK, 1987b, p. 239 [**O. scarabeus* HAVLÍČEK, 1987b, p. 240; OD] [=*Kantinatrypa* HAVLÍČEK, 1995, p. 58 (type, *K. gambrina* HAVLÍČEK, 1995, p. 59, OD]. Small to large, biconvex-dorsibiconvex; hypercline-adpressed, obscured area; small beak; foramen absent; ribs relatively coarse; surface bearing distinctive, fine concentric filae, with concentric growth lamellae, frills, or trail; anterior commissure rectimarginate to weakly plicate; pedicle callist moderate; deltidial plates absent; teeth with possible dental nuclei; cardinal process minute to absent; socket plates thin, with strong inner socket ridges; spiralia, jugal processes undescribed. [Distinguished from *Gotatrypa* by coarser ribs, distinct concentric filae, commonly prominent growth lamellae, frills.] *Silurian (upper Llandovery–Wenlock):* Eurasia.——FIG. 945,*3a–c.* **O. scarabeus,* Wenlock, Czech Republic; dorsal, ventral, posterior views, ×2.6 (Havlíček, 1987b).

?Omnutakhella LOPUSHINSKAYA, 1976, p. 66 [**O. bazhenovae;* OD]. Small, rounded, dorsibiconvex, noncarinate; protruding beak; small, orthocline area; transapical foramen; possible deltidial plates; weak, broadly plicate commissure; ribs fine to medium, weakly undulose; growth lamellae, frills absent; small teeth with dental cavities; delicate hinge plate with cardinal pit; thin socket plates; fewer

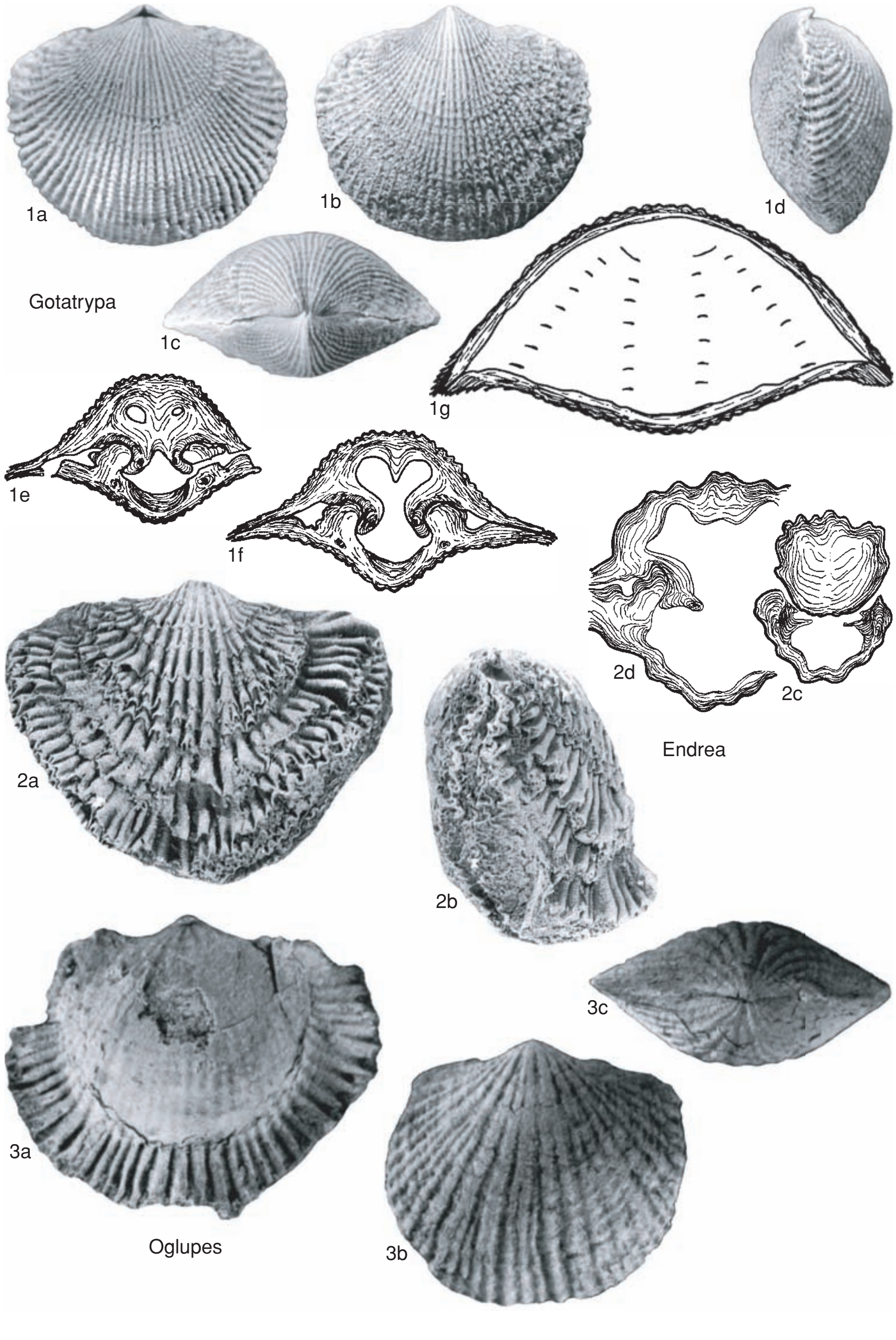

FIG. 945. Atrypidae (p. 1396).

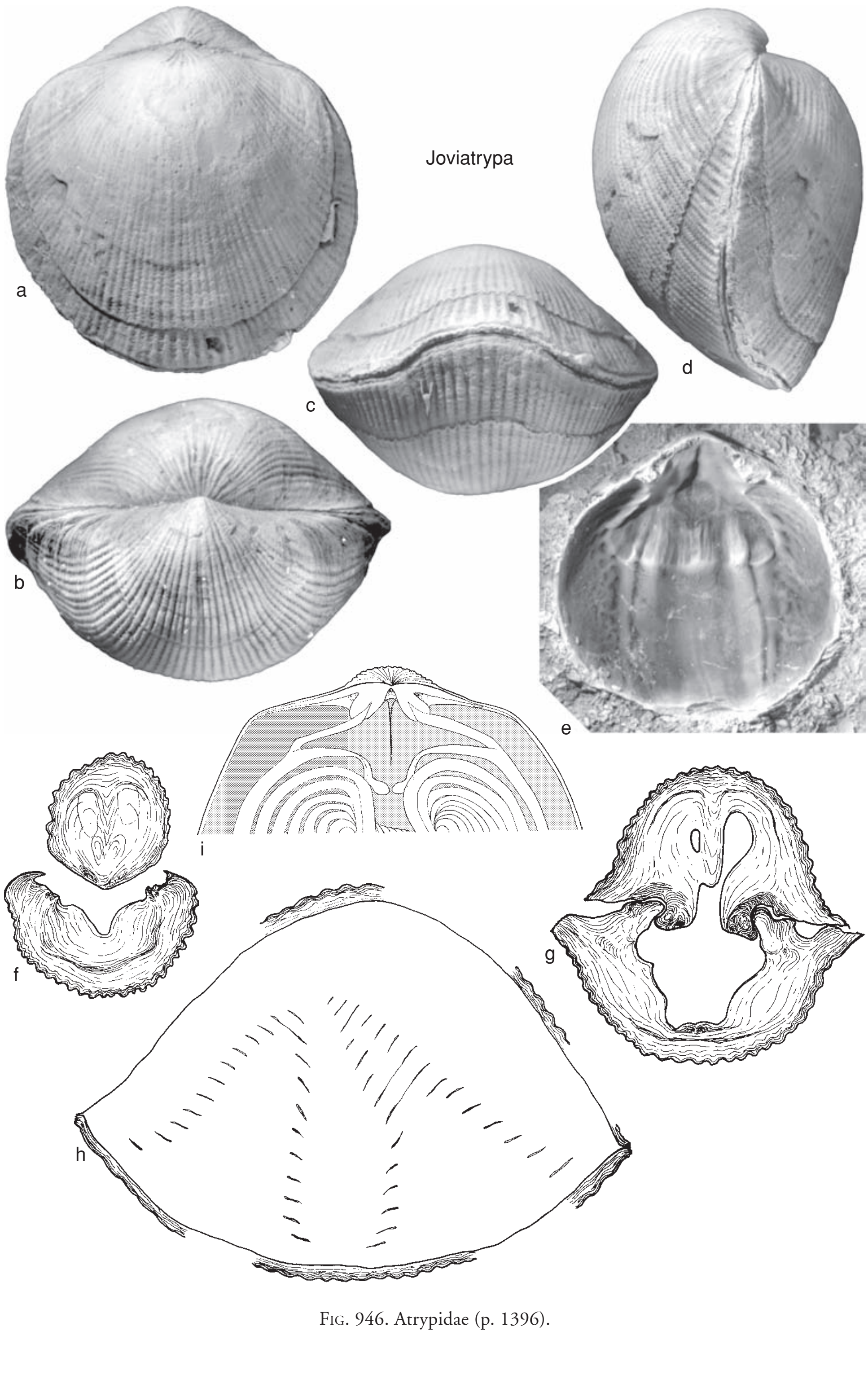

FIG. 946. Atrypidae (p. 1396).

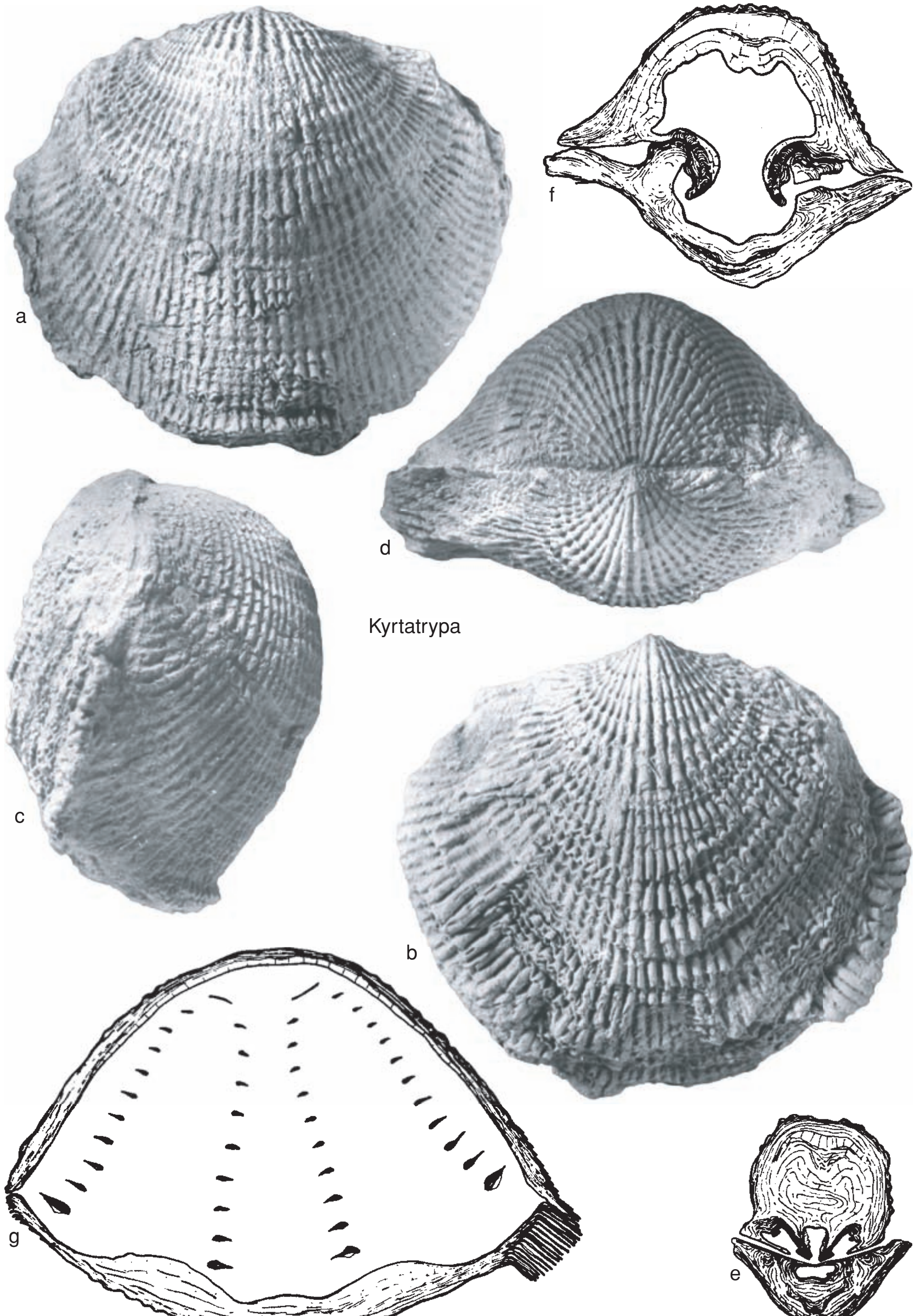

FIG. 947. Atrypidae (p. 1396).

than 5 to 6 dorsomedial spiralial whorls; crura, jugal processes undescribed. [Possible synonym of *Gotatrypa,* but for prominent dental cavities, lack of pedicle callist; similar to *Procarinatina* and *Dihelictera,* except in rounded shell, short hinge, weakly undulate ribs, lacking carination; differs from *Protatrypa* in small size, round outline, dorsibiconvex shape, dental cavities, short hinge, lacking carination; differs from *Sypharatrypa* in lacking growth lamellae, strong anterior fold.] *Silurian (Wenlock):* Siberian Platform.——FIG. 944,*3a–d.* **O. bazhenovae,* northern Siberia; *a–c,* dorsal, ventral, anterior views, ×3; *d,* serial section, ×7 (Lopushinskaya, 1976).

Procarinatina MIZENS & SAPELNIKOV, 1982, p. 18 [**Carinatina silurica* SAPELNIKOV, 1964, p. 9; OD]. Small to medium, biconvex, shield shaped to somewhat wide, flat; ventral valve strongly carinate; dorsal valve with widening median groove; protruding beak; small, apsacline-orthocline area; apical foramen; small deltidial plates; ribs fine to medium; ventral midribs raised; ribs interrupted by wavelike, closely spaced, short growth lamellae or interruptions; commissure rectimarginate to bilobate, or weakly sulciplicate; pedicle callist absent; short, wide teeth; relatively large dental cavities; hinge plate thick; crura, jugal processes, and spiralia undescribed. [Similar to *Protatrypa* in carination, but differing in having dental cavities, thin hinge plate with cardinal pit, sulciplicate commissure; differs from *Dihelictera* in strong carination, nature of growth lamellae, sulciplicate commissure.] *Silurian (Wenlock–Ludlow):* Urals.——FIG. 944,*2a–e.* **P. silurica* (SAPELNIKOV), lower Ludlow, eastern Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×1; *e,* serial section, ×6.5 (Mizens & Sapelnikov, 1982).

Protatrypa BOUCOT, JOHNSON, & STATON, 1964, p. 809 [**P. malmoeyensis* BOUCOT, JOHNSON, & STATON, 1964, p. 810; OD]. Medium size, biconvex-ventribiconvex; relatively flat, carinate ventral valve; small, distinct orthocline area; apical foramen; small deltidial plates; ribs weakly undulate to continuous; absent or very short growth lamellae; frills absent; commissure broadly rectimarginate; internally lacking thick pedicle callist; strong teeth with dental nucleus or minute dental cavities; hinge plates thick, low; cardinal pit lacking; prominent, bushy cardinal process in center of hinge plate; spiralia dorsomedial, fewer than 10 whorls; jugal processes tipped by small jugal plates. [Differs from *Atrypa* in flat, wide shape, orthocline area, strong cardinal process, and lacking frills, pedicle callist, and cardinal pit.] *Silurian (lower Llandovery):* North America, Europe, Siberia.——FIG. 948,*2a–g.* **P. malmoeyensis,* Rhuddanian, Norway; *a–d,* dorsal, ventral, anterior, lateral views, ×2; *e–f,* serial sections; *g,* reconstruction of brachidia, ×2.5 (Copper, 1995).

Rugosatrypa RZHONSNITSKAIA, 1975, p. 98 [**R. tschernyschewi* RZHONSNITSKAIA, 1975, p. 99; OD; *vid. Spinatrypina tschernyschewi* RZHONSNITSKAIA, 1964, p. 101, *nom. nud.,* no description]. Small to medium, usually shield shaped, dorsibiconvex to convexoplane; small, distinct orthocline area; protruding beak; apical foramen, deltidial plates in all growth stages; ribs relatively fine, *Atrypa*-like with undulose, short, growth lamellae in regular concentric rows; frills absent; commissure rectimarginate to weakly plicate; shell relatively thin; pedicle callist thin to absent; teeth moderately strong; prominent dental cavities; hinge plate modest; socket plates thin; crura delicate; spiralia, jugal processes undescribed. [Shell generally *Atrypa*-like in shape, rib structure, growth lamellae, but possessing orthocline area, deltidial plates, dental cavities, lacking thick pedicle callist, frills; similar to *Endrea* externally, but more finely ribbed, smaller sized.] *Silurian (?Ludlow), Lower Devonian (Lochkovian–Emsian):* Eurasia, North America.——FIG. 948,*1a–e.* **R. tschernyschewi,* Emsian, southern Siberia; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e,* detail of ornamentation, ×4 (Rzhonsnitskaia, 1975).

?Togatrypa HAVLÍČEK, 1987a, p. 76 [**T. fantomas;* OD]. Small to medium, moderately dorsibiconvex; beak adpressed; area absent; foramen transapical or absent; deltidial plates lacking; ribs coarse, undulose, *Spinatrypa*-like; interrupted by wavelike concentric lamellae extended as less than 5-mm-wide commissural frills; rectimarginate commissure; thick pedicle callist; short, solid teeth with lateral processes, lacking nuclei or cavities; socket plates thin, subvertically oriented; crura small; spiralia and jugal processes undescribed. [Possibly synonymous with or ancestral to *Atryparia;* may be mistaken for *Spinatrypa,* but spines absent, with short frills, pedicle callist; similar to *Atrypa* and *Gotatrypa* internally, especially in pedicle callist, hinge plate, teeth, but with very coarse ribs.] *Lower Devonian (Lochkovian–Pragian):* Czech Republic.——FIG. 948,*3a–f.* **T. fantomas,* Lochkovian; *a–d,* dorsal, ventral, posterior, lateral views, ×2; *e–f,* serial sections, ×5 (Havlíček, 1987a).

Zygospiraella NIKIFOROVA, 1961, p. 237 [**Terebratula duboisi* DE VERNEUIL, 1845, p. 97; OD] [=*Megumatrypa* HARPER, 1973, p. 72 (type, *M. glencoensis,* OD); *Cryptospira* LAURIE, 1991, p. 100 (type, *C. intraplicata* LAURIE, 1991, p. 101, OD)]. Small, planoconvex to ventribiconvex, lacking distinct carination; small orthocline area; apical-transapical foramen; ribs continuous, anteriorly interrupted by short growth interruptions; frills absent; rectimarginate to weakly sulcate commissure; short teeth; small dental cavities; hinge plate shallow; wide cardinal pit; small crural bases; partly feathered crura; mediodorsal spiralia with fewer than 6 whorls; jugal processes tipped by small jugal plates. [Hinge plates, jugal processes, and crura as in *Protatrypa,* but differing in small size, convexity, lack of carination, presence of cardinal pit.] *Silurian (lower Llandovery):* Eurasia, North America, Tasmania. ——FIG. 949*a–d.* **Z. duboisi* (DE VERNEUIL), Rhuddanian, Estonia; serial sections, and reconstruction of brachidia, ×5 (Copper, 1982).——FIG. 949*e–j. Z. planoconvexa* (HALL), Rhuddanian,

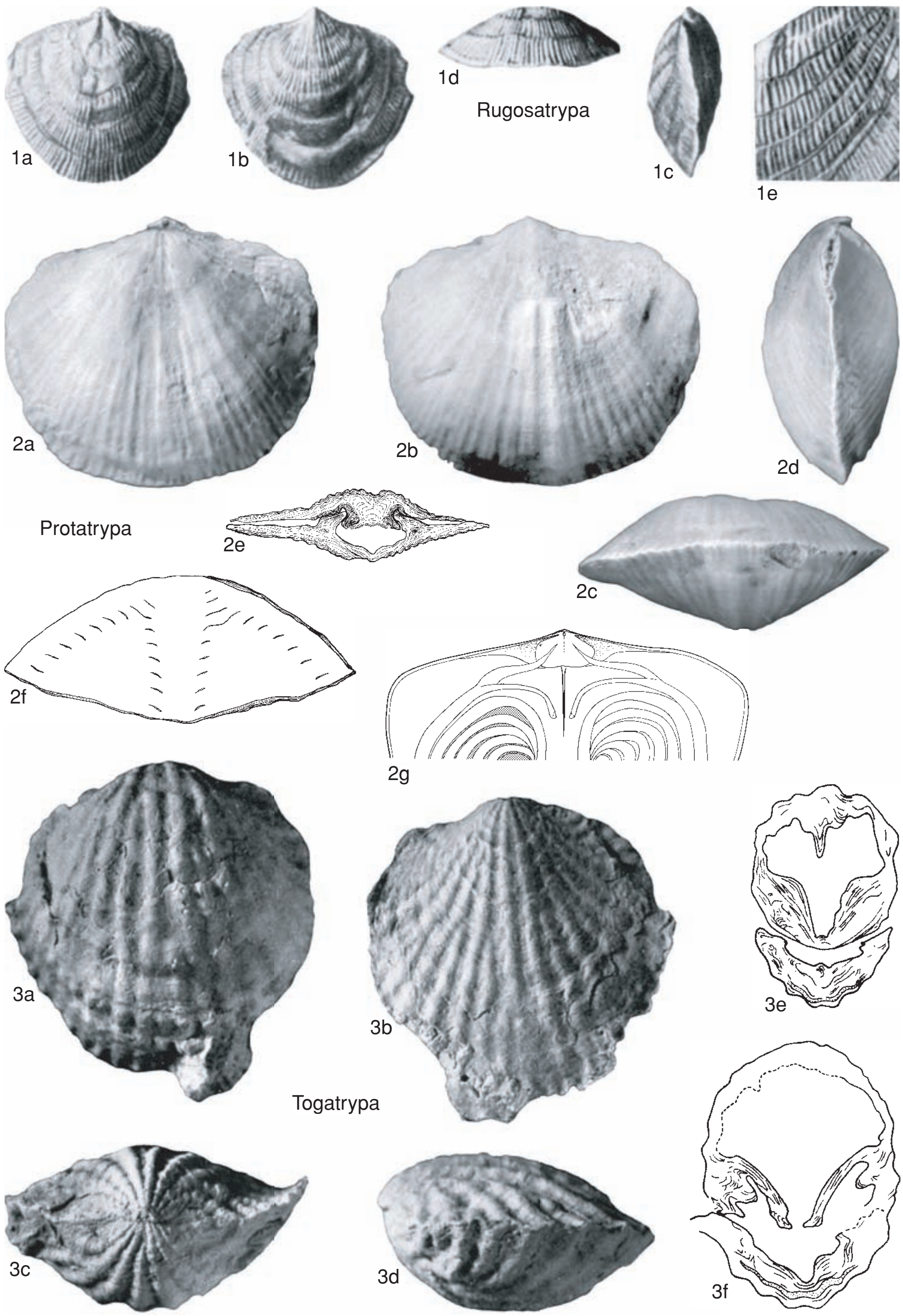

FIG. 948. Atrypidae (p. 1400).

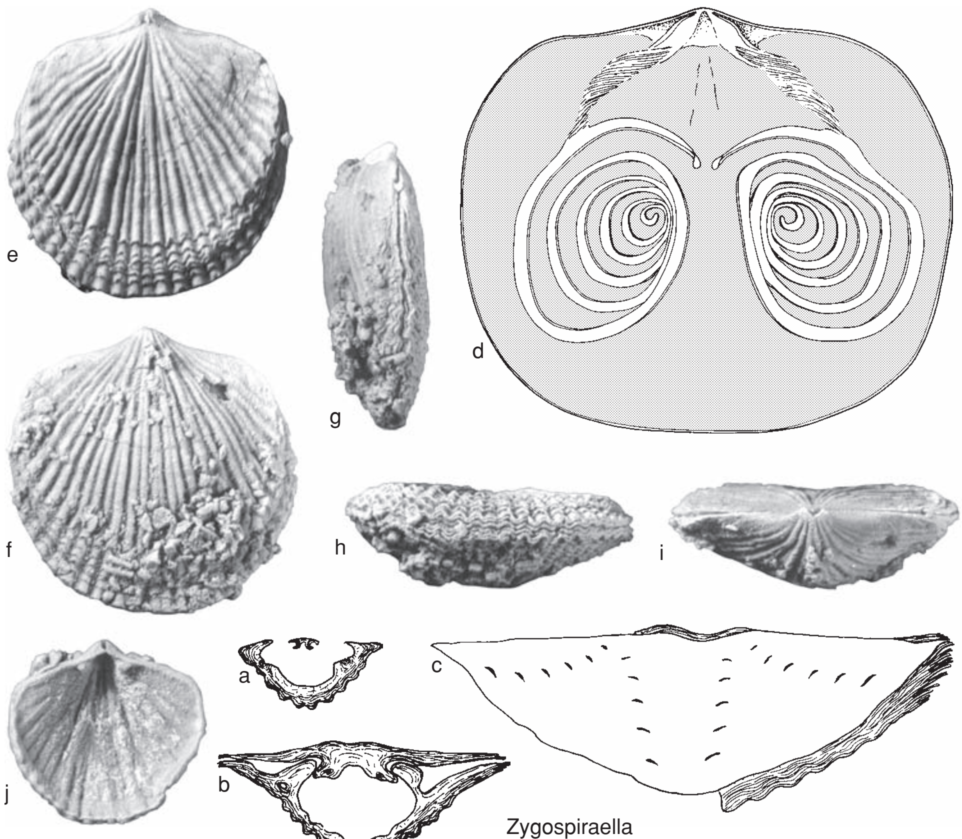

FIG. 949. Atrypidae (p. 1400–1402).

eastern Canada; dorsal, ventral, lateral, anterior, posterior views, internal ventral valve, ×2 (Copper, 1982).

Subfamily INVERTININAE Copper & Chen, 1995

[Invertininae COPPER & CHEN, 1995, p. 251]

Small to medium, fine, tubular to imbricately ribbed, lacking carination; short growth lamellae; frills absent; prominent orthocline-procline area; valves commonly asymmetrical, fixosessile-cemented via ventral valve apex; pedicle callist normally well developed, commonly with pedicle collar pressed against thick deltidial plates; teeth strong, solid, lacking dental cavities; muscle field commonly raised on solid platform; hinge plates thick, spiralia mediodorsal; jugal processes small. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Invertina COPPER & CHEN, 1995, p. 254 [**Atrypa aspera* var. *sinensis* VON RICHTHOFEN, 1883, p. 83; OD]. Small to medium, elongate, planoconvex-ventribiconvex (weakly convex ventral valve); orthocline-anacline area; apical-transapical foramen; small deltidial plates; ribs fine to medium, imbricate, intersected by numerous, closely spaced, short growth lamellae (spines absent); internally moderate pedicle callist integrated with deltidial plates; teeth solid, strong, with lateral lobes; small cardinal process in cardinal pit overlapping inner socket ridges; crura short, partly fibrous, extended from long inner socket ridges; dorsomedial spiralia with fewer than 8 whorls; jugal processes terminating in small, stubby jugal plates. [Externally similar to *Spinatrypina* but planoconvex, with solid teeth, pedicle callist, lacking dental cavities; differs from *Falsatrypa* and *Kerpina* in normal bilateral symmetry, smaller area, coarser ribs; differs from *Iowatrypa*

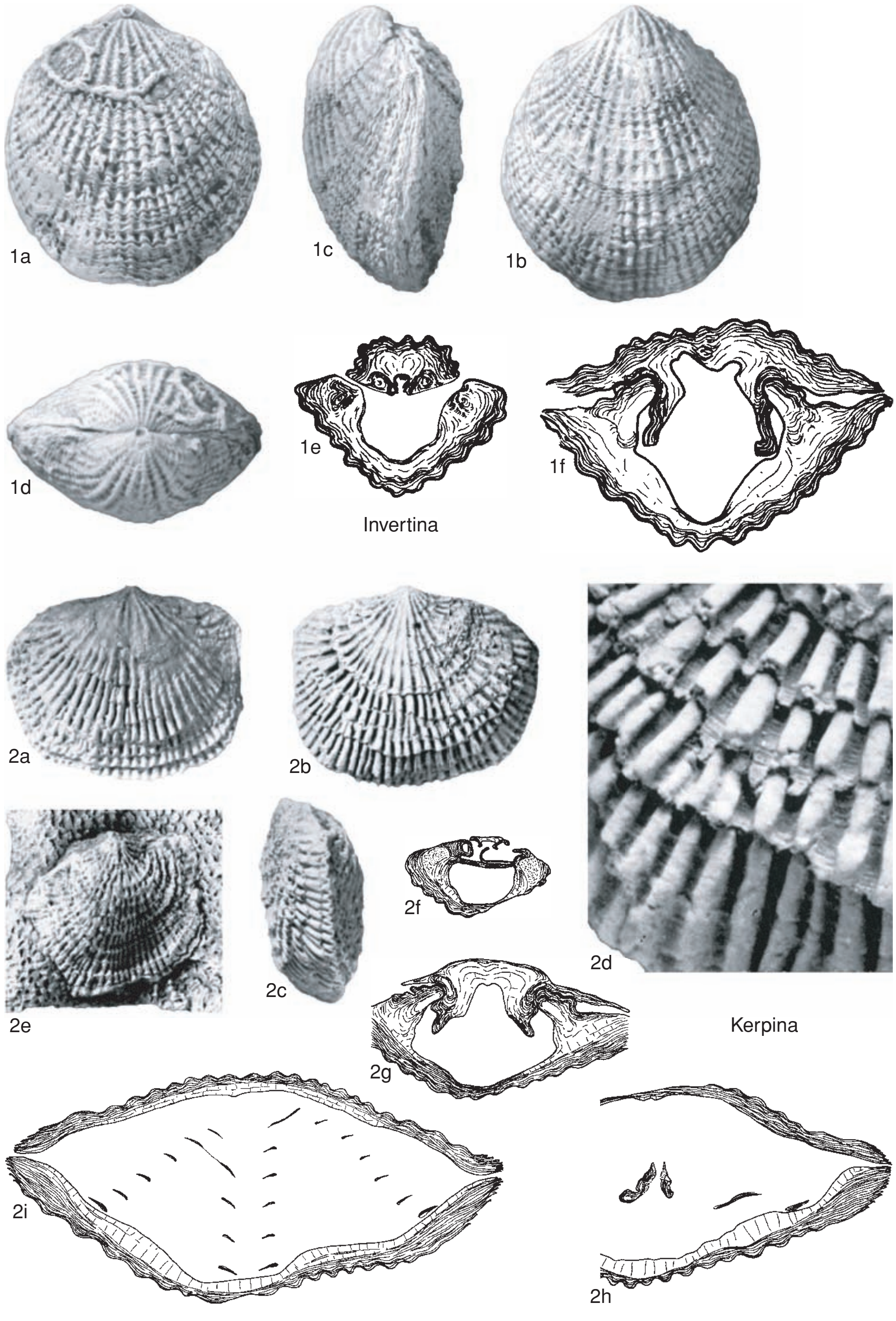

FIG. 950. Atrypidae (p. 1402–1404).

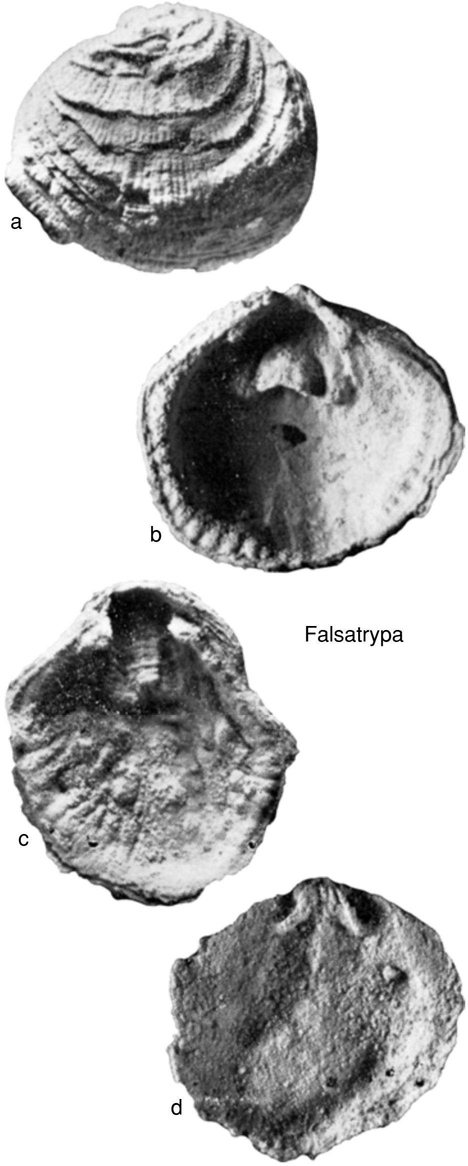

FIG. 951. Atrypidae (p. 1404).

in imbricate-tubular ribs.] *Middle Devonian (Givetian):* China, North Africa.——FIG. 950,*1a–f.* **I. sinensis* (VON RICHTHOFEN), lower Givetian, Sichuan; *a–d,* dorsal, ventral, lateral, posterior views, ×2; *e–f,* serial sections, ×5 (new).

?**Falsatrypa** HAVLÍČEK, 1956, p. 584 [**F. admiranda;* OD]. Small, usually asymmetric (possibly fixosessile), ventribiconvex-planoconvex; wide, deformed orthocline-apsacline area; apical foramen; deltidial plates; fine, tubular-imbricate ribs; rectimarginate commissure; short, overlapping growth lamellae; teeth solid, lacking dental cavities; crura, spiralia, jugal processes undescribed. [Poorly preserved, rare genus of problematic affinity (*vid.* HAVLÍČEK, 1967a), assigned by HAVLÍČEK (1987a) to Lissatrypidae; possibly synonymous with *Kerpina,* but more finely ribbed, smaller.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Czech Republic.——FIG. 951*a–d.* **F. admiranda,* Emsian; *a–c,* ventral external, internal, internal views, approximately ×4; *d,* dorsal internal view, approximately ×6 (Havlíček, 1987a).

Kerpina STRUVE, 1961, p. 333 [**K. vineta vineta;* OD] [=*Adaptatrypa* STRUVE, 1980, p. 412 (type, *A. heckeri,* OD)]. Small to medium, usually with asymmetric growth (commonly fixosessile), variable convexity from ventribiconvex-concavoconvex; proportionally large, very wide, sharp edged, often twisted, procline-orthocline area; large apical foramen; relatively wide deltidial plates; fine to medium tubular-imbricate ribs; overlapping, short growth lamellae; rectimarginate to weakly plicate commissure; pedicle collar conjunct to thick deltidial plates; teeth solid, lacking dental cavities; spiralia dorsomedial, with fewer than 8 whorls; jugal processes curved together in V-shape, tipped by jugal plates. [Possibly synonymous with *Falsatrypa,* but brachidia for *Falsatrypa* undescribed.] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian, ?lower Givetian):* western Europe, Urals (western slopes).——FIG. 950,*2a–i.* **K. vineta vineta,* upper Eifelian, Germany; *a–c,* dorsal, ventral, lateral views, ×2; *d,* enlarged detail ornament, ×8; *e,* specimen fixed to alveolitid coral, ×2; *f–i,* serial sections, ×4 (Copper, 1967e).

Subfamily PSEUDOGRUENEWALDTIINAE Rzhonsnitskaia, Yudina, & Sokiran, 1997

[*nom. correct.* COPPER, herein, *pro* Pseudogruenewaldtinae RZHONSNITSKAIA, YUDINA, & SOKIRAN, 1997, p. 57]

Ventribiconvex to planoconvex, small to large shells, ribbing as in Atrypinae, lacking carination and with no frills or only short growth lamellae (less than 1 mm); beak orthocline-anacline; pedicle callist to collar variably developed, teeth strong, lacking dental cavities, muscle field normally raised on thick platform, thick hinge plates; spiralia mediodorsal, small jugal processes. *Upper Devonian (Frasnian):* worldwide.

Pseudogruenewaldtia RZHONSNITSKAIA, 1960b, p. 48 [**P. tschernyschewi;* OD]. Medium to large, inflated ventribiconvex-biconvex, rounded to elongate; small, hypercline area, obscuring deltidial plates; large transapical foramen, beak anacline-hypercline; ribs fine, interrupted by numerous, closely spaced growth lamellae; shell wall thick; pedicle callist

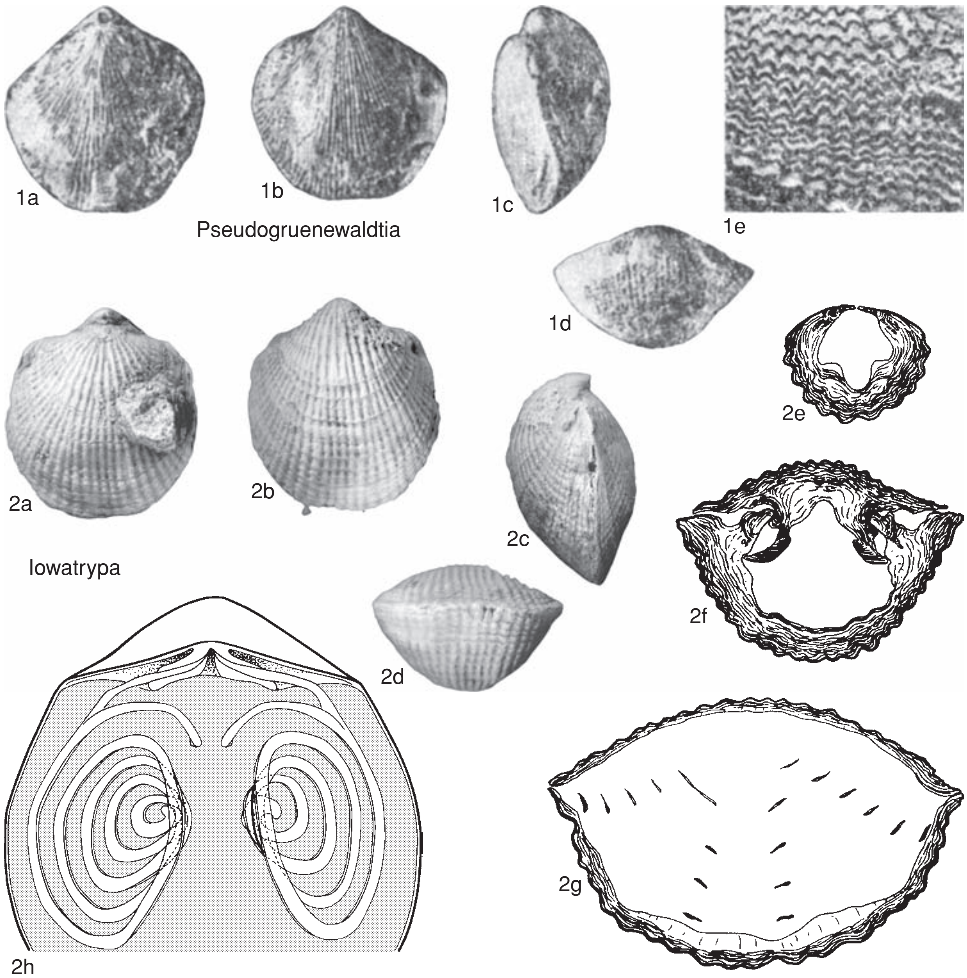

FIG. 952. Atrypidae (p. 1404–1405).

divided by central groove; hinge plate strong; cardinal pit small; socket plates thin; spiralia mediodorsal; crura, jugal processes undescribed. [Differs from closely related *Iowatrypa* in larger shell, hypercline area with large transapical foramen, lack of deltidial plates, raised muscle platform; distinguished from *Anatrypa* by microornament of overlapping growth lamellae; distinguished from *Gruenewaldtia* by lack of septally raised muscle platform.] *Upper Devonian (Frasnian):* northern Urals, Poland, Germany.——FIG. 952,*1a–e.* **P. tschernyschewi,* Timan, Russia; *a–d,* dorsal, ventral, lateral, anterior views, ×1; *e,* detail of macroornament, ×4 (Rzhonsnitskaia, 1964).

Iowatrypa COPPER, 1973c, p. 495 [**Atrypa owenensis* WEBSTER, 1921, p. 14; OD]. Small, elongate to equidimensional, planoconvex-ventribiconvex; commonly with short, straight hinge; small, orthocline-anacline area; apical foramen; minute deltidial plates; ribs relatively fine, *Atrypa*-like; numerous, tightly spaced, non-deflected, very short growth lamellae; commissure rectimarginate; interior with relatively thick ventral valve; usually thick pedicle callist or collar; short teeth with notch for crura; small dental cavities or nuclei; incised muscle scars; prominent, thickened ventral muscle platform; crural bases Z-shaped; crura short, stubby; spiralia dorsomedial, fewer than 8 whorls; jugal processes thick, ending in minute jugal plates. [Similar to *Pseudogruenewaldtia,* but smaller, ventribiconvex-planoconvex shell, possessing apical foramen, deltidial plates, and raised ventral muscle platform.] *Upper Devonian (Frasnian):* North America, Europe, Urals, China.——FIG. 952,*2a–h.* **I. owenensis* (WEBSTER), upper Frasnian, Iowa; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e–g,* serial sections; *h,* reconstruction of brachidia, ×5 (new).

Subfamily SPINATRYPINAE Copper, 1978

[Spinatrypinae COPPER, 1978, p. 297]

Atrypides with ribs disrupted into waves, commonly producing nodular surface macroornament; commonly spinose or imbricate; growth lamellae short, may be projected up to about 10 mm as irregular spines from rib crests; ventral valve noncarinate; usually small beak; small orthocline-anacline area; deltidial plates reduced or covered; apical-transapical foramen; rectimarginate to plicate commissure; pedicle callist thin to moderate; pedicle collar rarely developed; teeth with dental cavities, lateral lobes; small cardinal process in cardinal pit; spiralia dorsomedial, about 15 whorls in large shells; jugal processes normally terminating in stubby, short jugal plates. [Considerable infrageneric and infraspecific variability in convexity and spinosity for Wenlockian to Emsian forms suggests that such ancestral taxa as *Eospinatrypa, Punctspinatrypa,* and *Oglu* may be synonymous or should be considered as subgenera; ancestry of subfamily lies with Plectatrypinae.] *Silurian (?Telychian, Wenlock)–Upper Devonian (Frasnian).*

Spinatrypa STAINBROOK, 1951, p. 196, *nom. nov. pro Hystricina* STAINBROOK, 1945, p. 49, *non* MALLOCH, 1932 [**Atrypa hystrix* var. *occidentalis* HALL, 1858a, p. 515; OD] [=*Plicspinatrypa* RZHONSNITSKAIA in RZHONSNITSKAIA & others, 1998, p. 322 (type, *Spinatrypina plicata* RZHONSNITSKAIA, 1975, p. 124, OD, *vid. Spinatrypina plicata* RZHONSNITSKAIA, 1964, p. 108, *nom. nud.*)]. Medium to large, dorsibiconvex to convexoplane; small orthocline-hypercline area; foramen apical-transapical; deltidial plates commonly lost or obscured by beak incurvature; ribs coarse to very coarse, rarely becoming almost smooth; strong, wavelike growth lamellae developing into coarse, irregular spines up to 15 mm long; moderately to strongly plicate commissure; interior with thin pedicle callist or collar; teeth large, with accessory lobes; dental cavities small to prominent (i.e., strong dental plates); hinge plates strong; crura curved, feathered; dorsal spiralia with 8 to 15 widely spaced whorls; long jugal processes terminating in large, spatulate jugal plates. [Distinguished from *Isospinatrypa* and *Spinatrypina* by large size, very coarse, undulose ribs, long spines, more prominent area, deltidial plates, larger dental cavities. STAINBROOK first described the genus as *Hystricina* (1945), which turned out to be preoccupied, so he substituted *Spinatrypa* (1951). When he cited the type he indicated *Atrypa aspera* var. *occidentalis,* for he misread the original HALL description that said *Atrypa hystrix* var. *occidentalis* (corrected, but not by STAINBROOK). In 1938, moreover, STAINBROOK had already raised *occidentalis* to species rank, which he had forgotten about by 1945. RZHONSNITSKAIA described *Plicspinatrypa* as part of a wider paper by her and others in 1998 (she alone is listed as author of the genus). The type of *Plicspinatrypa* is cited as *Spinatrypina plicata* RZHONSNITSKAIA, 1964; unfortunately in 1964 she never described the species and just published a single figure. She finally described the species *plicata* in 1975, which then validates the species.] *Middle Devonian (?upper Eifelian, Givetian)–Upper Devonian (Frasnian):* worldwide.——FIG. 953*a–c*. **S. occidentalis* (HALL), Iowa, USA; dorsal, posterior, lateral views, ×2 (new).——FIG. 953*d–e. S. spinosa* (HALL), Givetian, New York, USA; internal views of ventral, dorsal valves, ×2 (new).——FIG. 953*f–g. S. curvirostra* COPPER, lower Givetian, Germany; serial sections, ×3 (Copper, 1967d).

?Catatrypa MIZENS, 1993, p. 3 [**C. schemachensis;* OD]. Small, convexoconcave to questionably convexoplane, ventral valve almost flat; protruding beak, catacline-apsacline area; small apical foramen; ribs coarse, with concentric lamellae, spines; internal structures undescribed except for massive crura, lack of dental cavities. [Distinguished from other spinatrypids by flattened ventral valve, prominent area with catacline-apsacline beak; similar to *Oglu* in convexity, but lacks hypercline beak of *Oglu,* and has apsacline area with apical foramen; possibly a synonym of davidsoniid *?Rugodavidsonia,* with comparable asymmetry, ribs, area, and foramen; may also be aberrant *?Kerpina.*] *Middle Devonian (Eifelian):* western slopes of Urals.——FIG. 954,*1a–c*. **C. schemachensis;* ventral, dorsal, lateral views, ×3 (Mizens, 1993).

Eospinatrypa COPPER, 1973c, p. 496 [**Atrypa nodostriata* HALL, 1852, p. 272; OD] [=*Morinatrypa* HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 165 (type, *M. mergli,* OD]. Small to medium, round to elongate or shield shaped, biconvex; small, orthocline area; apical (rarely transapical) foramen; minute deltidial plates; weak anterior fold; ribs few, coarse, bifurcating ventrally, intercalating dorsally, weakly raised ventral midrib pair; spines absent, rarely capidulate; short, weakly deflected, undulose growth lamellae; thin wall; pedicle callist thin or lacking; small, delicate teeth; small dental cavities; hinge plates thin; crural bases rounded; crura short; dorsomedial spiralia, fewer than 8 whorls; nodose jugal processes; thin, scooplike jugal plates. [Distinguished from *Spinatrypa* by small size, lack of spines, delicate tooth and socket structure, fewer spiralial whorls.] *Silurian (?Telychian, Wenlock–Přídolí):* North America, Eurasia.——FIG. 955,*1a–c*. **E. nodostriata* (HALL), Wenlock, New York; *a–c,* dorsal, ventral, posterior views, ×2 (Copper, 1973c).——FIG. 955,*1d–g. Eospinatrypa* sp., upper Wenlock, Gotland; *d–f,* serial sections; *g,* reconstruction of brachidia, ×5 (new).

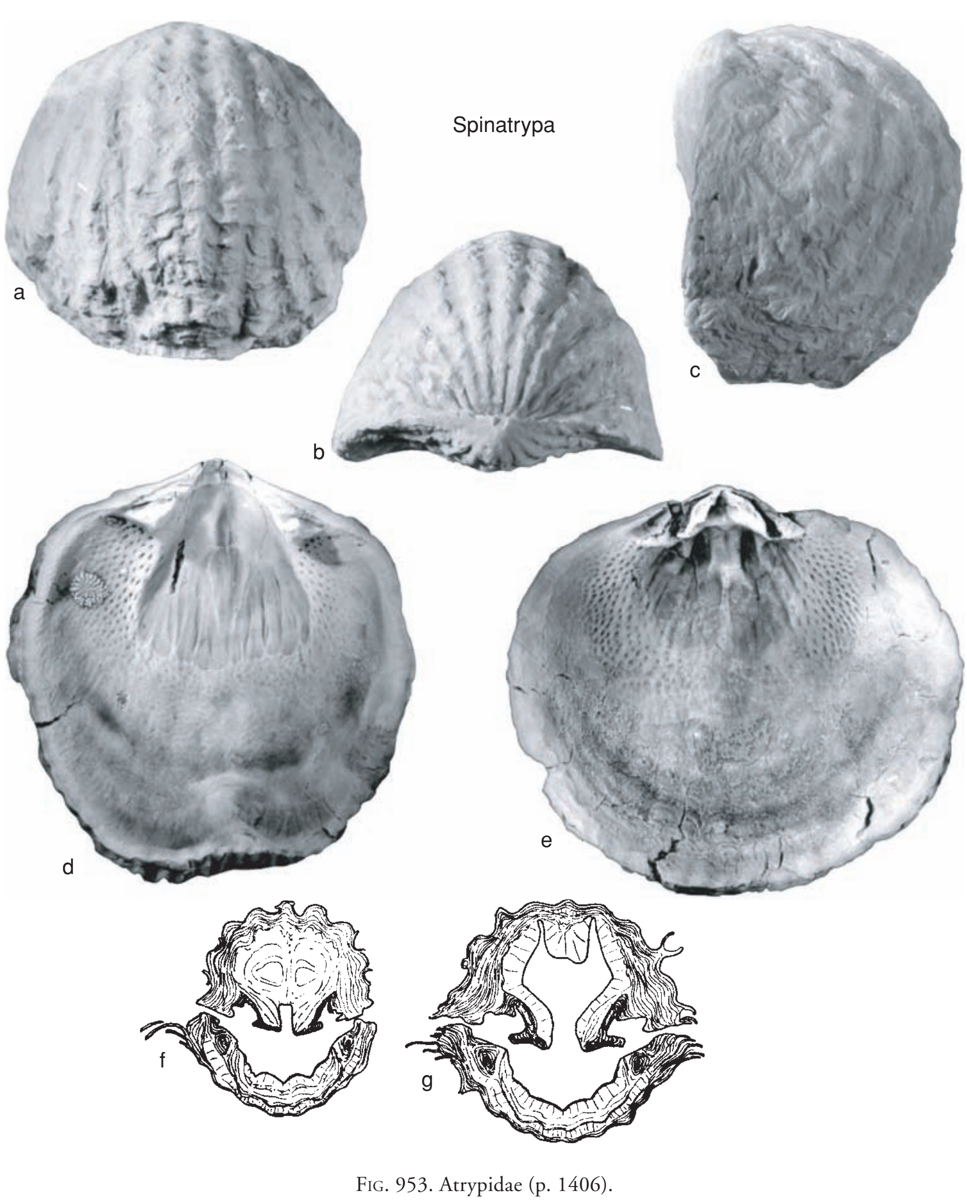

FIG. 953. Atrypidae (p. 1406).

?Gibberosatrypa MARKOVSKII & RZHONSNITSKAIA in RZHONSNITSKAIA & others, 1998, p. 316 [**Atrypa gibberosa* MARKOVSKII, 1989, p. 90; OD]. Medium size, relatively coarsely ribbed; subquadrate to subcircular shell, subcarinate ventrally, with broad, flat fold anteriorly; interior unknown. [Coarser ribs suggest *Spinatrypa* derivation, with some external similarities to *Carinatrypa* and *Mogoliella;* original material described by MARKOVSKII (1989) resembles spinatrypid; assignment unclear.] *Upper Devonian (Frasnian):* Urals, Russian Platform.——FIG. 956,*1a–d*. **G. gibberosa* (MARKOVSKII), upper Frasnian, southwestern Urals; dorsal, ventral, lateral, anterior views, ×2 (Rzhonsnitskaia & others, 1998).

Invertrypa STRUVE, 1961, p. 334 [**Spinatrypa kelusiana* STRUVE, 1956, p. 385; OD]. Small to medium, ventribiconvex-planoconvex-concavo-convex; small, hypercline area; foramen transapical; deltidial plates absent or minute, obscured by beak; anterior commissure rectimarginate, rarely weakly sulcate; ribs coarse, undulose to nearly flat, ending in 4 to 5 mm long, straight spines, especially on ventral valve; strongly developed ventral midrib keel

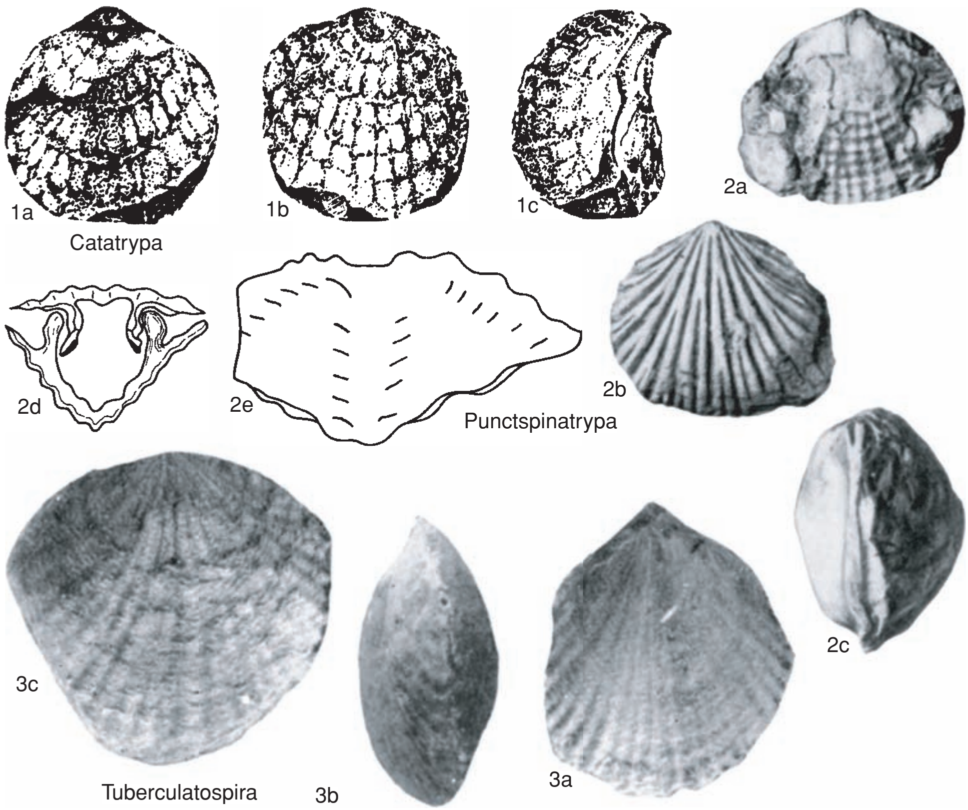

FIG. 954. Atrypidae (p. 1406–1412).

from 2 ribs; internally shell relatively thick; teeth short; small dental cavities; crura feathered; spiralia dorsomedial, fewer than 10 whorls; jugal processes with minute jugal plates. [Distinguished from *Spinatrypa* by small size, reversed convexity, rectimarginate commissure, relatively strong ventral midrib plan, obscured hypercline area; distinguished from *Isospinatrypa* by almost flat ribs, hypercline area, absence of deltidial plates, enlarged ventral midrib pair; distinguished from *Oglu* by reversed convexity.] *Middle Devonian (upper Eifelian–lower Givetian):* Europe, northwestern Canada.——FIG. 955,*2a–h.* **I. kelusiana* (STRUVE), upper Eifelian, ?lower Givetian, Germany; *a–d,* ventral, lateral, ventral, dorsal views of 2 specimens, ×2; *e–g,* serial sections, ×4 (Copper, 1967d); *h,* reconstruction of brachidia, ×4 (Copper, 1967b).

Isospinatrypa STRUVE, 1966, p. 155 [**Terebratulites asper* VON SCHLOTTHEIM [sic], 1813, pl. 1, fig. 7 (description, VON SCHLOTHEIM, 1820 in 1820–1823, p. 263); OD; modified to *aspera* by KOENIG, 1825, p. 3] [=?*Hanusitrypa* HAVLÍČEK, 1967a, p. 443 (type, *H. hanusi,* OD)]. Small to medium; biconvex to weakly dorsibiconvex, shield shaped to elongate; small orthocline-anacline area; blunt beak; minute deltidial plates flanking apical-transapical foramen; ribs medium sized, well defined; ventral midribs only slightly raised; short, wavy growth lamellae ending in short, irregular spines on both valves; rectimarginate to weakly plicate commissure; thin pedicle callist; stubby teeth; small dental cavities; spiralia dorsomedial, fewer than 12 closely spaced whorls; jugal processes short, tipped by small, blunt jugal plates. [Distinguished from *Spinatrypa* by small size, finer, well-defined ribs, short spines; distinguished from *Invertrypa* by biconvexity; possibly synonymous with *Oglu* but with reduced pedicle callist, clearly defined ribs.] *Lower Devonian (?Lochkovian, Emsian)–Middle Devonian (lower Givetian):* worldwide.——FIG. 956,*3a–i.* **I. aspera* (VON SCHLOTHEIM), upper Eifelian, Germany; *a–d,* dorsal, ventral, posterior, posterior views, ×2; *e–f,* internal view dorsal, ventral valve, ×2; *g–i,* serial sections, ×4 (Copper, 1967d).

?Oglu HAVLÍČEK, 1987a, p. 81 [**Terebratula semiorbis* BARRANDE, 1847, p. 454; OD]. Small to medium, elongate-equidimensional, dorsibiconvex-convexoplane; hypercline area; deltidial plates lacking;

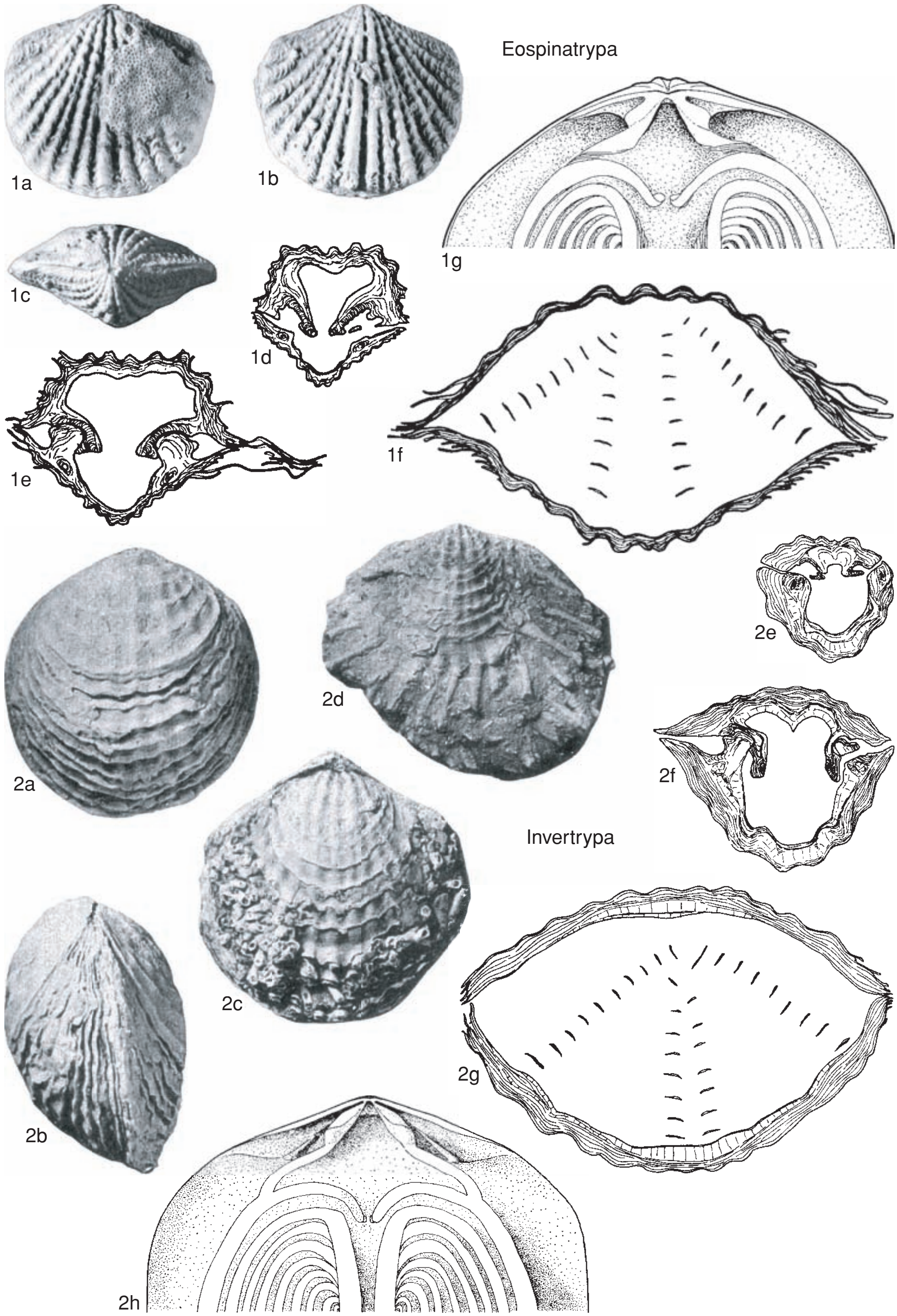

FIG. 955. Atrypidae (p. 1406–1408).

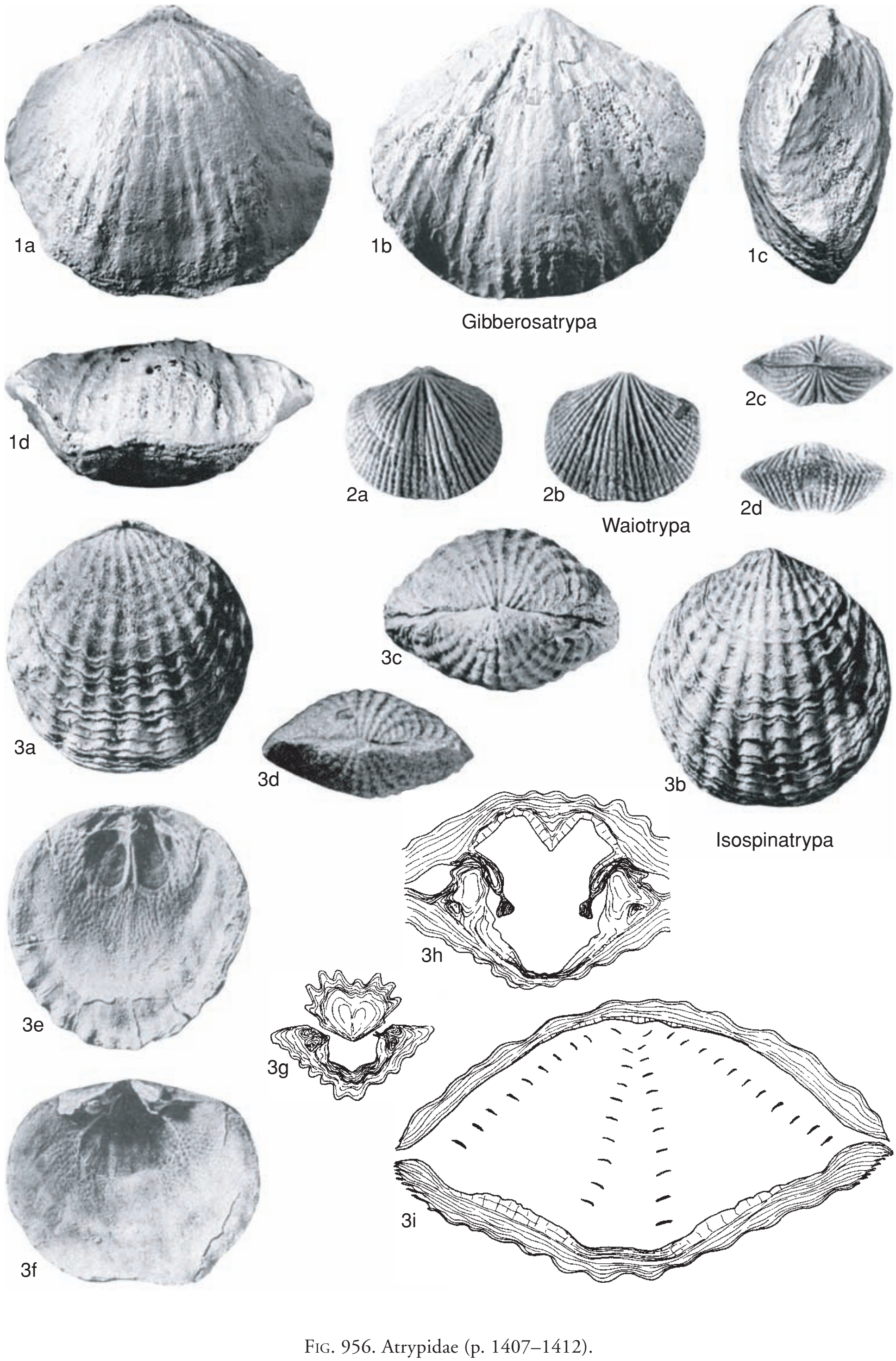

FIG. 956. Atrypidae (p. 1407–1412).

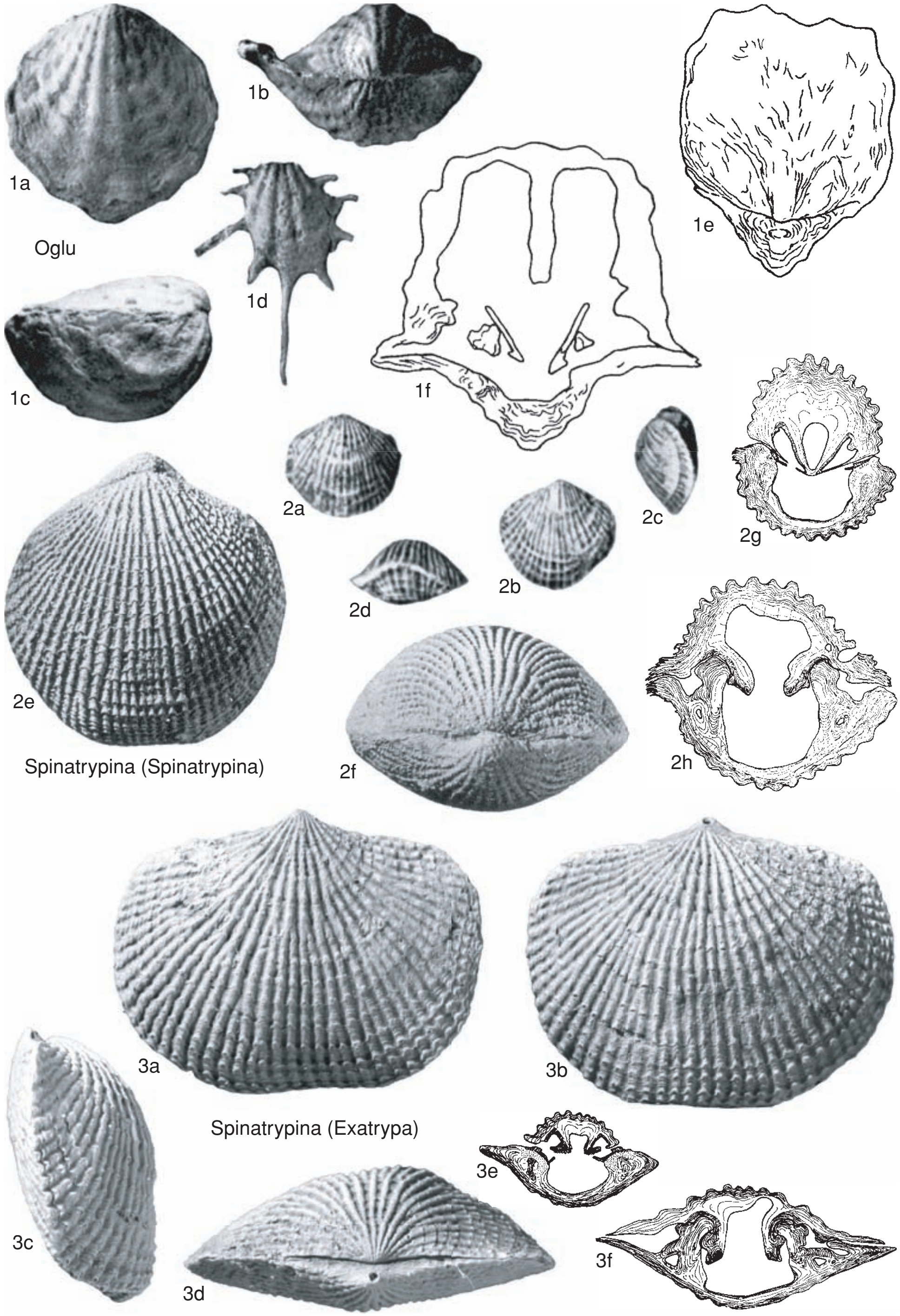

FIG. 957. Atrypidae (p. 1408–1412).

foramen transapical or lacking; relatively few, expanding, rarely bifurcating, undulose ribs, strong ventral midrib pair; simple growth lamellae on ventral valve; short spines possibly limited to dorsal valve; rectimarginate commissure; thick pedicle callist; solid teeth; crura strongly arcuate; spiralia, jugal processes undescribed. [Possible synonym of *Eospinatrypa* or *Punctspinatrypa,* differing in reversed convexity; distinguished from *Isospinatrypa* and *Eospinatrypa* by thick pedicle callist, possible restriction of spines to brachial valve, hypercline area, convexoplane shell; lack of deltidial plates. Differences between *Isospinatrypa, Oglu,* and *Punctspinatrypa* are relatively minor, and may not be sufficient to allow even subgeneric distinction.] *Lower Devonian (Pragian–Emsian):* Europe, northern Africa, Urals.——FIG. 957,*1a–f.* **O. semiorbis* (BARRANDE), Pragian, Czech Republic; *a–c,* ventral, posterior, lateral views, approximately ×3.7; *d,* dorsal valve, ×1.5; *e–f,* serial sections, ×5 (Havlíček, 1987a).

?Punctspinatrypa RZHONSNITSKAIA, 1975, p. 116 [**Atrypa rejensis* KHODALEVICH, 1951, p. 79; OD] [=*Atrypunculus* HAVLÍČEK, 1987a, p. 94 (type, *A. hians* HAVLÍČEK, 1987a, p. 95, OD)]. Medium, ventribiconvex-planoconvex, rounded to elongate; hypercline area; concealed deltidial plates, foramen; well-developed ventral midrib pair forming weak carination; ribs coarse, posteriorly relatively straight, interrupted by regular, short growth lamellae along commissure, lacking wavelike interruptions; spines undescribed (shell nonfenestrate); commissure rectimarginate to very weakly plicate; slender, vertically oriented teeth; small dental cavities; slender socket plates; spiralia, jugal processes undescribed. [Fenestrae or punctae attributed to genus absent in topotype specimens of type species, are possibly borings. Convexity, midrib pair as in *Invertrypa,* but internal comparison unavailable; possibly synonymous with *Oglu,* but for convexity, which may be variable.] *Lower Devonian (Pragian–Emsian):* Europe, Urals, central Asia.——FIG. 954,*2a–e.* **P. rejensis* (KHODALEVICH), Pragian, eastern slopes, Urals; *a–c,* dorsal, ventral, lateral views, ×1; *d–e,* serial sections, approximately ×3 (Rzhonsnitskaia, 1975).

Spinatrypina RZHONSNITSKAIA, 1964, p. 101 [**S. margaritoides;* OD] [=*Sibirispira* ALEKSEEVA, 1968, p. 198 (type, *S. inflata* ALEKSEEVA, 1968, p. 200, OD)]. Small to medium, rounded, globose, biconvex to planar; short to longer hinge; small, orthocline area; protruding beak; apical foramen; deltidial plates; fine to medium-sized, tubular-imbricate ribs; spines lacking; short deflected, rhythmic growth lamellae producing strong imbrication; weakly plicate commissure; thin shell wall, lacking pedicle callist or collar; delicate, long teeth; small to large dental cavities; hinge and socket plates thin, delicate; crura straight or partly feathered; dorsomedial spiralia with fewer than 10 whorls; jugal processes tipped by small plates. [Distinct from *Spinatrypa* in fine, tubular-imbricate ribbing, delicate teeth with wide dental cavities; differs from *Atrypinella* and *Reticulatrypa* in larger size, short growth lamellae, coarser ribs, presence of dental cavities.] *Silurian (?Ludlow, Přídolí)–Upper Devonian (Frasnian)*: worldwide.

S. (Spinatrypina). Diagnosis as for genus, but smaller shells, biconvex to weakly dorsibiconvex; short hinge; small to medium dental cavities. *Silurian (?Ludlow, Přídolí)–Upper Devonian (Frasnian)*: worldwide.——Fig. 957,*2a–d.* **S. (S.) margaritoides,* Pragian, Siberia; dorsal, ventral, lateral, anterior views, ×1 (Rzhonsnitskaia, 1975).——FIG. 957,*2e–h. S. (S.) soetenica* (STRUVE), lower Givetian, Germany; *e–f,* dorsal, posterior views, ×2; *g–h,* serial sections, ×3 (Copper, 1967d).

S. (Exatrypa) COPPER, 1967c, p. 123 [**Terebratulites explanatus* VON SCHLOTHEIM, 1820 in 1820–1823, p. 263; OD; modified to *explanata,* QUENSTEDT, 1871 in 1868–1871, explanation to pl. 42]. Similar to *Spinatrypina,* except for normally relatively flat, wide shell, long hinge, wide orthocline-apsacline area, long deltidial plates, rectimarginate commissure. *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian):* worldwide.——FIG. 957,*3a–f.* **S. (E.) explanata* (VON SCHLOTHEIM), lower Frasnian, Germany; *a–d,* ventral, dorsal, lateral, posterior views, ×2; *e–f,* serial sections, ×3 (Copper, 1967c).

?Tuberculatospira XIAN, 1988, p. 223 [**T. elegans;* OD]. Small, ovoid, ventribiconvex; protruding orthocline area; apical foramen flanked by deltidial plates; ribs medium; short growth lamellae; finely wrinkled filose microornament; inner shell wall tuberculate; weakly plicate commissure; thin pedicle callist; teeth with possible dental cavities; brachidia undescribed. [Enigmatic genus, doubtful atrypoid (synonymous with ?*Neocoelia*), or possibly synonymous with *Spinatrypina,* except for external microornament of wrinkled filae.] *Lower Devonian (Emsian)–Middle Devonian (lower Eifelian):* southwestern China (Sichuan).——FIG. 954,*3a–c.* **T. elegans,* lower Eifelian; dorsal, lateral views, detail of ornament, ×5.5 (Xian, 1988).

Waiotrypa BALINSKI, 1997, p. 429 [**W. sulcicarina* BALINSKI, 1997, p. 430; OD]. Small, biconvex, ventrally weakly carinate, dorsally sulcate; commissure rectimarginate to weakly sulcate; small orthocline area, apical foramen, deltidial plates. Surface finely, imbricately ribbed, slightly raised ventral midrib pair. Interior with prominent dental cavities; muscle scars deeply impressed, not raised; spiralia, jugal processes undescribed. [Ribbing, biconvexity, impressed muscle scars, and large dental cavities suggest assignment to *Spinatrypina* species-group, particularly the finely ribbed type of *Exatrypa.*] *Upper Devonian (Frasnian):* western Europe, North America.——FIG. 956,*2a–d.* **W. sulcicarina,* Poland; dorsal, ventral, posterior, anterior views, ×2 (Balinski, 1997).

Subfamily VARIATRYPINAE Copper, 1978

[Variatrypinae COPPER, 1978, p. 292]

Medium to large shells; long, straight ribs, commonly interrupted by widely spaced growth lamellae (expansive frills may produce shells more than 150 mm wide); rarely weakly carinate; normally projecting beak; distinct orthocline-anacline area; prominent, hollow, wrinkled deltidial plates; apical foramen; variably developed pedicle callist, sometimes leading to pedicle collar; teeth with small to large dental cavities; weak to strong, comblike cardinal process in cardinal pit and inner socket ridges; dorsally to dorsomedially directed spiralia in large shells, often with many whorls; long, posteroventral jugal processes tipped by central to ventral, inwardly curved jugal plates. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Variatrypa COPPER, 1966b, p. 12 [**Desquamatia ajugata* COPPER, 1965a, p. 316; OD] [=*Peetzatrypa* RZHONSNITSKAIA, 1975, p. 95 (type, *Dentatrypa? tschumyschensis* RZHONSNITSKAIA, 1968e, p. 142, OD); *Pesterevatrypa* RZHONSNITSKAIA, 1975, p. 93 (type, *P. malosalairica,* OD); *Lichnatrypa* WANG & RONG, 1986, p. 144 (type, *L. decora* WANG & RONG, 1986, p. 146, OD)]. Medium to large, usually shield shaped, dorsibiconvex; relatively long hinge; pointed beak; prominent orthocline area; apical foramen; large deltidial plates commonly corrugated, interlocking; ribs fine to medium, continuous, lacking growth lamellae, may be extended beyond shell margin as single trail; fine concentric filae microornament; commissure gently to strongly plicate; thin pedicle callist; rare pedicle collar; hollow deltidial plates separated from pedicle callist-collar; strong teeth with large dental cavities; thin hinge socket plates; cardinal pit lined by comblike cardinal process; crura highly feathered; spiralia with fewer than 15 whorls; jugal processes hook shaped. [Differs from *Desquamatia* by continuous, uninterrupted ribs, lack of frills, large dental cavities, thin hinge socket plates; differs from *Anatrypa* in dorsibiconvexity, nature of deltidial plates, pedicle callist.] *Lower Devonian (Emsian)–Middle Devonian (Givetian), Upper Devonian (?Frasnian):* worldwide.——FIG. 958,*1a–h*. **V. ajugata* (COPPER), lower Givetian, Germany; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×1; *f–h,* serial sections, ×4 (Copper, 1965a).

Anatrypa NALIVKIN, 1941, p. 172 [**Orthis micans* VON BUCH, 1840, p. 56; OD]. Medium, ventribiconvex-planoconvex, rounded outline; protruding beak, orthocline area; large apical foramen; prominent deltidial plates; finely ribbed; growth lamellae, frills, trail absent; rectimarginate commissure; pedicle callist absent; slender teeth, with accessory lobes; large dental cavities; thin shell wall; delicate hinge plates; crura feathered; spiralia dorsomedial, fewer than 10 whorls; jugal processes terminating in V-shaped plates. [Distinguished from *Variatrypa* and *Radiatrypa* in convexity, lack of projecting trail, nature of deltidial plates inside pedicle cavity.] *Upper Devonian (Frasnian):* Europe, Urals, North America.——FIG. 958,*2a–f.* **A. micans* (VON BUCH), Syas River, Russian Platform; *a–d,* dorsal, ventral, posterior, anterior views, ×2; *e–f,* serial sections, ×5 (new).

Desquamatia ALEKSEEVA, 1960a, p. 421 [**Atrypa (Desquamatia) khavae* ALEKSEEVA, 1960a, p. 423; OD] [=*Cleiothyris* PHILLIPS, 1841, p. 55, *nom. oblit.,* no type species described; *Desquamatia (Synatrypa)* COPPER, 1966b, p. 10 (type, *Desquamatia subzonata* BIERNAT, 1964, p. 319, OD); *Carinatinella* GRATSIANOVA, 1967, p. 97 (type, *C. concentrica,* OD); *Tenuiatrypa* RZHONSNITSKAIA, 1975, p. 91 (type, *T. subsalairica,* OD); *Peshiatrypa* XIAN in XIAN & JIANG, 1978, p. 298 (type, *Atrypa peshiensis* GRABAU, 1931b, p. 181, OD)]. Small to large, ovoid to shield shaped, biconvex to dorsibiconvex; beak small to medium; orthocline-hypercline area; small, commonly obscured foramen; minute deltidial plates; ribs fine to medium, in some coarsening distally, interrupted by regular, concentric growth lamellae; frills short to wide, concentrated around commissure, rarely preserved; commissure weakly to strongly plicate; thin pedicle callist separated from deltidial plates; teeth with small to large dental cavities; hinge plate weak to strong; crura feathered; dorsal spiralia with up to 20 whorls; jugal processes terminating in hooklike jugal plates. [Distinguished from other variatrypinids by nature of growth lamellae and rib size.] *Lower Devonian (Pragian)–Upper Devonian (Frasnian):* worldwide.

D. (Desquamatia). Small to medium, ovoid, rounded outline, inflated, biconvex-weakly dorsibiconvex; relatively short hinged; beak small; short, orthocline-hypercline area; ribs fine to very fine, interrupted by regular, densely spaced concentric growth lamellae; frills short, concentrated around commissure, rarely preserved; commissure weakly plicate; thin pedicle callist separated from deltidial plates; teeth with distinct dental cavities; hinge plate strong; dorsal spiralia with about 10 to 12 whorls. [Distinguished from *D. (Independatrypa)* and *D. (Seratrypa)* in smaller size, inflated, more biconvex shape, finer ribs, closely spaced growth lamellae, absence of large frills.] *Lower Devonian (Pragian)–Middle Devonian (Givetian), Upper Devonian (?Frasnian):* worldwide.——FIG. 959,*2a–c.* **D. (D.) khavae* (ALEKSEEVA), lower Eifelian, eastern slopes, Urals; *a–b,* dorsal, ventral views, ×1; *c,* serial section, ×1.6 (Alekseeva, 1960a).

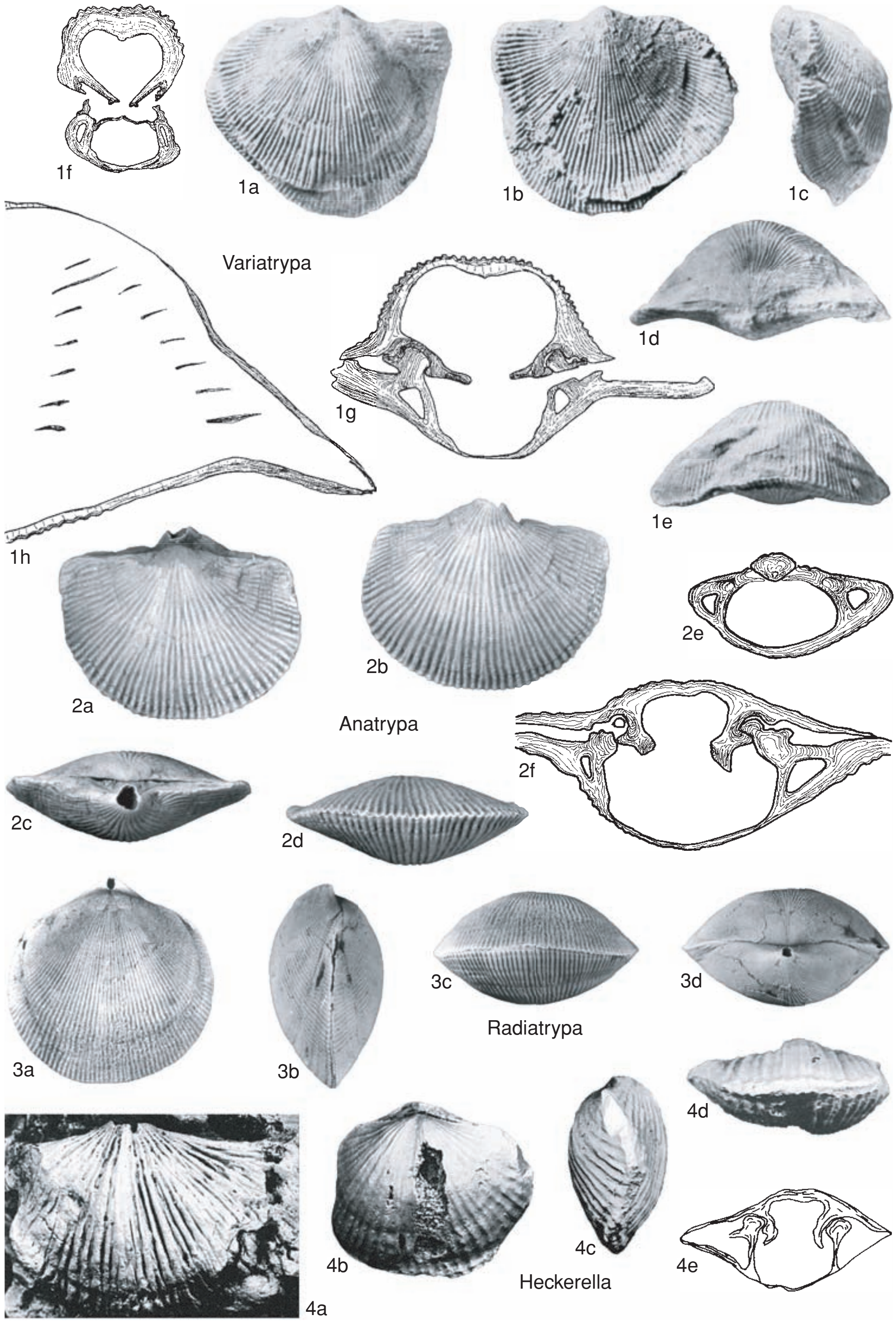

FIG. 958. Atrypidae (p. 1413–1419).

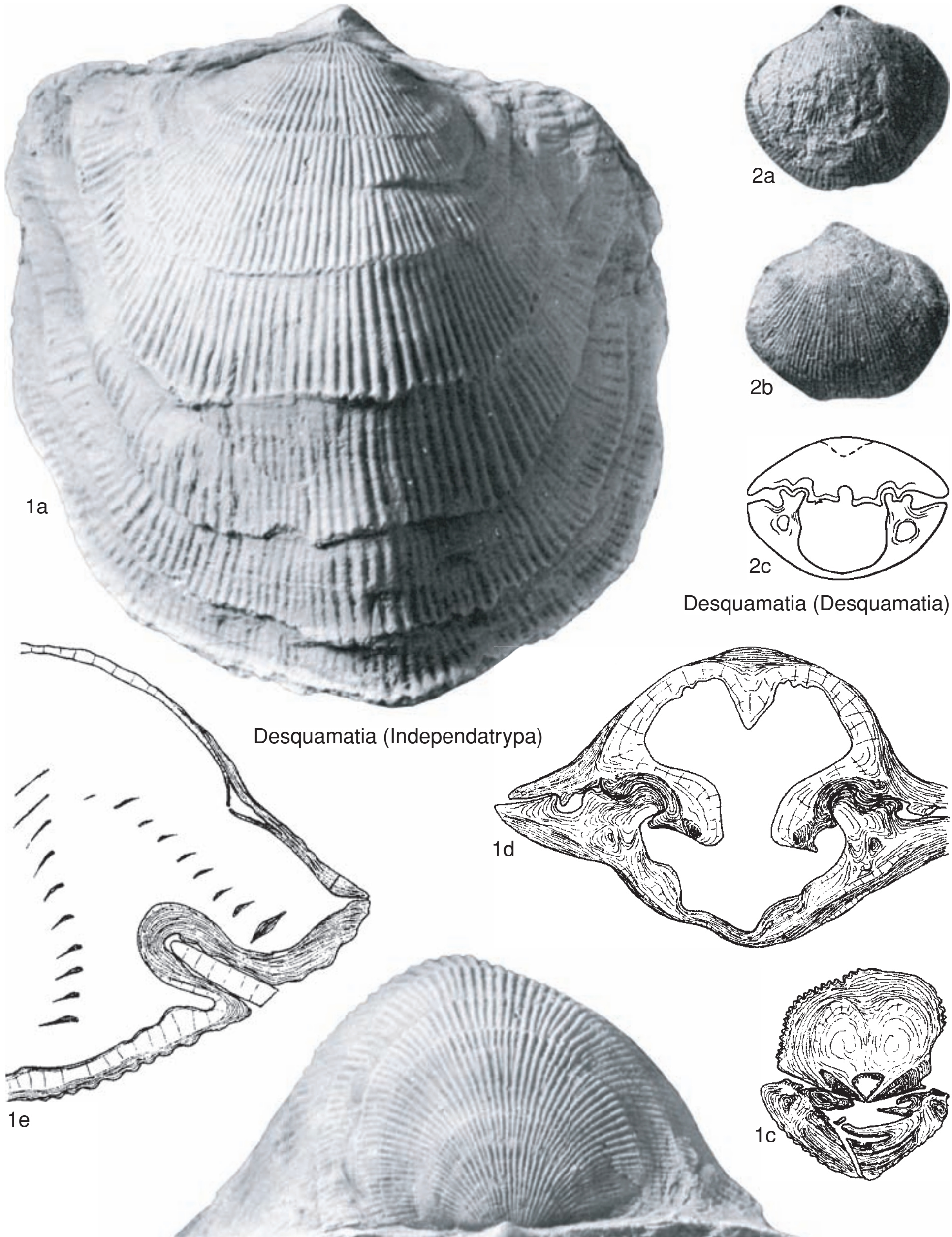

FIG. 959. Atrypidae (p. 1413–1416).

D. (Independatrypa) COPPER, 1973c, p. 493 [**Atrypa independensis* WEBSTER, 1921, p. 15; OD] [=*Puanatrypa* XIAN in XIAN & JIANG, 1978, p. 302 (type, *P. guanziyaoensis,* OD)]. Large to very large, dorsibiconvex to convexoplane, shield shaped; orthocline-anacline area; pointed beak; inflated umbo; apical foramen flanked by hollow deltidial plates; ribs medium, but coarsening slightly distally; widely spaced (2 to 15 mm) growth lamellae with fine concentric filae; wide, multiple frills commonly expanding shell to about 150 mm width; commissure moderately to strongly plicate; interior with thick callist or free pedicle collar; deltidial plates separated from pedicle callist; strong teeth with lateral lobes, prominent dental cavities; socket plates relatively thin; hinge plate thick; comblike cardinal process lining cardinal pit, inner socket ridges; crural bases thick, ball-like; crura feathered; spiralia dorsomedial, up to 20 whorls; jugal processes long, tipped by V-shaped jugal plates. [Distinct from *D. (Desquamatia)* by larger size, dorsibiconvexity, shield shape, widely spaced, large frills; differs from *D. (Seratrypa)* by shield-shape, less inflated shell, prominent pedicle callist, sturdy hinge socket plates.] *Middle Devonian (Eifelian–Givetian):* worldwide.——FIG. 959, *1a–b.* **D. (I.) independensis* (WEBSTER), middle Givetian, Iowa, USA; dorsal, posterior views, ×2 (Copper, 1973c).——FIG. 959,*1c–e. D. (I.) zonata* (SCHNUR), middle Eifelian, Germany; serial sections, ×3 (Copper, 1966b).

D. (Seratrypa) COPPER, 1967c, p. 132 [**Terebratulas pectinatas* SCHRÖTER, 1777, p. 382; OD] [=*Filiatrypa* CHEN Yuan-ren, 1983, p. 309 (type, *F. typica,* OD)]. Medium to large, ovoid-rounded outline, globose, biconvex-dorsibiconvex; ventral valve inflated posteriorly; very small anacline-hypercline area; short hinge; foramen and deltidial plates small or obscured; fine ribs apically, flattening, coarsening and expanding anteriorly; wide, 5- to 10-mm-spaced, concentric growth lamellae, upturned and overlapping distally, commonly producing large, coarsely ribbed frills; concentric filae absent; commissure gently plicate; moderately sized teeth; small dental cavities, may be reduced to dental nuclei; socket plate thin, slender; crura delicate; spiralia with more than 10 whorls; long jugal processes posterocentrally located, large; hook-shaped jugal plates. [Distinguished from other *Desquamatia* by ovoid instead of shield shape, short hinge, coarsening ribs lacking concentric filae, lack of pedicle callist-collar, slender cardinalia.] *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian):* Eurasia, North America.——FIG. 960*a–g.* **D. (S.) pectinata* (SCHRÖTER), lower Frasnian, Germany; *a–d,* dorsal, ventral, lateral, posterior views, ×2; *e–f,* serial sections, ×3 (Copper, 1967c); *g,* reconstruction of brachidia, ×3 (Copper, 1967b).

Devonatrypa RZHONSNITSKAIA, 1964, p. 93 [**Atrypa waterlooensis* WEBSTER, 1921, p. 18; OD] [=*Desquamatia (Neatrypa)* STRUVE, 1966, p. 137 (type, *D. (N.) europaea* STRUVE, 1966, p. 140, OD, =*Terebratulites priscus* VON SCHLOTHEIM, 1820 in 1820–1823, p. 262, SD COPPER, 1967c, p. 134); *Sibiratrypa* RZHONSNITSKAIA, 1975, p. 100 (type, *S. vassinensis,* OD)]. Medium to large, convexoplane, subquadrate to elongate; beak blunt; small, hypercline area; transapical foramen; deltidial plates reduced to lost in ontogeny; ribs coarse, rarely bifurcating-intercalating; growth lamellae widely spaced; frills absent; pedicle callist thin; teeth strong, blunt, with dental nuclei; dental cavities unknown; crural bases knoblike; crura feathered; dorsally directed spiralia, fewer than 13 to 15 whorls; jugal processes tipped by small, blunt jugal plates. [Distinguished from *Desquamatia* by convexoplane shell, coarse ribs, lack of concentric filae, adult deltidial plates, dental cavities, frills.] *Upper Devonian (Frasnian):* Eurasia, North America.——FIG. 961*a–e.* **D. prisca* (VON SCHLOTHEIM), lower Frasnian, Germany; *a–c,* dorsal, lateral, posterior views, ×2; *d–e,* serial sections, ×3 (Copper, 1967c).

Heckerella RZHONSNITSKAIA & SOKIRAN, 2000, p. 426 [**Anatrypa heckeri* NALIVKIN, 1941, p. 173; OD]. Medium size, moderately biconvex, rectimarginate; ventral valve weakly carinate from 2 midribs, dorsal valve slightly sulcate; commissure broadly rectimarginate to weakly paraplicate; small protruding beak, orthocline area, apical foramen and small deltidial plates; ribs fine, tubular, with weak growth interruptions, lacking growth lamellae, frills, or trail; large dental cavities, moderately slender teeth; weak hinge plate, small crural bases; spiralia and jugal processes undescribed. [Presence of filae in rib troughs suggest affinity with *Desquamatia* group, but shell is also broadly similar to *Gibberosatrypa,* from which it differs by a more elongate hinge, dorsal sulcus, and narrower ribs; overall affinity uncertain.] *Upper Devonian (lower Frasnian, ?middle Frasnian):* Europe.——FIG. 958,*4a–e.* **H. heckeri* (NALIVKIN), lower Frasnian, Shelon River, Russian Platform; *a–d,* ventral, dorsal, lateral, anterior views, ×1.5; *e,* serial section, ×3 (Rzhonsnitskaia & Sokiran, 2000).

Pseudoatrypa COPPER, 1973c, p. 492 [**Atrypa devoniana* WEBSTER, 1921, p. 19; OD]. Medium size, convexoplane, weakly convex to anteriorly weakly resupinate ventral valve, subrounded outline; small anacline-hypercline area; apical-transapical foramen; small deltidial plates reduced to lost in adult shell; fine tubular ribs interrupted by closely spaced, regular growth lamellae, crowded anteriorly; frills unknown; commissure weakly to moderately plicate; interior with thin or no pedicle callist; teeth small; dental cavities reduced; hinge socket plates delicate; crura feathered; spiralia dorsal, with fewer than about 12 whorls; jugal processes tipped by small jugal plates. [Distinguished from *Desquamatia* by rounded, ovoid shape, smaller size, closely spaced, less rhythmic growth lamellae, lack of frills, reduction of area, deltidial plates; from *Atrypa* by its minimal pedicle callist, *Desquamatia*-

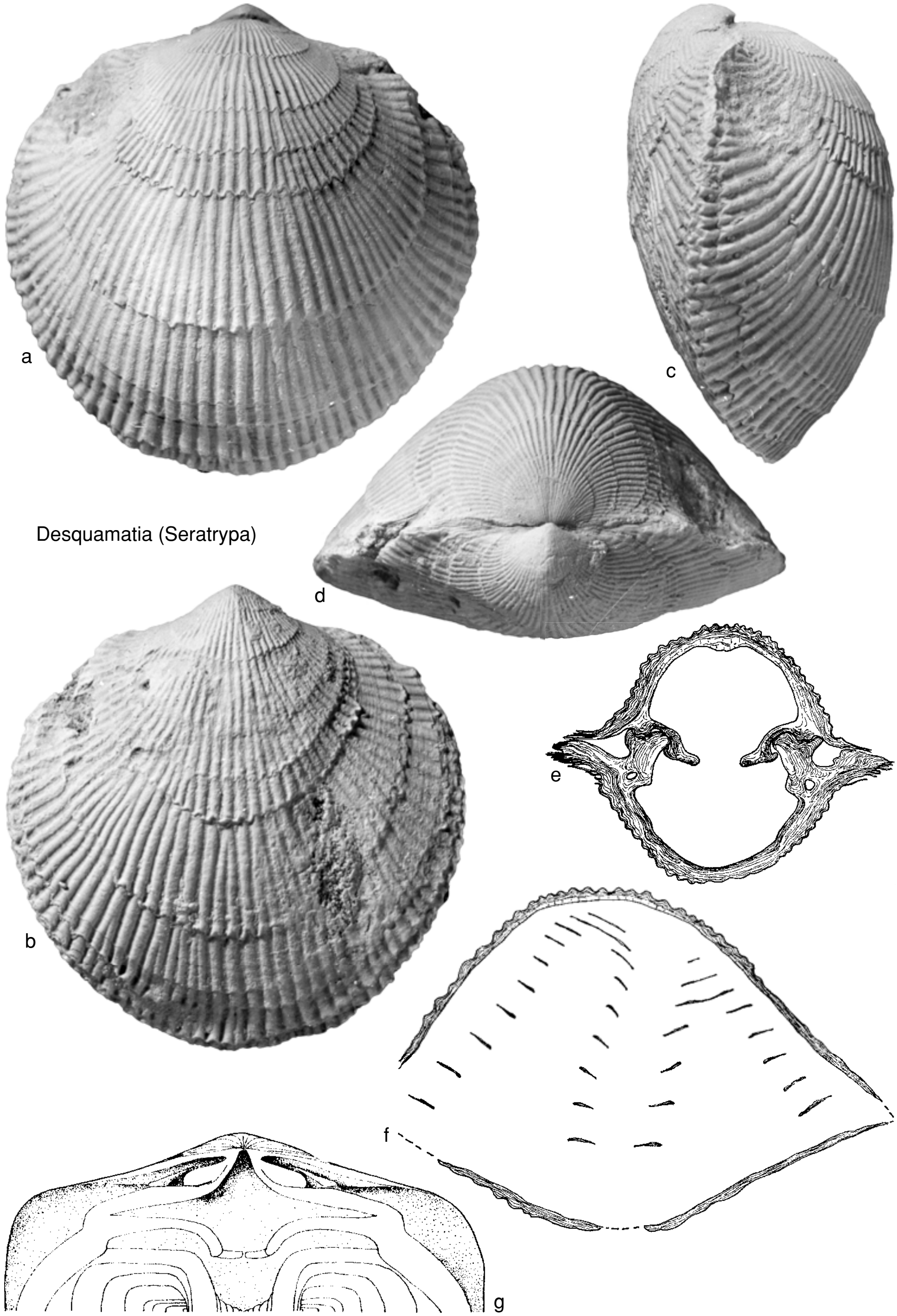

FIG. 960. Atrypidae (p. 1416).

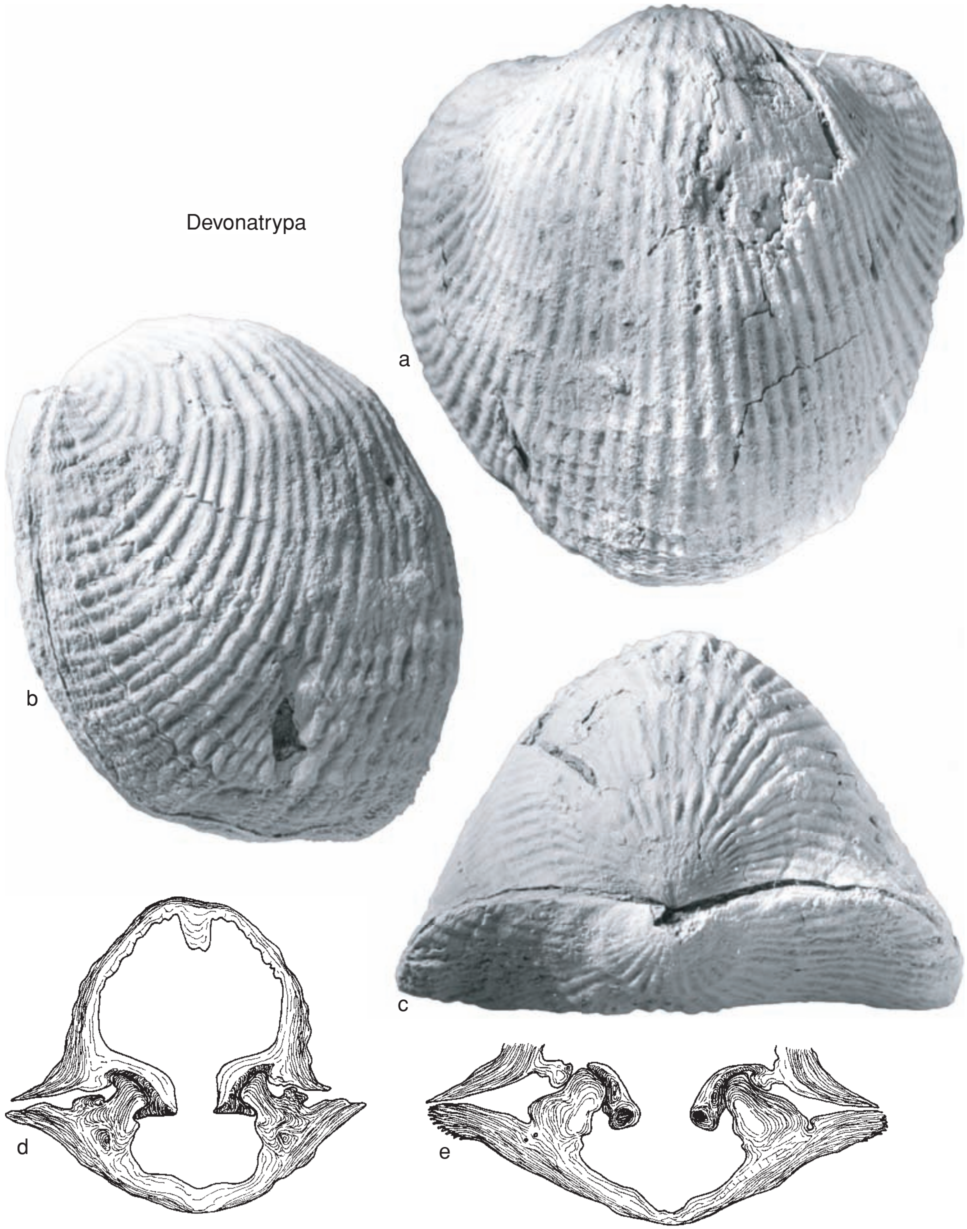

FIG. 961. Atrypidae (p. 1416).

like ribs in early growth stages, teeth with dental cavities, nature of hinge socket plates, brachidia.] *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian):* North America, Eurasia, Australia.——FIG. 962,*1a–d.* **P. devoniana* (WEBSTER), Frasnian, Iowa, USA; dorsal, ventral, posterior, lateral views, ×2 (Copper, 1973c).

Radiatrypa COPPER, 1978, p. 293 [**Atrypa gregeri* ROWLEY, 1900, p. 264; OD] [=*Paratrypa* L. I. MIZENS in G. A. MIZENS & L. I. MIZENS, 1997, p. 21 (type, *P. orbi* G. A. MIZENS & L. I. MIZENS, 1997, p. 21, OD]. Small to medium, rounded to ovoid, biconvex to weakly dorsibiconvex; orthocline area; minute apical foramen; distinct deltidial

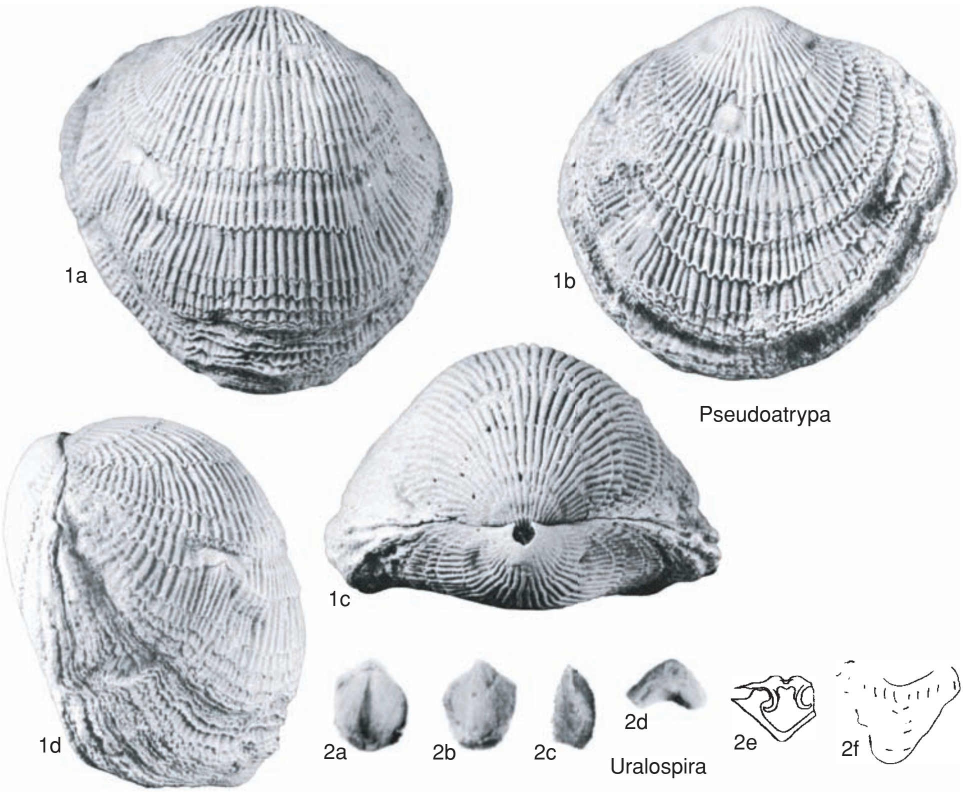

FIG. 962. Atrypidae (p. 1416–1419).

plates; ribs ultrafine, continuous; growth lamellae or frills lacking; rectimarginate to weakly plicate commissure; interior with short teeth; small dental cavities; delicate hinge plates; jugal processes and spiralia undescribed. [Similar to *Anatrypa,* but for biconvexity, smaller globose shell, nature of pedicle callist, deltidial plates. Material ascribed to *Paratrypa* by MIZENS & MIZENS lacks internal characters of karpinskiniids.] *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian):* North America, Urals, Russian Platform.——FIG. 958,*3a–d.* **R. gregeri* (ROWLEY), lower Frasnian, Missouri, USA; dorsal, lateral, anterior, posterior views, ×2 (new).

Uralospira MIZENS, 1977b, p. 82 [**U. tenuicostata;* OD]. Small, planoconvex-concavoconvex, elongate; ventrally subcarinate, dorsally deeply sulcate; prominent orthocline area; protruding beak; apical foramen; small deltidial plates; very fine continuous ribs to nearly smooth appearance; growth lamellae, frills absent; V-shaped sulcate commissure; deeply incised ventral muscle field; short, blunt teeth; slender socket plates; cardinal pit; crura arched laterally; mediodorsal spiralia with fewer than 5 whorls; jugal processes curved. [Differing from *Variatrypa* and *Desquamatia* by small size, sulcate commissure, subcarinate ventral valve, lack of frills.] *Lower Devonian (Pragian–Emsian):* Urals, central Asia, Altai-Salair.——FIG. 962,*2a–f.* **U. tenuicostata,* Pragian, eastern slopes, Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e–f,* serial sections, ×3.6 (Mizens, 1977b).

Family ATRYPINIDAE McEwan, 1939

[Atrypinidae MCEWAN, 1939, p. 619, *partim; emend.,* COPPER, herein]

Shells small to medium, plicate or rarely sulcate, commonly carinate ventrally; ribbed, less commonly secondarily smooth; ribs interrupted by short growth lamellae or growth lines; frills lacking; usually small orthocline area; distinct deltidial plates surrounding apical foramen; teeth solid or with small dental cavities; small dorsomedial spiralia with relatively few whorls; strong, short jugal processes, generally lacking terminal jugal plates. *Ordovician (lower Caradoc)–Lower Devonian (Emsian).*

Subfamily ATRYPININAE McEwan, 1939

[*nom. transl.* COPPER, herein, *ex* Atrypinidae MCEWAN, 1939, p. 619] [=Gracianellinae JOHNSON, 1973b, p. 1013]

Small, ventribiconvex to planoconvex shells; relatively few coarse ribs, less commonly smooth; usually strongly carinate apically, with raised ventral midribs; short growth lamellae, sometimes slightly imbricate; commissure weakly sulcate to weakly plicate; small but distinct area with deltidial plates; small apical foramen; teeth solid or with small dental cavities; spiralia dorsomedial, few whorls; jugal processes strong, thick. *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian).*

Atrypina HALL in HALL & CLARKE, 1893, p. 161 [**Leptocoelia imbricata* HALL, 1859b, p. 246; OD; *vid.* HALL, 1894, p. 815]. Small, suboval to subquadrate; planoconvex to subconcavoconvex to ventribiconvex; short hinge; minute orthocline to anacline area; beak small, projecting; apical foramen flanked by small triangular deltidial plates; relatively few, coarse expanding ribs, rarely bifurcating or intercalated, with strong ventral midrib pair; sulcus usually lined by strong dorsal midrib; anterior concentric growth lamellae very short or absent, apically lacking or missing in small shells, may have strong concentric ridges; commissure weakly sulcate to rectimarginate to weakly plicate. [Distinct from *Gracianella* by its stronger ribs, strong plicate commissure, roofed-over cardinal pit and fused hinge plate, externally by small size, very coarse ribs.] *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian):* North America, Eurasia.

A. (Atrypina). External description as for genus except in having plicate commissure, strongly defined ventral fold; internally pedicle cavity lined with thin callist continuous with deltidial plates; small teeth; distinct dental cavities; hinge plate strong, raised, divided by small cardinal pit, roofed over anteriorly by conjunct to fused inner socket plates; crura minute; spiralia mediodorsally directed, fewer than 6 thick, wide whorls; central jugal processes ending in small, ringed to crescentic jugal plates. *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian):* North America, Eurasia.——FIG. 963,*1a–c*. **A. (A.) imbricata* (HALL), lectotype, Emsian, New York, USA; dorsal, ventral, and anterior views, ×2 (new).——FIG. 963,*1d–g*. *A. (A.)* sp. cf. *A. (A.) barrandii,* Wenlock, United Kingdom; serial sections showing hinge plate, jugal processes, and reconstruction of brachidia, ×5 (new).

A. (Atrypinopsis) RONG & YANG, 1981, p. 232 [**A. biconvexa;* OD]. Similar to *Atrypina* except for stronger dorsal midrib producing more strongly plicate to plicosulcate commissure. [Some *Atrypina* also with weakly plicate commissure from dorsal midrib; brachidia undescribed.] *Silurian (lower Llandovery):* China, ?northwestern Canada.——FIG. 963,*2a–d*. **A. (A.) biconvexa,* China; *a–c,* dorsal, ventral, and anterior views, ×2; *d,* serial section, ×3.2 (Rong & Yang, 1981).

Gracianella JOHNSON & BOUCOT, 1967, p. 868 [**G. lissumbra* JOHNSON & BOUCOT, 1967, p. 871; OD] [=*Claratrypa* HAVLÍČEK, 1987b, p. 240 (type, *C. clarula,* OD)]. Very small to small, rounded to lenticular outline, relatively flat, roughly biconvex shell; hinge short; small, flat apsacline-orthocline area; apical foramen flanked by small deltidial plates; variable surface ornament from ribbed to nearly entirely smooth, sometimes capillose; weak to strong concentric growth lines, with or without growth lamellae; ventrally weakly to strongly carinate, with carina consisting of single or double, normally fused midrib pair; sulcus dorsal, weak to strong, narrow; weakly sulcate-rectimarginate commissure; interior with small, raised, ventral muscle platform; minute crura; dorsomedial spiralia of fewer than 7 whorls; jugal processes ending in ring-shaped jugal plates. *Silurian (middle Llandovery)–Lower Devonian (Lochkovian):* North America, Eurasia, Australia.

G. (Gracianella). Description as for genus, but relatively flat shell; ribbed variably to nearly entirely smooth; ribs continuous; weak concentric growth lines, lacking growth lamellae; ventrally weakly to strongly carinate, with carina consisting of single or double, fused midrib pair; spiralia and jugal processes undescribed. [Some *G. (Gracianella)* species appear to intergrade with *G. (Sublepida).*] *Silurian (Wenlock)–Lower Devonian (Lochkovian):* North America, Eurasia, Australia.——FIG. 963,*5a–g*. **G. (G.) lissumbra,* Ludlow, Nevada, USA; *a–e,* dorsal, ventral, lateral, posterior, anterior views; *f–g,* ventral, dorsal valve interiors, ×5 (Johnson & Boucot, 1967).

G. (Guangyuania) SHENG, 1975, p. 81 [**Quangyuania* [sic] *ovalia;* OD; *nom. correct.* COPPER, herein, *pro Quangyuania*]. Small, rounded, planoconvex-ventribiconvex; distinct ventral keel, dorsal sulcus; prominent orthocline area; deltidial plates parted by apical foramen; shell surface apically usually partly ribbed, carinate, but smooth distally, ornamented by rhythmic, concentric, capillose ridges on shell surface; commissure weakly sulcate; teeth with minute apical dental cavities, solid distally; hinge plates thick, with narrow V-shaped cardinal pit lined by small cardinal process; thick crura; 4 to 5 thick, mediodorsal spiralial whorls; jugal processes ending in small, ringlike jugal plates. [Similar to *G. (Gracianella)* in interior structure of hinge, orthocline area, and apical ribs, but differing in strong, bushy, concentric, capillate ridges on shell surface, similar to capillae in

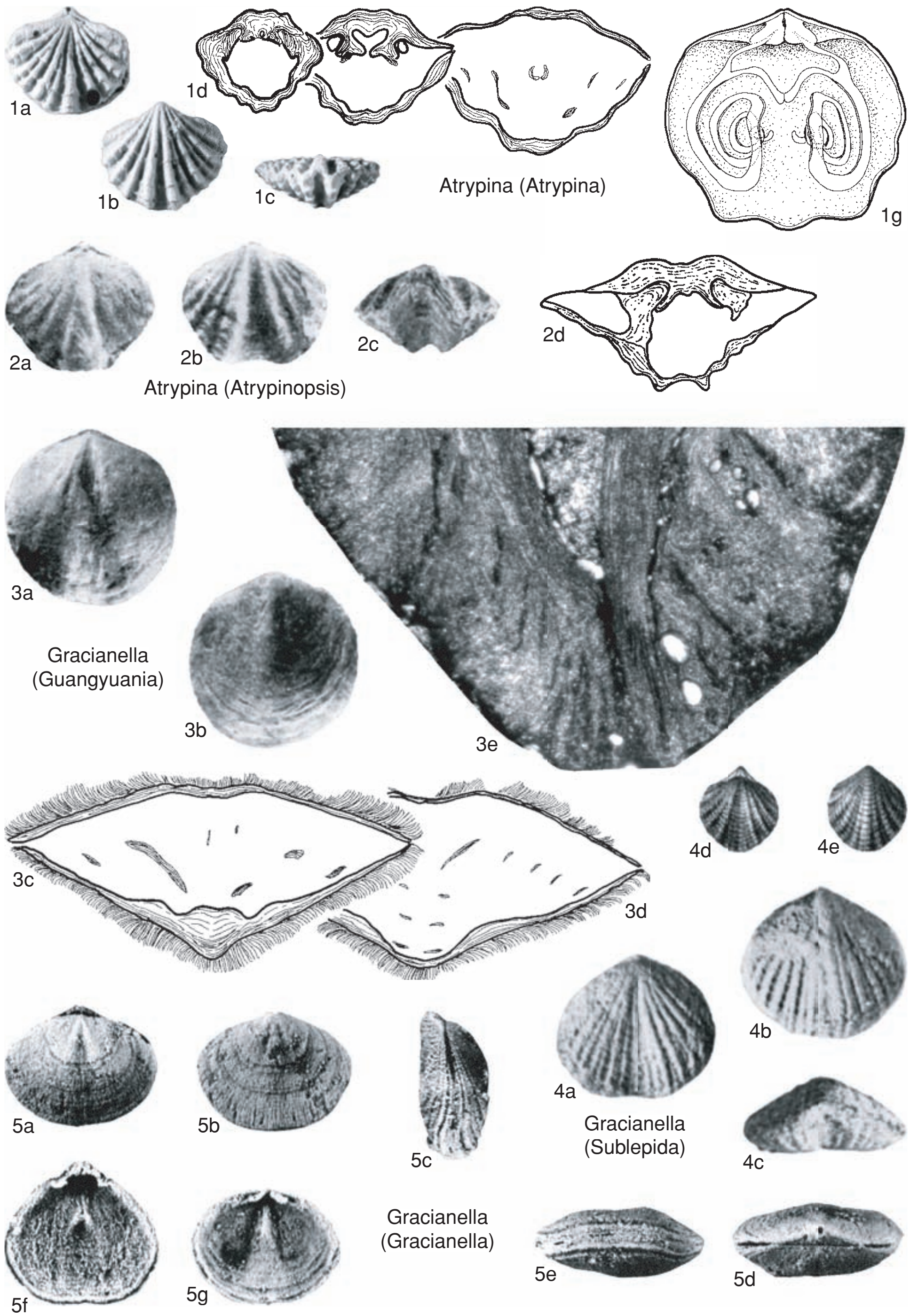

FIG. 963. Atrypinidae (p. 1420–1422).

Lissatrypa; differs from *G. (Sublepida)* in loss of ribs, presence of cardinal pit on hinge plate.] *Silurian (middle Llandovery–Wenlock):* southwestern China (Sichuan, Guizhou, southern Shaanxi).——FIG. 963,*3a–e.* **G. (G.) ovalia,* middle Llandovery, northern Sichuan; *a–b,* dorsal and ventral views, ×2 (Sheng, 1975); *c–d,* serial sections, ×5; *e,* peel photograph of capillose shell microornament, ×30 (new).

G. (**Sublepida**) MIZENS & SAPELNIKOV, 1982, p. 16 [**Terebratula sublepida* DE VERNEUIL, 1845, p. 96; OD]. Small, weakly ventribiconvex-planoconvex; ventrally carinate; dorsally sulcate; small orthocline-anacline area; apical foramen; deltidial plates; completely covered by ribs intersected by short, overlapping growth lamellae; commissure sulcate; interiorly thick ventral shell; raised muscle field; teeth solid, lacking dental cavities; hinge plate thick, lacking cardinal pit; dorsomedial spiralia with 4 to 6 thick whorls; ring- to hook-shaped jugal plates terminating processes. [Differs from *G. (Gracianella)* and *G. (Guangyuania)* in presence of ribs, short growth lamellae completely covering shell.] *Silurian (Ludlow–Přídolí):* southern and central Urals, central Asia, North America.——FIG. 963,*4a–e.* **G. (S.) sublepida* (DE VERNEUIL), Přídolí, southern and central Urals; *a–c,* dorsal, ventral, and anterior views, ×3 (Mizens & Sapelnikov, 1982); *d–e,* lectotype, dorsal and ventral views, ×2 (de Verneuil, 1845).

Subfamily CLINTONELLINAE Poulsen, 1943

[Clintonellinae POULSEN, 1943, p. 40, *partim; emend.,* COPPER, herein]

Small to medium-sized, rarely large, rounded, biconvex, often rhynchonelliform shell, lacking carination; weakly sulcate to moderately plicate commissure; ribs fine to very fine, evenly sized, continuous, lacking concentric growth lamellae or frills; shell thinly walled, lacking pedicle callist; dental cavities distinct to large; hinge plate thin to modest; spiralia with fewer than 8 to 11 whorls; ventroposterior jugal processes, possibly lacking jugal plates. [Although some genera commonly reported in upper Ashgill from Russia, definitive taxa unknown; neanic specimens may be confused with Rhynchonellida, or with some Spirigerininae.] *Silurian (Llandovery)–Lower Devonian (Emsian).*

Clintonella HALL in HALL & CLARKE, 1893, p. 159 [**C. vagabunda* HALL in HALL & CLARKE, 1893, p. 160; OD; *vid.* HALL, 1894, p. 160] [=*Pronalivkinia* RUKAVISHNIKOVA, 1977, p. 134 (type, *Nalivkinia (Pronalivkinia) numerosa,* OD); ?*Dabashanospira* FU, 1982, p. 170 (type, *Pentlandella sinicus,* SD FU, 1975, p. 107); *Dabashanospira* FU, 1984, p. 379 (type, *Pentlandella sinicus* FU, 1975, p. 107, OD)]. Small to medium, elongate to rounded, globose, biconvex, noncarinate; small beak; anacline area with apical foramen, minute deltidial plates; ribs fine to medium, continuous; rib troughs ornamented by concentric filae; growth lamellae lacking; commissure roughly rectimarginate to weakly plicate; interior with thin wall; teeth delicate; prominent dental cavities; hinge plate thin, divided by small cardinal pit; crura laterally arched; spiralia and jugal processes undescribed. [Differs from *Alispira* in generally elongate, globose shell, weakly plicate-rectimarginate commissure, lack of carination.] *Silurian (middle Llandovery–Wenlock):* North America, Siberia, Kazakhstan, China.——FIG. 964,*2a–b.* **C. vagabunda*, upper Llandovery, New York, USA; exterior ventral valve, interior dorsal valve, ×4 (Boucot & Johnson, 1970).——FIG. 964,*2c–j. C. anticostiana* (TWENHOFEL), middle Llandovery, Anticosti, Canada; *c–g,* dorsal, ventral, posterior, lateral, anterior views, ×2; *h–i,* serial sections, ×5; *j,* enlargement of microfilae ornament, ×38 (new).

Alispira NIKIFOROVA, 1961, p. 243 [**Zygospira (Alispira) gracilis* NIKIFOROVA, 1961, p. 244; OD]. Small; rounded to subtriangular outline; ventribiconvex-biconvex; ventrally weakly carinate; small orthocline area; apical foramen flanked by minute deltidial plates; ribs fine, continuous; sulcate-rectimarginate commissure; interior with thin shell; short teeth; small dental cavities; hinge plate with minute cardinal pit; inner socket ridges nearly touching; small, fibrous, laterally directed crura; dorsomedial spiralia with fewer than 6 whorls; jugal processes subhorizontal, terminating in center of shell. [Similar internally to *Clintonella,* externally finely ribbed, smaller in size, shield shaped, with weak carination, sulcate commissure, lacking globose-elongate shape.] *Silurian (Llandovery–Wenlock):* Siberia, China, ?North America.——FIG. 965,*1a–g.* **A. gracilis* (NIKIFOROVA), Llandovery, western Siberia; *a–c,* dorsal, ventral, and anterior views, ×2; *d–f,* serial sections, ×5; *g,* dorsal apex, ×12 (new).

Anabaria LOPUSHINSKAYA, 1965, p. 27 [**Catazyga rara* NIKIFOROVA, 1961, p. 248; OD]. Small to medium, rounded outline, biconvex-dorsibiconvex; orthocline-anacline area; small beak; apical foramen; minute deltidial plates; ribs fine, continuous, posterolateral shell flanks almost smooth; growth interruptions rare; moderately U-shaped, plicate commissure; interior with thin shell; small teeth with large lateral cavities; delicate hinge plates leading to feathery crura; dorsal spiralia with fewer than 8 whorls; jugal processes undescribed. [Differs from *Clintonella* in finer ribs, rounded, dorsibiconvex shape, and wide, U-shaped anterior fold; similar to *Beitaia,* except in coarser ribs, lower anterior fold.] *Silurian (?upper Llandovery, Wenlock):* Siberia.——FIG. 964,*1a–g.* **A. rara* (NIKIFOROVA), ?upper

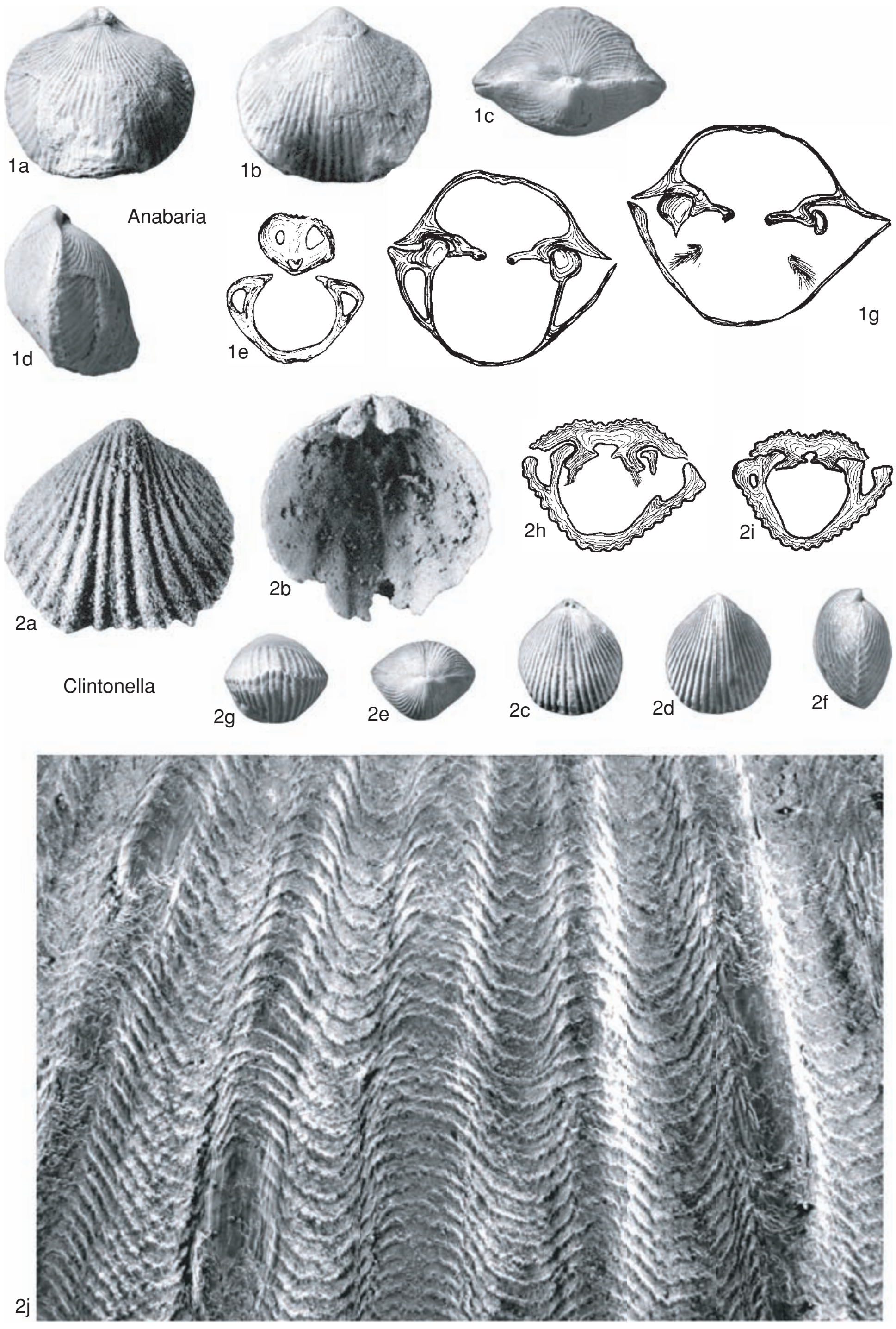

FIG. 964. Atrypinidae (p. 1422–1425).

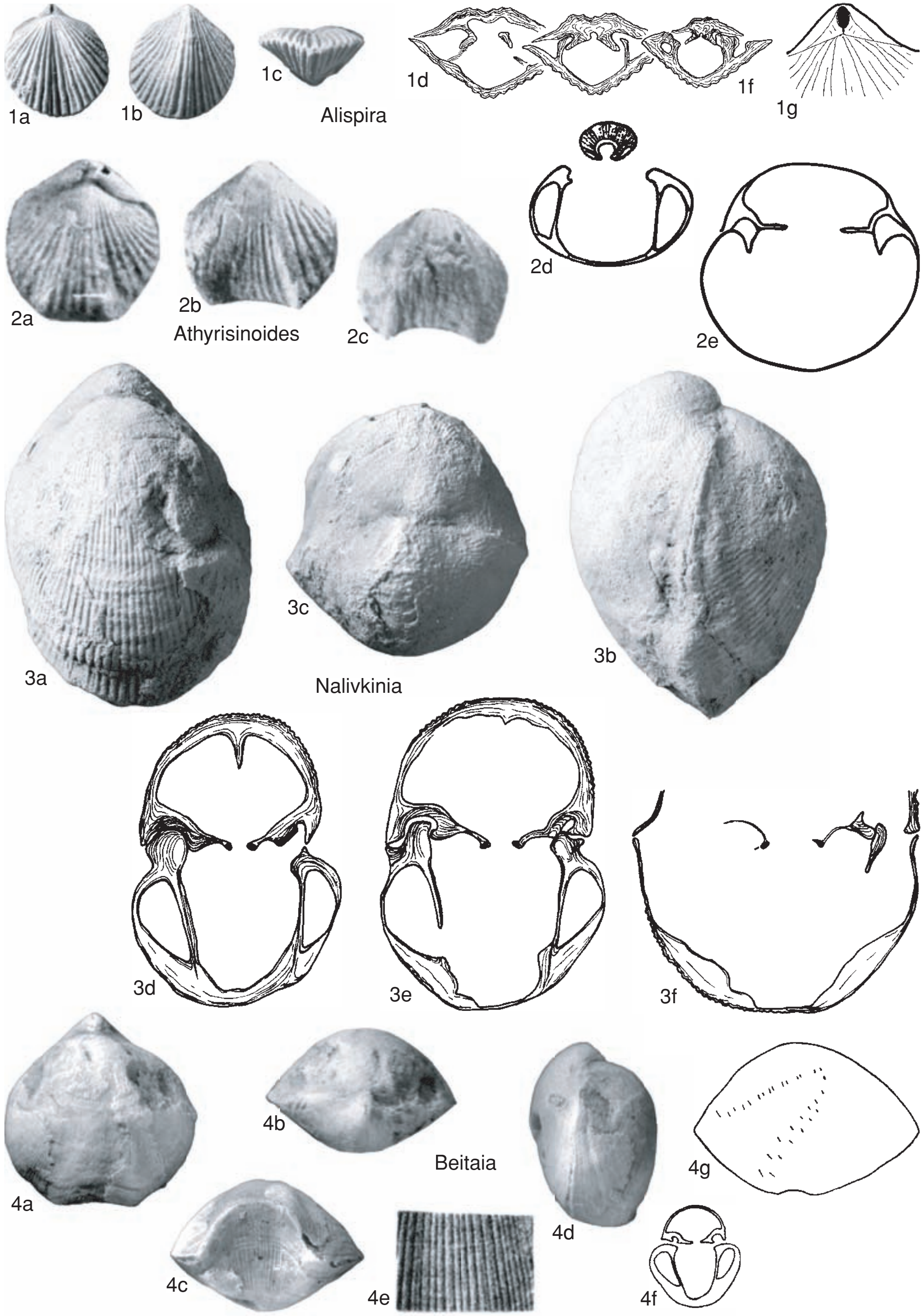

FIG. 965. Atrypinidae (p. 1422–1425).

Llandovery; *a–d,* dorsal, ventral, posterior, lateral views, ×2; *e–g,* serial sections, ×5 (Copper, 1977a).

Athyrisinoides Jiang in Xian & Jiang, 1978, p. 303, *non Athyrisinoides* Chen & Wan in Chen, 1979, p. 18 (type, *A. typica* Chen & Wan in Chen, 1979, p. 20, OD), =*Athyrisinoidea* Chen & Wan, 1980, p. 105, obj.; *Neoathyrisina* Chen, 1990, p. 14, obj. [**A. shiqianensis;* OD] [=*Kritorhynchia* Rong & Yang, 1981, p. 215 (type, *K. seclusa,* OD)]. Small to medium; rounded to subquadrate, rhynchonelliform outline; small anacline area, obscuring apical foramen, deltidial plates; ribs medium size, coarsening distally; ribs defining sharp fold with flanking troughs on both valves; short, overlapping growth lamellae may be present; squared to U-shaped strongly plicate commissure; internally modest dental cavities; dental plates; cardinal pit lined by weak cardinal process; crura lateral; spiralia with fewer than 6 whorls, dorsomedial; jugal processes undescribed. [Distinguished from *Anabaria* by coarser ribs, sharply defined, *Plectatrypa*-like fold, and presence of very short growth lamellae; genus is homeomorphic with some athyrisinids (Athyridida), but distinguished by dorsally directed atrypoid spiralia. Regarding the synonymy of this genus, *Athyrisinoides* Jiang, 1978, an atrypid, has priority. *Athyrisinoides* Chen & Wan, 1979, an athyridid, is a junior homonym. Chen & Wan renamed their athyridid *Athyrisinoidea,* but since there is only one letter difference in the names, they renamed it again as *Neoathyrisina.*] *Silurian (middle Llandovery–upper Llandovery):* southwestern China (Guizhou).——Fig. 965,*2a–c.* **A. shiqianensis,* middle Llandovery; dorsal, ventral, and anterior views, ×1 (Jiang, 1978).——Fig. 965,*2d–e. A. seclusa* (Rong & Yang), middle Llandovery; serial sections, ×5 (Rong & Yang, 1981).

Beitaia Rong, Xu, & Yang, 1974, p. 199 [**B. modica;* OD]. Small to medium, ventribiconvex to nearly convexoplane, very finely ribbed to almost smooth septatrypiform shell; orthocline-anacline area; protruding beak; small apical foramen; deltidial plates; ribs very fine (costellate) to nearly invisible, lacking growth interruptions; distinct concentric growth filae; commissure with high, wide, U-shaped fold; interior with large dental cavities, long dental plates; delicate hinge plates; dorsally directed spiralia with fewer than 11 whorls; jugal processes delicate. [Differs from *Clintonella* in very fine ribs, high dorsal fold, and broader shell; from *Anabaria* by septatrypid shape, large and wide fold, very fine ribs; worn shells may be mistaken for *Septatrypa.*] *Silurian (middle Llandovery):* southern China (Guizhou, Hubei, Sichuan).——Fig. 965,*4a–g.* **B. modica,* middle Llandovery, Guizhou; *a–d,* dorsal, posterior, anterior, lateral views, ×2; *e,* enlargement of fine ribs, ×4 (Rong, Xu, & Yang, 1974); *f–g,* serial sections, ×2.5 (Rong & Yang, 1981).

Nalivkinia Bublichenko, 1927, p. 982 [**Atrypa gruenewaldtiaeformis* von Peetz, 1901, p. 147; OD]. Medium to large, globose, strongly biconvex; small, hypercline area; foramen transapical or obscured, absent; deltidial plates absent in adult shell; ribs fine; abundant, very short, growth lamellae or growth interruptions; commissure rectimarginate to weakly plicate; interior with large dental cavities; short, dorsoventrally oriented teeth; delicate socket plates; small bushy crura; spiralia dorsomedial, fewer than 6 whorls, jugal processes straight, nearly touching. [Distinguished from other clintonellinids by large size, incurved beak, presence of short concentric growth lamellae; distinguished from *Tibetatrypa* by large dental cavities, thinner shell, delicate socket plates, absence of strong anterior fold.] *Silurian (upper Llandovery–Ludlow):* southern Siberia, Altai.——Fig. 965,*3a–f.* **N. gruenewaldtiaeformis* (von Peetz), Wenlock, Kuznetsk basin; *a–c,* dorsal, lateral, posterior views, ×2; *d–f,* serial sections, ×5 (Copper, 1977a).

Tibetatrypa Copper & Hou, 1986, p. 287 [**T. xainzaensis* Copper & Hou, 1986, p. 289; OD]. Large to very large, rotund, elongate, ventribiconvex to biconvex; hypercline area; narrow beak; foramen and deltidial plates absent or obscured in adult shell; ribs fine; intersected at relatively wide intervals by growth interruptions, lacking growth lamellae; rectimarginate to weakly plicate commissure; internally thick shell wall, pedicle callist; deep pedicle groove; teeth with long, narrow, reduced dental cavities; thin socket plates; short crura; spiralia dorsal, 8 to 10 whorls; jugal processes delicate, tapering into small, flat jugal plates. [Differs from closely related *Nalivkinia* in its much larger size, minute dental cavities, and deep pedicle groove.] *Lower Devonian (Lochkovian–Emsian):* Tibet.——Fig. 966,*2a–g.* **T. xainzaensis,* Emsian; *a–c,* dorsal, lateral, posterior views, ×2; *d–f,* serial sections, ×5; *g,* reconstruction from serial sections, ×3 (Copper & Hou, 1986).

?Uncitispira Fu, 1982, p. 150 [**U. sinica;* OD]. Small, rounded; orthocline area; strongly protruding beak; apical foramen, deltidial plates; ribs fine, continuous; lacking growth lamellae; rectimarginate to weakly plicate commissure; interior with thin wall; small teeth; large dental cavities; hinge plate short and sturdy; small cardinal pit; dorsomedially directed spiralia with about 6 whorls; crura, jugal processes undescribed. [Possible synonym of *Anabaria,* or *Clintonella,* but with strongly pointed, extended beak.] *Silurian (upper Llandovery):* northwestern China (Gansu).——Fig. 966,*1a–d.* **U. sinica; a–c,* dorsal, lateral, anterior views, ×3; *d,* polished section, ×3 (Fu, 1982).

Subfamily PLECTATRYPINAE Copper, 1996

[Plectatrypinae Copper, 1996b, p. 914]

Small- to medium-sized shells; small orthocline-hypercline area; apical-transapical foramen; highly imbricate, highly arched ribs, may be terminated by blunt caps (capidulae), nonspinose; ventral valve usually strongly carinate with enlarged, diverging

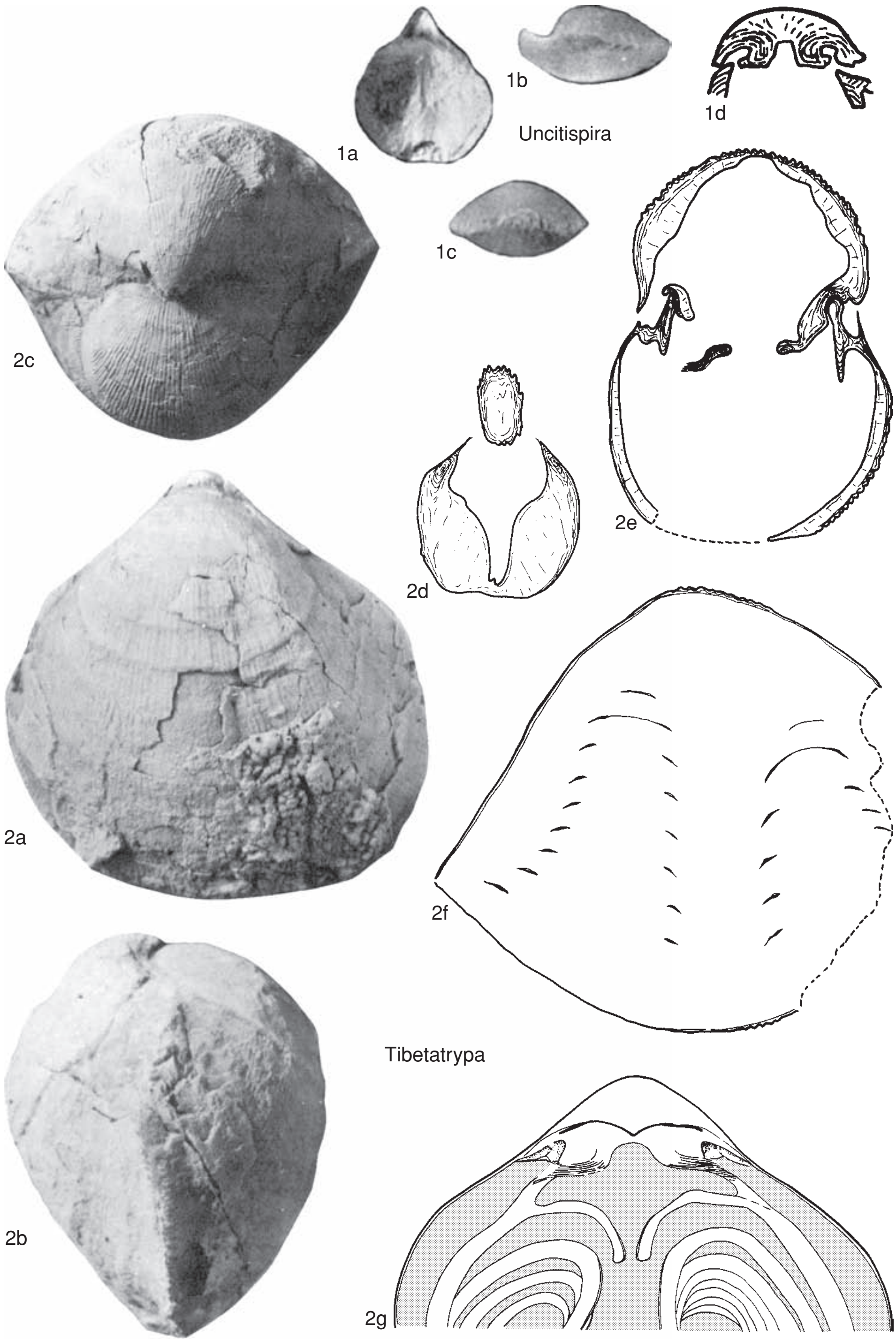

FIG. 966. Atrypinidae (p. 1425).

midribs separated by smaller ribs; short, overlapping, imbricate growth lamellae; frills absent; strongly plicate commissure; pedicle callist absent to very thin; teeth usually lacking dental cavities, but with nuclei; dorsomedial spiralia with fewer than 10 whorls; jugal processes far apart, terminated by small blunt jugal plates. *Ordovician (?Ashgill), Silurian (Llandovery–Ludlow, ?Přídolí).*

Plectatrypa COOPER, 1930, p. 278 [**Terebratula imbricata* J. de C. SOWERBY, 1839, p. 624; OD] [=*Imbricatospira* FU, 1982, p. 149 (type, *I. decora,* OD); *Imbricatospira* FU, 1985, p. 96 (type, *I. decora,* OD)]. Small to medium size, rounded, biconvex-dorsibiconvex; small pointed beak; anacline-hypercline area; apical-transapical foramen; deltidial plates normally not exposed; ribs medium to coarse, highly imbricate, with sharply projecting growth lamellae; strongly divergent, enlarged ventral midrib sets separated by wide sulcus, producing carination; strong, U-shaped anterior fold; internally thin to thick shell apically; pedicle callist thin to absent; deltidial plates extended into pedicle cavity as thin lining; teeth short, thick, medially directed, lacking dental cavities; delicate crural bases, fine crura; fewer than 8 dorsomedial, relatively widely spaced spiralial whorls; fine jugal processes curved laterally, terminating in delicate plates. [Distinct from *Sypharatrypa* in rib imbrication; distinct from *Xanthea* in finer ribs, lack of microornament.] *Silurian (Llandovery–Ludlow, ?Přídolí):* North America, Eurasia.

P. (**Plectatrypa**). Diagnosis as for genus, but includes only medium to coarsely ribbed, imbricate forms lacking capidulae; shell wall thin, hinge plate weak. *Silurian (Llandovery–Ludlow, ?Přídolí):* North America, Eurasia.——FIG. 967,*1a–g*. **P. (P.) imbricata* (SOWERBY), upper Wenlock, United Kingdom; *a–e,* dorsal, ventral, posterior, anterior, lateral views; *f–g,* serial sections, ×4 (new).——FIG. 967,*1h*. *P. (P.)* sp. cf. *P. (P.) imbricata,* upper Wenlock, Gotland; reconstruction of brachidia, ×4 (new).

P. (**Gutnia**) COPPER, 1996b, p. 915 [**G. capidula* COPPER, 1996b, p. 917; OD]. Small to medium, rounded outline; orthocline-anacline area; small, protruding beak; apical-transapical foramen; minute deltidial plates; ribs fine to very fine, evenly sized over shell surface; closely spaced imbricate growth lamellae; rib crests terminated by bulbous caps (capidulae); gently to strongly plicate anterior commissure; shell wall thick apically; deltidial plates hollow, distally retreating to sides of pedicle cavity; teeth short, anteriorly accommodating groove for crura; hinge plate sturdy; socket plates thin; crura very delicate; spiralia, jugal processes undescribed. [Differs from *Plectatrypa* in much finer ribs, presence of capidulae, lack of strong ventral midrib pair, lack of carination; internally similar but thick walled.] *Silurian (Wenlock):* western Europe, North America.——FIG. 967,*2a–g*. **P. (G.) capidula,* upper Wenlock, Gotland; *a–c,* dorsal, ventral, lateral views, ×3; *d–f,* serial sections, ×5; *g,* capidulae, ×20 (Copper, 1996b).

Sypharatrypa COPPER, 1982, p. 690 [**S. honora* COPPER, 1982, p. 692; OD]. Small to medium, biconvex-dorsibiconvex; protruding beak; small apsacline-orthocline area; rimmed apical foramen; small deltidial plates; ribs interrupted by relatively widely spaced, wavy, short growth lamellae, projecting 1 to 2 mm, subparallel to shell surface; rounded, plicate commissure; thin or no pedicle callist; small teeth; small dental cavities; dorsomedial spiralia with fewer than 6 whorls, jugal processes undescribed. [Externally similar in shape to *Eospirigerina* and *Schachriomonia,* but lacking carination and possessing wavelike, extended, short growth lamellae; differs from *Plectatrypa* in having coarser, wider ribs, without well-defined carination, rib imbrication.] *Ordovician (?Ashgill), Silurian (lower Llandovery–middle Llandovery):* eastern North America, western Europe.——FIG. 968*a–e*. **S. honora,* Rhuddanian, Manitoulin Island, Canada; *a–c,* dorsal, lateral, anterior views, ×2; *d,* dorsal view of large specimen showing growth lamellae, ×2; *e,* detail of dorsal beak, ×12 (new).

Xanthea COPPER, 1996b, p. 917 [**Atrypa imbricata* var. *lamellosa* LINDSTRÖM, 1861, p. 363; OD]. Small to medium, dorsibiconvex, wider than long or equidimensional; small orthocline-anacline area; protruding beak; apical to transapical foramen; small deltidial plates; ribs coarse, thicker apical midrib pair diverging rapidly, outlining sharp ventral sulcus; 2 to 4 ribs lining crest of strong, sharp dorsal fold; growth lamellae widely spaced, nonimbricate; microornament of zigzag filae; sharply plicate commissure; internally thick deltidial plates lining inside of pedicle cavity; pedicle callist absent; teeth solid, short, stubby; thick hinge plate; inner socket ridges expanded, globose; crura delicate; spiralia dorsomedial, fewer than 9 whorls; jugal processes delicate, terminating without touching. [Differs from *Plectatrypa* in very coarse ribs, widely spaced growth lamellae, zigzag, microornamental filae, larger size.] *Silurian (Telychian–Wenlock):* Europe.——FIG. 969*a–h*. **X. lamellosa* (LINDSTRÖM), lower Wenlock, Gotland; *a,* dorsal view, ×4; *b–d,* ventral, posterior, lateral views, ×2; *e–g,* serial sections, ×5; *h,* reconstruction of brachidia, ×5 (Copper, 1996b).

Subfamily SPIRIGERININAE Rzhonsnitskaia, 1974

[Spirigerininae RZHONSNITSKAIA, 1974, p. 57] [=Schachriomoniinae RUKAVISHNIKOVA, 1982, p. 46; Pectenospirinae POPOV, NIKITIN, & SOKIRAN, 1999, p. 646]

Small to medium size, inflated biconvex-dorsibiconvex; short hinge; small apsacline-anacline area; protruding beak; continuous

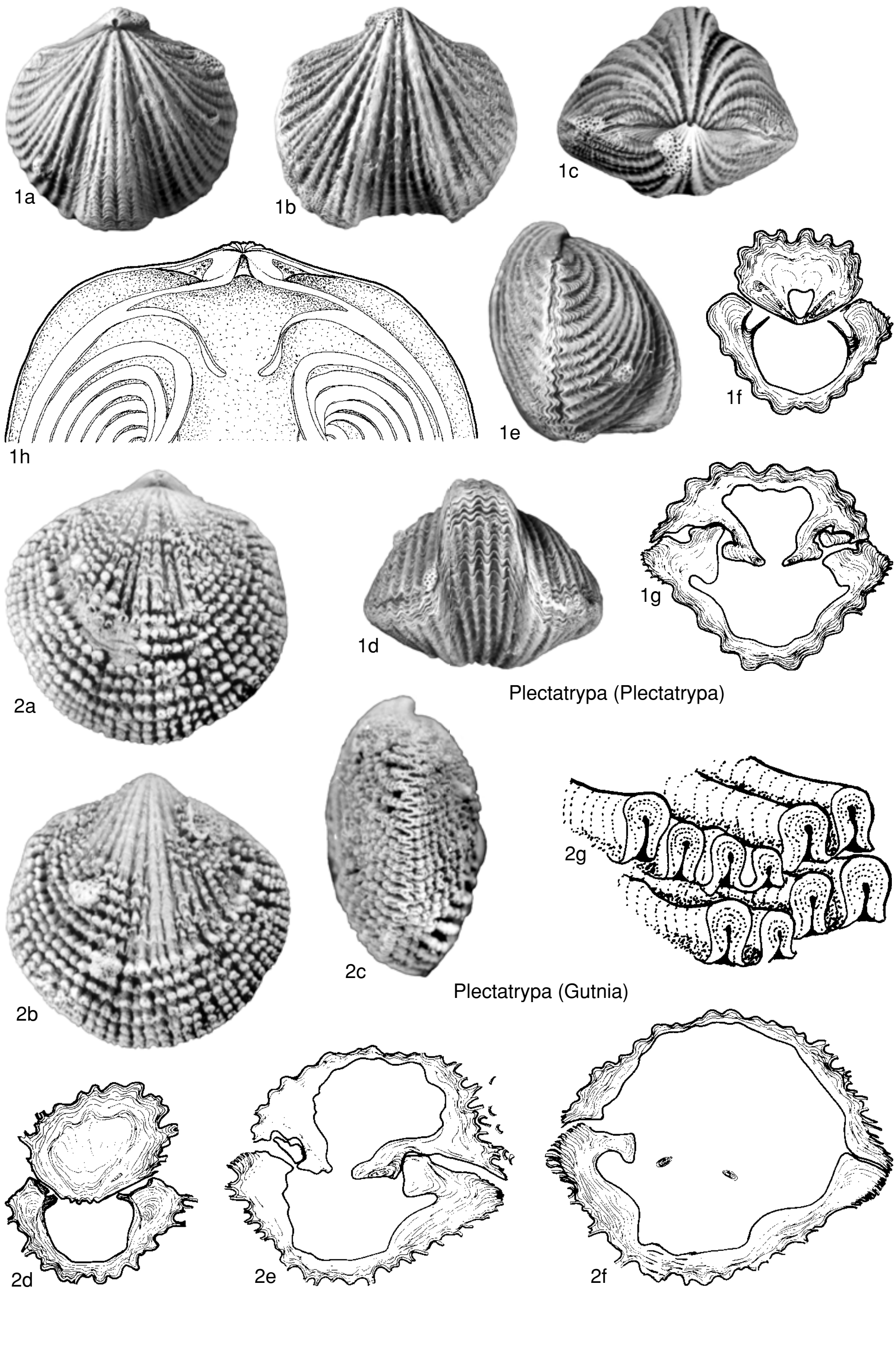

FIG. 967. Atrypinidae (p. 1427).

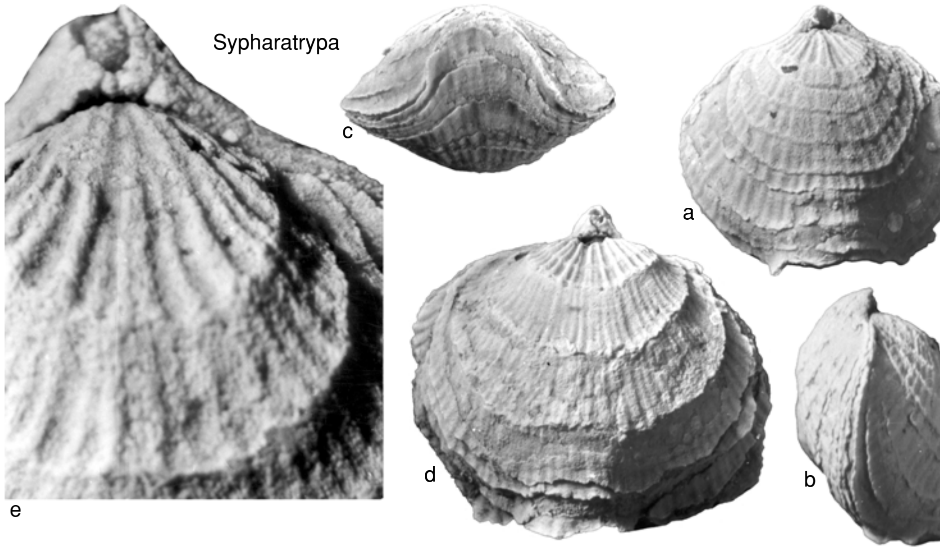

FIG. 968. Atrypinidae (p. 1427).

ribs, usually with strongly diverging ventral midrib pair producing pronounced carination; median sulcus on ventral valve; rarely weak concentric growth lamellae, rarely with trail, lacking frills; moderately to strongly plicate commissure; teeth solid or with small, rounded to slitlike dental cavities; feathery crura unknown; spiralia dorsomedially directed, fewer than 8 to 10 whorls; centroventral jugal processes recurved, with or without small jugal plates. *Ordovician (lower Caradoc)–Lower Devonian (Emsian).*

Spirigerina D'ORBIGNY, 1847, p. 268 [**Terebratula marginalis* DALMAN, 1828, p. 143; SD ALEKSEEVA, 1960b, p. 64, *vid.* D'ORBIGNY, 1850 in 1849–1852, p. 42] [=*Paraplectatrypa* ZENG & others, 1993, p. 375, *nom. nud.,* lacking description, only figures]. Medium size, subquadrate to pentagonal, dorsibiconvex; sharply pointed beak; triangular, orthocline area; apical foramen prominent; deltidial plates well developed; corrugate medium to coarse ribs, expanding distally, ventral midrib pair bi- to trifurcating with intervening sulcus filled by ribs; dorsal strongly bifurcating midrib; ribs ornamented by fine concentric filae, radial capillae; strong, angular-rounded, plicate commissure; internally thin pedicle callist; prominent hollow deltidial plates; strong, wide teeth; slitlike dental nucleus expanding to dental cavity anteriorly; thick central hinge plate; narrow cardinal pit; very thin socket plates; bulbous inner socket ridges; small, delicate crura; dorsal spiralia of fewer than 6 whorls, spiral lamellae widely spaced; jugal processes recurved in center, lacking jugal plates. *Silurian (middle Llandovery)–Lower Devonian (Emsian):* worldwide.——FIG. 970,*2a–i.* **S. marginalis* (DALMAN), Wenlock, Gotland; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×2; *f–h,* serial sections, ×5; *i,* reconstruction of left brachidium, ×5 (new).

?Australispira PERCIVAL, 1991, p. 169 [**A. disticha;* OD]. Medium size, globose-rounded, dorsibiconvex; broadly diverging ventral midribs separated by sulcus and numerous fine ribs; ribs tubular, continuous, expanding anteriorly to coarse; broadly plicate commissure; interior with blunt teeth; small dental cavities; spiralia dorsomedial, with about 7 whorls; possibly with posteroventrally located jugal processes. Smaller shells similar to *Sulcatospira,* but some gerontic shells with more robust shell, thicker shell wall. [PERCIVAL (1991) showed simple ventroposterior jugum, but silicification probably hides disconnected jugal processes. Similar to *Schachriomonia* but more finely ribbed, differing in strong globosity; neanic growth stages very similar to *Eospirigerina.*] *Ordovician (upper Caradoc):* Australia.——FIG. 970,*1a–h.* **A. disticha,* New South Wales; *a–d,* dorsal, ventral, lateral, anterior views; *e,* internal of dorsal valve; *f–g,* serial section; *h,* reconstruction of brachidia, ×2 (Percival, 1991).

Eospirigerina BOUCOT & JOHNSON, 1967a, p. 90 [**Zygospira putilla* HALL in HALL & CLARKE, 1895, p. 365, *vid.* HALL, 1894, p. 653; SD AMSDEN, 1974, p. 72; =*Atrypa praemarginalis* SAVAGE, 1913a, p. 84, OD, *vid.* AMSDEN, 1974, p. 72] [=*Zanclorhyncha* XU, 1979a, p. 96 (type, *Z. gentilis,* OD); *Eorhynchula* LIANG, 1983a, p. 284 (type, *E. yulangensis,* OD); *Neorhynchula* LIANG, 1983b, p.

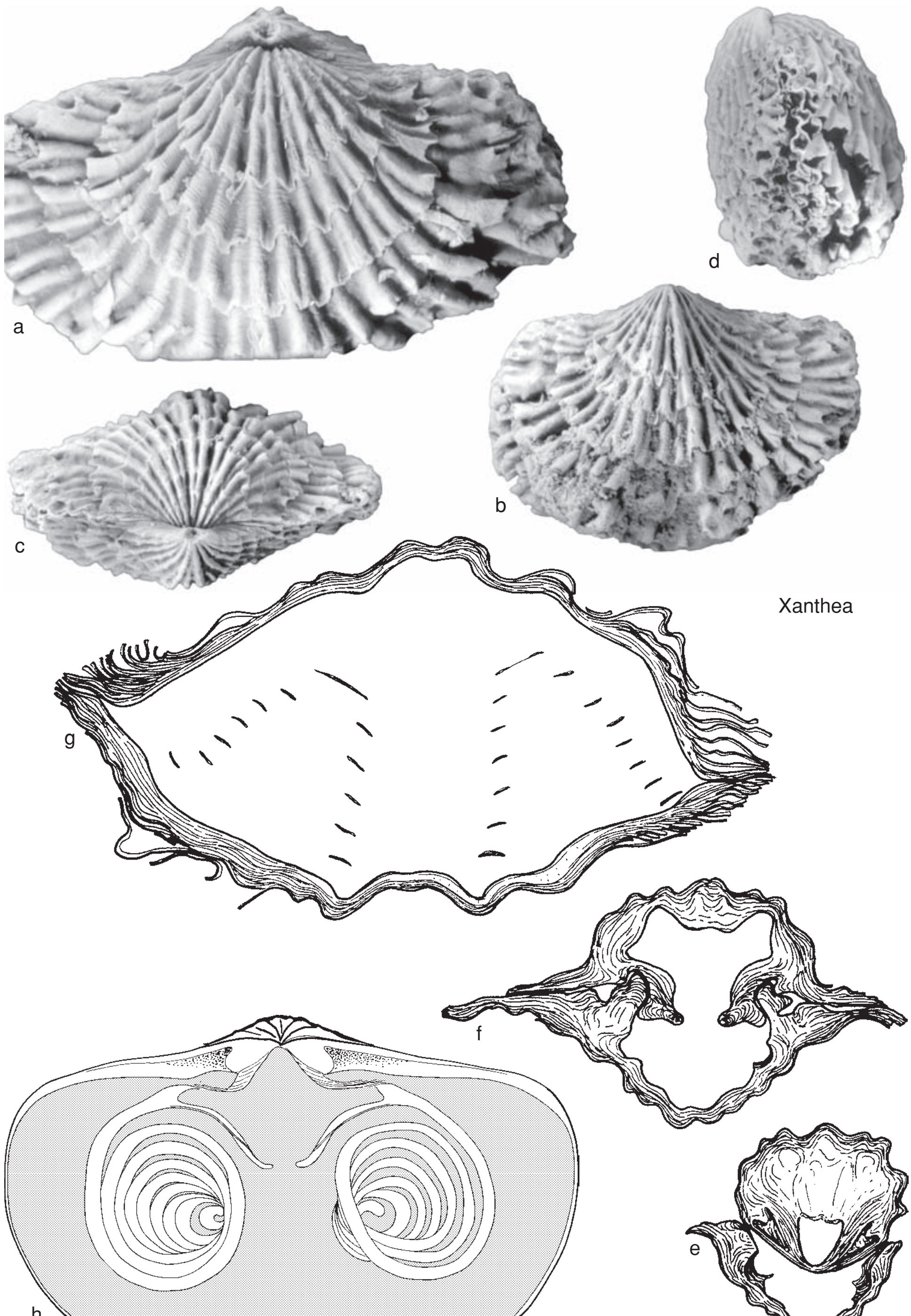

FIG. 969. Atrypinidae (p. 1427).

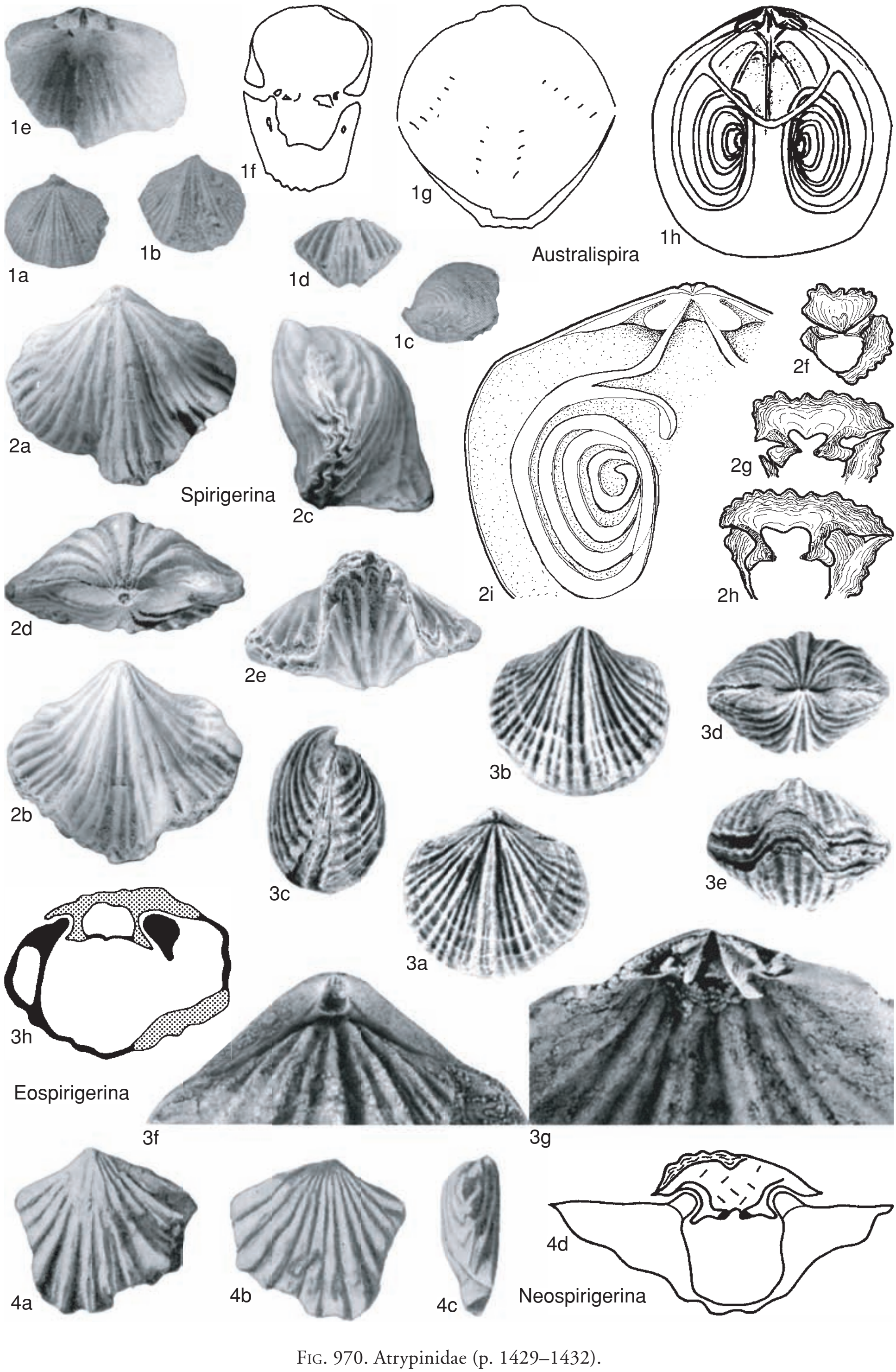

FIG. 970. Atrypinidae (p. 1429–1432).

284 (type, *N. jianglutangensis,* OD)]. Subquadrate to shield shaped, dorsibiconvex; small orthocline-anacline area; apical to transapical foramen, flanked by small deltidial plates; ribs fine to medium size, to fading laterally to sometimes nearly smooth, expanding and coarsening anteriorly; ventral diverging, furcating raised midrib clusters forming weak margins to ventral sulcus; ribs continuous or with partly developed growth lamellae anteriorly; strong, U-shaped anterior fold; short, stout teeth; small, subhorizontal, slitlike dental cavities; crura strong; dorsomedial spiralia with fewer than 12 whorls; jugal processes delicate. [Distinguished from *Spirigerina* by generally finer ribs, poorly defined midribs along fold margins, lacking microfilae, very short growth lamellae or growth interruptions commonly present, thin hinge plates; distinguished from *Qilianotryma* by coarser ribs, and rib-defined anterior fold; neanic specimens may be mistaken for *Atrypina.*] *Ordovician (middle Ashgill)–Silurian (Llandovery):* worldwide.——FIG. 970,*3a–h.* **E. putilla* (HALL), upper Ashgill, Missouri, USA; *a–e,* dorsal, ventral, lateral, posterior, and anterior views, ×2; *f–g,* dorsal interior, exterior, ×5; *h,* serial section, ×3 (Amsden, 1974).

Neospirigerina RZHONSNITSKAIA, 1975, p. 72 [**Plectatrypa ossa* NALIVKIN, 1960, p. 381; OD]. Medium size, weakly dorsibiconvex to flat, rhynchonelliform shell; protruding strong beak; small, apsacline-orthocline area; prominent deltidial plates, apical foramen; ribs coarse, nonbifurcating, with weakly defined midrib pair; rectimarginate to weak, broadly plicate commissure; internally broad, blunt teeth, possibly lacking dental cavities; massive hinge plate; slender socket plates with small inner socket ridges; spiralia and jugal processes undescribed. [Differentiated from *Spirigerina* by its very coarse, nondividing ribs, flat shell, weak anterior fold, lack of dental cavities; possibly synonymous with *Plesicarinatina.*] *Lower Devonian (Lochkovian–Emsian):* Siberia, Urals, Kazakhstan, central Asia.——FIG. 970,*4a–d.* **N. ossa* (NALIVKIN), Pragian, Urals; *a–c,* dorsal, ventral, lateral views, ×2 (Nalivkin, 1960); *d,* serial section at hinge plate, ×2 (Rzhonsnitskaia, 1975).

?Ogilviella LENZ, 1968, p. 180 [**O. rotunda* LENZ, 1968, p. 181; OD] [=?*Arctispira* SMITH, 1980, p. 66 (type, *A. canadensis,* OD)]. Small, rotund, biconvex-ventribiconvex, carinate ventrally; small orthocline area; minute deltidial plates; apical foramen; continuous ribs expanding distally; growth lamellae absent; ventral carina produced by raised midrib pair(s) matched by sulcus on brachial valve; rectimarginate to sulcate commissure; interior with thin shell wall; small teeth, minute dental cavities; thin hinge plates; crura, jugal processes, and spiralia undescribed. [Differs from *Spirigerina* by small size, lack of wide anterior fold, absence of ribs between raised ventral midrib pair, lack of ventral sulcus, sulcate-rectimarginate commissure; internal structure of brachidia unknown.] *Lower Devonian (Lochkovian–Pragian):* northern Canada, Australia.——FIG. 971,*1a–f.* **O. rotunda,* Pragian, Yukon, Canada; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e–f,* dorsal, ventral interiors, ×3.5 (Lenz, 1968).

?Otarella RUKAVISHNIKOVA, 1982, p. 46 [**O. multicostata;* OD; *nom. nud.*]. No known published description nor figures of genus or type species. *Ordovician (upper Ashgill)–Silurian (lower Llandovery):* Kazakhstan.

Pectenospira POPOV, NIKITIN, & SOKIRAN, 1999, p. 648 [**P. pectenata;* OD]. Small, ventribiconvex, acuminate shell, plicate with anterior, dorsal, smooth fold expressed as small posterior sulcus on ventral valve; high apical angle with narrow orthocline beak; ventral valve with 2 divergent main ribs flanked by smaller ribs; interior with large dental cavities, spiralia simple with fewer than 2 whorls, dorsomedially directed; centrodorsal, short jugal processes. [Earliest known spirigerinid, defined from others by small size and simple spiralium directed dorsomedially.] *Ordovician (lower Caradoc–middle Caradoc):* Kazakhstan, northwestern China (Qinghai).——FIG. 971,*2a–d.* **P. pectenata,* Anderken Formation, Kazakhstan; *a–c,* dorsal, ventral, anterior views, ×4; *d,* reconstruction of brachidia, approximately ×12 (Popov, Nikitin, & Sokiran, 1999).

Qilianotryma XU Hankui, 1979b, p. 97 [**Q. mirabile;* OD] [=*Euroatrypa* ORADOVSKAYA in NIKIFOROVA, ORADOVSKAIA, & POPOV, 1982, p. 63 (type, *E. tajmyrica* NIKIFOROVA, 1982, p. 65, OD); *Ovalospira* (*Orthocarina*) FU, 1982, p. 158 (type, *O. carinatiformis,* OD)]. Medium size, wide, subquadrate to subrounded, spirifer shaped; relatively long hinge; small, protruding, orthocline area; deltidial plates; apical foramen; broad, U-shaped anterior fold; ribs fine to very fine, evenly sized, bifurcating and intercalating; interior with short, broad teeth; slitlike to rounded dental cavity; dorsomedial-dorsal spiralia with fewer than 8 whorls; posteroventral jugal processes almost touching. [Similar to *Eospirigerina,* but relatively wide shell with very fine ribs, i.e., costellate ornamentation; ribbing as in *Beitaia* (Clintonellinae), but with *Eospirigerina*-like shell, small dental cavities, and sturdy teeth.] *Ordovician (upper Caradoc)–Silurian (Llandovery):* China (Qinghai), Urals, Kazakhstan, central Asia, *upper Caradoc;* Estonia, China (Qinling Mountains), *Llandovery.*——FIG. 971,*3a–c.* **Q. mirabile,* Ashgill, Qinghai; *a–b,* dorsal and posterior views, ×2; *c,* polished section, ×2.5 (Xu, 1979b).——FIG. 971,*3d. Q. tajmyrica* NIKIFOROVA, Ashgill, Taimyr, Russia; detail of shell surface, ×4 (Nikiforova, 1982).

Schachriomonia NIKIFOROVA, 1978, p. 118 [**S. schachriomonica* NIKIFOROVA, 1978, p. 119; OD]. Medium size; medium to coarsely ribbed; rounded to subquadrate outline; lacking strong midribs, but slightly carinate, with weak, concentric growth lamellae; small orthocline-anacline area; protruding beak; small deltidial plates; apical foramen; weakly plicate to rectimarginate commissure; thick walled; teeth with small dental cavities; spiralia dorsomedial; separated jugal processes. [Differs from

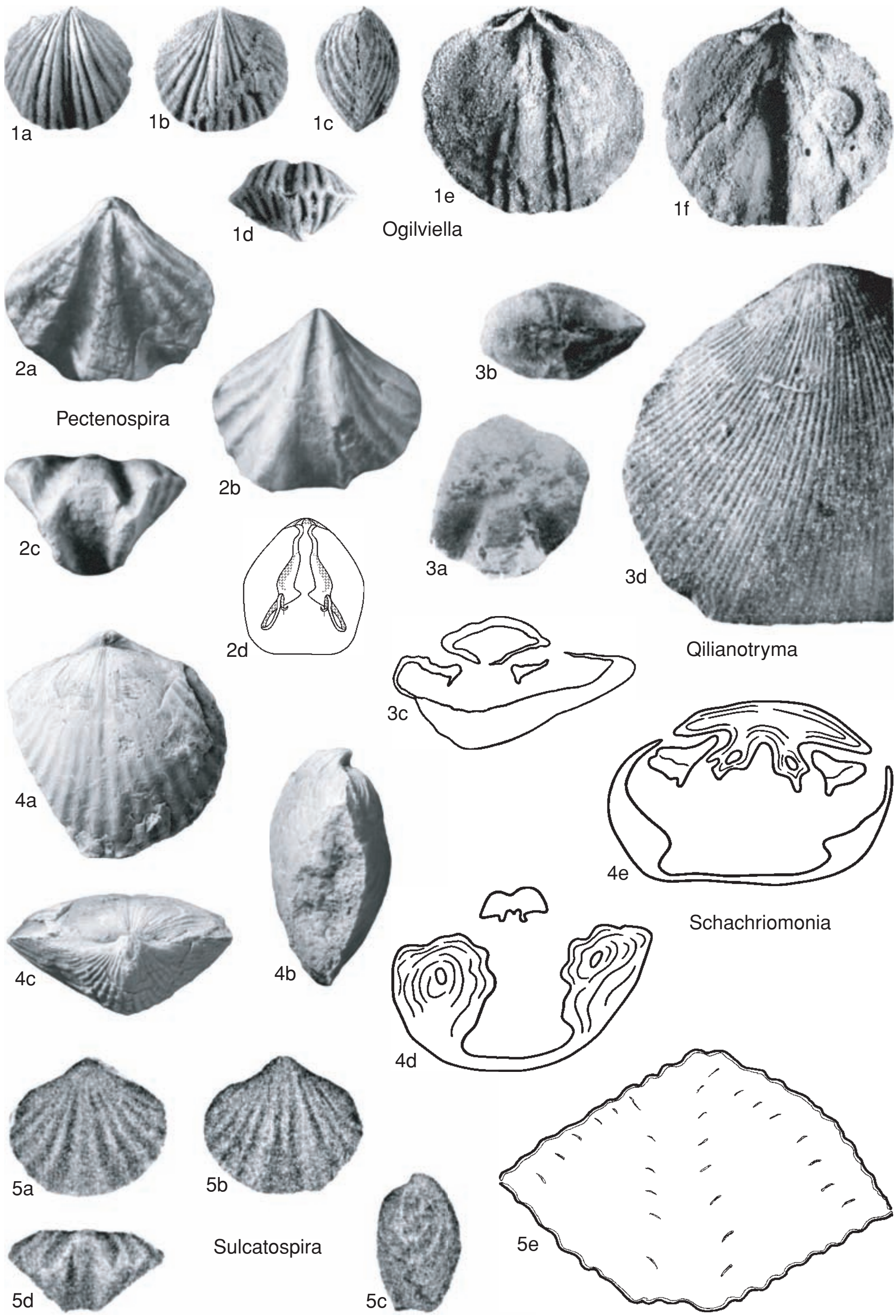

FIG. 971. Atrypinidae (p. 1432–1434).

Eospirigerina in coarser ribs, lack of strong carination, wider area; very similar to ?*Australispira,* except in convexity and lack of strong carination.] *Ordovician (Ashgill), Silurian (?Llandovery):* Kazakhstan, central Asia, Altai.——FIG. 971,*4a–e.* **S. schachriomonica,* Ashgill, Shakhriomon, Uzbekistan; *a–c,* dorsal, lateral, posterior views, ×2 (new); *d–e,* polished sections, ×3.5 (Nikiforova, 1978).

Sulcatospira XU, 1979c, p. 109 [**Zygospira* (*Sulcatospira) plicata* XU, 1979c, p. 110; OD] [=*Antizygospira* FU, 1982, p. 146 (type, *A. liquanensis,* OD); *Ovalospira* FU, 1982, p. 157 (type, *O. ovalis,* OD); *Taoqupospira* FU, 1982, p. 159 (type, *T. dichotoma,* OD); *Kuzgunia* MISIUS, 1969 (ms.) in KLENINA, 1984, p. 113 (type, *Zygospira parva* RUKAVISHNIKOVA, 1956, p. 162, OD); *Kuzgunia* MISIUS, 1986, p. 186 (type, *K. asiatica,* OD)]. Small, rounded to subquadrate, weakly carinate; minute orthocline area; triangular beak; small deltidial plates flanking apical foramen; tubular, expanding coarse ribs with ventral, diverging midrib pair, producing carination; plicate-sulciplicate commissure; short teeth; small, rounded dental cavities; small, bulbous hinge plates; dorsomedial spiralia with fewer than 8 whorls; slender, long jugal processes posteromedial, lacking jugal plates. [Differs from superficially similar *Zygospira* in being plicate instead of sulcate, with jugal processes instead of jugum; differs from *Eospirigerina* and *Spirigerina* in small size, expanding coarse ribs.] *Ordovician (?middle Caradoc, upper Caradoc–Ashgill):* China, Kazakhstan, Altai, central Asia, Australia.——FIG. 971,*5a–d.* **S. plicata,* Ashgill, Qinghai, northwestern China; dorsal, ventral, lateral, anterior views, ×3 (Xu, 1979c).——FIG. 971,*5e.* **S. parva* (RUKAVISHNIKOVA), Ashgill, Kazakhstan; serial section of spiralia, ×5 (new).

Superfamily PUNCTATRYPOIDEA Rzhonsnitskaia, 1960

[*nom. transl.* COPPER, herein, *ex* Punctatrypinae RZHONSNITSKAIA, 1960a, p. 262; *emend.,* COPPER, herein]

Ribbed atrypoids, with imbricate growth lamellae or short lamellae with fine grooves, ranging from ancestral, finely ribbed, nodose forms with short growth lamellae, lacking fenestrae, to shells with anterior fenestrae developed in concentric rows, open along actively growing anterior commissure, sealed posteriorly; dorsomedially directed spiralia with fewer than 10 whorls; jugal processes with short jugal plates. *Silurian (Aeronian)–Middle Devonian (Eifelian).*

Family PUNCTATRYPIDAE Rzhonsnitskaia, 1960

[*nom. transl.* COPPER, herein, *ex* Punctatrypinae RZHONSNITSKAIA, 1960a, p. 262]

Diagnosis as for superfamily. *Silurian (Aeronian)–Middle Devonian (Eifelian).*

Subfamily PUNCTATRYPINAE Rzhonsnitskaia, 1960

[Punctatrypinae RZHONSNITSKAIA, 1960a, p. 262] [=Crassipunctatrypinae WANG, COPPER, & RONG, 1983, p. 1085]

Punctatrypids with secondary layer modified to develop concentrically, radially aligned, round to oval fenestrae, open around commissure, posteriorly sealed off during growth, penetrating primary and secondary shell layers to shell interior; fenestrae (not punctae) oriented oblique or normal to shell surface (fenestrae absent in teeth, hinge, and socket plates); short growth lamellae may protrude as ribbed or smooth frills with angular narrow grooves, partly covering fenestrae; teeth solid; hinge plate usually thick. *Lower Devonian (middle Lochkovian)–Middle Devonian (Eifelian).*

Punctatrypa HAVLÍČEK, 1953, p. 8 [**P. nalivkini;* OD]. Small, elongate to rounded, biconvex, non-carinate; narrow hinge; protruding beak; small orthocline area; apical foramen flanked by triangular deltidial plates; finely ribbed; short, imbricate growth lamellae, closely spaced along commissure; single, vertical fenestra on each rib crest; weak, small dorsal sulcus posteriorly; rectimarginate commissure; solid, strong, short teeth, lacking dental cavities; thick hinge plate; narrow cardinal pit; large inner socket ridges; short crura; spiralia, jugal processes undescribed. [Distinguished by small, rounded, biconvex shell, evenly developed, fine ribs.] *Lower Devonian (middle Lochkovian)–Middle Devonian (Eifelian):* Eurasia, North America.——FIG. 972,*2a–g.* **P. nalivkini,* Emsian, Czech Republic; *a–d,* dorsal, ventral, posterior, anterior views, ×3.5; *e,* interior of ventral valve, ×3.7 (Havlíček, 1987a); *f,* SEM view of ventral valve interior, ×25.5 (new); *g,* external view of shell with fenestrae, ×30 (Wang, Copper, & Rong, 1983).

Crassipunctatrypa MIZENS & RZHONSNITSKAIA, 1979, p. 63 [**Punctatrypa crassiconcentrica* MIZENS, 1977b, p. 93; OD]. Small to medium, rounded,

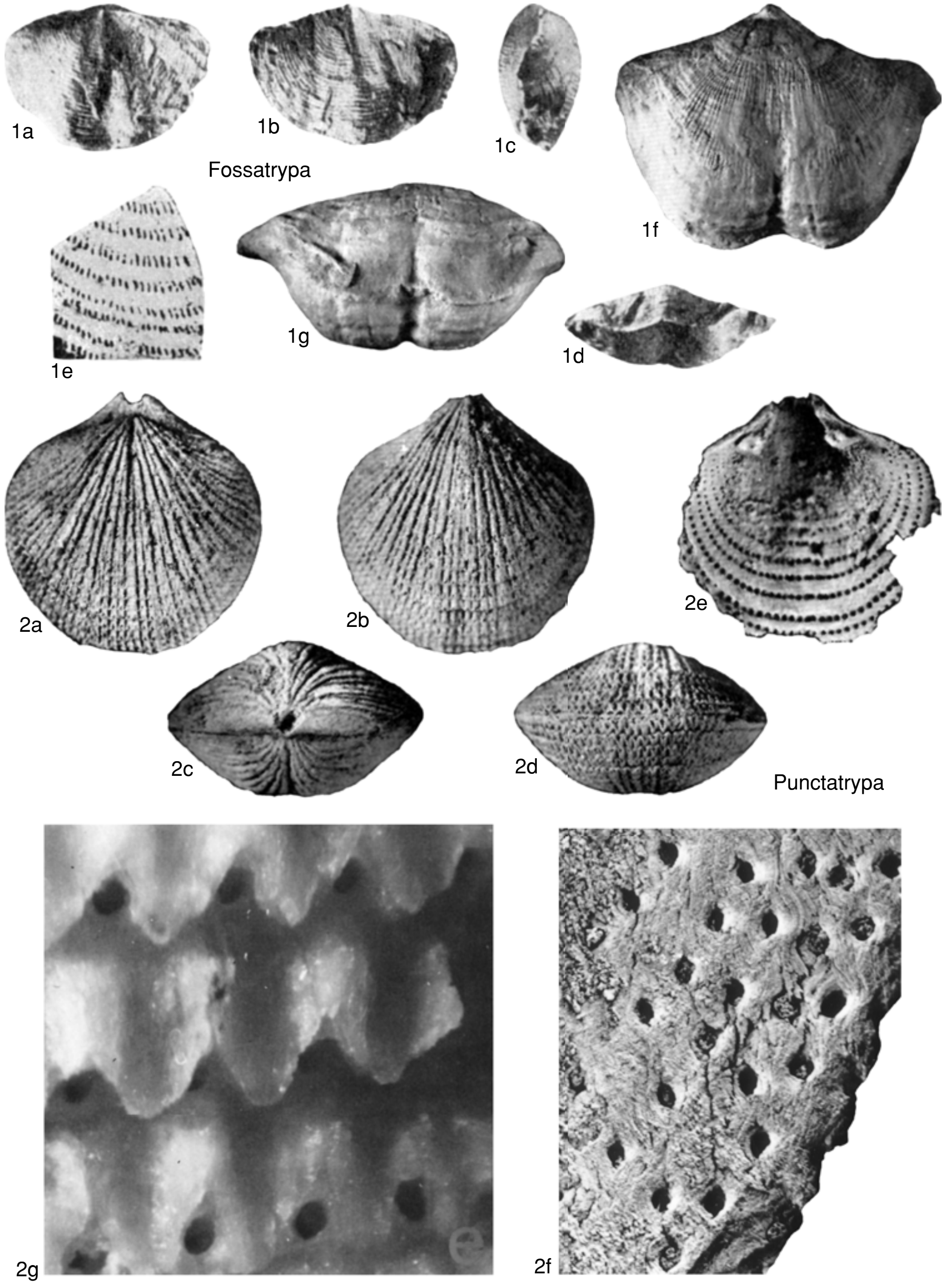

FIG. 972. Punctatrypidae (p. 1434–1437).

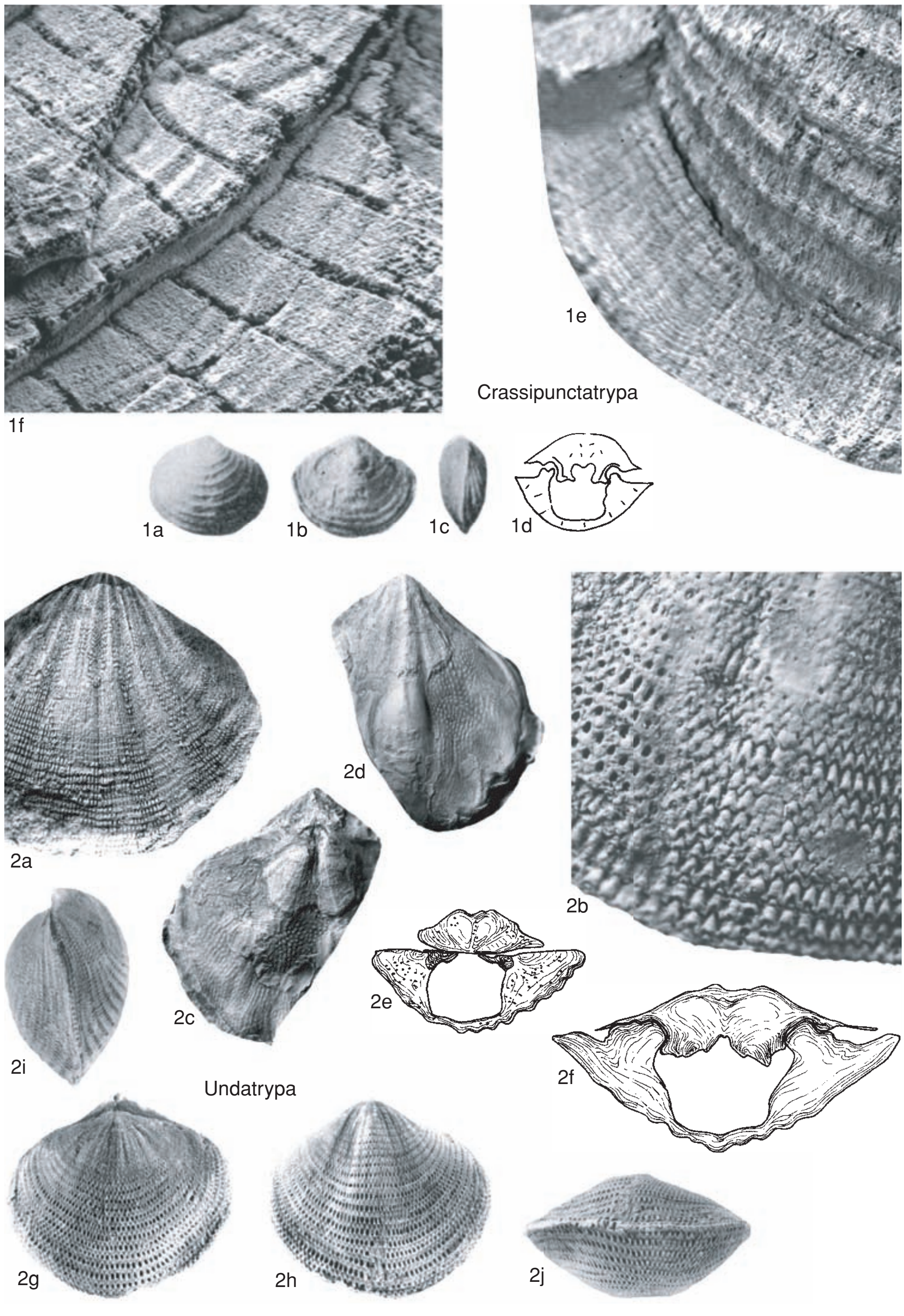

FIG. 973. Punctatrypidae (p. 1434–1438).

biconvex; small beak; minute anacline-orthocline area; apical foramen bisecting deltidial plates; surface covered by very fine ribs posteriorly, tending to fade anteriorly, ribbing absent on growth lamellae; concentric, flat, weakly deflected growth lamellae protruding as overlapping, flat frills, possessing narrow, radial, linear grooves; concentric anterior fenestrae partially roofed over by growth lamellae; commissure rectimarginate to weakly plicate; solid teeth; hinge plates delicate; spiralia, jugal processes undescribed. [Distinguished from *Punctatrypa* and others by its unique, flat growth lamellae with radiating linear grooves, rib loss anteriorly, hidden fenestrae.] *Lower Devonian (upper Pragian)–Middle Devonian (middle Eifelian):* Urals, central Asia, Tian Shan.——FIG. 973,*1a–f.* **C. crassiconcentrica* (MIZENS), Emsian, Turkestan; *a–c,* dorsal, ventral, lateral views, ×1; *d,* serial section, ×2.5 (Mizens, 1984); *e,* SEM view of growth lamellae, ×14; *f,* SEM view of fenestrae, ×43 (new).

Fossatrypa MIZENS & RZHONSNITSKAIA, 1979, p. 62 [**Punctatrypa fossa* BREIVEL, 1959, p. 56; OD] [=*Araneatrypa* HAVLÍČEK, 1987a, p. 90 (type, *Terebratula arachne* BARRANDE, 1847, p. 457, OD)]. Medium, biconvex, wider than long, long hinged, weakly carinate posteroventrally; hypercline-anacline area; beak incurved, obscuring foramen, deltidial plates; ribs fine, not overprinted by coarser ribs; short, concentric lamellae creating appearance of granules at rib crests, overlying oval fenestrae beneath; anterior fenestrae diagonal to shell surface; frills absent; commissure ligate or rectimarginate; interior with solid teeth; laterally arched crura; dorsomedial spiralia with about 6 whorls, jugal processes undescribed. [Differs from other punctatrypinids by its long hinge, wide spiriferoid shell, lack of overprinted ribs. "*Terebratula*" *granulifera* BARRANDE, 1847, lacks fenestrae and cannot be assigned to this genus.] *Lower Devonian (Pragian–Emsian), Middle Devonian (Eifelian):* eastern Urals, Carnic Alps, Czech Republic.——FIG. 972,*1a–e.* **F. fossa* (BREIVEL), ?lower Eifelian, ?middle Eifelian, eastern slopes, Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×3; *e,* enlarged view of macroornament, approximately ×10 (Breivel, 1959).——FIG. 972,*1f–g. F. arachne* (BARRANDE), Pragian, Czech Republic; dorsal, posterior views, ×1.4 (Havlíček, 1987a).

Sinopunctatrypa WANG, COPPER, & RONG, 1983, p. 1081 [**Punctatrypa (Sinopunctatrypa) saetulosa;* OD]. Small, ventribiconvex-planoconvex; weakly keeled or unkeeled; apsacline-orthocline area; small beak; apical foramen; wrinkled deltidial plates; fine ribs completely covering shell, intersected by short growth lamellae; ventral midrib pair raised; 2 or more vertical small fenestrae per rib; commissure sulcate to weakly plicate; interior with solid teeth; hinge plates broad; wide cardinal pit; dorsomedial spiralia with fewer than 8 whorls; jugal processes undescribed. [Distinct from other punctatrypinids in having 2 or more fenestrae per rib, instead of

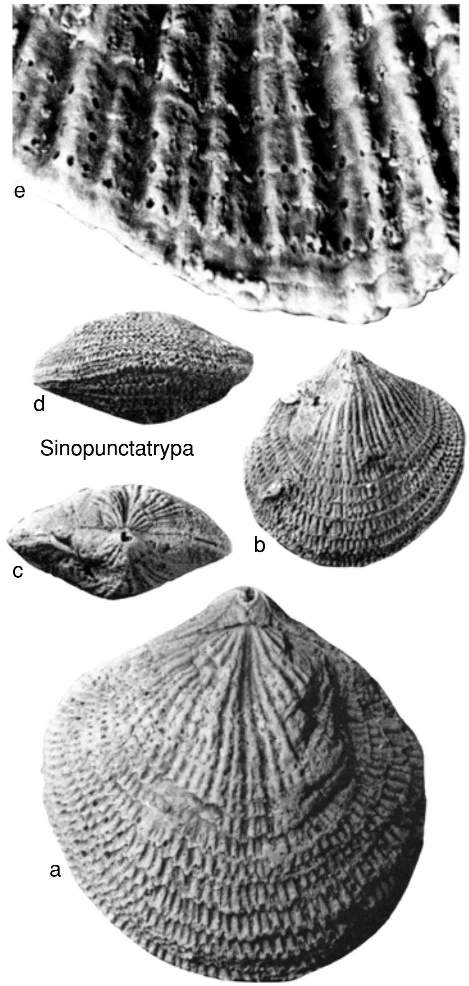

FIG. 974. Punctatrypidae (p. 1437).

single fenestra on each rib crest.] *Lower Devonian (Emsian):* southern China (Guangxi).——FIG. 974*a–e.* **S. saetulosa* (WANG, COPPER, & RONG), lower Emsian; *a,* dorsal view, ×5; *b–d,* ventral, posterior, anterior views, ×3; *e,* detail of ventral valve, ×15 (Wang, Copper, & Rong, 1983).

Undatrypa COPPER, 1978, p. 302 [**Terebratula munieri* GRUENEWALDT, 1854, p. 581[13]; OD] [=*Munieratrypa (Munieratrypa)* MIZENS & RZHONSNITSKAIA, 1979, p. 60 (type, *Punctatrypa munieri dichotomoplicata* RZHONSNITSKAIA, 1960a, pl. 56,*4ab, nom. nud.,* no description, OD, *vid.* RZHONSNITSKAIA, 1975, p. 156]. Small to medium, flattened, biconvex; carinate posteroventrally, sulcate dorsally; moderately long hinge; small orthocline area; protruding beak; apical foramen flanked by deltidial plates; ribs fine, posteriorly overprinted by coarse, strong ribs, fading anteriorly; ventral midribs producing keel; anterior, diagonal fenestrae at intersections of growth lamellae and finer ribs; commissure rectimarginate to weakly plicate; thick shell wall; solid teeth; hinge plates strong; spiralia dorsomedial, fewer than 10 whorls; jugal processes undescribed. [Distinguished from other Punctatrypinae by having fine ribs overprinted with coarse ribs.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Urals, southwestern Europe, China, northern Canada.——FIG. 973,*2a–f.* **U. munieri* (GRUENEWALDT), Emsian, eastern slopes, Urals; *a,* ventral view, ×2.5; *b,* macroornament, fenestrae, ×12; *c–d,* dorsal, ventral interiors, ×2.5; *e–f,* serial sections, ×5 (Copper, 1978).——FIG. 973,*2g–j. U. bellatula* (WANG, COPPER, & RONG), Emsian, Guangxi, China; dorsal, ventral, lateral, anterior views, ×3 (Wang, Copper, & Rong, 1983).

Subfamily ATRYPINELLINAE new subfamily

[Atrypinellinae COPPER, herein]

Finely ribbed, small to medium, biconvex, sometimes bilobate shells, commonly ventrally subcarinate; finely ribbed; short, evenly spaced, slightly imbricate growth lamellae; fenestrae absent; narrow to wide hinge; orthocline beak; distinct deltidial plates; apical foramen; thin shell, small dental cavities or nuclei. [Taxa resembling *Punctatrypa,* but lacking fenestrae, e.g., *Atrypinella granulifera* (BARRANDE, 1879b), may be assigned here.] *Silurian (Aeronian)–Lower Devonian (Emsian).*

Atrypinella KHODALEVICH, 1939, p. 45 [**Atrypa (Atrypinella) biloba;* OD]. Small to medium, rounded, globose, bilobate to biconvex; both valves normally sulcate, ventral valve subcarinate posteriorly; finely ribbed, with decorticated shell giving granulose appearance; closely spaced, flat, short growth lamellae; ligate to rectimarginate commissure; short teeth, possessing nuclei or small dental cavities; hinge socket plates thick; dorsal spiralia with fewer than 6 whorls; jugal processes thin, ventromedial to medial, almost touching. [Differs from *Reticulatrypa* in subcarinate, bisulcate shell; includes well-known *A. granulifera* (BARRANDE, 1879b).] *Silurian (Přídolí)–Lower Devonian (Emsian):* Urals, central Asia, western Europe, arctic Canada.——FIG. 975,*1a–d.* **A. biloba* (KHODALEVICH), Lochkovian, Urals; dorsal, ventral, lateral, anterior views, ×1 (Khodalevich, 1939).——FIG. 975,*1e–f. A. losvensis* (KHODALEVICH), upper Lochkovian–lower Pragian, eastern slopes, Urals; serial sections, ×2 (Mizens, 1984).

?Istokina BREIVEL & BREIVEL, 1988, p. 81 [*?*Spinatrypa bobrovkensis* MIZENS, 1977a, p. 50; OD]. Small, biconvex-ventribiconvex, rounded, subcarinate; moderately long, straight hinge; area orthocline; apical foramen; small deltidial plates; fine, imbricate-undulose ribs; bifurcating midrib pair producing weak keel on ventral valve; median sulcus on dorsal valve; very short, less than 2 mm, deflected growth lamellae; rectimarginate to weakly plicate commissure; pedicle callist absent; solid teeth; vertically oriented, long crura; spiralia, jugal processes undescribed. [Affinity uncertain; possibly synonymous with *Atrypinella* from which it differs in more wavy ribs, carination, apparent absence of dental cavities or nuclei; similar to finely ribbed *Plectatrypa* in sculpture, but lacking strong ventral carination.] *Silurian (Přídolí):* Urals.——FIG. 975,*3a–e.* **I. bobrovkensis* (MIZENS), eastern slopes; *a–d,* dorsal, ventral, lateral, anterior views, ×1 (Mizens, 1977a); *e,* enlarged view of dorsal macroornamentation, ×3 (Breivel & Breivel, 1988).

Limbatrypa COPPER, 1982, p. 700 [**L. leptostriata;* OD]. Relatively flat, weakly biconvex, ventrally weakly carinate; wide hinge; small, pointed beak; prominent orthocline area; apical foramen; deltidial plates; very finely ribbed; growth lamellae right-angled, short, less than 5 mm; rectimarginate commissure; teeth with dental cavities; crura, spiralia, jugal processes silicified, undescribed. [Similar to *Atrypinella* in rib fineness, granulose appearance at growth lamellae, but with relatively flat, wide shell, sharply deflected (about 90°), short lamellae, lack of bisulcation; affinities with Atrypinae, Variatrypinae, or Atrypinellinae uncertain.] *Silurian (Aeronian–Wenlock):* North America, Urals, central Asia.——FIG. 975,*4a–e.* **L. leptostriata,* Telychian, Manitoulin, eastern Canada; *a–d,* dorsal, ventral, posterior, lateral views, ×2 (Copper, 1982); *e,* detail of dorsal macroornamentation, ×5 (new).

Reticulatrypa SAVAGE, 1970, p. 663 [**R. fairhillensis;* OD]. Rounded, subcircular to ovate, globose, biconvex, weakly carinate or noncarinate; small orthocline area; apical foramen; minute deltidial plates; finely ribbed; imbricate ornamentation produced by less than 1-mm-spaced, short growth lamellae; rectimarginate to flat, widely plicate commissure; shell wall thin; teeth with possible dental cavities; muscle scars weakly incised; hinge plate delicate; spiralia of fewer than 6 whorls, dorsally directed; jugal processes undescribed (from silicified type material). [Ornamentation similar to possibly congeneric *Atrypinella,* but lacking strong bisulcation of type species; differs from *Limbatrypa* in imbricate ornamentation; affinities with Atrypinellinae uncertain, possibly referable to Atrypinae.] *Silurian (?Přídolí), Lower Devonian (Lochkovian–Pragian):* Australia, ?Europe, ?Urals, ?northwestern Canada.——FIG. 975,*2a–e.* **R. fairhillensis,* Pragian, New South Wales; *a–d,* dorsal, ventral, posterior, anterior views; *e,* lateral view of spiralium, ×3 (Savage, 1970).

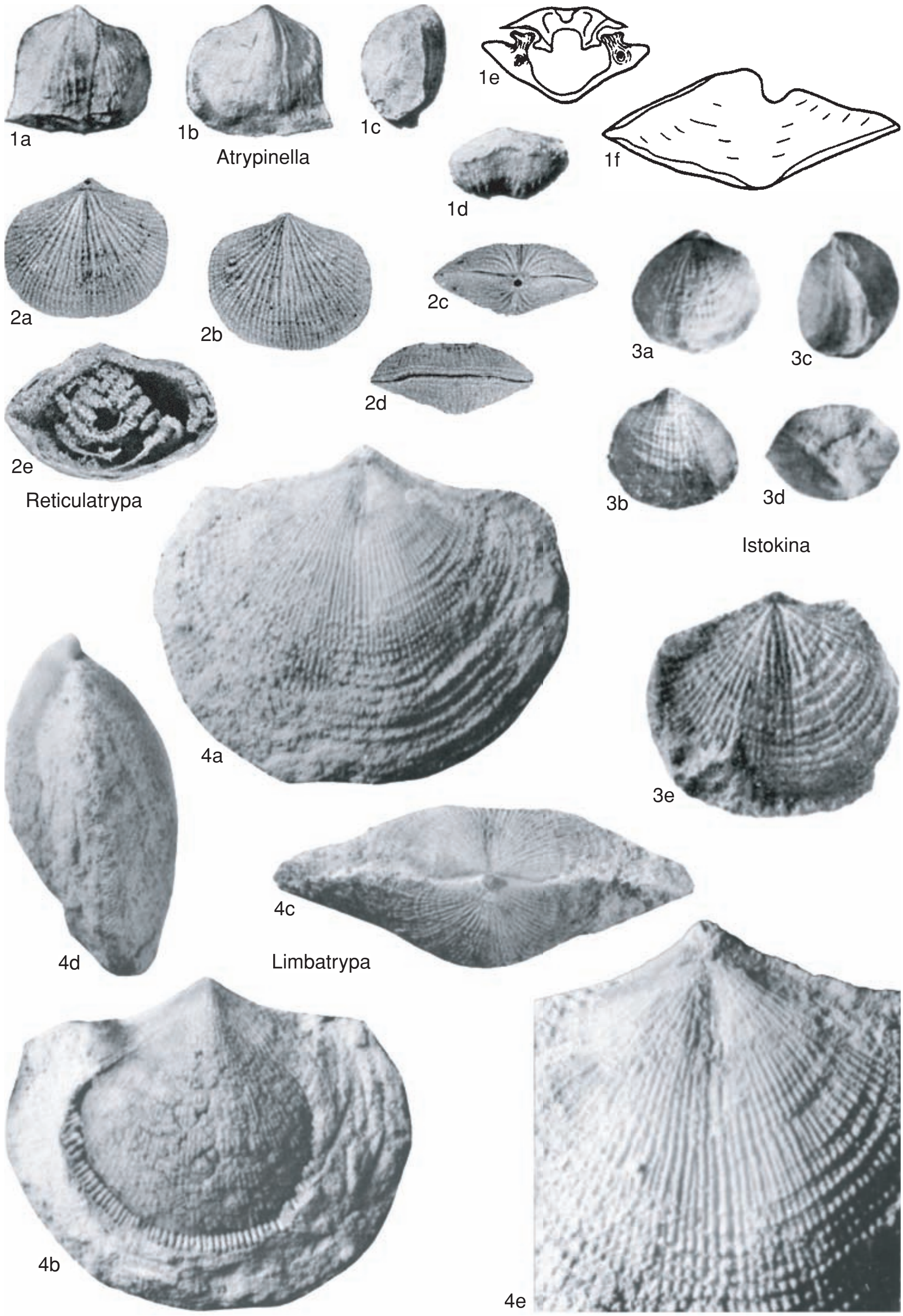

FIG. 975. Punctatrypidae (p. 1438).

Suborder ANAZYGIDINA Copper, 1996

[Anazygidina COPPER in COPPER & GOURVENNEC, 1996, p. 82] [=Zygospiridae WAAGEN, 1883, p. 449, *partim*]

Ribbed, small shells with sulcate-rectimarginate commissure; astrophic to strophic hinge; small orthocline area, beak; apical foramen; deltidial plates lacking or minute; teeth solid or with small dental cavities; simple spiralia medially to dorsomedially directed, normally fewer than 10 whorls; complete U- or W-shaped jugum. *Ordovician (?Llandeilo, Caradoc)–Silurian (Ludlow, ?Přídolí).*

Superfamily ANAZYGOIDEA Davidson, 1883

[*nom. transl.* COPPER, herein, *ex* Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim; emend.* COPPER, herein] [=Zygospiroidea WAAGEN, 1883, p. 446, *partim; emend.,* MUIR-WOOD, 1955, p. 91]

Characters as for suborder. *Ordovician (?Llandeilo, Caradoc)–Silurian (Ludlow, ?Přídolí).*

Family ANAZYGIDAE Davidson, 1883

[Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim; emend.,* COPPER, herein] [=Zygospiroidea WAAGEN, 1883, p. 446, *partim; emend.,* MUIR-WOOD, 1955, p. 91]

Small, ventribiconvex to planoconvex, ribbed shells; astrophic hinge; small area; sulcate to rectimarginate commissure; spiralia directed medially to dorsomedially with few whorls; simple jugum located dorsally to centrally. *Ordovician (?Llandeilo, Caradoc)–Silurian (Ludlow, ?Přídolí).*

Subfamily ANAZYGINAE Davidson, 1883

[*nom. transl.* COPPER, herein, *ex* Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim; emend.,* COPPER, herein] [=Zygospiridae WAAGEN, 1883, p. 446, *partim; emend.,* MUIR-WOOD, 1955, p. 91]

Small, weakly to strongly carinate, ventribiconvex to planoconvex anazygids with sulcate commissure; simple medially to dorsomedially directed spiralia with few whorls, central to anterodorsal jugum arising anterolaterally. *Ordovician (?Llandeilo, Caradoc)–Silurian (Sheinwoodian).*

Anazyga DAVIDSON, 1882, p. 128 [**Atrypa recurvirostra* HALL, 1847, p. 140; OD] [=*Hallina* WINCHELL & SCHUCHERT, 1892, p. 291 (type, *H. saffordi,* OD); *Nuria* MISIUS, 1986, p. 199 (type, *N. mediasiatica,* OD)]. Small, ventribiconvex, rounded to elongate, noncarinate; short hinge; protruding beak; small orthocline area; minute apical foramen; deltidial plates minute or lacking; ribs fine, anteriorly slightly expanding, bifurcating-intercalating; sulcate commissure; interior thin shelled; small, medially directed teeth with minute dental cavities; small, delicate hinge plate; crura vertical; spiralia medially directed, normally fewer than 5 whorls, occupying only part of shell interior; jugum flat, dorsomedially located, near shell anterior. [Distinguished from *Zygospira* by rounded-elongate shape, lack of carination, fine ribs, short hinge, medially oriented spiralia.] *Ordovician (?Llandeilo, Caradoc, ?middle Ashgill):* worldwide.——FIG. 976,*2a–i.* **A. recurvirostra* (HALL), Caradoc, New York, USA; *a–d,* dorsal, ventral, anterior, lateral views, ×3; *e–h,* serial sections, ×5; *i,* reconstruction of brachidium, ×5 (new).

Zygatrypa COPPER, 1977a, p. 307 [**Zygospira paupera* BILLINGS, 1866, p. 46; OD]. Small, strongly carinate, ventribiconvex-planoconvex; narrow hinge; beak minute, pinched; small anacline to hypercline area; minute deltidial plates; apical-transapical foramen; shell almost smooth to partly ribbed, ribs coarsening distally, shell generally smooth on lateral flanks; where present, 6 to 8 ribs occupying ventral carina; broadly sulcate commissure; interior relatively thick walled; short teeth with dental nuclei, dental cavities lacking; hinge plate stout; crura short, laterally directed; spiralia dorsomedial, fewer than 5 whorls; jugum curved, posterodorsal, almost resting on dorsal valve floor. [Distinguished from *Zygospira* by its thick shell wall, trend toward lateral or total rib loss, fine ribs on ventral carina, lack of dental cavities, and posteriorly located jugum.] *Silurian (Llandovery–Sheinwoodian):* North America, western Europe.——FIG. 976,*3a–h.* **Z. paupera* (BILLINGS), Telychian, Anticosti, Canada; *a,* ventral view, ×4; *b–c,* dorsal, anterior views, ×3; *d–e,* serial sections, ×5; *f–g,* camera lucida drawings, ×6; *h,* reconstruction of brachidia, ×5 (Copper, 1977a).

Zygospira HALL, 1862, p. 154 [**Producta modesta* SAY in HALL, 1847, p. 141; OD] [=*Pusillagutta* MISIUS, 1986, p. 210 (type, *P. gibbera* MISIUS, 1986, p. 211, OD)]. Small, ventribiconvex-planoconvex; ventral valve strongly to weakly carinate; weakly sulcate dorsal valve; long hinge; small orthocline-anacline area; minute beak; apical-transapical foramen; deltidial plates minute to absent; ribs medium (coarse ribs on ventral carina), expanding distally, generally nonbifurcating; growth interruptions common, rare, slightly overlapping anterior growth lamellae; commissure sulcate; interior thinly walled; minute, medially directed teeth with dental cavities; brachidia delicate; crura small, laterally directed; spiralia dorsomedially directed with fewer than 8 whorls, filling much of shell interior; jugum posteromedial to dorsal, in mid-anterior of shell. [Distinguished from *Anazyga* by wider hinge line, carination, coarser ribs, dorsomedially directed spiralia.] *Ordovician (Caradoc–Ashgill):* worldwide.——FIG. 976,*1a–h.* **Z. modesta* (SAY), middle

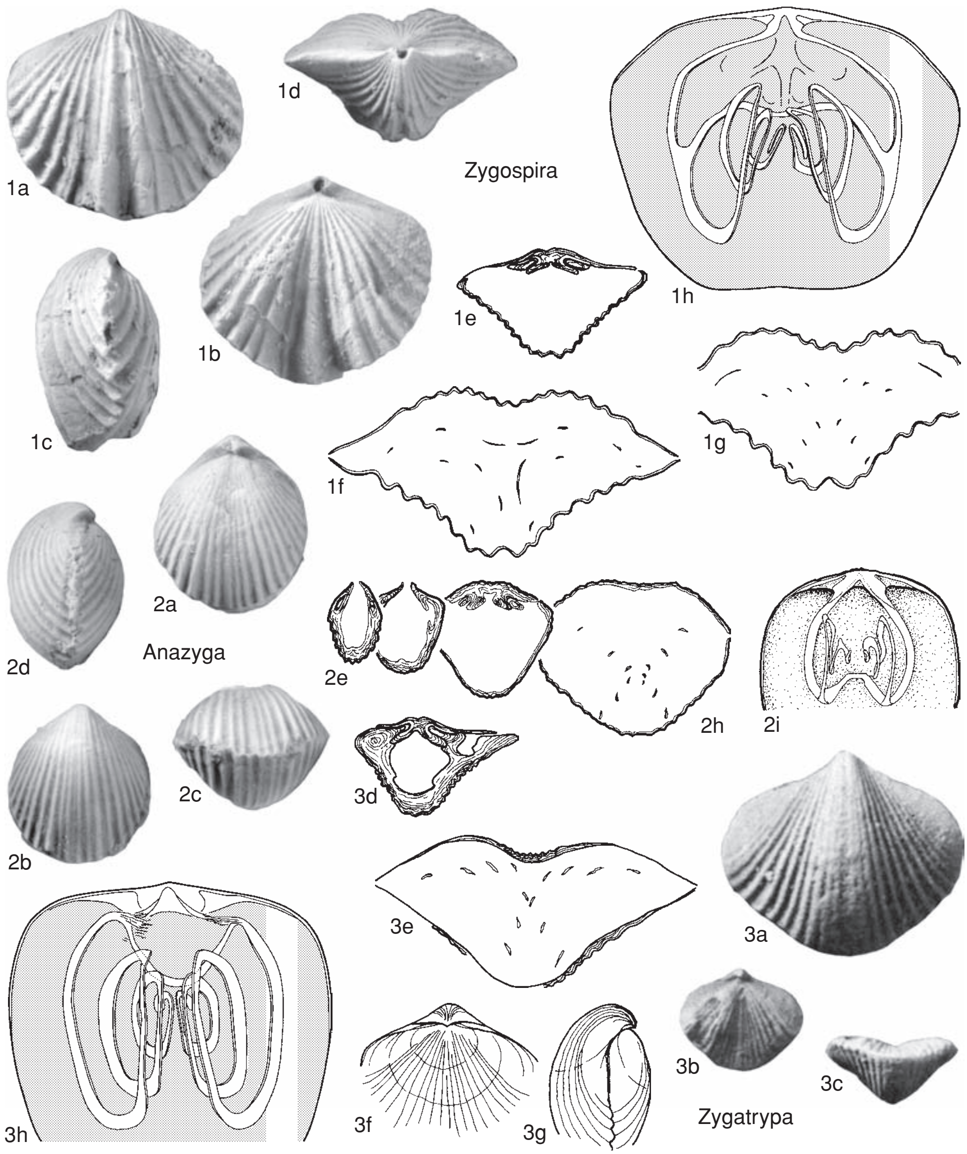

FIG. 976. Anazygidae (p. 1440).

Ashgill, Ohio, USA; *a–d,* ventral, dorsal, lateral, posterior views, ×3; *e–g,* serial sections with jugum, spiralia, ×5; *h,* reconstruction of brachidium, ×5 (Copper, 1977a).

Subfamily CATAZYGINAE Copper, 1977

[Catazyginae COPPER, 1977a, p. 311]

Ribbed, elongate to rounded, biconvex to dorsibiconvex, lacking ventral carination; rectimarginate commissure; small, narrow, anacline-hypercline area; minute foramen; deltidial plates obscured to absent; thick shell wall; prominent pedicle callist; dental cavities small to absent; dorsomedial to dorsal spiralia; simple central to ventrocentral jugum. *Ordovician (upper Caradoc)–Silurian (Llandovery).*

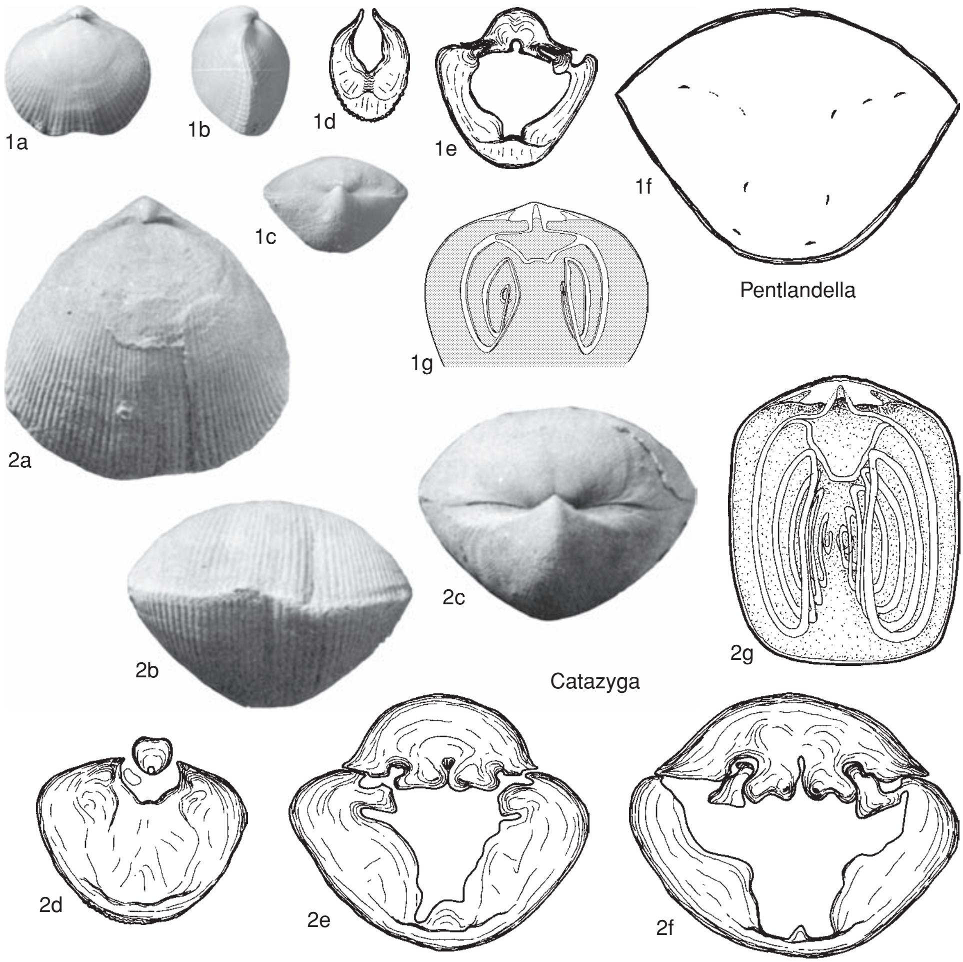

FIG. 977. Anazygidae (p. 1442–1443).

Catazyga HALL in HALL & CLARKE, 1893, p. 157 [**Athyris headi* BILLINGS, 1862, p. 147; OD; *vid.* HALL, 1894, p. 601] [=*Orthonomaea* HALL in HALL & CLARKE, 1893, p. 159 (type, *Orthis ?erratica* HALL, 1847, p. 288, OD, *vid.* HALL, 1894, p. 601); *Septacatazyga* DISTLER, 1972, p. 194, *nom. nud.* (type, *Catazyga homeospiroides* ROSS & DUTRO, 1966, p. 19, OD); *Salairella* SEVERGINA, 1984, p. 45 (type, *Catazyga salairica* SEVERGINA, 1960a, p. 403, OD); *Eonalivkinia* VLADIMIRSKAYA, 1985, p. 155 (type, *E. hondelensis,* OD)]. Small to medium, globose-elongate, biconvex-ventribiconvex; short, narrow hinge; small anacline to hypercline area; obscured pedicle opening; minute deltidial plates; finely ribbed; rarely fine concentric growth filae; weakly sulcate-rectimarginate to weakly plicate commissure; thick pedicle callist; muscle scars strongly incised; teeth stubby, curved, with or without dental cavity; hinge plate massive; bulbous crural bases; crura short; mediodorsal spiralia with fewer than 10 whorls; simple, posteromedial, U-shaped jugum. [Distinguished from *Anazyga* by large size, thick shell wall, nature of hinge plate, posterior location of jugum.] *Ordovician (upper Caradoc–Ashgill):* North America, Eurasia.——FIG. 977,*2a–g.* **C. headi* (BILLINGS), middle Ashgill, Québec, Canada; *a–c,* dorsal, posterior, anterior views, ×2; *d–f,* serial sections, ×5 (Copper, 1977a); *g,* reconstruction of brachidia, ×3 (new).

Pentlandella BOUCOT, 1964b, p. 104 [**Rhynconella* [sic] *pentlandicus* HASWELL, 1865, p. 31; OD]. Small, ventribiconvex, subpentagonal outline; small, hypercline area; beak minute; apical-transapical foramen; deltidial plates lost; very fine ribs; fine to almost smooth shell; commissure rectimarginate to weakly plicate; interior with thick shell wall; partly raised ventral muscle field; short, solid teeth; hinge plate small, with central cardinal

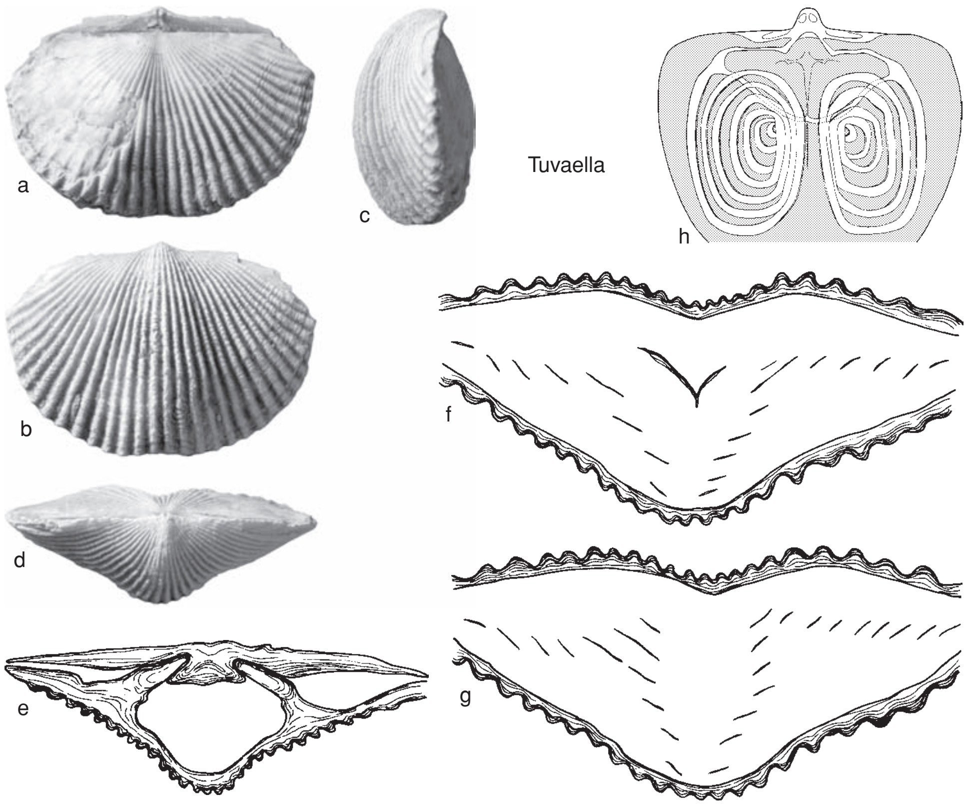

FIG. 978. Anazygidae (p. 1443).

pit; delicate crura; posteromedial to mediodorsal spiralia with fewer than 5 whorls; W- to U-shaped, ventroposterior jugum. [Distinguished from *Catazyga* by small, pentagonal shell, very fine ribs, weak hinge plate, raised ventral muscle field, reduced number of spiralial whorls. Holotype and paratypes preserved as molds in sandstones.] *Silurian (Llandovery):* Europe, North America.——FIG. 977,*1a–g*. *P. tenuistriata* RUBEL, Telychian, Estonia; *a–c,* dorsal, lateral, posterior views, ×2; *d–f,* serial sections, ×5; *g,* reconstruction of brachidium, ×3.5 (Copper, 1977a).

Subfamily TUVAELLINAE Alikhova, 1960

[*nom. transl.* COPPER, herein, *ex* Tuvaellidae ALIKHOVA, 1960, p. 190; *emend.,* COPPER, herein]

Medium to large, relatively flat, orthoid to spiriferoid shape, ribbed; wide, flat ventral area; sulcate commissure; long, strophic hinge; delthyrium with deltidial plates, apical foramen; notothyrium, chilidium lacking; teeth solid; dorsomedial spiralia with fewer than 10 whorls; jugum large, dorsomedial. *Silurian (upper Llandovery–Ludlow, ?Přídolí).*

Tuvaella CHERNYSHEV, 1937, p. 12 [**T. rackovskii;* OD]. Medium to large, long hinged, flat, ventribiconvex-planoconvex-dorsibiconvex; ventral valve carinate, dorsal sulcate; large, wide orthocline-anacline area; small, slitlike apical foramen, or foramen may be absent; prominent deltidial plates; continuous ribs expanding anteriorly, lacking raised, ventral midribs; distinct concentric growth filae; commissure sulcate; interior with solid, broad teeth, lacking accessory projections; hinge plate massive; cardinal pit absent; raised, but flat cardinal process; crura laterally directed; postero- to mediodorsally directed spiralia of fewer than 10 whorls; jugum dorsomedial, V-shaped, possessing ventrally directed crest. [Differs from other anazygids in large size, spiriferoid shape, solid teeth, V-shaped jugum.] *Silurian (upper Llandovery–Ludlow, ?Přídolí):* Tuva, Altai, Mongolia, Xinjiang, northeastern China.——FIG. 978*a–h*. **T. rackovskii,* upper Llandovery, Tuva; *a–d,* dorsal, ventral, lateral, posterior views, ×2; *e–g,* serial sections, ×5; *h,* reconstruction of brachidium, ×2.5 (Copper, 1977a).

Suborder DAVIDSONIIDINA Copper, 1996

[Davidsoniidina Copper, 1996a, p. 593]

Ribbed or smooth atrypoids, lacking growth lamellae; rarely with wide single frill (trail); strophic-astrophic hinge; relatively prominent, wide orthocline-apsacline area; deltidial plates with apical foramen, or foramen lost by total closure of delthyrium; dorsomedially directed spiralia with fewer than 10 whorls; ventroposterior jugal processes commonly terminating in large boss. *Silurian (Ludlow)–Middle Devonian (Givetian).*

Superfamily DAVIDSONIOIDEA King, 1850

[*nom. transl. et correct.* Copper, 1996a, p. 593, *ex* Davidsonidae King, 1850, p. 81; *emend.,* Copper, 1996a, p. 593]

Generally wide, flat, biconvex to dorsibiconvex, strophic shell, with wide area, deltidial plates, and apical foramen, usually liberosessile or cemented by pedicle valve (pedicle opening fully sealed by deltidial plates); rarely with commissural trail; multiple frills, growth lamellae absent; muscle scars, vascular canals atrypoid, dorsomedially to dorsally directed spiralia, commonly impressed as grooves in ventral valve; jugal processes ventroposterior, may terminate in jugal boss. *Silurian (?Ludlow, Přídolí)–Middle Devonian (Givetian).*

Family DAVIDSONIIDAE King, 1850

[*nom. correct.* Copper, 1978, p. 306, *pro* Davidsonidae King, 1850, p. 81; *emend.,* Copper, 1978, p. 306]

Smooth, rarely radially corrugate or concentrically wrinkled shell; cemented or free-living, convex ventral valve; commonly flat to concave dorsal valve; trail absent; strophic hinge; teeth solid; spiralia dorsally directed, usually centered over spiral grooves on raised cones of ventral valve; jugal processes touching. *Silurian (Přídolí)–Middle Devonian (Givetian).*

Davidsonia Bouchard-Chantereaux, 1849, p. 92 [**D. Verneuillii;* OD]. Medium to large, commonly asymmetrical, wider than long, subquadrate to rounded in outline, smooth, flat to ventribiconvex-planoconvex; cemented ventral valve thick in gerontic stages, usually cemented to hard substrates from apex to commissure, rarely free; dorsal valve flat to weakly concave; enlarged, flat, normally apsacline area; pointed, triangular beak; delthyrial cavity normally completely sealed by conjunct deltidial plates (foramen, deltidium, chilidium absent); surface smooth to concentrically wrinkled; rectimarginate commissure; pedicle collar lining apical cavity; teeth solid; hinge plate short, thick, lacking cardinal pit, capped by prominent, bushy cardinal process; crura projected from inner socket ridges; spiralia, rarely preserved, impressed in grooves of raised cones on ventral valve, fewer than 6 whorls, dorsally directed; jugal processes undescribed (except as fragments). [Distinct from other davidsoniids in fixosessile cementation of ventral valve, common asymmetry, lack of foramen.] *Lower Devonian (Emsian)–Middle Devonian (upper Givetian):* Europe, central Asia, China, USA (Nevada).——Fig. 979,*1a–f.* **D. verneuillii,* upper Eifelian, Germany; *a–c,* exterior dorsal view, interior ventral valve (cemented to alveolitid coral), interior dorsal valve, ×2 (new); *d–f,* serial sections, ×5 (Copper, 1978).

Prodavidsonia Havlíček, 1956, p. 564 [**P. dalejensis;* OD] [=*Quasidavidsonia* Havlíček, 1987a, p. 106 (type, *Prodavidsonia vicina* Havlíček, 1967b, p. 215, OD)]. Symmetrical, wider than long, flat, planoconvex to weakly concavoconvex to weakly ventribiconvex; weakly carinate, weakly convex ventral valve; weakly convex, flat, posteriorly sulcate dorsal valve; shell liberosessile; wide apsacline-orthocline area; slightly projecting beak; apical foramen flanked by deltidial plates; smooth to weakly concentrically ornamented surface; commissure rectimarginate to weakly sulcate; teeth solid; hinge plate *Davidsonia*-like with small cardinal process; spiralial grooves impressed in raised cones of ventral valve; spiralia, jugal processes undescribed. [Spiralial grooves in ventral valve, muscle scars as in *Davidsonia,* but more weakly impressed; differs in having apical foramen, liberosessile ventral valve (uncemented to substrate), bilateral symmetry, wider than long shape.] *Lower Devonian (?Pragian, Emsian)–Middle Devonian (lower Givetian):* western Europe, Urals.——Fig. 979,*2a–e.* **P. dalejensis,* Emsian, Czech Republic; *a–d,* dorsal, ventral, anterior, posterior views, ×2 (new); *e,* interior ventral valve, ×3 (Havlíček, 1987a).

Rugodavidsonia Copper, 1996a, p. 597 [**Davidsonia woodwardiana* de Koninck, 1855, p. 284; OD]. Small to medium, planoconvex-concavoconvex, rounded to ovoid outline, usually asymmetrical; short hinge line; ventral valve apex flattened, cemented or liberosessile apically; strongly protruding beak; large, flat area; deltidial plates narrow, high, completely sealing delthyrium; foramen absent; rectimarginate commissure; smooth apically, coarsely ribbed ornamentation distally; ventral valve

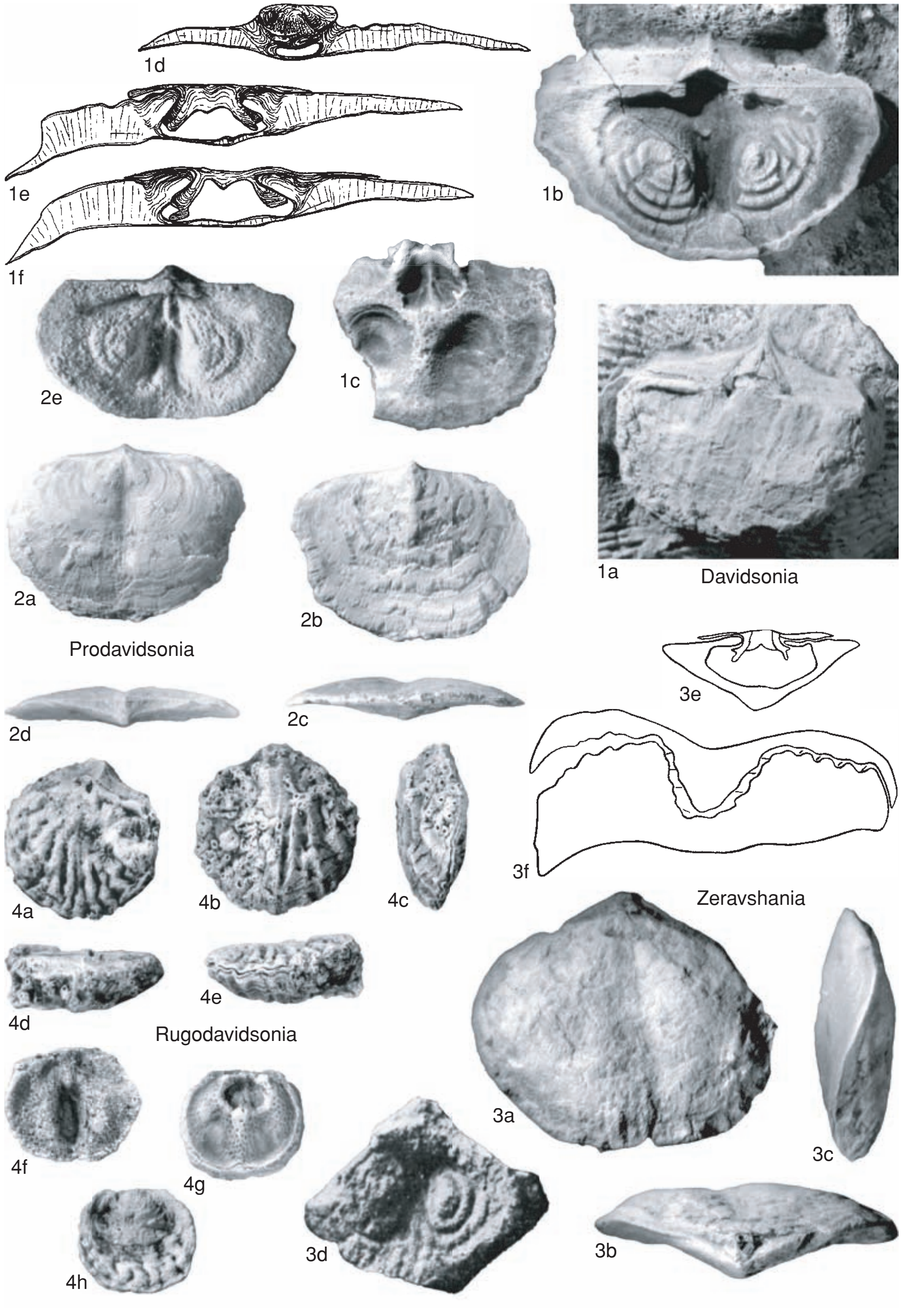

FIG. 979. Davidsoniidae (p. 1444–1446).

with central cones accommodating dorsally directed spiralia from opposing valve, lacking spiralial grooves; muscle scars, gonadal pits atrypoid; short hinge plate, protruding partially into delthyrial cavity; crura, spiralia, jugal processes undescribed. [Differs from *Davidsonia* in presence of coarse radial ribs, rounded-elongate shape, liberosessile ventral valve, lack of spiralial grooves in ventral valve; homeomorphic with Permian orthotetids, but differing in lack of notothyrium, chilidium.] *Middle Devonian (upper Eifelian–Givetian):* Europe, USA (Nevada), southern China.——Fig. 979,*4a–h.* **R. woodwardiana* (de Koninck), upper Eifelian, Belgium; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×2; *f–h,* interior ventral valve, interior and exterior of same dorsal valve, ×2 (new).

Zeravshania Menakova, 1983, p. 66 [**Z. pachyvalvata* Menakova, 1983, p. 68; OD]. Small, smooth, flat, weakly biconvex to planoconvex; relatively short hinge line; ventrally strongly carinate, dorsally sulcate; protruding beak; small apsacline area; minute apical foramen at apex of deltidial plates; commissure weakly sulcate to rectimarginate to weakly plicate to ligate; thick shell wall; strong ventral, dorsal median septa; spiralial grooves weakly to strongly impressed into conical thickenings of ventral valve; teeth solid; spiralia dorsally directed, fewer than 4 whorls; jugal processes touching. [Most similar to *Prodavidsonia,* but differing in smaller size, reduced area, strong carination, sulcate-ligate commissure.] *Silurian (Přídolí)–Lower Devonian (Lochkovian):* central Asia, Urals (eastern slopes).——Fig. 979,*3a–f.* **Z. pachyvalvata,* Přídolí, Zeravshan, Tadzhikistan; *a–c,* dorsal, posterior, lateral views, ×2 (new); *d,* interior of ventral valve, ×2; *e–f,* serial sections with spiralia, ×5 (Menakova, 1983).

Family CARINATINIDAE Rzhonsnitskaia, 1960

[*nom. transl.* Copper, 1996a, p. 600, *ex* Carinatininae Rzhonsnitskaia, 1960a, p. 261] [=Davidsoniatrypidae Havlíček, 1987a, p. 100]

Usually relatively flattened, commonly carinate (secondary loss of carination), biconvex-dorsibiconvex, mostly strophic shells, with prominently enlarged area (not anacline-hypercline), foramen, continuous ribs, wide trail (where preserved). Relatively thick hinge plates, jugal processes commonly with enlarged ends, spiralia nearly always dorsally directed, may or may not be impressed into ventral valve. *Silurian (?Ludlow), Lower Devonian (Pragian)–Middle Devonian (Givetian).*

Carinatina Nalivkin, 1930a, p. 104 [**Orthis arimaspus* Eichwald in von Buch, 1840, p. 108; OD; *vid.* d'Eichwald, 1861, p. 216] [=*Zejszneria* Siemiradzki, 1920, p. 172, *nom. oblit.* (type, *Orthisina davyi* Barrois, 1886, p. 194); ?*Salairina* Alekseeva, 1970, p. 131 (type, *S. misera,* OD); *Kaplicona* Havlíček, 1987a, p. 101 (type, *Biconostrophia conifera* Havlíček, 1967b, p. 209, OD); ?*Klukatrypa* Havlíček, 1987a, p. 95 (type, *K. klukovensis,* OD)]. Medium to large, flat, biconvex, strongly carinate; strophic hinge; wide apsacline-orthocline area; apical foramen, deltidial plates; coarsely ribbed, with 2 to 4 raised ventral midribs forming carina; broad, flat fold to rectimarginate commissure; broad, ventral rim surrounded by wide trail (5 to 15 mm) with ribs replaced by fine costellae; pedicle collar fused into deltidial plates; teeth with prominent dental cavities; thick hinge plate with bushy cardinal process; crura laterally divergent; spiralia dorsal, only rarely, weakly impressed as grooves into ventral valve, fewer than 10 whorls; jugal processes undescribed. [Differs from *Biconostrophia* in having dental cavities, spiralia normally not impressed into ventral valve; differs from *Eifelatrypa* in possessing ventral carination, teeth with dental cavities. Possibly occurs in the Frasnian in Timan.] *Lower Devonian (Pragian)–Middle Devonian (lower Givetian):* Eurasia, North America, *Pragian–lower Givetian.*——Fig. 980,*1a–g.* **C. arimaspa* (Eichwald), middle Eifelian, Urals; *a–e,* ventral, ventral (smaller shell), dorsal, lateral, anterior views, ×2 (Copper, 1978); *f–g,* serial sections, ×2 (Rzhonsnitskaia, 1975).

Biconostrophia Havlíček, 1956, p. 562 [**B. spirifera* Havlíček, 1956, p. 563; OD] [=*Davidsoniatrypa* Lenz, 1968, p. 182 (type, *D. johnsoni,* OD)] [?*Biconostrophia (Cherkesovaena)* Havlíček, 1987a, p. 103 (type, *B. sinelkovaensis* Cherkesova, 1980, p. 171, OD)]. Medium to large, semicircular outline, flat to weakly biconvex, ventrally carinate to weakly resupinate; wide, long, strophic hinge; shell widest at hinge; apsacline-orthocline beak; apical foramen; wide deltidial plates; ribs coarse distally, tubular, expanding, rarely bifurcating; single or double ventral midrib pair producing keel; trail unknown; muscle scars incised in ventral valve, slightly raised on platform in dorsal valve; solid teeth; raised cardinal process; cardinal pit absent; spiralia strongly impressed into cones on ventral valve, fewer than 6 whorls; jugal processes undescribed. [Similar to and possibly synonymous with *Carinatina,* but lacking dental cavities, spiralia impressed into ventral grooves as in *Davidsonia*. *Cherkesovaena* is possibly pseudopunctate (Cherkesova, 1980), otherwise identical to *Biconostrophia.*] *Lower Devonian (Pragian–Emsian):* Europe, Urals, Australia, North America.——Fig. 981,*3a–d.* **B. spirifera* (Havlíček), Emsian, Czech Republic; *a–b,* dorsal, ventral views; *c–d,* internal views of dorsal, ventral valves, ×1.5 (Havlíček, 1967b).

Carinatrypa Copper, 1973c, p. 496 [**Spinatrypa dysmorphostrota* Crickmay, 1960, p. 13; OD] [=*Hergetatrypa* Havlíček, 1987a, p. 97 (type, *Carinatina minuta* Siehl, 1962, p. 188, OD)].

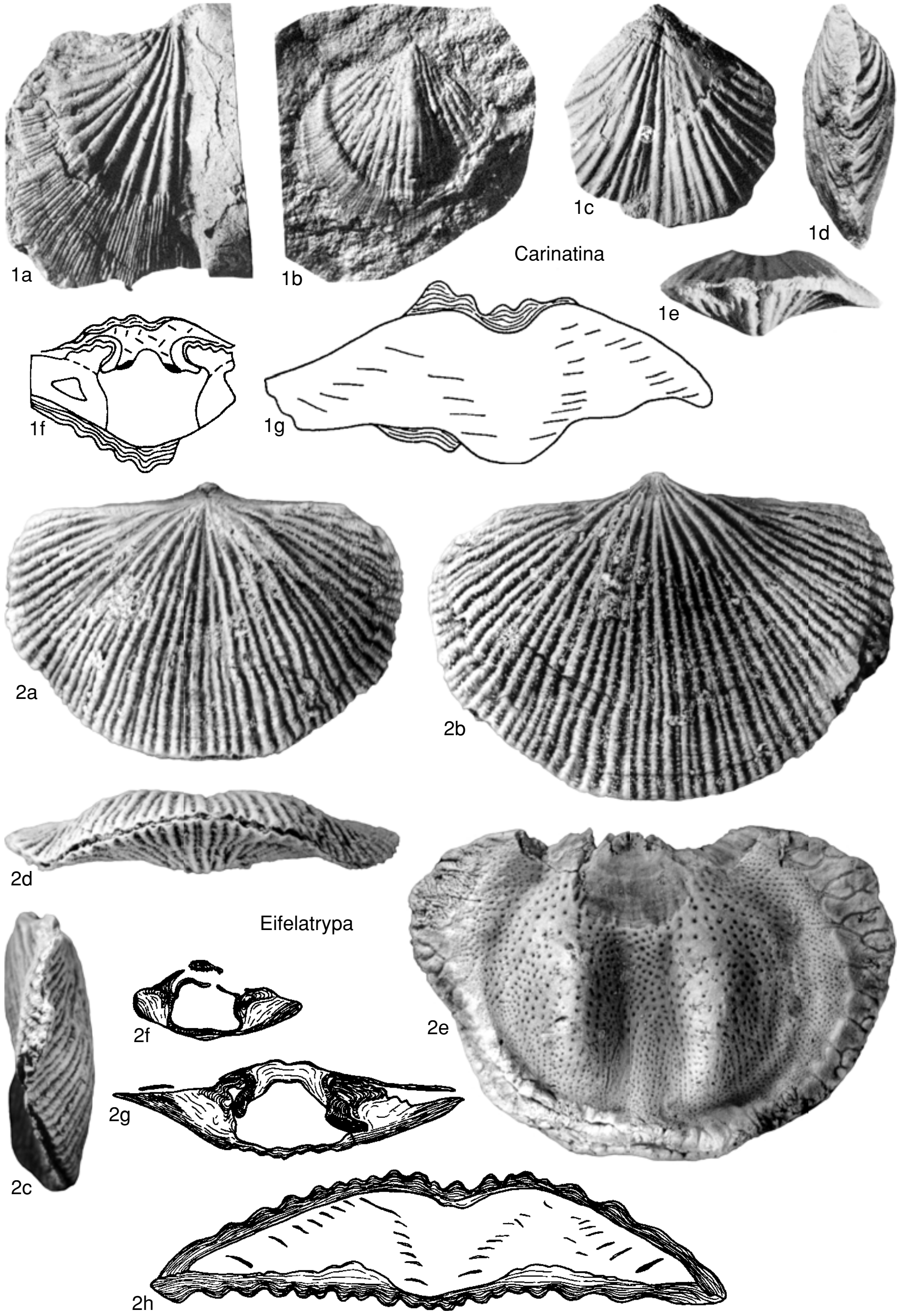

FIG. 980. Carinatinidae (p. 1446–1450).

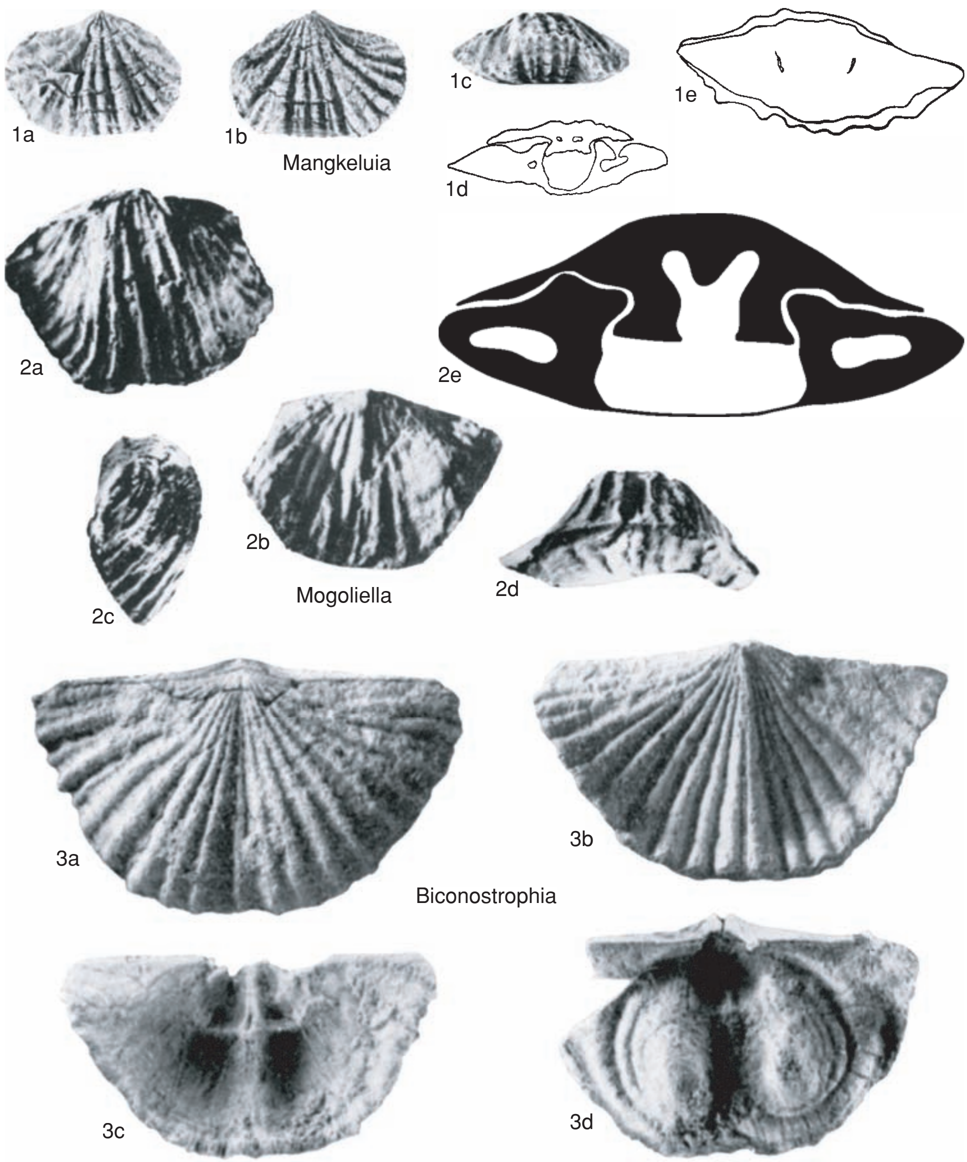

FIG. 981. Carinatinidae (p. 1446–1450).

Medium to large, dorsibiconvex, ventroapically carinate; small protruding beak; apsacline-orthocline area; apical foramen, deltidial plates; coarse tubular ribs, usually with concentric growth lamellae; trail with rib coarsening; moderately to strongly plicate commissure; thin shell; pedicle collar absent; teeth with large dental cavities; thin hinge, socket plates; crura delicate; dorsal spiralia with fewer than 10 whorls (not impressed into ventral valve); jugal processes with small, hooked jugal plates. [Differs from *Carinatina* and *Biconostrophia* in strong dorsal convexity (expansion of spiralia), high anterior fold, skirt with rib coarsening (instead of fine costellae), hinge plate divided by cardinal pit; possibly synonymous with *Mogoliella.*] *Middle Devonian (?upper Eifelian, Givetian):* northwestern Canada, USA (Michigan), western Europe, Russian Platform.——FIG. 982,*1a–e. C. dysmorphostrota* (CRICKMAY), lower Givetian, Northwest Territories; *a–d,* dorsal, ventral, lateral, posterior views, ×2; *e,* internal ventral valve, ×2 (Copper, 1978).

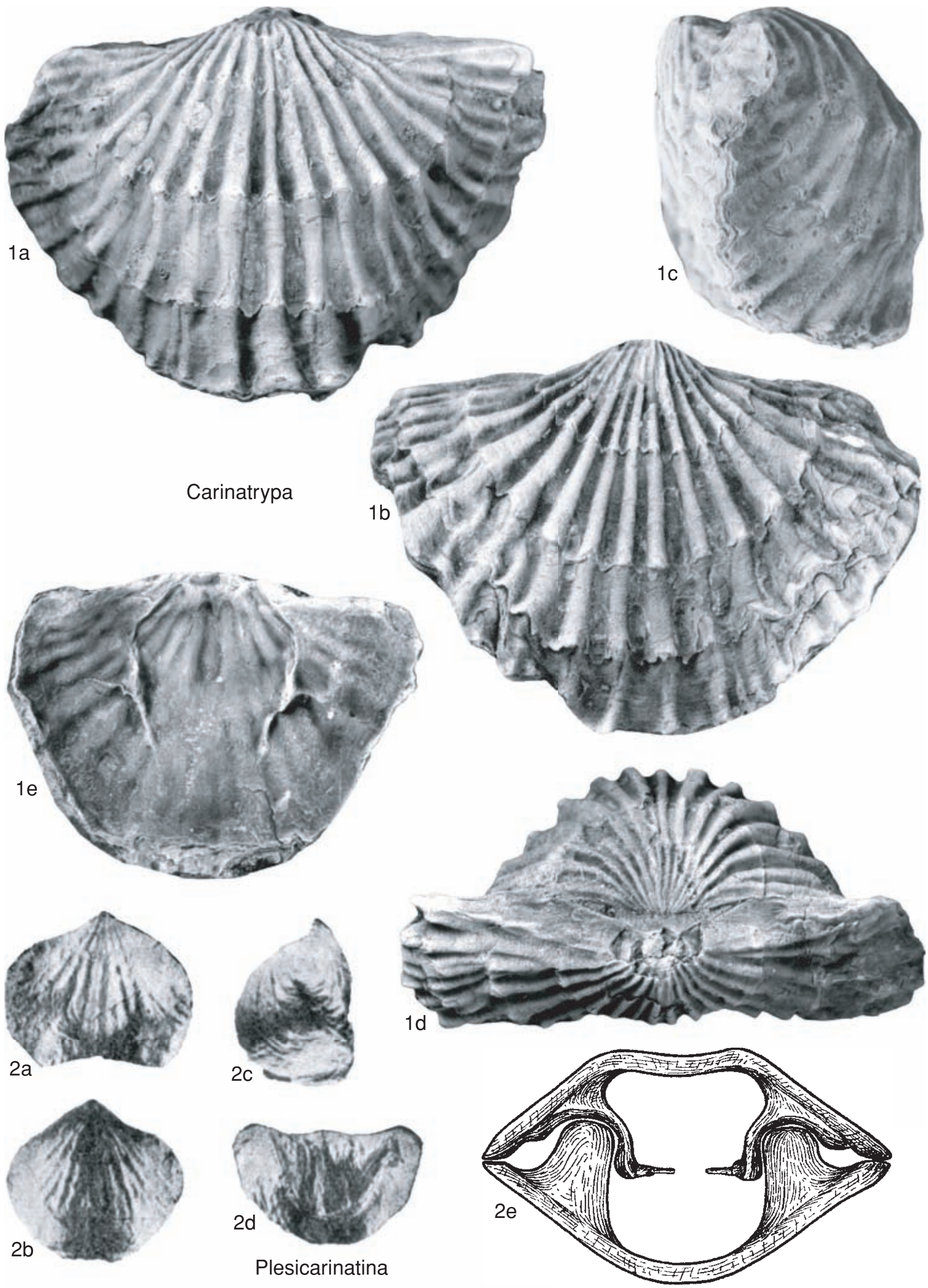

FIG. 982. Carinatinidae (p. 1446–1450).

Eifelatrypa COPPER, 1973c, p. 497 [**Atrypa reticularis* var. *plana* KAYSER, 1871, p. 545; OD]. Medium to large, widest between hinge and midshell; round hinge corners; biconvex, strophic, lacking ventral carination (except neanic shells); area apsacline-orthocline; prominent apical foramen; wide deltidial plates; ribs fine, tubular, even over whole shell; trail with fine ribs continuing from main shell; rectimarginate; interior pedicle collar continuous with deltidial plates; solid teeth; hinge plate wide, thick, lacking cardinal pit, capped by large, bushy cardinal process; crural bases large, extended from bulbous inner socket ridges; spiralia weakly incised into cones on thickened ventral valve; dorsal spiralia with about 8 to 10 whorls; thick jugal processes with large, bosslike jugal plates. [Differs from *Carinatina* and *Biconostrophia* by loss of carination, finer ribs, lack of costellae on trail, nature of hinge socket plates, crura, jugal boss.] *Middle Devonian (Eifelian–Givetian):* Europe, Urals, southern China.——FIG. 980,*2a–h.* **E. plana* (KAYSER), upper Eifelian, Germany; *a–e,* dorsal, ventral, lateral, anterior views, internal view ventral valve, ×2 (new); *f–h,* serial sections, ×4 (Copper, 1978).

?Mangkeluia XU Hankui, 1991, p. 318 [**M. extensa;* OD]. Small to medium, wider than long, round, dorsibiconvex, globose; ventral valve weakly carinate; small, orthocline area; protruding beak; apical foramen, deltidial plates; ribs expanding anteriorly, tubular; widely spaced, partly imbricate growth lamellae; low, broadly plicate commissure; stout, broad teeth; distinct dental cavities; hinge plate thick; crural bases stout; crura slender; spiralia, jugal processes undescribed. [Similar to small forms of *Carinatrypa* or *Mogoliella,* differing in small shell, hinge plates; possible rhynchonellid, lack of data on brachidia makes identification as atrypid doubtful.] *Lower Devonian (Emsian):* northwestern China (Xinjiang).——FIG. 981,*1a–e.* **M. extensa; a–c,* dorsal, ventral, anterior views, ×1.5; *d–e,* serial sections, ×1 (Xu Hankui, 1991).

Mogoliella ISHNAZAROV, 1972, p. 69 [**M. sukokentica* ISHNAZAROV, 1972, p. 72; OD] [?=*Sulciplicatatrypa* ZHANG Fengming, 1983, p. 336 (type, *Spinatrypa (Sulciplicatatrypa) xinjiangensis* ZHANG Fengming, 1983, p. 337, OD)]. Large, widest at hinge, dorsibiconvex, ventral valve weakly carinate; orthocline-apsacline area; protruding beak; prominent apical foramen; deltidial plates; strongly divergent, coarse ribs, ventrally raised midrib pairs; weak, short concentric growth lamellae partly developed; broad anterior fold; stout teeth; wide dental cavities; crural bases thick; dorsal spiralia with 10 to 12 whorls; jugal processes undescribed. [Externally very similar, possibly synonymous with *Carinatrypa.*] *Middle Devonian (Givetian):* Uzbekistan, China (Xinjiang).——FIG. 981,*2a–e.* **M. sukokentica,* Uzbekistan; *a–d,* dorsal, ventral, lateral, anterior views, ×1.5; *e,* sketch of polished view, ×4 (Ishnazarov, 1972).

?Plesicarinatina MIZENS, 1977b, p. 89 [**Plectatrypa? carpulenta* BREIVEL, 1959, p. 65; OD]. Equidimensional, inflated dorsibiconvex-convexoplane, carinate posteriorly; coarsely ribbed; fine concentric filae; trail present; narrow, protruding beak; apsacline-orthocline area; large apical foramen; deltidial plates; strong, U-shaped anterior fold; solid teeth; thick hinge plate, lacking cardinal pit; dorsally directed spiralia of fewer than about 7 whorls; jugal processes undescribed. [Possible junior synonym of *Neospirigerina,* but with weak carination and trail indicating carinatinid affinities.] *Silurian (?Ludlow, Přídolí)–Middle Devonian (lower Eifelian):* Urals.——FIG. 982,*2a–e.* **P. carpulenta* (BREIVEL), lower Eifelian; *a–d,* ventral, dorsal, lateral, anterior views, ×3; *e,* serial section, ×4 (Breivel, 1959).

Superfamily PALAFERELLOIDEA Spriestersbach, 1942

[*nom. transl.* COPPER, 1996a, p. 599, *ex* Palaferellinae SPRIESTERSBACH, 1942, p. 187; *emend.,* COPPER, 1996a, p. 599]

Ventribiconvex to dorsibiconvex, rectimarginate to weakly plicate; ribbed shells, lacking growth lamellae, frills; rarely with fringing commissural skirt; distinct area, deltidial plates, apical foramen; relatively thick shell wall, pedicle callist continuous with deltidial plates; strong teeth, hinge plates; spiralia dorsal-dorsomedial; jugal processes. *Silurian (Ludlow)–Middle Devonian (Givetian).*

Family PALAFERELLIDAE Spriestersbach, 1942

[*nom. transl.* COPPER, 1996a, p. 599, *ex* Palaferellinae SPRIESTERSBACH, 1942, p. 187]

Strongly biconvex to ventribiconvex, ribbed shells, lacking growth lamellae, frills; small apsacline-hypercline area, apical foramen; deltidial plates fused with pedicle callist-collar complex; thickened muscle platforms raised above shell floor by 2 or more septa in both valves. *Lower Devonian (?upper Emsian), Middle Devonian (Eifelian–Givetian).*

Gruenewaldtia CHERNYSHEV, 1885, p. 46 [**Terebratula latilinguis* SCHNUR, 1851, p. 7; OD] [=*Palaferella* SPRIESTERSBACH, 1942, p. 187 (type, *P. rhenana,* OD)]. Medium to large, rounded, globose, biconvex-ventribiconvex; umbo inflated; orthocline-anacline, rarely hypercline area; small apical foramen, deltidial plates; fine-medium ribs; concentric filae; rectimarginate to weakly plicate commissure; thick shell wall; pedicle callist or collar continuous with deltidial plates; interior of inner part of deltidial plates forming flange alongside foramen; muscle platforms on both valves raised above shell floor by 2 or more septa; ventral muscle platform larger than dorsal; hinge plate strong; crural bases small; crura laterally directed; dorsomedially directed spiralia with fewer than 15 whorls; disjunct, posteroventral jugal processes, terminating in spinose boss. [Distinct from homeomorphic *Desatrypa*

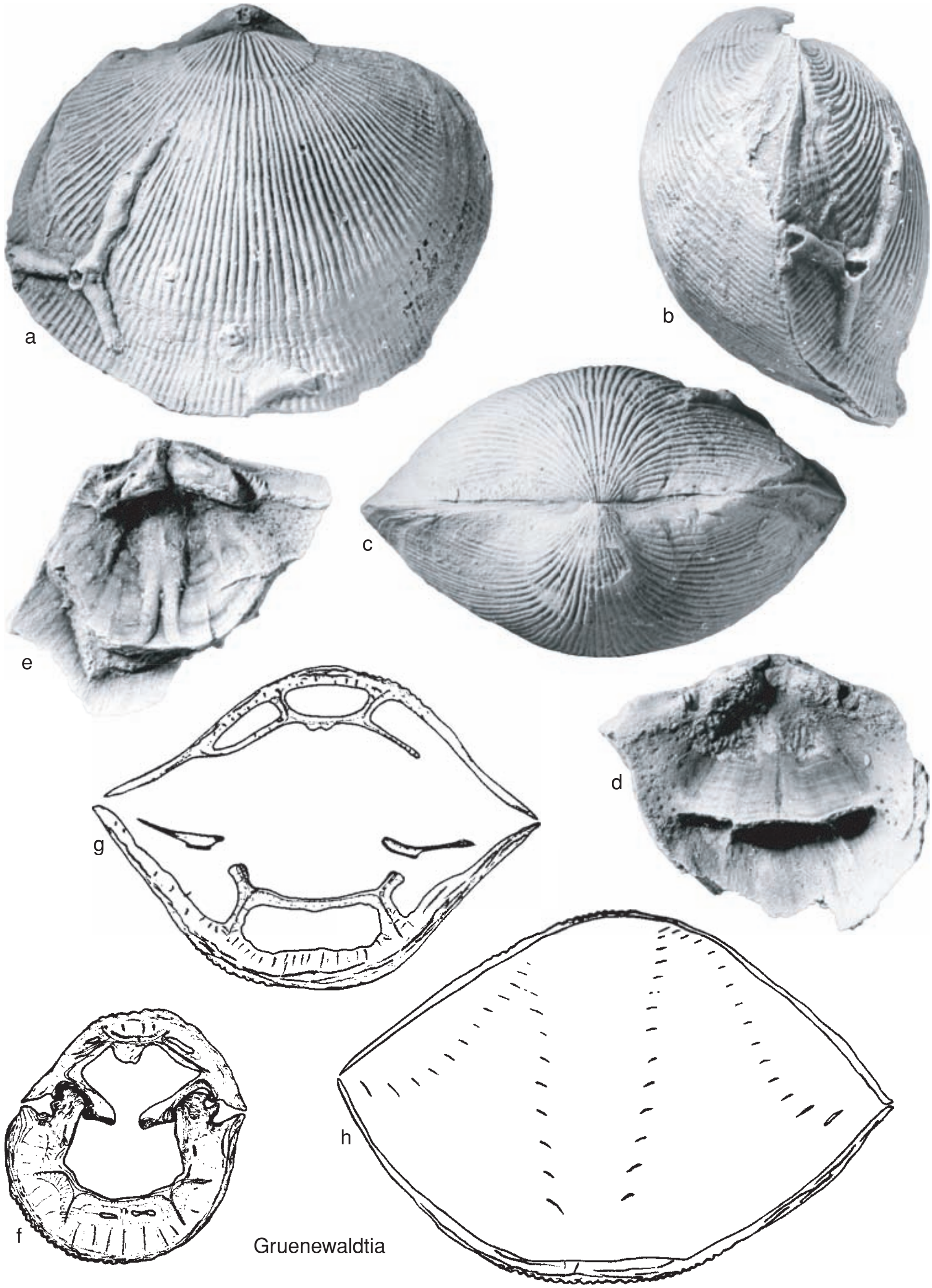

FIG. 983. Palaferellidae (p. 1450–1452).

and probably ancestral *Neokarpinskia* in septally raised muscle platforms. Early species have more septa supporting muscle platform, are smaller, more coarsely ribbed.] *Lower Devonian (?upper Emsian), Middle Devonian (Eifelian–Givetian):* Europe, Urals, Novaya Zemlya, Armenia, Uzbekistan, Siberia, arctic Canada.——FIG. 983*a–h*. **G. latilinguis* (SCHNUR), middle Eifelian, Germany; *a–c,* dorsal, lateral, posterior views; *d–e,* interior of ventral, dorsal valves with muscle platforms; *f–h,* serial sections, ×2 (new).

Family KARPINSKIIDAE Poulsen, 1943

[*nom. transl.* COPPER, 1996a, p. 600, *ex* Karpinskiinae POULSEN, 1943, p. 40; *emend.,* COPPER, herein]

Dorsibiconvex-convexoplane, thick shell wall, weakly apsacline-orthocline area (never anacline-hypercline), beak prominent, apical foramen large; ribs fine to coarse, always fine apically; commissure rectimarginate or very weakly plicate; muscle scars incised posteriorly with raised anterior edges, vascular canals strongly raised as prominent ridges; spiralia dorsally directed, jugal processes poorly known. *Silurian (Ludlow)–Middle Devonian (Givetian).*

Subfamily KARPINSKIINAE Poulsen, 1943

[Karpinskiinae POULSEN, 1943, p. 40; *emend.,* COPPER, 1996a, p. 600]

Elongate, commonly laterally compressed shells, biconvex to strongly dorsibiconvex to convexoplane; narrow apsacline-orthocline area; prominent apical foramen, deltidial plates; rectimarginate commissure; ribs fine posteriorly, usually coarser anteriorly, less commonly bifurcating-intercalating, rarely partly smooth shell; pedicle callist-collar common; commonly prominent ventral vascular ridges; teeth solid or with dental cavities; spiralia dorsally directed, jugal processes poorly known. *Silurian (Ludlow)–Middle Devonian (Givetian).*

Karpinskia CHERNYSHEV, 1885, p. 48 [**K. conjugula;* OD]. Medium to large, highly elongate, narrow, rectangular to triangular, laterally compressed, roughly squared in anterior view, dorsibiconvex, convexoplane; protruding beak; short hinge; acute hinge angle; apsacline-orthocline area; prominent apical foramen; thick deltidial plates; ribs fine apically, nonbifurcating, to very coarse anteriorly, zigzag at commissure; wide, high, subrectangular, plicate commissure; thick shell wall; weak vascular ridges; medium to thick pedicle callist-collar; long, narrow teeth; elongated dental cavities; thick hinge plate; long, thin socket plates; small crural bases, crura; dorsally directed spiralia with fewer than 13 whorls; jugal processes undescribed. [Pedicle callist, deltidial plates, and hinge structure as in *Vagrania* and *Mimatrypa* but differentiated by highly elongate shell, squared shape in transverse section, fine ribs posteriorly changing to very coarse ribs along commissure.] *Lower Devonian (Emsian):* southern Europe, Urals, central Asia, China (Xinjiang).——FIG. 984,*1a–g.* **K. conjugula,* Emsian, western slopes, Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×1; *e–g,* serial sections, ×2.5 (Mizens, 1984).

Crassatrypa MIZENS, 1977a, p. 54 [**Atrypa diversa* SAPELNIKOV, 1968, p. 128; OD]. Small, triangulate to elongate, narrow hinge angle, biconvex to weakly dorsibiconvex, rhynchonelliform shape; highly protruding beak; apsacline-orthocline area; prominent apical foramen and deltidial plates; 8 to 10 coarse expanding ribs, rarely bifurcating or intercalating; anterior growth interruptions; rectimarginate to weakly plicate commissure; interior with long, solid teeth; narrow hinge plates with deep cardinal pit; small, delicate socket plates, crura; spiralia dorsally directed, fewer than 10 whorls; jugal processes undescribed. [Differentiated from *Karpinskia* by small size, coarser ribs posteriorly, rhynchonelliform shape; differs from *Vagrania* by its elongate outline, anteriorly coarse ribs.] *Silurian (Ludlow–Přídolí):* Urals (eastern slopes).——FIG. 984,*2a–e.* **C. diversa* (SAPELNIKOV), lower Ludlow; *a–c,* dorsal, ventral, lateral views, ×1; *d–e,* serial sections, ×5.5 (Mizens & Sapelnikov, 1982).

Eokarpinskia RZHONSNITSKAIA, 1964, p. 103 [**Karpinskia nalivkini* NIKIFOROVA, 1937b, p. 23; OD]. Small, elongate to subtriangulate, inflated (rounded in cross section), biconvex, laterally weakly compressed, maximum width anteriorly; narrow, acute hinge angle; narrow area with smooth curved flanks; apical-transapical foramen; surface with smooth appearance, very finely ribbed; rectimarginate-bisulcate commissure; thin pedicle callist; long teeth with elongated dental cavities; thin, curved dental plates; socket plates thin, curved; crura, spiralia, jugal processes undescribed. [Distinguished from *Neokarpinskia, Karpinskia,* and *Crassatrypa* by very fine ribs leading to nearly smooth appearance, biconvexity, rounded cross section; differs from similarly shaped *Tectatrypa* (Lissatrypinae) by possessing fine ribs, dental cavities, thin socket plates.] *Silurian (Přídolí)–Lower Devonian (Lochkovian):* Kazakhstan, Urals, ?arctic Canada.——FIG. 984,*3a–d.* **E. nalivkini* (NIKIFOROVA), Přídolí, Kazakhstan; *a–c,* dorsal, ventral, lateral views, ×2; *d,* serial section, ×5 (Nikiforova, 1937b).

Mimatrypa STRUVE, 1964a, p. 436 [**Terebratula prisca* var. *flabellata* ROEMER, 1844, p. 66; OD] [=*Toquimaella* JOHNSON, 1967, p. 876 (type, *T. kayi,* OD); ?=*Megaplectatrypa* ZHANG Yan, 1981a, p. 386 (type, *M. simplex,* OD)]. Small to large, convexoplane-dorsibiconvex; flat adult ventral valve, weakly convex apically; shell outline rounded to subelongate, narrow hinge angle; apsacline-orthocline area; large apical-transapical foramen; fine ribs apically,

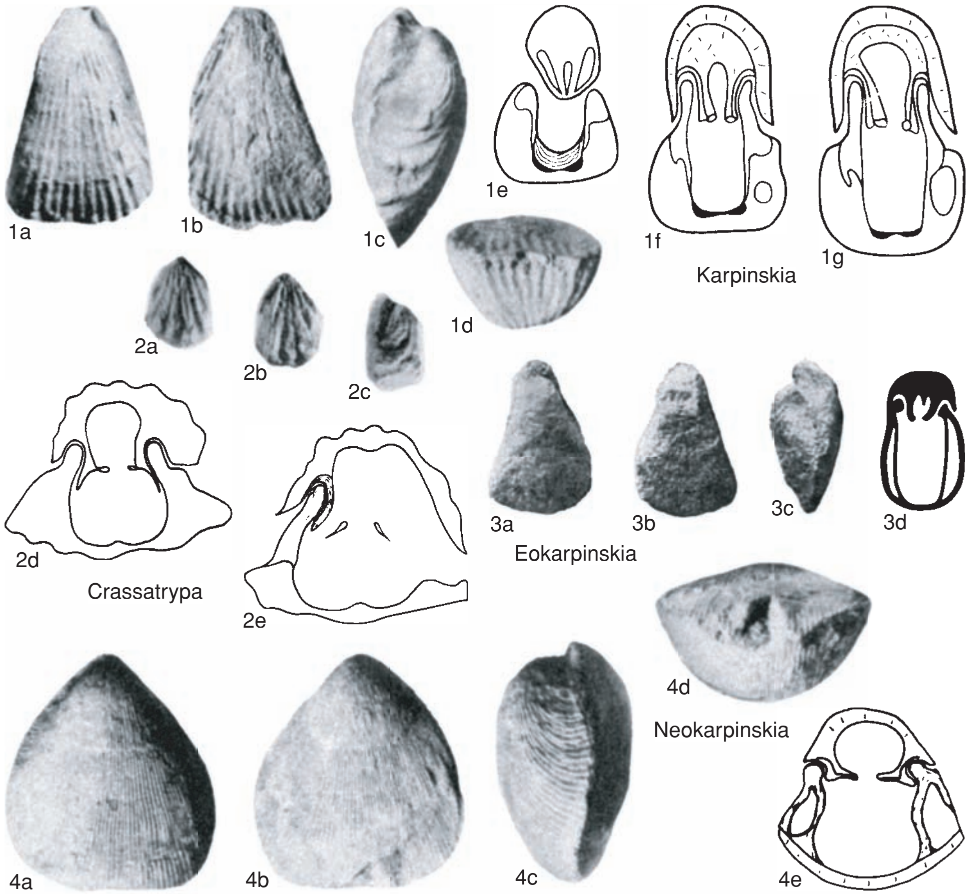

FIG. 984. Karpinskiidae (p. 1452–1456).

coarsening distally, rarely bifurcated or intercalated; microornament of fine concentric filae, growth interruptions; rectimarginate commissure; thick shell wall; hollow deltidial plates fused with pedicle callist or collar; muscle scars posteriorly incised but raised anteriorly; ventral vascular ridges prominently raised; teeth solid; hinge plate thickly reinforced by secondary layer; socket plates thin; small, rounded cardinal pit; minute, delicate crural bases, crura; dorsomedially directed spiralia, up to 21 closely spaced whorls; jugal processes undescribed. [Distinguished from *Karpinskia* by its wide, broader shell (neanic shells difficult to distinguish from *Karpinskia*), ovate cross section, solid teeth lacking dental cavities, distinct vascular ridges; differs from *Vagrania* by its flat ventral valve, apically highly angular beak, narrow hinge angle, anteriorly very coarse ribs.] *Lower Devonian (Emsian)–Middle Devonian (Givetian):* Eurasia, North America.——FIG. 985*a–h.* **M. flabellata* (ROEMER), upper Eifelian, Germany; *a–e,* dorsal, ventral, posterior, anterior, lateral views, ×2; *f–g,* serial sections, ×2 (new); *h,* internal dorsal valve, ×2 (Struve, 1964a).

Neokarpinskia MIZENS, 1977b, p. 95 [**Karpinskia fedorovi* var. *ivdeli* KHODALEVICH, 1937, p. 67; OD] [=*Parakarpinskia* ZHANG Yan, 1983b, p. 589 (type, *P. striata,* OD); *Parakarpinskia* ZHANG Yan, 1985, p. 347 (type, *P. striata,* OD, *nom. duplic.*)]. Medium to large, dorsibiconvex, triangular hinge angle; elongate, pear shaped, rounded in cross section; small apsacline area; narrow beak; apical-transapical foramen; small deltidial plates; ribs fine, continuous, lacking clear growth interruptions; commissure rectimarginate to weakly plicate; pedicle callist absent; teeth with long, elongate dental cavities; cardinal pit lined by bushy process; small delicate socket plates; medium dorsal septum lacking; crura minute, dorsal to laterodorsal spiralia, fewer than

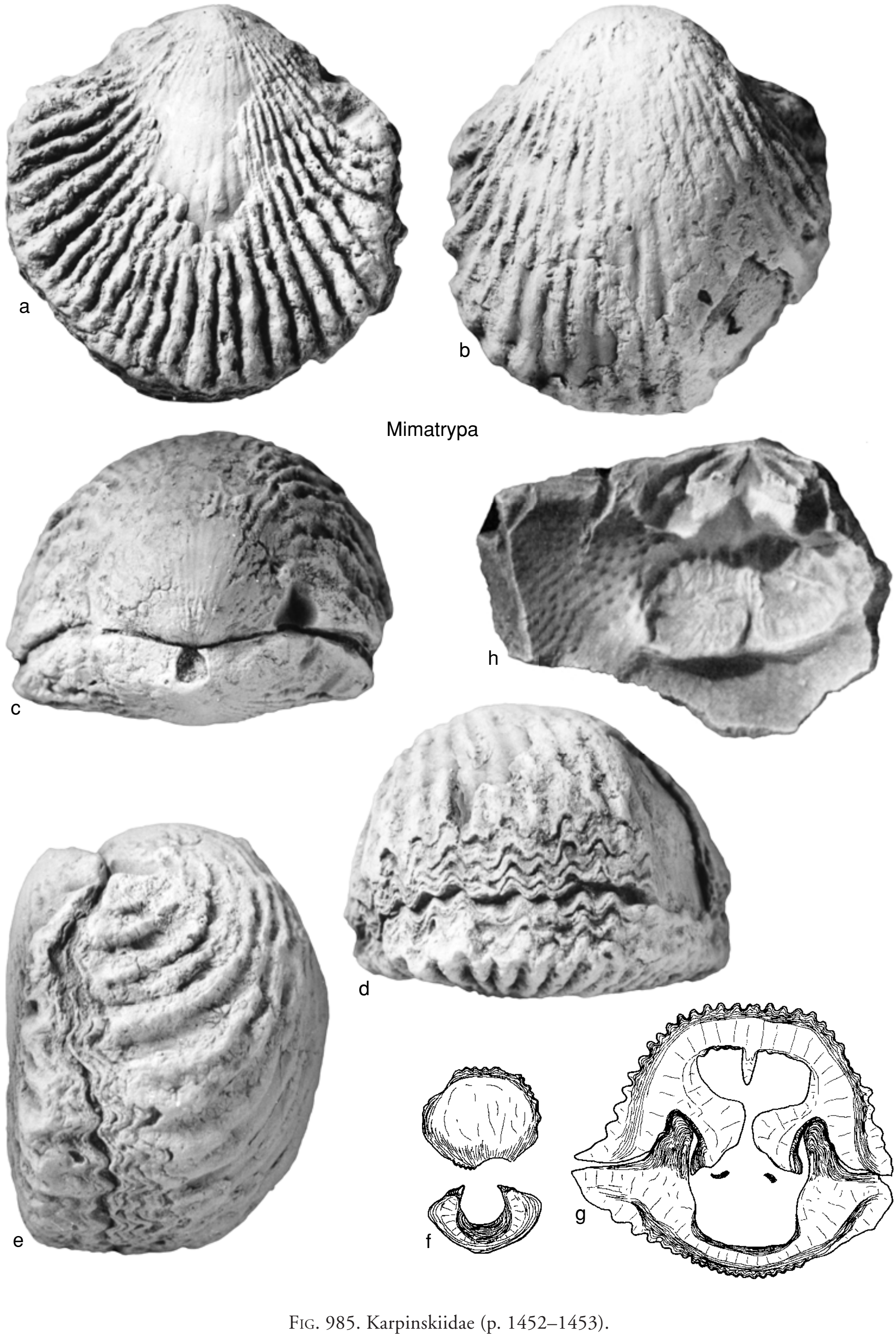

FIG. 985. Karpinskiidae (p. 1452–1453).

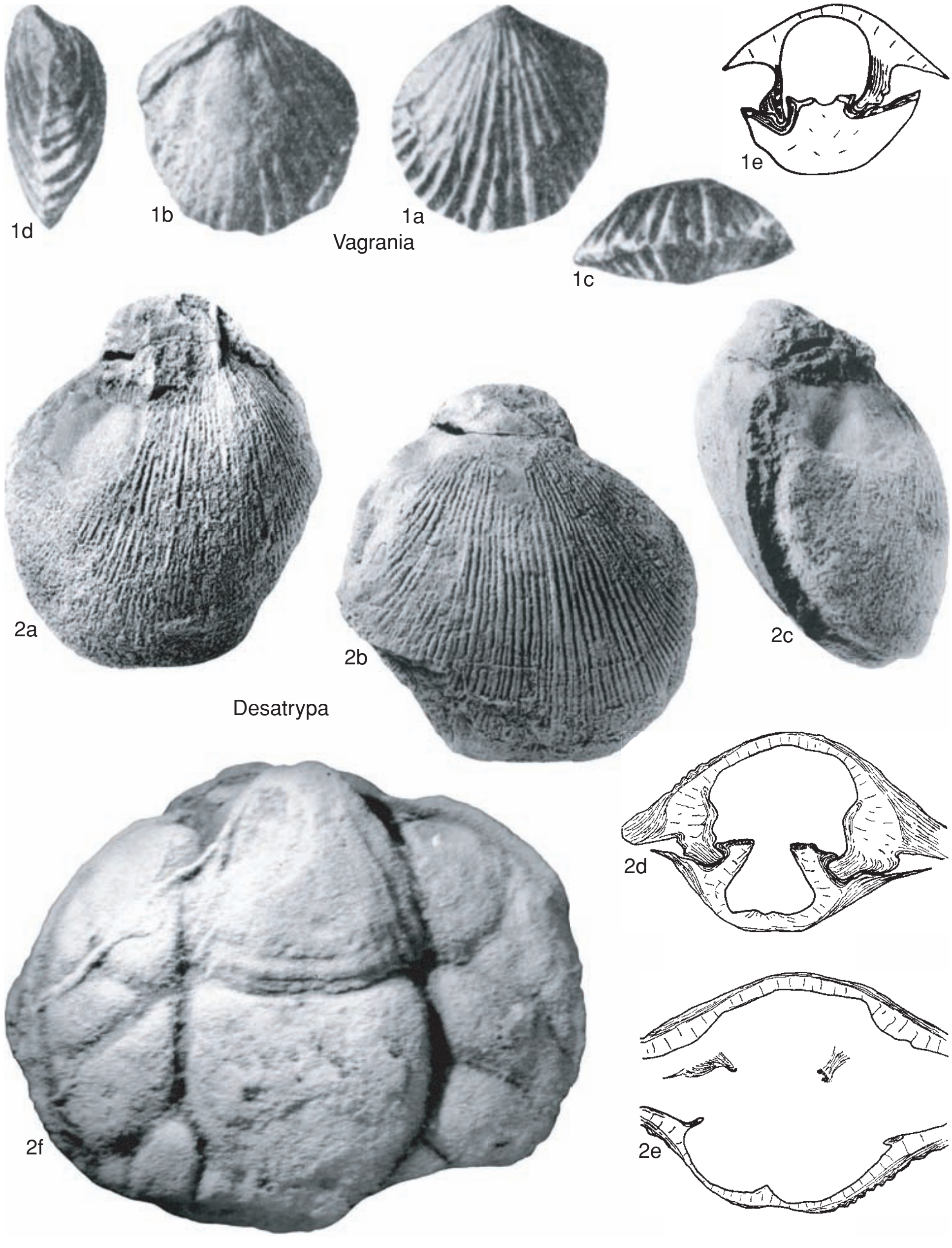

FIG. 986. Karpinskiidae (p. 1456–1457).

16 whorls; jugal processes undescribed. [Distinguished from *Karpinskia* by very fine ribs covering entire shell surface, rounded cross section, lack of lateral compression, numerous spiral whorls; from superficially similar *Gruenewaldtia* by lack of septally raised muscle platforms.] *Lower Devonian (?lower Pragian, middle Pragian–Emsian):* Urals (eastern slopes), central Asia, China (Gansu).——

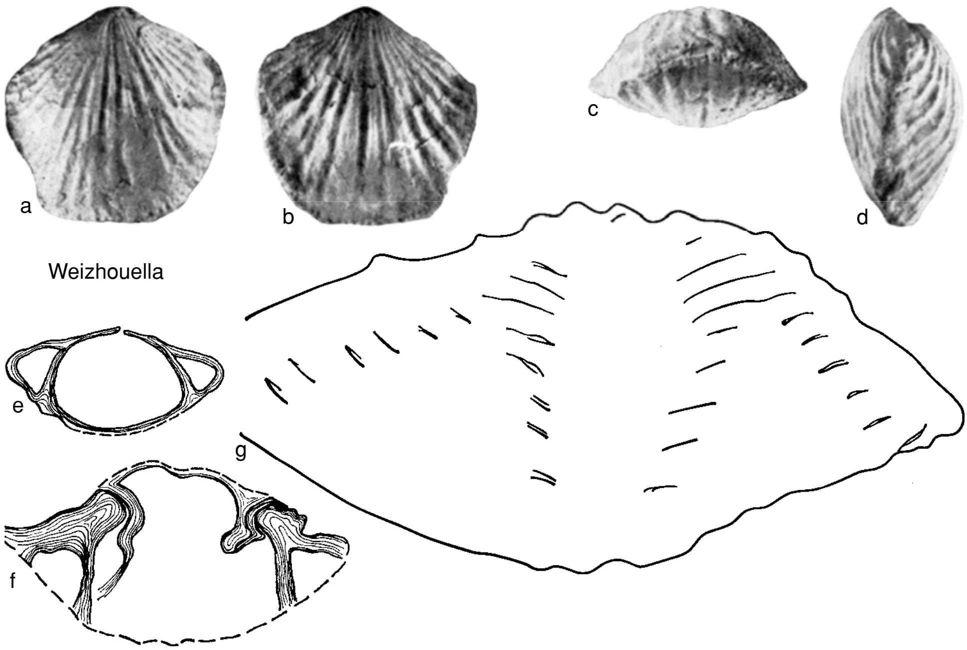

FIG. 987. Karpinskiidae (p. 1457).

FIG. 984,*4a–e*. **N. ivdeli* (KHODALEVICH), Emsian, eastern slopes, Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×1 (Mizens, 1984); *e,* serial section, ×2.5 (Mizens, 1977b).

Subfamily VAGRANIINAE Alekseeva, 1995

[Vagraniinae ALEKSEEVA, 1995, p. 49; *emend.,* COPPER, 1996a, p. 600]

Biconvex-dorsibiconvex, rounded shells; prominent beak, area, deltidial plates, apical foramen; tubular ribs normally bifurcating or intercalating; usually fine concentric filae; frills, growth lamellae lacking; thick hinge plates, usually strongly raised vascular ridges, incised muscle scars. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian).*

Vagrania ALEKSEEVA, 1959, p. 389 [**Atrypa kolymensis* NALIVKIN, 1936, p. 17; OD] [=*Dentatrypa* BREIVEL, 1959, p. 57, obj.; *Totia* RZHONSNITSKAIA & MIZENS, 1977, p. 20 (type, *Atrypa intermediafera* KHODALEVICH, 1951, p. 62, OD)]. Small to medium, rounded, biconvex; prominent apsacline-orthocline area; apical foramen; ribs medium to coarse, consistently spaced, bifurcating ventrally, intercalating dorsally; rectimarginate to weakly plicate commissure; large deltidial plates fused into collar; teeth with prominent dental cavities; strong ventral vascular ridges; hinge plate thick; crural bases, crura delicate; spiralia dorsomedial, fewer than 20 whorls; jugal processes terminating in jugal plates curving away from each other. [Distinguished from *Mimatrypa* by its convexity, bifurcating and intercalating coarser ribs, dental cavities; differs from *Desatrypa* by having dental cavities (dental plates), coarser ribs. *Totia* has been distinguished from *Vagrania* by its somewhat finer ribs and the presence of microornamental tubercles, but these characters appear to be variable.] *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Europe, Urals, arctic Canada, southern China.——FIG. 986,*1a–e.* **V. kolymensis* (NALIVKIN), upper Emsian, ?lower Eifelian, Kolyma, northeastern Siberia; *a–d,* dorsal, ventral, anterior, lateral views, ×1; *e,* serial section, ×2 (Rzhonsnitskaia & Mizens, 1977).

Desatrypa COPPER, 1964, p. 363 [**Atrypa desquamata* SOWERBY, 1840b, explanation to pl. 56, fig. 19–20; OD] [=*Lixatrypa* HAVLÍČEK, 1987a, p. 78 (type, *L. ponderosa* HAVLÍČEK, 1987a, p. 80, OD)]. Medium to large, moderately biconvex-dorsibiconvex, rounded outline; prominent beak; orthocline area; large apical foramen surrounded by deltidial plates; fine to medium, even, bifurcating or intercalating ribs; commissure rectimarginate to weakly plicate; pedicle callist or collar continuous from deltidial plates; posteriorly incised muscle scars raised anteriorly on solid platform; distinctive ventral vascular

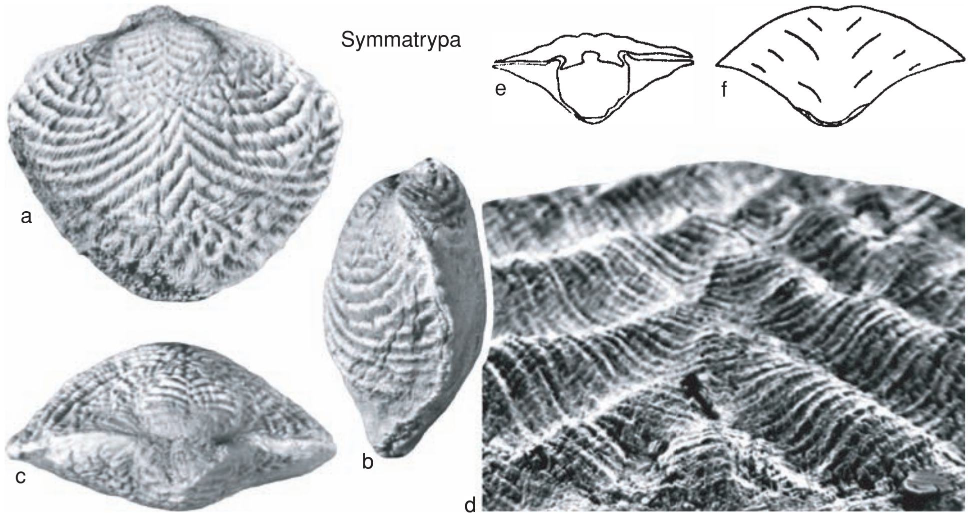

FIG. 988. Symmatrypidae (p. 1457).

ridges; solid teeth; hinge plates thick, massive; crura small, delicate; dorsal spiralia with about 15 whorls; jugal processes undescribed. [Identical to *Vagrania* in strongly raised vascular ridges, pedicle callist and deltidial plate complex, hinge plates, crura, brachidia, but with larger, more finely ribbed shell, solid teeth lacking dental cavities. Genus commonly homeomorphic with *Variatrypa* (Variatrypinae).] *Lower Devonian (Pragian)–Middle Devonian (upper Givetian):* western Europe, ?China.——FIG. 986, *2a–f.* **D. desquamata* (SOWERBY), upper Givetian; *a–c,* dorsal, ventral, lateral views, ×1; *d–e,* serial sections, United Kingdom, ×2 (Copper, 1965a); *f,* internal mold of ventral valve, Germany, ×2 (new).

?Weizhouella CHEN Yuanren, 1983, p. 322 [**W. shuimoensis;* OD]. Medium to large, dorsibiconvex; prominent orthocline-anacline area, beak; apical-transapical foramen; wide deltidial plates; ribs coarse, expanding distally; moderately plicate commissure; shell wall thin; pedicle callist absent; pallial sinuses weak; teeth strong with large dental cavities; crura long, fibrous; spiralia dorsal, about 12 whorls; ventral jugal processes ending in small stubby plates. [Problematic genus, similar to *Vagrania* externally in ribs, shape, but lacking vascular ridges, pedicle callist-deltidial plate complex, thick hinge plate; possibly synonymous with *Carinatrypa* or *Mogoliella* (Carinatinidae) in thin shell wall, lack of pedicle callist, nature of hinge plate, dental cavities, but lacks carination, trail.] *Middle Devonian (Eifelian–Givetian):* southern China (Sichuan).——FIG. 987*a–g.* **W. shuimoensis,* Givetian; *a–d,* dorsal, ventral, anterior, lateral views, ×1; *e–g,* serial sections, approximately ×4 (Chen Yuanren, 1983).

Family SYMMATRYPIDAE Mizens, 1989

[*nom. transl.* COPPER, herein, *ex* Symmatrypinae MIZENS, 1989, p. 48]

Shell surface with strong, diagonal, divaricate rib structure; lacking concentric growth lamellae, frills; small orthocline area; protruding beak; deltidial plates; apical foramen; teeth solid; hinge plate thick; spiralia dorsomedial; disjunct jugal processes. *Silurian (Ludlow–Přídolí).*

Symmatrypa MIZENS & SAPELNIKOV, 1975, p. 43 [**S. piceaplicata;* OD]. Small to medium, weakly to moderately biconvex, ovoid to shield shaped; small orthocline area; apical foramen, deltidial plates; ribs subradially diverging from plane of symmetry to produce divaricate, subconcentric growth undulations; rectimarginate commissure; thin pedicle callist, deltidial plates possibly fused; solid teeth; thick hinge plate; spiralia dorsomedial, with 4 to 5 widely spaced whorls; crura, jugal processes undescribed. [Affinities of this exotic genus appear to lie with Davidsoniidina and Palaferelloidea, possibly derived from *Gracianella;* superficially homeomorphic with *Kulumbella* (Pentamerida), but with area, deltidial plates, spiralia.] *Silurian (Ludlow–Přídolí):* Urals (eastern slopes).——FIG. 988*a–f.* **S. piceaplicata,* lower Ludlow; *a–c,* dorsal, lateral, posterior views, ×3; *d,* SEM detail of divaricate ornament, ×44 (new); *e–f,* serial sections, ×5.5 (Mizens, 1989).

Suborder LISSATRYPIDINA Copper, 1996

[Lissatrypidina COPPER in COPPER & GOURVENNEC, 1996, p. 81]

Shell smooth, rarely corrugated or undulose, may be covered with fine, projecting capillae or fibers of secondary shell; spiralia medially to dorsomedially directed; jugum complete to incomplete or absent in most Ordovician forms; jugal processes and plates in most Siluro-Devonian taxa. *Ordovician (Llandeilo)–Upper Devonian (Frasnian).*

Superfamily LISSATRYPOIDEA Twenhofel, 1914

[*nom. transl.* COPPER, herein, *ex* Lissatrypinae TWENHOFEL, 1914, p. 31; *emend.,* COPPER, herein]

Diagnosis as for suborder, but excludes forms assigned to superfamily Protozygoidea, i.e., those possessing medially directed spiralia, lacking a jugum or with incomplete jugum. [Excludes Glassiidae with medial spiralia; the internal structure of many lissatrypoids is unknown and requires description.] *Ordovician (Caradoc)–Middle Devonian (Eifelian).*

Family LISSATRYPIDAE Twenhofel, 1914

[*nom. transl.* COPPER, herein, *ex* Lissatrypinae TWENHOFEL, 1914, p. 31; *emend.,* COPPER, herein]

Smooth or covered by fine radial and concentric capillose ornament, biconvex-dorsibiconvex, with variably thick shell wall, small ventral beak, minute apical foramen, rectimarginate to plicate commissure; solid teeth lacking dental cavities; normally separate jugal processes with simple to complex, curved terminal jugal plates, rarely jugum; spiralia dorsomedially to dorsally directed. *Silurian (Llandovery)–Middle Devonian (Eifelian).*

Lissatrypa TWENHOFEL, 1914, p. 31 [**L. atheroidea* TWENHOFEL, 1914, p. 33; OD] [=*Spondylobolus* M'COY, 1851, p. 407, *nom. oblit.* (type, *S. craniolaris,* OD); ?*Loilemia* REED, 1936, p. 116 (type, *L. proxima,* OD); *Nanospira* AMSDEN, 1949a, p. 203 (type, *N. parvula,* OD); *Lissatrypoidea* BOUCOT & AMSDEN, 1958, p. 159 (type, *Nucleospira concentrica* HALL, 1859b, p. 223, OD); *Buceqia* HAVLÍČEK, 1984, p. 109 (type, *Terebratula obolina* BARRANDE, 1847, p. 404, OD); *Solitudinella* GODEFROID, 1991, p. 108 (type, *S. hollardi* GODEFROID, 1991, p. 110, OD)]. Small to medium, biconvex-dorsibiconvex-planoconvex; usually smooth (shells may preserve fine, concentrically aligned, radial capillae); apical to transapical foramen; small deltidial plates (commonly resorbed or covered by beak in adult shells); rectimarginate to gently plicate commissure; thick shell wall, pedicle callist, distinct collar; muscle scars commonly deeply incised, may be separated by septum, with V-shaped ventral adductors; short, solid teeth; thickened to bulbous hinge plate; cardinal pit commonly lost, overgrown or suppressed by massive crural bases in adult shells, covered by small cardinal process; dorsomedial spiralia with fewer than 7 to 8 whorls; short, bulky, posterior jugal processes terminating in thick, ringlike jugal plates. [Differs from *Australina* in thick shell, nature of hinge plate, pedicle callist-collar. The name *Spondylobolus* has not been used in more than 140 years and is abandoned.] *Silurian (middle Llandovery)–Middle Devonian (Eifelian):* worldwide.——FIG. 989,*5a–h.* **L. atheroidea,* middle Llandovery, Anticosti, Canada; *a–d,* dorsal, ventral, posterior, lateral views, ×3 (Copper, 1973a); *e–g,* serial sections, ×5; *h,* reconstruction of brachidia, ×3 (new).

Atrypellina MENAKOVA & NIKIFOROVA, 1986, p. 66 [**Lissatrypa caudata* NIKIFOROVA, 1949, p. 16; OD]. Small, dorsibiconvex, subquadrate-pentagonal outline; maximum width near hinge; narrow anacline area; small apical foramen separating deltidial plates; ventral, angular V-shaped sulcus, dorsal V-shaped fold; sharp, angular, plicate commissure; interior with short, small solid teeth; small hinge plate separated by cardinal pit; jugal processes posteromedial; spiralia dorsomedial, fewer than 7 whorls. [Distinct from *Meifodia, Cerasina,* and other lissatrypids by its subquadrate-pentagonal shape, very sharp, V-shaped fold-sulcus.] *Silurian (Přídolí):* central Asia, Urals.——FIG. 989,*3a–g.* **A. caudata* (NIKIFOROVA), Turkestan; *a–d,* dorsal, ventral, lateral, anterior views, ×3; *e–f,* serial sections, ×3.7; *g,* reconstruction of brachidia, ×5.5 (Menakova & Nikiforova, 1986).

Atrypoidea MITCHELL & DUN, 1920, p. 271 [**Meristina(?) australis* DUN, 1904, p. 318; OD] [=*Atrypella* KOZLOWSKI, 1929, p. 173 (type, *Atrypa prunum* DALMAN, 1828, p. 133, OD); *Lingatrypa* MIZENS, 1985, p. 10 (type, *Terebratula linguata* VON BUCH, 1834, p. 101, OD); *Globatrypa* MIZENS & SAPELNIKOV, 1985, p. 10 (type, *Merista globus* CHERNYSHEV, 1885, p. 5, OD)]. Medium to large, globose, wide to elongate, convexoplane-dorsibiconvex; shell smooth, may be partly corrugate on anterior fold; small apical-transapical foramen; deltidial plates in neanic shells; orthocline-anacline area in small shells, hypercline area in large shells; weak to strongly plicate commissure; thick shell wall with muscle scars weakly incised; solid teeth; relatively delicate hinge, socket plates; small crural bases;

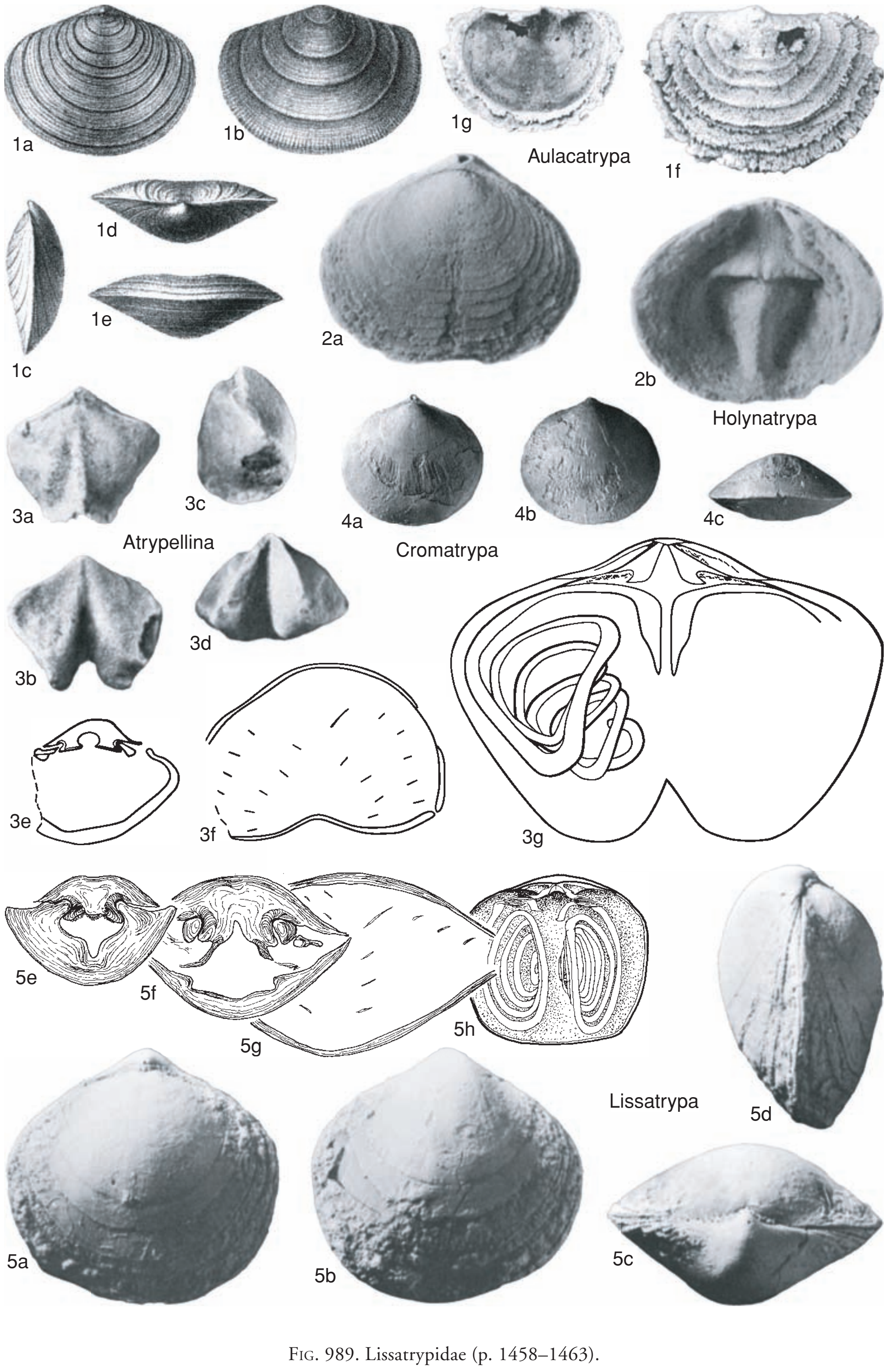

FIG. 989. Lissatrypidae (p. 1458–1463).

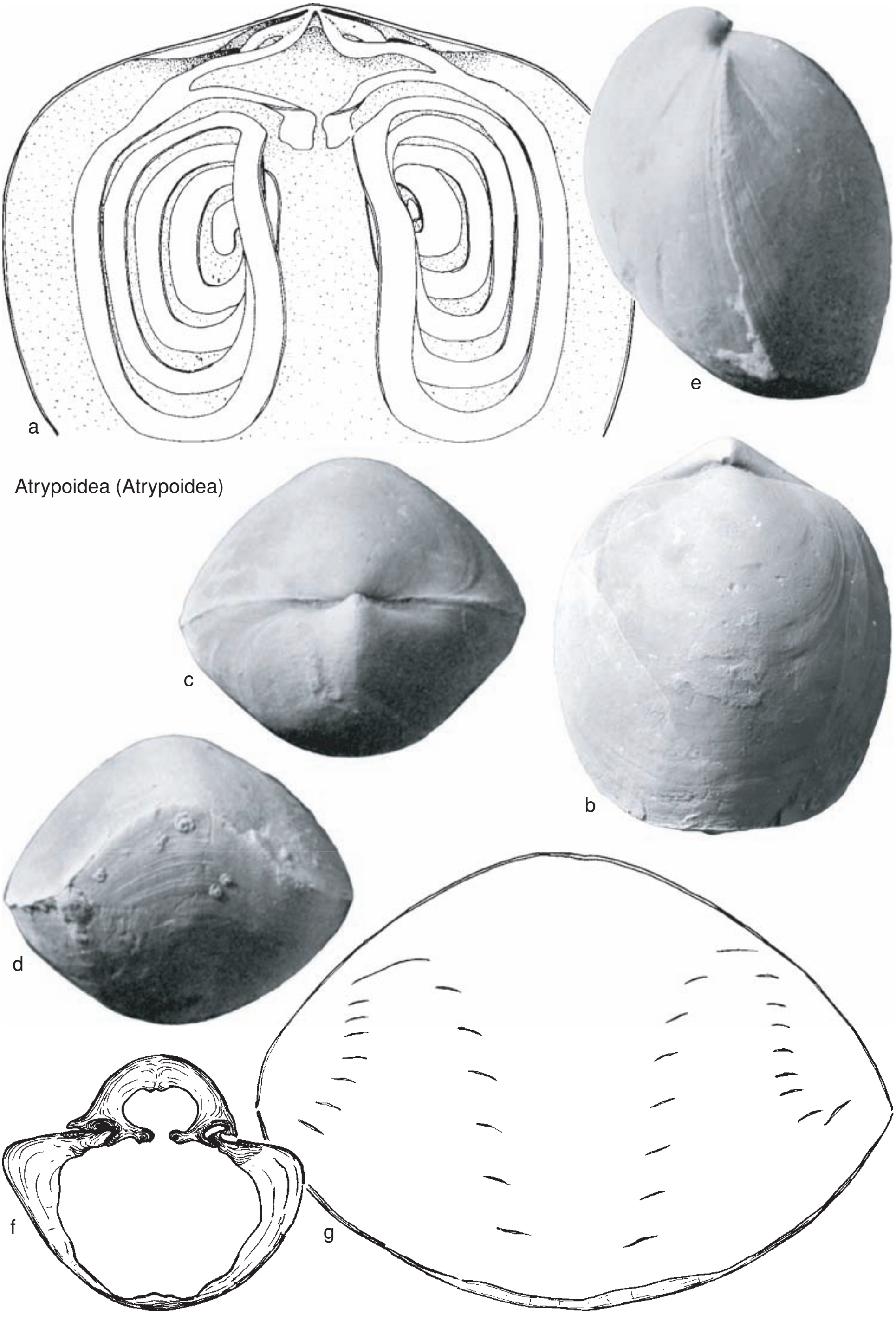

FIG. 990. Lissatrypidae (p. 1461).

dorsal-dorsolateral spiralia; ventrally positioned jugal processes with bulky jugal plates. [Differs from *Lissatrypa* and *Meifodia* in inflated size, elongate shape, hinge plates, stumpy jugal processes.] *Silurian (?middle Llandovery, Wenlock–Přídolí), Lower Devonian (?Lochkovian):* China, Urals, *?Aeronian;* worldwide, *Wenlock–Přídolí;* Czech Republic, *?Lochkovian.*

A. (**Atrypoidea**). Description as for genus, but biconvex-dorsibiconvex; broad, U-shaped to subangular, plicate commissure; thick shell wall, with muscle scars lobate, weakly incised; dorsal-dorsolateral spiralia with fewer than 14 whorls; posteroventral jugal processes with bulky jugal plates. [Differs from *Lissatrypa* in size, shape, outline, hinge plates, stumpy jugal processes; differs from *A. (Lissatrypella)* by convex ventral valve; infrapopulation variability encompasses wide shape variation in *Lingatrypa* and *Globatrypa.*] *Silurian (?middle Llandovery, Wenlock–Přídolí), Lower Devonian (?Lochkovian):* China, Urals, *?Aeronian;* worldwide, *Wenlock–Přídolí;* Czech Republic, *?Lochkovian* (Havlíček, 1987a).——FIG. 990*a.* **A. (A.) australis* (DUN), Ludlow, New South Wales, Australia; reconstruction from serial sections, ×4 (Copper, 1977b).——FIG. 990*b–g. A. (A.) prunum* (DALMAN), middle Ludlow, Gotland; *b–e,* dorsal, posterior, anterior, lateral views, ×2; *f–g,* serial sections, ×4 (Copper, 1977b).

?A. (**Lissatrypella**) SAPELNIKOV & MIZENS, 1982, p. 30 [**Atrypa kuschvensis* CHERNYSHEV, 1893, p. 60; OD]. Medium, round outline, flat ventral valve; convexoplane to weakly dorsibiconvex; small, anacline-hypercline area; apical foramen; small, obscured deltidial plates; broadly plicate commissure; interior with solid teeth, straight hinge plate, long slender jugal processes, dorsomedial spiralia with about 8 whorls. [Possibly synonymous with *A. (Atrypoidea),* distinguished only by variable characters such as broad, flattened, convexoplane shape, low anterior fold, possible deltidial plates in adult shells; possibly synonymous with *Tectatrypa,* except in plicate commissure. CHERNYSHEV's types are small, *Lissatrypa*-like, round shells, not corresponding to the description of the subgenus.] *Silurian (upper Wenlock–Přídolí), Lower Devonian (?Lochkovian):* eastern Urals, central Asia, northern Canada, *upper Wenlock–Přídolí;* Czech Republic, *?Lochkovian* (HAVLÍČEK, 1987a, p. 107).——FIG. 991*a–f.* **A. (L.) kuschvensis* (CHERNYSHEV), lower Ludlow, eastern slopes, Urals; *a–d,* dorsal, ventral, anterior, lateral views, ×1; *e–f,* serial sections, ×3.5 (Sapelnikov & Mizens, 1982).

?Aulacatrypa HAVLÍČEK, 1987b, p. 241 [**Atrypa squama* BARRANDE, 1879b, pl. 82; OD; *emend.,* HAVLÍČEK, 1990c, p. 203] [=*Johnsoniatrypa* ZHANG Ning, 1989b, p. 8 (type, *J. imbricata,* OD)]. Very small (less than 5 mm), weakly biconvex-planoconvex; widest at long, straight hinge; orthocline-apsacline area; open delthyrium, possibly lacking deltidial plates; slightly overlapping, concentric growth lamellae with fine capillae (spinulose); weakly sulcate to rectimarginate commissure; teeth solid; cardinal pit dividing hinge plate; crura, spiralia, and jugal processes undescribed. [Similar to ?*Lissatrypa* in possessing concentrically aligned capillae, but differing in very small size, thin shell, convexity, long hinge, large area, delicate hinge plate; possibly synonymous with *Australina,* with which it shares convexity, hinge plate structure.] *Silurian (Wenlock):* Czech Republic, arctic Canada.——FIG. 989,*1a–e.* **A. squama* (BARRANDE), Czech Republic; dorsal, ventral, lateral, posterior, anterior views, approximately ×6 (Barrande, 1879b).——FIG. 989,*1f–g. A. imbricata* (ZHANG), arctic Canada; dorsal valve exterior, interior, ×6 (Zhang Ning, 1989b).

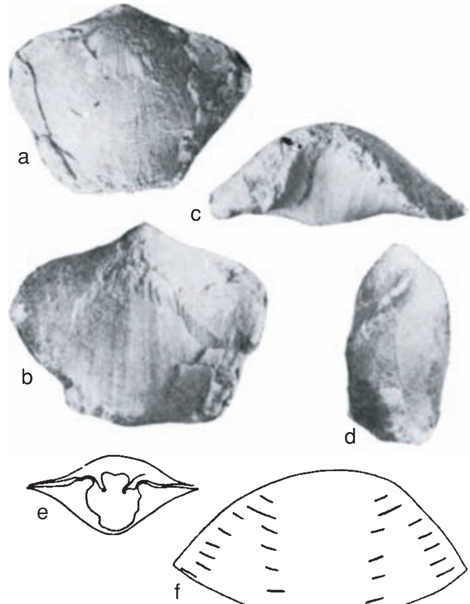

FIG. 991. Lissatrypidae (p. 1461).

Australina CLARKE, 1913, p. 348 [**A. jachalensis;* OD; *emend.,* COPPER, HÜNICKEN, & BENEDETTO, 1988, p. 533]. Small to medium; planoconvex-concavo-convex; long, narrow sulcus on dorsal valve; rounded outline; surface smooth, capillae unknown; beak adpressed; minute area; transapical foramen obscured; deltidial plates possibly absent; rectimarginate to weakly sulcate commissure; internally, weak pedicle callist; teeth stubby, medially directed, solid; socket plates strong, separated by distinct cardinal pit; cardinal process absent; dorsomedial spiralia with fewer than 5 whorls; jugal processes undescribed. [Distinguished from

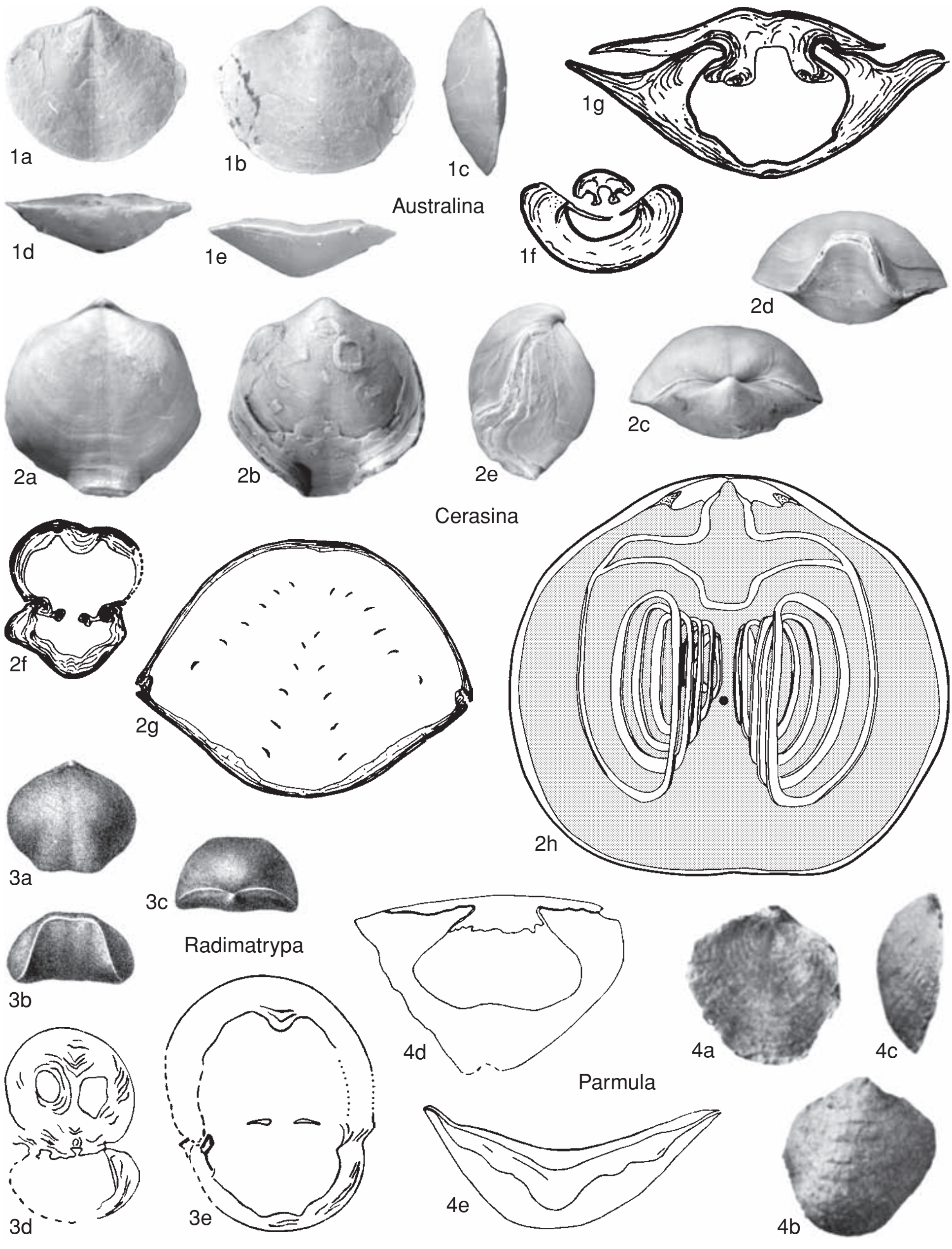

FIG. 992. Lissatrypidae (p. 1461–1463).

Lissatrypa by convexity, hinge plate with cardinal pit, lack of thick pedicle callist or collar; similar to *Aulacatrypa,* but larger, lacking straight hinge line.] *Silurian (?upper Wenlock, Ludlow–Přídolí):* South America, ?northern Africa, Australia, Czech Republic, ?China.——FIG. 992,*1a–g.* **A. jachalensis,* Ludlow, Argentina; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×2; *f–g,* serial sections, ×5 (Copper, Hünicken, & Benedetto, 1988).

Cerasina COPPER, 1995, p. 850 [**C. pycnata* COPPER, 1995, p. 851; OD]. Small to medium, elongate to equidimensional, rounded-subquadrate, dorsibiconvex-biconvex; narrow, hypercline area; foramen usually transapical; deltidial plates obscured by incurved beak, commonly lost; sharp, U-shaped anterior fold; interior with thick shell; dorsally directed solid teeth; thin hinge plate; small, apical, rounded ventral septum; broad dorsal septum; small crura; spiralia dorsomedial, about 8 whorls; dorsally positioned, simple jugum. [*Septatrypa*-like shape, but lacking dental cavities, delicate cardinalia internally; most similar to *Meifodia,* but distinguished by dorsally located, primitive jugum instead of separated jugal processes and a smaller, narrower shell with more sharply defined anterior fold.] *Silurian (lower Llandovery–middle Llandovery):* North America.——FIG. 992,*2a–h.* **C. pycnata,* lower Llandovery, Anticosti; *a–e,* dorsal, ventral, posterior, anterior, lateral views, ×2; *f–g,* serial sections, ×5; *h,* reconstruction of brachidia, ×5 (Copper, 1995).

?Cromatrypa HAVLÍČEK, 1987b, p. 240 [**C. orbis;* OD]. Small, smooth, rounded outline, biconvex to weakly dorsibiconvex; minute orthocline area; small deltidial plates with apical foramen; rectimarginate commissure; ventral *vascula media* long, straight, diverging; massive hinge plate with cardinal pit; probably dorsomedial spiralia; jugal processes undescribed. [Problematic genus; possibly synonymous with *Levispira* except in rounded shape, convexity; possibly synonymous with *Lissatrypa,* but adult shells possess exposed deltidial plates, apical foramen, small orthocline area; dorsomedial spiralia, but spiralia undescribed (HAVLÍČEK, personal communication, 1990).] *Silurian (Ludlow):* Czech Republic.——FIG. 989,*4a–c.* **C. orbis;* dorsal, ventral, anterior views, ×3.2 (Havlíček, 1987b).

?Holynatrypa HAVLÍČEK, 1973, p. 339 [**H. crucifera;* OD]. Similar to *Lissatrypa,* but generally very small shell, planoconvex; ventral valve with triangular, raised muscle platform, supported by raised median septum; brachidia undescribed. [Affinities unknown, possibly not atrypide.] *Lower Devonian (Emsian):* Czech Republic.——FIG. 989,*2a–b.* **H. crucifera,* upper Emsian; dorsal view, interior ventral valve, ×5.5 (Havlíček, 1998a).

Levispira MIZENS, 1975b, p. 47 [**L. eifeliensis* MIZENS, 1975b, p. 48; OD]. Small to medium, elongate, planoconvex-ventribiconvex; keeled ventral valve; strongly protruding beak; small orthocline area; apical foramen; minute deltidial plates; rectimarginate to weakly sulcate commissure; solid teeth; dorsal hinge plate thick; small cardinal pit; mediodorsal spiralia with fewer than about 6 whorls; jugal processes touching medially. [Possibly synonymous with *Cromatrypa* except in elongate shape, convexity, sulcate commissure; distinguished from *Lissatrypa* by keeled, elongate, sulcate shell, convexity, orthocline area, exposed deltidial plates; possibly synonymous with *Shrockia.*] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* Urals.——FIG. 993,*2a–f.* **L. eifeliensis,* upper Emsian–lower Eifelian, eastern slopes; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e–f,* serial sections, ×3 (Mizens, 1975b).

Meifodia WILLIAMS, 1951, p. 106 [**Hemithyris subundata* M'COY, 1851, p. 394; OD] [=*Tyrothyris* ÖPIK, 1953, p. 15 (type, *T. tyro,* OD)]. Medium, equally wide as long or wider than long, dorsibiconvex; straight hinge; small anacline-hypercline area usually obscuring apical-transapical foramen; deltidial plates commonly lost in adult shells; prominent, broad, angular, anterior fold on commissure; solid teeth; ventral valve with long, slightly arcuate, subparallel vascular canals; hinge plate divided by cardinal pit; straight, horizontal inner socket ridges; dorsomedially directed spiralia with fewer than 10 whorls; long, simple, posteroventrally located jugal processes, with hooklike jugal plates. [Distinct from *Cerasina* in the possession of ventral jugal processes (instead of dorsal jugum), wide shell with broad fold; differs from *Australina* by its convexity, strong anterior fold; may be confused with septatrypinids, but for solid teeth lacking dental cavities.] *Silurian (Llandovery):* Eurasia, North America.——FIG. 993,*1a–h.* **M. subundata* (M'COY), Rhuddanian, United Kingdom; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e–g,* serial sections, ×5; *h,* reconstruction of brachidia, ×5 (Copper, 1995).

?Parmula MENAKOVA & BREIVEL, 1987, p. 110 [**P. orbus* NIKIFOROVA & MENAKOVA, 1987, p. 112; OD]. Very small to small, concavoconvex-planoconvex; smooth or with numerous weak, overlapping concentric growth lamellae; minute anacline-hypercline area; obscured, small foramen; deltidial plates absent; thick shell wall; long, straight, median ventral septum almost to commissure; teeth solid; possibly dorsomedial spiralia with 2 to 4 whorls; jugal processes said to be present. [Homeomorphic with the athyridids *Dayia* or *Dnestrina,* with which it shares long ventral septum, but said to have atrypoid spiralia (original types lack intact brachidia); possibly synonymous with dwarfed *Lissatrypa, Levispira,* or *Shrockia.*] *Silurian (upper Llandovery–Přídolí):* Turkestan, Tian Shan, Urals, Hudson Bay Lowlands, Canada.——FIG. 992,*4a–e.* **P. orbus* NIKIFOROVA & MENAKOVA, Přídolí, Zeravshan Range, Turkestan; *a–c,* dorsal, ventral, lateral views, ×3; *d–e,* serial sections, ×6.5 (Menakova & Breivel, 1987).

?Radimatrypa HAVLÍČEK, 1990c, p. 161 [**R. zelaria;* OD]. Small to medium, dorsibiconvex, smooth; small, hypercline area, lacking (or obscuring) foramen, deltidial plates; broadly plicate commissure; thick shell wall; solid teeth, probably lacking dental cavities; crura, spiralia, jugal processes undescribed. [Problematic genus; externally homeomorphic with *Septatrypa* or *Cerasina;* internally apparently similar to *Lissatrypa* in solid teeth, but dental cavities may be infilled.] *Lower Devonian (Emsian), Middle Devonian (?Eifelian):* Czech Republic.——FIG. 992,*3a–e.* **R. zelaria,* upper Emsian; *a–c,* dorsal, anterior, posterior views, ×1 (Barrande, 1879b); *d–e,* serial sections, ×5 (Havlíček, 1990c).

?Shrockia BOUCOT & SMITH, 1978, p. 268 [**S. twenhofeli* BOUCOT & SMITH, 1978, p. 271; OD]. Large, smooth, elongate, planoconvex-ventribiconvex; obscured hypercline area; deltidial plates unknown; sulcate commissure; brachidia unknown.

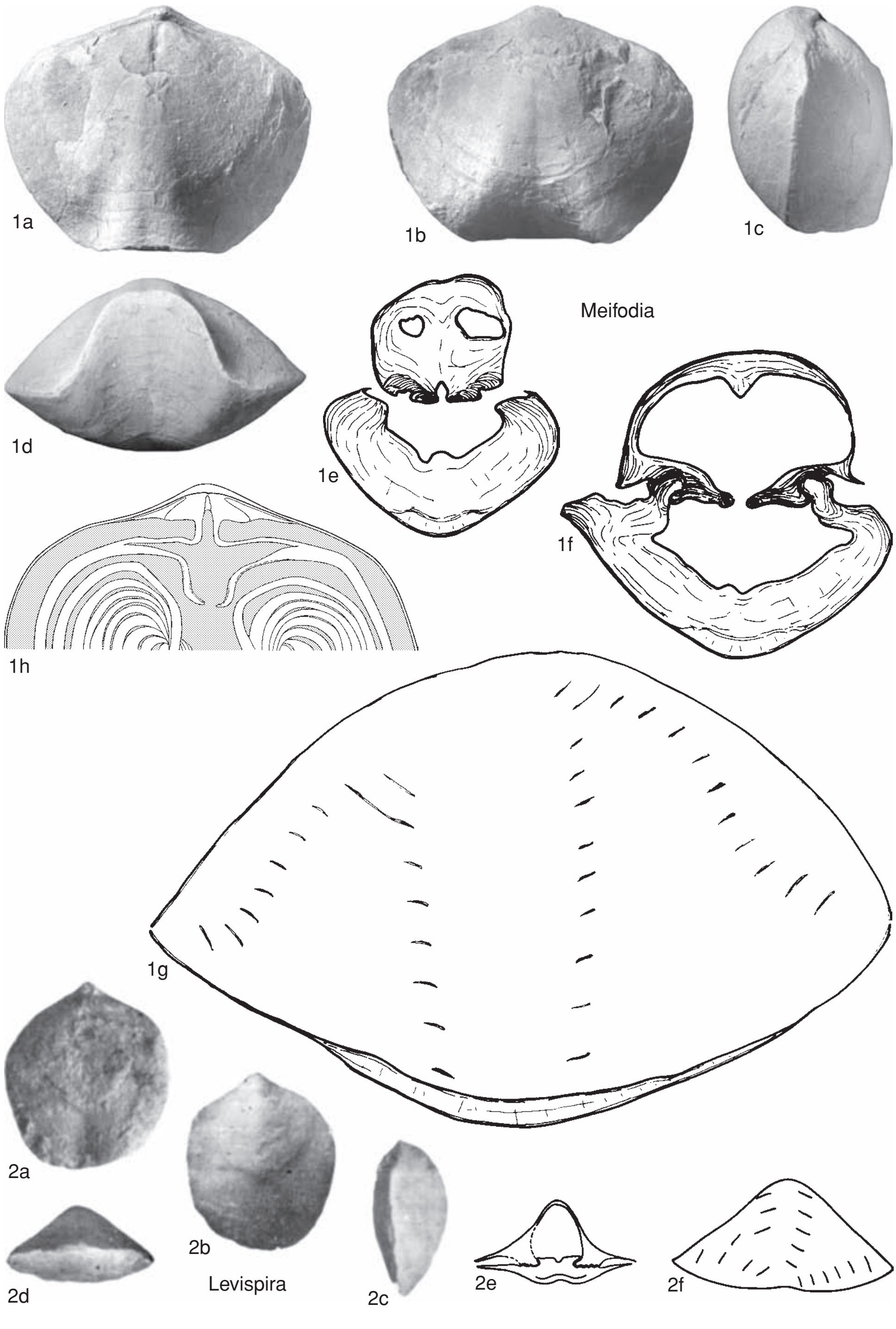

FIG. 993. Lissatrypidae (p. 1463).

[Externally like *Dayia* but with much larger shell; questionable atrypid since internal structure of poorly preserved shell unknown, shell may be deformed; elongate outline as in *Atrypoidea,* except for reversed convexity, sulcate commissure; possibly synonymous with *Levispira* or *Parmula,* but much larger in size.] *Silurian (Ludlow):* Newfoundland. ——FIG. 994,*2a–e.* **S. twenhofeli; a–c,* dorsal, posterior, ventral views, ×1; *d,* serial section, ×1.8; *e,* serial section, ×1.6 (Boucot & Smith, 1978).

?Tectatrypa MIZENS, 1973, p. 44 [**Merista tectiformis* CHERNYSHEV, 1893, p. 44; OD]. Small to medium, convexoplane, elongate to subtriangulate, laterally compressed; narrow beak; anacline area; possible small deltidial plates; apical foramen; high, broad, rounded, U-shaped anterior fold; interior with thick shell; solid, inwardly directed teeth; hinge plate slender; dorsally directed spiralia of fewer than 8 whorls; jugal processes undescribed. [Possibly synonymous with *Atrypoidea (Lissatrypella),* but with smaller, more globose, elongate shell; differs from smooth *Eokarpinskia* in hinge plate, lack of dental cavities.] *Silurian (upper Wenlock–Ludlow):* Urals. ——FIG. 994,*1a–f.* **T. tectiformis* (CHERNYSHEV), upper Wenlock, eastern slopes; *a–d,* dorsal, ventral, lateral, anterior views, ×1; *e–f,* serial sections, ×4 (Sapelnikov & Mizens, 1982).

Family SEPTATRYPIDAE Kozlowski, 1929

[*nom. transl.* COPPER, herein, *ex* Septatrypinae KOZLOWSKI, 1929, p. 30; *emend.,* COPPER, herein]

Small to medium, smooth, rarely corrugated, dorsibiconvex shells, generally with high anterior fold; large dental cavities with or without dental plates; thin, delicate hinge, socket plates; spiralia dorsomedially directed, with fine, narrow lamellae; spiralia dorsomedial; central to ventral jugum (Ordovician forms), or jugal processes (Siluro-Devonian forms). *Ordovician (Caradoc)–Lower Devonian (Emsian), Middle Devonian (?Eifelian).*

Subfamily SEPTATRYPINAE Kozlowski, 1929

[Septatrypinae KOZLOWSKI, 1929, p. 30] [=Atrypopsinae POULSEN, 1943, p. 40]

Smooth, thinly shelled, dorsibiconvex; may possess anterior corrugations (ribs); usually weakly to strongly plicate; large dental cavities; fragile hinge plates; dorsal septum very short to nearly absent; dorsomedially directed spiralia; delicate, long, ventrally to centrally located jugal processes. *Silurian (Llandovery)–Lower Devonian (Emsian), Middle Devonian (?Eifelian).*

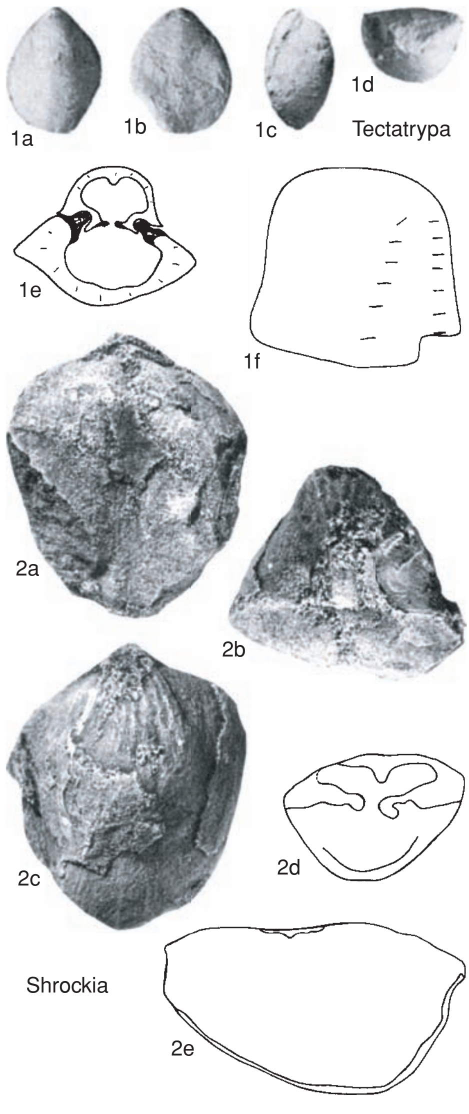

FIG. 994. Lissatrypidae (p. 1463–1465).

Septatrypa KOZLOWSKI, 1929, p. 176 [**S. secreta;* OD] [=*Dubaria* TERMIER, 1936, p. 1266 (type, *D. lantenoisi,* OD); *Atrypopsis* POULSEN, 1943, p. 44 (type, *A. varians,* OD); *Rhynchatrypa* SIEHL, 1962, p. 199 (type, *Terebratula thetis* BARRANDE, 1847, p. 349, OD); *Barkolia* ZHANG Quan, 1981, p. 97 (type, *B. typica,* OD)]. Medium, rounded to subtriangulate-subquadrate, dorsibiconvex; ventral valve relatively flat to concave posteriorly in specimens with high fold; shell smooth or corrugated; pinched beak; small anacline-hypercline area; minute apical-transapical foramen, obscuring small deltidial plates; shell smooth to corrugated; high, strongly defined, U-shaped plicate commissure;

thin shell wall; delicate teeth with large dental cavities flanked by thin dental plates; hinge, socket plates delicate, subhorizontal; distinct cardinal pit; variable weak, short dorsal septum [septalium-like structure in specimens with strong dorsal convexity]; crura delicate; dorsal spiralia with fewer than 8 whorls; posteromedial jugal processes ending in long, delicate jugal plates. [Differs from *Idiospira* in presence of ventrally located jugal processes. Contrary to published literature, Llandovery species externally, internally indistinguishable from later forms]. *Silurian (Aeronian)–Lower Devonian (Pragian):* worldwide.

S. (**Septatrypa**). Description as for genus, but only smooth species included. [Differs from *S. (Hircinisca)* in absence or rare appearance of anterior corrugations; differs from *Idiospira* in presence of jugal processes.] *Silurian (Aeronian)–Lower Devonian (Pragian):* worldwide.——FIG. 995,*1a–d.* **S. (S.) secreta,* Lochkovian, Podolia, Ukraine; dorsal, ventral, lateral, anterior views, ×2 (Nikiforova, Modzalevskaya, & Bassett, 1985).——FIG. 995,*1e–h. S. (S.)* sp., Wenlock, Gotland; *e–g,* serial sections; *h,* reconstruction of brachidia, ×5 (new).

S. (**Hircinisca**) HAVLÍČEK, 1960, p. 241 [**Atrypa Sappho* [*sic*] var. *hircina* BARRANDE, 1879b, pl. 90, fig. IV; OD; no original description of types]. Identical to *S. (Septatrypa)* internally, but variably up to 7 or 8 anterior corrugations along fold-sulcus producing rhynchonelliform shape, appearance of anterior ribs; population variants of *Septatrypa sensu stricto* also possess weak corrugations. *Silurian (middle Wenlock)–Lower Devonian (Lochkovian):* Europe, Morocco, North America, Urals, central Asia, ?southern China. ——FIG. 995,*2a–g.* **S. (H.) hircina* (BARRANDE), upper Wenlock, Czech Republic; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×1; *f–g,* serial sections, ×4.6 (Havlíček & Plodowski, 1974).

Becscia COPPER, 1995, p. 853 [**B. scissura;* OD]. Small, smooth, biconvex; 2 strong, divergent ventral corrugations separated by sulcus; commonly 1 or 2 lateral corrugations; small orthocline-anacline area; apical foramen; minute deltidial plates; multiplicate commissure; shell wall thin; teeth delicate; large, elongate dental cavities; inner socket ridges fused over cardinal pit; thin hinge, socket plates; mediodorsal spiralia with fewer than 4 whorls; centrodorsally located jugal processes. [Differs from *Hircinisca* in its prominent ventral, divergent pair of corrugations, producing *Atrypina*-like form, internally by fused inner socket ridges; differs from *Atrypina* in lack of growth lamellae or imbrication, centrodorsal jugal processes, large dental cavities.] *Silurian (Llandovery):* North America, ?United Kingdom, Urals.——FIG. 995,*3a–h.* **B. scissura,* Rhuddanian, Anticosti; *a–e,* dorsal, ventral, lateral, posterior, anterior views, ×3; *f–g,* serial sections; *h,* reconstruction of brachidia, ×5 (Copper, 1995).

?Cerberatrypa HAVLÍČEK, 1990c, p. 162 [**C. cerberus* HAVLÍČEK, 1990c, p. 163; OD]. Small to medium, cordate to pentagonal outline, biconvex; small, orthocline-anacline area; apical foramen; small deltidial plates; rectimarginate-plicate commissure; delicate hinge plates; large dental cavities; crura, spiralia, jugal processes unknown. [Problematic genus similar to *Septatrypa* but cordate shape, weak dorsal fold: may possibly be athyridid.] *Lower Devonian (Emsian), Middle Devonian (?Eifelian):* Czech Republic.——FIG. 995,*4a–c.* **C. cerberus,* Emsian; dorsal, ventral, anterior views, ×2 (Havlíček, 1990c).——FIG. 995,*4d. C. dissidens* (BARRANDE), Emsian; serial section, ×6 (Havlíček, 1990c).

Subfamily IDIOSPIRINAE new subfamily

[Idiospirinae COPPER, herein]

Septatrypidae with posterodorsally located jugum. *Ordovician (Caradoc–Ashgill), Silurian (?Llandovery).*

Idiospira COOPER, 1956a, p. 690 [**Camerella panderi* BILLINGS, 1859b, p. 302; OD]. Small to medium, ovoid, biconvex-dorsibiconvex, smooth to weakly corrugated anteriorly; small, orthocline-hypercline area; apical foramen; deltidial plates obscured, minute; usually corrugated, subangular to rounded, plicate commissure; teeth with large dental cavities; weak dorsal septum; thin socket plates; spiralia dorsomedial with fewer than 6 whorls; posterodorsal jugum. [Externally similar to *Septatrypa* or *Hirciniscа,* but smaller shell, possessing jugum instead of jugal processes, thicker hinge plate.] *Ordovician (middle Caradoc–Ashgill), Silurian (?Llandovery):* North America, Eurasia.——FIG. 996,*1a–h.* **I. panderi* (BILLINGS), middle Caradoc, Ontario, Canada; *a–e,* dorsal, ventral, lateral, anterior, posterior, ×3; *f–g,* serial sections; *h,* reconstruction of brachidia, ×4 (Copper, 1986b).

?Webbyspira PERCIVAL, 1991, p. 163 [**W. principalis;* OD]. Medium size, wide, dorsibiconvex-biconvex, smooth, only rarely corrugate; small, anacline area; foramen, deltidial plates unknown; broadly plicate commissure; thick walled; long, narrow dental cavities; moderate to strong dorsal septum; dorsomedial spiralia with fewer than 8 whorls; nature of discrete jugal processes or jugum unknown. [Differs from externally similar *Meifodia* in having dental cavities; differs from *Septatrypa* in broad shell, low anterior fold, narrow dental cavities, socket plates, jugal processes; differs from *Idiospira* in larger size, broad shell. Original description cites jugal processes; if correct, *Webbyspira* should be assigned to the Septatrypinae.] *Ordovician (Caradoc):* Australia. ——FIG. 996,*2a–g.* **W. principalis,* New South Wales; *a–d,* dorsal, posterior, lateral, anterior views, ×2; *e–f,* serial sections, ×2; *g,* reconstruction of brachidia, ×2 (Percival, 1991).

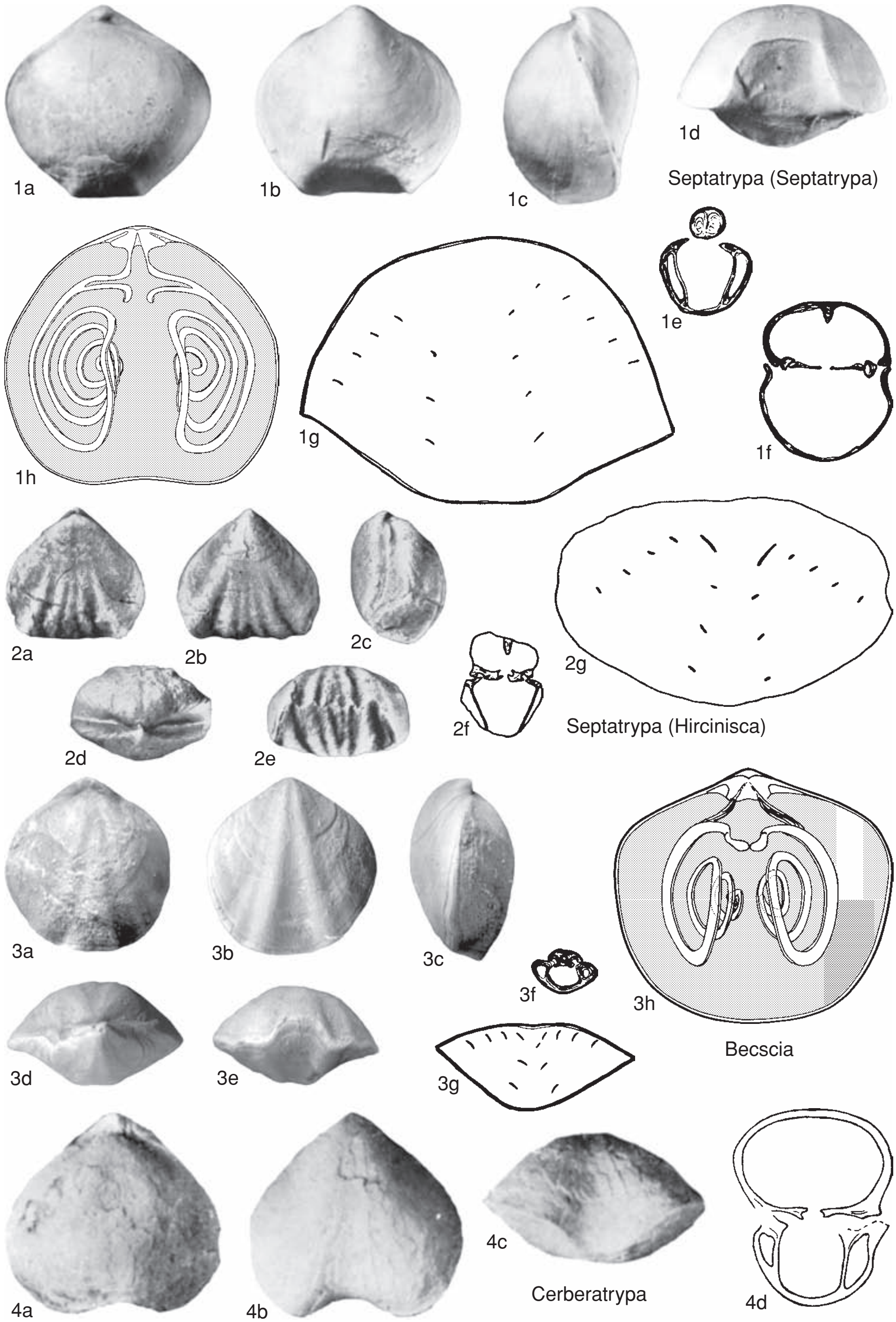

FIG. 995. Septatrypidae (p. 1466).

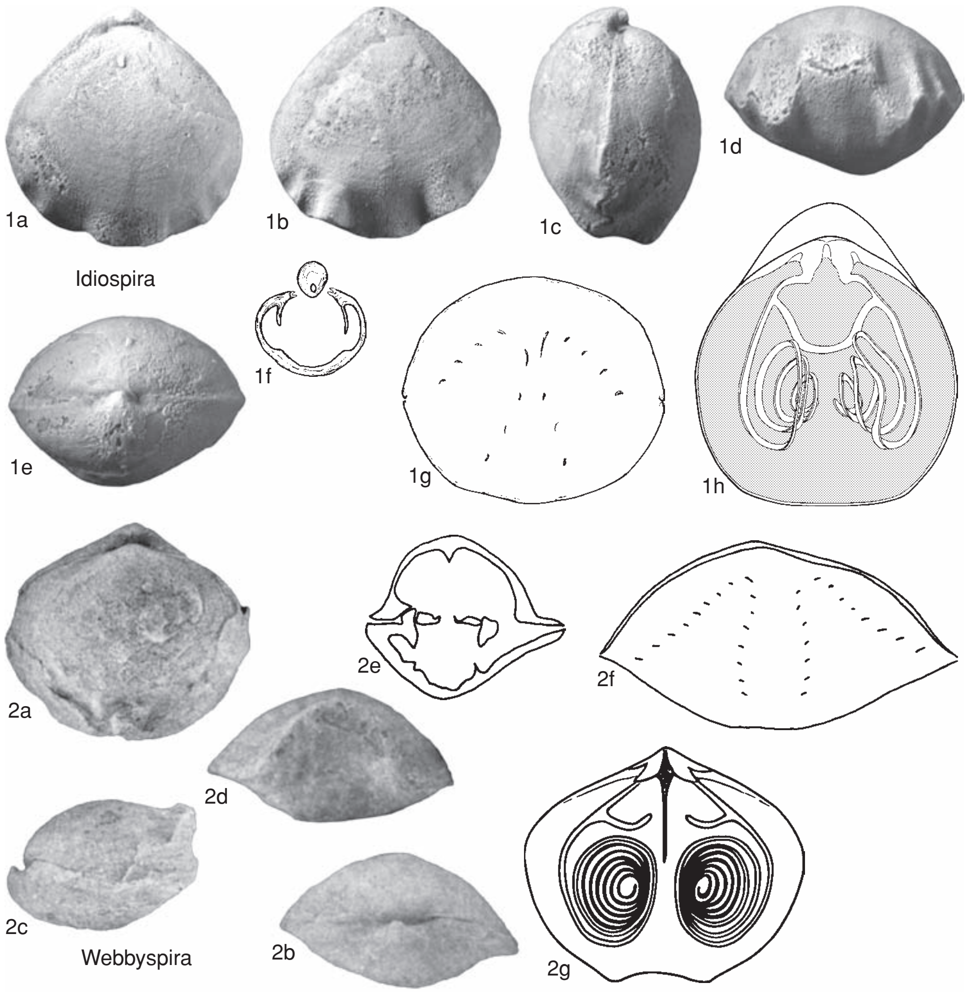

FIG. 996. Septatrypidae (p. 1466).

Superfamily GLASSIOIDEA Schuchert & LeVene, 1929

[*nom. transl.* COPPER, herein, *ex* Glassiinae SCHUCHERT & LEVENE, 1929a, p. 20; *emend.,* COPPER, 1986b, p. 852]

Small to medium, smooth, biconvex, commonly ligate shells; thick walled; sturdy hinge socket plates, solid teeth usually reinforced by exposed or buried dental plates; dental cavities in later taxa; spiralia medially directed, barrel shaped, scooped toward jugal processes; jugal processes terminated by small to large jugal plates. *Silurian (?upper Llandovery, Wenlock)–Upper Devonian (Frasnian).*

Family GLASSIIDAE Schuchert & LeVene, 1929

[*nom. transl.* COPPER, herein, *ex* Glassiinae SCHUCHERT & LEVENE, 1929a, p. 20; *emend.,* COPPER, 1986b, p. 852]

Diagnosis as for superfamily. *Silurian (?upper Llandovery, Wenlock)–Upper Devonian (Frasnian).*

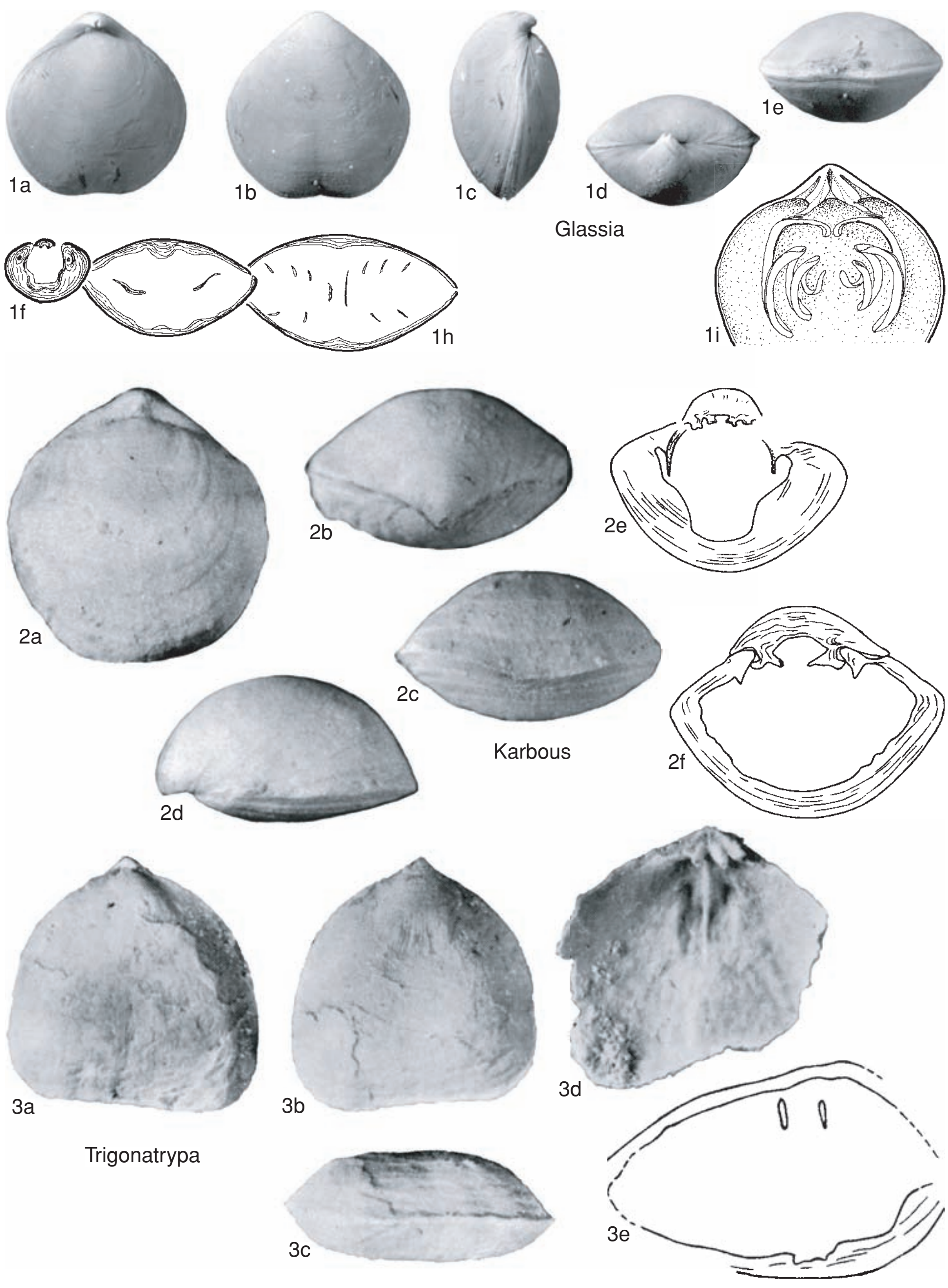

FIG. 997. Glassiidae (p. 1469–1470).

Glassia DAVIDSON, 1881a, p. 11 [**Atrypa obovata* J. de C. SOWERBY, 1839, p. 618; OD; *typum invalidum,* belongs to *Lissatrypa; ergo,* type revised to *Glassia elongata* DAVIDSON, 1881b, p. 148; *vid.* COPPER, 2001] [=*Cryptatrypa* SIEHL, 1962, p. 196 (type, *Terebratula philomela* BARRANDE, 1847, p. 387, OD)]. Small, biconvex to weakly ventribiconvex, rounded to elongate; small anacline-hypercline area; beak obscuring minute apical-transapical foramen; deltidial plates minute or absent; commissure ligate (both valves sulcate) to rectimarginate; thick shell wall; medium septum common in both valves; teeth distally solid or with minute apical dental cavities; buried dental plates; thick, squared hinge plate divided by narrow cardinal pit; spiralia barrel shaped, medially directed, fewer than 6 whorls; ventroposterior jugal processes terminating in hooks. [The originally and unfortunately designated type species of *Glassia, G. obovata* (Sowerby), is a species of *Lissatrypa* (family Lissatrypidae), with dorsally directed spiralia; Davidson (1881b) correctly identified *Glassia elongata* with medially directed spiralia, typical of the family Glassiidae as defined by Schuchert and LeVene (1929a) and used by Davidson in his diagnosis of the genus. This species was then selected as type (Copper, 1996b).] *Silurian (?upper Llandovery, Wenlock–Ludlow, ?Přídolí):* western Europe, Urals, ?northern Canada.——Fig. 997,*1a–e*. **G.* sp. cf. *G. elongata* (Davidson), Wenlock, Gotland; dorsal, ventral, lateral, posterior, anterior views, ×3 (new).——Fig. 997,*1f–i*. **G. elongata* (Davidson), Wenlock, United Kingdom; *f–h,* serial sections, ×5; *i,* reconstruction of brachidium, ×5 (new).

Karbous Havlíček, 1985a, p. 236 [**K. aperinus;* OD]. Small to medium, smooth, rounded to elongate to subrectangular outline, ventribiconvex; beak inflated; small, anacline-hypercline area; apical foramen flanked by minute deltidial plates; rectimarginate to weakly plicate commissure; squared pedicle cavity; teeth with dental cavities, dental plates; hinge plate with cardinal pit, lacking process; inner socket ridges flat; crura, spiralia, jugal processes unknown. [Similar to *Glassia* internally but differing in larger size, ventribiconvex-planoconvex shape, lack of sulci on either valve, expanded anacline-hypercline area, foramen, small dental cavities outlining dental plates; distinguished from *Peratos* by small dental cavities, small area; distinguished from *Lissatrypa* by hinge plate with distinct cardinal pit, straight inner socket ridges, prominent dental cavities. Havlíček (1990c, p. 159) stated that spiralia are dorsal, providing no figures; this is contradicted by *Glassia*-like hinge plate, tooth structure, but brachidia need confirmation.] *Lower Devonian (Lochkovian–Emsian):* western Europe, Urals, central Asia, ?China.——Fig. 997,*2a–f.* **K. aperinus,* upper Emsian, Czech Republic; *a–d,* dorsal, posterior, anterior, lateral views, ×3.5; *e–f,* serial sections, ×5.2 (Havlíček, 1985a).

?Nanatrypa Sapelnikov & Mizens, 1982, p. 12 [**Lissatrypa (Nanatrypa) bisinuata* Sapelnikov & Mizens, 1982, p. 13; OD]. Small, globose, rounded, biconvex; ventral, dorsal valve with well-developed median sulcus; minute, anacline area; small beak; minute apical foramen; deltidial plates undescribed; anterior commissure ligate, rectimarginate; internally thick shell apically; solid teeth, no dental cavities described; hinge plate divided by rounded cardinal pit; inner socket ridges *Glassia*-like; spiralia, jugal processes undescribed. [Homeomorphic with *Glassia,* which is occasionally ligate, i.e., bisinuate; lack of data on brachidia precludes comparison with Lissatrypinae or Glassiinae.] *Silurian (Ludlow):* Urals (eastern slopes), Czech Republic.——Fig. 998,*2a–e.* **N. bisinuata* (Sapelnikov & Mizens), eastern slopes, Urals; *a–d,* dorsal, ventral, lateral, anterior views, ×2; *e,* polished section, ×5 (Sapelnikov & Mizens, 1982).

Peratos Copper, 1986b, p. 856 [**P. arrectus* Copper, 1986b, p. 859; OD]. Medium to large, rounded to subquadrate outline, weakly biconvex; prominent orthocline area; strong protruding beak; apical foramen; prominent deltidial plates; rectimarginate commissure; thick shell wall; median septa lacking in either valve; large, subpyramidal dental cavities; long, straight dental plates; medially directed, barrel-shaped spiralia with 4 to 6 whorls; jugal processes posteromedial, terminating in large, spoon-shaped, incurved jugal plates. [Distinguished from *Karbous* by its large, orthocline area, biconvexity, internally by large dental cavities, free, straight dental plates; distinguished from *Glassia* in larger size, prominent orthocline area, lack of sulci, wide dental cavities, jugal processes.] *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* Europe, Urals (western slopes).——Fig. 998,*1a–h.* **P. arrectus,* upper Eifelian, Germany; *a–d,* dorsal, lateral, anterior, posterior views, ×3; *e–g,* serial sections, ×4; *h,* reconstruction of brachidia, ×4 (Copper, 1986b).

?Trigonatrypa Havlíček, 1990c, p. 154 [**Meristella holynensis* Havlíček, 1956, p. 613; OD]. Small to medium, triangulate-spatulate outline, widest anteriorly; weak anterior sulcus on dorsal valve; narrow, angular, apsacline-orthocline area; minute deltidial plates flanking apical foramen; rectimarginate commissure; thick shell wall; distally distinct dental cavities; possible dental plates; hinge socket plates delicate; jugal processes, spiralia undescribed. [Unusual for its triangulate shape, differentiating it from *Glassia* and *Karbous,* but spiralia undescribed; comparable in shape to *Tectatrypa,* which is more elongate; lack of data for brachidia makes assignment to Lissatrypidina or Atrypida questionable (possible rhynchonellide).] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Czech Republic.——Fig. 997,*3a–e.* **T. holynensis* (Havlíček), Emsian; *a–d,* dorsal, ventral, anterior views, internal dorsal valve, ×3; *e,* serial section, ×10 (Havlíček, 1990c).

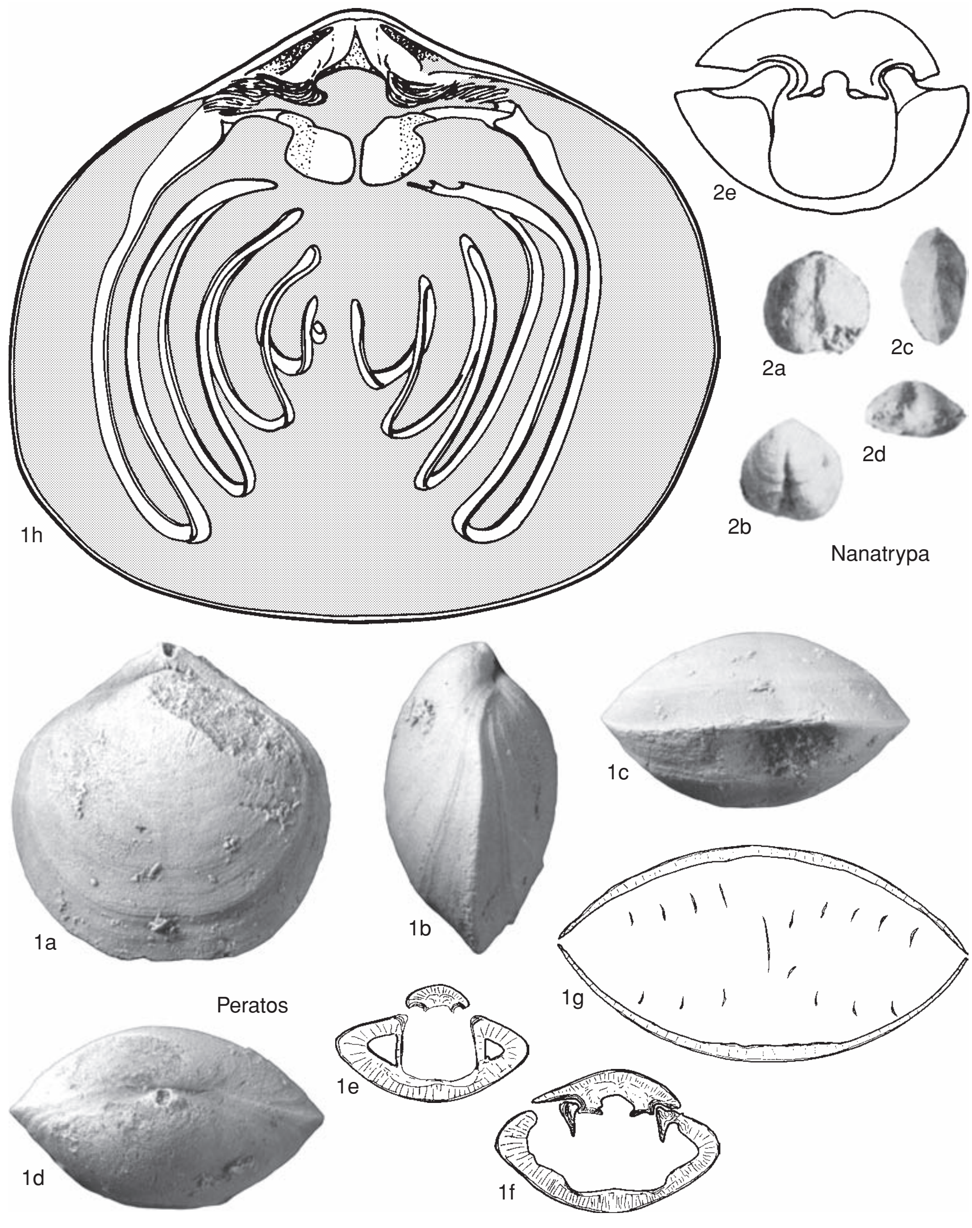

FIG. 998. Glassiidae (p. 1470).

Superfamily PROTOZYGOIDEA Copper, 1986

[*nom. transl.* COPPER, herein, *ex* Protozyginae COPPER, 1986b, p. 834; *emend.,* COPPER, herein]

Small shelled, smooth Lissatrypidina with medially directed spiralia of few whorls or less than 1 whorl, jugum, partial jugum, or no jugum. *Ordovician (Llandeilo–Ashgill), Silurian (?Llandovery).*

Family PROTOZYGIDAE Copper, 1986

[*nom. transl.* COPPER, 1995, p. 848, *ex* Protozyginae COPPER, 1986b, p. 834]

Protozygoids with small, ventribiconvex-planoconvex, thin-walled shell; sulcate to rectimarginate commissure; may be smooth to weakly corrugate or weakly ribbed; planar to conical spiralia with few whorls, or less than 1 whorl; jugum complete or incomplete, anterodorsal to medial. *Ordovician (Llandeilo–Ashgill), Silurian (?Llandovery).*

Protozyga HALL in HALL & CLARKE, 1893, p. 141 [**Atrypa exigua* HALL, 1847, p. 141; OD]. Small, rounded, normally smooth or slightly corrugate anteriorly, planoconvex-ventribiconvex; small, anacline-hypercline area; minute apical foramen; deltidial plates minute or absent; sulcate commissure; thin shell wall; teeth with large dental cavities; small cardinalia; crura delicate, ventrolateral; medially to mediodorsally directed spiralia, usually fewer than 3 whorls; ventrocentral, U-shaped jugum. [Differs from *Manespira* in spiralia of multiple whorls, complete jugum, posterior absence of corrugations.] *Ordovician (Caradoc):* worldwide.——FIG. 999,*3a–i.* **P. exigua* (HALL), lower Caradoc, New York, USA; *a–e,* dorsal, ventral, lateral, anterior, posterior views, ×5; *f–g,* serial sections, ×5 (Copper, 1986b); *h–i,* dorsal, lateral reconstruction of brachidium, ×10 (new).

Manespira COPPER, 1986b, p. 839 [**Hallina nicolleti* WINCHELL & SCHUCHERT, 1892, p. 293; OD]. Small, rounded outline, ventribiconvex-biconvex-planoconvex; commonly weakly ventrocarinate; neanic shell smooth, adult corrugated anteriorly; weak, diverging midrib pair on ventral valve; commonly with small fold developed on dorsal sulcus; area minute; very small beak; minute foramen; deltidial plates unknown; unisulcate to bisulcate commissure; thin shell wall; minute teeth; small dental cavities; thin, narrow hinge plates; medially directed spiralia with 1 whorl or part whorl; anterior to central, complete or incomplete jugum. [Distinct from *Protozyga* in its very simple spiralium (usually 1 whorl or fewer), incomplete jugum, commonly more frequent corrugations along adult commissure.] *Ordovician (Llandeilo–Caradoc):* North America, Europe.——FIG. 999,*1a–i.* **M. nicolleti* (WINCHELL & SCHUCHERT), lower Caradoc, Minnesota, USA; *a–e,* dorsal, ventral, lateral, anterior, posterior views, ×4; *f–g,* serial sections, ×6 (Copper, 1986b); *h–i,* reconstruction of brachidium, ×10 (new).

Xysila COPPER, 1995, p. 848 [**X. astaca* COPPER, 1995, p. 849; OD]. Small, elongate, ventribiconvex, globose, noncarinate; hypercline area; small, inflated beak; transapical foramen; deltidial plates unknown; smooth shell lacking corrugations or ribs; commissure weakly sulcate to ligate; both valves usually with narrow median sulcus; interior with thick shell apically; minute teeth with dental cavities; strong dorsal septum; crura sharply laterally geniculated; medially directed spiralia; jugum beginning anteriorly, joining dorsocentrally. [Similar to *Cyclospira* in shape and medially directed spiralia, but possessing simple jugum, lacking corrugations along commissure. *Xysila* could be assigned to Cyclospiridae, if alternately derived from *Cyclospira* via later addition of jugum, but ancestry seems more probable with Protozygidae. *Xysila* probable ancestor to Glassiidae.] *Ordovician (Ashgill), Silurian (?Llandovery):* North America, *Ashgill;* western Europe, *?Llandovery.*——FIG. 999,*2a–i.* **X. astaca,* Ashgill, Anticosti, Canada; *a–e,* dorsal, ventral, lateral, anterior, posterior views, ×3; *f–g,* serial sections, ×5; *h–i,* reconstruction of brachidia, ×5 (Copper, 1995).

Family CYCLOSPIRIDAE Schuchert, 1913

[Cyclospiridae SCHUCHERT, 1913, p. 410; *emend.,* COPPER, herein]

Small, smooth or weakly corrugated, planoconvex-ventribiconvex-biconvex; sulcate to rectimarginate; medially directed spiralia of fewer than 4 whorls; jugum absent. *Ordovician (?Llandeilo, Caradoc–Ashgill).*

Cyclospira HALL in HALL & CLARKE, 1893, p. 146 [**Orthis bisulcata* EMMONS, 1842, p. 396; OD] [=*Triplecella* WILSON, 1932, p. 399 (type, *T. diplicata,* OD); *Aulidospira* WILLIAMS, 1962, p. 252 (type, *A. trippi,* OD); ?*Cyclorhynchia* BARANOV, 1994, p. 29 (type, *Cyclospira globosa* ROZMAN, 1964a, p. 189)]. Small, ventribiconvex-planoconvex, subtriangulate to elongate; strongly convex ventral valve, weakly convex to planar dorsal valve; small area anacline-hypercline; apical-transapical foramen; sulcate-bisulcate commissure; shell thickly walled; teeth solid or with small, slitlike dental cavities or nuclei; medially directed spiralia with normally fewer than 4 whorls; jugum or jugal processes absent. [Distinguished from homeomorphic protozyginids by absence of jugum; distinguished from *Rozmanospira* by presence of more than 1

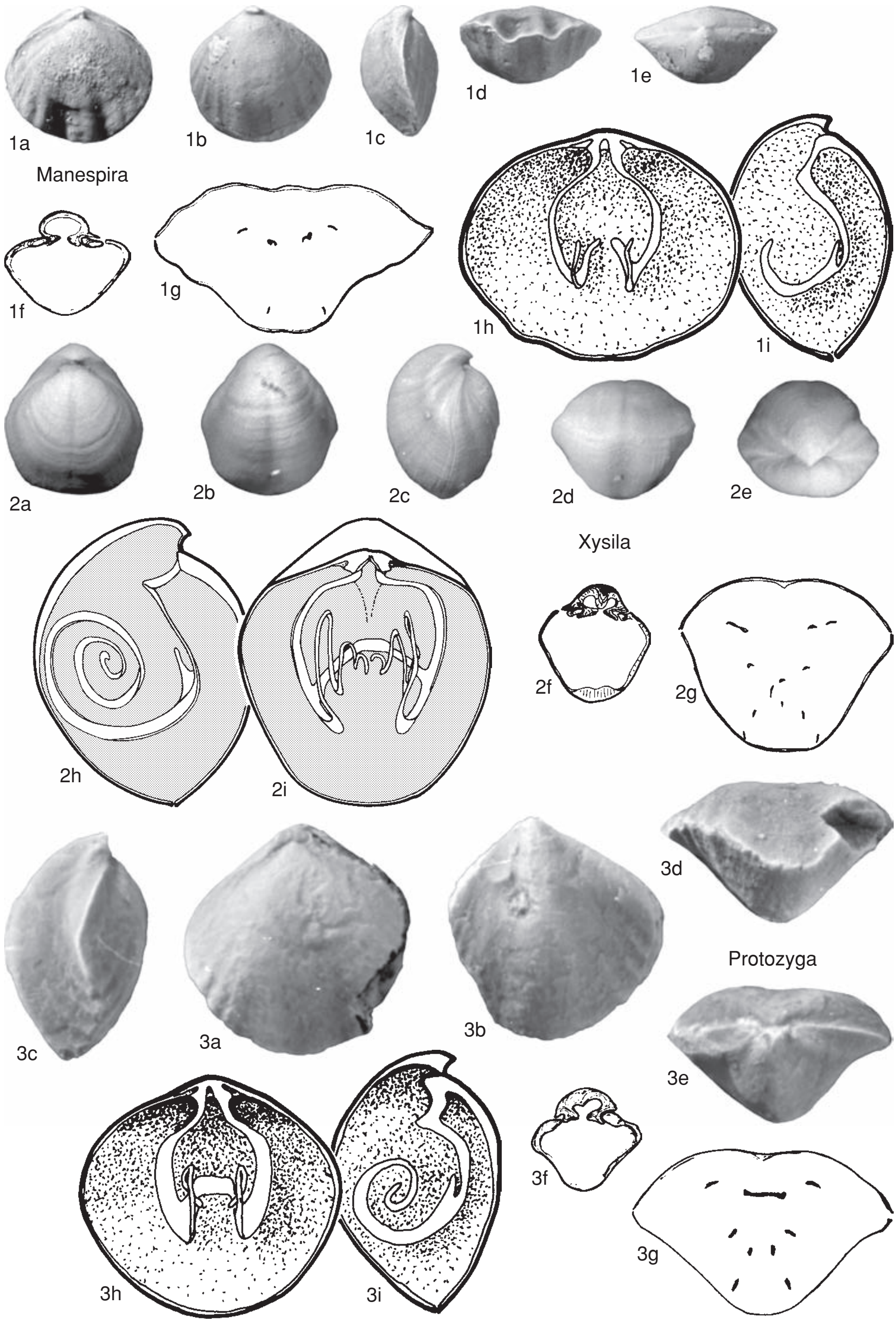

FIG. 999. Protozygidae (p. 1472).

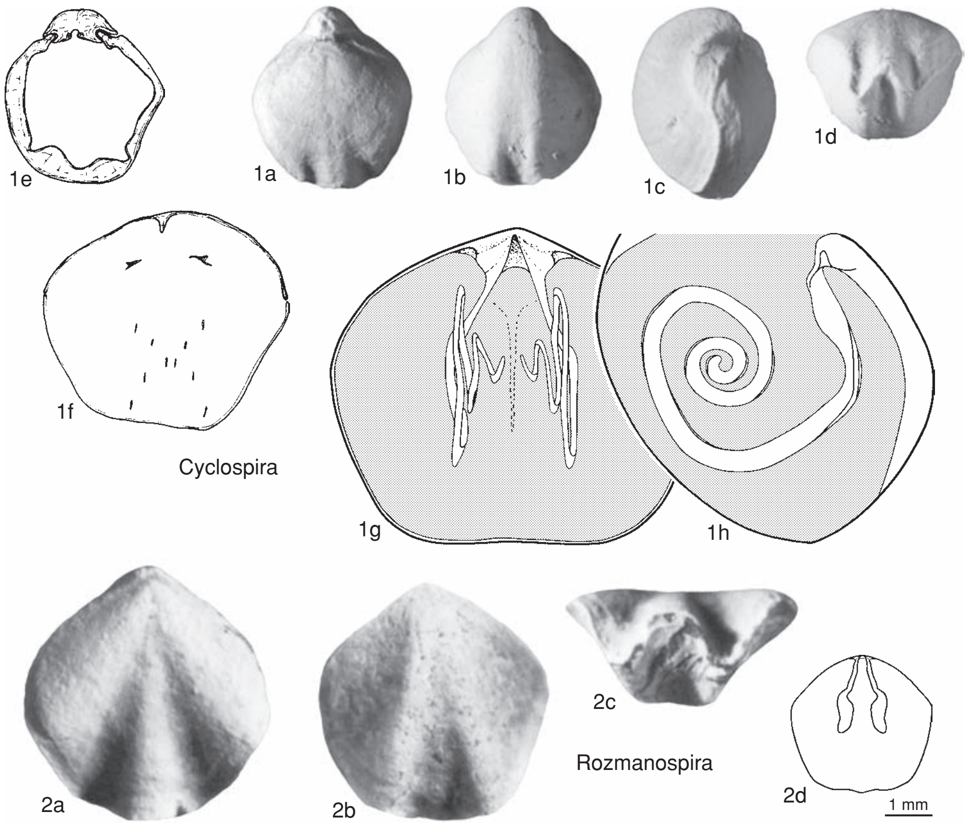

FIG. 1000. Cyclospiridae (p. 1472–1474).

spiral whorl. The synonym *Aulidospira* is also listed by ALVAREZ & RONG, herein, p. 1570, as a genus in the subfamily Meristinae, family Meristidae. See discussion of examination of type specimen in COPPER, 1986b, p. 849.] *Ordovician (Caradoc–Ashgill):* North America, Eurasia.——FIG. 1000,*1a–h.* **C. bisulcata* (EMMONS), upper Caradoc, New York, USA; *a–d,* dorsal, ventral, lateral, anterior views, ×3; *e–f,* serial sections, ×5; *g–h,* dorsal and lateral reconstruction of brachidia, ×5 (Copper, 1986b).

Rozmanospira POPOV, NIKITIN, & SOKIRAN, 1999, p. 645 [**Oligorhynchia mica* NIKITIN & POPOV, 1984, p. 156; OD]. Cyclospirinid with minute, smooth ventribiconvex shell, moderate to angular, dorsal anterior fold; small, incurved beak, minute pedicle opening; interior with short teeth, small dental cavities; divergent crura leading to medially directed, less than single revolution spiral whorl aligned in plane of symmetry; no jugum or jugal processes. [Differs from *Cyclospira* in its smaller shell, very simple partial spiral whorl.] *Ordovician (?Llandeilo, lower Caradoc–middle Caradoc):* Kazakhstan.——FIG. 1000,*2a–d.* **R. mica* (NIKITIN & POPOV), lower Caradoc; *a–c,* dorsal, ventral, and anterior views, ×10; *d,* reconstruction of brachidium, ×12 (Popov, Nikitin, & Sokiran, 1999).

ATHYRIDIDA

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ORDER ATHYRIDIDA

As here defined the order Athyridida includes the suborders Athyrididina, Retziidina, and Koninckinidina. All three suborders are characterized by a shell with a subcircular ventral foramen, in meso- to permesothyridid position and open or closed delthyrium, commonly obscured by the dorsal beak. Internally, cyrtomatodont hinge teeth articulate with dental sockets of variable shape depending on the degree of development of the cardinalia.

The athyridides, as the spiriferides, spiriferinides, and atrypides, developed a calcareous support for the lophophore in the form of spires disposed in cones. The apices of the cones were directed laterally in the athyrididines and retziidines and ventrally in the koninckinidines. Typically, the umbonal blades of the spiralium are sharply bent posterodorsally (posteroventrally in the koninckinidines) from the distal ends of the crura. A more or less elaborate jugum joined the dorsal half of the primary lamellae of each cone. In different stocks within the athyridides, accessory jugal lamellae intercoiled with primary volutions of the main spiralia to the apex of each cone.

More detailed accounts of the morphological variation displayed by the Athyridida are given below in the introductions to the systematic descriptions of each suborder.

SUBORDER ATHYRIDIDINA

The shells of athyrididines display great external morphological variability. Commonly moderately to strongly rostrate and unequally biconvex, the shell may also be planoconvex (e.g., *Lochengia*) or concavo-convex (e.g., *Galeatathyris*). Shapes vary from more or less globose, almost equidimensional, with varied outline (subcircular, e.g., *Nucleospira;* elongate oval to rounded pentagonal, e.g., *Athyris;* subtriangular in *Janiceps;* rhomboidal in *Triathyris*), to very transverse, winged shapes (e.g., *Anathyris*) with also less transverse forms having strongly carinate folds on their opposed valves (e.g., *Plicathyris*).

Athyrididines have a variety of folding patterns. Alternate folding may be uniplicate, parasulcate, or rarely sulcate. Alternate folding in which a variably developed median plica in the dorsal valve is opposed to a sulcus in the ventral valve (uniplicate) may develop two small sulci lateral to the median fold of the dorsal valve (parasulcate), or forms with folding practically opposed, with a median sulcus in both valves bounded laterally by two folds (bilobate) that may be strongly carinate (metacarinate). The great diversity of the anterior commissures of these brachiopods, resulting from different hydrodynamic models, includes a type of folding (mixed folding) in addition to those previously described by Buckman (1907, 1918), Thomson (1927), and Williams and Rowell (1965b). Mixed folding (see Alvarez, 1990) is characterized by the presence of unequal folds that tend to be opposed in the middle and most lateral parts of the shell and to alternate in the intervening sectors. Shells with this type of folding tend to have median ventral and lateral dorsal folds that bifurcate. The bifurcated elements have variable development (Fig. 1001). Less common is the radial, ribbed ornamentation of the retzielloids and some athyridoids (athyrisinins, misoliins, and some athyridins); the fine, delayed costation progressively developed medially in *Cardiothyris* and *Triathyris,* and in the pradoiins; or the peculiar ornament of fine lines folded in a zig-zag, chevronlike pattern as in *Septathyris.*

One of the more obvious and, in some, even spectacular characteristics of athyridide shells is the development of varied growth

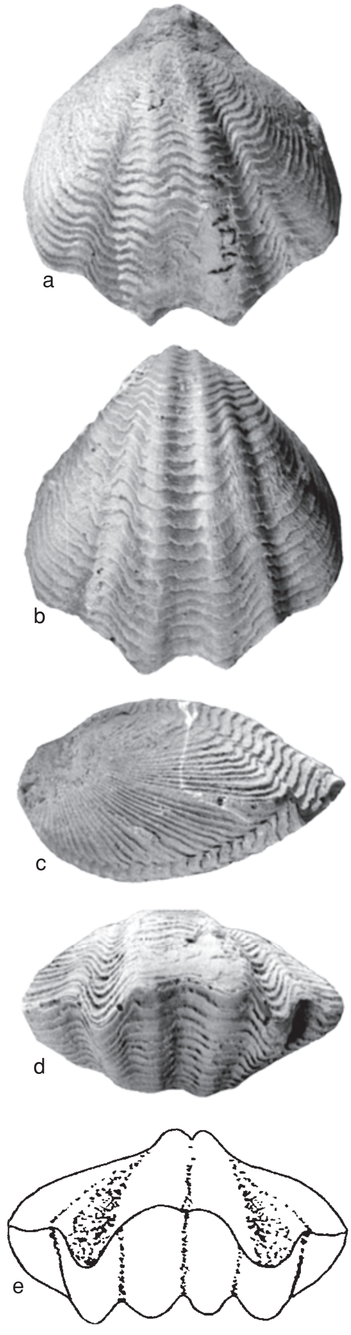


FIG. 1001. Mixed folding pattern in *Hexarhytis bonarensis* ALVAREZ; *a–e,* dorsal, ventral, lateral, anterior, and stylized anterior view, DPO 23921, ×2.5 (Alvarez, 1990).

lamellae (Fig. 1002–1003). The nature of these lamellae is a more significant character than, for example, folding and sulcation, which changed during ontogeny. The ornamentation present on the exteriors of most athyridide shells seems to have formed simply by regularly spaced concentric steps that are more or less strongly developed (e.g., Fig. 1002.6). In radial or longitudinal sections this ornamentation occurs as shelly extensions protruding from the surfaces of the valves at regular intervals and at different angles depending on the species (see ALVAREZ & BRUNTON, 1991). Commonly there are also differences in size, shape, and orientation between the lamellae in the dorsal and ventral valves (ALVAREZ, BRIME, & CURRY, 1987; ALVAREZ, 1990). In most Devonian genera (e.g., the plicathyridins) the lamellae are strongly recurved toward the surface of the valve (Fig. 1003.1, 1003.3) instead of being more or less flat tangents to the outer surface of the shell as happens in most meristelloids. In *Pachyplax,* the lamella are thick and overlap strongly so that the combination of lamellae and the entrapped sediment between them gives a rough, rugose external appearance to the shells. In any of the widely spaced growth lamellae of *Brimethyris* there are up to eight fine growth lines and a papillose microornamentation affecting both the primary layer and apparently most superficial secondary fibers (ALVAREZ, 1990, pl. 1,*2–5*). Some Late Devonian and Carboniferous genera developed long, delicate lamellae that are rarely preserved, with or without fine radiating striations (e.g., *Actinoconchus, Lamellosathyris*) or, as in *Cleiothyridina* and allied genera, the concentric shell lamellae project anteriorly and anterolaterally as flat, spinelike outgrowths, rectangular in section, that appear to be solid (Fig. 1004.1). In the long-ranging *Nucleospira,* both valves are ornamented with irregularly but commonly anteriorly concentrated growth lines and concentrically arranged fine spines of irregular diameter that project radially at high angles from the valve

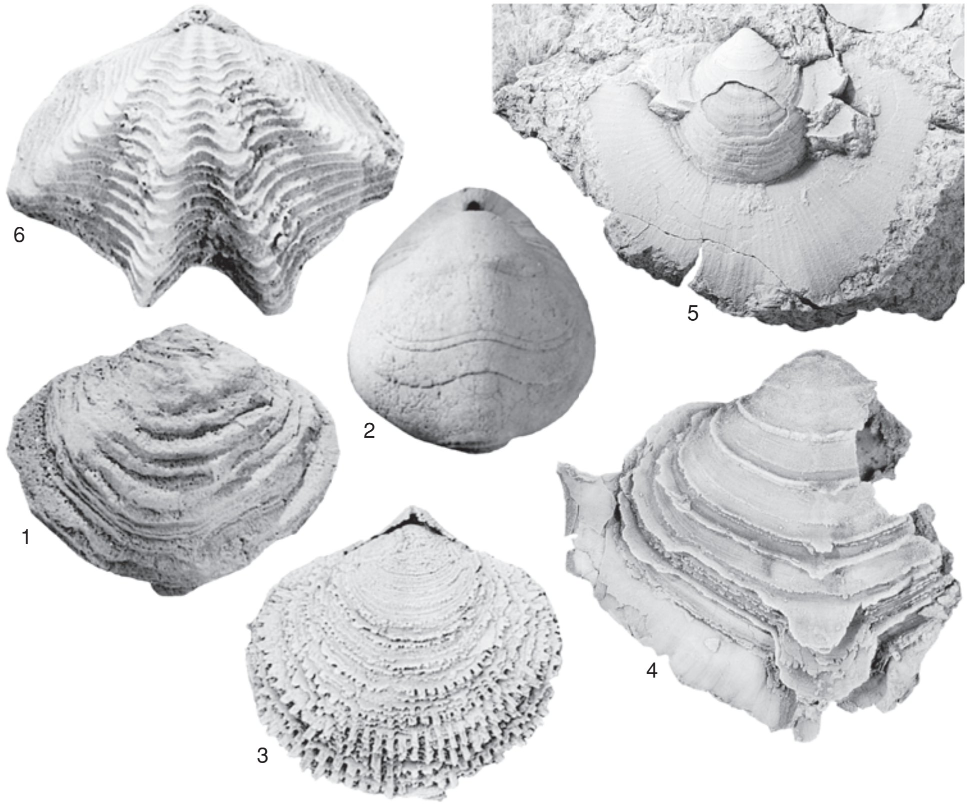


FIG. 1002. Athyridide growth lamellae; *1,* thick lamellae of *Pachyplax transversa* ALVAREZ & BRUNTON, DPO 18642, ×2.5 (Alvarez & Brunton, 1990a); *2,* flat lamellae on silicified specimen of *Spirigerella derbyi* WAAGEN, USNM 212887, ×2 (Grant, 1976; photograph courtesy of the late R. E. Grant); *3, Cleiothyridina fimbriata* (PHILLIPS); silicified specimen showing numerous, concentric, imbricated growth lamellae that project anteriorly as flat, spine-like outgrowths of rectangular section (these appear to be solid), BMNH BB 63452, ×3 (Brunton, 1984; photograph courtesy of C. H. C. Brunton); *4,* preserved marginal shelly flanges on silicified specimen of *Lamellosathyris lamellosa* (LÉVEILLÉ), BMNH BB 63398, ×2 (Brunton, 1984; photograph courtesy of C. H. C. Brunton); *5, Actinoconchus paradoxus* M´COY showing extensive lamellae near the commissure, BMNH BB B5392, ×1.5 (Brunton, 1980; photograph courtesy of C. H. C. Brunton); *6,* regularly spaced concentric lamellae of *Plicathyris ezquerrai* (DE VERNEUIL & D'ARCHIAC), EM 20232, ×3 (Alvarez, 1990).

surfaces (Fig. 1004.2). In some genera, as *Hexarhytis,* it is possible to recognize patches of radially disposed crenulations superimposed on the growth lamellae (see ALVAREZ, 1990, pl. 1,*1;* pl. 24,*19,21*). These are insufficiently developed to be spines but may be openings from which sensitive setae extended along the anterior margin of the mantle, similar to those present in specimens of recent species of *Terebratulina.* All these lamellae seem to have grown by successive outward transgression and regression of the mantle epithelium responsible for secretion of shell at the shell margin (see ALVAREZ, CURRY, & BRIME, 1985; ALVAREZ, BRIME, & CURRY, 1987; BRUNTON & ALVAREZ, 1989; ALVAREZ & BRUNTON, 1990b, 1991; BRUNTON, 1991). Such shells as the Carboniferous *Actinoconchus* or Devonian *Pachyplax* rapidly grew a pair of long lamellae at their valve margins. The lamellae at the edge of each valve grew parallel or subparallel to each other and temporarily formed the functional edges of the shell. Then mantle regression

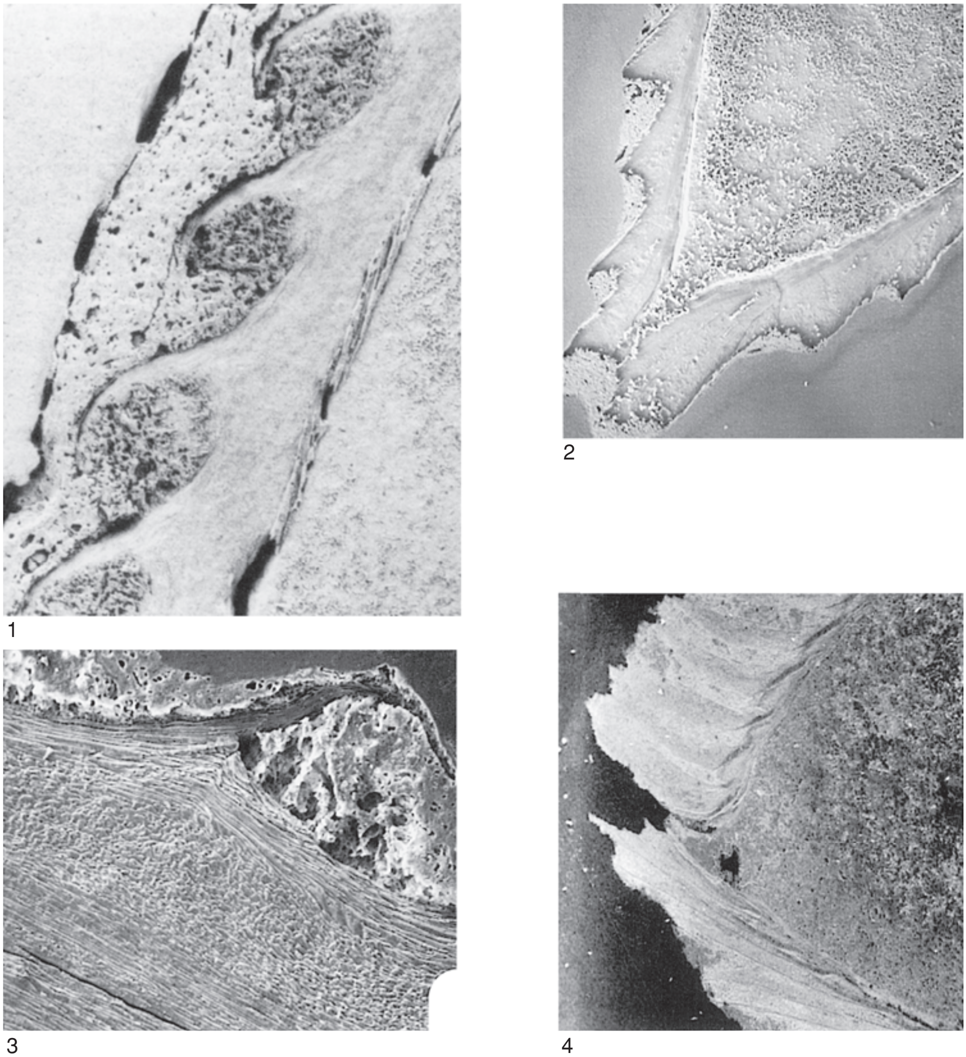
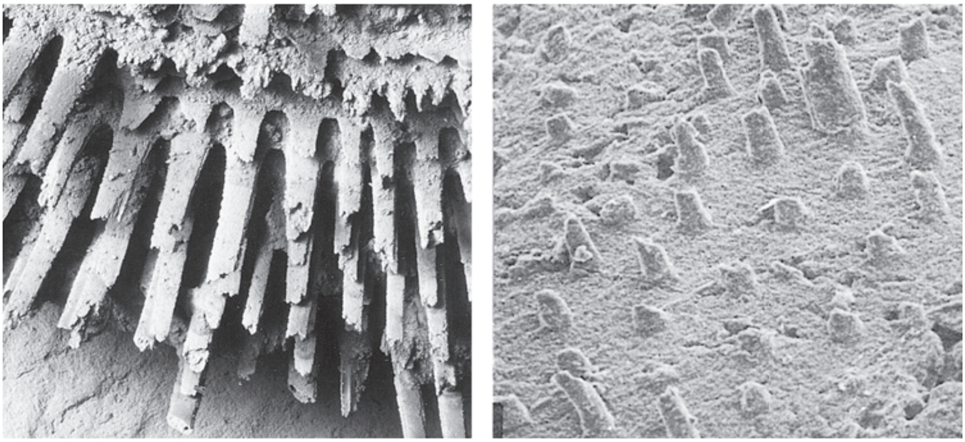


FIG. 1003. SEM photographs of longitudinal sections of athyridide shells showing size, shape, and disposition of growth lamellae; *1, Hexarhytis campomanesi* (DE VERNEUIL & D'ARCHIAC), DPO 16972, ×70 (Alvarez, Brime, & Curry, 1987); *2, Pachyplax elongata* ALVAREZ & BRUNTON, DPO 18740, ×15 (Alvarez & Brunton, 1990a); *3, Anathyris phalaena* (PHILLIPS), DPO 24484, ×166 (Alvarez, 1990); *4, Pachyplax transversa* ALVAREZ & BRUNTON, DPO 21160, ×19 (Alvarez & Brunton, 1990a).

took place, back to the true valve margin, which by this stage was left behind internally, well posterior to the margins of the lamellae (Fig. 1005.2). As forward growth was resumed between the pair of lamellae, the true valve edges grew obliquely toward each other for a short distance. This growth both increased the size of the valve and increased the depth of the mantle cavity, but at the same time it separated the inner surfaces of the lamellae so that space was left for the development of the next pair of lamellae. This development took place as a result of a change in direction of the growth of the mantle at a low angle away from the surfaces of the valves.



1 2

FIG. 1004. External spinose ornamentation present in *1, Cleiothyridina fimbriata* (PHILLIPS), detail of the anterior region of silicified dorsal valve showing concentric, imbricated, growth lamellae that project anteriorly as flat, spine-like outgrowths of rectangular section (these appear to be solid), BMNH BB 63452, SEM, ×12 (Alvarez, 1999b); *2, Nucleospira carlukensis* (DAVIDSON), detail of the anteromedial region of silicified ventral valve showing microspinous ornamentation, BMNH BB 61625, SEM, ×150 (Brunton, 1984; photograph courtesy of C. H. C. Brunton).

Posteriorly, the ventral valve has an area or palintrope, poorly delimited laterally by the umbonal ridges or not differentiated, usually containing a round pedicle foramen and triangular delthyrium. The opening is commonly obscured by the dorsal beak and usually laterally restricted by narrow deltidial plates that widen toward the base of the delthyrium and that may meet and interlock medially as in *Septathyris.* In *Anisactinella* the delthyrium is partially covered by a unique and irregularly triangular, flat or slightly curved, symphytium (the atypical pseudodeltidium of BENIGNI & FERLIGA, 1992), which bears no relationship to the foramen that, in this genus, occupies a supra-apical position (see BENIGNI & FERLIGA, 1992).

The ventral umbo of most athyrididines and retziidines has been partly destroyed by the expanding foramen, which commonly occupies a transapical, meso- to permesothyridid or more rarely epithyridid, position. Exceptionally the pedicle emerged between the apex of the ventral umbo and the hinge; subapical foramina with deltidial plates are present in the Silurian *Didymothyris* and young *Nucleospira,* while in mature *Nucleospira* a triangular, externally concave plate (deltidium) covers the delthyrium.

In most athyrididines, the beak of the ventral valve is divided internally into three unequal cavities by the dental plates, more or less parallel to the plane of symmetry. The wider central cavity is called the delthyrial cavity or pedicle chamber. The two lateral, narrower subtriangular cavities are the lateral apical cavities (Fig. 1005.1a). Between the dental plates, some didymothyridins have a peculiar structure, the pedicle support or pedicle fulcrum of RUBEL and MODZALEVSKAYA (1967) and MODZALEVSKAYA (1985), which consists of two curved plates formed of secondary-layer shell material deposited parallel to the dental plates. These curved plates divide the posterior portion of the delthyrial cavity into three parts, two laterally and a quite small one ventrally. They probably did not act as a real fulcrum for lifting but as a support for the pedicle. *Collarothyris,* an externally similar didymothyridin, instead has a dorsally convex delthyrial plate.

Pedicle collars, delthyrial plates, and other structures related to the pedicle are not easy to use as diagnostic characters because of

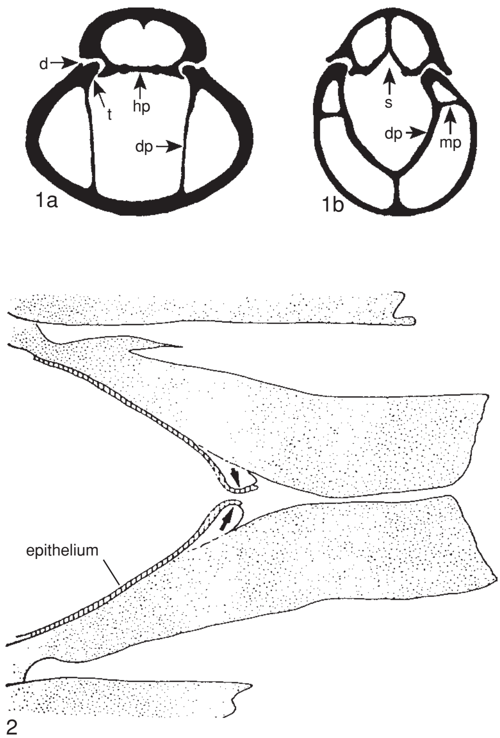


FIG. 1005. *1,* Enlarged drawings of transverse sections of *1a,* an athyridoid, ×3, and *1b,* a meristelloid, ×8, showing articulation and disposition of posteriorly placed structures: *d,* denticulum; *dp,* dental plates; *hp,* hinge plate; *mp,* mystrochial plates; *s,* septalium; *t,* tooth (new); *2,* stylized longitudinal section of anterior shell edge of *Pachyplax* showing bases of 2 pairs of most recently formed lamellae and true valve margins (*arrowed*) (adapted from Alvarez & Brunton, 1991, and Brunton, 1991).

their irregular and only sporadic calcification and preservation. Complete rings or pipelike structures similar to the ones developed in the retziidines do not occur in the athyrididines, but it seems clear that there was a trend toward greater complexity of ventral umbonal structures during Permian and Triassic times. Many specimens of Permian genera (*Spirigerella*) have a relatively small pedicle foramen bridged internally by a pair of plates that are analogous to the delthyrial plates of spiriferides. These plates slid past the dorsal beak as it entered the ventral valve during opening of the shell. They are conjunct in large adult specimens, disjunct in young adults, and incipient in juveniles. When conjunct, they cut off the foramen from the visceral chamber of the shell to leave the foramen as a mere recess, suggesting that the pedicle atrophied in adults. Triassic genera (*Tetractinella, Dioristella*) also possess more or less thick delthyrial plates that may be supported by a short septum as in *Clavigera.* Toward the apex of the beak, this plate contributes to the thickening of the cavity and may serve as a sessile pedicle collar, as in *Oxicolpella,* or it may be very complex, filling the delthyrial cavity almost completely, as in *Majkopella.* Such structures are not free in the manner of pedicle collars but fused laterally to the valve wall.

Commonly the dental plates support the hinge teeth, reinforce the umbonal region of the valve, and possibly act as places of attachment for the muscles. Their variability is closely related to that of the external morphology of the beak. In the athyrididines there is neither an angular difference nor a

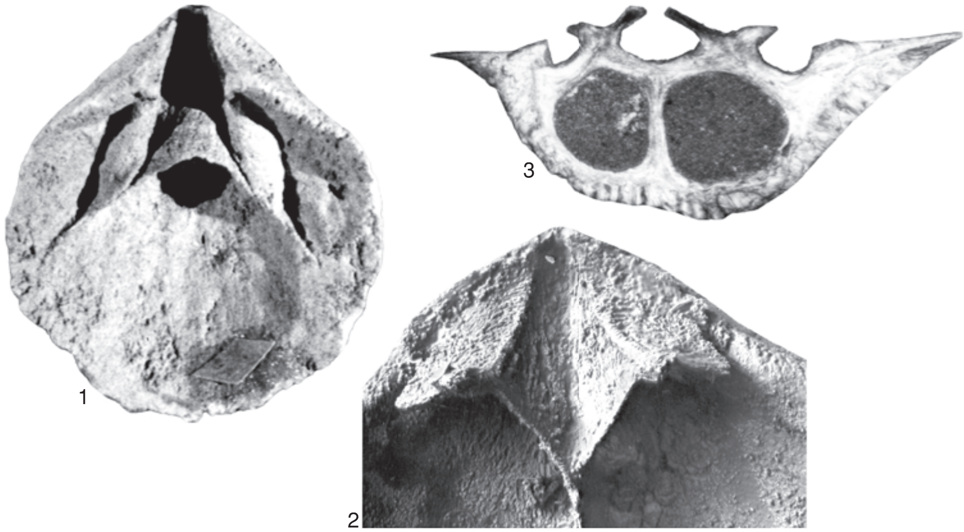


FIG. 1006. *1,* Ventral shoe-lifter in *Camarium typum* HALL, I1540, Hall collection, ×3 (Alvarez & Brime, 2000); *2,* septalium in *Meristella lata* (HALL), USNM 497416, SEM, ×10 (new); *3,* transverse section of *Retziella minor* (HAYASAKA), cardinalia, DPO F24241, ×10 (new).

clear groove separating the dental plate into components of a ventral adminiculum and dental flange, as commonly happens in the narrowly hinged spiriferides (BRUNTON, ALVAREZ, & MACKINNON, 1996, fig. 8), but these terms are helpful when describing, for example, the dental plates of some Triassic athyridoids (*Ochotathyris, Dioristella*) that are weakly developed anteroventrally (short adminicula) but strongly developed below the teeth (long dental flanges). The lateral apical cavities can be partly or completely filled by secondary shell material in adult specimens of some genera (*Meristella, Majkopella*). The posterior thickening observed in some specimens seems to have had a functional significance in relation to the acquisition of a more suitable orientation so that the center of gravity of the shell moved posteriorly to a position close to the point of attachment. As in other groups of articulated brachiopods, athyrididine dental plates can converge and fuse above the floor of the ventral valve in a spondylium, usually elevated above the floor by the septum duplex formed by coalescence of the dental plates. The spondylium resembles a deep, boat-shaped trough in the posterior part of the valve and becomes shallow and scoop shaped anteriorly where the dental plates terminate and only the base persists. In *Camarophorella* and some other genera, the spondylium may be supported not only by the median septum but also by more or less well-developed plates (mystrochial plates) that are confined to the umbonal region and extend anteriorly and laterally to the valve wall, nearly parallel to the plane of the lateral commissure (Fig. 1005.1b). Some genera, as *Camarium,* developed an arched platform (shoe-lifter) of secondary shell (with a chamber or cella beneath) that bore part of ventral muscle field (Fig. 1006.1).

A variably developed median septum is present in the ventral valve of some genera. In *Nucleospira* the medium septum is long, projecting from the umbonal cavity toward the anterior commissure. In some diplospirellins such as *Anisactinella quadriplecta,* the median septum is not elevated. At about one-third the total length of the valve, it thickens and stops (in some instances making a pronounced protrusion), branching into two elevated lateral septa and a small median septum. In others, as *Diplospirella wissmanni,* it appears initially as a thin ridge growing from a low, broad platform, subsequently becoming more massive and triangular in section (Benigni & Ferliga, 1990, 1992).

ARTICULATION

Athyridides normally have strong teeth and sockets. The hinge teeth are cyrtomatodont, commonly subrectangular to ovate in section. This type of dentition allows great flexibility in growth, remaining functional during ontogeny even in those athyridides that commonly have dorsal and ventral umbos very close together in their adult stages. In some genera, as in *Anisactinella,* teeth are massive, directed posteromedially, and supported by thick, poorly differentiated plates that seem to have grown from the anterior side of the symphytium in a posterolateral direction instead of posteroanteriorly, the common situation. The cyrtomatodont hinge teeth fit dental sockets of variable shape, narrow near the umbones and widening anterolaterally. They are bordered internally by normally prominent inner socket ridges and externally by less well-developed outer socket ridges. The shape of the dental sockets depends on the degree of development of the inner socket ridges, which usually rise ventrally and then curve laterally overhanging the socket. In some specimens the ventral end of the inner socket ridge fits against a groove or small cavity (crural fossette) in the inner part of the tooth, thus aiding articulation. In addition, the posterior edge of the cardinal area of the ventral valve (denticulum) is articulated with a socket present in the outer socket ridges of the dorsal valve (accessory socket). A small ridge on the outer socket ridge also inserts into the socket (denticular cavity) between the tooth and the posterior edge of the valve (Fig. 1005.1). The articulation described above is reinforced by the cardinalia and, in the more transverse forms, by the posterior edges of both valves that remained in contact during opening and closing movements. In most transverse forms (e.g., *Anathyris*) the palintrope is a morphological artifact allowing opening of the shell. The combined action of all these structures prevents lateral movement of one valve against the other.

CARDINALIA

In athyridides, as in other articulated groups, a wedge of shell, the outer hinge plate, is laid down between the inner socket ridge and the growth traces of the paired crura. Inner hinge plates, extending medially from the crural bases, commonly form a trough supported by the dorsal median septum that is Y-shaped in cross section. This is the usual form of a septalium (Fig. 1006.2). Less commonly the inner hinge plates fuse directly to the valve floor, forming a V-shape in cross section (sessile septalium; e.g., *Charionella*). The meristelloids characteristically have septalia of different types and shapes. A functional relationship between adjustor muscles and the inclined plates forming the sides of the septalium (inner hinge plates) is not clear in fossil groups; therefore the term crural plate is commonly used for these inclined plates (Brunton, Alvarez, & MacKinnon, 1996). A cruralium is present in some meristelloids (e.g., *Rowleyella*). The cruralium extends anteriorly much farther than a septalium, commonly well anterior of the distal ends of the sockets or to the origins of the crura. In some retziellids, as *Retziella,* paired plates extend ventromedially over shallow septalia from the outer hinge plates (Rong & others, 1994). These covering plates resemble posteriorly an incomplete connectivum (Havlíček, 1961), but evidence from serial sections (Fig. 1006.3) shows them to differ from the situation that occurs in most rhynchonellides (see discussion by Brunton, Alvarez, & MacKinnon, 1996).

In athyridoids the inner hinge plates extend medially from the crural bases, commonly parallel to the commissure (Fig. 1007). In hyattidinins they do not meet medially, but in all other athyridoids the inner hinge plates are well developed (although they may not be differentiated medianly), forming a hinge plate (Fig. 1007). When the crural bases do not form ridges on the surface of the hinge plates, it is difficult to differentiate outer and inner hinge plates, and a single plate (cardinal plate) extends between the inner socket ridges. In some diplospirellins (*Diplospirella*), the hinge plate is not parallel to the commissure but is steeply inclined posterodorsally, delimiting a triangular depression at the apex of the cardinalia (cardinal pit of BENIGNI & FERLIGA, 1990, p. 45 and fig. 4).

In many earlier athyridides, either the hinge plate or cardinal plate is perforated posteromedially by a hole connecting the beak chamber to its ventral surface. This dorsal foramen (Fig. 1007.1–1007.2), first described and figured by KING (1850), has been termed a visceral foramen by several authors (e.g., BEECHER, 1892, p. 147; HALL & CLARKE, 1894, p. 819; SCHUCHERT, 1897, p. 113) in the belief that it served as an anal opening. Other authors, however, considered that this foramen accommodated the dorsal ends of the diductor muscles (COOPER & GRANT, 1976a; ALVAREZ & BRUNTON, 1990b; BRUNTON, ALVAREZ, & MACKINNON, 1996). During the evolution of athyridides the diductor muscles probably migrated from the dorsal beak via the dorsal foramen to the hinge plates, as can be observed during the ontogeny of *Eohemithiris* (ALVAREZ & BRUNTON, 1990b; BRUNTON, ALVAREZ, & MACKINNON, 1996). In geologically younger taxa, the adult diductor muscles attached to the posterior region of the hinge plate where exaggerated shelly flanges (cardinal flanges) grew at the posterior ends of the inner socket ridges (Fig. 1007.3). The dorsal foramen shows signs of having been overgrown or filled by shell late in ontogeny. This suggests that the foramen may commonly have been a functional feature in adult athyridides in the geologically earliest stocks but was reduced to a nonfunctional canal that was subsequently infilled in most Late Paleozoic and Mesozoic species.

The detailed development and appearance of cardinal flanges among adults varies considerably within the athyridides, although in most they seem also to have aided articulation by overhanging the posterior ends of the sockets and in sealing the posterior valve margin by curving ventroposteriorly into the ventral beak cavity (Fig. 1007.3b). In some taxa, as *Anathyris, Composita,* and *Anisactinella* (DAGYS, 1974; ALVAREZ, 1990; BENIGNI & FERLIGA, 1992; BRUNTON, ALVAREZ, & MACKINNON, 1996), there are grooves on the lateral surfaces of the cardinal flanges fitting against different denticulum-like structures protruding from the ventral valve below the teeth. In some Triassic species of *Anisactinella,* a well-developed, subrectangular cardinal flange abuts the symphytium and seems to prevent excessive anterior opening of the shell (BENIGNI & FERLIGA, 1992). The main function of the cardinal flanges in many genera, however, was as the site of attachment for the diductor muscles. In Devonian genera (e.g., *Pachyplax*) and some species of *Composita*, these elevated flanges are confined posteriorly on the hinge plate and became serrated myophores. In others, diductor myophores spread over most of the ventral surface of a reduced but heavily thickened cardinal plate, as in some examples of *Lamellosathyris* (Fig. 1008.1) or Permian *Composita* (Fig. 1007.3c).

In general the athyridides display a phylogenetic trend from Devonian genera, with no cardinal flanges or only small ones and an open dorsal foramen, to late Paleozoic genera that lost the dorsal foramen and developed strong cardinal flanges that became united into a single structure (some with paired diductor pits, as in *Spirigerella;* Fig. 1008.2). Such a structure resembles the cardinal process (DAVIDSON, 1853b) of most orthides and strophomenides *s.l.,* but its

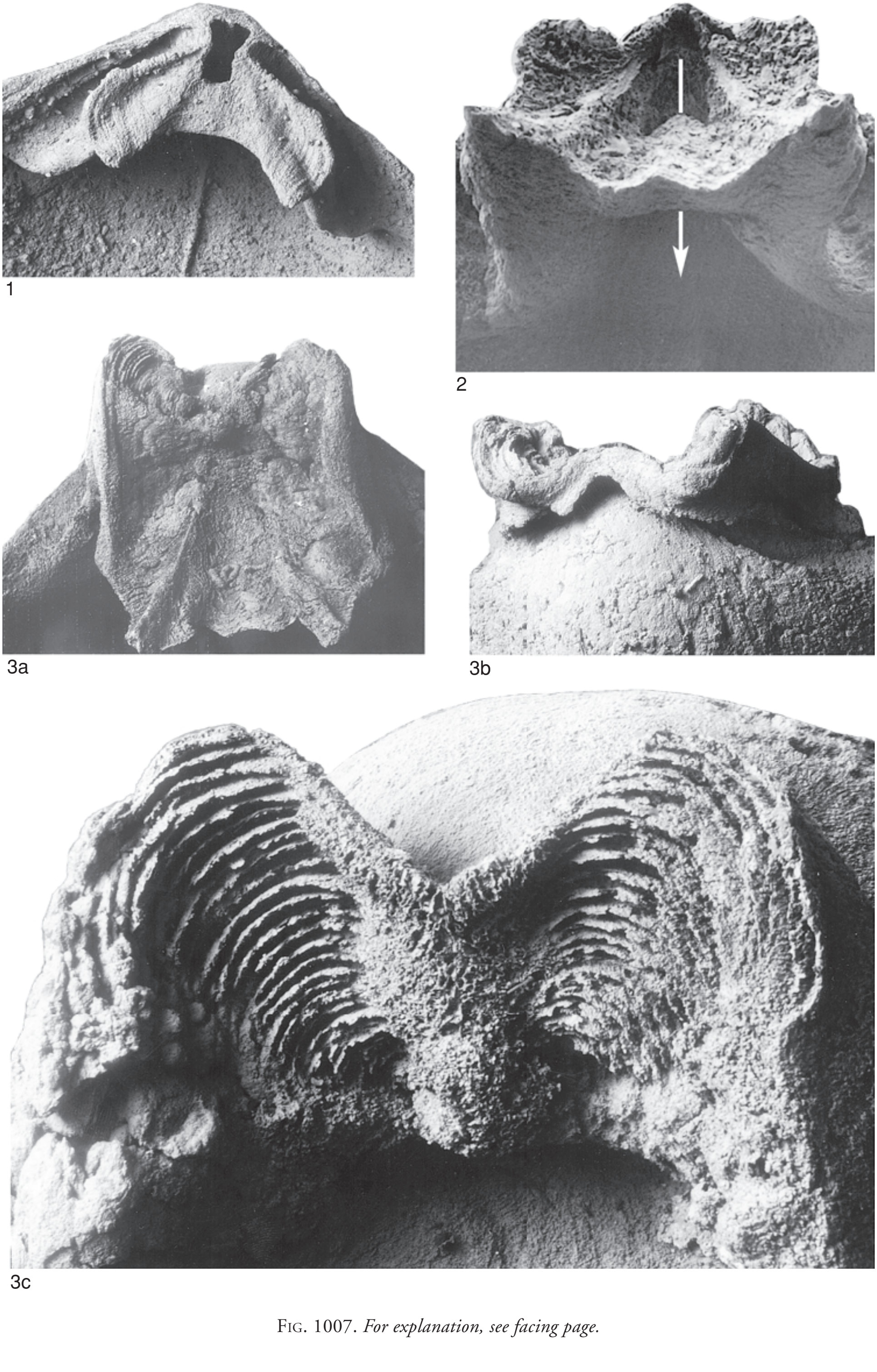


FIG. 1007. *For explanation, see facing page.*

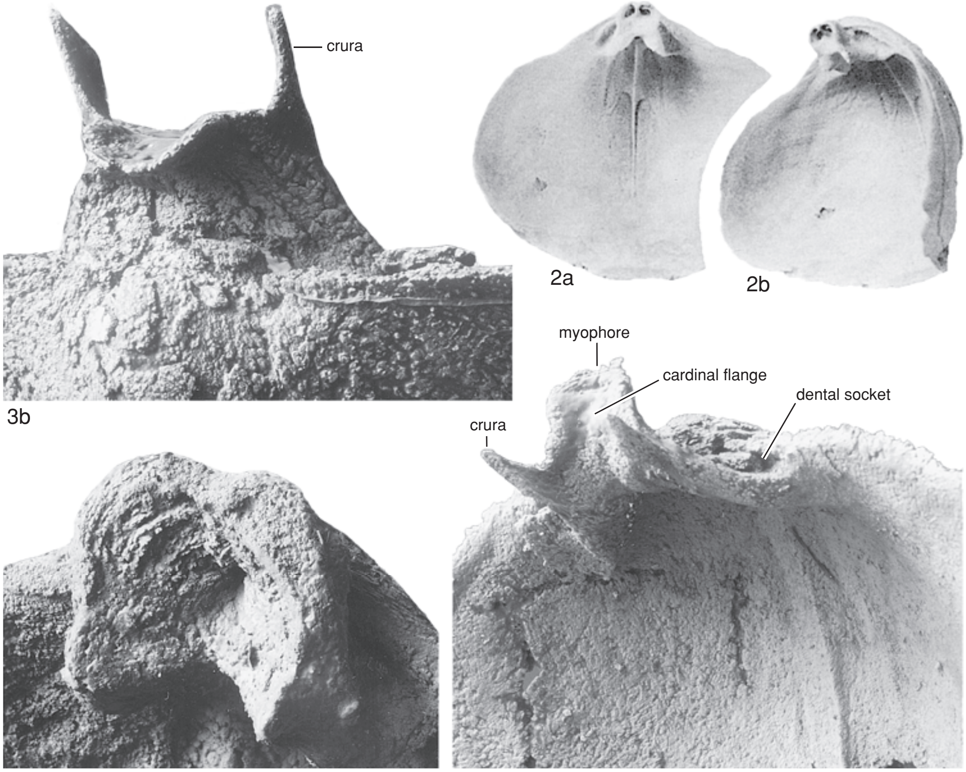


FIG. 1008. *1, Lamellosathyris lamellosa* (Léveillé), cardinalia in which diductor myophores spread over most of ventral surface of reduced, but heavily thickened, cardinal plate, BMNH BB 63399, SEM, ×10 (Brunton, Alvarez, & MacKinnon, 1996); *2a–b, Spirigerella derbyi* Waagen, dorsal interior straight on and tilted showing pair of diductor myophore pits surrounded by strong and unified cardinal flange, USNM 212890, ×2 (Grant, 1976; photographs courtesy of the late R. E. Grant); *3a–b, Nucleospira carlukensis* (Davidson); *3a,* anterolateral view of cardinalia showing dental sockets, crura, and myophore on distal, ventral face of united cardinal flanges, BMNH BB63459, SEM ×22; *3b,* oblique posterior view of same specimen showing crura and posteriorly recurved cardinal flange with no trace of myophores externally, BMNH BB63459, SEM, ×28 (Brunton, Alvarez, & MacKinnon, 1996).

FIG. 1007. SEM photographs showing different athyridoid cardinalia: *1, Cleiothyridina seriata* Grant, cardinalia with posteriorly enlarged dorsal foramen, USNM 486331, ×5.7 (Brunton, Alvarez, & MacKinnon, 1996); *2, Pachyplax gyralea* Alvarez & Brunton, cardinalia showing ventral opening to dorsal foramen (*arrowed*), general dorsal convexity of inner hinge plates with their slight ventral surface median ridge, and prominent shelly flanges posteriorly on inner socket ridges, DPO 25013, ×35 (Alvarez & Brunton, 1990a); *3a–c, Composita crassa* Cooper & Grant; *3a,* ventral view of cardinalia showing broken crura, crural bases, and cardinal flanges, united and elevated posteriorly on hinge plate, USNM 153009h, ×8 (Brunton, Alvarez, & MacKinnon, 1996); *3b,* posterior, slightly posterolateral view of dorsal umbo showing prominent cardinal flanges that, curving ventroposteriorly into ventral beak cavity, restrict delthyrial space and help with sealing of posterior shell margin, USNM 485991, ×8 (Brunton, Alvarez, & MacKinnon, 1996); *3c,* enlarged view of well-preserved serrated myophores on cardinal flange, USNM 485990, ×30 (Brunton, Alvarez, & MacKinnon, 1996).

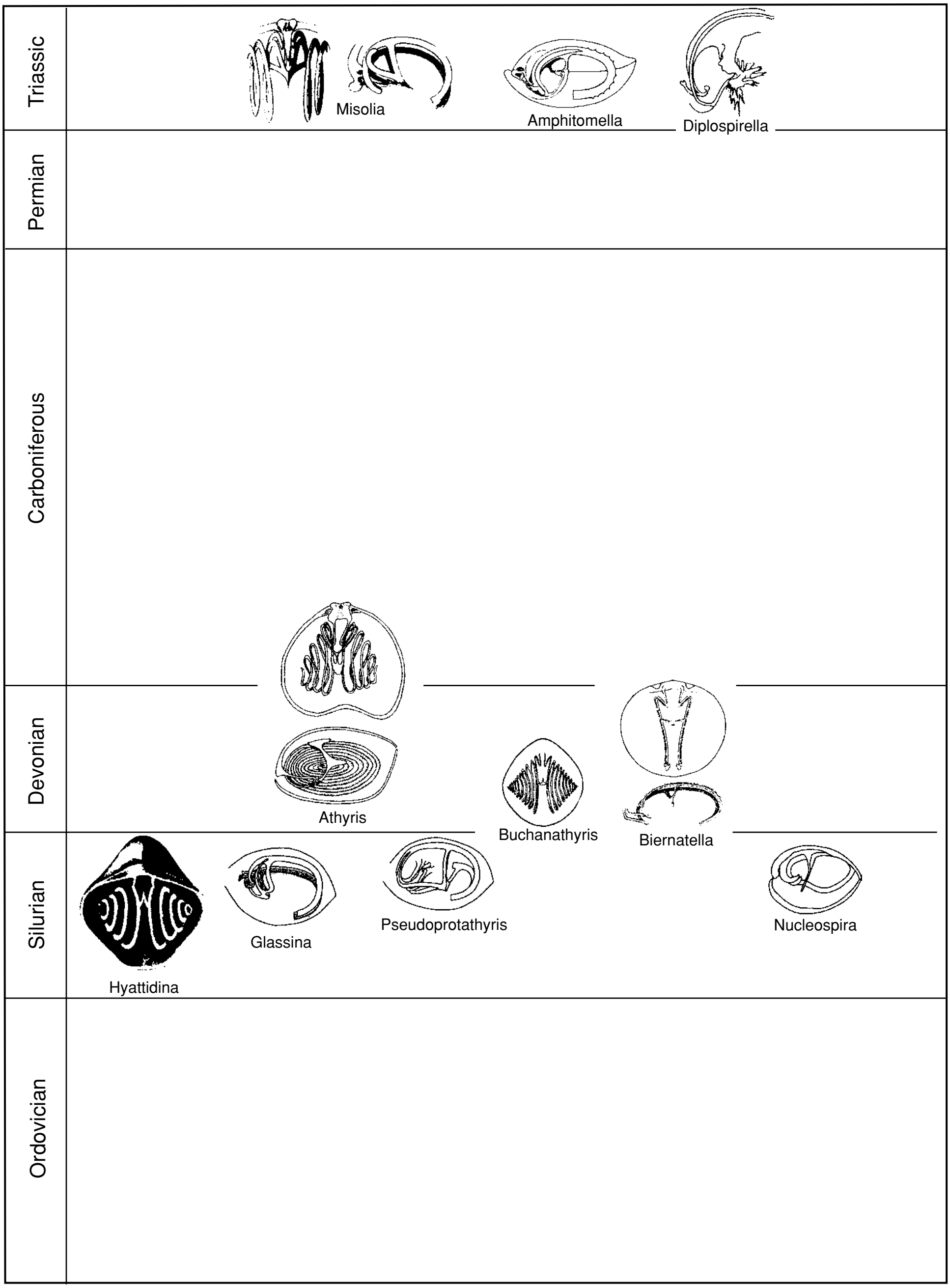


FIG. 1009. Main types of athyridoid and nucleospiroid brachidium (new).

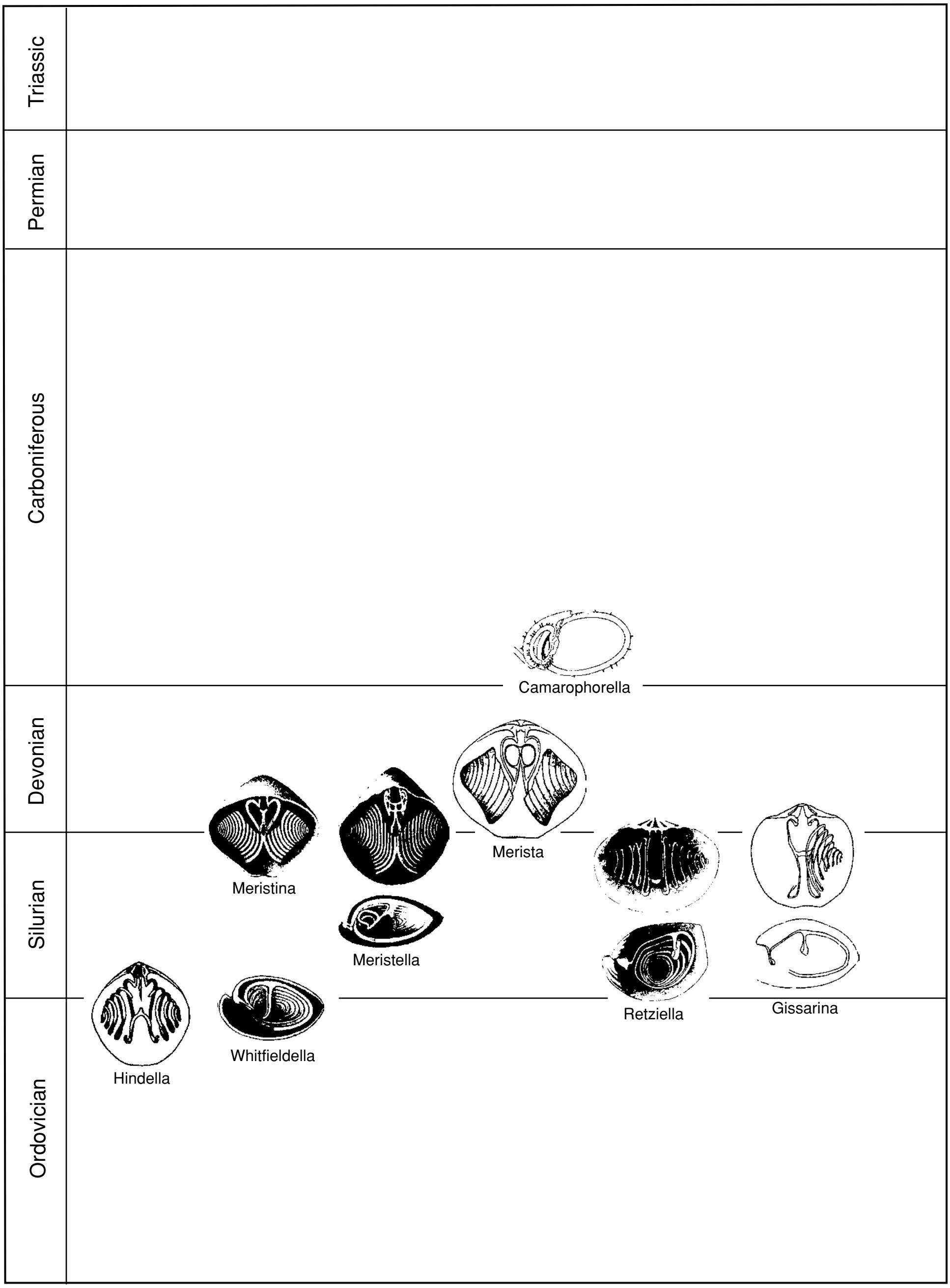


FIG. 1010. Main types of meristelloid and retzielloid brachidium (new).

position on the cardinal plate and its origin show it to be different (BRUNTON, ALVAREZ, & MACKINNON, 1996). In *Nucleospira* the juvenile seat of diductor muscle attachment was on small cardinal flanges posteriorly placed between the crural bases. By adulthood a fused and exaggerated cardinal flange had grown posteroventrally, carrying the myophores deeply into the ventral umbo (Fig. 1008.3). The posterior face of this structure is entirely smooth, indicating that it was covered by outer epithelium responsible for its secretion; it bears no trace of the myophore growth (BRUNTON, ALVAREZ, & MACKINNON, 1996, fig. 20a–b). In most athyridides, a relatively low ridge or myophragm of secondary shell developed medianly between paired muscle scars, typically separating adductor muscle scars. This structure contrasts with the meristelloid septum, a high, bladelike structure that may be seen in cross section as a strong inward flexure in the secondary layer fibers, normally originating close to the primary to secondary layer boundary.

Analyses, description, and comparison of such internal structures as dental plates, pedicle collars, cardinalia, brachidia, dorsal median septa, and the myophragm are especially difficult when reconstructing them from serial sections made from one (or at best a few) specimens. The myophragm and septum are easily misunderstood if compared from serial sections of specimens of different ages or convexity or if the sections were made at different angles in the different specimens.

BRACHIDIUM

The brachidium is a highly fragile structure feebly connected to the cardinalia and thus subject to postmortem mechanical damage from infilling with coarse sediment. It is easily obliterated during diagenesis. Silicified material presenting preserved brachidia is scarce. Consequently the brachidium and particularly the jugal structure have been clearly observed in only a few genera, and there is almost no information about growth or intraspecific variation. The configuration of this important structure is known for fewer than 50 percent of the genera commonly considered as athyridides. Until their jugal structure is determined, a confident decision concerning the relationship between genera and suprageneric taxa cannot be made, and remains speculative.

A pair of small calcareous supports, the crura, commonly extend ventrally or anteroventrally from the anterior edge of the cardinal plate, parallel to or converging slightly toward the plane of symmetry. After some distance, the crura give rise to the primary lamellae of the brachidium. In athyrididines and retziidines, the umbonal blades of the spiralia curve posteriorly, passing close to the sockets or inner socket ridges, and then curve toward the front, parallel with the plane of symmetry. They thus differ from spiriferides and spiriferinides in which the primary lamellae of the spiralia are direct prolongations of crura. The primary lamellae of atrypides typically curve laterally from the crura parallel with the commissural plane. It is reasonable to assume that the umbonal blades spring from the crura (see discussion by ALVAREZ, 1999a), but forms in which the brachidium is discontinuous with the crura have been recorded among Paleozoic Athyridida (COPPER, 1986a, 1986b; COPPER in COPPER & GOURVENNEC, 1996) and Triassic species (BENIGNI & FERLIGA, 1990).

Two different interpretations of the growth of spiralia have been proposed by SAMTLEBEN (1972) and MACKINNON (1971, 1974). In the athyridides, secondary fibers seem to have been secreted only on the basal side of the spire. The opposite side (the one facing the apex of the spiral cone or apical side) does not bear secondary layer mosaic. This single-sided growth pattern is quite distinct from the double-sided growth pattern of atrypides and spiriferides (MACKINNON, 1974, 1991). The primary lamellae continue in a helical fashion as a set of spires, whose number varies depending on the size and

TABLE 18. States of 37 characters used in cladistic analyses (Fig. 1011) of the order Athyridida (new).

1. size: small (0); moderate (1); large (2); very large (3).
2. lateral profile: biconvex (0); plano or concavoconvex (1).
3. radial ornament: smooth (0); plica (1); ribs (2); fine lines (3); delayed costation (4).
4. spines: absent (0); rounded (1); tabular (2); hollow (3); fimbriae (4).
5. growth lines: absent (0); weak (1); strong (2).
6. frills: absent (0); short (1); long (2).
7. fold and sulcus: absent (0); weak (1); strong (2); fold both valves (3); sulcus both valves (4).
8. adult folding: alternate (0); opposite (1); mixed (2).
9. palintrope: reduced (0); moderate (1); extensive (2).
10. palintrope orientation: catacline-apsacline (0); apsacline (1); apsacline-orthocline (2); orthocline (3).
11. hinge line: strophic (0); almost strophic (1); astrophic (2).
12. hinge line width: short (0); medium (1); long (= greatest shell width) (2).
13. pedicle opening: hypothyridid (0); meso-permesothyridid (1); permeso-epithyridid (2); epithyridid (3).
14. delthyrium: open (0); partially covered (1); completely covered (2).
15. pedicle supports: absent (0); pedicle collar (1); delthyrial plate (2).
16. dental plates: absent (0); short (1); medium (2); long, not extending as ridges anteriorly along muscle scars (3); long extending (4); indistinct (5).
17. mystrochial plates: absent (0); present (1).
18. ventral shoe-lifter: absent (0); present (1).
19. spondylial structure: absent (0); present (1).
20. ventral median septum: absent (0); short (1); long, supporting spondylium (2); long, not related to spondylium (3).
21. ventral muscle field: deeply impressed (0); moderately (1); weakly (2).
22. cardinal plate: absent (0); without inner hinge plate (1); disjunct (2); apically perforate (3); not perforate and thick (4); not perforate, inner hinge plates short, supported by high septum (5); not perforate, inner hinge plates very short or absent, low dorsal median septum or myophragm present (6).
23. cardinal process: absent (0); moderate (1); strong (2).
24. myophragm: absent (0); present (1).
25. dorsal median septum: absent (0); short, moderately high (1); short, very high (2); long, moderately high (3); long, very high (4).
26. septalium: absent (0); deep, narrow, and partially covered (1); shallow and partially covered (2); deep, narrow, and uncovered (3); shallow and uncovered (4); wide and uncovered (5).
27. cruralium: absent (0); present (1).
28. dorsal shoe-lifter: absent (0); present (1).
29. brachidium: absent (0); present, tips directed laterally (1); ventrally (2).
30. primary lamellae: absent (0); curving posterodorsally from crura (1); curving laterally from crura (2).
31. jugum: absent (0); present between spiral cones (1).
32. lateral branches of jugum: absent (0); vertical (1); inclined anteriorly (2); posteriorly (3); strong posteriorly (4); almost parallel to commissural plane (5).
33. jugal saddle: absent (0); directed anteriorly (1); directed posteriorly (2).
34. jugal stem: absent (0); short (1); long (2).
35. arms of the jugum: absent (0); present (1).
36. accessory jugal lamellae: absent (0); free and short (1); reunite with stem (2); reunite with lateral branches of jugum (3); free, ending near lateral branches of jugum (4); free, intercalated with spiralia to apex (5); secondarily connected with spiralia (6).
37. shell structure: impunctate (0); punctate (1).

morphology of the specimens, to produce spiral cones with the apex directed laterally, anterolaterally, or ventrally (in koninckinidines). The anterior half of the more basal whorls is much longer than the posterior half; apical whorls are more nearly circular or oval. Variation of shell convexity does not appear to have altered significantly the direction of the axes of the cone. The number of whorls in a spiral cone may vary with each genus and, depending on the size of the individuals, also with different species of one

TABLE 19. Character-state matrix used in PAUP analysis (Fig. 1011) of characters as listed in Table 18. 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
Ancistrorhynchidae	1	0	2	0	0	0	1	0	0	2	2	0	0	0	0	2	0	0	0
Athyridinae	2	0	0	0	2	1	1	0	0	1	2	0	1	0	0	2	0	0	0
Athyrisininae	2	0	2	0	2	2	2	0	0	2	2	1	1	0	0	2	0	0	0
Camarophorellinae	1	0	0	0	1	0	0	1	0	3	2	0	1	0	0	3	1	0	1
Clavigerinae	3	0	1	0	1	1	4	1	2	3	0	2	2	0	0	2	0	0	0
Cleiothyridininae	2	0	0	2	2	2	1	0	0	2	2	0	1	0	0	1	0	0	0
Comelicaniinae	3	0	1	0	1	1	1	0	1	2	1	2	0	0	0	1	0	0	0
Didymothyridinae	1	0	0	0	1	0	1	0	0	2	2	0	9	9	9	1	0	0	0
Diplospirellinae	0	0	0	0	1	0	0	1	0	3	2	0	2	0	0	1	0	0	0
Helenathyridinae	0	0	0	4	1	1	0	1	0	2	2	0	9	9	0	1	0	0	0
Hungarispirinae	0	0	1	0	1	0	4	1	2	3	1	2	2	2	0	0	0	0	0
Hustediinae	1	0	1	0	1	0	1	0	1	3	1	1	1	2	1	0	0	0	0
Hyattidinidae	1	0	0	0	1	9	2	0	0	2	2	0	9	0	0	1	0	0	0
Koninckinoidea	1	1	0	0	0	0	1	0	0	2	0	2	9	9	0	2	0	0	0
Lochengiinae	3	0	0	0	2	1	0	1	0	3	2	1	1	0	0	0	0	0	0
Meristellinae	2	0	0	0	1	0	1	0	0	2	2	0	1	1	0	5	0	0	0
Meristinae	2	0	0	0	1	0	1	0	0	2	2	0	1	0	0	4	1	1	0
Misoliinae	2	0	2	0	1	0	0	1	0	3	2	0	2	9	0	1	0	0	0
Mongolospiroidea	1	0	0	0	0	0	0	1	0	3	2	0	1	2	0	1	0	0	0
Neoretziinae	2	0	1	0	1	0	9	9	1	3	1	1	2	2	1	0	0	0	0
Nucleospiroidea	1	0	0	1	1	0	1	0	0	1	1	1	0	2	2	0	0	0	0
Ochotathyridinae	3	0	0	0	1	0	1	0	0	2	2	0	2	0	2	5	0	0	0
Parazygidae	1	0	2	3	2	1	1	0	0	1	2	1	1	2	1	2	0	0	0
Plectospirinae	0	0	1	0	1	0	1	0	1	2	1	1	1	2	0	0	0	0	0
Plicathyridinae	2	0	1	0	2	2	2	2	1	3	1	1	1	0	0	2	0	0	0
Pradoiinae	2	0	4	1	1	9	4	1	1	3	2	0	1	0	0	2	0	0	0
Retzielloidea	1	0	2	0	1	0	1	0	1	2	2	0	1	0	0	1	0	0	0
Retziidae	2	0	2	0	1	0	1	0	1	2	2	0	2	2	1	0	0	0	0
Rhynchospirinidae	1	0	2	0	2	0	1	0	0	1	2	1	1	2	9	9	0	0	0
Rowleyellinae	0	0	0	0	1	0	0	1	0	3	2	0	1	0	0	3	1	0	1
Septathyridinae	2	0	3	0	1	0	2	0	0	2	2	1	1	2	0	3	0	0	0
Spirigerellinae	2	0	0	0	1	1	1	0	0	2	2	0	1	0	0	2	0	0	0
Tetractinellinae	1	0	1	0	2	1	1	1	1	3	1	1	2	0	2	2	0	0	0
Triathyridinae	2	0	3	0	1	0	3	1	0	2	2	0	3	1	0	1	0	0	0
Trigonirhynchiidae	1	0	2	0	0	0	1	0	0	2	2	0	0	1	0	2	0	0	0
Whitfieldellinae	2	0	0	0	1	0	0	1	0	2	2	0	1	0	0	1	0	0	0
Xenosariinae	1	0	0	0	1	0	4	1	0	2	1	0	0	0	0	0	0	0	0

genus. This variation is small, however, and not useful taxonomically.

There is no apparent evolutionary trend toward an increase or decrease of spiral lamellae in the cones. A relationship between size, shape, and disposition of brachidium whorls, folds, and anterior projections of the shell was noted for several genera, as well as a relationship between shape, size, and jugal arch; the location of the median folds of the shell; and the disposition of the anterior commissure (ALVAREZ, 1990, fig. 154–156, 159; BENIGNI & FERLIGA, 1992).

Near the middle or in the posterior third of the primary lamella on the ventral edge is a jugal process (the lateral branch of the jugum), that projects anteriorly, anteroventrally, ventrally, or more rarely posteriorly until it joins the lateral branch of the jugum from the opposed spiral cone to form the jugal arch. This arch can be acute, as in most meristelloids, or rounded (commonly in athyridoids). The lateral branches may arise near the middle of the dorsal part of the primary lamellae (which is the approximate midpoint of the dorsal valve) or posterior or

TABLE 19. *(Continued).*

Character no.	20	21	22	23	24	25	26	27	28	29	30	31	22	33	34	35	36	37
Ancistrorhynchidae	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Athyridinae	0	2	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Athyrisininae	0	2	3	9	9	0	0	0	0	1	1	1	2	1	2	1	1	0
Camarophorellinae	2	9	0	0	0	4	4	0	1	1	1	1	2	9	2	1	3	0
Clavigerinae	1	0	4	2	1	0	0	0	0	1	1	1	2	9	2	1	1	0
Cleiothyridininae	0	1	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Comelicaniinae	0	2	3	2	0	0	0	0	0	1	1	1	9	9	9	9	4	0
Didymothyridinae	0	2	3	0	1	0	0	0	0	1	1	1	9	1	2	1	4	0
Diplospirellinae	0	2	4	2	1	0	0	0	0	1	1	1	2	0	2	1	5	0
Helenathyridinae	0	2	3	0	0	0	0	0	0	1	1	1	2	9	2	1	5	0
Hungarispirinae	0	2	6	2	0	4	0	0	0	1	1	1	0	0	2	1	5	1
Hustediinae	0	2	6	2	0	1	0	0	0	1	1	1	2	0	2	0	0	1
Hyattidinidae	0	2	2	9	0	0	0	0	0	1	1	1	9	0	0	0	0	0
Koninckinoidea	0	2	0	9	0	0	0	0	0	2	2	1	5	0	9	1	5	0
Lochengiinae	0	2	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Meristellinae	0	0	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Meristinae	0	9	0	0	0	4	4	0	0	1	1	1	3	0	2	1	3	0
Misoliinae	0	2	4	2	1	0	0	0	0	1	1	1	2	0	9	9	4	0
Mongolospiroidea	0	9	9	9	0	4	0	0	0	1	1	1	2	0	0	0	0	1
Neoretziinae	0	2	6	2	0	4	0	0	0	1	1	1	2	0	2	1	6	1
Nucleospiroidea	3	2	0	2	1	0	0	0	0	1	1	1	1	0	2	0	0	0
Ochotathyridinae	0	2	4	2	1	0	0	0	0	1	1	1	2	1	2	1	4	0
Parazygidae	0	2	5	1	1	0	0	0	0	1	1	1	2	2	0	0	0	1
Plectospirinae	0	2	6	9	0	3	0	0	0	1	1	1	1	0	2	0	0	1
Plicathyridinae	0	2	3	1	1	0	0	0	0	1	1	1	2	1	2	1	4	0
Pradoiinae	0	2	3	1	1	0	0	0	0	1	1	1	2	1	2	1	1	0
Retzielloidea	0	2	0	0	0	3	2	0	0	1	1	1	1	9	0	0	0	0
Retziidae	0	2	6	2	0	0	0	0	0	1	1	1	2	0	2	1	0	1
Rhynchospirinidae	0	2	5	1	0	1	0	0	0	1	1	1	1	2	0	0	0	1
Rowleyellinae	2	9	0	0	0	4	5	1	1	9	9	9	9	9	9	9	9	0
Septathyridinae	0	2	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Spirigerellinae	0	2	3	2	0	0	0	0	0	1	1	1	1	1	2	1	4	0
Tetractinellinae	0	2	4	2	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Triathyridinae	0	2	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Trigonirhynchiidae	0	2	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0
Whitfieldellinae	0	2	0	0	0	2	1	0	0	1	1	1	1	0	1	0	0	0
Xenosariinae	0	2	3	0	0	0	0	0	0	1	1	1	9	9	9	9	9	0

anterior to it but are always parallel to the plane of symmetry. Lateral branches may be a straight rod or ribbon that is smooth or spiny laterally, more or less twisted, or even folded back and forked dorsally. In the plicathyridins, the lateral branches of the jugum arise almost perpendicular to the primary lamellae and project ventrally for a short distance, up to a point at which they curve abruptly laterally or anterolaterally; they then project anteroventrally at a low angle until they join as a jugal arch (ALVAREZ, 1976, 1990). In some diplospirellins (*Anisactinella*), the lateral branches of the jugum are very short or absent, fusing with the thickened primary lamellae ventrally, which curl up toward the plane of symmetry until they coalesce in a massive jugum (BENIGNI & FERLIGA, 1992). Although the spiralium and jugum are continuous structures that are difficult to delineate as separate entities or with possible different functions of their own, we use such terms as primary lamella, umbonal blade, lateral branch, saddle, arch, and stem since we consider them useful in defining some morphological areas.

TABLE 20. Synapomorphy scheme for internal nodes of cladogram shown in Figure 1011 (new).

Node	Character states		
1	31:1		
2	29:1	30:1	
3	25:2		
4	26:1		
5	26:2		
6	26:4		
7	17:1	36:3	
8	19:1	20:2	28:1
10	3:3		
11	22:2		
12	22:3		
23	22:4		
28	37:1		
29	22:5		
31	22:6		

In the athyridides and retziidines the jugum is placed between the spiral cones, not below them (near the dorsal interior), and consists of a single complete structure that connects both spiralial cones instead of acting as a lever for movement of the spiralium as suggested by COPPER (1967b) for the jugal processes of atrypid genera. The jugal arch may project anteriorly as a more or less well-developed saddle of variable shape and size, sometimes with a spinous anterior edge. In some genera (diplospirellins) it is thickened by variously developed apophyses directed ventrally, laterally, anteriorly, or dorsally, which commonly have long, thin spines. Less frequently, the jugal arch has a miniature saddle directed posteriorly from the posterior extremity of which a little spiniform process extends straight backward (BEECHER & CLARKE, 1889). This occurs in early meristelloids (*Hindella, Whitfieldella*) and some athyridoids (*Buchanathyris, Johnsonathyris*). Rarely, the jugum takes the form of a backwardly inclined cross with its upper tips curved outward without a spiniform process or saddle (*Glassina*), or the jugum rests on a high dorsal median septum (*Camarophorella*). The posterior end of the jugal arch usually extends as a calcareous appendix (jugal stem) that may be spinose, protruding straight, or elbow shaped and directed posteriorly, posteroventrally, or ventrally finally reaching a position close to the crural ends (some *Hindella, Nucleospira*). A median septum may be present on the saddle, extending backward as far as the jugal stem in *Spirigerella.* The jugal stem may bifurcate distally, giving rise to two short stubs, jugal arms (*Meristina*) that may extend as accessory jugal lamellae that may rejoin the stem (*Meristella*) or the lateral branches of the jugum (*Merista*). In most athyridids, accessory jugal lamellae diverge and curve into a more or less complete loop or half circle that is parallel to that of the primary lamellae and lies between them and the secondary lamellae (although always closer to the former) and ending posteriorly or near the origin of the lateral branches of the jugum. In a few genera (*Pseudoprotathyris, Missolia*) the accessory jugal lamellae extend posterodorsally directly from the jugum or anteriorly pointed jugal saddle. The accessory lamellae may extend, intercoiling with primary lamellae (diplospirellins, helenathyridins). When composed of two lamellae, the primary (principal) lamella is commonly larger, and the accessory lamellae are smaller and more slender. Both primary and accessory lamellae may have long, thin fimbriae distributed along their external edges (Fig. 1009–1010).

In groups such as the athyridids with few external characters with many variants and with quite complex and at the same time poorly known interiors, it is not easy to envisage phyletic lineages. Phylogenetic relationships among athyridides *s.l.* were analyzed using outgroup methods of polarity determination. Information was compiled on 37 morphological characters of skeletal anatomy well displayed in the athyridides *s.l.,* including valve form and ornament, hinge region, and dorsal and ventral valve interior, especially the cardinalia and spiralium and shell structure (see Tables 18 and 19). Except for those related to the

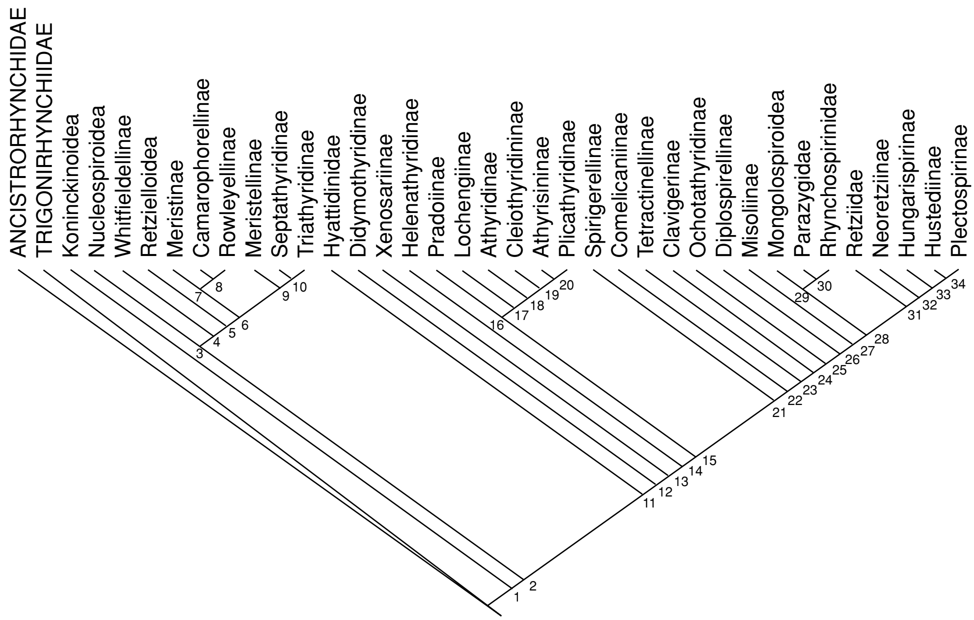


FIG. 1011. Second of the three equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 20; see also Table 18–19 (new).

external ornamentation (the cardinalia and the character of the shell substance, punctate or not), all other characters were equally weighted. Four characters (numbers 3, 5, 6, and 25) were weighted three times greater than the others; three characters (numbers 22, 23, and 26) five times greater; and the character (punctate or impunctate) of the shell structure (number 37) 13 times. The character numbers 6 (frills), 22 (cardinal plate), 23 (cardinal process), and 26 (septalium) in Table 18 were ordered. None was constrained to be irreversible. Ordovician rhynchonellides, commonly considered as ancestral to athyridides (e.g., IVANOVA, 1967; RUDWICK, 1970; GRUNT, 1989; ALVAREZ & CARLSON, 1998; ALVAREZ, RONG, & BOUCOT, 1998), were specified as the outgroup. The analysis yielded three equally most-parsimonious cladograms, each of length 367 and consistency index of 0.488 (0.484 excluding uninformative characters). The cladogram was rooted at an internal node with a basal polychotomy. Agreement between the stratigraphical first appearance of athyridid subfamilies and their cladistic rank was quite good except for the koninckinoids, suggesting that both outgroup and traditional paleontological methods indicate a similar direction of character polarity in the evolution of the group (Fig. 1011–1012). In the fifty percent majority-rule consensus cladogram, all nodes are supported by one hundred percent of the cladograms. Synapomorphies for internal nodes of the cladogram (Fig. 1011) are shown in Table 20. The topology of the consensus diagram is almost identical to cladogram two (Fig. 1011). The koninckinoids appear at the base of the cladogram. Typically they have a plano- or concavoconvex lateral profile, the tips of the spiralia are directed dorsomedially, and the primary lamella of the spiralium (umbonal blades) curves laterally from the crura. The nucleospiroids are smooth but have fine solid spines that cover the entire shell (Fig. 1004.2). The nucleospiroids appear at the base of two sister groups: the Meristelloidea,

	Meristelloidea	Meristellidae Triathyrididae Meristidae
Athyrididina	Athyridoidea	Hyattidinidae Athyrididae Diplospirellidae
	Nucleospiroidea	Nucleospiridae
	Retzielloidea	Retziellidae
	Retzioidea	Retziidae Neoretziidae
Retziidina	Rhynchospirinoidea	Rhynchospirinidae Parazygidae
	Mongolospiroidea	Mongolospiridae
Koninckinidina	Koninckinoidea	Koninckinidae

FIG. 1012. Chronostratigraphic range of athyridid suprageneric taxa (new).

characterized by inner hinge plates forming a septalium, and the Athyridoidea, characterized by horizontal inner hinge plates, forming a hinge plate (Fig. 1005.1; Fig. 1006.2; Fig. 1007; Fig. 1008.1–1008.2). The retzielloids, plicate or costate rhynchonelliform athyrididines *s.l.,* cluster with the meristelloids, partially due to their short and slightly covered septalium (Fig. 1006.3). The Whitfieldellinae are at the base of the meristelloids and the meristids appear as their most derived group. *Hyattidina* appears ancestral to the athyridoids, and the Spirigerellinae and the Comelicaniinae occur at the base of the diplospirellids, athyridids with derived characters as the possession of an imperforate cardinal plate and well- to strongly developed cardinal flanges (Fig. 1007.3; Fig. 1008.1–1008.2). The athyrisinids cluster within the athyridids. Finally, the retziidines appear at the end of the cladogram as the most derived group.

The classification here proposed is based on a mix of external and internal characters that persisted during unbroken lineages. It is hierarchical, so characters are mentioned at their first appearance and may not be repeated at lower taxon levels. Thus, several taxon levels have to be read to gain the most complete description of a subfamily or genus. More detailed analyses of the phylogenetic relationships among higher taxa of the athyridides and spire-bearing brachiopods in general was done by ALVAREZ and CARLSON (1998) and ALVAREZ, RONG, and BOUCOT (1998).

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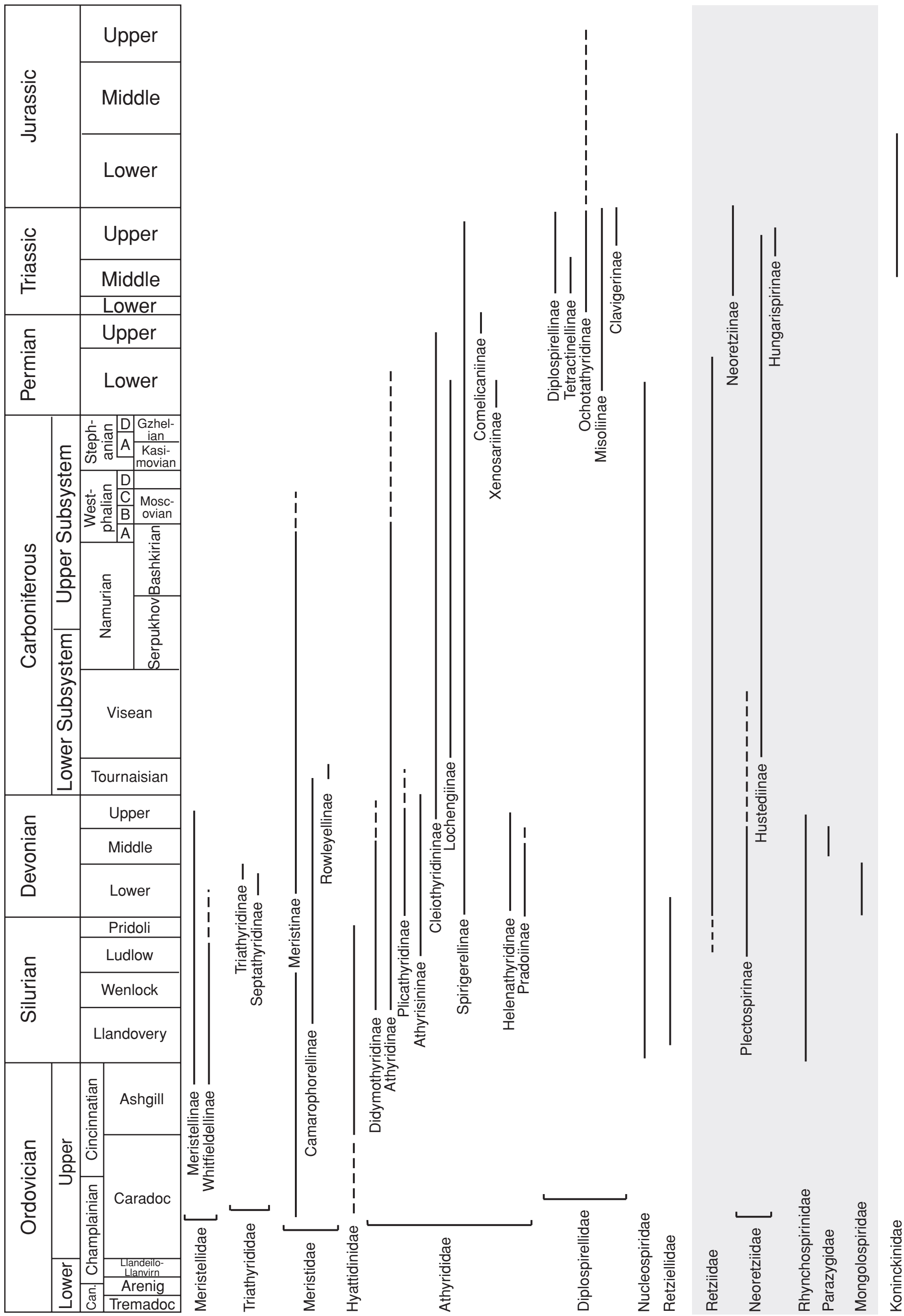

FIG. 1012. *(Continued).*

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Order ATHYRIDIDA Boucot, Johnson, & Staton, 1964

[*nom. transl.* Dagys, 1974, p. 152, *ex* suborder Athyridoidea Boucot, Johnson, & Staton, 1964, p. 815; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 833]

Biconvex, rarely concave or planoconvex, smooth, ribbed or plicate articulated shells; commonly astrophic, rarely strophic; concentric ornamentation more or less developed or absent; occasionally with solid or hollow spines; commonly with alternate folding in adults, less frequently opposite or mixed; ventral cardinal area (palintrope) commonly well developed in later forms; ventral beak commonly with circular foramen, in meso- to permesothyridid (rarely submesothyridid) position, and open or closed delthyrium; different type of pedicle support may be present; dental plates commonly absent in later forms; cardinal plate or septalium commonly present; umbonal blades of spiralia sharply bent from tips of crura commonly in posterodorsal direction, posterolateral in koninckinidines; spiral cones commonly laterally directed, ventrally in koninckinidines; more or less elaborate jugum joins primary lamellae of each conus; accessory lamellae of different disposition and length may be present; shell commonly impunctate, punctate in retziidines; tertiary layer may be present. *Upper Ordovician (Caradoc)–Lower Jurassic, ?Upper Jurassic.*

Suborder ATHYRIDIDINA Boucot, Johnson, & Staton, 1964

[*nom. correct.* Boucot, Johnson, & Staton, 1965, p. 654, *pro* suborder Athyridoidea Boucot, Johnson, & Staton, 1964, p. 815; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 834] [=suborder Rostrospiracea Moore, 1952, p. 221]

Astrophic to strophic, slightly to strongly rostrate athyridides with concentric growth lamellae in various states of expression that occasionally project anteriorly and anterolaterally as flat, spinelike outgrowths, rectangular in section, that appear to be solid; ventral cardinal area (palintrope) reduced to moderately developed, apsacline to orthocline; delthyrium commonly concealed by beak of dorsal valve; dental plates commonly present; outer hinge plates variably developed, inner hinge plates forming septalium or flat hinge plate apically perforated in other than late forms, inner hinge plates rarely absent or not fused medially; jugal saddle variably developed or absent; jugal stem and accessory jugal lamellae commonly present; shell impunctate; tertiary layer may be present. *Upper Ordovician (Caradoc)–Upper Triassic (Norian), ?Upper Jurassic.*

Superfamily ATHYRIDOIDEA Davidson, 1881

[*nom. correct.* Alvarez & Brunton, 1993, p. 310, *pro* Athyridacea Boucot, Johnson, & Staton, 1965, p. 654, *nom. correct. pro* Athyracea Williams, 1956, p. 284, *nom. transl. ex* Athyridae Davidson, 1881a, p. 4; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 840] [=Rostrospiracea Schuchert, 1929, p. 21 (invalid name not based on a family group)]

Athyrididines commonly subequally biconvex, rarely concave or planoconvex; anterior margin may be emarginate; numerous growth lines commonly with short to long frills that may project anteriorly and anterolaterally as flat spinelike outgrowths, rectangular in section, that appear to be solid, except in early and some late forms; dorsal fold and ventral sulcus variably developed or absent; shallow sulcus may develop in both valves; ribs or costae may be present;

foramen small to medium size, in meso- to permesothyridid position; delthyrium concealed by beak of dorsal valve, rarely by symphytium; ventral median septum may be present in late forms; pedicle support may be present, simple in early forms, elaborate in Permian and Triassic genera; cardinal plate flat, thin, subtriangular, inner hinge plates separated by narrow fissure or fused medially and apically perforated by usually large foramen in early forms, subquadrate, commonly thick, not pierced apically in most late Paleozoic forms; cardinal flanges poorly developed or absent in early forms and serrated, moderately to strongly developed, may become united into single structure in most Permian and Triassic forms; jugum commonly projecting anteriorly as jugal saddle and posteroventrally as thin jugal stem that bifurcates into accessory jugal lamellae that terminate posterior of lateral branches of jugum or intercalate with spiralial loops up to apex; rarely, the accessory jugal lamellae extend posterodorsally directly from jugal saddle. *Upper Ordovician (?Caradoc, Ashgill)–Upper Triassic (Norian), ?Upper Jurassic.*

Family ATHYRIDIDAE Davidson, 1881

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1964, p. 817, *pro* Athyridae DAVIDSON, 1881a, p. 4]

Small to very large athyridoids; dental plates commonly of medium length, short or absent in late forms; pedicle supports commonly absent (except *Didymothyris* and *Collarothyris*); ventral muscle field weakly to moderately impressed; cardinal plate subtriangular to subtrapezoidal (absent in some helenathyridins), apically perforate, dorsal foramen may be infilled in gerontic individuals; cardinal flanges poorly developed or absent; late Carboniferous and Permian forms with thicker cardinal plate, dorsal foramen commonly small, may be infilled in latest stocks, and cardinal flanges serrated, moderately to strongly developed. [Athyridae as proposed by PHILLIPS, 1841 or M'COY, 1844 is not an available group name under Art. 11.7 (ICZN, 1999; see ALVAREZ, BRIME, & BRUNTON, 1980 for discussion).] *Silurian (Wenlock)–Upper Triassic.*

Subfamily ATHYRIDINAE Davidson, 1881

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1964, p. 819, *pro* Athyrinae WAAGEN, 1883, p. 450, *nom. transl. ex* Athyridae DAVIDSON, 1881a, p. 4]

Shell small to large, moderately rostrate; commonly with numerous, short to very long growth lamellae, flat or radially striated; dorsal fold commonly low and ventral sulcus shallow; dental plates of medium length (except *Protathyris*), thin subparallel, slightly concave; lateral branches of jugum almost vertical, starting midway along length of dorsal valve; jugal saddle well developed (except *Johnsonathyris*); accessory jugal lamellae terminating slightly posterior of lateral branches of jugum. *Silurian (?Wenlock, Ludlow)–Carboniferous (Bashkirian), ?Lower Permian.*

Athyris M'COY, 1844, p. 146 [**Terebratula concentrica* VON BUCH, 1834, p. 103; SD KING, 1850, p. 136] [=*Cliothyris* AGASSIZ, 1846, p. 90, obj.; *Spirigera* D'ORBIGNY, 1847, p. 268, obj.; *Spirithyris* QUENSTEDT, 1868 in 1868–1871, p. 30, obj.; *Euthyris* QUENSTEDT, 1869 in 1868–1871, p. 442, obj.]. Small- to medium-sized, dorsi- to strongly dorsibiconvex, equidimensional to slightly transverse, rounded subpentagonal shells covered by numerous, regular, thin, and slightly lamellose growth lines; uniplicate anterior commissure with ill-defined fold in anterior half of adult shell and relatively narrow sulcus originating at ventral beak, groovelike posteriorly but widening strongly anteriorly to about half width of very flat ventral valve; ventral muscle field moderately impressed; cardinal plate flat or slightly concave ventrally; low myophragm may be present. *Devonian, ?Lower Carboniferous:* cosmopolitan.——FIG. 1013*a–g*. **A. concentrica* (VON BUCH), Eifelian, Eifel, Germany; *a–e,* neotype, dorsal, ventral, lateral, anterior, and posterior views, SMF 5480, ×2; *f–g,* ventral and lateral views showing reconstructed jugum (Alvarez, Brunton, & Struve, 1996).——FIG. 1014*a–s*. **A. concentrica* (VON BUCH), Eifelian, Eifel, Germany; tangential serial sections, parallel to commissural plane, 1.8, 2.2, 2.5, 2.9, 3.3, 3.6, 3.8, 4.2, 4.6, 5.0, 5.4, 5.8, 5.9, 6.5, 6.6, 7.0, 7.2, 7.3, 11.0 mm from dorsal valve, SMF 50013 (Alvarez, Brunton, & Struve, 1996).——FIG. 1014*t–ii*. *A. concentrica murchisoni* BRICE, Upper Devonian, Ferques, France; transverse serial sections 0.6, 1.1, 2.0, 2.8, 3.3, 3.9, 4.2, 5.0, 6.2, 6.9, 7.8, 8.3, 8.8, 9.3, 11.3, 11.5 mm from ventral umbo, BMNH BD12052 (Alvarez, Brunton, & Struve, 1996).——FIG. 1013*h*. *A. spiriferoides* (EATON), Givetian, Michigan, USA; posterolateral view of open shell showing jugum, ventral up, I1106, Hall collection, ×2.5 (new).——FIG. 1013*i*. *A. waratahensis* (TALENT),

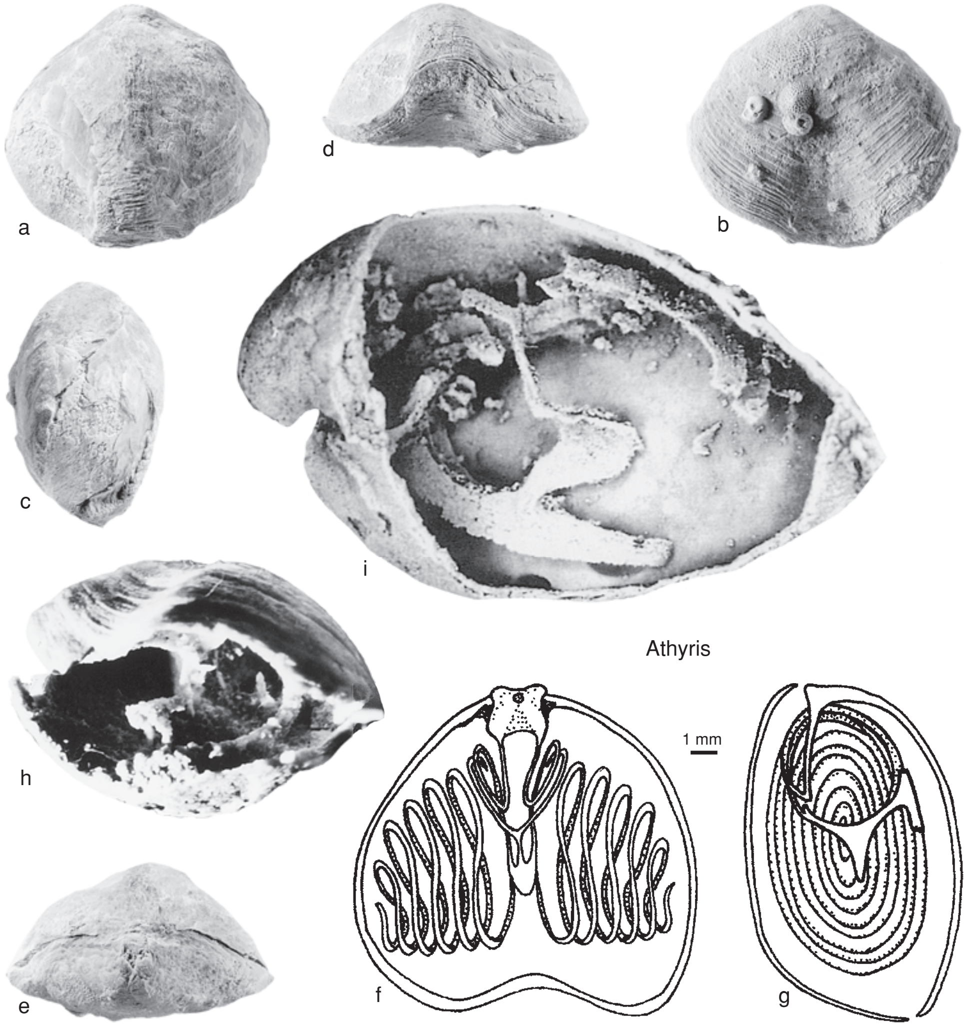

FIG. 1013. Athyrididae (p. 1497–1498).

Lower Devonian, New South Wales, Australia; lateral view of broken specimen showing jugum, ventral up, ANU 18998, approximately ×5(Alvarez, 1999a; photograph courtesy of B. D. E. Chatterton).

Actinoconchus M'COY, 1844, p. 149 [**A. paradoxus;* M] [=*Actinoconchus* M'COY in GRIFFITH, 1842, p. 18, *nom. nud.*]. Medium to large, biconvex, elongate oval, subcircular to transversely oval shells, very long, flat, delicate, radially striated, nonspinose flanges of shell from rugae or strong growth lines on both valves; dorsal fold and ventral sulcus absent or with shallow sulci on both valves forming ligate anterior; internal characters imperfectly known; jugum essentially as in *Athyris.* [*A. paradoxus* was the only species described under *Actinoconchus* so it must be considered the type by monotypy. DAVIDSON (1859) placed *A. paradoxus* into subjective synonymy with *Athyris planosulcata* (PHILLIPS, 1836) and many authors have accepted this. We agree with CARTER (1967) and BRUNTON (1980) in believing the two species to be distinct and so retain the name *A. paradoxus* for the type species of *Actinoconchus.*] *Upper Devonian (upper Famennian)–Upper Carboniferous (Bashkirian), ?Lower Permian:* southern China, *upper Famennian;* Europe, North America, Middle East, China, Australia, *Viséan–Bashkirian;* northeastern China, ?India, *?Lower Permian.*——FIG. 1015,*1a–b.* **A. paradoxus,* Viséan, Kildare, Ireland; *a,* lectotype viewed

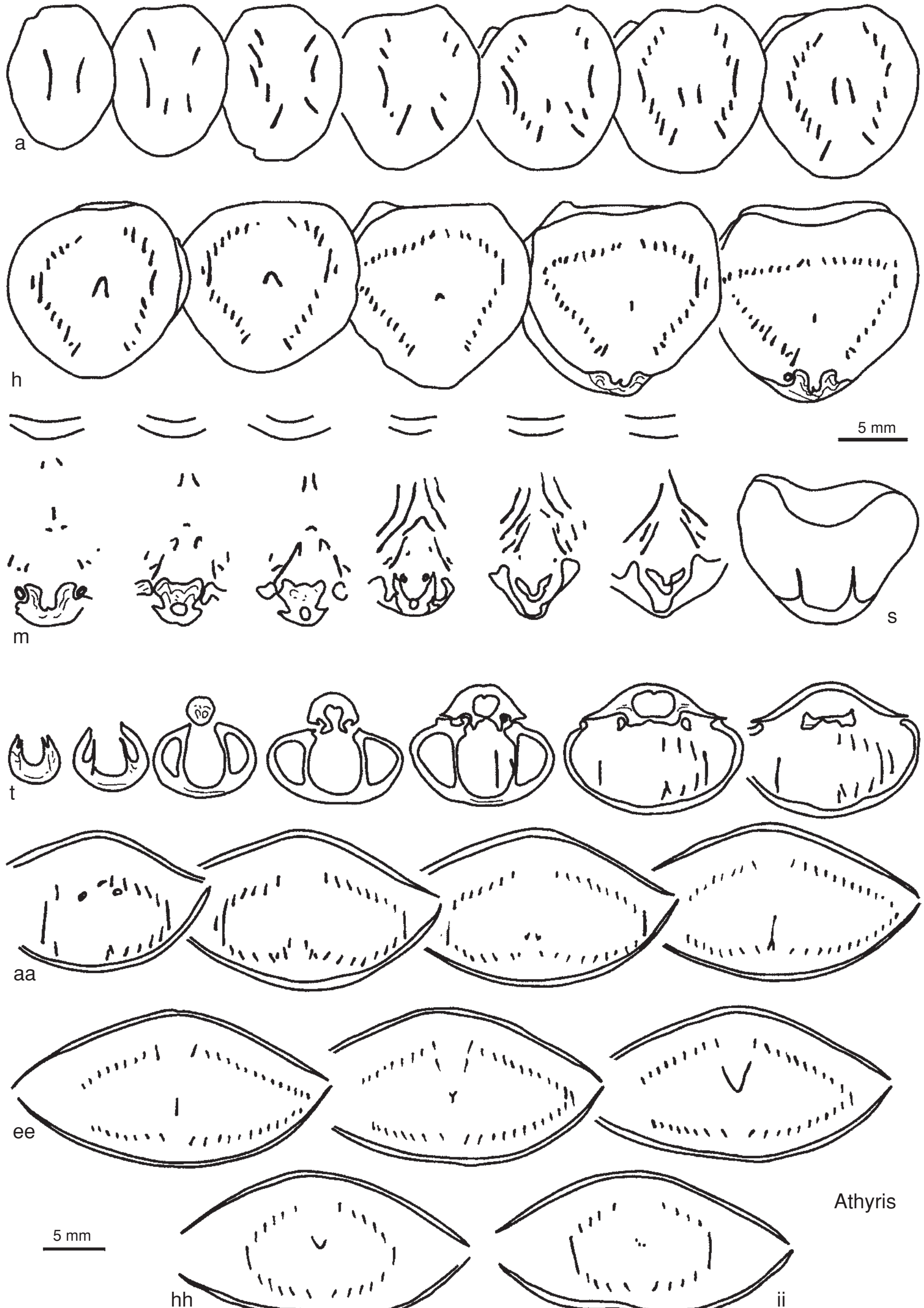

FIG. 1014. Athyrididae (p. 1497–1498).

dorsally, NMING: F6660, Griffith Collection; *b,* ventral view showing flanges, BMNH B5392, Davidson Collection, ×1.5 (Brunton, 1980; photographs courtesy of C. H. C. Brunton).——FIG. 1015,*1c–d. A. planosulcata* (PHILLIPS), Lower Carboniferous, Yorkshire, England; ventral and lateral views showing jugum (Glass in Davidson, 1882). [See also Fig. 1002.5, p. 1477, in introduction.]

Alvarezites STRUVE, 1992, p. 559 [**Athyris (Alvarezites) wolfarti;* OD]. Large to very large, dorsibiconvex, slightly wider than long; hinge line almost straight, slightly shorter than maximum width, subtriangular to transversely subelliptical shells with fold and sulcus distinct in anterior half of adult shell; growth lamellae irregular, densely crowded, delicate, rarely coarse; lateral apical cavities commonly infilled with secondary shell material; ventral muscle field fan shaped, distinctly depressed only posteriorly; myophragm weakly developed. *Middle Devonian (Eifelian):* Germany (Eifel).——FIG. 1015,*2a–c.* **A. wolfarti,* middle Eifelian; holotype, dorsal, ventral, and anterior views, SMF 54650, Struve Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

Atrythyris STRUVE, 1965, p. 218 [**A. atryplicata;* OD]. Similar to *Athyris,* but biconvex, with fine radial ornamentation somewhat similar to that of some atrypids; hinge plate slightly depressed medially. [The plicate exterior and umbonal interiors of Chinese specimens assigned to this genus are typically athyrisinin.] *Middle Devonian:* Germany, France, ?China.——FIG. 1015,*4a–d.* **A. atryplicata,* middle Eifelian, Eifel, Germany, SMF 18946, Struve Collection; *a–c,* holotype, dorsal, ventral, and anterior views, ×1.5; *d,* detail of ornamentation, ×10 (Struve, 1965).

Brimethyris ALVAREZ, RONG, & BOUCOT, 1998, p. 842 [**Terebratula subconcentrica* DE VERNEUIL & D'ARCHIAC, 1845, p. 463; OD]. Medium to large, biconvex, slightly wider than long, rounded subpentagonal shells, with imbricate, widely spaced growth lamellae on any of which are up to 8 growth lines; papillose microornamentation affecting both primary layer and apparently most superficial secondary fibers; shallow ventral sulcus and flat, or slightly depressed medianly, dorsal fold beginning in posterior third of shell; internally essentially as in *Athyris* with reduced outer hinge plates and cardinal flanges, hinge plate almost flat with gentle longitudinal crest. *Lower Devonian (Emsian):* Spain.——FIG. 1016*a–g.* **B. subconcentrica* (DE VERNEUIL & D'ARCHIAC), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, D855, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* ornamentation, ×9; *g,* ornamentation, DPO 17925, ×10 (Alvarez, 1990). ——FIG. 1017*a–cc.* **B. subconcentrica* (DE VERNEUIL & D'ARCHIAC), upper Emsian; transverse serial sections 1.15, 1.65, 1.85, 2.15, 2.75, 2.95, 3.35, 3.70, 4.15, 4.40, 4.65, 4.80, 5.35, 5.60, 6.35, 6.65, 6.90, 7.70, 8.25, 8.50, 8.80, 9.00, 9.35, 9.70, 9.90, 10.45, 10.85, 11.90, 12.00 mm from ventral umbo, DPO 17831 (adapted from Alvarez, 1990).

Bruntonites STRUVE, 1992, p. 559 [**Athyris (Bruntonites) mellingeni;* OD]. Similar to *Athyris,* but strongly biconvex, subcircular to broadly ovate in outline, fold and sulcus slightly developed only anteriorly; delthyrial cavity rather wide; myophragm very weak, commonly absent. *Middle Devonian (Eifelian):* Germany (Eifel).——FIG. 1015,*3a–c.* **B. mellingeni* (STRUVE), middle Eifelian, Gondelsheim; holotype, dorsal, ventral, and anterior views, SMF 54700, Struve Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

Eifyris STRUVE, 1992, p. 561 [**Terebratula eifliensis* SCHNUR, 1853, p. 192; OD]. Similar to *Athyris,* but ventribiconvex, longer than wide, subovate, moderately to strongly rostrate; sinus mostly shallow with median groove, fold mostly low or indistinct, more or less short; delthyrial cavity wide; myophragm long. *Middle Devonian (Eifelian):* Germany (Gerolstein).——FIG. 1018,*3a–b.* **E. eifliensis* (SCHNUR), middle Eifelian; lectotype, dorsal and ventral views, GPIBo S10, Schnur Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

?Gonathyris BARANOV, 1994, p. 30 [**G. ovata;* OD]. Shells resembling *Protathyris* but with hinge plate reportedly massive, pierced in its anterior part and serving as base for denticulate cardinal process; spiralia and jugum poorly known. [This genus requires revision.] *Lower Devonian (Pragian):* eastern Siberia, Yakutsk.——FIG. 1018,*1a–d.* **G. ovata;* holotype, dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/17, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov).

Imacanthyris GRUNT, 1991, p. 71 [**I. bortegensis;* OD]. External shape as in *Pachyplax* with bigger size and regular, thinner lamellose extensions covered with fine radial striations; internally resembling *Athyris;* jugum unknown. *Lower Devonian (Lochkovian):* Mongolia.——FIG. 1015,*5a–d.* **I. bortegensis;* holotype, dorsal, ventral, lateral, and anterior views, PIN 3385/2071, ×1 (Grunt, 1991).

Johnsonathyris SAVAGE, EBERLEIN, & CHURKIN, 1978, p. 381 [**J. adrianensis;* OD]. Small, strongly biconvex, subglobular, subcircular to subpentagonal; beaks incurved, foramen minute; weak dorsal fold and ventral sulcus developed anteriorly; commissure strongly uniplicate; fine growth lamellae crossed by regularly developed fine costellae; dental plates dorsally convergent, lateral apical cavities narrow; cardinal plate thin, flat, small, imperforate, medially crested; myophragm absent; jugum placed anterior of midlength, without saddle, stem, or accessory lamellae. *Upper Devonian (Famennian):* USA (Alaska).——FIG. 1018,*2a–n.* **J. adrianensis; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 223913, ×2 (Savage, Eberlein, & Churkin, 1978); *f–m,* transverse serial sections 0.4, 0.5, 0.7, 0.8, 0.9, 3.4, 4.9, 5.4 mm from ventral umbo (adapted from Savage, Eberlein, & Churkin, 1978); *n,* ventral view showing reconstructed spiralium with jugum, USNM 223915 (Savage, Eberlein, & Churkin, 1978).

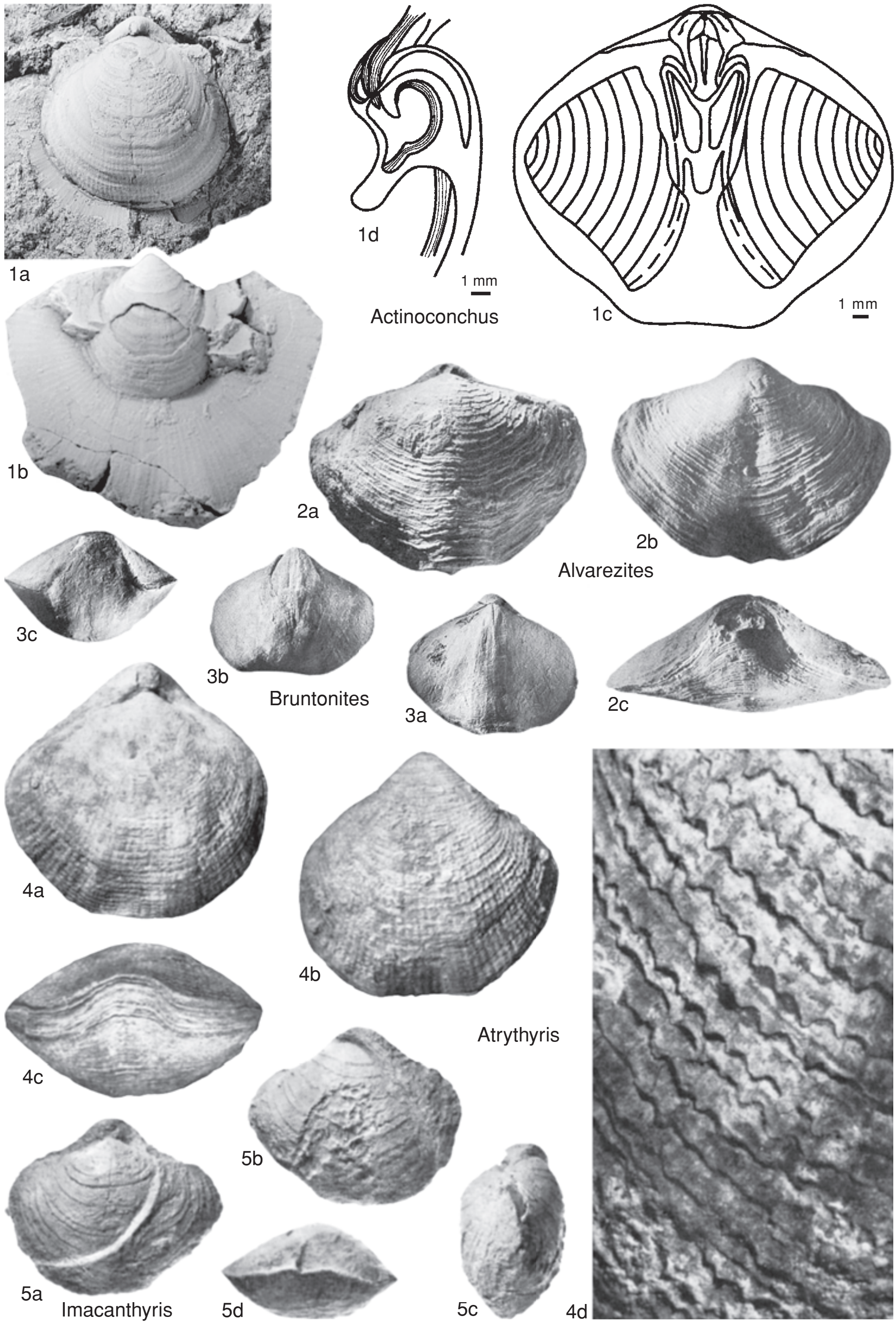

FIG. 1015. Athyrididae (p. 1498–1500).

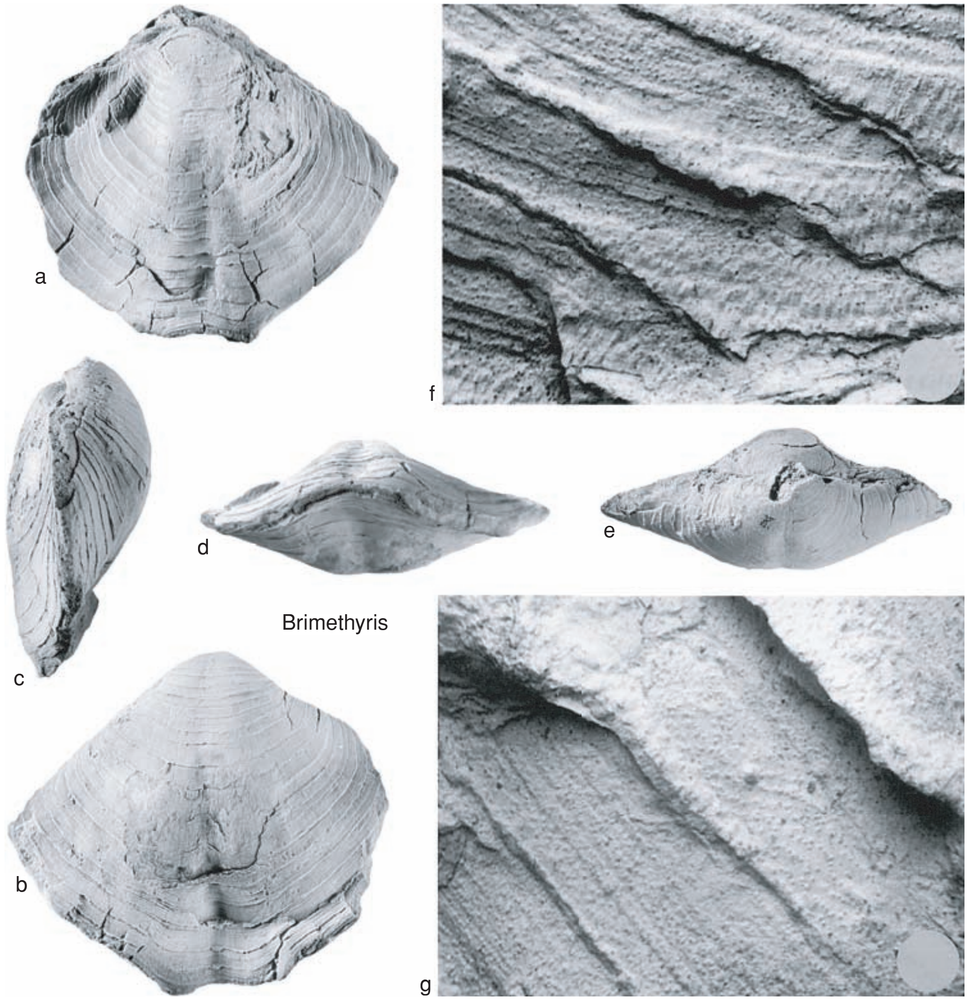

FIG. 1016. Athyrididae (p. 1500).

Lamellosathyris JIN & FANG, 1983, p. 147 [**Spirifer lamellosus* LEVEILLE, 1835, p. 39; OD]. Large, biconvex, subcircular to transversely elliptical shells, with long, radially corrugated shell flanges extending from rugae of both valves, with ventral sulcus and low dorsal fold with or without shallow median groove; dental plates slightly divergent dorsally, may become partially buried by secondary shell thickening during ontogeny; dorsal foramen small; cardinal flanges, more or less developed, projecting posteroventrally; low myophragm present; jugum, located at about midlength of first whorl of spiralia, essentially as in *Athyris* but accessory jugal lamellae shorter or absent. *Upper Devonian (Famennian)–Lower Carboniferous (Viséan):* ?Armenia, North America, *Famennian;* Elbourz, southwestern China (Yunnan), Europe, North America, *middle Tournaisian–Viséan.*——FIG. 1019,*2a–r.* **L. lamellosa* (LEVEILLE); *a–d,* neotype, dorsal, ventral, anterior, and posterior views, upper Tournaisian, Tournai, Belgium, BMNH B20138, Piret Collection, ×1; *e,* interior of silicified specimen, upper Tournaisian, Tournai, Belgium, BMNH BB62961, Piret Collection, ×3 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *f–r,* transverse serial sections 2.2, 3.5, 3.7, 4.3, 4.7, 5.7, 6.9, 8.5, 12.5, 15.2, 15.7, 15.9, 17.9 mm from ventral umbo, lower Viséan, western Yunnan, China (adapted from Jin & Fang, 1983). [See also Fig. 1002.4, p. 1477, and Fig. 1008.1, p. 1485, in introduction.]

?Meristospira GRABAU in GRABAU & SHERZER, 1910, p. 158 [**M. michiganensis;* OD]. Small to medium, subcircular or transversely oval biconvex shells; with or without faintly developed dorsal fold and ventral

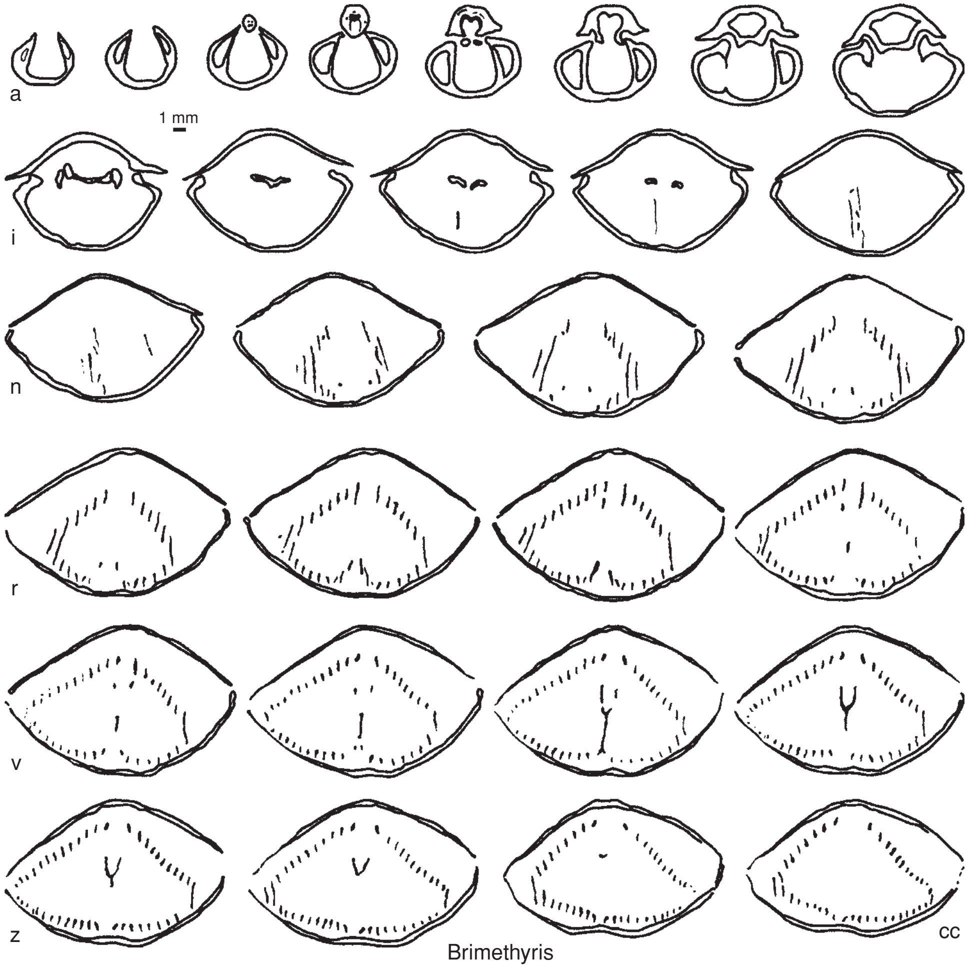

FIG. 1017. Athyrididae (p. 1500).

sulcus; growth lines not lamellose; a few low lateral plications may be present; dental plates subparallel, of moderate length; cardinal plate flat; dorsal myophragm present; spiralia and jugum unknown. [This genus requires revision.] *Middle Devonian:* USA (Michigan, Ohio), Canada (Ontario), ?China.——FIG. 1019,*1a–c.* **M. michiganensis,* Michigan; *a,* posterior internal mold both valves, ×3; *b–c,* lateral and ventral views of internal mold, ×2 (Grabau & Sherzer, 1910).

Pachyplax ALVAREZ & BRUNTON, 1990a, p. 31 [**P. transversa;* OD]. Resembling *Athyris* with small-sized, biconvex, rectimarginate to slightly uniplicate shells; valve surface covered by numerous, irregular, and very thick concentric lamellose extensions, formed by many layers of secondary fibers. *Lower Devonian (upper Emsian):* northwestern Spain.——FIG. 1020*a–v.* **P. transversa,* León; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, DPO 18642, ×1.5; *f–u,* transverse serial sections 0.70, 1.70, 2.00, 2.20, 2.70, 3.05, 3.80, 4.20, 4.55, 5.20, 5.60, 6.20, 6.50, 7.00, 8.95, 9.00 mm from ventral umbo, DPO 21154 (adapted from Alvarez & Brunton, 1990a); *v,* jugum, DPO 21154 (Alvarez & Brunton, 1990a).——FIG. 1020*w–x. P. gyralea* ALVAREZ & BRUNTON, Asturias; *w,* dorsal interior, DPO 25015, ×8; *x,* ventral interior, DPO 25010, ×9 (Alvarez & Brunton, 1990a). [See also Fig. 1003.2, 1003.4, p. 1478, and Fig. 1007.2, p. 1484, in introduction.]

Protathyris KOZLOWSKI, 1929, p. 223 [**P. praecursor;* SD GRABAU, 1932b, p. 90]. Similar to *Greenfieldia* externally and to *Athyris* internally, but shell wall thin, dental plates thin and very short; cardinal plate triangular, delicate, trilobed anteriorly, the central lobe being the largest and most concave, dorsal foramen large, cardinal flanges absent; dorsal myophragm may be present. *Silurian (?Wenlock,*

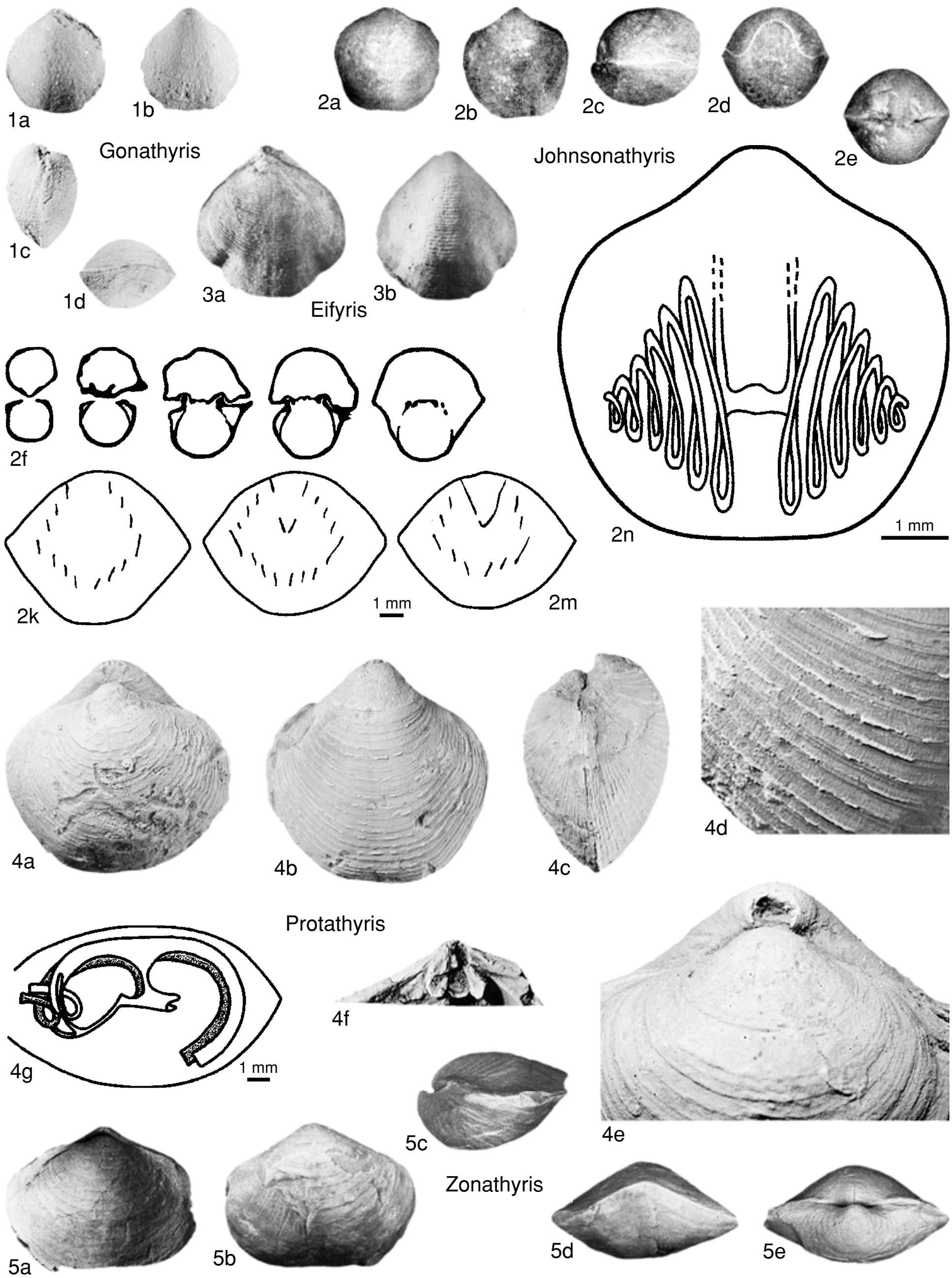

FIG. 1018. Athyrididae (p. 1500–1505).

Ludlow)–Lower Devonian (Emsian): North America, Europe, Asia, Australia.——FIG. 1018,*4a–g*. **P. praecursor,* Lochkovian, Podolia, Russia; *a–c,* neotype, dorsal, ventral, and lateral views, CNIGR 125/11475, ×2; *d,* enlargement of ornament of ventral valve, CNIGR 125/11475, ×5; *e,* posterior part of conjoined valves showing foramen, CNIGR 68/11475; *f,* cardinalia, CNIGR 8/10001, ×6 (Nikiforova, Modzalevskaya, & Bassett, 1985; photographs courtesy of T. L. Modzalevskaya); *g,* lateral

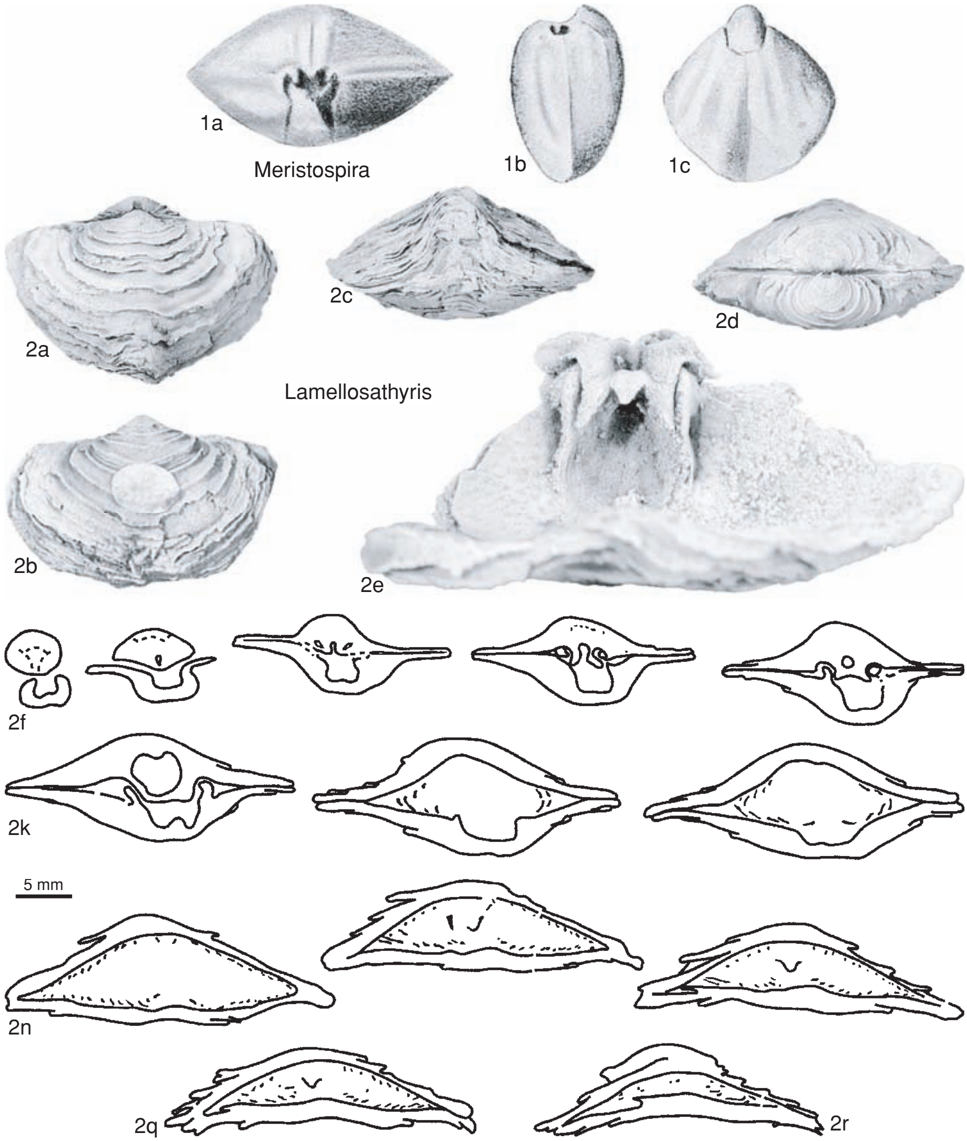

FIG. 1019. Athyrididae (p. 1502–1503).

view of jugum (adapted from Modzalevskaya, 1985).

Zonathyris STRUVE, 1992, p. 563 [**Terebratula cassidea oculta* QUENSTEDT, 1871 in 1868–1871, p. 460; OD]. Similar to *Alvarezites,* but biconvex, fold very faint, sinus weak to moderately developed, restricted to anterior part; growth lamellae delicate, regular, conspicuously spaced, on any of which are several weak growth lines. *Middle Devonian (Eifelian–Givetian):* Germany (Gerolstein).——FIG. 1018,*5a–e.* **Z. oculta* (QUENSTEDT); holotype, dorsal, ventral, lateral, anterior, and posterior views, IMGPT 3/51/95, ×1 (Alvarez, Brunton, & Struve, 1996).

Subfamily ATHYRISININAE
Grabau, 1931

[Athyrisininae GRABAU, 1931a, p. 509]

Shell small to large, moderately to strongly rostrate, ribbed or costate; growth

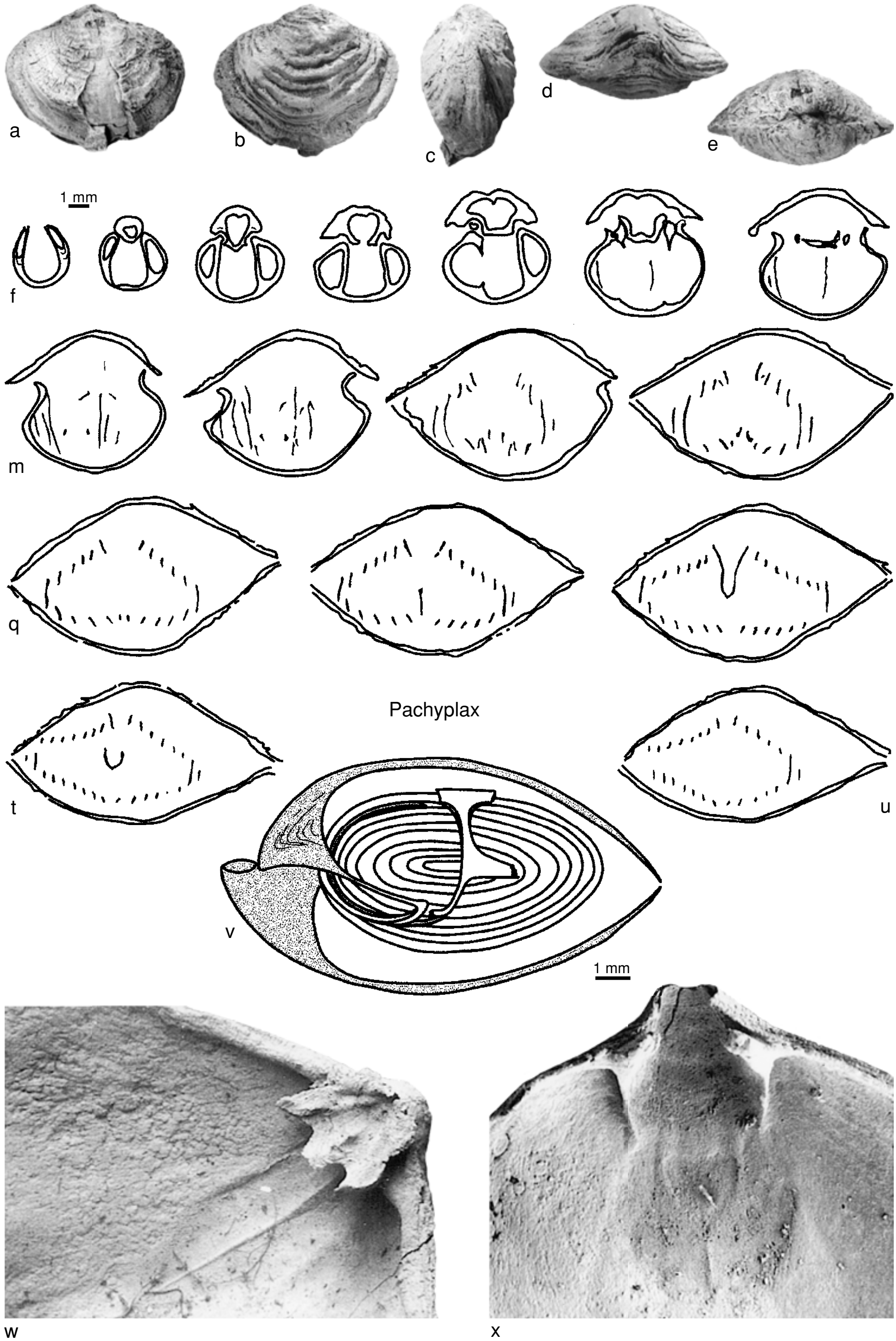

FIG. 1020. Athyrididae (p. 1503).

lamellae variably developed, may be squamose; fold and sulcus variably developed or absent; dental plates, when present, commonly short, converging dorsally; dorsal myophragm poorly developed, commonly absent; cardinal plate and jugum essentially as in *Athyris. Silurian (upper Ludlow)–Middle Devonian (Givetian).*

Athyrisina HAYASAKA in YABE & HAYASAKA, 1920, p. 176 [**A. squamosa;* OD] [=*Kwangsia* GRABAU, 1931a, p. 204 (type, *K. yohi,* OD); *Plectospirifer* GRABAU, 1931a, p. 379 (type, *P. heimi,* OD); *Kwangsiella* GRABAU, 1932a, p. 82 (type, *K. yohi,* OD); *Pseudoathyrisina* CHEN, 1979, p. 17 (type, *P. fasciata,* OD); *Athyrisinopsis* ZHANG Yan, 1983a, p. 354 (type, *A. uniplicata,* OD)]. Medium to large, rounded to transversely elliptical, ventribiconvex shell; ventral sulcus and dorsal fold usually well developed; pauciplicate to costellate, radial elements may bifurcate; concentric lamellae usually well developed; dental plates thin, short, dorsally convergent; lateral apical cavities very narrow; cardinal plate perforated apically by minute foramen, low myophragm may be present; lateral branches of jugum inclined anteriorly, starting posterior to middorsal valve length, accessory jugal lamellae short. *Lower Devonian (lower Emsian)–Middle Devonian (Givetian):* southern China (Sichuan, Guizhou, Guangxi, Yunnan), northwestern China (Western Qinling, southeastern Gansu, western Shaanxi).——Fig. 1021,*4*a–*jj.* **A. squamosa,* upper Emsian, Shuimogou, northern Sichuan; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, ×1 (new; photographs courtesy of the late Chen Yuan-ren); *f–jj,* serial sections 1.7, 2.4, 2.6, 2.8, 3.0, 3.4, 3.8, 4.05, 4.6, 5.1, 6.7, 7.6, 8.6, 9.8, 9.9, 11.4, 11.8, 12.5, 13.0, 13.9, 15.4, 15.7, 16.0, 16.25, 16.7, 17.3, 17.9, 18.25, 18.4, 18.7, 19.1 mm from ventral umbo (new).

Homeathyris MODZALEVSKAYA, 1997, p. 209 [**H. insularis;* OD] [=*Homeathyris* MODZALEVSKAYA in MODZALEVSKAYA & others, 1994, p. 66, *nom. nud.; Homeathyris* MODZALEVSKAYA, 1994b, p. 147, *nom. nud.*]. Similar to *Squamathyris* but bigger, with sulcus in both valves and without growth lamellae. Silurian (Ludfordian): Russia (Arctic Russia, southern island of Novaya Zemlya, Dolgii Island, western slopes of Central Urals).——FIG. 1021,*2a–b.* **H. insularis,* Dolgii; holotype, ventral and lateral views, CNIGR 2/12918, ×1 (Modzalevskaya, 1997).

?Ikella TIAZHEVA, 1972, p. 205 [**I. numerosa;* OD]. Small to medium, costate shells; elongate subelliptical, biconvex, fold and sulcus commonly absent; costae rounded, bifurcating or not, in corresponding position on each valve; delthyrium with narrow deltidial plates; dental plates absent; cardinal plate present; myophragm absent; spiralium and jugum unknown. [Insufficiently described and figured.] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* Russia (Bashkirkostan, western slopes of Southern Urals).

Parathyrisina WANG in WANG, YU, & WU, 1974, p. 41 [**P. bella;* OD; =*Athyrisina tangnae* HOU, 1963, p. 416] [=*Athyrisinoides* CHEN & WAN, 1978, p. 351 (type, *A. typica,* OD); *Athyrisinoidea* CHEN & WAN in WAN, 1980, p. 105 (type, *A. typica,* OD); *Neoathyrisina* CHEN, 1988b, p. 36, obj.]. Small to medium, transverse subelliptical to subcircular outline; pedicle opening large; ventral sulcus and dorsal fold rounded, well developed, without radial elements; lateral slopes bearing 3 or more round costae; interior and jugum essentially as in *Athyrisina. Lower Devonian (upper Pragian–lower Emsian):* northwestern China (western Qinling), southern China (Guangxi, Sichuan).——FIG. 1022*a–x.* **P. tangnae* (HOU), Guangxi; *a–d,* dorsal, ventral, lateral, and anterior views, NIGP 23624, ×2 (new); *e–x,* transverse serial sections 1.0, 2.1, 2.5, 2.9, 3.2, 3.5, 3.8, 4.3, 5.2, 5.8, 6.2, 7.25, 9.6, 10.5, 10.9, 11.3, 11.9, 12.3, 12.7, 14.5 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Wang & Rong, 1986).

Pseudohomeospira NIKIFOROVA, 1970, p. 139 [**P. polaris;* OD]. Small, biconvex, elongate oval, costate shells; ventral sulcus and dorsal fold weakly developed anteriorly; costae subangular, bifurcating in fold and sulcus; hypothyridid pedicle opening may be partially closed by deltidial plates; pedicle collar present; short ventral septum may be present apically; dental plates and dorsal interior essentially as in *Athyrisina;* spiralia directed laterally, jugum unknown. *Silurian (Přídolí):* Russia (Arctic Russia, Vaigatch, southern island of Novaya Zemlya, western Polar and Central Urals).——FIG. 1021,*1a–b.* **P. polaris,* Vaigatch; holotype, dorsal and ventral views, TsNIGRA 159/10331, ×2 (Nikiforova, 1970; photographs courtesy of T. L. Modzalevskaya).

Squamathyris MODZALEVSKAYA, 1981, p. 153 [**S. glacialis;* OD]. Medium size, biconvex, subpentagonal to longitudinally oval, ribbed shells; ventral sulcus and dorsal fold moderately developed; squamose surface of growth lamellae; ventral valve moderately to strongly rostrate; hypothyridid pedicle opening restricted laterally by deltidial plates; ventral interior as in *Didymothyris;* spiralia directed laterally, jugum unknown. *Silurian (Ludfordian):* Russia (Arctic Russia, Vaigach, Dolgii Island, southern island of Novaya Zemlya).——FIG. 1021,*3a–d.* **S. glacialis,* Novaya Zemlya; *a–c,* holotype, dorsal, ventral, and lateral views, TsNIGRA 9/12011, ×1; *d,* ventral valve internal mold, ×3 (Modzalevskaya, 1981; photographs courtesy of T. L. Modzalevskaya).

Subfamily CLEIOTHYRIDININAE Alvarez, Rong, & Boucot, 1998

[Cleiothyridininae ALVAREZ, RONG, & BOUCOT, 1998, p. 842]

Shell medium to large, moderately rostrate; numerous, concentric, imbricate, very close growth lamellae projecting anteriorly

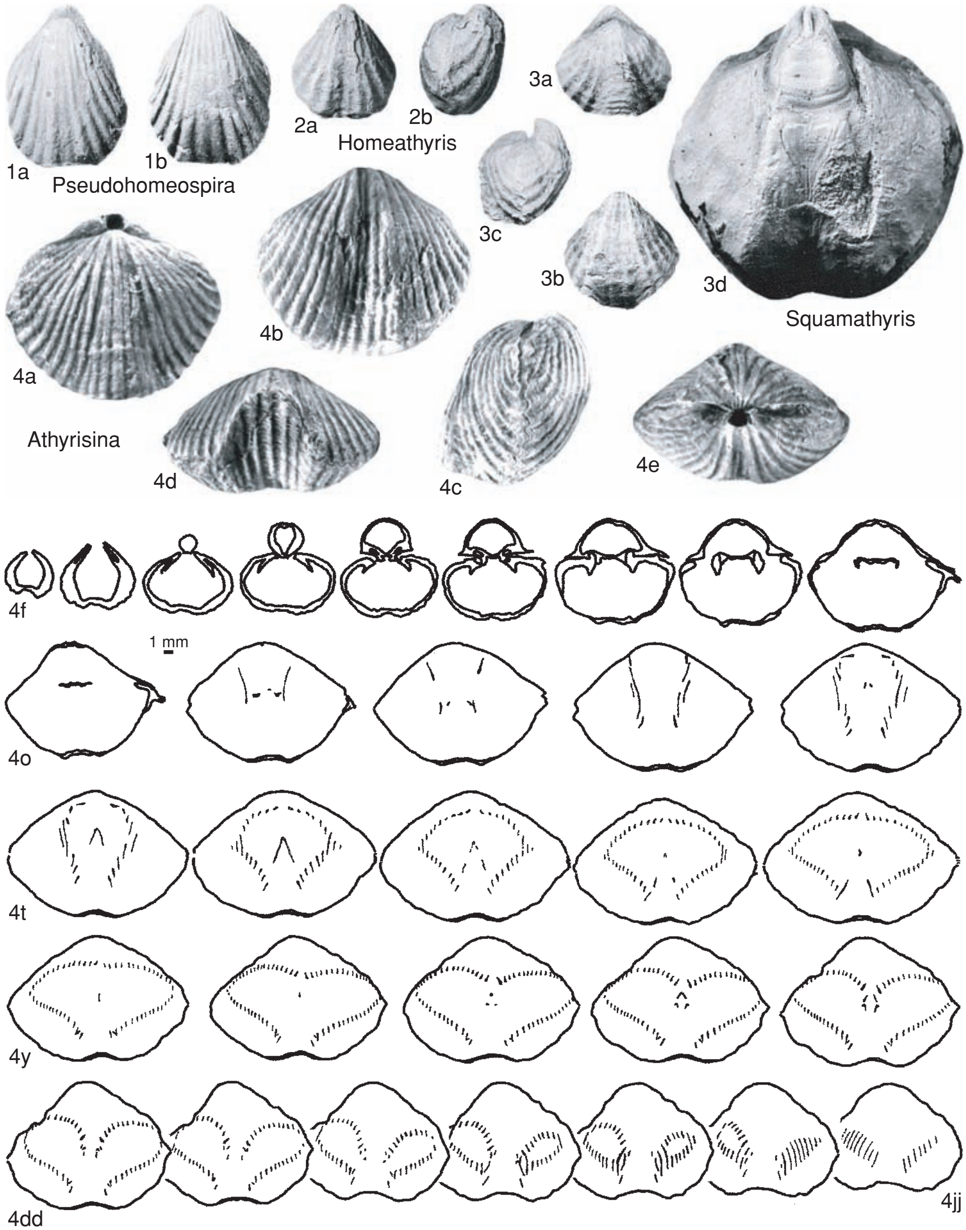

FIG. 1021. Athyrididae (p. 1507).

and anterolaterally as flat, solid spines; faint dorsal fold and ventral sulcus developed anteriorly; dental plates short, low, dorsally divergent, may become partially buried by secondary shell thickening; cardinal plate subtriangular; outer hinge plates well developed and ventrally concave, conjunct inner hinge plates subtrapezoidal, short, wide, and

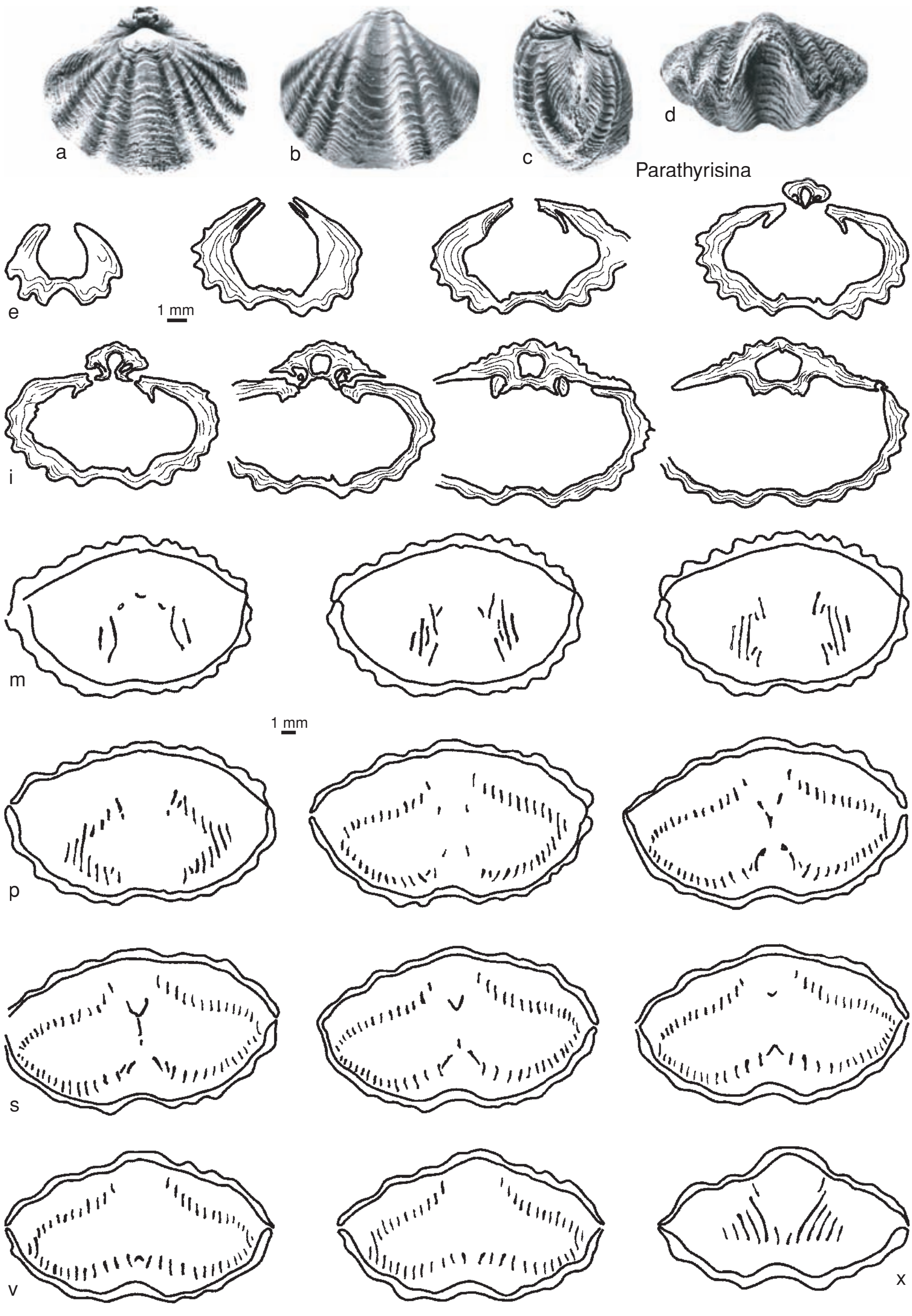

FIG. 1022. Athyrididae (p. 1507).

usually flat and situated more dorsally than outer hinge plates; posteroventrally projecting striate cardinal flanges variously developed; low myophragm present; jugum essentially as in *Athyris* with longer accessory jugal lamellae commonly terminating anterior to lateral branches; tertiary layer may be present. *Upper Devonian (Famennian)–Upper Permian (Kazanian, ?Tatarian).*

Cleiothyridina BUCKMAN, 1906, p. 324, *nom. nov. pro Cleiothyris* KING, 1850, p. 137 [**Atrypa pectinifera* J. de C. SOWERBY, 1840 in 1840–1846, p. 14; validated by ICZN Opinion 1041, 1976, p. 210] [=*Cliothyris* HALL & CLARKE, 1893, p. 90, obj., *non* AGASSIZ, 1846; *Cleiothyridellina* WATERHOUSE, 1978, p. 82 (type, *C. accoliformis,* OD); *Gerankalasiella* GRETCHISHNIKOVA, 1996, p. 423 (type, *G. gerankalasiensis,* OD); *Kjarkiella* GRETCHISHNIKOVA, 1996, p. 424 (type, *K. kjarkiensis,* OD)]. Medium-sized, transversely elliptical to longitudinally ovate, subequally biconvex shells. [*Cleiothyridellina,* from the Upper Permian of Nepal, is said to differ by having swollen shells, flat cardinal plate, and very short and low median septum, usually absent at maturity; *Gerankalasiella* and *Kjarkiella* from the Tournaisian of Transcaucasia are said to differ by having wider growth lamellae and spiral brachidium having a higher number of whorls (*Gerankalasiella*), while *Kjarkiella* has a larger size, high shell convexity, and very dense, narrow growth lamellae, weakly divided at margins.] *Upper Devonian (Famennian)–Upper Permian (Kazanian, ?Tatarian):* cosmopolitan.——FIG. 1023*a–e.* **C. pectinifera* (SOWERBY), Kazanian, ?Tatarian, Durham, United Kingdom; *a–d,* lectotype, dorsal, ventral, lateral, and posterior views, BMNH B61055, Sowerby Collection, ×2 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *e,* jugum, approximately ×4.5 (Davidson, 1857).——FIG. 1023*f–g. C. seriata* GRANT, Artinskian, southern Thailand; *f,* cardinalia, USNM 497424, ×16.5; *g,* anterior view into articulated umbones showing cardinalia and articulation, USNM 497425, ×14 (new). [See also Fig. 1002.3, p. 1477, Fig. 1004.1, p. 1479, and Fig. 1007.1, p. 1484, in introduction.]

Bajtugania GRUNT, 1980, p. 97 [**B. netschaevi;* OD]. Similar to *Cleiothyridina,* but with thick shell; dental plates absent; more or less prominent ridge joining thick cardinal plate at posterodorsal end; dorsal foramen may be overgrown. *Upper Permian (Kazanian):* Russian Platform, Verkhoyansk, Mongolia.——FIG. 1024,*1a–bb.* **B. netschaevi,* Russian Platform; *a–b,* holotype, dorsal and ventral views, PIN 1511/2695, ×1 (Grunt, 1980); *c–k,* transverse serial sections 1.3, 1.7, 2.6, 2.8, 3.1, 3.2, 3.4, 3.7, 4.4 mm from ventral umbo, PIN 3599/105; *l–bb,* tangential serial sections, parallel to commissural plane, 1.6, 2.7, 3.4, 3.7, 4.7, 5.3, 5.9, 6.1, 7.1, 7.2, 7.4, 7.5, 7.6, 7.7, 7.9, 8.0, 8.1 mm from dorsal valve, PIN 3599/829 (adapted from Grunt, 1986).

Carteridina ALVAREZ, RONG, & BOUCOT, 1998, p. 842 [**Spirigera prouti* SWALLOW, 1860, p. 649; OD]. Very large, transverse, dorsibiconvex shells resembling *Cleiothyridina,* with large growth lamellae; without dental plates and myophragm. *Lower Carboniferous (Tournaisian–Viséan):* USA (Missouri, New Mexico, Texas).——FIG. 1025,*1a–e.* **C. prouti* (SWALLOW), Tournaisian, Texas; dorsal, ventral, lateral, anterior, and posterior views, USNM 154774, ×2 (Carter, 1967).

Crinisarina COOPER & DUTRO, 1982, p. 92 [**Cleiothyridina reticulata* STAINBROOK, 1947, p. 326; OD]. Similar to *Cleiothyridina* with pentagonal outline, strongly uniplicate anterior commissure. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America.——FIG. 1025,*4a–k.* **C. reticulata* (STAINBROOK), Famennian, New Mexico, USA; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 200928, ×1; *f,* spines, ×4 (Cooper & Dutro, 1982); *g–k,* transverse serial sections 2.4, 2.8, 3.2, 3.6, 8.1 mm from ventral umbo, USNM 341941 (adapted from Cooper & Dutro, 1982).

?Deltachania WATERHOUSE, 1971, p. 217 [**D. acanthatia;* OD]. Similar to *Cleiothyridina,* but reportedly without hinge plate; spiralium and jugum unknown. [This genus requires revision.] *Upper Carboniferous (Moscovian):* Canada (northern Yukon).——FIG. 1024,*2a–d.* **D. acanthatia; a–b,* holotype, dorsal and ventral views of internal mold, GSC 26422, ×1; *c,* dorsal view, GSC 26418, ×1; *d,* rubber mold of cardinalia articulated with fragment of ventral valve, anterior view, GSC 26422, ×2 (Waterhouse, 1971).

?Himathyris WATERHOUSE, 1986b, p. 214 [**Athyris gerardi* DIENER, 1899, p. 56; OD]. Large shells with almost flat ventral valve, growth lamellae similar to those on *Actinoconchus,* with fine radial ribs and reportedly flat, small, erratically developed spines on only some lamellae; interior poorly known. [This genus requires revision. Date on publication is 1985, but volume 3 of *Contributions to Himalayan Geology* was published in 1986.] *Upper Permian (Tatarian):* India, Spiti.——FIG. 1025,*3.* **H. gerardi* (DIENER); lectotype, ventral view, GSI 6295, ×1 (Diener, 1899).

Leiothycridina GRUNT, 1980, p. 64 [**L. okensis;* OD]. Similar to *Cleiothyridina* but with poorly differentiated dental plates; very flat cardinal plate with longer inner hinge plates and thicker shell with well-developed tertiary layer; spiralia and jugum unknown. *Lower Carboniferous (Viséan–lower Namurian):* Belgium, England, France, Russia, Tian Shan, southern China, Japan.——FIG. 1025,*2a–i.* **L. okensis,* Viséan, Moscow syncline, Russia; *a–d,* holotype, dorsal and ventral valves viewed externally and internally, PIN 544/468, ×1 (Grunt, 1980); *e–i,* transverse serial sections 2.2, 2.5, 2.7, 3.7, 3.9 mm from ventral umbo, PIN 544/288 (adapted from Grunt, 1980).

Pinegathyris GRUNT, 1980, p. 88 [**Terebratula royssiana* VON KEYSERLING, 1846, p. 237; OD]. Similar to *Cleiothyridina,* but bigger, frequently

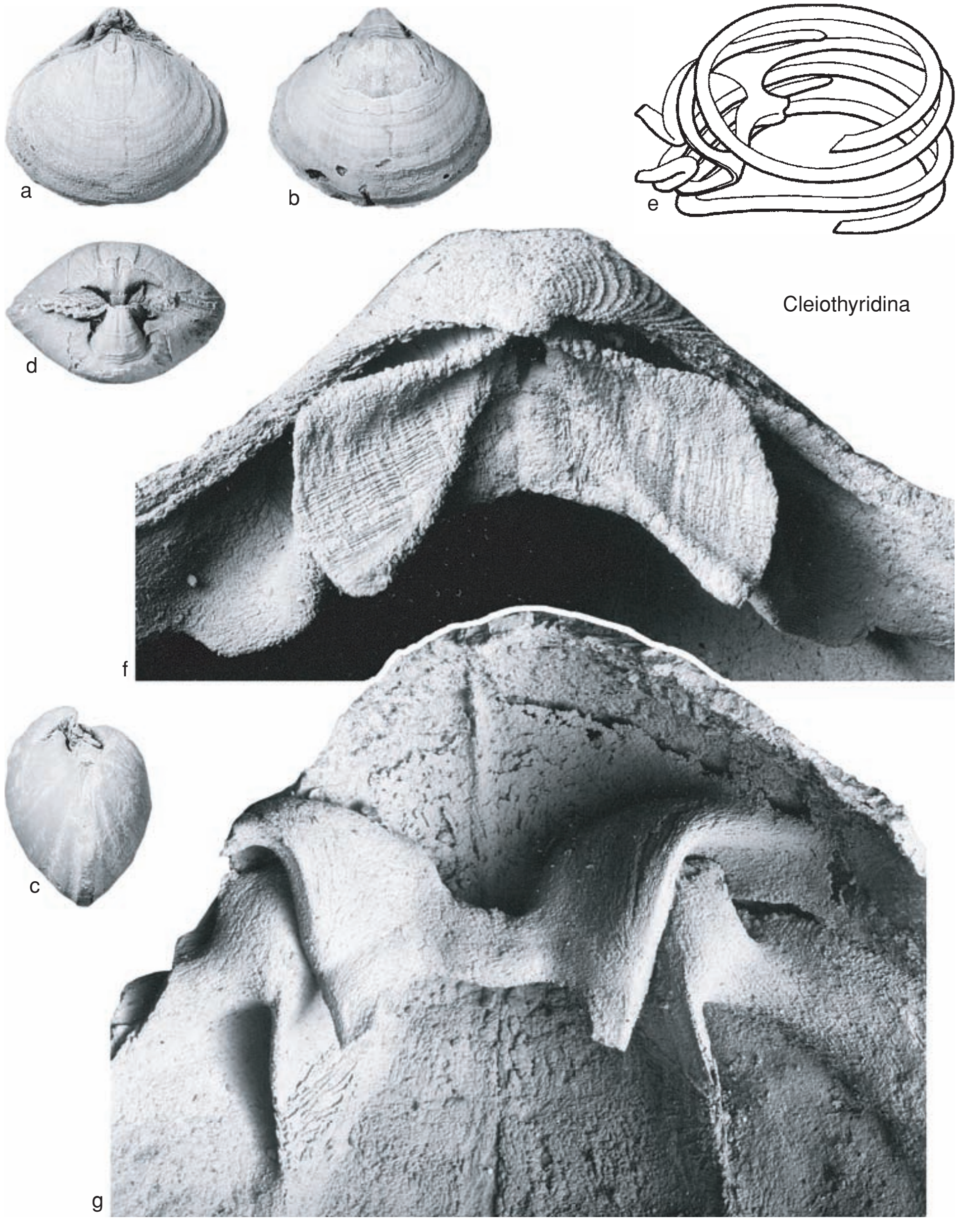

FIG. 1023. Athyrididae (p. 1510).

with winged overall aspect, well-defined subtrapezoidal ventral palintrope, almost straight hinge line equal or slightly shorter than maximum width; internally similar to *Bajtugania* but with low myophragm. *Lower Permian (Kungurian)–Upper Permian (Kazanian):* Kanin Peninsula, Spitzbergen, *Kungurian–Kazanian;* Russian Platform, *Kazanian.*——FIG. 1026,*2a–l.* **P. royssiana* (VON KEYSERLING), Kazanian, Russian Platform; *a–c,* dorsal, ventral, and anterior views, PIN 1120/845, ×1 (Grunt, 1980); *d–l,* transverse serial sections 8.9, 10.5, 11.9, 13.6, 14.2, 16.1, 16.2, 17.9, 18.8 mm from ventral umbo, PIN 1511/2302 (adapted from Grunt, 1986).

?Rawdonia PEOU, 1979, p. 190 [**R. nasharae;* OD]. Ventral valve exterior similar to *Cleiothyridina;*

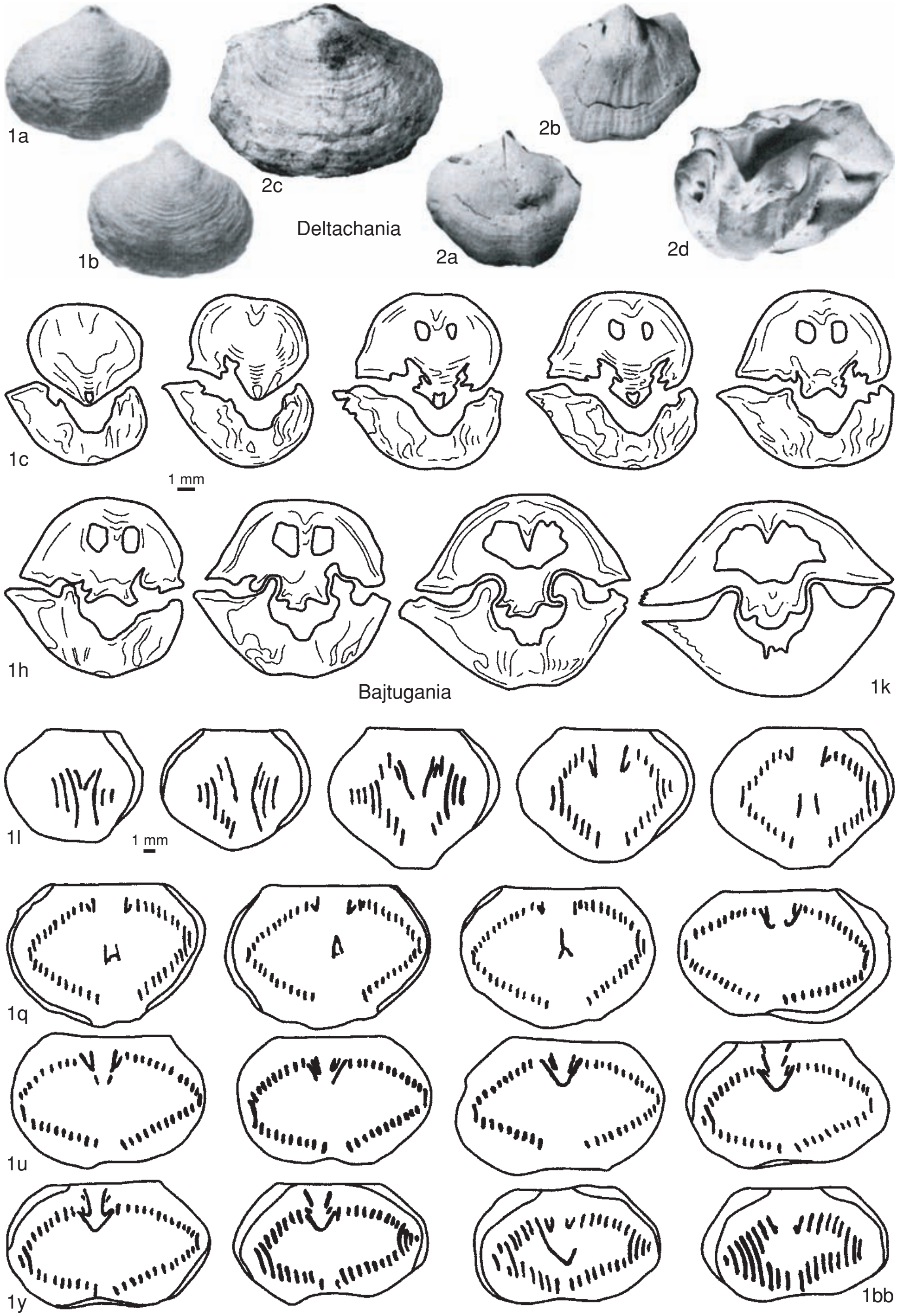

FIG. 1024. Athyrididae (p. 1510).

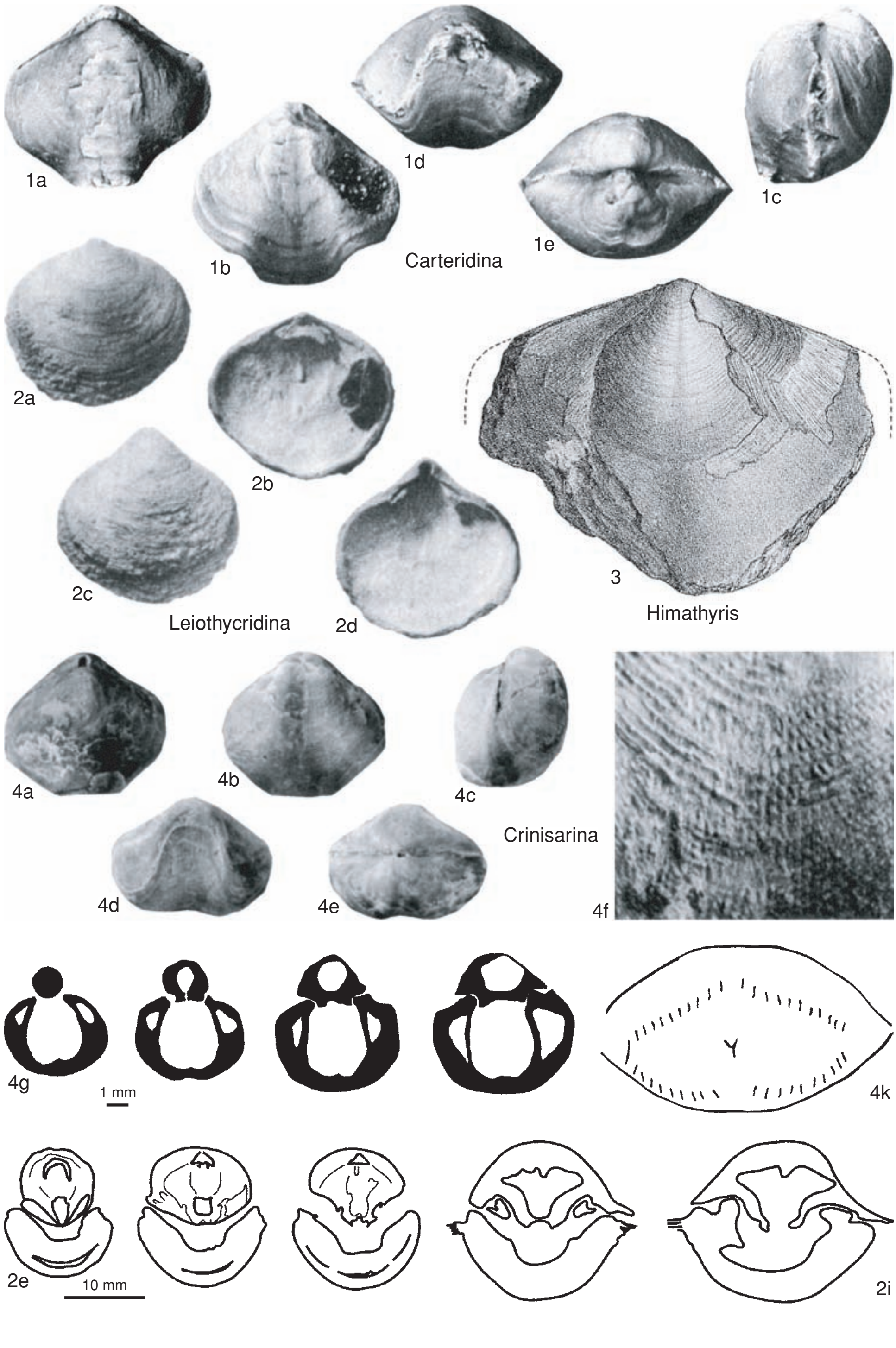

FIG. 1025. Athyrididae (p. 1510).

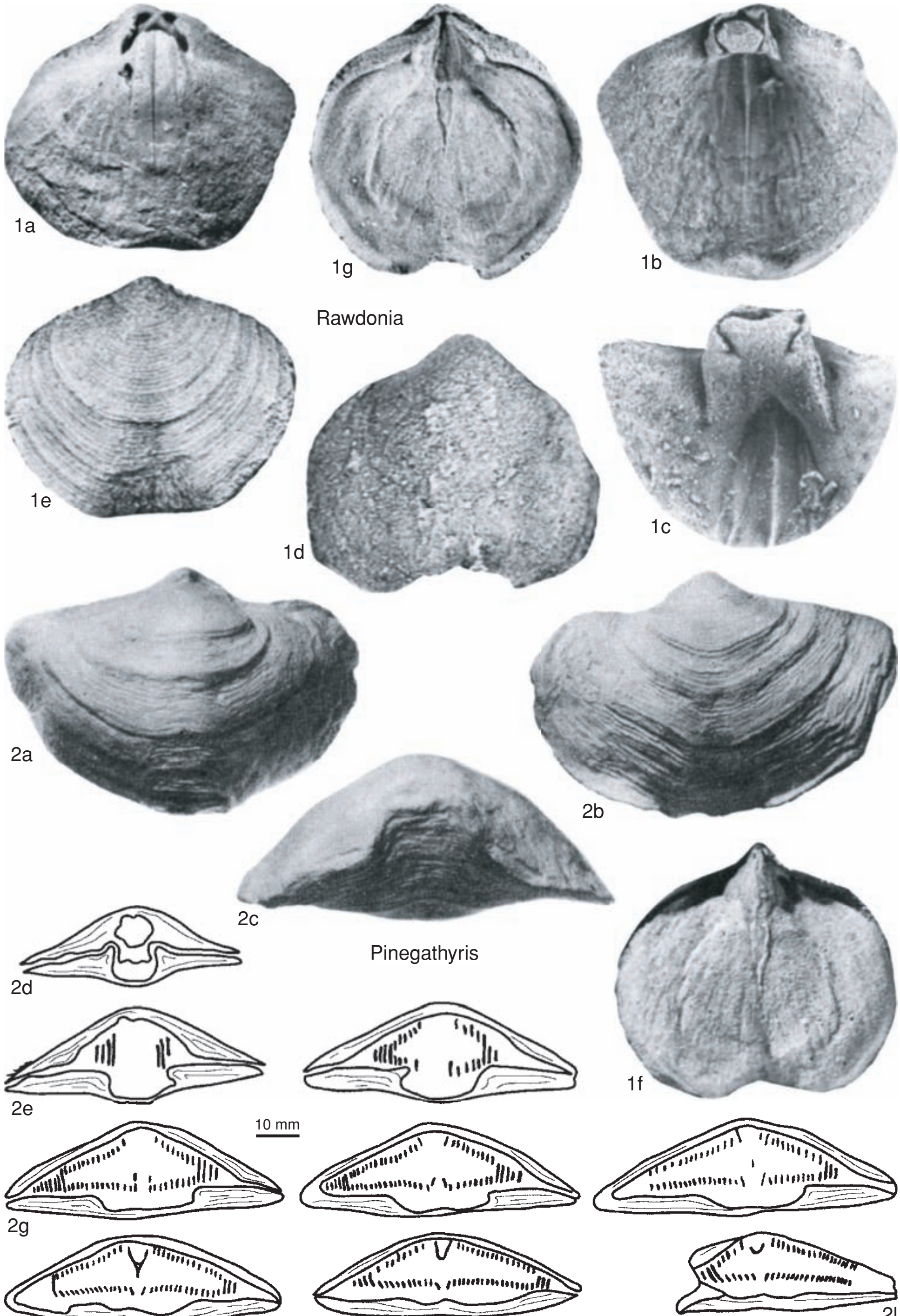

FIG. 1026. Athyrididae (p. 1510–1515).

dorsal valve smooth (?); poorly known. [Although the shells were found in the same beds, they were not conjoined. There is therefore the possibility that the smooth dorsal valves and the ornamented ventral valves do not belong to the same genus. This genus requires revision.] *Lower Carboniferous (Viséan):* Australia (New South Wales).——FIG. 1026,*1a–g.* **R. nasharae; a,* holotype, internal mold of dorsal valve, NUF 4128, ×2.5; *b,* holotype, ventral view of rubber mold, ×3; *c,* anterior view of rubber mold, ×5.7; *d,* exterior of dorsal valve (?), NUF 4116; *e,* exterior of ventral valve, ×2.5, NUF 4113; *f–g,* internal mold of ventral valve and rubber mold, NUF 4123, ×2.5 (Peou, 1979).

Subfamily COMELICANIINAE Merla, 1930

[*nom. correct.* POSENATO, 1989, p. 385, *pro* Comelicaniidae MERLA, 1930, p. 22, *nom. imperf.*]

Shell large to extremely large, smooth, with fine growth lines, commonly with 2 pairs of folds, more or less developed, on each valve; transverse, with greatest shell width at hinge margin; hinge line almost straight; ventral palintrope moderate to extensive, hypothyridid pedicle opening without deltidial plates, commonly obscured by beak of dorsal valve; pedicle supports absent; dental plates faintly developed or absent, low dental flanges may support teeth; cardinal plate triangular to subquadrangular and thick; cardinal flanges well developed; dorsal foramen infilled; median septum absent, but low dorsal myophragm may develop; jugum essentially as in *Athyris. Upper Permian (Changhsingian).*

Comelicania FRECH, 1901, p. 551 [*?*Spirifer megalotis* STACHE, 1878, p. 139; SD SCHUCHERT & LEVENE, 1929a, p. 43] [=*Spitispirifer* WATERHOUSE & GUPTA, 1986, p. 48 (type, *S. bisulcata,* OD); *Alatothyris* WATERHOUSE & GUPTA, 1986, p. 51 (type, *Spirifer Haueri* STACHE, 1878, p. 140, OD)]. Externally similar to *Anathyris;* dental plates thin and short; ventral and dorsal muscle fields deeply impressed, may be divided by low myophragm; cardinal plate subrectangular, rather thick, commonly with shallow longitudinal depression. *Upper Permian (Changhsingian):* southern Alps.——FIG. 1027,*1a–c.* **C. megalotis* (STACHE); *a,* holotype, ventral view of plaster replica, Monte Croce di Comelico, MGBW 3780, Stache Collection, ×1 (Posenato, 1998; photograph courtesy of R. Posenato); *b–c,* dorsal and posterior views, Sass de Putia, MDSGF PK1, ×1 (Posenato, 1989; photographs courtesy of R. Posenato).——FIG. 1028*a–m. C.* sp.; transverse serial sections 2.6, 4.6, 5.6, 9.0, 10.9, 11.7, 14.5, 15.5, 17.0, 20.2, 22.8, 24.5, 27.2 mm from ventral umbo, Val Brutta, MDSGF VB110 (adapted from Posenato, 1998).——FIG. 1027,*1d–e. C.* sp.; ventral and lateral views of reconstructed jugum, Val Brutta, MDSGF VB110 (Posenato, 1998).

Gruntallina WATERHOUSE & GUPTA, 1986, p. 51 [**Comelicania triangularis* GRUNT, 1965, p. 252; OD]. Similar to *Comelicania,* but much smaller; internally with very low dental flanges supporting teeth, transverse, smaller and flatter cardinalia with underlying median ridge. Jugum unknown. *Upper Permian (Changhsingian):* Transcaucasus.——FIG. 1027,*2a–g.* **G. triangularis* (GRUNT); *a–b,* holotype, dorsal and ventral views, Dzhul'fa Gorge, PIN 2073/551, ×1 (Grunt, 1965); *c–g,* transverse serial sections 0.8, 1.2, 1.5, 2.0, 2.5 mm from ventral umbo, PIN 2073/551 (adapted from Grunt, 1965).

Subfamily DIDYMOTHYRIDINAE Modzalevskaya, 1979

[Didymothyridinae MODZALEVSKAYA, 1979, p. 50]

Small to medium, strongly convex, moderately to strongly rostrate; growth lines weak, commonly without frills; dorsal fold and ventral sulcus commonly weak and narrow; dental plates thin and commonly short; ventral muscle field weakly impressed; cardinal plate commonly thin, flat, triangular, apically perforated by large foramen; cardinal process absent or rudimentary; jugal saddle moderately developed or absent; jugal arch may project posteroventrally as thin jugal stem, bifurcating into short accessory jugal lamellae, or as short horizontal and posteriorly directed stemlike process; shell thin valved, without tertiary layer. *Silurian (Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Famennian).*

Didymothyris RUBEL & MODZALEVSKAYA, 1967, p. 238 [**Terebratula? didyma* DALMAN, 1828, p. 146; OD]. Small to medium, unequally biconvex, elongate oval to rounded pentagonal smooth shells, sometimes with fine growth lines; ventral valve sulcate, dorsal valve with flat or slightly depressed median fold; anterior margin faintly emarginate; ventral beak high, slightly curved; hypothyridid pedicle opening partially closed by deltidial plates; low dorsal beak does not conceal delthyrium. Dental plates converging dorsally, anteriorly only dental flanges support teeth; large delthyrial chamber with 2 variably developed curved plates, formed of secondary layer, medially and apically situated, parallel to dental plates and joined with them at their posterodorsal end; very low dorsal myophragm may be present; cardinal plate and jugum essentially as in

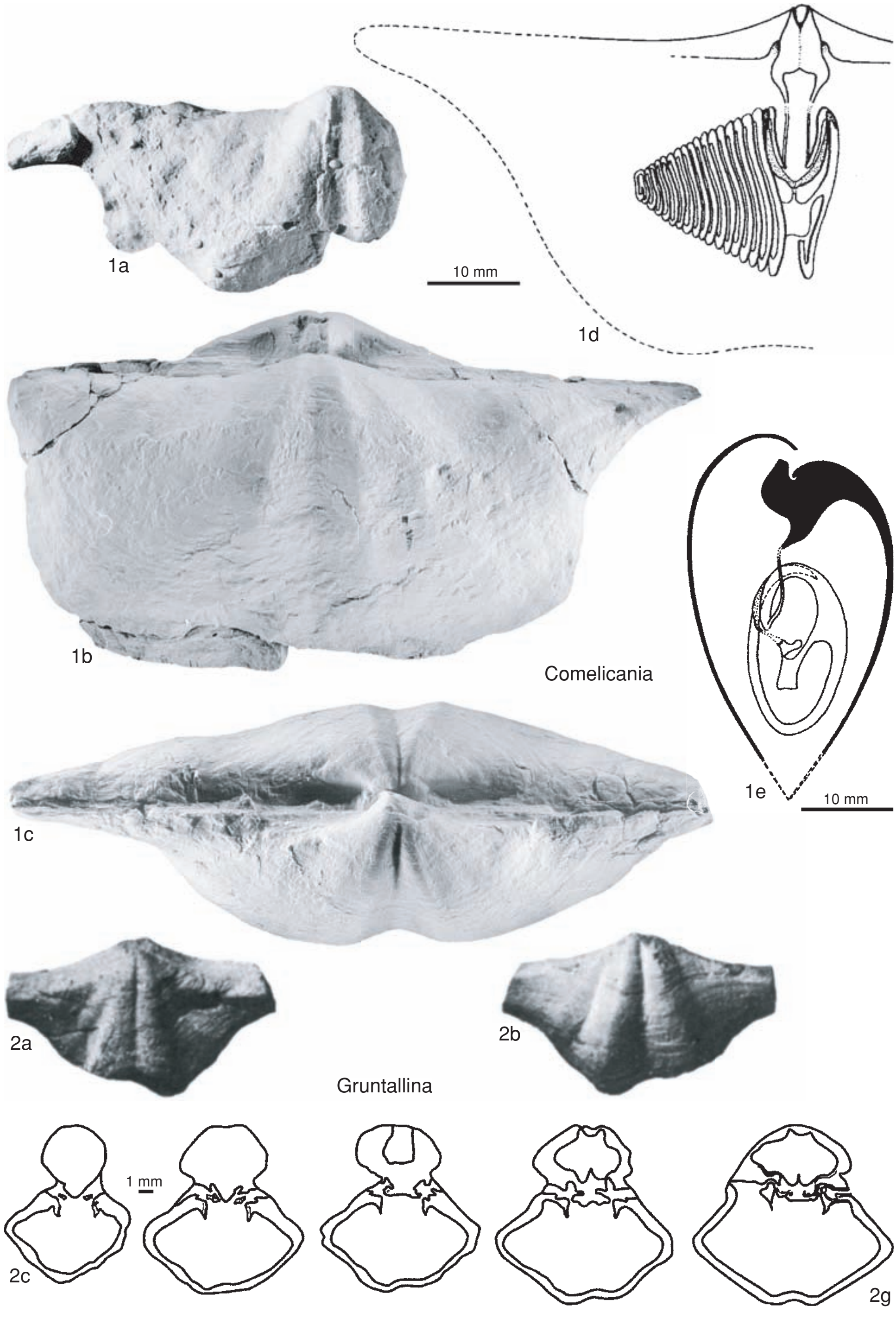

FIG. 1027. Athyrididae (p. 1515).

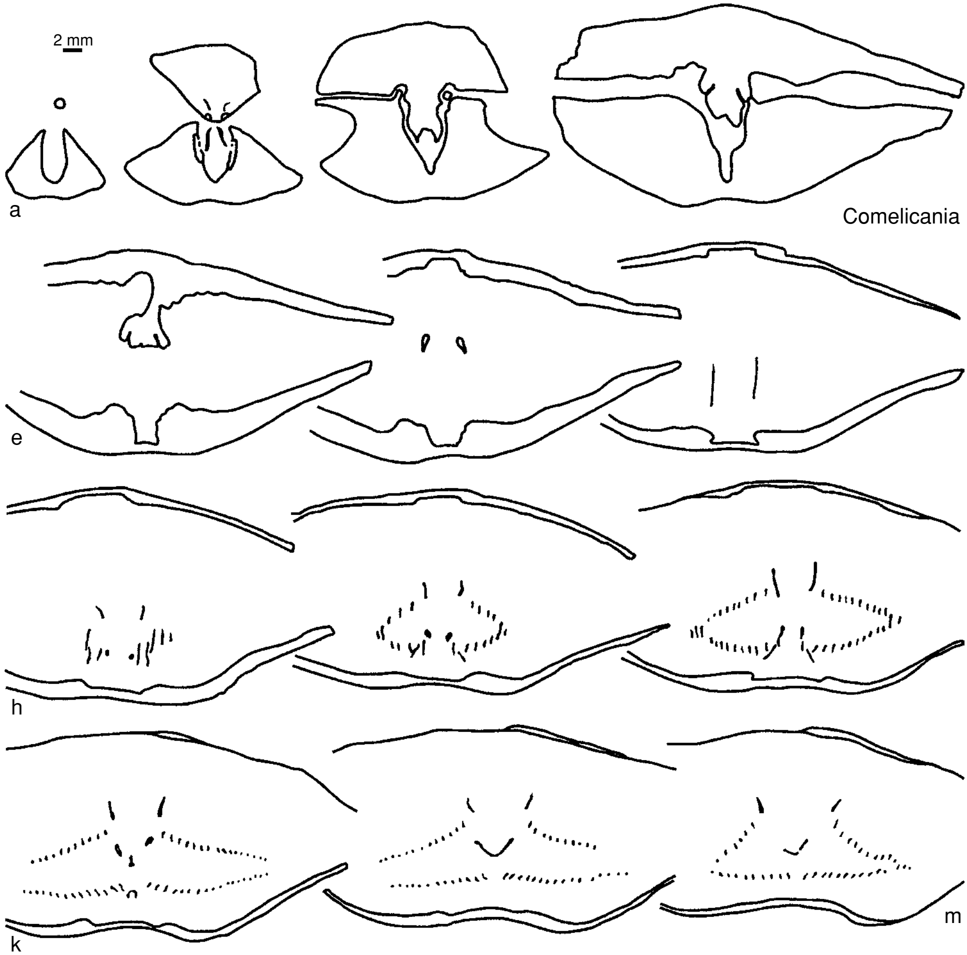

FIG. 1028. Athyrididae (p. 1515).

Athyris. Silurian (Wenlock–Ludlow, ?Přídolí): Estonia, ?Sweden, *Wenlock–Ludlow;* Gotland, Latvia, Podolia, Novaya Zemlya, Vaigach, Dolgii, Kotelmi, Chernova uplift, western circumpolar, northern, and central Urals, western Saian, ?Yukon, *Ludlow;* Salair, Altay, *Ludlow, ?Přídolí.*——FIG. 1029,*1a–w.* **D. didyma* (DALMAN), Ludlow, Estonia; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, TAGI BR 2629, ×2; *f,* ventral valve prepared to show dental and median plates, TAGI BR 2584, ×3; *g,* specimen polished to show ventral umbo structures, CNIGR 4/9742, ×1.5 (Rubel & Modzalevskaya, 1967; photographs courtesy of T. L. Modzalevskaya); *h–v,* transverse serial sections 0.7, 1.2, 1.5, 2.0, 2.4, 2.6, 3.0, 3.6, 4.0, 4.2, 5.1, 6.4, 7.8, 8.7, 9.1 mm from ventral umbo, distance from ventral umbo to first section approximate, CNIGR 69/11964; *w,* lateral view of jugum (adapted from Modzalevskaya, 1985).

Buchanathyris TALENT, 1956, p. 36 [**B. westoni;* OD]. Medium shell, subequally biconvex, subcircular to subelliptical in outline; with or without faintly developed dorsal fold and ventral sulcus; dental plates of medium length, medially concave; dorsal median septum or myophragm absent; lateral branches of jugum beginning posterior to middorsal valve length, inclined slightly anteriorly, united in acute jugal arch (without saddle), situated at middorsal valve length, pointed backward as short stemlike process, without bifurcations. *Lower Devonian (Pragian–lower Emsian):* Australia (Victoria, New South Wales), ?China.——FIG. 1029,*2a–n.* **B. westoni,* lower Emsian, Victoria; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, NMV P127838, ×1.5 (new; photographs courtesy of A. Sandford); *f–m,* transverse serial sections 0.50, 1.25, 1.50, 1.75, 2.00, 2.25, 2.50, 3.00 mm from ventral umbo, distance from ventral umbo to first

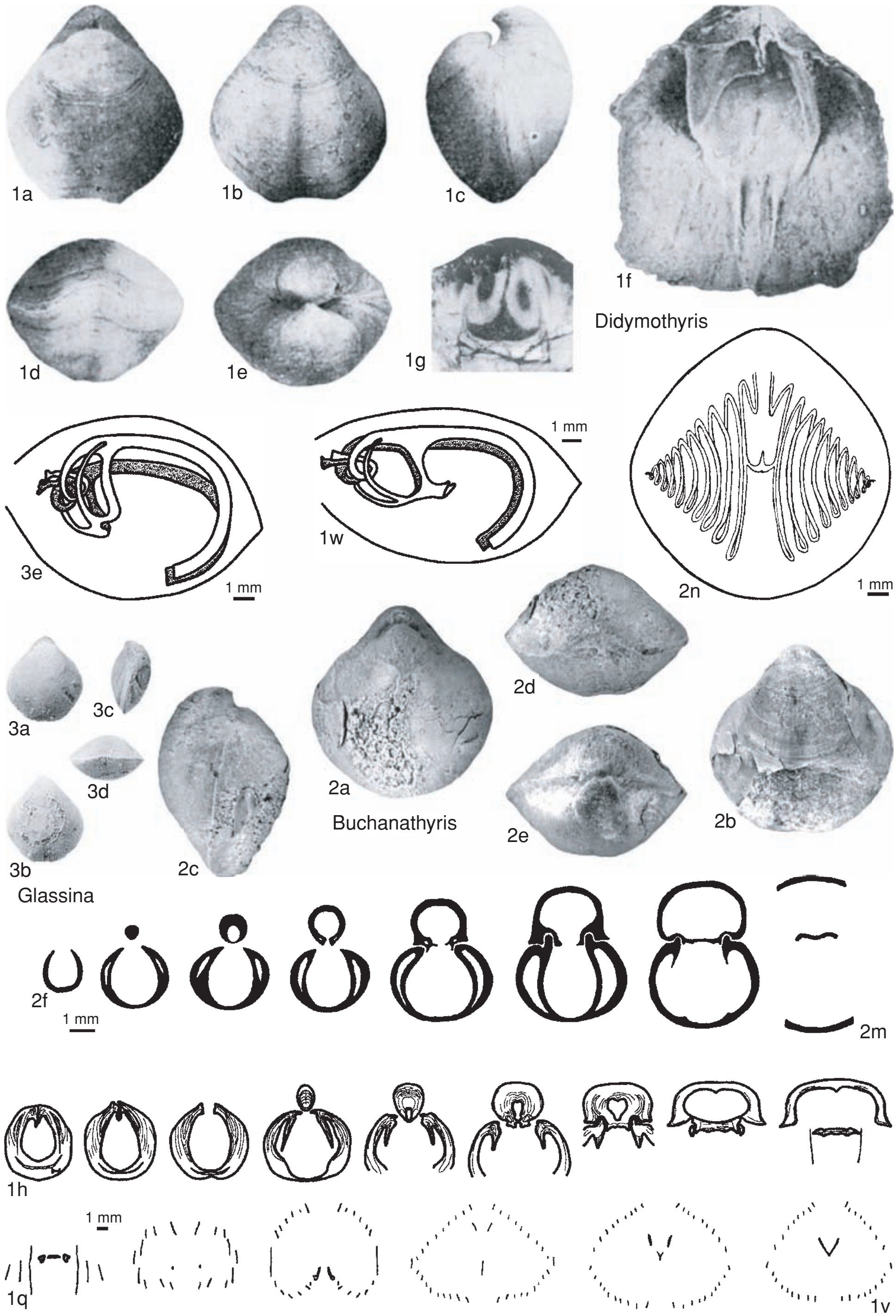

FIG. 1029. Athyrididae (p. 1515–1519).

section approximate (adapted from Talent, 1956); *n,* brachidium (Talent, 1956).

Collarothyris Modzalevskaya, 1970, p. 155 [**Meristella canaliculata* Veniukov, 1899, p. 143; OD]. Similar to *Didymothyris* but having dorsally convex delthyrial plate, instead of apically situated curved plates, parallel to dental plates. *Silurian (Přídolí):* Podolia, Estonia, Latvia, Novaya Zemlya, Dolgii, Vaigach, Chernyshev uplift, Bol'shezeml'-skaia Tundra, western circumpolar, northern, and central Urals.——Fig. 1030,*1a–e.* **C. canaliculata canaliculata* (Veniukov), Podolia; *a–d,* lectotype, dorsal, ventral, lateral, and anterior views, IGN 367/165, ×2 (Modzalevskaya, 1994a; photographs courtesy of T. L. Modzalevskaya); *e,* dorsal view of ventral beak of articulated specimen showing deltidial plates and pedicle support, CNIGR 15/ 9742, ×6 (Rubel & Modzalevskaya, 1967; photograph courtesy of T. L. Modzalevskaya).——Fig. 1030,*1f–w. C. canaliculata lata* (Chernyshev & Iakovlev), Bol'shezeml'skaia Tundra, Russia; *f–m,* transverse serial sections illustrating the development of cardinalia, 1.1, 1.3, 2.3, 2.4, 2.5, 2.8, 3.1, 3.4 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Modzalevskaya, 1970); *n–v,* transverse serial sections illustrating development of brachidium, 3.7, 4.5, 5.4, 5.8, 6.2, 6.6, 7.2, 7.3, 7.6 mm from ventral umbo, distance from ventral umbo to first section approximate, CNIGR 77/11964; *w,* lateral view of jugum (adapted from Modzalevskaya, 1985).

Dogdathyris Baranov, 1994, p. 31 [**D. horridula;* OD]. Similar to *Leptathyris* but reportedly with low median septum in ventral valve; jugum with long stem and short accessory jugal lamellae. *Lower Devonian (Emsian):* eastern Siberia, Yakutsk.——Fig. 1031,*1a–m.* **D. horridula; a–d,* holotype, dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/15, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov); *e–m,* transverse serial sections 0.4, 1.6, 2.7, 3.6, 4.7, 6.2, 6.7, 7.0, 8.0 mm from ventral umbo, GM YaRGTs 208/32 (adapted from Baranov, 1994).

Glassina Hall & Clarke, 1893, p. 98 [**Terebratula laeviuscula* J. de C. Sowerby, 1839, p. 631; OD]. Small, elongate subelliptical to subpentagonal, subequally moderately biconvex shells; slight median depression near front in ventral valve; anterior margin truncated or slightly emarginate; ventral beak small, incurved with minute oval foramen; hinge plate supported by median septum extending about one-third length of shell; jugum backward inclined X with upper tips curved outward, without jugal stem and saddle. *Silurian (Wenlock–Ludlow):* United Kingdom, Podolia, Gotland, Novaya Zemlya, Vaigach, ?Ontario.——Fig. 1029,*3a–d.* **G. laeviuscula* (Sowerby), Wenlock, Shropshire, England; *a–d,* dorsal, ventral, lateral, and anterior views, BMNH B5389(3), Davidson collection, ×2 (new; photographs courtesy of S. Long).——Fig. 1029,*3e. G. pentagona* Modzalevskaya, Ludlow, Podolia; lateral view of reconstructed jugum (adapted from Modzalevskaya, 1979).

Greenfieldia Grabau in Grabau & Sherzer, 1910, p. 148 [**G. whitfieldi;* OD]. Medium, subequally biconvex, elongate trigonal to subpentagonal shells, with or without faint sulcus on both valves; cardinal plate with narrow outer hinge plates and short, inner plates commonly fused medianly; dorsal median septum or myophragm absent; jugum as in *Buchanathyris. Silurian (Ludlow):* USA (Ohio, Michigan), Novaya Zemlya, Vaigach, Dolgii, Bol'shezemlia Tundra, China (?Yunnan).——Fig. 1031,*2a–b.* **G. whitfieldi,* Michigan, USA; dorsal and ventral interior molds, ×1 (Grabau & Sherzer, 1910).——Fig. 1031,*2c. G.* sp., Michigan, USA; jugum, USNM 487828, ×10 (Boucot, Alvarez, & Leibold, 1997).

?Jarovathyris Havlíček, 1987b, p. 241 [**Atrypa canaliculata* Barrande, 1879b, p. 89; OD]. Similar to *Glassina* but with narrow sulcus starting on dorsal umbo and unisulcate anterior commissure; internally with low myophragm, spiralia and jugum unknown; interior poorly known. [This genus requires revision.] *Silurian (Ludlow)–Lower Devonian (Lochkovian):* Czech Republic (central Bohemia).——Fig. 1030,*2a–d.* **J. canaliculata* (Barrande), upper Ludlow; lectotype, dorsal, ventral, lateral, and anterior views, L 23357, ×2 (Havlíček, 1990d).

Leptathyris Siehl, 1962, p. 212 [**L. gryphis;* OD]. Subequally biconvex, small to medium size, subcircular, elongate or transverse shell; ventral beak suberect; open delthyrium and minute foramen; commonly faintly bisulcate; few, widely spaced growth lines; shell thick in umbonal region; lateral apical cavities narrow, dental plates of medium length, subparallel; cardinal plate depressed, medially crested; stout myophragm may be developed; jugum as in *Buchanathyris. Lower Devonian (Emsian)–Middle Devonian (Givetian), Upper Devonian (?Famennian):* Germany, Bohemia, Salair, southern Siberia, southern China, USA (Nevada, Alaska), Canada, *Emsian–Givetian;* ?Poland, *Famennian.*——Fig. 1032*a–j.* **L. gryphis,* Eifelian, Eifel, Germany; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GIB Nr23, ×1.5; *f–j,* transverse serial sections 1.6, 1.7, 1.8, 2.0, 2.1 mm from ventral umbo, distance from ventral umbo to first section approximate (Siehl, 1962).——Fig. 1032*k–w. L. salaraica* Iazikov, Emsian, Salair; transverse serial sections 6.3, 7.8, 10.3, 10.9, 11.8, 13.1, 13.9, 15.2, 15.8, 16.1, 17.0, 17.2, 17.5 mm from ventral umbo, TSGM 839-15 (adapted from Iazikov, 1988).

Pseudoprotathyris Modzalevskaya, 1979, p. 59 [**Protathyris infantile* Kozlowski, 1929, p. 230; OD]. Small, subpentagonal, ventribiconvex shell; anteriorly faint sulcus in both valves; anterior margin may be slightly emarginate; dental plates subparallel; myophragm absent; inner hinge plates fused medially and dorsally concave; outer plates and crural bases projecting ventrally at right angle at anterior end of cardinal plate; lateral branches of

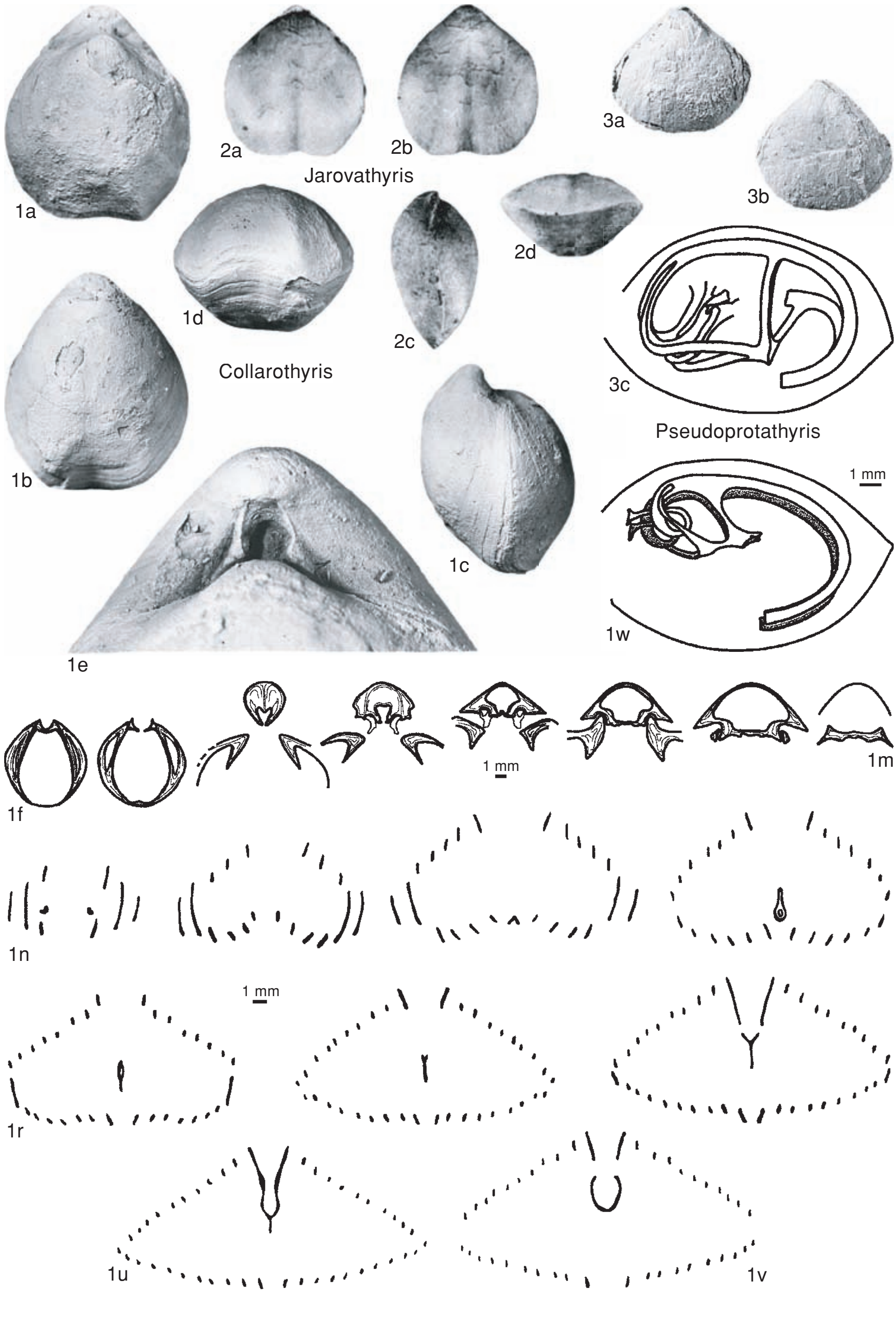

FIG. 1030. Athyrididae (p. 1519–1522).

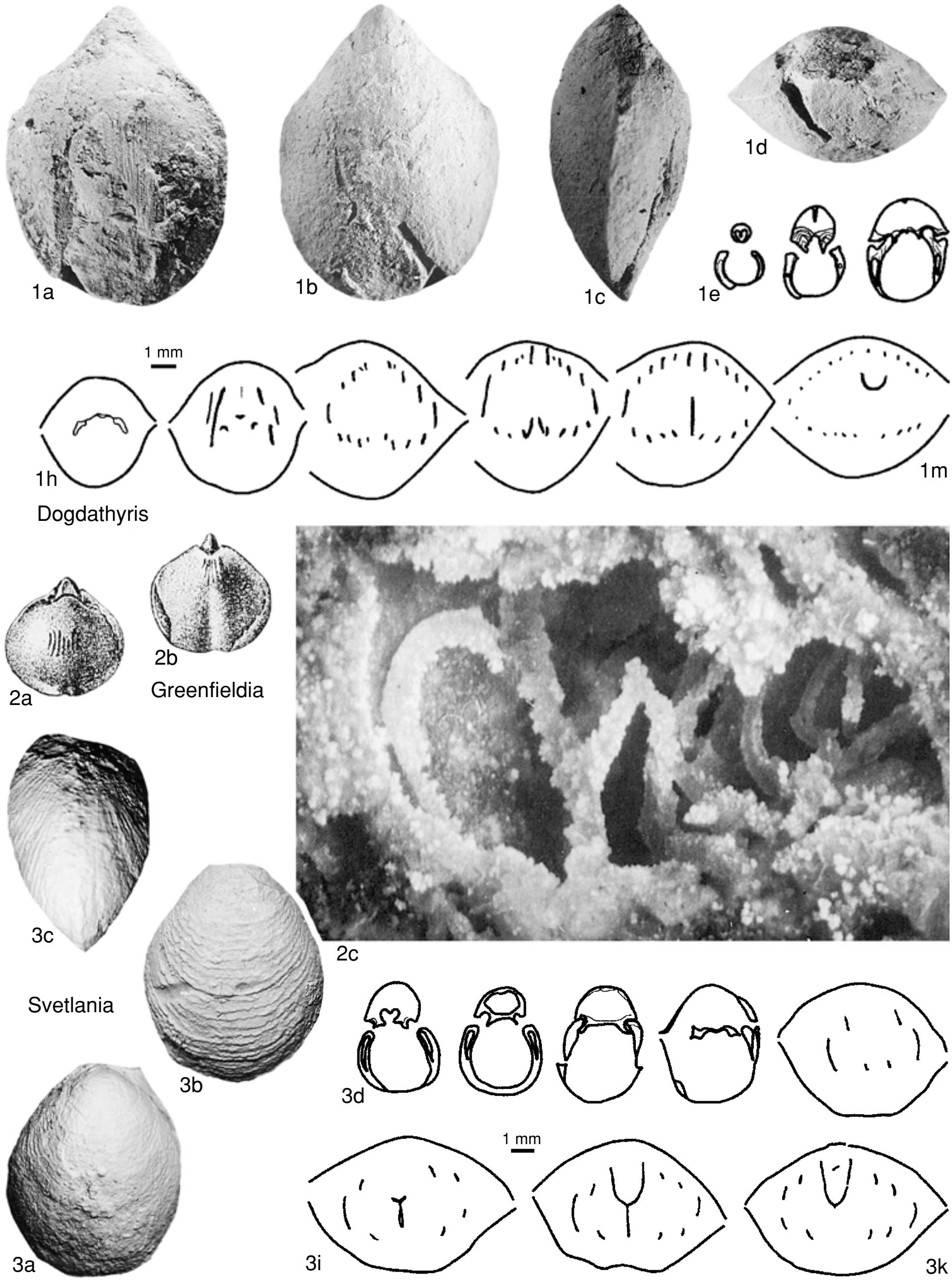

FIG. 1031. Athyrididae (p. 1519–1522).

jugum vertical; jugum anteriorly situated, without saddle and stem, projecting posteriorly up to dorsal valve midlength, there dividing into 2 accessory jugal lamellae posteriorly and dorsally directed, between primary and secondary lamellae, to end quite posteriorly to lateral branches of jugum. *Silurian (Wenlock)–Lower Devonian (Lochkovian):* Russia (Podolia), Bohemia, USA (Maryland), Arctic Canada.——FIG. 1030,*3a–c*. **P. infantilis* (KOZLOWSKI), Přídolí, Podolia; *a–b,* neotype, dorsal and

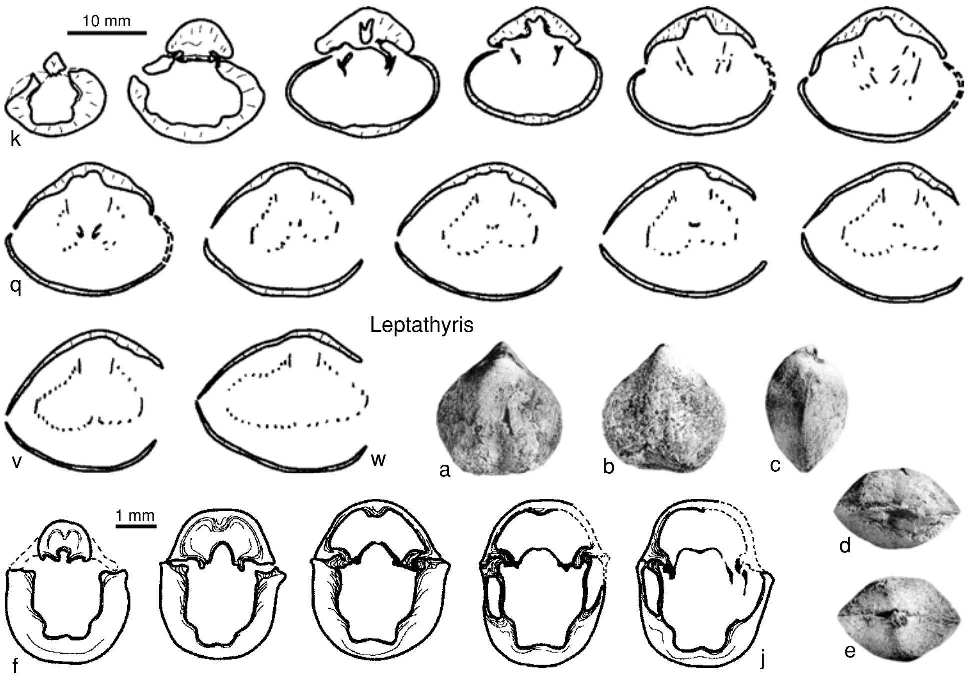

FIG. 1032. Athyrididae (p. 1519).

ventral views, CNIGR 14/11712, ×4 (Modzalevskaya, 1979; photographs courtesy of T. L. Modzalevskaya); *c,* lateral view showing reconstructed jugum, CNIGR 25/11712, approximately ×8 (adapted from Modzalevskaya, 1979).

Svetlania BARANOV, 1982, p. 48 [**S. rara;* OD]. Medium, elongate subelliptical, ventribiconvex shell; rectimarginate or with anterior faint sulcus in ventral valve; numerous lamellose growth lines; dental plates dorsally convergent; myophragm absent; cardinal plate with anterior median ridge; jugum with vertical lateral branches, long vertical stem, and reportedly short accessory jugal lamellae. *Lower Devonian–Middle Devonian:* eastern Siberia (Yakutsk). ——FIG. 1031,*3a–k*. **S. rara,* lower Emsian; *a–c,* holotype, dorsal, ventral, and lateral views, ventral umbo cut, YaTGU Museum 142/23, ×3 (Baranov, 1982; photographs courtesy of V. V. Baranov); *d–k,* transverse serial sections 1.2, 1.4, 1.6, 2.0, 3.2, 3.7, 3.8, 4.1 mm from ventral umbo, distance from ventral umbo to first section approximate, YaTGU Museum 142/26 (adapted from Baranov, 1982).

Subfamily HELENATHYRIDINAE Dagys, 1974

[Helenathyridinae DAGYS, 1974, p. 154]

Shell small, slightly rostrate, numerous growth lines; dorsal fold and ventral sulcus commonly absent; ventral beak short, suberect, with hypothyridid pedicle opening, with (*Eobiernatella, Sphaerathyris*) or without narrow deltidial plates; ventral area small, commonly orthocline; dental plates short to medium length, subparallel, or converging slightly ventrally, present until latest Givetian; cardinal plate apically perforate in Early Devonian, absent in Late Devonian; cardinal process absent; without dorsal septum or myophragm; lateral branches of jugum almost vertical, starting middorsal valve length; jugal saddle commonly absent, poorly developed and spiny when present; short, posteroventrally directed stem may be present; accessory jugal lamellae branching from ventral side of jugum, extending posterodorsally, and intercalating with spiralial loops to apex; thick shelled after Early Devonian. *Lower Devonian–Upper Devonian (Frasnian).*

Helenathyris ALEKSEEVA, 1969, p. 1157 [**H. plana;* OD]. Subcircular, weakly biconvex; growth plates covered with very fine fimbriae; dental plates short; cardinal plate apically perforate, inner sockets ridges and outer hinge plates projecting ventrolaterally.

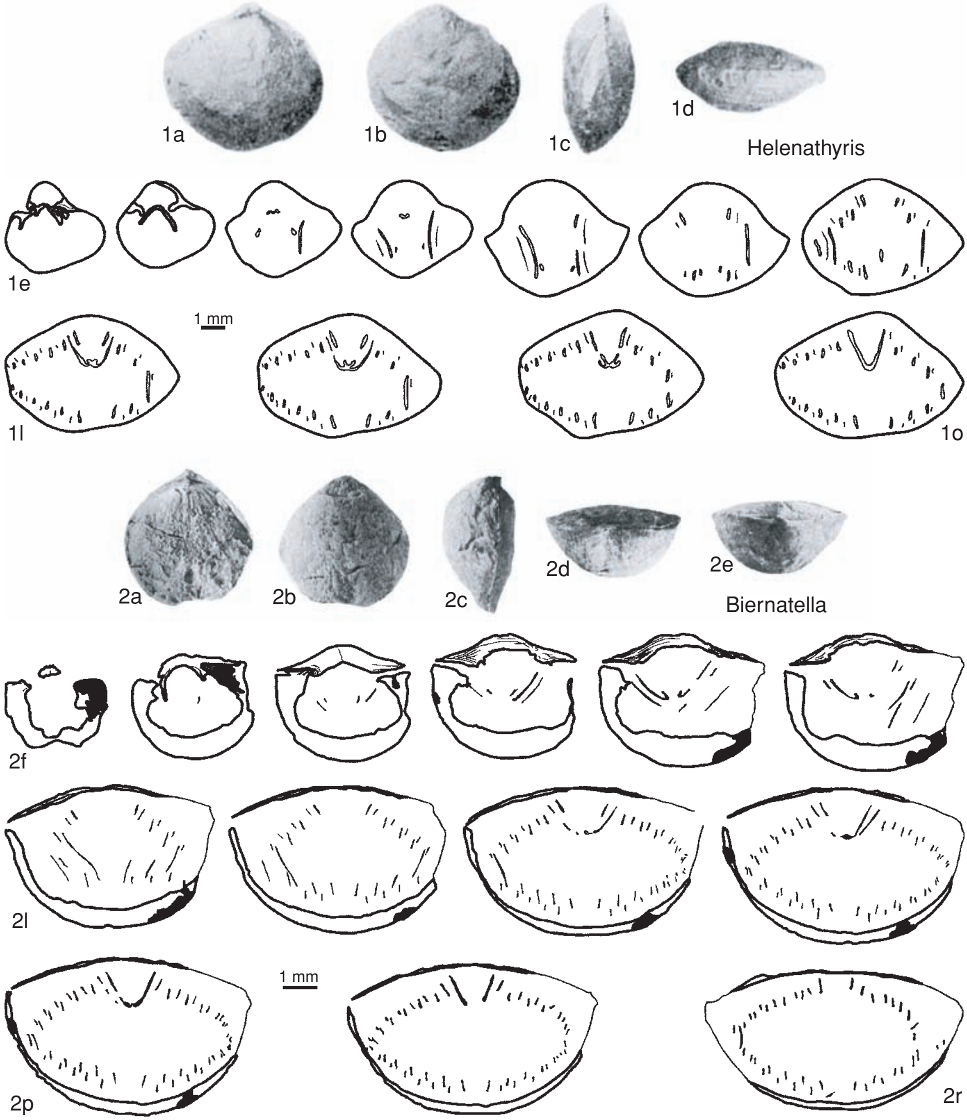

FIG. 1033. Athyrididae (p. 1522–1523).

Lower Devonian: northeastern Russia (Cherskogo Mountains).——FIG. 1033,*1a–o.* **H. plana; a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 340/1, ×2 (Alekseeva, 1969); *e–o,* transverse serial sections 1.7, 1.8, 1.9, 2.2, 2.4, 3.0, 3.8, 4.2, 4.3, 4.5, 4.6 mm from ventral umbo, IGiG 340/2 (adapted from Alekseeva, 1969).

Biernatella BALINSKI, 1977, p. 179 [**B. polonica;* OD] [=*Sedjulina* LIASCHENKO, 1985, p. 17 (type, *S. timanica,* OD)]. Elongate oval to subcircular, ventribiconvex; smooth, concentric lines weak, numerous; weak median sulcus may be present anteriorly; thick shelled. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Poland, western Russia.——FIG. 1033,*2a–r.* **B. polonica,* Frasnian, Kraków area, Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ZPAL Bp XXIII/31g, ×2 (Balinski, 1977); *f–r,* transverse serial sections 0.6, 0.8. 1.0, 1.15, 1.35, 1.5, 2.0, 2.3, 2.8, 2.9, 3.0, 3.15, 3.4 mm from ventral umbo, ZPAL Bp XXIII/30e (adapted from Balinski, 1977).

Eobiernatella BALINSKI, 1995b, p. 138 [**E. rackii;* OD]. Similar to *Biernatella* externally and to

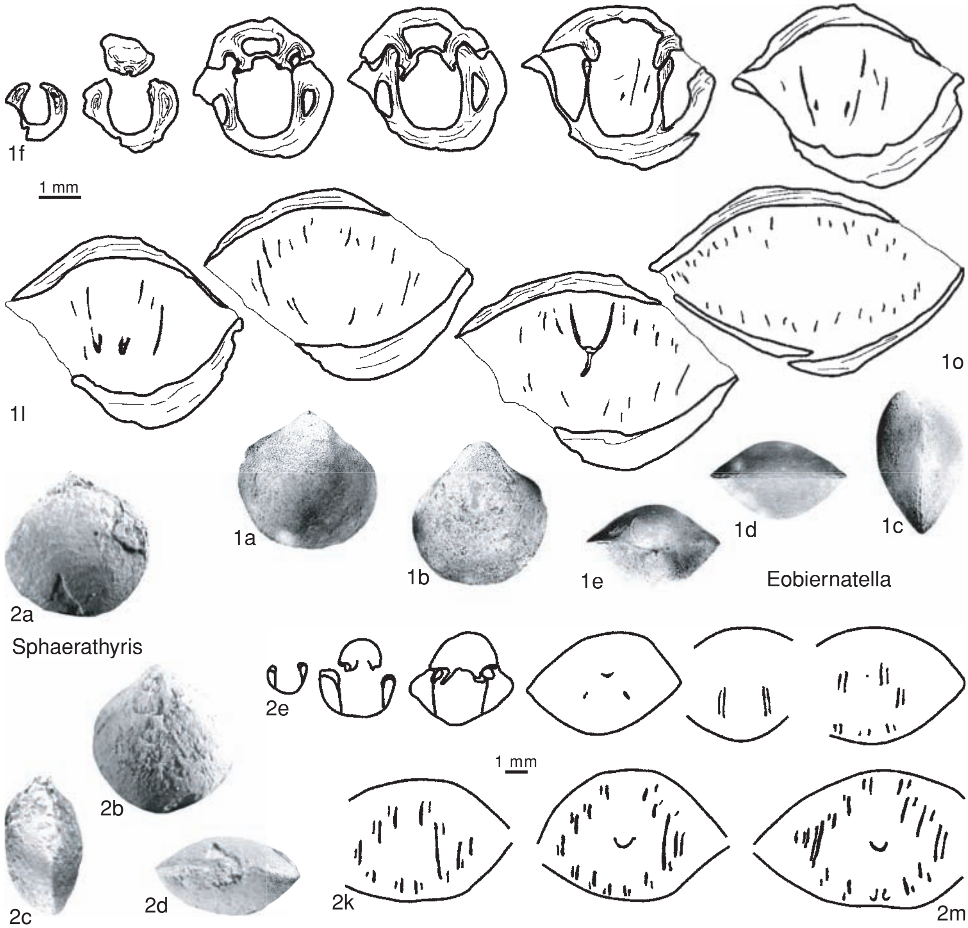

FIG. 1034. Athyrididae (p. 1523–1524).

Helenathyris internally; thick shelled. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Poland, Russia, ?Pyrenees.——FIG. 1034,*1a–o*. **E. rackii,* Givetian, Holy Cross Mountains, Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ZPAL Bp XXXVIII/7, ×2 (Balinski, 1995b); *f–o,* transverse serial sections 0.4, 0.6, 1.2, 1.4, 1.8, 2.1, 2.3, 2.9, 3.1, 4.1 mm from ventral umbo (adapted from Balinski, 1995b).

Sphaerathyris BARANOV, 1994, p. 34 [**S. repentina*; OD]. Similar to *Helenathyris* but differing in smooth exterior, delthyrium reportedly covered by deltidial plates, longer dental plates, and lack of stem in jugum. *Lower Devonian (upper Pragian–Emsian):* eastern Siberia, Yakutsk.——FIG. 1034,*2a–m*. **S. repentina,* Emsian; *a–d,* dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/20, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov); *e–m,* transverse serial sections 0.1, 0.4, 0.8, 1.3, 1.8, 2.1, 2.8, 3.3, 3.5 mm from ventral umbo, GM YaRGTs 208/42 (adapted from Baranov, 1994).

Subfamily LOCHENGIINAE Ching & Yang, 1977

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 842, *ex* Lochengiidae CHING & YANG, 1977, p. 412]

Shell very large, slightly to moderately rostrate; growth lines fine or lamellose, commonly plicate or costate; dorsal fold and ventral sulcus poorly developed or absent; dental plates short or absent; cardinal plate subtrapezoidal; cardinal flanges variably developed when present; jugum essentially as in *Athyris. Lower Carboniferous (Viséan)–Lower Permian.*

Lochengia Yoh, 1929, p. 70 [**L. lochengensis* Ching & Yang, 1977, p. 412; SD Jin, 1983, p. 227; =*Lochengia holoensis* Grabau, 1931a, p. 478, *nom. nud.; Cryptospirifer lochengensis* Grabau, 1931c, p. 405, *nom. nud.*] [=*Flexathyris* Grunt, 1980, p. 61 (type, *F. prokofjevi,* OD)]. Ventribiconvex to planoconvex or slightly concavoconvex, transversely oval, thick shells; dorsal fold faintly developed or absent, shallow ventral sulcus present from umbo; surface commonly with numerous, simple, round plicae variably developed; growth lines lamellose, closely and regularly spaced; very fine ribbing may be present in sulcus; ventral beak thick, strongly curved, foramen in meso- to permesothyridid position; dental plates moderately thick, short, low, converging slightly dorsally; cardinal plate thin, almost flat. [The genus is usually credited to Grabau (1931a, p. 478) although Yoh (1929, p. 70) should be considered its author (see Alvarez & Rong, 1995, p. 604).] *Lower Carboniferous (Viséan, ?Serpukhovian):* southern China (Guangxi), Russia (eastern Urals), Ukraine (Donetsk).——Fig. 1035,*1a–c.* **L. lochengensis* (Ching & Yang), Guangxi; holotype, dorsal, ventral, and lateral views, NIGP 70738, ×1 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Cryptospirifer Grabau, 1931c, p. 405 [**C. omeishanensis* Huang, 1933, p. 44; SD Wang, Ching, & Fang, 1964, p. 512]. Biconvex, transverse to subcircular or elongate oval, massive shells; without dorsal fold and ventral sulcus; few growth lines irregularly spaced; ventral beak short, strongly curved concealing small foramen; cardinal plate ventrally concave; cardinal flanges well developed; dorsal myophragm present. [The genus was credited by some authors to Huang (1933) although Grabau (1931b, p. 405) should be considered as author (see Alvarez & Rong, 1995, p. 604–605).] *Lower Permian:* southern China, Iran, Turkey, Armenia.——Fig. 1035,*4a–b.* **C. omeishanensis* Huang, Sichuan, southern China; holotype, ventral and posterior views, NIGP 4708, ×0.5 (Huang, 1933; photographs courtesy of Jin Yu-gan).

Galeatathyris Jin, 1983, p. 230 [**G. galeata;* OD]. Similar to *Lochengia* but clearly concavoconvex, with low ventral fold and wide and flat ears. *Lower Carboniferous (Viséan, ?Serpukhovian):* southern China.——Fig. 1035,*2a–c.* **G. galeata,* Guangxi; holotype, dorsal, ventral, and lateral views, NIGP 70750, ×0.5 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Titanothyris Ching & Hu, 1982, p. 253 [**T. subplicata;* OD]. Biconvex, subcircular to transversely oval shells, without dorsal fold and ventral sulcus; numerous coarse costae increasing in number anteriorly by bifurcation or intercalation; growth lines fine, growth lamellae stronger, more widely and randomly spaced; ventral beak short, strongly curved, concealing foramen; dental plates absent; cardinal flanges more or less developed; jugum unknown. *Lower Permian:* southern China.——Fig. 1035,*3a.* **T. subplicata,* western Sichuan; holotype, dorsal view, NIGP 70753, ×0.5 (Jin, 1983).——Fig. 1035,*3b. T. striata,* northwestern Hunan; detail of external ornamentation of ventral valve, NIGP 707555, ×0.5 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Subfamily PLICATHYRIDINAE Alvarez, 1990

[Plicathyridinae Alvarez, 1990, p. 93]

Shell medium to very large; anterior margin emarginate; moderately to strongly rostrate; ventral cardinal area (palintrope) moderate to extensive, covered by numerous, fine, and very closely spaced growth lines; dorsal cardinal area reduced; valve surfaces covered by numerous, concentric, fine, imbricate lamellae projecting outwardly; folding mixed (opposite medially and laterally, alternate between these zones); dental plates commonly of medium length, thin, slightly concave medianly, subparallel or converging dorsally; hinge plate rather wide, concave, and commonly with the median part projecting anteroventrally, giving plate a generally lobate aspect; outer hinge plates reduced; cardinal flanges moderately developed (well developed in *Anathyrella*); dorsal myophragm commonly present; jugum essentially as in *Athyris* with lateral branches of jugum starting in posterior third of primary lamellae, almost perpendicular to them, to a point at which they curve abruptly laterally or anterolaterally; they then project anteroventrally at a low angle before joining as jugal arch; anterior edge of jugal saddle spiny; jugal stem vertical. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian), ?Lower Carboniferous.*

Plicathyris Khalfin, 1946, p. 56 [**Terebratula Ezquerra* de Verneuil & d'Archiac, 1845, p. 467; OD]. Large, elongate to transverse shells, outline palmate; hinge line almost straight, rather shorter than maximum width; with median and outer lateral folds of dorsal valve and inner median and lateral folds of ventral valve starting at apex, well defined, sometimes carinate; inner lateral folds poorly developed or absent; outer median folds gentle and rounded; ventral cardinal area reduced. [The genus *Plicathyris* Khalfin, 1946 was placed in subjective synonymy with *Anathyris* von Peetz, 1901, by Boucot, Johnson, & Staton, 1965, p. 662. For validation of *Plicathyris* Khalfin, 1946 and discussion of its type species see Alvarez, 1990, p. 93–94]. *Lower Devonian (Pragian)–Upper Devonian*

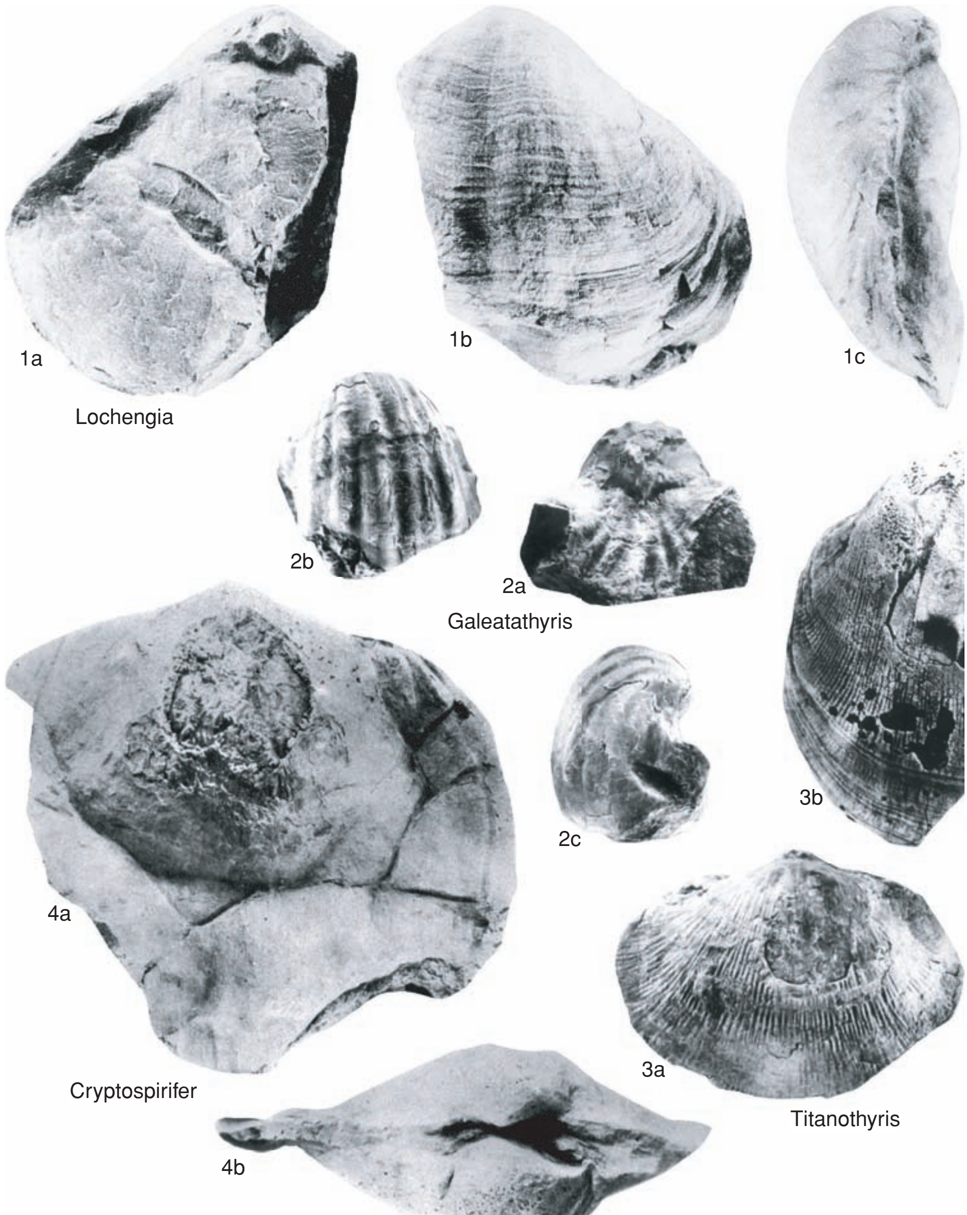

FIG. 1035. Athyrididae (p. 1525).

(lower Frasnian): northwestern Spain, France, Belgium, *Pragian–Emsian;* Kuznetsk, Altay, Salair, *upper Givetian–lower Frasnian.*——FIG. 1036*a–v.* **P. ezquerrai* (DE VERNEUIL & D'ARCHIAC), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Asturias, Spain, EM 20109, de Verneuil Collection, ×1; *f,* growth lamellae in posterior area, Asturias, Spain, EM 20109, de Verneuil Collection, ×7; *g,* growth lamellae in posterior area, Asturias, Spain, EM 20109, de Verneuil Collection, ×17 (Alvarez, 1990); *h–v,* transverse serial sections 1.15, 1.35, 2.00, 2.30, 2.60, 3.25,

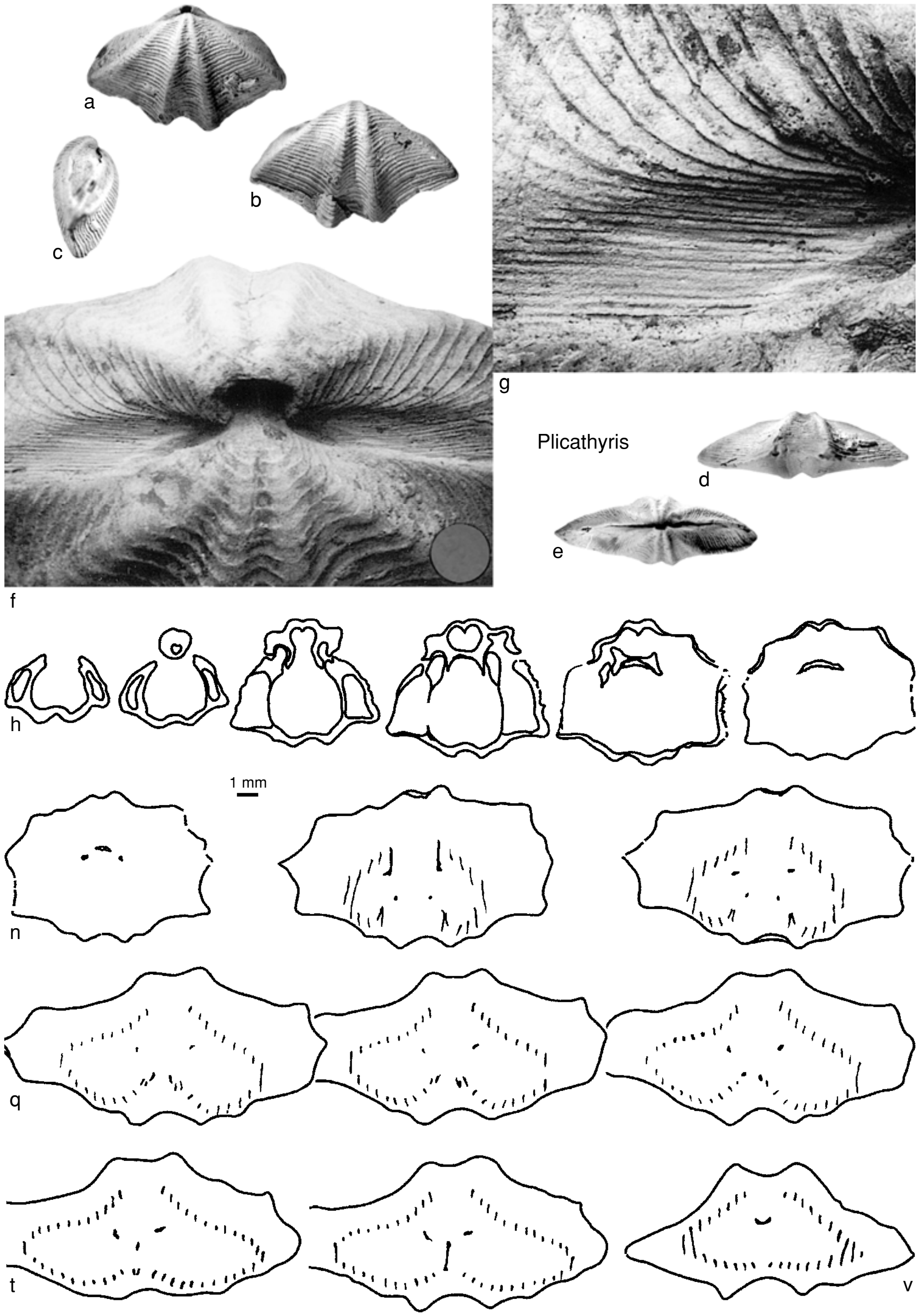

FIG. 1036. Athyrididae (p. 1525–1528).

3.85, 5.80, 6.30, 7.70, 7.80, 7.90, 8.45, 8.60, 10.30 mm from ventral umbo, León, Spain, DPO 19444 (adapted from Alvarez, 1990).——FIG. 1037*a–q.* **P. ezquerrai* (DE VERNEUIL & D'ARCHIAC), upper Emsian; *a–p,* tangential serial sections, parallel to commissural plane, 1.60, 1.90, 2.30, 2.40, 2.60, 2.85, 3.30, 3.75, 3.90, 4.05, 4.35, 4.45, 4.60, 4.85, 4.90, 5.00 mm from ventral valve, León, Spain, DPO 19442; *q,* lateral view of reconstructed jugum, León, Spain, approximately ×5 (adapted from Alvarez, 1990). [See also Fig. 1002.6, p. 1477, in introduction.]

Anathyrella KHALFIN in GRATSIANOVA, SINCHENKO, & KUL'KOV, 1961, p. 476 [**Anathyris ussoffi* KHALFIN, 1933, p. 112; OD]. Medium to large, transverse shells with widely flaring flanks; dorsal fold and ventral sulcus well developed, sometimes hypertrophically; hinge line almost straight, equal or slightly shorter than maximum width; ventral cardinal area rather high, subtrapezoidal, concave; thick-shelled ventral valve with poorly differentiated dental plates; may have pedicle support resembling that of early didymothyridins; stout subquadrate cardinal plate with dorsal foramen reportedly present, filled late in growth; thick cardinal flanges projecting strongly into delthyrial cavity; jugum unknown. [According to GRATSIANOVA & DAGYS (1983) all athyridid descriptions in GRATSIANOVA, SINCHENKO, & KUL'KOV (1961) were made by the editor of the volume, L. L. KHALFIN, although this does not appear in the table of contents; the date on the publication is 1960, but GRATSIANOVA (1975, p. 72) cites this publication as 1960 (1961) and *Nomenclator Zoologicus* (EDWARDS & VEVERS, 1975) also lists *Anathyella* [*sic*] as 1961. Note that *ussovi* is deemed to be an incorrect subsequent spelling for *ussoffi.*] *Upper Devonian (Frasnian):* northeastern Kuznetsk basin, Gorno-Altay.——FIG. 1038,*1a–d.* **A. ussoffi* (KHALFIN), northeastern Kuznetsk basin; dorsal, ventral, anterior, and posterior views, ×1 (new; photographs courtesy of T. L. Modzalevskaya).——FIG. 1038,*1e–m. A. peetzi* (KHALFIN), Gorno-Altay; transverse serial sections, distances for serial sections not indicated, TsGM 470-21b (adapted from Gratsianova & Dagys, 1983).

Anathyris VON PEETZ, 1901, p. 134 [**Spirifera phalaena* PHILLIPS, 1841, p. 71; SD SCHUCHERT & LEVENE, 1929a, p. 29]. Medium to very large transverse shells with overall winged outline; hinge line almost straight, equal to or slightly shorter than maximum width; folding almost opposite and anterior commissure straight in juveniles, passing during ontogeny to develop a clearer mixed folding; ventral cardinal area well defined, rather high, subtrapezoidal, concave, ranging from apsacline to almost catacline in lateral regions to strongly curved anacline centrally; area covered by numerous, close and horizontal, well-marked growth lines; foramen in permesothyridid position; delthyrium wide, triangular, open or partially restricted laterally by narrow deltidial plates; internally similar to *Plicathyris* but with thicker teeth and dental plates; in late growth stages of some specimens dorsal foramen filled. [For discussion of its type species and other species included, see ALVAREZ, 1990, p. 206–207. The inclusion of *A. rhomboidalis* from the Lower Carboniferous of Hunan, China, may extend the range from the Upper Devonian, Frasnian, but assignment uncertain.] *Lower Devonian (Emsian)–Upper Devonian (Frasnian), ?Lower Carboniferous:* northwestern Spain, France, northern Africa, Saudi Arabia, *Emsian;* England, Czech Republic, Timan, Kuznetsk Basin, North America, *Middle Devonian;* Timan, Urals, Kuznetsk basin, Afghanistan, *Frasnian;* ?Hunan, *?Lower Carboniferous.*——FIG. 1039*a–x.* **A. phalaena* (PHILLIPS); *a,* lectotype, ventral view, Middle Devonian, Devon, United Kingdom, GSM 6866, Phillips Collection, ×1 (Alvarez, 1990; photograph courtesy of D. E. Butler); *b–f,* dorsal, ventral, lateral, anterior, and posterior views, upper Emsian, Asturias, Spain, EM 20142, de Verneuil Collection, ×1 (Alvarez, 1990); *g–w,* transverse serial sections 0.80, 1.40, 1.70, 3.00, 3.40, 4.00, 5.75, 6.20, 8.25, 8.75, 9.00, 9.70, 11.00, 11.50, 12.80, 15.50, 18.85 mm from ventral umbo, upper Emsian, Asturias, Spain, DPO 24481, ×1.5 (adapted from Alvarez, 1990); *x,* dorsal view of winged specimen, upper Emsian, León, Spain, DPO 24777, ×1.5 (Alvarez, 1990). [See also Fig. 1003.3, p. 1478, in introduction.]

Hexarhytis ALVAREZ, 1990, p. 157 [**H. bonarensis;* OD]. Medium to large, equidimensional to elongate shells with generally lobate outline; slightly curved hinge line, rather narrower than maximum width; both valves with 6 unequal bifurcating folds; ventral cardinal area poorly defined, not very high, triangular, concave; internally similar to *Plicathyris* but dental plates thinner and shorter. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Spain, France, Transcaucasus, Saudi Arabia.——FIG. 1040*a–bb.* **H. bonarensis,* upper Emsian, León, Spain; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, DPO 23838, ×1 (Alvarez, 1990); *f–bb,* transverse serial sections 0.20, 0.60, 1.15, 1.45, 1.50, 1.55, 1.95, 2.15, 2.45, 2.80, 3.45, 3.55, 3.80, 4.20, 4.55, 4.65, 4.80, 4.85, 5.25, 5.55, 6.05, 6.75, 7.15 mm from ventral umbo, DPO 23839 (adapted from Alvarez, 1990). [See also Fig. 1001, p. 1476, and Fig. 1003.1, p. 1478, in introduction.]

Sulcathyris DÜRKOOP, 1970, p. 190 [**S. periplicata;* OD]. Medium to large, ventribiconvex, strongly rostrate, subcircular to subpentagonal shells; anterior margin slightly emarginate; ventral sulcus starting at apex, dorsal median fold flat or divided by narrow, shallow furrow, 2 wide folds may develop anterolaterally in both valves, parasulcate folding with anterior and lateral commissures in same plane; internally similar to *Athyris* but with deep, narrow sulcus in posteriormost part of cardinal plate, dorsal foramen reportedly present. *Middle Devonian (Eifelian):* western Afghanistan, Iran.——FIG. 1038,*2a–p.* **S. periplicata,* western Afghani-

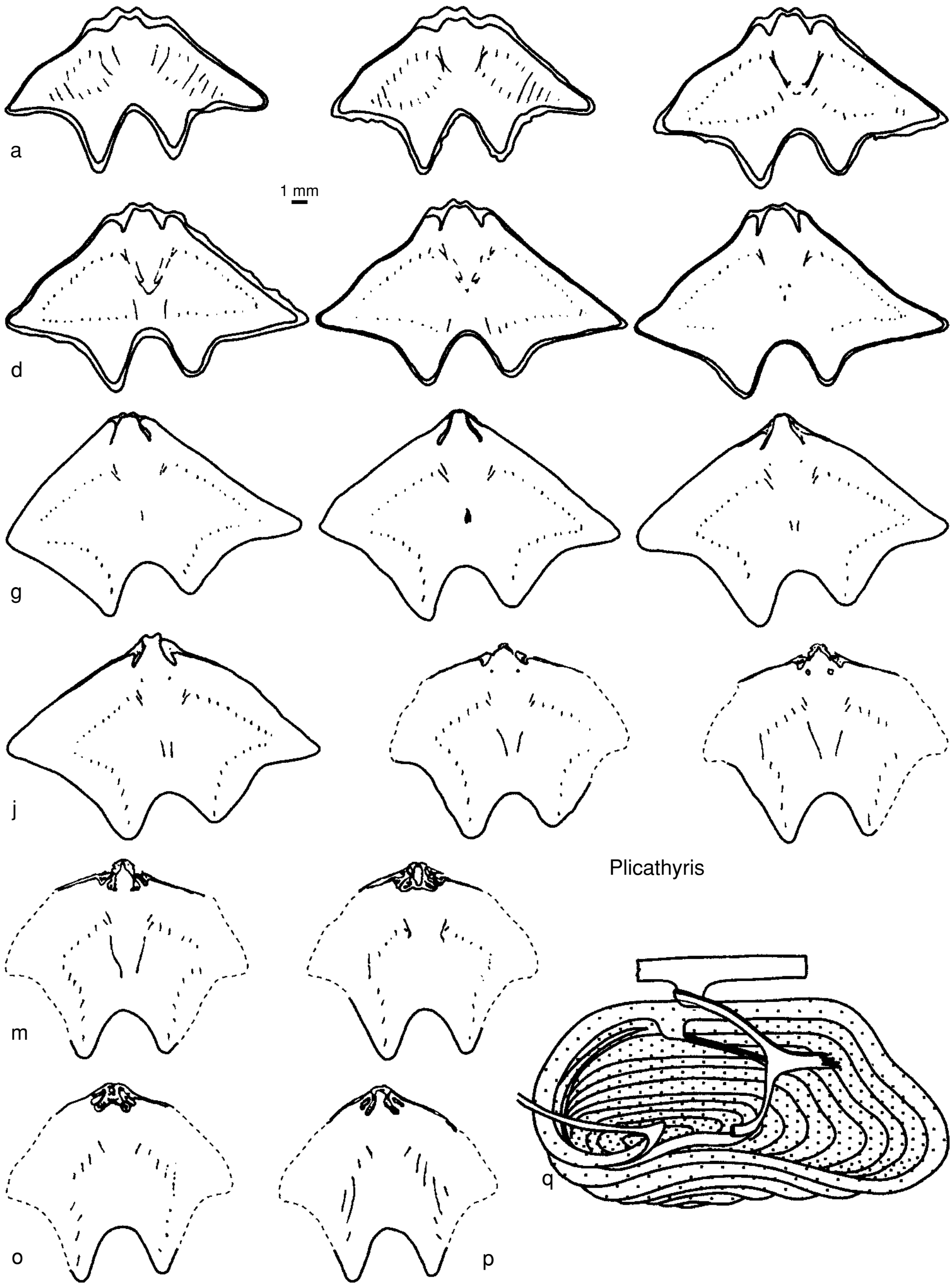

FIG. 1037. Athyrididae (p. 1525–1528).

stan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GPIBo 91, ×1.5 (Dürkoop, 1970); *f–k,* transverse serial sections showing cardinalia, 1.9, 2.6, 2.7, 3.1, 3.4, 4.0 mm from ventral umbo, GPIBo 93; *l–o,* transverse serial sections showing spiralium, 6.8, 8.6, 10.0, 10.4 mm from ventral umbo, GPIBo 95; *p,* jugum, approximately ×10 (adapted from Dürkoop, 1970).

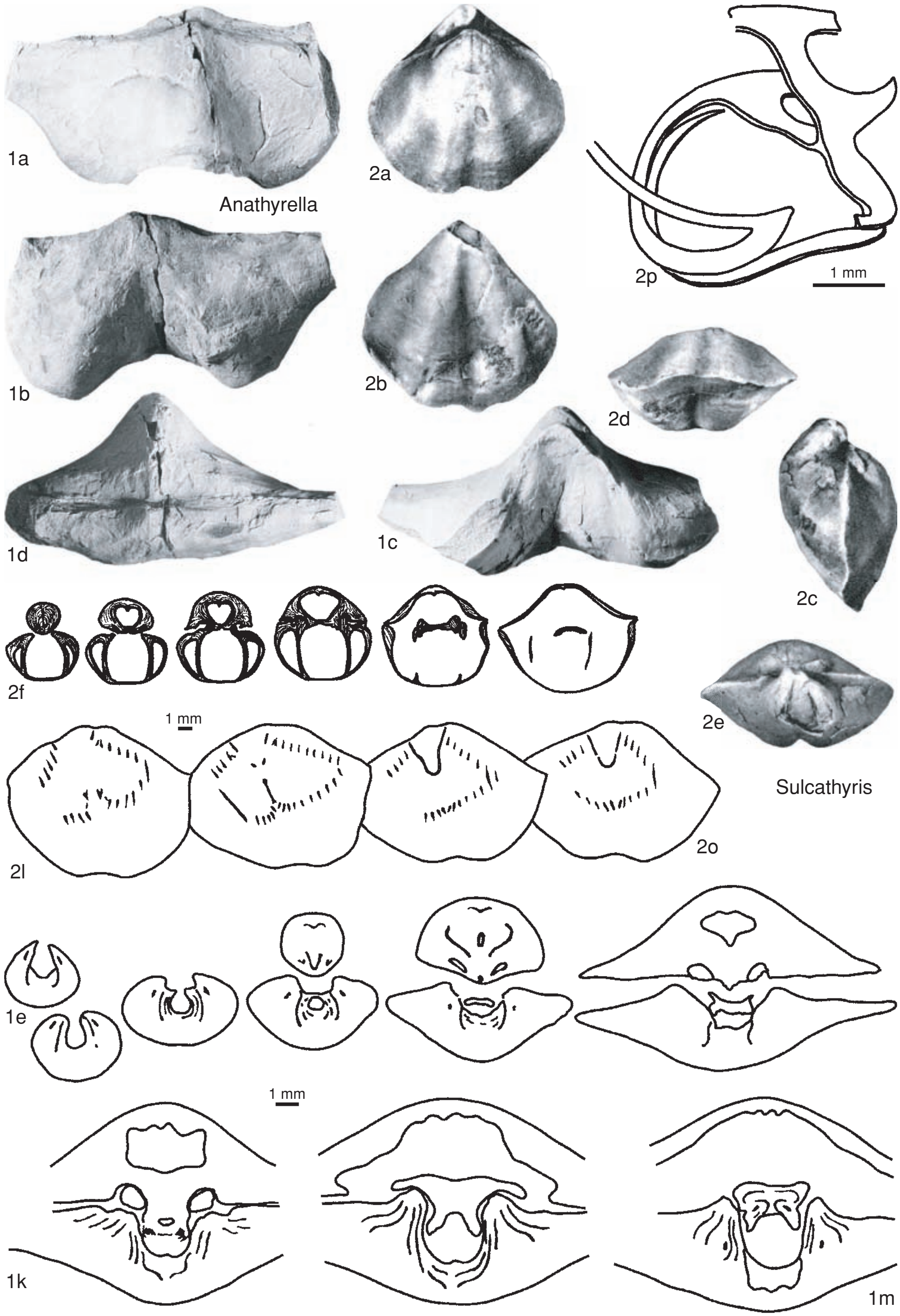

FIG. 1038. Athyrididae (p. 1528–1529).

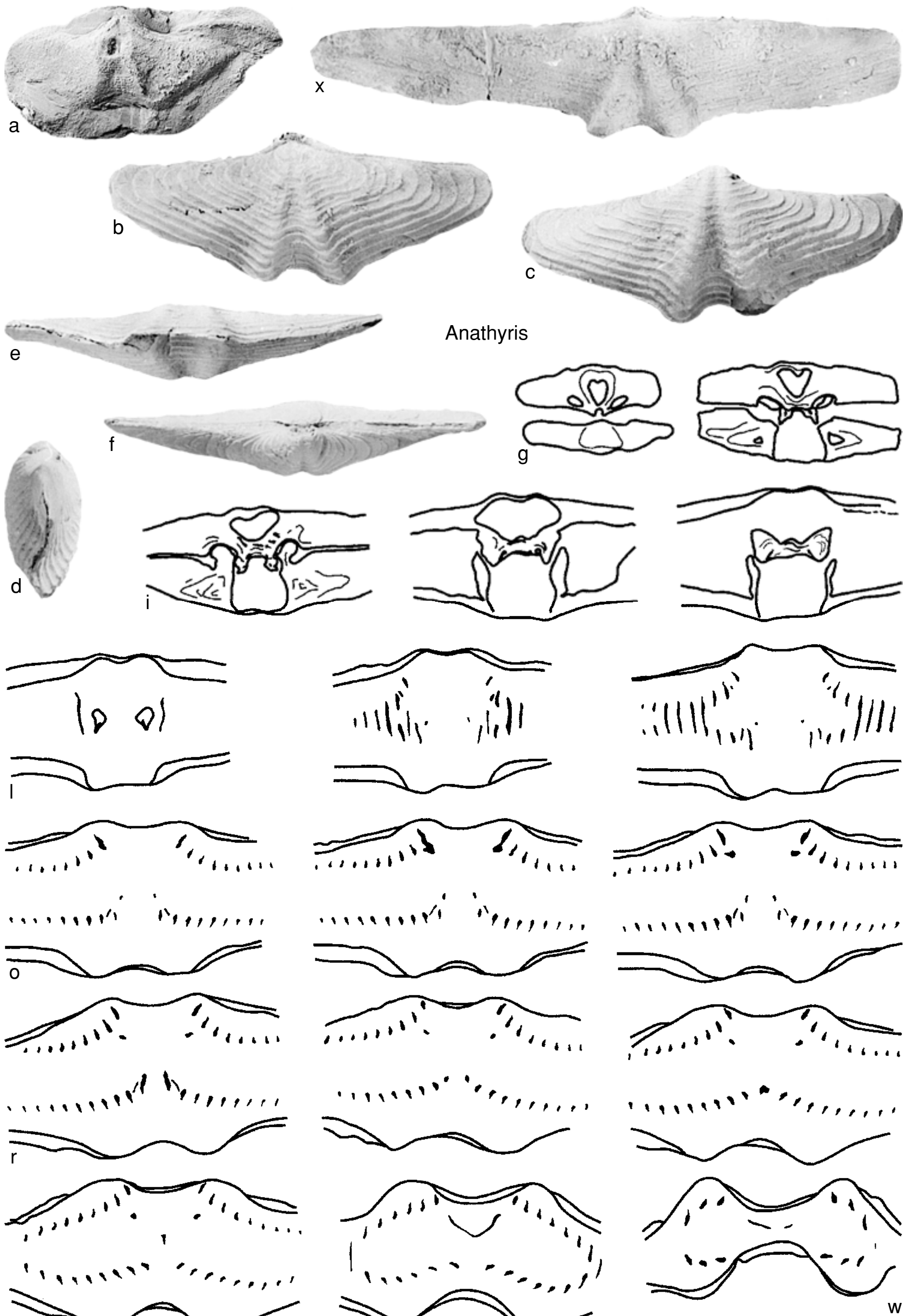

FIG. 1039. Athyrididae (p. 1528).

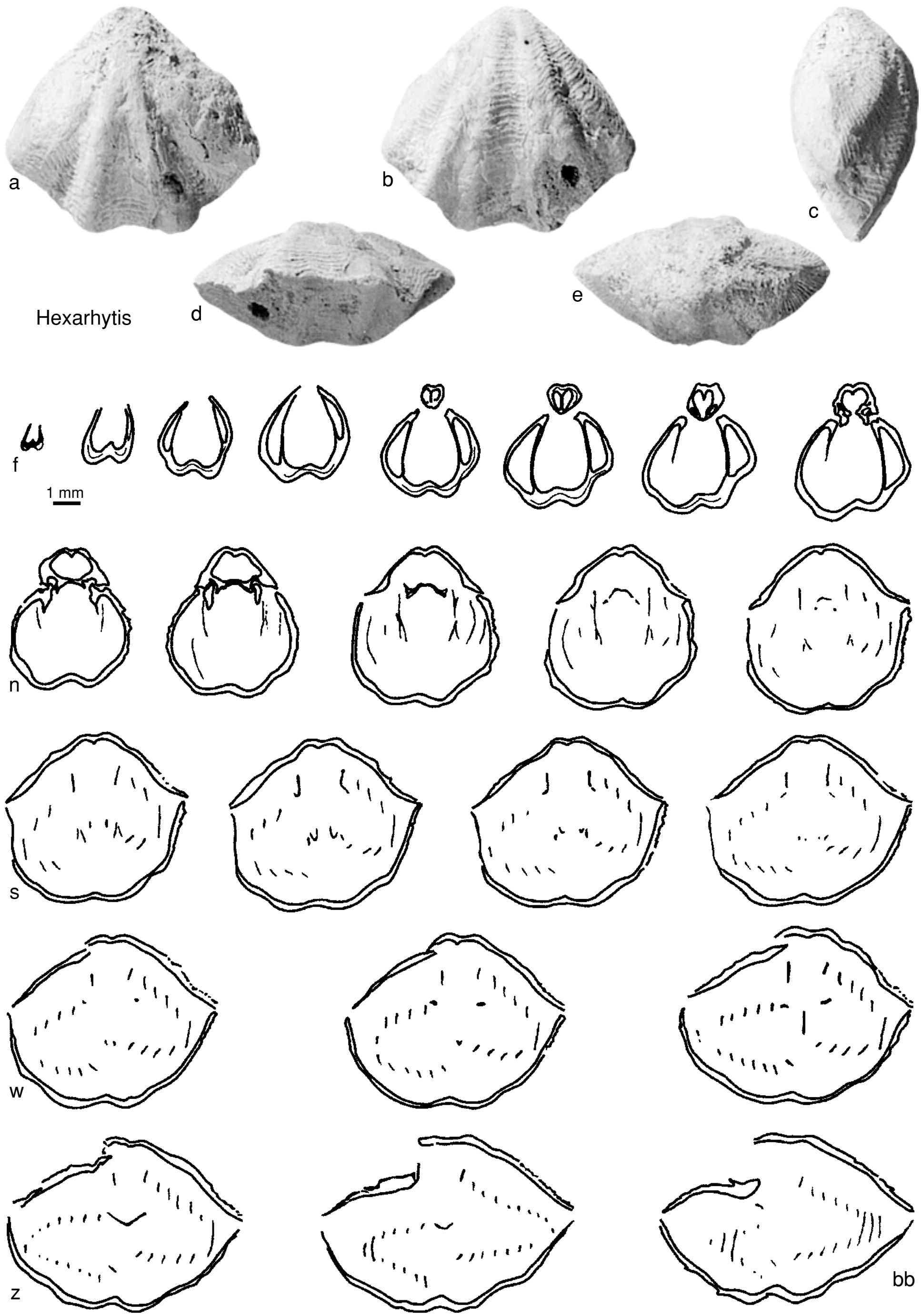

FIG. 1040. Athyrididae (p. 1528).

Subfamily PRADOIINAE García-Alcalde, 1986

[Pradoiinae García-Alcalde, 1986, p. 65]

Shell medium to large, slightly rostrate, ventral umbo moderately curved; median sulcus in both valves and opposite folding; anterior margin emarginate; lateral profile commonly compressed anteriorly; exterior with fine delayed costation progressively developed medially and few, weak, growth lines, without frills; wedgelike microornament usually present; interior as in Plicathyridinae but commonly with very narrow lateral apical cavities and very short accessory jugal lamellae. *Lower Devonian (Lochkovian)–Middle Devonian (lower Eifelian, ?Givetian).*

Pradoia Boucot, Johnson, & Staton, 1965, p. 665 [**Terebratula toreno* de Verneuil & d'Archiac, 1845, p. 469; OD]. Elongate subpentagonal with faint sulcus, starting in umbo, in both valves; dorsal profile bilobate; fine delayed costation and wedgelike microornament with narrowest part directed anteriorly, commonly quincuncially disposed. [Authorship of this genus is usually credited to Comte (1938, p. 43); however, he did not designate a type for the genus. The first unequivocal designation of the type species seems to be that of Boucot, Johnson, & Staton, 1965; thus they validated the name in their publication.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian, ?Givetian):* Spain, *upper Emsian–lower Eifelian;* Armenia, *?Givetian.*——Fig. 1041*a–t.* **P. torenoi* (de Verneuil & d'Archiac), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Asturias, Spain, D866, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f–r,* transverse serial sections 1.7, 3.1, 4.2, 5.0, 5.3, 6.6, 7.1, 7.6, 7.9, 8.5, 8.7, 9.0, 9.9 mm from ventral umbo, Asturias, Spain, DPO 424 (adapted from García-Alcalde, 1971); *s,* detail of external microornamentation, León, Spain, DPO F24244, ×18; *t,* detail of external microornamentation, León, Spain, DPO F24244, ×44 (new).

?Dichozygopleura Renouf, 1972, p. 121 [**D. dichozygopleura;* OD]. Elongate subelliptical; faint sulcus in anterior two-thirds of both valves; few growth lines usually present; strong ribs in posterolateral region of shell, curving anterolaterally; cardinal plate flat, with small dorsal foramen apically, dental cavities ventrally covered posteriorly; jugum unknown. [This genus requires revision.] *Lower Devonian:* France.——Fig. 1042,*2a–b.* **D. dichozygopleura,* Brittany; *a,* rubber impression of dorsal exterior mold, LPB 1186; *b,* rubber impression of ventral exterior mold, LPB 1161, ×2 (Renouf, 1972).

Guaxa García-Alcalde, 1986, p. 67 [**G. iberica;* OD]. Similar to *Pradoia* externally but with ribs stronger, present over entire valve and curving anterolaterally; ventral interior and cardinalia essentially as in *Athyris;* jugum poorly known. *Lower Devonian (Lochkovian–Pragian):* Spain.——Fig. 1042,*1a–d.* **G. iberica,* Teruel; holotype, dorsal, ventral, lateral, and anterior views, DPO 112.096, ×1 (García-Alcalde, 1986).

Quadriloba Alvarez, Rong, & Boucot, 1999, p. 547, *nom. nov. pro Tetraloba* Alvarez, Rong, & Boucot, 1998, p. 843, *non Tetraloba* Lee, 1983, Collembola [**Terebratula collettii* de Verneuil, 1850, p. 173; OD]. Resembles elongate *Plicathyris* but without lamellose growth lines; surface ornamentation similar to that of *Pradoia;* interior as in *Plicathyris* but with very narrow lateral apical cavities. [The names *colletei* and *colletti* are incorrect subsequent spellings of *collettii.*] *Lower Devonian (Emsian):* northwestern Spain.——Fig. 1042,*3a–r.* **Q. collettii* (de Verneuil), upper Emsian, León; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, D867, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* detail of external microornamentation, DPO F24245, ×11; *g,* detail of external microornamentation, DPO F24245, ×44 (new); *h–r,* transverse serial sections 1.7, 2.9, 4.2, 4.7, 5.6, 6.1, 6.2, 6.6, 6.8, 7.0, 7.4 mm from ventral umbo (adapted from García-Alcalde, 1971).

Subfamily SPIRIGERELLINAE Grunt, 1965

[Spirigerellinae Grunt, 1965, p. 237; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 843]

Small to extremely large, subpentagonal, subtrigonal, elongate or transversely oval in outline; bi- to dorsibiconvex with convexity moderate to strong; moderately rostrate; ventral sulcus and dorsal fold variably developed; lateral plications may develop; growth lines very fine, closely and regularly spaced; growth laminae stronger, more widely and randomly spaced; pedicle supports absent (delthyrial plate may be present in *Spirigerella*); dental plates thin and short (may form spondylium, e.g., *Araxathyris, Rectambitus*); cardinal plate commonly subquadrangular, thick in late Carboniferous and Permian taxa; inner hinge plate triangular, slightly lowered to plane of outer hinge plates in oldest species; well-developed

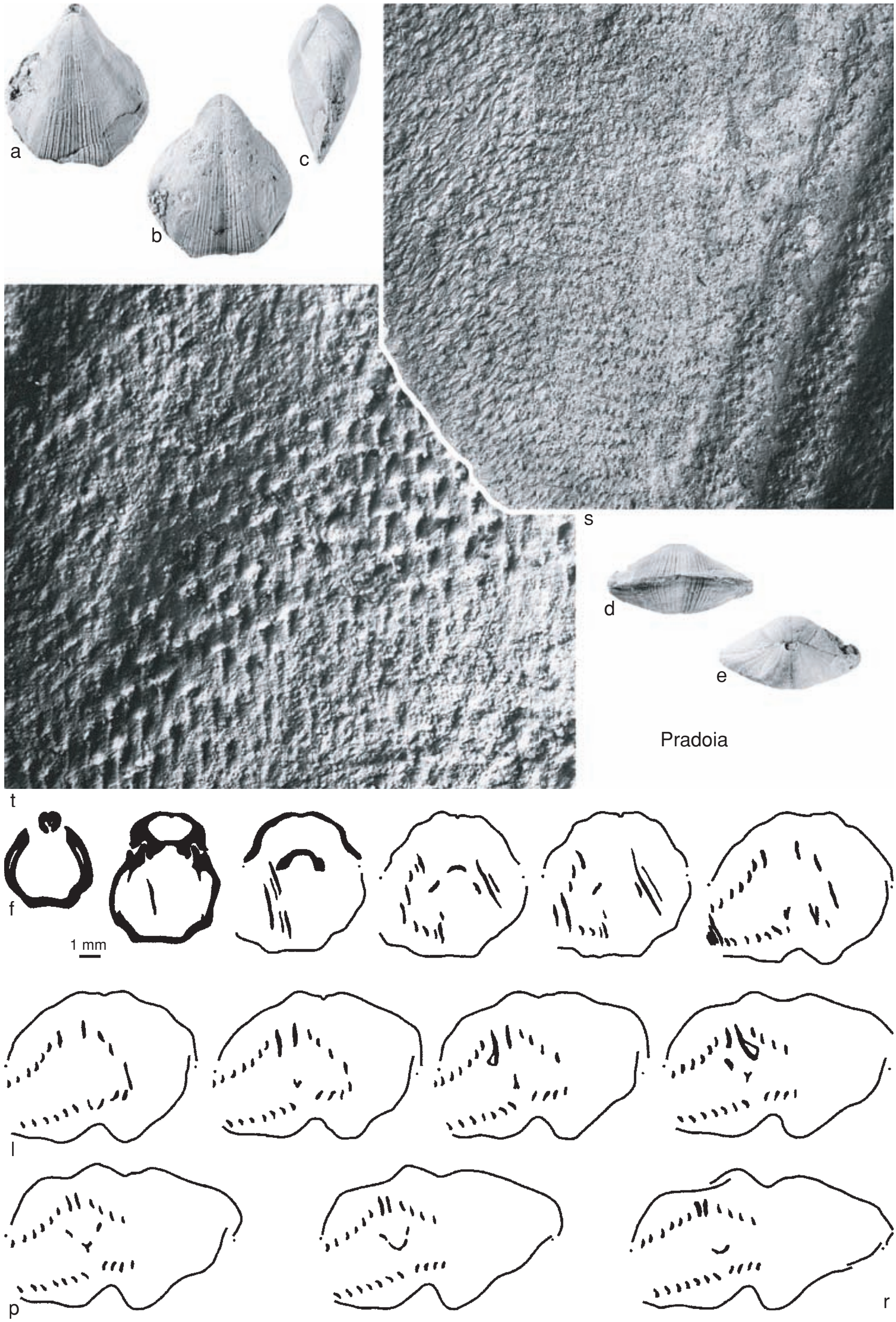

FIG. 1041. Athyrididae (p. 1533).

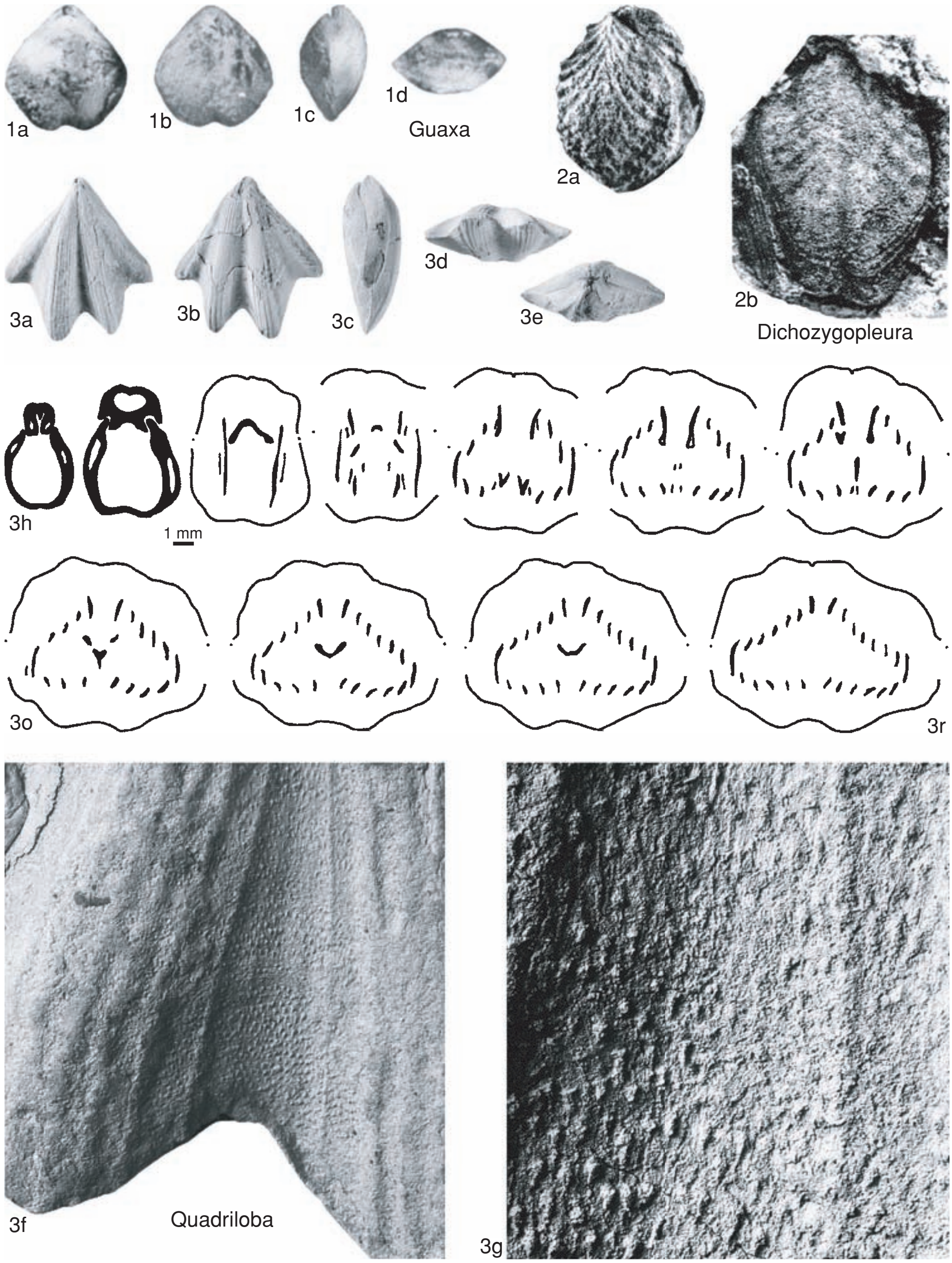

FIG. 1042. Athyrididae (p. 1533).

divergent crural bases; concave, serrated cardinal flanges moderately to strongly developed mainly in Permian species; dorsal foramen commonly small, may be infilled in latest stocks; dorsal myophragm may be present; jugum essentially as in *Athyris;* tertiary layer may be present. *Lower Devonian (Pragian)–Upper Triassic.*

Spirigerella WAAGEN, 1883, p. 450 [**S. derbyi;* SD OEHLERT, 1887a, p. 1300] [=*Juxathyris* LIANG, 1990, p. 270 (type, *J. apionucula,* OD)]. Bi- to dorsibiconvex or convexiplane, isometric or subovate massive shells commonly widest anterior to midlength; strong, broad dorsal fold and ventral sulcus; uniplicate or parasulcate anterior commissure; ventral beak short, strongly incurved, concealing small foramen; nearly flat palintrope; dental plates, if present, buried in secondary shell material that is strongly developed in umbonal cavities; more or less developed delthyrial plate may be present; high, massive, cardinal plate; outer hinge plates reduced; cardinal flanges may be unified, strongly developed, serrated, ventrally concave, with deeply impressed pair of diductor pits; dorsal myophragm commonly present; jugum essentially as in *Athyris,* but lateral branches of jugum originating before valve midlength, projecting anteroventrally; median bladelike elevation on saddle extending backward as far as jugal stem; tertiary layer may be present apically. [*Juxathyris,* from Middle to Upper Permian of southern China, is said to differ by having inner socket ridges superseded by high and large processes that take the shape of phoenix coronet (*sic*).] *Upper Carboniferous–Upper Permian:* Slovakia, Croatia, Hungary, Italy, Turkey, Iran, Pakistan, Nepal, Kashmir, western Malaysia, Timor, northeastern and southern China, Western Australia, Argentina.——FIG. 1043,*1a–g.* **S. derbyi,* Kazanian, Salt Range, Pakistan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GSI 3407, Waagen collection, ×1 (new; photographs courtesy of R. K. Biswas); *f,* ventral interior, USNM 212888, ×2 (Grant, 1976); *g,* lateral view of jugum, approximately ×4 (Waagen, 1883). [See also Fig. 1002.2, p. 1477, and Fig. 1008.2, p. 1485, in introduction.]

Araxathyris GRUNT, 1965, p. 240 [**Spirigera protea* ABICH, 1878, p. 55; OD]. Medium to large, moderately to strongly biconvex, transversely oval to subpentagonal, inflated shells; ventral sulcus and dorsal fold wide and flat anteriorly, bearing distinct median groove starting at apex; 2 poorly developed lateral plications may bound sulcus; anterior commissure para- to bisulcate; growth laminae widely and irregularly spaced; short, thin, medially concave dental plates forming narrow sessile spondylium; cardinal plate thin, narrow, subtriangular, apically perforated by small foramen; cardinal flanges well developed; tertiary layer present. *?Lower Permian, Upper Permian:* ?northern China, *?Lower Permian;* southern Alps, Transcaucasus, Iran, southern China (Sichuan, Shaanxi), northwestern China (Qinghai), Thailand.——FIG. 1044*a–c.* **A. protea* (ABICH), Transcaucasus; lectotype, dorsal, ventral, and anterior views, LGI 66/99, ×1 (Grunt, 1965).——FIG. 1044*d–p. A. felina* (ARTHABER), Transcaucasus; transverse serial sections, 6.7, 6.9, 7.2, 7.7, 8.2, 8.9, 9.7, 10.6, 11.8, 12.2, 12.9, 13.4, 17.5 mm from ventral umbo, PIN 2073/547 (adapted from Grunt, 1965).——FIG. 1044*q–x. A. abichi* (ARTHABER), Transcaucasus; tangential serial sections, parallel to commissural plane, 3.1, 4.8, 5.7, 6.5, 7.0, 7.3, 8.1, 8.7 mm from dorsal valve, PIN 3599/833 (adapted from Grunt, 1986).

Cardiothyris ROBERTS, 1971, p. 178 [**C. bisulcata;* OD]. Medium, subcircular to subpentagonal or elongate oval, subequally biconvex, thin shells; poorly rostrate, bearing small pedicle foramen in epithyridid position; sinus on each valve of equal depth, resulting in rectimarginate commissure; emarginate outline; external ornament of prominent, simple, widely spaced capillae crossed by few, fine, concentric growth lines; dental plates short, thin, subparallel; muscle scars weakly defined; cardinal plate subquadrate, robust, divided into 2 concave portions by median furrow and pierced apically, close to dorsal umbo, by minute dorsal foramen; cardinal flanges moderately developed; dorsal myophragm very low or absent; spiralia and jugum unknown. *Lower Carboniferous (Tournaisian):* northwestern Australia, USA (Missouri, Illinois).——FIG. 1045,*1a–o.* **C. bisulcata,* northwestern Australia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, CPC 8245, ×1.5; *f–o,* transverse serial sections 0.3, 0.5, 0.8, 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.7 mm from ventral umbo, CPC 11102 (Roberts, 1971).

Composita BROWN, 1845, p. 131 [**Spirifer ambiguus* SOWERBY, 1822 in 1821–1822, p. 105; OD] [=*Seminula* HALL & CLARKE, 1893, p. 93, *non* M'COY, 1844, p. 158; *Gruntathyris* GRETCHISHNIKOVA, 1996, p. 417 (type, *G. innae,* OD)]. Moderately to strongly biconvex, subovate, subpentagonal or subtrigonal shells, commonly widest near midlength, dorsal fold and ventral sulcus variably developed, may extend to umbonal region or be restricted to anterior part, fold may be flat or slightly depressed medianly; anterior commissure uniplicate to parasulcate; ventral beak thick, rounded, foramen large, ovate, in epi- to permesothyridid position; delthyrium completely filled by dorsal umbo without deltidial plates; dorsal foramen infilled other than in early forms. [Date on BROWN's publication is 1849, but parts 24–28 (p. 117–136) containing *Composita* (p. 131) were published in 1845 (see C. D. SHERBORN, 1905, p. 359).] *Upper Devonian (Famennian)–Upper Permian:* cosmopolitan.——FIG. 1043,*2a–c.* **C. ambigua* (SOWERBY), Viséan, Derbyshire, England; *a–b,* lectotype, dorsal and ventral views, BMNH B 61041, ×1.5 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *c,* ventral view of dorsal interior showing jugum, approximately ×3 (Davidson, 1861). [See also Fig. 1007.3, p. 1484, in introduction.]

Densalvus CARTER, 1991, p. 88 [**Athyris crassicardinalis* WHITE, 1860, p. 229; OD]. Similar to *Planalvus* but with strongly inflated ventral valve and weakly convex dorsal valve; dorsal fold and ventral sulcus absent; without ridges defining areas on either side of delthyrium; surface weakly and finely capillate; dorsal valve thick shelled; spiralia and

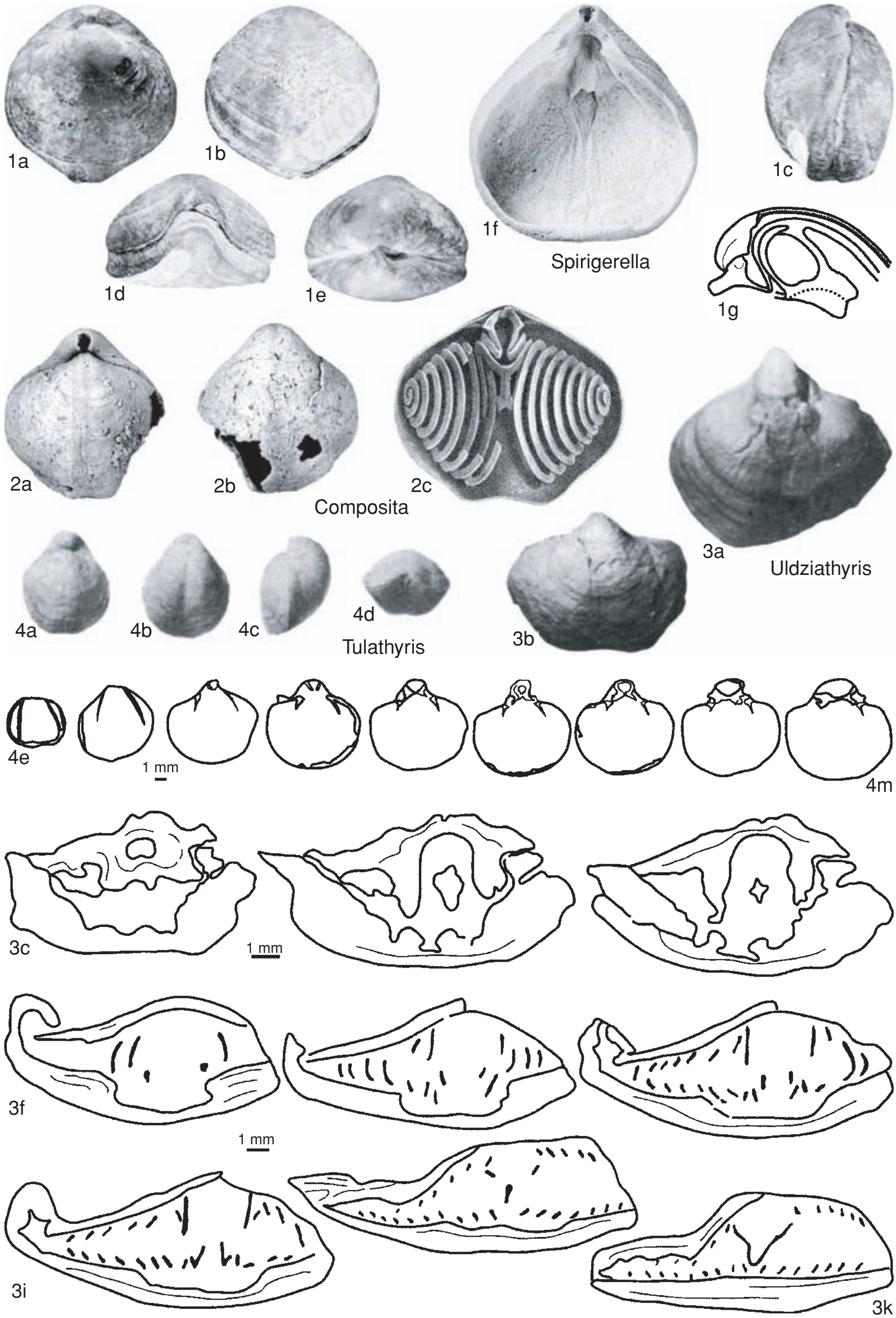

FIG. 1043. Athyrididae (p. 1536–1544).

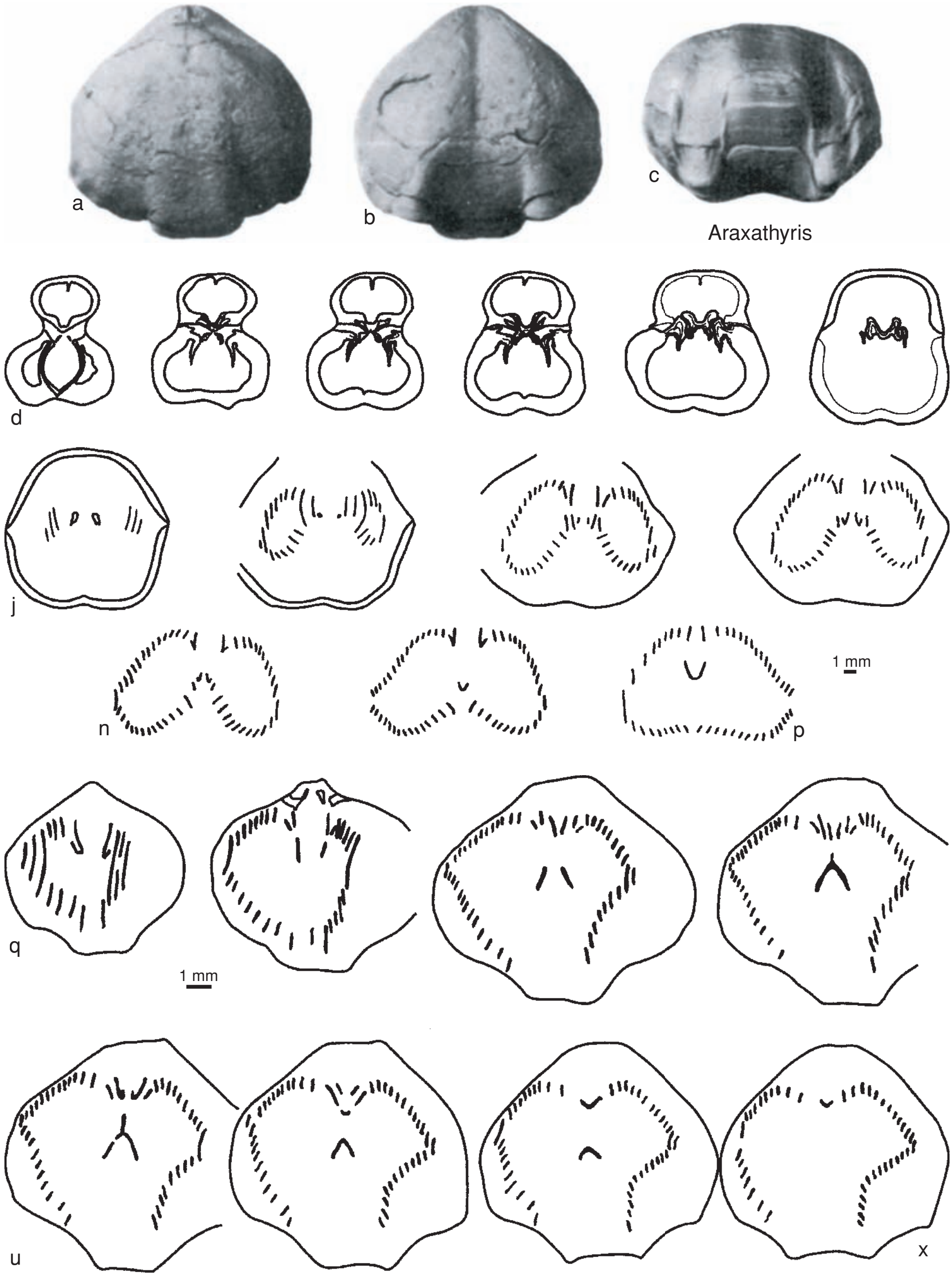

FIG. 1044. Athyrididae (p. 1536).

jugum unknown. *Lower Carboniferous (lower Tournaisian):* USA (Iowa, Missouri).——FIG. 1046,*1a–g.* **D. crassicardinalis* (WHITE); *a–d,* lectotype, ventral valve with dorsal cardinalia attached, ventral, dorsal, lateral, and posterior views, Iowa, UM 66073, White Collection, photographs courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA; *e,* posterior view, Iowa, UM

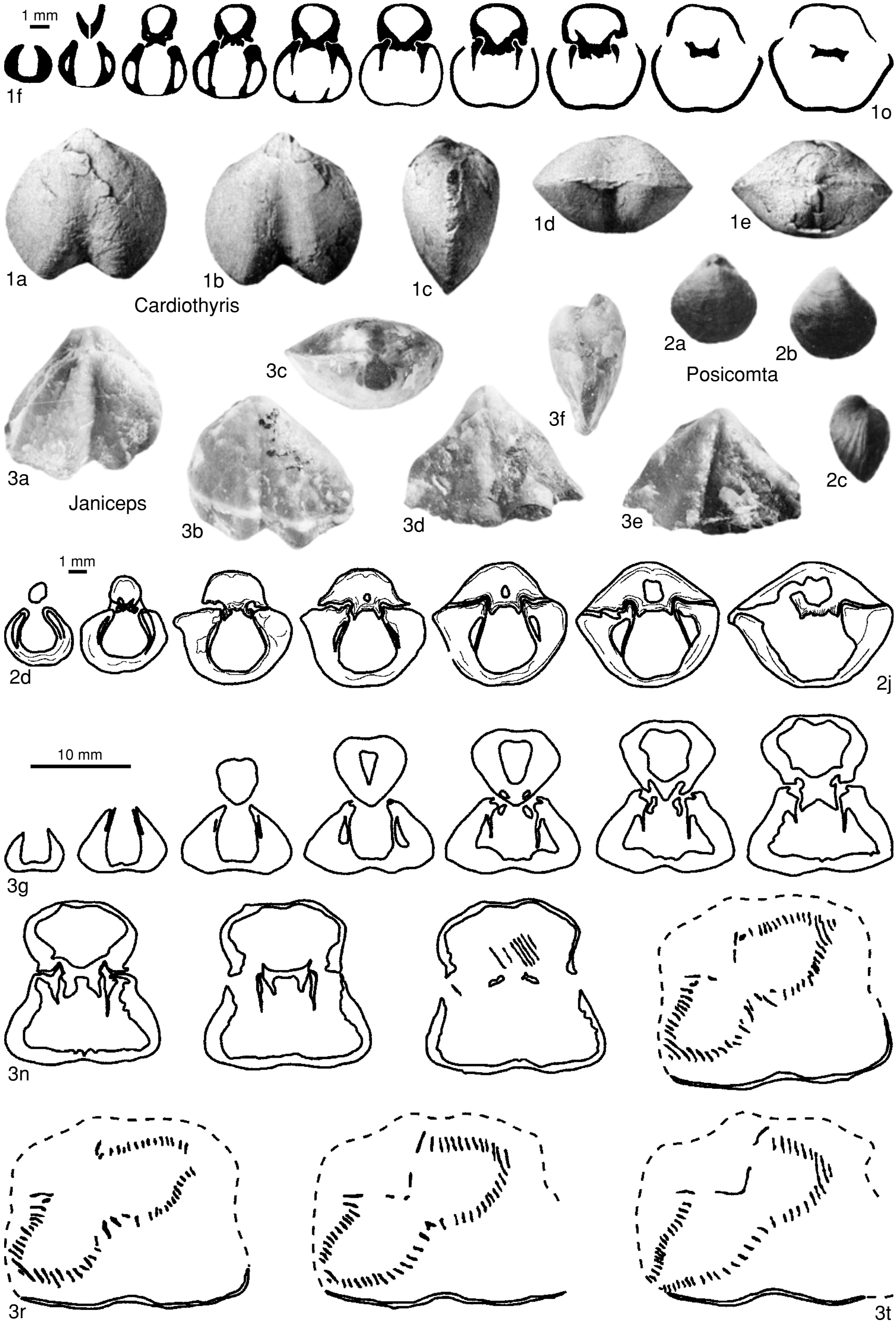

FIG. 1045. Athyrididae (p. 1536–1540).

66075, White Collection, photograph courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA; *f–g,* dorsal valve, external and internal views, Missouri, UC 9817, Weller Collection, ×3 (Carter, 1991; photographs courtesy of J. L. Carter).

Iniathyris BEZNOSOVA, 1963, p. 312 [**I. topkensis;* OD]. Externally similar to *Composita;* ventral interior, dental plates, and greatly thickened umbonal region as in *Nordathyris,* but without prismatic layer and having less impressed muscle field; dorsal interior and spiralium poorly known. *Lower Carboniferous (Tournaisian):* Russia (Kuznetsk basin), Kazakhstan, China, USA (Iowa).——FIG. 1047,*1a–d.* **I. topkensis,* Kuznetsk basin; holotype, dorsal, ventral, lateral, and posterior views, PIN 760/4470, ×1 (Beznosova, 1963).

Janiceps FRECH, 1901, p. 551 [**Spirigera peracuta* STACHE, 1878, p. 152; SD SCHUCHERT & LEVENE, 1929a, p. 70]. Medium to large, subequally biconvex, usually triangular shells with maximum width at anterior third of shell, very close to front, more rarely subrhomboidal to pentagonal; each valve usually bearing 2 pair of rounded unequal folds starting at apex and widening moderately anteriorly; ventral cardinal area more or less defined; dental plates thin and short, may be buried in secondary shell material that is strongly developed in umbonal cavities, low dental flanges may support teeth anteriorly. [The outline of some *Janiceps* species resembles that of young *Comelicania* (e.g., POSENATO, 1998). But, until better preserved specimens of *Janiceps* can be studied, this genus is provisionally included in the Spirigerellinae due to its adult external morphology and internal characters. The relationship between *Janiceps* and *Comelicania* and their taxonomic position within the Athyrididae requires revision.] *Upper Permian (Changhsingian):* Italy (southern Alps), Armenia.——FIG. 1045,*3a–t.* **J. peracuta* (STACHE), upper Changhsingian, southern Alps; *a–c,* dorsal, ventral, and posterior views, Monte Croce di Cornelico, MGBW 3797-b, Stache Collection; *d–f,* dorsal, ventral, and lateral views, Monte Croce di Cornelico, MGBW 3797-a, Stache Collection, ×2; *g–t,* transverse serial sections 0.50, 1.55, 3.55, 4.50, 4.95, 5.30, 5.55, 5.80, 6.40, 7.45, 10.70, 11.25, 12.55, 14.05 mm from ventral umbo, Val Brutta, MDSGF J06 (new; photographs and serial sections courtesy of R. Posenato).

Nordathyris GRUNT, 1977a, p. 73 [**N. bulkanensis;* OD]. Medium to large, subequally biconvex, transverse subelliptical to subpentagonal massive shell; narrow sulcus extending from ventral beak, widening considerably toward anterior margin; dorsal fold may be divided by narrow and shallow furrow, variably developed, lateral folds may be present; lateral apical cavities narrow and minute; ventral muscle field moderately to deeply impressed in thick umbonal region; high, massive cardinal plate; cardinal flanges well developed; tertiary layer present. *Upper Carboniferous (Bashkirian):* northeastern Russia (Kolyma-Omolonsk massif).——FIG. 1046,*3a–q.* **N. bulkanensis; a–c,* holotype, dorsal, ventral, and anterior views, PIN 2840/461, ×1 (Grunt, 1977a); *d–i,* transverse serial sections 0.6, 2.3, 2.5, 2.6, 3.8, 3.9 mm from ventral umbo, PIN 2840/460 (adapted from Grunt, 1977a); *j–q,* tangential serial sections, parallel to commissural plane, 1.1, 2.0, 3.2, 5.5, 6.6, 7.1, 7.4, 7.6 mm from dorsal valve, PIN 2840/465 (Grunt, 1986).

Planalvus CARTER, 1971, p. 248 [**P. gibberosa;* OD]. Small to medium size, longitudinally to transversely ovate, dorsibiconvex shells, ventral valve almost flat; broad, shallow sulcus originating in posterior third of ventral valve, dorsal valve with high median fold, but poorly defined laterally; surface lamellose, lamellae finely striated and apparently fringed with minute solid spines; gently curved beak, not prominent, truncated by circular meso- to permesothyridid foramen; beak ridges subangular, defining areas on either side of open delthyrium; ventral valve with thick shell, without dental plates; subtrapezoidal cardinal plate, imperforate apically; variably developed cardinal flanges project slightly posteroventrally within delthyrial cavity; wide, conjunct inner hinge plates flat or slightly concave ventrally; outer hinge plates reduced, difficult to distinguish from inner socket ridges, which slightly overhang sockets; posteriormost part of cardinal plate resting on short, thin median ridge extending as low myophragm to midshell. [The brachidium of the type species seems to be different from those of French species; if subsequent investigations show that their morphology is different, the French species must be separated into a new genus externally homeomorphic with *Planalvus.*] *Lower Devonian (Pragian)–Lower Carboniferous (Viséan):* France, *Pragian, ?lower Emsian;* Spain, *Famennian;* North America, *Tournaisian–Viséan.*——FIG. 1048*a–t.* **P. gibberosa,* Tournaisian, Iowa, USA; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, UI X-3435; *f,* dorsal interior, UI X-3441-2, ×3 (Carter, 1971); *g–t,* transverse serial sections 0.2, 0.6, 1.4, 1.8, 2.0, 3.4, 3.6, 4.0, 4.4, 4.6, 5.0, 5.4, 5.8, 6.2 mm from ventral umbo, USNM 176844 (adapted from Carter, 1972).——FIG. 1048*u–dd. P. rufus* RACHEBOEUF, COPPER, & ALVAREZ, Pragian, Armorican Massif, France; transverse serial sections 1.6, 1.9, 2.0, 2.4, 2.7, 3.4, 3.6, 3.8, 4.4, 4.8 mm from ventral umbo, IGR 10298 (adapted from Racheboeuf, Copper, & Alvarez, 1994).

Posicomta GRUNT, 1986, p. 120 [**P. gundarensis;* OD]. Shells resembling *Composita* with smaller size, dorsal fold and ventral sulcus poorly developed, possibly with narrow groove and much thicker shell; spiralia and jugum unknown. *Upper Permian:* Pamir, Tajikistan, southern Thailand.——FIG. 1045,*2a–j.* **P. gundarensis,* Darvaz, Tajikistan; *a–c,* holotype, dorsal, ventral, and lateral views, PIN 3599/814-382, ×1 (Grunt, 1986); *d–j,* transverse serial sections 0.8, 1.6, 2.6, 3.0, 3.3, 3.6, 3.9 mm from ventral umbo, PIN 3599/835 (adapted from Grunt, 1986).

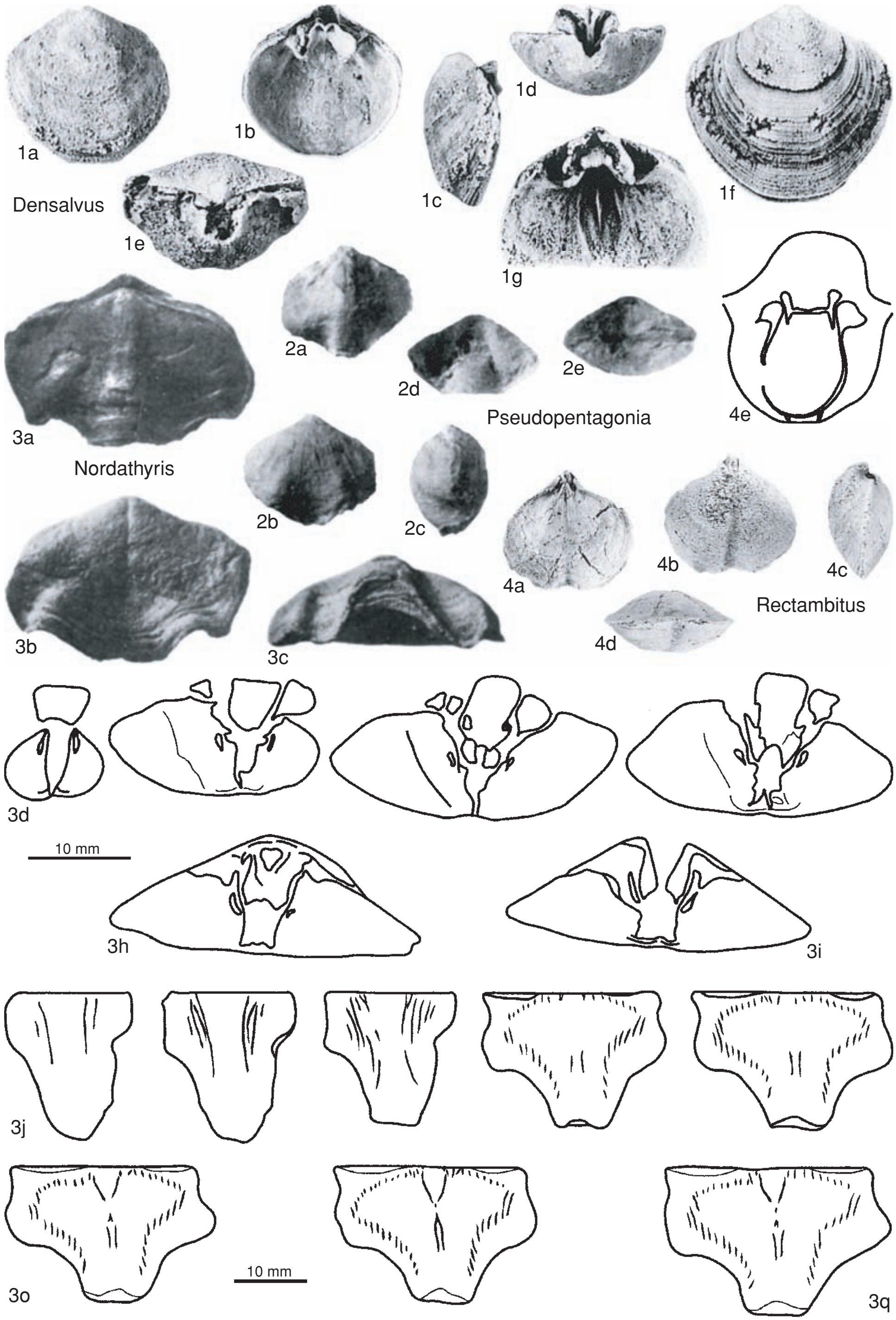

FIG. 1046. Athyrididae (p. 1536–1544).

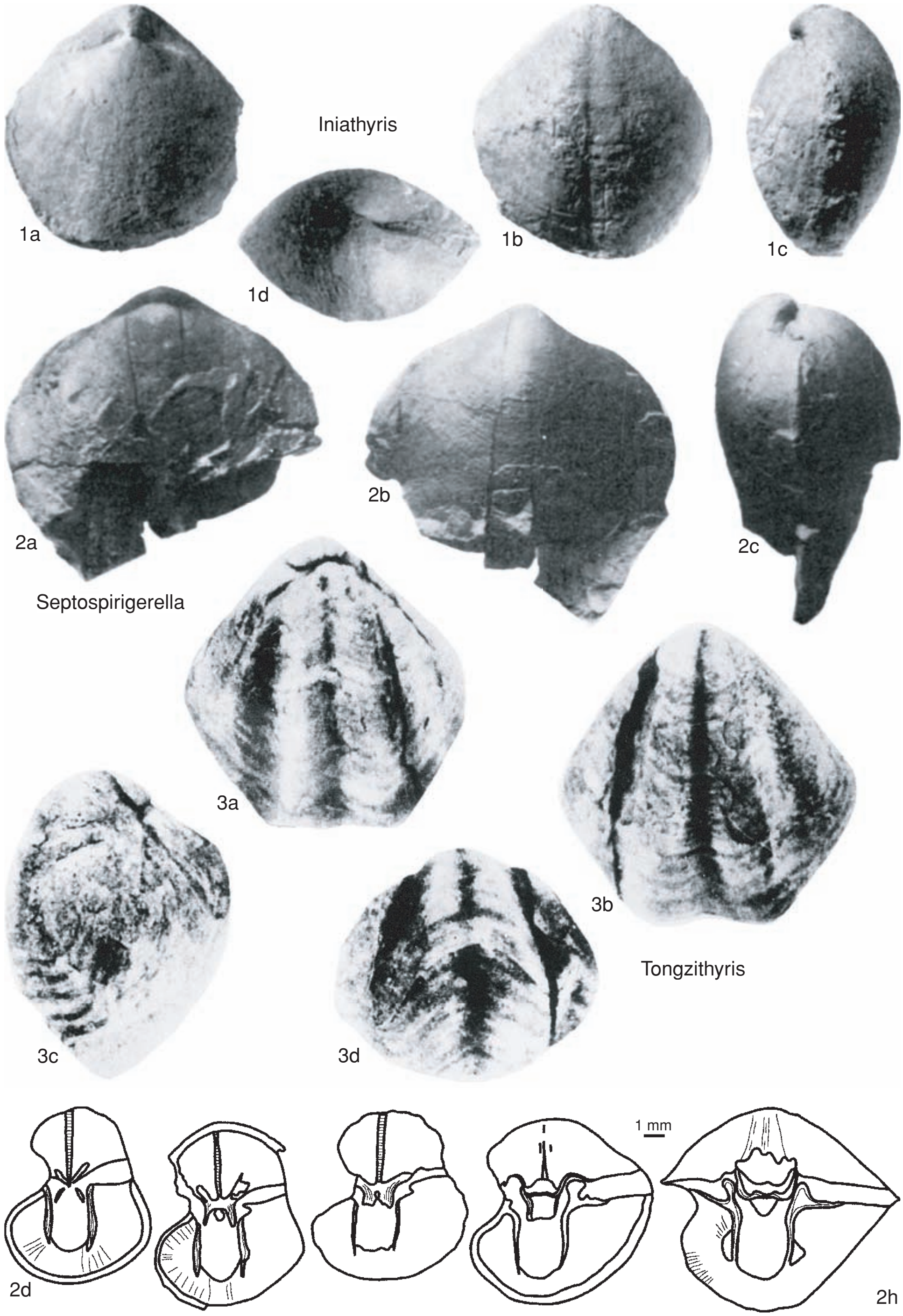

FIG. 1047. Athyrididae (p. 1540–1544).

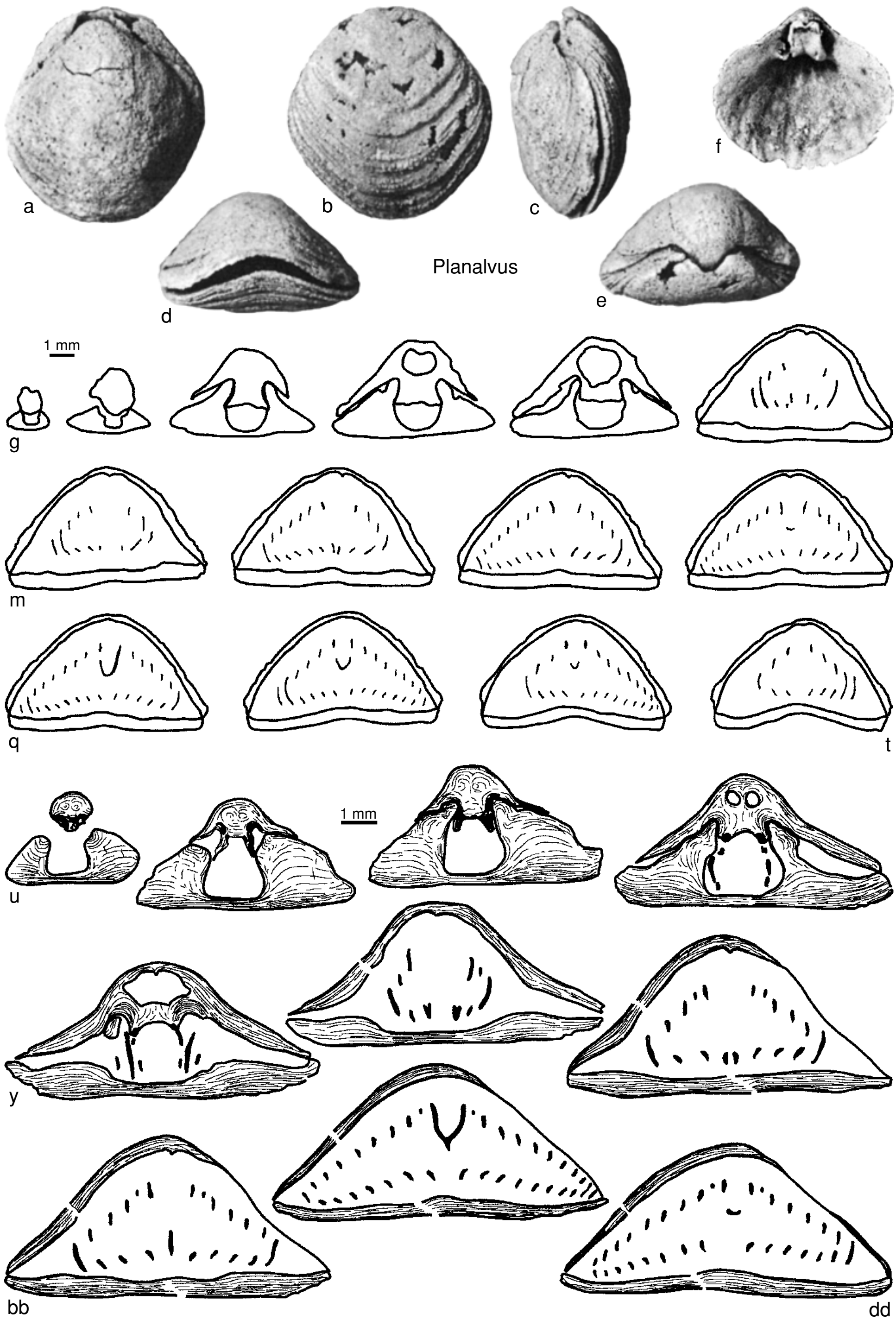

FIG. 1048. Athyrididae (p. 1540).

Pseudopentagonia Beznosova, 1963, p. 315 [**P. injensis;* OD]. Dorsibiconvex shell, similar to *Nordathyris* but with dental plates delicate, without apical thickening in both valves and without prismatic layer. *Lower Carboniferous (Tournaisian):* Kazakhstan, Russia (Kuznetsk basin).——Fig. 1046,*2a–e.* **P. injensis,* Kuznetsk basin; holotype, dorsal, ventral, lateral, anterior, and posterior views, PIN 760/4485, ×1 (Beznosova, 1963).

?Rectambitus Xu & Grant, 1994, p. 50 [**Araxathyris bisulcata* Liao, 1980, p. 268; OD]. Small to medium with rectimarginate, slightly emarginate, anterior commissure; spondylium supported anteriorly by low, broad median septum; jugum unknown. [May be synonymous with *Araxathyris.*] *Upper Permian (Changhsingian):* southern China (Guizhou, Shaanxi).——Fig. 1046,*4a–e.* **R. bisulcatus* (Liao), Guizhou; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Liao, 1980; photographs courtesy of Liao Zhuo-ting); *e,* transverse serial section showing spondylium supported by low, broad septum, USNM 456173, approximately ×3 (adapted from Xu & Grant, 1994).

Septospirigerella Grunt, 1965, p. 237 [**S. baissalensis;* OD]. Similar to *Spirigerella* without dorsal fold and ventral sulcus, ventral beak moderately curved; more or less prominent short ridge joining thick cardinal plate at posterior end; spiralia and jugum unknown; tertiary layer present. *Upper Permian–Upper Triassic:* Armenia, Iran, Transcaucasus, Thailand, *Upper Permian;* China (Sichuan), *Upper Triassic.*——Fig. 1047,*2a–h.* **S. baissalensis,* Upper Permian, Transcaucasus; *a–c,* holotype, dorsal, ventral, and lateral views, PIN 2073/626, ×1 (Grunt, 1965); *d–h,* transverse serial sections 3.9, 4.3, 4.4, 4.9, 5.4 mm from ventral umbo, PIN 2073/485 (adapted from Grunt, 1965).

Tongzithyris Ching, Liao, & Fang, 1974, p. 313 [**T. episulcata;* OD]. Similar to *Araxathyris* but larger and thick shelled, bearing 1 or 2 folds on lateral slopes; dorsal foramen absent; dorsal myophragm may be present; jugum unknown. *Upper Permian (Changhsingian):* southern China.——Fig. 1047, *3a–d.* **T. episulcata,* Tongzi, northern Guizhou; holotype, dorsal, ventral, lateral, and anterior views, NIGP 22501, ×1 (Ching, Liao, & Fang, 1974; photographs courtesy of Jin Yu-gan).

Tulathyris Grunt, 1976, p. 78 [**Athyris vogdti* von Peetz, 1893, p. 59; OD]. Shells resembling *Composita* with smaller size and thinner-shelled valves; cardinal plate subtriangular, cardinal flanges poorly developed; spiralia and jugum unknown. *Lower Carboniferous (Tournaisian):* Moscow syncline, Donets basin, northern Kyrgyzstan, Kuznetsk Basin, ?Kazakhstan, ?Verkhoyansk.——Fig. 1043, *4a–m.* **T. vogdti* (von Peetz), Tula, Russia; *a–d,* dorsal, ventral, lateral, and anterior views, PIN 544/150(9), ×1 (Grunt, 1980); *e–m,* transverse serial sections 0.9, 1.9, 2.0, 2.2, 2.3, 2.4, 2.5, 2.7, 3.0 mm from ventral umbo, PIN 544/1375 (adapted from Grunt, 1980).

Uldziathyris Grunt, 1977b, p. 82 [**U. tikhonovi;* OD]. Similar to *Composita* with coarse lamellae projecting slightly outwardly in anterior part of shell, dental plates very short, ventral muscle field moderately to deeply impressed in thick umbonal region; cardinal plate thick, with median, ridgelike process directed ventrally, dorsal foramen absent. *Lower Carboniferous:* western Mongolia.——Fig. 1043,*3a–k.* **U. tikhonovi; a,* holotype, internal mold of ventral valve, PIN 3158/85; *b,* ventral view, PIN 3158/87, ×1 (Grunt, 1977b); *c–e,* transverse serial sections 3.1, 3.5, 4.1 mm from ventral umbo, PIN 3158/93 (adapted from Grunt, 1977b); *f–k,* transverse serial sections 5.5, 6.6, 7.7, 8.8, 11.7, 14.8 mm from ventral umbo, PIN 3158/93 (adapted from Grunt, 1986).

Subfamily XENOSARIINAE Cooper & Grant, 1976

[*nom. transl.* Grunt, 1984, p. 70, *pro* Xenosariidae Cooper & Grant, 1976a, p. 2170]

Shell small, slightly rostrate; lenslike outline, with narrow sulcus extending from beak in both valves; anterior margin bisulcate; smooth, with only regular, fine, infrequent, growth lines; frills absent; beak of ventral valve small, pointed, straight; ventral area narrow, apsacline; hypothyridid pedicle opening without deltidial plates; valves thin shelled; dental plates wholly absent; teeth small; no septum in either valve, no dorsal myophragm; socket ridges prominent, short, thick, defining wide sockets; outer hinge plates very narrow or absent, hinge plate short, inconspicuous, ventrally concave, triangular, with small, oval foramen; crura short, stout, projecting ventrally at high angle at anterior end of cardinal plate; cardinal flanges absent; jugum poorly known, seemingly as in *Glassina. Lower Permian (Artinskian–Kungurian).*

Xenosaria Cooper & Grant, 1976a, p. 2170 [**X. exotica;* OD]. Moderately dorsibiconvex shells with swollen umbonal regions; anterior commissure rectimarginate; narrowly notched anterior margin; flanks bounding sulcus moderately swollen, lateral slopes gentle in ventral, moderate in dorsal valve. *Lower Permian (Artinskian–Kungurian):* USA (western Texas).——Fig. 1049*a–g.* **X. exotica,* Bell Canyon Formation, Hegler Member; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 153459e, ×2; *f,* dorsal interior, USNM 153459g; *g,* ventral interior, USNM 153459c, ×4 (Cooper & Grant, 1976a; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

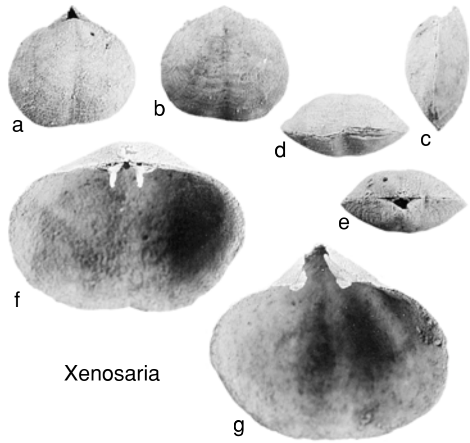

FIG. 1049. Athyrididae (p. 1544).

Family DIPLOSPIRELLIDAE Schuchert, 1894

[*nom. transl.* GRUNT, 1980, p. 51, *ex* Diplospirellinae SCHUCHERT, 1913, p. 418, *nom. correct. pro* Diplospirinae SCHUCHERT, 1894, p. 106, *nom. imperf.; emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 844]

Small to large, commonly small shells; foramen commonly small, in permesothyridid position; dorsal fold and ventral sulcus commonly faint or absent, shallow sulcus may develop in both valves; costae may be present; dental plates commonly short; median septum and pedicle support may be present; cardinal plate subquadrate, not pierced apically, commonly thick; moderately to strongly developed cardinal flanges, commonly serrated; low myophragm usually present. *Lower Permian (Artinskian)–Upper Triassic (Norian), ?Upper Jurassic.*

Subfamily DIPLOSPIRELLINAE Schuchert, 1894

[*nom. correct.* SCHUCHERT, 1913, p. 418, *pro* Diplospirinae SCHUCHERT, 1894, p. 106, *nom. imperf.*]

Commonly small; dorsal fold and ventral sulcus variably developed, commonly faint, more or less rounded plications may be present in both valves; growth lines weak, growth lamellae absent; delthyrium commonly concealed by beak of dorsal valve, rarely by symphytium; dental plates short, fused with lateral wall of valve or absent; median septum may be present; cardinal plate robust, inner socket ridges high and thick; cardinal flanges moderately to well developed; dorsal myophragm may be present; accessory jugal lamellae long, commonly continuing intercoiled with primary volutions of spiralia to ends. *Middle Triassic (Anisian)–Upper Triassic (Norian).*

Diplospirella BITTNER, 1890, p. 297 [**Terebratula wissmanni* MÜNSTER, 1841, p. 64; OD]. Elongate to transversely oval or subpentagonal, anterior commissure rectimarginate or weakly uniplicate or sulcate; ventral median septum extending for two-thirds length of valve; hinge plate thin, steeply inclined posterodorsally; cardinal flanges moderately developed; myophragm extending to half length of valve, distally flanked by short ridges; jugum posteriorly situated, projecting posteroventrally as long stem from which accessory jugal lamellae lead off, jugal saddle thick, with spiny apophysis. *Upper Triassic (Carnian):* Alps, Sicily, Carpathians, Caucasus, southeastern Pamir.——FIG. 1050,*1a–x.* **D. wissmanni* (MÜNSTER), Cortina d'Ampezzo area; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, MPUM 5823/9, ×2; *f,* cardinalia, ×20 (Benigni & Ferliga, 1990; photographs courtesy of C. Benigni); *g–w,* transverse serial sections 1.1, 2.0, 2.9, 3.3, 3.6, 3.95, 4.2, 4.3, 4.5, 4.65, 4.85, 5.1, 5.35, 5.7, 6.05, 6.22, 6.35 mm from ventral umbo, MPUM 5819/20 (adapted from Benigni & Ferliga, 1990); *x,* lateral view of reconstructed jugum, ×12 (Benigni & Ferliga, 1990).——FIG. 1050,*1y. D. sufflata* (MÜNSTER), Cortina d´Ampezzo area; spiny jugal saddle, MPUM 5827/29, ×40 (Benigni & Ferliga, 1990).

?Amphitomella BITTNER, 1890, p. 298 [**Terebratula hemisphaeroidica* VON KLIPSTEIN, 1845, p. 222; OD]. Similar to *Diplospirella,* but with strongly developed median septum in dorsal valve and single spiralium. [Although all other features are typically diplospirelline, the development of short accessory jugal lamellae makes the subfamily assignment uncertain. Further study of Triassic athyridoids is necessary to understand their affinities (see also comments in BENIGNI & FERLIGA, 1995).] *Upper Triassic (Carnian):* Alps.——FIG. 1051,*1a–x.* **A. hemisphaeroidica* (VON KLIPSTEIN), Cortina d'Ampezzo area; *a–d,* ventral, lateral, anterior, and posterior views, MPUM 5863/42, ×4; *e,* dorsal interior, MPUM 5858/74, ×7.5; *f,* ventral interior, MPUM 5858/75, ×11 (Benigni & Ferliga, 1995; photographs courtesy of C. Benigni); *g–i,* transverse serial sections of posterior part of cardinalia, 1.15, 1.20, 1.35 mm from ventral umbo, MPUM 5858/61; *j–w,* transverse serial sections showing development of internal structures, 1.20, 1.30, 1.35, 1.50, 1.60, 1.70, 1.95, 2.30, 2.70, 2.85, 3.05, 3.35, 3.80, 4.70 mm from ventral umbo, MPUM 5858/63 (adapted from Benigni & Ferliga, 1995); *x,* lateral view of

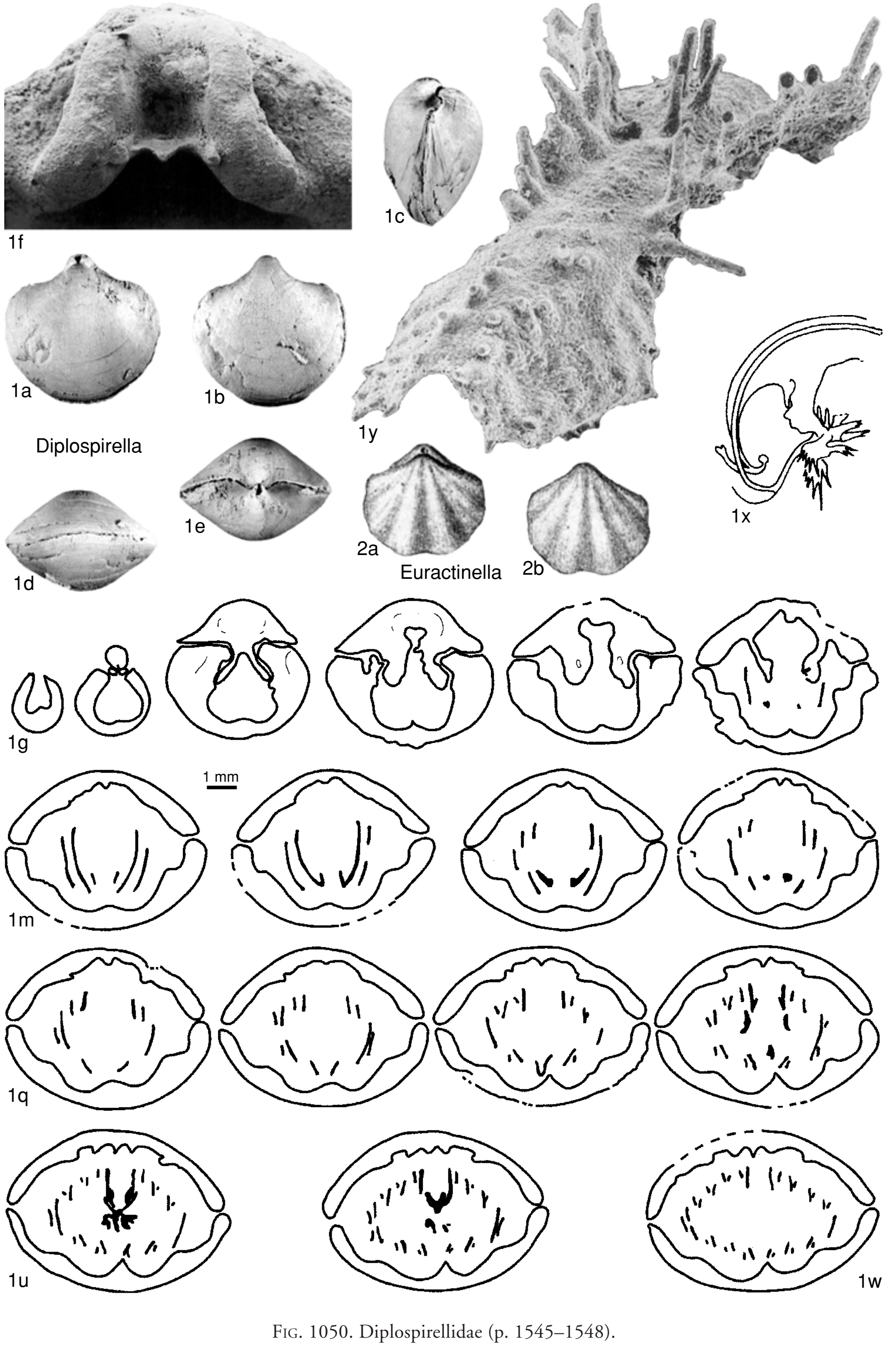

FIG. 1050. Diplospirellidae (p. 1545–1548).

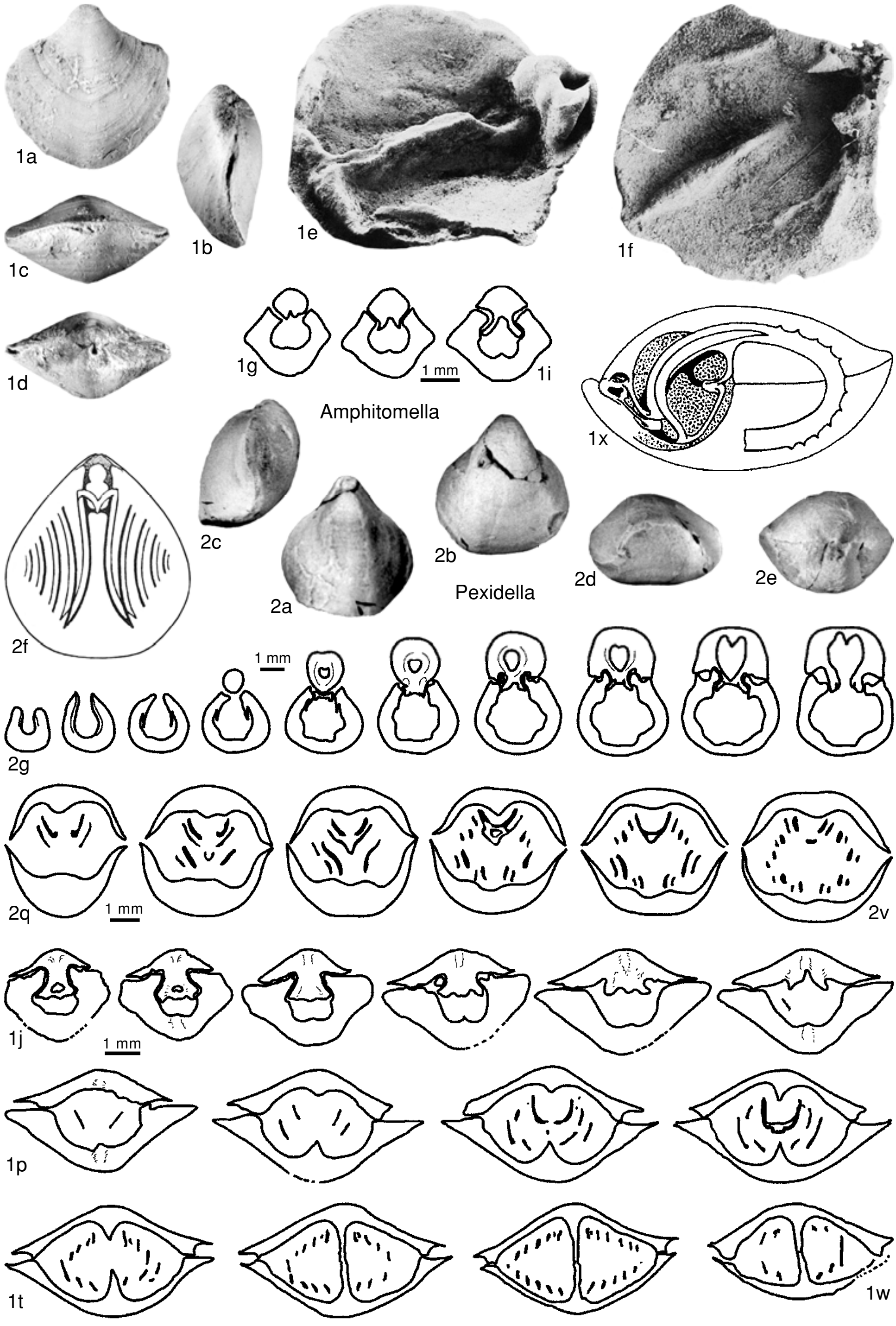

FIG. 1051. Diplospirellidae (p. 1545–1548).

reconstructed jugum, approximately ×6.5 (Benigni & Ferliga, 1995).

Anisactinella BITTNER, 1890, p. 302 [**Terebratula quadriplecta* MÜNSTER, 1841, p. 58; OD]. Small to medium, subtrapezoidal to subpentagonal shells; hinge line almost rectilinear; plicate ventral sulcus and dorsal fold defined laterally by sharp plicae, lateral surfaces commonly smooth; ventral cardinal area well defined, rather high, triangular, slightly concave, orthocline; delthyrium partially covered by symphytium (arcuate to flat); foramen supra-apical; ventral low median septum may be present; cardinal plate subtrapezoidal, ventrally concave, with median ridge; cardinal flange well developed, semicircular to subrectangular, projecting strongly into delthyrial cavity; jugum as in *Pexidella.* [The number and development of plicae shows a high degree of variability in the assigned specimens.] *Middle Triassic (Anisian)–Upper Triassic (Carnian):* Dinarides, Southern Alps, Lucania, Bakony Mountains, Carpathians, northwestern China (Qinghai).——FIG. 1052*a–u.* **A. quadriplecta* (MÜNSTER); *a–e,* dorsal, ventral, lateral, anterior, and posterior views, Ladinian, Cortina d'Ampezzo area, MPUM 5847/9, ×3; *f,* posterior view, showing cardinal flange, Ladinian, Cortina d'Ampezzo area, MPUM 5849/4, ×6; *g,* posterior view, showing cardinal flange, Triassic, Cortina d'Ampezzo area, MPUM 5847/20, ×13 (Benigni & Ferliga, 1992; photographs courtesy of C. Benigni); *h–u,* transverse serial sections 0.8, 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 1.7, 1.8, 1.95, 2.05, 2.15, 2.45 mm from ventral umbo, distance from ventral umbo to first section approximate, Carnian, Hungary (adapted from Dagys, 1974).——FIG. 1052*v–ff. A. maurensis* TADDEI RUGGIERO, Ladinian, Lucania, Italy; transverse serial sections 0.76, 1.12, 1.22, 1.47, 1.60, 1.84, 2.50, 3.36, 5.10, 5.30, 5.70 mm from ventral umbo (Taddei Ruggiero, 1968).

Euractinella BITTNER, 1890, p. 302 [**Terebratula contraplecta* BRAUN in MÜNSTER, 1841, p. 59; OD]. Suboval shells, without fold and sulcus; low rounded plications may be developed in corresponding positions on each valve; interior poorly known. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* southern Alps.——FIG. 1050,*2a–b.* **E. contraplecta* (BRAUN); holotype, dorsal and ventral views, ×2 (Münster, 1841).

Pexidella BITTNER, 1890, p. 300 [**Spirifer strohmayeri* SUESS, 1855, p. 27; OD]. Elongate oval; commonly with dorsal fold and ventral sulcus; posterior part of both valves may be strongly thickened by secondary shell material; jugum, posteriorly situated, originates from very wide umbonal blades, giving rise directly to accessory jugal lamellae. *Middle Triassic (Anisian)–Upper Triassic (Norian):* Carpathians, Alps, Dinarides, Balkans, Caucasus, Nepal, Pamir, *Anisian–Norian;* USA (southeastern Alaska), ?Chile, *Upper Triassic.*——FIG. 1051,*2a–v.* **P. strohmayeri* (SUESS), Norian; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, Mühltal, Austria, USNM 497419, ×1.5 (new); *f,* ventral view showing brachidium, Mühltal, Austria, ×2 (Bittner, 1890); *g–v,* transverse serial sections 0.6, 0.9, 1.1, 1.3, 1.4, 1.6, 1.8, 1.9, 2.1, 2.3, 2.7, 2.9, 3.0, 3.2, 3.4, 3.5 mm from ventral umbo, distance from ventral umbo to first section and between sections *p* and *q* approximate, northwestern Caucasus, IGiG 394/275 (adapted from Dagys, 1974).

Subfamily CLAVIGERINAE Waterhouse, 1975

[*nom. transl.* GRUNT, 1984, p. 70, *ex* Clavigeridae WATERHOUSE, 1975, p. 14]

Large, subpentagonal to subtrapezoidal; commonly with long straight hinge line and cardinal areas more or less well defined in both valves; dorsal fold and ventral sulcus faintly developed, or shallow sulcus may develop in both valves; surface with growth laminae; dental plates short, subparallel, slightly separated from thick lateral walls; pedicle support present, commonly complex; cardinal plate massive; cardinal flanges strongly developed; myophragm commonly present; jugum essentially as in *Athyris* with lateral branches of jugum originating before valve midlength, projecting anteroventrally; accessory jugal lamellae commonly very short and anteriorly serrated; shell massive, tertiary layer usually thick. *Upper Triassic.*

Clavigera HECTOR, 1879, p. 538 [**C. bisulcata* HECTOR in THOMSON, 1913, p. 50; SD THOMSON, 1919, p. 412] [=*Hectoria* TRECHMANN, 1918, p. 233, OD, obj.; *Hectorina* FINLAY, 1927, p. 533, *nom. nov. pro Hectoria* TRECHMANN, 1918, p. 233, *non Hectoria* CASTELNAU, 1873, Pisces, *nec Hectoria* TEPPER, 1889, Orthoptera; *Clavigerina* MARWICK, 1946, p. 30, *lapsus pro Clavigera*]. Transverse shell with shallow median sulcus in both valves, bordered by more or less rounded ridge on either side; anterior commissure rectimarginate to faintly uniplicate; hinge line straight, almost equal to maximum width; ventral cardinal area low and wide, concave, apsacline to anacline, faintly striated; foramen small, in meso- to permesothyridid position, closed at maturity; dental plates diverging slightly dorsally, very short ventral median septum may support apically situated delthyrial plate; divergent muscle scars strongly marked; very high cardinal plate commonly with shallow longitudinal depression; accessory jugal lamellae very short. *Upper Triassic (Norian–Rhaetian):* New Caledonia, New Zealand, Chile. ——FIG. 1053,*1a–f.* **C. bisulcata* HECTOR, Rhaetian, New Zealand; *a,* holotype, dorsal view, ×1 (Thomson, 1913); *b–f,* transverse serial sections 11.0, 14.0, 16.5, 18.5, 21.5 mm from ventral

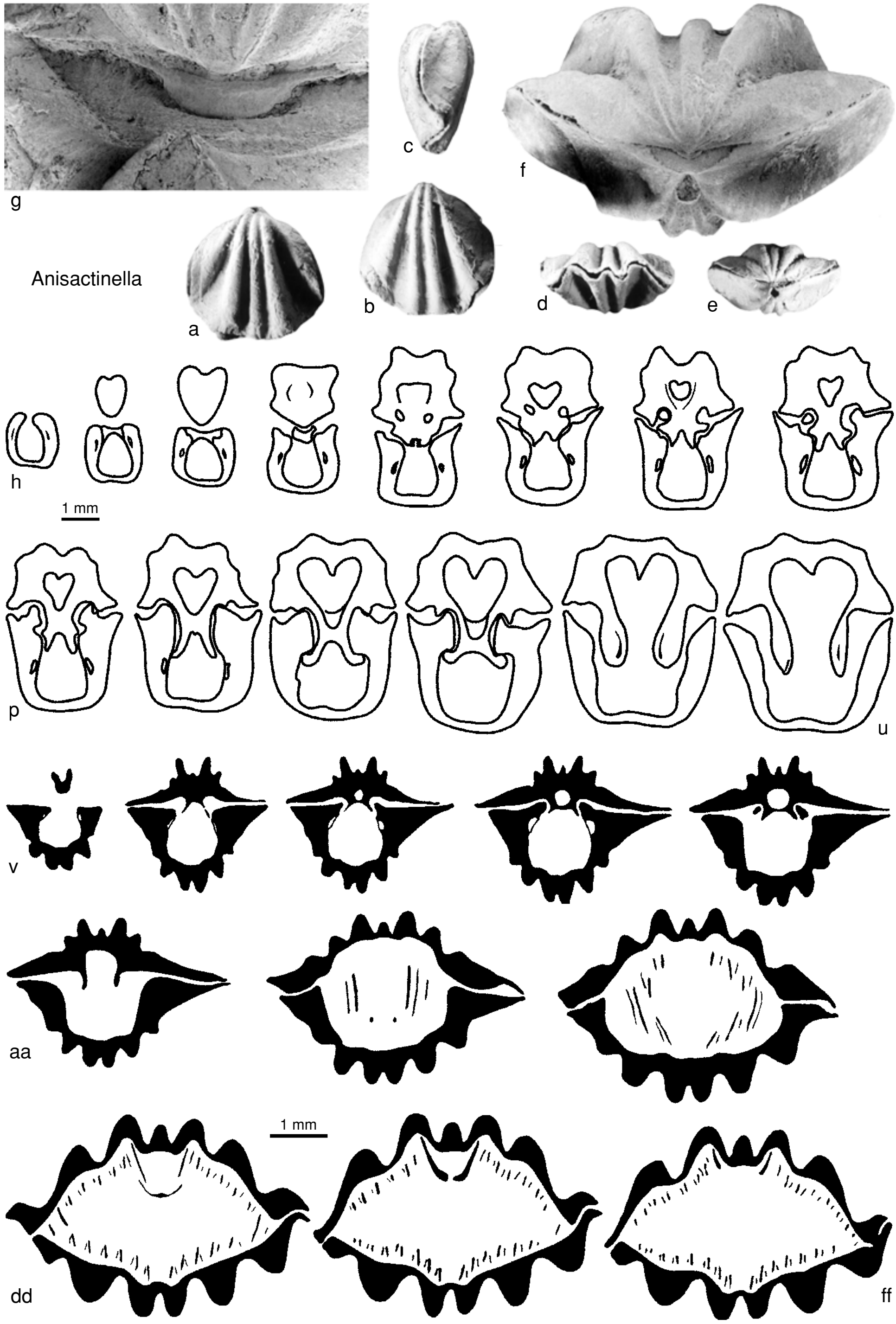

FIG. 1052. Diplospirellidae (p. 1548).

umbo, NZGS br1297 (adapted from Waterhouse, 1975).——FIG. 1053,*1g–k*. *C.* sp.; posterodorsal, ventral, lateral, anterior, and posterior views of internal mold, DPO F24246, ×1 (new).

Majkopella MOISSEIEV in DAGYS, 1962, p. 61 [**Athyris worobievi* MOISSEEV, 1947a, p. 76; OD]. Subequally biconvex, rounded subpentagonal to transverse semielliptical shells; hinge line nearly straight, equal or slightly shorter than maximum width; ventral cardinal area low, long, with almost parallel margins; pedicle collar complex, almost completely filling delthyrial cavity; cardinal plate as in *Oxycolpella.* [The name *Majkopella* is commonly credited to DAGYS (1962). We agree with DAGYS (1962, 1974) and accept MOISSEIEV (in DAGYS, 1962) as author.] *Upper Triassic:* Crimea, Carpathians, Balkans, Turkey, Caucasus, ?southern China (Sichuan).——FIG. 1053,*2a–o*. **M. worobievi* (MOISSEIEV), Rhaetian, northern Caucasus; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, IGiG 166/101, ×1 (Dagys, 1962; photographs courtesy of the late A. S. Dagys); *f–o,* transverse serial sections 0.6, 1.2, 1.7, 2.1, 2.6, 3.2, 4.3, 4.8, 6.2, 7.2 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Dagys, 1962).

Oxycolpella DAGYS, 1962, p. 68 [**Spirigera oxycolpos* SUESS, 1854, p. 45[17]; OD; =*Spirigera oxycolpos* SUESS, 1853, p. 287, *nom. nud.*] [=*Dictyonathyris* XU, 1978, p. 287 (type, *D. lanaensis,* OD)]. Round to rounded pentagonal; growth laminae irregular; large foramen; thick delthyrial plate; sessile pedicle collar may be present; cardinal plate massive, subquadrate; cardinal flanges strongly developed, serrated, ventrally concave, projecting into delthyrial cavity. [Type species is usually credited to EMMRICH, 1853, p. 356; however he gave no description or figure. The first to fulfill the conditions of availability was SUESS (1854) who therefore has been credited with authorship (PEARSON, 1977).] *Upper Triassic:* Slovakia, Bavaria, southern Austria, Hungary, Romania, Turkey, Iran, Himalayas, Pamir, southern and northwestern China, New Caledonia, New Zealand, northern Chile.——FIG. 1054*a–bb.* **O. oxycolpos* (SUESS), Rhaetian, Austria; *a–d,* lectotype, dorsal, lateral, anterior, and posterior views, MGBW 1074, ×1 (Pearson, 1977); *e–q,* transverse serial sections 2.3, 3.1, 3.9, 4.5, 11.6, 12.8, 15.0, 15.5, 16.0, 16.3, 16.9, 17.7, 19.3 mm from ventral umbo, MGBW PC.Nr.69 (adapted from Pearson, 1977); *r–bb,* transverse serial sections 0.8, 2.4, 3.6, 5.0, 6.1, 6.6, 7.7, 8.5, 9.2, 10.0, 11.1 mm from ventral umbo, distance from ventral umbo to first section approximate, northern Caucasus (adapted from Dagys, 1962).

Subfamily MISOLIINAE Dagys, 1996

[Misoliinae DAGYS, 1996, p. 89]

Commonly small, rarely large, elongate oval, costate; fold and sulcus faint or absent; growth lines commonly numerous and weak; dental plates poorly developed; cardinal plate slightly concave ventrally; swollen cardinal flanges moderately to strongly developed; jugum without jugal stem, short accessory jugal lamellae extend posterodorsally directly from anteriorly pointed jugal saddle. *Lower Permian (Artinskian)–Upper Triassic (Norian).*

Misolia VON SEIDLITZ, 1913, p. 172 [**M. misolica;* OD]. Large, moderately to strongly biconvex, elongate-oval; costae may bifurcate anteriorly; foramen large, in meso- to permesothyridid position; deltidial plates conjunct. *Upper Triassic (Norian):* Indonesia, Moluccas, Timor, Oman, ?India, ?China, northwestern Australia.——FIG. 1055,*1a–g*. **M. misolica,* Indonesia; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–g,* ventral and lateral views of jugum, ×2 (von Seidlitz, 1913).

?**Anomactinella** BITTNER, 1890, p. 300 [**Terebratula flexuosa* MÜNSTER, 1841, p. 59; OD]. Small, circular to elongate oval or pentagonal shells; umbones smooth, anterior half of valves prominently costate, with costae in corresponding position on each valve, commissure denticulate in dorsal view; ventral interior, cardinalia, and brachidium poorly known. [This genus requires revision.] *Middle Triassic (?Ladinian), Upper Triassic (Carnian):* southern Alps.——FIG. 1055,*2a–b*. **A. flexuosa* (MÜNSTER); dorsal and ventral views, ×1 (Bittner, 1890).

?**Pentactinella** BITTNER, 1890, p. 300 [**Terebratula quinquecostata* MÜNSTER, 1841, p. 59; SD HALL & CLARKE, 1894, p. 977]. Small, oval to subcircular or rhomboidal; each valve with 5 to 16 coarse costae in corresponding position; costae may bifurcate anteriorly; commissure strongly denticulate in dorsal view; foramen small, in permesothyridid position; structure of jugum unknown. [This genus requires revision.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* southern Alps, southern Italy, Slovakia, Romania.——FIG. 1055,*5a–b*. **P. quinquecostata* (MÜNSTER), Carnian, San Cassiano, Italy; dorsal and ventral views, ×2.5 (Taddei Ruggiero, 1968).——FIG. 1055,*5c–g*. *P. scandonei* TADDEI RUGGIERO, Ladinian, Lucania, Italy; transverse serial sections 0.68, 0.9, 1.06, 1.2, 1.62 mm from ventral umbo (Taddei Ruggiero, 1968).

?**Stolzenburgiella** BITTNER, 1903, p. 508 [**S. bukowskii;* OD]. Medium, elongate or transverse subpentagonal; costae in corresponding position on each valve; foramen dotlike; ventral interior, cardinalia, and brachidium poorly known. [This genus requires revision.] *Triassic:* Dinaric Alps, *Anisian;* Slovakia, *Ladinian;* Malaysia, *Triassic.*——FIG. 1055,*3a–c*. **S. bukowskii,* Anisian, Bosnia; dorsal, ventral, and anterior views, ×2 (Bittner, 1903).

?**Uncinella** WAAGEN, 1883, p. 494 [**U. indica;* M]. Medium, biconvex, longitudinally subelliptical, ribbed shells commonly without fold and sulcus; foramen labiate in epithyridid position; delthyrium

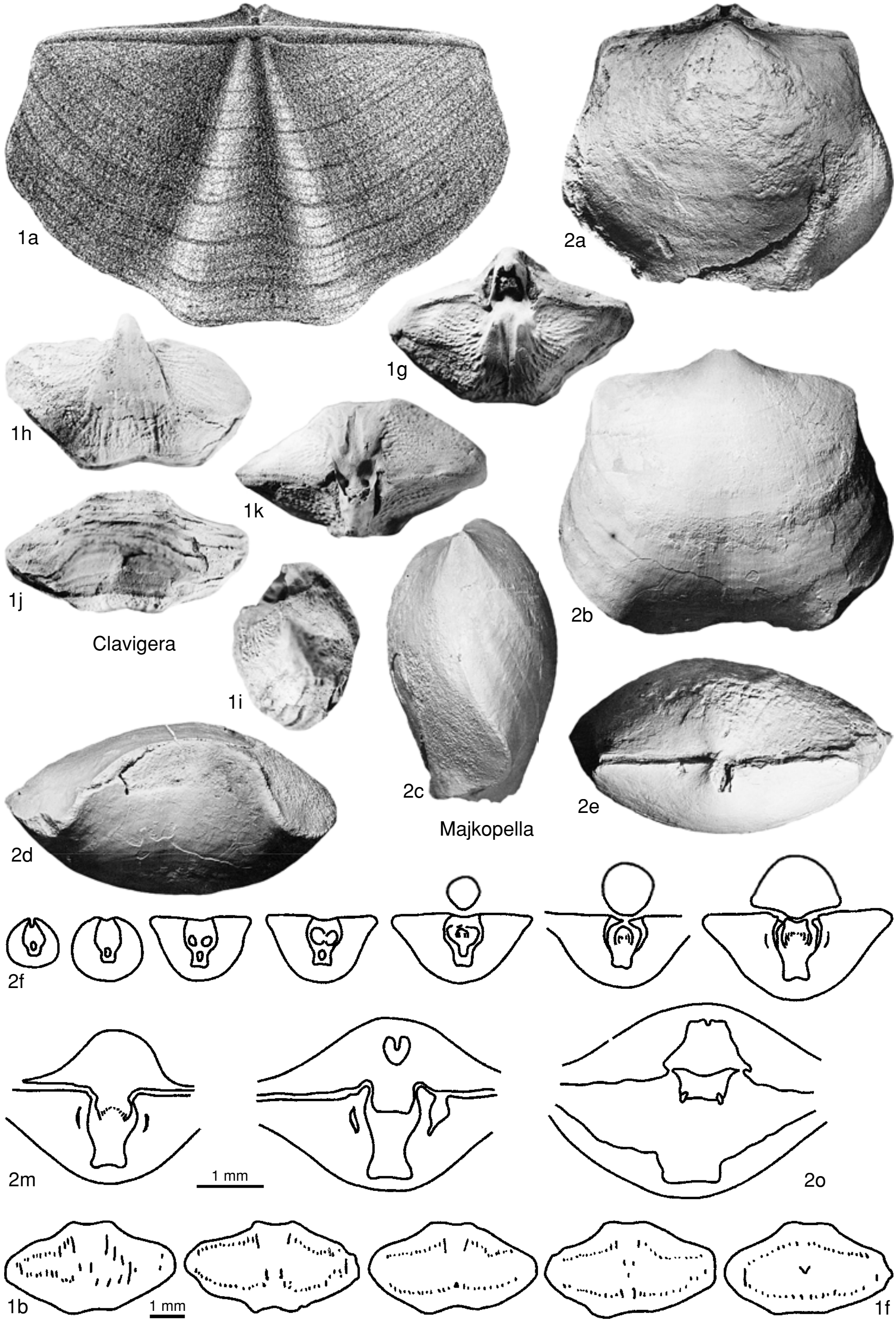

FIG. 1053. Diplospirellidae (p. 1548–1550).

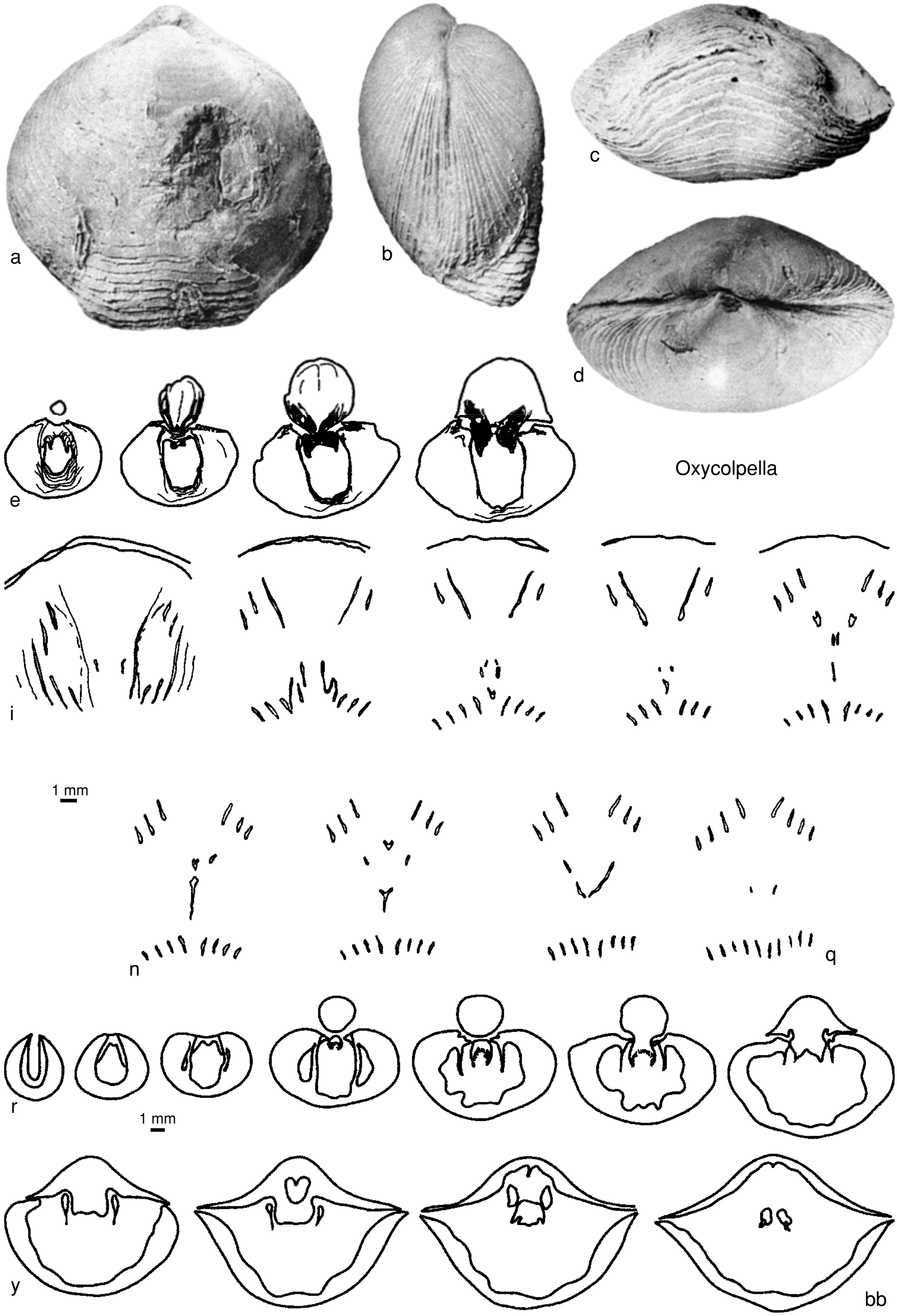

FIG. 1054. Diplospirellidae (p. 1550).

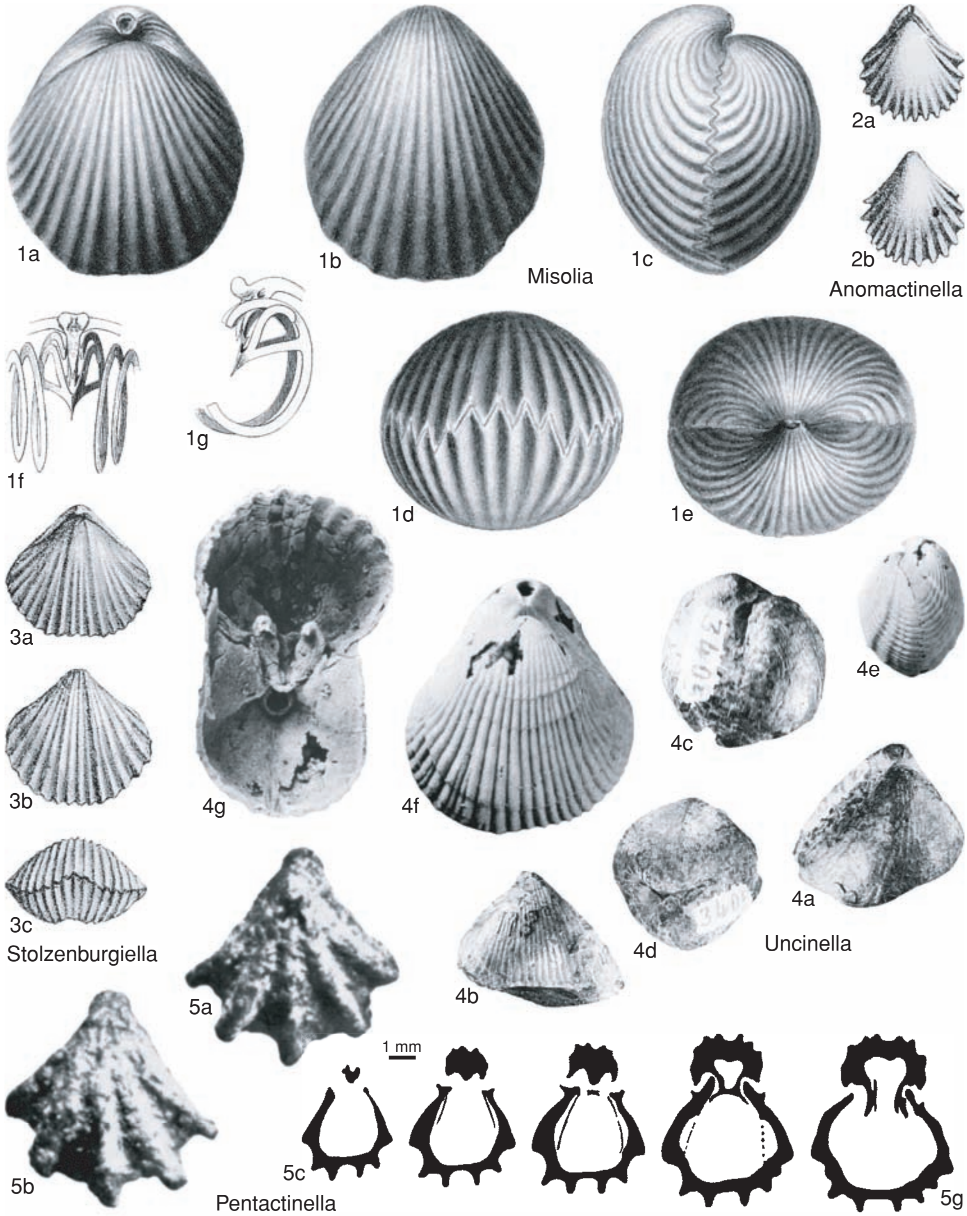

FIG. 1055. Diplospirellidae (p. 1050–1055).

with conjunct deltidial plates; dental plates absent, short pedicle collar may be present; hinge plate widely divided; cardinal process with large median knob and posteroventrally directed, well-developed cardinal flanges; crura ribbonlike, myophragm absent; spiral brachidium have been reported but not described or illustrated; jugum unknown. [Systematic position uncertain; this genus requires revision.] *Lower Permian (Artinskian):* Pakistan, southern Thailand, Cambodia, ?Vietnam, ?China.——FIG. 1055,*4a–f.* **U. indica,* Pakistan; *a–d,* holotype, dorsal, ventral, lateral, and posterior views, GSI 3405, Waagen collection, ×1 (new; photographs courtesy of R. K. Biswas); *e,* lateral view, ×1; *f,* dorsal view, USNM 212772, ×2 (Grant, 1976).——FIG. 1055,*4g. U. siamestris* GRANT, Artinskian,

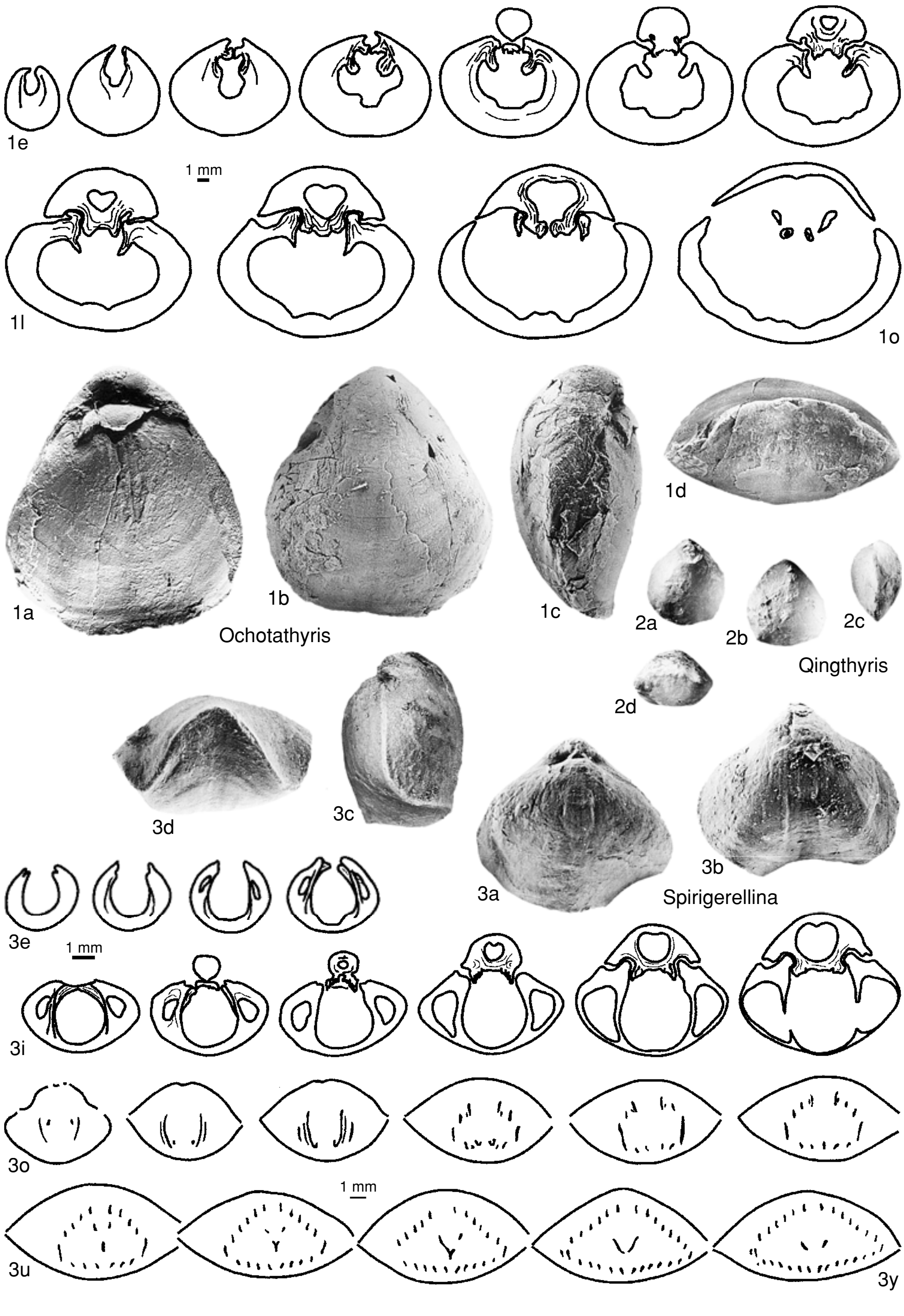

FIG. 1056. Diplospirellidae (p. 1555–1556).

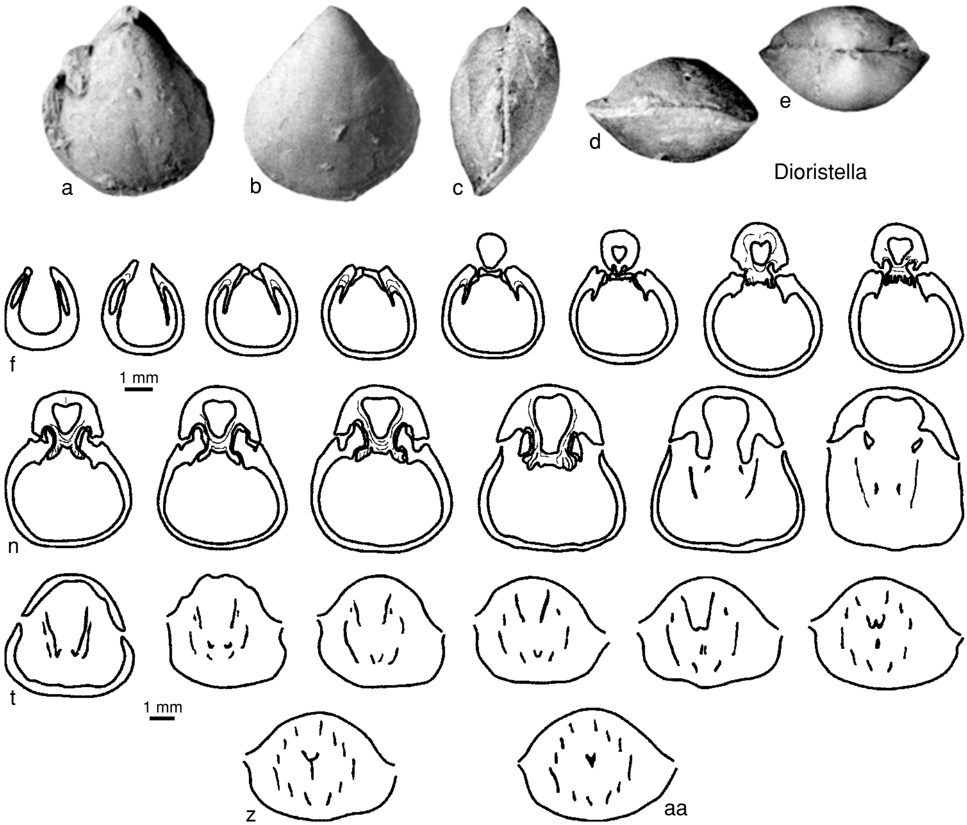

FIG. 1057. Diplospirellidae (p. 1555–1556).

Thailand; interior of articulated shell showing cardinalia and articulation, USNM 212770, ×2 (Grant, 1976).

Subfamily OCHOTATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Ochotathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 844]

Small to large, commonly elongate-oval; dorsal fold and ventral sulcus variably developed, commonly faint; growth lines faintly expressed, growth lamellae absent; dental plates short, converging dorsally, only dental flanges support massive teeth anteriorly; delthyrial plate present; cardinal plate commonly high and thick; cardinal flanges serrated, commonly well developed; low myophragm usually present; jugum essentially as in *Athyris* with short accessory jugal lamellae, jugal saddle poorly developed or absent; tertiary layer may be present. *Lower Triassic (Scythian)–Upper Triassic (Norian), ?Upper Jurassic.*

Ochotathyris DAGYS, 1974, p. 159 [**Oxycolpella ochotica* DAGYS, 1965, p. 132; OD]. Medium to large, oval to longitudinally triangular shells with dorsal fold and ventral sulcus faintly developed; beak thick, strongly incurved; faintly developed sessile pedicle collar may be present; tertiary layer thick. *Upper Triassic (Norian), ?Upper Jurassic:* Russia (Primorya, Siberia), USA (Arctic Alaska), *Norian;* northwestern China, Qinghai, *?Upper Jurassic.*——FIG. 1056,*1a–o.* **O. ochotica* (DAGYS), Norian, Primorya; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 290/118, ×1 (Dagys, 1974; photographs courtesy of the late A. S. Dagys); *e–o,* transverse serial sections 2.0, 3.2, 3.7, 4.2, 5.0, 5.7, 6.3, 7.0, 8.4, 8.9, 9.4 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Dagys, 1965).

Dioristella BITTNER, 1890, p. 299 [**Terebratula indistincta* BEYRICH, 1863, p. 34; SD HALL &

CLARKE, 1894, p. 969]. Small, commonly nonsulcate, longitudinal furrows may be developed in both valves; lateral branches of jugum lead off from umbonal blades until joining anteroventrally, jugal stem long, projecting posteroventrally with low angle, accessory jugal lamellae normally free. *Upper Triassic (Carnian):* southern Alps, Carpathians, Caucasus, Pamir.——FIG. 1057*a–aa*. **D. indistincta* (BEYRICH), St. Cassian, southern Tyrol; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497421, ×3 (new); *f–aa,* transverse serial sections 0.2, 0.5, 0.7, 0.9, 1.0, 1.1, 1.2, 1.4, 1.6, 1.7, 1.9, 2.1, 2.3, 2.4, 2.7, 3.0, 3.2, 3.4, 3.5, 3.7, 3.9, 4.2 mm from ventral umbo, distance from ventral umbo to first section and between sections *s* and *t* approximate, IGiG 394/265 (adapted from Dagys, 1974).

?Qingthyris XU & LIU, 1983, p. 126 [**Q. variabilis;* OD]. Medium size with variable outline; interior poorly known, reportedly without dental plates but possibly with bilobed cardinal process and posterior median ridge in dorsal valve; spiralia and jugum unknown. [May be synonymous with *Dioristella.*] *Middle Triassic:* northwestern China (Qilian Mountains).——FIG. 1056,*2a–d*. **Q. variabilis;* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Xu & Liu, 1983; photographs courtesy of Xu Guirong).

Spirigerellina DAGYS, 1974, p. 160 [**S. pygmaea;* OD] [=*Compositella* XU & LIU, 1983, p. 124 (type, *C. planosulcata,* OD)]. Small, rounded pentagonal to transversely oval shells with variably developed dorsal fold and ventral sulcus that may bear median furrow; anterior commissure uniplicate to parasulcate; cardinal flanges low; jugum without saddle. *Lower Triassic (Scythian)–Upper Triassic (Carnian):* Alps, Dinarids, Carpathians, Primorya, Caucasus, Nepal, Siberia, Kazakhstan, Mongolia, southern Qilian, Chaidam, northwestern China. ——FIG. 1056,*3a–y*. **S. pygmaea,* Scythian, Mangylschak, Kazakhstan; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 394/76, ×2.5 (Dagys, 1974; photographs courtesy of the late A. S. Dagys); *e–y,* transverse serial sections 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.1, 2.3, 2.5, 2.7, 3.0, 3.2, 3.4, 3.6, 4.1, 4.4, 4.7, 5.3, 5.6, 5.8, 6.0 mm from ventral umbo, distance from ventral umbo to first section and between sections *n* and *o* approximate, IGiG 394/84 (adapted from Dagys, 1974).

Subfamily TETRACTINELLINAE Grunt, 1986

[Tetractinellinae GRUNT, 1986, p. 7]

Medium, externally resembling *Plicathyris;* dental plates of medium length, converging slightly dorsally; delthyrial plate present; cardinal plate thin, high; cardinal flanges serrated, moderately developed; short dorsal myophragm may be present; jugum essentially as in *Athyris* with short jugal saddle and accessory jugal lamellae terminating anteriorly of lateral branches of jugum. *Middle Triassic.*

Tetractinella BITTNER, 1890, p. 300 [**Terebratulites trigonellus* VON SCHLOTHEIM, 1820 in 1820–1823, p. 271; SD HALL & CLARKE, 1894, p. 977]. Shell commonly with 4 narrow, cusplike plications in corresponding position on each valve, separated by wide, flat interspaces; anterior commissure straight or slightly deflected dorsally. *Middle Triassic:* Alps, Dinarids, Carpathians, Balkans, Caucasus, Pamir, ?China.——FIG. 1058*a–x*. **T. trigonella* (VON SCHLOTHEIM); *a–e,* dorsal, ventral, lateral, anterior, and posterior views, southern Tyrol, USNM 497420, ×1.5 (new); *f,* lateral view of jugum, southern Tyrol, ×4 (Bittner, 1890); *g–x,* transverse serial sections 1.0, 1.4, 1.8, 2.1, 2.4, 2.6, 2.8, 3.3, 3.8, 4.0, 4.2, 5.2, 5.9, 6.4, 6.9, 7.3, 7.7, 8.1 mm from ventral umbo, distance from ventral umbo to first section approximate, Caucasus, IGiG 394/273 (adapted from Dagys, 1974).

Family HYATTIDINIDAE Sheehan, 1977

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 841, *ex* Hyattidininae SHEEHAN, 1977, p. 29; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 841]

Astrophic, medium, moderately to strongly convex and rostrate shell; with or without ventral sulcus and dorsal fold; growth lines weak, without frills; dental plates thin and short; pedicle supports absent; ventral muscle field impressed, without longitudinal striations; cardinal plate thin, flat, triangular, inner hinge plates separated by narrow fissure; no cardinal process; no dorsal median septum or myophragm; lateral branches of jugum originating before valve midlength, projecting backward and joining in narrow jugal arch; jugal saddle and stem absent; without tertiary layer. *Upper Ordovician (?Caradoc, Ashgill)–Silurian (Přídolí).*

Hyattidina SCHUCHERT, 1913, p. 415, *nom. nov. pro Hyattella* HALL & CLARKE, 1893, p. 61, *non* LENENDFELD, 1891 [**Atrypa congesta* CONRAD, 1842, p. 265; OD]. Biconvex shells with pentagonal outline, covered with numerous growth lines; ventral sulcus and dorsal fold may be accentuated by bounding furrows; slightly divergent diductor scars enclose linear adductors. *Upper Ordovician (?Caradoc, Ashgill)–Silurian (Ludlow):* Scotland, Ireland, *?Caradoc, Ashgill;* North America, United Kingdom, Ireland, Norway, Russian Platform, Siberian Platform, *Ludlow.*——FIG. 1059,*1a–g*. **H. congesta* (CONRAD), Ludlow, Clinton Group, New York, USA; *a–e,* neotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 31132, Hall

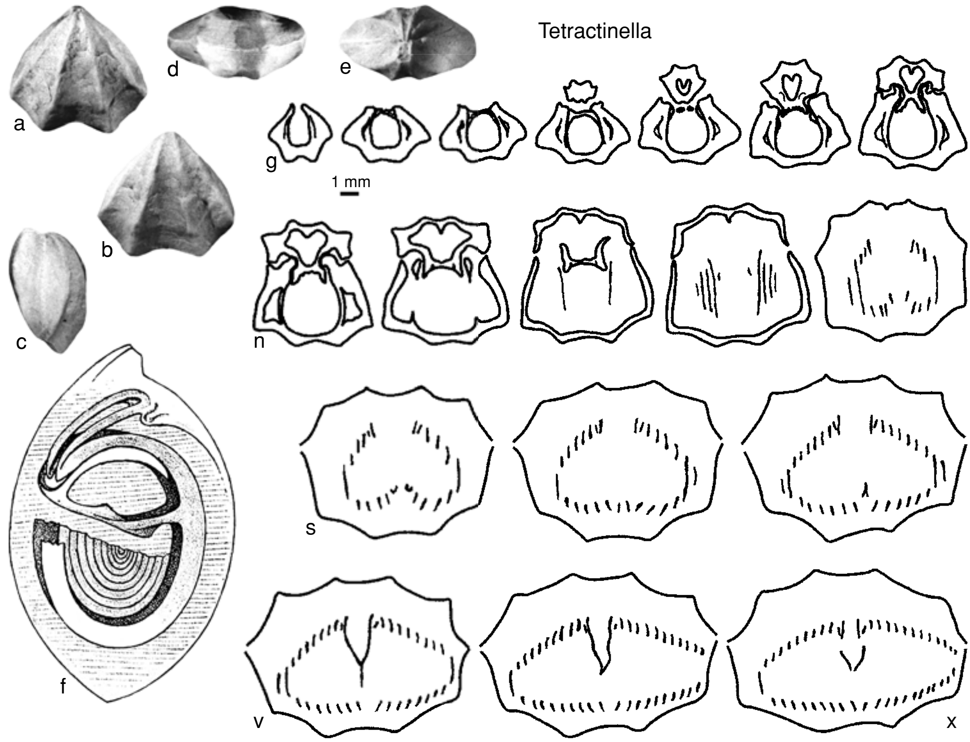

FIG. 1058. Diplospirellidae (p. 1556).

collection, ×2; *f,* cardinalia, I1420, Hall collection, ×17 (Alvarez & Brime, 2000); *g,* cardinalia, USNM 497423, ×20 (new).

?**Argella** MENAKOVA & NIKIFOROVA, 1986, p. 68 [**A. pirum;* OD]. Similar to *Hyattidina* but strongly inflated; base of delthyrium closed by short deltidial plates; crura ventrally directed. [*Argella* was identified by its authors as a meristelloid, presumably on the basis of the overall external morphology. Other features, such as the absence of septalium and dorsal septum, however, are more typically athyridoid. It has some similarities with the didymothyridins and the hyattidins. Revision of dorsal and ventral posterior internal structures is required to confirm its affinities.] *Silurian (Přídolí):* Tajikistan.——FIG. 1059,*2a–w.* **A. pirum; a–d,* holotype, dorsal, ventral, lateral, and anteroventral views, ×2 (Menakova & Nikiforova, 1986; photographs courtesy of T. L. Modzalevskaya); *e–u,* transverse serial sections 0.8, 1.2, 1.4, 1.8, 2.0, 2.05, 2.15, 2.2, 2.8, 3.2, 3.5, 3.6, 3.8, 4.0, 4.4, 4.9, 5.4 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 31/6228 (adapted from Menakova & Nikiforova, 1986); *v–w,* ventral and lateral views of jugum, TsNIGRA 31/6228 (Menakova & Nikiforova, 1986).

Superfamily MERISTELLOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 447, *pro* Meristellacea DAGYS, 1974, p. 231, *nom. transl. ex* Meristellinae WAAGEN, 1883, p. 449; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 834]

Athyrididines commonly smooth; moderately to strongly rostrate, ventral umbo moderate to strongly curved; narrow and astrophic hinge line; concentric growth lamellae poorly developed or absent; dorsal fold and ventral sulcus commonly weak or absent; ventral cardinal area (palintrope) reduced; pedicle opening commonly present as foramen, in meso- to epithyridid position, and delthyrium open or partially covered by deltidial plates (completely in *Septathyris*); shell tending to be thick, particularly in the umbonal region; pedicle support absent; distinct dental plates commonly present, may be reinforced by mystrochial plates or shoelifter (meristids) or form spondylial structure

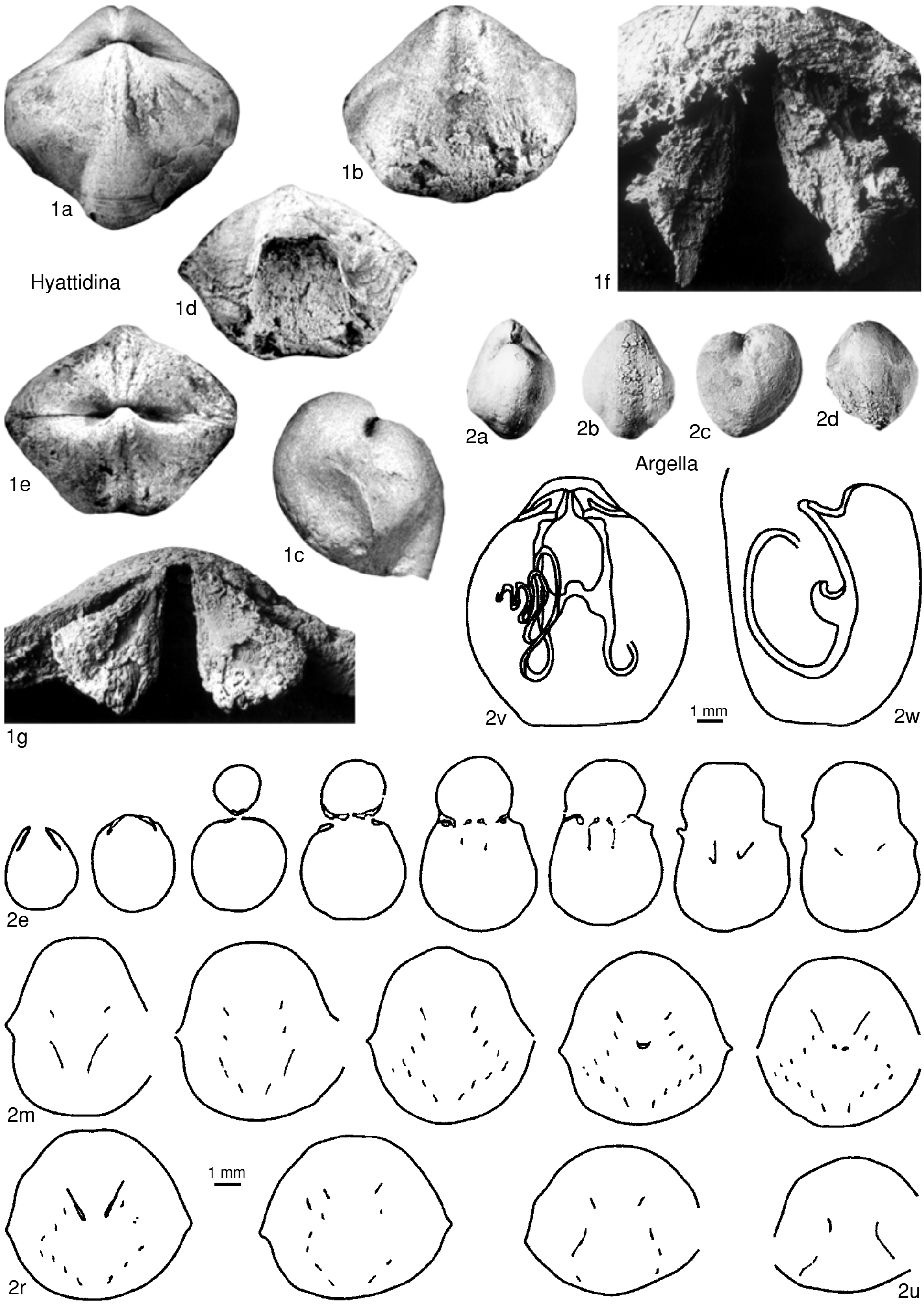

FIG. 1059. Hyattidinidae (p. 1556–1557).

(camarophorellins and rowleyellins); inner hinge plates present, forming septalium; long and high dorsal median septum commonly present; dorsal shoe-lifter may be present in some meristids; simple to complex jugum, jugal saddle absent, accessory jugal lamellae, when present, reunited with lateral branches of jugum or with jugal stem. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Family MERISTELLIDAE Waagen, 1883

[*nom. transl.* HALL & CLARKE, 1894, p. 840, *ex* Meristellinae WAAGEN, 1883, p. 449; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 835]

Commonly large, strongly convex, with dorsal valve equally or less convex than ventral; dental plates subparallel, long (possibly extending anteriorly to flank muscle scars) in Ordovician and Silurian genera, short to obsolescent in Devonian genera; ventral muscle field commonly deeply impressed, fan shaped, widening anteriorly; bulbous pedicle callist with a short constriction anteriorly commonly present; septalium commonly deep and narrow, but wide and shallow in late forms; other structures strengthening the muscle system, or supporting dental plates, absent; tertiary layer may be present. *Upper Ordovician (Ashgill)–Upper Devonian (lower Frasnian).*

Subfamily MERISTELLINAE Waagen, 1883

[Meristellinae WAAGEN, 1883, p. 449; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Acute jugal arch projecting as long stem, moderately inclined posteriorly, may bifurcate into accessory jugal lamellae that may reunite with stem. *Upper Ordovician (Ashgill)–Upper Devonian (lower Frasnian).*

Meristella HALL, 1859a, p. 78 [**Atrypa laevis* VANUXEM, 1842, p. 120; SD MILLER, 1889, p. 354; validated ICZN Opinion 1899, 1998a, p. 131]. Subequally biconvex shells, commonly longer than wide; ventral beak strongly incurved at maturity, frequently concealing foramen, with delthyrium commonly obscured by beak of dorsal valve; deltidial plates may be exposed in early growth stages; with or without dorsal fold and ventral sulcus that may affect only anterior commissure; dental plates short, obsolescent; ventral muscle field flaring widely laterally; broad and shallow supported septalium; septum extending anteriorly to about midvalve length; acute jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae then reuniting with stem; tertiary layer present. *Silurian (?upper Přídolí), Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* northeastern USA, *?upper Přídolí;* North America, Morocco, Mauritania, France, Belgium, Poland, Bohemia, Altay, Kazakhstan, eastern Urals, Chinese Altay, southeastern Australia, *Lochkovian;* Venezuela, *Pragian;* Spain, Bohemia, *Emsian;* Germany, *Eifelian.*——FIG. 1060*a–e.* **M. laevis* (VANUXEM), Lochkovian, Lower Helderberg Group, New York, USA; neotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33581, Hall collection, ×1.5 (Alvarez & Brime, 2000).——FIG. 1060*f–k. M. walcotti* HALL & CLARKE, Lower Devonian, Ontario, Canada; *f–g,* dorsal and anterior views of specimen prepared to show spiralium and jugum, I1573, Hall collection, ×1.5 (Alvarez, Rong, & Boucot, 1998); *h–i,* ventral and posterior views of specimen prepared to show spiralium and jugum, I1573, Hall collection, ×1.5 (new); *j–k,* lateral and ventral views of jugum (Hall & Clarke, 1893).——FIG. 1060*l–m. M. arcuata* (HALL), Lochkovian, Lower Helderberg Group, New York, USA; ventral and lateral views showing jugum (Glass, 1882).——FIG. 1060*n. M. atoka* GIRTY, Haragan, Oklahoma, USA; detail of growth lines and faintly developed radial ornamentation on flat growth lamella, USNM 497422, ×18 (new). [See also Fig. 1006.2, p. 1481, in introduction.]

Arctomeristina AMSDEN, 1978, p. 33 [**A. compressa;* OD]. Similar to *Hindella* externally and to *Meristina* internally; dorsal valve with short septalium supported by high, bladelike septum extending forward for approximately one-half valve length on mature shells; jugum projecting posteriorly, jugal bifurcations unknown. *Silurian (Wenlock):* North America, ?Russia (Tuva).——FIG. 1061,*2a–j.* **A. compressa,* Wenlock, Oklahoma, USA; *a–d,* holotype, dorsal, ventral, lateral, and posteroventral views, OU 8505, ×1 (Amsden, 1978); *e–j,* transverse serial sections 4.0, 4.44, 4.9, 6.4, 6.7, 7.6 mm from ventral umbo (adapted from Amsden, 1978).

Charionella BILLINGS, 1861, p. 148 [**Atrypa scitula* HALL, 1843, p. 171; OD]. Similar to *Meristella* but having a sessile septalium. *Lower Devonian (lower Emsian)–Upper Devonian (lower Frasnian):* North America.——FIG. 1062,*2a–f.* **C. scitula* (HALL); *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Givetian, New York, USA, I1215, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f,* ventral view of septalium, Middle Devonian, Ontario, Canada, I1214, Hall collection, ×11 (new).

Charionoides BOUCOT, JOHNSON, & STATON, 1964, p. 817 [**Meristella doris* HALL, 1860a, p. 84; OD].

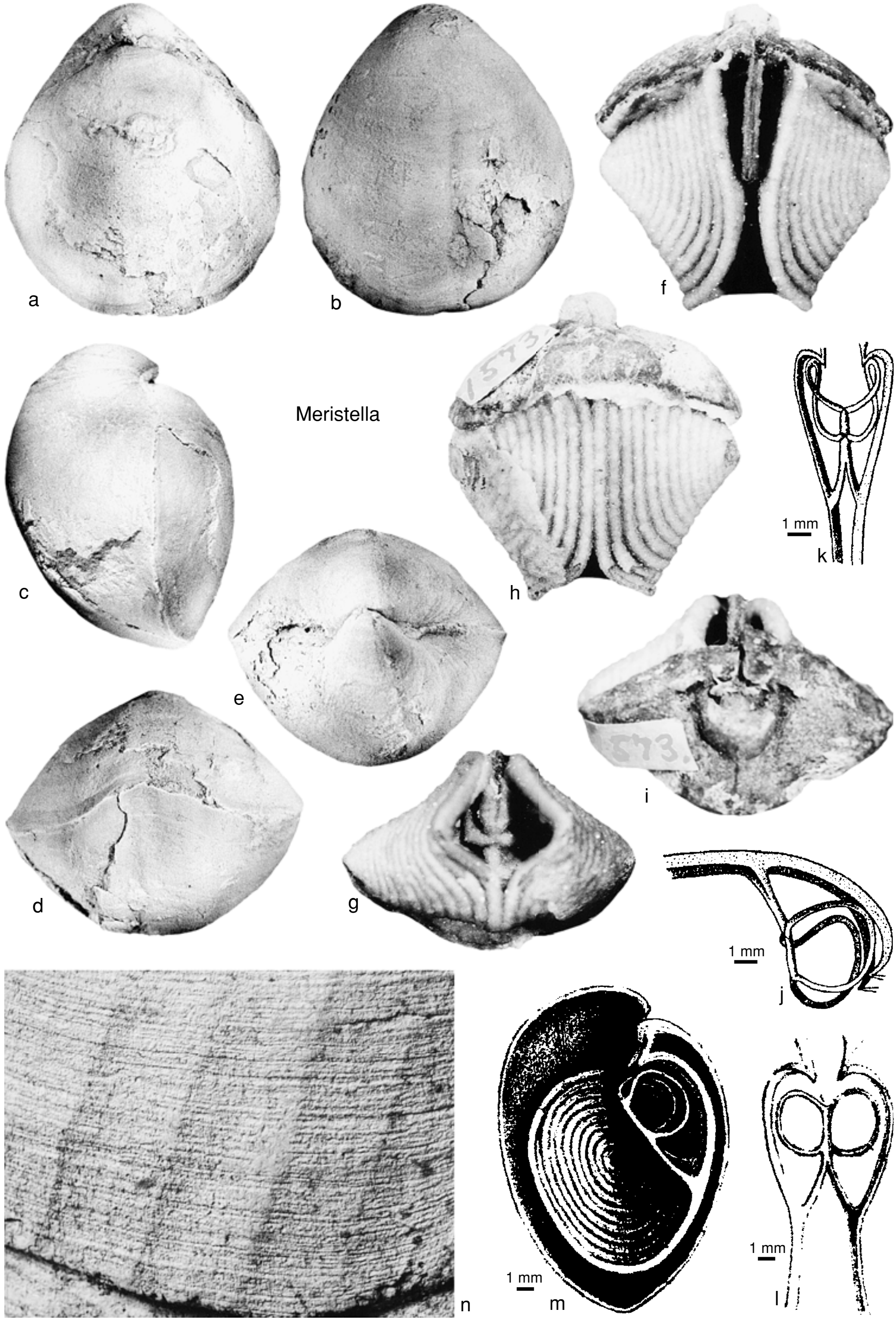

FIG. 1060. Meristellidae (p. 1559).

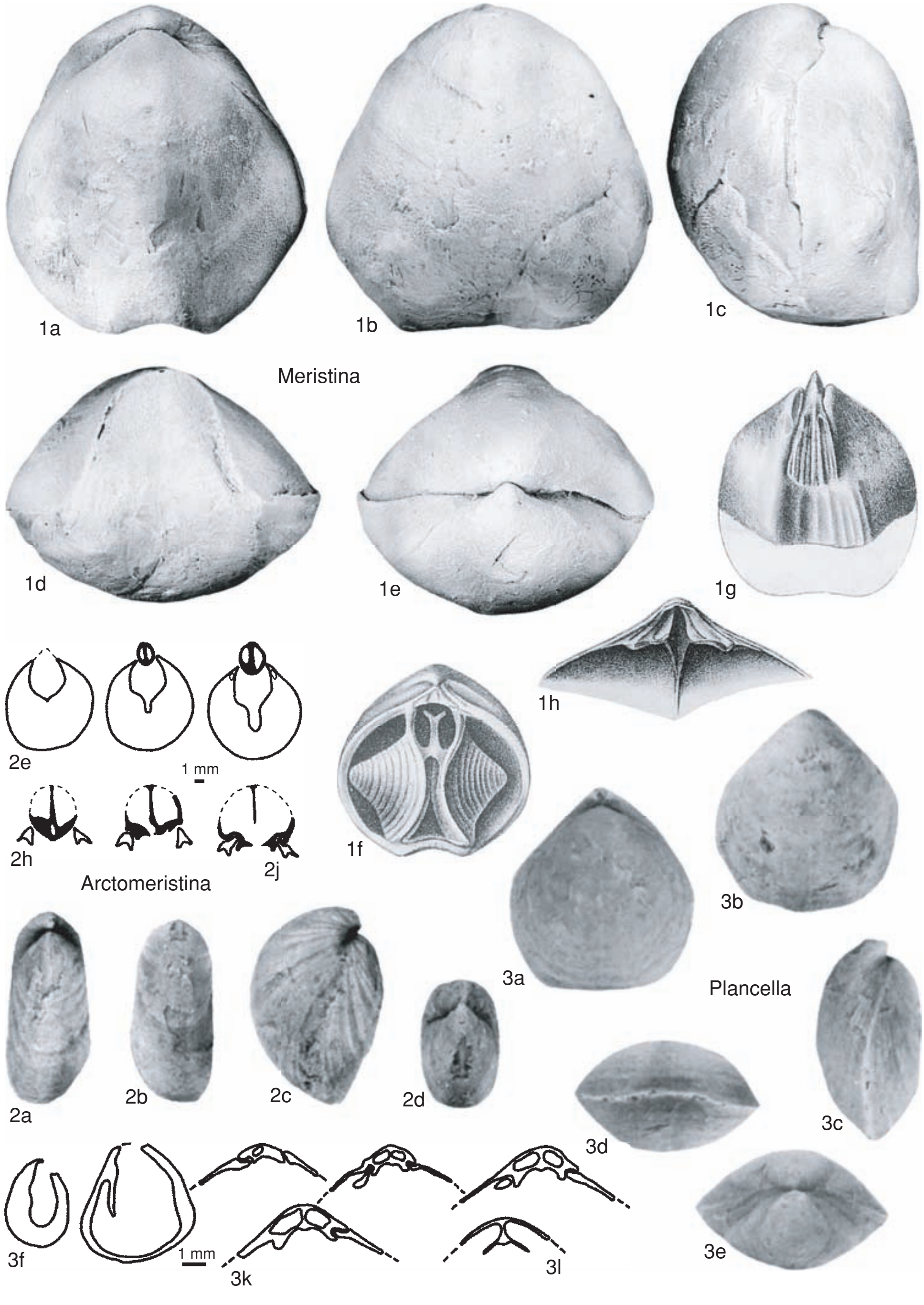

FIG. 1061. Meristellidae (p. 1559–1566).

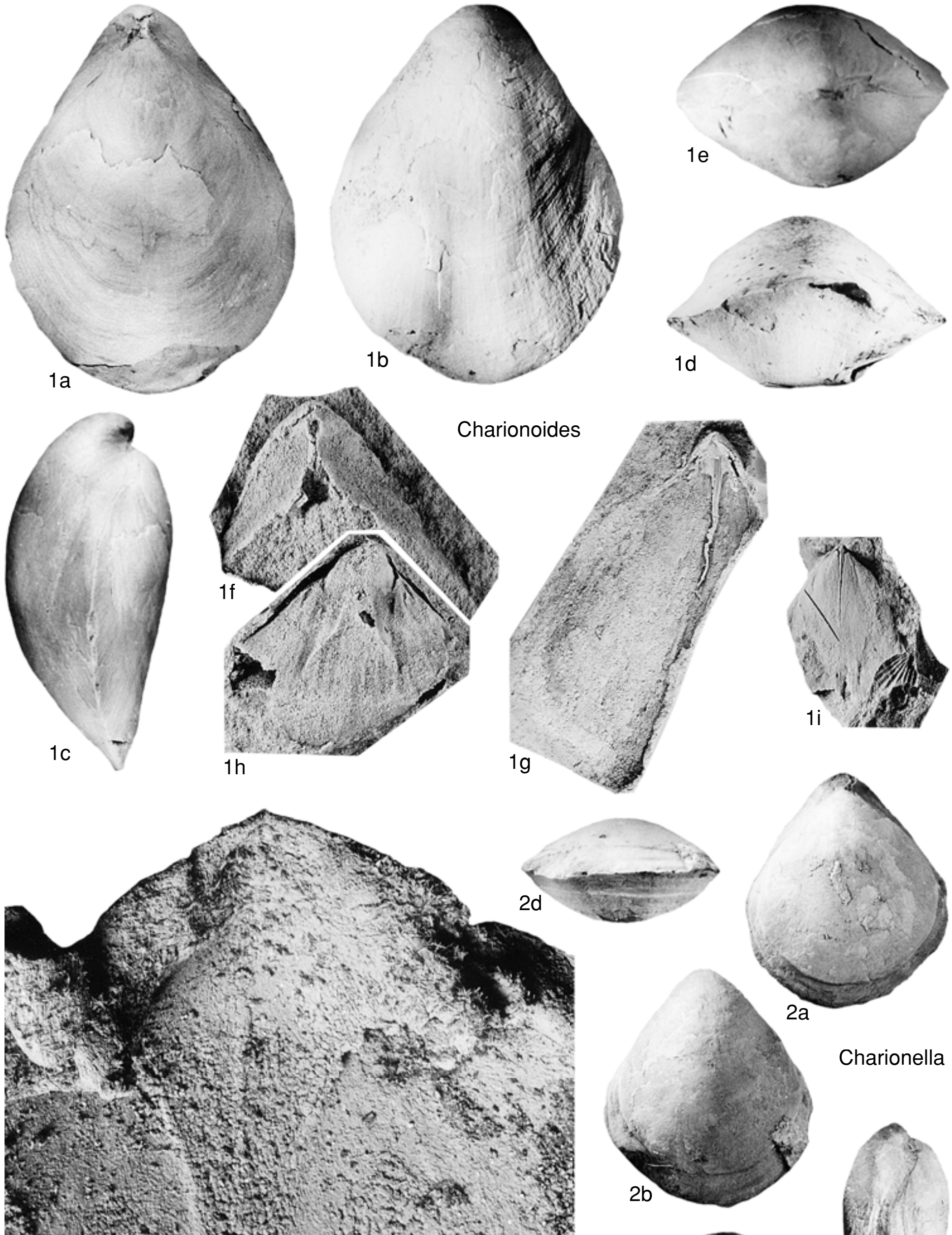

FIG. 1062. Meristellidae (p. 1559–1563).

Similar to *Charionella* but with ventral beak only slightly incurved; internally ventral valve with short dental plates, and muscle field less strongly impressed than in *Meristella;* dorsal valve septalium longer than in *Charionella,* being sessile posteriorly but elevated on short median septum anteriorly; spiralium and jugum unknown. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* eastern North America.——FIG. 1062,*1a–e.* **C. doris* (HALL), Emsian, New York, USA; lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 3071B, Hall collection, ×1.5 (Alvarez & Brime, 2000).——FIG. 1062,*1f–i. C.* sp. cf. *C. doris* (HALL), Emsian, Maine, USA; *f,* dorsal view of ventral beak, ×3; *g–h,* dorsal valve interior and ventral valve interior mold, ×2; *i,* dorsal interior mold, ×1 (Boucot, Johnson, & Staton, 1964).

Hindella DAVIDSON, 1882, p. 130 [**Athyris umbonata* BILLINGS, 1862, p. 144; OD] [=*Cryptothyrella* COOPER, 1942, p. 233 (type, *Whitfieldella quadrangularis* FOERSTE, 1906, p. 327, OD)]. Medium to large, elongate, subequally to ventribiconvex shells of variable outline commonly ranging from subrectangular to pyriform; ventral beak strongly incurved; dorsal fold and ventral sulcus absent or poorly developed, less frequently with narrow and shallow sulcus extending from umbo of ventral valve, and from about one-third posterior length of dorsal valve to anterior margin; few but strong growth lines; long, medially convex or dorsally convergent dental plates bounding deeply impressed muscle field; narrow, deep, and partially covered septalium, sessile or supported by median septum extending quite anteriorly as low ridge; lateral branches of jugum commonly originate well anteriorly, projecting backward at low angle, semicircular jugal arch projecting posteriorly as short, straight, and undivided stem; tertiary layer may be present. [*Cryptothyrella* COOPER differs only in minor changes in shell size and shape and in having longer, medially convex dental plates that bound a deeper, impressed muscle field (see GAURI & BOUCOT, 1970; SHEEHAN, 1977). The jugum of *Cryptothyrella* is more posteriorly placed, with jugal stem very long, posteroventrally directed, finally reaching a position close to crural ends. These differences are likely to reflect nothing more than specific variability and therefore the two genera are herein considered as synonoyms (see RONG, 1979; RONG & YANG, 1981; WANG Yu & others, 1984). Detailed revision of internal variability on species assigned to these two genera is needed.] *Upper Ordovician (Ashgill)–Silurian (Llandovery):* North America, Peru, Venezuela, Argentina, Sweden, Norway, Estonia, United Kingdom, Ireland, Czech Republic, southern Alps, Sardinia, Turkey, Altay-Sayan, Kazakhstan, Tuva, ?Thailand, southern and western China (Tibet), Burma.——FIG. 1063*a–v.* **H. umbonata* (BILLINGS), Ashgill, Anticosti Island, Canada; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497418, ×1.5 (new); *f–u,* transverse serial sections 0.8, 1.1, 1.5, 1.7, 2.1, 2.9, 3.1, 3.4, 4.0, 4.4, 5.9, 6.6, 7.1, 7.4, 7.9, 8.0 mm from ventral umbo, BMNH BB94780 (new); *v,* dorsal valve interior and brachidium (Glass in Davidson, 1882).

?Imdentistella GRUNT, 1991, p. 68 [**I. khabtagaica;* OD]. Similar to *Meristella* but differing in presence of axial groove in roof-shaped dorsal valve, complete absence of dental plates, and presence of incipient cardinal flanges; muscle field, spiralium, and jugum unknown. *Lower Devonian (lower Emsian):* Russia (Mongolia), eastern Gobi.——FIG. 1064,*1a–d.* **I. khabtagaica,* Mongolia; holotype, dorsal, ventral, lateral, and anterior views, PIN 3385/2055, ×1 (Grunt, 1991).

?Meristelloides ISAACSON, 1977, p. 175 [**Meristella Riskowskyi* ULRICH, 1893, p. 64; OD]. Similar to *Meristella* but with stout and shorter dorsal median septum; diductor muscle scars weakly impressed on ventral valve; poorly known, hence generic status uncertain. [The name *Meristelloides* is commonly attributed to BRANISA (1965) but this name was made available by ISAACSON (1977). The authorship and date are his and not those of BRANISA (1965) since in the latter paper the name was not accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (Art. 13.1.1, ICZN, 1999).] *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Bolivia, Brazil, Peru, Argentina, South Africa.——FIG. 1064,*2a–t.* **M. riskowskyi* (ULRICH), Emsian, ?lower Eifelian, Bolivia; *a–c,* dorsal, lateral, and anterior views, USNM 209105, ×1.8; *d,* dorsal view, USNM 209104, ×1.5 (Isaacson, 1977); *e–t,* transverse serial sections 2.0, 4.0, 5.25, 7.0, 7.5, 8.25, 9.0, 9.75, 11.5, 13.0, 14.0, 16.0, 17.5, 18.5, 19.5, 20.0 mm from ventral umbo (adapted from Isaacson, 1977).

Meristina HALL, 1867b, p. 299 [**Meristella maria* HALL, 1863a, p. 212; SD DALL 1877, p. 49] [=*Whitfieldia* DAVIDSON, 1881b, p. 156 (type, *Atrypa tumida* DALMAN, 1828, p. 134, SD DAVIDSON, 1882, p. 83; although the name *Whitfieldia* is commonly attributed to DAVIDSON (1882, p. 107) this name was already made available by DAVIDSON (1881b, p. 156)]. Externally and internally similar to *Meristella* but commonly with well-developed dental plates extending anteriorly as ridges, subparallel or slightly divergent, bounding a narrow, deep, and longitudinally striate muscle field; narrow and deep supported septalium, and jugal stem bifurcating into 2 short arms at its posteroventral end; tertiary layer may be present. [Fixation of type species is usually credited to HALL, 1867b by original designation. When *Meristina* was established by HALL (1867b, p. 299), however, no nominal species was explicitly designated as type species, and as there are two species, *M. maria* and *M. nitida,* included within the genus there is no type by indication (type by monotypy, Article 68.3, ICZN, 1999). According to Article 69.1.1 (ICZN,

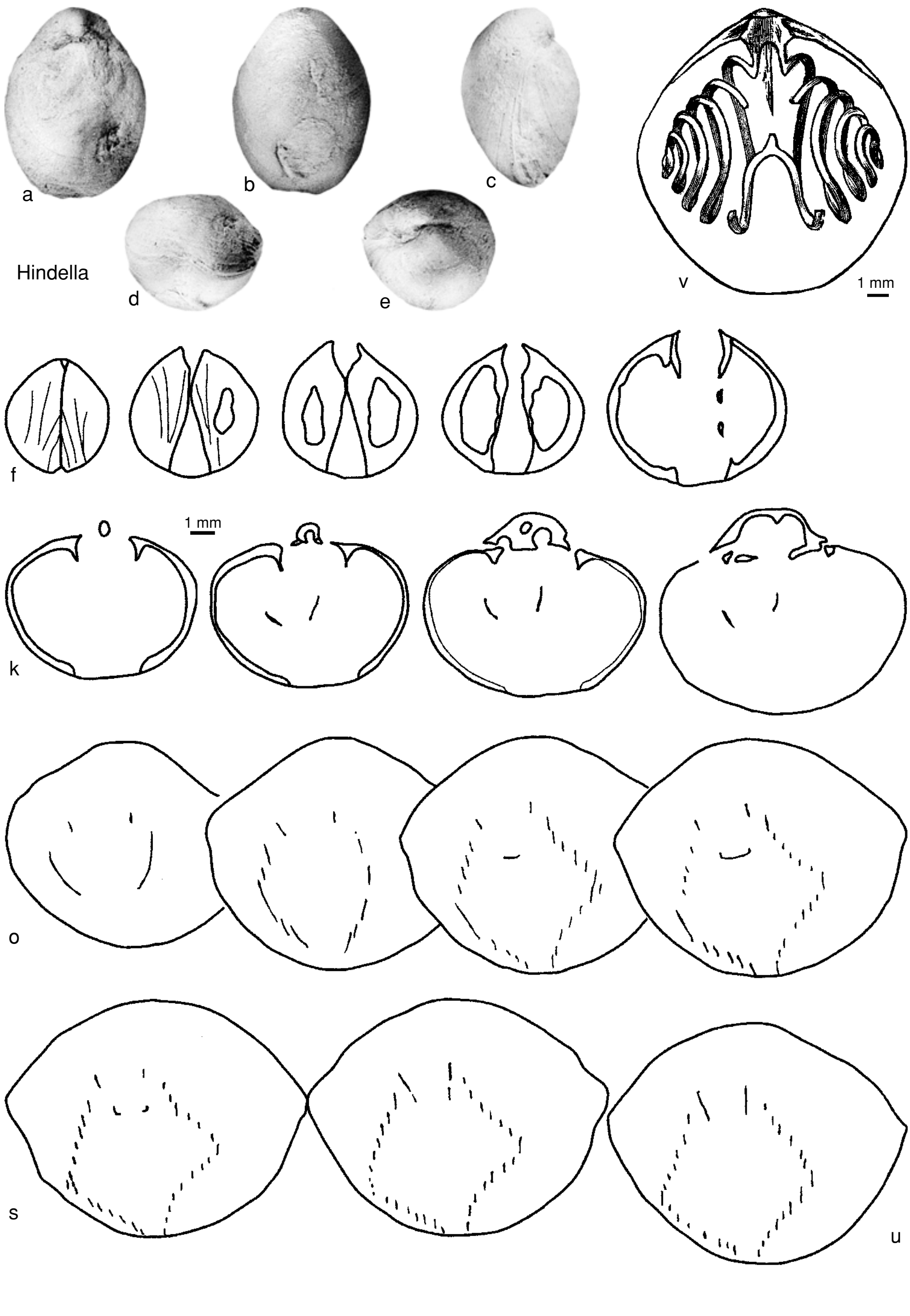

FIG. 1063. Meristellidae (p. 1563).

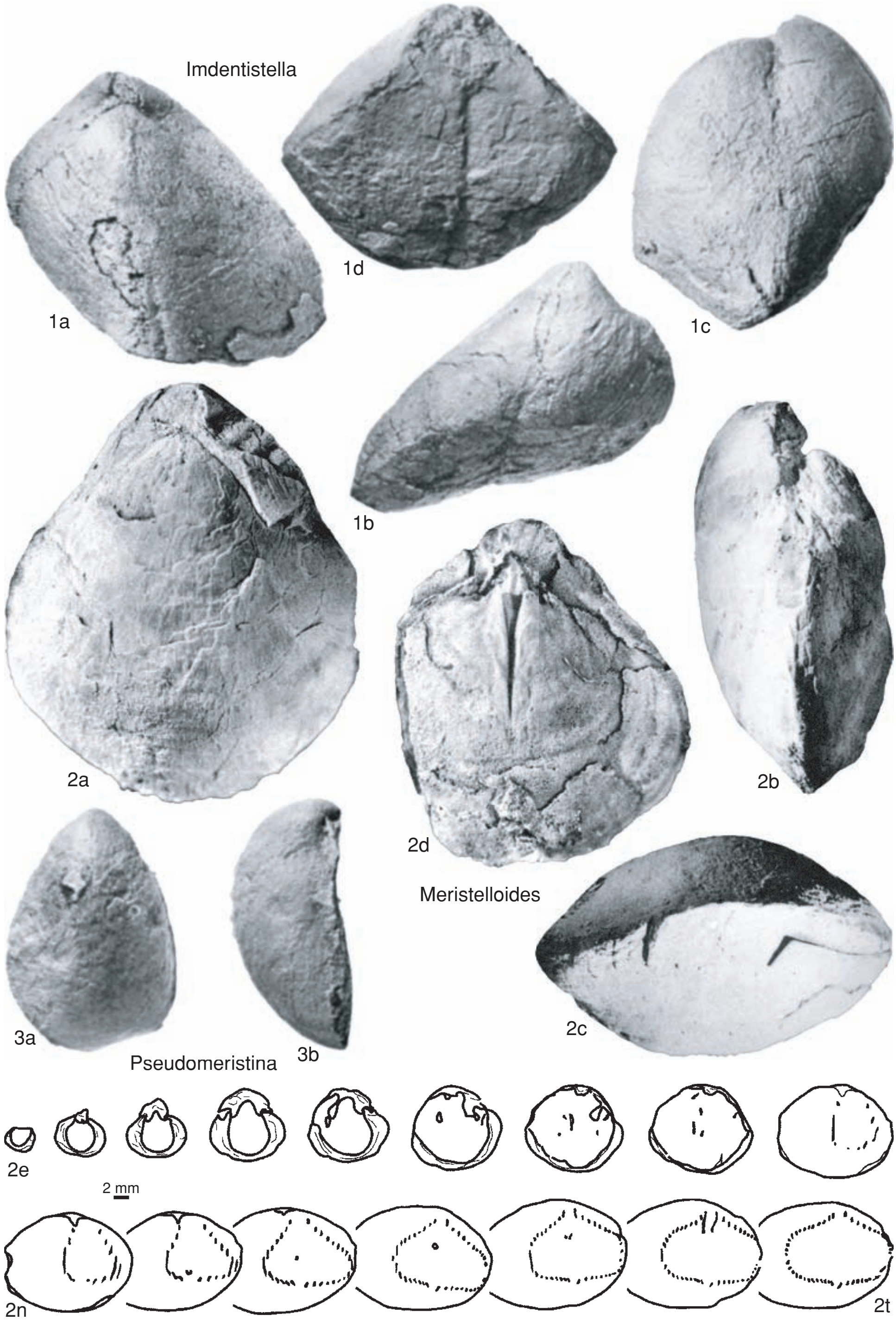

FIG. 1064. Meristellidae (p. 1563–1566).

1999), it is DALL (1877) who should be given the credit for the subsequent designation of *M. maria* as type species for *Meristina.*] *Silurian (Llandovery)–Middle Devonian (Givetian):* New Brunswick, Nova Scotia, Venezuela, Ireland, Novaya Zemlya, Siberia, *Llandovery;* North America, Podolia, Estonia, Lithuania, Bohemia, Gotland, United Kingdom, Ireland, southeastern Australia, *Wenlock;* Lithuania, northern China (Xinjiang, Heilongjiang), *Ludlow;* North America, *Lower Devonian–Middle Devonian (Givetian).*——FIG. 1061,*1a–h.* **M. maria* (HALL), Waldron, Indiana, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 36616, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f–g,* interior showing brachidium, and ventral valve internal mold, ×1; *h,* dorsal interior showing septalium, ×2 (Hall & Clarke, 1895).

Pentagonia COZZENS, 1846, p. 158 [**P. peersii;* OD] [=*Goniocoelia* HALL, 1861, p. 101 (type, *Atrypa uniangulata* HALL, 1861, p. 101, =*Atrypa unisulcata* CONRAD, 1841, p. 56, OD)]. Bi- to dorsibiconvex shells, pentagonal to hexagonal outline; ventral valve with very broad sulcus bounded by angular divergent carinae, lateral slopes abrupt; dorsal valve with broad, rounded fold commonly with narrow medial groove, 2 narrow folds could develop in posterolateral region of dorsal valve; ventral muscle impression essentially as in *Meristella;* dental plates short; low dorsal median septum continuing posteriorly as faint median ridge on massive cardinal plate arising vertically from bottom of valve so as to present erect, concave anterior face, top of plate extended posteriorly as scoop-shaped concavity; jugal stem without bifurcations. *Lower Devonian (Emsian)–Middle Devonian:* North America, Colombia, Venezuela.——FIG. 1065*a–e.* **P. peersii,* Emsian, Kentucky, USA; dorsal, ventral, lateral, anterior, and posterior views, AMNH 37546, Hall collection, ×1.5 (new).——FIG. 1065*f–h. P. unisulcata* (CONRAD), Middle Devonian, New York, USA; *f,* anterior view of broken specimen showing part of spiralium and jugum, I1722, Hall collection, ×5 (new); *g,* ventral view of cardinalia, I1721, Hall collection, ×14 (new); *h,* ventral valve interior, ×1 (Hall & Clarke, 1895).

?Plancella AMSDEN, 1985, p. 11 [**P. turkiensis;* OD]. External features and ventral valve interior similar to *Whitfieldella;* wide and shallow supported septalium as in *Meristella;* spiralium and jugum unknown. [This genus requires revision.] *Lower Devonian (Pragian):* USA (Oklahoma).——FIG. 1061,*3a–l.* **P. turkiensis; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, OU 10276, ×2 (Amsden, 1985); *f–l,* transverse serial sections 0.7, 1.3, 3.2, 3.8, 4.2, 5.8, ? mm from ventral umbo (adapted from Amsden, 1985).

?Pseudomeristina GRUNT, 1991, p. 65 [**P. rozmanae;* OD]. Similar to *Meristina* but differing in shell wall and dental lamellae being composed of prismatic calcite; spiralium and jugum unknown. *Silurian (Wenlock–Ludlow):* Russia (Mongolia, Altay region), ?northeastern China.——FIG. 1064,*3a–b.* **P. rozmanae,* upper Wenlock–lower Ludlow, Mongolia; holotype, ventral and lateral views, PIN 3385/2002, ×1 (Grunt, 1991).

Subfamily WHITFIELDELLINAE Alvarez, Rong, & Boucot, 1998

[Whitfieldellinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Ventral umbo moderately curved; dental plates short and dorsally convergent; ventral muscle field weakly impressed, without longitudinal striations; septalium shallow, short, partially covered, supported by high and short median septum; jugal stem may be thick and spiny. *Upper Ordovician (Ashgill)–Silurian, Lower Devonian (?Lochkovian).*

Whitfieldella HALL & CLARKE, 1893, p. 58 [**Atrypa nitida* HALL, 1843, table 14,*5;* OD (note that the figure on p. 12 is erroneously numbered as 13 when it should be 14; see HALL figure explanations)]. Biconvex, elongate trigonal to subpentagonal; with or without faint sulcus on both valves; lateral branches of jugum originating at approximately midlength of dorsal valve, vertical or projecting backward at high angle. *Upper Ordovician (Ashgill)–Silurian, Lower Devonian (?Lochkovian):* south-central USA, Tadzhikistan, southwestern China (Guizhou), *Ashgill;* North America, Europe, Siberia, southern China, *Silurian;* North America, *?Lochkovian.*——FIG. 1066,*2a–s.* **W. nitida* (HALL), Silurian, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 31290, Hall collection, ×3; *f–h,* dorsal, ventral, and posterior views, AMNH 40799, Hall collection, ×1 (Alvarez & Brime, 2000); *i–r,* transverse serial sections 2.9, 3.1, 3.5, 4.6, 7.5, 7.6, 8.1, 8.4, 9.3, 10.5 mm from ventral umbo, GSC 98796 (adapted from Jin, Caldwell, & Norford, 1993); *s,* lateral view showing jugum (Glass, 1882).

Koigia MODZALEVSKAYA, 1985, p. 37 [**Hindella extenuata* RUBEL, 1970, p. 48; OD]. Biconvex, elongate-oval to rounded, medium shells; with or without faint sulcus on ventral valve; deltidial plates partially covering delthyrium; foramen in epithyridid position; internally similar to *Whitfieldella. Silurian (Llandovery):* Estonia, eastern Siberia.——FIG. 1067,*1a–dd.* **K. extenuata* (RUBEL), Estonia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, TAGI BR2546, ×2 (Rubel, 1970; photographs courtesy of T. L. Modzalevskaya); *f,* dorsal umbo showing foramen and delthyrium partially covered by deltidial plates, TAGI BR 3859, ×6 (Modzalevskaya, 1985; photographs courtesy of T. L. Modzalevskaya); *g–cc,* transverse serial sections 0.2, 0.5, 0.7, 1.0, 1.1, 1.2,

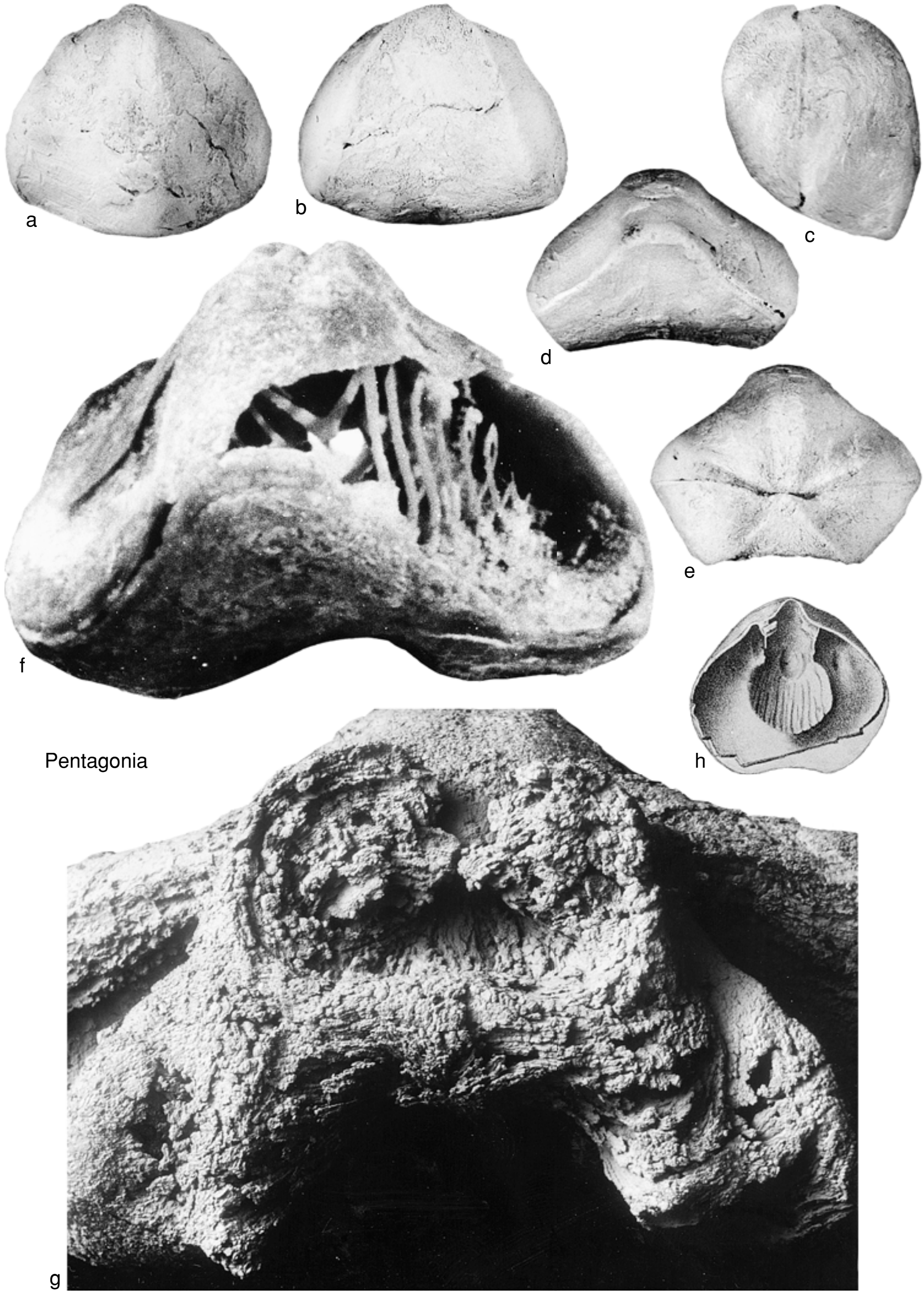

FIG. 1065. Meristellidae (p. 1566).

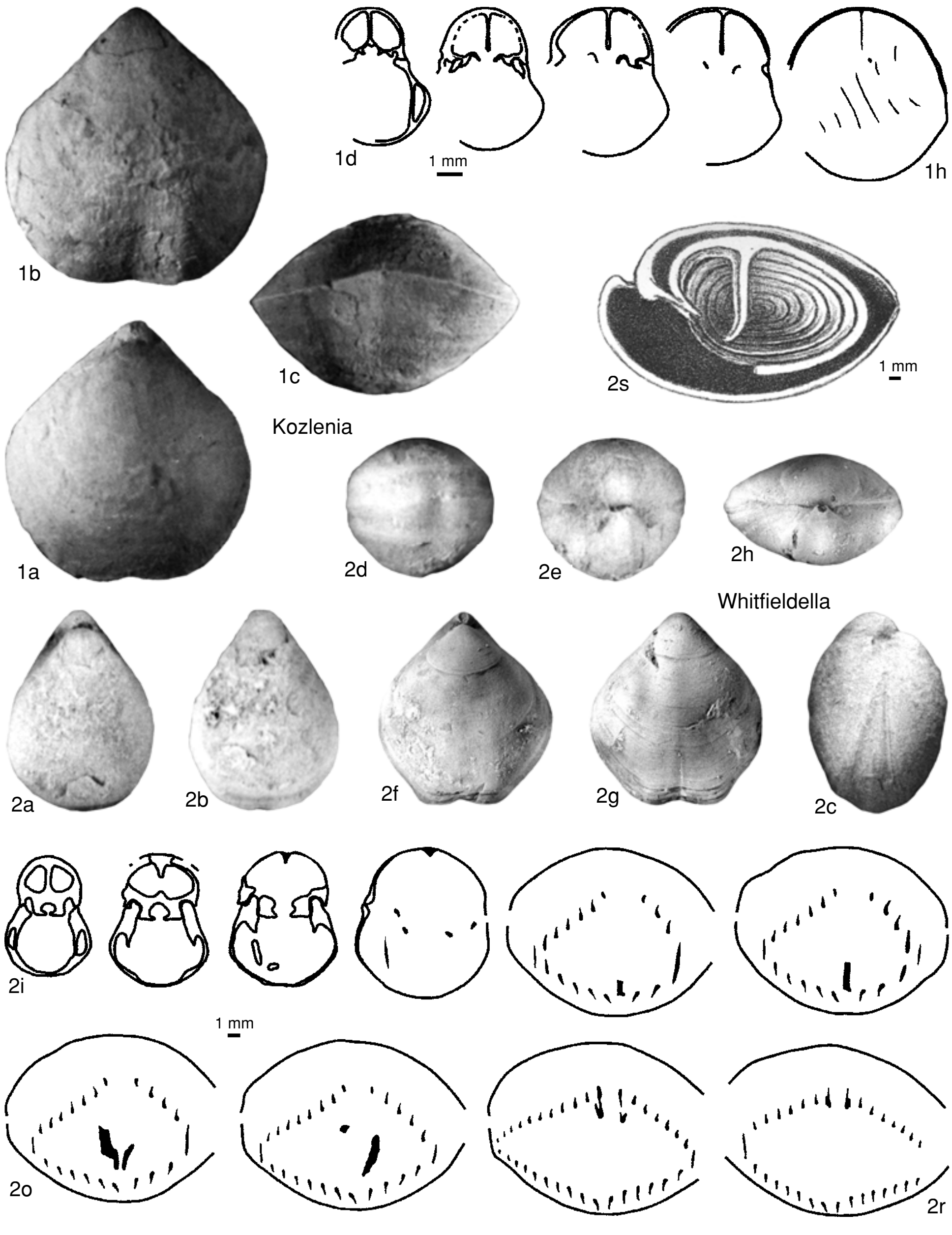

FIG. 1066. Meristellidae (p. 1566–1570).

1.4, 1.6, 1.8, 2.0, 2.2, 2.8, 3.4, 3.6, 4.0, 4.3, 4.5, 4.6, 4.8, 4.9, 5.2, 5.6, 6.9 mm from ventral umbo, distance approximate from ventral umbo to first section and to section *o,* TAGI BR 2545 (adapted from Rubel, 1970); *dd,* brachidium, approximately ×5.5 (Rubel, 1970).

Kozlenia Havlíček, 1987b, p. 241 [**K. kozlensis;* OD]. Similar to *Whitfieldella,* with short and shallow sulcus in ventral valves of mature specimens, dorsal fold absent; internally with thin and high median septum supporting septalium along entire length; jugum unknown. *Silurian (upper Llandovery–*

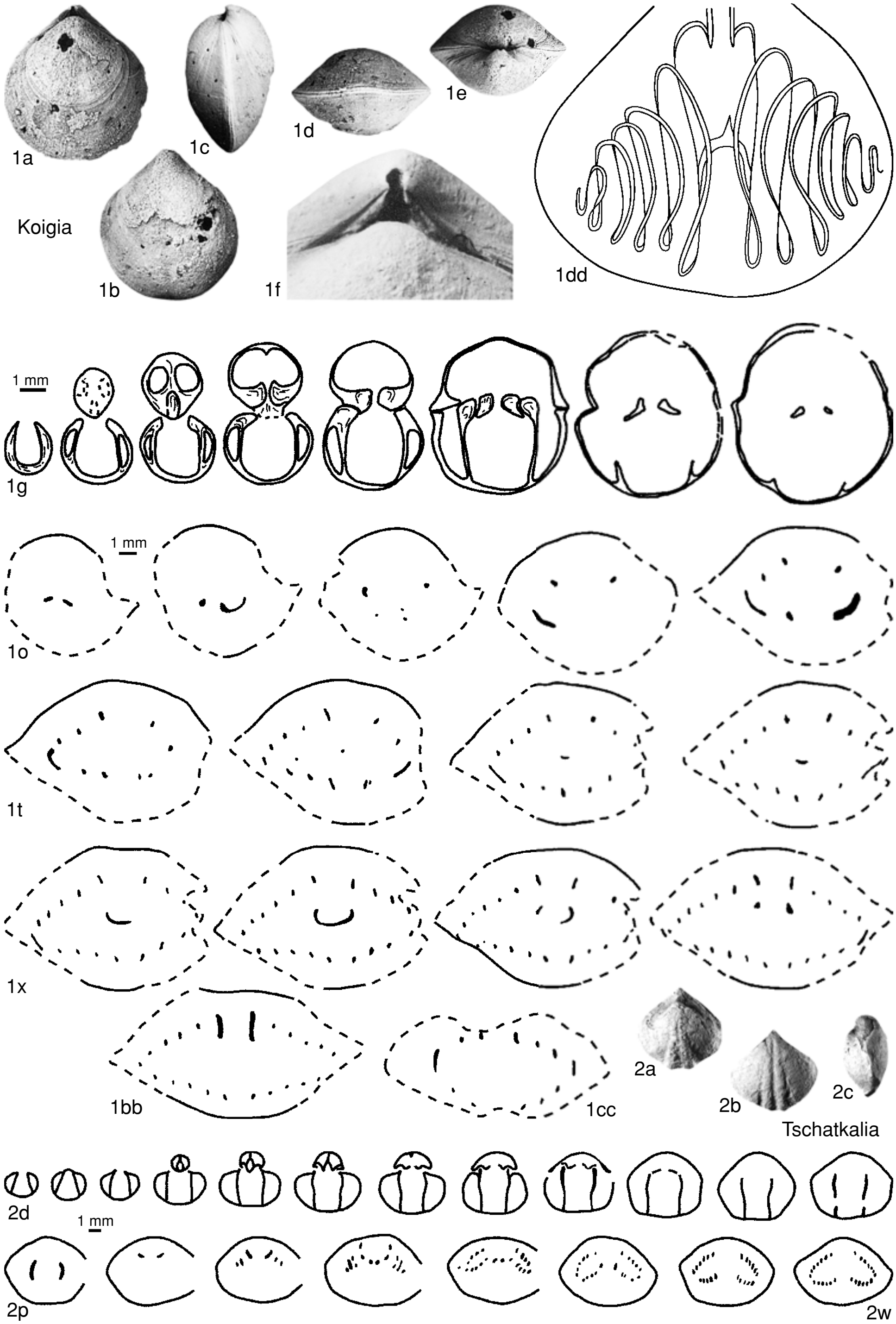

FIG. 1067. Meristellidae (p. 1566–1570).

Wenlock): Bohemia.——FIG. 1066,*1a–h.* **K. kozlensis; a–c,* holotype, dorsal, ventral, and anterior views, VH 4138a, ×3.5 (Havlíček, 1987b); *d–h,* transverse serial sections 2.1, 2.2, 2.4, 2.7, 3.5 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Havlíček, 1990d).

Tschatkalia NIKIFOROVA, 1964, p. 85 [**T. unica;* OD]. Small, ventribiconvex shells of triangular to pentagonal outline; ventral valve with narrow sulcus bounded by rounded plicae; rounded fold, extending from dorsal umbo, commonly with narrow medial groove; deltidial plates present; internally similar to *Koigia,* but with longer dental plates, often recurved in middle; jugum unknown. *Silurian (Llandovery–Wenlock):* Fergana, Kazakhstan.——FIG. 1067,*2a–w.* **T. unica,* Llandovery, Fergana; *a–c,* holotype, dorsal, ventral, and lateral views, CNIGR 36/8201, ×1 (Nikiforova, 1964; photographs courtesy of T. L. Modzalevskaya); *d–w,* transverse serial sections 1.5, 2.0, 2.4, 3.2, 3.6, 3.7, 3.9, 4.0, 4.3, 4.5, 4.6, 4.7, 5.2, 5.6, 5.7, 5.8, 6.0, 6.3, 6.4, 6.7 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Nikiforova, 1964).

Family MERISTIDAE Hall & Clarke, 1895

[Meristidae HALL & CLARKE, 1895, pl. 42]

Small to large size; biconvex; moderate to strong adult valve convexity; mystrochial plates and shoe-lifter possibly strengthening dental plates; spondylial structure, supported along entire length by septum, may be present; septalium shallow or deep and wide in late forms; other structures strengthening the dorsal muscle system may be present. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Subfamily MERISTINAE Hall & Clarke, 1895

[*nom. transl.* SCHUCHERT, 1929, p. 22, *ex* Meristidae HALL & CLARKE, 1895, pl. 42]

Shell small to large; dental plates possibly extending anteriorly as thickened ridges, shoe-lifter supporting dental plates, if not (as in *Amerista*), then very steeply, laterally inclined area for muscle attachment similar to that of *Merista,* mystrochial plates may be present; septalium shallow, narrow, supported by high and thin median septum; dorsal shoe-lifter may be present; acute jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae that reunite with lateral branches of jugum. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Merista SUESS, 1851, p. 150 [**Terebratula herculea* BARRANDE, 1847, p. 26; SD SUESS in DAVIDSON, 1856, p. 85]. Biconvex, elongate or transverse shells of rounded subpentagonal outline, with dorsal fold and ventral sulcus commonly developed anteriorly; dental plates short or may be produced anteriorly as thickened ridges that unite with outer part of medially placed shoe-lifter process along its lateral edges, shoe-lifter process with form of posteriorly plunging roof-shaped plate; mystrochial plates present; small septalium supported by high and thin median septum; accessory jugal lamellae reunite with lateral branches of jugum. [No nominal species were assigned to *Merista* when the genus was erected by SUESS (1851). No species was associated with *Merista* until 1854 when SUESS (1854, p. 62–63) assigned 3 species to the genus: *T. herculea, T. passer,* and *T. tumida;* no type species was designated. The first indication of a type species is that of SUESS (in DAVIDSON, 1856, p. 85), who designated *T. herculea* as type species of *Merista.*] *Silurian (Llandovery)–Middle Devonian:* southern Siberia, Altay, Canada, *Llandovery;* Canada, *Wenlock;* Venezuela, Mexico, south-central USA (Oklahoma, Tennessee), *Ludlow;* northeastern USA (Maine), *Ludlow or Přídolí;* Bohemia, Poland, Kazahkstan, Altay, Inner Mongolia, *Lower Devonian;* Germany, ?Burma, *Middle Devonian.*——FIG. 1068,*1a–k.* **M. herculea* (BARRANDE), Lower Devonian, Bohemia, Czech Republic; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497417, ×1.5 (new); *f–i,* transverse serial sections 1.4, 2.2, 2.9, 3.6 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr70 (adapted from Siehl, 1962); *j–k,* ventral and lateral views of brachidium (Glass, 1882).

Amerista BOUCOT & BLODGETT in BOUCOT, BLODGETT, & STEWART, 1997, p. 287 [**A. carillobravoi;* OD]. Similar to *Merista* but with very steeply, laterally inclined area for muscle attachment in ventral valve instead of shoe-lifter. [The diagnosis is presently based on ventral valves because conjoined valves were not found; dorsal valves are only questionably assigned to *Amerista.*] *Silurian (upper Wenlock–Ludlow):* northeastern Mexico (Sierra Madre Oriental).——FIG. 1068,*2a–b.* **A. carillobravoi;* holotype, impression and rubber replica of ventral valve interior, IGM 6938a, ×2 (Boucot, Blodgett, & Stewart, 1977; photographs courtesy of R. B. Blodgett & A. J. Boucot).

Aulidospira WILLIAMS, 1962, p. 252 [**A. trippi;* OD]. Ventribiconvex, small shell, with broad, shallow sulcus in dorsal valve and wide median ventral fold separated from pair of inconspicuous folds in

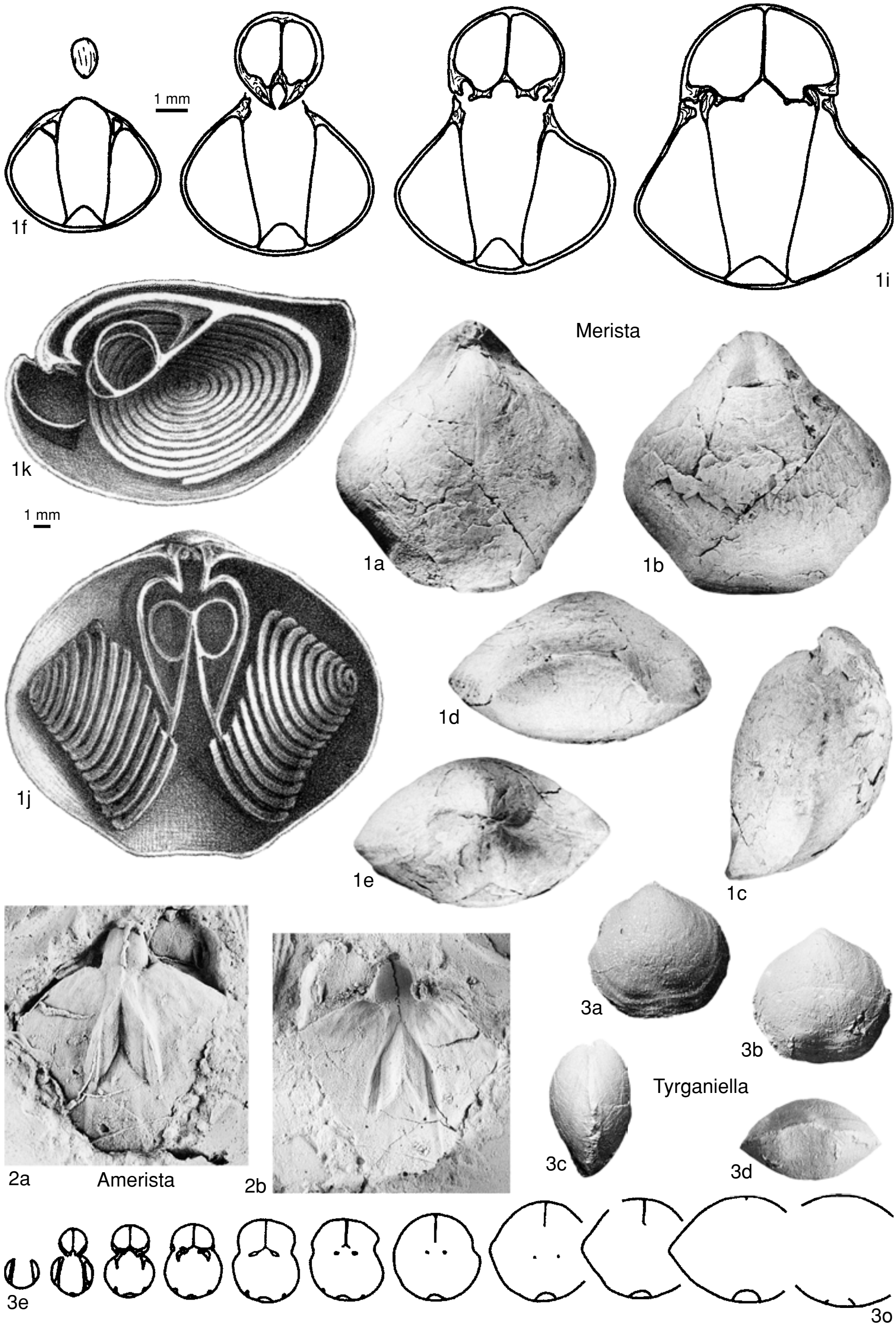

FIG. 1068. Meristidae (p. 1570–1572).

flattened posterolateral areas by pair of widely divergent and shallow, rounded sulci; dental plates attached to ventral side of small, nearly flat, shoe-lifter process; cardinalia poorly known; myophragm present, median septum absent; rudimentary spiralia coiled in plane parallel to median plane, jugal structure unknown. [The genus is also listed by P. Copper, herein, p. 1472, as a junior synonym of *Cyclospira* Hall in Hall & Clarke, 1893. This ambiguity should be resolved when the brachiojugal structure of *Aulidospira* is known.] *Upper Ordovician (Caradoc, ?Ashgill):* Great Britain, ?Bohemia, ?Quebec.——Fig. 1069,*1a–f.* **A. trippi,* Great Britain; *a,* holotype, lateral view of ventral internal mold, BMNH BB 27653, ×6; *b,* rubber replica of dorsal exterior, BMNH BB 27656, ×4.5; *c–d,* ventral and lateral views of complete shell, BMNH BB 27655; *e,* dorsal view of internal mold, BMNH BB 27654; *f,* ventral view of internal mold, BMNH BB 27657, ×6 (Williams, 1962).

Camarium Hall, 1859, p. 42 [**C. typum;* OD]. Similar to *Merista* but without mystrochial plates. [The name *Camarium* was published by Hall (1859a) without designation of a type species, but as one of the originally included new nominal species (Art. 67.2.1, ICZN, 1999) was given the name *C. typum;* that species must be considered as the type species by original designation (Art. 68.2.2, ICZN, 1999; by indication according to the ICZN, 3rd ed., 1985). Hall (1860a, 1862) then listed this genus as being identical with *Merista* (subjective synonym; see also Boucot, Johnson, & Staton, 1965, p. 658). Later, Amsden (1968) validated *Camarium* Hall after discovering that it lacks the mystrochial plates present in *Merista* Suess.] *Lower Devonian (Lochkovian)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian):* USA (Maryland, New York), Germany, Bohemia, Gorno-Altay, *Lower Devonian–Middle Devonian;* Australia (New South Wales), USA (Texas), *Tournaisian;* Canadian Arctic Archipelago (Ellesmere), *upper Bashkirian or lower Moscovian.*——Fig. 1069,*2a–e.* **C. typum,* Lochkovian, USA (Maryland); *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 34713, Hall collection, ×1.5 (Alvarez & Brime, 2000). [See also Fig. 1006.1, p. 1481, in introduction].

Dicamara Hall & Clarke, 1893, p. 73 [**Atrypa plebeia* Sowerby, 1840a, pl. 56,*12–13;* SD Hall & Clarke, 1894, p. 966; =*Terebratula scalprum* Roemer, 1844, p. 68]. Similar to *Merista* but without mystrochial plates and having shoe-lifter process, bisected by median septum in dorsal valve. [Fixation of type species is usually wrongly credited to Hall & Clarke by original designation. The first unequivocal designation of the type species seems to be that of Hall & Clarke, 1894, p. 966.] *Lower Devonian–Middle Devonian:* Poland, Czech Republic (Moravia), Germany, France, northwestern Spain, Salair, Kazakhstan, India, Algeria.——Fig. 1069,*4a–l.* **D. plebeia* (Sowerby), Middle Devonian, Eifel, Germany; *a,* dorsal view, USNM 497413, ×1.5 (Alvarez, Rong, & Boucot, 1998); *b–e,* ventral, lateral, anterior, and posterior views, USNM 497413, ×1.5 (new); *f–l,* transverse serial sections 0.6, 1.1, 1.4, 1.8, 2.3, 2.5, 3.2 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr71 (adapted from Siehl, 1962).

Dicamaropsis Amsden, 1968, p. 85 [**Merista parva* Thomas, 1926, p. 400; OD]. Similar to *Dicamara* but having mystrochial plates and rather flat septalium with knob in center; spiralium and jugum unknown. *Silurian (upper Llandovery–Wenlock):* southwestern China (Sichuan), *upper Llandovery (upper Telychian);* southern and central USA, *Wenlock.*——Fig. 1069,*3a–j.* **D. parva* (Thomas), Wenlock, Arkansas, USA; *a–c,* lectotype, dorsal, ventral, and posterior views, YPM 25745, ×3 (Amsden, 1968); *d–j,* transverse serial sections 0.5, 0.6, 0.8, 1.0, 1.2, 1.5, 2.1 mm from ventral umbo (adapted from Amsden, 1968).

Tyrganiella Kul'kov in Alekseeva & others, 1970, p. 167 [**T. repentina;* OD] [=?*Paramerista* Su, 1976, p. 206 (type, *P. brevisepta,* OD)]. Externally similar to *Merista,* but differing internally in having more rounded shoe-lifter process not attached to very short dental plates; spiralium and jugum unknown. [The name of the type species of ?*Paramerista* was spelled as *brevisepta* and *breviseptata* in the work in which it was established; following Articles 24.2.2 and 32.2.1 (ICZN, 1999), the name of *brevisepta* is chosen in this revision. The inclusion of ?*Paramerista* from the Lochkovian and Pragian of Inner Mongolia, northern China, may extend the range from the Lochkovian; but interiors are poorly known and assignment uncertain.] *Lower Devonian (Lochkovian, ?Pragian):* Russia (western Siberia, northeastern Salair), northern China.——Fig. 1068,*3a–o.* **T. repentina,* northeastern Salair; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 326-104, ×2 (Alekseeva & others, 1970; photographs courtesy of T. L. Modzalevskaya); *e–o,* transverse serial sections 0.5, 0.7, 0.8, 1.0, 1.2, 1.3, 1.4, 1.6, 1.9, 2.1, 2.3 mm from ventral umbo, IGiG 326-106 (adapted from Alekseeva & others, 1970).

Subfamily CAMAROPHORELLINAE Schuchert, 1929

[Camarophorellinae Schuchert, 1929, p. 22]

Medium-sized meristids with spondylium; mystrochial plates may be present; septalium deeply concave, supported by long, high median septum; dorsal shoe-lifter may be present; jugum posteriorly situated, consisting of complex, inverted, troughlike structure with small saddle, resting on

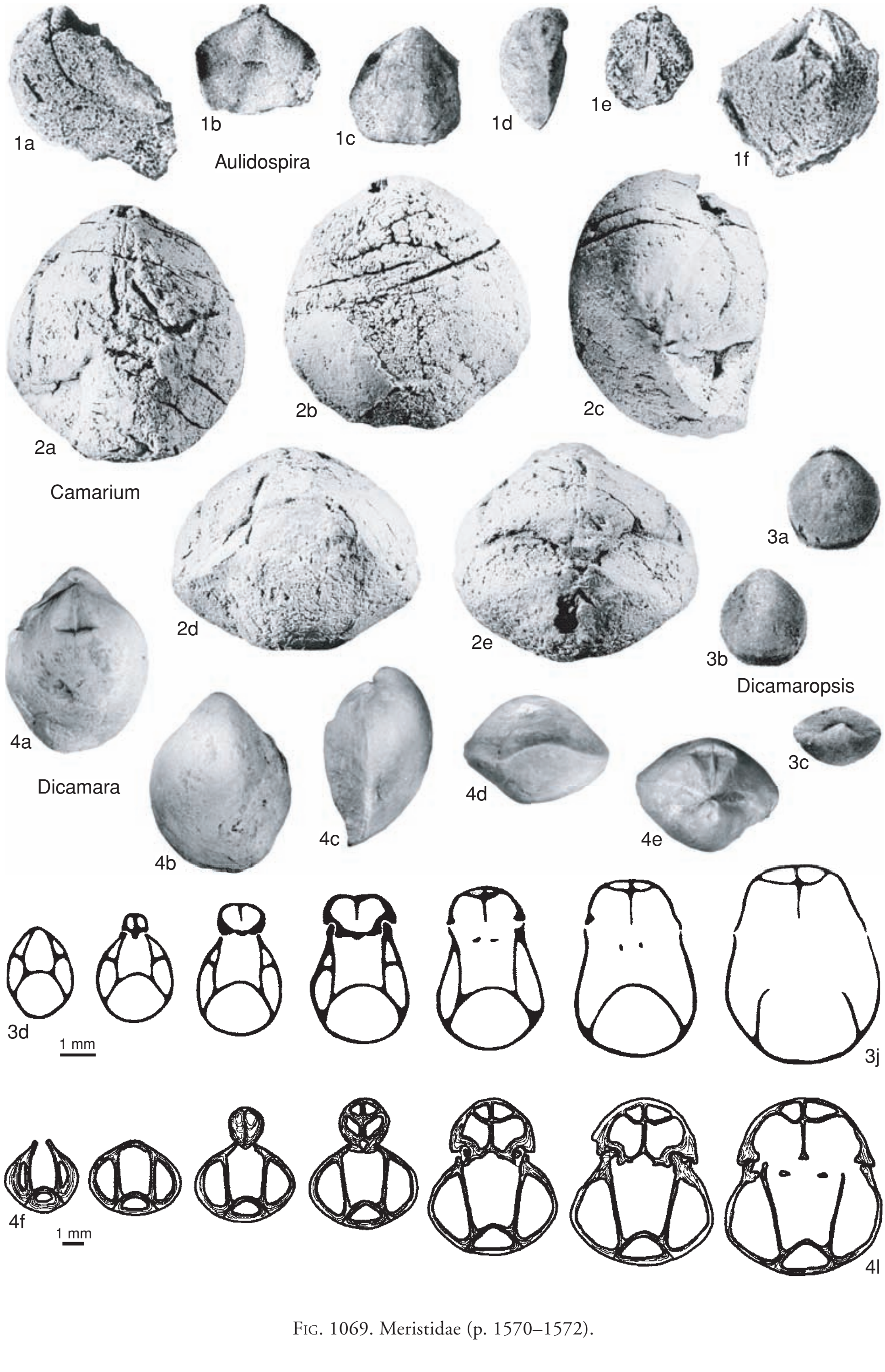

FIG. 1069. Meristidae (p. 1570–1572).

median septum, projecting backward as complex stem with lateral expansions that bifurcate into 2 spiny accessory jugal lamellae recurving dorsally, then anteriorly rejoining lateral branches of jugum near base. *Silurian (upper Llandovery)–Lower Carboniferous (Tournaisian).*

Camarophorella HALL & CLARKE, 1893, p. 215 [**Pentamerus lenticularis* WHITE & WHITFIELD, 1862, p. 295; OD]. Transversely subovate, subcircular or elongate biconvex shells with dorsal fold and ventral sulcus poorly developed or absent; fine growth lines may be crossed by irregular, fine radial lines; well-developed dental plates, laterally buttressed by mystrochial plates, converging to form spondylium duplex rising slightly on long, low median septum; dorsal shoe-lifter present; inner shell surfaces of both valves finely and densely papillose. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America.——FIG. 1070*a–b*. **C. lenticularis* (WHITE & WHITFIELD), middle Tournaisian, Iowa, USA; *a,* view of internal cast of ventral valve, ×3; *b,* view of internal cast of dorsal valve, UM1356a–b, ×3 (new; photographs courtesy of J. L. Carter).——FIG. 1070*c–f*. *C. mutabilis* HYDE, lower upper Tournaisian, Ohio, USA; *c,* posterior view of internal cast, ×2 (Carter, 1991); *d,* detail of external ornamentation and papillose inner surface, CMNH 69571a–b, ×10 (new; photographs courtesy of J. L. Carter); *e–f,* ventral and lateral views of jugum (Hyde, 1908).——FIG. 1070*g–w*. *C. buckleyi* (ROWLEY), upper Famennian, Missouri, USA; transverse serial sections 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.2, 2.6, 3.0, 3.6, 3.8, 4.0, 5.0, 5.4, 6.0, 6.6 mm from ventral umbo, CMNH 34950 (adapted from Carter, 1991; courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA).

Camarospira HALL & CLARKE, 1893, p. 82 [**Camarophoria eucharis* HALL, 1867b, p. 368; OD]. Externally similar to *Merista;* internally similar to *Camarophorella* but without mystrochial plates and dorsal shoe-lifter process; jugum unknown. *Middle Devonian:* North America, ?China.——FIG. 1071,*1a–e*. **C. eucharis* (HALL), Givetian, Ontario, Canada; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, I1174, Hall collection, ×1.5 (Alvarez & Brime, 2000).

?Liocoelia SCHUCHERT & COOPER, 1931, p. 248 [**Pentamerus proximus* BARRANDE, 1879b, p. 96; OD]. Similar to *Camarospira* but with mystrochial plates and much higher septum supporting spondylium; dorsal interior and spiralium poorly known; jugum unknown. [This genus requires revision.] *Silurian (upper Llandovery–Ludlow):* Bohemia.——FIG. 1071,*2a–e*. **L. proxima* (BARRANDE), upper Llandovery–Wenlock; *a–b,* lectotype, dorsal and ventral views, L24919 Barrande collection, ×1.4 (Havlíček, 1990d); *c–e,* transverse serial sections 1.7, 2.8, 3.0 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Havlíček, 1990d).

Subfamily ROWLEYELLINAE Alvarez & Brunton, 1995

[Rowleyellinae ALVAREZ & BRUNTON, 1995, p. 606]

Small-sized meristids with spondylium, supported by median septum, and mystrochial plates; dorsal valve with shallow septalium, short shoe-lifter, and long cruralium supported by long, high median septum; jugum unknown. *Lower Carboniferous (upper Tournaisian).*

Rowleyella WELLER, 1911, p. 447 [**Terebratula fabulites* ROWLEY, 1900, p. 265; OD]. Externally and internally similar to *Camarophorella* but also with cruralium. [The genus *Rowleyella* WELLER, 1911 was placed in subjective synonymy with *Camarospira* HALL & CLARKE, 1893, by BOUCOT, JOHNSON, & STATON, 1965, p. 658. Later, CARTER (1991) validated *Rowleyella* WELLER, 1911 after noting internal dorsal shoe-lifter, similar to the one present in *Camarophorella* HALL & CLARKE, 1893 (see also ALVAREZ & BRUNTON, 1995 for discussion).] *Lower Carboniferous (upper Tournaisian):* USA (eastern Missouri and eastern Oklahoma).——FIG. 1072*a–m*. **R. fabulites* (ROWLEY), Missouri; *a–b,* lectotype, dorsal and ventral views, RX 165A, Rowley Collection, ×5; *c,* posterior view of silicified natural internal mold showing mystrochial plates and very short dorsal shoe-lifter process, CMNH 34945, ×8 (Carter, 1991; photographs courtesy of J. L. Carter); *d–m,* transverse serial sections 0.2, 0.45, 0.6, 0.65, 0.75, 0.9, 1.0, 1.3, 1.8, 2.0 mm from ventral umbo, CMNH 34949 (adapted from Carter, 1991; courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA).

Family TRIATHYRIDIDAE Alvarez, Rong, & Boucot, 1998

[Triathyrididae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Medium to very large meristelloids; moderately rostrate; subequally biconvex; moderate to strong adult valve convexity; ornament consisting of delayed costation progressively developed medially or fine lines folded in chevronlike pattern that follows outline of shell, growth lines weak or absent, not developed into frills; dental plates commonly short; ventral muscle field weakly impressed; septalium long, uncovered, deep and wide, supported by long, bladelike to robust, commonly high median septum; jugum thick,

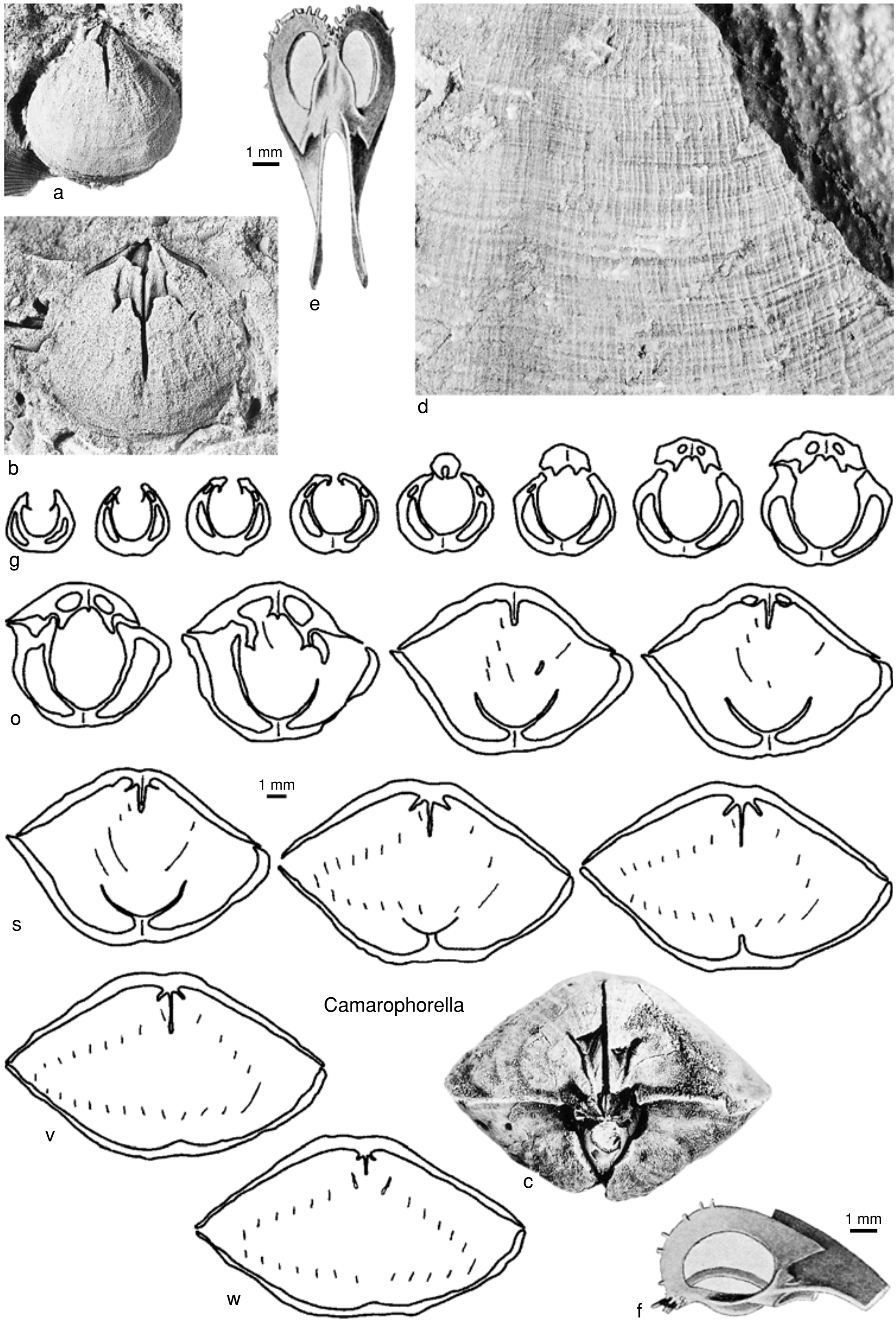

FIG. 1070. Meristidae (p. 1574).

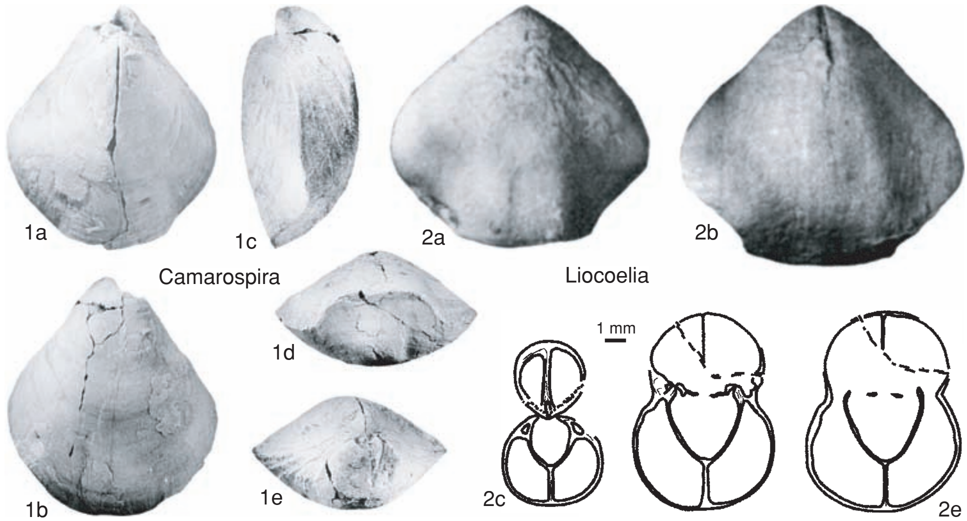

FIG. 1071. Meristidae (p. 1574).

accessory jugal lamellae reuniting with stem like that of some meristellins. *Lower Devonian (Pragian–upper Emsian).*

Subfamily TRIATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Triathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

External ornament of delayed costation progressively developed medially. *Lower Devonian (upper Emsian).*

Triathyris BOUCOT, JOHNSON, & STATON, 1965, p. 663 [**Terebratula mucronata* DE VERNEUIL, 1850, p. 171; OD]. Medium to large; equidimensional to elongate; commonly of rhomboidal outline; ventribiconvex with moderate adult valve convexity, compressed anterolaterally; clearly astrophic, short hinge line; ventral cardinal area reduced apsacline to orthocline; foramen in epithyridid position, delthyrium partially covered; growth lines weak and closely spaced; median plication on each valve raised to form anterior projection; anterior commissure almost straight; dental plates short, thin, medially concave; dorsal median septum very high. [Authorship of this genus is usually credited to COMTE (1938, p. 45); however, he did not designate a type for the genus. The first unequivocal designation of the type species seems to be that of BOUCOT, JOHNSON, & STATON, 1965 and thus they validated the name in their publication.] *Lower Devonian (upper Emsian):* Spain, ?France, ?Morocco.——FIG. 1073*a–v*. **T. mucronata* (DE VERNEUIL), Colle, León, Spain; *a–e,* lectotype, dorsal, ventral, lateral,

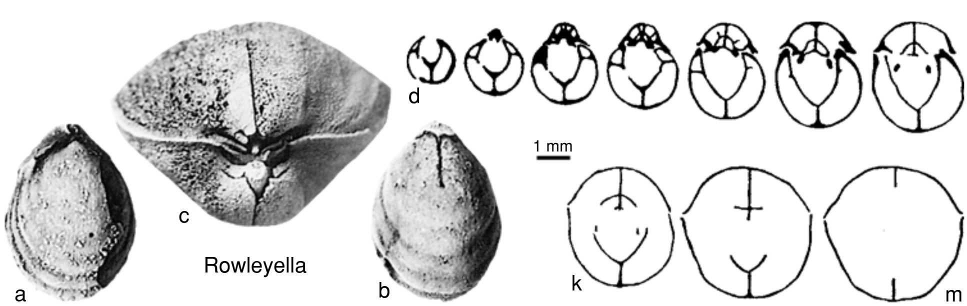

FIG. 1072. Meristidae (p. 1574).

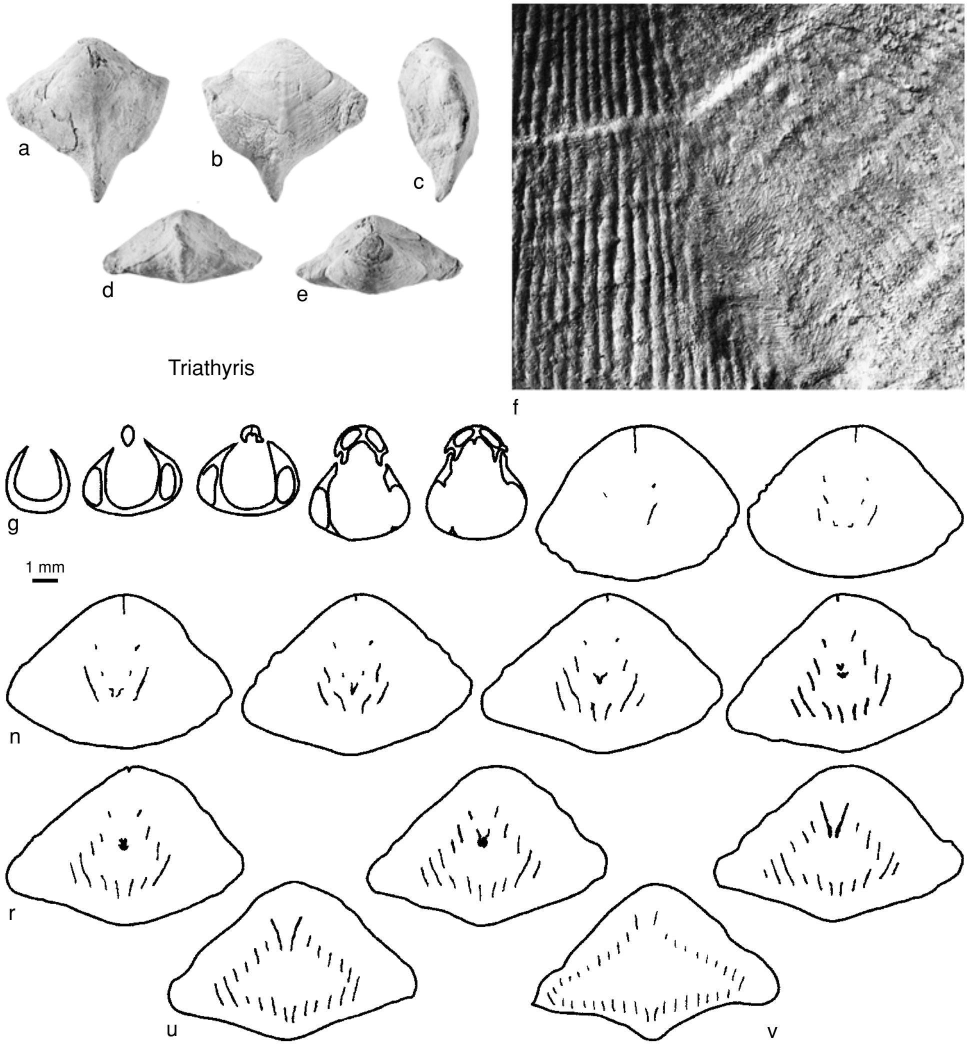

FIG. 1073. Triathyrididae (p. 1576–1577).

anterior, and posterior views, D868, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* external ornament on ventral valve, DPO F24240, ×13 (new); *g–v,* transverse serial sections 0.2, 0.9, 1.4, 2.4, 2.55, 6.5, 7.0, 7.2, 7.45, 7.8, 8.0, 8.2, 8.3, 8.6, 8.8, 9.8 mm from ventral umbo, DPO F24235 (Alvarez, Rong, & Boucot, 1998).

Subfamily SEPTATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Septathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Ornament of fine lines folded in chevron-like pattern with angles directed in postero-anterior direction. *Lower Devonian (Pragian–Emsian).*

Septathyris BOUCOT, JOHNSON, & STATON, 1964, p. 819 [**Athyris aliena* DREVERMANN, 1904, p. 258; OD]. Resembling *Anathyris* in external configuration but without lamellose growth lines; foramen in meso- to permesothyridid position, delthyrium completely covered by deltidial plates; dental plates thick, medially concave, not extending as ridges along muscle scars; dorsal median septum moderately high. *Lower Devonian (Pragian–Emsian):* Germany, Spain, northern Africa.——FIG. 1074*a–c*. **S. aliena* (DREVERMANN), Pragian, Germany; *a,* mold of exterior of dorsal valve, ×3; *b,* dorsal interior mold, ×1; *c,* rubber impression of dorsal interior

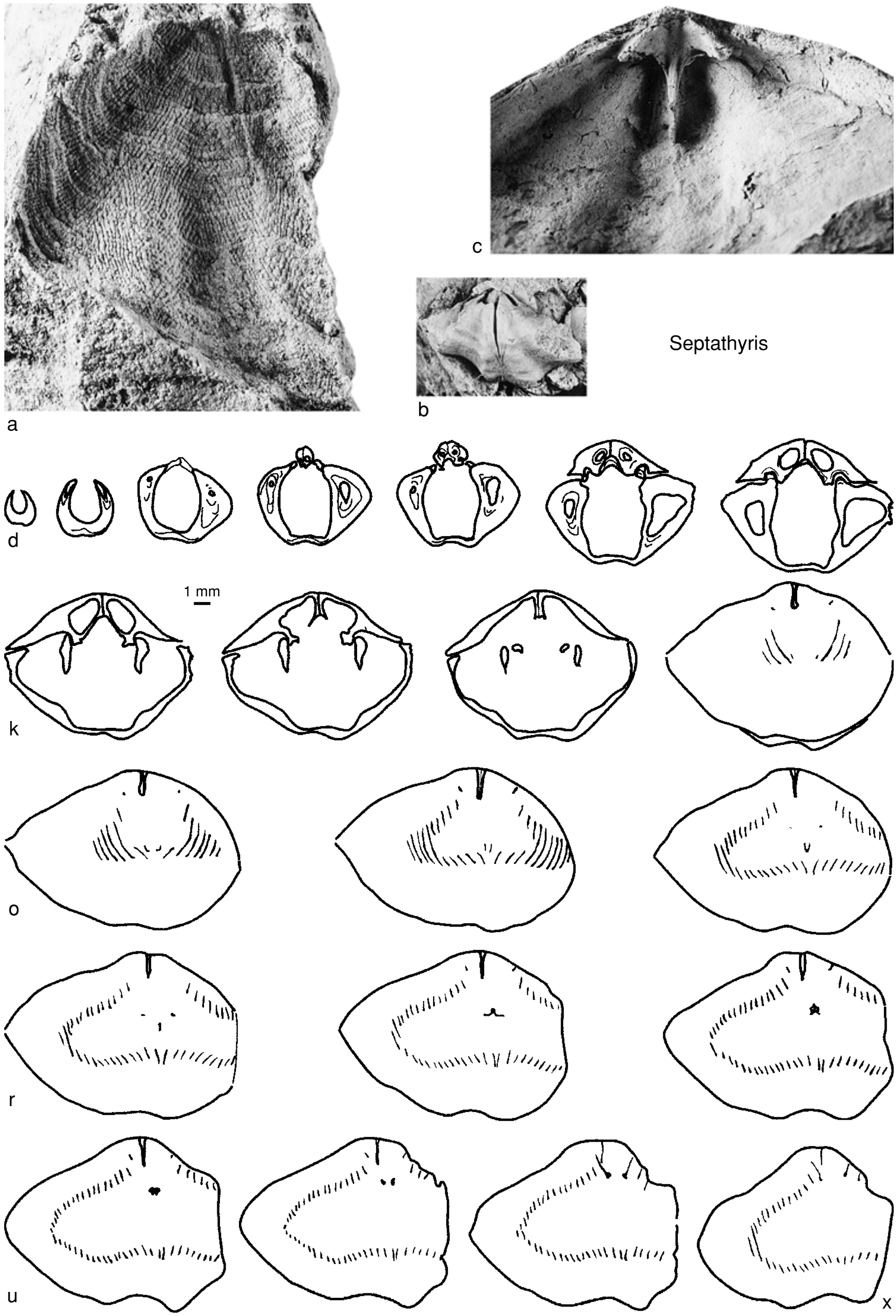

FIG. 1074. Triathyrididae (p. 1577–1579).

mold, ×2 (Boucot, Johnson, & Staton, 1964; photographs courtesy of the late J. G. Johnson).——Fig. 1074*d–x. S. cabrugnanensis* Alvarez, Rong, & Boucot, Emsian, Asturias, Spain; transverse serial sections 0.2, 1.4, 2.9, 3.7, 4.1, 5.2, 6.2, 7.4, 7.6, 7.9, 11.4, 12.1, 13.1, 14.0, 14.5, 15.4, 16.4, 17.1, 18.0, 19.3, 20.4 mm from ventral umbo, DPO F24236 (Alvarez, Rong, & Boucot, 1998).

Superfamily NUCLEOSPIROIDEA Davidson, 1881

[*nom. correct.* Harper, 1993, p. 448, *pro* Nucleospiracea Grunt, 1984, p. 70, *nom. transl. ex* Nucleospiridae Davidson, 1881a, p. 4; *emend.*, Alvarez, Rong, & Boucot, 1998, p. 844]

Smooth athyridines with irregularly and commonly anteriorly concentrated lamellose growth lines and concentrically arranged fine, solid spines covering entire shell and projecting radially at different angles from valve surface; hinge line from astrophic (very short in Permian species) to almost strophic, foramen small (e.g., Permian species), commonly absent; delthyrium commonly completely covered apically by concave plate; dental plates absent but delthyrial margins commonly thickened; low, long median ridge present in both valves, less developed in ventral valve of Permian species; cardinalia without inner hinge plates, strongly developed cardinal flange extending posteroventrally into ventral umbo; simple, acute jugum posteriorly situated, without jugal saddle but having long stem, accessory jugal lamellae absent; without tertiary layer. *Silurian (Llandovery)–Lower Permian (Sakmarian).*

Family NUCLEOSPIRIDAE Davidson, 1881

[Nucleospiridae Davidson, 1881a, p. 4]

Characters as for superfamily. *Silurian (Llandovery)–Lower Permian (Sakmarian).*

Nucleospira Hall in Davidson, 1858, p. 412 [**Spirifer ventricosus* Hall, 1857a, p. 57; M]. Small, moderately to strongly biconvex, subcircular to transversely broadly elliptical shells; ventral valve commonly with shallow median sulcus forming weakly uniplicate anterior commissure, or both valves shallowly sulcate, producing slight emargination of anterior outline; ventral cardinal area, apsacline, concave, nearly equilaterally triangular, commonly obscured by small incurved ventral beak; ventral diductor scars flabellate, feebly impressed, enclosing elongate adductor scars, restricted to umbonal cavity. [Authorship is usually credited to Hall (1859a); however the first to publish the name was Davidson (1858), who included *Nucleospira* Hall with an existing species, *N. ventricosa* Hall. This is adequate to make the generic name *Nucleospira* available with *N. ventricosa* as type species by monotypy; therefore, under Article 50.1 of the *Code* (ICZN, 1999), authorship of *Nucleospira* is Hall in Davidson, 1858.] *Silurian (Llandovery)–Lower Permian (Sakmarian):* cosmopolitan.——Fig. 1075*a–f.* **N. ventricosa* (Hall), Lochkovian, Lower Helderberg Group, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33416, Hall collection, ×2.5 (Alvarez & Brime, 2000); *f,* lateral view of jugum, approximately ×7 (Hall & Clarke, 1893).——Fig. 1075*g. N. cunctata* Cooper & Grant, Sakmarian, western Texas, USA; anterior oblique view of shell interior showing jugum and spires, USNM 154393g, ×8 (Cooper & Grant, 1976a; photograph courtesy of the late G. A. Cooper and the late R. E. Grant). [See also Fig. 1004.2, p. 1479, and Fig. 1008.3, p. 1485, in introduction.]

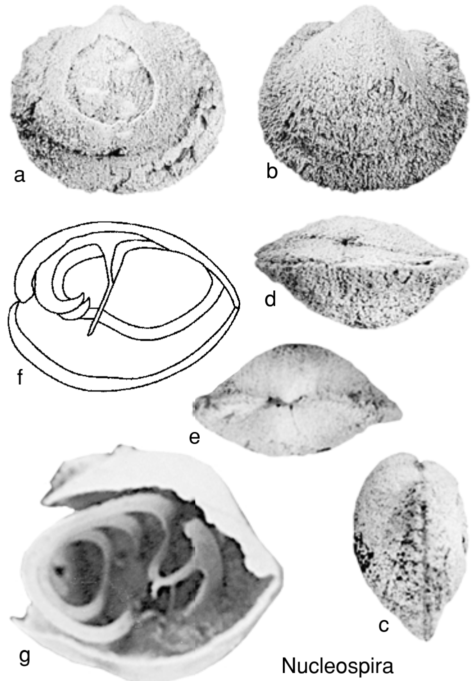

Fig. 1075. Nucleospiridae (p. 1579).

Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974

[*nom. correct.* ALVAREZ, RONG, & BOUCOT, 1998, p. 845, *pro* Retziellioidea MODZALEVSKAYA, 1996, p. 179, *nom. transl. ex* Retziellinae RZHONSNITSKAYA, 1974, p. 54]

Plicate or costate rhynchonelliform athyrididines of small to medium size; short and astrophic hinge line; bi- to ventribiconvex shells with moderate convexity in adult valves; fold and sulcus variably developed (sulcus may develop in both valves) commonly with ribs less developed than those on flanks, concentric growth lamellae may be present anteriorly; ventral cardinal area (palintrope) moderately developed; pedicle opening in meso- to permesothyridid position, delthyrium commonly open (completely covered by deltidial plates in *Gissarina*); pedicle support absent; short, dorsally convergent dental plates; outer hinge plates variably developed, inner hinge plates absent or forming short and shallow septalium partially covered by long, platelike, crural bases, supported by moderately high median septum; other structures strengthening the muscle system absent; jugum simple, medially or anteriorly situated, lateral branches vertical, very short jugal saddle and vertical stem may be present, accessory jugal lamellae absent; tertiary layer absent. *Silurian (upper Aeronian)–Lower Devonian (lower Emsian).*

Family RETZIELLIDAE Rzhonsnitskaya, 1974

[*nom. transl.* RONG & others, 1994, p. 546, *ex* Retziellinae RZHONSNITSKAYA, 1974, p. 59] [=Retzielinae RZHONSNITSKAYA, 1974, p. 59, *nom. imperf., nom. correct.* RONG & others, 1994, p. 547]

Characters as for superfamily. *Silurian (upper Aeronian)–Lower Devonian (lower Emsian).*

Retziella NIKIFOROVA, 1937a, p. 57 [**Retzia (Retziella) weberi;* OD] [=*Protathyrisina* CHU, 1974, p. 457 (type, *P. kütsingensis,* OD, =*Athyrisina minor* HAYASAKA in YABE & HAYASAKA, 1920, p. 183); *Stegospira* FU, 1982, p. 167 (type, *S. nucleola,* OD), see also FU, 1984, p. 374; *Gannania* FU, 1982, p. 168 (type, *G. spiriferoides,* OD); *Gannania* FU, 1984, p. 376 (type, *G. spireferoidea,* OD]. Shell with variably developed ventral sulcus and dorsal fold, both usually ribbed or plicate; well-developed apical septalium, shallow and partially covered by platelike crural bases and supported by short septum. *Silurian (upper Wenlock)–Lower Devonian (lower Lochkovian):* Kyrgyzstan, Tajikistan, China (Jilin, Inner Mongolia, Gansu, Sichuan, Yunnan, Guangxi), northern Vietnam, southwestern Tian Shan, ?North Korea, ?central Pamir, ?Afghanistan, ?eastern Iran, ?New Zealand.——FIG. 1076*a–w.* **R. weberi* (NIKIFOROVA), Přídolí, central Asia, southern Tian Shan, Fergana; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, VSEGEI W2456/50327, V. N. Weber Collection, 1885, ×2 (Nikiforova, 1937a; photographs courtesy of T. L. Modzalevskaya); *e–l,* serial sections, NIGP 121423-1; *m,* lateral view of sectioned specimen showing approximate position of serial sections; *n–v,* serial sections, NIGP 121423-1; *w,* lateral view of sectioned specimen showing approximate position of serial sections (adapted from Rong & others, 1994).——FIG. 1076*x–y. R. minor* (HAYASAKA), upper Ludlow–lower Přídolí, Yunnan; ventral and lateral views of reconstructed jugum, approximately ×3 (Rong & others, 1994). [See also Fig. 1006.3, p. 1481, in introduction.]

?Argorhynx HAVLÍČEK, 1992, p. 110 [**Monticola prokopensis* HAVLÍČEK, 1956, p. 541; OD]. Paucicostate rhynchonelliform shell with smooth umbonal regions; internally similar to *Gissarina*; spiralia poorly preserved, jugum unknown. [This genus requires revision.] *Lower Devonian (upper Pragian):* Prague basin (Bohemia).——FIG. 1077,6*a–c.* **A. prokopensis* (HAVLÍČEK); holotype, ventral, lateral, and anterior views, VH 3667, ×1.7 (Havlíček, 1956).

Gissarina MENAKOVA & NIKIFOROVA, 1986, p. 71 [**Parazyga ? argensis* NIKIFOROVA, 1949, p. 19; OD]. Similar to *Retziella* but sulcus may develop in both valves; delthyrium covered by deltidial plates; septalium and median septum extremely short or absent. *Silurian (Přidoli):* Tajikistan.——FIG. 1077,7*a–s.* **G. argensis* (NIKIFOROVA); *a–d,* holotype, dorsal, ventral, lateral, and anterior views, TsNIGRA 4/8639, ×2 (Nikiforova, 1949; photographs courtesy of T. L. Modzalevskaya); *e–j,* transverse serial sections showing umbonal regions 0.2, 0.55, 0.80, 0.95, 1.00, 1.45 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 19/6228; *k–q,* transverse serial sections showing cardinalia and brachidium 0.6, 1.2, 1.5, 2.25, 3.50, 4.90, 5.30 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 20/6228 (adapted from Menakova & Nikiforova, 1986); *r–s,* ventral and lateral views of reconstructed jugum (Menakova & Nikiforova, 1986).

Metathyrisina RONG & YANG, 1981, p. 246 [**M. merita;* OD]. Similar to *Retziella* with shorter and lower septalium arising somewhat forward of apex, outer hinge plates short. *Silurian (upper Aeronian):* southwestern China (northeastern Guizhou).——

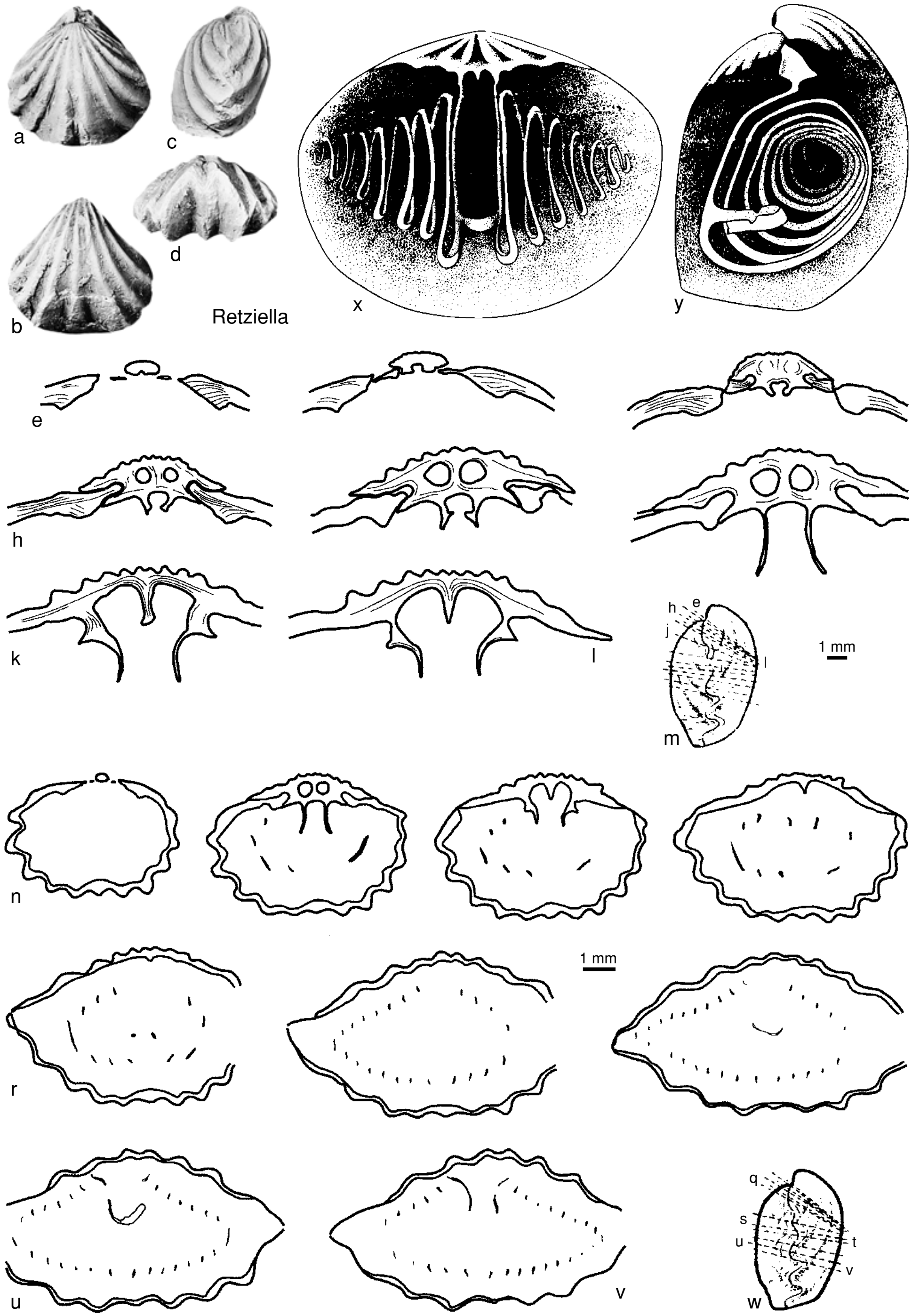

FIG. 1076. Retziellidae (p. 1580).

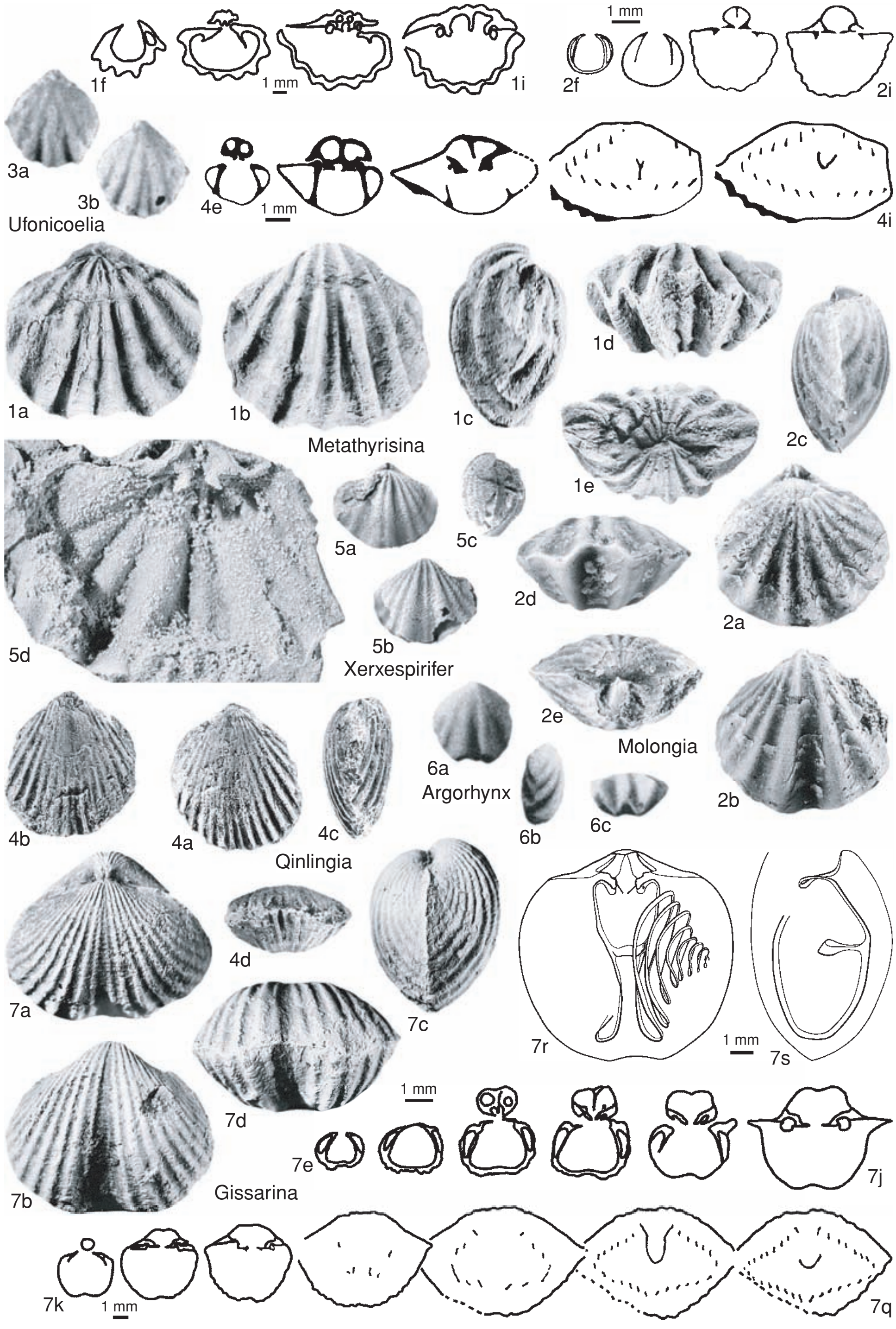

FIG. 1077. Retziellidae (p. 1580–1583).

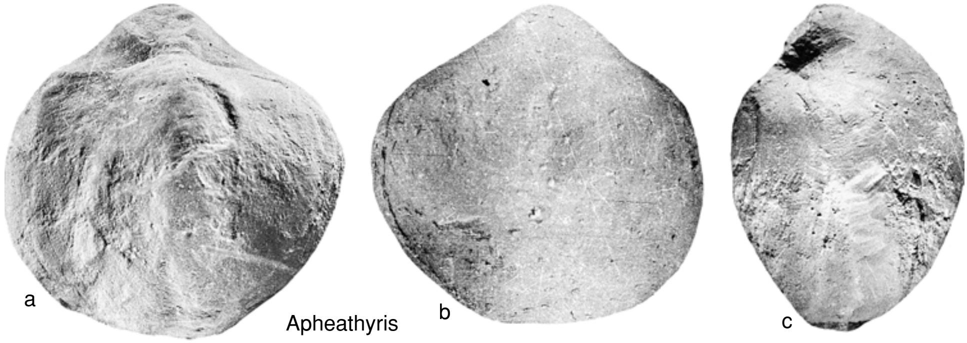

FIG. 1078. Uncertain (p. 1583).

FIG. 1077,*1a–i.* **M. merita; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, NIGP 44075, ×2.3 (Rong & Yang, 1981); *f–i,* transverse serial sections 0.5, 1.2, 1.9, 2.2 mm from ventral umbo (adapted from Rong & Yang, 1981).

Molongia MITCHELL, 1921, p. 546 [**M. elegans;* OD]. Shell with variably developed ventral sulcus and dorsal fold that may be plicate but is usually smooth; without dorsal median septum and septalium; short myophragm commonly present. *Silurian (Wenlock)–Lower Devonian (Lochkovian):* Australia (New South Wales, Victoria, Queensland).——FIG. 1077,*2a–i.* **M. elegans,* ?Wenlock, Ludlow, Molong, New South Wales; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, NIGP 121425, ×3 (Rong & others, 1994); *f–i,* transverse serial sections 0.3, 0.5, 0.8, 1.15 mm from ventral umbo (adapted from Rong & others, 1994).

Qinlingia RONG, ZHANG, & CHEN, 1987, p. 71 [**Q. bisulcata;* OD]. Similar to *Retziella* but having weak sulcus on each valve and jugal stem. *Lower Devonian (lower Lochkovian):* China (northwestern Sichuan).——FIG. 1077,*4a–i.* **Q. bisulcata; a–d,* holotype, dorsal, ventral, lateral, and anterior views, XAGM B108, ×2 (Rong, Zhang, & Chen, 1987); *e–i,* transverse serial sections 0.3, 0.6, 1.1, 4.2, 4.9 mm from ventral umbo (adapted from Rong, Zhang, & Chen, 1987).

?Ufonicoelia HAVLÍČEK, 1992, p. 112 [**Monticola torleyi* HAVLÍČEK, 1956, p. 576; OD]. Similar to *Argorhynx* but with ribs starting in umbo and having median costa in ventral valve; poorly known. [This genus requires revision.] *Lower Devonian (upper Pragian–lower Emsian):* Prague basin (Bohemia).——FIG. 1077,*3a–b.* **U. torleyi* (HAVLÍČEK); holotype, dorsal and ventral views, VH 177, ×4 (Havlíček, 1956).

?Xerxespirifer COCKS, 1979, p. 40 [**X. iranicus;* OD]. Shell with small but distinctive median rib in sulcus of ventral valve and corresponding trough in dorsal valve fold; concentric ornament of fine growth lines; cardinal process small; no inner hinge plates, no median septum; spiralium and jugum unknown. [This genus was erected by COCKS (1979) as an acrospiriferinine and was rejected from the spiriferidines by CARTER and others (1994), suggesting a rhynchonellid or leptocoeliid affiliation for the genus. Based mainly on external similarities it was placed herein within the retzielloids. While in proofs, BRICE (1999) placed part of the specimens illustrated by COCKS (1979) of *X. iranicus (*type species of *Xerxespirifer*), in the synonymy of *S. procerum (*type species of *Stegocornu* DÜRKOOP, 1970), therefore *Xerxespirifer* is also listed herein as a synonym of *Stegocornu* (rhynchonelloid) by N. SAVAGE, p. 1050. Careful revision of internal morphology is required to solve this ambiguity.] *Silurian (?Wenlock):* Iran.——FIG. 1077,*5a–d.* **X. iranicus,* Elburz; *a–c,* holotype, dorsal, ventral, and lateral views, BMNH BB 93453, ×1; *d,* dorsal interior and fragment of ventral valve above, BMNH BB 93462, ×3 (Cocks, 1979; photographs courtesy of L. R. M. Cocks).

Superfamily and Family UNCERTAIN

Apheathyris FU, 1982, p. 172 [**A. guyuanensis;* OD]. Poorly known. Large, elliptical to round pentagonal, ventribiconvex, smooth shell; with low dorsal fold and shallow ventral sulcus; interior poorly known, dental plates absent, outer hinge plates short and small, inner hinge plate absent, crura long, spiralia laterally directed. [When erected, this genus was included in the Athyrididina, Athyrididae; this genus needs revision.] *Upper Ordovician (lower Caradoc):* northern China (Shijiezigou, Guyuan, Ningxia).——FIG. 1078,*2a–c.* **A. guyuanensis;* holotype, dorsal, ventral, and lateral views, XAGM B993, ×1.5 (Fu, 1982).

RETZIIDINA

FERNANDO ALVAREZ and RONG JIA-YU

[University of Oviedo, Spain; and Nanjing Institute of Geology and Palaeontology]

All retziidines, as here considered, are endopunctate in contrast to the impunctate condition of athyrididines and koninckinidines. A tertiary layer is absent in the retziidines, being present in the koninckinidines and in some athyrididines. The ribbed or plicate (rarely smooth) shells of the retziidines and their cardinalia resemble those of the rhynchonellides from which they differ mainly in the calcification of a spiralium similar to those present in the athyrididines. The primary whorls of each spiral cone grew near the midline of the shell, coiled approximately parallel with the plane of symmetry, and were united by a posteriorly situated jugum, commonly spiny, but without a saddle and stem (Fig. 1079–1080). Accessory jugal lamellae are known in some genera. In the Neoretziinae the accessory jugal lamellae are secondarily connected to the spiralia, and in the Hungarispirinae they are intercalated with spiralial loops to the apex (Fig. 1079). In the three retziidine superfamilies a pedicle collar is commonly present, but the dental plates are extremely short or absent. A cardinalia is present and is more like the cardinal plate of the athyrididines than the septalium of meristelloids and retzielloids (Fig. 1081–1082). The outer hinge plates are well developed in contrast to the inner hinge plates, which are commonly short, without a dorsal foramen, or absent. Moderately to strongly developed cardinal flanges protrude posteroventrally (Fig. 1082), and a moderate to very high dorsal median septum is commonly present beneath the cardinal plate. Externally, *Parazyga* diverged from other ribbed rhynchospirinoids through the development of numerous, long, hollow spines anteriorly or anterolaterally directed and not known in any other athyridid taxa (see ALVAREZ, 1999b). The mongolospiroids differ from all other retziidines in the smoothness of the shell, a character sufficiently important in itself to warrant a different superfamilial grouping.

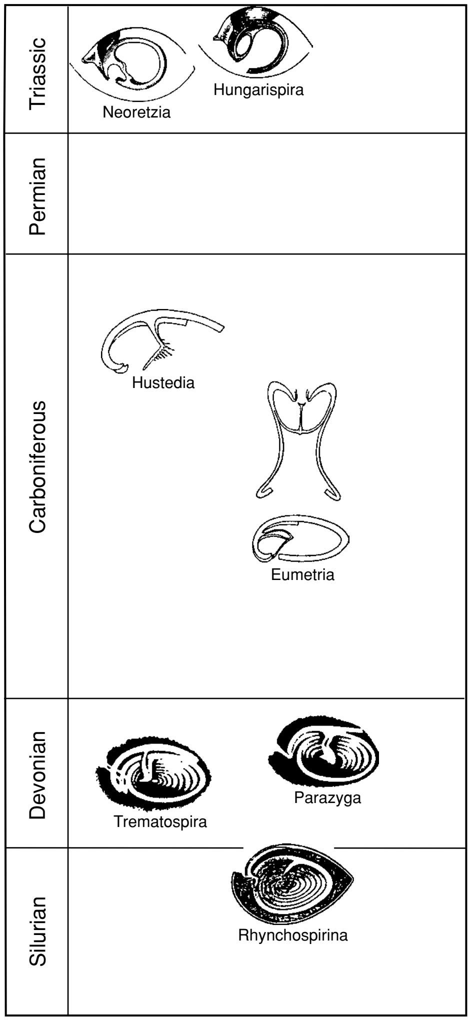

FIG. 1079. Main types of retziidine brachidium (Alvarez, 1999).

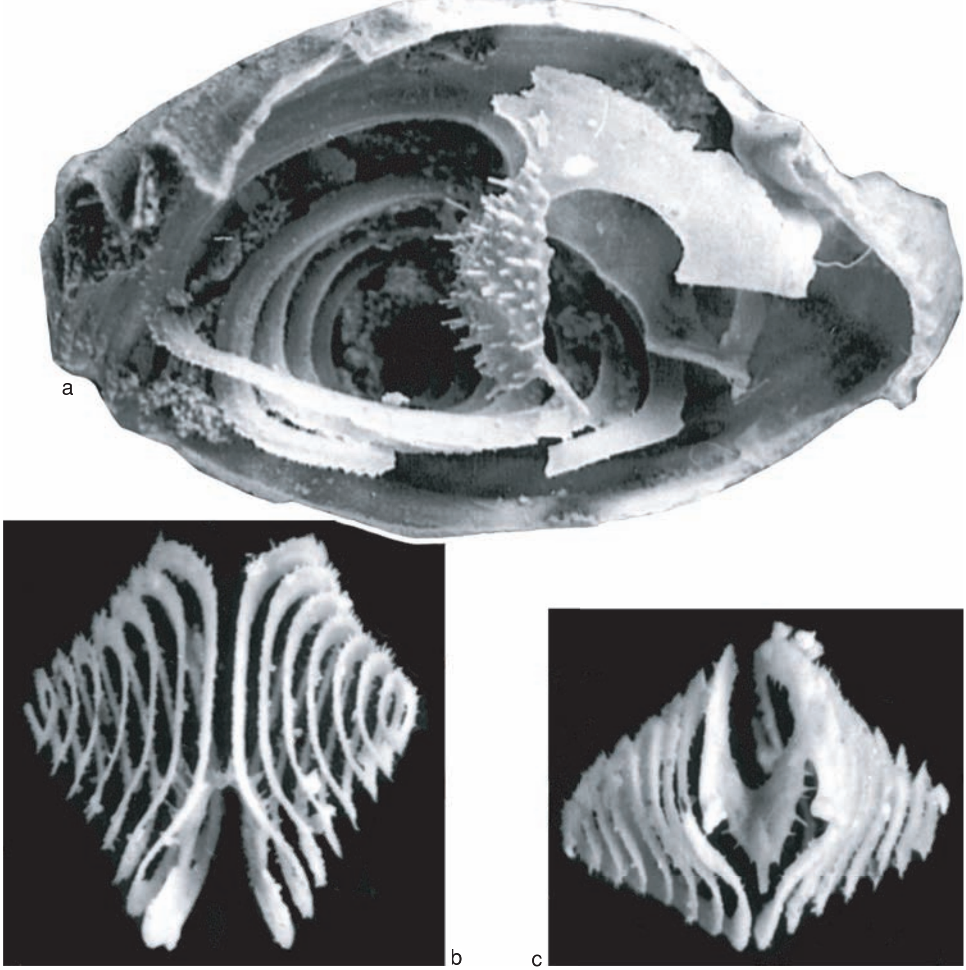

FIG. 1080. *a,* Side view of broken specimen of *Hustedia pugilla pugilla* COOPER & GRANT, showing large, spiny jugum, USNM 154482b, ×10; *b–c,* ventral and posterior views of complete and spiny spiralium with jugum, USNM 154482a, ×8 (Alvarez, 1999; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

Suborder RETZIIDINA Boucot, Johnson, & Staton, 1964

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1965, p. 649, *pro* suborder Retzioidea BOUCOT, JOHNSON, & STATON, 1964, p. 813; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Ribbed or plicate, rarely smooth, with or without spines, moderately to strongly rostrate, astrophic to almost strophic athyridides *sensu lato;* commonly with distinct ventral area and umbo moderately to strongly curved; delthyrium commonly completely covered; pedicle collar commonly present; dental plates commonly absent; hinge plate without dorsal foramen, commonly short or absent; outer hinge plates well developed; cardinal flanges moderately to strongly developed; moderate to very high dorsal median septum commonly present; jugum commonly spiny and posteriorly

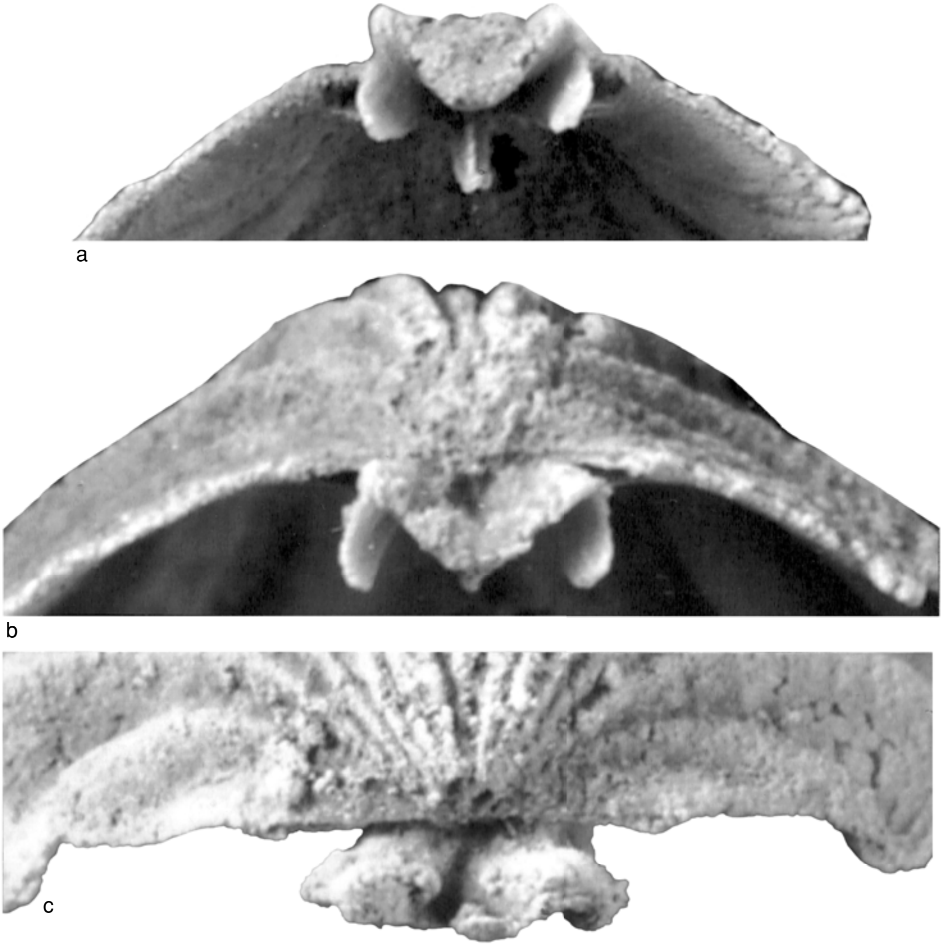

FIG. 1081. *a–c, Hustedia glomerosa* COOPER & GRANT, ventral, posteroventral, and posterior views of cardinalia, USNM 154455a, ×10 (new; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

situated; jugal saddle absent; short, roof-shaped process directed posteriorly from jugum may be present; jugal stem may be present; accessory jugal lamellae commonly absent, rarely secondarily connecting with spiralial (Neoretziinae) or intercalating with spiralial loops to the apex (Hungarispirinae); shell substance punctate (punctae simple, nonbranching, in oldest taxa, branching intensively in the Triassic Neoretziinae and Hungarispirinae); tertiary layer absent. [WATERHOUSE (1981), considering that the suborder Retziidina (sensu BOUCOT, JOHNSON, & STATON, 1964) differs substantially from spiriferides, atrypides, and athyridides, proposed placing it in a separate order, Retziida. WATERHOUSE provides as a diagnosis for the order the one given by BOUCOT, JOHNSON, & STATON (1964) for the suborder but did not discuss its contents. Most authors prefer to consider the retziidines as a suborder (the most derived within the athyridides; e.g., ALVAREZ, RONG, & BOUCOT, 1998) rather than as an independent order. Doing so reduces the number of paraphyletic groups named in the phylogenetic analysis of the spirebearers (see discussion by ALVAREZ & CARLSON, 1998).] *Silurian (lower Llandovery)–Upper Triassic (upper Norian).*

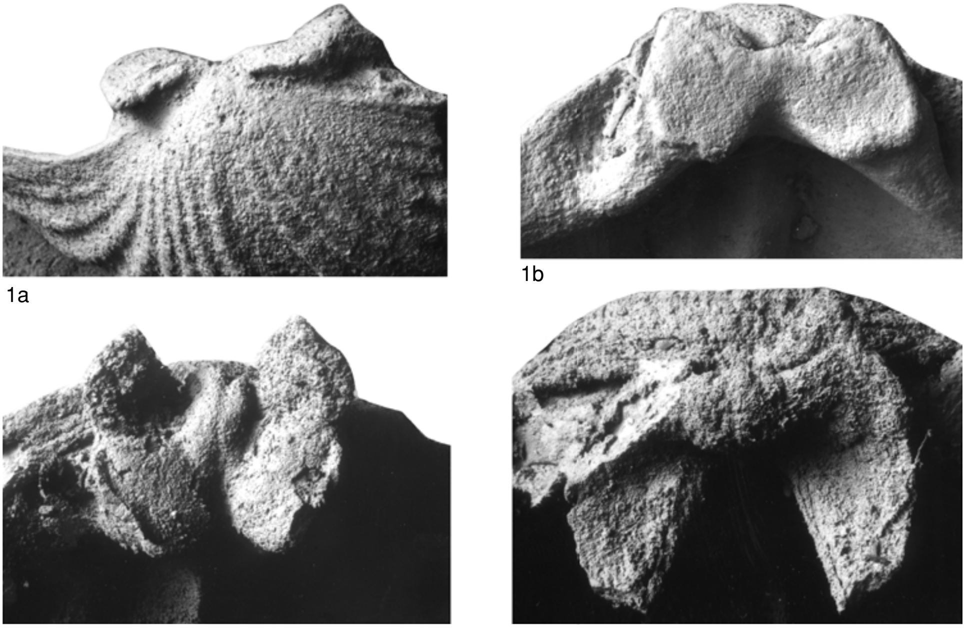

FIG. 1082. *1a–b,* Posterior (SEM, ×22) and ventral (SEM, ×20) views of *Homoeospira evax* (HALL), cardinalia, USNM 497429 (new); *2,* ventral view of *Trematospira multistriata* (HALL), cardinalia, I2120, Hall collection, SEM, ×9; *3,* ventral view of *Rhynchospirina formosa* (HALL), cardinalia, I1859, Hall collection, SEM, ×20 (Alvarez & Brime, 2000).

Superfamily RETZIOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 448, *pro* Retziacea BOUCOT, JOHNSON, & STATON, 1964, p. 813, *nom. transl. ex* Retziinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Retziidines clear astrophic to almost strophic in younger taxa, with strongly to very strongly rostrate shells, ribbed or costate in younger taxa; growth lines weak, closely spaced; frills not developed; alternate adult folding to opposite folding in younger taxa (neoretziidines); ventral cardinal area (palintrope) moderate to extensive in younger taxa, apsacline to orthocline; dental plates absent (except *Retzia*); cardinal plate nonperforate; cardinal flanges developed moderately to strongly, in younger taxa; dorsal median septum present, except in *Eumetria,* and very high in *Retzia* and Triassic taxa; jugal stem present and long; arms and differently developed accessory jugal lamellae may be present, especially in younger taxa. *Silurian (upper Ludlow)–Upper Triassic (upper Norian).*

Family RETZIIDAE Waagen, 1883

[*nom. transl.* HALL & CLARKE, 1894, p. 840, *ex* Retziinae WAAGEN, 1883, p. 486; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Astrophic shell commonly large; subequally biconvex, elongate-oval costate, commonly without fold and sulcus; median and flank costae same width; deltidial plates conjunct; foramen in permesothyridid position; ventral umbo strongly curved; pedicle collar commonly present; arms of jugum present but not developed into accessory jugal lamellae. *upper Silurian (?Ludlow), Lower Devonian–Lower Permian.*

Retzia KING, 1850, p. 137 [**Terebratula adrieni* DE VERNEUIL & D'ARCHIAC, 1845, p. 471; OD] [=*Trigeria* BAYLE, 1878, pl. 13, obj.]. Thin but high dental plates; pedicle collar well developed; cardinal flanges, thin and flat, projecting posteroventrally; hinge plate short, in comparison with long, flat outer hinge plates, supported by high, thin median septum; jugum projecting posteroventrally as long stem that may give rise to short, pronglike bifurcations or become thick and spiny. *upper Silurian (?Ludlow), Lower Devonian–Lower Carboniferous (Viséan):* ?Fergana, ?Urals, ?Inner Mongolia, *?Ludlow;* Spain, France, Germany, Kuznetsk, Altay, Novosibirsk area, southern China (Guangxi), *Lower Devonian–Middle Devonian;* Donetz, Kuznetsk, Kazakhstan, Siberia, northeastern China, *Upper Devonian–Lower Carboniferous (Viséan).*——FIG. 1083,*1a–aa.* **R. adrieni* (DE VERNEUIL & D'ARCHIAC), upper Emsian, Asturias, Spain; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, D852, de Verneuil Collection, ×1 (new; photographs courtesy of N. Podevigne); *f–r,* transverse serial sections showing umbonal regions 0.20, 0.60, 0.80, 1.10, 1.30, 1.50, 2.10, 2.30, 2.60, 2.70, 2.90, 3.30, 3.60 mm from ventral umbo, DPO/F24242; *s–z,* transverse serial sections showing cardinalia and brachidium 1.30, 1.60, 5.00, 5.60, 6.00, 6.30, 6.40, 6.60 mm from ventral umbo, DPO/F24243 (new); *aa,* lateral view of jugum (Hall & Clarke, 1893).

Acambona WHITE, 1865, p. 27 [**A. prima;* OD]. Externally similar to *Eumetria* but slightly longer and finely costate; pedicle collar present; cardinal flanges moderately developed, projecting posteriorly; spiralia and jugum unknown. [Although WHITE's contribution was presented to the Boston Society of Natural History on February 5, 1862, the papers presented to the Society during the years 1862 and 1863 were published in 1865 in volume IX of the Proceedings.] *Lower Carboniferous (upper Tournaisian–lower Viséan):* North America, ?Belgium, ?Kazakhstan, ?Mongolia.——FIG. 1083,*2a–b.* **A. prima,* Iowa; dorsal and lateral views, ×1 (Weller, 1914).

Eumetria HALL, 1863b, p. 59 [**Retzia vera* HALL, 1858a, p. 704; SD WAAGEN, 1883, p. 487]. Symphytium gently incurved; foramen in permesothyridid position; dental plates absent; incipient pedicle collar poorly developed or absent; hinge plate raised high above dorsal valve floor by outer hinge plates; high cardinal flanges ventrally forked; median septum absent; lateral branches of jugum originating well posteriorly, projecting anteriorly at low angle; jugal arch projecting posteroventrally as long, straight stem bifurcating into short arms. [Fixation of type species is usually credited to HALL (1863b) or DALL (1877). HALL, however, did not explicitly designate a species as type species for *Eumetria* and included more than one, therefore it is not possible to apply the principle of monotypy, and DALL (1877, p. 28) gave two types for *Eumetria: Retzia vera* HALL and *R. serpentina* DE KONINCK. The first unequivocal designation of the type species seems to be that of WAAGEN (1883, p. 487), who properly considered *Retzia vera* HALL, as the type of the genus (Article 69.1; ICZN, 1999).] *Lower Carboniferous–Lower Permian:* North America, Belgium, Kazakhstan, Kuznetsk basin, Siberia, Verkhoyansk, northeastern and southern China, ?Australia (New South Wales), *Lower Carboniferous;* Spitzbergen, Verkhoyansk, *Upper Carboniferous;* USA (Maryland), *Lower Permian.*——FIG. 1084*a–e.* **E. vera* (HALL), Viséan–lower Serpukhovian, Illinois, USA; dorsal, ventral, lateral, anterior, and posterior views, USNM 497426, ×1.5 (new).——FIG. 1084*f–r. E. osagensis* (SWALLOW), Lower Carboniferous, Alberta, Canada; transverse serial sections 1.1, 2.1, 2.4, 2.8, 3.6, 4.2, 5.4, 7.0, 7.4, 8.6, 9.4, 10.0, 11.2 mm from ventral umbo, GSC 63347 (adapted from Carter, 1987).——FIG. 1084*s–v. E. verneuiliana* (HALL), Viséan–lower Serpukhovian, Indiana, USA; *s,* jugum, ventral view; *t,* jugum, lateral view (adapted from Hall & Clarke, 1893); *u,* interior view of articulated but incomplete shell showing cardinalia and large ventral pedicle opening, I 1392, ×9.7; *v,* interior view of articulated shell (ventral up) showing articulation and cardinalia with ventrally projecting, widely forked cardinal flanges, I 1392, ×13.7 (Brunton, Alvarez, & MacKinnon, 1996).

Family NEORETZIIDAE Dagys, 1972

[*nom. transl.* GRUNT, 1986, p. 7, *ex* Neoretziinae DAGYS, 1972, p. 103; *emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 845]

Shell commonly small, except in *Neoretzia;* almost strophic; anterior margin may be emarginate; ventral umbo moderately curved in old taxa but straight in several Triassic taxa; ventral cardinal area commonly orthocline; deltidial plates conjunct; pedicle collar may be present; arms of jugum only present in some Triassic taxa in which they continue into accessory jugal lamellae secondarily connected with spiralial (Neoretziinae) or intercalated with spiralial loops to apex (Hungarispirinae). *Silurian (upper Ludlow)–Upper Triassic (upper Norian).*

Subfamily NEORETZIINAE Dagys, 1972

[Neoretziinae DAGYS, 1972, p. 103]

Shell small to large (*Neoretzia*); convexity moderate to strong; strongly to very strongly rostrate; ventral umbo straight or nearly so; costate; fold and sulcus absent or narrow sulcus from umbo present in both valves; moderate to extensive ventral cardinal area; dorsal median septum very high and long; accessory jugal lamellae connect secondarily with spiralia. *Middle Triassic (Anisian)–Upper Triassic (upper Norian).*

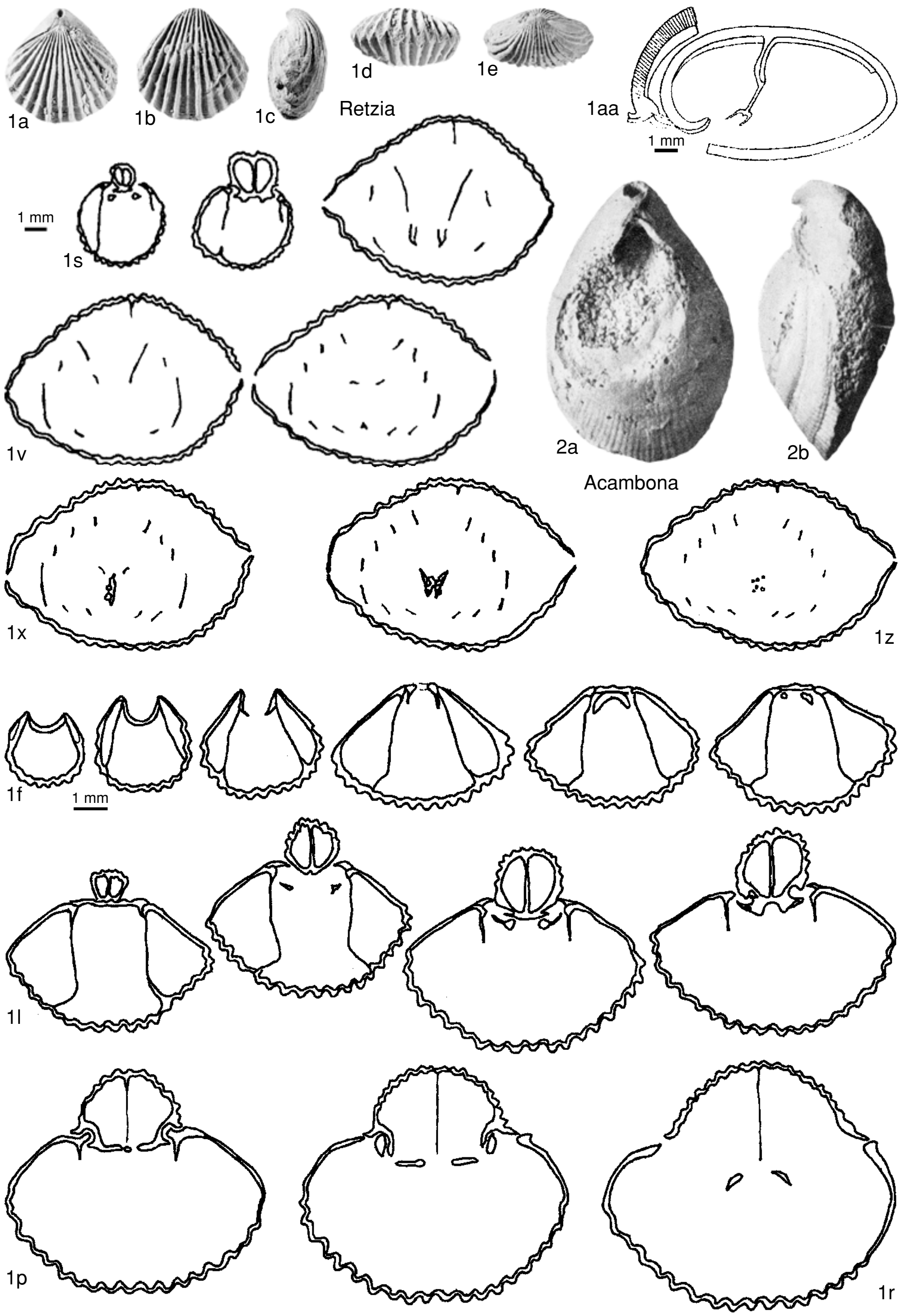

Fig. 1083. Retziidae (p. 1587–1588).

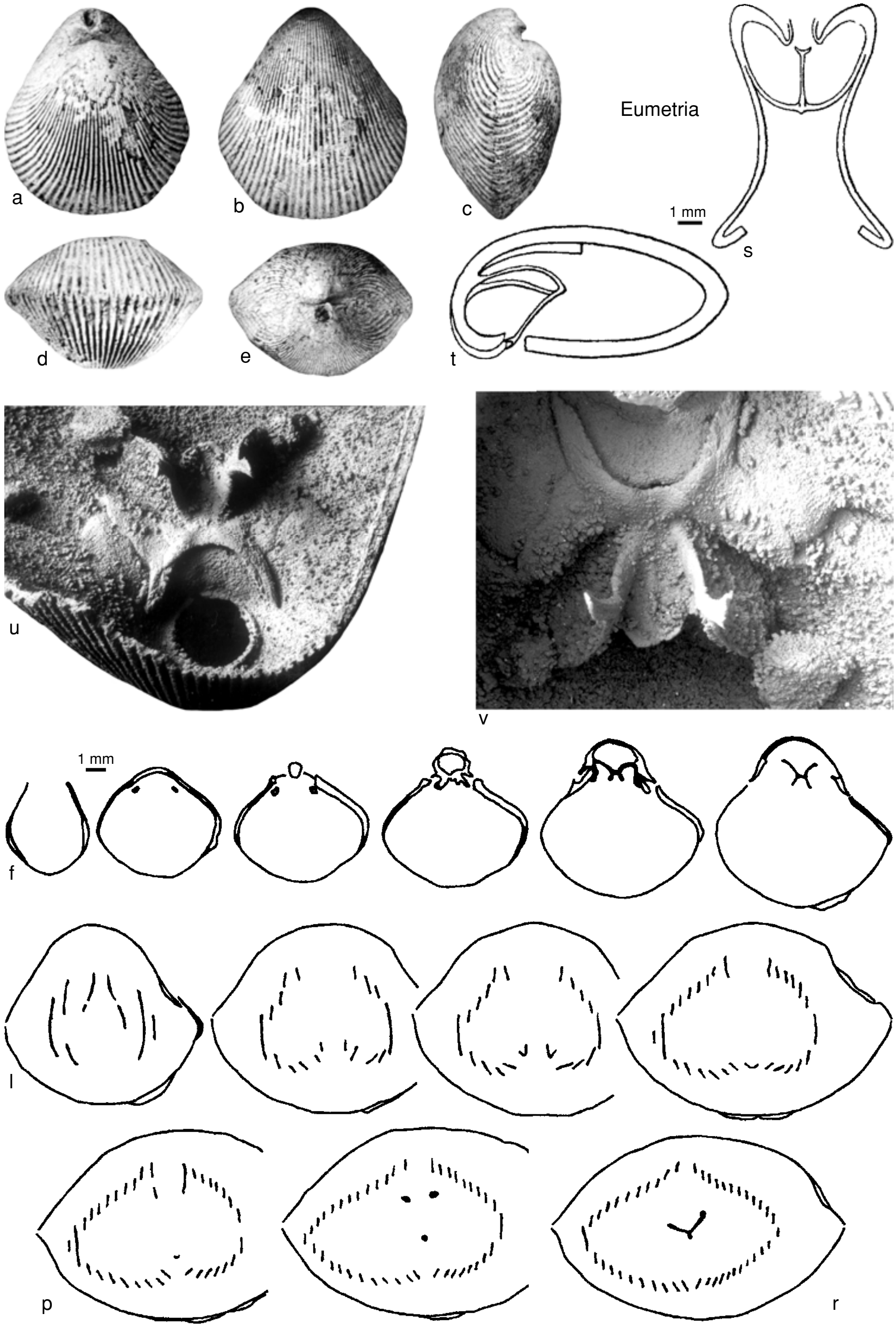

FIG. 1084. Retziidae (p. 1588).

Neoretzia Dagys, 1963, p. 130 [**Retzia superbescens* Bittner, 1890, p. 281; OD; =*Waldhemia superba* Suess in Davidson, 1856, p. 48]. Subequally biconvex, elongate oval shells with few subangular costae; ventral valve beak nearly straight, foramen in permesothyridid position; internally similar to *Retzia* but without dental plates and with much thicker cardinal flanges and hinge plates; jugum very posteriorly situated, projecting anteroventrally as a complex stem that rejoins primary lamellae on ventral half. *Middle Triassic (Anisian)–Upper Triassic (upper Norian):* Slovakia, *Anisian;* Austria, Hungary, Romania, Crimea, Iran, Caucasus, Himalayas, Pamir, southern and western China (Tibet), *Upper Triassic.*——Fig. 1085,*1a–s.* **N. superba* (Suess), Rhaetian; *a,* holotype, ventral view, Hirtenberg, Austria, MGBW 3828, ×1.3 (Pearson, 1977); *b–d,* dorsal, ventral, and lateral views, northern Caucasus, IGiG 47/2443, ×1 (Dagys, 1963; photographs courtesy of the late A. S. Dagys); *e–r,* transverse serial sections 0.3, 0.8, 1.8, 3.3, 3.7, 4.2, 4.5, 4.9, 6.1, 6.9, 7.6, 8.3, 8.6, 9.1 mm from ventral umbo, distance from ventral umbo to first section approximate, northern Caucasus (adapted from Dagys, 1963); *s,* jugum, lateral view, northern Caucasus, approximately ×1.8 (Dagys, 1974).

Cassianospira Dagys, 1972, p. 103 [**Retzia loczyi* Bittner, 1900, p. 29; OD]. Very small, strongly inequivalve, elongate subpentagonal shells, with few subangular costae and narrow dorsal sulcus with fine median costa extending from umbo; ventral beak very high and straight; symphytium wide and high; foramen in submesothyridid position; pedicle collar absent; cardinal flanges and hinge plate thick, supported by long septum; jugum not well known, stem essentially as in *Neoretzia. Upper Triassic (Carnian):* southern Alps, Carpathians, Hungary. ——Fig. 1085,*2a–m.* **C. loczyi* (Bittner), Hungary; *a–d,* dorsal, ventral, lateral, and anterior views, IGiG 394/287, ×3 (Dagys, 1963; photographs courtesy of the late A. S. Dagys); *e–m,* transverse serial sections 0.6, 1.7, 1.8, 2.1, 2.65, 3.2, 3.4, 3.7, 3.9 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/289 (adapted from Dagys, 1972).

Subfamily HUNGARISPIRINAE Dagys, 1972

[Hungarispirinae Dagys, 1972, p. 101]

Shell small; convexity of adult valves moderate; very strongly rostrate; ventral umbo straight; costate; narrow sulcus from umbo present in both valves; ventral cardinal area extensive; dorsal median septum very high and long; accessory jugal lamellae free and intercalated with spiralial loops to apex. *Upper Triassic (Carnian).*

Hungarispira Dagys, 1972, p. 102 [**Retzia aracanga* Bittner, 1900, p. 30; OD]. Similar to *Cassianospira* but multicostate, foramen in permesothyridid position, jugum projecting posteroventrally as long stem, accessory jugal lamellae continuing intercalated with spiralial loops to apex. *Upper Triassic (Carnian):* Italy, Hungary.——Fig. 1086,*1a–t.* **H. aracanga* (Bittner), Hungary; *a–d,* dorsal, ventral, lateral, and anterior views, IGiG 394/284, ×3 (Dagys, 1972; photographs courtesy of the late A. S. Dagys); *e–s,* transverse serial sections 0.8, 1.6, 1.8, 2.4, 2.6, 2.8, 3.0, 3.1, 3.2, 3.4, 3.5, 3.75, 3.9, 4.1, 4.7 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/286 (adapted from Dagys, 1972); *t,* jugum, lateral view (Dagys, 1974).

Subfamily HUSTEDIINAE Grunt, 1986

[Hustediinae Grunt, 1986, p. 7; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 847]

Small to medium shell; convexity strong in adult valves (except *Hustedtiella*); strongly rostrate; ventral umbo moderately curved; ribbed (adult shell with fewer than 15 ribs); fold and sulcus, if present, weak and restricted to anterior one-third valve length or narrow sulcus from umbo may develop in both valves; ventral cardinal area moderate; pedicle collar present; dorsal median septum moderately high and short; arms and accessory jugal lamellae absent. *Carboniferous (Tournaisian)–Upper Triassic (Carnian).*

Hustedia Hall & Clarke, 1893, p. 120 [**Terebratula mormoni* Marcou, 1858, p. 51; OD]. Subequally biconvex, elongate-oval, costate shells; commissure strongly plicate and slightly uniplicate, rectimarginate, or sulcate; emarginate; costae simple with same width in median region as in flanks, slightly raised median costa on dorsal valve may be present; symphytium transversely flat, longitudinally gently concave; foramen in submeso- to permesothyridid position; blunt hinge teeth elongate transversely along hinge; pedicle collar short; hinge plate thick, strongly recurved to extend posteriorly along inner face of symphytium, rather short; bladelike crura slightly divergent and directed almost ventrally; short, ligulate process extending forward from base of hinge plate; short median septum in apex beneath hinge plate, extending forward as low median ridge; lateral branches of jugum originating quite posteriorly, projecting anteroventrally as spiny lamellae that join medianly and project posteroventrally in long, sharp, spiny stem. *Carboniferous (Tournaisian)–Permian (Tatarian):* cosmopolitan. ——Fig. 1087,*1a–e.* **H. mormoni* (Marcou), Upper Carboniferous, Nebraska, USA; dorsal, ventral, lateral, anterior, and posterior views, USNM

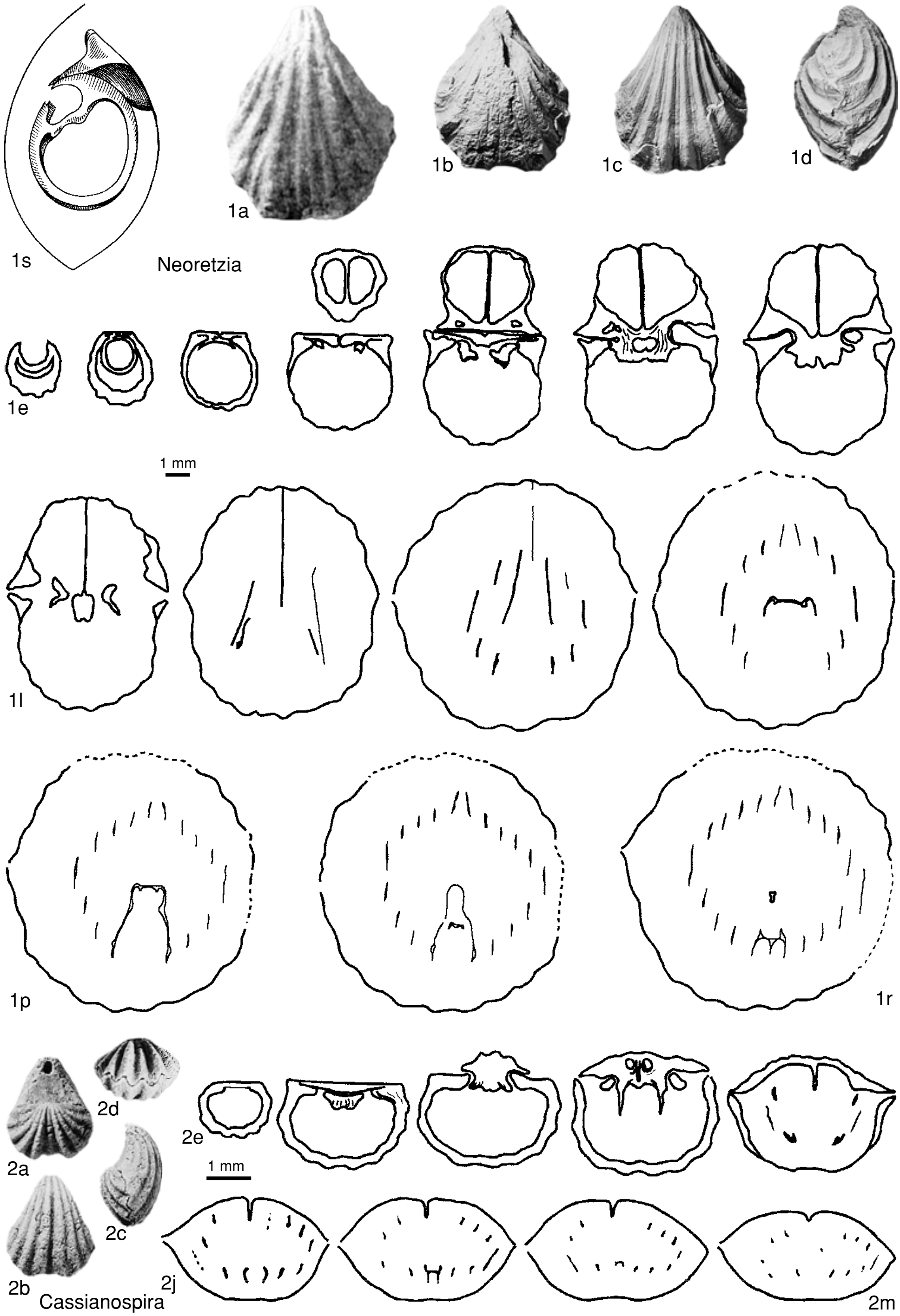

FIG. 1085. Neoretziidae (p. 1591).

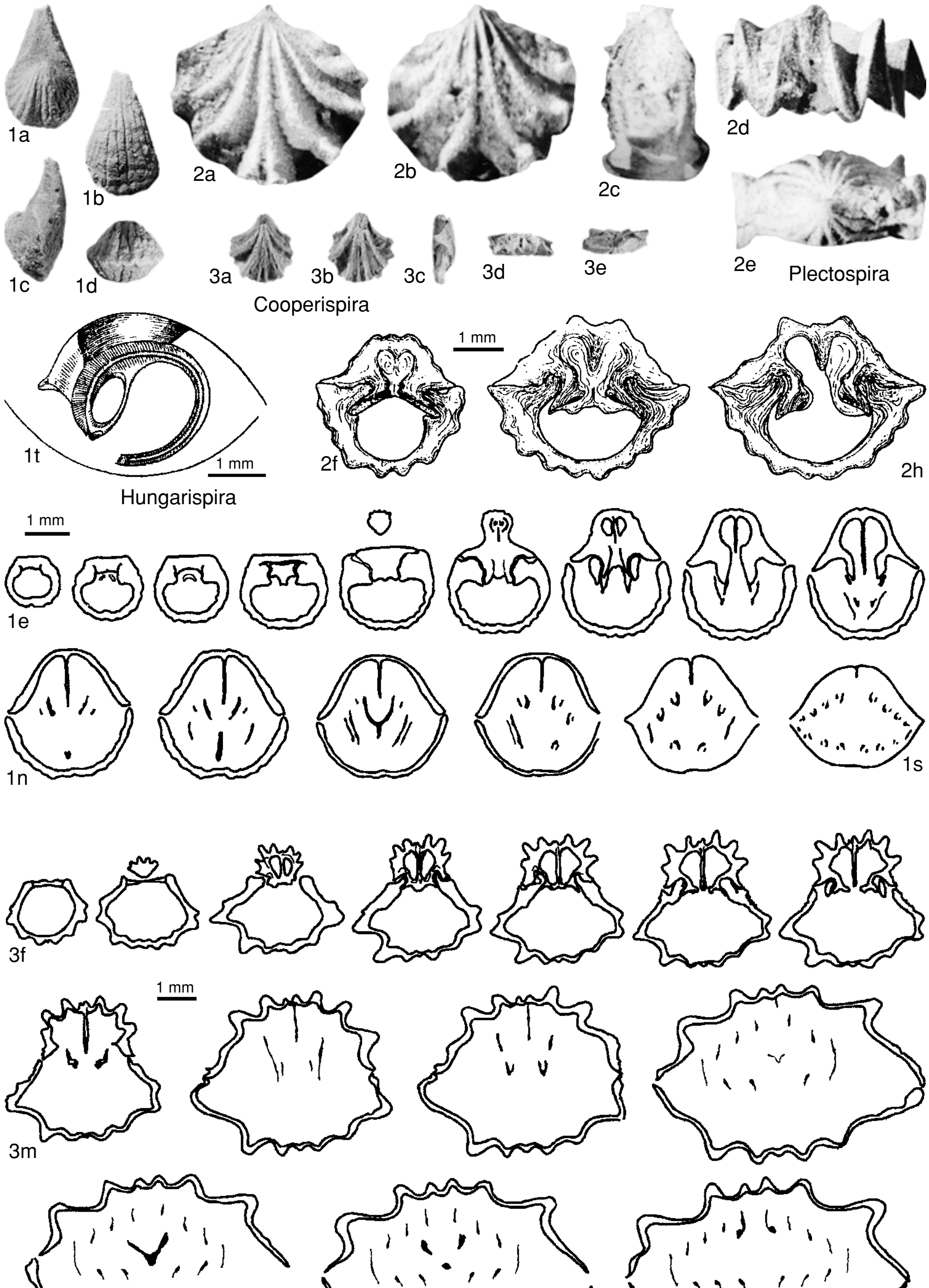

FIG. 1086. Neoretziidae (p. 1591–1596).

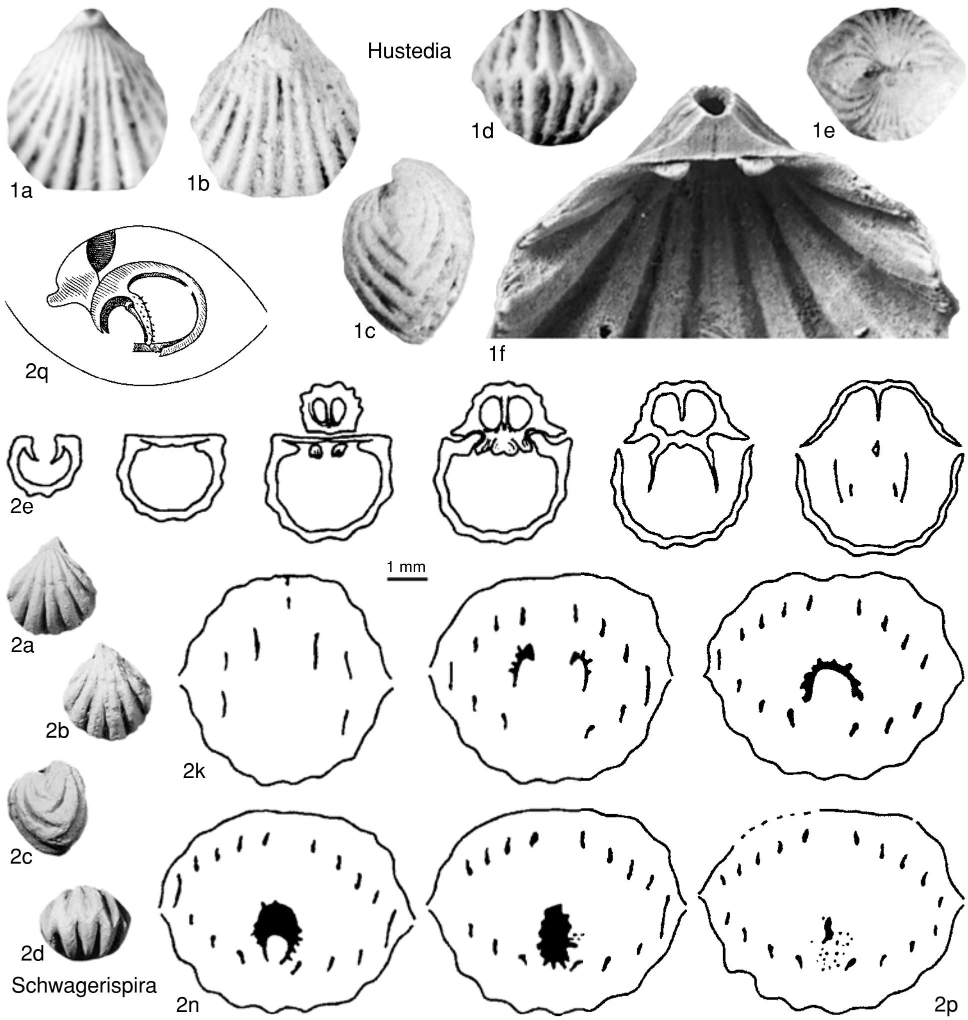

FIG. 1087. Retziidae (p. 1591–1595).

497428, ×3 (new).——FIG. 1087,*1f. H. glomerosa* COOPER & GRANT, Permian, Texas, USA; ventral umbo viewed dorsally, USNM 154456, ×4 (Cooper & Grant, 1976b). [See also Fig. 1080–1081, p. 1585–1586, in introduction.]

Hustedtiella DAGYS, 1972, p. 100 [**H. planicosta;* OD] [=*Hustediella* DAGYS, 1974, p. 166, incorrect subsequent spelling]. Subequally biconvex, longitudinally oval shells with low, rounded costae. Ventral valve beak short, slightly incurved, foramen in mesothyridid position; cardinal plate essentially as in *Schwagerispira* but cardinal flanges less developed, septum shorter and thicker; jugum projecting posteroventrally as short, simple stem. *Lower Triassic:* Russia (Primorya), Romania.——FIG. 1088,*2a–s.*H. planicosta,* upper Scythian, Primorya; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 380/1, ×2 (Dagys, 1972; photographs courtesy of the late A. S. Dagys); *e–r,* transverse serial sections 0.3, 0.6, 0.8, 0.9, 1.3, 1.6, 1.9, 2.1, 2.8, 3.1, 3.7, 4.5, 5.0, 5.3 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 380/3 (adapted from Dagys, 1972); *s,* jugum, lateral view, approximately ×4 (Dagys, 1974).

Schwagerispira DAGYS, 1972, p. 101 [**Retzia schwageri* BITTNER, 1890, p. 21; OD]. Subequally biconvex, subcircular shells with coarse, angular costae; foramen in permesothyridid position; cardinal flanges and hinge plates thick, supported by high, thin,

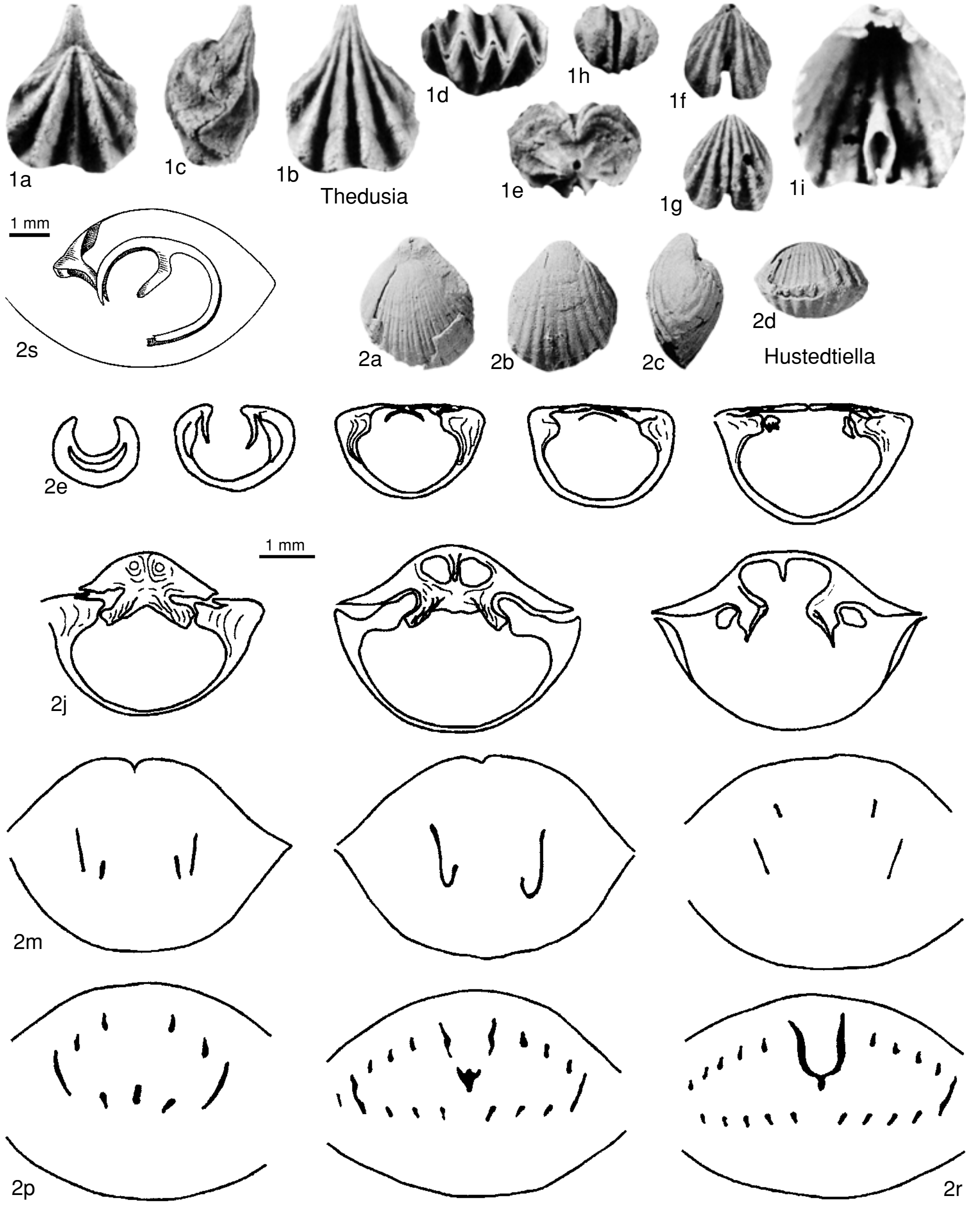

FIG. 1088. Retziidae (p. 1594–1596).

long septum; jugum essentially as in *Hustedia*. *Middle Triassic (Anisian)–Upper Triassic (Carnian):* Slovakia, Hungary, Bulgaria, Romania, Primorya, northwestern, southern, and central China, Qinghai.——FIG. 1087,*2a–q*. **S. schwageri* (BITTNER), Anisian, Bulgaria; *a–d,* dorsal, ventral, lateral, and anterior views, IGiG 394/281, ×2 (Dagys, 1972; photographs courtesy of the late A. S. Dagys); *e–p,* transverse serial sections 0.3, 0.5, 0.8, 1.05, 1.25, 1.45, 2.1, 2.5, 2.8, 2.9, 3.0, 3.2 mm from ventral umbo, distance from ventral umbo to first section approximate, IGiG 394/283 (adapted from Dagys, 1972); *q,* jugum, lateral view, approximately ×5.5 (Dagys, 1974).

Thedusia COOPER & GRANT, 1976b, p. 2806 [**Hustedia meekana trigonalis* GIRTY, 1909, p. 396;

OD]. Similar to *Hustedia* but smaller, dorsibiconvex, having more elongate ventral beak, ligate stage of folding with deep dorsal valve sulcus, and emarginate anterior. *Upper Carboniferous–Upper Permian (Capitanian):* southern China (Guangxi), *Upper Carboniferous;* USA (western Texas), *upper Sakmarian–Capitanian.*——FIG. 1088,*1a–e.* **T. trigonalis* (GIRTY), Capitanian, western Texas; dorsal, ventral, lateral, anterior, and posterior views, USNM 154499d, ×3 (Cooper & Grant, 1976b). ——FIG. 1088,*1f–i. T. discissa* COOPER & GRANT, upper Sakmarian–Artinskian, western Texas; *f–h,* dorsal, ventral, and anterior views, USNM 153264u, ×4; *i,* interior of ventral valve, USNM 154497e, ×11 (Cooper & Grant, 1976b).

Subfamily PLECTOSPIRINAE Alvarez, Rong, & Boucot, 1998

[Plectospirinae ALVAREZ, RONG, & BOUCOT, 1998, p. 847]

Shell small; convexity in adult valves strong; strongly rostrate; ventral umbo moderately curved; ribbed (adult shell having fewer than 15 ribs); fold and sulcus narrow and strong, present in entire valve, if costate, different from on flanks; dorsal median septum long and moderately high; arms and accessory jugal lamellae absent. *Silurian (upper Ludlow)–Middle Devonian (Givetian), ?Lower Carboniferous.*

Plectospira COOPER, 1942, p. 228, *nom. nov. pro Ptychospira* HALL & CLARKE, 1893, p. 112, *non* SLAVIK, 1869 [**Terebratula ferita* VON BUCH, 1835, p. 76; OD]. Subequally biconvex, pauciplicate shells of lenticular outline, dorsal fold commonly consisting of elevated median plication frequently with median groove in anterior part, which has corresponding ridge in sinus of opposite valve; foramen in submeso- to permesothyridid position; cardinal plate essentially as in *Homoeospira;* jugum projecting posteroventrally as very long, simple stem. *Silurian (upper Ludlow)–Middle Devonian (Givetian), ?Lower Carboniferous:* Europe, Altay, Kuznetsk, China, Australia (New South Wales), *upper Ludlow–Givetian;* North America, Verkhoyansk, Kuzbass, Kuznetsk, Mongolia, eastern Australia, *?Lower Carboniferous.*——FIG. 1086,*2a–h.* **P. ferita* (VON BUCH), Middle Devonian, Eifel, Germany; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497427, ×3 (new); *f–h,* transverse serial sections 1.50, 1.95, 2.15 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr75 (Siehl, 1962).

Cooperispira ALVAREZ, RONG, & BOUCOT, 1998, p. 847 [**Terebratula subferita* DE VERNEUIL, 1850, p. 174; OD]. Externally resembling *Plectospira* but with subpentagonal outline, elongate ventral beak, narrow and shallow sulcus on ventral valve, with fine median costa extending from umbo; dorsal valve with wider but also shallow sinus with fine median costa that bifurcates posteriorly, lateral plicae high, angular, sharp crested; foramen in permeso- to epithyridid position; dental plates and pedicle collar absent; cardinal plate essentially as in *Retzia;* jugum projecting ventrally as very short, simple stem. *Lower Devonian (Emsian):* northwestern Spain.——FIG. 1086,*3a–s.* **C. subferita* (DE VERNEUIL); *a–e,* dorsal, ventral, lateral, anterior, and posterior views, D690, de Verneuil Collection, ×3 (new; photographs courtesy of N. Podevigne); *f–s,* transverse serial sections 0.5, 1.2, 1.3, 1.5, 1.7, 1.8, 1.9, 2.0, 2.5, 2.7, 3.5, 3.6, 3.7, 3.9 mm from ventral umbo, DPO/F24239 (Alvarez, Rong, & Boucot, 1998).

Superfamily MONGOLOSPIROIDEA Alekseeva, 1981

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 847, *ex* Mongolospiridae ALEKSEEVA in ALEKSEEVA, MENDBAIAR, & ERLANGER, 1981, p. 108]

Clearly astrophic retziidines with moderately to strongly rostrate, completely smooth shells; ventral cardinal area (palintrope) moderately developed, almost orthocline; dental plates extremely short, supporting strong teeth; pedicle collar present; hinge plate supported by high, long median septum; jugum without stem. *Lower Devonian.*

Family MONGOLOSPIRIDAE Alekseeva, 1981

[*nom. correct.* GRUNT, 1986, p. 7, *pro* Mongolispiridae ALEKSEEVA in ALEKSEEVA, MENDBAIAR, & ERLANGER, 1981, p. 108, *nom. imperf.*]

Characters as for superfamily. *Lower Devonian.*

Mongolospira ALEKSEEVA, 1977, p. 63 [**M. turgensis;* OD] [=*Mongolispira* ALEKSEEVA, 1981, p. 108, incorrect subsequent spelling (Art. 33.3, ICZN, 1999)]. Subequally biconvex, elongate-oval, medium shells; dorsal fold and ventral sulcus absent; ventral valve beak high, incurved; deltidial plates conjunct; foramen in permesothyridid position. *Lower Devonian:* northwestern Mongolia.——FIG. 1089*a–l.* **M. turgensis; a–d,* holotype, dorsal, ventral, lateral, and anterior views, PIN 3602/1, ×2; *e,* dorsal view, PIN 3602/3, ×3.5 (Alekseeva, 1977; photographs courtesy of R. E. Alekseeva); *f–h,* transverse serial sections 0.8, 3.0, 4.3 mm from ventral umbo, showing ventral umbonal region and cardinalia, PIN 3602/8; *i–l,* transverse serial sections 3.0, 4.0, 4.5, 5.0 mm from ventral umbo, showing spiralium and jugum, PIN 3602/9 (adapted from Alekseeva, 1977).

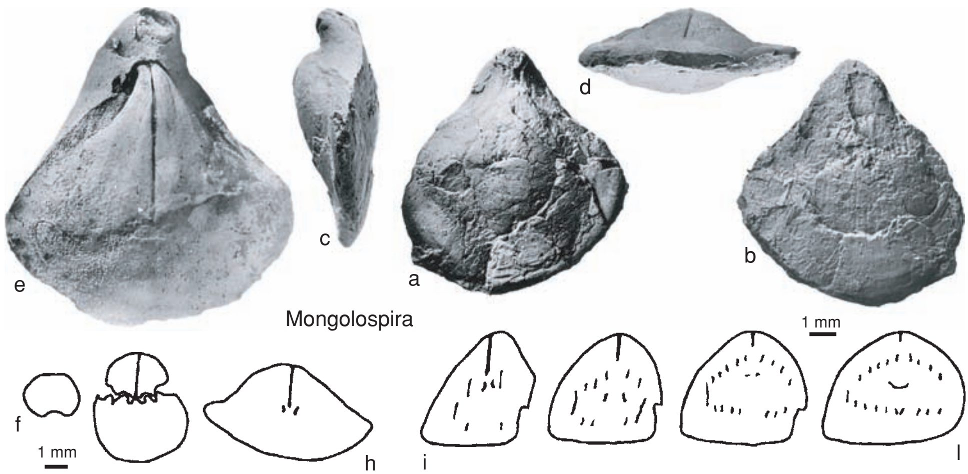

FIG. 1089. Mongolospiridae (p. 1596).

Superfamily RHYNCHOSPIRINOIDEA Schuchert, 1929

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 847, *ex* Rhynchospirinidae SCHUCHERT, 1929, p. 22]

Clear astrophic retziidines with moderately rostrate, ribbed shells (adult shells with more than 15 ribs); growth lines weak to strong and commonly widely spaced, may develop into short frills; hollow spines may be present; weak, alternate adult folding; ventral cardinal area (palintrope) reduced, apsacline; short dental plates supporting strong teeth may be present; hinge plate short or absent; jugum projecting backward as broad, short, roof-shaped process, jugal stem absent. *Silurian (lower Llandovery)–Upper Devonian (Frasnian).*

Family RHYNCHOSPIRINIDAE Schuchert, 1929

[Rhynchospirinidae SCHUCHERT, 1929, p. 22; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 847] [=Rhynchospirinae SCHUCHERT, 1894, p. 105]

Shell commonly large; ventral umbo strongly curved; deltidial plates commonly conjunct; short, moderately high dorsal median septum present, except in *Homoeospirella;* lateral branches of jugum vertical. [The reference to Article 39 of the Code made by BOUCOT, JOHNSON, & STATON (1965, p. 652) was based on the 1st Edition of the Code published in 1961. That article was modified in the 2nd Edition (1964) and had changed significantly by the 3rd Edition (1985) [see also 4th ed., 1999]. The new family-group name takes its own author and date, but does not take the priority of the name it has replaced, therefore the date 1894 should not be used. Similarly, the replacement generic name takes its own author and date but does not take the date of the name it replaced.] *Silurian (lower Llandovery)–Upper Devonian (Frasnian).*

Rhynchospirina SCHUCHERT & LEVENE, 1929b, p. 121, *nom. nov. pro Rhynchospira* HALL, 1859a, p. 29, *non* EHRENBERG, 1845 [**Waldheimia formosa* HALL, 1857a, p. 88; OD] [=*Rhyncospira* HALL, 1859b, p. 213, *nom. nud.*]. Externally similar to *Homoeospira* but deltidial plates conjunct and foramen in meso- to permesothyridid position; short dental plates may be present; incipient pedicle collar variably developed or absent; cardinal plate trapezoidal with flat cardinal flanges, projecting posteroventrally; hinge plate short (in comparison with long, flat outer hinge plates), thick, extending as transverse process between cardinal flanges and supported by short median septum extending anteriorly as low ridge. *Silurian (Wenlock)–Upper Devonian (Frasnian):* North America, Venezuela, Podolia, southwestern Urals, Mongolia, Gorno-Altay, western Qinling, Tibet, *Wenlock–Middle Devonian;* Gorno-Altay, *Upper Devonian.*——FIG. 1090,*1a–f.* **R. formosa* (HALL), Lochkovian, Lower Helderberg Group, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views,

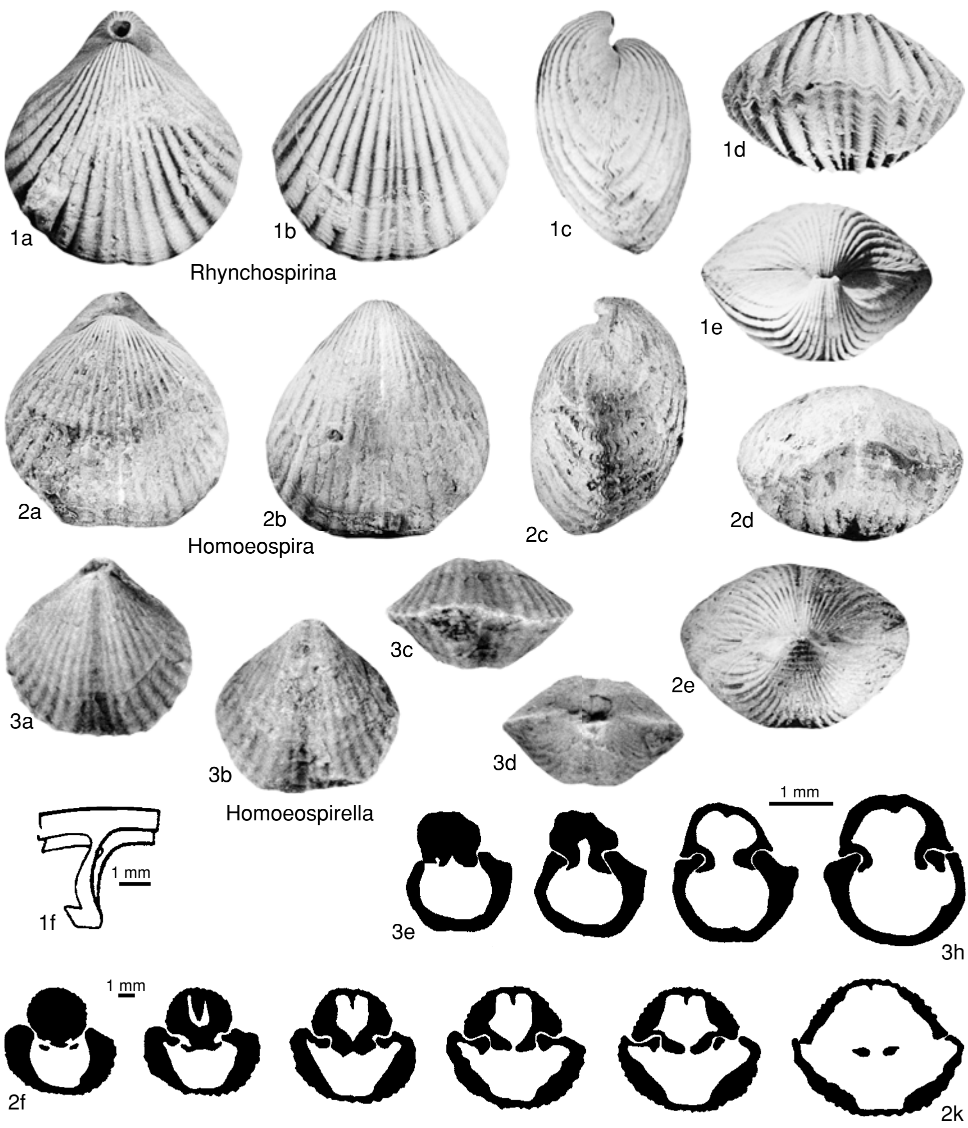

FIG. 1090. Rhynchospirinidae (p. 1597–1600).

AMNH 33399, Hall collection, ×2 (Alvarez & Brime, 2000); *f,* lateral view showing jugum (Hall & Clarke, 1893). [See also Fig. 1082.3, p. 1587, in introduction.]

Homoeospira HALL & CLARKE, 1893, p. 112 [**Rhynchospira evax* HALL, 1863a, p. 213; SD HALL & CLARKE, 1894, p. 986]. Subequally biconvex, elongate oval to subpentagonal costate shells, with or without poorly defined fold and sulcus, or shells may be faintly bisulcate; median costae narrower than costae on flanks; delthyrium may be open or restricted by disjunct or conjunct deltidial plates showing median fold; foramen in submeso- to permesothyridid position; dental plates absent; cardinal flanges poorly developed or absent, hinge plate extremely short, supported by stout median septum extending anteriorly as ridge; long, flat, anteriorly divergent outer hinge plates; jugum essentially as in *Trematospira.* [Fixation of type species is usually credited to SCHUCHERT (1897, p. 231), although the first unequivocal designation of the type species seems to be that of HALL & CLARKE (1894, p. 986). *Homeospira* is a frequent incorrect subsequent spelling of *Homoeospira.*] *Silurian (Wenlock)–Lower Devonian (Lochkovian):* North America, ?Argentina, United Kingdom, Gotland,

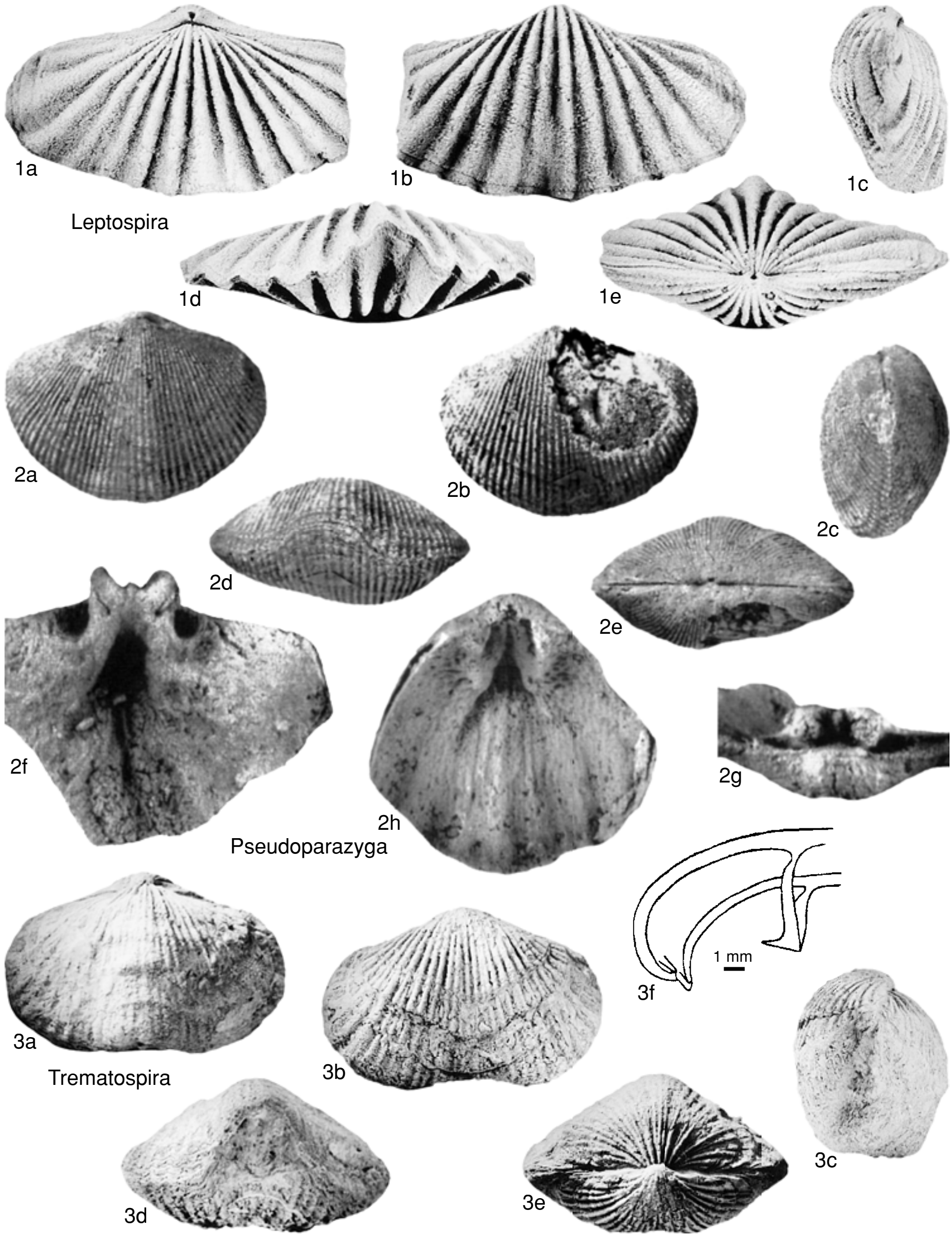

FIG. 1091. Rhynchospirinidae (p. 1600–1601).

Bohemia, Estonia, Ukraine, Vaigach, ?China, *Wenlock–Ludlow;* Poland, Belgium, *Lochkovian.* ——FIG. 1090,*2a–k.* **H. evax* (HALL); *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, upper Wenlock, Waldron, Indiana, USA, AMNH 36619, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f–k,* transverse serial sections 3.8, 4.0, 4.1, 4.6, 4.7, 5.0 mm from ventral umbo, Wenlock, Newson Station, Tennessee, USA, OU 6289 (adapted from Amsden, 1968). [See also Fig. 1082.1, p. 1587, in introduction.]

Homoeospirella AMSDEN, 1968, p. 90 [**H. costatula costatula;* OD]. Resembling *Homoeospira* in external and internal configuration but hinge plate and

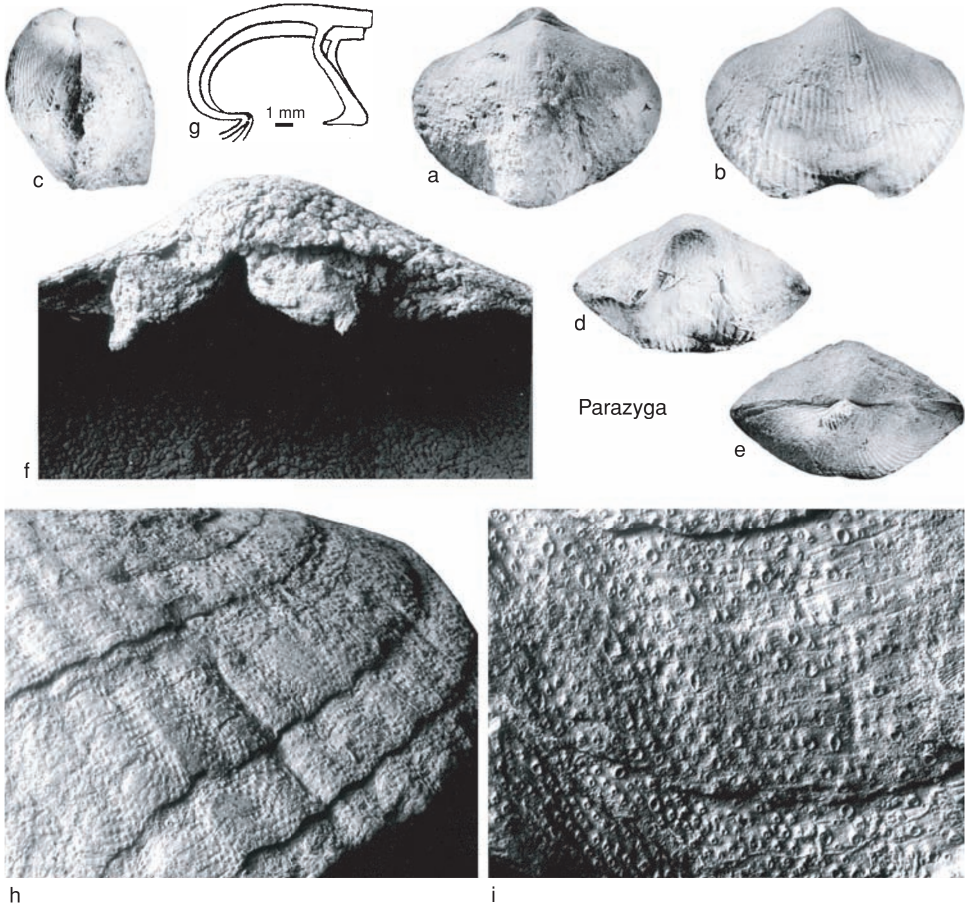

FIG. 1092. Parazygidae (p. 1601).

dorsal median septum absent; spiralia and jugum unknown. *Silurian (lower Llandovery–Wenlock), Lower Devonian (?Pragian):* Wales, *lower Llandovery;* USA (Oklahoma, Arkansas), *Wenlock;* USA (southern Oklahoma), *?Pragian.*——FIG. 1090,*3a–h.* **H. costatula costatula,* Wenlock, Oklahoma, USA; *a–d,* holotype, dorsal, ventral, anterior, and posterior views, OU 6401, ×1 (Amsden, 1968); *e–h,* transverse serial sections 0.4, 0.5, 0.7, 0.8 mm from ventral umbo, OU 8439 (adapted from Amsden, 1968).

Leptospira BOUCOT, JOHNSON, & STATON, 1964, p. 814 [**Trematospira costata* HALL, 1859a, p. 27; OD]. External shape as in *Trematospira,* but pauciplicate; cardinalia as in *Rhynchospirina;* spiralia and jugum unknown. [The name *Trematospira costata* is commonly attributed to HALL (1859b, p. 210) but this name was made available by HALL (1859a, p. 27) since in the latter paper the name was accompanied by an indication (Art. 12.2, ICZN, 1999).] *Lower Devonian (Lochkovian)–Upper Devonian (lower Frasnian):* central and northeastern USA.——FIG. 1091,*1a–e.* **L. costata* (HALL), Lochkovian, Lower Helderberg Group, New York, USA; lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 2461, Hall Collection, ×2 (Alvarez & Brime, 2000).

Pseudoparazyga JOHNSON, 1970b, p. 181 [**Trematospira cooperi* MERRIAM, 1940, p. 82; OD]. Similar to *Trematospira* with pedicle collar present and dental plates absent; spiralia and jugum unknown. *Lower Devonian:* USA (Nevada).——FIG. 1091,*2a–h.* **P. cooperi* (MERRIAM); *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 96372, ×1; *f–g,* interior and posterior views of dorsal valve, USNM 157161, ×3; *h,* ventral valve interior, USNM 157163, ×1.5 (Johnson, 1970b).

Trematospira HALL, 1859a, p. 27 [**Spirifer multistriatus* HALL, 1857a, p. 59; SD HALL & CLARKE, 1893, p. 126; validated ICZN Opinion 1900, 1998b, p. 133]. Subequally biconvex, transverse oval, costate shells, commonly with dorsal fold and ventral sulcus; costae subangular, approximately same width in medial regions as flanks, bifurcating anteriorly; deltidial plates conjunct; foramen in mesothyridid position; short dental plates may be present; greatly elevated cardinal plate deeply divided by median longitudinal groove, thick cardinal flanges projecting into pedicle cavity; small bilobate process may be developed between cardinal flanges, supported by short median septum extending anteriorly as low ridge, frequently obsolete; short, acute, and simple process extending horizontally backward from jugum. *Lower Devonian (Lochkovian–Pragian):* North America.——FIG. 1091,*3a–f.* **T. multistriata* (HALL), Lochkovian, Helderberg Group, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33375, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f,* lateral view of jugum (Hall & Clarke, 1893). [See also Fig. 1082.2, p. 1587, in introduction.]

Family PARAZYGIDAE Alvarez, Rong, & Boucot, 1998

[Parazygidae ALVAREZ, RONG, & BOUCOT, 1998, p. 847]

Shell medium with numerous, long, hollow spines anteriorly or anterolaterally directed; ventral umbo moderately curved; moderately long and thick, medially concave dental plates; pedicle collar; triangular outer hinge plates well developed, projecting posteriorly as thin, flat cardinal flanges; crural bases strongly divergent, inner hinge plates absent; dorsal myophragm present; lateral branches of jugum inclined anteriorly. *Middle Devonian (Givetian).*

Parazyga HALL & CLARKE, 1893, p. 127 [**Atrypa hirsuta* HALL, 1857a, p. 168; SD HALL & CLARKE, 1894, p. 995]. Subequally biconvex, transversely oval, subcircular or elongate shells with sparse lamellose growth lines; dorsal fold and ventral sulcus commonly present; costae simple, numerous, fine, rounded at same width across shell; conjunct deltidial plates present or absent; foramen in permesothyridid position; dental plates stout; jugum as in *Trematospira* but with lateral branches slightly inclined anteriorly. [Fixation of type species is usually credited to SCHUCHERT (1897, p. 301), but the first unequivocal designation of the type species is that of HALL and CLARKE (1894, p. 995).] *Middle Devonian (Givetian):* North America.——FIG. 1092*a–i.* **P. hirsuta* (HALL), Hamilton Group, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, I1714, Hall collection, Albany, ×1.5; *f,* cardinalia, I1716, Hall collection, ×12 (Alvarez & Brime, 2000); *g,* lateral view of jugum (Hall & Clarke, 1893); *h,* exterior with spines, USNM 497414, ×9.5; *i,* exterior with spines, USNM 497414, ×19 (Alvarez, 1999b).

KONINCKINIDINA

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Since the koninckinidines first came to the notice of paleontologists in the mid-nineteenth century, they have been a source of controversy, particularly with regard to their systematic position. Because of their highly distinctive concavoconvex outline and typically strophic shell, koninckinidines have in the past been regarded by various authors as somewhat unusual strophomenides (COWEN & RUDWICK, 1966; DAGYS, 1973), whereas others have regarded them as spiriferides *sensu lato* (DAVIDSON, 1884; BOUCOT, JOHNSON, & STATON, 1965; WILLIAMS, 1968; BRUNTON & MACKINNON, 1972; HARPER & others, 1993). MUIR-WOOD (1965) included the Early Jurassic superfamily Cadomelloidea within the Chonetidina, but the subsequent discovery by COWEN and RUDWICK (1966) of a spiral brachidium within *Cadomella davidsoni,* which was included in the genus *Cadomella* by MUIR-WOOD (1965), was considered sufficient grounds for synonymizing the Cadomelloidea with the Koninckinoidea. The type species of *Cadomella, C. moorei* (DAVIDSON), however, is now considered to be morphologically and taxonomically quite distinct from *C. davidsoni* (which is herein placed in

Koninckodonta), thus prompting the dissociation of the cadomelloids from the koninckinidines. In this revision, the Cadomelloidea are placed in *incerta sedis* (see volume 5 of *Treatise* Part H, Brachiopoda, Revised, in preparation).

Suborder KONINCKINIDINA Harper, 1993

[Koninckinidina HARPER in HARPER & others, 1993, p. 450]

Smooth, strophic, concavoconvex shells with well-developed interareas in both valves; dental plates absent; spiralia directed ventrolaterally; jugum with accessory lamellae continuing between primary volutions of spiralia to their ends; shell impunctate; tertiary layer present. *Middle Triassic–Lower Jurassic.*

Superfamily KONINCKINOIDEA Davidson, 1853

[*nom. correct.* HARPER in HARPER & others, 1993, p. 450, *pro* Koninckinacea BOUCOT, JOHNSON, & STATON, 1964, p. 820, *nom. transl. ex* Koninckinidae DAVIDSON, 1853b, p. 92]

Quadrate to subtriangular, strongly concavoconvex, smooth shells with very narrow mantle cavity. Pedicle foramen generally very small and permesothyrid to epithyrid. Beak ridges well defined. Hinge line either wide with low, well-developed interareas, or narrow with interareas replaced largely by palintropes in both valves; triangular delthyrium occupied by smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. Cardinalia consisting of posteromedian myophore bounded by a pair of robust inner socket ridges from near distal extremities of which extend a pair of slender, anteroventrally directed, pronglike crura. Brachidium consisting of ventrolaterally directed, paired spiral lamellae; broader, dorsal, primary spiral lamellae diverging from crura at sharp angle and uniting medially in a jugum; narrower, ventral, accessory lamellae originating on jugum and intercoiled with dorsal, primary spiral lamellae to their ends. Secondary layer fibers large and rhomboidal in cross section; thick, prismatic, tertiary shell layer present; impunctate. *Middle Triassic–Lower Jurassic.*

Family KONINCKINIDAE Davidson, 1853

[Koninckinidae DAVIDSON, 1853b, p. 92]

Characters as for superfamily. *Middle Triassic–Lower Jurassic.*

Koninckina SUESS in DAVIDSON, 1853b, p. 92 [**Producta leonhardi* WISSMANN, 1841, p. 68; OD] [=*Koninckia* SUESS in WOODWARD, 1854, p. 231, *nom. null.*]. Smooth, strongly concavoconvex shells, variably subquadrate in outline with low ventral umbo that is strongly incurved in adults; hinge line straight and well developed; posterolateral shell margins commonly alate; very small epithyrid pedicle foramen and very low interareas commonly obscured by excessive curvature in umbones in adults. [Location of type specimen unknown.] *Upper Triassic:* Italy (Dolomites), Dinaric Alps, Carpathians, Caucasus, Pamirs, Laos, China, Indonesia.——FIG. 1093,*1a–c*. **K. leonhardi* (WISSMANN), Dolomites; dorsal, lateral, anterior views, ×5 (new).——FIG. 1093,*1d*. *K. leopoldi austriae* BITTNER; dorsal interior showing spiral brachidium, ×2 (Bittner, 1890).

Amphiclina LAUBE, 1866, p. 28 [**Producta dubia* MÜNSTER, 1841, p. 68; OD]. Subpentagonal to subtriangular in outline with prominent, acuminate umbo; small permesothyrid pedicle foramen; narrow, triangular interareas located medially between prominent dorsal and ventral palintropes; smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. [Location of type specimen unknown.] *Upper Triassic:* Dolomites, Carpathians, Dinaric Alps, Balkans, Caucasus, Pamirs, Himalayas, Primor'ye region.——FIG. 1093,*2a–d*. *A. amoena* BITTNER, Dolomites, Italy; *a,* dorsal view, ×2.4 (Brunton & MacKinnon, 1972); *b–d,* ventral, lateral, anterior view, ×1 (Bittner, 1890).

Amphiclinodonta BITTNER, 1888, p. 288 [**A. liasina;* OD]. Smooth, gently concavoconvex shells, outline subtriangular, with strongly acuminate ventral umbo and very narrow hinge line; very small permesothyrid pedicle foramen; very small, narrow, triangular interareas; submarginal tubercles well developed on valve interiors. *Upper Triassic–Lower Jurassic:* Dolomites, Carpathians, Dinaric Alps, Austria, Pamirs, *Upper Triassic;* Dolomites, *Lower Jurassic.* ——FIG. 1093,*3a–c*. **A. liasina,* Liassic, Austria; dorsal, lateral, anterior views, ×2 (Bittner, 1888).——FIG. 1093,*3d–e*. *A. zugmayeri* BITTNER, Upper Triassic, Austria; ventral valve interior, oblique view of ventral valve interior, ×2 (Bittner, 1890).

Carinokoninckina JIN & FANG, 1977, p. 59 [**Koninckina expansa* BITTNER, 1890, p. 132; OD] [=*Ctenokoninckina* XU, 1978, p. 283]. Externally similar to *Koninckina* but ventral interior bearing

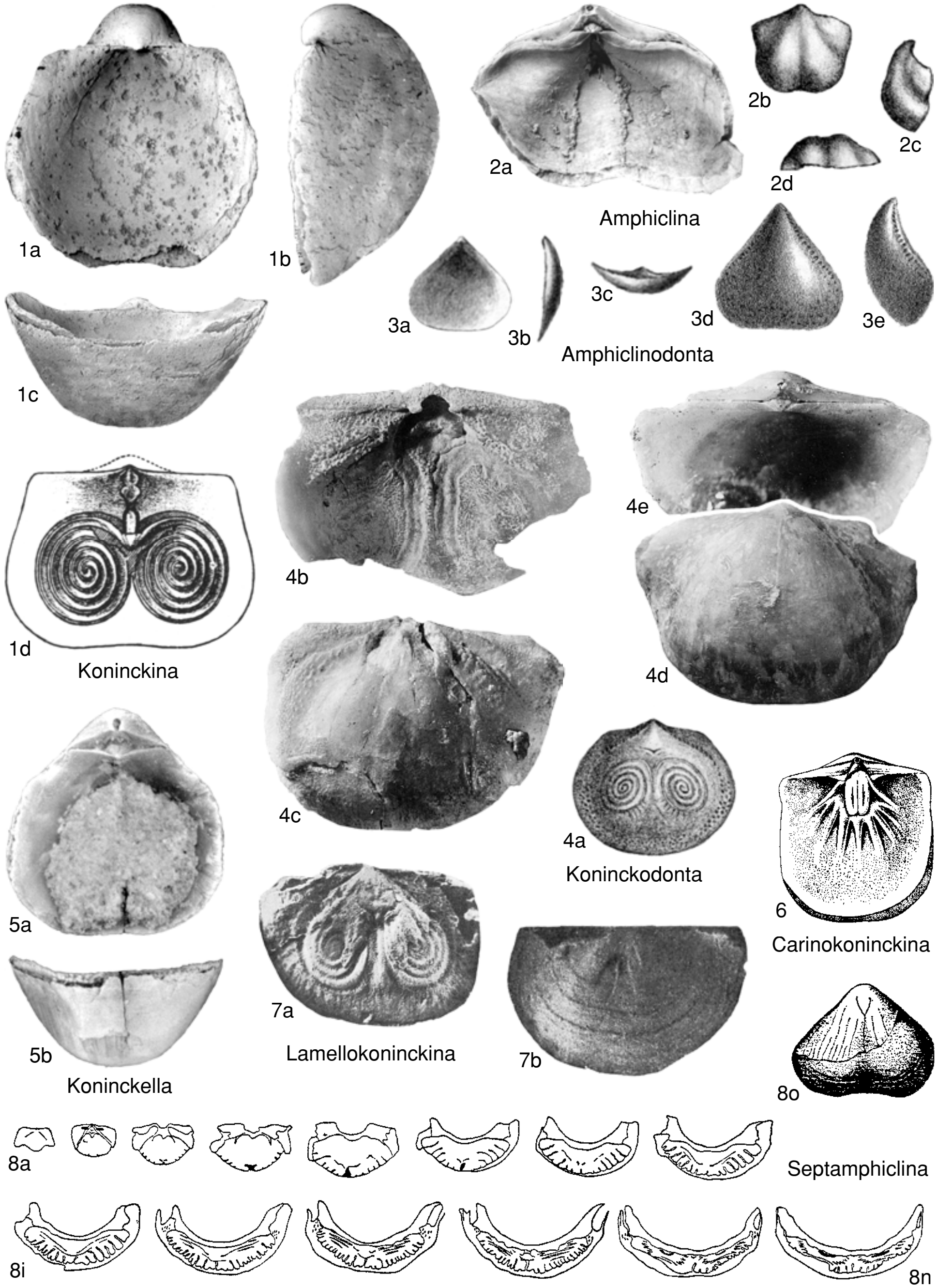

FIG. 1093. Koninckinidae (p. 1602–1604).

many (possibly pallial) ridges extending radially from ventral muscle scars. [May be synonymous with *Koninckina.* Location of type specimen unknown.] *Upper Triassic:* China.——FIG. 1093,*6. C. jindingensis* JIN & FANG; ventral valve interior, ×3 (Jin & Fang, 1977).

Koninckella MUNIER-CHALMAS, 1880, p. 280 [**Leptaena liasiana* BOUCHARD in DAVIDSON &

MORRIS, 1847, p. 250; OD]. Similar to *Koninckina* but rounded subtriangular in outline and with less curvature of ventral umbo; hinge line generally less than half maximum width; narrow, triangular interareas clearly visible in adults; small permesothyrid pedicle foramen; smooth, convex symphytium arching over small, commonly trilobed, posteromedian callosity in dorsal valve. [Location of type specimen unknown.] *Middle Triassic–Lower Jurassic:* France, Austria, Italy (Dolomites).——FIG. 1093,*5a–b*. *K. triadica* BITTNER, Upper Triassic, Dolomites; dorsal, anterior view, ×8.5 (new).

Koninckodonta BITTNER, 1893, p. 137 [**K. fuggeri;* OD]. Concavoconvex, smooth, transversely subquadrate with rounded lateral margins, hinge line generally greater than half maximum width, ventral interarea low and wide, small permesothyrid pedicle foramen; smooth, convex symphytium; valve interiors strongly tuberculate around valve margins. *Lower Jurassic:* Austria, France.——FIG. 1093,*4a*. **K. fuggeri;* dorsal interior, ×2 (adapted from Bittner, 1893).——FIG. 1093,*4b–e*. *K. davidsoni* (EUDES-DESLONGCHAMPS); *b–c,* ventral, dorsal interior; *d–e,* ventral, dorsal exterior, ×2 (Davidson & Morris, 1847).

Lamellokoninckina JIN & FANG, 1977, p. 57 [**L. heqingensis;* OD]. Similar in external outline to *Koninckina* but bearing concentric growth lamellae, which are adorned with very fine radial striae. [May be synonymous with *Koninckina*.] *Upper Triassic:* China.——FIG. 1093,*7a–b*. **L. heqingensis,* Yunnan; dorsal valve interior, dorsal exterior showing concentric growth lamellae, ×4 (Jin & Fang, 1977).

Septamphiclina JIN & FANG, 1977, p. 57 [**S. qinhaiensis;* OD]. Similar to *Carinokoninckina* but submarginal tubercles well developed on valve interiors. [May be synonymous with *Amphiclinodonta*.] *Upper Triassic:* China.——FIG. 1093,*8a–o*. **S. qinhaiensis,* Yunnan; *a–n,* transverse serial sections, ×3 (adapted from Jin & Fang, 1977); *o,* part ventral exterior, part ventral internal mold showing multisepta (possibly pallial markings), ×3 (Jin & Fang, 1977).

UNCERTAIN

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The three spire-bearing families Dayiidae, Anoplothecidae, and Kayseriidae, and the Leptocoeliidae, have commonly been classified in the superfamily Dayioidea (=Dayiacea) alongside the Atrypoidea (e.g., SCHUCHERT, 1896; RZHONSNITSKAIA, 1960a; BOUCOT, JOHNSON, & STATON, 1964, 1965; JOHNSON, 1970b). Based on the orientation of the spiral cones and the type of jugum, COPPER (COPPER, 1973b, 1973c, 1986a; COPPER & GOURVENNEC, 1996) assigned the *Coelospira* (*Bifida* and *Kayseria* included) and *Dayia* groups to the Athyridida and assigned *Cyclospira* to the lissatrypids. Later, CAMPBELL and CHATTERTON (1979) considered that the Dayioidea, as defined by BOUCOT, JOHNSON, and STATON (1965), were not a natural group. They separated the ribbed from the smooth dayioids and placed *Kayseria* in the family Kayseriidae. More recently HARPER and others (1993) considered the spiriferids and atrypids as different orders, placing the athyrids, retziids, dayiids, koninckinids, and spiriferidinids, all with subordinal rank, into the order Spiriferida. Other authors (e.g., DAGYS, 1996; ALVAREZ & CARLSON, 1998; ALVAREZ, RONG, & BOUCOT, 1998) did not include the dayioids (*sensu* BOUCOT, JOHNSON, & STATON, 1965) within the athyridides or considered their inclusion debatable (GRUNT, 1989).

The Leptocoeliidae, despite having some similarities with the Anoplothecidae, were considered as rhynchonelloids by COCKS (1978) because of the absence of evidence for a spiralial apparatus. This was accepted by HARPER and others (1993) and SAVAGE (1996); see also Leptocoeliidae (p. 1081 herein).

Based on the presence of ventrolaterally directed spiralia and a simple or complex jugum, the Dayiidae, Anoplothecidae, Kayseriidae, and Uncitidae (placed as uncertain in the previous *Treatise* (MOORE, 1965, p. 649) are here excluded from the Atrypida (COPPER, 1973b, 1973c, 1986a). ALVAREZ and CARLSON (1998) and ALVAREZ, RONG, and BOUCOT (1998) considered their accommodation within the Athyridida *sensu lato* as problematic. The principal reasons for uncertainty over their classification are their spiralial characteristics, including umbonal blades curving posterolaterally almost parallel with the commissural plane; an acute jugum resembling that of most meristelloids but placed below the spiral cones near the dorsal valve interior; grooved spiralial whorls or with double spiralial lamellae arising from the outer side of grooved whorls, or with accessory lamellae that intercalate with spiralial loops up to the apex, resembling that of some athyrididines and retziidines; the type of articulation with nearly vertical short, stubby, platelike teeth fixed directly to sides of valve; the unusual cardinalia; and the distinctive, long, narrow, strongly divergent ventral diductor scars, present in the so-called smooth dayioids. COPPER (herein) interprets both the Dayiidae (because of shell shape, dentition, and laterally directed spiralia), and the Anoplothecidae and Kayseriidae (because of similarities in their complex jugal structures, and possession of grooved or double spiralial whorls), as being Athyridida. These features are unknown in any Spiriferida.

Suborder UNCERTAIN
Superfamily DAYIOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 449, *pro* Dayiacea RZHONSNITSKAIA, 1960a, p. 264, *nom. transl. ex* Dayiinae SCHUCHERT, 1913a, p. 409, *nom. correct. pro* Dayinae WAAGEN, 1883, p. 486; *emend.,* ALVAREZ & COPPER, herein]

Smooth, with or without fine growth lines, ventribiconvex to planoconvex or weakly concavoconvex, impunctate shells; distal ends of crura strongly divergent laterally; spiralia ventrolaterally directed; jugum simple, medially to anteriorly located. *Silurian (?Llandovery, Wenlock–Přídolí), Lower Devonian (?Lochkovian).*

Family DAYIIDAE Waagen, 1883

[*nom. transl.* RZHONSNITSKAIA, 1960a, p. 264, *ex* Dayiinae SCHUCHERT, 1913a, p. 409, *nom. correct. pro* Dayinae WAAGEN, 1883, p. 486; *emend.,* ALVAREZ & COPPER, herein] [=Protozeugidae TWENHOFEL, 1914, p. 29]

Characters as for superfamily. *Silurian (?Llandovery, Wenlock–Přídolí), Lower Devonian (?Lochkovian).*

Dayia DAVIDSON, 1881c, p. 291 [**Terebratula navicula* J. de C. SOWERBY, 1839, p. 611; OD] [=*Daya* KOKEN, 1896, p. 240, incorrect subsequent spelling (Art. 33.3, ICZN, 1999)]. Small, longitudinally ovate to subcircular or subpentagonal, ventri- to planoconvex, relatively thick shell, mainly posterior of ventral valve; small, hypercline beak; commissure weakly sulcate-rectimarginate; teeth small, short, solid, dental plates absent; narrow groove for small ventral adductors; ventral diductor scars wide, diverging anteriorly; dorsal valve with long, low septum to near midshell, flabellate adductor scars; spiralia with 3 to 7 whorls; jugum angular, situated anteriorly, may project posteriorly as a short stem. Distinct from *Protozeuga* in relatively flat dorsal valve, more complex spiralium. *Silurian (Ludlow–Přídolí), Lower Devonian (?Lochkovian):* Ireland, United Kingdom, Baltic Basin, Ukraine, ?western slopes Urals.——FIG. 1094,*2a–u.* **D. navicula* (J. de C. SOWERBY), Ludlow, England; *a–c,* neotype, dorsal, anterior, and lateral views, Herefordshire, GSM 103291, ×2; *d–o,* transverse serial sections, 1.18, 1.95, 2.3, 2.51, 2.93, 3.98, 5.0, 5.91, 6.47, 7.03, 7.59, 7.8 mm from ventral umbo, distance from ventral umbo to first section approximate, Herefordshire, ×3 (Tucker, 1968); *p–q,* ventral and lateral views showing reconstructed spiralium and jugum, ×3 (new); *r–t,* dorsal, anterior, lateral views, Shropshire, ×2.3; *u,* view of specimen with most of its dorsal valve broken to show jugum and spiralium, Shropshire, ×3 (Glass in Davidson, 1882).

Protozeuga TWENHOFEL in SAVAGE, 1913a, p. 51 [**Waldheimia ? mawei* DAVIDSON, 1881b, p. 145; OD]. Very small shell (less than 3 to 4 mm wide), weakly ventribiconvex to planoconvex; sulcate commissure with small fold in sulcus to produce plicosulcate condition; teeth minute, solid; crura medial to slightly laterally directed; spiralia of fewer than 2 whorls; jugum simple, medial, apex slightly posteriorly directed. Distinguished from derived *Dayia* by its very small shell, weakly plicosulcate commissure, small spiralia with few whorls, smaller jugum. *Silurian (?Llandovery, Wenlock):* United Kingdom, Baltic Basin.——FIG. 1094,*1a–g.* **P. mawei* (DAVIDSON), Wenlock, Shropshire, United Kingdom; *a–d,* dorsal, ventral, lateral, and anterior views; *e,* anterior view showing plicosulcate anterior commissure, ×7.5 (Davidson, 1881b); *f–g,* ventral and lateral views of reconstructed spiralium and jugum, ×3 (new).

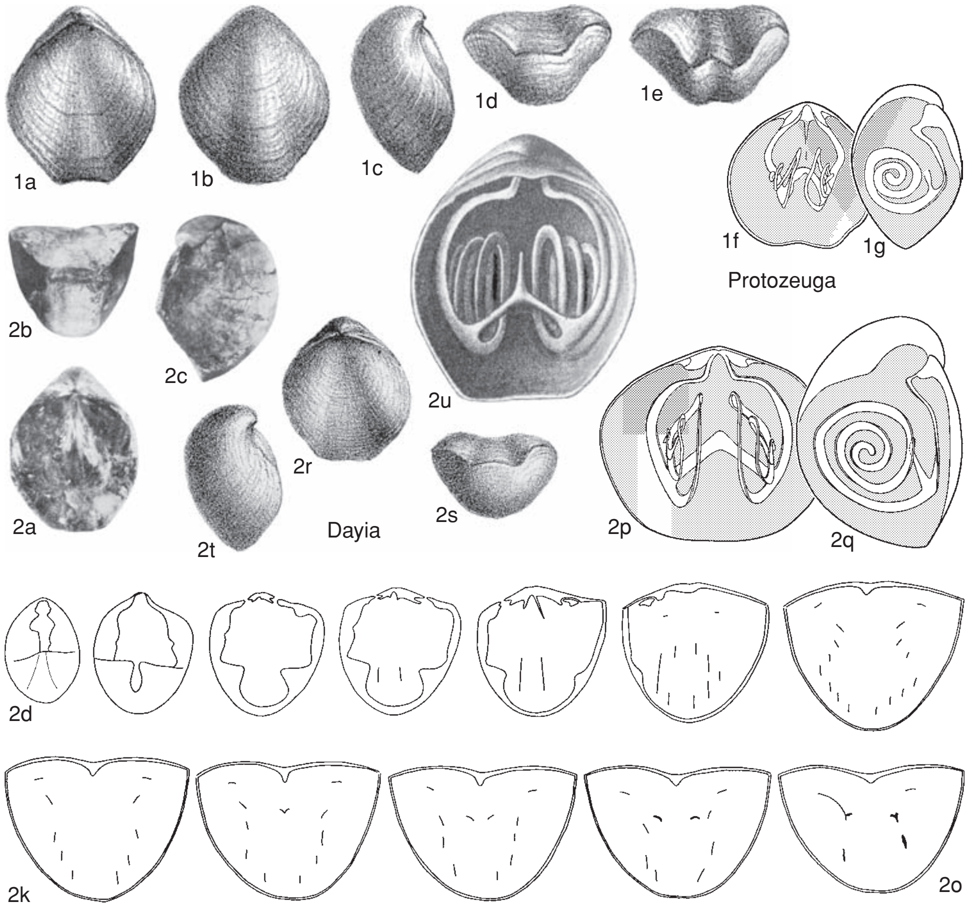

FIG. 1094. Dayiidae (p. 1605).

Superfamily ANOPLOTHECOIDEA Schuchert, 1894

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 835, *ex* Anoplothecinae SCHUCHERT, 1894b, p. 103; *emend.*, ALVAREZ & COPPER, herein]

Minute to medium, commonly ventribiconvex to concavoconvex, elongate to transversely oval shells, slightly rostrate, ventral umbo commonly moderate to strongly curved; narrow and astrophic hinge line; ventral cardinal area reduced, foramen small or absent, delthyrium open; surface with ribs or low, rounded plications commonly crossed by numerous, fine, regularly developed growth lines that could be lamellose; anterior commissure rectimarginate, unisulcate or biplicate; pedicle support absent; ventral valve commonly with thick shell, teeth short, solid, nearly vertical, dental plates absent; long median septum commonly present in both valves; cardinal process variably developed, inner socket ridges slightly overhanging sockets; umbonal blades of spiralia sharply bent from tips of crura in lateral (*Coelospira*) or posterolateral direction (*Kayseria*); spiral cones ventral to ventrolaterally directed; elaborate jugum joining primary lamellae of each cone, commonly sitting over median dorsal septum; with jugal stem that may be thick (*Coelospira*), may bifurcate distally into 2 short jugal arms (*Bifida*), or that may extend as long accessory jugal lamellae, continuing intercoiled with primary volutions of spiralia to ends (*Kayseria*); in some anoplothecids with grooved spiralial whorls, accessory lamellae derived from outer, ventral side of spiral whorl; frequently, the spiralia are spinose on their outer edges with jugum on its anterior edge; shell impunctate. *Silurian (?Wenlock, lower Ludlow)–Middle Devonian (Givetian).*

Family ANOPLOTHECIDAE Schuchert, 1894

[*nom. transl.* BOUCOT, JOHNSON, & STATON, 1964, p. 807, *ex* Anoplothecinae SCHUCHERT, 1894b, p. 103; *emend.,* ALVAREZ & COPPER, herein] [=Coelospiridae HALL & CLARKE, 1894, p. 840]

Ventribiconvex to concavoconvex shells; frequently with general naviculate aspect; lamellose growth lines may be numerous and regularly developed (e.g., *Anoplotheca, Bifida*) or only anteriorly developed (e.g., *Coelospira, Navispira*); spiral whorls grooved, jugal blade may develop from dorsal base of jugum and be directed ventroposteriorly toward jugal arms that may be short (e.g., *Bifida*) or long and fused with main spiralial whorls to make a groove. *Silurian (?Wenlock, lower Ludlow)–Middle Devonian (Givetian).*

Subfamily ANOPLOTHECINAE Schuchert, 1894

[Anoplothecinae SCHUCHERT, 1894b, p. 103]

Minute to medium, smooth or with ribs developed primarily toward umbones; growth lamellae commonly with fibrose or spinelike extensions; internally median septa well developed in both valves, often dividing posterior half of shell into 2 compartments; jugal arms short; laterally to ventrally directed spiralia of less than 7 whorls; spiralial whorls grooved. *Silurian (Přídolí)–Middle Devonian (Givetian).*

Anoplotheca SANDBERGER, 1855, p. 5 [**Terebratula venusta* SCHNUR, 1853, p. 180; OD; =*Productus lamellosus* SANDBERGER & SANDBERGER, 1856 in 1849–1856, p. 351] [=*Hoplotheca* BIGSBY, 1878, p. 36, obj.]. Medium, planoconvex to weakly ventribiconvex shells, with lenticular outline; ribs clearly present apically, shell commonly smooth anteriorly; about midventral valve a median rib starts, reaching anterior commissure; ventral valve with long thin septum dividing muscle field; dorsal muscle field strongly impressed; cardinal process prominent, bilobed; spiralia ventrally slightly laterally directed, 6 to 8 whorls; structure of jugum unknown. Differs from *Bifida* in larger size, less carinate shell, with weaker ribs. [This genus requires revision.] *Lower Devonian (Emsian):* Germany (Eifel region), France.——FIG. 1095*a–c.* **A. venusta* (SCHNUR), Eifel; *a–b,* dorsal and ventral views, ×1.5 (Hall & Clarke, 1895); *c,* mold of interior of ventral valve, USNM 140384, ×2 (Boucot, Johnson, & Staton, 1964).——FIG. 1095*d–e. A.* sp., upper Emsian, Germany; dorsal and ventral views of internal mold, USNM 140383, ×3 (Boucot, Johnson, & Staton, 1964).

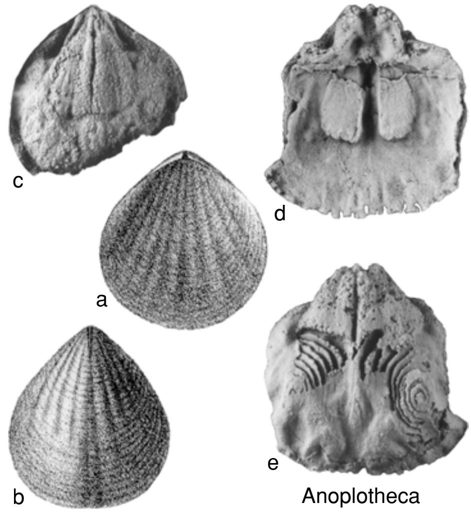

FIG. 1095. Anoplothecidae (p. 1607).

Bifida DAVIDSON, 1882, p. 27 [**Terebratula lepida* D'ARCHIAC & DE VERNEUIL, 1842, p. 368; OD] [=*Dahlispira* HAVLÍČEK, 1998, p. 119 (type, *Anoplotheca (Bifida) dahlia* HAVLÍČEK, 1956, p. 590)]. Small ventribiconvex shells, commonly with carinate ventral midrib pair; concentric growth lamellae, distinct, rhythmic, commonly developed as bushy, spinose external layer covering shell; commissure rectimarginate or weakly sulcate; short, small, solid teeth with inner notch for dorsal socket plates; strong ventral median septum; thick cardinal plate with weak cardinal process; crura medial, with high angles at junction with spiralia; spiralia grooved, with 3 to 7 whorls; jugal saddle resting on high dorsal septum, slightly projected as abortive accessory lamellae. Similarly grooved spiralia as in *Navispira* and *Coelospira,* but differing externally in small shell, very enlarged ventral midrib pair; differs from *Anoplotheca* mainly in smaller size, distinct concentric growth lamellae, and bushy spinose fibers. *Lower Devonian (Emsian)–Middle Devonian (lower Givetian):* Eurasia, North America.——FIG. 1096,*1a–p.* **B. lepida* (D'ARCHIAC & DE VERNEUIL);

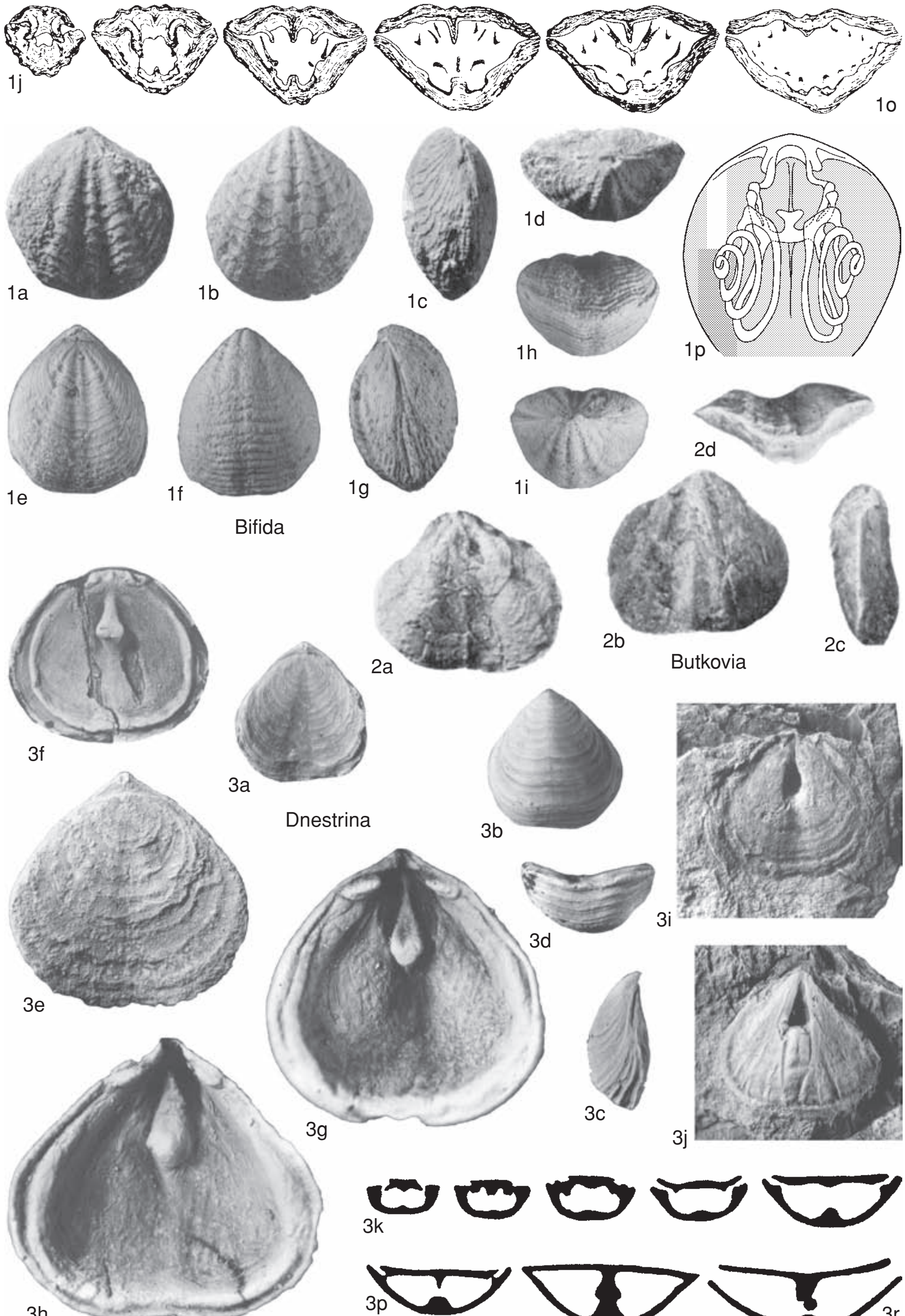

FIG. 1096. Anoplothecidae (p. 1607–1609).

a–d, dorsal, ventral, lateral, and posterior views, BMNH BB 58557, ×4 (Copper, 1973b); *e–i,* dorsal, ventral, lateral, anterior, and posterior views, USNM 140378, ×4 (Boucot, Johnson, & Staton, 1964); *j–o,* transverse serial sections, 0.9, 1.5, 1.9, 3.1, 3.4, 4.2 mm from ventral umbo, BMNH BB 58564, ×4 (adapted from Copper, 1973b); *p,* ventral view of dorsal interior showing reconstructed spiralium and jugum, BMNH BB 58564, ×5 (Copper, 1973b).

?Butkovia BARANOV, 1987, p. 113 [**B. eximia;* OD]. Very small, ventribiconvex to planoconvex shells; smooth except for strong ventral midrib pair and small rib in sulcus; thick shelled; small, protruding umbo, possibly lacking deltidial plates; sulcate to plicosulcate commissure; cardinalium massive, high dorsal septum strong; brachidia unknown. Similar to *Bifida, Anoplotheca,* and *Coelospirina* but lateral ribs and concentric ornamentation weakly developed or absent. [Interior poorly known; spiralia and jugum unknown; requires revision.] *Lower Devonian (Pragian–Emsian):* northeastern Siberia (Chilmaga Range, Kolyma).——FIG. 1096,*2a–d.* **B. eximia;* holotype, dorsal, ventral, lateral, and anterior views, YaTGU 120/40, ×5 (Baranov, 1987).

?Dnestrina NIKIFOROVA & MODZALEVSKAYA, 1968, p. 206 [**D. gutta;* OD]. Minute to small, concavo-convex to planoconvex, longitudinally ovate to subpentagonal shells covered by numerous, lamellose growth lines; ribs absent; dorsal sulcus shallow, originating in umbo, ventral median fold high but poorly defined laterally, anterior commissure rectimarginate to slightly sulcate; ventral interior relatively short, prominent, bulbous, widening anteriorly, ventral median septum dividing small muscle fields, pressed against similar median septum on dorsal valve that thickens medially, bifurcating slightly and sharply reduced anteriorly; cardinal process small; marginal borders present; spiralium and jugum unknown. Differs from *Anoplotheca* and *Bifida* in lacking ribs, and in prominent concentric growth lamellae. [Needs revision. When erected, this genus was included in the Atrypidae.] *upper Silurian (Přídolí):* Podolia, Moldavia, western Europe.——FIG. 1096,*3a–r.* **D. gutta,* Moldavia; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, CNIGR 1/9543, ×3 (Nikiforova & Modzalevskaya, 1968; photographs courtesy of T. L. Modzalevskaya); *e,* dorsal view showing pedicle foramen and lamellose growth lines, ×5.2 (new; photographs courtesy of T. L. Modzalevskaya); *f,* dorsal interior, ×4; *g,* ventral interior, ×6; *h,* ventral interior showing median septum and well-developed marginal borders, ×6; *i–j,* dorsal and ventral internal molds, ×4 (Nikiforova & Modzalevskaya, 1968; photographs courtesy of T. L. Modzalevskaya); *k–r,* transverse serial sections, 1.5, 1.7, 1.8, 2.1, 2.4, 2.7, 3.1, 4.6 mm from ventral umbo, distance from ventral umbo to first section approximate, ×5 (adapted from Nikiforova & Modzalevskaya, 1968).

Subfamily COELOSPIRINAE Hall & Clarke, 1895

[*nom. transl.* AMOS & BOUCOT, 1963, p. 441, *ex* Coelospiridae HALL & CLARKE, 1894, p. 840]

Coarsely ribbed, small shells lacking fibrous shell layer, distinct concentric growth lamellae; ventral midrib pair commonly clearly defined; weak ventral and dorsal median septa; complex jugum as in Anoplothecinae, but accessory lamellae fused into single spiralium with grooved spiral whorls. *Silurian (?Wenlock, lower Ludlow)–Middle Devonian (Givetian).*

Coelospira HALL, 1863b, p. 60 [**Leptocoelia concava* HALL, 1857a, p. 107; OD]. Small, ventribiconvex to planoconvex, longitudinally to transversely ovate shells with evenly convex profile; surface with numerous, relatively fine ribs, commonly median ventral ribs tending to be smaller than laterals; poorly developed growth lines commonly occurring at irregular intervals, few growth lamellae may develop anteriorly; anterior commissure rectimarginate to weakly sulcate; ventral diductor scars long, large, elliptical, broadening anteriorly, commonly divided by thin, bladelike median septum; platform elevating ventral muscle attachment area poorly developed or absent, cavity anterior to adductor scars much shallower than in *Navispira;* short, solid teeth, dental sockets well developed, inner socket ridges broadly divergent, may extend anterolaterally parallel to internal dorsal valve margin; cardinal process commonly bilobate to trilobate; a broad and posteriorly thick crest commonly dividing small, posterior, adductor scars, quickly narrowing anteriorly, separating broad triangular anterior adductor scars. Differs from *Navispira* in lack of prominent, carinate ventral midrib pair. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* North America, Venezuela, Argentina, Turkey, northern China, Australia.——FIG. 1097,*4a–d.* **C. concava* (HALL), Lochkovian, Albany County, New York, USA; *a,* lectotype, ventral view, AMNH 28456; *b,* ventral view, AMNH 28461; *c,* dorsal view, AMNH 28457; *d,* ventral valve internal mold, Gaspé, Lochkovian, USNM 156281, ×3 (Boucot & Johnson, 1967b).

?Coelospirella SU, 1976, p. 202 [**C. dongbeiensis;* OD]. Small, plano- to concavoconvex shells, resembling *Navispira* but with weak ribs that do not bifurcate; internally short dental plates were reported, but additional information (provided by SU Yangzheng, 2001) confirms that dental plates are absent and that spiralium and jugum are as in *Coelospira.* Said to differ from *Coelospira* by lacking bifurcating ribs, from *Bifida* in convexity, from *Anoplotheca* by its muscle area and vascular marking, from *Coelospirina* by convexity, type of cardinal process, and nature of ventral muscle field. [Poorly represented

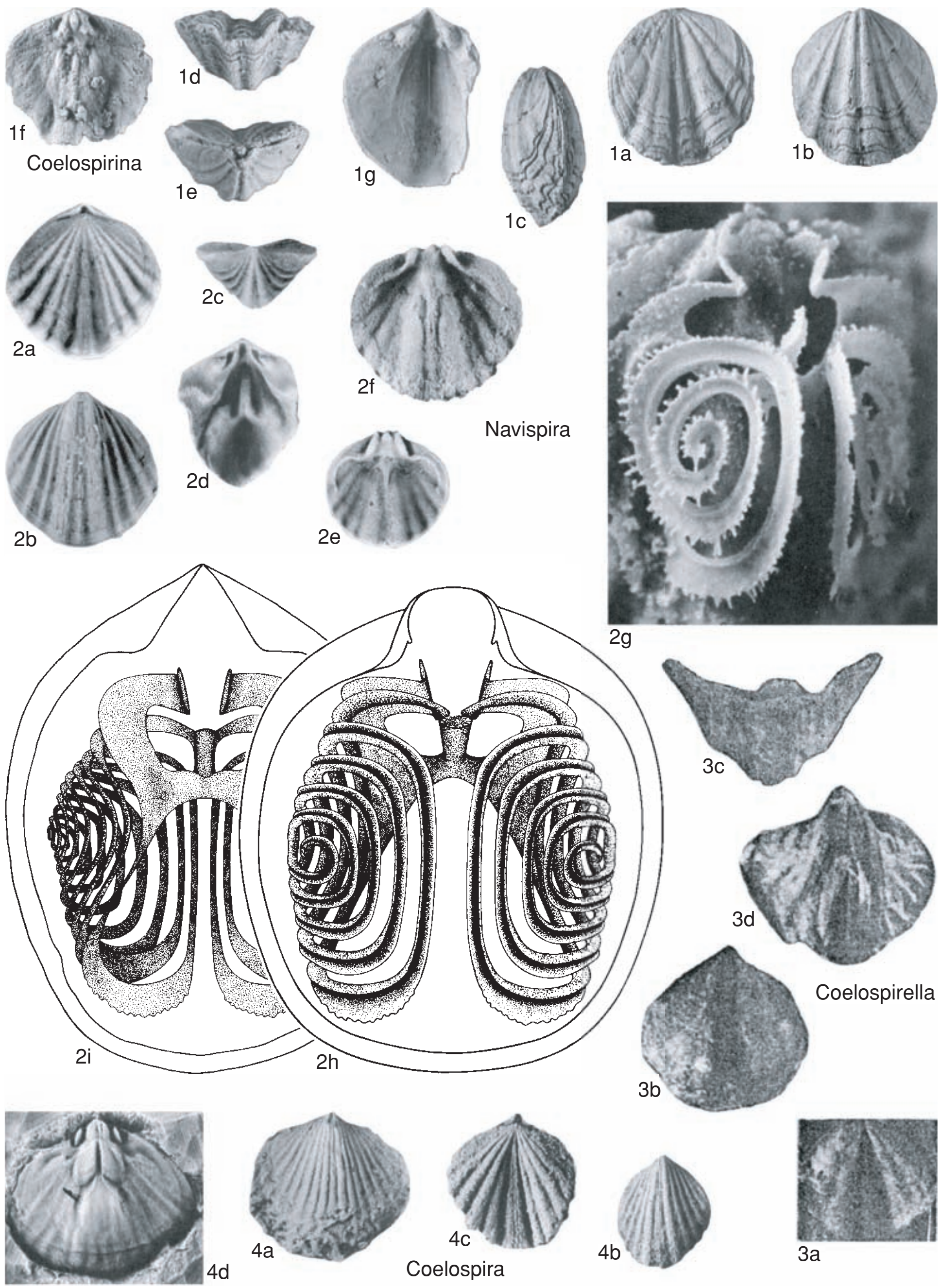

FIG. 1097. Anoplothecidae (p. 1609–1612).

and known, requires revision.] *upper Silurian (Přídolí)–Lower Devonian (Emsian):* Inner Mongolia, northern China, Kazakhstan, eastern Russia.——FIG. 1097,*3a–d*. **C. dongbeiensis,* Emsian, Inner Mongolia, northern China; *a,* dorsal view, NS12014; *b,* ventral view, NS12003; *c,* posterior view, NS12303; *d,* internal mold of ventral valve, NS12006, ×3 (Su, 1976).

Coelospirina HAVLÍČEK, 1956, p. 586 [**C. modica;* OD]. Shells resembling *Coelospira* with few irregularly spaced, anteriorly concentrated growth lamellae; stronger and sharply edged plications; cardinal

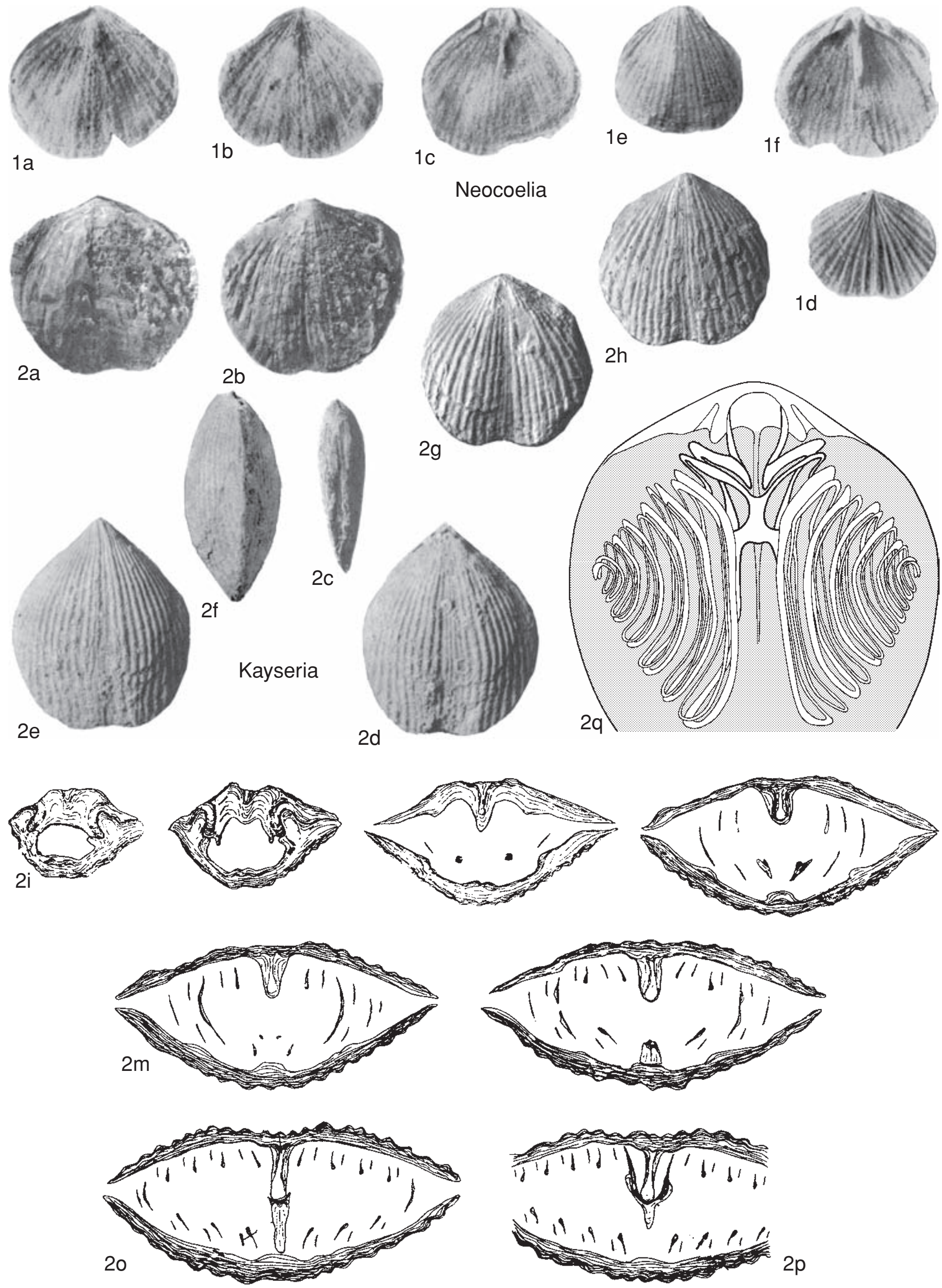

FIG. 1098. Kayseriidae (p. 1612).

process not bilobed; spiralia and jugum poorly known. [Requires revision. May be synonymous with *Coelospira.*] *Lower Devonian (upper Emsian):* Czech Republic, Germany, Gorno-Altay.——FIG. 1097,*1a–g.* **C. modica,* Zlichov Limestone, Praha-Hlubocepy, Czech Republic; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 140379; *f,* dorsal valve interior, USNM 140380; *g,* ventral valve interior, USNM 140379, ×3 (Boucot, Johnson, & Staton, 1964).

Navispira AMSDEN, 1983b, p. 1253 [**Anoplotheca (Coelospira) saffordi* FOERSTE, 1903, p. 709; OD].

Similar to *Coelospira,* but smaller, longitudinally ovate, with strong ventral midrib pair, producing carination, separated by smaller central rib; ventral diductor scars relatively narrow and small, separated by short, stout median septum commonly thickening anteriorly; ventral muscle attachment area elevated on platform of thickened shell material, thinning abruptly at its anterior margin to produce conspicuous cavity; dorsal interior similar to *Coelospira,* but with cardinal process smaller and knoblike or absent. *Silurian (?Wenlock, lower Ludlow)–Lower Devonian (Emsian):* North America, Venezuela, Bolivia, Gotland, Kazakhstan, *Ludlow;* North America, *Lochkovian;* Australia, *Emsian.*——Fig. 1097,*2a–d.* **N. saffordi* (Foerste), Ludlow, Perrysville Quadrangle, Tennessee; *a–b,* dorsal and ventral views, USNM 339088; *c,* posterior view, USNM 339091; *d,* interior of ventral valve, USNM 339090, ×4 (Amsden, 1983b).——Fig. 1097,*2e. N. virginia* (Amsden), Ludlow, Jeannette Quadrangle, Tennessee; interior of dorsal valve, USNM 339093, ×4 (Amsden, 1983b).——Fig. 1097,*2f–g. N. kennethensis* (Boucot & Johnson), Ludlow, Logansport, Indiana; *f,* dorsal valve interior, USNM 156318, ×4; *g,* ventral, slightly lateral, view of brachiojugal structures, USNM 156320, ×10 (Boucot & Johnson, 1967b).——Fig. 1097,*2h–i. N. dayi* Chatterton, Emsian, New South Wales, Australia; ventral and dorsal views of reconstructed brachiojugal structures, approximately ×10 (Campbell & Chatterton, 1979).

Family KAYSERIIDAE Boucot, Johnson, & Staton, 1964

[Kayseriidae Boucot, Johnson, & Staton, 1964, p. 807; *emend.,* Alvarez & Copper, herein]

Weakly biconvex shells with median sulcus in both valves and opposite folding, anterior margin slightly emarginate; numerous, fine ribs, evenly sized on flanks, being finer in the sulci; few growth lines crossing ribs at irregular intervals; deltidial plates and pedicle supports absent; teeth short, massive, nearly vertical, with notches for cardinalium, dental plates absent; median septum present in both valves; short, thick, imperforate apically, subtrapezoidal cardinal plate (without dorsal cavity below) with weak cardinal process; umbonal blades of spiralia sharply bent from tips of crura in posterolateral direction; spiral cones ventrolaterally directed, accessory lamellae long, continuing intercoiled with primary volutions of spiralia to ends; jugum resting on prominent dorsal septum and produced ventrally up to broad, flat, even concave, ventral median septum. *Middle Devonian (Eifelian–Givetian).*

Kayseria Davidson, 1882, p. 21 [**Orthis lens* Phillips, 1841, p. 65; OD]. Medium, rather flat, subcircular to subpentagonal or elongate oval shell, with tiny, slightly curved, ventral beak and minute foramen; 2 thick ribs may define sulcus laterally on both valves; rare growth lamellae projecting outwardly; ragged-edged cardinal process internally. *Middle Devonian (Eifelian–Givetian):* Eurasia.——Fig. 1098,*2a–c.* **K. lens* (Phillips), upper Eifelian, Devon, England; lectotype, dorsal, ventral, and lateral views, GSM 50872, ×2 (Copper, 1973b).——Fig. 1098,*2d–f. K. nohnensis* Copper, lower Eifelian, Eifel, Germany; holotype, dorsal, ventral, and lateral views, BMNH BB 58563, ×2 (Copper, 1973b).——Fig. 1098,*2g–q. K. dividua* (Schnur), lower Eifelian, Eifel, Germany; *g–h,* dorsal and ventral views, BMNH BB 59010, ×2 (Copper, 1973b); *i–p,* transverse serial sections, 0.9, 1.2, 1.9, 2.6, 3.1, 3.6, 4.2, 4.5 mm from ventral umbo, BMNH BB 59010, ×5 (adapted from Copper, 1973b); *q,* ventral view of dorsal interior showing reconstructed spiralium and jugum, BMNH BB 59010, ×5 (Copper, 1973b).

Family UNCERTAIN

?Neocoelia McKellar, 1966, p. 2 [**N. boucoti;* OD]. Shell with very numerous, fine, low ribs, most of which bifurcate; ventral muscle field poorly defined with a short, low septum; teeth solid, lacking dental cavities; cardinal process small, bilobate; dorsal median septum high, extending to midline; spiralium and jugum unknown. [Poorly represented and known, requires revision. When erected, *Neocoelia* was regarded as a close relative to *Anoplotheca* and *Kayseria,* with its shape suggesting closer affinity to the former. In the absence of revision of this genus, Alvarez prefers to regard it tentatively as belonging to the Anoplothecidae, while Copper suggests a closer relationship with *Kayseria,* of which *Neocoelia* seems to be an early relative.] *Lower Devonian (?Emsian), Middle Devonian (Eifelian)*: Australia (Queensland).——Fig. 1098,*1a–f.* **N. boucoti; a–b,* holotype, external mold of dorsal valve and rubber mold, GSQ F3696; *c,* holotype, rubber mold of dorsal interior, GSQ F3696; *d,* rubber mold of dorsal valve exterior, GSQ F9537; *e,* rubber mold of incomplete ventral valve exterior, GSQ F3695; *f,* rubber mold of dorsal interior, GSQ F3689, ×2 (McKellar, 1966).

Superfamily UNCITOIDEA d'Orbigny, 1847

[*nom. transl.* Jux & Strauch, 1966, p. 177, *ex* Uncitidae d'Orbigny, 1847, p. 268]

Diagnosis as for family. *Middle Devonian (Givetian).*

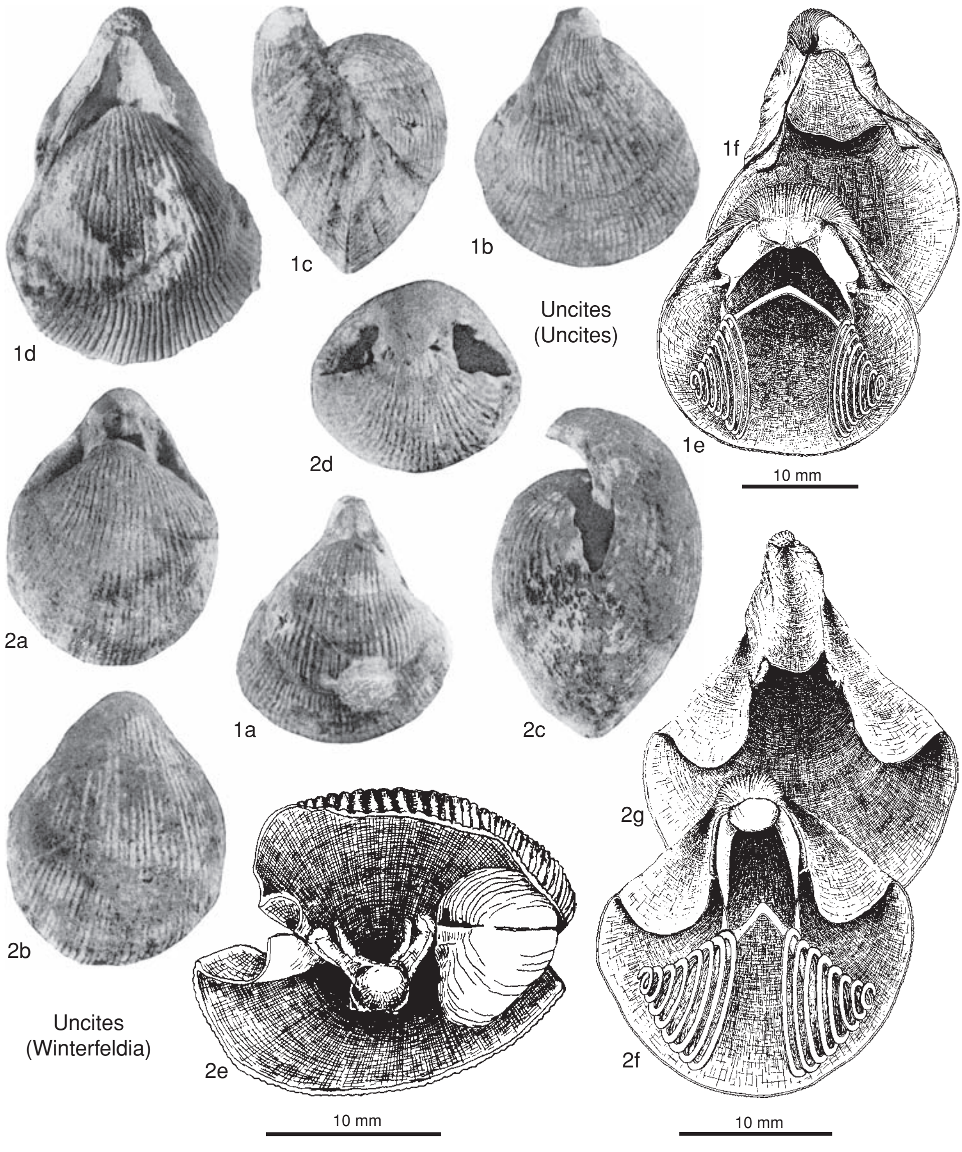

FIG. 1099. Uncitidae (p. 1614).

Family UNCITIDAE d'Orbigny, 1847

[Uncitidae D'ORBIGNY, 1847, p. 268]

Impunctate, ribbed, asymmetric, large-beaked shells with deltidium; ventrolaterally directed spiralia, simple, posteriorly located jugum. [Commonly, the family Uncitidae is attributed to WAAGEN (1883, p. 487, 494) as a subfamily, later raised to family rank by SCHUCHERT (1929, p. 22). However, it had been made available already by D'ORBIGNY (1847, p. 268; see JUX & STRAUCH, 1966; MANCEÑIDO, OWEN, & MORRIS, 1993, p. 197).] *Middle Devonian (Givetian).*

Uncites Defrance in de Blainville, 1825, p. 630 [**Terebratulites Gryphus* [sic] von Schlotheim, 1820 in 1820–1823, p. 259; OD; =*Uncites gryphoides* Defrance, 1827, p. 152]. Evenly ribbed, biconvex, generally elongate, highly variable, asymmetrical shells; shell wall thick, massive; very large, talonlike, protruding, pointed, ventral beak; concentric growth lines present, irregularly spaced; flanks lateral to delthyrium, smooth; foramen absent, but some shells possessing koskinoid perforations; large delthyrium occupied by single, concave deltidium, rarely with medial separation into separate plates; teeth solid, lacking dental plates or cavities; no clear median septa evident in either valve; muscle impressions weak; massive cardinalium; spiralia lateral to ventrolateral, with 6 or more whorls; simple, arched jugum pointed posteriorly. [For discussion of *Uncites* see Jux & Strauch, 1966.] *Middle Devonian (Givetian):* Eurasia, western Europe, China, Vietnam.

U. (**Uncites**). Beak with narrow smooth flanks; large, triangular, concave deltidium; hinge plate short, in comparison with long, flat outer hinge plates, short, laterally divergent crura; 6 or more lateroventral spiral whorls; simple wide jugum. Distinct from *Winterfeldia* in lacking brood pouches and possessing broad cardinal plate, widely diverging crura, wide jugum. *Middle Devonian (Givetian):* Eurasia, China, ?North America.——Fig. 1099,*1a–f.* **U. (U.) gryphus* (von Schlotheim), Germany; *a–c,* lectotype, dorsal, ventral, and lateral views; *d,* dorsal view, ×1; *e–f,* interiors of dorsal, ventral valves (Jux & Strauch, 1966).

U. (**Winterfeldia**) Spriestersbach, 1942, p. 197 [**U. paulinae* Winterfeld, 1895, p. 658; OD]. Generally smaller than *Uncites,* and distinguished by presence of brood pouches (parathyridia), W-shaped cardinal margin; narrow cardinal plate with thick process on top, medial and subparallel crura, narrow jugum, widely spaced spiralial whorls. *Middle Devonian (Givetian):* western Europe.——Fig. 1099,*2a–g.* **U. (W.) paulinae* Winterfeld, upper Givetian, Germany; *a–d,* lectotype, dorsal, ventral, lateral, and posterior views; *e,* interior view of brood pouches, ×1; *f–g,* interiors of dorsal, ventral valves (Jux & Strauch, 1966).

UNCERTAIN

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Order, Suborder, and Family UNCERTAIN

Weibeia Fu, 1982, p. 171 [**W. spiriferoides;* OD]. Small shell, subequally biconvex, subpentagonal, with growth lines, dorsal fold and ventral sulcus slightly developed only anteriorly; interior poorly known, dental plates and crural plates high and parallel; spiralia and jugum unknown. Poorly known, needs revision. [When erected, this genus was included in the Athyrididina, Meristellidae.] *Upper Ordovician (lower Caradoc):* northern China (Dongzhuang, Liquan, Shaanxi Province).——Fig. 1100*a–e.* **W. spiriferoides;* holotype, dorsal, ventral, lateral, anterior, and posterior views, ×3 (Fu, 1982; photographs courtesy of Fu Li-pu).

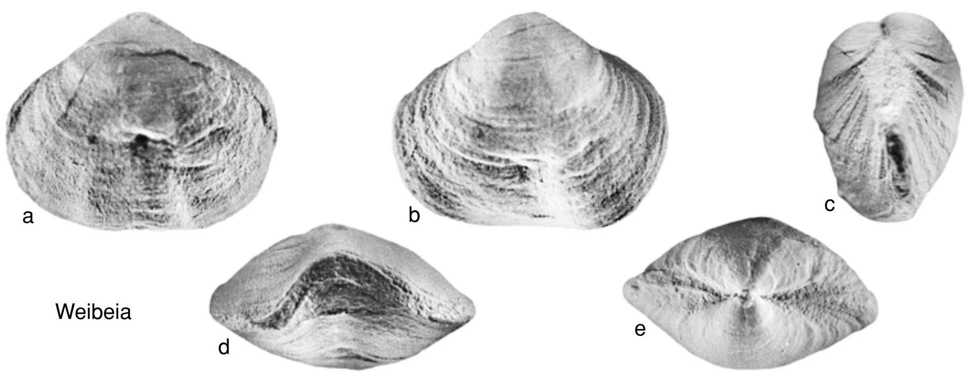

Fig. 1100. Uncertain (p. 1614).

NOMENCLATORIAL NOTE

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KATUNIELLA, NEW NAME FOR THE GENUS *KATUNIA*, KULKOV, 1963 (BRACHIOPODA, RHYNCHONELLIDA) PREOCCUPIED BY *KATUNIA* ROMANENKO, 1962 (ARTHROPODA, TRILOBITA)

During preparation of the manuscript for volume 4 of the revised brachiopod *Treatise on Invertebrate Paleontology,* Jill Hardesty, Assistant Editor for the *Treatise,* Paleontological Institute, University of Kansas, kindly informed me that the rhynchonellid genus name *Katunia* KULKOV, 1963, p. 54, is preoccupied by a trilobite genus published by ROMANENKO and ROMANENKO, 1962, p. 25 (see p. 1139 herein). I communicated with Dr. Nikolay KULKOV suggesting he publish a replacement name and he responded asking that, as he has now retired, I publish the replacement name *Katuniella*. According to Article 60 of ICZN rules (1999) I here propose the name *Katuniella* KULKOV, with reference to his letter (personal communication, 24 October, 2000), as replacement name for *Katunia* KULKOV, 1963, not *Katunia* M. F. ROMANENKO (*in* M. F. Romanenko, & E. V. Romanenko, 1962). The type species for *Katuniella* is *Katunia subtrigonata* KULKOV, 1963, p. 54.

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NOMENCLATORIAL NOTE

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BONDAREVIA, NEW NAME FOR THE GENUS *TRISEPTATA* BONDAREV, 1965 (BRACHIOPODA, PENTAMERIDA) PREOCCUPIED BY *TRISEPTATA* HOSHIDE, 1958 (PROTOZOA, SPOROZOA)

In 1965, Bondarev (in Bondarev & others, 1965) erected the genus *Triseptata* to distinguish an unusual porambonitoid brachiopod known from several dozen isolated dorsal and ventral valves, and one complete, articulated, but deformed specimen. The specimens were collected from the lower Arenig (Lower Ordovician) of Novaya Zemlya. These large costellate brachiopods with a rectimarginate commissure possess a pseudospondylium and cardinal process characteristic of Huenellidae, accessory septa, a notothyrial platform, and an elevated dorsal adductor muscle field characteristic of Clarkellidae, and a septalium characteristic of Syntrophiidae (Carlson, herein, p. 935). This unusual combination of porambonitoid features prevented Bondarev from referring this genus to an established family, thus it was relegated to Porambonitoidea Incertae familiae. In the process of revising the brachiopod volumes of the *Treatise on Invertebrate Paleontology,* it was discovered that the name *Triseptata* was preoccupied by a sporozoan *Triseptata* Hoshide, 1958 (see p. 931 herein). *Triseptata* Bondarev, 1965 is thus an objective homonym requiring a replacement name, according to Article 60 of the International Code of Zoological Nomenclature (1999). I propose the name *Bondarevia nomen novum* as a replacement for *Triseptata* Bondarev, 1965, not *Triseptata* Hoshide, 1958. *Bondarevia* derives from the surname of V. I. Bondarev, the author of the brachiopod genus. The type species of *Bondarevia* is *B. nelidovi* Bondarev in Bondarev & others, 1965, p. 34. *Bondarevia* is monospecific, with *B. nelidovi* the only species recognized thus far (see also Bondarev, 1968; Sapelnikov, 1980, 1985).

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