TREATISE ON
INVERTEBRATE PALEONTOLOGY

Prepared under Sponsorship of
The Geological Society of America, Inc.

The Paleontological Society *The Society of Economic Paleontologists and Mineralogists*
The Palaeontographical Society *The Palaeontological Association*

Directed and Edited by
RAYMOND C. MOORE

Part H
BRACHIOPODA

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TREATISE ON INVERTEBRATE PALEONTOLOGY

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EDITORIAL PREFACE

The aim of the *Treatise on Invertebrate Paleontology,* as originally conceived and consistently pursued, is to present the most comprehensive and authoritative, yet compact statement of knowledge concerning invertebrate fossil groups that can be formulated by collaboration of competent specialists in seeking to organize what has been learned of this subject up to the mid-point of the present century. Such work has value in providing a most useful summary of the collective results of multitudinous investigations and thus should constitute an indispensable text and reference book for all persons who wish to know about remains of invertebrate organisms preserved in rocks of the earth's crust. This applies to neozoologists as well as paleozoologists and to beginners in study of fossils as well as to thoroughly trained, long-experienced professional workers, including teachers, stratigraphical geologists, and individuals engaged in research on fossil invertebrates. The making of a reasonably complete inventory of present knowledge of invertebrate paleontology may be expected to yield needed foundation for future research and it is hoped that the *Treatise* will serve this end.

The *Treatise* is divided into parts which bear index letters, each except the initial and concluding ones being defined to include designated groups of invertebrates. The chief purpose of this arrangement is to provide for independence of the several parts as regards date of publication, because it is judged desirable to print and distribute each segment as soon as possible after it is ready for press. Pages in each part bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part.

The outline of subjects to be treated in connection with each large group of invertebrates includes (1) description of morphological features, with special reference to hard parts, (2) ontogeny, (3) classification, (4) geological distribution, (5) evolutionary trends and phylogeny, and (6) systematic description of genera, subgenera, and higher taxonomic units. In general, paleoecological aspects of study are omitted or little emphasized because comprehensive treatment of this subject is given in the *Treatise on Marine Ecology and Paleoecology* (H. S. LADD, Editor, Geological Society of America, Memoir 67, 1957), prepared under auspices of a committee of the United States National Research Council. A selected list of references is furnished in each part of the *Treatise*.

Features of style in the taxonomic portions of this work have been fixed by the Editor with aid furnished by advice from representatives of the societies which have undertaken to sponsor the *Treatise*. It is the Editor's responsibility to consult with authors and co-ordinate their work, seeing that manuscript properly incorporates features of adopted style. Especially he has been called on to formulate policies in respect to many questions of nomenclature and procedure. The subject of family and subfamily names is reviewed briefly in a following section of this preface, and features of *Treatise* style in generic descriptions are explained.

In December, 1959, the National Science Foundation of the United States, through its Division of Biological and Medical Sciences and the Program Director for Systematic Biology, made a grant in the amount of $210,000 for the purpose of aiding the completion of yet-unpublished volumes of the *Treatise*. Payment of this sum was provided to be made in installments distributed over a five-year period, with administration of disbursements handled by the University of Kansas. Expenditures planned are primarily for needed assistance to authors and may be arranged through approved institutions located anywhere. Important help for the Director-Editor of the *Treatise* has been made available from the grant, but no part of his stipend has come from it. Grateful acknowledgment to the Foundation is expressed on behalf of the societies sponsoring the *Treatise*, the University of Kansas, and innumerable individuals benefited by the *Treatise* project.

ZOOLOGICAL NAMES

Many questions arise in connection with zoological names, especially including those that relate to their acceptability and to alterations of some which may be allowed or demanded. Procedure in obtaining answers to these questions is guided and to a large extent governed by regulations published (1961) in the *International Code of Zoological Nomenclature* (hereinafter cited simply as the *Code*). The prime object of the *Code* is to promote stability and universality in the scientific names of animals, ensuring also that each name is distinct and unique while avoiding restrictions on freedom of taxonomic thought or action. Priority is a basic principle, but under specified conditions its application can be modified. This is all well and good, yet nomenclatural tasks confronting the zoological taxonomist are formidable. They warrant the complaint of some that zoology, including paleozoology, is the study of animals rather than of names applied to them.

Several ensuing pages are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*. Terminology is explained, and examples of style employed in the nomenclatural parts of systematic descriptions are given.

TAXA GROUPS

Each taxonomic unit (taxon, pl., taxa) of the animal and protistan kingdoms belongs to some one or another rank in the adopted hierarchy of classificatory divisions. In part, this hierarchy is defined by the *Code* to include a species-group of taxa, a genus-group, and a family-group. Units of lower rank than subspecies are excluded from zoological nomenclature and those higher than superfamily of the family-group are not regulated by the *Code*. It is natural and convenient to discuss nomenclatural matters in general terms first and then to consider each of the taxa groups separately. Especially important is provision that within each taxa group classificatory units are coordinate (equal in rank), whereas units of different taxa groups are not coordinate.

FORMS OF NAMES

All zoological names are divisible into groups based on their form (spelling). The first-published form (or forms) of a name is defined as original spelling (*Code,* Art. 32) and any later-published form (or forms) of the same name is designated as subsequent spelling (Art. 33). Obviously, original and subsequent spellings of a given name may or may not be identical and this affects consideration of their correctness. Further, examination of original spellings of names shows that by no means all can be distinguished as correct. Some are incorrect, and the same is true of subsequent spellings.

Original Spellings

If the first-published form of a name is consistent and unambiguous, being identical wherever it appears, the original spelling is defined as correct unless it contravenes some stipulation of the *Code* (Arts. 26-31), 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 unambiguous 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* (Arts. 26-31), including its provision for automatic emendations of minor sort.

Incorrect original spellings are any that fail to satisfy requirements of the *Code,* or that represent an inadvertent error, or that 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 wherever found. For example, a name originally published with a diacritic mark, apostrophe, diaeresis, 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 is accompanied by inserting "e" after the vowel.

Subsequent Spellings

If a name classed as a subsequent spelling is identical with an original spelling, it is distinguishable as correct or incorrect on the same criteria that apply to the original spelling. This means that a subsequent spelling identical with a correct original spelling is also correct, and one identical with an incorrect original spelling is also incorrect. In the latter case, both original and subsequent spellings require correction wherever found (authorship and date of the original incorrect spelling being retained).

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 (except that such changes as altered terminations of adjectival specific names to obtain agreement in gender wtih associated generic names, of family-group names to denote assigned taxonomic rank, and corrections for originally used diacritic marks, hyphens, and the like are excluded from spelling changes conceived to produce a different name).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If demonstrably intentional, the change is designated as an emendation. Emendations are divisible into those classed as justifiable and those comprising all others classed as 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 that differ in any way from original spellings, other than previously noted exceptions, and that are not classifiable as emendations 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

Available Names

An available zoological name is any that conforms to all mandatory provisions of the *Code*. Such names are classifiable in groups which are usefully recognized in the *Treatise*, though not explicitly differentiated in the *Code*. They are as follows:

(1) So-called *"inviolate names"* include all available names that are not subject to any sort of alteration from their originally published form. They comprise correct original spellings and commonly include correct subsequent spellings, but include no names classed as emendations. Here belong most generic and subgeneric names, some of which differ in spelling from others by only a single letter.

(2) Names may be termed *"perfect names"* if, as originally published (with or without duplication by subsequent authors), they meet all mandatory requirements, needing no correction of any kind, but nevertheless are legally alterable in such ways as changing the termination (e.g., many species-group names, family-group names, suprafamilial names). This group does not include emended incorrect original spellings (e.g., *Oepikina*, replacement of *Öpikina*).

(3) *"Imperfect names"* are available names that as originally published (with or without duplication by subsequent authors) contain mandatorily emendable defects. Incorrect original spellings are imperfect names. Examples of emended imperfect names are: among species-group names, *guerini* (not *Guérini*), *obrienae* (not *O'Brienae*), *terranovae* (not *terra-novae*), *nunezi* (not *Nuñezi*), *Spironema rectum* (not *Spironema recta*, because generic name is neuter, not feminine); among genus-group names, *Broeggeria* (not *Bröggeria*), *Obrienia* (not *O'Brienia*), *Maccookites* (not *McCookites*; among family-group names, Oepikidae (not Öpikidae), Spironematidae (not Spironemidae, incorrect stem), Athyrididae (not Athyridae, incorrect stem). The use of "variety" for named divisions of fossil species, according to common practice of some paleontologists, gives rise to imperfect names, which generally are emendable (*Code*, Art. 45e) by omitting this term so as to indicate the status of this taxon as a subspecies.

(4) *"Vain names"* are available names consisting of unjustified intentional emendations of previously published names. The emendations are unjustified because they are not demonstrable as corrections of incorrect original spellings as defined by the *Code* (Art. 32,c). Vain names have status in nomenclature under their own authorship and date. They constitute junior objective synonyms of names in their original form. Examples are: among species-group names, *geneae* (published as replacement of original unexplained masculine, *geni*, which now is not alterable), *ohioae* (invalid change from original *ohioensis*); among genus-group names, *Graphiodactylus* (invalid change from original *Graphiadactyllis*); among family-group names, Graphiodactylidae (based on junior objective synonym having invalid vain name).

(5) An important group of available zoological names can be distinguished as *"transferred names."* These comprise authorized sorts of altered names in which the change depends on transfer from one taxonomic rank to another, or possibly on transfers in taxonomic assignment of subgenera, species, or subspecies. Most commonly the transfer calls for a change in termination of the name so as to comply with stipulations of the *Code* on endings of family-group taxa and agreement in gender of specific names with associated generic names. Transferred names may be derived from any of the preceding groups except the first. Examples are: among species-group names, *Spirifer ambiguus* (masc.) to *Composita ambigua* (fem.), *Neochonetes transversalis* to *N. granulifer transversalis* or vice versa; among genus-group names, *Schizoculina* to *Oculina (Schizoculina)* or vice versa; among family-group names, Orthidae to Orthinae or vice versa, or superfamily Orthacea derived from Orthidae or Orthinae; among suprafamilial taxa (not governed by the *Code*), order Orthida to suborder Orthina or vice versa. The authorship and date of transferred names are not affected by the transfers, but the author responsible for the transfer and the date of his action may appropriately be recorded in such works as the *Treatise*.

(6) Improved or *"corrected names"* include both mandatory and allowable emendations of imperfect names and of suprafamilial names, which are not subject to regulation as to name form. Examples of corrected imperfect names are given with the discussion of group 3. Change from the originally published ordinal name Endoceroidea (TEICHERT, 1933) to the presently recognized Endocerida illustrates a "corrected" suprafamilial name. Group 6 names differ from those in group 5 in not being dependent on transfers in taxonomic rank or assignment, but some names are classifiable in both groups.

(7) *"Substitute names"* are available names expressly proposed as replacements for invalid zoological names, such as junior homonyms. These may be classifiable also as belonging in groups 1, 2, or 3. The glossary appended to the *Code* refers to these as "new names" *(nomina nova)* but they are better designated as substitute names, since their newness is temporary and relative. The first-published substitute name that complies with the definition here given takes precedence over any other. An example is *Mareita* LOEBLICH & TAPPAN, 1964, as substitute for *Reichelina* MARIE, 1955 (*non* ERK, 1942).

(8) *"Conserved names"* include a relatively small number of species-group, genus-group, and family-group names which have come to be classed as available and valid by action of the International Commission on Zoological Nomenclature exercising its plenary powers to this end or ruling to conserve a junior synonym in place of a rejected "forgotten" name *(nomen oblitum)* (Art. 23,b). Currently, such names are entered on appropriate "Official Lists," which are published from time to time.

It is useful for convenience and brevity of distinction in recording these groups of available zoological names to employ Latin designations in the pattern of *nomen nudum* (abbr., *nom. nud.*) and others. Thus we may recognize the preceding numbered groups as follows: (1) *nomina inviolata* (sing., *nomen inviolatum,* abbr., *nom. inviol.*), (2) *nomina perfecta (nomen perfectum, nom. perf.),* (3) *nomina imperfecta (nomen imperfectum, nom. imperf.),* (4) *nomina vana (nomen vanum, nom. van.),* (5) *nomina translata (nomen translatum, nom. transl.),* (6) *nomina correcta (nomen correctum, nom. correct.),* (7) *nomina substituta (nomen substitutum, nom. subst.),* (8) *nomina conservata (nomen conservatum, nom. conserv.).*

Unavailable Names

All zoological names which fail to comply with mandatory provisions of the *Code* are unavailable names and have no status in zoological nomenclature. None can be used under authorship and date of their original publication as a replacement name *(nom. subst.)* and none preoccupies for purposes of the Law of Homonymy. Names identical in spelling with some, but not all, unavailable names can be classed as available if and when they are published in conformance to stipulations of the *Code* and they are then assigned authorship and take date of the accepted publication. Different groups of unavailable names can be discriminated, as follows.

(1) *"Naked names"* include all those that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability, and in addition, if published before 1931, that were unaccompanied by a description, definition, or indication (Arts. 12, 16), and if published after 1930, that lacked accompanying statement of characters purporting to serve for differentiation of the taxon, or definite bibliographic reference to such a statement, or that were not proposed expressly as replacement *(nom. subst.)* of a pre-existing available name (Art. 13,a). Examples of "naked names" are: among species-group taxa, *Valvulina mixta* PARKER & JONES, 1865 (=*Cribrobulimina mixta* CUSHMAN, 1927, available and valid); among genus-group taxa, *Orbitolinopsis* SILVESTRI, 1932 (=*Orbitolinopsis* HENSON, 1948, available but classed as invalid junior synonym of *Orbitolina* D'ORBIGNY, 1850); among family-group taxa, Aequilateralidae D'ORBIGNY, 1846 (lacking type-genus), Hélicostègues D'ORBIGNY, 1826 (vernacular not latinized by later authors, Art. 11,e,iii), Poteriocrinidae AUSTIN & AUSTIN, 1843 (=fam. Poteriocrinoidea AUSTIN & AUSTIN, 1842) (neither 1843 or 1842 names complying with Art. 11,e, which states that "a family-group

name must, when first published, be based on the name then valid for a contained genus," such valid name in the case of this family being *Poteriocrinites* Miller, 1821).

(2) *"Denied names"* include all those that are defined by the *Code* (Art. 32,c) as incorrect original spellings. Examples are: Specific names, *nova-zelandica, mülleri, 10-brachiatus;* generic name, *M'Coyia, Størmerella, Römerina, Westgårdia;* family name, Růžičkinidae. Uncorrected "imperfect names" are "denied names" and unavailable, whereas corrected "imperfect names" are available.

(3) *"Impermissible names"* include all those employed for alleged genus-group taxa other than genus and subgenus (Art. 42,a) (e.g., supraspecific divisions of subgenera), and all those published after 1930 that are unaccompanied by definite fixation of a type-species (Art. 13,b). Examples of impermissible names are: *Martellispirifer* Gatinaud, 1949, and *Mirtellispirifer* Gatinaud, 1949, indicated respectively as a section and subsection of the subgenus *Cyrtospirifer; Fusarchaias* Reichel, 1949, without definitely fixed type-species (=*Fusarchaias* Reichel, 1952, with *F. bermudezi* designated as type-species).

(4) *"Null names"* include all those that are defined by the *Code* (Art. 33,b) as incorrect subsequent spellings, which are any changes of original spelling not demonstrably intentional. Such names are found in all ranks of taxa.

(5) *"Forgotten names"* are defined (Art. 23,b) as senior synonyms that have remained unused in primary zoological literature for more than 50 years. Such names are not to be used unless so directed by ICZN.

Latin designations for the discussed groups of unavailable zoological names are as follows: (1) *nomina nuda* (sing., *nomen nudum,* abbr., *nom. nud.*), (2) *nomina negata (nomen negatum, nom. neg.),* (3) *nomina vetita (nomen vetitum, nom. vet.),* (4) *nomina nulla (nomen nullum, nom. null.),* (5) *nomina oblita (nomen oblitum, nom. oblit.).*

VALID AND INVALID NAMES

Important distinctions relate to valid and available names, on one hand, and to invalid and 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 partly may be 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 name, generally the oldest. Obviously, no valid name can also be an unavailable name, but invalid names may include both available and unavailable names. Any name for a given taxon other than the valid name is an invalid name.

A sort of nomenclatorial no-man's-land is encountered in considering the status of some zoological names, such as *"doubtful names," "names under inquiry,"* and *"forgotten names."* Latin designations of these are *nomina dubia, nomina inquirenda,* and *nomina oblita,* respectively. Each of these groups may include both available and unavailable names, but the latter can well be ignored. Names considered to possess availability conduce to uncertainty and instability, which ordinarily can be removed only by appealed action of ICZN. Because few zoologists care to bother in seeking such remedy, the "wastebasket" names persist.

SUMMARY OF NAME GROUPS

Partly because only in such publications as the *Treatise* is special attention to groups of zoological names called for and partly because new designations are now introduced as means of recording distinctions explicitly as well as compactly, a summary may be useful. In the following tabulation valid groups of names are indicated in boldface type, whereas invalid ones are printed in italics.

DEFINITIONS OF NAME GROUPS

nomen conservatum (nom. conserv.). Name unacceptable under regulations of the *Code* which is made valid, either with original or altered spelling, through procedures specified by the *Code* or by action of ICZN exercising its plenary powers.

nomen correctum (nom. correct.). Name with intentionally altered spelling of sort required or allowable by the *Code* but not dependent on transfer from one taxonomic rank to another ("improved name"). (*See Code,* Arts. 26-b, 27, 29, 30-a-3, 31, 32-c-i, 33-a; in addition change of endings for suprafamilial taxa not regulated by the *Code.*)

nomen imperfectum (nom. imperf.). Name that as originally published (with or without subsequent identical spelling) meets all mandatory requirements of the *Code* but contains defect needing correction ("imperfect name"). (*See Code*, Arts. 26-b, 27, 29, 32-c, 33-a.)

nomen inviolatum (nom. inviol.). Name that as originally published meets all mandatory requirements of the *Code* and also is not correctable or alterable in any way ("inviolate name").

nomen negatum (nom. neg.). Name that as originally published (with or without subsequent identical spelling) constitutes invalid original spelling, and although possibly meeting all other mandatory requirements of the *Code*, cannot be used and has no separate status in nomenclature ("denied name"). It is to be corrected wherever found.

nomen nudum (nom. nud.). Name that as originally published (with or without subsequent identical spelling) fails to meet mandatory requirements of the *Code* and having no status in nomenclature, is not correctable to establish original authorship and date ("naked name").

nomen nullum (nom. null.). Name consisting of an unintentional alteration in form (spelling) of a previously published name (either available name, as *nom. inviol., nom. perf., nom. imperf., nom. transl.*; or unavailable name, as *nom. neg., nom. nud., nom. van.,* or another *nom. null.*) ("null name").

nomen oblitum (nom. oblit.). Name of senior synonym unused in primary zoological literature in more than 50 years, not to be used unless so directed by ICZN ("forgotten name").

nomen perfectum (nom. perf.). Name that as originally published meets all mandatory requirements of the *Code* and needs no correction of any kind but which nevertheless is validly alterable by change of ending ("perfect name").

nomen substitutum (nom. subst.). Replacement name published as substitute for an invalid name, such as a junior homonym (equivalent to "new name").

nomen translatum (nom. transl.). Name that is derived by valid emendation of a previously published name as result of transfer from one taxonomic rank to another within the group to which it belongs ("transferred name").

nomen vanum (nom. van.). Name consisting of an invalid intentional change in form (spelling) from a previously published name, such invalid emendation having status in nomenclature as a junior objective synonym ("vain name").

nomen vetitum (nom. vet.). Name of genus-group taxon not authorized by the *Code* or, if first published after 1930, without definitely fixed type-species ("impermissible name").

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nomina inviolata* or *nomina perfecta* (omitting from notice *nomina correcta* among specific names) and these are not discriminated. Names which are not accepted for one reason or another include junior homonyms, senior synonyms classifiable as *nomina negata* or *nomina nuda,* and numerous junior synonyms which include both objective *(nomina vana)* and subjective types; rejected names are classified as completely as possible.

NAME CHANGES IN RELATION TO TAXA GROUPS

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here because it is well understood and relatively inconsequential. When the form of adjectival specific names is changed to obtain agreement with the gender of a generic name in transferring a species from one genus to another, it is never needful to label the changed name as a *nom. transl.* Likewise, transliteration of a letter accompanied by a diacritical mark in manner now called for by the *Code* (as in changing originally published *bröggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornu-oryx* to *cornuoryx*) does not require *"nom. correct."* with it.

GENUS-GROUP NAMES

So rare are conditions warranting change of the originally published valid form of generic and subgeneric names that lengthy discussion may be omitted. Only elimination of diacritical marks of some names in this category seems to furnish basis for valid emendation. It is true that many changes of generic and subgeneric names have been published, but virtually all of these are either *nomina vana* or *nomina nulla.* Various names which formerly were classed as homonyms are not now, for two names that differ only by a single letter (or in original publication by presence or absence of a diacritical mark) are construed to be entirely distinct.

Examples in use of classificatory designations for generic names as previously given are the following, which also illustrate designation of type-species, as explained later.

Kurnatiophyllum THOMPSON, 1875 [**K. concentricum;* SD GREGORY, 1917] [=*Kumatiophyllum* THOMPSON, 1876 *(nom. null.); Cymatophyllum* THOMPSON, 1901 *(nom. van.); Cymatiophyllum* LANG, SMITH & THOMAS, 1940 *(nom. van.)*].

Stichophyma POMEL, 1872 [**Manon turbinatum* RÖMER, 1841; SD RAUFF, 1893] [=*Stychophyma*

Vosmaer, 1885 *(nom. null.)*; *Sticophyma* Moret, 1924 *(nom. null.)*].

Stratophyllum Smyth, 1933 [**S. tenue*] [=*Ethmoplax* Smyth, 1939 *(nom. van. pro Stratophyllum)*; *Stratiphyllum* Lang, Smith & Thomas, 1940 (*nom. van. pro Stratophyllum* Smyth) (non *Stratiphyllum* Scheffen, 1933)].

Placotelia Oppliger, 1907 [**Porostoma marconi* Fromentel, 1859; SD deLaubenfels, herein] [=*Plakotelia* Oppliger, 1907 *(nom. neg.)*].

Walcottella deLaubenfels, 1955 [*nom. subst., pro Rhopalicus* Schramm, 1936 (*non* Förster, 1856)].

Cyrtograptus Carruthers, 1867 [*nom. correct.* Lapworth, 1873 (*pro Cyrtograpsus* Carruthers, (1867), *nom. conserv.* proposed Bulman, 1955 (ICZN pend.)].

FAMILY-GROUP NAMES; USE OF *"NOM. TRANSL."*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) but all family-group taxa are defined as coordinate, signifying that for purposes of priority a name published for a taxon in any category and based on a particular type-genus shall date from its original publication for a taxon in any category, retaining this priority (and authorship) when the taxon is treated as belonging to a lower or higher category. By exclusion of -inae and -idae, respectively reserved for subfamily and family, the endings of names used for tribes and superfamilies must be unspecified different letter combinations. These, if introduced subsequent to designation of a subfamily or family based on the same nominate genus, are *nomina translata,* as is also a subfamily that is elevated to family rank or a family reduced to subfamily rank. In the *Treatise* it is desirable to distinguish the valid alteration comprised in the changed ending of each transferred family-group name by the abbreviation *"nom. transl."* and record of the author and date belonging to this alteration. This is particularly important in the case of superfamilies, for it is the author who introduced this taxon that one wishes to know about rather than the author of the superfamily as defined by the *Code,* for the latter is merely the individual who first defined some lower-rank family-group taxon that contains the nominate genus of the superfamily. The publication of the author containing introduction of the superfamily *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the unit.

Examples of the use of *"nom. transl."* are the following.

Subfamily STYLININAE d'Orbigny, 1851

[*nom. transl.* Edwards & Haime, 1857 (*ex* Stylinidae d'Orbigny, 1851)]

Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949

[*nom. transl.* Petrunkevitch, 1955 (*ex* Archaeoctonidae Petrunkevitch, 1949)]

Superfamily CRIOCERATITACEAE Hyatt, 1900

[*nom. transl.* Wright, 1952 (*ex* Crioceratitidae Hyatt, 1900)]

FAMILY-GROUP NAMES; USE OF *"NOM. CORRECT."*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of family-group units to another but most commonly involve correction of the stem of the nominate genus; in addition, they include somewhat arbitrarily chosen modification of ending for names of tribe or superfamily. Examples of the use of *"nom. correct."* are the following.

Family STREPTELASMATIDAE Nicholson, 1889

[*nom. correct.* Wedekind, 1927 (*pro* Streptelasmidae Nicholson, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944

[*nom. correct,* Petrunkevitch, 1955 (*pro* Palaeoscorpionidae Lehmann, 1944, *nom. imperf.*)]

Family AGLASPIDIDAE Miller, 1877

[*nom. correct.* Størmer, 1959 (*pro* Aglaspidae Miller, 1877, *nom. imperf.*)]

Superfamily AGARICIICAE Gray, 1847

[*nom. correct.* Wells, 1956 (*pro* Agaricioidae Vaughan & Wells, 1943, *nom. transl. ex* Agariciidae Gray, 1847)]

FAMILY-GROUP NAMES; USE OF *"NOM. CONSERV."*

It may happen that long-used family-group names are invalid under strict application of the *Code.* In order to retain the otherwise invalid name, appeal to ICZN is needful. Examples of use of *nom. conserv.* in this connection, as cited in the *Treatise,* are the following.

Family ARIETITIDAE Hyatt, 1874

[*nom. correct.* Haug, 1885 (*pro* Arietidae Hyatt, 1875) *nom. conserv.* proposed Arkell, 1955 (ICZN pend.)]

Family STEPHANOCERATIDAE Neumayr, 1875

[*nom. correct.* Fischer, 1882 (*pro* Stephanoceratinen Neumayr, 1875, invalid vernacular name), *nom. conserv.* proposed Arkell, 1955 (ICZN pend.)]

FAMILY-GROUP NAMES; REPLACEMENTS

Family-group names are formed by adding letter combinations (prescribed for family and subfamily but not now for others) to the stem of the name belonging to genus (nominate genus) first chosen as type of the assemblage. The type-genus need not be the oldest in terms of receiving its name and definition, but it must be the first-published as name-giver to a family-group taxon among all those included. Once fixed, the family-group name remains tied to the nominate genus even if its name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* (Art. 39) requires replacement of a family-group name only in the event that the nominate genus is found to be a junior homonym, and then a substitute family-group name is accepted if it is formed from the oldest available substitute name for the nominate genus. Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family group-name, but for purposes of the Law of Priority, they take the date of the replaced name. Numerous long-used family-group names are incorrect in being *nomina nuda,* since they fail to satisfy criteria of availability (Art. 11,e). These also demand replacement by valid names.

The aim of family-group nomenclature is greatest possible stability and uniformity, just as in case of other zoological names. Experience indicates the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of different workers as to the synonymy of generic names founded on different type-species may not agree and opinions of the same worker may alter from time to time. The retention similarly of first-published family-group names which are found to be based on junior objective synonyms is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. To displace a much-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.

Replacement of a family-group name may be needed if the former nominate genus is transferred to another family-group. Then the first-published name-giver of a family-group assemblage in the remnant taxon is to be recognized in forming a replacement name.

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 for any of these assemblages, 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. Also, every family containing differentiated subfamilies must have a nominate *(sensu stricto)* subfamily, which is based on the same type genus as that for the family, and the author and date set down for the nominate subfamily invariably are identical with those of the family, without reference to whether the author of the family or some subsequent author introduced subdivisions.

Changes in the form of family-group names of the sort constituting *nomina correcta,* as previously discussed, do not affect authorship and date of the taxon concerned, but in publications such as the *Treatise* it is desirable to record the authorship and date of the correction.

SUPRAFAMILIAL TAXA

International rules of zoological nomenclature as given in the *Code* (1961) are limited to stipulations affecting lower-rank categories (infrasubspecies to superfamily). Suprafamilial categories (suborder to phylum) are either unmentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Arts. 59-69) proposed to adopt rules for naming suborders and higher taxonomic divisions up to and including phylum, with provision for designating a type-genus for each, hopefully in such manner as not to interfere with the taxonomic freedom of workers. Procedures for applying the Law of Priority and Law of Homonymy to suprafamilial taxa were outlined and for dealing with the names for such units and their authorship, with assigned dates, when 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 XVth 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 which 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, if a class or order was defined by some author at a given date, using chosen morphologic characters (e.g., gills of pelecypods), this should not be allowed to freeze nomenclature, taking precedence over another later-proposed class or order distinguished by different characters (e.g., hinge-teeth of pelecypods). Even the fixing of type-genera for suprafamilial taxa might have small value, if any, hindering taxonomic work rather than aiding it. At all events, no legal basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the Editor of the *Treatise* from making "rules" for dealing with suprafamilial groups of animals described and illustrated in this publication. At least a degree of uniform policy is thought to be needed, especially for the guidance of *Treatise*-contributing 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 which 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, (a) with a capital initial letter, (b) without diacritical mark, apostrophe, diaeresis, or hyphen, and (c) if component consisting of a numeral, numerical adjective, or adverb is used, this must be written in full (e.g., Stethostomata, Trionychi, Septemchitonina, Scorpiones, Subselliflorae). No uniformity in choice of ending for taxa of a given rank is demanded (e.g., orders named Gorgon*acea,* Millepor*ina,* Rugos*a,* Scleractin*ia,* Stromatopor*oidea,* Phalang*ida*).

(2) Names of suprafamilial taxa may be constructed in almost any way, (a) intended to indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa), (b) based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina), or (c) arbitrary combinations of letters, (e.g., Yuania), but none of these can be allowed to end in -idae or -inae, reserved for family-group taxa. A class or subclass (e.g., Nautiloidea), order (e.g., Nautilida), or suborder (e.g., Nautilina) named from the stem of an included genus may be presumed to have that genus (e.g., *Nautilus*) as its objective type. 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 nomenclatural distinction between suprafamilial and family-group taxa which 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; superfamily Bellerophontacea M'Coy, 1851; family Bellerophontidae M'Coy, 1851). Family-group names and suprafamilial names are not coordinate.

(3) The Laws of Priority and Homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatural stability and the avoidance of confusion these laws are widely accepted by zoologists 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 change(s) cannot rationally be judged to alter the authorship and date of the taxon as published originally. (a) A name revised from its previously published rank is a "transferred name" *(nom. transl.)*, as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* Moore, 1955 (*ex* suborder Corynexochida Kobayashi, 1935)]

(b) A name revised from its previously published form merely by adoption of a different termination, without changing taxonomic rank, is an "altered name" *(nom. correct.)*. Examples follow.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* Moore, 1952 (*pro* order Disparata Moore & Laudon, 1943)]

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* Harrington & Leanza, 1957 (*pro* suborder Agnostini Salter, 1864)]

(c) A suprafamilial name revised from its previously published rank with accompanying change of termination (which may or may not be intended to signalize the change of rank) is construed to be primarily a *nom. transl.* (compare change of ending for family-group taxa -idae to -inae, or vice versa, and to superfamily) but if desired it could be recorded as *nom. transl. et correct.*

Order ORTHIDA Schuchert & Cooper, 1931

[*nom. transl.* Moore, 1952 (*ex* suborder Orthoidea Schuchert & Cooper, 1931)]

(5) The authorship and date of nominate subordinate and superordinate 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.

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* Teichert, 1963 (*pro* order Endoceroidea Teichert, 1933)]

Suborder ENDOCERINA Teichert, 1933

[*nom. correct.* Teichert, 1963 (*pro* suborder Endoceracea Schindewolf, 1935, *nom. transl. ex* order Endoceroidea Teichert, 1933)]

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* Teichert, 1963 (*ex* superorder Endoceratoidea Shimanskiy & Zhuravleva, 1961, *nom. transl. ex* order Endoceroidea Teichert, 1933)]

(6) A suprafamilial taxon may or may not contain a family-group taxon or taxa having the same type-genus, and if it does, the respective suprafamilial and family-group taxa may or may not be nominate (having names with the same stem). The zoological *Code* (Art. 61) affirms that "each taxon [of any rank] has, actually or potentially, its type." Taxa above the family-group level which may be designated as having the same type-genus (such designations not being stipulated or recognized by any articles of the zoological *Code*) are considered to have identical authorship and date if the stem of names employed is the same (illustrated in preceding paragraph), but otherwise their authorship and date are accepted as various. Examples showing both suprafamilial and familial taxa in a group of spiders follow.

Class ARACHNIDA Lamarck, 1801

[*nom. correct.* Newport, 1830 (*pro* class—not family—Arachnidae Lamarck, 1801) (type, *Araneus* Clerck, 1757, validated ICZN, 1948)]

Subclass CAULOGASTRA Pocock, 1893

[type, *Araneus* Clerck, 1757]

Superorder LABELLATA Petrunkevitch, 1949

[type, *Araneus* Clerck, 1757]

Order ARANEIDA Clerck, 1757

[*nom. correct.* Dallas, 1864 (*pro* Araneidea Blackwall, 1861, *pro* Araneides Latreille, 1801, *pro* Aranei Clerck, 1757, validated ICZN, 1948) (type, *Araneus* Clerck, 1757)]

Suborder DIPNEUMONINA Latreille, 1817

[*nom. correct.* Petrunkevitch, 1955 (*pro* Dipneumones Latreille, 1817) (type, *Araneus* Clerck, 1757)]

Division TRIONYCHI Petrunkevitch, 1933

[type, *Araneus* Clerck, 1757]

Superfamily ARANEOIDEA Leach, 1815

[*nom. transl.* Petrunkevitch, 1955 (*ex* Araneides Leach, 1815) (type, *Araneus* Clerck, 1757)]

Family ARANEIDAE Leach, 1815

[*nom. correct.* Petrunkevitch, 1955 (*pro* Araneadae Leach, 1819, *pro* Araneides Leach, 1815) (type, *Araneus* Clerck, 1757)]

Subfamily ARANEINAE Leach, 1815

[*nom. transl.* Simon, 1892 (*ex* Araneidae Leach, 1815) (type, *Araneus* Clerck, 1757)]

TAXONOMIC EMENDATION

Emendation has two measurably distinct aspects as regards zoological nomenclature. These embrace (1) alteration of a name itself in various ways for various reasons, as has been reviewed, and (2) alteration of taxonomic scope or concept in application of a given zoological name, whatever its hierarchical rank. The latter type of emendation primarily concerns classification and inherently is not associated with change of name, whereas the other type introduces change of name without necessary expansion, restriction, or other modification in applying the name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleozoologists, who have signified emendation of 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 may accompany the name, with statement of the author and date of the emendation. On the other hand, a multitude of workers concerned with systematic zoology think that publication of *"emend."* with a zoological name is valueless, because more or less alteration of taxonomic sort is introduced whenever a subspecies, species, genus, or other assemblage of animals is incorporated under or removed from the coverage of a given zoological name. 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 radical revisions are put forward, generally with published statement of reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as aid to subsequent workers in taking account of the altered nomenclatural usage and as indication that not to-be-overlooked discussion may be found at a particular place in the literature. Authors of contributions to the *Treatise* are encouraged to include records of all specially noteworthy emendations of this nature, using the abbreviation *"emend."* with the name to which it refers and citing the author and date of the emendation.

In Part G (Bryozoa) and Part D (Protista 3) of the *Treatise,* the abbreviation *"emend."* is employed to record various sorts of name emendations, thus conflicting with usage of *"emend."* for change in taxonomic application of a name without alteration of the name itself. This is objectionable. In Part E (Archaeocyatha, Porifera) and later-issued divisions of the *Treatise,* use of *"emend."* is restricted to its customary sense, that is, significant alteration in taxonomic scope of a name such as calls for noteworthy modifications of a diagnosis. Other means of designating emendations that relate to form of a name are introduced.

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE-SPECIES

The name of the type-species of each genus and subgenus is given next following the generic name with its accompanying author and date, or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names for this species is cited, accompanied by an asterisk (*), with notation of the author and date of original publication. An exception in this procedure is made, however, if the species was first published in the same paper and by the same author as that containing definition of the genus which it serves as type; in such case, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date, for this saves needed space. Examples of these two sorts of citations are as follows:

Diplotrypa NICHOLSON, 1879 [**Favosites petropolitanus* PANDER, 1830].

Chainodictyon FOERSTE, 1887 [**C. laxum*].

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

Acervularia SCHWEIGGER, 1819 [**A. baltica* (=**Madrepora ananas* LINNÉ, 1758)].

It is judged desirable to record the manner of establishing the type-species, whether by original designation or by subsequent designation.

Fixation of type-species originally. The type-species of a genus or subgenus, according to provisions of the *Code,* may be fixed in various ways originally (that is, in the publication containing first proposal of the generic name) or it may be fixed in specified ways subsequent to the original publication. Fixation of a type-species originally may be classified as automatic if the new genus was introduced for a single species (monotypy), or if the names of species referred to the genus are objectively synonymous. In addition, fixation of a type-species originally may be established in several ways by original designation, as by explicit statement given by an author, by use of *typus* or *typicus* as a new specific name, and by absolute tautonymy (e.g., *Mesolobus mesolobus*). According to convention adopted in the *Treatise,* the absence of indication as to the manner of fixing the type-species is to be understood as signifying fixation of the type-species in one way or another originally. Where an author wishes to specify the mode of original fixation, however, this may be done by such abbreviations as "M" (monotypy), "OS" (objective synonymy), and "OD" (original designation), the first- and last-mentioned being most common and the other very rare.

Fixation of type-species subsequently. The type-species of many genera are not determinable from the publication in which the generic name was introduced and 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, and in the *Treatise* fixation of the type-species 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 date of publishing the subsequent designation. Some genera, as first described and named, included no mentioned species and these necessarily lack a type-species until a date subsequent to that of the original publication when one or more species are assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type-species and in the *Treatise* this subsequent monotypy is indicated by the letters "SM." Of course, the first publication containing assignment of species to the genus which originally lacked any included species is the one concerned in fixation of the type-species, and if this named 2 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" and "SM" as employed in the *Treatise* follow.

Hexagonaria GÜRICH, 1896 [**Cyathophyllum hexagonum* GOLDFUSS, 1826; SD LANG, SMITH & THOMAS, 1940].

Muriceides STUDER, 1887 [**M. fragilis* WRIGHT & STUDER, 1889; SM WRIGHT & STUDER, 1889].

Another mode of fixing the type-species of a genus that may be construed as a special sort of subsequent designation is action of the International Commission on 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 (generally) reference to the appropriate numbered Opinion.

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 2 or more distinct taxonomic units, however, it is necessary to differentiate such homonyms, and 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, *Callopora* HALL, 1851, introduced for Paleozoic trepostome bryozoans, is invalid because GRAY in 1848 published the same name for Cretaceous-to-Recent cheilostome bryozoans, and BASSLER in 1911 introduced the new name *Hallopora* to replace HALL's homonym. The *Treatise* style of entry is:

Hallopora BASSLER, 1911, *nom. subst.* [*pro Callopora* HALL, 1851 (*non* GRAY, 1848)].

In like manner, a needed replacement generic name may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is avoided). The requirement that an exact bibliographic reference must be given for the replaced name commonly can be met in the *Treatise* by citing a publication recorded in the list of references, using its assigned index number, as shown in the following example.

Mysterium deLaubenfels, _nom. subst._ [_pro Mystrium_ Schrammen, 1936 (ref. 40, p. 60) (_non_ Roger, 1862)] [_*Mystrium porosum_ Schrammen, 1936].

For some replaced homonyms, a footnote reference to the literature is necessary. A senior homonym is valid, and in so far as the _Treatise_ is concerned, such names are handled according to whether the junior homonym belongs to the same major taxonomic division (class or phylum) as the senior homonym or to some other; in the former instance, the author and date of the junior homonym are cited as:

Diplophyllum Hall, 1851 [_non_ Soshkina, 1939] [_*D. caespitosum_].

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

Homonyms by misidentification. When an author uses a generic name for species not congeneric with the type-species, it is needful to record the misuse of the generic name, even though this is only determinable subjectively. In the _Treatise_ homonyms by misidentification are cited in synonymies as illustrated in the following example.

Asmussia Pacht, 1849 [_*A. membranacea_] [=_Posidonomya_ Pacht, 1852 (_non_ Bronn, 1834); _Estheria_ Jones, 1856 (_non_ Robineau-Desvoidy, 1830; _nec_ Rueppell, 1837)].

Synonymic 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 which they have in hand is not actually the original one. Although the names were separately published, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymic homonyms and in the _Treatise_ the junior one of these is indicated by the abbreviation "jr. syn. hom."

Identical family-group names not infrequently are published as new names by different authors, the author of the later-introduced name 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 are nomenclatural homonyms, based on the same type-genus, and they are also synonyms. Wherever encountered, such synonymic homonyms are distinguished in the _Treatise_ as in dealing with generic names.

SYNONYMS

Citation of synonyms is given next following record of the type-species and if 2 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. Examples showing _Treatise_ style in listing synonyms follow.

Calapoecia Billings, 1865 [_*C. anticostiensis;_ SD Lindström, 1883] [=_Columnopora_ Nicholson, 1874; _Houghtonia_ Rominger, 1876].

Staurocyclia Haeckel, 1882 [_*S. cruciata_ Haeckel, 1887] [=_Coccostaurus_ Haeckel, 1882 (obj.); _Phacostaurus_ Haeckel, 1887 (obj.)].

A synonym which also constitutes a homonym is recorded as follows:

Lyopora Nicholson & Etheridge, 1878 [_*Palaeopora? favosa_ M'Coy, 1850] [=_Liopora_ Lang, Smith & Thomas, 1940 (_non_ Girty, 1915)].

Some junior synonyms of either objective or subjective sort may take precedence desirably over senior synonyms wherever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a generic assemblage. This requires action of ICZN using its plenary powers to set aside the unwanted name and validate the wanted one, with placement of the concerned names on appropriate official lists. In the _Treatise_ citation of such a conserved generic name is given in the manner shown by the following example.

Tetragraptus Salter, 1863 [_nom. correct._ Hall, 1865 (_pro Tetragrapsus_ Salter, 1863), _nom. conserv._ proposed Bulman, 1955, ICZN pend.] [_*Fucoides serra_ Brongniart, 1828 (=_Graptolithus bryonoides_ Hall, 1858)].

ABBREVIATIONS

Abbreviations used in this division of the *Treatise* are explained in the following alphabetically arranged list.

Abbreviations

Abhandl., Abhandlung(en)
Acton., Actonian
aff., *affinis* (related to)
Afghan., Afghanistan
Afr., Africa, -an
Ala., Alabama
Alb., Albian
Alg., Algeria
Alta., Alberta
Am., America, -n
Ann., Anñaes, Annales, Annual
ant., anterior
Appalach., Appalachians
approx., approximately
Apt., Aptian
Arbeit., Arbeiten
Arch., Archipelago, Archives, Archivos
Arct., Arctic
Arg., Argentina
Ariz., Arizona
Ark., Arkansas
art., article
Artinsk., Artinskian
Ashgill., Ashgillian
Asti., Astian
Atl., Atlantic
auctt., *auctorum* (of authors)
Aus., Austria

Bajoc., Bajocian
Balt., Baltic
Barrem., Barremian
Bathon., Bathonian
B.C., British Columbia
Bd., Band
Bedfords., Bedfordshire
Beil., Beilage
Belg., Belgium, Belgique
Berrias., Berriasian
Boh., Bohemia
Bol., Bolivia
brach.v., brachial valve
Br.I., British Isles
Brit., Britain, British
Bull., Bulletin

C., Central
ca., circa
Calif., California
Callov., Callovian
Cam., Cambrian
Can., Canada
Canad., Canadian
Caradoc., Caradocian
Carb., Carboniferous
card., cardinal
Carib., Caribbean
Carn., Carnian
Cenoman., Cenomanian
cf., *confer* (compare)
Chemung., Chemungian
Chester., Chesterian
Cincinnati., Cincinnatian
circ., circular
Clinton., Clintonian
cm., centimeter
Coblenz.. Coblenzian
Coll., Collection(s)
Colo., Colorado
Colom., Colombia
congl., conglomerate
Contrib., Contribution(s)
cosmop., cosmopolitan
Couvin., Couvinian
Cret., Cretaceous
Czech., Czechoslovakia

Dan., Danian
D.C., District of Columbia
decort., decorticated
Deerpark., Deerparkian
Denbighs., Denbighshire
Denkschr., Denkschrift(en)
Denm., Denmark
Derbys., Derbyshire
Desmoines., Desmoinesian
Dev., Devonian
Devon., Devonshire
diagram., diagrammatic
Distr., District
Dol., Dolomite
Domer., Domerian
dors., dorsal

E., East
ed., editor
edit., edition
e.g., *exempli gratia* (for example)
Eifel., Eifelian
enl., enlarged
emend., *emendatus(-a)*
Ems., Emsian
Eng., England
Eoc., Eocene
equiv., equivalent, -s
err., *errore* (by error)
Est., Estonia
et al., *et alii* (and others, persons)
etc., *et cetera* (and others, objects)
Etroeungt., Etroeungtian
Eu., Europe
exfol., exfoliated
ext., exterior

F., Formation
fam., family
Famenn., Famennian
fig., figure, -s
Förhandl., Förhandlingar
Forhandl., Forhandlinger
Fr., France, French, Français, -e
Frasn., Frasnian
Ft., Fort

G.Brit., Great Britain
Gedinn., Gedinnian
Geol., Geology, Geological, Geologische, etc.
Ger., Germany, German
Givet., Givetian
Glos., Glocestershire
Gotl., Gotland
Gotland., Gotlandian
Gr., Group
Greenl., Greenland
Gt., Great
Guadalup., Guadalupian

Hamilton., Hamiltonian
Handl., Handlingar
Hauteriv., Hauterivian
Helderberg., Helderbergian
Hemis., Hemisphere
Herefords., Herfordshire
Hettang., Hettangian
hom., homonym
Hung., Hungary, Hungarica

I., Isle
ICZN, International Commission of Zoological Nomenclature
i.e., *id est* (that is)
Ill., Illinois
illus., illustration, -s
incl., including
incompl., incomplete
indet., indetermined
Ind., Indiana
Ind.O., Indian Ocean
Indon., Indonesia
Inf., Inferior
int., interior
Ire., Ireland
Is., Island, -s
Izv., Izvestiya

Jahrb., Jahrbuch
Jahrg., Jahrgang
Jct., Junction
Jour., Journal
jr., junior
Jur., Jurassic

Kans., Kansas
Kazakh., Kazakhstan
Kimmeridg., Kimmeridgian
Kinderhook., Kinderhookian
Ky., Kentucky

L., Low., Lower
lat., lateral
Leonard., Leonardian
Lias., Liassic
Llandeil., Llandeilian
Llandover., Llandoverian

Llanvirn., Llanvirnian
loc. cit., *loco citato* (in the place cited)
long., longitudinal
Longvill., Longvillian
Ls., Limestone
Ludlov., Ludlovian

m., meter
M., **Mid.**, Middle
M, monotypy
Maastricht., Maastrichtian
mag., magnification
Mag., Magazin, Magazine
max., maximum
Maysvill., Maysvillian
Md., Maryland
Medit., Mediterranean
Mem., Memoir, -s, Memoria, Memorie
Mém., Mémoire, -s
Meramec., Meramecian
Mex., Mexico
Mich., Michigan
Minn., Minnesota
Mio., Miocene
Miss., Mississippi, Mississippian
Mitt., Mitteilungen
mm., millimeter, -s
Mo., Missouri
Mohawk., Mohawkian
Mon., Monograph, Monographia
Mongol., Mongolia
Mont., Montana
Morrow., Morrowan
Moscov., Moscovian
Mts., Mountains

n., new
N., North
N.Am., North American, -n
Namur., Namurian
Nat., Natural
Natl., National
N.B., New Brunswick
NE., Northeast
Neb., Nebraska
Neocom., Neocomian
Neog., Neogene
Neth., Netherlands
Nev., Nevada
Newf., Newfoundland
N.J., New Jersey
N.Mex., New Mexico
no., number
nom. conserv., *nomen conservatum* (conserved name)
nom. correct., *nomen correctum* (corrected or intentionally altered name)
nom. imperf., *nomen imperfectum* (imperfect name)
nom. neg., *nomen negatum* (denied name)
nom. nov., *nomen novum* (new name)
nom. nud., *nomen nudum* (naked name)
nom. null., *nomen nullum* (null, void name)
nom. oblit., *nomen oblitum* (forgotten name)
nom. subst., *nomen substitutum* (substitute name)
nom. transl., *nomen-translatum* (transferred name)
nom. van., *nomen vanum* (vain, void name)
nom. vet., *nomen vetitum* (impermissible name)
Nor., Norian
Nov., Novitates
N.Scotia, Nova Scotia
NW., Northwest
N.W.T., Northwest Territories
N.Y., New York
N.Z., New Zealand
N.Zem., Novaya Zemlya

O., Ocean
obj., objective
OD, original designation
Okla., Oklahoma
Oligo., Oligocene
Onondag., Onondagan
Ont., Ontario
Ool., Oolite
Opin., Opinion
Ord., Ordovician
Ore., Oregon
Osag., Osagian
Oxford., Oxfordian

p., page, -s
Pa., Pennsylvania
Pac., Pacific
Pak., Pakistan
Paleoc., Paleocene
Paleog., Paleogene
Paleoz., Paleozoic
ped.v., pedicle valve
pend., pending
Penin., Peninsula
Penn., Pennsylvanian
Perm., Permian
Permocarb., Permocarboniferous
Philip., Philippines
pl., plate, -s, plural
Pleist., Pleistocene
Pliensbach., Pliensbachian
Plio., Pliocene
Pol., Poland
Port., Portugal
Portland., Portlandian
post., posterior
Proc., Proceedings
Prof., Professional
Prov., Province
pt., part, -s
publ., publication, published

Qtzt., Quartzite
Quart., Quarterly
Que., Quebec
Queensl., Queensland

Rec., Recent, Record
reconstr., reconstructed, -ion
Rept., Report
Rhaet., Rhaetian
Richmond., Richmondian
Rozpr., Rozpravy

S., South, Sea
Sakmar., Sakmarian
S.Am., South America
Santon., Santonian
Scand., Scandinavia
S.Car., South Carolina
Scot., Scotland
SD, subsequent designation
S.Dak., South Dakota
SE., Southeast
sec., section, -s
Senon., Senonian
sep., separate
ser., series, serial, etc.
Sh., shale
Shrops., Shropshire
Sib., Siberia
Siegen., Siegenian
Sil., Silurian
Sinemur., Sinemurian
sing., singular
Sitzungsber., Sitzungsberichte
Skrift., Skrifter
s.l., **s.lat.**, *sensu lato* (in the wide sense, broadly defined)
SM, subsequent monotypy
Somerset., Somersetshire
sp., species (spp., plural)
spec., special, specimen
Spitz., Spitzbergen
sr., senior
s.s., **s.str.**, *sensu stricto* (in the strict sense, narrowly defined)
Ss., Sandstone
St., Saint
Stirlings., Stirlingshire
Str., Strait, -s
subfam., subfamily
subj., subjective
superfam., superfamily
suppl., supplement
SW., Southwest
Swed., Sweden
Switz., Switzerland
syn., synonym

Tasm., Tasmania
Tenn., Tennessee
Terr., Territory, -ies
Tert., Tertiary
Tex., Texas
Tithon., Tithonian
Toarc., Toarcian
Tournais., Tournaisian
Trans., Transactions
transl., translated, translation
transv., transverse
Tremadoc., Tremadocian
Trenton., Trentonian
Trias., Triassic
Turon., Turonian

U., Up., Upper
Univ., Universidad, Università, Universität, Université, Universitets, University
Ural., Uralian
U.S., United States
USA, United States (America)
USSR, Union of Soviet Socialist Republics

v., volume, -s
Va., Virginia
Valangin., Valanginian
var., variety
Venez., Venezuela
vent., ventral
ventrolat., ventrolateral
Verhandl., Verhandlungen
Vict., Victoria
Virgil., Virgilian
Volg., Volgian
Vt., Vermont

W., West
Wash., Washington
Wenlock., Wenlockian
Westphal., Westphalian
Whiterock., Whiterockian
Wilts., Wiltshire
W.Ind., West Indies
Wis., Wisconsin
Wolfcamp., Wolfcampian
Wyo., Wyoming

Yorks., Yorkshire
Yugosl., Yugoslavia

Z., Zone
Zech., Zechstein
Zeitschr., Zeitschrift

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a selected list of references to paleontological literature consisting primarily of recent and comprehensive monographs available but also including some older works recognized as outstanding in importance. The purpose of giving these references is to aid users of the *Treatise* in finding detailed descriptions and illustrations of morphological features of fossil groups, discussions of classifications and distribution, and especially citations of more or less voluminous literature. Generally speaking, publications listed in the *Treatise* are not original sources of information concerning taxonomic units of various rank but they tell the student where he may find them; otherwise it is necessary to turn to such aids as the *Zoological Record* or Neave's *Nomenclator Zoologicus*. References given in the *Treatise* are arranged alphabetically by authors and accompanied by index numbers which serve the purpose of permitting citation most concisely in various parts of the text; these citations of listed papers are enclosed invariably in parentheses and except in Part C, are distinguishable from dates because the index numbers comprise no more than 3 digits. The systematic descriptions given in Part C are accompanied by a reference list containing more than 2,000 entries; the index numbers for them are marked by an asterisk.

The following is a statement of the full names of serial publications which are cited in abbreviated form in the *Treatise* lists of references. The information thus provided should be useful in library research work. The list is alphabetized according to the serial titles which were employed at the time of original publication. Those following it in brackets are those under which the publication may be found currently in the *Union List of Serials,* the United States Library of Congress listing, and most library card catalogues. The names of serials published in Cyrillic are transliterated; in the reference lists these titles, which may be abbreviated, are accompanied by transliterated authors' names and titles, with English translation of the title. The place of publication is added (if not included in the serial title).

The method of transliterating Cyrillic letters that is adopted as "official" in the *Treatise* is the so-called Anglo-American method given by the Geographical Society of London. It follows that names of some Russian authors in transliterated form derived in this way differ from other forms, possibly including one used by the author himself. In *Treatise* reference lists the alternative (unaccepted) form is given enclosed by square brackets (e.g., Chernyshev [Tschernyschew], T. N.; Gekker [Hecker], R. F.).

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Akademiya Nauk Kazakhskoy SSR, Izvestiya. Alma-Ata.
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[1] R. or K. preceding a serial title stands for all forms meaning royal, imperial, e.g., Royale, Reale, Königliche, Kaiserliche, Kongelig, etc.

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SOURCES OF ILLUSTRATIONS

At the end of figure captions an index number is given to supply record of the author of illustrations used in the *Treatise,* reference being made either (1) to publications cited in reference lists or (2) to the names of authors with or without indication of individual publications concerned. Previously unpublished illustrations are marked by the letter "n" (signifying "new") with the name of the author.

STRATIGRAPHIC DIVISIONS

Classification of rocks forming the geologic column as commonly cited in the *Treatise* in terms of units defined by concepts of time is reasonably uniform and firm throughout most of the world as regards major divisions (e.g., series, systems, and rocks representing eras) but it is variable and unfirm as regards smaller divisions (e.g., substages, stages, and subseries), which are provincial in application. Users of the *Treatise* have suggested the desirability of publishing reference lists showing the stratigraphic arrangement of at least the most commonly cited divisions. Accordingly, a tabulation of European and North American units, which broadly is applicable also to other continents, is given here.

Generally Recognized Divisions of Geologic Column

EUROPE	NORTH AMERICA
ROCKS OF CENOZOIC ERA	**ROCKS OF CENOZOIC ERA**
NEOGENE SYSTEM^{1}	**NEOGENE SYSTEM**^{1}
Pleistocene Series (including Recent)	Pleistocene Series (including Recent)
Pliocene Series	Pliocene Series
Miocene Series	Miocene Series
PALEOGENE SYSTEM	**PALEOGENE SYSTEM**
Oligocene Series	Oligocene Series
Eocene Series	Eocene Series
Paleocene Series	Paleocene Series
ROCKS OF MESOZOIC ERA	**ROCKS OF MESOZOIC ERA**
CRETACEOUS SYSTEM	**CRETACEOUS SYSTEM**
Upper Cretaceous Series	**Gulfian Series (Upper Cretaceous)**
Maastrichtian Stage^{2}	Navarroan Stage
Campanian Stage^{2}	Tayloran Stage
Santonian Stage^{2}	Austinian Stage
Coniacian Stage^{2}	
Turonian Stage	
Cenomanian Stage	Woodbinian (Tuscaloosan) Stage
	Comanchean Series (Lower Cretaceous)
	Washitan Stage
Lower Cretaceous Series	
Albian Stage	Fredericksburgian Stage
	Trinitian Stage
Aptian Stage	
	Coahuilan Series (Lower Cretaceous)
Barremian Stage^{3}	Nuevoleonian Stage
Hauterivian Stage^{3}	
Valanginian Stage^{3}	Durangoan Stage
Berriasian Stage^{3}	
JURASSIC SYSTEM	**JURASSIC SYSTEM**
Upper Jurassic Series	**Upper Jurassic Series**
Portlandian Stage^{4}	Portlandian Stage
Kimmeridgian Stage	Kimmeridgian Stage
Oxfordian Stage	Oxfordian Stage
Middle Jurassic Series	**Middle Jurassic Series**
Callovian Stage (or Upper Jurassic)	Callovian Stage (or Upper Jurassic)
Bajocian Stage	Bathonian Stage
Bathonian Stage	Bajocian Stage

Lower Jurassic Series (Liassic)	**Lower Jurassic Series (Liassic)**
Toarcian Stage	Toarcian Stage
Pliensbachian Stage	Pliensbachian Stage
Sinemurian Stage	Sinemurian Stage
Hettangian Stage	Hettangian Stage
TRIASSIC SYSTEM	**TRIASSIC SYSTEM**
Upper Triassic Series	**Upper Triassic Series**
Rhaetian Stage[5]	(Not recognized)
Norian Stage	Norian Stage
Carnian Stage	Carnian Stage
Middle Triassic Series	**Middle Triassic Series**
Ladinian Stage	Ladinian Stage
Anisian Stage (Virglorian)	Anisian Stage
Lower Triassic Series	**Lower Triassic Series**
Scythian Series (Werfenian)	Scythian Stage
ROCKS OF PALEOZOIC ERA	**ROCKS OF PALEOZOIC ERA**
PERMIAN SYSTEM	**PERMIAN SYSTEM**
Upper Permian Series	**Upper Permian Series**
Tartarian Stage[6]	Ochoan Stage
Kazanian Stage [7]	Guadalupian Stage
Kungurian Stage	
Lower Permian Series	**Lower Permian Series**
Artinskian Stage[8]	Leonardian Stage
Sakmarian Stage	Wolfcampian Stage
CARBONIFEROUS SYSTEM	
Upper Carboniferous Series	**PENNSYLVANIAN SYSTEM**
Stephanian Stage	**Kawvian Series (Upper Pennsylvanian)**
	Virgilian Stage
	Missourian Stage
Westphalian Stage	**Oklan Series (Middle Pennsylvanian)**
	Desmoinesian Stage
	Bendian Stage
	Ardian Series (Lower Pennsylvanian)
	Morrowan Stage
	MISSISSIPPIAN SYSTEM
	Tennesseean Series (Upper Mississippian)
Namurian Stage	Chesteran Stage
Lower Carboniferous Series	
Visean Stage	Meramecian Stage
	Waverlyan Series (Lower Mississippian)
Tournaisian Stage	Osagian Stage
Strunian Stage	Kinderhookian Stage
DEVONIAN SYSTEM	**DEVONIAN SYSTEM**
Upper Devonian Series	**Chautauquan Series (Upper Devonian)**
Famennian Stage	Conewangoan Stage
	Cassadagan Stage
Frasnian Stage	**Senecan Series (Upper Devonian)**
	Chemungian Stage
	Fingerlakesian Stage

Middle Devonian Series	**Erian Series (Middle Devonian)**
Givetian Stage	Taghanican Stage Tioughniogan Stage
Couvinian Stage	Cazenovian Stage
Lower Devonian Series	**Ulsterian Series (Lower Devonian)**
Coblenzian Stage	Onesquethawan Stage Deerparkian Stage
Gedinnian Stage	Helderbergian Stage
SILURIAN SYSTEM	**SILURIAN SYSTEM**
Ludlow Series	**Cayugan Series** Includes age equivalents of middle and upper Ludlow (in New York)
Wenlock Series	**Niagaran Series** Includes age equivalents of upper Llandovery, Wenlock, and lower Ludlow (in New York)
Landovery Series	**Medinan Series** Includes age equivalents of lower and middle Llandovery (in New York)
ORDOVICIAN SYSTEM	**ORDOVICIAN SYSTEM**
	Cincinnatian Series (Upper Ordovician)
Ashgill Series	Richmondian Stage Maysvillian Stage Edenian Stage
Caradoc Series	**Champlainian Series (Middle Ordovician)** Mohawkian Stage Trentonian Substage Blackriveran Substage
Llandeilo Series **Llanvirn Series**	Chazyan Stage
Arenig Series **Tremadoc Series**[9]	**Canadian Series (Lower Ordovician)**
CAMBRIAN SYSTEM	**CAMBRIAN SYSTEM**
Upper Cambrian Series	**Croixian Series (Upper Cambrian)** Trempealeauan Stage Franconian Stage Dresbachian Stage
Middle Cambrian Series	**Albertan Series (Middle Cambrian)**
Lower Cambrian Series	**Waucoban Series (Lower Cambrian)**
EOCAMBRIAN SYSTEM	**EOCAMBRIAN SYSTEM**
ROCKS OF PRECAMBRIAN AGE	**ROCKS OF PRECAMBRIAN AGE**

RAYMOND C. MOORE

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[1] Considered by some to exclude post-Pliocene deposits.

[2] Classed as division of Senonian Subseries.

[3] Classed as division of Neocomian Subseries.

[4] Includes Purbeckian deposits.

[5] Interpreted as lowermost Jurassic in some areas.

[6] Includes some Lower Triassic and equivalent to upper Thuringian (Zechstein) deposits.

[7] Equivalent to lower Thuringian (Zechstein) deposits.

[8] Equivalent to upper Autunian and part of Rotliegend deposits.

[9] Classed as uppermost Cambrian by some geologists.

PART H
BRACHIOPODA

By Alwyn Williams, A. J. Rowell, H. M. Muir-Wood, Charles W. Pitrat, Herta Schmidt, F. G. Stehli, D. V. Ager, A. D. Wright, G. F. Elliott, T. W. Amsden, M. J. S. Rudwick, Kotora Hatai, Gertruda Biernat, D. J. McLaren, A. J. Boucot, J. G. Johnson, R. D. Staton, R. E. Grant, and H. M. Jope

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INTRODUCTION
By Alwyn Williams

[The Queen's University, Belfast]

Brachiopods are solitary marine animals commonly anchored to the substratum by a fleshy stalk or pedicle. The soft parts are protected by a pair of valves of variable organic and mineral composition, that cover the ventral and dorsal surfaces and project forward to enclose a cavity in which is suspended a filamentar feeding organ or lophophore. The body is regionated but the coelom indistinctly so and there is no real evidence of cephalization, so that only a small fold above the mouth can doubtfully be identified as the protosome, and the principal nerve center is located below the esophagus. The digestive tract is normally recurved and in articulate brachiopods it terminates blindly; metanephridia and an open circulatory system are present.

More than 1,600 brachiopod genera have been described and, judging from current research, the number is likely to increase substantially during the next decade or so. This high taxonomic activity is mainly a measure of the long and rich history of a group of animals that is now in decline. About 70 genera are found in the seas today where they constitute a negligible part of Recent marine faunas compared with the dominance and diversity of their ancestors during, for example, Caradocian time when three times as many genera are known to have existed. Nonetheless, they are still as widely distributed as they have ever been, so that living and fossil species are available in every continent.

Such a profusion of brachiopod species in time and space inevitably led to an early appreciation of their distinctive morphology. MUIR-WOOD (19) has recorded that their fossil remains attracted attention even in the Middle Ages and that from the late 16th century onward, they were regularly figured by naturalists, like GESNER, FABIO COLONNA, PLOT, etc., under a variety of names, including the pre-Linnean designation of "Terebratula" by LLHYD. The term "lamp-shell" which alludes to a likeness between the lateral profile of the terebratulid shell and the outline of a Grecian lamp, although frequently cited today as an established nontechnical name for the phylum, does not seem to have been used until the latter part of the 18th century (19).

Despite this familiarity with brachiopod shells, the practice of indiscriminately grouping all bivalves together prevailed until the close of the 18th century. LINNÉ, for example, used the generic name *"Anomia"* for Recent and fossil species of brachiopods and pelecypods, and the first adequate illustrations of internal characteristics of Recent species were not published by PALLAS (21) until 1766, only a decade earlier than the founding by MÜLLER of the first valid brachiopod genus, *Terebratula*. Indeed, even when CUVIER (4), guided by his anatomical studies of *Lingula anatina,* proposed the familial group of "Brachiopodes" (formalized by DUMÉRIL, 5) for certain "acephalous Mollusca," he did so in the belief that the uncoiled lophophore performed the same function as the molluscan foot, a fallacy that is unfortunately perpetuated in the collective name adopted by him for the group (*βραχίων*-arm, and *πούς*-foot).

During the 19th century, many aspects of brachiopod organization and history were rewardingly explored. OWEN, HUXLEY, HANCOCK, and BLOCHMANN carried out notable researches on the anatomy of brachiopods; LACAZE-DUTHIERS, KOVALEVSKIY, MORSE, MÜLLER, and SHIPLEY on their embryology, and DAVIDSON and HALL on their fossil record. Consequently by the time BEECHER (1) came to synthesize a classification for the phylum (1891), not only had many of the fundamental differences between the inarticulate and articulate brachiopods been discovered but many opinions had also been expressed on the status of the Brachiopoda within the animal kingdom.

It was inevitable that bivalved brachiopods should first be classified as mollusks. Such a procedure was adopted by CUVIER, LAMARCK, MENKE, and others early in the last century and, although doubts about its merits were soon forthcoming, it persisted for many years even as an expression of affinity (8). Meanwhile, comparative studies carried out by HANCOCK (10) on the newly understood bryozoans, led him to believe that they were closely related to both tunicates and brachiopods, and prompted HUXLEY (12) to emend MILNE-EDWARDS' molluscan "subphylum" Molluscoides to include not only bryozoans and tunicates but also brachiopods. In the course of reiterating the relationship implied in the recognition of the "Molluscoida" ("Molluscoidea" had already been proposed in place of Molluscoides and is the better-known formal version of this taxon), HUXLEY (13) rejected any suggestion of molluscan affinity for the group and later supported MORSE's contention (18) that the Brachiopoda should be grouped with the Annelida.

The debate over the molluscan or annelid affiliations of the Molluscoidea continued for some time but is really less important than the correct identification of those groups that are most closely related to brachiopods. Following KOVALEVSKIY's demonstration (15, 16) of the chordate affinities of tunicates and the precise nature of phoronid development, and NITSCHE's segregation (20) of ectoproct and entoproct bryozoans, CALDWELL (3) inferred that ectoprocts, phoronids, brachiopods, and sipunculoids were closely linked. BLOCHMANN (2) came to the same conclusion and HAECKEL (9) erected the phylum Prosopygia to accommodate all four groups. It was HATSCHEK (11), however, who expressed the relationships most satisfactorily when he excluded sipunculoids from a new phylum, Tentaculata, which embraced the Brachiopoda and two new classes, the Ectoprocta and Phoronida.

HATSCHEK's arrangement, usually with the classes elevated to phyla and grouped under the designations of Tentaculata, Lophophorata (14) or an emended Molluscoidea, has been generally adopted even in classifications of the animal kingdom that are basically different. Hence all three groups in close association have been assigned to the Protostomia by GROBBEN (6), the Coelomata or Bilateria by MARCUS (17) and the Oligomeria by HADŽI (7). It is still, however, unresolved whether brachiopods are part of an evolutionary plexus leading to either arthropods and mollusks as postulated by GROBBEN and MARCUS, or chordates as envisaged by HADŽI, or whether they and other lophophorates evolved independently of the remaining coelomates from the Protozoa.

The insignificance of brachiopods among modern marine faunas has undoubtedly been responsible for their neglect during the 20th century as living organisms worthy of intensive study. A glance at the bibliographies for the chapters on "Anatomy" and "Ecology" is alone sufficient to emphasize the need for a comprehensive reappraisal of their anatomy, function, and mode of life. Little is known about the nervous and circulatory systems, especially of articulates; while many basic histological and physiological problems on shell growth, for example, have yet to be solved. Adequate embryological studies are so few and even conflicting in certain fundamental matters, like the origin of the coelom, that they have tended to raise more questions than have been answered. Even less information is available on the relationship between the living brachiopod and its environment. As is stated in the chapter on "Ecology," much more reliable data are required on such elementary aspects of brachiopod life as feeding habits, respiration, and population distributions and structures, before most of the fossil evidence can be interpreted with any confidence. Clearly such deficiencies as these preclude any definitive conclusions on the organization of living forms and reduce the prospects of significant advances in paleontological research.

The preponderance of paleontological data has had a profound effect on the mode of study and classification of the Brachiopoda in that variation in the exoskeleton has always been accepted as the chief gauge of diversity of the phylum and relationships within it. In some respects, this bias has its advantages since it ensures a similar systematic approach to both living and extinct forms. Less desirable features include the creation of a large and complicated terminology mainly to draw attention to minor differences in shell morphology. Altogether about 700 terms have been employed in past descriptions of brachiopods and despite the pruning indulged in during the compilation of the glossary, about 500 still survive. A number of the established terms are justifiable because each conveys through one word or phrase the subtle complexity of a particular characteristic which would otherwise have to be described at some length in a variety of languages. Others, however, are either synonyms in that they are used for structures of the same origin in different fossil groups or have been coined for unimportant growth variants of a well-known feature. Consequently in the chapter on "Morphology" and in the accompanying glossary, an attempt has been made to relate shell differences to processes of growth and to identify homologous features in unrelated groups, in the hope of achieving a consistent terminology of manageable proportions that will act as a deterrent to any further maintenance of elaborate private vocabularies.

All classifications of the Brachiopoda have been based on variation in the exoskeleton. In some, the type of lophophore support is the prime factor in taxonomic segregation; in others, much more arbitrary differences, like the form of the shell, have served in this capacity. Even BEECHER's classification, exploiting the nature of the pedicle opening, which enjoyed so much popularity earlier in this century, was really an exercise in interpretative shell morphology. The chief merit of such classifications is their applicability to extinct as well as living groups: but since they are founded on changes in a few exoskeletal features that have all reappeared in independent stocks several times during brachiopod evolution, they neither epitomize phylogeny nor provide suitable morphological keys for generic dissociation.

In the classification adopted for the *Treatise,* great importance is still attached to the morphology of the shell. But the practice of using a few characters to subdivide the phylum has been discarded in favor of building up higher taxa from assemblages of related genera. This scheme not only accords more closely with known phylogenetic relationships, as is shown in the chapters on "Evolution and Phylogeny" and "Classification," but is also more adaptable for the accommodation of further discoveries.

The systematic sections of this volume include diagnoses of nearly 1,700 genera assembled in 202 families, 48 superfamilies, 11 orders, and 2 classes, all also requiring description and discussion. Such an undertaking could not have been completed without the cooperation of a large number of colleagues who readily gave contributors to this volume valuable information and access to brachiopod collections.

Dr. G. A. COOPER of the U.S. National Museum deserves special mention for providing so many of us with access to the collections at the Museum, photographs of type-species and, above all else, the benefits of his unique experience of the phylum. Other colleagues to whom we are indebted include: Mr. D. E. B. BATES, University College of Wales; Dr. F. BARTHEL, Bayerische Staatsammung für Paläontologie, Munich; Dr. W. C. BELL, University of Texas; Dr. W. T. DEAN, British Museum (Natural History); Dr. F. DEMANET, Institut Royal des Sciences Naturelles de Belgique; Dr. C. O. DUNBAR, Yale University; Dr. A. GORYANSKY, Leningrad University; Dr. V. HAVLÍČEK, Ústřední Ústav Geologický, Prague; Dr. J. G. HELMCKE, Berlin; Mrs. S. HOOD, formerly Queen's University, Belfast; Dr. V. JAANUSSON, Geologiska Institutionea, Stockholm; Dr. R. P. S. JEFFERIES, British Museum (Natural History); Dr. M. LINDSTRÖM, Lund University; Dr. J. C. MENDES, Universidade de São Paulo, Brazil; Dr. O. I. NIKIFOROVA, V.S.E.G.E.I., Leningrad; Dr. A. A. ÖPIK, Bureau of Mineral Resources Geology and Geophysics, Canberra; Dr. A. R. PALMER, U.S. National Museum; Miss M. E. PUGH, Imperial College of Science and Technology, London; Dr. A. RÕÕMUSOKS, Geological Institute, Tartu, Estonian S.S.R.; Dr. M. A. RZHONSNITSKAYA, Leningrad; Dr. P. SARTENAER, Institut Royal des Sciences Naturelles de Belgique; Prof. O. H. SCHINDEWOLF, Tübingen; Dr. A. N. SOKOLSKAYA, Paleontological Institute, Moscow; Dr. NILS SPJELDNAES, Universitetet Oslo; Dr. T. TJERNVIK, Lindesberg, Sweden; Dr. A. VANDERCAMMEN, Institut Royal des Sciences Naturelles de Belgique.

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BRACHIOPOD ANATOMY

By Alwyn Williams and A. J. Rowell
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GENERAL CHARACTERS

The soft parts of all living brachiopods (21) are enclosed by a pair of valves which typically are bilaterally symmetrical but dissimilar in size, shape, and even ornamentation. Posteriorly the valves may be attached to the substratum by a variably developed stalk, the **pedicle**, which normally emerges from the ventral or **pedicle valve** (Fig. 1). The dorsal or **brachial valve** is generally smaller than the pedicle valve, both of which constitute the shell. The body occupies the posterior part of the space inside the shell and the body wall is prolonged forward and folded as a pair of **mantles** lining the anterior inner surfaces of the valves to enclose the brachial or **mantle cavity** (Fig. 2). The body space or **coelomic cavity** accommodates the digestive, excretory, and reproductive organs, as well as muscle systems, some of which are responsible for movements of the valves relative to each other, including opening of the shell (gape). The mantle cavity is separated from the body by the **anterior body wall** and contains the feeding organ or **lophophore** (Fig. 1; 2,*A*). A nervous and a primitive circulatory system are present.

Despite the similarities outlined above, Recent Brachiopoda may be allocated to one of two clearly defined classes, the Inarticulata and Articulata. Modern representatives of these two groups are fundamentally different in certain aspects of their development and also in their gross morphology. Both valves of articulate brachiopods are invariably calcium carbonate and articulated by complementary teeth and sockets, while the brachial valve is commonly equipped with outgrowths forming **lophophore supports** (Fig. 2,*B*). The inorganic content of inarticulate valves, in contrast, is calcium phosphate and only exceptionally (Craniacea) calcium carbonate, and no outgrowths are developed for either articulation or lophophore support. This

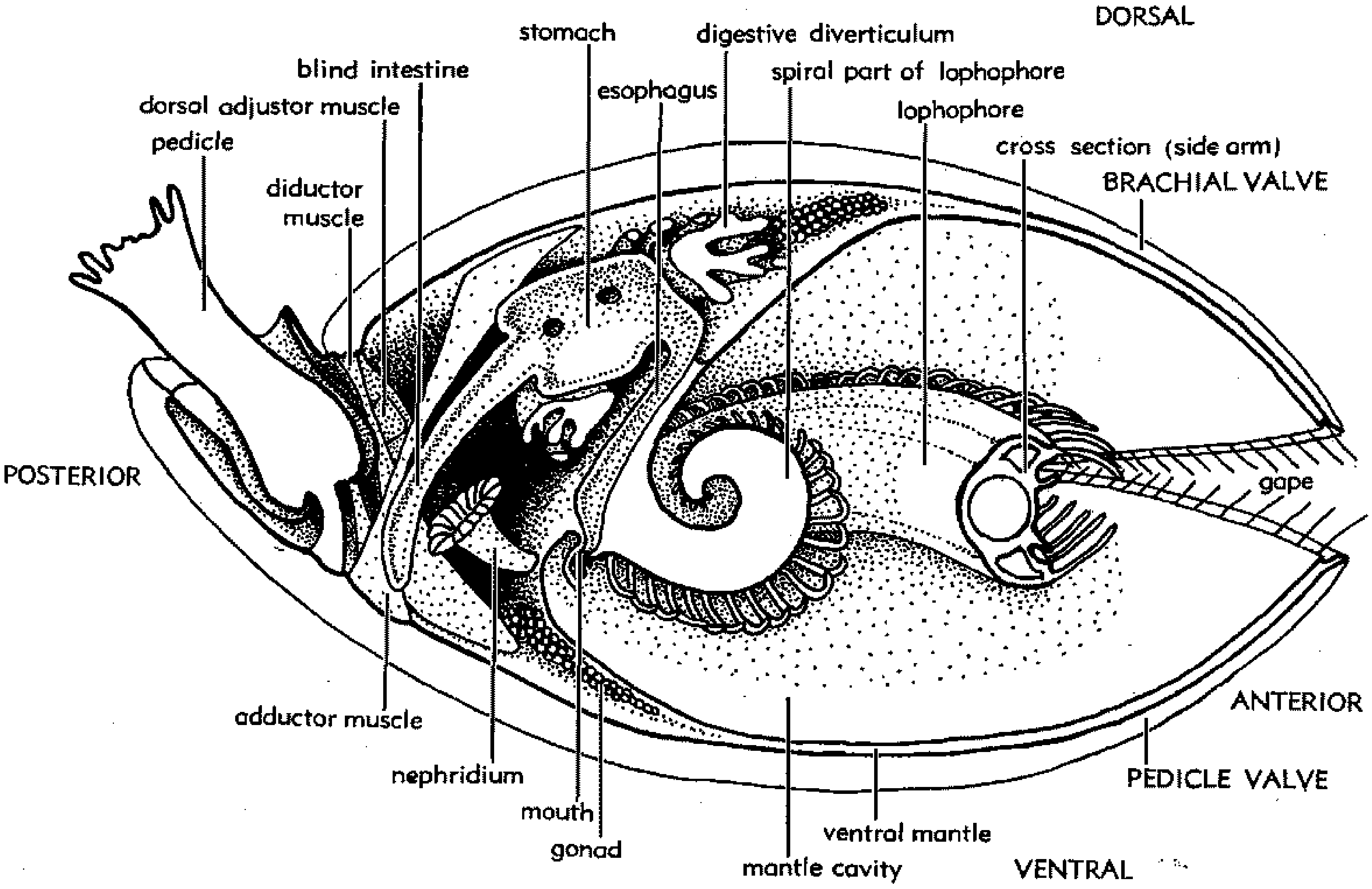

Fig. 1. Diagrammatic representation of principal organs of brachiopod typified by *Terebratulina* (48).

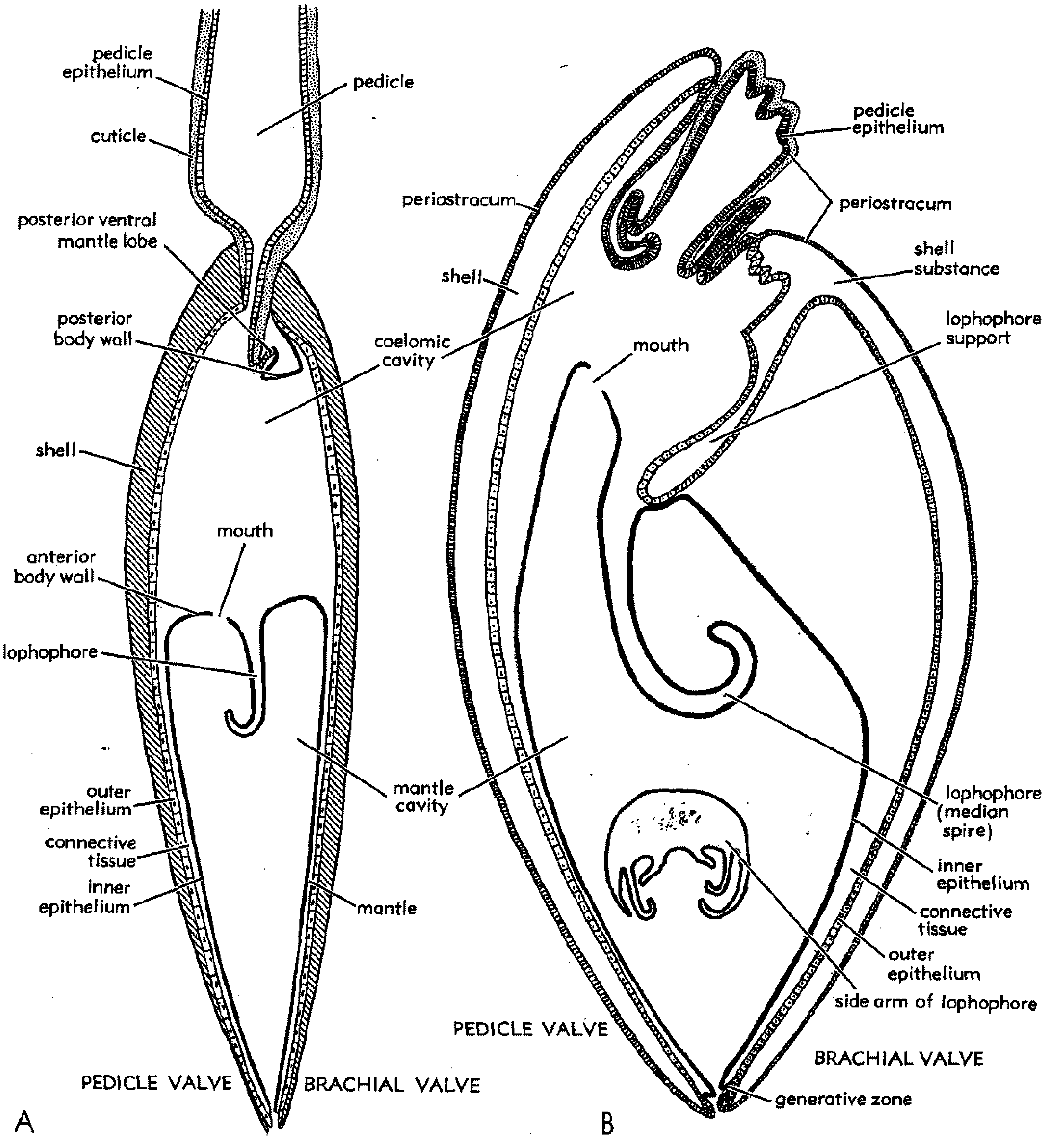

FIG. 2. Generalized representation of distribution of epithelium *(A)* in lingulids (47) and *(B)* terebratulids (44).

lack of articulation permits rotation in the plane of the margins or commissure of inarticulate valves, and consequently the musculature of the group is commonly more complex. Other internal differences are even more profound. The pedicle of articulate brachiopods develops from a primary segment of the larva, while that of the inarticulates arises from evagination of the inner surface of part of the ventral mantle. Finally, the alimentary canal of the articulates ends blindly, while that of the inarticulates terminates in an anus.

In both groups, the body wall consists of an outer layer of ectodermal **epithelium** resting on a thin connective tissue layer and lined internally by a ciliated coelomic epithelium (peritoneum). In the mantles coelomic space is greatly reduced, being limited to a number of canals, and the coelomic epithelium is correspondingly restricted in distribution. The ectodermal epithelium is responsible, among other things, for the secretion of the shell and its outgrowths, and since these are the sole remains of fossil brachiopods, it seems appropriate to begin with an account of the morphology and function of this tissue.

The external epithelium is differentiated into four distinctive zones. Posteriorly, it underlies and secretes a cuticular cover for the pedicle and is known as **pedicle epithelium** (Fig. 2,*A*,*B*). Anteriorly, it forms the selectively ciliated surface to the lophophore and also the cuboidal epithelium, which constitutes the outer and inner layers of the mantles. The **outer epithelium** secretes the shell; the **inner epithelium**, which, as previously noted, is ciliated, lines the mantle cavity, forming not only the inner surfaces of the mantle lobes but also the body wall joining the two mantles. Both outer and inner epithelia are continuous with a generative zone which in all living brachiopods (except craniaceans) is located in a sharp fold at the mantle edge. Here the cells are columnar and form an asymmetrical, bilobed structure with a long tapering outer

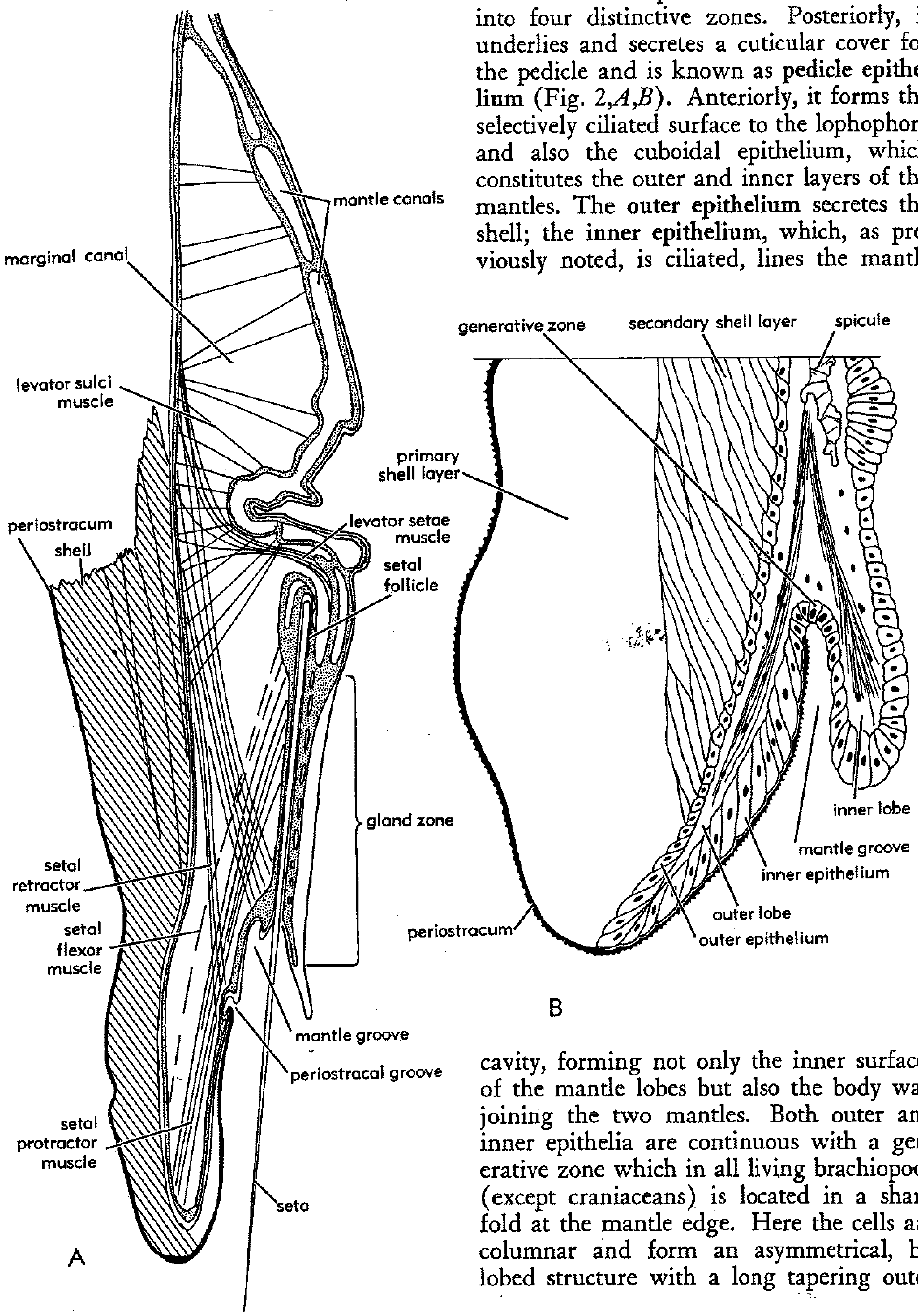

FIG. 3. Sections through anterior mantle margins of *(A) Lingula* (12) and *(B)* generalized articulate brachiopod (44).

lobe extending to the very edge of the shell and a more posteriorly situated, rounded inner lobe. The lobes are separated by a deep groove **(mantle groove)** from which arise the **setae**, the chief tactile organs of the brachiopod and a thin organic cover to the shell **(periostracum)** (Fig. 3).

The outer epithelium is therefore continuous posteriorly with the pedicle epithelium and anteriorly with the inner epithelium of the mantles. Nonetheless the boundaries of each are clearly defined and are important to an understanding of shell growth.

MANTLES

In inarticulates, the ventral and dorsal mantles are always discrete, even posteriorly about the pedicle, where a strip of body wall intervenes between the two mantle edges (Fig. 2,*A*). Over most of the area of the mantles, the inner and outer epithelium are separated only by a thin layer of connective tissue. The epithelium is typically cuboidal, and except for a peripheral zone usually occupied by the mantle groove, the inner epithelium is ciliated. Secretory cells are interspersed with cuboidal epithelium. In both mantles of the lingulids and discinids secretory cells are concentrated in a subperipheral zone roughly coincident with the base of the setae (Fig. 3,*A*).

Outgrowths of the mantle which pervade the inarticulate shell are entirely ectodermal in origin and develop at the margins of the mantles (Fig. 4,*A*). The protoplasmic strands seen as projections into the shell of *Lingula* and *Discinisca* are extremely fine and their detailed structure is still unknown. In contrast, the **caeca** of *Crania* are quite large and have a very characteristic arborescent appearance (Fig. 4,*B*), "branching" toward the outside of the shell. They arise from a peripheral zone of outer epithelium where the cells are larger than over the remainder of the mantle and strongly directed outward.

The mantle margin of *Crania* is relatively simple since the genus lacks the setae, mantle groove, and **marginal canal** found in lingulids and discinids (Fig. 3,*A*). However, a narrow peripheral zone of relatively high epithelial cells appears to secrete the periostracum on the mantle cavity or inner side of the mantle (Fig. 4,*A*). The periostracum of lingulids and discinids arises in a similar position but is secreted by a limited number of cells in the **periostracal groove**, a narrow furrow situated on the outer lip of the mantle groove (Fig. 3,*A*).

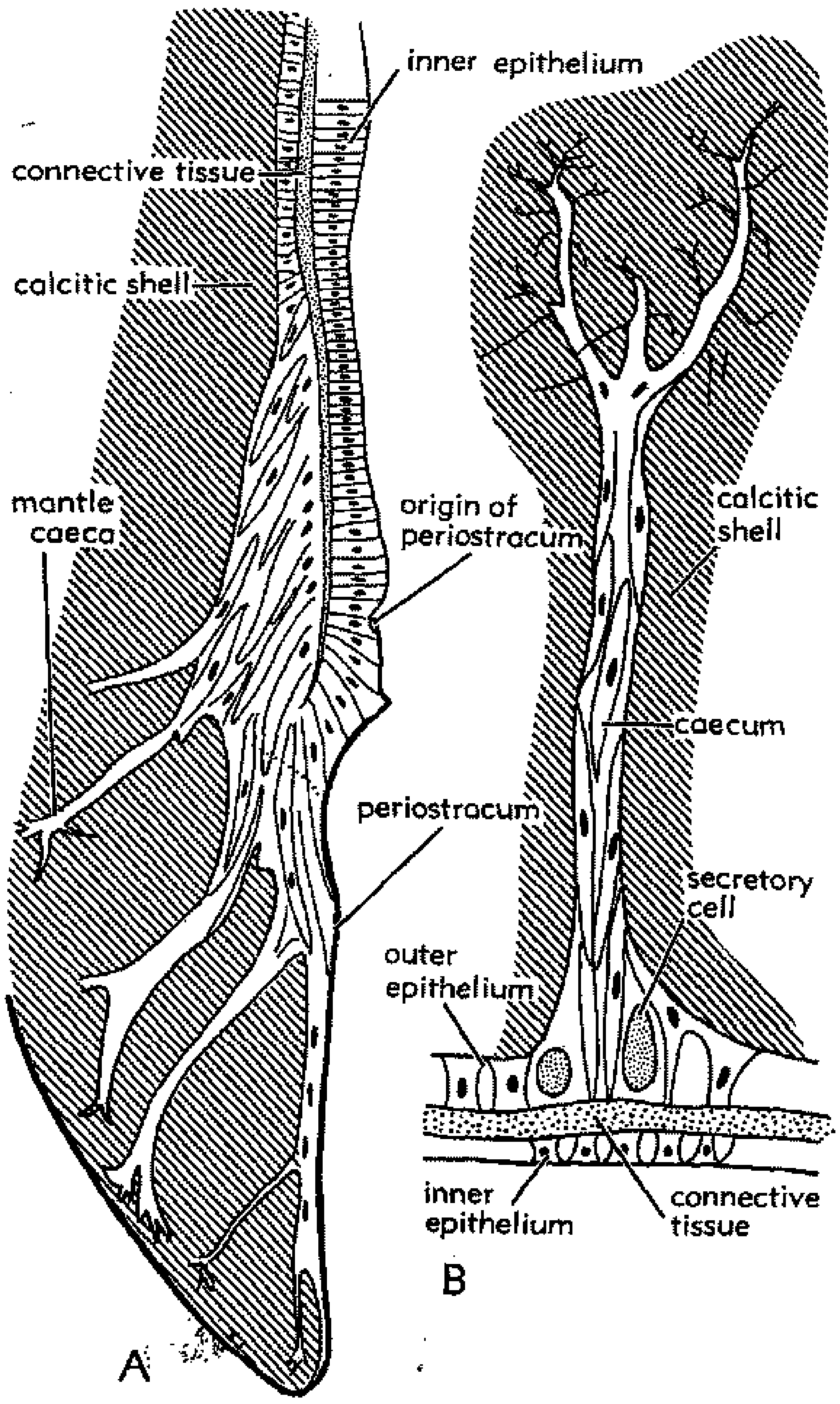

FIG. 4. Morphological features of *Crania: (A)*, section through mantle margin; *(B)*, mantle caecum (12).

The setae are developed peripherally in both valves and are only absent in the lingulids near the pedicle. Those of discinids are characteristically barbed, bearing numerous fine projections. Each seta arises from a tubelike invagination of epithelium into the connective tissue of the mantle groove and is secreted by one or more cells at the base of the follicle.

In the lingulids and discinids a large marginal canal is developed in the connective tissue of both mantles (Fig. 3,*A*). This runs peripherally around both mantle margins and is rather wider anteriorly than pos-

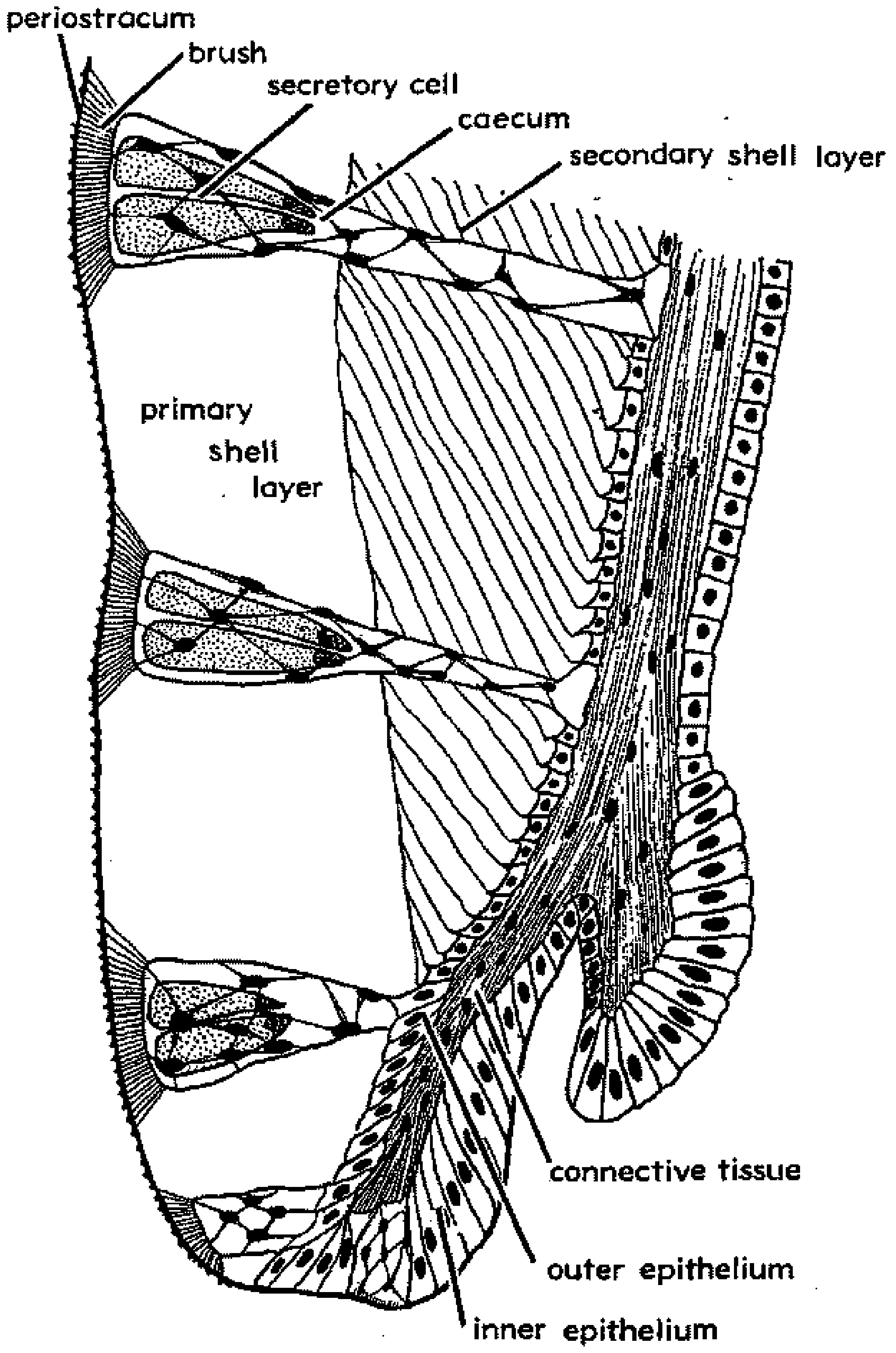

Fig. 5. Origin and growth of terebratulid caeca (44). [Noteworthy is absence of external openings to punctae (containing caeca) in shells of living terebratulids.]

teriorly. In both valves the marginal canals, which are particularly conspicuous in the lingulids, occur on the shell side of the **mantle canals** and **setal follicles** and are not in communication with the body cavity or its extensions (Fig. 3,*A*). They contain a well-developed musculature which controls movement of the setae and mantle margin. In *Discinisca* the musculature is relatively simple, consisting of radially arranged bundles of fibers attached to the base of the setal follicles peripherally and to the shell side of the marginal canal wall toward the center of the valve. The marginal musculature in *Lingula* is more complex. Five separate groups of muscles are present in the marginal canal (Fig. 3,*A*), and an additional three groups of muscles run through the connective tissue of the proximal end and inner side of the setal follicles. This elaborate musculature is undoubtedly used in formation of the setal tubes during feeding.

The mantle edge of articulate brachiopods is always clearly differentiated into an outer and inner lobe separated by a mantle groove (Fig. 3,*B*). The periostracum is spun out from the closed end of the groove and remains adherent to the inner surface of the outer lobe as far as the tip; thereafter it becomes increasingly separated from the outer epithelium by the intercalation of the growing calcareous shell. The periostracum is not a uniformly thick sheet because commonly it is differentially thickened into bars arranged in a honeycomb pattern, as in *Macandrevia*, or rarely in a diamond pattern, as in *Terebratulina*.

A complication in the details of these relationships arises in portions of the mantle containing setae. Here, the mantle groove persists as a notch on the inner surface of the outer lobe and still gives rise to the periostracum; but it is no longer bounded by the inner lobe, which is separated from it by the seta and its follicle. Such an arrangement is very like that characteristic of the lingulids (compare, Figs. 3,*A* and 7). A difference is noted, however, in that the mantle groove of the lingulids appears to be always internal of the persistent periostracal groove, whereas the mantle groove of articulate brachiopods is coincident with the "periostracal notch" between the follicles. Whether this difference is really a reflection of the very much greater density of setae along the lingulid mantle edge remains to be seen.

The posterior migration of caecal outgrowths from the outer lobe of the mantle edge in punctate shells (Fig. 5) shows that the groove is an epithelial generative zone responsible for enlargement of the shell. The origin and disposition of the periostracum suggest that the actual generative zone is the closed end of the mantle groove (44). If this is so, the entire outer lobe is the region of proliferation and differentiation for the continuously migrating outer epithelial cells and the inner lobe serves a similar function for the inner epithelium.

At the tip of the outer lobe a physiological change[1] must occur within the migrating

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[1] A comparable change, but generally involving the secretion of calcium phosphate, presumably also occurs at the tip of the outer lobe of inarticulate brachiopods.

columnar epithelial cells which had hitherto been secreting periostracum, because here they begin depositing a two-layered calcareous shell, an outer **primary layer** and an inner **secondary layer** (Fig. 3,*B*; 5). The primary layer is secreted only by those columnar cells forming the outer boundary of the outer lobe so that it is a continuous sheet, the thickness of which is related to the number of cells involved in its secretion. The layer has a finely fibrous texture with the long axes of the fibers coincident with their crystallographic *c*-axes and normal to the shell surface; it is entirely inorganic in composition and must have been deposited extracellularly. Immediately behind the primary layer the cells of the underlying epithelium become cuboidal and begin to secrete the secondary layer, which may continue over the entire surface of the outer epithelium within the peripheral outer lobe. The layer is therefore variable in thickness and consists of long, thin fibers of calcite disposed at low, oblique angles to the primary layer. Each fiber is well defined, for it is secreted by one cell only and is enclosed in a delicate cytoplasmic sheath which probably represents a greatly extended cell membrane so that deposition was intracellular. The *c*-axes of the secondary layer are oblique to the long axes of the fibers but parallel with those of the primary layer, and the distinction between the two layers is due ultimately to the intracellular secretion of the former and the extracellular deposition of the latter.

All internal features of the brachiopod skeleton, like the articulatory devices of teeth and sockets, complex as well as simple supports for the lophophore, elaborate platforms for the insertion of muscle bases, etc., are composed of secondary shell, and their growth is due to accelerated secretion in localized zones of the outer epithelium (44). The only calcareous deposits not built up in this way are irregular bodies or spicules occurring within the connective tissue of the mantle and lophophore of some articulate brachiopods. They are secreted by mesenchymous cells, and although they are densely developed in certain brachiopods like *Terebratulina* and *Fallax* (Fig. 6), and have also rarely been found loose in fossil thecideaceans, they never contribute to the solid skeleton.

As in most inarticulates, follicles occur at regular intervals along the mantle edge of articulate brachiopods and bear one, or exceptionally two or more, ringed setae (Fig. 7). Movement of the setae is also controlled by muscles attached to the follicular bases which are served not by a marginal canal but by terminal branches of the mantle canal system.

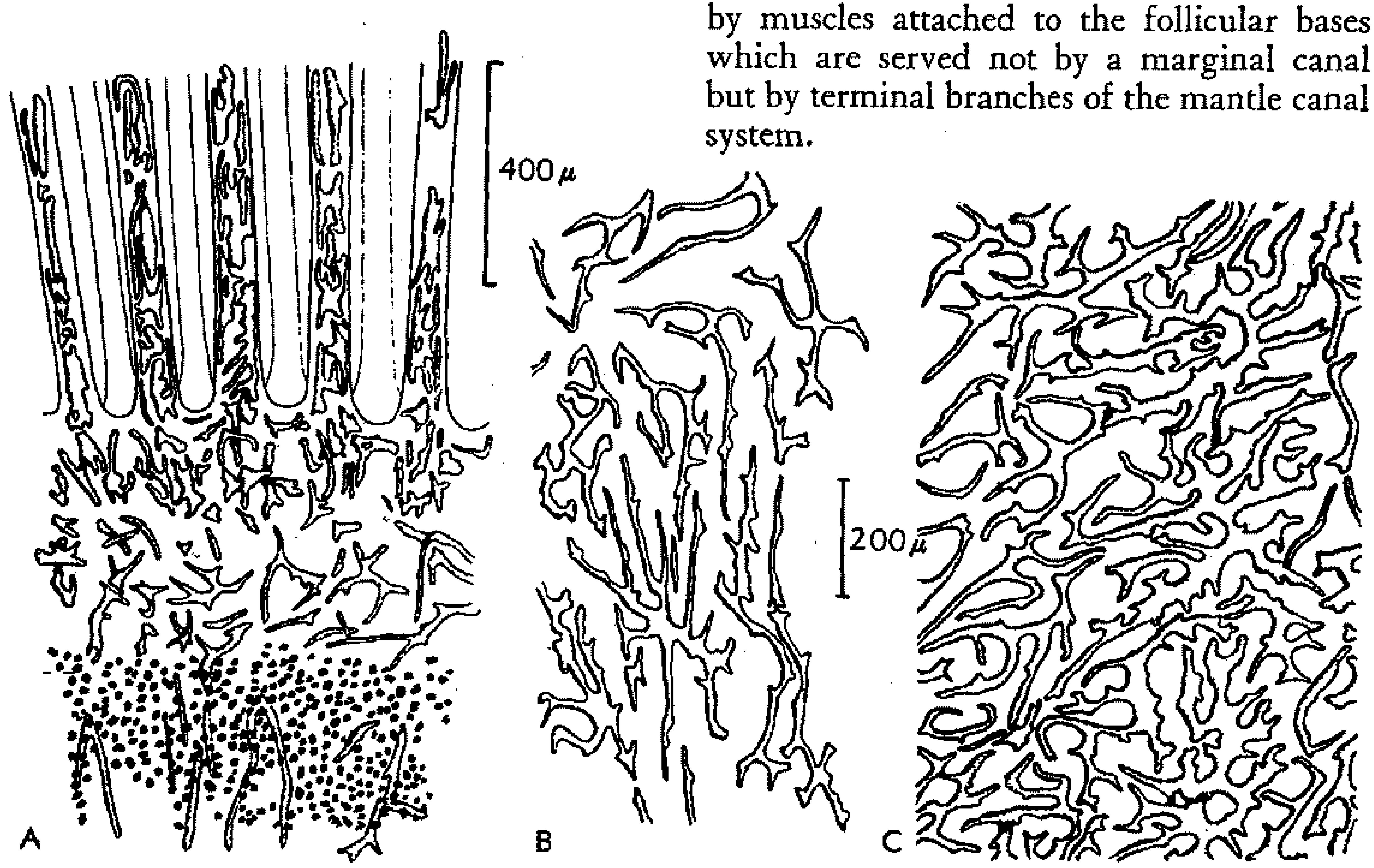

FIG. 6. Spiculation in *Fallax dalliniformis* ATKINS: *(A)* of ablabial filaments and lophophore, *(B)* of body wall, and *(C)* of mantle over gonad (6).

The growth of the shell leading to a triple stratification of periostracum, primary layer of calcite, and secondary layer of calcite is typical of all living articulate brachiopods (Fig. 3,*B*; 5). But the terebratuloid shell is also characterized by the presence of numerous caecal evaginations of the mantle (**endopunctate** condition) (Fig. 5) in contrast to their absence in Recent rhynchonelloid[1] shells (**impunctate** condition) (Fig. 3,*B*). Each caecum first appears along the inner surface of the outer lobe as a small bud consisting of a few large cells but is not fully differentiated until it reaches the tip. At this stage it is cup-shaped and is connected with the periostracum by numerous fine cytoplasmic strands (**brush**) radiating from a membranous cover to a conical lumen. As the caecum migrates posteriorly along the outer lobe a few elongated mucus gland cells appear within the lumen. The entire secretory portion of the caecum to the tips of its brush is completely encased in the calcite of the primary layer and at the junction of the primary and secondary layers a stalk, connecting the cup with the outer epithelium, is formed. As the valves expand peripherally, the caeca come to occupy an increasingly intramarginal position and may keep pace with the progressive thickening of the encasing secondary shell substance by convergence of adjacent stalks to give a branching effect, as in *Terebratulina.*

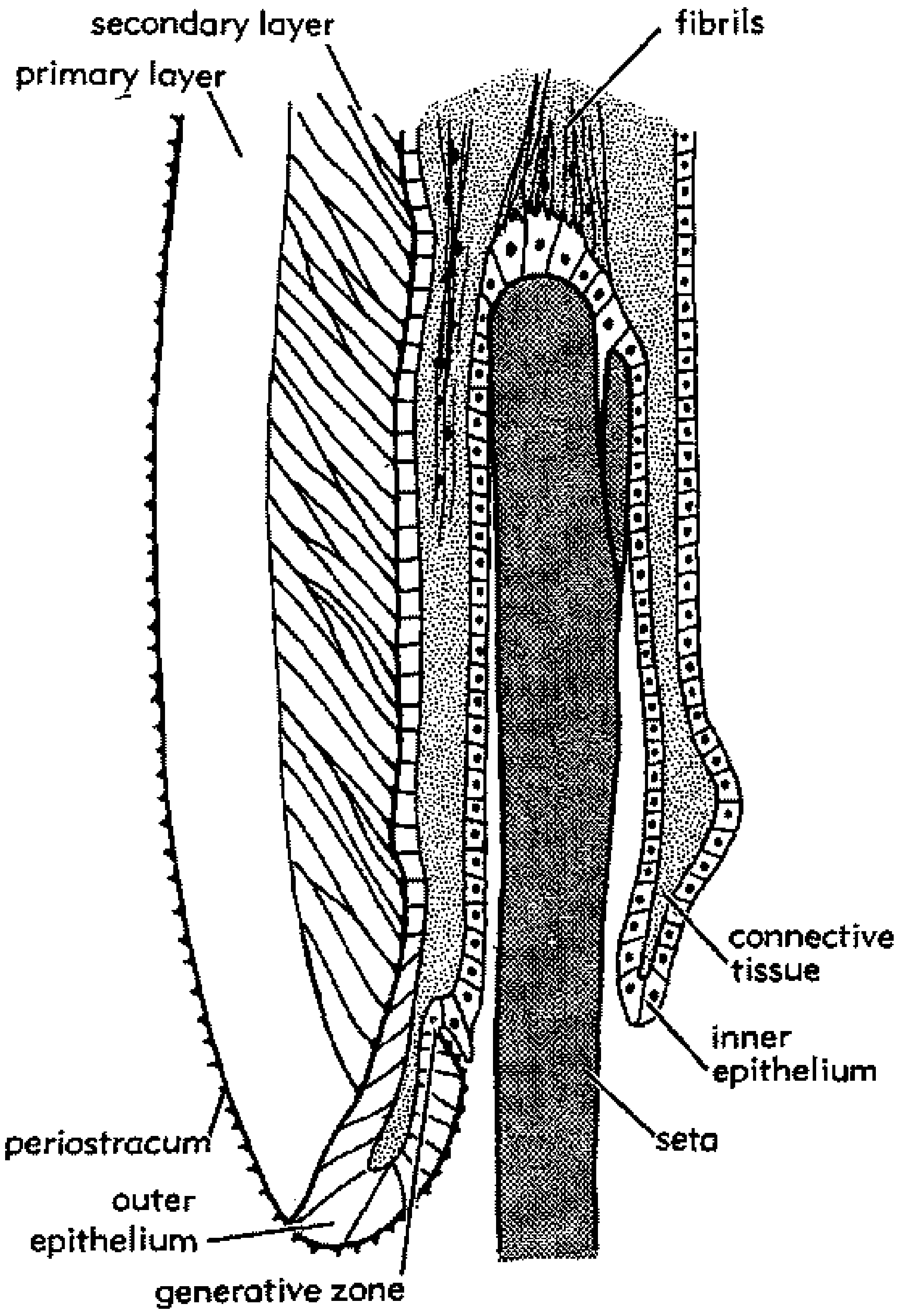

Fig. 7. Generalized diagram of mantle edge of *Terebratulina* showing follicle with seta (48).

The growth of the valves outlined above is typical of any free mantle edge corresponding to the gape of articulate shells, but posteriorly around the pedicle and in the region where the valves articulate an important modification occurs.

The shell of an articulate brachiopod may be compared with a pair of very asymmetrical cones built up from the apices (umbones) by retardation of growth in a pair of short inner posterior sectors which are represented externally by triangular sur-

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[1] **Vernacular designations of brachiopods.** It is a common and useful practice in writing about fossils to employ vernacular terms (common nouns, almost invariably in plural form, and adjectives) for assemblages of various taxonomic rank, but mostly suprageneric. Such terms appear in all *Treatise* volumes. In dealing with the Brachiopoda, however, problems have been encountered in this area, because no consistent procedure in anglicizing formal zoological names has been agreed on by authors and accepted editorially. Typescripts submitted for publication have referred to brachiopod groups called "rhynchonelloids," "rhynchonellaceids," "chonetids," "scaphelasmatinids" and numerous others. What are these? Should readers understand that "-oids" indicates a brachiopod group resembling and related to the genus from which the first part of the name is derived, without connotation of any particular taxonomic assemblage (order, suborder, superfamily, family, subfamily, genus)? Some authors are unconcerned about this, whereas others think that each particular taxonomic category needs to be specified. The termination "-aceans" (not "-aceids") is satisfactory for superfamilies, and "-ids" is appropriate for family-rank groups but in my opinion inappropriate for other assemblages.

Belatedly (that is, after very much *Treatise* typescript had been set in galleys) Rowell & Williams have advocated rejection of "-oids" for vernacular names of brachiopod groups, despite general acceptance of them by paleontologists and despite their own usage of them in earlier-submitted typescripts. Their objection to "-oids" stemmed from asserted ambiguity of its taxonomic signification or at least its insufficient precision in referring to orders, suborders, superfamilies, or some other assemblage. As substitute they recommended that groups of ordinal rank (e.g., Orthida) should be referred to as "-ides" (e.g., orthides), and those of subordinal rank (e.g., Orthidina) as "idines" (e.g., orthidines). Superfamilies (e.g., Orthacea) can be cited readily in vernacular terms with the termination "-aceans" (e.g., orthaceans) and families (e.g., Orthidae) with ending in "-ids" (e.g., orthids). For subfamily-rank groups they proposed adoption of anglicized names ending in "-ins" (e.g., Orthinae, orthins). Adjectival words for each of these categories are derived simply by dropping the "s" of plural nouns. This scheme has the merit of allowing precise taxonomic groups to be cited for reference but it is objected to by some highly qualified *Treatise* advisers as too technical and complicated, thus very unlikely to win acceptance by paleontologists, either specialists on brachiopods or others.

Editorial decision is to accept the anglicized designations of brachiopod taxonomic groups proposed by Rowell & Williams wherever this can be accommodated without resetting of type but to retain such vernacular names as "orthoids," "strophomenoids," "productoids," and others where used by authors without (in editorial opinion) appreciable uncertainty of meaning.—R. C. Moore.

faces **(cardinal areas)** rutted by transverse lines of interrupted growth (growth lines). Each cardinal area usually slopes anteriorly from the umbo toward that of the opposing valve and the two rarely match in size, for the dorsal cardinal area is commonly little more than a narrow ledge. The inner edges of cardinal areas (posterior margins) are always contiguous and are so maintained by a fusion of the mantle lobes (44). Thus at lateral limits of cardinal areas, the mantle edges come together so that the inner and outer lobes of the pedicle valve lie closely adjacent to their counterparts in the brachial valve. The effects of fusion may then be traced inwardly toward the median plane of the shell. The inner lobes lose their identity and fall away anteriorly to become the inner epithelium of the anterior body wall, while the outer lobes form a common generative zone in front of the posterior margin (Fig. 8). The fused outer lobes control growth of both cardinal areas, which are covered by a thick periostracal pad between the posterior margins and extending from the outer edge of one cardinal area to the other where it is continuous with the periostracal sheets secreted by the free mantle edges of both valves. In this manner the hinge line is completely sealed by the periostracal pad, which is deeply inserted into growth lines of the cardinal areas. Lateral expansion of cardinal areas is apparently not due to a progressive fusion of free mantle lobes but to an actual growth expansion of the lateral edges of the initial area of mantle fusion. Medially, along a line which completely encircles the external base of the pedicle, the shell-secreting generative zone of the posterior margin is confluent with the principal growing edge of the pedicle epithelium. The changing relationships that occur between these two distinct epithelial zones during the growth of the animal are discussed below.

PEDICLE

The majority of Recent brachiopods are attached to the substratum during life by a pedicle. However, the pedicle of the Inarticulata is only analogous with that of articulate brachiopods because the origin and morphology of the organ is completely different in the two classes.

In both families of living inarticulate brachiopods possessing a pedicle, lingulids

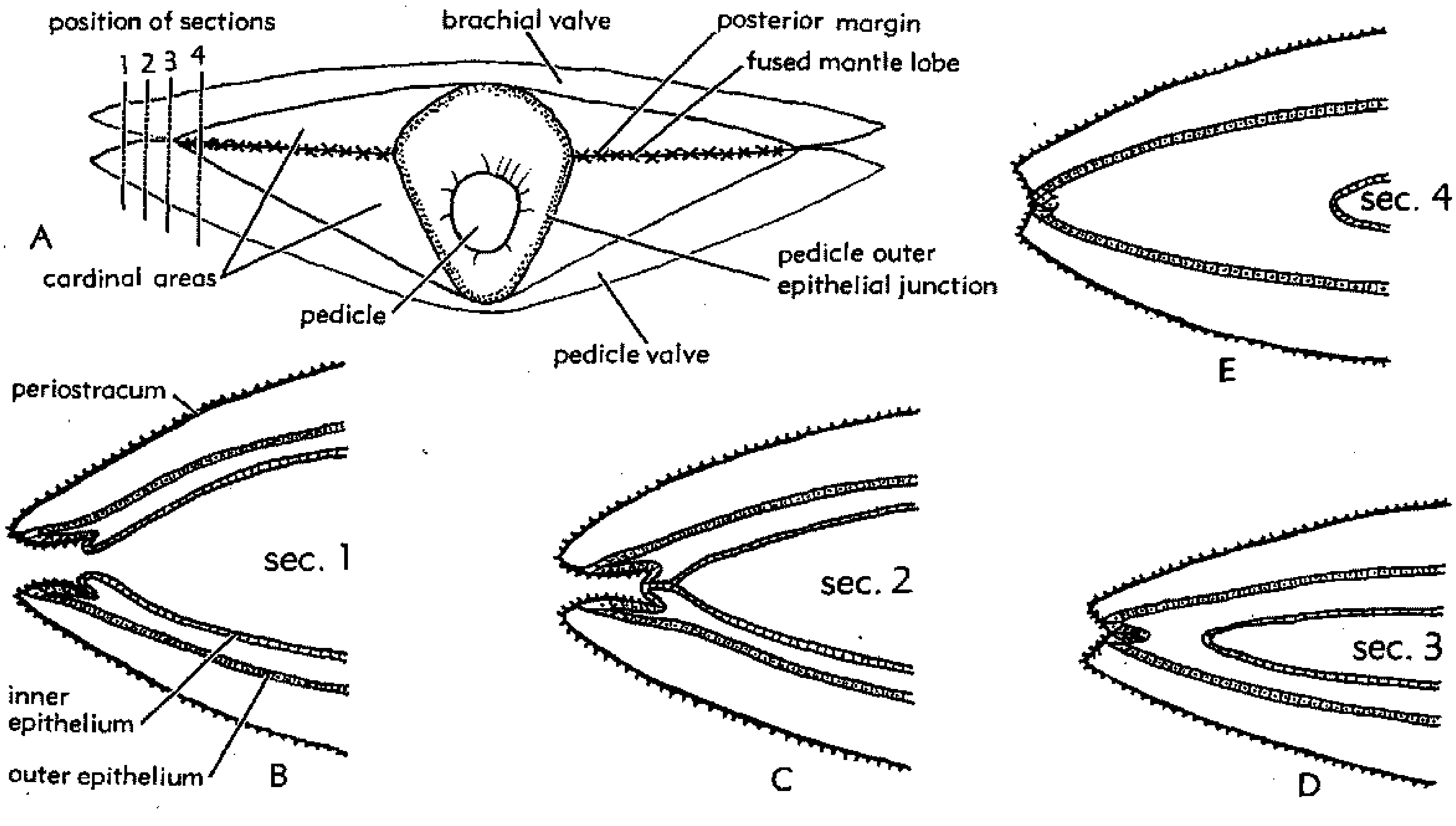

FIG. 8. Stylized sections showing relationship between dorsal and ventral mantle edges of articulate brachiopods along posterior end of gape and the posterior margin: *(A)* posterior view of shell showing location of sections; *(B-E)* successive sections 1-4 (48).

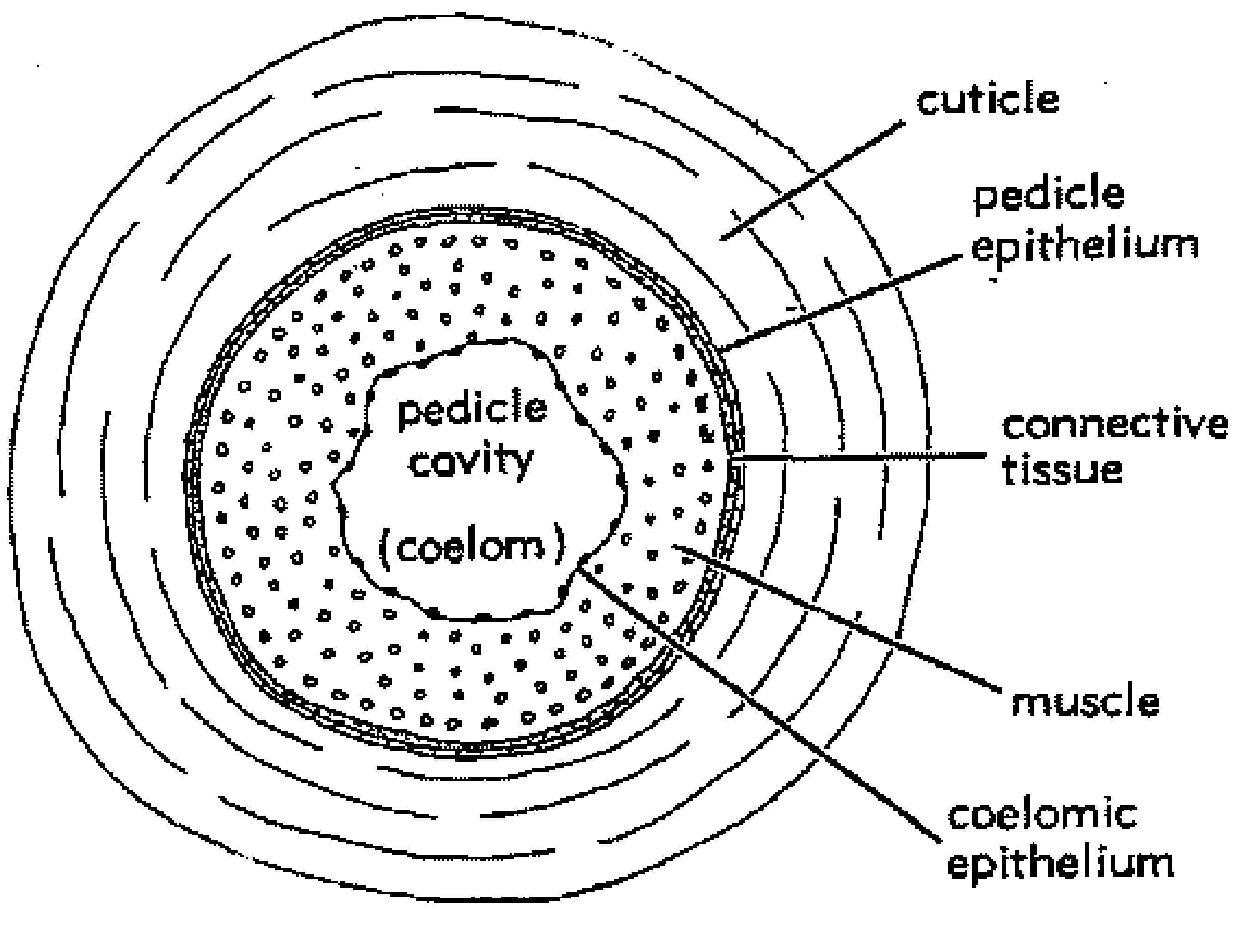

FIG. 9. Section through pedicle of *Lingula* (40).

and discinids, the organ arises as an outgrowth of the inner epithelium of the ventral mantle and is attached only to the pedicle valve (Fig. 2,*A*). Its epithelium is continuous with that of the ventral body wall and shows many similarities to it. The pedicle epithelium is covered externally by a thick layer of chitinous **cuticle**, continuous with the periostracum (Fig. 9). Internally it rests on a connective tissue layer which separates the pedicle epithelium from the coelomic epithelium lining the **pedicle cavity** (12).

In modern representatives of the lingulids and discinids a considerable difference is seen in the gross form and musculature of the pedicle, a difference that undoubtedly reflects the different mode of life of the two groups. The pedicle of the lingulids, which live in burrows, is invariably long and flexible, commonly several times the length of the shell. In the discinids, on the other hand, which live attached to a hard substratum, the pedicle is very short and the pedicle muscles are very strongly developed, permitting movement of the shell normal to the surface of attachment, as well as a variety of controlled rotational and tilting adjustments.

The thick cuticular layer ensheathing the pedicle of *Lingula* is transparent in life. Below this layer, the thin pedicle epithelium shows a marked thickening at the distal swelling (ampulla) of the pedicle. Underlying the pedicle epithelium a thin layer of connective tissue lies externally to a thick muscle layer. The individual muscle fibers are long and are attached at both ends to the connective tissue. The fibers are arranged longitudinally along a helical spiral, two directions of coiling are present, clockwise and counterclockwise, and contraction of the fibers causes a reduction in length of the pedicle. Thin coelomic epithelium separates the muscle layer from the pedicle cavity (Fig. 9), which varies in width along its length, broadening gradually from a sharp contraction immediately in front of the distal ampulla. Where the pedicle enters the valves it is strongly flattened and the pedicle coelom is likewise constricted to form the narrow pedicle canal opening into the body cavity to the right of the umbonal muscle. Gland cells, which apparently supply the secretion used to bind grains of sand into the sand tube surrounding the pedicle, are located on the posterior lateral body walls.

In *Discinisca* the basic structure of the pedicle is the same, but the muscle layer in the wall of the pedicle is not as well developed. The principal pedicle muscles of *Discinisca* consist of three pairs located in the pedicle coelom which they nearly fill. A large pair of rectus muscles run dorsoventrally through the pedicle and are attached to its distal end, and to the shell at the sides of the pedicle opening. Additional are two pairs of oblique muscles, the pedicle oblique median muscles and oblique external muscles (Fig. 10). At the proximal end of the pedicle the pedicle coelom is restricted to a narrow pedicle canal by a sphincter, which controls the opening into the body cavity.

Members of the only other inarticulate family represented in the seas today, the

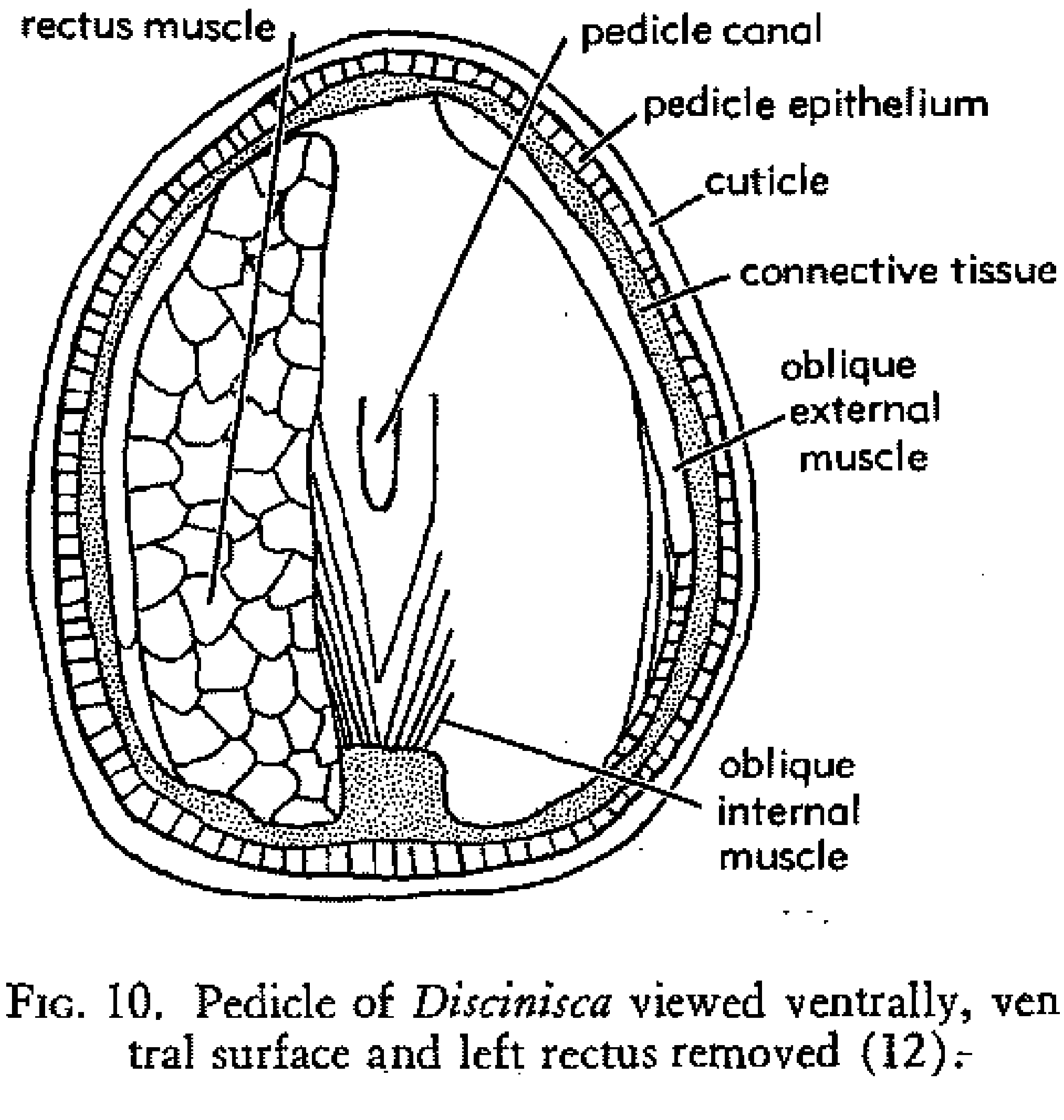

FIG. 10. Pedicle of *Discinisca* viewed ventrally, ventral surface and left rectus removed (12).

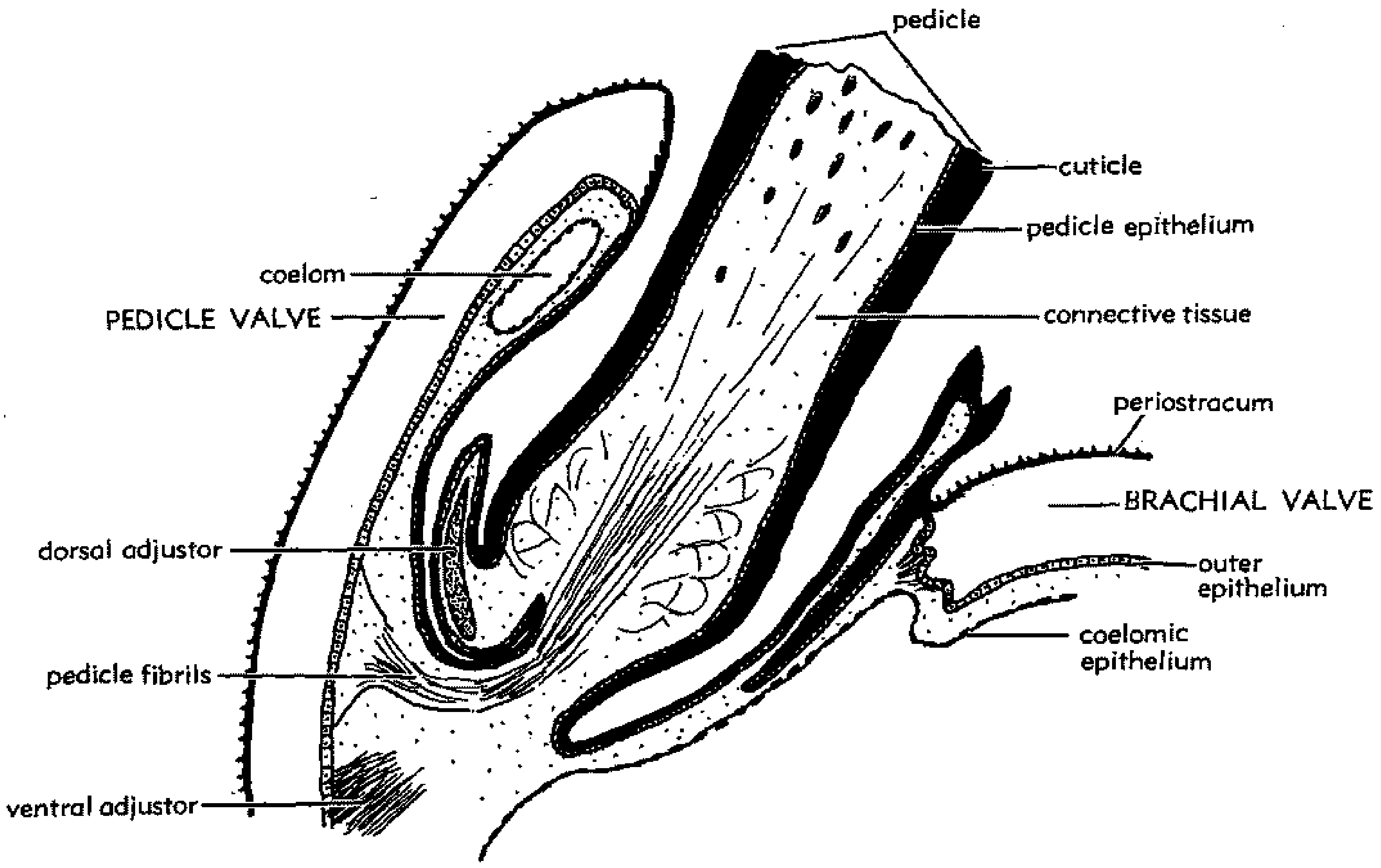

FIG. 11. Generalized diagram showing tissue distribution within pedicle of *Terebratulina* (48).

Craniidae, lack a pedicle at all known stages of development and are attached by cementation of all or part of the pedicle valve to foreign objects; the cementation seemingly is effected by adhesive properties of the periostracum.

The pedicle of the articulate brachiopods is essentially a solid cylinder of variable length and diameter with a core of connective tissue enveloped in pedicle epithelium and the outer chitinous cuticle. The proximal end tends to be bulbous and in Recent rhynchonelloids and terebratuloids is accommodated within the umbonal region of the pedicle valve in what is usually referred to as a capsule but which actually consists of a deep infold of pedicle epithelium and cuticle (Fig. 11). The distal end may also be bulbous or splayed with many rootlike extensions acting as adherent "holdfasts" to the substratum; rarely, as in *Chlidonophora*, the pedicle is divided into a series of long, slender filaments. The connective tissue forming the pedicle axis is made up of longitudinal fibrils which may pass anteroventrally to the floor of the pedicle valve and form a small scar of attachment (the "median adjustor" or "pedicle muscle scar"). The tissue is not, however, part of the muscle system of the brachiopod, for the movement of the shell about the pedicle is controlled by adjustor or pedicle muscles attached to the pedicle and the interiors of both valves. The adjustor muscles normally consist of two sets. The ventral pair arise from the dorsolateral surface of the pedicle and pass ventrally to become inserted on the floor of the pedicle valve lateral to the diductor muscles. The dorsal pair, arising ventrolaterally, are attached to either the hinge plate or socket plates of the brachial valve, as in *Hemithiris* and *Magellania* or, less commonly, anterior to the hinge plate on the floor of the valve, as in *Terebratulina*. In adult *Lacazella*, which is cemented to the substratum, neither the pedicle nor its muscle system is developed.

Since the pedicle of inarticulate brachiopods is exclusively an extension of the ventral body wall, the posterior part of the ventral mantle edge lies entirely outside the organ and never fuses with the part of the dorsal mantle edge, from which it is separated by the posterior body wall. The pedicle of articulate brachiopods, however, although largely accommodated by a median opening (delthyrium) in the ventral cardinal area, is confluent with the body wall of both valves and this leads to complications unknown in the inarticulates. The junction between the epithelia responsible

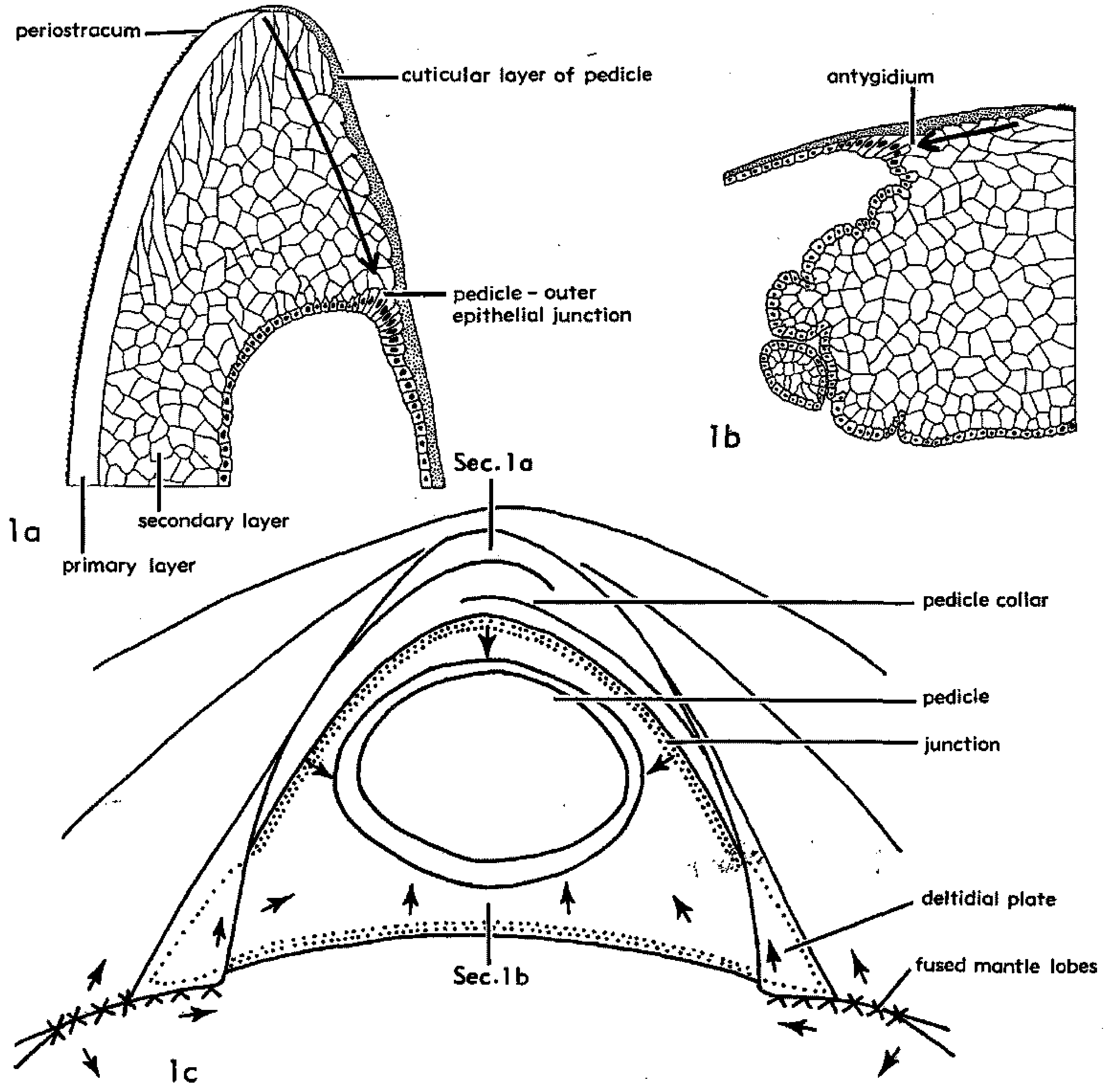

Fig. 12. Disposition and growth of outer-pedicle epithelial junction in articulate brachiopods; *1a,b,* partial sections; *1c,* posterior part of pedicle valve showing position of *1a,b* (arrows indicate direction of migration of proliferated outer or pedicle epithelium) (48).

for the secretion of the shell and the pedicle cuticle is sharply defined throughout the life of an articulate brachiopod. In its unmodified form it is subcircular to suboval in outline and lies mainly within the pedicle valve, that is, ventral of its intersection with the fused mantles controlling the growth along the posterior margins. The junction is responsible for the proliferation of the pedicle epithelium but in a manner which suggests that it is not a generative zone along its entire length for two types of epithelium like the closed end of the mantle groove. Thus, as growth proceeds, the junction becomes a zone of excessive secretion in the pedicle valve and here it retreats anteriorly, leaving behind a semicircular ridge of secondary calcite, the **pedicle collar,** coated on its inner side by a thick cuticle which is deeply inserted along irregular growth lines in the calcareous ridge. Along its dorsal edge, a very much slower retreat of the junction occurs, which is directed ventrally, not anteriorly, and leaves behind an external cuticle with insertions into a faint ridge of secondary calcite **(antygidium)** (Fig. 12). The most important aspect of this type of growth is the contrasting activities of the epithelia forming the junction. The secretion of primary shell substance takes place

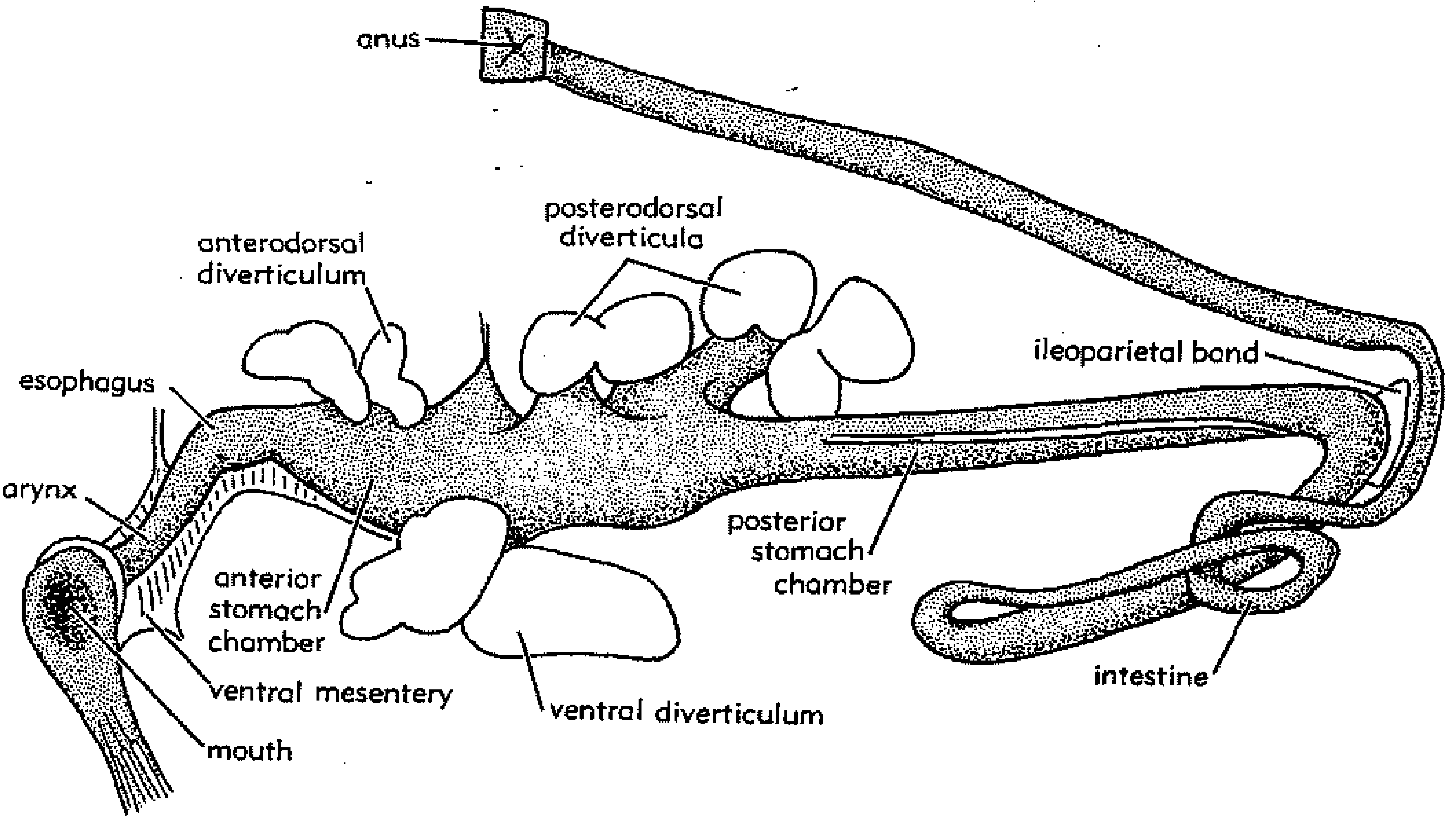

FIG. 13. Alimentary canal of *Lingula,* showing coiled anterior portion of intestine depressed and straight posterior portion elevated (17).

only along the posterior margin up to the intersection of the fused mantle lobes with the outer-pedicle epithelial junction. No primary shell is ever deposited at the junction within either the delthyrium or notothyrium, so that the outer epithelium encircling the pedicle is proliferated only by the fused mantle lobes at their two points of intersection with the pedicle epithelium. The pedicle epithelium, on the other hand, is responsible for the steady growth of the pedicle, including the deep infolds of cuticle and epithelium around the capsule. Hence, although circumferential enlargement is controlled at the posterior margin, the entire pedicle epithelium, at least along the junction, must continue to function as a generative zone (Fig. 12).

In most living brachiopods, the delthyrial opening of the adult shell is restricted by the growth of lateral plates **(deltidial plates)** so that the pedicle emerges through a variably placed foramen. Such modifications can involve complicated growth readjustments around the umbones of both valves and are more appropriately described in the chapter on shell morphology.

The shell growth of the thecideacean *Lacazella,* which lacks a pedicle, is not known in detail, but the arched, imperforate, triangular area of primary and secondary shell (pseudodeltidium) lying between the teeth ridges was evidently secreted by outer epithelium; and along the entire width of the hinge line the mantle lobes of both valves are fused and produce a periostracal pad.

ALIMENTARY CANAL

All brachiopods possess a well-developed alimentary tract. In the inarticulates its length is considerably greater than the length of the body cavity and it is consequently folded to varying degree. In this class, in contrast to the articulate brachiopods, the alimentary canal terminates in an anus.

In all members of the phylum the mouth is a transverse slit situated medianly in the brachial groove where the two arms (brachia) of the lophophore unite. This opens into the pharynx, a short, dorsally curved, muscular tube, which is embedded in the bases of the brachia. Behind the anterior body wall, the gut is continued as the esophagus, a relatively short tube of uniform diameter, which leads into the stomach. The stomach varies in shape in different genera, but in all of them it is the most expanded part of the alimentary canal and is supported in varying degree by mesenteries, gastroparietal and ileoparietal bands.

The stomach of living inarticulates extends posteriorly along the median line and in *Glottidia, Lingula,* and *Discinisca* is attached by part of the ileoparietal band to the posterior body wall. In *Crania,* however, it curves ventrally forward toward the left before reaching the extreme posterior end of the coelomic cavity (12). The

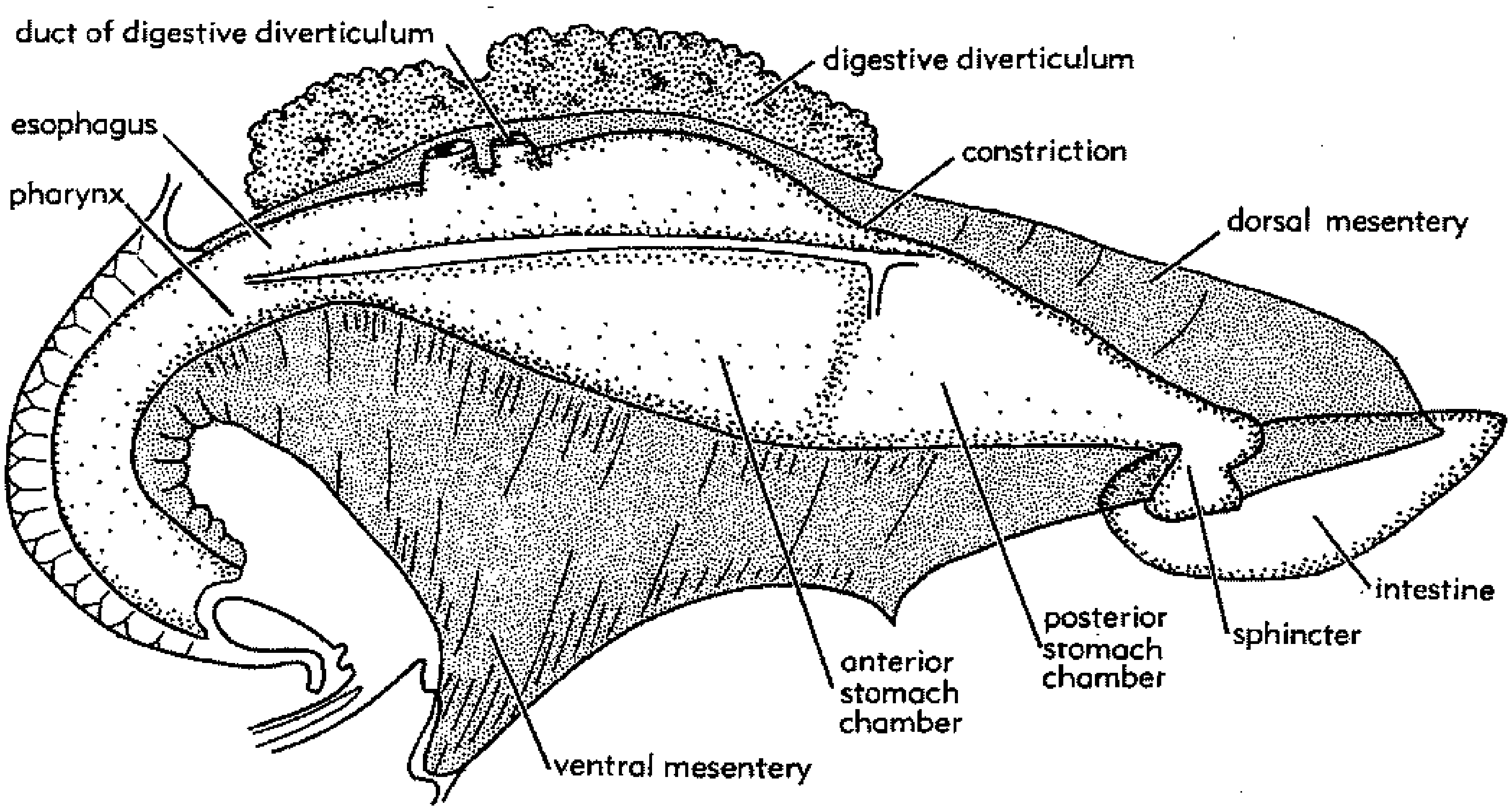

Fig. 14. Alimentary canal of *Crania* viewed from left side (left diverticulum removed) (18).

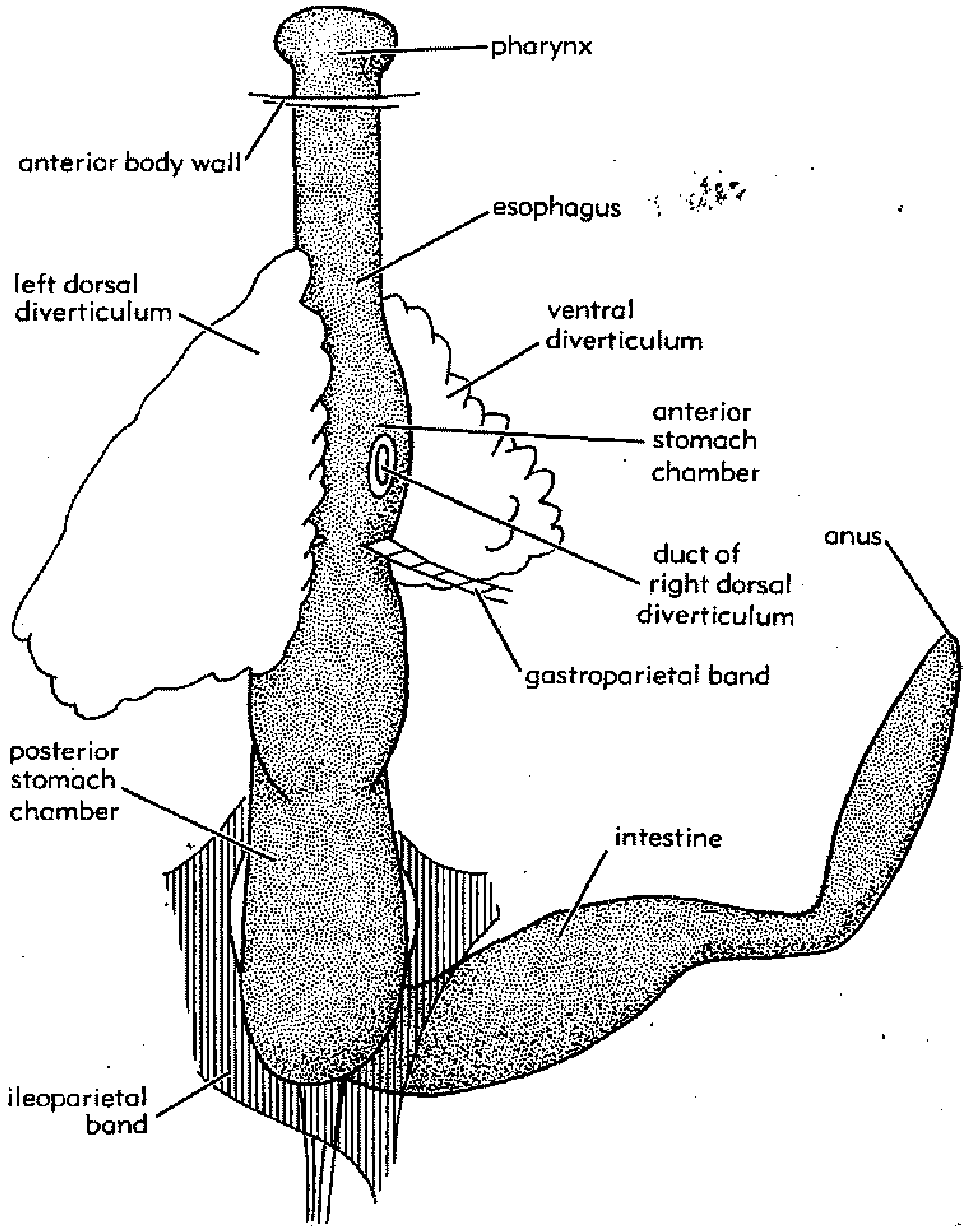

Fig. 15. Alimentary canal of *Discinisca* viewed dorsally (right diverticulum removed) (23).

stomach itself is divisible into an anterior and posterior chamber. This division is most marked in the lingulids where the anterior chamber is a thin-walled sac capable of considerable dilation in contrast to the thicker-walled, much narrower posterior chamber (Fig. 13). In *Crania* and the discinids the external difference between the two chambers is less conspicuous, but they are separated by a constriction (Fig. 14, 15).

Behind the sphincter, which limits the stomach posteriorly, is the intestine, the course of which differs considerably in the three inarticulate families with Recent representatives. The intestine of the lingulids is a slender thin-walled tube which bends to the left and forms a free loop before returning to the posterior end of the coelomic cavity. It then turns to the right and follows an oblique course anteriorly to open at an anus on the right body wall. Another sphincter controls the opening of the anus. In the discinids the course of the very much shorter intestine is somewhat similar. From the stomach it turns to the right toward the lateral body wall and then obliquely forward in a dorsal direction, to open at an anus on the right body wall. *Crania* differs considerably from the previous genera in that its intestine is capable of considerable dilation and its course is markedly different. It has the form of an inverted V with the apex directed anteriorly. From the sphincter at the end of the stomach it continues anteriorly and then bends back acutely to open at an anus medially placed on the posterior margin. Although the anus is on the mid-line, it lies to the right of the attachment of the ventral and dorsal mesenteries

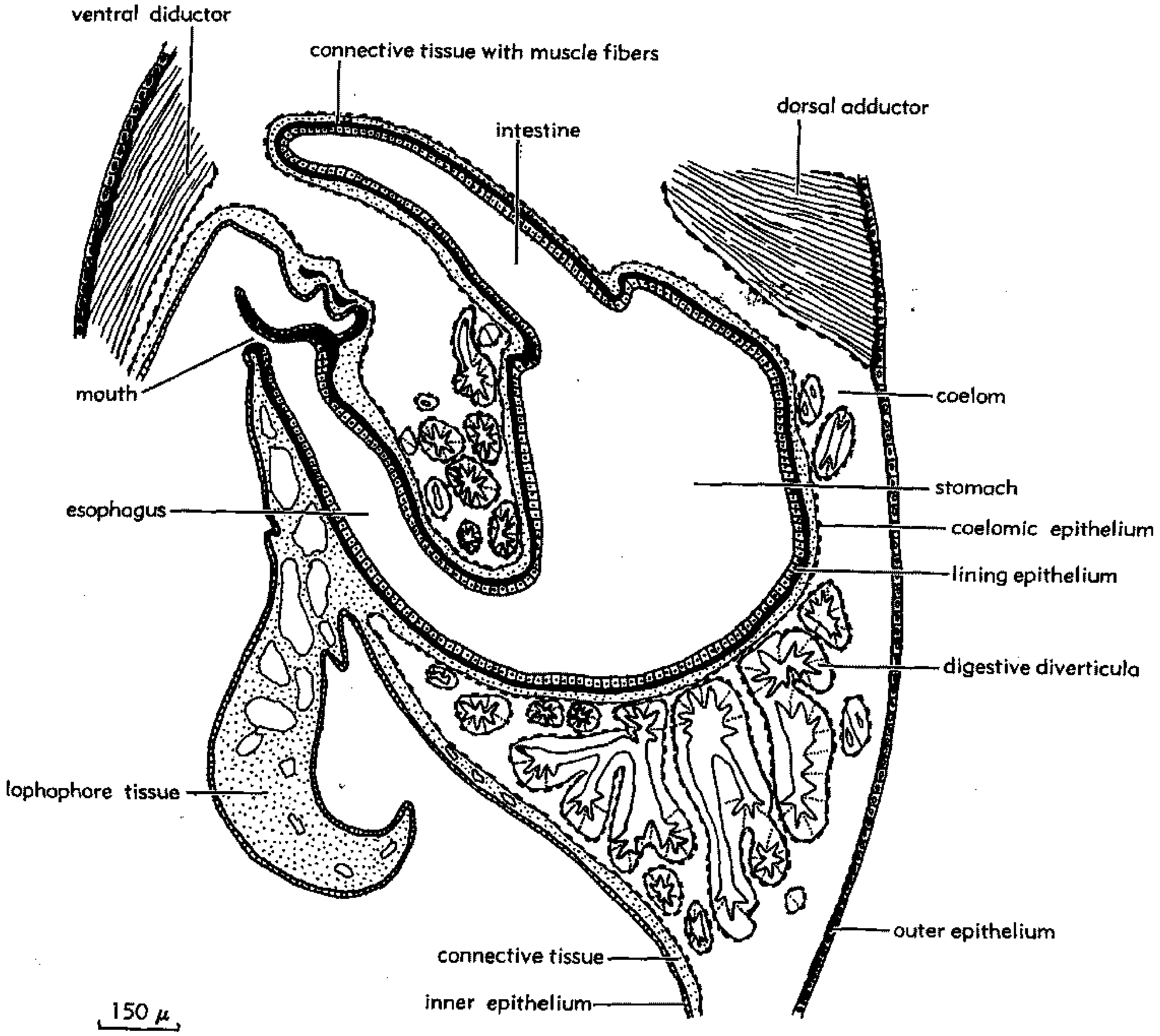

Fig. 16. Generalized longitudinal section of body of *Terebratulina* showing disposition of alimentary canal and diverticula relative to anterior body wall and brachial cavity (48).

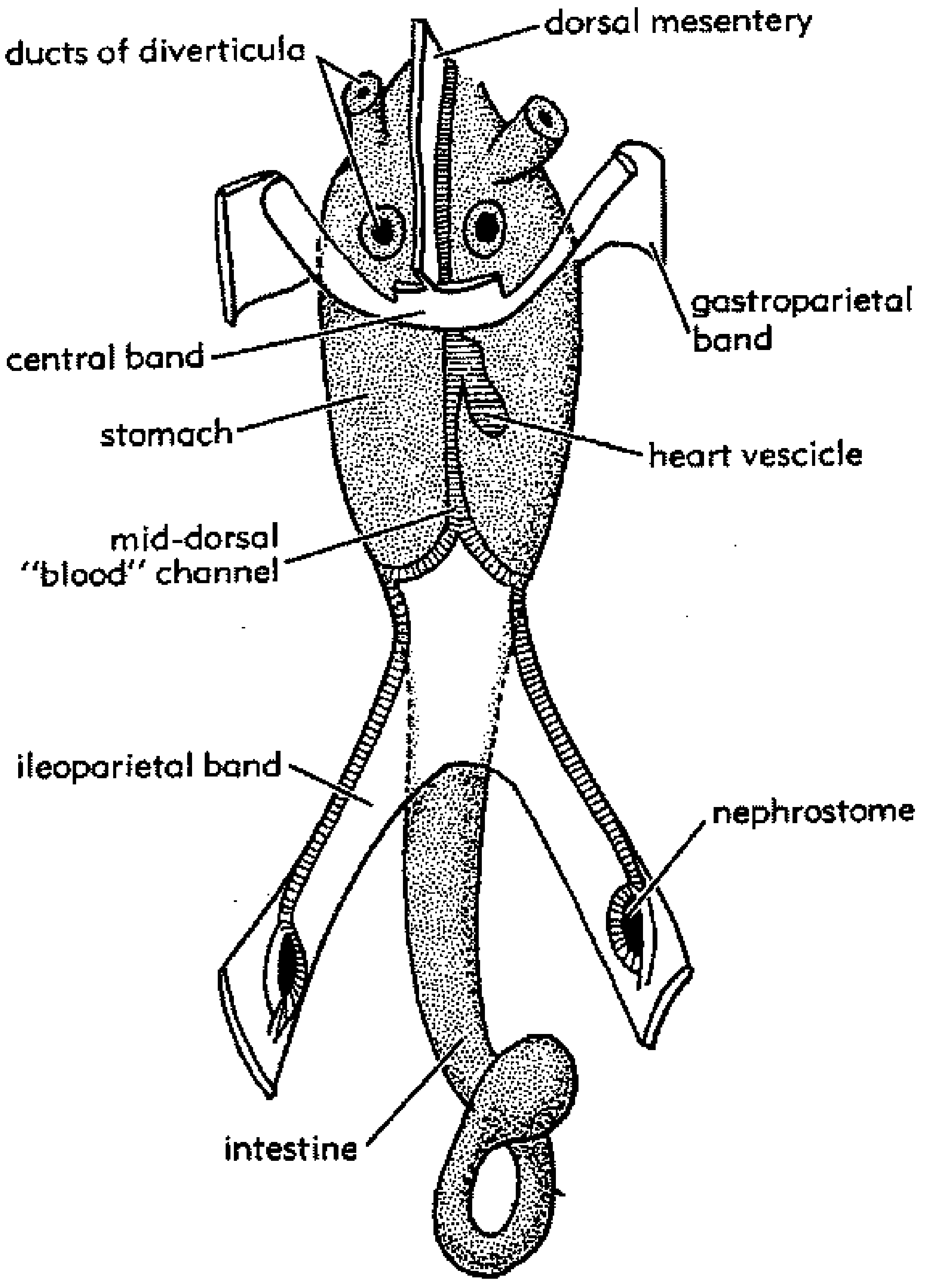

FIG. 17. View of part of alimentary canal of *Hemithiris psittacea* (GMELIN) showing distribution of main mesenteries (21).

to the intestine. In this respect the intestine may be thought of as opening on the right-hand side of the animal, as in other families of the inarticulates, although the anus is much more posteriorly placed in *Crania* than in the other genera (18).

Among articulate brachiopods the disposition of the alimentary canal is somewhat different in that the relatively longer esophagus is more strongly anterodorsally inclined before it bends abruptly into the relatively short stomach (Fig. 16). The stomach passes mid-dorsally into a tapering intestine directed posteroventrally and terminating blindly as either a blunt end supported by mesentery (Fig. 16) or exceptionally, as in *Hemithiris*, as a bulbous end twisted upon itself and hanging free (Fig. 17).

The digestive diverticula (or liver) open through ducts into the stomach, and are such conspicuous features of the coelomic cavity that they can almost conceal the stomach. Four diverticula are present in *Lingula*, three dorsal and one ventral, each opening through a separate duct into the stomach. The three dorsal diverticula consist of a single anterior diverticulum on the mid-line and a posterior pair left and right of the axis of the stomach, slightly behind the place of attachment of the gastroparietal band. The diverticula are not all of the same size in the adult, the right posterior dorsal being the largest and the anterior dorsal the smallest, but they all have a similar structure. Each diverticulum consists of a fixed number of lobes, seven in the right posterodorsal, two in the left posterodorsal, and four lobes in both the ventral and anterodorsal diverticula. The main duct of each diverticulum bifurcates shortly after leaving the stomach and from the bifurcation a number of lobular ducts arise which serve the lobes. The lobes consist of repeatedly branching ducts terminating in bunches of blind sacs (acini) (17).

In *Crania* only a pair of diverticula are present, both dorsally placed and separated by the dorsal mesentery. Each diverticulum is divided into two lobes and their basic structure is similar to the lobes in *Lingula*.

Discinisca has three diverticula (23), all of them situated in front of the gastroparietal band, a dorsal pair and a single, unpaired ventral diverticulum. Their detailed structure is unknown. They open into the stomach through separate ducts, but apparently are not divided into lobes, their terminal portions being long tubules.

Crania and *Lingula* both have a ciliated epithelial groove running along the stomach (17, 18). In *Lingula* this arises in the right posterodorsal diverticulum, traverses all the lobes of this organ and emerges to run along the dorsal surface of the posterior stomach chamber. The epithelial groove in *Crania* lies longitudinally along the floor of the anterior chamber of the stomach and is continued into the posterior chamber, rising dorsally from the floor to the roof of the chamber by the right lateral wall.

The diverticula of articulate brachiopods are less well known. They commonly consist of a pair of posterior lobes and a pair of larger anterior lobes, symmetrically arranged about the dorsal mesentery, which communicate with the stomach through one to three pairs of ducts. In detail, such diverticula are apparently like those of

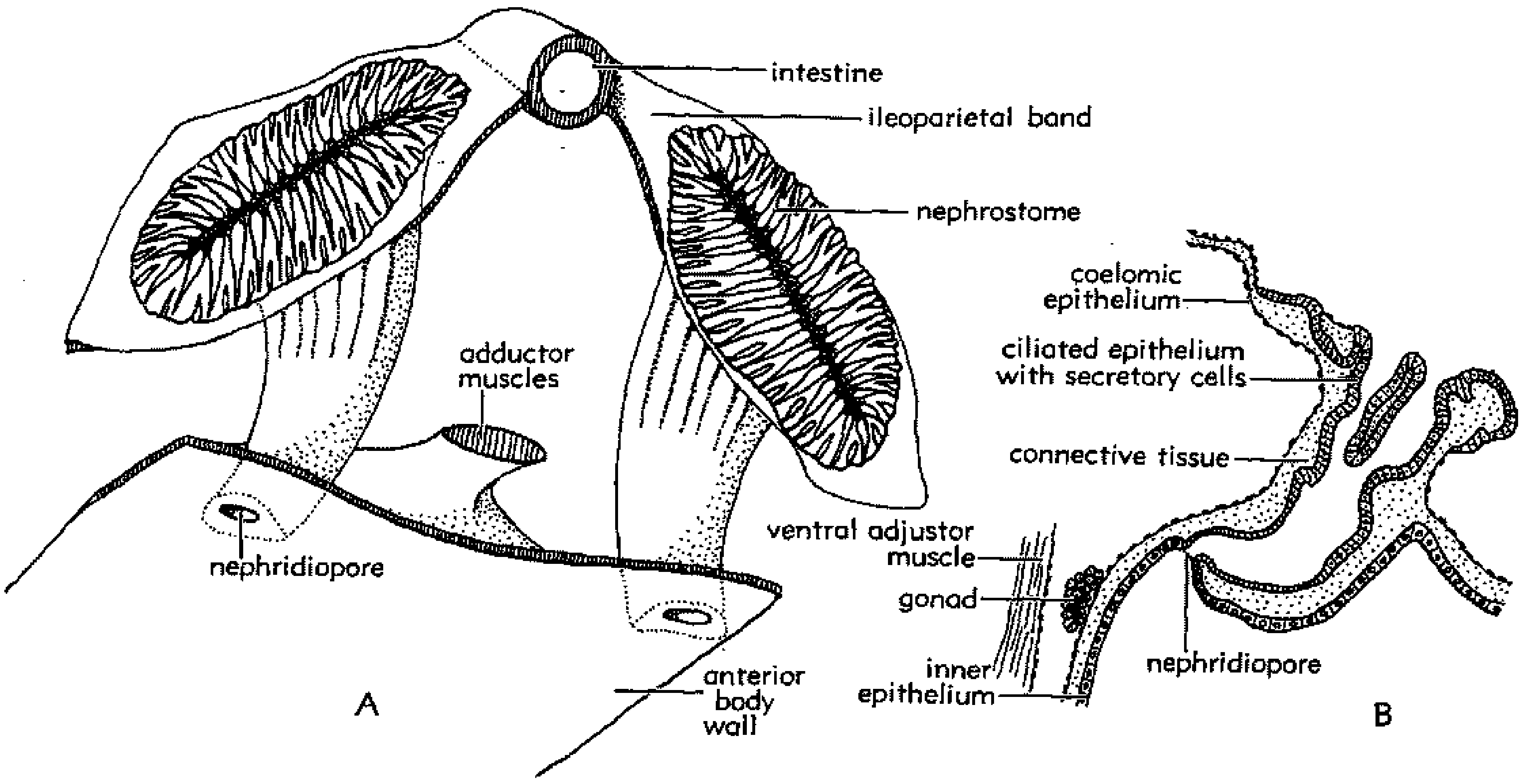

FIG. 18. Generalized diagrams showing *(A)* attitude of nephridia of *Terebratulina* relative to anterior body wall and *(B)* structure of nephridium as seen in longitudinal section (48).

Lingula, but differences are seen in at least *Argyrotheca* and *Lacazella*, where the diverticula consist respectively of six to eight pairs and 10 to 16 pairs of elongate tubules.

As far as is known, the histology of the gut of all living brachiopods is broadly similar (Fig. 16). The inner surface of the alimentary canal is lined with a simple columnar endodermal epithelium which rests on a basement membrane forming the inner surface of a connective tissue stroma. The epithelial cells are tall and slender in the pharynx and esophagus of *Crania* and are shorter elsewhere. They have a similar distribution in *Lingula*, but in this genus the epithelial lining of the posterior stomach also consists of tall cells. This epithelium is ciliated in all of the gut except the acini of the digestive diverticula. Interspersed between the normal epithelial cells are mucus cells and some wandering phagocytes. The latter also occur in the lumen of the stomach, digestive diverticula and intestine of *Lingula* (17).

Embedded in the outer part of the connective tissue stroma, which lies external to the basement membrane, are two sheets of muscle fibers. The fibers are arranged in an inner circular layer and an outer longitudinal sheet and are developed in the wall of all of the alimentary canal. They appear to be smooth in the stomach and intestine of all brachiopods, but the esophageal muscles of certain rhynchonelloids and terebratuloids are known to be striated. Where it is free, the canal is lined externally by a thin ciliated coelomic epithelium.

EXCRETORY SYSTEM

The brachiopod excretory organs consist of one or exceptionally, as in rhynchonelloids, two pairs of metanephridia, which also serve as gonoducts in that sex cells are discharged through them from the body cavity.

Although there is some variation in detail, the shape of the nephridia is similar in all living brachiopods. The nephridial opening within the coelomic cavity consists of a broad funnel-shaped nephrostome with a ruffled inner surface. Each nephrostome is continued anteriorly by a narrow tube, usually ventrally placed against the lateral body wall and opening into the mantle cavity through a small nephridiopore on the anterior body wall, close to the mid-line and ventral to the mouth (Fig. 18). The posterior pair of nephrostomes of the rhynchonelloids and the nephrostomes of all other brachiopods are supported by the ileoparietal band and the anterior pair, when present, by the gastroparietal bands.

The nephridia of the lingulids are broad and relatively long and the nephrostomes are turned laterally, away from the mid-line,

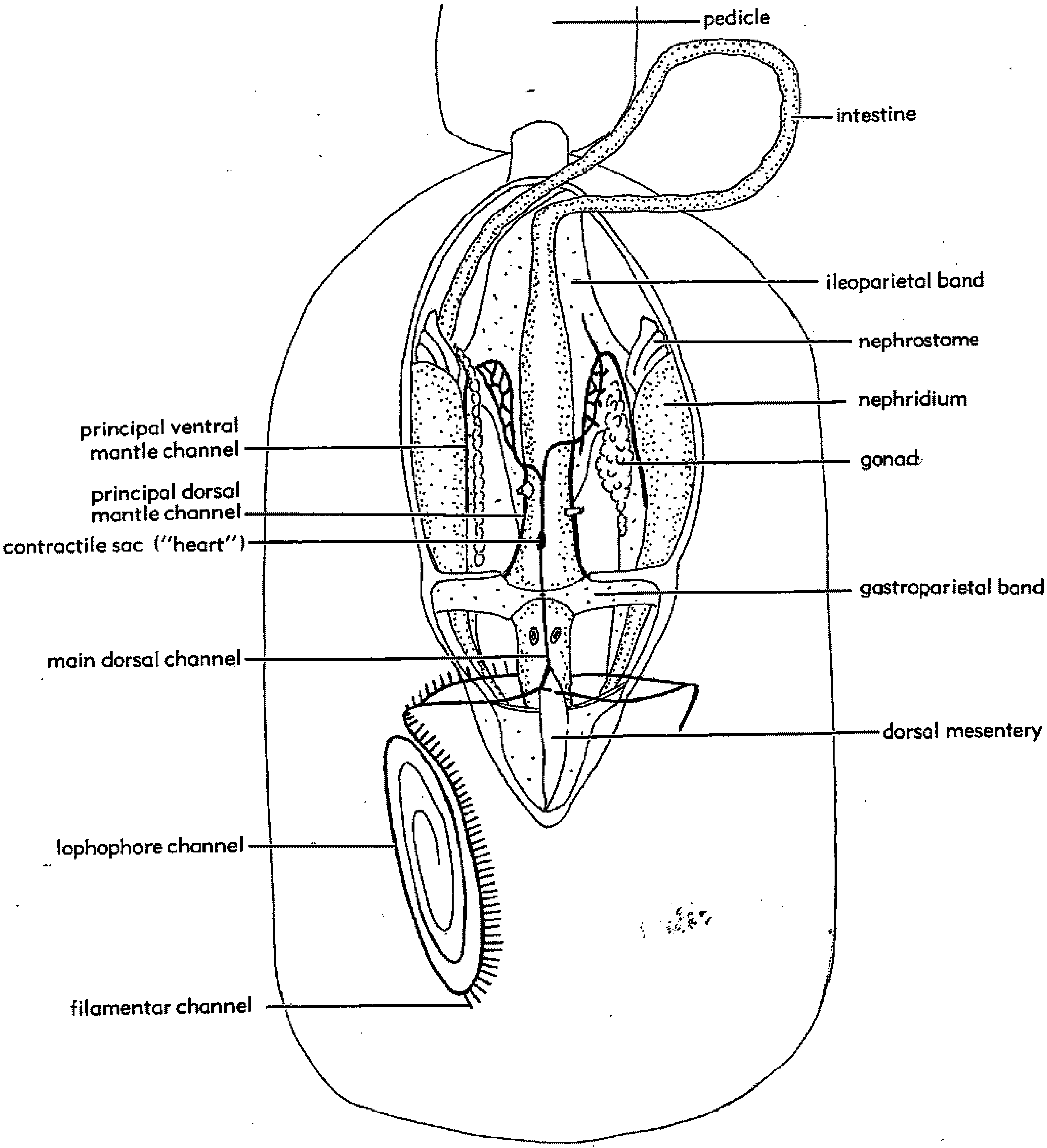

FIG. 19. Generalized diagram of circulatory system of *Lingula* (40).

to face the lateral body wall (Fig. 19). In the discinids and craniids, the nephridia are relatively shorter, the nephrostomes facing dorsally and slightly medially in the former family, while in the Craniidae they open medially. In the articulates, the nephrostomes appear to be consistently oriented to face dorsally or dorsomedially.

Histologically, as far as is known, the structure of the nephridia is similar in all living brachiopods. The inner surface is covered by ciliated epithelium with interspersed secretory cells. This layer is separated from the outer layer of coelomic epithelium by a connective tissue, which is differentially thickened in the ruffled surface of the nephrostomes (Fig. 18).

COELOM

The muscles, alimentary canal, excretory organs and all or part of the sexual organs, constituting the "body" of the brachiopod, are lodged in the posterior part of the shell within a coelom which also contains a fluid and may be divided by vertical and transverse mesenteries. Other coelomic spaces exist within the lophophore and mantle lobes and also in the pedicle of inarticulate brachiopods and theoretically the entire coelom may be divided into protocoel, mesocoel, and metacoel (22). These divisions are not very meaningful in that they have not been identified in embryological studies. But the coelomic spaces of the lophophore have been recognized as possible representatives of the protocoel and mesocoel and the body cavity with its extensions into the mantles and pedicle as the metacoel. More often than not, however, there is communication between at least part of the lophophore coelom and the body cavity and it is not proposed to use the terminology of this hypothetical threefold division of the coelom in the subsequent account.

The coelom and the organs and connective tissue it contains, including muscle bands and the mesenteries, are lined with a flat, ciliated coelomic epithelium (Fig. 16).

All coelomic spaces of living brachiopods contain a fluid which, in the main body cavity and its extensions, is a coagulable liquid carrying a variety of free cells. These include spherical or slightly irregular coelomocytes, phagocytic amoebocytes, and the so-called spindle bodies that are known only in the lingulids. KAWAGUTI (24) has found that the coelomocytes of *Lingula* contain a red pigment, hemerythrin. This pigment has a limited ability to carry oxygen which is released on the reduction of hemerythrin to a colorless form. The reaction is reversible and in all probability fulfills a respiratory function.

BODY CAVITY

The body cavity is normally traversed by a number of flat sheets of connective tissue (mesenteries) locally pervaded with fine muscle fibers. Dorsal and ventral mesenteries that run from the alimentary canal to the respective body walls are present in all living brachiopods but are incompletely developed, except in *Crania*, where the body cavity is divided into two separate compartments by them (12). In addition, two lateral pairs of mesenteric bands usually connect the alimentary canal to the body wall and give some support to it and other organs within the body cavity. The anterior pair, forming the gastroparietal band, which is absent in *Crania*, is relatively narrow and extends on both sides from the stomach, near the digestive diverticula, to the lateral

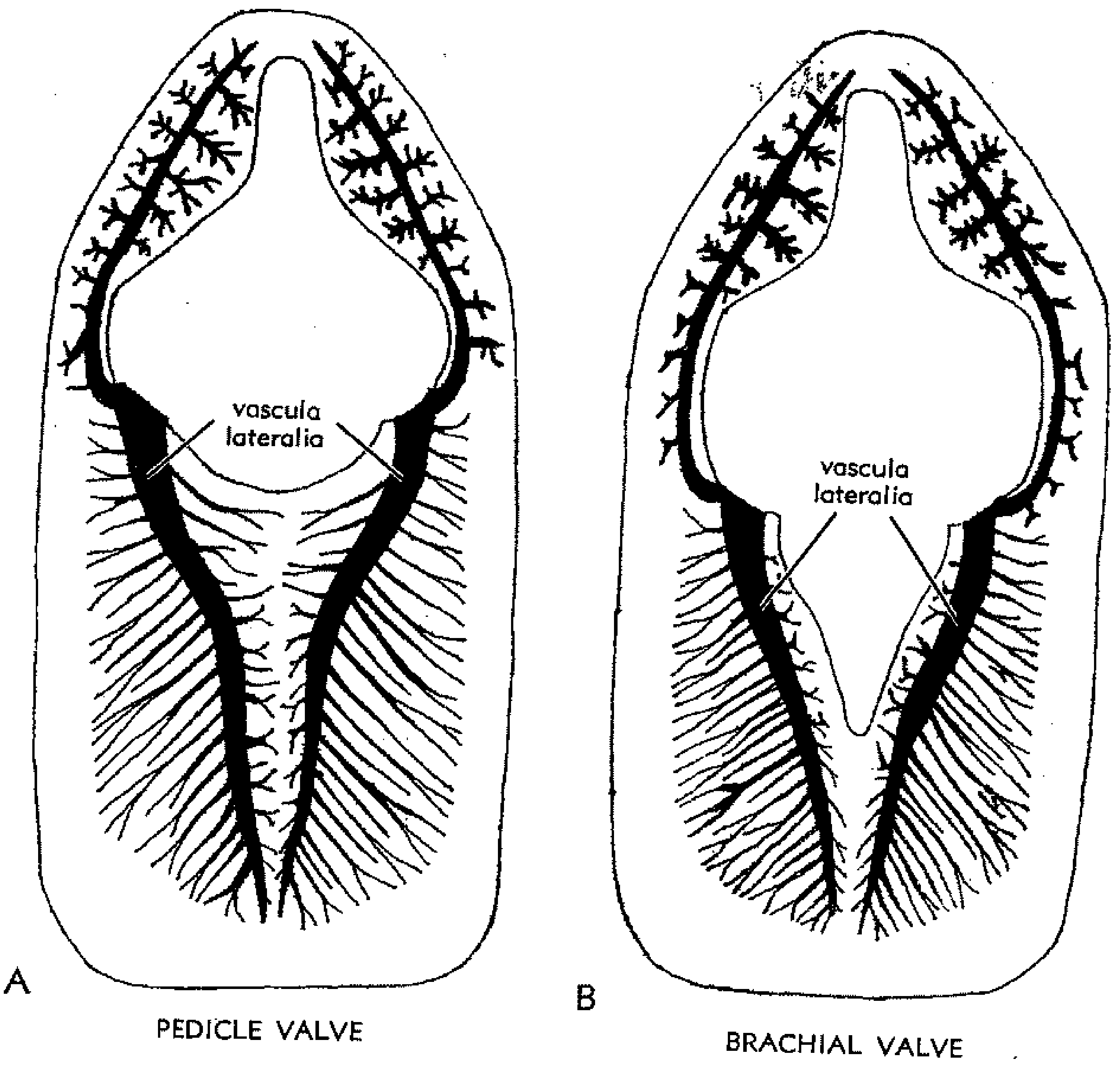

FIG. 20. Mantle canals of *Lingula* (12).

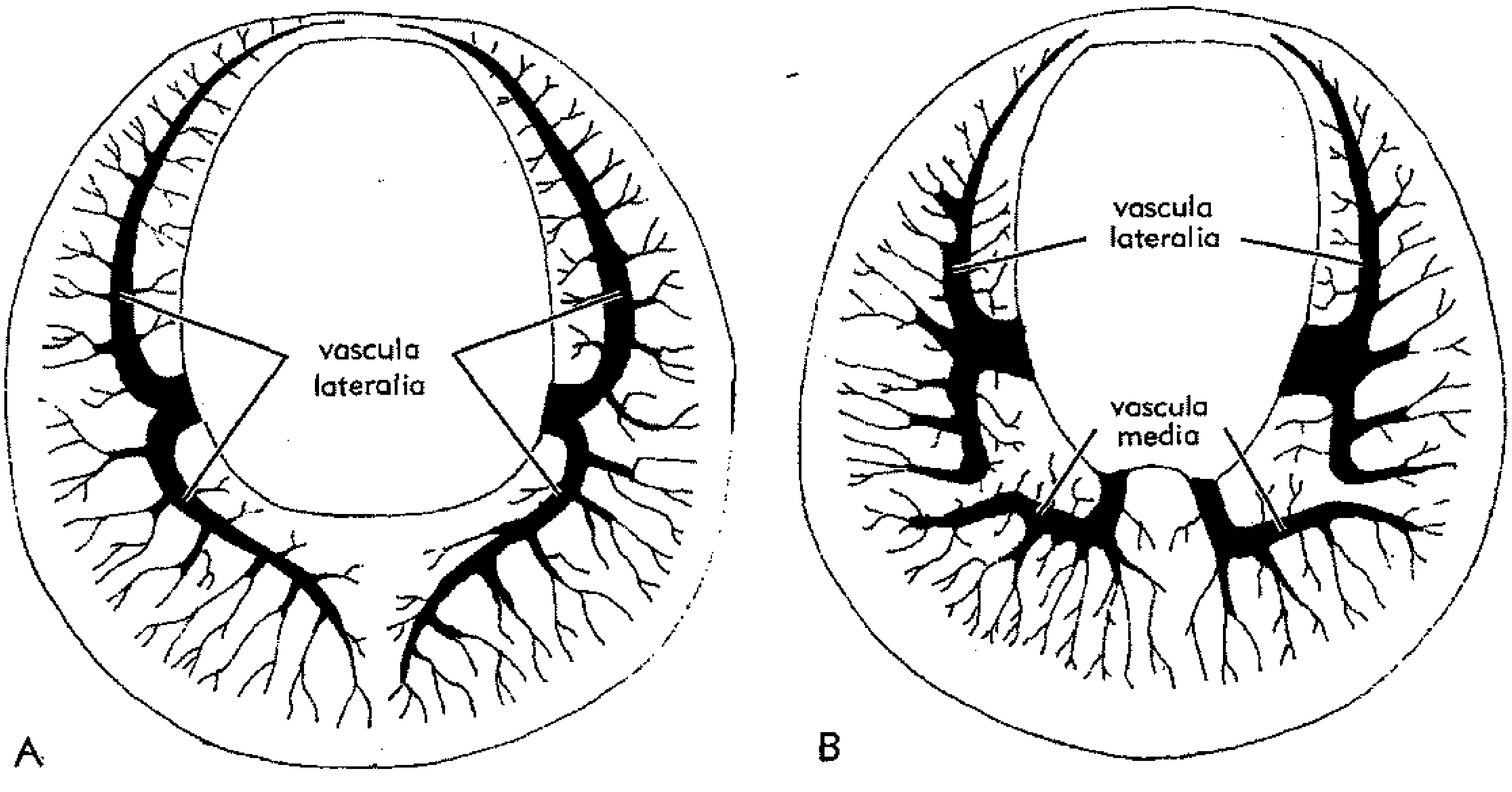

FIG. 21. Mantle canals of *Discinisca* (12).

body wall. The ileoparietal band has more complex ramifications but essentially it extends between the lateral body walls and the stomach, along which it may persist for some distance posterior to the gastroparietal band. In addition to affording support to the posterior ends of the excretory organs, it carries some or all of the gonads (Fig. 17, 19).

MANTLE CANALS

The mantle canals are long tubular extensions of the body cavity into the mantles. They are lined with ciliated coelomic epithelium and in the inarticulates at least a thin muscle layer underlies the epithelium on the side facing the mantle cavity.

In Recent inarticulates two main canals *(vascula lateralia)* enter each mantle from the body cavity. In *Discinisca*, two more main canals *(vascula media)* occur in the dorsal mantle. The principal canals of the lingulids and discinids open into the body cavity through muscular valves and branch repeatedly to produce a large number of minor canals which end blindly and are distributed throughout most of the mantles (Fig. 20; 21). In *Crania*, each principal canal gives rise to a small number of second- or exceptionally third-order branches and further differs from its counterpart in other living inarticulates not only in the absence of a muscular valve at its junction with the body cavity but also in containing part of the gonads (Fig. 22).

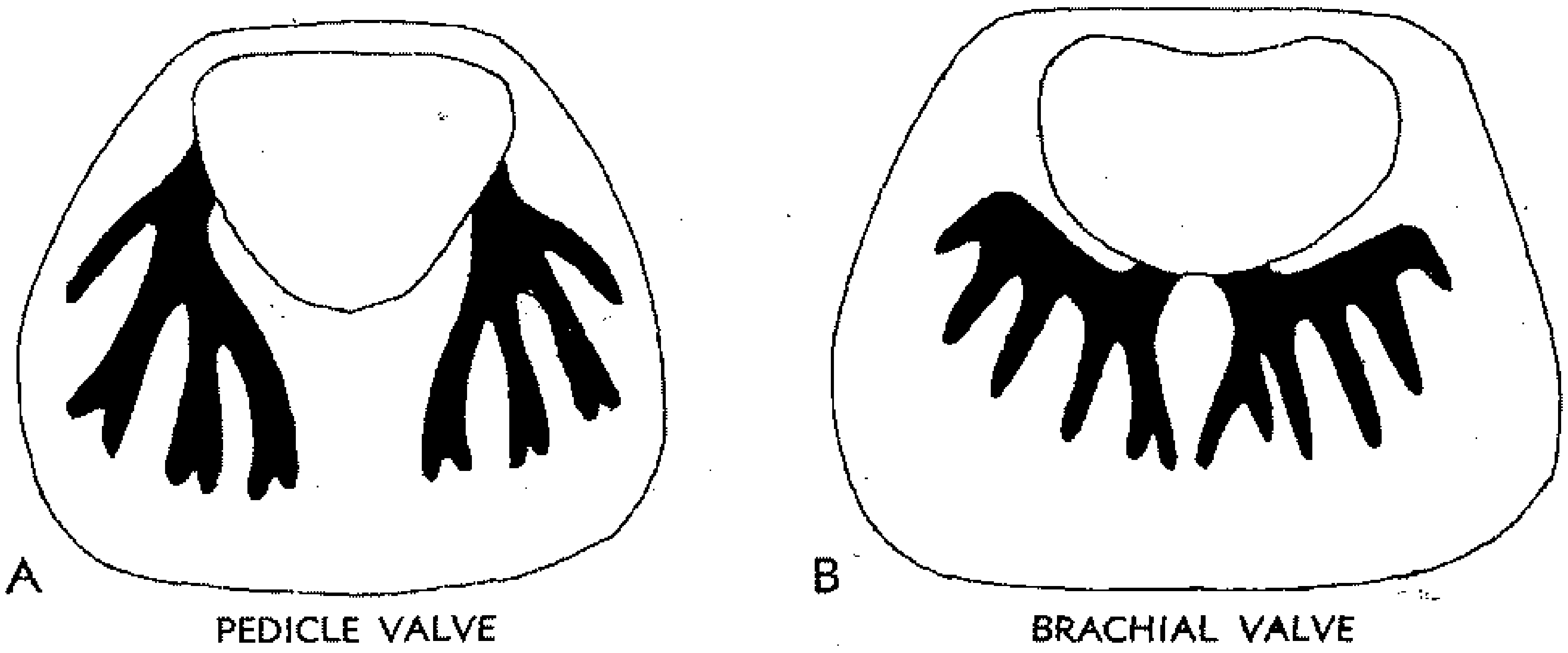

FIG. 22. Mantle canals of *Crania* (12).

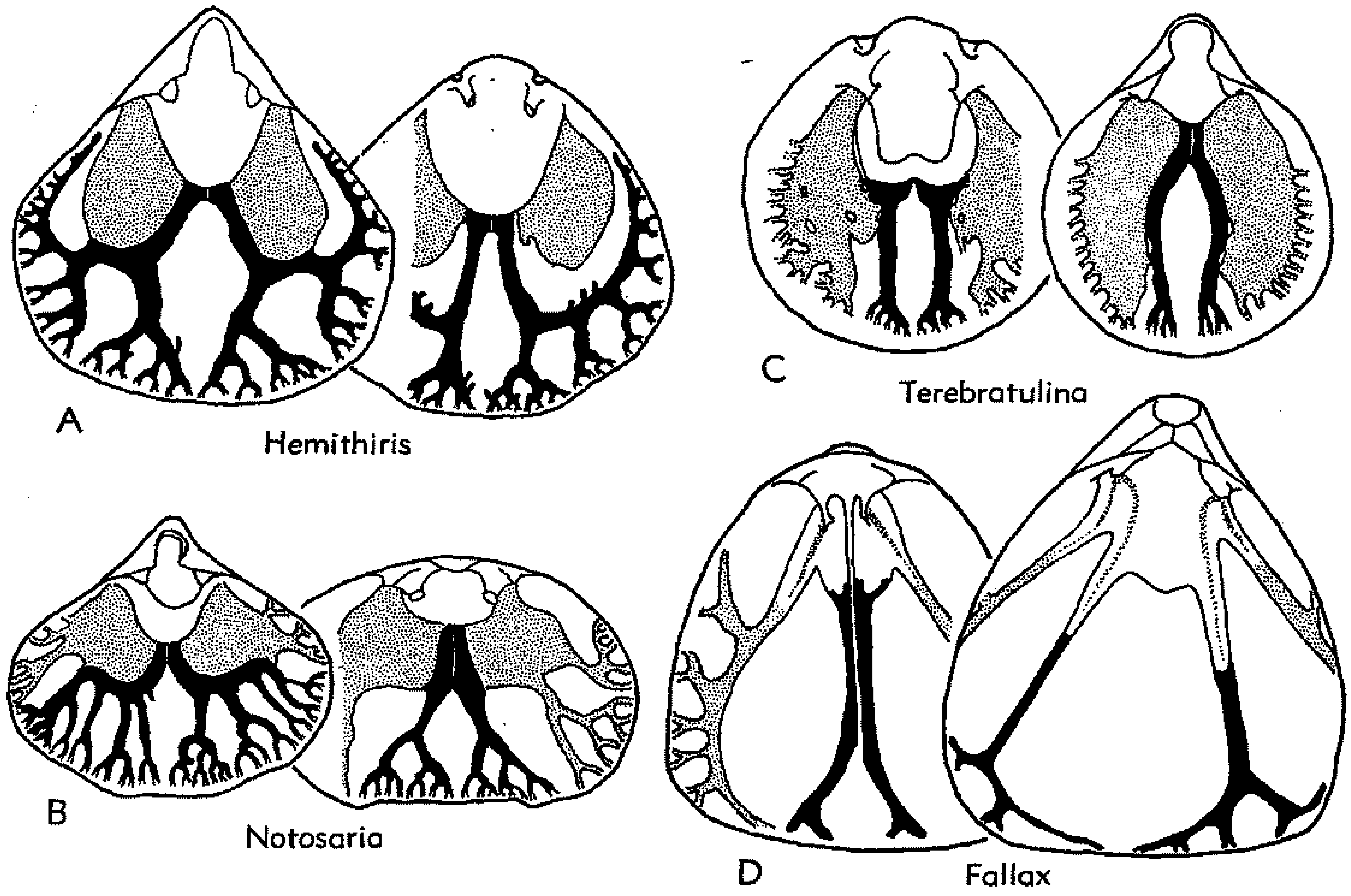

FIG. 23. Mantle canal systems of Recent rhynchonellids *(A, B)* and terebratulids *(C, D)*; *vascula media* black, *vascula genitalia* and gonadal sacs stippled, *A-C* (44), *D* (6).

In Recent Rhynchonellida and Terebratulida, two pairs of principal canals occur in each mantle (44), but the patterns become complicated because some, but not all, invariably act as repositories for part of the gonads (Fig. 23). In the rhynchonellaceans, for example, each mantle contains a pair of submedian canals *(vascula media)* curving posterolaterally and branching repeatedly toward the mantle edge. In *Hemithiris* the *vascula media* are flanked by a pair of short broad canals *(vascula genitalia)* which are unbranched saclike extensions of the body cavity containing the gonads (Fig. 23,*A*). In *Notosaria* the pattern is identical except that the *vascula genitalia*, although still saclike proximally, branch repeatedly toward the mantle margin, and the *vascula media* are correspondingly abbreviated (Fig. 23,*B*). In all known terebratuloids the pattern is similar to that of *Notosaria* in that the *vascula genitalia* are branched and the *vascula media* restricted peripherally (Fig. 23,*C*); but in some genera, like *Macandrevia, Pumilus, Fallax* (Fig. 23,*D*), and *Magellania* gonads are also found in the *vascula media.*

The ciliated epithelium lining the canals is responsible for the circulation of coelomic fluid. In the lingulids, this is regular and controlled in that the ciliary beat aided by a median ridge apparently separates an outgoing current from a return flow in each canal (Fig. 24). A similar epithelial ridge also located medianly on the canal wall adjacent to the shell is known in *Discinisca* and *Terebratalia*, where it may perform the same task.

The principal function of the mantle canals is respiratory and an unusual adaptation is seen in the lingulid *Glottidia* (30). In this genus, the peripheral minor canals in the anterior part of the shell bear a number of projections (Fig. 24). These small, thin-walled, tubular saclike extensions (gill ampullae) project into the mantle cavity, thereby increasing the surface area of the mantle canal system.

MUSCULATURE

The main muscle system of living brachiopods is responsible for the movement of the brachial valve relative to the pedicle valve

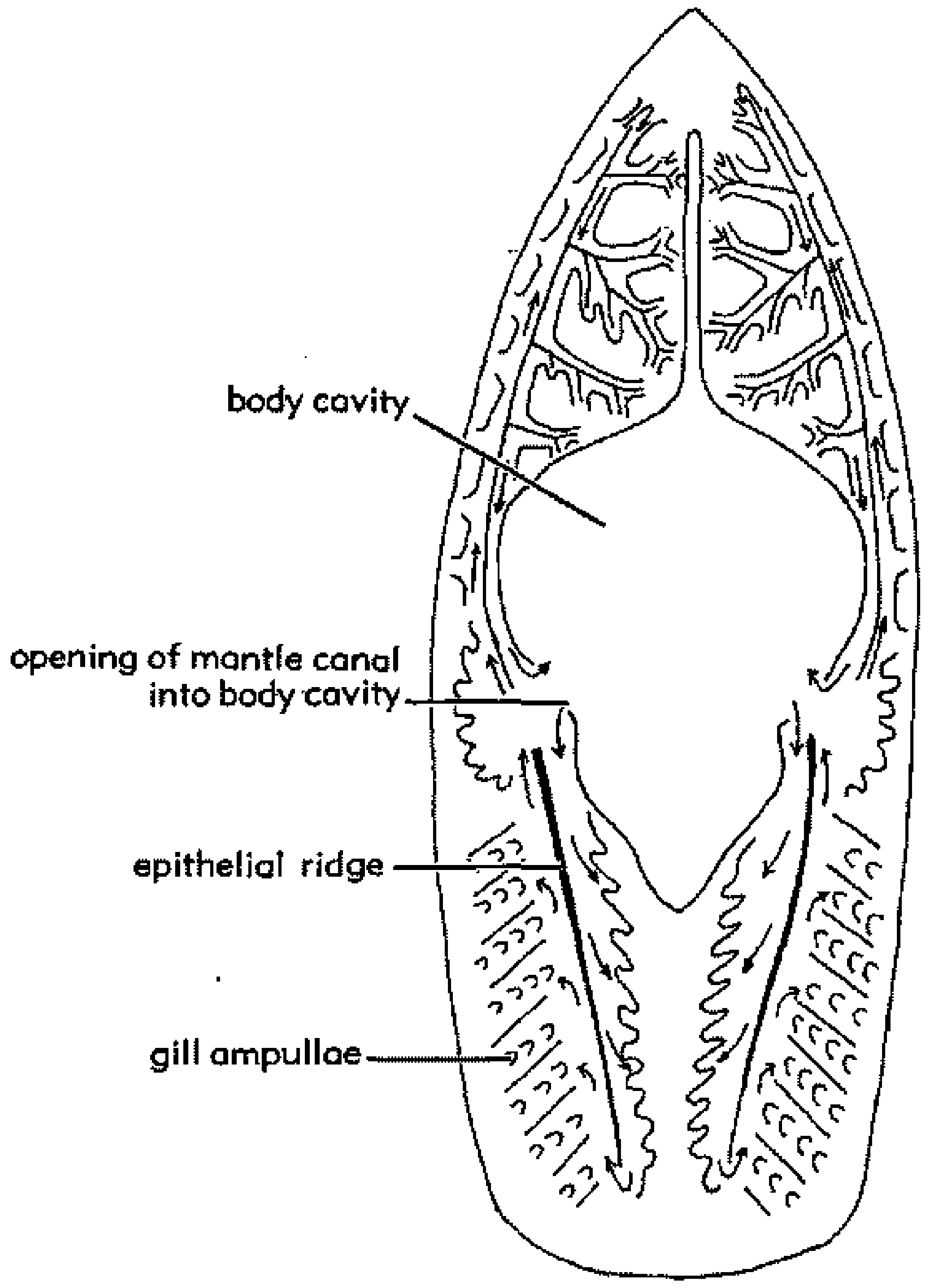

Fig. 24. Circulation in dorsal mantle canals of *Glottidia* (30).

and of the entire shell about the pedicle. The principal movement in both articulate and inarticulate shells is an opening and closing of the valves in the plane of bilateral symmetry. But the arrangement of muscle sets is fundamentally different in the two groups because the absence of a hinging device in the inarticulates permits rotation and even sliding of the valves in the plane of the commissure. The muscles are usually smooth (although the striated type is certainly known in the lophophore filaments and also the posterior adductors of some terebratuloids like *Pumilus*) and, within the body cavity, are encased in a thin sheath of coelomic epithelium. Where the muscles are attached to the shell the intervening outer epithelium becomes modified to a series of striated cells containing tonofibrils. Such areas of attachment are commonly seen on the inner surfaces of the valves as impressions (muscle scars) because of the significantly slower rate of secondary shell secretion by the modified epithelium.

In articulate brachiopods the muscle system responsible for the opening and closing of the shell includes a set of adductors which pass from one valve to the other in front of the posterior margin and set of diductors which are typically inserted, at least in the brachial valve, posterior to the fulcrum (hinge axis) represented by articulating teeth and sockets (Fig. 25). The adductors arise from a pair of ventrally located scars placed postero-medianly in the pedicle valve, but each bifurcates in its passage toward the

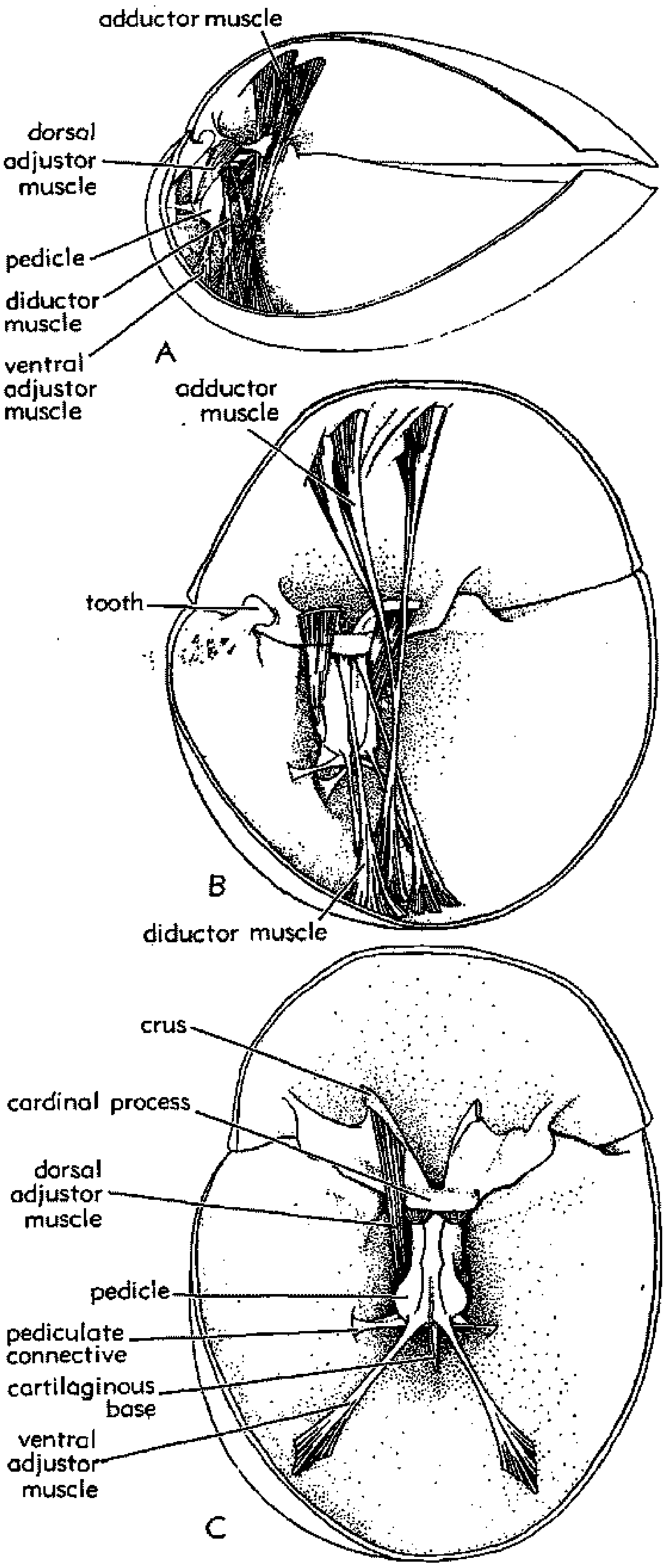

Fig. 25. Musculature of *Gryphus vitreus* (Born), *(A)* lateral and *(B)* anterolateral views and *(C)* anterior view of pedicle with its musculature (20).

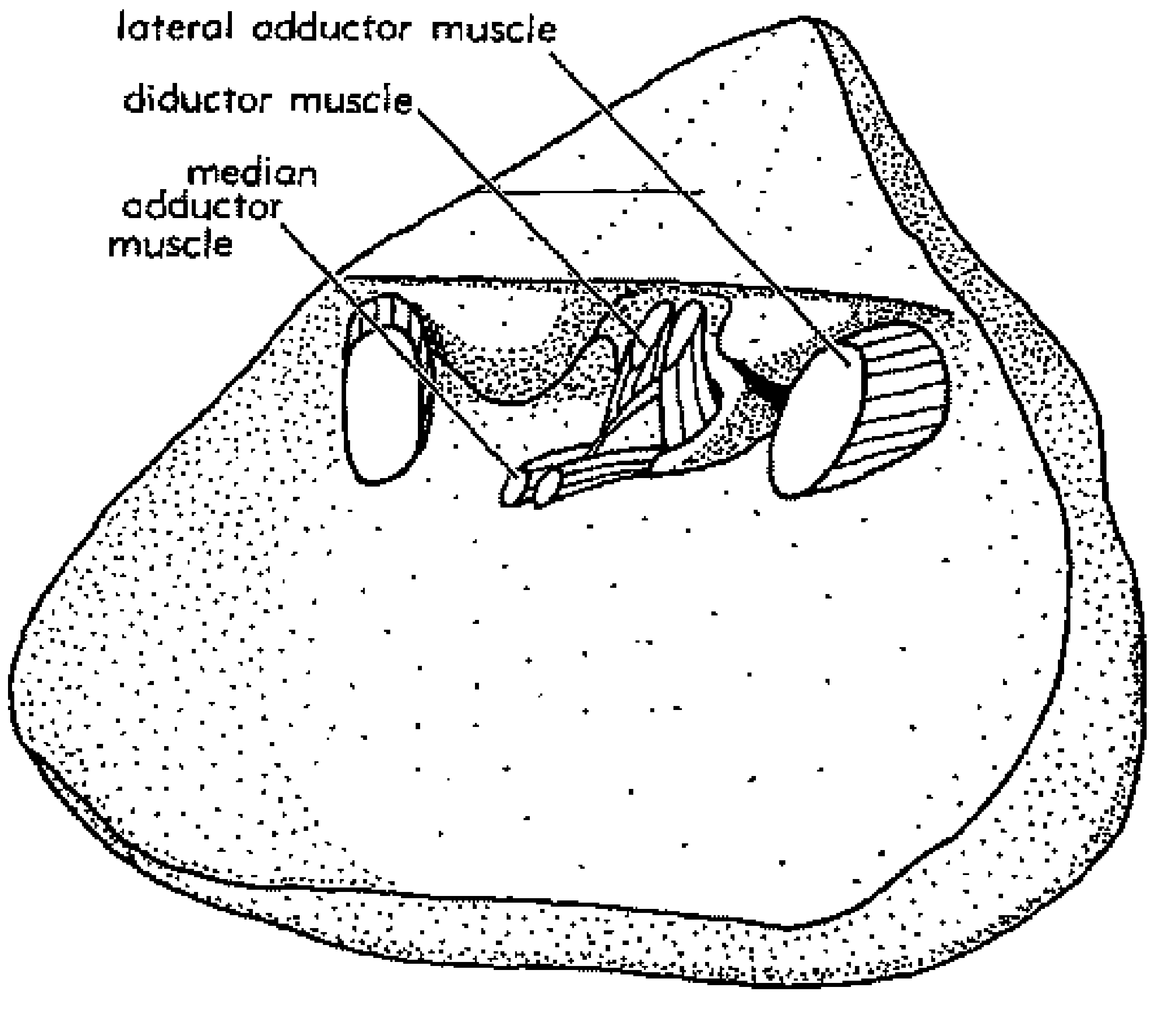

FIG. 26. Musculature of *Thecidellina,* brachial valve removed (47).

brachial valve so that four dorsal attachment scars are situated anteromedianly of the hinge region. In the thecideaceans a pair of adductors occupy the median position characteristic of other articulate brachiopods but do not divide dorsally; in addition, an extra pair of adductor muscles occupy posterolateral positions just in front of the hinge line and presumably prevent any lateral movements that might arise from an articulation which is sufficiently loose to allow the brachial valve to open at right angles to the cemented pedicle valve (Fig. 26).

The diductor muscles are inserted immediately in front of the beak of the brachial valve, commonly in, or at the side of, a cardinal process, *i.e.,* posterior to the hinge axis of the shell. From this position they pass anteroventrally and splay out to occupy a pair of large attachment areas in the pedicle valve, commonly on either side of the adductor bases. The only exception to this relationship is found in certain terebratellaceans (e.g., *Platidia*) in which the dorsal umbo is resorbed to accommodate the pedicle (Fig. 27). In such shells the dorsal attachment areas are in front of the hinge axis and the ventral areas posterior, thus reversing the normal arrangement. A pair of slender accessory diductors are also usually present, passing from the cardinal process to become inserted on a small pair of attachment areas situated posteriorly to the ventral adductors.

The contrast between the sudden closure and gradual opening of a shell suggests that the latter movement depends as much on the relaxation of the adductor muscles as on the contraction of the diductors. During a snap closure, the shell also rotates about, and moves backward along, the pedicle, which thus seems to be shortened. This movement is brought about by contraction of the adjustors pulling the proximal end of the pedicle deep into the body cavity, but it is believed that, since the diductors are intimately associated with the connective tissue around the base of the pedicle, their contraction during the opening of the shell would assist in ejecting the pedicle, thus moving the shell forward to an erect position.

In addition to opening and closing the valves, rotation and sliding are possible in Recent inarticulates. The muscles that control these movements are necessarily more complex than those of the articulates. Basically they consist of two groups. The first group consists of two pairs of muscles that pass more or less directly dorsoventrally through the body cavity. They are usually the largest sets in the animal, and, although they are known under different names in different families, they are all concerned with the closure of the shell. The second group includes a variable number of oblique muscles controlling the rotational and longitudinal movements.

In *Lingula* the muscles responsible for the closure of the shell consist of a pair of central muscles near the middle of the valves and effectively an umbonal muscle, which is actually made up of two very unequal bundles of fibers (Fig. 28). The larger

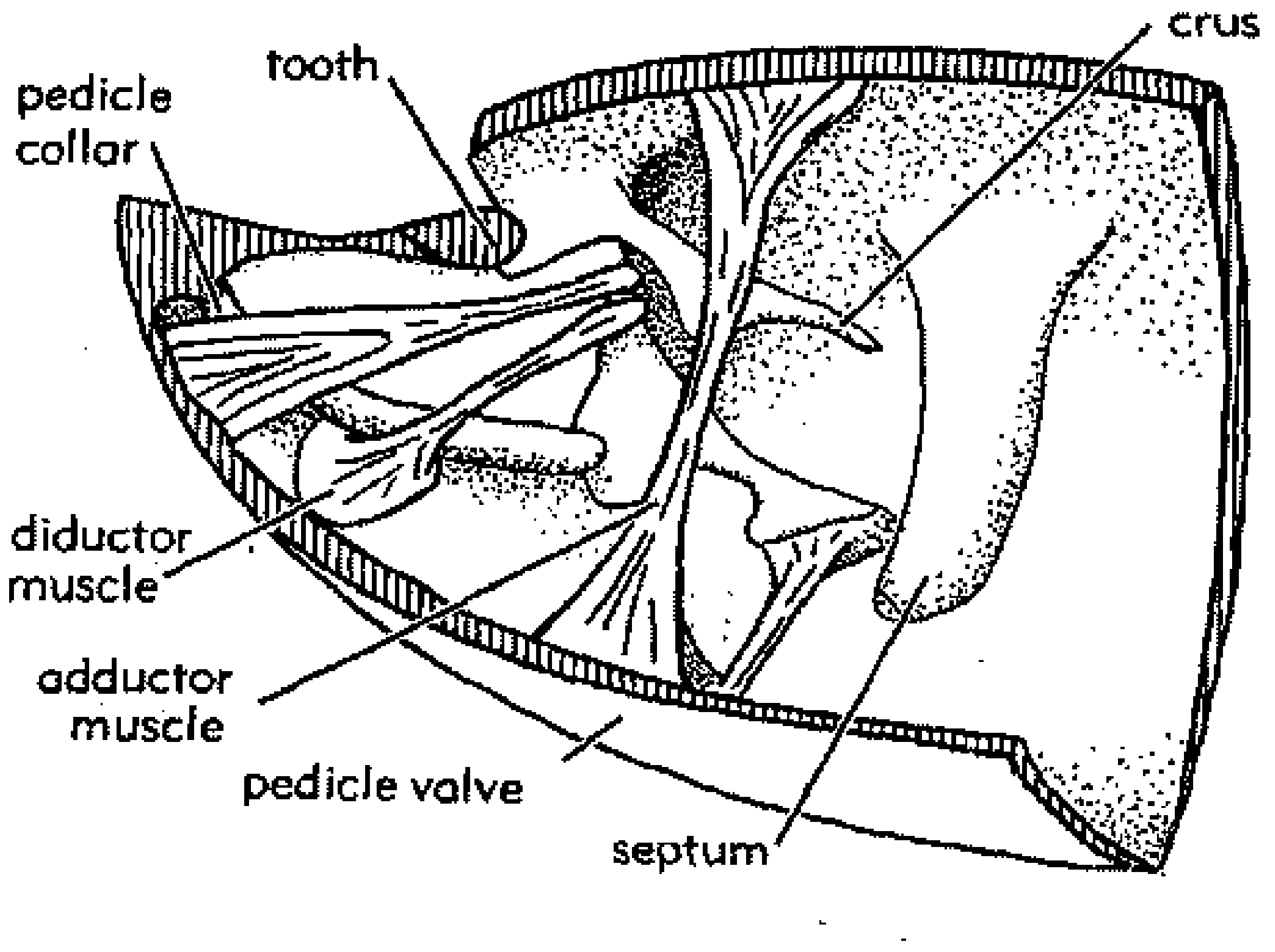

FIG. 27. Musculature of *Platidia annulata* ATKINS (48).

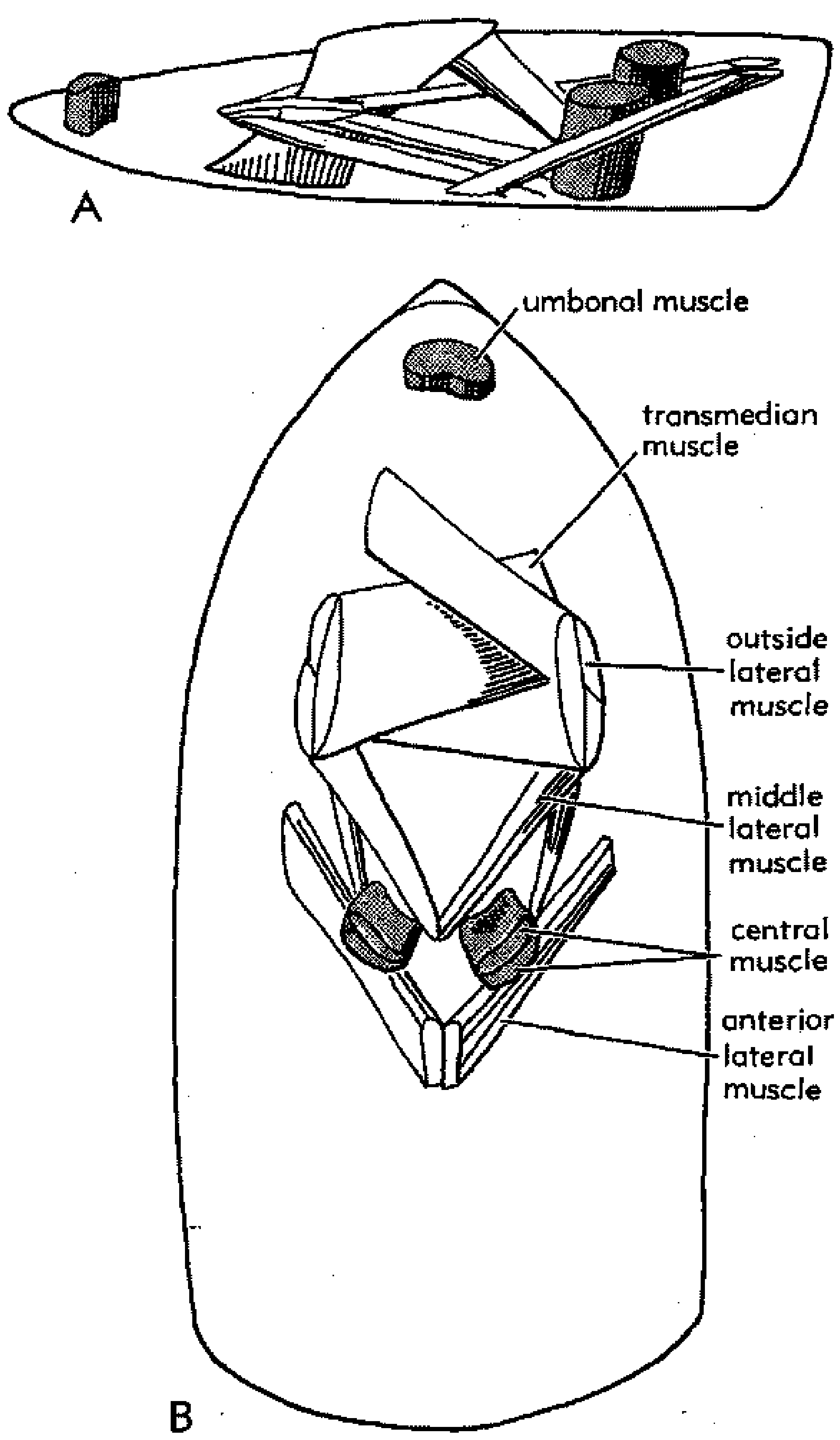

FIG. 28. Muscle system of *Lingula* viewed *(A)* laterally and *(B)* dorsally (14).

bundle of the umbonal muscle runs directly dorsoventrally; but the smaller, flat bundle which is inserted on the pedicle valve in front of the main bundle, spirals around the latter and is inserted on the brachial valve posterior to it (12). Both central muscles consist of a double bundle of fibers passing directly dorsoventrally. Four pairs of oblique muscles are present, three of which, the middle laterals, outside laterals, and transmedians, form a composite scar in the brachial valve. The middle laterals arise between the central muscles in the pedicle valve and pass obliquely backward to be inserted on the brachial valve, immediately in front of the scar of the outside laterals. These outside lateral muscles converge slightly anteriorly from the brachial valve and are inserted on the pedicle valve lateral of the centrals. The third pair of muscles, the transmedians, are the largest of the oblique muscles and form the inner part of the composite scars. The right transmedian muscle runs ventrally from the brachial valve to become attached on the left side of the pedicle valve. The left transmedian splits just below its insertion on the brachial valve, and the two branches cross over the right transmedian to become fixed to the right side of the pedicle valve. This is the usual condition of the transmedians, but the left transmedian of a few brachiopods may be undivided (14). The fourth pair of muscles, with an oblique course, are the anterior laterals. These are inserted on the pedicle valve posterolateral of the outside lateral muscles and rise anteriorly to become attached to both the brachial valve and the anterior body wall near the mid-line of the valve.

The muscle system of *Glottidia* is basically similar to that of *Lingula* (30), but those of other Recent genera are somewhat simpler, since they have fewer oblique muscles.

In the discinids (Fig. 29,*1a,b*), two pairs of adductor muscles, a small posterior pair and a large anterior pair, run directly dorsoventrally between the valves. Each anterior adductor consists of a small median and a much larger lateral bundle of muscle fibers. Three pairs of oblique muscles occur, all of them relatively long and thin in comparison with adductors. The internal obliques arise from near the center of the pedicle valve and diverge posteriorly so as to become inserted on the brachial valve slightly anterolateral of the attachment of the posterior adductors. The oblique lateral muscles originate on the pedicle valve anterolaterally of the posterior adductors, near the side wall of the body, and run forward to be inserted on both the brachial valve and the anterior body wall close beside the main bundle of the anterior adductors. The third pair of oblique muscles, the posterior obliques, arise on the pedicle valve, slightly in front and median of the site of attachment of the oblique laterals. They pass dorsally and converge posteriorly, becoming inserted on the brachial valve close together near the mid-line, slightly in front of the posterior margin.

The principal muscles of *Crania* are similar to those of *Discinisca*, but rather simpler.

Two pairs of adductors occur, the anterior set consisting of two bundles of fibers. The oblique internals occupy a similar position to those of the discinids but follow a more S-shaped course. The oblique laterals originate on the pedicle valve at the side of the posterior adductors and are attached not to the brachial valve but to the anterior body wall (Fig. 29,*2a,b*).

The correlation of the muscles of the lingulids, discinids, and craniids is based on form, assumed function, and more fundamentally on their innervation (12). The posterior and anterior adductors of the craniids and discinids are considered to be the homologues of the lingulid umbonal and central muscles, respectively. The transmedian, outside, and middle lateral oblique muscles of the lingulids, which are attached only to the shell, may be correlated with discinid oblique posterior and oblique internal muscles and with the oblique internals of *Crania*, all of which are similarly attached.

The opening of the valve of all of these genera is thought to be effected by contraction of the posterior adductors or umbonal muscle and relaxation of the anterior adductors or their homologues. The action is probably assisted and partly controlled by the various oblique muscles and dermal muscles of the body wall.

LOPHOPHORE

The brachiopod feeding organ, the **lophophore,** which may also assist in respiration, is a filamentous appendage disposed symmetrically about the mouth and typically suspended from the anterior body wall, extending into the mantle cavity. The fully developed lophophore is essentially a variably disposed tube bearing a pair of ridges along its length bordering the brachial (or food) groove. The frontal ridge forms a flap, the brachial lip (or fold), which is actually a lateral extension of the preoral lobe in front of the slitlike mouth; the other (abfrontal ridge), forms a broad base to the filaments (Fig. 30). The entire surface of the lophophore consists of inner epithelium, with tall, slender, selectively ciliated cells and ciliated columnar cells forming the epidermis of the filaments and the lophophore, respectively. Mucus-gland cells are usually more abundantly interspersed within the epithelium of the lophophore, but in *Lingula* at least, they are also arranged in definite longitudinal rows along the filaments (15).

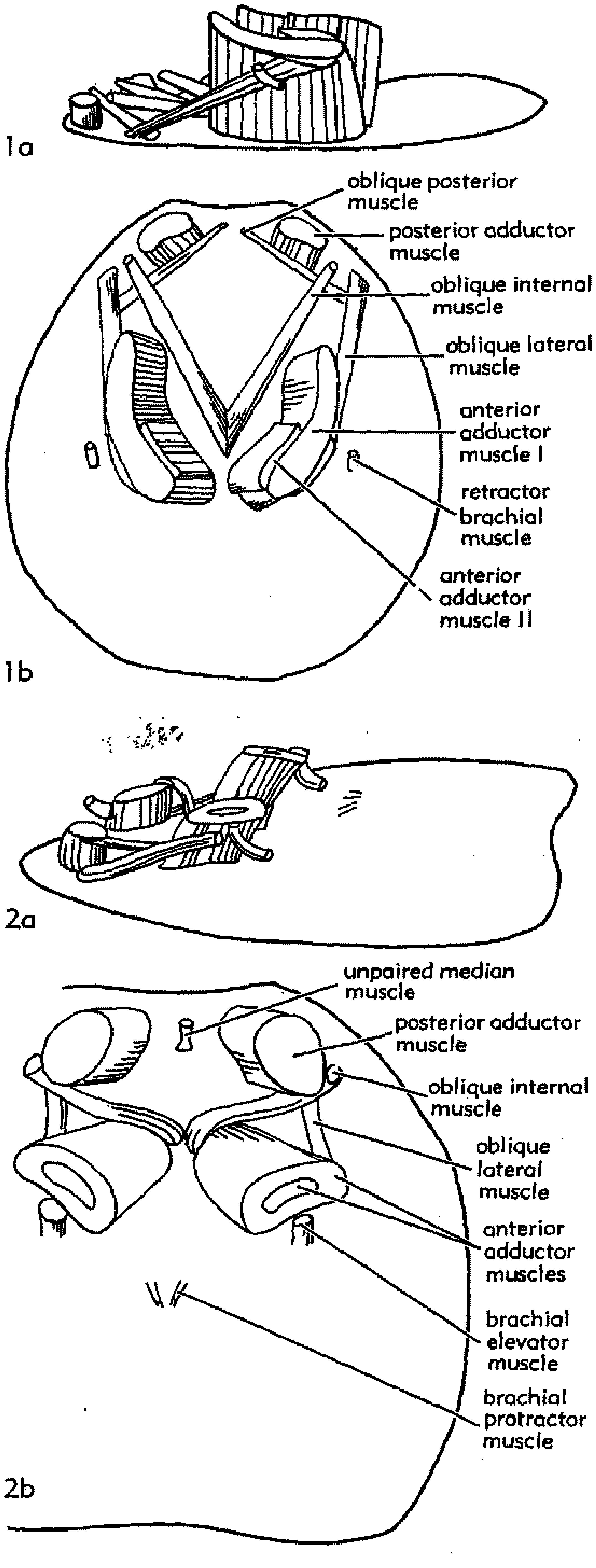

FIG. 29. Muscle systems of *(1a,b) Discinisca* viewed laterally and dorsally (14), and *(2a,b) Crania* viewed laterally and dorsally (14).

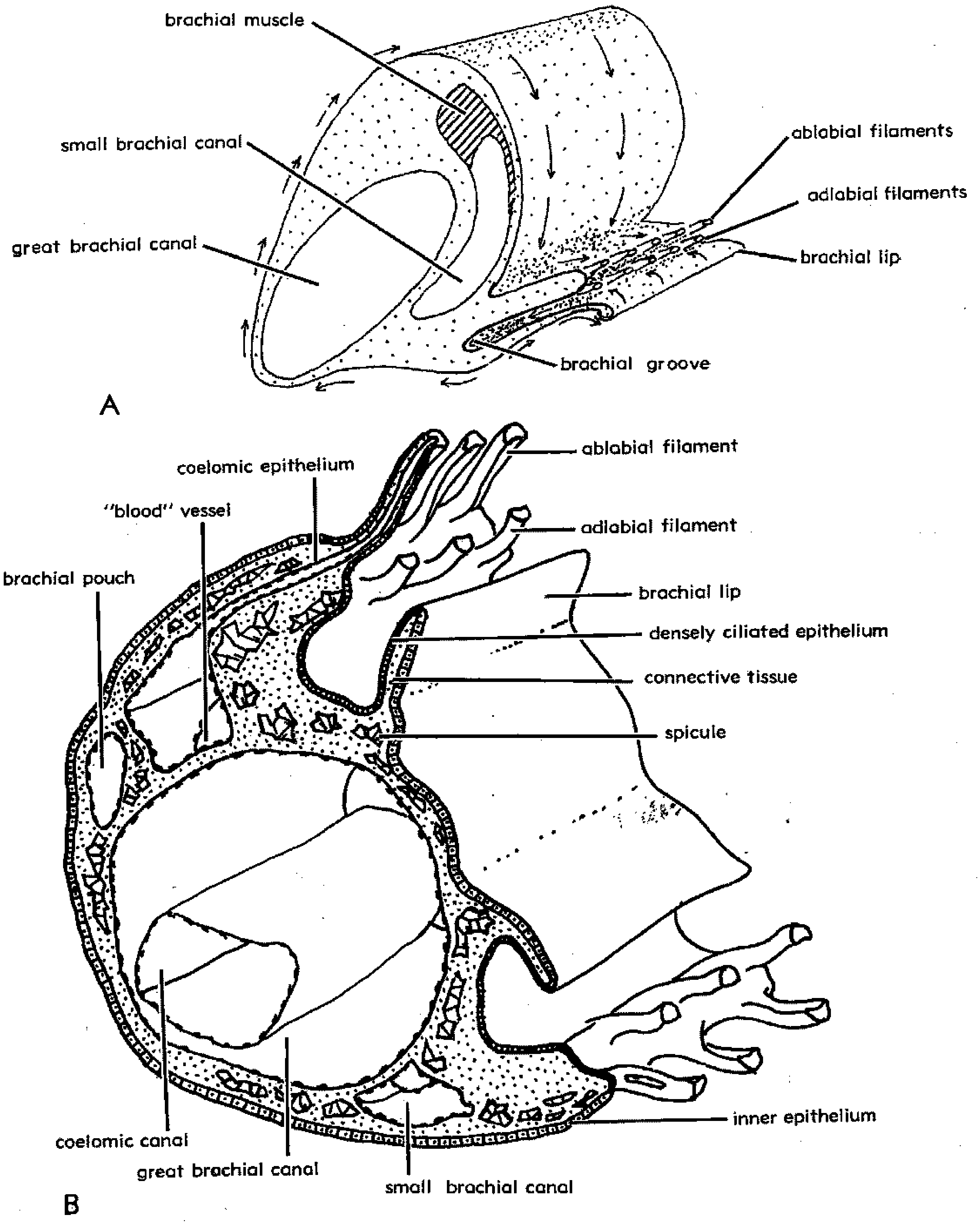

FIG. 30. Diagrammatic sections of *(A)* brachium of *Lingula* with arrows showing direction of ciliary beat (15), and *(B)* side arm of *Terebratulina* (48).

Two liquid-filled canal systems, lined by coelomic epithelium and embedded in a firm collaginous connective tissue, occupy the axes of the lophophore and the filamentous base. The former, the **great brachial canal,** is closed off from the body cavity, at least during the life of the adult, and in inarticulates it is also divided into two separate cavities symmetrically disposed about the mid-line. The latter, the **small brachial canal,** gives off a branch into each filament (filamentar canal) and except in some inarticulates (craniids, discinids), opens into the body cavity around the esophagus. Although this generalized pattern is typical of all living brachiopods, a number of minor complications characterize the inarticulates. Thus, in *Lingula* and to a lesser extent in

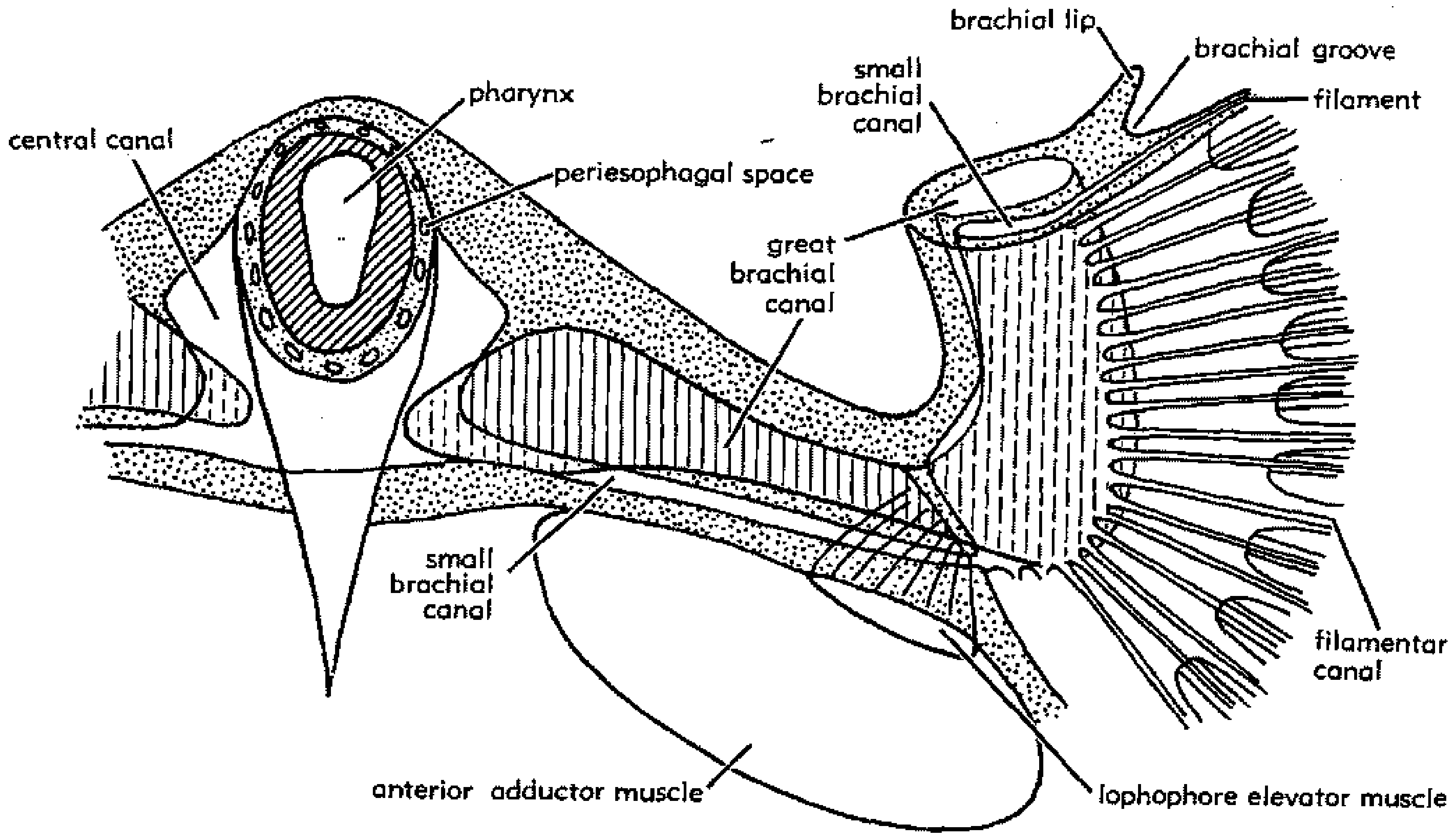

FIG. 31. Diagrammatic representation of canal systems in lophophore of *Crania* (12).

Discinisca, the proximal ends of the great brachial canals are divided into several lobes (12), and the course of the canals in the region of the esophagus is further complicated by infolding of narrow pouches of the main body cavity. Moreover, where the lophophore is attached to the anterior body wall of inarticulates, the small brachial canals contract abruptly (Fig. 31). They are then continued medially as narrow tubes, which in *Crania* and *Discinisca* open into a large median central canal developed in the supporting tissue of the lophophore, on the ventral side of the pharynx (Fig. 31, 32). In *Lingula*, although the two small brachial canals are connected medially, the central canal is poorly developed. In all inarticulate genera, the connective tissue surrounding the pharynx contains a number of small interconnected chambers, the **periesophagal spaces** which are in connection with the small brachial canals (Fig. 32) (12). In *Discinisca* and especially *Lingula* a further extension of the small brachial canal system is found in coelomic spaces of the **brachial lip.** Thus the small brachial canal system in inarticulates consists of interconnected elements which include the **filamentar canals**, small brachial canals, central canal, periesophagal spaces, and lacunae in the brachial lip.

No complications on this scale affect the cavity systems of the articulates. In terebratellaceans like *Pumilus*, the small brachial canals arise laterally from pouchlike extensions of the main body cavity and although these have been called periesophageal sinuses (3), they are not infolded in the manner of the inarticulate periesophageal canals (Fig. 33). The body cavity is also prolonged as a pair of brachial pouches along the medianly facing surfaces of the terebratuloid side arms (Fig. 30). These pouches extend forward more or less to the same degree as the skeletal loop, so that they are only incipiently developed in the septate *Pumilus* but extend to the tip of the side arms of the long-looped *Macandrevia.*

The lophophore is apparently not capable of much extensible movement, even in the inarticulate brachiopods, which not only lack skeletal support for the organ but also have the best-developed musculature. Within the inarticulate lophophore, a pair of strongly developed brachial muscles arise from the connective tissue at the constricted proximal end of the small brachial canal and extend along the length of the canal in each brachium.

Some of the inarticulates have additional muscles attached to the lophophore, the apparent function of which is to control the position of the organ relative to the brachial valve and anterior body wall. Thus the discinids and craniids both possess a pair of small "brachial retractor muscles," which

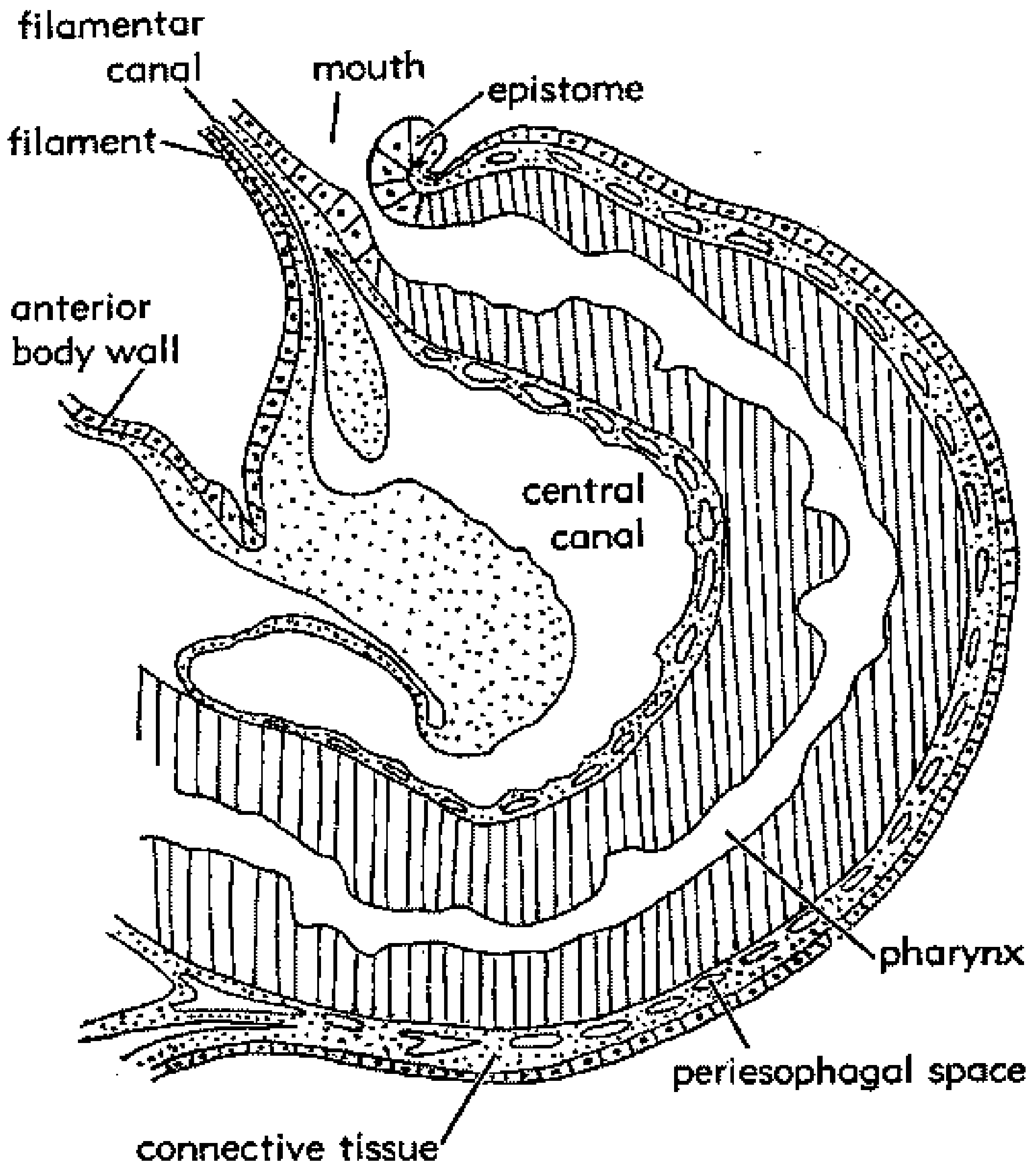

FIG. 32. Median section through lophophore and pharynx of *Crania* (12).

arise from the brachial valve lateral to the attachment of the anterior adductors. A further two pairs of muscles occur only in the craniids. A pair of stout brachial-elevator muscles inserted on the brachial valve anterolateral of the anterior adductors are attached at their other extremity to the connective tissue at the base of the brachial muscle. A pair of small brachial-protractor muscles placed anteromedially are also present (Fig. 29,2*a*,*b*).

In the supported lophophores of articulate brachiopods, the muscle fibers do not show the same degree of organization. They are more numerous, however, in the spirally coiled free brachia **(spirolophe)** of the rhynchonelloids than in lophophores associated with a complex skeletal support, which may be made even more rigid by the development of irregular plates of calcite (spicules) within the connective tissue (Fig. 6,*A*).

The filaments, which are responsible for activating water flow through the lophophoral apparatus and for diverting food particles into the brachial groove, whence they are conveyed to the mouth, are of two distinctive types in most adult brachiopods. On either side of the mouth are the first-formed filaments of the **trocholophe,** the ringlike lophophore that is attached to the anterior body wall and even part of the dorsal mantle of larvae and juvenile shells. The actual number of these filaments, which, except in lingulids and discinids, are arranged in a single row, varies at least from one genus to another according to the size of the fully developed trocholophe (45). Their frontal surface (facing the brachial lip) forms a broadly rounded ridge bearing cilia that beat with the length of the filament, in contrast to the two sets of longer lateral cilia that beat across the length of the filament from the frontal to the abfrontal surface. The abfrontal surface appears to be sparsely ciliated in all brachiopods, with exception of the lingulids, in which they are as densely distributed as on the frontal surface (Fig. 34).

In a minority of brachiopods like *Argyrotheca* and *Dyscolia*, this type of filament alone is also characteristic of adults. But with the transformation of the trocholophe

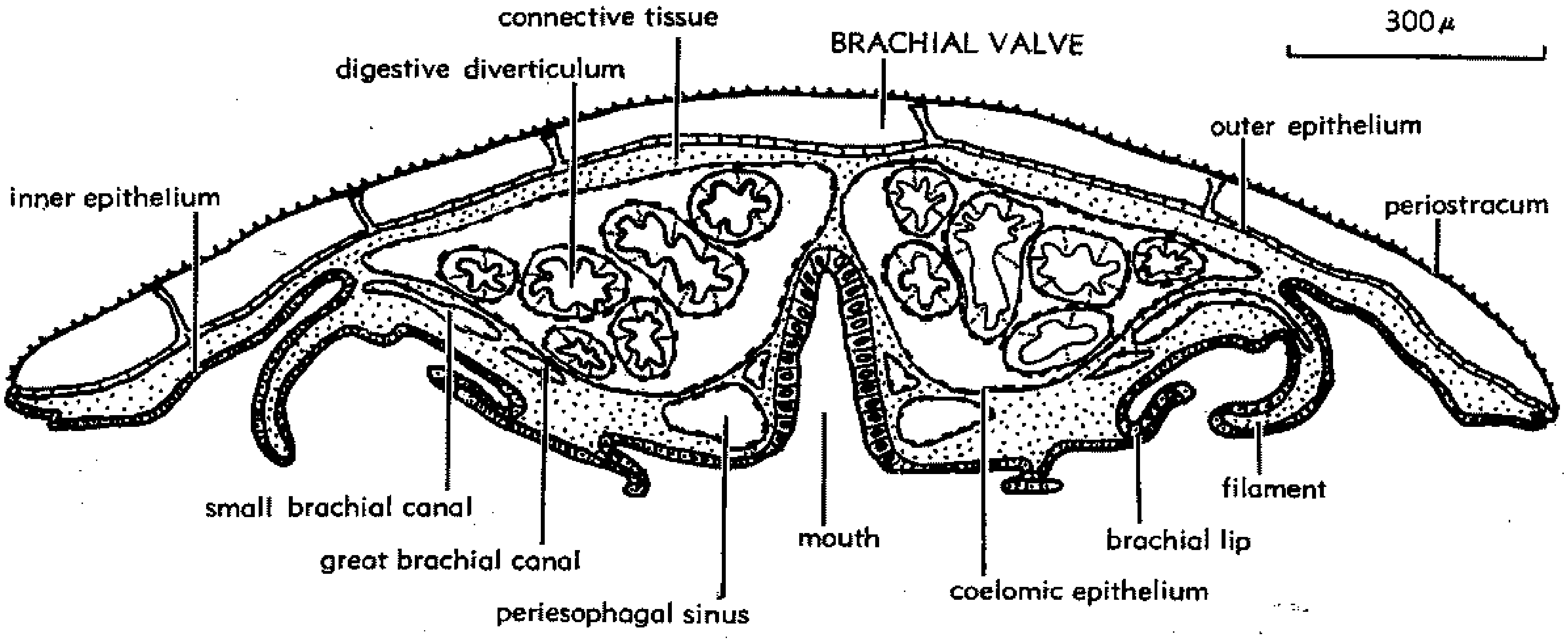

FIG. 33. Sections of brachial valve of *Pumilus antiquatus* ATKINS showing periesophageal sinuses (3).

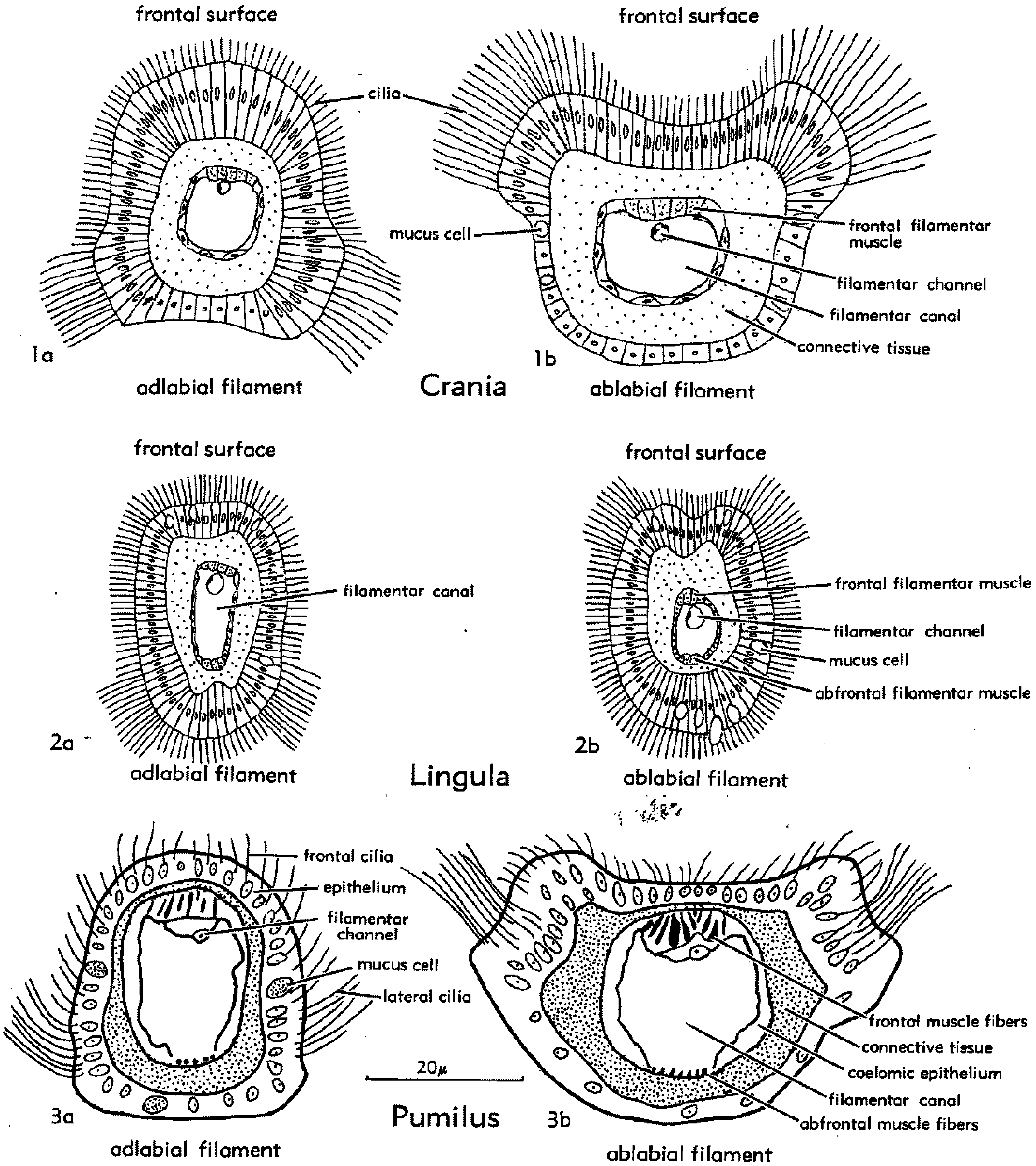

FIG. 34. Diagrammatic sections through adlabial and ablabial filaments of inarticulates (*1a,b, Crania,* 12; *2a,b, Lingula,* 15) and a terebratellacean (*3a,b, Pumilus antiquatus* ATKINS, 3).

into the more complex attitudes found in most adult shells a second set of filaments appears and alternates with the ridged frontal types (adlabial filaments). Filaments of this second series (ablabial filaments) are longer and appear on the filamentous ridge at a greater distance from the brachial lip than those of the first series; and although they are ciliated in the manner of the ablabial filaments their frontal surface is a shallow groove (Fig. 34). In lingulids and discinids all of the filaments are arranged in a double row; even those of the mouth segment are differentiated into ridged adlabial and grooved ablabial types and do not merely represent a post-larval crowding of trocholophous adlabial filaments.

The internal organization of both series is similar to a subepidermal layer of connective tissue and an inner layer of coelomic epithelium lining the filamentar canal. Throughout the length of the filament ex-

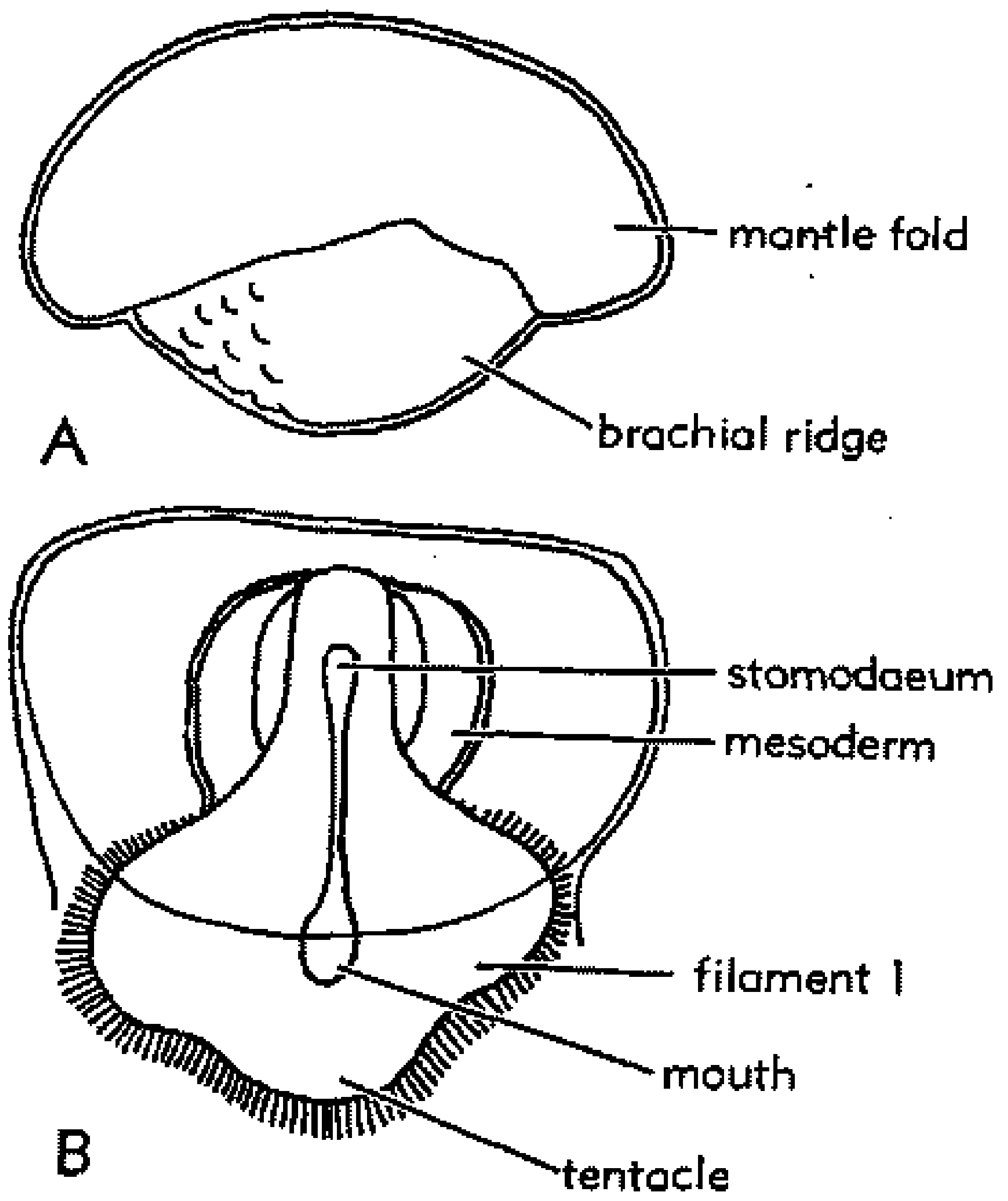

FIG. 35. *Lingula* embryo *(A)* with brachial ridge and mantle fold, and larva *(B)* with one pair of filaments (46).

tends the nerve lodged in the base of the epithelium of the frontal surface and frontal and abfrontal muscles within the coelomic epithelium; also a blood vessel (filament channel) occurs within the filamentar canal, commonly attached to the coelomic epithelium beneath the frontal surface (Fig. 34). All muscle fibers appear to be smooth in *Lingula,* but in *Crania, Notosaria,* and many terebratuloids, most if not all of the fibers in the more strongly developed group (concentrated beneath the frontal surface) are striated.

The disposition of the adult lophophore is so intimately related to its early growth that it is best described in relation to the development of that organ.

In all living inarticulates the lophophore is first differentiated in the free-swimming larval stage. Details of its earliest growth, however, are known only in *Lingula* although there is no reason why they should not be regarded as typical for the class (46). In *Lingula,* the lophophore develops from a moundlike, densely ciliated brachial ridge which initially is invaginated ventromedianly to form the rudimentary mouth (Fig. 35,*A*). The ridge then flattens ventrodorsally and assumes a triangular outline with the two posterior angles forming the first pair of rudimentary filaments and the anterior apex the earliest manifestation of the median tentacle (Fig. 35,*B*). The second pair of filaments are added anteriorly on either side of the median tentacle. At the same time a part of the lophophore immediately posterior to the mouth becomes elevated ventrally so that the mouth is shifted to a central position, where it becomes flanked anteriorly by a transverse ridge, the preoral lobe or **epistome.** A third pair of filaments arises between the median tentacle and the second pair and proliferation of filaments continues from the generative zones on either side of the tentacle so that the lophophore assumes the form of a filamentous ring with the earliest filaments situated posteriorly (trocholophe). The trocholophous stage is known in craniids and discinids, as well as in the lingulids. At varying stages in the proliferation of filaments (four to five pairs in *Crania,* 15 pairs or more in *Lingula*) the median tentacle disappears and the two generative zones at the tips of a pair of brachia (or arms) gradually move apart to define a median indentation (schizolophous condition). At about this phase in growth of *Crania* the adlabial and ablabial filaments arise in alternating series. The preoral lobe is then undergoing lateral expansion concentric with the filament bases to form the juvenile brachial lip. Exceptionally, as in *Pelagodiscus,* the schizolophe is characteristic of the adult, but with further growth of the lophophore in other genera, the generative zones are pushed away as the apices of two ever-increasing spires (spirolophe) directed dorsally in the craniids, ventrally in the discinids, and medianly in the lingulids.

The best accounts of the origin of the lophophore in articulate brachiopods are those of PERCIVAL (35, 36) for *Notosaria nigricans* (SOWERBY) and *Terebratella inconspicua* (SOWERBY), but some inconsistencies appear, especially with regard to growth of the brachial lip, which, according to ATKINS (9), arise from misinterpretation of the development in the latter species.

As the larvae of *Notosaria* settle, the surface of the apical lobe becomes modified into a low central mound surrounded by a broad margin (Fig. 36,*A*). Two crescentic slits appear at the base of the mound (dorsal one first), and ultimately join as the central mound sinks from sight (Fig. 36,*B,C*). Concomitant with depression of the central mound, the margin becomes broken by a gap on the dorsal side to form a horseshoe-shaped rim with two ends touching and with an outline becoming hexagonal as the rudiments of the first three pairs of filaments become differentiated. The central mound now reappears as an azygous lobe which moves into the gap in the rim and

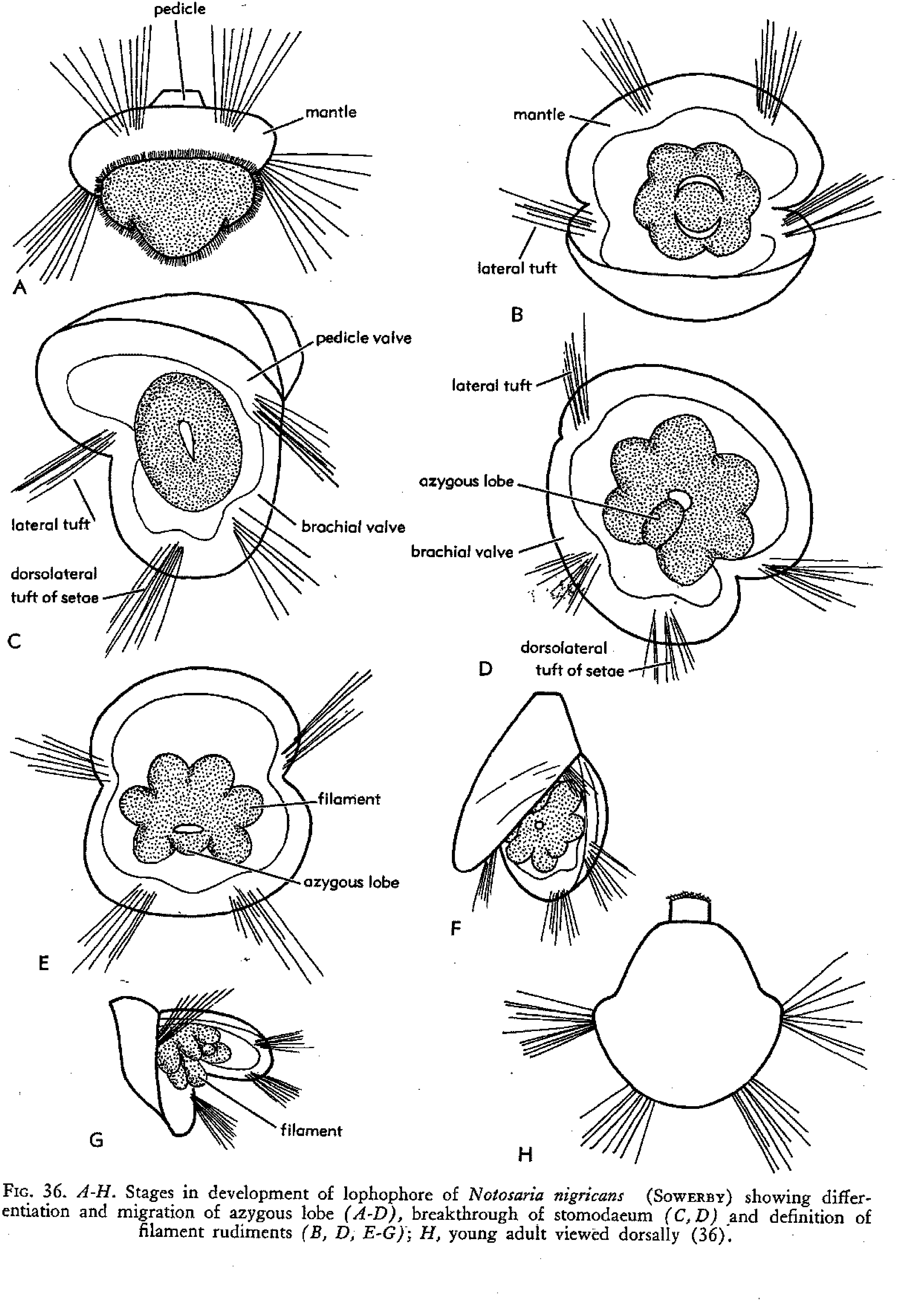

Fig. 36. *A-H.* Stages in development of lophophore of *Notosaria nigricans* (Sowerby) showing differentiation and migration of azygous lobe *(A-D),* breakthrough of stomodaeum *(C,D)* and definition of filament rudiments *(B, D, E-G)*; *H,* young adult viewed dorsally (36).

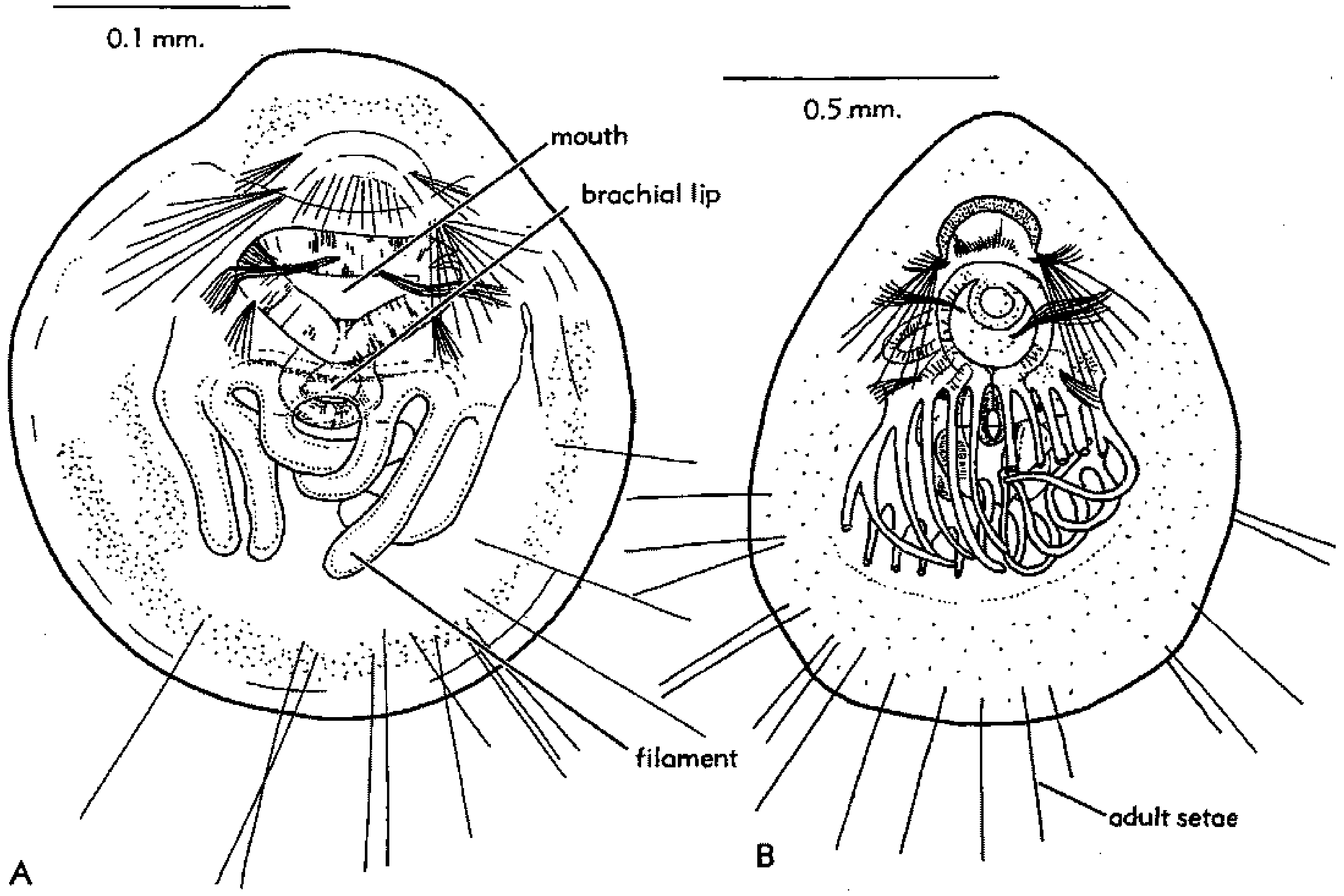

FIG. 37. Young adult of *Notosaria nigricans* (SOWERBY); *A*, with 6 filaments and brachial lip above mouth; *B*, with 10 pairs of filaments and well-developed brachial lip (36).

is the rudiment of the brachial lip (Fig. 36, *D,E*). The first-formed filaments continue to elongate and new ones are formed simultaneously at both ends of the arc on each side of the azygous lobe, which is modified into a thin hood projecting toward the middle of the oral field. When eight pairs of filaments have appeared, this brachial lip enlarges toward the filaments to form a crescentic flap concentric with their bases and partially covering the juvenile mouth (Fig. 37).

PERCIVAL's description (35) of the development of the lophophore of *Terebratella* differs from the process outlined above especially in formation of the brachial lip, which he claimed arises as a rapid posterior extension of the anterior border between the latest pair of filaments, when eight pairs have appeared (Fig. 38,*A*). ATKINS (9), however, maintained that the brachial lip of *Terebratella* and also of a number of terebratuloid (Fig. 39) and rhynchonelloid species, developed by anterolateral extension on either side of a small, preoral lobe in the manner of *Notosaria* (Fig. 38,*B,C*). Her material did not include early postlarval spats available to PERCIVAL, but her observations so endorse the differentiation of the lophophore of *Notosaria* that this may be taken as the typical mode of development in articulate brachiopods. At this stage of development PERCIVAL also recorded that in *Terebratella* the rudiments of the first three pairs of filaments do not appear simultaneously, as in *Notosaria*, but in a definite order with the posterior pair arising first, followed by the lateral, then the anterior pair (Fig. 40). This suggests a migration of two generative zones, responsible for the proliferation of filaments toward a contiguous anteromedian position on the rudiment of the filamentous base. Whether PERCIVAL was mistaken in believing the lateral and anterior pair to be initially absent, as claimed by ATKINS, remains to be seen.

With the formation of about eight pairs of filaments the lophophore consists of a posteromedian mouth with a preoral brachial lip rapidly expanding anterolaterally, surrounded by a circular and expanding base bearing filaments that are being added in pairs from two contiguous generative zones situated anteromedianly in a position formerly occupied by the azygous lobe. This represents the **trocholophous stage** (Fig. 39). The lophophore base is attached to the dorsal mantle and anterior body wall and con-

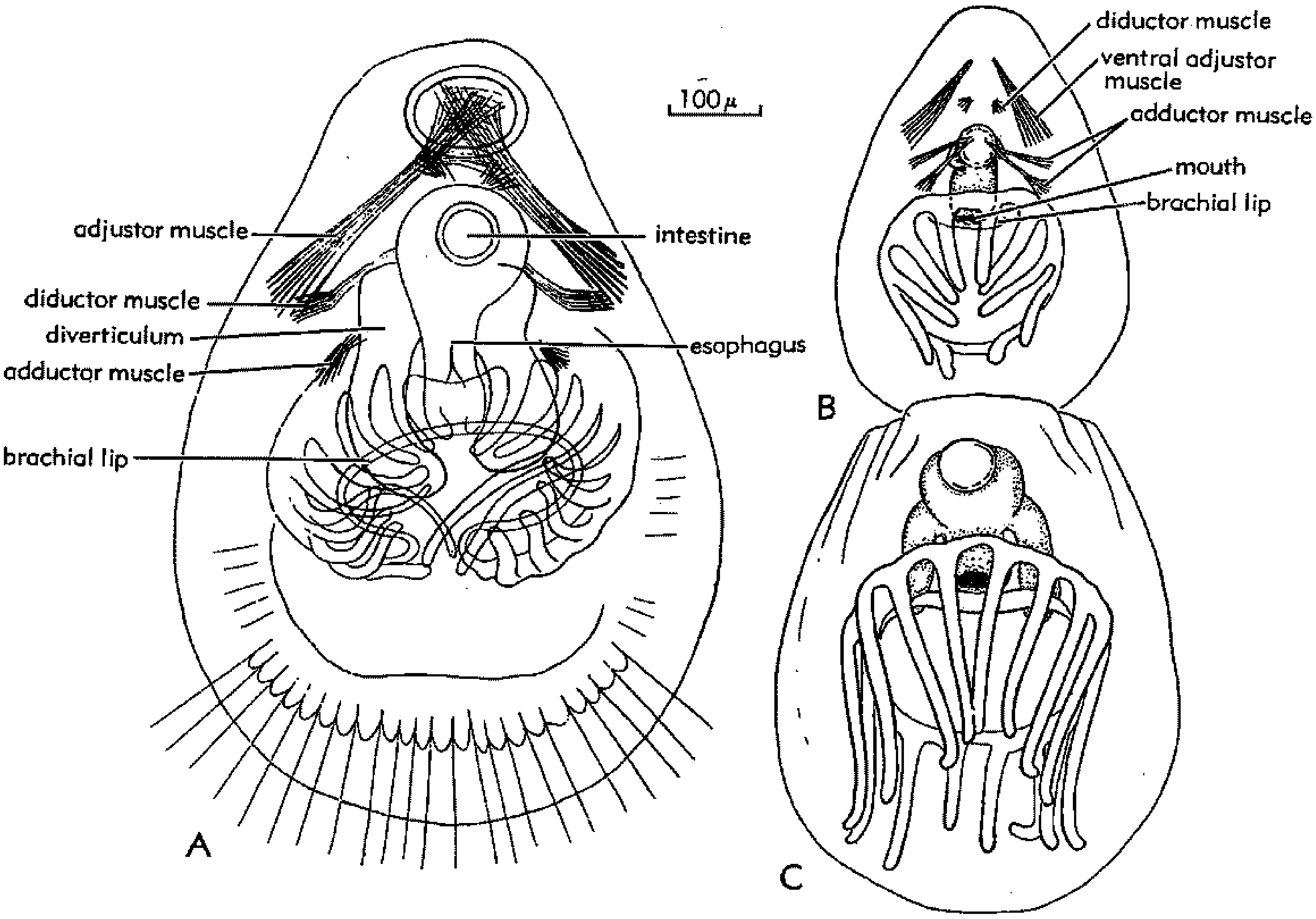

FIG. 38. Origin of brachial lip of *Terebratella inconspicua* (SOWERBY), *(A)* according to PERCIVAL (35) and *(B, C)* ATKINS (9).

tains only the small brachial canal, so that it is really the filamentar base. At this stage of development all filaments have ridged frontal surfaces and exceptionally, as in *Dyscolia* and probably *Gwynia*, the adult lophophore simply consists of an expanded trocholophe equipped solely with adlabial filaments.

The lophophores of adult *Argyrotheca, Megathiris,* and *Thecidellina* also bear a single series of adlabial filaments, but they are folded into either two or four lobes,

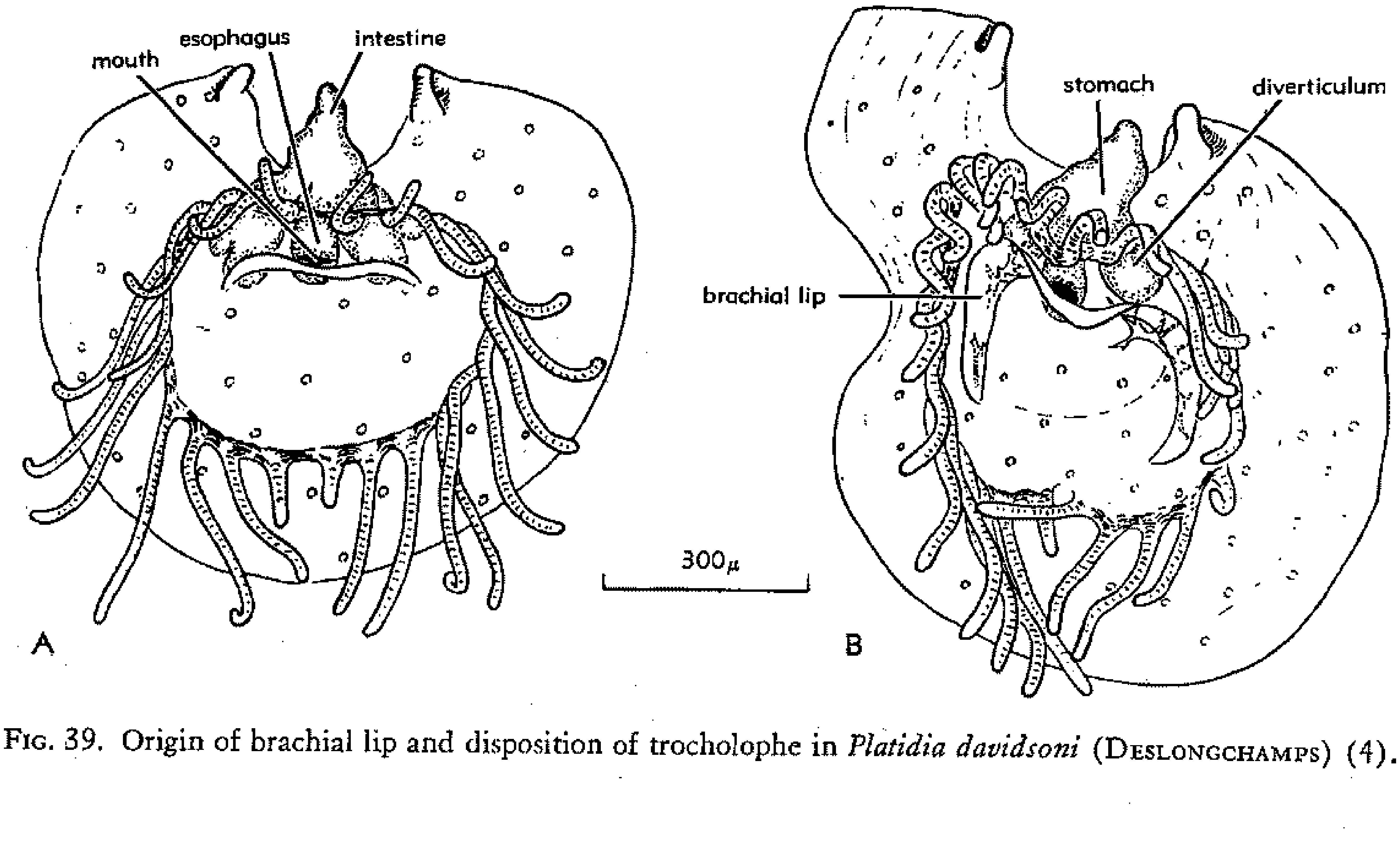

FIG. 39. Origin of brachial lip and disposition of trocholophe in *Platidia davidsoni* (DESLONGCHAMPS) (4).

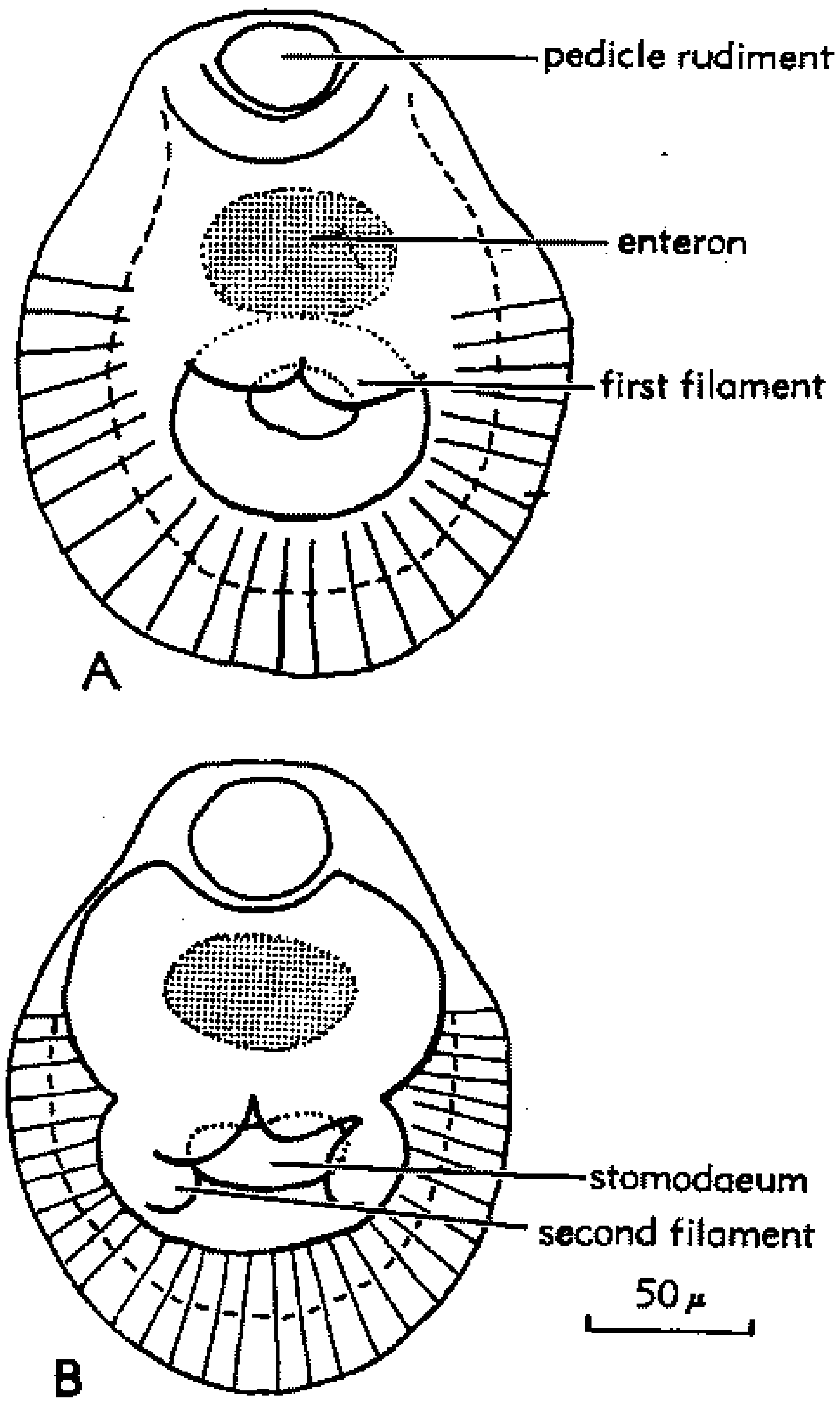

FIG. 40. Origin of filament rudiments during development of *Terebratella inconspicua* (SOWERBY) (35).

with the generative zone forming a continuous posterior tip across the median ridge. Despite some inconsistency in nomenclature, it seems better to refer to such structures as "bilobed" or "quadrilobed" trocholophes in order to recognize their simple arrangement of filaments (Fig. 41,*A*,*B*; 42). For in most articulates as in the craniids, after the formation of a variable number of adlabial filaments, about eight pairs in *Terebratella inconspicua,* 18 pairs in *Platidia davidsoni* (DESLONGCHAMPS), an alternating series of ablabial filaments with grooved frontal surfaces is also proliferated. At the same time the generative zones may become separated by a median septum, as in the terebratellaceans, or directed posteriorly in such a way that the circular disposition of the trocholophe is deformed by a median indentation. This is the **schizolophous stage** in which, as in the inarticulates, the lophophore is identified for the first time as consisting of a pair of brachia, each terminating in a medianly situated generative zone (Fig. 41,*C*). The schizolophe is characteristic of adult *Pumilus.* Both the trocholophe and schizolophe are disposed more or less in the same plane and further lengthening of the brachia can continue only if subsidiary indentations of schizolophe take place (**ptycholophous stage**). Alternatively, the generative

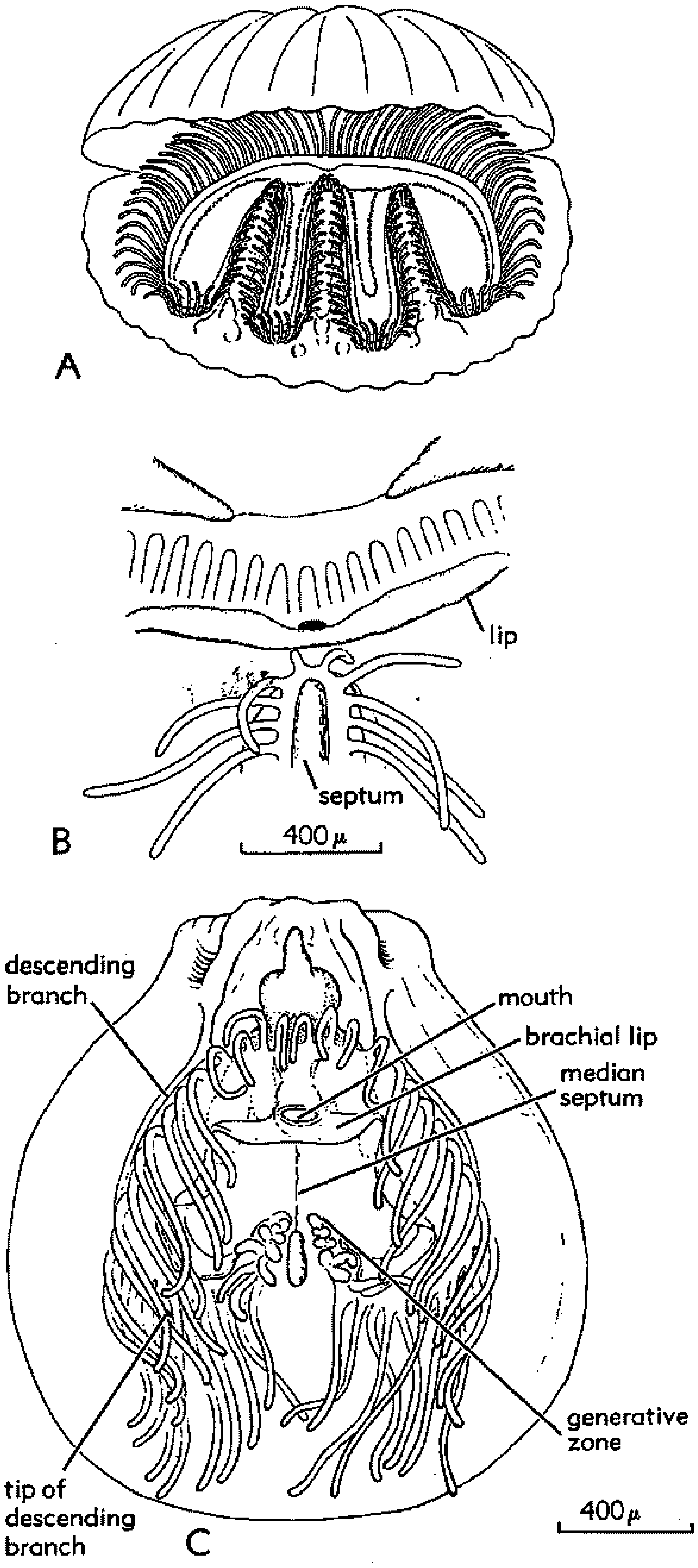

FIG. 41. *A*. Quadrilobed trocholophe of *Megathiris detruncata* (GMELIN) (7).——*B*. Details of generative tip of *Agyrotheca cordata* (RISSO) (7).——*C*. Schizolophe of *Macandrevia cranium* (MÜLLER) (5).

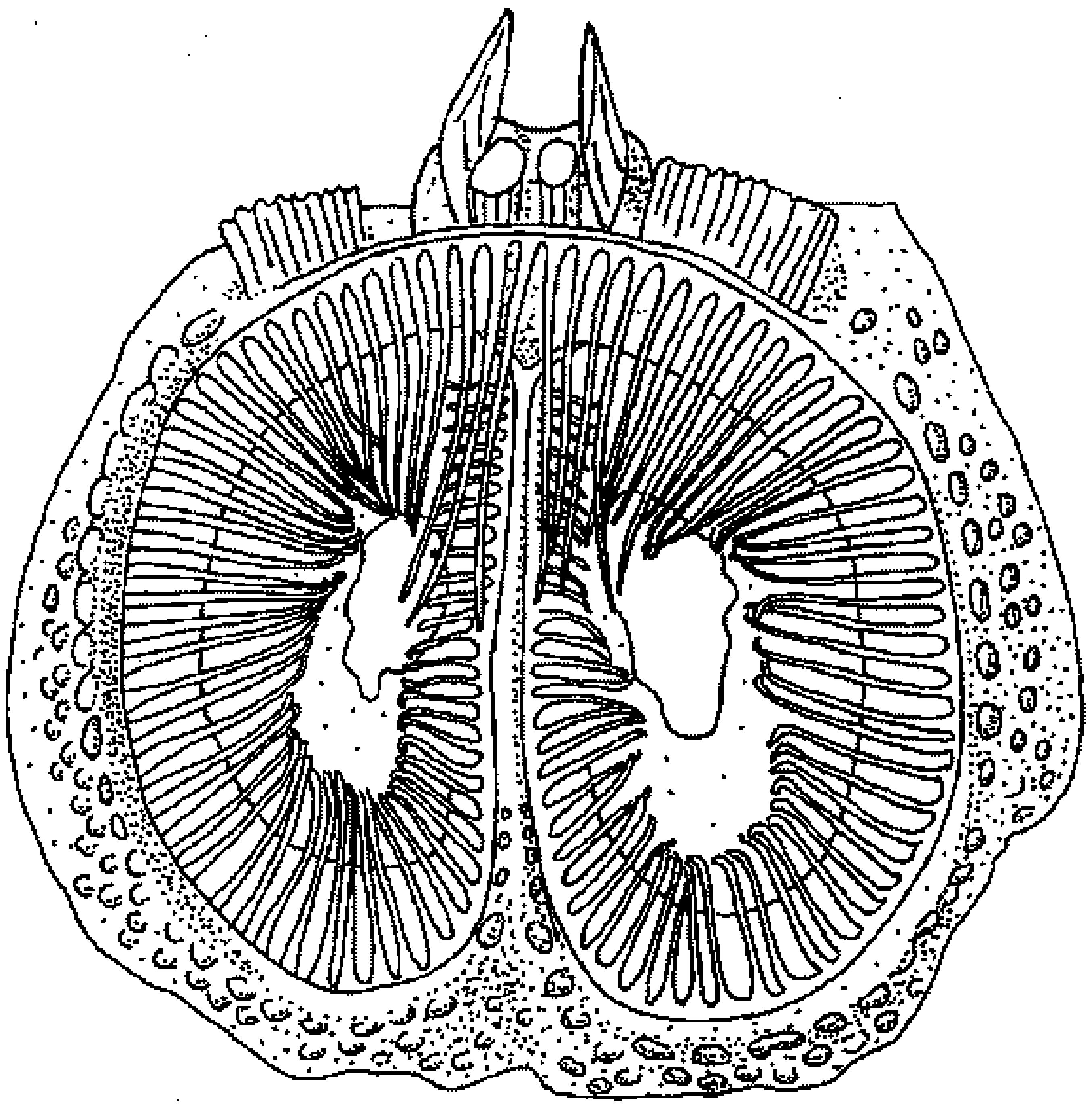

FIG. 42. Bilobed trocholophe of *Thecidellina* (47).

zones may move spirally away from their median position to form the dorsally directed spirolophes of the rhynchonelloids (Fig. 43,*2a,b*). In contrast, the generative zones of the terebratuloid lophophore remain in median position and increase in length of the brachia is initially accommodated by development of a pair of long loops (side arms) equivalent to the proximal whorls of the spirolophe but rotated to lie more or less parallel with the plane of shell symmetry (Fig. 43,*1a,b*). This is the **zygolophous stage** and is usually precursory to the ultimate **plectolophous stage**, so characteristic of most terebratuloids, in which the terminal portions of the brachia also move away from the anterior body wall by coiling in the median plane (Fig. 44).

NERVOUS SYSTEM

A central nervous system is present in all brachiopods. Among the articulates it is only well known in *Gryphus* (Fig. 45) although its ramifications are probably typical of the class. The system consists of a smaller, transverse supraenteric ganglion and a larger subenteric ganglion, lying respectively above and below the esophagus near its junction with the anterior body wall. The ganglia are joined by one or more circumenteric connectives. The subenteric ganglion and the connectives are responsible for the innervation of the lophophore, the

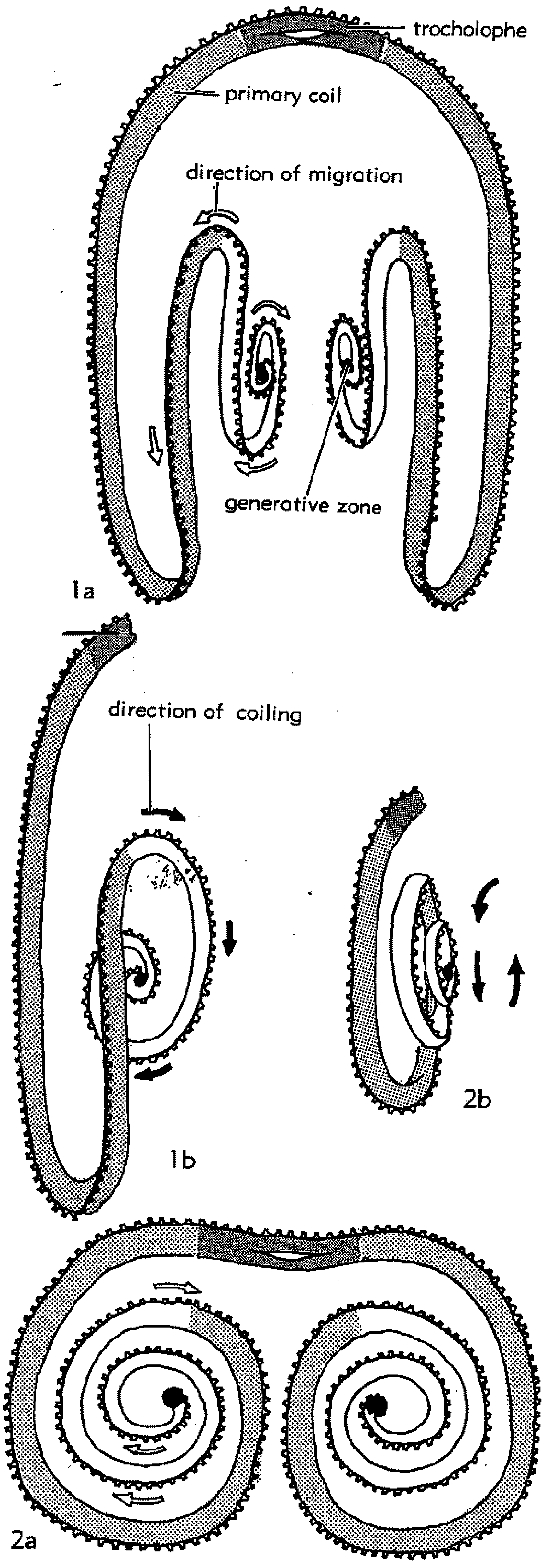

FIG. 43. Stylized ventral and lateral views of *(1a,b)* terebratulid plectolophe and *(2a,b)* rhynchonellid spirolophe, showing positions of original trocholophes, primary coils, and generative zones (45).

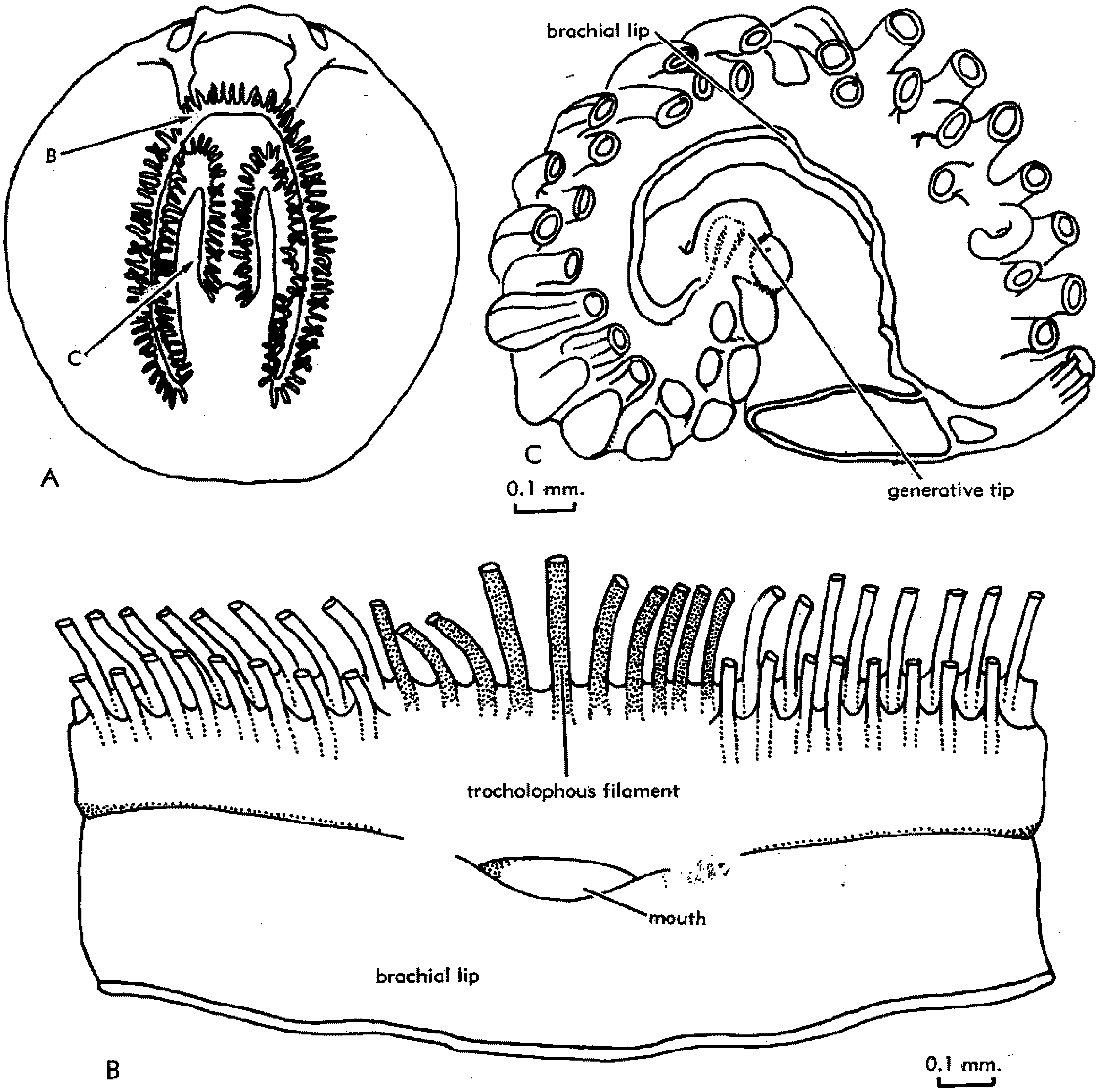

FIG. 44. Plectolophe of *Terebratulina (A)*, with enlargements showing arrangement of trocholophous filaments behind mouth *(B)* and one of median generative zones *(C)* (45).

former giving rise laterally to a pair of nerves that activate the brachial lip and the latter forming branches (accessory and lower brachial nerves) that serve the brachia and filaments. A pair of main lateral and a number of ancillary branches arise from the subenteric ganglion to innervate the dorsal mantle lobe. The ventral mantle lobe, the adductor muscles, and the pedicle are served by a pair of thick, subparallel branches passing posteriorly from the same ganglion.

The nervous system of inarticulate brachiopods differs importantly from that of the articulates in the absence of a supraenteric ganglion and also possibly in its location in the base of the epithelium, rather than in the connective tissue.

The principal nervous mass is the subenteric ganglion, which in the lingulids and *Discinisca* is medially placed, beneath the esophagus, in the epidermis of the anterior body wall. Two principal nerve trunks diverge laterally from the ganglion and give rise to the circumenteric connectives which pass in front of the esophagus to complete the circumenteric ring. In *Crania*, the subenteric ganglion is divided into two parts which occur in the epidermis of the lateral body wall, lateral to the anterior adductor muscles; circumenteric connectives complete the circumenteric ring (Fig. 46-48).

The main brachial nerves for the lophophore branch laterally from the circumenteric connectives. They are developed in the epithelium near the base of the brachial lip and give rise to the filamentar nerves.

The nerves associated with the ventral and dorsal mantle arise from the subenteric ganglion and split into numerous fine branches. In *Discinisca* and *Lingula* the branches of the mantle nerves are joined at their distal end to form ventral and dorsal marginal mantle nerves. These are ringlike nerves following the periphery of the mantle and are found on the inner side of the follicles. In *Crania* both follicles and marginal nerves are absent.

The pedicle in *Discinisca* and *Lingula* is provided with a pair of nerves which branch from the subenteric ganglion or from ring-shaped lateral nerves located in the body wall. The course of the nerves to the various muscles is seen in diagrams (Fig. 46-48).

A nervous plexus in the base of the epithelium lining the alimentary canal has been detected by BLOCHMANN (12).

No special sensory cells have been observed in adult brachiopods. Statocysts containing small statoliths are present in larval *Lingula* and *Discinisca* and also in the juvenile forms after settling (46). They may persist in adult lingulids because MORSE (30) has recorded their presence in two species of *Lingula,* although it is noteworthy that he did not find them in *Glottidia,* and BLOCHMANN (12) was unable to confirm their existence in *Lingula.*

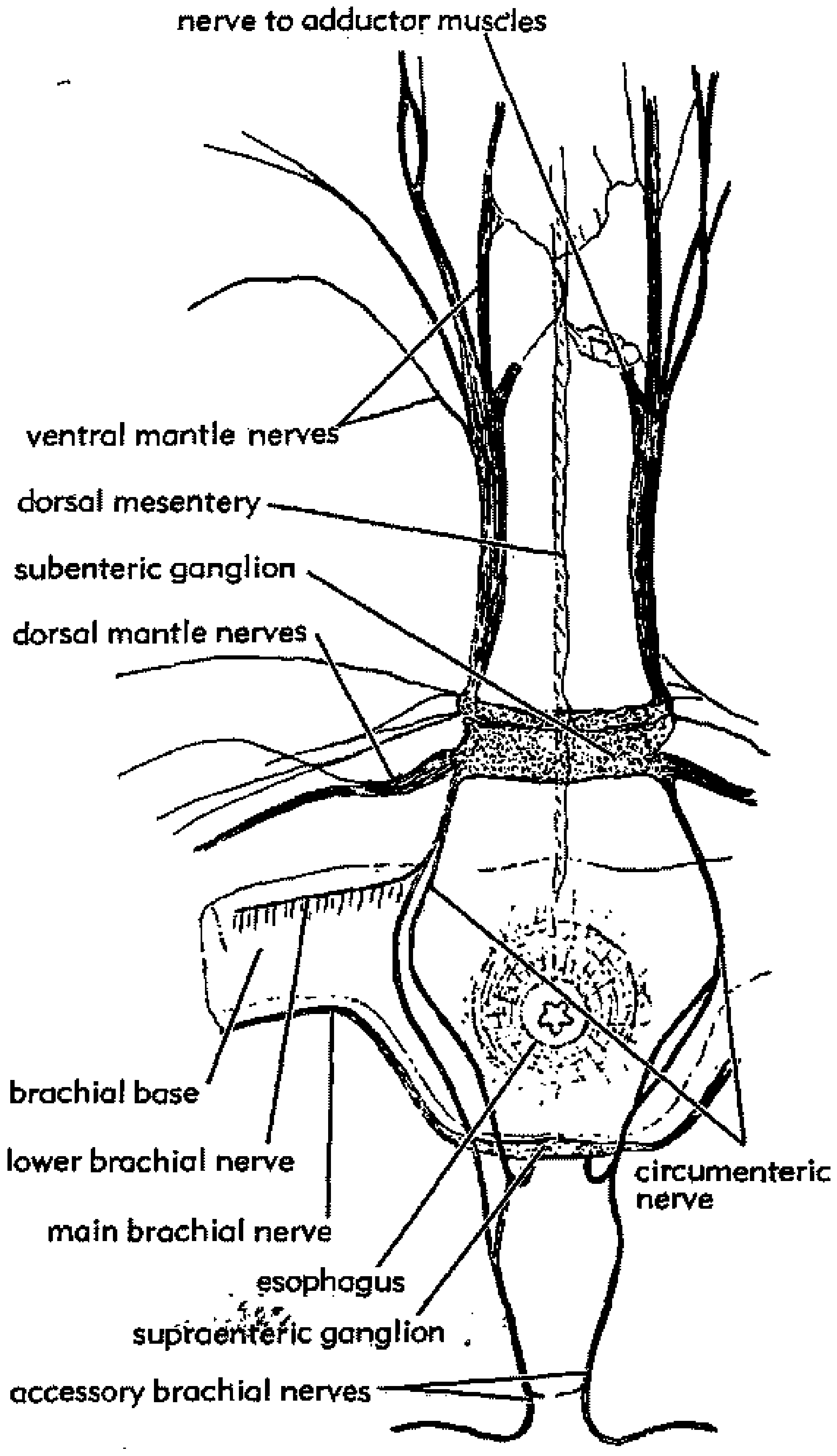

FIG. 45. Nervous system of *Gryphus vitreus* (BORN) (11).

CIRCULATORY SYSTEM

An open circulatory system containing a coagulable colorless fluid free of cells is variably developed in all living brachiopods. It is imperfectly known, especially in the articulates, although throughout the phylum it appears to conform to a basic pattern best known in *Lingula* and *Crania.* Essentially the system is served by one or more contractile appendages ("heart") of a main mid-dorsal channel, which is supported by the dorsal mesentery in the vicinity of the stomach. The heart of *Lingula* and probably of other brachiopods is crudely differentiated as a chamber with an outer layer of coelomic epithelium underlain by a thick layer of circularly disposed muscle fibers but without an inner endothelial lining. The main channel is similarly constructed, except that the muscle fibers are helicoidal, but all branches consist solely of continuous channels within the connective tissue.

The course of the principal channels is basically alike in *Crania* and *Lingula,* although in the former genus several contractile sacs fulfill the function of one, or rarely, more appendages in *Lingula* (Fig. 19). In front of the heart the main dorsal channel runs forward dorsal of the esophagus and bifurcates to serve each brachium of the lophophore. Inside the lophophore, the branch runs ventrally and laterally in the central canals to the entrance of the brachial canal. At this point another branch arises and runs medianly in the ventral part

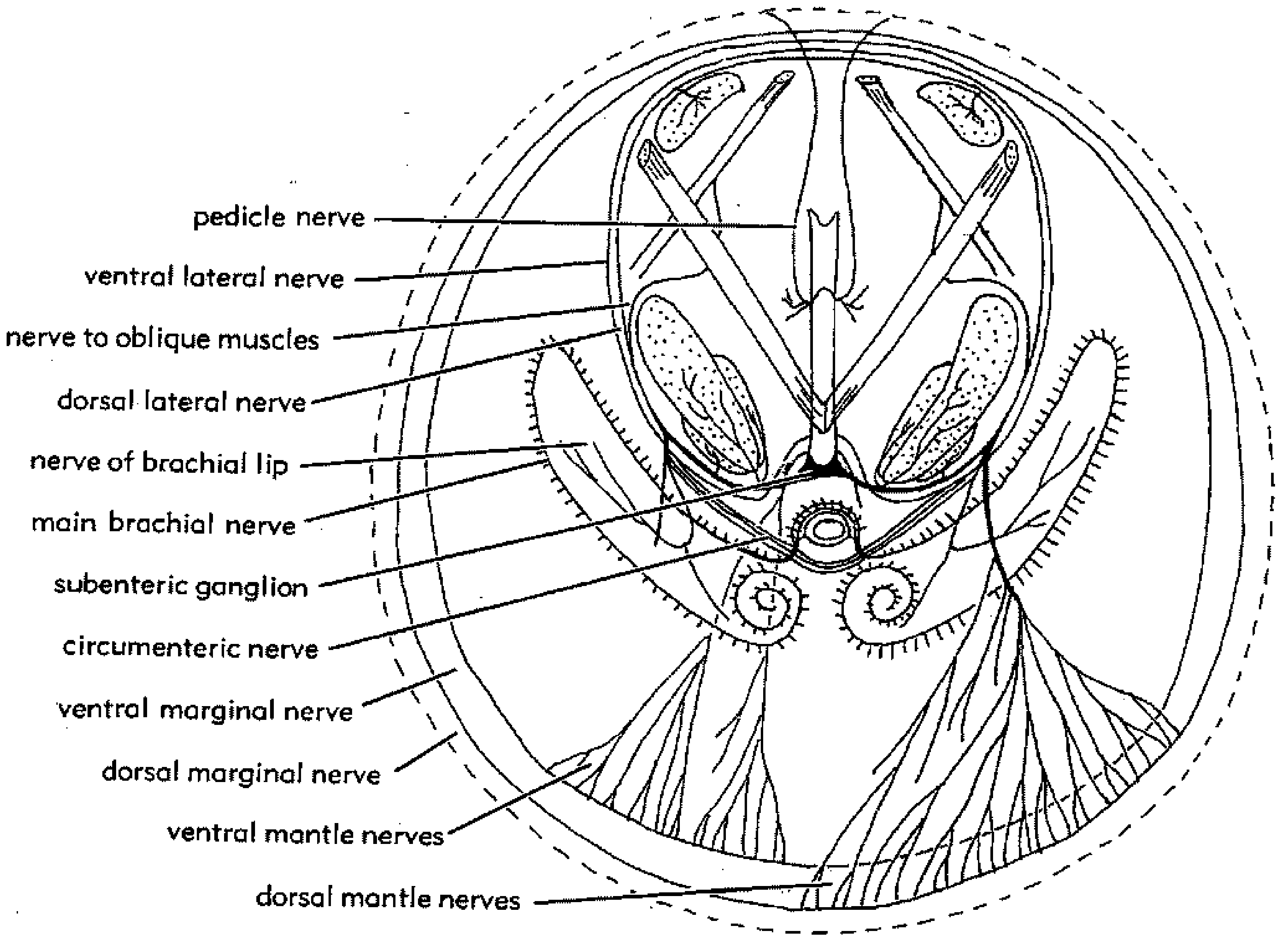

FIG. 46. Diagram of nervous system of *Discinisca* (mantle nerves only shown anteriorly) (12).

of the central canal to connect with the corresponding branch in the other brachium. In this way the circulatory system of both brachia is joined by a connective blood channel ventral of the esophagus. The main branch in each brachium continues along the length of the small brachial canal. The lophophore circulatory system terminates as blind filamentar channels arising from the small brachial or ventral connective channels (12).

Behind the heart, the main dorsal channel splits into a left and right branch, each of which runs ventrally for a short distance before bifurcating into anterior and posterior branches; these two pairs of branches form the dorsal and ventral mantle channels, respectively. The two dorsal mantle channels pass to the anterior body wall along the outer surface of the alimentary canal, on either side of the mid-line. They are then inserted into the dorsal mantle canal and send a branch, which ends blindly in each branch of the mantle canal system.

The ventral mantle channels follow a more complex course before they reach the ventral mantle canals. The course of these channels is different in *Crania* and *Lingula*, but in both genera, they, or their branches, supply the ileoparietal bands and associated gonads and form a network of small channels in this region. Both channels then run anteriorly along their respective nephridia and at the front turn laterally to be inserted in the ventral mantle canals, sending branches into the ramifications of the mantle canal system.

Discinisca is apparently aberrant in the very poor development of its circulatory system (12). The channels in the lophophore are developed normally and are like those

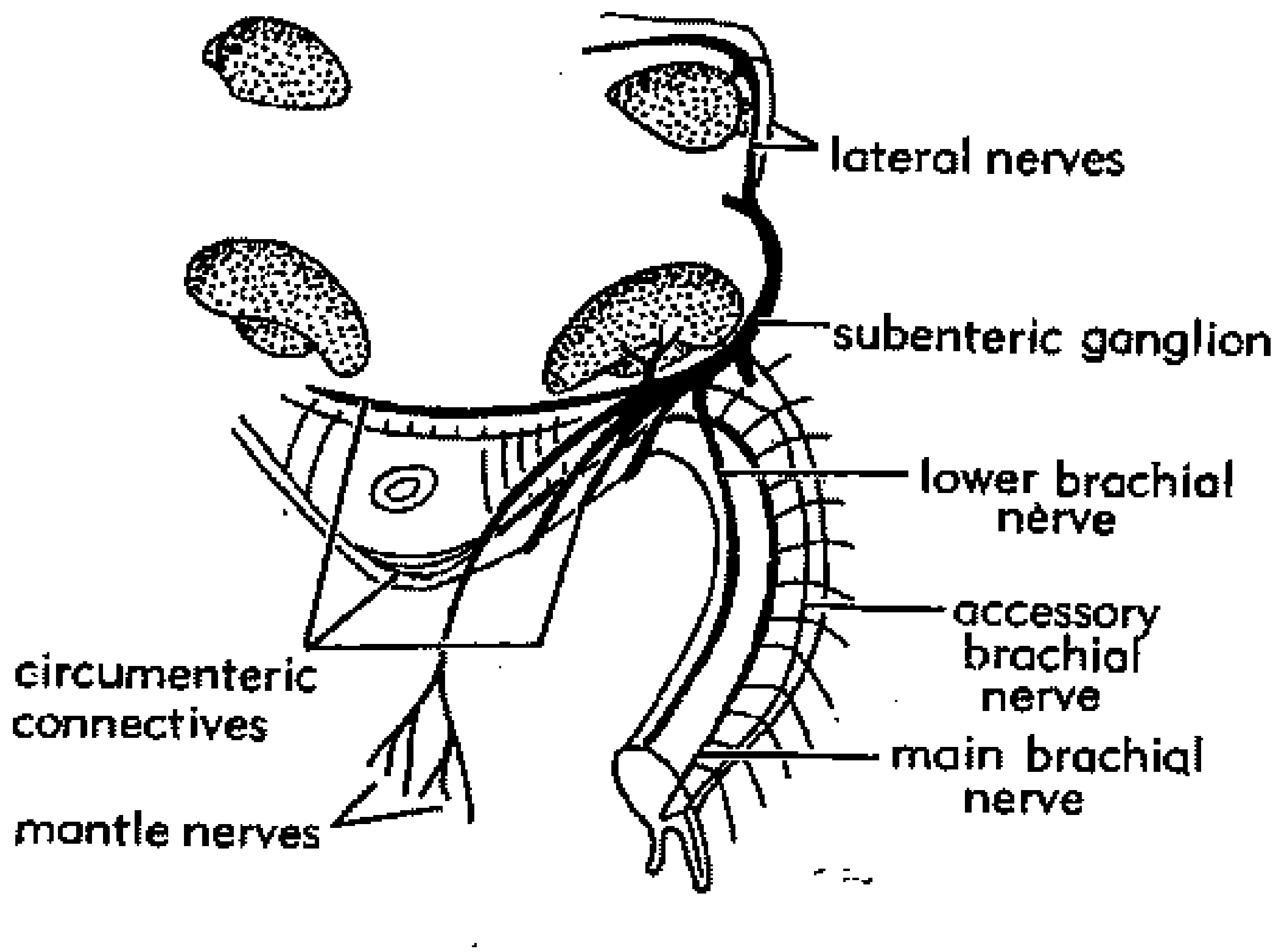

FIG. 47. Diagram of nervous system of *Crania* (mantle nerves only shown anteriorly) (12).

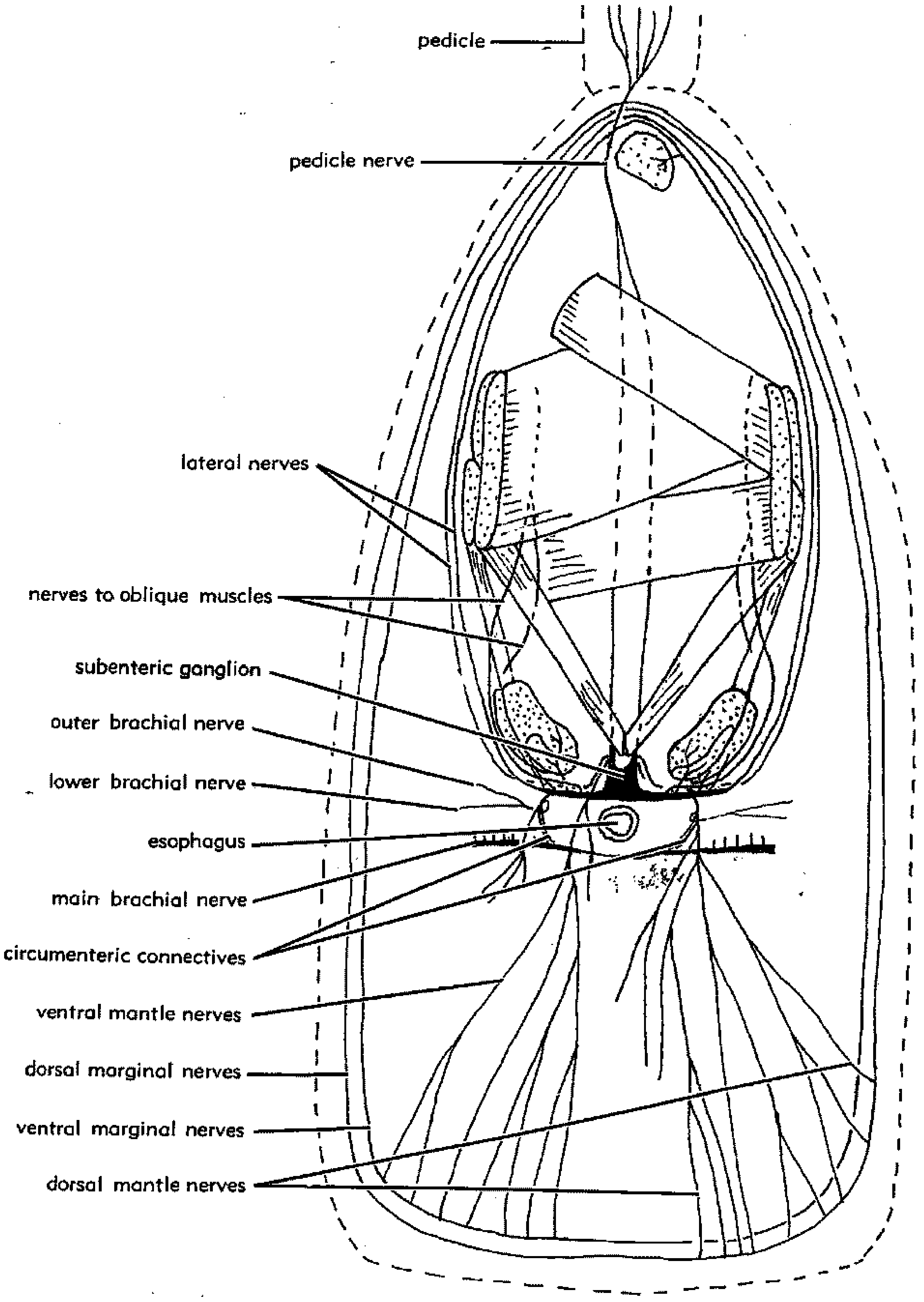

Fig. 48. Diagram of nervous system of *Lingula* (mantle nerves only shown anteriorly) (12).

in *Crania* and *Lingula*, but the remainder of the system appears to be absent.

REPRODUCTIVE SYSTEM

Most brachiopods are apparently dioecious, although some species of *Argyrotheca, Pumilus,* and *Platidia* are known to be hermaphroditic and it is also possible that an alternation occurs in the production of sex cells of *Fallax.* Sexual dimorphism is known in *Lacazella,* but the sexes of other brachiopods are only distinguishable by color of the ripe gonads: the testes tend to be white or pale yellow and the ovaries deep yellow to red-brown.

The sex cells develop from folds of the coelomic epithelium, usually located in the body cavity of the inarticulates and mantle canals of the articulates. Two pairs of gonads are commonly present in all brachiopods, but they show consistent differences in location and disposition.

Two pairs of gonads develop in the lingulids, confined to the ileoparietal band which ramifies and branches wtihin them (40). The dorsal pair appears along the free edges of that part of the ileoparietal band running along the sides of the alimentary canal, while the ventral pair occurs on the section of the ileoparietal band supporting the nephridia. In the discinids, the gonads develop on the ileoparietal band but are also present on the free ventral edge of the gastroparietal band. The distribution of the gonads in the craniids, however, is like that of the articulates because, although gonads are found on the ileoparietal band, a conspicuous pair develops in the canals of both ventral and dorsal mantles; when ripe they completely fill the mantle canal systems (12).

The gonads of articulate brachiopods, like those of *Crania,* are mainly developed from the coelomic epithelium lining the inner sides of coelomic embayments and canals within the mantles. The organs may also extend into the body cavity, especially on the ventral side where they may reach posteriorly as far as the nephrostomes. In the rhynchonellaceans the gonads are contained in the *vascula genitalia* either as two pairs of sacs representing anterolateral extensions of the body cavity (e.g., *Hemithiris*) (Fig. 23,*A*), or as sacs that give off branching canals towards the mantle edges (e.g., *Notosaria*) (Fig. 23,*B*). Accommodation within greatly distended *vascula genitalia* are also characteristic of *Terebratulina* (Fig. 23,*C*), and *Megerlina.* But in the ventral mantles of *Macandrevia, Magellania, Fallax* (Fig. 23,*D*), etc., each gonad, which tends to be long and relatively thin, is doubled back upon itself to occupy the *vascula media,* as well as the *vascula genitalia.*

Two pairs of gonads are also found in *Pumilus* but are differently disposed within its limited canal system. The ventral pair develops within the *vascula media,* while the dorsal pair, which occurs mainly in the body cavity, extends anterolaterally into the short, saclike *vascula genitalia.* In contrast, only one pair of gonads develop in *Argyrotheca* and *Lacazella,* a dorsal pair in the former and a ventral pair in the latter.

BREEDING AND DEVELOPMENT

Information on the breeding season of brachiopods is still too scanty to permit any generalizations. The breeding habits of *Lingula* are best known, but even so, the data are inadequate to cover possible variations arising from its wide geographical distribution. In Japan, Yatzu (46) concluded that *Lingula* spawns from mid-July to the end of August, with, according to more recent work, a peak in early August. *Lingula* off the south coast of Burma, however, spawns during December and February (42) while in the southern part of the Red Sea, Ashworth (2) found larvae whose stages of development indicated spawning in May and September, possibly as part of a continuous breeding season extending from early March to September. A detailed study of the breeding habits of *Lingula* from Singapore has been carried out by Chuang (16), who presents very strong evidence for a succession of spawnings throughout the year. Larvae in growth stages with two or three pairs of lophophore filaments were taken during June to November inclusive as well as January and February; while some females in collections made during the remaining months had ripe ovaries. Breeding as continuous as this is probably due to the prevalence of optimum conditions, like constant sea temperatures, throughout the year.

Among other inarticulates the following information is noteworthy. Paine (34) has recently published the results of a study on the larval and postlarval ecology of *Glottidia pyramidata,* in which he reports that in northern Florida breeding begins in the early spring at a water temperature of 20°C-22°C and lasts some nine months, whereas in southern Florida the evidence suggests that spawning occurs throughout most of the year. Larval *Pelagodiscus atlanticus* have been taken in the late summer or early autumn, suggesting a spawning during the summer months. There is also a shortage of information concerning the spawning season of *Crania.* Rowell (38) considered that *Crania anomala* off the northwest coast of Scotland spawns in April and again in November, but that there was inadequate information to decide whether there was a succession of spawnings in the summer. Joubin (23) found that the gonads in a Mediterranean species of this genus contained eggs in November but were most distended in May.

Among the articulates, it may be significant that in New Zealand, the only locality in the Southern Hemisphere for which reliable information is available, spawning takes place in the winter months. It is known to occur in *Notosaria* during May and June (36) and in *Terebratella* during April and May (35), and although it has not been observed in *Pumilus* the gonads of that genus are ripe in June and late May (3). In the Northern Hemisphere, however, the breeding season seems to vary greatly. *Terebratulina septentrionalis* from northeastern United States certainly spawns during April to August inclusive, and Morse (29) believed that this species breeds continuously throughout the year. Ripe gonads were found in *Platidia davidsoni* dredged off the coast of France during June and July (4). This condition suggests summer breeding in this species too, although ripe eggs have also been recorded in shells taken from the same area in February. The gonads of *Dallina septigera* collected from approximately the same area in November were ripe, as were those of *Gryphus vitreus* recovered from the Mediterranean in December (28). These two species, then, may possibly have a limited winter breeding season.

When ripe, the discharged sex cells leave the body cavity and the mantle canals to enter the mantle cavity through the nephridia, which in *Pumilus* are distensible and act as temporary stores (3). Only a minority of species brood the fertilized egg up to the free-swimming larval stage, either in the mantle cavity or even in specialized receptacles. The fertilized eggs of *Terebratella inconspicua* generally attach themselves, before final release, to the inner surfaces of the mantles (35). But in *Notosaria nigricans* (36) and *Liothyrella antarctica* (13) some of the lophophore filaments interweave to form a temporary brood basket. In *Lacazella* the fertilized eggs attach themselves to swollen portions near the ends of a pair of lophophore filaments that have been inserted into a median brood pouch occupying a depression in the pedicle valves of females (27). Probably the most unusual specialization is found in *Argyrotheca* in which the nephridia become enlarged to act as brood pouches (41).

SPAWNING

Spawning has been observed only in *Lingula anatina* (46, 16), *Terebratulina septentrionalis* (29), and *Glottidia pyramidata* (34). In these species the eggs are ejected into the sea from the mantle cavity, through the median exhalant current and fertilization is external. If considerable numbers of eggs are released quickly, they are enveloped in mucus and form large clumps or sheets. Spawning is well known in *Lingula anatina* from Singapore (16), where the young females become capable of producing ova when they are a year to a year and a half old. They remain sexually mature throughout a considerable size range, for spawning has been observed in specimens with pedicle valve lengths varying between 14.3 and 46 mm. Any one individual does not release all of its ova during the initial burst of spawning, for the process extends over several months as subsidiary phases, separated by rest intervals. The number of ova shed is great; the maximum recorded for one female is 28,600 in 104 days, although the average for large adults is about two-thirds of this value. Individual females of *Glottidia pyramidata* likewise do not release all their eggs during the initial burst of spawning, for Paine (34) considers that reproductive activity extends over a 3- or 4-month period. The number of ova released during a single burst of spawning varies greatly, but may be enormous, a maximum of 47,000 being recorded from one female. Seemingly the early and late phases of spawning are smaller, but Paine (34) estimates that one female will shed in the order of 150,000 ova during her total spawning period. In contrast with *Lingula,* females commence spawning when 6 to 9 months old, but this early onset of sexual maturity is undoubtedly related to their much shorter life span.

Sexual maturity is not attained in *Terebratella* until individuals are more than one year old, and Percival (36) noted that both sexes of *Notosaria* were capable of reproduction when they were between 9 and 20 mm. long and produced between 4,000 and 8,000 eggs in a season. Indeed, judging from various accounts, it seems likely that most brachiopods become sexually mature when they attain about one-third to one-half the size of an average adult.

DEVELOPMENT

The full development of the brachiopod from the fertilized egg is reliably known for *Lingula* (46), *Terebratella* (35), and *Notosaria* (36). Supplementary information is also available for the prelarval stages of *Terebratulina* (19), *Argyrotheca* (25,26, 37), and *Lacazella* (27, 25,26), and for the larval or early postlarval stages of *Glottidia, Discinisca, Pelagodiscus* (31,32), and *Crania* (38). The scarcity of detailed records and the controversial nature of some that are available make it impossible to generalize on brachiopod ontogeny with certainty. Nonetheless, the fundamental differences between inarticulate and articulate brachiopods are nowhere better shown than in the contrasted development of representative species. Apart from the significantly greater duration of the free-swimming stage of the inarticulates, there are other, more important differences. Internally, the coelomic spaces of the inarticulates are said to be schizocoelic in that they arise by a hollowing-out of the mesoderm, whereas those of the articulates are enterocoelic, developing as pouches from the enteron. The articulate embryo is soon differentiated into an anterior lobe and rudiments of the pedicle and mantle, the latter subsequently undergoing reversal. In contrast, the inarticulate embryo consists simply of an apical brachial ridge and the mantle rudiment, which does not undergo reversal during growth; the pedicle arises much later as an evagination of the ventral mantle.

The development of *Lingula anatina* has been described in detail by YATSU (46), who reared early larvae to the stage where they possessed three pairs of lophophore filaments, and obtained later stages in plankton collections from Misaki Harbor. Some variation appears between YATSU's Japanese material and other scattered records of larval *Lingula* as to the age, expressed in terms of the number of pairs of lophophore filaments, at which various structures and organs appear. The sequential pattern of development, however, is the same. YATSU found that after fertilization of the eggs a hollow blastula is formed by regular cleavage which at the 30- to 40-cell stage develops into a gastrula by invagination. The gastrula is subsequently flattened in an anterior-posterior direction and the external opening of the archenteron, the blastopore, is closed. A ringlike flap arises by outward growth of the ectoderm, which becomes partially divided into two by diametrically opposed depressions. This flap marks the first stage in development of the mantle. In front of the flap and partially covered by it is the brachial ridge from which the lophophore subsequently develops (Fig. 35,*A*). An invagination of the ventral median part of the brachial ridge gives rise to the stomodaeum, which soon communicates with the archenteron to form the larval alimentary canal. This phase coincides with the appearance of the first pair of rudimentary filaments on the brachial ridge, the subsequent growth of which has already been outlined in the section dealing with the lophophore. Shortly afterward the ringlike flap becomes completely divided into two mantles, which grow rapidly to assume a semicircular form and almost enclose the brachial ridge. The mantles now secrete a thin chitinous shell in one piece, folded across the posterior margin. Internally, the mesoderm, which has been proliferated by the endoderm, lies laterally to the alimentary canal. At this stage too, the young animal escapes by rupturing the egg membrane and becomes free-swimming, using the lophophore for propulsion (Fig. 35,*B*).

Subsequent development is most conveniently described in stages defined by the regular appearance of new lophophore filaments. Thus, by the time two pairs of filaments are present, the coelomic cavities have been hollowed out of the mesoderm and are developing as schizocoeles. The anterior part of the mesoderm becomes mesenchymatous and migrates into the recently formed rudimentary lophophore canal system, which communicates with the body cavity.

At the stage defined by three pairs of

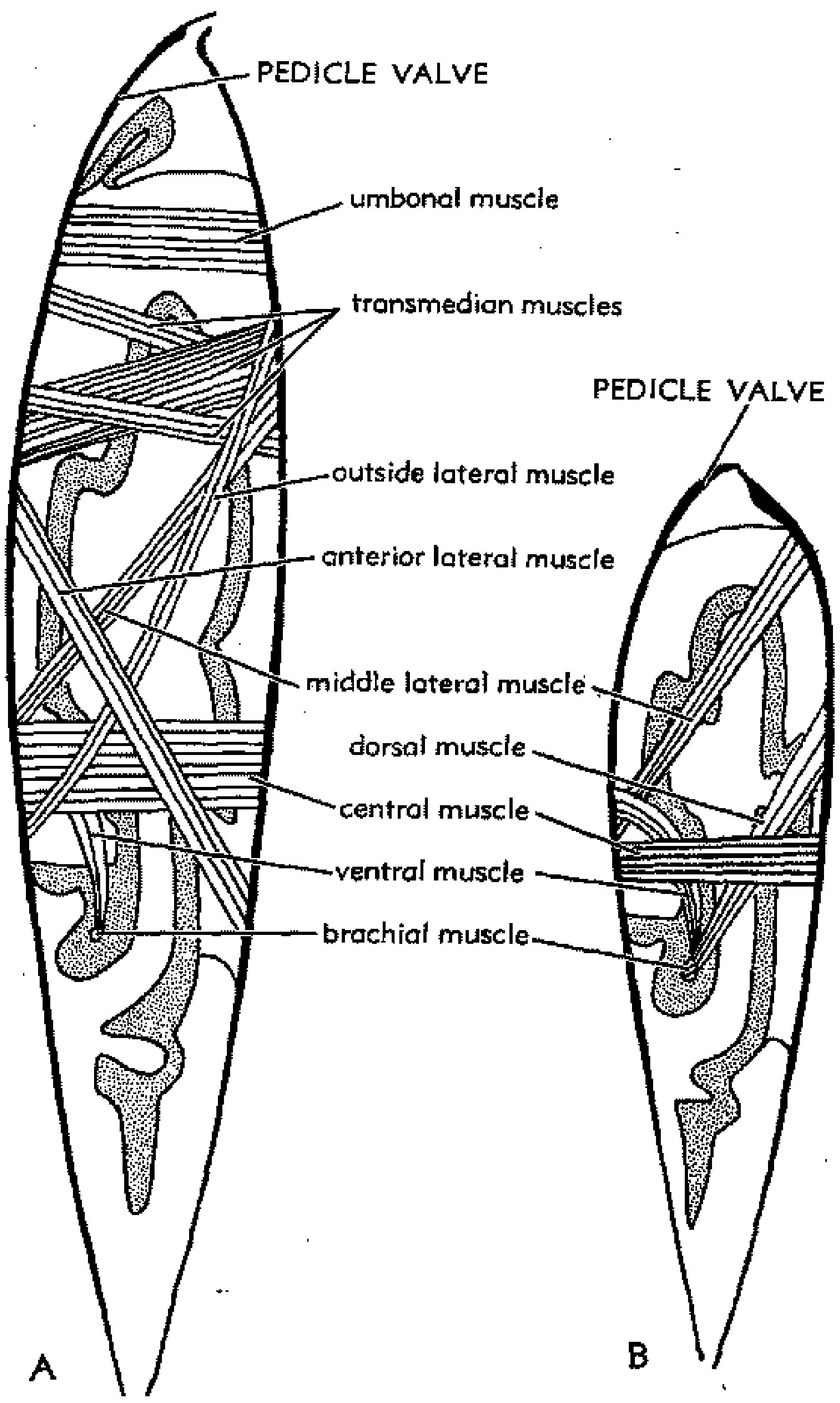

FIG. 49. Diagrammatic sections through *Lingula* larva showing muscle development *(A)* with eight pairs of filaments, *(B)* with five pairs of filaments (46).

filaments, the first pair of muscles appear, but they are characteristic only of the free-swimming stage, since they degenerate after the animal becomes attached. These ventral muscles arise from the ventral mantle and pass forward from the posterior end of the esophagus to the brachial canal at about the level of the mouth (Fig. 49,*B*). At this stage too, the filamentar muscles and the filamentar canals are present, the latter being diverticula of the lophophore canal system.

With the appearance of the fourth pair of filaments, the alimentary canal begins to differentiate into its adult components. The posterior dorsal digestive diverticula and intestine first appear together with the small ciliated mid-gut and by the time the ninth pair of filaments have arisen, the animal has a functional anus and rudiments of all the digestive diverticula.

The nephridia first appear as a pair of cell strands at the five-pair-filament stage. At the same time, the first adult muscles, the centrals and middle laterals, are formed along with another pair of larval muscles, which are located dorsally and degenerate before two more pairs of filaments are added. The remainder of the adult muscles develop before the ninth pair of filaments are added to the lophophore (Fig. 49,*A*), by which time the nephridia are already conspicuous (Fig. 50). Meanwhile, the mantle canals have developed as prolongations of the body cavity into the mantle when the lophophore possessed eight pairs of filaments.

The pedicle was first seen by YATSU at the six-pair-filament stage. It arises from the posterior end of the ventral mantle as a hollow hemispherical projection of the inner epithelium communicating through a narrow lumen with the body cavity. By the nine-pair-filament stage it has increased in length and is twisted but still totally enclosed by both valves. The pedicle of specimens examined by ASHWORTH (2) originated in the same way, but the organ did not appear until 11 pairs of filaments had developed.

In captivity, YATSU's specimens attached themselves to the substratum at the ten-pair-filament stage, when they were about 650μ long. Attachment does not always occur quite as early as this, for ASHWORTH observed free-swimming larvae with 15 pairs of filaments. This discrepancy may

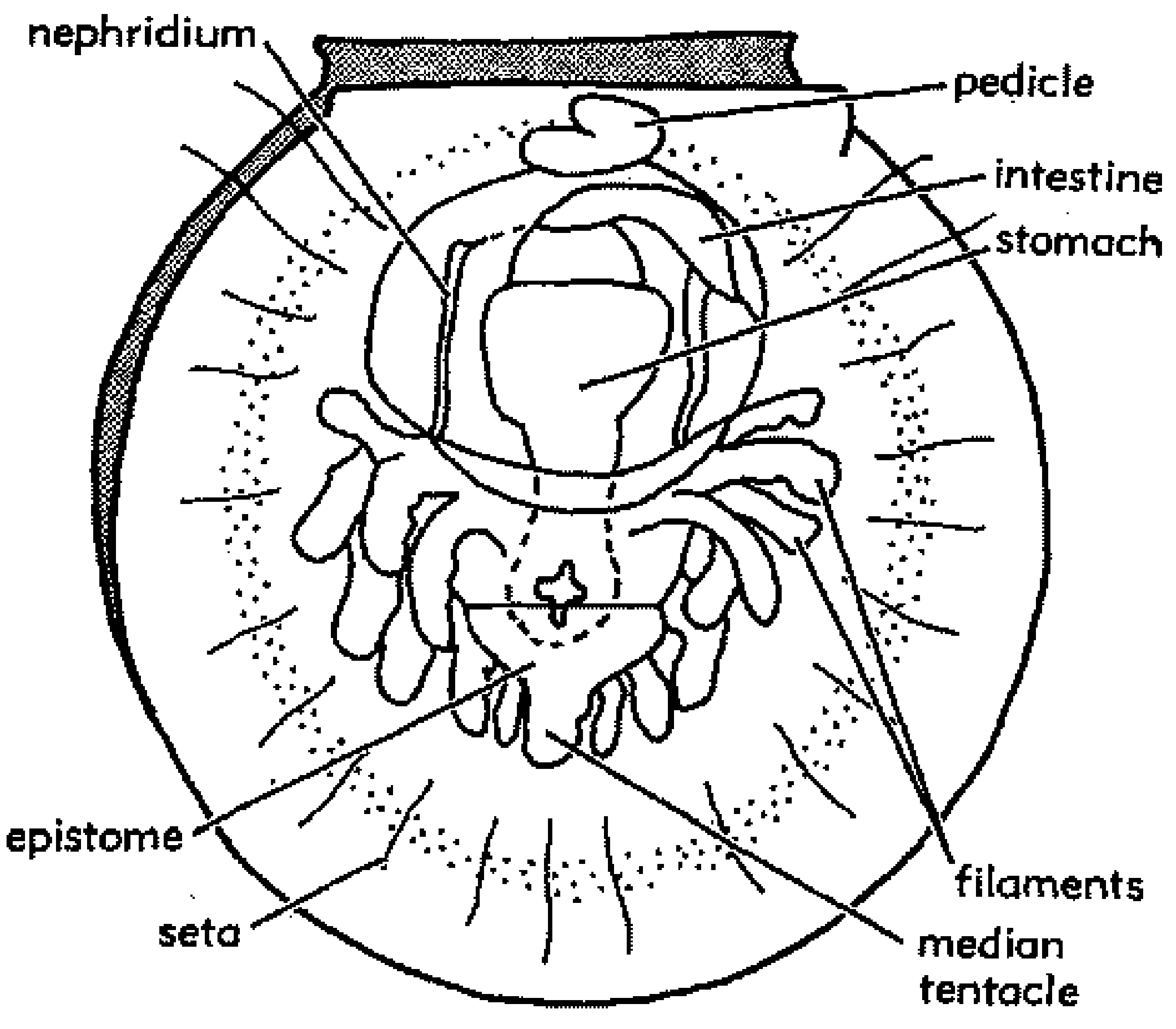

FIG. 50. Larval *Lingula* with eight pairs of filaments, viewed ventrally (musculature omitted) (46).

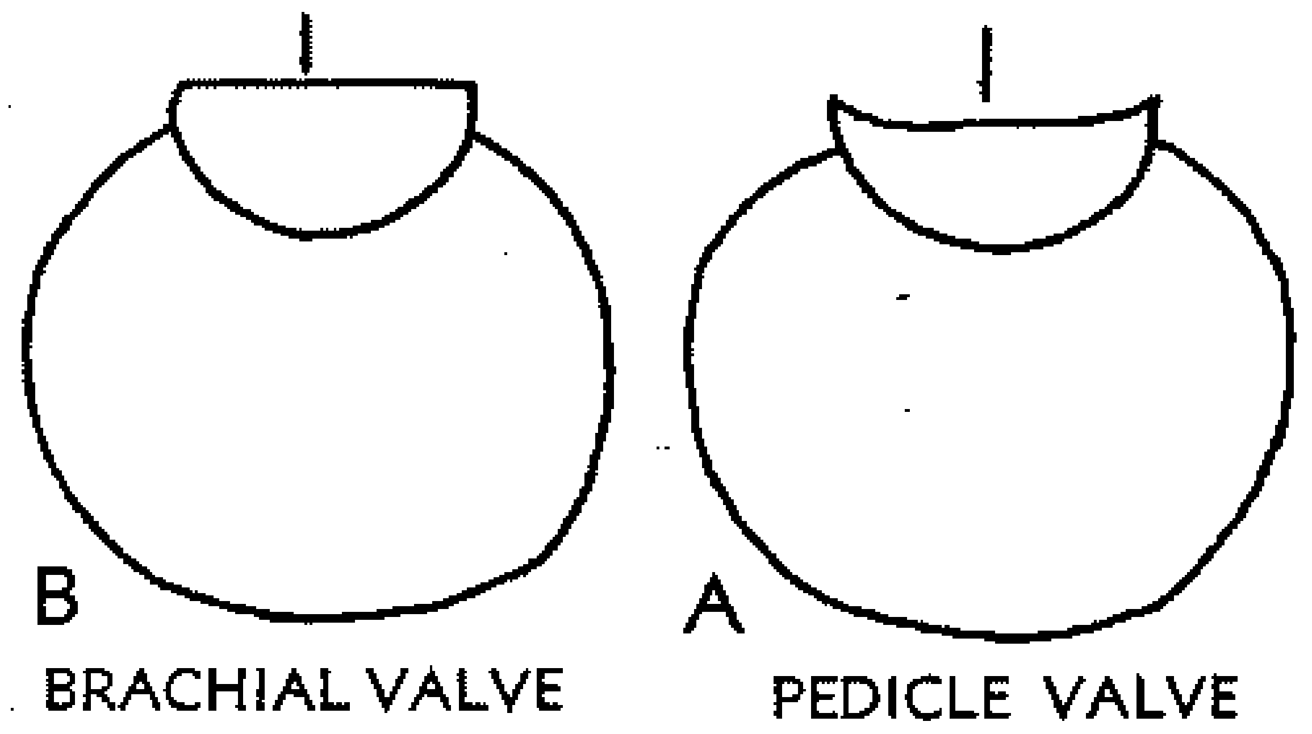

FIG. 51. Outline of shell of *Lingula* 0.5 mm. long (47).

be due to either specific differences or artificial conditions under which the Japanese larvae were reared—for example, differences in depth of water, for PAINE (34) considers that deeper water and lack of bottom contact tend to retard the age at which settling occurs. Immediately prior to attachment the pedicle is protruded and secretes a gelatinous substance which is viscous at first, but subsequently hardens.

On adopting the sedentary mode of life, the lophophore ceases to be a locomotory organ and by means of its cilia induces circulation of water in the mantle cavity. With this change in function, the more persistent, ventral pair of larval muscles degenerate. Considerable changes affect the lophophore itself, involving not only its transformation into a schizolophe but also the development of a partition which divides the brachial canal into two, the future great and small brachial canals.

Increase in the size of the mantle and shell is continuous throughout these early developmental stages. As has been noted, the shell first appears as a very thin cuticle over the entire external surface of the mantle when the animal has a single pair of filaments. At this stage, the shell is a circular lamella folded double along one of its diameters (the "hinge line").

When three pairs of filaments are present, the two valves, still joined together, attain the protegulum stage of BEECHER. Each valve is almost a semicircle; the "hinge line" is about 280μ wide and does not increase with subsequent growth of the shell. The ends of the "hinge line" project laterally as a pair of small ears (termed "teeth" by YATSU).

Further growth of the shell is now confined to the anterior and lateral margins so that the valves become almost circular in outline by the time the seventh pair of filaments appear on the lophophore (Fig. 51). Later growth is so much more rapid along the anterior margin that the shell quickly elongates and an elliptical outline is attained about the 15-pair-filament stage. The thin cuticle, which initially joins the valves, is ruptured along the "hinge line" before the appearance of the eighth pair of filaments. The break develops nearer the brachial valve, so that the pedicle valve ends posteriorly in a thin lamella, a remnant of the fold, which is bent dorsally to overlap the thickened margin of the other valve (Fig. 49,*A*). Concomitantly the shell, which at first is colorless and transparent, acquires a brownish tint along the margins. At the posterior end the superficial layers are bright green.

Setae first appear along the margin of the mantle during growth of the seventh pair of filaments. At first they are very short and by the time the next pair of filaments are added project beyond the edge of the shell only at the posterolateral corners. Subsequent to attachment of the animal, growth of the setae is very rapid and unequal, those along the anterior and anterolateral borders becoming relatively long (some 300μ) and assisting in producing currents of water within the mantle.

The rate of growth up to this stage of development when the animal has become attached to the substratum and has acquired all adult organs, is relatively fast when compared with articulate genera. PAINE (34) considers that the larval life of *Glottidia pyramidata*, living in shallow water, is about 20 days, but that settlement may be retarded for individuals which have drifted seaward over deeper water. YATSU found that *Lingula* has 15 pairs of filaments when it is about 800μ long and 630μ wide, some six weeks after the eggs have been fertilized. Subsequent growth is mainly concerned with increases in size and shell thickness and further elaboration of existing organs.

More than 30 discinid larvae have been described, the majority belonging to the cosmopolitan species *Pelagodiscus atlanticus*. All the larvae of this species have been found in approximately the same stage of development, with four pairs of lophophore

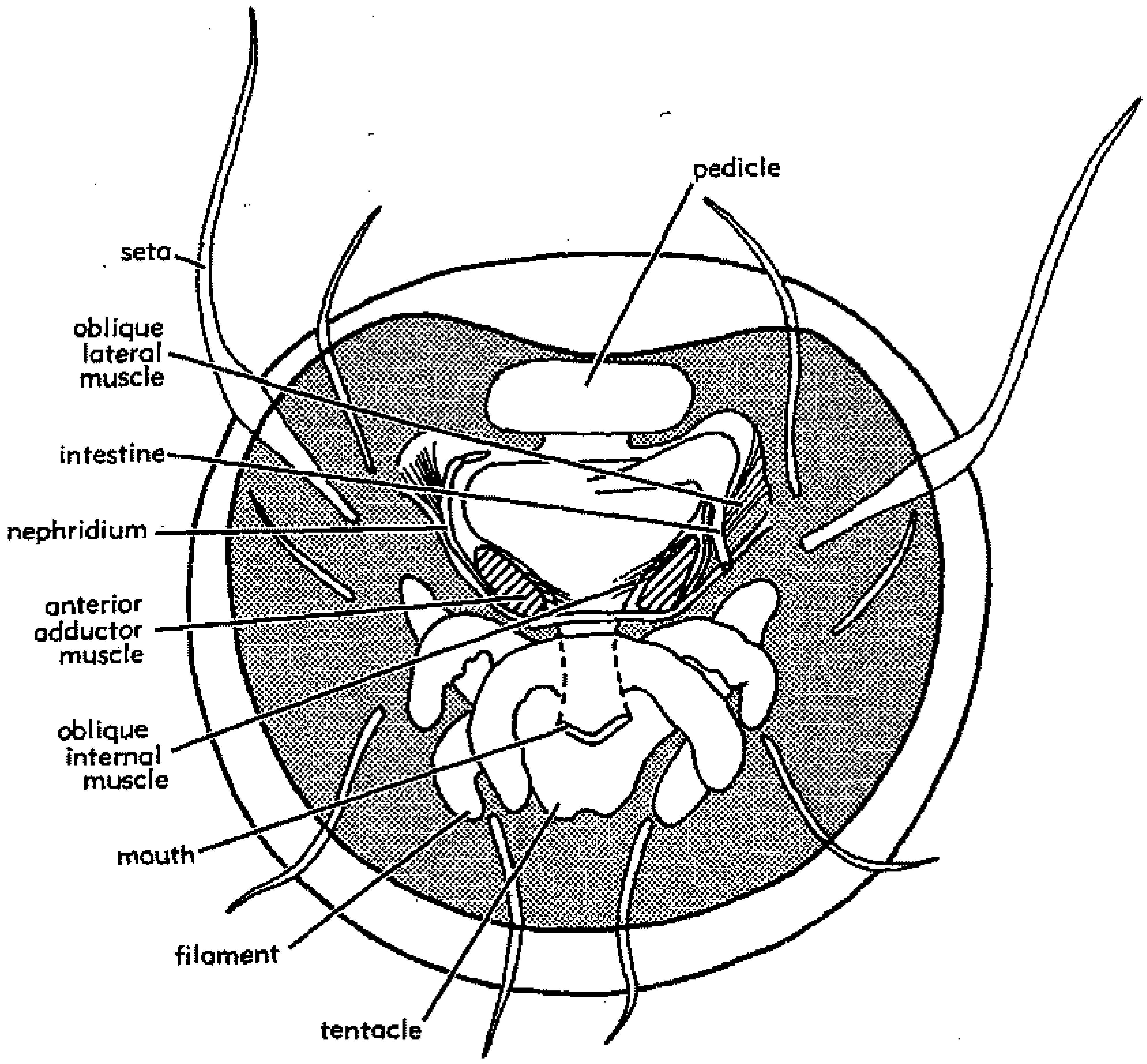

FIG. 52. Larval *Pelagodiscus* with four pairs of filaments, viewed ventrally (minor setae in dorsal valve omitted) (2).

filaments. They were all taken in shallow water (less than 200 m. deep), well above the known upper limit of the bathymetric range of adult *Pelagodiscus* and it is probable that earlier stages remain in the deeper water. Little information about settling is available but MÜLLER observed that larvae studied by him remained free-swimming for a maximum of five or six days. Presumably they became attached while still at the four-pair-filament stage.

The two thin valves of the larvae are roughly circular in outline, with a width of 400μ to 500μ, and are held together only by the body wall and muscles. Characteristically there are five pairs of principal setae (Fig. 52). The anterior four pairs are attached to the pedicle valve, those placed farthest back being much larger and broader than the others. The fifth pair of principal setae occur posteromedianly in the dorsal mantle where they are associated with about 30 pairs of minor setae developed along the lateral and anterior margins. The lophophore, which at this stage contains coelomic spaces and associated musculature, is basically similar to that of *Lingula*, but the filaments are relatively thicker and the median tentacle is only a broad projection of the anterior margin. Within the body cavity, the alimentary canal is functional and the intestine opens on the right side of the body wall through an anus. The digestive diverticula are not developed, but the wall of the gut is already differentiated. Nephridia and statocysts are present and the musculature is well advanced, although the posterior adductor muscles are not yet formed. A pedicle rudiment occurs, confined within the valves, and as in *Lingula,* it is a projection from the inner surface of the ventral mantle (Fig. 53). A pair of larval sense organs, the so-called "eye spots," are developed on the lateral body walls.

On settling, the pedicle is protruded from the valves through the notch at the posterior margin of the pedicle valve. The eye spots are lost, larval setae replaced by adult ones, and the median tentacle reduced in size shortly after settling. Detailed information on the later growth of the animal is still unavailable.

Very little is known of the larval stages of other discinids and a few that have been taken as plankton cannot be specifically recognized with certainty. YATSU has ob-

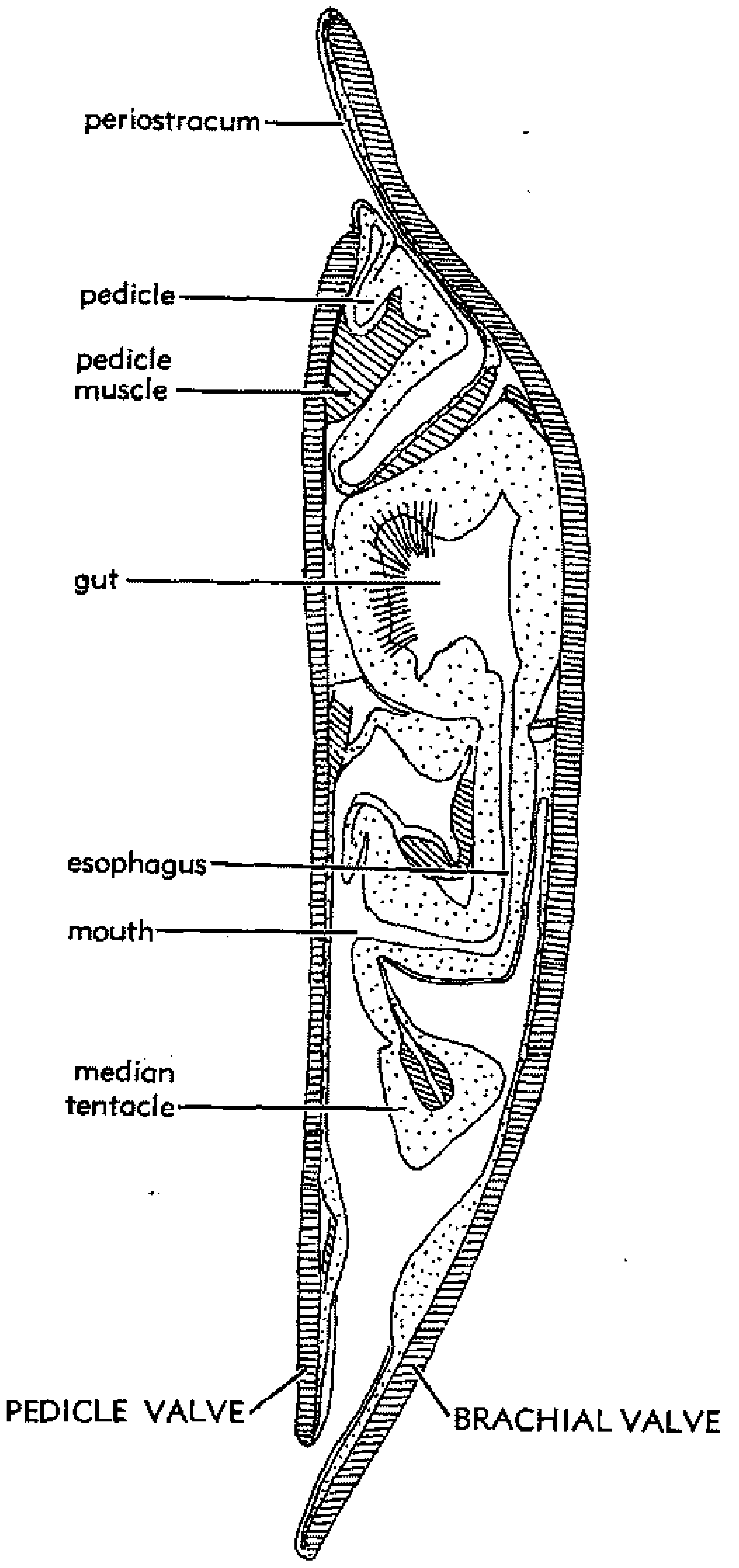

FIG. 53. Diagrammatic median longitudinal section of larval *Pelagodiscus* with four pairs of filaments (not shown because located laterally from mid-line) (2).

served young *Discinisca laevis* which were already attached at the six-pair-filament stage. Morphologically they are similar to *Pelagodiscus* that had recently settled.

Free-swimming stages of *Crania* are still completely unknown, but some of the early postlarval stages have been described for *Crania anomala* (38). The animal settles relatively early in its development, compared with other inarticulates, for it becomes attached during the stage of three pairs of lophophore filaments, when it is about 200 to 300μ long (Fig. 54,*A*). At this size the dorsal mantle has already secreted a thin conical calcareous shell covered by periostracum, but the ventral mantle is invested only in a periostracal layer, which apparently cements the animal to the substratum (Fig. 54,*B*).

No trace of a pedicle is known in attached *Crania* at any stage of development, although possibility exists that a pedicle is present in free-swimming forms. At the youngest stage known, the animal shows an early development of many adult features. With exception of the lophophore protractor and anal muscles, the adult muscle system is already present. The alimentary canal is developed, but ends blindly and lacks digestive diverticula, which first appear at about the ten-pair-filament stage as pouchlike outgrowths of the anterodorsal stomach wall. The anus originates rather earlier, when the animal has five pairs of filaments. The nephridia first occur at the nine-pair-filament stage as two rows of cells embedded in the connective tissue of the lateral body walls. They do not develop a lumen or become functional until the animal has acquired about 16 pairs of filaments. In the earlier stages of development, the lophophore possesses a median tentacle and is rather like that of *Lingula*, but loss of the median tentacle when the lophophore has four or five pairs of filaments and the onset of the schizolophous condition during pro-

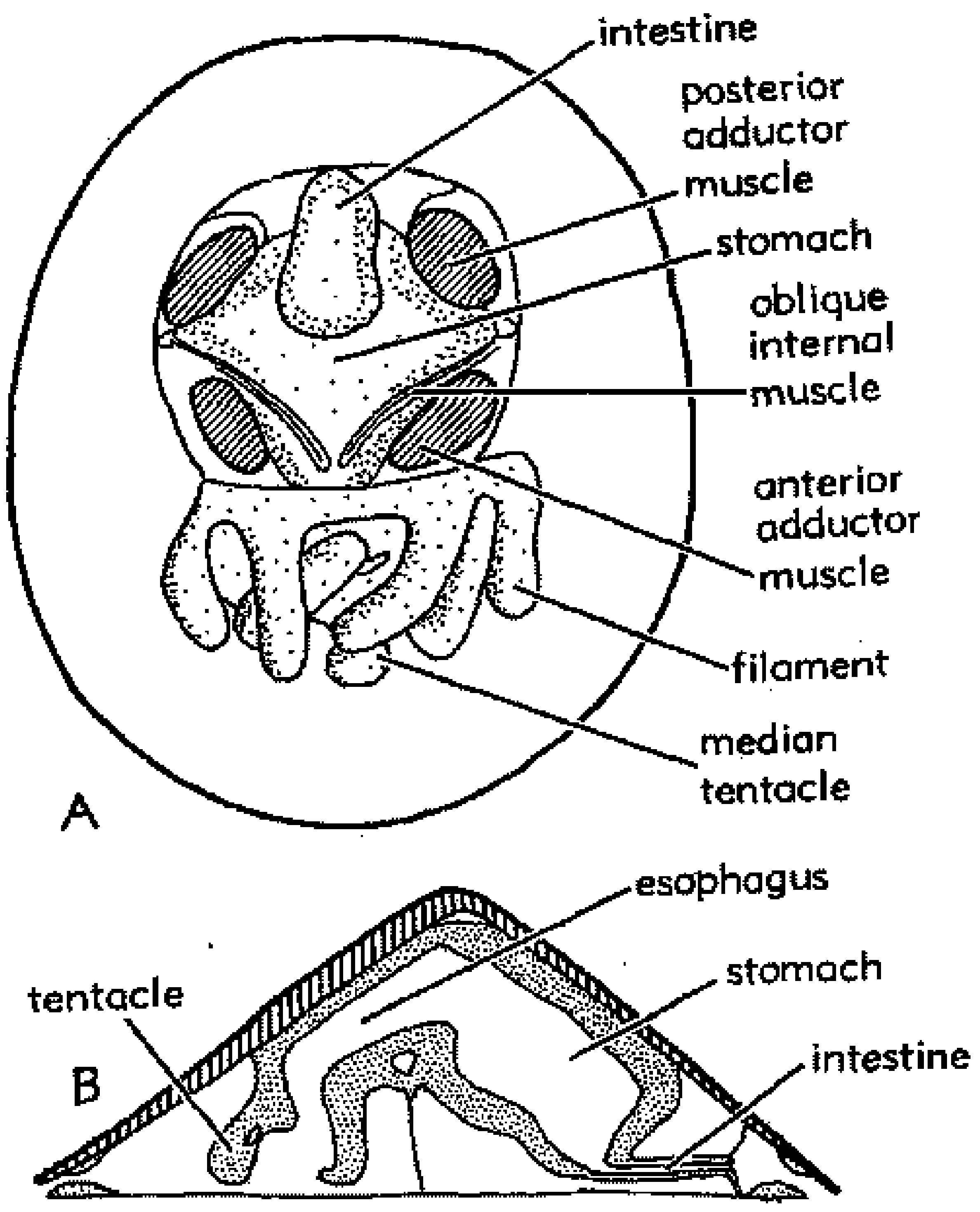

FIG. 54. Young *Crania*, recently attached, with three pairs of filaments, *(A)* viewed ventrally and *(B)* in diagrammatic median section (38).

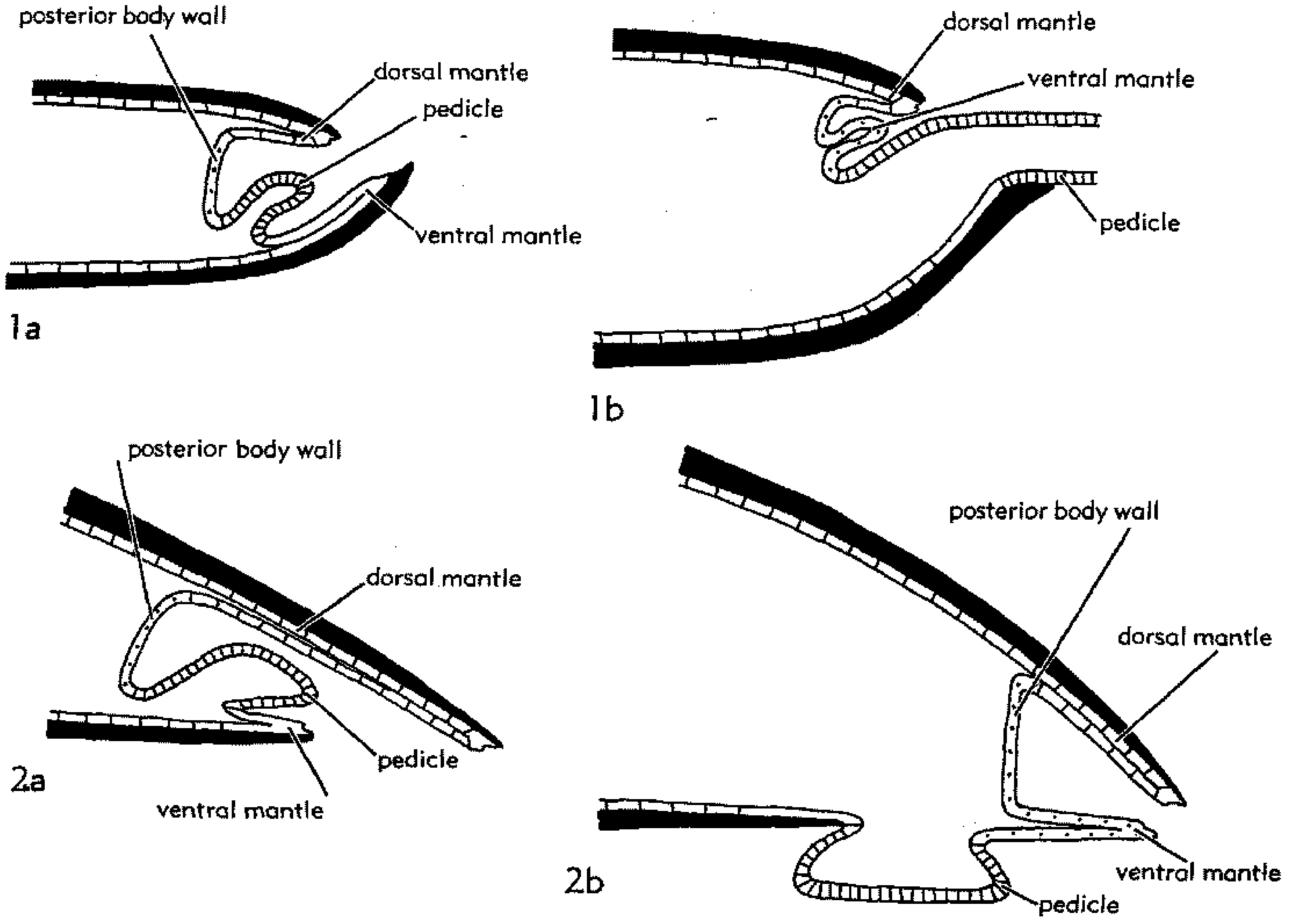

FIG. 55. Diagrammatic longitudinal median section through *(1a)* young lingulid prior to settling, *(1b)* adult lingulid, *(2a)* young discinid prior to settling, *(2b)* adult discinid (47).

liferation of the seventh pair of filaments occurs earlier in *Crania* than in *Lingula*.

Comparison of the morphology of the posterior region of adult lingulids and discinids with that of young forms which have not settled, but which have developed a pedicle enclosed between the valves, reveals considerable differences in the distribution of epithelium. These are important in a consideration of later shell growth.

In both families the pedicle is initiated as an evagination of the inner surface of the ventral mantle immediately behind the posterior body wall, the juvenile mantle continuing on the posterior side of the pedicle to the margin of the valve. At some later developmental stage prior to settling, probably closely associated with the protrusion of the pedicle, this organ comes to assume a position entirely posterior to the tissue which formed the posterior sector of the juvenile ventral mantle. The change in relative position must also be associated with transformation of the juvenile ventral mantle lobe, for in adults the tissue immediately in front of the pedicle comprises a single layer of outer epithelium lining the body cavity. However, since the ventral mantle is intact in discinids and lingulids after settling, it follows that subsequent to, or possibly contemporaneously with, the loss of the posterior sector of the juvenile mantle, a flap of epithelium is developed which is continuous anterolaterally with the remainder of the ventral mantle. This sector of the adult mantle can only have developed from, or have been proliferated by, the tissues which initially formed the posterior body wall of the young animal prior to settling. It is separated by the pedicle from the tissue which was involved in the corresponding sector of the juvenile mantle (Fig. 55). The secretory behavior of this posterior sector of the adult ventral mantle and the extent to which it is integrated with the remainder of the mantle are of fundamental importance in determining the form of the adult shell, and as such they are better discussed in the section dealing with morphology of the shell.

The most comprehensive account of development among articulate brachiopods is that given by PERCIVAL (36) for *Notosaria nigricans*. A spherical blastula is developed

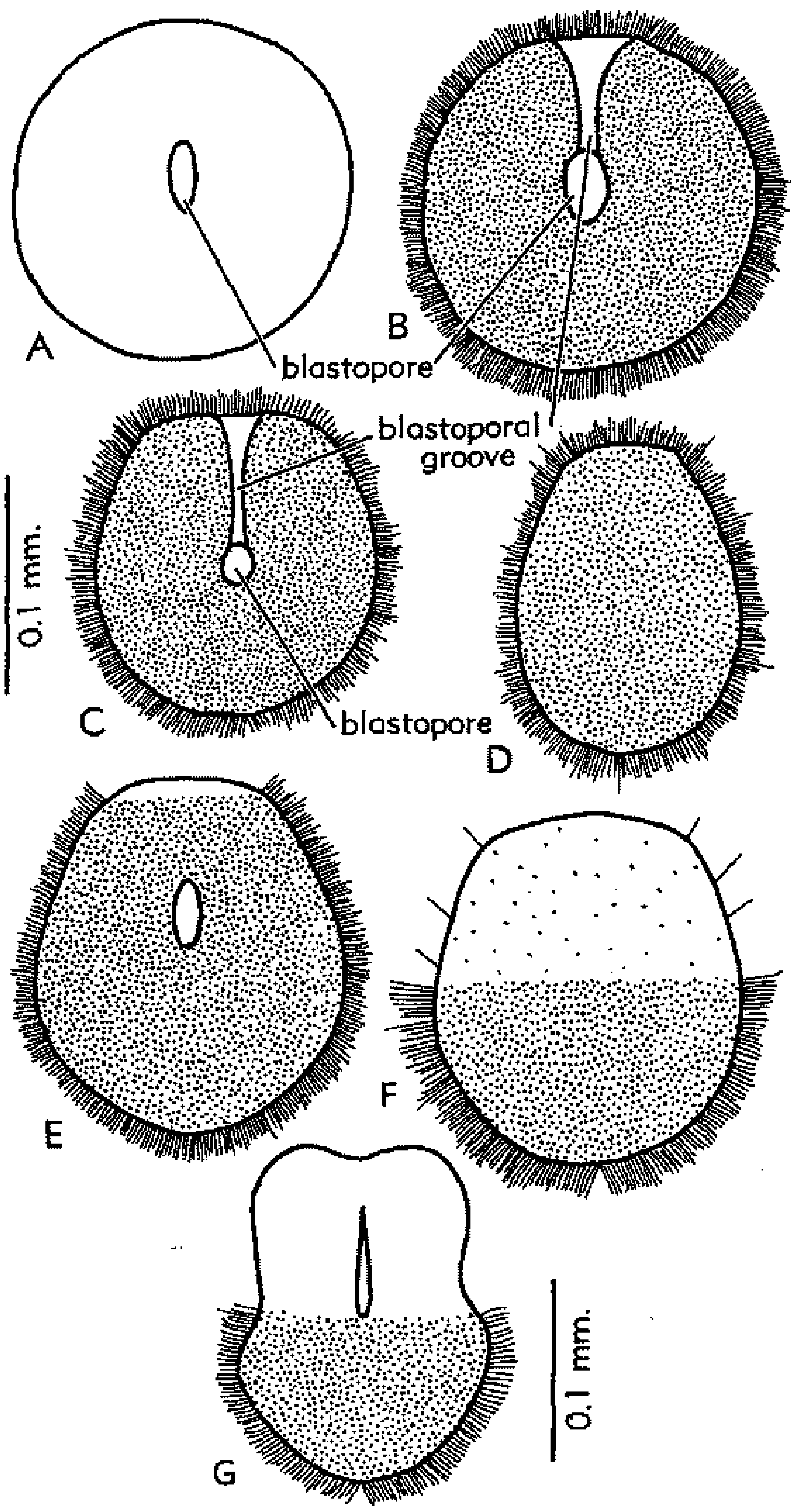

FIG. 56. *A-G*. Stages in the development of the gastrula of *Notosaria nigricans* (SOWERBY), showing closing of the blastopore, deepening of the blastoporal groove, loss of cilia posteriorly, and beginnings of body differentiation (*D* is side view of *C*) (36).

at the eight-cell stage and normally consists of subequal blastomeres which arise by a slightly oblique or, more rarely, a radial cleavage of the fertilized egg. Gastrulation is effected by invagination of the coeloblastula and the blastopore soon becomes oval within a wide depression, which is continued in the future posterior direction as a groove (Fig. 56, *A-D*). Quite early in the development of the gastrula its entire surface is ciliated, but as it assumes the shape of a blunt wedge, the cilia disappear from its flattened posterior end (Fig. 56,*E,F*). The rounded, ciliated anterior part may now be identified as the anterior lobe. The blastopore, which has meanwhile been reduced to a small pit, is located in the base of the anterior lobe and the blastoporal groove still remains as a trace in the mid-line of the slightly narrower and bilobed posterior part (Fig. 56,*G*). But with the differentiation of the mantle rudiment, the blastopore closes and the groove disappears.

The mantle rudiment first appears as a transverse ridge on the dorsal side of the posterior part of the embryo, separated from the anterior lobe by a well-developed constriction (Fig. 57,*A*). The ridge is enlarged posteroventrally, ultimately to form a continuous mantle rudiment which is quite distinct from a posterior unciliated lobe (the pedicle rudiment) and bears two pairs of long setal tufts located dorsally and dorsolaterally. The anterior lobe is now separated from the rest of the body by the encircling constriction and is further characterized by the appearance of an apical tuft of long cilia and about 48 marginal "eye spots." The cilia disappear before settling, but the eye spots persist for some time after metamorphosis. The pedicle rudiment tends to be partially enclosed by a sheath of mantle rudiment, which at this stage grows posteriorly and becomes lobed along its posterior margin about each tuft of setae (Fig. 57,*B-D*). Cilia also appear on the ventral surface of the mantle rudiment and aid the embryo in its movement over the substratum, although the cilia of the anterior lobe are responsible for its gyratory propulsion through the water prior to settling (Fig. 57,*E,F*).

Concurrently with these external changes, profound internal modifications occur (Fig. 58). The formation of the blastoporal groove results in the depression of its floor as a partition in contact with the ectoderm on the opposite surface of the gastrula. In this way the archenteron is divided into an anterior sac, "the enteron," penetrated by the blastopore, and a pair of posterolateral diverticula. The enteron lengthens with the long axis of the body and its endoderm remains temporarily in contact with the blastopore, now reduced to a pit. The diverticula grow forward on each side between the enteron and ectoderm as a pair of mesodermal bodies and then divide into posterior and anterior parts to occupy respectively the future pedicle and the remaining body regions. As the mantle grows, its mesoderm is not easily distinguishable from the ectoderm, in contrast to the clarity of the two hollow mesodermal masses within the pedicle rudiment. At this stage of development, muscle fibers appear within these posterior mesodermal bodies which later become the adjustors and possibly also the diductors.

The larva of *Notosaria* remains free-swimming from two to seven days before it settles, attaching itself to the substratum by a secretion from the tip of the pedicle lobe. The mantle then shortens and thickens by rolling upward so that the setal tufts become directed first horizontally, then anteriorly (Fig. 36,*A*). Meanwhile, the apical lobe becomes contracted longitudinally to form a low central mound surrounded by a ring-like margin containing the "eye spots." The mound continues to subside and is eventually separated from the peripheral ring by a pair of growing crescentic slits (Fig. 36,*B*). With the union of these slits and the sinking of the central mound, the processes leading to the definition of the lophophore are initiated (Fig. 36,*C-H*); they are outlined in the description of the lophophore. The mantle rudiment, while still disposed as a short cone, secretes a protegulum as a pair of discrete, thin valves. A dorsoventral flattening then occurs accompanying the differentiation of a smaller brachial valve with the former dorsolateral tufts of setae, now located anteriorly, and a larger pedicle valve bearing the remaining pair of tufts posterolaterally. At first the valves lie well within the mantle edges but later growth reverses the relationship. This dorsal-ventral flattening also affects the apical lobe (now modified into a rudimentary ring, six filaments, and a brachial lip surrounding a stomodaeum) which spreads onto the inner surface of the brachial valve (Fig. 37,*A*,*B*).

The longitudinal contraction that follows the settling of the larva is accompanied by a dorsoventral reorientation of the long axis of the enteric mass, the rudiment of the alimentary canal (gut) (Fig. 58,*E-F*). In this position, it develops a lumen and makes contact with the stomodaeum along the ventral crescentic slit. However, before an open connection is established between the stomodaeum and the gut rudiment, two pairs of muscles are present in addition to the adjustor. They lie anterolaterally and posteriorly to the mid-gut and are the adductors and diductors respectively. The muscles are at first unlined within the cavities that have reappeared in the mesoderm. But subsequent to opening of the stomodaeum into the mid-gut rudiment, an epithelial lining appears in the cavities between the gut and muscles. With the enlargement of these cavities toward each other, the dorsoventral mesenteries, which support the alimentary

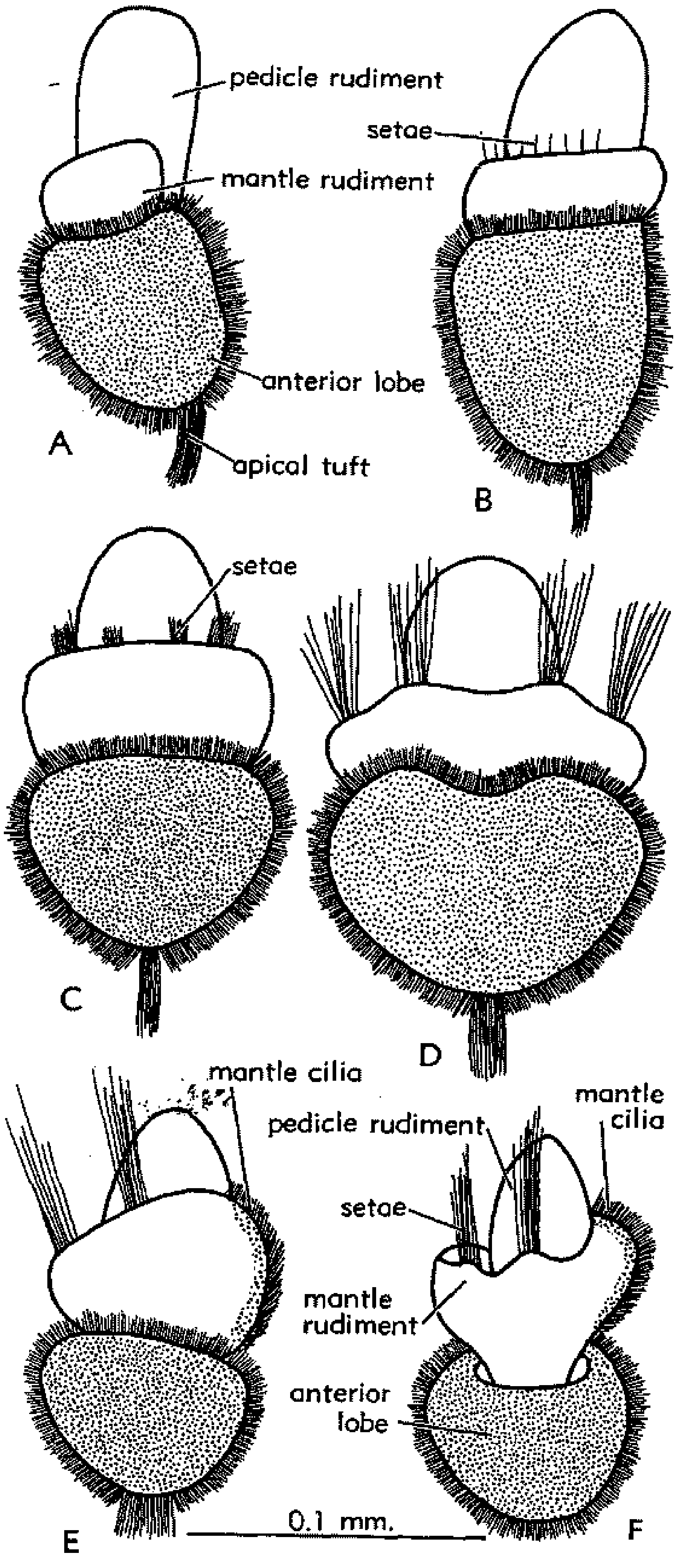

FIG. 57. *A-F*. Stages in differentiation of the anterior lobe, mantle, and pedicle rudiments of the larva of *Notosaria nigricans* (SOWERBY) (36).

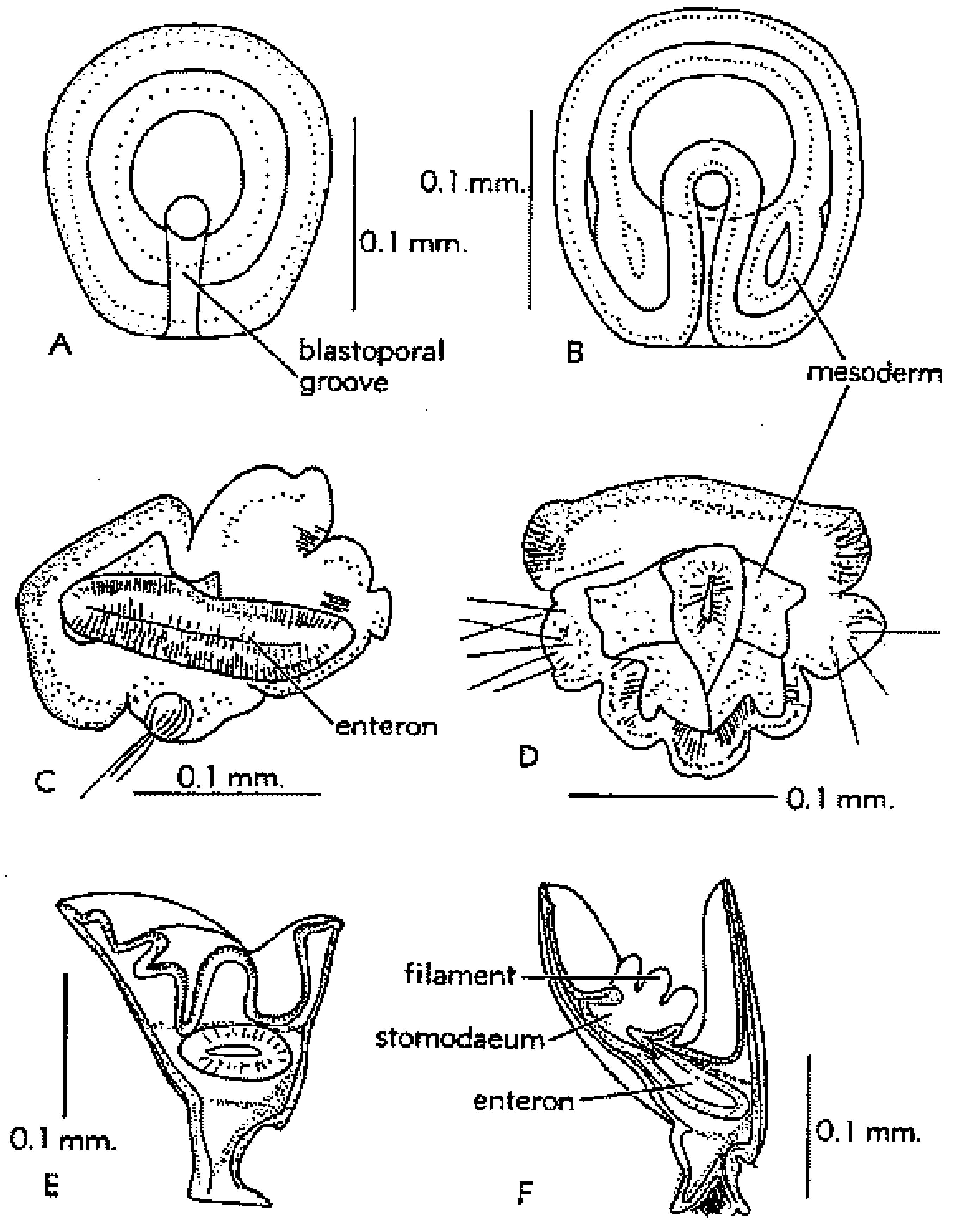

FIG. 58. *A-F*. Stages in internal development of *Notosaria nigricans* (SOWERBY), *A,B,* showing origin of mesodermal masses in late gastrula; *C, D,* longitudinal and horizontal sections of late embryo and larva showing enteron and two pairs of mesodermal masses; *E, F,* longitudinal sections of young adult before and after breakthrough of stomodaeum (36).

canal, are formed; and about the time that ten pairs of filaments are present on the lophophore, rudimentary digestive diverticula also project into the body cavity. A pair of ciliated ducts representing the anterior nephridia of adults first appear at the six-pair-filament stage; the posterior pair develop later.

Traces of filamentar canals are seen when three pairs of filaments are first differentiated, and by the time another pair have been added, circulatory canals continuous with the periesophageal canals are developed.

When allowance is made for a misidentification of the juvenile valves, which was later corrected, the development of *Terebratella* is similar to that of *Notosaria*. PERCIVAL (36) remarked on differences in development of the lophophore, notably those involving growth of the brachial lip and the first three pairs of filaments. But, as has been pointed out elsewhere, the differences may prove to be unimportant; the pattern of growth is more likely to be that seen in *Notosaria*. Other differences are mainly matters of timing. The free-swimming life of the *Terebratella* larva is variable but, with average duration of about 30 hours, is distinctly shorter than that of *Notosaria*. Indeed, it may be said that the entire development of *Terebratella* is accelerated, so that not only do the mesodermal cavities appear by the four-pair-filament stage but also the first outgrowths of the digestive diverticula.

In general, less satisfactory accounts describing the larval growth of other articulates confirm the pattern of development outlined above, although some noteworthy discrepancies may be due to faulty observation. CONKLIN (19) investigated the free-swimming stages of *Terebratulina septentrionalis* and reported that tufts of long setae are not developed along the edge of the mantle rudiment and that the diverticulum, which later forms the mesoderm, is partitioned off from the anterior (*not* posterior) end of the archenteron. This diverticulum is later constricted by the growth of the enteron into two lobes, which elongate but do not divide, as in *Notosaria*. The anomalous location of the entercoelic sac when it first arises has been commented on by PERCIVAL (35), who pointed out that CONKLIN used preserved material and might have been mistaken in his orientation of specimens at this stage of development. In *Argyrotheca*, according to KOVALEVSKIY (25, 26), SHIPLEY (43), and PLENK (37), the diverticula arise as a pair of lateral pouches pinched off from the sides of the archenteron. They then spread along the sides of the enteron and meet ventral to it. Both KOVALEVSKIY and SHIPLEY also record that the first three pairs of filaments arise in the same way as those of *Terebratella*, by spreading around the oral disc from either side of the first-formed posterior pair.

The embryology of *Lacazella* is the most difficult of all to understand, mainly because it has only been sketchily outlined in a rarely seen paper by KOVALEVSKIY (25). According to this account, gastrulation is effected by delamination (*not* invagination) and the mantle lobes are defined before reversal takes place. This differentiation is then followed by atrophy of the ventral mantle rudiments and the deposition of chitinous plates on both the inner surface of the dorsal mantle rudiment and the adjacent surface of the pedicle rudiment. The plates have been respectively identified as the beginnings of the brachial valve and a delthyrial cover; BEECHER (10) believed that the pedicle valve was formed later and subsequently ankylosed to this cover. Such interpretations cannot be accepted without further investigations. Admittedly important modifications of larval development are to be expected in cemented brachiopods, like *Lacazella*, that lack a pedicle. Nonetheless, it is important to note that KOVALEVSKIY's illustrations were not based upon prepared sections and the plate homologized by BEECHER with the delthyrial cover could well have been a stylized representation of a ring of chitin around a degenerating pedicle rudiment (1, 44).

LENGTH OF LIFE

Crania has survived in the laboratory for more than a year and its rate of growth suggests that its life span can be greatly in excess of a year. This is borne out by the size distribution within a sample of *C. anomala* off northwestern Scotland, which led ROWELL (38) to conclude that in this area the animals were capable of living for four or five years.

YATSU (46) found that in Misaki Bay (Japan) it took a year for *Lingula* to attain a shell length of 5 mm., and assuming that the rate of growth was constant, he concluded that maximum adult size indicated a life of five years or more. CHUANG (18a), however, working on *Lingula anatina* from Singapore, has found that although the rate of growth varies, in general it is inversely proportional to length of the individual. He obtained direct evidence that the animals live more than five years and considers that the life span varies probably between six and twelve years. The life span of *Glottidia pyramidata* off Florida is seemingly much shorter (34), with a maximum probably in the order of 20 months.

Very little information has been published on the life span of discinids. PAINE (33) found that size variation in a sample of *Discinisca strigata* from Mexico was normally distributed, and thought it likely that these animals were annuals. Other interpretations of this curve are possible, however, and more data still are required.

Articulate brachiopods are known to be less hardy than inarticulates under laboratory conditions, but the only noteworthy comments on longevity are those for *Terebratella inconspicua*. From the size distributions of his samples, PERCIVAL (35) concluded that adults lived for about four years. RUDWICK's sampling (39) provided entirely different patterns of distribution with fewer peaks. Despite this difference, he maintained that since rate of growth decreases with increasing age, the life span of surviving individuals with the largest shells is probably much greater than four years.

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ADDITIONAL SOURCES OF ILLUSTRATIONS

(47) **Rowell, A. J.**, new

(48) **Williams, Alwyn**, new

MORPHOLOGY

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[The Queen's University of Belfast and Nottingham University]

SHELL FORM

The brachiopod shell which is normally bilaterally symmetrical about the longitudinal median plane (plane of symmetry) consists of two dissimilar valves and is oriented according to the growth and disposition of the soft parts. That region of the shell from which the pedicle emerges and which normally represents the first-formed part of each valve is posterior, so that the median portions at the opposite ends of the shell margin constitute the anterior (Fig. 59). The valve that accommodates most, if not all, of the pedicle is referred to as the **pedicle valve**; it is typically larger than the opposing **brachial valve.** The valves are also called ventral and dorsal respectively in recognition of their orientation relative to the body axis; and although these terms are less meaningful in identification of the valves, they are nonetheless correct and may be retained for describing the disposition of various features. Dimensions measured to give some indication of shell size, outline and profile are conventionally taken in the manner shown in Figure 59.

The growth of the brachiopod valve subsequent to the secretion of the protegulum may proceed in three different ways (49) (Fig. 60). In certain inarticulates like the discinids, deposition by an expanding mantle edge continues around the entire margin of the protegulum which, as a result of this process of holoperipheral growth, migrates forward away from the posterior margin toward the center of the adult valve (Fig. 60,*1a,b*). In other inarticulates like the lingulids, although the posterior margins are thickened by some growth, nearly all the

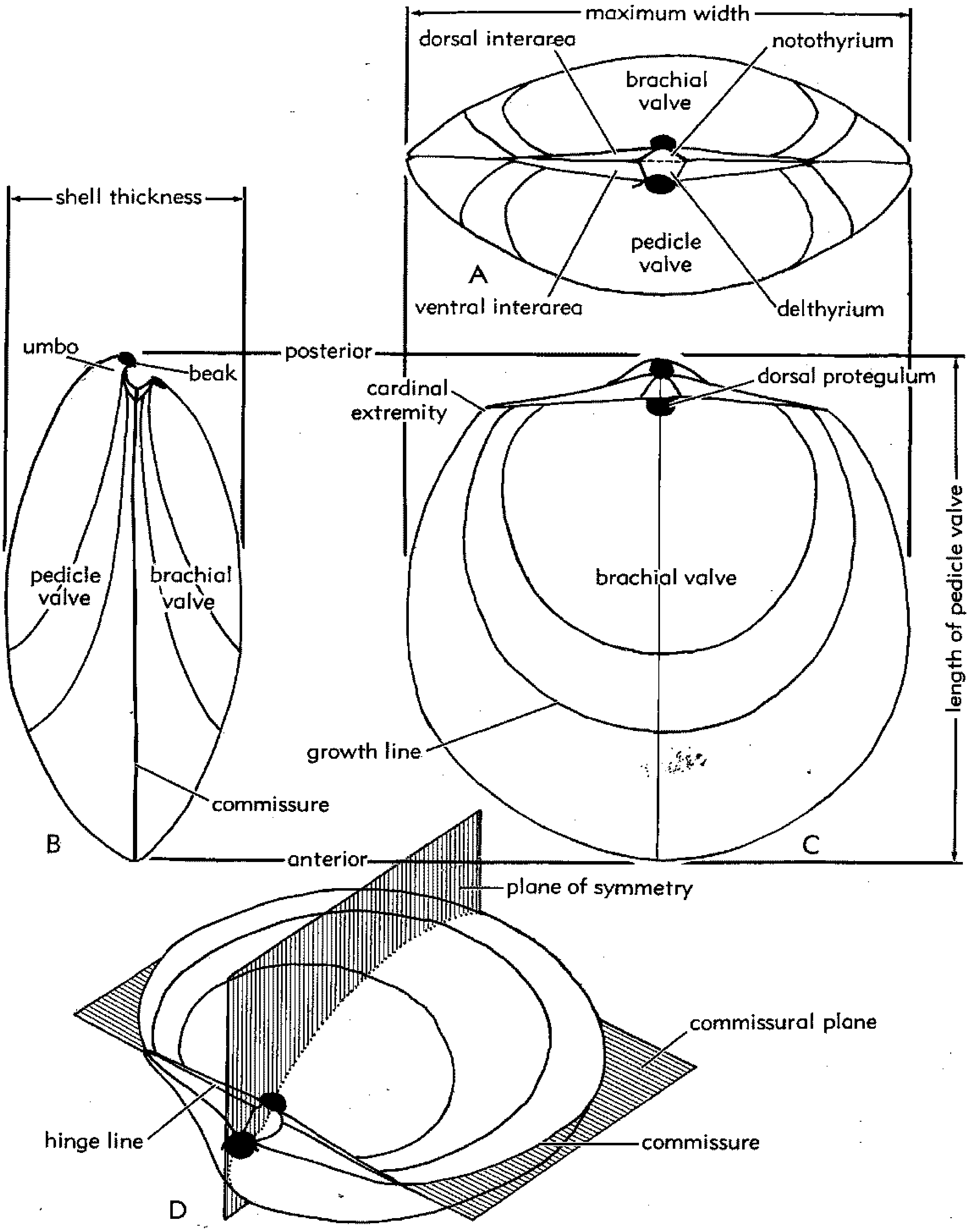

FIG. 59. External features of generalized enteletacean brachiopod seen in posterior *(A)*, left lateral *(B)*, dorsal *(C)*, and dorsolateral *(D)* views (65).

new shell is added to the lateral and anterior margins (hemiperipheral growth) so that the protegulum remains in posteromedian position (Fig. 60,*3a,b*). The third type of growth affecting inarticulates (e.g., some acrotretaceans and paterinaceans), which is known as mixoperipheral, is really a modification of holoperipheral growth in that the posterior surface of a valve is inclined anteriorly toward the other valve (Fig. 60,*2a,b*). Such a surface has been called a palintrope (49), but the term has limited use in this context because changes in growth directions, involving transitions between holoperipheral and mixoperipheral patterns, are common among brachiopods. Mixoperipheral growth is pre-eminently characteristic of the articulate brachiopods (Fig. 60,*5a,b*), especially in the definition in both valves of a planar or curved triangular shelf (**cardinal area**) subtended between each apex and the posterior ends of the lateral margins (cardinal extremities) (Fig. 59). The growth of the cardinal area is controlled at its free edge (posterior margin). In many genera the posterior margin is parallel to the hinge axis (i.e., the line about which the valves rotate during opening or closing of the shell) and forms a true hinge line, the growing edge of the posterior margin of the two valves being identical in extent. Shells in which both conditions are fulfilled are referred to as strophic (40) (Fig. 61) and the cardinal areas of these shells as **interareas.** The ventral interarea of such shells is commonly larger than the dorsal and both may be variously inclined relative to the surface containing the boundary line (commissure) between the anterior and lateral margins of the valves (Fig. 59). As can be seen in Figure 61,*C*, the disposition of interareas relative to the "plane" of commissure (the "normal plane" of RUDWICK) may vary by more than 180°. The commonest attitude adopted by the ventral and dorsal interareas is apsacline and anacline, respectively, and the rarest conditions are probably the procline and hypercline, which represent aspects

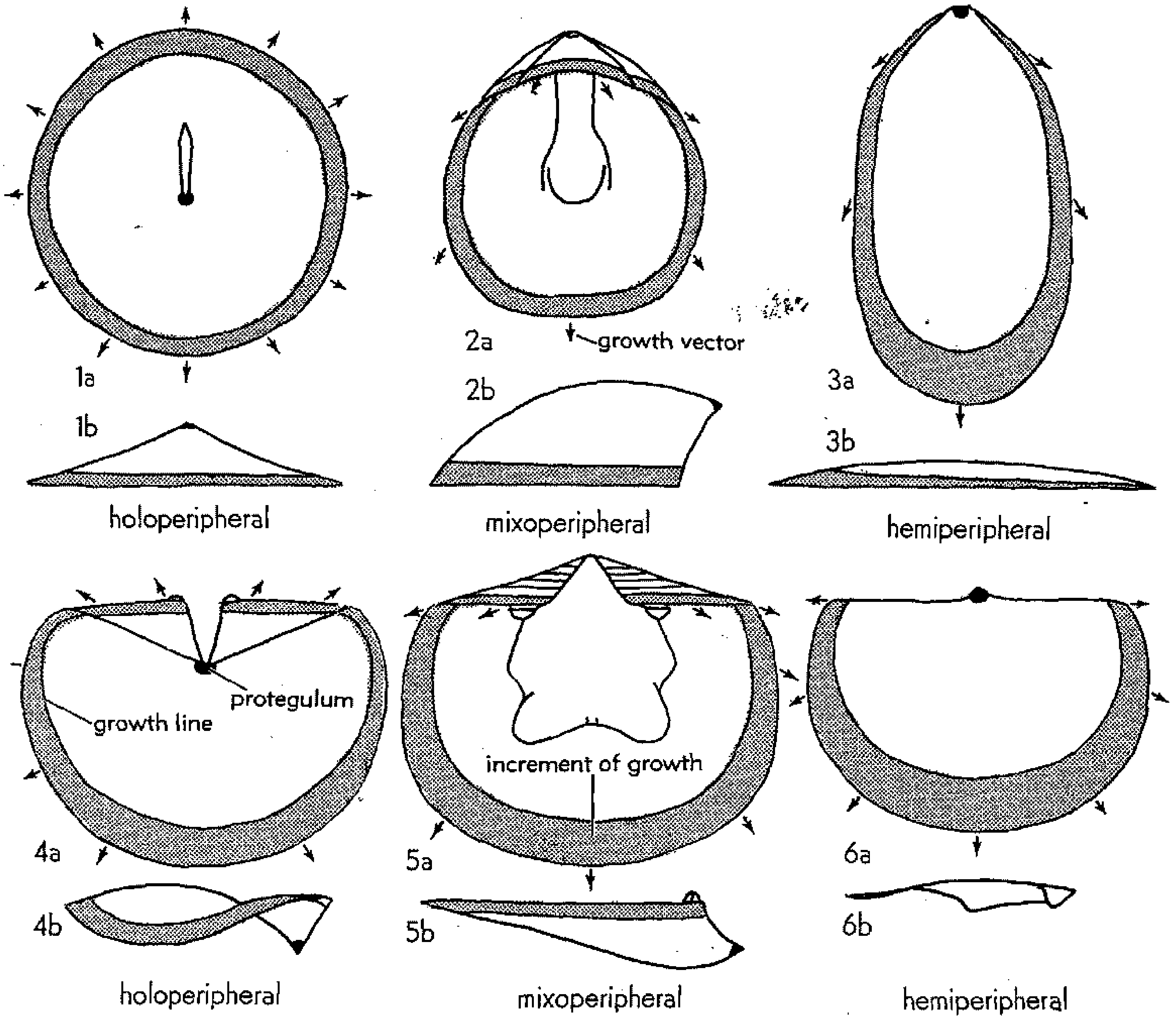

FIG. 60. Nature of shell growth as typified by holoperipheral increase in pedicle valves in ventral and lateral views of *Orbiculoidea (1a,b)* and *Plaesiomys (4a,b)*; mixoperipheral increase in pedicle valves in dorsal and lateral views of *Apsotreta (2a,b)* and *Dinorthis (5a,b)*; and hemiperipheral increase in brachial valves in dorsal and lateral views of *Lingula (3a,b)* and *Productus (6a,b)* (64).

of holoperipheral growth. Among wide-hinged orthoids, strophomenoids, and spiriferoids, the interareas form very obtuse-angled triangles, but extreme lateral reduction of the hinge line led to rostrate shells like *Perditocardinia* in which the apical angle of the interareas is narrowly acute. A conical pedicle valve, due to excessive for-

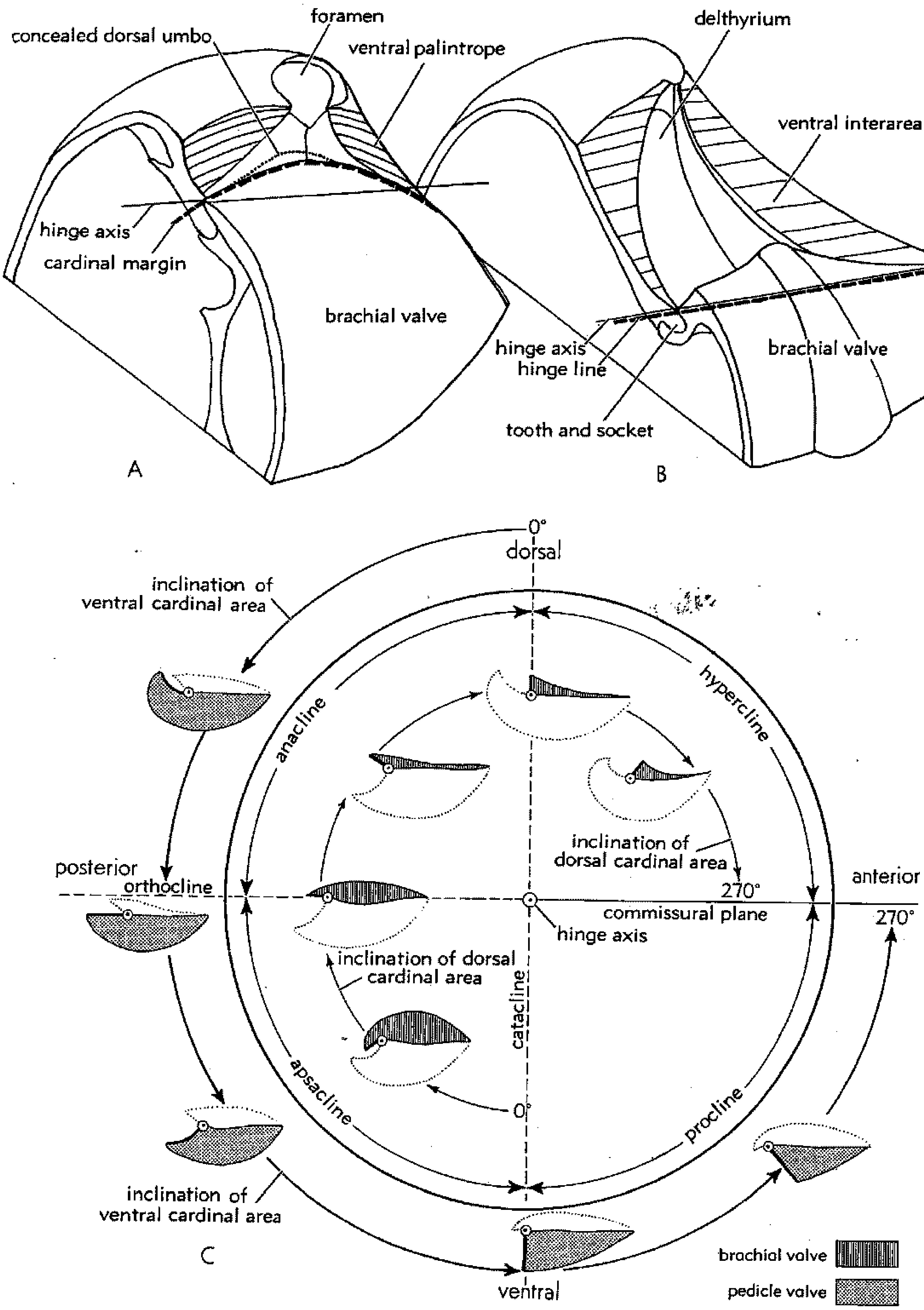

FIG. 61. Posteromedian regions of (*A*) nonstrophic and (*B*) strophic shells, with (*C*) a chart showing the various attitudes of cardinal areas about the hinge axis relative to the commissural plane (65).

ward growth of the ventral interarea, is characteristic of a number of genera (e.g., *Onychotreta, Scacchinella, Syringothyris*), whereas a suppression of forward growth, as in the majority of productoids, led to linear interareas and "hemiperipheral" expansion of the brachial valve.

Rostrate shells are also characteristic of nonstrophic terebratuloids, rhynchonelloids, and atrypoids, in which homologues of the interareas are greatly reduced or absent and homologues of the hinge lines are short and curved, so that their traces only intersect the hinge axis (Fig. 61). Rudwick (40) prefers to use the terms "palintrope" and "cardinal margin" to distinguish these vestiges from the well-developed interareas and hinge lines, respectively, of strophic shells. This distinction may seem academic, because the free edge of the dorsal umbo which protrudes into the delthyrial cavity of the pedicle valve of the nonstrophic shell (i.e., most of the cardinal margin as understood by Rudwick) is no more an integral part of the hinge line than are the notothyrial edges of strophic brachial valves. However, if reference is made exclusively to those posterior surfaces and edges lateral of the points of articulation (i.e., to the arcs underlain by fused mantle lobes), the differences described by Rudwick are valid.

Irrespective of the different types of growth, the protegula occupy the apices (or beaks) of the valves, and the shell region immediately around the apex is referred to as the **umbo** (Fig. 59). The attitude of the ventral beak can vary from being in the commissural plane (straight) to a dorsally directed inclination of up to 150° to that plane (strongly curved). Typically the cardinal areas of articulate brachiopods, immediately beneath apices of the valves, are notched by a pair of triangular openings—the delthyrium of the pedicle valve, which normally accommodates the pedicle, and the notothyrium of the brachial valve, which usually is filled with the attachment base (cardinal process) for the dorsal ends of the diductor muscles (Fig. 59). Both of these openings may be partially or completely covered by shell outgrowths described below.

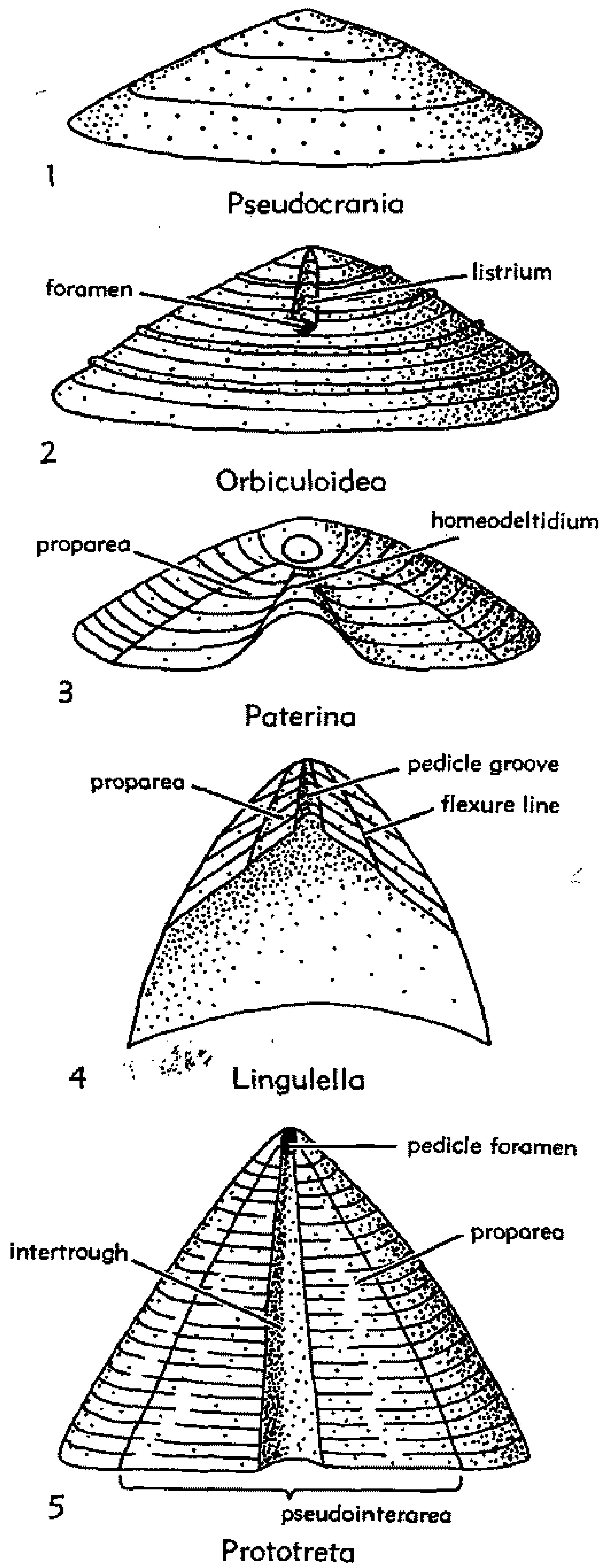

Fig. 62. Modifications of posterior sector of pedicle valve of some inarticulate brachiopods; *1*, craniacean *(Pseudocrania)*; *2*, discinacean *(Orbiculoidea)*; *3*, paterinacean *(Paterina)*; *4*, lingulacean *(Lingulella)*; *5*, acrotretacean *(Prototreta)* (63).

The posterior surface of the inarticulate valve may be completely unmodified and comparable with the anterior and lateral slopes, as in the majority of craniaceans (Fig. 62,*1*). More commonly some differentiation occurs especially in the pedicle valve. The simplest modification is some form of opening such as a notch or a slit

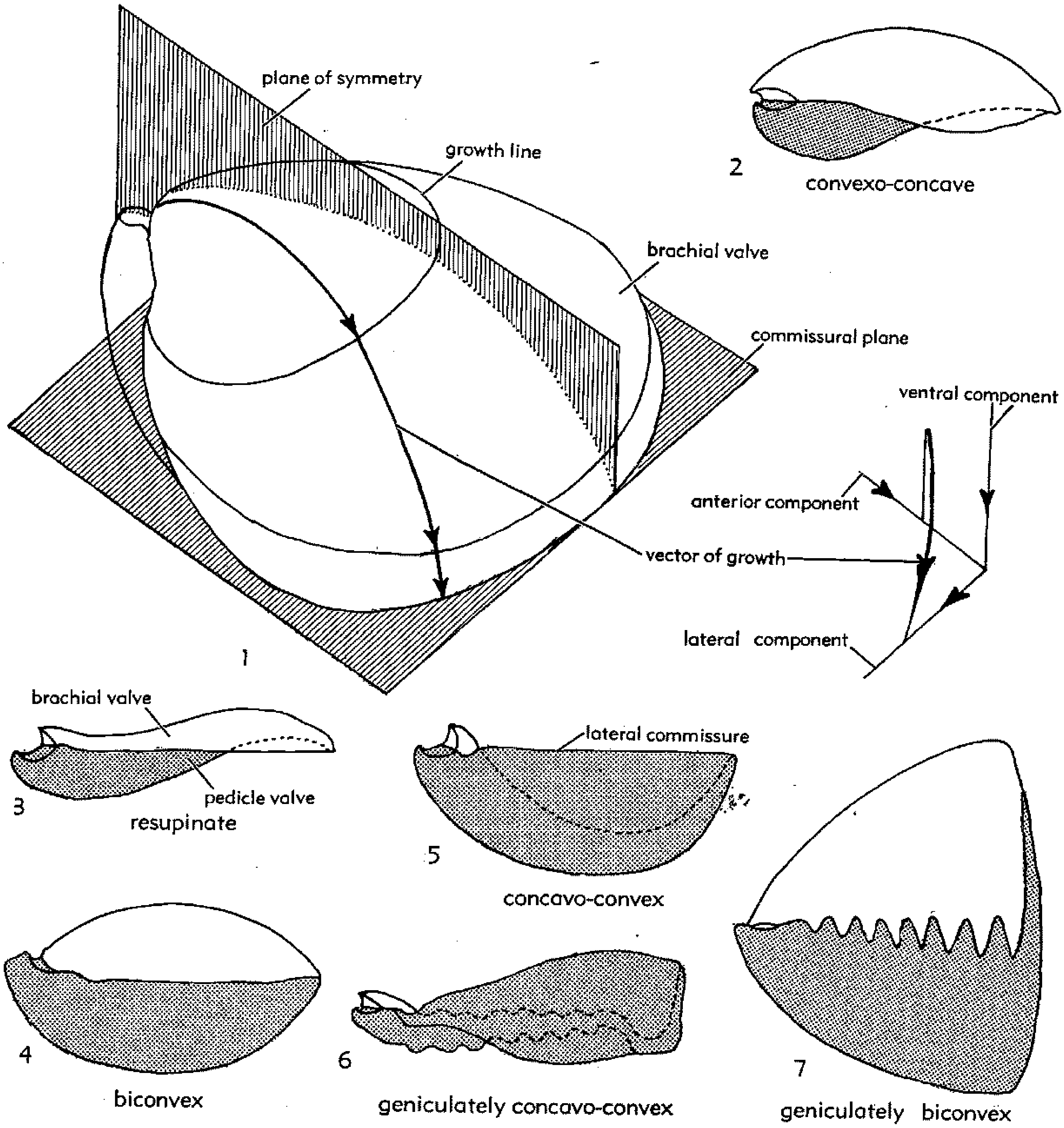

Fig. 63. Components of growth in brachiopod shells (*1*), with illustrations of various types of lateral profiles (*2-7*) (65).

for the pedicle (e.g., discinids) while a flattened surface (pseudointerarea) on the posterior margin of either valve is characteristic of many groups (Fig. 62,*3-5*). Thus, in the paterinaceans the pseudointerarea of the pedicle valve consists of a pair of flattened triangular areas (propareas) marked off from the posterolateral regions of the valve by a break in slope and separated by the delthyrium. The ventral pseudointerarea of lingulaceans, in contrast, is approximately orthocline in disposition and the two triangular propareas flank a pedicle groove. These basic patterns, with minor modifications, also occur in other inarticulate groups and can involve the posterior margin of the brachial valves. An orthocline or anacline dorsal pseudointerarea, which may be divided medially as in many acrotretids, is commonly developed, although other less complex modifications may occur.

The protegula of living and extinct brachiopods suggest that in both transverse and longitudinal profiles, the unspecialized shape of the adult shell is biconvex (Fig. 63). Ideally, then, three components of growth relative to the median and commissural planes of the shell may be recognized and vectors of growth, traced on the shell surface from the protegulal node, may be resolved according to these axes. They are an anterior component parallel with the intersection of both planes, a ventral or dorsal one normal to the commissural plane, and a lateral one normal to the median plane. In general, the pedicle valve is not only larger in outline but deeper than the brachial valve, but every conceivable variation in this relationship was attained during brachiopod evolution. Thus among the strophomenoids, chonetoids, and productoids, the more usual adult profile was concavo-convex, that is, with a brachial valve becoming concave beyond the protegulal node and the pedicle valve continuing its initial convexity (Fig. 63,*5*). A reversal in growth direction was also common, so that the biconvexity of the protegulum was modified to a concavo-convex relationship in young shells, which in turn gave way to a convexo-concave attitude during adult stages of growth. This type of growth is known as **resupination** (Fig. 63,*2*). Such reversals in direction of growth were also accentuated by an angular deflection of one or both valves (**geniculation**) due to a marked reduction or cessation of the radial components of growth. Such deflections are directed either toward the other valve (e.g., *Enantiosphen, Sphaerirhynchia,* Fig. 63, *6,7*), or in the same direction to define a disc, commonly with an internal confining ridge (submarginal ridge) and a trail (Fig. 63,*6*). The disc corresponds more or less to that part of the shell occupied by the body and lophophore, and the trail may be directed dorsally or ventrally and may even reverse direction as in some leptaenids.

A common modification of the profile of inarticulate brachiopods is the development of a conical valve. Both valves of *Orbiculoidea* may be subconical but it is more usual for only one valve to become conical, such as the acrotretid pedicle valve and the discinid brachial valve. This profile is very much less common in the articulate brachiopods, the most spectacular being the cone-shaped pedicle valve of *Richthofenia,* which encloses a sunken subcircular brachial valve.

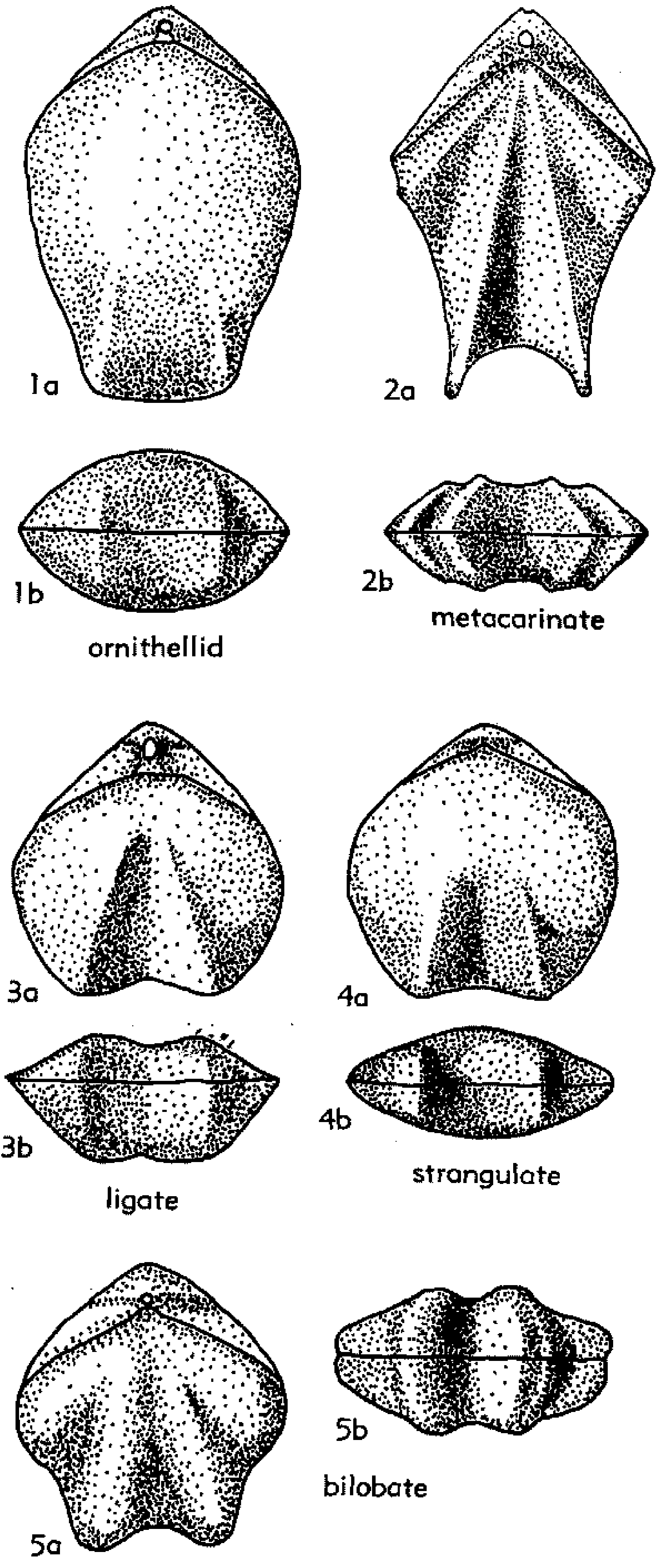

FIG. 64. Types of opposite folding; *1-5,* dorsal and anterior views of indicated stages (63).

The brachiopod outline varies greatly, apart from the more orthodox transversely semioval, subcircular, elongately oval, and subtriangular appearance of wide- to short-hinged shells. Some of the more bizarre forms include the saucer-like, incurved, or conical pedicle valve of the oldhaminoids, with highly lobed dorsal structure which may have consisted of a vestigial brachial valve and a large internal plate supporting the lophophore; the tubelike pedicle valve of the productoid *Proboscidella*; and the terebratuloid *Pygope*, pierced subcentrally by a hole which was sealed off by anteromedian fusion of a deeply indented (emarginate) anterior margin. Both outline and profile of the shell may be considerably modified by radially disposed deformations which display a variety of form and amplitude. The major, radial elevations of the valve surface are **folds** and the complementary major depressions are **sulci.** These broad deformations grade down into minor features (costae, costellae) which are produced in a comparable manner but are normally regarded as part of the ornament and as such are discussed in detail elsewhere.

In terms of their effect on the commissure, folds and sulci fall into two broad groups, and it is apparent that the deformations of these two groups arose in different ways (40). In one group, the folds and sulci are developed opposite each other in the two valves (**opposite folding**), a fold being opposed to a fold and the commissure remaining straight (rectimarginate) (Fig. 64). These deformations may be regarded as being produced by localized anomalies of the radial growth component, which is the vector sum of the anterior and lateral components; since the commissure is not deflected, they do not involve anomalies in the vertical component. Deformations produced in this way have their maximum expression when the valve is strongly convex.

In the second group, the folds and sulci are complementary to one another (**alternate folding**), a fold in one valve being opposed by a sulcus in the other, and the commissure becomes correspondingly undulated by deflections directed dorsally (**plicae**) and ventrally (**sinuses**). The commoner arrangements of this type are shown in Fig. 65, but these are not necessarily constant throughout ontogeny, because during growth a median sulcus may be replaced by a fold and vice versa. Deformations of the alternate type commonly involve localized anomalies of the vertical growth component either acting alone or in conjunction with localized anomalies of the radial component. If the anomalies are entirely in the vertical component, the deformations will have their maximum expression on a plane valve and be less conspicuous on a highly convex one.

SHELL STRUCTURE AND ORNAMENTATION

The shell structure of living and extinct articulate brachiopods may be referred to one of three conditions: **impunctate, endopunctate,** and **pseudopunctate.** The triple stratification of the shell described in the chapter on "Anatomy" is known or presumed to be normally true of at least the first two types, although the periostracum is never preserved on fossil shells. The thin primary layer is difficult to detect except in well-preserved, unaltered specimens. It is, however, immediately recognizable in the spiriferoids, thecideaceans, pentameraceans, and at least the later porambonitaceans, *Anastrophia* and *Camarella,* as well as fossil terebratuloids and rhynchonelloids. In these groups it is always cryptocrystalline and fairly constant in thickness except for consistent variations related to the development of radial and concentric ornamentation as in the atrypoids (Fig. 66). The boundary between the primary and secondary layers is commonly so sharply defined that one can reasonably assume all obliquely disposed fibers of the inner secondary layer to have been enclosed in cytoplasmic sheaths. Variations do occur. In the thecideaceans and some terebratellaceans (56) the fibers of the secondary layer are disposed at high angles to the external shell surface in a series of bundles forming the cores of internal tubercles (Fig. 67). Among the spiriferoids and pentameroids, a third calcareous layer is commonly found (the prismatic layer of Alexander, 1) which although distinct in appearance is simply a modification of the secondary layer (Fig. 66). It consists of coarse prisms of calcite in continuity with underlying, earlier formed, obliquely disposed fibers and is commonly well developed in those parts of the shell occupied by the muscle bases, which suggests that it

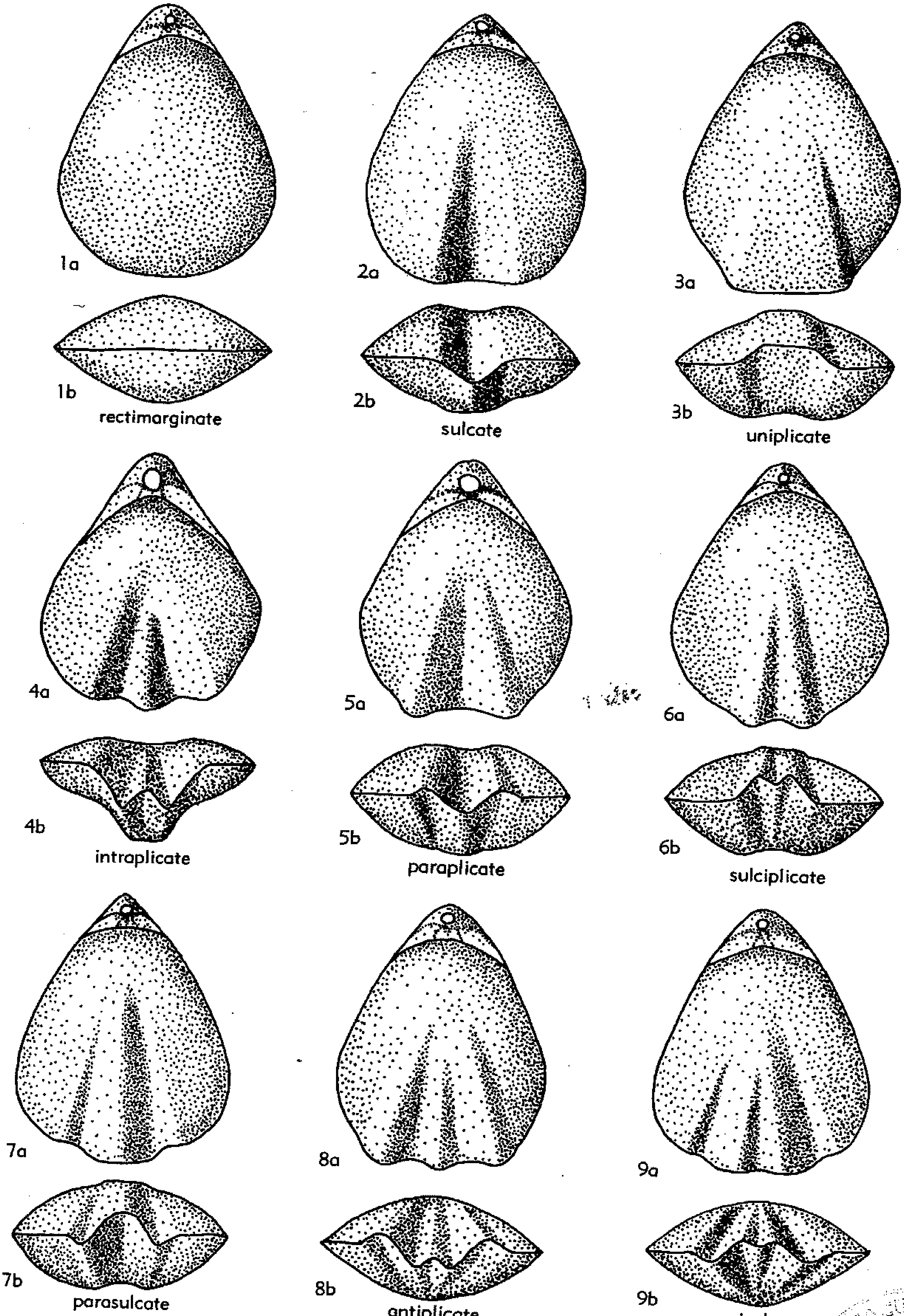

FIG. 65. Types of alternate folding; *1-9*, dorsal and posterior views of indicated stages (63).

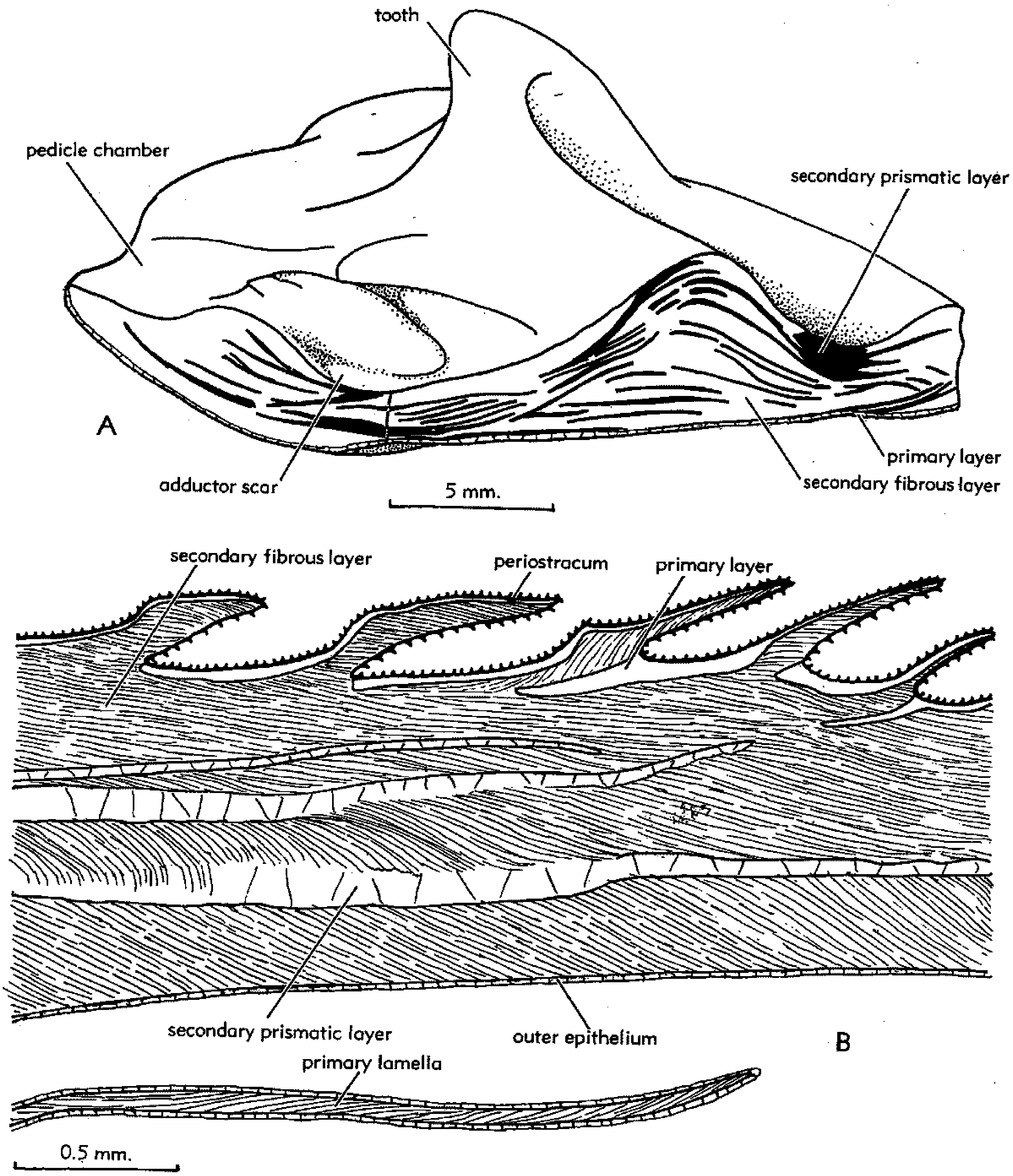

Fig. 66. Stylized sections showing (*A*) distribution of prismatic shell within secondary layer of posterior part of pedicle valve of *Atrypa* sp., M.Dev., USA, and (*B*) inferred relationships during life with periostracum and outer epithelium (65).

could be secreted extracellularly by adult outer epithelium associated with tonofibrils. In respect of surface detail, the exterior of the primary layer of well-preserved fossils is seen to be made up of slightly convex minute polygons like those associated with the periostracal net of living brachiopods (Fig. 68); and the internal surface of the secondary layer is appropriately differentiated into a fine mosaic consisting of the ends of the fibers within their organic sheaths (Fig. 69). The dimensions of the bases of the fibers which make up the mosaic are supposedly sufficiently constant within a species to be used systematically (10).

The primary layer in its typical form is also found sporadically on the shell surface of orthoids and clitambonitoids. This impersistence is usually attributed to mechanical abrasion or solution during fossilization, but it may be that in these groups, the primary shell was very thin, although not invariably so, because exaggerated concentric ornamentation (as in *Glyptorthis*) consists mainly of primary shell substance.

The impunctate shell appears to be the most primitive, because, as yet, no endopunctate or pseudopunctate brachiopods have been recorded from strata older than the Ordovician, while the Cambrian articulate shell (as typified by *Nisusia*) is comparable in structure with that of the younger impunctate stocks and was presumably also deposited by the outer mantle lobe and the

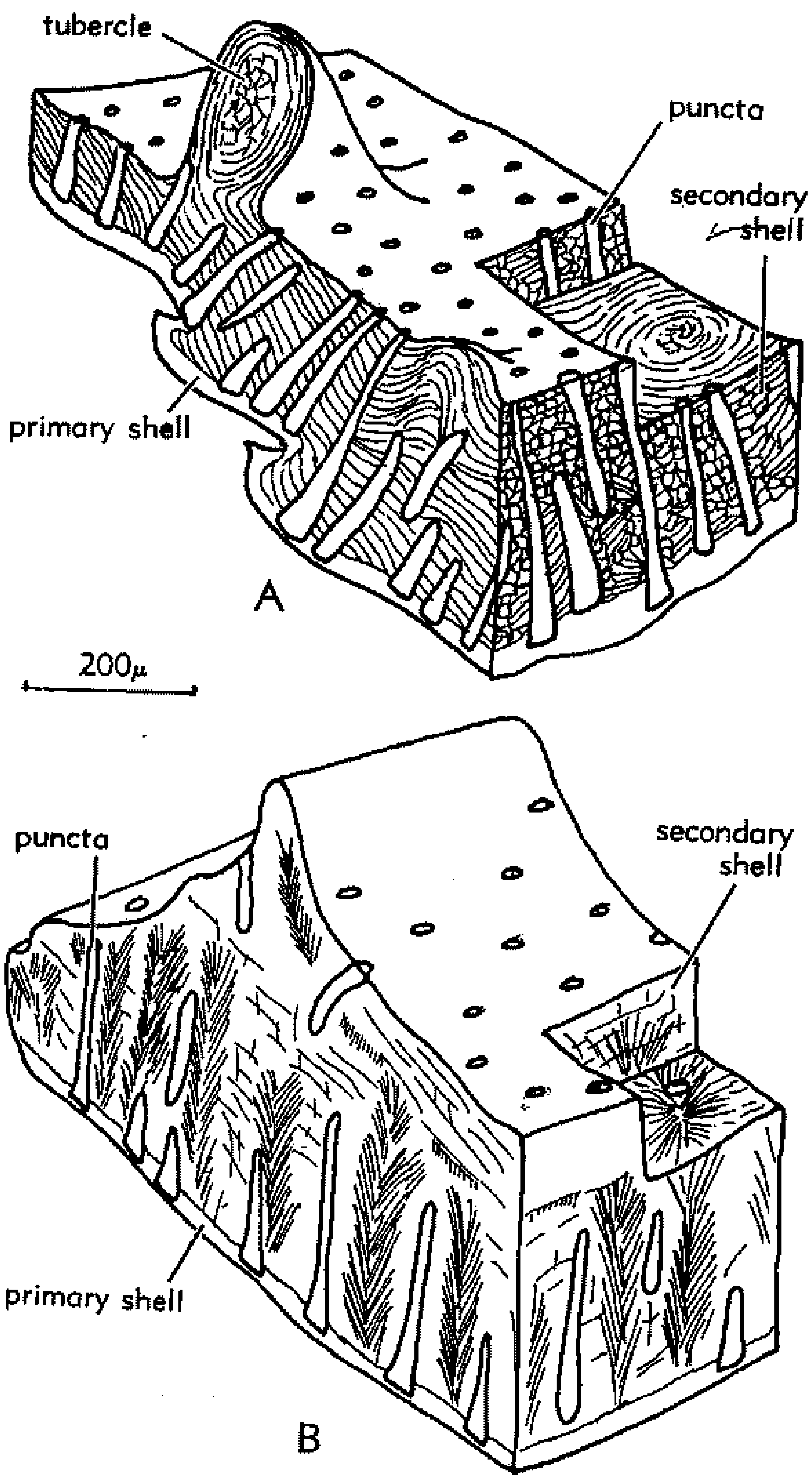

Fig. 67. Sections showing shell structure of *Megerlia truncata* (Linné) *(A)*, and *Lacazella mediterranea* (Risso) *(B)* (65).

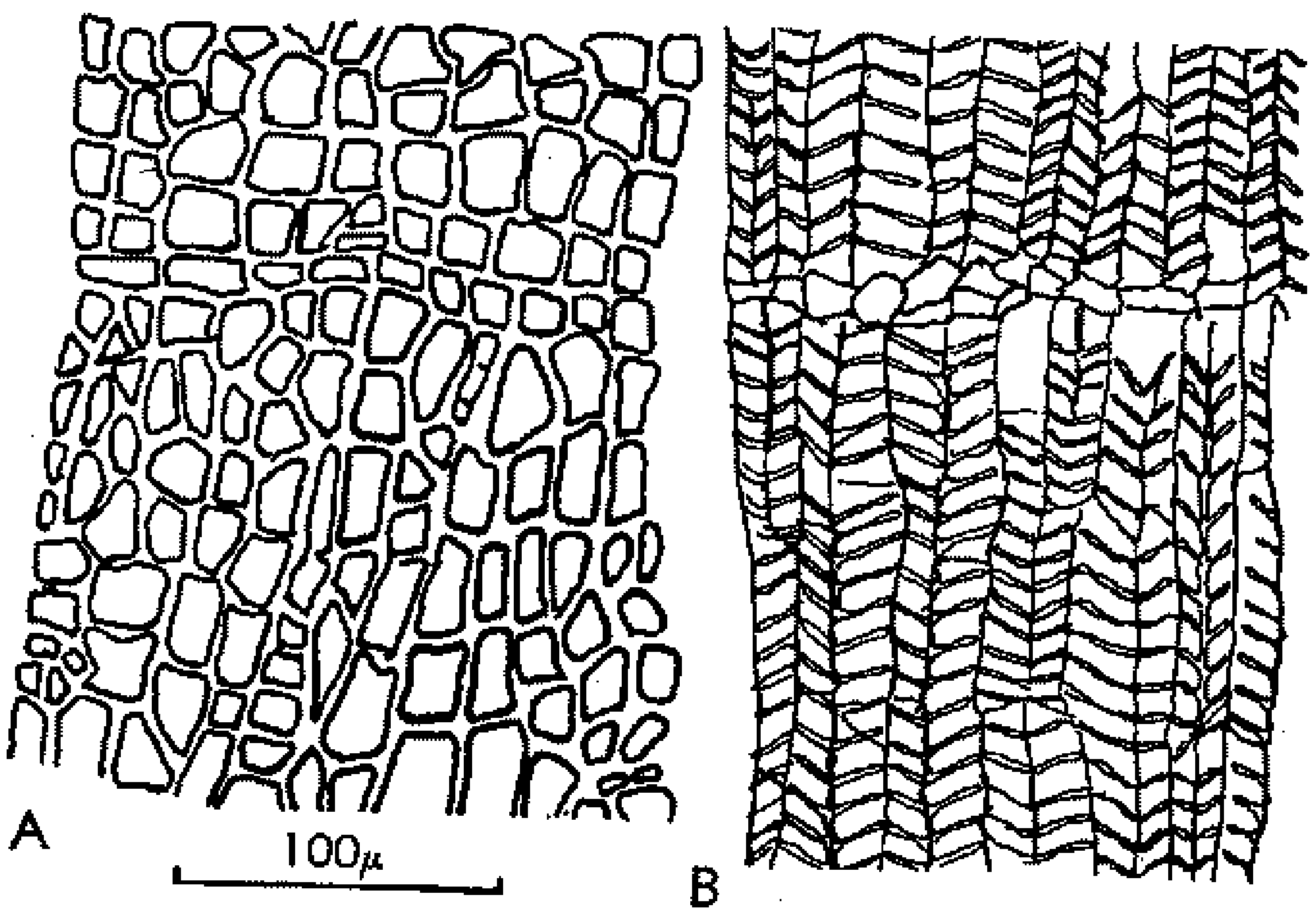

Fig. 68. Impressions of periostracal cover to exteriors of *(A) Hemithiris psittacea* (Gmelin) and *(B) Notosaria nigricans* (Sowerby), prepared as cellulose acetate peels (65).

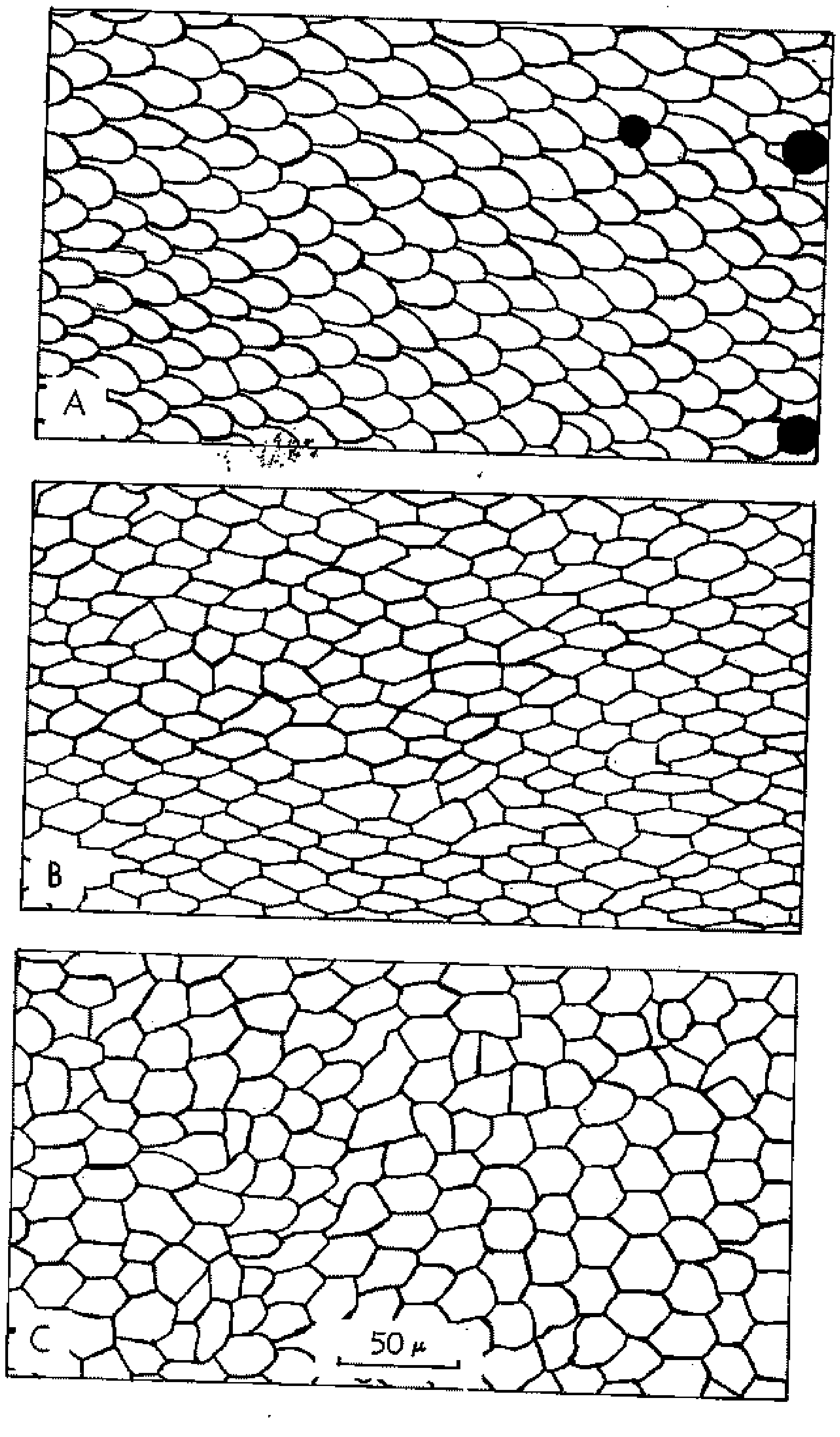

Fig. 69. Shell mosaic of *(A) Terebratulina caputserpentis* (Linné) and *(B) Hemithiris psittacea* (Gmelin), with *(C)* impression of epithelium underlying muscle base of latter, all prepared as cellulose acetate peels (65).

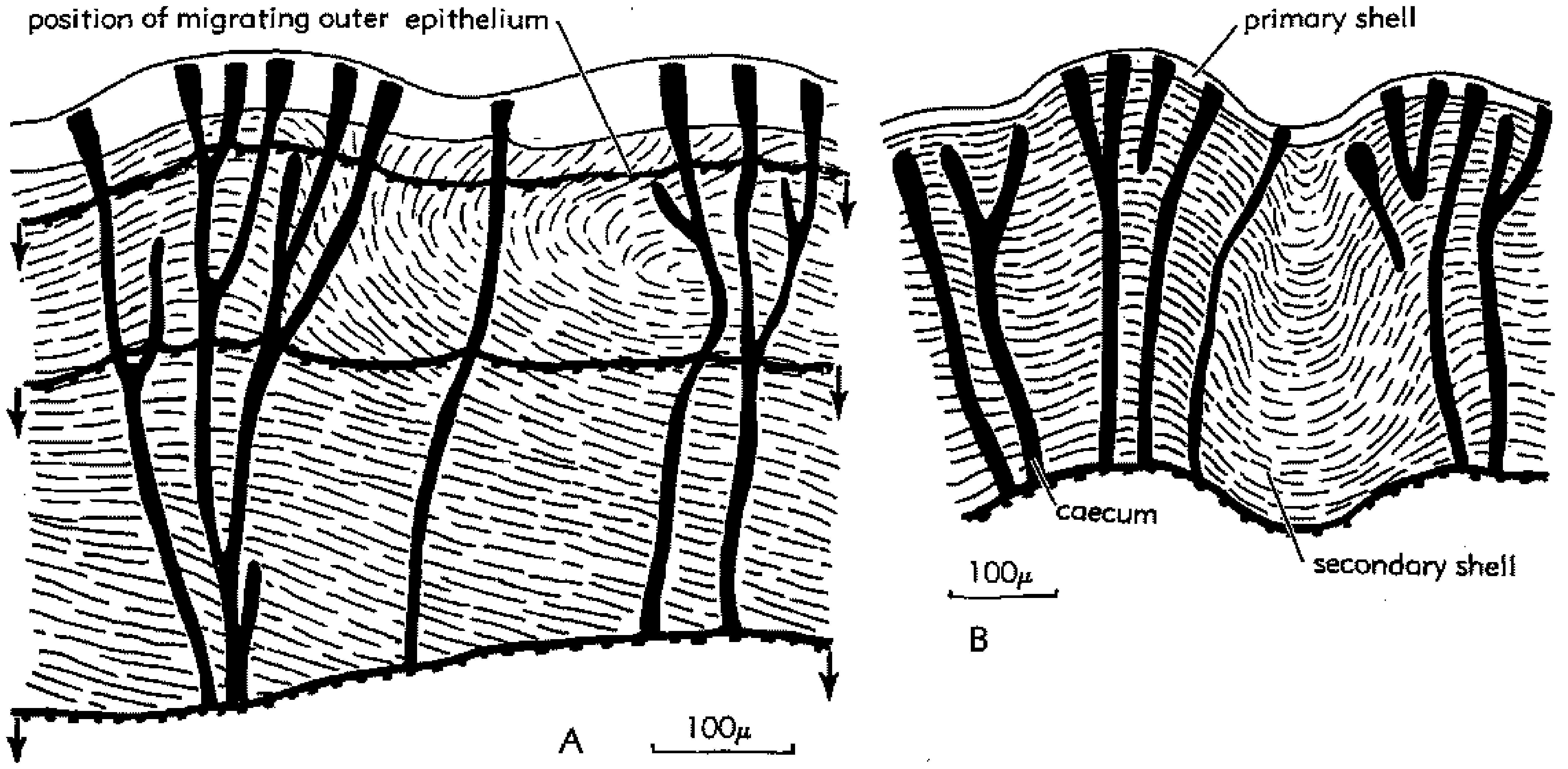

Fig. 70. Branching caeca seen in cross sections of *(A) Rhipidomella* sp., M.Dev., USA, and *(B) Terebratulina caputserpentis* (Linné) (65).

outer epithelium. Indeed, so great is the time lag before the first appearance of endopunctate and pseudopunctate stocks that they were most probably derived from impunctate ancestors.

The shells of all extinct endopunctate brachiopods are comparable in morphological detail to those of living terebratuloids (Fig. 70). The punctae have the same kind of conical distal end and although canopies of calcite, which in living brachiopods lie penetrated by caecal brushes, are rarely seen, even in fossil terebratuloids, it is reasonable to assume that all punctae were occupied by caeca proliferated at the mantle edge. The punctae may be single or they may branch freely when the caecal cups bud off singly but come to share a common secondary stalk of outer epithelium which is pinched up from the mantle by deposition of the surrounding secondary shell (Fig. 70). The diameter of the cups varies greatly (although 30 to 50μ seems to be representative), as does the density of their incidence (Fig. 71,*A*). In radially ornamented shells, punctation is commonly concentrated in strips coincident with ornamentation (Fig. 71,*C*); it may also develop in distinct rows concentric with, or oblique to, the lines of growth (Fig. 71,*B*), or it may be sporadically or densely distributed with no apparent sense of pattern.

Punctation is invariably characteristic of the enteletaceans and terebratuloids. It is also known in the thecideaceans, certain spiriferoids, and exceptionally even in the rhynchonelloids *(Rhynchopora)*. It is unlikely that this similarity in shell structure reflects any close relationship between the various groups; more probably the incorporation of secretory cells within the brachiopod shell, in the manner characteristic of living terebratuloids, occurred repeatedly during brachiopod evolution and became a persistent feature of independent stocks. Indeed, the only prerequisite for the initial development of caeca in impunctate shells, or their degeneration in endopunctate brachiopods to give rise to impunctate descendants, is the presence of secretory glands in the primary layer (57); and it is significant that superficial perforations (**exopunctae**) which might have accommodated the cups of impersistent caeca are preserved in fossil shells. Exopunctae, however, might have arisen in a number of ways. Those typical of the plaesiomyids and plectorthids seem to have represented the incipient development of hollow costellae (Fig. 72). They are formed by a regularly occurring inward sag of the mantle edge away from the sharply angular margins of the principal ribs while deposition continued and ultimately sealed off the re-entrant as a short, oblique cylindrical hollow. The exopunctae of *Crurithyris* are the bases of hollow spines (24) which almost certainly enclosed columnar epithelium sealed off from the mantle at the junction of the primary and secondary layers, while others like those in the rhynchonellid *Porostictia* (12) are definite pits and must also have contained, temporarily at least, epithelium budded off from the mantle edge.

In most strophomenoids, productoids, chonetoids, and some clitambonitoids, the shell is penetrated by rods of calcite (**taleolae**) in a manner reminiscent of true punctation (57). The general shell condition is referred to as pseudopunctation.

The shell structure of strophomenoids differs from that of most articulate brachiopods in lacking a clearly differentiated primary layer over most of the shell surface and in being, with rare exceptions, pseudopunctate. Many references (e.g., 55) have been made to the existence of an outer shell layer like that of the terebratuloid primary layer in members of this group, but its full and invariable development has always been inferred from the structure of the interareas and the origin of the pseudopuncta within the rest of the shell. Thus in strophomenoids and also chonetoids, the interareas are made up of inner fibrous layer and an outer layer, composed of either cryptocrystalline calcite or very fine calcite fibers disposed normal to the external surface, which thickens gradually toward the hinge line and which must have been secreted at the mantle edge in the manner of the true primary layer (see Fig. 116). This differentiation led to the assumption that a similar "pri-

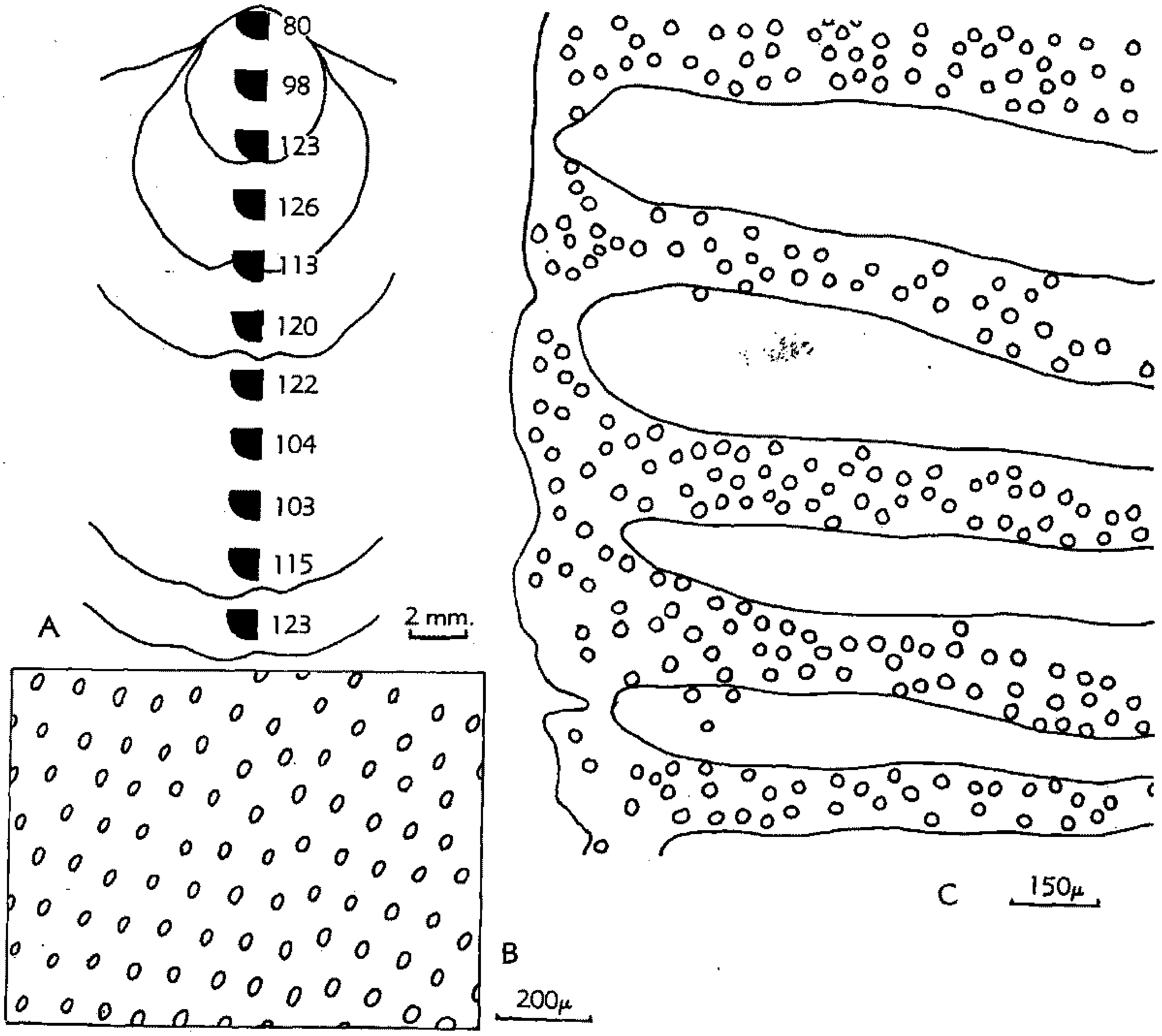

FIG. 71. Distribution of endopunctae showing *(A)* number of punctae occurring in sectors with radius of 1 mm. along mid-line of brachial valve of *Magellania flavescens* (LAMARCK) and *(B)* details of their arrangement; also *(C)* concentration of punctae in crests of costellae as seen along edge of brachial valve of *Terebratulina caputserpentis* (LINNÉ) *(B, C,* prepared as cellulose acetate peels of shell surfaces) (65).

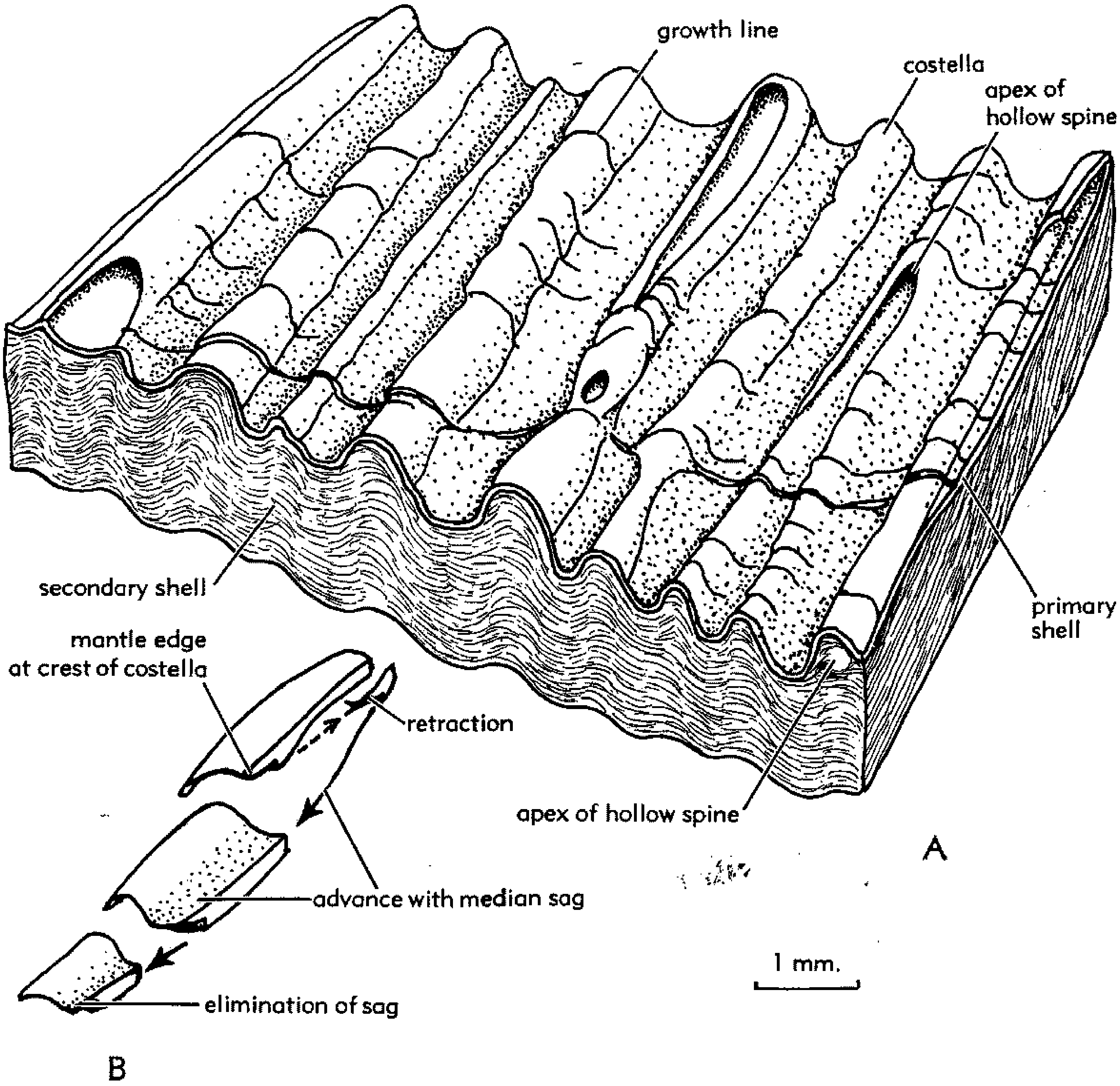

FIG. 72. Part of pedicle valve of *Plaesiomys subquadrata* (HALL), U.Ord., USA, showing *(A)* nature of hollow costellae and *(B)* inferred path of mantle edge during formation of hollow rib (65).

mary" layer was also deposited along the mantle edges responsible for the growth of the rest of the shell but was so thin as to have been dissolved away or recrystallized into an unrecognizable state during fossilization. Such modifications would account for its never having been positively identified over the remainder of the shell surface and also for the absence of pits corresponding to the pseudopunctae on the external surfaces of well-preserved shells.

Sections of Upper Silurian and Lower Carboniferous limestones, however, have shown skeletal remains of rhynchonelloids, spiriferoids, and terebratuloids, all with a nonfibrous primary layer, side by side with those of leptaenids (and also stropheodontids in the older limestones), the shells of which were undifferentiated except along the interareas. This confirms the impression gained from a detailed study of about 40 strophomenoid genera that the homologue of the terebratuloid primary layer over much of the strophomenoid shell consists of the outermost layers of calcite fibers which are disposed parallel with the external surface and are indistinguishable from the inner secondary layer, except for a scattering of pseudopunctae throughout the latter.

The strophomenoid arrangement is also characteristic of at least some chonetoids, but in some productoids like *Dictyoclostus*

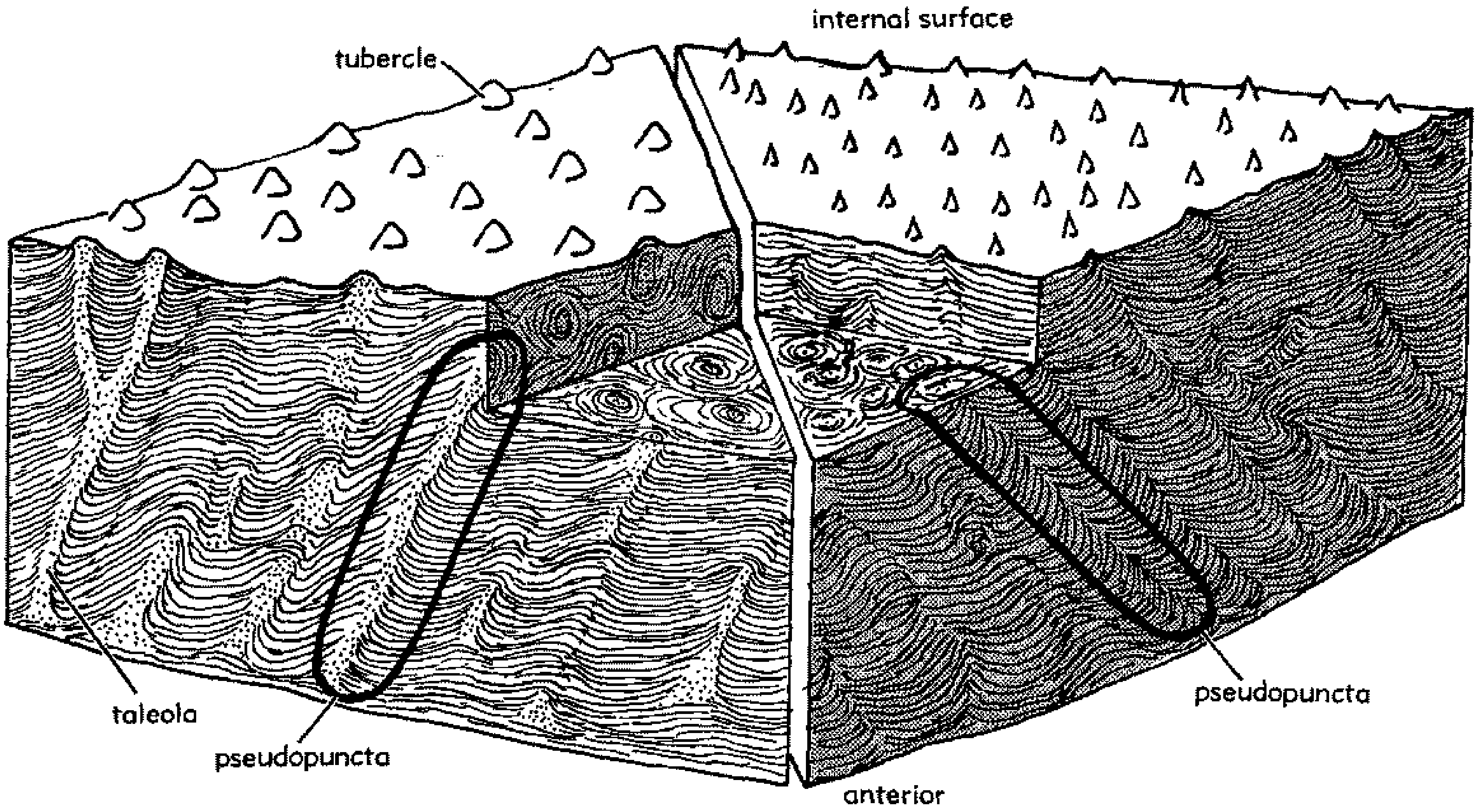

FIG. 73. Idealized sections of strophomenoid shell showing disposition and structure of pseudopunctae (65).

an identifiable primary layer is found, especially in the vicinity and along some of the external spines (see Fig. 88). It is significant that such spines occur in juxtaposition with others lacking any differentiation of an outer calcareous layer and that, unlike the terebratuloid primary layer, it is distinguishable from the underlying fibers, with which it is parallel, only in being uniformly thicker. Its differentiation, therefore, might have taken place in the productoids independently of other articulate brachiopods and even to a variable degree in different stocks because VEEVERS (52, 53) has reported its presence on both valves of *Productella* and on only the pedicle valve of *Avonia.*

Pseudopunctation has been described in a number of conflicting ways, due mainly to either imperfect preservation and inadequate preparation of thin sections purporting to show its structure, or a too limited survey of the stocks that are characterized by this condition. It has been interpreted as a form of endopunctation modified by a calcification of caecal outgrowths from the mantle (46); a series of conical puckerings of the inner shell layers (45, 48); and tubercles built up around rods of calcite (taleolae) (28, 57). Irrespective of origin, the fibers contributing to the formation of all pseudopunctae are buckled into a series of superimposed cones and are commonly obtusely and acutely deflected along the respective posterior and anterior surfaces of the cones. The pseudopunctae are consequently markedly asymmetrical in longitudinal section with their apices directed inwardly and anteriorly to protrude from the internal surfaces of both valves as tubercles (Fig. 73). Among certain strophomenaceans (like *Strophomena*), gonambonitaceans, and many davidsoniaceans (*Derbyia*), the pseudopunctae are composed solely of fibrous cones one within another; but in leptaenids, stropheodontids, productoids, and chonetoids, taleolae, as cleaved rods of granular calcite surrounded by deflected fibers, occupy the axial regions of pseudopunctae. The taleolae almost invariably occur singly and extend continuously throughout the pseudopunctae, although they are known to bifurcate in *Leptagonia* and may be superficially indented at their tuberculate ends, as in some leptaenids and stropheodontids. There is, however, no conclusive evidence that the axes of taleolae were ever occupied by epithelial extensions from the mantle in the manner of caeca. Clay minerals have rarely been identified within taleolae of *Leptaena* (46), but their presence is more likely to reflect an accident of preservation than any deep invagination of the mantle. Indeed, the reflexed attitude

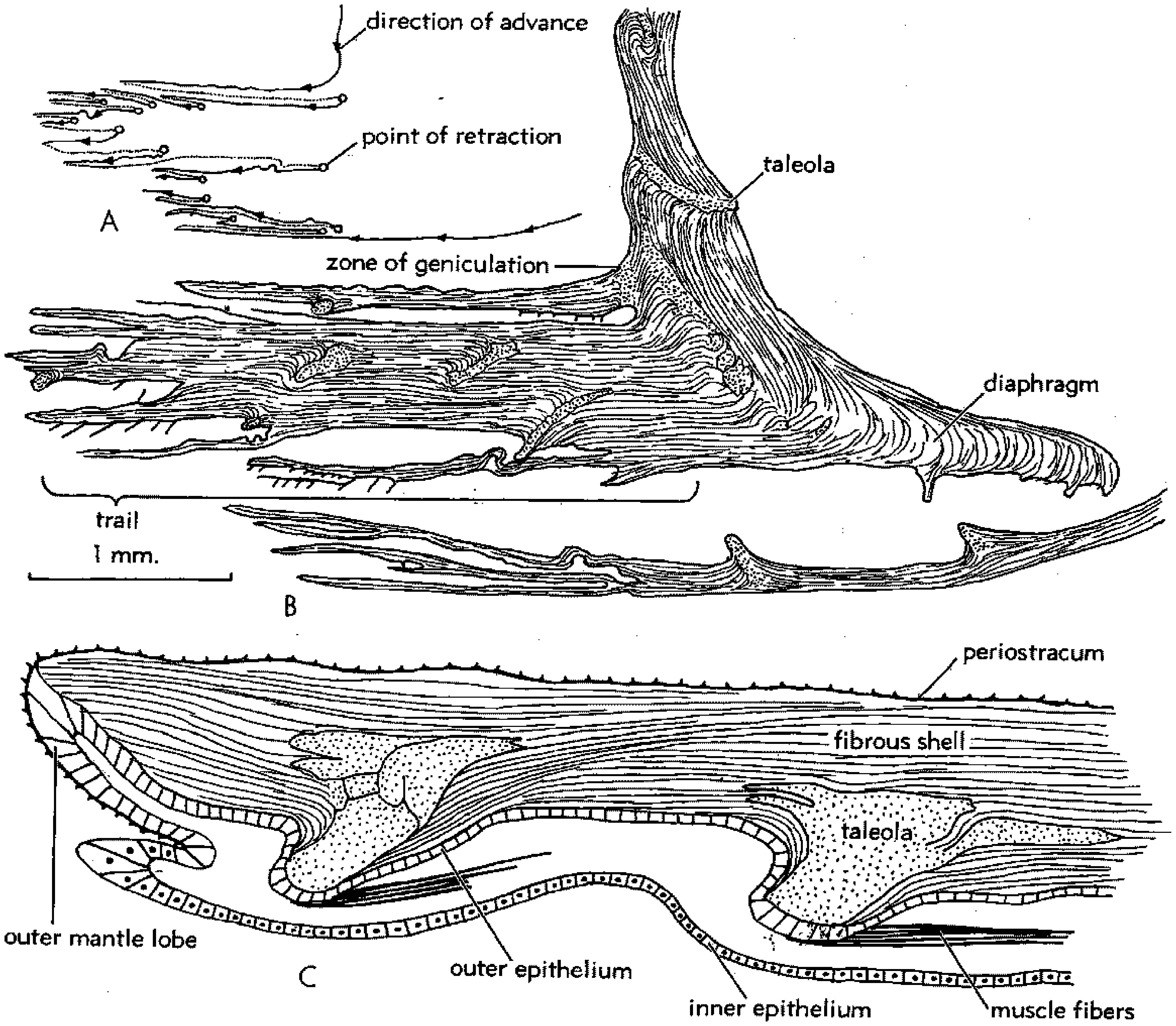

FIG. 74. Stylized sections through trail of *Leptaena* sp., U.Sil., USA, showing *(A)* inferred path of migration for mantle edge, *(B)* detail of mantle edge, and *(C)* inferred relationship between shell and mantle (65).

of the surrounding fibers are proof that the tubercles were contained in evaginated cups of outer epithelium and the only indication of endopunctation among the strophomenoids is found in *Streptorhynchus* as a series of penetrative canals occupying the axes of outwardly directed fibrous cones (48).

Clearly a close relationship exists between pseudopunctae with taleolae and those lacking them, for the presence of taleolae must ultimately have depended upon subtle histological differences within the outer epithelium. The taleolae are comparable in texture with both the terebratuloid primary layer and the areas of muscle attachment in strophomenoids, so that their growth was probably controlled by small islands, each of a few cells of either columnar epithelium or epithelium associated with tonofibrils, within the main spread of cuboidal epithelium responsible for the secretion of the rest of the shell. Sections of the trail of *Leptaena* show that they arose early but behind the inferred position of the outer mantle lobe (Fig. 74). They are, therefore, unlikely to represent imperfectly developed primary shell secreted by persistent patches of columnar epithelium that survived from the tip of the outer mantle lobe, and were more probably the seats of tendonous attachments. This interpretation is consistent with the fact that the mantle edges must have been greatly retractable in many pseudopunctate brachiopods, although, as can be seen in *Leptaena*, incipiently developed pseudopunctae at least were not necessarily permanent sites for tendons.

Pseudopunctae without taleolae are less specialized than those possessing them, since only evaginations of an otherwise undiffer-

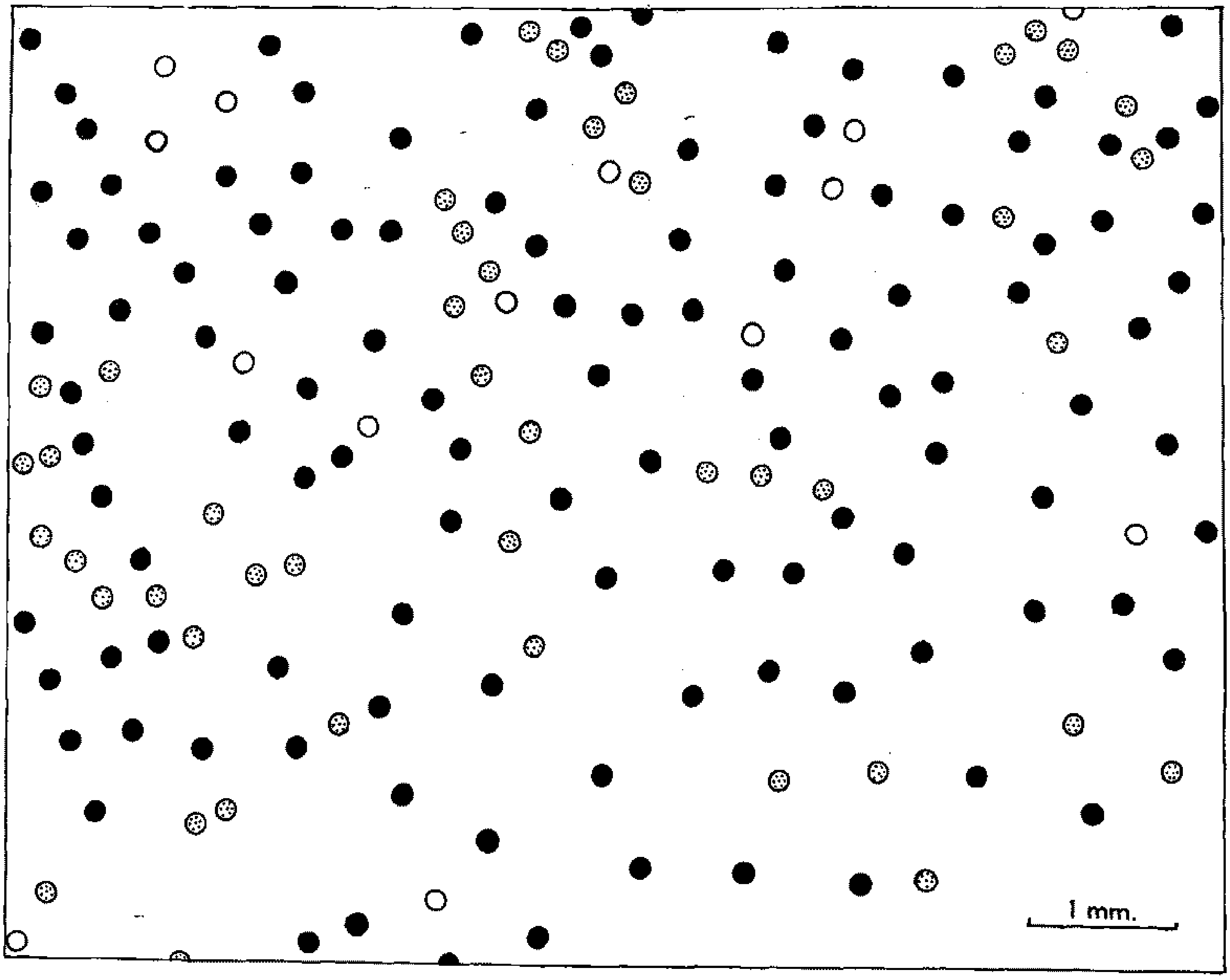

FIG. 75. Distribution of pseudopunctae within small portion of shell of brachial valve of *Rafinesquina nasuta* (CONRAD), U.Ord., USA (solid black circles representing persistent pseudopunctae, open circles impersistent pseudopunctae originating just within external shell surface, and dotted circles impersistent pseudopunctae originating well within secondary shell), prepared from tangential serial sections (65).

entiated cuboidal epithelium were necessary for growth of taleola-lacking pseudopunctae, which possibly supported too few mantle fibrils to promote the secretion of taleolae. It is likely, however, that both types of pseudopunctae are closely related and that taleolae were a later development; they are unknown in certain primitive stocks like the gonambonitaceans, stophomenids, and some of the early davidsoniaceans that must have descended from the impunctate *Fardenia* stocks. It is difficult to judge if both types occur together in the same shell because the disposition and impersistence of pseudopunctae with taleolae are such that random cuts of the pseudopunctae will be present in any section of the shell and will include lateral, tangential, and transverse portions of the reflected fibers simulating pseudopunctae without taleolae. For the same reason, sections normally show pseudopunctae affecting only parts of the shell, as well as extending throughout the entire inner layer, giving an impression that the pseudopunctae are more commonly impersistent and that they arose anywhere during the growth of the shell (Fig. 73). It can be demonstrated, however, that the majority of pseudopunctae originated near the mantle edge and persisted throughout the growth of the shell (Fig. 75).

Traces of repair are found on the exterior of many brachiopod shells, and include especially those carried out subsequent to the malfunction or damage of the mantle edge. The commonest manifestation consists of a semiconical depression of the shell surface with a steep base more or less coincident with a growth line and a shallowing apex directed anteriorly (Fig. 76,*C*). It resulted from a localized and abrupt inward sag of the mantle edge and its gradual

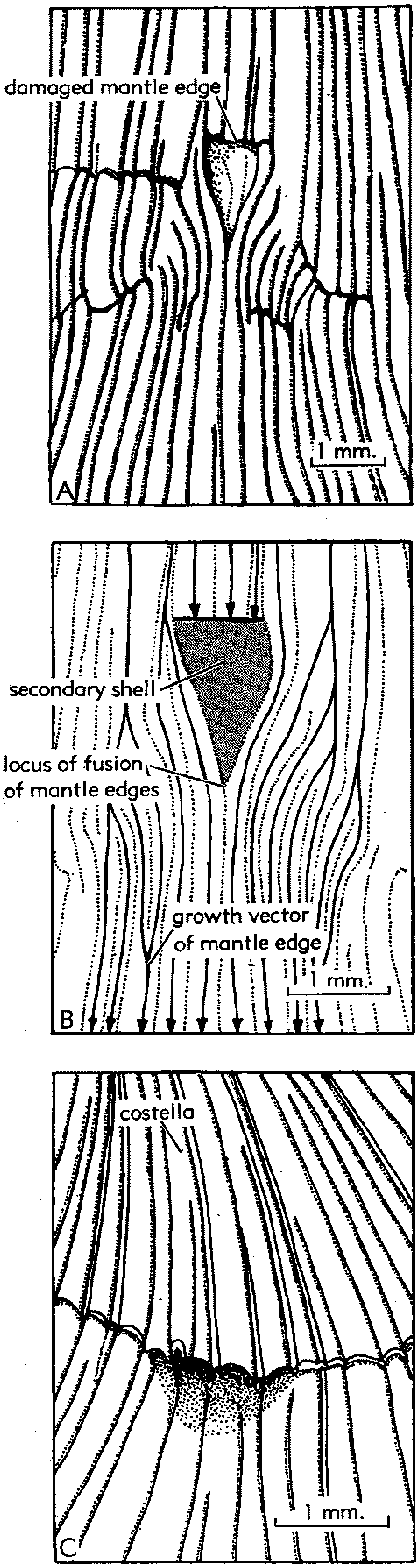

Fig. 76. Shell repair in *Rafinesquina nasuta* (Conrad), U.Ord., USA, showing *(A)* inferred relationships of area of repair with *(B)* undamaged growing mantle edges and *(C)* shell-repair following sag of mantle edge in *Rhipidomella* sp., U.Sil., USA (65).

elimination during the continued forward growth of the mantle edge. More spectacular malformations arose during temporary or permanent damage of the mantle edge and their origin is best understood in relation to the disruption of radial ornamentation in finely costellate shells (Fig. 76,*A*). When injury to part of the mantle edge was sufficiently severe to impede forward growth the space anterior to the zone of damage became constricted and ultimately sealed off by the encroachment and fusion of the flanking unaffected parts which thereby restored a fully functional and continuous mantle edge. Such encroachment involves an abnormal proliferation of tissue towards the area of injury, as is shown by the increased number of costellae given off to converge in that direction (Fig. 76,*B*). Concomitantly, the space immediately in front of the damaged part of the mantle edge became closed by outer epithelium which originated behind the flanking parts of the mantle edges as they moved forward, and was responsible for the deposition of a cover of secondary shell.

No triple stratification closely comparable with that of the articulate shells is known among either the calcareous or phosphatic shells of the inarticulate brachiopods. Intracellular deposition of inorganic shell material is very rare and seemingly occurs only in the Craniidae, and even in this family its secretion is localized, and it does not constitute the entire secondary layer similar to that of the articulates. The structure of the punctate, calcareous shell of the craniids is best known in the Recent *Crania anomala*, but this appears to be typical of the family (Fig. 77,*1*). Two layers may be recognized in the calcareous shell of the brachial valve, although the junction between them may be rather diffuse. Immediately beneath the periostracum is a thin outer layer within which the punctae "branch" arborescently. This layer varies somewhat in thickness and may be absent locally; it is commonly colored pale brown

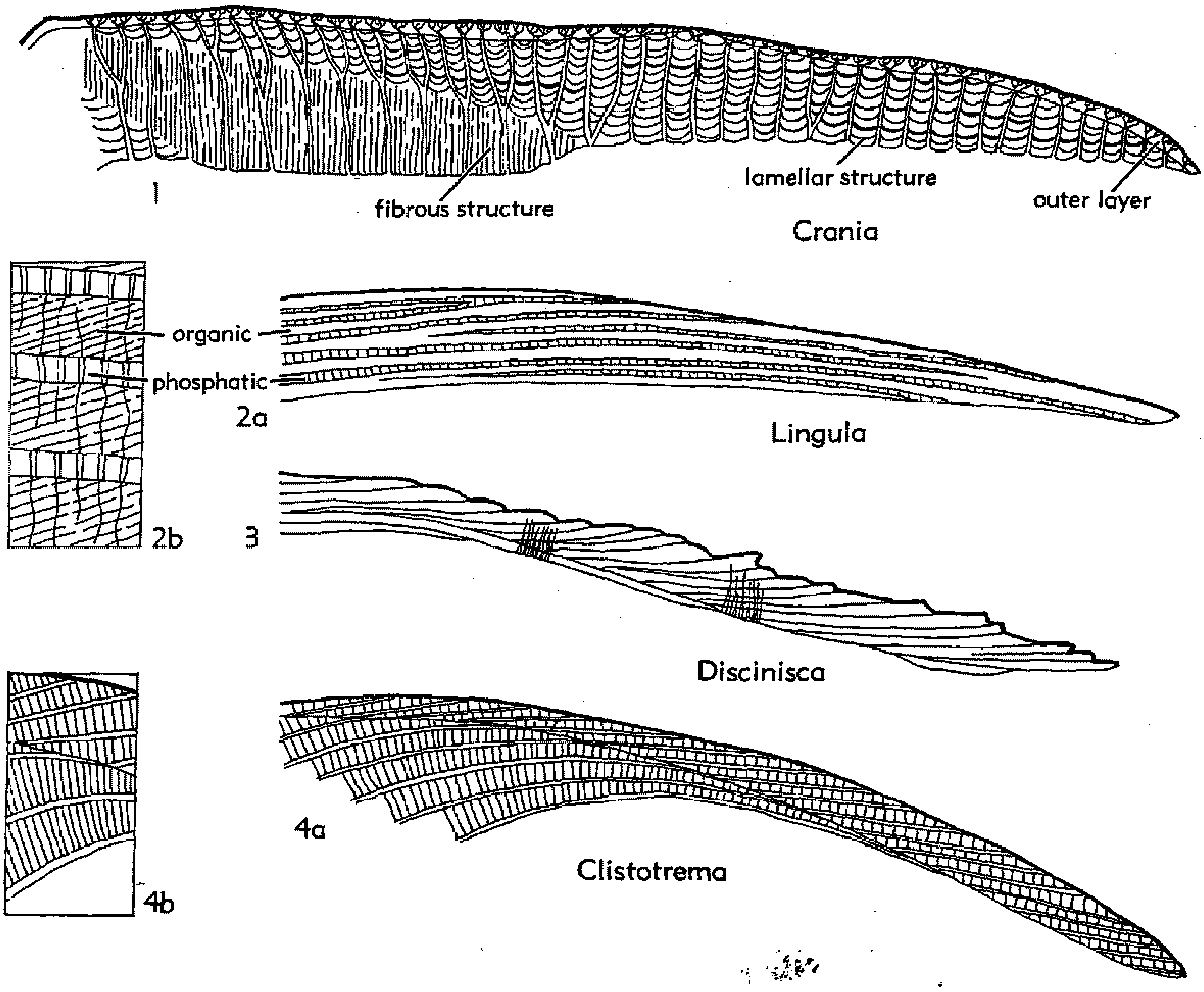

FIG. 77. Stylized thin sections of brachial valves of some inarticulate brachiopods with enlargements showing punctae in organic and phosphatic layers *(2b)* and disposition of fibers *(4b)* (63).

or yellow, but otherwise is relatively clear and apparently structureless. In young shells the calcite crystals forming the layer can be seen to be oriented at a high angle to the shell surface (38). Much of the remainder of the valve, comprising the inner layer, has a characteristically strong lamellar structure. The lamellae are oblique to the shell surface and are commonly thicker peripherally than toward the apex of the valve; they are not plane but are festooned between the punctae, sagging ventrally between adjacent perforations. Under high magnifications what appears to be a fibrous structure of the calcite runs parallel to the lamellae, but the more conspicuous breaks between the calcareous lamellae and also, according to BLOCHMANN (8), many of the finer ones, are formed by membranous sheets of organic material secreted between the calcite. This organic material is seemingly absent in the outer calcareous layer. A further complication of the shell structure is associated with the site of attachment of the muscles, where the tonofibrils secrete fibrous calcite intracellularly (12). These patches of fibrous calcite, which are more sparsely punctate than the remainder of the valve, radiate obliquely outward and ventrally from the apex, marking the track of the muscle scars during progressive growth of the animal. The fibers, in contrast with those of the secondary layer of the articulate shell, are disposed approximately normal to the inner surface of the valve. The structure of the pedicle valve, which is commonly thinner, is basically similar to that of the brachial. In *Crania anomala* the most conspicuous differences between the two are the relatively poor development of the inner lamellar layer of the pedicle valve in addition to the reduced density of punctae, which rarely branch.

The complex craniid shell structure is

clearly a reflection of the varied physiological behavior of the outer epithelium. The cells of the mantle margin secrete only calcite and produce the thin outer layer. With increasing growth of the animal these cells move away from the periphery to occupy a more internal position and there develop a more complex secretory behavior, for the extracellular deposition of calcite of the outer epithelium (with exception of the peripheral zone) is commonly interrupted by the secretion of thin membranous sheets of organic material found in the inner layer of the shell. Thus, these cells are capable of secreting alternately either calcite or organic material. The continuity and disposition of these organic membranous sheets suggest that they are the simultaneous response of part of the outer epithelium to some physiological requirement of the animal. Superimposed upon this pattern is the additional modification of secretory behavior produced when normal outer epithelial cells acquire a tonofibril structure as they become associated with the muscle bases. The tonofibrils secrete calcite intracellularly, but they do not continuously alternate between the deposition of calcite and organic material, for in this part of the shell the organic lamellae are absent and organic material is restricted to what are presumably greatly extended cell walls bounding the fibrous prisms of calcite.

The shell structure of other calcareous-shelled inarticulate brachiopods, which are all impunctate, is not known in as much detail as the craniids, recrystallization proving a common obstacle, particularly in the Cambrian obolellids. The calcareous shell of the craniopsids, trimerellids and obolellids shows no trace of intracellularly secreted fibrous material, and similarly no thin outer layer deposited by peripherally placed cells and comparable with the craniid outer shell layer has been detected. All these shells show a crude layering, the lamellae making an oblique angle with the outer shell surface. It is probable that the calcite was secreted extracellularly, but it is not known whether the break between lamellae represents a small hiatus in secretion of calcite or whether, in life, it was occupied by a thin organic sheet homologous with those found in the craniid shell.

All Recent phosphatic inarticulate brachiopods have a shell consisting of a number of lamellae which are particularly conspicuous in the lingulids, where they are emphasized by their alternating composition (26). In *Lingula* itself, the lamellae are disposed subparallel with the surface of the valves, the phosphatic bands being commonly relatively thick in part of the shell covering the body cavity and thinning out laterally and anteriorly (Fig. 77,*2*). These phosphatic lamellae were described by GRATIOLET (26) as consisting of short prisms set normal to the shell surface, but this has not been confirmed, and it is possible that he confused some of the punctae with a prismatic structure. Each organic band itself consists of extremely fine lamellae sloping obliquely forward from the inside to the external side of the valve. The disposition of the phosphatic and organic bands relative to the outer surface of the valve and the outer epithelium which secretes them shows that although the adult shell consists of a large number of lamellae, only a few are being actively secreted at any particular stage in the growth of the animal (Fig. 77,*2*). The outer epithelium is divided into a number of zones which are arranged roughly subparallel with the margin of the valve, zones which secrete phosphatic material being interspaced between those which deposit organic matter. The position of these zones relative to the valve margin is not constant during growth, for the detailed structure of the shell shows that they have a tendency to migrate outward away from the body cavity toward the edge of the shell, and the outer epithelium at any point must alternate in its ability to secrete phosphatic and organic material.

The shell of *Discinisca* differs from that of *Lingula* both in the distribution of the organic material and in details of the shell structure (Fig. 77,*3*). Beneath the periostracum of *Discinisca* the shell is of uniform composition, the phosphatic material being dispersed in an organic groundmass (9). The shell is composed of a large number of lamellae, distribution of which tends to divide it rather crudely into two layers. The outer layer consists of oblique lamellae which crop out on the outer surface of the valve and are stacked one above the other, so that in section they resemble tiles on a roof. In the brachial valve, the lamellae are commonly thickest submarginally, thinning and usually dying out before the apex is reached. They are commonly secreted by only the marginally placed cells of the outer epithelium, but in some the majority of the outer surface of the mantle is involved. Their orientation suggests that, in contrast to the lingulids, significant increase in the size of the shell is invariably accompanied by the secretion of new lamellae in this layer. Although the more apically placed cells of the outer epithelium may be involved in the secretion of the lamellae of the outer layer of the shell, more commonly

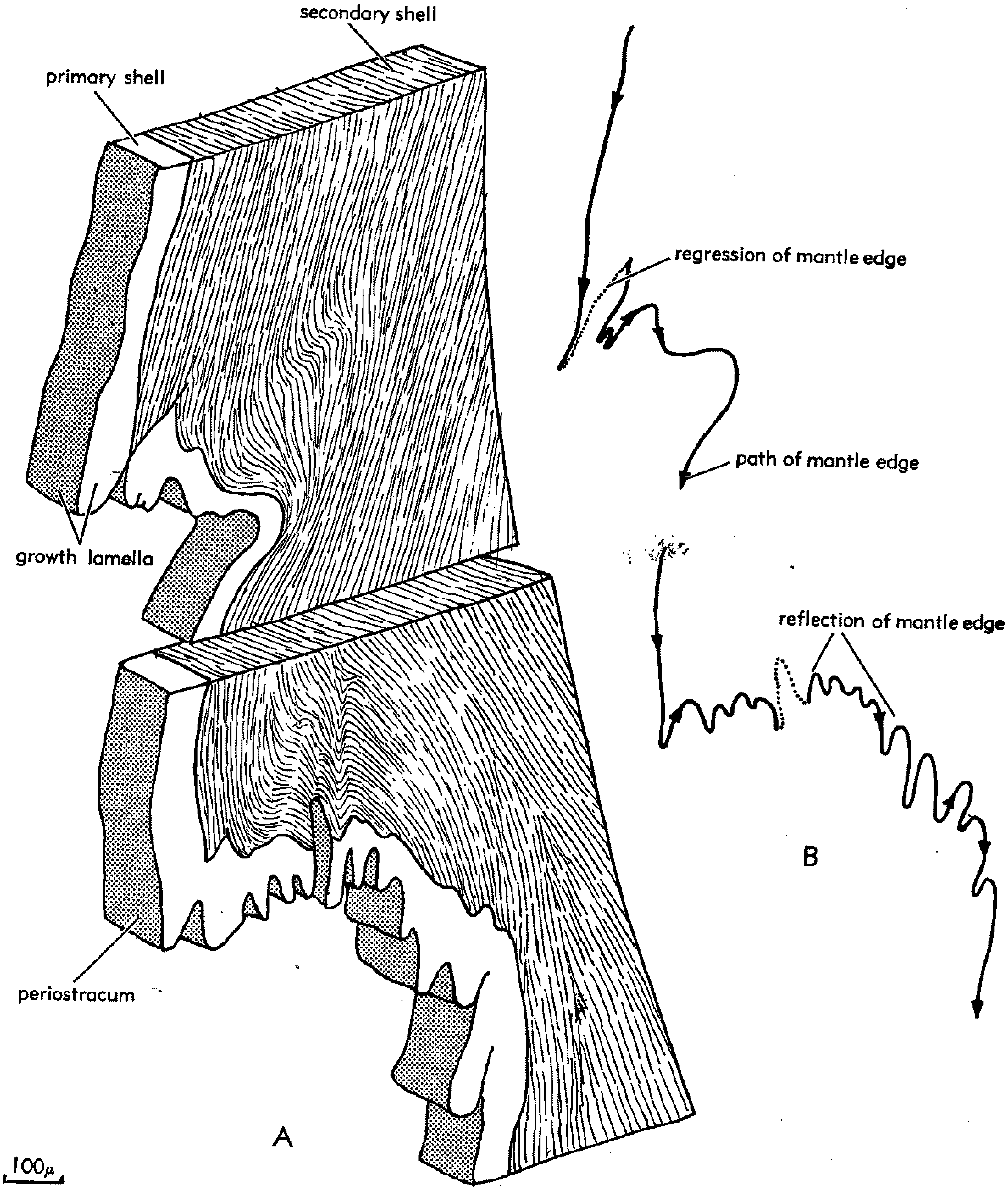

Fig. 78. Structure of portion of brachial valve of *Notosaria nigricans* (Sowerby) showing *(A)* nature of lamellae and *(B)* inferred path of mantle edge responsible for the deposition of portion illustrated in *A* (65).

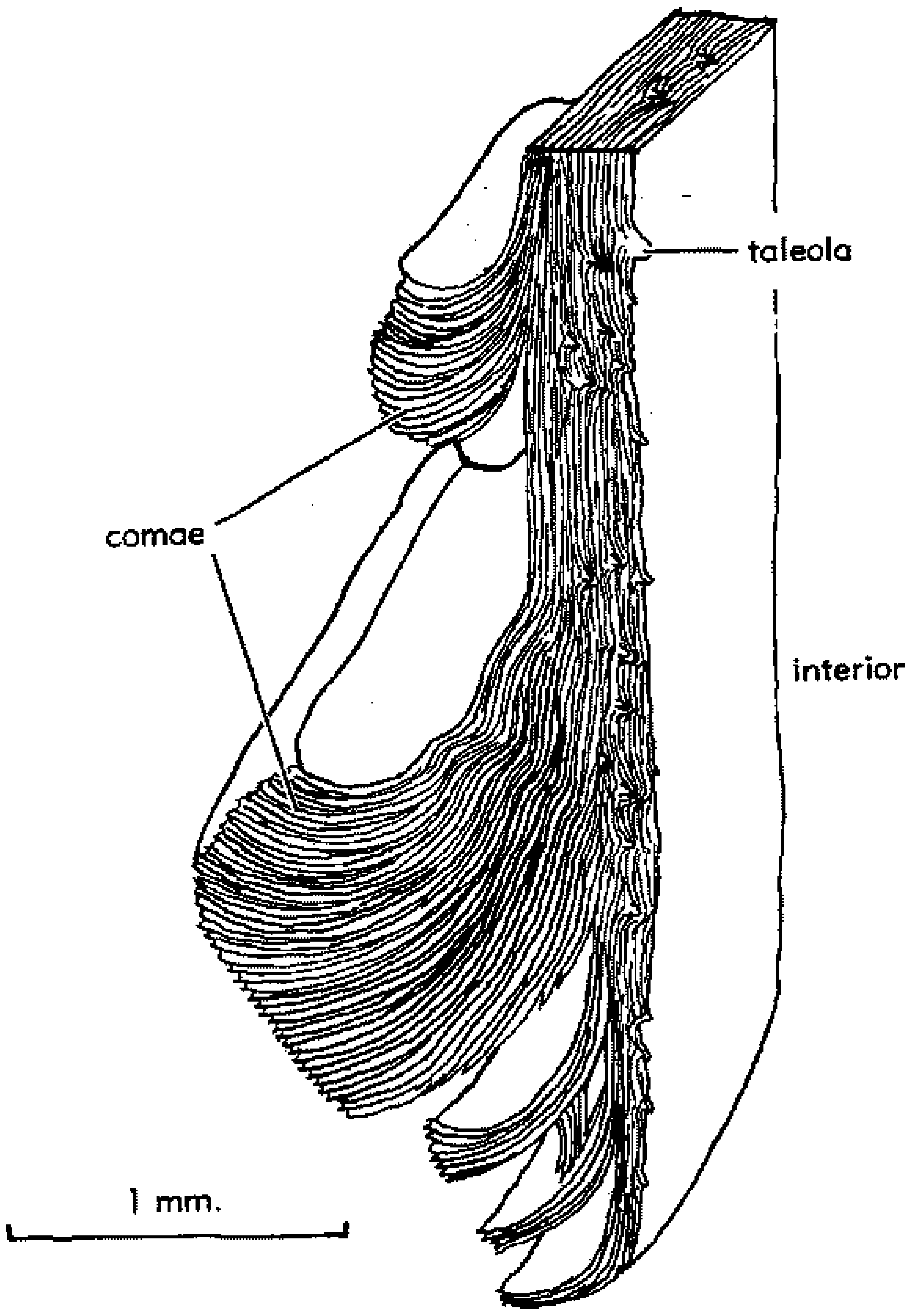

FIG. 79. Stylized section through brachial valve of *Bimuria* sp. cf. *B. buttsi* COOPER, M.Ord., Scot. (65).

they deposit lamellae subparallel with the inner surface of the valve which overstep the previously formed lamellae of the outer layer and form an inner shell layer.

The shell structure of fossil phosphatic-shelled inarticulate brachiopods is known for only a limited number of genera. The lingulaceans, with exception of the calcareous-shelled craniopsids, apparently have a shell structure closely resembling that of living *Lingula* and *Glottidia*. Similarly the shell structure of *Disciniscà* appears to be typical of the discinaceans.

In the acrotretid shell the distribution of lamellae shows some similarity with the discinid pattern; an outer layer which consists of relatively short lamellae strongly oblique to the shell surface and secreted by only the periphery of the mantle and an inner layer secreted subsequently by the remainder of the outer epithelium (Fig. 77, *4*). Although the shell is now seemingly made up mainly of calcium phosphate, both shell layers include two distinctly different types of lamellae which alternate with each other. The thicker lamellae, forming the bulk of the shell, have a strongly fibrous structure, the fibers being arranged normal to the lamellae. The thinner intervening bands lack the conspicuous fibrous structure and may represent material of organic origin that has been phosphatized during diagenesis of the enclosing sediments. The shell structure of the paterinaceans is poorly known. Their valves consist of a number of lamellae disposed subparallel with the shell surface and some specimens show a suggestion of the discinid pattern with the shell divided into two layers by differing orientation of the lamellae.

The punctation of Recent *Crania* is known to be due to the development of caecal evaginations from the outer epithelium (see Fig. 4), and since this condition is typical of all known species of fossil craniids it is probable that the shell was always permeated by branching caeca. It is feasible to assume that projections from the mantle occupied the coarse apertures in the phosphatic meshwork of *Dictyonites*, since no inner shell layer is known, but it is impossible to determine whether these projections were caeca. The extensions of the mantle into the shell of other living inarticulates like *Lingula* and *Discinisca* are extremely fine, and although BLOCHMANN (9) has recorded projections of the mantle epithelium into the shell of *Lingula* it is probable that many of these are cytoplasmic strands, rather than caeca. CHAPMAN (13) has reported the existence of fine perforations within the shell of Silurian lingulids which may have accommodated similar strands. In the lingulids, the punctae are consistently coarser in the phosphatic layers and may be virtually invisible in the organic lamellae of dried shells. The punctae of *Discinisca* are unusual in branching toward the inner surface of the valves (9).

The external surfaces of the protegulum are smooth, but a variety of distinctive features, usually arranged concentrically and radially, may develop during postlarval growth and are referred to as ornamentation. In many species the shells remain smooth except for the sporadic occurrence of concentric lines which are commonly more conspicuous and more closely spaced toward the periphery of gerontic specimens. These are known as **growth lines**, although they do in fact represent periods of shell

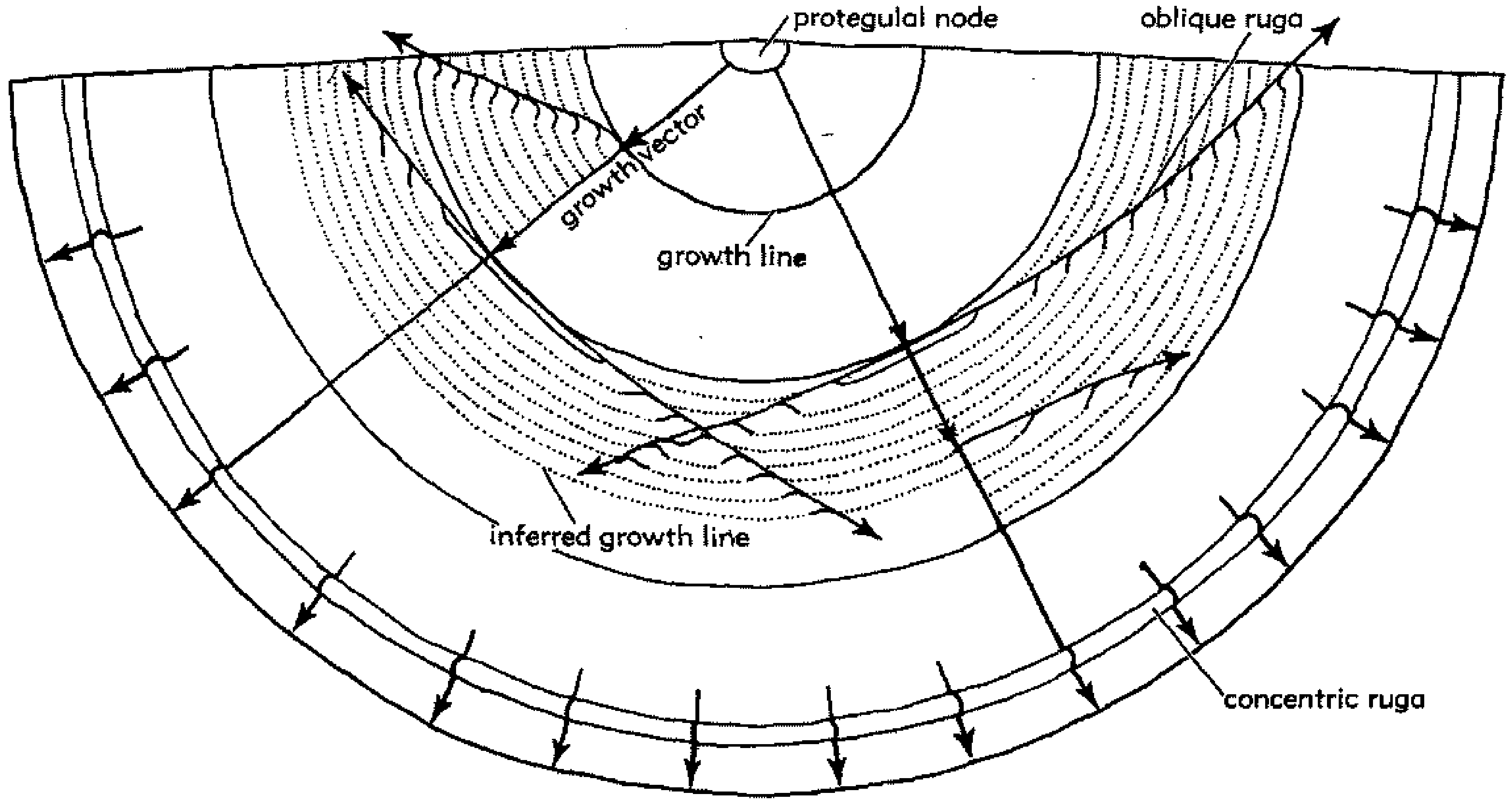

Fig. 80. Diagrammatic illustration of nature and origin of oblique and concentric rugae (65).

deposition when forward growth was in abeyance, so that their occurrence is controlled by environmental factors such as temperature (Fig. 59). Regularly spaced concentric outgrowths (lamellose or imbricate condition) which may be made up of secondary as well as primary shell are also characteristic of many genera (Fig. 78). These lamellose extensions may also be prolonged as spines (e.g., *Tegulorhynchia*) or may be so thickened as to form knobby protuberances (comae) that give the shell a gnarled appearance (e.g., *Bimuria*) (Fig. 79). Irrespective of the unusualness of these various features, however, they were all covered by adherent periostracum and deposited by a retractible mantle edge involved in a gradual retreat when the primary layer is doubled back or reflected upon itself or in a sudden regression when no duplication of primary shell is evident. The growth of lamellose skirts in several inarticulate genera was probably controlled by similar contractions of the mantle margins.

Another form of oblique or concentric ornamentation is the wrinkling of the shell surface (rugation) which is especially characteristic of the strophomenoids, productoids, and chonetoids but is also known rarely in other groups (e.g., *Kulumbella, Iru*). The **rugae** may be continuous and concentric, as in *Leptaena*, where they are precursory to formation of the trail, which may be regarded, in that genus, as an indefinite continuation of the anterior face of the last-formed ruga; or impersistent and oblique, like those of *Sowerbyella* (Fig. 80). Rarely, as in *Ptychoglyptus*, the rugae are concentrically disposed but so interrupted at their junctions with the more accentuated elements of radial ornamentation that they are broken up into a series of chevron-like or oblique strips. Exceptionally also, two or more sets of oblique rugae may develop, intersecting at obtuse or acute angles (e.g., *Bellimurina, Kulumbella*).

Rugae were formed by a deflection of the mantle edge through an arc of 180 degrees along an axis which was disposed in any direction except that of the radial vector relative to the mantle periphery (deflections normal to the mantle margin giving rise to radially disposed features like ribs, folds, etc.). The concentric arrangement of *Leptaena* was the simplest condition in that it involved a simultaneous deflection of the growing mantle edges along the entire commissure anterior to the hinge line. An obliquely disposed ruga arose through a localized deflection of the mantle edges at any point along the margins and during subsequent growth the deflection was transmitted laterally either in one or both directions along an axis traced out by the rugae in a full-grown shell. In this manner two

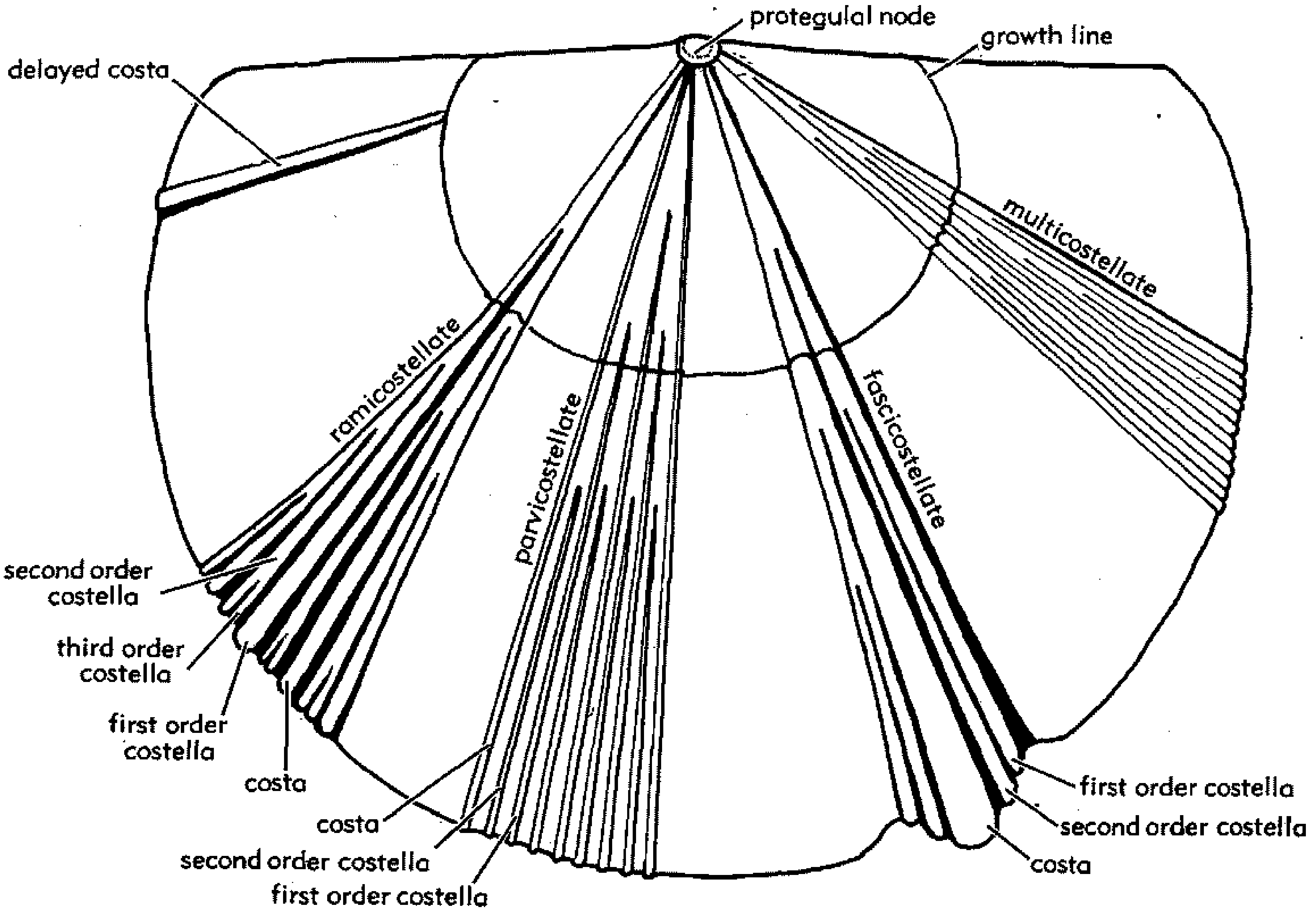

FIG. 81. Diagrammatic illustration of more important types of brachiopod radial ornamentation (65).

or more sets of rugae may have developed a complicated pattern of intersections (Fig. 80).

The raised concentric ridges or threadlike lines (**fila**) ornamenting the valves of some inarticulates, like *Schizotreta* and *Rhysotreta*, must have formed in the manner of small scale rugae by the periodic deflection of part or all of the mantle edge into a wave.

All radial ornamentation (**ribs**) is due to a persistent or impersistent deflection of the mantle edges along vectors radiating from the protegulal nodes, so that every variety in size and shape can be found (Fig. 81). The basic element is a well-defined elevation of the shell surface, triangular to rounded in transverse section and of variable amplitude and wave length, which arises at the protegulal node and almost invariably extends to the margins of adult shells. Such a feature is known as a **costa**, whereas a **costella**, which may be of comparable thickness and shape, does not arise at the margin of the brephic shell but by branching from or intercalation between costae at any stage during subsequent growth. Defined in this way according to the point of origin of the features, the terms have a different meaning from that understood by many students who have used them in a necessarily arbitrary manner to imply a relative coarseness in texture, which is better expressed as a frequency count for a standard arc at a stipulated distance from the beak. In a few species (e.g., triplesiaceans, rhynchonelloids, etc.), the radial ornamentation may first appear along an arc of growth well beyond the protegulal node and it is suggested that this pattern be called delayed costation or delayed costellation if first or higher orders of costellae are involved. Certain brachiopods, especially the strophomenoids, are characterized by a finely textured ornamentation consisting of costae and several orders of costellae, all of which arise by intercalation. This pattern is usually referred to as **parvicostellate** (as opposed to **ramicostellate,** which implies an origin solely by branching, as in most orthoids); and when the costae and certain costellae are accentuated to segregate the ornamentation into a series of sectors, the condition is referred to as unequally parvicostellate. When the costellate and rami-

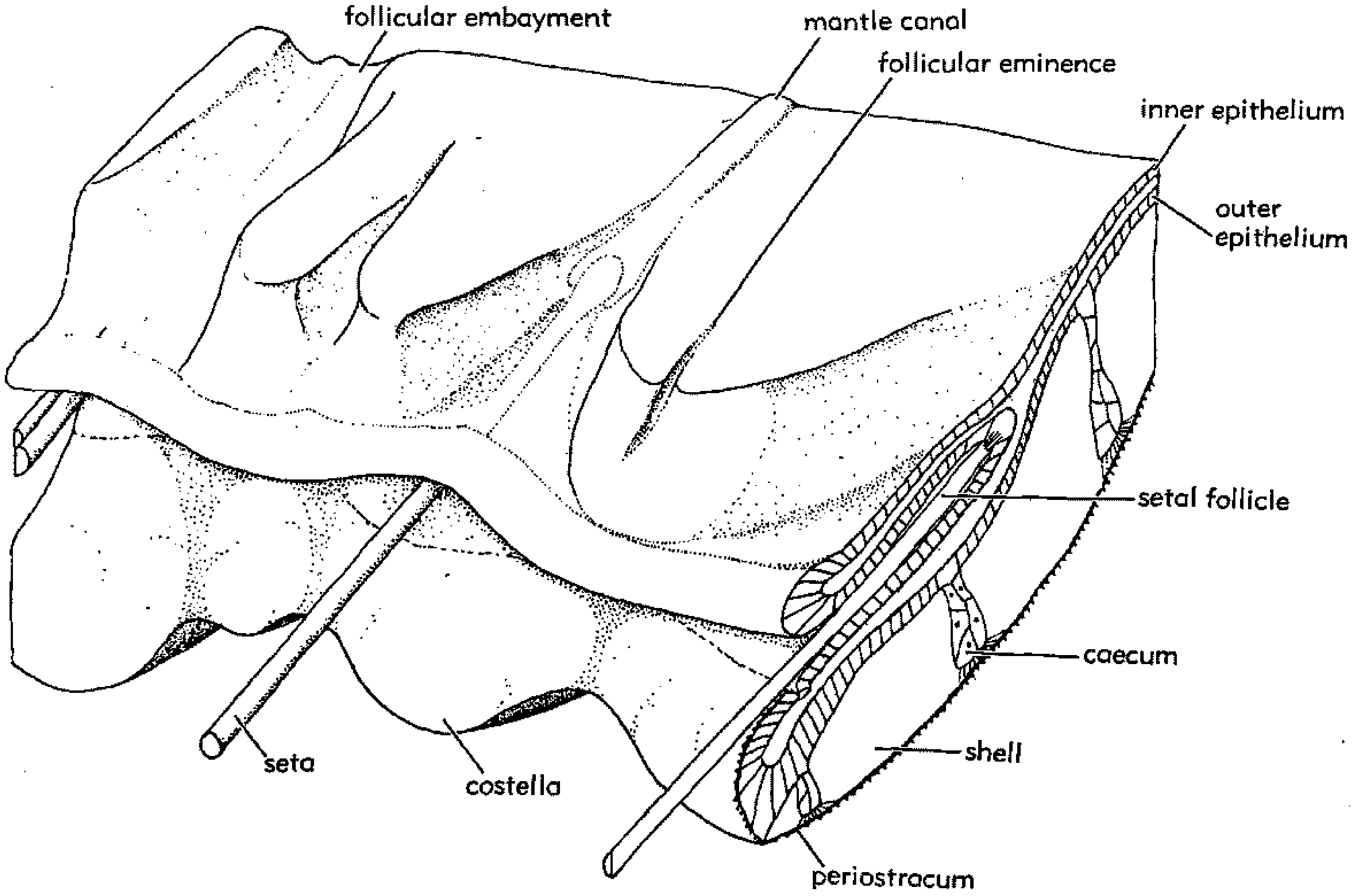

FIG. 82. Inferred relationships between mantle edge and shell margin in typical enteletacean (65).

costellate patterns are so evenly divided as to give an appearance of a uniformly fine ornamentation they are referred to as **multicostellate** (e.g., *Schizophoria*), whereas the segregation of these patterns into conspicuous bundles is called **fascicostellation** (e.g., *Fascicostella*).

The costellate radial ornamentation of some extinct brachiopods is probably related to the distribution of setae along the mantle edge in the style characteristic of Recent *Terebratulina* (compare Fig. 82). Along the edge of the *Terebratulina* valve, the secondary shell layer is not uniformly distributed, for it is indented by a series of V-shaped embayments, underlying the crests of fully formed ribs and pointing posteriorly. Each embayment accommodates a follicle containing one or two setae or, very rarely, two follicles separated by a narrow ridge. The interspace of two adjacent ribs mutually coincides with a V-shaped eminence on the internal surface of the valve, pointing anteriorly but ending abruptly just inside the zone of the valve edge which is occupied by the mantle lobes. As the shell grows, each eminence develops a slight median furrow which begins to widen and deepen into an embayment, later to be occupied by a new follicle. Fully developed follicles appear relatively suddenly along the mantle edges of dissected specimens, but it is likely that they are first differentiated within the mantle groove when the eminence, corresponding to the intercostellate spaces on the outer surface, is first indented by a median furrow, that is just before a new costella, containing the developing embayment, branches off from its parent (61). When the *Terebratulina* shell is closed, the crenulated commissures of the valves interlock in such a way that the eminences of one valve fit into the embayments of the other valve. The edges of both valves, corresponding to the zone of the mantle lobes, remain slightly parted and parallel to each other and thus facilitate the continuous deposition of the shell, as well as the movements of the setae which protrude between each costella and the complementary eminence of the other valve.

The setal arrangement in *Terebratulina* with its well-developed incostellate spaces is quite distinct from that of *Hemithiris*,

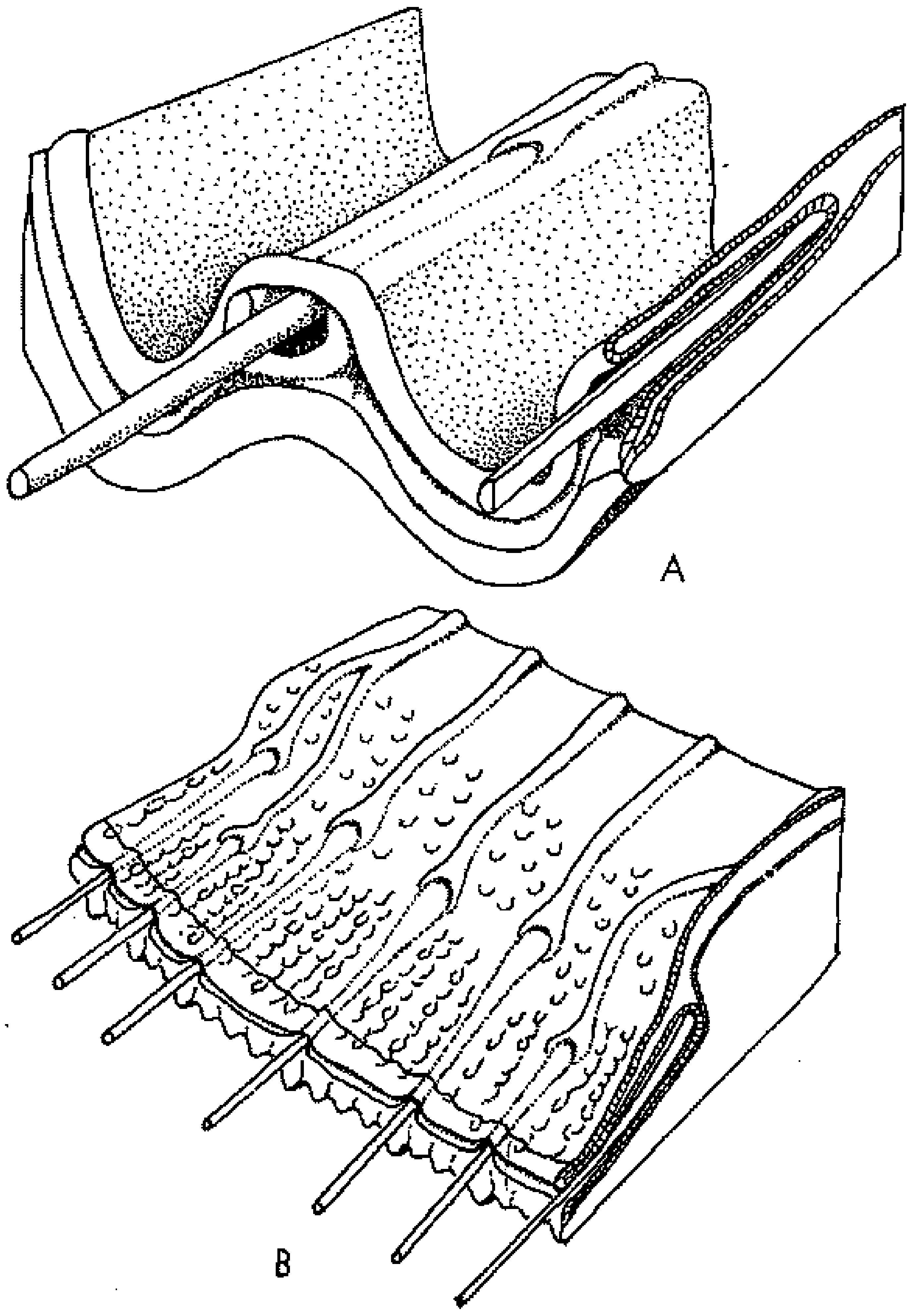

FIG. 83. Inferred relationships between mantle edge and shell margin in *Hesperorthis (A)* and *Sowerbyella (B)* (65).

which is ornamented by low-rounded ribs separated by linear interspaces. In the latter genus the follicles occur at regular intervals along the mantle edge, irrespective of external ornamentation, and apart from a marginal occurrence of slight ridges corresponding with the interspaces there is no differentiation of the internal edges of the shell. This lack of indication of setae on the internal surfaces is also true of smooth shells like *Macandrevia* and of the coarsely costellate *Terebratalia* in which the radial ornamentation may be regarded as a superimposed crenulation of the commissure not affecting the distribution of setae.

The morphology of the inner marginal edge of costellate fossil shells like those of the enteletaceans is so like that of *Terebratulina* that a similar arrangement of setae probably obtained (Fig. 82). A comparable pattern was also characteristic of costate shells (e.g., *Hesperorthis, Plaesiomys, Orthambonites*) (Fig. 83,*A*). In such stocks as these, the costae are represented internally by grooves and the interspaces by V-shaped or bluntly rounded eminences indented by a median furrow which is shallower than the groove but about as long. Judging from comparisons with living brachiopods and the impressions of peripheral branches of the mantle canals on the interiors of fossil shells like *Cyrtonotella* (37), it is feasible to assume that follicles occupied at least the median furrows. The arrangements in other costellate orthoids and cliambonitoids seem to have been more primitive in that no well-differentiated eminences, coincident with the intercostellate spaces, were developed and it seems likely that the follicles occupied short grooves corresponding to the crests of the costellae. The absence of distinct grooving at the inner margins of adult shells of *Atrypa* suggests that as in *Hemithiris,* there was no relationship between the incidence of setae and costellae in fossil species with this style of radial ornamentation. *Enteletes, Meekella,* and other brachiopods with strong costae superimposed upon a finely costellate ornamentation probably possessed a follicle distribution unaffected by the coarser ribbing, as in *Terebratalia.* The parvicostellate ornamentation of the strophomenoids may well have reflected a high density of setae at the shell margin. In *Sowerbyella,* for example, deeply incised, short grooves, each ending posteriorly as a pit in the peripheral rims of secondary shell, occur at regular intervals along the lateral and anterior margins (Fig. 83,*B*). These grooves probably contained follicles. They underlie the crests of all costae and older generations of costellae and are separated from each other by low, flat, rectangular-ended eminences that correspond to as many as 5 or 6 younger costellae. Here and there slight pits and furrows indent the eminences and probably represent the early development of follicular grooves. Thus, at any one stage of growth, setae protruded from beneath about one-quarter of the costellae.

Some rhynchonelloids (e.g., *Sphaerirhynchia*) which are highly globose when adult and which develop a vertical zone formed when anterior and lateral growth is in abeyance show an unusual modification of the anterior and lateral margins of the valves. The interspaces between costae or costellae are elongated to form long, slender marginal spines which lie against the inner surface of the costae or costellae involved in the vertical zone of the opposing valve. Conceivably, these spines had some protective function when the shell was open, as they form a regular grille across the gape (44) (Fig. 84).

The valve margins of Recent setae-bearing inarticulate brachiopods, lingulids, and discinids are smooth, and it is only in the craniids, which lack setae, that modifications of the periphery of the valves occur. In *Crania anomala*, the modifications in the brachial valve are superficially similar to the eminences and furrows of *Terebratulina* but are very much finer and associated with the development of the punctae. A narrow peripheral zone bears numerous, very fine, radially disposed ridges separated by narrow grooves in which the punctae are located. With growth of the shell, the ridges increase in number by bifurcation, but apically they are buried by the later-formed lamellae of the secondary shell layer (Fig. 85). The margin of the pedicle valve of this species, as in many post-Paleozoic craniids, is minutely pustulose, and the punctae are not regularly arranged but are grouped in the depressions of the shell between the pustules (8).

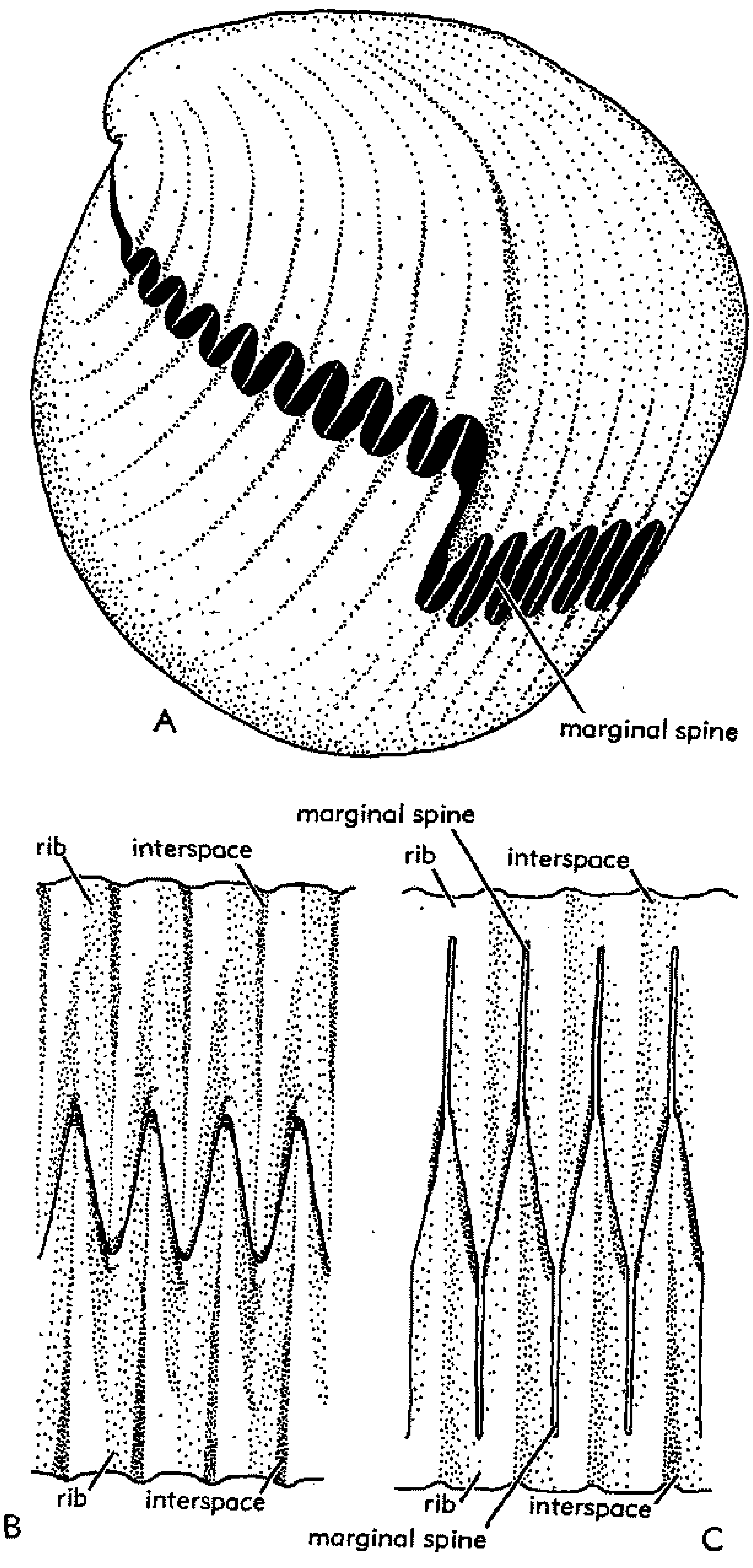

FIG. 84. Marginal spines of *Sphaerirhynchia*; *A*, oblique anterolateral view of open shell showing grille formed by spines; *B*, detail of part of anterior commissure, viewed externally; *C*, detail of part of anterior commissure, viewed internally, showing relation of spines and interspaces (63).

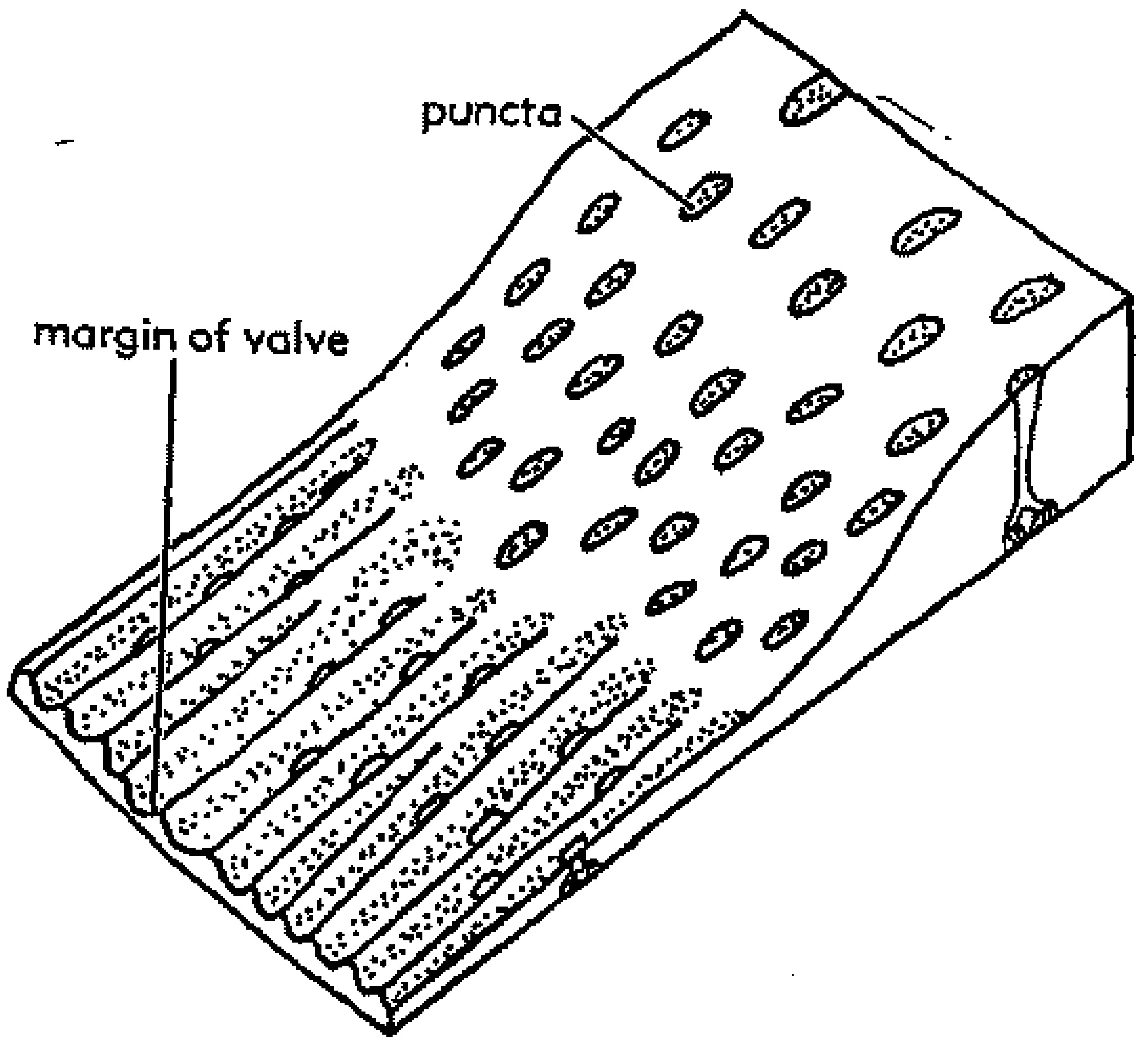

FIG. 85. Small segment of posterior margin of brachial valve of *Crania anomala* viewed internally, punctae initially located in grooves separated by low ridges (63).

The brachiopod shell may also be finely to coarsely ornamented by a series of outgrowths on the inner, as well as the outer, surfaces, generally cylindroid to conical in habit and referred to as granules, tubercles, or spines. In terms of growth, two distinct categories may be recognized. The fine granules of *Platystrophia* and *Lingulasma*, the tear-shaped tubercles of *Spinocyrtia*, and the spines along the ribs of *Dictyothyris* (Fig. 86) represent solid excrescences on the external surface of the valves fashioned out of primary shell at the tip of the outer mantle lobe. The spines of *Tegulorhynchia*, *Spinilingula*, etc., normally represent curved, triangular prolongations of the lamellae, but

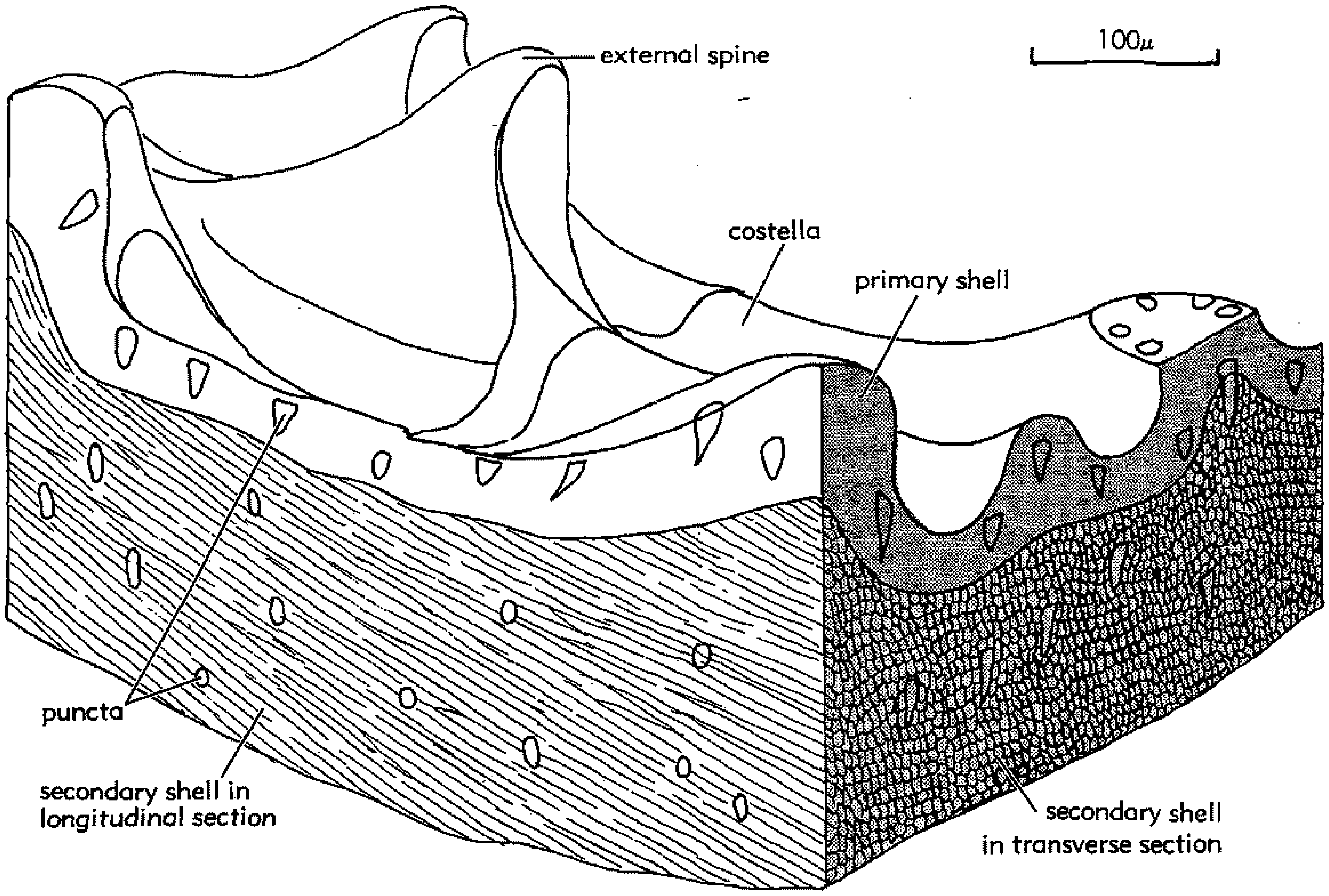

FIG. 86. Section of pedicle valve of *Dictyothyris coarctata* (PARKINSON), M.Jur., Eng., showing relationships of external spines with primary and secondary shell layers (65).

may also develop into hollow cylinders which must have been secreted around retractable epithelial outgrowths from the tips of the outer lobes and which were subsequently sealed off by deposition of the secondary shell layer. The double-barreled spines of *Phricodothyris* were probably formed in the same way by pairs of adjacent epithelial outgrowths (25) (Fig. 87).

The hollow productoid, chonetoid, rhynchonelloid, and siphonotretacean spines that also open into the shell interior were formed in a different way (Fig. 88). Many of these spines must have continued to increase in length throughout life of the animal. But increments could only have been added at the distal ends which must have been occupied by persistent generative tips capable of proliferating outer epithelium to line the lengthening axial canals and thereby maintain the processes of shell secretion (57). Since all spines were first differentiated at the shell margin, it is likely that the tips were actually isolated bits of the outer epithelial lobes that simply retained the generative properties of that part of the mantle. In all probability, continuity of the periostracal layer was maintained by the activity of the apical cells making up these generative tips and it is feasible that, in some spines, these were responsible for the secretion of a chitinous pad by which they became attached to the substratum. These epithelial evaginations were commonly sealed off by later deposition, especially in the body cavity, in which event growth of the spines ceased and the axial canals end blindly within the secondary shell layer.

Striking color patterns are rarely developed in the Brachiopoda. The presence of periostracum usually imparts a brown tinge to shells, but the underlying calcareous or chitinophosphatic material commonly provides the basic colors of the brachiopods. In inarticulate brachiopods, browns, or more rarely, green or cream colors predominate, while among the articulate brachiopods creams to pinks are common, especially among the terebratuloids, although whites and blue grays (e.g., *Hemithiris*) are also known. Original color variations are less certainly diagnosed in fossil groups because even consistently variegated patterns may be related to post-mortem differential stain-

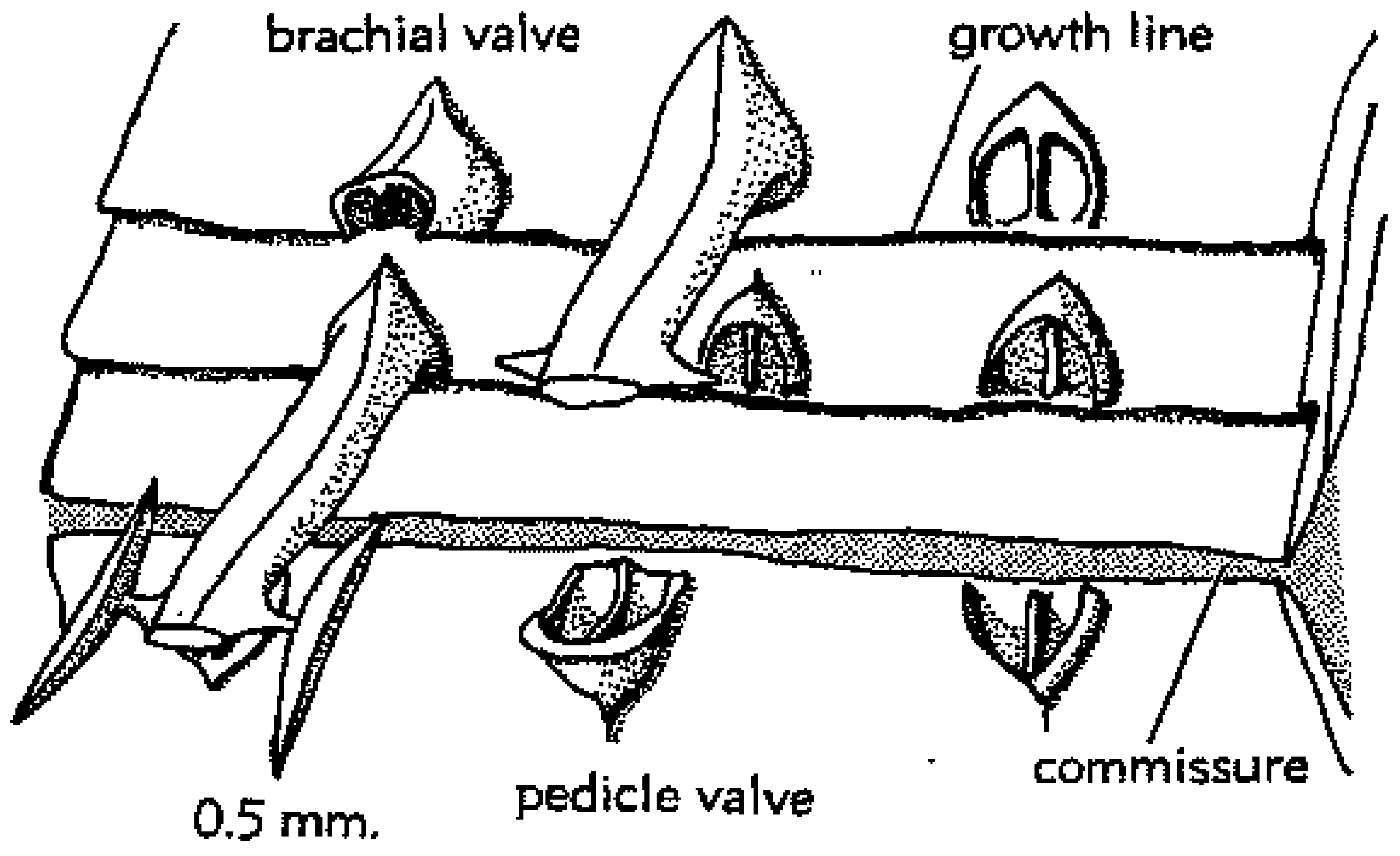

FIG. 87. Double-barreled spines of *Phricodothyris* sp., L.Carb., N.Ire. (65).

ing particularly of punctate shells that were subjected to selective penetration. A small number of species (23), however, show variations in light and dark grays or browns that evidently arose during shell growth. They are first found in Devonian shells and are indeed best known in terebratuloid species of that period. The variations include concentric alternations of light and dark hues as in *Cranaena, Hamburgia,* and *Subrensselandia,* as well as radial alternations and spotted patterns in members of the first two genera (14). CLOUD has remarked that concentric changes could have resulted during phases of slower shell growth involving a relative concentration of color-inducing compounds which are more diffuse in the more quickly growing bands. He also noted that the radial bands of *Cranaena* coincided with the principal canals of the mantle lobes, although this coincidence is not true for the numerous, somewhat irregular, radial bands of *Coenothyris vulgaris* (SCHLOTHEIM).

MODIFICATIONS OF PEDICLE OPENING

The pedicle of young Recent articulate brachiopods protrudes posteriorly through the delthyrial opening, which, during further growth, is generally restricted by the development of lateral **deltidial plates** defining the foramen. The relationship between the unmodified delthyrium and the pedicle-outer epithelial junction has already been discussed, and the growth of coverings to the delthyrium has to be reviewed in this context. The delthyrium is bounded by a pair of progressively divergent ridges representing the continuously growing teeth. That part of the pedicle epithelium initially attached to the apices of both valves

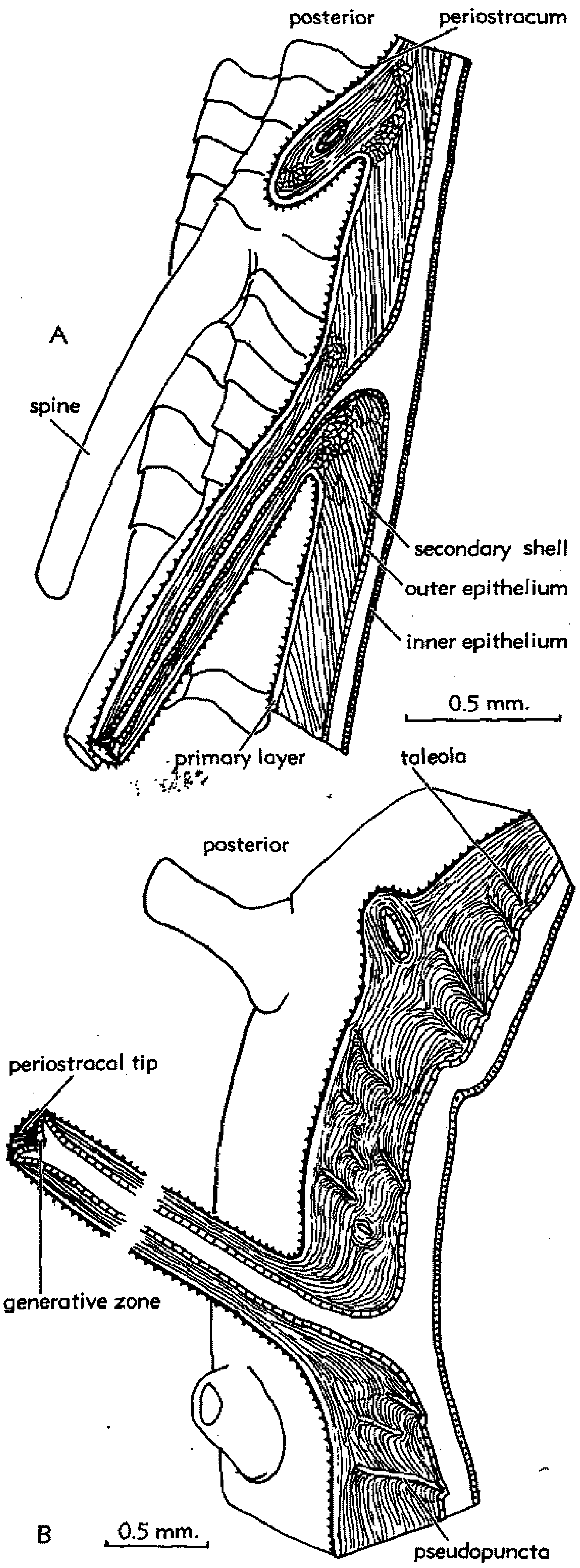

FIG. 88. Reconstructions showing inferred relationships between mantle and shell spines *(A)* in *Acanthothiris spinosa* (LINNÉ), M.Jur., Eng., and *(B)* in *Productella* sp., U.Dev., USA (65).

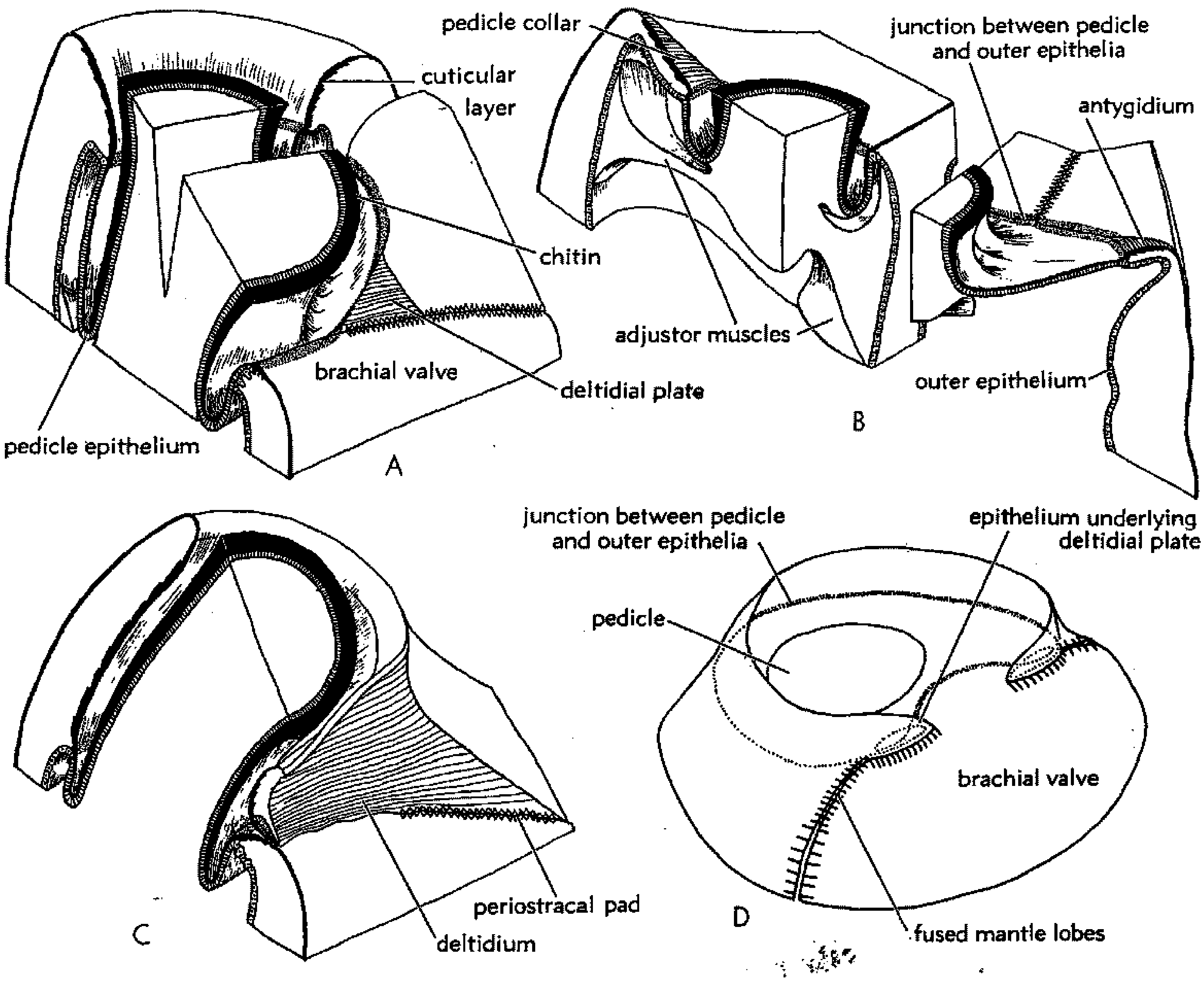

Fig. 89. Relationships between pedicle and shell in *(A) Terebratulina* and *(C) Laqueus*, with *(B)* inferred restoration of them in *Hesperorthis australis* Cooper, M.Ord., USA, and *(D)* diagrammatic representation of course of junction between pedicle and outer epithelia in *Laqueus* prior to fusion of epithelium underlying deltidial plates *(A-C, 57; D, 65)*.

is fixed; but lateral expansion along the posterior margin during the growth of the ventral cardinal area causes the epithelial junction to assume an oval outline, with an increasing proportion of the circumference within the pedicle valve (compare Fig. 89,*D*). It is this widening gap between the diverging teeth ridges and the boundary of the pedicle epithelium which is filled by deltidial plates. The inner surfaces of the deltidial plates are necessarily continuous laterally with the pedicle collar, but the outer surfaces are made up of primary shell. They are therefore deposited by outer lobes of outer epithelium, continuous at least with the ventral part of the fused mantle lobes at the posterior margin (57) and are like a pair of triangular flaps, posterior to the dorsal beak, with their bases expanding toward the median plane. In rostrate brachiopods with the dorsal pedicle zone not projecting beyond the hinge axis (e.g., *Terebratulina*), the plates remain discrete, flanking the dorsal sheet of pedicle epithelium (Fig. 89,*A*). In other living brachiopods, however (e.g., *Magellania, Laqueus*), the growth of the dorsal umbo well into the pedicle valve shifts the dorsal pedicle boundary anteroventrally from the expanding bases of the deltidial plates, which, continuing to grow toward each other, ultimately meet medially to form a single structure (**deltidium**). If the outer epithelial sheets underlying the deltidial plates fuse medially, the line of junction on the deltidium is lost and a **symphytium** results (Fig. 89,*C*). The edge of the pedicle capsule now appears to be restricted to the foramen of the pedicle valve, although a dorsomedian strip of pedicle epithelium is still connected with the posterior edge of the brachial valve (Fig. 89,*D*). The position of the foramen relative to the deltidium and the ventral beak can vary through migration and resorption, and a number of terms are in general use to indicate its location (Fig. 90).

The open delthyrium and its dorsal counterpart, the notothyrium, are typical of the great majority of orthacean, enteletacean, and pentameroid brachiopods, and it is safe to assume that the junction between the pedicle and outer epithelia in such forms as these coincided with the boundaries of the diamond-shaped aperture made up of both notches (Fig. 89,*B*). Some modification did occur. The pedicle collar (pedicle or apical plate) was quite commonly developed by retreat of the ventral edge of the junction, and deltidial plates fusing to form either a deltidium or notodeltidium (16) are known to have developed independently in *Barbarorthis* and *Phragmophora.* The unmodified notothyrial edges acted as attachment surfaces for the pedicle junction in precisely the same way as those of the delthyrium, so that lateral or apical extensions of them (the so-called "chilidial plates" and "chilidium" of *Hesperorthis, Nicolella, Valcourea,* etc.) arose in exactly the same manner as the deltidia. The spiriferoids display a greater variation in delthyrial modification owing to repeated atrophy of the pedicle and the common, extravagant development of the ventral interarea. The sunken delthyrial plate of *Syringospira, Syringothyris,* etc., is the homologue of the elevated pedicle collar of the living terebratulacean *Agulhasia.* In *Syringospira* (Fig. 91), the gap between the delthyrial plate and the brachial valve was closed by the deposition of a series of concentric layers (the largest basal layer overlapping the posterior surface of the delthyrial plate) secreted by the ventral and lateral edges of the outer epithelium of the junction moving posterodorsally. This abnormal structure (stegidium of Cooper, 15) was clearly related to a dorsal migration and ultimate atrophy of the pedicle and a similarly induced condition is known in stocks like *Mucrospirifer* which lacked delthyrial plates. An apically situated, imperforate delthyrial cover is found in some spiriferoids like *Eospirifer* and also rarely in the pentameroids (14) and was deposited by outer epithelium at the ventral edge of a pedicle undergoing atrophy. The delthyrial cover

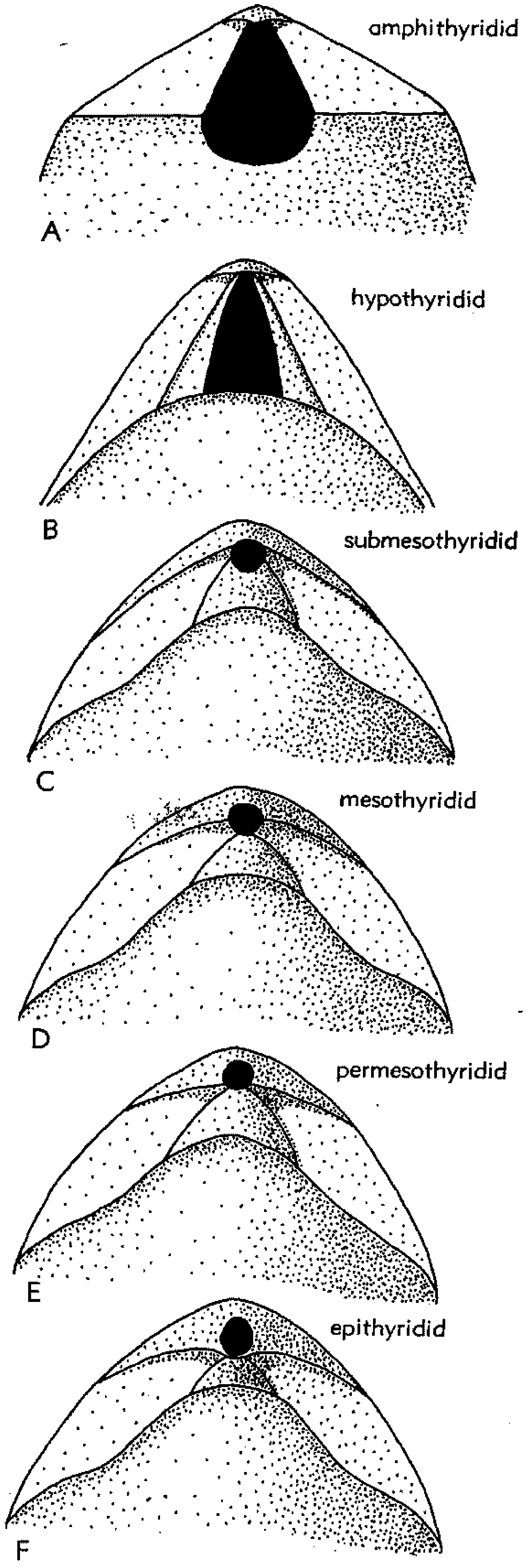

Fig. 90. Classification of some articulate brachiopods based on position of pedicle opening relative to beak ridges (63).

of *Cyrtina*, with its subcentrally placed foramen (see Fig. 120), was probably formed by a similar secretion of the apical portion of the cover, combined with deposition of a symphytium dorsal of the foramen.

The covers to the delthyrium and notothyrium of the strophomenoids, referred to respectively as **pseudodeltidium** and **chilidium,** were deposited in an entirely different way. The young shells of a sufficient number of independent stocks are now known to suggest that the junction between the outer and pedicle epithelia was restricted, throughout growth, to the pedicle valve. In such first-formed shells the pedicle opening occurs supra-apically (3) within the pedicle valve and is commonly enclosed in a high calcareous ring (pedicle sheath) (Fig. 92,*B*). The pedicle junction, therefore, must have lain within the edge of the ring, so that the pseudodeltidium lying dorsal of it was an integral part of the interarea, and its development was in no way dependent upon the presence of the pedicle but on secretion of its dorsal edge by an outer lobe of outer epithelium (57) (Fig. 92,*A*). The deposition of the chilidium must have been controlled in exactly the same way by outer epithelium as were the entire margins of both valves, a condition comparable with that involving the growth of the inarticulate shell. In early strophomenoids, as well as the billingsellaceans and kutorginaceans, which also possess such covers, the dorsal edge of the pseudodeltidium is not flush with the hinge line but concave to it; and although the chilidium may protrude into the gap, it is not entirely filled, so that a well-defined posteromedian gape commonly is found. The gape may have been bridged by periostracum secreted by an isthmus of outer epithelium homologous with the zone of fused mantle lobes (Fig. 92,*C*); alternatively it may have been closed by an inner epithelial strip homologous with part of the posterior body wall of the inarticulate brachiopods (Fig. 92,*D*).

Despite the lack of information about development of the delthyrial covers in the clitambonitoids and triplesiaceans, it is likely that they too were homologous with the strophomenoid pseudodeltidia, and the

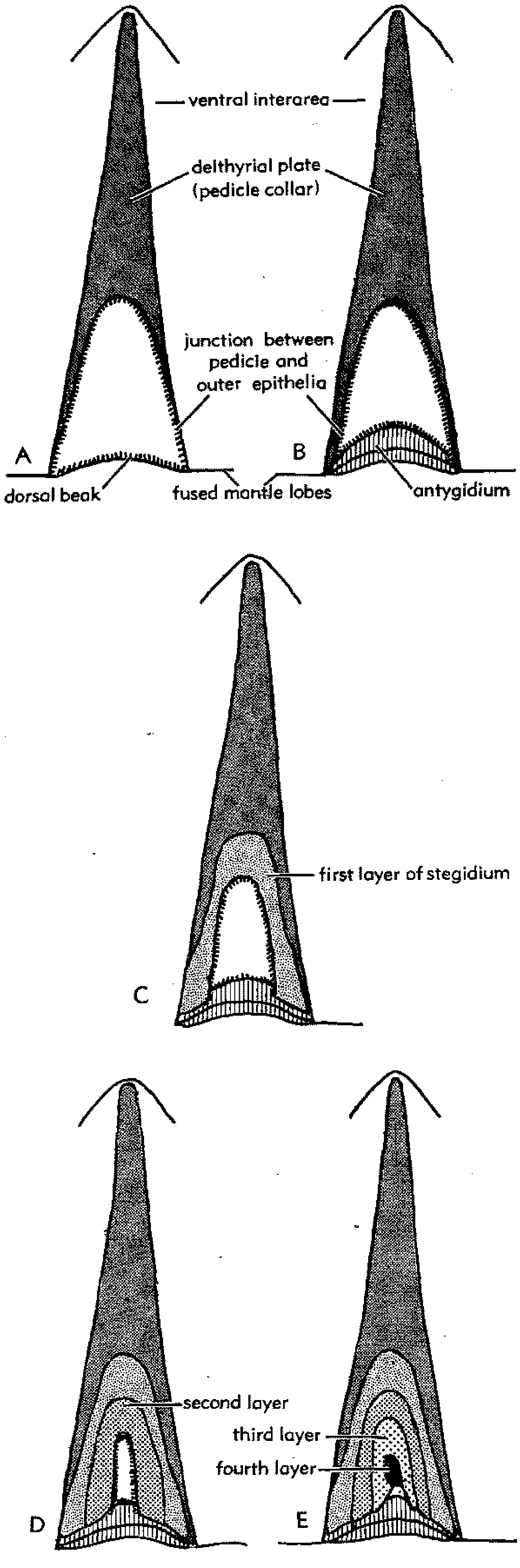

FIG. 91. Stages in deposition of the stegidium of *Syringospira prima* KINDLE, U.Dev., USA (65).

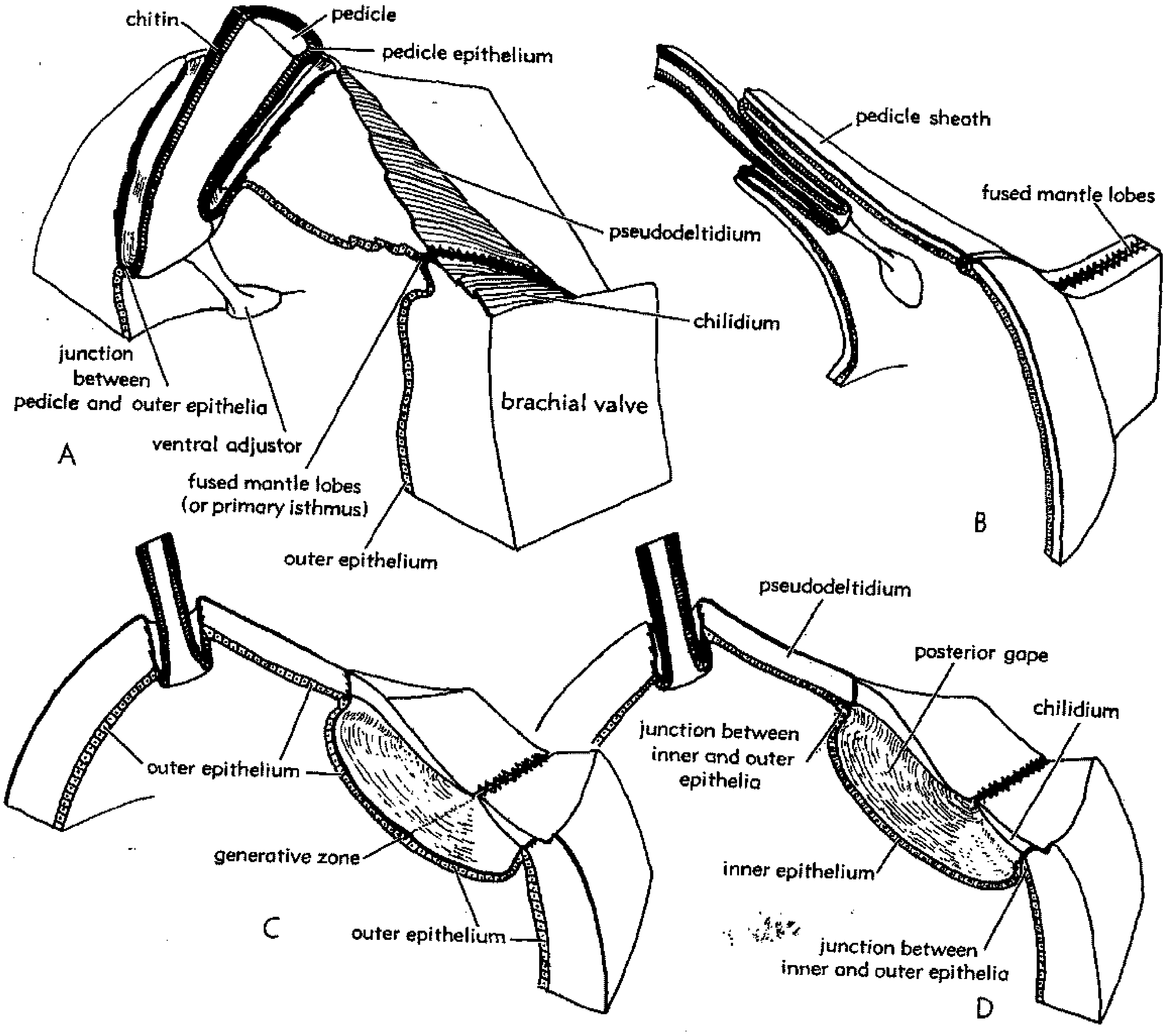

FIG. 92. Inferred relationships between the pedicle and pedicle opening *(A)* in adult *Leptaena, (B)* young *Fardenia, (C)* adult *Nisusia* on assumption that the posterior gape was closed by a primary isthmus of outer epithelium or an extension of fused mantle lobes, and *(D)* adult *Nisusia* on assumption that the posterior gape was closed by a posterior body wall of inner epithelium (65).

presence of an inner calcareous pedicle tube in the triplesiaceans can only be explained on this assumption (62). The pseudodeltidium may be resorbed along with the beak of the pedicle valve, as in *Leptaena, Macrocoelia,* etc., and if the cover in the clitambonitoids has been correctly homologized it may not develop at all (e.g., *Apomotella*). A loss of pedicle occurred in the majority of the strophomenoids and all productoids and chonetoids, the pedicle valves of which were commonly cemented to the substratum, probably by a sticky periostracal pad that gave rise to a cicatrix of attachment.

Among the inarticulates, *Paterina* and its allies alone have features recalling the articulate pattern. In these stocks, the arrangement of structures that are assumed to have been associated with a pedicle is reminiscent of certain strophomenoids in that all or part of the delthyrium and notothyrium are covered by externally convex plates (**homeodeltidium** and **homeochilidium**, respectively). However, no indication is found that an apical or supra-apical foramen ever existed, and it is usually supposed that the pedicle emerged between the two plates (Fig. 93,*A*). If this were so, the plates would be the homologues of the pedicle collar and orthacean "chilidium." Alternatively, it is possible that no pedicle developed in postlarval stages, at least, and that the gape was underlain by inner epithelium of

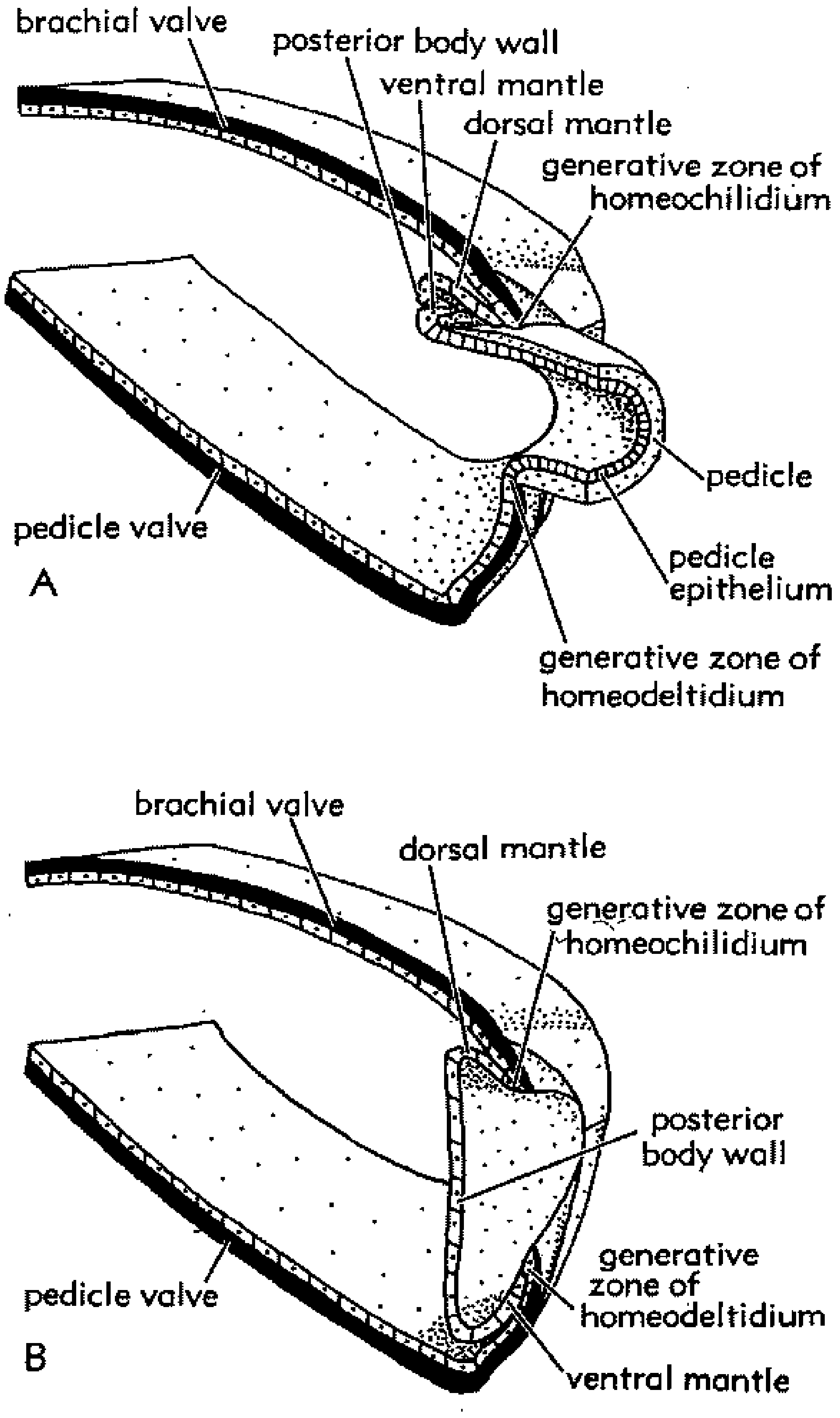

FIG. 93. Stylized reconstruction (with median longitudinal section) of posterior part of paterinid showing alternative interpretations of epithelium-and-shell relations (anterior body wall omitted): *(A)* inferred to possess pedicle, *(B)* inferred to lack pedicle (63).

the posterior body wall in the inferred manner of the gape between the true pseudodeltidium and chilidium (Fig. 93,*B*).

There is less uncertainty about the presence or absence of a pedicle in the remainder of the Inarticulata, although considerable variation is observed in form of the posterior sector of the shell and nature of the pedicle opening. Much of this variation is controlled by the secretory behavior of a narrow posteromedian strip of the ventral mantle which lies posterior or dorsal of the pedicle of the attached animal. This sector of the mantle is seemingly developed later than the remainder, after the formation of the pedicle rudiment, and its appearance is probably associated closely with protrusion of the pedicle between the valves prior to settling (p. *H*51).

The ventral pseudointerareas of most Lingulida are indented medially by a pedicle groove which is homologous with the pedicle collar of the articulate brachio-

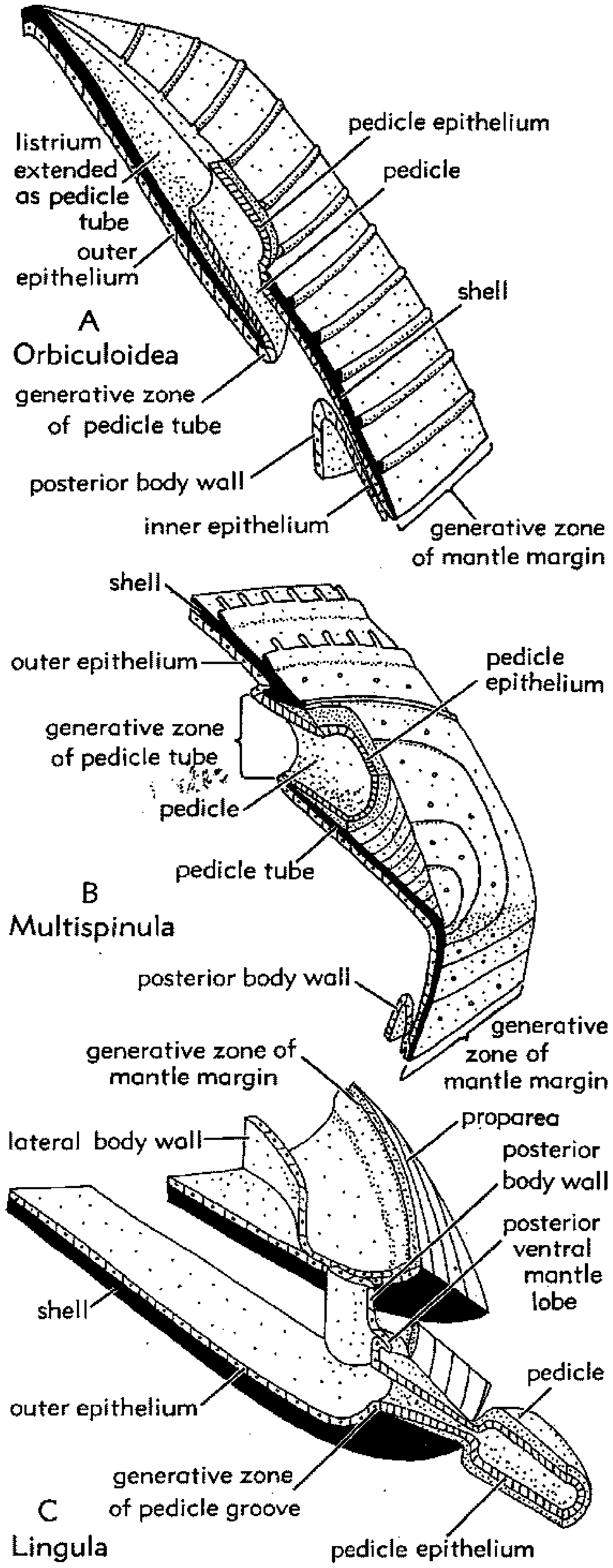

FIG. 94. Stylized reconstruction of posterior part of pedicle valve with longitudinal section showing inferred epithelium-and-shell relations in *(A) Orbiculoidea*, *(B) Multispinula*, both viewed externally, *(C)* observed epithelium-and-shell relations in *Lingula*, viewed internally (63).

pods, for it is secreted by outer epithelium at its junction with the pedicle epithelium. The flanking propareas and the entire pseudointerarea of the brachial valve are secreted independently by the outer lobes along the posterior segments of the ventral and dorsal mantles, respectively. In these forms the posteromedian sector of the ventral mantle is greatly reduced in size and takes no part in the secretion of the shell (Fig. 94,*C*).

In some modern discinaceans (e.g., *Discinisca*) the homologous posterior sector of the ventral mantle, although oriented differently to lie posterior of the pedicle, also plays no part in the secretion of the mineralized shell; but in contrast to the Lingulida, it does secrete the outer, chitinous periostracal layer. The same relationship probably existed in the trematids, for in this family, although growth of the pedicle valve was essentially holoperipheral, the posterior margin of the valve is broken by a variably shaped opening which extends radially from the apex. The secretory behavior of the posterior sector of the ventral mantle of many young discinids was probably similar, for their triangular pedicle opening, breaching the posterior margin of the valve, is broadly comparable with the pedicle opening of adult trematids; during later life in many genera, however, this sector of the mantle acquired the ability to secrete shell material in continuity with that deposited by the remainder of the ventral mantle, and the posterior margin of the adult shell is entire (e.g., *Orbiculoidea, Discina*) (Fig. 94,*A*). In the discinaceans, posterior migration of the pedicle tends to enlarge the triangular opening between it and the apex of the valve, which is commonly filled by a plate (**listrium**), growing posteriorly and secreted by the anterior part of the junction of the pedicle and outer epithelia (Fig. 94). The free margin of the listrium in the Orbiculoideinae projects internally, posterior of the external pedicle foramen, as a distinct pedicle tube lying against the previously formed shell of the

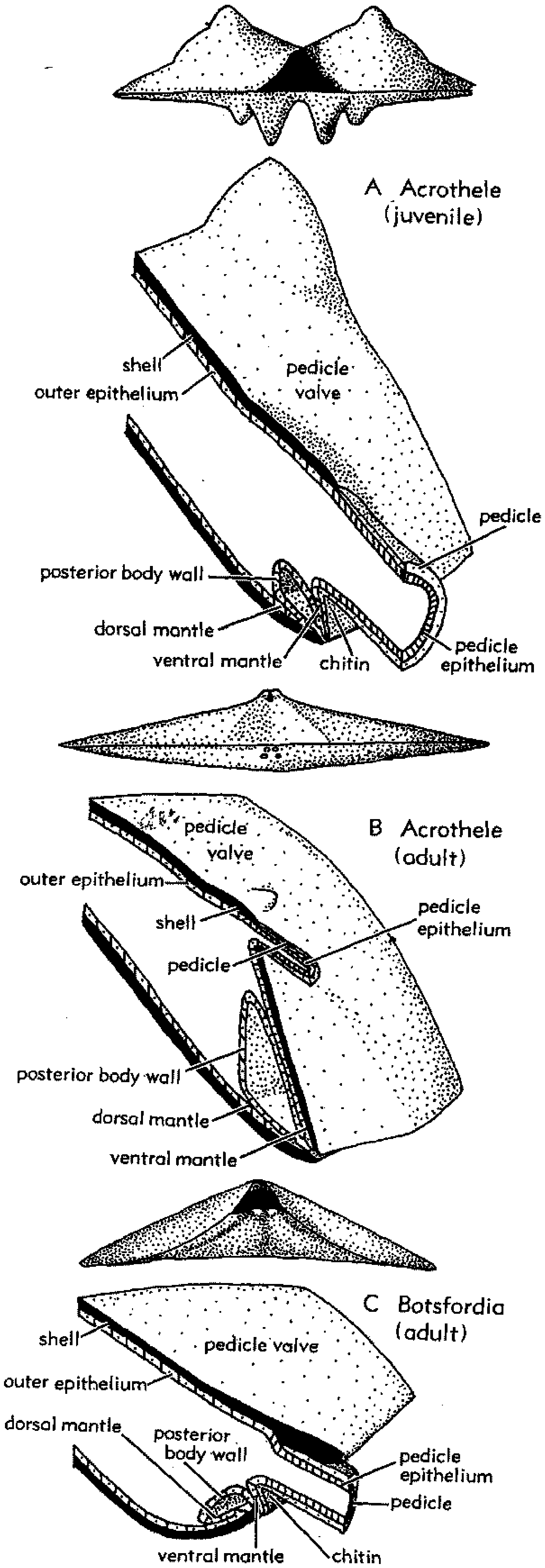

FIG. 95. Posterior views of shell and stylized reconstructions with longitudinal median section of posterior part of shell showing inferred epithelium-and-shell relations of *(A)* young *Acrothele*, *(B)* adult *Acrothele*, *(C)* adult *Botsfordia* (anterior body wall omitted in *A-C*) (63).

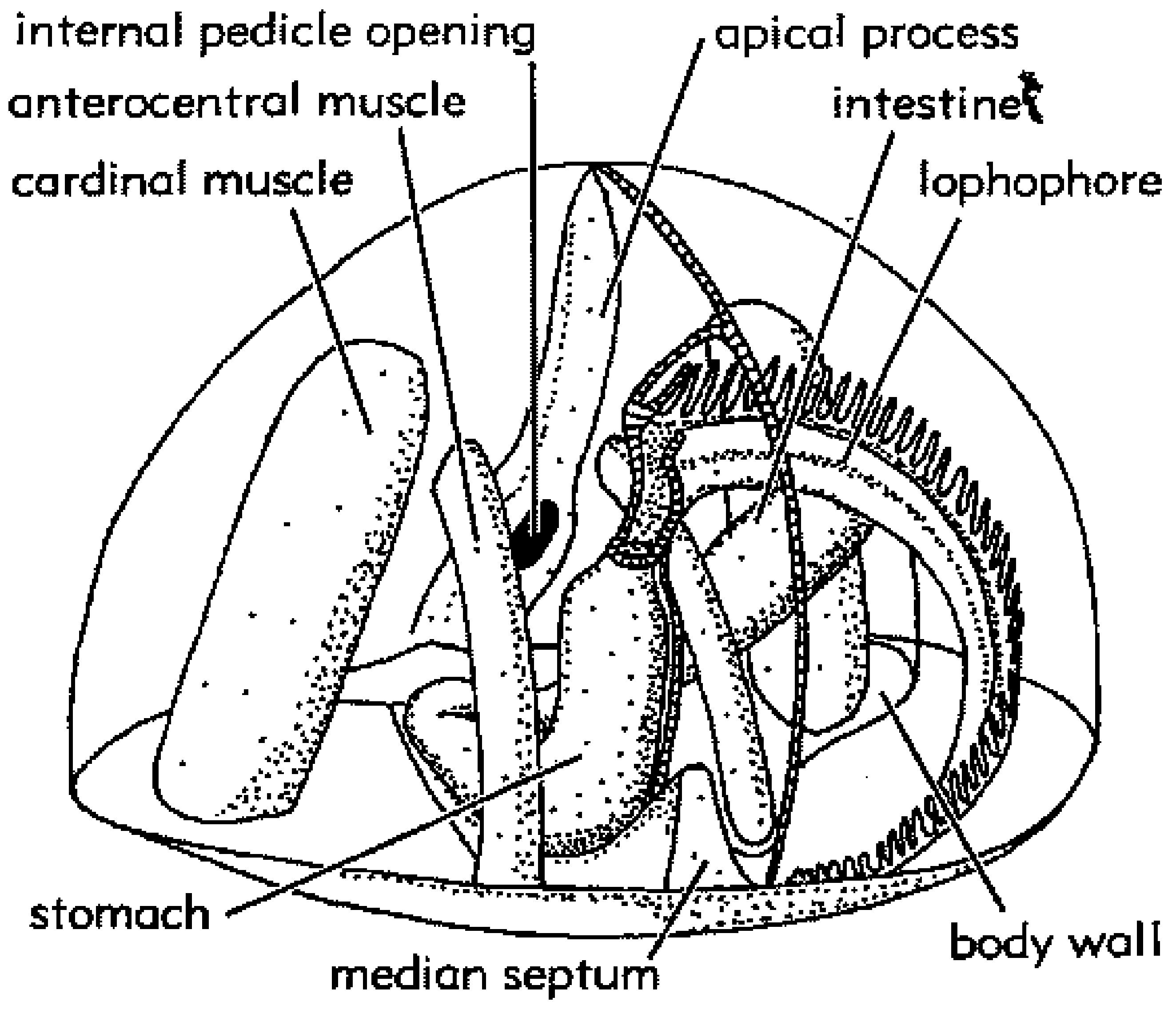

FIG. 96. Stylized reconstruction of *Ceratreta* with inferred location of musculature, lophophore and alimentary canal, shell treated as transparent (63).

posteromedian part of the pedicle valve. In older animals the pedicle tube may be almost completely buried by the deposition of later secondary shell. The pedicle opening of some living and many extinct discinaceans is contained within an elongately oval depression of the shell to which the expanded pedicle is attached externally.

In the majority of adult acrotretaceans the posterior margin of the pedicle valve is entire and is commonly flattened to produce a strongly developed pseudointerarea, but it is presumed that in their very earliest stages, generally unknown, the pedicle opening intersects the posterior margin of the valve. This is true in *Acrothele* (Fig. 95), but in this genus and probably most acrotretaceans, the posterior sector of the mantle rapidly begins to secrete shell material to produce the entire ventral pseudointerarea. The posterior slope of the acrotretid pedicle valve is usually slightly indented or raised along a median sector (intertrough, deltoid pseudointerarea) (Fig. 62). These features seem to have had nothing to do with the development or disposition of the pedicle which lay ventral of their growing edge, although they may conceivably reflect the later-formed posteromedian sector of the ventral mantle. In the majority of acrotretaceans there is a very limited posterior migration of the pedicle opening, which is usually located near the apex of the valve and which may be prolonged internally by a differential thickening (**apical process**) secreted by outer epithelium around the

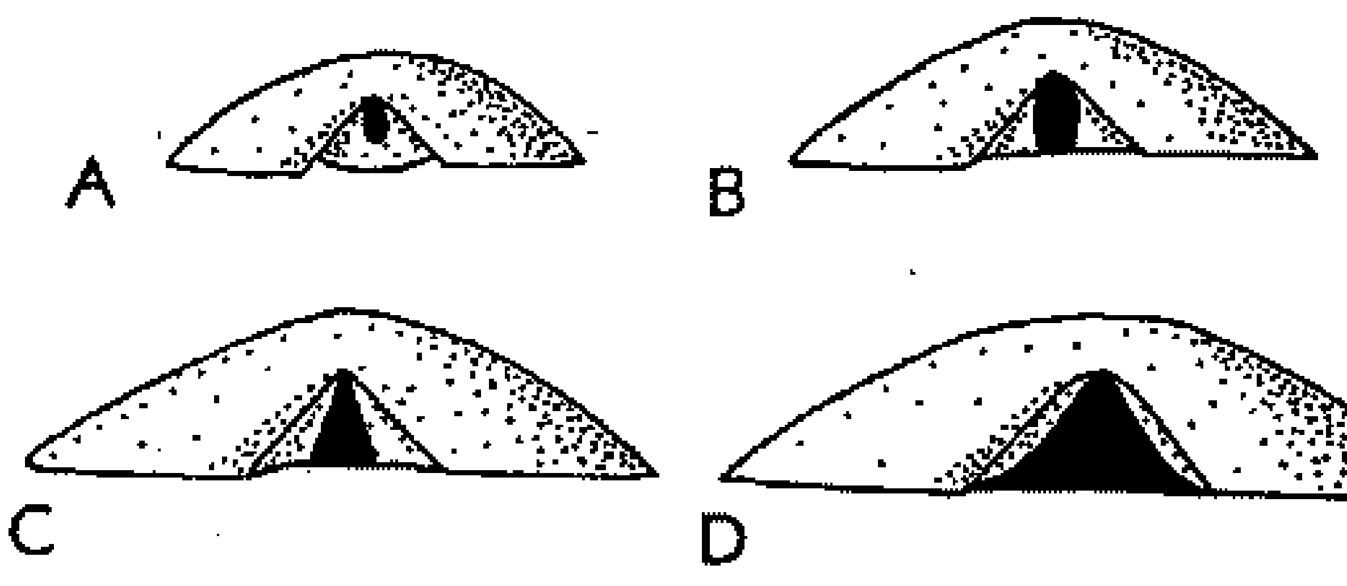

FIG. 97. Development of pedicle opening of *Curticia minuta*, posterior view of pedicle valve: *A*, youngest stage known, 1.1 mm. wide; *B*, dorsally directed resorption causes pedicle opening to breach posterior margin of shell; *C, D*, pedicle opening more widely triangular, with increasing size of shell (39).

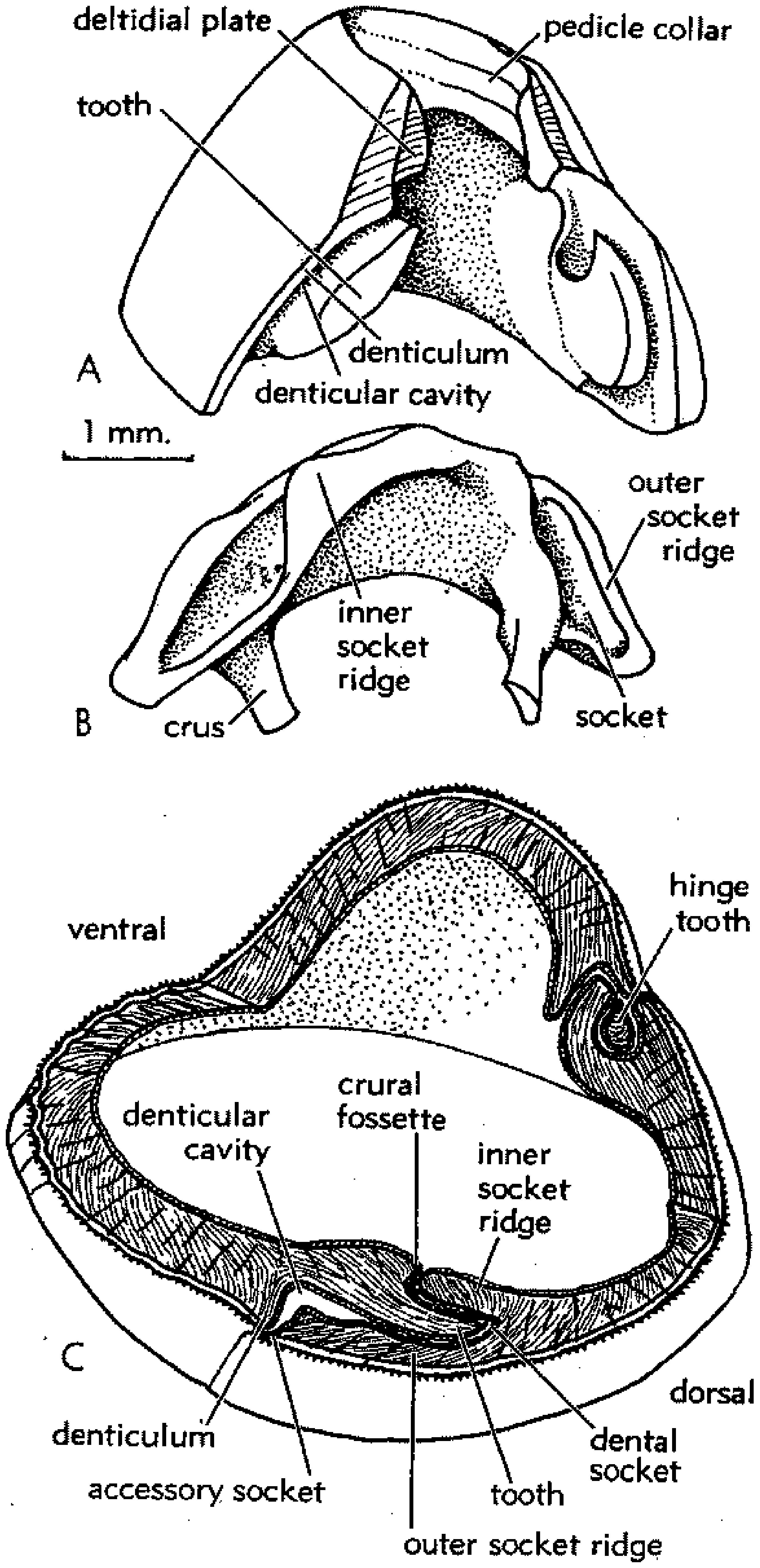

FIG. 98. Articulatory features of *(A)* pedicle valve and *(B)* brachial valve of *Terebratulina caputserpentis* (LINNÉ), also *(C)* as seen in transverse and submedian sections (65).

junction (Fig. 96). Rarely, as in the curticiids, the pedicle migrated posterodorsally and the posterior margin of the valve was breached by resorption to produce a triangular pedicle opening (Fig. 97) (39).

The botsfordiids also have a triangular pedicle opening that breaches the posterior margin of the valve. This could have been formed in a comparable manner to that of the curticiids or, alternatively, it may have been produced by an adult perpetuation of the arrangement found in young *Acrothele*, with secretory failure of the posteriomedian sector of the ventral mantle. Although quite small specimens of *Botsfordia* are known, the form of the pedicle opening is always comparable to that of the adult, with no indications of any resorption on the curticiid pattern, and in this family failure to secrete (rather than migration of the pedicle) appears to be the more likely explanation for the unusual pedicle opening (Fig. 95). The acrotretacean anacline to orthocline dorsal pseudointerarea, although differing in details of form, is homologous with that of the lingulaceans, being secreted by the posterior sector of the outer lobe of the dorsal mantle.

In the siphonotretaceans, the ventral pseudointerarea is entire, and the arrangement of the pedicle junction relative to the ventral mantle edge is like that inferred for the triplesiaceans. The pedicle opening of adult siphonotretaceans lies well forward of the ventral beak and its position is due to an anterior migration by resorption. The posterior part of the track is restricted by a superficial plate or an internally protruding tube secreted by the junction of the outer and pedicle epithelia migrating anteriorly or anterodorsally (Fig. 94,*B*).

Neither pedicle nor pedicle opening is known in the craniaceans, which either lived free on the sea floor or, more commonly, attached themselves to the substratum by cementation of all or part of the pedicle valve, the ventral periostracum seemingly functioning as the cementing medium.

ARTICULATION

The articulate brachiopods are pre-eminently characterized by a pair of **teeth** in the pedicle valve which fit into a pair of depressions or **sockets** in the brachial valve (Fig. 98). The teeth are composed entirely of secondary shell deposited within invaginations of outer epithelium. The track of their growth invariably defines the margins of the delthyrium, so that they protrude from beneath the ventral cardinal area on either side of the delthyrium or its cover. The teeth may be circular to triangular in cross section and are commonly supported by a pair of variably disposed

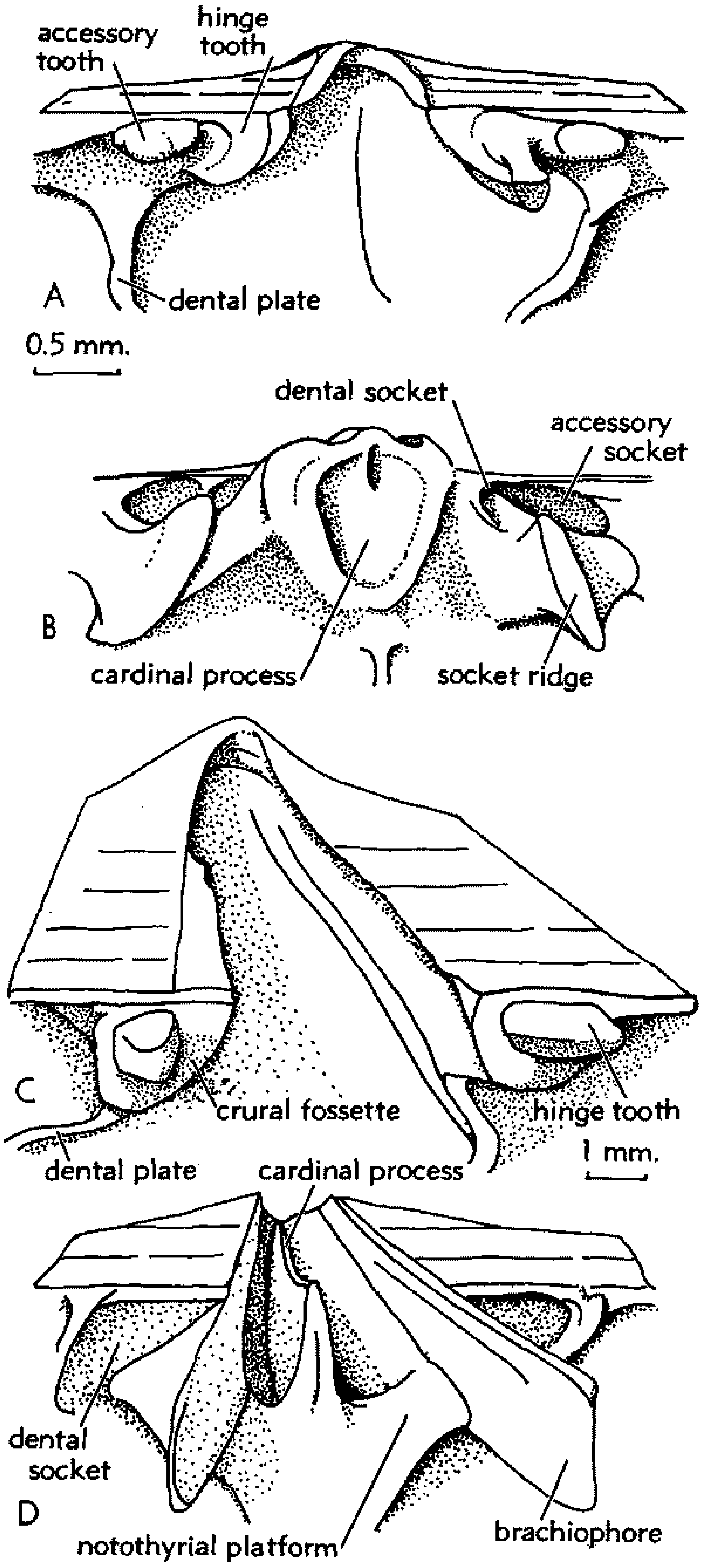

Fig. 99. Articulating outgrowths of *(A, B) Leptellina tennesseensis* Ulrich & Cooper and *(C, D) Hesperorthis australis* Cooper, M.Ord., USA (65).

plates, also built up exclusively of secondary shell and known as **dental plates** (Fig. 99, *A,C*). The dorsal surfaces of the teeth may be blunt or sharp, smooth or crenulated, and further complicated by minor grooves and apophyses, which fit snugly with complementary features associated with the socket. The **crural fossette** is perhaps the commonest of these minor modifications (Fig. 99, *C*). It consists of a groove located on the

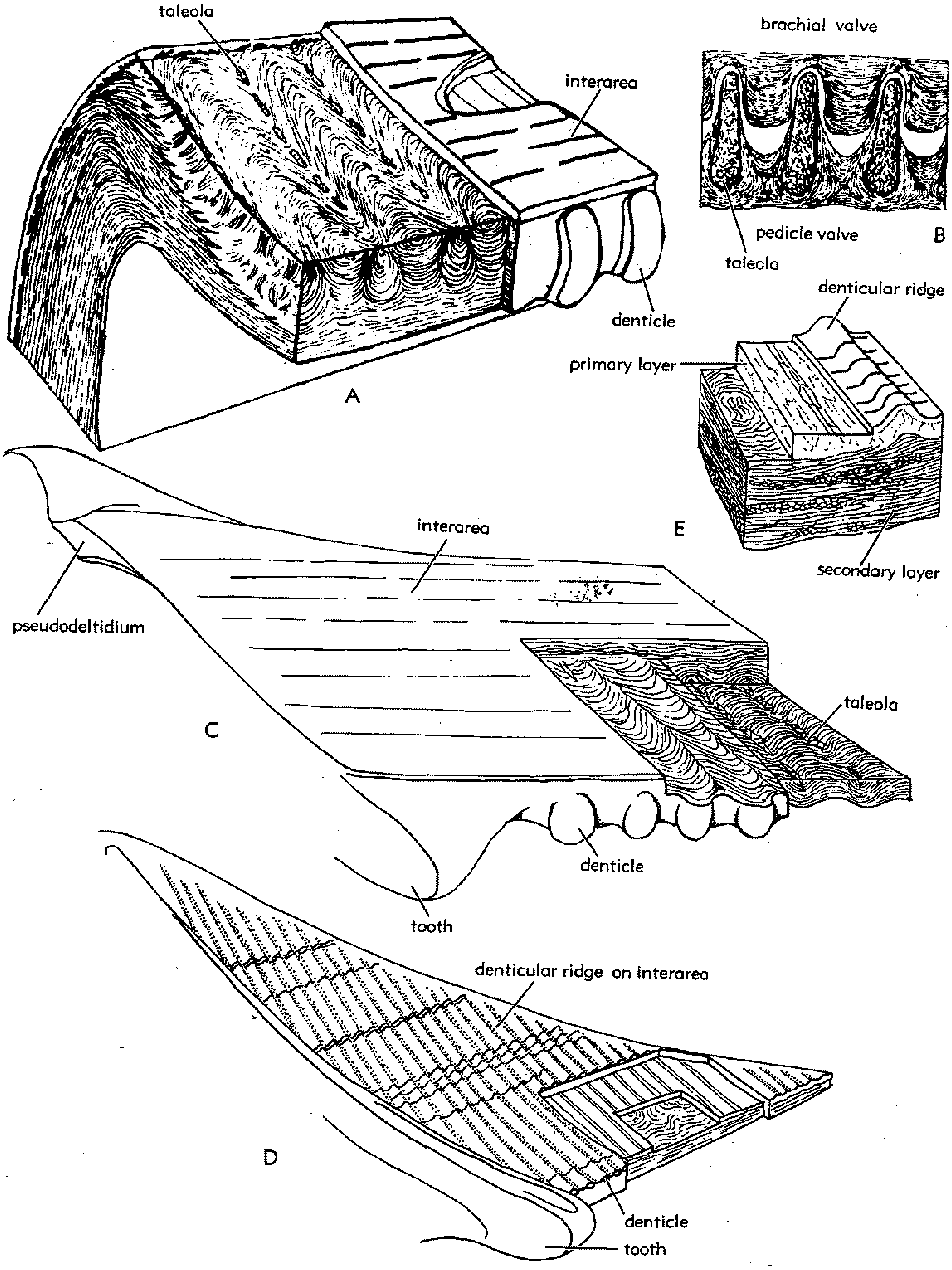

FIG. 100. Denticular structures of stropheodontids (idealized): *A, Pholidostrophia* sp., M.Dev., USA; *B, Plectodonta transversalis* WAHLENBERG, M.Sil., Eng.; *C-E, Tenticospirifer* sp., U.Dev., USA (*A,B,* 55; *C-E,* 65).

inner (anteromedian) side of the tooth and accommodates the posterolateral edge of the ventral wall of the brachiophore (43). A more unusual arrangement, which is especially characteristic of the plectambonitaceans, involves the growth of a pair of accessory teeth lateral to the teeth bordering the delthyrium and separated by a pair of deep grooves (35) (Fig. 99,*A*). Two pairs of sockets are found in the brachial valve, one on either side of the socket ridges, the posterior surfaces of which fit into the grooves between the teeth.

It is inevitable that, since the tooth and socket are fashioned from secondary shell, the former is commonly separated from the valve margin by a groove that receives the variably thickened or undercut dorsal margin forming the posterior edge of the socket. A number of conflicting terms have been used to describe this relationship, but the following selections seem to be the most appropriate, although they do not necessarily have historical precedence. Thus **denticulum** (31) may be used for the posterior edge of the pedicle valve margin (e.g., *Digonella*) or of the symphytium (e.g., *Laqueus*). For the prominence of secondary shell along the posterior edge of the socket, **outer socket ridge** affords the best description; while the grooves accommodating the denticulum and outer socket ridge are best referred to as **accessory socket** and **denticular cavity** (Fig. 98).

The teeth may be supplemented or, rarely, replaced by a series of smaller protuberances extending lateral to the teeth and in a complementary arrangement along the posterior margin of both valves. In spiriferoids, such denticles are small crenulations of primary and adjacent secondary shell underlying the interareas (Fig. 100,*D,E*), as are the denticles found in many plectambonitaceans except that each of them appears to have been built up around a taleola (Fig. 100,*C*). The stropheodontid denticulation, in contrast, only arises after the fusion of widely divergent, platelike teeth and dental plates, following the posterior migration of the latter, although in this group too, the denticles contain taleolae (55) (Fig. 100,*A,B*). The denticulation of the chonetoid *Eodevonaria* and the productoid *Ctenalosia* appears to be most closely related in development to that of the stropheodontids (33).

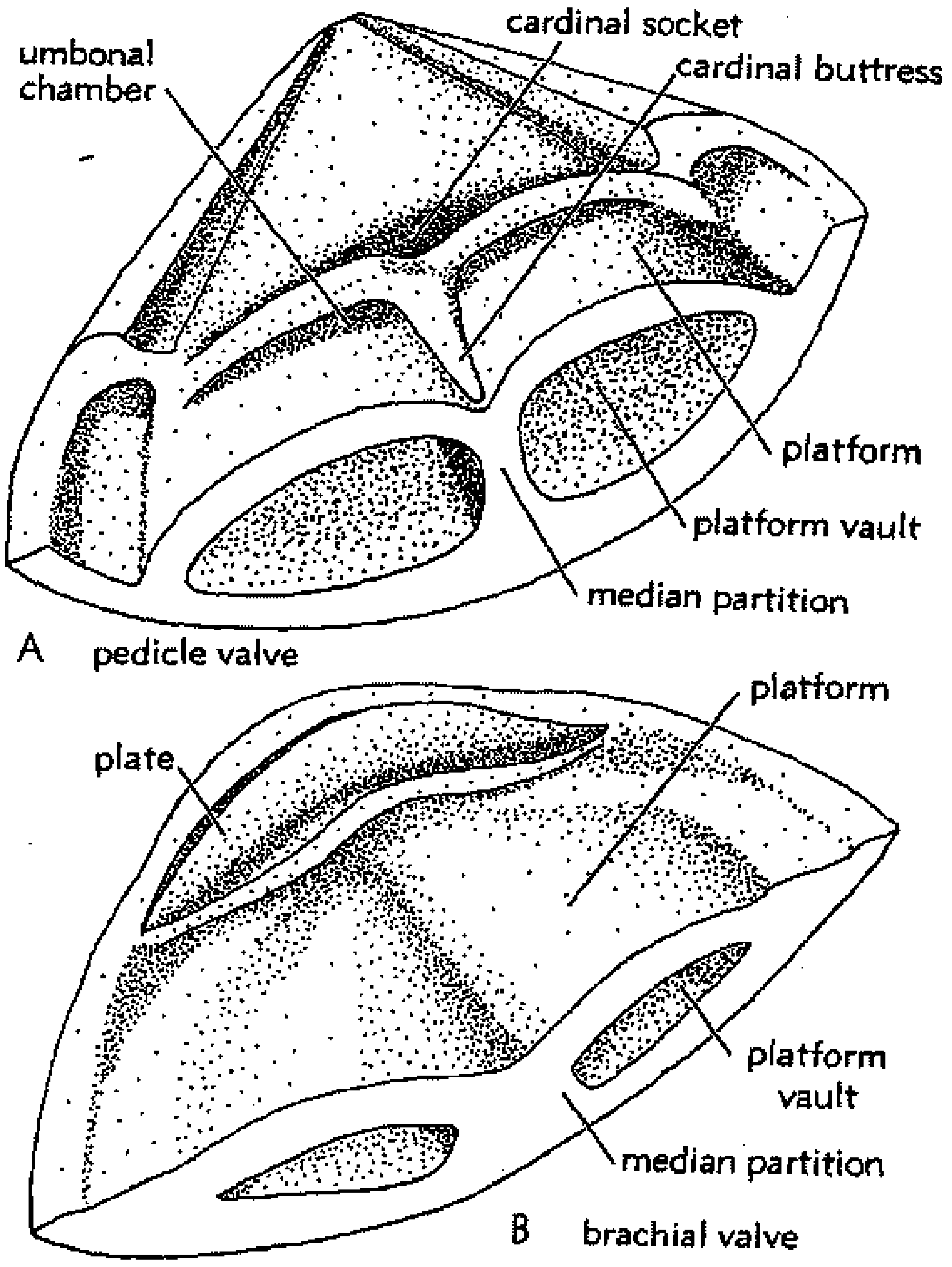

Fig. 101. Morphology of posterior region of *(A)* pedicle valve and *(B)* brachial valve of *Dinobolus* (63).

Although the majority of inarticulate brachiopods lack any form of articulation between the valves, which are merely held together by muscles, aided by the body wall, hinge structures are known in a few genera. An unusual type of articulation occurs in *Dinobolus* and probably in other genera of the Trimerellacea (51). On the posterior margin of the brachial valve is a single, medially placed plate which fits into a corresponding cardinal socket in the pedicle valve (Fig. 101). These structures probably contributed little toward holding the valves together, but they would have inhibited any relative rotational or sliding movements between the valves. What is probably another form of primitive articulation, which developed quite independently of that of the Trimerellacea, occurs in the acrotretid genus *Linnarssonella* (7). In this genus the typical acrotretid dorsal pseudointerarea is modified by the development of a groove on both propareas, which are elevated ventrally immediately in front of

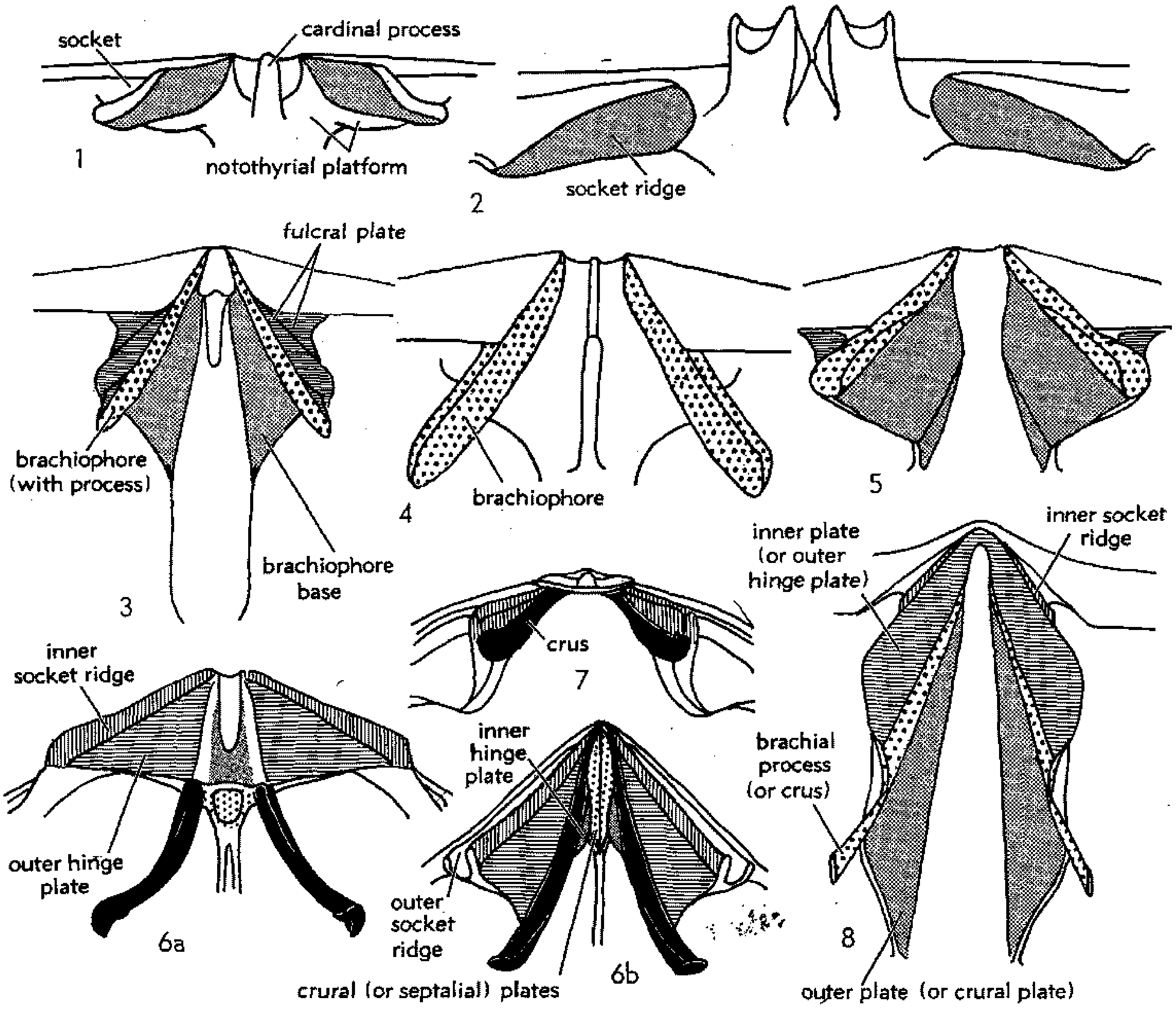

Fig. 102. Cardinalia of *(1) Billingsella, (2) Strophomena, (3) Dalmanella, (4) Hesperorthis, (5) Imbricatia, (6a,b)* a camarotoechiid, *(7) Notosaria,* and *(8) Gypidula,* all ventral views (65).

the grooves. The grooves may have functioned as sockets receiving the dorsal edge of the pedicle valve, but the latter bears no distinct structures or thickenings interpretable as teeth, and it is possible that the elevated propareas may only have restricted relative rotational and sliding movements of the valves without occurrence of any positive articulation. A similar form of constraining mechanism, or possibly full articulation, is also present in the obolid *Dicellomus* (6), for the posterolateral margins of the brachial valve bear conspicuous grooves, but details of the corresponding margin of the pedicle valve are unknown. In *Linnarssonella* and *Dicellomus* the supposed sockets can, of course, be only analogous with true sockets, because they were developed on the shell surface and not as modifications of inner layers of the shell.

The plates or ridges defining the sockets in the brachial valves of articulate brachiopods are part of structural modifications of varying complexity found in the dorsal umbo and collectively referred to as the **cardinalia.** The several pieces comprising the cardinalia are composed of secondary shell and, apart from defining the sockets, afford attachment areas for musculature and even include the bases of processes giving support to the lophophore. This diversity of function has naturally given rise to a wide variety of features (Figs. 102, 103), and since combinations of them tend to be characteristic of major taxa, a complicated terminology, frequently incompatible with that employed for other groups, has grown up for each taxon. An important element of the cardinalia is a medially situated outgrowth(s) (**cardinal process**), which is commonly developed as an attachment area for the dorsal ends of the diductors. This fea-

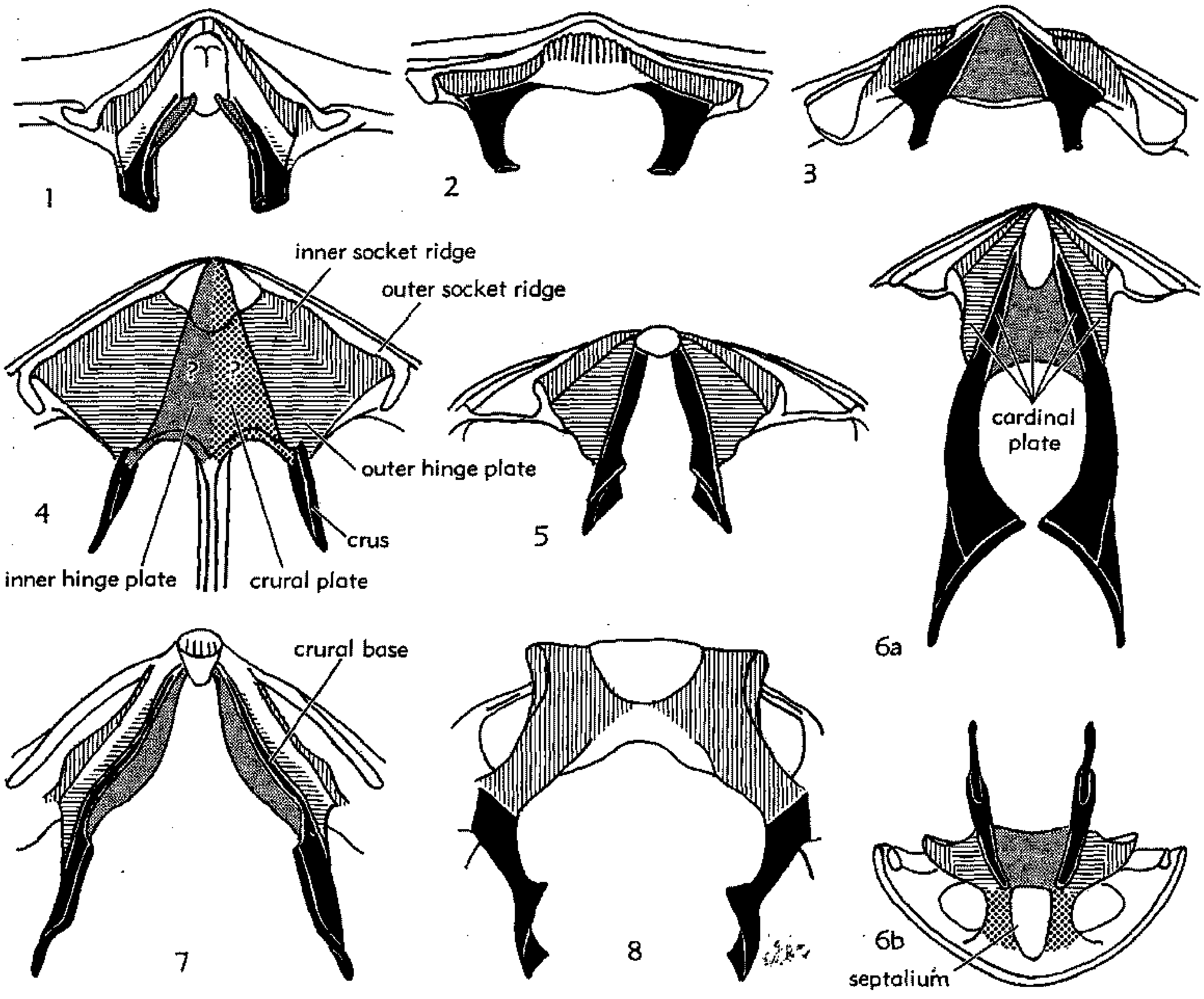

FIG. 103. Cardinalia of *(1) Crenispirifer, (2) Neospirifer, (3)* young *Cleiothyridina, (4) Laqueus, (5) Dallithyris, (6a,b) Nanothyris, (7) Terebratula,* and *(8) Terebratulina,* all ventral views except *6b,* which is posterior (65).

ture is more conveniently dealt with when considering the shell modifications due to the insertion of muscles concerned with relative movements of valves.

The most primitive arrangement is found in the billingsellaceans (Fig. 102,*1*), where a pair of widely divergent plates bound the notothyrium and also act as inner walls to sockets which are excavated within the secondary shell uniting the plates with the edge of dorsal interarea. Medially, the proximal ends of the plates may be encased by lateral extensions of a low-lying deposit of secondary shell which forms the floor of the notothyrium (**notothyrial platform**). These plates have been called brachiophores in the belief that prolongations of their ventroposterior edges gave support to the lophophore. Such processes however, are unknown in the billingsellaceans, in which the plates do not extend beyond the lateral edges of the sockets, and are only rarely developed incipiently among the strophomenoids and clitambonitoids; and even in later orthoids they rarely extended sufficiently anteroventrally to reach the inferred position of the anterior body wall. In all, it seems preferable to use the term **socket ridge** for widely divergent structures of limited extension like those of the billingsellaceans, strophomenoids, etc. (Fig. 102,*2*) (55). Certainly an exclusive function of articulation may be inferred for the socket ridges of stropheodontids which became vestigial or even disappeared subsequent to the loss of teeth in members of that family (55).

The orthacean arrangement represents a significant advance in that the shell outgrowths (**brachiophores**) that serve to define the ventral limits of the sockets were rotated to point anterolaterally and were also prolonged as blade-shaped or rodlike processes beyond the limits of the sockets (43). Disposed in this manner, the brachiophores are free of the posterior margin and in many orthids (e.g., *Hesperorthis*) are supported by a well-developed notothyrial platform (Fig. 102,*4*). The sockets are excavated in secondary shell deposited between the brachiophores and the posterior margin but in other orthoids their anterolateral limits may be defined by concave plates (**fulcral plates**), which are partially or completely elevated above the valve floor (Fig. 102,*3*). The forward growth of the brachiophores and their processes, as in most enteletaceans and many orthaceans, was accompanied by the forward growth of connections between the brachiophores and the floor of the brachial valve, as a pair of plates supporting the upper part of the brachiophore. These plates may be disposed at varying angles to the median plane of symmetry and have generally been called "supporting plates" only when they converge towards the dorsal median ridge. It seems best, however, to refer to them as **brachiophore bases**, irrespective of inclination (61).

It is significant that the ventral adjustor scars are first indisputably identified in the orthaceans and enteletaceans, and judging from anatomical reconstruction, the only sites for the attachment of the dorsal adjustor muscles were the inner faces of their well-developed brachiophores (61).

The cardinalia of early porambonitaceans consist essentially of fulcral plates and brachiophores (50) with bases variably convergent onto the floor of the valve (Fig. 102,*5*). The brachiophore processes may be negligible in the older stocks but were very well developed in some younger forms like *Camerella*. Furthermore, a raised ridge is commonly found standing above the posterior edge of the brachiophore, but intervening between it and the concave socket of the fulcral plate. Theoretically, at least, this ridge could have arisen either as an upgrowth along the contact between the fulcral plate and the brachiophore or within the fulcral plate as an inner restriction to a small posterolateral socket. These arrangements are reminiscent of the patterns characteristic of many spiriferoids and rhynchonelloids, respectively. In both conditions, the raised ridge is at least analogous with the rhynchonelloid "inner socket ridge" and that part of the fulcral plate, which now intervenes between the inner socket ridge and the brachiophore, is homologous with the outer hinge plate (Fig. 102,*6,7*). One other modification is noteworthy. In camerellids, for example, the brachiophore bases converge toward the floor of the valves, either uniting with or fusing to form a median septum. This structure is usually referred to as a cruralium, but since it did not contain the dorsal ends of the adductor muscles, it is more correctly spoken of as a **septalium** (see Fig. 128).

The use of an entirely different terminology for the pentameracean cardinalia is not a reflection of any radical departure from porambonitacean morphology but of historical precedent. In general, the cardinalia are only better developed, or, as with the homologues of the brachiophore bases, are only differently disposed. Nonetheless the extended brachiophore of the pentameraceans is known as the brachial process (crus); the brachiophore base as the outer plate; and the fulcral plate, with or without modification like the inner socket ridge, as the inner plate (42) (Fig. 102,*8*). Such terminology is so divorced from that employed for other groups that it may be worthwhile discarding it in favor of the terminology for either the porambonitacean or, preferably, the rhynchonellacean cardinalia.

In the remaining groups of articulate brachiopods, some sort of calcareous support to the lophophore was almost invariably developed, so that greatly prolonged homologues of the brachiophores and their processes, the **crura**, are the dominant element of the cardinalia. The crura, which are commonly strongly curved, divergent apophyses extending anteroventrally, are known in living brachiopods to pass forward on either side of the esophagus to make contact with the anterior body wall and posterior part of the lophophore on either side of the mouth; and it is highly probable that all processes so named in fossil rhynchonelloids, terebratuloids, and spiriferoids performed a similar function.

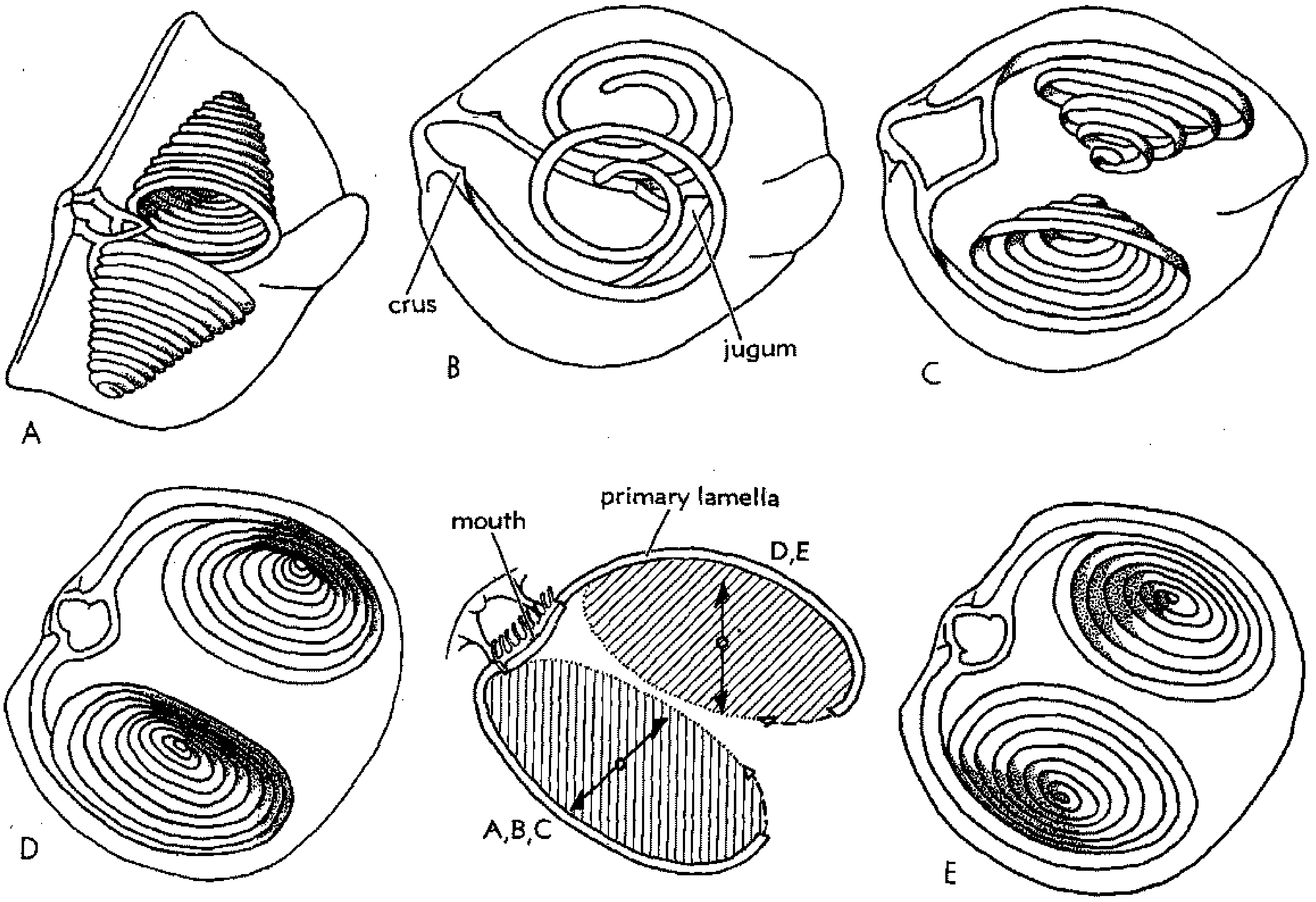

FIG. 104. Stylized representation of various attitudes adopted by primary lamellae of the spiralia relative to planes parallel with the plane of symmetry (as in *A,B,C*) and parallel with the commissural plane (as in *D, E*) (65).

Only rarely, as in *Enteletes* and *Skenidioides,* were the brachiophores sufficiently prolonged and suitably disposed to give support to the lophophore (57). The crura, therefore, represent an important advance in brachiopod organization and are associated with other features of the cardinalia that are distinctive enough to warrant a different terminology from that used for the more primitive groups. Apart from the replacement of the fulcral plate by a fully differentiated inner socket ridge and outer hinge plate, the rhynchonelloid crura were commonly underlain by a pair of plates (**crural plates**) that converged to form a septalium (Fig. 102,*6*), but these could also have arisen from the sides of the crura rather than from their anterior margin. Another pair of plates (inner hinge plates) could also have grown from the sides of the crura to meet medially as a cover to the septalium (Fig. 102,*6b*).

The cardinalia of Paleozoic terebratuloids (14) are very like those of the rhynchonelloids, although the crural plates, defining the septalium, may be subparallel, as in *Nanothyris* (Fig. 103,*6*), or convergent, as in *Globithyris.* The inner hinge plates are normally well developed, and together with the posterior faces of the crura and the outer hinge plates, constitute the cardinal plate (Fig. 103,*6a*). The median elements of the cardinalia of Mesozoic and Recent terebratuloids (49) are commonly greatly modified or incomplete so that it is difficult to be certain about their relationships with similarly disposed structures of older groups. The simplest arrangement is that of *Terebratulina* (Fig. 103,*8*) which consists of crura springing directly from high inner socket ridges. In other terebratuloids, like *Dallithyris,* outer hinge plates are differentiated (Fig. 103,*5*); and in a minority like *Terebratula* a pair of discrete inner hinge plates were also developed (Fig. 103,*7*). The cardinalia of *Laqueus,* in contrast, include a pair of plates, arising at sides of the crura and converging on to the dorsal median septum, which have been called both inner hinge plates and crural plates (Fig. 103,*4*). But until more is known about their origin, it seems preferable to refer to them as crural plates, which at least reflects their disposition relative to the rest of the cardinalia and the floor of the brachial valve.

The cardinalia of many spiriferoid brachiopods, especially the spiriferacean and atrypacean stocks, are reminiscent of *Terebratulina* in that the crura arose directly from well-developed inner socket ridges (e.g., *Neospirifer*) (Fig. 103,*2*). Less commonly, thin strips representing outer hinge plates (e.g., *Plectatrypa*), crural bases and inner hinge plates (e.g., *Crenispirifer*) were developed (Fig. 103,*1*). Among *Athyris* and its allies (like *Cleiothyridina*), the fusion of the inner hinge plates to form a median horizontal plate, subtended between the inner surfaces of the crura or the inner socket ridges, commonly took place (Fig. 103,*3*).

The cardinalia of many articulate brachiopods are also connected with spirally coiled, calcareous ribbons (**spiralia**) or calcareous **loops** (Figs. 104, 105). The spiralia and loops are greatly variable in form and attitude and, indeed, may have arisen in different ways. Nonetheless, two aspects of their growth and disposition seem to have been common to them all. First, they represent outgrowths from the crura, extending well into the brachial cavity and, like the crura, were contained in sheaths of outer epithelium responsible for their growth and enlargement by controlled processes of secretion and resorption (57). (The only exception seems to have been the spiralia of *Thecospira* which were connected by short apophyses to the cardinal process, although they were probably deposited in a like fashion.) Secondly, although the loops grew independently of the lophophores, in living terebratuloids they are intimately associated with that organ and the disposition of both loops and spires in extinct stocks suggests that they performed a similar function of support.

As far as is known from the development of spiralia in a few species (5), the first structure formed was an elongately oval loop (centronelliform loop) by the anteromedian fusion of a pair of curved prongs extending from the crura. The small size of the shell at this stage in growth suggests that the loop supported a trocho-

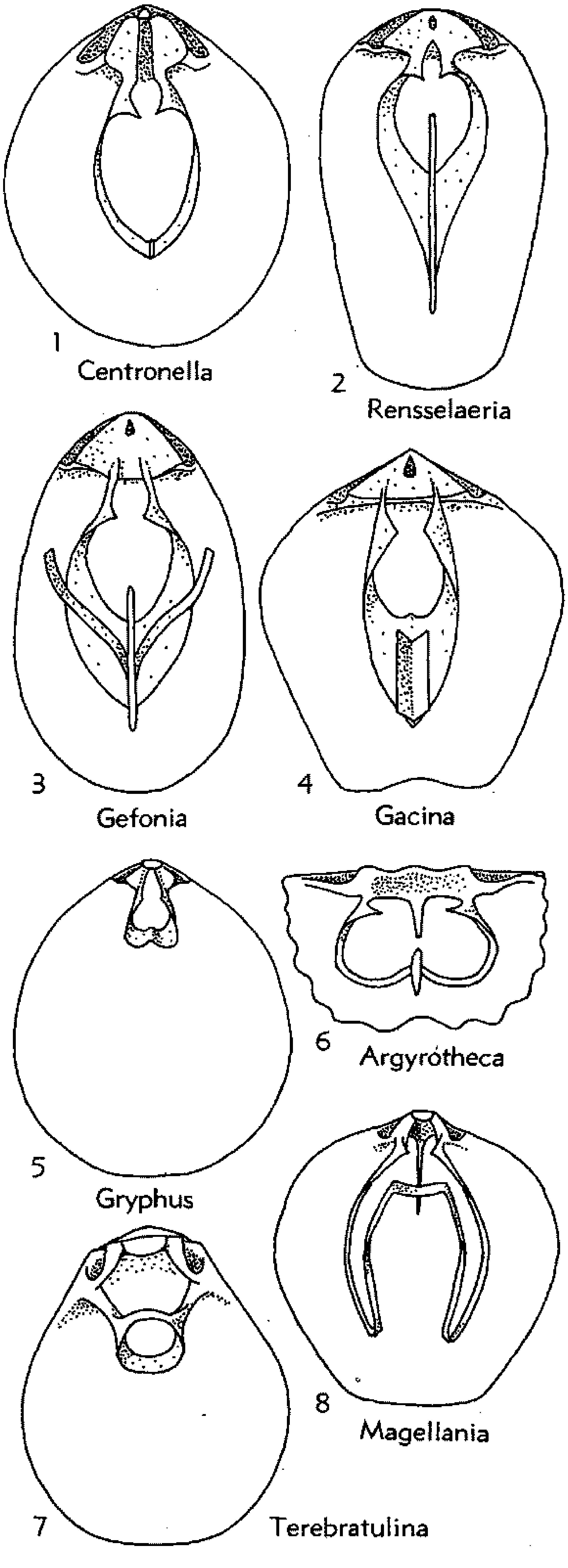

FIG. 105. Some loop forms in the Terebratulida: *1, Centronella*; *2, Rensselaeria*; *3, Gefonia*; *4, Gacina*; *5, Gryphus*; *6, Argyrotheca*; *7, Terebratulina*; *8, Magellania* (*1, 2,* Cloud; *3, 4,* Stehli; *5, 7, 8,* Rowell, n; *6,* Thomson).

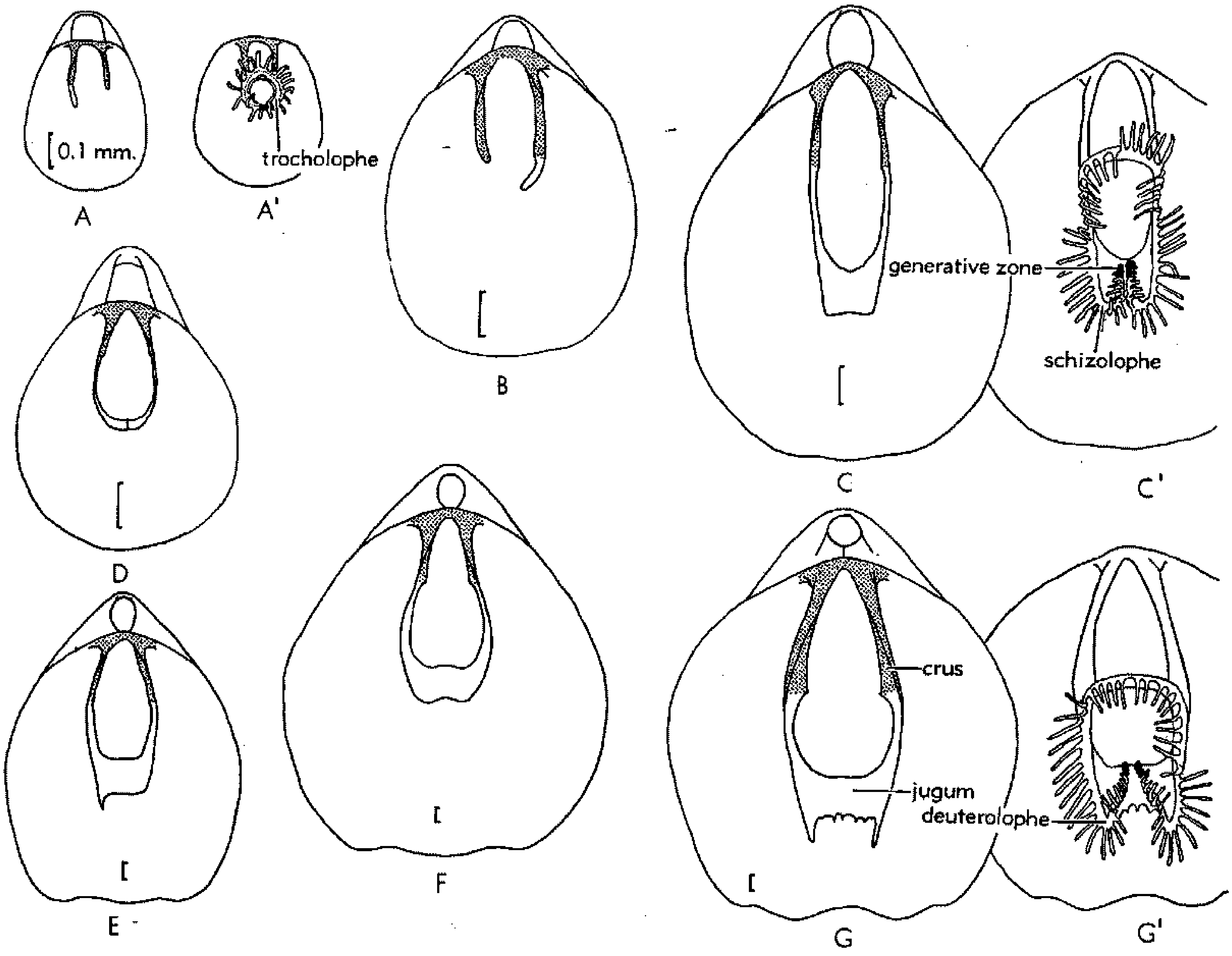

FIG. 106. *A-G*. Growth of the brachidial apparatus of *Protozyga elongata* COOPER, with reconstructions of the trocholophe *(A')* and the schizolophe *(C', G')* (60).

lophous or schizolophous lophophore (Fig. 106). During subsequent enlargement, differential resorption took place, so that the transverse part of the loop became truncated anteriorly to form a band (**jugum**) with a pair of short apophyses at the anterolateral corners. These prolongations represent the beginnings of the first pair of coils (**primary lamellae**) of the spiralia. But the inferred arrangement of the lophophore may *not* be a simple spirolophe coincident with the calcareous ribbons of the spiralia (41), for, if the paired generative zones of the early schizolophe were retained medially on the jugum, which must have been the original position, the growth of the primary lamellae would have been accompanied by an anterolateral lobation of the lophophore to fit around the peripheries of the calcareous ribbons (57). In these circumstances the doubled lophophore (deuterolophe) borne by the spiralia would have been homologous with the side arms of *Terebratulina* (Fig. 107,*B,D*). Moreover, the elaboration of the jugum in some spire-bearing brachiopods, which must also have been due to secretion and resorption by ensheathing outer epithelium, may indicate the retention of the generative zones of the lophophore in a median position on the jugum. In a number of genera this structure developed into a spinose platform and also gave rise to a posteriorly directed process (jugal stem) which bifurcated in a number of stocks (e.g., *Athyris*) to form a pair of arcs (arms of jugum) lateral to the primary lamellae; and in certain unrelated genera (e.g., *Kayseria*, *Diplospirella*) the arms continued to grow into a pair of spires (**accessory lamellae**) coextensive with the primary spiralia (Fig. 108). If the generative zones of the lophophore moved away from the jugum at all, it is at least as likely that they did so posteriorly along the jugal stem and then laterally in association with the accessory lamellae; and if this is so, it is these single

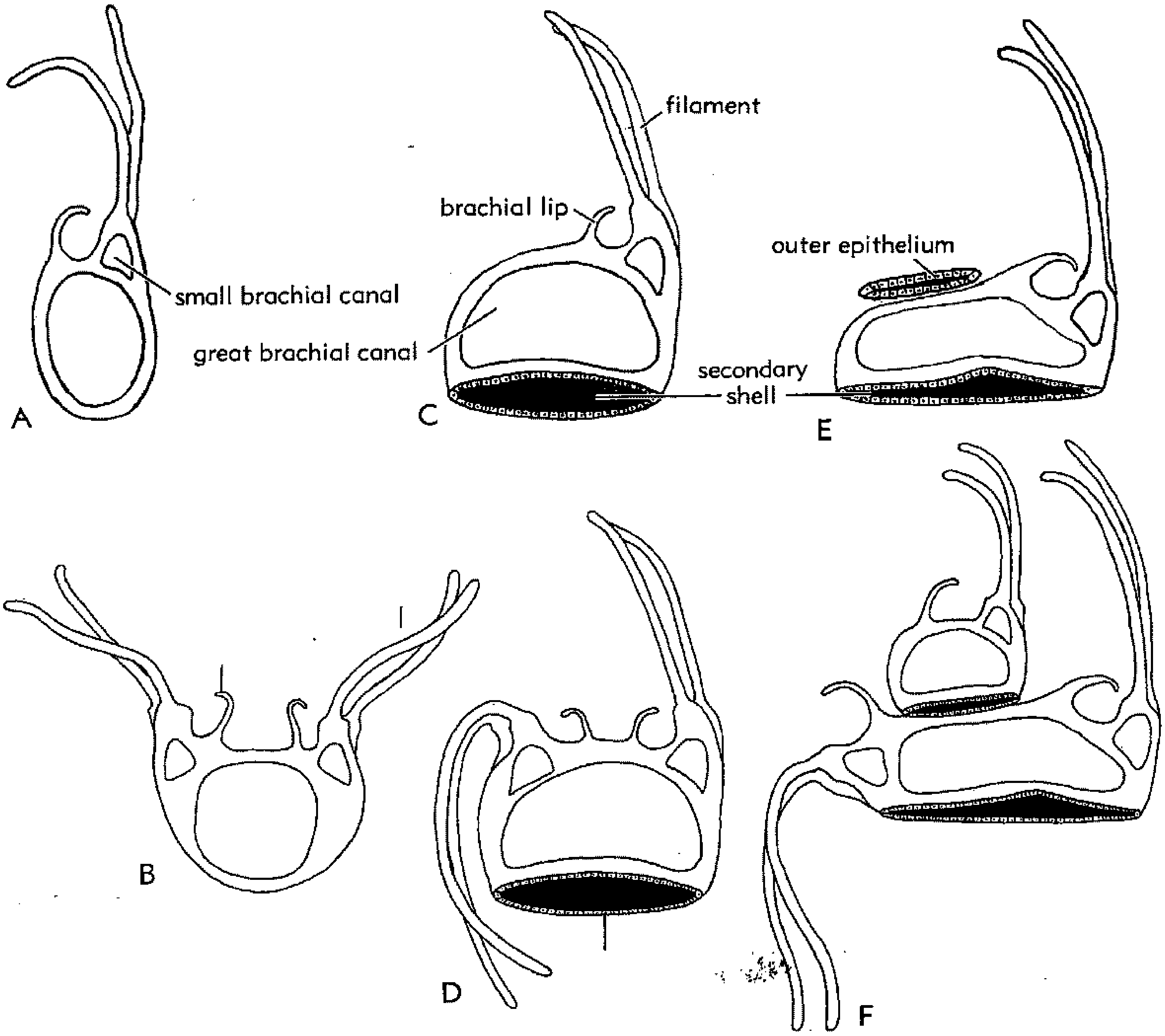

FIG. 107. Diagrammatic cross sections of *(A)* brachium of *Notosaria* and *(B)* side arm of *Terebratulina* with inferred lophophore restorations of *(C, D)* spiriferoids and *(E, F)* athyridaceans according to whether they should be homologized with *A* (as in *C* and *E*) or with *B* (as in *D* and *F*) (65).

elements of the lophophore which are to be homologized with the rhynchonelloid spirolophe, not the deuterolophe, which is really equivalent to the side arms of the terebratuloid (Fig. 107,*F*).

The jugum is unknown in a number of spire-bearing brachiopods. In many poorly investigated stocks, the absence could well be ascribed to the breakage of such a delicate structure during burial of the shell. In others, its absence may have been due to resorption, which is known partially to have affected the juga of certain adult spiriferoids and atrypoids. But in a few stocks like *Cyclospira,* no jugum has been found in well-preserved adult shells and if it proves that the spiralia developed directly from the crura and not by modification of a loop, it is more likely that the spiralia gave support to a spirolophe, rather than a deuterolophe (compare Fig. 107,*A,C*).

The calcareous ribbons of the spiralia are commonly wafer-like but they may be differentially thickened or impersistently spinose (fimbriate) along one side or the other; or folded upon themselves to a varying degree, to give a V-shaped cross section (e.g., *Thecospira*). The spiralia may be oriented to take up almost any attitude within the mantle cavity, but all of them are variants of five basic dispositions (Fig. 104). The simplest arrangement (e.g., *Protozyga*) consists of a pair of planospiral calcareous ribbons, parallel with the longitudinal median plane of symmetry of the shell. This attitude is essentially adopted by the primary lamellae of *Spirifer* and *Zygospira,* but the ribbons are drawn out into spires with apices di-

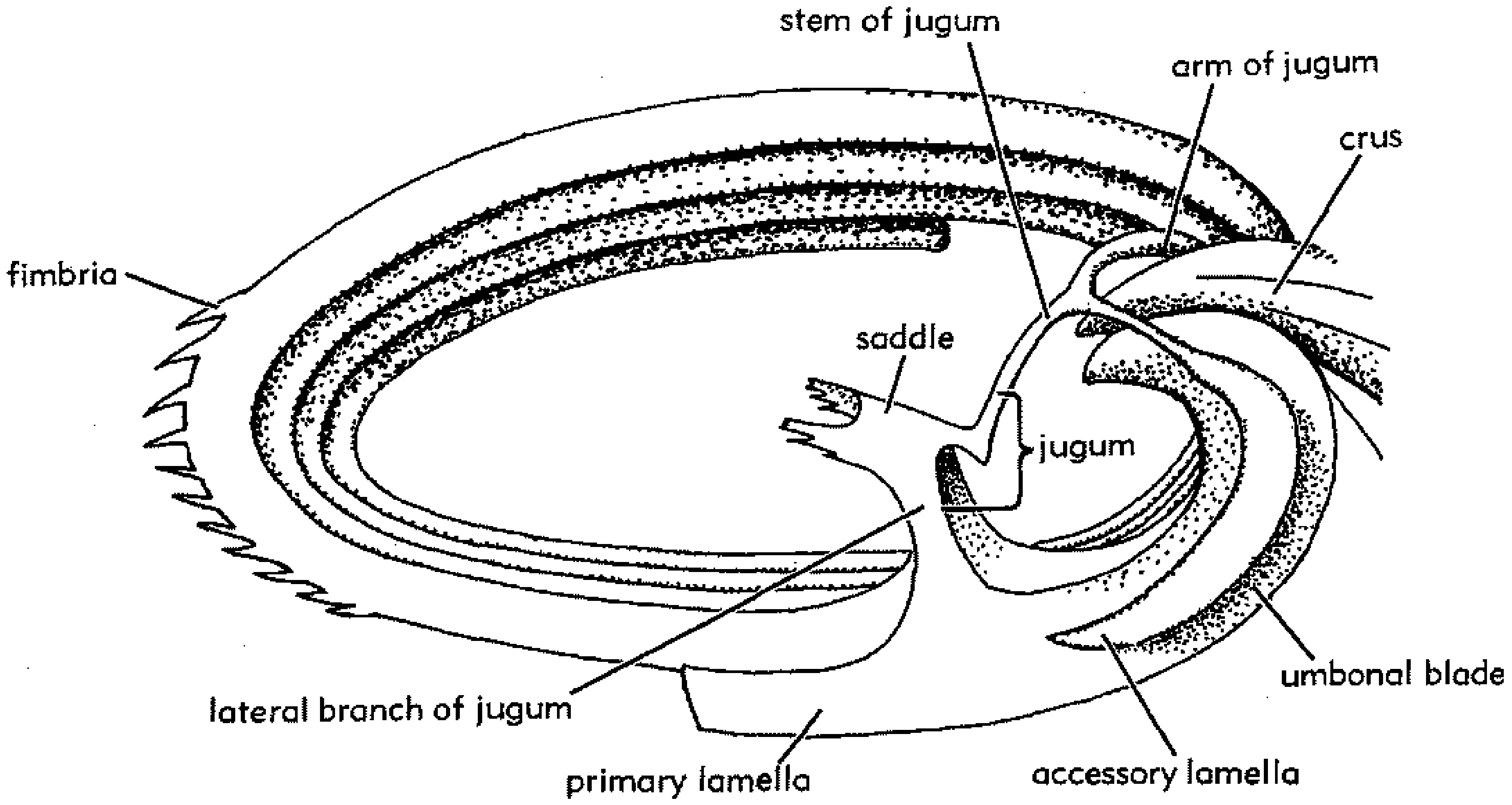

FIG. 108. Structure of spiralium in *Athyris* (27).

rected laterally and centrally, respectively. The primary lamellae of *Atrypa* and *Cyrtina,* on the other hand, are more or less normal to the plane of symmetry, with apices of the spiralia directed dorsally and ventrally, respectively. Judging from the inferred disposition of the lophophore between the ends of the crura and along the calcareous ribbons, the zygospirid pattern could have been derived from the protozygid by extension of the apices of the spiralia toward the center, and the atrypid and cyrtinids by rotation of the primary lamellae through 90°, accompanied by apical extensions dorsally or ventrally. The spiriferid arrangement, however, is quite different, for it involved an eversion of the lophophore as well as a rotation relative to the mouth segment (41).

Calcareous ribbons composed of secondary shell may also extend from the distal ends of the crura to form a closed structure known as the loop, which is especially characteristic of the terebratuloids. The loop varies greatly, not only in form but also in its origin and growth; yet it gives support to a plectolophous lophophore in the great majority of adult living terebratuloids, an association that probably also obtained for most fossil members of the group.

The simplest arrangement is found in Paleozoic terebratuloids like *Centronella* and consists of a band suspended between the crura; the band is lanceolate anteriorly where it tends to form a broad pointed blade (**echmidium**). This is the centronelliform loop (50) (Fig. 105,*1*), which was probably associated with a trocholophe or early schizolophe. Such a loop persisted in some adult shells with little modification, apart from enlargement of the outer edge and resorption along the inner edge, as in *Rensselandia,* with or without peripheral spines (e.g., *Stringocephalus*). In other stocks a median plate (**vertical plate**) normal to the anterior blade of the loop developed (e.g., *Rensselaeria,* Fig. 105,*2*) which may further divide (e.g., *Gacina,* Fig. 105,*4*) or give rise to a pair of bands diverging posterolaterally (e.g., *Gefonia,* Fig. 105,*3*) in a manner which suggests that the generative tips of a highly modified schizolophous lophophore moved out in the same direction (Fig. 105,*4*). More important modifications included the development of short and long loops morphologically like those of living terebratuloids. Thus in *Cranaena,* median resorption and deposition accompanied by lateral enlargement of a centronelliform loop gave rise to a short truncate loop in which a pair of descending branches are clearly identifiable, in the manner of modern *Terebratulina,* and must also have supported a plectolophe (Fig. 105,*7*). In *Cryptacanthia* (19) and related stocks, however, resorption and deposition were accompanied by an accelerated forward growth of the anterolateral corners of the loop to

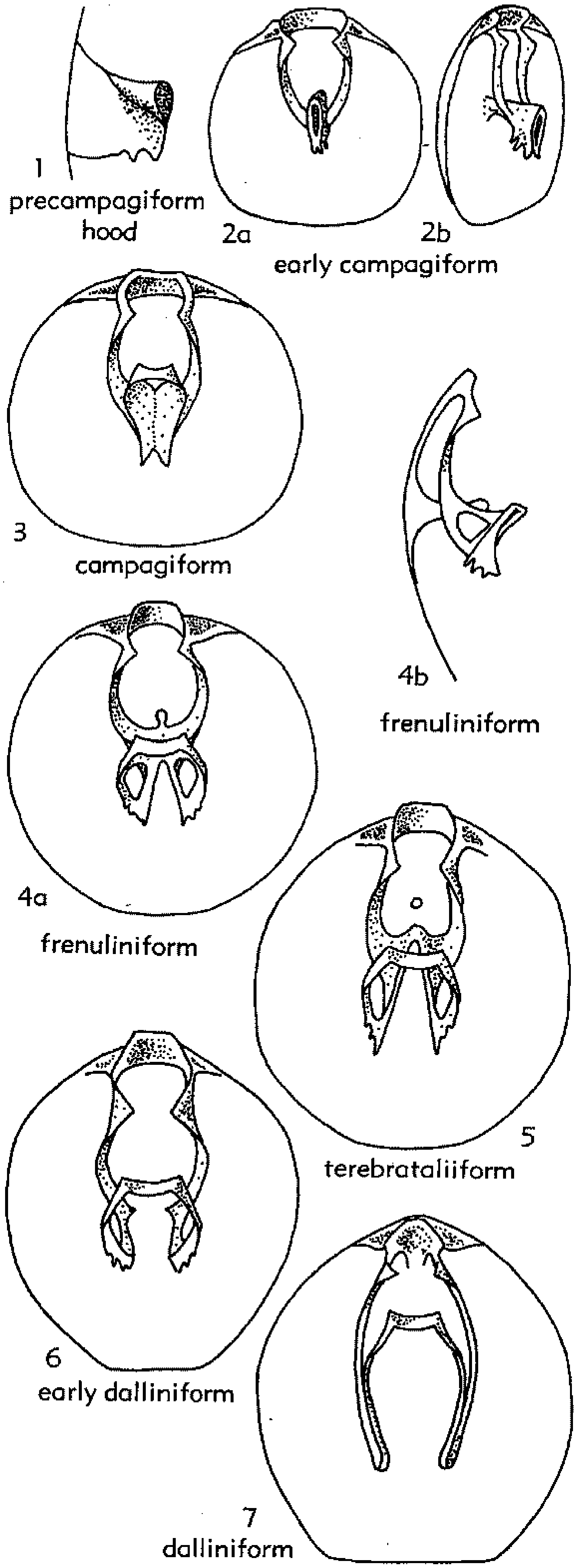

Fig. 109. Stages in loop development of *Cryptacanthia prolifica: 1,* ventral view of precentronelliform stage; *2,* ventral view of centronelliform stage with development of echmidium; *3a,b,* ventral and oblique lateral views of early cryptacanthiiform stage showing development of hood on anterior tip of echmidium; *4a,b,* ventral and lateral views of cryptacanthiiform stage, descending branches still joined medially with remnant of echmidium intact posteriorly; *5,* ventral view of early glossothyropsiform stage, descending branches separate (19).

define a pair of ascending branches connected by a transverse band, as well as the descending branches. The resulting glossothyropsiform loop is similar to the long loops of some living terebratellaceans, which are fashioned, however, in an entirely different way (Fig. 109).

The growth of the terebratellacean loop (22) is linked with the development of a dorsal median septum (or septal pillar), which first makes its appearance as a high platelike outgrowth of secondary shell inserted in the posterior indentation of the schizolophe (Fig. 110). A ring or cone (hood) of secondary shell is then secreted along the posterior face of the septum and by enlargement and modification may be transformed into the ascending branches and transverse band. At about the same time as the appearance of the hood, descending branches appear as prolongations growing anteriorly from the crura to meet and fuse with either the septum or a pair of posteriorly directed upgrowths from it. Further growth and modification by resorption may ultimately give rise to a long recurved loop entirely free of septal support (e.g., *Macandrevia*) in which the descending and ascending branches form the dorsal and ventral boundaries, respectively, of the side arms; and the transverse band joining the ascending branches gives support to the medially coiled spirolophe (Fig. 110). Alternatively the resorption of the median septum and the anteromedian surface of the hood may be arrested so as to leave connections (**connecting bands**) between the descending branches and remnants of the median septum (e.g., *Terebratella*) (Fig. 111).

The development of the terebratellacean free loop, therefore, involves a complex series of metamorphoses; and since the adult loops of living and extinct terebratellacean stocks together typify nearly all possible variations within such a series, distinctive stages in development have been named after genera. In this way an extensive terminology indicating the nature of the loop

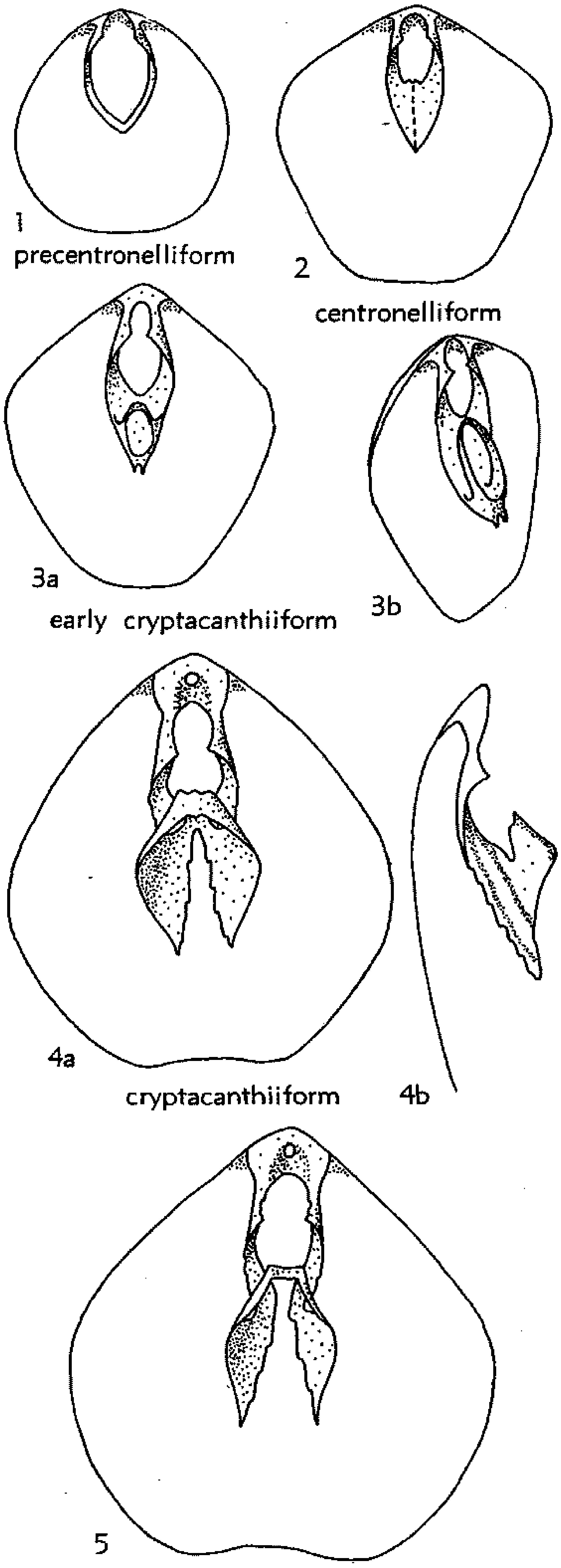

FIG. 110. Growth stages in development of dalliniform loop: *1*, lateral view of precampagiform hood; *2a,b*, ventral and oblique lateral views of early campagiform growth stage; *3*, ventral view of campagiform growth stage; *4a,b*, ventral and lateral views of frenuliniform growth stage; *5*, ventral view of terebrataliiform growth stage; *6*, ventral view of early dalliniform growth stage, *7*, ventral view of dalliniform growth stage (Rowell, after 49).

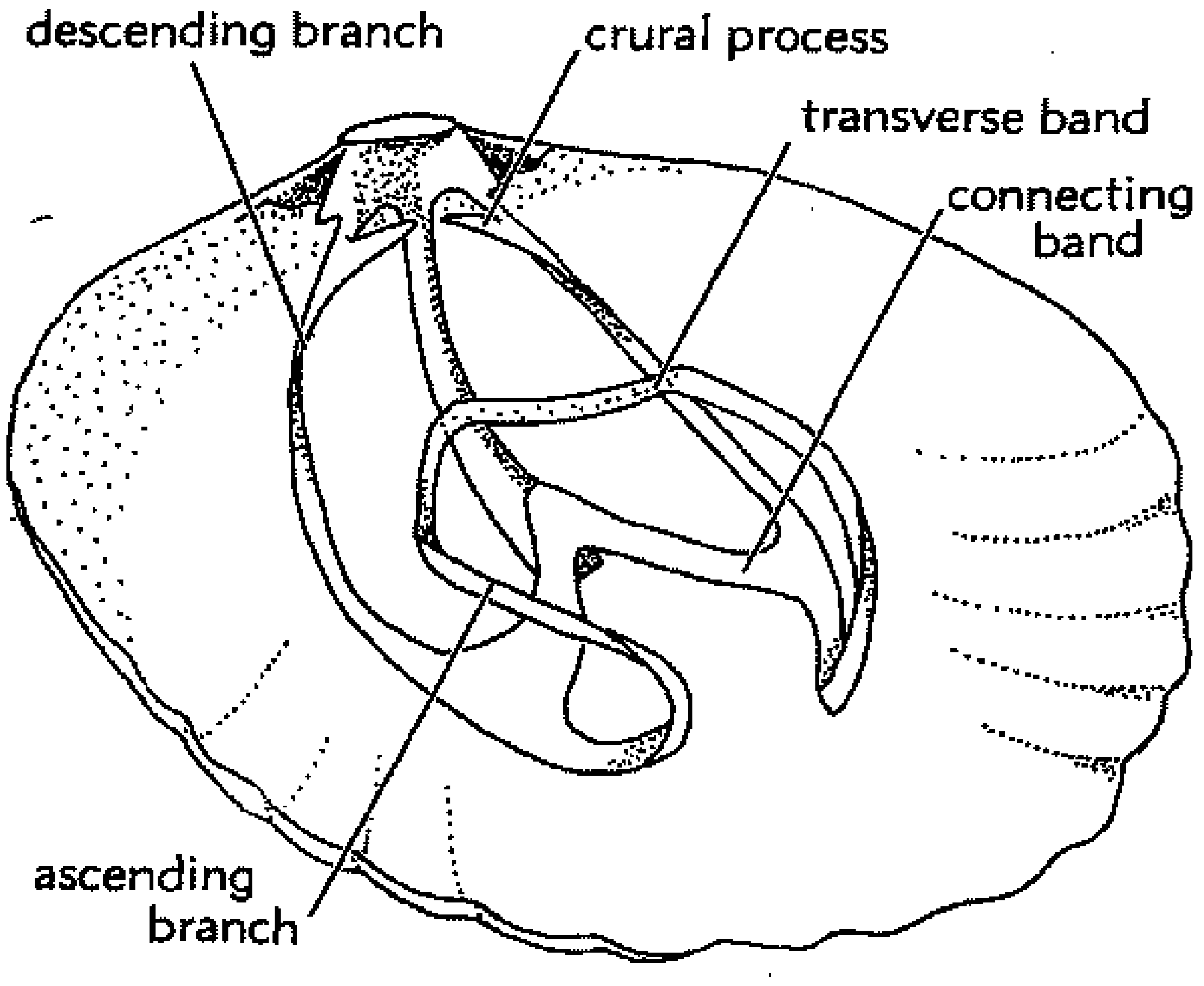

FIG. 111. Morphology of terebratellid loop (early terebratelliform growth stage) (63).

has been built up and is fully illustrated in the systematic section dealing with the terebratuloids. In the meantime it is worth noting that in the kraussinids, structures associated with the septa are the first to appear, and the descending branches appear later or not at all (22). In *Argyrotheca* (Fig. 105,6), the descending branches unite with an undifferentiated median septum to support a trocholophe (4).

Apart from the terebratuloids and immature spiriferoids, loops are found in only the pentameracean *Enantiosphen* and the enteletacean *Tropidoleptus* (Fig. 112). The bilobate loop of the former seems to have developed by accelerated anterolateral growth as well as general enlargement (with resorption) from a young subcircular structure and may have supported a modified schizolophe. The growth of the *Tropidoleptus* loop, on the other hand, was dependent on the development of a dorsal median septum and the inferred arrangement seems to have been like that of terebratellaceans, although the lophophore it supported was much more likely to have been spirolophous in the plane of commissure rather than plectolophous (60).

Despite the lack of structures comparable with crura, certain internal features of the brachial valves of strophomenoids, chonetoids, and productoids seem also to have functioned as supports to the lophophore (57). Among the plectambonitaceans, a variably elevated, semicircular, medially cleft disc (**lophophore platform**), like that of *Leptellina*, is commonly found and may

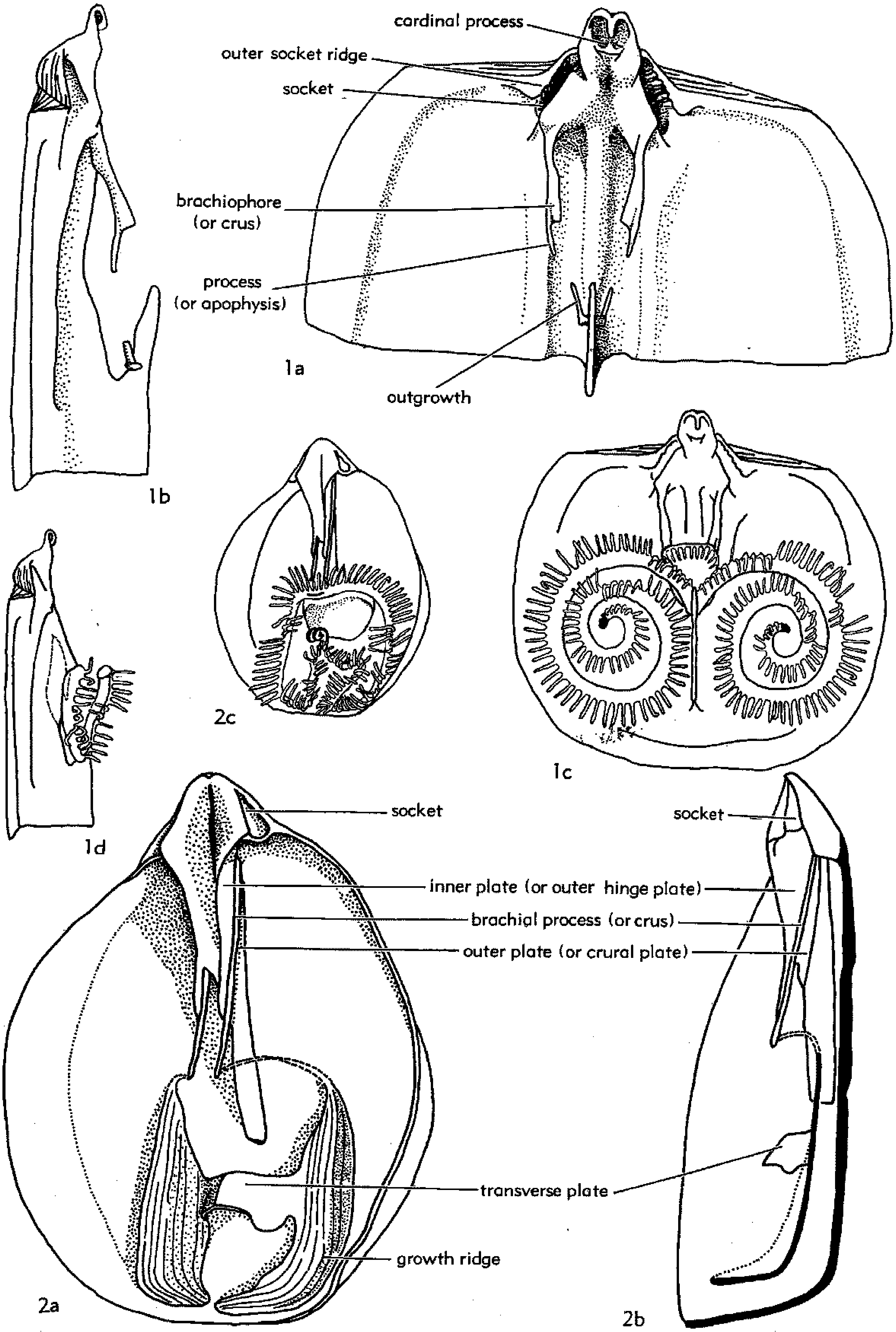

Fig. 112. Internal morphology of brachial valve in *(1a)* ventral and *(1b)* lateral views of *Tropidoleptus carinatus* Conrad, M.Dev., USA, with *(1c,d)* inferred restoration of lophophore in ventral and lateral views; and of brachial valve in *(2a)* ventral and *(2b)* lateral views of *Enantiosphen vicaryi* (Davidson), M.Dev., Eng., with *(2c)* inferred restoration of lophophore in ventral view (60).

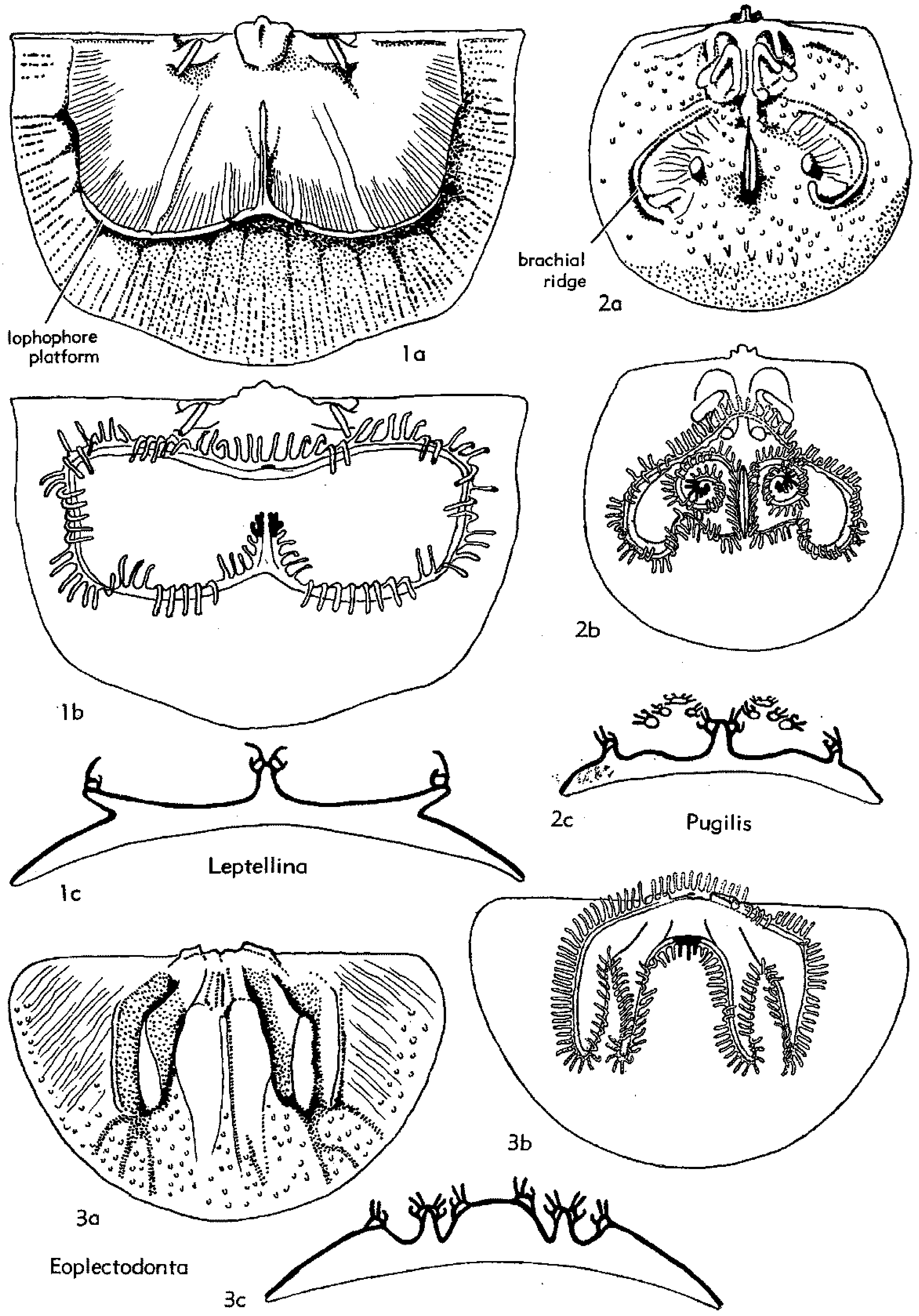

FIG. 113. Internal features of brachial valves of *Leptellina (1a-c)* and inferred restorations of the lophophore viewed ventrally and in transverse section, also of *Pugilis (2a-c)* and *Eoplectodonta (3a-c)* (65).

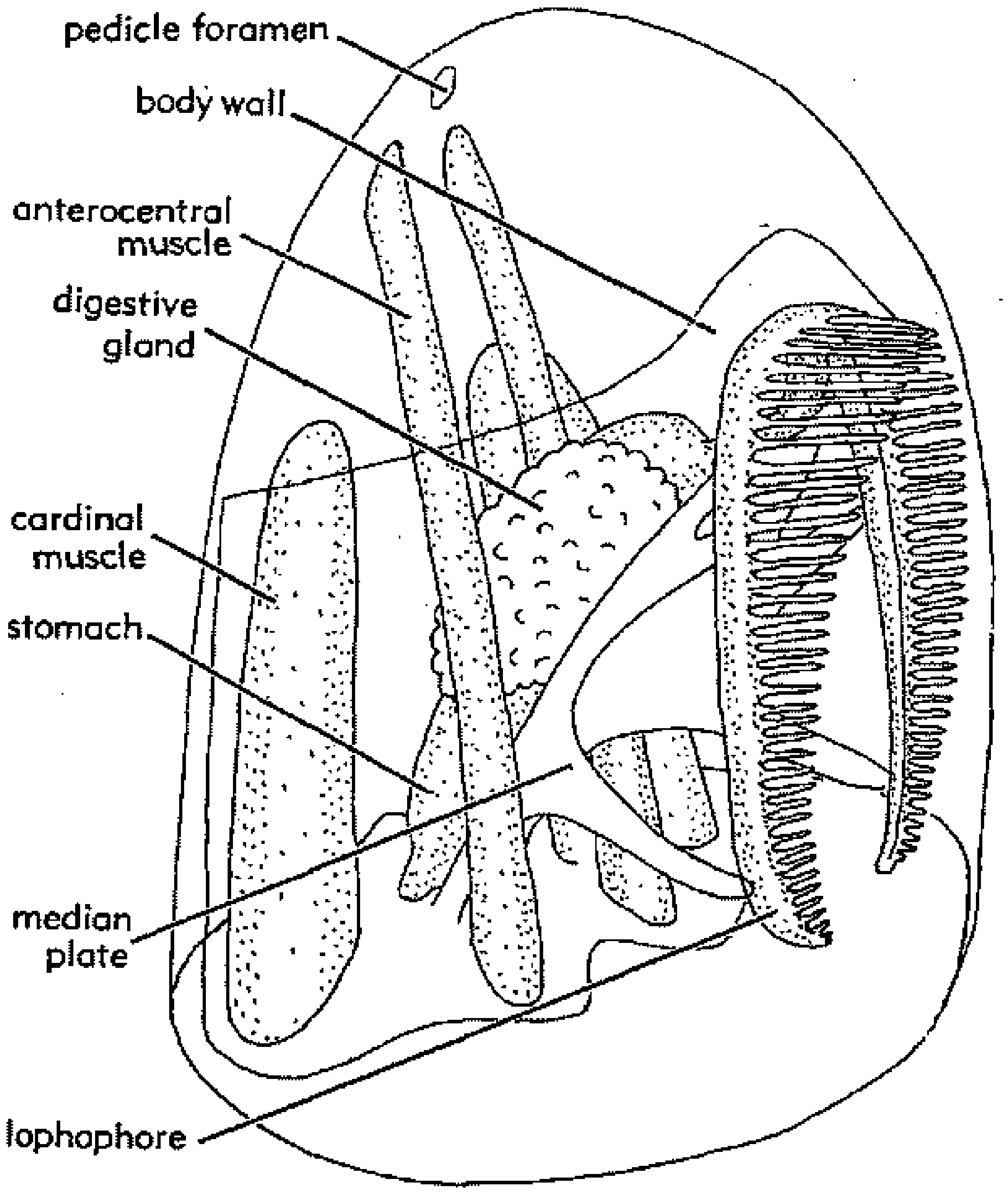

FIG. 114. Stylized reconstruction of *Ephippelasma* with inferred location of lophophore, musculature, and alimentary canal, shell treated as transparent (63).

be interpreted as having borne a schizolophous lophophore (Fig. 113,*1a-c*). The deeply divided, elongately oval platform of *Bimuria* or the pair of long, U-shaped sets of ridges of the strophomenacean *Christiania* must have functioned in a similar way; although like the divergent oval areas of the sowerbyellids, which are not only bounded submedially by ridges but also divided by a pair of divergent lateral septa, the structures may have supported a lobate trocholophe rather than a ptycholophe (Fig. 113,*3a-c*). Indeed, attached and modified trocholophes or schizolophes seem to have been the more likely kind of plectambonitacean lophophore, although spiral impressions in *Leptestia jukesi* (DAVIDSON) suggest that in this stock, at least, the development was not arrested in the schizolophous stage but continued to the spirolophous climax.

Most strophomenaceans and davidsoniaceans were probably equipped with unsupported low spirolophes directed ventrally or dorsally and rarely, as in *Leptaena* and *Davidsonia*, an accommodating differential thickening of the shell has left impressions of spiral coils on the floor of the valves. The productoids, however, together with later chonetoids and rare strophomenaceans (e.g., *Leptaenisca, Leptodonta*), are characterized by a pair of ridges arising between the posterior and anterior pair of dorsal adductor scars and recurving to define a pair of anterolateral areas commonly occupied by a smooth raised mound of secondary shell, or even twisted into two or three convolutions (e.g., *Leptaenisca*). These features are called **brachial ridges,** in the belief that they gave support to the lophophore. They are exceptionally associated with subconical impressions directed ventrally, which might represent differential thickening to accommodate the spirolophous part of a lophophore (e.g., *Levitusia, Gigantoproductus*). The ensemble suggests a plectolophous arrangement but with the side arms remaining adnate to the brachial valve and the spirolophe disposed as a pair of low spires in the same plane, so that both parts were aligned normal to their attitude in terebratuloids (Fig. 113,*2a-c*).

It has also been suggested that the brachial ridges may represent traces of the mantle canal system, such as sites of gonocoels, mainly because they commonly arise from the dorsal muscle field in a position occupied by the *vascula myaria* of orthoids and strophomenoids (33). The mantle canal systems of the productoids are unknown, but traces of radiating peripheral canals seen in *Peniculauris* terminate abruptly against the well-developed brachial ridges. This dissociation is even better seen in *Leptaenisca* and *Leptodonta,* both of which belong to groups that are known not to possess any feature like brachial ridges in the mantle canal system. Indeed, the elongately oval platforms of *Stipulina,* which are clearly elevated structures incorporating the brachial ridges, are so like the lophophore platforms of the plectambonitaceans that any function other than support to the feeding organ is difficult to imagine.

Among inarticulate brachiopods there are no prolongations of the shell which indisputably functioned as lophophore supports; but projections from the brachial valve of a few acrotetid genera may have given support to the lophophore and anterior body wall. This would appear to be the most probable function of the saddle-shaped plate of *Ephippelasma* (18), which arises from a

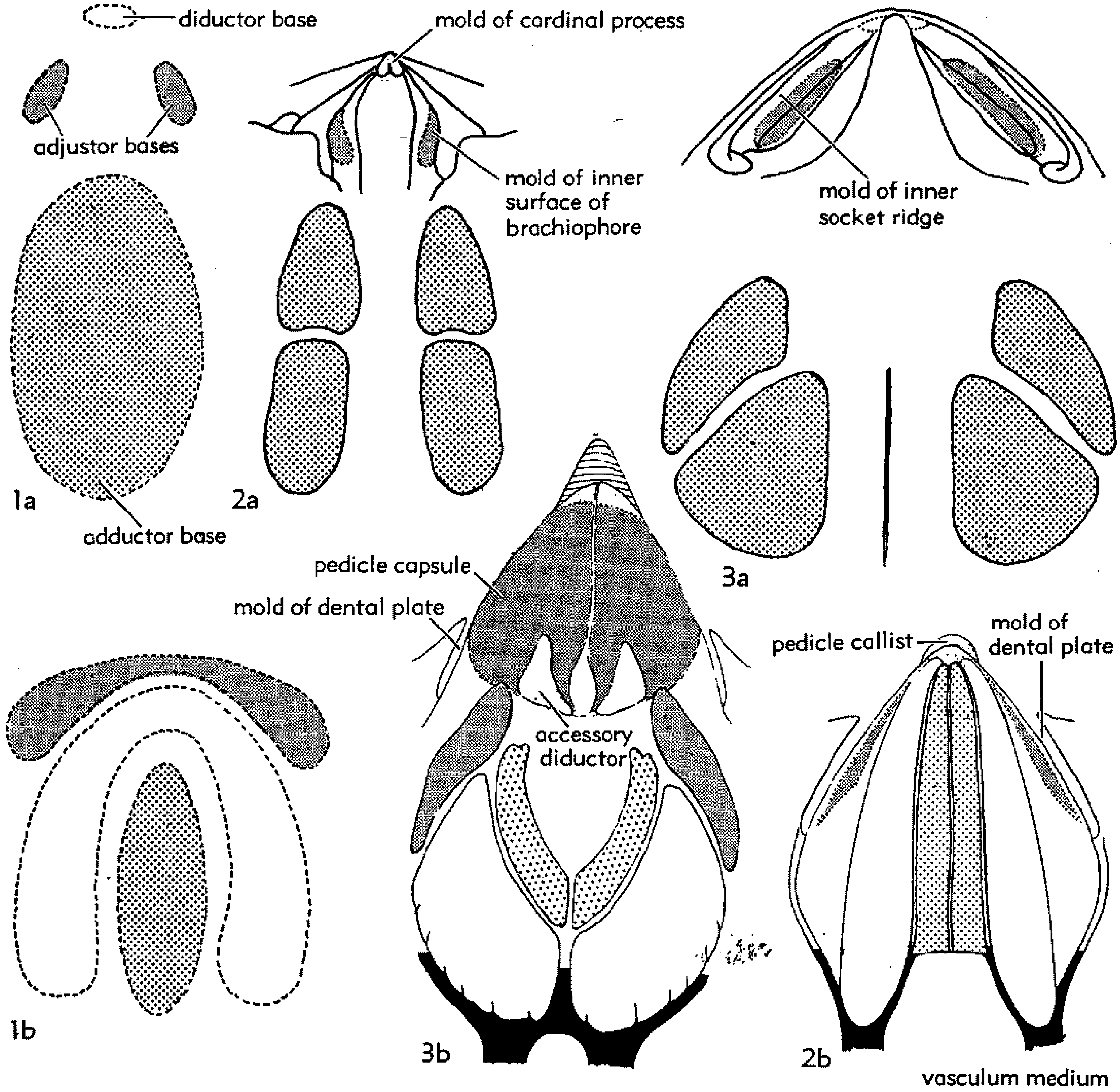

FIG. 115. Diagrammatic representation of principal muscle marks in *(1a)* dorsal and *(1b)* ventral interiors with examples of corresponding actual scars seen in *Dalmanella wattsi* (BANCROFT), M.Ord., Eng. *(2a,b)* and *Hemithiris psittacea* (GMELIN) *(3a,b)* (65).

relatively narrow base slightly behind the center of the valve and expends ventrally and anteriorly to terminate in a number of slender projections (Fig. 114). These projections are disposed with a crude symmetry about the median plane and their tips roughly fall on an imaginary surface which is inclined posteroventrally to make a high angle with the plane of commissure. The mouth in *Ephippelasma* presumably lay in the plane of symmetry, as in all Recent brachiopods, and must have opened along the crest line of the median plate or ventrally of this line. All adult individuals of *Ephippelasma* are small enough to suggest that their lophophores were probably trocholophous or schizolophous; and if the tips of the projections from the median plate touched the anterior part of the body wall, the limited brachial cavity could conveniently have accommodated a trocholophe (or schizolophe) only when the organ was oriented approximately parallel with the plane defined by the tips of the projections. In this attitude, the median projection could have supported the lophophore immediately dorsal of the mouth, with the laterally placed prongs embedded in the posterior arcs of the trocholophous ring on either side of the mouth.

Many other acrotretid genera have a thin bladelike median septum, usually subtriangular in lateral profile and attached basally along its length to the brachial valve. The posteroventral edge of the median septum is commonly unmodified, but it may bear a slender triangular plate (e.g., in *Torynelasma*) or it may be narrowly expanded and digitate in a plane more or less normal to the septum (e.g., in *Angulotreta, Prototreta*). In all these forms, the medially situated mouth must have lain on, or ventral of, the free edge of the septum, which dorsally may have supported the generative tips of a trocholophe or schizolophe. The modifications on the posteroventral edge of the septum, however, are generally too narrow to have given much support to the lophophoral arcs lateral of the mouth.

MUSCULATURE

The muscles of most articulate brachiopods that leave their impressions (**muscle marks**) on the shell interior consist of two sets passing between the valves (**diductors, adductors**) and another two sets controlling the pedicle (**ventral** and **dorsal adjustors**). In the pedicle valve, all muscle marks tend to be grouped together to form a muscle field, which is ideally differentiated into a median adductor muscle mark contained posteriorly by two incomplete arcs of inner diductors and outer adjustors (Fig. 115,*1b, 2b,3b*). The attachments areas in the brachial valve, however, are generally much more scattered (Fig. 115, *1a,2a,3a*). The adductor field commonly consists of an anterior and a posterior pair of marks, with one of each pair discernible on either side of the median line and well forward of the cardinalia, which accommodated both the dorsal adjustors and dorsal ends of the diductors, usually along the inner faces of the hinge plates (or brachiophores) and on a posteromedian outgrowth of secondary shell (cardinal process), respectively.

The muscle marks can vary not only in their relative position but also in the clarity of their impression. They may be deeply inserted or raised above the general level of the valve floor, or even greatly elevated on elaborate platforms. The definition of muscle marks in brachiopod shells is normally a function of age, so that the ultimate area of attachment attained in adult stages of growth (**muscle scars**) is much more easily seen than the impressions in young or immature valves. This clarity is due mainly to differential secretion but can also result from a change in the texture of that part of the secondary layer affording attachment. Deposition by the modified epithelium underlying the muscle bases is commonly slower than elsewhere, so that the muscle marks are sunk below the level of adjacent shell. Indeed, even when the entire muscle field is raised above the valve floor on thick deposits of secondary shell, the marks themselves may be deeply impressed on the platform. Such impressions usually include a variable number of strip-like indentations (**muscle tracks**) disposed parallel with the adjacent boundaries of the muscle scars, which represent the course of migration for the muscle bases during shell growth.

The migration of muscle bases can involve two aspects of growth. First, the proportions of the field relative to those of the valve may remain constant, or they may undergo changes at any stage in growth by an accelerated expansion in size of either the valve or the muscle field. Greatly extended and splayed impressions (**flabellate muscle scars**) are commonly found in the adult pedicle valves of many stocks and usually result from an acceleration in the spread of the muscle bases. Secondly, irrespective of any changes in relative growth rates, there is always an absolute increase in the area occupied by the muscle bases, which may be greater along some vectors than others, so that the outline of the muscle marks may change significantly during growth.

The histological changes that make possible this increase in size are well seen in *Terebratulina* (Fig. 116,*A*), and were probably also typical of extinct groups. Fibers, together with an intervening sheet of connective tissue, are proliferated along the anterior and lateral boundaries of the muscles and spread over the inner surface of outer epithelium. As they become incorporated into the main mass of muscle, both connective tissue and associated outer epithelium become modified by the passage through them of tonofibrils. The muscle marks probably correspond to the area of modified epithelium and it is evident from the existence of muscle tracks that, like growth of the shell, distinct pauses occur in expansion of the muscle fields. Physiological changes within the modified outer epithe-

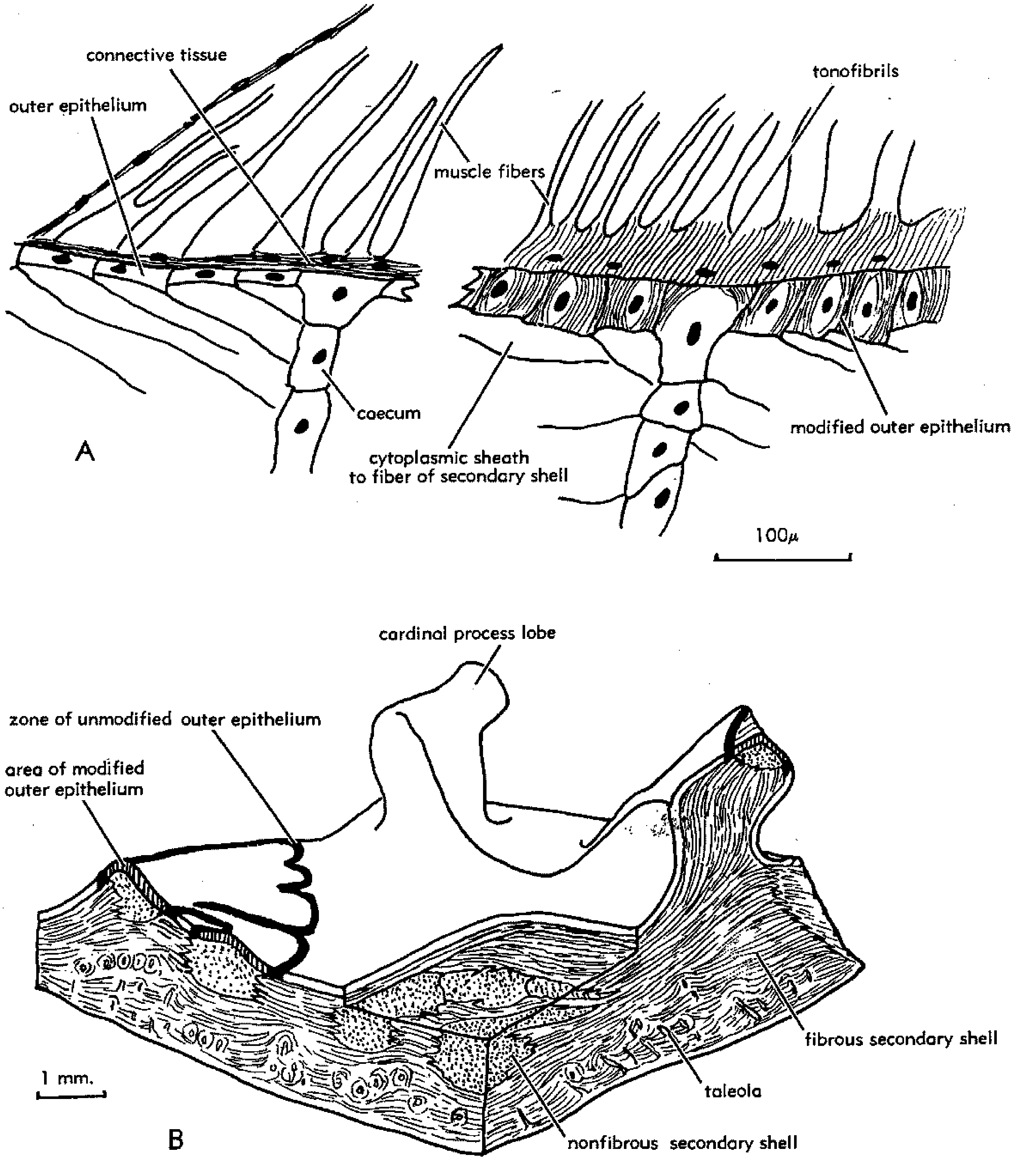

FIG. 116. Relationship (*A*) between diductor muscle base and shell of *Terebratulina caputserpentis* (LINNÉ) as seen at, and well within, the muscle boundary (to left and right respectively); and inferred relationship (*B*) between outer epithelium and muscle fields of *Strophonelloides* sp., U.Dev., USA (65).

lium underlying the muscle bases were probably responsible for differences in shell deposition that commonly characterize the muscle scars of later strophomenoids and productoids which are usually convoluted (dendritic impressions) in a manner that reflected the intricate lobation of the muscle bases. In these stocks, the shell making up the attachment areas for the muscles consists of cryptocrystalline calcite (55), which was probably deposited extracellularly by modified epithelium, inserted deeply within and encroaching anteriorly over the fibrous layers (Fig. 116,*B*). Differences in texture may also be found in other articulate groups but are usually related to re-orientations of fibers within the secondary shell as in *Schizophoria* (52); or to concentrations of prismatic secondary shell, as in some spire-bearing brachiopods and pentameroids (42),

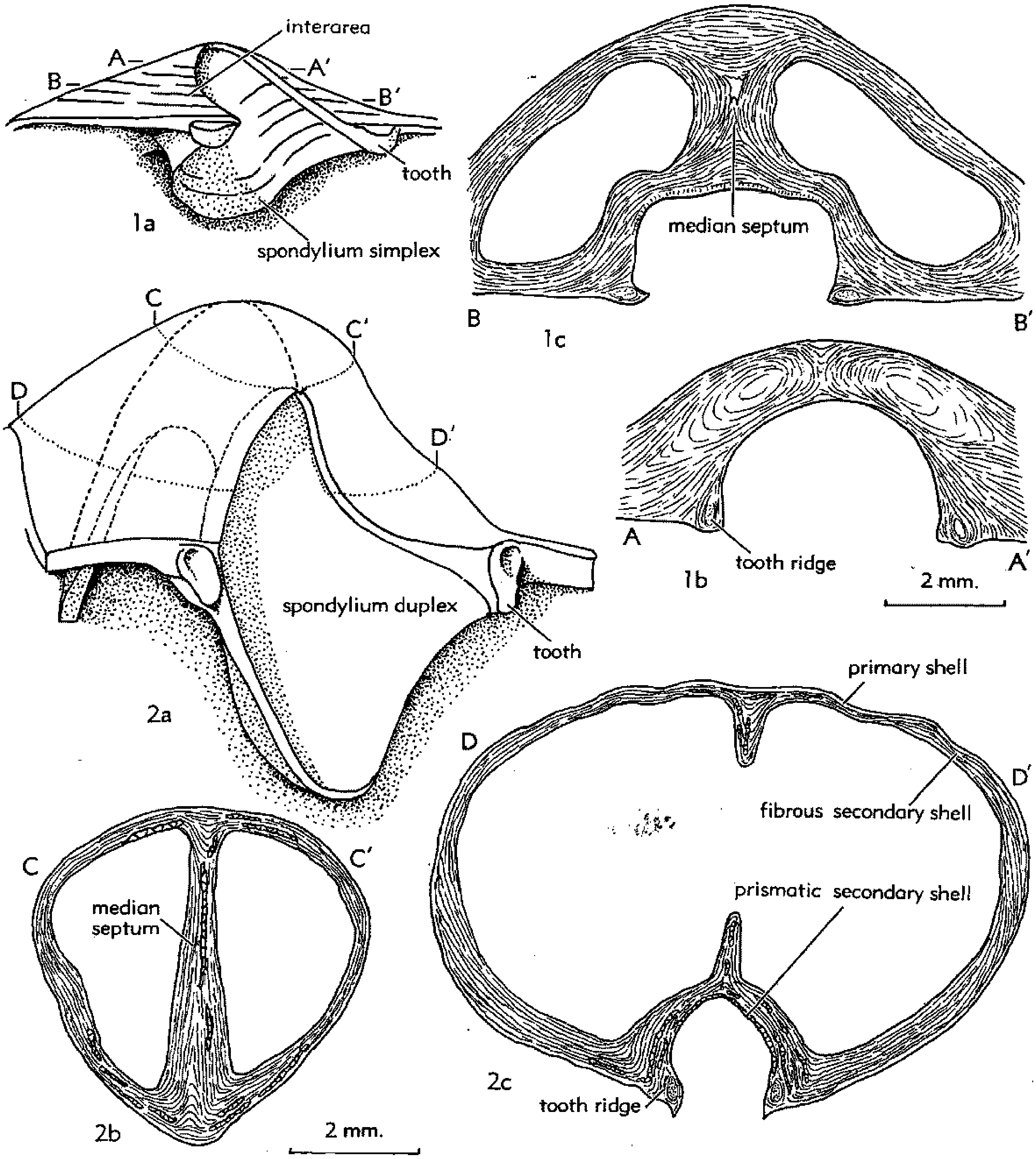

FIG. 117. Pedicle valves showing (1) spondylium simplex of *Skenidioides craigensis* REED, M.Ord., Scot., and *(2)* spondylium duplex of *Gypidula dudleyensis* SCHUCHERT, U.Sil. (Wenlock.), Eng.; *1a,* oblique view showing location of transverse sections, *1b,c; 2a,* oblique view showing location of transverse sections, *2b,c* (65).

which, however, is not restricted exclusively to the main muscle-bearing bases (21).

The growth and distribution of platforms and apophyses to accommodate the various sets of muscles controlling shell movement are related to both the function and grouping of the muscles. The ventral muscle field tends to be located posteriorly of the transverse mid-line and, apart from details of outline, its relative size probably does not vary greatly throughout the majority of articulate brachiopods. An important difference, however, is noted in location of the field within the valve, since those of rhynchonelloids, spiriferoids, and terebratuloids are well forward of the umbonal chamber which accommodated the pedicle base, whereas the orthoid, strophomenoid, and

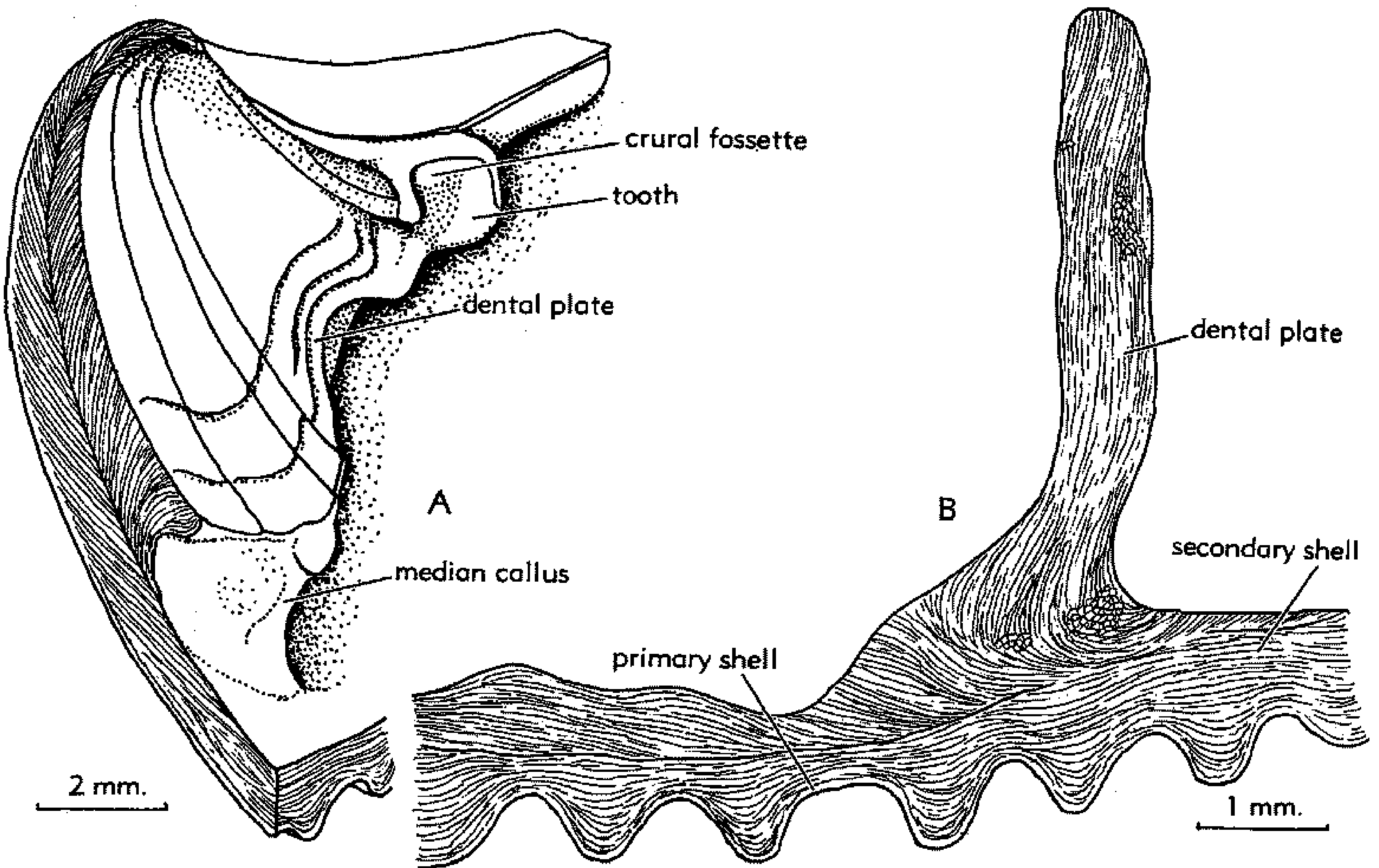

FIG. 118. *A*, Structure of pseudospondylium of *Glossorthis tacens* ÖPIK, M.Ord., USSR, with *(B)* transverse section showing relationship between dental plate and floor of pedicle valve (65).

porambonitacean fields typically occupied all available wall space within the delthyrial chamber, and usually did not extend very much forward of it (61) (Fig. 115,*2b*,*3b*). One of the consequences of this posterior location in the older brachiopods is that the dental plates commonly afforded attachment for the ventral adjustors and, by convergence toward each other, for an increasing area of the ventral diductor and adductor bases as well. Convergent dental plates that united with each other in such a way as to elevate the entire ventral muscle field above the floor of the pedicle valve constitute a **spondylium** (Fig. 117).

The spondylium is pre-eminently characteristic of the clitambonitoids, pentameroids, and stenoscismataceans, but it is also found in other unrelated stocks such as the orthacean *Skenidioides,* the davidsoniacean *Ombonia,* and the stringocephalacean *Amphigenia*; and a complicated terminology, partly reflecting this diversity of origin, is now used to indicate various stages in spondylial development. KOZLOWSKI (28) named the slightly convergent dental plates that grew directly from the floor of the pedicle valves of certain porambonitaceans like *Huenella,* the **spondylium discretum.** This arrangement is, however, identical with that of most orthaceans and the term is acceptable only where clear evidence indicates that such a disposition was precursory to growth of a spondylium. Structures involving discrete dental plates are also known as **pseudospondylia** (43) if the anterior part of the ventral muscle field is elevated on an undercut callosity which may be prolonged anteromedianly as a ridge (Fig. 118). Pseudospondylia have frequently been designated sessile spondylia, but it is preferable to restrict the use of this latter term, with its implications of a true spondylial relationship, to structures formed by dental plates that unite with each other on the floor of the pedicle valve (e.g., *Sicelia*).

Spondylia formed by the convergence of dental plates above the floors of adult valves may be free of septal support, as in *Protorthis* and *Holorhynchus,* and presumably represent an anteromedian growth from a juvenile sessile spondylium. More commonly the spondylium is supported by a median septum or ridge of variable length. KOZLOWSKI (28) distinguished between two types of septal support. In the **spondylium sim-**

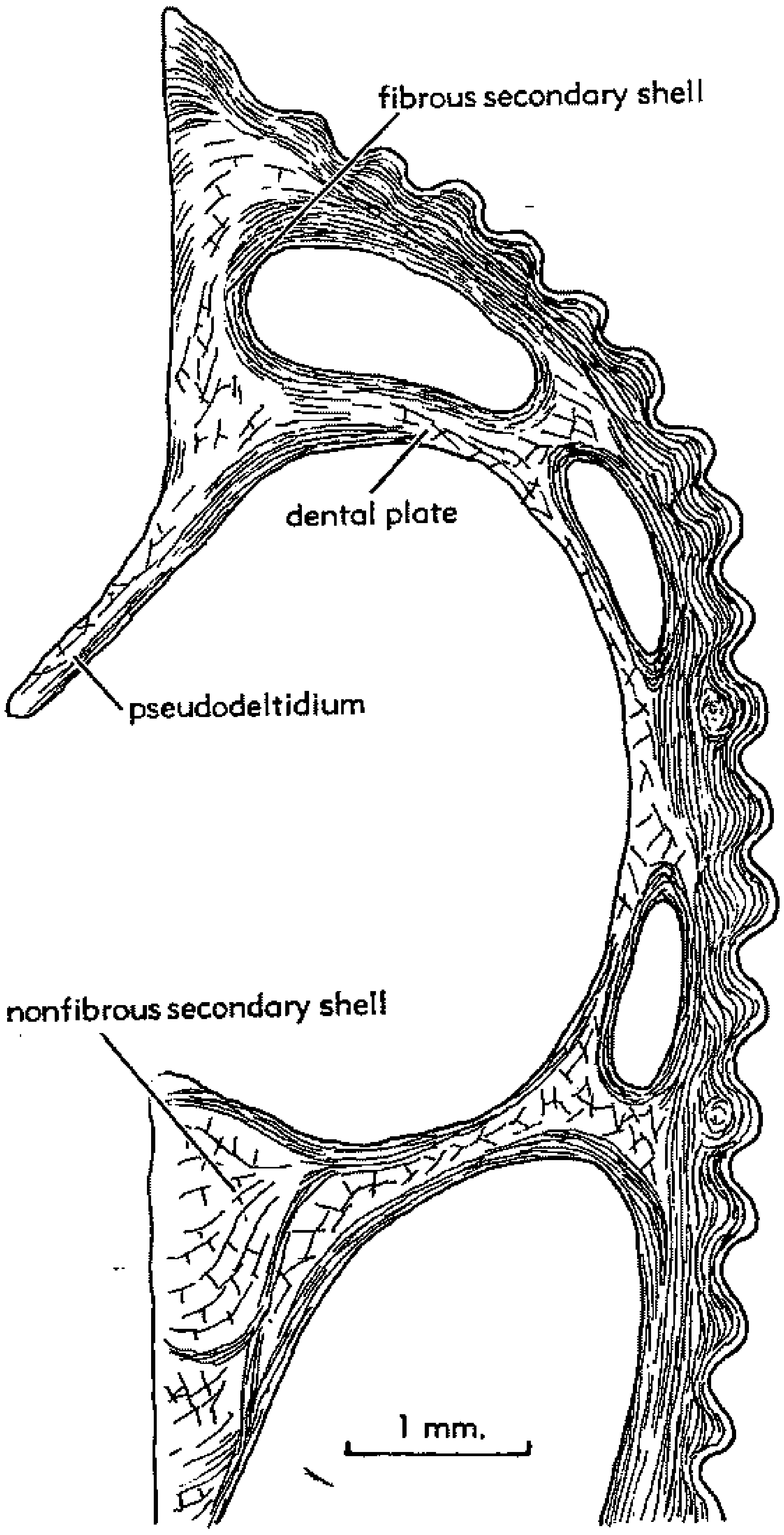

FIG. 119. Section through spondylium triplex of pedicle valve of *Antigonambonites planus* (PANDER), L.Ord., Baltic (65).

plex of *Skenidioides,* for example, the median septum consists of secondary calcite disposed in such a way as to suggest the incremental growth of a single structure. A low elevation of secondary shell commonly trailed anteriorly from the septum along the floor of the valve and became buried during the subsequent thickening and forward growth of the entire apparatus so that anterior sections of the adult spondylium simplex appear to show a dichotomy in the ventral end of the septum (Fig. 117,*1a-c*). KOZLOWSKI believed that this kind of arrangement evolved by the elevation of the entire pseudospondylium above the floor of the valve, rather than by a convergence of dental plates. In contrast, a thin plate of prismatic calcite (intraseptal lamella) appeared invariably to occupy the median plane of the septum supporting the pentameracean **spondylium duplex**; and its presence led KOZLOWSKI to conclude that such a septum was formed by the incomplete fusion of the dental plates (Fig. 117,*2a-c*). He also assumed that the spondylium duplex was derived from the spondylium discretum by the convergence of the ventral parts of the dental plates toward each other.

The differences between the spondylia simplex and duplex may not be as fundamental as is generally believed (60). The intraseptal lamella has been described as having an enlarged base at the junction of the septum with the spondylium and as thinning out toward the floor of the valve, a disposition that is compatible with the prevalent interpretation of its origin. But ST. JOSEPH (42) and AMSDEN (2) have observed that the dorsal end of the intraseptal lamella can be continuous with extensive deposits of prismatic calcite lining the spondylium. Moreover, serial sections show that in at least some pentameracean genera (e.g., *Antirhynchonella, Pentamerella, Gypidula*) the prismatic calcite along the median plane of the septum is disposed more like a series of disconnected lenticles than a continuous sheet and in some planes of section is no more concentrated medially than elsewhere throughout the septum or spondylium (Fig. 117,*2b*). The distinctiveness of the spondylium duplex may therefore have resulted from the secretory activities of the outer epithelium of the pentameraceans, which, unlike that of the skenidiids, was capable of depositing prismatic calcite (57); and not from an imperfect fusion of dental plates. This interpretation would account for a more random distribution of the two different types of spondylia than was formerly believed possible. For a spondylium simplex has been identified in the syntrophiids and a spondylium duplex in the stenoscismataceans and camerellids; the spondylium of *Amphigenia* is truly duplex in that the dental plates are seen to unite into a median "septum" (11).

Complications also arise in the use of the term spondylium triplex (37) for an apparatus with a variably developed triseptate support which is especially characteristic of certain gonambonitaceans (Fig. 119). In the genera described by ÖPIK, the median and lateral (or accessory) septa underlying the spondylium were fashioned during early stages of growth by a pair of subconical hollows that developed between the floor of the valve and a sessile spondylium as it diverged in an anterolateral direction. In *Antigonambonites*, at least, the lateral septa acted as posterior partitions between the *vascula media* and *vascula genitalia* of the ventral mantle so that their growth may have been conditioned by the relationship between the ventral mantle canals and the body cavity. The term may therefore be used for the spondylia of some porambonitaceans, like *Tetralobula*, in which accessory septa, posteriorly underlying the spondylium, are also lateral boundaries to the ventral *vascula media*. It has been used, but is less appropriate, except in a strictly morphological sense, for the structure found in *Polytoechia*, which appears to consist of a pair of subparallel dental plates containing a pseudospondylial platform elevated on a median septum.

The apparatus found in the pedicle valve of *Cyrtina* (Fig. 120) is not a spondylium in the sense that its posterior elements gave support to the entire ventral muscle field. It consists of a long, high, bladelike, median septum to which the short, convergent, dental plates are ankylosed just below the posterior edge. A pair of lateral struts are subtended between the inner surfaces of the dental plates and the posteriorly protruding part of the median septum to define a small chamber (**tichorhinum**), suboval in section and extending from the umbo to the dorsal edge of the median septum. The tichorhinum is actually a chamber within a larger one bounded by an arched deltidium and the dental plates which must have contained the pedicle. Within such an arrangement, the tichorhinum, which may be incompletely partitioned (28), probably accommodated the base of the pedicle (the so-called unpaired median pedicle muscle) with the ventral adjustors attached to the anterolateral surface of the dental plates; and the ventral ends of the adductor and diductor muscles inserted on either side of the median septum anterior to its junction with the dental plates. In respect of their convergence into a median septum well posterior of the ventral muscle field, the dental plates are like the short dental ridges

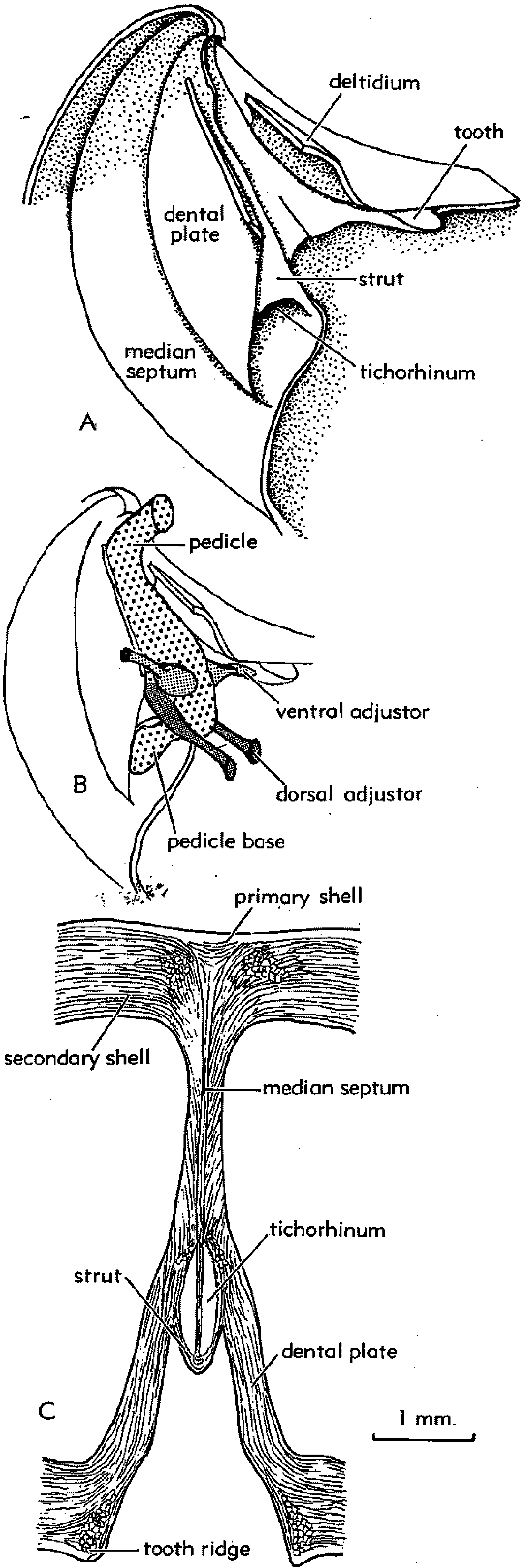

FIG. 120. *A*, Tichorhinum of *Cyrtina* sp., L.Carb., N.Ire., with *(B)* inferred disposition of the pedicle and its muscles, and *(C)* section showing tichorhinum of *Cyrtina* sp., M.Dev., USA (65).

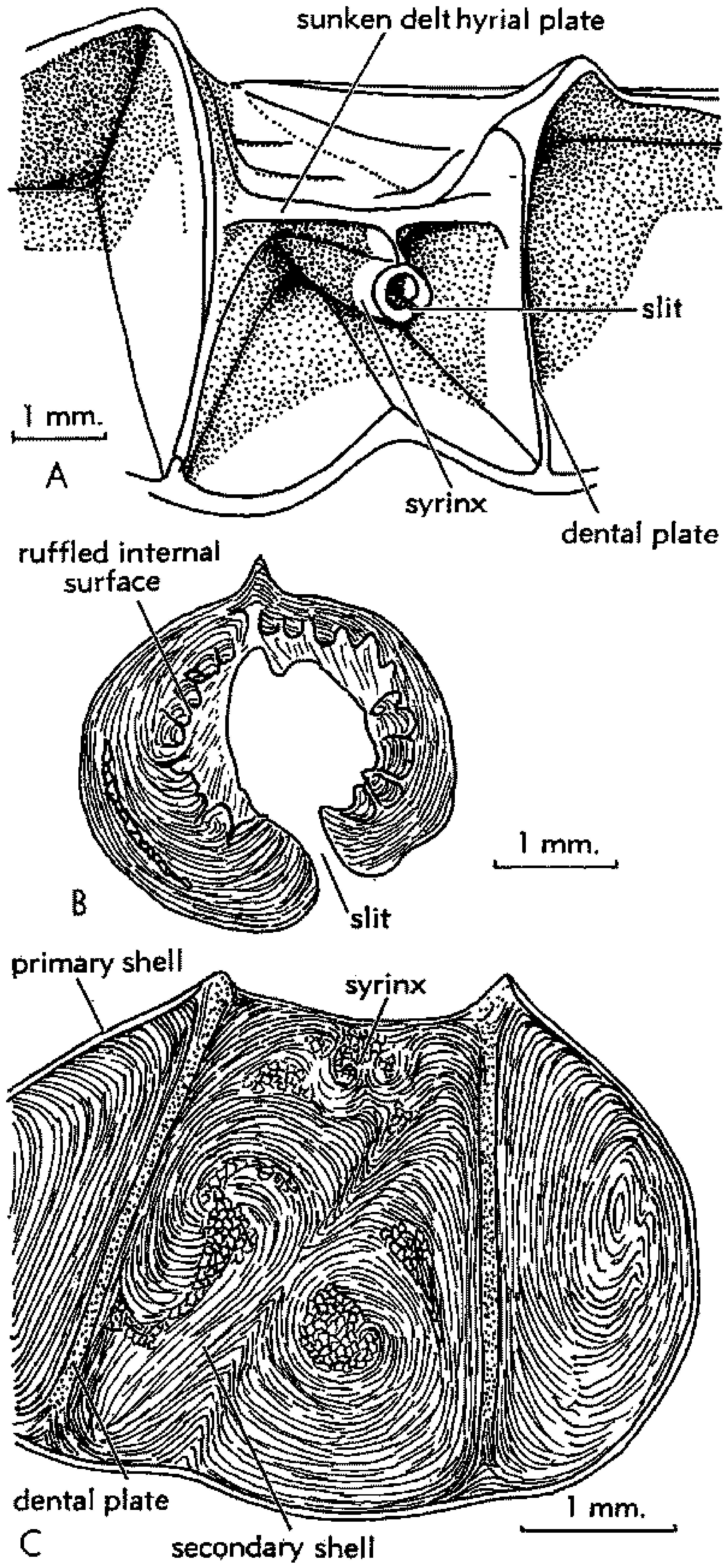

FIG. 121. *A*, Ventral interior of *Syringothyris cuspidata exoleta* NORTH, L.Carb., Eng., with *(B)* transverse sections of free dorsal end of syrinx and *(C)* of apex (65).

of certain davidsoniaceans (e.g., *Orthotetes*), which also form a small chamber that has been incorrectly called a spondylium. Contrary to general opinion, the syrinx of *Syringothyris* (Fig. 121) may have performed same functions as the tichorhinum. The sunken plate (delthyrial plate) within the delthyrium, to which the syrinx is attached, is probably homologous with the pedicle collar and would thus have lain anteroventrally to the pedicle or its remnant. If this were so, the syrinx would have been deposited by outer epithelium around the attached end of the pedicle base which also

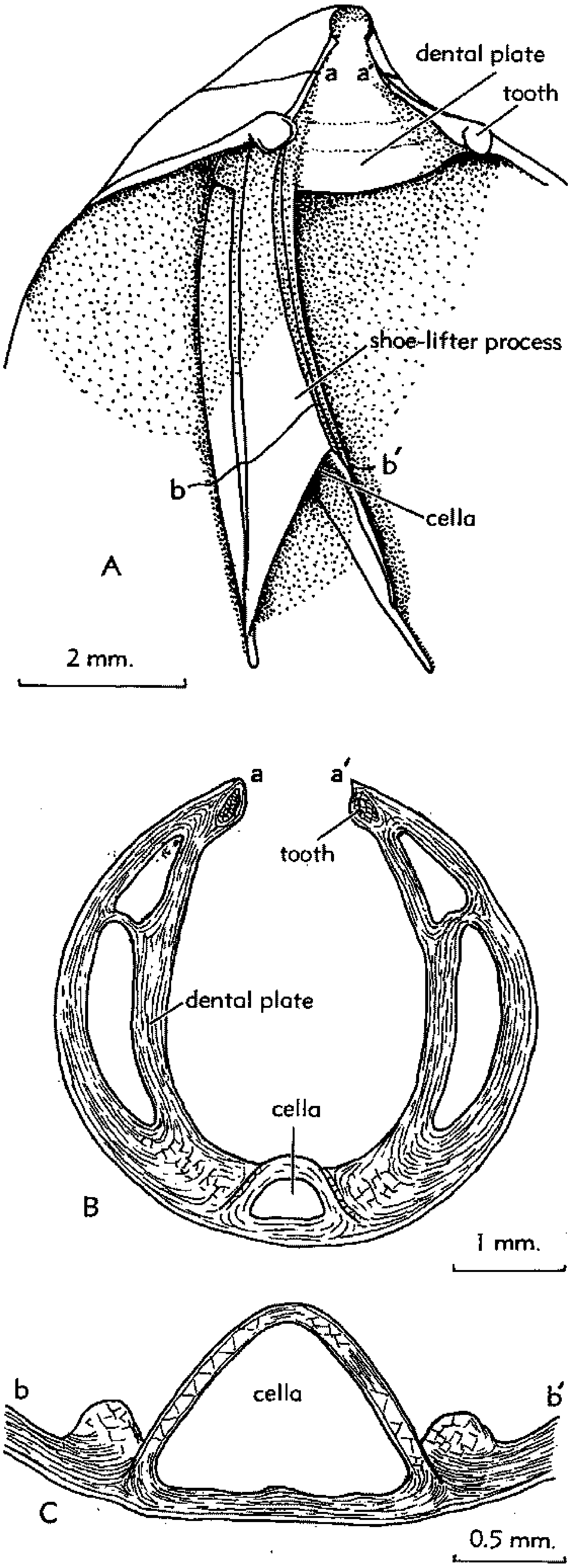

FIG. 122. Pedicle valve of *Merista tennesseensis* HALL & CLARKE, M.Sil., USA, showing shoe-lifter process; *A*, oblique view showing location of transverse sections, *B*, *C* (65).

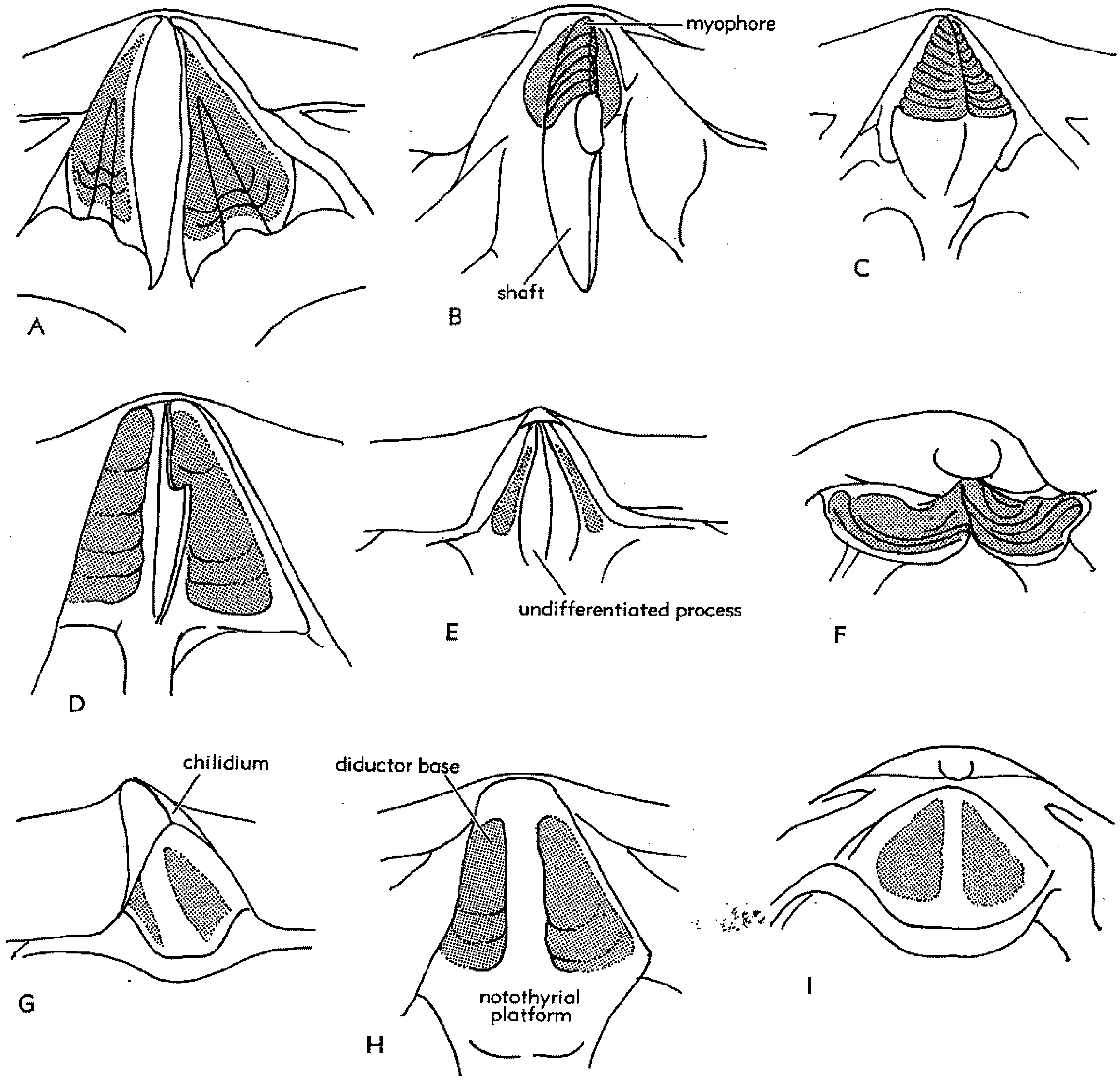

FIG. 123. Various types of cardinal processes: *(A)* development of subsidiary ridges flanking median septum of *Glossorthis,* with *(B, C)* differentiation of myophore and shaft in *Hebertella* and *Dinorthis*; *(D, E)* simple partition of *Glyptorthis* and *Bimuria* and *(F)* transverse area of muscle insertion of *Notosaria;* *(G-I)* undifferentiated areas for dorsal diductor attachment of *Leptella, Nothorthis,* and *Terebratulina* (65).

protruded anteriorly through the split on the syrinx. This interpretation is consistent with the pattern of muscle impressions on the floor of the pedicle valve, the closed ventral end of the syrinx and the sporadic development of a deltidium or stegidium posterior of the sunken plate. One other type of muscle platform was developed among certain spire-bearing brachiopods (27) such as *Merista* and its allies (Fig. 122). It consists of a transverse partition (**shoe-lifter process**) extending across the posterior part of the pedicle valve to define an open, hemipyramidal chamber (**cella**). The process was formed by deposition of secondary shell within an infold of outer epithelium elevated above the floor of the pedicle valve even in early stages of growth so that in some genera (e.g., *Aulidospira*), the dental plates encroached forward over the inner surfaces of the partitions. A similar structure, which bears a strong median septum, is found in *Parenteletes.*

The dispersion of the attachment areas of the diductor and adductor muscles within the brachial valve has led to independently derived modifications of the dorsal interior. In general, the former are inserted near or at the notothyrial apex and posterior of the articulatory fulcral

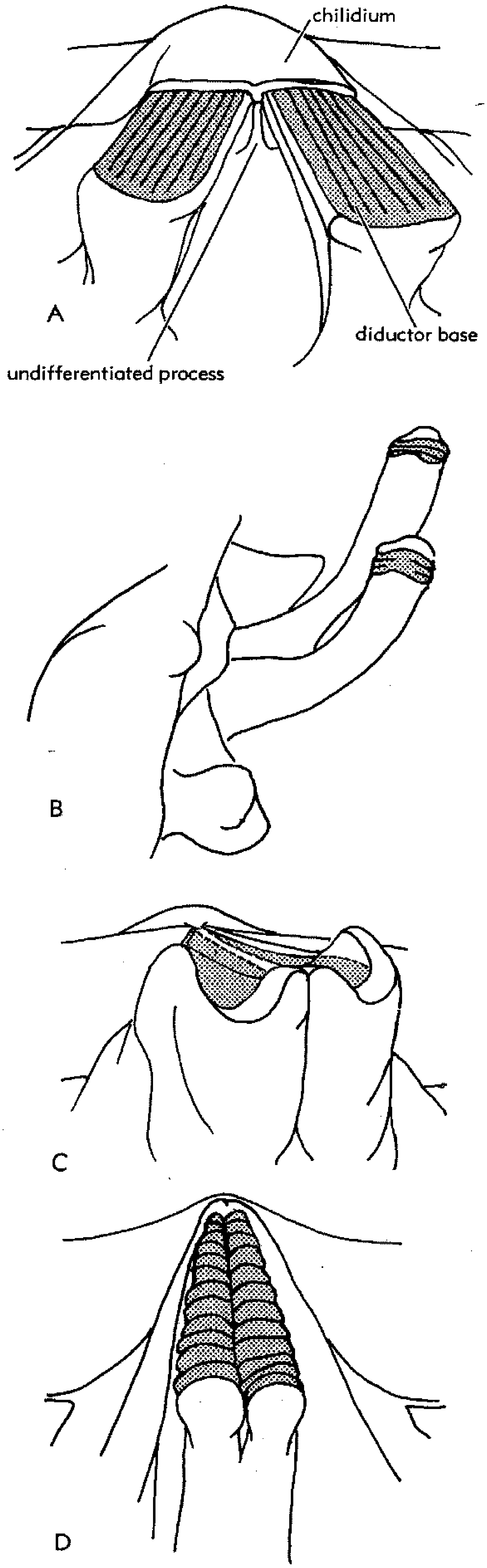

Fig. 124. Various types of bilobed cardinal processes: *A, Rafinesquina,* with vestige of median undifferentiated process; *B, Oxoplecia*; *C, Resserella*; *D, Dalmanella* (65).

points to provide a third order lever; and the latter submedially on the valve floor and well forward of the hinging mechanism. Ideally, both muscle sets are attached symmetrically about the median plane, the diductors to a pair of small bases, the adductors to two pairs of relatively large scars (Fig. 115,*1a,2a,3a*); and this symmetry of insertion has led to many morphological changes especially around the dorsal beak.

In primitive articulate brachiopods, the dorsal ends of the diductor muscles were implanted on the notothyrial platform or, if this infilling was absent, on the inner sides of the brachiophores where they meet to define the notothyrial apex (Fig. 123, *G,H*). Accelerated deposition of secondary calcite by the strip of outer epithelium between the discrete muscle bases commonly led to the outgrowth of a variably defined median partition as in the orthaceans, plectambonitaceans, and even a few porambonitaceans (e.g., *Diaphelasma*). Such an outgrowth is referred to as a cardinal process, irrespective of whether it separated the areas for muscle insertion or whether it served as a surface for attachment (Fig. 123,*D,E*). Thus, in some orthaceans, most enteletaceans and early rhynchonelloids (like *Orthorhynchula*), the muscle bases migrated medially to occupy the lateral and posterior surfaces of the partition (Fig. 123,*B,C*). Concomitant with this specialization, the median process became enlarged and differentiated into a **shaft** surmounted by a swollen head (**myophore**) which was crenulated by a series of thin plates of secondary calcite, thereby increasing the area for muscle attachment (Fig. 123,*B,C*). In many enteletaceans (e.g., *Dalmanella*) the discrete nature of the muscle bases gave rise to a bilobed cardinal process by the development of a cleft on the posterior face of the myophore during its ventral growth (Fig. 124,*D*). In *Resserella*, each lobe of the divided myophore is bordered ventrally and laterally by a narrow, smooth ridge of secondary shell, which acted as a boundary to the central crenulated faces of muscle attachment (differentiated bilobed process)

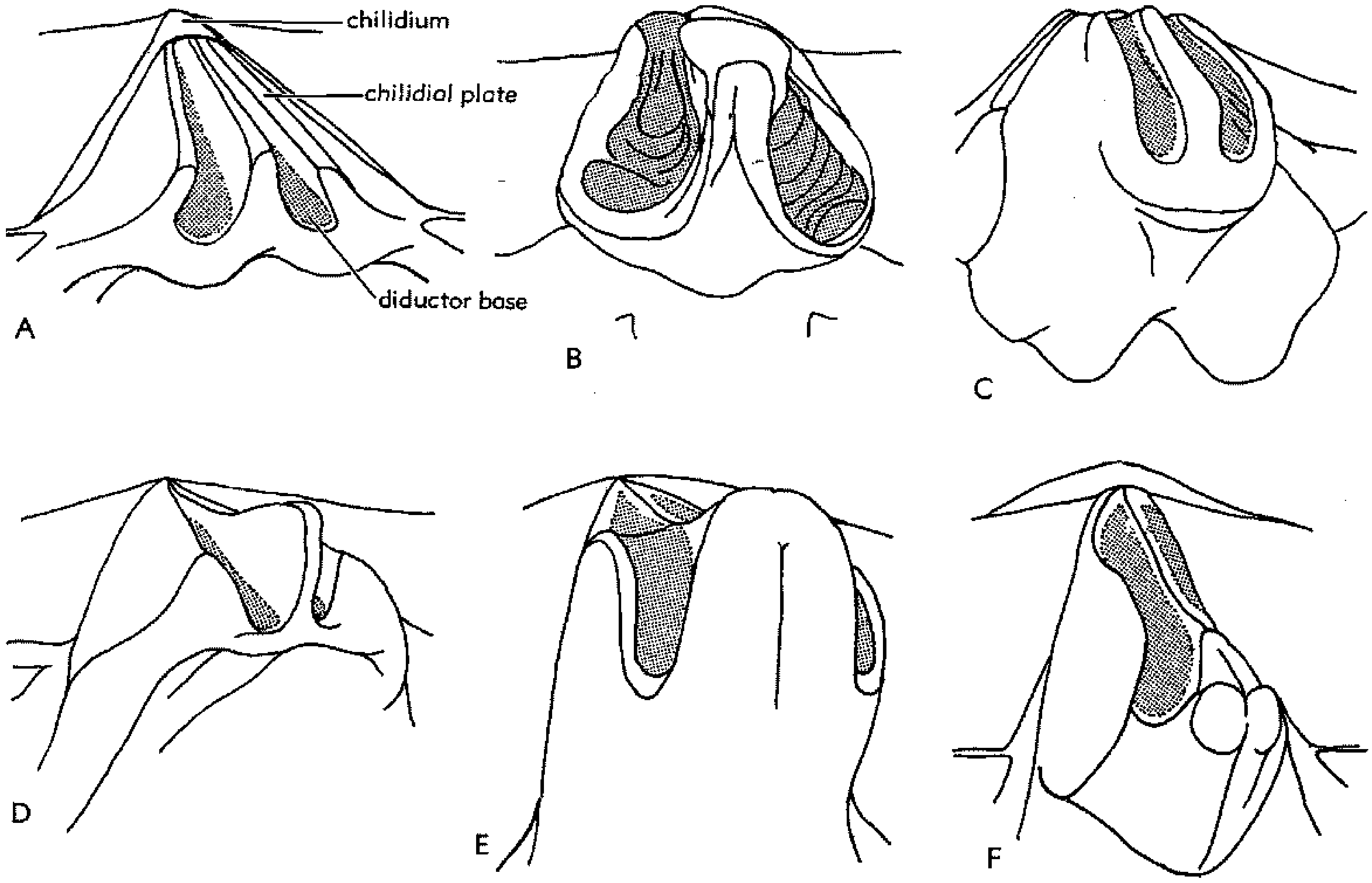

Fig. 125. Various types of trilobed cardinal processes: *A, Sowerbyella*; *B, Pugilis*; *C, Prionothyris*; *D, Orthidiella*; *E, Resserella*; *F, Paucicrura* (65).

(Fig. 124,*C*); and in some species, the two inner adjacent boundary ridges also became ankylosed and expanded posteriorly to simulate a trilobed myophore (Fig. 125,*E*). Alternatively, as in *Paucicrura*, the ventroposterior edge of the myophore expanded at a greater rate than the crenulated areas to form a high median crest and with the development of smooth lateral and ventral boundaries to the attachment areas, a differentiated trilobed process came into being (Fig. 125,*F*), which is a reversion to the condition that prevailed in stocks with a simple median partition except, of course, for elevation of the entire arrangement above the floor of the notothyrium (61).

This pattern of elaboration, related to the posteroventral growth of the cardinal process and a migration of the muscle bases onto its distal surfaces, was repeated again and again during evolution of the articulate brachiopods and can be illustrated by a brief consideration of Paleozoic stocks.

Apart from unusual orthoids, like the triplesiaceans with their grotesquely exaggerated bilobed processes (Fig. 124,*B*), and the orthidiellids with their trilobed structures formed by the outgrowth of lateral ridges that supported the muscle bases (Fig. 125,*D*), the plectambonitaceans show some resemblances to the enteletacean elaboration. A trilobed condition, for example, was attained among the sowerbyellids (Fig. 125,*A*) by the posteroventral growth of the median partition and a pair of lateral plates bounding the notothyrium elevated as a single element above the hinge line. In the brachial valve of *Bilobia*, on the other hand, a basically trilobed arrangement became bilobed by the development of a cleft in the high median crest (36); and in *Anoptambonites*, the cardinal process consists of a median ridge and up to six lower lateral ridges simulating the transverse "comb" of many spiriferoids (58).

Among the strophomenaceans, davidsoniaceans, productoids, and chonetoids, variation in the morphology of the cardinal process was ultimately related to modifications of a bilobed structure (Fig. 124,*A*). This bilobation, however, did not result from a dichotomy of the median partition as in the enteletaceans but to the posteroventral growth of flanking lateral ridges (compare Fig. 123,*A*). Such ridges supported the muscle bases and are found in a few clitam-

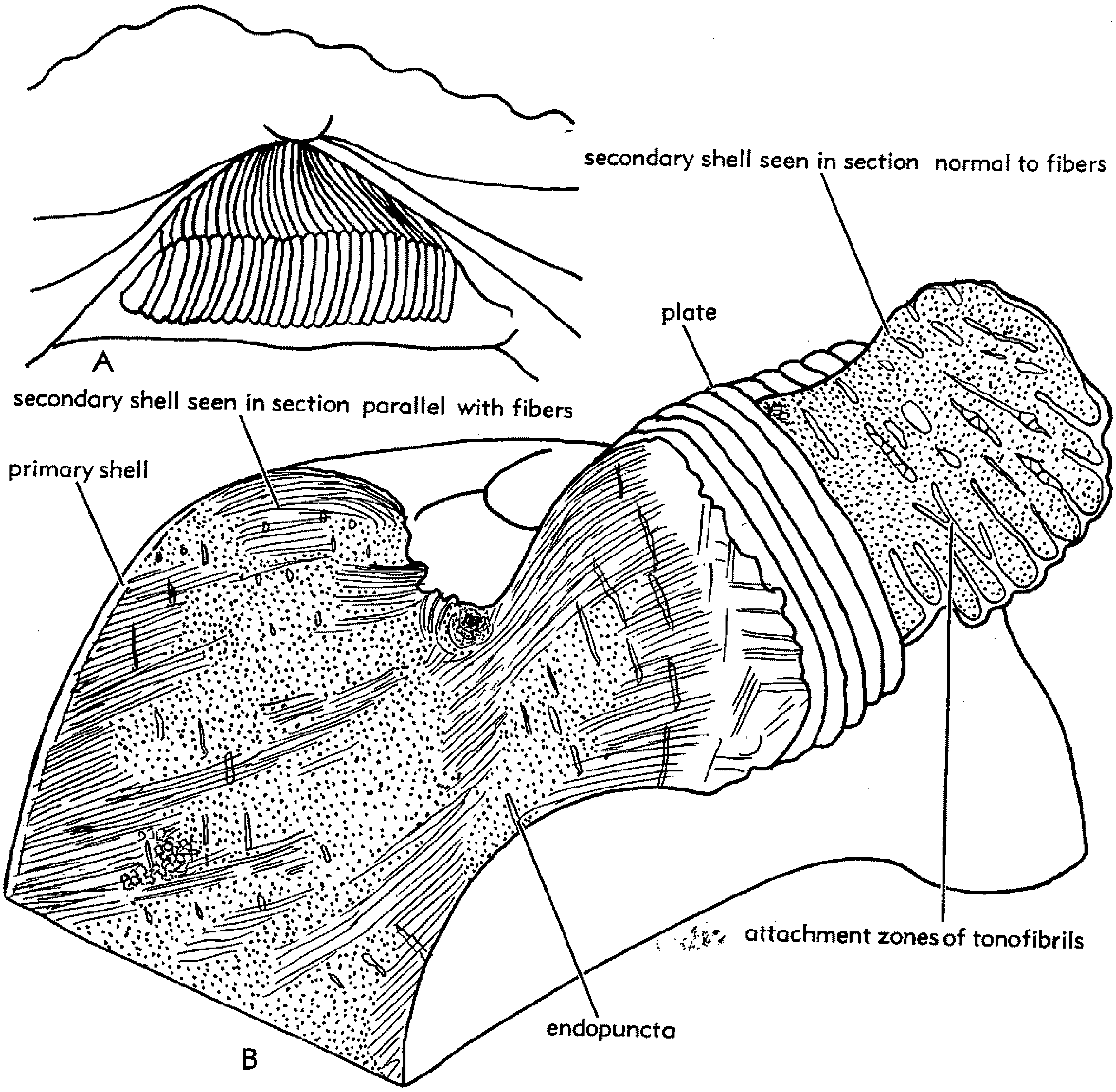

FIG. 126. Cardinal process of *(A) Neospirifer* and *(B) Terebratalia transversa* (SOWERBY) in median and tangential sections showing associated shell structure (65).

bonitoids (e.g., *Clinambon*) and especially in the orthidiellids (50). But their development in the strophomenaceans was accompanied by an atrophy of the median ridge and the differentiation of the greatly expanded posterior surfaces into crenulated zones with smooth boundaries (Fig. 124,*A*). In many chonetoids and productoids, the cardinal process lobes are slightly divergent and their boundaries are so exaggerated that they have a quadrilobed appearance. In other genera, the inner boundaries are more or less ankylosed to each other and the entire process is referred to as trilobed (Fig. 125,*B*); and in a few genera (e.g., *Titanaria*), the cardinal process consists simply of a median lobe with a crenulated dorsoposterior face, a reversion that may have resulted from the atrophy of the lateral boundaries. Other modifications (33) that recall those of earlier independent stocks include the bilobed cardinal process of *Scacchinella,* which is as long and deeply forked as that of any triplesiacean, and the tendency for the productoid processes to overhang a conical hollow (**alveolus**) in a manner reminiscent of the undercut cardinal process of the sowerbyellids.

No elaborate cardinal process ever developed among the pentameraceans. It was also less prevalent among the rhynchonelloids, spiriferoids, and terebratuloids than among the orthoids or strophomenoids, so that even in many Recent articulate brachiopods (e.g., *Hispanirhynchia, Dallina*), the attachment areas for the dorsal ends of the diductor muscles are nothing more than roughened surfaces beneath the beak. Modifications similar to those already discussed do occur, however. A simple, elongate, or transverse surface which is slightly elevated and tuberculate or crenulated is fairly common (Fig. 123,*I*) (e.g., *Rhynchotrema, Emanuella, Terebratulina*). A bilobed cardinal process comparable with the enteletacean structure is known in such genera as *Cryptopora, Ambocoelia,* and *Agulhasia.* Unusual variants include the forked, triplesiid-like process of *Stringocephalus* and the bilobed transverse outgrowth of *Notosaria,* with its transversely crenulated posterior face overhung by the dorsal beak (Fig. 123,*F*). A trilobed process like that of *Paucicrura* is also found in *Meganteris* and *Prionothyris* (Fig. 125,*C*); and a quadrilobate structure, reminiscent in section of the productoid arrangement, in *Eucharitina.* But perhaps the most novel kind of cardinal process developed in the rhynchonelloids, spiriferoids, and terebratuloids is a transverse ridge with a ventral face composed of thin plates aligned normal to the long axis of the ridge which, in thin section, give the cardinal process the appearance of a comb (Fig. 126).

The attachment areas for the dorsal ends of the adductor muscles normally consist of four scars impressed on the floor of the brachial valve at a variable distance anterior of the cardinalia. The scars may differ in size and arrangement, but they are commonly disposed in the median area of the valve with the posterior pair flanking the more closely placed anterior pair (Fig. 115, *3a*). Modification by differential secretion of secondary calcite is minor except for the deposition of a median ridge that normally extends anteriorly from the vicinity of the cardinalia to separate the right and left set of adductor impressions (**myophragm**). The muscle field may, however, be raised above the floor of the valve in a number of different ways which deserve a brief review.

The best-known elevated structure for the reception of the dorsal adductor bases is the cruralium which, like its ventral counterpart, the spondylium, is especially characteristic of the pentameraceans (28). It was formed by the forward growth of the outer plates underlying the base of the brachial

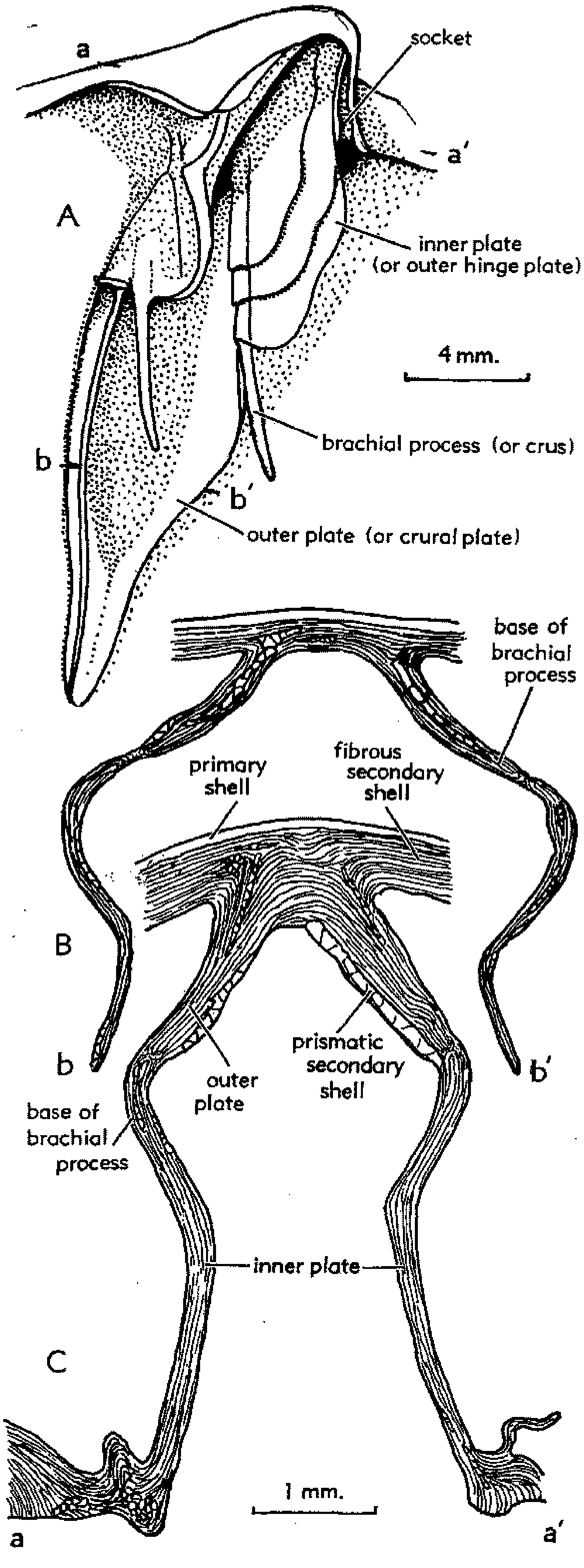

FIG. 127. Parts of brachial valves of *Gypidula*: *A, G.* sp., M.Dev., USA, with convergent outer plates simulating sessile cruralium; *B, C,* transverse sections of *G. dudleyensis* SCHUCHERT, U.Sil. (Wenlock.), Eng., in planes indicated on *A* (65).

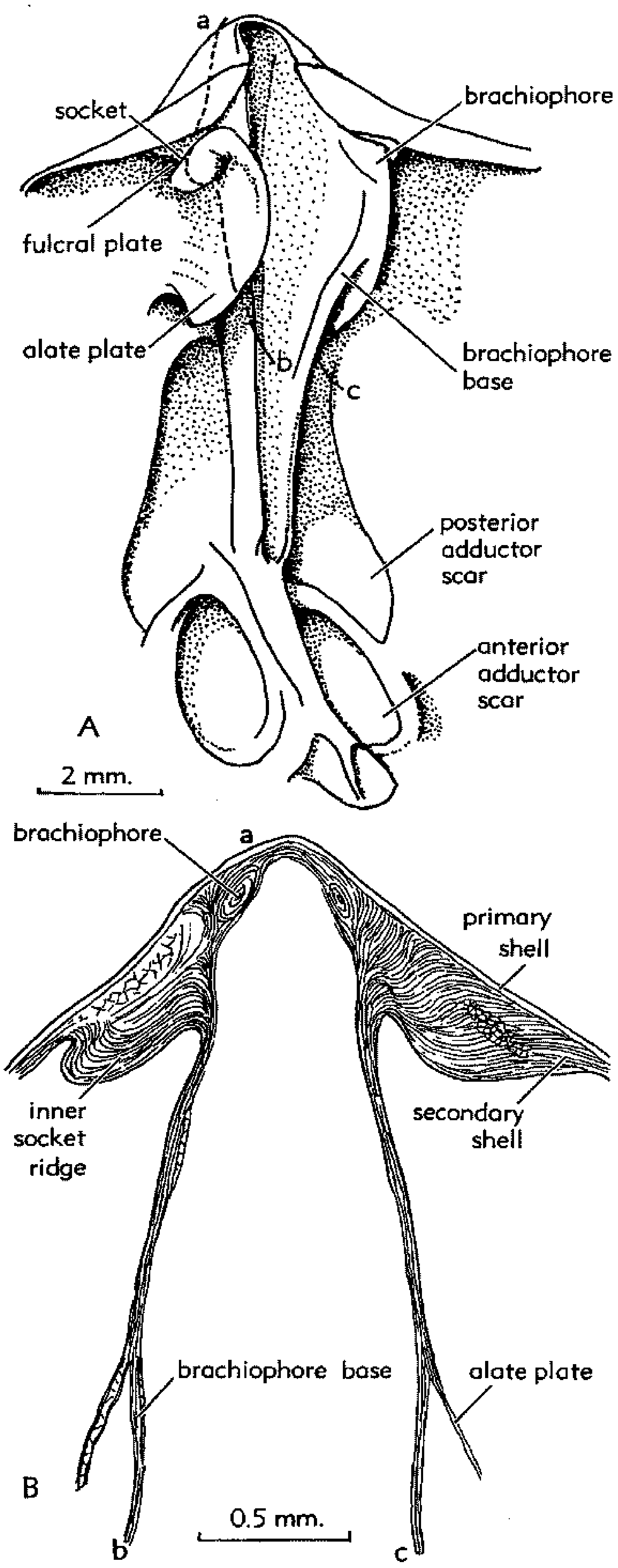

FIG. 128. Part of brachial valve of *Anastrophia* sp., M.Sil., Eng., showing *(A)* cardinalia relative to dorsal adductor field, and *(B)* oblique section along line indicated in *A* (65).

processes to receive part or all of the adductor muscle field. The plates may be subparallel to divergent (e.g., *Pentamerus*) or variably convergent (e.g., *Gypidula*, Fig. 127) so that they grow forward along the floor of the valve independently of each other to enclose a strip of the valve floor. Alternatively, they may converge to unite with each other at their junction with the valve floor, the sessile cruralium of *Barrandella*, or above the valve floor to which they are joined by a median septum. The median septum of *Sieberella* is reported to have been developed independently of the

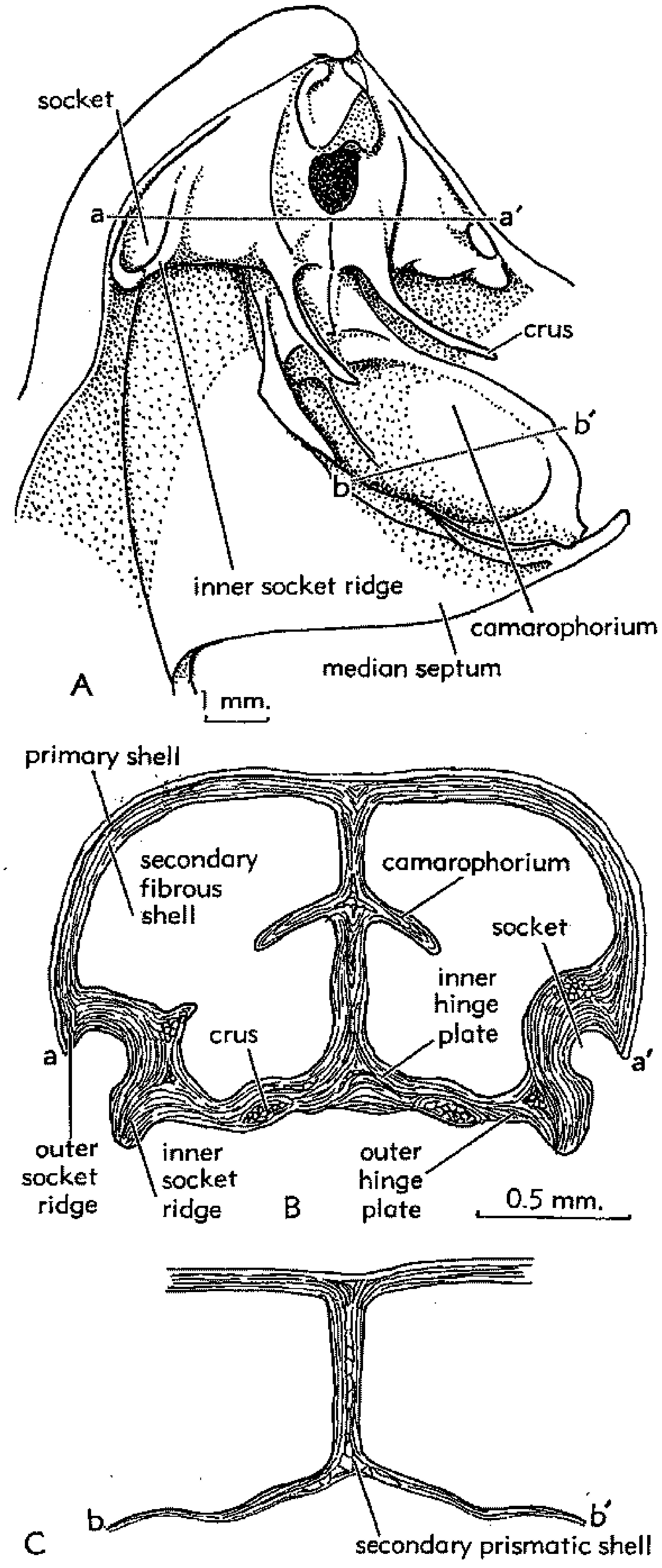

FIG. 129. *A*, Camarophorium of *Camerophoria* sp., M.Perm., USA; *B, C*, transverse sections of camarophorium of *Camerophoria* sp., U.Dev., USA, with approximate location of cuts indicated on *A* (65).

plates; but in some species of *Pentamerella* it is known to have been formed by the ankylosis of the converging plates.

The term cruralium has been used for structures which may have originated in the same way as that characteristic of the pentameraceans but which could not have given support to the dorsal adductor field. The elevated troughs found in the brachial valves of the syntrophiids and parastrophinids (Fig. 128) or of the skenidiids and *Kayserella*, for example, were formed by the convergence of the brachiophore bases onto the valve floor or a median septum, but they all lie well posterior of the adductor scars and are more like septalia than cruralia, as originally understood by HALL & CLARKE (27). Moreover, although the spoonlike apparatus in the brachial valve of stenoscismataceans gives support to the dorsal adductor muscles, its growth around a high median septum was independent of the crura and it is more appropriately called a **camarophorium** or torynidium (17) (Fig. 129). The spyridium of *Spyridiophora* (20) and some aulostegids also supported the dorsal adductor muscles but on the transversely flattened posteroventral surfaces of a pair of subparallel plates that grew vertically from the floor of the brachial valve on either side of a low median septum (Fig. 130,*A*). These plates are quite different in disposition from the braceplates (55) of stropheodontids like *Douvillina* (Fig. 130, *B*), which grew anteromedially of the adductor field and are more likely to have given support to the median segment of the lophophore on either side of the mouth. In contrast, the apparatus subtended between the brachiophores and median septum of *Mystrophora* (16) did accommodate the dorsal adductor bases and is correctly called a cruralium.

In some genera (e.g., *Hypsomyonia*), the growth of a high median septum was accompanied by the elevation of the anterior boundaries to the dorsal adductor field above the floor of the valve. KOZLOWSKI (28) has proposed the term pseudocruralium for this kind of structure, but it hardly seems necessary so to distinguish it from raised callus rims of secondary calcite that commonly defined the limits of the scars.

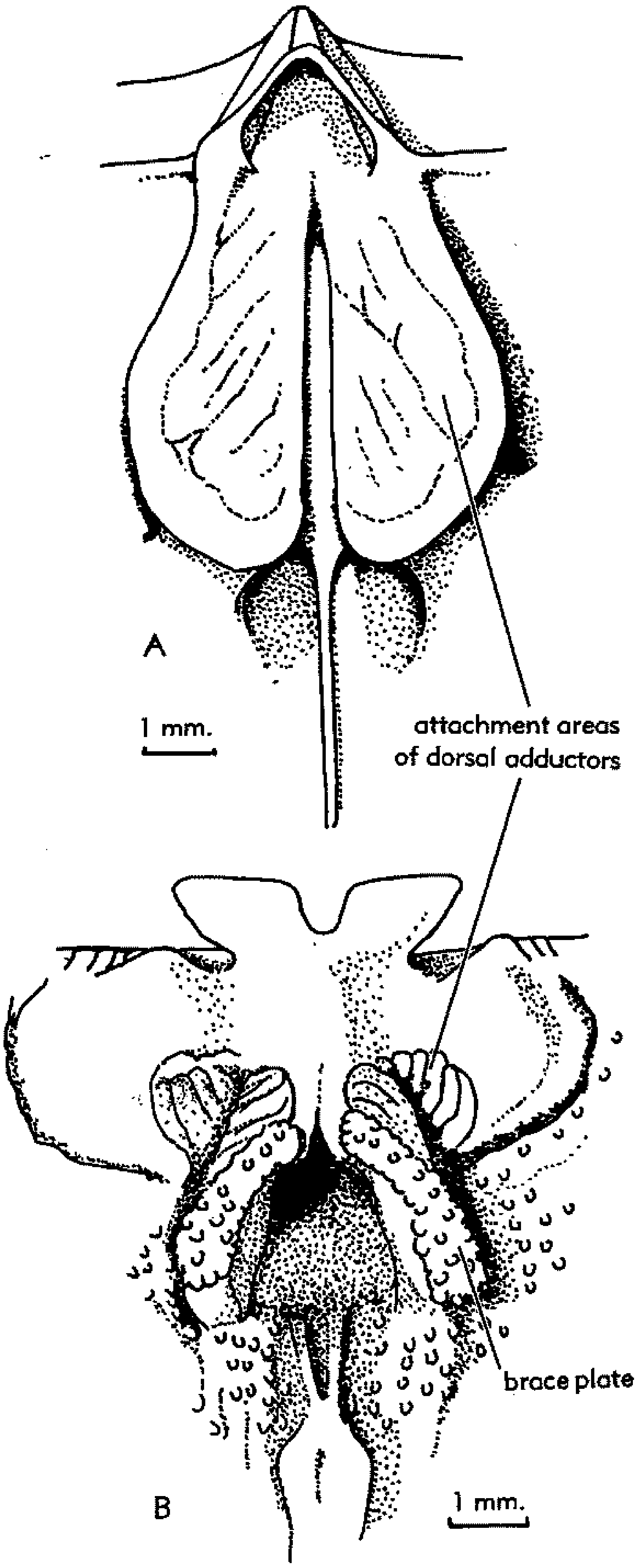

FIG. 130. Stylized representations of *(A)* subdued spiridium of *Echinosteges*, based on *E. tuberculatus* (R. E. KING), M.Perm., USA, and *(B)* braceplates of *Douvillina*, based on *D. arcuata* (HALL), U.Dev., USA (65).

Apart from septa that clearly played a part in accommodating muscle bases (myophragms), found in either valve, a minority of articulate brachiopods (e.g., *Phragmorthis, Skenidioides, Mystrophora*, etc.) were equipped with septa that stood so high above the floor of the brachial valve as to divide the mantle cavity into two

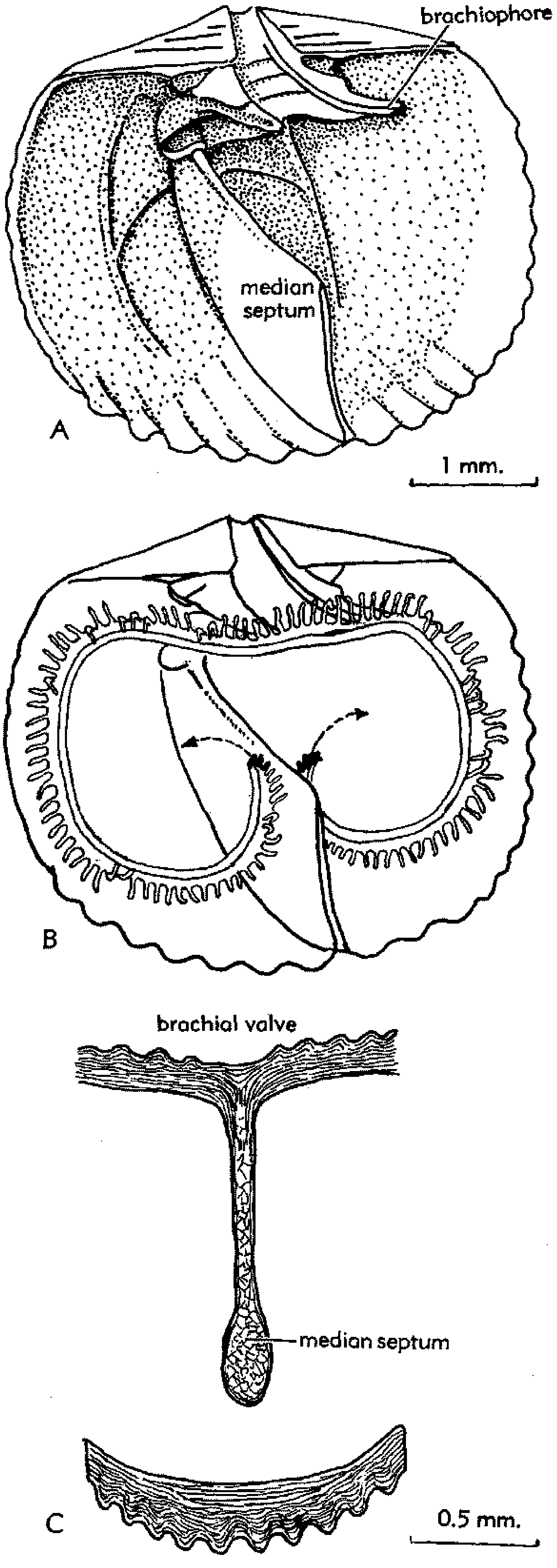

Fig. 131. *A,* Dorsal interior of *Phragmorthis* sp. cf. *P. buttsi* Cooper, M.Ord., Scot., with *(B)* inferred disposition of lophophore about median septum and *(C)* transverse mid-section through shell to show relationship of septum to pedicle valve (65).

compartments (Fig. 131). A septum of this kind usually rises steeply to its apex along its posterior edge, whereas the anteroventral edge tends to fall away more gently, in a curve conforming to the anteromedian longitudinal profile of the pedicle valve. This characteristic profile and the closeness of the fit with the pedicle valve, when the shell was closed, suggest that the septum was associated with the lophophore. It is unlikely, however, that the septum gave support to the lophophore, although it may have assisted in the separation of the left and right halves of that organ during its schizolophous growth, in a manner reminiscent of comparable outgrowths in the brachial valves of terebratellaceans. Transverse partitions, again unrelated to the insertion of muscle bases, are also found in the pedicle valves of such independent stocks as richthofeniids (33), scacchinellids (54), and *Syringospira* (15) (in which they are known as blisters). All shells so equipped have very deep conical or subpyramidal pedicle valves which must have grown at such a faster rate than the enlargement of the contained soft parts that the viscera migrated continually in a dorsal direction, thereby creating space between the internal surface of the valve and the outer epithelium, which was then sealed off by deposition of a partition of secondary calcite (Fig. 132).

Muscle scars and, more rarely, muscle tracks are developed in the inarticulate brachiopods and are impressed on the inner surface of the valves by differential secretion of the outer epithelium associated with the muscle bases, and in this sense they are closely comparable with the scars and tracks of the articulate brachiopods. Commonly this differential secretion merely involves a reduced rate of deposition of shell material, the shell underlying the muscle scars being similar in structure and composition to the remainder of the valve. The physiological changes of the epithelium at the base of the muscles may, however, be more marked, as in *Crania,* where the modified epithelium is responsible for the deposition of calcite intracellularly, in marked contrast to the extracellular secretion which characterizes the remainder of the outer epithelium.

Within any Recent inarticulate genus the

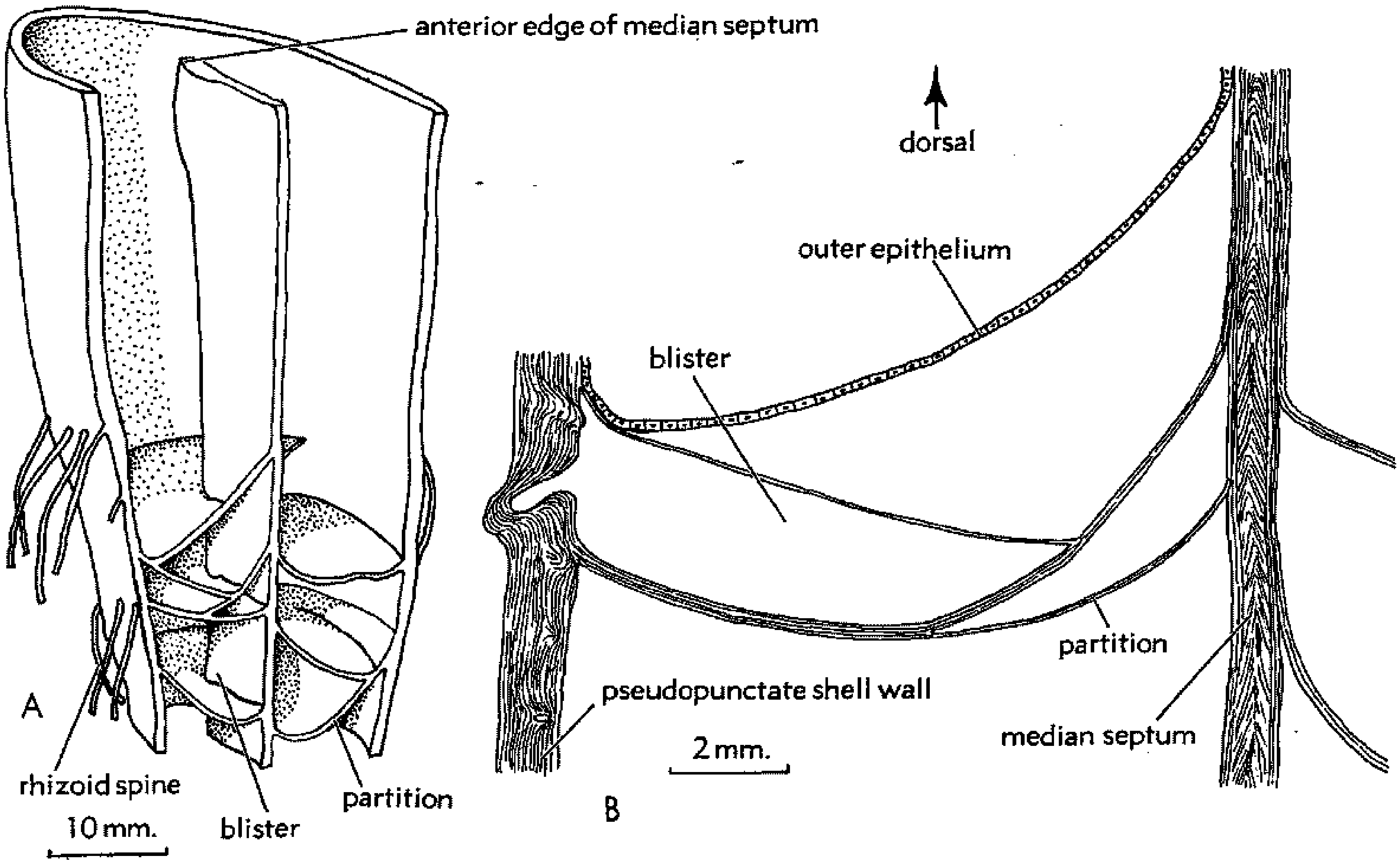

FIG. 132. *A*, Pedicle valve of *Scacchinella americana* STEHLI, L.Perm., USA, cut parallel with and anterior to interarea, with (B) section showing inferred relationship between transverse partitions and outer epithelium (65).

muscles fall into two groups, the adductors and the oblique muscles (see Figs. 28-29). Basically there are two pairs of adductors, the muscles of each pair being symmetrically disposed relative to the median line of the valve; the posterior pair are situated close to the posterolateral boundary of the body wall, while the anterior pair are placed well forward in the body cavity. Both pairs pass more or less directly dorsoventrally between the valves. The homologue of the posterior pair of adductors is strongly modified in Recent lingulids to form a single umbonal muscle consisting of two very unequal bundles of fibers (p. *H27*), but the homologues of the anterior adductor muscles, known as the central muscles in this family, do not deviate from the basic pattern. The oblique muscles are usually more slender than the adductors and are commonly longer; as their name implies, they traverse the body cavity obliquely, either in a dominantly anteroposterior direction or laterally. Although the number of oblique muscles is constant within any of the families of Recent inarticulate brachiopods, considerable variation exists between the families, the lingulids having four pairs, the discinids three, and the craniids only two pairs. In all families, the function of the oblique muscles appears to be similar, to assist the adductors in opening and closing the valves, and to control the relative longitudinal and lateral displacements of them.

Compared with the articulate brachiopods, the muscles of the inarticulates differ, not only in their function, but also in their distribution. The muscle bases of the inarticulates are commonly more peripherally placed within the body cavity and they are not grouped to form a well-defined muscle field in either valve. There is also another important difference. With a few exceptions (e.g., thecideaceans), the number of shell muscles is constant within the Articulata, in contrast to the variable number of oblique muscles found among inarticulates. This variation of the oblique muscles, combined with the delicacy of the impression of their attachment surface to the shell, makes it extremely difficult, and in some instances impossible, to reconstruct the entire muscle system for extinct stocks.

Within any one superfamily, the scattered evidence suggests that although the relative position of individual muscles is variable, the number of muscles is commonly constant. Thus, among the Lingulacea, with

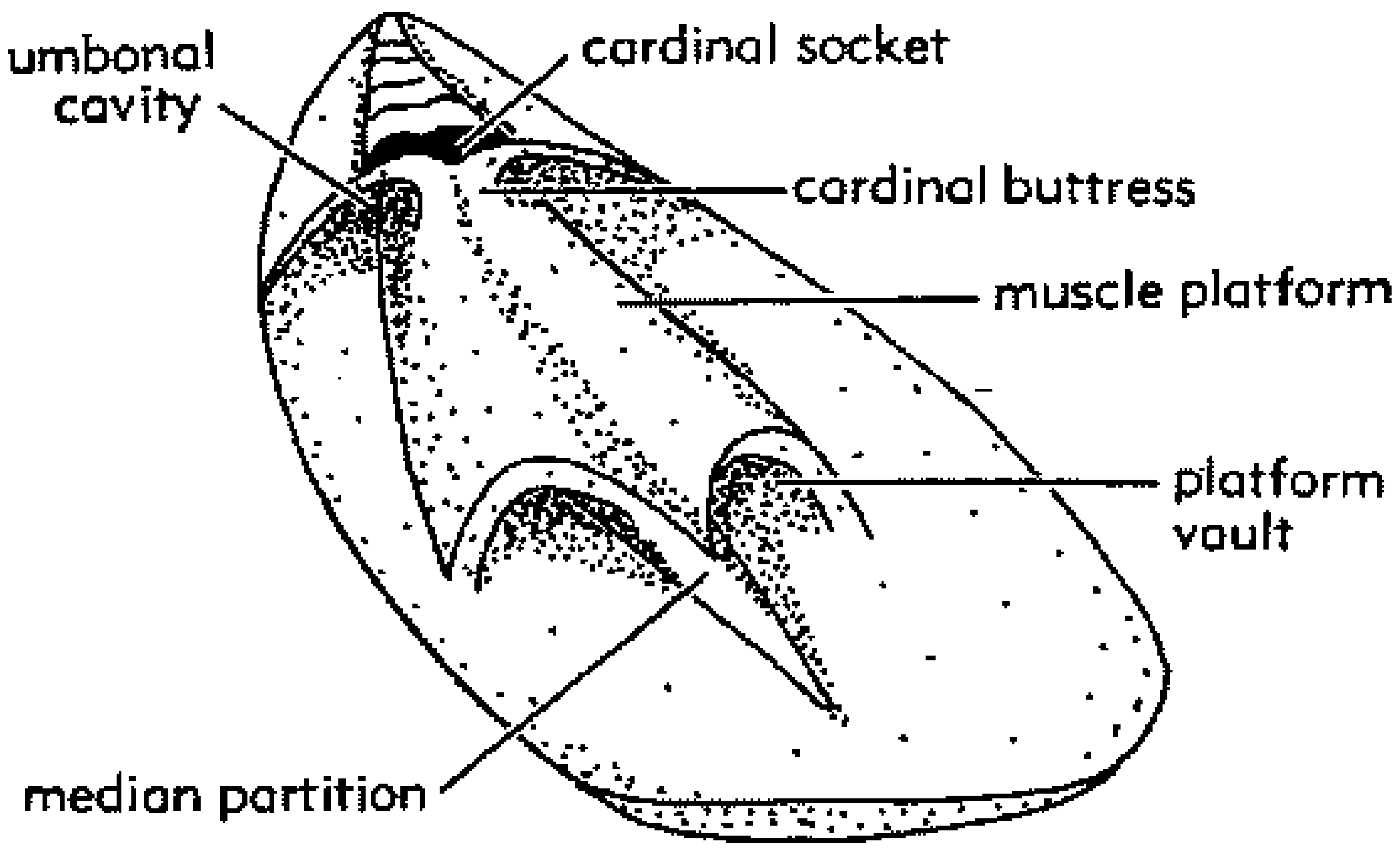

FIG. 133. Morphology of pedicle valve of *Trimerella* (63).

the possible exception of some of the paterulids and craniopsids, the basic muscle pattern appears to have been comparable with that of *Lingula.* The development of transmedian muscles, which cross the body cavity laterally as they pass from pedicle to brachial valve, is unknown outside the superfamily, although they may have occurred also in the trimerellaceans. Some variation in the relative positions of the muscles does occur and is seen for example in *Obolus* and *Pseudolingula* (29, 30). In the former genus, the transmedians do not form composite scars with the middle and outside lateral muscles on the brachial valve as they do in *Lingula* and the umbonal muscle consists of two subequal bundles of fibers which form separate scars on the pedicle valve and which unite to form a single scar on the brachial valve. In *Pseudolingula,* the umbonal muscle of *Lingula* is represented by two separate bundles of fibers which form a pair of posteriorly placed scars in both valves. Unfortunately, it is not known how persistent or widespread are these deviations from the *Lingula* pattern within the superfamily.

The details of the muscle system of the trimerellaceans (which, together with the lingulaceans, constitute the Lingulida) are still inadequately known. Within this superfamily there is a marked tendency for the development of muscle platforms in both valves. In the older genera (e.g., *Eodinobolus*), these are poorly developed and are little more than a thickening of the posterior part of the valve, but they are extravagantly developed in younger forms like *Trimerella.* In *Trimerella* (Fig. 133) the platforms are hollow anteriorly and are elevated high above the valve floor, being supported medially by a median partition, which projects in front of the platform and divides the cavity beneath it into two subtubular vaults. The entire platform was invested in and secreted by outer epithelium. During the earlier stages of growth of the animal, the front edge of the platform and the median partition grew anteriorly and the posterior ends of the vaults were progressively infilled with shell material secreted by the infolds of epithelium lining them. There are at least two and possibly three pairs of scars on the muscle platforms of both valves, with an additional minimum of at least two pairs of rather elongated scars on the floor of both valves, lateral to the platforms, forming the sides and ends of the so-called "crescent." The overall distribution of the scars suggests that the muscle system may have been of the *Lingula* type, but more information is required to confirm this hypothesis. Muscle platforms occur in other Lingulida stocks. Low platforms occur in *Lingulops* and most of the craniopsids, usually in both valves, but they may be restricted to the ventral one. These platforms are developed as low thickenings of the valve floor, their anterior margin may be slightly excavated and is always abruptly flexed above the inner surface of the valve. As in the trimerellids, they carried some of the musculature, but more laterally placed muscles were commonly inserted in the floor of the valve, lateral of the platform. Higher platforms are developed in *Lingulasma* and *Andobolus.* In the former genus, the platforms are broadly comparable to the trimerellacean development; they are internally gently concave and that of the brachial valve is hollow anteriorly and is supported by a median septum. In *Andobolus* the muscle platform, which is present only in the brachial valve, is strongly bifid, with a deep median groove separating the two halves; in transverse cross section the platform has the appearance of a pair of rabbit ears. The distribution of muscle scars on the platform of this rare genus is unknown.

Among the Obolellida the muscle scars are commonly only lightly impressed and the full complement of muscles is probably still unknown. Two pairs of scars are usually seen in the pedicle valve, one pair (the larger), posterolaterally placed, and a second pair, close together, near the middle of the valve. Judging from the distribution of the muscle scars of other inarticulate brachiopods these are possibly the homologues of the posterior and anterior adductors. In the brachial valve three pairs of scars are commonly recognizable, two pairs close together, posterolaterally located in front of the pseudointerarea, with a third pair situated near the center of the valve. Additional muscles probably existed, however, for there are indications of a third pair of muscle scars in the pedicle valve of *Bicia,* situated in front of the better-impressed, medianly placed pair. Similarly, there are indications of a fourth pair of scars in the brachial valve of *Trematobolus,* in a position which would agree with that of the anterior lateral muscles of *Lingula.* These scars have not been identified in other genera referred to the order, however, and at present the muscle system cannot be reconstructed confidently.

In the Acrotretida, the complement of shell muscles of the craniids has seemingly been constant throughout the history of the stock. There is some variation in the relative size and position of the anterior and posterior adductors, but both pairs of muscles undoubtedly existed. The scars of the oblique muscles are not known in all genera referred to the family, but traces of them are frequently preserved and it appears probable that they possessed two pairs of oblique muscles similar to those of Recent *Crania.*

Only the adductor muscle scars are known in fossil discinaceans and extinct representatives of this superfamily possessed two pairs of these muscles, located in a broadly comparable position to those of modern *Discina* and *Discinisca.* It is not known whether, like these genera, they also possessed three pairs of oblique muscles; even in Recent shells, the impressions of these muscles are exceedingly faint.

Among the Acrotretacea, particularly the acrotretids, two pairs of muscle scars are commonly fairly conspicuous in both valves. The pedicle valve bears a pair of large cardinal muscle scars on the posterolateral or posterior slopes of the valve and a much smaller pair of apical pits, usually located near its apex. The brachial valve has a complementary pair of large cardinal scars posterolaterally placed and a small pair of scars near the center of the valve. A further unpaired scar, the posteromedian, situated on the posterior end of the median septum of the acrotretids has been described, but its existence is doubtful. A number of reconstructions of the muscle system are possible, but the one here illustrated (Fig. 96, 114) is based on the assumption that the posteromedian muscle, if it exists, is a body muscle not attached to the pedicle valve. The principal muscle scars are all assumed to be sites of attachment of single muscles, because no specimen shows evidence suggesting that they are composite. It is difficult to homologize acrotretacean muscles with those of other members of the Acrotretida, but it appears possible that the cardinal muscles are equivalent to the posterior adductors of the discinaceans and craniaceans, and the anterocentral muscles, which form the apical pits in the pedicle valve and the small, centrally placed scars in the brachial valve, are the homologues of the anterior adductors. Additional scars which could be referred to oblique muscles have not been observed and these muscles may not have been present in this group. The form of the posterior margin of the brachial valve in many genera suggests that oblique movement would have been restricted if not entirely inhibited. Opening of the valves in the group was probably largely controlled by dermal muscles in the body wall. Another interpretation of these muscles, which cannot be entirely dismissed, is that the cardinal muscles are homologues of both the posterior and anterior adductors and that the anterocentral muscles are oblique muscles.

The muscles of the remaining superfamily of the Acrotretida, the Siphonotretacea, are poorly known. Only one pair of relatively large scars may be definitely recognized in each valve, and these possibly may be homologues of the acrotretacean cardinal muscle scars.

The internal morphology of the Paterinida, unfortunately, is only imperfectly known for a limited number of genera. Impressions on the internal surface of the shell are very delicate and it is difficult to be confident of their origin, but what are seemingly muscle tracks suggest that the musculature of this order differed considerably from that of the remainder of the inarticu-

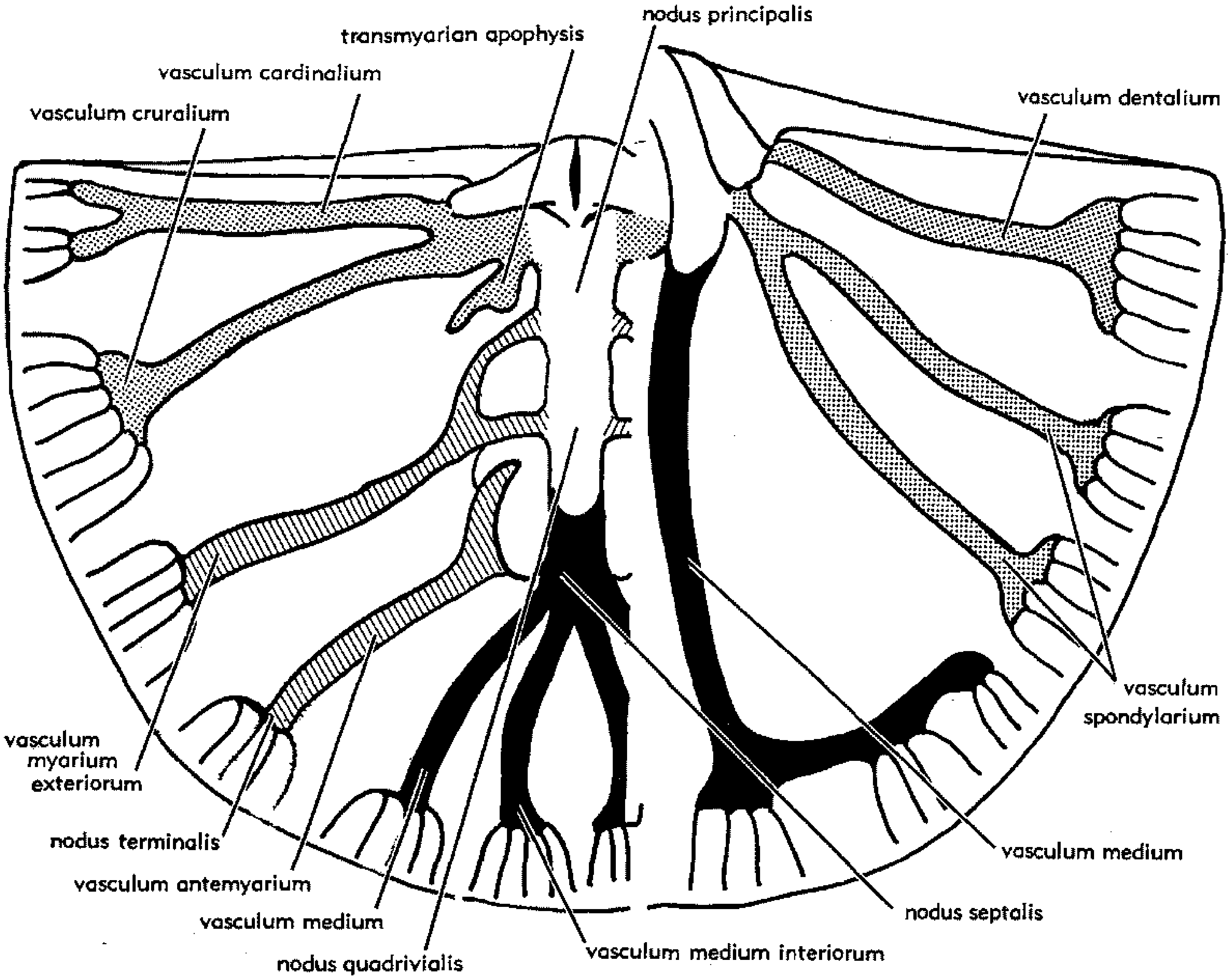

Fig. 134. Idealized canal systems in brachial (to left) and pedicle (to right) valves of primitive articulate brachiopod to illustrate terminology used by Öpik (37) (65).

late brachiopods. All of the scars recognized produce narrowly triangular tracks radiating from the apex. In the pedicle valve two such tracks diverge slightly anteriorly, terminating near the center of the valve, whereas in the brachial valve there are seemingly two pairs of tracks, one pair diverging anterolaterally and a second pair forming a single medianly located depression. The location of these tracks, if they are correctly interpreted as muscular in origin, in some ways is more reminiscent of the muscle system of the articulate brachiopods than the Inarticulata.

MANTLE CANAL SYSTEMS

The system of canals that pervaded the mantles of fossil brachiopods may be reconstructed by deciphering a series of impressions on the interiors of both valves. These impressions consist of a number of grooves or ridges, more or less symmetrically disposed on either side of the longitudinal mid-line, which are commonly seen to emanate from the vicinity of the muscle scars. They arose by differential deposition of secondary shell because these strips of outer epithelium arching the canals secreted shell material at a slower or, less commonly, faster rate than over the mantle generally.

The fine distal branches of all canals that terminate just within the shell margins are known to connect with the setal follicles in living articulate brachiopods. The disposition of impressions of terminal branches relative to the grooves and eminences along the internal margins of fossil shells suggest that this relationship always has obtained.

Interpretable patterns are rare and in general are more likely to be found not only in gerontic specimens but also, for some obscure reason, in older stocks (e.g., orthoids, strophomenoids, porambonitaceans), and it is symptomatic of this geological circumstance that the first analytical study of the patterns was prepared by Öpik (37). He showed that arrangements deduced from a study of the clitambonitoids were sufficiently consistent to merit special terminology (Fig. 134). Some of the terms have been proposed for details of canal intersection or location within what must have been the body cavity and are not important in any

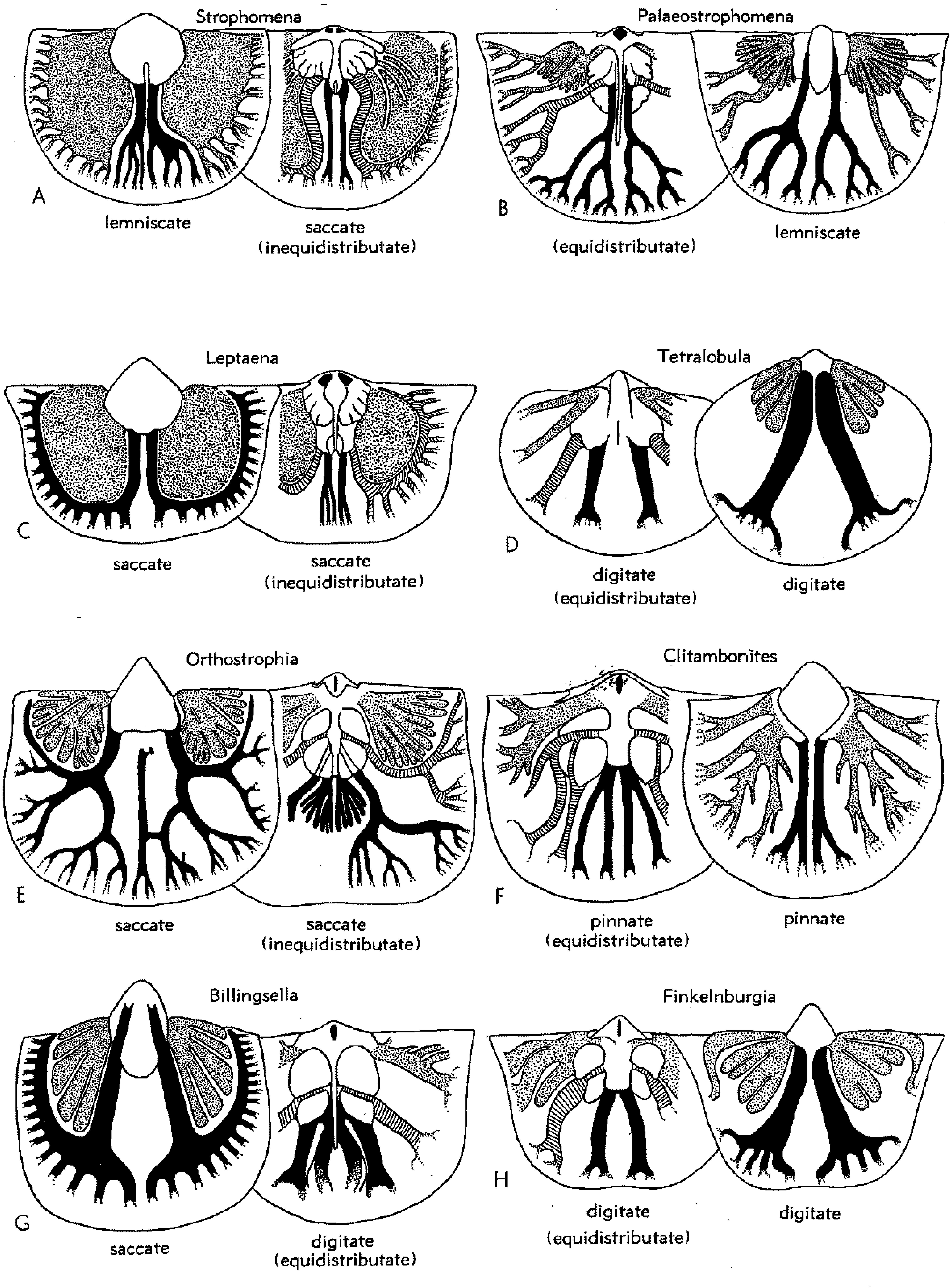

Fig. 135. Mantle canal systems of selected brachiopods; in each example brachial valve is inner figure and pedicle valve outer (*vascula media* in solid black, gonadal sacs and *vascula genitalia* stippled, *vascula myaria* ornamented by closely spaced lines) (57).

comparative survey. But having regard for what is now known of the patterns in fossil and living shells, all canals can ultimately be related to three principal pairs of extensions of the body cavity into the mantles (57). They are the *vascula media,* which arise anteromedially of the muscle fields; the *vascula myaria,* which originate between or within muscle bases and which are unequivocally identifiable mainly in brachial valves with their widely separated posterior and anterior adductor attachments; and the *vascula genitalia,* which normally occupy the posterolateral areas of the mantles. These last vary from peripheral branches given off from pouches within the mantles that contain the gonads (gonocoels) to a complex of branches (including, according to Öpik's terminology, combinations of *vascula dentalia* and *myaria* and of *vascula cardinalia* and *cruralia* in the ventral and dorsal mantles, respectively). In adult shells, however, they are always associated with the gonads, which may occur elsewhere within mantle canals but are invariably present in the posterolateral areas.

A survey of the known patterns of articulate brachiopods shows that they can be assigned to a few standard types, which were probably derived from those characteristic of Cambrian shells. Thus, in *Billingsella* (Fig. 135,*G*), circulation within the ventral mantle was apparently effected by a pair of *vascula media* which curved arcuately within the shell margin and presumably served the peripheral mantle lobes with their setae. This arrangement is not far removed from that of certain living inarticulates (e.g., *Lingula*). But the ventral mantle of *Billingsella* also contained a pair of pouchlike sinuses lying wholly posterior to the arcuate *vascula media,* which were probably homologous with similarly disposed gonocoels of *Hemithiris* (see Fig. 23,*A*); and this entire pattern is referred to as the saccate condition (57). The projection of the gonads into the mantle is rare among inarticulate brachiopods but was always characteristic of the articulate brachiopods and was, in fact, the main source of subsequent development.

The beginning of a profound modification of the saccate condition is seen in impressions on the ventral interior of *Finkelnburgia* (Fig. 135,*H*). The gonocoels projected laterally almost as far as the mantle edge (digitate condition) and must have served not only as sexual receptacles but also as circulatory channels because the lateral arcs of the *vascula media* were correspondingly reduced. In most younger stocks, this tendency is carried to conclusion. The *vascula media* became greatly abbreviated, although never entirely suppressed, while the *vascula genitalia,* which originated as a pair of gonocoels, also became the dominant circulatory canals. In *Palaeostrophomena* the gonocoels are still pouchlike but gave rise to a series of canals (lemniscate condition) (Fig. 135,*B*); and in *Clitambonites* the pouches were entirely replaced by radially disposed *vascula genitalia* (pinnate condition) that presumably contained gonadal cords (Fig. 135,*F*).

The dorsal mantle canal systems, despite a basic difference in arrangement, underwent the same kind of changes as those described for the ventral mantle. In *Billingsella* and *Finkelnburgia,* digitate gonocoels were developed but the *vascula media* far less so than those of the ventral mantle because a third pair of primary canals appeared laterally between the posterior and anterior adductors *(vascula myaria)* (Fig. 135,*G*,*H*). These are probably best interpreted as principal branches of the *vascula media* with which they enveloped the submedian anterior adductor scars in such a way as to suggest that the muscles were responsible for a premature branching of what were really a pair of median canals.

Such digitate patterns as these did not represent the most primitive grade of differentiation. The dorsal mantle of some Cambrian forms, possibly stocks like *Eoorthis,* in which the patterns were not impressed on the shells, must have been saccate because a pair of pouchlike gonocoels were certainly typical of many Ordovician brachiopods (e.g., *Orthostrophia, Strophomena, Leptaena,* etc.) (Fig. 135,*A*,*C*,*E*), and the peripheral extensions of the other canals, especially the *vascula myaria* to cover the entire margin, suggest that they alone were responsible for circulation in the mantle (inequidistributate condition). More commonly, the digitate, lemniscate (e.g., *Palaeostrophomena*), or pinnate (e.g., *Clitambonites*) patterns prevailed, and the *vascula genitalia* also assisted in circulation (equidistributate condition). Öpik (37) figured a very instructive variation within the species *Cyrtonotella kukersiania.* In one specimen, the entire posterolateral periphery of the mantle was served by arcuate *vascula myaria,* while the lemniscate *vascula*

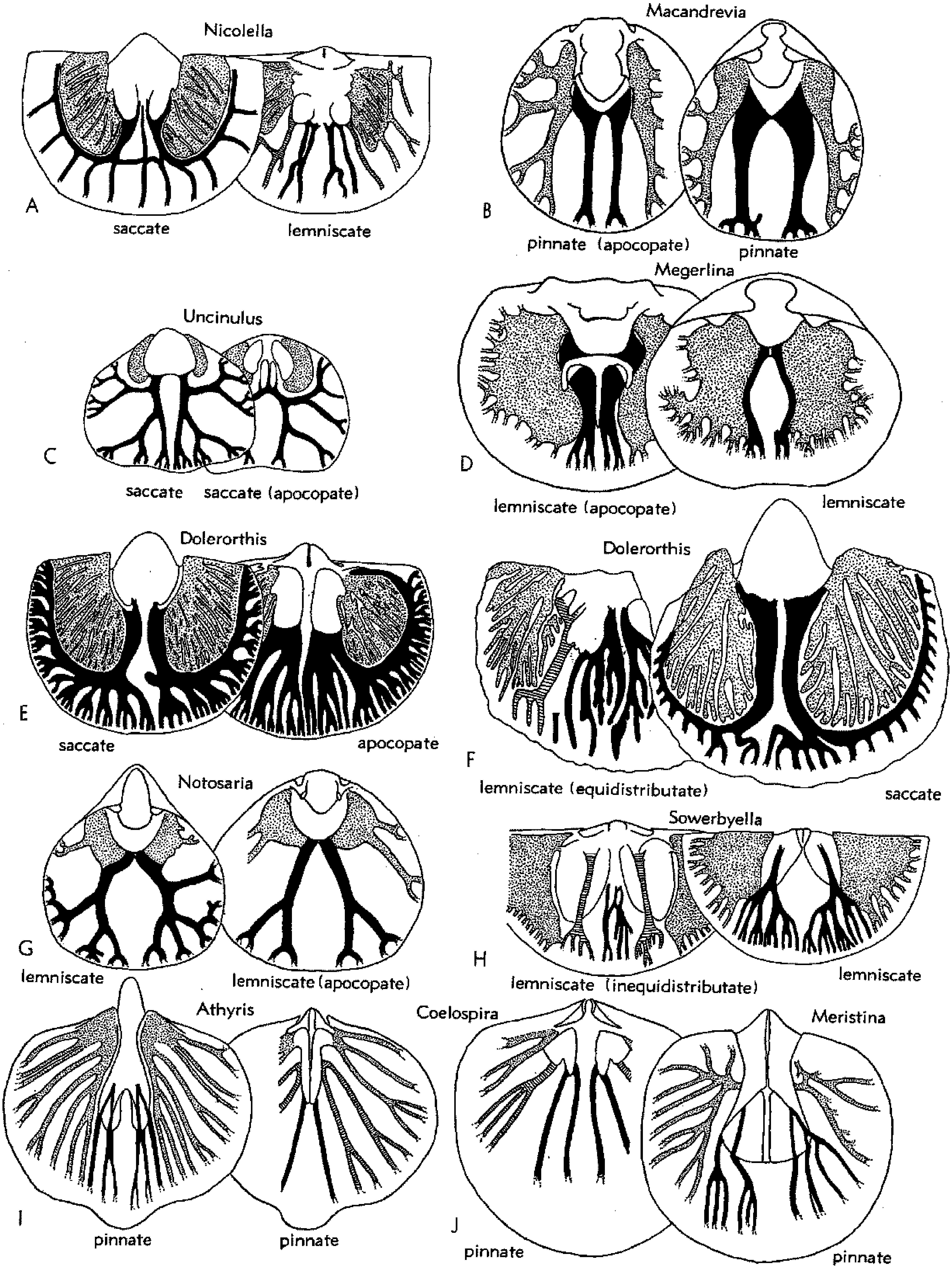

Fig. 136. Mantle canal systems of selected brachiopods, arrangement and shading as in Fig. 135 (*A,F,H,* 59; *C,* 52; *E,* 37; remainder, 57).

genitalia were limited within the arc. In another, the peripheral arcs of the *vascula myaria* were abbreviated and the posterolateral mantle margin, for about one-third its length, was pervaded by *vascula genitalia.* The same degree of variation probably obtained in the basically saccate to lemniscate dorsal mantle of *Nicolella actoniae* (59) (Fig. 136,*A*).

It is now evident that, although these different patterns are well defined, they really constitute morphological grades which were attained during the development of several independent stocks. The post-Cambrian orthaceans tended to retain a saccate ventral mantle, although, as in the orthids, plaesiomyids, and plectorthids, the arcs to the *vascula media* developed in the posterior part of the mantle and served the mantle edge by giving rise to a series of long radiating branches, while the small posterolateral gonocoels were supplemented by subsidiary median ones. The most radical departure from this condition is found in *Dolerorthis.* In later species of this genus, the ventral pattern was orthodoxly saccate, but that of the dorsal mantle consisted of greatly branched *vascula media* with complete lateral arcs and pouchlike gonocoels; the *vascula myaria* do not appear to have developed (apocopate condition) (Fig. 136, *E*). This simple arrangement seems to represent a degeneration from an equidistributate lemniscate pattern, as is seen in some Ordovician species (Fig. 136,*F*).

The triplesiaceans and clitambonitoids, which are contemporaries of the orthaceans, are decisively lemniscate and pinnate, respectively. The enteletaceans are also predominantly lemniscate in both valves, but the saccate condition was characteristic of the ventral mantle of *Paurorthis.*

Reconstructions of the strophomenacean and plectambonitacean mantles show a similar drift away from the primitive saccate condition. A few genera (e.g., *Titanambonites*) possessed saccate ventral mantles, but in both superfamilies the lemniscate or pinnate condition was more usual (e.g., *Strophomena, Strophonelloides, Plectodonta, Palaeostrophomena*) (Fig. 135, *A,B*; 136,*H*). The effects of sexual maturity can be seen in species of *Leptellina.* The basic ventral pattern is saccate, but the distension of the gonocoels became so great in some valves that they became amalgamated with the lateral arcs of the *vascula media* to simulate a lemniscate condition; and indeed, this process of "capture" may have been the chief process of development. The dorsal mantle systems of these groups are not well known. Among plectambonitaceans, the lemniscate equidistributate pattern of *Palaeostrophomena* and the pinnate inequidistributate patterns of *Plectodonta* and *Sampo* seem to be dominant, and this conclusion may also be true for the strophomenaceans, although in *Leptaena* and *Strophomena* the dorsal mantles were essentially saccate (Fig. 135,*A,C*).

The patterns of other groups (e.g., davidsoniaceans, spiriferoids, pentameroids) are rarely preserved and those of the chonetoids and productoids entirely unknown except for traces of *vascula media* belonging to what was possibly a lemniscate ventral mantle of *Rugosochonetes* (32). The davidsoniacean *Davidsonia* clearly had a saccate ventral mantle, but species of *Schuchertella* rarely show impressions of patterns more suggestive of expanded lemniscate (or pinnate) *vascula genitalia* and abbreviated median and submedian canals in both valves.

The patterns of atrypaceans are indifferently preserved but if *Atrypa* is representative, the mantle canal systems developed in members of the superfamily constituted an interesting modification (Fig. 137). Judging from the distribution of impressions of muscle ties found in the shell interior, the gonads occupied most of the disrupted mantles of both valves in adult specimens, although the courses of the principal canals can still be made out. VANDERCAMMEN & LAMBIOTTE (51) have plotted these for *Atrypa reticularis* but have also included patterns within the body cavity which were not canals but were produced by strips of unmodified outer epithelium within the muscle fields, etc. Ignoring these, however, one may see that the *vascula media* were poorly developed in the ventral mantle to give a modified saccate condition and were equally reduced in the dorsal mantle where also the *vascula myaria* and *vascula genitalia* were about equally developed (modified digitate condition). In contrast, a pinnate condition with destructive narrow radiating primary canals was probably the prevalent type of the athyridaceans (Fig. 136, *I,J*), and

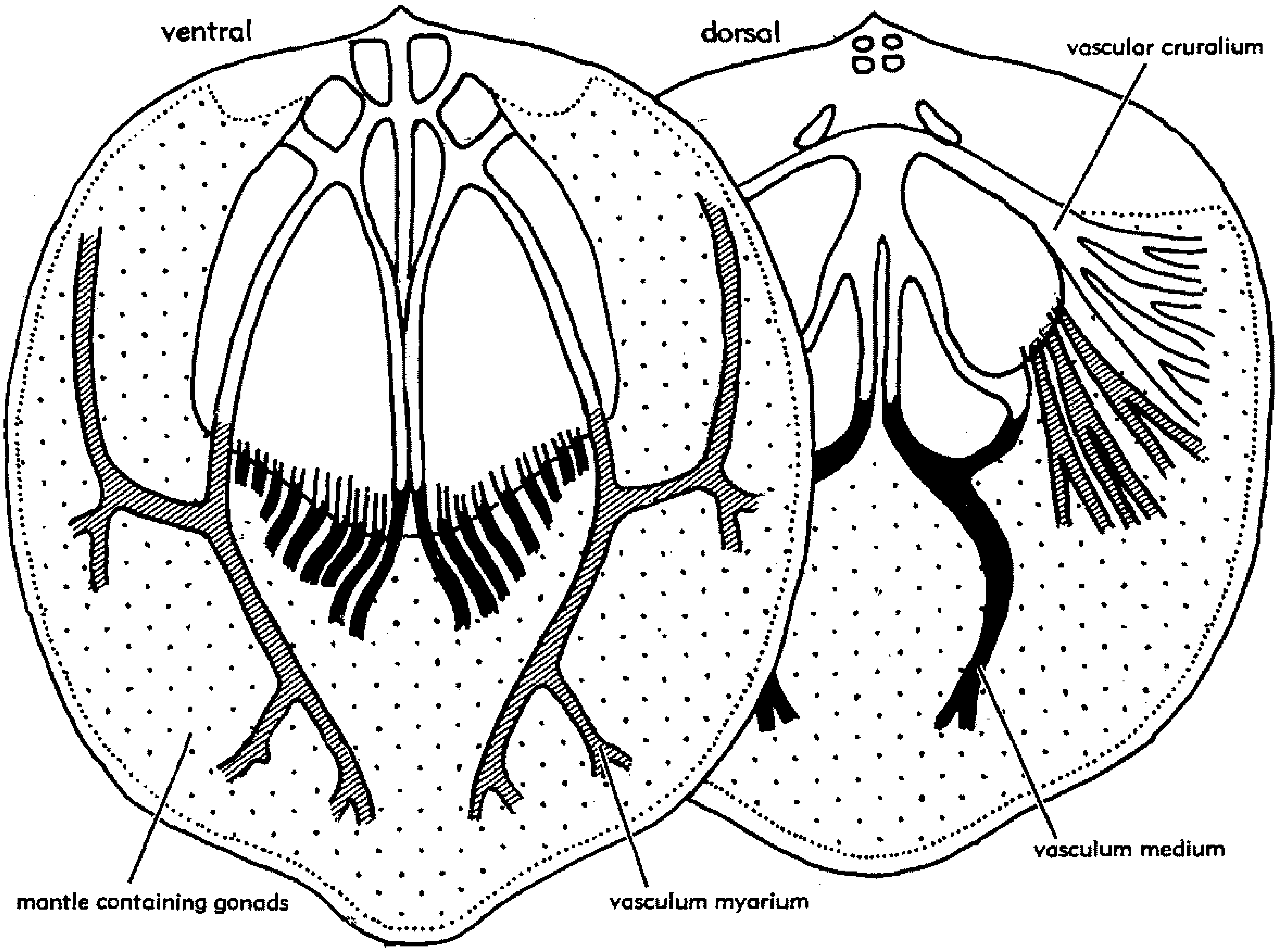

FIG. 137. Mantle canal system of sexually mature *Atrypa* (Williams, after 51).

was also possibly the representative pattern of the spiriferoids among which traces of a pinnate arrangement can rarely be found especially as impressions of the ventral mantle.

The two remaining major groups, the rhynchonelloids and terebratuloids, are represented by living species, the canal systems of which can be studied by injection preparations of the mantles. Both are unusual in that the pattern for the dorsal mantle is, and almost invariably was, apocopate. Yet it is fairly certain that the rhynchonelloid arrangement was independently derived from a saccate or lemniscate condition and the terebratuloids from a radial pinnate pattern.

Two contrasting patterns exist among Recent rhynchonelloids. The gonocoels in both mantles of *Hemithiris* are pouchlike and conform to the saccate condition, while those of *Notosaria* give off branches peripherally in the lemniscate manner (Fig. 136, *G*). Both these patterns occur in fossil forms. *Sphaerirhynchia*, *Fitzroyella*, and *Uncinulus* (Fig. 136,*C*) are saccate and *Leiorhynchus* lemniscate, but whether they constitute two persistently independent groups or whether the saccate stocks continually replenished the lemniscate ones is unknown. The latter conclusion is the more likely, because impressions on the interiors of *Pugnax* may show a saccate condition or one in which the gonocoels may have enlarged sufficiently to rupture into the lateral arcs of the *vascula media* and capture them.

In modern terebratuloids, the *vascula media* are subordinate to the lemniscate or pinnate *vascula genitalia,* and this relationship seems not to have varied greatly throughout their history. Even in Devonian times, when the terebratuloids first emerged as significant members of the brachiopod phylum, the pattern of some living terebratuloids like *Macandrevia* (Fig. 136,*B*) was already characteristic of stringocephalaceans (14). A few stocks (e.g., *Meganteris, Cranaena*) displayed the impressions of three or even four pairs of narrow sinuses radiating from the muscle scars of each valve in a manner reminiscent of the athyridaceans. It is possible, then, that the characteristic dorsal pattern was derived from a pinnate condition by atrophy of the *vascula myaria.* In some modern terebratellaceans (e.g., *Laqueus, Macandrevia, Pumilus*) gonadal cords also occur in the *vascula media,* and in some respects this development may be regarded as the climax of anatomical reorganization that began with the formation of the gonocoel in the mantle. It is not unique, however; the ventral mantle of *Plaesiomys* and the dorsal mantle of *Orthostrophia* possessed a pair of subsidiary saccate gonocoels situated anteromedianly between the *vascula media,* and in view of the poor data on mantle canal systems generally, it may well have been characteristic of other groups unrelated to the terebratuloids.

The mantle canal pattern of the inarticulate brachiopods is basically simpler than that of the articulates. Commonly, there is also some difference in function of the canals, for only in the Craniidae are the gonads known to be partially inserted into them; in all other Recent inarticulates the gonads are confined to the body cavity, and the canals have primarily a respiratory function.

The majority of inarticulates have a single pair of main trunks in the ventral mantle *(vascula lateralia)* and two pairs in the dorsal mantle, one pair *(vascula lateralia)* occupying a similar position to the single pair in the ventral mantle and a second pair projecting from the body cavity near the mid-line of the valve. For convenience, this latter pair may be termed the *vascula media,* but whether they are strictly homologous with the *vascula media* of the articulate brachiopods is difficult to determine. Similarly, it is impossible to be certain that the *vascula lateralia* are the homologues of the *vascula genitalia* of the articulates, although they do arise in a comparable position.

The basic pattern of one ventral and two dorsal pairs of canals is commonly developed in the lower Paleozoic Lingulida, the ventral *vascula lateralia* curve forward from a lateral position on the anterior body wall, subparallel with the shell margin; the dorsal *vascula lateralia* are similarly disposed and the *vascula media* diverge anteriorly from near the anterior lateral muscles. In *Broeggeria* and *Obolus* (Fig. 138,*B,C*) numerous minor canals branch off from either side of the main trunks and they and their ramifications permeate much of the mantle. These small branches are rarely seen in fossil forms, but it appears reasonable to suggest that they are probably present in the majority of the Lingulacea. The branches from the principal canals are relatively minor and in particular, the *vascula lateralia* extend forward without any major dichotomy or bifurcation (baculate condition).

The seemingly fundamental pattern of a pair of baculate *vascula lateralia* in each valve with a pair of *vascula media* in the dorsal mantle occurs in a number of stocks. In the siphonotretacean *Schizambon* and in *Obolella* (Fig. 138,*G,H*) the major canals are arranged similarly to those of *Obolus,* but minor branches from them are unknown. Among the acrotretaceans, although the slender principal canals of *Acrothele* give off delicate branches, the majority of the acrotretids appear to lack the fine ramifications of the vascular system (Fig. 138,*D,F*). In this family, a modification of the mantle canal system occurs, well displayed by *Conotreta,* in which the *vascula lateralia* rapidly branch into a number of subequal, radially disposed canals (pinnate condition) (Fig. 138,*E*). Although this branching commonly produces medially situated canals in the ventral mantle, whose position is similar to that of the dorsal *vascula media,* they are probably best regarded merely as branches of the *vascula lateralia,* since true *vascula media* are otherwise unknown in the pedicle valve of inarticulate brachiopods.

The ventral *vascula lateralia* of the craniids exhibit a modified form of the pinnate condition in which the branching is delayed. The same type of branching affects the single pair of principal canals in the dorsal mantle; these are probably the *vascula lateralia,* which in Recent *Crania* occupy a rather median position. The distribution of the canals in older genera of the family (e.g., *Petrocrania,* Fig. 138,*I*) suggests that the *vascula media* are absent in this family.

In the Recent lingulids, *Glottidia* and *Lingula,* and possibly in many closely related fossil representatives of the family, other modifications of the mantle canal system occur. The dorsal *vascula media* are not developed and the *vascula lateralia* in both valves divide immediately after leaving the body cavity (bifurcate condition), the smaller branch of each main canal extending posteriorly to supply the mantle lateral of the lateral body wall and the larger branch passing anteriorly and converging toward the mid-line of the valve. From these principal branches minor canals are given off comparable to those of *Broeggeria* and *Obolus*. The bifurcation of each of the *vascula lateralia* into anterior and posterior branches is not solely a function of

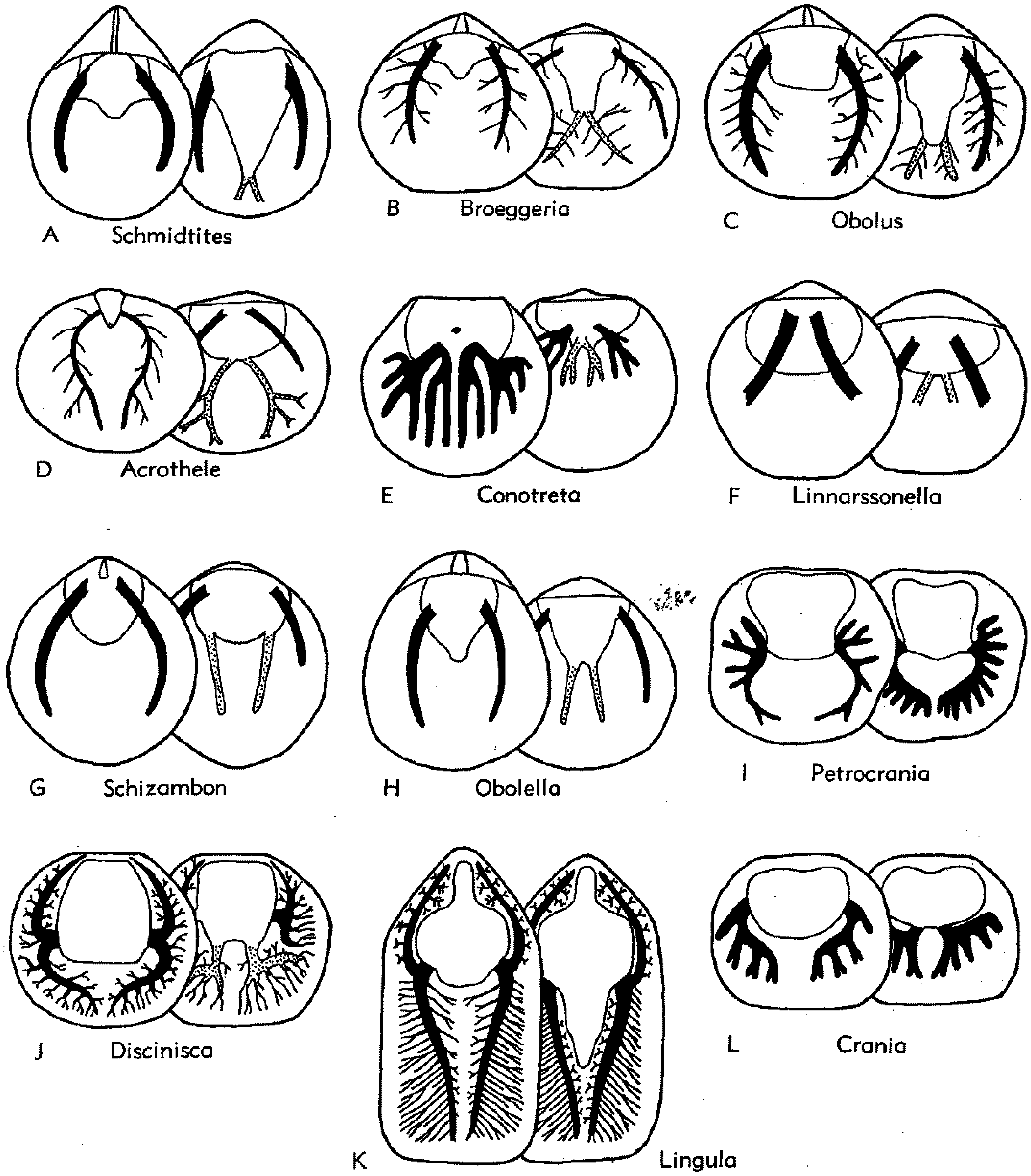

FIG. 138. Mantle canal patterns of some inarticulate brachiopods, pedicle valve on left, brachial valve on right, *vascula lateralia* in black, *vascula media* stippled: *A, Schmidtites* (baculate condition); *B, Broeggeria* (baculate condition); *C, Obolus* (baculate condition); *D, Acrothele* (baculate condition); *E, Conotreta* (pinnate condition); *F, Linnarssonella* (baculate condition); *G, Schizambon* (baculate condition); *H, Obolella* (baculate condition); *I, Petrocrania* (pinnate condition); *J. Discinisca* (bifurcate condition); *K, Lingula* (bifurcate condition); *L, Crania* (pinnate condition) (63).

the form of the shell, for in *Barroisella* and *Langella,* genera very similar in outline to some Recent *Lingula,* the *vascula lateralia* arise in a similar position and are comparable in form to those of *Obolus*. The bifurcation of these canals in the Recent lingulids appears to be more closely related to their relatively anterior origin and to the attenuated outline of the posterior part of the body cavity. Both these factors combine to produce a comparatively large area of mantle, posterolateral of the body cavity, which if it is to be supplied by the existing vascular system necessitates a relatively large, posteriorly directed branch from the *vascula lateralia.* The absence of the dorsal *vascula media* is more difficult to explain. It is not directly a consequence of the considerable forward extension of the body cavity, for in several Paleozoic Lingulida, particularly *Schmidtites,* the limit of the anterior body wall is placed relatively farther forward than that of *Lingula,* yet they still develop *vascula media.* The respiratory function of the *vascula media* of Paleozoic lingulaceans is performed in modern lingulids by the anterior branches of the *vascula lateralia* which converge medially.

A similar bifurcate condition of the *vascula lateralia* has also arisen independently in the Discinidae (Fig. 138,*J*), but in contrast to the lingulids, the dorsal *vascula media* are well developed. On phylogenetic grounds it is probable that the bifurcate *vascula lateralia* in this family were developed from the baculate condition of the acrothelids, but the condition of the *vascula lateralia* of the early discinaceans is quite unknown. In this family the mantle canal system is only known from Recent species, for the epithelium beneath the canals secretes at the same rate as the adjacent outer epithelium of the remainder of the mantle, and consequently the canals leave little or no trace of their position on the shell.

The mantle canal system of the Paterinida is unfortunately still unknown and a similar lack of differential secretion appears to have occurred in these forms, although it is possible that some of the scars, provisionally regarded as being associated with the muscles, may ultimately prove to be vascular in origin.

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ADDITIONAL SOURCES OF ILLUSTRATIONS

(63) **Rowell, A. J.,** new

(64) **———, & Williams, Alwyn,** new

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MORPHOLOGICAL TERMS APPLIED TO BRACHIOPODS

By Alwyn Williams and A. J. Rowell, with contributions by D. V. Ager, G. F. Elliott, R. E. Grant, H. M. Muir-Wood, and F. G. Stehli

The following glossary has been compiled to include terms used in descriptions of brachiopod shells, together with anatomical definitions necessary for understanding shell morphology. Terms most commonly used are in capitals (as **ADDUCTOR MUSCLES**); less important terms are printed in uncapitalized letters (as **accessory adductor scars**). Terms printed in italics are considered by some or all of the contributors to be superfluous or obsolete and therefore continued use of them by brachiopod workers is not recommended.

Glossary of Morphological Terms

accessory adductor scars. Pair of muscle scars in pedicle valve of daviesiellids lying anterior to principal adductor impressions; interpreted by Waagen (1884) as ancillary adductor bases.

accessory denticles. See denticles.

accessory dental socket (of Orthidina). *See* denticular cavity.

accessory diductor muscles. Pair of muscles branching posteroventrally from main diductor muscles and inserted in pedicle valve posterior to adductor bases (Fig. 115).

accessory lamellae. Pair of lamellae developed from arms of jugum and coiled parallel to main lamellae of spiralia (Fig. 108).

accessory septa. Two septa in brachial valve of some chonetoids situated between median septum and lateral septa. [Muir-Wood]

accessory socket. Depression in outer socket ridge articulating with denticulum (Fig. 98,*C*). [Muir-Wood] Also used for outer part of divided dental socket of plectambonitaceans (Fig. 99,*B*).

accessory tooth. Articulating process flanking hinge tooth of plectambonitaceans and fitting into accessory socket in brachial valve (Fig. 99,*A*).

ADDUCTOR MUSCLES. Muscles which contract to close shell. Two adductor muscles, each dividing dorsally, are commonly present in articulate brachiopods to produce single pair of scars located between diductor impressions in pedicle valve and 2 pairs (anterior, posterior) in brachial valve. Two pairs of adductor muscles (anterior, posterior) are commonly present in inarticulate brachiopods, passing almost directly dorsoventrally between valves (Fig. 1, 25, 115). (*See* central and umbonal muscles.)

adductor pits. Pair of depressions indenting anterior face of notothyrial platform of some orthoids for attachment of posterior adductor muscles.

ADJUSTOR MUSCLES. Two pairs of muscles in many articulate brachiopods branching from pedicle and responsible for moving shell relative to it; ventral pair attached posterolaterally from diductors, dorsal pair on hinge plates or floor of brachial valve behind posterior adductors (Fig. 1, 25, 29, 115).

adminiculum. See dorsal and ventral adminiculum.

alae. Winglike ears or cardinal extremities. [Muir-Wood]

alate plate. Flaplike extension of secondary shell arising from lateral surface of brachiophore base in porambonitaceans (Fig. 128).

alternate folding. Deflection of shell surface in which fold of one valve is opposed by sulcus of other (Fig. 65).

alveolus. Pit anterior to internal face of cardinal process. [Muir-Wood]

amphithyridid (foramen). Pedicle opening shared by delthyrium and groove in beak of brachial valve (Fig. 90,*A*).

anacline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

ancillary strut. Secondary shell material deposited between brachiophore base and median ridge in some orthoids.

angle of spines. External angle subtended by chonetoid external hinge spines with posterior margin of pedicle valve, measured in plane parallel with plane of commissure.

ANTERIOR. Direction in plane of symmetry or parallel to it away from pedicle and toward mantle cavity (Fig. 59,*B*).

anterior commissure. Anterior part of line of junction between valves.

anterior margin. Anterior edge of valve.

anterior lateral muscles. Pair of muscles in some Lingulida originating on pedicle valve posterolateral to central muscles, converging dorsally to their insertions anteriorly on brachial valve (Fig. 28).

anterolateral commissure. Anterolateral parts of line of junction between valves.

antiplicate (folding). Similar to paraplication but with fold developed along mid-line of median sulcus (reverse of episulcate) (Fig. 65). [Muir-Wood]

antron. Triangular gap due to incomplete fusion of cardinal process, buttress plates, and breviseptum in some productoids. [Muir-Wood]

antygidium. Low ridge of secondary shell near beak of brachial valve, covered externally by cuticle and deposited during ventral migration of junction of pedicle epithelium with outer epithelium (Fig. 12, 89).

apex. First-formed part of valve around which shell has grown subsequently (term usually restricted to valves having this point placed centrally or subcentrally).

apical angle. Angle subtended by umbonal slopes at umbo.

apical callosity. See pedicle callist; for inarticulate brachiopods, *see* apical process.

apical cavity. Undivided space beneath umbo in either valve.

apical plate. Dorsally enlarged pedicle collar partly closing apex of delthyrium.

apical process. Variably shaped protuberance in umbonal region of pedicle valve of some acrotretaceans which may contain pedicle tube (Fig. 96).

apocopate (mantle canal). Dorsal mantle-canal system with single pair of canals in addition to *vascula genitalia* (Fig. 136).

apsacline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

arcuifer (crura). Crura hammer-shaped in cross section, with arcuate heads concave toward each other (Fig. 1, 7,*4*). [Ager]

area. See cardinal area.

areola. See planarea.

arms. See brachia.

arms of jugum. Processes arising by bifurcation of distal end of jugal stem, which may become extended into accessory lamellae (Fig. 108).

ARTICULATION. Interlocking of 2 valves by projections along their posterior margins, commonly effected in Articulata by 2 ventral teeth fitting sockets of brachial valve but may be assisted or replaced by other projections and complementary pits (Fig. 98).

ascending branches (of loop). Two ventral elements of loop continuous anteriorly with ventrally recurved descending branches and joined posteriorly by transverse band (Fig. 111).

attrite (foramen). Opposite of telate, when ends of beak ridges are worn away. [Muir-Wood]

aulacoterma. Thickening on inside wall of richthofeniid pedicle valve against which brachial valve rests when shell is closed. [Muir-Wood]

auriculate (foramen). Opening bounded by deltidial plates bearing external rims or winglike extensions.

baculate condition (mantle canal). *Vascula lateralia* lacking major dichotomy or bifurcation (Fig. 138).

band. See connecting band and transverse band.

base of brachial process. Proximal part of pentameracean brachial process attached dorsally to outer plate and ventrally to inner plate (Fig. 127).

BEAK. Extremity of umbo, commonly pointed (Fig. 59,*B*). [Muir-Wood]

beak angle. Angle subtended between commissural plane and line bisecting beak of nonstrophic pedicle valve as seen in lateral profile, defined as straight (beak angle, 0-20°), nearly straight (20-30°), suberect (30-70°), erect (70-90°), incurved (more than 90°), corresponds to orthocline-anacline condition of strophic shells (Fig. 61).

beak ridges. More or less angular linear shell elevations extending from each side of umbo so as to delimit all or most of cardinal area. [Muir-Wood]

biconvex. Both valves convex (Fig. 63).

bifurcate condition (mantle canal). *Vascula lateralia* split into anterior and posterior branches immediately beyond point of leaving body cavity (Fig. 138).

bilobate (folding). Similar to strangulate stage but with sulci and folds both well developed (Fig. 63, 64). [Muir-Wood]

biplicate (folding). Alternate folding with 2 submedian folds in brachial valve separated by median sulcus; includes sulciplicate and episulcate conditions (Fig. 65).

biseptum. Double septum in pedicle valve formed by union of dental plates.

blister. Vesicles of secondary shell in umbonal and delthyrial chambers of some spiriferoids and productids (Fig. 132).

BODY CAVITY. Principal part of coelomic space, situated posteriorly, bounded by body wall and containing alimentary tract, nephridia, etc. (Fig. 1, 2).

brace plates. Narrowly diverging septa extending anteriorly of adductor muscle scars in some stropheodontids (Fig. 130).

BRACHIA. Two armlike projections from either side of mouth segment of lophophore, variably disposed but symmetrically placed about mouth (Fig. 1).

brachial bases. See inner socket ridge.

brachial branches. Narrow elevations of secondary shell contained within brachial ridge and converging anteromedially.

brachial cavity. See mantle cavity.

brachial lamellae. See lophophore platform.

brachial loop. See loop.

brachial muscles. Muscles in small brachial canal of inarticulate genera, arising from connective tissue at proximal ends of canals and extending along their length (Fig. 30).

brachial plate. One of pair of subvertical plates constituting pentameracean cardinalia and including inner plate, base of brachial process, and outer plate.

brachial process. Anteriorly directed blade or rodlike projection from pentameracean cardinalia (Fig. 102-107).

brachial protractor muscles. Pair of muscles in craniids which assist movements of lophophore, located anteromedially on brachial valve.

brachial retractor muscles. Pair of small muscles in brachial valve of discinids and craniids, located lateral to anterior adductor muscles.

brachial ridges. Narrow elevations of secondary shell extending laterally or anteriorly as open loop from dorsal adductor muscle field of some articulate brachiopods (Fig. 113,*2*).

BRACHIAL VALVE. Valve that invariably contains any skeletal support for lophophore and never wholly accommodates pedicle, commonly smaller than pedicle valve and having distinctive muscle-scar pattern (Fig. 59).

brachidium. Calcareous support for lophophore in form of loop or spires.

BRACHIOPHORES. Blades of secondary shell projecting from either side of notothyrium and forming anteromedian boundaries of sockets in orthoid, enteletacean, and porambonitacean brachial valves (Fig. 102).

brachiophore base. Basal (dorsal) part of brachiophore which joins floor of valve (Fig. 102,*3*).

brachiophore plate. See brachiophore base.

brachiophore process. Distal rodlike extension of brachiophore that possibly supported lophophore in some genera (Fig. 102,*8*).

brachiophore support. See brachiophore base.

breadth. See width.

brephic. Juvenile stage in shell development following secretion of protegulum, best seen on ribbed valves where it can be distinguished from protegulum by presence of growth lines and from neanic shells by absence of radial ornament.

breviseptum. Dorsal median septum not extending posteriorly to fuse with cardinal process. [Muir-Wood]

bridge. Posteromedian part of marginal flange of thecideacean brachial valve free of valve floor.

brush. Numerous fine cytoplasmic strands radiating from distal end of caecum and connected to periostracum of punctate shells of Articulata (Fig. 5).

buttress plates. See cardinal process buttress plates.

caecum. Evagination of outer epithelium projecting into endopuncta of shell (Fig. 5).

calcareocorneous. See chitinophosphatic.

calcarifer (crura). Crura said to be characterized by dorsally directed process at distal end of each crus (Fig. 1, 2,*2*). [Ager]

callist. See pedicle callist.

callus. Any excessive thickening secondary shell located on valve floor (Fig. 118).

camera. See cella.

camarophorium. Spoon-shaped, adductor-bearing platform in stenoscismatacean brachial valve supported by median septum and derived independently of cardinalia (Fig. 129).

campagiform (loop). Term for growth stage of the loop of dallinids marked by proportionally large hood without lateral lacunae, position of attachment of descending branches to septum and hood varying in different genera (Fig. 110,*2*,*3*). [Elliott]

campagiform hood. Large, commonly funnel-shaped structure without lateral lacunae, with descending branches attached to median septum by transverse processes.

canalifer (crura). Variant of radulifer type, folded longitudinally in form of dorsally facing channel or gutter (Fig. 20,*11*). [Ager]

capilla. Very fine radial ridge on outer surface of shell. *See* costa.

capillate. Ornamented by capillae.

capsular muscles. Longitudinal fibers in connective tissue of pedicle of articulate brachiopods, may be attached to floor of pedicle valve.

cardinal angle. Angle between hinge line and posterolateral margins of shell.

cardinal area. Posterior sector of articulate valve exclusive of delthyrium or notothyrium (may be interarea, planarea, or palintrope) (Fig. 61,*A*,*B*).

cardinal buttress. Vertical plate or ridge supporting cardinal socket in some trimerellids, dividing cavity beneath beak into 2 umbonal chambers (Fig. 101).

cardinal extension. Thecideacean cardinal process.

cardinal extremities. Terminations of posterior margin (Fig. 59,*C*).

cardinal facet. See cardinal socket.

cardinal margin. Curved posterior margin of shell, homologous with hinge line of strophic shells but not parallel with hinge axis (Fig. 61,*A*).

cardinal muscle scar. Posterolaterally placed muscle scars in acrotretaceans and obolellaceans (Fig. 96).

cardinal plate. Plate extending across posterior end of brachial valve, consisting laterally of outer hinge plates and medially of either conjunct inner hinge plates or single plate, commonly perforated posteriorly (Fig. 103,*6*).

CARDINAL PROCESS. Blade or variably shaped boss of secondary shell situated medially in posterior end of brachial valve and serving for separation or attachment of diductor muscles (Fig. 99, 123-125).

cardinal process buttress plates. Two vertical converging or diverging plates which extend anteriorly from cardinal process and in some shells unite with breviseptum. [Muir-Wood]

cardinal process lobes. Projections forming all or part of cardinal process and bearing muscle bases (Fig. 116).

cardinal process shaft. Ridge- or stalklike proximal part of cardinal process which supports myophore (Fig. 123).

cardinal socket. Transverse depression on posterior margin of trimerellacean pedicle valve which receives plate or tooth of brachial valve (Fig. 101).

CARDINALIA. Outgrowths of secondary shell in posteromedian region of brachial valve, associated with articulation, support of lophophore, and muscle attachment; include, for example, cardinal process, socket ridges, crural bases and their accessory plates (Fig. 102).

carina. Major angular elevation of valve surface, externally convex in transverse profile and radial from umbo.

catacline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

cella. Any chamber contained between floor of valve and elevated muscle-bearing platform, best known as inverted V-shaped chamber beneath shoe-lifter process (Fig. 122).

central muscles. Anteriorly or medially placed pair of muscles in Lingulida, originating on pedicle valve and passing anterodorsally to brachial valve (Fig. 28).

centronellid stage (of folding). Terebratuloid brachial valve sulcate umbonally.

centronelliform (loop). Simple lanceolate loop suspended free of valve floor, commonly bearing median vertical plate in addition to echmidium (Fig. 105,*1,2*; 109,*2*).

cheniothyridid stage (of folding). *See* ligate stage.

CHILIDIAL PLATES. Pair of posterior platelike extensions of notothyrial walls, commonly forming lateral boundaries of cardinal process (Fig. 125).

CHILIDIUM. Triangular plate covering apex of notothyrium, commonly convex externally and extending for variable distance ventrally over proximal end of cardinal process (Fig. 92,*A*; 124).

chitinophosphatic (shell). Consisting dominantly of some form of calcium phosphate and chitin.

chlidonophorid (loop). Short loop with converging but not fused crural processes, and transverse band not well differentiated from descending branches. [Muir-Wood]

cicatrix of attachment. Flattening of pedicle valve umbo, representing place of cementation of shell to foreign object. [Muir-Wood]

cilifer (crura). Variant of radulifer type, flattened in plane of commissure, forming direct prolongations of horizontal hinge plates, then turning parallel to plane of symmetry as slightly crescentic blades. [Ager]

cinctid stage (of folding). *See* opposite folding.

cincture. External concentric incision in either valve of some productoids, corresponding to internal ridge or diaphragm. [Muir-Wood]

circinate (lophophore). Consisting of 2 elongate diverging brachia coiled distally into short laterally directed spires, as in cryptoporids.

cirri socles. Obsolete term for spicules at base of filamentar appendages to lophophore. *See* spicules.

coma (pl., **comae**). Concentrically disposed impersistent and irregular protuberances composed of primary and secondary shell on external shell surface of some plectambonitaceans (Fig. 79).

COMMISSURE. Line of junction between edges or margins of valves (Fig. 59, *B,D*).

commissural plane. Plane containing cardinal margin and either commissure of rectimarginate shell or points on anterior commissure midway between crests of folds in both valves (Fig. 59,*D*).

concavo-convex (shell). Brachial valve concave, pedicle valve convex (Fig. 63).

conjunct deltidial plates. Deltidial plates in contact anterodorsally of pedicle.

connecting bands (of loop). Parts of terebratellacean loop that join descending branches to median septum (e.g., terebratelliform, terebrataliiform loops) or ascending and descending branches posterior to their anterior curvature (e.g., laqueiform loops) (Fig. 111). [Elliott]

convexo-concave (shell). Brachial valve convex, pedicle valve concave (Fig. 63).

convexo-plane (shell). Brachial valve convex, pedicle valve plane.

COSTA. Radial ridge on external surface of shell originating at margin of protegulal node (Fig. 81). Also, any coarse rib, without reference to origin. [In this context, which is the commoner usage, **costella** is a fine rib, and **capilla** a very fine rib; and among productoids and chonetoids the term "costate" is used when there are fewer than 15 ribs in a width of 10 mm., "costellate" for 15 to 25 ribs per 10 mm., and "capillate" for more than 25 ribs per 10 mm. (Muir-Wood). This usage gives no indication of the nature of radial ornamentation and any quantitive definitions related to the incidence of ribs at the shell margins are necessarily arbitrary. Thus, in brachiopods ornamented by ribs which increase in wave length during growth, shells of the same species could be described as capillate, costellate, or costate according to their size.]

costate. Shell radially ornamented exclusively by costae.

COSTELLA. Radial ridge on external surface of shell not extending to margin of protegulal node but arising by bifurcation of existing costae or costellae or by intercalation between them. Also used for a fine rib irrespective of origin. *See* costa.

costellate. Shell radially ornamented by costae and costellae.

crenulations. See denticles.

crescent. Submarginal feature in trimerellids consisting of posteromedian raised "crown" and anterolateral depressions comprising "sides" and "ends"; crown occurs on site of cardinal socket in pedicle valve, whereas sides and ends are possibly muscle scars.

crown of crescent. See crescent.

CRURA (sing., **crus**). Two processes which extend from cardinalia or septum to give support to posterior end of lophophore; distal ends may also be prolonged into primary lamellae of spire or descending branches of loop (Fig. 103).

crural band. Ribbon of secondary shell joining crural processes ventrally.

crural bases. Parts of crura united to hinge plates and separating inner and outer hinge plates when present (Fig. 103,*7*).

crural fossette. Cavity on inner face of tooth receiving posteroventral edge of brachiophore or crural plate when valves are closed (Fig. 99,*C*; 118).

crural keel. Dorsal extension of crus beyond junction with flange.

crural lobe. Strongly developed, posteroventrally elevated inner socket ridge in atrypaceans.

crural pit. Cavity near floor of valve separating brachiophore base and fulcral plate in some orthoids.

crural plate. Plate extending from inner edge of outer hinge plate or crural base to floor of brachial valve, may fuse medially with counterpart to form septalium; *see* septalial plate (Fig. 102,*6*). Rejected as general term for platelike structures of orthoid cardinalia (Bancroft, 1928). For pentameroids, *see* brachial plate.

crural point. See crural process.

crural process. Pointed portion of crus directed obliquely inward and ventrally (Fig. 111). [Elliott]

crural trough. See septalium.

cruralium. Spoon-shaped structure of brachial valve formed by dorsal union of pentameracean outer plates (or homologues) and bearing adductor muscles.

cruralium discretum. Outer plates attached independently of each other to floor of pentameracean brachial valve to enclose dorsal adductor field.

cryptacanthiiform (loop). Loop composed of descending branches fused distally to form echmidium, which bears hood on ventral anterior end; with continued growth echmidium becomes deeply cleft anteriorly but still connected with descending branches (Fig. 109,*3*,*4*).

cryptonelliform (loop). Long loop unsupported in adults by median septum and having narrow transverse band. [Stehli]

curvature of beak. Curvature of ventral beak toward brachial valve; *see* beak angle.

cuticle. Chitinous cover of pedicle.

cyclothyridid (foramen). *See* auriculate.

cynocephalous (folding). Having exaggerated, very sharp fold in brachial valve, especially in rhynchonelloids (e.g., *Homoeorhynchia*), supposedly resembling dog's head (Fig. 15). [Ager]

cystose (shell). Vesicles of secondary shell deposited in deep pedicle valves by dorsally migrating outer epithelium.

dalliniform (loop). Dallinid loop arrangement in which long descending branches recurve into ascending branches which meet in transverse band, all free of valve floor, morphologically similar to magellaniform and cryptonelliform loop (Fig. 110,*6*,*7*). [Elliott]

delayed costation (or **costellation**). Ribs first appearing at some distance outside of protegulal node (Fig. 81).

deltarium discretum. Impersistent thickening along posterolateral edges of delthyrium.

delthyrial angle. Angle subtended by margins of delthyrium.

delthyrial callosity. See apical callosity.

delthyrial carinae. See teeth ridges.

delthyrial cavity. See delthyrial chamber.

delthyrial chamber. Cavity beneath umbo of pedicle valve bounded by dental plates, if present, or by posterolateral shell walls, if dental plates absent.

delthyrial foramen. Relatively large aperture for emergence of pedicle through open delthyrium unmodified by plates; occurs in earliest growth stages, rare in adults.

delthyrial plate. Plate within delthyrial chamber of some spiriferoids, extending variable distance from apex between dental plates (probably homologue of pedicle collar) (Fig. 91, 121).

delthyrial supporting plate. See dental plate.

DELTHYRIUM. Median triangular or subtriangular aperture bisecting ventral cardinal area or pseudointerarea, commonly serving as pedicle opening (Fig. 61,*B*).

deltidial cover. Externally concave plate in some pentameraceans closing posterior end of delthyrium (probably homologue of pedicle collar).

deltidial grooves. Lines delimiting thecideacean pseudodeltidium in species with this structure not flush with ventral area. [Elliott]

DELTIDIAL PLATES. Two plates growing medially from margins of delthyrium, partly or completely closing it (Fig. 89,*A*; 98,*A*).

deltidial ridges. Two narrowly triangular ridges reputed to separate homeodeltidium and propareas of trimerellids.

deltidium. Cover of delthyrium formed by conjunct deltidial plates, line of junction of plates visible (Fig. 89,*C*).

dental lamellae. See dental plates.

DENTAL PLATES. Variably disposed plates of secondary shell underlying hinge teeth and extending to floor of pedicle valve (Fig. 99, 119).

dental ridges. See teeth ridges.

DENTAL SOCKETS. Excavations in posterior margin of brachial valve for reception of hinge teeth (Fig. 98,*B*,*C*).

dental valve. See pedicle valve.

denticles. Small, sharp, protruding ridges that alternate with complementary sockets located along cardinal margin or hinge line of both valves (Fig. 100); for denticles of orthoid cardinalia *see* outer socket ridge.

denticular cavity. Groove on outer side of teeth which receives projection from outer socket ridge (Fig. 98). [Muir-Wood]

denticular plate. Obtusely triangular plate lateral to delthyrium, bearing denticles and fused with dental plate, developed in stropheodontids.

denticulated cardinal margin. Posterior margin of both valves bearing denticles, fitting into complementary sockets.

denticulated commissure. Zigzag commissure due to interfingering of angular ribs.

denticulum (pl., **denticula**). Small toothlike termination of cardinal area, usually in pedicle valve, commonly articulating with accessory socket in outer socket ridge (Fig. 98). [Muir-Wood]

depth. See thickness.

descending branches. Two dorsal elements of loop extending distally from crura and recurved ventrally at anterior ends (Fig. 111).

descending lamellae. See descending branches.

deuterolophe. Spirally coiled part of lophophore bearing double brachial fold and double row of paired filamentar appendages, homologous with side arms of plectolophe (Fig. 106,*G'*).

deuterolophous (adj.). Pertaining to deuterolophe.

diaphragm. Thin crescentic plate of secondary shell developed around visceral disc of brachial valve and restricting gap between brachial valve and trail of pedicle valve (Fig. 74). [Muir-Wood]

dictyothyridid stage (of folding). *See* pliciligate.

DIDUCTOR MUSCLES. Muscles serving to open valves of articulate brachiopods, commonly consisting of 2 pairs attached to brachial valve immediately anterior to beak, usually to cardinal process; principal pair commonly inserted in pedicle valve on either side of adductor muscles and accessory pair posterior to them (Fig. 115).

digitate (brachidium). Thecideacean brachidium with brachial branches extending inward from marginal flange. [Elliott]

digitate (mantle canal). Posterior part of *vascula genitalia* projecting laterally nearly to mantle margin, with corresponding abbreviation of *vascula media* or *vascula myaria* (Fig. 135).

disjunct deltidial plates. Plates not in contact anterodorsally of pedicle.

divaricator muscles. See diductor muscles.

divided hinge plates. Plates not united medially.

dorsal. Direction toward brachial valve from pedicle valve.

dorsal adjustor muscles. See adjustor muscles.

dorsal adminiculum. Dorsal part of dental plate.

dorsal denticulum. See outer socket ridge.

dorsal foramen. Posteriorly located perforation of cardinal plate which may encroach on beak of brachial valve; also used for so-called "perforation" of brachial valve representing passage between bases of cardinal-process lobes in some strophomenoids.

dorsal valve. See brachial valve.

dorsibiconvex. Brachial valve more convex than pedicle valve.

dorsiconvex. See dorsibiconvex.

dotted brachial ridges. Ridges of thecideacean brachidium represented by rows of small separate pustules. [Elliott]

double-barrelled spines. External spines of primary shell having oval cross section and commonly barbed, bearing fine longitudinal furrow on posterior surface and partially enveloping anterior chamber which is incompletely divided by median partition (Fig. 87).

double deltidial plates. Pair of deltidial plates, each of which is seen in certain transverse sections to consist either of 2 parallel plates or of one plate nearest hinge line buttressed by another disposed at angle to it (e.g., *Cirpa,* Fig. 11,*2*). [Ager]

double median septum. More or less elevated median plate in pentameroid brachial valve formed by union of 2 septal plates.

dyscoliid stage (of lophophore). Details unknown but probably trocholophe.

ear. Flattened or pointed extremity of shell subtended between hinge-line and lateral commissure.

ear baffle. Extension of lateral ridge across ear inside some productoids. [Muir-Wood]

echmidium. Spear-shaped plate formed during ontogeny of loop by fusion of anterior ends of descending branches (Fig. 109,*2*).

elytridium. Convex puckered cover of delthyrium in aulostegids. [Muir-Wood]

emarginate. Median segment of anterior commissure deflected posteriorly.

endopuncta (pl., **endopunctae**), Perforation of shell not extending to its external surface, occupied by caecal prolongation of outer epithelium (Fig. 5, 126).

endopunctum (pl., *endopuncta*). *See* endopuncta.

endospines. Fine, solid or hollow spines on interior of shell.

entering valve. See brachial valve.

ephebic. Mature.

episulcate (folding). Resembling parasulcate but with median fold of brachial valve indented by median sulcus (Fig. 65,*9*).

epithyridid (foramen). Pedicle opening wholly within ventral umbo and ventral from beak ridges (Fig. 90,*E*).

equidistribute (mantle canal). *Vascula genitalia, vascula myaria,* and *vascula media* all well developed and contributing to mantle canal circulation (Fig. 135).

erect beak. *See* beak angle.

erect spines. Spines projecting at high angle (75-90°) from shell surface. [Muir-Wood]

euseptoidum. See myophragm.

euseptum. Primary septum; *see* septum.

everted stage (of folding). *See* uniplicate.

exopuncta (pl., **exopunctae**). Perforation of external shell surface commonly restricted to primary layer and never penetrating to internal surface.

exopunctum (pl., *exopuncta*). *See* exopuncta.

extremities. See cardinal extremities.

falcifer (crura). Crura arising on dorsal side of hinge plates and projecting into brachial valve as broad bladelike processes (Fig. 1, 14). [Ager]

false cardinal area. See cardinal area or pseudointerarea; term previously used for any poorly defined cardinal area or pseudointerarea.

false pedicle groove. See intertrough.

fascicostellate. Ornament of costae and costellae bundled into fascicles (Fig. 81).

fibrous layer. See secondary layer; term commonly used as alternative in articulate brachiopods in which the secondary layer is exclusively fibrous.

filum (pl., **fila**). Fine concentric ridge on external surface of shell.

fimbria (pl., **fimbriae**). Spinelike projection from spiralia or jugum; also used for spinose projection on margin of growth lamella, as in *Spinilingula* (Fig. 108).

flange (of crus). Lateral projection from crus formed by anterior extension of part of outer hinge plate adjacent to crural base.

flange (dyscoliid). Incurved lateral and anterior margins of both valves. [Muir-Wood]

flanks. See lateral slopes.

flap. See posterior flap.

flexure line. Line extending from beak to anterior border of both ventral propareas in some linguIaceans, marked by deflection of growth lines (Fig. 62,*4*).

FOLD. Major elevation of valve surface, externally convex in transverse profile and radial from umbo.

foramen. *See* pedicle foramen; term commonly used with this meaning (Fig. 61,*A*).

foraminal sheath. See pedicle sheath.

foraminal tube. See pedicle tube.

free. Animal not attached to substratum.

free spondylium. Spondylium unsupported by septum.

frenuliniform lacuna. Lateral hole in hood produced by resorption during dallinid loop development subsequent to campagiform growth stage. [Elliott]

frenuliniform (loop). Term for growth stage in dalliniform loop development when lateral resorption gaps occur in hood and before resorption of shell occurs posterior to gaps (Fig. 110,*4*). [Elliott]

frill. Relatively large lamella projecting well beyond general contour of valve, deposited by margin of highly retractile mantle.

fulcral plate. Small plate raised above floor of brachial valve extending between posterior margin and brachiophore base and bounding socket anterolaterally (Fig. 102,*3*).

furrow. See interspace.

fused hinge plates. Hinge plates joined together along mid-line as far as hinge line or in front of it, with no development of septalium (e.g., *Cirpa*). [Ager]

gape. Anterior and lateral opening of shell.

gastrothyridid (foramen). Pedicle opening limited to pedicle valve.

geniculate. Abrupt and more or less persistent change in direction of valve growth producing angular bend in lateral profile (Fig. 63).

genital area. Part of shell underlain by saccate gonocoel or posterior part of digitate or lemniscate gonocoel.

genital markings. Radial ridges or pits on inside of shell within genital area.

ginglymus. Secondary interarea in pedicle valve of some productoids serving to close gap between valves and to assist in articulation. [Muir-Wood]

glossothyropsiform (loop). Loop developed from cryptacanthiiform stage by final resorption of posterior part of echmidium and consisting of 2 descending branches unconnected posteriorly, bearing 2 broad ascending elements joined by wide transverse band (Fig. 109,*5*).

granule. See tubercle.

growth lamella. Concentric outgrowth of shell deposited by retractile mantle margin, smaller than frill (Fig. 78).

growth line. Concentric line on outer surface of shell formed when anterior and lateral growth of shell temporarily was in abeyance (Fig. 80).

gutter. Anterior recurvature of trail of one or both valves, possibly serving as strainer or stabilizer. [Muir-Wood]

haemal valve. See brachial valve.

halteroid spines. Long external hollow spines, commonly 4 to 6, symmetrically placed, acting as strutlike supports. [Muir-Wood]

height. In biconvex, plano-convex, and convexo-plane shells height equals thickness, being maximum dimension normal to length and width; in concavo-convex and convexo-concave shells height is maximum distance measured normal to length in plane of symmetry between shell and line joining beak and anterior margin (Fig. 59).

hemiperipheral growth. New shell material added anteriorly and laterally but not posteriorly (Fig. 60).

hemispondylium. Two small plates within thecideacean ventral umbo, usually free of valve floor and side walls but commonly supported by median septum and bearing median adductor muscles. [Elliott]

hemisyrinx. Conical chamber extending medially along floor of clitambonitoid spondylium and delineated posteriorly by pair of discrete lateral ridges.

hemisyrinx ridge. Ridge forming posterolateral boundary of hemisyrinx.

hemithyridid stage (of shell structure). *See* impunctate shell.

henidium. Conjunct deltidial plates that lose line of junction during late stages of growth.

hinge. Often used loosely for either hinge line or cardinal margin.

hinge area. See cardinal area.

hinge axis. Line joining points of articulation about which valves rotate when opening and closing (Fig. 61,*A,B*).

hinge line. Straight posterior margin of shell parallel with hinge axis; also used as synonym of cardinal margin (Fig. 61,*B*).

hinge plate. *See* inner hinge plate, outer hinge plate.

hinge platform. Solid secondary shell platform extending between socket ridges of terebratellacean cardinalia. [Elliott]

hinge projections. Projections of fused inner socket ridges and crural bases, visible externally posterior to dorsal umbo. [Elliott]

hinge socket. *See* dental socket.

hinge spines. Hollow spines developed in chonetoids in row along posterior margin of ventral interarea on either side of umbo and continuous with cylindrical hollow, commonly deflected passageways through interarea, often called roots of spines. [Muir-Wood]

HINGE TEETH. Two principal articulating processes situated at anterolateral margins of delthyrium and articulating with dental sockets in brachial valve (Fig. 98).

hinge trough. V- or U-shaped depression formed by fusion of bifurcated median septum with combined socket ridges and crural bases of some terebratellaceans. [Elliott]

hinge width. Lateral extent of hinge line.

holcothyridid stage (of folding). *See* paraplicate.

holoperipheral growth. Increase in valve size all around margins, in posterior as well as anterior and lateral directions (Fig. 60).

HOMEOCHILIDIUM. Externally convex triangular plate closing almost all or only apical part of notothyrium in Paterinida; spelled homoeochilidium by some authors (Fig. 93).

HOMEODELTIDIUM. Externally convex triangular plate closing almost all or only apical part of delthyrium in Paterinida; spelled homoeodeltidium by some authors (Fig. 62,*3*; 93).

hood. Arched plate of secondary shell arising from echmidium of *Cryptacanthia* or median septum of dallinids. *See* campagiform hood (Fig. 109, 110).

hypercline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

hypothyridid (foramen). Pedicle opening located below or on dorsal side of beak ridges with umbo intact (Fig. 90,*B*). [Muir-Wood]

imbricate (ornament). *See* lamellose.

impunctate (shell). Shell lacking endopunctae or pseudopunctae.

inclination of cardinal area or pseudointerarea. Commonly used terms for inclination of cardinal area or pseudointerarea in either valve based on convention of viewing specimen in lateral profile with beaks to left and brachial valve uppermost, referring cardinal area to its position within one of 4 quadrants defined by commissure plane and plane normal to it and symmetry plane, touching base of cardinal areas (Fig. 61). Cardinal area lying on continuation of commissure plane is **orthocline.** Moving clockwise, cardinal area in first quadrant (top left) is weakly to strongly **anacline**; in second quadrant (top right) weakly to strongly **hypercline.** Moving counter-clockwise from orthocline position, cardinal area lying in bottom left quadrant is weakly to strongly **apsacline**; at 90° to orthocline it is **catacline**; and continuing counter-clockwise into bottom right quadrant cardinal area is weakly to strongly **procline** (Fig. 61,*C*).

incurved beak. *See* beak angle.

inequidistribute (mantle canal). *Vascula genitalia* of dorsal mantle saccate and contributing little to canal circulation (Fig. 135).

inner carbonate layer. *See* secondary layer.

inner hinge plates. Pair of subhorizontal plates in cardinalia of some rhynchonelloids, spiriferoids and terebratuloids located median of crural bases and fused laterally with them (Fig. 102,*6*).

inner plates. Pair of subvertical plates in cardinalia of some pentameraceans lying on ventral side of base of brachial process and fused dorsally with it; *see* brachiophore base for orthoids (Fig. 102,*8*).

inner socket ridge. Ridge of secondary shell commonly overhanging dental socket and forming its inner or anterior margin (Fig. 98; 102,*6*).

interarea. Posterior sector of shell with growing edge at hinge line; also, more commonly used for any plane or curved surface lying between beak and posterior margin of valve and bisected by delthyrium or notothyrium (Fig. 61,*B*).

intercalary lamellae. *See* accessory lamellae.

intercalation. Costella arising by insertion between costae or costellae, not by bifurcation of existing costa or costella (Fig. 81).

intercamarophorial plate. Short, low median septum on posterior mid-line of camarophorium in stenoscismataceans, extending to underside of hinge plate but independent of median septum duplex. [Grant]

interconnecting bands. *See* connecting bands.

intercostal sulci. *See* interspace.

internal oblique muscles. Pair of muscles in some inarticulates, originating on pedicle valve between anterior adductors and passing posterolaterally to insertions on brachial valve located anterolaterally from posterior adductor muscles (Fig. 29).

interspace. Flat or externally concave sectors of shell between adjacent costae or costellae (Fig. 84).

intertext (folding). Alternate folding with opposed sulci and carinae equal in amplitude.

intertrough. Median, narrowly triangular furrow dividing pseudointerarea of pedicle valve of some acrotretaceans (Fig. 62,*5*).

intraplicate (folding). Form of alternate folding with pedicle valve bearing median fold indented by shallower median sulcus (Fig. 65,*4*).

intraseptal lamella. Sheet of prismatic calcite of varying persistency found in median septum of spondylium duplex.

inverted stage (of folding). *See* sulcate.

ismeniform (loop). *See* campagiform loop.

jugal processes. Pair of ventromedially directed outgrowths from primary lamellae of spiralia which do not coalesce.

jugal stem. Ventroposteriorly directed continuation of jugum which by bifurcation may give rise to accessory lamellae posteriorly.

JUGUM. Medially placed connection of secondary shell between 2 primary lamellae of spiralia (Fig. 108).

kingeniform (loop). Adult dallinid loop in which tendency to retain campagiform hood during development leads to broad sheetlike transverse band with connecting bands leading to septum in addition to normal ones joining descending branches with septum. [Elliott]

labiate (foramen). Exaggerated marginate foramen in which dorsal edge is prolonged liplike. [Stehli]

lacuna. *See* frenuliniform lacuna.

lamella. Sheetlike extension of primary and even underlying secondary shell deposited by retractile mantle margin on external shell surface; also used for calcareous ribbon comprising spiralium and coiled extension from arm of jugum.

lamellar layer. *See* primary layer.

lamellose. Ornament consisting of overlapping growth lamellae.

laqueiform (loop). Dallinid loop pattern in which posterior connecting bands from ascending to descending branches are retained during enlargement and proportional thinning during change from frenuliniform to terebrataliiform loop. [Elliott]

lateral areas. General term for portions of ventral palintrope to left and right of delthyrial structures. [Elliott]

lateral branch (of jugum). Part of jugum continuous with primary lamella (Fig. 108).

lateral cavities. See umbonal cavities.

lateral commissure. Lateral part of line of junction of valves.

lateral margin. Lateral edge of valve.

lateral oblique muscles. Pair of muscles in some inarticulates, originating on pedicle valve anterolaterally from posterior adductor muscles and passing anterodorsally to insertions either on brachial valve and anterior body wall against anterior adductors (Discinidae) or entirely on anterior body wall (Craniidae) (Fig. 29).

lateral slopes. Valve surfaces on either side of median sector of shell.

leiolophid stage (of lophophore). Obsolete term for embryonic brachial structure before appearance of filamentar appendages of lophophore.

lemniscate (mantle canal). Gonocoel still saclike but giving rise to branches that extend to posterolateral margins with corresponding peripheral reduction of *vascula media* and *vascula myaria* (Fig. 136).

LENGTH (of valve). Distance from most posterior point of value, normally umbo, to farthest point on anterior margin measured on commissural plane in plane of symmetry or parallel with it (Fig. 59,*C*).

lenticular stage (of folding). Both valves gently and subequally biconvex, anterior margin rectimarginate.

ligate stage (of folding). Opposite folding with single sulcus in one valve opposed by single sulcus in other, commissure rectimarginate (Fig. 64, *3*). [Elliott]

limbus. Flattened inner margin of inarticulate valve.

lingual extension. See linguiform extension.

linguiform extension. Anterior tongue-shaped extension of either valve. [Muir-Wood]

liothyrinid stage (of folding). *See* lenticular stage.

lirae. Fine ridges and grooves.

LISTRIUM. Plate in some discinaceans closing anterior end of pedicle opening which has migrated posteriorly (Fig. 62,*2*; 94,*A*).

longitudinal axis. Intersection of planes of commissure and symmetry.

LOOP. Support for lophophore composed of secondary shell and extending anteriorly from crura as closed apparatus, variably disposed and generally ribbon-like with or without supporting septum from floor of brachial valve (Fig. 105).

lophidium. Inverted V-shaped projection of median posterior part of brachial valve or of external face of cardinal process, helping to close gap in delthyrium in some productoids. [Muir-Wood]

LOPHOPHORE. Feeding organ with filamentar appendages, symmetrically disposed about mouth, typically suspended from anterior body wall but may be attached to dorsal mantle; occupies mantle cavity (Fig. 1).

lophophore platform. Bilobed or U-shaped disc of secondary shell with anterior edge elevated above floor of plectambonitacean brachial valve; probably supported lophophore (Fig. 113,*1*).

lophrothyridid stage (of folding). *See* uniplicate.

magadiform (loop). *See* campagiform loop.

magadiniform (loop). Type of terebratellid loop or loop growth stage marked by completed descending branches from cardinalia to median septum, with ringlike structure on septum representing early ascending portion of loop. [Elliott]

magaselliform (loop). *See* magelliform loop.

magellanian stage (shell). *See* punctate (shell).

magellaniform (loop). Type of free terebratellid loop consisting of long descending branches recurved into ascending branches which meet in transverse band; morphologically similar to dalliniform loop. [Elliott]

magelliform (loop). Type of terebratellid loop or loop growth stage, in which bases of septal ring on median septum meet and fuse with attachments of completed descending branches. [Elliott]

main flanks. See lateral slopes.

maniculifer (crura). Derived from radulifer type, with handlike processes at end of straight, ventrally directed crura (Fig. 1, 25,*2*). [Ager]

MANTLE. Prolongation of body wall as fold of ectodermal epithelium (Fig. 1,*2*).

MANTLE CANALS. Flattened, tubelike extensions of body cavity into mantle.

MANTLE CAVITY. Anterior space between valves bounded by mantle and anterior body wall and containing lophophore (Fig. 1,2).

mantle papilla. See caecum.

mantle sinus. See mantle canal.

margin (of valve). Edge of valve.

marginal flange (of shell). *See* geniculation.

marginal flange (of thecideacean brachial valve). *See* subperipheral rim.

marginal ridge. Thickening along internal lateral and anterior margin of visceral disc of some productoids, usually in brachial valve. [Muir-Wood]

marginal spines. Long, slender prolongations of interspaces between ribs lying against inner surface of opposing valve when shell is shut and forming grille when shell is open (Fig. 84).

marginate (foramen). Pedicle foramen with thickened margin. [Stehli]

marsupial notch. Small double notch or perforation in ventral edge of brachial bridge in some adult female thecideaceans marking passage of 2 specialized posteriorly directed filaments to which embryos are attached. [Elliott]

median. In plane of shell symmetry.

median partition. Median septum supporting anterior part or trimerellacean muscle platform and dividing cavity beneath platform into 2 vaults (Fig. 101).

median plane. *See* plane of symmetry.

megathyridid (posterior margin). Posterior margin long and straight.

megerliiform (loop). Terabratellacean loop with descending branches joining anterior projections from large ring on low median septum; differs from similar dallinid and terebratellid loops by appearance of well-developed ring before growth of descending branches. [Elliott]

mergifer (crura). Variant of radulifer crura, long, close together, parallel, arising directly from swollen edge of high dorsal median septum (Fig. 1, 8,*3*). [Ager]

mesothyridid (foramen). Pedicle opening located partly in ventral umbo and partly in delthyrium, beak ridges appearing to bisect foramen (Fig. 90,*D*). [Muir-Wood]

metacarinate stage (of folding). Opposite folding, carinae continuous and strongly developed (Fig. 64,*2*).

middle lateral muscles. Pair of muscles in some Lingulida originating on pedicle valve between central muscles and diverging slightly posteriorly before insertion on brachial valve (Fig. 28).

mixoperipheral growth. Differs from holoperipheral growth in that posterior sector of valve increases in size anteriorly and toward other valve (Fig. 60).

monticules. Small rounded nodes, commonly bearing spines. [Muir-Wood]

mosaic. Pattern on interior of valve formed by outlines of adjacent fibers of secondary shell layer (Fig. 69).

mouth segment (of lophophore). Median part of lophophore containing mouth, attached to anterior body wall and bearing single row of paired or unpaired filamentar appendages.

mucronate (cardinal margin). Cardinal extremities extended into sharp points.

muehlfeldtiform (loop). *See* megerliform.

multicostellate. Costellae increasing in number by bifurcation or intercalation but not varying greatly in size (Fig. 81).

muscle area. *See* muscle field.

muscle-bounding ridge. Elevation composed of secondary shell bounding part of muscle field.

muscle field. Area of valve in which muscle scars are concentrated.

muscle impression. Marks of muscle attachment.

muscle platform. Solid or undercut elevation of shell to which muscles are attached (Fig. 122, 133).

MUSCLE SCAR. More or less well-defined impression or elevation on valve representing final site of attachment of muscle (Fig. 115).

muscle track. Path of successive muscle impressions formed by migration of muscle base during growth.

myocoelidium. Chamber similar to spondylium but not formed by dental plates, serving for attachment of muscles (e.g., Richthofeniidae). [Muir-Wood]

myophore. Distal expanded part of differentiated cardinal process to which diductor muscles were attached (Fig. 123).

myophragm. Median ridge of secondary shell secreted between muscles and not extending beyond muscle field. [Muir-Wood]

mystrochial plates. Pair of small plates buttressing spondylium posterolaterally, as in *Amphigenia.*

neanic. Youthful stage at which generic characters of shell begin to be apparent.

nearly straight beak. *See* beak angle.

nepionic. See brephic.

neural valve. See pedicle valve.

nodus principalis. Point from which *vascula cruralia* or *vascula cardinalia* (or both) diverge in mantle canal system of brachial valve (Fig. 134).

nodus quadrivialis. Point from which *vascula intermyaria* diverge in mantle canal system of brachial valve (Fig. 134).

nodus septalis. Point from which *vascula media* diverge in mantle canal system of brachial valve (Fig. 134).

nodus terminalis. Point of origin of *vascula terminalia* in mantle canal systems (Fig. 134).

nonintertext (folding). Type of folding in which sulcus or carina of one valve is opposed by plane valve. [Elliott]

nonstrophic (shell). Shell with posterior margin not parallel with hinge axis (Fig. 61,*A*).

norellid stage (of folding). *See* sulcate.

notodeltidium. Plate completely filling delthyrium, formed by fusion of deltidial plates with eventual plugging of pedicle foramen by posterior retreat of junction between pedicle epithelium and outer epithelium.

notothyrial cavity. See notothyrial chamber.

notothyrial chamber. Cavity in umbo of brachial valve corresponding to delthyrial chamber of pedicle valve, bounded laterally by brachiophore bases (or homologues) or by posterolateral shell walls if brachiophore bases absent.

notothyrial platform. Umbonal thickening of floor of brachial valve between brachiophore bases (or homologues) (Fig. 99,*D*).

notothyridid (foramen). Pedicle opening in brachial valve, condition never completely attained.

NOTOTHYRIUM. Median subtriangular opening bisecting dorsal cardinal area or pseudointerarea (Fig. 59,*A*).

occlusor muscle. See adductor muscle.

oligopalmate. Mantle canal system with 2 pairs of principal canals in each mantle.

opercular. Lidlike, referring to brachial valve in some genera. [Muir-Wood]

opposite folding. Folding in which fold or sulcus in one valve is opposed by fold or sulcus in other, commissure remaining rectimarginate (Fig. 64).

ornament. Any outgrowth, minor deflection or nonpathological interruption in growth found on outer shell surface.

ornithellid stage (of folding). Characterized by presence of lateral carinae but without median sulci. (Fig. 64,*1*). [Muir-Wood]

orthocline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

orthoconate. Brachia coiled parallel with plane of commissure.

outer carbonate layer. See primary layer.

outer epithelium. Ectodermal epithelium adjacent to shell and responsible for its secretion (Fig. 2,3, 16).

outer hinge plates. Pair of concave or subhorizontal plates in cardinalia separating inner socket ridges and crural bases (Fig. 102,*6*).

outer mantle lobe. Outer peripheral part of mantle, separated by mantle groove from inner lobe, in articulate brachiopods responsible for secretion of primary shell layer (Fig. 3, 74).

outer plates. Pair of subvertical plates in pentameracean cardinalia with ventral surface fused to base of brachial process and dorsal edge attached to floor of valve or rarely septal plate (Fig. 102,*8*).

outer socket ridge. Low ridge bounding dental socket on outer lateral or posterior side (Fig. 98; 102,*6*).

outside lateral muscles. Pair of muscles in some Lingulida which originate on pedicle valve lateral to centrals and extend posteriorly to insertions behind middle lateral muscles on brachial valve (Fig. 28).

ovarian impression. See genital marking.

ovarian marking. See genital marking.

palintrope. Initially used for morphologically posterior sector of either valve which was reflexed to grow anteriorly (mixoperipheral growth); more recently used for curved surface of shell, bounded by beak ridges and cardinal margin of nonstrophic shells (differs from planarea in being curved in all directions) (Fig. 61,*A*).

pallial caecum. See caecum.

pallial lobe. See mantle.

pallial markings. See vascular markings.

pallial sinus. See mantle canal.

pallium. See mantle.

papillae. Regularly arranged endospines.

paradental lamella. See muscle-bounding ridge.

paraplicate (folding). Produced from sulcate stage by development of 2 folds in brachial valve bounding dorsal sulcus (Fig. 65,*5*).

parasulcate (folding). Form of alternate folding with brachial valve bearing sulcus on either side of median fold (Fig. 65,*7*).

parathyridium. Deep indentation of shell on either side of beak, formed by medially directed depression or flexure of posterolateral shell surface of both valves, particularly brachial (e.g., *Cardiarina*).

parvicostellate. Costellae numerous, arising entirely by intercalation between widely spaced costae (Fig. 81).

paucicostate. Costae distant and few.

paucicostellate. Costae and costellae distant and few.

paucispinose. With few spines.

PEDICLE. Variably developed, cuticle-covered appendage, commonly protruding from pedicle valve and responsible for attachment of animal to substratum (Fig. 1, 2).

pedicle callist. Localized thickening of secondary shell layer in apex of pedicle valve representing track of anterior migration of junction between pedicle epithelium and outer epithelium (Fig. 115).

pedicle collar. Complete or partial ringlike thickening of inner surface of ventral beak, continuous laterally with internal surface of deltidial plates, sessile, with septal support, or free anteriorly and secreted by anteriorly migrating outer epithelium at its junction with pedicle epithelium (Fig. 98, *A*).

pedicle epithelium. Ectodermal epithelium investing pedicle (Fig. 2).

PEDICLE FORAMEN. Subcircular to circular perforation of shell through which pedicle passes (Fig. 61,*A*).

pedicle furrow. External plate extending anteriorly from beak to pedicle foramen in some siphonotretaceans and obolellaceans (use not recommended because plate not invariably concave externally).

PEDICLE GROOVE. Commonly subtriangular groove dividing ventral pseudointerarea medially and affording passage for pedicle in many Lingulida (Fig. 62,*4*).

pedicle muscle scar. Scar of attachment on pedicle valve of longitudinal fibrils in connective tissue of pedicle of articulate brachiopods.

pedicle muscles. Any muscles associated with pedicle; in articulate brachiopods mostly synonymous with adjustor muscles and may include longitudinal fibrils in connective tissue of pedicle; in inarticulate brachiopods includes muscles developed within wall and coelom of pedicle (Fig. 25).

pedicle notch. Small subtriangular depression, posteromedially placed on limbus of paterulids, probably functioning as pedicle groove.

pedicle opening. Variably shaped aperture in shell through which pedicle emerges.

pedicle plate. Tongue-shaped shelly deposit inside labium of labiate foramen.

pedicle sheath. Externally directed tube projecting posteroventrally from ventral umbo, probably enclosing pedicle in young stages of development of some shells with supra-apical pedicle opening (Fig. 92,*B*).

pedicle tube. Internally directed tube of secondary shell continuous with margin of pedicle foramen and enclosing proximal part of pedicle (Fig. 94,*B*).

PEDICLE VALVE. Valve through which pedicle commonly emerges, usually larger than brachial valve (Fig. 1, 59).

peduncle. See pedicle.

perideltidial area. Discrete part of perideltidium.

perideltidial line. Break of slope marking outer boundary of perideltidial area.

perideltidium. Pair of slightly raised triangular parts of interarea flanking pseudodeltidium or lateral to it and characterized by vertical striae in addition to horizontal growth lines parallel to posterior margin.

periostracal pad. Thickened band of periostracum covering cardinal areas and spun out by fused mantle lobes along posterior margin of some articulate brachiopods (Fig. 89,*C*).

periostracum. Thin, organic external layer of shell (Fig. 74).

permesothyridid (foramen). Pedicle opening located mostly within ventral umbo (Fig. 90,*E*). [Muir-Wood]

pinnate (mantle canal). *Vascula genitalia* or *vascula lateralia* consisting exclusively of radially disposed canals (Fig. 135).

planareas. Two flattened areas developed, one on either side of posterior part of shell in place of more common single median interarea. [Ager]

plane commissure. See rectimarginate.

plane of symmetry. Plane bisecting shell symmetrically (Fig. 59,*D*).

plano-convex. Brachial valve flat, pedicle valve convex.

plate (of trimerellids). Single transverse, platelike projection from cardinal margin of brachial valve articulating with cardinal socket of pedicle valve (Fig. 101).

platform. Relatively broad solid or undercut elevation of inner surface of valve, commonly bearing muscles (Fig. 101).

platform (of Orthidina). *See* notothyrial platform and chamber.

platform line. Side bounding notothyrial chamber.

platform vaults. Two cavities beneath platform in some trimerellids, separated by median partition (Fig. 101).

platidiiform (loop). Loop consisting of descending branches from cardinalia to median septum, with only rudimentary prongs on septum representing ascending part of loop. [Elliott]

plectolophe. Lophophore in which each brachium consists of U-shaped side arm bearing double row of paired filamentar appendages but terminating distally in medially placed plano-spire normal to commissural plane and bearing single row of paired appendages.

plectolophous (adj.). Pertaining to plectolophe.

plectolophus (noun). *See* plectolophe.

pleuromal plates. Pair of "plates" in posterior part of delthyrial cavity of some spiriferoids immediately internal to dental plates, probably merely later infilling of delthyrial cavity.

plica. Major undulation of commissure with crest directed dorsally, commonly but not invariably associated with dorsal fold and ventral sulcus; also used, irrespective of commissure, as small carina or fold.

plication. See plica.

pliciligate stage (of folding). Having deep median ventral sulcus with strong bounding folds opposite low median dorsal fold bordered by shallow sulci. [Muir-Wood]

polypalmate. Mantle canal system with more than 4 principal canals in each mantle.

pore. See puncta.

POSTERIOR. Direction in plane of symmetry or parallel to it toward pedicle and away from mantle cavity (Fig. 59,*B*).

posterior flap. Reflexed to anteriorly directed extension of oldhaminoid pedicle valve lying dorsal to at least posteromedian part of brachial valve.

posterior margin. Posterior part of junction between edges of valves, may be hinge line or cardinal margin (Fig. 61).

posterior oblique muscles. Pair of muscles in discinaceans originating posterolaterally on pedicle valve and converging dorsally to insertions on brachial valve between posterior adductors (Fig. 29).

posterolateral commissure. Posterolateral parts of line of junction between edges of valves.

precampagiform flange. Lateral projections from early septal hood in loop development of some dallinids; may survive in later growth stages as small accessory structures on loop. [Elliott]

precampagiform hood. Tubular cone on posterior face of septal pillar, not fused with descending branches (Fig. 110,*I*).

prefalcifer (crura). Crura straight, in plane of commissure and slightly compressed, variant of falcifer crura (Fig. 1). [Ager]

pre-ismeniform (loop). *See* campagiform loop.

premagadiniform (loop). One of the early stages in terebratellid loop development marked by growth of descending branches from both cardinalia and median septum and their completion, and appearance of tiny hood developing into ring on septum. [Elliott]

prepygites stage (of folding). *See* intraplicate.

presocket line. Anterior or anterolateral side of triangular slot produced by brachiophore base (and fulcral plate if present) in internal mold of Orthidina.

primary lamella. First half whorl of each spiralium distal from its attachment to crus (Fig. 108).

PRIMARY LAYER (of shell). Outer shell layer immediately beneath periostracum deposited extracellularly by columnar outer epithelium of outer mantle lobe; in most articulate brachiopods forms well-defined calcareous layer devoid of cytoplasmic strands (Fig. 3, 78).

prismatic layer. See secondary layer.

procline. *See* inclination of cardinal area or pseudointerarea (Fig. 61,*C*).

prodeltidium. So-called "third plate" at one time thought to be developed in earlier embryonic growth of "atrematous," "neotrematous," and "protrematous" species, subsequently becoming more or less attached to either brachial atrematous) or pedicle valve.

PROPAREAS. Pair of subtriangular halves of pseudointerarea divided medially by various structures (e.g., homeodeltidium, intertrough, pedicle groove, etc.) (Fig. 62).

prosocket ridge. See socket ridge.

prostrate spines. Usually straight spines that lie prone on shell surface of some productoids. [Muir-Wood]

protegulal node. Apical portion of adult shell, commonly raised, representing site of protegulum and later growth up to brephic stage (Fig. 80).

protegulum. First-formed shell of organic material (chitin or protein), secreted simultaneously by both mantles (Fig. 60).

protractor muscle. See outside and middle lateral muscles in articulates; also used in articulate brachiopods for longitudinal fibrils in connective tissue of pedicle (*see* pedicle muscle scar).

pseudoarea. See pseudointerarea.

pseudobrace plate. Tuberculate ridges bearing dorsal adductor muscles.

pseudochilidium. See chilidium.

preudocruralium. Callus of secondary shell bearing dorsal adductor impressions and elevated anteriorly above floor of valve.

PSEUDODELTIDIUM. Single, convex or flat plate affording variably complete cover of delthyrium but invariably closing apical angle when foramen is supra-apical or absent and always dorsally enclosing apical foramen (Fig. 92,*A*).

PSEUDOINTERAREA. Somewhat flattened, posterior sector of shell of some inarticulate brachiopods secreted by posterior sector of mantle not fused with that of opposite valve (Fig. 62).

pseudopedicle collar. Sessile pedicle collar.

pseudopedicle groove. See intertrough.

pseudopuncta (pl., **pseudopunctae**). Conical deflection of secondary shell, with or without taleola, pointing inwardly and commonly anteriorly to appear on internal surface of valve as tubercle (Fig. 73).

pseudopunctate (shell). Possessing pseudopunctae.

pseudopunctum (pl., *pseudopuncta*). *See* pseudopuncta.

pseudoresupinate. Convexo-concave shells (Fig. 63, *2*).

pseudosockets. See secondary sockets.

pseudospondylium. Cup-shaped chamber accommodating ventral muscle field and comprising undercut callus of secondary shell contained between discrete dental plates (Fig. 118).

pseudoteeth. See secondary teeth.

pseudotelae. Pair of external projections resembling telae but produced by dorsal migration of pedicle cutting labiate foramen, not beak ridges.

ptycholophe. Lophophore with brachia folded into one or more lobes in addition to median indentation (Fig. 113,*3*).

ptycholophous (adj.). Pertaining to ptycholophe.

ptycholophus (noun). *See* ptycholophe.

puncta (pl., **punctae**). *See* endopuncta.

punctate (shell). Commonly used to describe shell possessing endopunctae.

punctum (pl., *puncta*). *See* endopunctum.

pygopid (loop). Short ringlike loop with slightly arched transverse band. [Muir-Wood]

quadriplicate (folding). Having 4 anterior folds and 3 intervening sulci. [Muir-Wood]

radulifer (crura). Hook-shaped or rodlike crura which arise on ventral side of hinge plate and project toward pedicle valve (Fig. 1). [Ager]

ramicostellate. Costellae numerous, arising entirely by branching (Fig. 81).

receiving valve. See pedicle valve.

rectimarginate. Having plane anterior commissure (Fig. 65,*1*).

recumbent spines. Slightly curved spines extending at angle of less than 45° to shell surface. [Muir-Wood]

reflexed interarea. Dorsal interarea hypercline.

remigrant (foramen). Pedicle opening which tends to move dorsally after initially migrating toward ventral beak.

resupinate. Reversal in relative convexity of postbrephic shells with convex pedicle valve which becomes concave and with concave brachial valve which becomes convex during successive adult stages of growth (Fig. 63).

reticulate (ornament). Subrectangular patterns on shell exterior, commonly involving nodelike enlargements, formed by intersection of concentric and radial elements of ornament.

retractor muscles. See anterior lateral muscles.

rhizoid spines. Spines resembling rootlets, serving for attachment either by entanglement or by extending along and cementing themselves to foreign surface (Fig. 132). [Muir-Wood]

rhynchonellid stage (of folding). *See* uniplicate.

ribs. Any radial ornament.

ridge. Relatively long narrow elevation of secondary shell, indicated in articulates to variable depth within underlying floor of valve by low, wide deflections of fibrous calcite normal to long axis of ridge, and in inarticulates by comparable deflections of shell lamellae.

rimmed (foramen). *See* auriculate.

ring. Precursor to ascending branches of terebratellid loop in premagadiniform growth stage, consisting of thin circular ribbon, narrow ventrally and broadening dorsally to its attachment on median septum.

rostellum. Low projection between anterior adductor muscle scars of pedicle valve of some craniaceans to which internal oblique muscles are attached.

rostral callosity. See delthyrial plate.

rostrate. With prominent beak of pedicle valve projecting over narrow cardinal margin.

rostrum. Beak of articulate brachiopods (*see* beak).

rostrum. Elevation of secondary shell on inner surface of brachial valve of some craniaceans in front of anterior adductor muscles, consisting of pair of low club-shaped protuberances forming seat of attachment for brachial protractor muscles.

RUGA (pl., **rugae**). Concentric or oblique wrinkling of external shell surface (Fig. 80).

saccate (mantle canal). *Vascula genitalia* pouchlike, without terminal branches, not extending to anterolateral periphery of mantle, functioning primarily as gonocoels (Fig. 135).

saddle. Median arched part of jugum between stem and lateral branches (Fig. 108).

scar. *See* muscle scar.

scar of pedicle attachment. See pedicle muscle scar.

schizolophe. Lophophore indented anteromedially to define pair of brachia which bear row of paired filamentar appendages, at least distally (Fig. 106, *C'*).

schizolophous (adj.). Pertaining to schizolophe.

schizolophus (noun). *See* schizolophe.

SECONDARY LAYER (of shell). Shell deposited by outer epithelium median of outer mantle lobes; in articulate brachiopods, layer secreted intracellularly as fibers bounded by cytoplasmic sheaths, or, less commonly, extracellularly as prismatic calcite (Fig. 5, 78,117).

secondary sockets. Pair of small depressions immediately posterodorsal of cardinal process lobes receiving secondary teeth.

secondary teeth. Pair of dorsally directed projections from ventral process fitting into secondary sockets of stropheodontid brachial valve.

septal pillar. High dorsal septum anterior to cardinalia, formed early in development of terebratellacean loop.

septal plates. Two plates which fuse to form duplex median septum in brachial valve of some pentameroids and bearing outer plates on their ventral surfaces.

septal plates. Various parts of cardinalia; *see* crural plates, hinge plates.

septalial plates. Crural plates forming floor of septalium and united with earlier-formed part of median septum (Fig. 102,*6*).

septalium. Troughlike structure of brachial valve between hinge plates (or homologues), consisting of septalial plates (or homologues) enveloping and buttressed by median septum; does *not* carry adductor muscles (Fig. 103,*6*).

septifer crura. Crura having form of septa that descend directly from dorsal side of hinge plates to floor of brachial valve (Fig. 1, 6,*1*). [Ager]

septum. Relatively long, narrow elevation of secondary shell, commonly bladelike; indicated in articulates within underlying floor of valve by persistent high, narrow deflections of fibrous calcite originating near primary layer, and in inarticulates by comparable deflections of shell lamellae (Fig. 120).

sessile cruralium. Cruralium united with floor of brachial valve without intervention of supporting median septum.

sessile spondylium. Spondylium united with floor of pedicle valve without intervention of supporting median septum.

seta (pl., **setae**). Chitinous bristle arising from invagination of mantle groove (Fig. 82).

shaft. *See* cardinal process shaft.

shell mosaic. *See* mosaic.

shell space. Cavity enclosed by conjoined valves.

shoe-lifter process. Arched platform of secondary shell attached posteriorly and laterally to floor of pedicle valve but sharply elevated and free medially, bearing part of ventral muscle field and lying between or supporting dental plates (Fig. 122).

sinus. Major undulation of commissure with crest directed ventrally, commonly but not invariably associated with ventral fold and dorsal sulcus; also used irrespective of commissure, as a synonym of sulcus.

siphonothyridid (foramen). Pedicle foramen continued internally as tube made up of exaggerated pedicle collar.

socket line. Posterior side of triangular slot in internal molds of orthoid and enteletacean brachiopods produced by brachiophore base (and fulcral plate, if present) and bounding impression of socket.

socket plate (of orthoids). *See* fulcral plate.

socket plate (of davidsoniaceans). Pair of plates supporting socket ridges, attached to cardinal process and resting on floor of brachial valve.

socket ridges. Linear elevations of secondary shell extending laterally from cardinal process and bounding margin of dental sockets; *see* also inner socket ridge and outer socket ridge (Fig. 99,*B*; 102,*2*).

socket valve. See brachial valve.

sockets. *See* dental sockets.

spicules. Small, irregular bodies of calcite which may be secreted within connective tissue of body wall, mantle, and lophophore (Fig. 3,*B*, *6*).

spine. Solid or hollow, cylindrical or, less commonly, elongate triangular projections from external shell surface (Fig. 72,*A*; 86-88).

spine apertures. Internal opening of spine bases.

spine ridge. Posterior trace of prostrate spine on shell exterior.

spinule bases or apertures. Small oval perforations in some chonetoids representing bases of spinules usually seen on summit of radial ornament and only penetrating external shell layer; possibly homologous with hollow ribs of some orthoids and enteletaceans. [Muir-Wood]

spinules. Spines of small diameter and approximately 1 or 2 mm. in length in chonetoids. [Muir-Wood]

spinulifer (crura). Variant of radulifer type, but with crura laterally compressed (Fig. 1). [Ager]

SPIRALIA (sing., **spiralium**). Pair of spirally coiled supports for deuterolophe or spirolophe, composed of secondary shell (Fig. 104).

spires. *See* spiralia.

spiriferid stage (of posterior margin). Shell very transverse, posterior margin long and straight.

spirolophe. Lophophore in which brachia are spirally coiled and bear single row of paired filamentar appendages (Fig. 43).

splanchnocoele. See body cavity.

spondylial cavity. Space enclosed by posterior part of spondylium and purported to be bounded by spondylial lining.

spondylial lining. Thin prismatic layer of secondary shell forming more or less continuous veneer on dorsal surface of pentameracean spondylium and entire deltidial cover (Fig. 117,*2*).

spondylium. Trough-shaped or spoonlike apparatus composed of dental plates in various stages of coalescence, usually with median septum, accommodating ventral muscle field (Fig. 117, 119).

spondylium discretum. Muscle-bearing chamber formed by slight convergence of dental plates which are attached separately to floor of valve.

spondylium duplex. Spondylium formed by convergence of dental plates and supported by variably developed median septum arising from floor of pedicle valve, septum supporting platform and attached to pedicle valve (Fig. 117,*2*).

spondylium pseudotriplex. See spondylium triplex.

spondylium simplex. Spondylium formed by convergence of dental plates and supported ventrally by variably developed simple median septum or ridge (Fig. 117,*1*).

spondylium triplex. Spondylium supported by median septum and 2 lateral septa (e.g., *Polytoechia*) (Fig. 119).

spondyloid (dental plates). Basal inner surfaces of dental plates thickened and coalesced to simulate spondylium.

spyridium. Cuplike apparatus affording attachment for dorsal adductor field and consisting of variably fused pair of subtriangular platforms elevated on subjacent ridges (Fig. 130). [Muir-Wood]

squamose. Having irregular and ragged margin to concentric growth lamellae. [Muir-Wood]

stalk. See pedicle.

stegidium. Convex plate closing gap between delthyrial plate and spiriferoid brachial valve consisting of series of concentric layers deposited by outer epithelium associated wtih atrophying pedicle migrating dorsally (Fig. 91).

stolidium. Thin marginal extension of one or both valves forming narrow to broad frill protruding at distinct angle to main contour of shell, as in stenoscismataceans. [Grant]

straight beak. *See* beak angle.

strainer spines. See endospines.

strangulate stage (of folding). Form of opposite folding, sulcus in each valve with incipient carinae (Fig. 64,*4*).

striae. Fine grooves or incisions.

strophic (shell). Shell with true hinge line parallel to hinge axis (Fig. 61,*B*).

suberect beak. *See* beak angle.

suberect spines. Spines inclined to shell surface at angles between 45°-75°. [Muir-Wood]

subintertext folding. Alternate folding with opposing sulci and carinae of unequal amplitude.

submarginal ridge (of productoids). Thickening of interior of either valve parallel to anterior margin of visceral disc. [Muir-Wood]

submegathyridid (posterior margin). Posterior margin approximately straight and slightly less than maximum width of shell.

submesothyridid (foramen). Pedicle opening located partly in ventral umbo, but mainly in delthyrium (Fig. 90,*C*).

subperipheral rim. Elevation of secondary shell concentric to margin of valve and just within it.

subplectolophous (lophophore). Plectalophous lophophore in which there is an incipient median coil. [Muir-Wood]

subspondylial chamber. See umbonal cavity.

subterebratulid (posterior margin). Posterior margin considerably less than maximum width of shell, but not strongly curved.

sulcate (folding). Form of alternate folding with brachial valve bearing median sulcus and anterior commissure median sinus (preferably not termed inverted stage) (Fig. 65,*2*).

sulciplicate (folding). Form of alternate folding with brachial valve bearing median fold indented by shallower median sulcus (Fig. 65,6).

SULCUS. Major depression of valve surface, externally concave in transverse profile and radial from umbo.

supporting plates (of orthoids). *See* brachiophore bases.

supporting septum (of hemispondylium). Median septum attached to floor of thecideacean pedicle valve and supporting concave plates of hemispondylium.

supra-apical foramen. Pedicle foramen initially located in ventral umbo away from apex of delthyrium.

symbolothyridid (pedicle opening). Pedicle opening shared by both valves.

symphytium. Deltidial plates fused dorsally or anteriorly from pedicle foramen and lacking median line of junction.

syndeltarium. See deltidial cover.

syrinx. Tube of secondary shell medially located on ventral side of delthyrial plate and split along its ventro-anterior surface (Fig. 121).

taleola (pl., **taleolae**). Cylinder of granular calcite in axial region of some pseudopunctae (Fig. 73).

taxolophous lophophore. Rudimentary lophophore with filamentar appendages not completely encircling mouth.

teeth. *See* hinge teeth.

teeth ridges. Linear elevations bounding delthyrium laterally, representing growth track of hinge teeth and commonly forming low elevations on internal surface of cardinal area in absence of dental plates.

telae (sing., **tela**). Pair of pointed terminations of beak ridges projecting into and beyond pedicle opening, formed by apical migration of pedicle.

terebrataliiform (loop). Type of dallinid loop or growth stage consisting of long descending branches with connecting bands to median septum, then recurving into ascending branches which meet in transverse band; morphologically similar to terebratelliform loop (Fig. 110,5). [Elliott]

terebratelliform (loop). Type of terebratellid loop or growth stage consisting of long descending branches with connecting bands to median septum, then recurving into ascending branches which meet in transverse band; morphologically similar to the terebrataliiform loop (Fig. 111). [Elliott]

terebratulid stage (of folding). *See* sulciplicate.

terebratulid (posterior margin). Strongly curved posterior margin much less than maximum width of shell.

terebratuliform (loop). Short, typically U- or W-shaped loop found in most terebratulaceans (Fig. 105,5).

terebratuliniform (loop). Short loop in which crural processes are fused medially to complete ring or boxlike apparatus (Fig. 105,7).

THICKNESS. Maximum dimension normal to length and width (Fig. 59,*B*).

tichorhinum. Small, suboval chamber, with or without median partition, formed by medially directed struts arising from dental plates converged on to median septum in spiriferoid pedicle valve; probably accommodated base of pedicle (Fig. 120).

tongue. See linguiform extension.

torynidium. See camarophorium.

track. *See* muscle track.

trail. Extensions of shell in either valve anterior to visceral disc (Fig. 74). [Muir-Wood]

transmedian muscles. Pair of muscles in some Lingulida anterior to umbonal muscle; one muscle originating on left side of pedicle valve rising dorsally to be inserted on right side of brachial valve, second muscle originating on right side of pedicle valve and inserted on left side of brachial (Fig. 28).

transmuscle septa. Assemblage of narrow elevations comprising one median and 2 pairs of diverging laterals associated with strophomenacean dorsal adductor field.

transverse band. Connecting lamella joining posterior ends of ascending branches of loop (Fig. 111).

transverse delthyrial plate. See delthyrial plate.

transverse plate (of spiriferoids). *See* delthyrial plate.

transverse plate (of stringocephalacean loop). *See* echmidium.

trocholophe. Lophophore disposed as ring surrounding mouth, bearing either single row of unpaired (or more rarely double row of paired) filamentar appendages (Fig. 106,*A'*).

trocholophous (adj.). Pertaining to trocholophe.

trocholophus (noun). *See* trocholophe.

tropoconate. Brachia coiled parallel with plane of symmetry.

trough. See hinge trough.

tubercle. Any fine, low, rounded protuberance on either surface of valve, irrespective of origin (Fig. 73).

UMBO. Apical portion of either valve containing beak (Fig. 59,*B*).

umbonal angle. *See* apical angle.

umbonal blade. Part of primary lamella of spiralium extending between lateral branch of jugum and distal end of crus (Fig. 108).

umbonal chambers. Pair of posterolaterally located cavities in either valve; in pedicle valve bounded by dental plates (cardinal buttress in trimerellids) and shell walls; in brachial valve limited medially by crural plates (or homologues) and shell walls (Fig. 101).

umbonal muscle. Single muscle occurring in some Lingulida, thought to be homologous with posterior adductors; consists of 2 bundles of fibers, posteriorly and slightly asymmetrically placed (Fig. 28).

umbonal slopes. Region of shell surface adjacent to umbo. [Muir-Wood]

uniplicate (folding). Form of alternate folding with pedicle valve bearing median sulcus and anterior commissure median plica (Fig. 65,*3*).

uniseptum. See septum.

unisulcate. See sulcate.

unpaired median muscle scar. Scar of attachment of base of pedicle to ventral floor; *see* pedicle muscle scar.

varix (pl., *varices*). *See* growth line.

vascula (sing., **vasculum**). Any identifiable branches of mantle canal system.

vascula antemyaria. Pair of mantle canals in brachial valve located between *vascula media exteriora* and *vascula myaria exteriora* (Fig. 134).

vascula arcuata. Any mantle canals which are curved subparallel with lateral or anterior margin of shell and which peripherally give off *vascula terminalia.*

vascula cardinalia. Posterior branches, subparallel with posterior margin of reduced *vascula cruralia,* commonly in digitate condition (Fig. 134).

vascula cruralia. Posterolaterally located pair of mantle canals in dorsal mantle of articulate brachiopods, into which gonads were inserted; varying from saccate to pinnate in outline (Fig. 134).

vascula dentalia. Pair of posteriorly located mantle canals in pedicle valve of articulate brachiopods into which gonads were inserted (Fig. 134).

vascula genitalia. Mantle canals of articulate brachiopods which contain gonads; may consist of *vascula dentalia* and *vascula spondyliaria* in pedicle valve and *vascula cruralia* and *vascula cardinalia,* if developed, in brachial valve.

vascula intermyaria. Posteromedian parts of *vascula myaria,* segments passing between anterior and posterior adductor scars, distal continuations of which form *vascula myaria exteriora.*

vascula lateralia. Laterally located pair of mantle canals developed in both valves of inarticulate brachiopods (Fig. 21, 138).

vascula media. Pair of mantle canals in either valve, medially located, projecting anteriorly from body wall (Fig. 134).

vascula media exteriora. Lateral branches from bifurcated *vascula media.*

vascula media interiora. Inner, medianly located branches of bifurcated *vascula media* (Fig. 134).

vascula myaria. Simple or branched pair of mantle canals arising between anterior and posterior adductor muscle scars of brachial valve of some articulate brachiopods (Fig. 134).

vascula myaria exteriora. Anterior continuations of *vascula intermyaria* outside adductor muscle scars (Fig. 134).

vascula myaria ventri. See vascula spondyliaria.

vascula spondyliaria. Pair of mantle canals located between *vascula media* and *vascula dentalia* of pedicle valve, receiving gonads (Fig. 134).

vascula terminalia. Terminal branches of mantle canals of articulate brachiopods, supplying setae (Fig. 134).

vascular markings. Impressions of mantle canals on shell interior.

vascular sinus. See mantle canal.

vascular trunks. Any major branches of mantle canal system.

venter. Median region of productoid shell between lateral slopes. [Muir-Wood]

ventral. Direction toward pedicle valve from brachial valve.

ventral adjustor muscles. *See* adjustor muscles.

ventral adminiculum. Ventral part of dental plate.

ventral dental socket. See denticular cavity.

ventral process. Median callus of secondary shell underlying pseudodeltidium and projecting dorsally to fit between lobes of cardinal process.

ventral valve. See pedicle valve.

ventrally biplicate (folding). *See* antiplicate.

ventribiconvex. Both valves convex, pedicle valve more strongly so than brachial.

vertical plate (of stringocephalaceans). Plate of secondary shell more or less in plane of symmetry and borne on echmidium.

vertical zone. Part of valve secreted normal to commissure plane.

vestibule. Subcylindrical prolongation of pedicle valve dorsal of brachial valve.

virgate (hinge plates or crural bases). Straight and erect. [Muir-Wood]

visceral area. Part of shell enclosing body cavity.

visceral cavity. See body cavity, also used to include both true body cavity and mantle cavity of productoids.

visceral disc. Part of shell posterior to geniculation.

visceral foramen. See dorsal foramen.

WIDTH. Maximum dimension normal to plane of symmetry (Fig. 59,*A*).

xenidium. See pseudodeltidium.

zeilleriid stage (of folding). *See* bilobate stage.

zeilleriid (loop). Having long loop, not attached to dorsal septum in adult. [Muir-Wood]

zygidium. Collar-like structure uniting lateral ridges on dorsal side of cardinal process and functioning like lophidium in some productoids. [Muir-Wood]

zygolophe. Lophophore in which each brachium consists of straight or crescentic side arm bearing 2 rows of paired filamentar appendages.

zygolophous (adj.). Pertaining to zygolophe.

zygolophus (noun). *See* zygolophe.

COMPOSITION OF BRACHIOPOD SHELL

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INTRODUCTION

A study of shell structure and morphology, if it is to be used to understand evolutionary development, must be seen in relation to the fundamental biochemistry and metabolic processes of shell growth. Brachiopods must thus be considered as having exoskeletons similar in function to other invertebrate exoskeletons, with a general pattern underlying their structure and metabolic biochemistry, but with significant differences.

Shell growth is a chain of interlinked processes biochemically regulated so that the result is morphologically recognizable as producing heritable features; an understanding of its biochemistry may therefore contribute to classification on a rational basis. The adult shell is dead tissue which can have only repairs or additions to the inner layer, but during growth it takes an integral part in the basic metabolic processes of the animal. In assessing the relative phylogenetic or morphogenetic importance of the organic constituents, it is necessary to see them as interrelated parts of a functional system and to differentiate rejected or waste products from substances concerned in growth processes both structural and regulatory. There is an underlying homogeneity in biochemical processes of most living organisms and refined variants in the general pattern must be sought. There may nevertheless be some biochemical species variants such as in amino-acid constitution of specific proteins, which, if detected, may be a decisive factor in classification. Specific proteins may be specific by virtue of the order of array of amino acids, or of their actual amino-acid constitution; the latter holds promise of heritable characteristics potentially detectable even in fossil material. Functional variants of composition may occur, however (e.g., inner layer of the ligament of marine lamellibranchs has a different protein constitution from the remainder of the shell, thought to be correlated with its specialized function, 5). Sterols may be informative; in echinoderms and sponges the nature of the sterol present in different groups of the organism seems to have phylogenetic significance (6). Certain marine invertebrates (some anthozoans and sponges) are able to concentrate bromine and iodine and convert them into bromo- and iodoscleroproteins (24), in this respect differing greatly from their utilization of chloride, which has a role in controlling osmotic pressure. The bromoscleroproteins do not appear to have a definite composition but the iodoscleroproteins have this, and thus have contributed to a more precise definition of the systematic position of the Gerardiidae (Hexacorallia).

A start has been made toward understanding the biochemistry of morphogenesis, and compounds such as mucopolysaccharides are evidently involved. Neutral mucopolysaccharides (a class of compounds which includes chitin) and especially acid mucopolysaccharides are found in connective tissue where they probably play a part in the morphogenesis of the fibrous material (11). The shell mosaic of articulate brachiopods, for example, which is believed to be specifically diagnostic, is the pattern on the inside of the shell made by the ends of the calcite fibers and must be a reflection of the cross section of the cytoplasmic sheath within which they grow, and which is presumably genetically controlled.

The brachiopod shell resembles exoskeletons of arthropods and mollusks in consisting of proteinaceous layers secreted onto the outer surface of the body by a single layer of epidermal cells, strengthened by deposition of inorganic compounds (chiefly of calcium) and may contain much chitin. Exoskeletons of arthropods and mollusks contain also other organic constituents such as tanning agents and lipids, presumably equally essential in brachiopod shells. The periostracum is usually thin; it is mainly organic but may contain a relatively high proportion of iron (about 10 percent in some areas in *Lingula*) (17). It is resistant to abrasion and relatively impermeable to fluids though remaining elastic to some extent.

There are two main types of brachiopod shells, depending on whether the inorganic material is predominantly calcium phosphate or calcium carbonate. Phosphatic shells contain a high proportion of organic material, 25 to 52 percent (7, 28) (Table 1), which is mainly chitin and protein (Table 2). Carbonate shells contain a much lower proportion of organic material (0.93-4.7 percent) (7), largely protein, along with small amounts of material which is estimated as hexosamine but which could have been derived from some mucosubstance other than chitin. Organic substances such as lipids are present in both types of shells (17).

These major distinctions of composition provide a broad basis for classification of the organisms. The articulate shell is invariably carbonate, the inarticulate mainly phosphatic; the Craniidae have carbonate shells but are grouped with the inarticulates which they resemble anatomically. A number of forms are difficult to fit into either group: the Cambrian kutorginids, for example, are important in being among the most primitive brachiopods, but although their shell is calcareous, its true structure and detailed composition have yet to be determined. It would be valuable to know whether this shell had contained any chitin or significant amounts of phosphate.

INORGANIC CONTENT

The main inorganic constituent of brachiopod shell structure is calcium phosphate in inarticulates (lingulids 74.7-93.7 percent, *Discinisca* 75.2 percent), and calcium carbonate in articulates (94.6-98.6 percent) and craniids (87.8-88.6 percent) (7,28) (Table 1). There are usually small amounts of phosphate in carbonate shells (e.g., about 0.5 percent in *Crania*), and carbonate in phosphatic shells (1-4 percent in lingulids;[1] 8.6 percent in *Discinisca*). $MgCO_3$ is almost always found in small amounts. It has not yet been shown whether these lesser constituents (or indeed others found in smaller amounts) are concentrated in specific locations or diffused generally through the shell structure. Small amounts of Al_2O_3, Fe_2O_3 and SiO_2 are found in all forms, and other elements have been shown in some species (Sr, which tends to follow Ca, in *Macandrevia* (26), *Hemithiris psittacea* (23), and *Lingula anatina* (28); B_2O_3 in *L. anatina* and *Terebratula vitrea* (14) and traces of Cu, Ba, Ti, and Zr in *L. anatina* (28). Lingulid shells have a high concentration of F, 1.6 percent (4), 1.91 percent (28), shown by McConnell (X-ray powder diffraction patterns, 21) to be present as carbonate fluorapatite (francolite). F is toxic to many biological systems, and such amounts in the shell may represent removal from the system by fixation. *Lingula anatina* has about 0.5 percent Mn_3O_4 (28).

Some of these elements are functional in brachiopods and are essential to the shell in so far as it is part of the living tissue of the animal; others are apparently merely ingested incidentally from the environment.

Ca, the major mineral constituent of shell structure, has also a physiological role in maintaining differential osmotic pressures and in stimulating muscular movement. Mg is variable; it is ingested from sea water and from green algae, and in traces it is needed for some enzyme systems; but the large amounts in *Crania anomala* and *Discinisca lamellosa* are probably incidental. Deposition of Mg by some marine invertebrates has been said to be greater in warm waters than in cold (7), but this is not so in brachiopods, since *Crania anomala* (Norway coast) with a cold-water habitat has a high proportion of $MgCO_3$ (Table 1). Part of the Fe is functional, in oxygen transporters and transfer; hemoglobin is the respiratory blood pigment in brachiopods (28), and hemerythrin has been found in *Lingula unguis* [=*L. anatina*] (18). Cu, Mn and perhaps other elements of variable valency are also essential in traces as components of specific enzyme systems. Si is sometimes found in exoskeletons and spicules (though not in brachiopods). On the other hand, Al and B have no known physiological function relevant here.

Analysis of fossil forms shows that while there may be secondary deposition of carbonate, sulfate, and fluoride, there need be little replacement of phosphate by carbonate, a concentration of 85.89 percent $Ca_3(PO_4)_2$ has been reported in the Ordovician *Obolus appollinis* Eichwald (22).

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[1] The high values for calcium carbonate in some lingulids in Table 1 may be due to inclusion of sulphate.

Table 1. *Inorganic Constituents of Recent Inarticulate and Articulate Brachiopoda*

INDEX	Organic matter	Ash (a)	MgO	$FePO_4$	$Ca_3P_2O_8$	$CaSO_4$	$CaCO_3$	$MgCO_3$	$(Al,Fe)_2O_3$	SiO_2	Other
A	0.93	99.07	---	---	tr.	0.36	98.61	0.93	0.04	0.06	---
B	1.00	---	---	---	0.61	---	98.39	tr.	tr.	---	---
C	4.73	95.27	---	---	tr.	1.18	96.78	1.37	0.15	0.52	---
D	2.55	---	---	---	tr.	2.40	94.60	1.05	tr.	---	---
E	1.55	98.45	---	---	tr.	0.36	98.30	0.68	0.48	0.18	---
F	2.00	---	0.60	---	0.18	0.90	96.20	---	tr.	---	0.30 (b)
G	1.24	---	---	---	tr.	0.85	96.20	1.20	0.40	0.60	---
H	1.99	---	---	---	0.12	---	95.98	1.40	0.15	---	---
I	2.65	97.35	---	---	0.38	0.55	98.20	0.49	0.23	0.15	---
J	---	---	---	---	0.27	0.75	98.06	0.92	---	---	---
K	---	---	---	---	---	---	---	0.45	---	---	---
L	3.52	96.48	---	---	0.57	1.72	88.59	8.63	0.27	0.22	---
M	4.30	---	1.80	---	0.28	2.15	87.80	3.40	tr.	---	---
N	40.00	60.00	---	---	91.74	2.93	1.18	2.70	0.54	0.91	---
O	39.50	60.50	---	---	89.99	4.18	4.25	0.79	0.29	0.50	---
P	42.60	57.40	---	3.61	77.17	---	12.19	---	---	tr.	7.03 (c)
Q	38.70	61.30	2.80	---	85.79	---	11.75	---	---	---	---
R	---	---	---	0.77	84.94	---	10.76	2.94	---	0.18	---
S	37.90	62.10	---	0.76	85.32	---	11.12	3.03	---	0.17	---
T	37.00	63.00	---	---	74.73	---	---	1.71	1.16	0.49	---
U	25.00	75.00	---	---	75.17	8.37	8.35	6.68	0.58	0.85	---
	Organic	Ash	CaF_2	Mn_3O_4	P_2O_5	Indet.	CaO	MgO	Fe_2O_3		Other
V	---	---	---	---	23.20	---	30.19	---	---	---	1.52 (d)
W	52.10	47.90	3.93	0.46	42.99	1.44	50.66	0.30	0.22	---	---

(a) Per cent of dry matter. (b) CaO. (c) $Mg_3P_2O_8$. (d) F.

NATURE OF ORGANIC CONTENT OF SHELLS

The chief organic constituents of brachiopod shells are protein and chitin. Protein is determined quantitatively by analysis of the amino-acid assemblage obtained on hydrolysis (Tables 2 and 3). Chitin is demonstrated qualitatively but specifically by the chitosan test and quantitatively by estimation of its breakdown product, glucosamine (Table 2). Hyman (16), using the chitosan test, showed that the shell and pedicle cuticle of *Lingula* contained chitin, as did the shell of *Discinisca lamellosa* and the membrane covering the slot in its ventral valve but not the apex of its dorsal valve. *Crania anomala* gave a negative chitosan test. The shells of articulate forms (*Terebratulina retusa, T. transversa,* and *Laqueus californicus*) also gave negative chitosan tests, but the cuticle of the pedicle was chitinous.

Three main categories of organic components are distinguished within the brachiopod shell. They form the periostracum and any caecal strands which represent invaginations of the outer epithelium. They may also form part of the shell structure as cytoplasmic sheaths to calcite fibers.

Lingulid shells and the secondary layer of craniids have organic substances, including protein interleaved with the inorganic. In lingulids, chitin is present, as well as protein, possibly as alternating monolayers. Fraenkel & Rudall (13) from X-ray studies suggested this structure in insect cuticles. In craniids there is no chitin (17) (Table 2). *Discinisca* has both chitin and protein but distributed uniformly throughout the shell, not in layers.

The secondary layer of articulates and craniids at the muscle attachments have cell-wall material enclosing each calcite fiber, contributing phospholipids, steroids, proteins, and polysaccharides. Endopunctate forms have outer epithelium intruded as caeca into the shell structure. Their primary layer contains mucin-like material (possibly acid or neutral mucopolysaccharides) and strands of cytoplasm forming the brush, as well as epithelial cell material; their secondary layer contains epithelial cell wall and cell contents. Cells, while undergoing periodic mitosis during shell growth, would contain such substances as DNA of the nucleus, RNA, phospholipids, enzymes, and mucoprotein of the cytoplasm. The caeca of craniids are made up of epithelial cell material possibly containing mucus. Lingulid and discinid shells are traversed by fine cytoplasmic strands (mucoprotein possibly) which may contain intracellular fluid or mucus.

The periostracum of all shell types is mainly organic, in phosphatic shells chitin and protein, and in carbonate shells protein without chitin (17). The protein of all shells may be quinone tanned as in lamellibranch shells (5) and some arthropods (9). There may also be a lipid component, for in insect cuticles a sterol operates in the tanning and a straight chain paraffin forms the outermost layer (9, 10).

The dark brown color of the periostracum of *Lingula* is due to iron, probably as ferric hydroxide, in places forming about 10 percent of its weight. The iron tends to be distributed in bands following growth lines, the regions representing embryonic or young growth of the shell containing much

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Explanation of Table 1

[Specimens, localities, and index numbers for references given in list at end of this chapter are indicated by capital letters at left margin of table, as follows.——(A) *Gryphus cubensis* (Pourtalès), Florida (7).——(B) *Gryphus* sp., Florida, Cuba (27).——(C) *Terebratulina septentrionalis* (Gray), Maine (Eastport) (7).——(D) *T. caputserpentis* (Linné),? (19).——(E) *Laqueus californicus* (Koch), Calif. (Esteros Bay) (7).——(F) *Macandrevia cranium* (Müller),? (19).——(G) *M. cranium* (Müller), 68°12'N, 15°40'E (26).——(H) *M. cranium* (Müller), Lofoten Is. (26).——(I) *Hemithiris psittacea* (Gmelin), Shetland Is. (7) ——(J) *H. psittacea* (Gmelin), Barents Sea (25). ——(K) *H. psittacea* (Gmelin), ?(12).——(L) *Crania anomala* (Müller), Norway coast (7).——(M) *C. anomala* (Müller), ?(19).——(N) *Lingula anatina* Lamarck, Japan (Higo) (7).——(O) *L. anatina* Lamarck, Philippine Is. (Iloilo) (7).——(P) *L. anatina* Lamarck, ?(8).——(Q) *Lingula ovalis* Reeve, Sandwich Is. (20).——(R) *L. ovalis* Reeve, ?(15).——(S) *L. ovalis* Reeve, ?(15).——(T) *Glottidia pyramidata* (Stimpson), North Carolina (7).——(U) *Discinisca lamellosa* (Broderip), Peru (7).——(V) *Lingula anatina* Lamarck, Ceylon (3).——(W) *L. anatina* Lamarck, Ceylon (28). (Question marks indicate no locality cited.)]

less proportion of iron than older regions. The iron, presumably taken in from the environment, becomes deposited in the periostracum as unused material. The young, fast-growing shell, therefore, receives a smaller proportion of iron than slow-growing parts of more mature growth. Brachiopods have iron-containing respiratory pigments (hemoglobin or hemerythrin): it is not yet clear whether their iron is drawn from this reserve in the periostracum or whether their breakdown products contribute thereto.

The periostracum of *Lingula* appears laminated in pigmented areas; the outermost layer may be very dark brown, the underlayer, amber-colored. Protein (67.9 percent) and chitin (10.6 percent) have been demonstrated from the periostracum. The protein contains most of the amino

TABLE 2. *Organic Content of Recent Brachiopod Shells*
[BV=brachial valve; P=pedicle; PV=pedicle valve]

Specimen	Location of Sample	Chitin as Hexosamine (a)	Protein (a)
1. Lingula sp.	PV, no periostracum	18.0	---
	BV, no periostracum	12.0	---
	PV, periostracum only	8.2	---
	BV, periostracum only	7.0	---
	P cuticle, inner layer	26.2	---
	P cuticle, outer layer	20.8	---
2. Lingula sp.	BV, with periostracum	20.3	22.0
3. Lingula sp.	PV+BV, periostracum only	10.6	59.8
4. Glottidia pyramidata (Stimpson)	PV, with periostracum	9.6	---
	BV, with periostracum	9.6	---
	P cuticle, inner + outer	19.6	---
5. Discinisca lamellosa (Broderip)	PV, with periostracum	4.5	---
	BV, with periostracum	3.3	7.0
	PV+BV, periostracum only	3.2	10.9
	PV+BV, with periostracum	20.6(b,c)	---
	PV+BV, with periostracum	3.8(c,d)	---
6. Crania anomala (Müller)	BV, with periostracum	0.09	0.54
7. Crania anomala (Müller)	BV, protegulum only	0.0	---
8. Notosaria nigricans (Sowerby)	PV, with periostracum	0.05	0.16
	BV, with periostracum	0.02	1.7
9. Macandrevia cranium (Müller) Magellania flavescens (Lamarck)	PV+BV, periostracum only	0.0	---
10. Macandrevia cranium (Müller)	PV+BV, with periostracum	0.07	1.9
11. Laqueus californicus (Koch)	PV+BV, periostracum only	0.4	21.1
12. Terebratalia transversa (Sow'by)	PV+BV, periostracum only	0.5	10.6

(a) Percent of shell dry weight. (b) Percent of organic matter.
(c) C and H analysis by Mr. Dunn, Microanalysis Lab., Queen's University
(d) Percent of water.

acids of structural animal proteins with very high proportions of alanine, arginine, and proline. Cystine was not found, but there is a small amount of hydroxyproline (Tables 2, 3) (17). In *Discinisca lamellosa* the periostracum has been shown to have chitin (3.2 percent) and protein (14.3 percent), high arginine, alanine, glutamic acid and some hydroxyproline.

The periostracum of *Laqueus californicus*

TABLE 3. *Amino Acids in Brachiopod Shells*

Amino acids	Specimens													
	A	B	C	D	E	F	G	H	I	J	K	L	M	N
Aspartic acid	+	+	0	–	+	15.6	16.6	22.6	14.9	23.5	+	+	+	–
Glutamic acid	+	+	0	–	+	9.1	12.2	10.4	7.5	5.8	+	+	+	+
Cystine	+	+	–	–	–	–	–	–	0.3	0.3	–	–	–	–
Serine	+	+	0	–	–	8.9	4.7	9.3	9.7	7.0	–	+	+	–
Threonine	0	0	0	–	–	4.5	5.4	7.4	3.2	3.7	–	+	+	–
Glycine	++	++	++	+	+	7.2	29.1	16.5	31.5	32.4	+	++	++	+
Alanine	++	+	+	–	–	13.2	23.1	8.1	1.6	4.1	+	+	+	+
Proline	++	0	–	–	–	4.5	0.6	0.9	3.3	1.1	+	+	0	–
Valine	+	+	0	–	–	5.4	2.2	3.9	1.6	2.3	+	+	0	+
Methionine	0	–	0	–	–	–	–	–	–	–	–	–	–	–
Leucine/isoleucine	+	+	0	–	–	8.6	0.9	5.1	5.5	1.9	+	+	0	+
Phenylalanine	++	+	+	+	+	2.4	0.2	2.0	4.6	0.7	–	++	++	–
Tryptophane	+	+	+	+	–	–	–	–	0.9	–	–	–	–	–
Tyrosine	+	+	+	+	–	3.1	0.2	6.0	7.8	1.2	–	–	0	–
Lysine	+	+	0	+	–	2.7	0.4	0.7	0.8	0.7	–	0	0	–
Histidine	+	+	+	+	–	5.5	7.1	6.7	5.5	11.3	–	++	++	–
Arginine	+	+	+	–	–	7.3	3.3	0.5	1.2	3.9	–	–	–	–
Hydroxyproline	+	0	0	–	–	2.1	1.2	–	–	–	–	–	–	–
μM amino acids per gram (fossil or matrix)	–	–	–	–	–	–	–	–	–	–	–	0.5	0.3	0.5

[Explanation: O indicates no amino acid detected; +, amino acids present in small or moderate amounts; ++, amino acids present in high proportion; figures indicate percent of total amino acid residues present; μM (micromoles) denotes measure proportional to number of molecules per unit mass. Specimens analyzed are identified by letters, as follows: RECENT (whole shells):——(A) *Discinisca lamellosa* (BRODERIP).——(B) *Lingula* sp.——(C) *Crania anomala* (MÜLLER).——(D) *Notosaria nigricans* (SOWERBY).——(E) *Macandrevia cranium* (MÜLLER). RECENT (periostracum only, showing minimal number of amino acid residues):——(F) *Lingula* sp.——(G) *Discinisca lamellosa* (BRODERIP).——(H) *Crania anomala* (MÜLLER).——(I) *Laqueus californicus* (KOCH).——(J) *Terebratalia transversa* (SOWERBY). FOSSIL:——(K) *Spirifer* sp. (Carboniferous Ls.); *Atrypa* sp. (Wenlock Sh.); *Plectothyris fimbria* (SOWERBY), Jurassic.——(L) *Linoproductus* sp. (Carboniferous Ls.).——(M) Carboniferous Ls. matrix.——(N) *Plaesiomys (Dinorthis) subquadrata* HALL & CLARKE (Ordovician) (2). (Jope, n)] contains no chitin but yields about 0.4 percent hexosamine from some mucosubstance. Protein 21.8 percent was found, consisting of most of the usual structural animal amino acids including cystine but no hydroxyproline and high proportions of tyrosine, phenylalanine, proline, and glycine (Tables 2, 3) (17). As in *Lingula*, the periostracum of *Laqueus* contains iron in the form of ferric hydroxide, but in very much smaller amounts. The periostracum of *Terebratalia transversa* like that of *L. californicus* contains no chitin but 0.5 percent hexosamine; its protein (13.3 percent) has high arginine and glycine values.

The periostracum of the inarticulate *Crania* follows the pattern of the carbonate shells of the articulates in containing protein but no chitin. The formation of chitin is apparently associated with the presence of phosphate or its deposition, rather than carbonate, and is not a property of hingeless forms as such. The inarticulate *Crania*, anomalous with its carbonate shell and lack of chitin, may be seen as a transition between inarticulates and articulates.

Analysis of the organic content of impunctate articulate shells is without complications in that they contain structural material only; all other groups, however, contain some incorporated epithelial cell material in the form of caeca, and significant analytical data can only be obtained after differential micro dissections.

The organic content of the intrusive caeca differs only from that of impunctate shells (epithelial cell walls of cytoplasmic sheaths) in containing mucin-like material and cell contents: mucoprotein, DNA, and RNA, when the mantle cells are proliferating. The organic content of the primary layer alone (of endopunctate forms) will give data for caecal cup material (epithelial cell wall), mucus, and cell contents; that of the secondary layer will give data for the caecal stalks (epithelial cell wall and cell contents) along with material of the cytoplasmic sheaths.

Lingulid and discinid shells have fine cytoplasmic strands intruded into the shell structure. These shells, however, have a high organic content and the proportion from the cytoplasmic strands will be slight.

Crania has punctae formed of epithelial cell material; these branch in the outer calcareous layer which otherwise contains no organic material. Analysis of the organic material of the outer layer will therefore give an estimate of the epithelial cell material which can be deducted from that found in the inner layer.

Carbonate shells contain small amounts of protein (about 0.5-2 percent) and very small amounts of hexosamine (<0.1 percent) derived more likely from a mucosubstance than from chitin, since hexosamine is a very common constituent of animal cell and connective tissue. Phosphatic shells contain relatively large amounts of chitin (*Lingula*, 20 percent, *Discinisca*, about 4 percent) and also protein (*Lingula*, 22 percent, *Discinisca*, 7 percent) (Table 2) (17). The chitin was estimated as hexosamine and so may contain small amounts of hexosamine from mucosubstances.

Impunctate articulate shells (e.g., *Notosaria nigricans*) contain about 1 percent of protein and about 0.05 percent hexosamine (Table 2) (17): material derived from the cell wall of the cytoplasmic sheaths. Lingulids have 22 percent protein and 20 percent chitin: material derived from the organic interleaves of the laminated shell structure, possibly alternating monolayers of chitin and protein. The "punctae" of lingulids are fine, and small amounts of protein and hexosamine from them will be included in the values given in Table 2. The protein from the whole shell of *Lingula* contains most of the common animal structural amino acids and is fairly rich in glycine; certain areas of the shell have also a green organic pigment. *Notosaria* contains the common amino acids of structural proteins but is not rich in glycine (Table 3) (17).

Endopunctate forms (e.g., *Macandrevia* and *Crania*) contain invaginated material from the epithelium. Their hexosamine content is a little higher than that of impunctate *Notosaria*, about 0.1 percent, and their protein content is low (0.5 percent in *Crania*, about 2 percent in *Macandrevia*) (Table 2) (17). In *Macandrevia* this material is derived from the cytoplasmic sheaths and caecal material including mucin, also from the thin periostracum. In *Crania*, the organic material comes from interleaves of the inner shell layer, cytoplasmic sheaths to calcite fibers at sites of muscle attachments, epithelial cell material forming the punctae and from the periostracum. The protein of *Crania* is rich in glycine and is unusual in containing little or no aspartic and glutamic acids.

Discinids contain smaller amounts of protein and chitin than lingulids (Table 2). Their protein is rich in glycine, alanine, proline, and phenylalanine, and like *Lingula,* contains hydroxyproline, characteristic of collagenous proteins.

ORGANIC COMPOSITION OF FOSSILS

In fossil material, even of great age, recognizable fragments of these organic constituents are perserved. Proteins themselves may survive with their specific properties unchanged for 1,000 years (e.g., in the shell of *Mya arenaria*). In Pleistocene specimens of *Mercenaria mercenaria*, 1 to 5 percent of the peptide bonds are broken (10^4—10^5 years), giving more soluble protein fragments; in Miocene specimens all the peptide links are broken and only amino acids remain (1). Amino acids vary in their stability toward oxygen and temperature, only the more stable ones tending to be preserved in fossils. The more commonly found amino acids are alanine, glycine, glutamic acid, leucene, isoleucene, proline, valene, aspartic acid. These occur in *Atrypa reticularis* (Linné) (Wenlock Sh.), *Spirifer* sp. (Carb. Ls.) and in *Plectothyris fimbria* (Sowerby) (Jur.) (17), also (except proline) in *Plaesiomys (Dinorthis) subquadrata* (Hall & Clarke (Ord.) (2) (Table 3).

Organic materials to some extent may accumulate in fossils by perfusion from the surrounding sedimentary rock. *Linoproductus* sp. contained all the amino acids that were present in its containing matrix of Carboniferous Limestone, but had a higher concentration of them and in addition contained several amino acids not found in the limestone matrix (17) (Table 3). The *Linoproductus* shell contained 0.5 micromoles (μM) amino acids per gram fossil; the limestone matrix contained 0.3 μM amino acids per gram.

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EVOLUTION AND PHYLOGENY

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The chronology of morphological changes that represent evolution of the brachiopod shell can be really assessed only by comparative studies of continuous series of interrelated assemblages from given segments of the geological column. The opportunities for following the detailed course of even small skeletal alterations in this manner, however, are so reduced by the fortuitous nature of the geological record that nearly all statements on brachiopod evolution are inferential. They involve either deductive interpolations between the alleged end products of lineages (17, 46), or an inductive evaluation of the disparity between unrelated contemporary stocks (2). Both methods are attempts to estimate the drift away from common ancestry. The former approach is likely to lead to the identification of a more immediate relationship and tends to give a sense of continuous incremental change in features of minor taxonomic importance. The latter is generally concerned with more remote affinities and, more often than not, appears to reveal the sudden introduction or elimination of morphological features with great systematic weight. These apparent differences in the importance, as well as the pace, of morphological changes have led to a belief that they reflect varying scales of evolution. In fact, as the study of any well-documented group shows, the taxonomic importance of a feature is normally a function of the number of species to which it became common. Moreover, although no one doubts that evolution can proceed at greatly varying rates, all morphological discontinuities must ultimately be due to breaks in the geological record and are more likely to be met within the search for the common ancestry of independent stocks which, unlike the study of lineages, cannot be conducted selectively according to the completeness of the record.

Many fallacies can therefore arise from reviewing brachiopod evolution on such fragmentary evidence as we now have and within a classificatory framework which is at best an uneasy compromise with those evolutionary processes that are known to have affected the phylum. Nonetheless, it is still possible not only to demonstrate the repetitive nature of evolution but also to give some indication of the complex morphological and inferred anatomical changes that led to the emergence of the several major groups within the phylum.

It is symptomatic of the long and rich history of the brachiopods that few morphological features of the shell are unique to a particular stock. Such convergences vary from the repetition of one character, like the superposition of costation on finely costellate shells of *Orthis* and *Nikiforovaena*, to faithful mimicries of a complex of characters involving the entire external appearance of the shell (5, 7). Indeed, homeomorphy of this sort is so rife that when it is attended by a convergent likeness of internal characters as well, as in *Pionodema* and *Doleroides* (8), real difficulties are encountered in dissociating one stock from another. The repetitive appearance of internal features was also widespread throughout the phylum. Many of them are admittedly only analogous. The spread of denticles along the hinge lines of stropheodontids and possibly of the chonetacean *Eodevonaria*, for example, differs from that affecting the hinge lines of some plectambonitaceans in that it was preceded by fusion of the dental plates with the secondary shell of the interareas. In all three groups however, the denticles arose well within the secondary layer and were built up about taleolae, in contrast to those of the spiriferoids which were fashioned mainly from the primary shell layer. Other features are clearly homologous. Thus, no distinction can at present be drawn between the endopunctation of the enteletaceans and of the terebratulids, retziaceans, and many spiriferoids, which almost certainly arose in the last three groups independently of the first.

The extent to which the diversity of one group anticipated or repeated the trends in other groups is well illustrated by members of the Orthida. Insofar as the complex of stocks comprising this order probably was ancestral to all articulate brachiopods, some variation leading to morphological resemblances with the primitive antecedents of other later groups is to be expected. Yet the order also includes extinct lineages, clearly divorced from the main flow of descent, but foreshadowing to a remarkable degree many characteristics of the later phases in the evolution of the articulate brachiopods.

The modal orthoid shape includes a subquadrate outline, a biconvex profile, and a sulcate anterior commissure with well-developed interareas and hinge lines, but modifications in the first three attributes led to the strophomenacean appearance of *Cyrtonotella* and *Valcourea* and the spiriferacean habit of *Platystrophia*, while the pronounced emargination of *Dicoelosia* is suggestive of the trends that resulted in the emergence of the terebratulacean *Pygope*. The elongation of the ventral interarea is seen in the hesperorthids and skenidiids but was greatly exaggerated in the clitambonitaceans, which look like some later davidsoniaceans, and again in the triplesiacean *Onychotreta* which is very like the terebratuloid *Terebrirostra* (42). The interareas of *Productorthis*, in contrast, were sufficiently vestigial to persuade early students of the phylum, like Pander, that this lower Ordovician stock was a productid which, like its supposed relatives, also lacked a pedicle; whereas the reduction of both hinge lines and interareas, as in *Perditocardinia* and *Cyclocoelia*, anticipated the nonstrophic condition typical of the rostrate terebratuloids. Such trends were commonly accompanied by subtle changes in ornamentation that enhanced the homeomorphic properties of the stocks. The radial ornamentation of *Valcourea*, with its strong development of intercalated costellae, is fine enough to be mistaken for the parvicostellate condition of strophomenoids; and the lamellose and coarsely costellate condition of *Productorthis* recalls the exterior of *Reticulatia.* Strongly overlapping lamellae are especially characteristic of the glyptorthids and the spinose prolongations of *Spinorthis* are homologous with those of the atrypacean *Spinatrypa* and the rhynchonellacean *Tegulorhynchia.* Both the pseudodeltidium and the open delthyrium are typical of the orthids; but it is significant that, before the group became extinct, deltidial plates, which must have grown in the same way as those characteristic of rhynchonellid, terebratulid, and spiriferid shells, appeared independently in *Barbarorthis* and *Phragmophora.*

The internal characters also underwent changes that were echoed by contemporary or later stocks. The spondylia of the protorthids, skenidiids, and clitambonitaceans were developed independently of one another and of those diagnostic of the pentameraceans and later porambonitaceans; while the septate, muscle-bearing structure in the pedicle valve of *Parenteletes* is no different in function or origin from the meristinid shoe-lifter process. The pseudopunctate gonambonitaceans, which are only on balance assigned to the Orthida, include *Antigonambonites,* with a denticulate hinge line comparable with that of the spiriferids. The appearance of a cardinal process on the notothyrial platform, first as a median partition to segregate the dorsal ends of the diductor muscles which were later accommodated by the differentiation of the partition into a bilobed to trilobed myophore, with shaft, was a trend parallel with those that led to the elaboration and diversification of the strophomenoid cardinal processes. The orthid mantle canal systems show every conceivable variation achieved in later stocks, from the primitive saccate condition (e.g., *Billingsella*) to the advanced pinnate (e.g., *Clitambonites*) and apocopate (e.g., *Dolerorthis*) arrangements (Fig. 139). Finally, it is noteworthy that the brachiophores of a number of orthids were sufficiently prolonged to act as supports to the lophophore in the manner of crura. These processes are, for example, rodlike in *Skenidioides* and broad and bladelike in *Laticrura,* reminiscent respectively of the radulifer and falcifer crura of the rhynchonellaceans. In *Tropidoleptus,* apophyses from the brachiophores joined with outgrowths from a dorsal median septum to form a loop which, in certain aspects of growth, was like that of the terebratellaceans and must also have given support to the lophophore.

With the exception then of certain features, like the internally communicating hollow spines of productaceans and the rhynchonellacean *Acanthothiris,* or the calcareous spires of spiriferoids and the strophomenacean *Thecospira,* the morphological variability of the Orthida seems to have anticipated the diversity that arose during the subsequent evolution of the articulate brachiopods. There were, of course, recombinations of characters and changes in emphasis, both ontogenetic and phylogenetic, which produced new stocks. Such relationships are complex and the details of descent are still unknown, but the main paths of evolution can be traced with some confidence. Taxonomically the chief discontinuities in the morphological links from one group to another appear mostly at the superfamily or subordinal level. This classificatory aspect of evolutionary digression essentially reflects the systematic limit to which the procedure of assembling groups together by detailed morphological comparison can be taken. It may also have a more profound implication, in being the taxonomic level at which successful neotenous changes become identifiable. Either way, it is convenient to take the superfamily as a basic unit for discussing the significance of evolutionary changes within the phylum.

One other aspect of evolution requires some comment before discussing the details of brachiopod phylogeny. It has long been known, if only through the remarkable geological record of *Lingula,* that some stocks are more persistent than others and that they are easily outnumbered by their short-lived relatives. This variability in longevity is, of course, a manifestation of the experimental nature of evolutionary processes and has been used by SIMPSON (35) as an index of evolutionary rates in the expectation that some quantitative comparisons can be made between phyla. Unfortunately, the raw data, whether they are species or genera, cannot be quantified with any degree of confidence (49). The known range of a stock is only as objective an estimate of its actual existence as hazards of the geological record will allow. Moreover, the subjective nature of taxonomic procedure frequently makes it difficult to distinguish "monographic" bursts (12) from real accelerations in evolutionary diversification. Consequently, no attempt has been made to calculate evolutionary rates for various brachiopod groups, although histograms (Fig. 140) have been prepared to show the incidence of extinct articulate and inarticulate genera according to their absolute ages in HOLMES' time scale (20). The details of these frequency distributions are obviously influenced by the estimated duration of systems and their major divisions, since generic ranges can only be expressed in terms of the grosser stratigraphic units. Nonetheless the distributions are of some value in that their positive skews reveal the clear preponderance of genera with relatively short ranges.

Representatives of all four orders of inarticulate brachiopods are present in the Lower Cambrian, but, as with the earliest known articulates, the Orthida, there is as yet inadequate information, on a world-wide basis, to comment on the sequence of appearance of the orders. Hence it is not known whether they were all independently derived from a remote common ancestor or whether there is a fundamental regularity in the succession of their appearance with one order arising from another. In the absence of chronological information, one is forced to rely solely on morphological comparison to assess affinities.

Two of the orders are represented in modern seas, the Lingulida by two and the Acrotretida by six or seven genera. Internally, these genera show many resemblances in their soft anatomy, as discussed elsewhere. In the musculature, for example, the posterior and anterior adductors of Recent Acrotretida may be homologized with the umbonal and central muscles of the lingulids. Indeed, there is more resemblance between the musculature in Recent members of these two orders (like *Lingula* and *Discinisca*) than between Cambrian representatives (e.g., *Linnarssonella* and *Lingulella*), an anomaly that must be a measure of convergence. Moreover, the known ontogenetic histories of living inarticulates are basically similar and probably the two orders were initially fairly closely related to each other, although no ancestral-descendent relationship between them can be postulated.

Less is known of the other two orders, Obolellida and Paterinida. The Obolellida had a relatively short existence, for they became extinct by the close of Middle Cambrian times. They differed from Cambrian members of the other three orders in having a calcareous shell. They also show a remarkable variation in the position of the pedicle opening, a character which is usually relatively stable within an order. In some genera, the pedicle either emerged between the valves or possibly atrophied; in others it passed through a foramen located apically or well forward of the apex of the pedicle valve (31). The musculature is not well known in detail, but seems to correspond with the basic pattern of the Lingulida and Acrotretida, with two sets of muscles so placed as to suggest homology with the posterior and anterior adductors. It appears probable that the Obolellida are related to these two orders, but all details of their phylogenetic position are quite unknown.

The Paterinida are even more problematic. They first appear in the Lower Cambrian and were long thought to be restricted to the Cambrian, but are now known to range as high as the Middle Ordovician (10). They resemble the majority of inarticulate brachiopods in having phosphatic shells and in lacking articulation between the valves; but what is considered to be the muscle pattern, although still incompletely known, is basically different from that of other inarticulates. All recognizable scars produce narrowly triangular tracks radiating from the beak of each valve, and it is not possible to homologize them with the anterior and posterior adductors of other inarticulate orders. The posterior margin of the Paterinida has some similarities with that of the kutorginaceans and the articulate billingsellaceans. In all three, a median gap separates the covers to the apical parts of the delthyrium and notothyrium, although this opening in the Paterinida may possibly be only analogous with that of the other two groups in which it definitely did not function as a pedicle foramen. The resemblance of *Paterina* to the protegulum of many brachiopods prompted several earlier writers (19, 34) to regard the stock as the an-

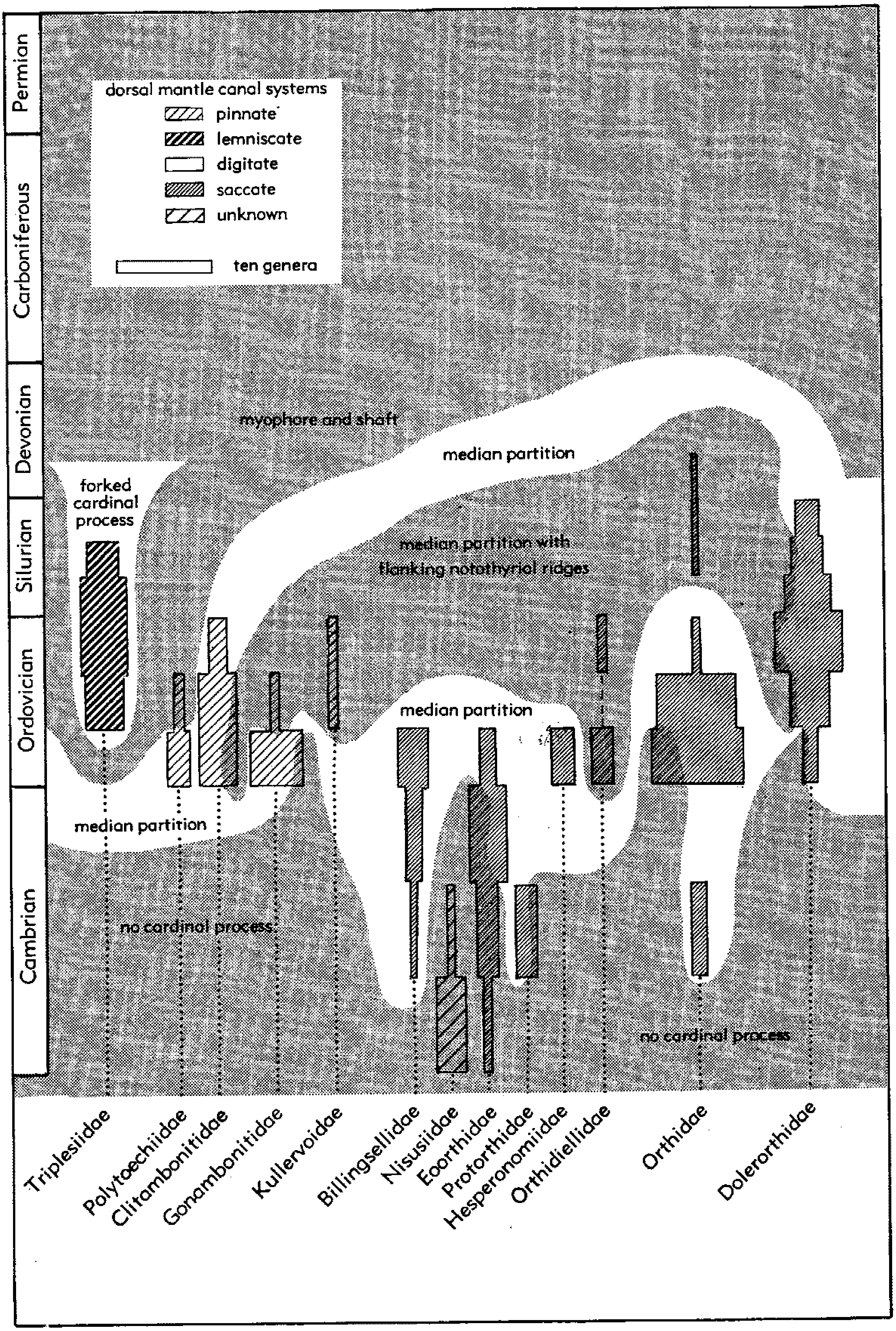

Fig. 139. Variation in cardinal process and dorsal mantle canal system in Orthida (54).

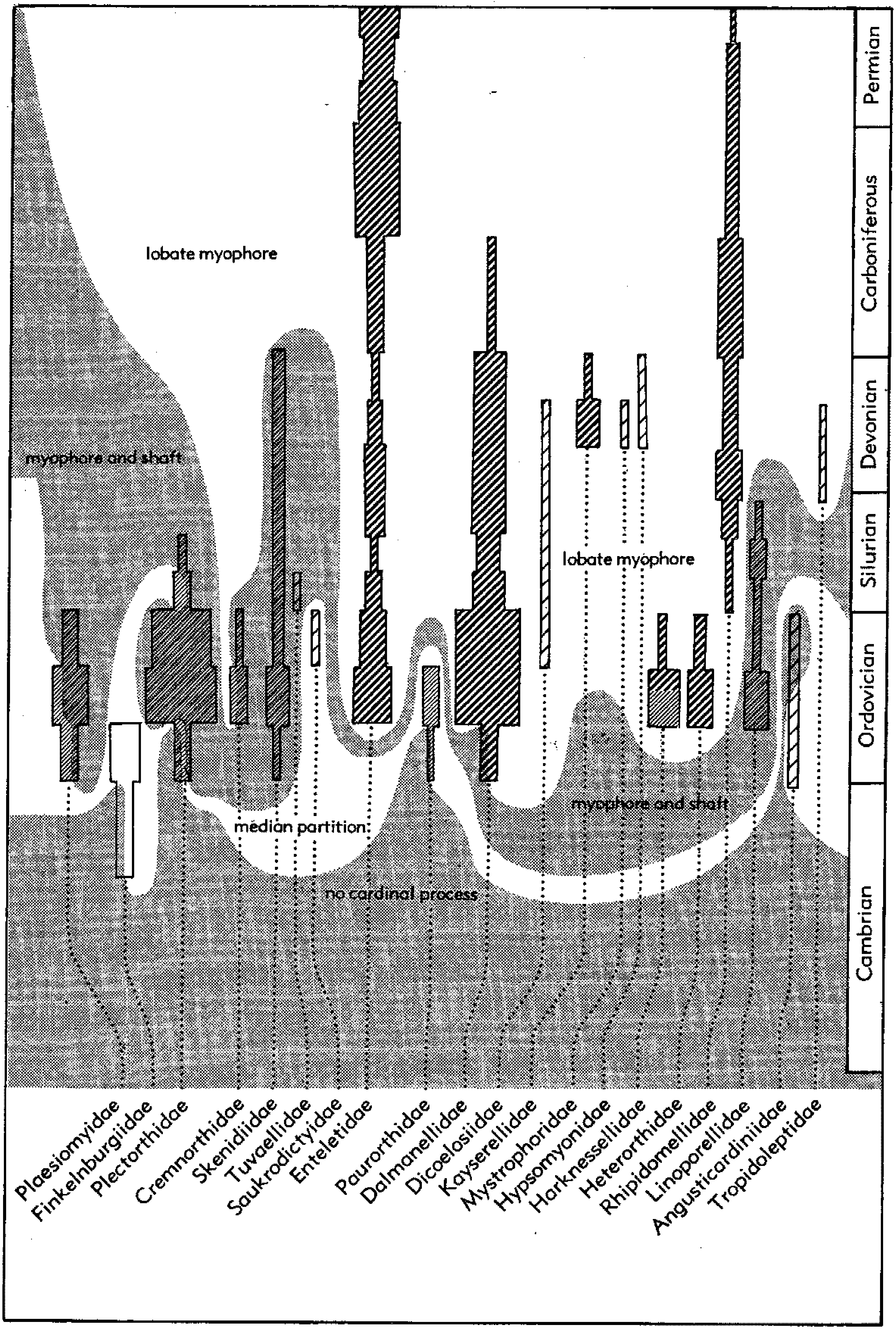

FIG. 139. (*Continued from facing page.*)

cestral radicle of the Brachiopoda. This relationship is unlikely because what is known of the paterinid internal markings precludes such a role.

The distinction between the Inarticulata and Articulata is also obscured by the existence of the Kutorginida, which, like the Paterinida, possess a conflicting assemblage of characters.

The kutorginaceans have been regarded as inarticulates by some students (18) and as early articulates by others (25), but on balance they do perhaps show greater similarities with the latter than the former. This likeness includes the calcareous nature of the shell, the variably developed cardinal areas, the pseudodeltidium with an apical or supra-apical foramen, and the postero-

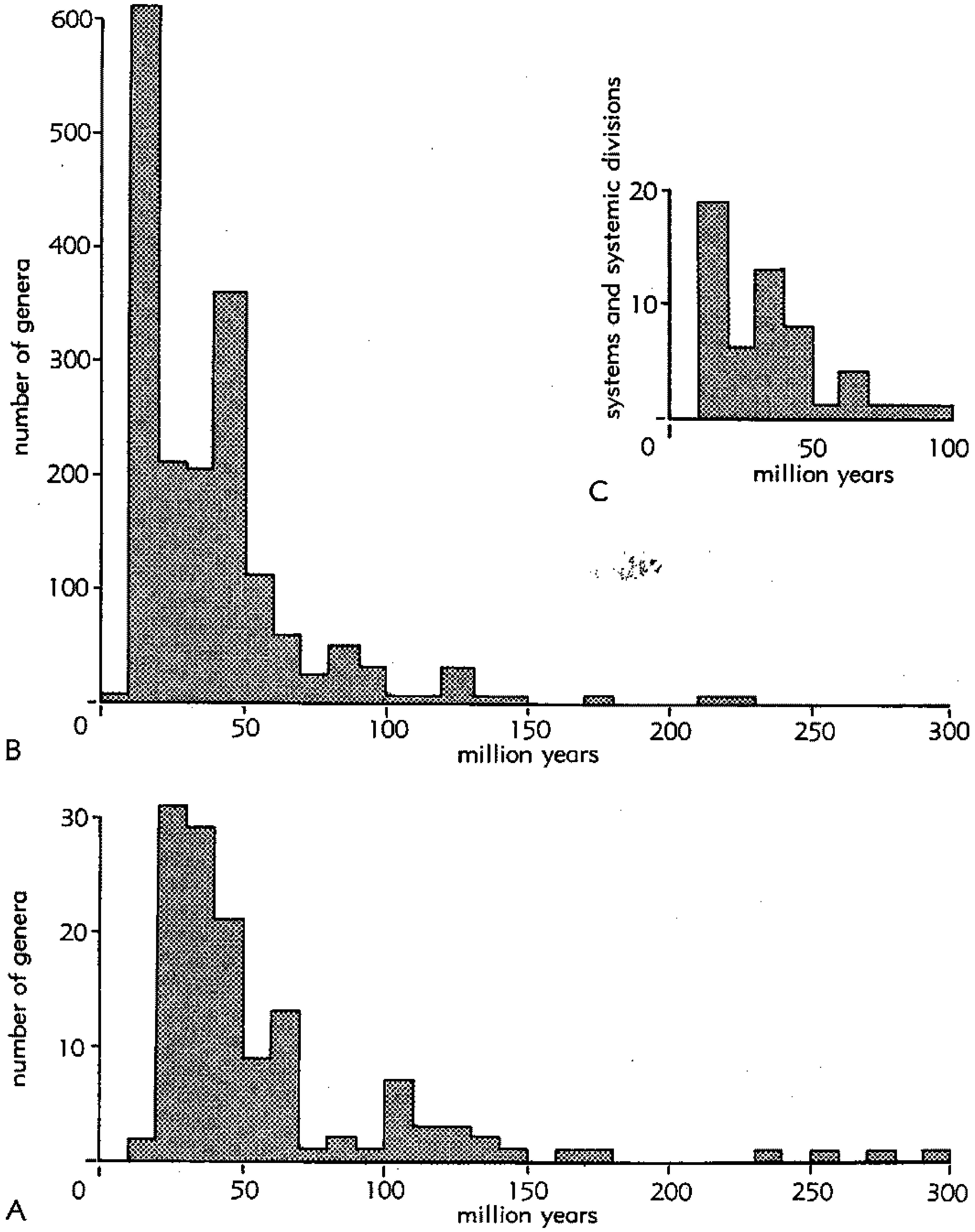

FIG. 140. Histograms representing frequency of *(A)* extinct inarticulate genera and *(B)* extinct articulate genera in stated segments of geologic time, and *(C)* absolute time-frequency distribution of post-Cambrian geologic periods and epoch divisions, showing that variations depicted in *A* and *B* mainly reflect estimated generic longevity in terms of geologic systems and series (54).

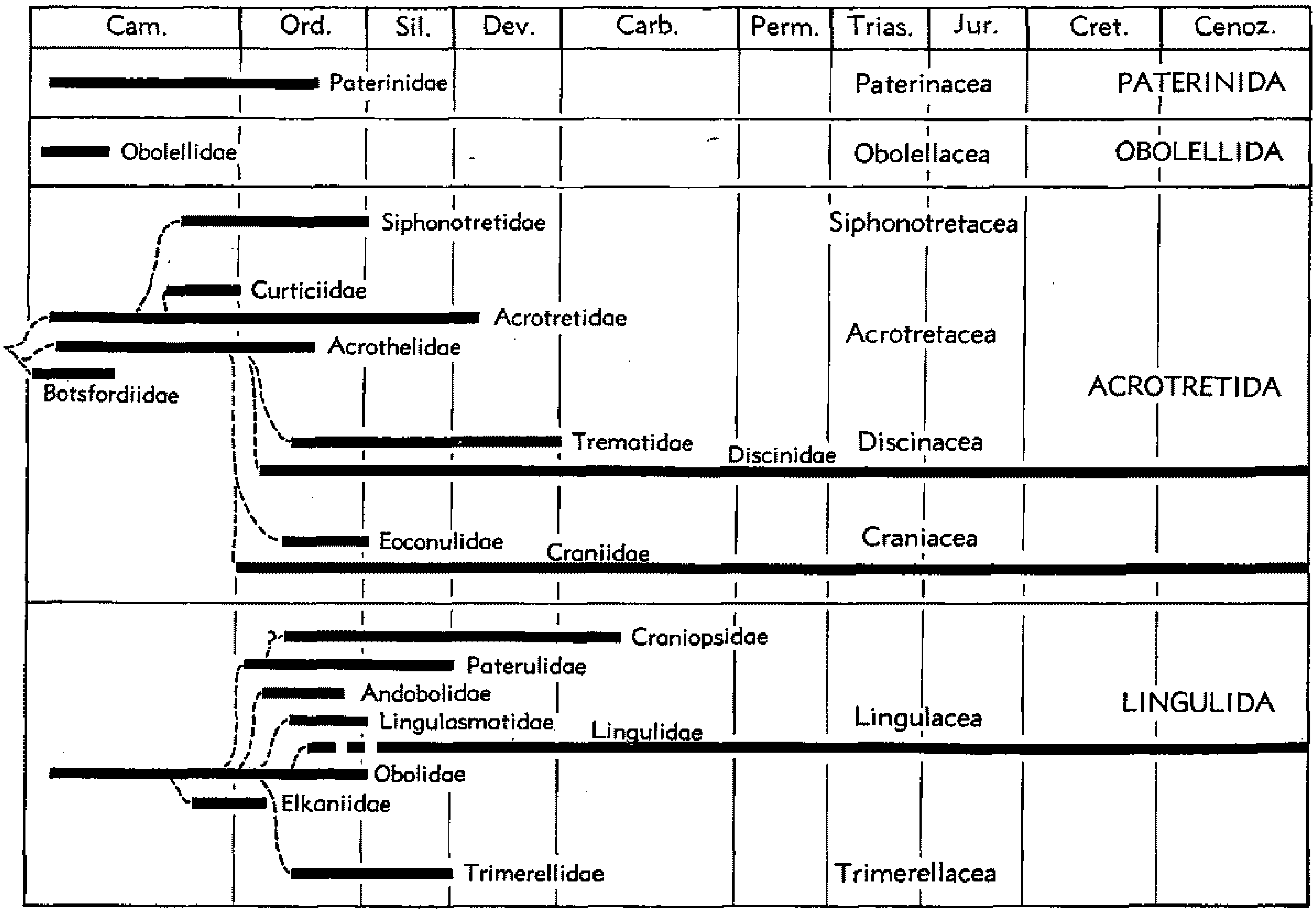

FIG. 141. Inferred relationships and approximate stratigraphic ranges of families in Inarticulata (53).

median location of the muscle scars. The inferred distribution of musculature and mantle canal systems, however, is difficult to reconcile with any categorical articulate organization.

An unusual modification of the pedicle valve characterizes the calcareous-shelled Dictyonellidina, a small group whose precise affinities are obscure and whose homogeneity is not beyond dispute. The group consists of the eichwaldiids and isogrammids, both of which bear a triangular opening extending anteriorly from the umbo of the pedicle valve. This opening is closed, except along the anterior side of the triangle, by a depressed plate fused with the remainder of the valve along the lateral margins of the triangular slot. The extreme similarity of this modification in both stocks suggests some degree of affinity between them rather than convergence. Although the eichwaldiids have been regarded as inarticulate brachiopods by some authors (18), the assemblage of characters possessed by the group, particularly by the later isogrammids [Dictyonellidina], which have a well-developed cardinal process and functional articulation, strongly suggests that they are articulate brachiopods with anomalous shell structure and pedicle opening.

Uncertainties, similar to those attending any inquiry into the affinities between inarticulate ordinal groups, also affect a review of evolutionary relationship within the groups, and are again due to significant gaps in the geological record, Indeed, so restricted are the obolellid and paterinid records that only the Acrotretida and the Lingulida afford any evidence of evolutionary processes (Fig. 141).

By early Cambrian times the Acrotretida were already represented by three well-established stocks, two of which (acrothelids and botsfordiids) are morphologically alike. The principal difference between these stocks is that the pedicle emerged through a triangular delthyrium which remained open in adult botsfordiids but, in adult acrothelids, was confined to a foramen at or slightly posterior of the apex by the growth of a pseudointerarea or an undifferentiated posterior margin. The fact that the botsfordiids are, on the whole, older suggests that they may have been the ancestral stock from which the acrothelids were derived by acquisition of an entire margin. Further, if the Lower Ordovician *Orbithele* is a true acrothelid, a convergence toward morphology of the Orbiculoideinae later took place in the development of a small pedicle tube.

The precise relationship between the third stock, the acrotretids, and the acrothelids or botsfordiids is unknown. Yet the number of features in common suggests that they are related, because the early acrotretids differ importantly only in having a median pit or groove dividing the variably developed dorsal pseudointerarea into two propareas, and in having an internal thickening near the beak of the pedicle valve (apical process). In the evolution of later acrotretids, changes in the apical process, position of the pedicle foramen, and form of the dorsal pseudointerarea and median septum played an important part.

The Linnarssoniinae [Acrotretidae] were the most conservative stock in that the dorsal pseudointerarea and median ridge remained weakly developed, although a secondary loss of the apical process also took place in later forms, like *Opisthotreta.* The dorsal pseudointerarea of their later contemporaries, the Acrotretinae, on the other hand, were well developed throughout stock history and the dorsal median ridge was commonly expanded into a bladelike septum independently in many members. In this stock, the foramen remained apical or immediately posterior of the apex and the apical process was commonly strong, although, as in the Linnarssoniinae it was secondarily lost in some later species.

Despite the gaps in the post-Cambrian record, it is likely that the Acrotretinae were ancestral to most of the later acrotretids. The Ceratretinae [Acrotretidae], for example, probably arose from them during Late Cambrian times by the elaboration of the apical process into a buttress bearing the internal pedicle opening, and a concomitant dorsoposterior migration of the external foramen. The Scaphelasmatinae [Acrotretidae], first known in the Middle Ordovician, may, in turn, have been derived from the Ceratretinae, to which they bear a strong external resemblance, by reduction and eventual loss of the apical process. Alternatively, the Scaphelasmatinae diverged from Ordovician acrotretids by adopting the external form of the Ceratretinae. The isolated occurrences of the Torynelasmatinae and Ephippelasmatinae [both Acrotretidae] present similar problems concerning descent. Their derivation from the Acrotretinae would have involved the loss of the apical process, a familiar theme in acrotretid history (Fig. 142), and the obsolescence of the dorsal pseudointerarea in the Ephippelasmatinae, a return to the condition typical of the Linnarssoniinae. The elaboration of the sporadically appearing acrotretid median septum reached its climax in the complex, saddle-shaped plate of the Ephippelasmatinae, which possibly represented the only successful trend towards a lophophore support among inarticulate brachiopods.

Curticiids, which are characterized by an open triangular delthyrium, show an interesting return to the botsfordiid condition. The musculature and pseudointerarea of young specimens, which have a closed pedicle foramen, are similar to those of the Acrotretinae, but during growth the constricting part of the ventral pseudointerarea was lost by dorsally directed resorption (32).

Relatively little is known about the origin of the siphonotretaceans. In this group, the pedicle foramen migrated anteriorly with growth of the shell and the track of the pedicle opening was closed to a variable extent by a plate or pedicle tube. Walcott (43) suggested that *Schizambon* developed from the obolellacean *Trematobolus,* but this appears most unlikely. Although the two genera are superficially alike, there are many differences, including shell composition, and it is probable that the elongate pedicle track, common to them both, is an example of homeomorphy (31). The majority of siphonotretaceans are spinose, but this feature probably developed subsequent to the emergence of the stock, because the Upper Cambrian *Dysoristus,* which in other respects seems to be closely related to *Schizambon,* is ornamented only by growth lines. The dorsal pseudointerarea of *Dysoristus* and the slightly younger *Helmersenia* shows some resemblance to the acrotretacean arrangement with a median pit separating the propareas; it is therefore possible that the

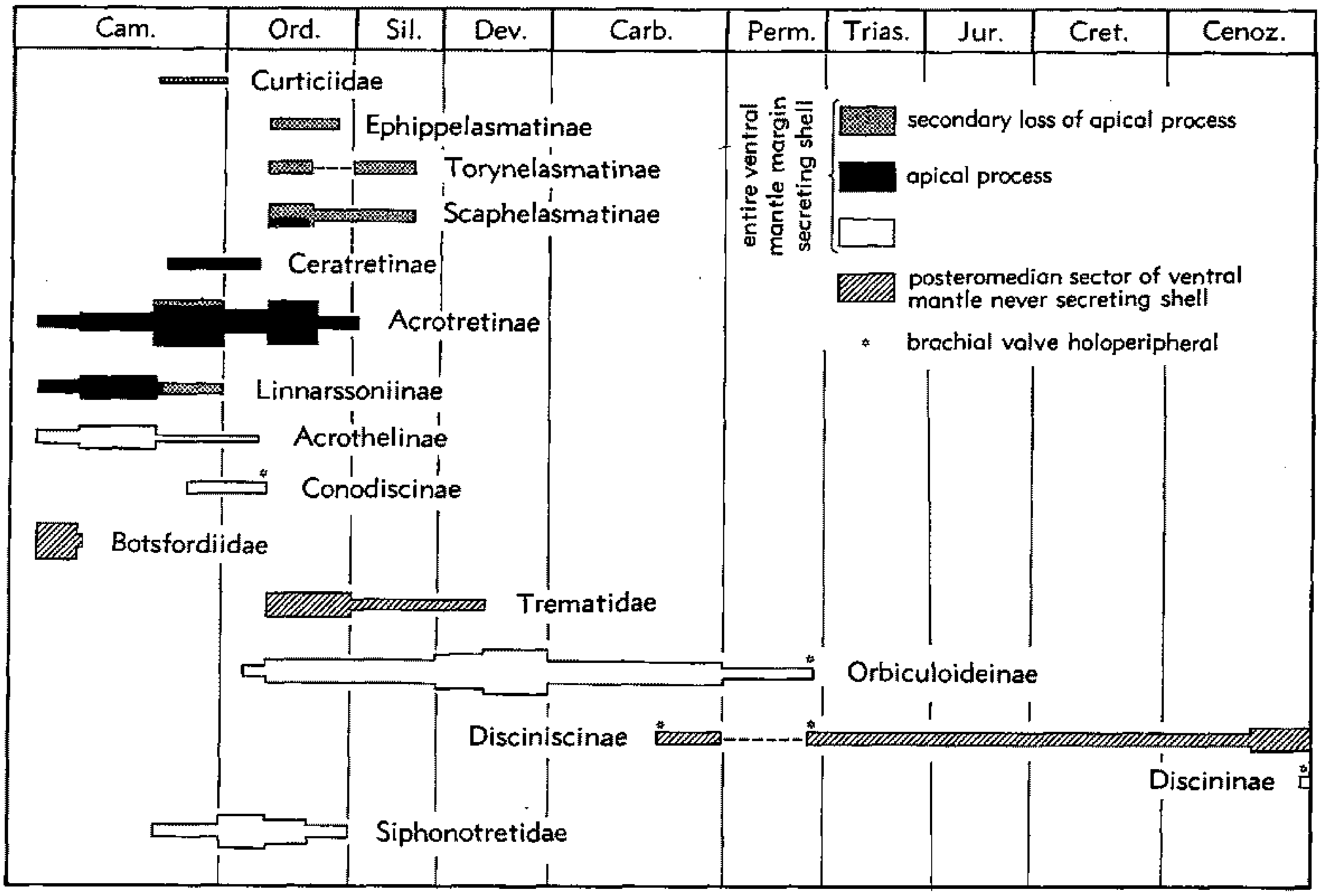

FIG. 142. Diagrammatic representation of evolutionary trends in Acrotretidina (53).

siphonotretaceans were derived from the acrotretaceans.

The discinaceans are first recorded from the Ordovician and, whereas it is almost certain that they arose from the acrotretaceans, it is also probable that the acrothelids were their ancestors (Fig. 141). Early in the history of the group two stocks were developed, which probably remained quite distinct from each other during their subsequent evolution. The trematids, in the manner of most acrotretaceans, retained a marginal beak in the brachial valve; but the pedicle emerged through a triangular opening which breached the posterior margin of the circular to subcircular pedicle valve in all stages of growth, and the only constriction of the opening resulted from the growth of the listrium at its apex (Fig. 142). In the discinids, which also appeared in the Ordovician, the dorsal marginal beak was lost, for the growth of the brachial valve was holoperipheral. Moreover, the pedicle opening of the earliest members, the Orbiculoideinae, became closed by an entire posterior margin in the adult shell, and the listrium was commonly elaborated to form a posterodorsally directed pedicle tube. Later discinids, the Disciniscinae, which must have descended from the Orbiculoideinae, show a reversion to the trematid condition in the pedicle valve because the pedicle opening intersected the posterior margin throughout life and a pedicle tube never developed from the listrium. Only living members of the third discinid stock, the Discininae, are known. The geological record indicates that they must have been derived from the Disciniscinae, with which they share an unmodified listrium, but they resemble the Orbiculoideinae in possessing a pedicle track that extends only a limited distance down the posterior slope of the pedicle valve.

The origin of the last group assigned to the Acrotretida, the Craniidina, is rather obscure; but it appears probable that they arose from either the acrothelids or the discinaceans, admittedly by fundamental changes in their physiology and soft anatomy. The majority of the craniaceans belong to a homogeneous stock, the craniids, characterized by calcareous, punctate shells and the lack of a pedicle in all known growth stages.

Apart from changes in surface ornament and the distribution of mantle canals and to a lesser extent musculature, the only common modification, which may have been repeated during stock history, was the development of the limbus in those forms which were free-living or attached only by the apical region of the pedicle valve. The phosphatic-shelled eoconulids resemble the craniids in the holoperipheral growth of the brachial valve, and the inferred cemented habit of the pedicle valve. Their shell composition suggests that they were more primitive than the craniids, although their rare occurrence at about the same time as early craniids may indicate an aberrant line of descent from a common ancestor.

The Lingulida, like the Acrotretida, were also represented in the Lower Cambrian by stocks that were sufficiently differentiated to imply either a substantial previous history or a rapid evolution. These early obolids possessed a deep pedicle groove separating the ventral propareas and a conspicuous dorsal pseudointerarea. They were probably ancestral to both the paterulids and the elkaniids. The latter stock developed a posteromedian thickening in both valves by the coalescence of oblique lamellae. The former was characterized by a limbus in both valves and a greatly reduced pedicle notch in the pedicle valve; exceptionally, as in *Lingulops*, a low muscle platform is found in both valves, a recurrent trend in many groups assigned to the order. It is possible that the craniopsids arose out of the paterulids especially by the acquisition of a calcareous shell. Three other small groups evolved from the main obolid stock during Ordovician times, the spinose *Acanthambonia*, *Andobolus* with its very high, bifid dorsal muscle platform valve, and *Lingulasma* which possessed a dorsal muscle platform supported by a high median septum as well as a ventral one.

The Lingulidae, which certainly occur in the Silurian but are also reported from the Ordovician, were derived from the Obolidae by the obsolescence of the pseudointerareas in both valves. It is, however, unknown whether they descended directly from the Lingulellinae [Obolidae], or whether the Glossellinae [Obolidae] constitute an intermediate stage in which only the dorsal pseudointerarea was reduced. The Lingulidae have been very stable throughout their history. Many Recent species show a remarkable resemblance to some of their Silurian ancestors, and the stock has formed the dominant element of post-Paleozoic inarticulate brachiopod faunas.

The trimerellaceans are first recorded from the Middle Ordovician and appear to have become extinct by the end of the Silurian. They display an unusual combination of important features in having a calcareous shell with a primitive form of articulation (29) and in probably lacking a pedicle. It is much more likely that they were descended from the main obolid stock than from other contemporary Lingulida, although it is evident that their emergence was due to major physiological and morphological changes. It is significant, for example, that early species had a typical obolid outline and profile, but low muscle platforms had already developed internally. During their subsequent history the shells commonly became obese and the muscle platforms, which were correspondingly high, became deeply excavated.

The earliest known articulate brachiopods are Lower Cambrian representatives of the billingsellaceans *(Nisusia, Eoconcha, Matutella)* and orthaceans *(Eoorthis)*. Allowing for the inadequacies of the geological record, it is a moot point which group is stratigraphically older. Much more important (9) is the undeniable evidence that the pseudodeltidium and chilidium are at least as old as the open delthyrium and notothyrium, and, from anatomical considerations, are even likely to have been the more primitive condition, so that initially it was the loss and *not* the growth of delthyrial and notothyrial covers that represented a significant evolutionary step away from the articulate ancestral archetype. These features, therefore, together with the impunctate shell, the flat-lying socket ridges and the variably developed cardinal process consisting of a median partition on the notothyrial platform, constituted the basic ingredients of billingsellacean morphology; and despite the lack of transitional forms, it is likely that six groups of Ordovician brachiopods, which were also equipped with a pseudodeltidium, were derived from such a radicle.

Two of these groups, the triplesiaceans

and clitambonitaceans, retained an impunctate shell but diverged principally by the acquisition of a forked cardinal process and a spondylium, respectively. The differentiation of the triplesiacean cardinal process was accompanied by a reduction of the dorsal interarea and some elaboration of the socket ridges (52) but without a rotation into the orthacean attitude, except in *Epacroplecia*. Some of the trends that affected the group before its extinction in Late Silurian times included an elongation of the ventral interarea *(Onychotreta)*, a reversal of the modal uniplicate condition *(Brachymimulus)*, and the development of an asymmetrical twist to the shell *(Streptis)*.

The clitambonitoids have been exhaustively studied by Öpik (30), and perhaps the most obvious general development in the clitambonitaceans, apart from the spondylium, was the pinnate mantle canal systems in both valves. One of the more tantalizing problems in reviewing clitambonitoid relationships is that of the affinities of the gonambonitaceans, which are regarded as being closely related to the clitambonitaceans. It is, however, significant that the shell substance is pseudopunctate and the spondylium a "triplex" rather than a "simplex" structure; and in view of certain other features, like the development of an incipient bilobed cardinal process in *Antigonambonites* and the impersistent rugation of *Raunites*, it may prove that the group was closer to the strophomenoids and only convergent toward the clitambonitaceans. One further comment remains to be made about the clitambonitoids. The delthyria and notothyria of the Atelelasmatinae [Clitambonitidae] and Anomalorthinae [Gonambonitidae] are open, but whether this lack of pseudodeltidium and chilidium involved any basic anatomical modification like that inferred for the orthaceans is unknown.

The three remaining Ordovician groups, which are assumed to have arisen from the billingsellaceans, also show a curious anomaly in shell composition. For two of them (plectambonitaceans, strophomenaceans) it is reasonable to visualize a common ancestor differing from the billingsellacean prototype in being concavo-convex and in possessing a parvicostellate ornamentation and a pseudopunctate shell. The earliest known davidsoniaceans (mid-Ordovician *Gacella* and *Fardenia*) are, however, impunctate and biconvex; and although they appear to have typical strophomenacean interiors, especially in the presence of a well-developed bilobed cardinal process, they could well represent an independent but convergent line of descent.

The divergence between the plectambonitaceans and strophomenaceans [Strophomenida] may be illustrated by differences in their cardinal processes. The plectambonitacean arrangement, stripped of its many variations, was essentially derived by an elaboration of the median partition on the notothyrial platform, whereas the bilobed strophomenacean process came into being by the forward and posterior growth of the areas flanking a median partition that underwent atrophy. Trends in both groups included the atrophy of the pedicle in adult shells of several stocks. This loss was precursory to cementation of the pedicle valve in the strophomenaceans *Liljevallia* and *Leptaenisca* and to the development of perforations through the ventral interarea of the plectambonitacean *Eochonetes*, which presumably contained anchoring strands of epithelium. Other trends among the plectambonitaceans include the spread of denticles along the hinge lines of independent stocks (e.g., Plectambonitinae, sowerbyellids) and the growth of lophophore platforms among the leptellinids and, later, among sowerbyellids by the coalescence and elevation of spinelike septules disposed in arcs. Indeed, the lophophore platform is so distinctively plectambonitacean that the similarly equipped *Christiania*, with its strophomenacean bilobed cardinal process, poses a systematic dilemma. It may well represent an aberrant line of descent independent of both groups, especially since the stock appears to have developed a pseudopunctate shell somewhat later than its inception (36).

The most widespread changes affecting the strophomenaceans involved repeated resupination and geniculation, and among the stropheodontids these were superimposed on a series of heterochronous parallel trends related to the loss of the pedicle and the spread of denticles along the hinge lines. Such trends included the fusion (and resultant loss of identity) of both the pseudodeltidium and chilidium with their containing interareas and the atrophy of the socket ridges or their realigned growth as ancillary struts to the cardinal process (46). As is to be expected in dorsoventrally compressed shells, elevations of secondary shell for the attachment of muscle bases were rarely developed (like the "pseudospondylium" of *Douvillina* and *Leptagonia*), and no true spondylium is known.

In spite of the problematic origin of the davidsoniaceans [Strophomenida], the group itself was sufficiently homogeneous to be traced without any profound break into the Permian. The earliest indications of pseudopunctation are at present found in some of the early Devonian stocks (e.g., *Schellwienella, Davidsonia*), and there seems to be little doubt that the condition was a late characteristic of the group (48). Thomas (41) has also reported punctation in Permian species of *Streptorhynchus,* but it has yet to be confirmed whether this condition is strictly comparable with the endopunctation of the Enteletacea or Terebratulida. A few trends are noteworthy. The adult pedicle was lost and the foramen sealed before the end of the Ordovician, as in species of *Fardenia.* A secondary attachment by cementation of the ventral beak, however, became prevalent during the Devonian Period, and was later attended by a gross elongation of the pedicle valve in some forms like the Permian *Meekella.* Internally, the two most significant changes affected the dental plates which became either obsolescent and disappeared, as in the schuchertellids, or exaggerated and even convergent so as to form a spondylium *(Perigeyerella).* In most stocks it seems unlikely that the socket plates were well enough developed to give support to the lophophore, although impressions of a spirolophe, disposed in the plane of commissure, are preserved in the shell of davidsoniids. In the Triassic stock *Thecospira,* however, a pair of calcareous spires gave support to the lophophore. Each apparently was suspended from the cardinal process by a short apophysis, an arrangement quite different from the crural support found in the Spiriferida, but one to be expected in an aberrant davidsoniacean.

The remaining post-Ordovician pseudopunctate groups, with exception of the oldhaminoids, appear to have identifiable antecedents. Muir-Wood (26), in reviewing origin of the chonetoids, has referred to the possibility that the group is polyphyletic. The bulk of the stocks are feasibly derived from a generalized form, in many respects comparable with the earliest known chonetoid *Strophochonetes.* Its basic characters probably included a smooth to costellate, concavo-convex shell with perforations along the ventral interarea, which may have been continuous with external spines, and a functional pedicle in at least the early growth stages. Internally there was a ventral median septum and a more variable dorsal one which may have been flanked by lateral septa; also present is a cardinal process variably lobate in ventral and posterior aspects, probably derived by longitudinal cleavage of an arched median outgrowth (comparable with the sowerbyellid arrangement) with or without lateral subsidiary ridges. All these attributes became manifest during plectambonitacean evolution. *Eochonetes,* for example, has a perforate ventral interarea, and although its decisively sowerbyelline interior militates against a role as an ancestral stock, it is highly likely that a paedomorphic introduction of such perforations in Aegiromeninae [Sowerbyellidae], such as in *Chonetoidea,* provided the link. The Devonian *Chonostrophia,* on the other hand, with a resupinate shell bearing an unequally parvicostellate ornamentation and distinctive musculature, may have been derived from the strophomenaceans (26).

Once established, the chonetoids did not undergo any spectacular change. The daviesiellids were affected by gross increases in size and thickness of the pedicle valve but the genera assigned to the family may represent the end products of a series of convergences rather than closely related stocks (26). Variation also occurred in the development of the dorsal septa and in the disposition and growth of the spines external to the ventral perforations; the repeated loss and acquisition of radial ornamentation are also noteworthy.

The origins of the productoids have been reviewed by Muir-Wood & Cooper (27). They concluded that the strophomenacean *Leptaenisca,* with cemented pedicle valve, simple teeth and socket ridges, bilobed cardinal process, and spirally disposed brachial ridges, conforms most satisfactorily to the inferred ancestral type. The two features indicative of a trend away from the orthodox strophomenoids toward the nascent productoids, are, of course, the ventral attachment of the shell by cementation and the brachial ridges, neither of which is unique to *Leptaenisca.* Brachial ridges occur in the Leptodontellinae [Stropheodontidae] and the problematic davidsoniacean *Irboskites*; and the cementing habit was achieved by the stropheodontid *Liljevallia* and contemporary davidsoniaceans (e.g., *Schuchertella, Irboskites*). These occurrences show how new characters can arise in a number of independent stocks and at opportune moments in evolution and in appropriate combinations can contribute toward the establishment of an entirely new group involving, in the case of productoids, the paedomorphic acquisition of spines.

Subsequent to their introduction, the productoids underwent what is probably the most prolific diversification in the brachiopod phylum, giving rise to an unprecedented number of bizarre stocks. By Early Devonian time the two principal antecedents to the strophalosiaceans and productaceans, *Devonalosia* and *Spinulicosta*, respectively, had appeared (27). Both are concavo-convex with small teeth and sockets and a modified bilobed cardinal process. But the spines, which are rare on the brachial valve of *Spinulicosta* and absent from that of *Devonalosia*, were already acquiring specialized functions, because, in addition to protective recumbent spines present in both, steadying spines were as characteristic of the former stock as were clasping spines of the latter. Both interareas (together with pseudodeltidium) were moreover present in *Devonalosia* but were obsolescent in *Spinulicosta.* These differences foreshadowed the divergent paths of strophalosiacean and productacean evolution.

Strophalosiaceans remained fixed throughout adult life by clasping and attachment spines, and they tended to retain primitive features like the interareas which were rarely absent from both valves, as in *Spyridiophora.* The teeth and sockets also persisted in the strophalosiids, and in *Ctenalosia,* a series of small cones with complementary sockets were proliferated along the hinge line to simulate denticulation.

The most spectacular trends within the strophalosiaceans [Productidina] were undoubtedly those involving the disproportionate growth of the pedicle valve. Umbonal lengthening was attended by a gross extension of the ventral interarea, as in the aulostegids with a medially raised elytridium simulating the pseudodeltidium, and in the scacchinellids, in which repeated deposition of cystose plates concomitantly reduced the shell space. Among teguliferinids and richthofeniaceans, the pedicle valves grew like cones which were attached apically, and the brachial valves relatively reduced to function as a lid commonly sunk well within the periphery of the pedicle valve.

Productaceans [Productidina] may have been fixed as spats by ringlike attachment spines or by cementation of the ventral beak but were detached for most of their lives. This free sedentary habit was successfully maintained by trends toward redistributions of spines into dense, symmetrical clusters (e.g., *Peniculauris*) or to their reduction to a few strong symmetrically placed ones (e.g., *Muirwoodia*). In respect of other features, the modifications of strophomenid morphology found in *Spinulicosta* were carried to a conclusion. Reduced interareas (with pseudodeltidium and chilidium) survived only in the Productellidae and Kansuellinae, although secondary structures simulating them (ginglymus) were rarely developed (e.g., *Reticulatia*). Similarly, teeth and sockets persisted only in the productellids, and even in that group were weak and not invariably present. The bilobed cardinal process, in contrast, underwent a series of changes that were convergent toward conditions prevalent in the chonetaceans. In general, as can be seen in the leioproductids, the submedian sides of the lobes became adjacent and incompletely fused to form a trilobed structure. Further modifications involved the lengthening or shortening of the shaft, and a dorsal rotation of the myophore, as well as an accentuation of the median crest, as in the dictyoclostids. The climax to this last trend is found in *Striatifera* and *Titanaria,* in which the lateral boundaries to the process atrophied, and the attachment areas were located on a median crest continuous with the dorsal median ridge, recalling the arrangement in certain orthoids.

The precise affinities of the oldhaminoids [Oldhaminidina], the last group which is inequivocally related to the pseudopunctate stocks just discussed, constitute a major problem in determining the pattern of descent among articulate brachiopods. Speculation on oldhaminoid ancestry is further complicated by the possibility that the dorsal part of the shell may have consisted of a vestigial brachial valve and a very much larger plate of secondary shell which acted as an internal supporting plate to a schizolophous or ptycholophous lophophore (38, 45). Assuming, however, that this condition, if it existed, arose paedomorphically, a number of features, other than pseudopunctation, indicate its strophomenid ancestry. Thus the earliest-recorded oldhaminoid, *Poikilosakos*, possesses a nonspinose cemented pedicle valve, which extends well beyond the limits of the "brachial valve" in all directions and lacks a true cardinal area, although secondary "teeth" are present and the weak cardinal process is distinctly bilobed. Taken in isolation, these characteristics are not conclusively diagnostic, but collectively they suggest a productoid ancestry in general and a richthofeniacean one in particular. The lack of spines does detract somewhat from this inferred derivation. But, when the unique growth relationships between the valves are considered, it can be appreciated that the stock came into being only after a fundamental anatomical reorganization had taken place in which the loss of spines would have been a minor event. FREDERIKS (16) believed that the oldhaminoids were descended from the marginiferids, but his chief reason for doing so was to account for the bilobation of the "brachial valve" which seems to be less important than other features.

During their brief recorded existence throughout Pennsylvanian and Permian times, many novel shapes were assumed by the oldhaminoids, dependent upon the extent to which the pedicle valve was attached. Internal changes involving the asymmetrical development of the ventral muscle impressions also took place. The most conspicuous trend, however, was an increase in the lobation of the "brachial valve," and a complementary development of ridges or septa in the pedicle valve, which were either normal to, and more or less symmetrical about the median plane, or less commonly subparallel with the median incision.

In comparison with the articulate brachiopods already discussed, the most important difference displayed by the earliest known eoorthids [Orthida], like *Wimanella*, is the open delthyrium. This condition was typical of all Cambrian and the great majority of younger orthaceans and enteletaceans, although, as in orthidiellid *Trematorthis*, dolerorthid *Barbarorthis*, plaesiomyids *Campylorthis* and *Valcaurea*, tuvaellid *Tuvaella*, and kayserellid *Phragmophora*, deltidial covers were secreted in a number of independent stocks. A further change, with implications of an equally profound anatomical reorganization, was introduced soon after the inception of the group. The ventral boundaries of the sockets in the eoorthids and *Protorthis* are flat-lying ridges; but by mid-Cambrian time, in the protorthid *Arctohedra* and the orthids *Bohemiella* and *Oligomys*, they had undergone a rotation toward the median plane. In this attitude, which is typical of the orthaceans and enteletaceans, the brachiophores became elongated in a ventral direction and were commonly equipped with processes. As unsupported rods or blades, like those of the orthids and dolerorthids respectively, it is unlikely that their functions were very different from those of the billingsellacean socket ridges. In Upper Cambrian finkelnburgiids, however, the brachiophores were supported by bases reaching to the floor of the valve, and the sockets were normally defined by fulcral plates. This arrangement is characteristic of the plectorthids, cremnorthids, skenidiids, and Evenkininae [Plaesiomyidae] (an independent derivation from the plaesiomyid pattern) and dominant in the enteletaceans. In some of these stocks the brachiophores were sufficiently prolonged to have acted as supports for the lophophore.

Such changes as these indicate the close affinities that existed between the orthaceans and enteletaceans and there seems little reason to doubt that the latter arose out of the former by the acquisition of an endopunctate shell. Indeed, judging from the many morphological differences between the orthid-like Paurorthidae, the nearly rostrate Angusticardiniidae, and the remaining endopunctate stocks with advanced cardinalia, it is possible that the enteletacean group was polyphyletic.

Other trends affecting the orthaceans and enteletaceans have been referred to in the introduction to this chapter; but those leading to the diversification of the cardinal process and mantle canal systems are noteworthy (Fig. 139).

The cardinal process is absent or rudimentary in the eoorthids and also in early members of many other stocks, including enteletaceans (e.g., *Paurorthis*), orthids (e.g., *Poramborthis*), dolerorthids (e.g., *Lepidorthis*) and finkelnburgiids (e.g., *Diparelasma*). Once established as a median partition, however, it became the seat of attachment for the medially migrating diductor muscle bases in the plectorthids and later plaesiomyids and thereby differentiated into myophore and shaft. Further elaboration occurred in the enteletaceans, which led, for example, to the formation of a trilobed process. The trilobed process is also found rarely among the orthaceans, but that of the orthidiellids at least was differently derived by the posterior growth of the notothyrial ridges flanking a high median plate, a style that is reminiscent of primitive strophomenaceans.

The basic patterns of the orthacean mantle canal systems are more primitive in some respects than those of the billingsellaceans because the saccate arrangement prevailed in both valves not only in the eoorthids but even in relatively late stocks such as the plaesiomyids, plectorthids, many orthids, and paurorthids. More advanced patterns, involving an enlargement of the gonocoels and a redistribution of the peripheral canals, were developed independently in many orthaceans. Thus the dorsal systems were digitate in the hesperonomiids and orthidiellids, and digitate to apocopate in the dolerorthids. In the finkelnburgiids both canal systems were digitate and in the enteletaceans dominantly lemniscate.

In summary, it may be remarked that the history of the orthaceans is sufficiently well known to illustrate the evolutionary processes of parallelism, convergence, and uneven progress of character changes within the group, so that advanced and primitive features combine to characterize various stocks (Fig. 139).

The Pentamerida form a homogeneous group of such modest variation and range that the main trends contributing to its evolution are obvious. Taxonomically, the principal feature for identification of the group is the spondylium, but this structure was a relatively late development. Indeed, judging from the Cambrian porambonitaceans (e.g., *Cambrotrophia*), the chief difference from orthacean contemporaries, with which they shared an open delthyrium, discrete dental plates, and rudimentary brachiophores, was the presence of a dorsal fold. Thereafter, a series of changes progressing at varying rates in different stocks became evident.

Discrete dental plates survive as a feature of some Ordovician stocks (e.g., *Xenelasma, Stenocamera, Lycophoria, Porambonites*). Yet by Late Cambrian time, every stage from a pseudospondylium to a spondylium simplex had been attained by the huenellids and clarkellids. The spondylium simplex was a dominant feature of many Ordovician porambonitaceans, as was the so-called "spondylium duplex" of the parastrophinids and the great majority of pentameraceans. Only the free spondylium of *Holorhynchus*, recalling that of the orthacean *Protorthis*, represented any noteworthy departure.

The rudimentary brachiophores of the ancestral stocks also underwent orderly transformation. By Late Cambrian time they had become well defined, flanked by small fulcral plates, and with their bases (brachiophore plates) reaching to the floor of the brachial valve, and disposed either divergently (e.g., *Mesonomia*, early clarkiids) or convergently (e.g., *Plectotrophia*). With rare exceptions (e.g., *Porambonites*), convergent brachiophore bases, either contributing to or associated with a dorsal median septum, became the dominant arrangement of the younger porambonitaceans. Such a structure has mistakenly been called a "cruralium" but it never enclosed the dorsal adductor bases of porambonitaceans. The pentameracean cardinalia in general differs from that of the porambonitaceans only in being better developed. Hence the homologues of the brachiophores probably gave support to the lophophore in all pentameracean stocks, compared with only a few late porambonitaceans (e.g., camerellids, parastrophinids). Moreover, although the homologues of the brachiophore bases were mainly discrete (e.g., *Pentamerus*), they also converged to form a true cruralium (e.g., *Pentameroides*), and even underwent atrophy as in the stricklandiids (4, 44) and the virgianids. The climax to this trend in improvement of the brachiophores as devices for the support of the lophophore is represented by the growth of a calcareous loop from the ends of the crura of *Enantiosphen* (50). This stock, which was without issue, did not contribute to the evolution of the articulate brachiopods, but the development of its loop was nonetheless a striking repetition of those processes that resulted in the establishment of the spiriferid and terebratulid calcareous supports.

Some of the changes that affected the pentamerid exterior also merit mention. The dorsal fold and ventral sulcus, although variably expressed, were always characteristic of the porambonitaceans but of only a minority of pentameraceans (e.g., *Barrandina*, *Clorinda*). Most pentameracean shells were either rectimarginate (e.g., Pentamerinae) or sulcate (e.g., *Gypidula*), and the difference between the two groups is an added reason for supposing that the Mid-Ordovician parallelelasmatids are really porambonitaceans and *not* early pentameraceans. The change in outline, arising from the reduction of both interareas and hinge lines were typical of the early porambonitaceans, was more uniform. Later, porambonitaceans (e.g., camerellids, parastrophinids) and most pentameraceans became nonstrophic, although the stricklandiids and the pentamerids *Aliconchidium* and *Pleurodium* were strophic, possibly through a secondary growth of the cardinal area.

Consideration of the origin and descent of the Rhynchonellida, Terebratulida, and Spiriferida is essential to any discussion of brachiopod evolution, because members of the first two orders, along with the problematic thecideids, constitute the only articulates surviving today. It is, moreover, appropriate to review them together because there are many indications that they were originally closely related to one another. In some respects this affinity isolates them from other extinct stocks and suggests that, with appearance of the rhynchonellids (oldest and least specialized of the groups) articulate brachiopods attained a third phase of anatomical modification as fundamental as that which is believed to have taken place during the derivation of the orthaceans from the billingsellaceans.

The oldest rhynchonellids yet recovered are the early Chazyan *Sphenorhynchia*, *Ancistrorhyncha*, *Dorytreta*, and *Rostricellula* (which is also known from the upper Llanvirn of Wales) and the late Chazyan *Oligorhynchia*. They are all sufficiently distinctive, not only from other contemporary groups but also from one another, to suggest that they had already diverged significantly from their presumed common ancestry. It is nonetheless profitable to enumerate the chief characteristics shared by this assorted lot. They include a rostrate impunctate shell with a vestigial to obsolescent ventral cardinal area, an open delthyrium which may be restricted by rudimentary deltidial plates, divergent dental plates supporting laterally set teeth, and sockets fashioned from fulcral plates and bounded by ridges which are separated from strong crura by outer hinge plates. The crural bases may be supported by plates convergent on to the floor of the brachial valve (e.g., *Oligorhynchia*) or on to a median septum (septalium of *Rostricellula*). In addition, *Rostricellula* is normally strongly uniplicate and *Ancistrorhyncha* less so, while *Dorytreta* and *Sphenotreta* are sulcate and *Oligorhynchia* intraplicate. Many of these features occur singly in contemporary orthaceans; but as a combination (excluding the sulcate anterior commissure and the rudimentary deltidial plates) they decisively reveal a porambonitacean ancestry. One can therefore think of the rhynchonellids as having been derived out of the porambonitaceans simply by a precocious development of crura and the elimination of any tendency to form a spondylium. The last factor may have been linked with a subtle but highly significant shift in the ventral seats of muscle attachment. For in *Rostricellula*, and all rhynchonellids, terebratulids, and spiriferids with well-preserved muscle impressions, the ventral adductor and diductor scars are well forward of the delthyrial cavity which accommodated the pedicle base. Such a redistribution distinguishes these three groups from all other articulate brachiopods. In Recent species it is an adult expression of mantle reversal which may therefore have become a feature of the embryonic development of articulate brachiopods only with the emergence of the rhynchonellids (51).

The Rhynchonellida are the most conservative group of articulate brachiopods, for they have survived to the present day with so few changes that the great majority of them, irrespective of their range, are instantly recognizable. Traces of cardinal areas persist only in certain Ordovician stocks (e.g., *Orthorhynchula, Orthorhynchuloides, Drepanorhyncha*), thereafter an exaggerated secondary expansion of posterior margins was confined to a few Triassic forms (e.g., *Dimerella, Halorella*). The most significant deviations were the appearance of endopunctation in the short-lived *Rhynchopora* and the acquisition of a spondylium "duplex" and a camarophorium by the stenoscismataceans. Neither of these is likely to signify polyphyly, and the only other indication of a disruptive change within the group seems to have been the neotenous advent of the dimerellids.

The essential stability of the group is reflected in both external and internal characteristics. A uniplicate commissure, normally associated with a well-developed dorsal fold and ventral sulcus, is the commonest condition of the shell, and its effects may be spectacularly exaggerated by a dimorphic segregation into high- and low-convexity species within closely related stocks, as in the Hebetoechiinae [Uncinulidae]. This arrangement, however, was repeatedly modified by reversals during growth, or by the retention or a later ventrally directed folding of the straight margins of the brephic shell. The rectimarginate commissure is found in some Orthorhynchulinae [Rhynchotrematidae], Uncinulidae (e.g., *Plethorhyncha, Uncinulus*), and Septalariinae [Camarotoechiidae] (e.g., *Pseudopugnax*). The sulcate condition is characteristic of *Sphenotreta* (a replacement of the dorsal sulcus by a fold took place in adult growth stages of *Dorytreta*), early Mesozoic dimerellids, and Recent Cryptoporidae and Basiolinae. An asymmetry in shell growth, like the more subdued manifestations in the triplesiaceans, also affected the stenoscismatacean *Camerisma* and some Mesozoic and Recent stock among the Dimerellidae, Cyclothyridinae, Basiolinae, and Erymnariidae.

Similarly, the fine to coarsely costate ornamentation, which is characteristic of the majority of rhynchonellids, was repeatedly suppressed at various stages of growth in a number of independent stocks. The commoner modifications entailed the persistence of the smooth condition of the brephic shell throughout adult growth as in the dimerellids *Rhynchonellina* and *Norella*, the basiliolid *Basiliola*, and some species of the camerophoriacean *Psilocamara*; or a variable delay in the onset of radial ornamentation during growth of the shell, which is especially characteristic of the Rhynchonellidae. More rarely, as in the Camarotoechiinae, the costae became obsolescent and died away in the late phases of shell enlargement.

The principal internal changes, apart from the growth of the stenoscismatacean spondylium and camarophorium, affected the cardinalia, because even the mantle canal systems seem to have been basically saccate with continual lemniscate elaborations (48). The crura certainly underwent a number of repeated modifications in their attitude and morphology, the historical consequences of which have still to be studied. The cardinal process was less important than in other groups, because it appeared only sporadically during rhynchonellid evolution, yet its appearance frequently involved morphological repetition—the bilobed process, for example, is known among Devonian eatoniids, Rhaetic austrirhynchids, and the Eocene to Recent *Cryptopora*.

The earliest known member of the Spiriferida, the mid-Ordovician *Protozyga*, is essentially a loop-bearer, because in the older species, the homologues of the distal parts of the primary lamellae are commonly only a pair of apophyses extending from the anterolateral corners of a closed calcareous ribbon. Such a structure was formed by the median fusion of a pair of prongs growing forward from well-developed crura and, at this juncture in brachiopod history, was entirely novel. The shape of the loop and the small size of the early spire-bearers in comparison with contemporary articulate brachiopods (Fig. 143) suggest that the loop functioned as a support to the ringlike trocholophe typical of living juveniles. Other features, like obsolescence of cardinal areas, presence of incipient deltidial plates, well-defined primary and secondary layers of the impunctate shell, and arrangement of the cardinalia, are diagnostic of ancestry. Thus, when all aspects of its morphology are considered, *Protozyga* is reasonably interpreted to have been derived paedomorphically out of the Rhynchonellida (50). This development seems to have been the source of most, if not all, spiriferoid and terebratuloid evolution. Other Ordovician spire-bearers (e.g., *Zygospira, Hallina, Catazyga*) can certainly be attributed to the same common ancestor, although the spiralium of *Cyclospira*, which lacks a jugum at least in adult shells, may have grown as discrete calcareous ribbons during post-trocholophous stages of lophophore development, to support a spirolophe (48).

From these beginnings the spire-bearing brachiopods proliferated along a number of independent lines of descent during the Paleozoic and early Mesozoic with important changes in form and internal organization.

One of the striking distinctions maintained throughout the history of the Spiriferida was the obsolescence of cardinal areas in the atrypoids, retzioids and athyridoids in contrast to their retention among spiriferoids. The rostrate shell was typical of even the oldest known atrypoids, because rarely did either traces of interareas survive, as in *Catazyga*, or secondary, straight hinge lines grow, as in some Carinatininae [Atrypidae] and koninckinaceans. Strongly developed interareas and wide hinge lines were nonetheless characteristic of the earliest known spiriferoids, the eospiriferids, and delthyridids; and since these stocks first appeared toward the end of the Early Silurian, it is probable that their strophic condition was acquired during their derivation from a rostrate atrypoid. Subsequently, some reduction took place as in the reticulariids, but, more commonly, the ventral interarea was repeatedly lengthened in the hemipyramidal pedicle valves of the cyrtiids, cyrtinids, syringothyridids, cyrtospiriferids (e.g., *Syringospira*), etc.

Another feature stabilized in the spiriferoids was the strong dorsal fold (with complementary ventral sulcus) which was almost invariably present. In only a few stocks, like some ambocoeliids, the brachythyridid *Palaeochoristites*, elythids, and martiniids, did the dorsal fold tend to become weak and disappear. It was also common enough in the remaining spire-bearers, but was never dominant to the same extent, so that even among the most primitive stock, the zygospirids, every condition, from sulcate to uniplicate, prevailed.

Radial ornamentation showed a similar variation in constancy. The atrypoids were normally devoid of radial ornamentation and persistently so in some stocks like the dayiids and lissatrypids, although others (e.g., atrypids) varied from smooth to costellate. Stabilization, however, took place in the retzioids, which were costate to costellate, and also in the athyridoids, which may have been coarsely plicate, as in *Tetractinella*, but almost invariably lacked radial ornamentation. At first sight, the spiriferoids appear to vary greatly, in much the same way as the atrypids, from smooth (elythids and many martiniids) to costellate (exceptionally in the cyrtinids, commonly in the cyrtospiriferids, brachythyridids, etc.). Yet the earliest stocks to some extent were all very finely costellate or capillate, and the fact that traces of this primitive ornamentation have been found in all stocks suggests that the more conspicuous ornamentation, or lack of it, is a secondarily imposed feature.

The shell structure of the Spiriferida is normally impunctate, but, as in the Orthida, the endopunctate condition was commonly attained. Indeed, the group provides very good evidence for both the acquisition and loss of caeca in independent stocks. Thus, the late Silurian to Permian retziaceans were persistently endopunctate, whereas the suessiaceans which first appeared in middle Silurian time, include certain early Mesozoic relatives (e.g., *Hirsutella, Suessia*) that are reputedly impunctate. Similarly the impunctate *Odontospirifer* and Licharewiinae [Syringothyrididae] appear to have arisen from the endopunctate spiriferinids and syringothyridids, respectively; and the su-

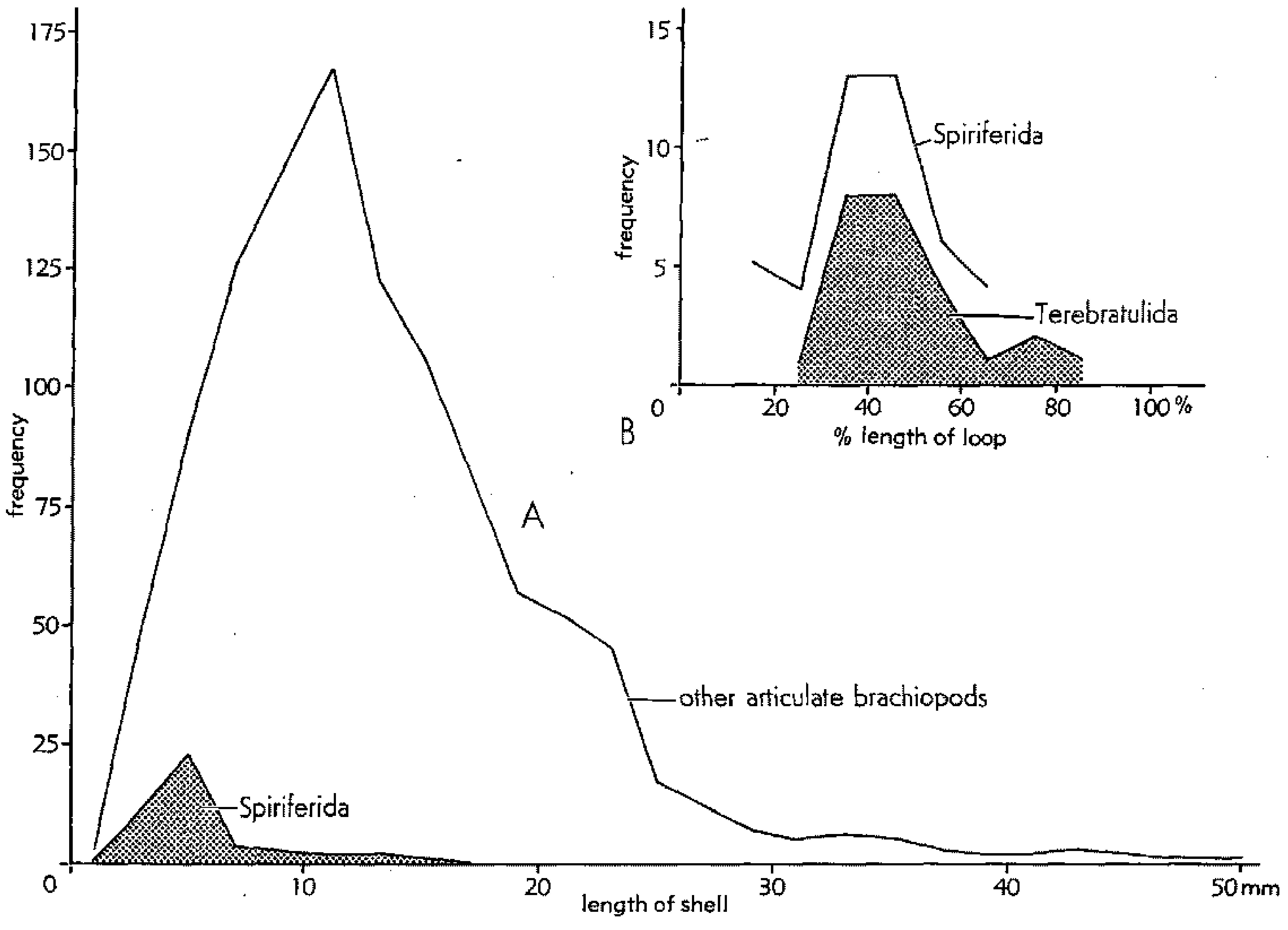

FIG. 143. *A*, Frequency distribution of longest pedicle valves recorded in type descriptions of 46 Ordovician spiriferid species (shaded area) and of 1, 113 other contemporary species of articulate brachiopods (unshaded area). *B*, Frequency distribution of lengths of "loops" (measured from dorsal umbones to posterior edges of transverse bands and juga) relative to length of brachial valves in Silurian and Devonian genera of terebratulids (25) (shaded area) and spiriferids (45) (unshaded area) (50).

perficial pits of the martiniids may be the relics of impersistent caeca.

The spiriferid interior is dominated by the spiralia, which may be disposed at any angle to the median plane of symmetry. Yet, as RUDWICK (33) has pointed out, there are actually a limited number of basic attitudes, only one of which tends to be consistently adopted within an established group, although, as one would expect, all are found in the earliest stocks. The orientations, assumed by the spiralia of *Protozyga* and *Zygospira*, for example, are different enough to have been the sources of all subsequent evolution. In the former, the umbonal blades and at least part of the primary lamellae were aligned parallel with the median plane; in the latter, they were deflected to be more or less normal to the median plane. The zygospirid pattern was probably the model from which all atrypid attitudes were derived by the dorsal or dorsomedian extension of the spires, and also the prototype for the dayiacean spires, which were elaborated by lateral or ventral extension. In most members of the retzioids, athyridoids, and spiriferoids, the umbonal blades and primary lamellae were retained more or less parallel with the median plane, as in *Protozyga*, and the spires extended laterally. Reversions toward the basic zygospirid condition did take place in some younger stocks (e.g., cyrtinids, koninckinaceans) by rotation of the umbonal blades toward the commissural plane. The continued growth of processes from the jugal stem also led to the development of accessory lamellae co-extensive with the primary spiralia in the Devonian Anoplothecinae [Anoplothecidae] (e.g., *Bifida*) and again in the Triassic Diplospirellinae [Athyrididae] and koninckinaceans. But the most astonishing change seems to have affected the leptocoeliids, because no spiralia have ever been seen in any member of this stock, not even in some 200 well-preserved specimens of *Eocoelia* sectioned by NIKIFOROVA (28). Hence, it is possible that the lophophores of leptocoeliids were without the intricate calcareous support of other Spiriferida.

The cardinalia of the Spiriferida were only selectively modified during the evolution of the group. Among the more primitive atrypoid stocks, the cardinalia were usually divided or disjunct and consisted of socket ridges and variably disposed crural plates, which rarely converged to form a septalium in the Septatrypinae [Lissatrypidae], with or without intervening strips of outer hinge plates. Inner hinge plates, becoming conjunct, were developed in a number of independent stocks (e.g., the atrypids *Alispira* and *Gruenewaldtia,* some lissatrypids, and the early dayiacean *Cyclospira*). In most spiriferoids the unspecialized divided cardinalia prevailed, with repeated atrophy or forward growth of the crural plates, because only in spiriferaceans like *Dimegelasma* were the inner hinge plates conspicuously developed. Among the retzioids and athyridoids, on the other hand, the cardinalia not only included conjunct inner hinge plates, but were also consolidated to form a strong cardinal plate. This structure was supported by crural plates in the retzioids, while among the athyridoids it became imperforate (as in the meristellids) and was further elaborated by extravagant forward growth so that it varied from the enlarged concave trough, typical of the meristellids, to the high, recurved plate of the nucleospirids.

Other important internal changes, which were mainly concerned with accommodating the muscle bases, took place only sporadically but did result in the appearance of some unusual structures. The commonest was the growth of a ventral median septum, which was strongly developed in certain spiriferoids (e.g., delthyridids) and is known to have borne muscles in at least the spiriferinids. The tichorhinum of the cyrtinids and a transverse plate of the suessiids, each of which was an outgrowth along the posterior edge of a high median septum, probably received the bases and musculature of pedicles, as did the variably developed syrinx suspended beneath the delthyrial plate of the syringothyridids. True spondylia were rare and included the simplex type found in the reticulariid *Bojothyris* and a structure in *Camarophorella* which simulated the spondylium triplex. In general, the ventral muscle bases of the atrypoids and athyridoids were inserted on the floor of the valve, and any changes in this arrangement involved the secretion of a platform rather than a septum. Thus the muscle bases were accommodated on a solid platform in *Septatrypa* or on a platform supported by septa in *Gruenewaldtia*; but in the dayiacean *Aulidospira* and again in the meristinids, the shoe-lifter process appeared.

Elevated muscle-bearing structures were rarely secreted in the brachial valves. The crural plates were greatly extended in the ambocoeliids and provided a cruralium which was either sessile (e.g., *Metaplasia*) or elevated on a septum (e.g., *Prosserella*). Similar arrangements also occurred in the Meristellinae [Meristellidae] (e.g., *Charionoides*) and suessiaceans (e.g., *Suessia*), but the most unusual structures were the dorsal homologues of the shoe-lifter process which were developed in the brachial valves of the athyridaceans *Dicamara* and *Camarophorinella.*

The Terebratulida are the youngest ordinal group to emerge during evolution of the Brachiopoda, because the earliest known representatives like the stringocephalaceans *Podolella, Mutationella,* and *Brachyzyga* (22) do not appear until the end of Silurian times. In respect of their origin, their most important features include a rostrate, endopunctate shell with variably developed deltidial plates and hinge plates which may unite medially to complete a cardinal plate, well-defined crural processes, and a loop. The loops varied greatly in outline, even within a single species of *Mutationella,* and partly they anticipated the diversity of shapes that were ultimately characteristic of the younger, more stable, Devonian stocks (6). Despite the paucity of information on ontogenetic development of these loops, it can be safely assumed that they were formed by processes of secretion and resorption from a simple, lanceolate centronelliform loop, which is common to the early growth stages of *Cranaena* (37) and *Dielasma* (3). The centronelliform loop is identical with that found in young *Zygospira* shells (3) and is strictly homologous with the *Protozyga* apparatus. It must therefore have given support to a trocholophe or a schizolophe, with the generative zones disposed contiguously about a median plate whenever that structure developed (48). In adult *Rensselandia, Centronella,* and the majority of *Mutationella,* etc., this fundamental lanceolate pattern was retained. A more important modification, however, was manifest in many stocks like *Cranaena, Dielasma,* and a minority of adult *Mutationella.* It was brought about by resorption of the anteromedian part of the centronelliform loop and refashioning of the corroded connection into a transverse, posteriorly curved band making acute angles with the descending branches. This transformation must have been closely comparable with the definition of the spiriferid jugum, and there can be little doubt that those portions of the terebratulid and spiriferid apparatuses lying posteriorly to the band and jugum, respectively, were identical in origin. Even in adult shells the "loops" thus defined by transverse bands, and juga are similar in proportion (Fig. 143).

The terebratulid loop, then, was probably derived from the spiriferid brachial skeleton simply by a suppression of the growth of the calcareous spires. Moreover, since the development of spires was preceded by the secretion of a loop, it may be assumed that the earliest terebratulids were small generalized shells of pre-Ludlow age, barely distinguishable from the juveniles of contemporary, endopunctate, rostrate retzioids with cardinal plates, from which group they were probably neotenously descended (50).

The loop has so dominated the terebratulid interior and has undergone so many complex changes, ontogenetically as well as phylogenetically, that its modification has come to be regarded as the epitome of terebratulid evolution. Certainly the initial diversity and instability of primitive terebratulid loops and the ultimate survival of only the short, terebratulacean and the long, terebratellacean types are classic illustrations of radiation and selection (7). Thus it may be confidently inferred that the retention of an enlarged centronelliform loop which had undergone only minor alterations in shape (e.g., in adult *Rensselandia, Centronella,* etc.) signified the persistence of a trocholophe or early schizolophe, but that the differentiation of a transverse band in the dielasmatids, for example, indicated the beginnings of plectolophous side arms (48). Indeed, Stehli (37) has maintained that there is a direct line of descent from early Devonian, short-looped stocks, like the dielasmatids and cranaenids, to modern terebratulaceans. This phylogenetic link would have incurred little more than the suppression of the lanceolate shape of the first-formed loop of terebratulaceans and in later stocks (e.g., *Terebratulina*) an exaggerated growth of the crural processes so that they tended to meet medially, thereby completing a calcareous ring for lophophore support.

The development and disposition of the short loops characteristic of the terebratuloids have remained remarkably stable throughout time, although some gross changes did occur in the late Paleozoic. In *Centronelloidea* (40), for example, a pair of projections grew anteriorly from the junctions of the descending branches with the transverse band and presumably gave support to the side arms of a plectolophe, as did similar projections in the Lower Devonian stringocephalacean *Cimicinella.* A more profound change found in *Gefonia* and *Timorina* (37, 39) involved the retention in adult shells of a modified centronelliform loop bearing a pair of long divergent processes. The arrangement is unique and, if the generative tips of the lophophore had migrated out of the median plane along with the growing points of the calcareous processes, represented an unsuccessful trend towards the re-establishment of a spirolophous attitude by the lophophore.

The adult loop of a number of Triassic genera (e.g., *Cubanithyris, Nucleatula*) was also typically centronelliform with a ventrally directed plate medially disposed on the echmidium. In *Wittenburgella,* however, this plate extended both ventral and dorsal of the echmidium (12b): and in young *Rhaetina* the dorsal extension is known (12a, 12c) to have united with the floor of the brachial valve, although with further growth the entire vertical plate was resorbed and the echmidium transformed into the transverse band of the adult dielasmatid loop.

Long-looped terebratulids are also found in the Lower Devonian but their relationships with terebratellaceans are more controversial.

It is generally agreed that not all stringocephalaceans equipped with long loops that probably supported a plectolophe were directly related to the terebratellaceans. The side arms of *Cimicinella*, for example, must have been strengthened by a pair of long processes that grew in place of discrete descending and ascending branches, while the medially coiled part of the *Meganteris* lophophore must have been contained between slightly convergent processes originating from the crura. The long slender loop of *Cryptonella*, however, is strikingly like that of Recent terebratellaceans such as *Macandrevia*. Hence Stehli (37) has concluded that the cryptonellids were the ultimate ancestors from which all zeilleriaceans and terebratellaceans were derived, and that the nature of the foramen tends to confirm these inferred relationships.

Further study of Paleozoic terebratulids is required to test the feasibility of this interpretation. As Elliott (13, 15) has pointed out, the first-formed calcareous support for the terebratellacean lophophore has always included a dorsal median septum or pillar upon which the later development of other parts of the apparatus is dependent. Nothing is known of the ontogeny of the cryptonellid loop, although it may well have arisen simply by differential anterolateral growth of a short dielasma-like loop (48). In fact, Cooper (11) has shown that even growth of the loop of late Carboniferous *Cryptacanthia*, which included the differentiation of a hood, did not involve the secretion of any septal support. Stehli (37) has invoked paedomorphism to account for the part played by the median septum in the growth of the terebratellacean loop, and has referred to the discovery by Muir-Wood (24) of a connecting band attached to the descending branch of a young *Digonella*, to support his thesis of the descent of the terebratellaceans from the cryptonellids through the zeilleriaceans. This band, however, was not attached to the median septum, and although it may have been a remnant of connections that existed in earlier growth stages, it does not necessarily indicate a metamorphosis related to that of the true terebratellacean loop. As for paedomorphism, it is well to remember that a plectolophe is normally developed in living terebratulides, irrespective of the nature of the supporting loop, because the generative tips are maintained in the median plane throughout growth (50). Hence, if a plectolophe were to develop, any elaboration of a calcareous apparatus following the insertion of a median septum between the contiguous tips of a trocholophe must include complex processes of differential growth and resorption similar to those affecting terebratellacean loops. Yet the earliest stages in the development of the descending branches up to their fusion with the median septum are the same for both terebratulaceans and terebratellaceans. It is, therefore, even possible that the terebratellaceans arose out of some short-looped stock which was characterized by a slight dorsal shift of the tropholophe and the early and accelerated growth of a median septum and the descending branches.

The phylogenetic importance of the zeilleriaceans has yet to be assessed because even the homogeneity of the group is not beyond dispute. Thus Dagis (12a, 12c) in his study of the ontogeny of the Triassic *Zeilleria moisseievi* failed to find any connection between the loop and median septum, although the loop of the smallest specimen, about 5 mm. long, differed greatly from its adult form. It consisted of broad descending lamellae, fused together anteriorly and bearing a hood in which the elements of wide ascending branches, connected posteriorly by a narrower transverse band, were already discernible. The subsequent growth and resorption of the loop recall characters of *Cryptacanthia*, and earlier development of the loop leading to definition of the hood (although as yet unknown) may also have been comparable. Furthermore, Babanova (1a) has recently described some stages of loop development in three species which she has referred to *Aulacothyris*, a genus which is commonly placed in the zeilleriids. These specimens displayed the characteristic stages of dallinid loop ontogeny, however, and she concluded that *Aulacothyris* should be reassigned to this family. Until more is known of the loop development of genera placed in the Zeilleriidae, the possibility of incorrect familial assignments cannot be ignored and it may be premature to attach too much importance to the presence of connecting bands between the loop and median septum unless a substantial part of the ontogeny is also known.

Whatever the origin of the terebratellaceans, a series of distinct trends affected the metamorphoses and phylogeny of their loops and were due to variations in the rate of growth of the descending branches and in the style of supports arising from the median septum.

In the dallinids, which include the earliest terebratellaceans yet found, the descending branches have always developed early to unite with the sides of a septum that, even in this growth stage, normally bears a hood in the process of differentiation. In the later-appearing terebratellids, on the other hand, the descending branches become ankylosed to outgrowths from the septum and the crest of the ascending branches is fashioned out of a ring, not a hood. In both stocks, the culmination of a series of changes which involve the resorption of the septal support and connecting bands, gives freely hanging recurved loops, although during the proliferation of generic stocks, development was arrested at any stage to provide a variety of adult loops. The most interesting of such retardations were those that gave rise to late Cretaceous *Megathyris*, with its attached loop consisting exclusively of descending branches and supporting a lobate trocholophe, and post-Cretaceous *Platidia*, with its short loop and short discrete ascending branches supporting a schizolophe. Indeed, in both these stocks neotenous effects seem to become increasingly important in Recent times, because the trocholophe of the megathyridid *Gwynia* is unsupported and the brachial valve bears only traces of an attached loop, while the schizolophe of the platidiid *Amphithyris* is supported solely by a median septum.

Neotenous simplification of the adult brachial apparatus has also affected the kraussinids, which first appeared in early Tertiary time out of the terebratellids. In contrast to other terebratellaceans, the descending branches developed later than the septal ring to form an attached loop (as in *Megerlia*) or did not develop at all (as in Recent *Pumilus*), in which the schizolophe is supported by only a low septum bearing a pair of divergent projections. Clearly, the morphology of Recent stocks like *Gwynia, Amphithyris,* and *Pumilus* has become so generalized through neotenous influences that profound internal changes are possible in the future.

In respect of other features, the evolution of the Terebratulida seems to have been as conservative as that of the Rhynchonellida. Trends that led to gross changes in form of the shell of other groups also affected the terebratulids but were, on the whole, rare. The commonest were those that repeatedly gave rise to the intricate folding of the anterior commissure. Rarer changes include asymmetrical growth, which tended to be characteristic of the stringocephalids, deepening emargination that became incorporated as a subcentral hole through pygopid shells by anteromedian union of the shell lobes during subsequent growth; likewise rare is elongation of the ventral umbo (e.g., *Terebrirostra*) and growth of wide hinge lines (e.g., *Antigoniarcula, Megathiris*). Internally, the loss of dental plates in several independent lines of descent, such as later terebratulaceans and the terebratellids, and the less common elaboration of the cardinal process, as in *Stringocephalus* and *Eudesia*, are noteworthy. More important internal changes, however, which included some striking examples of similar, heterochronous trends (Stelhi, 775, p. 196) affected the cardinalia; and, in general, led to the elimination of the cardinal and crural plates so typical of the older stocks.

Any discussion on the origin of the Thecideidina is, at present, compromised by an abundance of imperfectly known or understood facts about living, as well as extinct, species. From its first appearance in the Triassic, the group has been so distinctive morphologically that there has never been much doubt about its homogeneity, but a great deal about its relationship with other contemporary articulate brachiopods. Even more disconcerting are the inconsistencies and obscurities in the only detailed studies ever carried out on the development and anatomy of living *Lacazella* (21, 23). In all thecideaceans, the loss of the pedicle has been accompanied by a growth of the ventral interarea as one piece continuous across the delthyrial region. The median part between the teeth may be gently arched into what is described as a pseudodeltidium, although it is commonly nothing more than a bulge accommodating the high dorsal surface of the cardinal process. Yet nothing is known of the epithelial relationships along the hinge except those inferred by Williams (47).

Kovalevskiy's account of the development of *Lacazella mediterranea* is incomplete and ambiguous. It does indicate that a pedicle rudiment is formed in the larval stages but he asserts that the rudiment of the ventral mantle undergoes atrophy and that ventral shell is first secreted on the dorsal side of the thoracic segment. This is the "third shell" of Beecher, which was believed by him to be a discrete piece, representing the adult pseudodeltidium and fusing only later with the true pedicle valve. Kovalevskiy's diagram showing this stage of development, however, is a longitudinal median profile and, as Arber (1) has pointed out, does not preclude the so-called "third shell" from being simply a stage in the secretion of a pedicle valve that is continuous around a ringlike mantle rudiment without any ventral lobular extension. Indeed, the three most important facts to emerge from Kovalevskiy's description of *Lacazella* embryology are: first, the larval commissural plane divides the mantle rudiment so much more obliquely than in other modern articulates that its posterior trace is entirely dorsal of the pedicle rudiment. Secondly, the pedicle rudiment is supra-apical; and thirdly, only the dorsal segment of the original mantle rudiment undergoes reversal. Excluding the related *Thecidellina*, such characteristics as these are not manifest, as far as is known, in the development of any other living brachiopods; but they are reminiscent of certain phases in the inferred development of the Strophomenida (48). This similarity, however, is as likely to be an expression of convergence, due to independently attained obliquity of the commissural plane and loss of pedicle, as of affinity, and a survey of thecideacean morphology tends to promote the candidature of other groups as possible ancestors to the thecideaceans.

It is generally agreed that thecideacean antecedents are to be sought among articulate groups existing during Permo-Triassic times. Of these, only the Rhynchonellida and the last remnants of the Orthida can be immediately dismissed as unlikely sources, because the thecideaceans have much in common with members of the other orders then extant, *viz.*, the Strophomenida, Spiriferida, and Terebratulida. The loss of the pedicle, the acquisition of a cemented habit, and the development of a strong, wide ventral interarea continuous with the delthyrial cover, are recurrent themes in brachiopod history and are not only typical of late davidsoniaceans and chonetoids but also of some suessiaceans like *Thecocyrtella*. The thecideacean shell is well differentiated into primary and secondary layers, as in the Spiriferida and Terebratulida. It is also endopunctate (14), yet strongly tuberculate internally in a manner suggestive of pseudopunctation. The tubercles, however, also compare closely with those occurring sporadically in *Megerlina* (47), and, in general, the shell structure is more like that of the Spiriferida and Terebratulida than of the Strophomenida.

Internally, the development of posterolateral adductor muscles is unique, but the growth of ridges to support the lophophore has occurred repeatedly in the brachial valve of articulate brachiopods during their evolution. Kozłowski (22) figured an instructive comparison between the arrangement of the lophophore supports of *Lacazella* and *Thecidella* and similarly disposed ridges in the plectambonitacean *Plectodonta*. The partially attached loop of *Megathyris* is another noteworthy homologue, which, moreover, bears an expanded trocholophe with a single row of filaments as in the lobate lophophore supported by the thecideacean apparatus. Such supports as these evidently arise paedomorphically and do not necessarily signify any close relationship. The cardinalia and associated structures, on the other hand, are less equivocal. The thecideacean cardinal process is not an independent outgrowth from the dorsal posterior margin but a single plate formed by the exaggerated posteromedian growth of the inner socket ridges; while the brachial bridge represents the median fusion of processes projecting inwardly from short crura that, in early growth stages at least, are seen to arise from the inner surfaces of the socket ridges. None of these features are found in the Strophomenida but all of them commonly occur together in the Spiriferida and Terebratulida.

The organization of the ventral interior is not very helpful in search for thecideacean antecedents, although the presence of strong teeth suggests that productoids and oldhaminoids need not be seriously considered. In all, even the remaining pseudopunctate groups, the chonetoids and davidsoniaceans, seem less likely to have been the source of the thecideaceans than the terebratelloids or suessiaceans.

The principal changes affecting thecideaceans during their existence led to the elaboration of the apparatus supporting the lophophore, which seems to have taken place independently and heterochronously in a number of stocks (14). The simplest arrangement involved the coalescence of submarginal tubercles and the growth of septa to form a strongly bilobed structure, commonly closed posteriorly by the median fusion of the crural processes. The development of brachial ridges was also common, as well as subsidiary infolds of each lobe, which were either aligned more or less with the median axis, as in *Lacazella* and *Eudesella*, or radially disposed *(Thecidiopsis)*. This variation in pattern must have been accompanied by an identical infolding of a basically bilobed lophophore, which, despite such complications, probably never bore a double row of filaments.

The most significant aspect of any outline of brachiopod history, like the one given above, is the complexity of the inferred relationships within the phylum. Admittedly some complications are attributable to incompleteness of the geological record and an imperfect understanding of shell morphology. Yet the inescapable conclusion remains that the confusing intricacies of the general evolutionary design are mostly expressions of the repeated intervention of the same trends during the development of several stocks. The elaboration of muscle-bearing platforms is a good example of how progressive specialization of this sort contributed to the morphological diversity of many groups, because in varying degree it affected every articulate order, as well as the Lingulida. These recurrent trends, dramatic as they are, have nonetheless tended to obscure the more fundamental changes that contributed to the cumulative morphological drift away from the generalized organization of the earliest stocks. Indeed, when such trends are set aside, it appears that the most profound shifts were the consequence of changes in shell composition, pedicle accommodation, and muscle distribution, and of the introduction of articulation and skeletal supports for the lophophore.

The most important change in the shell composition of fossil brachiopods was that which led to the distinction between shells in which the inorganic content was dominantly either a calcium phosphate salt or calcium carbonate (Fig. 144). It is probably equally significant that the very much higher proportion of organic material in the phosphatic shells of living species contains chitin, which is absent even from the periostracum of modern calcareous shells, and it seems reasonable to assume that this relationship always obtained. Although both shell types occur together in the Lower Cambrian, the chitinophosphatic condition may well represent the more primitive state from which the earliest calcareous-shelled groups, the obolellaceans and billingsellaceans, evolved. This change, which seems to have been irreversible, certainly took place in several stocks during the Ordovician, because (like the relationship between the calcareous craniids and the chitinophosphatic Acrotretina) craniopsids and trimelleraceans can be accounted for only by assuming an independent derivation from the Lingulida.

Despite the polyphyletic origin of the calcareous shell, a subtle differentiation of its structure took place during derivation of the articulate brachiopods, which isolates them from other groups with a similar shell composition. The secondary layer of the articulates has always been secreted intracellularly, at least at the mantle edge, whereas a fibrous secondary shell is unknown among the inarticulates, except for the craniids, where it always has been impersistent and confined to the migratory regions of muscle attachment.

The differences between the endopunctate, pseudopunctate, and impunctate stocks are less important to the main progress of evolution than the attention they have attracted would suggest, because the first two were polyphyletically derived from impunctate ancestors. Indeed, the stabilization of

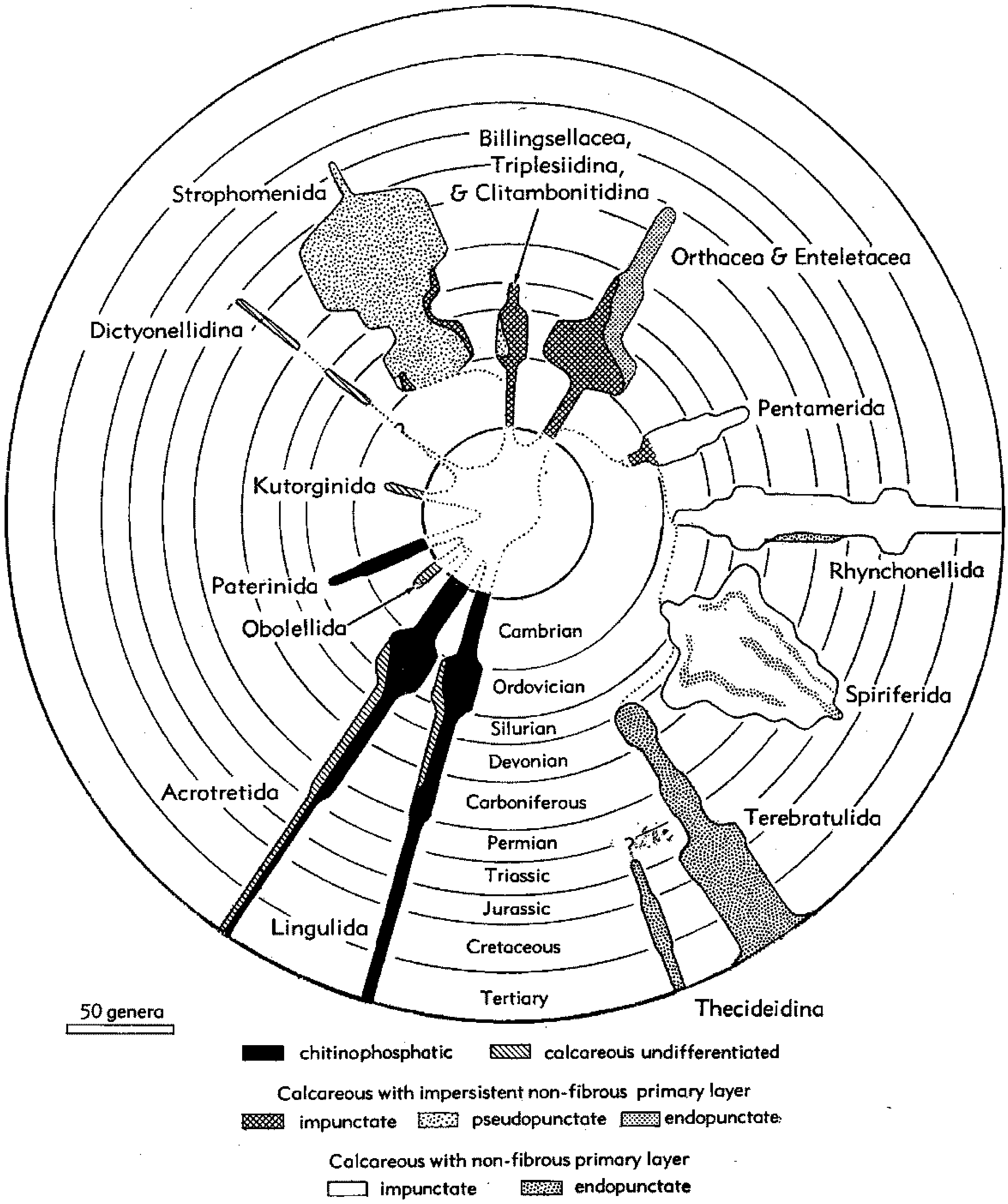

FIG. 144. Variation in shell composition and structure of brachiopod groups (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

a well-differentiated nonfibrous primary layer was probably more significant. The layer seems to have occurred impersistently among the Strophomenida and Orthida; but in at least the later Pentamerida and in all the Rhynchonellida, Spiriferida, and Terebratulida it was invariably present and very well defined (Fig. 144). Hence, if the primary layer of the latter groups is regarded as an inorganic sheet deposited extracellularly to intervene between the periostracum and the secondary shell with its protein sheaths, the course of evolution in shell composition involved the progressive reduction of organic material in the exoskeleton.

In Recent species of the chitinophosphatic Lingulida and Acrotretida, and probably throughout the history of both groups, the

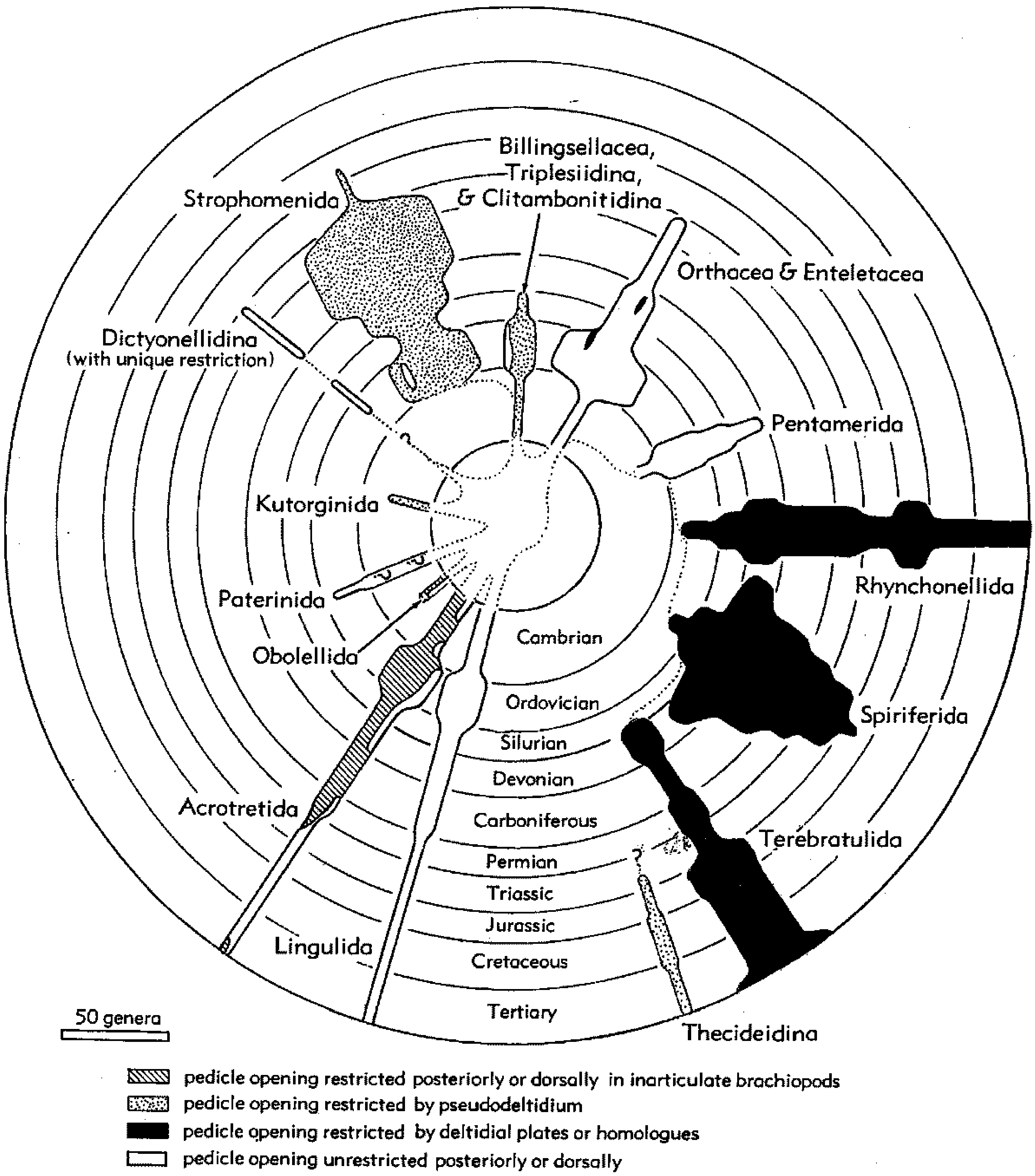

Fig. 145. Variation in structure of pedicle valve of brachiopods accommodating pedicle (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

pedicle is merely an extension of the outer layer of the adult ventral body wall, invariably located within the ventral mantle margin. There is also good morphological evidence for assuming that both mantles were always separated, even posteromedially, by a variably developed body wall of inner epithelium. The mantle edges never fused, but from time to time in some Acrotretida the posteromedian margin of the ventral mantle secreted a strip of shell continuous with the rest of the valve, which restricted the pedicle opening to the apical region of the valve. The most important aspect of this variation is the persistence of the posterior body wall even in stocks having a physically restricted pedicle. The variable accommodation developed for the pedicle of the obolellaceans can be explained in the same way. The paterinaceans present a greater problem because their morphology offers no unique interpretation, but it is likely that they also had a posterior body wall.

The anatomy of living articulates is a less reliable guide to the distribution of soft parts in extinct ancestral stocks, because greater morphological changes took place during the evolution of the class than in the inarticulates (Fig. 145). The pseudodeltidium of the Strophomenida and certain Orthida, for example, cannot profitably be compared even with that of the problematic thecideids. Thus the development of the pseudodeltidium in extinct stocks provided with a functional pedicle must have entailed the existence of a continuous ventral mantle edge, which was responsible for the secretion of shell restricting the pedicle to one valve throughout all known growth stages. There is, moreover, a conspicuous median gap between the pseudodeltidium and chilidium of the billingsellaceans and other primitive stocks, which, since it led into the body cavity, must have been effectively sealed. It is possible that fused ventral and dorsal mantle lobes provided this cover, but in view of the size of the gap in early forms, it is more likely that the mantle edges were not fused, at least over this region, and that the cover consisted of a sheet of inner epithelium suspended between the mantle edges. According to this interpretation, certain primitive articulates may have possessed the homologue not only of the inarticulate posterior body wall but even of the inarticulate pedicle.

The disappearance of the median gap in later Strophomenida may have been associated, as in the tight fit of lingulid valves, with a reduction of the posterior body wall, and the absence of a pseudodeltidium in a few clitambonitoids may have represented a secretory failure of the posteromedian sector of the ventral mantle comparable with that observed in *Discinisca*.

The appearance of the eoorthids marked an important step toward the type of pedicle accommodation characteristic of living Rhynchonellida and Terebratulida. In all such articulates, the growth of restrictive plates and even entire covers to the delthyrium was common enough, but it occurred polyphyletically in several independent stocks and was always a later modification of an open delthyrium (Fig. 145). This homogeneity of basic pattern suggests that in all these groups (Orthacea, Enteletacea, Pentamerida, Rhynchonellida, Spiriferida, Terebratulida) the pedicle developed from a rudiment differentiated in the larval stage, and in absence of the posterior body wall was in contact with both mantle margins, which were fused along the posterior margins lateral of it. The only exception to this arrangement seems to have been the entire pseudodeltidium of the thecideaceans. The embryology of living species is poorly known, but undoubtedly there was an initial differentiation of a pedicle rudiment in the manner of rhynchonellids and terebratulids. The larval commissural plane, however, divides the mantle rudiment (prior to its reversal) so much more obliquely than in other modern articulates that its posterior trace is entirely dorsal of the pedicle rudiment. This rotation of the plane of mantle division and the alleged atrophy of the rudiment of the ventral mantle lobe may be responsible not only for the anomalous structure of the pedicle valve but also for the emergence of a stock bearing such ambiguous morphological evidence of its ancestors.

The acquisition of an efficient hinging device was the most consistent difference between the inarticulate and articulate brachiopods (Fig. 146). Other, cruder forms of pivoting one valve on the other are known among the inarticulates and an analogous modification was evolved in *Linnarssonella*. But unmistakable though weak teeth and sockets bordering the delthyrium and notothyrium, respectively, were developed by the billingsellaceans and persisted throughout the history of the articulate brachiopods with remarkably little replacement or obsolescence, except among the productoids.

In a way which illustrates the interdependence between morphological features, the development of lophophore supports as outgrowths from the dorsal posterior margin, which was exclusive to articulate brachiopods, was related to the stabilization of articulation (Fig. 146).

In the Billingsellacea, Strophomenida, Triplesiacea, Clitambonitidina, and early Orthacea (e.g., eoorthids) the dental sockets were bounded internally by ridges of secondary shell more or less parallel with the hinge line. In remaining articulates, the

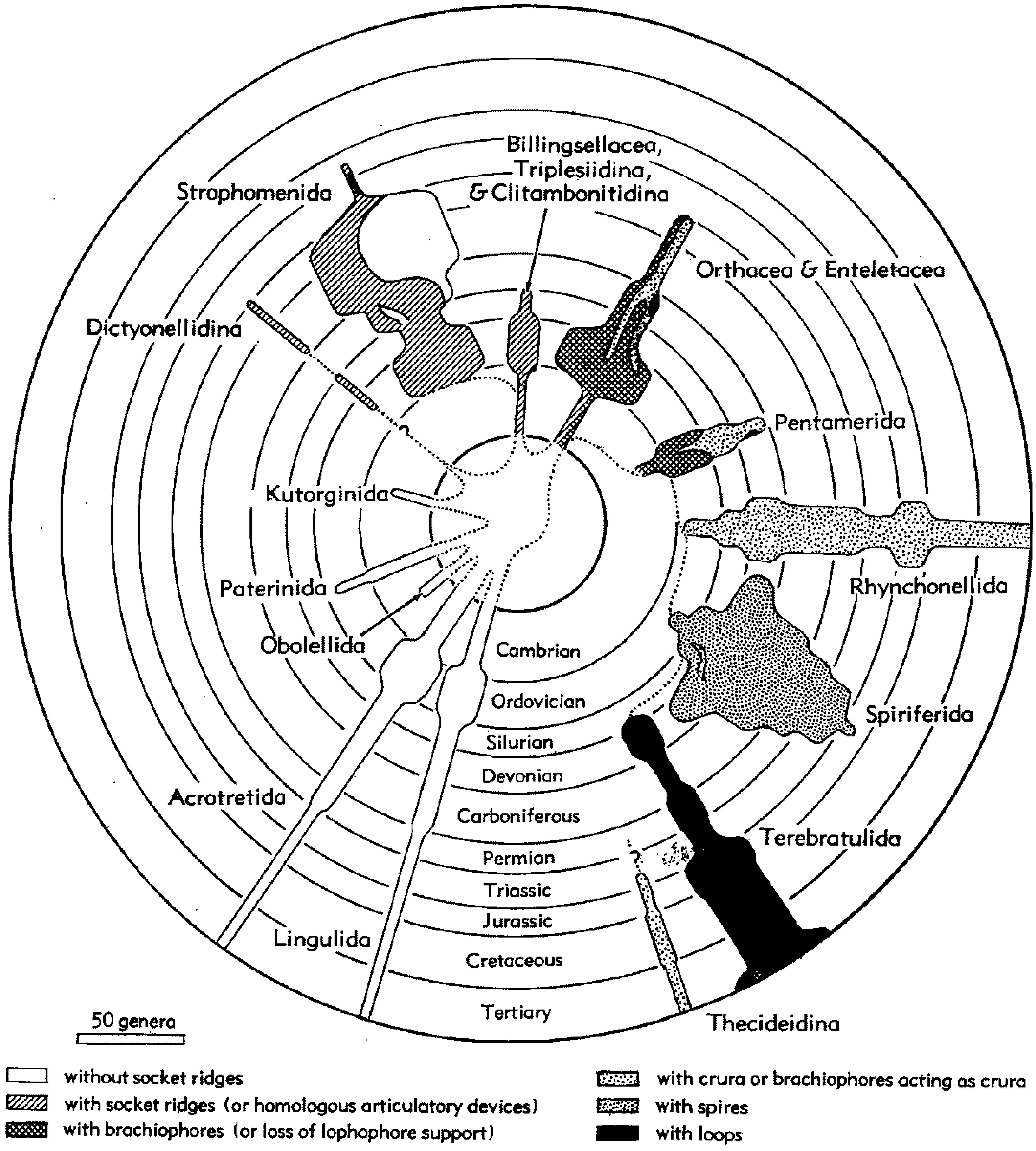

FIG. 146. Diversity of dorsal articulatory devices and associated supports for lophophore in brachiopod groups (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

ridges became rotated toward the median plane and, in addition to functioning as socket boundaries, became extended toward the anterior body wall, where they gave support to the mouth segment of the lophophore. This elaboration of the socket ridges took place independently in some orthaceans and enteletaceans; but in later Pentamerida, Rhynchonellida, Spiriferida, and Terebratulida, it resulted in the appearance of the crura, which, in due course, became further extended into loops and spires. Nothing quite like this arrangement is known among either the inarticulates or the billingsellacean-like articulates in which all plates, platforms, or septa interpreted as lophophore supports grew directly from the floor of the brachial valve. Even the spiralia of the aberrant davidsoniacean *Thecospira* were not suspended from the socket ridges but from the base of the cardinal process. The growth of a dorsal septum to provide some lophophore support also took place in groups equipped with crura or their homologues. It is characteristic of the terebratelloids, for example, and the crura are lost in *Gwynia*, *Amphithyris*, and *Pumilus*, as well as the thecideaceans. In such stocks as these, however, vestiges of the loop or median septum or an elaborate platform, all attached to the floor of the brachial valve, represent only a reversion to the primitive condition.

One of the most interesting consequences of the development of articulation and the crural type of lophophore support was the anatomical reorganization that necessarily took place within the body cavity. Both the distribution and function of the muscle system were greatly affected. Its adaptation to opening and closing the valves exclusively on a lever system about a hinge axis led, in all articulate brachiopods, to the disappearance of the oblique muscles so characteristic of the inarticulates, and in turn to a more median concentration of the attachment bases. Further modification of the system also occurred with the development of a pedicle from a differentiated rudiment, which was accompanied by the attachment of its controlling adjustors not only to the pedicle valve but also to the brachial valve. These systems, whether they included adjustors or not, were initially grouped in such a way as to occupy the delthyrial cavity of the pedicle valve and the notothyrial cavity and posteromedian part of the floor of the brachial valve. This arrangement is typical of the Strophomenida, Orthida, and Pentamerida. The anterior extension of the ventral muscle field well beyond the limits of the delthyrial cavity occurred widely in all three groups, and the common presence of a pedicle callist indicated that the base of the pedicle was depressed relative to the apex of the pedicle valve. Any interpretive reconstructions of the disposition of the muscles in such shells, however, suggest that the base of the pedicle, even when it developed from a rudiment, was never more than a flat sheet extended into ventral and dorsal adjustors. The arrangement found in the Rhynchonellida, Spiriferida, and Terebratulida is strikingly different in that the delthyrial cavity was always occupied by the retractable base of the pedicle and, in consequence, the ventral muscle field was displaced anteriorly. It is significant that this considerable overlap between the posterior region of the shell and the proximal part of the pedicle is seen in young growth stages and represents an incomplete recovery of the mantle subsequent to its reversal. It is therefore feasible to assume that mantle reversal took place only in the Rhynchonellida, Spiriferida, and Terebratulida.

Little can be said about evolution involving anatomical changes apart from those that accompanied revelatory modifications of the shell. It is noteworthy, however, that some evidence concerning the redistribution of organs within the body cavity can be got from a study of the impressions of mantle canal systems, especially with regard to position of the gonads. Thus, it is significant that in living chitinophosphatic brachiopods the gonads are carried on the mesenteries well within the body cavity. Assuming this location to be the primitive one, the first important changes are seen to have occurred in the early articulate brachiopods, like the billingsellids and huenellids. In these, and apparently without exception in all articulate brachiopods, part or all of the gonads migrated out of the body cavity initially to occupy posterolateral pouches within the mantles. Already, as in the dorsal mantles of early stocks, the pouches were beginning to branch and subsequently they provided terminal canals for increasing arcs of the mantle edges, with a concomitant reduction of the principal circulatory canals. This change, therefore, which took place independently in most stocks, resulted in structures that performed the dual function of storing gonads and circulating the body fluid. Such economy was achieved independently in many groups (e.g., clitambonitoids, spiriferids, terebratulids) by total reduction of the primitive gonadal sacs to slender, radiating canals so well integrated with the mantle canal systems generally that, as in the terebratelloid *Fallax*, gonadal cords are also present in the *vascula media*. This series of changes did not, of course, take place uniformly. The primitive gonadal sacs, for example, are retained in living rhynchonellids, whereas the sex organs of the inarticulate craniids protrude into radiating canals within the mantles in the manner of more advanced articulates.

Two other important anatomical differences, seen in Recent brachiopods but unlikely ever to be confidently inferred from shell morphology, are worth a brief note.

It has been claimed that certain external openings, located posteromedially in the brachial valves of some Paleozoic articulate brachiopods, accommodated the anus in various stages of atrophy, thereby providing a link between living representatives of the two classes. The perforations may be either the median gap in a bilobed cardinal process or an imperfectly sealed cardinal plate. The impersistency of these holes, even in members of the same stock, and the secondary nature of their origin seems to preclude such a function. It is likely, therefore, that they were covered by periostracum or an extension of the pedicle cuticle.

The last important anatomical difference between living chitinophosphatic and calcareous-shelled brachiopods concerns the arrangement of the lophophore filaments. In the former group, both ablabial and adlabial filaments are present throughout all growth stages of the lophophore. In the latter, the ablabial set is absent in the trocholophe (the filaments of which are exclusively adlabial and disposed in a single row), appearing only with onset of the schizolophous condition. Assuming that the invariable presence of paired filaments is the more primitive condition, the arrangement characteristic of living articulates could have evolved by suppression of the outer ablabial filaments during the trocholophous stage of development. Such a trend is carried to its conclusion in the lophophores of living megathyridids and thecideids, which bear only adlabial filaments even in adult stages of growth. Nothing, of course, is known about the filament arrangement in extinct groups, but changes like those referred to must have occurred at least twice, because the filaments of the craniid trocholophe are also adlabial and disposed in a single row.

In summary, it may be said that four morphological characteristics, each really an assemblage of features, help to distinguish articulate from inarticulate brachiopods. They are (1) shell composition and structure, (2) articulation by teeth and sockets, (3) lophophore support from the posterior margin of the brachial valve, and (4) distribution of the musculature. Two inferences based on known anatomical distinctions may also be considered because they complete a gradient of change linking modern inarticulate and articulate brachiopods. They depend upon interpretations of the delthyrium and its various covers and on the location of muscle bases in extinct stocks. If they are correct, they give some indication of the nature of the pedicle and the occurrence of mantle reversal during early postlarval stages of growth.

The morphological differences do not coincide entirely with the conventional systematic boundaries between the two classes. The musculature of the Paterinida, for example, is not distributed peripherally within the inferred body cavity in the manner of orthodox inarticulates, and the typical articulate lophophore support is only rarely developed in the Orthida, Strophomenida, and early Pentamerida. The two inferences certainly conflict with present class groupings. They have led to the assumption that the pedicle of the Billingsellacea, Clitambonitidina, Triplesiacea, and Strophomenida arose from the ventral body wall in the inarticulate fashion. It is also believed that mantle reversal was first introduced into articulate ontogeny during the evolution of the Rhynchonellida (Fig. 147).

These conclusions emphasize the basic homogeneity of the phylum and show how living articulate species represent the culmination of divergence from ancestors close to primitive inarticulates. Hence, if the Cambrian chitinophosphatic forms were nearer the archetypal brachiopod than any other contemporary stocks, five structural grades may be distinguished as follows: (1) The first group comprises the Obolellida, Acrotretida, and Lingulida, which were involved only in the acquisition of a calcareous shell in some groups. (2) The Paterinida stand alone among the inarticulates in showing some regrouping of the muscle bases toward the median areas of the shell, although their scars are inadequately understood. (3) The Billingsellacea, Clitambonitidina, Triplesiacea, and Strophomenida make up a third group, which acquired a calcareous shell with an intercellularly se-

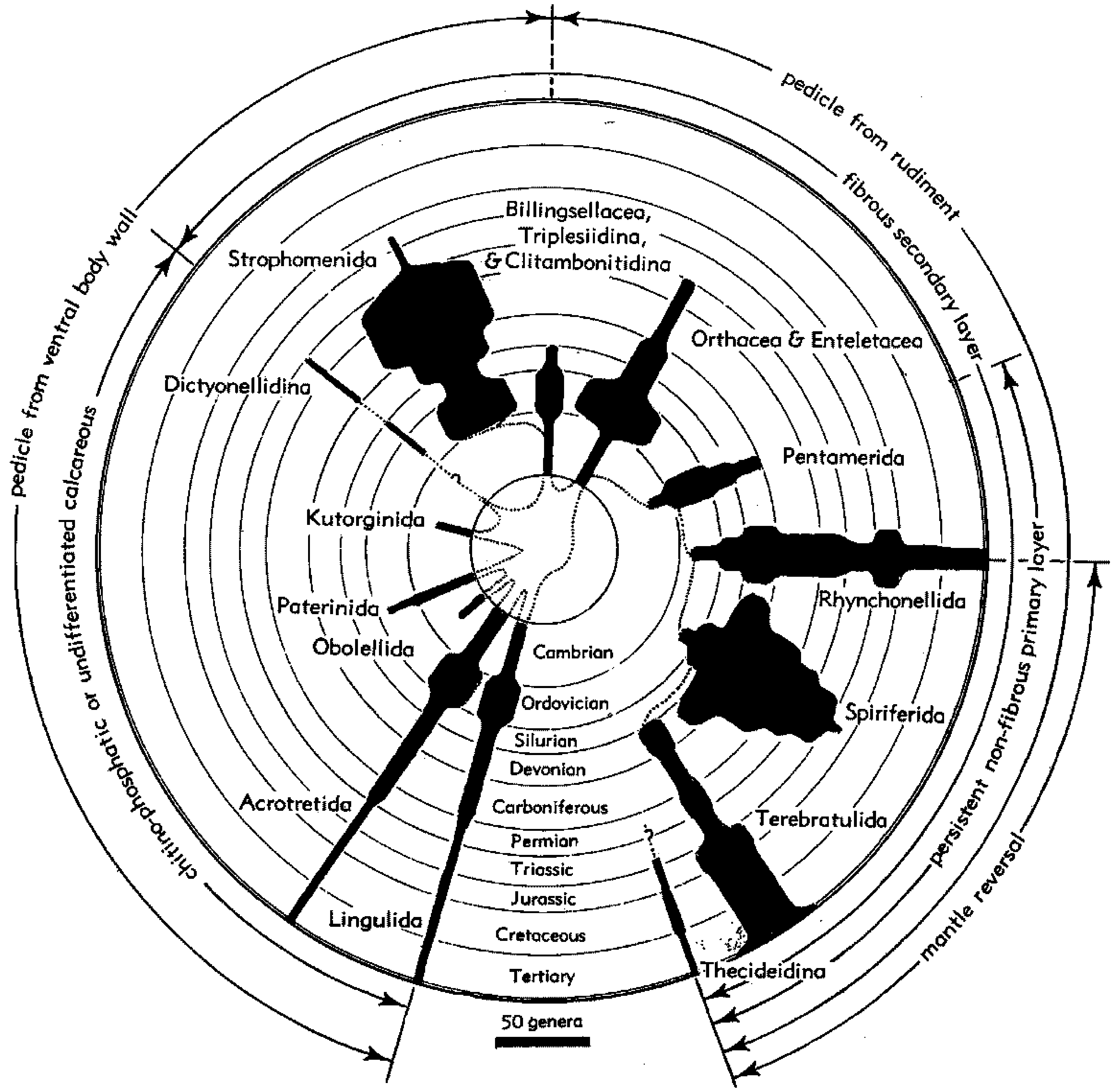

Fig. 147. Phylogeny of Brachiopoda with indications of some principal features developed during evolution (thickness of plot for each group approximately proportional to average number of genera in each system) (54).

creted secondary layer but a sporadically developed nonfibrous primary layer, teeth and sockets, and a medially arranged muscle system without obliques. (4) The fourth group includes the Orthacea, Enteletacea, and Pentamerida, with the pedicle originating from a differentiated rudiment of the larva; both a persistent primary layer and fully developed crura (or homologues) appeared in some of the later orthaceans and enteletaceans and all later Pentamerida. (5) Lastly, as a climax to all earlier changes, a persistent primary layer, functional lophophore supports (rarely secondarily lost) and mantle reversal became characteristic of all Rhynchonellida, Spiriferida, and Terebratulida.

In general, these grades can accommodate all members of the phylum, although there are three small stocks the precise affinities of which have yet to be decided. The Kutorginida include a few Cambrian genera with a superficial resemblance to the billingsellaceans; but teeth and sockets have never been identified positively in them, and the internal impressions, although including elements that are medially disposed, are unlike those of any articulate. They may have originated independently of all known articulate and inarticulate stocks. The Dictyonellidina are likely to have developed from some articulate ancestor, as yet unidentifiable, possibly through gross paedomorphic changes in the early eichwaldiids.

The origin of the thecideaceans presents a similar problem, mainly due to alleged anomalies in their development and to their cemented habit and supposed strophomenoid shell structure and pseudodeltidium. In fact, these features either have been mistakenly interpreted or are not as important in deciding the affinities of the group as they seem to be, and it is quite possible that the group was derived paedomorphically out of the suessiaceans or terebratuloids.

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ADDITIONAL SOURCES OF ILLUSTRATIONS

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ECOLOGY AND PALEOECOLOGY

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INTRODUCTION

Living brachiopods are comparatively rare and insignificant members of the faunas of the present day, and their study has therefore been neglected by zoologists. This neglect is especially serious in the field of ecology. Few Recent species have ever been observed alive, and fewer still have been the subject of any thorough ecological analysis. Most of our information is fragmentary, and comes from widely scattered sources, such as accounts of dredging operations, systematic descriptions of species, etc. In this chapter, therefore, all statements about the ecology of brachiopods include the implicit qualification that they are true only as far as our extremely imperfect information extends.

This neglect of brachiopod ecology is reflected in the poor quality and dubious validity of much published work on their paleoecology. Many conjectures about the paleoecology of brachiopods have been made in apparent ignorance of the physiology, life habits, etc., of living species, or even in ignorance of their basic anatomy. Other work purporting to deal with their paleoecology merely records characteristic assemblages of species, characteristic associations between species and their enclosing sediments, or characteristic patterns of geographical distribution. Without any truly ecological interpretation, such records cannot be regarded as more than raw material for future paleoecological work.

In these circumstances, a brief account of the ecology and paleoecology of brachiopods cannot hope to be definitive, and will necessarily be fragmentary and uneven in its coverage. Most generalizations about the ecology of the phylum will unavoidably represent no more than our knowledge of one or a few species. Even the limits of "ecology" are debatable. Here it is taken to include at least some aspects of the physiology and functional morphology of brachiopods (i.e., "autecology"). The relation of individual brachiopods to each other, to other organisms, and to the general inorganic environment (i.e., "synecology"), about which even less is known, is treated much more briefly.

Almost all living brachiopods are marine, benthonic, epifaunal, sessile suspension-feeders. This mode of life probably has been characteristic of the phylum as a whole throughout its history. A few brachiopods, however, seem to have modified it in one direction or another. A few were probably epiplanktonic and a few possibly nektobenthonic. Some may have become deposit-feeders or even in a limited sense carnivores. Some were virtually infaunal, and a few still are. Probably none has ever invaded any truly nonmarine habitat.

RELATION TO SUBSTRATUM

Most brachiopods are and were sessile benthonic organisms. Their relation to the substratum is therefore of the greatest ecological importance and is reflected in many major features of morphology. All living brachiopods are permanently attached to the substratum, generally by a pedicle, more rarely by cementation of the ventral valve. Unlike byssally-attached bivalve mollusks, there is no evidence that any brachiopod (except possibly a lingulid) can change its position of attachment after the larval stage, or that if uprooted it can re-establish itself elsewhere.

The pedicles of inarticulates and articulates differ in structure and embryonic origin, and are evidently not homologous, but in most respects they are functionally equivalent.

The pedicle of an articulate develops from the caudal segment of the larva. It is a tough, solid, "cartilaginous" cylinder, covered with a thick chitinous cuticle. Its distal end is attached very firmly and rigidly to the material of the substratum, presumably by a sticky secretion. Its proximal end projects through the posterior body wall into the cœlom. Obliquely inserted pedicle muscles connect the pedicle to the inner surface of the valves. Their contraction enables the whole shell to be rotated laterally and to a lesser extent dorsoventrally around the immobile pedicle.

The pedicle of an inarticulate brachiopod develops from the posterior edge of the ventral mantle, the caudal segment being unrepresented in the larva. The inarticulate pedicle is a highly muscular cylinder with a central lumen connected to the cœlom. Its distal end is firmly attached to the substratum by a sticky secretion; proximally it remains intimately connected to the ventral mantle. There are no pedicle muscles external to the pedicle, but the muscle fibers within the pedicle serve the same function, enabling the shell to be rotated, elevated, or depressed relative to the substratum (the central lumen acting as a hydrostatic skeleton for extension of the pedicle).

In most living brachiopods, both inarticulate (e.g., *Discinisca*) and articulate (e.g., most Terebratulida), the pedicle is very short, and the shell is closely attached to some material on the substratum. The pedicle not only acts as an anchor, but also supports the weight of the shell and holds it in position relative to the substratum. The pedicle has this dual function even in the early growth stages, immediately after the larva has settled; and there is good reason to regard it as the "standard" mode of attachment to the substratum. Most living species seem to require, or at least to prefer, a hard material for attachment, such as a surface of rock, shell, or coral. Thus many species are most abundant on bottom environments such as boulders or stony gravel, coarse shell gravel, or coral debris. On bottoms of finer-grained sediments, such brachiopods would be restricted to sites of attachment such as shells or other fragments of hard material. It is possible that many fossil brachiopods were so restricted. Specimens are occasionally found in their position of life, with the pedicle foramen pressed closely against the surface of another shell (14), or lying in a cluster around an isolated pebble.

At least a few living brachiopods (e.g., *Kraussina*, *Terebratulina*, *Magasella*) are able to attach themselves to "soft" materials such as algal stems, ascidian tests and "horny" worm tubes. These and other organic materials would not normally be preserved in the fossil state; therefore, after death the brachiopod shells might be buried in a soft muddy sediment without preserving any trace of the original material of attachment. This probably accounts in part for the abundance of fossil brachiopods in fine-grained sediments.

Another explanation of the same fact is that the pedicles of many brachiopods may have been adapted to anchor the shell directly into the sediment itself. This is known in a few living species. The pedicle is relatively long, but like those of more normal brachiopods it serves to anchor the shell and hold it in position close to the surface of the substratum. In a few articulates (e.g., *Terebratulina*) the distal end of the pedicle is split into fine rootlets, which are apparently able to perforate calcareous material by means of an acid secretion. In *Terebratulina* the rootlets can penetrate the shell fragments in a fine shell gravel; in *Chlidonophora* the pedicle is even longer and more finely divided, and the rootlets penetrate the tests of *Globigerina* within a soft substratum of *Globigerina* ooze. Pedicles with branching rootlets leave no distinctive trace on the shells of brachiopods, and may have been much more abundant among fossil brachiopods than they are among living species.

The pedicles of living lingulids are also able to anchor the shell into soft sediment (e.g., sandy mud), not by divided rootlets but by a sticky secretion from the whole distal surface of the pedicle. Although at the present day this kind of pedicle is closely related to an aberrant infaunal mode of life, it is possible that some fossil lingulids (and perhaps other inarticulates) were attached epifaunally by similar pedicles.

It is possible that the pedicles of a few articulates and inarticulates were attached to "soft" materials not on the sea floor but in the surface waters. This epiplanktonic mode of life has been suggested principally for a few species (chiefly *Lingulida, Acrotretida, Rhynchonellida*) which are found in "black shale" and similar facies. They are accompanied by few if any other organisms that were certainly benthonic, and there is good evidence that the sediment accumulated in anaerobic conditions; they may have been attached to floating vegetation.

Any pedicle that actively supports the whole shell must be relatively stout, whether the attachment is to hard or soft materials. In a fossil shell this is shown by a relatively large pedicle foramen. On this criterion there is little doubt that the "standard" mode of attachment has been extremely common throughout the history of the phylum. Most other varieties of attachment or support seem to be derived from the standard mode, the pedicle being supplemented or replaced by other structures during ontogeny (13).

One very common derivative involves the use of shell material to weigh down the posterior end of the shell. In many living articulates (e.g., *Gryphus*, *Neothyris*) the shell is thickened internally in the umbonal region in such a way that it retains its orientation relative to the substratum even if the pedicle attachment is cut. The pedicle has thus lost much or all of its supporting function, but it retains its function of anchorage. Such shells are effectively tethered by the pedicle and cannot be swept away by currents or wave scour; yet the shell is maintained in its orientation without the tonic contraction of the pedicle muscles. In fossil shells this mode of support is shown not only in the posterior thickening of one or both valves, but also in the relatively small size of the pedicle foramen; in an ontogenetic series the foramen can be seen to have failed to enlarge in proportion to the growth of the whole shell.

In the ontogeny of many fossil brachiopods this process was carried to completion, and the pedicle finally atrophied. This is shown either by the gradual shrinking and final plugging of the foramen, or by a progressive incurving of the ventral umbo and final blocking of the foramen. After atrophy of the pedicle, the shell must have been maintained both in orientation and in position on the substratum purely by means of its weight. Such shells would be nominally "free" and unattached, but probably they lay immobile on the surface of the substratum or with the umbonal region slightly buried. With the posterior side downward, most of the commissure would have been held clear of the substratum in an oblique or even vertical plane.

Some brachiopods with reduced or atrophied pedicles seem to have developed other structures, in addition to or in place of shell thickening, as means of maintaining the position and orientation of the shell on a soft substratum. Thus the long lateral alae of some spiriferoids (e.g., *Mucrospirifer*) may have had a ski-like function, spreading the weight of the shell over a greater area of the substratum. In some other spiriferoids (e.g., *Cyrtia, Syringothyris*) the ventral cardinal area was modified into a broad flat base, which could have had the same function. In one genus *(Syringospira)* the area of this flat base was increased still further by the development of thin lateral frills. Frills that extend all around both valve edges (e.g., *Atrypa*) can also be interpreted, though perhaps with less confidence, as structures for supporting the shell on a soft substratum.

In most Strophomenida the pedicle (inferred from its foramen) ceased to grow or atrophied altogether at a very early stage in ontogeny, and the shell must have become free while still quite small. Generally there was a concurrent development of a gently concavo-convex shell form. This was probably an adaptation for lying freely on a soft substratum (24). By passing through the phase of pedicle attachment at an early stage of growth, even small fragments of shell, etc., would have been adequate as sites for initial settlement of the larvae; but thereafter the brachiopods would have been independent of any attachment materials whatever. With the shell lying on its convex valve, the commissure would have been held slightly above the surface of the substratum. If overturned by bottom currents, a vigorous "snapping" of the valves could have turned the shell back into its original orientation; if covered with sediment, a similar reaction would lift the shell off the substratum or at least shift it posteriorly into a different position. Such movements can be proved possible by experiments with working models, and they would be analogous to those known in living pectinid mollusks. It is even possible that, like some pectinids, various Strophomenida with gently concavo-convex shells may have been able to swim, if only as an occasional protective reaction to escape from potential predators.

But most Strophomenida passed during ontogeny from a gently to a strongly concavo-convex shell form (the change, if fairly sudden, being shown by geniculation of the shell). This probably represents a reversion to a sessile or immobile mode of life. The shell was probably large and heavy enough, commonly by great internal thickening of one or both valves, not to be overturned by any currents; the commissure could have been held slightly above the surface of the sediment, while allowing the convex valve to become quite deeply sunk within it. Some of the thinner and lighter shells may in effect have "floated" in a semiliquid sediment of very fine mud or ooze. Strongly concavo-convex shells are especially characteristic of the productoids, but they occur in many other Strophomenida, and occasionally are found in other articulate groups (e.g., *Koninckina, Amphiclina*). Some markedly plano-convex shells (e.g., *Productorthis, Ambocoelia*) may have had the same habit. The position of living productoids in particular has been the subject of much speculation (15, 21), since they differ from modern brachiopods perhaps more widely than any other extinct group. It is now fairly certain, however, that all strongly concavo-convex brachiopods must have lived in the manner described above; only by resting with the convex valve on or in the substratum, and with the commissure therefore held clear of the substratum, would they have been able to feed and to respire. At least some of them, as suggested above, may have adopted a virtually infaunal mode of life, with only the margins of the valves projecting above the surface, and perhaps with the concave valve itself filled with sediment. In such a position the brachiopod would have been well protected from predators.

The cemented brachiopods show a series of adaptations parallel to those found in pedicle-attached groups. Cemented brachiopods are represented today by both inarticulates (e.g., *Crania*) and articulates (e.g., *Lacazella*). The shell material secreted by the ventral mantle is laid down in intimate contact with a hard substratal material. In *Crania* the larva settles at an early stage of development, and becomes cemented immediately by the ventral protegulum; a pedicle is never developed. In *Lacazella* the larva settles by its caudal segment as in other articulates; the later stages of growth have not been fully described, but the larval pedicle must be replaced very soon by cementation of the ventral valve, for no trace of a pedicle foramen can be seen on the adult shell.

Initially, the ventral mantle edge remains in contact with the substratum, so that the whole surface of the ventral valve is cemented. In a few brachiopods (e.g., *Crania, Davidsonia, Poikilosakos, Leptalosia*) this simplest variety of cementation is or was retained throughout life. This undoubtedly provides the strongest form of attachment known in brachiopods (it is significant that *Crania* occurs in more strongly current-swept environments than any other living brachiopod). But such attachment is restricted, of course, to hard materials (generally rock surfaces or shells, but exceptionally stems of crinoids).

More usually the ventral mantle-and-valve edge rises away from the attachment surface at some stage in ontogeny, leaving an area of cementation around the ventral umbo. This may give a relatively weaker attachment than complete cementation, but it also raises the commissure away from the substratum. This variety of cemented attachment is common among the Craniacea, Thecideacea (including the living *Lacazella*), Davidsoniacea, and Lyttoniacea. In the Strophalosiacea the initial cemented attachment was generally supplemented by a series of struts or props, formed by tubular rhizoid spines (outgrowths of the ventral valve edge) which are themselves cemented distally to the substratum (e.g., *Aulosteges, Heteralosia*). This allowed the commissure to be raised from the substratum without sacrificing the strength of attachment.

The coralloid shell form can be regarded as an extreme development of this mode of attachment. The ventral valve became deeply conical in shape; it was cemented by its apex, and also (in Strophalosiacea) by a tangle of rhizoid spines. Occasionally these shells even formed reeflike masses. The dorsal valve was reduced to a lidlike operculum (e.g., *Scacchinella, Gemmellaroia*) or modified still more radically (e.g., *Teguliferina, Richthofenia*).

Many brachiopods passed through a cemented stage but later outgrew the cemented attachment and lay freely on or in the substratum. As in shells attached initially by a pedicle, this development is commonly associated with the concavo-convex shell form (e.g., *Oldhamina, Bactrynium*). The initial cementation is shown by an attachment area at the ventral umbo. In Strophalosiacea the rest of the ventral valve commonly bears spines of various kinds (e.g., *Strophalosia, Institella*). Some such spines, but not necessarily all, may have served to root the shell firmly into a soft substratum.

This habit was more characteristic of the Productacea. Their initial attachment by the ventral umbo was generally superseded at a very early stage, and in some may have been omitted altogether. In the next stage of growth they were commonly attached, by a ringlike pair of small clasping spines, to some slender cylindrical object (e.g., crinoid stem, spine of another productoid, or perhaps a plant stem or some other unpreserved object). But generally the shell seems to have outgrown even this attachment at a fairly early stage of growth, and thereafter it probably lay, like other concavo-convex shells, with the ventral valve resting on or floating in the soft or loose substratum. Its stability in this position was commonly aided by the development of rhizoid or halteroid spines, which probably penetrated the sediment or became entangled in it, or perhaps extended across its surface. The vermiform spines found in the concave dorsal valves of a few productoids (e.g., *Dasyalosia, Echinauris*) could have helped to retain sediment within the dorsal valve, so that only the valve edges projected visibly above the surface of the substratum.

This virtually infaunal mode of life is analogous to that of the only fully infaunal brachiopods, the lingulids. Although they are perhaps the most intensively studied living brachiopods, they are also some of the most aberrant of all brachiopods, living or fossil. Living lingulids build deep vertical burrows, generally in sandy mud, and are attached to the base of the burrow by the distal portion of the long muscular pedicle. The shell is held vertically within the burrow, with the anterior edge scarcely projecting above the surface of the substratum (3). When the lingulid is disturbed, contraction of the pedicle withdraws the shell into the deeper part of the burrow. Fossil lingulids preserved perpendicular to the bedding have been recorded from as far back as the Ordovician, and indicate the same highly aberrant mode of life (9). It is not certain, however, that all lingulids were infaunal burrowers; this mode of life is not reflected in any distinctive feature of the shell itself, and many fossil lingulids may have been epifaunal.

SENSORY AND PROTECTIVE MECHANISMS

Living brachiopods have only one protective reaction in response to unfavorable circumstances in the external environment. The valves can be closed rapidly and tightly by contraction of the adductor muscles.

As in bivalve mollusks the adductors are differentiated into "quick" and "catch" portions; in at least some species these are composed of striated and unstriated muscle respectively. In inarticulates it is the anterior adductors that are divided into two portions; in articulates the anterior adductors are "quick," the posterior adductors "catch." The "quick" muscles snap the shell shut; the "catch" muscles, contracting more slowly, then hold the valves firmly together. When the shell is closed the valve edges fit tightly together along the commissure, sealing all the living tissues of the body (except the pedicle) from contact with the environment. The brachiopod can survive for periods of at least several hours with the shell tightly closed. It is significant that such tightly fitting valve edges have only rarely been abandoned in the history of the phylum (e.g., Teguliferinidae, Richthofeniidae, Oldhaminidina). The closure of the shell may be accompanied by a movement of the whole shell on the pedicle, drawing the shell nearer the substratum or (in lingulids) into its burrow, or merely rotating it into a different orientation.

This protective reaction is evoked by the stimulation of sensory mechanisms. In living brachiopods the sensory receptors seem to be confined to the extreme edges of the mantle lobes (and possibly also the pedicle). No special receptor organs have been discovered, but the mantle edges are sensitive to light, touch, and chemical stimuli. They are richly supplied with nerves leading to the central ganglia, through which there is a simple reflex circuit to the adductors. Under natural conditions a protective closure of the shell is produced, for example, in response to a shadow falling on the shell, or to a moving organism touching the shell. Clearly this serves to protect the brachiopod from potential predators or other organisms that might interfere with its delicate feeding mechanisms. In addition, the mantle edges seem to be able to detect water that is highly turbid, brackish, or poorly oxygenated.

These mechanisms are essentially uniform in all living brachiopods, and it is reasonable to infer that they were also common to all fossil brachiopods. The tightly fitting valve edges, and the scars of the adductors, are of course preserved. Among articulates the common twofold division of the adductor scars suggests that the muscles were differentiated into "quick" and "catch" portions as in living species. Many modifications of the valve edges of fossil brachiopods can be interpreted as adaptations of the sensory mechanisms at the mantle edges. In a few rhynchonelloids (e.g., *Uncinulus, Hypothyridina*) the valve edges are modified into uniformly spaced internal spines, which could have covered the apertures of the open shell with a sensitive "grille." In a much larger number of rhynchonelloids, but also in members of many other articulate groups, the valve edges are modified into distinctive zigzag forms; this could have reduced the distance between the sensitive mantle edges without any corresponding reduction in the area of the apertures (20). Although many varieties of tubular external spines were used for attachment and support, some others apparently were not, and may have functioned as sensitive "antennae," for at their open distal ends the sensitive mantle-edge tissue would have been extended outward from the rest of the shell. Examples of possibly sensory spines include the fine prostrate spines of many productoids, the posterior spines of most Chonetacea, and the tubular spines of a few other articulates (e.g., *Acanthothiris*). The long narrow extensions of the valve edges in the homeomorphic genera *Tetractinella* and *Cheirothyris* could have had a similar function.

The chitinous setae that project from the mantle edges of most living brachiopods serve to extend the tactile sensitivity outward from the mantle. Generally the setae are short, merely forming a fringe around the edges of the apertures. In a few genera (e.g., *Discinisca, Notosaria, Terebratulina*) the setae are much longer, and cover the apertures with a sensitive grille. The spacing of such setae determines the maximum size of objects that can approach the apertures without causing a protective closure of the shell. During growth of the brachiopod the spacing of the setae is kept fairly constant by intercalation of new setae. In *Terebratulina* the setae correspond in position to the growing edges of the external costellae. The spatial pattern of branching costellae on the valve surfaces therefore reflects precisely the temporal pattern of growth and intercalation of the array of setae. Similar patterns of branching costellae on the valves of many fossil articulates (especially Orthida and Strophomenida) probably reflect the existence of similar grilles of sensitive setae. But not all costellae in living brachiopods correspond in position to the setae (e.g., *Notosaria*). Other evidence of marginal setae in fossil brachiopods is shown occasionally by internal grooves shaped like the setal follicles of living brachiopods. In exceptional conditions the setae themselves have been preserved. A few living brachiopods (e.g., *Crania, Lacazella*) have no setae at all; they may have been lacking in earlier Craniacea and Thecideacea, and perhaps also in other groups. The setae of lingulids are highly specialized; not only are they sensitive, but they are also equipped with a complex musculature and are used in the maintenance of the burrow and to form siphon-like apertures (3).

FEEDING AND DIGESTION

As in other sessile invertebrates, organs of feeding are elaborate and conspicuous parts of the body and are of great ecological importance. The lophophore is never preserved in fossil brachiopods, but indirect evidence of the feeding system is shown in many important features of morphology.

All living brachiopods are ciliary suspension-feeders. The lophophore acts as a combined pump and filter. Its ciliated filaments divide the mantle cavity into separate inhalant and exhalant chambers; when the shell is open they also divide the gape between the valve edges into separate inhalant and exhalant apertures. The lateral cilia on the filaments draw water from the inhalant into the exhalant chamber, and thus create a one-way circulation of water currents, the current system, through the mantle cavity (19). As the water passes between the filaments, many of the suspended particles collide with the filaments and are carried by frontal cilia to the food groove at the base of the filaments. Cilia in the food groove transport the particles along the brachium to the mouth. There is no qualitative sorting of the particles; the material reaching the mouth may therefore include a high proportion of silt or other material without food value. The food particles are chiefly diatoms and dinoflagellates.

The ingested material passes through the esophagus to the stomach. From here it is sucked by muscular action in and out of the diverticula ("liver"), where most of the digestion takes place (4). The digestion is mainly intracellular, though phagocytes may be important. Undigested material is returned to the stomach and passed on to the intestine, which contains a rotating thread of mucus (but not a crystalline style) and is probably concerned chiefly with the consolidation of rejected material into fecal pellets. In inarticulates the pellets are ejected from the anus by peristalsis in the intestine; in articulates they are returned through the stomach and ejected from the mouth by antiperistalsis in the esophagus. In either case they are then transported by mantle cilia to the edge of the mantle, and finally ejected from the shell by the periodic snapping of the valves.

Although no qualitative sorting of particles occurs during normal feeding, rejection mechanisms are highly developed (3). Occasional particles too large to be accepted within the food groove may be allowed to pass directly into the exhalant chamber by the contraction of one or more filaments. Such particles are then transported by mantle cilia to the mantle edge. More radical rejection mechanisms, which interrupt the feeding process on part or all of the lophophore, are evoked by the presence of unusually large quantities of suspended particles. The lateral cilia stop beating, so that the circulation of water currents ceases and no further particles enter the mantle cavity. The frontal cilia reverse their direction of beat (or, in *Lingula*, adjacent tracts of frontal cilia may begin beating away from the food groove); and mucus is secreted by the filaments. The particles are trapped in the mucus and swept by the reversed cilia to the tips of the filaments and then by mantle cilia to the edge of the mantle. The mass of pseudofeces which collects there is finally ejected from the shell by vigorous snapping of the valves. In natural conditions this rejection process serves to prevent the lophophore from becoming choked by a sudden influx of sediment. Very rarely, another rejection mechanism has been observed: the lateral cilia reverse their direction of beat, so that the whole current system is reversed in direction, and the particles are ejected from the mantle cavity through the inhalant apertures.

It is noteworthy that the snapping of the valves, though perhaps primarily a protective reaction, is also of great importance in the ejection of feces and pseudofeces. When the brachiopod is feeding undisturbed, the valves are snapped shut at fairly regular intervals, but they reopen immediately so that feeding is scarcely interrupted.

These mechanisms of feeding, digestion, and rejection are essentially uniform in living brachiopods of all groups, and may have been general in the past. Only in the form of the lophophore and the consequent current system is there much diversity, but even in this the basic structure and function of the lophophore remain constant. The lophophore always divides the mantle cavity into separate chambers and apertures, so that all the water is filtered once, but only once, during its passage through the mantle cavity. This accords with analogous enclosed suspension-feeding systems in other organisms (e.g., bivalve and some gastropod mollusks, ascidians, etc.).

The lophophore and current system become increasingly complex during the ontogeny of most species. This is related to increase in absolute size, and apparently reflects the increasing filtering capacity required by the metabolism of the growing animal (19). Thus, many species of unusually small size retain as adults the simpler forms of lophophore, which in larger species are confined to an early growth stage.

In brachiopods with trocholophes and schizolophes, the valves gape apart fairly widely and the filaments project forward like a bell. Water is drawn through a median inhalant aperture into the interior of the "bell" and after being filtered escapes laterally. In *Pumilus* the orientation of the inhalant aperture is shifted farther from the substratum by a ventral deflection in the commissure (i.e., ventral fold, dorsal sulcus). Trocholophes and schizolophes are almost invariably found in brachiopods of very small size, generally early growth stages. The only brachiopod with trocholophe in the adult stage is the very small *Gwynia*, which for long was thought to be the young of some other genus (the very large *Dyscolia* is also said to have a trocholophe, but has not been observed alive). Schizolophes are found in the adults of small thecideids (e.g., *Thecidellina*), megathyridids (e.g., *Argyrotheca*) and kraussinids (e.g., *Pumilus*). Small fossil species in these and other groups may also have had schizolophes, especially if their supporting structures (grooves, loops, etc.) can be shown to be comparable to those of living species. Other fossil structures alleged to have supported schizolophes (e.g., "lophophore platforms" of plectambonitaceans, "brachial ridges" of productoids) bear no close resemblance to the supports of schizolophes in living brachiopods, and their function is much more dubious.

The growth of a schizolophe into a ptychlophe increases the length of the rows of filaments and therefore the filtering capacity; but the current system is altered very little (it has only been studied fully in *Megathyris,* but *Lacazella* is probably similar). The valves continue to gape apart widely, and the water is drawn into the interior of the lophophore through a median inhalant aperture. Fossil megathyridids and thecideids have similar multilobed loops and grooves respectively, which probably supported similar ptycholophes. Some thecideaceans seem to have had ptycholophes of far greater complexity than any living species (e.g., *Vermiculothecidea, Bactrynium*). These have some resemblance to the multilobed plates (?dorsal valves) of Oldhaminidina, but interpretation of the latter is more problematic.

The growth of a schizolophe into a spirolophe also increases the size and filtering capacity of the lophophore, but it involves profound alterations of the current system. The brachia are coiled into conical spirals; according to the direction of coiling, the interiors of the spirals may form part of either the inhalant chamber (e.g., *Lingula, Crania, Notosaria*) or the exhalant chamber (e.g., *Discinisca*). The orientation of the spirals within the mantle cavity varies widely, but there is generally a median exhalant aperture flanked by paired inhalant apertures. This involves a complete reversal of the schizolophous arrangement of the apertures. During the early growth of the spirolophe the original median inhalant aperture is gradually split in two by a new exhalant aperture, while the original lateral exhalant apertures are shifted posteriorly and reduced in size or even lost.

Spirolophes are found at the present day without significant difference in both inarticulates and articulates, and they may also have been the most widespread form of lophophore among fossil brachiopods.

Spiral impressions are preserved on the inner surfaces of the valves of some Strophomenida (e.g., *Davidsonia, Gigantoproductus*), and these suggest spirolophes similar to those of living species.

The spiral brachidia of Spiriferida are more problematic. In general form they strongly resemble the spirolophes of living brachiopods. If interpreted as supports for spirolophes, their direction of coiling makes it possible to reconstruct their current systems (16). The interiors of the spirals would have formed part of either the inhalant chamber (most Atrypidina) or the exhalant chamber (all other Spiriferida). In either case there would have been a median exhalant aperture flanked by paired inhalant apertures. On an alternative interpretation (25), based on a different conception of the relation between lophophore and brachidium, the spiralia would have supported a deuterolophe with double rows of filaments; the median aperture would then have been inhalant and the lateral apertures exhalant. But this latter interpretation involves a current system in which the water would have been filtered twice during its passage through the mantle cavity; such a system is unknown not only in living brachiopods but also in living suspension-feeders of any phylum, and it would be highly inefficient.

The growth of a schizolophe through a zygolophe into a plectolophe involves changes analogous to those leading to a spirolophe. The inhalant chamber comprises the interior of the lateral arms of the zygolophe, supplemented in the plectolophe by the interior of the median coil; the rest of the mantle cavity is the exhalant chamber. The apertures are transformed during ontogeny as in the growth of a spirolophe; generally there is a median exhalant aperture flanked by paired inhalant apertures, with vestigial exhalant apertures posteriorly. The current systems of zygolophes and plectolophes depend for their efficacy on the development of the tissues flooring the lateral arms and median coil. They are affected very little by the great diversity in the nature of the supporting structures (short and long loops, etc.). Zygolophes and plectolophes are confined to living, and perhaps also to fossil, Terebratulida.

In many living articulates with spirolophes, zygolophes, and plectolophes, a gentle median deflection develops in the commissure during ontogeny. This invariably marks the position of the median exhalant aperture. Deflections may be either dorsal or ventral in direction (i.e., uniplicate or sulcate, respectively). They are never deep enough to isolate the median from the lateral apertures when the valves are gaping apart. Nor are they clearly related to the position of the shell on the substratum; they do not, for example, necessarily direct the filtered water away from the substratum. Similar weak median deflections are very common among fossil articulates of most groups; they too probably mark the positions of median apertures. In some species the median deflection became very deep in the later stages of ontogeny, and may then have served to separate the apertures from one another, or to direct the jet of filtered water well away from the inhalant apertures or the substratum. Among brachiopods, unlike bivalve mollusks, the apertures are never separated by means of erected or fused portions of the mantle edges, though exceptionally (lingulids) the setae are modified to serve this function.

It is possible that some fossil brachiopods may have abandoned the normal suspension-feeding found in all living species. For example, the peculiar morphology on one aberrant productoid *(Prorichthofenia)* can be interpreted in terms of a feeding mechanism analogous to that of the living septibranch mollusks (17). A rhythmic opening and closing of the highly modified dorsal valve could have sucked water in and out of the mantle cavity. As in septibranchs, the particles obtained in this way might have been much larger and more varied than those obtained by a ciliary suspension-feeder; and the animal might have been a deposit-feeder or even, in a limited sense, a carnivore. The lophophore, although thus losing its normal pumping function, might have retained its function of collecting captured particles and transporting them to the mouth. The morphology of richthofeniids can be interpreted as being especially well adapted to such a feeding mechanism; but a similar feeding process could have been utilized by many less aberrant productoids, and may even have been characteristic of the whole group.

The aberrant morphology of the Oldhaminidina, which has been the subject of much discussion (22), may also reflect some unusual mode of feeding. The "dorsal valve" (if such it is) is lobed in a manner that closely resembles the lobed ptycholophes of Thecideacea, though on a much larger scale. The hinge and musculature were apparently abnormal and commonly asymmetrical, but there is no reason to suppose that they were nonfunctional. When closed, the "dorsal valve" fits precisely on to the corresponding ridges on the ventral valve; and unless it was able to open, the "body" of the brachiopod would have been permanently sealed off from all contact with the environment.

RESPIRATION, CIRCULATION, AND EXCRETION

Very little is known about the physiology of respiration and excretion in living brachiopods, or about the functions of the so-called blood vessels and the mantle canals. The lophophore was originally regarded as a respiratory organ, since it has an obvious superficial resemblance to the gills of many aquatic animals. Although it is now clear that it is primarily a feeding organ, its large surface area may be important for gaseous exchange, and the filaments are certainly supplied with a system of vessels (branches of the small brachial canal, and "blood vessels"). The thin body wall and mantle surfaces may also be important; in *Glottidia* the mantle surface is extended into thin-walled ampullae projecting into the mantle cavity. Most inarticulates have broad closely packed mantle canals, giving a large area for gaseous exchange; and the canals themselves have a crude ciliary circulation in communication with the coelom. Most articulates have much narrower mantle canals, which do not seem well adapted for respiration; as they are finely divided and terminate at the mantle edge, they may serve rather for the transport of metabolites to the growing tissues there. In any case, whatever the exact site of gaseous exchange, it is clear that the lophophore is important at least indirectly in respiration, in that it creates a flow of water through the mantle cavity. The function of the "blood vessels" is extremely uncertain; there is no respiratory pigment. The products of excretion are ingested by phagocytes in the coelom and drawn by ciliary currents into the nephridia, which perforate the body wall. They are ejected into the mantle cavity, and leave the shell in suspension in the exhalant currents.

REPRODUCTION

The sexes are separate in almost all living brachiopods (*Argyrotheca* and possibly *Platidia* are hermaphrodite). The gonads are similar in size and position in both sexes; at maturity they extend from the coelom into the proximal parts of the mantle canals. Living brachiopods become sexually mature long before the average "adult" size is reached, i.e., morphologically "juvenile" individuals may be capable of reproduction.

Little thorough study has been made of the breeding seasons of living brachiopods. In tropical water *Lingula* seems to spawn at intervals throughout the year (5), but in temperate water it has a more limited breeding season. Scattered observations on the larvae of other temperate-water brachiopods suggests that they too probably have a limited breeding season in spring or summer.

Like other sessile invertebrates, brachiopods probably have some mechanism for ensuring a co-ordinated release of sperm and ova. When spawning occurs, the sperm and ova are released from the gonads and expelled through the nephridia (which thus act as gonoducts) into the mantle cavity. The sperm pass directly to the exterior in the exhalant current. The ova are yolky, relatively large and few. In most species they too pass out of the mantle cavity, and fertilization takes place externally. The larvae are then planktonic throughout their earlier stages of development.

In a few articulates the ova are retained in the mantle cavity of the female, and fertilization takes place there, the sperm entering with the inhalant current. The larvae are then released at a somewhat later stage of development, and probably settle on to the substratum after a very short planktonic phase. *Argyrotheca* and *Lacazella* have special brood pouches, formed by modification of the nephridia and the body wall, respectively. Traces of a brood pouch like that of *Lacazella* have been found in a fossil thecideid *(Bifolium)*. The pouches found in some specimens of *Uncites* were formed by invagination of the shell; they are closely analogous to the brood pouches of a living bivalve mollusk *(Thecalia)*. The female of the living *Gwynia*, like many other members of the interstitial fauna of marine sand, broods only a very small number of larvae.

Whether or not the larvae are brooded, successful reproduction clearly depends on the chances of fertilization, and hence, as in other sessile invertebrates, on a close proximity between the breeding individuals. This probably accounts for the fact that living brachiopods are almost always very patchy in distribution, dense colonies being separated from one another by areas of apparently similar environment in which brachiopods are rare or absent.

Another probable factor is the very short planktonic period of most brachiopods, for this limits their powers of dispersal. In most living species the larva is planktonic only for a few hours before settling permanently on the substratum. Some of the inarticulates (e.g., *Lingula* and *Discinisca*, but not *Crania*) have developed a much more extended planktonic period of several days or even weeks. The larva develops much further, into an actively swimming and feeding organism, before settling finally on to the substratum; such larvae have often been taken in mid-oceanic plankton.

The presence of possible brood pouches is the only primarily sexual dimorphism that can be detected in fossil brachiopods. Dimorphism in general form of the shell has been claimed in several fossil brachiopods (e.g., *Cyrtospirifer*, *Dielasma*), and may be a secondary sexual character.

POPULATION STRUCTURE

Very little is known about the rates of growth and mortality in brachiopod populations. Growth lines on the shells of some species, especially those from shallow water, are sometimes grouped together in fairly regular "annual rings," which probably represent seasonal conditions unfavorable for shell growth (18, 23). This indirect evidence, which has yet to be checked by long-term study of growing individuals, suggests that sexual maturity may be reached after two or three years, and that shell growth continues at a gradually decreasing rate throughout life, some individuals having a life span of seven or eight years or perhaps even longer. These tentative figures are based on a study of *Waltonia inconspicua*; but probably different species vary greatly.

The age distribution or even the size distribution of a population cannot easily be determined, because the extremely patchy settlement of the individuals makes it difficult to collect a representative sample. Observations on shallow-water species, which can be studied easily *in situ*, suggest a fairly symmetrical distribution about a mean corresponding to a "mature" shell form. Generally no great preponderance of small and young individuals is found, which implies that if a high rate of juvenile mortality affects populations, it must occur in the larval stage before or at spatfall. Once an individual has survived the larval period and settled successfully on to a suitable substratum, it has a relatively good chance of surviving to maturity. In detail, the distribution is commonly bimodal or multimodal; this may be due either to the growth of successive year-classes of individuals, or to their irregular settlement.

Most assemblages of fossil brachiopods have a rather similar symmetrical size distribution; even where the state of preservation is good and there is little risk of collection bias, small shells are generally rare. This has been used to argue that such assemblages cannot be true life-assemblages, that the shells have drifted from their position of life, or that the smallest shells have been winnowed out after death by bottom currents or destroyed by predators. It is true that empty brachiopod shells, especially the normal biconvex forms, can be shifted even by very gentle currents, and it is also probable that such movements may produce few apparent signs of abrasion or breakage. Many or most fossil brachiopods may indeed have been shifted a little from their position of life; but it has yet to be proved that fossil assemblages do not usually approximate to life-assemblages. If, as the slender available evidence of living species suggests, the highest rate of juvenile mortality occurs before or at spatfall, fossil assemblages would not be expected to contain any preponderance of small shells. This conclusion is supported by an analysis of fossil brachiopods preserved in well-defined "clusters" or "nests," which almost certainly represent undrifted life-assemblages (11). These show a roughly symmetrical size distribution, which in detail may be bimodal or multimodal.

So-called "dwarf" faunas of fossil brachiopods have been described frequently, but their ecological significance is uncertain (6). Although some may be due to true physiological dwarfing by unfavorable conditions, others may be due to a relatively high early mortality, or to a concentration of small shells by drifting after death.

Many populations of living brachiopods show a high degree of variability, especially in characters such as shell form, length-breadth-height ratios, etc. In a few instances it is clear that some of the variation is purely phenotypic, depending on factors such as the degree of exposure. It is probable that many similar intraspecific variants in fossil brachiopods have been described as separate "species."

BIOTIC RELATIONS

Almost nothing is known about predators on living brachiopods. Potential predators, by analogy with known predators on sessile mollusks, may include fishes, crustaceans, starfishes, and gastropods. It is possible that predation may be relatively heavy during the earlier stages of growth, while the shell is small, thin, and not yet camouflaged by encrusting organisms.

Numerous fossil brachiopod shells show injuries which were healed by subsequent regeneration at the valve edges. Like similar injuries in the shells of living bivalve mollusks, they may have been due to attempted predation. An analysis of injuries to some Carboniferous productoids, for example, suggested that they were due to *(a)* sharp bites, possibly by the horny beaks of cephalopods, and *(b)* broader crushing bites, possibly by the flat crushing teeth of elasmobranch fishes such as *Petalodus*. Circular borings with bevelled edges, which almost certainly indicate predation by carnivorous gastropods, are found occasionally in brachiopod shells as far back as the Upper Ordovician.

True parasitism is little known in living brachiopods and difficult to establish in fossils. Parasitic trematodes have been reported in *Glottidia* and monocystid protozoa in *Crania*. In a Devonian *Atrypa*, the boring organism *Diorygma* maintained an aperture on the inner side of the shell, opening into the mantle cavity, and was probably parasitic (2). Other boring organisms, possibly sponges or "worms," utilized the shells of some other Paleozoic brachiopods, but probably only for protection; their adverse effect on the brachiopods was probably mild.

The shells of living brachiopods commonly are thickly encrusted with other sessile organisms, especially in shallow water where there may be intense competition for settling space (18). Like the brachiopods themselves, these organisms are predominantly suspension-feeders (e.g., sponges, hydroids, tube worms, bryozoans, young brachiopods). Similar encrusting organisms, or at least those with preservable hard parts, are commonly found on the shells of fossil brachiopods (1); they include sponges, small corals, tube worms, bryozoans, and other brachiopods. Some of these organisms may have colonized the brachiopod after death, using the shell merely as a piece of hard substratum on an otherwise soft bottom. But some probably encrusted the brachiopod during life, if only because the dangers of sedimentation would have been lessened by the frequent snapping movements of the host shell. A few of these organisms clearly grew in such a way as to maintain themselves at the valve edges of the brachiopod, suggesting that they intercepted the food-bearing currents created by the brachiopod. One such organism was the coral *Aulopora*, and it has been suggested that the nematocysts of the coral conferred some protection on the brachiopod, making the association mutually beneficial. In fact, however, any encrustation might be of some mutual benefit; while the brachiopod provides the encrusting organisms with settling space, the latter may serve to camouflage the brachiopod and protect it from predators.

Color marking on the shell may also be a form of camouflage. It occurs on the shells of a few living brachiopods from shallow water (e.g., *Argyrotheca, Frenulina*), and traces of color patterns have been seen on the shells of a few fossil brachiopods (e.g., *Cranaena*).

INORGANIC FACTORS

At the present day, all brachiopods normally live in water of full marine salinity, almost all are intolerant of any lowering of the salinity, and none are adapted to brackish- or fresh-water conditions. The lingulids can survive occasional brief periods of immersion in brackish or fresh water (e.g., a tropical storm while exposed at low tide); but they do so by closing their shells tightly and by retreating into their burrows, i.e., by temporarily suspending all normal metabolic activities. No other living brachiopods possess even this limited tolerance of nonmarine conditions.

The evidence of sediments and associated faunas suggests that the environments of fossil brachiopods were also invariably marine. The presence of fossil lingulids unaccompanied by other brachiopods is not a reliable indicator of brackish conditions of deposition. Such assemblages may indicate conditions that were normally marine but liable to occasional brief periods of brackish water. But lingulids are ecologically abnormal in several other respects, and other explanations are therefore possible.

All living brachiopods seem to require well-oxygenated water, and are not known from environments such as black organic-rich muds. This seems to be true also of fossil brachiopods. With certain exceptions, fossil brachiopods are conspicuously absent from the "black-shale" facies. The few that do occur are most plausibly interpreted as epiplanktonic, living suspended from floating vegetation or other organisms in the surface waters, away from the poorly oxygenated bottom conditions.

It is possible that living brachiopods, like other marine invertebrates, are limited in their distribution by narrow ranges of temperature tolerance, especially perhaps for reproduction, but of this little is known. At the present day, brachiopod faunas are most abundant and diverse in cool and temperate waters. Those found in subtropical or tropical latitudes are mainly confined to deeper water; the exceptions, which are presumably adapted to relatively high temperatures, include (among others) species of *Lingula, Glottidia, Discinisca,* and *Frenulina.* There is no apparent correlation between the size of brachiopods and the climatic region in which they live.

It is clearly hazardous to extrapolate such frail evidence to fossil brachiopods. The ecology of living species does not encourage the use of fossil species as indicators of paleotemperature. Nevertheless, certain fossil brachiopods have a circumscribed geographical distribution which does not seem to be attributable to limitations of present outcrops, original bottom conditions, possibilities of dispersal, etc., and which may be climatic in origin. In the Permian, for example, the Enteletidae, Richthofeniidae, and Oldhaminidae have a distinctive circumglobal distribution which may represent the tropical and subtropical belt of the time. The Permian brachiopod faunas within this belt are certainly remarkable for the diversity, abundance, and large size of many of their species, which recalls the character of the tropical molluscan faunas (but not brachiopod faunas) of the present day.

As in other marine animals, the range in depth of brachiopods is probably related closely to their range of temperature tolerance. The greatest abundance of living species occurs in the shallower waters of the continental shelves. Most of these species are limited to depths of a few hundred meters, but some extend through a remarkable range from shallow water into abyssal depths (e.g., *Terebratulina retusa* to 3,600 m.; *Macandrevia cranium* to 4,000 m.). A few species are confined to abyssal depths (e.g., *Abyssothyris wyvillei, Chlidonophora chuni*); none are known from hadal faunas. At the opposite extreme, very few species extend into the littoral (intertidal) zone. Here the chief limitations are of course the reduced time available for feeding and the risk of desiccation. Species of *Lingula, Glottidia,* and *Discinisca,* among the inarticulates, and *Terebratalia* and *Waltonia,* among the articulates, are known to extend up to mid-tide level. At low tide the lingulids retreat into their burrows; the other brachiopods can only close their shells tightly, but they tend to occur in situations where they are protected from desiccation (e.g., undersides of boulders). None of these species, however, is more than marginally intertidal; all of them are most abundant below low-tide level.

Like the evidence of temperature, that of depth is too indecisive to allow extrapolation to fossil brachiopods. Moreover, it is clear that many modes of life, some of which may have been related to definite conditions of depth, are unrepresented among the surviving species of the present day. It has been asserted that brachiopods as a phylum have tended to migrate into deeper water in the course of time; but this is doubtful, except in the most general sense that brachiopods have become less abundant members of the shallow-water faunas. Few fossil brachiopods can be used as indicators of depth; but the occurrence of fossil lingulids without other brachiopods may, if there are no indications of toxic conditions, be taken to reflect possibly littoral (intertidal) conditions of deposition.

It is commonly asserted that living brachiopods require clear water and cannot tolerate turbid conditions. While this perhaps may be true of some species, it is certainly not true of all. For example, among the shallow-water species that can be studied *in situ,* the inarticulate *Lingula* and the articulate *Waltonia* are well adapted to living in water that is generally turbid. Few if any direct observations on turbidity have been made on deeper-water brachiopods, but at least some species are known from muddy bottoms, and some can tolerate turbid conditions in laboratory aquaria. Tolerance of turbidity is clearly related to the feeding mechanisms. The digestive system, like that of other unselective suspension-feeders, is adapted to the extraction of food particles from a relatively large volume of other material (silt, etc.); and the highly developed rejection mechanisms enable the brachiopod to cope with any sudden large influx of inorganic material in suspension. In the last resort, the shell can be tightly closed, and can remain closed for several hours. Living brachiopods are less well adapted, however, to cope with any substantial sedimentation; unlike bivalve mollusks, for example, they lack the mobility to maintain themselves at the surface of a substratum on which rapid sedimentation is taking place (the infaunal burrowing habit of the lingulids gives them in this respect a unique advantage among brachiopods). Small or young brachiopods, especially, have to keep their shells clear of sediment by frequent and vigorous snapping of the valves and by turning around on the pedicle. Some species are commonly found in positions (e.g., undersides of boulders) which afford not only protection but also relative freedom from sedimentation.

A high tolerance of turbidity, with lesser tolerance of actual sedimentation, is likely to have been a general characteristic of brachiopods in the past; for there is no reason to suppose that the controlling physiological characters have changed radically. This is confirmed by the fact that fossil brachiopods commonly are abundant in muddy or silty sediments and in fine-grained limestones. Perhaps in some instances such sediments accumulated discontinuously, giving long periods without active sedimentation; but many must represent bottom environments of high turbidity with at least some degree of sedimentation.

Living brachiopods are generally found in bottom conditions that are relatively quiet and not swept by powerful currents. Those that occur in shallow turbulent water are commonly confined to the more protected micro-environments. This ecological preference, however, is probably dependent simply on the mode of anchorage of the shell. Attachment by a pedicle is probably not strong enough to withstand highly turbulent conditions. It is significant that *Crania,* with its ventral valve firmly cemented to a rock surface even in the earliest stages of growth after settlement, is able to survive on rocky bottoms with strong current action.

The mode of anchorage of the shell clearly influences to a great extent the types of substratum that can be utilized by brachiopods. Since most living species seem to be dependent on hard material for attachment, they are correspondingly limited to bottom environments in which such materials (rock, shell, coral, etc.) are abundant. This, however, is not a reliable guide to the ecology of fossil brachiopods, since many fossil species may have shared with the living *Chlidonophora* the ability to root into soft sediments. Others apparently lived freely on the surface of such sediments, or were stabilized by other means (spines, etc.). The living *Gwynia,* by its extremely small size and by other adaptations, is able to utilize the "difficult" environment of marine sand, as a member of the interstitial fauna.

Brachiopods were common members of "reef" faunas during the Paleozoic, but have been rare in similar environments in more recent periods. This has been attributed to the predation of the brachiopod larvae by coral polyps (10). But at the present day coral reefs support a large fauna of other organisms, some of which have planktonic larvae. The more sheltered parts of reefs should provide abundant sites of attachment suitable for brachiopods; yet very few (e.g., *Frenulina*) are in fact found there. It may be significant that deep-water ahermatypic corals, on the other hand, characterize an environment in which living brachiopods may be abundant. Brachiopods may have been rare on true reefs since the Paleozoic simply because the conditions of temperature or depth are generally unsuitable, or because predation by fishes, etc., is too great.

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CLASSIFICATION

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The history of brachiopod classification reveals a bewildering succession of taxonomic practices which have varied greatly in utility and popularity but have not yet given rise to a scheme that meets with general and lasting approbation. The principal reason for this confusion is, of course, the never-ending search for a classification that is not only workable and decisive in its application but also consistent with the known facts of brachiopod evolution, a requisite of special significance for a phylum founded mainly on paleontological data. These two qualifications, desirable though they be, are essentially incompatible with each other. Taxonomic procedure is a practical method of segregating organisms into identifiable groups, each with a clearly defined status within a classificatory scheme, whereas the theory of evolution postulates continuity between all such groups within the framework of time. This incompatibility has long been known, but the problems generated by attempts to satisfy both conditions in a classification of the Brachiopoda were not fully appreciated until some 50 years after Beecher (2, 3) had published his classic systematized interpretation of brachiopod phylogeny. Indeed, so important are his writings to the development of a sophisticated brachiopod classification that it is convenient to review various procedures adopted in the past according to whether they were proposed before or after the period 1891 to 1929, when the impact of Beecher's ideas was most felt. Since, however, the full history of brachiopod systematics has recently been admirably summarized by Muir-Wood (31), the following account is concerned only with a comparison of those classifications that have most influenced modern practices.

The earliest classifications involving more than one suprageneric group, like those of Menke (29), von Buch (9, 10), Gray (18), Phillips (37), M'Coy (27) and King (22) were attempts to formalize the profound differences existing between genera that were then known and at the same time to provide a simplified key for quick diagnosis. Thus King recognized ten families (one embracing the coral *Calceola*), while von

Buch contrived to establish a hierarchical arrangement dependent primarily on external form. But a feasible monothetic classification, i.e., one in which the diagnostic set of features for any taxon is unique (47), did not appear until 1848, when Gray (19) proposed to assign the brachiopods to two subclasses, the Ancylopoda and Helictopoda, based on the disposition of the lophophore and the structure of the shell (a third unnamed category for the rudist pelecypods was also tentatively listed). This segregation was carried to its logical conclusion. The Ancylopoda, which were described as having "recurved" brachia, were further divided into those with lophophores forming "hoops" (i.e., plectolophes), the Ancylobrachia; or "sunk into grooves" (e.g., thecideid lobate trocholophes), the Cryptobrachia. Again, among the Helictopoda a distinction was drawn between those in which the spirally disposed brachia were either supported by variably developed outgrowths from the "hinge margin" (Sclerobrachia) or lacking any such support (Sarcibrachia). In this way Gray disposed of 8 families accommodating nearly 1,000 fossil species.

The most interesting feature of this classification was the assurance with which Gray interpreted the anatomy of extinct groups. With commendable perspicacity, he indicated a relationship between rhynchonellids, pentamerids and spiriferids; and in concluding that an unsupported spirolophe was typical of his Productidae (comprising *Orthis, Leptaena, Strophomena,* etc.) was able to effect an integrated classification for both living and fossil species. No fundamental distinction, however, was drawn between the articulates and inarticulates, for the latter were all included as families in the Sarcibrachia, although Deshayes (16) had already proposed the segregation of species with free (Libres) or articulated (Articules) valves, and Owen (36) was shortly to erect two orders, Lyopomata and Arthropomata, on these differences and others like shell composition and proportions of viscera to shell space.

Gray's scheme was accepted by many systematists (e.g., King, 23, and, with some emendation, Bronn, 7) although others, like M'Coy (28) and Davidson (15) continued to recognize only familial divisions. Davidson's reluctance to indulge in any monothetic classification was particularly noteworthy. After devoting his life to an unrivalled study of the phylum, he would not commit himself to anything more than assigning the 139 genera ultimately recognized by him to 29 suprageneric groupings, 7 of which were listed as Tretenterata King (=Inarticulata Huxley) and the remainder as Clistenterata King (=Articulata Huxley). Incidental comments on the lack of fossil evidence in support of the theory of evolution suggest that Davidson found no relationships between these groups that were strong enough to warrant any closely integrated classification, although he was obliged to use the superfamilial rank. Throughout his researches Davidson carefully discriminated in an appropriate systematic manner between family (-idae) and subfamily (-inae). Yet in bringing together all the loop- and spire-bearing brachiopods, he used the collective nouns "Terebratulacea" and "Spiriferacea," listed as "families," but actually embracing several orthodox families and subfamilies. Davidson was thus among the first to appreciate the need for a taxonomic rank intermediate between family and order.

Waagen's classification (52) was altogether much more elaborate, for like that of Gray, it was essentially monothetic and consisted of inarticulate suborders based on the presence and attitude of the pedicle, and articulate suborders founded mainly on the nature of the lophophore supports. Neither procedure was original. The former feature had been used for suprageneric classification by von Buch (11) and Eudes-Deslongchamps (17), and the latter by Gray; but Waagen employed them with a much greater understanding of their classificatory merits. He was certainly the first to attempt any subordinal arrangement of the inarticulates which he knew by Owen's term Lyopomata. Thus the Gasteropegmata was erected for forms, like the craniids, that lacked a pedicle and were attached by their "ventral valve"; the Daikaulia embraced the discinids, siphonotretids and genera which would now be included in the trematids and acrothelids, all with a pedicle which "pierces one of the valves"; his third suborder, the Mesokaulia, included the lingulids, obolids and trimerellids which WAAGEN believed had a pedicle that protruded between the valves. The articulates (i.e., Arthropomata of OWEN) were divided into four suborders, the Kampylopegmata for brachiopods with "curved" skeletal supports to the lophophore, the Helicopegmata for those with spiral skeletal supports, the Aphaneropegmata for those without any calcareous lophophore supports, and the Coralliopsida for the Richthofenidae.

Even in the light of contemporary knowledge, there were incongruities to WAAGEN's scheme, like the exalted rank of the richthofeniids, which, in contrast to the lyttoniids, had been separated at the subordinal level from the productids, and the assignment of the rhynchonellids and thecideids, as well as all loop-bearing brachiopods, to the Kampylopegmata. These weaknesses were generally recognized by others who used the classification, and emendations accordingly were made. ZITTEL (61), for example, replaced the Kampylopegmata by the Ancylopegmata, which included all the loop-bearers (compare the Ancylobrachia of GRAY), and the Ancistropegmata for brachiopods like the rhynchonellids that were equipped with crura. In this manner modified versions of WAAGEN's classification continued in use as late as 1949 (49), and would probably have enjoyed a much wider popularity if SCHUCHERT had not so actively promoted BEECHER's classification as one that faithfully reflected brachiopod evolution.

BEECHER's ordinal segregation of the Brachiopoda (2) was undoubtedly inspired by the Haeckelian theory of recapitulation. His prefatory remarks include references to the efficacy of HYATT's law of morphogenesis and to methods of elucidating the evolutionary history of phyla by applying the "principles of growth, acceleration of development, and mechanical genesis" in the light of the "geological sequence of genera and species." Therefore, he believed that the study of a relatively few stocks, the selection of which was fortuitously determined by what was then known of brachiopod ontogeny would provide the key to a broad classification in harmony with the main evolutionary changes affecting the group.

According to BEECHER, the generalized morphology of the brachiopod protegulum represents the most primitive condition of the shell and is closely comparable with that of adult *Paterina*, which may therefore be regarded as typifying the "early primordial form." Subsequent diversification of the phylum was essentially related to an increasing dissimilarity in the form and relationship of the valves and to a ventral migration of the pedicle. BEECHER recognized that one of the most distinctive features to develop in the brachial valve was a skeletal support for the lophophore. Yet he maintained that internal structures like these grew independently of the valves and could safely be ignored in any interpretation of brachiopod history based on shell form. In contrast, the type of pedicle opening and even the length of pedicle were regarded as important factors in shell growth and, in the belief that they indicated the existence of four distinct groups which came into being during the evolution of the phylum, BEECHER proposed four new orders, the Atremata and Neotremata to embrace all inarticulate genera, and the Protremata and Telotremata to include all articulates. The diagnoses of these taxa include comments on the nature of the protegulum and subsequent shell growth and on the occurrence of articulation and supports for the lophophore; but, judging from the preamble to his classification, BEECHER gave pride of place to the location of the pedicle opening. Thus, the pedicle of the Atremata was described as lying in the commissural plane and emerging between both valves, while that of the Neotremata was stated to be disposed normal to the commissural plane and confined to the "lower" valve where the pedicle opening may be a slit opening posteriorly or entirely surrounded by shell and even subcentrally located. The Protremata were believed to have been derived from the Neotremata, although the pedicle opening remained in a submarginal position and posterodorsally was either constricted by a pseudodeltidium *(Strophomena)* or open through resorption of that structure *(Orthis)*. BEECHER also noted that the pedicle of young Telotremata is oriented like that of the Atremata but with further growth of the shell is normally restricted to the pedicle valve by deltidial plates. The affinities suggested by such comparisons were contrary to those implicit in the recognition of the Articulata and Inarticulata and led Beecher to reject these terms (or their synonyms) as formal taxa. His comparative review (3) of the embryology of certain brachiopods belonging to all four orders seemed to vindicate his earlier conclusions because he interpreted Kovalevskiy's study (24) of the development of the "protrematous" *Lacazella* as showing the pseudodeltidium to originate independently of the pedicle valve.

The repercussions of this ingenious analysis were not immediately felt. The classification used by Hall & Clarke in their definitive review of the Brachiopoda (20), for example, was an inconsistent mixture of earlier schemes; although three of Beecher's orders were used, the systematic validity of the Inarticulata and Articulata was still upheld. Waagen's division of the inarticulates into three suborders was adopted in its original form, except for a minor etymological correction of two subordinal names to Mesocaulia and Diacaulia, and the listing of Atremata as an alternative to the former. The adoption of Beecher's Protremata and Telotremata as ordinal taxa for the articulates was, however, attended by some important changes within the latter group, which was divided into three suborders, Rostracea (first used by Schuchert) for the rhynchonellids, Ancylobrachia (of Gray) for the loop-bearers, and Helicopegmata (of Waagen) for the spire-bearers. The text accompanying this classification suggests that Hall & Clarke accepted Beecher's ideas on brachiopod phylogeny without realizing how irreconcilable they were with those systematic treatments of the phylum based solely on morphological comparison. This incompatibility was, however, fully appreciated by Schuchert, who for the next quarter of a century conducted a prolific and spirited defense of Beecher's thesis that classifications must be founded on the facts of evolution.

In 1893, Schuchert (42) was content to employ Beecher's orders as subdivisions of the Lyopomata (Inarticulata) and Arthropomata (Articulata), but by 1897 he had completely revised (43) the brachiopod classification, then embracing more than 6,000 species, to conform strictly with *his* interpretation of the evolutionary history of the phylum. Walcott (53) had already shown that, in contrast to the brachiopod protegulum, *Paterina* possesses a "cardinal area." Yet Schuchert persisted in the belief that the ancestor to the phylum must have been like the protegulum and continued to use the term "Paterina" to denote this theoretical stage in brachiopod evolution. The "third shell," identified by Beecher in the development of *Lacazella* and named the "prodeltidium" by Hall & Clarke, was the source of even greater speculation. Schuchert, consolidating tentative observations by Müller (32) and Brooks (8), not only homologized the prodeltidium with a "plate somewhat loosely attached to the ventral shell" of *Discinisca,* but also with a posteromedian thickening in the brachial valve of *Lingula.* He therefore concluded that the prodeltidium, supposedly secreted by the pedicle, was invariably present except in the Telotremata, and was attached to the pedicle valves of the Neotremata and Protremata and to the brachial valve of the Atremata. On this basis he was able to define two superorders: the Homocaulia, embracing the Atremata and Telotremata, and the Idiocaulia containing the Neotremata and Protremata. Since this grouping is contrary to that resulting from the use of Inarticulata and Articulata, Schuchert sought to show that the latter categories had neither phylogenetic nor morphological worth. Hence, he contended that the so-called "perforations" in the "dorsal beaks" of a number of fossil Protremata and Telotremata must have been anal openings; that articulation was developed in many Atremata and even in the Neotremata, yet was hardly functional in the protrematous *Kutorgina*; and that the Telotremata were represented in the Lower Cambrian by *"Protorhynchia antiquata"* (now referred to *Swantonia,* a genus of uncertain taxonomic position) and must have evolved from the Atremata and not from the protrematous orthids as postulated by Hall & Clarke (20).

The infraordinal classification advocated by Schuchert in 1897 involved the standardization of taxa with the termination

"-acea" (previously used by Waagen and Davidson for suprafamilial units of varying rank) as superfamilies. In this manner, 31 families were arranged within 10 superfamilies, the atrematous Obolacea and Lingulacea, the telotrematous Rhynchonellacea, Terebratulacea and Spiriferacea, the neotrematous Acrotretacea, Discinacea and Craniacea, and the protrematous Strophomenacea and Pentameracea.

In all but the last of his later writings on the Brachiopoda, Schuchert maintained these views on the nature and phylogenetic importance of the relationship between the pedicle and the shell. Some strictly systematic rearrangements were promulgated from time to time but no allowance was made for the growing body of evidence that was steadily undermining the very foundations of his classifications. In 1913 he again emphasized (44) the need to build a classification on "the history of the class (chronogenesis) and the ontogeny of the individual," and declared that there are "certain primary characters," like the nature of the pedicle opening and the stages of shell development, which can be used to define orders, while "persistent internal characters" may be employed for superfamilial division. The classification put forward had been enlarged by the addition of three superfamilies, the Rustellacea (Atremata), Siphonotretacea (Neotremata) and Orthacea (Protremata). More significantly, Walcott's studies of the Cambrian brachiopods (54) had caused Schuchert to shift the Kutorginacea from the Protremata to the Atremata and to acknowledge that the Telotremata first appeared not in the Lower Cambrian but in the Ordovician. He did not, however, realize how contradictory these revisions were to the arguments he had used in 1897 for the abolition of the Inarticulata and Articulata and the derivation of the Telotremata from the Atremata rather than the Protremata. In fact, the sole concession made by Schuchert was to conclude that the Telotremata and Neotremata had evolved from the Obolacea (Atremata) and the Protremata from the Kutorginacea (by then transferred to the Atremata), a relationship that necessitated the abandonment of the superorders Homacaulia and Idiocaulia.

Even in 1929 Schuchert (with LeVene) continued (46) to use Beecher's orders (together with Palaeotremata of Thomson) as the basis for the classification of the 700 or so brachiopod genera then known. In all, 56 families were recognized and distributed among 19 superfamilies, five of which were new. One of these, the Paterinacea, was removed to the Palaeotremata. The others, Trimerellacea (Atremata), Clitambonacea (Protremata), Rostrospiracea and Atrypacea (Telotremata) simply represented hierarchical promotions of families within the same orders to which they had been assigned in 1913. Indeed, Schuchert did not admit any suspicions about the validity of his phylogenetic and systematic practices until 1932 when he held it likely (45) that the Telotremata arose from the Protremata and the "prodeltidium" had been misinterpreted. By then, however, the Beecher-Schuchert classification had become so firmly established in literature that even when its inadequacies were known, paleontologists were generally content to recast it rather than advocate its discard. Kozlowski (25), for example, in his systematic study of the Silurian brachiopods of Poland used Beecher's orders but, in contradiction to the reasoning that led to their erection, assigned the Atremata and Neotremata to the Inarticulata and the Protremata and Telotremata to the Articulata. After demonstrating the polyphyletic origin of the spondylium, he also moved the Pentameracea from the Protremata to the Telotremata in the misapprehension that what delthyrial covers developed in that group originated in the same way as the telotrematous deltidia.

The chief reason for the survival of the Beecher-Schuchert classification for so long after the exposure of the fallacies that had prompted its construction was, paradoxically, Thomson's critique on brachiopod morphology and systematics (50). In an enquiry into the naturalness of Beecher's orders, he reviewed embryological researches that flatly contradicted the generalizations propounded by Beecher and later assumed by Schuchert, and pointed out further deficiencies that had arisen from their disregard of the delthyrium, articulation, and shell structure. Thomson concluded that in living brachiopods differences in the development of the pedicle are far more fundamental than the nature of the pedicle opening, and since these were associated with other distinguishing features that had previously been used for the separation of the Inarticulata (or Lyopomata) and Articulata (or Arthropomata), he urged the continued recognition of two similarly constituted subclasses. For this purpose he proposed Gastrocaulia and Pygocaulia, which were broadly synonymous with the Inarticulata and Articulata, respectively, but, in his estimation, sufficiently different in content and emphasis to warrant new names. Actually, the changes introduced by him for the definition of his new subclasses were much less important than the revision he considered necessary at the ordinal level. Thus, he maintained that the Neotremata as understood by BEECHER and SCHUCHERT was diphyletic and he revised the grouping of the inarticulates by assigning the Obolacea, Lingulacea and Siphonotretacea to the Atremata, and the Paterinacea, Acrotretacea, Discinacea and Craniacea to the Neotremata. The rearrangement of the articulates was equally drastic because, although the Orthacea, Strophomenacea and Pentameracea were still allocated to the Protremata, and the Rhynchonellacea, Spiriferacea, and Terebratulacea to the Telotremata, a new order, Palaeotremata, was introduced for the Kutorginacea and Rustellacea with their undifferentiated shell and incompletely developed articulation and delthyrium. In effect, the emendations advised by THOMSON were incompatible with the intention behind BEECHER's orders. Yet so established had those orders become that, in contrast to his treatment of the subclasses, THOMSON preferred to recast their diagnoses entirely rather than abandon them for a new classification. This ambivalence, especially in conjunction with his well-reasoned criticisms, was undoubtedly the signal for excessive caution from other paleontologists and greatly extended the life of a classification that had long ceased to have any intrinsic merit.

The response to the mounting evidence that militated against the retention of BEECHER's orders was varied. Some students, like KUHN (26) were content to accept THOMSON's emended version of the classification *in toto* and do nothing more than change the status of some taxa. Others adopted bits of it. This selective practice seems to have been started by ULRICH & COOPER (51), who used THOMSON's subclasses as well as the orders Atremata and Neotremata; although in describing the articulates they omitted reference to any rank above the subordinal level, a position then held by their Orthoidea, Strophomenoidea and Syntrophioidea. No explanation was given for this action, but in 1944, COOPER (13) produced a provisional systematic arrangement of the phylum and briefly listed the reasons for introducing certain emendations. COOPER's classification was basically that of THOMSON, although he had by that time reverted to the use of Inarticulata and Articulata in preference to Gastrocaulia and Pygocaulia, respectively. He retained the Atremata and Neotremata but transferred the Siphonotretacea back to the latter order. The only articulate order to survive, however, was the Palaeotremata. The remaining articulate genera were assembled into superfamilies which in turn were grouped together according to shell structure. Thus, the impunctate Articulata contained the Orthacea, Clitambonacea, Syntrophiacea [Porambonitacea], Pentameracea, Triplesiacea, Rhynchonellacea, Spiriferacea, Atrypacea and Rostrospiracea; the pseudopunctate Articulata, the Strophomenacea and Productacea: and the punctate Articulata, the Dalmanellacea [Enteletacea], Terebratulacea and Punctospiracea. COOPER emphasized that such an arrangement, based on shell structure, was not intended as a "genetic classification" but as an informal guide for quick identification of genera. This qualification was reiterated in 1956 when the same scheme was used in his study of Ordovician brachiopods (14), although the subclasses Gastrocaulia and Pygocaulia were reinstated without comment.

Despite the cautionary note struck by COOPER, his views stimulated contrasted systematic activity. Both ROGER (38) and MOORE (30) adopted the orders Atremata, Neotremata and Palaeotremata as understood by COOPER (13). ROGER also accepted COOPER's demonstration of the systematic value of shell structure but not his criticisms of the Protremata and Telotremata, because in a gesture of uninhibited compromise he set up five composite orders, the Protremata Impunctata, Protremata Pseudopunctata, Protremata Punctata, Telotremata Impunctata, and Telotremata Punctata. Moore, on the other hand, concurred with Cooper on the need to abandon the Protremata and Telotremata, but concluded that the grouping of superfamilies solely on shell structure was inconsistent with other morphological evidence and should not be formalized. Instead, he proposed the elevation of most suborders then known to ordinal rank (the "Clitambonitoidea" were not included presumably through oversight), thereby filling the gap in the hierarchy left by the rejection of the Protremata and Telotremata. Excluding members of the Palaeotremata, all articulate genera were assigned to twelve suborders (denoted by the termination—"-acea") and seven orders—("-ida"). They were (1) Orthida (including the Orthacea and Dalmanellacea [Enteletacea]), (2) Pentamerida (Syntrophiacea [Porambonitacea], Pentameracea), (3) Triplesiida, (4) Rhynchonellida (Rhynchonellacea, Rhynchoporacea), (5) Strophomenida (Strophomenacea, Productacea), (6) Spiriferida (Atrypacea, Spiriferacea, Rostrospiracea, Punctospiracea), (7) Terebratulida.

In her history of brachiopod classification, Muir-Wood (31) went even further toward the abolition of Beecher's classification. She discarded the order Palaeotremata and assigned the Kutorginacea to the Orthoidea (the Rustellacea being cited as *"incertae sedis"*). She also predicted that a comprehensive revision of the inarticulates would lead to the rejection of the Atremata and Neotremata, although they were provisionally retained in the classification presented by her. She foresaw difficulties in using shell structure or any other single character as the basis for an ordinal classification of the articulates and, pending the completion of several independent studies that were then being undertaken for the *Treatise,* used only suborders and superfamilies to accommodate the 108 articulate families known at that time. In this manner 15 suborders were recognized: Orthoidea, Dalmanelloidea, Clitambonitoidea, Syntrophioidea, Pentameroidea, Triplesioidea, Strophomenoidea, Oldhaminoidea, Productoidea, Rhynchonelloidea, Atrypoidea, Spiriferoidea, Chonetoidea, Terebratuloidea and Terebratelloidea, of which the last three were new.

The shortcomings of the systematic schemes propounded by Beecher and Schuchert have all been stated at one time or another but are worth reiterating at this juncture.

The chief attraction of Beecher's thesis has always been his contention that a few features, and especially the pedicle opening, not only provide a simple classificatory key for the Brachiopoda but also indicate the main lines of descent within the phylum. The principal novelty of the resultant classification was undoubtedly the assumption that the Telotremata were not related to the Protremata but derived out of the Atremata. Yet even in the light of contemporary knowledge, Beecher was not really justified in arriving so confidently at such controversial conclusions. He interpreted the relationship between the pedicle and the shell in much too mechanistic a fashion and naively ignored both the anatomy of that organ and the structure of various openings accommodating it. The studies of Hancock (21), which must have been known to him, had already shown how much the pedicle of *Lingula* differed from those of *Terebratulina* and *Hemithiris,* while the likeness between the open delthyria of certain Protremata and Telotremata, as pointed out by Thomson (50), ought at least to have been considered.

Apart from the attitude of the pedicle, the distinction drawn between the protrematous and telotrematous delthyrial covers also played an important rôle in ordinal diagnosis. The difference as then understood depended entirely on Beecher's opinion (3) that the third shell (prodeltidium) of the Protremata was secreted not by the mantle but by the pedicle and only later became ankylosed to the pedicle valve during subsequent growth. Since its publication, this assertion has been the subject of increasing criticism, culminating in the proof that the pseudodeltidium has always been similar in shell structure to the rest of the valve, even in *Lacazella* (56, 57), and that Beecher misinterpreted Kovalevskiy's work (1). The shell substance figured by Kovalevskiy as originating on the pedicle rudiment and homologized by Beecher with the pseudodeltidium is not, as he believed, a discrete plate but the lateral view of a ring continuous with the pedicle valve.

Finally, the location of the teeth of articulate brachiopods invariably flanking the delthyrium and fitting into dorsal sockets, the differences between the muscle systems of the inarticulates and articulates, and the fibrous nature of the secondary shell shown by CARPENTER (12) to be typical of the articulates, should not have been so lightly disregarded by BEECHER during his enquiry into the relationship between the Protremata and Telotremata.

It may be said that the mistakes perpetrated by BEECHER are only obvious in retrospect, but even so, their perpetuation by SCHUCHERT is less excusable. By 1913, when SCHUCHERT repeated without any basic modification his views on brachiopod phylogeny, BLOCHMANN (5, 6) had decisively demonstrated the essential anatomical homogeneity of the inarticulates, and YATSU (60) had shown that the development of *Lingula* is greatly different from that of living articulates and does not include the secretion of a third shell. In the face of this evidence and that of WALCOTT (54) on the post-Cambrian origin of Telotremata, the views held by SCHUCHERT are inexplicable.

In a bid to retain BEECHER's orders there has been a tendency to revise their diagnoses in such a way as to emphasize the exclusiveness rather than the derivation of their chief characteristics. Such emendations were really attempts to change a phylogenetic classification into a monothetic one. THOMSON (50), for example, contrasted the hemiperipheral succeeded by mixoperipheral growth of both valves of the Atremata with the holoperipheral growth of, at least, the pedicle valve of the Neotremata. But, since he included the Obolacea, Lingulacea, and Siphonotretacea in the former order and the Paterinacea, Acrotretacea, Discinacea, and Craniacea in the latter order, he was obliged to concede that in members of both taxa the pedicle might have emerged between both valves or through an opening of the pedicle valve. The important differences cited for the segregation of the articulates (excluding the Palaeotremata) were for the Protremata "ventral delthyria closed only by impunctate deltidia" and "brachial supports absent or rudimentary"; and for the Telotremata "ventral delthyria partially or completely closed by deltidial plates, pseudodeltidia or symphytia which are punctate in punctate shells," and "brachial supports generally well developed." Even generalized statements of this sort, however, do not promote the merits of BEECHER's orders sufficiently to warrant their retention, as can be shown by reviewing some of the discrepancies.

In terms of shell growth, THOMSON was justified in assigning the Paterinacea to the Neotremata. But the nature of the posterior opening between the valves is anomalous and apart from the subconical form of the pedicle valve there are few resemblances between the paterinaceans and other genera included within the Neotremata. The only satisfactory solution, as was realized by COOPER (14), is to place *Paterina* and its related genera in a taxon outside both the Atremata and Neotremata, but this, of course, means that "holoperipheral growth" as a taxonomic feature is no longer unique to members of the Neotremata. Other examples may be cited which contradict any reasonably designed diagnoses for the two orders. *Curticia* has commonly been regarded as belonging to the Atremata (54) because adults have a triangular opening in the posterior margin of the pedicle valve. This opening, however, is not homologous with the lingulid pedicle groove. It was formed during ontogeny by a dorsally directed resorption of the shell and the pedicle was initially restricted to a small slitlike foramen near the apex of the valve. Hence, juvenile *Curticia* would undoubtedly be placed in the Neotremata and indeed many of the characters of the genus suggest that it was derived from some acrotretacean stock (40). Similar difficulties arise in the classification of the Obolellidae. *Alisina,* with an apical pedicle foramen, and *Trematobolus,* which has a pedicle foramen opening anterior of the apex, would unquestionably be referred to the Neotremata. Yet *Obolella* and *Magnicanalis,* which in all other respects appear to have been very closely related, would have to be placed in the Atremata, since their pedicle seemingly emerged between the valves.

Morphological differences between the Protremata and Telotremata are even less exclusive. Like that of the Telotremata, the delthyrial cover developed in any protrematous stock is deposited by outer epithelium in exactly the same way as the shell and is therefore similar in microstructure to the rest of the pedicle valve (57). Moreover, the protrematous cover is not always a pseudodeltidium. Deltidial plates, identical in genesis with those of the telotremates, are known in the orthacean *Barbarorthis* and the enteletacean *Phragmophora,* and the apical plates commonly found in the spiriferides are also known among the pentameraceans.

The use of the lophophore skeletal supports to distinguish between the Protremata and Telotremata is contrary to the advice of Beecher, but even when employed in the manner advocated by Thomson, no mutually exclusive scheme of classification, consistent with other morphological data, can be arranged. Among groups assigned to the Protremata, apophyses that probably functioned like the telotrematous crura, are known in a minority of Orthidina (57) and in most pentameraceans; while loops developed in the enteletacean *Tropidoleptus* and the pentameracean *Enantiosphen* (58) and spiralia in the davidsoniacean *Thecospira* (55). Among members of the Telotremata, the spiriferide leptocoeliids lacked spiralia (33) and in a few terebratulides, like *Gwynia,* it has long been known that only vestiges of a loop or dorsal median septum are retained for the support of the lophophore.

In summary, it may be said that no possible benefit can accrue from the retention of Beecher's classification or any emended version of it that contrives to maintain any of the original assumptions on which it was based. It in no way reflects brachiopod phylogeny as we now understand it, nor can it be adopted as a workable morphological key for the quick identification of brachiopod groups.

Following the collapse of Beecher's classification only a few attempts have been made to erect a monothetic classification. The use of shell structure in the classification of articulates has lately exercised some attraction but, although the impunctate, endopunctate, and pseudopunctate shell types are all distinctive enough to be categorized, the resultant classification would be intolerably artificial. Abundant evidence now suggests that although pseudopunctate and endopunctate brachiopods descended from impunctate stocks, all three shell conditions reappeared continually during evolution of the phylum. The earliest endopunctate enteletaceans, the paurorthids, angusticardiniids, and dalmanellids are so unlike in other features that they possibly arose independently of one another from diverse orthaceans. The rhynchonellide *Rhynchopora* was certainly unrelated to any other endopunctate group, and although the Terebratulida appear always to have been endopunctate, the relationships within their probable ancestors, the Spiriferida, are complex. The earliest spire-bearers are all impunctate but the endopunctate condition ultimately became characteristic of four distinct groups, three of which, the suessiaceans, spiriferinids, and syringothyridids, are reputed to include some impunctate descendants. The relationship between the impunctate and pseudopunctate conditions, surprisingly enough, is also complex. The latter type of shell is generally thought of as being exclusively diagnostic of the Strophomenida. In fact, it is also characteristic of the Gonambonitacea (35), and although this group may actually have had a common ancestry with the Plectambonitacea rather than the Clitambonitacea, with which it is now associated systematically, the impunctate condition of certain Strophomenida, like early species of *Christiania* (48), the plectambonitacean *Ukoa* (34), and early davidsoniaceans (57) is equally misleading.

Deficiencies of a classification based exclusively on lophophore supports have been recognized generally since the turn of the century, but they did not deter Beurlen (4) from proposing a monothetic scheme based on the known or inferred disposition of the lophophore. He erected two orders: the Orthoconata, to include the Orthacea, Triplesiacea, Clitambonitacea, Strophomenacea, Dalmanellacea [Enteletacea], Rhynchonellacea, Atrypacea, and Terebratulacea; and the Tropoconata to embrace the Syntrophiacea [Porambonitacea], Pentameracea, and Spiriferacea. According to Beurlen, who relied mainly on shell shape to interpret the attitude of the lophophore, orthoconate brachiopods possessed a lophophore disposed as a pair of low spires lying in the plane of the commissure with the apices directed submedianly; in the tropoconates, the spiral brachia were normal to the commissural plane, thereby conforming with the strong biconvexity and reduced hinge line of primitive stocks. Neither ordinal diagnosis, of course, is consistent with the attitude of the terebratulide plectolophe, but a much graver fault is the unprecedented systematic importance given to shell shape on the assumption that it invariably reflects one of two basic attitudes of the lophophore. The prevalence of homeomorphy throughout the history of the phylum shows how unsuited this feature is for the construction of an acceptable classification. Among the orthacean plectorthids alone, such great variation in shell shape is found that it is possible to draw close comparisons with members of other superfamilial groups. *Plectorthis* is gently biconvex and would probably be classified as a typical orthoconate brachiopod. Its near relatives, however, include *Herbertella,* dorsibiconvex like *Atrypa, Cyclocoelia,* almost rostrate in the rhynchonellid fashion, and *Platystrophia,* strongly reminiscent of *Spirifer,* all of which would have to be assigned to different suborders or even orders.

The disadvantages of any monothetic classification of the Brachiopoda have been reviewed by Williams (57), who demonstrated that all such schemes proposed in the past are incompatible with the evolutionary history of the phylum. This limitation does not necessarily preclude the use of a monothetic classification, provided that it always is acknowledged to be only a catalogue of brachiopods, deliberately arranged for the quick identification of stocks. A grouping of the articulates based upon differences in shell structure or lophophore supports as used by Cooper and Waagen respectively, falls into this category. No one, however, admits to being entirely satisfied with a classification which is merely a key to the identification of specimens. An awareness of the effects of evolution so pervades paleontological thought that preference is rightly given to those schemes purporting to reflect the main lines of descent. Hence the attraction exercised by classifications like those of Beecher, Schuchert, and Beurlen derives not so much from their simplicity as from the claim that they represent a synopsis of the history of the phylum. Brachiopod evolution, however, so obviously pursued a far more complicated course than is indicated by such classifications that they do not even constitute plausible monothetic groupings. It can be shown that every character which has played a fundamental role in classifications of this kind arose independently in unrelated stocks, and the inescapable conclusion is that no satisfactory ordinal arrangement will ever emerge from the use of a few selected features of shell morphogeny.

It is apparent then that the only way to erect a classification which approximates to brachiopod evolution and is at the same time utilitarian is to build one up from a series of basic units—the genus is best suited for this purpose in paleontology—by a process of continual morphological comparison. Such a classification is more objective than one contrived by the fragmentation of predetermined orders because each character is assigned a taxonomic value largely uninfluenced by preconceptions. Moreover, morphological comparison is the paleontological measure of affinity, so that when genera are assembled into families, families into superfamilies, and so on, it becomes evident that each taxon within the hierarchy spanned by a particular group is typified by a certain combination of features which commonly can be related to morphogenetic developments within the group. This does not mean that the hierarchical status of character combinations for any one group of brachiopods can be used unconditionally for similar character combinations in any other group, as advocated by Schuchert (43). Each group should be built up separately, because features which persist unmodified in one group and have therefore a high systematic value, appear only sporadically or are subject to extreme variation in another group and so possess a low systematic value. In effect, the classificatory importance of a character is normally a function of the number of species (or genera) in which it appears. Thus variably developed deltidial plates or symphytia are always present in members of the Terebratulida and so have a diagnostic value at the ordinal level. Yet the occurrence of deltidial plates in *Barbarorthis,* of the Hesperorthinae, a well-defined group deserving no more than a subfamilial rank in the orthacean hierarchy, does not necessitate the separation of that genus from its hesperorthin relatives and its promotion to ordinal rank.

The range of each genus compared with that of the group to which it is morphologically related can also affect the design of a classification, because the variability of even persistent characters was frequently an inverse function of time as measured by phyletic existence. Thus the form of the loop in established terebratulides is sufficiently stable to play a very important part in classification, but it is highly variable even within a generic stock when the order first appeared (25). Consequently, if the diverse loops found in early Devonian *Mutationella* were assigned the taxonomic value they undoubtedly possess in stabilized Mesozoic Terebratellidina, almost every individual would constitute a genus and every population a family.

The time range of a genus is another important factor influencing taxonomic procedure. Along with detailed morphological comparison it serves to distinguish convergent elements in unrelated and related groups. Many paleontologists (e.g., KOZLOWSKI, 25) have commented on the similarity between dorsal interiors of thecideaceans and certain plectambonitaceans. On morphological grounds these two groups might appear to have some affinity but there cannot be any genetic relationship between them, because the last plectambonitacean is recorded from the Middle Devonian and the earliest thecideacean from the Triassic. A more striking example of external and internal homeomorphy exists between the orthacean *Phragmorthis* and the enteletacean *Mystrophora* (14). Apart from differences in shell structure, only minor morphological details serve to separate them; yet heterochronous convergence is the only explanation for this likeness because the former is restricted to the Ordovician and the latter to the Devonian.

These considerations led WILLIAMS (57) to emphasize the value of superfamilies as taxa made up of demonstrably related stocks. It remains to be seen whether, through processes of systematic trial and error, this rank has become, as suggested by him, a rough measure of successful paedomorphic changes that have dictated the course of brachiopod evolution. Nonetheless the superfamilies, as at present conceived, are highly distinctive taxa. Genera included in the Davidsoniacea, for example, can be confidently described as constituting a basically homogeneous group diversified by the loss or exaggerated growth of dental plates, the differential development of cardinal area, the acquisition of pseudopunctation and secondary ornamentation, etc. Yet the affinities of their impunctate progenitors can only be described vaguely as strophomenidine.

Although superfamilies can be defined in terms of distinctive character combinations, their contents are not necessarily morphologically unique. Indeed, as disputes over superfamilial affiliations of a minority of genera, like *Christiania,* show, some stocks exhibiting morphological overlap between allied superfamilies can be expected to have persisted beyond the early stages of group divergence, thereby indicating the more feasible ways of combining superfamilies into suborders and orders. WILLIAMS contended that the articulate superfamilies, except for the Triplesiacea and Thecideacea, could be marshalled into six groups, each typified by a well-known brachiopod (*Orthis, Strophomena, Pentamerus, Rhynchonella, Spirifer, Terebratula*) epitomizing the generalized morphology of its group. No formal taxa were then proposed for these groups, although it was pointed out that the complex processes of morphological duplication that characterized brachiopod evolution make it impossible to define the assemblages by diagnoses that are not mainly repetitive. The superfamilies making up the groups were: (1) *Orthis* group: Orthacea, Dalmanellacea [Enteletacea], Clitambonitacea, ?Triplesiacea; (2) *Pentamerus* group: Syntrophiacea [Porambonitacea], Pentameracea, ?Triplesiacea; (3) *Strophomena* group: Plectambonitacea, Strophomenacea, Orthotetacea, Oldhaminacea [Lyttoniacea], Productacea, Richthofenacea, Chonetacea, Cadomellacea; (4) *Rhynchonella* group: Rhynchonellacea, Stenoscismatacea; (5) *Spirifer* group: Atrypacea, Spiriferacea, Athyracea [Athyridacea]; (6) *Terebratula* group: Terebratulacea, Terebratellacea, ?Thecidacea [Thecideacea].

In the introduction to the brachiopod section of the *Osnovy Paleontologii* (41), SARYCHEVA reiterated the arguments given above for building up a classification from a generic foundation and presented what was admitted to be a provisional arrangement constructed in this manner. The most significant advance was the abandonment of BEECHER's Atremata and Neotremata and the allocation of inarticulate genera to six orders embracing 11 superfamilies: (1) Rustellida: Rustellacea; (2) Lingulida: Obolacea, Lingulacea, Trimelleracea; (3) Craniida: Craniacea; (4) Acrotretida: Acrotretacea, Discinacea; (5) Siphonotretida: Obolellacea, Siphonotretacea; (6) Kutorginida: Paterinacea, Kutorginacea.

No explanation was given for this revision in either the introduction or the systematic chapter on the inarticulates prepared by GORYANSKY, and the orders appear to have been introduced to produce some degree of parity between the ordinal classification of the Inarticulata and Articulata. Articulata genera were assembled into 8 orders and 26 superfamilies: (1) Orthida: Orthacea, Rhipidomellacea, Enteletacea, Clitambonitacea; (2) Pentamerida: Porambonitacea, Camerellacea, Pentameracea; (3) Strophomenida: Plectambonitacea, Strophomenacea, Stropheodontacea, Orthotetacea; (4) Productida: Chonetacea, Productacea, Lyttoniacea; (5) Rhynchonellida: Rhynchonellacea, Rhynchoporacea; (6) Atrypida: Cyclospiracea, Atrypacea, Coelospiracea, Dayiacea; (7) Spiriferida: Spiriferacea, Delthyriacea, Spiriferinacea; (8) Terebratulida: Terebratulacea, Terebratellacea, ?Thecidacea [Thecideacea]. In addition, the Triplesiacea, which were believed to have features in common with the Pentamerida and Strophomenida, and the Athyracea [Athyridacea], which were considered to be an unnatural grouping, were listed as *incertae ordinis*, as were the Eichwaldiidae, although near relatives, the Isogrammidae, were assigned to the Productida.

The classification used herein has also been built up by continual morphological comparison of genera, subfamilies, families, etc. It is the product of several contributors and at suprafamilial levels consists of 48 superfamilies, 20 suborders, and 11 orders. For purposes of comparisons with earlier classifications, it is necessary to list only orders and their constituent superfamilies, which are: (1) Lingulida: Lingulacea, Trimerellacea; (2) Acrotretida: Acrotretacea, Discinacea, Siphonotretacea, Craniacea; (3) Obolellida: Obolellacea; (4) Paterinida: Paterinacea; (5) Kutorginida: Kutorginacea; (6) Orthida: Billingsellacea, Orthacea, Enteletacea, Clitambonitacea, Gonambonitacea, Triplesiacea; (7) Strophomenida: Plectambonitacea, Strophomenacea, Davidsoniacea, Chonetacea, Cadomellacea, Strophalosiacea, Richthofeniacea, Productacea, Lyttoniacea; (8) Pentamerida: Porambonitacea, Pentameracea; (9) Rhynchonellida: Rhynchonellacea, Stenoscismatacea, Rhynchoporacea; (10) Spiriferida: Atrypacea, Dayiacea, Retziacea, Athyrisinacea, Athyridacea, Koninckinacea, Cyrtiacea, Suessiacea, Spiriferacea, Spiriferinacea, Reticulariacea; (11) Terebratulida: Stringocephalacea, Cryptonellacea, Dielasmatacea, Terebratulacea, Zeilleriacea, Terebratellacea.

The first four orders constitute the Inarticulata; the last six, together with the Eichwaldiacea and Thecideacea as *incertae ordinis*, the Articulata. The Kutorginida cannot at present be assigned confidently to either class.

This classification differs importantly from that adopted for the *Osnovy Paleontologii*. The rejection of the Atremata and Neotremata was certainly opportune but reinvestigation of inarticulate genera has shown that a number of emendations of GORYANSKY's classification are necessary. The order Lingulida is accepted with only minor changes in content. The Acrotretida is also deemed valid but it has been enlarged to embrace not only the forms assigned to it by GORYANSKY, but also the majority of genera comprising his Craniida, which is now regarded as superfluous. Changes of this kind are always, in the last resort, subjective, but since it is highly probable that the craniaceans developed from either the acrothelids or discinaceans, it appears desirable to indicate this relationship taxonomically. The Siphonotretida of GORYANSKY is considered to be polyphyletic and to embrace two distinct stocks

(39). The phosphatic-shelled siphonotretaceans, whose early members suggest that they may have developed from the acrotretaceans, have been emended and transferred to the Acrotretida. The calcareous-shelled Obolellacea (emended), on the other hand, are here regarded as sufficiently distinctive morphologically to merit a separate order, the Obolellida. The Kutorginida, as proposed by GORYANSKY, is likewise thought to include two independently derived groups. The order is retained for the kutorginaceans and also the poorly known *Rustella,* which thereby loses its ordinal status: but the phosphatic-shelled paterinaceans are now known to differ greatly from all other brachiopods in the posterior margins of both valves and have been promoted to a new order, the Paterinida.

The reduction of articulate orders from eight to six is consistent with the superfamilial groupings advocated by WILLIAMS (57) and has led to the demotion of the Productida and Atrypida, proposed in the *Osnovy Paleontologii,* to suborders. This revision is ultimately a matter of preference, but, as shown in the chapter on Evolution, there is little doubt about the origin of either group and the taxonomic distance between Strophomenidina and Productidina or the Atrypidina and the Spiriferidina is considered to be significantly less than that between any of the orders recognized here. The order Triplesiida, proposed by MOORE, has also been rejected. WRIGHT (59) has recently reviewed the possible affinities of this group and his conclusions justify its classification as a suborder of the Orthida. Indeed, only two subordinal groups remain to be placed within the present scheme, the Dictyonellidina (Eichwaldiacea) and the Thecideidina; their relationships with other articulates have already been explored in the chapter on Evolution.

The infraordinal arrangement of the articulates is quite different from that put forward by Russian contributors to the *Osnovy Paleontologii,* both in the number and grouping of the superfamilial units. In contrast to ALICHOVA's treatment of the Orthida, WRIGHT has found no reason to retain her Rhipidomellacea, as well as the Enteletacea, while WILLIAMS believes that the morphological heterogeneity of the Orthacea and Clitambonitacea as described by her, can be reduced profitably by using some stocks previously assigned to them as the basis for the new superfamilies Billingsellacea and Gonambonitacea, respectively. Similarly, WILLIAMS believes that stropheodontids are not sufficiently different from other members of the Strophomenacea to warrant a separate superfamily within the Strophomenida, as proposed by SOKOLSKAYA; and although the Productida of SARYCHEVA, LIKHAREV, and SOKOLSKAYA has not been retained, MUIR-WOOD has continued to recognize the Cadomellacea, as well as the Chonetacea, and the Strophalosiacea and Richthofeniacea, as well as the Productacea, as necessary superfamilial assemblages.

In her preparation of the Pentamerida, NIKIFOROVA erected a new superfamily (Camerellacea) and used Porambonitacea for the remaining porambonitaceans, whereas BIERNAT prefers to retain both groups within the Porambonitacea; the remaining group, the Pentameracea as prepared by AMSDEN, conforms more or less with that of NIKIFOROVA. The higher ranks of the Rhynchonellida as set out by AGER, GRANT, MCLAREN, and SCHMIDT differ from those used by RZHONSNITSKAYA, LIKHAREV and MAKRIDIN in the continued recognition of the Stenoscismatacea, in addition to the Rhynchonellacea and Rhynchoporacea.

The spire-bearing brachiopods show the most radical differences in treatment. Not only is the order Atrypida RZHONSNITSKAYA relegated to subordinal status by BOUCOT, JOHNSON & STATON, but both the Cyclospiracea and Coelospiracea are discarded and their contents reallocated, mainly to the Dayiacea. Moreover the Athyracea, as understood by LIKHAREV, MAKRIDIN, NIKIFOROVA, and RZHONSNITSKAYA has been promoted to two suborders, Retziidina and Athyrididina, each sufficiently diverse in morphology to warrant the recognition of two superfamilies, the Retziacea and Athyrisinacea, and the Athyridacea and Koninckinacea, respectively. In a like manner, PITRAT's studies of the Spiriferidina have led him to propose a classification quite different from IVANOVA's arrangement of the Spiriferida. The genera assigned by IVANOVA to the Delthyriacea have been redistributed, partly to the Spiriferacea and partly to two new superfamilies, the Cyrtiacea and Reticulariacea, while the Cyrtinidae and Suessidae have been removed from the Spiriferinacea, as understood by Ivanova, and assembled into the new superfamily Suessiacea. Lastly, the twofold division of the Terebratulida into the Terebratulacea and Terebratellacea as used by Likharev, Makridin, and Rzhonsnitskaya has proved quite inadequate for Muir-Wood, Elliott, Hatai, and Stehli in their classification of the order. Genera included in the former superfamily are here allocated to two suborders (and three superfamilies), the Centronellidina (Stringocephalacea) and Terebratulidina (Terebratulacea and Dielasmatacea); and those attributed to the latter are now distributed among the Cryptonellacea and Zeilleriacea, as well as the Terebratellacea.

In conclusion, it seems appropriate to offer a few words in defense of the systematic procedure adopted here. The classification is far more complicated than any monothetic scheme, but, because it has been built up by empirical methods of morphological comparison, it has two important advantages. First, it is sufficiently versatile in its construction to survive drastic revisions of any of its ordinal sections. Second, since it involves all characters initially used to define genera and subsequently repeatedly sieved to determine the limits of each successive rank within the systematic hierarchy, it is bound to reflect to some degree or other the phylogenetic complexities of brachiopod evolution. As in any other classification, all taxa are admittedly subjective, but this concerns their ranking rather than their relationships with one another, which are real in so far as one can rely on shell morphology to reflect true affinities among extinct stocks. Hence, it is the nature and composition of the major groups making up the phylum that should be scrutinized closely, rather than their ranges within the systematic hierarchy which change with the fashion of the time.

Few paleontologists would now dispute the validity and status of the Inarticulata and Articulata as classes within the phylum Brachiopoda. The morphological, anatomical and embryological differences between them, which are fully discussed in the appropriate systematic sections, are decisive enough in living representatives. But morphological interpretation suggests that, within the dimension of brachiopod history, some of these distinctions are lost and that definable boundaries, which are also indicative of affinities, can only be maintained between the two classes if the Kutorginida are excluded from both. This dilemma is not new, as is shown by the way the allocation of *Kutorgina* (with *"Rustella"*) vacillated between the Protremata and Atremata of Beecher and Schuchert. In isolating the stock as an order of uncertain systematic allegiance, it is anticipated that further study will confirm its derivation independently of both the articulates and inarticulates (see chapter on Evolution) and lead to its recognition as a distinct class.

The Inarticulata and Articulata, as interpreted herein, embrace four and six orders, respectively, which can be arranged in a gradient of change from the Lingulida at one end to the Terebratulida at the other. It might, therefore, be argued that, with some revision of existing orders, a more refined classification involving subclasses to indicate these inferred relationships, might be achieved. Thus, in the chapter on Evolution, reasons are advanced for segregating the phylum (excluding the Kutorginida) into the following five grades: (1) Lingulida, Obolellida, Acrotretida; (2) Paterinida; (3) Strophomenida, Clitambonitidina, Triplesiidina, Billingsellacea; (4) Pentamerida, Orthacea, Enteletacea, ?Dictyonellidina; and (5) Rhynchonellida, Spiriferida, Terebratulida, ?Thecideidina. The differences between them are not based on any one set of characters, as was used by Beecher to establish his fourfold division of the phylum. The Paterinida are isolated from other inarticulates because the pattern of their muscle impressions is unique; the Strophomenida, etc., are separated from other articulates because their pedicle is inferred to have developed in the same way as that of the inarticulates: while the fifth group is believed to be the only one characterized by mantle reversal. Nonetheless, it is at least premature to erect subclasses on interpretations such as these and nothing is gained by recasting the Orthida to conform with the segregation adopted for the third and fourth groups. The pseudodeltidium is mainly diagnostic of the nature of the pedicle in stocks assigned to the third group, but is not one of those persistent features that provide an unambiguous classification, because it is wanting in a few Clitambonitidina and Strophomenida. Moreover, although the morphology of the Clitambonitidina is reminiscent of both the Strophomenida and Orthidina, the modal characters of the Billingsellacea and Triplesiidina are certainly more like those of early Orthacea than primitive Strophomenidina.

A total of 232 subfamilies, 202 families, 48 superfamilies, and 20 suborders have been used to accommodate the 1,700 or so brachiopod genera described to date. About one-fifth of these suprageneric categories are new, but most of them represent promotion of pre-existing taxa, and in view of the fact that this compilative work is the most comprehensive review of the phylum to be undertaken since 1913, the treatment is not unduly lavish. All suprageneric taxa, with the exception of those assigned to the Dictyonellidina and Thecideidina, have been incorporated within the ordinal classification. It is possible that the former group will prove to have arisen independently of other articulates and so merit ordinal status, but the latter is more likely to be ultimately allocated to the Spiriferida, Terebratulida, or even the Strophomenida.

Finally, it is noteworthy that diagnoses of all suprageneric taxa have been so composed as to emphasize their definitive characteristics. The repetitious nature of diagnoses for suprafamilial groups, however, may prove disconcerting at first, because, in many of them, only changes in emphasis serve to indicate the individuality of the group. This morphological overlap is, of course, a manifestation of the replicating processes in evolution. The modal features of the Strophomenida, for example, are unique and include a concavo- to planoconvex, strophic, pseudopunctate, unequally parvicostellate shell with pseudodeltidium and chilidium, bilobed cardinal process, teeth and socket ridges without brachiophores, and muscle bases impressed directly on the internal surfaces of valves. Yet genera, rightly assigned to the order, may lack one or more of all these characters, while everyone of them is known to occur among members of the Orthida. Despite such convergences, most genera can be referred immediately to their ordinal groups and even the closest homeomorphs identified unequivocally.

OUTLINE OF CLASSIFICATION

The following outline of the classification of the Brachiopoda summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each family group and higher-rank taxon.[1] Where a single number is given, it refers to genera; where two numbers are given, the second indicates subgenera. Authorship of the systematic descriptions is indicated by recording with each division the initial letters of the author's name as shown by the tabulation below:

Authorship of Systematic Descriptions

Ager, D. V.	A
Amsden, T. W.	AM
Biernat, Gertruda	B
Boucot, A. J.	BO
Elliott, G. F.	E
Grant, R. E.	G
Hatai, Kotora	H
Johnson, J. G.	J
McLaren, D. J.	ML
Muir-Wood, H. M.	MW
Pitrat, Charles W.	P
Rowell, A. J.	R
Schmidt, Herta	SC
Staton, R. D.	ST
Stehli, F. G.	S
Williams, Alwyn	W
Wright, A. D.	WR

Main Divisions of Brachiopoda

- Inarticulata *(class)* (129). *L.Cam.-Rec.* (R)
  - Lingulida *(order)* (51). *L.Cam.-Rec.* (R)
    - Lingulacea *(superfamily)* (46). *L.Cam.-Rec.* (R)
      - Lingulidae (7). *?Ord., Sil.-Rec.* (R)
      - Obolidae (27). *L.Cam.-U.Ord.* (R)
        - Obolinae (10). *L.Cam.-M.Ord.* (R)
        - Lingulellinae (6). *L.Cam.-U.Ord.* (R)
        - Glossellinae (7). *L.Ord.-U.Ord.* (R)
        - Acanthamboniinae (1). *M.Ord.-U.Ord.* (R)
        - Subfamily Uncertain (3). *Ord., ?Sil.* (R)
      - Elkaniidae (3). *U.Cam.-L.Ord.* (R)
      - Lingulasmatidae (1) *M.Ord.-U.Ord.* (R)
      - Andobolidae (1). *Ord.* (R)
      - Paterulidae (3). *Ord.-Sil.* (R)
      - Craniopsidae (4). *M.Ord.-L.Carb.* (R)
    - Trimerellacea *(superfamily)* (5). *M.Ord.-U.Sil.* (R)
      - Trimerellidae (5). *M.Ord.-U.Sil.* (R)
  - Acrotretida *(order)* (65). *L.Cam.-Rec.* (R)

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[1] Numbers given in the following tabulation are exclusive of genera recorded in the Addendum.

Acrotretidina *(suborder)* (50). *L.Cam.-Rec.* (R)
Acrotretacea *(superfamily)* (32). *L.Cam.-Dev.* (R)
Acrotretidae (21). *L.Cam.-U.Sil., ?L.Dev.* (R)
Acrotretinae (8). *?L.Cam., M.Cam.-U.Ord.* (R)
Linnarssoniinae (3). *L.Cam.-U.Cam.* (R)
Ceratretinae (2). *U.Cam.-L.Ord.* (R)
Scaphelasmatinae (3). *M.Ord.-U.Sil.* (R)
Torynelasmatinae (2). *M.Ord., ?U.Sil.* (R)
Ephippelasmatinae (1). *M.Ord., ?U.Ord.* (R)
Subfamily Uncertain (2). *Ord.* (R)
Curticiidae (1). *U.Cam.* (R)
Acrothelidae (6). *L.Cam.-L.Ord.* (R)
Acrothelinae (4). *L.Cam.-L.Ord.* (R)
Conodiscinae (2). *?M.Cam., U.Cam., ?L.Ord.* (R)
Botsfordiidae (3). *L.Cam., ?M.Cam.* (R)
Botsfordiinae (2). *L.Cam., ?M.Cam.* (R)
Neobolinae (1). *L.Cam.* (R)
Family Uncertain (1). *L.Ord.* (R)
Discinacea *(superfamily)* (11). *Ord.-Rec.* (R)
Trematidae (2). *M.Ord.-Dev.* (R)
Discinidae (9). *Ord.-Rec.* (R)
Orbiculoideinae (5). *Ord.-Perm.* (R)
Disciniscinae (3). *?Carb., ?Trias., L.Jur.-Rec.* (R)
Discininae (1). *Rec.* (R)
Superfamily and Family Uncertain (2). *L.Ord.-Dev.* (R)
Siphonotretacea *(superfamily)* (5). *U.Cam.-Ord.* (R)
Siphonotretidae (5). *U.Cam.-Ord.* (R)
Craniidina *(suborder)* (15). *?M.Cam., L.Ord.-Rec.* (R)
Craniacea *(superfamily)* (15). *?M.Cam., L.Ord.-Rec.* (R)
Craniidae (11). *?M.Cam., L.Ord.-Rec.* (R)
Eoconulidae (1). *M.Ord.-U.Ord.* (R)
Genera Doubtfully Referred to Craniacea (3). *Ord.-L.Sil.* (R)
Obolellida *(order)* (5). *L.Cam.-M.Cam.* (R)
Obolellacea *(superfamily)* (5). *L.Cam.-M.Cam.* (R)
Obolellidae (5). *L.Cam.-M.Cam.* (R)
Paterinida *(order)* (7). *L.Cam.-M.Ord.* (R)
Paterinacea *(superfamily)* (7). *L.Cam.-M.Ord.* (R)
Paterinidae (4). *L.Cam.-M.Ord.* (R)
Genera Doubtfully Referred to Paterinida (3). *L.Cam.-L.Ord.* (R)
Addendum, Class Inarticulata (1). *M.Ord.* (R)
Ptychopeltidae (1). *M.Ord.* (R)
Class Uncertain (3). *L.Cam., ?M.Cam.* (R)
Kutorginida *(order)* (3). *L.Cam., ?M.Cam.* (R)
Kutorginacea *(superfamily)* (3). *L.Cam., ?M. Cam.* (R)
Kutorginidae (2). *L.Cam., ?M.Cam.* (R)
Yorkiidae (1). *L.Cam.* (R)
Articulata *(class)* (1584;44). *L.Cam.-Rec.* (A,AM, B,BO,E,G,H,J,ML,MW,P,R,SC,ST,S,W,WR)
Orthida *(order)* (189;9). *L.Cam.-U.Perm.* (W, WR)
Orthidina *(suborder)* (156;7). *L.Cam.-Perm.* (W,WR)
Billingsellacea *(superfamily)* (8). *L.Cam.-L.Ord.* (W)
Billingsellidae (4). *M.Cam.-L.Ord.* (W)
Nisusiidae (4). *L.Cam.-M.Cam.* (W)
Orthacea *(superfamily)* (82;7). *L.Cam.-U.Dev.* (W)
Eoorthidae (7). *L.Cam.-L.Ord.* (W)
Protorthidae (3). *M.Cam.* (W)
Hesperonomiidae (3). *L.Ord.* (W)
Orthidiellidae (5). *L.Ord.-U.Ord.* (W)
Orthidae (21). *M.Cam.-L.Dev.* (W)
Orthinae (17). *M.Cam.-L.Dev.* (W)
Productorthinae (3). *Ord.* (W)
Poramborthinae (1). *L.Ord.* (W)
Dolerorthidae (11). *L.Ord.-U.Sil.* (W)
Dolerorthinae (1). *M.Ord.-U.Sil.* (W)
Hesperorthinae (5). *L.Ord.-U.Sil.* (W)
Glyptorthinae (5). *L.Ord.-U.Sil.* (W)
Plaesiomyidae (7;7). *Ord.* (W)
Plaesiomyinae (5;7). *Ord.* (W)
Evenkininae (1). *M.Ord.* (W)
Metorthinae (1). *L.Ord.* (W)
Finkelnburgiidae (4). *U.Cam.-L.Ord.* (W)
Plectorthidae (14). *L.Ord.-U.Sil.* (W)
Plectorthinae (10). *L.Ord.-L.Sil.* (W)
Platystrophiinae (2). *M.Ord.-U.Sil.* (W)
Cyclocoeliinae (1). *U.Ord.* (W)
Rhactorthinae (1). *M.Ord.-U.Ord.* (W)
Cremnorthidae (2). *M.Ord.* (W)
Cremnorthinae (1). *M.Ord.* (W)
Phragmorthinae (1). *M.Ord.-U.Ord.* (W)
Skenidiidae (3). *L.Ord.-U.Dev.* (W)
Tuvaellidae (1). *L.Sil.* (W)
Saukrodictyidae (1). *U.Ord.* (W)
Enteletacea *(superfamily)* (66). *L.Ord.-U.Perm.* (WR)
Enteletidae (17). *M.Ord.-U.Perm.* (WR)
Enteletinae (4). *M.Carb.-U.Perm.* (WR)
Draboviinae (6). *M.Ord.-U.Ord.* (WR)
Schizophoriinae (7). *U.Ord.-U.Perm.* (WR)
Paurorthidae (2). *L.Ord.-M.Ord.* (WR)
Dalmanellidae (20). *L.Ord.-L.Carb.* (WR)
Dicoelosiidae (1). *U.Ord.-M.Dev.* (WR)
Kayserellidae (4). *M.Dev.-U.Dev.* (WR)
Kayserellinae (1). *M.Dev.* (WR)
Prokopiinae (3). *M.Dev.-U.Dev.* (WR)
Mystrophoridae (1). *M.Dev.* (WR)
Hypsomyoniidae (1). *M.Dev.-U.Dev.* (WR)
Harknessellidae (4). *M.Ord.-U.Ord.* (WR)
Heterorthidae (3). *M.Ord.-U.Ord.* (WR)
Rhipidomellidae (5). *L.Sil.-U.Perm.* (WR)
Linoporellidae (5). *M.Ord.-U.Sil.* (WR)
Angusticardiniidae (2). *L.Ord.-U.Ord.* (WR)
Tropidoleptidae (1). *L.Dev.-U.Dev.* (WR)
Clitambonitidina *(suborder)* (23;2). *Ord.* (W)

Clitambonitacea *(superfamily)* (13;2). *Ord.* (W)
Polytoechiidae (4). *L.Ord.-M.Ord.* (W)
Clitambonitidae (9;2). *Ord.* (W)
Clitambonitinae (7;2). *Ord.* (W)
Atelelasmatinae (2). *L.Ord.-M.Ord.* (W)
Gonambonitacea *(superfamily)* (10). *Ord.* (W)
Gonambonitidae (9). *Ord.* (W)
Gonambonitinae (6). *L.Ord.-M.Ord.* (W)
Anomalorthinae (3). *L.Ord.* (W)
Kullervoidae (1). *M.Ord.-U.Ord.* (W)
Triplesiidina *(suborder)* (10). *L.Ord.-Sil.(Wenlock.).* (WR)
Triplesiacea *(superfamily)* (10). *L.Ord.-U.Sil. (Wenlock.).* (WR)
Triplesiidae (10). *L.Ord.-U.Sil.* (WR)
Order Uncertain (4). *M.Ord.-Perm.* (R)
Dictyonellidina *(suborder)* (4). *M.Ord.-Perm.* (R)
Eichwaldiacea *(superfamily)* (4). *M.Ord.-Perm.* (R)
Eichwaldiidae (2). *M.Ord.-U.Sil.* (R)
Isogrammidae (2). *Carb.-Perm.* (R)
Strophomenida *(order)* (375;26). *L.Ord.-L.Jur.* (MW,W)
Strophomenidina *(suborder)* (150;26). *Ord.-Trias.* (W)
Plectambonitacea *(superfamily)* (53;4). *Ord.-Dev.* (W)
Plectambonitidae (6). *L.Ord.-M.Ord.* (W)
Plectambonitinae (3). *L.Ord.-M.Ord.* (W)
Ahtiellinae (3). *L.Ord.-M.Ord.* (W)
Taffiidae (4). *L.Ord.(U.Canad.-Whiterock.).* (W)
Leptestiidae (15). *L.Ord.-U.Ord.* (W)
Leptestiinae (11). *L.Ord.-U.Ord.* (W)
Isophragmatinae (3). *L.Ord.-M.Ord.* (W)
Taphrodontinae (1). *L.Ord.* (W)
Leptellinidae (12). *L.Ord.-U.Sil.* (W)
Leptellininae (4). *L.Ord.-L.Sil.* (W)
Leptellinae (2). *L.Ord.* (W)
Leptestiininae (6). *M.Ord.-U.Sil.* (W)
Sowerbyellidae (14;4). *Ord.-M.Dev.* (W)
Sowerbyellinae (6;4). *Ord.-M.Dev.* (W)
Ptychoglyptinae (1). *Ord.* (W)
Xenambonitinae (1). *M.Ord.-U.Ord.* (W)
Aegiromeninae (6). *M.Ord.-L.Sil.*
Bimuriidae (2). *M.Ord.*
Strophomenacea *(superfamily)* (68;20). *Ord.-Carb.* (W)
Strophomenidae (29;2). *M.Ord.-L.Dev.* (W)
Strophomeninae (9). *M.Ord.-U.Sil.* (W)
Furcitellinae (4). *M.Ord.-L.Sil.* (W)
Rafinesquininae (4;2). *M.Ord.-U.Ord.* (W)
Glyptomeninae (5). *L.Ord.-M.Ord.* (W)
Oepikinae (5). *M.Ord.-U.Ord.* (W)
Leptaenoideinae (2). *U.Sil.-L.Dev.* (W)
Foliomenidae (1). *U.Ord.*
Christianiidae (1). *Ord.* (W)
Leptaenidae (10). *M.Ord.-L.Carb.* (W)
Stropheodontidae (27;18). *U.Ord.-U.Dev.* (W)
Stropheodontinae (7;10). *U.Ord.-U.Dev.*
Leptostrophiinae (5). *L.Sil.-U.Dev.* (W)
Douvillininae (6;2). *U.Sil.-U.Dev.* (W)
Pholidostrophiinae (2;4). *U.Sil.-M.Dev.* (W)
Shaleriinae (3;2). *L.Sil.-Dev.* (W)
Leptodontellinae (3). *L.Dev.-M.Dev.* (W)
Liljevalliinae (1). *M.Sil.* (W)
Davidsoniacea *(superfamily)* (29;2). *Ord.-Trias.* (W)
Davidsoniidae (3). *L.Dev.-M.Dev.* (W)
Meekellidae (11;2). *M.Ord.-Perm.* (W)
Meekellinae (9;2). *Dev.-Perm.* (W)
Fardeniinae (2). *M.Ord.-U.Sil.* (W)
Schuchertellidae (7). *Dev.-Perm.* (W)
Schuchertellinae (4). *Dev.-Perm.* (W)
Streptorhynchinae (3). *Carb.-Perm.* (W)
Orthotetidae (7). *Carb.-Perm.* (W)
Orthotetinae (4). *Carb.-Perm.* (W)
Derbyiinae (3). *Carb.-Perm.* (W)
Thecospiridae (1). *Trias.* (W)
Chonetidina *(suborder)* (29). *?U.Ord., L.Sil.-L.Jur.(U.Lias.).* (MW)
Chonetacea *(superfamily)* (29). *?U.Ord., L.Sil.-U.Perm.* (MW)
Chonetidae (23). *?U.Ord., L.Sil.-U.Perm.* (MW)
Chonetinae (1). *L.Dev.-L.Carb.* (MW)
Strophochonetinae (1). *?U.Ord., L.Sil.-L.Dev.* (MW)
Devonochonetinae (4). *M.Sil.-M.Dev.* (MW)
Anopliinae (5). *L.Dev.-L.Perm.* (MW)
Retichonetinae (1). *L.Dev.-L.Carb.(Miss.).* (MW)
Rugosochonetinae (7). *L.Dev.-U.-Perm.* (MW)
Chonetinellinae (3). *U.Carb.(Penn.).-U.Perm.* (MW)
Semenewiinae (1). *L.Carb.(Tournais.-Visean).* (MW)
Eodevonariidae (1). *L.Dev.-M.Dev.* (MW)
Chonostrophiidae (1). *U.Sil.-M.Dev.* (MW)
Daviesiellidae (4). *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.).* (MW)
Daviesiellinae (1). *L.Carb.(Visean.).* (MW)
Delepineinae (2). *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.).* (MW)
Airtoniinae (1). *L.Carb.(Visean).* (MW)
Suborder and Family Uncertain (1). *L.Carb. (Tournais.).* (MW)
Cadomellacea *(superfamily)* (1). *L.Jur.(U.Lias.).* (MW)
Cadomellidae (1). *L.Jur.(U.Lias.).* (MW)
Productidina *(suborder)* (179). *L.Dev.-Perm.* (MW)
Strophalosiacea *(superfamily)* (42). *L.Dev.-Perm.* (MW)
Strophalosiidae (15). *L.Dev.-U.Perm.* (MW)
Strophalosiinae (5). *M.Dev.-U.Perm.* (MW)

- Heteralosiinae (9). *L.Dev.-U.Perm.* (MW)
- Ctenalosiinae (1). *L.Perm.* (MW)
- Teguliferinidae (3). *U.Carb.(Penn.)-L.Perm., ?U.Perm.* (MW)
- Aulostegidae (18). *U.Penn.-U.Perm.* (MW)
- Aulosteginae (3). *L.Perm.-U.Perm.* (MW)
- Echinosteginae (8). *U.Penn.-L.Perm.* (MW)
- Chonosteginae (3). *U.Carb. or L.Perm., ?Perm.* (MW)
- Institellinae (1). *L.Perm., ?U.Perm.* (MW)
- Rhamnariinae (2). *L.Perm.-U.Perm.* (MW)
- Costellariinae (1). *L.Perm.* (MW)
- Sinuatellidae (1). *L.Carb.-U.Carb.(Namur.).* (MW)
- Chonetellidae (1). *?L.Perm., U.Perm.* (MW)
- Spyridiophoridae (1). *U.Penn.-L.Perm.* (MW)
- Tschernyschewiidae (1). *L.Perm.-U.Perm.* (MW)
- Scacchinellidae (2). *U.Penn.-L.Perm., ?U. Perm.* (MW)
- Richthofeniacea *(superfamily)* (6). *L.Perm.-U.Perm.* (MW)
- Richthofeniidae (5). *L.Perm.-U.Perm.* (MW)
- Richthofeniinae (2). *L.Perm.-U.Perm.* (MW)
- Prorichthofeniinae (1). *L.Perm.* (MW)
- Gemmellaroiinae (2). *L.Perm.* (MW)
- Family Uncertain (1). *Perm.* (MW)
- Loczyellinae (1). *Perm.* (MW)
- Productacea *(superfamily)* (131). *L.Dev.-U. Perm.* (MW)
- Productellidae (16). *Up.L.Dev.-U.Miss.* (MW)
- Productellinae (9). *L.Dev.-L.Miss.* (MW)
- Chonopectinae (7). *U.Dev.-L.Carb.(L.Miss.-U.Miss).* (MW)
- Institinidae (3). *L.Carb.(Visean), ?U.Carb.* (MW)
- Leioproductidae (11). *M.Dev.-L.Perm.* (MW)
- Leioproductinae (7). *U.Dev.-L.Perm.* (MW)
- Devonoproductinae (2). *M.Dev.-U.Dev.* (MW)
- Productininae (2). *L.Miss.-L.Carb.(Visean).* (MW)
- Overtoniidae (19). *U.Dev.-L.Perm., ?U.Perm.* (MW)
- Overtoniinae (16). *U.Dev.-L.Perm., ?U.Perm.* (MW)
- Plicatiferinae (1). *L.Carb.(Visean).* (MW)
- Institiferinae (2). *L.Carb.(Visean).* (MW)
- Marginiferidae (22). *L.Carb.-U.Perm.* (MW)
- Marginiferinae (8). *L.Carb.-U.Perm.* (MW)
- Costispiniferinae (8). *U.Miss.-U.Perm.* (MW)
- Retariinae (5). *U.Carb.(Moscov.-Ural.)-L. Perm.* (MW)
- Probolioniinae (1). *L.Perm.*
- Productidae (2). *L.Carb.(Visean)-U.Carb. (Westphal.).* (MW)
- Echinoconchidae (8). *L.Carb.(Miss.)-U.Perm.* (MW)
- Echinoconchinae (7). *L.Carb.(Miss.)-L.Perm.* (MW)
- Waagenoconchinae (1). *U.Penn.-U.Perm.* (MW)
- Buxtoniidae (11). *U.Dev.-U.Perm.* (MW)
- Buxtoniinae (9). *U.Dev.-U.Perm.* (MW)
- Juresaniinae (2). *U.Carb.(L.Penn.-U.Penn.)-L.Perm.* (MW)
- Dictyoclostidae (16). *L.Carb.(Tournais.-Visean)-U.Perm.* (MW)
- Dictyoclostinae (14). *L.Carb.(Tournais.-Visean)-U.Perm.* (MW)
- Horridoniinae (1). *Perm.* (MW)
- Levitusiinae (1). *L.Carb.(Visean).* (MW)
- Linoproductidae (18). *L.Carb.(L.Miss.-U. Miss.)-U.Perm.* (MW)
- Linoproductinae (11). *L.Carb.(L.Miss).-U. Perm.* (MW)
- Proboscidellinae (1). *L.Carb.(Visean).* (MW)
- Monticuliferinae (1). *L.Perm., ?U.Perm.* (MW)
- Paucispiniferinae (3). *U.Carb.(Penn.)-U. Perm.* (MW)
- Striatiferinae (2). *L.Carb.(Visean)-Perm.* (MW)
- Gigantoproductidae (5). *U.Dev.-U.Carb.(Namur.).* (MW)
- Gigantoproductinae (2). *L.Carb.(Visean).* (MW)
- Semiplaninae (2). *U.Dev.-U.Carb.(Namur.).* (MW)
- Kansuellinae (1). *L.Carb.(Visean).* (MW)
- Oldhaminidina *(suborder)* (16). *U.Carb.-U. Trias.* (W)
- Lyttoniacea *(superfamily)* (16). *U.Carb.-U. Trias.* (W)
- Lyttoniidae (10). *U.Carb.-Perm.* (W)
- Poikilosakidae (4). *U.Carb.-Perm.* (W)
- Bactryniidae (1). *U.Trias.(Rhaet.).* (W)
- Spinolyttoniidae (1). *U.Perm.* (W)
- Pentamerida *(order)* (84;3). *M.Cam.-U.Dev.* (B, AM)
- Syntrophiidina *(suborder)* (40;3). *M.Cam.-L. Dev.* (B)
- Porambonitacea *(superfamily)* (40;3). *M.Cam.-L.Dev.* (B)
- Eostrophiidae (1). *M.Cam.* (B)
- Huenellidae (6). *U.Cam.-L.Ord.* (B)
- Huenellinae (4). *U.Cam.-L.Ord.* (B)
- Mesonomiinae (2). *U.Cam.-L.Ord.* (B)
- Tetralobulidae (4). *L.Ord.* (B)
- Alimbellidae (2). *L.Ord.* (B)
- Clarkellidae (8). *U.Cam.-U.Ord.* (B)
- Syntrophopsidae (3). *L.Ord.* (B)
- Lycophoriidae (1). *L.Ord.-M.Ord.* (B)
- Porambonitidae (1;3). *L.Ord.-L.Sil.* (B)
- Syntrophiidae (2). *L.Ord.* (B)
- Syntrophiinae (1). *L.Ord.* (B)
- Xenelasmatinae (1). *L.Ord.* (B)
- Brevicameridae (1). *Ord.* (B)
- Camerellidae (7). *L.Ord.-Sil.* (B)

- Camerellinae (6). *L.Ord.-Sil.* (B)
- Stenocamarinae (1). *L.Ord.* (B)
- Parastrophinidae (4). *M.Ord.-L.Dev.* (B)
- Pentameridina *(suborder)* (44). *?M.Ord., U.Ord.-U.Dev.* (AM)
  - Pentameracea *(superfamily)* (44). *?M.Ord., U.Ord.-U.Dev.* (AM)
    - ?Parallelelasmatidae (4). *M.Ord.* (AM)
    - Stricklandiidae (5). *L.Sil.-U.Sil.(Wenlock.).* (AM)
    - Virgianidae (3). *U.Ord.-L.Sil.* (AM)
    - Pentameridae (31). *U.Ord.-U.Dev.* (AM)
      - Pentamerinae 13). *U.Ord.-L.Dev.* (AM)
      - Gypidulinae (14). *L.Sil.-U.Dev.* (AM)
      - Clorindinae (4). *Sil.-M.Dev.* (AM)
    - Enantiosphenidae (1). *M.Dev.* (AM)
- Rhynchonellida *(order)* (270;2). *M.Ord.-Rec.* (A,G,ML,SC)
  - Rhynchonellacea *(superfamily)* (258;2). *M.Ord.-Rec.* (A,ML,SC)
    - Ancistrorhynchidae (2) *M.Ord.* (SC)
    - Oligorhynchiidae (4). *M.Ord., ?Sil.* (SC)
    - Rhynchotrematidae (14). *M.Ord.-M.Dev.* (SC)
      - Rhynchotrematinae (7). *M.Ord.-L.Dev.* (SC)
      - Orthorhynchulinae (7). *M.Ord.-M.Dev.* (SC)
    - Trigonirhynchiidae (13). *M.Ord.-L.Carb.(Miss.).* (ML-SC)
    - Uncinulidae (19;2). *Sil.-U.Dev., ?Perm.* (SC)
      - Uncinulinae (7;2). *L.Dev.-U.Dev., ?Perm.* (SC)
      - Hebetoechiinae (8). *Sil.-M.Dev.* (SC)
      - Hypothyridininae (3). *Sil.-U.Dev.* (SC)
      - Hadrorhynchiinae (1). *M.Dev.(Givet.).* (SC)
    - Eatoniidae (7). *Sil.-L.Dev.* (SC)
    - Pugnacidae (6). *L.Dev.-L.Carb.* (SC)
    - Family Uncertain (?aff. Pugnacidae) (5). *Sil.-L.Carb., ?Perm.* (SC,ML)
    - Camarotoechiidae (20). *?L.Sil., U.Sil.-Perm.* (SC)
      - Camarotoechiinae (16). *?L.Sil., U.Sil.-Perm.* (SC)
      - Septalariinae (4). *L.Dev.-M.Dev., ?U.Perm.* (SC)
    - Camerophorinidae (1). *M.Dev.* (ML)
    - Yunnanellidae (7). *?M.Dev., U.Dev., ?L.Miss.* (ML-SC)
    - Dimerellidae (21). *?Dev., Trias.-L.Cret.* (A)
      - Dimerellinae (1). *Trias.* (A)
      - Rhynchonellininae (10). *U.Trias.-U.Jur.* (A)
      - Norellinae (7). *M.Trias.-U.Jur., ?L.Cret.* (A)
      - Halorellinae (2). *?Dev., Trias.* (A)
      - Peregrinellinae (1). *?Dev., M.Jur.-L.Cret.* (A)
    - Tetracameridae (3). *L.Carb.(Miss.).* (ML)
    - Rhynchotetradidae (3). *L.Carb.-L.Perm.* (ML)
    - Wellerellidae (30). *L.Carb.-U.Cret.* (SC,A)
      - Wellerellinae (9). *L.Carb.-U.Perm.* (SC)
        - Wellerella Group (2). *U.Carb.-Perm.* (SC)
        - Pseudowellerella Group (4). *Permocarb.-U.Perm.* (SC)
        - Allorhynchus Group (3). *L.Carb.-U.Perm.* (SC)
      - Cirpinae (13). *Trias.-U.Jur.* (A)
      - Lacunosellinae (8). *L.Jur.-U.Cret.* (A)
    - ?Cardiarinidae (1). *Penn.* (ML)
    - Rhynchonellidae (60). *Trias.-U.Cret.* (A)
      - Rhynchonellinae (4). *Trias.-U.Jur.* (A)
      - Acanthothyridinae (3). *M.Jur.-U.Jur.* (A)
      - Tetrarhynchiinae (23). *U.Trias.-L.Cret.* (A)
      - Cyclothyridinae (30). *L.Jur.-U.Cret.* (A)
    - Septirhynchiidae (1). *U.Jur.* (A)
    - Austrirhynchiidae (1). *Trias.* (A)
    - Cryptoporidae (1). *Eoc.-Rec.* (A)
    - ~Basiliolidae (9). *Cret.-Rec.* (A) FOM,
      - Basiliolinae (6). *Eoc.-Rec.* (A)
      - Aphelesiinae (1). *Eoc.-Plio.* (A)
      - Aetheiinae (2). *Cret.-Mio.* (A)
    - Hemithyrididae (4). *Eoc.-Rec.* (A)
    - Frieleiidae (5). *?Eoc., ?Mio., Plio.-Rec.* (A)
    - Erymnariidae (1). *Eoc.* (A)
    - Family Uncertain (20). *M.Ord.-L.Perm.* (S,ML)
  - Stenoscismatacea *(superfamily)* (11). *M.Dev.-U.Perm.* (G)
    - Atriboniidae (7). *M.Dev.-U.Perm.* (G)
      - Atriboniinae (3). *M.Dev.-L.Perm.* (G)
      - Psilocamarinae (4). *U.Carb.-U.Perm.* (G)
    - Stenoscismatidae (4). *M.Dev.-U.Perm.* (G)
      - Stenoscismatinae (2). *M.Dev.-U.Perm.* (G)
      - Torynechinae (2). *?U.Carb., L.Perm.* (G)
  - Rhynchoporacea *(superfamily)* (1). *Miss.-Perm.* (ML)
    - Rhynchoporidae (1). *Miss.-Perm.* (ML)
- Spiriferida *(order)* (305). *M.Ord.-Jur.* (BO,J,ST,P)
  - Atrypidina *(suborder)* (56). *M.Ord.-U.Dev.* (BO,J,ST)
    - Atrypacea *(superfamily)* (42). *M.Ord.-U.Dev.* (BO,J,ST)
      - Atrypidae (29). *M.Ord.-U.Dev.* (BO,J,ST)
        - Zygospirinae (8). *M.Ord.-L.Sil.* (BO,J,ST)
        - Atrypininae (1). *L.Sil.-L.Dev.* (BO,J,ST)
        - Carinatininae (9). *U.Ord.-M.Dev.* (BO,J,ST)
        - Atrypinae (8). *L.Sil.-U.Dev.* (BO,J,ST)
        - Karpinskiinae (1). *Sil.-M.Dev.* (BO,J,ST)
        - Palaferellinae (2). *L.Dev.-M.Dev.* (BO,J,ST)
      - Lissatrypidae (12). *M.Ord.-M.Dev.* (BO,J,ST)
        - Lissatrypinae (6). *L.Sil.-M.Dev.* (BO,J,ST)
        - Septatrypinae (6). *M.Ord.-M.Dev.* (BO,J,ST)
      - Family and Subfamily Uncertain (1). *Sil.* (BO,J,ST)
    - Dayiacea *(superfamily)* (13). *M.Ord.-M.Dev.* (BO,J,ST)
      - Dayiidae (4). *M.Ord.-L.Dev.* (BO,J,ST)
        - Cyclospirinae (1). *M.Ord., ?L.Sil.* (BO,J,ST)
        - Dayiinae (2). *U.Sil.(Wenlock.)-L.Dev.* (BO,J,ST)

Aulidospirinae (1). *M.Ord., ?U.Ord.* (BO,J,ST)

Anoplothecidae (4). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)

Coelospirinae (1). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)

Anoplothecinae (3). *L.Dev.-M.Dev.* (BO,J,ST)

Kayseriidae (1). *M.Dev.* (BO,J,ST)

Leptocoeliidae (4). *L.Sil.-M.Dev.* (BO,J,ST)

Superfamily Uncertain (1). *M.Dev.* (BO,J,ST)

Uncitidae (1). *M.Dev.* (BO,J,ST)

Retziidina *(suborder)* (16). *U.Sil.(Wenlock.)-Trias.* (BO,J,ST)

Retziacea *(superfamily)* (11). *U.Sil.(Wenlock.)-Perm.* (BO,J,ST)

Retziidae (9). *L.Dev.-Perm.* (BO,J,ST)

Rhynchospirinidae (2). *U.Sil.-L.Dev.* (BO,J,ST)

Athyrisinacea *(superfamily)* (5). *M.Dev.-Trias.* (BO,J,ST)

Athyrisinidae (5). *M.Dev.-Trias.* (BO,J,ST)

Athyrididina *(suborder)* (46). *U.Ord.-Jur.* (BO,J,ST)

Athyridacea *(superfamily)* (41). *U.Ord.-Trias.* (BO,J,ST)

Meristellidae (13). *U.Ord.-U.Miss.* (BO,J,ST)

Meristellinae (6). *U.Ord.-U.Dev.* (BO,J,ST)

Meristinae (2). *L.Sil.-M.Dev.* (BO,J,ST)

Camarophorellinae (2). *M.Dev.-Miss.* (BO,J,ST)

Hindellinae (3). *U.Ord.-L.Dev.* (BO,J,ST)

Athyrididae (27). *U.Sil.(Wenlock.)-Trias.* (BO,J,ST)

Protathyridinae (4). *U.Sil.(Wenlock.)-M.Dev.* (BO,J,ST)

Athyridinae (10). *L.Dev.-Trias.* (BO,J,ST)

Diplospirellinae (4). *Trias.* (BO,J,ST)

Subfamily Uncertain (9). *L.Dev.-Trias.* (BO,J,ST)

Nucleospiridae (1). *U.Sil.-L.Carb.(Miss.).* (BO,J,ST)

Koninckinacea *(superfamily)* (5). *Trias.-Jur.* (BO,J,ST)

Koninckinidae (5). *Trias.-Jur.* (BO,J,ST)

Spiriferidina *(suborder)* (185). *L.Sil.-L.Jur.* (P)

Cyrtiacea *(superfamily)* (28). *L.Sil.-Perm.* (P)

Cyrtiidae (9). *L.Sil.(Llandover.)-M.Dev.(Couvin.).* (P)

Cyrtiinae (3). *L.Sil.(U.Llandover.-Dev.(Ems.-?Couvin.).* (P)

Eospiriferinae (6). *L.Sil.(Llandover.)-M.Dev.(Couvin.).* (P)

Ambocoeliidae (19). *?U.Sil., L.Dev.-Perm.* (P)

Suessiacea *(superfamily)* (12). *Sil.-L.Jur.* (P)

Cyrtinidae (11). *Sil.-U.Trias.* (P)

Suessiidae (1). *L.Jur.* (P)

Spiriferacea *(superfamily)* (89). *L.Sil.-U.Perm.* (P)

Delthyrididae (21). *L.Sil.(Llandover.)-M.Dev.(Couvin.).* (P)

Delthyridinae (5). *U.Sil.(Wenlock.)-M.Dev.(Couvin.).* (P)

Acrospiriferinae (10). *L.Sil.(Llandover.)-U.Dev.(Frasn.).* (P)

Kozlowskiellininae (2). *U.Sil.(Wenlock.)-L.Dev.(Ems.).* (P)

Paraspiriferinae (3). *L.Dev.(Siegen.)-M.Dev.(Couvin.).* (P)

Cyrtinopsinae (1). *M.Dev.(Couvin.).* (P)

Mucrospiriferidae (5). *L.Dev.(Ems.)-L.Carb.(Visean).* (P)

Fimbrispiriferidae (1). *L.Dev.(Ems.)-M.Dev.Givet.).* (P)

Spinocyrtiidae (6). *L.Dev.(Ems.)-U.Dev.(Frasn.).* (P)

Syringothyrididae (15). *U.Dev.-U.Perm.* (P)

Syringothyridinae (7). *U.Dev.-Perm.* (P)

Licharewiinae (8). *U.Carb.-U.Perm.* (P)

Costispiriferidae (5). *L.Dev.(Siegen.)-U.Dev.(Frasn.), ?L.Carb.* (P)

Cyrtospiriferidae (13). *?M.Dev., U.Dev.(Frasn.)-L.Carb.(Visean).* (P)

Spiriferidae (10). *L.Carb.-Perm.* (P)

Brachythyrididae (12). *?U.Dev., L.Carb.-Perm.* (P)

Family Uncertain (1). *U.Dev.(Frasn.).* (P)

Spiriferinacea *(superfamily)* (19). *L.Carb.-L.Jur.* (P)

Spiriferinidae (19). *L.Carb.-L.Jur.* (P)

Reticulariacea *(superfamily)* (36). *?U.Sil., L.Dev.-Perm., ?Trias.* (P)

Reticulariidae (18). *?U.Sil., L.Dev.-L.Carb., ?U.Carb.-Trias.* (P)

Elythidae (7). *M.Dev.-Perm.* (P)

Martiniidae (11). *L.Carb.-Perm., ?Trias.* (P)

Superfamily and Family Uncertain (1). *Dev., ?L.Carb.* (P)

Suborder, Superfamily, and Family Uncertain (2). *Carb.-L.Jur.* (P)

Terebratulida *(order)* (290;4). *L.Dev.-Rec.* (MW,S,E,H)

Centronellidina *(suborder)* (39). *L.Dev.-Perm.* (S)

Stringocephalacea *(superfamily)* (39). *L.Dev.-U.Perm.* (S)

Centronellidae (12). *L.Dev.-M.Dev.* (S)

Centronellinae (2). *L.Dev.-M.Dev.* (S)

Rensselaeriinae (5). *L.Dev.-M.Dev.* (S)

Eurythyridinae (3). *L.Dev.* (S)

Meganteridinae (2). *L.Dev.* (S)

Stringocephalidae (7). *M.Dev.* (S)

Rensselandiinae (3). *M.Dev.* (S)

Bornhardtininae (1). *M.Dev.* (S)

Stringocephalinae (3). *M.Dev.* (S)

Rhipidothyrididae (5). *L.Dev.-M.Dev.* (S)

Rhipidothyridinae (2). *M.Dev.* (S)

Globithyridinae (3). *L.Dev.* (S)

Mutationellidae (13). *L.Dev.-Perm.* (S)

Brachyzyginae (1). *L.Dev.* (S)

Mutationellinae (8). *L.Dev.-M.Dev.* (S)
Cimicinellinae (1). *L.Dev.* (S)
Cryptacanthiinae (3). *?L.Dev., Miss.-U.Perm.* (S)
Family Uncertain (2). *M.Dev.-U.Miss.* (S)
Terebratulidina *(suborder)* (132;2). *L.Dev.-Rec.* (S,MW)
Dielasmatacea *(superfamily)* (42;2). *L.Dev.-U.Trias., ?L.Jur.* (S,MW)
Cranaenidae (5). *L.Dev.-Miss.* (S)
Cranaeninae (3). *L.Dev.-U.Miss.* (S)
Girtyellinae (2). *Miss.* (S)
Dielasmatidae (24). *L.Carb.-U.Trias., ?L.Jur. (Lias.).* (S,MW)
Dielasmatinae (13). *L.Carb.-U.Trias.* (S, MW)
Centronelloideinae (1). *U.Miss.* (S)
Nucleatulinae (3). *U.Trias., ?L.Jur.(Lias.).* (MW)
Juvavellinae (5). *U.Trias.* (MW)
Subfamily Uncertain (2). *M.Trias.-L.Jur.(M. Lias.-U.Lias.).* (MW)
Heterelasminidae (4). *U.Dev.-U.Perm.* (S)
Notothyrididae (5;2). *U.Miss.-U.Perm.* (S)
Labaiidae (3). *M.Penn.-U.Perm.* (S)
Family Uncertain (1). *Perm.* (S)
Terebratulacea *(superfamily)* (90). *U.Trias.-Rec.* (MW)
Orthotomidae (1). *L.Jur.(M.Lias.).* (MW)
Terebratulidae (56). *U.Trias.-Rec.* (MW)
Terebratulinae (41). *U.Trias.-Rec.* (MW)
Sellithyridinae (3). *L.Cret.-U.Cret.(Cenoman.).* (MW)
Rectithyridinae (5). *L.Cret.-U.Cret.* (MW)
Gibbithyridinae (3). *U.Cret.(Cenoman.-Senon.).* (MW)
Carneithyridinae (2). *U.Cret.(Senon.-Dan.).* (MW)
Inopinatarculinae (1). *U.Cret.(Santon.).* (MW)
Subfamily Uncertain (1). *U.Jur.(Oxford.).* (MW)
Cheniothyrididae (1). *M.Jur.(U.Infer.Ool.).* (MW)
Dictyothyrididae (1). *M.Jur.(Bathon.)-U.Jur. (Oxford.-?Kimmeridg.).* (MW)
Tegulithyrididae (1). *U.Jur.(Callov.).* (MW)
Pygopidae (5). *?L.Jur.(Lias.), M.Jur.-L.Cret. (Neocom.).* (MW)
Dyscoliidae (4). *?U.Jur., U.Cret.(Cenoman.)-Rec.* (MW)
Cancellothyrididae (21). *?L.Jur.-?M.Jur., U. Jur.-Rec.* (MW)
Cancellothyridinae (6). *U.Jur.-Rec.* (MW)
Chlidonophorinae (3). *U.Cret.-Rec.* (MW)
Eucalathinae (2). *?U.Cret., Rec.* (MW)
Agulhasiinae (1). *Rec.* (MW)
Orthothyridinae (1). *U.Cret.* (MW)
Subfamily Uncertain (8). *L.Jur.(Gt.Ool. Ser.)-L.Cret.(Apt.-Alb.).* (MW)
Terebratellidina *(suborder)* (117;2). *L.Dev.-Rec.* (MW,E,H,S)
Cryptonellacea *(superfamily)* (4). *L.Dev.-Perm.* (S)
Cryptonellidae (4). *L.Dev.-Perm.* (S)
Zeilleriacea *(superfamily)* (22). *Trias.-L.Cret.* (MW)
Zeilleriidae (21). *Trias.-L.Cret.* (MW)
Eudesiidae (1). *M.Jur.(Bathon.).* (MW)
Terebratellacea *(superfamily)* (91;2). *U.Trias.-Rec.* (E,H)
Megathyrididae (5). *U.Cret.-Rec.* (E,H)
Platidiidae (2). *Eoc.-Rec.* (E,H)
Kraussinidae (6). *Mio.-Rec.* (H)
Dallinidae (39;2). *U.Trias.-Rec.* (E,H)
Dallininae (14;2). *L.Cret.-Rec.* (E)
Gemmarculinae (1). *L.Cret.-U.Cret.* (E)
Kingeninae (4). *U.Jur.-U.Cret.* (E)
Trigonellininae (3). *L.Jur.-U.Jur.* (E)
Frenulininae (3). *Mio.-Rec.* (H)
Nipponithyridinae (5). *Mio.-Rec.* (H)
Subfamily Uncertain (9). *U.Trias.-L.Cret.* (E)
Terebratellidae (32). *L.Cret.-Rec.* (E,H)
Terebratellinae (7). *Oligo.-Rec.* (H)
Bouchardiinae (3). *U.Cret.-Rec.* (E,H)
Magadinae (9). *L.Cret.-Rec.* (E,H)
Trigonoseminae (3). *U.Cret.* (E)
Neothyridinae (10). *Oligo.-Rec.* (H)
Laqueidae (4). *Mio.-Rec.* (H)
Laqueinae (1). *Mio.-Rec.* (H)
Pictothyridinae (2). *Plio.-Rec.* (H)
Kurakithyridinae (1). *Plio.* (H)
Family Uncertain (3). *Jur.-Rec.* (E,H,MW)
Suborder, Superfamily, and Family Unknown (2). *Eoc.-Mio.* (MW)
Order Uncertain (12). *Trias.-Rec.* (E)
Thecideidina *(suborder)* (12). *Trias.-Rec.* (E)
Thecideacea *(superfamily)* (12). *Trias.-Rec.* (E)
Thecidellinidae (4). *Trias.-Rec.* (E)
Thecideidae (8). *L.Jur.-Rec.* (E)
Order, Suborder, and Family Uncertain (53). *M. Cam.-Trias.*

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STRATIGRAPHIC DISTRIBUTION

13.

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The known stratigraphic distribution of the Brachiopoda is a reflection not only of the evolutionary history of the phylum and the control exercised by shifting facies throughout time, but also of the fortuity of fossil preservation and paleontological tradition. The first two factors have determined the main pattern of distribution; the last two are responsible for its imperfect presentation. Any general survey of the brachiopods in time and space needs to take account of limitations of the available data and insofar as possible, to segregate the relative effects of nature and artifice.

By any standard of measurement, it appears that the phylum has passed through its climactic phase of evolution and is now in decline. In effect, brachiopods have been replaced by other invertebrates as the principal constituents of benthic marine faunas. This process seems to have been gathering momentum since early Mesozoic times but it followed an era of remarkable generic proliferation and phyletic diversity which, as shown graphically in Figs. 148-150, reached their acme during the Devonian. It is not surprising to find that the generic and superfamilial patterns of distribution are comparable, since frequency of the latter is normally a function of the former. Superfamilial ranges, however, provide a better picture of evolutionary design because the inauspicious beginnings and decimated endings of extinct groups are commonly obscured by the numerical preponderance of their more flourishing contemporaries. Thus all six articulate orders are represented in Devonian rocks (including the earliest Terebratulida and the last Pentamerida) and although four persisted into the Jurassic they included the last of the Strophomenida and Spiriferida. In fact, since the Ordovician and Devonian, when maxima of eight orders were simultaneously in existence, there has been a steady reduction in the more basic diversity of the phylum.

The occurrence of living brachiopods in almost every known marine environment from brackish-water tidal flats (e.g., *Lingula*) to abyssal regions over 5,000 m. deep (e.g., *Abyssothyris*) is undoubtedly a relic of past adaptability. Certainly ample evidence suggests that extinct stocks, as burrowers, sedentary benthos, or even epiplankton, successfully colonized as many ecological niches as their modern descendants. Consequently, brachiopods have been

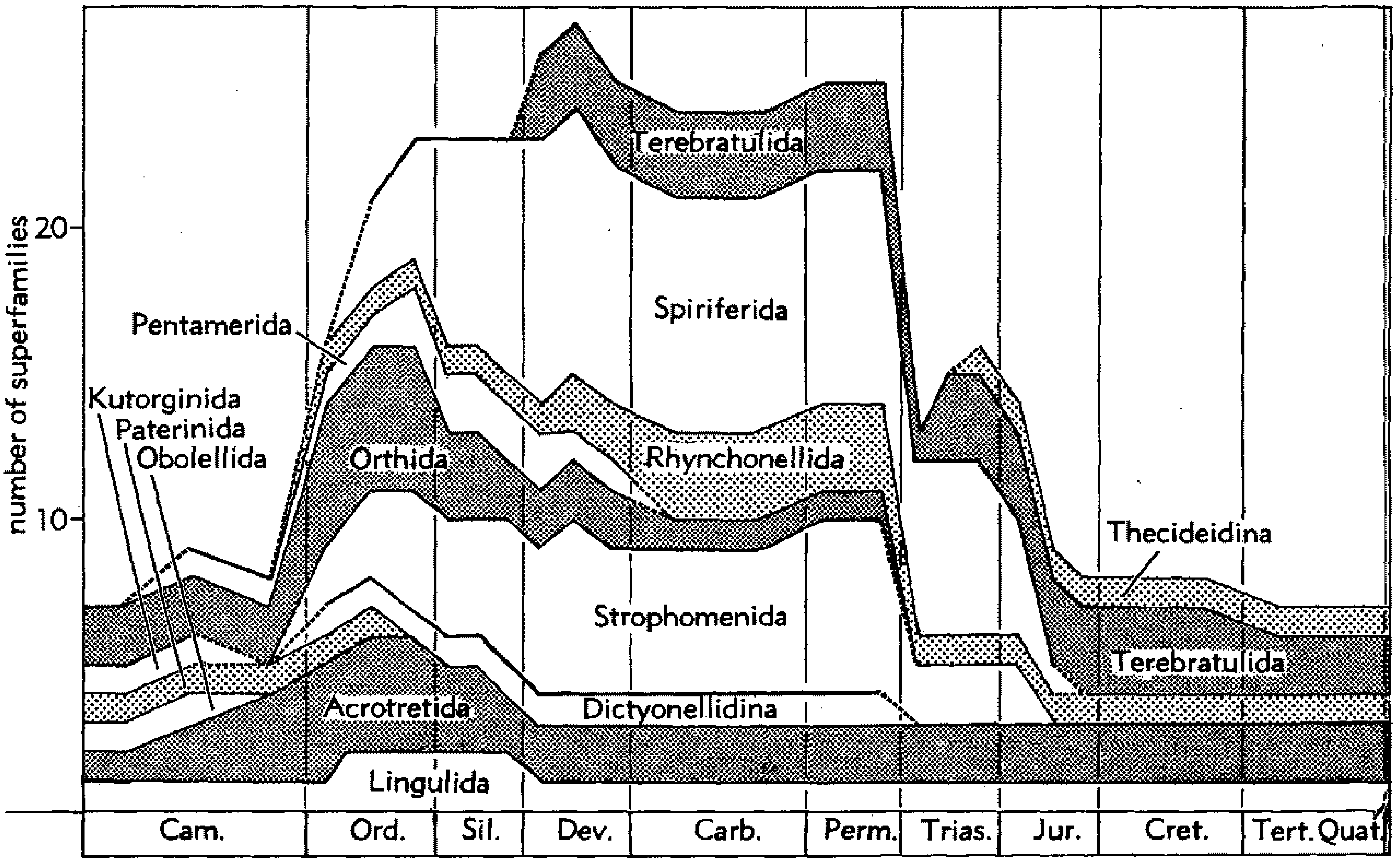

FIG. 148. Stratigraphic distribution of Brachiopoda according to number of superfamilies (5).

taken from most sedimentary rocks of marine origin, but with a clear majority from assorted shallow-water deposits. It is also becoming apparent that communities maintained by subtle differences in facies and associations endemic to major provinces were as common in the past as they are today. In all, the relationships between and within faunas in time and space have always been complex and are likely to be grossly misinterpreted through incompleteness of the fossil record.

Some of the effects of such facies controls may be identified in a time-frequency chart of all known genera (Fig. 149). The distribution shows the Late Silurian and Late Carboniferous as times of relatively few brachiopod genera, isolating the Ordovician, Devonian, and early Permian maxima from one another. This disparity can be explained in a number of ways. The minima may represent phases of depressed speciation immediately precursory to evolutionary accelerations affecting, for example, the Devonian Spiriferida and the Permian Strophomenida. They may represent faunas that for reasons of geographical inconvenience or personal taste have not been subjected to the same intensity of systematic research as, say, the Devonian assemblages. Yet it is also significant that the location of maxima and minima are mainly determined by systemic or subsystemic boundaries and, since these boundaries are related in general to important facies changes, generic variation could have been due to equally profound changes in past environments. Thus, the drop in number of genera recorded from the Upper Carboniferous coincided with the deposition of the largely nonmarine Coal Measures of Europe and North America, the two regions of the world with the longest tradition for systematic study of the brachiopods. Indeed, a good example of the difficulties involved in interpreting stratigraphic distributions of this sort is afforded by the Ordovician record.

The Ordovician was a period of unrivaled increase in the number of brachiopod genera. More than six times as many genera are recorded from the mid-Ordovician as from the Cambrian, and this proliferation

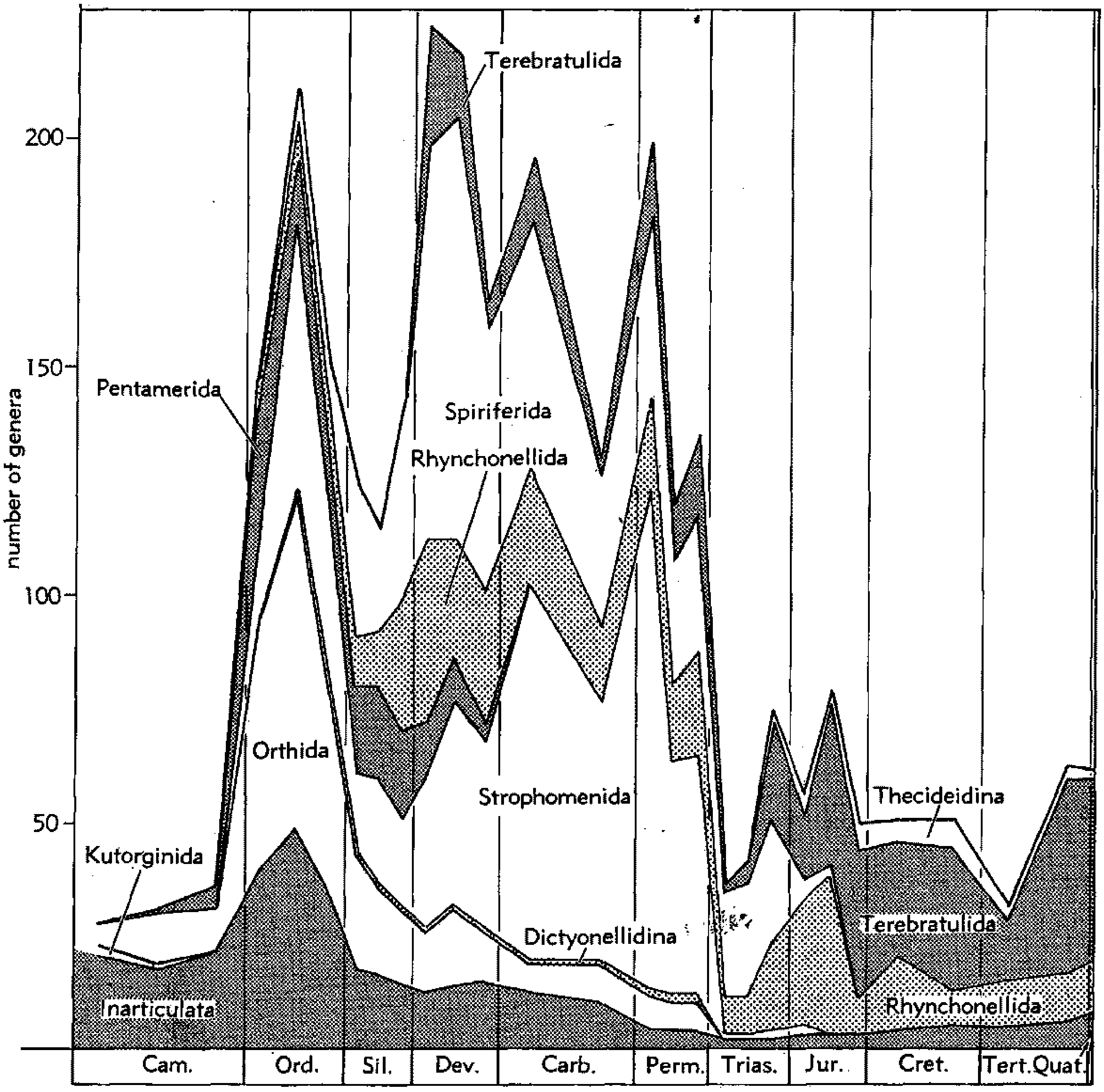

Fig. 149. Stratigraphic distribution of Brachiopoda according to number of genera (5).

is generally conceded to signify the most important radiation that affected the phylum. About 330 genera made their first appearance during the Ordovician, including 117 from the Early Tremadocian and 84 from oldest members of the Caradocian (or Porterfield) (Fig. 151). The former influx is as yet not well documented, but the latter is known to ~~coincide with a ma~~rine transgression that occurred during the ~~existence of the~~ ubiquitous graptolite ~~*Nemagraptus gracilis*~~ and seems to have affected much of the Northern Hemisphere.

By establishing new channels of communication between hitherto isolated basins and opening up newly flooded areas for exploitation by marine faunas, transgressions on this scale can promote ~~rapid migra~~tion and speciation, each contributing to an increase in the number of genera registered for a given area. Both influences seem to have been operative during early Caradocian times and may be identified in the following manner. A cluster analysis of brachiopod assemblages recovered from the shelly facies of North America and Europe ~~shows that~~ at least two ~~well-defined indig~~enous faunas existed in this part of the world during mid-Ordovician time (Fig. 152). One extended from Nevada to Scotland, the other from the eastern Baltic to North Wales, although both were affected by diversification, as can be seen in the low correlations of the Ward Cove and Spy

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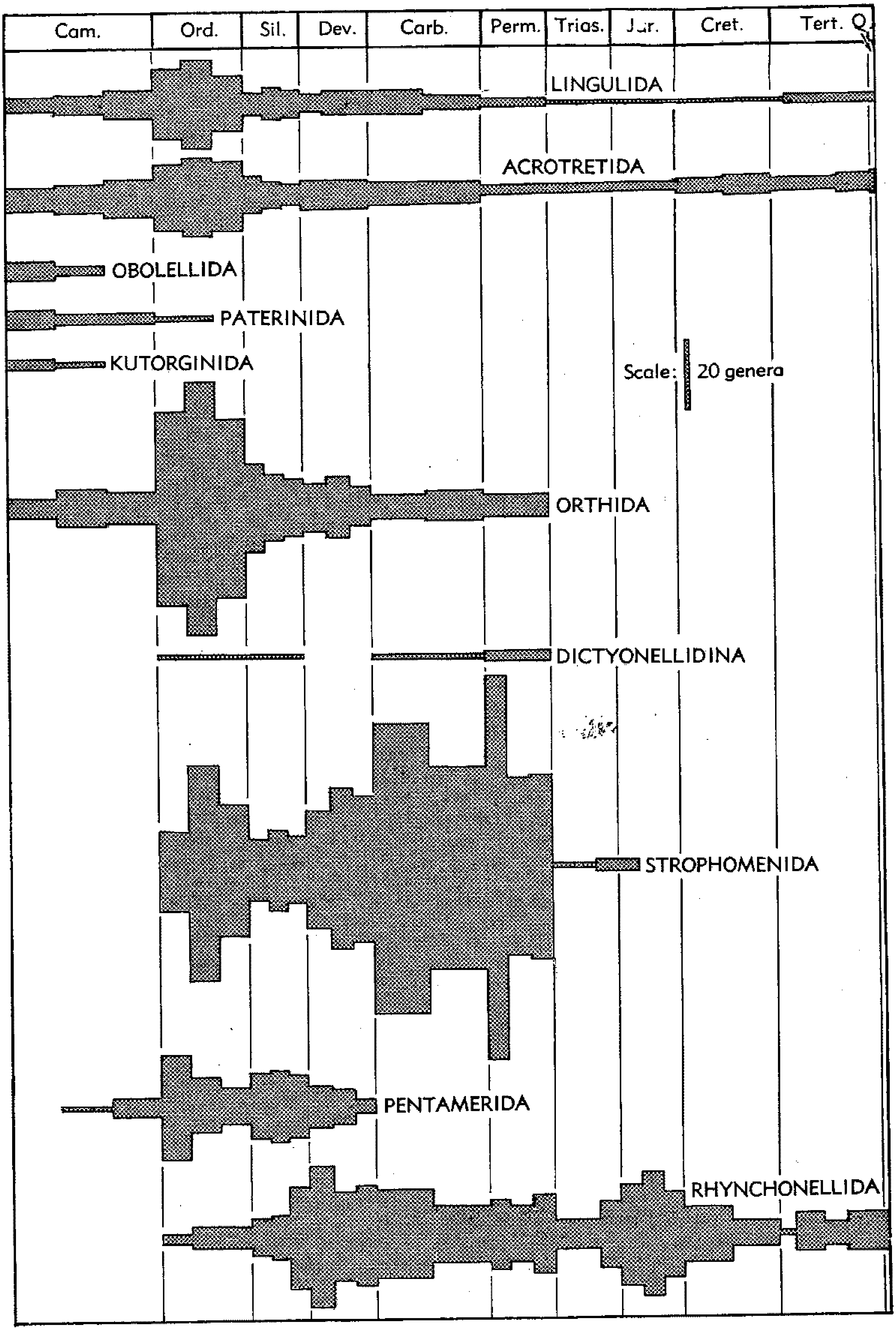

FIG. 150. Stratigraphic distribution of Brachiopoda in orders or suborders and proportionate to numbers of genera (5).

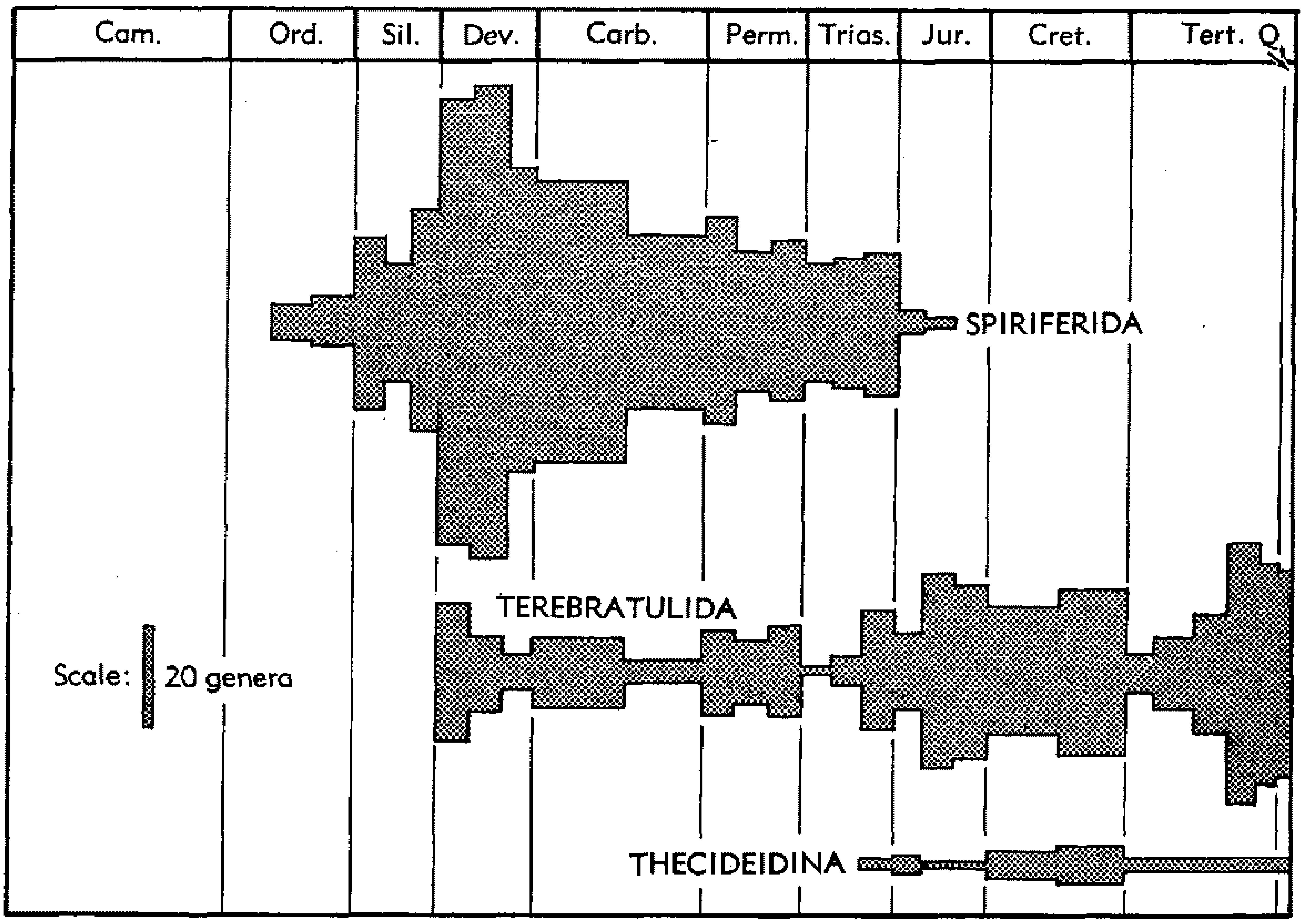

FIG. 150. *(Continued.)*

Wood Grit assemblages within their respective provinces. Various elements of the early Caradocian influx, however, appeared everywhere and can be segregated into two distinct groups. Among new genera, 52 of 84 belong to families or subfamilies already represented in one or both provinces and could conceivably have arisen by rapid speciation *in situ*. The remainder are the earliest members of families or subfamilies to which they have been assigned. They include inarticulates like the craniopsids, and scaphelasmatinids, and articulates like the dolerorthids, linoporellids, kullervoids, parastrophinids, xenambonitinids, bimuriids, and rafinesquinids. Such stocks are so different from their contemporaries that they must have had a long evolutionary history in an unidentified basin (or basins) which first became connected with the North American and European provinces during ~~mid-Ordovician time.~~ Moreover, it is possible that this massive immigration also included some members of the first group which had evolved more gradually elsewhere. Hence the sudden increase of genera registered for the mid-Ordovician may ~~not~~ be so realistic an index of an acceleration in evolution as is generally believed.

~~Complications comparable with~~ those outlined above must continually have affected the geological record of the Brachiopoda and important changes in distribution are to be expected as systematic study proceeds. It is possible, however, that sampling is already thorough enough to give a reasonably accurate picture of the relative importance of various groups from one system to another. Some idea of the changes in faunal composition that occurred throughout time may, therefore, be profitably gauged from the distributions shown in Figures 153 and 154, and the following comments may be appropriate.

Except for the Cambrian, the Paleozoic may be described as the era of the Orthida, Spiriferida, and Strophomenida. The inarticulates were certainly conspicuous elements in the earlier phases of brachiopod descent, for they comprise about two-thirds of the Cambrian faunas. Yet only the Acrotretida were comparable in generic representation with the Orthida, which soon became so prolific as to outnumber the entire

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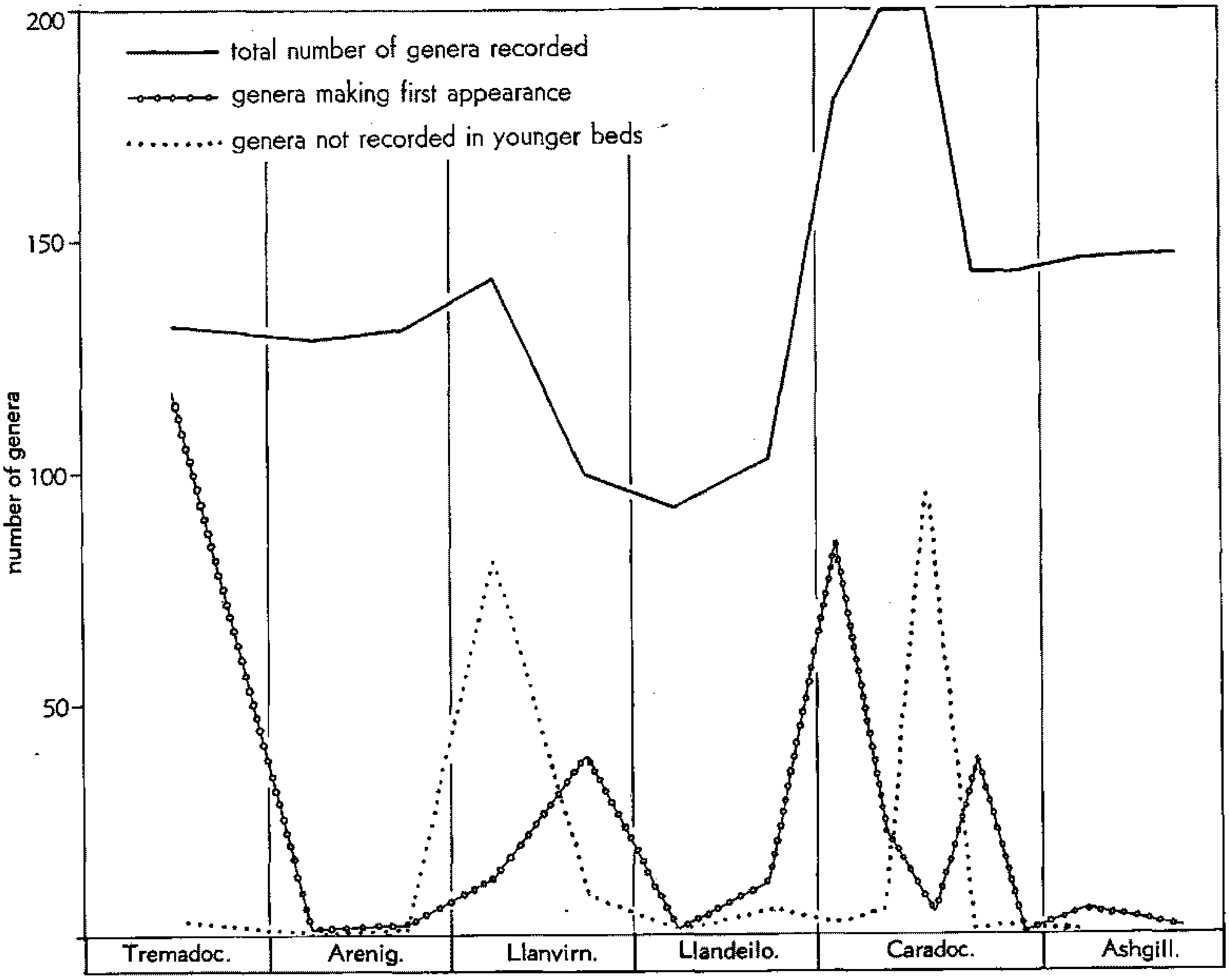

FIG. 151. Variations in total number and first and last appearances of brachiopod genera throughout Ordovician time (5).

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class of inarticulates by early Ordovician times. Throughout the Ordovician, the Orthida, notably orthaceans and enteletaceans, remained dominant. They embraced about one-third of the brachiopod faunas and their supremacy was never seriously challenged by either the Strophomenida, which superseded the inarticulates in the Middle and Late Ordovician successions as the second most diverse group, or the pentameroid porambonitaceans, which had first appeared in the mid-Cambrian and were quite common in the Early Ordovician. These oldest strophomenoids were initially represented exclusively by the plectambonitaceans and strophomenaceans, since the davidsoniaceans are not now recorded from successions older than Middle Ordovician. Of the remaining groups that arose during the period, early Rhynchonellida and Spiriferida were indisputably the most significant to future development of the phylum. The Clitambonitidina are noteworthy for their restricted range, being unknown outside the Ordovician; they were relatively rare constituents of most faunas, however.

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The history of the Spiriferida illustrates the rapidity with which new stocks may become established. By early Silurian time Athyrididina, Spiriferidina and especially Atrypidina amounted to about one-quarter of the total brachiopod faunas; and, apart from the mid-Silurian, when they were temporarily ousted by the strophomenoids (principally strophomenaceans), they remained dominant throughout the period. The replacement of the Orthida was equally decisive. They remained as the second most common group of brachiopods during the Early Silurian but thereafter their relative importance became greatly diminished, despite persistence of the enteletaceans and a minority of orthaceans into the Middle Paleozoic (triplesiaceans became extinct before

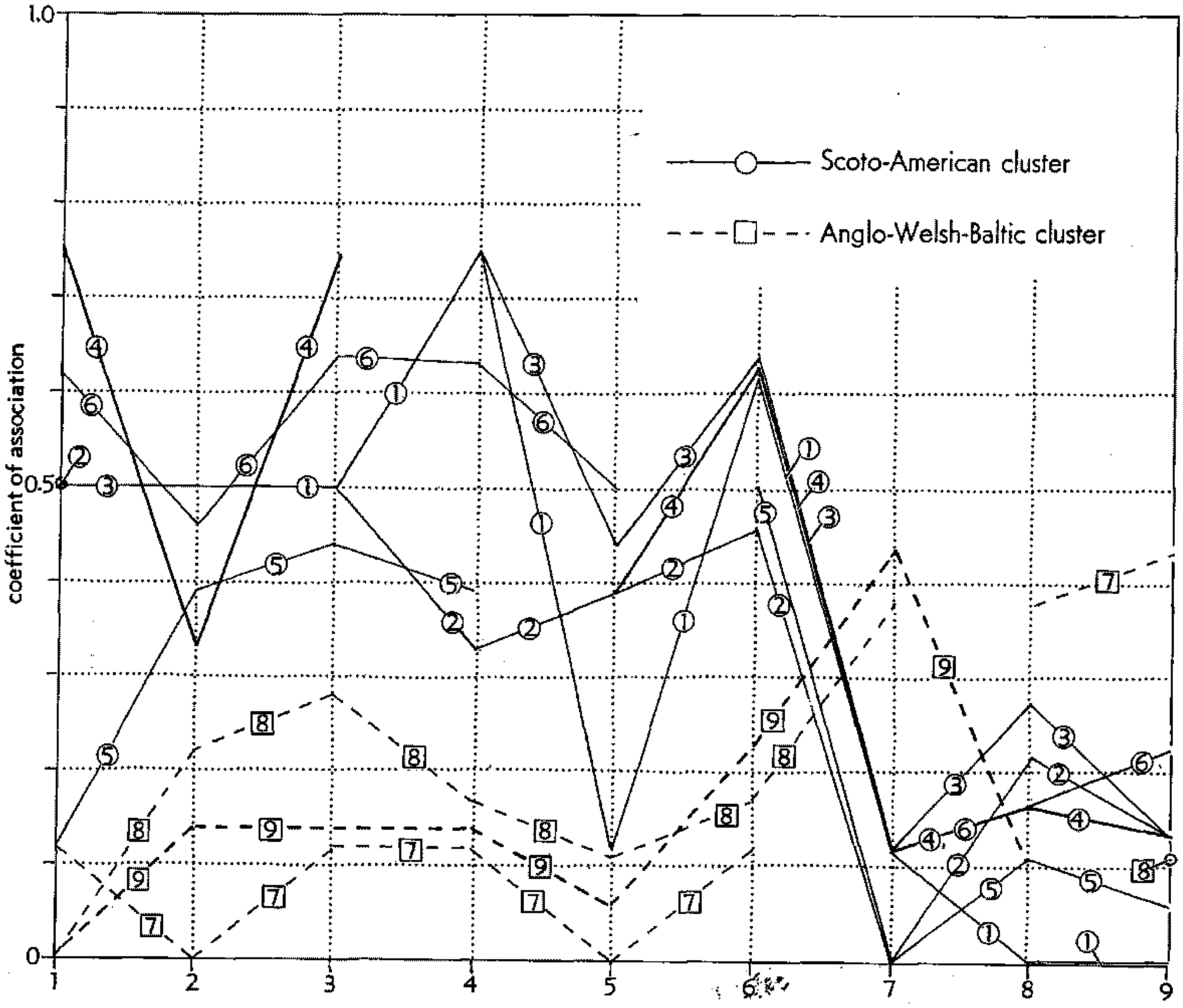


FIG. 152. Correlation profiles of nine Ordovician brachiopod faunas (*1,* Yellow Ls., Nev.; *2,* Mountain Lake, Okla.; *3,* Pratt Ferry and Little Oak, Ala.; *4,* Arline, Tenn.; *5,* Ward Cove, Va.; *6,* Stinchar Limestone, Scot.; *7,* Derfel Limestone, North Wales; *8,* Spy Wood Grit, Eng.; *9,* Kukruse Stage C_{II}, Eastern Baltic (refs. 1-4 and unpublished data). The coefficient of association was calculated by eliminating genera recorded in all successions and expressing the residue in common between any two faunas as a proportion of the smaller assemblage (5).

the end of the Silurian). Pentamerida, mainly pentameraceans, are widely regarded as typical of the Silurian as well as the Devonian. But this impression is a reflection of their restricted range, rather than their profusion, because they were consistently only the third most commonly occurring group and were even surpassed in respect of generic numbers by the Rhynchonellida throughout the Late Silurian. The most significant additions to the phylum during this period included the Spiriferida, Chonetidina, Stenoscismatacea, and Terebratulida, which first occur in transitional beds between the Silurian and Devonian.

Well more than one-third of the brachiopod genera recorded from the Devonian were Spiriferida, which persisted as the most important group throughout the period. There was, however, a subtle replacement within the order in that the spiriferaceans superseded the atrypaceans, which dwindled and became extinct by the end of the Devonian. Moreover, the rhynchonelloids were displaced by the strophomenoids as the second most common group throughout the Middle and Late Devonian. This transposition took place despite the extinction of the plectambonitaceans. It resulted from a late proliferation of the strophomenacean stropheodontids and particularly of the Productidina, which became the dominant Strophomenida during late Devonian times. The Terebratulida were initially conspicuous mainly through the advent of a number of centronellidine genera. They were, however,

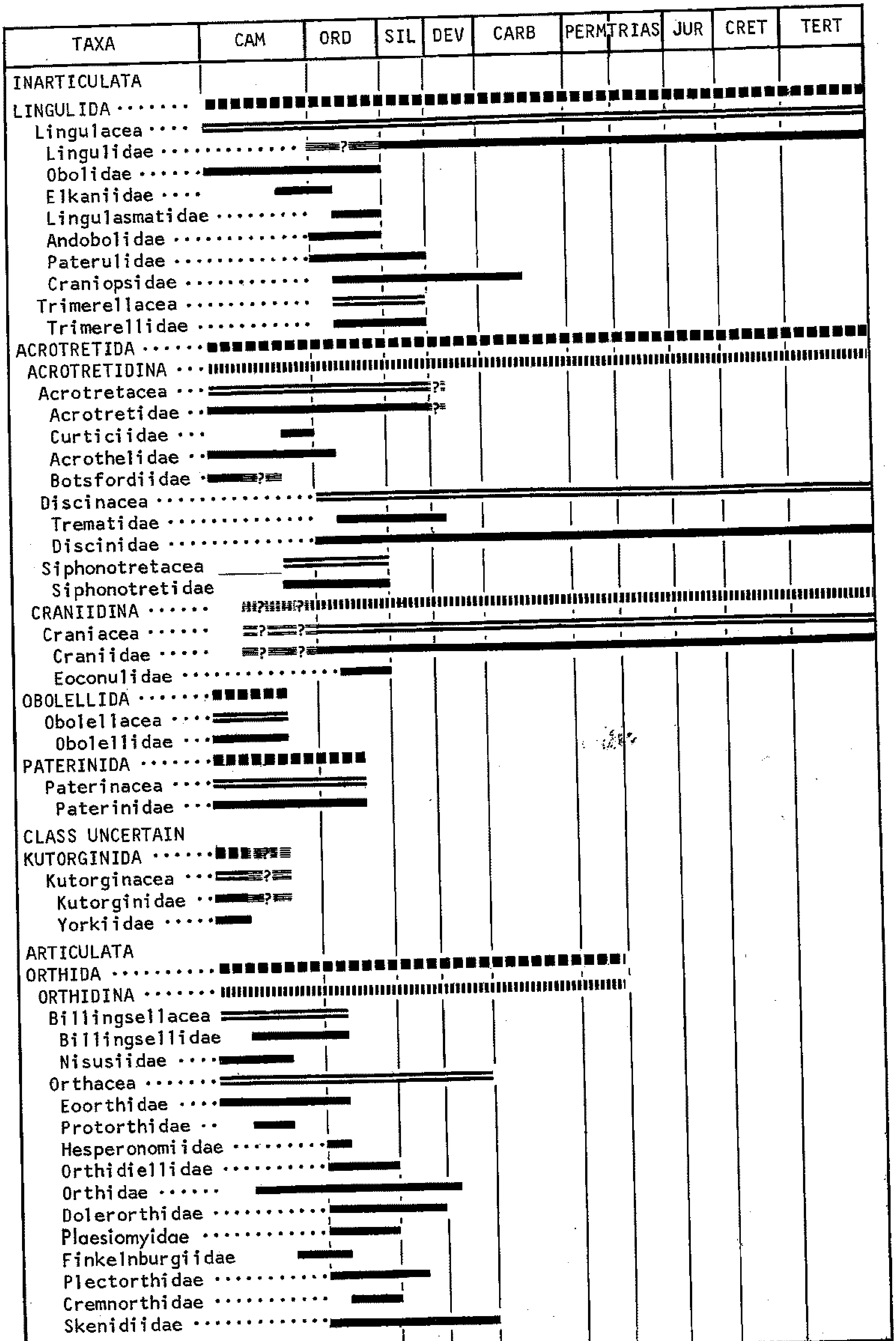


FIG. 153. Stratigraphic distribution of families and higher taxonomic units of Brachiopoda (5).

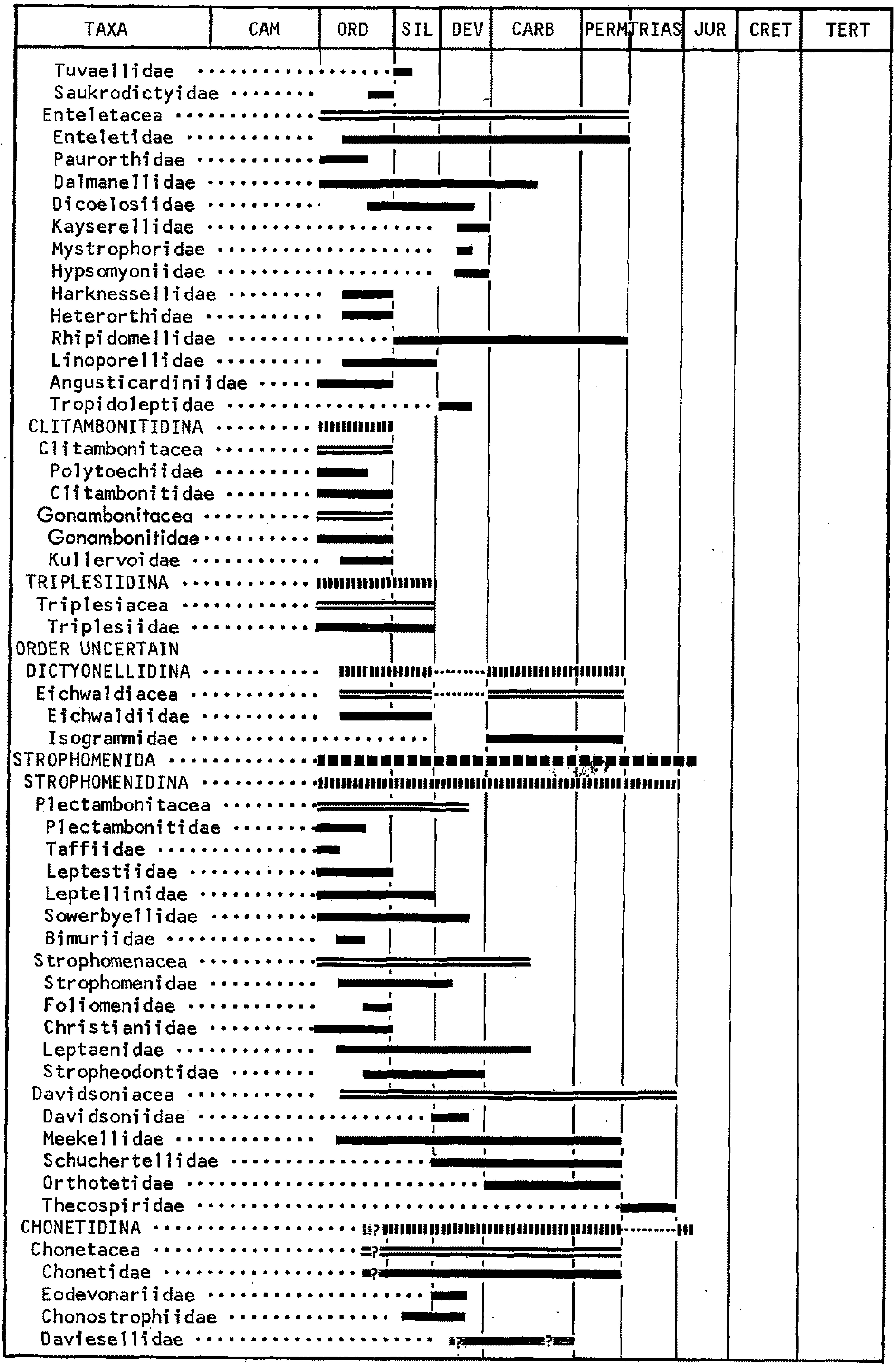


Fig. 153. (*Continued.*)

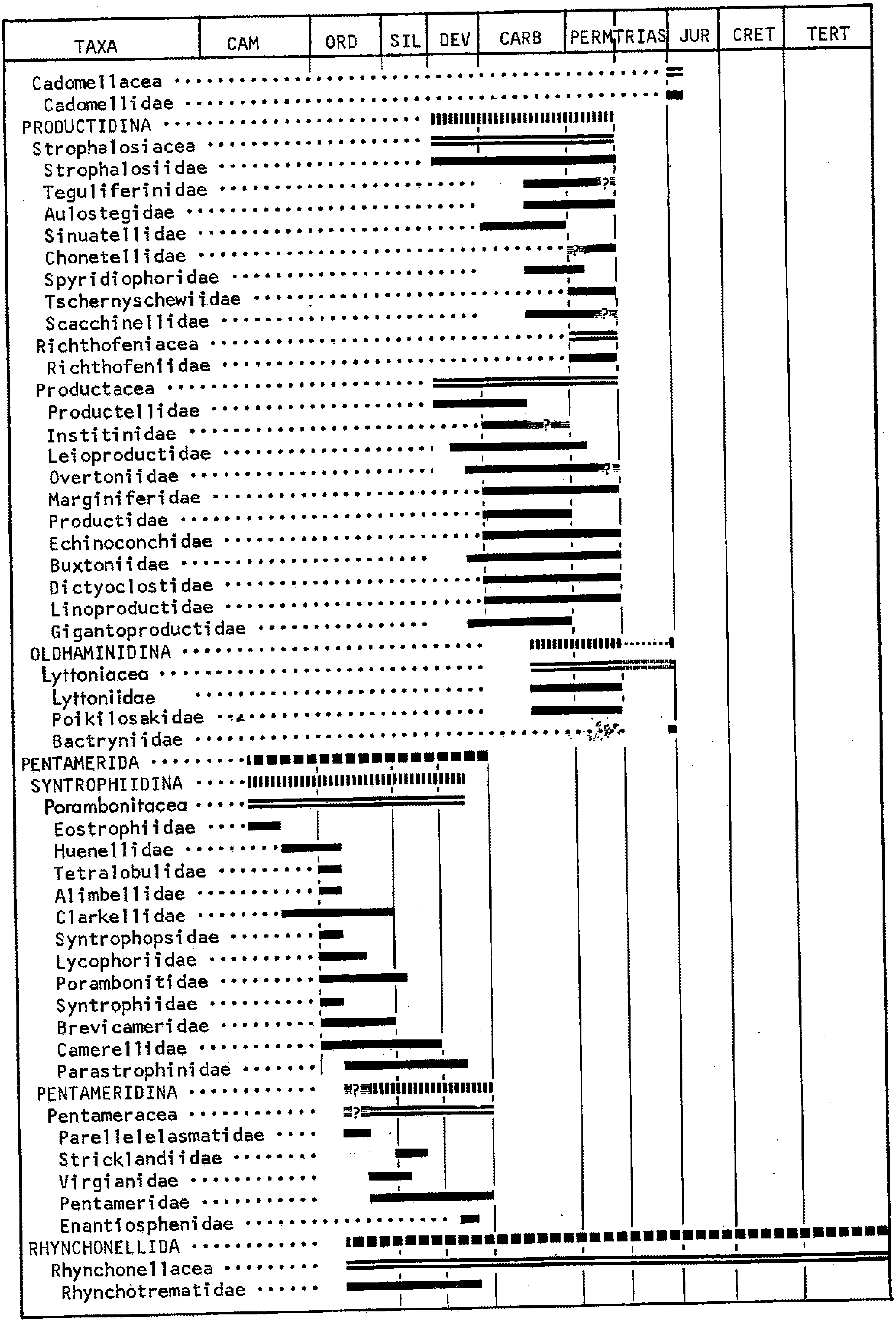
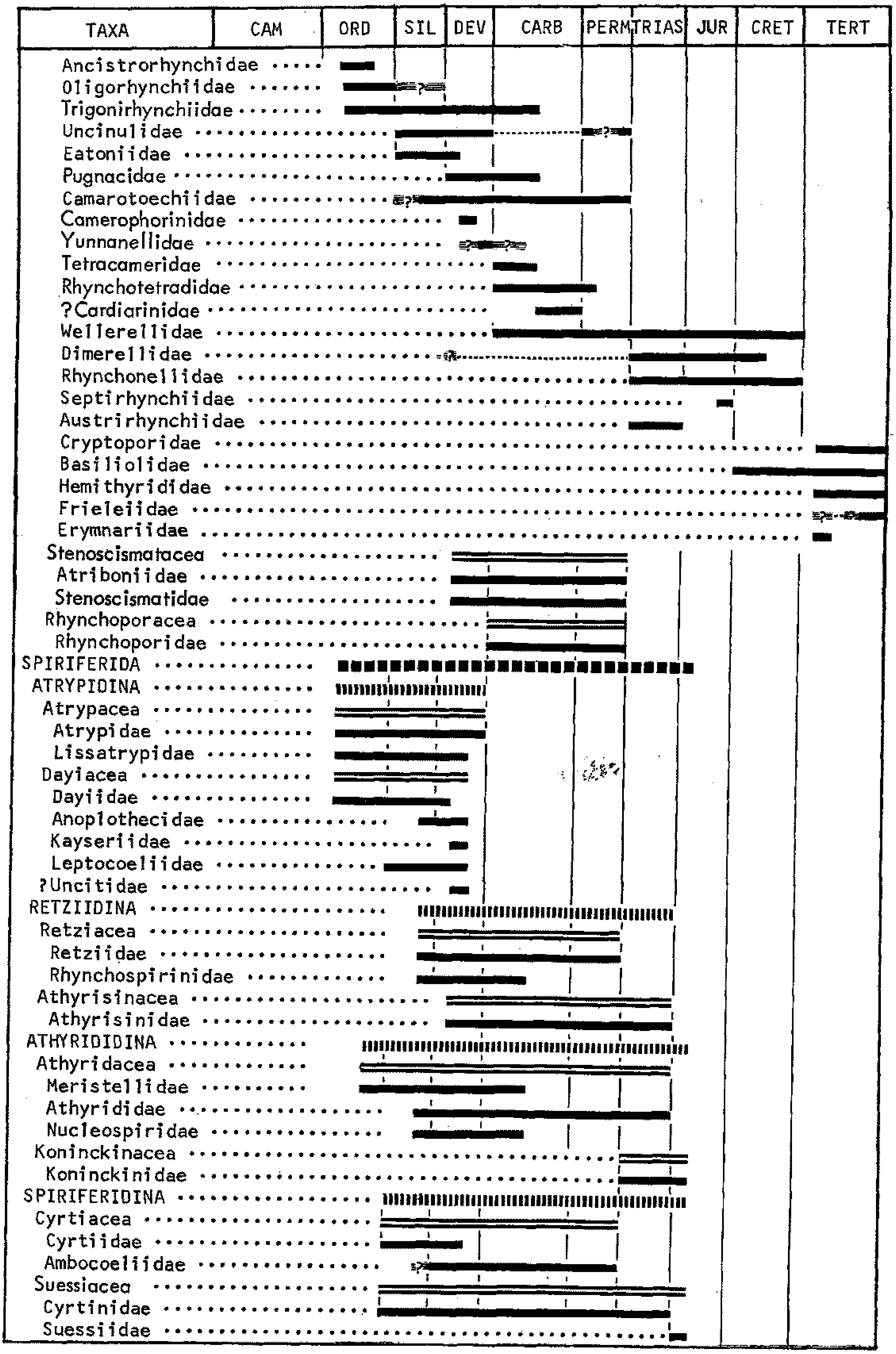


Fig. 153. (*Continued.*)



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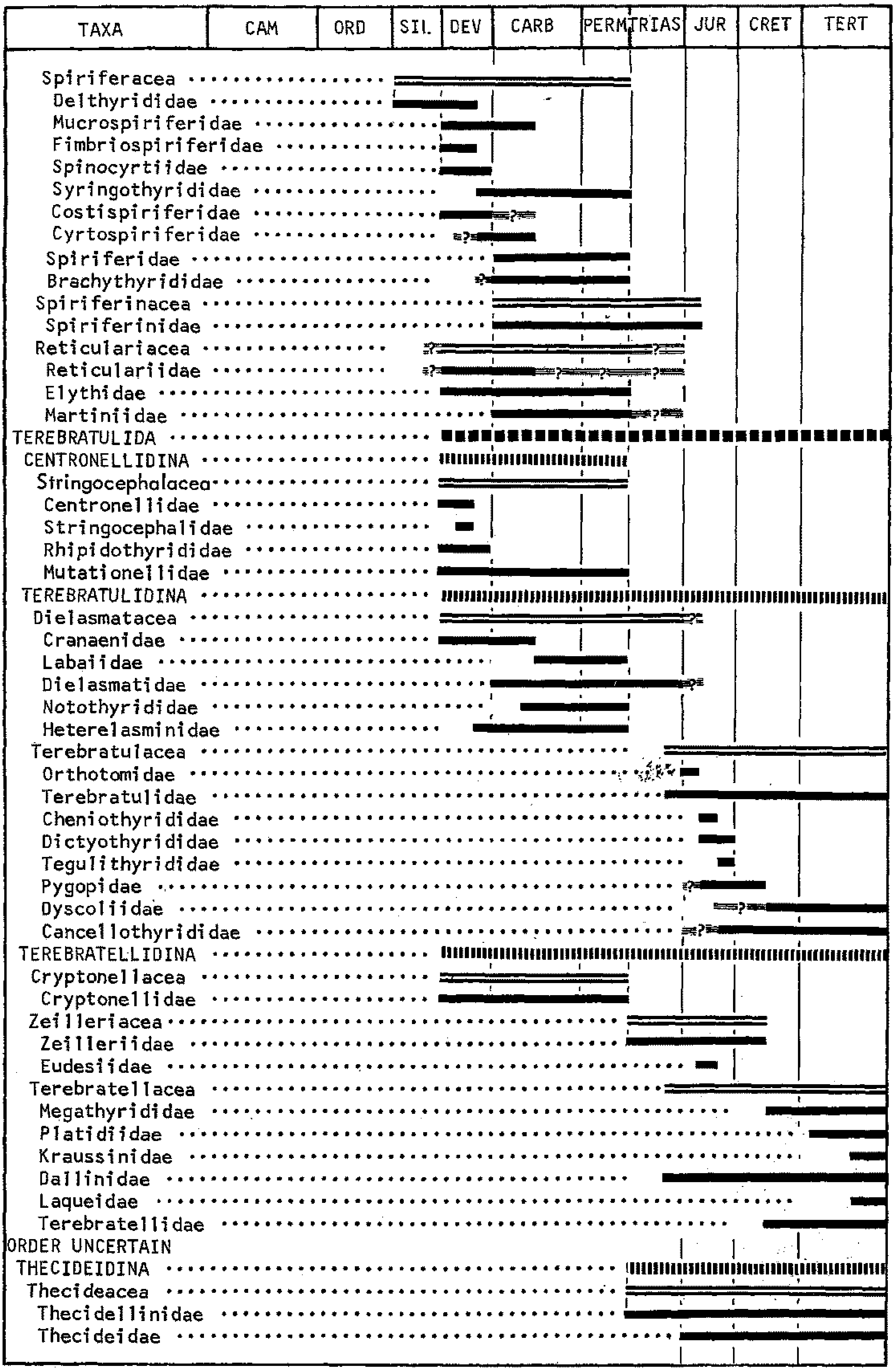

FIG. 153. *(Continued.)*

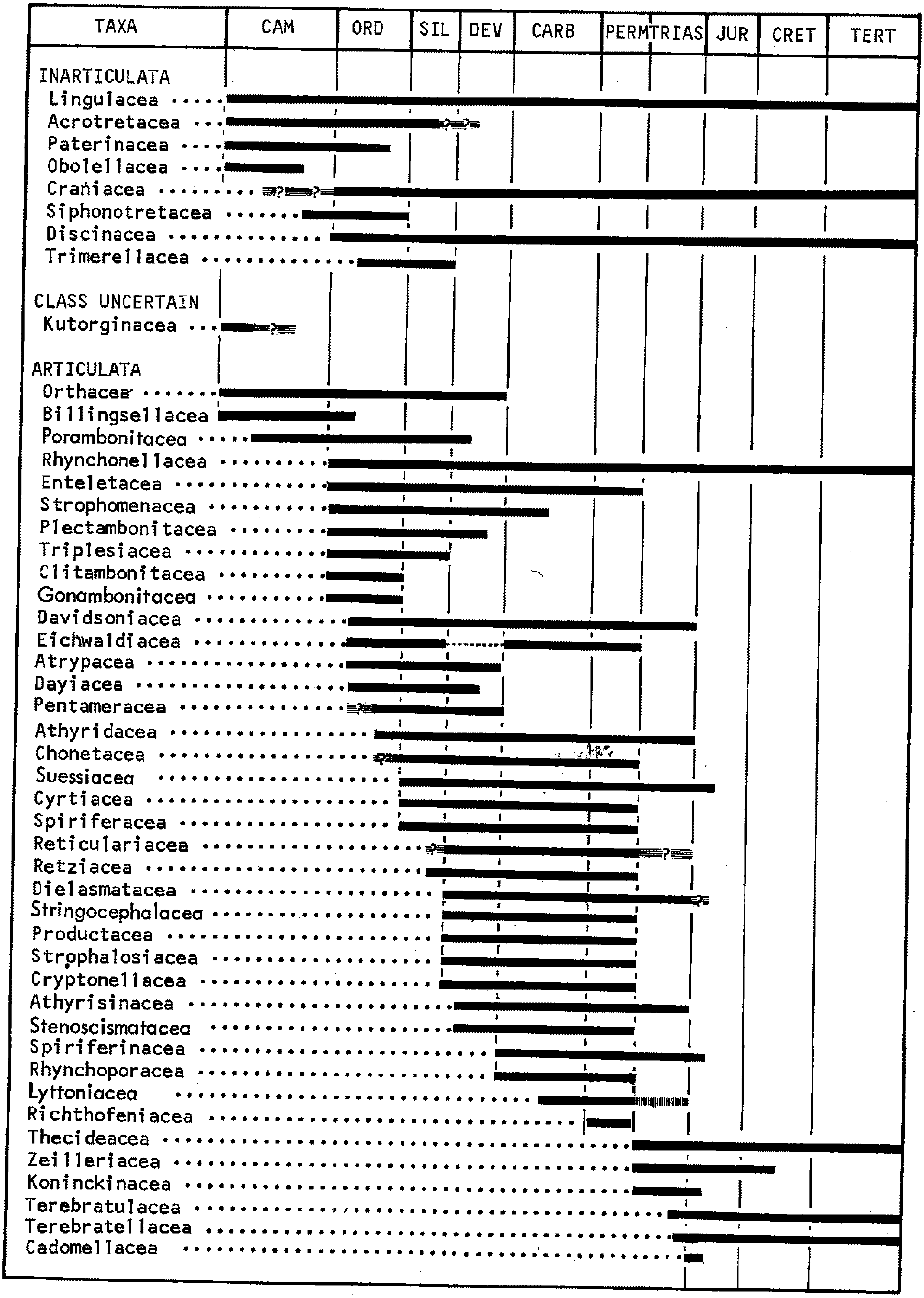

FIG. 154. Stratigraphic distribution of brachiopod superfamilies plotted according to order of their appearance (5).

less common than the Orthida throughout the rest of the period, although the orthaceans themselves became extinct before the beginning of the Carboniferous, leaving the enteletaceans as sole representatives of the order.

The ascendancy gained by the Productidina within the strophomenoid group became even more marked during the Permo-Carboniferous and indeed greatly contributed toward establishing the Strophomenida as the most diverse order throughout both periods. The productaceans formed the largest superfamily, with more genera during the Carboniferous than those assigned to all other groups. Yet by early Permian times, the chonetaceans, davidsoniaceans, Oldhaminidina, which are first known from the Late Carboniferous, and strophalosiaceans together became more numerous. The spiriferoids and especially the spiriferaceans and reticulariaceans, which thrived in more or less equal strength, were as consistently the second most commonly occurring group as were the rhynchonelloids the third. In fact, more than 80 percent of the brachiopod faunas then extant belong to these three orders and the remarkable changes that took place during the Mesozoic were mainly the consequence of a widespread extinction. Thus no member of the enteletaceans, productaceans, davidsoniaceans, richthofeniaceans, strophalosiaceans, spiriferaceans, cyrtiaceans, stenoscismataceans, rhynchoporaceans, Centronellidina, and dielasmataceans have yet been recovered from post-Paleozoic successions. This unprecedented reduction affected all taxonomic ranks of the Brachiopoda and not only marked the end of the Orthida, the first-established articulate order, but also the prelude to disappearance of the strophomenoids and spiriferoids. Admittedly, the spiriferoids, chiefly athyridaceans, survived in sufficient strength to become the commonest Triassic brachiopods; but along with a few strophomenoid derivatives they ultimately became extinct in the Jurassic.

With the elimination of such large and long-established orders, the Rhynchonellida and Terebratulida ultimately emerged as the dominant articulate brachiopods, although both groups remained subordinate to remnants of the Spiriferida during Triassic time. Throughout much of the Triassic and on into the Early Jurassic, the rhynchonellaceans were more numerous than the Terebratulida, which were represented mainly by the terebratulaceans. But by mid-Jurassic time, the terebratuloids, especially the terebratulaceans and zeilleriaceans, replaced the rhynchonelloids as the most prolific brachiopod order. This position has been maintained up to the present day by an increase in the number of terebratellacean stocks, which has more than counterbalanced the extinction of the zeilleriaceans and the decline of the terebratulaceans during Cretaceous time. The only other brachiopods living today are, significantly, descendants of two of the oldest orders, the inarticulate Lingulida and Acrotretida, and the youngest group to come into being, the thecideaceans.

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TECHNIQUES FOR PREPARATION OF FOSSIL AND LIVING BRACHIOPODS

By Alwyn Williams
[The Queen's University of Belfast]

Brachiopods have flourished at some period or another in nearly every type of marine environment since Cambrian times, so that, like representatives of many other phyla, their occurrence is registered in such a variety of ways that a number of techniques have come into use to facilitate the study of their record. These modes of preservation are all ultimately related to the degree to which closed or gaping shells or disarticulated valves remain unaltered after their burial. Skeletal remains may have been so unaffected by diagenesis as to permit detailed studies of their shell structure, a state of preservation that is found even among Cambrian articulate brachiopods. Quite commonly, however, the original shell substance has been partially or completely recrystallized or replaced by dolomite, pyrite, or silica. It may even have been dissolved away completely, without replacement, leaving external and internal molds which bear the impressions of exterior and interior surfaces of the shells or valves. Clearly, the techniques involved in the study of molds or altered shells serve only to reveal morphological detail, but those employed in the examination of unaltered shells may also furnish information on shell deposition and growth.

In general, molds are eminently satisfactory for purposes of morphological reconstruction, because the counterparts can be used to prepare casts of both internal and external features. A number of casting materials, including waxes and plastics (18) are widely favored but modeling clays, like plasticene, and various latex solutions, with or without plaster fills, are among the simplest and most efficient media in use. Plasticene, with a wetted surface to prevent adhesion, provides adequate impressions for day-to-day purposes; but permanent casts, especially of molds that accommodated long, obliquely disposed apophyses, are best obtained by using latex solution. Good casts free of air blisters are usually obtained by wetting the mold surface with a diluted detergent to reduce surface tension, and applying a thin first coat of latex carefully decanted into undercut indentations of the mold. Further coats should then be added to build up a thick but pliable cast. The translucency of dried natural latex is disadvantageous to the microscopic examination and photographing of casts even when they are coated by a sublimate like ammonium chloride, but casts can be opaquely colored by adding small quantities of india ink or organic dyes to the liquid latex stock.

A profitable examination of shells that have been recrystallized or dolomitized depends on how distinguishable they are from their containing matrix, which, more often than not, has been similarly affected. Selective silicification that has commonly resulted in the replacement of articulate shells in carbonate rocks, however, has proved a boon for the study of morphological variation.

The process of dissolving silicified organic remains out of carbonate rocks by dilute acids has been known for a long time (8, 21) but was not practiced on a large scale until the 1930's when Cooper began his systematic investigation of the American Ordovician brachiopods and his studies (5, 17) are a testimony to the efficacy of this technique. Dilute hydrochloric acid may be used to etch silicified shells out of limestone blocks, but this acid also attacks the unsilicified chitino-phosphatic shells of inarticulates and, following Bell (2), dilute acetic acid or the more quickly acting formic acid are now more popular etching agents because their use ensures the recovery of the inarticulate elements in the fauna. During etching, certain delicate structures, like loops or spires, that gradually appear may break away in the final stages of solution of their supporting matrix. To prevent such destructive collapses, Cooper (12) has used paraffin wax as a temporary embalming medium which may later be removed with xylol; and Cloud (4) has advocated the painting of those parts of the fossil content requiring strengthening and protection with cellulose acetate. Silicified shells recovered by etching are normally brittle and may even be hollow, and thus subject to collapse, because replacement may have been limited to thin external and internal skins to the original shells. It is therefore advisable to harden specimens by thinly painting them with liquids, like polyvinol acetate emulsion (12) or "lustrex" dissolved in acetone, which dry out to form a tough protective binding cover.

The preparation of unaltered shells and valves for examination is nearly always a more exacting task than those just described. Even when specimens have been washed out from clays and sands it is likely that adherent particles obscure the finer morphological details, and although the penetrative effects of ultrasonic tanks and detergents are invaluable aids in the final stages of cleaning, patches of matrix may still have to be removed by mechanical means. The simplest method, and also one over which the most delicate control can be exercised, is, of course, the scratching away of matrix with needles, either permanently mounted or held in chucks. COOPER (5) has found that if the needle points are beveled they can be used as fine chisels and such microscopic cutting edges greatly facilitate the scraping away of material and minimize the damage done to the shell surface. During such preparation, surfaces are best kept wet, not only to soften some types of matrix but also to accentuate the visible contrast between shell and matrix. Even for specimens in rock, the final cleaning is best performed in this manner, although there are other means for reducing the volume and toughness of the enclosing matrix.

Dental equipment with electrically driven cutting wheels and chisels or similarly fitted percussive implements can be safely used for removing much of the matrix. Certain chemicals like caustic potash (17), hydrogen peroxide, and gasoline (see SOHN in 16) have been used in an attempt to find effective methods of disintegrating argillaceous or arenaceous rocks. Carefully applied dilute acid may also be used to remove carbonate matrix (see, for example, 5), but, in general, such methods are only partially successful, because of the wide range of bonding properties of rock cements; accordingly, they should be regarded only as ancillary to the more painstaking process of mechanical dissection. Indeed, the rock containing brachiopods may be so intractable that removal of the shell, thereby providing external and internal molds, is an easier and less hazardous operation. Thus, dilute acid may be used to dissolve away shells embedded in noncarbonate rocks, especially tough mudstones and siltstones which give very fine external and internal impressions; although slight carbonate diffusion into the matrix immediately adjacent to the shell may ultimately leave the mold surfaces friable enough to require hardening.

Specimens embedded in matrix which is sufficiently calcareous to preclude the use of acids may be transformed into molds by calcining the shell. This method was first recorded by BUCKMAN (3), who suggested that specimens should be heated until the shell becomes powdery and then should be plunged into cold water. The technique can be very wasteful of material because most matrices, including the finely grained ferric ones which provide the best molds, are liable to crack and explode, not only during their immersion in water, but even while they are being heated. On the whole, the more cautious approach adopted by COOPER (5) of removing the calcined shell by dissection, rather than by slaking, is preferred.

Under certain conditions of deposition, buried shells may be so tightly closed as to contain only a small quantity of sediment, and during diagenesis the remaining shell space may become filled with clear calcite. Such a matrix has been used to great advantage in the study of internal features because, being soft and transparent, it can easily be cut and chiseled to expose the skeletal remains. In this medium it is possible even to dissect out such fragile structures as loops and spires (GLASS, 8). But, generally, nothing more is required for studies in the variation of lophophore supports (10) than to chisel away the anterior part of the shell of a number of specimens and then to clear the calcite of abrasive marks by controlled application of dilute acid. Such prepared surfaces coated with glycerine give satisfactory views of the entombed structures.

Other techniques that currently aid in the study of unaltered shells mostly involve the preparation of serial sections. Critical comments have been made in the past about these methods of investigation (14, 17); but they are only justifiable for those procedures which do not provide any permanent record of successive sections through a specimen except for camera lucida drawings or photographs of internal and external outlines of the shell substance. When carried out with all its modern refinements, however, serial sectioning gives an accurate picture not only of the gross morphology but also of the growth relationships and composition of the skeletal parts. Indeed, it can be claimed that no comprehensive review of morphological variation within a group of brachiopods is complete without the kind of supplementary information that is obtained only from the study of serial sections.

The most sophisticated procedure is based on taking impressions of differentially etched sections of a shell. It has been known to paleontology for at least 50 years but apparently was not used for the interpretation of brachiopod morphology until the 1930's when St. Joseph (15) carried out his investigations of lower Paleozoic articulates. Since then a number of refinements have improved the technique, and although individual taste gives rise to some variation in procedure, the following steps are known to yield satisfactory results. Before mounting a specimen for sectioning, it is usually necessary to produce a replica of it. Rubber compounds, like latex, are commonly used to make a pair of mold blocks of the specimen which can then be filled with a solidifying plaster and pressed together until a complete cast has annealed and set (11).

The mounting of a specimen within an appropriately sized block of an acid-resistant substance is essential for reasons that will soon become obvious. Plaster of Paris or dental plaster is still commonly employed for this purpose (11), but any one of the laminar resins (e.g., Marco Resin) is superior because it is much freer of air bubbles and more closely adherent to the external surface, thereby preventing any deep corrosion along this interface; and because the specimen can be clearly seen within such a medium and thus oriented to any desired position for sectioning. The external surface of the specimen may be intricately ornamented or friable or pervaded by microscopic cracks, so that it is advisable first to soak the shell in resin for some hours. In the meantime, the floor of a tray made out of aluminum foil or pliable plastic (individual ice cube trays are big enough for most specimens) is covered to a required depth with polymerizing resin. In due course this hardened resin provides a solid base on which to rest the soaked specimen and polymerizing resin is then added to immerse the specimen either in one operation or, if the shell is big, in successive stages to prevent the development of tension cracks during hardening. When the resin is completely polymerized, only the surface in contact with the atmosphere remains sticky (this can be cleaned with acetone) and the resin, which is easily ejected from the tray, is squared off relative to the preferred orientation of the contained specimen. The base of the prepared block is then soldered by beeswax to the attachment plate of a grinding machine that is calibrated to control the abrasive reduction of the top surface of the resin block by as little as 10μ. The Croft parallel grinding instrument (6), now manufactured by the Cutrock Engineering Co., Ltd., is the best known of these machines; but Hendry, Rowell, & Stanley (9) have recently described equipment which prepares the ground surfaces much more quickly.

Once mounted in position, the top surface of the block is ground down until the shell substance first appears. This exposed area of shell is then etched with dilute acid (dipping the surface about 15 times in 10 percent HCl is normally sufficient), washed, and allowed to dry. A negative impression of the prepared surface can be obtained in a number of ways. The common practice is to apply a thin coat of one of the commercial collodions or a similarly constituted laboratory preparation; for example, cleaned nonsafety film cut into small pieces and added to amyl acetate can be made to any required consistency (7) and has proved eminently successful. But good impressions can also be obtained more quickly by painting the etched surface with amyl acetate and pressing on to it a thin cellulose film. When the preparation has dried, it can be neatly

FIG. 155. Proximal oblique section of spine on brachial valve of *Acanthothiris spinosa* (LINNÉ), showing disposition of fibers in secondary layer, nonfibrous primary layer represented by black rim (cellulose peel, *ca.* ×200) (22).

peeled off the block by first lifting its edges with a razor blade. Subsequent to obtaining the first peel, the instrument is set to grind the block down by required thicknesses and at each interval a peel can be taken until the specimen has been completely abraded (Fig. 155).

Other methods of serial sectioning are practiced. They include the calcining of the shell and the differential staining of the matrix to enhance their contrast; and the drawing or photographing of successive sections (1, 11, 13); but they are certainly less efficient and informative than that described above. The great advantage of the preparation of peels is that they constitute a permanent record that can be used for future studies. Thus they can be projected like negative films to give enlarged photographic prints which in turn can be used as controls for the reconstruction of large-scale models in wax (20). Under high magnifications they show, in negative relief, such details of shell structure as the relationships between fibers comprising the secondary layers of articulate brachiopods. Indeed, these properties of cellulose acetate make it invaluable for rapidly preparing random sections of the shell as well as for determining fine details of the shell surface, like the shell mosaic, which can easily be reproduced without recourse to etching prior to the application of collodion (Fig. 156).

Finally, a few remarks about the preparation of living material seem appropriate here, because interpretive studies of fossil remains cannot really be conducted without reference to the relative distribution of soft parts in living brachiopods. Normally, anatomical sections are prepared by well-known biological techniques subsequent to the decalcification of the shell, the position of which, relative to its secreting epithelium, has to be inferred. It is, however, greatly to the advantage of the palaeontologist to be able to examine sections showing both shell substance and soft parts and the following procedure (19) gives satisfactory results.

A preserved specimen is bulk-stained with some suitable dye, like hematoxylin, and is then taken through a series of liquids in which the preservative is progressively re-

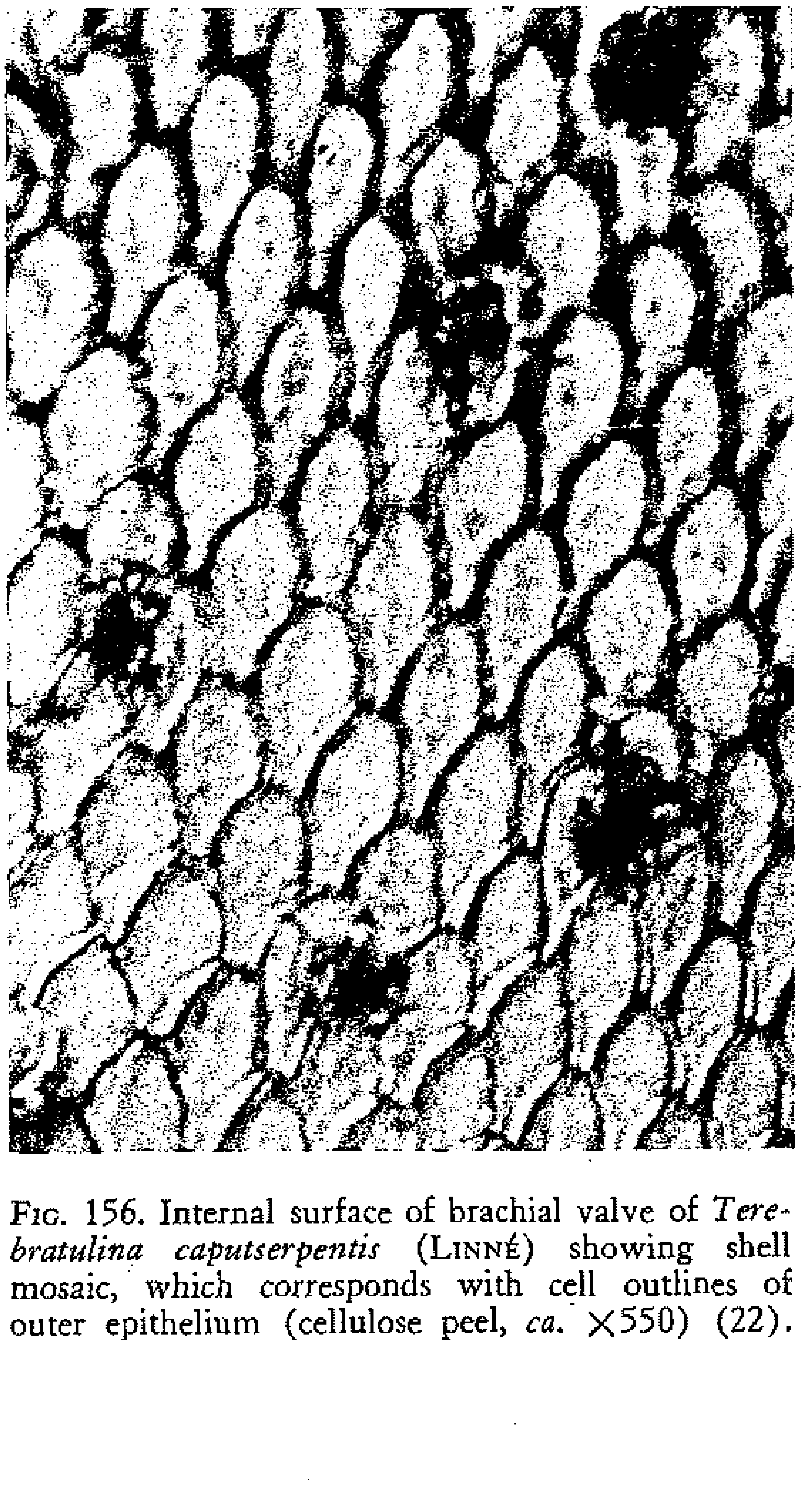

FIG. 156. Internal surface of brachial valve of *Terebratulina caputserpentis* (LINNÉ) showing shell mosaic, which corresponds with cell outlines of outer epithelium (cellulose peel, *ca.* ×550) (22).

FIG. 157. Part of section through posterior part of *Terebratulina caputserpentis* (LINNÉ) which has been bulk-stained and impregnated with resin before cutting, pedicle at top left, pedicle epithelium disposed in V at bottom left, pedicle valve with periostracum, primary and secondary shell and outer epithelium at right (*ca.* ×60) (22).

duced and acetone proportionately increased (Fig. 157). Once the pure acetone stage is reached the specimen is taken through a second series in which a laminar resin is increased at the expense of acetone (in respective proportions, for example, percentage ratios of 25/75, 50/50, etc.). The longer the interval of time between each transfer (2 or 3 days at least), the more complete the diffusion of increasing concentrations of laminar resin into the tissues. After soaking in laminar resin for a few days, the specimens can be mounted within polymerizing resin in the same way as a fossil shell, and the block containing the specimen can then be cut into a number of thin slices which, like those of rocks or minerals, can be prepared as microscope slides.

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SOURCE OF ILLUSTRATIONS

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SYSTEMATIC DESCRIPTIONS

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BRACHIOPODA

Phylum BRACHIOPODA Duméril, 1806

[Brachiopoda Duméril, 1806, p. 154] [=Palliobraches de Blainville, 1814, p. 179; Spirobrachiophora Gray, 1821, p. 238; Palliobrachiata de Blainville, 1824, p. 298; Brachionopoda Agassiz, 1848, p. 145; Brachionacephala Bronn, 1862, p. 224; Brachionoconchae Bronn, 1862, p. 228] [Diagnosis prepared by Alwyn Williams, The Queen's University, Belfast]

Solitary, marine, bivalved, coelomate invertebrates bilaterally symmetrical about median plane normal to surface of separation between valves; shell chitinophosphatic or calcareous, attached to substratum by muscular stalk (pedicle) or secondarily cemented or free and composed of commonly larger pedicle (ventral) valve and brachial (dorsal) valve lined by mantle extensions of body wall; epistome possibly represented by brachial fold in front of mouth, feeding organ (lophophore) filamentar, variably disposed and suspended between mantles; alimentary canal with or without anus; nervous system subepithelial, principal ganglion subenteric, located below esophagus; one, rarely two, pairs of metanephridia also acting as gonoducts; circulatory system open, commonly with dorsal contractile vescicle; coelom schizocoelic or enterocoelic; mostly dioecious. *L.Cam.-Rec.*

The term "Brachiopodes" was first used by Cuvier in 1805 (208a) for the "acephalous molluscs" *Lingula, Orbicula,* and *Terebratula,* but was not formalized until 1806 when Duméril (267a) proposed Brachiopoda as an order of Mollusca. Since then it has been customary to recognize the group either as a class of the Molluscoidea or Tentaculata, having equal status with the Ectoprocta and Phoronida, or latterly as a distinct phylum. From a palaeontological viewpoint, the promotion of the Brachiopoda to a phylum is taxonomically more realistic because the group, which includes some of the oldest known fossils, has always been decisively different from other invertebrates. Admittedly, embryological studies of living forms give some indication of the relationships between brachiopods and other phyla; but these supposed affinities are much more remote than those existing between inarticulate and articulate brachiopods. Moreover, comparative morphological studies of extinct brachiopods suggest that many distinguishing features of articulate groups were gradually derived from an archetypal stock that had much in common with some living inarticulates. These characteristics probably included an organic ectodermal skeleton consisting of two unarticulated valves; a pedicle that arose simply as an extension of the ventral body wall; a recurved gut with the anus located outside a ringlike lophophore containing the mouth; one pair of metanephridia; an open circulatory system; a nervous center including a subenteric ganglion located in the mesosome, and a triple regionated body with a poorly developed protosome undergoing atrophy. It is also likely that the development of the archetypal embryo involved radial cleavage, formation of the mouth at the blastopore and the differentation of a mantle rudiment which did not undergo reversal. No confident assertion can be made about the origin of the archetypal coelom because it is schizocoelic in at least one inarticulate species and enterocoelic in articulates: but in view of the homogeneity of the phylum, it is possible that the latter condition evolved from the former.

Such an assemblage of characters underlines both the individuality of the Brachiopoda and their affinity with the other lophophorates, the Ectoprocta and Phoronida. The larvae of all three phyla are best described as modified trochophores in which the mouth arises directly from the blastopore, although in respect of the brachiopod larva, the apical tuft is the only other point of resemblance with the trochophore. The presence of a lophophore, the lack of a well-defined protosome and the location of the main nerve centers in the mesosome are also typical of the three phyla. HYMAN (441a) assumed that the "horseshoe" shape of the phoronid and phylactolaematous lophophore represents the primitive lophophorate disposition. This is unlikely, since, as in the schizolophe, which is the nearest counterpart to the "horseshoe" arrangement among the brachiopods, a double arc of filaments containing the mouth can only arise by a growth distortion of an originally circular structure like that characteristic of young brachiopods and gymnactolaematous ectoprocts; and this must have been the generalized disposition.

Despite these similarities, the Brachiopoda are unique in a number of fundamental characteristics. From both Ectoprocta and Phoronida, they differ in having an ectodermal skeleton of two valves arranged ventrodorsally, chitinous setae (not always present and possibly matched by ectoproct vibracula), a principal ganglion that is subenteric (an auxiliary supraenteric ganglion occurs in articulates), an enterocoelic coelom (in articulates only), and an imperfect separation of the "mesocoel" and "metacoel" (except in *Crania* where a dividing septum is well developed). The phylum further differs from the Ectoprocta in the possession of metanephridia and a circulatory system, and from the Phoronida in the radial cleavage of the embryo and the open nature of the circulatory system.

These comparisons illustrate the dangers of categorizing the end products of evolution without allowing for the process itself. The brachiopods are certainly more likely to have been related to the ectoprocts and phoronids than to members of any other phylum. Yet so removed are they, through time and subsequent change, from a common ancestral design that whereas the phoronids fit reasonably well into the Protostomia, the brachiopods have many features that are more characteristic of the Deuterostomia. Many authors (e.g., 441a) have described the lophophorates as intermediaries between the protostomatous and deuterostomatous invertebrates. Even among living forms, such a relationship can only be demonstrated by a selective arrangement of data; whereas phylogenetic evidence suggests that the "deuterostomatous" characteristics of the brachiopods are more likely to have evolved independently of similar traits in other phyla. Indeed, in view of the long geological record of at least the brachiopods, there is some attraction in the speculation that certain of the more problematic invertebrate phyla, like the lophophorates, were derived independently from the Protozoa.

INARTICULATA

By A. J. Rowell
[Nottingham University]

Class INARTICULATA Huxley, 1869

[Inarticulata Huxley, 1869, p. 116] [=Lyopomata Owen, 1858, p. 339; Ecardines Bronn, 1862, p. 301; Pleuropygia Bronn, 1862, p. 301; Tretenterata King, 1873, p. 15; Gastrocaulia Thomson, 1927, p. 114]

Brachiopoda with chitinophosphatic or calcareous valves, punctate or impunctate, secondary layer never completely fibrous, periostracum chitinous in living species with phosphatic shells, of protein in calcareous-shelled forms; valves commonly held together only by muscles and body wall, rarely articulated and never by hinge teeth and dental sockets; lophophore never supported by shelly outgrowths from dorsal posterior margin; muscle system for opening and closing valves consisting of adductors and obliques (latter not demonstrable in acrotretaceans and neither pair identifiable in paterinaceans) with bases commonly located peripherally in body cavity. Pedicle of living species developing from ventral mantle and inferred to have originated in same manner in extinct groups. Coelom described as schizocoelic; shell, alimentary canal, and lophophore with median tentacle developing in larval stages of growth; settling without mantle reversal. Alimentary canal with functional anus, trocholophous stage of lophophore development with single (adlabial) or double (adlabial and ablabial) row of filaments. *L.Cam.-Rec.*

The major classification of the inarticulate brachiopods and the inferred evolution both within the class and between the classes have been discussed previously, but the possibility that two of the features which are typical of inarticulate brachiopods—origin of the pedicle from the ventral mantle and absence of mantle reversal—may also have occurred in some of the earlier articulate groups is worthy of reiteration. This possibility helps to emphasize the basic unity of the phylum and suggests that the two classes arose from a common ancestor whose early stages of development were probably similar in many respects to those of a living inarticulate. The two classes have seemingly diverged from this archetypal brachiopod, the inarticulates retaining many of its features which gradually were lost in the early phases of evolution of the Articulata.

There is a complete absence of articulation between the valves of all living inarticulate brachiopods and the majority of fossil forms. The shape of the dorsal pseudointerarea of many acrotretids, however, suggests that relative rotary and sliding movements between the valves was commonly inhibited, and in at least one genus (*Linnarssonella*), these movements were eliminated by the development of deep grooves which received the dorsal edge of the posterior margin of the pedicle valve. Interlocking structures along the posterior margin of both valves also arose independently in two other lower Paleozoic stocks, the obolid *Dicellomus* and the trimerellid *Dinobolus*. The form ot articulation in the latter genus is very unusual, since a ventral median socket receives a single toothlike projection from the brachial valve; but all these hinge structures are only analogous, not homologous, with those commonly developed in the articulates. The peripheral position of the muscle bases within the body cavity is probably associated with the absence of articulation and the relatively high degree of freedom of movement between the valves. A lateral position of the attachment base would, from the mechanical viewpoint, be particularly advantageous for those oblique muscles controlling relative rotary movements between the valves.

In all living inarticulate brachiopods the two mantle margins are entire and discrete; they are neither interrupted medially by the pedicle nor fused along the posterior margin, but invariably are separated from each other by inner epithelium of the body wall. This relationship is inferred to have characterized the entire class. The gross form of the shell is of course controlled by the secretory behavior of the entire margin of both mantles, although the shape of the immediate substratum or host may considerably modify the form of species attached by cementation. However, the important modifications of the pedicle valve, peripheral to the pedicle opening, are determined entirely by the secretory ability of a narrow posteromedian sector of the ventral mantle. This narrow sector is variably disposed relative to the pedicle; in *Lingula* it is but a slender fold enclosed between the valves and taking no part in their secretion, whereas in *Discina* it is well developed, lying entirely posterior of the pedicle and its shell secretion fully integrated with that of the remainder of the mantle lateral to it. The secretory ability of this narrow strip of epithelium may vary not only in different stocks but also during the ontogeny of any individual. In many genera which had the adult pedicle restricted to a foramen in the pedicle valve, it was not so constrained in younger stages of development, when the pedicle opening breached the posterior margin of the valve and the posteromedian sector of the mantle was not involved in shell secretion (e.g., *Acrothele*). The pattern of secretory behavior of this strip of epithelium is commonly constant within the larger taxa; in the lingulaceans, for example, this sector of the mantle is never associated with shell secretion, although considerable variations in some closely related stocks are observed. Thus, in trematids the pedicle opening intersects the shell margin at all stages of growth, whereas in the contemporaneous discinids, although the pedicle opening in the young stages is similar to that of the trematids, it becomes progressively isolated from the posterior margin of the shell by the secretory activity of the posteromedian sector of the mantle, and in the adult condition the posterior margin of the pedicle valve is entire. A similar variation is seen between the Recent genera *Discinisca* and *Discina* and this variation in secretory ability gives rise to one of the principal differences between the genera of the Cambrian obolellids.

The inarticulate brachiopod lophophore is never supported by a shelly outgrowth from the posterior margin of the brachial valve, but it may be inferred that the variably modified posteroventral surface of the median septum of some acrotretids may have afforded a degree of support for the mouth segment. The complex saddle-shaped plate of *Ephippelasma*, arising near the center of the brachial valve, may likewise be interpreted as a lophophore support, probably the most ambitious attempt among members of the class, but in the majority of genera the lophophore must have been unsupported by a solid skeleton and suspended freely in the mantle cavity. Spicular support, of the type developed in some terebratellaceans, is unknown in living inarticulates and there is no evidence for its existence in fossil forms. If the lophophore of extant genera provides a reliable guide, any rigidity the organ may have possessed must have been afforded by the high proportion of connective tissue and muscle, possibly aided by the hydrostatic "skeleton" of the lophophore canal system. During the ontogeny of modern inarticulates, the lophophore passes from the initial trocholophe through the schizolophous condition to culminate in a spirolophe. The only known exception is *Pelagodiscus*, whose lophophore does not advance beyond the schizolophous stage. The apices of the spires have various attitudes, and the form of the shell does not provide a very reliable guide to their disposition; thus in *Crania* the apices of the spires are dorsally directed, but those of *Discina* and *Discinisca* are inclined ventrally, although the gross form of their shell is not unlike that of *Crania*. Consideration of the relationship between size of the shell and form of the lophophore during the growth of living inarticulates (Williams & Wright, 1961, 879) suggests that in the smaller fossil genera, even when adult, the organ may have been only a schizolophe, or possibly a trocholophe.

Some variation may be noted of attachment of the inarticulate brachiopods to the substratum, which is reflected in the form or even absence of the pedicle. The modern lingulids are all burrowing animals attached to the bottom of the burrow by the distal end of a long contractile pedicle; a similar habit appears to have characterized their spatula-shaped ancestors at least as far back as the Ordovician. This mode of life is seemingly a very successful adaptation for an animal which lives in shallow water or even intertidally on a soft bottom. The ability to escape from a burrow blanketed by sediment and to form a new one if the previous burrow is disturbed in any way are obvious advantages when living in an environment in which the rate of sedimentation may locally be high. Withdrawal into the burrow will moreover assist in escaping predation and reduce the hazards of desiccation if intermittently exposed between tides. Living discinids are permanently attached by a much shorter pedicle and this method of attachment probably characterized the majority of inarticulate brachiopods. Loss of the pedicle, however, was a common trend in several stocks. The craniaceans probably never possessed a pedicle at any stage of their development and there is no evidence for its existence in either the craniopsids or trimerellids; in these genera growth of the pedicle was apparently suppressed, at least during postlarval stages. In the siphonotretacean *Helmersenia*, on the other hand, a pedicle was characteristic of the younger stages of growth but atrophied during later life when the pedicle foramen was progressively plugged and ultimately closed. Many genera which lack a pedicle lay free on the sea floor, but a cemented habit was adopted to varying degree in different stocks. Some of the early craniaceans were apparently unattached, but the majority were cemented by all or part of their pedicle valve to the substratum and although this valve is unknown in the acrotretid *Undiferina*, the irregular shape of the brachial valve suggests that this also was a cemented form. Attachment by cementation was developed independently in at least one craniopsid genus (*Craniops*), which bears a clearly defined cicatrix on the pedicle valve, but the majority of genera in the stock seemingly lay free on the sea floor, as did all the trimerellids.

Order LINGULIDA Waagen, 1885

[*nom. transl.* Kuhn, 1949, p. 99 (*ex* suborder Lingulacea Waagen, 1885, p. 754), *nom. correct.* Goryansky, 1960, p. 173 (*pro* order Lingulacea Kuhn, 1949, p. 99)] [*emend.* Rowell, herein] [=Mesokaulia Waagen, 1885, p. 754 (*partim*); Atremata Beecher, 1891, p. 354 (*partim*); Mesocaulia Hall & Clarke, 1894, p. 322 (*partim*)]

Shell of calcium phosphate with some layers of organic material, more rarely calcareous (Craniopsidae, Trimerellacea), very finely punctate or impunctate, biconvex, beak terminal in both valves (except in some Craniopsidae); pedicle emerging posteriorly between valves (pedicle apparently absent in Craniopsidae and Trimerellacea). [Habitat marine, but some lingulids tolerant of reduced salinity.] *L.Cam.-Rec.*

The order contains the two superfamilies Trimerellacea and Lingulacea. Many authors have recognized the superfamily Obolacea, proposed by Schuchert in 1896 for forms which are here included within the Lingulacea. There seems little justification for giving separate superfamilial status to this group (178), which differs only in relative details from the lingulids in the posterior margin of the valves, musculature, thickness of shell, and inferred length of pedicle. The superfamily name, Lingulacea, is determined by priority of the available family-group names.

Superfamily LINGULACEA Menke, 1828

[*nom. transl.* Schuchert, 1896, p. 306 (*ex* Lingulidae Gray, 1840, p. 155, *nom. correct. pro* Lingulaceae Menke, 1828, p. 56, *nom. imperf.*)] [incl. Obolacea King, 1846, *nom. transl.* Schuchert, 1896, p. 305 (*ex* Obolidae King, 1846, p. 28)]

Shell phosphatic (except in Craniopsidae), usually with some layers of organic material; valves subequal, pedicle valve in many forms slightly larger, bearing pedicle groove commonly separating orthocline, striated propareas (pedicle apparently absent in Craniopsidae); posterior margin of brachial valve may be merely thickened or possess pseudointerarea extending variable distance anteriorly as concave apical plate. *L.Cam.-Rec.*

Family LINGULIDAE Menke, 1828

[*nom. correct.* Gray, 1840, p. 155 (*pro* Lingulaceae Menke, 1828, p. 56, *nom. imperf.*)] [=fam. Lingulacea Menke, 1830, p. 95]

Elongate oval to spatulate in outline, more rarely subtriangular, gently biconvex; beak of pedicle valve with broadly triangular ventral depression or groove for passage of pedicle, posterolateral margins of valve thickened, striated, lacking flexure lines, but rarely forming well-defined triangular propareas. Beak of brachial valve with small, uninterrupted pseudointerarea, not extending as a plate into the valve. Principal musculature consisting of umbonal muscle, paired centrals, transmedians, anterior, outside and middle laterals. One pair of principal mantle canals (*vascula lateralia*) in each valve. Recent species with long, flexible pedicle, lophophore spirolophous, apices of spires medianly directed. *?Ord., Sil.-Rec.*

The lower stratigraphical range of the family is not precisely known. Many Ordovician species have been loosely referred to *Lingula*, but the internal structure of the valves is unknown and in these circumstances even the family assignment is doubtful.

All Recent lingulids live in burrows and this was probably a common mode of life in the family.

Lingula Bruguière, 1797, pl. 250 [**L. anatina* Lamarck, 1801, p. 141; ICZN pend.] [=*Pharetra* Bolton, 1798, p. 159 (type, *P. monoculoides*); *Ligula* Cuvier, 1798, p. 435 *(nom. null.)*; *Ligularius* Duméril, 1806, p. 170 *(nom. van.)*; *Lingularius* Schuchert & LeVene, 1929, p. 76 *(nom. null.)*]. Elongate, lateral margins gently convex to subparallel, ornament only of concentric growth lines; shell thin, slightly thickened in areas of muscle attachment. Internally without septa, low median ridge in brachial valve may be present extending from central scars to anterior lateral scars. *?Ord., Sil.-Rec.*, cosmop.——Fig. 158,*1*. **L. anatina* Lamarck, Rec., Andaman Is.; *1a,b*, ped. v. ext., int., ×1; *1c,d*, brach. v. ext., int., ×1 (Rowell, n).

Barroisella Hall & Clarke, 1892, p. 62 [**B. campbelli* Cooper, 1942, p. 228 *(nom. subst. pro Lingula subspatulata* Meek & Worthen, 1868, p. 437, *non* Hall & Meek, 1856; OD] [=*Barroisella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Elongate oval in outline, ornament of concentric growth lines; in pedicle valve propareas well developed for family, small but prominent, solid; large, median, elongate triangular scar extending forward half length of valve; brachial valve with low broad median ridge, bifurcating near middle of valve, between bifurcation second low ridge intercalated, probably bearing anterior lateral scars. *U.Dev.-Miss.*, N.Am.——Fig. 158,*2*. **B. campbelli* Cooper, U.Dev., USA(Ohio, *2a*; Ind., *2b,c*); *2a*, ped.v. int., ×4; *2b,c*, brach.v. int., int. impression, ×4, ×6 (*2a,b*, Rowell, n; *2c*, 555a).

Dignomia Hall, 1871, p. 2 [**Lingula alveata* Hall, 1863, p. 23; SM Hall, 1872, pl. 13]. Relatively large, wide, thin-shelled forms, long, conspicuous median ridge in both valves, with 2 low, broadly diverging ridges that extend anterolaterally from beak. *Dev.*, N.Am.——Fig. 158,*4*. **D. alveata* (Hall), M.Dev., USA(N.Y.); brach. v. int. impression, ×1 (Rowell, n).

Glottidia Dall, 1870, p. 157 [**Lingula albida* Hinds, 1845, p. 71; OD]. Externally similar to *Lingula*, but internally with 2 low septa in pedicle valve, diverging from beak extending forward about 0.3 length of shell; brachial valve with low median septum of similar length. *Eoc.-Rec.*, N.Am.-S.Am.-Eu.——Fig. 158,*3*. *G. palmeri* Dall, Rec., USA(Calif.); *3a*, ped.v. int., ×1; *3b*, brach. v. int., ×1 (Rowell, n).

Langella Mendes, 1961, p. 1 [**Lingula imbituvensis* Oliveira, 1930, p. 18; OD]. Similar to *Barroisella*, but having much shorter dorsal median ridge and lacking anterior intercalated ridge. *Permo-Carb.*, S.Am.——Fig. 158,*5*. **L. imbituvensis* (Oliveira), Tubarâo Ser., Brazil; *5a,b*, ped. v. and brach. v. int. impressions, ×6 (555a).

Lingulipora Girty, 1898, p. 387 [**Lingula (Lingulipora) williamsana*; OD]. Elongate oval in outline, shell relatively coarsely punctate, ornament of concentric growth lines and closely spaced, fine pustules with their long axis parallel to growth lines. Internal structure unknown. *M.Dev.-U.Carb.*, N.Am.-?W.USSR.——Fig. 158,*7*. **L. williamsana* (Girty), U.Dev., USA(Va.); brach. v. ext., ×3 (Rowell, n).

Trigonoglossa Dunbar & Condra, 1932, p. 35 [**Lingula nebrascensis* Meek, 1872, p. 158; OD]. Subtrigonal in outline, valves gently convex, ornament of strongly raised concentric lines separated by broad, flat interspaces. Posterior margin of pedicle valve internally like *Lingula*. *?Dev.-Carb.*, N.Am.-Eu.——Fig. 158,*6*. **T. nebrascensis* (Meek), Penn., USA(Tex.); ped. v. ext., ×1.5 (Rowell, n).

Family OBOLIDAE King, 1846

[Obolidae King, 1846, p. 28]

Rounded, suboval or elongate in outline, ornamented by growth lines rarely becoming lamellose or spiny; propareas of pedicle valve well developed. Principal musculature consisting of umbonal muscle that may be partly or completely divided into 2 separate muscles, paired centrals, transmedians, anterior, middle and outside laterals. *Vascula lateralia* of both valves baculate, converging slightly forward; *vascula media* of brachial valve commonly diverging from anterior projection of visceral area but adequately known only in Obolinae. *L.Cam.-U.Ord.*

Subfamily OBOLINAE King, 1846

[*nom. transl.* Dall, 1870, p. 154 (*ex* Obolidae King, 1846, p. 28)]

Rounded to suboval, flexure lines on ventral propareas; dorsal pseudointerarea well developed as striated, triangular plate divided into 2 propareas by poorly defined, broadly triangular, concave median depression (848). *L.Cam.-M.Ord.*

Obolus Eichwald, 1829, p. 274 [**O. apollinis*; SD Davidson, 1853, p. 135] [=*Ungula* Pander, 1830, p. 163 (type, *U. convexa*); *Ungulites* Bronn, 1848, p. 1342 *(nom. null.)*; *Obulus* Quenstedt, 1868, p. 732 *(nom. null.)*; *Euobolus* Mickwitz, 1896, p. 129 (obj.); *Eoobolus* Matthew, 1902, p. 94 (type, *Obolus (E.) triparilis* Matthew, 1902, p. 94; SD Rowell, herein)]. Subequivalve, circular to subtriangular in outline, gently convex;

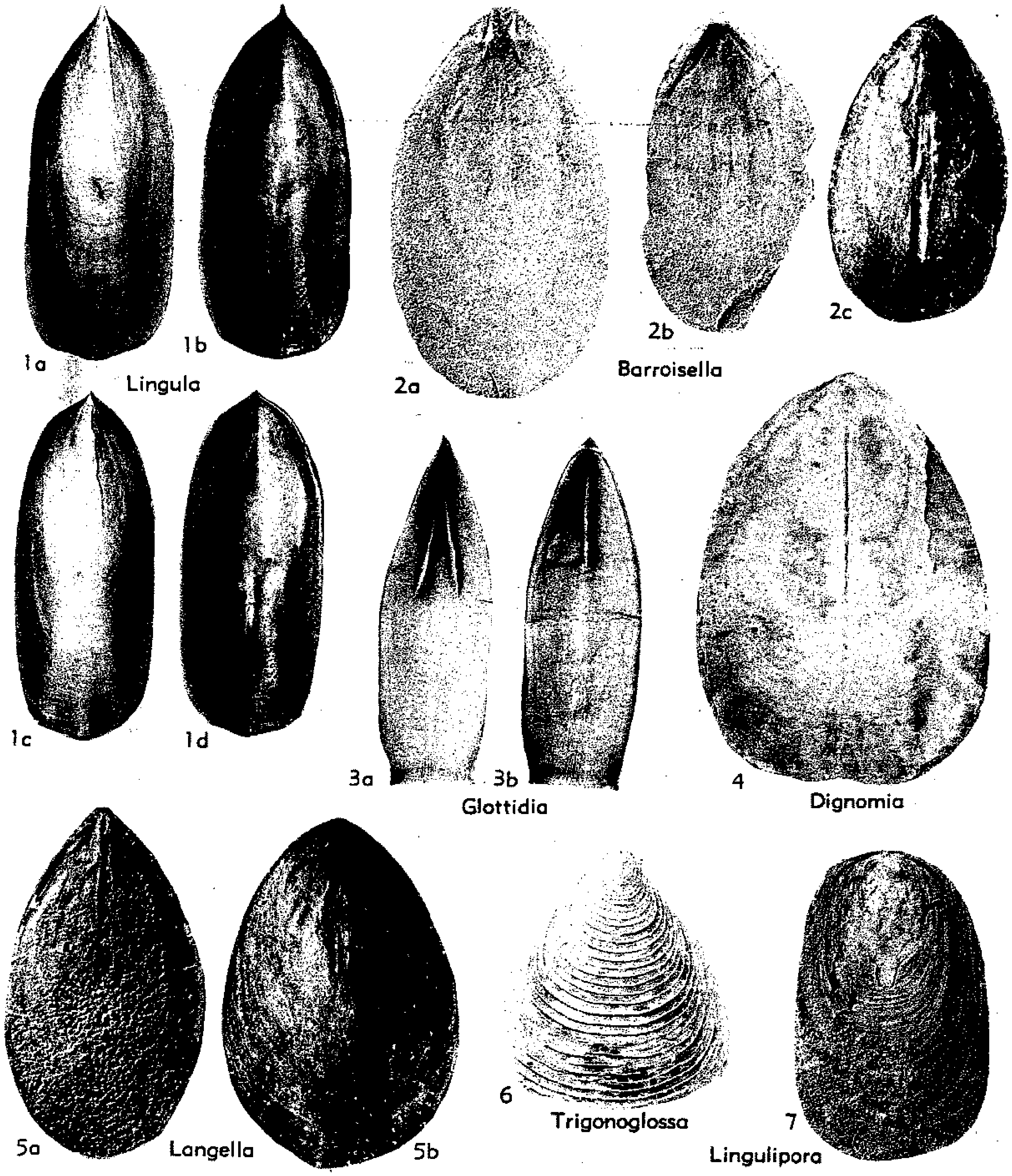


Fig. 158. Lingulidae (p. *H263*).

ornament of fine, concentric growth lines, fine radial ornament may be present; narrow, strongly defined pedicle groove; posterior half of pedicle valve thickened, indented by heart-shaped depression. Central, middle, and outside lateral muscles forming 2 composite scars anterolateral of depression, transmedians and anterior laterals forming 2 composite scars posterolateral of depression; posterior half of brachial valve thickened, anterior margin of thickening concave anteriorly; transmedians forming scars separate from combined middle and outside lateral scars, anterior lateral scars very anteriorly placed. *?L.Cam., M.Cam.-L.Ord., ?M.Ord.*, cosmop.——Fig. 159,*2*. **O. apollinis, L.Ord.*, Est.; *2a,b*, incompl. ped. v. ext., int., ×1.5; *2c,d*, incompl. brach. v. ext., int., ×2 (Rowell, n).

Aulonotreta Kutorga, 1848, p. 260 [**A. sculpta* (=**Obolus antiquissimus* Eichwald, 1843, p. 143); SD Hall & Clarke, 1894, p. 244] [=*Acri-*

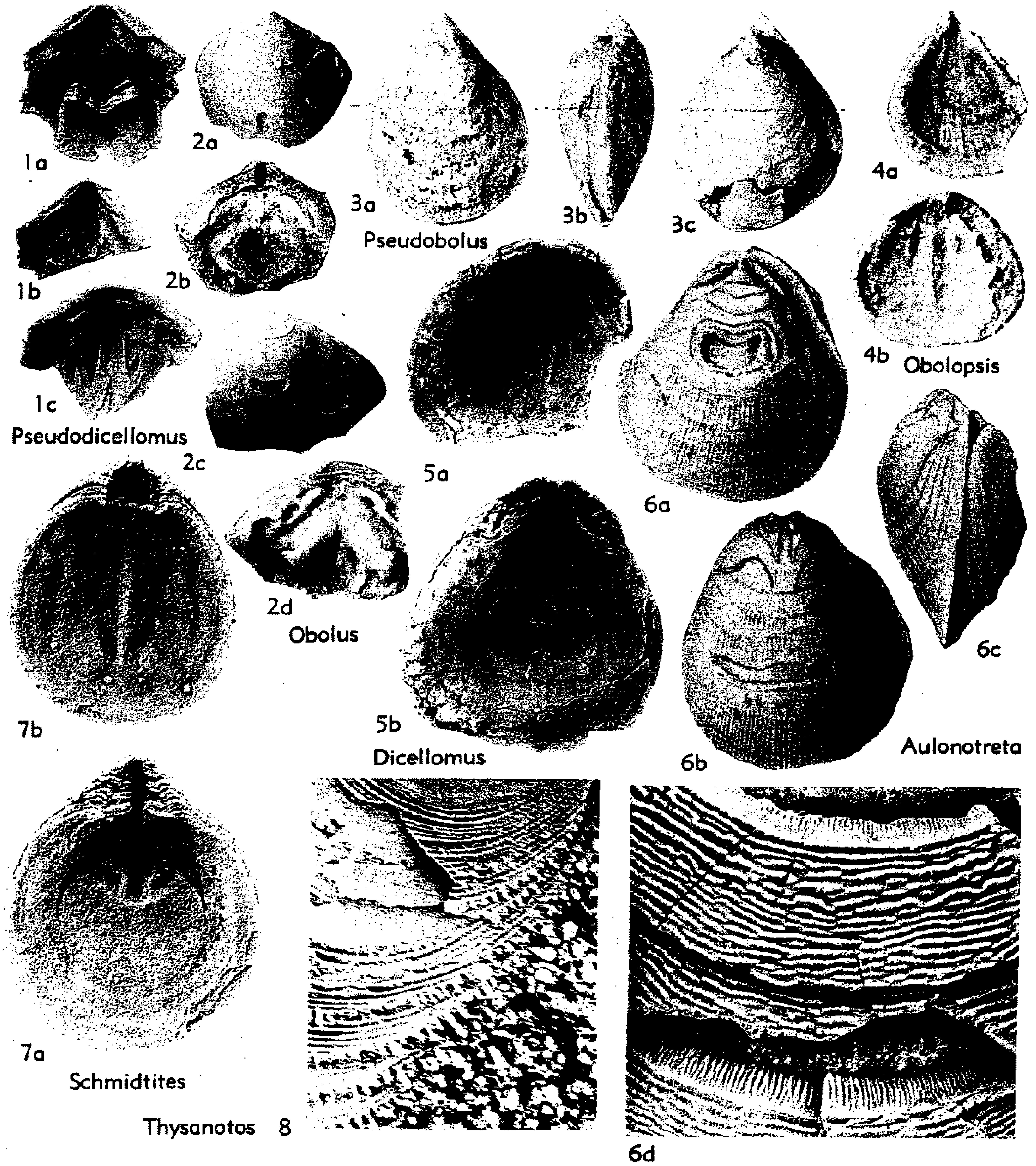


Fig. 159. Obolidae (Obolinae) (p. *H263-H266*).

tis Volborth, 1869, p. 212 (obj.)]. Similar to *Obolus*, but concentric ornament of discontinuous, rounded, raised lines. More strongly biconvex than *Obolus* and visceral area more posteriorly placed. *L.Ord.*, Eu.(E.Baltic).——Fig. 159,*6*. *_A. antiquissima_ (Eichwald), Est.; *6a,b,* ped. v. and brach.v. int. impressions, ×1.5; *6c,* both valves, int. impression lat., ×1.5; *6d,* detail of ornament, ×6 (*6a-c,* 848; *6d,* Rowell, n).

Dicellomus Hall, 1871, p. 3 [*_Lingula polita_ Hall, 1861, p. 24, proposed Rowell, 1962, Z.N.(S.) 1504, ICZN pend.]. Small, biconvex, thick shell in 3 layers, middle layer punctate; pair of elongate, narrow grooves occupying position of propareas in brachial valve; visceral area of pedicle valve thickened; musculature similar to *Obolus*, usually well impressed. *U.Cam.(Cedaria-Crepicephalus Zones)*, N.Am.——Fig. 159,*5*. *D. occidentalis* Bell, USA(Mont.); *5a,* brach.v. int., ×5; *5b,* ped.v. int., incompl., ×5 (66).

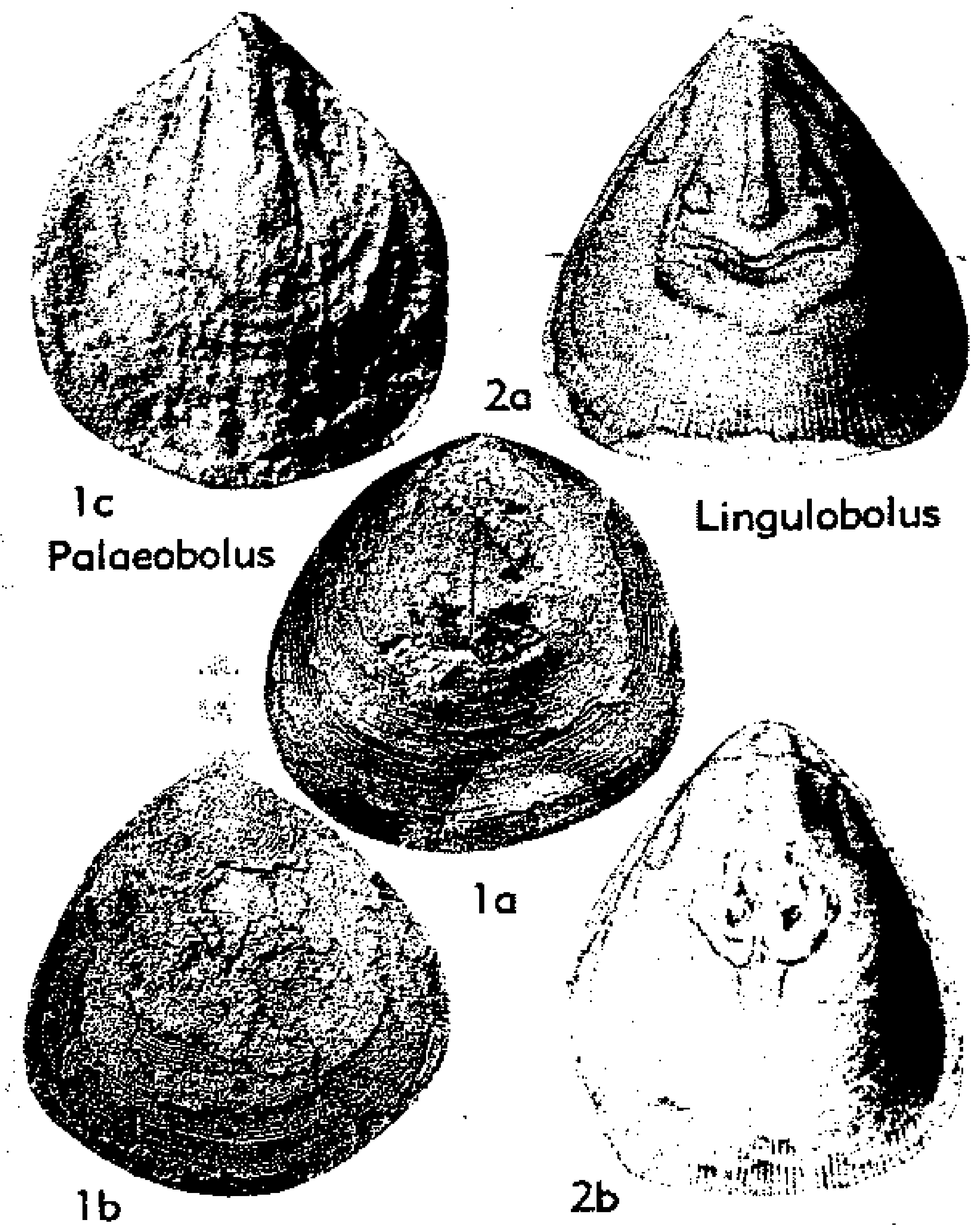


FIG. 160. Obolidae (Obolinae) (p. *H266*).

Lingulobolus MATTHEW, 1895, p. 260 [**Lingulella? affinis* BILLINGS, 1872, p. 468; OD] [=*Sphaerobolus* MATTHEW, 1895, p. 263 (type, *Lingulella? spissa* BILLINGS, 1872, p. 468)]. Large, oval to subtriangular in outline, strongly biconvex. Shell thick, ornament of concentric growth lines and fine radiating striae, thickened over visceral area of pedicle valve to form low platform of lamellar tissue. *L.Ord.*, N.Am.-?Eu.——FIG. 160,2. **L. affinis* (BILLINGS), Newf.; *2a,b,* ped. v. and brach. v. int. impressions, ×2 (848).

?**Obolopsis** SAITO, 1936, p. 349 [**O. margaritae*; OD]. Early obolids differing from *Obolus* in absence of striated pseudointerareas; posterior margins of both valves thickened. *L.Cam.*, Asia (Korea).——FIG. 159,4. **O. margaritae*; *4a,b,* incompl. ped. v. and brach. v. int., ×3 (703a).

Palaeobolus MATTHEW, 1899, p. 201 [**P. bretonensis;* OD] [=*Palaebolus* GORYANSKY, 1960, p. 173 *(nom. null.)*]. Suboval in outline, ventral *vascula lateralia* close together, only slightly diverging; externally similar to *Aulonotreta,* but less strongly convex and ornament more continuous. *M.Cam.,* N.Am.(N.Scotia).——FIG. 160,*1*. **P. bretonensis*; *1a,* brach. v. ext. exfoliated, ×2; *1b,c,* ped.v. ext., int. impression, both ×2 (*1c,* 848; *1a,b,* Rowell, n).

Pseudobolus COOPER, 1956, p. 194 [**Palaeoglossa gibbosa* WILLARD, 1928, p. 256; OD]. Slightly dorsibiconvex; similar to *Lingulobolus* externally, but lacking visceral platform in pedicle valve and musculature very poorly impressed. *M.Ord.*, N.Am.——FIG. 159,*3*. **P. gibbosus* (WILLARD), Murat F., USA(Va.); *3a-c,* ped. v. ext., both valves lat., brach. v. ext., all ×2 (189).

Pseudodicellomus BELL, 1962, p. 407 [**Dicellomus mosaicus* BELL, 1941, p. 216; OD]. Similar to *Dicellomus;* shell of 3 layers, middle one impunctate; pedicle groove widely triangular, external surface of valves minutely pitted. *U.Cam. (Conaspis Z.-Ptychaspis-Prosaukia Z.)*, N.Am.——FIG. 159,*1*. **P. mosaicus* (BELL), USA(Tex.); *1a,b,* incompl. ped. v. int., both ×3.5; *1c,* incompl. brach. v. int., ×3.5 (67).

Schmidtites SCHUCHERT & LEVENE, 1929, p. 121 [*nom. subst. pro Schmidtia* VOLBORTH, 1869, p. 208 (*non* BALSAMO-CRIVELLI, 1863)] [**Schmidtia celata* VOLBORTH, 1869, p. 209; OD]. Very similar to small *Obolus,* but posterior region of valves less strongly thickened and low median ridge present in central part of brachial valve. *L.Ord.*, Eu.(Baltic).——FIG. 159,*7*. **S. celatus* (VOLBORTH), Tremadoc., Est.; *7a,b,* ped. v. and brach. v. int., ×6 (Rowell, n).

Thysanotos MICKWITZ, 1896, p. 130 [**Obolus siluricus* EICHWALD, 1843, p. 7; OD] [=*Mickwitzella* WALCOTT, 1908, p. 70 (obj.); *Thysanotus* KOLIHA, 1926, p. 317 *(nom. null.)*]. Similar to thin-shelled *Obolus* but ornament of narrow, raised concentric lines which at fairly regular intervals bear row of fine spines. *L.Ord.*, Eu.——FIG. 159,*8*. **T. siluricus* (EICHWALD), Est.; detail of ornament, ×5 (Rowell, n).

Subfamily LINGULELLINAE Schuchert, 1893

[*nom. transl.* SCHUCHERT & LEVENE, 1929, p. 12 (*ex* Lingulellidae SCHUCHERT, 1893, p. 149)]

Elongate obolids, strong flexure lines on ventral propareas, dorsal pseudointerarea well developed as striated triangular plate divided into 2 propareas by poorly defined, broadly triangular, concave median depression. *L.Cam.-U.Ord.*

Lingulella SALTER, 1866, p. 333 [**Lingula davisii* M'COY, 1851, p. 405; SD DALL, 1870, p. 159] [=*Lingulella* SALTER, 1861, p. 98 *(nom. nud.)*; *Leptembolon* MICKWITZ, 1896, p. 130 (type, *Obolus (L.) lingulaeformis*)]. Elongate oval to subtriangular in outline, subacuminate; thin-shelled, external ornament of concentric growth lines, inner layers of shell with fine radial striae, visceral area may be pustulose. Musculature apparently like *Obolus*. *L.Cam.-M.Ord., ?U.Ord.,* cosmop.——FIG. 161,*3*. **L. davisii* (M'COY), U. Cam., Wales; *3a,* ped. v. int. impression, ×2; *3b,* brach. v. ext., ×2; *3c,d,* flattened int. impressions showing posterior margins, ped.v., brach.v., ×2 (Rowell, n).

Fordinia WALCOTT, 1908, p. 64 [**Obolus (Fordinia) perfectus*; OD]. Suboval outline; ornament of concentric growth lines; pedicle groove narrow, may continue as groove across thickened visceral region of pedicle valve, anterior margin of thickened area strongly concave, lateral margins bearing _vascula lateralia_; brachial valve with thickened area, posteriorly bearing broad, short median ridge, anterior of thickening low median ridge present in middle of valve. _M.Cam.-U.Cam.,_ N.Am.——Fig. 161,_1_. *_F. perfecta_ (Walcott), M.Cam., USA(Utah); _1a,_ incompl. ped. v. int., ×4; _1b,_ brach. v. int., ×4 (Rowell, n).

?**Lingulepis** Hall, 1863, p. 129 [*_Lingula pinnaformis_ Owen, 1852, p. 583; SD Dall, 1870, p. 161]. Strongly acuminate, ventral beak elongated, valves moderately convex; ornament of concentric growth lines; shell fairly thick, inner layers punctate, radially striated. [Genus inadequately known.] _?L.Cam., U.Cam., ?L.Ord.,_ N.Am.-?Greenl.-?Asia.——Fig. 161,_6_. *_L. pinnaformis_ (Owen), U.Cam., USA(Wis.); _6a,b,_ partly exfoliated ped. v., brach. v., ×3 (848).

Pseudolingula Mickwitz, 1909, p. 771 [*_Crania quadrata_ Eichwald, 1829, p. 273; OD]. Broad, subrectangular outline, ornament of concentric growth lines. Umbonal muscle divided, producing pair of scars in both valves, remainder of musculature similar to _Obolus_. _Ord.,_ N.Am.-Eu.——Fig. 161,_4_. *_P. quadrata_ (Eichwald), U.Ord., Est.; _4a,b,_ ped. v. and brach. v. ext., _4c,_ both valves lat., all ×1 (Rowell, n).

Spinilingula Cooper, 1956, p. 210 [*_S. intralamellata_; OD]. Internally similar to _Lingulella,_ but exterior lamellose, with short prone spines along anterior edge of lamellae. _M.Ord.,_ N.Am.(Ala.).——Fig. 161,_2_. *_S. intralamellata,_ Pratt Ferry F.;

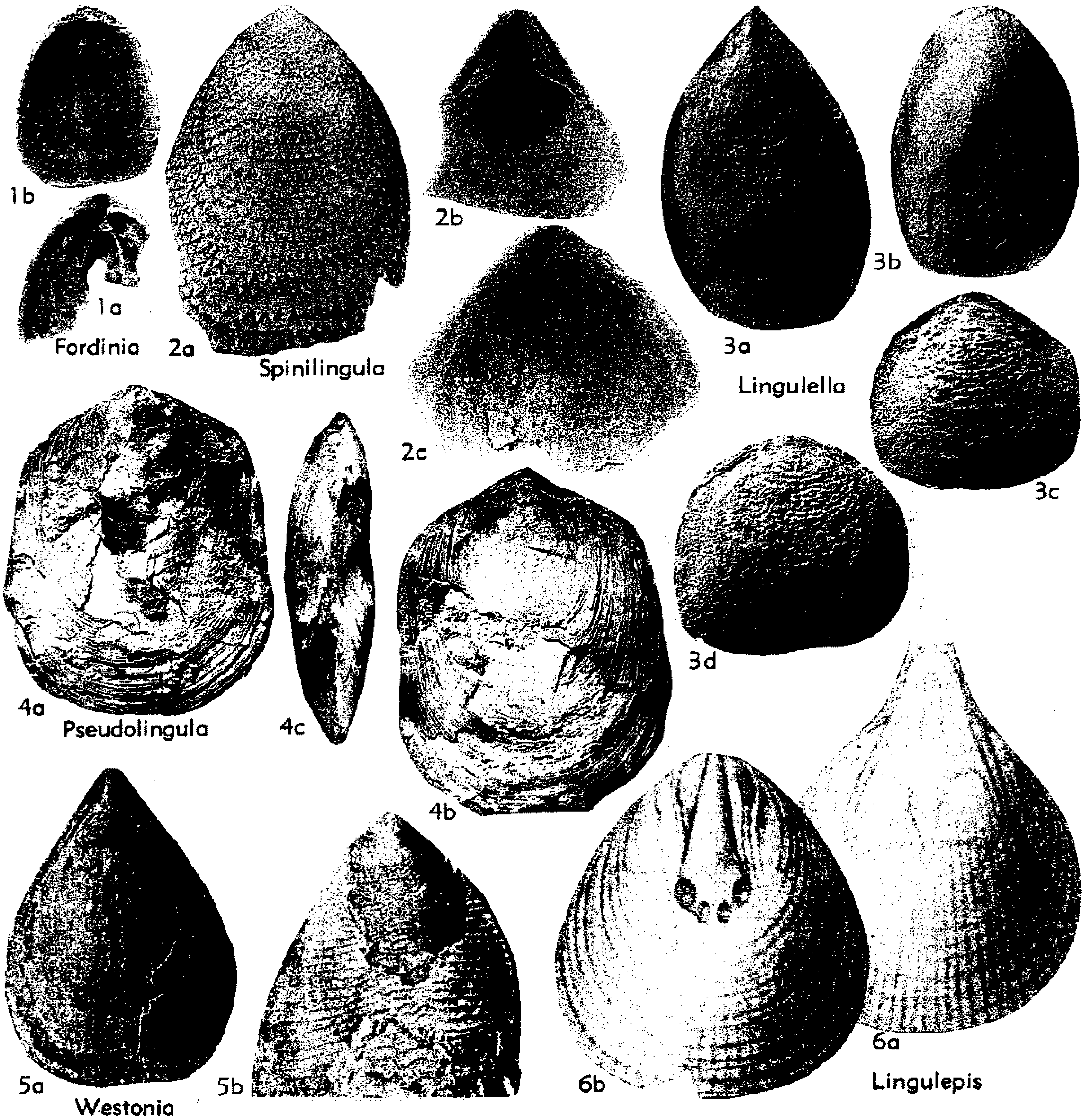


Fig. 161. Obolidae (Lingulellinae) (p. _H266-H268_).

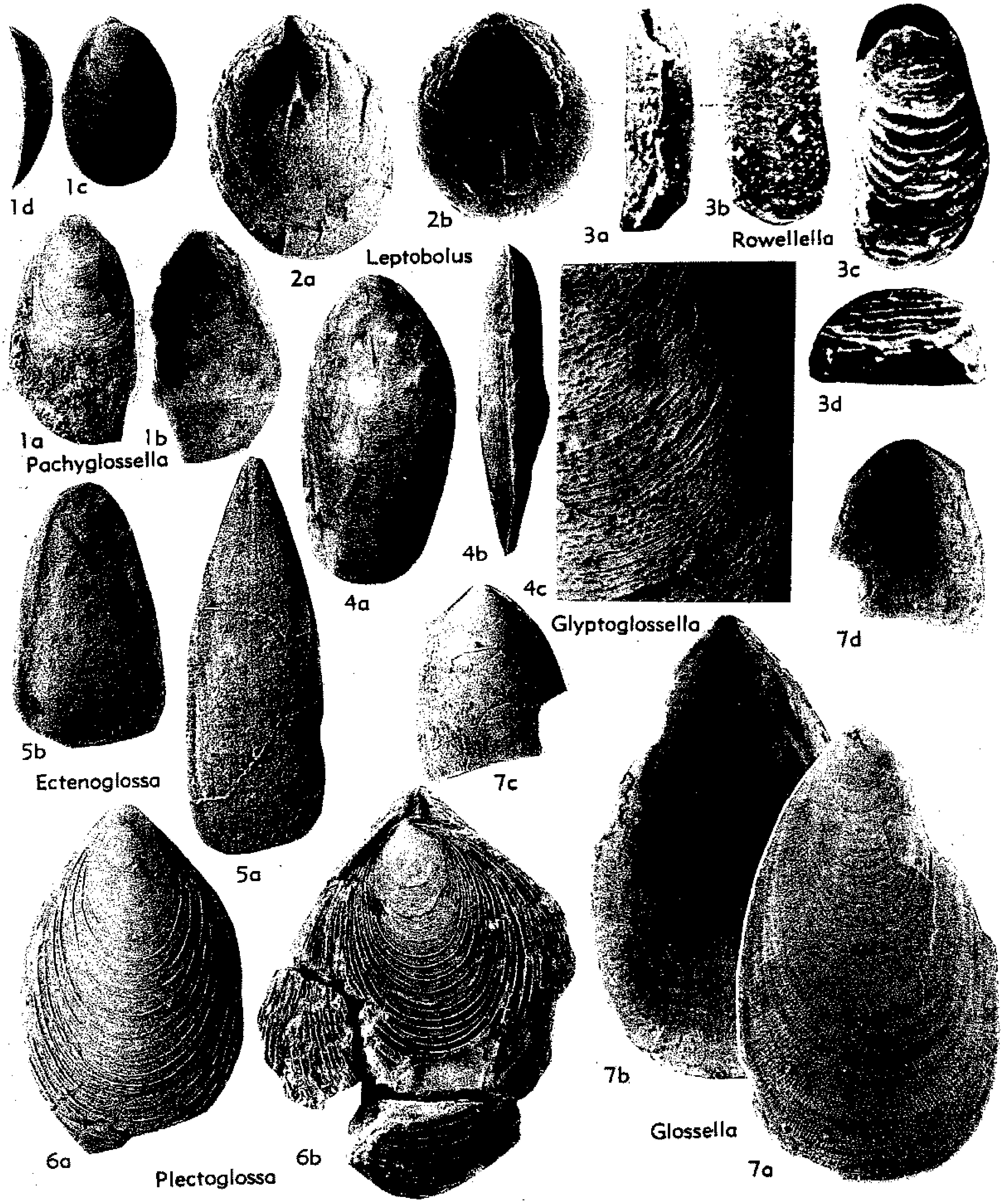


FIG. 162. Obolidae (Glossellinae) (p. H269).

2a, brach. v. ext., ×10; *2b,c*, incompl. ped. v. and brach.v. int., ×10 (189).

Westonia WALCOTT, 1901, p. 683 [**Lingula aurora* HALL, 1861, p. 24; OD]. Ovate-subtriangular outline, gently biconvex, ornament of fine concentric growth lines crossed by irregular, transverse lines, with zigzag pattern in middle of valves. *M.Cam.-M.Ord.*, N.Am.-Eu.-Asia.——FIG. 161,5. *W. linguloides* (KOBAYASHI), L.Ord., Alaska; *5a*, exfoliated ped. v., ×4; *5b*, detail of ornament, ×6 (825).

Subfamily GLOSSELLINAE Cooper, 1956

[Glossellinae COOPER, 1956, p. 213]

Elongate obolids, brachial valve lacking concave platelike pseudointerarea, posterior margin more or less thickened (189). *L. Ord.-U.Ord.*

Glossella Cooper, 1956, p. 228 [**G. papillosa*; OD]. Elongate oval outline, lateral margins subparallel to gently convex; ornament of concentric growth lines and radial rows of small granules similar to *Lingulasma*, but internally lacking septa or platforms; posterior margin of brachial valve sharply flexed, simulating propareas. *M.Ord.*, N.Am.-Eu.——Fig. 162,*7*. **G. papillosa*, Pratt Ferry F., USA (Ala.); *7a,b*, ped. v. ext., int., ×5; *7c,d*, brach. v. ext., int., ×4 (189).

Ectenoglossa Sinclair, 1945, p. 63 [**Lingula lesueuri* Rouault, 1850, p. 727; OD]. Relatively long, narrow shells, lateral margins subparallel; ornament of concentric growth lines; 2 short subparallel ridges extending anteriorly from beak of pedicle valve. *L.Ord.-M.Ord.*, N.Am.-Eu.——Fig. 162,*5*. **E. lesueuri* (Rouault), L.Ord., Eu.; *5a,b*, impression ped. v. and brach. v. int., ×1.5 (Rowell, n).

Glyptoglossella Cooper, 1960, p. 601 [*nom. subst. pro Glyptoglossa* Cooper, 1956, p. 226 (*non* Brenske, 1895)] [**Glyptoglossa cavellosa* Cooper, 1956, p. 227; OD]. Elongate oval outline; ornament of concentric lamellae scalloped along their anterior margins. Muscles attached to thickened area in both valves; brachial valve with median septum extending to middle of valve. *M.Ord.*, N.Am.-Eu.——Fig. 162,*4*. **G. cavellosa* (Cooper), Shippensburg F., USA(Pa.); *4a*, brach. v. ext., ×2; *4b*, both valves lat., ×2; *4c*, brach. v. ornament, ×6 (189).

Leptobolus Hall, 1871, p. 2 [**L. lepis*; SD Dall, 1877, p. 42] [=*Leptobulus* Hall, 1871 (*nom. neg.*)]. Relatively small, suboval in outline; median ridge in pedicle valve interior extending to center of valve and forking; brachial valve interior with 1 to 3 low ridges, lateral ridges variably developed. *M.Ord.-U.Ord.*, N.Am.——Fig. 162,2. **L. lepis*, Trenton F., USA(Ky.); *2a,b*, ped. v. and brach. v. int., ×12 (189).

Pachyglossella Cooper, 1960, p. 601 [*nom. subst. pro Pachyglossa* Cooper, 1956, p. 223 (*non* Hodgson, 1843; *nec* Fauvel, 1868)] [**Pachyglossa dorsiconvexa* Cooper, 1956, p. 225; OD]. Elongate elliptical, strongly biconvex, thick-shelled; ornament only of concentric growth lines. *M.Ord.*, N.Am.-Eu.——Fig. 162,*1*. **P. dorsiconvexa* (Cooper), Pratt Ferry F., USA(Ala.); *1a,b*, ped. v. ext. and int., ×5; *1c,d*, brach. v. ext. and lat., ×3 (189).

Plectoglossa Cooper, 1956, p. 222 [**P. oklahomensis*; OD]. Pseudointerarea of pedicle valve divided medianly by low fold; shell suboval in outline, valves ornamented by strong, elevated concentric lines. *M.Ord.*, N.Am.——Fig. 162,*6*. **P. oklahomensis*, USA(Okla.); *6a,b*, ped. v. and brach. v. ext., ×4 (189).

Rowellella Wright, 1963, p. 233 [**R. minuta*; OD]. Small, dorsibiconvex, elongate, subrectangular shells; lateral, and to lesser extent, anterior margins of brachial valve geniculate ventrally; ornament of fairly strong concentric lamellae. Internally, dorsal muscle field limited anteriorly by low W-shaped ridge. *U.Ord.*, Eu. (Ire.).——Fig. 162,*3*. **R. minuta*; *3a*, both valves lat.; *3b*, ped. v. ext.; *3c*, brach. v. oblique ext.; *3d*, brach. v. ant.; all ×30 (895a).

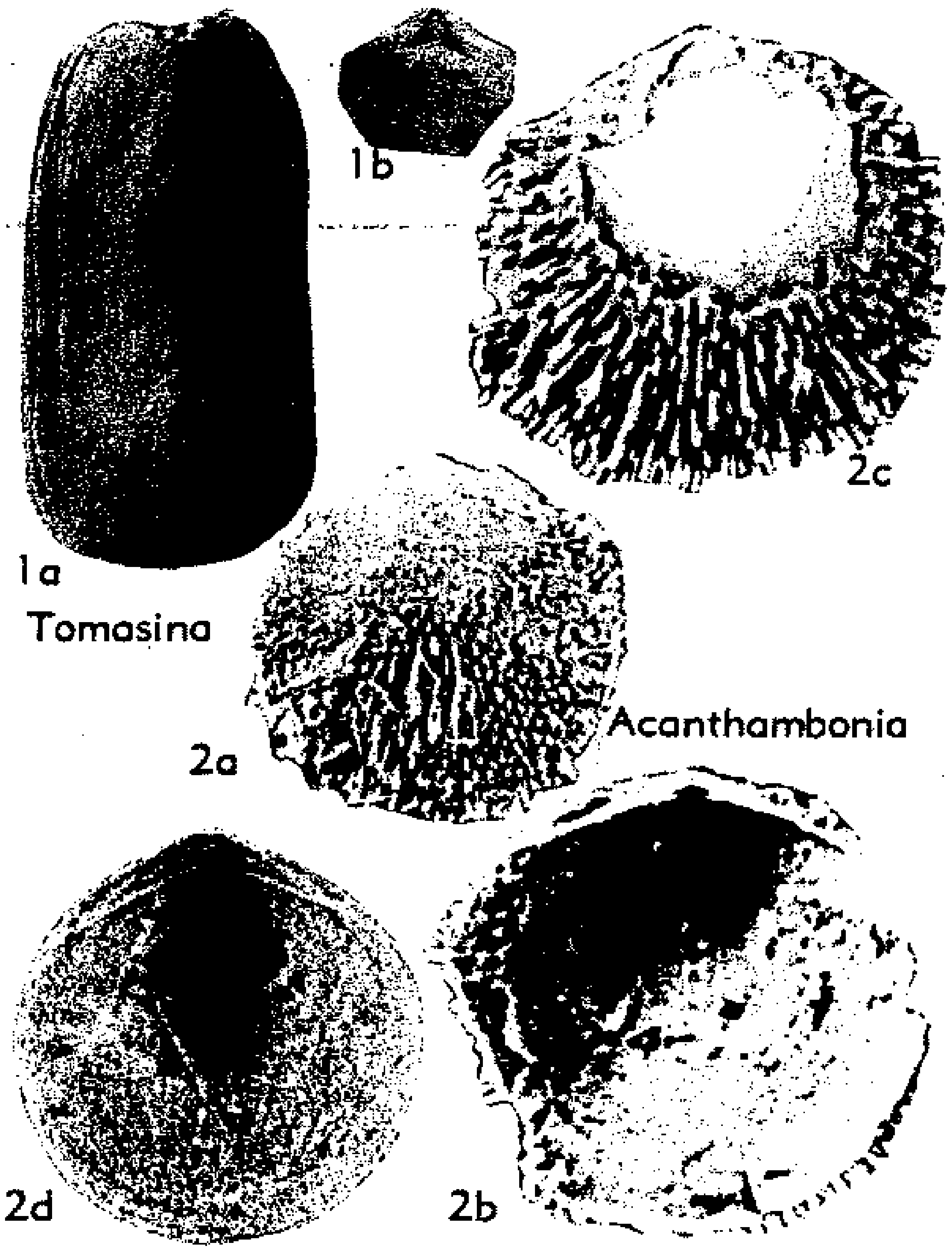


Fig. 163. Obolidae (Acanthamboniinae) *(2)*; (Subfamily Uncertain) *(1)* (p. *H269-H270*).

Subfamily ACANTHAMBONIINAE Cooper, 1956

[Acanthamboniinae Cooper, 1956, p. 211]

Small obolids, externally covered by abundant, minute, hairlike spines. Pedicle valve interior with narrowly triangular propareas separated by poorly developed pedicle groove, brachial pseudointerarea typical of family (189). *M.Ord.-U.Ord.*

Acanthambonia Cooper, 1956, p. 211 [**A. minutissima*; OD]. Suboval to subcircular in outline, biconvex. Muscle scars indistinguishable. *M.Ord.-U.Ord.*, N.Am.-Eu.(Ire.).——Fig. 163,*2*. *A. virginiensis* Cooper, Botetourt F., USA(Va.); *2a,b*, ped. v. ext. and int.; *2c,d*, brach. v. ext. and int., all ×15 (189).

Subfamily UNCERTAIN

Bistramia Hoek, 1912, p. 247 [**B. elegans*; OD] [=?*Pizarroa* Hoek, 1912, p. 246 (type, *P. quichuana*); *Tunarites* Cooper & Muir-Wood, 1951, p. 196 (*nom. subst. pro Tunaria* Hoek, 1912, p. 247

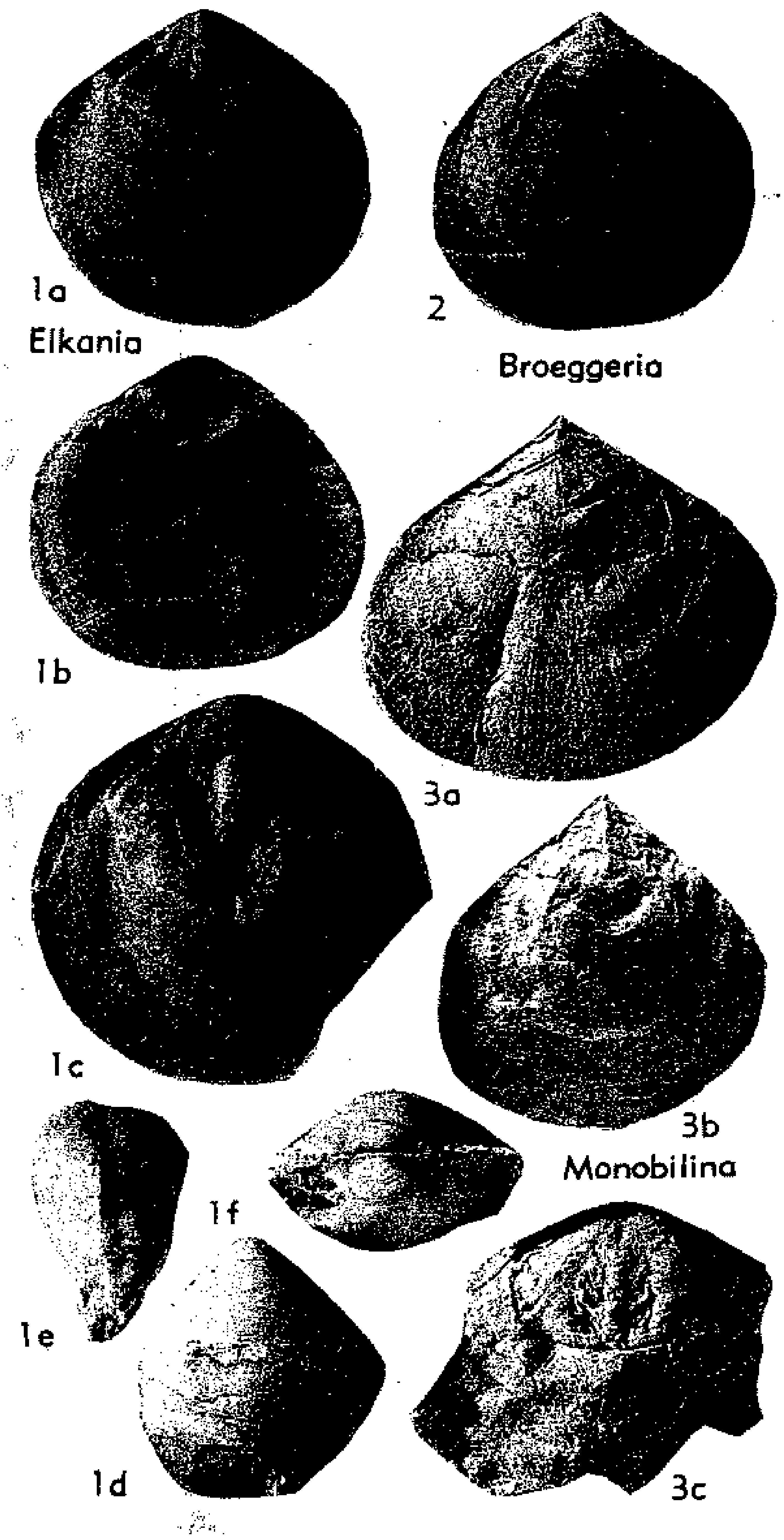


FIG. 164. Elkaniidae (p. *H*270).

(type, *Tunaria cochambina*), *non* Link, 1807)]. Transversely oval, ornament of concentric growth lines, beak marginal; shell finely punctate. [Details of posterior margin and internal structure unknown (488).] *Ord.*, S.Am.(Bol.).

Palaeoglossa Cockerell, 1911, p. 96 [*nom. subst. pro Glossina* Phillips, 1848, p. 370 (*non* Wiedemann, 1830)] [**Lingula attenuata* Sowerby, 1839, p. 641; OD] [=*Palaeoglossina* Dunbar & Condra, 1932, p. 35 *(nom. null.)*]. Pedicle valve acuminate, brachial valve suboval; ornament of fine growth lines. Internal structure of genus unknown. *Ord., ?Sil.*, Eu.-N.Am.

Tomasina Hall & Clarke, 1892, p. 65 [**Lingula criei* Davidson, 1881, p. 372; OD] [=*Tomasina* Hall & Clarke, 1891, p. 15 *(nom. nud.)*; *Thomasina* Bigot, 1927, p. 721 *(nom. null.)* (*non* Paeckelman, 1931)]. Elongate subrectangular in outline, valves gently convex, ornament of fine concentric growth lines. Beak of pedicle valve distinctly elevated above plane of commissure, triangular opening beneath beak into which posterolateral margins of valves are strongly reflected. *L.Ord.*, Eu.——FIG. 163,*1*. **T. criei* (Davidson), Sarthe; *1a*, latex impression, ped. v. int., ×1.5; *1b*, post. view latex impression ped. v. int., ×1.5 (Rowell, n).

Family ELKANIIDAE Walcott & Schuchert, 1908

[*nom. transl.* Schuchert & LeVene, 1929, p. 12 (*ex* Elkaniinae Walcott & Schuchert, 1908, p. 144)]

Subtriangular to subcircular in outline, propareas in pedicle valve well developed, posterior region of both valves thickened by number of platelike lamellae oblique to shell surface, dorsal muscle scars commonly impressed deeply in thickened area. Ventral *vascula lateralia* diverging anterolaterally from lateral margins of thickened area, dorsal *vascula lateralia* disposed similarly to those of pedicle valve, *vascula media* diverging slightly from mid-line in front of thickened area (825). *U.Cam.-L.Ord.*

Elkania Ford, 1886, p. 325 [*nom. subst. pro Billingsia* Ford, 1886, p. 466 (*non* de Koninck, 1876)] [**Obolella desiderata* Billings, 1862, p. 69; OD]. Ornament of concentric growth lines, moderate to strongly biconvex, beaks strongly incurved, thickened area in pedicle valve strongly developed, propareas inclined toward pedicle groove. *U.Cam.-L.Ord.*, N.Am.-?N.Afr.——FIG. 164,*1a-c*. **E. desiderata* (Billings), L.Ord.(Levis Sh.), Que.; *1a,b*, ped. v. int. impression, ped. v. int., ×4; *1c*, brach. v. int. impression, ×4 (825). ——FIG. 164,*1d-f*. *E. hamburgensis* (Walcott), *U.Cam.*, USA(Nev.); *1d*, brach. v. ext., ×3; *1e,f*, both valves lat., post., ×4 (825).

Broeggeria Walcott, 1902, p. 605 [*nom. correct.* Ulrich & Cooper, 1936, p. 618 (*pro Bröggeria* Walcott, 1902, p. 605, *nom. imperf.*)] [**Obolella salteri* Holl, 1865, p. 102; OD]. Similar to *Monobilina* but external shell without radial ornament. *U.Cam.-L.Ord.(Tremadoc.)*, N.Am.-Eu.-Asia(China)-?S.Am.(Arg.).——FIG. 164,*2*. **B. salteri* (Holl), U.Cam., Eng.; ped. v. int. impression, ×6 (Rowell, n).

Monobilina Salter, 1866, p. 334 [**Lingula plumbea* Salter, 1859, p. 50; OD]. Similar to *Elkania* but all shell layers with fine costellate ornament, valves less convex, beak of pedicle valve more pointed, less incurved; thickened area in pedicle valve less strongly developed. *L.Ord.*, Eu.——FIG. 164,*3*. **M. plumbea* (Salter), Wales; *3a,b*, ped. v. int. impressions, ×2: *3c*, brach. v. int. impression, ×1.5 (Rowell, n).

Family LINGULASMATIDAE
Winchell & Schuchert, 1893

[Lingulasmatidae Winchell & Schuchert, 1893, p. 149]

Medium to large lingulaceans, suboval to subrectangular in outline. Musculature of both valves borne on elevated platforms in posterior half of valve; platform of brachial valve supported anteriorly by high median septum (396). *M.Ord.-U.Ord.*

Lingulasma Ulrich, 1889, p. 383 [**L. schucherti*; OD] [=*Lingulelasma* Miller, 1889, p. 351 *(nom. null.)*]. Ornament of growth lines and fine granules. *M.Ord.-U.Ord.*, N.Am.-Eu.——Fig. 165,*1a,b*. **L. schucherti*, Richmond F., USA(Ill.); *1a,b*, wax casts of ped. v. and brach. v. int., ×1 (Rowell, n). ——Fig. 165,*1c*. *L. compactum* Cooper, Oranda F., USA(Va.); detail of ornament, ×8 (189).

Family ANDOBOLIDAE Kozlowski, 1930

[Andobolidae Kozlowski, 1930, p. 301]

Medium-sized lingulaceans with very high, strongly bifid platform in brachial valve extending forward about 0.25 length of valve from beak, platform free for short distance anteriorly; lateral margins of both valves strongly thickened. *Ord.*

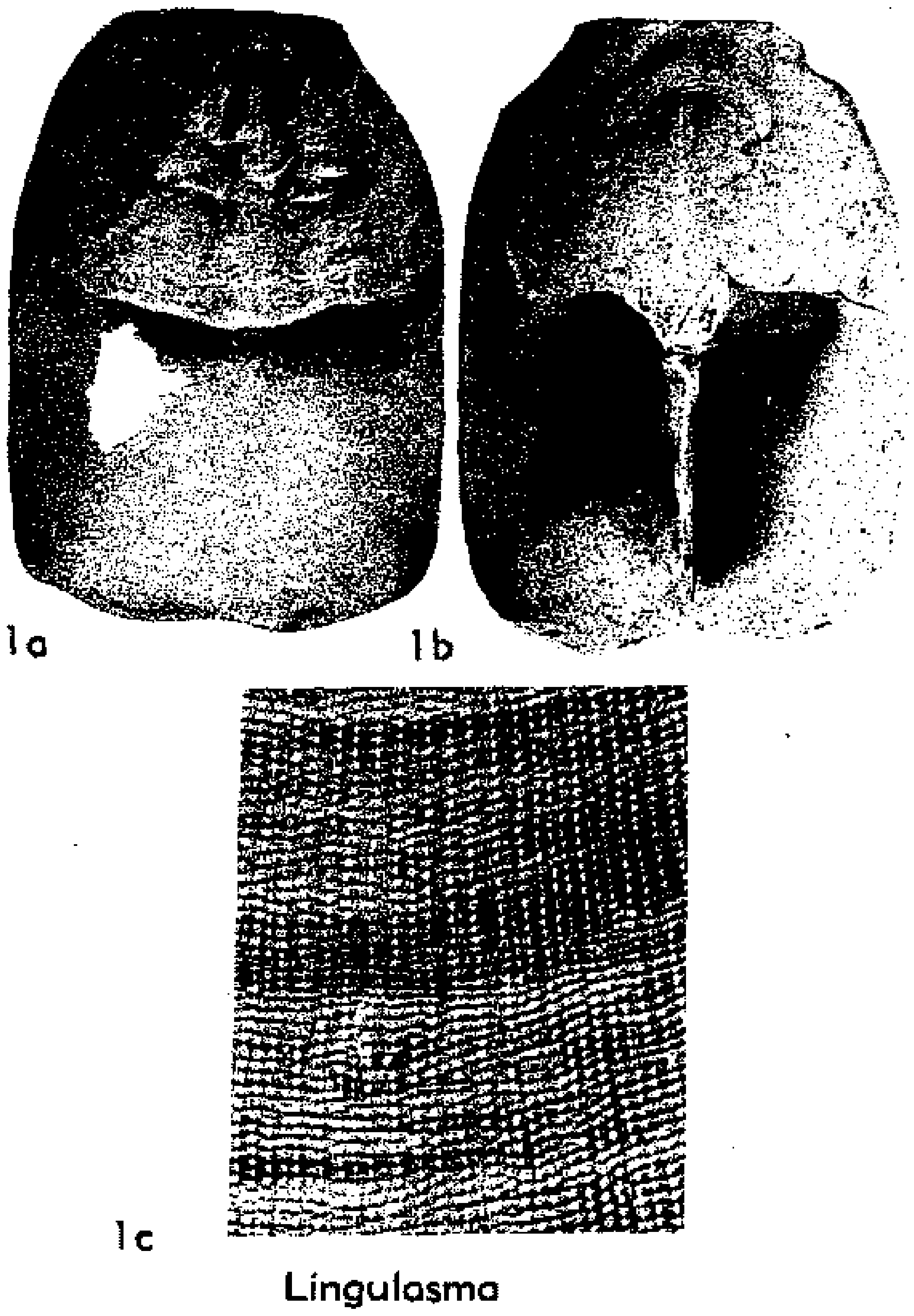


Fig. 165. Lingulasmatidae (p. *H*271).

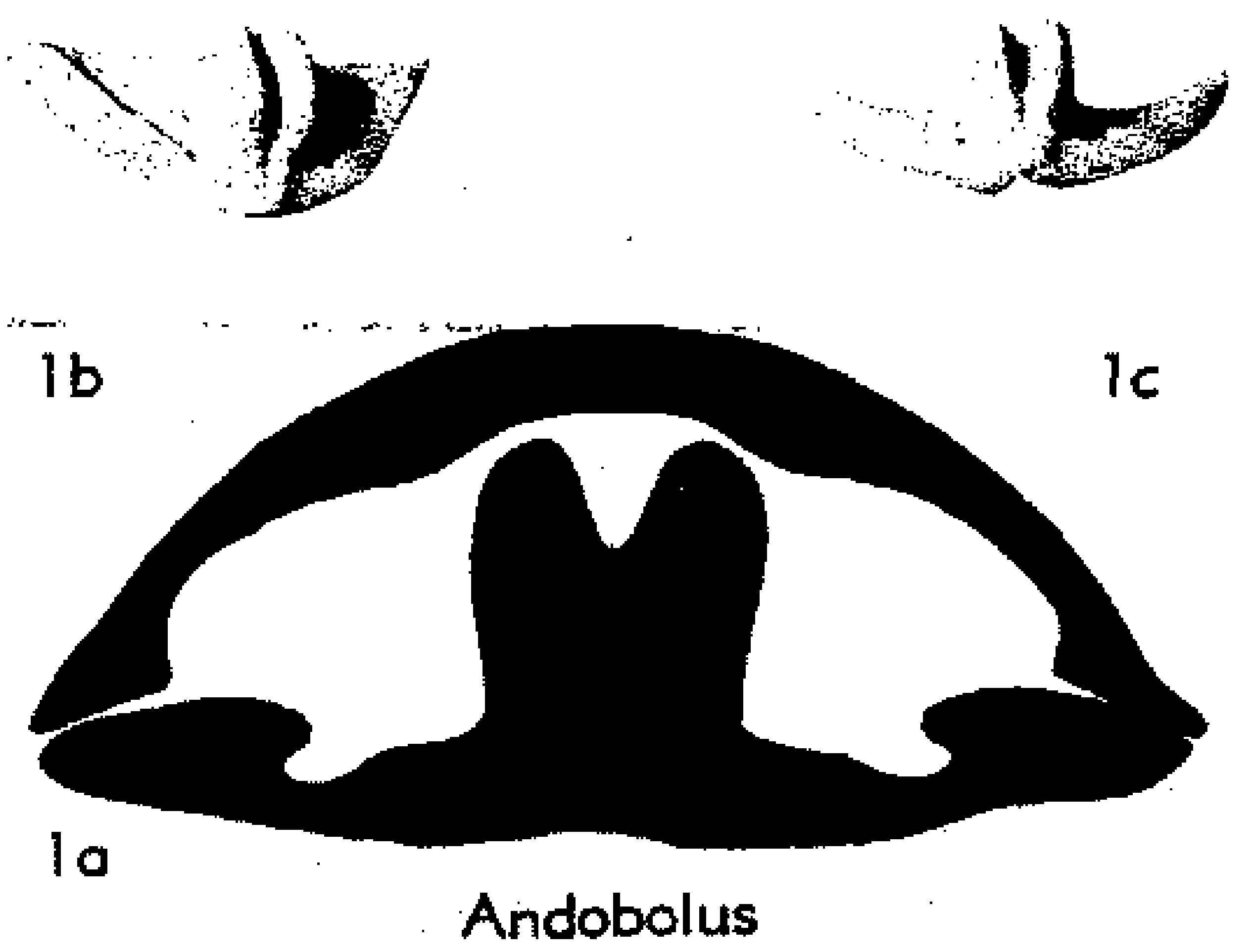


Fig. 166. Andobolidae (p. *H*271).

The systematic position of this family is somewhat doubtful, but the phosphatic shell, pedicle groove and gross form suggest that it is best regarded as an offshoot from the main obolid stock. The high platform is vaguely suggestive of the Trimerellidae, but several factors make it appear unlikely that the two families are closely related. The trimerellids are all essentially calcareous-shelled forms with platforms that differ considerably in details of morphology from those of *Andobolus*. Moreover, the contemporary Ordovician trimerellids have only very low, poorly developed platforms.

Andobolus Kozlowski, 1930, p. 295 [**A. jackowskii*; OD]. Oval in outline, ventribiconvex, brachial valve almost flat posteriorly, convex in anterior third, low sulcus near beak. Pedicle valve with triangular pedicle groove and internally with broad, low, flattened median ridge. *Ord.*, S.Am. (Bol.).——Fig. 166,*1*. **A. jackowskii*; *1a*, diagram. transv. sec. through both valves, brach. v. below, ×3; *1b,c*, oblique and post. views of wax reconstruction of post. part of brach. v. based on ser. secs., ×1 (*1a*, 488; *1b,c*, Rowell, n, based on sections by Kozlowski, 488).

Family PATERULIDAE Cooper, 1956

[Paterulidae Cooper, 1956, p. 236]

Relatively small phosphatic-shelled forms; subelliptical, linguloid to subcircular in outline, gently biconvex; limbus in both valves, low pedicle groove or notch in pedicle valve (189). *Ord.-Sil.*

The musculature of the 3 genera referred to the family is imperfectly known; it appears to be basically linguloid, particularly in *Lingulops* and *Elliptoglossa*, but that of *Paterula* is farther removed from this pattern. A similar situation appears to exist

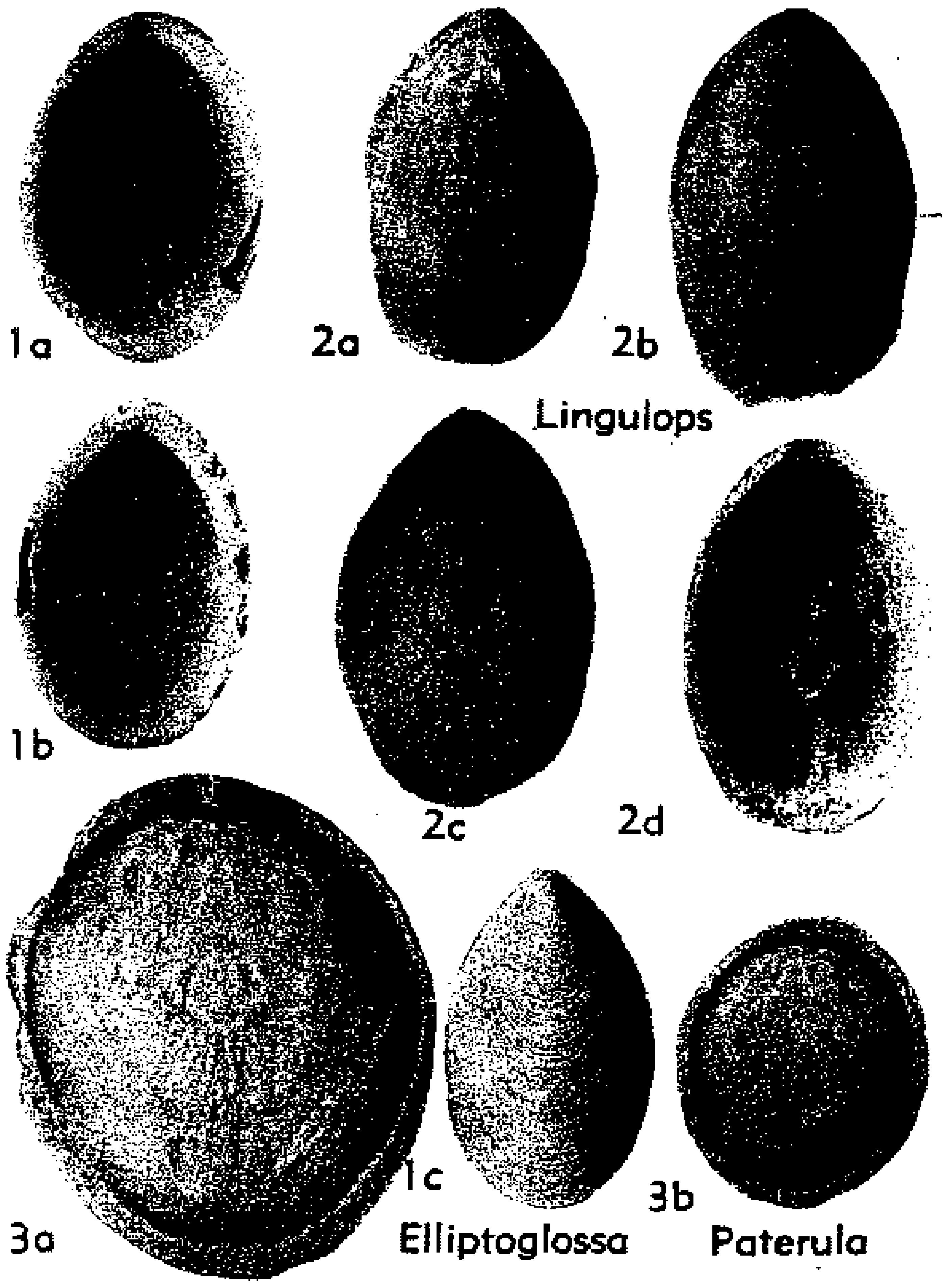


FIG. 167. Paterulidae (p. *H272*).

with the mantle canal system, although this is very poorly known. In *Lingulops* it is linguloid as far as it has been recognized, but the arrangement of the numerous fine canals in the pedicle valve of *Paterula* is unlike that of *Lingula*. It seems that *Paterula* has diverged farther than *Elliptoglossa* and *Lingulops* from the main linguloid stock, from which the family arose.

Lingulops has previously been placed with *Lingulasma* in the Lingulasmatidae. In their linguloid form, phosphatic shell, and the presence of some form of muscle platform, the two genera show some similarity. But *Lingulasma* has a very much larger shell, with characteristic beaded ornament and very high, strongly excavated platforms, the valves lacking a limbus. The presence of the latter in *Lingulops*, together with the low pedicle notch, size, and ornament, all suggest that the genus is better placed in the Paterulidae.

Paterula BARRANDE, 1879, p. 110 [**P. bohemica*; OD]. Shell thin, subcircular outline, brachial valve more convex than pedicle; pedicle valve with distinct pedicle notch, internally with 2 impressed lines, diverging slightly, extending to center of valve lateral of large central scar, numerous fine mantle canals radiating anteriorly and anterolaterally from central muscle scar, other muscle scars faintly impressed (189). *M.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 167,*3*. *P. perfecta* COOPER, M.Ord., USA(Ala.) *(3a)*, USA(Va.) *(3b)*; *3a*, ped. v. int. impression, ×15; *3b*, brach. v. int. impression, ×12 (189).

[Examinations of records indicates that *Paterula* BARRANDE, 1879, should be classed as a *nom. subst. pro Cyclus* BARRANDE, 1879, p. 110 (*non* DEKONINCK, 1841, p. 13) with type-species *Cyclus Bohemicus* BARRANDE, 1879, p. 110.]

Elliptoglossa COOPER, 1956, p. 241 [**Leptobolus? ovalis* BASSLER, 1919, p. 230; OD]. Subelliptical to linguloid in outline, subequally biconvex; pedicle groove low, inconspicuous. Muscle pattern basically linguloid, but imperfectly known and faintly impressed. *L.Ord.-U.Ord.*, N.Am.-Eu.——FIG. 167,*1*. **E. ovalis* (BASSLER), M.Ord., USA (Va.); *1a*, ped. v. int., ×8; *1b,c*, brach. v. int., ext., ×8 (189).

Lingulops HALL, 1872, p. 245 [**L. whitfieldi*; OD] [=*Ligulops* HALL, 1871, p. 2 *(nom. oblitum)*]. Externally like *Elliptoglossa*. In both valves anterior end of musculature borne on low platforms, that of brachial valve more strongly developed and may be slightly excavated anteriorly. Muscle pattern apparently basically linguloid, but except for anterior laterals and centrals of brachial valve poorly impressed. *Ord.-Sil.*, N.Am.——FIG. 167,*2*. *L. norwoodi* (JAMES), M.Ord., USA(Ky.); *2a*, ped. v. int. impression, ×6; *2b-d*, brach. v. ext., int. impression, int., all ×6 (189).

Family CRANIOPSIDAE Williams, 1963

[Craniopsidae WILLIAMS, 1963, p. 346] [=Pholidopsidae GORYANSKY, 1960, p. 177 (*nom. nud.*, not based on valid generic name)]

Shell calcareous, impunctate, biconvex, elliptical to linguloid in outline, with strong concentric ornament, which may be lamellose, growth holoperipheral or mixoperipheral. Apparently lacking a pedicle, attached by cementation or free. Central muscle scars strongly developed, usually on low solid platform. Smooth limbus present in both valves. *M.Ord.-L.Carb.*

At least one genus in the family, *Craniops*, was attached by cementation of the apical region of the pedicle valve. An attachment scar does not occur in *Paracraniops* or *Lingulapholis* and has not been described for the rather poorly known *Pseudopholidops*. None of these three genera possess a pedicle groove or foramen and it appears probable that at least in the adult stages a pedicle was absent and that the animals lay free on the sea floor.

The taxonomic position of the family is

debatable. The genera referred to it usually have been included in the Craniacea. They agree with members of that superfamily in possessing a calcareous shell and they show a resemblance to some of them in having a limbus. Possibly, however, these characters developed independently in the two stocks. Several differences between the Craniopsidae and the Craniidae support this point of view. In the former family the shell is impunctate, lacking the arborescent punctae of the Craniidae, and the characteristic muscle and mantle-canal patterns of the craniids, which are usually well preserved, cannot be recognized in the Craniopsidae. In the latter family, moreover, the lateral margins of the body cavity are commonly well marked by narrow, very elongated scars, probably the site of attachment of dermal muscles. Among Recent genera, dermal muscles are well developed only in the lingulids and, as Huene (439) has noted, *Craniops* is internally more like *Lingula* than *Crania*. At the present time, one cannot be dogmatic, but it seems unlikely that the Craniopsidae developed from early craniaceans or that they and the craniaceans diverged from a common ancestral stock.

Cooper (189) included *Craniops* in his new family Paterulidae, which he placed in the Trimerellacea. The genus shows some similarities with the Paterulidae, particularly with *Lingulops*, which is here included in that family. However, the differences in shell composition and to a lesser extent in growth form seem to preclude *Craniops* being included in the Paterulidae and merit the retention of a separate family, of uncertain origin, but possibly derived from some *Lingulops* stock.

Craniops Hall, 1859, p. 84 [**Orbicula? squamiformis* Hall, 1843, p. 108; OD] [=*Pholidops* Hall, 1859, p. 489 (obj.)]. Attached by cementation of apical region of pedicle valve, holoperipheral growth, apices posterior of center, muscle field in both valves bounded anteriorly by low platform. *M.Ord.-L.Carb.*, N. Am.-S. Am.-Eu.-Asia.——Fig. 168,*1*. *C. implicata* (Sowerby), U.Sil.(Wenlock.); *1a,b*, ped. v. ext., int., ×6; *1c,d*, brach. v. int., ext., ×6 (Rowell, n).

Lingulapholis Schuchert, 1913, p. 295 [**Pholidops terminalis* Hall, 1859, p. 490; OD]. Internally similar to *Craniops*, but differs in having mixoperipheral growth, producing terminal beaks and well-developed pseudointerareas in both valves. No cementation attachment scar. *M.Ord.-Dev.*, N. Am.-Eu.——Fig. 168,*3*. *L. calceola* (Hall & Clarke), Dev., USA(Tenn.); *3a*, ped. v. int., ×5; *3b,c*, brach. v. ext., int., ×5 (Rowell, n).

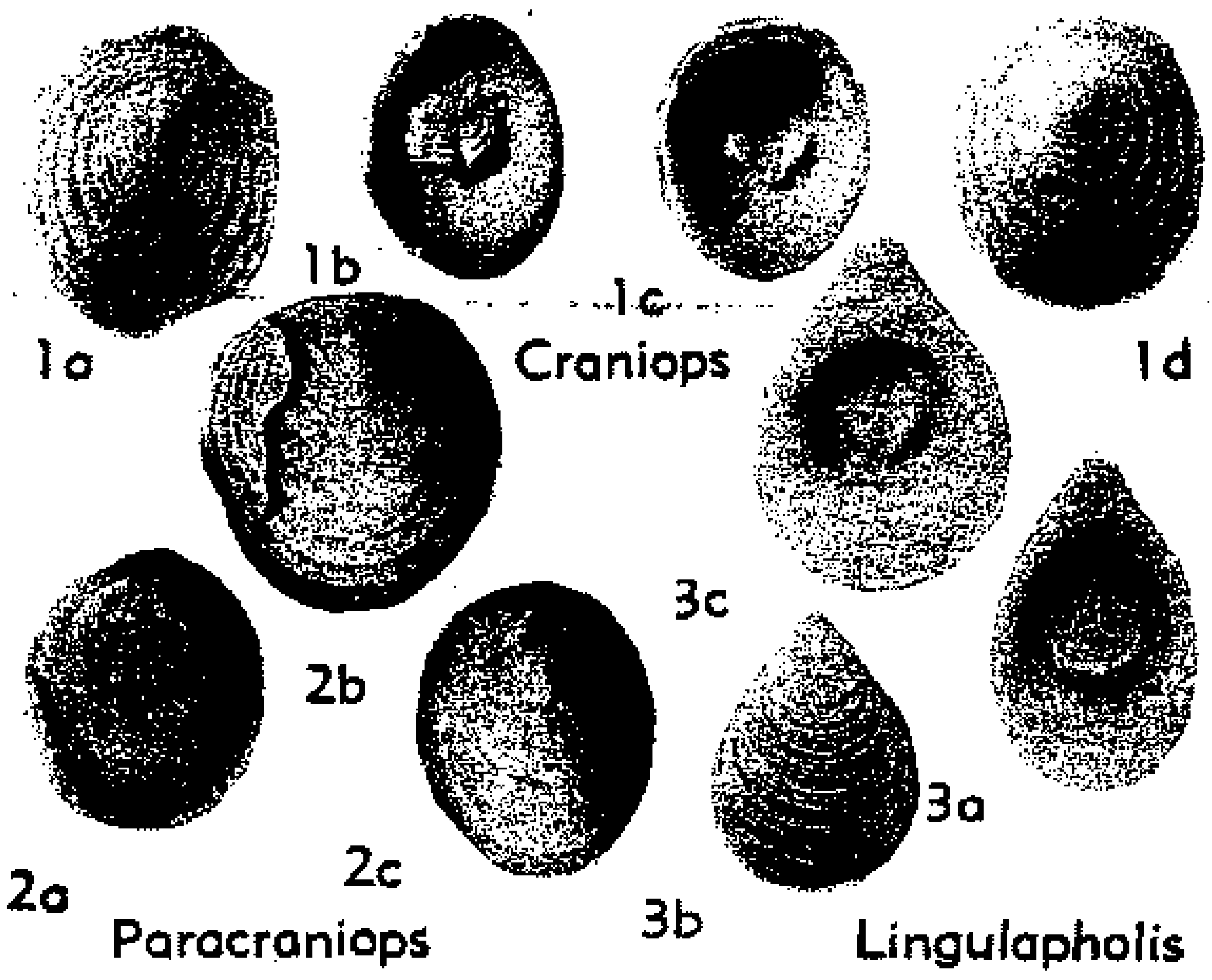


Fig. 168. Craniopsidae (p. *H*273).

Paracraniops Williams, 1963, p. 346 [**Craniops? pararia* Williams, 1962, p. 88; OD]. Outline and ornament similar to *Craniops*, differing in absence of attachment scar, of well-formed platform in brachial valve, and in presence of 2 low ridges in this valve diverging anterolaterally from apex. *M.Ord.*, Eu.-N.Am.——Fig. 168,*2*. **P. pararia* (Williams), Scot.; *2a*, ped. v. int. impression, ×4; *2b,c*, brach. v. ext., int. impression, ×4 (877).

Pseudopholidops Bekker, 1921, p. 64 [**P. scutellata*; OD]. Genus inadequately known; apparently similar to *Lingulapholis* but muscle platforms absent. *M.Ord.*, Eu.

Superfamily TRIMERELLACEA Davidson & King, 1872

[*nom. transl.* Schuchert & LeVene, 1929, p. 12 (*ex* Trimerellidae Davidson & King, 1872, p. 442)]

Large forms with thick calcareous shells, biconvex, inequivalved, elongate oval to transversely oval in outline, shell smooth except for growth lines; beak of pedicle valve prominent, pseudointerarea well developed, generally apsacline, divided into 2 propareas by triangular homeodeltidium. Internally, ventral umbo may be solid or divided into 2 umbonal chambers by cardinal buttress; muscle platforms present in both valves, solid or excavated, when excavated, cavity divided into 2 vaults by median partition that may extend anterior to platform. *M.Ord.-U.Sil.*

The musculature of this group is not well known. Both platforms appear to bear 2 or possibly 3 pairs of poorly defined scars, and additional pairs of scars occur in both valves lateral to the platform on the floor of the valve.

In *Dinobolus,* the valves possess a rudimentary form of articulation (606). A transverse plate on the posterior margin of the brachial valve fits into a corresponding depression, the cardinal socket, in the pedicle valve. No apical foramen is known and since the form of articulation prohibits the pedicle emerging between the valves the genus must have lain free on the sea floor. Other genera referred to the superfamily have not been found as well preserved as Norford's *Dinobolus* material, but the structure of their posterior margin, as far as known, is consistent with their having similar articulation.

Family TRIMERELLIDAE Davidson & King, 1872

[Trimerellidae Davidson & King, 1872, p. 442]

Characters of superfamily (245). *M.Ord.-U.Sil.*

Trimerella Billings, 1862, p. 166 [**T. grandis*; SD Dall, 1870, p. 160] [=*Gotlandia* Dall, 1870, p. 160 (type, *G. lindstroemi*)]. Large for family, elongate oval in outline, pseudointerarea of pedicle valve high, cardinal buttress broad, not extending onto ventral platform, umbonal cavities small or absent; platforms in both valves well developed, deeply vaulted, vaults separated by median partition that extends anterior to platform. *Sil.,* N.Am.-Eu.(Gotl.).——Fig. 169,*2a-d*. **T. grandis,* M.Sil., Ont.; *2a,b,* ped. v. int., int. impression, ×0.7; *2c,d,* brach. v. int., int. impression, ×0.7 (245).——Fig. 169,*2e*. *T. ohioensis* Meek, M.Sil., USA(Ohio); ext. (restored), ×0.7 (396).

Dinobolus Hall, 1871, p. 4 [**Obolus conradi* Hall, 1868, p. 368; OD] [=*Conradia* Hall, 1872, p. 107 (obj.)]. Pseudointerarea of pedicle valve relatively low, umbo solid or small umbonal cavities separated by cardinal buttress; ventral platform hollow anteriorly, vaults small, supporting median partition broadly triangular posteriorly, narrowing anteriorly; dorsal platform vaulted anteriorly, supported by short median ridge. *L.Sil.-U.Sil.,* Eu.-N.Am.——Fig. 169,*5*. **D. conradi* (Hall), M.Sil., Wis. *(5a,b),* Iowa *(5c)*; *5a,b,* ped. v. int., int. impression, ×1; *5c,* brach. v. int. impression, ×1 (396).

Eodinobolus Rowell, 1963, p. 37 [**Obolellina magnifica* Billings, 1872, p. 329; OD]. Early trimerellids, externally like *Dinobolus* but platforms not vaulted, dorsal platform very low, median ridges poorly developed or absent, umbo of pedicle valve solid. *M.Ord.-U.Ord.,* N.Am.-Eu.——Fig. 169,*3*. **E. magnificus* (Billings), M.Ord. (Rockland F.), Ont.; *3a,* ped. v. ext., ×1; *3b,c,* brach. v. ext., int., ×1 (189).

Monomerella Billings, 1871, p. 220 [**M. prisca*; SD Davidson & King, 1874, p. 155]. Cardinal buttress well developed, extending forward nearly to front of platform, umbonal cavities deep, tubular. Ventral platform solid, widest anteriorly where it is slightly excavated, median ridge short or absent. Dorsal platform similar to *Dinobolus. Sil.,* N.Am.-NW.Eu.-?Asia(Kazakhstan).——Fig. 169,*4*. **M. prisca,* M.Sil., USA(Ill.); *4a,b,* ped.v. int., int. impression, ×1; *4c,* brach. v. int. impression, ×1 (396).

Rhynobolus Hall, 1871, p. 5 [**Obolus galtensis* Billings, 1862, p. 168; SD Dall, 1877, p. 61] [=*Obolellina* Billings, 1871, p. 222 (obj.); *Rhinobolus* Hall & Clarke, 1892, p. 44 *(nom. van.)*]. Elongate oval in outline, pseudointerarea of pedicle valve high, platform inconspicuous posteriorly, anteriorly V-shaped in outline, steeply inclined posteriorly, umbo solid; dorsal platform low, not excavated, low median ridge may be present anterior to platform. *M.Sil.,* N.Am.-?Asia (Kazakhstan).——Fig. 169,*1*. **R. galtensis* (Billings), Ont.; *1a,b,* ped. v. int., brach. v. int., ×1 (396).

Order ACROTRETIDA Kuhn, 1949

[*nom. correct.* Goryansky, 1960, p. 178 (*pro* order Acrotretacea Kuhn, 1949, p. 101)] [emend. Rowell, herein] [=Daikaulia Waagen, 1885, p. 748 *(partim)*+Gasteropegmata Waagen, 1885, p. 744 *(partim)*; Neotremata Beecher, 1891, p. 354 *(partim)*]

Usually circular or subcircular in outline, shell phosphatic or punctate calcareous; pedicle opening, when present, confined to pedicle valve, growth of pedicle valve holoperipheral or mixoperipheral; shell secretion of brachial valve more variable, beak marginal to subcentral. *L.Cam.-Rec.*

The original concept of the order has been extended to include the craniaceans and the phosphatic-shelled genera which Rowell (680) grouped in the Siphonotretacea.

Suborder ACROTRETIDINA Kuhn, 1949

[*nom. transl.* Rowell, herein (*ex* order Acrotretida Kuhn, 1949, p. 101)] [=Daikaulia Waagen, 1885, p. 748 *(partim)*; Discinacea Waagen, 1885, p. 748 *(partim)*; Diacaulia Hall & Clarke, 1894, p. 323 *(partim)*]

Shell phosphatic, usually attached by pedicle throughout life. *L.Cam.-Rec.*

Superfamily ACROTRETACEA Schuchert, 1893

[*nom. transl.* Schuchert, 1896, p. 308 (*ex* Acrotretidae Schuchert, 1893, p. 150)]

Pedicle valve commonly conical to subconical, more rarely convex, pseudointerarea

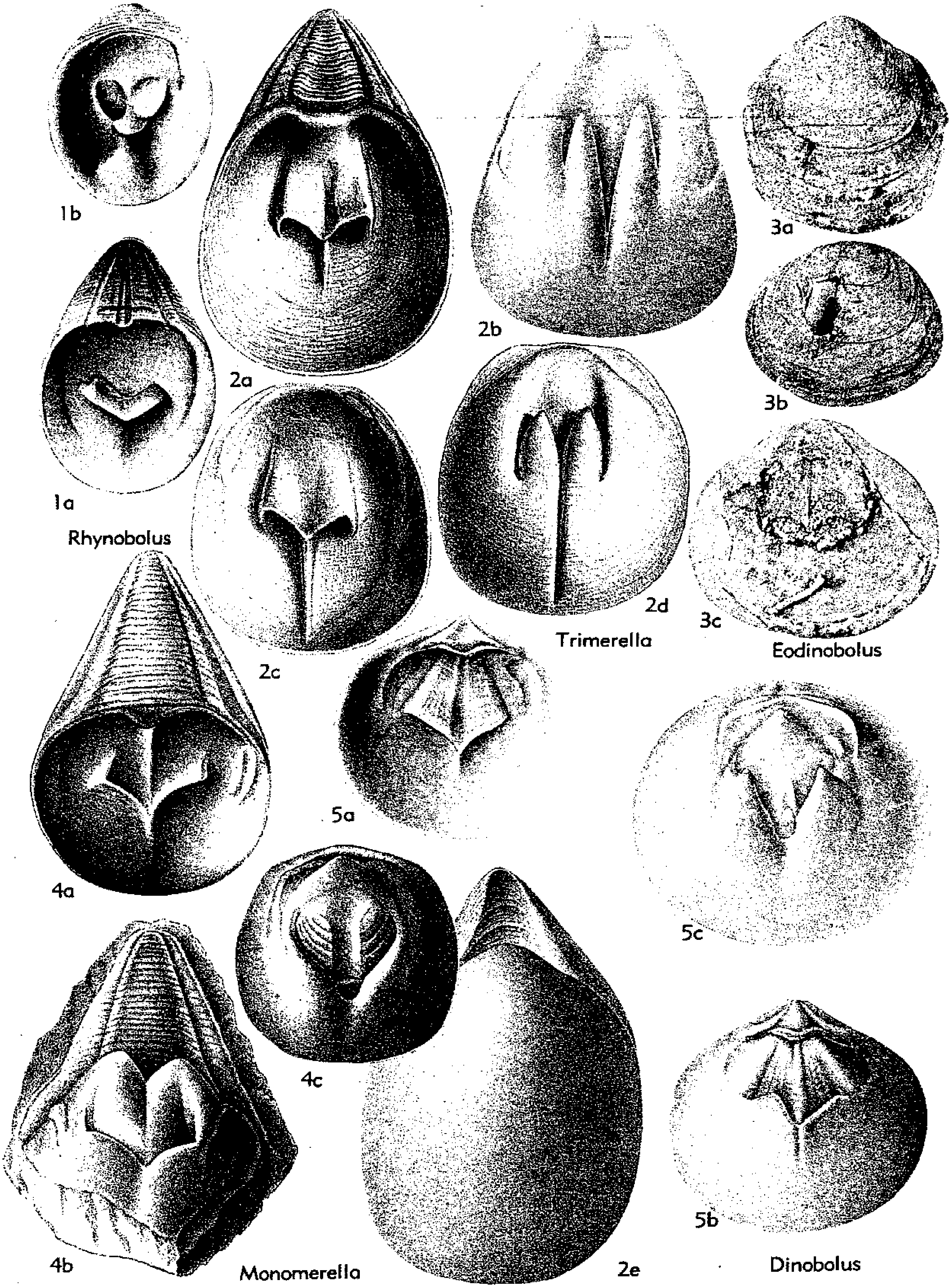


Fig. 169. Trimerellidae (p. *H*274).

usually present; pedicle opening typically a foramen at or slightly posterior to beak, less commonly an open triangular delthyrium; brachial valve usually with marginal beak, more rarely low cone (Conodiscinae); propareas variably developed; dorsal median ridge or septum usually present (189, 848). *L.Cam.-Dev.*

Family ACROTRETIDAE Schuchert, 1893

[Acrotretidae Schuchert, 1893, p. 150]

Generally small to minute; pseudointerarea of pedicle valve commonly divided by intertrough or deltoid pseudointerarea; pedicle foramen small, at or somewhat posterior to beak, may be simple perforation or continued internally as some form of tube, apical process present in many species; brachial valve gently convex to gently concave, marginal beak, pseudointerarea well developed to obsolescent, anacline to orthocline, median septum usually present, may be merely a ridge or absent. Muscle scars of pedicle valve include pair of relatively large cardinal scars posterolaterally placed and pair of small apical pits. Brachial valve bears pair of large cardinal scars posterolaterally situated and smaller pair of anterior scars close together, near center of valve; another more doubtful scar is medially placed immediately in front of pseudointerarea. Ventral mantle canal system typically consists of pair of baculate *vascula lateralia* (more rarely pinnate as in *Conotreta*); mantle canal system of brachial valve less well known but commonly comprises pair of baculate *vascula lateralia* that diverge anterolaterally from in front of beak, with additional, poorly impressed pair of *vascula media*. *L.Cam.-U.Sil., ?L.Dev.*

Acrotretids definitely range into the Upper Silurian (Chimney Hill Limestone, Oklahoma) in North America and Upper Silurian (Wenlock Limestone) in England, but the upper stratigraphic limit is not satisfactorily determined. Undoubted acrotretids, known only from their pedicle valves and as yet incapable of more than family assignment, occur in float material collected in New York, apparently associated with a Lower Devonian fauna (70).

Subfamily ACROTRETINAE Schuchert, 1893

[*nom. transl.* Matthew, 1903, p. 74 (*ex* Acrotretidae Schuchert, 1893, p. 150)]

Pedicle valve usually conical, more rarely convex, foramen circular at or immediately posterior to beak, apical process usually present; dorsal pseudointerarea well developed, divided into 2 propareas by triangular, concave median groove. *?L.Cam., M.Cam.-U. Ord.*

Acrotreta Kutorga, 1848, p. 260 [**A. subconica*; SD Davidson, 1853, p. 133]. Pedicle valve high, procline to catacline, with well-marked intertrough, internal structure unknown (848). [Genus inadequately known. Type material destroyed during World War II and satisfactory topotype material not yet found (Goryansky, personal communication, 1961). May be a senior synonym of *Conotreta*.] *?U.Cam., Ord.*, Eu.-?N.Am.-?Asia.

Angulotreta Palmer, 1955, p. 769 [**A. triangularis*; OD]. Pedicle valve moderately high, procline to catacline, narrow deltoid pseudointerarea present, internal pedicle opening at apex, apical process well developed, long, mainly on anterior slope of valve; in brachial valve median septum variably developed, strong to weak, may be digitate, posteriorly buttressing median groove. *U.Cam.*, N. Am.——Fig. 170,*1*. **A. triangularis, Aphelaspis* Zone, USA(Tex.); *1a-d*, ped. v. ext., lat., post., int., all ×10; *1e*, brach. v. int., ×10 (*1a-c,e*, 635a; *1d*, 67).

Apsotreta Palmer, 1955, p. 770 [**A. expansa*; OD]. Pedicle valve convex, apsacline, deltoid pseudointerarea low, wide; apical process on anterior slope, long, parallel-sided or expanding anteriorly; brachial valve similar to *Angulotreta*, septum not digitate. *U.Cam.*, N.Am.——Fig. 170,*2*. **A. expansa, Dunderbergia* Z. (USA(Tex.); *2a-d*, ped. v. ext., lat., post., int., all ×15; *2e*, brach. v. int., ×15 (Rowell, n).

Conotreta Walcott, 1889, p. 365 [**C. rusti*; OD] [=*Geinitzia* Hall, 1889, p. 43 (*nom. nud.*)]. Pedicle valve externally similar to *Angulotreta* but usually with fine intertrough, internally different, having pinnate *vascula lateralia* and apical process a large boss on anterior slope of valve which bounds internal pedicle opening anteriorly; brachial valve similar to *Angulotreta*, but propareas less well developed and cardinal scars more medianly placed. *Ord.*, N.Am.-Eu.——Fig. 170,*4*. *C. multisinuata* Cooper, M.Ord., USA(Va.); *4a-d*, ped. v. post., lat., int. cast, int. apical region, all ×6; *4e*, brach. v. int., ×10 (189).

Linnarssonella Walcott, 1902, p. 601 [**L. girtyi*; OD]. Similar to *Apsotreta* but apical process less well developed, posterolateral margins of dorsal propareas deeply grooved and median septum absent. *U.Cam.*, N.Am.——Fig. 170,*5*. **L. girtyi*, USA(S.Dak.); *5a,b*, ped. v. and brach. v. int., ×10 (Rowell, n).

Prototreta Bell, 1938, p. 405 [**P. trapeza*; OD] [=*Homotreta* Bell, 1941, p. 230 (type, *H. interrupta* Bell, 1941, p. 230)]. Similar to *Angulo-*

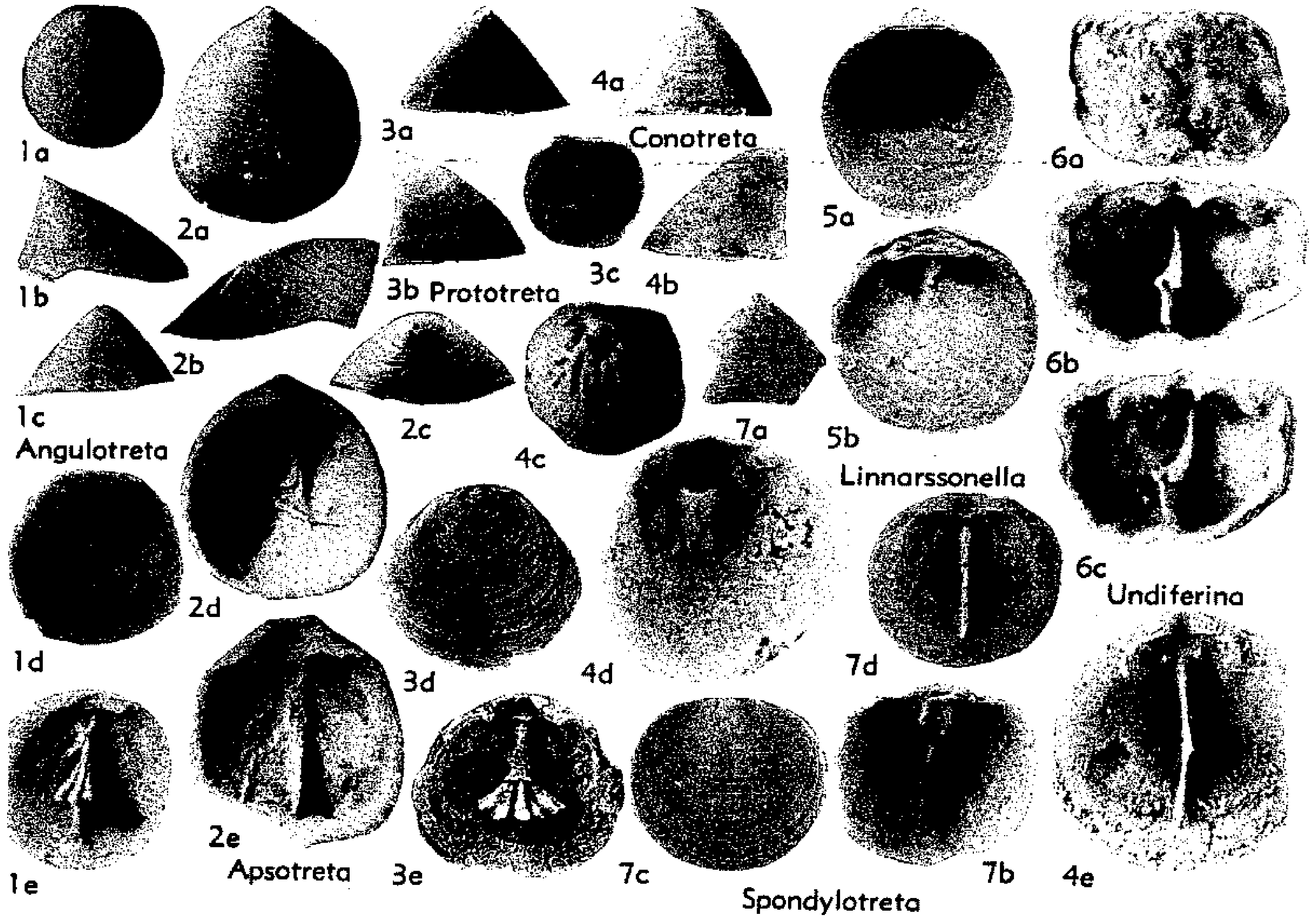


FIG. 170. Acrotretidae (Acrotretinae) (p. *H276-H277*).

treta, but pseudointerarea of pedicle valve divided by well-marked intertrough, internal pedicle foramen opening through apical process on posterior slope of valve. *?L.Cam., M.Cam.,* N.Am.-Eu.-Asia. ——FIG. 170,*3*. **P. trapeza, M.Cam.,* USA(Mont.); *3a-c,* ped. v. post., lat., int. apical region, ×6, ×6, ×8; *3d,e,* brach. v. ext., int., ×6 (65).

Spondylotreta COOPER, 1956, p. 255 [**S. concentrica*; OD]. Ornament of fine, elevated concentric lines, pedicle valve procline; pedicle tube on inner posterior surface of valve, continued as forked ridge, supported apically by median septum; brachial valve gently concave, internally similar to *Angulotreta* but septum not digitate nor buttressing median groove. *M.Ord.-U.Ord.,* N. Am.-Eu.(Ire.).——FIG. 170,*7*. **S. concentrica,* Pratt Ferry F., USA(Ala.); *7a,b,* ped. v. post., int., ×6, ×10; *7c,d,* brach. v. ext., int., ×6 (189).

Undiferina COOPER, 1956, p. 262 [**U. rugosa*; OD]. Pedicle valve unknown, possibly cemented form; brachial valve convex, subrectangular outline, ornament of irregular wrinkles, concave median groove, not buttressed by septum, separating short, well-developed propareas, septum strong, highest anteriorly, ventral edge may bear slightly digitate plate. *M.Ord.,* N.Am.(Ala.).——FIG. 170,*6*. **U. rugosa*; *6a-c,* brach. v. ext., int., int., ×8 (189).

Subfamily LINNARSSONIINAE Rowell, n. subfam.

Pedicle valve depressed conical to convex, foramen circular at or immediately posterior to beak, apical process anterior of internal pedicle opening; median groove in brachial valve small, propareas obsolescent. *L.Cam.-U.Cam.*

Linnarssonia WALCOTT, 1885, p. 115 [**Obolella transversa* HARTT, 1868, p. 644; OD] [=*Pegmatreta* BELL, 1941, p. 231 (type, *P. perplexa*)]. Pedicle valve a relatively low cone, procline rarely apsacline, apex thickened by callosity anterior to internal pedicle foramen, subcircular in outline, extending slightly on to anterior slope of valve; brachial valve with small median groove, propareas minute or absent, low median ridge. *L.Cam.-M. Cam., ?U.Cam.,* N.Am.-Eu.——FIG. 171,*2*. *L. sagittalis* (DAVIDSON), M.Cam., Wales; *2a,b,* ped. v. and brach. v. int. impressions, ×4 (Rowell, n).

Acrothyra MATTHEW, 1901, p. 303 [**Acrotreta proavia* MATTHEW, 1899, p. 203; SD WALCOTT, 1912, p. 716]. Elongate, strongly apsacline, pseudointerarea long, divided by intertrough; apical process on anterior slope of valve, elongate, expanding anteriorly, depressed in center, bounded by raised rim; brachial valve with median ridge. *M.Cam.,* N.Am.

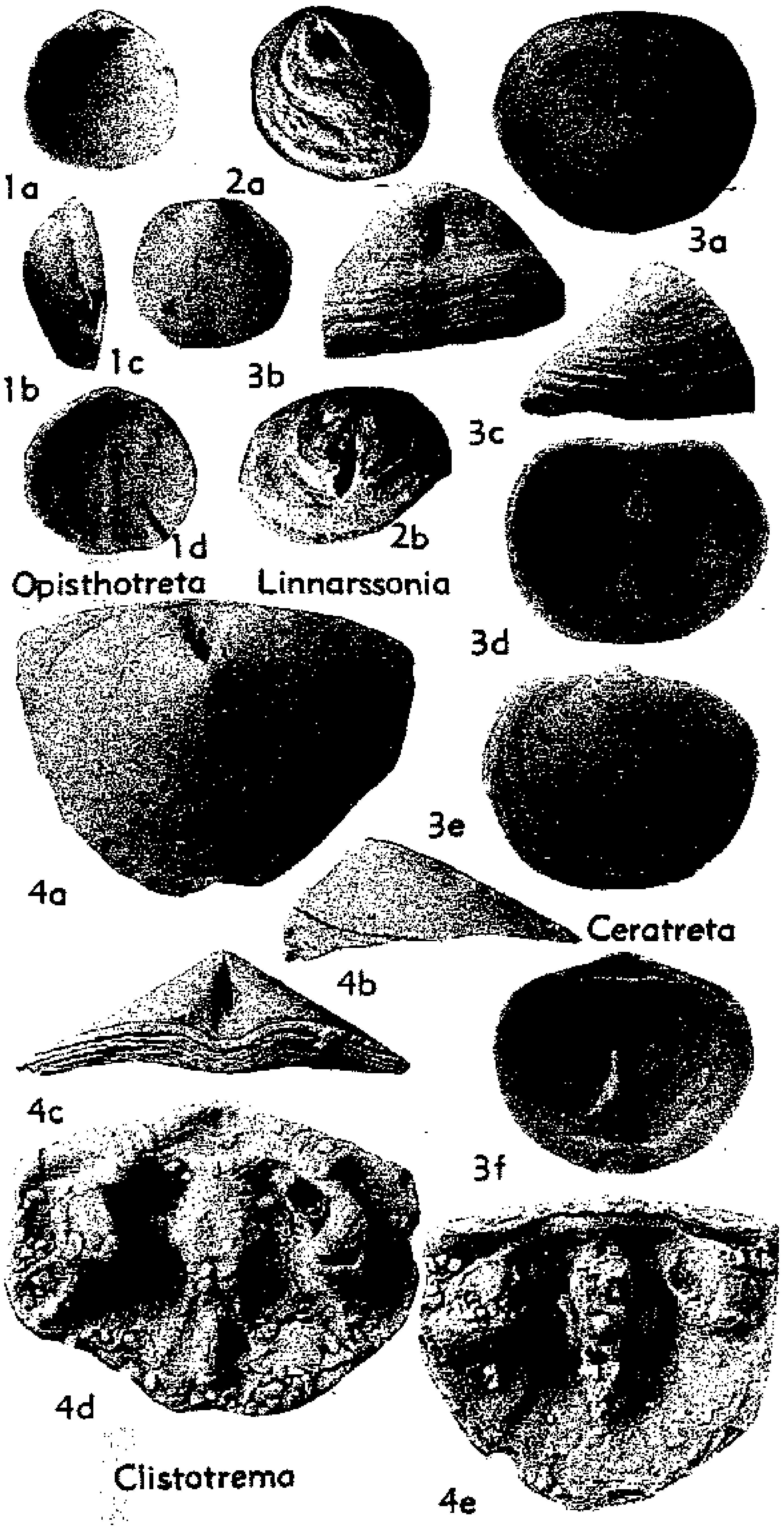


FIG. 171. Acrotretidae (Linnarssoniinae) *(1-2)*, (Ceratretinae) *(3-4)* (p. *H277-H278*).

Opisthotreta PALMER, 1955, p. 771 [**O. depressa*; OD]. Subcircular, pedicle valve low, apsacline, pseudointerarea small, concave; apical process very low, anteriorly expanding on anterior slope of valve; brachial valve with pitlike median groove, minute propareas and low median ridge. *U.Cam.*, N.Am.——FIG. 171,*1*. **O. depressa,* USA(Tex.); *1a,* ped. v. int.; *1b,* both valves lat.; *1c,d,* brach. v. ext., int., all ×15 (635a).

Subfamily CERATRETINAE Rowell, n. subfam.

Thick-shelled, pedicle valve conical, obtuse or rounded apex, intertrough well developed, external pedicle foramen elongated, apical process a ridge or buttress connecting anterior and posterior slopes of valve, bearing internal pedicle opening; brachial valve with well-developed median groove buttressed by median septum, propareas moderately well developed to obsolescent. *U. Cam.-L.Ord.*

Ceratreta BELL, 1941, p. 233 [**C. hebes*; OD]. Pedicle valve bluntly conical, procline; apical process a strong ridge mainly on posterior slope of valve, internal pedicle opening on ridge about halfway down posterior slope, median groove in brachial valve large, propareas absent, median septum abruptly pointed anteriorly. *U.Cam.* (*Conaspis* Z.), N.Am.——FIG. 171,*3*. **C. hebes,* USA(Mont.); *3a-d,* ped. v. ext., post., lat., int., ×12; *3e,f,* brach. v. ext., int., ×12 (Rowell, n).

Clistotrema ROWELL, 1963, p. 35 [*nom. subst. pro Orbicella* D'ORBIGNY, 1847, p. 269 (*non* DANA, 1846)] [**Orbicula buchii* DE VERNEUIL, 1845, p. 288; OD]. Large, very thick-shelled; pedicle valve obtusely conical, procline, pseudointerarea poorly defined, intertrough deep, external foramen in intertrough, one third distance down posterior slope; internal pedicle opening dorsally placed on extremely massive apical process which fills apical part of valve, extending as broad buttress across valve, widest anterior of internal pedicle opening, projecting into brachial valve. Muscle scars elevated on lamellar shell. Brachial valve with anacline propareas, cardinal muscle scars elevated as in pedicle valve. *L.Ord.*, USSR(N.W.).——FIG. 171, *4*. **C. buchii* (DE VERNEUIL), Tremadoc., Est.; *4a-c, e,* ped. v. ext. lat., post., int., ×5; *4d,* brach. v. int. ×5 (Rowell, n).

Subfamily SCAPHELASMATINAE Rowell, n. subfam.

Obtusely conical or conical with rounded apex. Intertrough usually well developed, foramen immediately posterior to apex; apical process a very low swelling, mainly anterior to foramen or absent. Brachial valve with median groove not buttressed by septum. Propareas variable, never large. [Possibly derived from the Ceratretinae.] *M.Ord.-U.Sil.*

Scaphelasma COOPER, 1956, p. 259 [**S. septatum*; OD]. Ornament lamellose peripherally; pedicle valve obtusely conical, foramen a short slit, apical process a low swelling nearly surrounding foramen; triangular median septum arising near center of valve. *M.Ord., ?U.Ord.,* N.Am.(Ala.)-?Eu.(Ire.).——FIG. 172,*1*. **S. septatum,* Pratt Ferry F., USA(Ala.); *1a-d,* ped. v. ext., post., lat., int., ×10; *1e,f,* brach. v. ext., int., ×10 (189).

Artiotreta IRELAND, 1961, p. 1138 [**A. parva*; OD]. Minute, thin-shelled; pedicle valve obtusely conical, foramen circular, internally pedicle apex slightly thickened anterior of foramen; brachial valve similar to *Scaphelasma* but median groove minute and propareas absent. *U.Sil.,* N.Am.

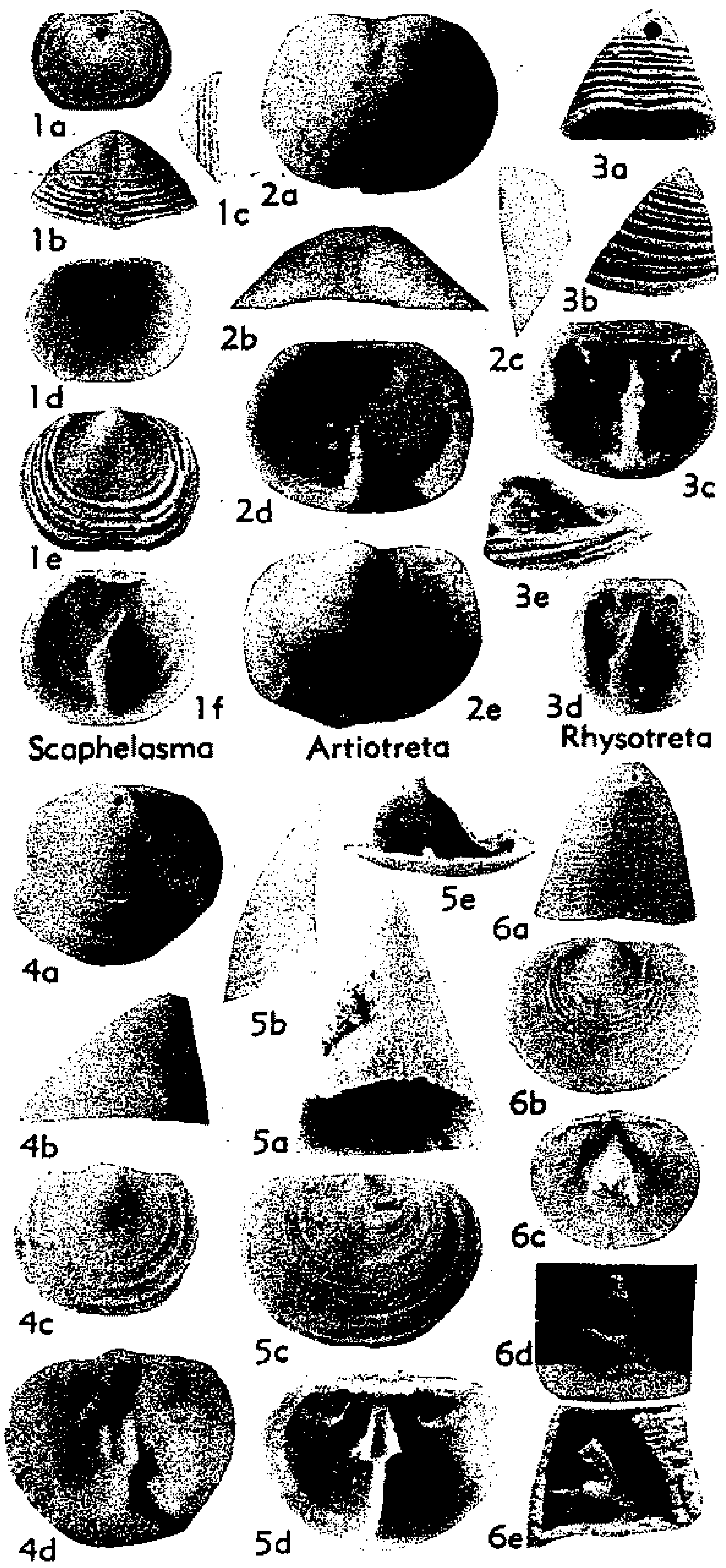


FIG. 172. Acrotretidae (Scaphelasmatinae) *(1-3)*, (Torynelasmatinae) *(4-5)*, (Ephippelasmatinae) *(6)* (p. *H278-H279*).

(Okla.).——FIG. 172,*2*. **A. parva*, Chimneyhill; *2a-c*, ped.v. ext., post., lat., ×40; *2d,e*, brach.v. int., ext., ×40 (Rowell, n).

?**Rhysotreta** COOPER, 1956, p. 258 [**R. corrugata*; OD]. Ornament of strong concentric rings; pedicle valve high, procline to catacline, foramen slightly posterior to apex, tear-shaped, no apical process; brachial valve concave, large pseudointerarea seemingly undivided, high median septum arising in front of beak. *M.Ord.*, N.Am.(Ala.).——FIG. 172,*3*. **R. corrugata*, Pratt Ferry F.; *3a,b*, ped.v. post., lat., ×10; *3c-e*, brach. v. int., int. oblique, lat., ×10 (189).

Subfamily TORYNELASMATINAE Rowell, n. subfam.

Pedicle valve conical with apical foramen minute, lacking apical process; brachial valve with undivided pseudointerarea, median septum arising slightly anterior to beak bearing shallow concave plate on its posteroventral edge. *M.Ord., ?U.Sil.*

Torynelasma COOPER, 1956, p. 257 [**T. toryniferum*; OD]. Pedicle valve acutely conical, apsacline, similar to *Acrothyra* but lacking apical process and well-defined pseudointerarea. Concave plate on median septum well developed. *M.Ord.*, N.Am. (Ala.).——FIG. 172,*5*. **T. toryniferum*, Pratt Ferry F.; *5a,b*, ped. v. post., lat., ×8; *5c-e*, brach. v. ext., int., lat., ×10 (189).

?**Acrotretella** IRELAND, 1961, p. 1139 [**A. siluriana*; OD]. Pedicle valve procline, pseudointerarea undivided; brachial valve with small pseudointerarea and delicate concave-plate on septum. *U.Sil.*, N. Am.(Okla.)-?Eu.(Eng.).——FIG. 172,*4*. **A. siluriana*, Chimneyhill, USA(Okla.); *4a,b*, ped.v. ext., lat., ×25; *4c,d*, brach.v. ext., int., ×25 (445a).

Subfamily EPHIPPELASMATINAE Rowell, n. subfam.

Pedicle valve conical, lacking apical process, foramen circular, apical; brachial valve with pitlike median groove, minute propareas, and complex saddle-like plate arising in front of beak and attached only at its posterior end. *M.Ord., ?U.Ord.*

Ephippelasma COOPER, 1956, p. 261 [**E. minutum*; OD]. Minute, pedicle valve high, catacline to apsacline, beak prominent, intertrough indistinct; brachial valve concave. *M.Ord., ?U.Ord.*, N.Am. (Ala.)-?Eu.(Ire.).——FIG. 172,*6*. **E. minutum*, Pratt Ferry F., USA(Ala.); *6a*, ped. v. post., ×20; *6b-d*, brach. v. ext., int., int. lat., ×20, ×15, ×15; *6e*, int. ped. v. and brach. v. lat., ×20 (189).

Subfamily UNCERTAIN

Hisingerella HENNINGSMOEN, 1948, p. 388 [**Atrypa? nitens* HISINGER, 1838, p. 77; OD]. Fine concentric ornament; pedicle valve a low cone, procline, narrow deltoid pseudointerarea, internal structure unknown except for long median ridge in brachial valve extending forward from beak. [Genus inadequately known.] *U.Ord.*, Scand.

Keyserlingia PANDER, 1861, col. 46 [**Orbicula reversa* DE VERNEUIL, 1845, p. 289; SD DALL, 1871, p. 75] [=*Kayserlingia* BEECHER, 1891, p. 354 *(nom. null.)*]. Small acrotretid, genus virtually unknown; pedicle valve subconical, with centrally placed apex. *L.Ord.*, Eu.(NW.USSR).

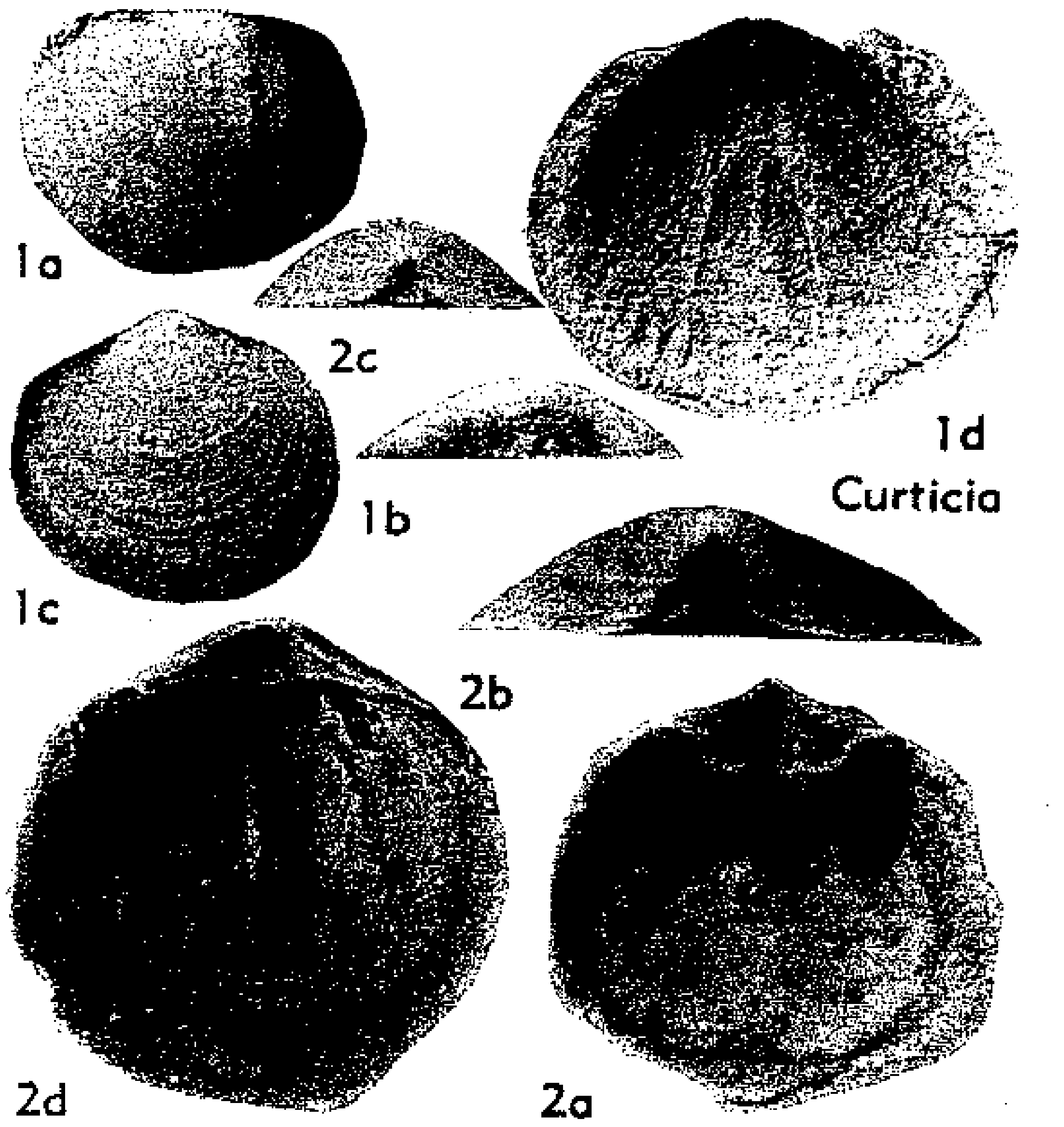


FIG. 173. Curticiidae (p. H280).

Family CURTICIIDAE Walcott & Schuchert, 1908

[Curticiidae WALCOTT & SCHUCHERT, 1908, p. 143]

Ventribiconvex acrotretaceans in which the early pedicle foramen is enlarged dorsally by subsequent resorption to produce a triangular pedicle opening that separates 2 discrete propareas; brachial valve similar to Acrotretinae (682). [The family is thought to be derived from the Acrotretinae.] *U.Cam.*

Curticia WALCOTT, 1905, p. 319 [**C. elegantula*; OD]. Characters of family. *U.Cam.*, N.Am.——FIG. 173,*1*. **C. elegantula,* USA(Minn.); *1a,b,* ped. v. ext., post., ×4; *1c,d,* brach. v. ext., int., ×4 (682).——FIG. 173,2. *C. minuta* BELL, USA (Mont.); *2a-c,* ped. v. int., post., post. young specimen, ×16; *2d,* brach. v. int., ×16 (682).

Family ACROTHELIDAE Walcott & Schuchert, 1908

[*nom. transl.* ROWELL, herein (*ex* Acrothelinae WALCOTT & SCHUCHERT, 1908, p. 146) (*incl.* Schizopholidacea SCHINDEWOLF, 1955, p. 556)]

Pedicle valve depressed conical, with excentric apex usually in posterior third of valve, pseudointerarea triangular, commonly not well defined, may be absent; foramen circular, apical, or elongate ellipsoidal slightly posterior to apex; mantle canal pattern not well known in all genera referred to family, but typically consists of baculate *vascula lateralia* in pedicle valve arising behind foramen, running short distance laterally before bending abruptly forward to run subparallel with lateral margins of valve. Brachial valve with pair of *vascula lateralia* arising near beak and diverging laterally, *vascula media* seemingly originating near center of valve and passing anterolaterally. Pedicle valve with pair of posterolaterally placed cardinal scars and second smaller pair of scars near apex of valve. Cardinal scars of brachial valve similarly placed, with second smaller pair of scars near center of valve, close to median ridge. *L.Cam.-L.Ord.*

It is probable that the acrothelids provided the ancestral stock for the discinacean Orbiculoideinae. In the possession of a pedicle tube the genus *Orbithele* shows some similarity with members of that subfamily.

Subfamily ACROTHELINAE Walcott & Schuchert, 1908

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

Brachial valve flat to gently convex, with marginal beak, internally with low median ridge extending forward from beak, never developed as septum; beaks of both valves commonly bearing short spines or tubercles. *L.Cam.-L.Ord.*

Acrothele LINNARSSON, 1876, p. 20 [**A. coriacea*; SD OEHLERT, 1887, p. 1270] [=*Dearbonia* WALCOTT, 1908, p. 78 (type, *D. clarki*); *Aerothele* CZARNOCKI, 1927, p. 742 *(nom. null.)*]. Ornament of fine concentric growth lines, usually with additional irregular wavy ridges bearing minute granules, producing fine granular ornament; 2 short spines on apex of pedicle valve immediately in front of elliptical foramen, 4 short spines arranged roughly in rectangle on beak of brachial valve; dorsal pseudointerarea an obtusely triangular plate adnate to inner surface of valve. *?L.Cam., M.Cam.,* Eu.-Asia-N.Am.-Australia-?N. Afr.——FIG. 174,2. **A. coriacea,* M.Cam., Sweden; *2a-c,* ped. v. ext., detail of apex, int., ×10, ×15, ×10; *2d-f,* brach. v. ext., detail of beak, post. int. (incomplete), ×10, ×15, ×10 (Rowell, n).

Orbithele SDZUY, 1955, p. 9 [**Discina contraria* BARRANDE, 1868, p. 104; OD]. External form similar to *Acrothele* but differing from it and other members of subfamily in having pedicle opening continued internally as posteriorly directed pedicle tube, pedicle valve with 2 pairs of muscle scars posterolateral to foramen, not coalescing to form pair of cardinal scars. *L.Ord.(Tremadoc.),* Eu.——FIG. 174,*4*. **O. contraria* (BARRANDE); ped. v. int. impression, ×5 (734a).

Redlichella WALCOTT, 1908, p. 89 [**Acrotreta granulata* LINNARSSON, 1876, p. 24; OD]. Externally similar to *Acrothele* with granular ornament; differs in larger, more deeply impressed dorsal cardinal muscle scars. *M.Cam.*, Eu. [Possibly best classed as subgenus of *Acrothele*.]

Schizopholis WAAGEN, 1885, p. 752 [**S. rugosa*; OD] [=*Discinolepis* WAAGEN, 1885, p. 749 (type, *D. granulata*)]. Pedicle opening long, narrow slit, originating just behind apex, not extending to posterior margin; without clearly defined pseudointerarea, apex of pedicle valve very excentric, near posterior margin, both valves ornamented by concentric growth lines. *L.Cam.*, Asia(Pak.).——FIG. 174,*1*. **S. rugosa*; *1a,b*, ped.v. ext., post., ×6; *1c,d*, brach. v. int. impression, ext. (partly exfoliated), ×6 (Rowell, n).

Subfamily CONODISCINAE Rowell, n. subfam.

Brachial valve depressed conical, beak subcentral. *?M.Cam., U.Cam., ?L.Ord.*

Conodiscus ULRICH & COOPER, 1936, p. 619 [**Acrothele burlingi* KOBAYASHI, 1935, p. 45; OD]. Ornament of concentric fila; pedicle valve similar to *Acrothele*, without pseudointerarea; brachial valve interior with low median ridge extending posteriorly from apex. *U.Cam., ?L.Ord.*, N.Am.——FIG. 174,*3*. **C. burlingi* (KOBAYASHI), USA (Alaska); *3a,b*, ped. v. ext. (partly exfoliated), int. impression, ×3, ×4; *3c*, brach.v. int. impression, ×3 (825).

?**Discinopsis** MATTHEW, 1892, p. 105 [**Acrotreta? gulielmi* MATTHEW, 1886, p. 37; OD] [=*Discinopsis* MATTHEW, 1889, p. 43 (*nom. nud.*)]. Genus poorly understood, known only from crushed material; possibly a synonym of *Acrothele*, described initially as having brachial valve with excentric apex. *M.Cam.*, N.Am.(N.B.).

Family BOTSFORDIIDAE Schindewolf, 1955

[*nom. transl.* ROWELL, herein (*ex* superfamily Botsfordiacea SCHINDEWOLF, 1955, p. 545)]

Pedicle valve convex, beak posteriorly placed, growth mixoperipheral, pseudointerarea clearly defined, apsacline, rarely catacline, divided into 2 propareas by open triangular delthyrium; *vascula lateralia* diverging anterolaterally from in front of beak, with 2 pairs of poorly defined subequal muscle scars, one pair posterolateral to mantle canal trunks, second pair posteriorly placed between trunks; brachial valve gently convex, marginal beak may bear 2 small tubercles; internally pseudointerarea, musculature, and mantle canal system similar to those of Acrothelidae (714). *L.Cam., ?M.Cam.*

The genera here included in the family have been classified variously in the past. *Botsfordia* and *Glyptias* have usually been included in the Obolellidae and *Neobolus* placed in a family of its own in the Trimerellacea. The pedicle opening and pseudointerareas of *Botsfordia* and *Neobolus* are

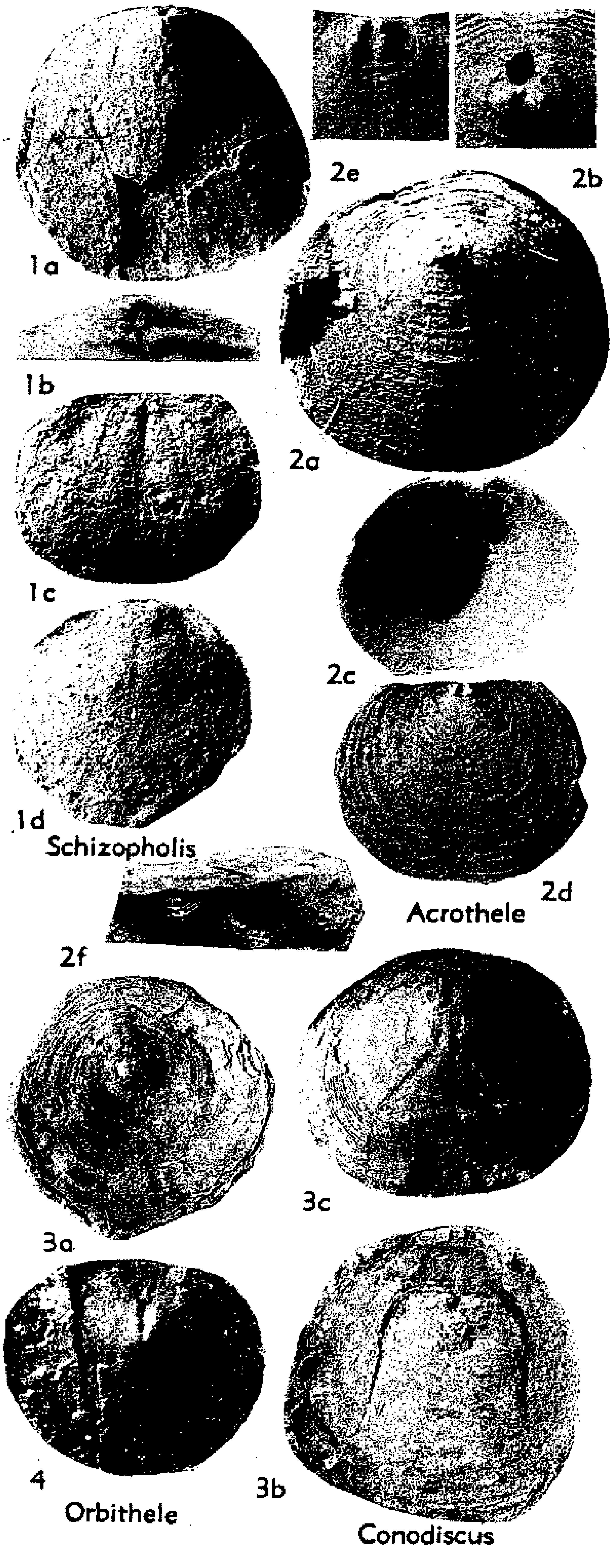


FIG. 174. Acrothelidae (Acrothelinae) (*1-2, 4*), (Conodiscinae) (*3*) (p. *H*280-*H*281).

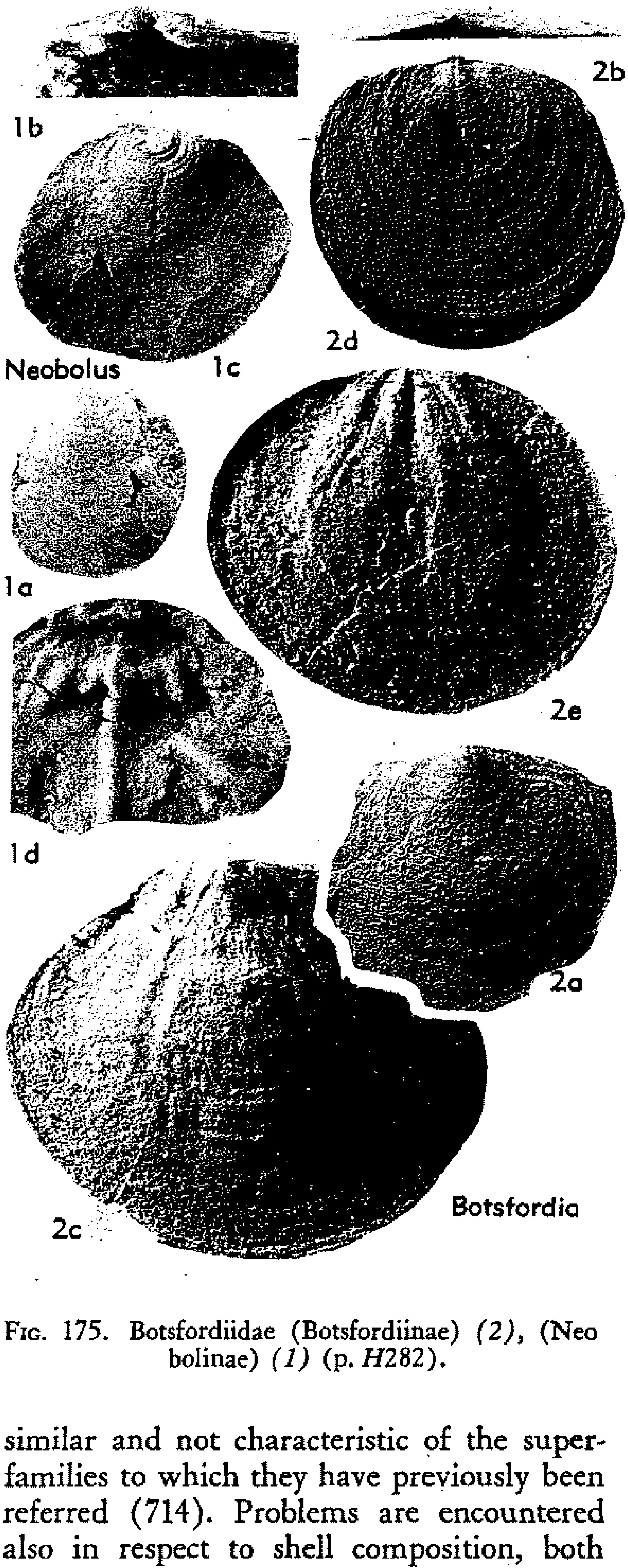


Fig. 175. Botsfordiidae (Botsfordiinae) *(2)*, (Neo bolinae) *(1)* (p. *H*282).

similar and not characteristic of the superfamilies to which they have previously been referred (714). Problems are encountered also in respect to shell composition, both the Obolellidae and Trimerellidae, as here restricted, having calcareous shells, whereas the genera under consideration have phosphatic ones. The relation of the genera of the Botsfordiidae with other stocks is not very clear, but the external and internal structures, particularly of the brachial valve of *Botsfordia,* suggest that they are probably related to the Acrothelidae.

Subfamily BOTSFORDIINAE Schindewolf, 1955

[*nom. transl.* Rowell, herein (*ex* Botsfordiidae Schindewolf, 1955, p. 545)]

Median ridge of brachial valve short, lacking dorsal platform. *L.Cam., ?M.Cam.*

Botsfordia Matthew, 1891, p. 148 [**Obolus pulcher* Matthew, 1889, p. 306; OD] [=*Mobergia* Redlich, 1899, p. 5 (type, *M. granulata*)]. Ornament of concentric growth lines and minute granules, latter may cover entire shell or only apical regions. *L.Cam., ?M.Cam.,* N.Am.-Asia-Greenl.——Fig. 175,*2*. *B. granulata* (Redlich), L.Cam., Pak.; *2a-c,* ped.v. ext., post., int. impression, ×8; *2d,e,* brach. v. ext., int. impression, ×8 (Rowell, n).

?Glyptias Walcott, 1901, p. 675 [**Lingula? favosa* Linnarsson, 1869, p. 356; OD]. Pedicle opening apparently as in family; ornament of concentric growth lines crossed locally by irregular raised lines producing pitted appearance (848). *L.Cam.,* Eu.(Scand.).

Subfamily NEOBOLINAE Walcott & Schuchert, 1908

[Neobolinae Walcott & Schuchert, 1908, p. 144]

Solid platform well developed internally in posterior part of brachial valve, bearing high process immediately in front of dorsal beak (714). *L.Cam.*

Neobolus Waagen, 1885, p. 756 [**N. warthi*; SD Oehlert, 1887, p. 1263] [=*Lakhmina* Oehlert, 1887, p. 1265 (*nom. subst. pro Davidsonella* Waagen, 1885, p. 762 (type, *D. linguloides*), *non* Munier-Chalmas, 1880; *nec* Frederiks, 1926)]. Ornament of fine concentric growth lines. *L.Cam.,* Asia(Pak.).——Fig. 175,*1*. **N. warthi*; *1a,b,* ped.v. ext. (incompl.), post., ×3, ×4; *1c,d,* brach. v. ext. (incompl.), int. (incompl.), ×4 (Rowell, n).

Family UNCERTAIN

Discotreta Ulrich & Cooper, 1936, p. 619 [**Acrothele levisensis* Walcott, 1908, p. 85; OD]. Both valves depressed subconical, ornament of fine growth lines, apices smooth, situated behind center; small foramen in pedicle valve immediately behind apex, bounded laterally by 2 short folds; internally, foramen surrounded by low rim, low median ridge extending to center of valve, central area of valve smooth, peripherally strongly pitted. Musculature unknown. Brachial valve lacking median ridge, anterior part of apex with 2 diverging subrectangular ?muscle scars extending to center of valve. *L.Ord.,* N.Am.——Fig. 176, *1*. **D. levisensis* (Walcott), Que.; *1a,b,* ped. v. ext., int., ×4, ×3; *1c,* brach. v. int., ×3 (825).

Superfamily DISCINACEA Gray, 1840

[*nom. transl.* Schuchert, 1896, p. 309 (*ex* Discinidae Gray, 1840, p. 155)]

Growth of pedicle valve holoperipheral,

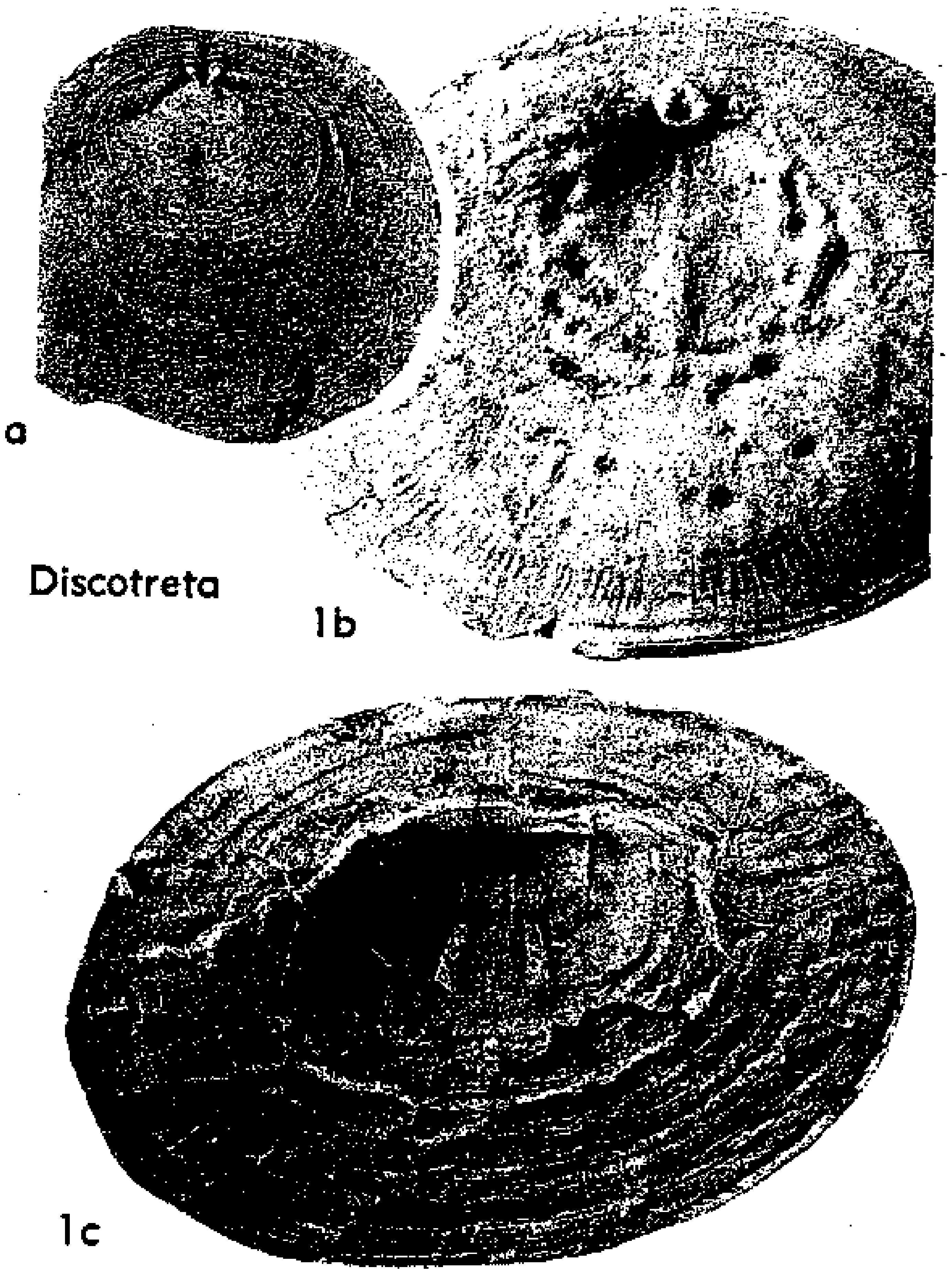


FIG. 176. Family Uncertain (p. *H*282).

that of brachial valve more variable, beak marginal to central; pedicle opening in young forms a triangular notch in posterior margin of pedicle valve, adult pedicle opening may be closed posteriorly or extend to margin of shell, anterior end of track of pedicle opening partially closed by listrium; pedicle valve without pseudointerarea (396). *Ord.-Rec.*

The shell structure of fossil discinaceans is unknown in detail. In Recent *Disciniscus* the shell is homogeneous, minutely punctate, and not in alternate organic and phosphate layers.

Recent species belonging to the superfamily are all shallow-water forms, with exception of *Pelagodiscus atlanticus,* which has a large bathymetric range, but is typically abyssal.

Family TREMATIDAE Schuchert, 1893

[Trematidae SCHUCHERT, 1893, p. 149]

Beak of brachial valve marginal, protruding beyond pedicle valve; pedicle opening extending to posterior margin of pedicle valve in all growth stages. *M.Ord.-Dev.*

Trematis SHARPE, 1848, p. 66 [**Orbicula terminalis* EMMONS, 1842, p. 395; SD DAVIDSON, 1853, p. 130]. Circular to suboval in outline, biconvex; surface of both valves ornamented by small superficial pits variably arranged, commonly in rough quincunx or in lines radiating from beak; pedicle valve with subcentral beak, convex, but depressed posteriorly, open pedicle notch in depression, margins of notch straight or concave toward mid-line; pseudointerarea of brachial valve adnate to inner surface of valve, low median ridge variably developed separating 2 bean-shaped composite muscle scars. *M.Ord.-U.Ord.,* N.Am.-Eu.——FIG. 177,*1*. *T. millipunctata* HALL, U.Ord., N.Am.; *1a,* ped. v. ext., exfoliated, ×2; *1b,c,* brach. v. ext., int., ×2, ×1.5; *1d,* both valves lat., ×2 (396).

Schizocrania HALL & WHITFIELD, 1875, p. 71 [**Orbicula? filosa* HALL, 1847, p. 99; OD]. Subcircular to subtriangular in outline, convexiplane to convexiconcave; brachial valve ornamented by fine costellae, pedicle valve by concentric fila, costellae may also occur. Pedicle valve circular in outline, pedicle opening broadly triangular, margins straight, listrium small; posterior margin of brachial valve slightly thickened, pair of elongate subtriangular muscle scars in posterior third of valve, second pair of poorly defined scars near center of valve. *Ord.-L.Dev.,* N.Am.-Eu.——FIG. 177,*2*. **S. filosa* (HALL), U.Ord., USA(Ohio, *2a,b*; N.Y., *2c*); *2a,* cluster of shells on strophomenoid, ×1; *2b,* ped. v. ext., ×2; *2c,* brach. v. int. impression, ×1.5 (*2a,* Rowell, n; *2b,c,* 396).

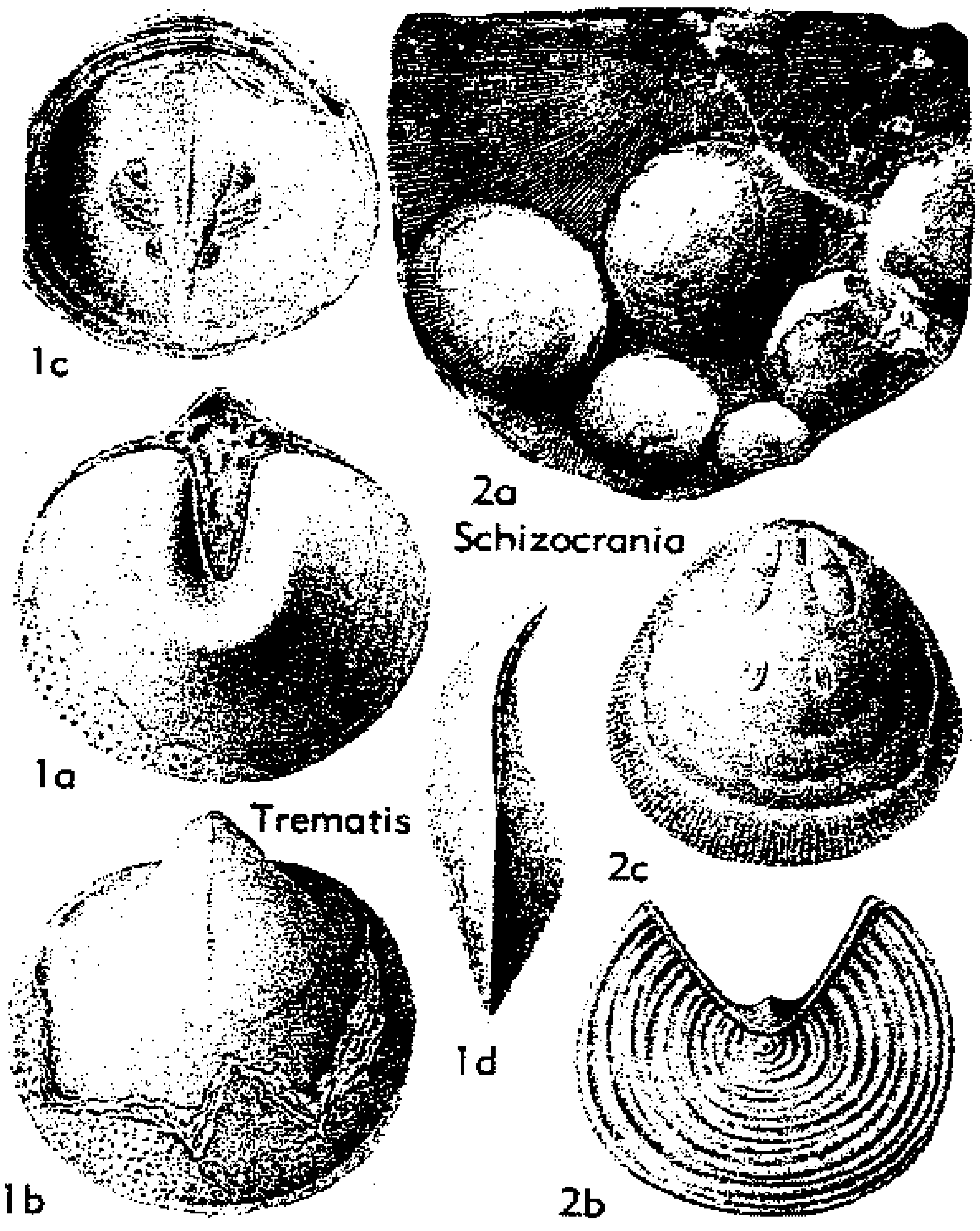


FIG. 177. Trematidae (p. *H*283).

Family DISCINIDAE Gray, 1840

[Discinidae Gray, 1840, p. 155] [=Orbiculidae M'Coy, 1844, p. 103]

Holoperipheral growth in brachial valve, which is usually conical to subconical; musculature consisting of 2 major pairs, anterior and posterior adductors, plus several pairs of oblique muscles, latter only adequately known in Recent species, which also possess

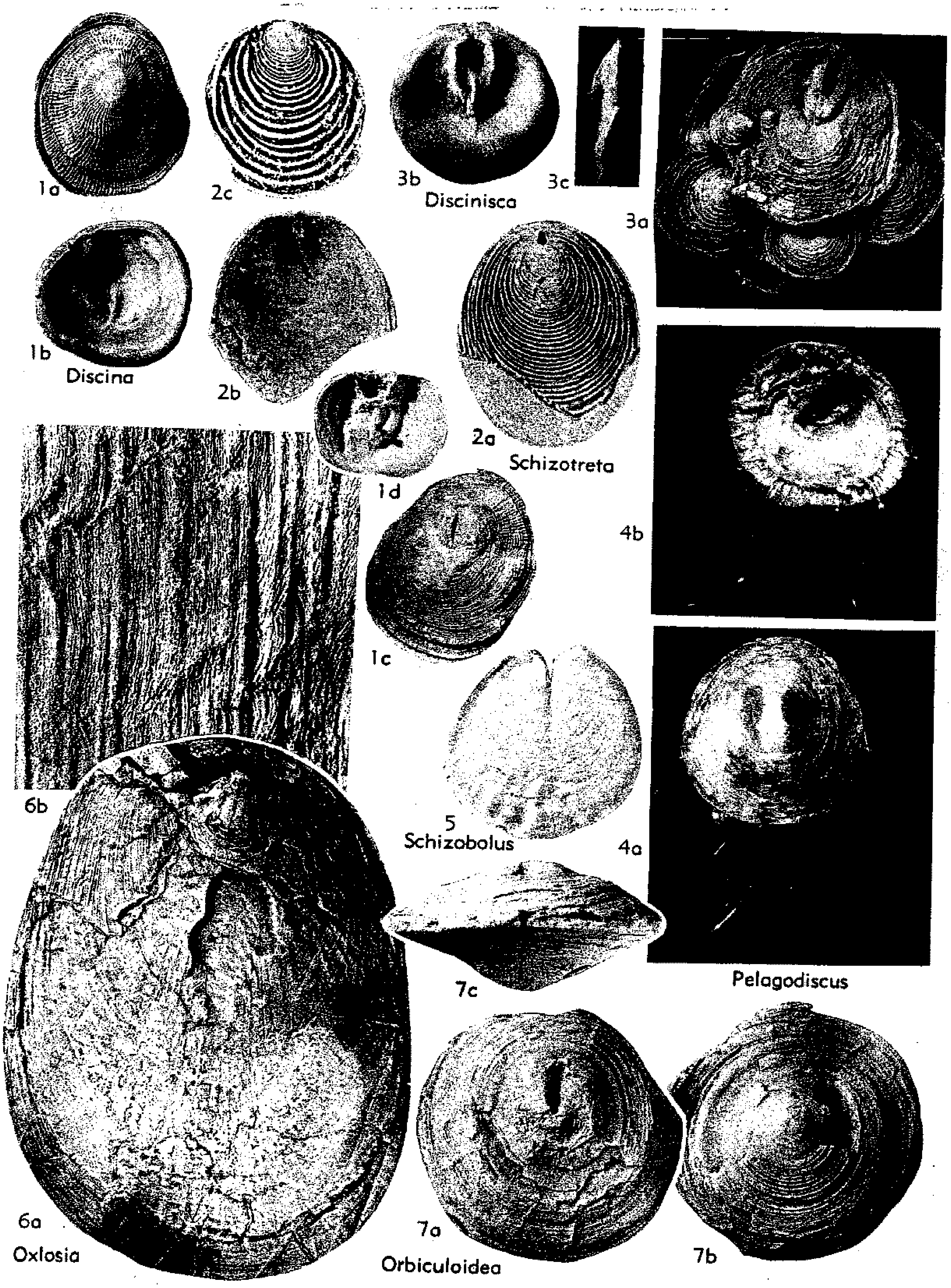


Fig. 178. Discinidae (Orbiculoideinae) *(2,7)*, (Disciniscinae) *(3-4)*, (Discininae) *(1)*; Family Uncertain *(5-6)* (p. *H*285-*H*287).

spirolophe or schizolophe, and have well-developed marginal setae (396). *Ord.-Rec.*

Subfamily ORBICULOIDEINAE
Schuchert & LeVene, 1929

[Orbiculoideinae Schuchert & LeVene, 1929, p. 13] [incl. Acrosaccidae Willard, 1928]

Adult pedicle notch not open at posterior margin, track of pedicle opening relatively narrow, extending variable distance from apex along posterior slope of valve; listrium may almost close pedicle track leaving only small foramen which is continued obliquely backward through shell as pedicle tube. *Ord.-Perm.*

Orbiculoidea d'Orbigny, 1847, p. 269 [**Orbicula forbesi* Davidson, 1848, p. 334; ICZN plenary powers proposed Rowell, 1962, Z.N.(S.)1506, ICZN pend.]. Concentric ornament of both valves varying from fine growth lines to well-developed fila; brachial valve conical to subconical, apex not depressed and submarginal, as in *Schizotreta*; pedicle valve subconical to gently concave, pedicle track narrow, closed anteriorly by listrium, foramen at posterior end of slit continued obliquely through shell to open internally in front of posterior margin; low median ridge may occur in brachial valve extending anteriorly from apex. *Ord.-Perm.*, cosmop.——Fig. 178,*7*. **O. forbesi* (Davidson), Sil.(Wenlock), Eng.; *7a*, ped. v. ext., partly exfoliated, ×4; *7b*, brach. v. ext., part exfoliated, ×4; *7c*, both valves, post., ×4 (Rowell, n).

Lindstroemella Hall & Clarke, 1890, p. 16 [**L. aspidium*; OD] [=*Lindstromella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*; *Lindstoemelia* Dunbar & Condra, 1932, p. 49 *(nom. null.)*]. Large, dorsibiconvex. Ornament of both valves strong concentric fila. Apex of brachial valve subcentral, internally with low median ridge anterior of apex, 2 ridges lateral of apex converging on median ridge, bounding anterior adductor scars; apex of pedicle valve central, pedicle opening long, narrow, sides in contact posteriorly, but not fused. *M.Dev.-Penn.*, N.Am.——Fig. 179,*1*. **L. aspidium*, M.Dev., USA(N.Y.); *1a*, ped. v. ext. impression, ×1; *1b*, brach. v. int., ×1 (396).

Lingulodiscina Whitfield, 1890, p. 122 [**Lingula exilis* Hall, 1860, p. 77; OD]. Genus poorly known, may be synonym of *Orbiculoidea*; apparently differs from that genus in having brachial valve elongate oval, almost linguloid in outline with beak submarginal. *Dev.*, N.Am.

Roemerella Hall & Clarke, 1890, p. 19 [**Orbicula grandis* Vanuxem, 1842, p. 152; OD] [=*Roemerella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Like large *Orbiculoidea* but having strongly concave pedicle valve with central apex and pedicle track on broadly elevated area within concave valve; brachial valve high cone with subcentral apex. *Dev.*, N.Am.-?Eu.

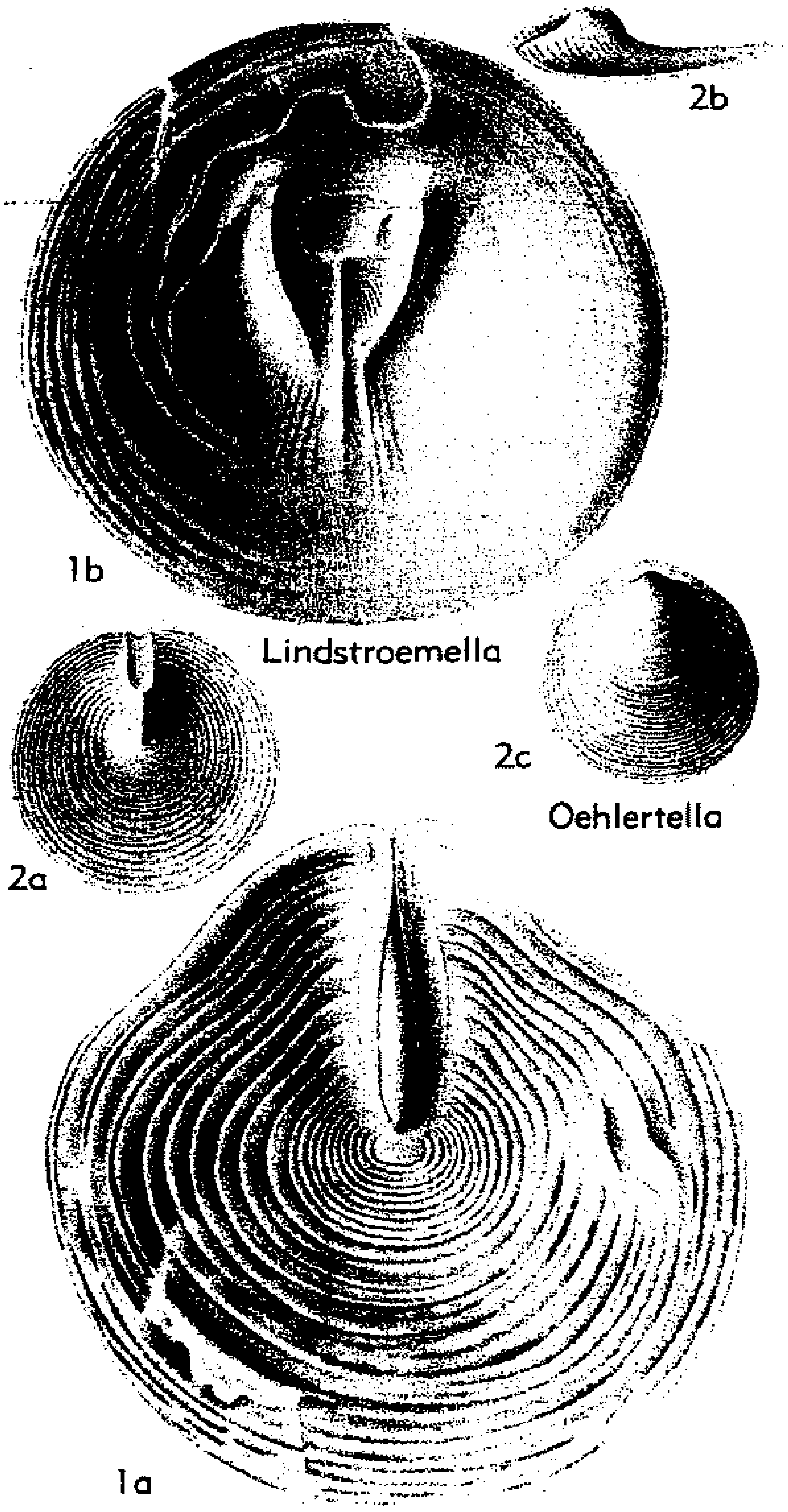


Fig. 179. Discinidae (Orbiculoideinae) *(1)*, (Disciniscinae) *(2)* (p. *H*285-*H*286).

Schizotreta Kutorga, 1848, p. 272 [**Orbicula elliptica* Kutorga, 1846, p. 123; OD] [=*Acrosaccus* Willard, 1928, p. 258 (type, *A. shuleri*)]. Both valves ornamented by well-developed concentric fila; brachial valve gently convex to flat in profile, beak submarginal; pedicle valve subconical, pedicle track and opening similar to *Orbiculoidea*, passage of pedicle through shell may produce low ridge on internal surface of posterior slope. *M.Ord.-Sil.*, N.Am.-Eu.-Asia.——Fig. 178,*2*. *S. corrugata* Cooper, Pratt Ferry F., USA(Ala.); *2a,b*, incompl. ped. v. ext., int., ×4; *2c*, brach. v. ext., ×6 (189).

Subfamily DISCINISCINAE Schuchert & LeVene, 1929

[Disciniscinae Schuchert & LeVene, 1929, p. 13]

Discinids with track of pedicle opening in broad depression of pedicle valve, track partially closed anteriorly by listrium, but pedicle tube not developed; pedicle opening lanceolate to suboval, separated from posterior margin of valve only by narrow band of periostracum. Ventral and dorsal *vascula lateralia* bifurcate, dorsal *vascula media* present. *?Carb., ?Trias., L.Jur.-Rec.*

In Recent species the pedicle is narrow where it emerges through the shell, but expands externally to fill the depressed area and is attached to its outer surface.

Discinisca Dall, 1871, p. 37 [**Orbicula lamellosa* Broderip, 1833, p. 124; OD]. Ornament variable, fine growth lines which may become lamellose, with or without fine ribs. Brachial valve convex to subconical, pedicle valve concave to slightly convex, with large depressed area around pedicle track, internally with small triangular median septum extending posteriorly from apex on to listrium. Lophophore spirolophous. *?Trias., L.Jur.-Rec.*, cosmop.——Fig. 178,*3*. **D. lamellosa* (Broderip), Rec., S.Am.; *3a*, cluster of valves, ped. v. and brach. v. ext., ×1; *3b,c*, ped. v. int., lat., ×1 (Rowell, n).

?Oehlertella Hall & Clarke, 1890, p. 15 [**Discina pleurites* Meek, 1875, p. 278; OD] [=*Oehlertella* Hall & Clarke, 1889, p. 43 *(nom. nud.)*]. Ornament of fine growth lines; dorsibiconvex, apex of brachial valve submarginal; pedicle valve similar to *Discinisca*, but pedicle opening more parallel-sided and lacking internal median septum. *Carb.(Miss.-Penn.)*, N.Am.-?Eu.——Fig. 179,*2*. **O. pleurites* (Meek), USA(Ohio); *2a,b*, ped. v. int., lat., ×1; *2c*, brach. v. ext., ×1 (396).

Pelagodiscus Dall, 1908, p. 440 [**Discina atlantica* King, 1868, p. 170; OD]. Similar to *Discinisca*, but smaller, very thin-shelled, lophophore schizolophous. *?Mio., Rec.*, cosmop.——Fig. 178,*4*. **P. atlanticus* (King), Rec., N.Pac.; *4a*, brach. v. ext.; *4b*, ped. v. ext., both under water at ×6 (Rowell, n).

Subfamily DISCININAE Gray, 1840

[*nom. transl.* Rowell, herein (*ex* Discinidae Gray, 1840, p. 155)]

Rather thick-shelled discinids, track of pedicle opening a very narrow slit not extending to margin of valve, not situated in conspicuous depression of valve. Pedicle opening partially closed anteriorly by grooved listrium that forms outer surface of irregular median septum projecting above pedicle opening. Pedicle tube absent. Mantle canal system similar to that of Disciniscinae. *Rec.*

Externally the only genus in the subfamily is similar to a thick-shelled *Orbiculoidea*. Contrary to Hall & Clarke (396), the pedicle emerged through the valve with a similar inclination to that of *Orbiculoidea*, i.e., with the pedicle inclined posteriorly from outside to inside of the valve. *Discina* differs from *Orbiculoidea* in its very narrow pedicle opening, complete absence of a pedicle tube, presence of ventral median septum and to a lesser extent, in ornament. Although a conspicuous depression of the ventral valve around the pedicle opening is absent, the pedicle has a similar form to that of *Discinisca;* it expands abruptly after passing through the valve and is attached to the outer surface of the shell.

Discina Lamarck, 1819, p. 236 [**D. ostreoides* (=**Crania striata* Schumacher, 1817, p. 102); OD]. Irregularly subcircular, biconvex to convexi-concave, apices subcentral, ornament of concentric growth lines and fine costellae. Interior of pedicle valve with subtriangular median septum extending short distance posterior of apex, partially closing pedicle opening. Lophophore spirolophous. *Rec.*, W.Afr.——Fig. 178,*1*. **D. striata* (Schumacher); *1a,b*, brach. v. ext., brach. v. int., both ×1.5; *1c,d*, ped. v. ext., int., ×1.5 (Rowell, n).

Superfamily and Family UNCERTAIN

The following 2 genera previously have been included in the Discinacea, but it is doubtful that they are closely related to any of the genera assigned to it.

Oxlosia Ulrich & Cooper, 1936, p. 619 [*nom. subst. pro Eunoa* Clarke, 1902, p. 606 *(non* Malmgren, 1867)] [**Eunoa accola* Clarke, 1902, p. 607; OD]. Large, thin-shelled, ornament of concentric growth lines modified by obscure radial lines; outline subcircular to elongate oval. Brachial valve a depressed cone, apex between center and posterior margin; pedicle valve inadequately known, apparently flat, apex in similar position to that of brachial valve, pedicle opening triangular, extending from close behind apex to posterior margin. Internal structures unknown (825). *L. Ord.*, N.Am.——Fig. 178,*6*. *O. perplexa* Ulrich & Cooper, Que.; *6a,b*, brach. v. ext., detail of ornament, ×1, ×10 (825).

Schizobolus Ulrich, 1886, p. 25 [**Discina truncata* Hall, 1863, p. 28 (=**Lingula concentrica* Vanuxem, 1842, p. 168); OD]. Elongate oval in outline, biconvex, shell thin, ornamented by fine growth lines. Pedicle valve with beak posteriorly placed, not marginal, pedicle opening a triangular notch extending from beak to posterior margin, no listrium; internally low ridge may extend forward from beak to center of valve. Brachial valve with short, straight posterior margin, beak position similar to pedicle valve, internally low

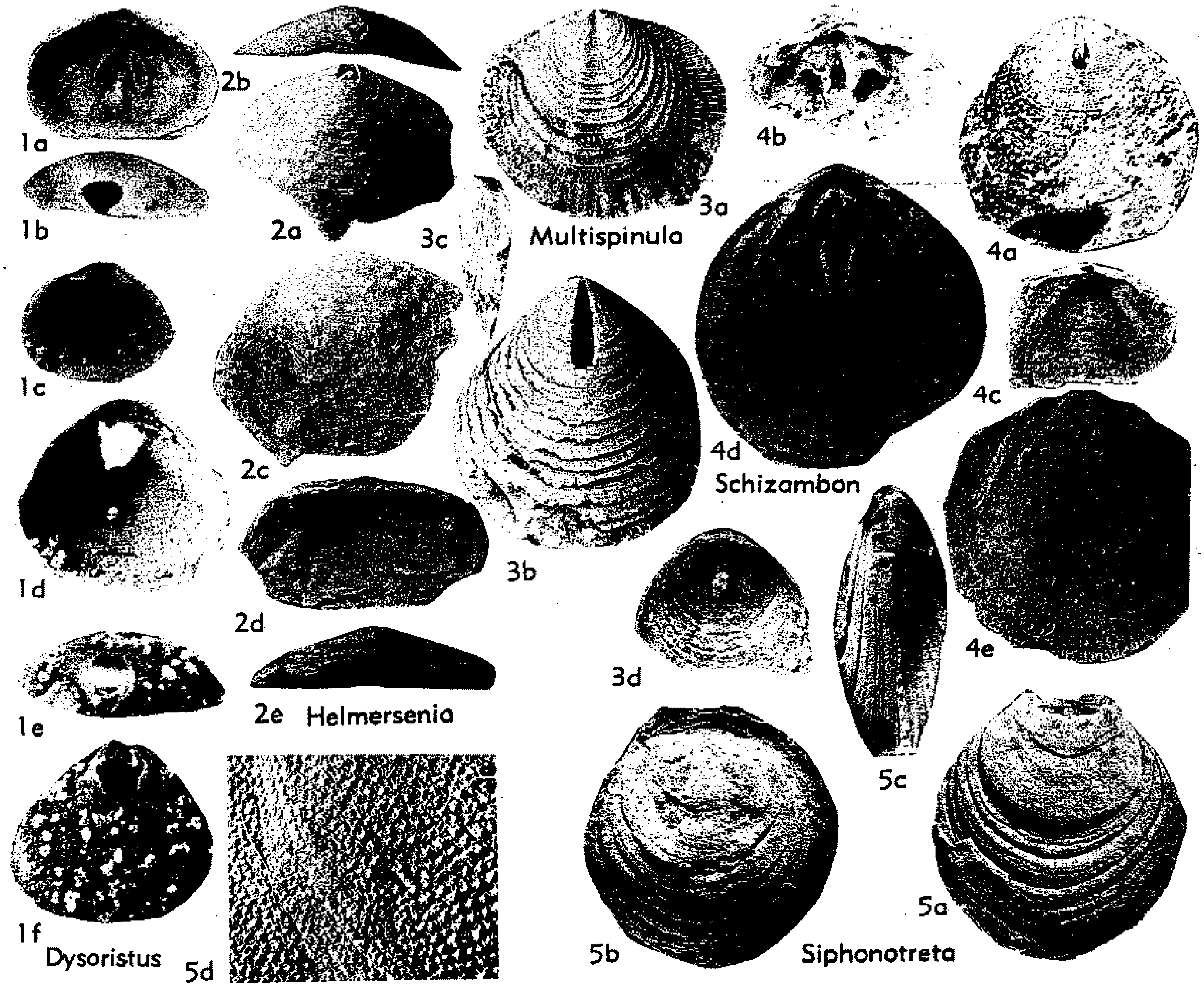


FIG. 180. Siphonotretidae (p. *H*288).

median ridge separates 2 faint subtriangular muscle scars in front of beak, pair of mantle canal trunks arising behind beak, passing forward, diverging slightly (396). *Dev.*, N.Am.-S.Am.——FIG. 178,*5*. **S. concentricus* (VANUXEM); ped. v. int. impression, ×5 (Rowell, n).

Superfamily SIPHONOTRETACEA Kutorga, 1848

[*emend.* ROWELL, 1962, p. 146; *nom. transl.* WALCOTT & SCHUCHERT, 1908, p. 145 (*ex* Siphonotretidae DALL, 1877, p. 62, *nom. correct. pro* fam. Siphonotretaeae KUTORGA, 1848, p. 253, *nom. imperf.*)]

Biconvex, usually ornamented by hollow spines; pedicle foramen circular and apical or may extend anteriorly, through resorption producing elongate triangular pedicle track; when elongate, posterior part of opening may be closed by plate which may be continued to form distinct anterodorsally directed pedicle tube; pseudointerarea of pedicle valve small or absent. Brachial beak marginal, pseudointerarea may be divided into 2 propareas by small pit (680). *U.Cam.-Ord.*

Musculature and mantle canal markings are inadequately known in the superfamily. A pair of large muscle scars in each valve, usually in the posterior third of the valve, other small impressions are occasionally seen that may be muscle scars. In both valves a pair of major mantle canals *(vascula lateralia)* arise near the beak and run forward roughly parallel with the margin of the shell. In well-preserved specimens of the brachial valve of *Schizambon* a second pair of trunks *(vascula media)* are seen that arise outside the muscle scars and converge toward the mid-line. It is not confidently known whether this second pair of mantle canal trunks is characteristic of the superfamily.

The origin of the superfamily is still uncertain, but the structure of the dorsal posterior margin, particularly that of the early genera, suggests that the acrotretaceans may have provided the ancestral stock.

Family SIPHONOTRETIDAE Kutorga, 1848

[*nom. correct.* Dall, 1877, p. 62 (*pro* Siphonotretaeae Kutorga, 1848, p. 253, *nom. imperf.*)]

Characters of superfamily. *U.Cam.-Ord.*

Siphonotreta de Verneuil, 1845, p. 286 [**Crania unguiculata* Eichwald, 1829, p. 274; SD Davidson, 1853, p. 131]. Suboval outline, ornament of fine concentric growth lines and scattered spine bases; foramen circular, apical, continued through thick beak as tube; pseudointerarea of pedicle valve large for family, strongly apsacline, its dorsal surface internally forming concave plate parallel to plane of commissure; pseudointerarea of brachial valve a flat plate overhanging interior of valve. *L.Ord.-M.Ord.*, Eu.-N.Am.-Asia-?Australia.——Fig. 180,*5*. **S. unguiculata* (Eichwald), USSR; *5a*, ped. v. ext., beak damaged; *5b*, brach. v. ext.; *5c*, both valves lat., all ×1.5; *5d*, detail of ornament, ×6 (Rowell, n).

Dysoristus Bell, 1944, p. 146 [**D. lochmanae*; OD] [=*Dysozistus* Goryansky, 1960, p. 182 (*nom. null.*)]. Without spines, foramen circular to tear-shaped, may be partly closed by plate posteriorly. Beak of pedicle valve marginal, internally with posterior plate like *Schizambon*, but not adnate; propareas of brachial valve extremely narrow, separated by depressed concave plate (680). *U.Cam.*, N.Am.——Fig. 180,*1a-c*. **D. lochmanae*, USA(Mont.); *1a*, brach. v. int., ×6; *1b,c*, ped. v. post., int., both ×10 (680).——Fig. 180, *1d-f*. *D. transversa* (Walcott), USA(Nev.); *1d-f*, ped. v. int., post., ext., all ×16 (680).

Helmersenia Pander, 1861, column 48 (no page numbers) [**Siphonotreta ladogensis* Zheremezhev, 1856, p. 73; SD Walcott, 1912, p. 367]. Externally similar to small *Siphonotreta*, but pseudointerarea of pedicle valve relatively smaller and extreme posterior tip of beak curved dorsally to form lip of foramen; pedicle opening sealed internally in adults. Brachial pseudointerarea divided into 2 triangular anacline propareas by median pit. *L.Ord.*, Eu.(Baltic).——Fig. 180,*2*. **H. ladogensis* (Zheremezhev), USSR; *2a,b*, incomplete ped. v. ext., post., both ×8; *2c-e*, incomplete brach. v. ext., int., post., all ×8 (680).

Multispinula Rowell, 1962, p. 147 [**Schizambon macrothyris* Cooper, 1956, p. 267; OD]. Like *Schizambon* but larger and thicker-shelled, differs in having small pseudointerarea in pedicle valve and submarginal beak, with anterior part of shell lamellose, bearing row of spines on front edge of lamellae; pedicle opening externally like *Schizambon*, but pedicle confined to tube. *M.Ord.-U.Ord.*, Eu.-N.Am.——Fig. 180,*3*. *M. subradiata* (Cooper), Arline F., USA(Tenn.); *3a*, brach. v. ext., ×3; *3b-d*, ped. v. ext., lat., incompl., int., ×3, ×2, ×2 (*3a-c*, 189; *3d*, 680).

Schizambon Walcott, 1884, p. 69 [**S. typicalis*; SD Oehlert, 1887, p. 1266] [=*Schizambonia* Oehlert, 1887, p. 1266 (*nom. null.*)]. Relatively thin-shelled, ornament of concentric growth lines, commonly with short discontinuous costellae, surface usually covered with fine spines. Pedicle track anterior to beak, elongate triangular, posterior part covered by plate; beak of pedicle valve marginal, internally with plate adnate to posterior surface of valve. Brachial pseudointerarea like *Siphonotreta* but very narrow. *U.Cam.-L.Ord.*, N.Am.-S.Am.-Greenl.——Fig. 180,*4a-c*. **S. typicalis*, USA(Nev.); *4a,b*, ped.v. ext., incompl. int., both ×6; *4c*, incompl. brach.v. int., ×6 (680).——Fig. 180,*4d,e*. *S. australis* Ulrich & Cooper, Arg.; *4d*, ped. v. int., ×6; *4e*, brach. v. int. impression, ×6 (825).

Suborder CRANIIDINA Waagen, 1885

[*nom. correct.* Rowell, herein (*pro* suborder Craniacea Waagen, 1885, p. 744] [=Gasteropegmata Waagen, 1885, p. 744 (*partim*); Gastropegmata Hall & Clarke, 1894, p. 326 (*partim*); Craniida Goryansky, 1960, p. 176 (*partim*)]

Shell strongly punctate, calcareous (except Eoconulidae); some free, many attached by cementation of all or part of pedicle valve to some other object, no forms known to have possessed pedicle; growth usually holoperipheral in both valves, more rarely mixoperipheral. *?M.Cam.*, *L.Ord.-Rec.*

Superfamily CRANIACEA Menke, 1828

[*nom. transl.* Schuchert, 1896, p. 310 (*ex* Craniidae King, 1846, p. 28, *nom. correct. pro* Craniaceae Menke, 1828, p. 56, *nom. imperf.*)]

Characters of the suborder. *?M.Cam.*, *L. Ord.-Rec.*

The Craniacea occur in the Lower Ordovician and are well developed by the Middle Ordovician when the superfamily was already represented by several genera. The extension of its time range into the Middle Cambrian is doubtful and is based on the occurrence of the poorly known "*Philhedra*" *columbiana* (Walcott) from British Columbia.

The systematic position of the genus *Eoconulus* is rather problematic. The low irregular cone suggests that it is the brachial valve of an animal which was attached by cementation of its pedicle valve, but the latter valve, however, is unknown. Internally, the relatively large posteriorly placed adductors recall the Craniidae, but no anterior adductors are known and the genus differs fundamentally from members of that

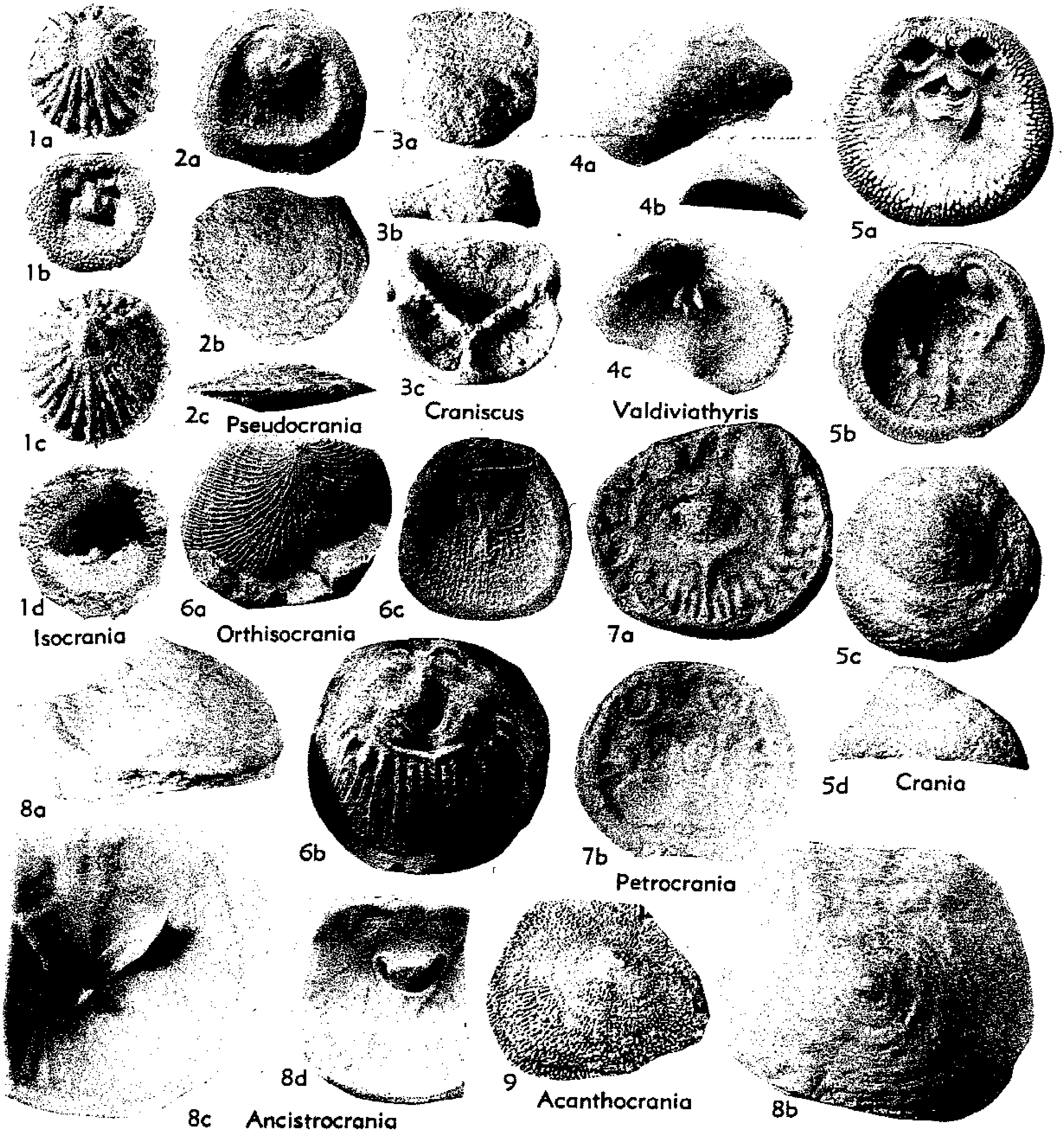


FIG. 181. Craniidae (p. *H*290-*H*291).

family in having a phosphatic shell. For these reasons the family Eoconulidae is introduced, since *Eoconulus* would not appear to be closely related to any other known craniacean. As COOPER, 1956 (189) has pointed out, the genus occurs with typical craniaceans and from what is known of its range cannot have been ancestral to them.

Family CRANIIDAE Menke, 1828

[*nom. correct.* KING, 1846, p. 28 (*pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*)] [=fam. Craniacea MENKE, 1830, p. 96; Craniadae FORBES, 1838, p. 38; incl. Valdiviathyrididae, *nom. correct.* ROWELL, herein (*pro* Valdiviathyridae HELMKE, 1940, p. 235, *nom. imperf.*)]

Shell calcareous, punctate, punctae in brachial valve branching arborescently toward distal end; brachial valve usually conical, pedicle valve subconical or convex when free, conforming to shape of surface of attachment when fixed. Principal muscles consist of two pairs of adductors traversing shell dorsoventrally and two pairs of oblique muscles. *Vascula lateralia* of both valves pinnate, *vascula media* seemingly absent. Recent species with anus posteriorly placed on mid-line of shell, no marginal setae (439). *?M.Cam., L.Ord.-Rec.*

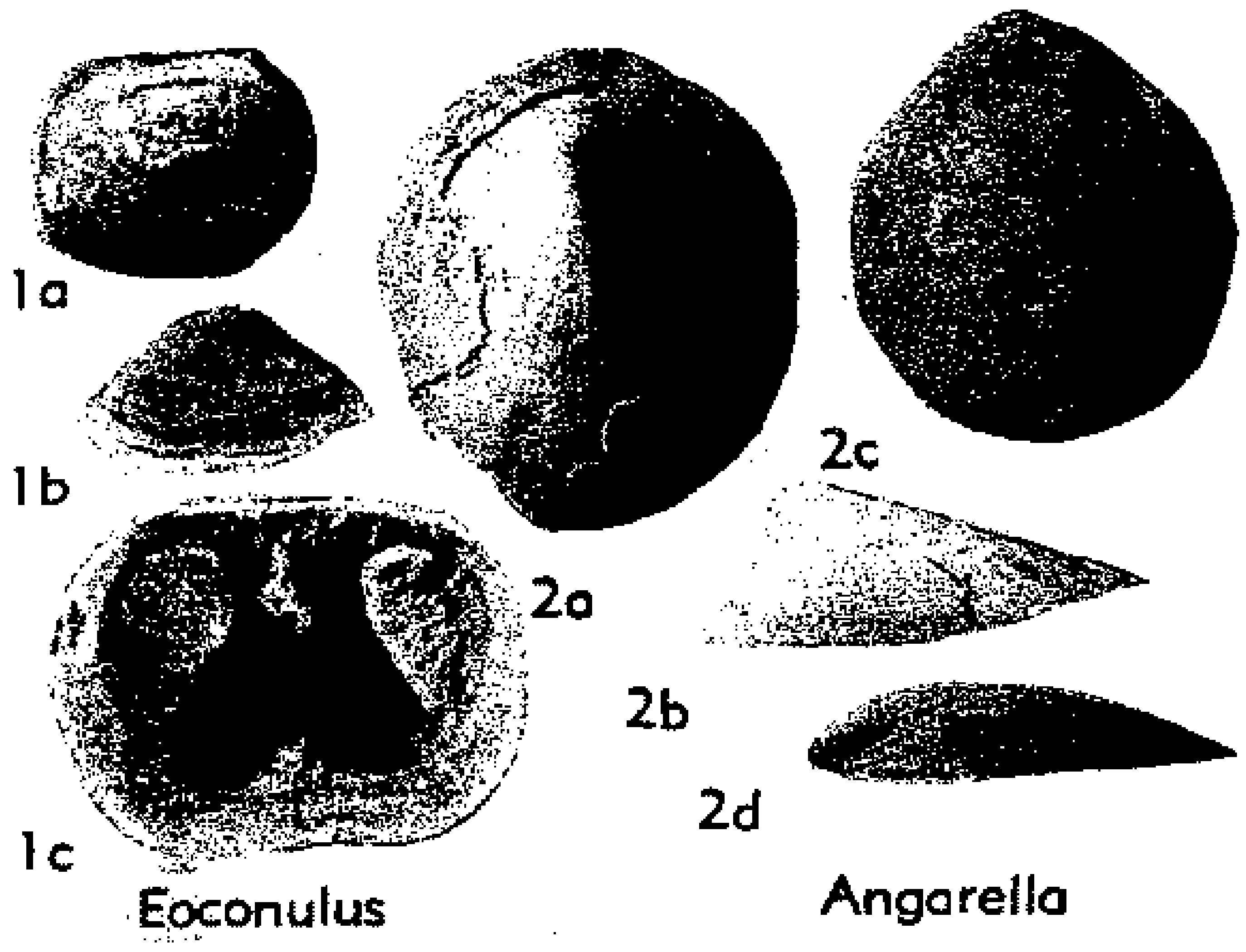


Fig. 182. Eoconulidae *(1)*; Superfamily and Family Uncertain *(2)* (p. *H*291).

Some Paleozoic species that belong to the family apparently lack a pedicle valve. These all appear to be forms that were attached by cementation. Presumably the ventral mantle secreted a periostracum that was responsible for the actual cementation, but did not secrete a calcareous shell. This condition is known as a transitory phase in the very early stages of development of the Recent *Crania anomala.*

Crania Retzius, 1781, p. 72 [**Anomia craniolaris* Linné, 1758, p. 700; SD Schmidt, 1818, p. 71] [=?*Criopus* Poli, 1791, p. 34 (type, *Anomia imperforata* Poli, 1791, p. 34) (*non* Gray, 1821); *Criopoderma* Poli, 1795, p. 255 (type, *Anomia turbinata* Poli, 1795, p. 189); *Orbicula* Cuvier, 1797, p. 435 (type, *Patella anomala* Müller, 1776, p. 237); *Orbicularius* Duméril, 1806, p. 170 *(nom. van.)*; *Criopododerma* Agassiz, 1836, p. 104 *(nom. van.)*; ?*Cryopus* Deshayes, 1836, p. 314 *(nom. null.)*; ?*Crania (Lissocrania)* Williams, 1943, p. 71 (type, *Crania dodgei* Rowley, 1908, p. 73)]. Attached by part or all of pedicle valve; ornament of concentric growth lines, low discontinuous radial lines present or absent; margins of both valves thickened, pustulose, may form limbus, anterior adductor scars close together; brachial valve conical to subconical. *?Carb., Cret.-Rec.,* cosmop.——Fig. 181,*5.* **C. craniolaris* (Linné), U.Cret., Sweden; *5a,* ped. v. int., ×2; *5b-d,* brach. v. int., ext., lat., all ×2 (Rowell, n).

Acanthocrania Williams, 1943, p. 71 [**Crania spiculata* Rowley, 1908, p. 74; OD] [=?*Choniopora* Schauroth, 1854, p. 546 (type, *C. radiata*)]. Attached, brachial valve conical, ornament of fine papillae or spines; anterior adductors usually larger than posterior adductors, margin of valve not thickened. Pedicle valve unknown, presumed thin or not calcified. *Ord.-Carb.,* N.Am.-Eu.——Fig. 181,*9. A. grandis* Cooper, Benbolt F., USA (Va.); brach. v. ext., ×1.5 (189).

Ancistrocrania Dall, 1877, p. 13 [*nom. subst. pro Cranopsis* Dall, 1871, p. 27 (*non* Adams, 1860)] [**Crania parisiensis* Defrance, 1819, p. 313; OD]. Similar to *Crania* but brachial valve interior bearing 2 slender, posterolaterally directed processes originating near apex, in part bearing anterior adductor scars; low short median septum may be present; valve margin not thickened; attached by entire surface of pedicle valve, margin of valve thickened. *Cret., ?Rec.,* Eu.——Fig. 181,*8.* **A. parisiensis* (Defrance), U.Cret., Eng.; *8a,* both valves lat. ext., ×2; *8b,c,* brach. v. ext., int., ×2; *8d,* ped.v. int., ×1 (*8a,d,* Rowell, n; *8b,c,* 681).

Craniscus Dall, 1871, p. 27 [**Crania tripartita* Münster, 1837, p. 297; OD]. Anterior adductor scars of brachial valve on 2 strong ridges extending posterolaterally from apex, united with median septum or ridge, structures dividing valve into 3 chambers; margins of valve not thickened. Pedicle valve of type-species unknown; in other species flat, attached by entire surface. *Jur.-Rec.,* Eu.-N.Am.-Australia-Japan-IndoPac.-Aleutian Is.——Fig. 181,*3.* **C. tripartitus* (Münster), Jur., Ger.(Thurnau); *3a-c,* brach. v. ext., lat., int., all ×4 (Rowell, n).

Isocrania Jaekel, 1902, p. 1062 [**Crania egnaburgensis* Retzius, 1781, p. 75; SD Schuchert & LeVene, 1929, p. 69]. Both valves conical to subconical, brachial valve usually higher than pedicle, strongly costellate, attached only by apical region of pedicle valve, limbus well developed in both valves, pustulose. *U.Cret.,* Eu.-Afr.-Asia.——Fig. 181,*1.* **I. egnaburgensis* (Retzius), Eng.; *1a,b,* ped.v. ext., int., ×4; *1c,d,* brach.v. ext., int., ×4 (Rowell, n).

Orthisocrania Rowell, 1963, p. 39 [**Pseudocrania divaricata* M'Coy, 1851, p. 388; OD]. Free, costellate ornament; both valves convex, with beak initially marginal and growth mixoperipheral, may later become holoperipheral, catacline to apsacline, ventral pseudointerarea and anacline dorsal pseudointerarea developed in young stages, retained in adults except in forms with later holoperipheral growth; limbus well developed in both valves, not pustulose. Anterior adductor scars conspicuous, usually larger than posterior pair; branches of mantle canal system numerous (10-30), scarcely interrupted medianly. *M.Ord.-U.Ord.,* Eu.——Fig. 181,*6.* **O. divaricata* (M'Coy); *6a,b,* ped. v. ext., int. impression, ×1.5; *6c,* brach. v. int., ×1.5 (Rowell, n).

Petrocrania Raymond, 1911, p. 229 [*nom. subst. pro Craniella* Oehlert, 1888, p. 101 (*non* von Schlotheim, 1820)] [**Craniella meduanensis* Oehlert, 1888, p. 102; OD] [=*Punctopatella* Grubbs, 1939, p. 559 (type, *P. corallifera*)]. Attached, pedicle valve thin; brachial valve conical, ornament of concentric growth lines, in some simulating ornament of host; characterized by pair of sigmoidal dorsal *vascula lateralia,* secondary canals branching off laterally; posterior adductors larger than anterior, margin of valves not thickened. *M.Ord.-Dev., ?Perm.,* Eu.-N.Am.-Asia.——Fig. 181,*7*. *P. hamiltoniae* (Hall), Ludlowville F., USA(N.Y.); *7a,* plasticene cast of ped.v. int., ×1.5; *7b,* plasticene cast of brach. v. int., ×1.5 (189).

Philhedra Koken, 1889, p. 465 [**P. baltica*; OD] [*non Philhedra* Schmidt, 1939] [=*Philedra* Bekker, 1921, p. 34 *(nom. null.)*; *Propatella* Grubbs, 1939, p. 558 (type, *P. magnacostata*)]. Similar to *Acanthocrania* but fine continuous or discontinuous costellate ornament; pedicle valve thin, commonly not calcified. *?M.Cam., L.Ord.-Carb.* N.Am.-Eu.-Asia.

Philhedrella Kozłowski, 1929, p. 28 [**Philhedra (Philhedrella) mimetica*; OD]. Genus inadequately understood, interior of valves unknown; erected for species similar to *Philhedra* but smooth, lacking costellae; pedicle valve thin or not calcified. *?Ord., U.Sil.,* Eu.

Pseudocrania M'Coy, 1851, p. 387 [**Orbicula antiquissima* Eichwald, 1840, p. 169 (=**Crania petropolitana* Pander, 1830, p. 100); SD Davidson, 1853, expl. Pl. 9] [=*Palaeocrania* Eichwald, 1854, p. 20 (obj.)]. Free, brachial valve conical, pedicle valve conical to flat, growth holoperipheral in both valves; ornament of growth lines and minute scattered papillae. Internally similar to *Orthisocrania. L.Ord.-M.Ord.,* Eu.(Balt.-Sweden-N.Ger.).——Fig. 181,*2*. **P. petropolitana* (Pander); *2a,* ped. v. int., ×1.5; *2b,* incompl. brach. v. ext., ×1; *2c,* both valves lat., ×1 (Rowell, n).

Valdiviathyris Helmcke, 1940, p. 237 [**V. quenstedti*; OD]. Pedicle valve unknown. Brachial valve similar to *Ancistrocrania,* but much smaller, thinner-shelled, processes more ventrally directed (681). *Rec.,* S.Ind.O.——Fig. 181,*4*. **V. quenstedti*; *4a-c,* brach. v. ext., lat., int., all ×6 (681).

Family EOCONULIDAE Rowell, n. fam.

Shell impunctate, phosphatic; brachial valve a low misshapen cone with pair of large adductor scars near posterolateral margins. *M.Ord.-U.Ord.*

Eoconulus Cooper, 1956, p. 282 [**E. rectangulatus*; OD]. Small to minute, probably attached by cementation of pedicle valve, latter unknown. *M.Ord.-U.Ord.,* N.Am.(Ala.-Va.)-Eu.(Ire.).——Fig. 182,*1*. **E. rectangulatus,* M.Ord., USA(Ala.); *1a-c,* brach. v. ext., lat., int., all ×15 (189).

GENERA DOUBTFULLY REFERRED TO CRANIACEA

Angarella, Pseudometoptoma, and *Eleutherocrania* are three rather similar genera which previously have been referred to the Craniidae (356), but their systematic position is debatable. Although their calcareous shells and some aspects of their gross shape recall this family, the microstructure of their impunctate shells differs markedly from that of the craniids. Moreover, although the musculature of these forms is not very well known, in *Angarella* the brachial valve shows a suggestion of 4 or 5 pairs of submarginally placed and bilaterally symmetrical muscles. Such a muscle pattern is unknown in the craniaceans, or indeed in any other brachiopod superfamily, but is similar to that of some monoplacophorans (Mollusca). Since the animals have been described as having 2 valves, however, a close relationship with the monoplacophorans is unlikely; much more must be known of the morphology of the 2 valves and their relationship to each other before the systematic position of these genera can be regarded as reasonably well established.

Angarella Asatkin, 1932, p. 486 [**A. jaworowskii*; OD]. Large forms with relatively high, conical brachial valve, flat to gently convex pedicle valve, both valves without limbus. Attached by cementation of apical region of pedicle valve, possibly becoming secondarily free. Shell calcareous, impunctate, in 2 layers. Musculature inadequately known. *Ord.,* Asia(E.Sib.-Urals-Kazakhstan).——Fig. 182,*2*. **A. jaworowskii,* Sib.; *2a,b,* brach. v. ext. exfoliated, lat., ×1; *2c,d,* ped. v. ext., lat., ×1 (Rowell, n).

Eleutherocrania von Huene, 1899, p. 294 [**E. gibberosa*; OD]. Similar to *Pseudometoptoma,* but pedicle valve strongly convex to subconical. *U.Ord.-L.Sil.,* Eu.(Est.).

Pseudometoptoma von Huene, 1899, p. 282 [**Metoptoma siluricum* Eichwald, 1842, p. 77; OD]. Free, externally like *Angarella,* but lacking attachment scar. *Ord.-L.Sil.,* Eu.(Baltic).

Order OBOLELLIDA Rowell, n. order

Shell essentially calcareous, biconvex, subcircular to elongate oval in outline. Pedicle valve with well-defined pseudointerarea; position of pedicle opening very variable, may emerge between valves, at apex of pedicle valve, or by subsequent resorption open anterior to apex of pedicle valve. Beak of brachial valve marginal. *L.Cam.-M.Cam.*

Superfamily OBOLELLACEA Walcott & Schuchert, 1908

[emend. Rowell, 1962, p. 137] [*nom. transl.* Goryansky, 1960, p. 180 (*ex* Obolellidae Walcott & Schuchert, 1908, p. 145)]

Ornament of concentric growth lines and

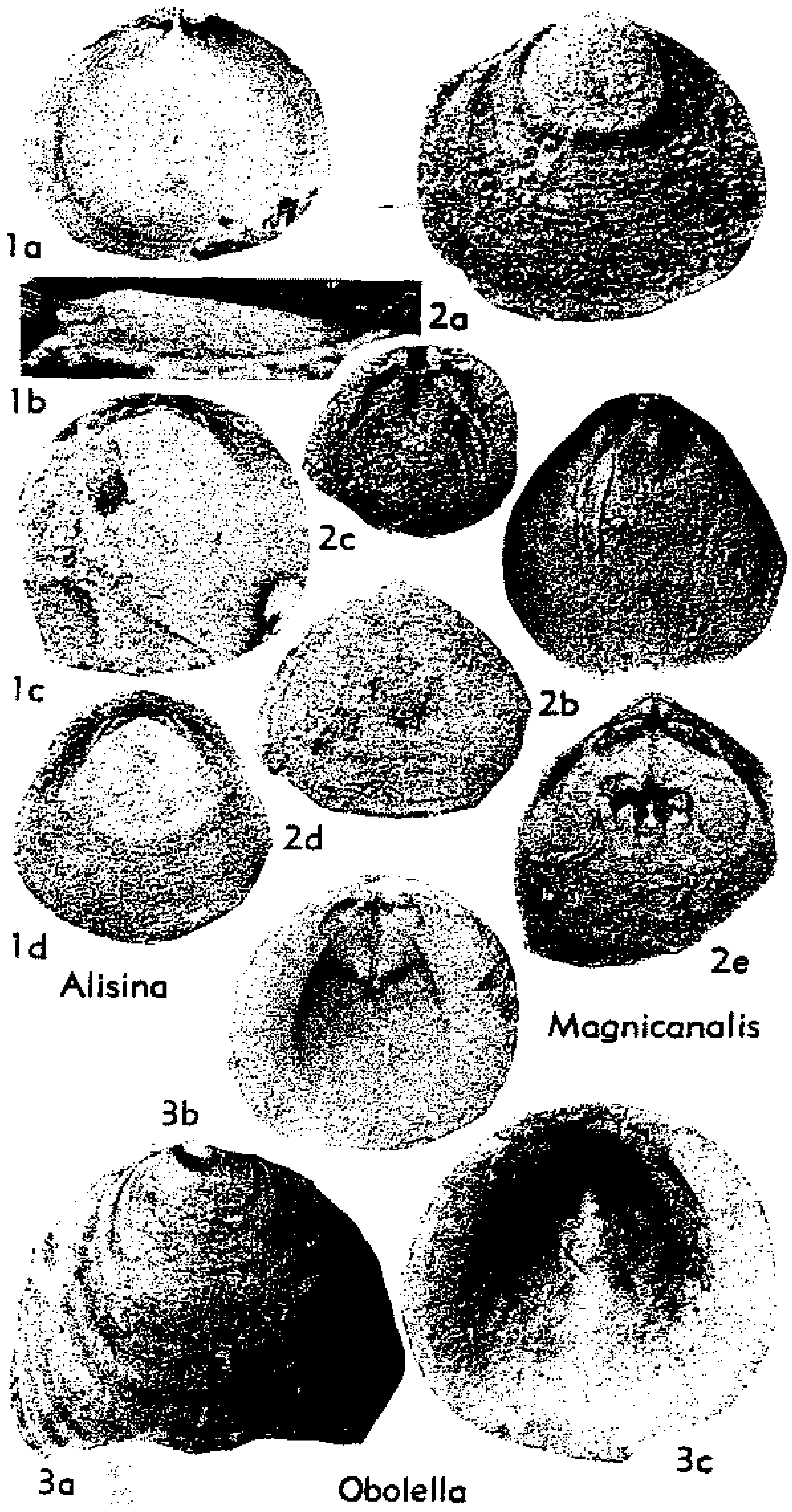


FIG. 183. Obolellidae (p. *H292-H293*).

fine radial striae. One pair of principal mantle canals *(vascula lateralia)* in pedicle valve diverging anterolaterally from in front of beak, posterior third of valve commonly thickened to produce very low, solid platform. Brachial valve with orthocline pseudointerarea, low median ridge variably developed, 2 pairs of principal mantle canals, one pair *(vascula lateralia)* diverging anterolaterally from in front of beak, second pair *(vascula media)* arising near center of valve, diverging slightly anteriorly; musculature in superfamily inadequately known but apparently a pair of cardinal scars in pedicle valve in front of propareas with second smaller pair of scars near mid-line, in front of ventral platform. Brachial valve with 2 pairs of cardinal scars, commonly united to form two scars immediately in front of propareas, third pair of muscle scars near center of valve. *L.Cam.-M.Cam.*

Family OBOLELLIDAE Walcott & Schuchert, 1908

[Obolellidae WALCOTT & SCHUCHERT, 1908, p. 145; emend. ROWELL, 1962, p. 138]

Characters of superfamily. *L.Cam.-M. Cam.*

The genera included in the family form a compact group, but one which displays remarkable variation in the nature of the pedicle opening. Superficially, some of the genera show a resemblance to the kutorginaceans, but they differ fundamentally from them in musculature, mantle canal pattern, and nature of the posterior margin of the brachial valve. The muscle scars of the obolellids are not concentrated medianly or elongated as in the kutorginaceans or articulates, and their distribution, with one or more pairs posterolaterally placed, agrees with the typical inarticulate pattern. It is unlikely that these posterolateral muscles are associated with the pedicle, since they are relatively deeply impressed and their position is more or less constant, irrespective of the position of the pedicle foramen, and it seems probable that they are the homologues of the posterior adductors of other inarticulates. The relationship of the family to remainder of the class is very obscure, however, since in shell composition and nature of the posterior margin of the pedicle valve they differ greatly from any other Cambrian stock and in spite of the small number of genera involved, the differences merit assignment of ordinal rank to the group.

The Obolellida form the oldest group of calcareous-shelled inarticulates, and its members are among the earliest elements that are known of brachiopod faunas. They were widely distributed and locally numerically abundant in the Early Cambrian, but the initial success of the stock was short-lived and it was extinct by the Middle Cambrian.

Obolella BILLINGS, 1861, p. 6 [**O. chromatica*; SD DALL, 1870, p. 163]. Variably developed pseudointerarea, apsacline to catacline; pedicle emerging through low groove which divides pseudointerarea medianly (680). *L.Cam., ?M.Cam.,* N.Am.-Greenl. - ?Asia - ?Australia.——FIG. 183,*3*. **O. chromatica,* L.Cam., Labrador; *3a,b,* incompl. ped.

v. ext., int., ×5, ×4; *3c,* brach. v. int. ×4 (*3a,* Bell, n; *3b,c,* 680).

Alisina Rowell, 1962, p. 141 [**Obolella atlantica* Walcott, 1890, p. 36; OD]. Pseudointerarea of pedicle valve apsacline to catacline, divided medianly by triangular elevation into 2 propareas; pedicle confined to narrowly conical pedicle tube sloping obliquely posteroventrally through thickened umbonal part of shell, foramen apical. *L.Cam.,* Eu.(Eng.)-N.Am.(Mex.).——Fig. 183,*1*. **A. atlantica* (Walcott), Newf.; *1a,b,* ped. v. int. impression; int. impression lat., ×4, ×5; *1c,d,* brach. v. int. impression showing pseudointerarea, int. impression, ×4 (680).

Bicia Walcott, 1901, p. 676 [**Obolella gemma* Billings, 1871, p. 218; OD]. Subtrigonal outline, beak of pedicle valve subacuminate, pseudointerarea orthocline to slightly apsacline, divided medianly by almost parallel-sided pedicle groove. Platform in pedicle valve well developed for family, posterolateral muscle scars deeply impressed. *L.Cam.,* N.Am.——Fig. 184,*1*. **B. gemma* (Billings), USA(N.Y.); *1a,b,* ped.v. ext., lat., ×5.3; *1c,* ped.v. int., ×7.5; *1d,* brach.v. int., ×4.4 (848).

Magnicanalis Rowell, 1962, p. 140 [**Obolella mobergi* Walcott, 1901, p. 673; OD]. Similar to *Obolella,* but with well-developed pseudointerarea in pedicle valve ornamented by strong growth lines crossed by deep hemiconical pedicle groove. *L.Cam.,* Eu.(Scand.).——Fig. 183,*2*. **M. mobergi* (Walcott), Sweden; *2a-c,* ped. v. ext., int. impression, incompl. int. (latex cast), all ×3; *2d,e,* brach. v. ext., incompl. int. impression, ×3 (680).

Trematobolus Matthew, 1893, p. 276 [**T. insignis;* OD] [=*Protosiphon* Matthew, 1897; p. 70 (type, *P. kempanum*); *Protosyphon* Goryansky, 1960, p. 181 *(nom. null.)*; *Trematobolos* Eastman, 1960, p. 288 *(nom. null.)*]. Large for family. Pseudointerarea of pedicle valve apsacline, divided medianly by groove. Pedicle track triangular, foramen at anterior end, about quarter length of valve in front of beak. Homeomorphic with *Schizambon. L.Cam.-M.Cam.,* N.Am.-Eu.-Asia(E. Sib.).——Fig. 184,*2*. *T. kempanum* (Matthew), L.Cam., N.B.; *2a-c,* ped. v. int. impression, incompl. int. impression showing pedicle opening, latex cast ext., ×1.6 *(2a,b)*, ×2 *(2c)*; *2d,e,* brach. v. int. impression, incompl. int. impression showing musculature, both ×1.6 (*2a,b,d,e,* 680; *2c,* Bell, n).

Order PATERINIDA Rowell, n. order

Shell phosphatic, rounded or elliptical in outline, growth usually holoperipheral in both valves. Pedicle valve convex to hemiconical, pseudointerarea divided by triangular delthyrium closed to variable extent by homeodeltidium. Brachial valve similar in external form, notothyrium partially closed by homeochilidium. *L.Cam.-M.Ord.*

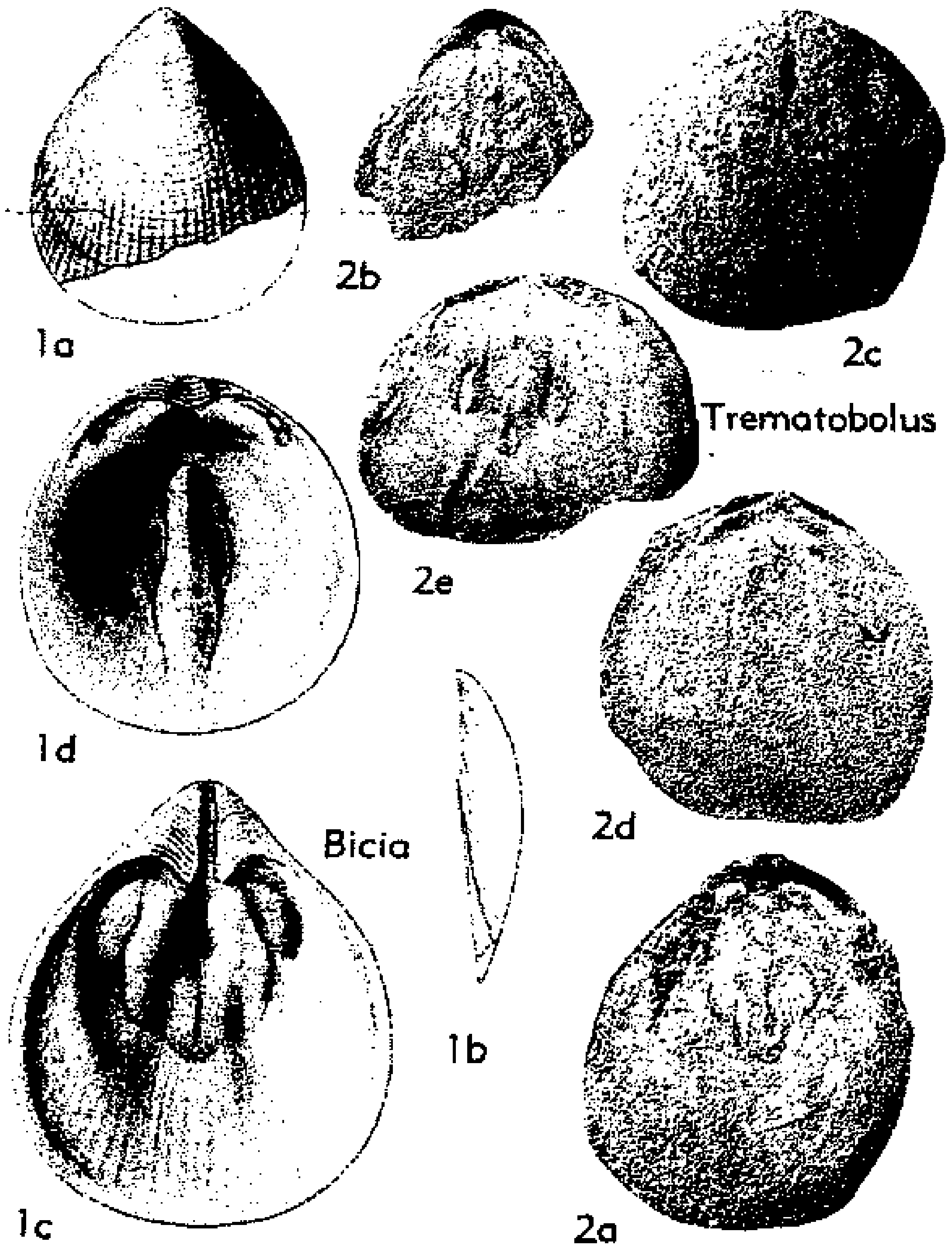


Fig. 184. Obolellidae (p. *H*293).

Superfamily PATERINACEA Schuchert, 1893

[*nom. transl.* Schuchert & LeVene, 1929, p. 11 (*ex* Paterinidae Schuchert, 1893, p. 148) incl. Dictyoninacea Cooper, 1956, p. 187]

Ventral pseudointerarea usually well developed, procline to apsacline, homeodeltidium convex. Brachial valve lower than pedicle valve, homeochilidium convex (65, 189). *L.Cam.-M.Ord.*

The paterinaceans are one of the earliest brachiopod stocks and originally were thought to be restricted to the Cambrian but are now known to range into the Middle Ordovician (189). The internal structure of many species referred to the superfamily is unknown and as Bell (65) has suggested, it is possible that some genera included in it are polyphyletic. The paterinaceans always have been difficult to place taxonomically; Schuchert (1893, 1897) included them in the Atremata, as did Walcott (1912) and while Thomson (1927) and Muir-Wood (1955) referred them to the Neotremata, Schuchert & LeVene

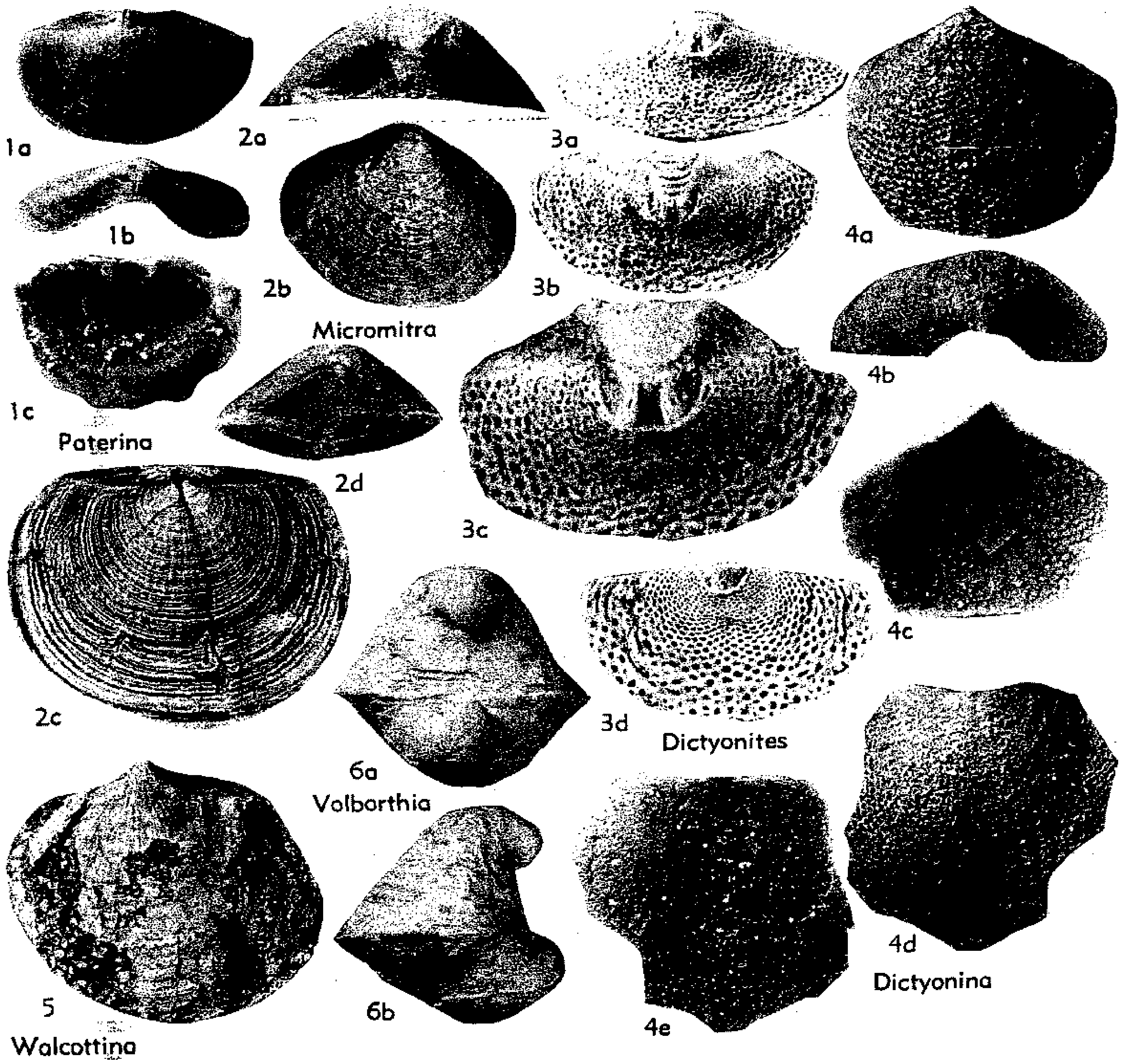


FIG. 185. Paterinidae *(1-4)*; ?Paterinida *(5-6)* (p. *H*295).

(1929) split the group, placing the Paterinidae in the Palaeotremata and the Micromitridae in the Atremata.

Superficially, the pedicle valve of the paterinaceans is somewhat similar to that of the acrotretaceans, but there are major differences. Characteristic of the superfamily is the absence of an apical pedicle foramen. It is usually assumed that the pedicle emerged between the valves and although this may well have occurred, the animals possibly may have lacked a pedicle (p. *H*89). In addition to the external differences between the paterinaceans and other inarticulate stocks, there are internal differences which together seem to be of sufficient magnitude to merit regarding the paterinaceans as a separate order. The lateral margins of the delthyrium are strengthened by broad diverging ridges in several genera and what are apparently muscle scars, although imperfectly known, all seemingly forming narrow triangular muscle tracks extending posteriorly to the beak. It is probable that we still do not know the position of all of the muscles, but in the pedicle valve there are two narrow tracks, diverging slightly forward and extending from the beak to near the mid-length of the valve. In the brachial valve two pairs of tracks occur, the larger pair extending forward from the beak to near the mid-length of the valve and forming a single median depression, with a much shorter pair, more externally placed, diverging anterolaterally. This pattern is quite unlike the muscle scar distribution of any other inarticulate brachiopod stock.

Family PATERINIDAE Schuchert, 1893

[Paterinidae Schuchert, 1893, p. 148; incl. Micromitridae Schuchert & LeVene, 1929, p. 11]

Characters of superfamily. *L.Cam.-M.Ord.*

Paterina Beecher, 1891, p. 345 [**Obolus labradoricus* Billings, 1861, p. 6; OD] [=*Iphidella* Walcott, 1905, p. 304 (*nom. subst. pro. Iphidea* Billings, 1872, p. 477, *non* Bayley, 1865) (type, *Iphidea bella* Billings, 1872, p. 477)]. Shell thin, seemingly single-layered, ornament of regular concentric fila. Homeodeltidium variably developed, usually large, lateral margins of delthyrium with 2 strong ridges on internal face uniting at apex of valve. *Cam.*, N.Am.-Eu.-Asia-Australia.——Fig. 185,*1*. **P. labradorica* (Billings), L. Cam., Labrador; *1a-c*, ped. v. ext., post., int., all ×10 (Rowell, n).

Dictyonina Cooper, 1942, p. 228 [*nom. subst. pro Iphidella* Walcott, 1912, p. 359 (*non* Walcott, 1905)] [**Trematis pannulus* White, 1874, p. 6; OD]. Ornament of small, superficial pits commonly formed by intersection of oblique raised lines. Homeodeltidium relatively small. *L.Cam.-M.Cam., ?U.Cam.*, N.Am.-Eu.-Asia.——Fig. 185, *4*. **D. pannula* (White), L.Cam., USA(Nev.); *4a-c*, ped. v. ext., post., int., all ×15; *4d,e*, incompl. brach. v. ext., int., both ×15 (Rowell, n).

Dictyonites Cooper, 1956, p. 187 [**D. perforata*; OD]. Umbonal region of both valves imperforate, bearing 2 short ridges in pedicle valve and single median ridge in brachial. Ventral pseudointerarea well developed, homeodeltidium large, dorsal pseudointerarea and homeochilidium relatively small, remainder of shell perforated by large pores, possibly covered by thin outer shell layer in life. Interior of pedicle valve with short apical median ridge; musculature unknown. *M.Ord.*, N. Am.(Ala.).——Fig. 185,*3*. **D. perforata*, Pratt Ferry F.; *3a-c*, ped. v. ext., oblique post., detail of umbo, ×10, ×10, ×15; *3d*, brach.v. ext., ×10 (189).

Micromitra Meek, 1873, p. 479 [**Iphidea? sculptilis*; OD] [=*?Icodonta* Bell, 1941, p. 212 (type, *I. typica*)]. Relatively thick shell of several layers, ornament basically reticulate, but variable, fine concentric fila crossed by costellae. Homeodeltidium and homeochilidium usually large, lateral margins of delthyrium apparently buttressed by ridges, as in *Paterina*. *Cam.*, N.Am.-Eu.-Asia-Australia.——Fig. 185,*2*. **M. sculptilis* (Meek), M.Cam., USA(Mont.); *2a,b*, ped. v. post., ext., ×6; *2c*, brach. v. ext., ×6; *2d*, both valves post. incompl., ×6 (65).

GENERA DOUBTFULLY REFERRED TO PATERINIDA

Mickwitzia Schmidt, 1888, p. 24 [**Lingula? monilifera* Linnarsson, 1869, p. 344; OD] [=*Causea* Wiman, 1902, p. 53 (type, *C. formosa*)]. Relatively large, oval to subcircular in outline, ventribiconvex. Shell of 3 layers, outer pustulose, middle with fine reticulate ornament, inner coarsely punctate. Pedicle valve with elevated apex submarginal or recurved over posterior margin of valve, pseudointerarea poorly defined, apparently without pedicle opening. Brachial valve with low submarginal apex. Internal structure unknown. *L. Cam.*, Eu.-?N.Am.——Fig. 186,*1*. **M. monilifera* (Linnarsson), Sweden; *1a-c*, ped. v. ext. exfoliated, lat., post., all ×1.5 (*1a*, Rowell, n; *1b,c*, 848).

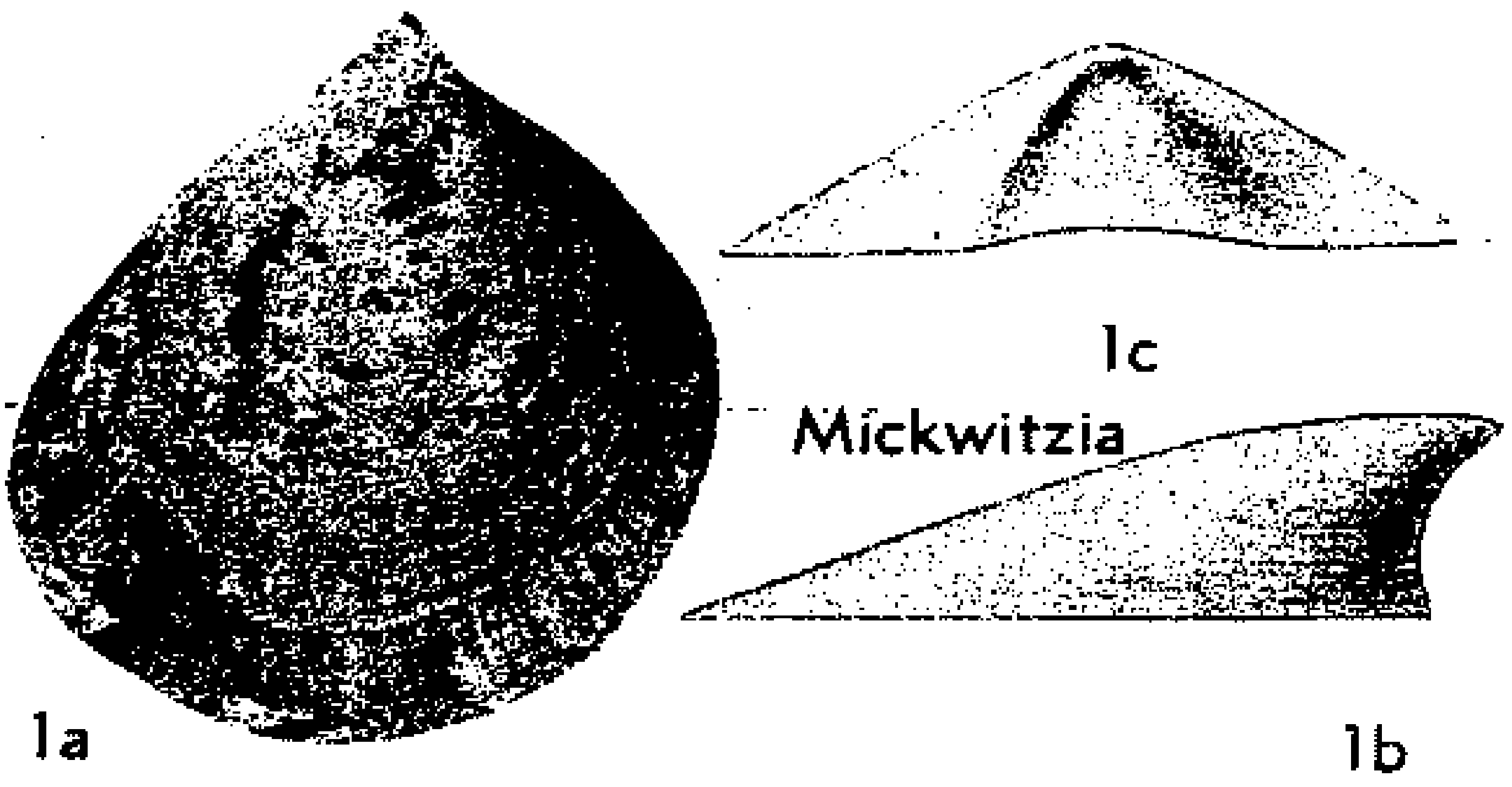


Fig. 186. ?Paterinida (p. *H*295).

Volborthia von Möller, 1870, p. 409 [**Acrotreta recurva* Kutorga, 1848, p. 277; OD]. Fairly large, transversely ovate in outline, posterior margin straight; pedicle valve conical, beak inflated, recurved over well-defined catacline pseudointerarea which is divided into propareas by narrow ridge, pedicle opening apparently absent in adults. Brachial valve strongly convex, beak similar to pedicle valve, small anacline pseudointerarea. Valves ornamented by concentric growth lines. Internal structure unknown. *L.Ord.*, Eu.(NW. USSR).——Fig. 185,*6*. **V. recurva* (Kutorga); *6a,b*, plaster cast of both valves post., lat., ×1.5 (Rowell, n).

Walcottina Cobbold, 1921, p. 334 [**W. lapworthi*; OD]. Pedicle valve transversely oval, convex, beak recurved above or behind straight posterior margin; pseudointerarea poorly defined, pedicle opening probably triangular delthyrium beneath beak. Brachial valve unknown. Shell apparently phosphatic, in 3 layers, outer layer with fine concentric fila, middle layer with radial striae, inner layer apparently smooth. *L.Cam.*, Eu.(Eng.).——Fig. 185,*5*. **W. lapworthi*; partly exfoliated ped. v., ×5 (Rowell, n).

CLASS INARTICULATA—ADDENDUM

The genus *Ptychopeltis* Perner was regarded as a monoplacophoran by Knight & Yochelson, who in the *Treatise* provisionally assigned it to the Archinacellidae (p. *I*81).

Horný (433a, 433b) has recently argued that the gross form of the shell and its internal markings are inconsistent with such a taxonomic position and based on the genus he has erected a new family (Ptychopeltidae) which he considers is best referred to the inarticulate brachiopods. As Horný noted, several features of *Ptychopeltis* are reminiscent of characters found in some Inarticulata, and if he is correct in considering the shell phosphatic, then, superficially at least, the genus shows a degree of resemblance to the discinaceans. Some characteristics of the shell, however, notably such features as the strong ?dorsally directed commissure deflection, are unknown in any undoubted inarticulate brachiopod, and until the second (?pedicle) valve is discovered or the musculature discerned, the affinity of the family with brachiopods can at best be regarded as only tentatively established. It has not yet been possible for me to examine material of the genus and Horný's (433b, p. 62) diagnosis therefore is reproduced in full.

Family PTYCHOPELTIDAE Horný, 1961

[Ptychopeltidae Horný, 1961, p. 299]

"Subovate arched, saddle-shaped shells with small blunt apex near or at the apical margin; aperture semicircular, not in a plane; lateral sides rounded, curved deeply downwards, the abapical (anterior) margin curved strongly upwards to form a distinct saddle which is not too well expressed in young stages; outer surface with faint, crowded radial striation, striae not bifurcated; shell lamellar, probably carbonatic-phosphatic; inner structure without visible scars except the median groove and series of numerous small marginal scars bordering the apical and lateral sides of the shell, corresponding probably to the pallial sinuses." *M.Ord.*

Ptychopeltis Perner, 1903, p. 42 [**P. incola*; OD]. Characters of family. *M.Ord.*, Eu.

Class UNCERTAIN

By A. J. Rowell

[Nottingham University]

Order KUTORGINIDA Kuhn, 1949

[*nom. correct.* Goryansky, 1960, p. 181 (*pro* order Kutorginacea Kuhn, 1949, p. 99)] [*emend.* Rowell, herein] [=Palaeotremata Thomson, 1927, p. 118; ?incl. order Rustellacea Kuhn, 1949, p. 99]

Shell calcareous, biconvex; cardinal area present in pedicle valve but not clearly demarcated in all specimens from remainder of valve, small apical foramen, delthyrium widely triangular, partially closed by pseudodeltidium; teeth seemingly absent. Brachial valve with variably developed cardinal area, notothyrium may be restricted apically by chilidium, cardinal process absent. Two principal mantle canals in both valves, with numerous radially arranged grooves, probably vascular in origin; muscle field in each valve narrow, elongate, near mid-line of valve. *L.Cam., ?M.Cam.*

Superfamily KUTORGINACEA Schuchert, 1893

[*nom. transl.* Walcott & Schuchert, 1908, p. 144 (*ex* Kutorginidae Schuchert, 1893, p. 151)] [?incl. Rustellacea Walcott, 1908, p. 143 (*partim*)]

Characters of order. *L.Cam., ?M.Cam.*

The superfamily is here considered to include the Kutorginidae and Yorkiidae. Previously, *Yorkia* has always been regarded as a calcareous-shelled inarticulate brachiopod, related in some way to *Obolella* (680), but the systematic position indicated for *Kutorgina* has been more varied. The latter genus has been placed in the Inarticulata by some workers (e.g., 356) and regarded as an early articulate brachiopod by other students (e.g., Muir-Wood, 1955). Recent work on the internal structure of *Kutorgina* and *Yorkia* strongly suggests that they are closely related to each other and only distantly to any other stock. The mantle canal system of both genera, particularly of the brachial valve, which is better known, is basically the same, with two, characteristic, crescentic, principal canals; the musculature of the two genera is also seemingly similar and the gross structure of the pedicle valves is comparable.

Although a separate order (Rustellida Kuhn) has been erected for *Rustella*, this poorly known genus is provisionally included in the Kutorginacea. A distinct possibility exists that the type-species of *Rustella*

(R. edsoni) is a *Kutorgina,* but the preservation of the material does not allow this relationship to be established beyond doubt (739b).

The problematic affinities of the kutorginaceans are discussed elsewhere (p. *H*196, *H*227).

Family KUTORGINIDAE Schuchert, 1893

[Kutorginidae Schuchert, 1893, p. 151; incl. Rustellidae Walcott, 1908, p. 143, and Schuchertinidae Walcott, 1908, p. 145]

Posterior margin of brachial valve unmodified, delthyrium widely triangular, pseudodeltidium relatively small. *L.Cam., ?M.Cam.*

Kutorgina Billings, 1861, p. 8 [**Obolella cingulata*; OD] [=*Koturgina* Billings, 1861, p. 8 *(nom. imperf.)*; *?Rustella* Walcott, 1905, p. 311 (type, *R. edsoni*)]. Cardinal area of pedicle valve orthocline, becoming anacline in old individuals which develop strongly convex valve; beak of brachial valve flexed abruptly above remainder of valve, notothyrium closed apically by small chilidium. Ornament of growth lines, lamellose peripherally, granular micro-ornament. *L.Cam.,* N.Am.-Eu.-Asia.——Fig. 187,*1a-c.* **K. cingulata* (Billings), USA(Vt.); *1a,* ped.v. ext.; *1b,* brach. v. ext.; *1c,* both valves lat., all ×1.5 (Rowell, n).——Fig. 187,*1d,e.* *K. reticulata* Poulson, E. Greenl.; *1d,e,* ped. v. int. impression, brach. v. int. impression, both ×1.5 (Rowell, n).

?Schuchertina Walcott, 1905, p. 323 [**S. cambria*; OD]. Genus poorly known, apparently similar to *Kutorgina,* but subequally biconvex. *M.Cam.,* N.Am.

Family YORKIIDAE Rowell, 1962

[Yorkiidae Rowell, 1962, p. 144]

Posterior margin of brachial valve bearing 2 narrowly triangular plates ornamented by lines parallel to their narrow base. *L. Cam.*

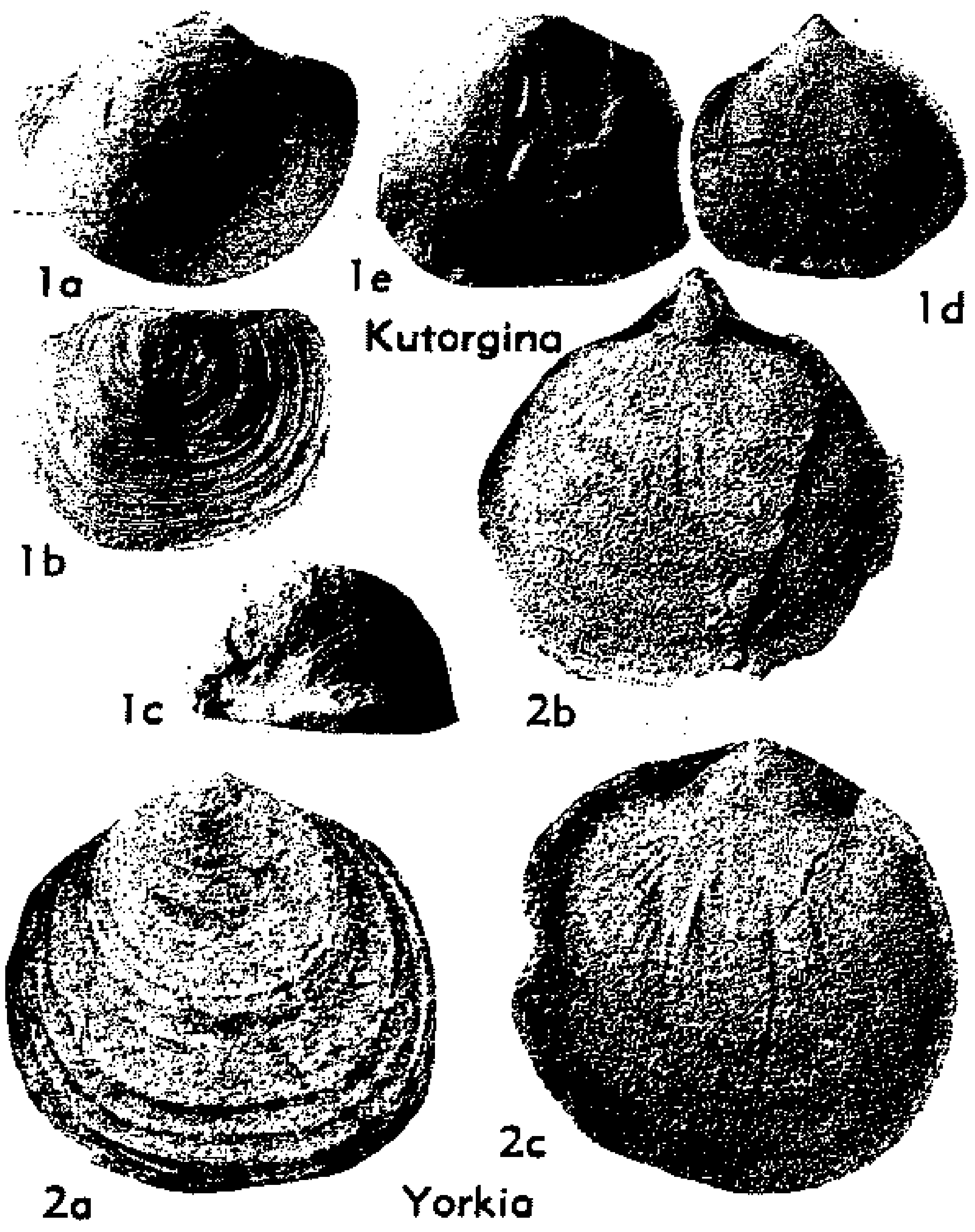


Fig. 187. Kutorginidae *(1)*; Yorkiidae *(2)* (p. *H*297).

Yorkia Walcott, 1897, p. 714 [**Y. wanneri*; OD] [=*Quebecia* Walcott, 1905, p. 320 (type, *Obolella circe* Billings, 1872, p. 219)]. Pedicle valve with small pointed beak abruptly flexed above remainder of valve, cardinal area apsacline to catacline, pseudodeltidium well developed. *L. Cam.,* N.Am.——Fig. 187,*2.* **Y. wanneri,* USA (Pa.); *2a,b,* ped. v. ext. (wax cast), int. impression, both ×2; *2c,* brach.v. int. impression, ×2 (680).

ARTICULATA

By D. V. Ager, T. W. Amsden, Gertruda Biernat, A. J. Boucot, G. F. Elliott, R. E. Grant, Kotora Hatai, J. G. Johnson, D. J. McLaren, H. M. Muir-Wood, Charles W. Pitrat, A. J. Rowell, Herta Schmidt, R. D. Staton, F. G. Stehli, Alwyn Williams, and A. D. Wright

Class ARTICULATA Huxley, 1869

[Articulata Huxley, 1869, p. 116] [=Arthropomata Owen, 1858, p. 336; Testicardines Bronn, 1862, p.301; Clistenterata King, 1873, p. 15; Pygocaulia Thomson, 1927, p. 116] [Diagnosis prepared by Alwyn Williams, Queen's University of Belfast]

Valves calcareous and impunctate, punctate or pseudopunctate, with fibrous or variably prismatic secondary layer and nonfibrous primary layer commonly well differentiated, periostracum of protein in living species; hinge teeth and dental sockets composed of secondary shell, well developed or rarely lost or replaced; socket ridges commonly modified as crura (or homologues) associated with rarer loops or spires to provide support for lophophore; musculature for opening and closing valves about hinge axis consisting of diductor and adductor sets with bases commonly grouped posteromedially. Pedicle of living species developing from larval rudiment and controlled by dorsal as well as ventral adjustor muscles, inferred to have originated in same way in many extinct groups or to have arisen as extension of ventral body wall in others. Larval development involving differentiation of anterior lobe and mantle and pedicle rudiments, coelom enterocoelic; shell, alimentary canal, and lophophore without median tentacle, appearing after settling with mantle reversal occurring in living species but inferred not to have taken place in some extinct stocks. Alimentary canal ending blindly, row of ablabial filaments arising in addition to adlabial set only in post-trocholophous stages of lophophore development. *L.Cam.-Rec.*

The division of the Brachiopoda into two distinct classes is undeniably validated, as has been recognized for more than a century, by basic morphological, anatomical, and embryological differences among living species.

The exoskeletons of Recent articulates are immediately distinguishable from those of living inarticulates in being invariably calcareous with well-defined primary and secondary layers and in possessing a tooth-and-socket system of valve articulation and secondary shell outgrowths of variably developed crura or loops which support the lophophore, or both. Within articulate shells, the absence of an anus, presence of a relatively complex pedicle that developed independently of the rest of the body from an embryonic rudiment, fusion of outer lobes of the mantles along the posterior margin, and the distinctive grouping of a simplified musculature are further indications of a fundamental divergence within the phylum. The embryological differences are equally significant. In contrast to living inarticulates, a reversal of the mantle rudiment, an enterocoelic derivation of the coelom and an absence of a median tentacle throughout the development of the lophophore are all characteristic of the articulates. Indeed, PERCIVAL (1944), admittedly in support of a mistaken belief that there was also a difference in body orientation, contended that the similarity between the articulates and inarticulates was an expression of convergence rather than common ancestry and advocated their separation into two phyla.

An interpretive study of brachiopod history, like that outlined in the chapter on "Phylogeny and Evolution," does not, however, support such radical taxonomic reform. On the contrary it suggests that all brachiopods were descended from the same ancestral stock and that the articulates diverged at a relatively faster rate by a series of basic modifications which were introduced at different times during phylogeny and only cumulatively represent the distinctiveness of the class. Certainly the differences between the oldest Articulata and Inarticulata are not always as decisive as those between Recent representatives; while the Lower Cambrian Kutorginida cannot be assigned confidently to either class and may have evolved independently.

The only tangible evidence for these conclusions is, of course, based on changes in morphology of the shell. In this respect articulation seems to have been the most persistent feature of the class, because primitive teeth and sockets are found even in billingsellaceans, whereas their absence, as in members of the Productidina, was invariably due to degeneration. The structure of the shell and the presence of calcareous supports for the lophophore are much less diagnostic. The primary layer is poorly differentiated in most species of the Orthida and Strophomenida, and the nonfibrous test of the Dictyonellidina is really like that of the calcareous-shelled inarticulates. Skeletal outgrowths that undoubtedly gave support to the lophophore are also relatively late features of articulate history and in their most typical forms as crura, loops, and spires are characteristic only of the later Pentamerida, Rhynchonellida, Terebratulida, and Spiriferida.

There are, moreover, certain morphological features of extinct articulate groups that may be taken to indicate equally profound embryological and anatomical changes. The absence of a well-defined chamber for reception of the pedicle base among the Orthida, Strophomenida, and Pentamerida suggests that mantle reversal first took place during emergence of the Rhynchonellida and became a feature of articulate development only in members of that order and the related Spiriferida and Terebratulida. The gap between the pseudodeltidium and chilidium of the billingsellaceans and early Strophomenida was more likely sealed by a posterior body wall of inner epithelium than by extensions of outer epithelium. This arrangement, together with the restriction of the pedicle-outer epithelial junction to the ventral apical regions by growth of pseudodeltidium in members of the Billingsellacea, Clitambonitidina, Triplesiidina and Strophomenida, suggests that in such species, the pedicle, like that of the inarticulates, was an extension of the ventral body wall. Hence, it is feasible to assume that the articulates were originally closely related to the inarticulates and that, although taxonomic segregation into two classes is warranted, differences become less important as both groups are traced back in time.

For reasons outlined in the chapter on "Classification," the Articulata are here divided into six orders embracing 37 superfamilies. Two additional suborders, the Dictyonellidina and the Thecideidina, each comprising a small number of genera but undeniably related to the Articulata, have not as yet been assigned to an ordinal group. The former may ultimately prove to have arisen independently of the remaining articulates, thereby meriting ordinal rank in the manner of the Kutorginida, Paterinida, and Obolellida. The ancestry of the Thecideidina is at present debatable, with the Spiriferida, Terebratulida, and the Strophomenida each qualifying, to a variable degree, for the role.

The distinctions drawn between the six orders are decisively diagnostic only in respect of their modal morphology. It is, for example, convenient and indeed desirable in gross comparison, to visualize typical Orthida as impunctate or endopunctate shells with an open delthyrium and brachiophores, Strophomenida as pseudopunctate with a pseudodeltidium and socket ridges, Pentamerida as impunctate with a spondylium and homologues of crura, Rhynchonellida as impunctate with deltidial plates and crura, Spiriferida as impunctate or endopunctate with a variable delthyrial cover and spiralia, and Terebratulida as endopunctate forms with deltidial plates and a loop. Yet so recurrent were the processes of evolution that no one character is either exclusive to an order or invariably exhibited by all its members and the distinctiveness of an order depends solely on its unique combination of all characters. Consequently, ordinal diagnoses are variably repetitive and indications of changes in character combinations are commonly more important guides to the individuality of the taxa than the prevalence of a single feature.

ORTHIDA

By Alwyn Williams and A. D. Wright

[Queen's University of Belfast and Nottingham University]

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, herein] [Materials for this order prepared by Alwyn Williams except Enteletacea and Triplesiidina by A. D. Wright]

Articulate brachiopods normally with unequally biconvex strophic shells and well-developed interareas and hinge lines; delthyrium and notothyrium open or less commonly closed by pseudodeltidium and chilidium, deltidial constrictions to delthyrium very rare. Ventral muscle field commonly not extending much beyond umbonal cavity, rarely elevated on spondylial or other structures of secondary shell. Cardinal process normally as median partition or differentiated into variably lobate myophore and shaft, rarely absent or forked; socket ridges commonly replaced by brachiophores with or without fulcral plates and convergent to divergent bases, less commonly bearing long processes which may have supported lophophore; lophophore inferred to have varied from schizolophous to spirolophous condition. Shell substance normally impunctate but also endopunctate and rarely pseudopunctate. *L.Cam.-U.Perm.*

The assignment of the Orthidina, Clitambonitidina, and Triplesiidina to the same ordinal group seems the best way to express the strong morphological affinities that exist between these primitive articulate brachiopods. All three suborders were mainly characterized by a strophic shell which lacked calcareous supports for the lophophore as well as a pedicle chamber. Indeed, only the forked cardinal process of the Triplesiidina and the spondylium of the Clitambonitidina

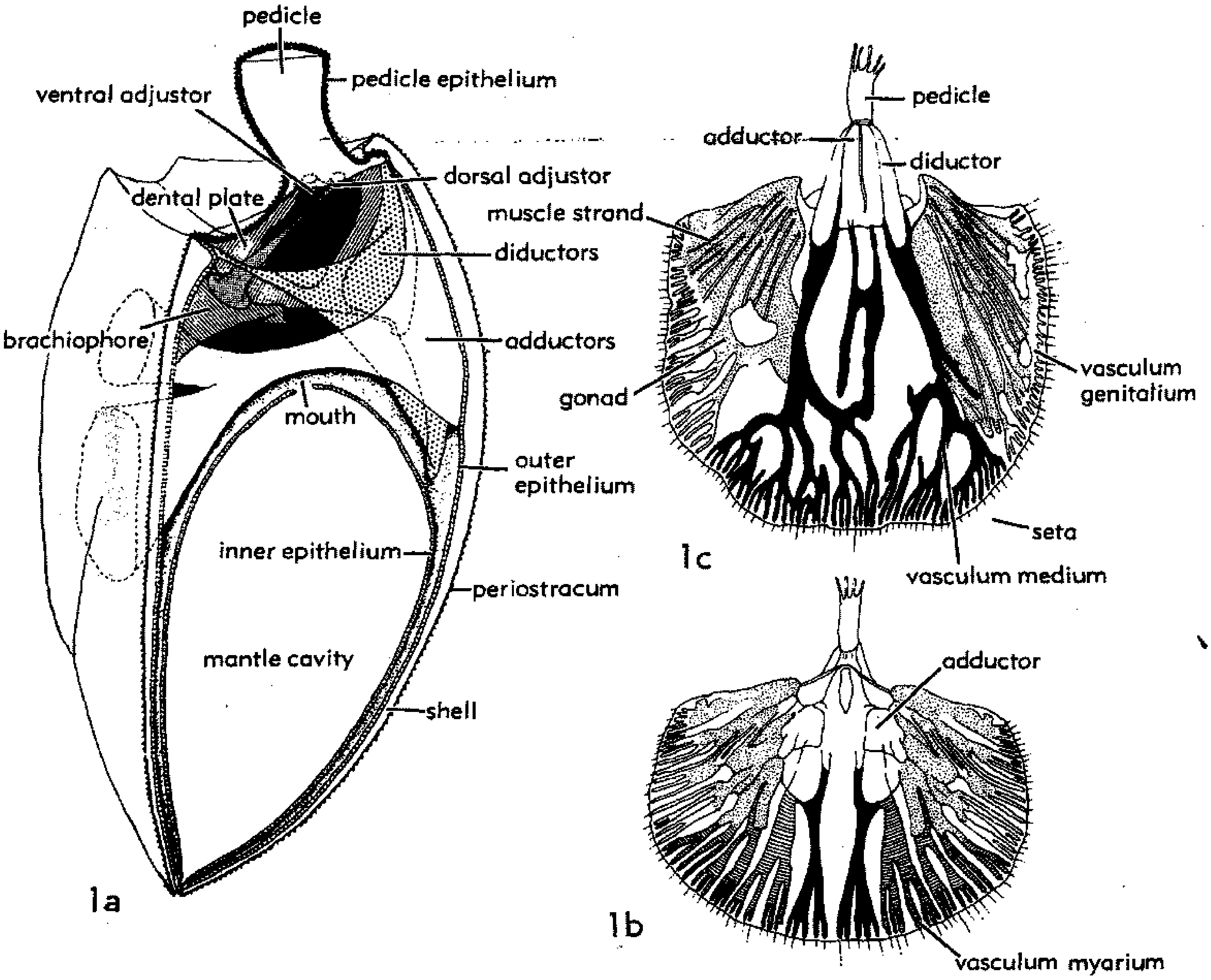


Fig. 188. *Howellites antiquior* (M'Coy); *1a,* stylized reconstruction of musculature; *1b,c,* inferred morphology of soft parts viewed from dorsal and ventral exteriors (880).

may be regarded as the pre-eminent requisites for distinction at the subordinal level, because the pseudodeltidium, which is the other principal feature of these two groups, is also present in the billingsellaceans. Admittedly, the possession of a pseudodeltidium may be sufficiently important in itself to warrant an entirely different grouping. Yet the billingsellaceans have a great deal more in common with early orthaceans than the Triplesiidina, for example, and the failure of the pseudodeltidium to develop in some Clitambonitidina indicates that the open delthyrium was not unique to the orthaceans and enteletaceans.

Suborder ORTHIDINA
Schuchert & Cooper, 1932

[*nom. correct.* Williams & Wright, herein (*pro* Orthoidea Schuchert & Cooper, 1932, p. 43)] [*emend.* Williams & Wright, herein]

Plano-convex to convexo-concave, costate to finely costellate or parvicostellate with superimposed costae, ventral interarea commonly curved, apsacline, delthyrium rarely closed by apically perforate pseudodeltidium or deltidium, chilidium rarely developed; teeth simple, ventral muscle field almost invariably impressed on valve floor and dental plates; cardinal process absent, simple, or differentiated into variably lobate myophore and shaft; sockets defined by ridges or outer surfaces or brachiophores with or without fulcral plates, brachiophores as short plates or rods, less commonly with processes and variably disposed supporting bases; dorsal adductor field quadripartite, normally divided by median ridgelike extension of notothyrial platform; mantle canal systems saccate to lemniscate; shell substance impunctate or punctate. *L.Cam.-Perm.*

The Orthidina, as here constituted, are an assemblage of extinct Paleozoic stocks that include the oldest known articulate brachiopods. They were especially prolific during Cambro-Ordovician times and became so diversified as to anticipate most of the morphological characteristics of other groups. Many of these stocks, however, were short-lived deviations from a small number of persistent lineages and have little effect on the modal design of the three superfamilies making up the suborder. Moreover, the differences between *Eosotrematorthis, Orthambonites,* and *Howellites,* which display the modal characteristics of the Billingsellacea, Orthacea, and Enteletacea, respectively, although important, actually include a minority of skeletal features, so that a representative orthoid can be satisfactorily defined.

The exterior of a typical member of the Orthidina is quite distinctive. It is that of a biconvex strophic shell, subquadrate in outline, with a maximum width anterior of a well-developed hinge line and a curved apsacline ventral interarea which is longer than an anacline dorsal interarea. A strong, median dorsal sulcus is normally present and the shell surface is usually costellate. Variations include the convexo-concave profile of many plaesiomyids, the bilobed outline of *Dicoelosia,* the reduced or mucronate hinge lines of *Angusticardinia* and *Skenidioides* respectively, the obsolescent interareas of *Productorthis,* the dorsal median fold of *Platystrophia* and of *Enteletes* with its additional superimposed radial plications; and the absence of radial ornamentation in *Kotujella* or the common occurrence of hollow ribs among enteletaceans and plectorthids. The most important external difference, however, is the persistence of a chilidium and pseudodeltidium among billingsellaceans and their absence in the orthaceans and enteletaceans. Chilidial-like structures are known in some hesperonomiids, productorthinids, and plaesiomyids, and deltidial plates were variably developed in a few independent stocks like *Trematorthis, Barbarorthis,* and *Phragmophora*; but the latter structures, at least, are not homologous with the billingsellacean pseudodeltidium, and, in general, the notothyria and delthyria of the orthaceans and enteletaceans remained uncovered.

Basic similarities are also evident internally, because only shell structure is as important as the presence of the pseudodeltidium in the superfamilial classification of the Orthidina. Thus, all enteletaceans are endopunctate, in contrast to the impunctate condition of billingsellaceans and orthaceans, although other morphological features suggest that the earliest known enteletaceans, the paurorthids, dalmanellids, and angusticardiniids, became endopunctate independently of one another.

The ventral muscle impressions of the Orthidina are normally subtriangular or bilobed in outline and confined to the posterior half of the pedicle valve (Fig. 188, 189). The umbonal chamber was never differentiated to receive the base of the pedicle as in other orders. It was occupied,

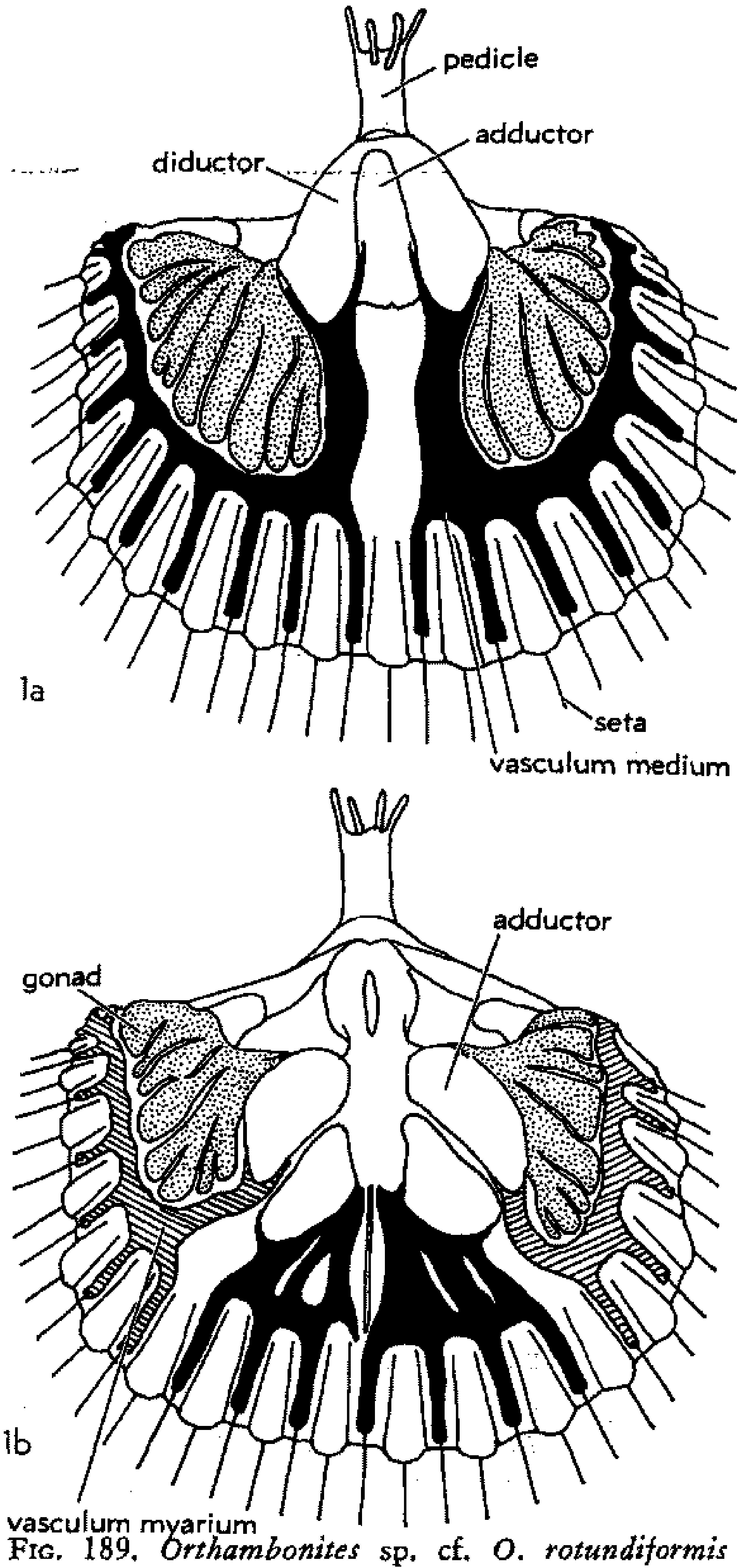


FIG. 189. *Orthambonites* sp. cf. *O. rotundiformis* COOPER; *1a,b,* stylized reconstruction of inferred morphology of soft parts viewed from the ventral and dorsal exteriors (Williams, n).

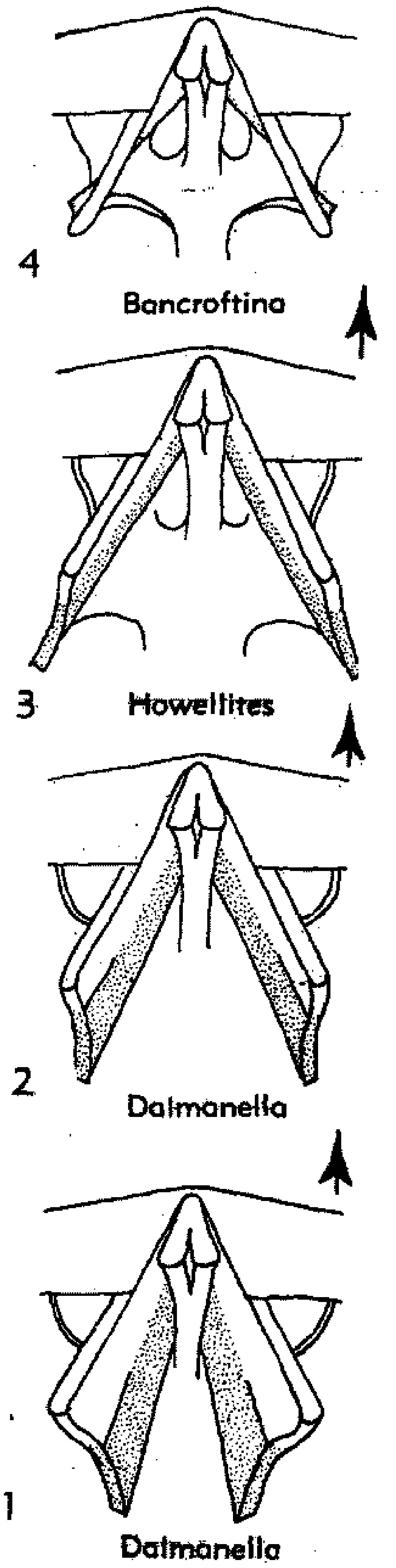


FIG. 190. Possible orthogenetic evolution of dalmanellid cardinalia involving lateral migration of brachiophore bases (shaded) from subtending an angle significantly less than that between tops of the brachiophores *(1)* to a not significantly smaller angle *(2)*, to a not significantly greater angle *(3)*, and to a significantly greater angle *(4)* (880).

solely by the muscle bases up to a variably developed pedicle callist, with the median adductor scars normally not enclosed anteriorly and the adjustors and lateral diductor lobes, at least in the orthaceans and enteletaceans, inserted on the inner surfaces of the dental plates (Fig. 188). In some stocks, like the plaesiomyids and heterorthids, the ventral muscle field was greatly splayed over the valve floor. In others, it was elevated on a spondylium (e.g., *Skenidioides*) or, as in *Parenteletes* and *Elasmothyris*, respectively, inserted on a shoe-lifter process or transverse plate. Yet such modifications as these were rare; indeed, the most important changes affecting the internal morphology were those that led to the diversification of the cardinalia.

The most commonly occurring cardinalia among the billingsellaceans, orthaceans, and enteletaceans are basically different from one another morphologically and, by inference, functionally. In all three groups, the notothyrial platform is normally well developed, as are the sockets for reception of the ventral teeth. In the billingsellaceans, the notothyrium is flanked by a pair of flat-lying plates or rods, more or less parallel with the hinge line, which acted principally as inner boundaries to the sockets, although they might also have received any dorsal adjustors that had developed. In the orthaceans and enteletaceans, on the other hand, the homologues of these socket ridges (brachiophores) are not only better developed rods or blades, which may be prolonged distally as processes, but subtend much greater angles with the hinge line. In this attitude they are more likely to have been elaborated into supports for the mouth segment of the lophophore. Moreover, the brachiophores of most enteletaceans and some orthaceans like the plectorthids are commonly supported by expanded bases and, together with fulcral plates, define sockets that are distally elevated above the floor of the brachial valve. The disposition of the brachiophore bases can vary greatly even within a series of closely related genera like those assigned to the Dalmanellidae. Using members of this family, it is possible to demonstrate a continuous gradient of change between arrangements in which the angle subtended by the brachiophore bases is significantly less or greater than that subtended by the tops of the brachiophores. Hence, although *Bancroftina, Dalmanella,* and *Howellites* are each characterized by a distinctive attitude, the last two genera together include species showing every conceivable variation in the disposition of the bases relative to the top of the brachiophores (Fig. 190). Generally, however, their attitude tends to be consistent in different stocks, so that they may converge onto a median septum to form a septalium, as in *Linoporella* and *Skenidioides*, or be widely divergent, as in *Enteletes*.

There are important differences in the origin and function of the diverse structures, collectively referred to as the cardinal process, that project posteriorly from the notothyrial platform. The lack of such outgrowths is relatively rare and represents the most primitive condition, although it is characteristic of species of the Ordovician enteletacean *Paurorthis*, while well-developed processes are found in such Cambrian stocks as *Billingsella* and the orthacean *Arctohedra*. In the majority of billingsellaceans and orthaceans, the commonest type of cardinal process consists of a median partition that effectively divides the posterior surface of the notothyrial platform into two halves, each of which received the dorsal ends of the diductor muscles. In a few stocks (e.g., *Dolerorthis, Hesperonomia*), the notothyrial areas flanking the median partitions were elaborated into ridges for reception of the diductor bases, and in the orthidiellids, these grew high and became fused with the median partition to form a trilobed process. In most orthaceans, however, further modification involved the migration of the diductor bases onto the posterolateral surfaces of the median partition, which, in consequence, is either indented by muscle impressions, as in some plectorthids or, more commonly, is differentiated into a bulbous crenulated myophore surmounting a thickened shaft, as in many plaesiomyids. This latter arrangement is prevalent among enteletaceans with the myophore mostly fashioned in a bilobed or trilobed manner, thereby separating the diductor bases from each other.

The dorsal ends of the adductor muscles were implanted posteromedially within the brachial valve of the Orthidina and normally left a pair of posterior and anterior scars on the valve floor on either side of a median ridge (Figs. 188, 189). The ridge was built up as a low anterior extension of the notothyrial platform and only rarely did it culminate in a high median septum, as in the cremnorthids, skenidiids, and kayserellids. In such stocks as these, the median septum effectively divided the mantle cavity into two compartments, each of which presumably contained a variably developed brachium; and in *Hyposmyonia* it also affords support for an elevated platform of secondary shell which accommodated the dorsal adductor bases. The most unusual modification is undoubtedly that found in *Tropidoleptus*, in which posteriorly directed outgrowths from a median septum became contiguous with greatly extended brachiophore processes to complete a loop, presumably for support of the lophophore.

Despite the variation that is known to have occurred in the mantle canal systems of the Orthidina, one of the least specialized patterns, comprising saccate and digitate distributions in the pedicle and brachial valves, respectively, is easily the most common among the billingsellaceans and orthaceans (Fig. 189). A lemniscate arrangement in both valves, on the other hand, is prevalent among the enteletaceans (Fig. 188). Yet these differences between superfamilies is not mutually exclusive. The ventral and dorsal patterns of the enteletacean paurorthids, for example, are saccate and digitate like most orthaceans, while those of the finkelnburgiids (digitate and digitate) and some plectorthids (saccate and digitate but with the gonads pervading the entire mantles) approach the enteletacean condition.

The dominance of the modal morphological assemblages outlined above is, of course, a reflection of the trends that characterized orthoid evolution. The billingsellaceans were really important only in their rôle as probable ancestors of the more advanced orthaceans, because they comprise an insignificant group, with only the more specialized members, equipped with a relatively well-developed articulation and a strong notothyrial platform, surviving into the Ordovician. In contrast, contemporary orthaceans not only underwent a remarkable radiation but also gave rise to four groups which persisted into the Silurian and did not become entirely extinct until the end of Devonian times. Two of these groups, the orthids and dolerorthids, epitomize the survival of a more primitive organization, whereas the plectorthids and skenidiids display a number of relatively advanced features.

The conservative nature of orthid and dolerorthid morphogeny is illustrated by the persistence of unsupported brachiophores, a simple cardinal process consisting of a median partition, rarely with ancillary notothyrial ridges, and a relatively small, compact ventral muscle field, largely confined to the umbonal chamber. Indeed, the dolerorthids seem to have diverged from their presumed ancestors, the orthids, only through the development of an advanced digitate to apocopate dorsal mantle canal system and a long ventral interarea, because other changes were duplicated in the orthids. Thus, the acquisition or suppression of costellae in related costate and costellate stocks is found in both families, while the strongly lamellose ornamentation of the glyptorthinids was repeated in the productorthinids, which also represented the climax of the trend that led to obsolescence of the short orthid interareas.

It is likely that the plectorthids, and even the skenidiids, arose from the older finkelnburgiids in late Cambrian times, because the brachiophores of all three groups are supported by expanded bases and the cardinal process was normally differentiated into myophore and shaft. Nonetheless, the most distinctive features of both the plectorthids and skenidiids were already established by early Ordovician times, including the high ventral interarea, spondylium, and high dorsal median septum of the latter family. Apart from a conspicuous lengthening of the ventral interarea in some species of *Mimella*, these features were not developed in the plectorthids, although a considerable diversification in other morphological aspects took place. Hollow ribs are a common characteristic of the plectorthinids and rhactorthinids, which also show an incipient development of a lamellose ornamentation. But the most divergent trends affecting external form were those that led to the emergence of mucronate and strongly plicate platystrophiinids and the contemporary rostrate cyclocoelinids. Internally, the most conspicuous changes affected the disposition of the brachiophore bases. Those of most plectorthids are convergent to subparallel and are associated with well-developed fulcral plates, but those of the mid-Ordovician *Rhactorthis* were so widely divergent as to define the sockets without the ancillary growth of fulcral plates.

The changes within the skenidiids were relatively minor, because, once established, the main characters, like the spondylium and brachiophore bases convergent onto a high median dorsal septum, remained more or less stable throughout stock history. In the course of time, however, a migration of the brachiophores toward the median plane probably occurred, because each fulcral plate of the Devonian stock *Skenidium* was sufficiently large to carry a subsidiary ridge as an inner boundary to the socket. This development is reminiscent of the definition of the inner socket ridges that took place during the evolution of the rhynchonellids, and it is probably also significant that in many skenidiids, the brachiophores were equipped with processes long enough to have given support to the mouth segment of the lophophore.

Three stocks of punctate enteletaceans appeared in the Lower Ordovician and include the earliest representatives of one of the three most successful enteletacean groups, the dalmanellids. The accompanying stocks, the primitive orthid-like paurorthids and the aberrant rhynchonelliform angusticardiniids, became extinct before the end of Ordovician times, and although the former achieved wide distribution during its relatively brief history, the latter was apparently restricted to Europe. The dalmanellids, on the other hand, were not only ubiquitous and persistent into the Lower Carboniferous but were also ancestral to the two other major groups, the enteletids and the rhipidomellids, both of which survived to the end of the Permian. Other divergences from the dalmanellids include the widespread *Dicoelosia*, with its distinctive bilobed outline, and less successful Devonian forms which were characterized by the presence of a strong dorsal median septum. Both these structural modifications were directed toward the longitudinal division of the mantle cavity, possibly as an aid to the feeding mechanism.

The dalmanellids differ from their presumed finkelnburgiid ancestors in the endopunctate condition of the shell and, ultimately, in their advanced cardinalia. The cardinalia of the early forms varied greatly, particularly in the attitude of the bases of the brachiophores relative to their tops. This variability, however, was reduced in time because divergent bases became standard in the later forms. The converse was true of the cardinal process, which initially progressed rapidly from the simple orthacean ridge to an undifferentiated bilobed type but became dominantly trilobed in the later forms, although still variable even within a single species. In such characters as these, together with the relatively small, compact ventral muscle field, which extends little beyond the umbonal chamber, and the rare development of hollow costellae, the dalmanellids constitute the least specialized enteletacean stocks.

The enteletids are represented in the Middle Ordovician by the drabovinids, which differ from contemporary dalmanellids in their very fine, hollow costellae, anteriorly extended ventral muscle field, and distinctive cardinalia. The cardinalia include a slender cardinal process with a crenulated, rather than distinctly lobate myophore, delicate, commonly tusklike brachiophores supported laterally by well-developed fulcral plates and dorsally by bases which may converge toward the median ridge, but with ridgelike anterior extensions on the valve floor directed medially toward the center of the adductor field. In late Ordovician times, this group was replaced by the schizophoriinids, in which the anterior extensions of the brachiophore bases diverge to contain the adductor field laterally. An accompanying trend was the relative deepening of the brachial valve to produce a dorsibiconvex profile, instead of the ventribiconvex to subequally biconvex profile of the Middle Ordovician forms. In the Carboniferous, the enteletinids evolved from a schizophoriinid stock. These new forms are morphologically very distinct, with their strongly globose form, abundant radial plications superimposed on the fine radial ornament, the internal strengthening of the dental plates and the high ventral median septum. These aberrant forms persisted alongside the standard *Schizophoria* until the end of the Permian.

The rhipidomellids are not known in pre-Silurian rocks, and although the heterorthids do show many similarities which suggest close affinities (or parallel development) it is difficult to envisage *Rhipidomella* as being a direct descendant of the rather specialized heterorthid genera at present known. Like the enteletids, the rhipidomellids possess a fine ornament of hollow costellae. Externally they differ in their subcircular outline, the shortness of their hinge lines and the shallowness of their valves, and show little tendency to develop fold or sulcus. A marked difference from the other two major groups is seen in the very large ventral muscle field in which the adductors are enclosed by the large diductor scars, the latter condition appearing only rarely in the dalmanellids. The cardinalia, too, are quite distinct from those of contemporary enteletids, especially in the swollen and lobate nature of the cardinal process and the strength of the brachiophores which bound the sockets without fulcral plates.

Like the contemporary *Schizophoria, Rhipidomella* was another successful, stable stock, persisting with little modification from early Silurian to late Permian times, and although it gave rise to several genera, none of these enjoyed the same degree of success as their progenitor.

Superfamily BILLINGSELLACEA Schuchert, 1893

[*nom. transl.* WILLIAMS, herein (*ex* Billingsellidae SCHUCHERT, 1893, p. 152)]

Delthyrium covered by arched pseudodeltidium perforated by apical foramen, chilidium present but variably developed. Teeth primitive, with or without dental plates; ventral muscle field impressed on floor of pedicle valve; cardinal process absent or as simple ridge; sockets simple, socket ridges bladelike, unsupported; ventral mantle canal system saccate, dorsal probably digitate. Shell substance impunctate. *L.Cam.-L.Ord.*

Family BILLINGSELLIDAE Schuchert, 1893

[Billingsellidae SCHUCHERT, 1893, p. 152]

Interareas and hinge lines well developed, pseudodeltidium strong, perforate apically, chilidium present; teeth large, dental plates variably developed, ventral muscle field with widely divergent diductor scars and large subtriangular adductor track commonly extending well anterior of umbonal cavity; cardinal process simple ridgelike, socket ridges as widely divergent short, unsupported blades, sockets cuplike; ventral canal system saccate, with proximal parts of *vascula media* divergent, dorsal digitate. *M. Cam.-L.Ord.*

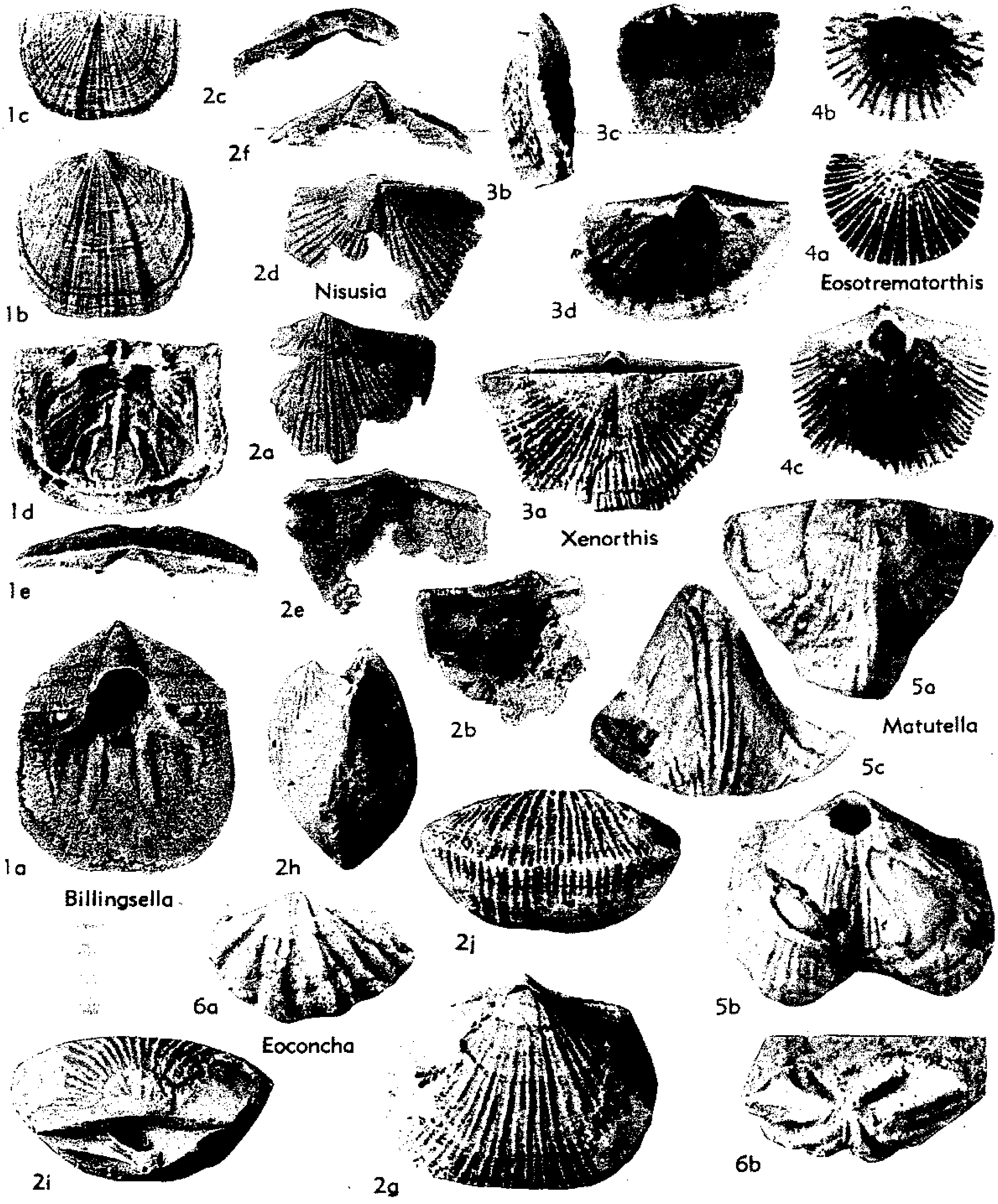


FIG. 191. Billingsellidae *(1, 3-4)*; Nisusiidae *(2, 5-6)* (p. *H*306-*H*307).

Billingsella Hall & Clarke, 1892, p. 230 [*_Orthis pepina_ Hall, 1863, p. 134; OD]. Subquadrate in outline, unequally biconvex, with long orthocline to apsacline interarea in deeper pedicle valve, subdued multicostellate to unequally parvicostellate. *M.Cam.-L.Ord.*, cosmop.——Fig. 191,*1*. *B. perfecta* Ulrich & Cooper, U.Cam.(Dry Creek), USA (Idaho-Wyo.); *1a*, ped. v. int., ×3; *1b*, ped. v. ext., ×2; *1c*, brach. v. ext., ×2; *1d,e*, brach. v. int., post., ×3 (825).

Cymbithyris Cooper, 1952, p. 5 [*_C. hami_; OD]. Like *Billingsella* but concavo-convex and lacking dental plates. *L.Ord.*, W.USA.

Eosotrematorthis Wang, 1955, p. 336 [*_E. sinensis_; OD]. Like *Billingsella* but strongly costellate. *L. Ord.*, China.——Fig. 191,*4*. *_E. sinensis_; *4a,b,* brach. v. ext., int., ×3; *4c,* ped. v., int., ×3 (852).

Xenorthis Ulrich & Cooper, 1936, p. 620 [**Strophomena stosei* Bassler, 1919, p. 250; OD]. Semioval in outline, subequally biconvex but with median fold in brachial valve; costellate and variably lamellose; interiors like those of *Billingsella* but dental plates rudimentary or absent; socket ridges rodlike, *?U.Cam.-L.Ord.,* E.USA-Ire.——Fig. 191,*3.* **X. stosei* (Bassler), U.Cam., USA (Md.); *3a,* brach. v. view of conjoined valves, ×2; *3b,* lat., ×2; *3c,* brach.v. int., ×4; *3d,* ped.v. int., ×3 (825).

Family NISUSIIDAE Walcott & Schuchert, 1908

[*nom. transl.* Schuchert & Cooper, 1931, p. 242 (*ex* Nisusiinae Walcott & Schuchert, 1908, p. 147)]

Interareas and hinge lines well developed, pseudodeltidium strong, foramen apical or anterior to apex through pedicle valve, chilidium variable; teeth rudimentary, dental plates absent, ventral muscle field rarely preserved but apparently with short adductor scar, and long divergent diductor scars; cardinal process absent or rudimentary; notothyrial platform rudimentary, socket ridges bladelike making acute angle with hinge line to define sockets; dorsal adductor scars, when present, as elongate impressions on either side of indistinct median ridge. *L.Cam.-M.Cam.*

Nisusia Walcott, 1905, p. 247 [**Orthisina festinata* Billings, 1861, p. 10; OD]. Subquadrate, subequally biconvex, with variable developed median sulcus in both valves, costellate, with beaded tuberculation along costellae at their intersections with strong concentric growth lines. *L.Cam.-M. Cam.,* N.Hemis.——Fig. 191,*2a-f.* **N. festinata* (Billings), L.Cam., USA(Va.); *2a-c,* brach. v. ext., int., post., ×2; *2d-f,* ped. v. ext., int., post., ×2 (176).——Fig. 191,*2g-j. N. deissi* Bell, M. Cam., USA(Mont.); *2g-j,* brach. v., ext., lat., ant. views of conjoined valves, ×2 (65).

Eoconcha Cooper, 1951, p. 4 [**E. austini*; OD]. Like *Nisusia* but coarsely costellate and with persistent median sulcus in brachial valve and fold in pedicle valve. *L.Cam.,* E.USA.——Fig. 191,*6.* **E. austini,* USA(Va.); *6a,* brach. v. ext., ×1.5; *6b,* post. view of ped. v. int. mold, ×2 (179).

Kotujella Andreeva, 1962, p. 87 [**K. calva*; OD]. Like *Matutella* but without radial ornamentation. *L.Cam.,* USSR.

Matutella Cooper, 1951, p. 6 [**M. clarki*; OD]. Subquadrate, with high narrow fold in brachial valve, costellate and sporadically imbricate; foramen large, excavated in floor of pedicle valve. *L.Cam.,* E.USA-USSR.——Fig. 191,*5.* **M. clarki,* USA(Va.); *5a,b,* brach. v. ext., ped. v. ext., ×2; *5c,* ant. view of ped. v., ×2 (179).

Superfamily ORTHACEA Woodward, 1852

[*nom. transl.* Walcott & Schuchert, 1908, p. 147 (*ex* Orthidae Woodward, 1852, p. 229)]

Delthyrium open, rarely constricted by deltidial plates or deltidium, chilidium rare; teeth simple, commonly with deep crural fossettes and supported by dental plates; ventral muscle field rarely supported by spondylium; cardinal process simple or differentiated, rarely absent; sockets simple or defined by fulcral plates, brachiophores commonly rodlike, less commonly with supporting bases convergent or divergent on floor of brachial valve; ventral mantle canal system commonly saccate, with proximal parts of *vascula media* convergent or divergent on to median plane, dorsal mantle canal system commonly digitate, rarely apocopate. Shell substance impunctate. *L.Cam.-U.Dev.*

Family EOORTHIDAE Walcott, 1908

[*nom. transl.* Schuchert & Cooper, 1931, p. 242 (*ex* Eoorthinae Walcott, 1908, p. 148)]

Interareas well developed, hinge lines wide, delthyrium and notothyrium open; teeth strong, commonly supported by receding dental plates, ventral muscle scar variably impressed on valve floor or pseudospondylium; cardinal process and notothyrial platform rudimentary, socket ridges widely divergent, bladelike, making acute angles with hinge line to define sockets; ventral mantle canal system saccate with proximal parts of *vascula media* divergent. *L. Cam.-L.Ord.*

Eoorthis Walcott, 1908, p. 102 [**Orthis remnicha* Winchell, 1886, p. 317; OD]. Subquadrate in outline; subequally biconvex, finely costellate, with variably superimposed secondary costation; ventral muscle field impressed on valve floor, subtriangular, with wide adductor track extending beyond diductor scars; cardinal process rudimentary, notothyrial platform scarcely raised off floor of brachial valve but supporting socket ridges, median ridge low. *U.Cam.,* USA-USSR.——Fig. 192,*4.* **E. remnicha* (Winchell), USA(Mont.); *4a,b,* brach. v. ext., int., ×2; *4c,* ped. v. int., ×3; *4d,* post. portion of brach. v., ×3 (65).

Apheorthis Ulrich & Cooper, 1936, p. 620 [**Eoorthis lineocostata* Walcott, 1924, p. 508; OD] [=*Apheoorthina* Havlíček, 1949, p. 99 (type, *A. ferrigena*)]. Like *Eoorthis* but with fascicostellate radial ornamentation and pseudospondylium in pedicle valve; cardinal process generally strong. *U.Cam.-L.Ord.,* N.Hemis.-S.Am.——Fig. 192,*1.* **A. lineocostata* (Walcott), U.Cam.(Manitou), USA(Colo.); *1a, 1b,* ped. v. ext., int., ×2; *1c,d,*

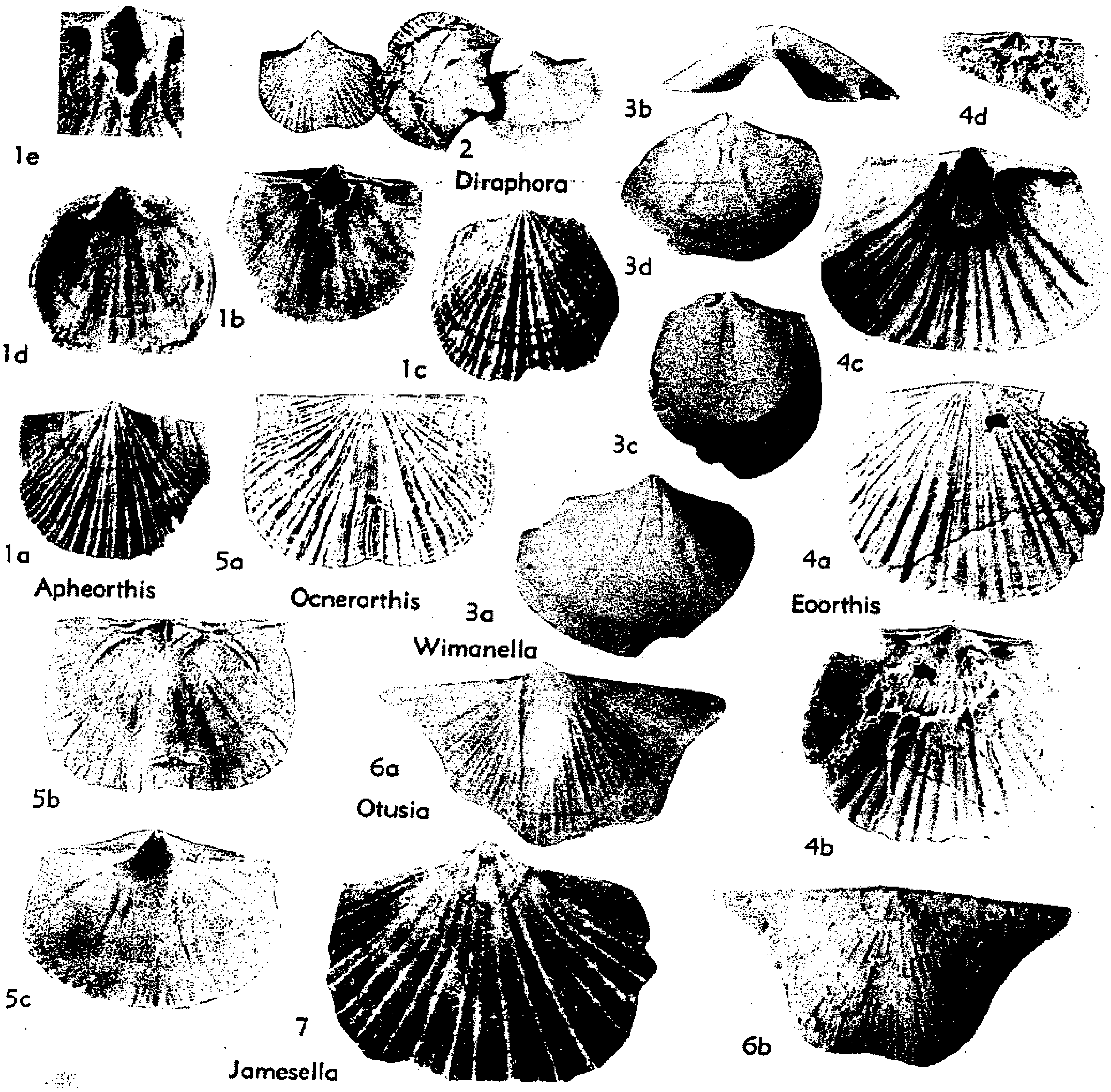


Fig. 192. Eorthidae (p. _H_307-_H_309).

brach. v. ext., int., ×2; _1e,_ post. portion of ped. v. enlarged to show pseudospondylium, ×4 (825).

Diraphora Bell, 1941, p. 243 [*_Eoorthis bellicostata_ Walcott, 1924, p. 505; OD]. Like _Wimanella_ but costellate. _M.Cam.,_ W.N.Am.——Fig. 192,_2._ *_D. bellicostata_ (Walcott), USA(Mont.); 2 ped. v. exts., 1 ped. v. int. mold, ×1.5 (65).

Jamesella Walcott, 1905, p. 252 [*_Orthis perpasta_ Pompeckj, 1896, p. 515; OD]. Like _Eoorthis_ but coarsely costellate. _?M.Cam.-U.Cam.,_ Eu. [The systematic position of this genus is uncertain. The type-species is reported as having an open delthyrium, but Walcott (1912, p. 733) described a pseudodeltidium in the species _Jamesella kuthani_ Pompeckj.]——Fig. 192,_7. J._ sp. cf. _J. perpasta_ (Pompeckj), U.Cam., Boh.; ped. v. int., ×2 (729).

Ocnerorthis Bell, 1941, p. 251 [*_O. cooperi_; OD]. Subquadrate in outline, unequally biconvex to plano-convex, costellate; interiors like those of _Eoorthis_ but without dental plates and with strong notothyrial platform and cardinal process. _U.Cam.-L.Ord.,_ N. Am.(W. USA)-Eu.(Czech.).——Fig. 192,_5._ *_O. cooperi,_ U.Cam., USA(Wyo.); _5a,b,_ brach. v. ext., int., ×3; _5c,_ ped. v. int., ×3 (65).

Otusia Walcott, 1905, p. 246 [*_Orthis sandbergi_ Winchell, 1886, p. 318; OD]. Transversely semioval and mucronate in outline, subequally biconvex, with strong median sulcus in brachial valve, costellate; interiors like those of _Eoorthis. U.Cam.,_ N.Am.(USA).——Fig. 192,_6._ *_O. sandbergi_ (Winchell), Mont.; _6a,_ ped. v. ext., ×4; _6b,_ brach. v. ext., ×3 (65).

Wimanella Walcott, 1908, p. 98 [*_W. simplex_; OD]. Subquadrate in outline, unequally biconvex, with pedicle valve more convex, shell surface without radial ornamentation; dental plates variably developed; delthyrial cavity with low short median ridge, adductor scars small, subcircular, flanked but not enclosed by divergent diductors; notothyrial platform absent, cardinal process absent or obscure. *?L.Cam., M.Cam.*, N.Am.——FIG. 192,*3*. *W. rossensis* RESSER, M.Cam., Can.(B.C.); *3a,b*, normal, post. views of ped. v. int. mold, ×3; *3c,d*, brach. v. int., ped. v. int., molds, ×2 (65).

Family PROTORTHIDAE
Schuchert & Cooper, 1931

[Protorthidae SCHUCHERT & COOPER, 1931, p. 242]

Interareas well developed, hinge lines wide, delthyrium and notothyrium open; teeth small, ventral muscle field supported by free spondylium; cardinal process and notothyrial platform variably developed, brachiophores bladelike and variably disposed; ventral mantle canal system saccate with proximal parts of *vascula media* divergent. *M.Cam.*

Protorthis HALL & CLARKE, 1892, p. 231 [**Orthis billingsi* HARTT in DAWSON, 1868, p. 644; OD]. Transversely subquadrate in outline, subequally biconvex, costellate; notothyrial platform shallow, median ridge absent, cardinal process absent, brachiophores short, widely divergent. *M.Cam.*, E.N.Am. ——FIG. 193,*7*. **P. billingsi* (HARTT), Can.(N. B.); ped. v. int., ×2.5 (729).

Arctohedra COOPER, 1936, p. 210 [**A. minima*; OD]. Like *Protorthis* but with subpyramidal pedicle valve and with well-developed cardinal process, notothyrial platform, and median ridge; brachiophores long and less divergent. *M.Cam.*, N. Am.——FIG. 193,*3a,b*. **A. minima*, USA(Alaska); *3a*, ped. v. ext., ×6; *3b*, brach. v. int., ×10 (176). ——FIG. 193,*3c,d*. *A. mertiei* COOPER, USA(Alaska); *3c,d*, ped. v. int., post., ×6 (176).

Loperia WALCOTT, 1905, p. 287 [**Protorthis (Loperia) dougaldensis*; OD]. Like *Protorthis* but convexo-concave and with low thick cardinal process. *M.Cam.*, E.Can.

Family HESPERONOMIIDAE
Ulrich & Cooper, 1936

[Hesperonomiidae ULRICH & COOPER, 1936, p. 621]

Interareas variable in length, hinge lines wide, delthyrium open, chilidium poorly developed; ventral muscle field subquadrate, extending beyond umbonal region; cardinal process as simple ridge, not ankylosed to variably developed notothyrial ridges, brachiophores short, rodlike; ventral mantle canal system saccate, dorsal digitate. *L.Ord.*

Hesperonomia ULRICH & COOPER, 1936, p. 621 [**H. planidorsalis*; OD]. Pedicle valve gently convex, brachial valve plane to concave, with feeble median sulcus, finely or rarely coarsely multicostellate; dental plates short, receding, diductor scars extending beyond but not enclosing adductor. *L.Ord.*, N.Am.——FIG. 193,*4*. **H. planidorsalis*, Sarbach, Can.(Alta.); *4a,b*, brach.v. ext., int., ×2; *4c*, ped. v. int., ×2 (825).

Hesperonomiella ULRICH & COOPER, 1936, p. 622 [**Protorthis porcias* WALCOTT, 1924, p. 504; OD]. Like *Hesperonomia* but unequally biconvex and with gentle median sulcus in shallower brachial valve. *L.Ord.*, N.Am.——FIG. 193,*8*. *H. minor* WALCOTT, Pogonip, USA(Utah); *8a*, ped. v. int., ×3; *8b*, brach. v. int., ×2 (189).

Jivinella HAVLÍČEK, 1949, p. 94 [**Orthis incola* BARRANDE, 1879, p. 94; OD]. Like *Hesperonomiella* but more coarsely costellate and with pseudospondylium in pedicle valve; notothyrial ridges strong. *L.Ord.*, Eu.(Czech.).

Family ORTHIDIELLIDAE
Ulrich & Cooper, 1936

[Orthidiellidae ULRICH & COOPER, 1936, p. 621]

Interareas and hinge lines of variable length, deltidium sporadically developed; ventral muscle field subtriangular, commonly extending in front of umbonal region, cardinal process developed as high ridge ankylosed to pair of notothyrial ridges simulating trilobed structure cemented to simple rod- or bladelike brachiophores by secondary shell; ventral mantle canal sytem saccate, with proximal parts of *vascula media* divergent, dorsal digitate. *L.Ord.-U.Ord.*

Orthidiella ULRICH & COOPER, 1936, p. 621 [**O. longwelli*; OD]. Unequally biconvex and wide-hinged, with deeper, commonly carinate pedicle valve and sulcate brachial valve costellate; delthyrium commonly restricted by apical plate simulating imperforate deltidium, teeth massive, with deep fossettes, dental plates short; diductor scars usually extending well beyond but not enclosing broad median adductor scar, brachiophores rodlike, variable in length, mainly encased in secondary shell. *L.Ord.*, N.Am.(W.USA).——FIG. 193,*5*. **C. longwelli*, Pogonip, Nev.; *5a*, brach. v. of conjoined valves, ×4; *5b*, ped. v. int., ×2; *5c*, ped. v. ext., ×3; *5d*, brach. v. int., ×4 (825).

Eostrophomena WALCOTT, 1905, p. 256 [**Strophomena (Eostrophomena) elegantula*; OD]. Concavo-convex, unequally parvicostellate with widely spaced costae and finely imbricate, delthyrium open, notothyrium with convex chilidium; teeth strong, dental plates short, ventral muscle field short and wide, slightly cordate, with diductor lobes extending slightly beyond anterior edge of wide adductor impressions, subperipheral rims strong in both valves; cardinal process simple, flanked by high chilidial plates which also support widely divergent rodlike brachiophores; dorsal adductor scars quadripartite, impressed on

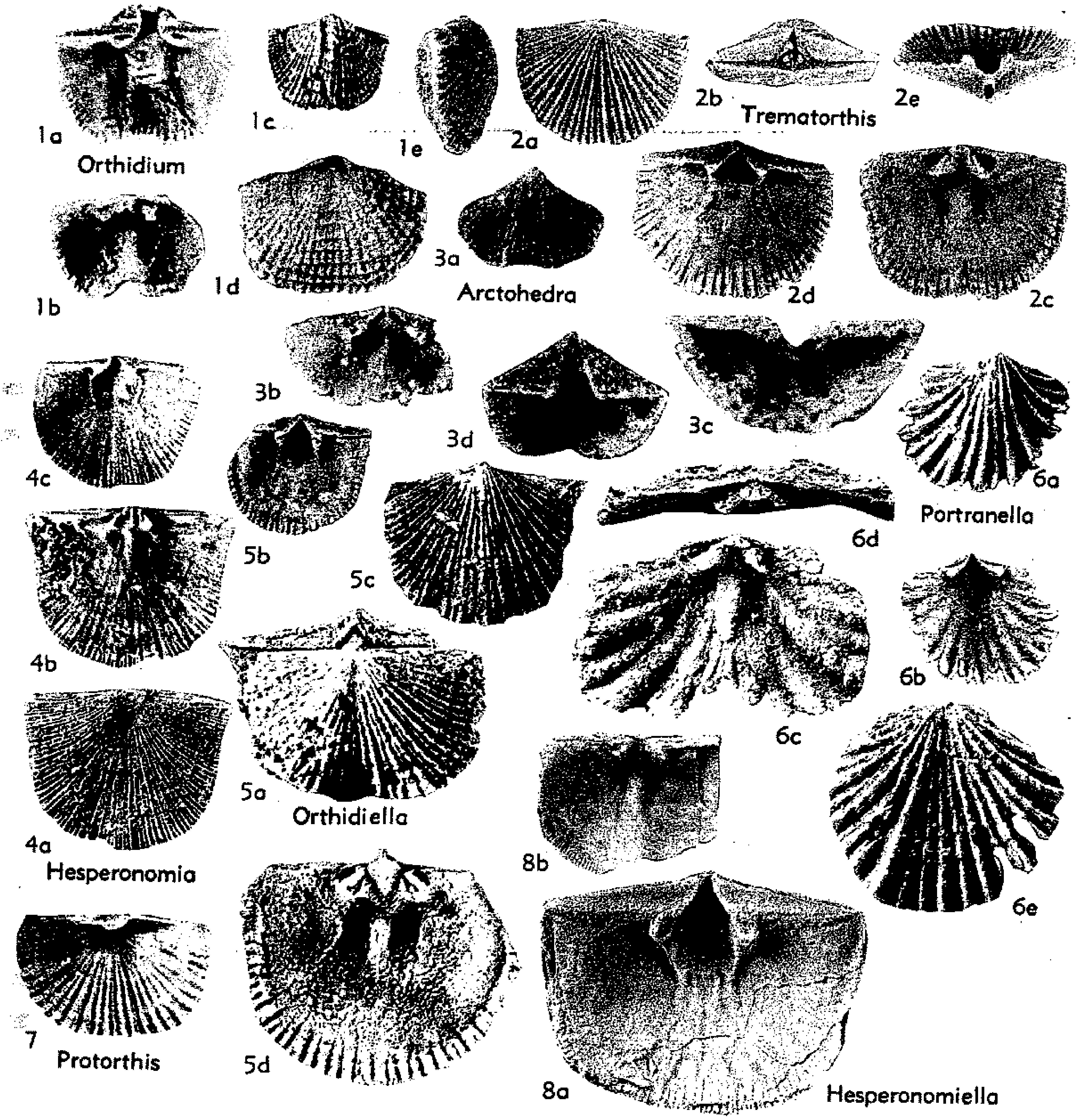


FIG. 193. Protorthidae _(3,7)_; Hesperonomiidae _(4,8)_; Orthidiellidae _(1-2, 5-6)_ (p._H309-H311_).

either side of median septum extending to subperipheral rim. [Good specimens recently collected by Dr. T. E. TJERNVIK show that this genus, which was previously known only as a ventral exterior and a poorly preserved dorsal interior, is an orthidiellid and differs from other members of that family in its parvicostellate ornamentation and concavo-convex profile.] _L.Ord._, Sweden.——FIG. 193A,_1_. *_E. elegantula_ (WALCOTT), Tremadoc. (_Apatokephalus serratus_ Zone), Västergötland _(1a,b)_, Biludden _(1c)_; _1a,b_, brach.v. int., ped.v. int., ×2; _1c_, exfoliated ped.v. ext., ×2 (Williams, n).

Orthidium HALL & CLARKE, 1892, p. 244 [*_Orthis gemmicula_ BILLINGS, 1862, p. 75; OD]. Strongly biconvex, commonly with high ventral umbo and like _Orthidiella_ but with strongly imbricate concentric ornamentation and without apical plate in delthyrium. _L.Ord._, N.Am.——FIG. 193,_1a-c_. *_O. gemmicula_ (BILLINGS), Can.(Que.); _1a,b_, ped. v. int., brach. v. int., ×6; _1c_, ped. v. ext., ×4 (825).——FIG. 193,_1d-e_. _O. bellulum_ (ULRICH & COOPER), Pogonip, USA(Nev.); _1d,e_, brach. v. ext., lat. view of conjoined valves, ×4 (189).

Portranella WRIGHT, 1964, p. 167 [*_P. angulocostellata_; OD]. Like _Orthidiella_ but with short hinge line, coarsely costellate ornamentation and without apical plate in delthyrium. _U.Ord._, Ire.

——Fig. 193,*6*. **P. angulocostellata*; *6a,b*, ped. v. ext., int., ×2.5; *6c,d*, brach. v. int., post. views, ×3; *6e*, brach.v. ext., ×2 (895b).

Trematorthis Ulrich & Cooper, 1938, p. 112 [**T. masoni*; OD]. Like *Orthidiella* but with perforate deltidium, bladelike brachiophores and lower cardinal process. *L.Ord.*, N.Am.——Fig. 193,*2*. **T. masoni*, Pogonip, USA(Nev.); *2a,b*, brach. v., post. views of conjoined valves, ×3; *2c*, brach. v. int., ×4; *2d,e*, normal, post. views of ped. v. int., ×3 (189).

Family ORTHIDAE Woodward, 1852

[Orthidae Woodward, 1852, p. 229]

Interareas and hinge lines of variable length, delthyrium open, notothyrium rarely covered by chilidium; teeth with crural fossettes, dental plates variably disposed, ventral muscle field short, not extending much beyond umbonal cavity, commonly suboval, median adductor scars not enclosed by diductors; cardinal process simple, ridgelike, brachiophores rodlike, unsupported; ventral mantle canal system saccate, dorsal mantle canal system saccate to digitate. *M.Cam.-L. Dev.*

Subfamily ORTHINAE Woodward, 1852

[*nom. transl.* Schuchert & Cooper, 1931, p. 243 (*ex* Orthidae Woodward, 1852, p. 229)]

Interareas short incurved, hinge lines wide; notothyrium not covered by chilidium; dental plates short, receding, divergent. *M.Cam.-L.Dev.*

Orthis Dalman, 1827, p. 93 [**O. callactis* Dalman, 1828, p. 93, 96; SD Davidson, 1853, p. 101]. Subquadrate to semioval in outline, plano-convex, dorsal sulcus subdued; costate, with costae and interspaces bearing fine parvicostellae; ventral muscle field suboval, with long adductor scars; cardinal process as thin ridge within notothyrial cavity, brachiophores divergent, dorsal adductor quadripartite, proximal parts of ventral *vascula media* adjacent to each other along median plane. *L.Ord.*, *?M.Ord.*, cosmop.——Fig. 194,*7*. **O. callactis* Dalman, L.Ord., USSR; *7a-c*, ped. v. brach. v., post. views of conjoined valves, ×2; *7d*, brach. v. int., ×2 (729).

Archaeorthis Schuchert & Cooper, 1931, p. 243 [**Orthis electra* Billings, 1865, p. 79; OD]. Subcircular in outline, with narrow hinge line, unequally biconvex, pedicle valve commonly subcarinate, dorsal sulcus variably developed, costellate; ventral interior like that of *Orthis* but with large teeth and elongate callosity extending in front of muscle field; brachiophores short, divergent, cardinal process absent. *L.Ord.*, *?M.Ord.*, N.Am.-Eu.——Fig. 194,*2*. *A. biconvexa* Cooper, Womble Sh., USA(Okla.); *2a,b*, ped. v. ext., int., ×3; *2c*, brach. v. int., ×3 (189).

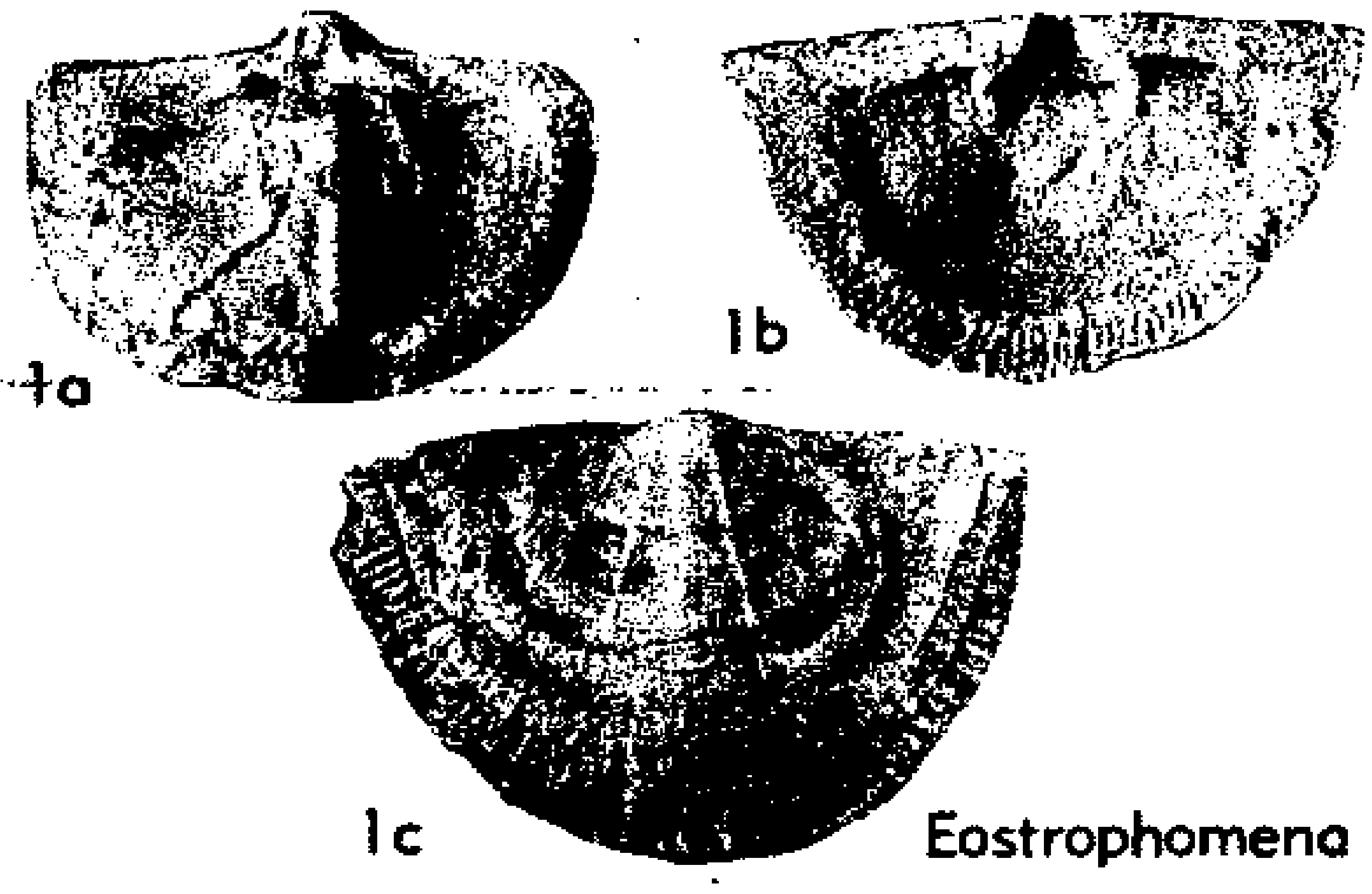


Fig. 193A. Orthidiellidae (p. *H*309).

Bohemiella Schuchert & Cooper, 1931, p. 242 [**Orthis romingeri* Barrande, 1879, p. 203; OD] [=*Shiragia* Kobayashi, 1935, p. 70 (type, *S. biloba*)]. Transversely suboval in outline, plano- to concavo-convex with broad shallow sulcus; costellate; teeth small, dental plates rudimentary, ventral muscle field small, subtriangular; cardinal process simple widening anteriorly, brachiophores long, triangular in section, proximal parts of ventral *vascula media* divergent. *M.Cam.*, Eu.(Czech.). ——Fig. 194,*1*. **B. romingeri* (Barrande); *1a*, brach.v. view of conjoined valves, ×2; *1b*, ped.v. int., mold, ×2; *1c*, brach.v. int., ×2 (729).

Cyrtonotella Schuchert & Cooper, 1931, p. 243 [**Orthis semicircularis* Eichwald, 1829, p. 276; OD] [=*Planidorsa* Schuchert & Cooper, 1931, p. 244 (type, *P. bella*)]. Semioval in outline, concavo-convex, costellate; teeth small, dental plates widely divergent, ventral muscle scar subrhomboidal; cardinal process thick, high, brachiophores short, subparallel with hinge line to define slitlike sockets; proximal parts of ventral *vascula media* adjacent to each other at median plane. *M.Ord.*, N.Hemis.——Fig. 194,*10a,b*. **C. semicircularis* (Eichwald), USSR; *10a,b*, brach.v., post. views of conjoined valves, ×1 (729).——Fig. 194,*10c,d*; 195,*1*. *C. kukersiana* (Wysogorski), CII, USSR; *10c*, brach.v. int., ×1; *10d*, ped.v. int. mold, ×1 (710); 195,*1*, brach.v. int., ×2.25 (621).

Glossorthis Öpik, 1930, p. 82 [**G. tacens*; OD]. Subquadrate in outline, unequally biconvex, with variable median sulcus in shallower brachial valve, costate to coarsely costellate; ventral muscle field impressed on tonguelike pseudospondylium between slightly divergent dental plates and supported anteriorly by low ridge; cardinal process ridgelike, flanked by low notothyrial ridges. *M.Ord.*, Eu.——Fig. 194,*8*. **G. tacens*, CII, Est.; *8a,b*, brach.v. ext., int., ×1.5; *8c*, ped.v. int., ×1.5 (729).

Lenorthis Andreeva, 1955, p. 69 [**L. girardi*; OD]. Like *Orthis* but unequally biconvex, with costate to coarsely costellate radial ornamentation and divergent proximal parts of ventral *vascula media*. *L.Ord.-M.Ord.*, cosmop.——Fig. 194,*9*. *L. mostellerensis* (Cooper), M.Ord.(Porterfield), USA (Ala.); *9a,b*, brach.v., lat., views of conjoined

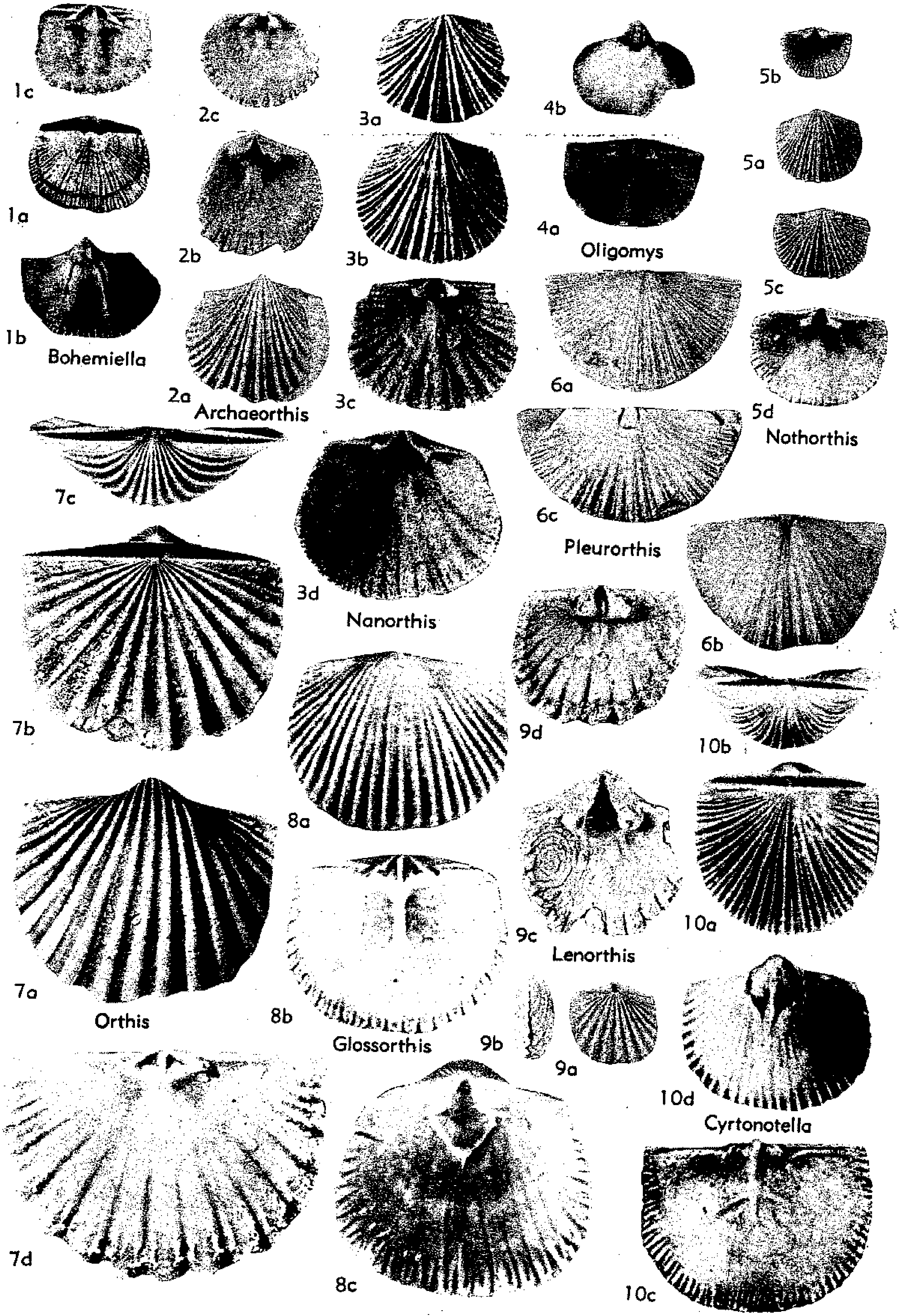


FIG. 194. Orthidae (Orthinae) (p. *H*311, *H*313).

valves, ×1; *9c,d,* ped.v. int., brach.v. int., ×2 (189).

Nanorthis Ulrich & Cooper, 1936, p. 621 [**Orthis hamburgensis* Walcott, p. 73; OD]. Like *Archaeorthis* but with small teeth, rudimentary cardinal process and notothyrial platform built up mainly around brachiophores to simulate supports; ventral muscle field with subtriangular adductor scars and narrow subcrescentic diductors; proximal parts of ventral *vascula media* divergent. *L.Ord.*, cosmop. ——Fig. 194,*3*. **N. hamburgensis* (Walcott), Canad., USA(Nev.-Colo.); *3a,b,* brach.v. ext., ped.v. ext., ×3; *3c,* brach.v. int., ×6; *3d,* ped.v. int., ×4 (825).

Nothorthis Ulrich & Cooper, 1938, p. 106 [**N. delicatula*; OD] [=*Althorthis* Andreeva, 1960, p. 288 (type, *A. kinderlensis*)]. Like *Nanorthis* but more transverse in outline and with well-developed notothyrial platform. *L.Ord.-M.Ord.*, N.Am.-Scot. ——Fig. 194,*5*. **N. delicatula,* L.Ord.(Canad.-Whiterock.), Can.(Que.); *5a-c,* ped.v. ext., ped.v. int., brach.v. ext., ×3; *5d,* brach.v. int., ×4.5 (189).

Oligomys Schuchert & Cooper, 1931, p. 243 [**Orthis exporrecta* Linnarsson, 1876, p. 12; OD]. Transversely oval in outline, unequally biconvex to plano-convex, finely parvicostellate with superimposed secondary costellation; teeth small, dental plates obsolete, ventral muscle field suboval, small, with adductor track widening anteriorly and extending beyond diductors; brachiophores short, widely divergent, cardinal process thickened anteriorly; proximal parts of ventral *vascula media* divergent, dorsal mantle canal system digitate. *M.Cam.*, NW.Eu.——Fig. 194,*4*. **O. exporrectus* (Linnarsson), Sweden; *4a,* brach.v. int., ×2.5; *4b,* ped.v. int. mold, ×2.5 (729).

Orthambonites Pander, 1830, p. 80 [**O. transversa;* SD Dall, 1877, p. 51]. Like *Orthis* but biconvex and with costate to coarsely costellate radial ornamentation. *L.Ord.-M.Ord.*, cosmop.——Fig. 196,*4*. *O. calligramma* Dalman, M.Ord., USSR; *4a-c,* brach.v., lat., post. views of conjoined valves, ×2 (729); *4d,* ped.v. int., ×1; *4e,* brach.v. int., ×2 (710).

Orthostrophia Hall, 1883, pl. 36, figs. 32-34 [**Orthis strophomenoides* Hall, 1857, p. 46; OD]. Subquadrate, subequally biconvex to resupinate, with median dorsal sulcus, costellate; ventral muscle field short, subtriangular, with wide adductor track; cardinal process expanded anteriorly, commonly flanked by discrete notothyrial ridges; mantle canal systems saccate but ventral *vascula media* short, divergent, with arcs limited to posterior half of valve and giving rise to branches anteriorly. *M.Sil.-L.Dev.*, N.Am.-Eu.——Fig. 196, *2*. *O. strophomenoides parva* Amsden, L.Dev. (Haragan), USA(Okla.); *2a,b,* ped.v., ant. views of conjoined valves, ×1; *2c,* lat. view of conjoined valves, ×1; *2d,e,* ped.v. int., portion of brach.v. int., ×2 (106).

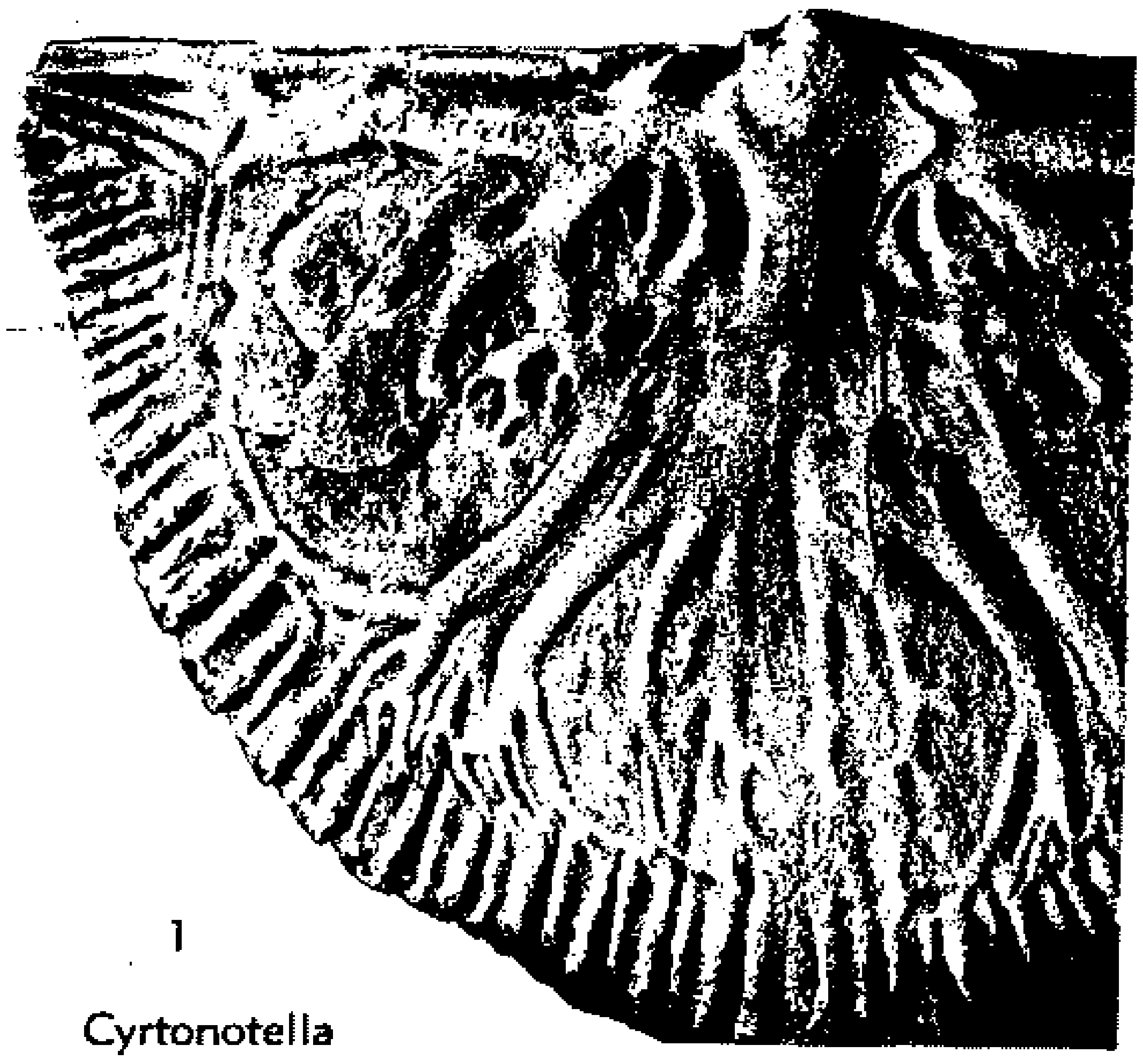


Fig. 195. Orthidae (Orthinae) (p. *H*311).

Pleurorthis Cooper, 1956, p. 329 [**P. fascicostellata*; OD]. Transversely subquadrate in outline, subequally biconvex, brachial valve commonly deeper, with median sulcus passing into broad median fold in adult shells; multicostellate to fasciocostellate; interiors like those of *Orthis*. *L.Ord.*, E.N.Am. ——Fig. 194,*6*. **P. fascicostellata,* Whiterock, Can.(Que.); *6a,* brach.v. ext., ×1; *6b,c,* brach.v. int., ped.v. int. molds, ×2 (189).

Prantlina Havlíček, 1949, p. 250 [*Orthis desiderata* Barrande, 1848, p. 59; OD]. Like *Taphrorthis* but with very gently convex to plane, vaguely sulcate brachial valve; cardinal process ridgelike, strong. *L.Ord.*, Eu.(Czech.).

Ranorthis Öpik, 1939, p. 119 [**R. norvegica*; OD]. Like *Nanorthis* but elongately semioval in outline with carinate pedicle valve, and gently convex to plane brachial valve with sharp, narrow median sulcus. *L.Ord.*, Eu.——Fig. 196,*5*. **R. norvegica,* Expansusschiefer, Nor.; *5a,* brach.v. ext., ×4; *5b,* brach.v. int. mold, ×4; *5c,* ped.v. int. mold, ×8 (622).

Riograndella Kobayashi, 1937, p. 422 [**R. subcircus*; OD]. Like *Taphrorthis* but with subparallel dental plates and without median ridge in elongately oval ventral muscle field. Age unknown, Bol.

Sinorthis Wang, 1955, p. 327 [**S. typica*; OD]. Like *Prantlina* but with elongately oval ventral muscle field and proximal parts of ventral *vascula media* divergent. *L.Ord.*, China.——Fig. 196,*3*. **S. typica,* Fenhsiang; *3a,* brach.v. view of conjoined valves, ×3; *3b,c,* ped.v. int., brach.v. int., ×3 (852).

Taphrorthis Cooper, 1956, p. 326 [**T. emarginata*; OD]. Subquadrate in outline, unequally biconvex with less deep, medianly sulcate brachial valve, costellate; teeth small, dental plates, short, divergent, ventral muscle field subcordate, divided

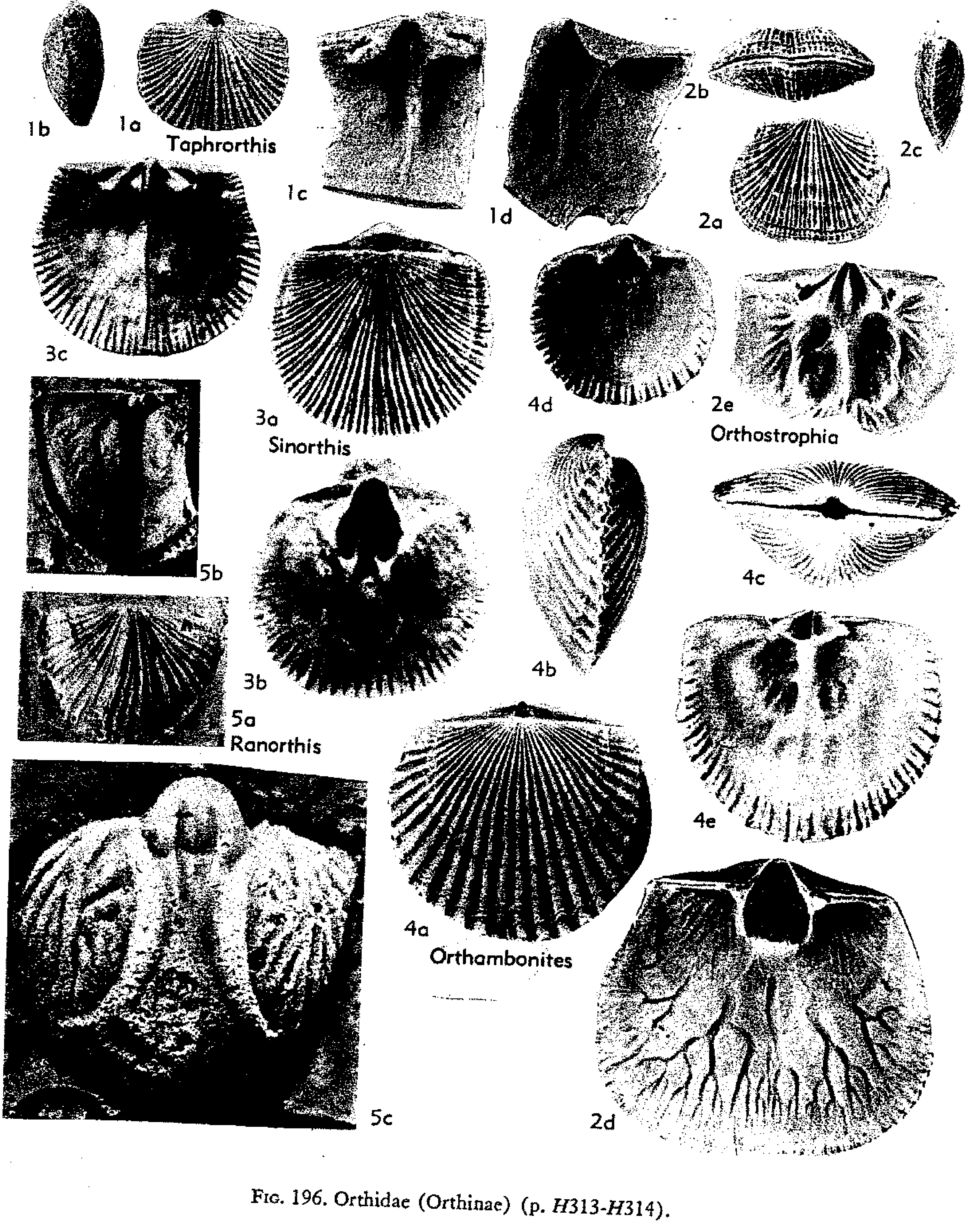


Fig. 196. Orthidae (Orthinae) (p. *H*313-*H*314).

by low median ridge prolonged anteriorly; cardinalia like those of *Orthis* with poorly developed cardinal process; proximal parts of ventral *vascula media* adjacent to each other at median plane. *M.Ord.*, N.Am.-Scot.-Ire.——Fig. 196,*1*. **T. emarginata*, Porterfield, USA(Tenn.-Ala.); *1a,b*, brach. v., lat. views of conjoined valves, ×2; *1c*, fragment of brach.v. int., ×3; *1d*, fragment of ped.v. int., ×2 (189).

Subfamily PRODUCTORTHINAE Schuchert & Cooper, 1931

[Productorthinae Schuchert & Cooper, 1931, p. 243]

Imbricate to strongly lamellose, interareas very short to vestigial, hinge lines wide; notothyrium commonly covered with variably developed chilidium; dental plates short, receding, divergent. *Ord.*

Productorthis Kozlowski, 1927, p. 9 [**Productus obtusus* Pander, 1830, p. 87; OD]. Subquadrate, concavo-convex to unequally biconvex, pedicle valve deep, with swollen umbo, interareas vestigial, costate to costellate, with greatly extended and crowded concentric lamellose frills; teeth small, dental plates subparallel, short, bounding high callus impressed by wide adductor scars and narrow diductors that also encroach on to dental plates; cardinal process high, thick, bearing di-

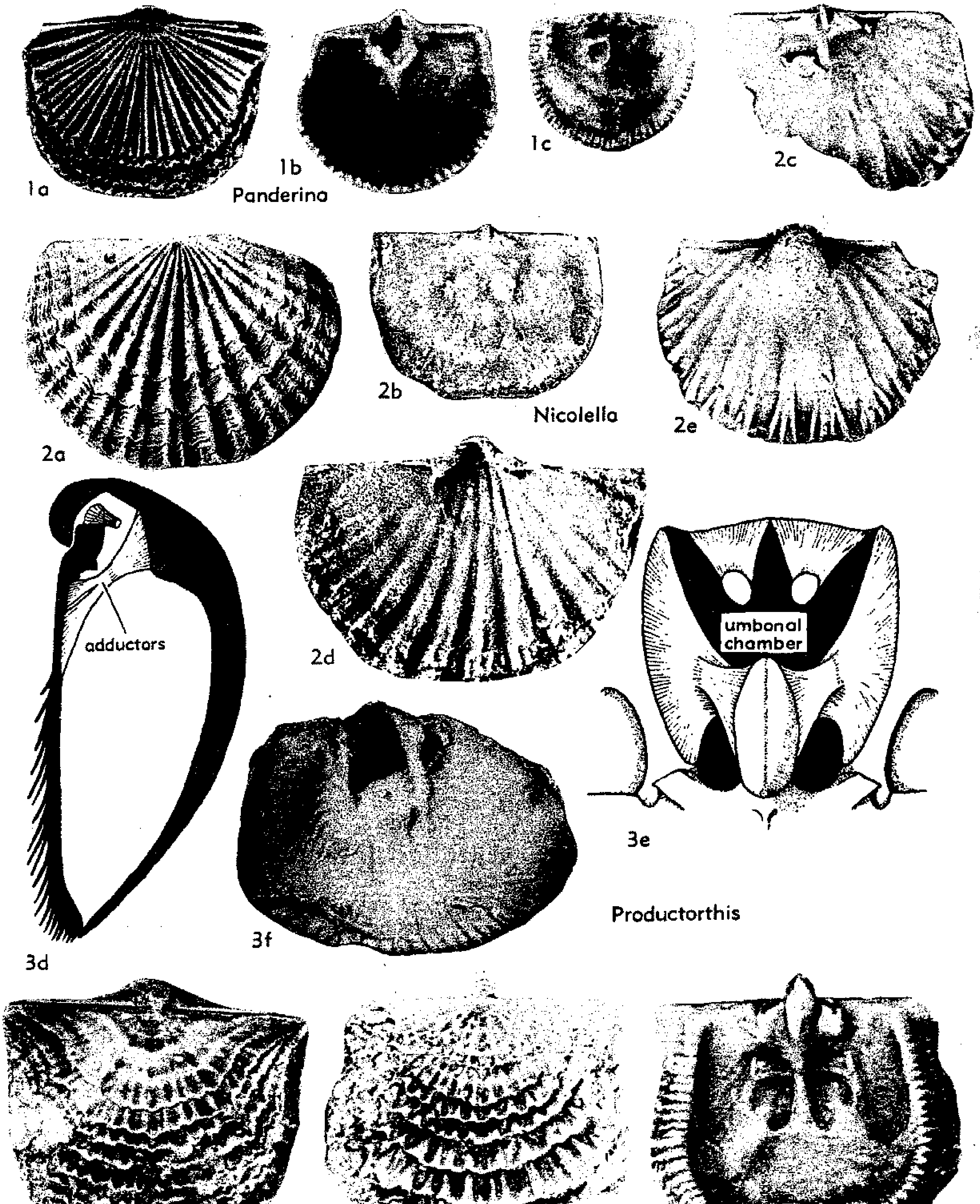


Fig. 197. Orthidae (Productorthinae) (p. *H*315-*H*316).

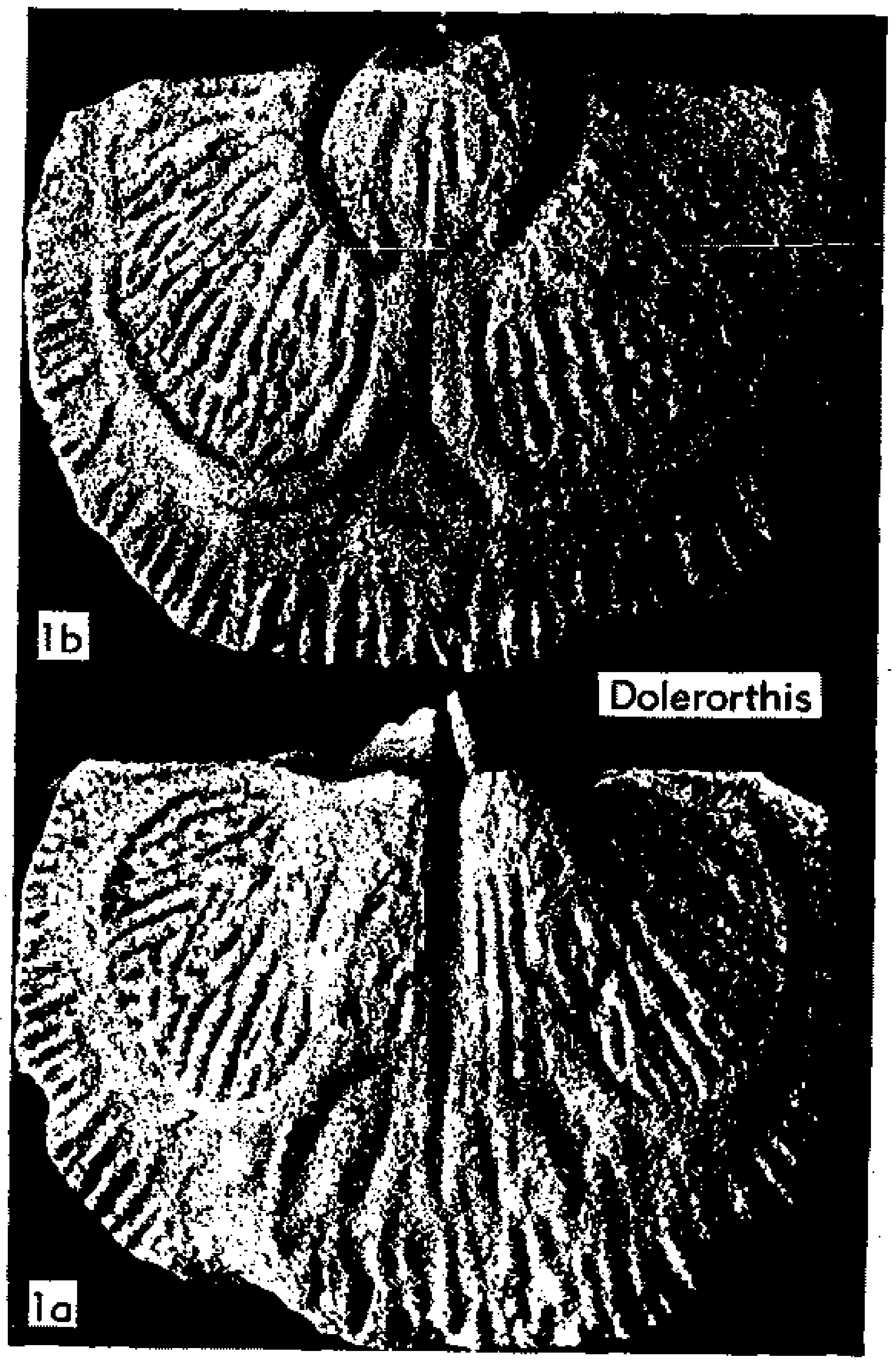


FIG. 198. Dolerorthidae (Dolerorthinae) (p. *H*316).

ductor scars posterolaterally, chilidium vestigial, brachiophores short, encased in secondary shell to define cup-shaped sockets; dorsal adductors scars quadripartite, with lobate anterior pair; ventral mantle canal system saccate, with *vascula media* greatly divided medianly. *L.Ord.-M.Ord.*, cosmop. ——FIG. 197,*3a-c*. *P. parallela* PANDER, L.Ord., USSR; *3a*, brach.v. view of conjoined valves, ×3; *3b,c*, brach.v. ext., int., ×3 (729).——FIG. 197, *3d-f*. *P. mitchelli* WILLIAMS, M.Ord., Eire; *3d*, reconstructions showing inferred disposition of muscles in median-lat. view, ×3; *3e*, ant. view of umbonal chamber, ×6; *3f*, vent. int., ×2.5 (876).

Nicolella REED, 1917, p. 860 [**Orthis actoniae* SOWERBY, 1839, p. 639; OD]. Externally like *Productorthis* but with less convex pedicle valve and relatively well-developed interareas, chilidium strong; dental plates divergent, ventral muscle field subcordate, diductor scars not enclosing narrow adductors; cardinal process high, brachiophores widely divergent, anterior adductor scars not bilobed. *M.Ord.-U.Ord.*, Eu.-N.Am.——FIG. 197,*2*. **N. actoniae* (SOWERBY), U.Ord.(Acton.), Eng.; *2a*, brach.v. ext., ×1.5; *2b,c*, brach.v. int., ×1.5; *2d,e*, ped.v. int., ped.v. int. mold, ×1.5 (Williams, n).

Panderina SCHUCHERT & COOPER, 1931, p. 243 [**Productus abscissus* PANDER, 1830, p. 86; OD]. Like *Productorthis* but with very short incurved ventral interarea and narrow plane dorsal interarea; cardinal process low, not united with short brachiophores. *L.Ord.*, Eu.-USSR.——FIG. 197,*1a*. **P. abscissa* (PANDER), USSR; *1a*, brach.v. view of conjoined valves, ×2 (729).——FIG. 197,*1b,c*. *P. tetragonum* (PANDER), B_1, USSR; *1b,c*, ped.v. int., brach.v. int., ×1.5 (729).

Subfamily PORAMBORTHINAE Havlíček, 1950

[*nom. transl.* WILLIAMS, herein (*ex* Poramborthidae HAVLÍČEK, 1950, p. 58)]

Interareas short, incurved, hinge lines wide; notothyrium not covered by chilidium; dental plates long, convergent on to floor of pedicle valve. *L.Ord.*

Poramborthis HAVLÍČEK, 1949, p. 107 [**P. klouceki*; OD]. Semicircular in outline, subequally biconvex, finely multicostellate; ventral muscle field long, with narrow adductor scar; cardinal process and notothyrial platform rudimentary; proximal parts of *vascula media* divergent. *L.Ord.*, Eu.(Czech.).

Family DOLERORTHIDAE Öpik, 1934

[Dolerothidae ÖPIK, 1934, p. 180]

Ventral interareas long; hinge lines wide; teeth with oblique fossettes, supported by receding dental plates, ventral muscle field elongately subtriangular to subcordate with rounded anterior margins of diductor scars commonly extending beyond but not enclosing lanceolate adductors usually contained by low ridges; cardinal process ridgelike, rarely absent, brachiophores commonly as pair of long blades, triangular in section; ventral mantle canal system saccate with *vascula media* converging medianly. *L.Ord.-U.Sil.*

Subfamily DOLERORTHINAE Öpik, 1934

[Dolerorthinae ÖPIK, 1934, p. 180]

Strong concentric imbrication not developed, delthyrium and notothyrium open; dorsal mantle canal system apocopate. *M. Ord.-U.Sil.*

Dolerorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis interplicata*; OD]. Unequally biconvex to convexo-concave, costate to costellate; cardinal process flanked by variably developed notothyrial ridges. *M.Ord.-U.Sil.*, N.Hemis.——FIG. 199,*5*. *D. duftonensis* (REED) *prolixa* WILLIAMS, Caradoc, Wales; *5a,b*, ped.v., brach.v. exts., ×1.5; *5c*, brach. v. int., ×2 (Williams, n).——FIG. 198,*1*. *D. rustica osiliensis* (SCHRENK), U.Sil.(Jaani Stage), Balt.; *1a,b*, dors., vent. int. molds, ×3 (621).

Subfamily HESPERORTHINAE Schuchert & Cooper, 1931

[Hesperorthinae SCHUCHERT & COOPER, 1931, p. 243]

Strong concentric imbrication not devel-

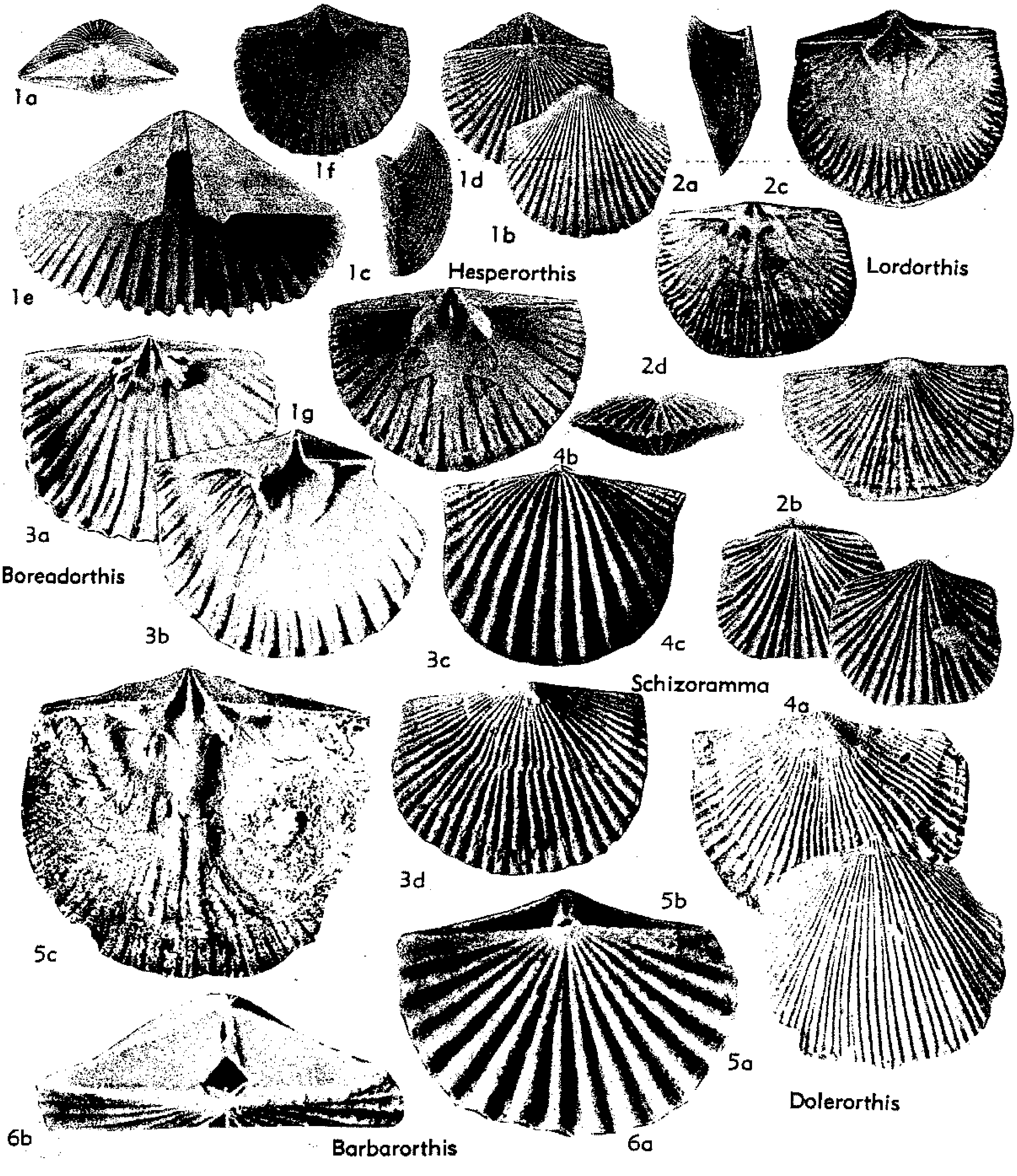


FIG. 199. Dolerorthidae (Dolerorthinae) *(5)*, (Hesperorthinae) *(1-4,6)* (p. *H*316-*H*318).

oped, apical plate or deltidium and antigydium sporadically developed; dorsal mantle canal system digitate. *L.Ord.-U.Sil.*

Hesperorthis SCHUCHERT & COOPER, 1931, p. 244 [**Orthis tricenaria* CONRAD, 1843, p. 333; OD]. Plano- to gently concavo-convex, with high pedicle valve, costate, with very fine parvicostellae in the interspaces; apical plate and antigydium commonly developed especially in later species; median parts of ventral *vascula media* long, arcuate branches subperipheral. *L.Ord.-U.Sil.*, N.Hemis.——FIG. 199,*1a-e*. **H. tricenaria* (CONRAD), L.Ord., USA; *1a-d*, post., ped.v., lat., brach.v. views of conjoined valves, ×1; *1e*, post. view of ped.v., ×2 (189).——FIG. 199,*1f,g*. *H. australis* COOPER, L. Ord., USA(Tenn.); *1f*, ped.v. int., ×1; *1g*, brach. v. int., ×2 (189).

Barbarorthis ÖPIK, 1934, p. 183 [**B. foramenifera*; OD]. Like *Hesperorthis* but with perforate deltidium covering delthyrium. *U.Ord.*, Eu.——FIG. 199,6. **B. foramenifera*, F₁, Est.; *6a,b*, brach.v., post. views of conjoined valves, ×5 (621).

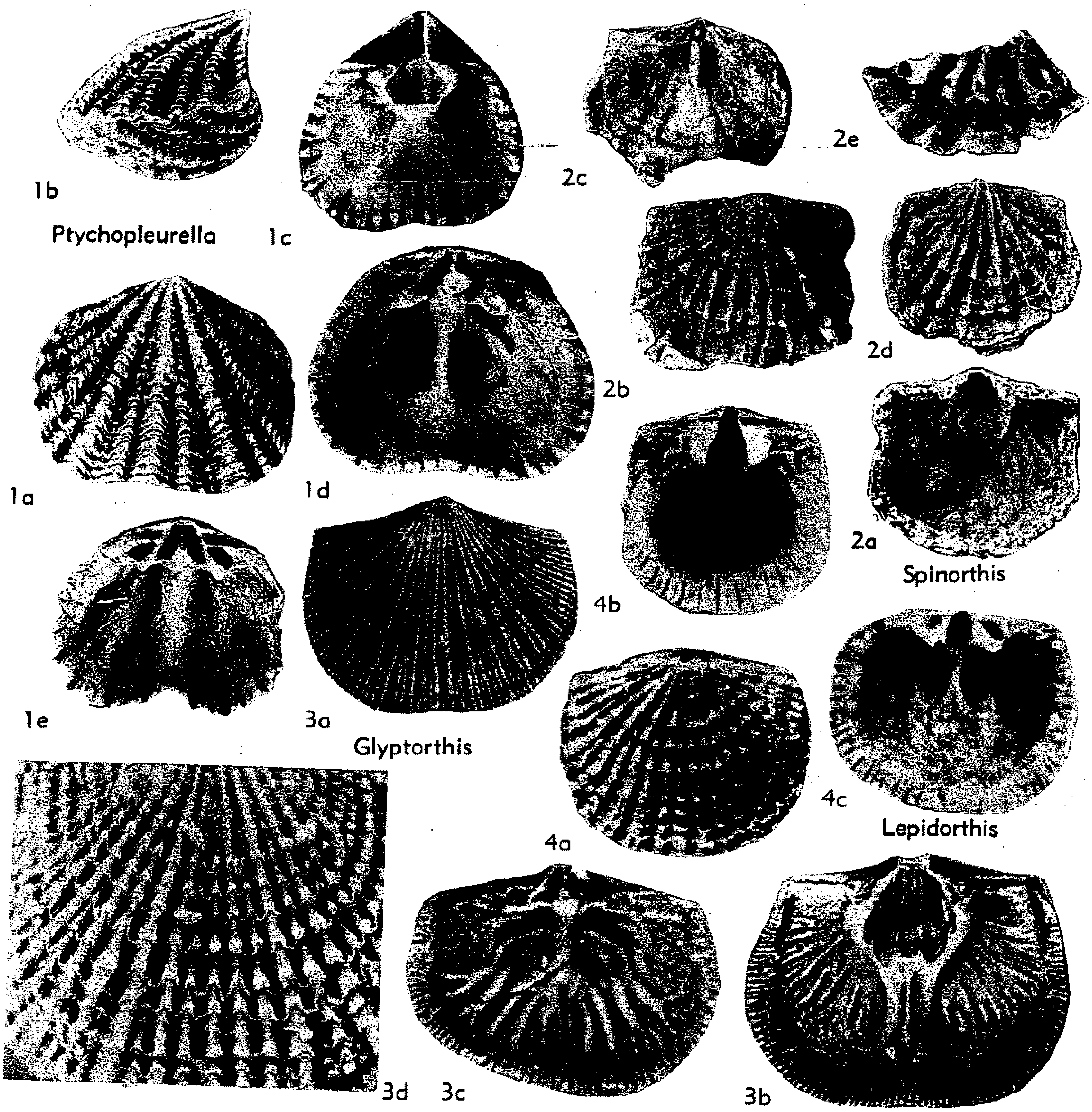


Fig. 200. Dolerorthidae (Glyptorthinae) (p. *H*319).

Boreadorthis Öpik, 1934, p. 184 [**B. crassa*; OD]. Like *Hesperorthis* but with strongly and uniformly convex brachial valve. *U.Ord.*, Eu.——Fig. 199,*3*. **B. crassa,* F_1, Est.; *3a,b,* brach.v. int., ped. v. int., ×2; *3c,* brach.v. ext., ×1.5 (621).——Fig. 199,*3d*. *B. recula aequivalvata* Öpik, F_1, Est.; ped. v. ext., ×1.5 (621).

Lordorthis Ross, 1959, p. 446 [**L. variabilis*; OD]. Like *Hesperorthis* but with plane brachial valve of young shells becoming convex in adult shells and costellate radial ornamentation. *U.Ord.*, N.Am. (W.USA).——Fig. 199,*2*. **L. variabilis*; *2a,* lat. view of conjoined valves, ×1; *2b,* ped.v. ext., ×1; *2c,d,* ped.v. int., brach.v. int., ×1 (678).

Schizoramma Foerste, 1909, p. 77 [**Hebertella (Schizonema) fissistriata*; OD] [=*Schizonema* Foerste, 1909, p. 77 (type, *H. (Schizonema) fissistriata*)]. Like *Lordorthis* but with plane to uniformly convex and impersistently sulcate brachial valve and variably developed notothyrial ridges flanking cardinal process; median parts of ventral *vascula media* variable in length. *Sil.,* N.Hemis. ——Fig. 199,*4*. *S. hami* Amsden, U.Sil.(Henryhouse), USA(Okla.); *4a-c,* ped.v., ant., brach.v. views of conjoined valves, ×1 (30).

Subfamily GLYPTORTHINAE
Schuchert & Cooper, 1931

[Glyptorthinae Schuchert & Cooper, 1931, p. 243]

Costate to costellate, with strong concentric imbrication disposed as frills or even drawn out as spines; delthyrium and notothyrium open, dorsal mantle canal system digitate. *L.Ord.-U.Sil.*

Glyptorthis Foerste, 1914, p. 257 [**Orthis insculpta* Hall, 1847, p. 125; OD]. Unequally biconvex, with deeper brachial valve bearing strong median sulcus, delthyrium open, triangular, ornamentation variably costellate, with strong imbrication commonly produced into frills; ventral adductor scars broad, rarely longer than diductor scars and commonly raised on median elevation of secondary shell extending forward into anterior half of valve; cardinal process ridgelike. *M.Ord.-L.Sil.*, N.Hemis.——Fig. 200,*3a-c*. **G. insculpta* (Hall), U.Ord.(Richmond.), USA(Ohio); *3a-c*, ped.v. ext., ped.v. int., brach.v. int., ×1.5 (729).——Fig. 200,*3d*. *G. costellata* Cooper, M.Ord. (Bromide), USA(Okla.); portion of brach. surface, ×4 (189).

Eridorthis Foerste, 1909, p. 223 [**Plectorthis (Eridorthis) nicklesi* Foerste, 1909; SD Schuchert & Le Vene, 1929, p. 58]. Like *Glyptorthis* but with dorsal median sulcus replaced by fold in adult shells. *M.Ord.-L.Sil.*, N.Am.-Eu.

Lepidorthis Wang, 1955, p. 330 [**L. typicalis*; OD]. Like *Glyptorthis* but without cardinal process. *L. Ord.*, China.——Fig. 200,*4*. **L. typicalis*, Fenhsiang; *4a*, brach.v. view of conjoined valves, ×3.5; *4b,c*, ped.v. int., brach.v. int., ×2.5 (852).

Ptychopleurella Schuchert & Cooper, 1931, p. 244 [**Orthis bouchardi* Davidson, 1847, p. 64; OD]. Like *Glyptorthis* but with subpyramidal pedicle valve and narrowly triangular delthyrium commonly restricted by lateral plates; radial ornamentation commonly costate or coarsely costellate, with raised costae bounding dorsal sulcus. *M.Ord.-U.Sil.*, cosmop.——Fig. 200,*1*. **P. bouchardi* (Davidson), Wenlock, Eng.; *1a,b*, ped.v., lat. views of conjoined valves, ×3.5; *1c*, ped.v. int., ×3; *1d,e*, brach.v. ints., ×2.5, ×3.5 (Williams, n).

Spinorthis Wright, 1964, p. 184 [**S. geniculata*; OD]. Like *Glyptorthis* but with adult shell geniculated dorsally and lamellae prolonged into suberect spines; dorsal interarea reduced. *U.Ord.*, Eire.——Fig. 200,*2*. **S. geniculata*; *2a,b*, ped.v. int., ext., ×2; *2c,d*, brach.v. int., ext., ×2; *2e*, fragment of shell, ×3.5 (895b).

Family PLAESIOMYIDAE Schuchert, 1913

[*nom. transl. et correct.* Williams, herein (*ex* Plaesiomiinae Schuchert, 1913, p. 382)] [=Dinorthidae Schuchert & Cooper, 1931, p. 244]

Ventral interareas variably disposed, hinge lines wide; delthyrium and notothyrium rarely covered by deltidium and chilidium; ventral muscle field subquadrate, extending well beyond umbonal region; mantle canal system saccate, with proximal parts of *vascula media* short, divergent. *Ord.*

Subfamily PLAESIOMYINAE Schuchert, 1913

[*nom. correct.* Williams, herein (*pro* Plaesiomiinae Schuchert, 1913, p. 382)]

Mostly convexo-concave, with short rodlike brachiophores and cardinal process well differentiated into crenulated myophore and shaft. *Ord.*

Plaesiomys Hall & Clarke, 1892, p. 196 [**Orthis subquadrata* Hall, 1847, p. 126; OD]. Convexo-concave to unequally biconvex, pedicle valve commonly shallowly sulcate, costate to costellate, deltidium absent; teeth with oblique fossettes, dental plates short; ventral muscle field bilobed anteriorly, with diductor scars enclosing central oval adductors; adjustors prominent. *M.Ord.-U.Ord.*, cosmop.

P. (Plaesiomys). Variably convexo-concave, ventral interarea apsacline; radial ornamentation costellate. *M.Ord.-U.Ord.*, N.Hemis.——Fig. 201,*5*. **P. (P.) subquadrata* (Hall), U.Ord.(Richmond.), USA(Ohio); *5a,b*, ped.v., lat. views of conjoined valves, ×1; *5c,d*, brach.v. ext., int., ×1; *5e*, ped.v. int., ×1 (740).

P. (Dinorthis) Hall & Clarke, 1892, p. 195 [**Orthis pectinella* Conrad & Emmons, 1842, p. 394; OD] [=*Diorthis* Kobayashi, 1937, p. 12 (*nom. nud.*)]. Resembling *P. (Plaesiomys)* but radial ornamentation costate, exceptionally with incipient costellae. *M.Ord.*, N.Hemis.——Fig. 201, *3a,b*. **P. (D.) pectinella* (Conrad), Trenton., E.USA.; *3a*, ped.v. view of conjoined valves, ×1; *3b*, brach.v. ext., ×1 (740).——Fig. 201,*3c-e*. *P. (D.) holdeni* (Willard), Elway, USA (Tenn.); *3c*, lat. view of conjoined valves, ×1; *3d,e*, ped. v. int., brach.v. int., ×2 (189).

P. (Pionorthis) Schuchert & Cooper, 1931, p. 244 [**Orthis sola* Billings, 1866, p. 12; OD]. Like *P. (Plaesiomys)* but subequally biconvex. U.Ord., N.Am.——Fig. 201,*4*. *P. (P.) sola* (Billings), Richmond., USA(Ind.); lat. view of conjoined valves, ×1.5 (729).

P. (Retrorsirostra) Schuchert & Cooper, 1931, p. 244 [**Orthis carleyi* Hall, 1847, p. 120; OD]. Like *P. (Plaesiomys)* but with procline ventral interarea. *U.Ord.*, N.Hemis.——Fig. 201,*6*. **P. (R.) carleyi* (Hall), Richmond., USA(Ohio); *6a,b*, ped.v. lat. views of conjoined valves, ×1; *6c*, ped.v. int., ×1 (740).

Austinella Foerste, 1909, p. 224 [**Orthis kankakensis* McChesney, 1861, p. 77; SD Bassler, 1915, p. 1002]. Like *Plaesiomys (Pionorthis)* but with linear adductor track in pedicle valve broadening anteriorly and not enclosed by diductor scars. *U. Ord.*, N.Am.-Eu.

Campylorthis Ulrich & Cooper, 1942, p. 621 [**Strophomena deflecta* Conrad, 1843, p. 332; OD]. Like *Plaesiomys* and convexo-concave to unequally biconvex but finely costellate and with well-developed, apically perforate deltidium and chilidium. *M.Ord.*, USA-Scot.——Fig. 201,*1*. **C. deflecta* (Conrad), Platteville, USA(Wis.); *1a-d*, post., brach.v., lat., ped.v. views of conjoined valves, ×1 (189).

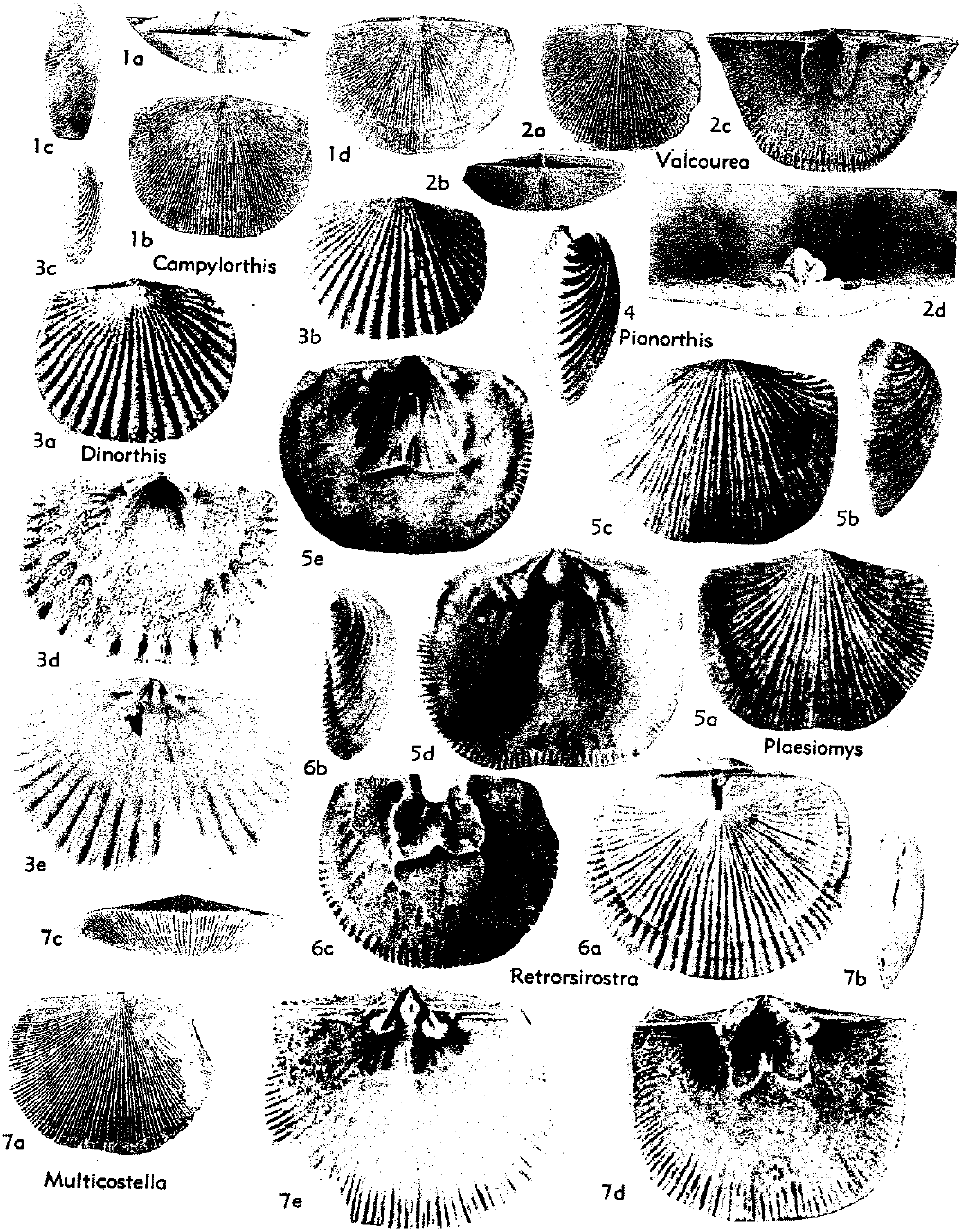


Fig. 201. Plaesiomyidae (Plaesiomyinae) (p. *H*319-*H*321).

Multicostella Schuchert & Cooper, 1931, p. 244 [**Orthis? saffordi* Hall & Clarke, 1892, p. 217; (OD]. Like *Campylorthis* but lacking deltidium and chilidium. *M.Ord.*, N.Hemis.

M. (Multicostella). Subequally biconvex, commonly with narrow median fold in pedicle valve and median sulcus in brachial valve dying away anteriorly. *M.Ord.*, N.Hemis.——Fig. 201,*7*. *M. (M.) semisulcata* Cooper, Lincolnshire, USA (Tenn.); *7a-c*, ped.v., lat., ant. views of conjoined valves, ×1; *7d,e*, ped.v. int., brach.v. int., ×2 (189).

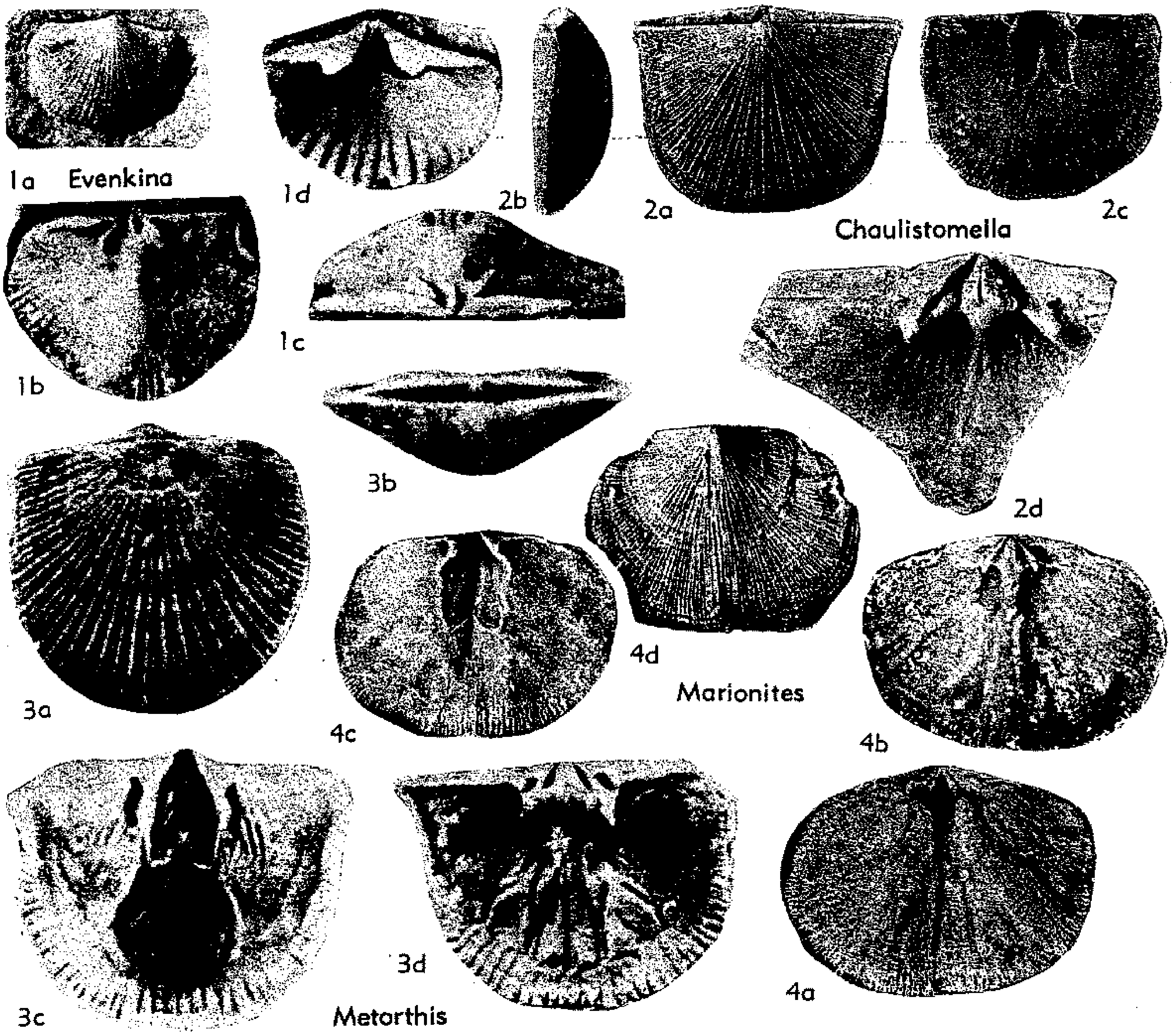


FIG. 202. Plaesiomyidae (Plaesiomyinae) *(2,4)*, (Evenkininae) *(1)*, Metorthinae *(3)* (p. *H*321-*H*322).

M. (Chaulistomella) COOPER, 1956, p. 432 [**C. inequistriata*; OD]. Resupinate in profile, with pedicle valve concave anteriorly and brachial valve uniformly convex; ventral median fold obscure. *M.Ord.*, E.N.Am.-Scot.——FIG. 202,*2*. **M. (C.) inequistriata*, Wardell, USA(Va.); *2a,b*, ped.v., lat. views of conjoined valves, ×1; *2c*, ped.v. int., ×1; *2d*, brach.v. int., ×2 (189).

M. (Marionites) COOPER & MUIR-WOOD, 1951, p. 195 [*pro Marionella* BANCROFT, 1928, p. 181 (*non* COBB, 1922)] [**Marionella typa* BANBROFT, 1928, p. 181; OD]. Resupinate in profile and with median fold, commonly sharp and narrow, in pedicle valve. [The differences between *M. (Marionites)* and *M. (Chaulistomella)* are too finely drawn to be worth even subgeneric recognition. Nonetheless there is a distinct possibility that they typify European and American species groups that evolved independently of each other.] *M.Ord.*, G.Brit.——FIG. 202,*4*. **M. (M.) typa* (BANCROFT), Caradoc, Eng.; *4a,b*, brach.v. int. and int. mold, ×1; *4c,d*, ped.v. int. and ext., ×1 (Williams, n).

Valcourea RAYMOND, 1911, p. 239 [**Plaesiomys strophomenoides* RAYMOND, 1905, p. 370; OD]. Convexo-concave with wide hinge line and well-developed deltidium and chilidium, narrow carinate median fold common in pedicle valve, radial ornamentation finely costellate; interiors like those of *Dinorthis* but with subperipheral rim in pedicle valve and median crest to myophore of cardinal process. *L.Ord.-M.Ord.*, N.Am.-Scot.——FIG. 201, *2a-c*. **V. strophomenoides* (RAYMOND), M.Ord. (Crown Point), USA(N.Y.); *2a,b*, ped.v., post. views of conjoined valves, ×2; *2c*, ped.v. int., ×3 (189).——FIG. 201,*2d*. *V. deckeri* COOPER, M.Ord.(Tulip Creek), USA(Okla.); *2d*, brach.v. post. view, ×3 (189).

Subfamily EVENKININAE Williams, n. subfam.

Unequally biconvex to plano-convex, with long bladelike divergent brachiophores rest-

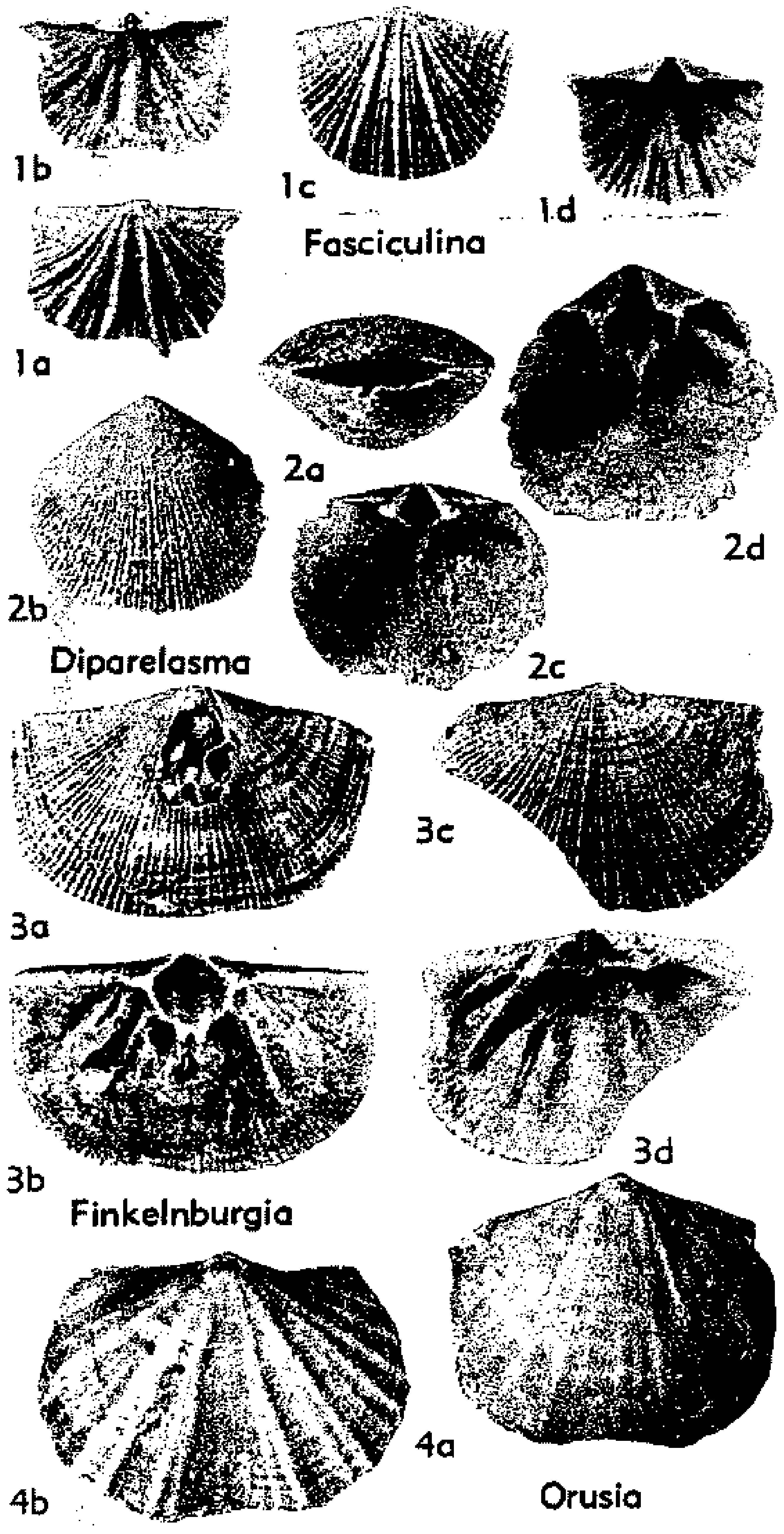


FIG. 203. Finkelnburgiidae (p. *H*322).

ing on floor of brachial valve throughout their entire length and poorly differentiated cardinal process. *M.Ord.*

Evenkina ANDREEVA, 1961, p. 96 [**E. anarbensis*; OD]. Subquadrate in outline, dorsal median sulcus present, costellate. *M.Ord.*, Sib.——FIG. 202,*1*. **E. anarbensis*; *1a*, ped.v. ext., ×2; *1b*, brach.v. int., ×3; *1c*, post. view of brach.v., ×3; *1d*, ped. v. int., ×4 (602).

Subfamily METORTHINAE Williams, n. subfam.

Plano-convex, with bladelike brachiophores raised above floor of brachial valve and undifferentiated cardinal process. *L. Ord.*

Metorthis WANG, 1955, p. 333 [**M. alata*; OD]. Subquadrate in outline, costellate; notothyrial edges elevated as chilidial plates. *L.Ord.*, China. ——FIG. 202,*3*. **M. alata*; *3a,b*, brach.v., post. views of conjoined valves, ×2.5; *3c,d*, ped.v. int., brach.v. int., ×2.5 (852).

Family FINKELNBURGIIDAE Schuchert & Cooper, 1931

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 54 (*ex* Finkelnburgiinae SCHUCHERT & COOPER, 1931, p. 243)]

Interareas and hinge lines well developed, delthyrium and notothyrium open; teeth small, dental plates divergent, ventral muscle field variable; brachiophores with subparallel to convergent bases, fulcral plates small; mantle canal systems of both valves digitate. *U.Cam.-L.Ord.*

Finkelnburgia WALCOTT, 1905, p. 277 [**F. finkelnburgi*; OD]. Semioval in outline, subequally biconvex with variable developed dorsal median sulcus, costellate to unequally parvicostellate, rarely with hollow costellae; ventral muscle field of adductor and divergent diductor scars expanding anteriorly, impressed on raised callus of secondary shell between dental plates; cardinal process, simple, ridgelike, brachiophore bases convergent onto floor of brachial valve. *U.Cam.-L.Ord.*, N.Hemis. ——FIG. 203,*3*. *F. buttsi* ULRICH & COOPER, U. Cam., USA(Va.); *3a,b*, ped.v. ext., int., ×2; *3c,d*, brach.v. ext., int., ×2 (825).

Diparelasma ULRICH & COOPER, 1936, p. 623 [**D. typicum*; OD]. Like *Finkelnburgia* but subcircular in outline, with relatively short hinge line; radial ornamentation evenly multicostellate; cardinal process absent to simple; brachiophore bases convergent onto median ridge in brachial valve. *L. Ord.*, N.Am.——FIG. 203,*2*. **D. typicum*, U. Canad., USA(Ala.); *2a*, post. view of conjoined valves, ×2; *2b-d*, ped.v. ext., brach.v. int., ped.v. int., ×2 (825).

Fasciculina COOPER, 1952, p. 7 [**Orthis desmopleura* MEEK in HAYDEN, 1872, p. 295; OD]. Like *Finkelnburgia* but coarsely fascicostellate. *L.Ord.*, N. Am. (W.USA).——FIG. 203,*1*. *F. fasciculata* COOPER, Okla.; *1a,b*, brach.v. ext., int., ×2; *1c,d*, ped.v. ext., int., ×2 (181).

Orusia WALCOTT, 1905, p. 273 [**Anomites lenticularis* WAHLENBERG, 1821, p. 66; OD]. Like *Diparelasma* but without pseudospondylium in pedicle valve and cardinal process in brachial valve; brachiophore bases subparallel, united with floor of valve. *U.Cam.*, *?L.Ord.*, N.Hemis.——FIG. 203,*4*. **O. lenticularis* (WAHLENBERG), U.Cam., Sweden; *4a,b*, ped.v., brach.v. int. molds, ×5 (Williams, n).

Family PLECTORTHIDAE Schuchert & Le Vene, 1929

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 243 (*ex* Plectorthinae SCHUCHERT & LEVENE, 1929, p. 14)]

Interareas and hinge lines of variable length, delthyrium and notothyrium open; teeth with oblique fossettes, supported by strong dental plates extending anteriorly, ventral muscle field variable but commonly elongately cordate; cardinal process almost invariably present and differentiated into crenulated myophore and shaft in adult shells; brachiophore bases either convergent

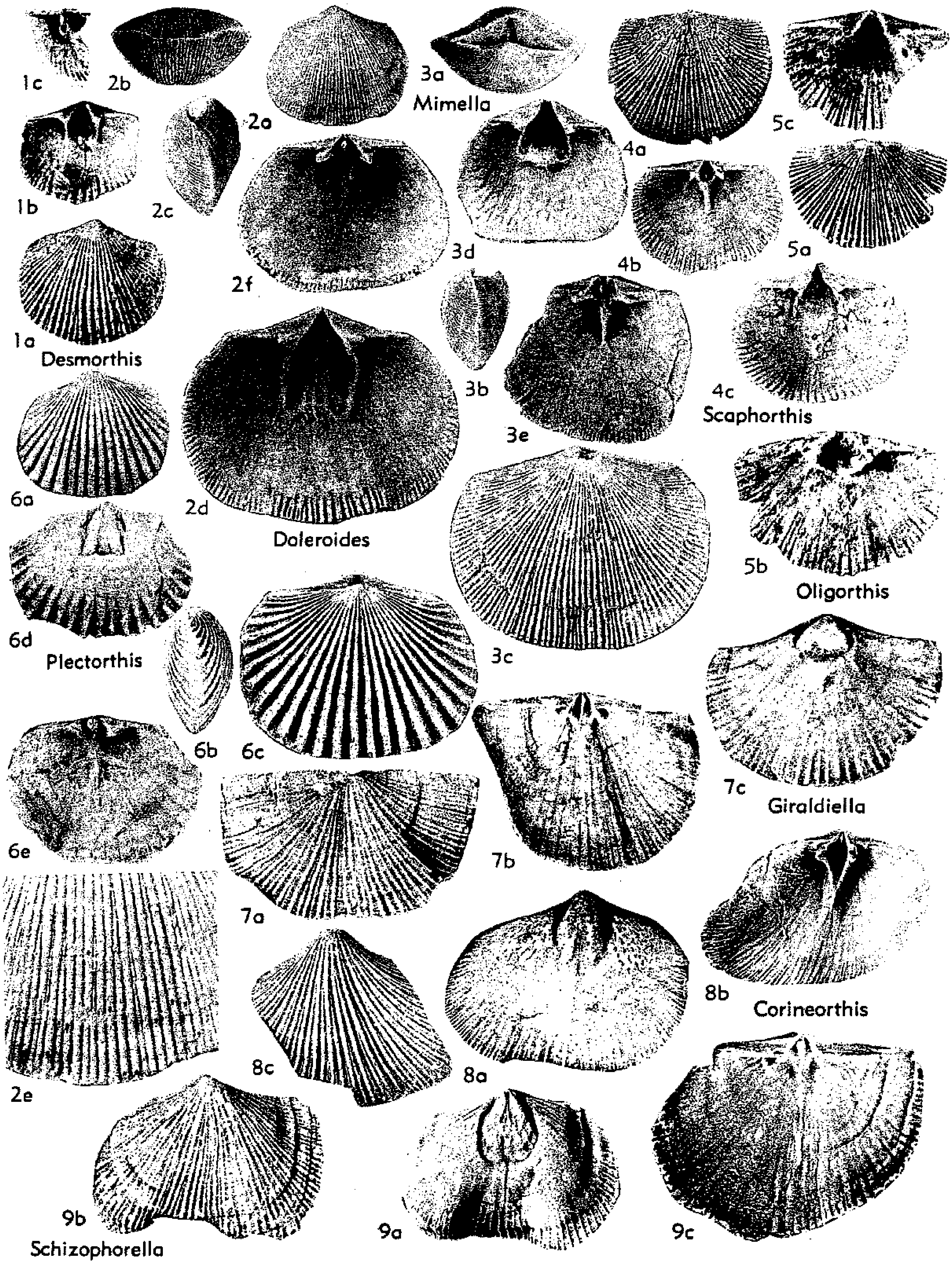


Fig. 204. Plectorthidae (Plectorthinae) (p. *H*324).

onto floor of brachial valve near junction of cardinal process and median ridge dividing quadripartite adductor scars and ankylosed to concave fulcral plates, or rarely divergent and replacing fulcral plates; ventral and dorsal mantle canal systems saccate. *L.Ord.-U.Sil.*

Subfamily PLECTORTHINAE
Schuchert & Le Vene, 1929

[Plectorthinae Schuchert & LeVene, 1929, p. 14]

Costellate, with well-developed interareas and wide hinge lines, dorsal median fold absent or subdued; brachiophore bases either convergent or rarely subparallel. *L.Ord.-L.Sil.*

Plectorthis Hall & Clarke, 1892, p. 194 [**Orthis plicatella* Hall, 1847, p. 122; OD]. Subequally biconvex, with short, curved apsacline ventral interarea, coarsely costellate, commonly with one generation branching near umbones so as to simulate costate radial ornamentation, dorsal median sulcus shallow; ventral muscle scar cordate with subcrescentic diductor scars enclosing linear adductor track. *M.Ord.-U.Ord.*, N.Hemis.——Fig. 204,*6*. *P. ponderosa* Cooper, M.Ord.(Martinsburg), USA(Va.); *6a,b*, ped.v., lat. views of conjoined valves, ×1; *6c*, brach.v. view of conjoined valves, ×1.5; *6d*, ped.v. int. mold, ×1; *6e*, brach.v. int., ×1.5 (189).

Corineorthis Stubblefield, 1939, p. 67 [**C. decipiens*; OD]. Unequally biconvex to resupinate, with strongly convex, medianly sulcate brachial valve, costellate, with hollow costellae and strong regular imbrication simulating exopunctae in intercostellate grooves; ventral muscle field elongately cordate, diductors not enclosing long adductor scars which commonly are divided by groove. *M.Ord.*, G.Brit.——Fig. 204,*8*. *C. pustula* Williams, L.Llandeil., Wales; *8a*, ped.v. int. mold, ×1.5; *8b*, brach.v. int., ×1.5; *8c*, ped.v. ext., ×2 (Williams, n).

Desmorthis Ulrich & Cooper, 1936, p. 624 [**D. nevadensis*; OD]. Like *Plectorthis* but with hollow costellae, apical plate in delthyrium, simple ridgelike cardinal process and subparallel brachiophore bases. *L.Ord.*, N.Am.(W.USA).——Fig. 204,*1*. **D. nevadensis*, Pogonip, Nev.; *1a*, ped.v. ext., ×2; *1b,c*, ped.v. int., brach.v. int., ×3 (189).

Doleroides Cooper, 1930, p. 375 [**Orthis gibbosa* Billings, 1857, p. 296; OD] Like *Plectorthis* but costellate, with swollen hollow costellae and commonly with dorsal broad median fold indented by faint impersistent median sulcus; ventral muscle scar elongatedly cordate, with elliptical adductor field divided by single ridge and not enclosed by diductor scars. *M.Ord.*, N.Am.-Scot.——Fig. 204, *2a-e*. **D. gibbosus* (Billings), Decorah, USA (Minn.); *2a-c*, ped.v., ant., lat. views of conjoined valves, ×1; *2d*, ped.v. int., ×2; *2e*, portion of shell enlarged showing hollow costellae, ×2 (189).——Fig. 204,*2f*. *D. tennesseensis* Cooper, Lebanon, USA(Tenn.); *2f*, brach.v. int., ×2 (189).

Giraldiella Bancroft, 1949, p. 5 [**Orthis protensa* Sowerby, 1839, p. 638; OD]. Subequally biconvex or resupinate, with medianly sulcate brachial valve more convex, costellate; ventral muscle field short, subtriangular, with wide adductor scars; cardinal process linear, socket plates well developed, subparallel with dorsal hinge line. *L.Sil.*, G.Brit.——Fig. 204,*7*. **G. protensa* (Sowerby), U.Llandover., Wales; *7a,b*, brach.v. ext., int., ×2; *7c*, ped.v. int. mold, ×2 (Williams, n).

Hebertella Hall & Clarke, 1892, p. 198 [**Orthis sinuata* Hall, 1847, p. 128; OD]. Like *Doleroides* but convexo-concave or unequally biconvex, with wide fold in brachial valve and with wide diductor scars not enclosing elongately suboval adductor scars borne on double ridge. *M.Ord.-U.Ord.*, N. Am.-Ire.——Fig. 205,*5*. **H. sinuata* (Hall), U. Ord.(Maysvill.-Richmond.), USA; *5a-c*, ped.v., brach.v., lat. views of conjoined valves, ×1; *5d,e*, brach.v. int., ped.v. int., ×1 (740).

Mimella Cooper, 1930, p. 375 [**Pionodema globosa* Willard, 1928, p. 274; OD]. Like *Hebertella* but unequally biconvex, with long, slightly curved, catacline to apsacline ventral interarea and with ventral muscle field consisting of long subparallel, deeply impressed diductor scars not enclosing long, anteriorly expanding elevated adductor track. *M.Ord.*, N.Hemis.——Fig. 204,*3*. **M. globosa* (Willard), Porterfield, USA (*3a-c,e*, Va., *3d*, Tenn.); *3a,b*, post., lat views of conjoined valves, ×1; *3c*, ped.v. ext., ×2; *3d,e*, ped.v. int., brach.v. int., ×1 (189).

Oligorthis Ulrich & Cooper, 1936. p. 624 [**O. arbucklensis*; OD]. Like *Desmorthis* but more finely costellate and without cardinal process and apical plate in delthyrium. *L.Ord.*, N.Am.(W. USA).——Fig. 204,*5*. **O. arbucklensis*, Canad., Okla., *5a*, brach.v. ext., ×3; *5b*, brach.v. int., ×4; *5c*, ped.v. int., ×3 (825).

Scaphorthis Cooper, 1956, p. 502 [**S. virginiensis*; OD]. Subcircular in outline with short hinge line, unequally biconvex, with short, curved apsacline interarea in deeper pedicle valve, costellate; ventral muscle scar short, subcordate, with wide median adductor scar; cardinal process with thin bladelike myophore. *M.Ord.-U.Ord.*, N.Am.(E. USA)-Scot.-Ire.——Fig. 204,*4*. **S. virginiensis*, M.Ord.(Porterfield), USA(Va.); *4a-c*, brach.v. ext., brach.v. int., ped.v. int., ×2 (189).

Schizophorella Reed, 1917, p. 858 [**Orthis fallax* Salter, 1846, p. 72; OD]. Like *Corineorthis* but with greater convexity of brachial valve accentuated by strong median fold in adult shells; ventral muscle field long, with subparallel lateral boundaries formed of dental plates and their anterior extensions, adductor scar long and narrow with faint double ridges like *Hebertella*. *U.Ord.*, G.Brit.-

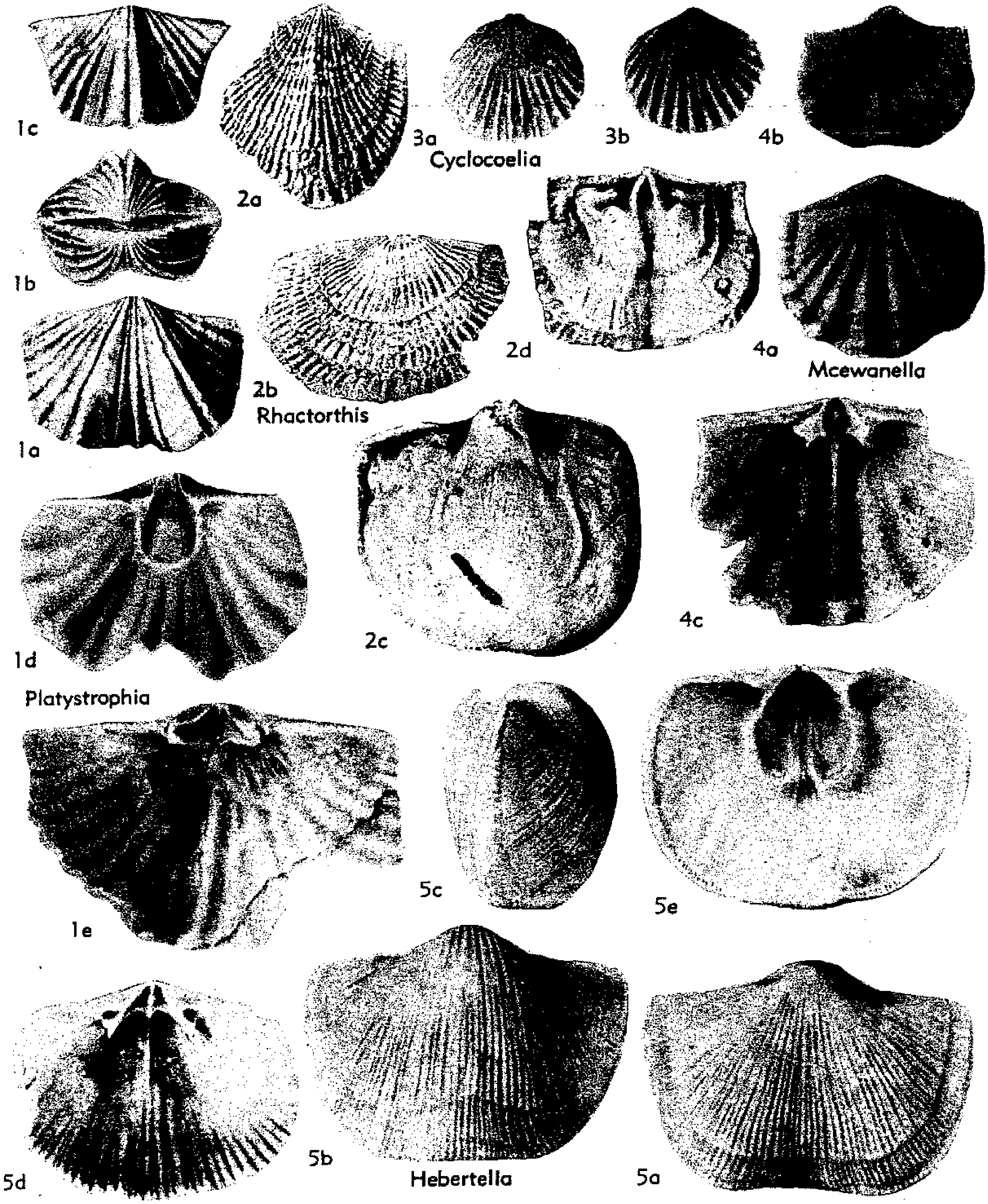


FIG. 205. Plectorthidae (Plectorthinae) *(5)*, (Platystrophiinae) *(1, 4)*, (Cyclocoeliinae) *(3)*, (Rhactorthinae) *(2)* (p. *H*324-*H*326).

Ire.——FIG. 204,*9*. *S. fallax* (SALTER), Scot.; *9a*, ped.v. view of int. mold of conjoined valves, ×1.5; *9b*, ped.v. ext., ×1.5; *9c*, brach.v. int., ×2 (Williams, n).

Subfamily PLATYSTROPHIINAE Schuchert & Le Vene, 1929

[Platystrophiinae SCHUCHERT & LEVENE, 1929, p. 14]

Costate to costellate, with large subequal interareas and wide hinge lines, dorsal median fold strongly developed; brachiophore bases convergent. *M.Ord.-U.Sil.*

Platystrophia KING, 1850, p. 105 [**Terebratulites biforatus* VON SCHLOTHEIM, 1820, p. 265; OD]. Spiriferoid in outline, hinge line commonly mu-

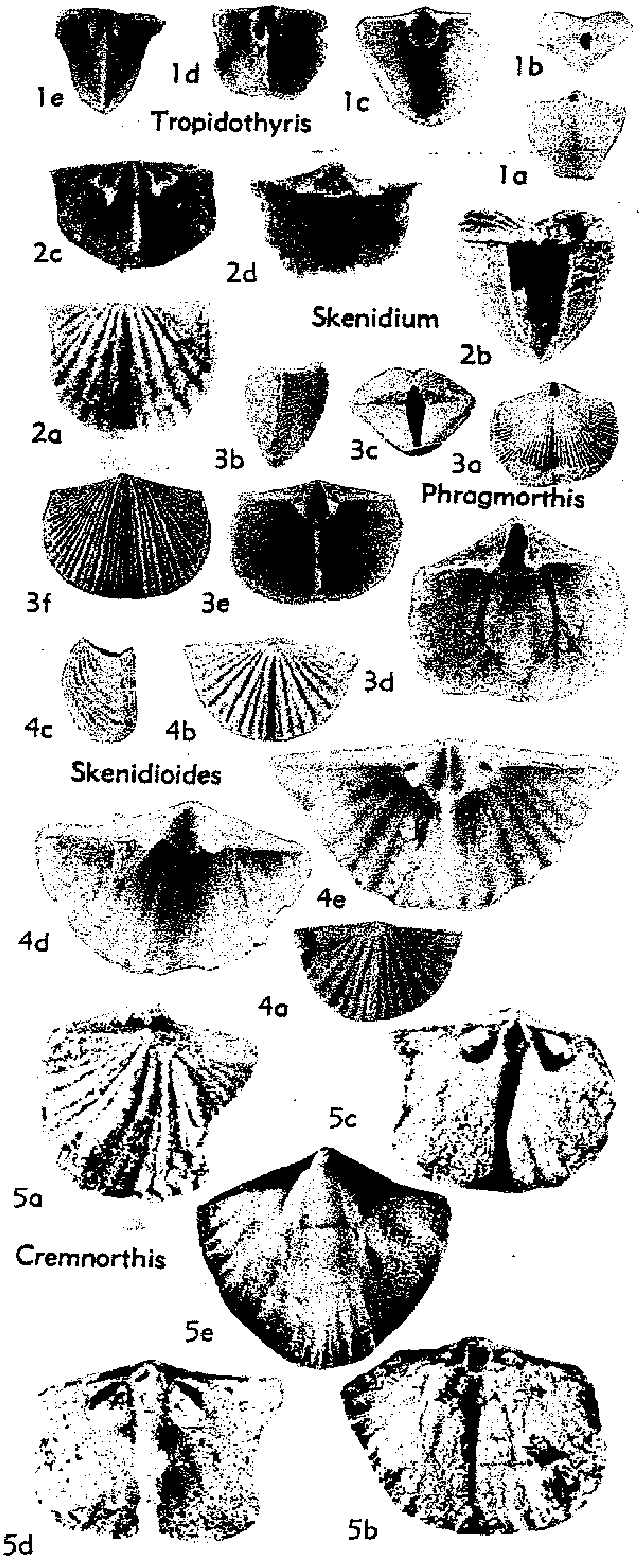


Fig. 206. Cremnorthidae (Cremnorthinae) *(5)*, (Phragmorthinae) *(3)*; Skenidiidae *(1-2, 4)* (p. *H326-H327*).

cronate, strongly biconvex, costate and finely pustulose; ventral muscle field elongate, with broad adductor scars and commonly elevated on platform of secondary shell in adult valves; cardinal process low, ridgelike. *M.Ord.-U.Sil.(Wenlock.)*, cosmop.——Fig. 205,*1*. *P. laticosta* Meek, U.Ord. (Maysvill.), S.USA; *1a,b*, ped.v., post. views of conjoined valves, ×1 (740); *1c*, brach.v. ext., ×1 (740); *1d,e*, ped.v. int., brach.v. int., ×1.5 (729).

Mcewanella Foerste, 1920, p. 197 [**Platystrophia fernvalensis* McEwan, 1919, p. 428 (=**Hebertella lineolata* Savage, 1918, p. 267); OD]. Like *Platystrophia* but with costellate radial ornamentation commonly superimposed on costate arrangement of *Platystrophia*. *M.Ord.-U.Ord.*, N.Am.(USA)-G. Brit.-Eire.——Fig. 205,*4*. *M. raymondi* Foerste, U.Ord., USA(Mo.); *4a*, brach.v. view of conjoined valves, ×2; *4b*, ped. v. int., ×1; *4c*, brach. v. int., ×2 (740).

Subfamily CYCLOCOELIINAE Schuchert & Cooper, 1931

[Cyclocoeliinae Schuchert & Cooper, 1931, p. 243]

Costate to coarsely costellate, with small interareas and very short hinge lines, dorsal fold faint; brachiophore bases convergent. *U.Ord.*

Cyclocoelia Foerste, 1909, p. 227 [**Atrypa sordida* Hall, 1847, p. 148; OD] [=*Encuclodema* Foerste, 1912, p. 227 (obj.)]. Rhynchonelliform in outline; shell thin, muscle scars not impressed. *U.Ord.*, N.Am.(E.USA).——Fig. 205,*3*. **C. sordida* (Hall), Cincinnati(Maysvill.), Ohio; *3a,b*, brach.v. int., ext., ×2 (729).

Subfamily RHACTORTHINAE Williams, 1963

[Rhactorthinae Williams, 1963, p. 371]

Costellate, with well-developed interareas and wide hinge lines, dorsal median sulcus well developed; brachiophore bases divergent, curving laterally so as to define sockets; cardinal process with crenulated myophore and shaft continuous with median ridge. *M. Ord.-U.Ord.*

Rhactorthis Williams, 1963, p. 371 [**R. crassa*; OD]. Unequally biconvex, with deep pedicle valve, multicostellate, with hollow costellae; dental plates short, receding, ventral muscle field subpentagonal, with wide aductor scars not enclosed by narrow divergent diductors. *M.Ord.-U.Ord.*, G.Brit.-Eire. ——Fig. 205,*2*. **R. crassa*, M.Ord.(Longvill.), Wales; *2a,b*, ped.v. ext., brach.v. ext., ×3; *2c*, ped.v. int. mold, ×3.5; *2d*, brach.v. int. mold, ×6.5 (Williams, n).

Family CREMNORTHIDAE Williams, 1963

[Cremnorthidae Williams, 1963, p. 377]

Strongly biconvex, with deep narrow dorsal sulcus, delythrium and chilidium open; ventral muscle field short, subtriangular, dental plates short, stout, receding; cardinal process simple or differentiated, continuous with high dorsal median septum, subtriangular in outline, extending almost to anterior margin and dividing elongately oval dorsal adductor field; ventral mantle canal system saccate, with divergent *vascula media,* dorsal system unknown. *M.Ord.*

Subfamily CREMNORTHINAE Williams, 1963

[*nom. transl.* Williams, herein (*ex* Cremnorthidae Williams, 1963, p. 377)]

Adductor scar in ventral muscle field wide; cardinal process trilobed; brachiophores short, widely divergent, with bases curved laterally to define semioval sockets. *M.Ord.*

Cremnorthis Williams, 1963, p. 378 [**C. parva*; OD]. Fascicostellate, with angular costae and costellae. *M.Ord.,* Wales.——Fig. 206,*5*. **C. parva*; *5a,* brach.v. view of conjoined valves, ×6; *5b,c,* brach.v. mold, int., ×7, ×8.5; *5d,* brach.v. int., ×9.5; *5e,* ped.v. int. mold, ×6.5 (Williams, n).

Subfamily PHRAGMORTHINAE Williams, n. subfam.

Ventral muscle field undifferentiated; cardinal process ridgelike; brachiophores long, bases convergent onto median septum, socket plates well developed. *M.Ord.-U.Ord.*

Phragmorthis Cooper, 1956, p. 508 [**P. buttsi*; OD]. Multicostellate, with some costellae swollen. *M.Ord.-U.Ord.,* N.Am.-Scot.——Fig. 206,*3*. **P. buttsi,* M.Ord.(Porterfield), USA (*3a-c,* Va., *3d-f,* Tenn.); *3a-c,* brach. v., lat., post. views of conjoined valves, ×2; *3d,e,* ped.v. int., brach.v. int., ×4; *3f,* brach.v. ext., ×4.5 (189).

Family SKENIDIIDAE Kozlowski, 1929

[*nom. correct.* Schuchert & Cooper, 1931, p. 243 (pro Scenidiidae Kozlowski, 1929, p. 46]

Subpyramidal, with open delthyrium and chilidium; ventral muscle field contained in free or supported spondylium; brachiophores long, slender, commonly with bases convergent on high median septum and united laterally to socket plates or to hinge plates containing sockets; cardinal process simple or differentiated into shaft and crenulated myophore; dorsal adductor field shield-shaped, impressed on either side of septum; mantle canal systems rarely preserved. *L. Ord.-U.Dev.*

Skenidium Hall, 1860, p. 70 [**Orthis insignis* Hall, 1859, p. 173; SD Hall & Clarke, 1892, p. 241]. Pedicle valve high, with procline to apsacline interarea, brachial valve plane to gently convex, with median sulcus, costate to coarsely costellate; spondylium free anteriorly, supported apically by small septum; cardinal process linear, not continuous with median septum; large slightly concave plates lateral to brachiophores sharply indented near junction with hinge line to form sockets. *L.Dev.-U.Dev.,* cosmop.——Fig. 206,*2*. **S. insigne* (Hall), L.Dev., USA(N.Y.); *2a,b,* brach.v., post. view of conjoined valves, ×4; *2c,d,* brach.v. int., ped.v. int., ×4 (729).

Skenidioides Schuchert & Cooper, 1931, p. 243 [**S. billingsei*; OD]. Like *Skenidium* but with cardinal process commonly differentiated into shaft and compressed myophore and continuous with median septum; plates lateral to brachiophores, narrow, entirely and deeply concave to form sockets. *L.Ord.-U.Sil.,* cosmop.——Fig. 206,*4*. *S. costatus* Cooper, M.Ord.(Porterfield), USA(Va.-Tenn.); *4a-c,* ped.v., brach.v., lat. views of conjoined valves, ×4; *4d,e,* ped.v. int., brach.v. int., ×6 (189).

Tropidothyris Cooper, 1956, p. 507 [**T. pentagona*; OD]. Like *Skenidioides* but subpentagonal in outline, with smooth or faintly plicate external surface and with subparallel brachiophore bases attached to floor of brachial valve. *M.Ord.,* N.Am. (E.USA).——Fig. 206,*1*. **T. pentagona,* Porterfield, Ala.; *1a,b,* brach.v., post. views of conjoined valves, ×5; *1c,* ped.v. int., ×8; *1d,e,* brach.v. ints., ×8 (189).

Family TUVAELLIDAE Alichova, 1960

[Tuvaellidae Alichova, 1960, p. 190]

Interareas well developed, hinge line wide, deltidium and chilidium present, teeth strong, supported by receding dental plates, ventral muscle field elliptical; cardinal process short and thick, notothyrial platform wide. *L.Sil.*

Tuvaella Chernyshev, 1937, p. 11 [**T. rackovskii*; OD]. Costate, plano-convex to unequally biconvex, with deep median sulcus in brachial valve. *L.Sil.,* E.USSR.——Fig. 207,*1*. **T. rackovskii*; *1a-c,* ped.v., brach.v., post. views of conjoined valves, ×2 (710).

Family SAUKRODICTYIDAE Wright, 1964

[Saukrodictyidae Wright, 1964, p. 218]

Interareas short, hinge line wide, delthyrium and notothyrium open; costae and costellae developed within honeycomb network ornamenting shell surface; teeth supported by short strong dental plates; cardinal process simple, brachiophores short, divergent, with bases convergent onto notothyrial platform, fulcral plates absent. *U.Ord.*

Saukrodictya Wright, 1964, p. 218 [**S. hibernica*; OD]. Unequally biconvex, with strong median fold in deeper pedicle valve; ventral muscle field

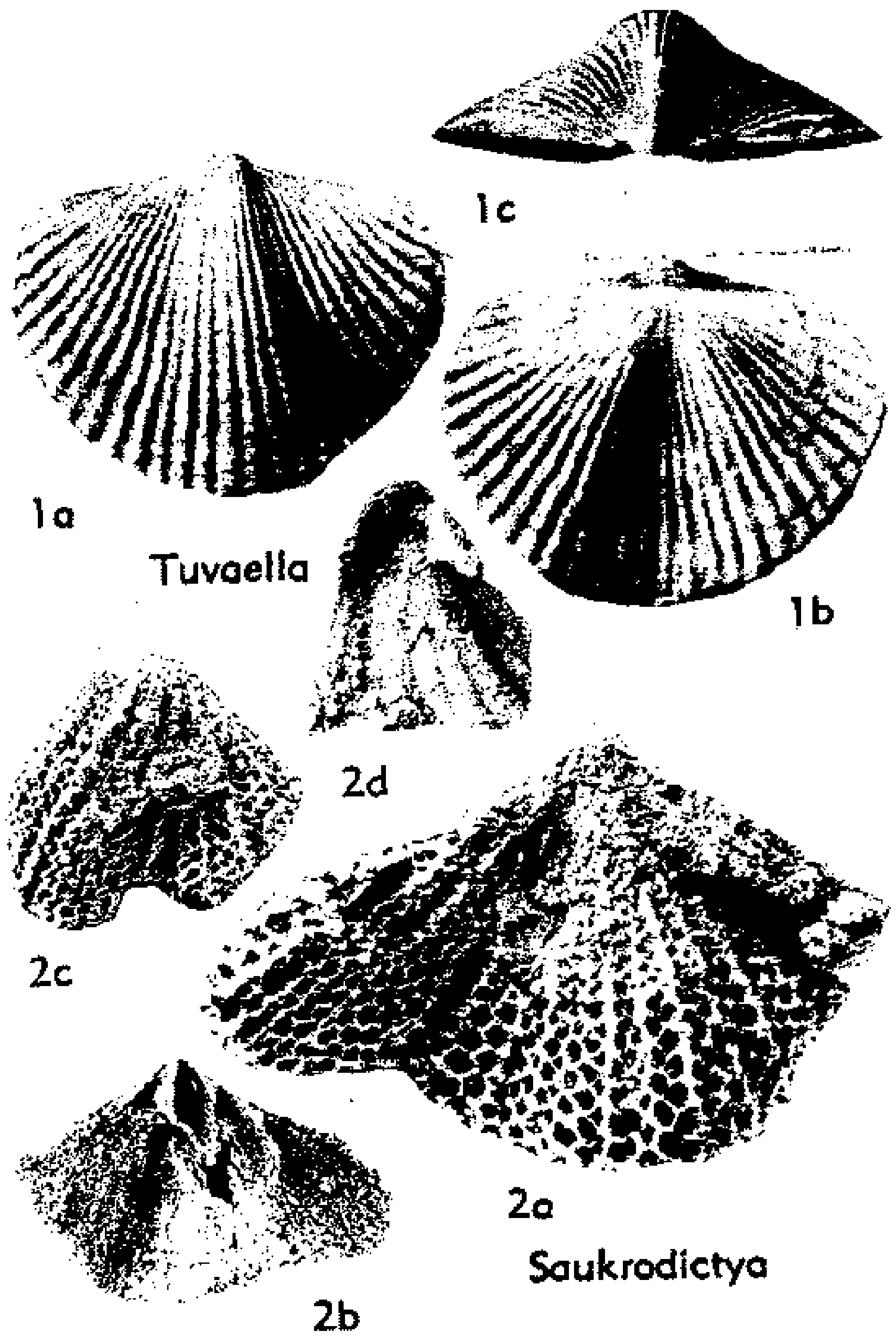


Fig. 207. Tuvaellidae *(1)*; Saukrodictyidae *(2)* (p. *H327-H328*).

poorly preserved, dorsal adductor field elongately subquadrate. *U.Ord.(Ashgill.)*; Eire.——Fig. 207, 2. **S. hibernica*; *2a,* incomplete brach.v. ext., ×9; *2b,* incomplete brach.v. int., ×5; *2c,d,* incomplete ped.v. ext., int., ×5 (895b).

Superfamily ENTELETACEA Waagen, 1884

[*nom. transl.* Alichova, 1960, p. 193 (*ex* Enteletinae Waagen, 1884, p. 548); *emend.* Wright, herein]
[Materials for this superfamily prepared by A. D. Wright]
[Appreciation and thanks are expressed to the Trustees of the British Museum (Natural History) for permission to reproduce several illustrations from Williams, 1963 (ref. 878)]

Delthyrium and notothyrium open, rarely constricted by plate or plates; teeth supported by variably developed dental plates, ventral muscle field impressed on floor of pedicle valve, exceptionally raised above valve floor; cardinal process of lobate myophore and shaft, rarely simple or absent; sockets simple or defined by fulcral plates, brachiophores with bases convergent or divergent on floor of brachial valve, rarely extended to produce calcareous support to lophophore. Ventral mantle canal system commonly lemniscate, rarely saccate, dorsal lemniscate to digitate and pinnate. Shell substance punctate. *L.Ord.-U.Perm.*

Recent investigations show that the name applied to the superfamily of punctate orthoid-like brachiopods, Dalmanellacea, is incorrect according to present taxonomic procedure.

The Dalmanellacea were first given superfamilial status by Schuchert & Cooper (1931, p. 245), the principal character used to separate this superfamily from the Orthacea being the punctate nature of the shell (p. 242). Since 1931, the name has been generally accepted in the literature concerned with brachiopod classification (e.g., Cooper, 1944, p. 351; Moore, 1952, p. 220; Muir-Wood, 1955, p. 87; Williams, 1956, p. 284).

In the latest classificatory work, the Russian "Treatise" (Osnovy), Alichova divides the punctate orthoid stocks into two superfamilies Rhipidomellacea and Enteletacea (1960, p. 183). Here the Rhipidomellacea include the family Dalmanellidae, the name Dalmanellacea being replaced on grounds of priority, Alichova attributing the Dalmanellidae to Schuchert, 1929, and the Rhipidomellidae to Schuchert, 1913. However, as all categories in the family group are of co-ordinate status in nomenclature, and as a change in rank of a taxon within the family group does not affect authorship, there is no justification for the use of Rhipidomellacea instead of Dalmanellacea, as both superfamilies are ascribable to Schuchert, 1913, the diagnosis of the Dalmanellinae being given before Rhipidomellidae (p. 382 of that work).

With respect to the Enteletacea, the subfamily Enteletinae was erected by Waagen (1884, p. 548) as a subfamily of the Orthidae, and accordingly it antedates any other family taxon within the punctate orthoid stocks. The division of these forms by Alichova into two distinct groups at superfamilial level seems entirely unjustified on morphological considerations; thus, on the grounds of priority, the name Enteletacea has been adopted for the entire superfamily.

The change of superfamilial name may initially be inconvenient. Although both *Dalmanella* and *Enteletes* are equally widespread and well-known stocks, the former, appearing early in the evolution of the group (Middle Ordovician), is relatively unspecialized and is generally considered to be close to the basic stock from which the other members of the superfamily evolved. *Enteletes,* on the other hand, is an aberrant and specialized form, only appearing in Carboniferous and Permian times; from these considerations *Dalmanella* would appear to provide the better type-genus.

These grounds, however, in no way justify an appeal for the retention of the Dalmanellacea, which is accordingly suppressed in favor of Enteletacea.

Family ENTELETIDAE Waagen, 1884

[*nom. transl.* ALICHOVA, 1960, p. 194 (*ex* Enteletinae WAAGEN, 1884, p. 548); *emend.* WRIGHT, herein] [=Schizophoriidae SCHUCHERT & LEVENE, 1929, p. 15]

Variably biconvex, ventral interarea curved, apsacline, dorsal interarea shorter, commonly curved, anacline to strongly apsacline, delthyrium and notothyrium open, costellae fine, hollow, rarely with strong superimposed radial plications, fold and sulcus variably developed; ventral muscle field with prominent diductor scars, extending beyond but not enclosing adductor scars, which may be situated on median septum; extravagant development of dental plates and ventral median septum in later genera. Cardinal process with lobate myophore and shaft; stout, commonly tusklike brachiophores with bases varying in attitude, fulcral plates present; median septum absent or low, dividing subquadrate adductor field; ventral mantle canal system probably lemniscate, dorsal pinnate. *M.Ord.-U.Perm.*

Subfamily ENTELETINAE Waagen, 1884

[Enteletinae WAAGEN, 1884, p. 548]

Strongly biconvex or globose, with abundant strong radial plications anteriorly; dental plates and ventral median septum invariably well developed, pedicle callist very small or absent; brachiophore bases containing adductor field posterolaterally. *M.Carb.-U.Perm.*

Enteletes FISCHER DE WALDHEIM, 1825, p. 6 [**E. glabra* FISCHER DE WALDHEIM, 1830, pl. 26, figs. 6, 7; SM] [=*Anteletes* D'ORBIGNY, 1850 (*nom. null.*); *Enteles* SCHELLWEIN, 1892 (*nom. null.*); *Syntrilasma* MEEK & WORTHEN, 1865, p. 277 (type, *Spirifer hemiplicatus* HALL, 1852); *Syntrielasma* MEEK & WORTHEN, 1866, p. 321 (*nom. van.*)]. Small to medium-sized, globose, dorsibiconvex, strongly plicate anteriorly, with dorsal fold and ventral sulcus; dental plates strong,

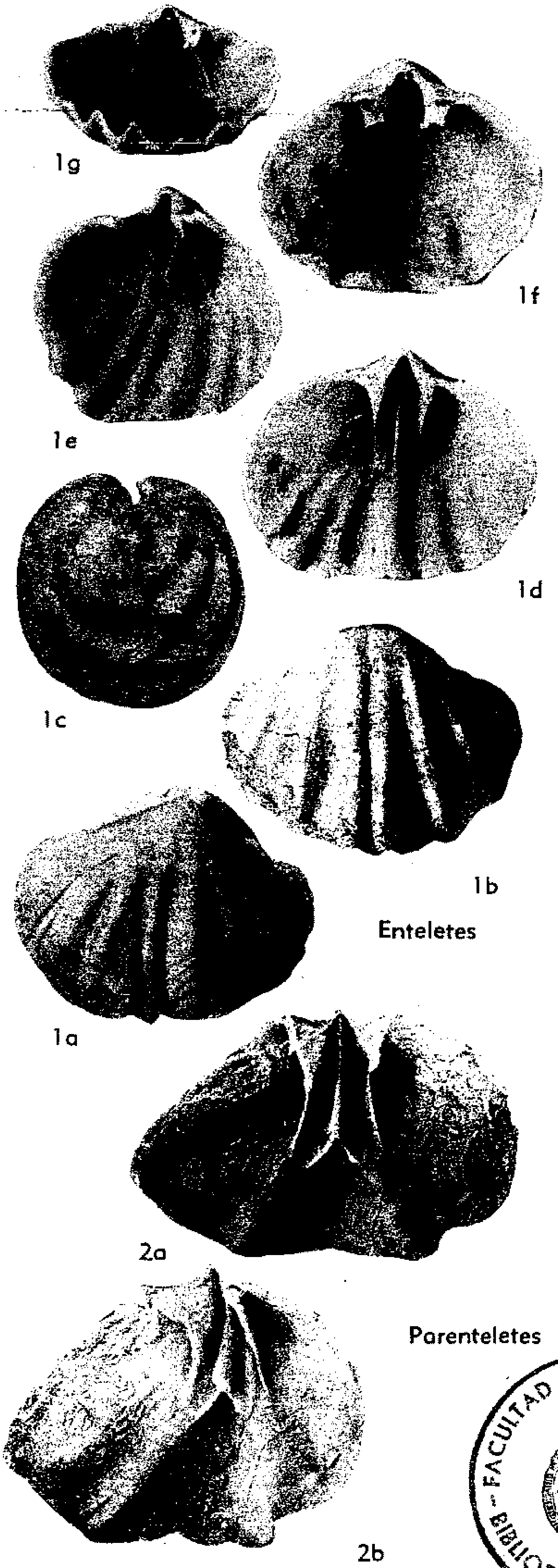


FIG. 208. Enteletidae (Enteletinae) (p. H329-H330).

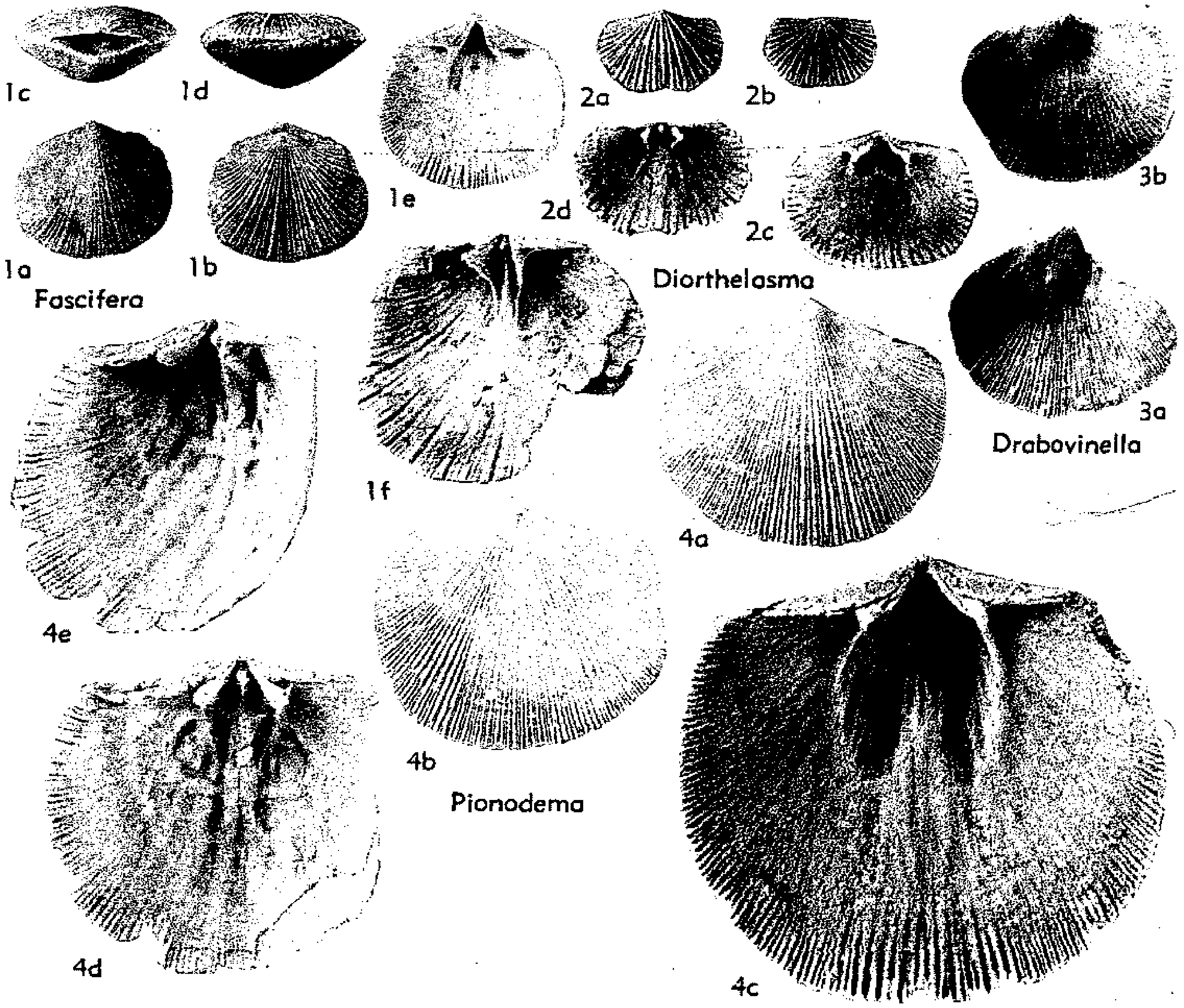


FIG. 209. Enteletidae (Draboviinae) (p. *H*331-*H*332).

subparallel, median septum strong, rising to crest near abruptly truncated anterior end, ventral muscle field narrowly restricted; cardinal process small, crenulated, on shallow notothyrial platform, brachiophores stout, tusklike, with strong, divergent bases; low, narrow median septum commonly developed, small posterior adductor scars lateral to larger anterior pair. *U.Carb.-U.Perm.*, widespread. ——FIG. 208,*1a-c*. *E. lamarcki* (Fischer de Waldheim), U.Carb., USSR; *1a-c*, ped.v., brach.v., lat. views of conjoined valves, ×1 (729).——FIG. 208,*1d-g*. *Enteletes* sp., Perm.(WordF.), USA (Tex.,Glass Mts.); *1d,e*, normal, oblique views of ped.v. int., ×2; *1f,g*, normal, ant. views of brach. v. int., ×2 (178).

Enteletella Likharev, 1925, p. 719 [**E. nikschitchi*; OD]. Like *Enteletes*, but distinguished by convergence of dental plates to form spondylium. *U. Perm.*, USSR (Caucasus).

Enteletina Schuchert & Cooper, 1931, p. 247 [**Enteletes latesinuatus* Waagen, 1884, p. 559; OD]. Like *Enteletes* but with dorsal sulcus and ventral fold. *U.Carb.-U.Perm.*, Asia-?N.Am.

Parenteletes King, 1930, p. 48 [**P. cooperi*; OD]. Like *Enteletina* externally, but distinguished by presence of cella under anterior of ventral median septum. *U.Carb.-L.Perm.*, Eu.-Asia-N.Am.——FIG. 208,2. **P. cooperi*, L.Perm.(Wolfcamp.), USA (Tex.); *2a,b*, normal, oblique views of ped.v. int., ×2 (729).

Subfamily DRABOVIINAE Havlíček, 1950

[Draboviinae Havlíček, 1950, p. 45; *emend.* Wright, herein]

Profile lenticular, with pedicle valve commonly deeper than brachial valve, strong radial plications lacking; ventral median septum not strongly developed, pedicle callist usually present; anterior continuation of brachiophore bases converging on to median ridge and not containing adductor field posteriorly; brachiophore bases may converge directly on to median ridge. *M.Ord.-U.Ord.*

Drabovia Havlíček, 1950, p. 45 [**Orthis redux* Barrande, 1848, p. 49; OD]. Like *Fascifera*, but completely lacking median thickening to ventral muscle field. *M.Ord.*, Eu.-N.Afr.

?Comatopoma Havlíček, 1950, p. 54 [**C. bar-*

randei; OD]. Transversely subcircular, subequally biconvex, finely costellate, sulcate; ventral muscle field short, broad, commonly bilobate; cardinal process simple ridge, convergent brachiophore bases short, thin. *U.Ord.*, Boh.

Diorthelasma Cooper, 1956, p. 997 [**D. parvum*; OD]. Minute, transverse, ventribiconvex, with marked sulcus in shallow brachial valve; cordate ventral muscle field wide, short, pedicle callist not known, *vascula media* strongly divergent; cardinalia like *Fascifera*, dorsal adductor scars small, elongate, posterior pair situated lateral to anterior pair, median ridge lacking. *M.Ord.*, SE.USA-Scot. ——Fig. 209,*2*. **D. parvum*, Porterfield, USA (Ala.); *2a,b*, ped.v., brach.v. views of conjoined valves, ×4; *2c,d*, ped.v. int., brach.v. int., ×6 (189).

Drabovinella Havlíček, 1950, p. 50 [**Orthis drabovensis* Barrande, 1879, pl. 61, fig. 5; OD]. Transverse, commonly large, subequally biconvex, apparently without fold or sulcus; ventral muscle field narrowly triangular, thickening to adductor field completely lacking; cardinal process shaft and convergent brachiophore bases very closely apposed, continued anteriorly as long, low, subparallel ridges. *M.Ord.*, Boh.——Fig. 209,*3*. **D. drabovensis* (Barrande), Llandeil.; *3a,b*, ped.v. int., brach.v. int., ×1 (Wright, n).

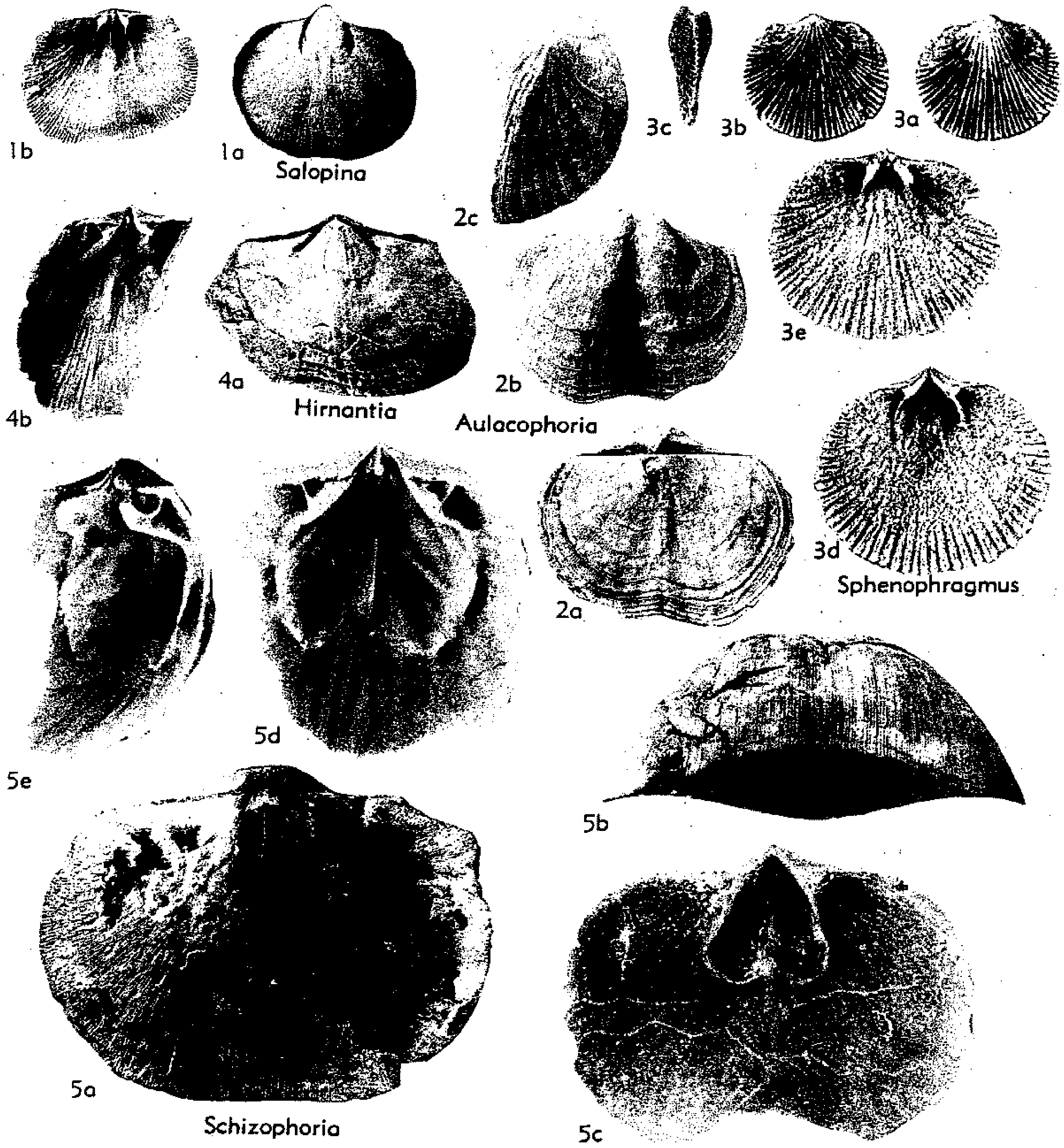


Fig. 210. Enteletidae (Schizophoriinae) (p. *H*332).

Fascifera Ulrich & Cooper, 1942, p. 620 [**F. subcarinata*; OD]. Distinguished from *Pionodema* by generally fascicostellate ornament, commonly persistent dorsal sulcus, poorly developed ventral median ridge, and narrower notothyrial platform with brachiophore bases variably convergent toward median ridge. *M.Ord.*, N.Am.-?Eu.(Scot.).——Fig. 209,*1a-e*. **F. subcarinata,* Wilderness, USA (Tenn.); *1a-d,* ped.v., brach.v., post., ant. views of conjoined valves, ×2; *1e,* ped.v. int., ×2 (189). ——Fig. 209,*1f*. *F. stonensis* (Safford), Wilderness, USA(Tenn.); *1f,* oblique brach.v. int., ×3 (189).

Pionodema Foerste, 1912, p. 139 [*pro Bathycoelia* Foerste, 1909 (*non* Amyot & Serville, 1843)] [**Orthis subaequata* Conrad, 1843, p. 333; OD]. Subcircular to transversely elliptical, ventribiconvex to subequally biconvex with narrow dorsal sulcus of young stages usually lost or reverting to low fold in adult; ventral muscle field with commonly subflabellate diductor scars and elongate semielliptical adductor scars on median thickening; cardinal process with small, crenulated, bilobate myophore and slender shaft, brachiophore bases suberect, bounding broad notothyrial platform, with anterior extensions convergent on to median ridge. *M.Ord.-U.Ord.,* N.Am.-Scot-?Asia.——Fig. 209,*4*. **P. subaequata* (Conrad), M.Ord.(Barnhart), USA(Mo.); *4a,b,* ped.v., brach.v. views of conjoined valves, ×2; *4c,* ped.v. int., ×2; *4d,e,* normal, oblique views of brach.v. int., ×2 (189).

Subfamily SCHIZOPHORIINAE Schuchert & LeVene, 1929

[Schizophoriinae Schuchert & LeVene, 1929, p. 15]

Biconvex young growth stages commonly developing deep brachial valve and less convex or resupinate pedicle valve, strong radial plications lacking; ventral median septum rarely well developed, pedicle callist usually present; brachiophore bases containing adductor field posterolaterally. *U.Ord.-U.Perm.*

Schizophoria King, p. 106 [**Conchyliolithus (Anomites) resupinatus* Martin, 1809, pl. 49, fig. 13, 14; OD]. Transversely elliptical, low dorsal fold and ventral sulcus commonly developed, rarely shallow sulcus in both valves; teeth strong, dental plates extending as low ridges bounding elongatedly bilobate to broadly cordate muscle field, divided medially by anteriorly elevated adductor ridge; cardinal process typically with large lobate myophore in young stages, less prominent in adult. *Sil.-Perm.,* cosmop.——Fig. 210,*5a,b*. **S. resupinata* (Martin), L.Carb., Eng.; *5a,b,* ped.v., ant. views of neotype, ×0.7 (87).——Fig. 210,*5c-e*. *S. iowensis* (Hall), U.Dev., USA(Iowa); *5c,* ped.v. int., ×2; *5d,e,* normal, oblique views of brach.v. int., ×2 (729).

Aulacophoria Schuchert & Cooper, 1931, p. 247 [**Orthis keyserlingiana* de Koninck, 1843, p. 230; OD]. Like *Schizophoria* but with deep dorsal sulcus and narrow ventral fold; ventral interarea commonly flat, catacline. *L.Carb.,* Eu.——Fig. 210,*2*. **A. keyserlingiana* (de Koninck), Eng.; *2a-c,* ped.v., brach.v., lat. views of conjoined valves, ×1 (Wright, n).

Enteletoides Stuckenberg, 1905, p. 59 [**E. rossicus*; OD]. Like *Schizophoria* but with dental plates and ventral median septum extravagantly developed as in *Enteletes*. *U.Carb.,* C.Asia.

Hirnantia Lamont, 1935, p. 313 [**Orthis sagittifera* M'Coy, 1851, p. 398; OD]. Dorsibiconvex, commonly with shallow dorsal sulcus, distinguished from more finely costellate *Schizophoria* by suboval ventral muscle field with subtriangular adductor scars impressed, with no median ridge or thickening; cardinal process with small myophore and long shaft. *U.Ord.-L.Sil.,* Eu.(G.Brit.).——Fig. 210,*4*. **H. sagittifera* (M'Coy), U.Ord.(Ashgill.), Wales; *4a,b,* ped.v. int. mold, brach.v. int., ×1.5 (Wright, n).

Orthotichia Hall & Clarke, 1892, p. 213 [**Orthis? morganiana* Derby, 1874, p. 29; OD] [=*Orthotichina* Chernyshev, 1914 (*nom. null.*)]. Like *Schizophoria,* but with strong dental plates extending to front of ventral muscle field as high ridges and strong median septum, intermediate in development between *Schizophoria* and *Enteletoides*. *U.Carb.-U.Perm.,* widespread.

Salopina Boucot, 1960, p. 3 [**Orthis lunata* Sowerby, 1839, p. 611; OD]. Distinguished from small *Schizophoria* by ventribiconvex profile, persistent dorsal sulcus and cordate ventral muscle field lacking median ridge. *U.Sil.-L.Dev.,* W.Eu.-E.N. Am.——Fig. 210,*1*. **S. lunata* (Sowerby), U.Sil. (Ludlov.), Eng.; *1a,* ped.v. int. mold, ×1.5; *1b,* brach.v. int., ×2 (Wright, n).

Sphenophragmus Imbrie, 1959, p. 365 [**S. nanus*; OD]. Small, subcircular shells, initially ventribiconvex with brachial valve becoming resupinate in adult stages; ventral muscle field cordate, impressed, no median ridge or thickening; cardinal process with high, posteriorly directed, trilobed myophore. *M.Dev.,* E.N.Am.-C.N.Am. ——Fig. 210,*3*. **S. nanus,* USA(Mich.); *3a-c,* ped.v., brach.v., lat. views of conjoined valves, ×2; *3d,e,* ped.v. int., brach.v. int., ×4 (445).

Family PAURORTHIDAE Öpik, 1933

[Paurorthidae Öpik, 1933, p. 11]

Small, subequally convex to ventribiconvex, ventral interarea typically curved, apsacline, dorsal interarea shorter, anacline, delthyrium open, rarely restricted by lateral plates, notothyrium open; ventral muscle field subtriangular, anteriorly thickened, with prominent median ridge developed anterior to field; cardinal process simple ridge or absent, brachiophores simple; ventral mantle canal system saccate, dorsal lemniscate to digitate. *L.Ord.-M.Ord.*

Paurorthis Schuchert & Cooper, 1931, p. 243 [**Orthambonites parva* Pander, 1830, p. 83; OD] [=*Nereidella* Wang, 1955, p. 338 (type, *N. typa*); *Paurorthina* Rubel, 1961, p. 187 (type, *P. resima*)]. Subcircular to subquadrate, sulcus in brachial valve, fascicostellate; ventral muscle field with adductor and median diductor lobes of variable size, median ridge commonly narrow, *vascula media* subparallel; brachiophores with bases greatly divergent relative to their tops, dorsal muscle field with small posterior and large anterior adductor scars, separated by strong median ridge. *L.Ord.-M.Ord.*, N.Eu.-N.Am.-Asia.——Fig. 211, *2a-d*. **P. parva* (Pander), L.Ord., USSR; *2a,b*, ped.v., brach.v. views of conjoined valves, ×2; *2c,d*, ped.v. int., brach.v. int., ×2 (729).——Fig. 211,*2e,f*. *Paurorthis sp.*, M.Ord.(Porterfield), USA (Tenn.); *2e,f*, ped.v. and brach.v. int. molds, ×2 (189).

Cyclomyonia Cooper, 1956, p. 974 [**C. peculiaris*]. Distinguished from *Paurorthis* by fine costellate ornament, initially subparallel ventral *vascula media* becoming widely divergent at front of broad median ridge, and dorsal posterior adductor scars arranged posterolateral to anterior pair. *M.Ord.*, E. USA.——Fig. 211,*1*. **C. peculiaris*, Porterfield, USA(Ala.); *1a,b*, ped.v. ext., int., ×2, ×3; *1c*, brach.v. int., ×4; *1d*, imperfect brach.v. int., ×3 (189).

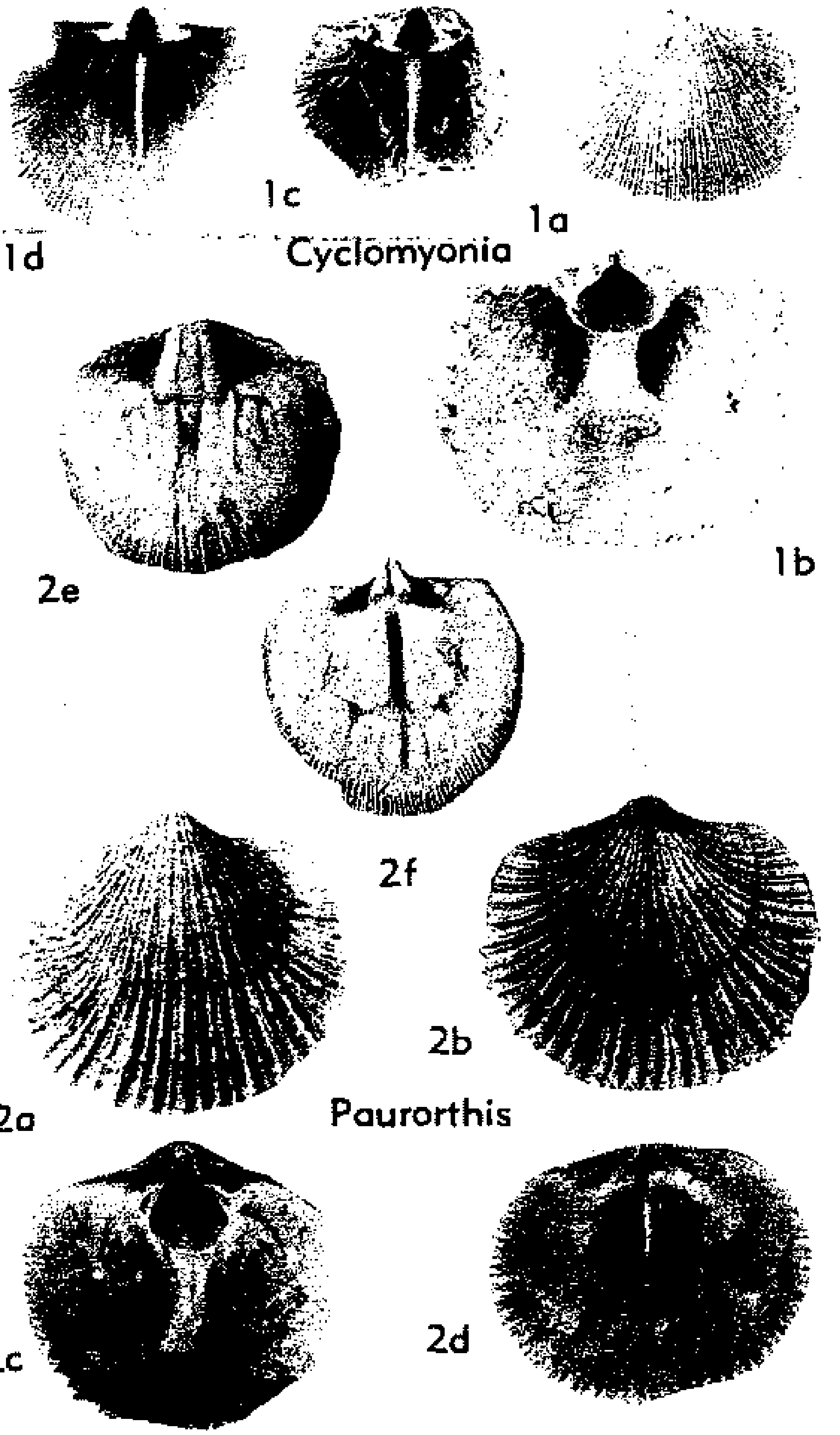


Fig. 211. Paurorthidae (p. *H*333).

Family DALMANELLIDAE Schuchert, 1913

[*nom. transl.* Schuchert & LeVene, 1929, p. 15 (*ex* Dalmanellinae Schuchert, 1913, p. 382)] [=Wattsellidae Schuchert & Cooper, 1931, p. 246; Isorthinae Schuchert & Cooper, 1931, p. 247; Onniellidae Öpik, 1933, p. 14]

Convexo-concave to plano-convex profile, ventral interarea curved, apsacline, dorsal interarea shorter, anacline, delthyrium and notothyrium open, coarsely fascicostellate to finely costellate ornament very rarely with hollow costellae, variably developed dorsal sulcus at least in young growth stages; ventral muscle field usually umbonal, broadly cordate to bilobed, with adductor scar rarely enclosed by median diductor lobes; cardinal process varying from simple ridge to elaborate trilobed myophore with shaft, bases of simple brachiophores variably disposed, fulcral plates commonly developed; dorsal adductor scar quadripartite, mantle canal system commonly lemniscate in both valves. *L.Ord.-L.Carb.*

Dalmanella Hall & Clarke, 1892, p. 205 [**Orthis testudinaria* Dalman, 1828, p. 115; OD] [=*Wattsella* Bancroft, 1928, p. 55 (type, *W. wattsi*); *Idiorthis* McLearn, 1924, p. 56 (type, *I. matura*); *Nocturnellia* Havlíček, 1950, p. 53 (type, *Orthis nocturna* Barrande, 1879)]. Subcircular, ventribiconvex, with variably developed dorsal sulcus, coarsely to finely costellate; ventral muscle field cordate, *vascula media* slightly divergent; cardinal process undifferentiated bilobed, brachiophore bases convergent onto median ridge, fulcral plates usually present. *L.Ord.-L.Sil.*, N.Hemis.——Fig. 212,*3a-e*. **D. testudinaria* (Dalman), U.Ord., Sweden; *3a-e*, ped.v., brach.v., lat., post., ant. views of conjoined valves, ×2 (880).——Fig. 212,*3f,g*. *D. wattsi* (Bancroft), M.Ord.(Marshbrook.), Eng.; *3f,g*, brach.v. int., ped.v. int. mold, ×1.5 (Wright, n).

Aulacella Schuchert & Cooper, 1931, p. 246 [**Orthis eifeliensis* Schnur, 1853, p. 213; OD]. Subequally biconvex, with low ventral fold and shallow dorsal sulcus, rarely reversed in adult shells; costellae hollow, ventral muscle scar elongatedly bilobate, *vascula media* slightly divergent; cardinal process usually trilobed, brachiophore bases greatly divergent relative to their tops. *M.Dev.-L.Carb.*, N.Hemis.——Fig. 212,*1*. **A. eifelensis* (de Verneuil), M.Dev.(Couvin.), Ger.-Pol.; *1a,b*, ped.v. ext., brach.v. ext., ×1.5; *1c*, brach.v. int., ×1.5 (729); *1d*, ped.v. int., ×2.5 (71).

Bancroftina Sinclair, 1946, p. 295 [*pro Raymondella* Whittington, 1938 (*non* Reed, 1935)] [**Raymondella typa* Whittington, 1938, p. 249, =*R. typa* Bancroft, 1933, p. 3 (*nom. nud.*); OD]. Ventral muscle field narrowly bilobate, initially subjacent *vascula media* becoming divergent anteriorly; cardinal process undifferentiated trilobed, brachiophore bases subparallel to hinge line, ancillary struts present, fulcral plates rare. *M.Ord.-U.Ord.*, G.Brit.-Ire.——Fig. 212,*4*. **B. typa* (Whittington), M.Ord.(Caradoc.), Eng.; *4a*, ped.v. int. mold, ×1.5; *4b,c*, brach.v. int. mold, cast, ×1.5 (Wright, n).

Cariniferella Schuchert & Cooper, 1931, p. 246 [**Orthis carinata* Hall, 1843, p. 267; OD]. Like *Aulacella* but typically convexo-concave profile with persistent narrow dorsal sulcus and sharp ventral fold; myophore trilobate. *U.Dev.*, N.Am.-W. Eu.-N. Afr.-C. Asia-Australia.——Fig. 212,*10*. **C. carinata* (Hall), USA(N.Y.); *10a,b*, ped.v. ext., brach.v. ext., ×1.5; *10c,d*, ped.v. and brach. v. int. molds, ×1.5 (729).

Cryptothyris Bancroft, 1945, p. 223 [**Resserella paracyclica* Bancroft, 1928, p. 56; OD] [=*Crassiorina* Havlíček, 1950, p. 36 (type, *Orthis notata* var. *crassior* Barrande, 1879)]. Ventribiconvex profile, with brachial valve feebly sulcate in early growth stages only; ventral muscle field cordate, diductor lobes not extending much beyond broad adductor, *vascula media* initially divergent; cardinal process undifferentiated bilobed, brachiophore bases slightly divergent relative to their tops, fulcral plates rare. *M.Ord.*, Eng.-Boh.——Fig. 212, *7*. **C. paracyclica* (Bancroft), Caradoc, Eng.; *7a,b*, ped.v. and brach.v. int. molds, ×3 (880).

Dedzetina Havlíček, 1950, p. 33 [**Parmorthis (Dedzetina) macrostomoides*; OD]. Like *Resserella*, but with convex brachial valve and divergent ventral *vascula media*. *U.Ord.(Ashgill.)*, Boh.

Diceromyonia Wang, 1949, p. 35 [**Orthis tersa* Sardeson, 1892, p. 331; OD]. Like *Paucicrura* but with ventral muscle field composed of adductor scar enclosed by greatly elongated diductor scars. *U.Ord.*, N.Am.——Fig. 212,*5*. **D. tersa* (Sardeson), USA(Iowa); ped.v. int., ×1.3 (851).

Eodalmanella Havlíček, 1950, p. 24 [**Orthis socialis* Barrande, 1879, pl. 63, fig. III, 1-7; OD]. Finely costellate, ventribiconvex, with wide hinge line, subcarinate pedicle valve and gently convex medially sulcate brachial valve; ventral muscle field broadly triangular, *vascula media* divergent; cardinal process simple, ridgelike, brachiophore bases greatly divergent relative to their tops. *L. Ord.(Llanvirn.)*, Boh.——Fig. 212,*2*. **E. socialis* (Barrande); *2a,b*, ped.v. int. mold and brach.v. int., ×2 (Wright, n).

Eremotrema Cooper, 1956, p. 959 [**E. biconvexum*; OD]. Like *Howellites*, but with fissured, trilobed cardinal process and ventral *vascula media* initially adjacent. *M.Ord.*, E.USA-Scot.——Fig. 212,*9*. **E. biconvexum*, Benbolt, USA(Va.); *9a-c*, brach.v., post., lat. views of complete shell, ×2; *9d*, ped.v. int., ×2; *9e*, brach.v. int., ×3 (189).

Fascicostella Schuchert & Cooper, 1931, p. 246 [**Strophomenes gervilii* Defrance, 1827, p. 152; OD]. Like *Resserella* but coarsely fascicostellate. *U.Sil.* (Pol.)-*L.Dev.*, Eu.-N.Afr.-C. Asia-Australia-N.Z.——Fig. 212,*6*. **F. gervilii* (Defrance), L. Dev., Boh.; *6a,b*, ped.v. ext., brach.v. ext., ×1.5 (729).

Heterorthina Bancroft, 1928, p. 59 [**H. praeculta*; OD] [=*Elsaella* Alichova, 1960, p. 192 (*pro Bekkerella* Rosenstein, 1943, *non* Reed, 1936) (type, *Bekkerella bekkeri* Rosenstein, 1943)]. Like *Onniella* but with convex pedicle valve, subplanar brachial valve and large splayed ventral diductor scars, bounded by ridges uniting anteromedially to enclose small adductor scar, and widely divergent ventral *vascula media*. *M.Ord.-U.Ord.*, Eu. (Eng.-Boh.-Est.)-?USA(Ohio).——Fig. 212,*8*. **H. praeculta*, M.Ord.(Caradoc.), Eng.; *8a,b*, ped.v. int. mold, and brach.v. int., ×1.5 (Wright, n).

Howellites Bancroft, 1945, p. 203 [**Resserella (Howellites) striata*; OD] [=*Mesodalmanella* Havlíček, 1950, p. 26 (type, *M. flava*)]. Ventribiconvex, finely costellate with high ventral umbo and gently convex sulcate brachial valve; ventral muscle field bilobate, *vascula media* slightly divergent and greatly divided; cardinal process undifferentiated bilobed, brachiophore bases slightly to greatly divergent relative to their tops, fulcral plates differentiated in some. *M.Ord.*, G.Brit.-Boh. ——Fig. 212,*11*. **H. striata* (Bancroft), Caradoc., Wales; *11a,b*, ped.v. ext., brach.v. ext., ×2.5; *11c*, ped.v. int. mold, ×2.5; *11d*, brach.v. int. mold, ×2.5; *11e*, brach.v. int., ×3.5 (878).

Isorthis Kozlowski, 1929, p. 29 [**Dalmanella (Isorthis) szajnochai*; OD]. Subequally biconvex profile, with shallow sulcus in brachial valve; ventral muscle field strongly bilobed, with long narrow diductor scars extending beyond thickened adductor ridge, *vascula media* divergent; cardinal process small, variably lobate, brachiophore bases divergent relative to tops, fulcral plates commonly developed. *Sil.-M.Dev.*, widespread.——Fig. 213, *3*. **I. szajnochai* (Kozlowski), U.Sil., Pol.; *3a-d*, ped.v., brach.v., lat., ant. views of conjoined valves, ×1; *3e*, brach.v. int., ×1.5 (Wright, n); *3f*, post. part of ped.v. int., ×1.5 (729).

Levenea Schuchert & Cooper, 1931, p. 246 [**Orthis subcarinata* Hall, 1857, p. 43; OD] [=*Dalmanellopsis* Khalfin, 1948, p. 208 (type, *D. septiger*)]. Like *Isorthis*, but profile ventribiconvex, with trilobed cardinal process and pentagonal ventral muscle field. *Sil.-M.Dev.*, N.Hemis. ——Fig. 213,*5*. **L. subcarinata* (Hall), L.Dev. (Birdsong), USA(Tenn.); *5a,b*, ped.v. int., brach. v. int., ×1.5 (729).

Mendacella Cooper, 1930, p. 377 [**Orthis uberis* Billings, 1866, p. 42; OD] [=*Dalejina* Havlíček, 1953, p. 5 (type, *D. hanusi*)]. Subequally biconvex profile; initial shallow sulcus of brachial

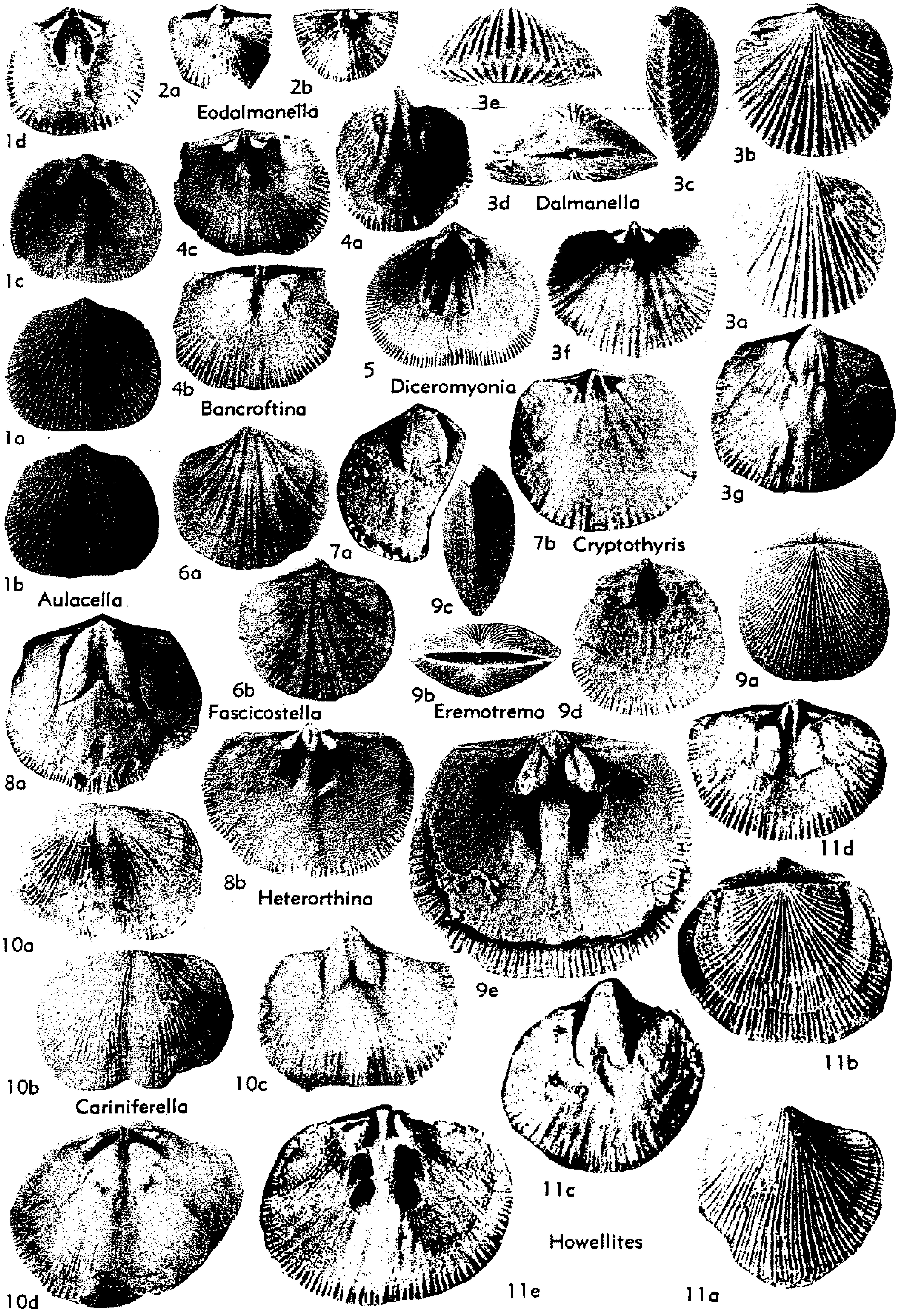


FIG. 212. Dalmanellidae (p. *H*333-*H*334).

valve replaced by fold in adult stages, with corresponding sulcus on adult pedicle valve, costellae hollow. Ventral muscle field bilobate, submedian diductor lobes extending beyond adductors; dental plates very short, commonly united with hinge line by secondary shell, *vascula media* slightly divergent. Cardinal process differentially bilobed to trilobed by fusion, brachiophore bases greatly divergent relative to tops, fulcral plates commonly developed. *U.Ord.-M.Dev.*, N.Am.-Eu.-C.Asia.——FIG. 213,*6*. **M. uberis* (BILLINGS), U.Ord.(Richmond.), Anticosti; *6a-c*, ped.v., brach.v., ant. views of complete shell, ×2 (Wright, n); *6d,e*, brach.v. int., ped.v. int., ×2 (729).

Onniella BANCROFT, 1928, p. 55 [**O. bröggeri*; OD] [=*Soudleyella* BANCROFT, 1945, p. 209 (type, *S. soudleyensis*)]. Gently ventribiconvex with wide hinge line, small ventral umbo and shallow, sulcate, brachial valve; ventral muscle scar widely cordate, mantle canal systems lemniscate with ventral *vascula media* slightly divergent and greatly divided; cardinal process undifferentiated bilobed, brachiophore bases greatly divergent relative to their tops, fulcral plates rare. *M.Ord.-U.Ord.*, Eu.-N.Am.——FIG. 213,*4*. *O. grandis* BANCROFT, M.Ord.(Acton.), Eng.; *4a*, ped.v. int. mold, ×2; *4b*, brach.v. int., ×1.5 (Wright, n).

Paucicrura COOPER, 1956, p. 956 [**Orthis rogata* SARDESON, 1892, p. 331; OD] [=*Cristiferina* COOPER, 1956, p. 961 (type, *C. cristata*)]. Ventribiconvex with gently convex sulcate brachial valve; ventral muscle field bilobate, *vascula media* divergent; cardinal process trilobed with median lobe forming variably developed crest, brachiophore bases divergent relative to their tops. *M. Ord.-U.Ord.*, N.Am.-Eu.——FIG. 213,*1*. **P. rogata* (SARDESON), M.Ord.(Trenton.), USA(Minn.); *1a-c*, ped.v., brach.v., post. views of complete shell, ×2; *1d*, brach.v. int., ×2 (189).

Proschizophoria MALLIEUX, 1912, p. 177 [**Orthis personata* ZEILER, 1857, p. 48; OD]. Large, convexo-concave, costellate, externally like *Schizophoria*; ventral muscle field broadly triangular; cardinal process with massive trilobed myophore continuous with long, thick, bladelike shaft; brachiophore bases divergent relative to their tops, continuous with ridge containing broadly suboval quadripartite adductor field. *Dev.*, W.Eu.-N.Afr.-C. Asia-E.N.Am.——FIG. 213,*8*. **P. personata* (ZEILER), L.Dev., Ger.; *8a,b*, brach.v. and ped.v. int. molds, ×0.7 (Wright, n), ×1.5 (729); *8c*, brach.v. cardinalia, ×1 (880).

Resserella BANCROFT, 1928, p. 54 [**Orthis canalis* J. DE C. SOWERBY in MURCHISON, 1839, p. 630, pl. 13, fig. 12a; OD] [=*Parmorthis* SCHUCHERT & COOPER, 1931, p. 246 (type, *Orthis elegantula* DALMAN, 1828)]. Ventribiconvex to plano-convex costellate shells with plane to gently convex brachial valve and deep pedicle valve; ventral muscle field small, cordate, *vascula media* adjacent for much of their length; teeth and sockets crenulated; cardinal process differentially bilobed to trilobed by fusion, brachiophore bases greatly divergent, commonly with fulcral plates, elongatedly oval dorsal adductor field bounded by low ridges. *Sil.*, widespread.——FIG. 213,*7*. *R. elegantula* (DALMAN), U.Sil.(Gotland.), Gotl.; *7a-c*, ped.v., brach. v., post. views of conjoined valves, ×2; *7d,e*, ped.v. int., brach.v. int., ×2 (729).

?**Teichertina** VEEVERS, 1959, p. 37 [**T. fitzroyensis*; OD]. Fascicostellate, ventribiconvex, transverse, with greatest width at hinge line; pedicle valve pyramidal, sulcus present in each valve, anterior margin emarginate; ventral muscle field possibly subapical; cardinal process bilobed, brachiophore bases subparallel to hinge line, fulcral plates present; brachial valve with quadripartite adductor field almost as long as valve; dorsal mantle canal system saccate-inequidistributate. *U.Dev.*, W.Australia.——FIG. 213,*2*. **T. fitzroyensis*; *2a-d*, ped.v., brach.v., lat., post. views of conjoined valves, ×3.5; *2e*, brach.v. int., ×3.5 (838).

Family DICOELOSIIDAE Cloud, 1948

[*nom. correct.* ROGER, 1952, p. 82 (*ex* Dicaelosiidae CLOUD, 1948, p. 374)] [=Bilobitidae SCHUCHERT & COOPER, 1931, p. 246]

Outline bilobed with emarginate anterior margin resulting from sulcus in each valve. Hinge line of variable width, but shorter than maximum valve width; ventral interarea apsacline, dorsal interarea shorter, anacline, delthyrium and notothyrium open. Ventral muscle field with adductor scars not enclosed by diductor scars; cardinal process with short, bilobed myophore and shaft, brachiophores long, bladelike plates. *U.-Ord.-M.Dev.*

Dicoelosia KING, 1850, p. 106 [=*Dicaelosia* KING, 1850 *(nom. null.)*; =*Bilobites* QUENSTEDT, 1869, p. 550 *(obj.)* *(non* RAFINESQUE, 1831; *nec* D'ORBIGNY, 1839; *nec* BRONN, 1848)] [**Anomia biloba* LINNÉ, 1767, p. 1154; OD]. Small, costellate, pedicle valve strongly convex, brachial valve varying from less convex to gently concave, with variably developed flattening of cardinal extremities; quadripartite dorsal adductor field rarely impressed. *U.Ord.-M.Dev.*, N.Am.-Eu.-C.Asia-Australia.——FIG. 214,*1*. **D. biloba* (LINNÉ), U.Sil. (Wenlock.), Gotl.; *1a-e*, ped.v., brach.v., lat., post., ant. views of conjoined valves, ×3; *1f,g*, ped.v. int., brach.v. int., ×5 (Wright, n).

Family KAYSERELLIDAE Wright, n. fam.

Ventribiconvex, ventral interarea curved, apsacline, dorsal interarea shorter, anacline, delthyrium open or with variably developed apical plate or notodeltidium, ornament cos-

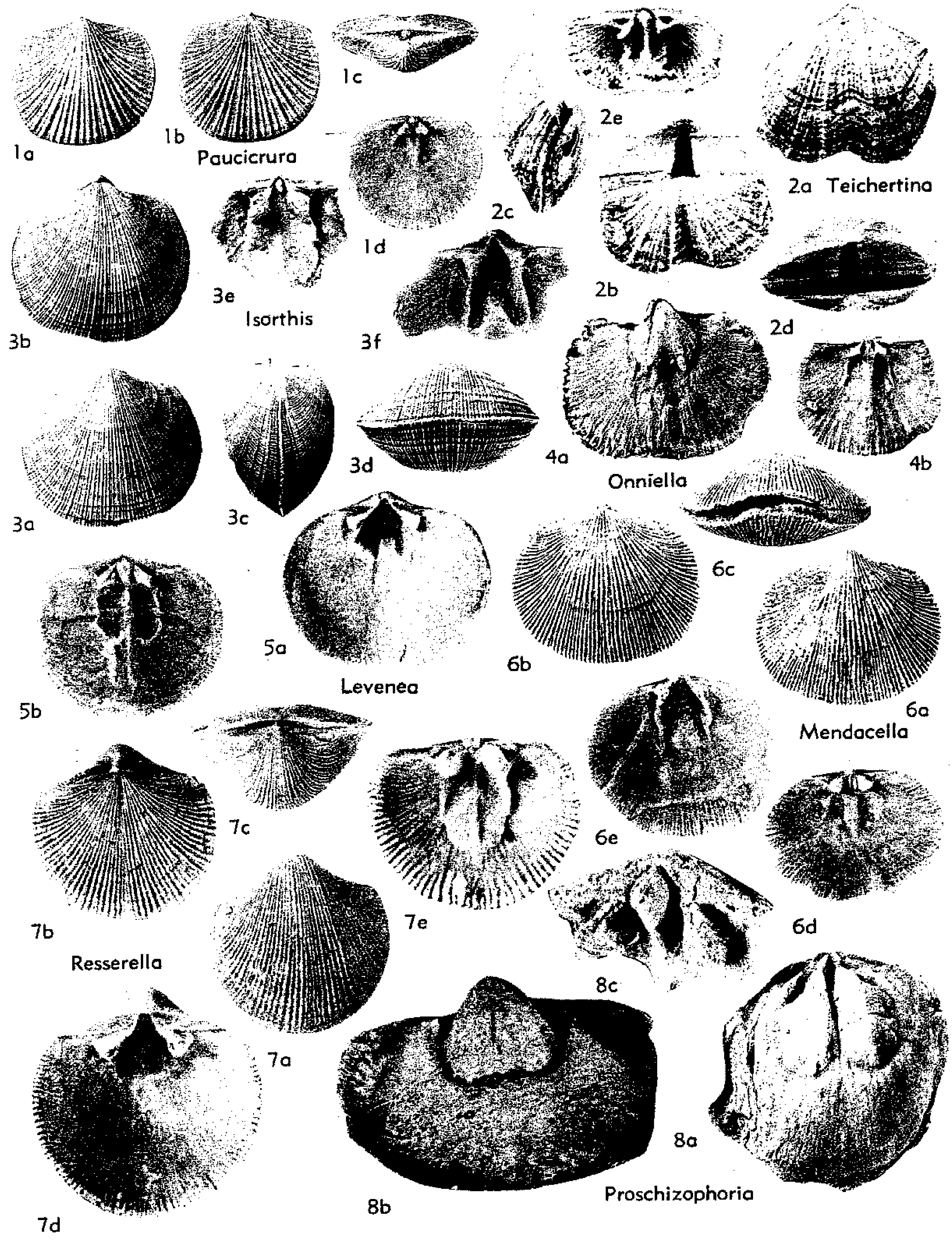


FIG. 213. Dalmanellidae (p. *H*334, *H*336).

tellate, sulcus in brachial valve; dental plates short, stout, receding; brachiophores short, stout, bases varying in attitude, fulcral plates commonly developed; shell space divided longitudinally by high dorsal septum of subtriangular outline, commonly extending ventrally to reach pedicle valve, and anteriorly almost to valve margin; ventral mantle canal system lemniscate, dorsal also probably lemniscate. *M.Dev.-U.Dev.*

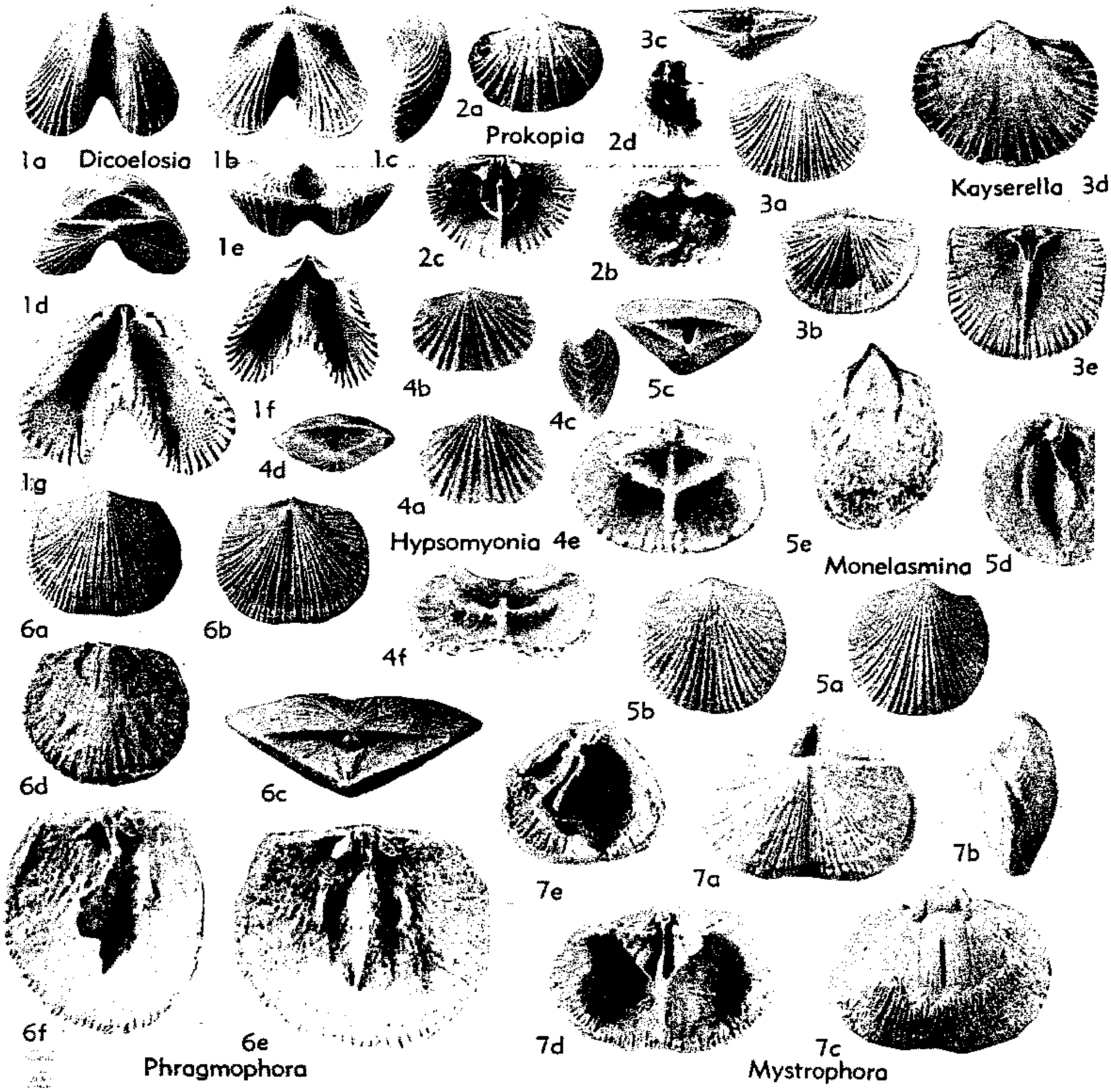


FIG. 214. Dicoelosiidae _(1)_; Kayserellidae (Kayserellinae) _(3)_, (Prokopiinae) _(2, 5-6)_; Mystrophoridae _(7)_; Hypsomyoniidae _(4)_ (p. _H336-H339_).

Subfamily KAYSERELLINAE Wright, n. subfam.

Cardinal process with bilobate myophore and slender shaft, brachiophore bases convergent on to median septum to form septalium. _M.Dev._

Kayserella Hall & Clarke, 1892, p. 259 [*_Orthis lepida_ Schnur, 1853, p. 218; OD]. Subcircular to transverse, delthyrium open; ventral muscle field short, wide, adductor scars wide; fulcral plates present, dorsal adductor field not impressed, presumably situated on valve floor. _M.Dev._, Eu.-E.N. Am.——Fig. 214,_3a-c_. *_K. lepida_ (Schnur), Ger.; _3a-c_, ped.v., brach.v., post. views of conjoined valves, ×2 (185).——Fig. 214,_3d,e_. _K. americana_ Cooper, USA(N.Y.); _3d,e_, ped.v. int. mold, brach. v. int., ×3 (185).

Subfamily PROKOPIINAE Wright, n. subfam.

Cardinal process with myophore and shaft bilobate, brachiophore bases suberect, anteriorly divergent, adductor field clearly defined by thickened margin. _M.Dev.-U.Dev._

Prokopia Havlíček, 1953, p. 5 [*_P. bouškai_; OD]. Small, subcircular to transverse, delthyrium containing flat apical plate; ventral muscle field indistinct; fulcral plates absent, adductor field suboval, divided by high median septum extending to anterior margin. _M.Dev._, Boh.——Fig. 214,_2_. *_P. bouskai_; _2a,b_, ped.v. ext., int., ×5; _2c,d_, brach.v. int., brach.v. int. (oblique), ×5 (Wright, n).

Monelasmina Cooper, 1955, p. 53 [*_Orthis deshayesi_ Rigaux, 1873, p. 50; OD]. Like _Prokopia_ but with small fulcral plates, subrectangular dorsal adductor field, apical plate apparently lacking; ventral muscle field subtriangular to elongatedly oval, adductor scars moderately wide, separating slender diductor scars, _vascula media_ slightly divergent, greatly divided. _U.Dev._, W.Eu.-W.Can.

——Fig. 214,*5*. **M. deshayesi*, Fr.; *5a-c*, ped.v., brach.v., post. views of conjoined valves, ×3; *5d*, brach.v. int. (oblique), ×4; *5e*, ped.v. int. mold, ×3 (185).

Phragmophora Cooper, 1955, p. 50 [**P. schnuri*; OD]. Subcircular, delthyrium closed by variably developed convex notodeltidium; ventral muscle field broadly triangular, adductor field wide, flanked by diductor scars of similar width, *vascula media* moderately divergent, greatly divided; fulcral plates commonly developed in larger shells, dorsal adductor field subquadrate, with median septum rarely reaching anterior margin. *M.Dev.*, Ger.-Pol.——Fig. 214,*6*. **P. schnuri*, Ger.; *6a,b*, ped.v., brach.v. views of conjoined valves, ×1; *6c*, post. view of conjoined valves, ×2; *6d*, ped.v. int. mold, ×1; *6e,f*, normal, oblique views of brach.v. int., ×2 (185).

Family MYSTROPHORIDAE Schuchert & Cooper, 1931

[Mystrophoridae Schuchert & Cooper, 1931, p. 246]

Ventribiconvex, with high apsacline ventral interarea, dorsal interarea shorter, anacline, delthyrium and notothyrium open; ventral muscle field with adductor scars not enclosed by slightly longer diductor scars; cardinal process with bilobate myophore and shaft united with very high median septum which supports well-developed cruralium, brachiophores long, ventrally directed, fulcral plates present. *M.Dev.*

Mystrophora Kayser, 1871, p. 612 [**Orthis areola* Quenstedt, 1871, p. 589; SD Williams & Breger, 1916, p. 61]. Transverse, pedicle valve of subpentagonal outline, costellate, sulcus in brachial valve; ventral adductor field broad, ?short median septum anteriorly at mid-valve, *vascula media* subparallel; dorsal median septum very high, cruralium divisible into 4 plates. *M.Dev.*, W.Eu.——Fig. 214,*7*. **M. areola* (Quenstedt), Ger.; *7a,b*, brach.v., lat. views of conjoined valves, ×1.5; *7c*, ped.v. int. mold, ×1.5; *7d,e*, normal, oblique views of brach.v. int., ×2 (185).

Family HYPSOMYONIIDAE Wright, n. fam.

Ventribiconvex, interareas well developed, delthyrium and notothyrium open; dental plates short, receding, ventral muscle field not well known; cardinal process with bilobate myophore and shaft, brachiophore bases subparallel to hinge line, fulcral plates absent, adductor scars situated on platform rising from valve floor in front of brachiophores, supported medianly by strong septum. *M.Dev.-U.Dev.*

Hypsomyonia Cooper, 1955, p. 52 [**H. stainbrooki*; OD]. Small, transverse, costellate, with sulcus in brachial valve. *M.Dev.-U.Dev.*, N.Am.-C. Eu.-W. Australia.——Fig. 214,*4*. **H. stainbrooki*, U.Dev., USA(Iowa); *4a-d*, ped.v., brach.v., lat., post. views of conjoined valves, ×5; *4e,f*, normal, ant. views of brach.v. int., ×7.5 (185).

Family HARKNESSELLIDAE Bancroft, 1928

[*nom. transl.* Alichova, 1960, p. 192 (*ex* Harknessellinae Bancroft, 1928, p. 173); *emend.* Wright, herein]

Transversely subquadrate, hinge line commonly mucronate, subequally biconvex to dorsibiconvex, ventral interarea apsacline, dorsal interarea commonly anacline to orthocline, delthyrium and notothyrium open, fascicostellate, prominent, commonly sharply angular, ventral fold and dorsal sulcus; ventral muscle field suboval to subpentagonal, diductor scars commonly extending only slightly anterior to narrowly rectangular adductor scars; cardinal process with lobate myophore and shaft, brachiophores variably disposed, notothyrial platform with deep adductor pits; mantle canal systems saccate to lemniscate. *M.Ord.-U.Ord.*

Harknessella Reed, 1917, p. 862 [**Orthis vespertilio* Sowerby, 1839, p. 640; OD]. Ventral muscle field subpentagonal, bilobed; brachiophores long, bladelike, bases convergent, fused or not fused to fulcral plates. *M.Ord.*, Eu.——Fig. 215,*4*. **H. vespertilio* (Sowerby), Caradoc., Eng.; *4a*, ped.v. ext., ×1; *4b,c*, ped.v. int. molds, ×1; *4d,e*, brach. v. int. mold, cast, ×1 (Wright, n).

Horderleyella Bancroft, 1928, p. 178 [**H. plicata*; OD]. Commonly small for family, coarsely fascicostellate; ventral muscle field small, suboval to rhomboidal; cardinalia small, crural pits and fulcral plates well differentiated. *M.Ord.*, Eng.-Wales. ——Fig. 215,*1*. **H. plicata*, Caradoc., Eng.; *1a,b*, ped.v. ext., brach.v. ext., ×1; *1c*, ped.v. int. mold, ×1; *1d,e*, brach.v. int. mold, cast, ×1 (Wright, n).

Reuschella Bancroft, 1928, p. 180 [**R. semiglobata*; OD] [=*Reushella* Alichova, 1960 (*nom. null.*)]. Like *Harknessella* but commonly larger with deep dorsal valve, coarser ornament, and shorter, more widely splayed brachiophores. *M. Ord.-U.Ord.*, Eu.-N.Am.——Fig. 215,*3a-d*. **R. semiglobata*, M.Ord.(Caradoc.), Eng.; *3a*, brach.v. ext., ×1; *3b,c*, brach.v. int. mold, cast, ×1; *3d*, cardinalia, ×2.5 (Wright, n).——Fig. 215,*3e*. *R.* sp. cf. *R. horderleyensis* Bancroft, M.Ord. (Caradoc.), Wales; ped.v. int. mold, ×1.0 (878).

Smeathenella Bancroft, 1928, p. 177 [**S. harnagensis*; OD]. Large, flatly dorsibiconvex, of strophomenoid appearance; ventral muscle field small, rhomboidal or anteriorly truncated; cardi-

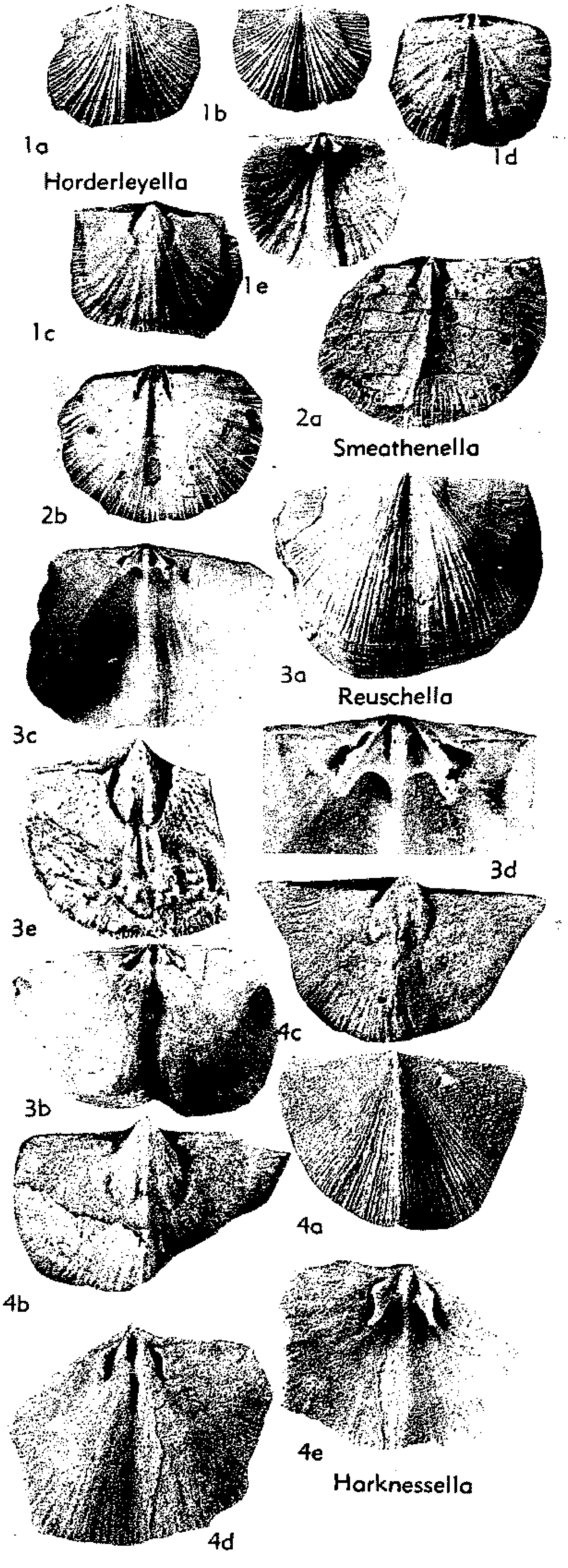


FIG. 215. Harknessellidae (p. H339-H340).

nal process small, brachiophores narrowly divergent, crural pits and fulcral plates not developed. *M.Ord.*, Eng.——FIG. 215,*2*. **S. harnagensis*; *2a,b*, ped.v. and brach.v. int. molds, ×1 (Wright, n).

Family HETERORTHIDAE Schuchert & Cooper, 1931

[Heterorthidae SCHUCHERT & COOPER, 1931, p. 246, *emend.* WRIGHT, herein]

Transversely subcircular to subquadrate with hinge line less than maximum shell width, concavo-convex to biconvex, ventral interarea apsacline, dorsal interarea anacline, delthyrium open, notothyrium open or with chilidium, typically finely costellate, rarely with ventral fold and dorsal sulcus; ventral muscle field large with long divergent, semicircular, commonly flabellate and scalloped, diductor scars with anterior ends widely separated, extending far beyond and not enclosing adductor scars; cardinal process narrow or semioval with commonly trilobate posteroventral surface, brachiophores ridge-like, fused to valve floor throughout their length, dorsal adductor field quadripartite, subcircular; dorsal mantle canal system lemniscate, ventral probably also lemniscate. *M.Ord.-U.Ord.*

Heterorthis HALL & CLARKE, 1892, p. 202 [**Orthis clytie* HALL, 1861, p. 90; OD]. Concavo-convex to plano-convex, chilidium well developed; ventral adductor scars small, commonly cordate; fulcral plates not differentiated; subperipheral ridge developed in adult valves. *M.Ord.-U.Ord.*, Eu.-E.N.Am.——FIG. 216,*1a,b*. **H. clytie* (HALL), M.Ord.(Trenton.), USA(Ky.); *1a,b*, ped.v. int., brach.v. int., ×1.5 (729).——FIG. 216,*1c-e*. *H. alternata* (SOWERBY), M.Ord.(Caradoc.), Eng.; *1c*, brach.v. ext., ×1.5; *1d,e*, ped.v. and brach.v. int. molds, ×1.5 (878).

Planoharknessella HAVLÍČEK, 1950, p. 42 [**P. planidorsa*; OD]. Plano-convex, with feeble fold and sulcus, chilidium lacking; ventral adductor scars poorly defined; crural pits small, fulcral plates feebly differentiated; subperipheral ridge lacking. *M.Ord.(Caradoc.)*, Boh.——FIG. 216,*2*. **P. planidorsa*; *2a*, brach.v. ext., ×2; *2b,c*, ped.v. and brach.v. int. molds, ×2 (403).

Svobodaina HAVLÍČEK, 1950, p. 38 [**Orthis inclyta* BARRANDE, 1879, pl. 67, fig. 1; OD] [=*Svobodiana* ALICHOVA, 1960 *(nom. null)*]. Subequally biconvex to dorsibiconvex, chilidium lacking; ventral adductor scars small, poorly defined anteriorly; fulcral plates rarely defined; subperipheral ridge lacking. *M.Ord.-U.Ord.*, Eu.——FIG. 216,*3*. **S. inclyta* (BARRANDE), M.Ord.(Caradoc.), Boh.; *3a,b*, ped.v. and brach.v. int. molds, ×1.5 (403).

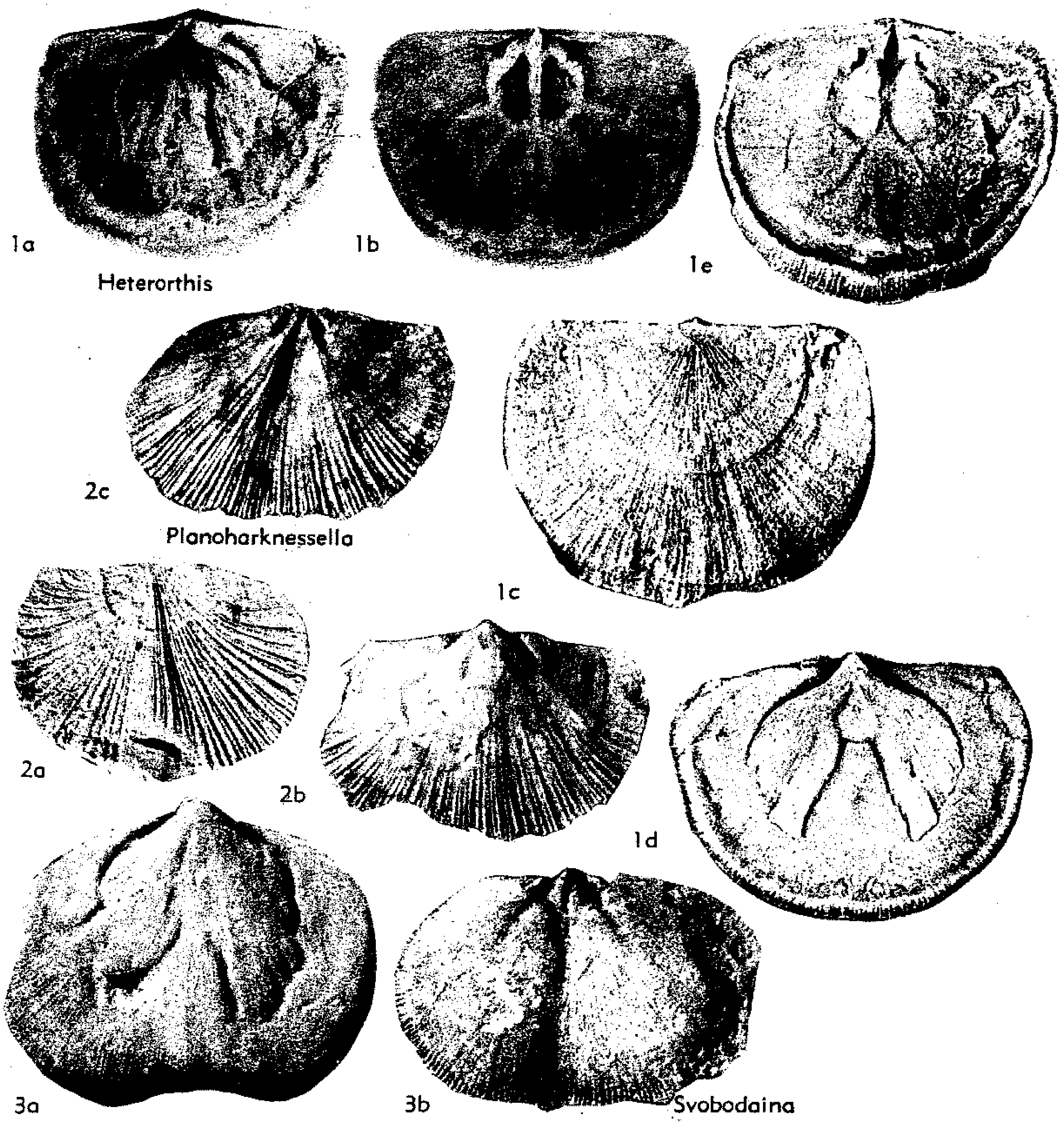


FIG. 216. Heterorthidae (p. *H*340).

Family RHIPIDOMELLIDAE Schuchert, 1913

[Rhipidomellidae SCHUCHERT, 1913, p. 382]

Dorsibiconvex to plano-convex, ventral interarea apsacline to orthocline, dorsal interarea commonly orthocline, both becoming much reduced; delthyrium open, notothyrium with chilidial plates developed rarely, costellae hollow, fold and sulcus commonly not well developed; ventral muscle field large, oval to cordate, adductor scars elliptical, completely enclosed by diductors commonly with scalloped margins; cardinal process with lobate myophore and short shaft, brachiophores commonly short, blunt, with suberect bases, fulcral plates absent; ventral and dorsal mantle canal systems lemniscate. *L.Sil.-U.Perm.*

Rhipidomella OEHLERT, 1890, p. 372 [*pro Rhipidomys* OEHLERT, 1887 (*non* WAGNER, 1844)] [**Terebratula michelini* LÉVEILLÉ, 1835, p. 39; OD] [=*Blairella* MILLER & GURLEY, 1896 (*nom. nud.*); *Pseudodicoelosia* BOUCOT & AMSDEN, 1958, p. 162 (type, *Rhipidomella oklahomensis* AMSDEN, 1951, p. 76); *Loganella* BOUCOT & AMSDEN, 1958, p. 164 (type, *Rhipidomella lehuquetiana* CLARKE, 1906, p. 202); *Rhipidomelloides* BOUCOT & AMS-

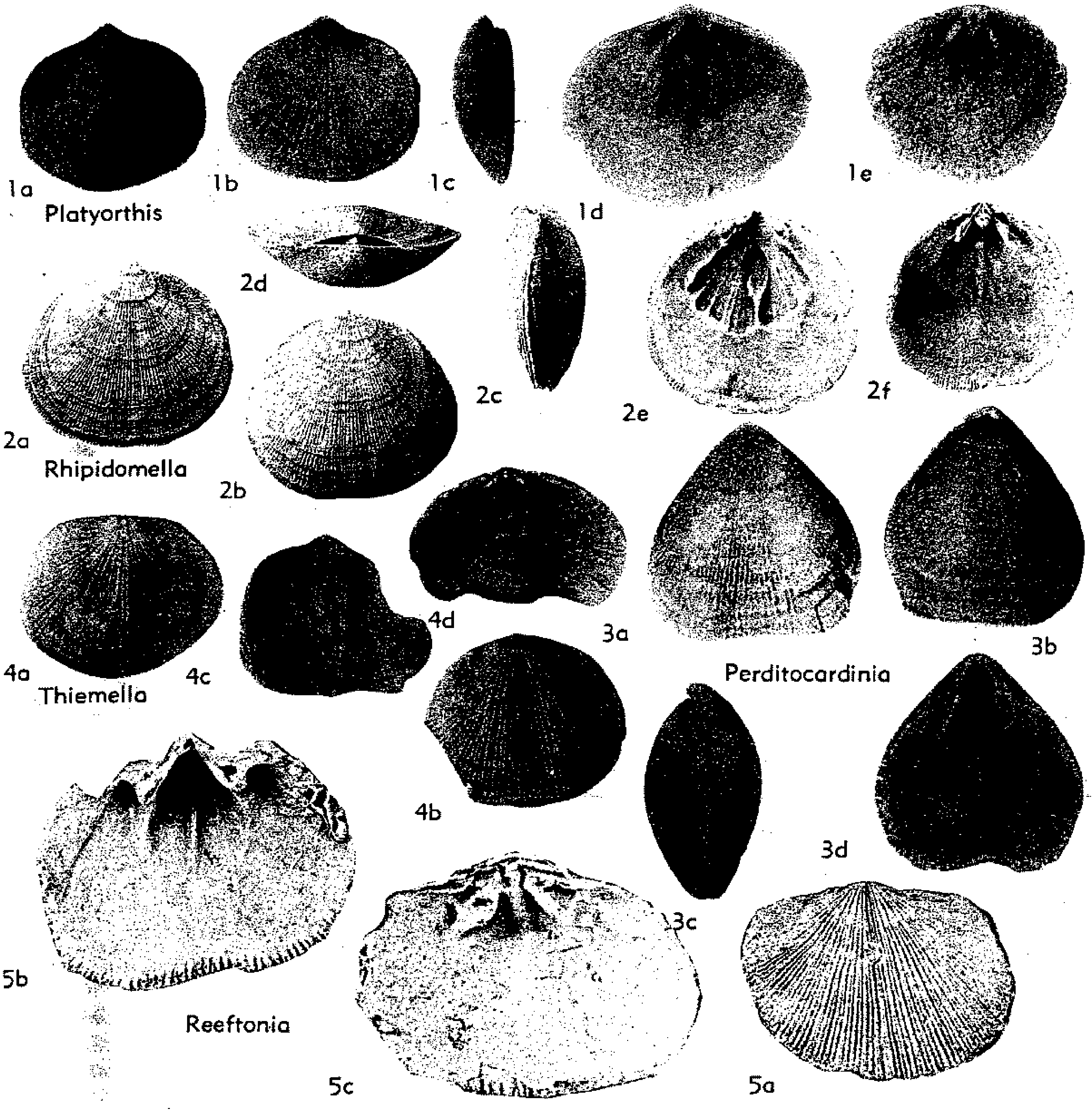


FIG. 217. Rhipidomellidae (p. H341-H343).

DEN, 1958, p. 165 (type, *Rhipidomella henryhousensis* AMSDEN, 1951, p. 74); *Strixella* BOUCOT & AMSDEN, 1958,. p. 170 (type, *Rhipidomella acutisulcata* AMSDEN, 1951, p. 75)]. Subcircular to subtriangular, dorsibiconvex, chilidial plates common in later forms; ventral muscle field suboval, diductor scars broad, with strongly scalloped margins, separated in front of adductor scars by ridge which rarely continues beyond muscle field. *L.Sil.-U.Perm.*, cosmop.——FIG. 217,*2*. **R. michelini* (LÉVEILLÉ), L.Carb., Belg.; *2a-d*, ped.v., brach.v., lat., post. views of conjoined valves, ×1; *2e,f*, ped.v. int., brach.v. int., ×1 (Wright, n). [The four nominal genera erected by BOUCOT & AMSDEN in 1958 (106) differ from *Rhipidomella* and from one another only in features that normally are variable even within the limits of species. Thus, *Pseudodicoelosia* presumably is distinguished by a pronounced dorsal sulcus, short hinge line, and emarginate front edge; *Loganella* by abbreviation of the interarea and fusion of the cardinalia; *Rhipidomelloides* by the presence of flat marginal crenulations internally, rather than rounded ones; and *Strixella* by having an angular dorsal sulcus. A relatively short hinge line, which characterizes the whole group, is not strongly pronounced in *Pseudodicoelosia* (as in *Perditocardinia* or *Dicoelosia*) and its anterior emargination, a feature developed to some extent in many species of *Rhipidomella*, is not always evident in the type-species (30, pl. 15, fig. 37). The conspicuous dorsal sulcus of *Pseudodicoelosia* and *Strixella* seems not to be a diagnostic character differing from the dorsal sulcus commonly present, although tending to be shallow or impersistent, in *Rhipidomella*. The association of *Pseudodicoelosia*, *Rhipidomelloides*, and *Strixella* in the same strata (U.Sil., Henryhouse F., Okla.) suggests that they may be simply "form species."]

Perditocardinia SCHUCHERT & COOPER, 1931, p. 246 [**Orthis dubia* HALL, 1858, p. 12; OD]. Like *Rhipidomella* but of rostrate form, with interareas obsolete and hinge line very narrow. *L.Carb.-M.Perm.*; N.Am.-S.Asia.——FIG. 217,*3*. **P. dubia* (HALL), Miss., USA(Ind.); *3a-c*, ped.v., brach.v., lat. views of conjoined valves, ×1; *3d*, ped.v. int., ×2 (729).

Platyorthis SCHUCHERT & COOPER, 1931, p. 246 [**Orthis planoconvexa* HALL, 1859, p. 168; OD]. Subcircular to subelliptical, plano-convex; ventral muscle field broad, suboval to slightly cordate, diductor scars rarely with scalloped margins; cardinal process with large bilobed or trilobed myophore and medianly cleft shaft. *U.Sil.-M.Dev.*, widespread.——FIG. 217,*1*. **P. planoconvexa* (HALL), L.Dev.(Deerpark.), USA(Md.); *1a-c*, ped.v., brach.v., lat. views of conjoined valves, ×1; *1d,e*, ped.v. int., brach.v. int., ×1.5 (729).

Reeftonia ALLAN, 1947, p. 436 [**R. marwicki*; OD]. Transversely elliptical, plano-convex, sulcus in brachial valve; ventral muscle field cordate, diductor scars without scalloped margins; cardinal process with small undivided myophore and short shaft. *L.Dev.*, N.Z.——FIG. 217,*5*. **R. marwicki*; *5a*, brach.v. ext., ×2; *5b,c*, ped.v. int., brach.v. int., ×2 (27).

Thiemella WILLIAMS, 1908, p. 59 [**T. villenovia*; OD]. Like *Rhipidomella* but with prominent dorsal sulcus and ventral fold, and elliptical to subcordate ventral muscle field with median ridge extending well beyond muscle field. *U.Dev.-L.Carb.*, E.USA-Ger.——FIG. 217,*4*. **T. villenovia*, U.Dev. (Chemung.), USA(N.Y.); *4a,b*, ped.v. ext., brach. v. ext., ×1.5; *4c,d*, ped.v. int. mold, brach.v. int., ×1.5 (729).

Family LINOPORELLIDAE Schuchert & Cooper, 1931

[Linoporellidae SCHUCHERT & COOPER, 1931, p. 247]

Subequally biconvex to ventribiconvex, ventral interarea long, curved, apsacline, dorsal interarea shorter, curved, anacline, delthyrium and notothyrium open, fold and sulcus rarely well developed; ventral muscle field variable, dental plates strong; cardinal process simple ridge, continuous anteriorly with median septum, brachiophores long, bladelike, with bases convergent on to strong median septum to form septalium, fulcral plates present; ventral mantle canal system possibly saccate, dorsal probably lemniscate. *M.Ord.-U.Sil.*

Linoporella SCHUCHERT & COOPER, 1931, p. 247 [**Orthis punctata* DE VERNEUIL, 1848, p. 343; OD]. Subcircular to transverse, ornament costellate with radial rows of pits in interspaces; ventral muscle field elongate, clearly defined by anterior continuation of dental plates, adductor scars on median ridge which becomes more pronounced on valve floor in front of muscle field; cardinal process with expanded myophore and thin shaft, dorsal adductor field elongatedly oval. *L.Sil.-U.Sil.*, N.W. Eu.-E.N.Am.——FIG. 218,*5*. **L. punctata* (DE VERNEUIL), U.Sil.(Gotland.), Sweden; *5a,b*, brach. v., lat. views of conjoined valves, ×2 (Wright, n); *5c,d*, ped.v. ext., int., ×1.5; *5e*, cardinalia, ×2 (729).

Elasmothyris COOPER, 1956, p. 983 [**E. concinnula*; OD]. Minute, transverse, ventribiconvex with sulcus in brachial valve, costellate; ventral muscle field on horizontal plate extending across delthyrial cavity between base of dental plates; cardinal process wtih expanded myophore. *M.Ord.*, E.USA.——FIG. 218,*2*. **E. concinnula*, Porterfield, Ala.; *2a-c*, ped.v., post., ant. views of conjoined valves, ×5; *2d,e*, ped.v. int., brach.v. int., ×8 (189).

Laticrura COOPER, 1956, p. 979 [**L. pionodema*; OD]. Subcircular, ventribiconvex, costellate with hollow costellae developed rarely; ventral muscle field subtriangular, adductor scars and median diductor lobes of similar size, apical plate variably developed; cardinal process without expanded myophore, brachiophores large, S-shaped in section, dorsal adductor field narrow, elongate. *M.Ord.-U.Ord.*, E.USA-Scot.-Ire.——FIG. 218,*7*. **L. pionodema*, M.Ord.(Porterfield.), USA(Va.); *7a-c*, ped.v., brach.v., lat. views of conjoined valves, ×2; *7d,e*, ped.v. int., brach.v. int., ×2, ×4; *7f*, ant. view of cardinalia, ×6 (189).

Orthotropia HALL & CLARKE, 1894, expl. pl. 84 [**O. dolomitica*; OD(M)]. Ventribiconvex, interior very close to *Linoporella* but probably without expanded myophore; ornament unknown. *U.Sil.(Wenlock.)*, USA(Wis.).

Salopia WILLIAMS, 1955, p. 409 [**Orthis salteri* DAVIDSON, 1871, p. 255; OD]. Distinguished from *Laticrura* by very high, almost catacline ventral interarea, suboval ventral muscle field, simple bladelike brachiophores and commonly broader dorsal adductor field. *M.Ord.*, Eng.——FIG. 218,*1*. **S. salteri* (DAVIDSON), Caradoc.; *1a-c*, vent., post., lat. views of ped.v. int. mold, ×2; *1d*, brach.v. int., ×2 (Wright, n).

Family ANGUSTICARDINIIDAE Schuchert & Cooper, 1931

[*nom. transl.* WRIGHT, herein (*ex* Augusticardiniinae SCHUCHERT & COOPER, 1931, p. 243)] [=Apatorthidae ÖPIK, 1933, p. 5]

Biconvex with short hinge line, interareas short, curved, ventral apsacline, dorsal anacline, delthyrium and notothyrium open,

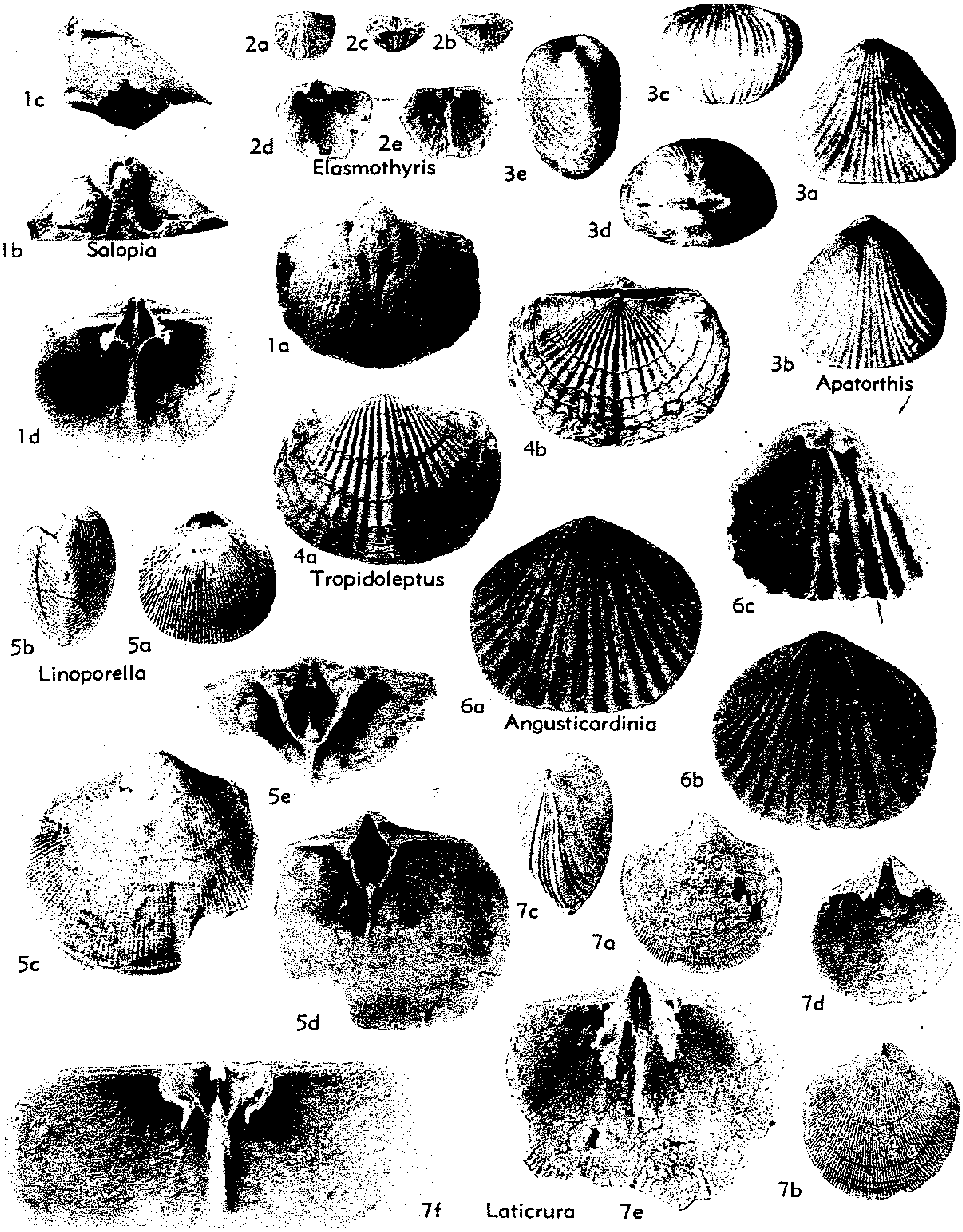


FIG. 218. Linoporellidae *(1-2, 5, 7)*; Angusticardiniidae *(3, 6)*; Tropidoleptidae *(4)* (p. *H*343-*H*346).

ornament of coarse subangular costae and costellae, dorsal fold and ventral sulcus variably developed; pedicle valve with small teeth supported by strong dental plates; cardinal process simple ridge or absent, brachiophores with bases convergent on to median septum; mantle canal systems unknown. *L.Ord.-U.Ord.*

The subfamily Angusticardiniinae, with the single genus *Angusticardinia*, was originally established as a subfamily of the Orthidae. ÖPIK (1933, p. 5-6) has indicated that

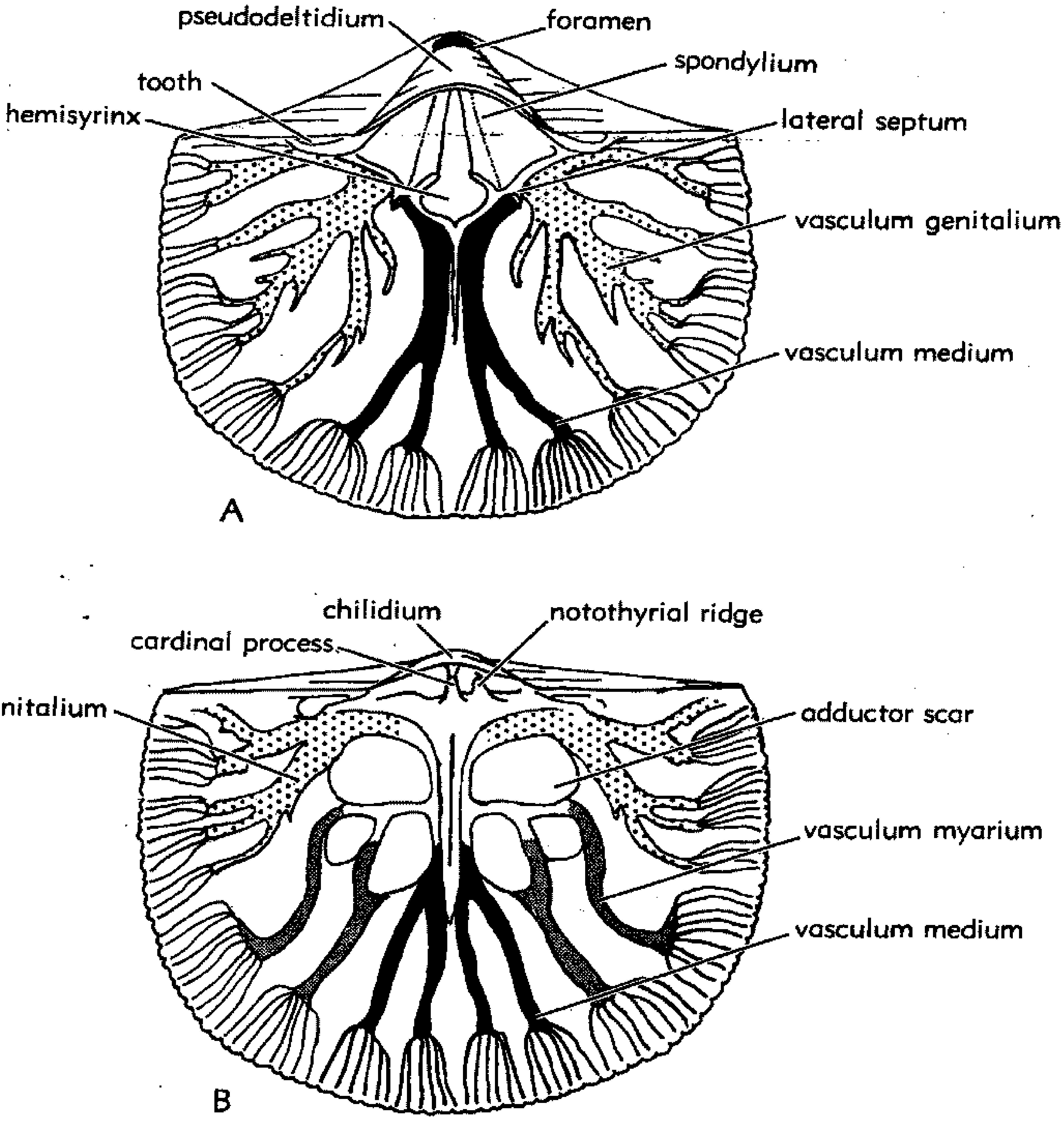


FIG. 219. Generalized illustrations of clitambonitidine pedicle valve *(A)* and brachial valve *(B)*, showing mantle canal systems of *Clitambonites* (after Öpik, 621).

the shell substance of *Angusticardinia* is probably punctate, although this is somewhat uncertain, as the examined shells have undergone recrystallization. The placing of the genus here with the punctate orthoid stocks is thus provisional; this necessitates suppression of the family Apatorthidae in favor of the Angusticardiniidae on grounds of priority.

Angusticardinia SCHUCHERT & COOPER, 1931, p. 244 [**Porambonites recta* PANDER, 1830, p. 97; OD]. Subcircular, small ears developed rarely, fold and sulcus feeble; cardinal process linear, brachiophores short, median septum prominent, dividing small quadripartite adductor scars. *L.Ord.*, E.Baltic-Boh.——FIG. 218,*6*. **A. recta* (PANDER), USSR; *6a,b*, ped.v., brach.v. views of conjoined valves, ×3; *6c*, brach.v. int., ×3 (729).

Apatorthis ÖPIK, 1933, p. 5 [**A. punctata*; OD]. Subtriangular, ears small but pronounced, fold and sulcus well developed, surface finely granulated; cardinal process absent? *M.Ord.-U.Ord.*, Est.——FIG. 218,*3*. **A. punctata*, M.Ord.; *3a-e*, ped.v., brach.v., ant., post., lat. views of conjoined valves, ×1.3 (620).

Family TROPIDOLEPTIDAE Schuchert, 1896

[*nom. transl.* SCHUCHERT & COOPER, 1932, p. 152 (*ex* Tropidoleptinae SCHUCHERT, 1896, p. 330)]

Hinge line wide, ventral interarea well developed, orthocline, delthyrium open; dorsal interarea shorter, anacline, notothyrium covered by antigydium. Teeth massive, outer sides strongly crenulated, separate from hinge line, supported by stout dental plates. High cardinal process with deep double diductor pit on ventral surface at posterior of thick notothyrial platform; anteriorly, pair of long crura develop apophyses which possibly form loop with posteriorly directed outgrowths from high anterior part of median septum. *L.Dev.-U.Dev.*

Tropidoleptus HALL, 1857, p. 151 [**Strophomena carinata* CONRAD, 1839, p. 64; OD]. Concavo-convex, subquadrate with narrow ventral fold and dorsal sulcus, ornamented by broad, rounded costae. *L.Dev.-U.Dev.*, Eu.-N.Afr.-N.Am.-S.Am.——FIG. 218,*4*. **T. carinatus* (CONRAD), M.Dev. (Hamilton), USA(N.Y.), *4a,b*, ped.v. ext., brach. v. ext., ×1 (Wright, n).

Suborder CLITAMBONITIDINA Öpik, 1934

[*nom. correct.* WILLIAMS, herein (*pro* Clitambonitoidea ÖPIK, 1934, p. 75]

Concavo-convex to convexo-concave, coarsely costellate to unequally parvicostellate, wide-hinged articulate brachiopods, commonly with long procline to apsacline ventral interarea and arched pseudodeltidium perforated by an apical foramen; shell substance impunctate or pseudopunctate. Teeth simple, rarely supplemented by denticles; ventral muscle field impressed exceptionally on floor of valve and on bounding dental plates, mostly on modified spondylium triplex or spondylium simplex; cardinal process usually a simple ridge fused posteriorly with strong, convex chilidium, rarely with ancillary ridges; socket ridges widely divergent, commonly ankylosed to strong, transverse notothyrial platform; dorsal adductor field quadripartite, normally divided by strong median ridge; mantle canal system in both valves pinnate with *vascula media*, *myaria*, and *genitalia* variably divided near nodes of origin. *Ord.*

DISCUSSION

The brachiopods classified as members of the Clitambonitidina constitute a fairly natural, but minor, group possessing a unique assemblage of morphological features, which, considered individually, are really more typical of other suborders within the phylum. This peculiarity is understandable in that Clitambonitidina have been recorded so far only from rocks of Ordovician age, a period when the definitive characters of many longer ranging groups were still being derived. Consequently, although they can be easily separated from other brachiopods, their "hybrid" qualities and the morphological instability of their contemporaries make it difficult to be certain about their origin.

With few exceptions, the Clitambonitidina are at first sight more like the Orthidina than any other group and the modal features of the 23 genera comprising the suborder confirm this impression (Fig. 219). Such characters include, for example, a biconvex, wide-hinged, costellate shell with a high ventral interarea and a simple ridgelike cardinal process, all of which are typically orthoid; and a pseudodeltidium pierced by a large apical foramen, a convex chilidium, and widely divergent socket ridges, which, together with the first set of characters, are so reminiscent of the billingsellid brachiopods that common ancestry seems the only acceptable explanation. Noteworthy variations of this basic pattern did occur and include the development of strong imbrication (e.g., *Clitambonites*), hollow costellae (e.g., *Tritoechia*), subsidiary notothyrial ridges flanking the cardinal process (e.g., *Clinambon*), and even the differentiation of the latter structure into a primitive myophore and shaft (e.g., *Eremotoechia*). Moreover, the pseudodeltidium (and to a lesser extent, the chilidium) is unknown among the Atelelasmatinae and Anomalorthinae so that the delthyrium of these stocks was open in the manner of the majority of the Orthidina. This loss of the pseudodeltidium does not seem to have arisen by resorption after its deposition. More probably it failed to develop during the differentiation of the young shell, which would account for the growth of low lateral plates flanking the delthyrium of *Atelelasma*. In any event, the pedicle must have remained functional throughout the life of most Clitambonitidina and was even additionally protected by an irregular, collar-like extension beyond the foramen of *Kullervo*, although ÖPIK (621, pl. 34, fig. 2b) has figured a remarkable seal of secondary shell plugging the foramen of *Antigonambonites planus* (PANDER).

The most conspicuous feature of the clitambonitoid shell is the spondylium, which, related as it is in its forward extension to

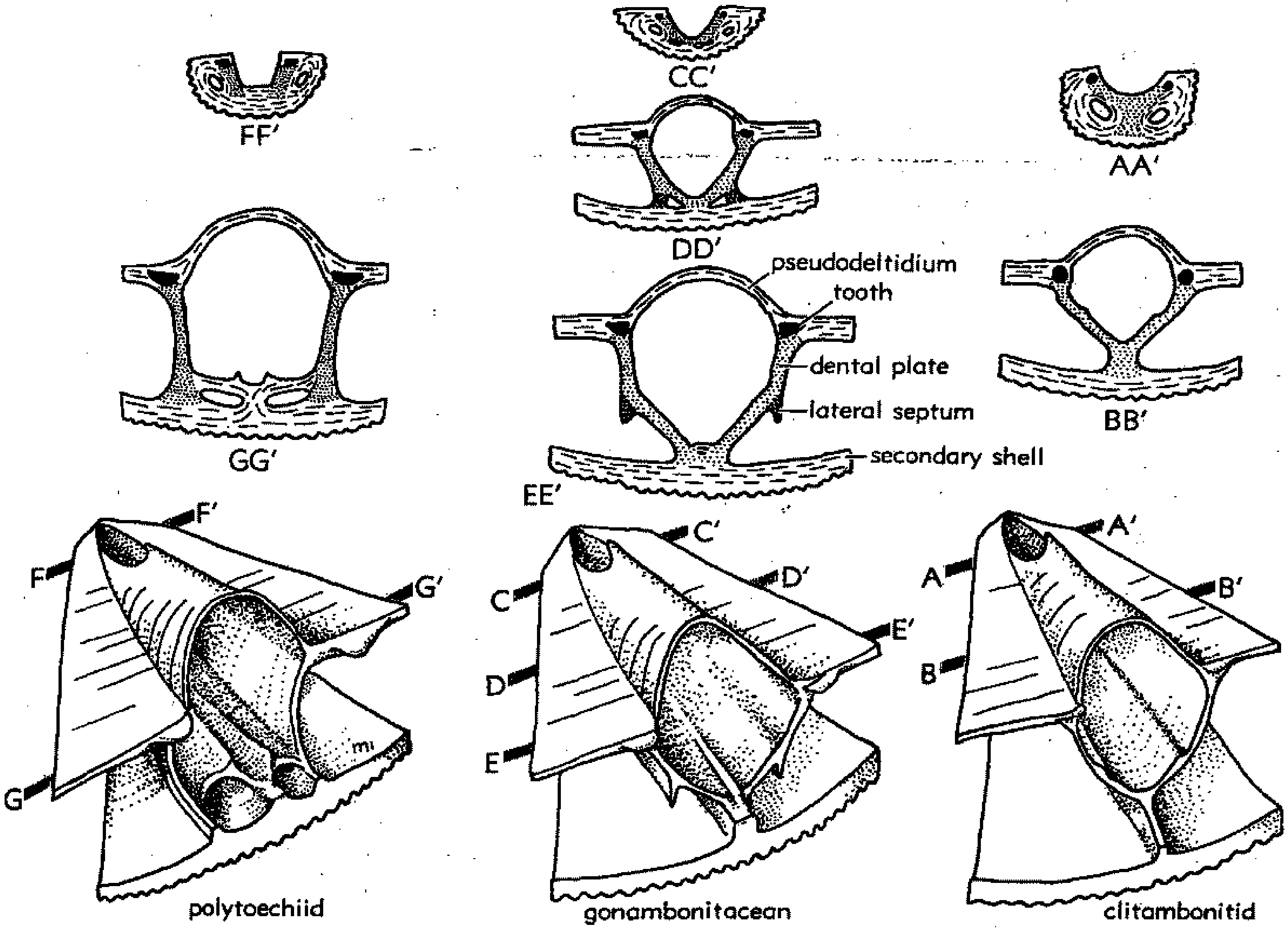


FIG. 220. Parts of three different clitambonitidine pedicle valves illustrating spondylia, with sections showing attitudes of the dental plates (Williams, n).

the exaggerated growth of the ventral interarea, commonly dominates the ventral interior (Fig. 220). Two greatly different types of support to the ventral muscle field were developed, dependent on whether the dental plates were subparallel to each other or convergent toward the floor of the pedicle valve, but a variety of arrangements were derived and are worthy of a brief note.

Among the polytoechiids the dental plates are disposed more or less parallel to each other and probably they gave support to at least the ventral adjustors, so that the ventral ends of both diductors and adductors were mainly inserted on the floor of the valve between the plates. This strip of floor, however, was built up as a raised solid platform by excessive deposition of secondary shell (pseudospondylium) and was commonly deeply undercut along its anterior margin on either side of a strong median ridge (Fig. 220). The resultant structure simulates a spondylium triplex in that it consists of a low platform accommodating the anterior part of the ventral muscle field and is supported by the bases of the containing dental plates and the median ridge.

The spondylium triplex of the gonambonitaceans was formed in an entirely different manner. Judging from sections through the spondylia of *Estlandia, Antigonambonites,* and *Progonambonites,* the structure in juvenile pedicle valves consisted essentially of a sessile spondylium formed by the convergence of the dental plates on to the floor of the valve (Fig. 220). The junction between the spondylium and the valve floor, however, was broken by a pair of conical hollows (presumably occupied by evaginations of shell-secreting outer epithelium) to form a triple septate base. In some genera (e.g., *Antigonambonites*) the spondylium continued to grow close to the floor of the valve and the lateral and median septa persisted as low supports. Yet in adult shells of other genera little or no trace of lateral septa are found in either high or sessile spondylia (*Oslogonites* and *Lacuna-*

rites, respectively), which therefore look very like the simple spondylia of the clitambonitids. Indeed, the gross morphology of the adult ventral interior can be misleading because in certain clitambonitids (e.g., *Atelelasma*) a pair of thin partitions that separated the *vascula media* and *genitalia* are commonly preserved on the under surface of the spondylium in a position occupied by the lateral septa of the Gonambonitacea.

The clitambonitid spondylium simplex is also formed by convergence of the dental plates but in this structure they become confluent above the valve floor (Fig. 220). Öpik (621, p. 22) reconstructed a morphogeny of the spondylium simplex from sections of an adult valve of *Clitambonites adscendens* Pander. He concluded that the arrangement in juvenile valves consisted of a pair of discrete dental plates flanking a median septum which became united into a single structure by secondary shell secretion during subsequent growth. Unfortunately, no young clitambonitid shells were available to test this interpretation, but prepared serial sections of *Clitambonites* sp. suggest that at any stage during growth the median septum extended in front of the convergent portions of the dental plates. Hence, during further enlargement of the spondylium, the septum was buried between later-deposited parts of the dental plates and now appears as an independent structure in thin sections.

The impressions of the ventral muscle field found on the surfaces of spondylia show that the arrangement was typically orthoid, with a broad undifferentiated adductor scar occupying the median zone and the diductors and ventral adjustors inserted on the sides, the latter just in front of the junctions with the teeth. Independently in both *Clinambon* and *Kullervo*, a pair of ridges grew toward each other partially to enclose a subconical chamber (hemisyrinx) for the reception of the ventral ends of the adductor muscles.

The Clitambonitidina, probably more than any other group of brachiopods, display in wonderful detail the impressions of the mantle canals on the internal surfaces of the shell (Fig. 219). Variation in pattern has been discussed in detail by Öpik (621) but essentially all genera show an abbreviation of the peripheral ramification of the *vascula media*, with a concomitant expansion in branching of the *vascula myaria* and *genitalia* (the pinnate condition of Williams, 875).

In the following systematic account of the Clitambonitidina, it is proposed to recognize two superfamilies, viz., the Clitambonitacea and the Gonambonitacea. The most important classificatory difference between these two groups, as at present constituted, is that the shell of the clitambonitaceans is impunctate, whereas that of the gonambonitaceans is pseudopunctate. Whether this contrast is a reflection of a strophomenoid rather than an orthoid ancestry for the gonambonitaceans cannot be profitably debated at present; but it may be significant that such typical strophomenoid features as unequally accentuated parvicostellae with interrupted rugation and denticular hinge lines are also known in the gonambonitaceans *Raunites* and *Anchigonites*, respectively. Either way, the Gonambonitacea present some remarkable examples of homeomorphy.

Superfamily CLITAMBONITACEA Winchell & Schuchert, 1893

[*nom. correct.* Cooper, 1956, p. 511 (*pro* Clitambonacea Schuchert & LeVene, 1929, p. 15, *nom. transl. ex* Clitambonitidae Winchell & Schuchert, 1893, p. 377)]

Plano-convex to biconvex multicostellate, with ventral muscle field impressed on floor and dental plates of pedicle valve on rudimentary spondylium triplex or on spondylium simplex; shell substance impunctate. *Ord.*

Family POLYTOECHIIDAE Öpik, 1934

[*nom. transl.* Williams, herein (*ex* Polytoechiinae Öpik, 1934, p. 76)] [=Tritoechiidae Ulrich & Cooper, 1936, p. 624]

Ventral interarea apsacline; strong, convex pseudodeltidium perforated apically. Ventral muscle field impressed either on valve floor between and along subparallel dental plates or on callus of secondary shell elevated anteriorly from valve floor and supported medially by ridge as rudimentary spondylium; notothyrial edges high, continuous with curved socket ridges, chilidium poorly developed. *L.Ord.-M.Ord.*

Polytoechia Hall & Clarke, 1892, p. 239 [**Hemipronites apicalis* Whitfield, 1886, p. 300; OD] [=*Deltatreta* Ulrich in Butts, 1926, p. 100

(type, *D. fillistriata* Butts, 1926; SD Schuchert & Cooper, 1932, p. 108); *Deltorthis* Ulrich in Poulsen, 1927, p. 297 (*pro Waagenia* Hall, 1889, *non* Kriechbaumer, 1874) (obj.); *Martellia* Wirth, 1936, p. 300 (type, *Orthisina giraldii* Martelli, 1901)]. Unequally biconvex, multicostellate. Ventral muscle field slightly elevated as spondylium triplex with median groove formed by convergence of 2 plates on to median septum; socket ridges supported by low, oblique plates uniting with valve floor as anterior boundary to notothyrial cavity; cardinal process simple. *L.Ord.*, N.Am.——Fig. 221,*2*. *P. subcircularis* (Cooper), USA(Okla.); *2a,b*, brach.v. int. and ext., ×3; *2c*, tilted view of ped.v. int., ×3 (181).

Eremotoechia Cooper, 1956, p. 513 [**E. cloudi*; OD]. Like *Tritoechia* but without hollow costellae, with more swollen dorsal umbo, and with cardinal process differentiated into short shaft and lobate myophore. *M.Ord.*, E.USA-Scot.——Fig. 221,*4*. **E. cloudi*, Porterfield, USA(Tenn.); *4a,b*, ped.v. and lat. views of conjoined valves, ×1; *4c*, ped.v. int., ×1; *4d*, brach.v. int., ×2 (189).

Pomatotrema Ulrich & Cooper in Schuchert & Cooper, 1932, p. 109 [**P. muralis*; OD]. Like *Tritoechia* but plano-convex and without swollen hollow costellae within multicostellate ornamentation. *L.Ord.*, N.Am.——Fig. 221,*3*. **P. murale*, U.Canad., USA(Okla.); *3a,b*, brach.v. int. and ext., ×2; *3c*, ped.v. int., ×2 (825).

Tritoechia Ulrich & Cooper, 1936, p. 624 [**Deltatreta typica* Schuchert & Cooper, 1932, p. 206; OD]. Unequally biconvex, multicostellate with scattered hollow costellae. Ventral muscle field inserted on floor of valve and along inner surfaces of long, slightly divergent dental plates with median ridge extending in front of slightly raised anterior margin to muscle field; cardinal process simple. *L.Ord.*, N.Am.-Eu.——Fig. 221,*1*. **T. typica* (Schuchert & Cooper), M.Canad., USA (Okla.); *1a,b*, tilted views of ped.v. int., ×1; *1c*, ped.v. ext., ×1; *1d,e*, brach.v. int. and ext., ×2 (189).

Family CLITAMBONITIDAE
Winchell & Schuchert, 1893

[Clitambonitidae Winchell & Schuchert, 1893, p. 377]

Ventral interarea variably inclined; pseudodeltidium and chilidium variably developed. Ventral muscle field impressed on spondylium simplex. *Ord.*

Subfamily CLITAMBONITINAE
Winchell & Schuchert, 1893

[*nom. transl.* Schuchert & Cooper, 1931, p. 245 (*ex* Clitambonitidae Winchell & Schuchert, 1893, p. 377)]

Pseudodeltidium arched; perforated by apical foramen; chilidium strong, continuous with widely divergent socket ridges. *Ord.*

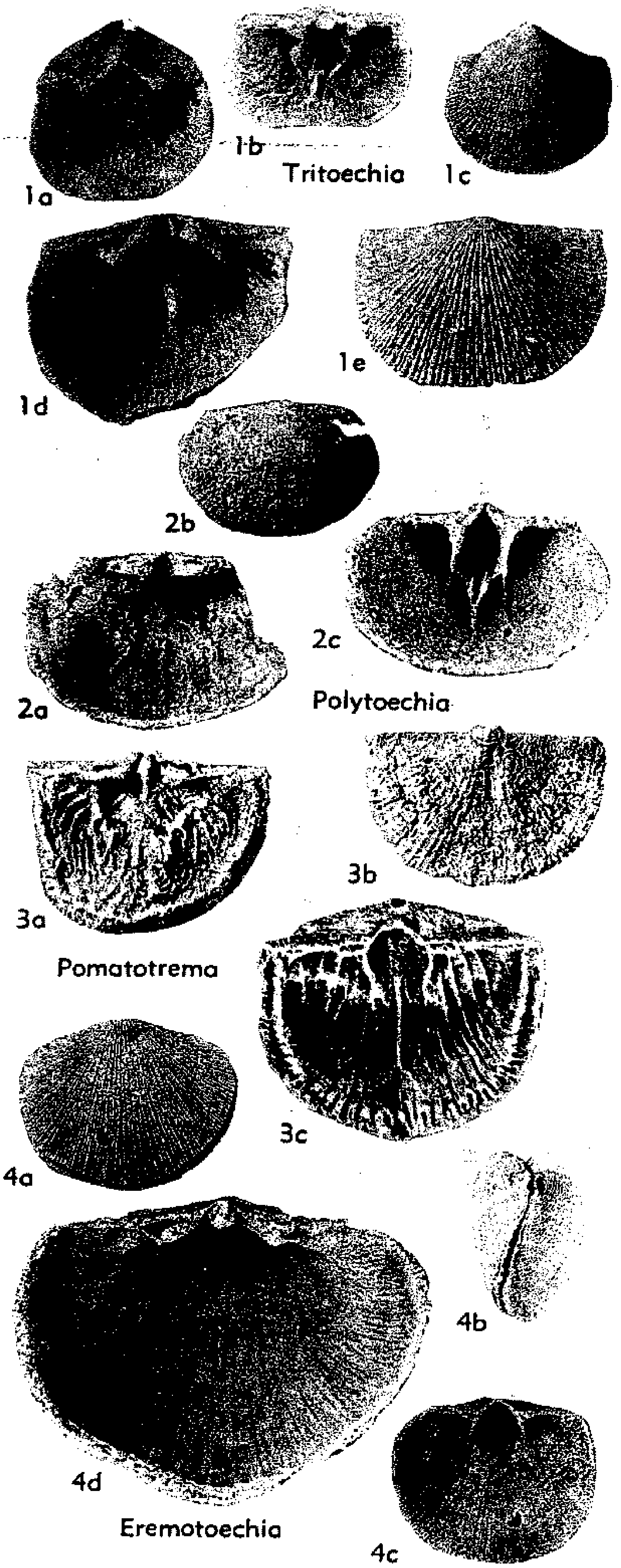


Fig. 221. Polytoechiidae (p. *H*348-*H*349).

Clitambonites Agassiz, 1846, p. 90 [**Pronites adscendens* Pander, 1830, p. 71; SD Hall & Clarke, 1892, p. 234] [=*Pronites* Pander, 1830, p. 71 (obj.); *Orthisina* d'Orbigny, 1847, p. 267 (obj.)]. Pedicle valve with procline to apsacline

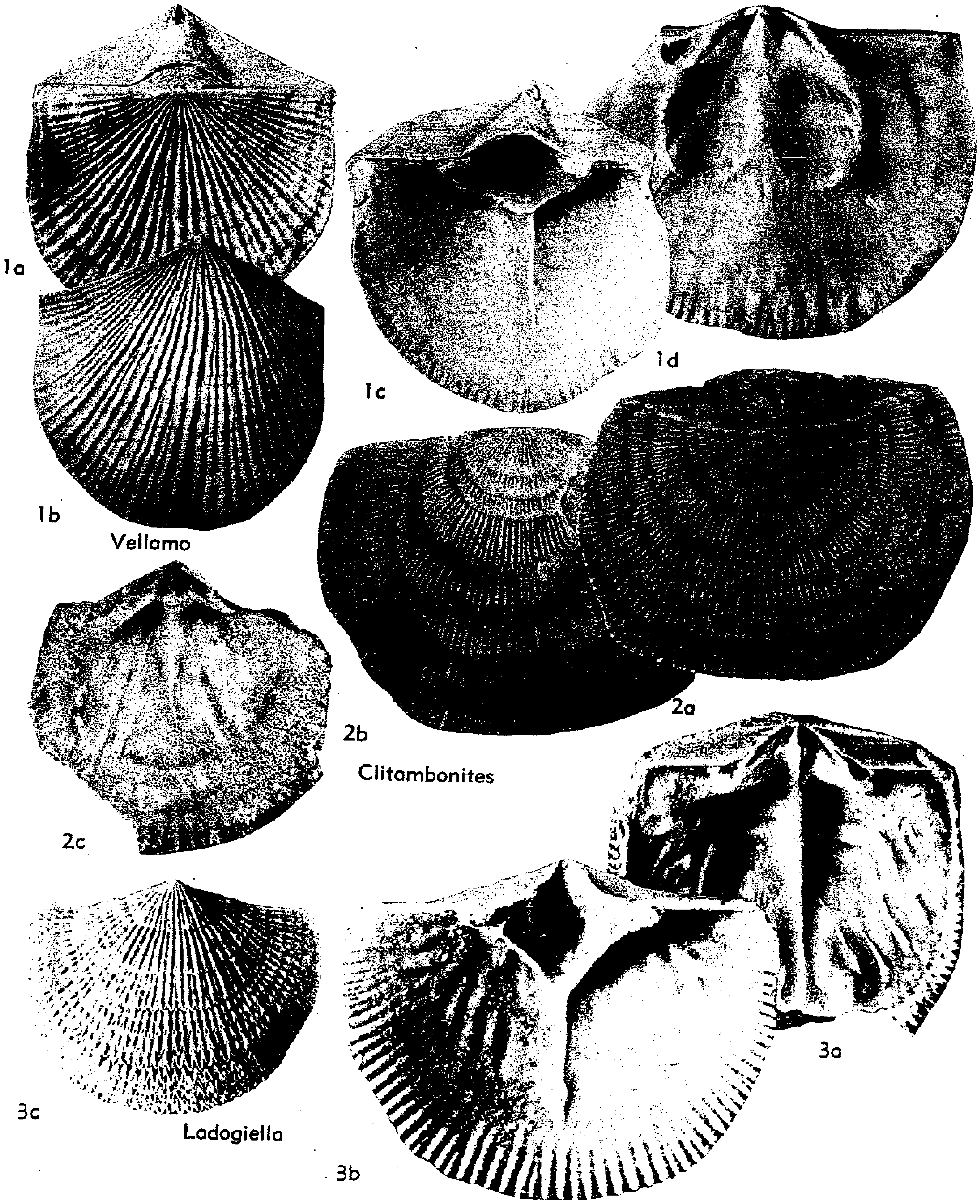


Fig. 222. Clitambonitidae (Clitambonitinae) (p. *H*349-*H*352).

interarea, brachial valve convex, multicostellate and imbricate; chilidium small, cardinal process simple. *L.Ord.-M.Ord.*, Eurasia. [*See* note, p. *H*904.]

C. (Clitambonites). Coarsely costellate and grossly, irregularly imbricate, with subpyramidal pedicle valve and gently convex brachial valve. *L.Ord.-M.Ord.*, Eurasia.——Fig. 222,2. **C.* (*C.*) *adscendens* (Pander), L.Ord.(B_{III}), USSR; *2a,b*, ped.v. and brach.v. views of conjoined valves, ×1.5; *2c*, brach.v. int., ×2 (Rõõmusoks, n).

C. (Hemipronites) Pander, 1830, p. 74 [**Hemipronites tumida* Pander, 1830; SD Dall, 1877, p. 31]. Strongly biconvex with finely costellate

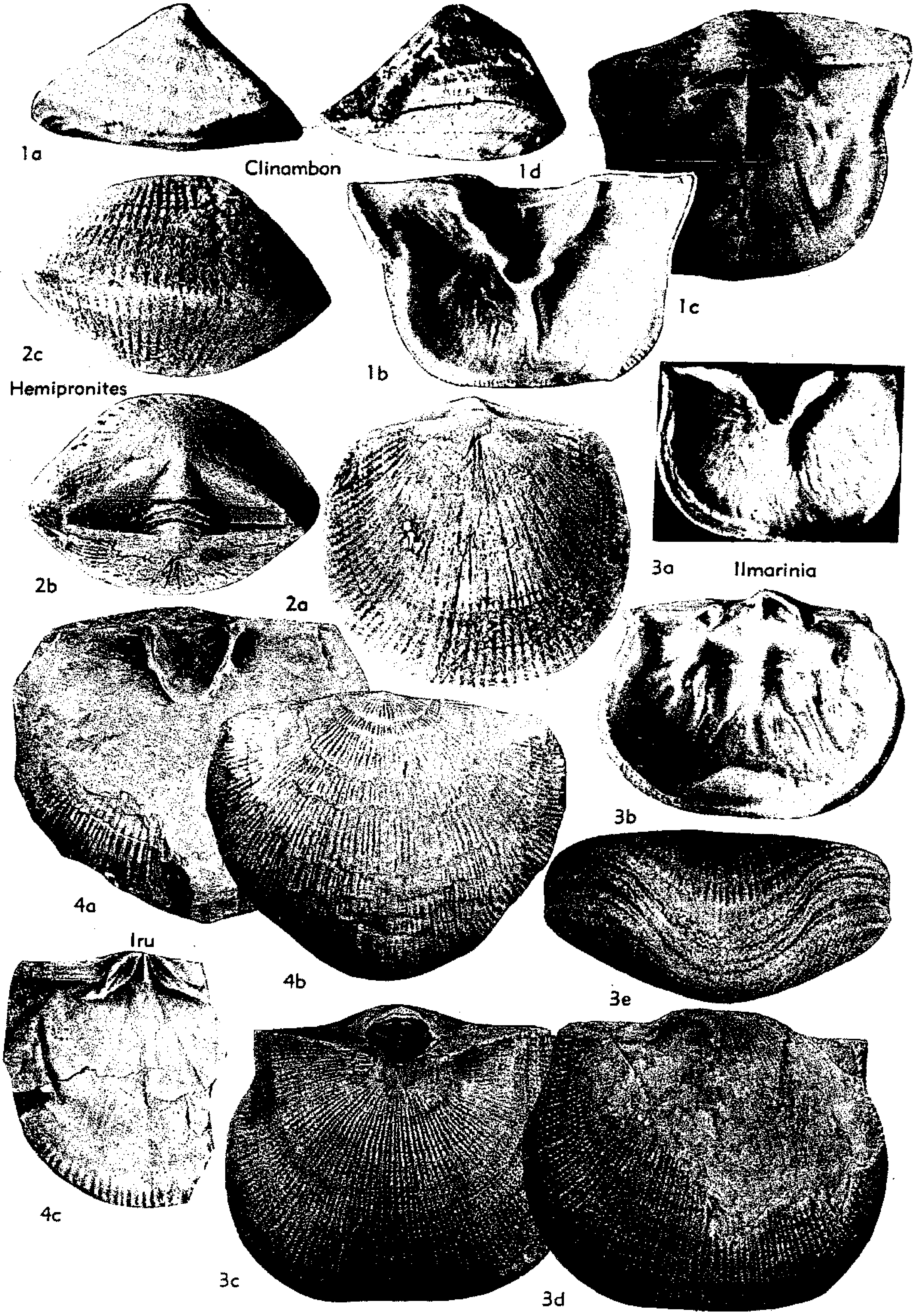


Fig. 223. Clitambonitidae (Clitambonitinae) (p. *H*350, *H*352).

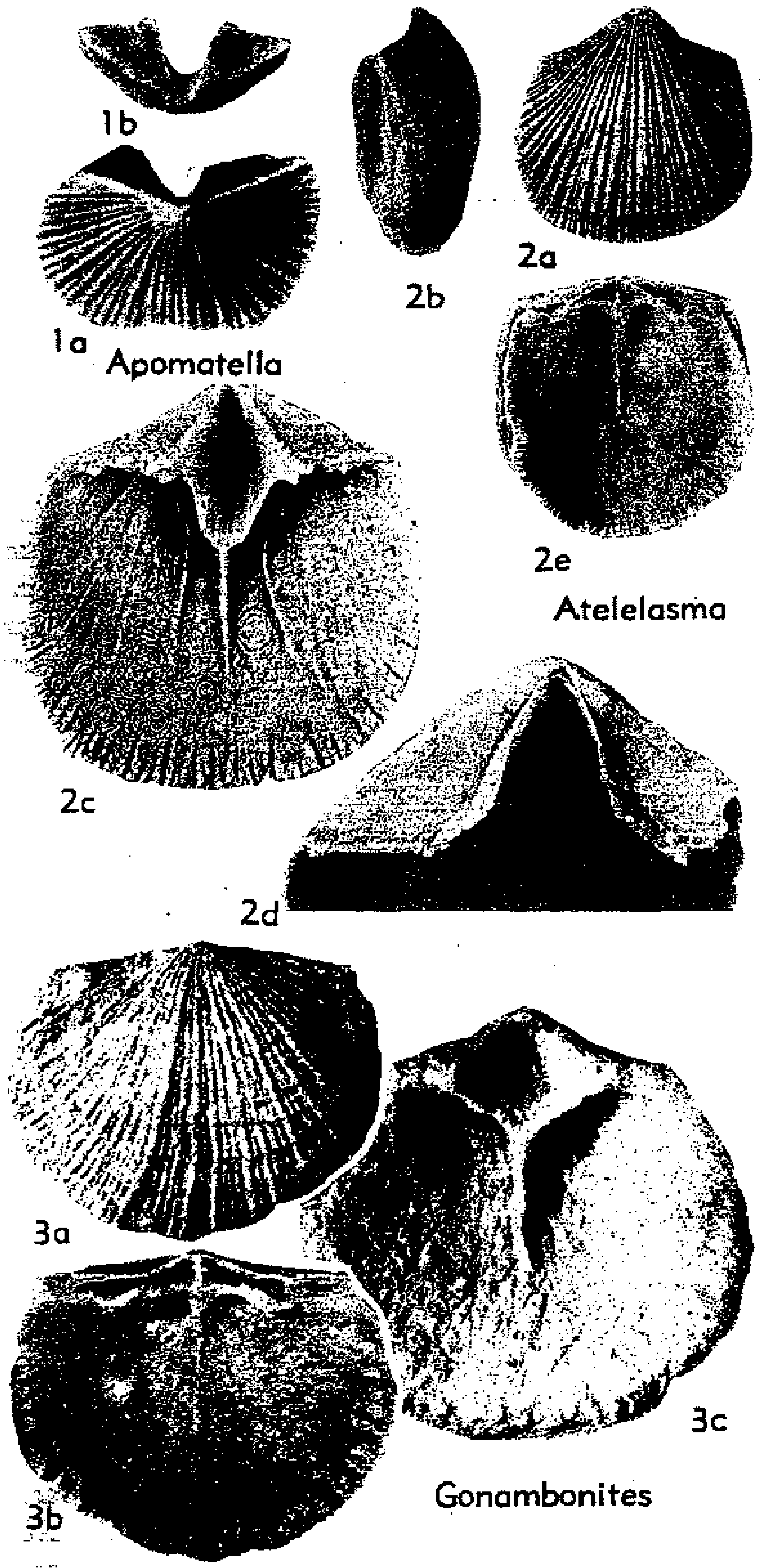


FIG. 224. Clitambonitidae (Atelelasmatinae) *(1,2)*; Gonambonitidae (Gonambonitinae) *(3)* (p. *H*352-*H*353).

radial ornamentation and subdued imbrication. *L.Ord.*, E.Eu.-China.——FIG. 223,*2*. **C. (H.) tumida* (PANDER), L.Ord., E.Baltic; *2a-c*, brach. v., post., ant. views of conjoined valves, ×4.5 (Williams, n).

Clinambon SCHUCHERT & COOPER, 1932, p. 115 [**Anomites anomala* VON SCHLOTHEIM, 1822, p. 65; OD]. Like *Clitambonites* but not imbricate and with strongly procline ventral interarea; spondylium constricted by pair of inwardly directed ridges forming hemiconical chamber anteriorly; chilidium large, cardinal process flanked by subsidiary ridges. *M.Ord.*, USSR.——FIG. 223, *1a-c*. **C. anomalus anomalus* (SCHLOTHEIM), DI-DIII; E.Baltic; *1a*, ant. view of conjoined valves, ×1; *1b,c*, ped.v. and brach.v. int., ×1 (621).——FIG. 223,*1d*. *C. anomalus praecedens* (ÖPIK), DI, E.Baltic; *1a*, lat. view of conjoined valves, ×1 (621).

Ilmarinia ÖPIK, 1934, p. 125 [**Orthisina sinuata* PAHLEN, 1877, p. 44; OD]. Unique in possessing dorsal fold and ventral sulcus, otherwise like *Clinambon* but without constricted spondylium and with large, open foramen. *M.Ord.-U.Ord.*, Baltic.——FIG. 223,*3*. **I. sinuata* (PAHLEN), U. Ord.(FIC), E.Baltic; *3a,b*, ped.v. and brach.v. int., ×1 (621); *3c-e*, ped.v., brach.v. ant. views of conjoined valves, ×1.5 (Rõõmusoks, n).

Iru ÖPIK, 1934, p. 89 [*Orthisina concava* PAHLEN, 1877, p. 17; OD]. Strongly convexo-concave costellate and imbricate. Spondylium sessile; cardinal process flanked by subsidiary ridges; socket ridges hatchet-shaped; dorsal median ridge absent; notothyrial platform weak. *L.Ord.*, USSR.——FIG. 223, *4*. **I. concava* (PAHLEN), BIII, W.Russian Platform; *4a,b*, ped.v. int., brach.v. ext., ×1.5; *4c*, brach.v. int., ×2 (Rõõmusoks, n).

Ladogiella ÖPIK, 1934, p. 93 [**L. imbricata*; OD]. Externally like *Clitambonites* but with more strongly convex brachial valve, shorter ventral interarea and finer ornamentation. Spondylium sessile; chilidium vestigial; cardinal process massive, lanceolate and flanked by well-developed subsidiary ridges. *L.Ord.*, USSR.——FIG. 222,*3*. **L. imbricata*, E.Baltic; *3a*, brach.v. int., ×3; *3b*, ped.v. int., ×5; *3c*, ped.v. ext., ×3 (621).

Pahlenella SCHUCHERT & COOPER, 1931, p. 245 [**Orthis trigonula* EICHWALD, 1840, p. 148; OD]. Like *Vellamo* but concavo-convex, with prominent ventral fold and dorsal sulcus and with quadripartite dorsal adductors impressed on sessile shield-shaped plate of secondary shell. *L.Ord.*, USSR.

Vellamo ÖPIK, 1930, p. 212 [**Orthis verneuili* EICHWALD, 1841, p. 51; OD]. Like *Clitambonites* but not imbricate and with flat or gently convex brachial valve and high subpyramidal, commonly asymmetrical, pedicle valve; foramen large and invariably open; cardinal process simple. *M.Ord.-U.Ord.*, N.Hemis.——FIG. 222,*1*. **V. verneuili* (EICHWALD), U.Ord.(FIab), E.Baltic; *1a,b*, brach. v. and ped.v. views of conjoined valves, ×1.5; *1c,d*, ped.v. and brach.v. int., ×2 (Rõõmusoks, n).

Subfamily ATELELASMATINAE Cooper, 1956

[Atelasmatinae COOPER, 1956, p. 516]

Pseudodeltidium lacking, chilidium variably developed. *L.Ord.-M.Ord.*

Atelelasma COOPER, 1956, p. 517 [**A. perfectum*; OD]. Pedicle valve subpyramidal, with procline to apsacline interarea, brachial valve gently convex, multicostellate, commonly with swollen and hollow costellae; delthyrium restricted laterally by elevated plates; chilidium well developed; cardinal process simple. *M.Ord.*, N.Am.-Eu.——FIG. 224,*2*. **A. perfectum*, Porterfield, USA(Tenn.); *2a,b*, ped.v., lat. views of conjoined valves, ×1; *2c,d*, ped.v. int. and post. views, ×2; *2e*, brach.v. int., ×1 (189).

Apomatella Schuchert & Cooper, 1931, p. 245 [**Orthisina ingrica* Pahlen, 1877, p. 48; OD]. Like *Atelelasma* but lacking hollow costellae, lateral plates to delthyrium and chilidium. *L.Ord.*, Eu.——Fig. 224,*1*. **A. ingrica* (Pahlen), B_{II}, Baltic; *1a,b*, ped.v. ext. and post. views, ×1 (729).

Superfamily GONAMBONITACEA Schuchert & Cooper, 1931

[*nom. transl.* Williams, herein (*ex* Gonambonitinae Schuchert & Cooper, 1931, p. 245)]

Concavo-convex to convexo-concave, costellate to unequally parvicostellate, with ventral muscle field impressed on spondylium triplex; shell substance pseudopunctate. *Ord.*

Family GONAMBONITIDAE Schuchert & Cooper, 1931

[*nom. transl.* Rubel, 1963, p. 92 (*ex* Gonambonitinae Schuchert & Cooper, 1931, p. 245)] [=Estlandiidae Öpik, 1934, p. 129]

Ventral interarea variably inclined, pseudodeltidium and chilidium variably developed; spondylium triplex sessile to elevated; anterior impressions of dorsal adductors commonly smaller than posterior. *Ord.*

Subfamily GONAMBONITINAE Schuchert & Cooper, 1931

[Gonambonitinae Schuchert & Cooper, 1931, p. 245]

Pseudodeltidium well developed, perforated by an apical foramen which may be closed in adult shells; chilidium strong, continuous with widely divergent and well-differentiated socket ridges supported by strong extensions of notothyrial platform. *L.Ord.-M.Ord.*

Gonambonites Pander, 1830, p. 77 [**G. latus*; SD Schuchert & LeVene, 1929, p. 63]. Unequally biconvex to convexo-concave with high, apsacline ventral interarea; finely costellate to unequally parvicostellate; spondylium triplex elevated, notothyrial platform and median ridge strongly developed, cardinal process flanked by subsidiary ridges. *L.Ord.*(B_{III}), E.Baltic.——Fig. 224,*3*. **G. latus*, USSR(Leningrad); *3a,b*, brach.v. ext., int., ×2 (684a).——Fig. 224,*3c*. *G.* sp., USSR (Leningrad); ped.v. int., ×1.5 (684a).

Anchigonites Öpik, 1939, p. 136 [**A. conulus*; OD]. Like *Antigonambonites* but not resupinate, high pedicle valve remaining convex throughout growth and plane brachial valve becoming slightly concave. *L.Ord.*(B_{III}), Scand.-USSR.——Fig. 225,*2*. **A. conulus*, Norway; *2a-c*, brach.v. and ped.v. int. molds, brach.v. ext. cast, ×4 (622).

Antigonambonites Öpik, 1934, p. 147 [**Gonambonites plana* Pander, 1830, p. 78; OD]. Resupinate and costellate. Spondylium mostly sessile, with rudimentary median septum; hinge line denticulate; dorsal adductor scars, subquadrate, widely spaced with posterior pair larger. *L.Ord.*, Eu.——Fig. 225,*4*. **A. planus* (Pander) ($B_{II}\beta$), Estonia; *4a,b*, brach.v. and ped.v. int., ×1.5; *4c*, ped.v. ext., ×2; *4d*, ped. view of foramen with seal of secondary shell, ×12 (621).

Estlandia Schuchert & Cooper, 1931, p. 245 [**Orthisina marginata* Pahlen, 1877,p. 33; OD]. Unequally biconvex with high, apsacline ventral interarea; multicostellate, costellae arising by intercalation and traversed by undercut lamellae to give interrupted tubular appearance. Spondylium triplex elevated; cardinal process flanked by subsidiary ridges; notothyrial platform and median ridge strongly developed; posterior dorsal adductor scars quadrate and larger than subtriangular anterior pair; subperipheral rims strong in both valves. *M.Ord.*, Eu.——Fig. 225,*5a,b*. **E. marginata marginata* (Pahlen), (C_{II}), Estonia; *5a*, brach.v. ext., ×1.5; *5b*, ped.v. ext., ×2 (Rõõmusoks, n).——Fig. 225,*5c,d*. **E. marginata aspera* (Pahlen), (C_{II}), Estonia; *5c,d*, ped.v. and brach. v. int., ×2 (621).

Lacunarites Öpik, 1934, p. 175 [**L. ilmatar*; OD]. Strongly concavo-convex, coarsely costellate, with strong, widely spaced imbrication forming radial series of lacunae in interspaces. Spondylium sessile, traces of lateral septa absent. *L.Ord.*, USSR.——Fig. 225,*6*. **L. ilmatar*, (B_{III}), Estonia; ped.v. ext., ×3 (Rõõmusoks, n).

Raunites Öpik, 1939, p. 135 [*pro Rauna* Öpik, 1932, *non* Münster, 1839] [**Orthisina janischewskyi* Lessnikov, 1924, p. 153; OD]. Resupinate, unequally parvicostellate, and finely imbricate, exceptionally with impersistent posterolateral rugae; cardinal process without flanking subsidiary ridges, teeth and socket ridges obsolescent, dorsal median ridge absent. *L.Ord.*, USSR.——Fig. 225,*3a,b*. **R. janischewskyi* (Lessnikov), ($B_{II}\beta$-γ), Estonia; *3a*, brach.v. int., ×1.5; *3b*, ped.v. int., ×1 (621).——Fig. 225,*3c*. *R. wolchowiana* (Öpik), (B_{II}), USSR(Leningrad); brach.v. ext., ×2 (621).

Subfamily ANOMALORTHINAE Ulrich & Cooper, 1936

[*nom. transl.* Williams, herein (*ex* Anomalorthidae Ulrich & Cooper, 1936, p. 622)] [=Progambonitinae Rubel, 1963, p. 92]

Ventral interarea apsacline to anacline, delthyrium open, chilidium vestigal or lacking; spondylium triplex sessile to elevated. *L.Ord.*

The systematic position of *Anomalorthis* is uncertain. Ulrich & Cooper (825, p. 126) reported a sessile spondylium with traces of a median septum lying between the dental plates and also "scattered pseudopunctae like those occurring in the Strophomenacea." Nonetheless they concluded

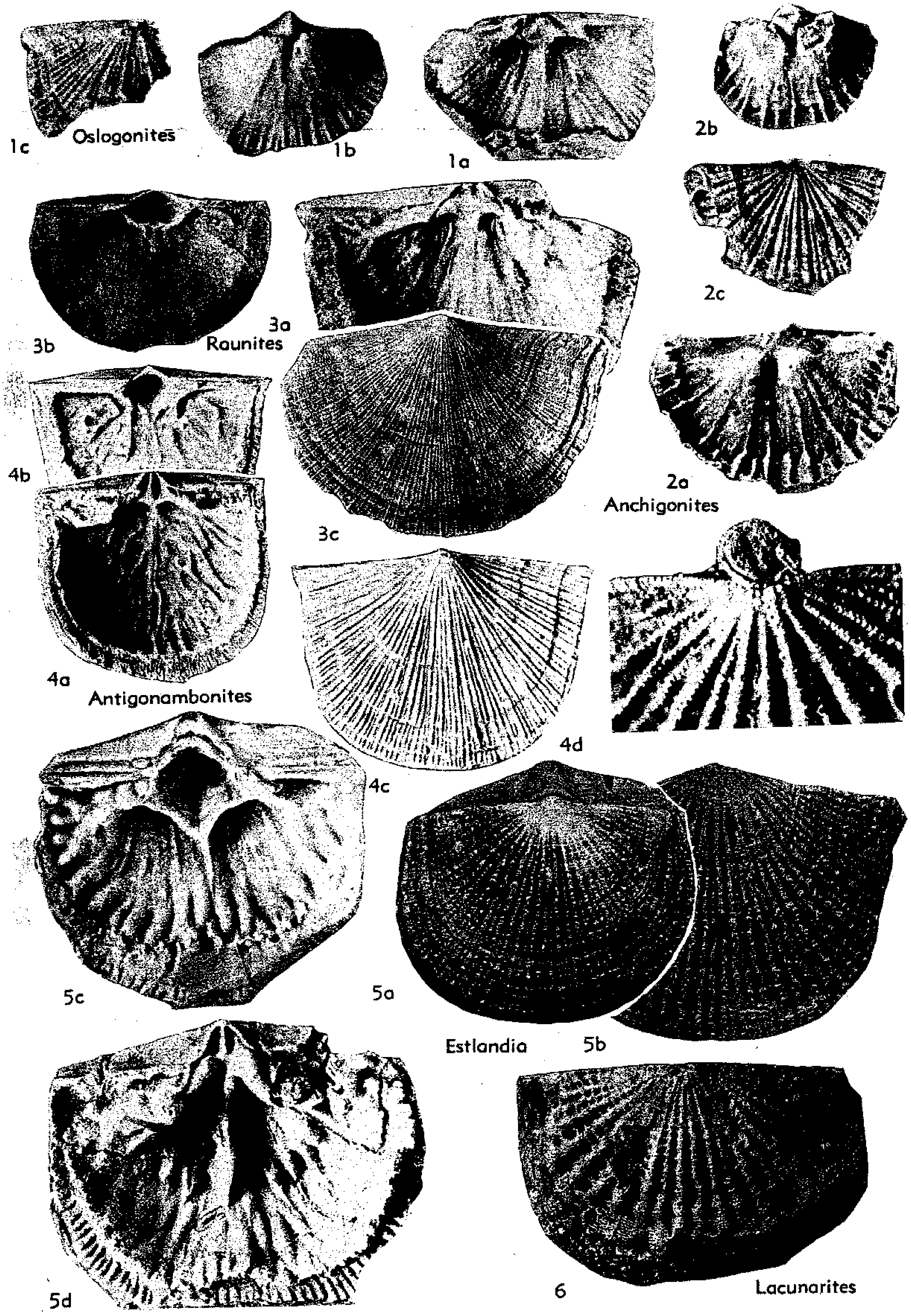


Fig. 225. Gonambonitidae (Gonambonitinae) *(2-6)*, (Anomalorthinae) *(1)* (p. *H*353, *H*355).

that the genus was more orthoid than clitambonitoid, especially in possessing "a flat imperforate deltidium." This structure is much more likely to be a raised pedicle callist or apical plate and despite the orthoid features of the genus it seems best to assign it to the Gonambonitacea.

Anomalorthis Ulrich & Cooper, 1936, p. 622 [**A. utahensis*; OD]. Unequally biconvex to convexi-concave, with long ventral interarea, finely multicostellate. Spondylium sessile; cardinal process simple, ridgelike. *L.Ord.*, W.USA.——Fig. 226,*1*. **A. utahensis*, Canad.-USA(Utah); *1a,b*, ped.v. int., lat. views, ×1; *1c*, brach.v. int., ×2; *1d*, ped.v. ext., ×2 (825).

Oslogonites Öpik, 1939, p. 133 [**O. costellatus*; OD]. Finely costellate, with flat to moderately convex brachial valve and high pedicle valve. Spondylium high with rudimentary lateral septa; notothyrial platform, concave, thin and bladelike, cardinal process absent, socket ridges weak. *L.Ord.*, Scand.——Fig. 225,*1*. **O. costellatus*, Expansusschiefer, Nor.; *1a-c*, brach.v. int., ped.v. int. mold, brach.v. ext., ×4 (622).

Progonambonites Öpik, 1934, p. 138 [**P. estonus*; OD]. Biconvex, finely imbricate to give costellate radial ornament beaded appearance; interior like that of *Oslogonites* except for presence of cardinal process. *L.Ord.*, Eu.——Fig. 226,*2*. **P. estonus*, (B_{III}), Estonia; *2a*, brach.v. ext., ×2.5; *2b,c*, post., ped.v. ext., ×1.5; *2d*, brach.v. int., ×2 (Röõmusoks, n).

Family KULLERVOIDAE Öpik, 1934

[Kullervoidae Öpik, 1934, p. 70]

Coarsely costellate and imbricate, with well-developed pseudodeltidium and chilidium. Spondylium triplex constricted anteromedially by pair of inwardly directed plates forming semiconical chamber (hemisyrinx), lateral septa rudimentary. *M.Ord.-U.Ord.*

Kullervo Öpik, 1932, p. 70 [**Gonambonites panderi* Öpik, 1930, p. 234; OD]. Brachial valve flat to gently convex, pedicle valve subpyramidal, costellae commonly no more conspicuous than imbrication posterolaterally; foramen commonly large, with high irregular lip. Cardinal process flanked by subsidiary ridges, dorsal adductor scars widely spaced, subpetaloid. *M.Ord.-U.Ord.*, N. Hemis.——Fig. 227,*1*. *K. complectens* (Wiman) *albida* (Reed), U.Ord.(Ashgill.), Eire; *1a-e*, int., tilted int. ext., post., posterolat. views of ped.v., ×3; *1f,g*, brach.v. int., ext., ×5 (Wright, n).

Suborder TRIPLESIIDINA Moore, 1952

[*nom. correct.* Wright, herein (*pro* suborder Triplesioidea Muir-Wood, 1955, p. 89, *nom. transl. ex* order Triplesiida Moore, 1952, p. 221)]

[Materials for this suborder prepared by A. D. Wright]

[Appreciation is expressed to the Trustees of the British Museum (Natural History) for permission to reproduce several illustrations from Wright, 1964 (ref. 895b)]

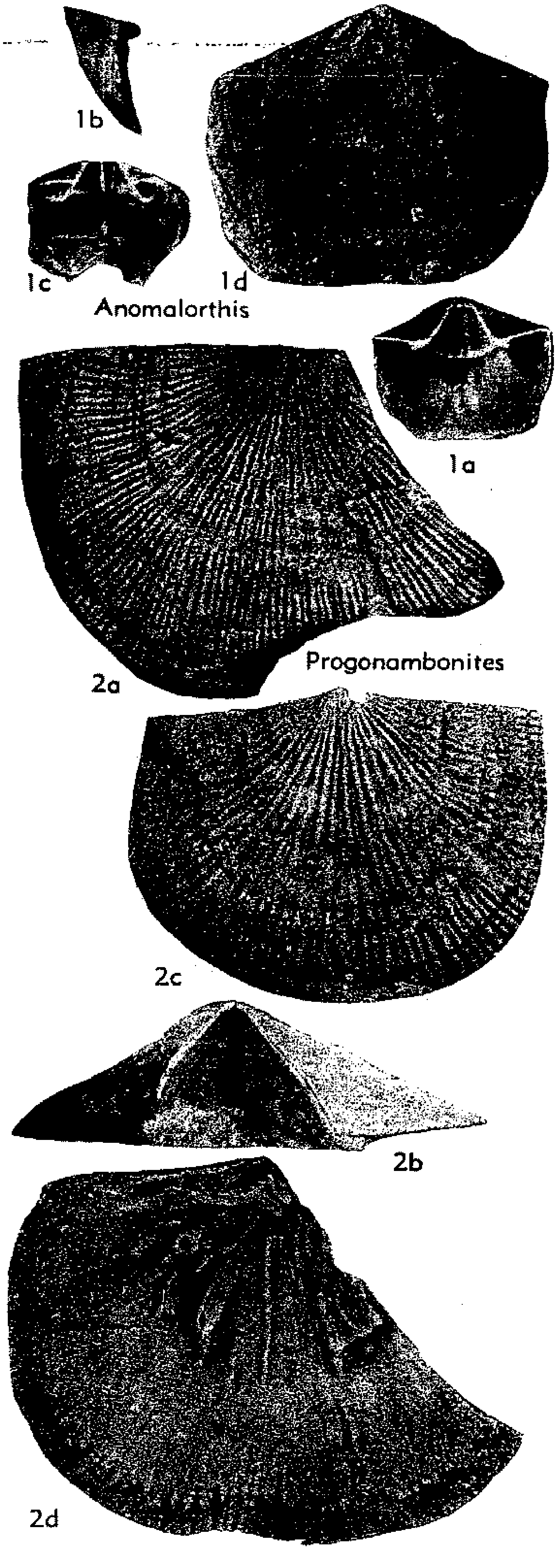


Fig. 226. Gonambonitidae (Anomalorthinae) (p. *H*355).

The Triplesiidina form a very distinctive

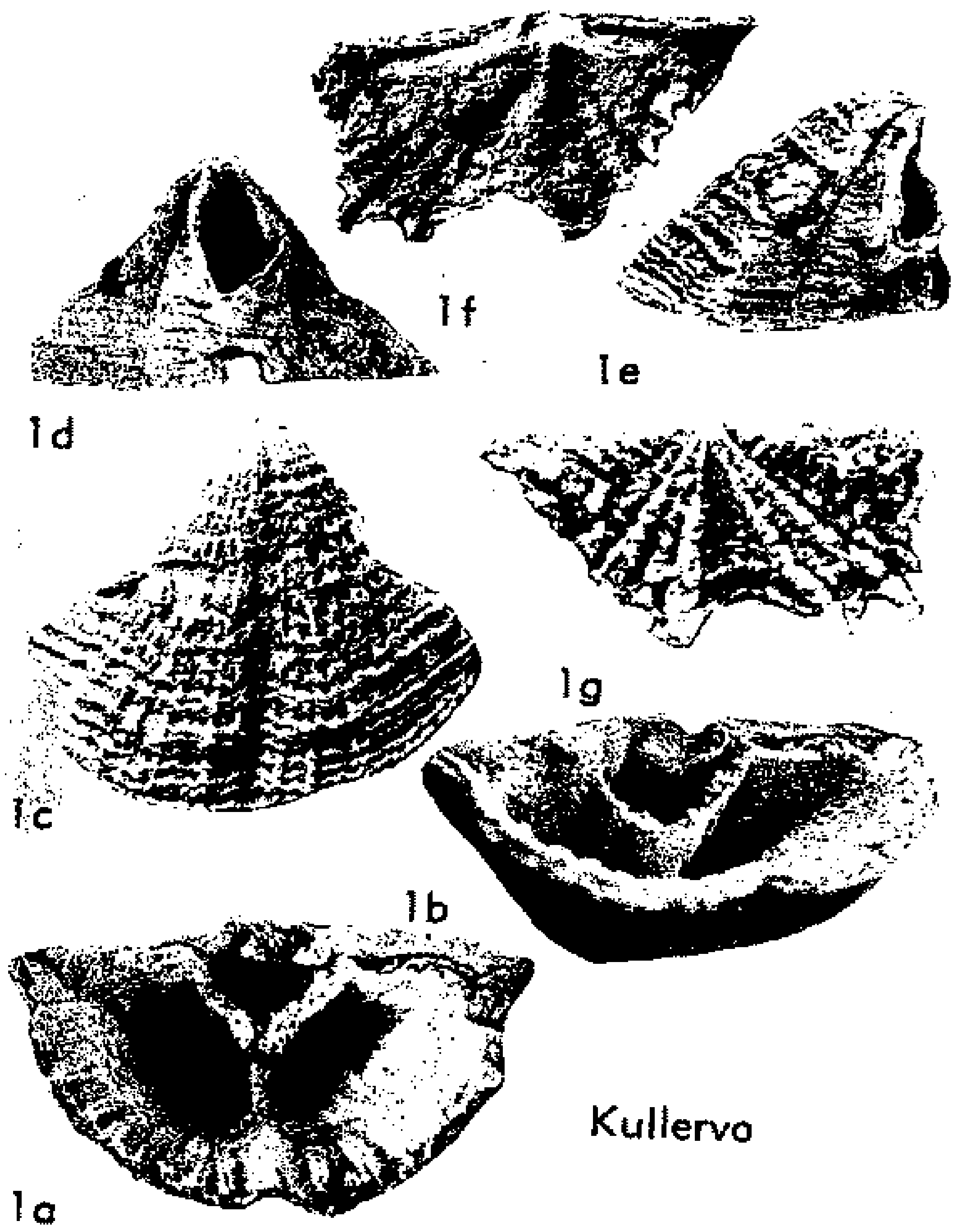


FIG. 227. Kullervoidae (p. *H355*).

and closely knit group among the articulate brachiopods. The external appearance is very variable, and before the internal structures were fully known, the various species and genera were assigned to such stocks as *Spirifer*, *Atrypa*, and *Orthis*. The discovery of the unusual and consistent nature of the cardinalia in the then known genera led SCHUCHERT (1913) to unite them into a single subfamily within the Strophomenidae. Subsequently the distinctive characters of the subfamily caused it to be elevated progressively to familial (ÖPIK, 1932), superfamilial (COOPER, 1944), and ordinal rank (MOORE, 1952); MUIR-WOOD (1955) reduced it to the present subordinal status. This suborder contains a single family, currently comprising ten genera.

The relationships of the Triplesiidina are now considered to lie with the Orthacea (WRIGHT, 1963), and they appear to have developed from a stock of small biconvex orthaceans in early Ordovician times. No possible transitional forms between the two stocks are yet known, and the earliest recorded genus, *Onychoplecia*, appearing in the Lower Ordovician Table Head Series of Newfoundland, already possessed the typical triplesiid characteristics. The group continued throughout the Ordovician and into the Silurian, being fairly widespread but rarely abundant. Although four genera were still present in the Wenlockian, representatives of the group are not known from the Ludlovian or later strata.

Biconvex, impunctate shells; ventral interarea with flat, medianly arched pseudodeltidium and apical foramen; dorsal interarea obsolete, cardinal process long, forked. *L.Ord.-U.Sil. (Wenlock.).*

The triplesioid shell varies greatly in outline from transversely elliptical (e.g., *Bicuspina*) to rounded (e.g., *Plectotreta*), tear-shaped (e.g., *Onychoplecia*) and elongate (e.g., *Onychotreta*). In profile the shell varies from biconvex to markedly dorsi-biconvex. A fold and sulcus are usually strongly developed, and are reflected in the presence of a uniplicate or, less commonly, sulcate anterior commissure. Asymmetrical shell development is typical of some genera (e.g., *Streptis*). Surface ornament is lacking, for example, in the smooth *Triplesia*; other forms show concentric growth lines, frills, and lamellae, commonly in combination with radial costae, costellae, or plications. It is these features of shell shape and ornament which provide the basis for generic distinction (823).

The pedicle valve interarea is normally curved, apsacline, and exceptionally is developed to great size (e.g., *Onychotreta*). The small foramen is restricted to the extreme apex of the delthyrium, and may resorb part of the ventral umbo, thus becoming situated anterior to the beak. The remainder of the delthyrium is filled by a flat pseudodeltidium, which lies flush with the interarea and which has a narrow fold running medianly from the foramen to the hinge line.

Internally, the pedicle valve may develop a more or less tubular passage for the pedicle between the foramen and valve interior. The teeth are normally supported by small dental plates. The muscle scars are only known for a few genera, where they consist of flabellate diductor scars surrounding, and all but enclosing, the cordate or lanceolate adductor scars. The meager evidence on the mantle canals indicates that they have a lemniscate pattern.

The brachial valve lacks an interarea, and the strongly convex dorsal umbo is tucked inside the pedicle valve. Internally, the valve possesses a long, forked cardinal process, which curves backward from its base at the posterior end of the brachial valve so as to extend into the ventral umbo. The myophores are located at the distal extremity of each prong, usually as deep grooves on the dorsal surface. On the posterior side of the shaft near its base is a calcareous hood, and lateral to it on either side is a short calcareous process which serves as the inner margin to the socket. The adult lophophore apparently is a dorsally directed spirolophe. In specimens showing muscle and mantle canal impressions, the dorsal muscle field has a larger anterior adductor pair and a smaller subcentral posterior pair, the latter being bounded laterally by a pair of gonocoels. The mantle canal patern is saccate (895).

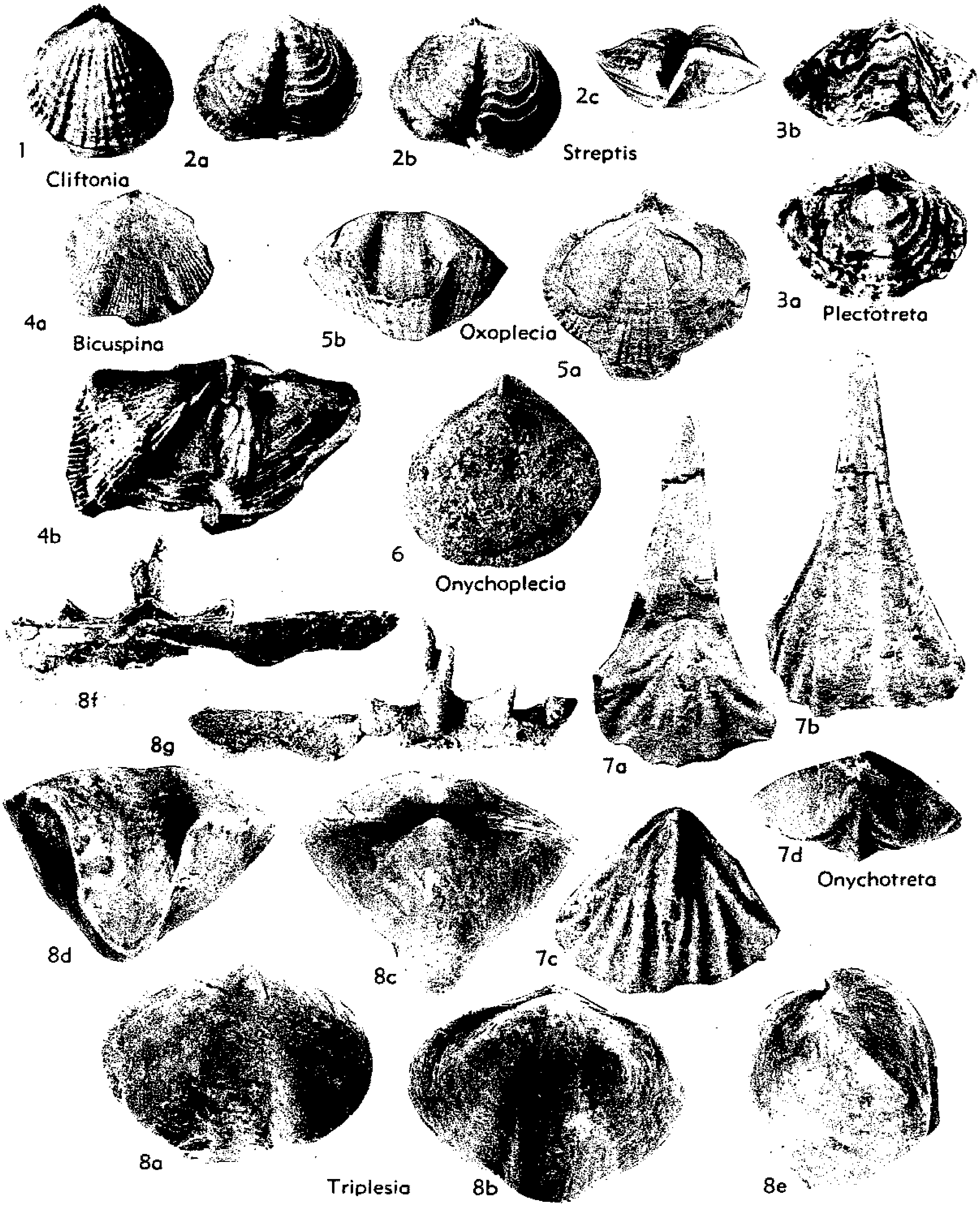


FIG. 228. Triplesiidae (p. *H358-H359*).

Superfamily TRIPLESIACEA Schuchert, 1913

[*nom. transl.* Cooper, 1944, p. 307 (*ex* Triplesiinae Schuchert, *nom. correct.* Schuchert & LeVene, 1929, p. 16, *pro* Tripleciinae Schuchert, 1913, p. 387)]

Characters of the family. *L.Ord.-U.Sil. (Wenlock.).*

Family TRIPLESIIDAE Schuchert, 1913

[*nom. transl.* Muir-Wood, 1955, p. 89 (*ex* Triplesiinae Schuchert, *nom. correct.* Schuchert & LeVene, 1929, p. 16, *pro* Tripleciinae Schuchert, 1913)]

Biconvex to markedly dorsi-biconvex, impunctate shells, normally with prominent undulation in anterior commissure. Pedicle-valve interarea with delthyrium closed by flat pseudodeltidium with narrow median fold extending anteriorly from small apical foramen. Brachial-valve interarea obsolete. Cardinal process long, forked, and directed backward, with hood commonly developed on posterior side of its base, and with short divergent processes on either side forming inner boundaries of sockets. *L.Ord.-U.Sil. (Wenlock.).*

Triplesia Hall, 1859, p. 44 [**Atrypa extans* Emmons, 1842; SD Hall & Clarke, 1892, p. 270] [=*Triplecia* Hall & Clarke, 1892 (obj.) *(nom. van.)*; *Dicraniscus* Meek, 1872, p. 279 (type, *D. ortoni*)]. Strongly trilobate, with pronounced dorsal fold and ventral sulcus; surface smooth, with only faint growth lines. *M.Ord.-U.Sil.(Wenlock.),* widespread.——Fig. 228,*8a-e*. **T. extans,* M.Ord.(Trenton.), USA(N.Y.); *8a-e*, ped.v. brach. v. post., ant., lat. views of complete shell, ×1.5 (895; Wright, n).——Fig. 228,*8f,g*. *T.* sp. cf. *T. insularis* (Eichwald), U.Ord.(Ashgill.), Ire.; dorsal and ventral views of cardinalia, ×5 (895b).

Bicuspina Havlíček, 1950, p. 18 [**Orthis cava* Barrande, 1848, p. 209; OD]. Transverse shells of spiriferoid outline; uniplicate, multicostellate, with well-developed pedicle tube. *M.Ord.-U.Ord.,* Eu.(Br.I.-Boh.-Est.).——Fig. 228,*4a*. **B. cava,* Llandeil., Boh.; ped.v. ext., ×1 (Havlíček, n).——Fig. 228,*4b*. *B. spiriferoides,* Caradoc., Br.I.; ped.v. int. mold, ×1.3 (895).

Brachymimulus Cockerell, 1929, p. 105 [*pro Mimulus* Barrande, 1879 (*non* Stimpson, 1860)] [**Mimulus perversus* Barrande, 1879, p. 109; OD]. Smooth form, close to *Triplesia* but with ventral fold and dorsal sulcus. *U.Ord.-L.Sil.,* Eu.-N.Am.

Cliftonia Foerste, 1909, p. 82 [**C. striata*; OD]. Externally like "small *Atrypa*" with subcircular outline and ornament of strong distant lamellae which undulate over costellae. *U.Ord.,* Ire.-Swed.; *L.Sil.,* EC.USA-Wales.——Fig. 228,*1*. *C. bellula* Ulrich & Cooper, L.Sil., USA(Okla.); brach.v., ext., ×2 (823).

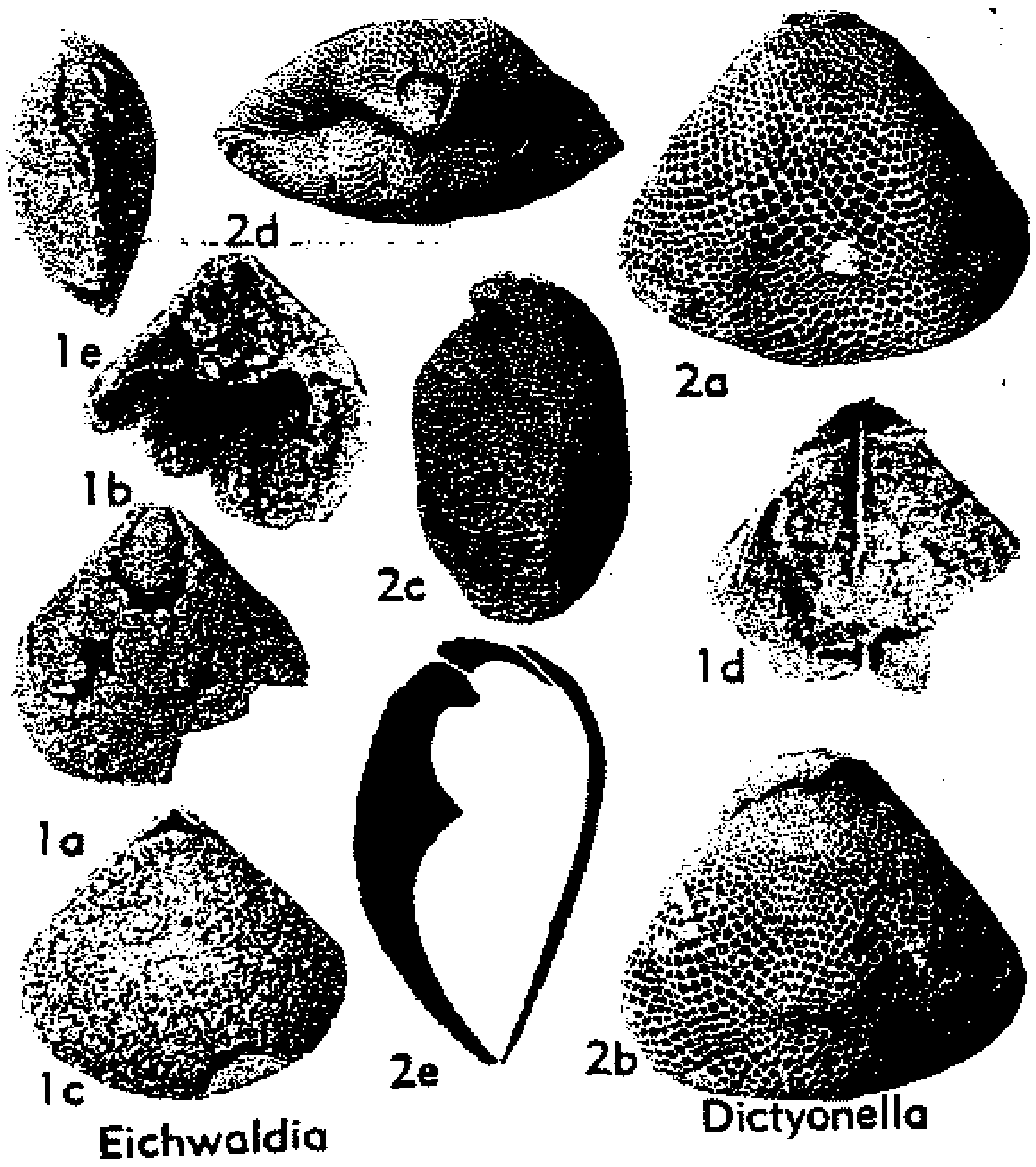


Fig. 229. Eichwaldiidae (p. *H*360).

Epacroplecia Williams, 1962, p. 155 [**Triplesia grayiae* Davidson, 1870, p. 198; OD]. Trigonal shell, with highly convex trilobate brachial valve and shallow pedicle valve; hinge short; finely costellate. Brachiophores subparallel, normal to hinge line, bladelike. *M.Ord.,* Scot.-?China.

Onychoplecia Cooper, 1956, p. 529 [**O. brevirostris*; OD]. Small form with tear-shaped outline, elongate beak and narrow hinge; narrowly lenticular in profile, smooth and uniplicate. *M.Ord.,* N. Am.(Newf.-N. Y.-Okla.-Tenn.).——Fig. 228,*6*. **O. brevirostris,* USA(Tenn.); brach.v. view of complete shell, ×2.5 (Wright, n).

Onychotreta Ulrich & Cooper, 1936, p. 339 [**O. mesleri*; OD]. Outline clawlike; pedicle valve greatly elongated, with very long interarea; dental plates long, parallel; brachial valve short; ornament coarsely costellate. *L.Sil.,* USA(Ark.).——Fig. 228,*7*. **O. mesleri*; *7a,b*, brach.v. view of complete shell, ped.v. ext., ×2; *7c,d*, brach.v. dorsal and post. views, ×2 (Wright, n).

Oxoplecia Wilson, 1913, p. 81 [**O. calhouni*; OD] [=*California* Bassler, 1915 *(nom. null.)*]. Roundly elliptical to transverse shells, uniplicate, characterized by well-developed costellate ornament and fine elevated concentric growth lines. Internally, may possess pedicle collar, but not pedicle tube. *M.Ord.-U.Sil.(Wenlock.),* Eu.-N.Am.——Fig. 228,*5*. **O. calhouni,* M.Ord.(Trenton.), Ont.; *5a,b*, brach.v., ant., views of complete shell, ×1.5 (Wright, n).

Plectotreta Ulrich & Cooper, 1936, p. 339 [**P. lindströmi*; OD]. Subcircular form characterized by strong concentric lamellae, and differentiated from *Streptis* by strong radial plications. *U.Sil. (Wenlock.),* NW.Eu.(Gotl.-Eng.).——Fig. 228,*3*. **P. lindströmi,* Gotl.; *3a,b*, brach.v., ant. views of complete shell, ×2 (Wright, n).

Streptis Davidson, 1881, p. 150 [**Terebratula grayi* Davidson, 1848, p. 331; OD]. Exterior with ornament of strong concentric lamellae, commonly developed into frills, and superimposed radial ribs. Uniplicate; usually showing marked asymmetry. *U.Ord.-U.Sil.*, N.Am.-Greenl.-Eu.——Fig. 228,*2*. **S. grayi*, U.Sil.(Wenlock.), Eng.; *2a-c*, ped.v., brach.v., ant. views of complete shell, ×3 (Wright, n).

ORDER UNCERTAIN—DICTYONELLIDINA

By A. J. Rowell
[Nottingham University]

Suborder DICTYONELLIDINA Cooper, 1956

[*nom. correct.* Rowell, herein (*pro* suborder Dictyonelloidea Cooper, 1956, p. 947)]

Shell calcareous, punctate; umbo of pedicle valve with inset, smooth, triangular umbonal plate. *M.Ord.-Perm.*

Superfamily EICHWALDIACEA Schuchert, 1893

[*nom. transl.* Rowell, herein (*ex* Eichwaldiidae Schuchert, 1893, p. 155)].

Characters of suborder. *M.Ord.-Perm.*

The most characteristic feature of the superfamily is the unusual modification of the umbo of the pedicle valve, nothing closely comparable to it being known in any other brachiopod stock. Extending anteriorly from the apex of the valve is a narrowly triangular smooth area, inset slightly below the level of the adjacent shell; this is the umbonal plate. It fills a triangular opening in the umbo and is attached by its lateral margins to the valve. Anteriorly, the umbonal plate is free and a broad, slitlike passage communicates between the inside and outside of the valve. This opening, although readily masked by crushing, is certainly present in the Eichwaldiidae and is recorded by Dittmar (260) in the Isogrammidae. As in all extinct groups, the interpretation of the functional anatomical significance of shell structures is difficult, but it is probable that this passage functioned as a pedicle opening, as was suggested by Hall & Clarke (1894).

Two families (Eichwaldiidae, Isogrammidae) are here included in the superfamily, differentiated from each other primarily by characters of the brachial valve. From what is known of their stratigraphical range, the two are separated from each other by a distinct time gap. The youngest Eichwaldiidae are recorded from the high Silurian and the Isogrammidae are first known from the Lower Carboniferous. Two alternative explanations of this hiatus are possible. The gap may be real, in which case the two families are not closely related, the resemblance between them indicating convergence rather than affinity, and the superfamily is polyphyletic. Alternatively, the absence of Devonian representatives may be explained in terms of failure of the fossil record. This negative approach is not very satisfactory, but in view of the rarity of the Isogrammidae and the close resemblance of the unusual modified ventral umbo of both families, it seems to be the most reasonable explanation.

The origin of this group of brachiopods is still unknown and there is even disagreement as to whether they should be referred to the Inarticulata or to the Articulata. Goryansky (1960, 356), for example, placed the Eichwaldiidae in the Inarticulata and the Isogrammidae in the Articulata. Muir-Wood (1955), taking a somewhat different view, referred both families to a suborder Incertae Sedis and assigned them to the articulates. The evidence on which to base a decision on this question is not very conclusive, but if the two families are regarded as related, then it appears on balance to favor the view that they are articulates. The calcareous shell suggests affinities with the Articulata, but, on the other hand, it is known that a calcareous shell has been developed independently in at least three and probably four separate inarticulate stocks. Similarly, the nature of articulation does not provide indisputable evidence of affinity, although that of *Isogramma* is reminiscent of the Articulata. It is the presence of a well-developed cardinal process in the Isogrammidae that suggests that they are articulates, for this structure, commonly developed in the Articulata, is unknown in any inarticulate stock.

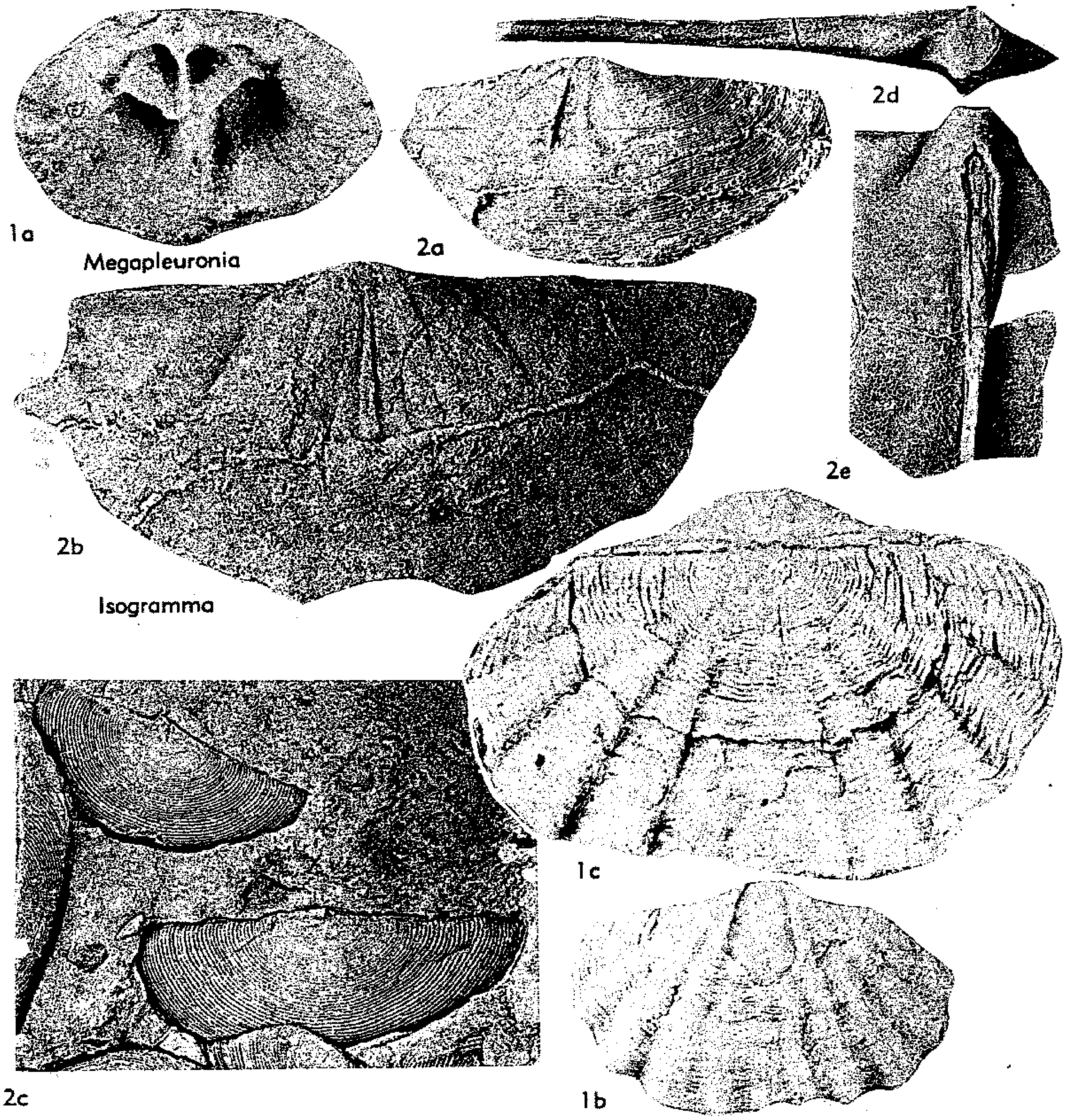


FIG. 230. Isogrammidae (p. *H*361).

Family EICHWALDIIDAE Schuchert, 1893

[Eichwaldiidae SCHUCHERT, 1893, p. 155]

Biconvex, triangular outline; long dental sockets in posterolateral margins of brachial valve, articulating with teeth in pedicle valve. *M.Ord.-U.Sil.*

Eichwaldia BILLINGS, 1858, p. 190 [**E. subtrigonalis*; OD]. External ornament only of fine concentric growth lines. Interior of brachial valve with prominent median septum extending nearly to anterior margin, small boss at posterior end of septum possibly functioning as cardinal process; musculature unknown. *M.Ord.*, Can.——FIG. 229, *1*. **E. subtrigonalis*, Rockland F., Ont.; *1a,b*, incompl. ped.v. ext., int., both ×2; *1c,d*, brach.v. ext., incompl. int., ×1, ×2; *1e*, both valves lat., ×1 (189).

Dictyonella HALL, 1868, p. 274 [**Atrypa coralifera* HALL, 1852, p. 281; OD] [=*Dyctionella* OEHLERT, 1887, p. 1267 (*nom. null.*)]. Very similar to *Eichwaldia*, differing in its ornament of rather coarse pits defined by intersecting, narrow, elevated lines. *Sil.*, N.Am.-Eu.-Asia.——FIG. 229,*2*. *D. capewelli* (DAVIDSON), Wenlock, Eng.; *2a*, ped. v. ext.; *2b*, brach.v. ext.; *2c*, both valves lat., *2d*, post.; *2e*, median long. sec., all ×3 (Rowell, n).

Family ISOGRAMMIDAE Schuchert & LeVene, 1929

[Isogrammidae Schuchert & LeVene, 1929, p. 18]

Shells transversely suboval in outline. Cardinal process with well-developed shaft, dental sockets relatively small, lateral to cardinal process (180). *Carb.-Perm.*

Isogramma Meek & Worthen, 1870, p. 36 [**Chonetes? millipunctatus* Meek & Worthen, 1870, p. 35; OD] [=*Aulacorhynchus* Dittmar, 1872, p. 2 (*non* Gould, 1834); *Aulacorhyna* Strand, 1928, *p. 37* (*nom. subst. pro Aulacorhynchus* Dittmar, 1872 (*non* Gould, 1834) (type, *Aulacorhynchus pachti* Dittmar, 1872, p. 2)]. Large, concavo-convex; strong concentric ornament of elevated fila. Myophore strong, shaft bifurcating around dorsal median ridge; musculature of brachial valve obscure, in pedicle valve adductor scars on inner surface of umbonal plate, subflabellate diductor scars lateral to plate (5). *Carb.-Perm.*, N.Am.-Eu.-Asia.——Fig. 230,*2a-c*. *I. texanum* Cooper, Penn. (Gaptank F.), USA(Tex.); *2a*, latex replica ped.v. ext., ×1; *2b*, ped.v. int. impression, ×2; *2c*, brach.v. ext. mold, ×1 (180).——Fig. 230,*2d,e*, *I. renfrarum* Cooper, Penn. (Gonzales Sh.); USA(Tex.); *2d,e*, detail of cardinal process, post., dors., both ×2 (180).

Megapleuronia Cooper, 1952, p. 117 [**Productus fabianii* Greco, 1947, p. 1; OD]. Biconvex or concavo-convex; costate, with concentric ornament of discontinuous, raised lines. Ventral interior unknown, dorsal interior with muscle platform supported by median septum. *Perm.*, Eu.——Fig. 230, *1a*. **M. fabianii* (Greco), Italy; brach.v. int., ×1 (180).——Fig. 230,*1b,c*. *M. grecoi* Cooper, Italy; *1b*, ped.v. ext., ×2; *1c*, brach.v. ext., ×3 (180).

STROPHOMENIDA

By Helen Muir-Wood and Alwyn Williams

[British Museum (Natural History) and Queen's University of Belfast]

Order STROPHOMENIDA Öpik, 1934

[*nom. transl.* Moore *in* Moore, Lalicker & Fischer, 1952, p. 221 (*ex* suborder Strophomenoidea Öpik, 1934, p. 75); emended H. M. Muir-Wood & Alwyn Williams, herein]
[Diagnosis prepared by Alwyn Williams]

Articulate brachiopods with plano- to concavo-convex, less commonly biconvex, resupinate or geniculated, shells; interareas lacking or vestigial to extravagantly developed, hinge lines rarely reduced; pseudodeltidium rarely absent, mostly strongly developed or continuous with ventral interarea, chilidium variably developed or indistinguishable from dorsal interarea; pedicle foramen, with sheath, supra-apical probably in all brephic shells but rarely open in adult shells, or attachment effected by cementation of pedicle valve with or without aid of open, tubular spines; spines may be present on brachial as well as pedicle valve, less commonly limited to margin of ventral interarea. Cardinal process rarely absent, elaborated from median partition or more commonly from pair of discrete lobes; socket ridges rarely strongly developed, commonly vestigial or absent; lophophore inferred to vary from schizolophous to spirolophous and attached plectolophous dispositions, less commonly supported by dorsal platforms or ridges, very rarely by calcareous spires. Ventral muscle field commonly expanded well beyond umbonal cavity, rarely borne on elevated structures; dorsal adductor field normally quadripartite rarely elevated. Shell substance pseudopunctate, very rarely impunctate. *L.Ord.-L.Jur.*

The Strophomenida constitute the largest ordinal group within the Brachiopoda, for the order embraces nearly 400 genera (including the largest and thickest shells known) distributed among nine superfamilies and four suborders. A taxonomic assemblage of this size inevitably includes a great variety of forms, but the morphological diversity displayed by members of the order is unprecedented, mainly because of the widespread adoption of an attached mode of life by cementation or spinous anchorage following the loss of a functional adult pedicle early in the evolutionary history of the group. Chonetidina and Productidina, for example, independently acquired spines or perforations containing outer epithelial strands by means of which support, through attachment to, or ramification within the substratum, was effected. A minority of strophomenaceans, most davidsoniaceans and all lyttoniaceans, on the other hand, remained attached for varying parts of their lives solely by cementation of the pedicle valves. Inflexible anchorage of this nature was probably the principal cause for repeated bizarre modifications in shell shape. Thus, conical shells were typical of late davidsoniaceans as well as richthofenaceans; but, whereas those of the former involved an exaggerated growth of the ventral interarea, those of the latter were the result of holoperipheral increase in the pedicle valve subsequent to loss of the interarea.

Despite this extraordinary variation in shell form, the order is basically a homogeneous group. With the discovery that pedicle sheaths were also developed in at least some young Productidina (BRUNTON, 1965) the supra-apical location of the functional foramen, commonly ventral of a well-developed pseudodeltidium, becomes the chief diagnostic feature of the Strophomenida, although it is also characteristic of some members of the Orthida. The attendant implication that the embryonic pedicle developed directly from the ventral body wall indicates, if correct, how primitive the Strophomenida were relative to most other articulate brachiopods. The pseudopunctate nature of the shell is not as invariably developed nor as exclusive to the order as is generally believed. The shells of a few plectambonitaceans and of early davidsoniaceans are impunctate, whereas *Estlandia* and other related Clitambonitidina are pseudopunctate, so that this particular condition of the test must have arisen polyphyletically.

Simple socket ridges are also typical of the Strophomenida, although they were lost in a minority of the Strophomenidina and in most Productidina, in which group they were commonly replaced by lateral ridges. In only a few plectambonitaceans and davidsoniaceans did elaboration of the ridges entail the growth of dorsally directed apophyses which may have been connected with the mouth segment of the lophophore in the manner of crura. Indeed, only the spiralia of *Thecospira* can be confidently compared with the more orthodox lophophore structures of other articulate orders. It is therefore not surprising to find that in plectambonitaceans, a few strophomenaceans, and many species of Productidina and Chonetidina, dorsal platforms, ridges, and endospines which are so arranged as to suggest their functioning as supports to the lophophore (the problems involved in interpreting the Oldhaminidina shell are discussed as an introduction to the systematics of that suborder). The endospines of Productidina probably also functioned as strainer devices.

Other features are less convincingly diagnostic of the order, although a few of them are still noteworthy. All variations of the plectambonitacean cardinal process, which include bifid and trifid structures, arose through modification of a simple median partition. In contrast, cardinal processes of the remaining Strophomenida, which may be extravagantly developed and greatly elaborated, were derived from a pair of ridge-like myophores that flanked a vestigial median partition only in the primitive, earlier strophomenaceans. Differences in the shell profile are also significant at the superfamilial level. The brephic shell of all Strophomenida was either biconvex or rarely convexo-plane (as in some strophalosiids) but this relationship was retained throughout later stages of growth only by members of the Davidsoniacea and an aberrant productacean (*Septarinia*). In all other Strophomenida are given below in the introductions to concavo-convex and was modified solely by resupination with or without geniculation; and in this respect most members of the order are immediately distinguishable from other articulate brachiopods.

More detailed accounts of the morphological variation displayed by the Strophomenida are given below in the introductions to the systematic descriptions of each suborder.

Suborder STROPHOMENIDINA
Öpik, 1934

[*nom. correct.* WILLIAMS, herein (*pro* suborder Strophomenoidea ÖPIK, 1934, p. 75] [Materials for this suborder prepared by ALWYN WILLIAMS]

Biconvex to concavo-convex or resupinate, smooth to unequally parvicostellate, wide-hinged articulate brachiopods, commonly with well-developed pseudodeltidium and chilidium; shell substance pseudopunctate, rarely impunctate. Teeth simple, rarely supplemented by accessory teeth and denticles or replaced by denticular plates; muscle bases rarely elevated above floor of valves; cardinal process commonly bilobed but also consisting of simple median ridge, rarely absent; mantle canal system in both valves saccate to lemniscate. *Ord.-Trias.*

The Strophomenidina brachiopods include a diverse host of stocks, mainly characteristic of the Paleozoic era, which, de-

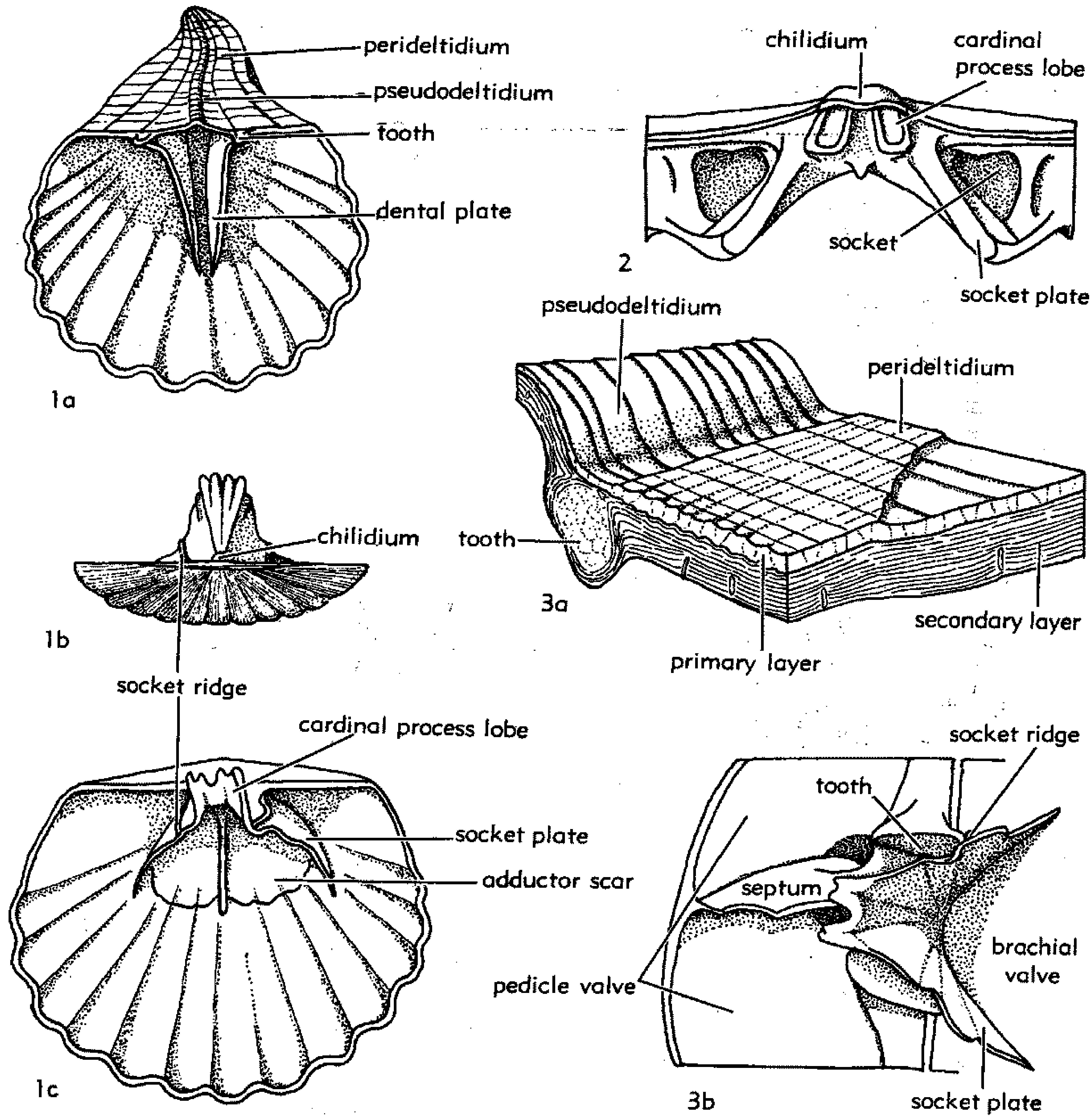


Fig. 231. Morphological features of davidsoniacean strophomenides (Williams, n). *1. Meekella*; *1a*, pedicle valve interior; *1b*, posterior view of brachial valve; *1c*, interior of brachial valve.——*2. Schuchertella*, showing chilidium and adjacent structures of brachial valve.——*3. Derbyia*; *3a*, oblique 3-dimension diagram showing structure of part of interarea; *3b*, view from inside shell looking toward beak.

spite a great deal of morphological variation, have a number of features indicative of common ancestry and collectively distinguishing them from the Productidina and Chonetidina.

The protegulum and brephic shells of all Strophomenidina, as far as known, are biconvex, a disposition maintained throughout the ontogeny of the davidsoniaceans, except for a minority (like some Schellwienella) in which the pedicle valve becomes concave in adult stages of growth. In contrast, the shell of all strophomenaceans and plectambonitaceans is concavo-convex in neanic stages at least, a relationship that never is eliminated completely even in resupinate stocks. The strophomenoid shell is typically widest at the hinge line and equipped with well-developed interareas, but among the davidsoniaceans a tendency toward reduction in width of the hinge line and in length of the dorsal interarea is seen.

The strophomenoid shell is ornamented in a variety of ways. The radial ornamenta-

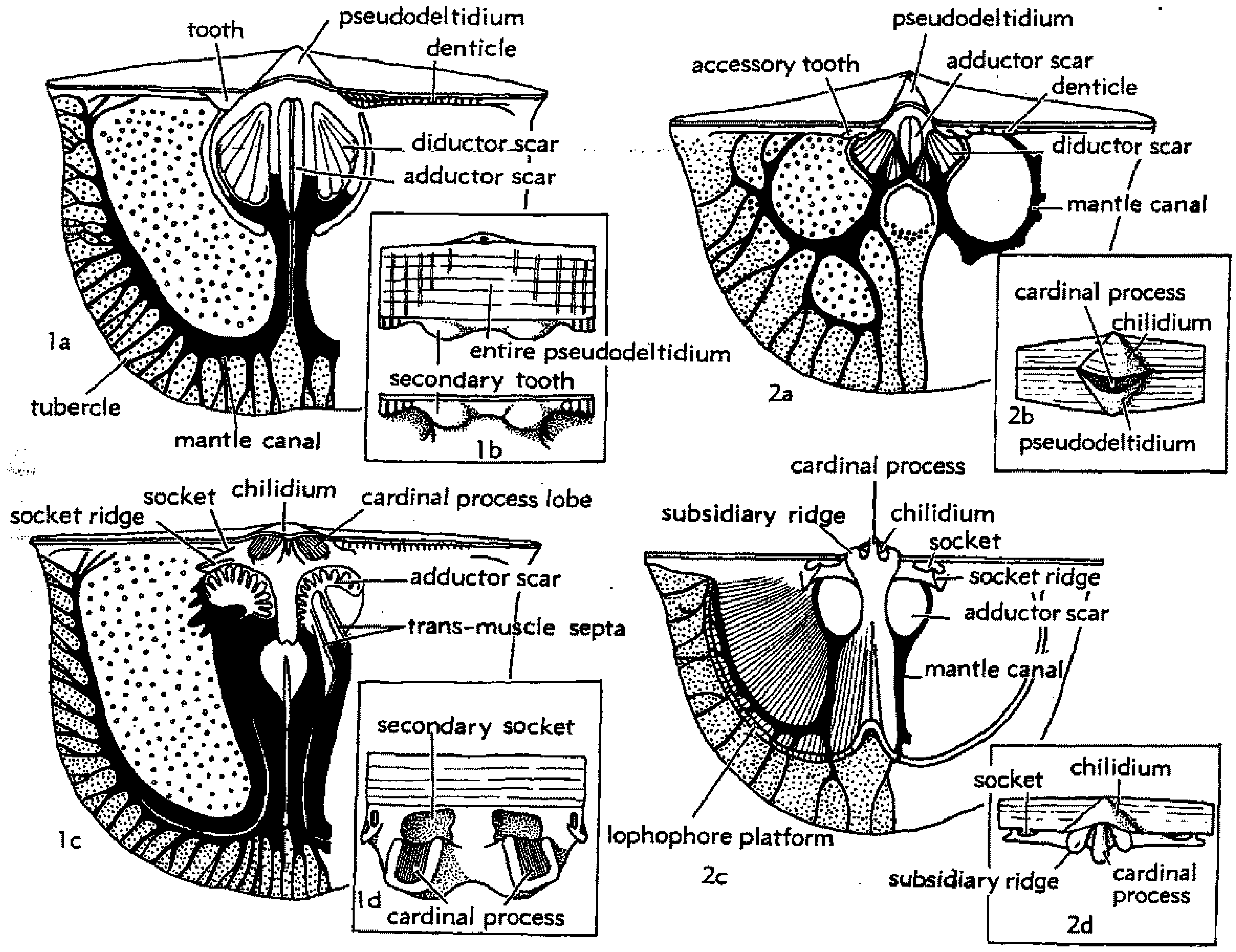


Fig. 232. Morphological features of earlier, less specialized strophomenide stocks (Williams, n).——*1.* Strophomenaceans; *1a*, stylized pedicle valve interior showing muscle scars and mantle canal pattern as developed in *Strophomena; 1b*, enlargements of median part of stropheodontid interarea; *1c*, brachial valve interior showing mantle canal pattern of *Strophomena*; *1d*, enlargement of median part of stropheodontid interarea.——*2.* Plectambonitaceans; *2a*, stylized pedicle valve interior showing mantle canal pattern as in *Leptestiina*; *2b*, enlargement of central part of interarea showing both valves; *2c*, stylized brachial valve interior showing mantle canal pattern as in *Leptestiina*; *2d*, enlargement showing chilidium and associated structures. The subsidiary ridges indicated in *2c* and *2d* also may be referred to as "notothyrial walls" or "chilidial plates" according to their origin.

tion is typically unequally parvicostellate but it disappears in such unrelated stocks as *Christiania, Bimuria, Pholidostrophia,* and *Thecospira,* and in late species of *Strophodonta* it is replaced by coarse secondary costellation. The shell may also be ornamented by fine lamellae or comae (as in many plectambonitaceans) and by concentric or impersistent rugae, as in most plectambonitaceans and strophomenaceans. All davidsoniaceans are characterized by a pair of triangular surfaces (perideltidium) forming part of the interarea of the pedicle valve and lying lateral to the pseudodeltidium, although not necessarily adjacent to it (Fig. 231, *1a, 3a*). Each surface is slightly elevated above the rest of the interarea, and in addition to being ornamented by growth lines parallel to the hinge line, is also feebly striated at right angles to the hinge line, the striations lying oblique to the perideltidial boundaries and not radiating from the umbo. Serial sections show that the perideltidial boundaries are represented by sharp deflections of both primary and secondary shell layers, the striations representing crenulations of the primary layer and part of the underlying secondary layer. No function has as yet been ascribed to the perideltidium.

In all plectambonitaceans, most strophomenaceans, and early davidsoniaceans, the pseudodeltidium and chilidium are well developed and they fit together so snugly that an exaggerated growth of one was matched by a complementary reduction of the other.

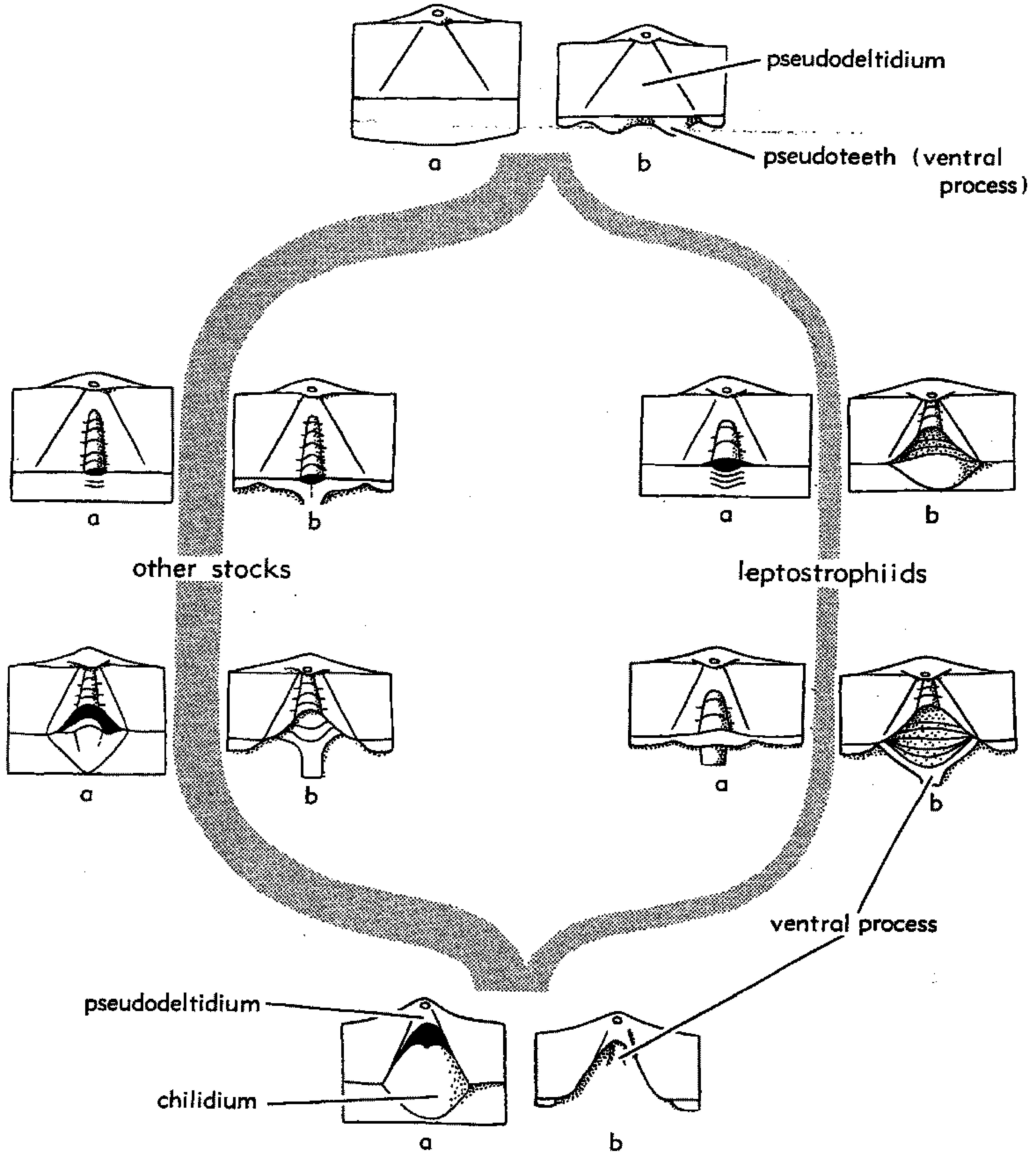


Fig. 233. Closure of delthyrium and loss of chilidium during evolution of stropheodontids (Williams, n). In most stocks, the delthyrium eventually was closed entirely by dorsal growth of the pseudodeltidium and ventral process on its inner side, without any pronounced concavity on the posterior surface of the ventral process. Among leptostrophiids, however, an evolutionary stage is seen in which the ventral process may be decidedly concave, simulating a spondylium, although certainly not homologous to it.

In early Strophomenidina (Fig. 232, *1c*) the chilidium, which usually is very much larger than the pseudodeltidium, probably functioned as a protective covering for the bases of the diductor muscles implanted on the notothyrial floor or on the cardinal process. It is therefore not surprising to find that among the stropheodontids the growth of the lobes of the cardinal process away from the hinge line was accompanied by a progressive elimination of the chilidium (871), so that in most Devonian representatives of the family the interarea of the brachial valve is entire, without a differentiated chilidium (Fig. 233). Concomitantly, the delthyrium ultimately became covered by an entire pseudodeltidium extending to the hinge line and disposed posteriorly in the

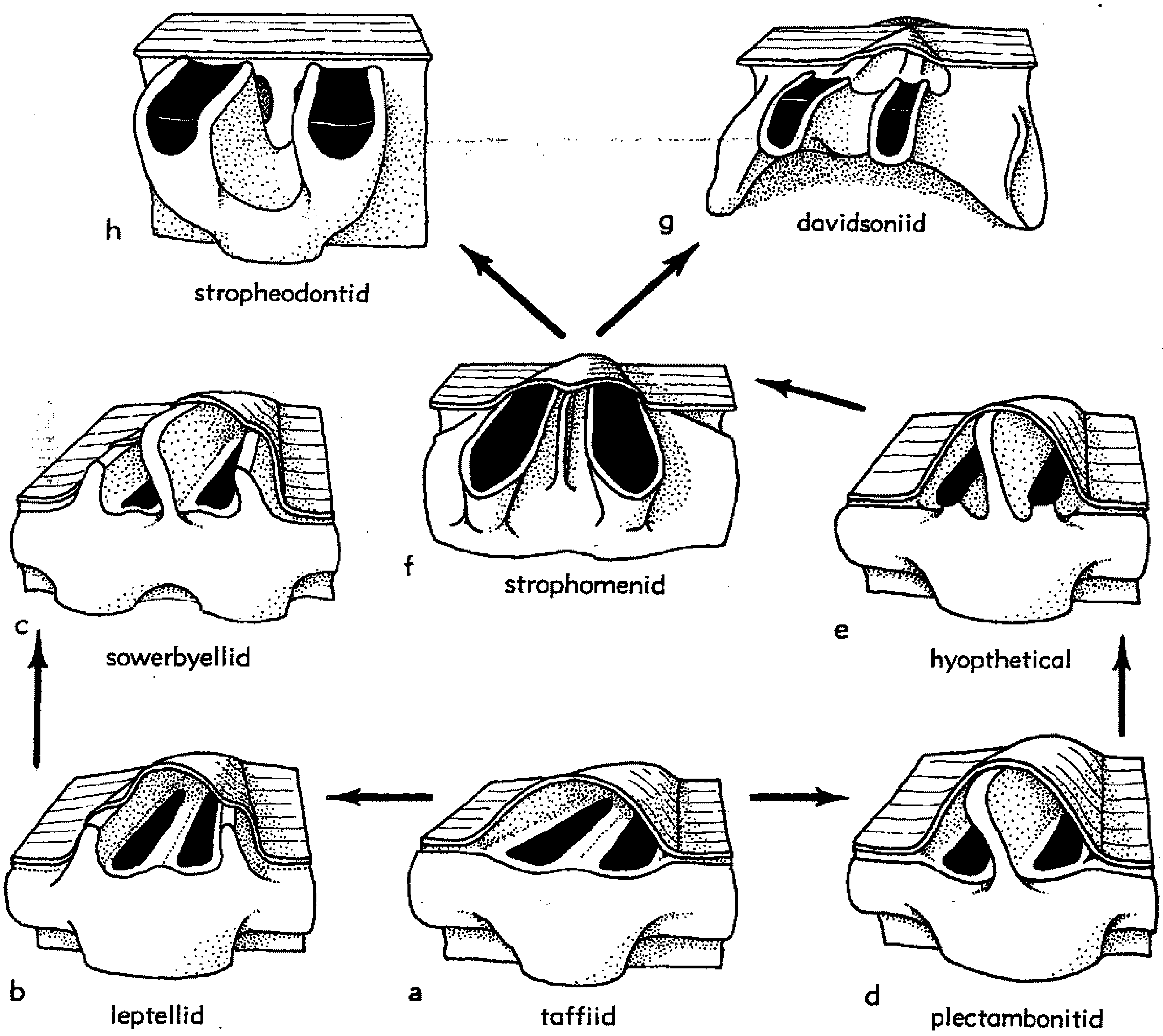


FIG. 234. Morphogeny of strophomenide cardinal process, with lines of presumed development indicated by arrows (black areas represent inferred seats of diductor muscle attachments) (Williams, n).

same plane as the interarea of the pedicle valve. In this ultimate stage the secondary shell deposit of the pseudodeltidium was fashioned into a pair of protuberances (secondary teeth) (Fig. 232, *1b*) which fit into the concave surfaces (secondary sockets, etc.) separating the cardinal process lobes from the interarea of the brachial valve.

A similar complementary growth of the pseudodeltidium and chilidium also apparently was connected with ventral growth of the cardinal process lobes and, accelerated by reduction in the interarea of the brachial valve, characterizes the davidsoniaceans (Fig. 231, *1*). Except for a few forms (e.g., *Thecospira*), however, the pseudodeltidium is never entire and usually it is sharply arched medianly to accommodate both a vestigial chilidium and the elevated posterior face of the cardinal process.

Modification of the notothyrial floor for attachment of the dorsal diductor muscle bases was diversely effected among the Strophomenidina (Fig. 234). In some early plectambonitaceans (e.g., *Taffia*), the diductor muscle bases must have been attached directly to the floor of the notothyrium, for no outgrowths which could have accommodated them are found on it.

A simple departure from this unspecialized condition consists of the growth of a median partition which usually extends from the notothyrial floor to the chilidium (as among the plectambonitids), thus dividing the notothyrium into two deep narrow chambers. This septum is conveniently referred to as a simple cardinal process but in all probability the diductor bases were attached to the notothyrial floor on either side of the septum. Further elaboration included the infilling of the notothyrium by the growth of lateral ridges subsidiary to the median septum and subtending with it a pair of grooves for the reception of the dorsal diductor bases.

A similar development is seen in other plectambonitaceans but it was accompanied by the posterior and ventral growth of the notothyrial walls as a pair of prominent ridges more or less continuous with the socket ridges. These are commonly referred to as chilidial plates, although it is noteworthy that their formation was in no way related to the growth of the chilidium, which normally covers their dorsal ends. In early members (e.g., *Leptella*), the chilidial plates simply acted as high lateral boundaries to the notothyrium or to a notothyrium containing a median cardinal process (e.g., *Bimuria*). Among sowerbyellids, however, the plates, together with the median septum, are not only firmly ankylosed to the notothyrial floor but also considerably elevated above the hinge line and prolonged ventrally to it, and since the muscle bases probably were inserted within the narrow slots formed by the median septum and the chilidial plates, the entire structure is analogous to a bilobed cardinal process with the lobes ankylosed to each other along the median plane.

The strophomenacean and davidsoniacean arrangement is quite distinct from that of the plectambonitacean, for the diductor muscles were attached not to the notothyrial floor but to a pair of outgrowths from it (bilobed cardinal process), each of which bore the muscle bases on its posterior face. Öpik (618, p. 61) has commented on the presence of a fine ridge lying medianly between the lobes of the cardinal process of many strophomenaceans and his suggestion that this ridge is a degenerate homologue of the plectambonitacean median partition is probably correct. Despite subsequent modification of the strophomenoid cardinal process, the fundamental bilobed pattern is maintained (e.g., stropheodontids and most davidsoniaceans, in which the notothyrium, as well as the chilidium, is vestigial or absent and in which the cardinal process lobes project for some distance into the umbonal region of the pedicle valve).

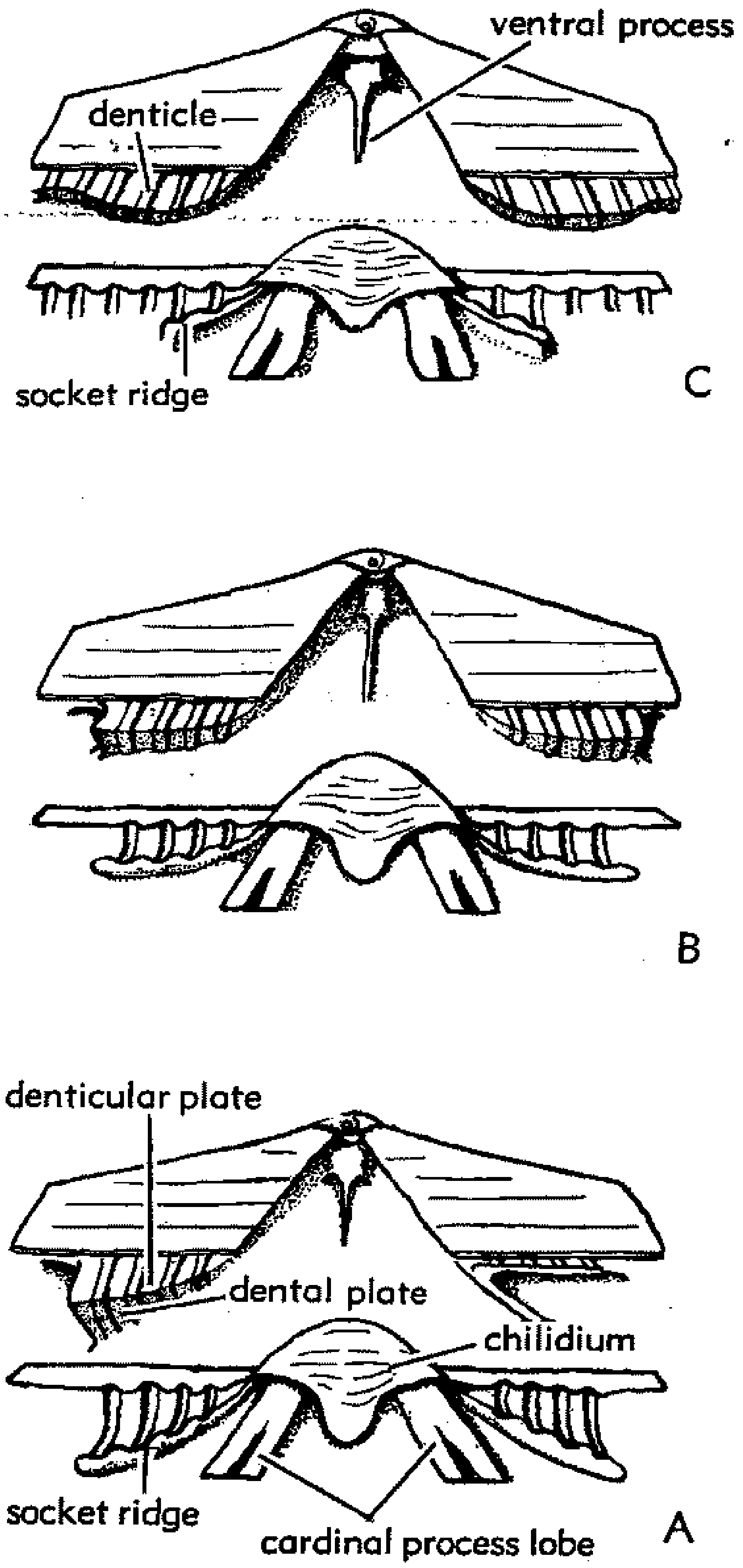


Fig. 235. Evolution of stropheodontid denticular structure associated with loss of dental plates, illustrated in sequence *A-C* (based on various Lower Silurian species of *Strophonella* (Williams, n).

A considerable variation in the articulatory devices also is displayed by the Strophomenidina. The simplest and seemingly the most primitive consisted of a pair of simple teeth, generally supported by dental plates in the pedicle valve, and a complementary pair of sockets in the brachial valve (Fig. 232, *1a,c*). In a number of plectambonitaceans, the teeth are flanked by a pair of similar protuberances (accessory teeth, Fig. 232, *2a*) which also are provided with accessory socket accommodation. In the earliest stropheodontids (871) the simple teeth consist of a pair of obtusely triangular plates which are fused along their dorsal edges to a pair of widely divergent dental plates to form a pair of hollow cones with the dorsal edges corrugated by as many as seven ridges (denticles). The sockets of the brachial valve are corrugated in a like manner. As the stocks evolved, so the dental plates migrated to the hinge line and finally fused with the teeth to form a thick, wide, denticular plate on either side of the delthyrium (Fig. 235). Subsequent to fusion, the remainder of the hinge line became progressively denticulate in all stropheodontid stocks, although with varying tempo. A denticulate hinge line is also characteristic of some plectambonitaceans, but in this group it is not preceded by any modification of the teeth and dental plates which persisted.

The development of deep conical pedicle valves among the davidsoniaceans was accompanied by the exaggerated growth of the dental plates, which became a pair of long deep blades sweeping down from the anterior faces of the teeth to the floor of the valve (Fig. 231, *1a*). They may be divergent (e.g., *Schellwienella*), parallel (e.g., *Meekella*), or in various stages of coalescence leading to the formation of a spondylium which may be sessile (e.g., *Sicelia*), supported by a median septum (e.g., *Geyerella*), or even free for most of its length (e.g., *Orthotetella*). Small chambers found in the umbo of *Orthotetes* by fusion of the posterior end of the ventral median septum with the anterior edges of unsupported teeth are in no way homologous with these muscle-bearing spondylia.

Another important feature of strophomenoid organization is the apparent, and in many stocks the undoubted, absence of any specialized structures associated with the cardinalia which gave support to the lophophore. Thus, in the stropheodontids, the pair of ridges forming the inner boundary of the sockets in early members have been referred to as "brachiophores." With the progressive spread of denticles along the hinge line in later stocks, the teeth-and-socket arrangement became vestigial and the ridges either disappeared entirely or, exceptionally (e.g., leptostrophias), became modified to form ankylosed buttresses to the cardinal process lobes (Fig. 236). It seems, then, that the ridges are nothing more than internal walls of the sockets and the function of lophophore support cannot be ascribed to them. This is equally true for Strophomenidina generally which are equipped with weak ridges (e.g., early stropheodontids). Within the davidsoniacean group also, no evidence is found to suggest that specialized structures supported the lophophore. The presence of strong, large teeth, the loss of the interarea of the convex brachial valve, and the pronounced ventral growth of the cardinal process all contributed to the development of a pair of socket plates extending from the floor of the valve to the sides of the cardinal process and bearing a pair of concave socket surfaces bounded laterally by socket ridges (Fig. 231, *1b,c 2, 3b*). Even in *Thecospira* the calcareous spires are not attached to any structures associated with the socket ridges but were supported by a pair of very short, scarcely differentiated outgrowths from the bases of the cardinal process lobes.

Öpik (619, p. 44) has come to a similar conclusion in his investigation of *Leangella*, in which the ridges defining the teeth sockets are especially prominent; and in the plectambonitaceans generally, it is highly likely that the so-called crural processes, or brachiophores, functioned only as socket-bounding ridges (Fig. 232, *1c,d, 2c,d*).

Little evidence as to the form of the strophomenacean lophophore can be adduced but some preserved impressions (e.g., *Leptaenisca*) indicate that it consisted of a pair of depressed spirally coiled brachia, a disposition compatible with the shell configuration. Impressions suggestive of a spirolophe are also found in certain species of the plectambonitacean *Titambonites*.

A spirolophous lophophore was apparently also characteristic of the davidsoniaceans; impressions of depressed coiled brachia are found in *Davidsonia*, and the brachia of *Thecospira* were evidently strengthened by the development of a pair of spirally coiled calcareous ribbons. These spires form a pair of high cones extending well into the interior of the pedicle valve and it is probable that the lophophore of those davidsoniaceans, in which the depth of the shell was greatly increased by the exceptional growth of the pedicle valve, was similarly disposed.

Kozlowski (487), Öpik (619), and Wil-

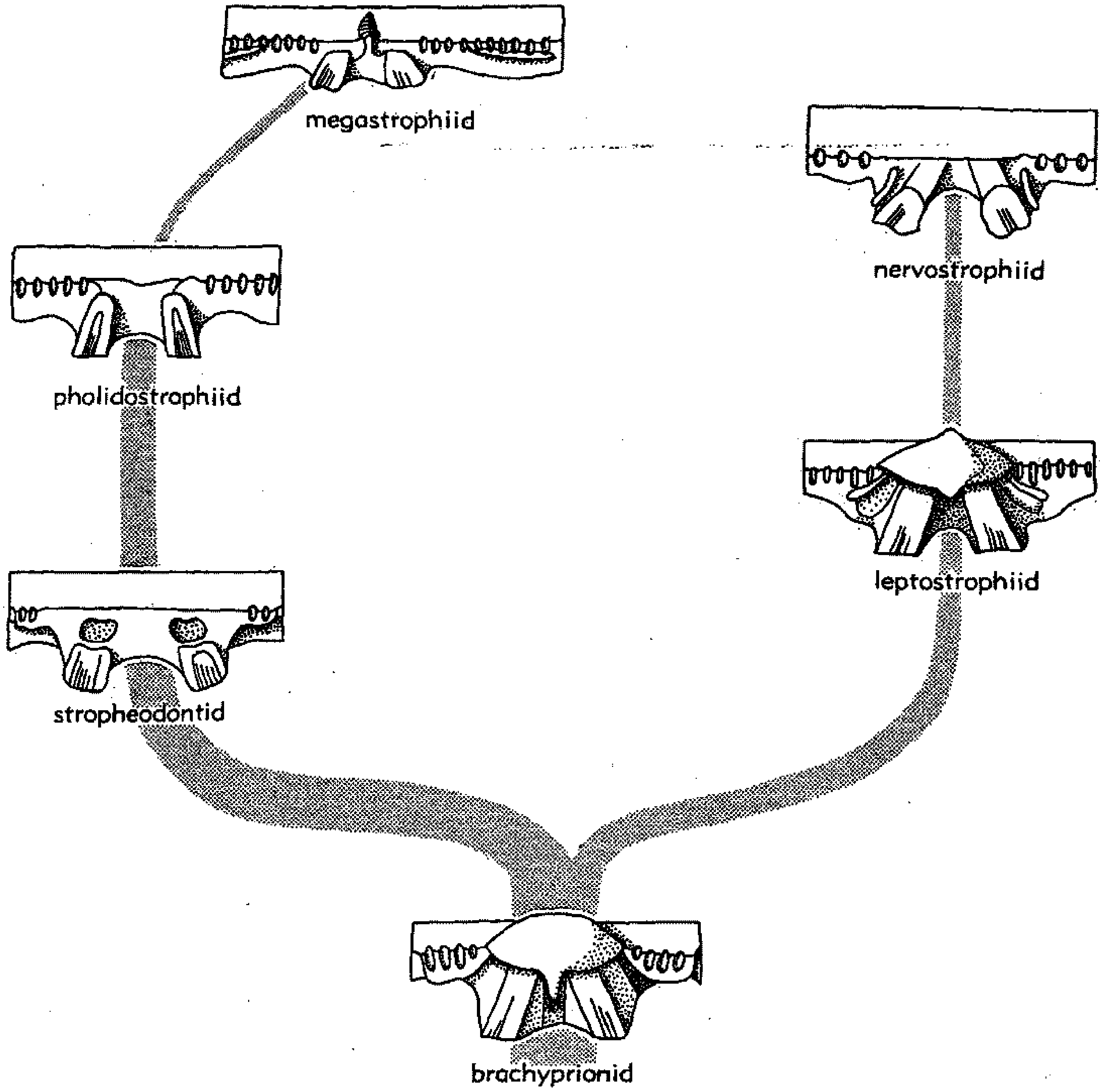


FIG. 236. Modification of socket ridges of brachial valve during evolution of stropheodontids (Williams, n). Most stocks show brachyprionid to pholidostrophiid patterns, with ultimate loss of ridges; megastrophiid forms are judged to belong in this group, for the articulatory ridges of Devonian members are secondary structures. The divergent branch of leptostrophiid and nervostrophiids is characterized by ankylosis of socket ridges to the cardinal process lobes.

LIAMS (875) have concluded that the strongly elevated and striated ridge often found in the plectambonitacean brachial valve (Fig. 232, *2c*) completely surrounding the posteromedian area (lophophore platform) represent the zone of attachment for the lophophore in a manner analogous to the lophophore-supporting structure of the thecideaceans. This interpretation is certainly the most plausible explanation for the development of such an extraordinary feature, and if it is correct, the supported lophophores were probably schizolophous or ptycholophous.

Elevated ridges are also found in the brachial valve of the strophomenacean *Christiania* and are strongly reminiscent of the plectambonitacean lophophore platform. In this stock, however, the partitions are disposed in two discrete loops and if the functional interpretation of these structures is correct, the lophophore was schizolophous.

Most of the morphogenetic trends outlined above, such as the complementary development of the pseudodeltidium and chilidium and the development of various types of cardinal processes, were important features of strophomenoid evolution but the main one was undoubtedly the loss of a functional pedicle in postneanic stages of growth of most stocks. It is probable that in all Strophomenidina the pedicle rudiment was differentiated sufficiently to function as an organ of attachment during early stages of development and at least in the majority of the strophomenaceans was provided with a calcareous protective sheath. In a number of adult plectambonitaceans and strophomenaceans, the persistence of an apical foramen suggests that the rudiment did, in fact, give rise to a pedicle which functioned throughout the life of the individual. But all adult stropheodontids, together with certain other strophomenaceans and many plectambonitaceans in which the foramen was sealed off by the secretion of secondary shell within the umbonal cavity of the pedicle valve, must have rested unattached in or on the sediments of the sea floor.

In terms of stock longevity, this specialized mode of existence does not seem to have been entirely successful; the stropheodontids originated, proliferated, and suffered extinction well within the time range of the pedicle-bearing *Leptaena.* It is also significant that the plectambonitaceans and strophomenaceans were replaced by the davidsoniaceans, for although the supposed ancester of this group, *Fardenia,* lost a functional pedicle in adult shells of all but the earliest species, the remainder retained an attached mode of life by cementation of the pedicle valve to a foreign body. Attachment by cementation was not restricted to the davidsoniaceans; it was also a feature of the stropheodontid *Lilljevallia,* and the strophomenids *Leptaenoidea* and *Leptaenisca,* although none of these flourished on the davidsoniacean scale.

Superfamily PLECTAMBONITACEA Jones, 1928

[*nom. transl.* Cooper & Williams, 1952, p. 332 (*ex* Plectambonitinae Jones, 1928, p. 394)]

Concavo-convex to resupinate Strophomenidina with cardinalia consisting of well-developed socket ridges and cardinal process, which, when present, is essentially a simple median ridge, with or without subsidiary lateral ridges and rarely expanded as a bulbous myophore; pseudodeltidium and chilidium present in variable degree; pedicle presumably functional in adult shells with persistent apical foramen, more commonly lost during ontogeny, so that mature shells were unattached; brachial valve generally equipped with elevated lobate platform presumed to have given support to a ptycholophous or schizolophous lophophore. *Ord.-Dev.*

Family PLECTAMBONITIDAE Jones, 1928

[*nom. transl.* Kozlowski, 1929, p. 108 (*ex* Plectambonitinae Jones, 1928, p. 394)]

Median cardinal process growing from notothyrial floor and ankylosed posteriorly to convex chilidium; pseudodeltidium large; apical foramen sporadically persistent in adult shells. Pedicle valve with pair of accessory teeth lying anterolaterally to 2 simple teeth; brachial valve without elevated lophophore platform, socket ridges flat-lying, subparallel with hinge line; subperipheral rims, possibly representing boundaries of brachial cavity, usually well developed in both valves; mantle canal systems poorly known but probably saccate in both valves. *L.Ord.-M.Ord.*

Subfamily PLECTAMBONITINAE Jones, 1928

[Plectambonitinae Jones, 1928, p. 394] [=Plectellinae Schuchert & Cooper, 1931, p. 245 (assigned to Clitambonitidae)]

Hinge line denticulate; pedicle valve with divergent diductor scars separated anteriorly by low broad plate or ridge and flanked by pair of variably developed, divergent ridges; adductor scars of brachial valve associated with variable number of low septa. *L.Ord.-M.Ord.*

Plectambonites Pander, 1830, p. 90 [**P. planissimus*; SD Hall & Clarke, 1892, p. 296]. Concavo-convex, unequally parvicostellate, with widely spaced accentuated costellae and strong concentric ridges breaking finer costellae into radial rows of tubercles, apical foramen persistent in adult shells. Dorsal adductor scars splayed about single pair of submedian septa and 3 pairs of radiating ridges. *M.Ord.,* Baltic.——Fig. 237,2. **P. planissimus,* C_1; *2a,b,* ped.v. and post views of conjoined valves, ×1.5 (Williams, n); *2c,* brach.v. int., ×2; *2d,* ped.v. int., ×3 (Rōōmusoks, n).

Ingria Öpik, 1930, p. 57 [**Orthisina nefedywi* Eichwald, 1860; OD] [=*Palinorthis* Ulrich & Cooper, 1936, p. 625 (type, *P. cloudi*)]. Resupinate, unequally parvicostellate, with narrow seg-

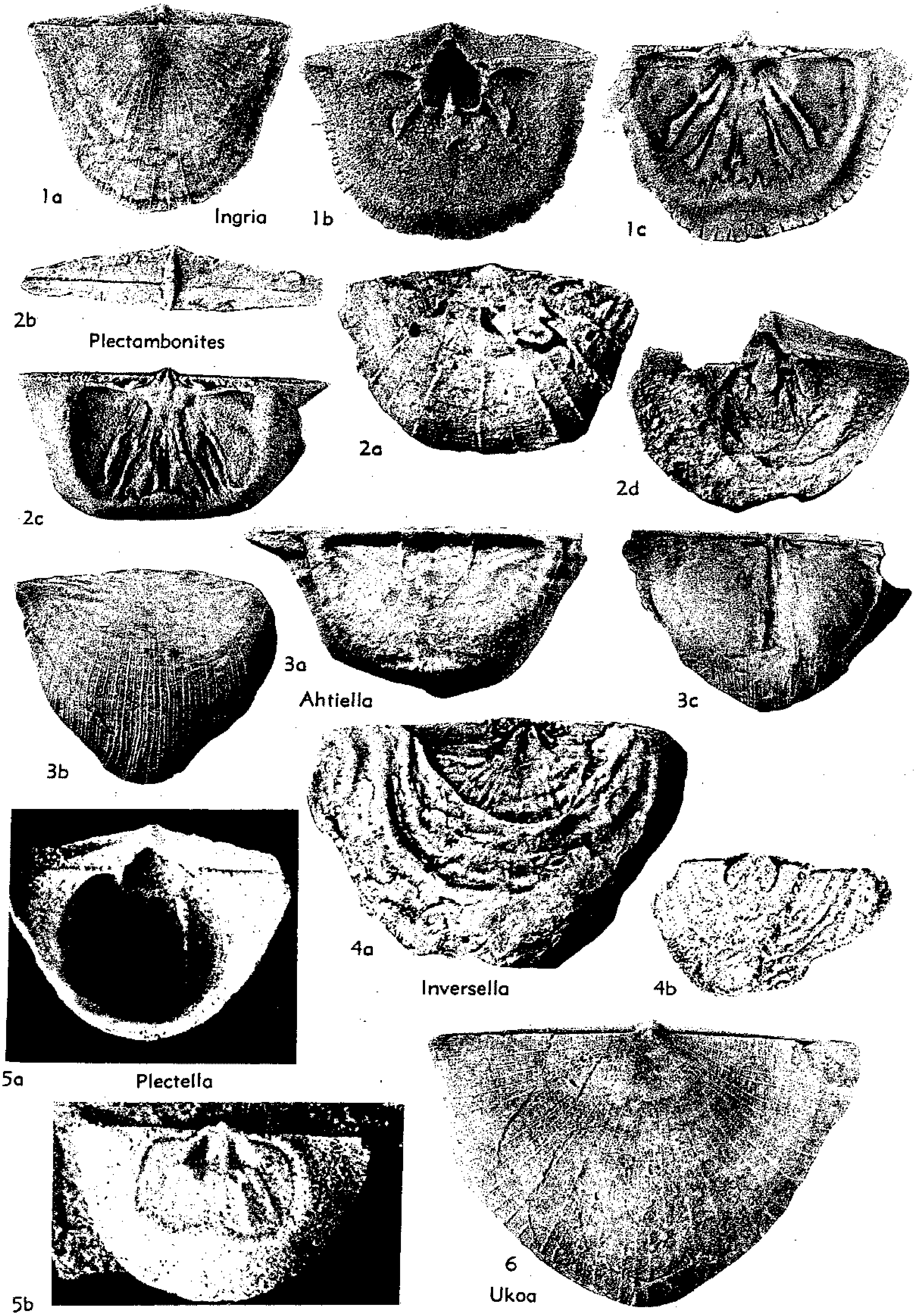


Fig. 237. Plectambonitidae (Plectambonitinae) *(1-2, 5)*, (Ahtiellinae) *(3, 4, 6)* (p. *H*370, *H*372).

ments defined by accentuated costellae, without apical foramen; brachial valve interior like that of _Plectella_. _L.Ord._, Eu.-N.Am.——Fig. 237,_1_. _I. cloudi_ (Ulrich & Cooper), Whiterock, USA (Nev.); _1a_, brach.v. view of conjoined valves, ×2; _1b,c_, ped.v. int., brach.v. int., ×2 (189).

Plectella Lamansky, 1901, p. 156 [*_Plectambonites uncinata_ Pander, 1830, p. 91; OD]. Like _Plectambonites_ but without apical foramen and with median ridge in brachial valve commonly bifurcating to contain another median ridge which extends forward flanked by 2 pairs of low or indistinct ridges. _L.Ord._(B_{I}), Baltic.——Fig. 237,_5_. *_P. uncinata_ (Pander), Est.; _5a_, ped.v. int., ×3; _5b_, brach.v. int. mold, ×3 (618).

Subfamily AHTIELLINAE Öpik, 1933

[Ahtiellinae Öpik, 1933, p. 19]

Resupinate, with smooth hinge lines and without elaborate septal apparatus in brachial valve. _L.Ord.-M.Ord._

Ahtiella Öpik, 1932, p. 37 [*_A. lirata_; OD]. Unequally parvicostellate, impersistently rugate, with dorsal sulcus and without apical foramen. Ventral muscle scar quadrate in outline, dorsal adductor scars impressed on either side of strong median septum. _L.Ord._(B_{III})-_M.Ord._(C_{I}), Baltic.——Fig. 237,_3a_. *_A. lirata_, M.Ord.(C_{I}); _3a_, ped.v. int., ×2 (Rõõmusoks, n).——Fig. 237,_3b,c_. _A. jaanussoni_ (Hessland), L.Ord., Sweden; _3b,c_, brach.v. ext. and int. mold, ×1 (Williams, n).

Inversella Öpik, 1933, p. 21 [*_I. borealis_; OD]. Like _Ahtiella_ but strongly geniculate and persistently rugate; without median septum in brachial valve. _L.Ord._(B_{III})-_M.Ord._(C_{I}), Baltic-Wales.——Fig. 237,_4a_. _I._ sp. cf. _I. borealis_, (B_{III}), Est.; _4a_, brach.v. ext. dissolved away posteromedianly to show mold of cardinalia, ×1.5 (Williams, n).——Fig 237,_4b_. _I._ sp., L.Ord., Wales; _4b_, ped.v. int., ×1.5 (Bates, n).

Ukoa Öpik, 1932, p. 33 [*_U. ornata_; OD]. Differs from _Ahtiella_ in being impunctate and having apical foramen and triangular muscle scar in pedicle valve. _L.Ord._(B_{III})-_M.Ord._(C_{I}), Baltic.——Fig. 237,_6_. *_U. ornata_, M.Ord.(C_{I}), Est.; brach.v. view of conjoined valves, ×1 (Rõõmusoks, n).

Family TAFFIIDAE Ulrich & Cooper, 1936

[Taffiidae Ulrich & Cooper, 1936, p. 625]

Subquadrate, faintly sulcate, unequally parvicostellate. Musculature and cardinalia orthoid-like; notothyrium covered completely by convex chilidium; teeth simple, supported by short dental plates; cardinal process absent or present as median ridge, exceptionally differentiated into myophore; pseudodeltidium variable in development, apical foramen small, only sporadically persistent in adult shells; subperipheral rims variably developed; mantle canal systems poorly known and variable: _L.Ord.(U.Canad.-Whiterock)_.

Taffia Ulrich, 1926, p. 99 [*_T. planoconvexa_ Butts in Ulrich, 1926, p. 100; OD]. Plano- to concavo-convex. Ventral muscle scar small, subtriangular, with diductor lobes not enclosing median adductor scar; socket ridges rodlike, cardinal process absent, dorsal subperipheral rim present; ventral mantle canal pattern saccate, dorsal probably digitate. _L.Ord.(U.Canad.)_, N.Am.——Fig. 238,_1_. *_T. planoconvexa_ Butts, USA(Ala.); _1a,b_, brach.v. ext. and int., ×1.5; _1c_, brach.v. view of conjoined valves, ×2; _1d_, ped.v. int., ×1.5 (189).

Aporthophyla Ulrich & Cooper, 1936, p. 625 [*_A. typa_; OD]. Like _Taffia_ but with simple cardinal process and without subperipheral rims inside margins of valves. _L.Ord.(Whiterock)_, N.Am.——Fig. 238,_2_. *_A. typa_, USA(Nev.); _2a_, brach.v. post. view, ×3; _2b_, ped.v. int. mold, ×1 (189).

Pelonomia Cooper, 1956, p. 699 [*_Orthis delicatula_ Billings, 1865, p. 217; OD]. Like _Taffia_ but with rudimentary pseudodeltidium, small median cardinal process and dorsal median ridge replaced by 2 submedian rows of strong tubercles. _L.Ord. (Whiterock)_, E.N.Am.(Newf.).

Toquimia Ulrich & Cooper, 1936, p. 626 [*_T. kirki_; OD]. Shallowly concavo-convex with brachial valve becoming flat or gently convex anteriorly. Ventral muscle scar subflabellate, with diductor lobes enclosing median adductor scar and ending anterolaterally in pair of subdued callosities; socket ridges in form of short, flat blades; cardinal process consisting of short median shaft and trilobed myophore; subperipheral rims prominent in both valves; dorsal mantle canal pattern lemniscate. _L.Ord.(Whiterock)_, N.Am.——Fig. 238,_3_. *_T. kirki_, USA(Nev.); _3a_, ped.v. int. mold, ×1; _3b_, brach.v. int. cast, ×2 (189).

Family LEPTESTIIDAE Öpik, 1933

[_nom. transl._ Williams, 1953, p. 6 (_ex_ Lepestiinae Öpik, 1933, p. 24)]

Simple teeth supplemented by pair of variably developed accessory teeth and with variable number of septa associated with dorsal adductor field; pseudodeltidium commonly narrow, arched, pedicle foramen persistent in adult shells of one stock only; socket ridges short, divergent and commonly pointed distally; dorsal and ventral mantle canal systems commonly saccate or digitate but lemniscate exceptionally. _L.Ord.-U.Ord._

Subfamily LEPTESTIINAE Öpik, 1933

[Leptestiinae Öpik, 1933, p. 24]

Unequally parvicostellate, with massive trilobed cardinal process differentiated posteriorly into high median crest flanked by pair of lower lateral ridges and continuous anteriorly with median septum. *L.Ord.-U.Ord.*

Leptestia Bekker, 1922, p. 362 [**L. musculosa*; OD] [=*Leptestia (Leptoptilum)* Öpik, 1930, p. 130 (type, *L. (L.) bekkeri*)]. Concavo-convex, commonly with strong concentric lamellae distally; ventral muscle scar suboval with wide adductor field not enclosed by diductor scars; dorsal median septum strong, dividing oval adductor field. *M.Ord.*, Baltic-Eire.——Fig. 239,*6*. **L. musculosa*, CII, Est.; *6a,b*, ped.v. and brach.v. int., ×1.5 (Williams, n).

Apatomorpha Cooper, 1956, p. 709 [**Rafinesquina pulchella* Raymond, 1928, p. 296; OD]. Concavo- or plano-convex, impersistently rugate posterolaterally. Ventral muscle scar large, bilobed, with diductors extending beyond median adductor; cardinal process bulbous, dorsal median septum strong, flanked by up to 3 pairs of narrowly divergent ridges. *M.Ord.(Porterfield)*, E.USA.——Fig. 239,*7*. **A. pulchella* (Raymond), Tenn.; *7a*, brach.v. view of conjoined valves, ×2;*7b,c*, brach. v. and ped.v. int. molds, ×3 (189).

Glyptambonites Cooper, 1956, p. 712 [**G. musculosus*; OD]. Like *Apatomorpha* but strongly rugate posterolaterally and even anteriorly, commonly with widely spaced accentuated costellae. Long, narrow, slightly divergent diductor scars in pedicle valve. *M.Ord.-U.Ord.*, E.N.Am.-Eu.(Scot.).——Fig. 239,*8*. **G. musculosus*, U.Ord.(Wilderness), USA(Va.); *8a*, ped.v. ext., ×2; *8b*, ped.v. int., ×1; *8c*, brach.v. int. cast, ×1.5 (189).

Goniotrema Ulrich & Cooper, 1936, p. 626 [**G. perplexum*; OD]. Like *Sowerbyites* but without callosities anterior to diductor scars in pedicle valve and strong submedian septa in brachial valve; pedicle foramen persistent in adult shells. *L.Ord.(Canad.)*, USA(Nev.).

Grorudia Spjeldnaes, 1957, p. 61 [**G. grorudi*; OD]. Like *Apatomorpha* but with poorly defined ventral muscle scar and short elevated platform for dorsal adductor scars flanking short median septum and pair of subparallel submedian septa. *M.Ord. (4aβ-4ba)*, Norway, Eire.——Fig. 239,*1*. **G. grorudi*, *4aβ*, Norway; *1a*, brach.v. int., ×4.5; *1b*, ped.v. int. mold, ×5 (Williams, n).

Hesperomena Cooper, 1956, p. 744 [**H. leptellinoidea*; OD]. Like *Leptestia* but with large ventral muscle scar including long, slender diductors, trilobed cardinal process projecting as shelf over notothyrial platform; dorsal adductor scars obscure; median septum low. *L.Ord.(Whiterock)*, USA(Nev.).——Fig. 239,*2*. **H. leptellinoidea*; brach.v. int., ×2 (189).

Palaeostrophomena Holtedahl, 1916, p. 43 [**Strophomena concava* Schmidt, 1958, p. 217; OD]. Like *Apatomorpha* but resupinate and commonly with widely spaced accentuated costellae. *M.Ord.*, Eu.-N.Am.——Fig. 239,*3*. **P. concava* (Schmidt), CII, Est.; *3a,b*, brach.v. ext., ped.v. int., ×1.5 (619).

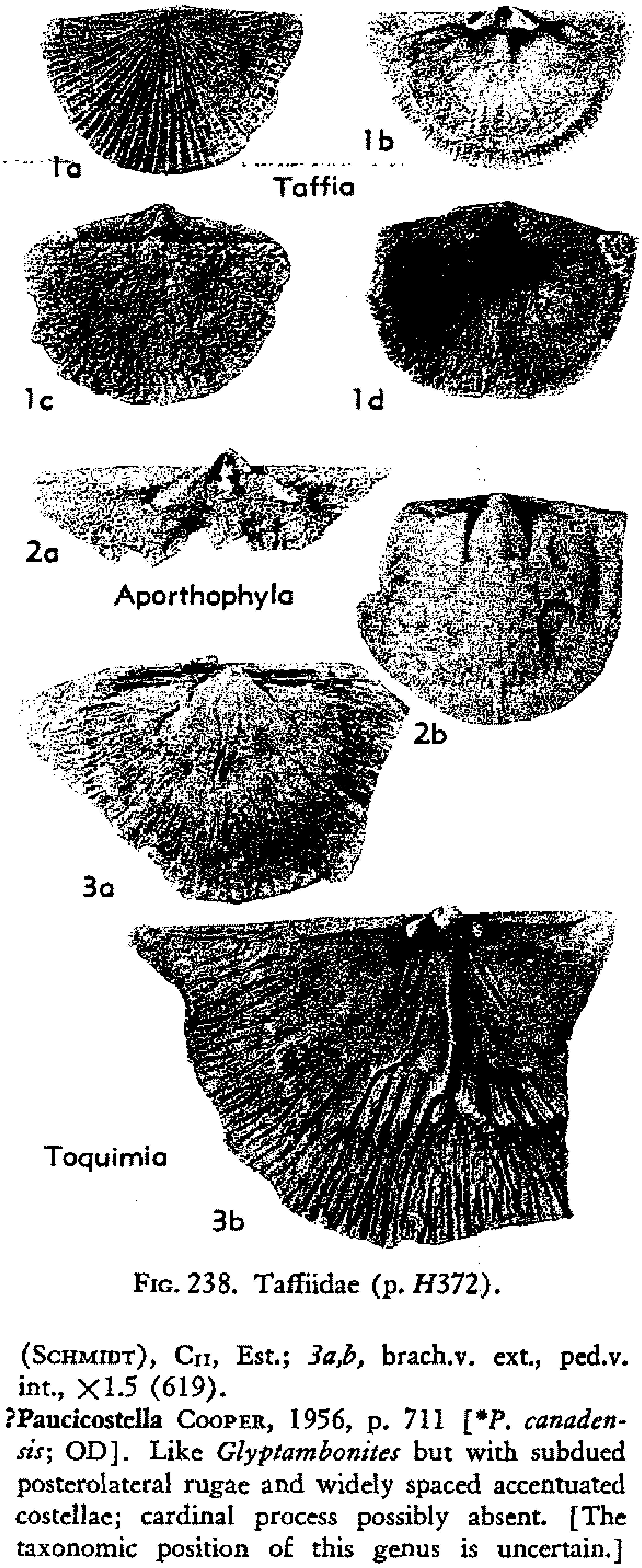


Fig. 238. Taffiidae (p. *H372*).

?Paucicostella Cooper, 1956, p. 711 [**P. canadensis*; OD]. Like *Glyptambonites* but with subdued posterolateral rugae and widely spaced accentuated costellae; cardinal process possibly absent. [The taxonomic position of this genus is uncertain.] *L.Ord.*, N.Am.(E.Can.).——Fig. 239,*4*. **P. canadensis*, Whiterock, Que.; *4*, ped.v. ext., ×2 (189).

Sowerbyites Teichert, 1937, p. 66 [**S. medioseptata*; OD]. Posterolateral rugae sporadically developed, accentuated costellae narrowly spaced, thickened concentric lamellae common distally. Ventral adductor scar small and within delthyrial cavity, diductor scars long, broad, divergent and ending in callosities; dorsal interior with strong median septum, submedian septa slightly divergent, weaker. *M.Ord.*, *?U.Ord.*, N.Am.-Greenl.-?Eu.——Fig. 239,*5*. *S. triseptatus* (Willard), M.Ord.,

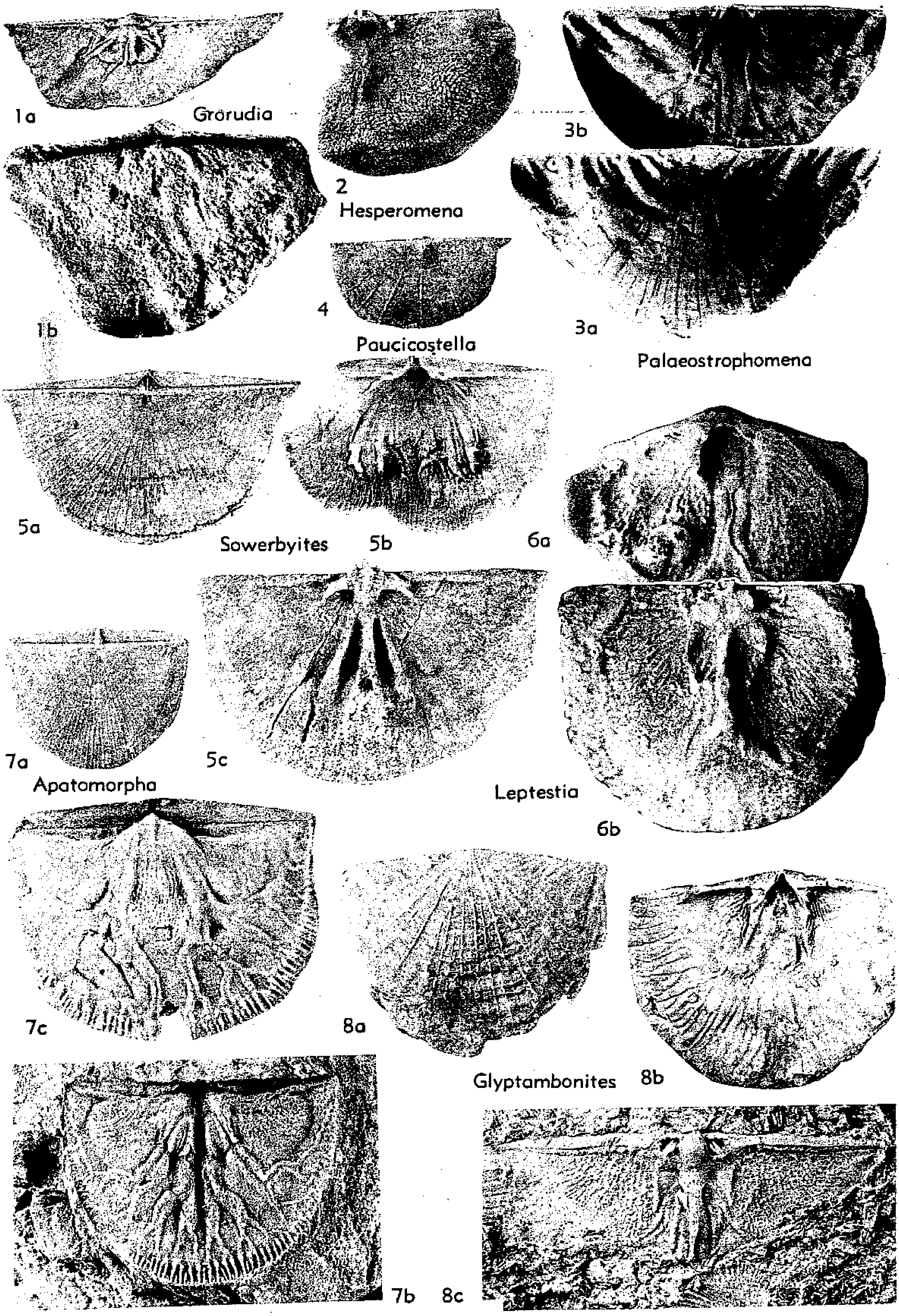


Fig. 239. Leptestiidae (Leptestiinae) (p. *H372-H373*).

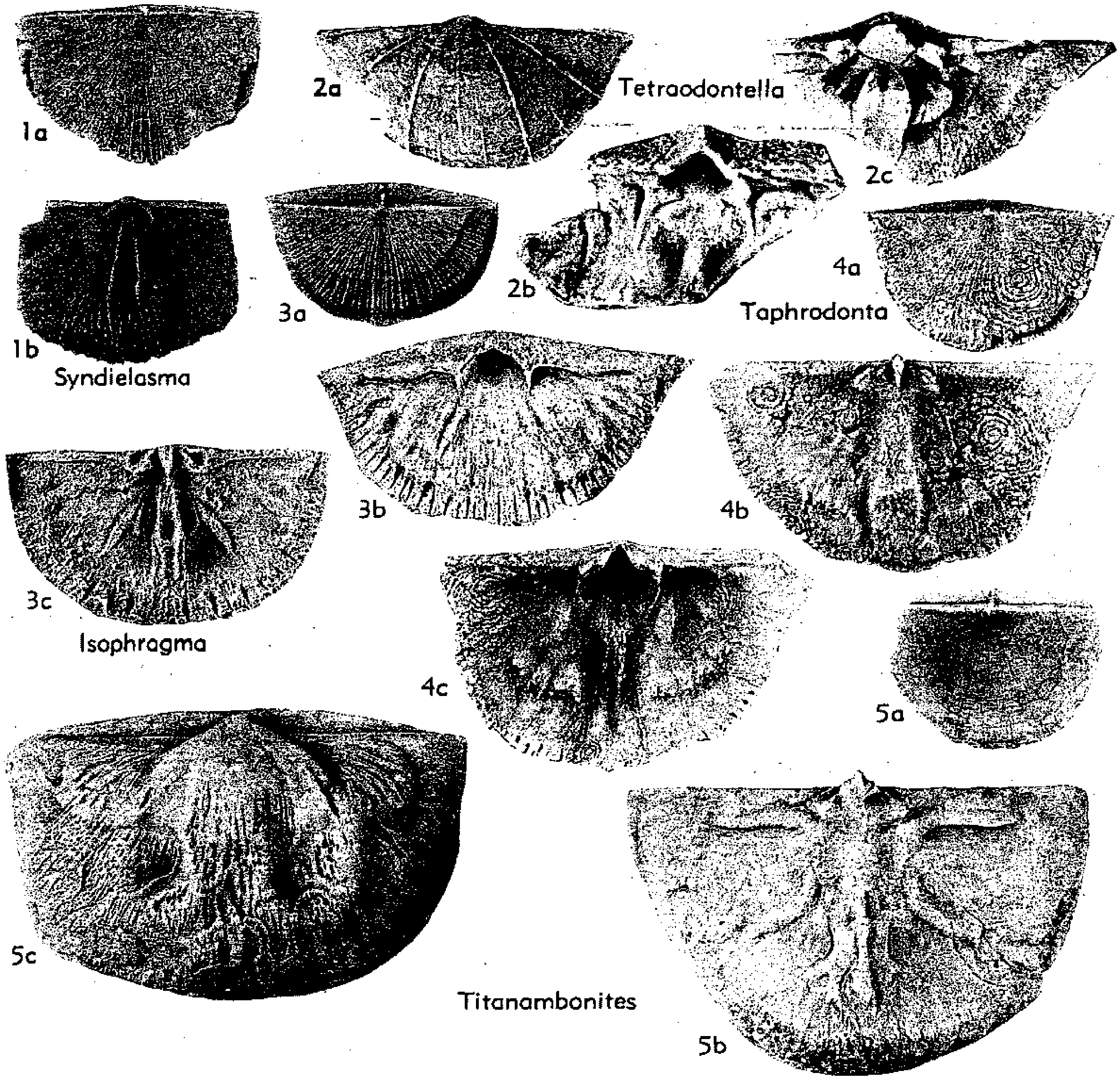


FIG. 240. Leptestiidae (Leptestiinae) *(5)*, (Isophragmatinae) *(1-3)*, (Taphrodontinae) *(4)* (p. *H375-H376*).

USA(Tenn.); *5a*, brach.v. view of conjoined valves, ×2; *5b*, ped.v. int., ×2; *5c*, brach.v. int., ×3 (189).

Spanodonta PRENDERGAST, 1935, p. 13 [**S. hoskingiae*; OD]. Like *Leptestia* but socket ridges united with trilobed cardinal process so as to project ventral of notothyrial platform. *M.Ord.*, W.Australia.

Titanambonites COOPER, 1956, p. 717 [**T. medius*; OD]. Like *Sowerbyites* but with finer parvicostellae crossed by regular concentric lamellae. Cardinal process bulbous; dorsal median ridge becoming strong anteriorly, dorsal submedian septa absent; strong ridges of secondary shell, parallel with and anterior to hinge line, conspicuous in both valves. *M.Ord.*, E.USA-Scot.——FIG. 240,*5*. **T. medius*, Porterfield, Tenn.; *5a*, brach.v. view of conjoined valves, ×1; *5b*, brach.v. int., ×1.5; *5c*, ped.v. int. mold, ×1.5 (189).

Subfamily ISOPHRAGMATINAE Cooper, 1956

[*nom. correct.* WILLIAMS, herein (*pro* Isophragminae COOPER, 1956, p. 733)] [=Syndielasmatidae COOPER, 1956, p. 742]

Costellate to unequally parvicostellate, with bulbous cardinal process generally not well differentiated into trilobed posterior face and pair of high, subparallel septa in brachial valve. *L.Ord.-M.Ord.*

Isophragma COOPER, 1956, p. 733 [**I. ricevillense*; OD]. Resupinate, with shallow dorsal sulcus replaced by fold in adult shells, costellate and commonly with widely spaced accentuated costellae. Dental plates short; ventral muscle scar subquadrate, with wide adductor trace; ventral subperipheral rim divided into several discrete callosities; suboval adductor field raised, divided by high submedian septa. *M.Ord.*, E.USA-Br.I.——FIG. 240,*3*. **I. ricevillense*, Porterfield, Tenn.; *3a*, brach.v.

view of conjoined valves, ×2; *3b,c*, ped.v. int., brach.v. int., ×3 (189).

Syndielasma Cooper, 1956, p. 742 [**S. biseptatum*; OD]. Concavo-convex unequally parvicostellate with narrowly spaced accentuated costellae, impersistent posterolateral rugae. Dental plates absent; ventral muscle scar indistinct; cardinal process bulbous, with trilobed posterior face; submedian septa long, slender. *L.Ord.(Whiterock)*, USA (Nev.).——Fig. 240,*1*. **S. biseptatum*; *1a*, brach. v. view of conjoined valves, ×2; *1b*, brach.v. int., ×3 (189).

Tetraodontella Jaanusson, 1962, p. 1 [**T. biseptata*; OD]. Like *Isophragma* but concavo-convex, with fine parvicostellae and widely spaced accentuated costellae, definite trilobed cardinal process, and smaller bilobed ventral muscle scar. *M.Ord.*(C_{II}), Baltic.——Fig. 240,*2*. **T. biseptata*, Viruan, Sweden; *2a*, ped.v. ext., ×4; *2b*, post. portion of ped.v. int., ×5; *2c*, post. portion of brach.v. int., ×4 (Williams, n).

Subfamily TAPHRODONTINAE Cooper, 1956

[*nom. transl.* Williams, herein (*ex* Taphrodontidae Cooper, 1956, p. 740)]

Unequally parvicostellate, with bladelike cardinal process and wide median ridge in brachial valve built up from 2 submedian septa. *L.Ord.*

Taphrodonta Cooper, 1956, p. 740 [**T. parallela*; OD]. Concavo-convex, ventral muscle scar cordate, diductor scars wide but not completely enclosing small adductors; subperipheral thickened ridge, interrupted by median sulcus, well developed in pedicle valve, with corresponding ridge in brachial valve. *L.Ord.(Whiterock)*, USA(Nev.).——Fig. 240,*4*. **T. parallela; 4a*, brach.v. view of conjoined valves, ×2; *4b*, brach.v. int., ×2; *4c*, ped.v. int., ×3 (189).

Family LEPTELLINIDAE Ulrich & Cooper, 1936

[*nom. transl.* Williams, herein (*ex* Leptellininae Ulrich & Cooper, 1936, p. 626)]

Concavo-convex, with simple teeth supplemented by variably developed accessory teeth and undercut platform, which probably gave support to lophophore in brachial valve; socket ridges commonly short, divergent and commonly sharp-edged distally. *L.Ord.-U.Sil.*

Subfamily LEPTELLININAE Ulrich & Cooper, 1936

[Leptellininae Ulrich & Cooper, 1936, p. 626]

Strong cardinal process differentiated into sharp median crest and lower lateral ridges on posterior face; lophophore platform wide, extending to posterolateral margins, with high median crest; ventral mantle canal pattern saccate to lemniscate, dorsal mantle canal pattern, digitate or lemniscate. *L.Ord.-L.Sil.*

Leptellina Ulrich & Cooper, 1936, p. 626 [**L. tennesseensis*; OD]. Unequally parvicostellate, with variably spaced accentuated costellae; commonly impersistently rugate posterolaterally, comae well developed distally in some species; apical foramen sealed in adult shells, pseudodeltidium large. Ventral muscle scar short, transversely bilobed, commonly with raised callosity between anterior lobes of diductor scars which do not enclose wide median adductor scar; cardinal process broad, set low relative to hinge line. *L.Ord.(Whiterock)-M.Ord. (Wilderness)*, N.Am.-Eu.(Scot.).——Fig. 241,*1*. **L. tennesseensis*, M.Ord.(Porterfield), USA (Tenn.); *1a*, brach.v. view of conjoined valves, ×2; *1b,c*, normal, post. views of brach.v. int., ×3; *1d*, ped.v. int., ×3 (189).

Anoptambonites Williams, 1962, p. 170 [**Leptaena grayae* Davidson, 1883, p. 171; OD]. Finely multicostellate, with accentuated costae, pseudodeltidium unknown. Ventral muscle scar small, cordate about low median ridge which is continuous apically with small "pedicle" chamber; cardinal process massive, differentiated posteriorly into median ridge and up to 6 lower lateral ridges, fused laterally with pair of curved plates to form semicircular structure projecting ventrally between socket ridges. *M.Ord.*, Scot.-W.USSR.——Fig. 241, *6*. **A. grayae* (Davidson), Caradoc., Scot.; *6a*, brach.v. view of conjoined valves, ×2.5; *6b,c*, ped.v. and brach.v. int., ×2.5 (877).

Leptelloidea Jones, 1928, p. 388 [**Plectambonites schmidti* Tornquist var. *leptelloides* Bekker, 1921, p. 68; OD]. Like *Leptellina* but with widely spaced accentuated costellae, high trilobed cardinal process with median depression on its ventral face, and long bilobed ventral muscle scar consisting of subcircular adductor scar enclosed by diductor lobes. *M.Ord.*, Baltic.——Fig. 241,*5*. **L. leptelloides* (Bekker), C_{Ic-II}, Est.; *5a*, brach.v. int., ×2; *5b,c*, ped.v. int., ext., ×2 (Williams, n).

Merciella Lamont & Gilbert, 1945, p. 655 [**Leptella (Merciella) vesper*; OD] [=*Leptestiina (Benignites)* Havlíček, 1952, p. 409 (type, **Strophomena primula* Barrande, 1879, p. 101)]. Like *Leptellina* but with widely spaced accentuated costellae and small ventral adductor scar enclosed by diductors, giving subcordate outline to small ventral muscle field. *U.Ord.(Ashgill.)-L.Sil. (Llandover.)*, Eu.——Fig. 241,*4*. **L. vesper*, Llandov.(C_6), Eng.; *4a,b*, brach.v. and ped.v. int. molds, ×2 (Williams, n).

Subfamily LEPTELLINAE Williams, n. subfam.

Smooth(?) or delicately unequally parvicostellate, with transversely subtriangular ventral muscle scar including wide adductor scar not enclosed by diductor lobes; socket

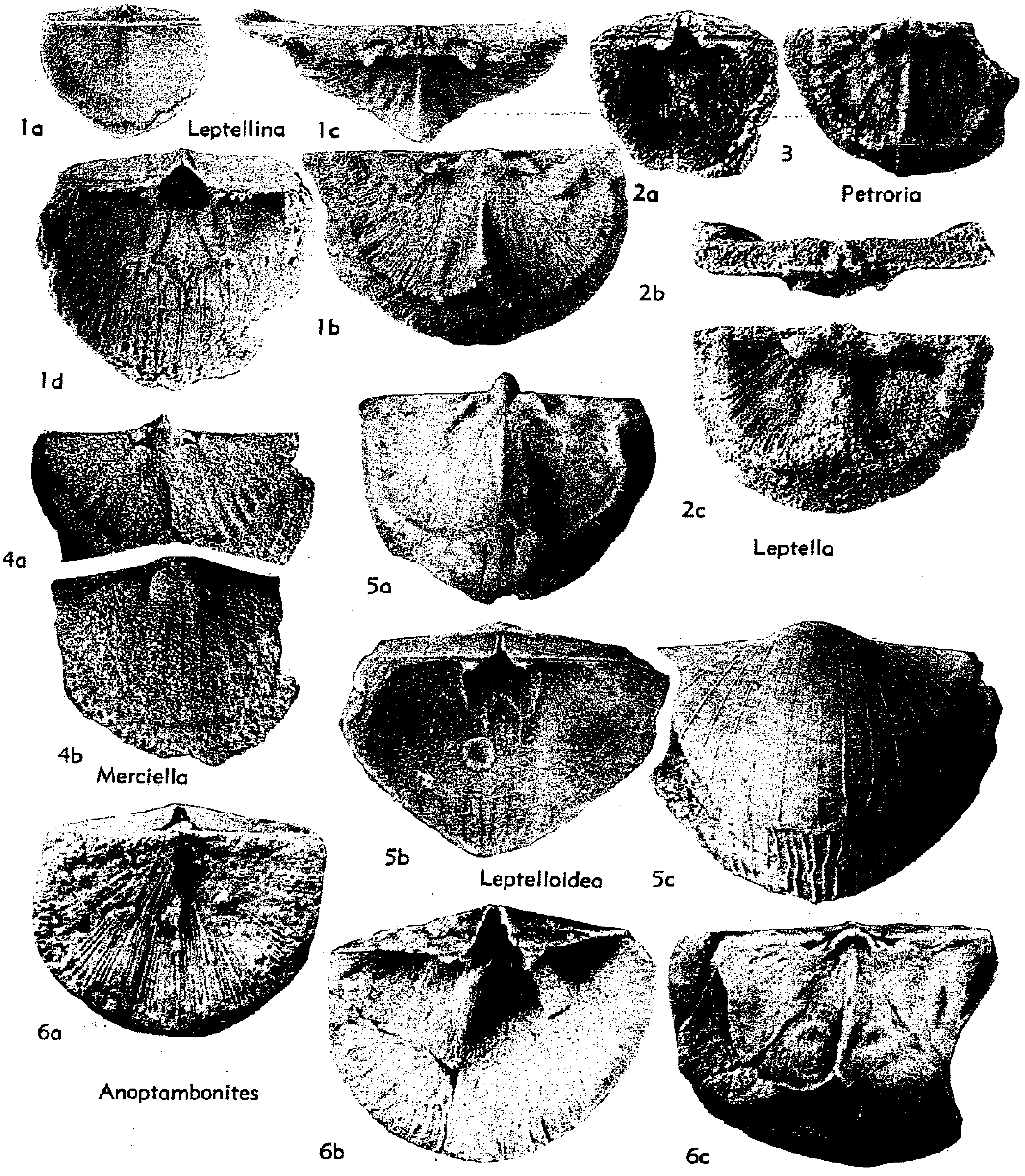


Fig. 241. Leptellinidae (Leptellininae) *(1,4,5,6)*, (Leptellinae) *(2-3)* (p. *H376-H377*).

ridges short, curved, continuous with pair of chilidial plates which are covered posteriorly by chilidium, socket ridges bounding median hollow underlain by thickened notothyrial platform; lophophore platform wide, extending to posterolateral margins, not greatly elevated medianly; ventral mantle canal pattern saccate. *L.Ord.*

Leptella Hall & Clarke, 1892, p. 293 [*non* Carus, 1880, p. 625 (incorrect subs. spelling *pro Lepetella* Verrill, 1880)] [**Leptaena sordida* Billings, 1862, p. 74; OD] [*non Leptella* Reuter, 1893]. Dorsal median ridge wide, ending anteriorly as median indentation of lophophore platform; dental plates short, ventral muscle scar limited anteriorly by broad median callosity. *L.Ord.(Whiterock)*, N. Am.——Fig. 241,*2*. **L. sordida* (Billings), Can. (Que.); *2a*, ped.v. int., ×3; *2b,c*, post., int. views of brach.v., ×6 (825).

Petroria Wilson, 1926, p. 27 [**P. rugosa*; OD]. Like *Leptella* but lacking ventral median callosity; dorsal median septum sharp, extending anteriorly of lophophore platform and dividing raised oval adductor area. *L.Ord.*, W.Can.-Eire.——Fig. 241,*3*. **P. rugosa*; brach.v. int., ×3 (189).

Subfamily LEPTESTIININAE Havlíček, 1961

[*nom. transl.* Williams, herein (*ex* Leptestiinidae Havlíček, 1961, p. 447)]

Strong cardinal process differentiated posteriorly into median crest and up to 3 pairs of lower lateral ridges; ventral muscle scar small, with median adductor scar enclosed by diductor lobes; lophophore platform small, originating just in front of socket ridges and strongly bilobed anteriorly; mantle canal patterns saccate to lemniscate. *M. Ord.-U.Sil.*

Leptestiina Havlíček, 1952, p. 409 [**L. prantli*; OD] [=*Dulankarella* Rukavishnikova, 1956, p. 135 (type, **D. magna*)]. Unequally parvicostellate, with variably spaced accentuated costellae. Ventral muscle scar transversely bilobed; cardinal process squat, trilobed posteriorly, lophophore platform transversely to elongately bilobed, culminating medianly in wide ridge. *M.Ord.-U.Ord.*, Eu.——Fig. 242,*4a,b*. **L. prantli*, U.Ord.(Ashgill.), Czech.; *4a,b*, ped.v. and brach.v. int., ×2 (Havlíček, n).——Fig. 242,*4c,d*. *L. oepiki* (Whittington), M.Ord.(Caradoc.), Wales; *4c,d*, ped.v. and brach.v. int., ×4.5 (Williams, n).

Bilobia Cooper, 1956, p. 759 [**B. hemisphaerica*; OD]. Unequally parvicostellate, with widely spaced accentuated costellae; ventral muscle scar strongly bilobed, with divergent diductors; median ridge sporadically developed anterior to ventral scar, generally as coalescent tubercles; cardinal process high, trilobed, but with cleft median crest; lophophore platform of 2 elongate pointed or rounded lobes separated by discrete median septum. *M.Ord.-U.Ord.*, Eu.-N.Am.——Fig. 242,*1*. **B. hemisphaerica*, M.Ord.(Wilderness), E.USA (Va., *1a,b*-Pa., *1c*); *1a*, brach.v. view of conjoined valves, ×2; *1b,c*, ped.v. and brach.v. int. molds, ×3 (189).

Diambonia Cooper & Kindle, 1936, p. 356 [**Plectambonites gibbosa* Winchell & Schuchert, 1895, p. 416; OD]. Like *Leangella* but with strong median septum anterior to muscle scar on pedicle valve. *M.Ord.-U.Ord.*, N.Am.-Eu.

Leangella Öpik, 1933, p. 42 [**Plectambonites scissa* Salter var. *triangularis* Holtedahl, 1916, p. 84; OD]. Unequally parvicostellate, with widely spaced accentuated costellae. Ventral muscle scar transversely bilobed; cardinal process high, commonly with 2 pairs of ridges flanking median crest on its posterior face; lophophore platform small, bilobed, culminating medianly in wide ridge; rounded or medianly pointed, sharp, subperipheral rim defining brachial cavity in brachial valve. *M.Ord.-U.Sil.*, Eu.-N.Am.——Fig. 242,*2a-c*. **L. scissa* (Salter), L.Llandover., Wales; *2a,b*, ped.v. int. mold and cast, ×5; *2c*, brach.v. int. cast, ×5 (Williams, n).——Fig. 242,*2d*. *L. segmentum* (Lindström), U.Sil.(Wenlock), Eng.; *2d*, brach.v. view of conjoined valves, ×5 (Williams, n).

Sampo Öpik, 1933, p. 35 [**S. hiiuensis*; OD]. Unequally parvicostellate, with widely spaced accentuated costellae; hinge line denticulate. Ventral muscle scar bilobed; cardinal process high, trilobed posteriorly with indentation along ventral face of median crest; lophophore platform elongately bilobed, commonly with 2 boundaries anteriorly and culminating in median ridge. *U.Ord.*, Eu.——Fig. 242,*5*. **S. hiiuensis*, F1a, Est.; *5a*, brach.v. view of conjoined valves, ×3; *5b,c*, ped. v. and brach.v. int., ×5 (619).

Tufoleptina Havlíček, 1961, p. 447 [**T. tufogena*; OD]. Like *Leangella* but with subperipheral rim in pedicle valve as well as brachial valve. *U.Sil. (Wenlock)*, Czech.——Fig. 242,*3*. **T. tufogena*; *3a*, brach.v. int., ×4; *3b*, ped.v. int. mold, ×4 (Havlíček, n).

Family SOWERBYELLIDAE Öpik, 1930

[*nom. transl.* Cooper, 1956, p. 774 (*ex* Sowerbyellinae Öpik, 1930, p. 144)]

Semicircular to semioval, unequally parvicostellate, with small pseudodeltidium, apical foramen rarely if ever persistent in adult shells. Simple teeth rarely supported by dental plates and rarely supplemented by denticles; variably bilobed ventral muscle scar with deeply inserted lanceolate adductor scars; chilidial plates fused with small flat-lying socket ridges and median ridge-like cardinal process to form inverted V which overhangs subcircular deep depression in place of notothyrial platform; dorsal septa and lophophore platform variably developed; ventral and dorsal mantle canal patterns digitate to lemniscate. *Ord.-M.Dev.*

Subfamily SOWERBYELLINAE Öpik, 1930

[Sowerbyellinae Öpik, 1930, p. 144]

Concavo-convex, with impersistent rugae commonly developed posterolaterally at acute angles to hinge line and with variable number of septa in brachial valve surrounding or associated with suboval raised areas which probably gave support to anterior portion of lophophore, as well as dorsal adductor bases. *Ord.-M.Dev.*

Sowerbyella Jones, 1928, p. 384 [**Leptaena sericea* Sowerby, 1839, p. 636; OD]. Parvicostellae either smooth or slightly beaded and variably segregated; ventral muscle scar small and bilobed, bounded

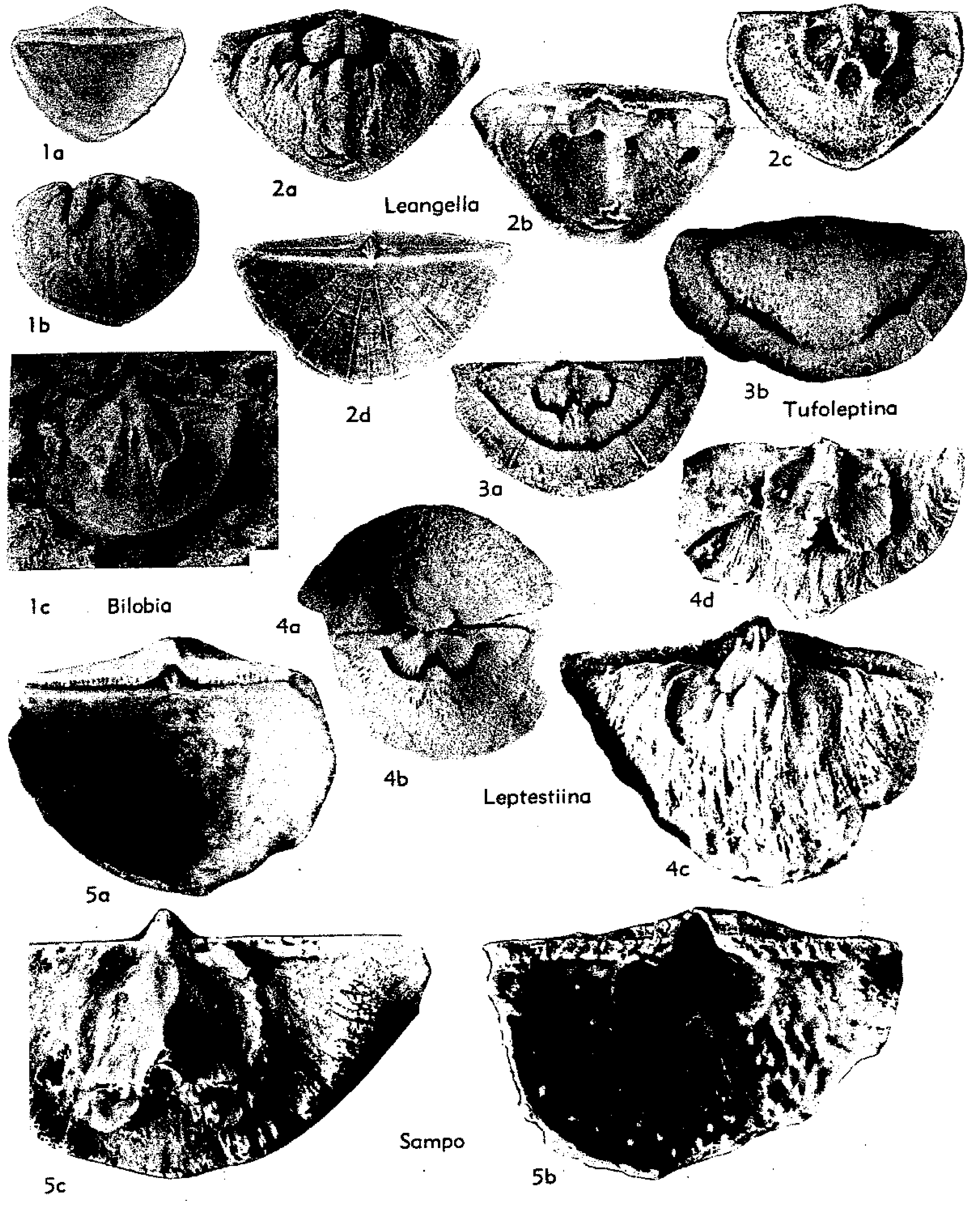


FIG. 242. Leptellinidae (Leptestiininae) (p. *H*377-*H*378).

posterolaterally by short dental plates and anteromedianly by pair of divergent ridges bifurcating from short median ridge bearing adductor scars; brachial valve with pair of strong submedian septa flanked by raised suboval areas, median ridge variably developed. *Ord.-L.Sil.*, cosmop.

S. (**Sowerbyella**). Parvicostellae segregated into narrow segments by many accentuated costellae; median ridge in brachial valve weak or absent. *Ord.-L.Sil.*, cosmop.——FIG. 243,*1*. **S.* (*S.*) *sericea* (SOWERBY), M.Ord.(Caradoc), Eng.; *1a,b*, brach.v. ints., ×3.5, ×2; *1c,d*, brach.v. int. and ext., ×3; *1e*, ped.v. int. mold, ×3; *1f*, brach.v. ext., ×2.5 (Williams, n).

S. (**Viruella**) RÕÕMUSOKS, 1959, p. 43 [**Sowerbyella liliifera* ÖPIK, 1930, p. 148; OD]. Like *S.* (*Sowerbyella*) but with small number of accentuated costellae dividing radial ornamentation

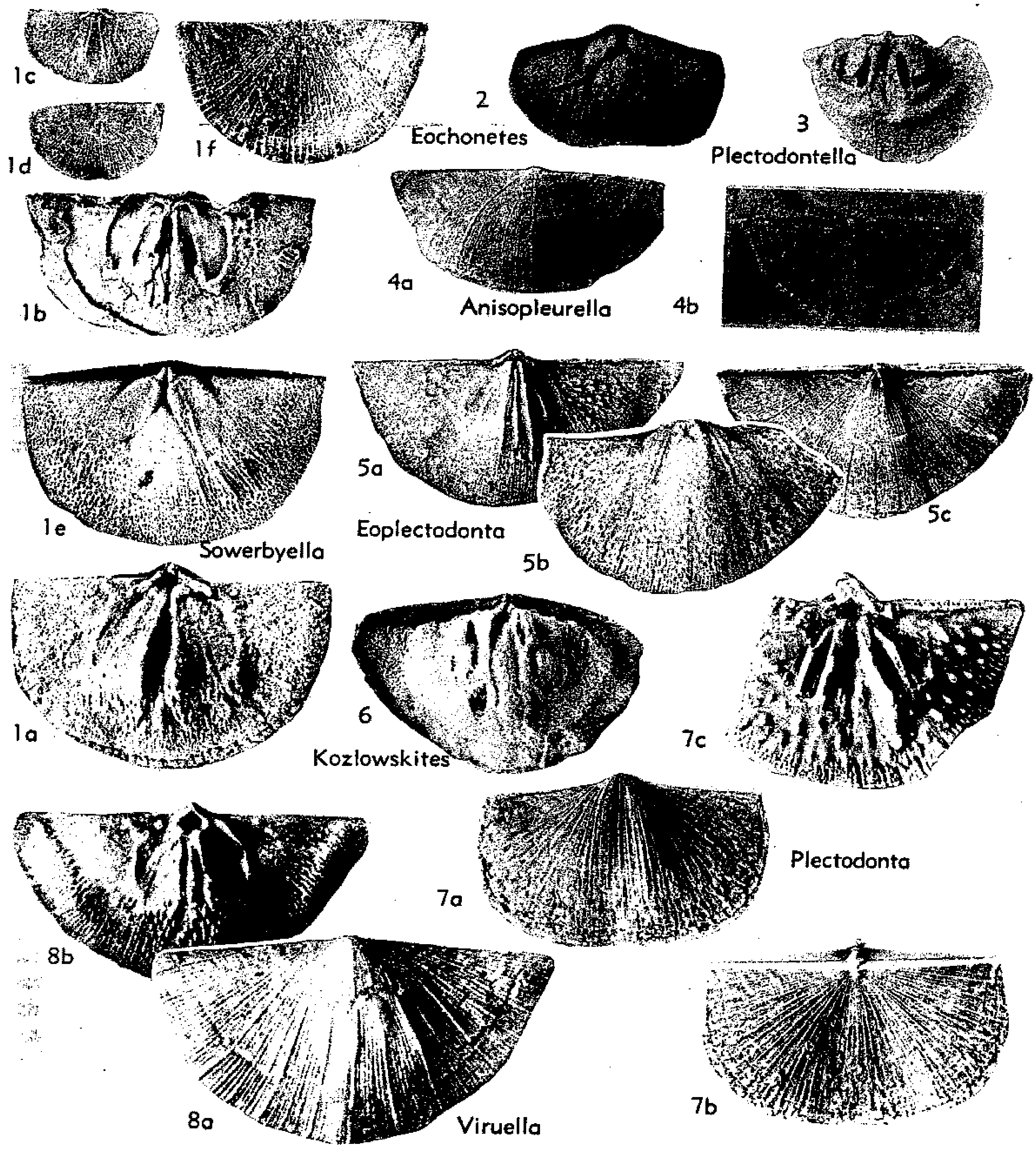


FIG. 243. Sowerbyellidae (Sowerbyellinae) (p. *H*378-*H*381).

into wide segments and strong median ridge in brachial valve standing high above flanking submedian septa. *L.Ord.(Llandeil.,* C_{1a}*)-M.Ord. (Caradoc.,* C_{III}), Eu.——FIG. 243,*8*. **S. (V.) liliifera* (ÖPIK), M.Ord.(Kukruse $\mathrm{C}_{II\alpha}$), Est.; *8a*, ped.v. ext., ×3.5; *8b*, brach.v. int., ×3 (676).

Anisopleurella COOPER, 1956, p. 804 [**A. inaequistriata*; OD]. Finely and unequally parvicostellate, with 3 accentuated costellae arising near umbo and disposed medianly and laterally, supplemented by few shorter ones. Ventral muscle scar bilobed, with divergent diductors and adductors borne on low median ridge; in brachial valve, submedian septa, narrowly divergent about low median ridge and continuous with outer pair of sublateral ridges to define 2 suboval areas each divided by divergent septum. *M.Ord.(Caradoc.)-U.Ord.(Ashgill.)*, Eu.-Am.——FIG. 243,*4*. **A. inquequistriata*, M.Ord. (Porterfield), USA(Tenn.); *4a*, ped.v. ext., ×4; *4b*, brach.v. int. mold, ×4 (189).

Eochonetes REED, 1917, p. 916 [**E. advena*; OD]. Like *Sowerbyella (Sowerbyella)* but with interarea of pedicle valve pierced by about 6 oblique narrow canals. *U.Ord.(Ashgill.)*, Scot.——FIG. 243,*2*. **E. advena*; ped.v. int. mold, ×1 (Williams, n).

Eoplectodonta KOZLOWSKI, 1929, p. 113 [**Sower-*

byella praecursor Jones, 1928, p. 437; OD] [=*Thaerodonta* Wang, 1949, p. 19 (type, *T. aspera*)]. Like *Sowerbyella (Viruella)* but with variably denticulate hinge line and with oval areas flanking dorsal submedian septa, well defined by raised lateral boundaries and containing pair of divergent ridges. *M. Ord. (Caradoc) - L. Sil. (Llandover.)*, cosmop.

E. (Eoplectodonta). Ventral muscle field divided by narrow median ridge that bifurcates to form anteromedian boundaries of divergent diductor scars. *M.Ord.-L.Sil.*, cosmop.——Fig. 243,*5*. **E. (E.) praecursor* (Jones), L.Llandov., Wales; *5a,b*, brach.v. and ped.v. int. molds, ×3; *5c*, brach.v. ext., ×3 (Williams, n).

E. (Kozlowskites) Havlíček, 1952, p. 406 [**Strophomena nuncia* Barrande, 1879, pl. 49, fig. III; OD]. Ventral adductor scars inserted on high short platform not dividing anteriorly, diductor scars subparallel. *U.Ord.(Ashgill.)*, Eu. (Czech.).——Fig. 243,*6*. **E. (K.) nuncia* (Barrande), ped.v. int. mold, ×3.5 (Williams, n).

Plectodonta Kozlowski, 1929, p. 112 [**P. mariae*; OD] [=*Dalejodiscus* Havlíček, 1961, p. 449 (type, *Strophomena comitans* Barrande, 1879, p. 101)]. Like *Eoplectodonta (Eoplectodonta)* but without dorsal median septum and with hinge line more or less entirely denticulate. *U.Sil.-M.Dev.*, cosmop.——Fig. 243,*7*. **P. mariae*, U.Sil.(Ludlov.), Pol.; *7a,b*, ped.v. and brach.v. views of conjoined valves, ×4; *7c*, brach.v. int., ×6 (Williams, n).

Plectodontella Havlíček, 1953, p. 9 [**P. redunca*; OD] [=*Ygera* Havlíček, 1961, p. 449 (type, *Y. ygerens*)]. Like *Plectodonta* but with elevated suboval areas in brachial valve contained by high boundaries formed by fusion of submedian septa with strong curved lateral ridges. *U.Sil.-M.Dev.*, cosmop.——Fig. 243,*3*. **P. redunca*, M.Dev. (Eifel.), Czech.; brach.v. int., ×3 (Havlíček, n).

Subfamily PTYCHOGLYPTINAE Cooper, 1956

[Ptychoglyptinae Cooper, 1956, p. 815]

Concavo-convex, unequally parvicostellate, with strongly accentuated costellae breaking concentrically disposed, narrow rugae into segments which may be chevron-shaped, or even strips oblique to costellae. Dental plates short, receding, ventral muscle scar small, slightly bilobed and without median ridge; median and submedian septa in brachial valve poorly developed. *Ord.*

Ptychoglyptus Willard, 1928, p. 283 [**P. virginiensis*; OD]. Commonly alate and thin-shelled, rarely geniculate. *Ord.(Whiterock-Porterfield)*, N.Am.-Eu.——Fig. 244,*6*. **P. virginiensis* M.Ord.(Porterfield), USA(Va.); *6a-c*, ped.v., brach.v., post. views of conjoined valves, ×2; *6d,e*, ped.v. int. and ext., ×3; *6f*, brach.v. int., ×4 (189).

Subfamily XENAMBONITINAE Cooper, 1956

[Xenambonitinae Cooper, 1956, p. 813]

Concavo-convex, finely costellate, brachial valve sulcate and geniculate anteriorly toward pedicle valve; dental plates vestigial, ventral muscle scar transversely bilobed; lophophore platform short, narrow, undercut and pointed anteromedianly. *M.Ord.-U. Ord.*

Xenambonites Cooper, 1956, p. 813 [**X. undosus*; OD]. Alate, accentuated costellae rarely developed and mainly as boundaries to ventral fold and in dorsal sulcus, posterolateral rugae parallel with hinge line. *M.Ord.(Porterfield)-U.Ord.(Trenton.)*, E.USA-Scot.——Fig. 244,*1*. **X. undosus*, M.Ord. (Porterfield), USA(Ala.); *1a*, ped.v. ext., ×4; *1b*, ant. view of conjoined valves, ×5; *1c*, brach.v. int., ×6; *1d*, ped.v. int., ×4 (189).

Subfamily AEGIROMENINAE Havlíček, 1961

[Aegiromeninae Havlíček, 1961, p. 450]

Plano- to concavo-convex, with short, narrow tract in brachial valve which probably gave support to lophophore as well as dorsal adductor bases, defined either by septules arranged in arc(s) or as elevated undercut platform; dorsal median septum always present. *M.Ord.-L.Sil.*

Aegiromena Havlíček, 1961, p. 450 [**Leptaena aquila* Barrande, 1848, p. 76; OD]. Concavo-convex, unequally parvicostellate but not well segregated into distinct segments. Dental plates short, receding, ventral muscle scar bilobed, with divergent diductor scars extending anterolaterally into raised, pustulose areas, contained posteromedianly by pair of ridges bifurcating from median ridge supporting adductor scars; lophophore platform in brachial valve bilobed but weakly defined by incomplete fusion of septule arcs. *M.Ord.-U.Ord.(Ashgill.)*, Czech. —— Fig. 244,*7*. **A. aquila* (Barrande), M.Ord.(Llandeil.-Caradoc.), Czech.; *7a,b*, ped.v. and brach.v. int. molds, ×2; *7c*, brach.v. view of conjoined valves, ×2 (Havlíček, n).

Aegiria Öpik, 1933, p. 55 [**A. norvegica*; OD]. Concavo-convex, finely costellate, and generally sulcate; dental plates short, receding, ventral muscle scar small, bilobed with adductor scars impressed on median ridge that bifurcate anteriorly to define anteromedian boundaries of divergent diductor scars, suboval lophophore platform well developed, undercut, median septum high. *L.Sil.*, Eu.——Fig. 244,*4*. **A. norvegica*, M.Llandover., Norway; *4a,b*, ped.v. and brach.v. int. molds, ×4 (Williams, n).

Alwynella Spjeldnaes, 1957, p. 85 [**A. osloensis*; OD]. Like *Aegiria* but with fine parvicostellae segregated into narrow segments by accentuated costellae, denticulate hinge line and without me-

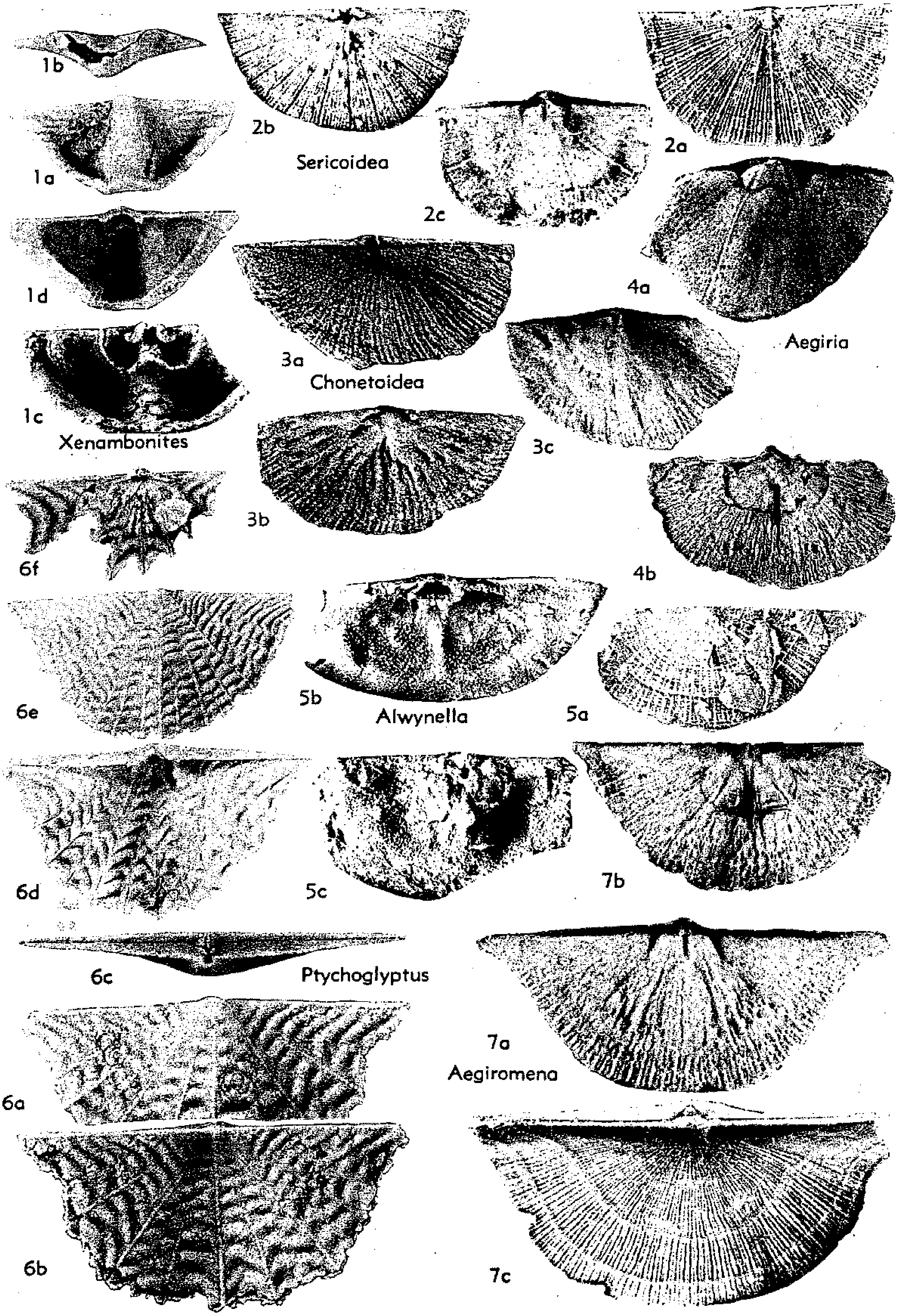


FIG. 244. Sowerbyellidae (Ptychoglyptinae) *(6)*, (Xenambonitinae) *(1)*, (Aegiromeninae) *(2-5, 7)* (p. *H*381, *H*383).

dian ridge dividing ventral muscle scar. _M.Ord.(4aa-β)_, Scand.——Fig. 244,_5_. *_A. osloensis, 4aβ_, Nor.; _5a,b,_ ped.v. ext. and int., ×4; _5c,_ brach.v. int., ×4.5 (Williams, n).

Chonetoidea Jones, 1928, p. 393 [*_Plectambonites papillosa_ Reed, 1905, p. 45; OD]. Like _Aegiria_ but with lophophore platform weakly defined by series of discrete or coalescing elongate tubercles usually disposed arcuately about median septum. _U.Ord.(Caradoc.)-L.Sil.(Llandover.),_ Eu.——Fig. 244,_3_. *_C. papillosa_ (Reed), Ashgill., Br.I.; _3a-c,_ brach.v. ext., brach.v. and ped.v. int. molds, ×4 (Williams, n).

Kassinella Borissiak, 1956, p. 50 [*_K. globosa_; OD]. Like _Aegiromena_ but plano-convex and with pair of posterolateral processes in each valve. _M. Ord.,_ USSR(Kazakh.).

Sericoidea Lindström, 1953, p. 473 [*_Leptaena sericea_ var. _restricta_ Hadding, 1913, p. 62; OD]. Like _Chonetoidea_ but with radial ornamentation unequally parvicostellate and segregated into well-defined segments by accentuated costellae; dorsal tubercles discrete. _M.Ord.-U.Ord.(Caradoc.),_ Eu.-N.Am.——Fig. 244,_2_. *_S. restricta_ (Hadding), M.Ord., Sweden; _2a,b,_ brach.v. ext. and int., ×7; _2c,_ ped.v. int., ×7 (Williams, n).

Family BIMURIIDAE Cooper, 1956

[Bimuriidae Cooper, 1956, p. 764]

Radial ornamentation lacking but with concentric lamellae commonly grossly thickened into comae; pedicle foramen persistent in adult shells. Teeth simple, dental plates obsolete; ventral muscle field not clearly impressed but probably large; ventral mantle canal pattern pinnate; socket ridges strong, widely divergent and continuous with high chilidial plates bounding notothyrium; cardinal process simple; chilidium apical or absent; brachial valve interior with 3 long, high median septa flanked by elongately oval callosites or subtriangular, elevated platforms, dorsal mantle canal pattern lemniscate or pinnate. _M.Ord._

Bimuria Ulrich & Cooper, 1942, p. 622 [*_B. superba_; OD]. Concavo-convex, with elongately oval callosities in brachial valve commonly contained laterally by pair of ridges which converge anteriorly toward outer median septa. _M.Ord.(Porterfield-Wilderness),_ N.Am.-Eu.——Fig. 245,_2_. *_B. superba,_ Porterfield, USA(Tenn.); _2a,_ brach.v. view of conjoined valves, ×1; _2b,_ ped.v. int., ×1.5; _2c,_ brach.v. int., ×2; _2d,_ post. view of brach.v. tilted to show cardinalia, ×3 (189).

Craspedelia Cooper, 1956, p. 772 [*_C. marginata_; OD]. Like _Bimuria_ but with anterior margin geniculate ventrally and elevated triangular platforms flanking median septa of brachial valve; median ridge or line of tubercles commonly developed in pedicle valve. _M.Ord.(Porterfield-Wilderness),_ N.Am.-Scot.——Fig. 245,_1_. *_C. marginata,_ Porterfield, USA(Ala.); _1a,_ brach.v. ext., ×5; _1b-d,_ ext., int., ant. views of ped.v., ×4; _1e,_ tilted view of brach.v. int., ×4 (189).

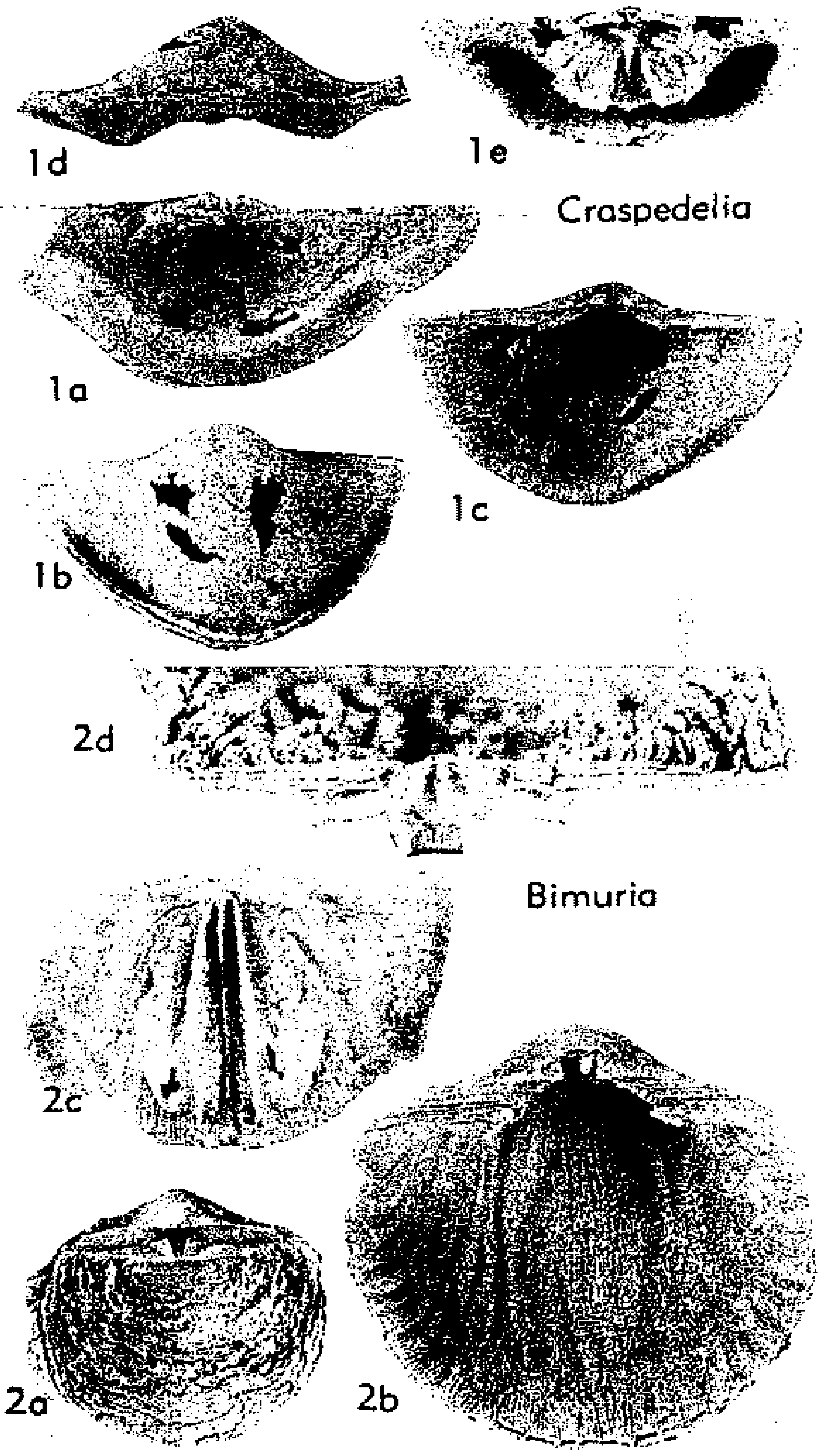


Fig. 245. Bimuriidae (p. _H_383).

Superfamily STROPHOMENACEA King, 1846

[_nom. transl._ Schuchert, 1896, p. 312 (_ex_ Strophomenidae King, 1846, p. 28)]

Concavo-convex to resupinate, with cardinalia consisting of strong to obsolescent socket ridges and bilobed cardinal process; delthyrium covered apically to completely by pseudodeltidium, chilidium well developed to absent; apical foramen sealed in some later stocks so that adult shells were unattached or exceptionally cemented by part of pedicle valve to substratum; brachial valve rarely equipped with raised supports for schizolophous or spirolophous lophophore. _Ord.-Carb._

Family STROPHOMENIDAE King, 1846

[Strophomenidae King, 1846, p. 28]

Concavo-convex to resupinate, rarely geniculate or rugate; apical foramen in adult shells small or (less commonly) closed, shells exceptionally attached by cementation; chilidium well developed, pseudodeltidium usually present but exceptionally resorbed in adult shells. Teeth simple, dental plates usually present; ventral muscle scar variable in outline; notothyrial platform anchor-shaped, dorsal adductor impressions subcircular to oval, traversed by 2 pairs of variable developed ridges (trans-muscle septa); mantle canal systems poorly preserved, but probably saccate in both valves of many genera. *M.Ord.-L.Dev.*

Subfamily STROPHOMENINAE King, 1846

[*nom. transl.* Gill, 1871, p. 26 (*ex* Strophomenidae King, 1846, p. 28)]

Resupinate, unequally parvicostellate, with small apical foramen and large pseudodeltidium. Dental plates short to obsolescent; ventral muscle scar subcircular to subquadrate, commonly with strong bounding ridges; notothyrial platform short but well developed, trans-muscle septa variably defined. Shell substance commonly finely and densely pseudopunctate. *M.Ord.-U.Sil.*

Strophomena Rafinesque in de Blainville, 1825, p. 513 [**S. rugosa* Rafinesque in de Blainville, 1825 (?conspecific with *Leptaena planumbona* Hall, 1847); SD King, 1846, p. 28] [=*Longvillia* Bancroft, 1933, p. 3 (type, *Strophomena grandis* Sowerby, 1839); *Öpikinella* Wilson, 1946, p. 199 (type, *O. affinis*); *S. (Drummuckina)* Bancroft, 1949, p. 12 (type, *S. (D.) agrestis*)]. Variably unequally parvicostellate. Teeth smooth or striated, dental plates obsolescent, ventral muscle scar subcircular to suboval, with strong lateral bounding ridges not united with strong median adductor ridge; trans-muscle septa variably developed. *M.Ord.-U.Ord.*, cosmop.——Fig. 246,*3*. *S. planumbona* (Hall), U.Ord.(Cincinnati.), USA (Ohio); *3a*, brach.v. int., ×1 (189); *3b,c*, brach.v. ext., lat. view of conjoined valves, ×1; *3d*, ped.v. int., ×2 (851).

Actinomena Öpik, 1930, p. 166 [**Strophomena (Actinomena) orta*; OD]. Gently resupinate and strongly unequally parvicostellate, with strong posterolateral rugae. Ventral muscle scar short, subquadrate, with high subparallel lateral bounding ridges and broad median adductor ridge; trans-muscle septa present. *M.Ord.*, Eu.(Est.-Eire).——Fig. 246,*5*. **A. orta* (Öpik), CII, Est.; *5a*, ped.v. int., ×1.5; *5b,c*, brach.v. ext. and int., ×1.5 (617).

Gunnarella Spjeldnaes, 1957, p. 149 [**Strophomena (Gunnarella) delta*; OD]. Like *Strophomena* but rarely geniculate and with strong concentric rugae interrupted by widely spaced accentuated costellae. *M.Ord.-U.Ord.*, N. Am.-N. Eu.——Fig. 246,*1*. *G. regulifera* (Wang), U.Ord.(Richmond.), USA(Iowa); *1a,b*, ped.v. and ant. views of complete shell, ×2 (851).

Luhaia Rõõmusoks, 1956, p. 1091 [**L. vardi*; OD]. Like *Strophomena* but strongly geniculate in ventral direction and with concentric rugae not broken by accentuated costellae; trans-muscle septa present. *U.Ord.*(FIC), W.USSR.——Fig. 246,*6*. **L. vardi*, Est.; *6a*, ped.v. view of conjoined valves, ×2; *6b*, brach.v. int. mold, ×2; *6c*, ped.v. ext., ×2 (Rõõmusoks, n).

Microtrypa Wilson, 1945, p. 144 [**M. altilis*; OD]. Like *Strophomena* but with submedian pair of trans-muscle septa well developed and lateral of forked medium extension of notothyrial platform. *M.Ord.*, N.Am.-Eu.

Pentlandina Bancroft, 1949, p. 11 [**Strophomena (Pentlandina) tartana;* OD]. Like *Luhaia* but lacking geniculation and with strong median fold in brachial valve; trans-muscle septa well developed, *L.Sil.-U.Sil.*, G.Brit.

Rhipidomena Cooper, 1956, p. 866 [**Strophomena tennesseensis* Willard, 1928, p. 285; OD]. Like *Tetraphalerella* but with large ventral muscle field occupying nearly half of internal area of pedicle valve, not enclosed by strong bounding ridges, dental plates absent, cardinalia small, trans-muscle septa subdued. *M.Ord.*, E.USA.——Fig. 246,*7*. **R. tennesseensis* (Willard), Porterfield, Va. *(7a,b)*, Tenn. *(7c)*; *7a*, ped.v. int., ×1; *7b*, brach.v. int., ×2; *7c*, lat. view of conjoined valves, ×1 (189).

Tetraphalerella Wang, 1949, p. 19 [**T. cooperi*; OD]. Like *Strophomena* but with small suboval adductor scar in ventral muscle field divided by short thin ridge and enclosed anteriorly by diductor scars; trans-muscle septa not developed; shell substance coarsely and densely pseudopunctate. *U.Ord.*, N.Am.——Fig. 246,*4*. **T. cooperi*, Richmond., USA(Iowa); *4a,b*, brach.v. int. and ext., ×1; *4c*, ped.v. int., ×1 (851).

Trigrammaria Wilson, 1945, p. 140 [**T. trigonalis*; OD]. Like *Strophomena* but with rounded dorsal median fold and with submedian pair of trans-muscle septa well developed in addition to median prolongation from notothyrial platform. *M. Ord.*, N. Am.——Fig. 246,*2*. *T. wilsoni* (Cooper), Wilderness, USA(N.Y.); *2a,b*, ped.v. and brach.v. ext., ×2 (189).

Subfamily FURCITELLINAE Williams, n. subfam.

Biconvex to concavo-convex or resupinate, costellate, with large foramen and pseudodeltidium. Ventral muscle scar small, subcircular to trapezoidal in outline, notothyrial platform and trans-muscle septa well de-

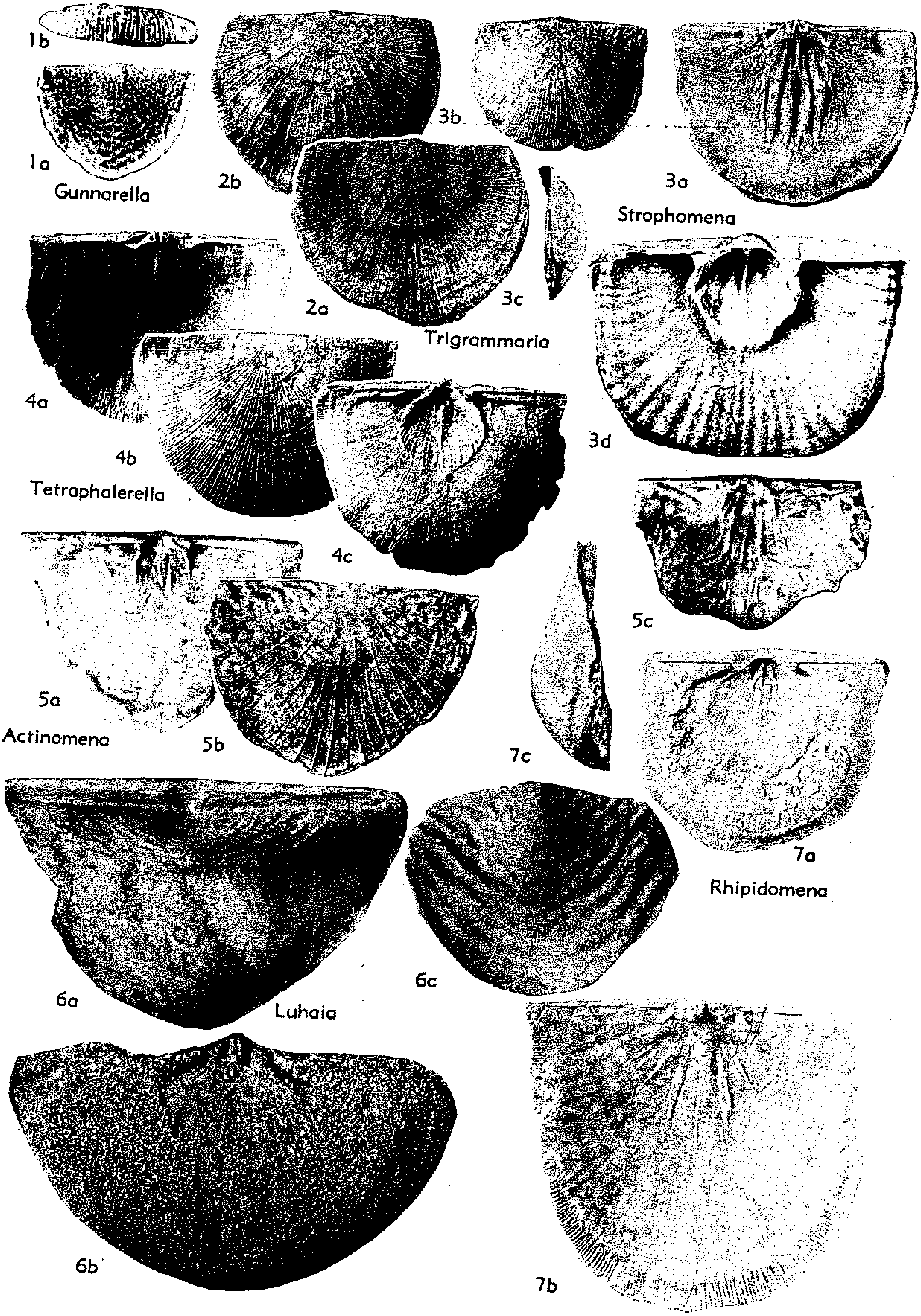


Fig. 246. Strophomenidae (Strophomeninae) (p. *H*384).

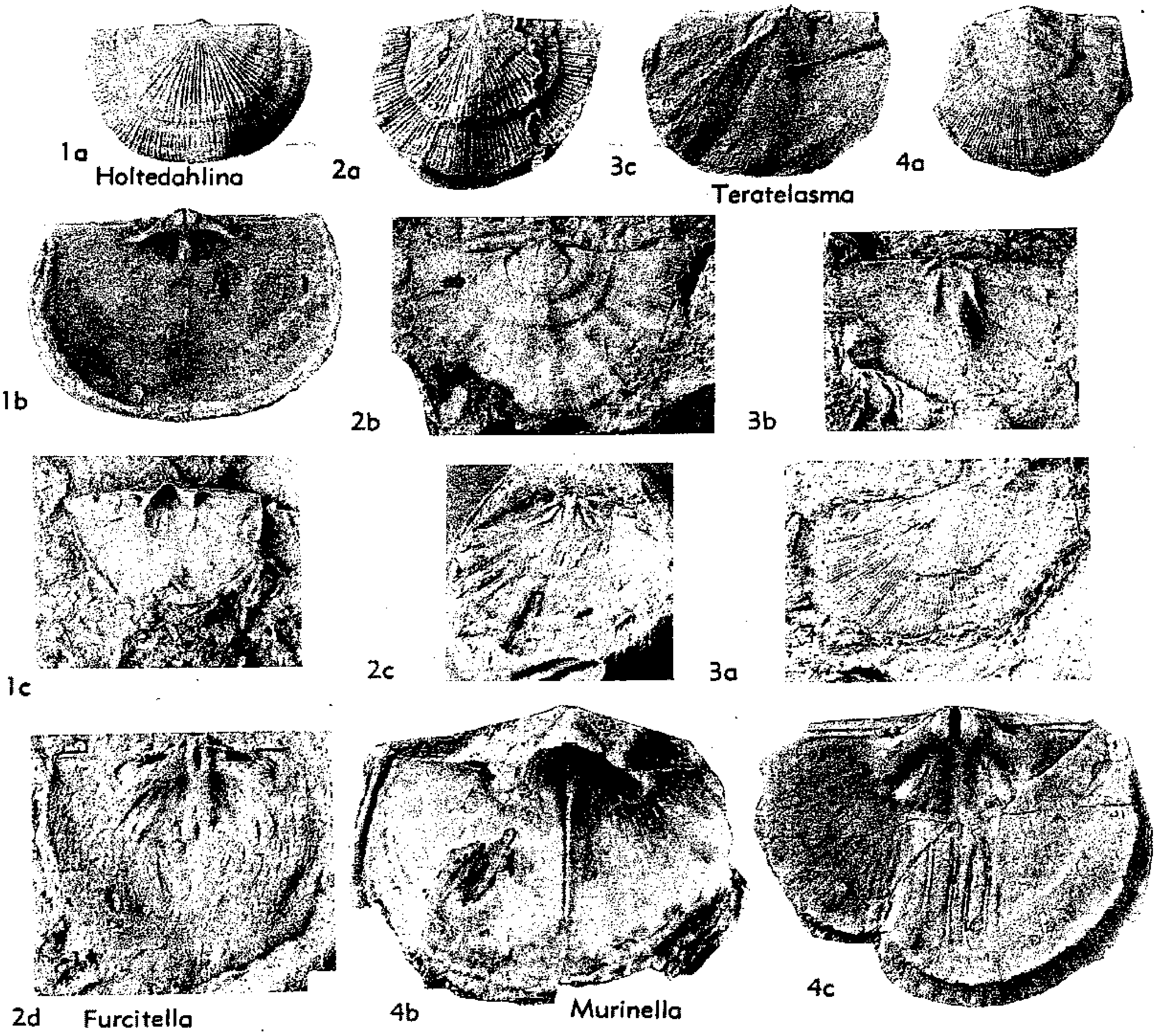


FIG. 247. Strophomenidae (Furcitellinae) (p. _H_384, _H_386).

veloped. Shell substance finely and densely pseudopunctate. _M.Ord.-L.Sil._

Furcitella COOPER, 1956, p. 875 [*_F. plicata_; OD]. Biconvex, with deeper brachial valve and pedicle valve commonly flattened to concave anteriorly; ventral muscle field trapezoidal, with strong bounding ridges; median ridge of notothyrial platform divided, trans-muscle septa normally well developed, with curved submedian septa. _M.Ord.-L.Sil._, N.Hemis.——FIG. 247,_2_. *_F. plicata_, M. Ord.(Wilderness), USA(Va.); _2a,c_, plasticene casts of ped.v. ext. and brach.v. int., ×2; _2b_, ped.v. int., ×2; _2d_, plasticene cast of brach.v. int. mold, ×3 (189).

Holtedahlina FOERSTE, 1925, p. 122 [*_Leptaena sulcata_ DE VERNEUIL, 1848, p. 350; OD]. Like _Furcitella_ but unequally biconvex, with dorsal median fold; trans-muscle septa poorly developed. _U.Ord._, N.Am.——FIG. 247,_1_. *_H. sulcata_ (DE VERNEUIL), Richmond., USA(Ohio); _1a_, brach.v. view of conjoined valves, ×1; _1b_, brach.v. int., ×1.5; _1c_, ped.v. int., ×1 (189).

Murinella COOPER, 1956, p. 844 [*_M. partita_; OD]. Biconvex but also concavo-convex in late growth stages of some species, costellate to unequally parvicostellate. Ventral muscle field subcircular, with strong bounding ridges, adductors separated by median ridge continuing anteriorly beyond muscle field; trans-muscle septa present, with long submedian pair; dorsal interior with strongly elevated subperipheral band. _M.Ord._, N.Am.——FIG. 247,_4_. *_M. partita_, Porterfield, USA(Okla.); _4a_, ped.v. ext., ×1; _4b,c_, ped.v. and brach.v. int., ×2 (189).

Teratelasma COOPER, 1956, p. 823 [*_T. neumani_; OD]. Gently biconvex, with narrow dorsal median sulcus. Ventral muscle field short and bilobed about median fold in ventral interior; trans-muscle septa well developed, with median septum, extending almost to anterior margin, pointed and strongly elevated posteriorly, and strong submedian septa. _M.Ord._, N.Am.(USA).——FIG. 247, _3_. *_T. neumani_; _3a,b_, plasticene casts of ped.v. ext., and brach.v. int., ×3; _3c_, ped.v. int. mold, ×3 (189).

Subfamily RAFINESQUININAE Schuchert, 1893

[Rafinesquininae SCHUCHERT, 1893, p. 153]

Concavo-convex, or rarely resupinate and geniculate, unequally parvicostellate, with small apical foramen and vestigial or resorbed pseudodeltidium; rugae concentric or impersistent posterolaterally. Ventral muscle scar subquadrate to subcircular,

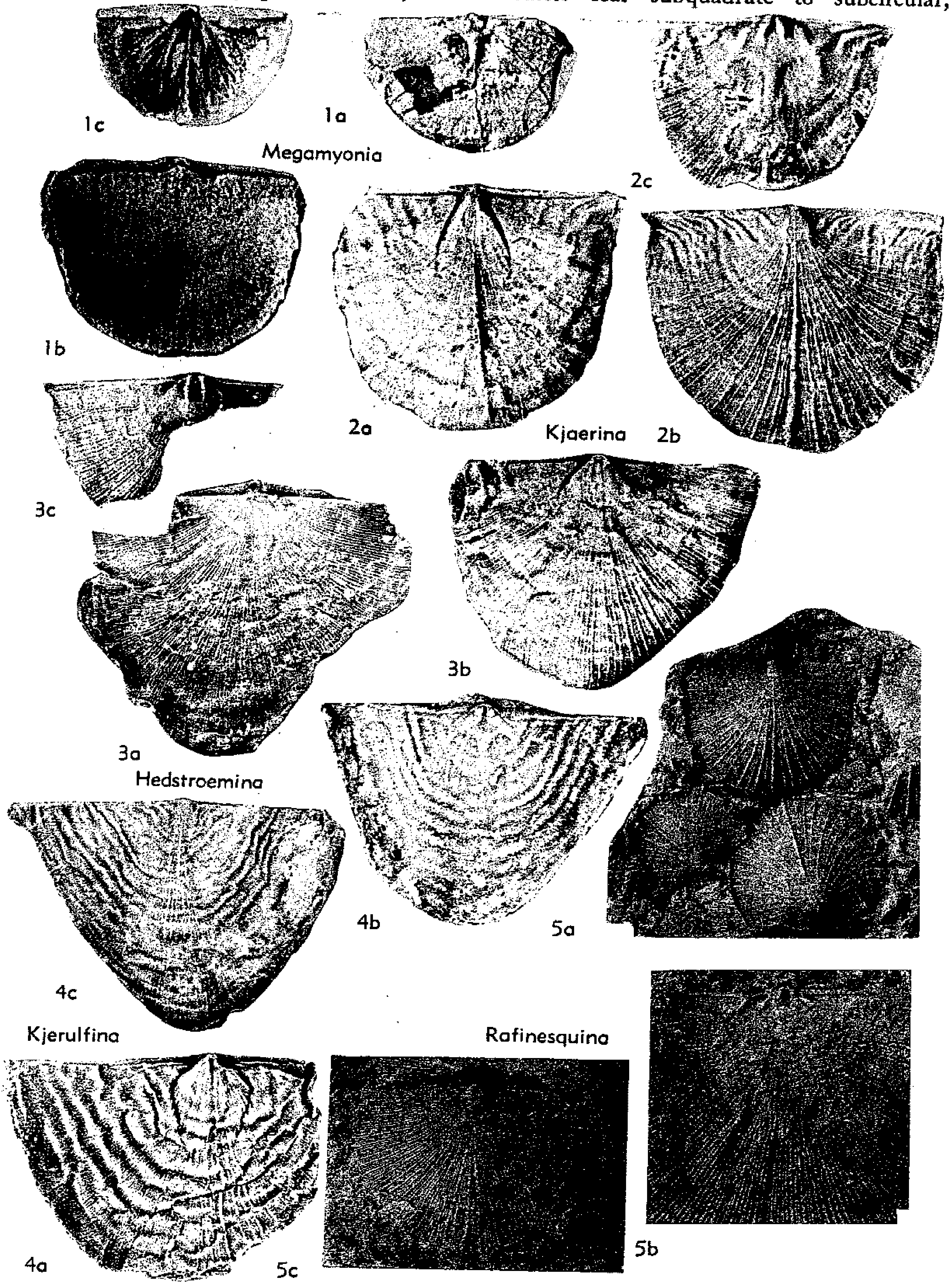


FIG. 248. Strophomenidae (Rafinesquininae) (p. *H*386-*H*388).

bounding ridges weak or absent; notothyrial platform small, cardinalia commonly delicate, trans-muscle weakly defined or absent; shell substance regularly and coarsely pseudopunctate. _M.Ord.-U.Ord._

Rafinesquina Hall & Clarke, 1892, p. 281 [*_Leptaena alternata_ Conrad, 1838, p. 115; OD] [=_Playfairia_ Reed, 1917, p. 866 (type, _Strophomena deltoidea_ Conrad, 1839, p. 63)]. Concavo-convex, unequally parvicostellate, commonly with thickened, conspicuous median costa, posterolateral rugae feeble, pseudodeltidium vestigial. Ventral muscle scar small, subcircular, weakly impressed, and without bonding ridges except for extensions of divergent dental plates; cardinalia delicate; notothyrial platform weak; trans-muscle septa not preserved. _M.Ord.-U.Ord._, N.Hemis.——Fig. 248,_5a_. _R. trentonensis_ (Conrad), M.Ord.(Wilderness-Trenton.), USA(N.Y.); _5a_, ext. views of 3 ped. valves, ×1 (189).——Fig. 248,_5b,c_. _R. planulata_ (Cooper), M.Ord.(Wilderness), USA(Va.); _5b_, brach.v. int., ×3; _5c_, ped.v. int., ×2 (189).

Kjaerina Bancroft, 1929, p. 43 [*_K. typa_; OD]. Like _Rafinesquina_ but with strong posterolateral rugae and lightly impressed, triangular ventral muscle scar, with low, subparallel bounding ridges. _M.Ord.-U.Ord._, Eu.

K. (Kjaerina). Brachial valve plane to shallowly concave; pedicle valve convex to geniculately convex; thickened median costae on pedicle valve conspicuous. _M.Ord._, Eu.——Fig. 248,_2_. *_K. (K.) typa_, Caradoc., Eng.; _2a_, ped.v. int., ×1.5; _2b_, ped.v. ext., ×2; _2c_, brach.v. int., ×2 (Williams, n).

K. (Hedstroemina) Bancroft, 1929, p. 56 [*_H. fragilis_; OD]. Concavo-convex valves commonly geniculate dorsally; thickened median costae rare. _M.Ord.-U.Ord._, Eu.——Fig. 248,_3_. *_K. (H.) fragilis_, Caradoc., Eng.; _3a_, brach.v. view of conjoined valves, ×1.5; _3b_, ped.v. int., ×1.5; _3c_, brach.v. int., ×2.5 (Williams, n).

Kjerulfina Bancroft, 1929, p. 59 [*_K. trigonalis_; OD]. Like _Kjaerina_ but resupinate, with ventrally directed geniculation and concentrically rugate disc. _U.Ord._, Eu.——Fig. 248,_4_. _K. polycyma_ (Bancroft), Caradoc., Eng.; _4a_, ped.v. int., ×1.5; _4b,c_, brach.v. int., ext., ×1.5 (Williams, n).

Megamyonia Wang, 1949, p. 32 [*_M. knighti_; OD]. Concavo-convex, with sharp dorsal geniculation, thick median costa commonly well developed, posterolateral rugae weak. Dental plates absent; ventral muscle field large subcircular; trans-muscle septa commonly absent, rarely variably and feebly developed. _U.Ord._, N.Am.——Fig. 248,_1_. *_M. knighti_, Richmond., USA(Iowa); _1a,b_, brach.v. int., ext., ×2; _1c_, ped.v. int., ×2 (851).

Subfamily GLYPTOMENINAE Williams, n. subfam.

Biconvex to concavo-convex, unequally parvicostellate, with apical foramen and moderately large pseudodeltidium; dental plates short to obsolescent, ventral muscle scar small, cordate to subcircular in outline; cardinal process lobes small, commonly united with curved socket ridges above weak notothyrial platform; trans-muscle septa variably developed. Shell substance mainly densely and finely pseudopunctate. _L.Ord.-M.Ord._

Glyptomena Cooper, 1956, p. 881 [*_G. sculpturata_; OD] [=_Oslomena_ Spjeldnaes, 1957, p. 161 (type, _O. osloensis_)]. Concavo-convex, commonly with strong short rugae posterolaterally. Teeth commonly tuberculate, dental plates short; ventral muscle field subcordate, with lateral bounding ridges; notothyrial platform weak; trans-muscle septa variably developed, submedian pair slightly curved. _M.Ord._, N.Am.-Eu.——Fig. 249,_1_. *_G. sculpturata_, Porterfield, USA(Va.); _1a,b_, brach.v. int., ext., ×2; _1c_, ped.v. int., ×2 (189).

?Hesperinia Cooper, 1956, p. 822 [*_H. kirki_; OD]. Plano- to slightly concavo-convex, parvicostellate; dental plates present, ventral muscle field unknown; notothyrial platform and trans-muscle septa poorly developed. Shell substance coarsely pseudopunctate. [The taxonomic position of this genus is uncertain.] _L.Ord.(Whiterock)_, USA (Nev.).——Fig. 249,_2_. *_H. kirki_; _2a,b_, ped.v., lat. views of conjoined valves, ×3; _2c_, brach.v. int., ×3 (189).

Mjoesina Spjeldnaes, 1957, p. 137 [*_Rafinesquina mjoesensis_ Holtedahl, 1916, p. 19; OD]. Concavo-convex, with brachial valve initially plane or slightly concave, but geniculate dorsally in adult stages of growth. Teeth striated; dental plates short; ventral muscle scar short, rhomboidal, with lateral bounding ridges; notothyrial platform and trans-muscle septa faint or absent. _M.Ord._, Eu.——Fig. 249,_3_. _M. rugata_ Williams, Scot.; _3a_, brach.v. int. cast, ×3; _3b_, ped.v. int. mold, ×2.5; _3c_, brach.v. ext. cast, ×2 (877).

Pionomena Cooper, 1956, p. 901 [*_P. neumani_; OD]. Like _Glyptomena_ but gently biconvex and with obsolescent dental plates. _M.Ord._, N.Am.-Scot.——Fig. 249,_5_. _P. pulchra_ (Cooper), Wilderness, USA(Pa.); ped.v. ext., ×2 (189).

Platymena Cooper, 1956, p. 879 [*_P. plana_; OD]. Like _Glyptomena_ but plano- to slightly concavo-convex and with obsolescent dental plates. _M.Ord._, N.Am.——Fig. 249,_4_. *_P. plana_, Porterfield, USA (Tenn.); _4a,b_, ped.v. int. and ext., ×2; _4c_, brach.v. int., ×2 (189).

Subfamily OEPIKINAE Sokolskaya, 1960

[_nom. correct._ Williams, herein (_pro_ Öpikinae Sokolskaya, 1960, p. 211)]

Concavo-convex, unequally parvicostellate, rarely costellate, with small apical foramen and variably developed pseudodeltidium; impersistent rugae common posterolaterally. Ventral muscle scar large, subcircular, with flabellate diductor scars enclosing adductor scars on either side of variably developed median ridge, bounding ridges weak or absent; notothyrial platform, cardinalia and trans-muscle septa commonly strongly developed. Shell substance densely and finely pseudopunctate. *M.Ord.-U.Ord.*

Oepikina Salmon, 1942, p. 589 [**Öpikina septata*; OD]. Concavo-convex, with convex or gently

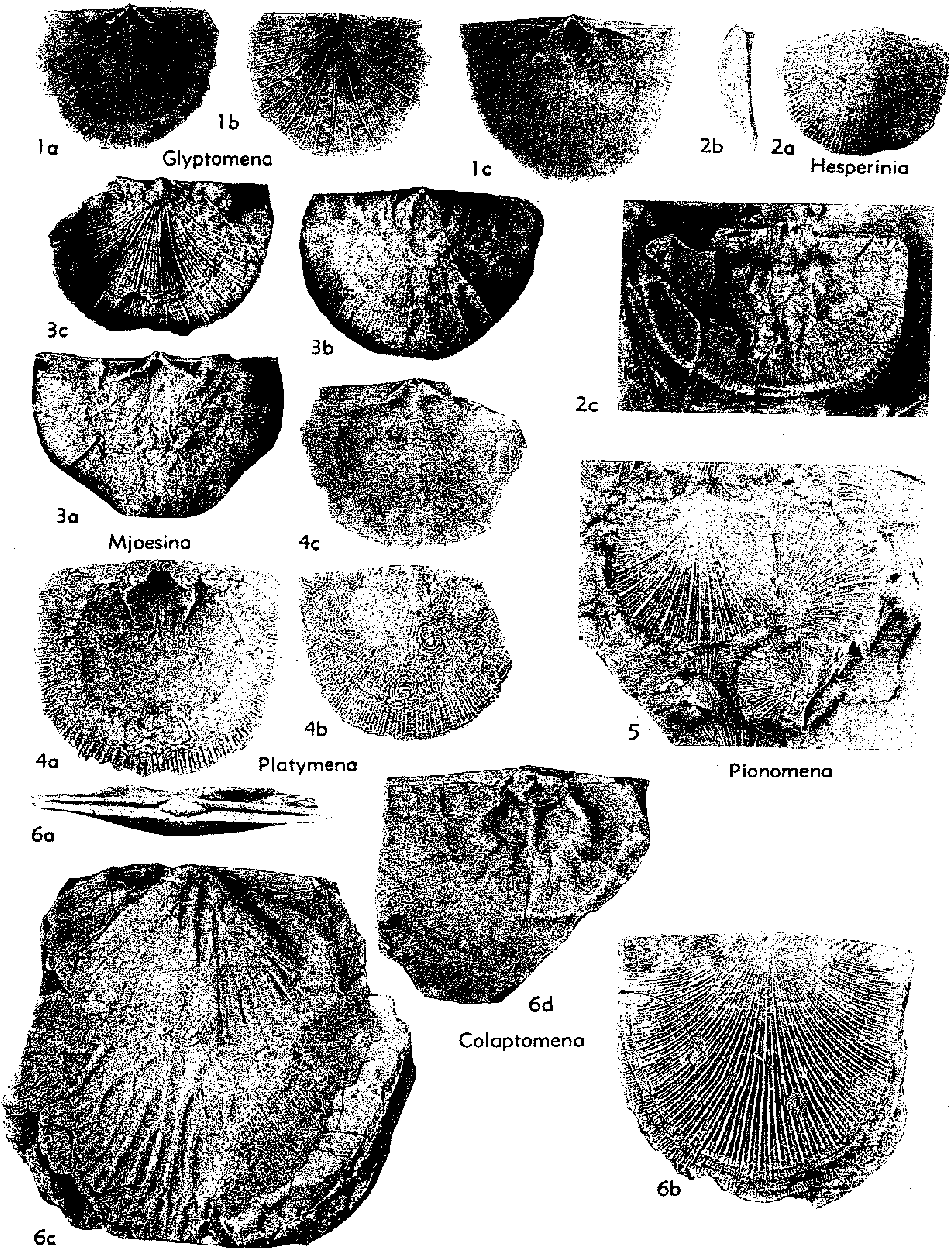


Fig. 249. Strophomenidae (Glyptomeninae) *(1-5)*, (Oepikinae) *(6)* (p. *H*388-*H*390).

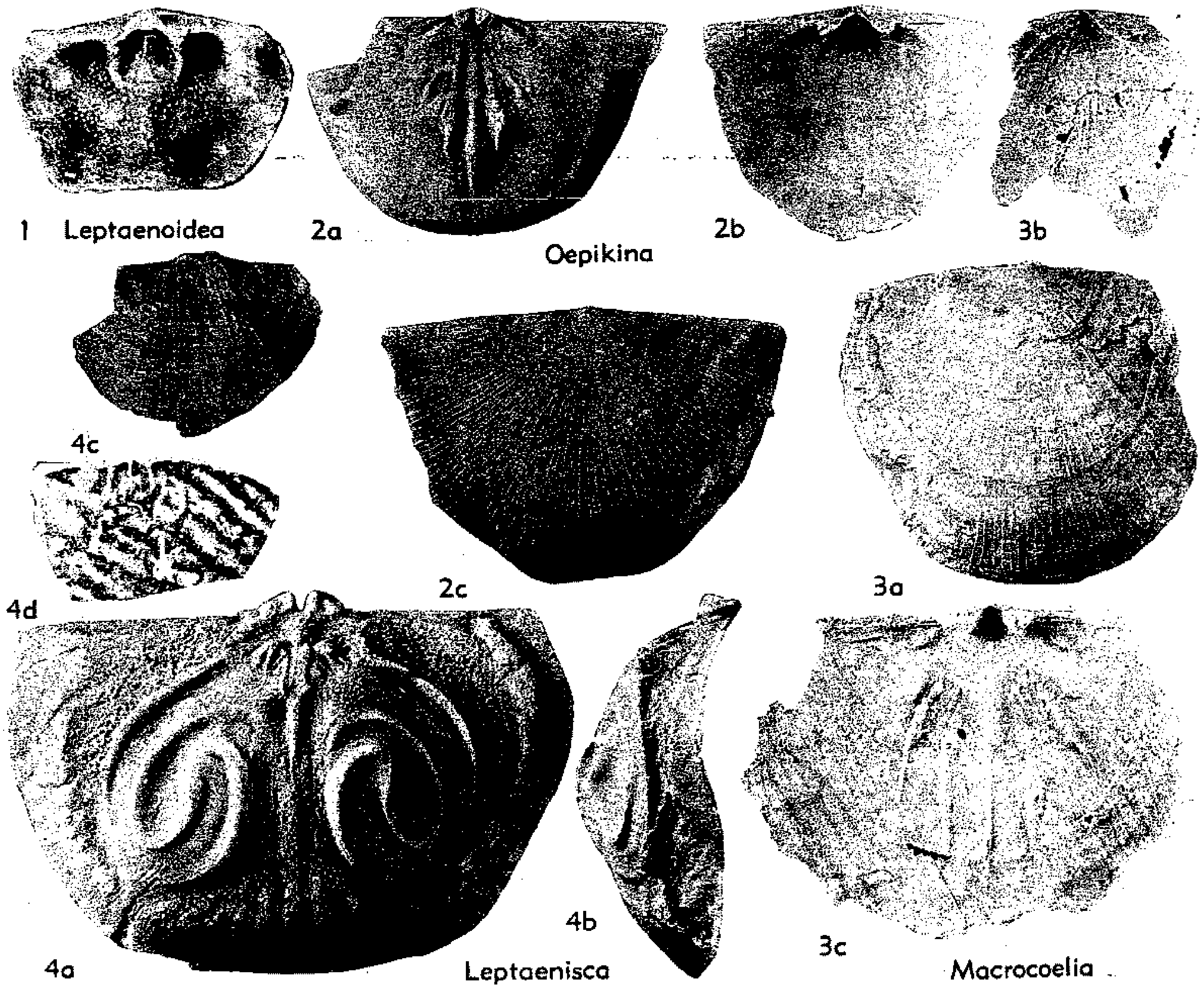


FIG. 250. Strophomenidae (Oepikinae) *(2-3)*, (Leptaenoideinae) *(1,4)* (p. *H*388-*H*390).

geniculate pedicle valve and dorsally geniculate brachial valve; unequally parvicostellate, pseudodeltidium small. Teeth commonly crenulate or tuberculate, dental plates widely divergent; trans-muscle septa strongly developed and high anteriorly, dorsal subperipheral rim conspicuous. *M.Ord.-U.Ord.*, cosmop.——FIG. 250,*2*. **O. septata,* M. Ord.(Wilderness), USA(Tenn.); *2a,b,* brach.v. and ped.v. int., ×2; *2c,* ped.v. view of conjoined valves, ×2 (189).

Colaptomena COOPER, 1956, p. 889 [**C. leptostrophoidea*; OD]. Like *Oepikina* but large, with compressed plano- to concavo-convex profile and resorbed pseudodeltidium; dental plates obsolescent, trans-muscle septa faint. *M.Ord.*, E.N.Am.-G.Brit.——FIG. 249,*6*. **C. leptostrophoidea,* Trenton., USA(Va.); *6a,* post. view of conjoined valves, ×1; *6b,* ped.v. ext., ×1; *6c,* ped.v. int. mold, ×1.5; *6d,* brach.v. int., ×1 (189).

Kirkina SALMON, 1942, p. 598 [**K. millardensis*; OD]. Concavo-convex, subequally parvicostellate, median and submedian septa in dorsal trans-muscle set, poorly developed; pedicle valve unknown. *L.Ord.*, W.USA(Nev.).

Maakina ANDREEVA, 1961, p. 170 [*Öpikina (M.) kulinnensis*; OD]. Like *Oepikina* but with costellate radial ornamentation. *M.Ord.*, USSR.

Macrocoelia COOPER, 1956, p. 890 [**M. obesa*; OD]. Like *Oepikina* but evenly concavo-convex, with small pseudodeltidium rarely resorbed, rudimentary or obsolescent dental plates and subdued trans-muscle septa. *M.Ord.*, N.Hemis.——FIG. 250, *3*. **M. obesa,* Porterfield, USA(Tenn.); *3a,* ped.v. view of conjoined valves, ×1;*3b,* ped.v. int., ×1; *3c,* brach.v. int., ×2 (189).

Subfamily LEPTAENOIDEINAE Williams, 1953

[Leptaenoideinae WILLIAMS, 1953, p. 8]

Parvicostellate, attached to foreign body by cementation of umbonal area of pedicle valve; shell substance coarsely pseudopunctate. *U.Sil.-L.Dev.*

Leptaenoidea HEDSTRÖM, 1917, p. 2 [**L. silurica*; OD]. Finely costellate, plano-convex; pedicle valve with short broad muscle scar, adductors borne on median ridge; interior of brachial valve unknown. *U.Sil.(Wenlock)*, Eu.——FIG. 250,*1*. **L.* sp. aff. *L. silurica,* Sweden; ped.v. int., ×4 (Williams, n).

Leptaenisca Beecher, 1890, p. 239 [**Leptaena concava* Hall, 1857, p. 47; SD Hall & Clarke, 1892, p. 300]. Unequally parvicostellate, concavo-convex, attached in young stages of growth only. Ventral muscle field longer than that of *Leptaenoidea*; dorsal interior bearing a pair of planospiral ridges. *U.Sil.-L.Dev.*, N.Am.——Fig. 250,*4a-c*. **L. concava* (Hall), L.Dev.(Haragan), USA(Okla.); *4a,b*, int., lat. views of brach.v. int., ×1.5; *4c*, ped.v. ext., ×1.5 (Cooper, n).——Fig. 250,*4d*. *L.* sp. cf. *L. concava* (Hall); *4d*, brach.v. int., ×4 (Williams, n).

Family FOLIOMENIDAE Williams, n. fam.

Plano-convex, lacking radial ornamentation; condition of apical foramen unknown, pseudodeltidium and chilidium well developed. Teeth simple, unsupported; ventral muscle field bilobed, with divergent diductors separated medianly by short median ridge and completely enclosing posteriorly located adductor scars; socket ridges subparallel with hinge line; submedian trans-muscle septa strong, median ridge faint; ventral mantle canal system probably digitate with divergent *vascula media*. *U.Ord.*

Foliomena Havlíček, 1952, p. 17 [**Strophomena folium* Barrande, 1879, p. 55, figs. 11-13; OD]. Transversely semioval in outline, shell surface ornamented by impersistent concentric rugae. *U. Ord.*, Czech.——Fig. 251,*2*. **F. folium* (Barrande); *2a,b*, brach.v. ext. and int., ×3; *2c*, ped. v. int., ×3 (Havlíček, n).

Family CHRISTIANIIDAE Williams, 1953

[Christianiidae Williams, 1953, p. 9]

Pseudodeltidium and chilidium, well developed, apical foramen persistent throughout ontogeny; some early species possibly impunctate, majority coarsely pseudopunctate. Teeth simple, supported by receding dental plates; ventral muscle field transversely bilobed; brachial valve with strong socket ridges and pair of long, discrete U-shaped ridges, presumably comprising supports for schizolophous lophophore; mantle-canal pattern digitate. *Ord.*

Christiania Hall & Clarke, 1892, p. 298 [**Leptaena subquadrata* Hall, 1883, pl. 46, figs. 32, 33; OD]. Elongately oval in outline, smooth or with faint fine costellae. Dorsal muscle field defined within posterior parts of loops either by obliquely or transversely directed ridges. *Ord.*, N.Hemis.——Fig. 251,*1*. **C. subquadrata* (Hall), M.Ord.(Porterfield), USA(Appalach.); *1a*, brach. v. view of conjoined valves, ×2; *1b,c*, int., post. views of brach.v. ×2; *1d,e*, int., post. views of ped.v., ×2 (189).

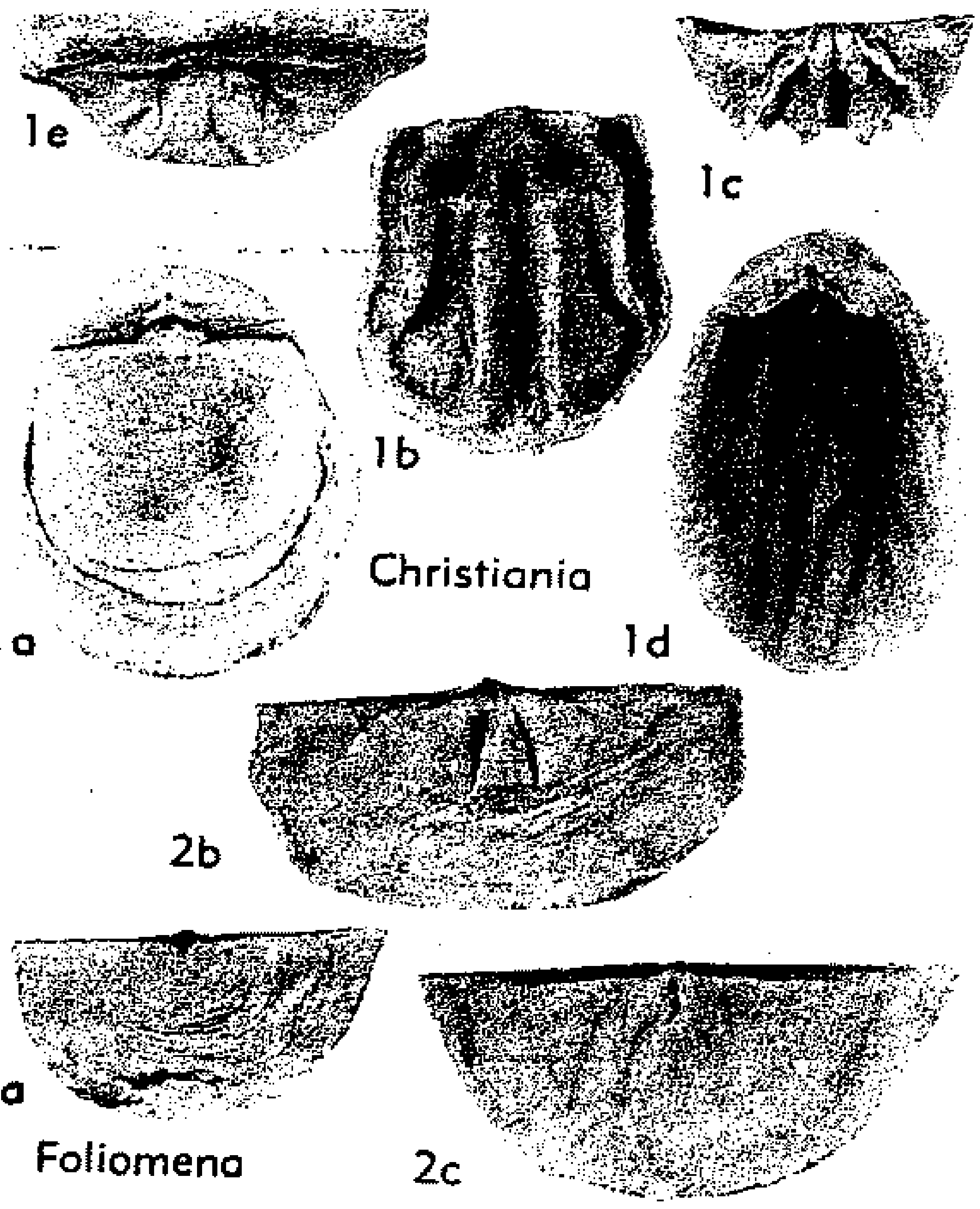


Fig. 251. Foliomenidae *(2)*; Christianiidae *(1)* (p. *H390-H391*).

Family LEPTAENIDAE Hall & Clarke, 1894

[Leptaenidae Hall & Clarke, 1894, p. 354]

Concavo-convex to biconvex, with variably developed geniculation directed dorsally or (rarely) ventrally; concentric rugae almost invariably present on disc; apical foramen large, persistent throughout ontogeny or rarely plugged by secondary shell, pseudodeltidium commonly present but exceptionally resorbed in adult shells, chilidium well developed. Teeth simple, supported by receding dental plates, ventral muscle scar suboval to subcircular with strong bounding ridges; cardinal process lobes strong and with socket ridges, supported by anchor-shaped extension of notothyrial platform embracing posterior ends of dorsal adductor scars; trans-muscle septa variably developed; mantle canal systems saccate to lemniscate; shell substance coarsely pseudopunctate. *M.Ord.-L.Carb.*

Leptaena Dalman, 1828, p. 93 [**L. rugosa* Dalman, 1828; SD King, 1846, p. 28] [=*Leptaenella* Frederiks, 1917, p. 89 (type, *Leptaena rhomboidalis ventricosa* Hall) (*non* Sarycheva & Sokolskaya, 1952); *Leptaenulopsis* Haupt, 1878, p. 59 (type, indeterminate young *Leptaena*)].

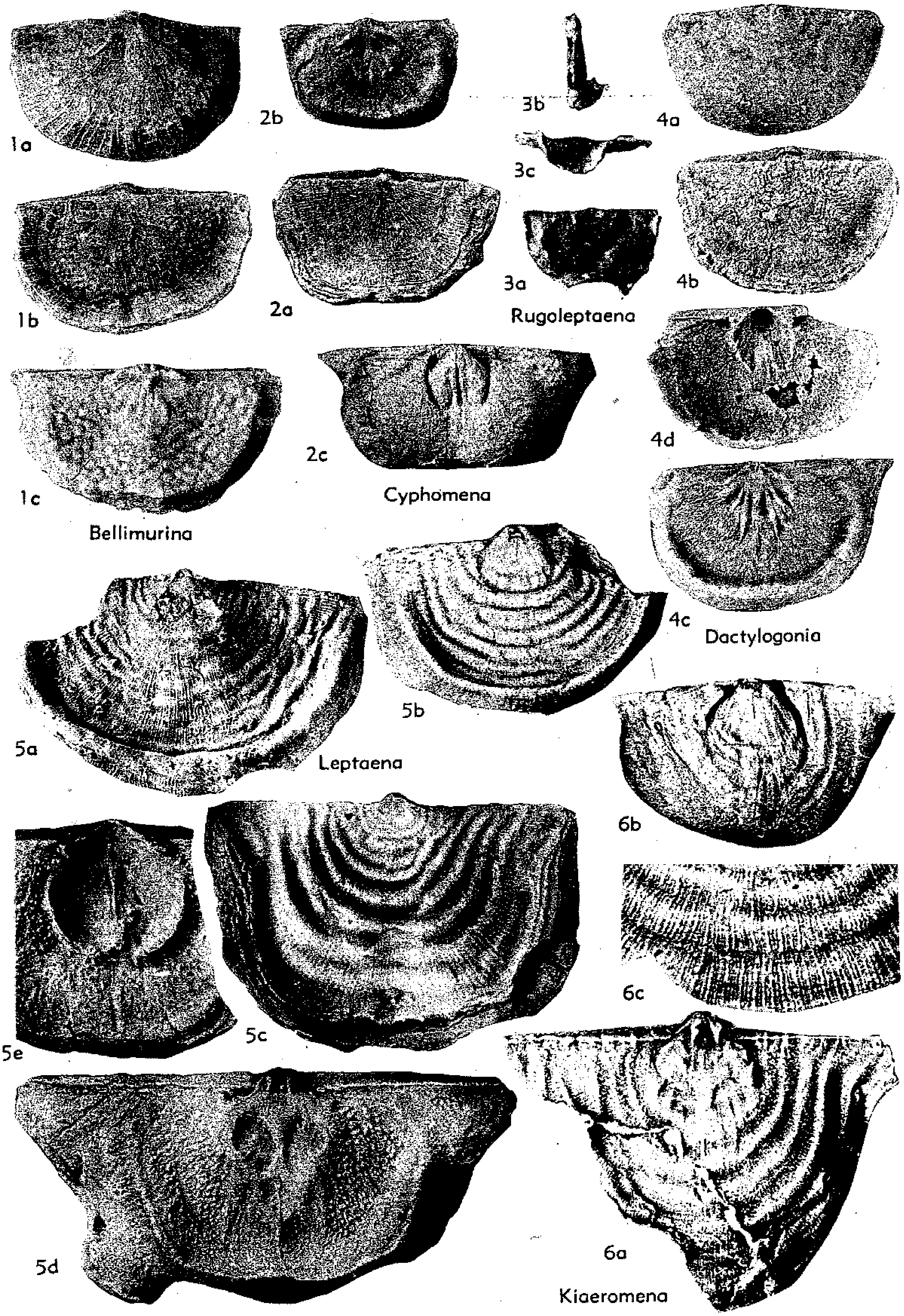


FIG. 252. Leptaenidae (p. *H*391, *H*393-*H*394).

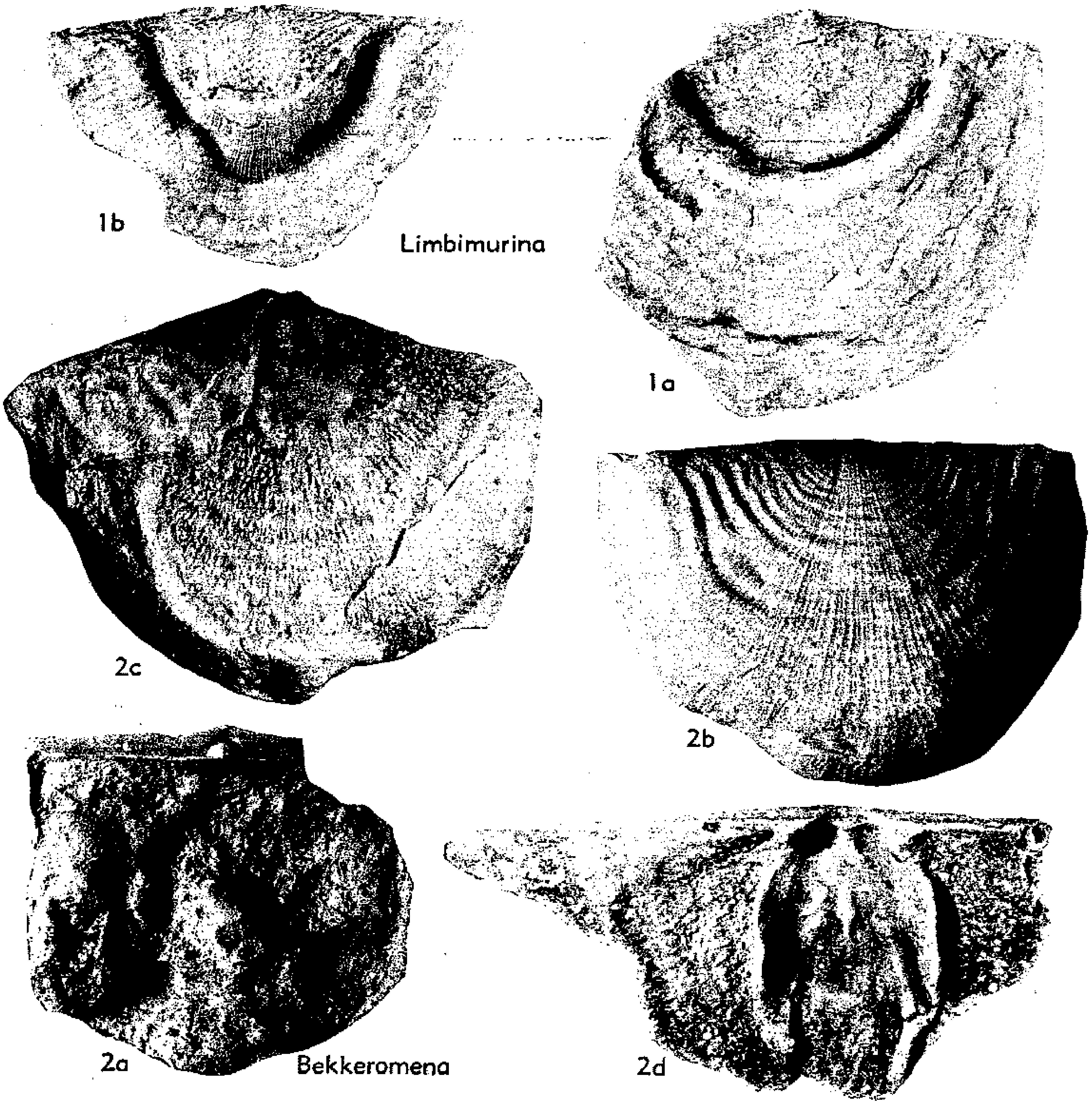


FIG. 253. Leptaenidae (p. *H*391, *H*393-*H*394).

Sharply geniculate with narrow ventrally projecting ridge separating disc from trail; finely and evenly costellate, concentric rugae strong; pseudodeltidium present or resorbed. Teeth smooth or crenulated, ventral muscle scar suboval to subcircular surrounded by ridges; dorsal trans-muscle septa including variably developed median septum, 2 long, curved submedian septa and 2 shorter, lateral septa. *M.Ord.-Dev.*, cosmop.——FIG. 252,*5a,b*. **L. rugosa*, U.Ord., Sweden; *5a,b*, brach.v. ext., ped.v. int. mold, ×1.5 (Williams, n).——FIG. 252,*5c-e*. *L. rhomboidalis* (WILCKENS), U.Sil., Eng.; *5c*, brach.v. ext., ×1.5; *5d,e*, brach.v. and ped.v. int., ×1.5 (Williams, n).

Bekkeromena RÕÕMUSOKS, 1963, p. 235 [**Strophomena semipartita* ROEMER, 1861, pl. 1, figs. 5-9, text-figs. 2-3; OD]. Like *Leptaena* but with unequally parvicostellate ornamentation, elongately subquadrate ventral muscle field, rounded geniculation without ventrally projecting ridge, and without trans-muscle septa. *U.Ord.*, *E.Eu.*——FIG. 253,2. **B. semipartita* (ROEMER), FIab-d, Est.; *2a*, brach.v. view of conjoined valves, ×1.5; *2b,c*, ped.v. ext., brach.v. int., ×1.5; *2d*, ped.v. int., ×2 (Rõõmusoks, n).

Bellimurina COOPER, 1956, p. 854 [**Leptaena charlottae* WINCHELL & SCHUCHERT, 1892, p. 288; OD]. Gently geniculate in dorsal direction, unequally parvicostellate with stronger costellae breaking up rugae into short zigzag sets. Ventral muscle scar short and wide; trans-muscle septa variably developed. *M.Ord.*, N.Am.-Eu.——FIG. 252,1. **B. charlottae* (WINCHELL & SCHUCHERT), Wilderness, USA (Minn.); *1a,b*, ped.v. and brach.v. views of conjoined valves, ×2; *1c*, brach.v. int., ×2 (189).

Cyphomena COOPER, 1956, p. 840 [**Leptaena homostriata* BUTTS, 1942, p. 110; OD]. Sharply geniculate in dorsal direction, finely costellate, impersistent rugae developed only posterolaterally;

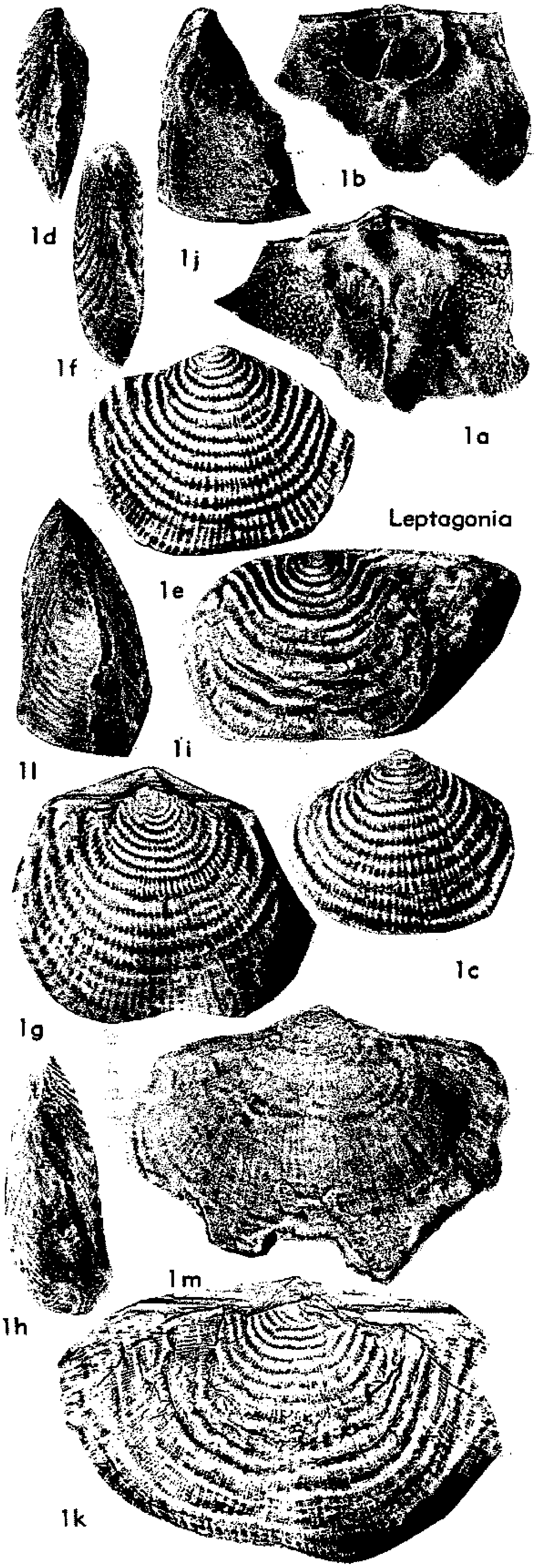


FIG. 254. Leptaenidae (p. *H*394).

ventral muscle scar small, elongately oval; trans-muscle septa strong. *M.Ord.*, USA-Scot.——FIG. 252,*2*. *C. angulata* (Cooper), Porterfield, Va. (*2a*), Pa. (*2b*), Md. (*2c*); *2a*, brach. v. view of conjoined valves, ×2; *2b*, brach.v. int., ×2; *2c*, ped.v. int. mold, ×3 (189).

Dactylogonia Ulrich & Cooper, 1942, p. 623 [**D. geniculata;* OD]. Sharply geniculated in dorsal direction, unequally parvicostellate, impersistent rugae posterolaterally, pseudodeltidium large. Teeth smooth, ventral muscle scar suboval normally with strong bounding ridges; dorsal trans-muscle septa well developed. *M.Ord.*, E.USA.-Scot.——FIG. 252,*4*. **D. geniculata*, Porterfield, USA(Tenn.); *4a,b*, ped.v. and brach.v. views of conjoined valves, ×2; *4c,d*, brach.v. and ped.v. int., ×2 (189).

Kiaeromena Spjeldnaes, 1957, p. 183 [**Leptaena kjerulfi* Holtedahl, 1916, p. 72; OD]. Like *Bekkeromena* but with subcircular ventral muscle field and weakly developed trans-muscle septa. *M.Ord.-U.Ord.* Eu.——FIG. 252,*6*. *K.* sp. cf. *K. kjerulfi* (Holtedahl), M.Ord.(4bβ), Eu.(Nor.); *6a*, brach.v. int., ×3; *6b*, ped.v. int., 2; *6c*, detail of ornamentation, ×4 (Williams, n).

Leptagonia M'Coy, 1844, p. 116 [**Producta analoga* Phillips, 1836, p. 215; SD Schuchert & LeVene, 1929, p. 74] [=*Pseudoleptaena* Williams, herein (*pro Leptaenella* Sarycheva & Sokolskaya, 1952, *non* Frederiks, 1917)]. Initially biconvex through resupination but with biconvexity accentuated in adult shells by ventral geniculation in brachial valve and dorsal geniculation in pedicle valve to give shelflike anterior margin commonly indented medianly or even laterally, and less commonly prolonged dorsally as a narrow trail; finely costellate, rarely with accentuated costellae, concentric rugae strong; pseudodeltidium present or resorbed. Teeth crenulated, ventral muscle field subcircular, impressed on raised cup of secondary shell suported by median ridge; dorsal adductor field impressed posteriorly on subtriangular elevation culminating in high median septum. *L.Carb.*, Eurasia.——FIG. 254,*1*. **L. analoga* (Phillips), Carb., Wales; *1a,b*, fragments of brach.v. and ped.v. ints., ×1.5; *1c,d*, ped.v. ext., lat., ×1.5; *1e,f*, ped.v. ext. lat., ×1.5; *1g,h*, brach.v. ext., lat., ×1.5; *1i,j*, ped.v. ext., lat., ×1; *1k,l*, brach.v. ext., lat. ×1; *1m*, brach.v. ext., ×1, views of 6 complete specimens (Williams, n).

Limbimurina Cooper, 1956, p. 851 [**L. insueta;* OD]. Ventrally directed ridge surrounding disc greatly exaggerated to give ventral, then dorsal direction to geniculation; surface ornamentation like that of *Bellimurina;* interiors like those of *Leptaena*. *M.Ord.*, USA.——FIG. 253,*1*. **L. insueta*, Wilderness, USA(Penn.); *1a,b;* ped.v. and brach.v. ext., ×2 (189).

Notoleptaena Gill, 1951, p. 191 [**N. linguifera;* OD]. Like *Leptaena* but geniculate in ventral direction and with anteromedian zone of ventral trail projecting dorsally to fit into deep, complementary incision in brachial valve. *L.Dev.*, Australia.

Rugoleptaena Havlíček, 1956, p. 24 [**Rugoleptaena hornyi;* OD]. Like *Notoleptaena* but with anteromedian parts of both ventral and dorsal trails deflected dorsally as tongue. *U.-Sil-L.Dev.*, Eu.——Fig. 252,*3*. *R. emarginata* (Barrande), U.Sil., Pol.; *3a-c*, brach.v. ext., lat., ant. views of brach.v., ×1 (487).

Family STROPHEODONTIDAE Caster, 1939

[Stropheodontidae Caster, 1939, p. 26]

Lacking functional pedicle and with simple teeth and dental plates replaced by denticles subsequently spreading along hinge line; socket ridges abbreviated subsequent to loss of dental plates becoming obsolescent or disappearing completely, exceptionally forming buttresses to cardinal process lobes; pseudodeltidium initially small, apical, becoming progressively larger and in some stocks ultimately closing delthyrium completely; chilidium initially massive becoming degenerate and in some stocks ultimately completely lost; mantle canal patterns in both valves probably lemniscate; shell substance densely pseudopunctate. *U.Ord.-U. Dev.*

Subfamily STROPHEODONTINAE Caster, 1939

[Stropheodontinae Caster, 1939, p. 28]

Unattached, concavo-convex or resupinate, with parvicostellate radial ornamentation commonly modified or even supplanted by secondary plicate or costellate patterns, concentric rugae rare; ventral muscle scar subcircular to subquadrate; dorsal adductor scars commonly impressed on elevated platforms in late stocks. *U.Ord.-U.Dev.*

Strophodonta Hall, 1850, p. 348 [**Leptaena demissa* Conrad, 1842, p. 258; OD] [=*Stropheodonta* Hall, 1852, p. 63 *(nom. van.)*]. Concavo-convex, ventral muscle field elongately oval, with diductor scars anterolateral to lanceolate adductor scar. *U.Ord.-U.Dev.*, cosmop.

S. (Strophodonta). Finely costellate, also secondarily ornamented by plicae or costellae; pseudodeltidium complete, no chilidium; no dental plates, socket-ridge obsolescent; strong muscle scars. *Dev.*, cosmop.——Fig. 255,*4*. *S. (S.)* sp. aff. *S. (S.) demissa* (Conrad), M.Dev., USA (Mich.); *4a,b*, ped.v. ext., ×2, ×1.5; *4c,d*, ped.v. and brach.v. int., ×1.5 (871).

S. (Brachyprion) Shaler, 1865, p. 63 [**Strophomena leda* Billings, 1860, p. 55; OD]. Parvicostellate; delthyrium progressively closed by pseudodeltidium, chilidium degenerate; no dental plates, socket ridges abbreviated. *L.Sil.-L.Dev.*, cosmop.——Fig. 255,*1*. *S. (B.)* sp., L.Dev.(Haragan), USA(Okla.); *1a,b*, ped.v. int. and ext., ×1.5; *1c*, brach. v. int., ×1.5 (871).

S. (Eostropheodonta) Bancroft, 1949, p. 9 [**Orthis hirnantensis* M'Coy, 1851, p. 395; OD]. Finely parvicostellate to fascicostellate; delthyrium open, chilidium massive; dental plates short, socket ridges strong; muscle scars faint. *U.Ord.-L.Sil.*, Eu.——Fig. 255,*3a-c*. **S. (E.) hirnantensis* (M'Coy), U.Ord.(Ashgill.), Wales; *3a*, ped. v. int. mold, ×2.5; brach.v. int., ×3; *3c*, ped.v. ext., ×1.5 (Williams, n).——Fig. 255,*3d,e*. *S. (E.) siluriana* (Davidson), U.Ord., Br.I.; *3d,e*, brach.v. ext. and ped.v. int. molds, ×2.5, ×10 (conical mold of hollow between expanded tooth and dental plate figured on left of ped.v. umbonal mold removed on right to show denticulate nature of both tooth and plate) (870).

S. (Rhenostrophia) Boucot, 1960, p. 483 [**Orthis subarchnoidea* d'Archiac & de Verneuil, 1842, p. 372; OD]. Like *S. (Strophodonta)* but strongly geniculate in dorsal direction. *L.Dev.*, E.Can.-Eu.

Cymostrophia Caster, 1939, p. 48 [**Leptaena stephani* Barrande, 1879, p. 308; OD] [=*Corrugatella* Khalfin, 1948, p. 236 (obj.)]. Finely parvicostellate segregated into wide sectors by strongly developed costellae that also interrupt close concentric rugation; ventral muscle field subcircular with well-developed posterolateral ridges; dorsal interior unknown. *U.Sil.-L.Dev.*, N.Hemis.

C. (Cymostrophia). Pseudodeltidium almost complete, with slight median fold, hinge line almost entirely denticulate. *L. Dev.*, N.Hemis.——Fig. 255,*2*. **C. (C.) stephani* (Barrande), Czech.; *2a,b*, ped.v. ext. and int. mold, ×1 (871).

C. (Idioglyptus) Northrop, 1939, p. 172 [**I. stigmatus;* OD] [=*Pioglyptus* St. Joseph, 1941, p. 8 *(nom. null.)*]. Hinge line denticulate for less than half of its length; interiors unknown. *U.Sil.*, E.N.Am.

Megastrophia Caster, 1939, p. 36 [**Strophomena (Strophodonta) concava* Hall, 1857, p. 140; OD] [=*Dictyostrophia* Caster, 1939, p. 40 (type, *D. cooperi*)]. Large concavo-convex, unequally parvicostellate. Ventral muscle field transversely oval, diductor scars lying laterally to adductor. *Sil.-M.Dev.*, N.Hemis.

M. (Megastrophia). Pseudodeltidium entire but with sharp median fold, chilidium vestigial. Dorsal adductor scars borne on foliaceous platforms. *M.Dev.*, N.Hemis.——Fig. 255,*5*. *M. (M.)* sp. aff. **M. (M.) concava* (Hall), USA (N.Y.); *5a*, brach.v. view of conjoined valves, ×1; *5b*, ped.v. int., ×1; *5c*, brach.v. int., ×1.5 (871).

M. (Protomegastrophia) Caster, 1939, p. 36 [**Leptaena profunda* Hall, 1852, p. 61; OD]. Pseudodeltidium progressively developed but not

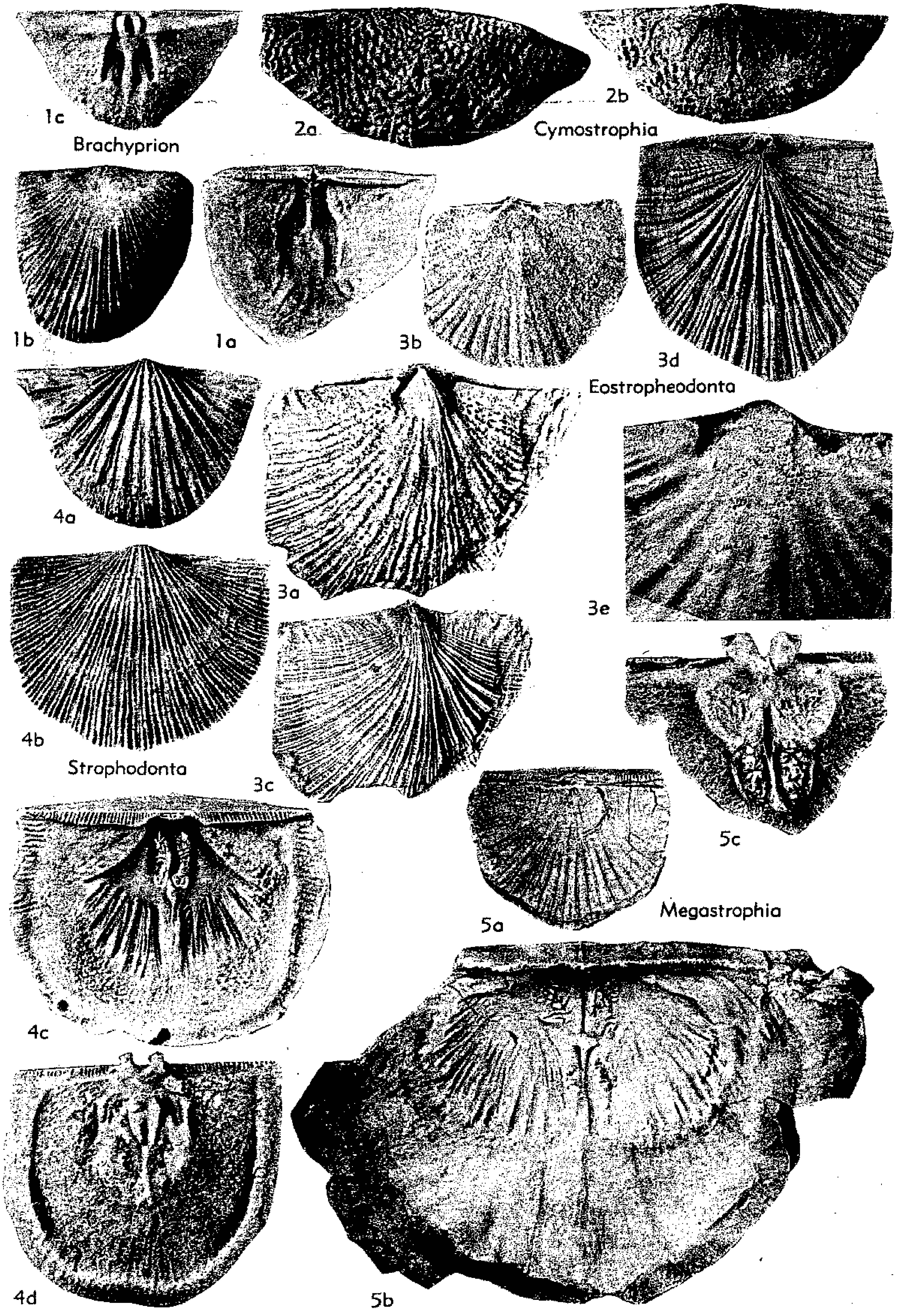


FIG. 255. Stropheodontidae (Stropheodontinae) (p. *H*395).

completely filling delthyrium, chilidium strong to obsolescent. Dorsal adductor scars faintly impressed on valve floor. *L.Sil.-L.Dev.*, Eu.-N.Am. ——FIG. 256,4. *_M. (P.) profunda_ (HALL), M.Sil.(Racine), USA(Wis.); *4a*, ped.v. int. mold, ×1; *4b*, brach.v. int. mold, ×1.5 (871).

Plicostropheodonta SOKOLSKAYA, 1960, p. 214 [*_Orthis murchisoni_ D'ARCHIAC & DE VERNEUIL, 1842, p. 371; OD]. Like *Megastrophia (Megastrophia)* but with secondary ornament of strong coarse costae and subperipheral rim in brachial valve. *L.Dev.-M.Dev.*, Eurasia-N.Afr.

Radiomena HAVLÍČEK, 1962, p. 471 [*_Orthis irregularis_ ROEMER, 1844, p. 75; OD]. Like *Megastrophia (Megastrophia)* but strongly geniculate in dorsal direction and with accentuated

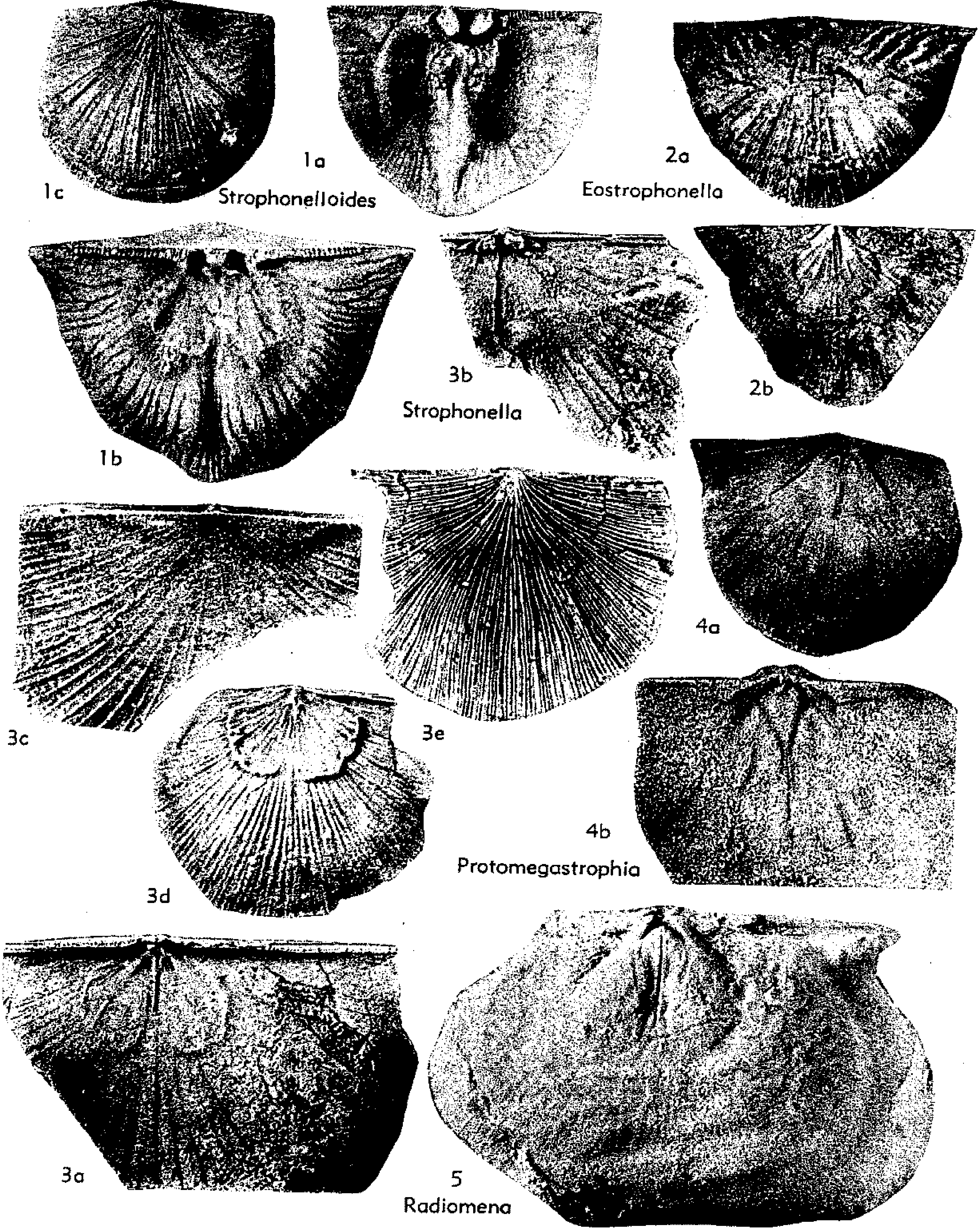


FIG. 256. Stropheodontidae (Stropheodontinae) (p. *H395*, *H397-H398*).

costellae dying away on trail to give undifferentiated parvicostellate ornamentation anteriorly; pseudodeltidium without median fold. *M.Dev.*, C.Eu.——Fig. 256,*5*. **R. irregularis* (Roemer); ped.v. int. mold, ×1 (Havlíček, n.).

Strophonella Hall, 1879, p. 153 [**Strophomena semifasciata* Hall, 1863, p. 210; SD Hall & Clarke, 1892, p. 291] [=*Strophoprion* Twenhofel, 1914, p. 25 (type, *Brachyprion geniculatum* Shaler, 1865, p. 63)]. Resupinate, radial ornament unequally parvicostellate with superimposed secondary costellation in some late stocks, rugae impersistent posterolaterally; pseudodeltidium progressively degenerate; ventral muscle scar subcircular to subquadrate. *L.Sil.-L.Dev.*, N.Hemis.

S. (Strophonella). Pedicle valve without dental plates, ventral muscle scar subquadrate, bounded laterally and anteriorly by low interrupted ridges with petaloid appearance. *U.Sil.-L.Dev.*, N.-Hemis.——Fig. 256,*3a-c*. **S. (S.) semifasciata* (Hall), U.Sil., USA(Tenn.); *3a,b*, ped.v. and brach.v. int., ×1.5; *3c*, brach.v. view of incomplete shell, ×1.5 (871).——Fig. 256,*3d*. *S. (S.)* sp., L.Dev., USA(Tenn.); ped.v. int., ×1 (871).——Fig. 256,*3e*. *S. (S.)* sp. cf. *S. (S.) cavumbona* (Hall), L.Dev., USA(Tenn.); brach.v. ext., ×1 (871).

S. (Eostrophonella) Williams, 1950, p. 281 [**Strophonella davidsoni* Holtedahl, 1916, p. 64; OD]. Pedicle valve with dental plates; ventral muscle scar subcircular. *L.Sil.*, Eu.——Fig. 256,2. *S. (E.) eothen* (Bancroft), L.Sil., Wales; *2a,b*, brach.v. and ped.v. int. mold, ×1 (871).

Strophonelloides Caster, 1939, p. 106 [**Strophodonta reversa* Calvin, 1878, p. 728; OD] [=*Chemungia* Caster, 1939, p. 106 (type, *Strophodonta caelata* Hall, 1867, p. 112)]. Like *S. (Strophodonta)* but resupinate. *U.Dev.*, N.-Am.——Fig. 256,1. **S. reversa* (Calvin), Cerro Gordo, USA(Iowa); *1a,b*, brach.v. and ped.v. int., ×1; *1c*, brach.v. view of conjoined valves, ×1 (871).

Subfamily LEPTOSTROPHIINAE Caster, 1939

[*nom. transl.* Williams, herein (*ex* tribe Leptostrophiini Caster, 1939, p. 73)]

Unattached, concavo-convex, biplanate or rarely resupinate, with costellate to unequally parvicostellate radial ornamentation, less commonly broken at irregular intervals to give subspinose (nervate) appearance; rugae impersistent posterolaterally or rarely concentric. Ventral muscle scar subtriangular and commonly splayed; dorsal adductor scars impressed on floor of brachial valve with variably developed posterolateral bounding ridges. *L.Sil.-U.Dev.*

Leptostrophia Hall & Clarke, 1892, p. 288 [**Stropheodonta magnifica* Hall, 1857, p. 54; OD] [=*Rhytistrophia* Caster, 1939, p. 86 (type, *Stropheodonta beckii* Hall, 1859, p. 191)]. Gently concavo-convex to biplanate, parvicostellate, subdued concentric rugae generally present posterolaterally and rarely covering entire shell; pseudodeltidium never complete, chilidium becoming degenerate. Socket ridges initially widely divergent, later adjacent to cardinal process lobes. *Sil.-Dev.*, cosmop.——Fig. 257,*6*. *L.* sp., *L.Dev.*, USA(Tenn.); *6a*, brach.v. int., ×1.5; *6b*, ped.v. int., ×2 (Williams, n).

Gamphalosia Stainbrook, 1946, p . 33 [**G. tenuissima;* OD]. Like *Nervostrophia* but resupinate. *U.Dev.*, N.Am.(Iowa).

Maoristrophia Allan, 1947, p. 440 [**M. neozelanica;* OD]. Costellate, plano-subconvex, with narrow median fold in pedicle valve, hinge line incompletely denticulate. Ventral muscle scar subtriangular; socket ridges short, stout, dorsal median ridge flanked anteriorly by pair of low curved ridges. *L.Dev.*, N.Z.——Fig. 257,*5*. **M. neozelanica; 5a-c*, rubber casts of brach.v. int., brach.v. ext., ped.v. int., ×1 (27).

Nervostrophia Caster, 1939, p. 79 [**Strophomena nervosa* Hall, 1843, p. 266; OD] [=*Sulcatostrophia* Caster, 1939, p. 81 (type, *Leptostrophia camerata* Fenton & Fenton, 1924, p. 96); *Pseudodouvillina* Stainbrook, 1945, p. 26 (type, *P. euglyphea*)]. Concavo-convex, rarely sulcate, unequally parvicostellate with stronger costellae irregularly broken into several short lengths (nervate); pseudodeltidium complete, with or without median fold, chilidium vestigial or absent. Socket ridges parallel to sides of cardinal process lobes and fused with them. *M.Dev.-U.Dev.*, cosmop.——Fig. 257,*3*. *N. rockfordensis* (Fenton & Fenton), *U.Dev.*, USA(Iowa); *3a*, brach.v. int., ×2; *3b*, ped.v. ext., ×1; *3c*, ped.v. int., ×1.5 (871).

Protoleptostrophia Caster, 1939, p. 75 [**Strophomena blainvillii* Billings, 1874, p. 28; OD]. Like *Leptostrophia* but without socket ridges in brachial valve. *M.Dev.*, N.Am.——Fig. 257,*1a,b*. **P. blainvillii* (Billings), Silica Sh., USA(Ohio); *1a,b*, plasticene casts of brach.v. and ped.v. int., ×1 (871).——Fig. 257,*1c*. *P.* sp., Silica Sh., USA(Ohio); *1c*, ped.v. ext., ×1 (871).

Subfamily DOUVILLININAE Caster, 1939

[*nom. transl.* Williams, herein (*ex* tribe Douvillinini Caster, 1939, p. 70)]

Unattached concavo-convex to resupinate, with unequally parvicostellate radial ornamentation. Ventral muscle scar suboval to transversely subquadrate, with well-developed bounding ridges; socket ridges short to obsolescent, dorsal adductor scars variably impressed on floor of brachial valve posterior to pair of narrowly divergent ridges. *U.Sil.-U.Dev.*

Douvillina Oehlert, 1887, p. 1282 [**Orthis dutertrei* Murchison, 1839, p. 253; OD]. Con-

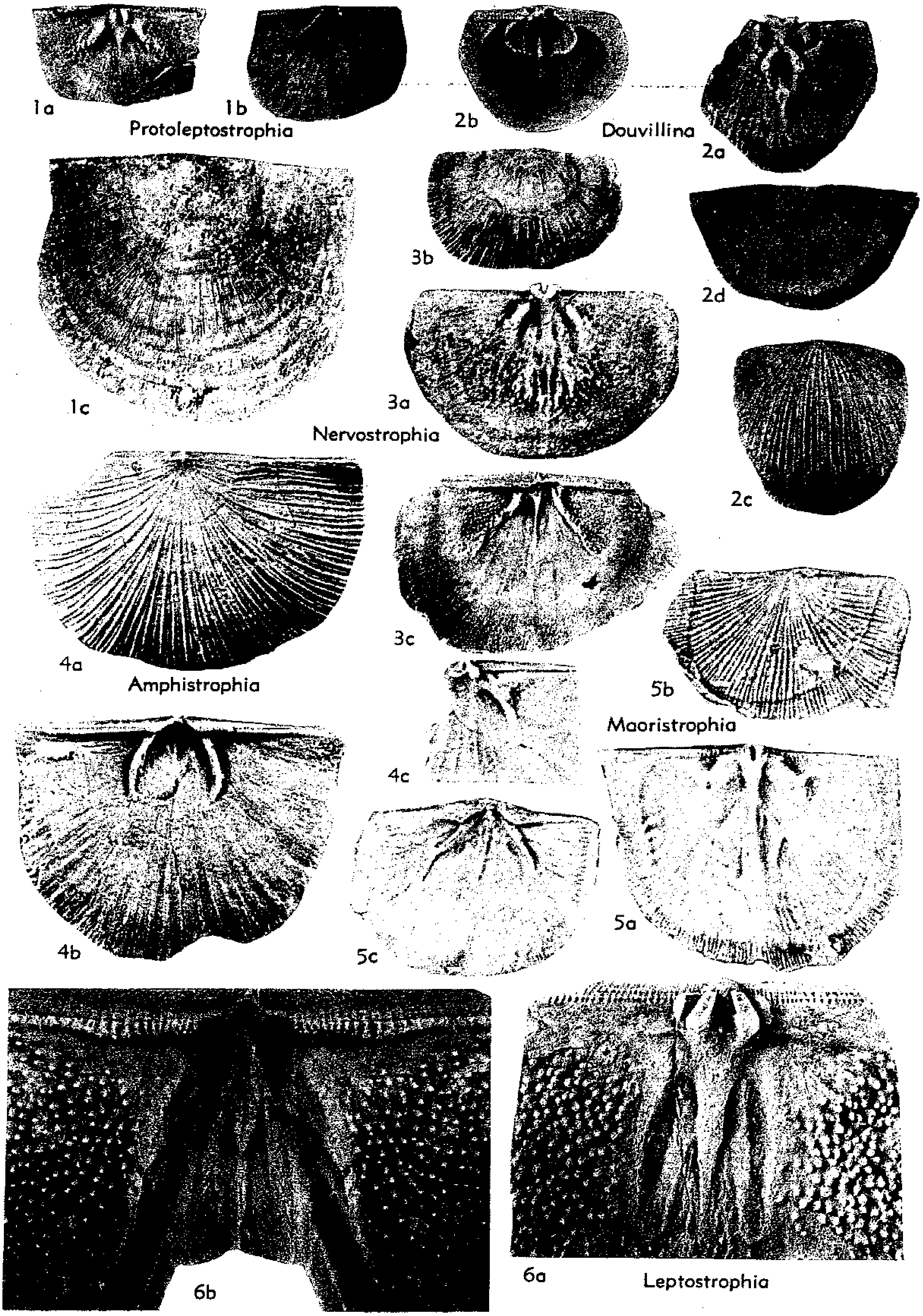


FIG. 257. Stropheodontidae (Leptostrophiinae) *(1,3,5,6)*, (Douvillininae) *(2,4)* (p. *H*398, *H*400).

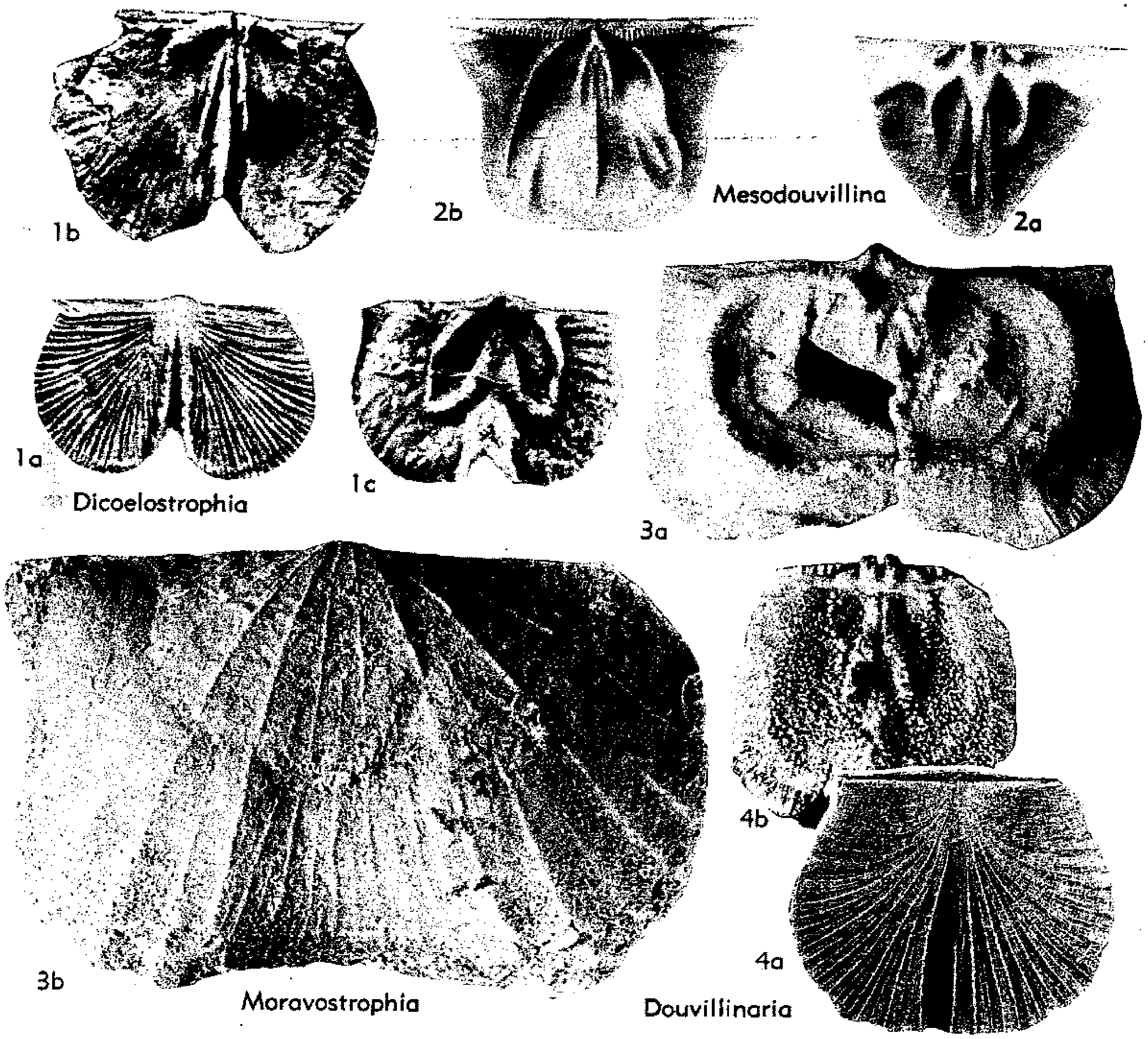


Fig. 258. Stropheodontidae (Douvillininae) (p. _H_400-_H_401).

cavo-convex, unequally parvicostellate. Ventral muscle scar ultimately completely bounded by ridges. _U.Sil.-U.Dev.,_ N.Hemis.

D. (Douvillina). Medianly folded pseudodeltidium complete, chilidium vestigial. Socket ridges obsolescent; ventral muscle scar transversely subquadrate, bounded anteriorly by raised ridges commonly to form a raised cup; ridges anterior to dorsal adductor scars, tuberculate, strong, and curving toward each other. _Dev.,_ N.Hemis.——Fig. 257,_2a-c_. _D. (D.) arcuata_ (Hall), U.Dev.-(Hackberry), USA(Iowa); _2a-c,_ brach.v. int., ped.v. int., ped.v. ext., ×1.5 (871).——Fig. 257,_2d_. _D. (D.)_ sp., M.Dev.(Hamilton), USA (Va.), _2d,_ ped.v. int. mold, ×1 (871).

D. (Mesodouvillina) Williams, 1950, p. 281 [*_Stropheodonta (Brachyprion) subinterstrialis_ var. _seretensis_ Kozlowski, 1929, p. 97; OD]. Pseudodeltidium incomplete, chilidium becoming degenerate. Ventral muscle scar suboval with lateral bounding ridges; socket plates short, ridges anterior to dorsal adductor scars low. _U.Sil.,_ N.Hemis.——Fig. 258,_2_. *_D (M.) subinterstrialis seretensis_ (Kozlowski), U.Sil. (Czortkov), Pol.; _2a,b,_ brach.v. int., ped.v. int., ×2 (487).

Amphistrophia Hall & Clarke, 1892, p. 292 [*_Strophomena striata_ Hall, 1843, p. 104; OD]. Resupinate, with incompletely developed pseudodeltidium and massive chilidium. Ventral muscle scar suboval, bounded by strong, curved lateral ridges. _U.Sil.,_ cosmop.——Fig. 257,_4_. *_A. striata_ (Hall), Waldron, USA(Ind.); _4a-c,_ brach.v. view of conjoined valves, ped.v. int., incomplete brach.v. int., ×2 (871).

Dicoelostrophia Wang, 1955, p. 350 [*_D. punctatum,_ OD]. Like _Douvillina (Douvillina)_ but with resupinate, emarginate shell ornamented by branching costellae. _M.Dev.,_ China.——Fig. 258,_1_. *_D. punctata_; _1a,_ ped.v. ext., ×1.5; _1b,c,_ brach.v. int., ped.v. int., ×2 (852).

Douvillinaria Stainbrook, 1946, p. 24 [*_Stropheodonta variabilis_ Calvin, 1878, p. 727; OD]. Related to _Douvillina (Douvillina)_ but having resupinate shell reverting in adult forms to concavo-convex habit. _U. Dev.,_ N.Am.——Fig.

258,*4*. **D. variabilis* (Calvin), USA(Iowa); *4a,* brach.v. view of conjoined valves, ×2; *4b,* brach.v. int., ×2 (Williams, n).

Douvillinella Spriestersbach, 1925, p. 432 [**Strophеodonta filifer* Schmidt, 1912, p. 313; OD]. Like *Douvillina* (*Douvillina*) but resupinate. *M.Dev.-U.Dev.*, N.Hemis.

Moravostrophia Havlíček, 1962, p. 471 [**Stro-*

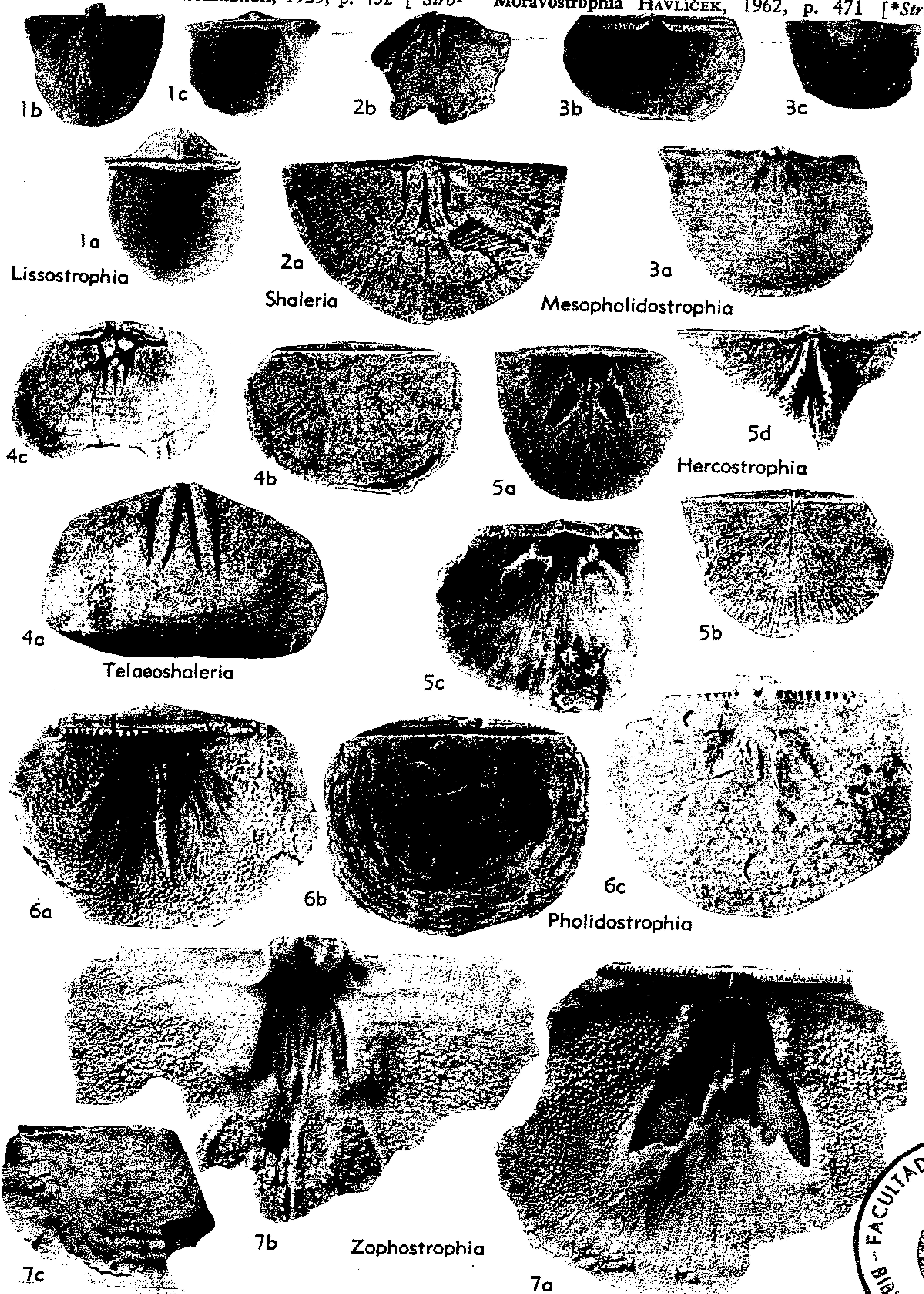


Fig. 259. Stropheodontidae (Pholidostrophiinae) *(1, 3, 6)*, (Shaleriinae) *(2, 4, 5, 7)* (p. *H*401-*H*403).

phomena interstrialis moravica Smyčka, 1897, p. 41; OD]. Like *Douvillina (Douvillina)* but with widely spaced accentuated parvicostellae, high subperipheral rim, and short, anteriorly located, median septum in brachial valve. *M.Dev.*, Czech.——Fig. 258,*3*. **M. moravica* (Smyčka); *3a*, brach.v. int., ×2; *3b*, ped.v. ext., ×2 (Havlíček, n).

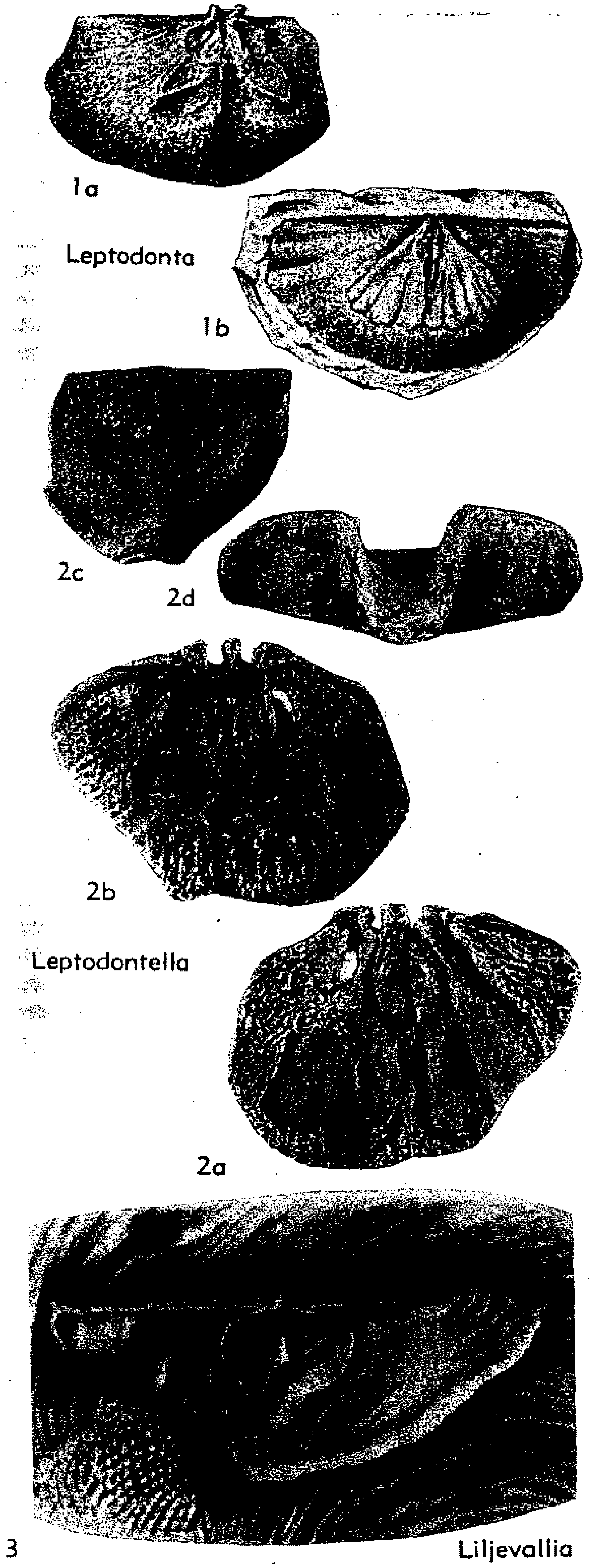


Fig. 260. Stropheodontidae (Leptodontellinae) *(1-2)*, (Liljevalliinae) *(3)* (p. *H*403).

Subfamily PHOLIDOSTROPHIINAE Stainbrook, 1943

[Pholidostrophiinae Stainbrook, 1943, p. 44]

Unattached, concavo-convex, lacking any surface ornamentation except growth lines. Ventral muscle scar elongately oval; socket ridges initially small, lost in later stocks, dorsal adductor scars impressed on floor of brachial valve. *U.Sil.-M.Dev.*

Pholidostrophia Hall & Clarke, 1892, p. 287 [**Strophomena nacrea* Hall, 1857, p. 144; OD]. Shell composed of thin lamellae of calcite giving nacreous sheen. *U.Sil.-M.Dev.*, N.Hemis.

P. (Pholidostrophia). Complete pseudodeltidium, no chilidium; socket ridges absent. *L.Dev.-M.Dev.*, N.Hemis.——Fig. 259,*6*. *P. (P.)* sp. aff. **P. (P.) nacrea* (Hall), M.Dev.(Hamilton), USA(N.Y.); *6a*, ped.v. int., ×2; *6b*, brach.v. view of conjoined valves, ×2; *6c*, brach.v. int., ×3 (871).

P. (Mesopholidostrophia) Williams, 1950, p. 278 [**P. (Mesopholidostrophia) nitens;* OD]. Pseudodeltidium incompletely developed, chilidium becoming degenerate, socket ridges abbreviated. *U.Sil.*, Eu.——Fig. 259,*3*. **P. (M.) nitens*, Gotl.; *3a,b*, brach.v. and ped.v. int., ×3; *3c*, ped.v. ext., ×2 (871).

Lissostrophia Amsden, 1949, p. 202 [**L. cooperi;* OD]. Like *Pholidostrophia* but with secondary layer of shell composed of fibrous calcite. *L.Sil.-L.Dev.*, N.Hemis.

L. (Lissostrophia). Complete pseudodeltidium; chilidium and socket ridges absent. *U.Sil.-L.Dev.*, N.Hemis.——Fig. 259,*1*. **L. (L.) cooperi*, U.Sil.(Henryhouse), USA(Okla.); *1a*, brach.v. view of conjoined valves, ×3; *1b,c*, brach.v. and ped.v. int., ×3 (871).

L. (Mesolissostrophia) Williams, 1950, p. 280 [**L. (Mesolissostrophia) pellucida;* OD]. Pseudodeltidium incompletely developed; chilidium and socket ridges becoming vestigial. *U.Sil.*, N.Hemis.

Subfamily SHALERIINAE Williams, n. subfam.

Unattached, concavo-convex to biplanate, with parvicostellate radial ornamentation, concentric rugae rare. Ventral muscle field including pair of long narrow, subparallel to divergent diductor scars, each bounded by more or less continuous ridges, rarely meeting above floor of valve to form narrow ring; dorsal adductor scars impressed posteriorly to 3 or 4 narrow ridges. *L.Sil.-Dev.*

Shaleria Caster, 1939, p. 33 [**Strophomena gilpini* Dawson, 1881, p. 341; OD] [=*Mclearnites*

Caster, 1945, *pro Mclearnia* Caster, 1939, p. 34 (type, *Brachyprion mertoni* McLearn, 1924, p. 61) (*non McLearnites* Crickmay, 1930)]. Concavo-convex, unequally parvicostellate. Ventral muscle scar bounded by pair of high lateral ridges and divided by bifurcated median ridge; socket ridges small, applied to sides of cardinal process lobes in late forms, dorsal adductor scar borne on 4 parallel ridges. *L.Sil-M.Dev.*, N.Hemis.

S. (Shaleria). Pseudodeltidium progressively developed but incomplete, chilidium progressively obsolescent; ventral muscle scar bounded by parallel lateral ridges and divided by median ridge which bifurcates at anterior end. *L.Sil.-L.Dev.*, N.Hemis.——Fig. 259,*2*. **S. (S.) gilpini* (Dawson), U.Sil., N.Scot.; *2a*, ped.v. int. mold, ×2; *2b*, plasticene cast of brach.v. int., ×2 (871).

S. (Telaeoshaleria) Williams, 1950, p. 281 [**S. (Telaeoshaleria) sulcata;* OD]. Pseudodeltidium entire, folded medianly, chilidium vestigial. Ventral muscle scar divided into 2 narrow, divergent parts by median ridge which bifurcates anteriorly; in brachial valve outer pair of ridges obsolescent, inner pair fused posteriorly, short median ridge anterior of dorsal adductor scars. *M.Dev.*, Eu.——Fig. 259,*4*. **S. (T.) sulcata*, Ger.(Eifel); *4a*, ped.v. int. mold, ×2; *4b*, brach.v., view of conjoined valves, ×2; *4c*, brach.v. int. mold, × 1.5 (871).

Hercostrophia Williams, 1950, p. 277 [**H. alpenensis*; OD]. Differs from *Shaleria (Telaeoshaleria)* especially in encirclement of divergent diductor scars by pair of rings formed by apices of bounding ridges, vestigial widely divergent socket ridges and persistence of outer pairs of divergent ridges in brachial valve. *M.Dev.*, N.-Am.——Fig. 259,*5a,b*. **H. alpenensis*, USA-(Mich.); *5a*, ped.v. int., ×2; *5b*, brach.v. view of conjoined valves, ×2 (871).——Fig. 259,*5c,d*. *H.* sp., USA(N.Y.); *5c,d*, ped.v. and brach.v. int., ×2 (871).

Zophostrophia Veevers, 1959, p. 63 [**Z. ungamica;* OD]. Like *Shaleria (Telaeoshaleria)* but dorsally geniculate, equally parvicostellate and weakly concentrically rugate externally. Ventral diductor scars strongly divergent, median adductor scar on raised platform. *U.Dev.*, W.Australia.——Fig. 259,*7*. **Z. ungamica; 7a,b*, ped.v. and brach.v. int., ×3.5; *7c*, ped.v. view of conjoined valves, ×1 (838).

Subfamily LEPTODONTELLINAE Williams, n. subfam.

Concavo-convex or resupinate, with unequally parvicostellate radial ornamentation. Ventral muscle scar triangular; socket ridges short, flanking cardinal process lobes; dorsal adductor scars bounded laterally by strong, raised ridges and impressed posterior to high median septum and curved or deflected brachial ridges defining slightly elevated areas. *L.Dev.-M.Dev.*

Leptodontella Khalfin, 1948, p. 253 [**Leptaena caudata* Schnur, 1854, p. 224; OD] [=*Glossostrophia* Williams, 1950, p. 282 (obj.) (type, *Leptaena caudata*); *Altaestrophia* Bublichenko, 1956 (type, *Leptodontella acuta* Khalfin, 1948)]. Resupinate by sharp, ventrally directed geniculation, with narrow median zone of trail projecting beyond profile of brachial valve like tongue. Dorsal median septum ending anteriorly in raised boss, brachial ridges curved. *L.Dev.-M.Dev.*, Eurasia.——Fig. 260,*2*. **L. caudata* (Schnur); *2a,b*, ped.v. and brach.v. int. molds, ×1.5; *2c*, brach.v. view of conjoined valves, ×1; *2d*, ant. view of conjoined valves, ×1.5 (871).

Leptodonta Khalfin, 1955, p. 237 [*pro Oehlertia* Khalfin, 1948 (*non* Perner, 1907)] [**Leptaena? leblanci* Rouault, 1851, p. 393; OD]. Like *Leptodontella* but concavo-convex and with sharply deflected brachial ridges. *M.Dev.*, Eurasia.——Fig. 260,*1*. **L. leblanci* (Rouault), Fr.; *1a*, brach.v. int., ×2; *1b*, ped.v. int. mold, ×1 (610).

Parastrophonella Bublichenko, 1956, p. 93 [**Strophomea anaglypha* Kayser, 1871, p. 628; OD]. Like *Leptodontella* but without dorsally projecting tongue. *M.Dev.*, Eurasia.

Subfamily LILJEVALLIINAE Williams, 1953

[*nom. correct.* Williams, herein (*pro* Liljevallinae Williams, 1953, p. 9)]

Attached to foreign body throughout ontogeny by cementation of pedicle valve. *M. Sil.*

Liljevallia Hedström, 1917, p. 9 [**L. gotlandica;* OD]. Pseudodeltidium arched, incompletely developed, ventral process low; hinge line denticulate for less than half of its length. Dental plates absent; ventral muscle scar subcircular, enclosed by bounding ridges except anteriorly; brachial valve unknown but cardinal process lobes inferred to be disjunct from position of accommodating holes drilled into ventral interarea. *M.Sil.*, Sweden.——Fig. 260,*3*. **L. gotlandica;* ped.v. int., ×2 (419).

Superfamily DAVIDSONIACEA King, 1850

[*nom. transl.* Williams, herein (*ex* Davidsoniinae King, 1850, p. 81)]

Functional pedicle present only in earliest known species; pedicle valve usually modified and cemented by umbo or greater part of shell surface to substratum, brachial valve invariably convex in young growth stages; pseudodeltidium commonly forming complete cover to delthyrium, chilidium well developed to obsolescent; cardinal process bilobed, in many forms greatly extended ventrally, ankylosed with variably disposed socket plates; lophophore probably spirolophous in all stocks, rarely impressed or supported by spirally coiled calcareous ribbons; mantle canal systems poorly known, probably saccate to lemniscate in both valves; shell substance commonly pseudopunctate but impunctate in older stocks. *M.Ord.-Trias.*

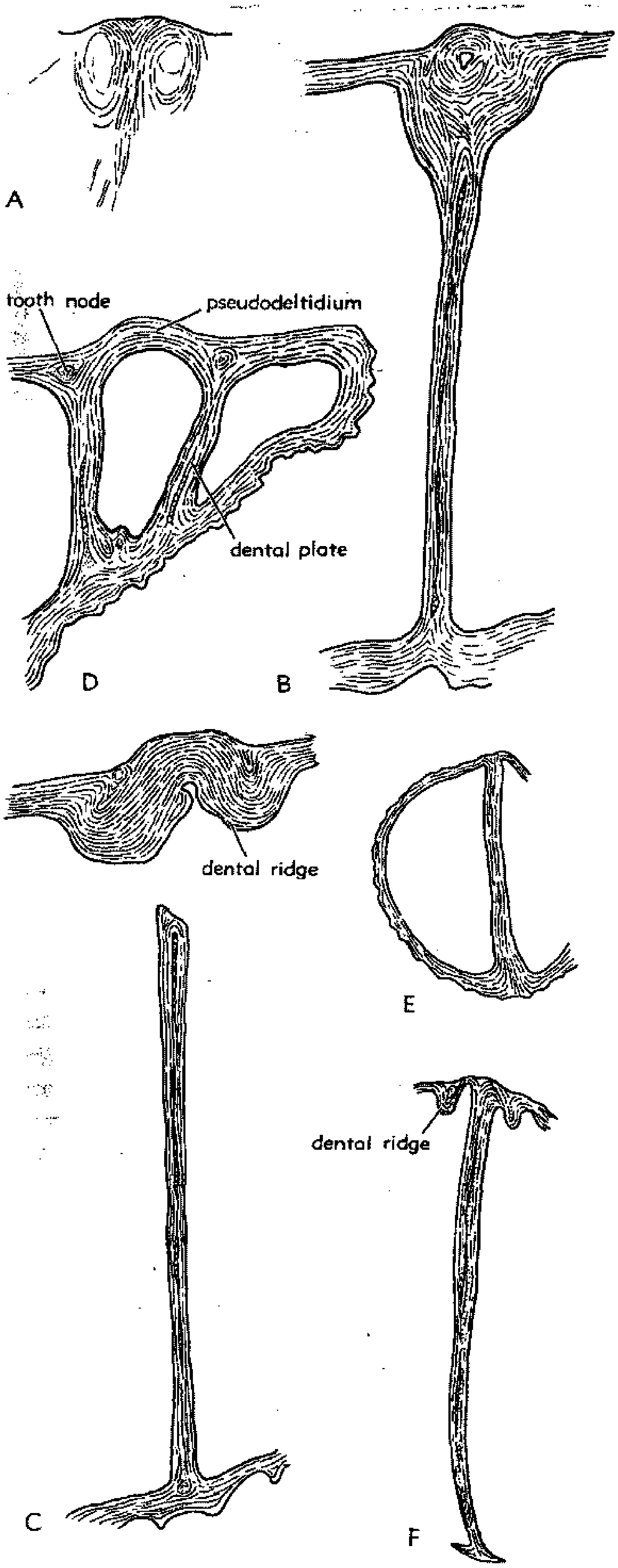


Fig. 261. Sections through the umbonal regions of davidsoniacean pedicle valve; *A-C*, *Orthotetes radiata* (Fischer), M.Carb.(C_2^{pd}), USSR, ×7; *D*, *Meekella* sp., Penn. (La Salle Ls.), USA, ×7; *E-F*, *Derbyia* sp. cf. *D. cymbula* Hall & Clarke, Perm., USA(Tex.), ×4.

Although the davidsoniaceans constitute a homogeneous group of brachiopods which is immediately distinguishable from other Strophomenida, they have never been satisfactorily classified. Many attempts have been made (Dunbar & Condra, 1932, 270; Williams, 1953, 872; Stehli, 1954, 773; and Thomas, 1958, 802) to arrange the increasing number of genera assigned to the superfamily into subordinate taxonomic groups that reflect the course of evolution and at the same time provide a workable basis for ready generic identification. All of them have been unsuccessful, owing mainly to persistent misinterpretation of the ventral interior of *Orthotetes* Fischer de Waldheim, the first davidsoniacean genus to be recognized. The specimens on which the type-species, *O. radiata*, was founded, were lost during the last century and, until recently, systematists have had to rely exclusively on an original illustration of a partially weathered pedicle valve to ascertain the main ventral features. This showed a tiny cavity, immediately anterior of the pseudodeltidium and contained by the teeth and the median septum apparently fused into a single unit, which has always been taken to be a spondylium. Accordingly, *Orthotetes* has been classified with davidsoniaceans possessing strongly developed dental plates which may or may not join just above the floor of the valve (Fig. 261). True dental plates, however, invariably formed the lateral boundaries of the ventral muscle field even when they converged high above the valve floor, as in *Ombonia*, whereas the ventral muscle scars of *Orthotetes* are impressed on the valve floor on either side of the median septum. The subpseudodeltidial cavity of *Orthotetes* is therefore in no way homologous with the spondylium of the meekellids, because it is formed not by the median fusion of dental plates but by secondary shell joining the median septum with a pair of ridges representing the anterior edges of unsupported teeth (Fig. 261). In this respect *Orthotetes* is much more like *Derbyia*, a fact recorded by SOKOLSKAYA in 1954 (755), although unfortunately ignored by her in the classification of the davidsoniaceans which she gave for the Russian Treatise (1960). Through the kindness of Dr. SOKOLSKAYA it has been possible to obtain specimens of *Orthotetes*, believed to be conspecific with *O. radiata*, and these have been used for sectioning. Comparisons of thin sections of *Orthotetes*, *Derbyia*, and *Meekella* show the fundamental difference between the dental ridges of the first two and the long dental plates of the last. These differences have furnished the basis for the classification given below.

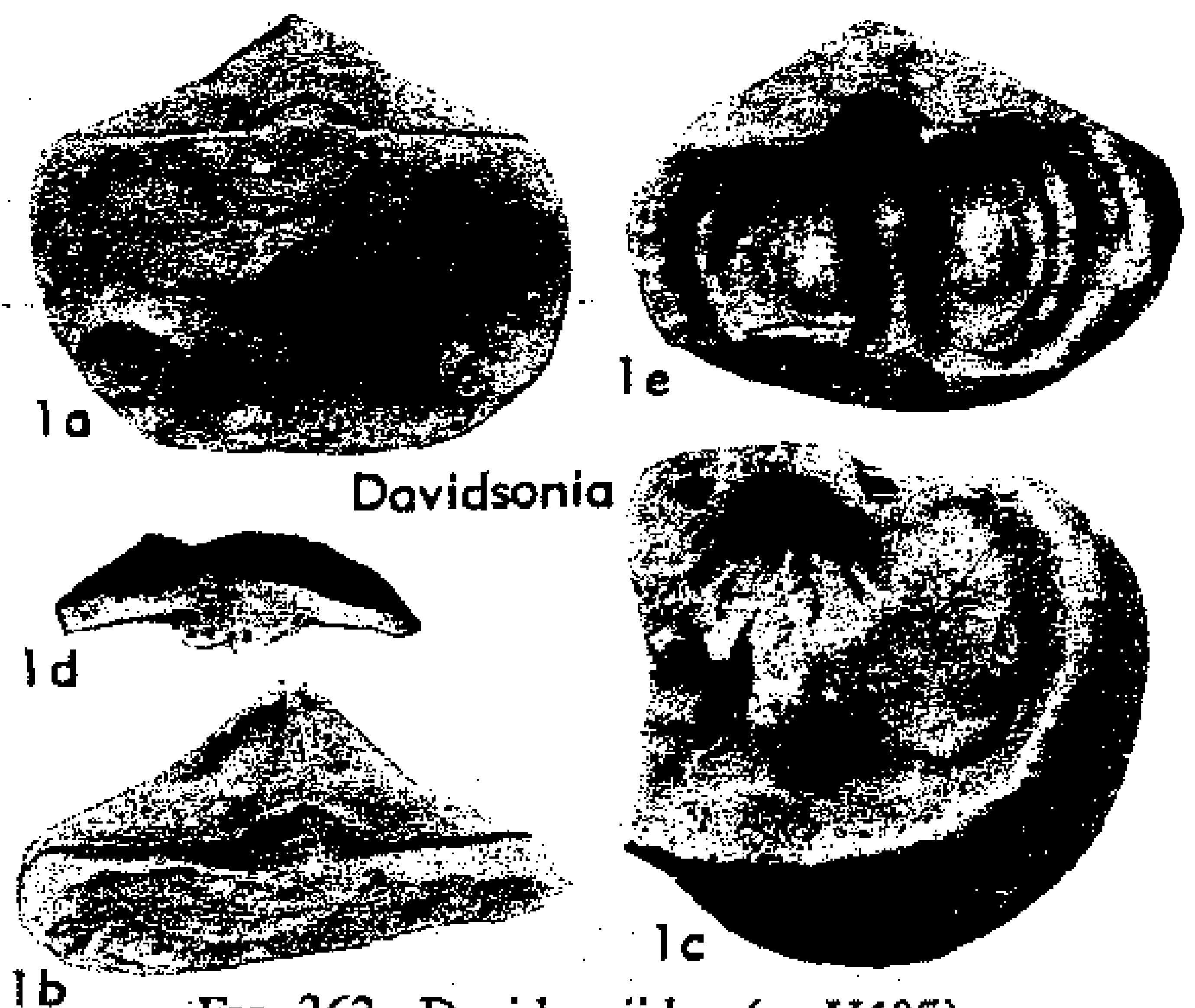


FIG. 262. Davidsoniidae (p. *H*405).

Family DAVIDSONIIDAE King, 1850

[*nom. correct.* WILLIAMS, herein (*pro* Davidsonidae KING, 1850, p. 81)]

Pseudodeltidium and chilidium well developed; teeth unsupported, ventral muscle scar small, suboval, restricted laterally and anteriorly by low ridges; socket plates recurved, united with dorsal posterior margin and with low cardinal process lobes that join anteriorly to form low median ridge; quadripartite dorsal adductor scars small, subcircular, divided by low median ridge; both valves with impressions of pair of brachia spirally coiled into about 6 convolutions forming 2 very low cones with apices directed dorsally; shell substance pseudopunctate. *L.Dev.-M.Dev.*

Davidsonia BOUCHARD, 1849, p. 92 [**D. verneuili*; OD]. Brachial valve convex, pedicle valve irregular, cemented to substratum by most of external surface throughout life; radial ornamentation lacking. *M.Dev.*, Eu.——FIG. 262,*1*. **D. verneuili*, Ger.; *1a,b*, brach.v., post. views of conjoined valves, ×1.5; *1c,d*, brach.v. int., post., ×1.5; *1e*, ped.v. int., ×1.5 (Cooper, n).

Biconostrophia HAVLÍČEK, 1956, p. 562 [**B. spirifera;* OD]. Like *Davidsonia* but with flat or slightly concave pedicle valve not attached to substratum except in very early growth stages and with coarsely costate radial ornamentation. *L.Dev.*, Eu.(Czech.).

Prodavidsonia HAVLÍČEK, 1956, p. 564 [**P. dalejensis;* OD]. Unattached, like *Biconostrophia* but with convex pedicle valve and without radial ornamentation as in *Davidsonia. M.Dev.*, Eu. (Czech.).

Family MEEKELLIDAE Stehli, 1954

[*nom. transl.* WILLIAMS, herein (*ex* Meekellinae STEHLI, 1954, p. 303)]

Teeth in pedicle valve supported by variably disposed dental plates; ventral muscle field subcircular to elongately oval, with flabellate diductor and posteromedian lanceolate adductor scars impressed either on floor of valve between dental plates or to varying degree on dental plates in their convergence toward spondylium; chilidium well developed to obsolescent. *M.Ord.-Perm.*

Subfamily MEEKELLINAE Stehli, 1954

[Meekellinae STEHLI, 1954, p. 303] [=Omboniinae SOKOLSKAYA, 1960, p. 218]

Cemented by ventral umbo, with socket plates ankylosed to cardinal process lobes and prolonged anterolaterally as pair of widely divergent supporting plates arising from floor of brachial valve, enclosing posteriorly dorsal adductor field; shell substance pseudopunctate. *Dev.-Perm.*

Meekella WHITE & ST. JOHN, 1867, p. 120 [**Plicatula striatocostata* Cox in OWEN, 1857, p. 568; OD]. Unequally biconvex, with deeply conical pedicle valve, finely costellate and radially plicate; dorsal interarea linear, chilidium vestigial; dental plates long, subparallel; cardinal process high. *Carb.-Perm.*, cosmop.——FIG. 263,*4*. *M. attenuata* (GIRTY), Perm.(Leonard.), USA(Tex.); *4a*, brach.v. view of conjoined valves; *4b,c*, ped.v. int., brach.v. int., all ×1.5 (Williams, n).

Geyerella SCHELLWIEN, 1899, p. 4 [**G. gemmellaroi;* OD] [=*Turriculum* DE GREGORIO, 1930, p. 26 (type, *T. imperans*)]. Like *Meekella* but with dental plates converging and coalescing toward middle of pedicle valve as narrow spondylium supported by median septum. *U.Carb.-Perm.*, cosmop. ——FIG. 263,*1*. *G.* sp., Perm., N.Am.; lat. view of conjoined valves, ×1.5 (Williams, n).

Ombonia CANEVA, 1906, p. 54 [**O. dieneri* LIKHAREV, 1932, p. 30; SD LIKHAREV, 1932, p. 26]. Like *Geyerella* but finely costellate and without radial plicae. *Perm.*, N.Hemis.——FIG. 263,*3*. *O.* sp., Perm.(Lamar), USA(N.Mex.); *3a,b*, 2 views of ped.v. int., ×2 (Williams, n).

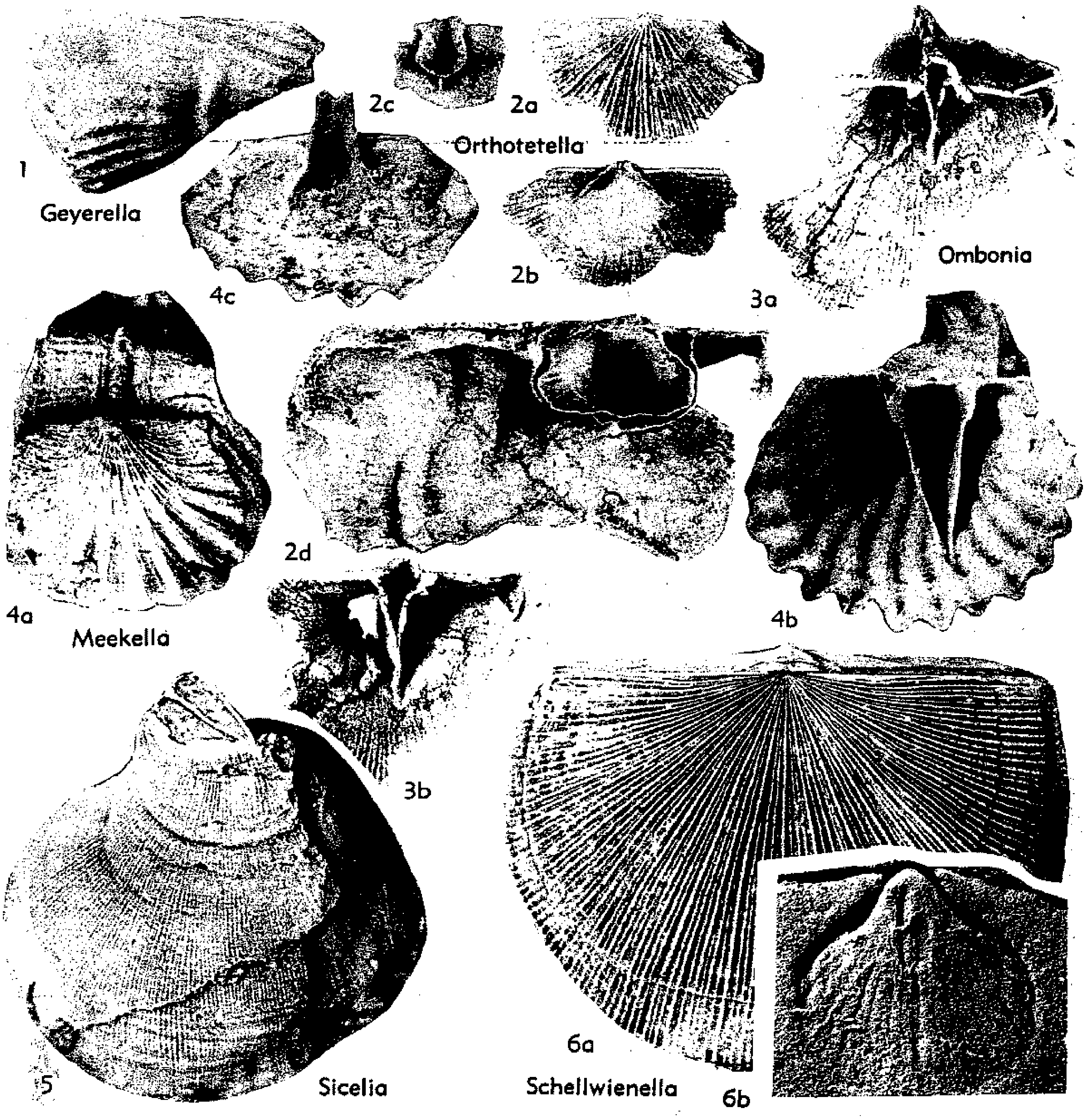


FIG. 263. Meekellidae (Meekellinae) (p. *H*405-*H*407).

Orthotetella R. E. King, 1931, p. 51 [*O. wolfcampensis; OD]. Biconvex to plano-convex, costellate; dorsal interarea and chilidium vestigial; dental plates strongly convergent to form deep conical spondylium supported posteriorly by short median septum; cardinal process low. *L. Perm.*, USA.——Fig. 263,*2*. *O. wolfcampensis; USA (Tex.); *2a,b*, brach.v. ext., int., ×1; *2c,d*, fragments of ped.v. ints., ×1 (773).

Orthothetina Schellwien, 1900, p. 8 [*Orthotetes persicus (Schellwien); SD Schuchert & LeVene, 1929, p. 91] [=*Hamletella* Hyasaka, 1953, p. 92 (type, *Streptorhynchus altus Hamlet, 1928)]. Like *Meekella* but without radial plicae. *Carb.-Perm.*, cosmop.

Perigeyerella Wang, 1955, p. 346 [*P. costellata; OD]. Biconvex, with conical pedicle valve, finely costellate, dorsal interarea and chilidium vestigial; dental plates becoming less convergent with growth so that spondylium with supporting median septum is characteristic of young pedicle valve and sessile spondylium or discrete dental plates typical of adult valves. *U.Perm.*, China.——Fig. 264,*1*. *P. costellata; *1a*, brach.v. view of conjoined valves, ×1; *1b-d*, serial secs. at intervals indicated on *1a*, ×2 (852).

Pseudoderbyia Likharev, 1934, p. 213 [*P. netschajewi; OD]. Costellate, ventral interior with sessile spondylium like that of *Sicelia*, containing independently developed short, median ridge; dorsal interior unknown. *L.Perm.*, USSR.

Schellwienella I. Thomas, 1910, p. 92 [*Spirifera crenistria Phillips, 1836, pl. 9, fig. 6; OD]. Biconvex to resupinate, pedicle valve commonly

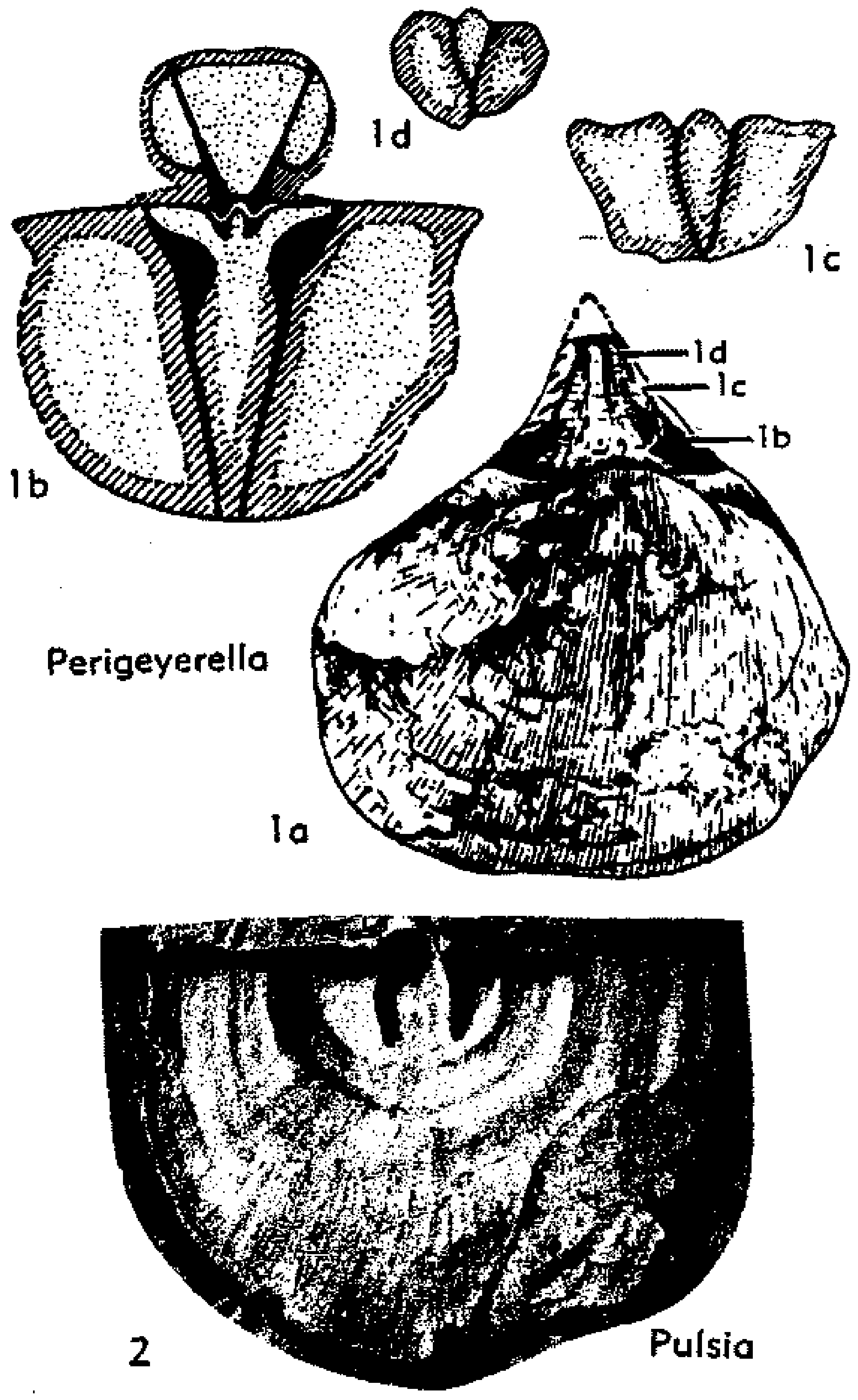


FIG. 264. Meekellidae (Meekellinae) (p. *H*406-*H*407).

less convex than brachial valve and distorted umbonally due to cementation; costellate; pseudodeltidium well developed, chilidium obsolescent; dental plates short, reaching to floor of pedicle valve; cardinal process low with discrete lobes. *Dev.-Carb.*, cosmop.

S. (Schellwienella) [=*Carlopsina* REED, 1954, p. 183 (type, *Spirifera radialis* PHILLIPS, 1836)]. Dental plates divergent. *Dev.-Carb.*, cosmop.——FIG. 263,6. *S. (S.)* sp. cf. *S. (S.) aspis* (SMYTHE), L.Carb., G.Brit.; *6a*, brach.v. view of complete shell, ×1.5; *6b*, mold of posteromedian region of ped.v. int., ×1.5 (Williams, n).

S. (Pulsia) IVANOV, 1925, p. 113 [**P. mosquensis;* OD]. Dental plates, subparallel, *Carb.*, USSR.——FIG. 264,2. **S. (P.) mosquensis,* U.Carb., ped.v. int., ×0.5 (755).

Sicelia GORTANI & MERLA, 1934, p. 284 [*pro Canavaria* MERLA, 1928 (*non* OPPENHEIM, 1899; *nec* GEMMELLARO, 1866)] [**Canavaria acropedion* MERLA, 1928, p. 70; OD] [=*Gemmellaria* FABIANI & RUIZ, 1933 (*non* MUNIER-CHALMAS, 1873)]. Unequally biconvex, with deep, distorted pedicle valve, finely costellate; dorsal interarea and chilidium vestigial; dental plates long, convergent, uniting with floor of pedicle valve to form elongately oval spondylium. *Perm.*, Eurasia.——FIG. 263,5. **S. acropedion* (MERLA), Perm.(Sosio), Italy; ped.v. ext. showing dental plates in partly dissected post. portion, ×2 (Williams, n).

Subfamily FARDENIINAE Williams, n. subfam.

Uncemented, rarely with functional pedicle in adult shells; socket plates short, divergent, cardinal process lobes low, discrete; pseudodeltidium and chilidium variably developed; shell substance impunctate. *M.Ord.-U.Sil.*

Fardenia LAMONT, 1935, p. 310 [**F. scotica;* OD] [=*Coolinia* BANCROFT, 1949, p. 7 (type, **Orthis? applanata* SALTER, 1846, p. 72); *Saughina* BANCROFT, 1949, p. 7 (type, *Strophomena pertinax* REED, 1917, p. 907); *Chilidiopsis* BOUCOT, 1959 (type, *Fardenia reedsi* AMSDEN, 1951, p. 84)]. Subequally biconvex to resupinate, costellate; pseudodeltidium variably developed, pedicle foramen rarely persistent in adult shells; dorsal interarea short, chilidium varying even in type-species from complete convex cover to one extending beyond apical areas only as lateral partitions flanking cardinal process lobes; dental plates and socket plates short, divergent. *M.Ord.-U.Sil.*,

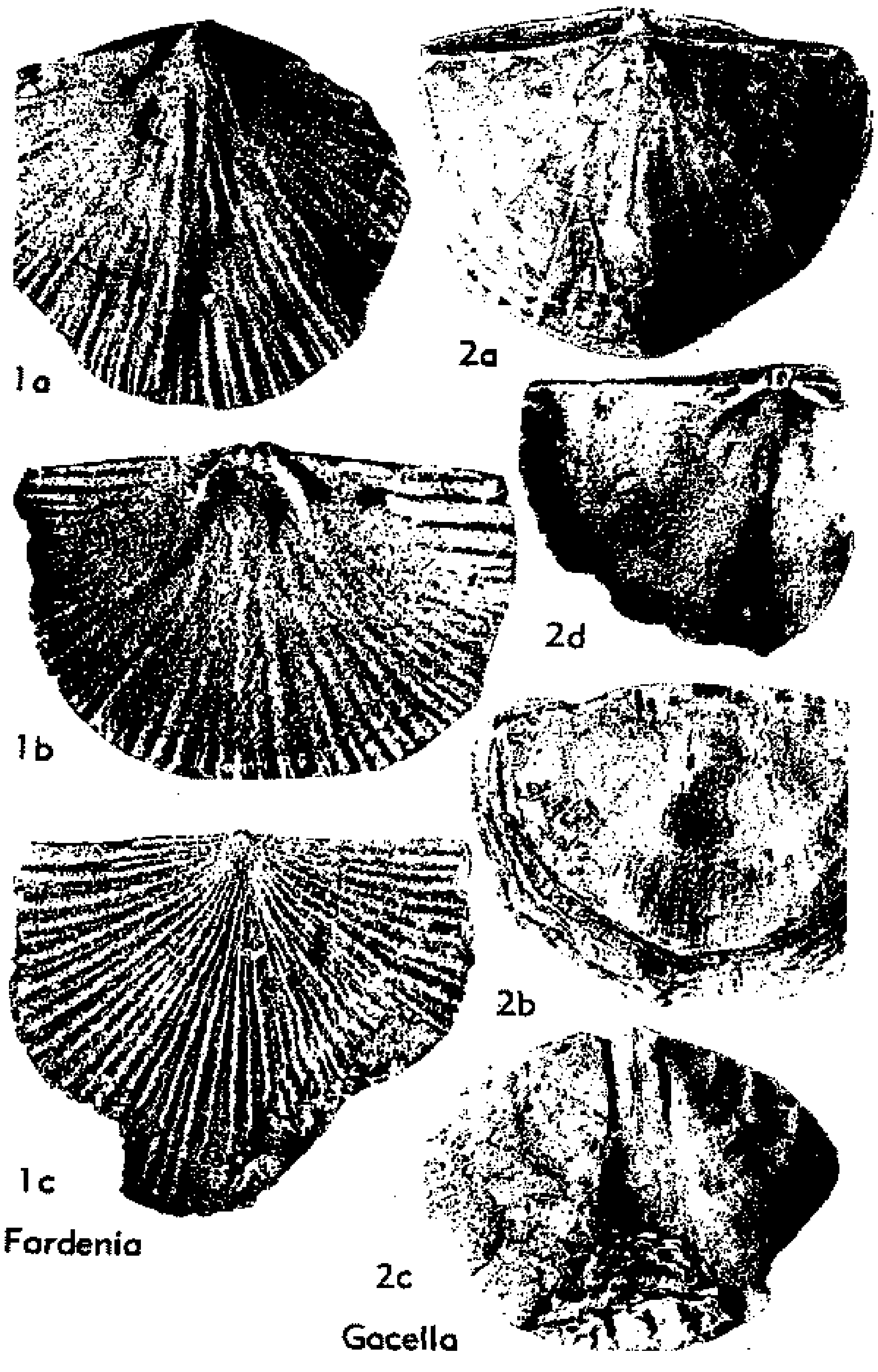


FIG. 265. Meekellidae (Fardeniinae) (p. *H*407-*H*408).

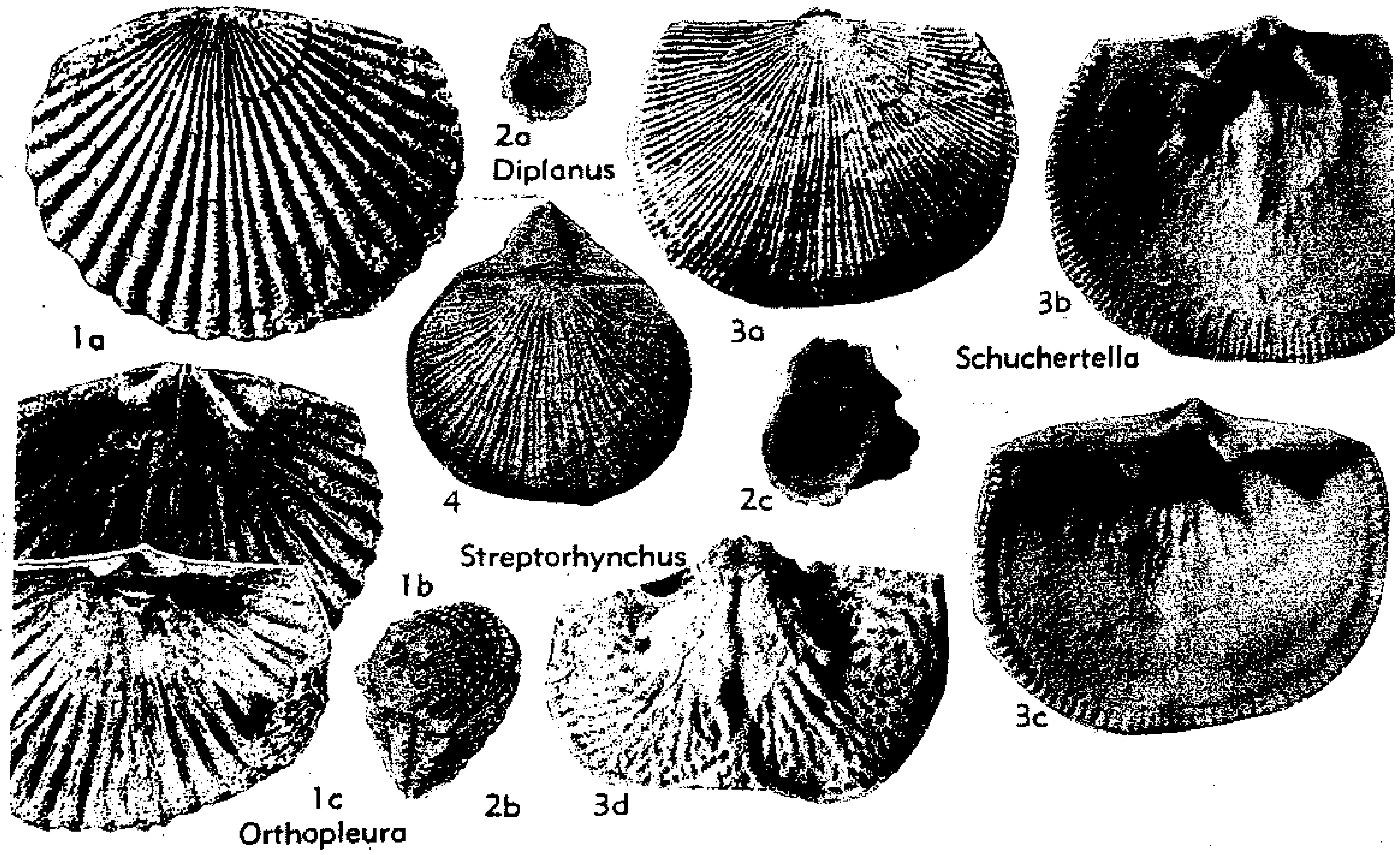


Fig. 266. Schuchertellidae (Schuchertellinae) *(1-3)*, (Streptorhynchinae) *(4)* (p. *H*408-*H*409).

cosmop.——Fig. 265,*1*. **F. scotica*; U.Ord.(Ashgill.), Scot.; *1a,* ped.v. int. mold, ×2.25; *1b,* brach.v. int., ×3.6; *1c,* brach.v. ext., ×2.7 (Williams, n).

Gacella Williams, 1962, p. 222 [**G. insolita;* OD]. Biconvex, with strong dorsal median fold, unequally parvicostellate, pseudodeltidium and chilidium well developed, pedicle foramen open throughout life; dental plates long, subparallel; ventral muscle field with narrow diductor and lanceolate adductor scars; socket plates widely divergent, subparallel with hinge line. *M.Ord.*, Scot.-SE.USA.——Fig. 265,*2*. **G. insolita,* Scot.; *2a,b,* brach.v., ped.v. views of conjoined valves, ×2.25; *2c,* ped.v. int. mold, ×2.25; *2d,* brach.v. int., ×2.25 (Williams, n).

Family SCHUCHERTELLIDAE Williams, 1953

[*nom. transl.* Stehli, 1954 (*ex* Schuchertellinae Williams, 1953, p. 9)]

Cemented by ventral umbo and with pair of unsupported teeth in pedicle valve; ventral muscle field subcircular to elongately oval with large flabellate diductor scars and more posteriorly located elongately oval adductor scars impressed on floor of pedicle valve; chilidium well developed to obsolescent. *Dev.-Perm.*

Subfamily SCHUCHERTELLINAE Williams, 1953

[Schuchertellinae Williams, 1953, p. 9]

Socket plates recurved, ankylosed to cardinal process lobes and dorsal posterior margin; dorsal adductor field variably impressed. *Dev.-Perm.*

Schuchertella Girty, 1904, p. 734 [**Streptorhynchus lens* White, 1862, p. 28; OD]. Plano-convex to biconvex, costellate, with costellae added by intercalation during shell growth; dorsal interarea linear; cardinal process lobes low, not united posteromedianly; median ridge dividing dorsal adductor field variably developed; shell substance impunctate. *L.Dev.-Perm.*, cosmop.——Fig. 266,*3*. *Schuchertella* sp. cf. *S. parva* (Hall), U.Dev.(Hackberry), USA(Iowa); *3a-c,* brach.v. ext., int., ped.v. int., ×1.5; *3d,* ped.v. int. mold, ×3 (Williams, n).

Diplanus Stehli, 1954, p. 229 [**Streptorhynchus lamellatum* R. E. King, 1930, p. 49; OD]. Like *Schuchertella* but with small, developed dorsal interarea and costate radial ornamentation interrupted by strong, irregular imbrication; shell substance pseudopunctate. *L.Perm.*, USA.——Fig. 266,*2*. **D. lamellatum* (King); *2a,* brach.v. int.; *2b,* sublat. view of complete shell; *2c,* ped.v. int., all ×1 (773).

Orthopleura Imbrie, 1959, p. 391 [**O. rhipis*; OD]. Like *Schuchertella* but biconvex with deeper pedicle valve, radial ornamentation costate, shell substance pseudopunctate. *M.Dev.*, N.Am.——Fig. 266,*1*. **O. rhipis,* M.Dev.(Onesquethaw-Taghanic), USA(Mich.); *1a-c,* brach.v. ext., int., ped.v. int., ×3 (445).

Schuchertellopsis Maillieux, 1939, p. 3 [**S. durbutensis;* OD]. Small, like *Schuchertella* but with pedicle valve completely cemented to foreign body throughout life. *U.Dev.*, Eu.

Subfamily STREPTORHYNCHINAE Stehli, 1954

[Streptorhynchinae STEHLI, 1954, p. 299]

Socket plates ankylosed to cardinal process lobes and prolonged anterolaterally as pair of widely divergent plates arising from floor of brachial valve and enclosing posteriorly dorsal adductor field; shell substance pseudopunctate. *Carb.-Perm.*

Streptorhynchus KING, 1850, p. 107 [**Terebratulites pelargonatus* VON SCHLOTHEIM, 1816, p. 28; OD] [=*Lepsius* DE GREGORIO, 1930, p. 24 (type, *L. favoritus*); *Mammosum* DE GREGORIO, 1930, p.25 (type, *M. ipsium*)]. Unequally biconvex, with conical pedicle valve, costellate, with variable texture; cardinal process lobes high, not united posteromedianly above low median ridge; chilidium vestigial. *Carb.-Perm.*, cosmop.——FIG. 266,*4*. **S. pelargonatus* (VON SCHLOTHEIM), Perm.(Zechstein), Ger.; brach.v. view of conjoined valves, ×2 (802).——FIG. 267,*1*. *S.* sp. cf. *pelargonatus* (SCHLOTHEIM), U.Perm. (Liveringa F.), W.Australia(Fitzroy Basin); incompl. brach.v. showing cardinal process, ant., ×2 (802).

?**Irboskites** BEKKER, 1924, p. 48 [**I. fixatus*; OD]. Brachial valve with dorsally deflected margin; pedicle valve irregularly convex, cemented to substratum by most of external surface throughout life, radial ornamentation lacking; teeth unsupported, ventral muscle field large, subcircular, commonly with raised adductor scars; cardinal process lobes high, socket plates divergent, arising from floor of brachial valve, dorsal median ridge strong and long, dividing deeply impressed subcircular dorsal adductor field. [The taxonomic position of this genus is uncertain but provisionally it is best accommodated within the Streptorhynchinae.] *M.Dev.*, USSR.——FIG. 267,*2*. **I. fixatus*, Est.; *2a*, ped.v. int., ×2; *2b*, brach.v. int., ×2; *2c*, ped.v. attached, ×1 (60).

Kiangsiella GRABAU & CHAO, 1927, p. 103 [*Orthotetes tingi* GRABAU, 1924, p. 359; OD]. Like *Streptorhynchus* but with strong secondary plications like coarse costae. *U.Carb.-Perm.*, cosmop. ——FIG. 267,*3*. *K. condoni* (THOMAS), Perm. (Artinsk.), Australia; brach.v. view of conjoined valves, ×1 (802).

Family ORTHOTETIDAE Waagen, 1884

[*nom. transl.* MCEWAN, 1939 (*ex* Orthotetinae WAAGEN, 1884, p. 576)]

Cemented by ventral umbo, with pair of unsupported teeth in pedicle valve; ventral muscle field subcircular to elongately oval, with larger flabellate diductor scars flanking lanceolate adductor scars and divided by variably developed median septum commonly continuous with inner surface of pseudodeltidium or less commonly ankylosed to short dental ridges forming anterior edges of teeth; shell substance pseudopunctate. *Carb.-Perm.*

Subfamily ORTHOTETINAE Waagen, 1884

[Orthotetinae WAAGEN, 1884, p. 576] [=Derbyoidinae THOMAS, 1958, p. 21]

Recurved socket plates ankylosed to cardinal process lobes and dorsal posterior margin; dorsal adductor field subcircular generally weakly impressed; dorsal interarea and chilidium mostly obsolescent. *Carb.-Perm.*

Orthotetes FISCHER DE WALDHEIM, 1829, p. 375 [**O. radiata* FISCHER DE WALDHEIM, 1850, p. 491; SD GIRTY, 1908, p. 186] [=*Werriea* CAMPBELL,

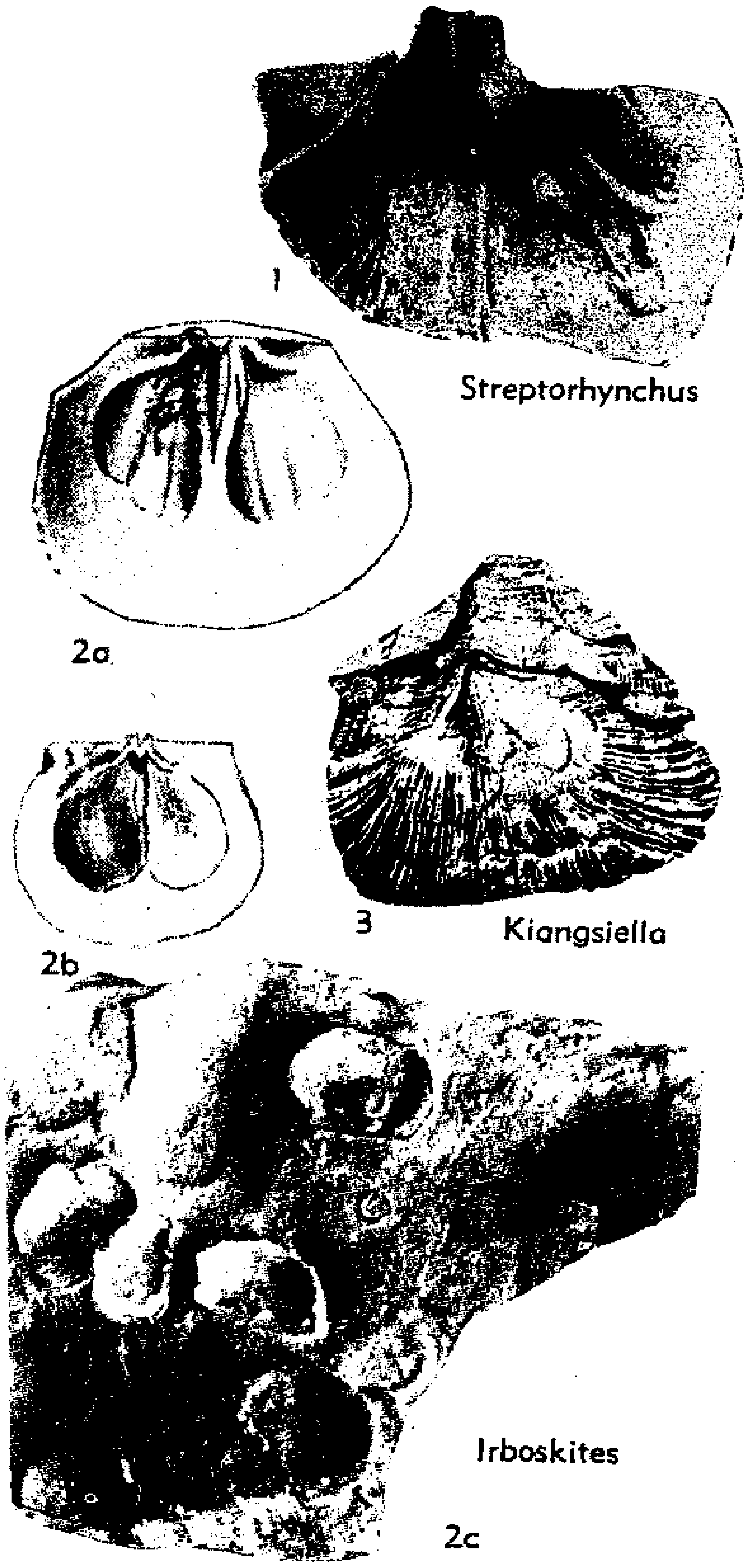


FIG. 267. Schuchertellidae (Streptorhynchinae) (p. *H*409).

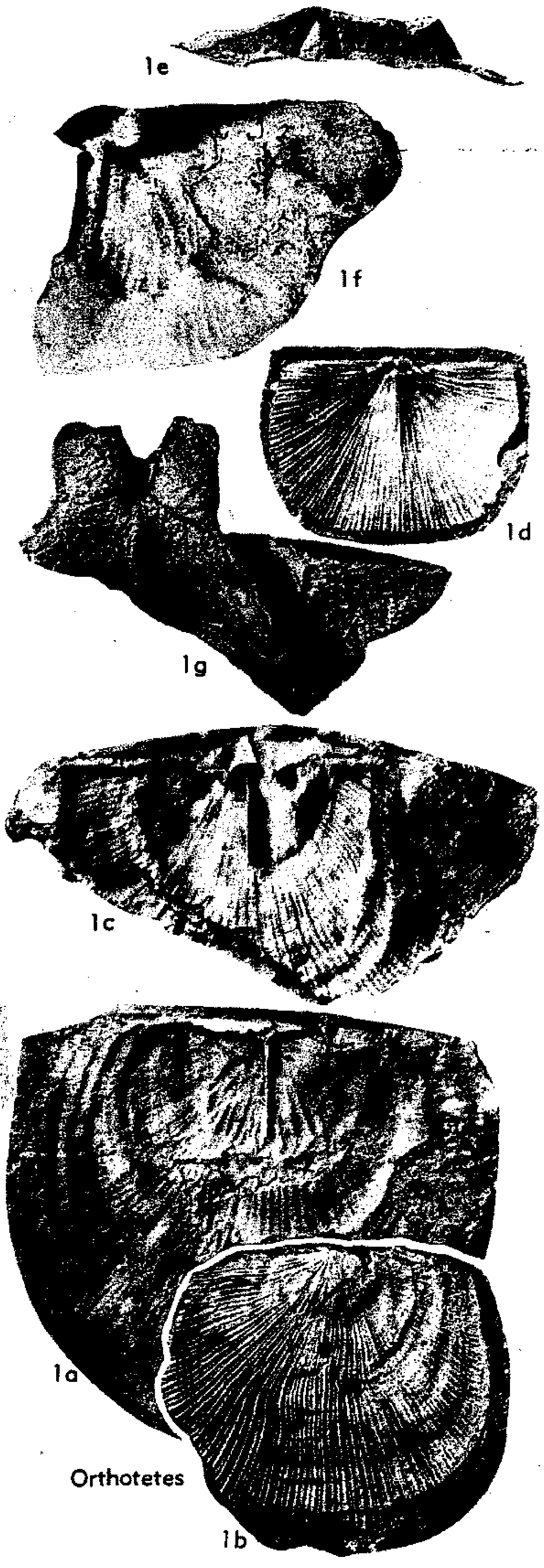


FIG. 268. Orthotetidae (Orthotetinae) (p. *H*409-*H*410).

1957, p. 44 (type, *W. australis*); *Permorthotetes* G. A. THOMAS, 1958, p. 82 (type, *P. callytharrensis*); *Pseudoorthotetes* SOKOLSKAYA, 1963, p. 96 (type, *P. borodencovensis*)]. Subequally biconvex to resupinate, finely costellate; dental ridges united by secondary shell substance to posterior edge of ventral median septum to define small delthyrial chamber commonly filled with secondary shell substance and less commonly extending anteromedianly for entire length of ventral interarea; cardinal process lobes fairly low, separate posteriorly but united into median ridge anteriorly. *M.Carb.-Perm.*, cosmop.——FIG. 268,*1a,b*. **O. radiata* (FISCHER DE WALDHEIM), M.Carb. (C_2^{pd}), USSR; *1a,b*, ped.v. int., ext., ×1 (755).——FIG. 268,*1c,d*. *O. plana* (IVANOV), U.Carb. (C_3^{ks}), USSR; *1c,d*, ped.v. int., brach.v. int., ×1 (755).——268,*1e-g*. *O. callytharrensis* (THOMAS), Perm., Aus.; *1e*, post. view of ped.v. int. mold, ×1; *1f*, ped.v. int., ×1; *1g*, post. view of detached cardinal process, ×2 (802).

Derbyoides DUNBAR & CONDRA, 1932, p. 114 [**D. nebrascensis;* OD]. Biconvex, with variable depth to pedicle valve; finely costellate; ventral median septum fused posteriorly with inner surface of pseudodeltidium; cardinal process lobes like those of *Orthotetes;* chilidum and dorsal interarea relatively well developed. *Penn.*, N.Am.——FIG. 269,*1*. **D. nebrascensis*, USA(Kans.-Neb.); *1a,b*, brach.v. int., ext., ×1; *1c*, vent. view of brach.v. cardinal region, ×1.5 (270).

Hipparionyx VANUXEM, 1842, p. 124 [**H. proximus* VANUXEM, 1842; SD HALL & CLARKE, 1892, p. 258]. Unequally biconvex, with gently convex pedicle valve, subcircular in outline, finely costellate; ventral muscle scar large with strong bounding ridges, median septum low, united umbonally with dental ridges; cardinal process lobes high, strongly divergent. *L.Dev.*, N.Am.——FIG. 269,*3*. **H. proximus* (VANUXEM), Oriskany; *3a*, brach.v. int., ×1; *3b*, ped.v. int. mold, ×1 (740).

Tapajotia DRESSER, 1954, p. 149 [**Streptorhynchus tapajotensis* DERBY, 1874, p. 37; OD]. Like *Derbyoides* but with weaker median septum in pedicle valve and with more strongly recurved socket plates parallel to dorsal hinge line and widely divergent cardinal process lobes. *U.Carb.-L.Perm.*, USSR-Brazil.——FIG. 269,*2*. **T. tapajotensis* (DERBY), U.Carb.(Penn.), Brazil; *2a*, brach.v. ext., ×1; *2b*, ped.v. int., ×1; *2c*, brach.v. int., ×2 (266).

Subfamily DERBYIINAE Stehli, 1954

[Derbyiinae STEHLI, 1954, p. 300]

Socket plates ankylosed to high cardinal process lobes and prolonged anterolaterally as pair of widely divergent supporting plates arising from floor of brachial valve and enclosing posteriorly dorsal adductor field; dorsal interarea and chilidium obsolescent. *Carb.-Perm.*

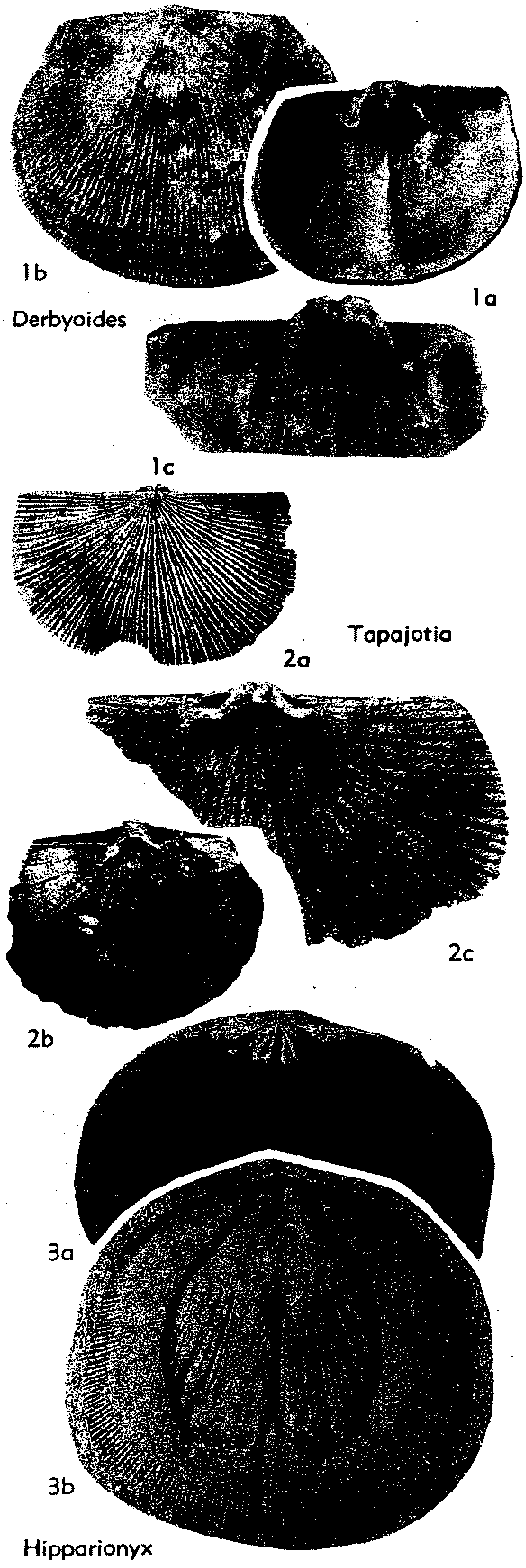


FIG. 269. Orthotetidae (Orthotetinae) (p. *H*410).

Derbyia WAAGEN, 1884, p. 576 [**P. regularis;* SD HALL & CLARKE, 1892, p. 262] [=*Derbyaeconcha* LIKHAREV, 1934, p. 507 (type, *Derbyia anomata* LIKHAREV, 1932, p. 20); *Grabauellina* LIKHAREV, 1934, p. 507 (type, *Derbyia mongolica* GRABAU, 1931, p. 259), *pro Derbyina* GRABAU, 1931 (*non* CLARKE, 1913)]. Biconvex, with variable depth of pedicle valve, finely costellate; ventral median septum strong, fused posteriorly with inner surface of pseudodeltidium; cardinal process lobes high, divergent posteriorly. *Carb.-Perm.*, cosmop.——FIG. 270,*1*. *D.* sp., Perm.(Leonard.), N.Am.(Tex.); *1a-c,* ped.v. int., brach.v. int., ext., ×1.5 (Williams, n).——FIG. 270,2. *D. cymbula* HALL & CLARKE, Perm., USA; post. view of conjoined valves, ×1.5 (Williams, n).

Licharewiella SOKOLSKAYA, 1960, p. 219 [**Derbya magnifica* LIKHAREV, 1939, p. 80; OD]. Like *Derbyia* but with median septum of pedicle valve continuous anteriorly with high transverse ridge. *L.Perm.*, USSR-Asia.

Plicatoderbya H. D. THOMAS, 1937, p. 14 [*Orthotetes magnus* BRANSON, 1930, p. 26; OD]. Like *Derbyia* but with shell additionally ornamented by broad radial plicae. *L.Perm.*, N.Am.

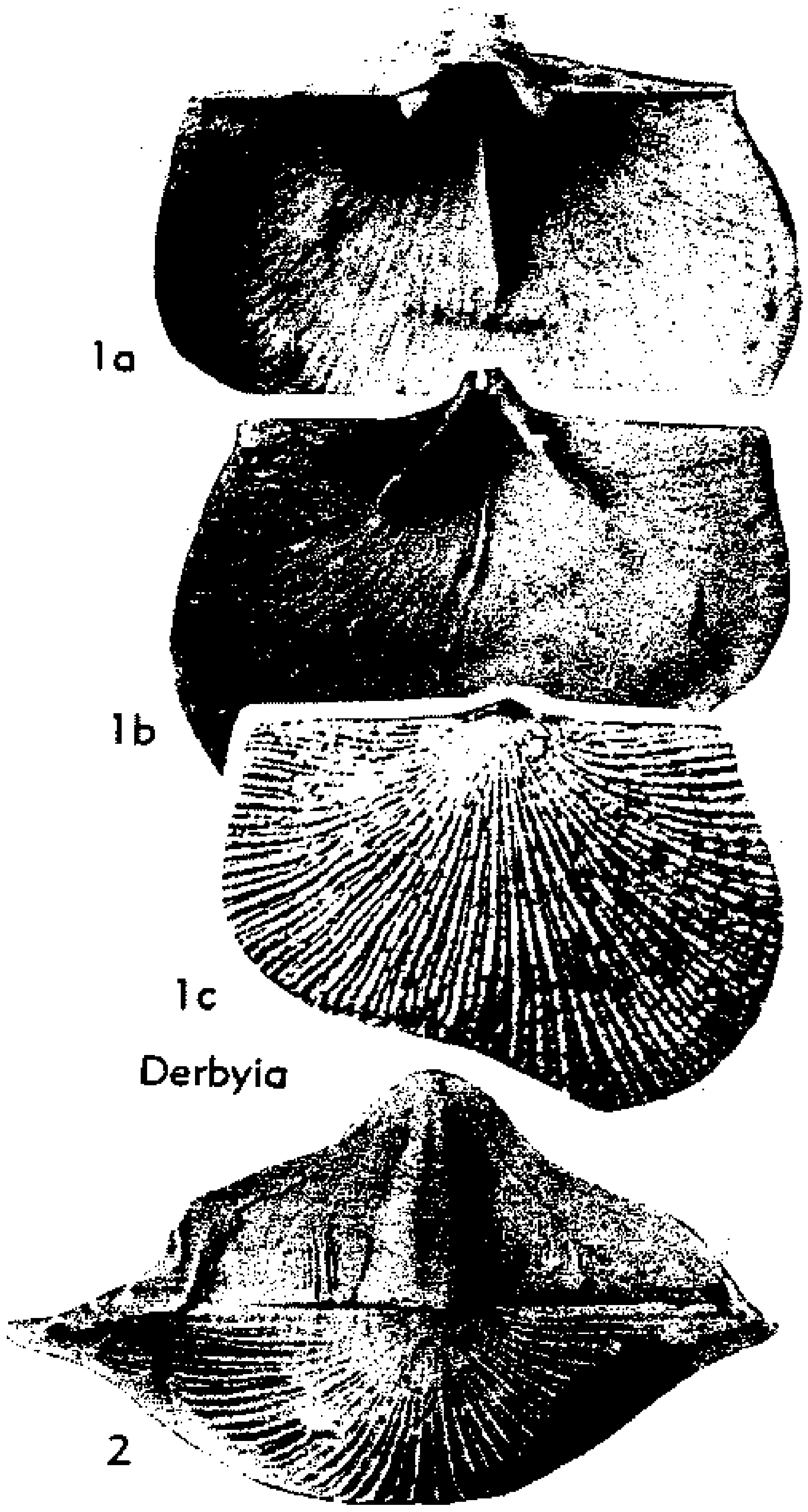


FIG. 270. Orthotetidae (Derbyiinae) (p. *H*410-*H*411).

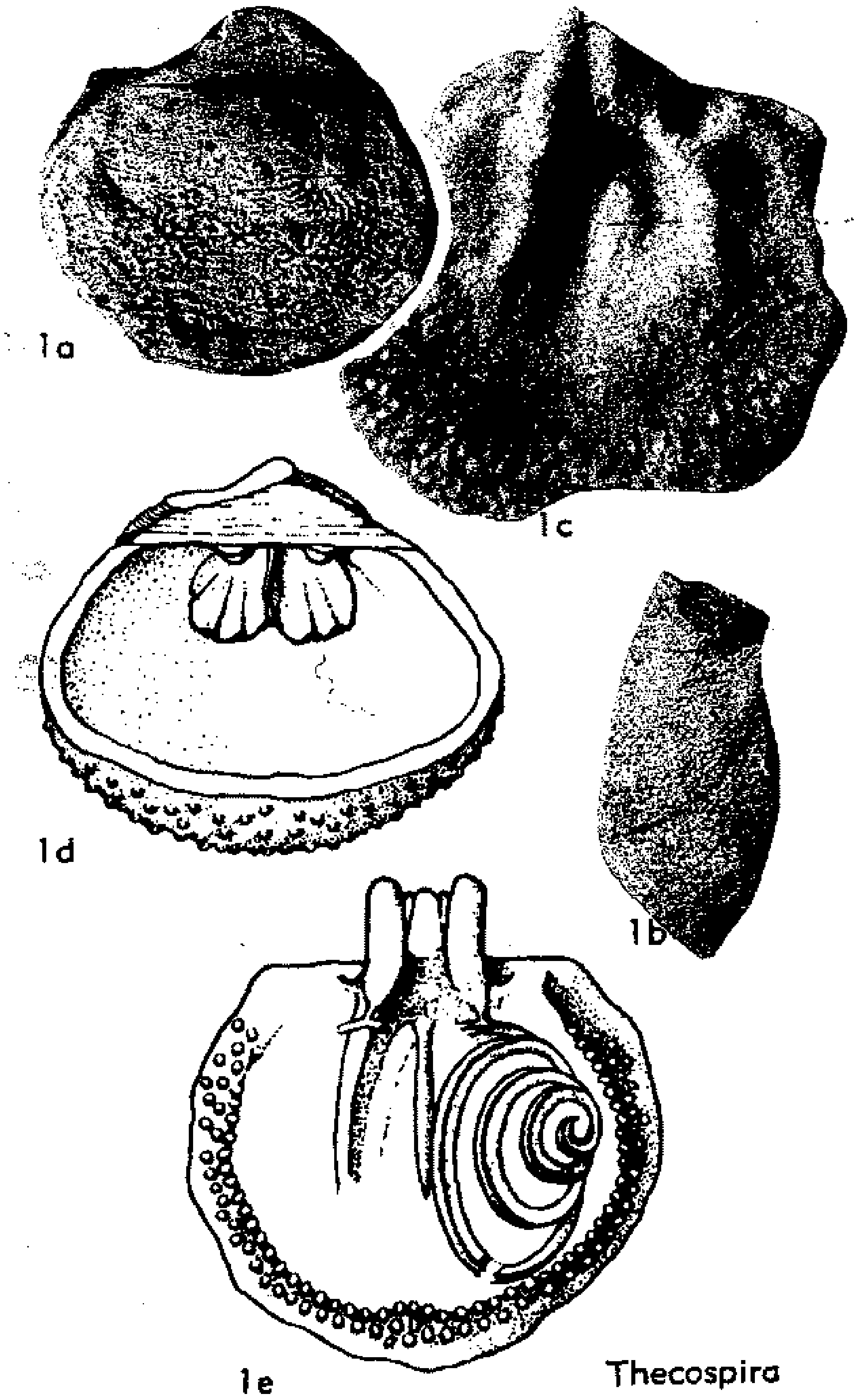


FIG. 271. Thecospiridae (p. H412).

Family THECOSPIRIDAE Bittner, 1893

[Thecospiridae BITTNER, 1890, p. 310]

Cemented by ventral umbo, ventral interarea entire, without differentiation of pseudodeltidium; dorsal interarea vestigial, chilidium absent; teeth unsupported, ventral muscle scar small, divided by low median septum; cardinal process high, functionally bilobed but united medianly to form tripartite structure, socket plates recurved but continuous anteriorly with pair of subparallel ridges containing dorsal adductor field divided by low median ridge; cardinal process bases prolonged into 2 short processes supporting pair of spirally coiled calcareous ribbons directed ventrolaterally; brachial ribbons sharply folded throughout length to give V-shaped cross section; shell substance pseudopunctate. *Trias.*

Thecospira ZUGMAYER, 1880, p. 152 [**Thecidea haidingeri* SUESS, 1854, p. 15; OD]. Exterior tuberculate, sporadically and impersistently rugate but without radial ornamentation. *Trias.*, Eu.——FIG. 271,*1*. **T. haidingeri* (SUESS), Alps; *1a,b*, brach.v., lat. views of conjoined valves, ×2; *1c*, brach. v. int., ×3; *1d,e*, brach.v., ped.v., ints., ×3 (Williams, n).

CHONETIDINA

[Materials for this suborder prepared by HELEN M. MUIR-WOOD]

[Appreciation and cordial thanks are expressed to the Trustees of the British Museum (Natural History) for permission to use numerous illustrations published in the MUIR-WOOD monograph on the Chonetoidea (586)]

The suborder Chonetidina as here defined includes the superfamilies Chonetacea and Cadomellacea.

The Chonetacea are at present divided into four families, 11 subfamilies and 30 genera.

The Cadomellacea comprise the single family Cadomellidae, containing one described genus, *Cadomella*. Although it lacks pseudopunctate shell structure, except in the innermost layer, it is grouped provisionally with the Chonetacea on account of its supra-apical foramen and the development of chilidial plates.

The Chonetacea have world-wide distribution, though many genera (e.g., *Daviesiella*) are only locally developed. The range of the superfamily is definitely from Early Silurian through Late Permian, a period of about 210 million years, but two imperfectly known species of Late Ordovician age may be true chonetids and this would extend the range still further (Fig. 272).

EXTERNAL MORPHOLOGY

The brachial valve is plane or concave and the pedicle valve more or less convex, except in *Chonostrophia*, where the convexity is reversed. In *Megachonetes* the two valves may be almost flat and the body cavity reduced to a minimum. The shell may be semicircular, alate, or quadrate, with the width normally exceeding the length. The hinge may be equal or less than the greatest width of the shell, with the cardinal extremities angular, rounded, or spinelike. The ears are more or less flattened, triangular, and slightly convex, and demarcated from the flanks by a shallow sulcus.

A narrow **interarea** is developed in each valve, that of the pedicle valve usually being twice the height of that of the brachial valve. The two interareas taper laterally and lie in the same plane or are set at an angle to one another. In some upper Paleozoic forms the dorsal interarea may be reflexed or bent anteriorly owing to development medianly of a secondary interarea in the pedicle valve. This serves to force the two umbones apart and make room for the growing external face of the cardinal process.

The **notothyrium** may be closed by the **chilidium**, a trigonal or subtrigonal, commonly medianly notched plate, developed at the base of the exterior of the cardinal process of some chonetoids (e.g., *Daviesiella*) (see Fig. 292,*1c*). The chilidium may be replaced by two narrow **chilidial plates** which are fused anteriorly and extend along the lateral margin of the triangular external face of the cardinal process. The latter serves to close part of the triangular **delthyrium** in the conjoined valves, the **pseudodeltidium** being as a rule a small crescentic or subtrigonal plate occupying the apex of the delthyrium. The delthy-

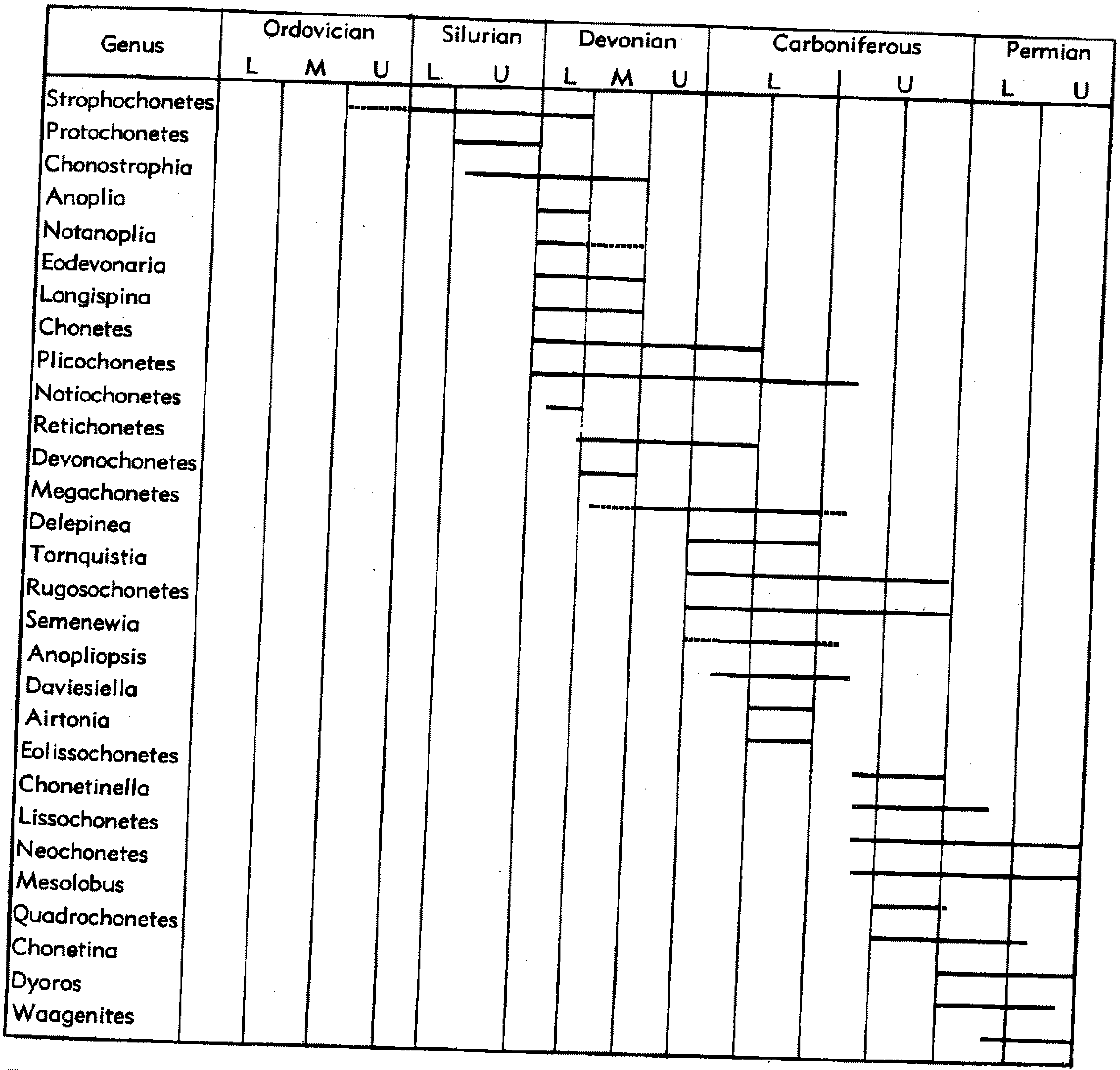


FIG. 272. Ranges of presently known chonetoid genera, with indicated duration of geologic-time divisions plotted in accordance with latest figures published by A. HOLMES (1959) (horizontal scale, 1 mm.=2.6 million years). Letters L, M, and U denote Lower, Middle, and Upper; in Silurian, L=Llandovery, U=Wenlock+Ludlow; in Devonian, L=Gedinnian+Siegenian+Emsian, M=Eifelian (Couvinian)+Givetian, U=Frasnian+Famennian; in Carboniferous, L=Tournaisian+Visean, U=Namurian+Westphalian (Mississippian corresponding to L+part of Namurian, and Pennsylvanian to U less part of Namurian) (Muir-Wood, n).

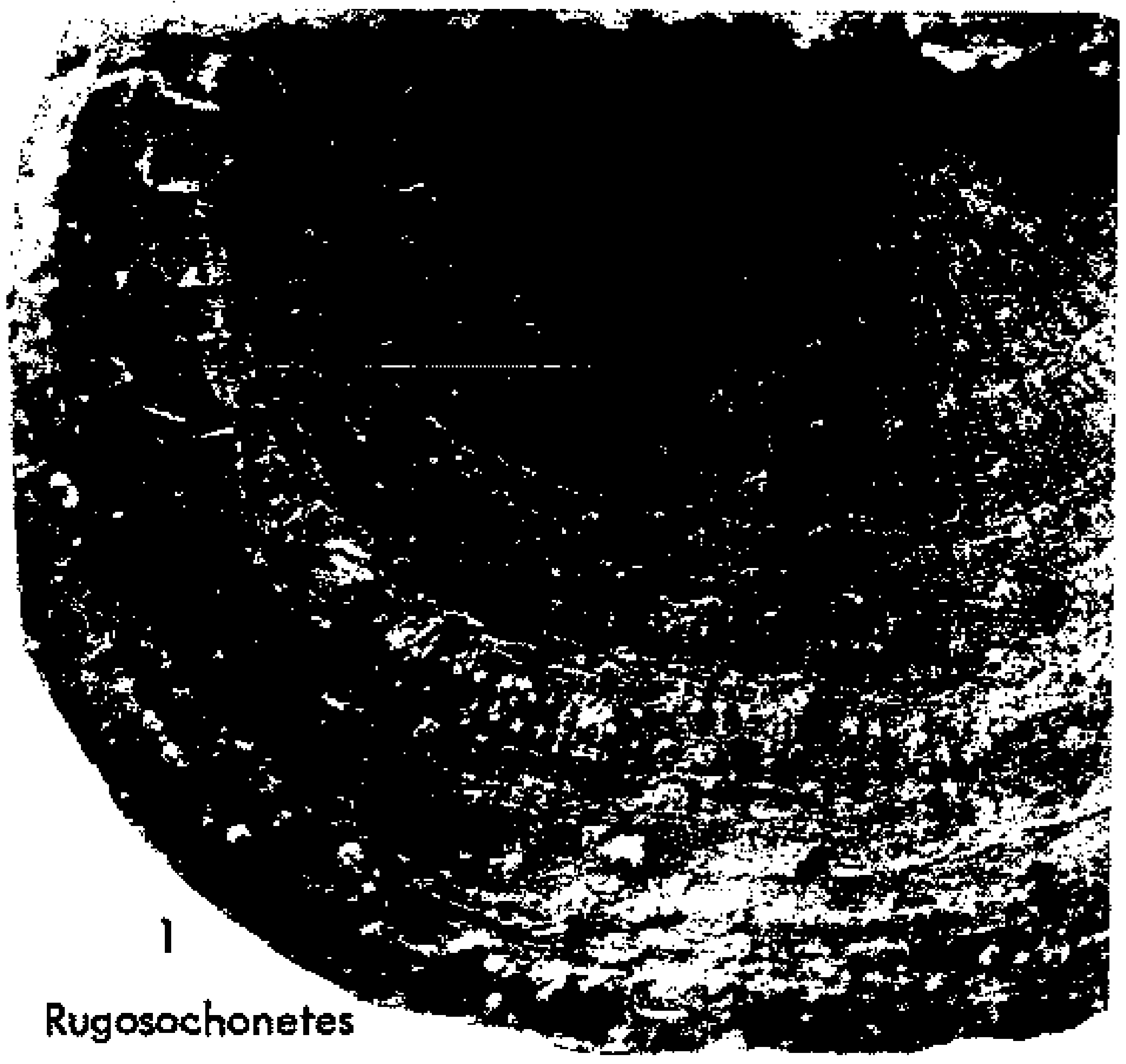


FIG. 273. Spinules in place of exterior of brachial valve of *Rugosochonetes hindi* MUIR-WOOD, U. Carb.(Namur.), Eng., ×6 (Muir-Wood, n).

rium is not occupied by a pedicle, but as in *Leptaena* and some stropheodontids, a supra-apical foramen may be developed, at least in some Silurian and Devonian forms, anterior to the ventral umbo in early growth stages, and this serves for the passage of a pedicle. A pedicle pipe is rarely preserved. The young chonetoid shell was probably attached by the pedicle to some external object and is, therefore, quite unlike young productoids. In the latter an attachment ring has been observed in the pedicle valve of very young shells in several genera, serving to attach the shell to a spine or some other small cylindrical object.

The ornament of chonetacean shells may be radial, or concentric, or both combined to give a netlike structure (e.g., *Retichonetes*), or the shell may be smooth, with only growth lines or lamellae (e.g., *Tornquistia, Lissochonetes*). The radial ornament consists of longitudinal ridges separated by intercostal sulci. Intercalated costae may occur on one valve and bifurcations on the other, but normally both occur on each valve.

When there are fewer than 15 ridges in a breadth of 10 mm. the ridges are referred to as **costae** (e.g., *Plicochonetes, Waagenites*); where 15 to 25 ridges occur in 10 mm. they are called **costellae** (e.g., *Daviesiella*); when more than 25 ridges are counted in 10 mm. they are termed **capillae** (e.g., *Chonetes*). The latter term replaces "striae," since these are incisions and not ridges.

The primary capillae and costellae usually extend from the umbo, and rarely from the hinge when they correspond in position to the spine bases. Most chonetids have radial ornament, and smooth forms may be derived from them by loss of ornament, usually first seen on the anterior third or half of the shell. More rarely, costellae are developed anteriorly in a posteriorly smooth species. Decorticated shells of smooth forms may appear capillate. The ears may be smooth and the remainder of the shell capillate.

Semenewia has concentric rugae and no radial ornament, and *Chonostrophia* has fine capillae inserted between slightly coarser costellae, as in some strophomenoids. Spines occur in a row on each side of the ventral umbo. The spines, ranging in number from 4 to 20, are set along the posterior edge of the interarea and are absent from the body of the shell and from the brachial valve. The form of the spines, whether straight or curved, their length, diameter, and angle of emergence—whether high-angled, oblique, or parallel to the hinge—is found to be more or less constant in a single species, and in species belonging to the same genus, and is of considerable importance in classification. The spines are tubular and they contained extensions of the mantle, but unlike productoid spines, were probably closed at the tip. They may exhibit growth lines. The roots of the spines extend through the interarea, in some shells at an angle to the externally projecting spine. In some species the roots may be curved instead of geniculated, whereas in other forms the spines extend straight through the interarea. The spine roots are not as a rule parallel, but in *Delepinea* the roots appear as parallel incisions when the interarea is decorticated. The inner openings of the roots can be seen as rounded apertures near the anterior margin of the interarea.

Fine spinules, a few millimeters in length, leave a trace of their existence in the elongated apertures on the summit of the capillae or scattered over the shell of smooth forms (Fig. 273). The spinules are seldom preserved in place but can often be detected as minute hairlike spines in the matrix enclosing a chonetid shell. They are very numerous on both valves in upper

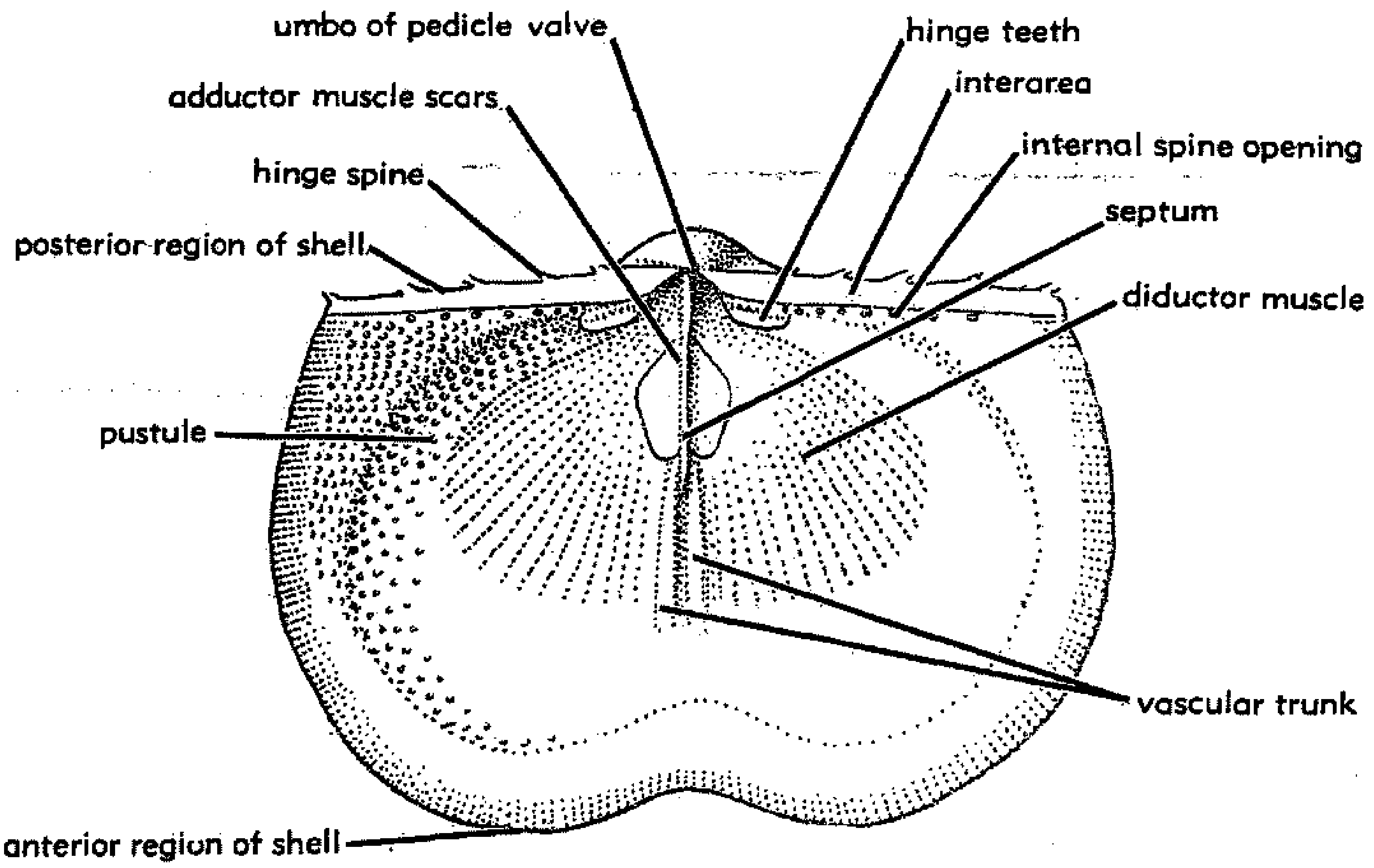


FIG. 274. Diagrammatic representation of internal morphology of pedicle valve of *Neochonetes pratti* (T. DAVIDSON), L.Perm., W.Australia, approx. ×2.5 (copyright, Trustees of British Museum, by permission).

Paleozoic forms. The spinules penetrate the outer, but not the inner shell layers, and when first formed at the shell margin each spinule would be filled with a small outgrowth of mantle and would be in communication with the shell interior. It was later sealed off by inner fibrous deposits. A median sulcus may be developed in the pedicle valve and a fold in the brachial valve (e.g., *Chonetina, Chonetinella*). An additional fold in the ventral median sulcus and a sulcus in the dorsal median fold may be developed in *Mesolobus*.

DIMENSIONS

The largest species all belong to the family Daviesiellidae and occur in the Lower Carboniferous, mostly in the Visean, and one genus extends its range into the Namurian. Species of *Delepinea* may attain a width of 8 to 10 inches and rival the Gigantoproductidae with their massive, thickened pedicle valve.

Specimens are referred to as small when their width is less than 0.75 in. or 20 mm., medium-sized when width is between 0.75 and 2 in., or 20 and 50 mm., large when the width exceeds 2 in. or 50 mm. Many chonetids are less than 20 mm. wide.

The length is measured along a vertical axis from the most posterior part of the ventral umbo to the anterior margin. The width is measured along the hinge or along the region of greatest width. The thickness is measured along an axis at right angles to length and width.

INTERNAL MORPHOLOGY

PEDICLE VALVE

The **hinge teeth** are developed as two bosses, one on each side of the anterolateral margin of the delthyrium (Fig. 274). They are usually elongated laterally and grooved longitudinally or transversely. A groove may separate the tooth from the anterior edge of the interarea and may articulate with the inner or outer ridges bounding the **hinge socket**. In *Eodevonaria* a denticulate hinge occurs and the hinge teeth and sockets are reduced.

Dental plates are normally absent but may be represented in some genera by ridges diverging from the umbo and extending as a raised rim along the outer margin of the diductor scars.

A ventral **median septum** is normally developed as a low ridge about one-third or one-half of the length of the pedicle valve. In *Protochonetes* the septum bifurcates posteriorly; in some genera it becomes more prominent and bladelike or fimbriate anteriorly.

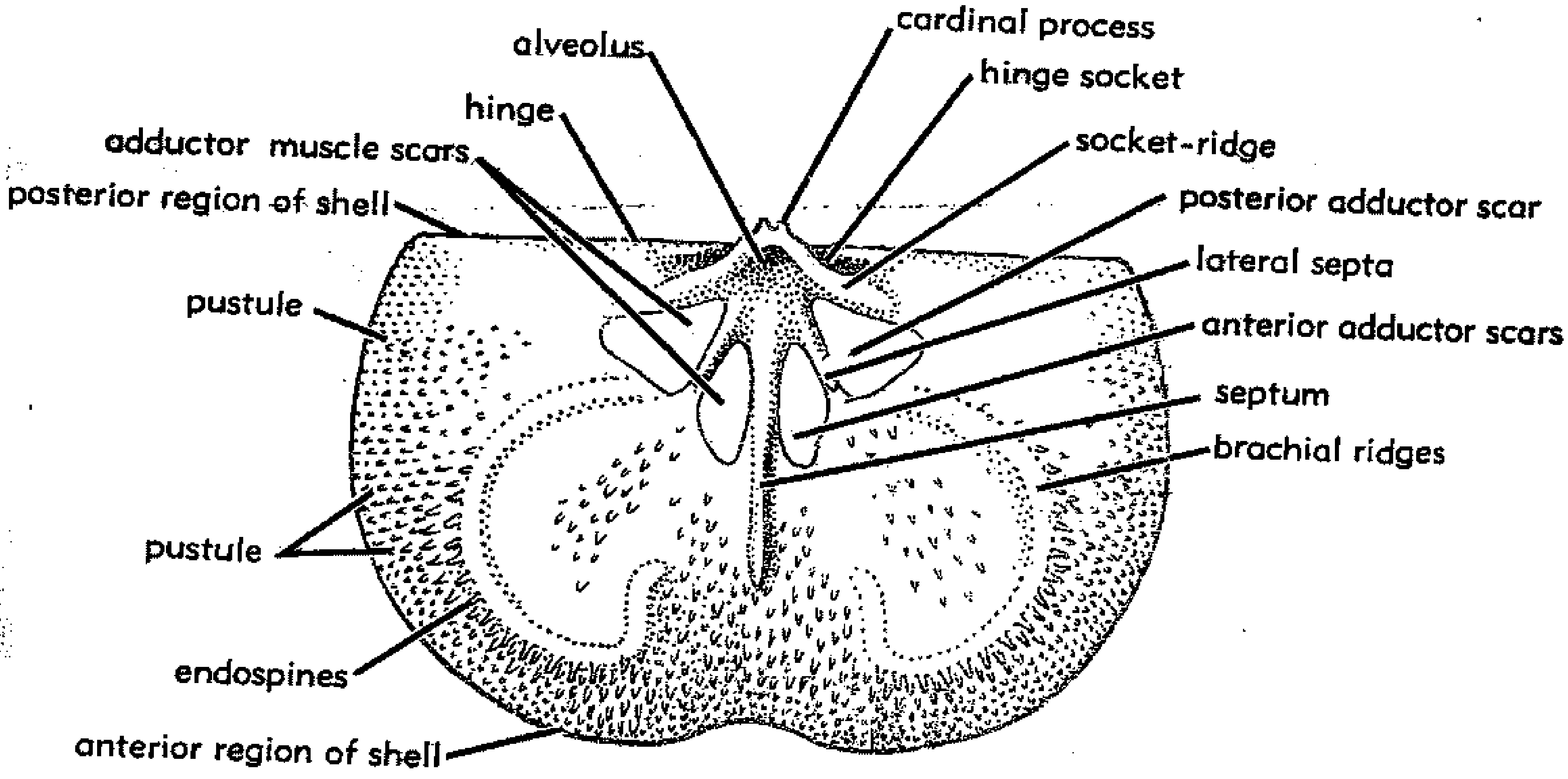


FIG. 275. Diagrammatic representation of internal morphology of brachial valve of *Neochonetes pratti* (T. DAVIDSON), L.Perm., W.Australia, approx. ×2.5 (copyright, Trustees of British Museum, by permission).

Articulation is effected by **adductor and diductor muscles,** in addition to hinge teeth and sockets. In the pedicle valve the diductor scars are usually pear-shaped, commonly ridged or furrowed, and in contact with the adductor scars along their inner margins. The adductor scars, usually four in number, are medianly placed and separated by the median septum. In smaller chonetoids the adductors are smooth. In *Daviesiella* the adductor scars are large and dendritic, and in part attached to the stout median septum. Small rounded accessory adductor scars are developed in genera belonging to the Daviesiellidae.

BRACHIAL VALVE

In the brachial valve the diductors are attached to grooves between the lobes of the outer face of the **cardinal process** (Fig. 275). The inner face of this process in larger chonetoids is short and bilobed or quadrilobed, but the outer face is large, trigonal, and lobed, with four, five, or six lobes. The dorsal adductor scars are commonly smooth and obscure but may be divisible into posterior (outer) and anterior (inner) scars. No pedicle muscle scars have been observed.

The inner face of the cardinal process may be separated from the median septum or **breviseptum** by a circular pit or **alveolus** (Fig. 276). The function of this pit, which also occurs in the Productellidae and Aulostegidae, is unknown. It may be a muscle pit, but as it appears to have been in open communication with the exterior, at least in early growth stages, it has been thought by some authors to be a visceral foramen, though no evidence is found to indicate that such exists in Recent articulate genera. In *Devonochonetes* and *Notiochonetes* the cardinal process is massive, trilobed, and supported by the septum.

The dental sockets are inserted at the base of the cardinal process and may be bounded by outer, as well as by inner, **socket ridges**

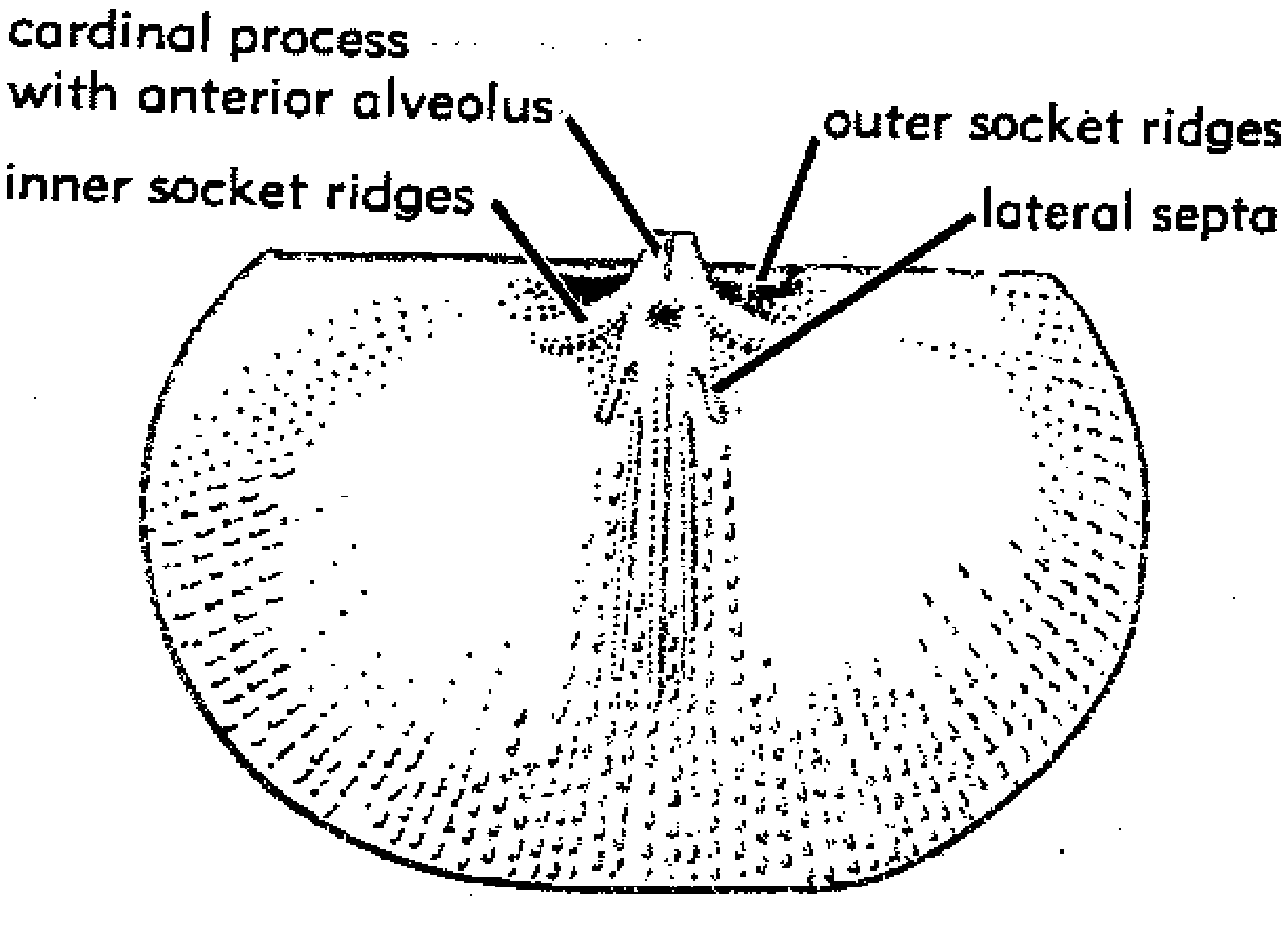


FIG. 276. Diagrammatic representation of internal morphology of brachial valve of *Chonetes sarcinulatus* (VON SCHLOTHEIM), L.Dev.(Ems.), Ger., showing three fine parallel septa and bilobate cardinal process with anterior alveolus, ×1.75 (copyright, Trustees of British Museum, by permission).

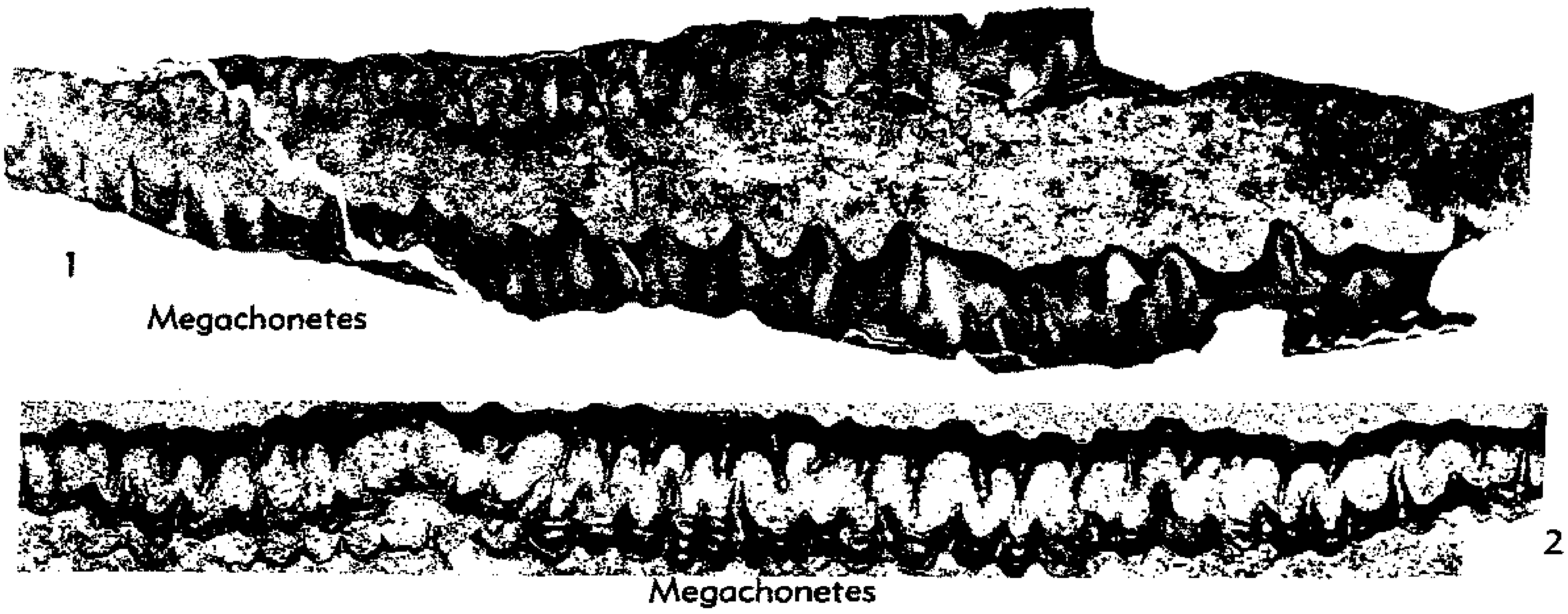


FIG. 277,*1,2*. Shell structure of *Megachonetes siblyi* (I. THOMAS), L.Carb.(U.Visean), G. Brit.; *1*, thin section through two valves showing taleolae as thin peaks with central canal clearly visible, ×10; *2*, thin section showing taleolae alternating with those of opposite valve and appearing as toothlike projections with central cavity, ×10 (Muir-Wood, n).

(Fig. 275, 276). The inner ridges are in contact with the cardinal process, and both inner and outer socket ridges probably assist in articulation of the shell.

In addition to the median septum there are usually two lateral septa, often referred to as **brachiophores.** These may have served as seat of attachment of the brachia, which may have been schizolophes or low spirolophes. Two additional septa, medially placed from the two lateral septa in some species, are referred to as **accessory septa.** Two or more diverging septa may replace the single dorsal median septum (e.g., *Chonetes s.s., Tornquistia, Anoplia*). In *Chonetina* and *Airtonia* a number of plate-like ridges are present.

The brachial ridges are seldom seen in Silurian and Devonian forms but in Carboniferous and Permian chonetoids they appear as low coiled, generally endospinose ridges.

SHELL STRUCTURE

The shell of chonetoids is pseudopunctate. It is composed of a thin, lamellar, outer layer and a thicker, fibrous, inner layer with rods (**taleolae**) formerly called spicules, or pseudopunctae, composed of nonfibrous calcite (Fig. 277, 278). The taleolae are perforated medianly and in the live animal were filled with outgrowths of mantle. They appear to be closely related to the external spines and spinules. They are commonly of two diameters and variable in length, and some taleolae may project into the shell cavity as rounded pustules or as endospines. The shell tends to be much thickened posteriorly, especially in the pedicle valve of the Daviesiellidae. The mode of formation of pseudopunctate shells and their relationship, if any, to true punctate shells (e.g., Mesozoic *Spiriferina*, in which external pustules are perforate) is not perfectly understood. The subject is at present under investigation.

LIFE HABITS

After early attachment by means of the pedicle, at least in Silurian and Devonian species, chonetid shells probably rested on the sea bottom with the brachial valve uppermost, the spines along the hinge serving as balancers, or for entanglement or attachment of the normally small, light shell. It has been suggested that the smaller forms may have floated.

The surface spinules may have served as strainers across the anterior gape of the valves, like the setae in Recent brachiopods. The endospines developed in both valves would serve the same purpose and help to keep out large particles or predators.

EVOLUTION

The superfamily Chonetacea is probably polyphyletic and derived from the Plectambonitacea and Strophomenacea. The Productidina are not thought to be derived from the Chonetidina.

Strophochonetes, the earliest chonetoid

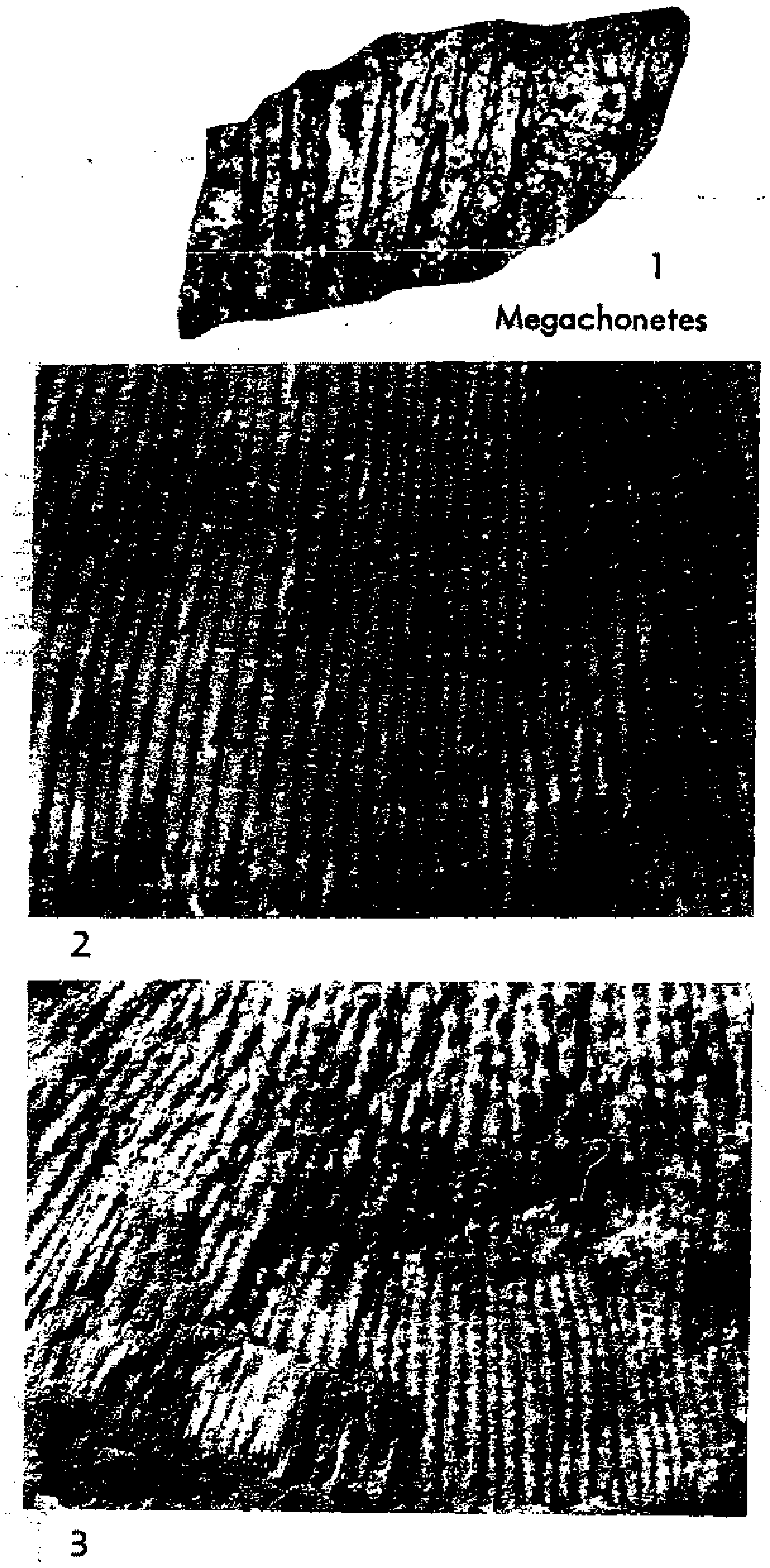


FIG. 278,*1-3*. Shell structure of *Megachonetes siblyi* (I. THOMAS), L.Carb.(U.Visean), Eng.(Derbys.); *1*, tang. sec. through shell showing rows of taleolae-like rows of beads, ×8.5; *2*, unweathered shell surface showing spinule apertures, ×7; *3*, weathered shell surface showing rows of taleolae, some with median perforation visible, ×7 (Muir-Wood, n).

now known, is capillate and has an enlarged median capilla, suggesting plectambonitid ancestry, although its musculature and the development of a median septum in each valve are chonetoid characters. Some species of *Anoplia* have oblique hollow tubes that penetrate the interarea, suggesting those of *Eochonetes* from the Upper Ordovician (Ashgillian) of Scotland (Ayrshire). *Eochonetes* has plectambonitacean musculature and external ornament and appears to be an offshoot of the Plectambonitacea.

The denticulate hinge of *Eodevonaria* is reminiscent of that of the plectambonitacean genus *Plectodonta,* which ranges from the Ordovician to the Devonian. The development of two or more diverging septa in the brachial valve can also be paralleled in the Plectambonitacea, but the ventral median septum is mainly a chonetoid character.

Chonostrophia, with reversed convexity of its valves, finer capillae and coarser costellae, as well as lobate diductor scars, suggests a strophomenoid ancestor, whereas *Devonoproductus* has spines developed as triangular projections from the hinge without any roots.

In spite of their long range small species of the Chonetacea remain practically unchanged. Except in number of spinules per capilla and better development of interareas and brachial ridges, Permian chonetoids are little more advanced or specialized than Silurian forms. This subject has been fully discussed by me elsewhere (586).

HOMEOMORPHY

A number of pairs of homeomorphs characterized by similar external form and ornament associated with dissimilar internal structures occur in the Chonetacea, as in other brachiopod superfamilies. For example, the large convex genus *Daviesiella* has been confused with *Airtonia,* the small capillate genus *Chonetes* with *Protochonetes,* the smooth genus *Anoplia* with *Tornquista* and *Lissochonetes,* and the sulcate genus *Chonetina* with *Chonetinella.* All these genera are easily distinguished by differences in their internal structure.

CLASSIFICATION

The classification employed here is based on external characters, including shell form, convexity, ornament, number of hinge spines and especially the angle of emergence of the spines, as well as on internal morphology, especially that of the brachial valve. A discussion of the present classification, as well as a history of the classification of the Chonetidina, is given by MUIR-WOOD (586).

TERMINOLOGY

Morphological terms applicable to the Chonetidina are partly the same as are employed for brachiopods generally, but others are largely or entirely restricted to this group. It is convenient to list and define the terms here.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CHONETIDINA

accessory septa. Two septa in brachial valve situated between median septum and lateral septa in some genera.

adductor muscle scars. Muscles serving to close valves and forming 2 or 4 scars of attachment in each valve, centrally or posteriorly located on each side of median septum.

adductor scars (accessory). Two subcircular muscle scars in *Daviesiella, Delepinea,* and *Megachonetes,* interpreted by Waagen (1884) as adductors and by Cope (1940) as diductors.

alveolus. Circular pit in some species at base of cardinal process separating it from median septum, and interpreted as visceral foramen in early growth stages or serving as muscle pit.

angle of spines. Angle formed by external hinge spines with hinge line or interarea.

bifurcation. Forking of capillae or costellae.

brachial bases. Term used by Imbrie (1959) for low ridgelike structures at base of cardinal process and thought by him to be homologous with orthoid brachiophores. A comparable structure observed in *Notiochonetes* was not interpreted as a brachiophore.

brachial ridges. Curved ridges extending from adductor muscle scars and possibly region of attachment of lophophore.

breviseptum. Septum not supporting cardinal process and anteriorly placed in some shells.

capillae. Fine radial ridges (more than 25 in 10 mm.) comprising external ornament of most chonetoid species.

chilidial plates. Two narrow diverging plates fused apically and in some shells developed along lateral margins of external face of cardinal process.

chilidium. Trigonal or subtrigonal plate developed in chonetoids at base of external face of cardinal process, and partly closing notothyrium; may be replaced by chilidial plates.

costae. Radial ridges on exterior of shell, broader than costellae (fewer than 15 in 10 mm.).

costellae. Radial ridges intermediate in width between capillae and costae (15 to 25 in 10 mm.).

delthyrium. Triangular opening in interarea of pedicle valve not serving for passage of pedicle, partly closed by pseudodeltidium and partly or wholly by exterior face of cardinal process.

dendritic. Having branched leaflike pattern; term used in connection with adductor muscle scars.

dental sockets. Hollows on each side of cardinal process serving for reception of hinge teeth, bounded on anterior margin by inner socket ridges, and in some shells by outer ridges along hinge margin.

diductor muscle scars. Opening muscles attached to cardinal process in brachial valve and forming large flabellate scars in pedicle valve.

endospines. Internal spines developed on interior of both valves, usually small papillae with central cavity in chonetoids (*see* taleolae).

fibrous layer. Inner shell layer formed of fine fibers commonly set at angle to shell surface, serving to thicken valves.

fold. Elevation in either valve, generally median and corresponding to sulcus in opposite valve.

hinge spines. Spines developed in row along posterior margin of pedicle-valve interarea on either side of umbo; roots of spines extending through ventral interarea generally at angle to external spines.

hinge teeth. Two peglike projections situated on anterior lateral margin of delthyrium and articulating with sockets in brachial valve.

imbricate. Having ornament consisting of overlapping lamellae.

interarea. Smooth or striated region along hinge of each valve bisected by delthyrium in pedicle valve and in some shells by notothyrium in brachial valve; formerly called cardinal area.

intercalation. Costella or capilla inserted between 2 other costellae or capillae.

lamellar layer. Outer shell layer, usually thin.

lateral septa. Short diverging ridges that tend to be anteriorly prominent and separated by median septum of brachial valve, but not as a rule in contact with it, possibly serving for attachment of lophophore; referred to by some authors as brachiophores, and by Imbrie (1959) as adductor dividing ridges.

notothyrium. Triangular opening in interarea of brachial valve, similar to delthyrium of pedicle valve.

papillae. Short, spinelike projections (endospines) which tend to be regularly arranged in interior of both valves.

protegulum. First-formed chitinous shell, only exceptionally preserved.

pseudopunctae. *See* taleolae.

reflexed interarea. Anterior curvature of interarea of brachial valve due to secondary growth along interarea of pedicle valve, forcing umbones of valves apart to permit growth of exterior face of cardinal process.

reticulate. Having netlike enlargements formed at point of intersection of rugae or growth-lines and radial capillae or costellae.

rugae. Concentric folds, rarely developed ornament in chonetids, except in *Semenewia.*

septum. Median vertical ridge in either valve, may support cardinal process in brachial valve.

socket ridges. Ridges extending laterally from cardinal process, commonly parallel to hinge and bounding anterior margin of hinge sockets; referred to by other authors as dental lamellae or brachiophores and by Imbrie (1959) as prosocket ridges. Outer socket ridges extend along hinge and posterior margin of sockets; these occur in *Chonetes s.s.* but are rarely developed in other genera.

spine apertures. Internal opening of spine bases on interior of pedicle valve just below interarea.

spinules. Minute spines of fine diameter and approximately 1 or 2 mm. in length, rarely preserved *in situ*.

spinule bases, or apertures. Small oval perforations usually seen on summit of costellae or capillae and only penetrating external shell layer; represent bases of fine spinules.

squamose. Having irregular and ragged margins; often used in referring to margins of concentric lamellae.

striae. Fine radial depressions or incisions.

sulcus. Depression in either valve, commonly deep and medianly placed, dividing valve into 2 parts; shallow sulcus may separate ears from venter.

supra-apical foramen. Pedicle foramen situated outside delthyrium and generally on ventral side of umbo.

taleolae. Nonfibrous calcite rods with central cavity which are developed in fibrous shell layer and may emerge into shell cavity as endospines.

Suborder CHONETIDINA Muir-Wood, 1955

[*nom. correct.* Muir-Wood, herein (*pro* suborder Chonetoidea Muir-Wood, 1955, p. 68)]

Articulate brachiopods with functional pedicle present in all growth stages or in early stages only, foramen supra-apical and outside delthyrium. Lophophore probably schizolophous or spirolophous. Valves normally concavo-convex except in one genus. Spine row normally developed along margin of pedicle-valve interarea; spinules represented by fine apertures on shell, or spines and spinules absent. Shell composed of thin outer lamellar layer and inner fibrous layer, with hollow pseudopunctae (taleolae) present, except in Cadomellacea. Endospines commonly in radial rows. *?U.Ord., L.Sil.-L.Jur.(U.Lias.).*

Superfamily CHONETACEA Bronn, 1862

[*nom. transl.* Shrock & Twenhofel, 1953, p. 317 (*ex* Chonetidae Bronn, 1862, p. 301)]

Small to large Chonetidina with functional pedicle only in early growth stages, and foramen rarely preserved. Interareas in each valve may be reflexed in brachial valve. Pseudodeltidium, chilidium, or chilidial plates and lobate cardinal process normally present. Brachial ridges and vascular markings preserved in some genera. Median septum in each valve, lateral septa in brachial valve probably acting as brachiophores. Adductor scars normally smooth, rarely dendritic, accessory adductors in one family. Shell substance lamellar and pseudopunctate. *?U.Ord., L.Sil.-U.Perm.*

Family CHONETIDAE Bronn, 1862

[Chonetidae Bronn, 1862, p. 301]

Small to medium in size; shell rarely thickened, externally smooth, capillate, costellate or lamellose, rarely rugose, spine row and spinules usually developed. Adductor scars smooth, no accessory adductors. One or more septa in brachial valve. *?U.Ord., L.Sil.-U.Perm.*

Subfamily CHONETINAE Bronn, 1862

[*nom. transl.* Waagen, 1884, p. 612 (*ex* Chonetidae Bronn, 1862, p. 301)]

Three or more fine, diverging septa in brachial valve, brachial ridges normally absent, cardinal process bilobed or quadrilobed, alveolus present; spine angle oblique (45 degrees). *L.Dev.-L.Carb.*

Chonetes Fischer de Waldheim, 1830, pl. 26, fig. 8,9 [**Terebratulites sarcinulatus* von Schlotheim, 1820, p. 256; SD de Verneuil, 1845, p. 240]. Shell small, semicircular; valves plano- or slightly concavo-convex; pseudodeltidium present; shell capillate, commonly becoming smooth or lamellose anteriorly; hinge sockets with curved inner and short outer socket ridges, no brachial ridges developed. *L.Dev.-U.Dev.*, Eu.(G.Brit.-Fr.-Ger.)-N. Am.-?Asia-N. Afr.-Australia; *L. Carb.*, Eu. (G. Brit.-Ger.).——Fig. 279,*1*. **C. sarcinulatus* (von Schlotheim), L.Dev. (Ems.), Ger.(Eifel.); *1a*, ped.v. and brach.v. ext., ×2; *1b*, ped.v. int. mold, ×1.5; *1c*, ped.v. int. (reconstr.) showing adductor scars (*ad*), diductor scars (*did*), ridge bounding post. margin of diductors (*r*), long median septum (*s*), ×1.75; *1d*, brach.v. (lectotype) int., ×2.5 (586).——Fig. 279,*2*. *C. plebejus* Schnur, L.Dev.(Ems.), Ger.(Eifel.); *2a*, ped.v. ext. and brach.v. int., ×2; *2b,c*, brach.v. int., ×3, ×2 (586).

Subfamily STROPHOCHONETINAE Muir-Wood, 1962

[Strophochonetinae Muir-Wood, 1962, p. 40]

Dorsal median septum short or absent, prominent lateral septa, alveolus sometimes developed, spinules present, spines long, vertical. *?U.Ord., L.Sil.-L.Dev.*

Strophochonetes MUIR-WOOD, 1962, p. 40 [**Chonetes cingulatus* LINDSTRÖM, 1860, p. 374; OD]. Small, hemispherical; valves plano- or slightly concavo-convex, pseudodeltidium and chilidial plates present, capillate, commonly smooth posteriorly and lamellose anteriorly, with median en-

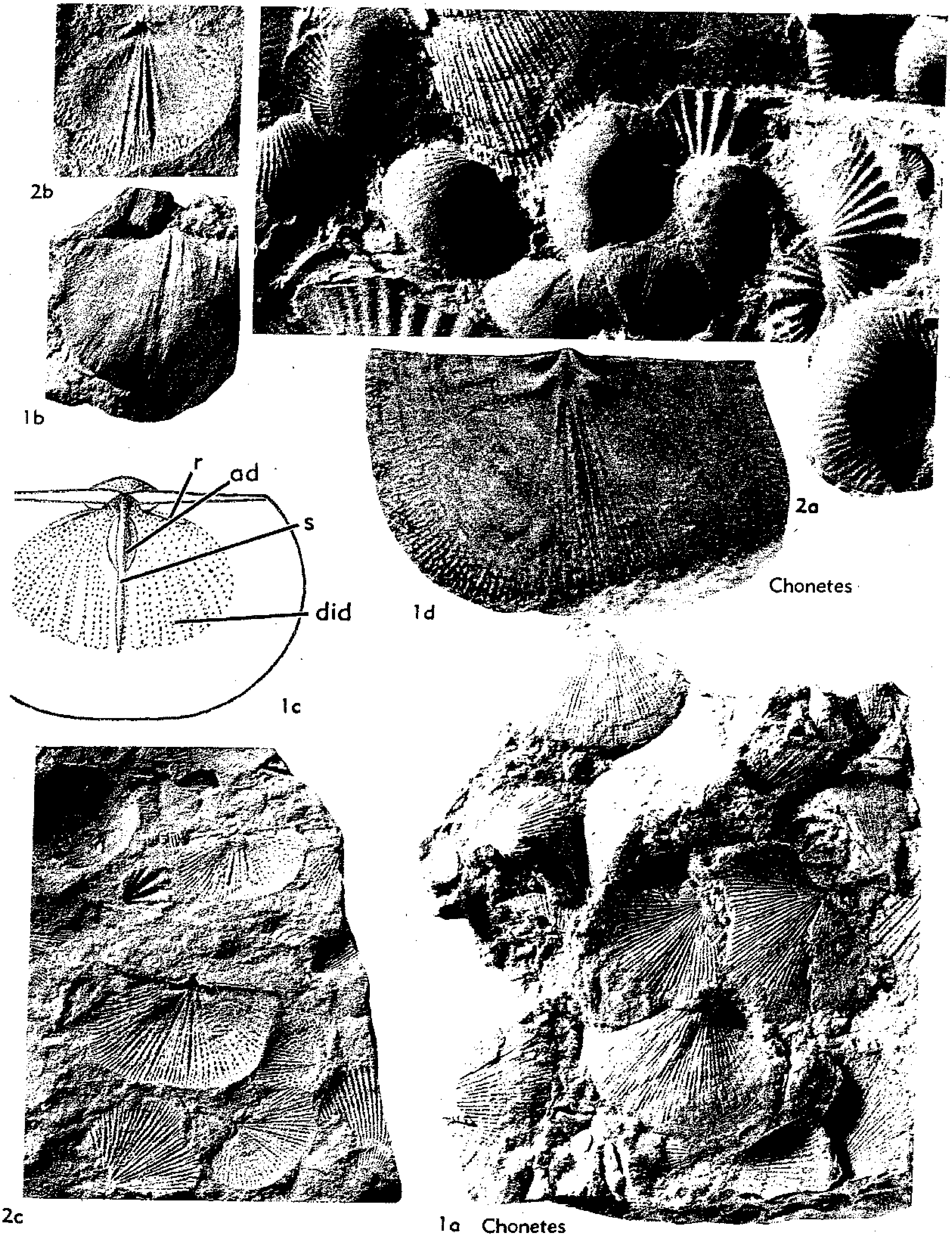


FIG. 279. Chonetidae (Chonetinae) (p. H420).

larged capilla in pedicle valve, socket ridges along hinge margin, no brachial ridges. *?U.Ord.*, N.Am. (Anticosti Is.)-Eu.(G.Brit.); *Sil.-L.Dev.*, Eu.-N. Am.(USA-Can.).——FIG. 280,*1*. *S. tenuicostatus* (OEHLERT), L.Dev., Fr.(Mayenne); brach.v. int., ×4 (586).——FIG. 280,2. **S. cingulatus* (LINDSTRÖM), U.Sil.(Wenlock.), Sweden(Gotl.); *2a*, ped.v. ext., ×2; *2b,c*, ped.v. ext. with long spines and prominent median capilla, brach.v. ext. showing capillae without strong median one, ×5; *2d*, slab with both ped.v. and brach.v. ext., ×3 (586).

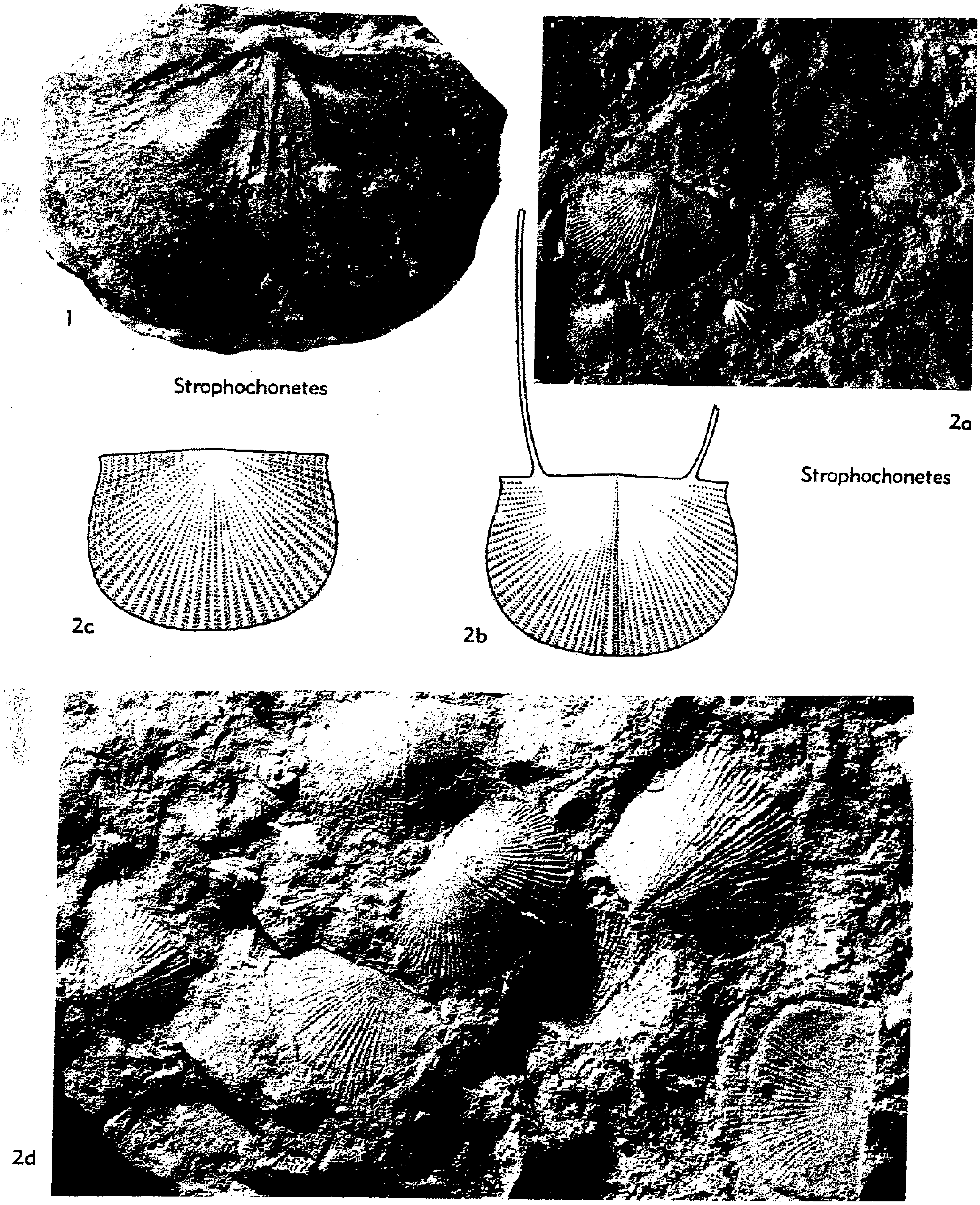


FIG. 280. Chonetidae (Strophochonetinae) (p. *H*420-*H*422).

Subfamily DEVONOCHONETINAE Muir-Wood, 1962

[Devonochonetinae Muir-Wood, 1962, p. 43]

Dorsal median septum supporting large prominent bilobate or trilobate cardinal process, breviseptum in one genus, lateral septa developed, brachial ridges rarely seen; spinules developed, spines low-angled. *M. Sil.-M.Dev.*

Devonochonetes Muir-Wood, 1962, p. 43 [**Strophomena carinata* Conrad, 1842, p. 257 (*non* Conrad, 1839, p. 64) (=*Chonetes coronatus* Hall, 1857, p. 146); OD]. Shell small or medium in size; valves moderately concavo-convex, pseudodeltidium and chilidium usually present, shell costellate or capillate, spinules not numerous, spine angle low, curved inner and short outer socket ridges present. *M.Dev.(Hamilton)*, N.Am.-N.Afr.——Fig. 281,*1*. **D. coronatus* (Hall), Hamilton(Kashong Sh.), USA(N.Y.); *1a-c*, ped. v. vent., lat., ant. views, ×2.5; *1d*, brach.v. view, ×2.5; *1e*, brach.v. int., ×2.5 (586).

Longispina Cooper, 1942, p. 230 [**Chonetes emmetensis* Winchell, 1866, p. 92; OD]. Small, subquadrate; valves strongly concavo-convex, pseudodeltidium and chilidium may be present, costellate or capillate, spines long, parallel to hinge, projecting from cardinal extremities, inner socket ridges short, brachial ridges rare. *L. Dev.-M.Dev.*, N. Am.(Can.-USA)-S. Am.——Fig. 282,*1*. **L. emmetensis* (Winchell), M.Dev. (Hamilton), USA(Mich.); *1a,b*, slab showing ped. v. ext., ×1, ×2; *1c*, brach.v. int. (reconstr.) showing faint brach. ridges *(br)*, knoblike card. process *(cp)*, median septum *(s)*, and short socket ridges *(sr)*, ×4; *1d*, ped.v. int. (reconstr.) showing long spines parallel to hinge, hinge teeth *(ht)*, and short median septum, ×4 (586).

Notiochonetes Muir-Wood, 1962, p. 48 [**Chonetes skottsbergi* Clarke, 1913, p. 29; OD]. Medium-sized; brachial valve flat, pedicle valve slightly convex, pseudodeltidium and ?chilidial plates present; shell finely costellate, with spine roots but external spines rarely preserved, cardinal process large, projecting ventrally, strong inner and outer socket ridges, breviseptum and strong lateral septa present, brachial ridges rare. *Up.L.Dev.*, E.Falkland Is.——Fig. 282,*2*. **N. skottsbergi* (Clarke); *2a*, ped.v. ext. mold showing capillation and spinule bases, ×2; *2b,c*, ped.v. int., with reconstr. showing small adductor scars *(ad)*, longitud. ridged diductor scars *(did)*, hinge teeth *(ht)*, and spine openings *(so)* near hinge, ×1 ×1.5; *2d,e*, wax squeeze of brach.v. int. mold, with reconstr. showing 2 pairs of adductor scars *(ad)*, broad card. process *(cp)*, inner socket ridges *(isr)*, lateral septa *(ls)*, and outer socket ridges *(osr)*, ×1, ×1.25; *2f*, post. view of card. process showing chilidial plates, each side of card. process *(chp)*, card. process *(cp)*, inner socket ridges *(isr)*, and outer socket ridges *(osr)*, ×4 (586).

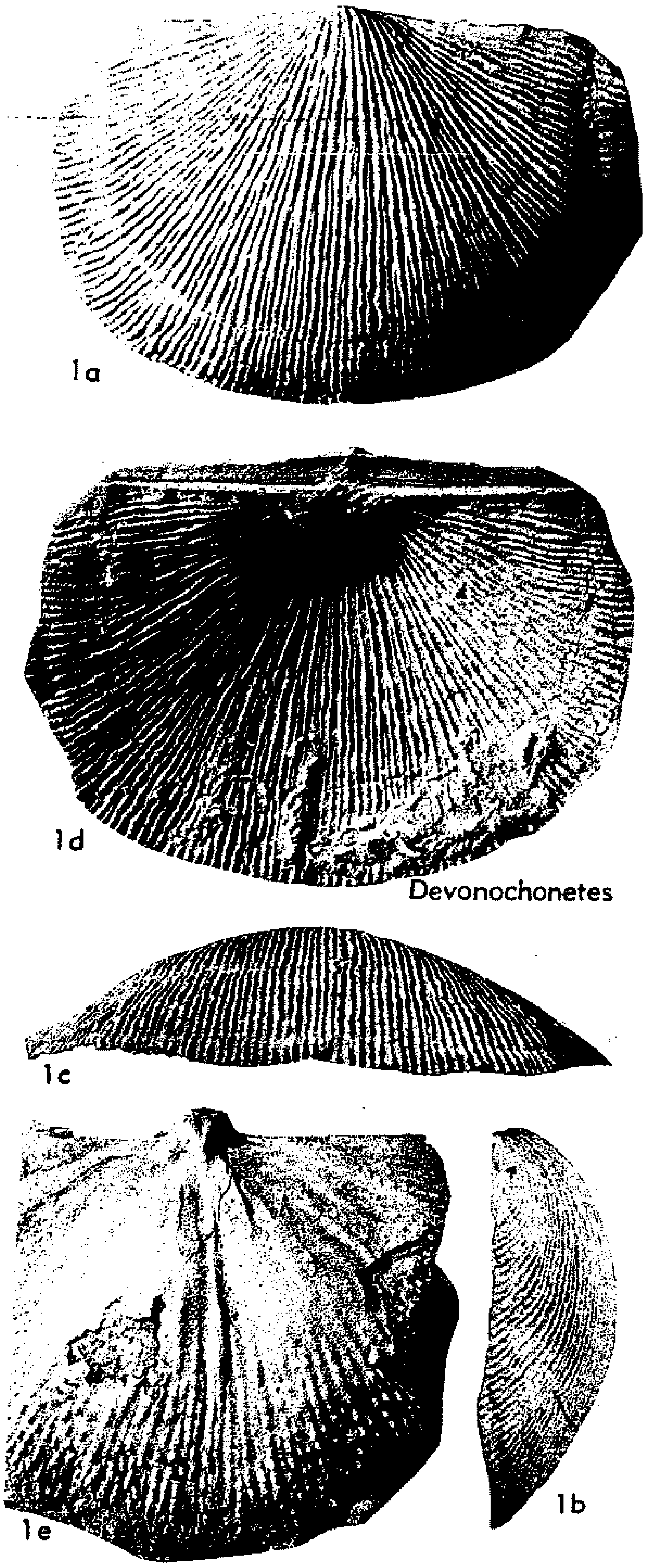


Fig. 281. Chonetidae (Devonochonetinae) (p. *H*423).

Protochonetes Muir-Wood, 1962, p. 50 [**P. ludloviensis*; OD]. Small to medium-sized; valves plano- to concavo-convex, pseudodeltidium small, chilidium may be present; shell capillate, spines oblique; ventral septum bifurcating posteriorly, dorsal septum long, anteriorly elevated, inner socket ridges short, curved. *Sil.(Wenlock.-Ludlov.)*, Eu.-N.Am.——FIG. 283,*1*. **P. ludloviensis*, U.Sil.(U.Ludlov.), Eng.(Shrops.-Herefords.); *1a,b*, ped.v. ext. (*1a*, holotype), ×3, ×4; *1c*, ped.v. int. mold showing post. bifurcating septum, ×3; *1d,e*, brach.v. int. (reconstr.) showing card. process (*cp*), lateral septa (*ls*), and socket ridges (*sr*), ×2.5 (586).——FIG. 283,*2*. *P. striatellus* (DALMAN), U.Sil., Sweden(Gotl.); *2a*, ped.v. ext.; *2b*, part of brach.v. view showing interarea; *2c*, ped.v. int. showing post. bifurcating median septum; all ×3 (586).

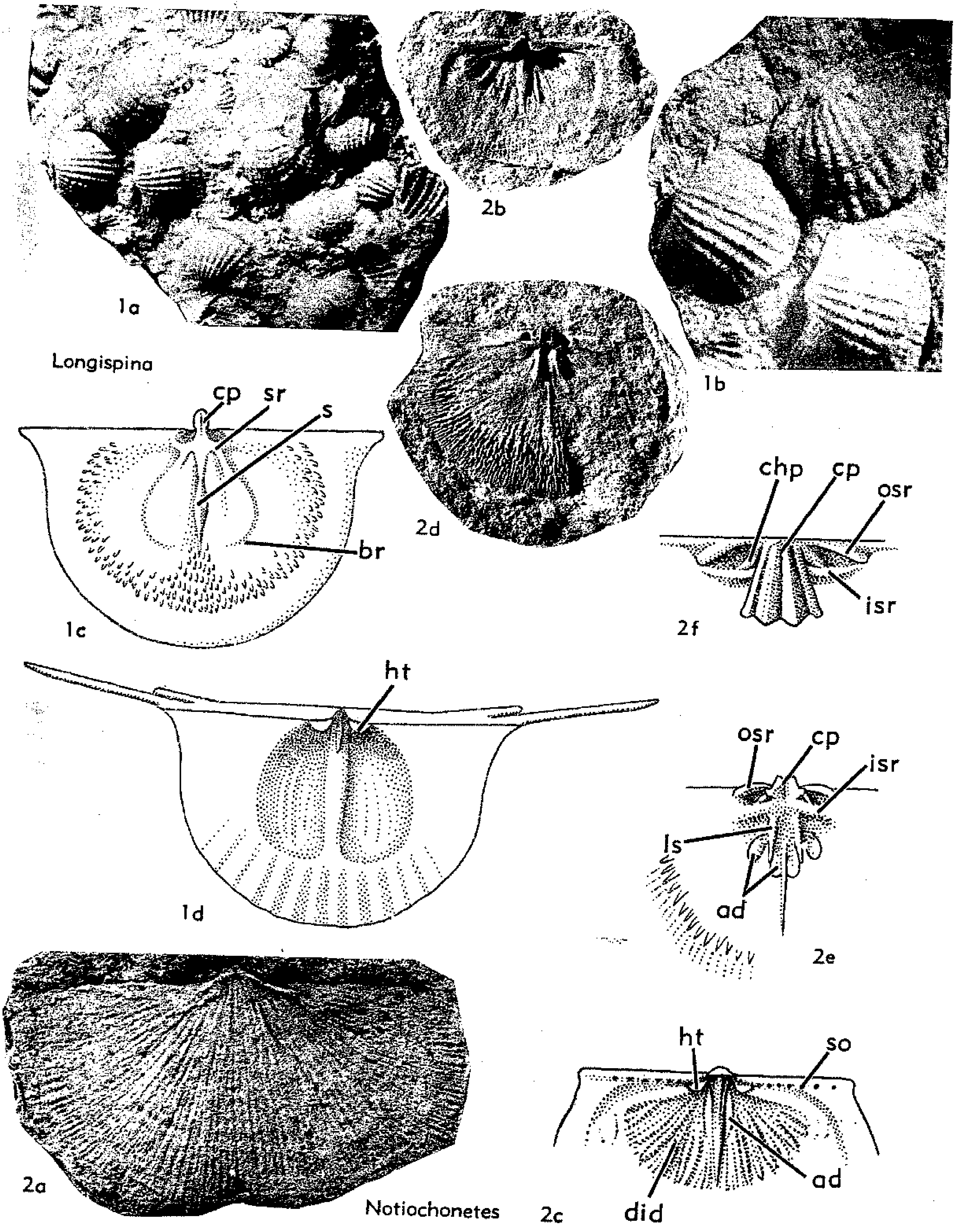


FIG. 282. Chonetidae (Devonochonetinae) (p. H423).

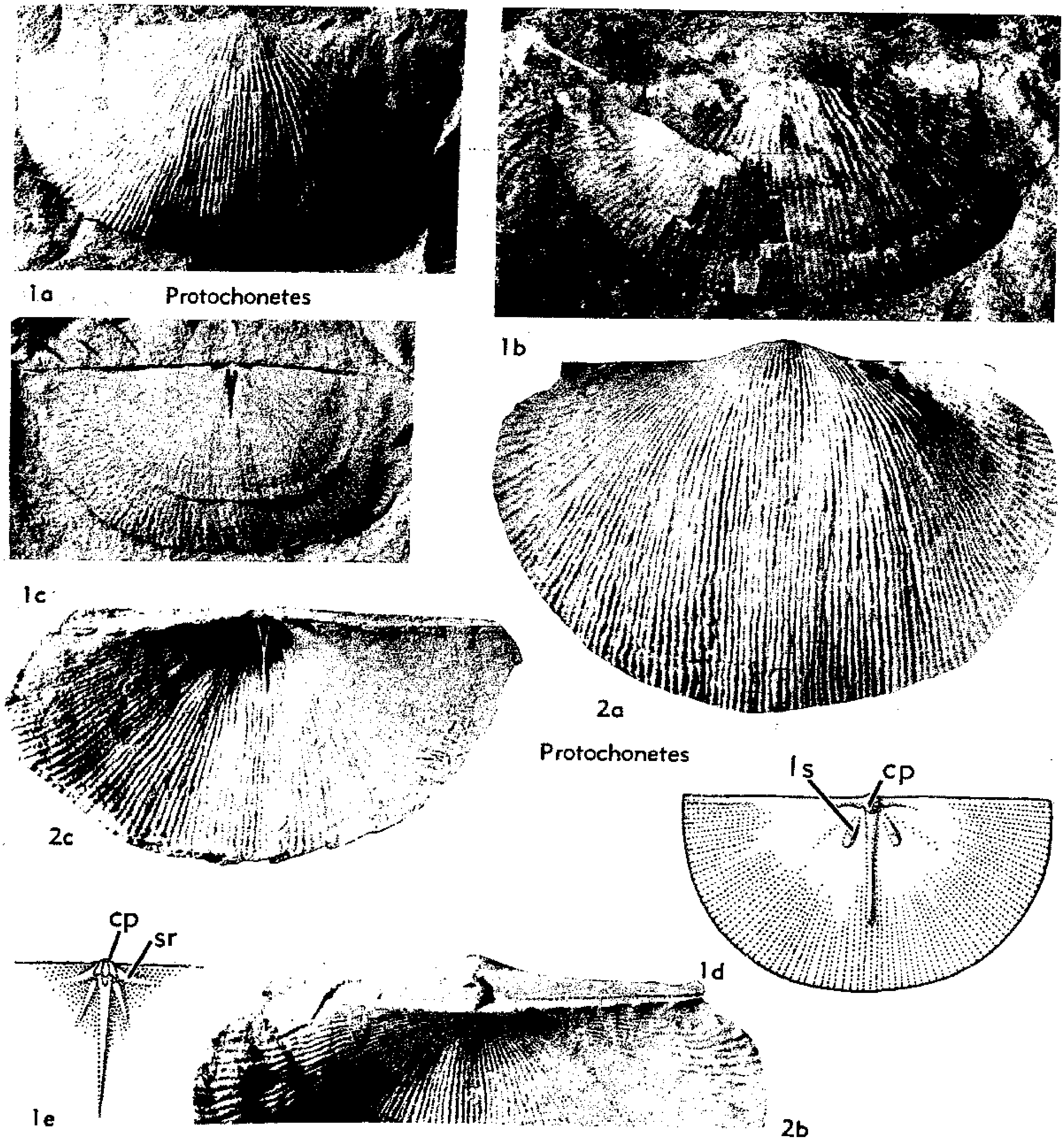


FIG. 283. Chonetidae (Devonochonetinae) (p. *H*423-*H*424).

Subfamily ANOPLIINAE Muir-Wood, 1962

[Anopliinae MUIR-WOOD, 1962, p. 53]

Two or more diverging plates or septa in one or both valves, dorsal median septum reduced or absent, no brachial ridges, cardinal process small, usually bilobed; shell normally smooth, external spines high-angled or spine roots only. *L.Dev.-L.Perm.*

Anoplia HALL & CLARKE, 1892, p. 309 [**Leptaena? nucleata* HALL, 1857, p. 47; OD(M)]. Small in size, semicircular; valves highly concavo-convex, interareas linear, pseudodeltidium present; shell smooth with growth lamellae, no spinules, spines usually absent, roots may be present; brachial valve with 2 diverging septa and short lateral septa, socket ridges long, crenulated. *L.Dev.*, N. Am. (USA-Can.) - Eu. (Belg. - Ger.) - N. Afr.- Australia(Victoria).——FIG. 284,*1*. **A. nucleata* (HALL), L.Dev.(Camden Chert), USA(Tenn.); *1a,b*, ped.v. vent., lat., ×4; *1c*, brach.v. view, ×4; *1d*, brach.v. int., ×4; *1e,f*, ped.v. and brach. v. int. (reconstr.) showing card. process *(cp)*, median septa *(s)*, socket ridges *(sr)*, ×6, ×8 (396).

Anopliopsis GIRTY, 1938, p. 281 [**Chonetina subcarinata* GIRTY, 1926, p. 27; OD]. Small trigonal shells, slightly concavo-convex; shell smooth with few lamellae, spines at high angle, brachial valve interior with median sulcus; pedicle valve with septum, both valves with radial platelike septa from umbo to anterior margin; socket ridges short curved. *L.Miss.-U.Miss.*, N.Am.(Tex.-Tenn.-Okla.).——FIG. 284,2. **A. subcarinata* (GIRTY), L.Miss.(Ft.Payne), USA(Tenn.); *2a*, ped.v. int. cast, ×5; *2b,c*, brach.v. int. with lamellae, ×5; *2d*, ped.v. int. cast, ×5 (351).

Chonetina KROTOW, 1888, p. 500 [*pro Chonetella* KROTOW, 1885, p. 274, 309 (*non* WAAGEN, 1884, p. 613) (obj.)] [**Chonetella artiensis* KROTOW,

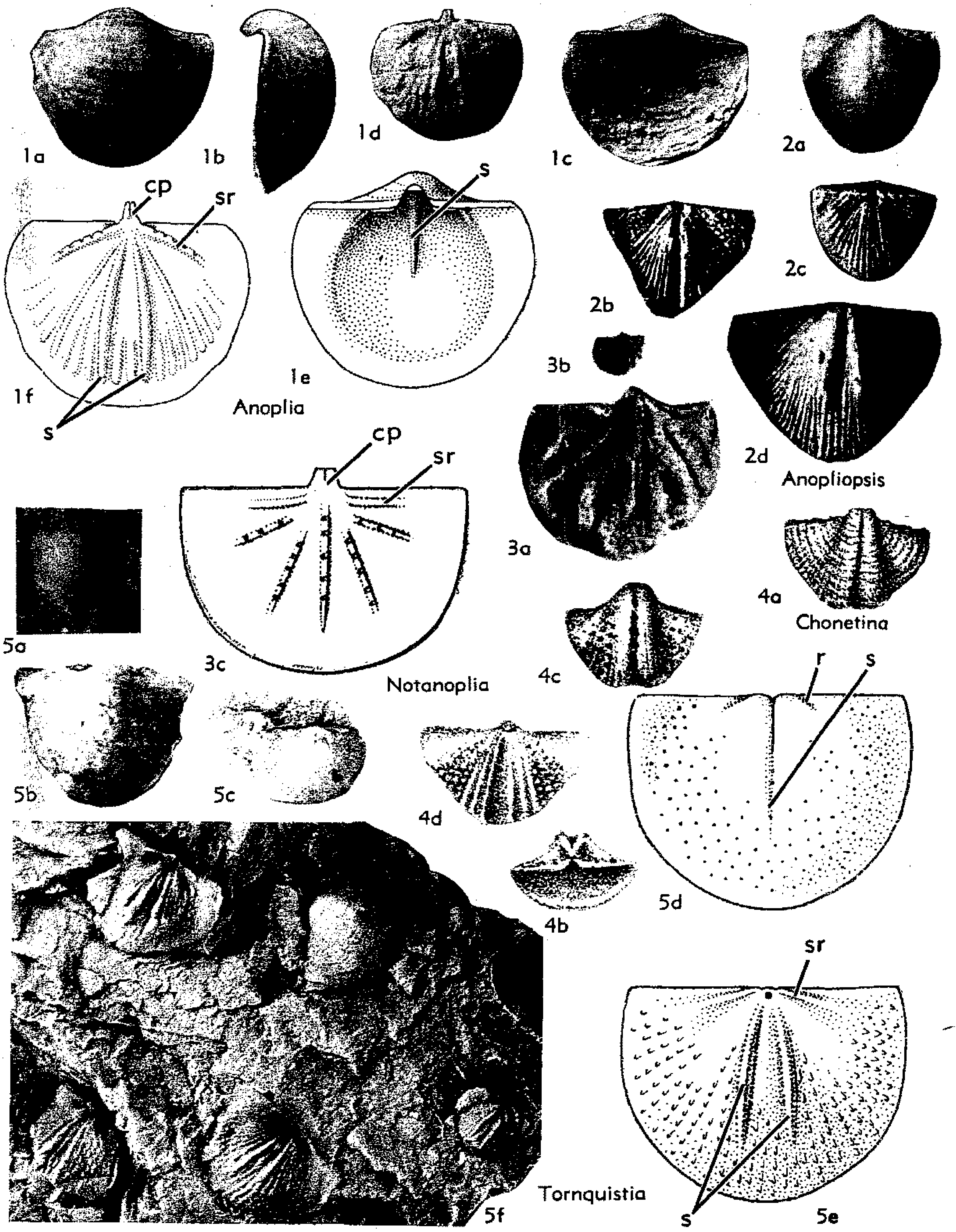


FIG. 284. Chonetidae (Anopliinae) (p. *H*425-*H*428).

1885, p. 275; OD]. Shell small, highly concavo-convex with dorsal median fold, and deep ventral sulcus; shell smooth, with growth lines, external spine row developed; brachial valve interior with several platelike septa formed from fused papillae, no true median septum. *L.Perm-U.Perm.*, Eu.-Asia.——Fig. 284,*4*. **C. artiensis* (Krotow), USSR(Urals); *4a,c,* ped.v. vent. and int. cast;

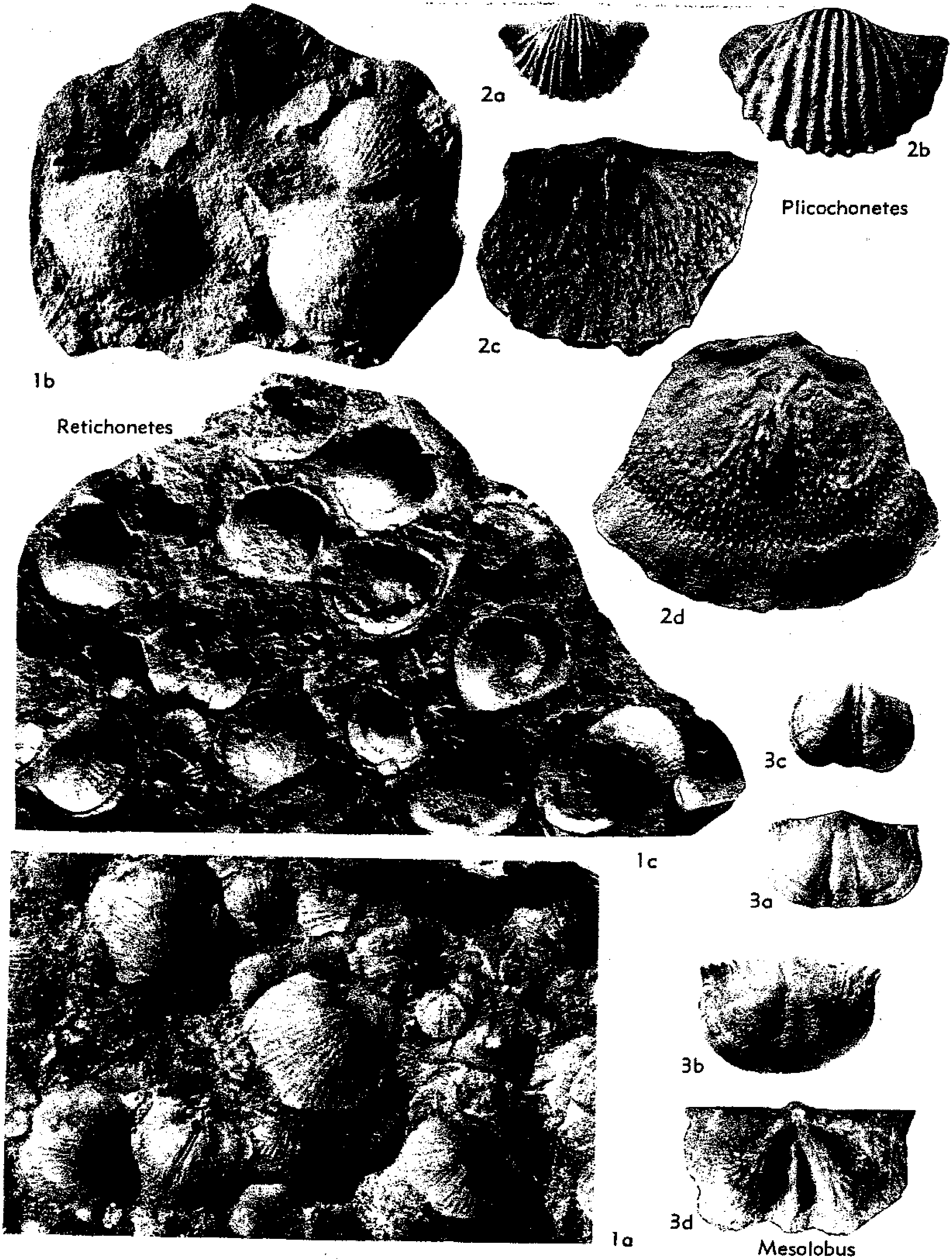


Fig. 285. Chonetidae (Retichonetinae) *(1)*, (Rugosochonetinae) *(2, 3)* (p. *H*428, *H*430).

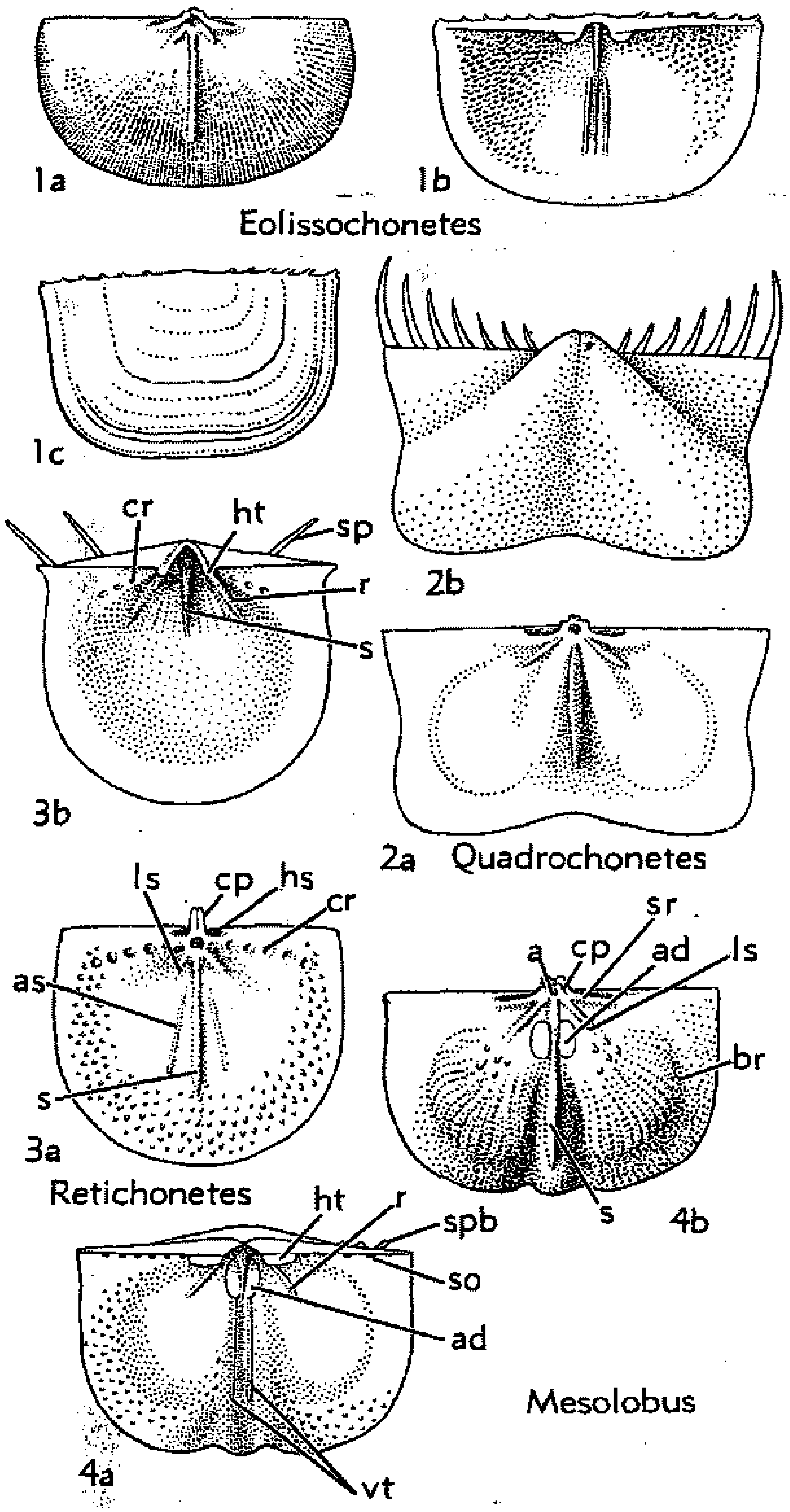


FIG. 286. Chonetidae (Retichonetinae) *(3)*, (Rugosochonetinae) *(1, 2, 4)* (p. *H*428, *H*430).

4b, ped.v. view showing interarea and umbo; *4d,* brach.v. int. cast showing int. plates; all ×3 (491).

Notanoplia GILL, 1950, p. 249 [**N. pherista*; OD]. Small, plano- or concavo-convex, shell smooth, with growth lines and rare capillae, no spine row present, both valves with long median septum and 2 or more accessory septa with row of pits along each septum, socket ridges extending along hinge. *L.Dev., ?M.Dev.,* Australia(Vict.-Tasm.).——FIG. 284,*3a,b. N. loyolensis* GILL, L.Dev. (base of Yeringian), Vict.; *3a,b,* ped.v. int., ×3.5, ×1 (338).——FIG. 284,*3c. N.* sp., L.Dev., Vict.; brach.v. int. (reconstr.) showing card. process *(cp)*, socket ridges *(sr)* and diverging septa with pits on top, ×5 (338).

Tornquistia PAECKELMANN, 1930, p. 227 [**Leptaena (Chonetes) polita* M'COY, 1855, p. 456; OD] [=*Paeckelmannia* LIKHAREV, 1934, p. 509 (obj.)]. Small, valves highly concavo-convex, ears well demarcated, shell smooth or faintly capillate when decorticated, spinules scattered, row of spines at high angle; brachial valve interior with 2 long diverging septa, median septum rare, alveolus present, socket ridges parallel to hinge. *L. Carb.-U. Carb.,* Eu.(G.Brit.-Eire-Ger.).——FIG. 284,*5.* **T. polita* (M'COY), L.Carb., Scot.(Stirlings.); *5a,b,* ped.v. vent. showing spine row, ×4; *5c,* ped.v. int. cast, ×3; *5d,e,* ped.v. int. cast and brach.v. int. (reconstr.) showing ridges diverging from hinge *(r)*, socket ridges *(sr)*, and septa *(s)*, in ped.v. represented by slit, ×8; *5f,* slab with 4 brach.v. int. and ped.v. cast, ×3 (632).

Subfamily RETICHONETINAE Muir-Wood, 1962

[Retichonetinae MUIR-WOOD, 1962, p. 62]

Median septum, lateral and accessory septa and alveolus present in brachial valve; hinge longitudinally ridged when decorticated, or crenulate; brachial ridges absent, spines oblique or high-angled (45 to 60 degrees). *L.Dev.-L.Carb.(Miss.).*

Retichonetes MUIR-WOOD, 1962, p. 62 [**Chonetes armatus* BOUCHARD-CHANTEREAUX in DE VERNEUIL, 1845, p. 241; OD]. Shell small, semicircular to subquadrate; valves moderately to highly concavo-convex, pseudodeltidium and chilidium developed, shell capillate or costellate, with growth lines or lamellae causing reticulation, spinules developed, socket ridges short, diverging from hinge. *L. Dev.-L. Carb.(Miss.),* Eu.(G. Brit.-Fr.-Belg.-Ger.-USSR)-Asia(Burma-Tibet)-W.Australia-N. Am.(Iowa-Md.-N. Y.).——FIG. 285,*1*; 286,*3.* **R. armatus* (BOUCHARD-CHANTEREAUX), U.Dev. (Frasn.), Fr.(Boulonnais); 285,*1a,* slab with several ped.v. ext. and single brach.v. int., ×2.5; 285,*1b,* ped.v. ext. (one with long spines) and brach.v. int., ×3; 285,*1c,* slab with brach.v. ext. and ped.v. int., ×2; 286,*3a,* brach.v. int. (reconstr.) showing alveolus separating median septum *(s)* from card. process *(cp)*, accessory septa *(as)*, rounded crenulations *(cr)*, hinge sockets *(hs)*, and lateral septa *(ls)*, ×2.7; 286, *3b,* ped.v. int. (reconstr.) showing hinge teeth *(ht)*, ridges along outer margin of diductor scar *(r)*, spines *(sp)*, crenulations *(cr)* and septum *(s)*, ×2.7 (586).

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

[Rugosochonetinae MUIR-WOOD, 1962, p. 64]

Median septum, lateral, and commonly accessory septa and alveolus developed in brachial valve; cardinal process bilobate or quadrilobate, brachial ridges prominent, dorsal interarea may be reflexed; shell capillate or smooth; median fold and sulcus variably developed; spines oblique (35 to 45 degrees) or high-angled. *L.Dev.-U.Perm.*

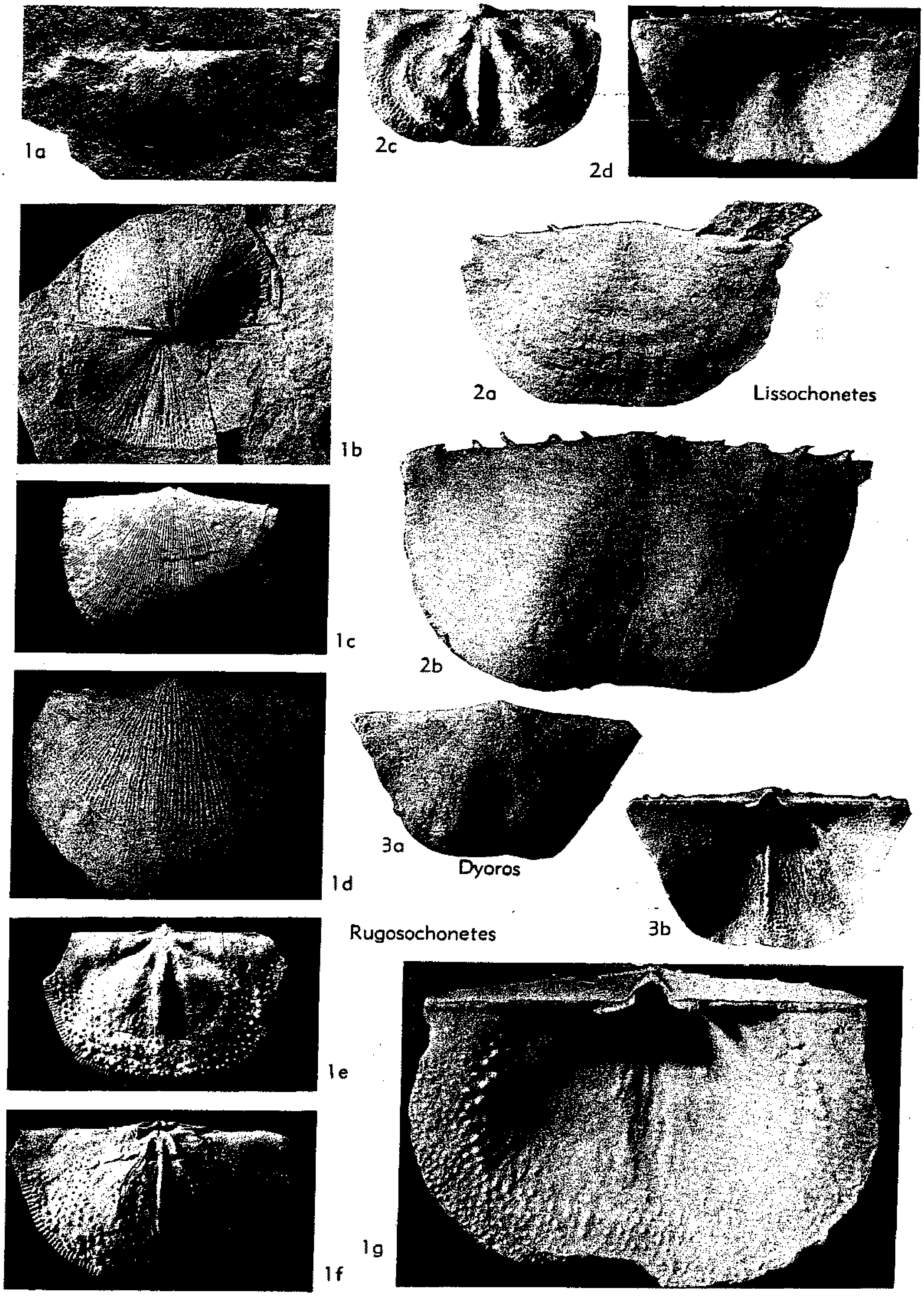


Fig. 287. Chonetidae (Rugosochonetinae) (p. *H*430).

Rugosochonetes Sokolskaya, 1950, p. 23 [*_Orthis hardrensis_ Phillips, 1841, p. 138; OD]. Shell small, plano- to slightly concavo-convex, dorsal interarea reflexed, pseudodeltidium and chilidium developed. Shell capillate, spinules numerous, dorsal median septum half of valve length, spines at angle of 45 to 60 degrees, socket ridges curved. _L.Carb.-U.Carb._, Eu.-Asia-Australia-N.Am.-?Afr.——Fig. 287,_1a,b_. *_R. hardrensis_ (Phillips), L.Carb.(Visean), Eng.(Yorks.); _1a_, ped.v. ext. with impression of spines along hinge, ×2; _1b_, ped.v. and brach.v. int. molds in contact along hinge, ×2 (586).——Fig. 287,_1c-g_. _R. celticus_ Muir-Wood, U.Carb.(Namur.), Scot.; _1c,d_, ped.v. ext., ×1.5, ×3; _1e,f_, brach.v. int., ×2; _1g_, ped.v. int., ×4 (586).

Dyoros Stehli, 1954, p. 312 [*_Chonetes consanguineus_ Girty, 1929, p. 409; OD]. Shell small to medium-sized, slightly concavo-convex, with median fold and sulcus; pseudodeltidium vestigial or absent, shell smooth except for growth lines, capillate if decorticated, spines oblique (30 to 45 degrees), dorsal septum long, socket ridges diverging from hinge. _L.Perm.-U.Perm._, N.Am.-?Eu.——Fig. 287,_3_; 288,_2_. _D. subliratus_ (Girty), Perm.(Word), USA(Tex.); 287,_3a,b_, ped.v. ext., int., ×1.5; 288,_2a,b_, brach.v. int., ×4, ×1.5; 288,_2c,d_, ped.v. int., ×4, ×6.5 (773).

Eolissochonetes Hoare, 1960, p. 220 [*_Chonetes laevis_ Keyes, 1888, p. 229 (_non_ Davidson, 1866) =*_E. keyesi_ Muir-Wood, 1962, p. 76; OD]. Differs from _Lissochonetes_ in its smaller dimensions and less marked ventral median sulcus, by development of long dorsal median septum and less defined brachial ridges. _M.Penn.(Desmoines.)_, N.Am.——Fig. 286,_1a_. *_E. keyesi_ Muir-Wood, USA (Mo.); brach.v. int., ×1.8 (429).——Fig. 286,_1b,c_. _E. bilobatus_ Hoare, USA(Mo.); _1b,c_, ped.v. int., ext., ×1.8 (429).

Lissochonetes Dunbar & Condra, 1932, p. 169 [*_Chonetes glaber_ Geinitz, 1866, p. 60 (_non_ Hall, 1857, p. 117)=_Chonetes geinitzianus_ Waagen, 1884, p. 621; OD]. Small to medium-sized; valves slightly concavo-convex with ill-defined fold and sulcus, pseudodeltidium present; shell smooth with fine growth lines and spinules, capillate if decorticated, spines long, at angle of about 40 degrees, dorsal septum may be anterior only or absent, socket ridges along hinge. _U.Carb._, Eu.-Asia-N.Afr.-Australia; _Penn.-Perm._, N.Am.-Asia.——Fig. 287,_2_. _L. geinitzianus_ (Waagen), U.Penn.(Virgil.), Neb. (_2a,b,d_), Ill. (_2c_); _2a,b_, ped.v. ext. with spine row, ×3.5; _2c,d_, brach.v. int., ext., ×3 (270).

Mesolobus Dunbar & Condra, 1932, p. 134, 159 [*_Chonetes mesolobus_ Norwood & Pratten, 1855, p. 27; OD]. Small, valves moderately concavo-convex, normally with ventral sulcus bearing median fold, and dorsal fold bearing median sulcus; pseudodeltidium and chilidium present; shell capillate or smooth, commonly lamellose; spines oblique, spinules numerous; dorsal median septum long, anteriorly elevated and serrated, inner socket ridges parallel to hinge. _Penn._, N.Am.; _?L.Perm._, Eu.——Fig. 285,_3_; 286,_4_. *_M. mesolobus_ (Norwood & Pratten), M.Penn. (Desmoines.), USA (Ill.); 285,_3a-c_, ped.v. ext., ×2.5, ×2, ×2; 285, _3d_, brach.v. int., ×4; 286,_4a_, ped.v. int. (reconstr.), showing adductor scar (_ad_), hinge teeth (_ht_), ridge along post. margin of diductor scars (_r_), int. spine openings (_so_), spine bases (_spb_), and vascular trunks (_vt_), ×4; 286, _4b_, brach.v. int. (reconstr.) showing alveolus (_a_), adductor scars (_ad_), brachial ridges (_br_), card. process (_cp_), lateral septa (_ls_), median septum (_s_), and socket ridges (_sr_), ×4 (270).

Plicochonetes Paeckelmann, 1930, p. 222, 306, 311 [*_Chonetes buchianus_ deKoninck, 1843, p. 208; OD]. Small to medium-sized, concavo-convex, pedicle valve medianly arched, pseudodeltidium small or absent; shell costate or costellate, rarely bifurcating, numerous growth lines, spines at high angle (55 to 70 degrees), spinules developed; septum in brachial valve extending half of its length or absent, inner socket ridges short, curved. _L.Dev.-U.Dev._, Eu.(Eng.-Fr.-Ger.)-Asia; _L.Carb.(Miss.)_, Eu. - Asia - N. Afr.-Australia-N. Am.; _U.Carb.(Namur.)_, Eu.(Eng.-Czech.).——Fig. 285, _2_. *_P. buchianus_ (deKoninck), L.Carb.(U.Visean) or U.Carb.(Namur.), Eng.(Yorks.); _2a,b_, ped.v. ext., ×1, ×1.5; _2c_, ped.v. int., ×3; _2d_, brach.v. int., ×3 (483).

Quadrochonetes Stehli, 1954, p. 309 [*_Chonetes quadratus_ Girty, 1929, p. 407 (_non C. uralica quadratus_ Bolkhovitinova & Markov, 1926, p. 26, _non_ Nikitin, 1890)=_Q. girtyi_ Stehli, 1954; OD]. Small, quadrate, strongly concavo-convex, with prominent dorsal fold and deep ventral sulcus, ears large; shell smooth, with spines at angle of 75 degrees; median septum of brachial valve low, extending about half of its length, brachial ridges obscure or absent, socket ridges short, curved. _Penn.-L.Perm._, N.Am.; _L.Perm._, Eu. (USSR).——Fig. 286,_2_. _Q. girtyi_, L.Perm. (Leonard), USA(Tex.); _2a,b_, brach.v. int., ped. v. ext., ×2.7 (773).

Subfamily CHONETINELLINAE Muir-Wood, 1962

[Chonetinellinae Muir-Wood, 1962, p. 85]

Internally near to Rugosochonetinae, but no accessory septa; median fold and sulcus usually strong; dorsal interarea commonly reflexed; shell capillate to costate; spinules numerous; spines parallel to hinge. _U.Carb. (Penn.)-U.Perm._

Chonetinella Ramsbottom, 1952, p. 13 [*_Chonetes flemingi_ Norwood & Pratten, 1855, p. 26; OD]. Small, bilobate, highly concavo-convex, with deep median sulcus and high fold, pseudodeltidium and chilidium rudimentary or absent; shell capillate, with spinules; cardinal process small, bilobed, with alveolus, median septum long, anteriorly elevated; socket ridges long, parallel to hinge, brachial ridges prominent. *U.Carb.(Penn.)*, Eu.-N.Am.-S.Am.; *L.Perm.*, N.Am.-Asia.——Fig. 288,*1*. *C. flemingi (Norwood & Pratten), Penn., Tex. *(1a-e)*, Ill. *(1f)*; *1a,b*, ped.v. ext., brach.v. ext., ×3; *1c,d*, ped.v. ext. with spines, brach.v. ext. and interarea, ×8; *1e,f*, ped.v. int., brach.v. int., ×3 (654).

Neochonetes Muir-Wood, 1962, p. 87 [*Chonetes dominus R. H. King, 1938, p. 259; OD] [=*Quadranetes* Sadlick, 1963, p. 721 (obj.)].

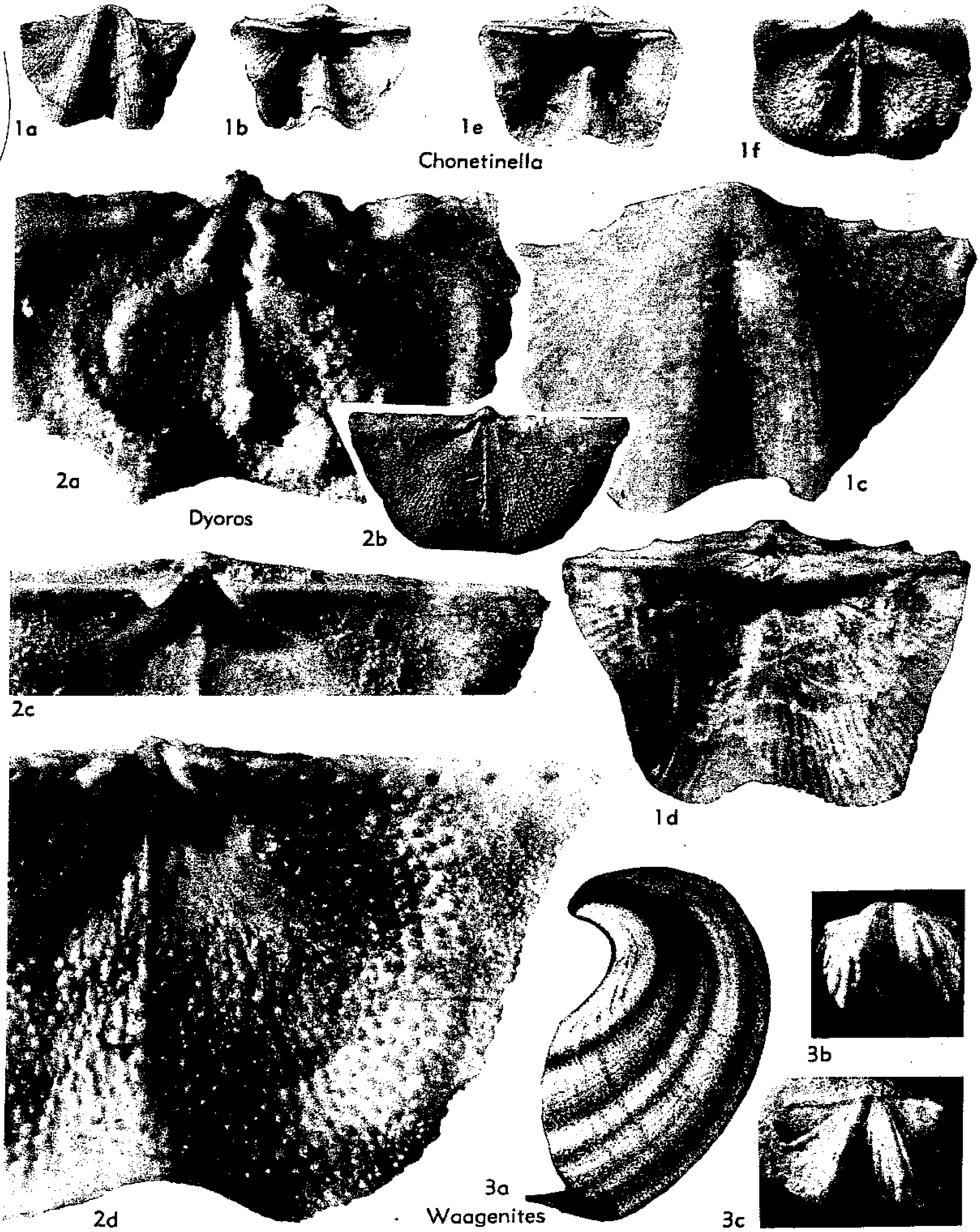


Fig. 288. Chonetidae (Rugosochonetinae) *(2)*, (Chonetinellinae) *(1,3)* (p. *H*430-*H*433).

Small to medium-sized, plano- to slightly concavo-convex, ventral valve may be sulcate; pseudodeltidium vestigial or absent, chilidium present; capillate or smooth anteriorly, many spinules, hinge spines numerous; median septum anteriorly elevated, with inner socket ridges and commonly outer ones also. *U.Carb.(Penn.)-U.Perm.*, cosmop.——Fig. 289,*1a,b*. *N. transversalis* (Dunbar & Condra), U.Penn., USA(Neb.); *1a,b*, ped.v. ext., brach.v. int., ×2 (471).——Fig. 289,*1c*. *N. granulifer* (Owen), Penn., USA(Ala.); ped.v. int., ×2 (471).——Fig. 289,*1d-g*. *N. dominus

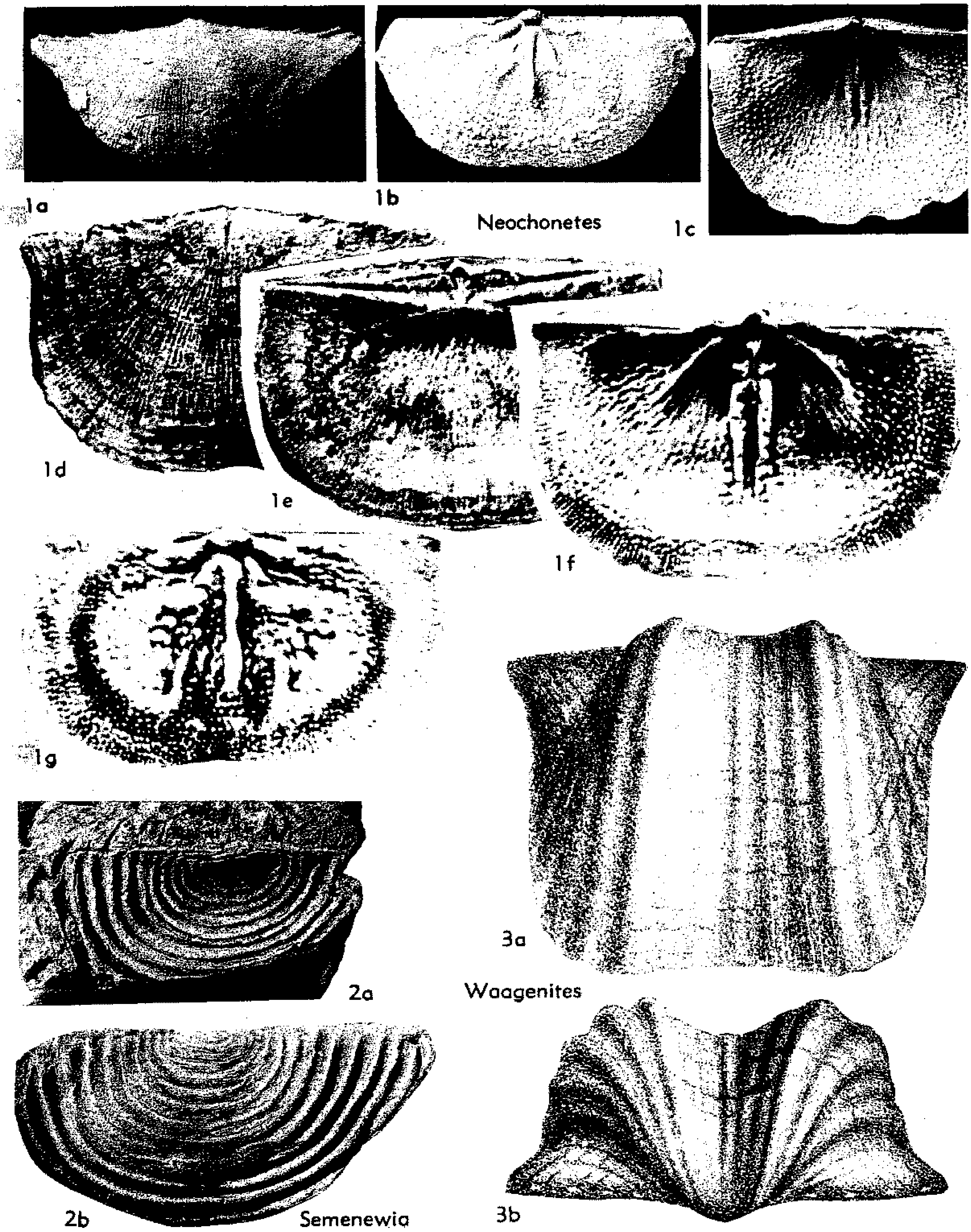


Fig. 289. Chonetidae (Chonetinellinae) *(1,3)*, (Semenewiinae) *(2)* (p. *H*431-*H*433).

(R. H. King), Penn., USA(Tex.); *1d,e*, ped.v. ext., brach.v. ext., ×3; *1f,g*, ped.v. int., brach.v. int., ×3 (471).

Waagenites Paeckelmann, 1930, p. 223 [**Chonetes grandicostus* Waagen, 1884, p. 638; OD] [=*Dienerella* Reed, 1931, p. 18 (obj.)]. Small, quadrate, pedicle valve highly convex, with deep median sulcus, no pseudodeltidium, umbo much incurved; valves with few coarse costae, or costellate, rarely capillate; ears large, smooth, dorsal septum medianly developed, socket ridges short. *U.Perm.*, Asia(Pak.-Timor)-?N.Am.-Arctic (Spitz.).——Fig. 288,*3*; 289,*3*. **W. grandicostus* (Waagen), U.Perm.(U.Productus Ls.), Pak.(Punjab); 288,*3a*, ped.v. lat., ×4; 288,*3b,c*, ped.v. ext., ×1.5, ×2; 289, *3a,b*, ped.v. ext., post., ×4 (845) (288,*3a*, 289,*3a,b*, after Waagen).

Subfamily SEMENEWIINAE Muir-Wood, 1962

[Semenewiinae Muir-Wood, 1962, p. 91]

Median septum in each valve, valves ornamented by concentric rugae, spines vertical. *L.Carb.(Tournais.-Visean).*

Semenewia Paeckelmann, 1930, p. 217, 224 [**Chonetes concentricus* deKoninck, 1874, p. 186; OD]. Small to medium-sized, semicircular, slightly concavo-convex, interareas low, pseudodeltidium present; shell with concentric rugae and no radial ornament, spinules developed; internal characters imperfectly known. *L.Carb. (Tournais.-Visean)*, Eu.——Fig. 289,*2*. **S. concentrica* (deKoninck), Visean, Belg.; *2a,b*, ped.v. ext. with curved erect spines, ×2 (483).

[**Subfamily Uncertain.—Eccentricosta, Nix,** *see* p. *H*904.]

Family EODEVONARIIDAE Sokolskaya, 1960

[Eodevonariidae Sokolskaya, 1960, p. 223]

Hinge denticulate, hinge teeth and sockets reduced; with long curving inner socket ridges, alveolus absent, strong dorsal septum and lateral septa, spines low-angled. *L.Dev.-M.Dev.*

Eodevonaria Breger, 1906, p. 534 [**Chonetes arcuatus* Hall, 1857, p. 76; SD, Schuchert & LeVene, 1929, p. 57]. Small to medium-sized, laterally extended, strongly concavo-convex, with incurved ventral umbo, pseudodeltidium developed; shell capillate, spinules rare; cardinal process bilobate or quadrilobate. *L.Dev.-M.Dev.*, Eu.-N.Afr.-S.Afr.-N.Am.-S.Am.——Fig. 290,*1*. *E. dilatata* (Römer), L.Dev.(Emsian), Ger.; *1a*, brach.v. int., ×1; *1b*, ped.v. int. with denticulate hinge, ×1; *1c,d*, squeeze of brach.v. int. with post. view showing card. process, ×2; *1e*, decorticated ped.v., ×1.5; *1f*, ped.v. int. (reconstr.) showing adductor scars *(ad)*, denticulate hinge *(dh)*, diductor scars *(did)*, and median septum *(s)*, ×1.25 (117).

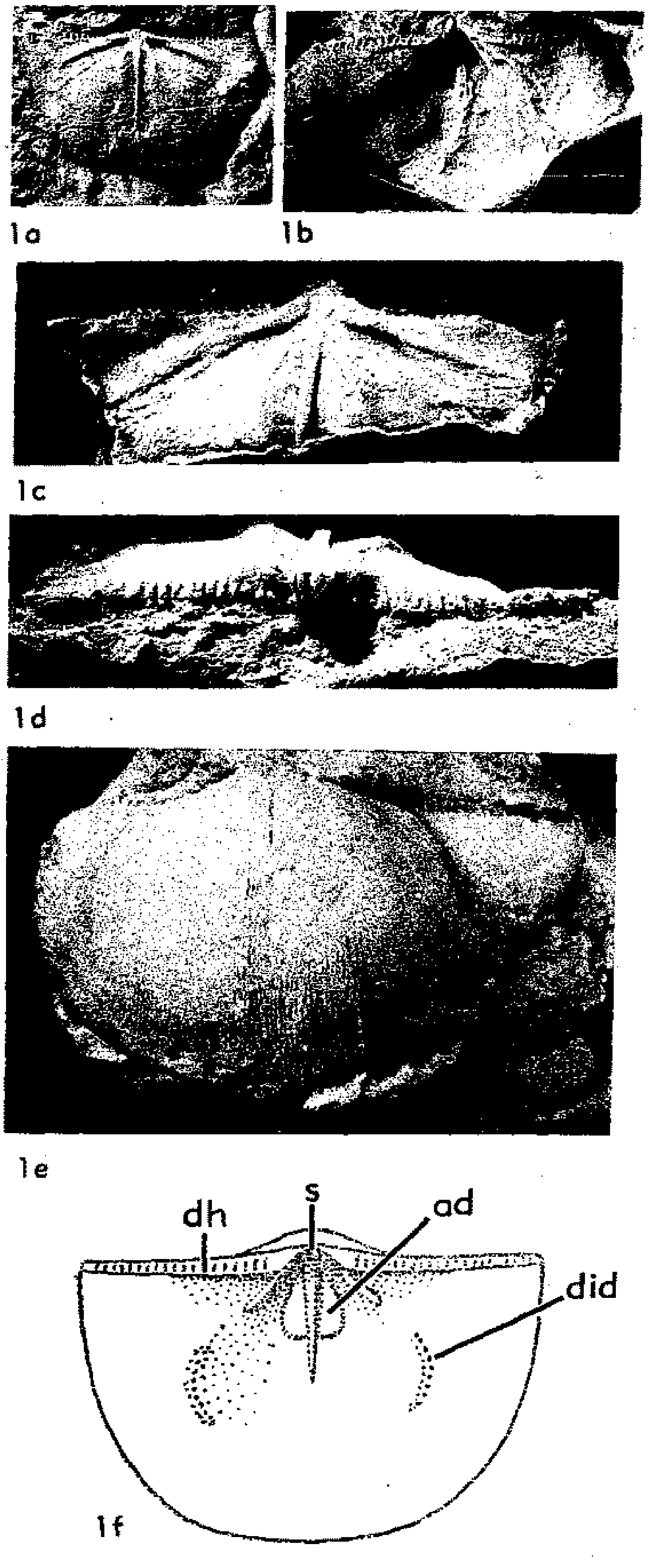


Fig. 290. Eodevonariidae (p. *H*433).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

[Chonostrophiidae Muir-Wood, 1962, p. 95]

Shell convexity reversed; ventral muscle area lobed, with raised rim, as in strophomenoids; ventral septum present, dorsal septum low or absent; cardinal process bilobate, supported laterally by short socket ridges. *U.Sil.-M.Dev.*

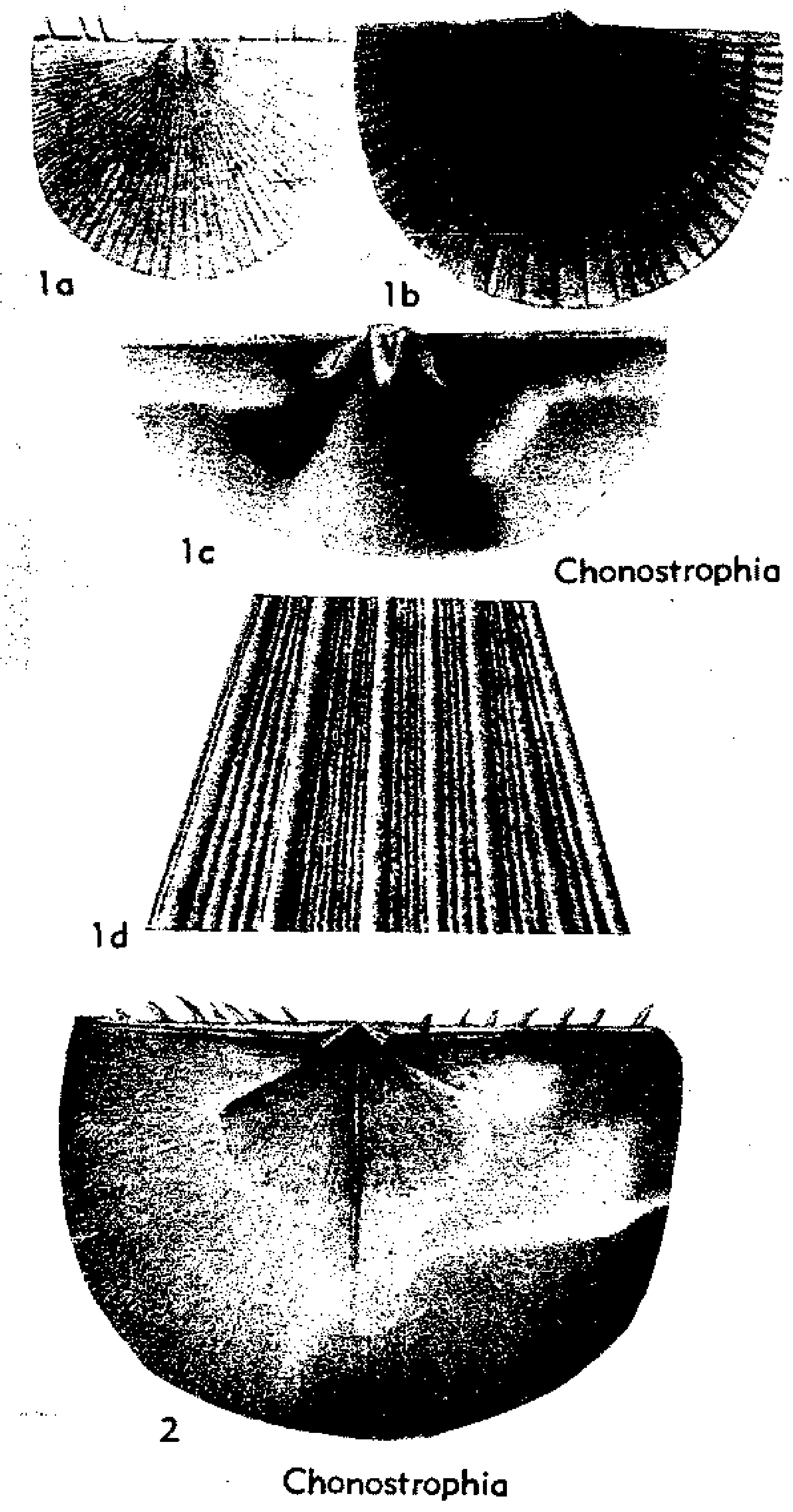


FIG. 291. Chonostrophiidae (p. *H*434).

Chonostrophia HALL & CLARKE, 1892, p. 310 [**Chonetes reversa* WHITFIELD, 1882, p. 213; OD (M)]. Medium-sized, semicircular, thin-shelled, pedicle valve resupinate, brachial valve slightly convex, interareas linear, pseudodeltidium present; valves costellate, with intervening capillae, spines long, vertical. *U.Sil.-M.Dev.*, N.Am.(Can.-USA)-S. Am.(Colombia-Bolivia-Argentina). ——FIG. 291,*1*. **C. reversa* (WHITFIELD), L.Dev.(U. Helderberg.), N.Am., Can.(Ont.) *(1a)*, USA (Ohio) *(1b-d)*; *1a,b*, ped.v. ext., ×2.5; *1c*, brach.v. int. showing card. process, ×9; *1d*, ext. ornament, ×9 (396).——FIG. 291,*2*. *C. complanata* (HALL), L.Dev.(Oriskany), USA(N.Y.); ped.v. int., ×1 (396).

Chonostrophiella (*see* p. *H*904).

Tulcumbella (*see* p. *H*905).

Family DAVIESIELLIDAE Sokolskaya, 1960

[Daviesiellidae SOKOLSKAYA, 1960, p. 223]

Medium-sized to large, pedicle valve usually thickened; median septum in each valve, cardinal process bilobate or quadrilobate; brachial ridges may be developed, adductor scars wholly or partly dendritic or striated, detached rounded accessory adductor scars present; rarely row of oblique or high-angled spines. *?M.Dev., U.Dev.-L. Carb., ?U.Carb.(Namur.).*

Subfamily DAVIESIELLINAE Sokolskaya, 1960

[*nom. transl.* MUIR-WOOD, 1962, p. 96 (*ex* Daviesiellidae SOKOLSKAYA, 1960, p. 223)]

Dorsal septum massive, supporting cardinal process, without alveolus, brachial ridges anteriorly directed, adductor scars dendritic; interareas low. *L.Carb. (Visean).*

Daviesiella WAAGEN, 1884, p. 613 [**Productus llangollensis* T. DAVIDSON, 1863, p. 277; SD OEHLERT, 1887, p. 1280]. Large, highly concavo-convex, pedicle valve massive, much thickened; pseudodeltidium lacking, chilidium present; capillate or costellate, external spine row not observed. *L.Carb.(Visean)*, Eu.(Eng.-Wales).——FIG. 292,*1*. **D. llangollensis* (DAVIDSON), Wales(Denbighs.); *1a,b*, ped.v. vent., lat., ×1; *1c*, interareas showing hinge teeth and chilidium of damaged specimen, ×2; *1d,e*, ped.v. int., brach.v. int., ×1 (201).

Subfamily DELEPINEINAE Muir-Wood, 1962

[Delepineinae MUIR-WOOD, 1962, p. 99]

Dorsal median septum fine, not supporting cardinal process, alveolus present, lateral septa short, brachial ridges not observed; pseudodeltidium and chilidium present, ventral interarea high, with spine roots as parallel incisions, some forms with external row of oblique spines. *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.).*

Delepinea MUIR-WOOD, 1962, p. 99 [**Productus comoides* J. SOWERBY, 1822, p. 31; OD]. Large, moderately concavo-convex; pedicle valve posteriorly thickened, layers weathering characteristically; capillate or costellate, spinules present, spine row rarely preserved. *L.Carb.(Tournais.-Visean)*, Eu.(G. Brit.-Fr.-Belg.-Ger.-USSR-N.Afr.-Asia.——FIG. 293,*1*. **D. comoides* (J. SOWERBY), Visean, Eng.(Westmorland); *1a,b*, ped.v. ext., brach.v. view, ×1 (586).——FIG. 293,*2*. *D. destinezi* (VAUGHAN), Visean, N.Ire.(Fermanagh); *2a,b*, ped.v. int. showing spine roots in interarea and accessory adductor scars, ×1 (586).——FIG. 293,*3*. *D. carinata* (GARWOOD), Visean, Eng.(Westmorland); *3a*, ped.v. ext., ×1; *3b*, brach.v. int., ×1 (586).

Megachonetes Sokolskaya, 1950, p. 42 [**Chonetes compressa* Sibly, 1908 (*non* Waagen, 1884, p. 630) =*C. siblyi* I. Thomas, 1919, p. 612 (also Paeckelmann, 1930, p. 274); OD]. Medium-sized to large, plano- to slightly concavo-convex, pedicle valve slightly thickened, interareas commonly high, shell finely capillate, spinules numerous, spines curved, extending at angle of 45 to 60 degrees. *?M.Dev.*, Eng.; *U.Dev.-L.Carb. (Tournais.-U.Visean), ?U.Carb.(Namur.),* Eu.(G. Brit.-Eire-Fr.-Belg.-Ger.-USSR)-?Asia-N.Afr. —— Fig. 294,*1*. *M. siblyi* (I. Thomas), L.Carb. (Visean), Eng.(Yorks.-Derbys.); *1a-c,* ped.v. vent., brach.v. ext. and lat. views, ×1.25; *1d,* brach.v. view showing interarea, ×2; *1e,* ped.v. post. with interarea and pseudodeltidium, ×1;

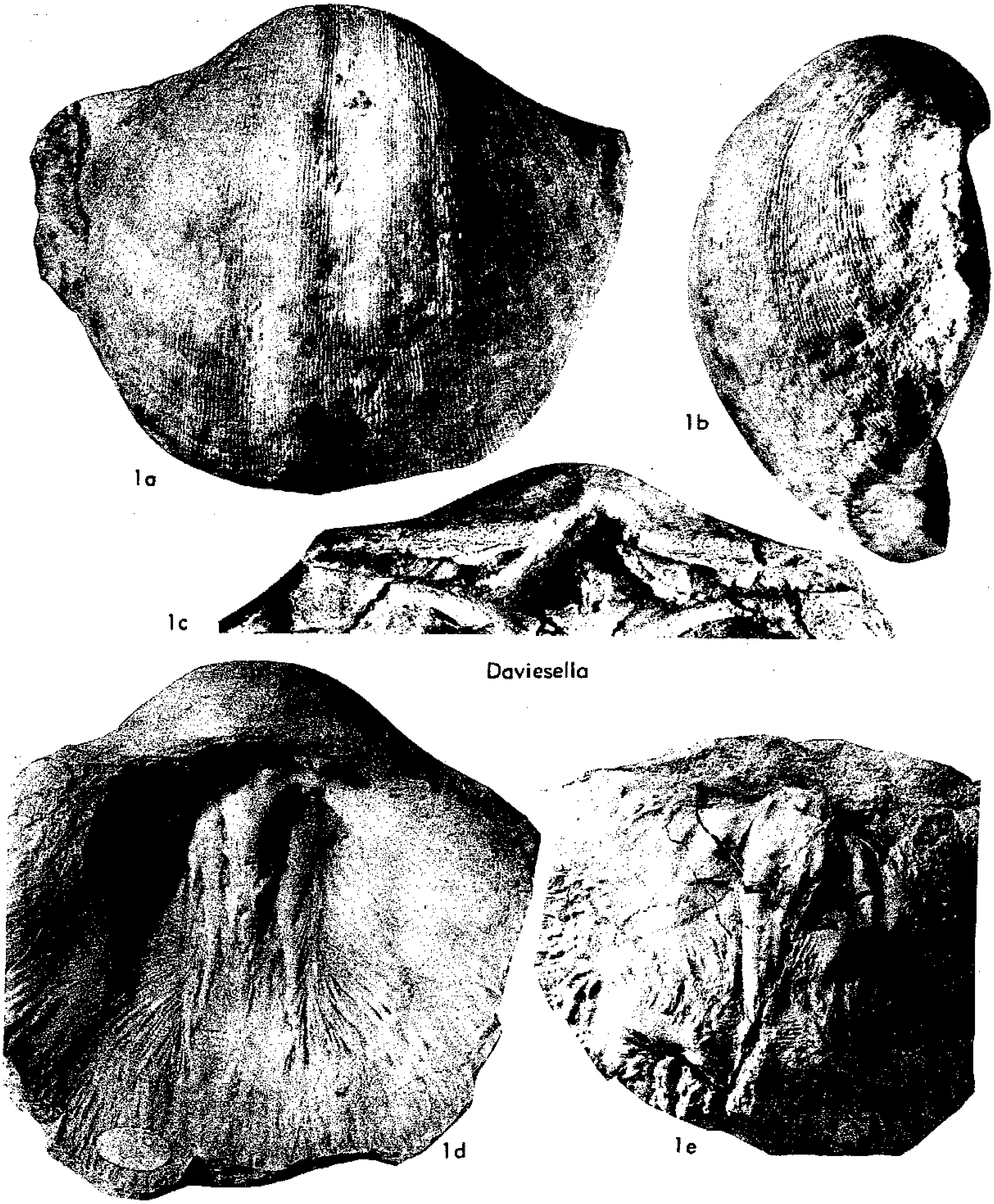


Fig. 292. Daviesiellidae (Daviesiellinae) (p. *H*434).

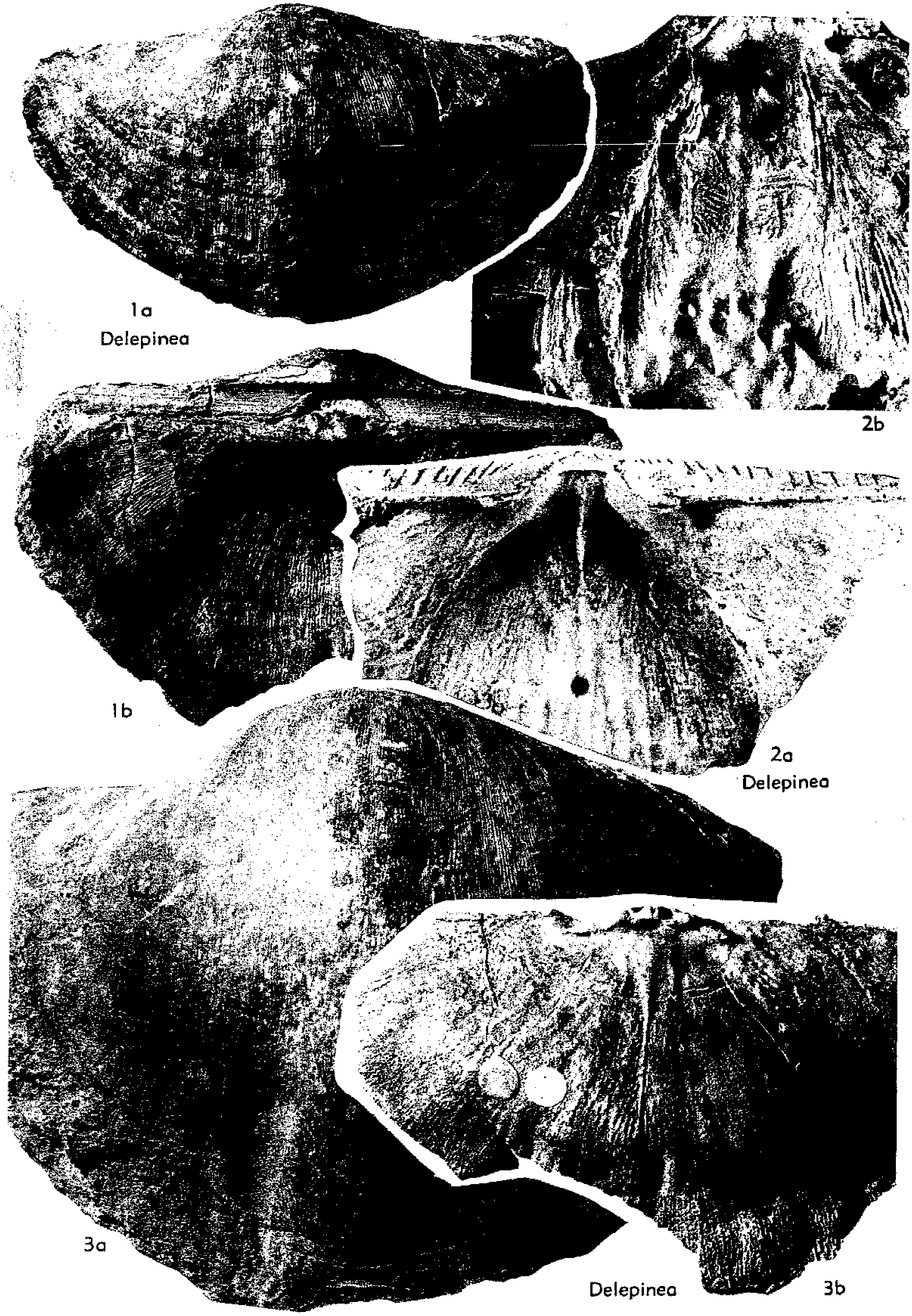


FIG. 293. Daviesiellidae (Delepineinae) (p. *H*434).

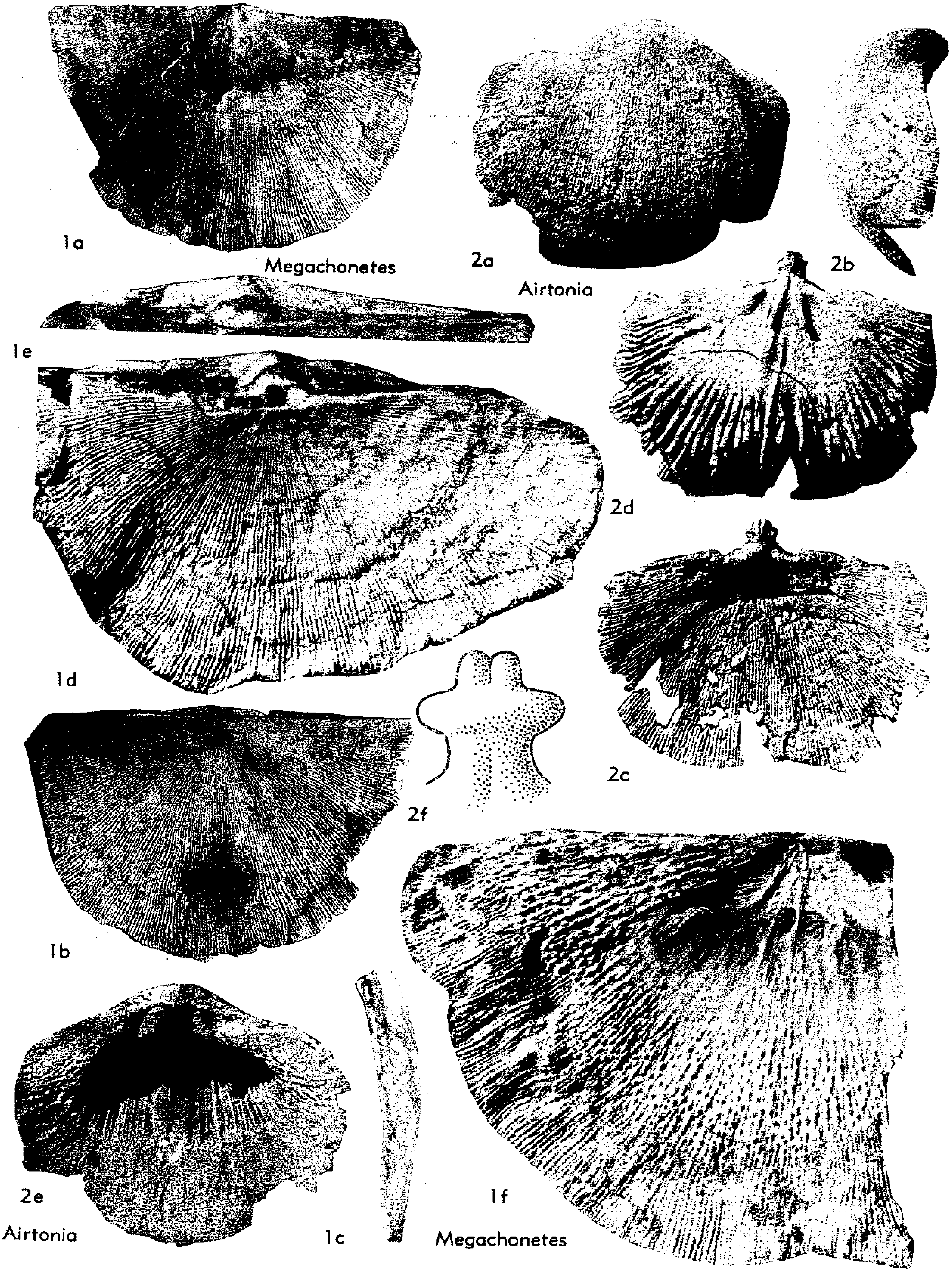


Fig. 294. Daviesiellidae (Delepineinae) *(1)*, (Airtoniinae) *(2)* (p. *H*435, *H*438).

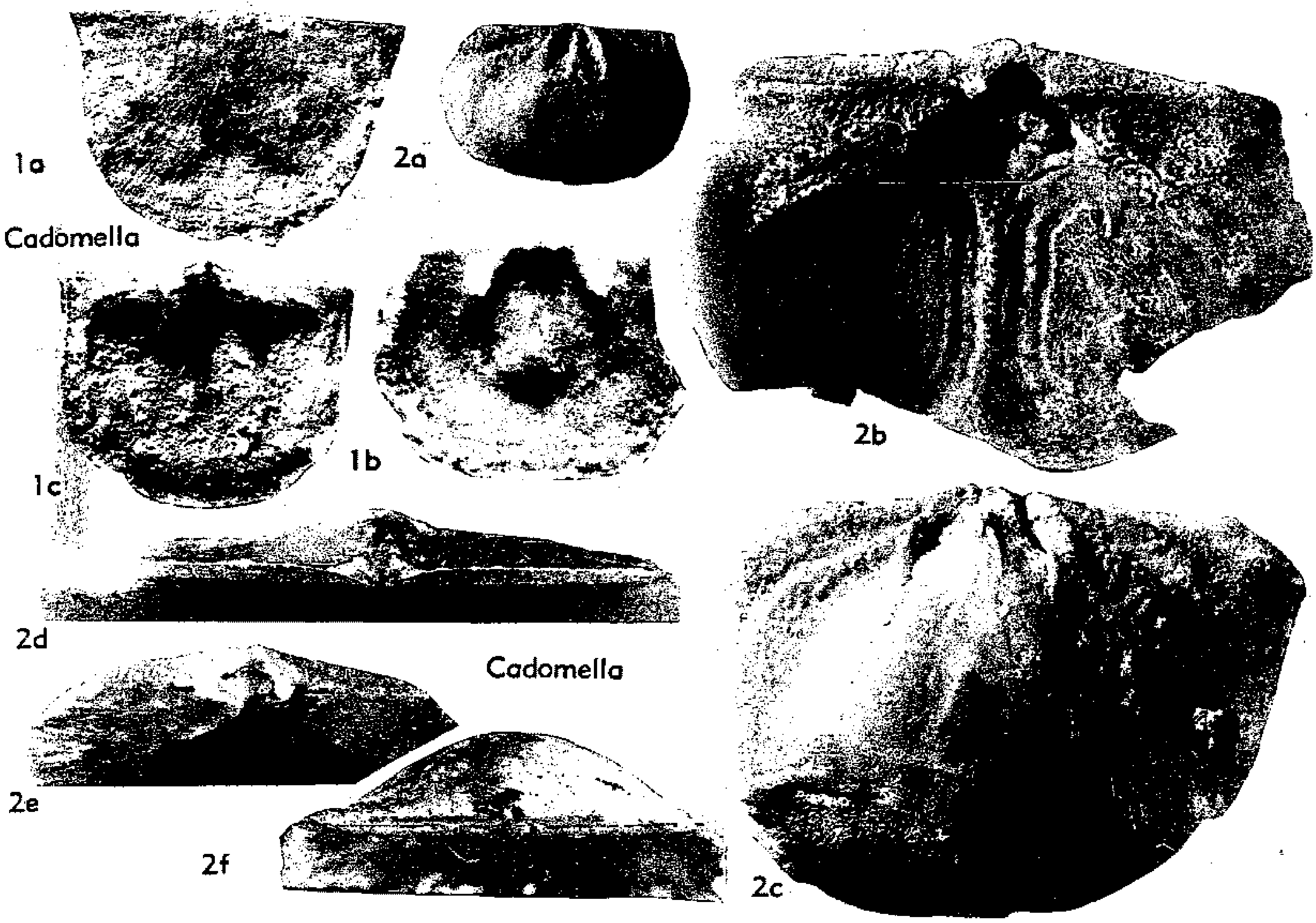


FIG. 295. Cadomellidae (p. *H438-H439*).

1f, ped.v. int. showing accessory adductor scars and pseudopunctate shell structure, ×2 (586).

Subfamily AIRTONIINAE Muir-Wood, 1962

[Airtoniinae MUIR-WOOD, 1962, p. 107]

Dorsal breviseptum and two strong diverging lateral septa extending from prominent trilobate or quadrilobate cardinal process; anterior ridges platelike; brachial ridges laterally directed, adductor scars not dendritic, ventral interarea low, no dorsal interarea. *L.Carb.(Visean).*

Airtonia COPE, 1934, p. 273 [**A. hudsoni*; OD]. Medium-sized, highly concavo-convex, small pseudodeltidium or posterior callosity; shell finely capillate, spine row along hinge. *L.Carb.(L.Visean),* Eu.(Eng.-Belg.-Fr.).——FIG. 294,*2*. **A. hudsoni,* Eng.(Yorks.); *2a,b,* ped.v. vent., lat., ×1; *2c,d,* brach.v. ext., int., showing prominent card. process, ×1; *2e,* ped.v. int., ×1; *2f,* card. process, ×5 (199).

Suborder and Family UNCERTAIN

Reticulatochonetes BUBLICHENKO, 1956, p. 97 [**R. lautus*]. Imperfectly known, possibly a productoid. Said to have concavo-convex valves with interareas and spines on ventral valve, reticulate ornament and bilobate cardinal process. *L.Carb. (Tournais.),* Asia(Kazakh.) (126).

Superfamily CADOMELLACEA Schuchert, 1893

[*nom. transl.* MUIR-WOOD, 1955, p. 90 (*ex* Cadomellinae SCHUCHERT, 1893, p. 153, *non* MUNIER-CHALMAS MS)]

Small forms having functional pedicle throughout life with apical foramen, interarea in each valve and hinge teeth and sockets; hinge spines not developed; shell structure lamellar, fibrous, with internal layer pseudopunctate. *L.Jur.(U.Lias).*

Family CADOMELLIDAE Schuchert, 1893

[*nom. transl.* MUIR-WOOD, 1955, p. 90 (*ex* Cadomellinae SCHUCHERT, 1893, p. 153)]

Median septa, brachial ridges and vascular markings variably developed, muscle area wholly or partly surrounded by raised rim, delthyrium closed by small triangular pseudodeltidium and by external face of lobate cardinal process, possibly bordered by chilidial plates. *L.Jur.(U.Lias).*

Cadomella OEHLERT in FISCHER, 1887, p. 1285 (*non* MUNIER-CHALMAS MS) [**Leptaena moorei* DAVIDSON, 1850, p. 17; OD]. Valves slightly concavo-convex, laterally elongated with greatest width along hinge, finely capillate or smooth;

low anterior septum in each valve, brachial ridges obscure. *L.Jur.(U.Lias.),* Eu.(Eng.-Fr.).——Fig. 295,*1.* **C. moorei* (Davidson), Fr.; *1a-c,* brach.v. ext. and int., ped.v. int., ×10 (Muir-Wood, n). ——Fig. 295,*2*; 296,*1. C. davidsoni* (Eudes-Deslongchamps), Fr.; 295,*2a,* brach.v. int., ×2; 295, *2b,* ped.v. int. with teeth and mantle-canal markings, ×4; 295,*2c,* brach.v. int. showing papillae and brachial ridges, ×4; 295,*2d,* interarea showing pseudodeltidium, ×4; 295,*2e,* hinge of both valves showing teeth, sockets, and exterior part of cardinal process, ×4; 295,*2f,* ped.v. foramen, ×4; 296,*1a,* brach.v. view of shell showing interareas, foramen, and ext. card. process, ×3; 296, *1b,* ped.v. view of shell, ×3 (224).

PRODUCTIDINA

[Materials for this suborder prepared by Helen M. Muir-Wood]

The suborder Productidina includes the largest, as well as the most bizarre and aberrant, brachiopods known at present. Owing to its world-wide distribution and range of about a hundred and fifty million years, a very considerable number of genera and species have been recognized. The ancestors of this remarkable group, as well as the relationship of the various families, are still uncertain. It has been cited as an example of explosive evolution on account of the rapid increase in numbers after the first appearance of the Strophalosiacea and Productacea in the Lower Devonian.

The suborder Productidina, as here defined, includes the superfamilies Strophalosiacea, Richthofeniacea, and Productacea. These are at present subdivided into 20 families and 39 subfamilies, and 179 genera.

RANGE AND DISTRIBUTION

The Productidina have a world-wide distribution, but are especially abundant in the Mississippian, Pennsylvanian, and Permian of North America.

The range of the two superfamiiles Strophalosiacea and Productacea is from Lower Devonian through Permian. The Richthofeniacea range from Pennsylvanian to Permian (Fig. 297).

The earliest strophalosiacean genus at present known is *Devonalosia* from an equivalent of the Onondaga Limestone of Gaspé Peninsula, Quebec, while *Spinulicosta* from the Onondaga of Ohio is the earliest productacean. In both these genera teeth and sockets are developed. An interarea occurs in each valve, with pseudodeltidium but no chilidium. The ornament is spinose in both *Devonalosia* and *Spinulicosta,* but the development of clasping spines and a cicatrix in *Devonalosia* indicates close attachment of the shell in this genus.

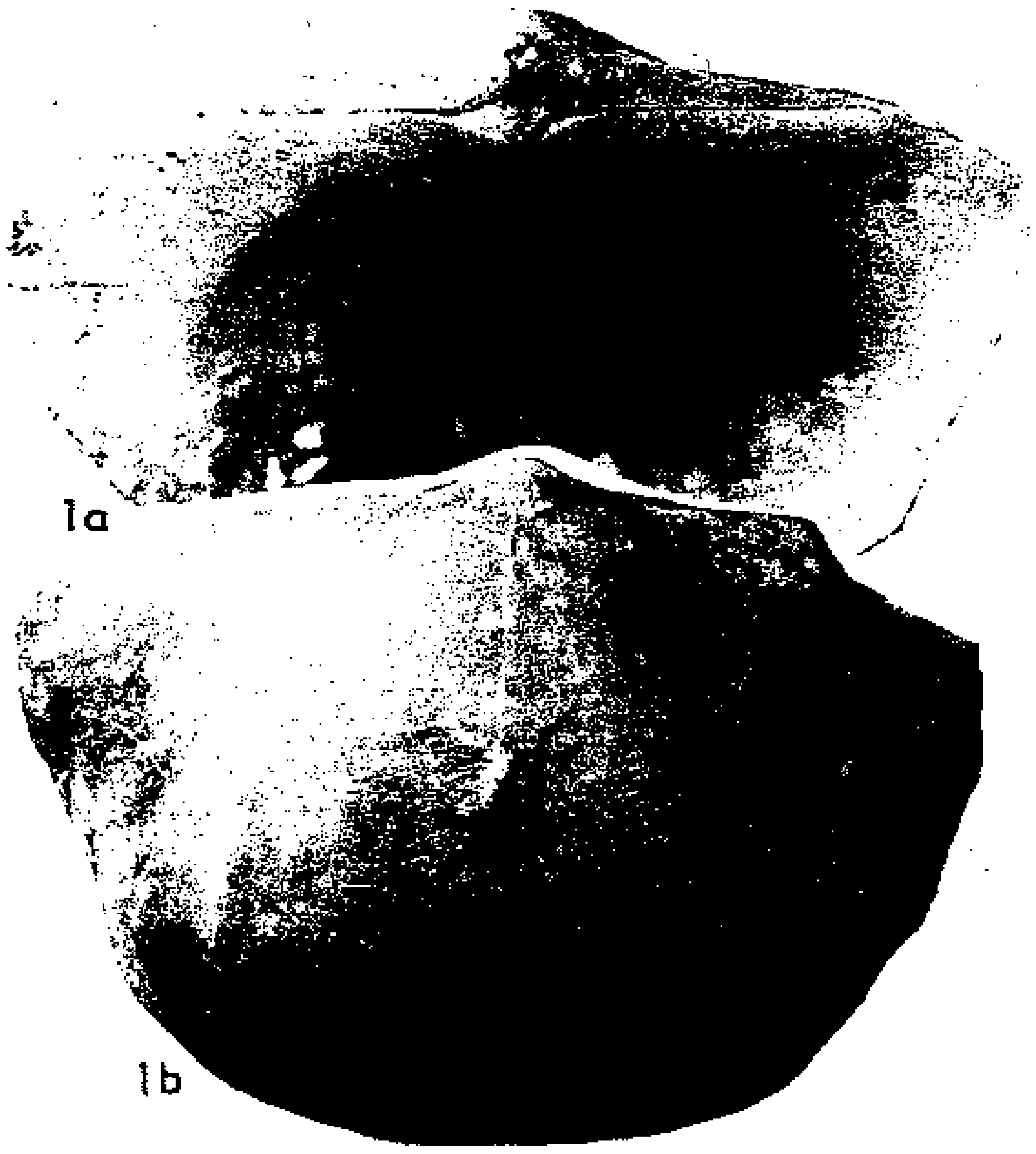


Fig. 296. Cadomellidae (p. *H*438-*H*439).

Both stocks are clearly unrelated to the chonetoids, formerly considered to be the ancestors of the productoids, and it is probable that they were derived from some Silurian or early Devonian strophomenoid, such as the genus *Leptaenisca,* in which brachial ridges are prominently developed.

The strophalosiaceans were not numerous in Devonian and Carboniferous times but were locally abundant in the Permian.

The productaceans abounded from the Upper Devonian onward, showing considerable variation in size and ornament. The largest brachiopods known—*Gigantoproductus* and *Titanaria,* from 12 to 15 inches in width—occurred in the upper part of the Lower Carboniferous, the former genus having an almost world-wide distribution, but both having a short duration.

In the Upper Carboniferous the number of genera declined somewhat, but a great increase occurred in the Permian when a multiplicity of new genera appeared, many

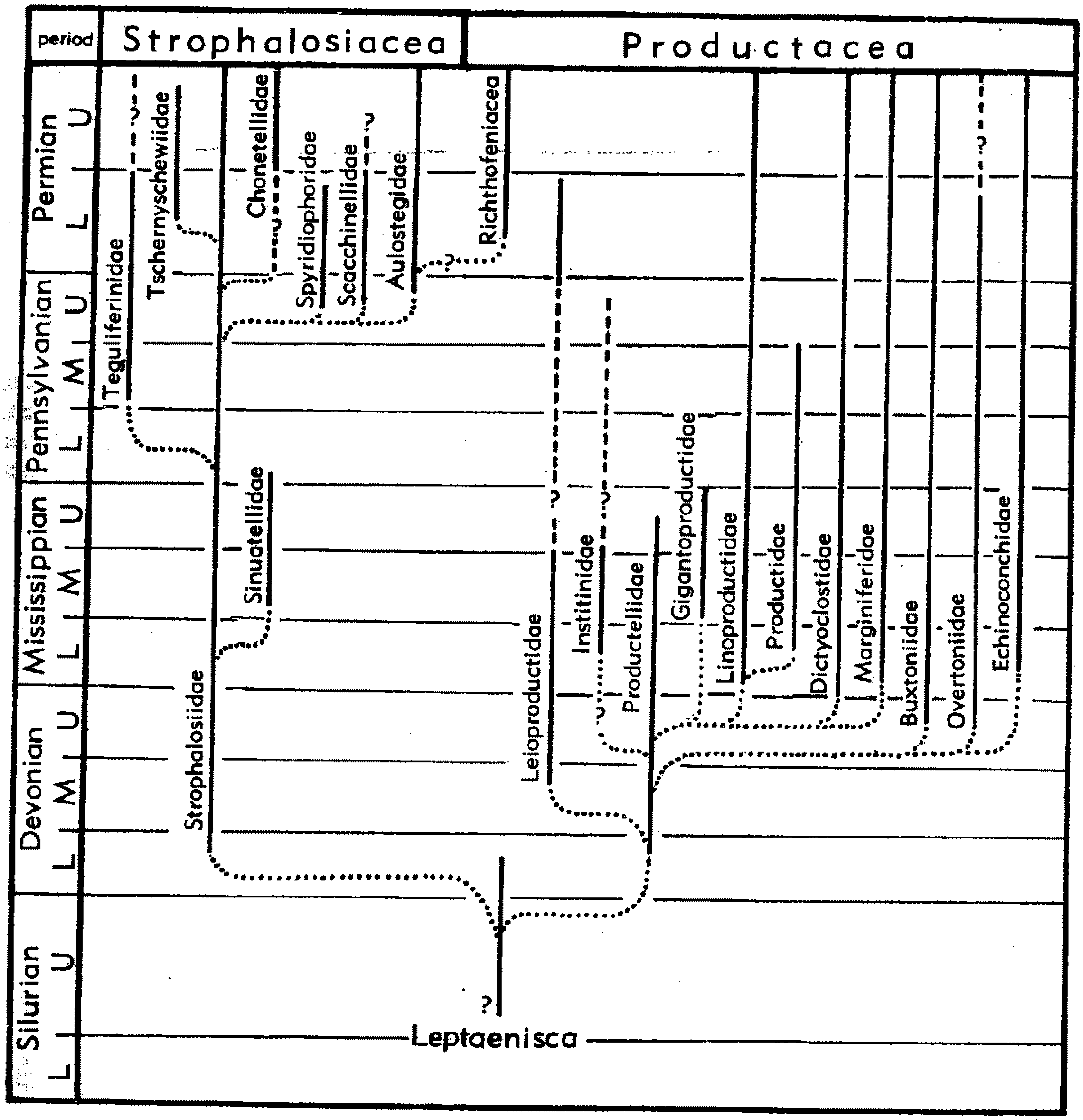


FIG. 297. Stratigraphic distribution and inferred phylogeny of productoid family assemblages (587).

of bizarre type, such as the richthofeniids and scacchinellids, with conical shells and rootlet spines, and other genera with extravagant development of spines and frills.

The productoids died out in the Permian, though some of the Triassic spiriferoids, such as *Koninckina* and *Koninckella,* with calcified dorsoventral spiralia, and *Thecospira,* with a pseudopunctate shell, may have been derived from the Productidina.

LIFE HABITS

No pedicle was developed in the productoids, and many species lived free and unattached. Such forms frequently had long, symmetrically placed spines to support the shell, so that the anterior margin was kept free from the mud of the sea bottom. Some species were attached to a foreign body by cementation of the umbo of the pedicle valve in the early growth stages, often assisted by clasping or attachment spines.

Examples of the young of a Mississippian productellid, *Orbinaria pyxidata* (HALL), have a ringlike structure on the umbo of the pedicle valve (Fig. 298), and it is suggested that this served to attach the young

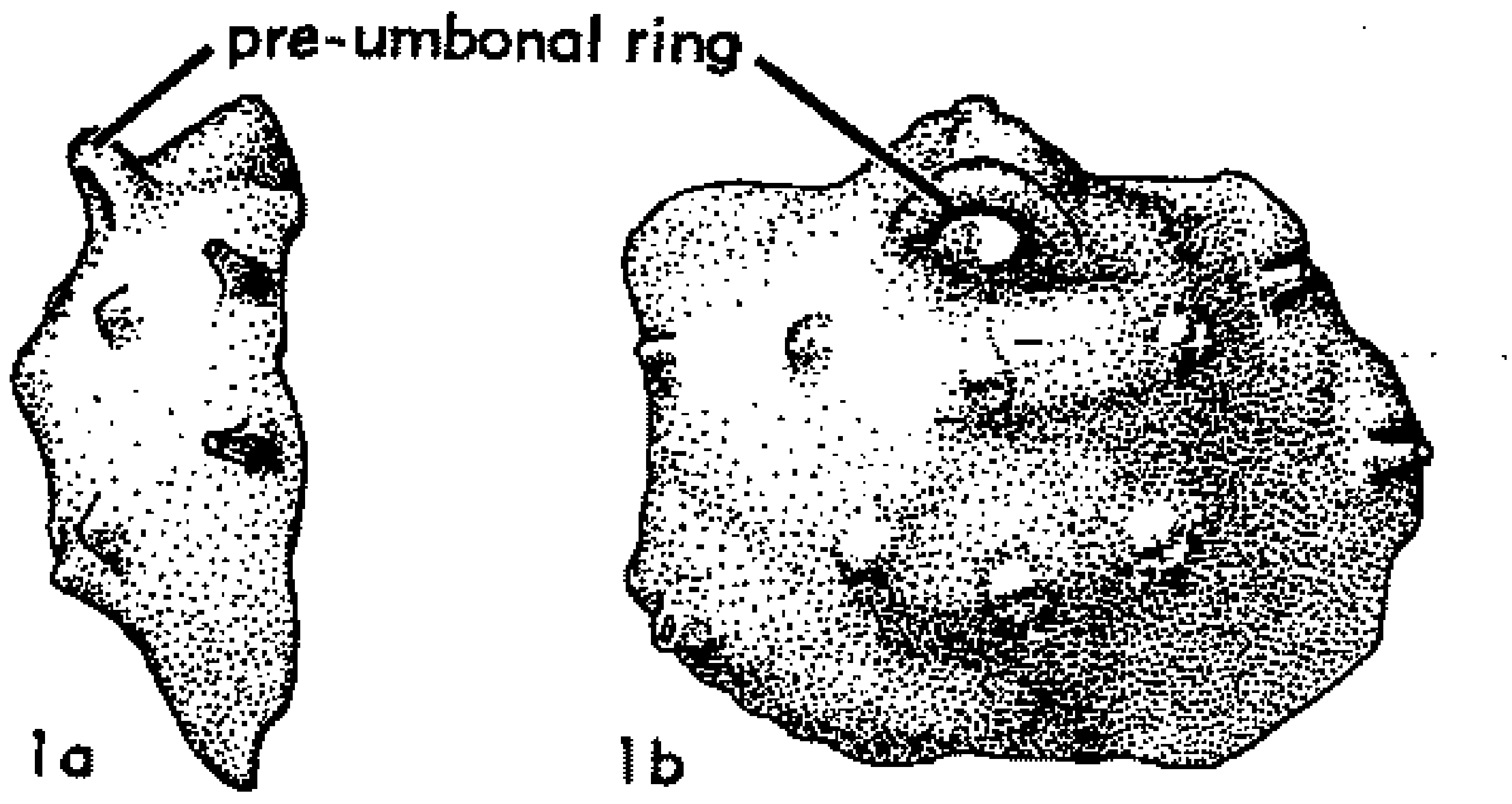


FIG. 298. Lateral and ventral views of juvenile *Orbinaria pyxidata* from the Louisiana Limestone (U.Dev. or L.Miss.) of Missouri, showing attachment ring on umbo, ×15 (587).

shell to a spine, possibly one on a parent's shell. A similar structure has been observed in young forms of *Megousia* and in some British forms and it may have been of common occurrence. In some small unnamed Permian shells from Texas the spines along the hinge are inclined toward the umbo, forming a ring which probably served for attachment in early growth stages, and a similar ringlike development of hinge spines has been observed in a number of adult forms.

The long creeping spines, in well-preserved specimens of *Antiquatonia*, certainly served to steady the shell and to attach it to some foreign object, while the large brush of rhizoid spines preserved in silicified specimens from the Texas Permian reefs must have served for entanglement and support.

Many specimens have been observed in what must have been their original position of growth, with the brachial valve uppermost, and the anterior margin lifted free of the sea-bottom mud.

Straining devices to prevent foreign particles or attacking organisms from entering the shell are elaborately developed, and consist of rims, frills, and anterior gutter-like or tubelike development of the trail, or the development of prostrate spines from the anterior margin, which would project across the anterior gape of the shell like a sieve. The interior or endospines in the two valves also tend to interlock in a mesh, and this is especially well developed in the richthofeniids and forms a sievelike strainer in *Coscinarina* from the Permian of Sicily.

EXTERNAL MORPHOLOGY

The shell consists of a flat or concave, or rarely, convex brachial valve, and a convex pedicle valve. Both valves may be geniculated and develop a long or short trail. The **trail** of one or both valves may develop flattened rims, or may be recurved to form a gutter or coil (Fig. 299). In the aberrant forms belonging to the Richthofeniidae and Scacchinellidae, the pedicle valve is conical and the brachial valve opercular, forming a lid.

The median part of the valve is known as the **venter** and this slopes down on either side to join the **lateral slopes** or **flanks.** The pedicle valve tapers posteriorly to form the **umbo,** which terminates in a more or less acute **beak.** The umbo may be truncated by a **cicatrix** of attachment of variable size and development. A corresponding rounded swelling may occur in the brachial valve.

The two valves are united along the **hinge,** which may be the widest part of the shell. The lateral extremities of the hinge, usually trigonal in outline, are known as **ears.** In some of the more primitive families (e.g., Productellidae, Strophalosiidae) an **interarea** is developed in each valve. In the Aulostegidae only the pedicle valve has an interarea. The **delthyrium** and **notothy-**

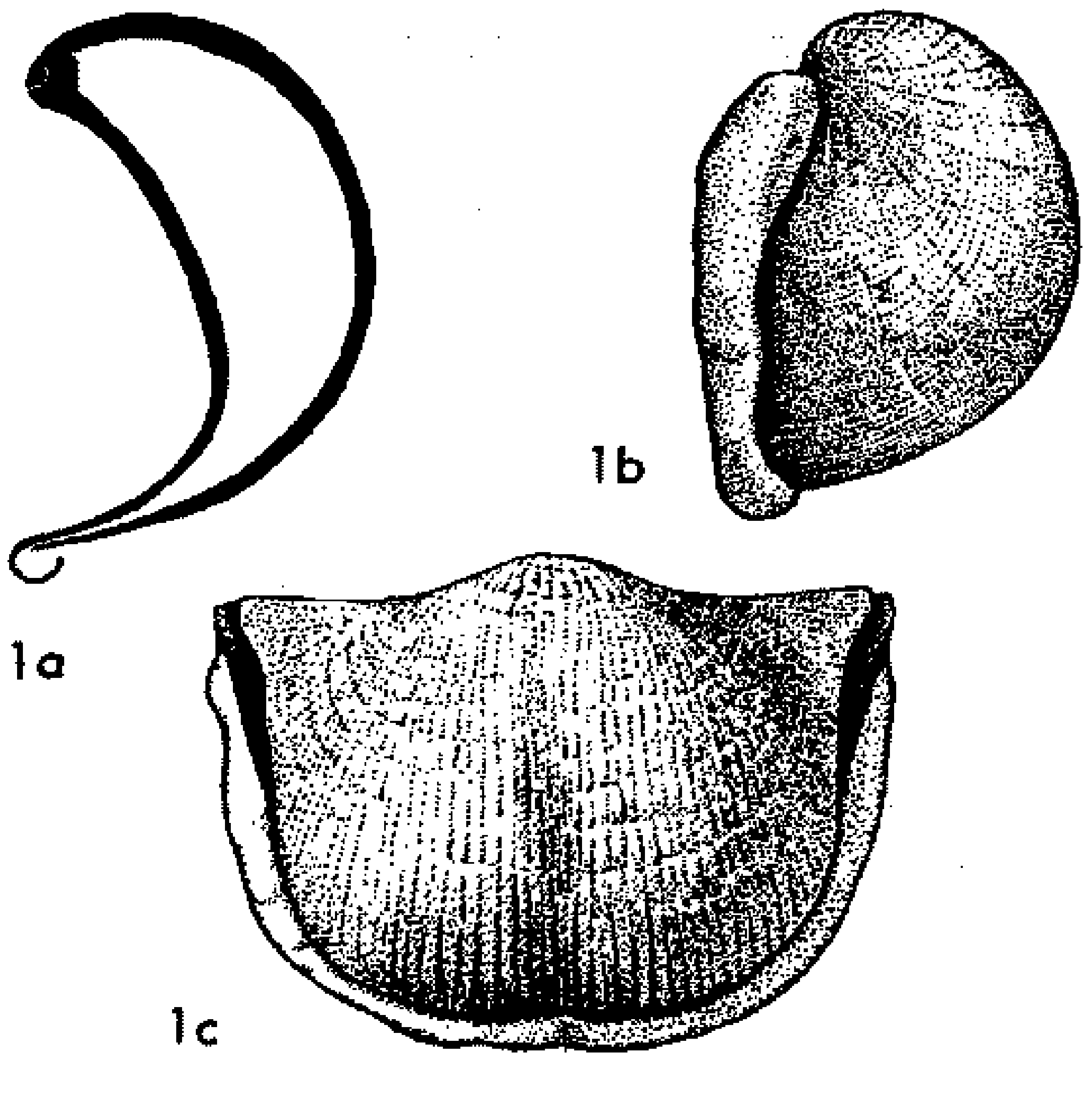


FIG. 299. *Auloprotonia aulacophora* MUIR-WOOD & COOPER (U.Miss., Okla.), showing specialized gutter formed by reflexed margin of brachial valve; *1a*, long. sec., ×0.75; *1b,c,* lat. and vent. views, latter showing openings of gutter near ears of shell, ×0.75 (587).

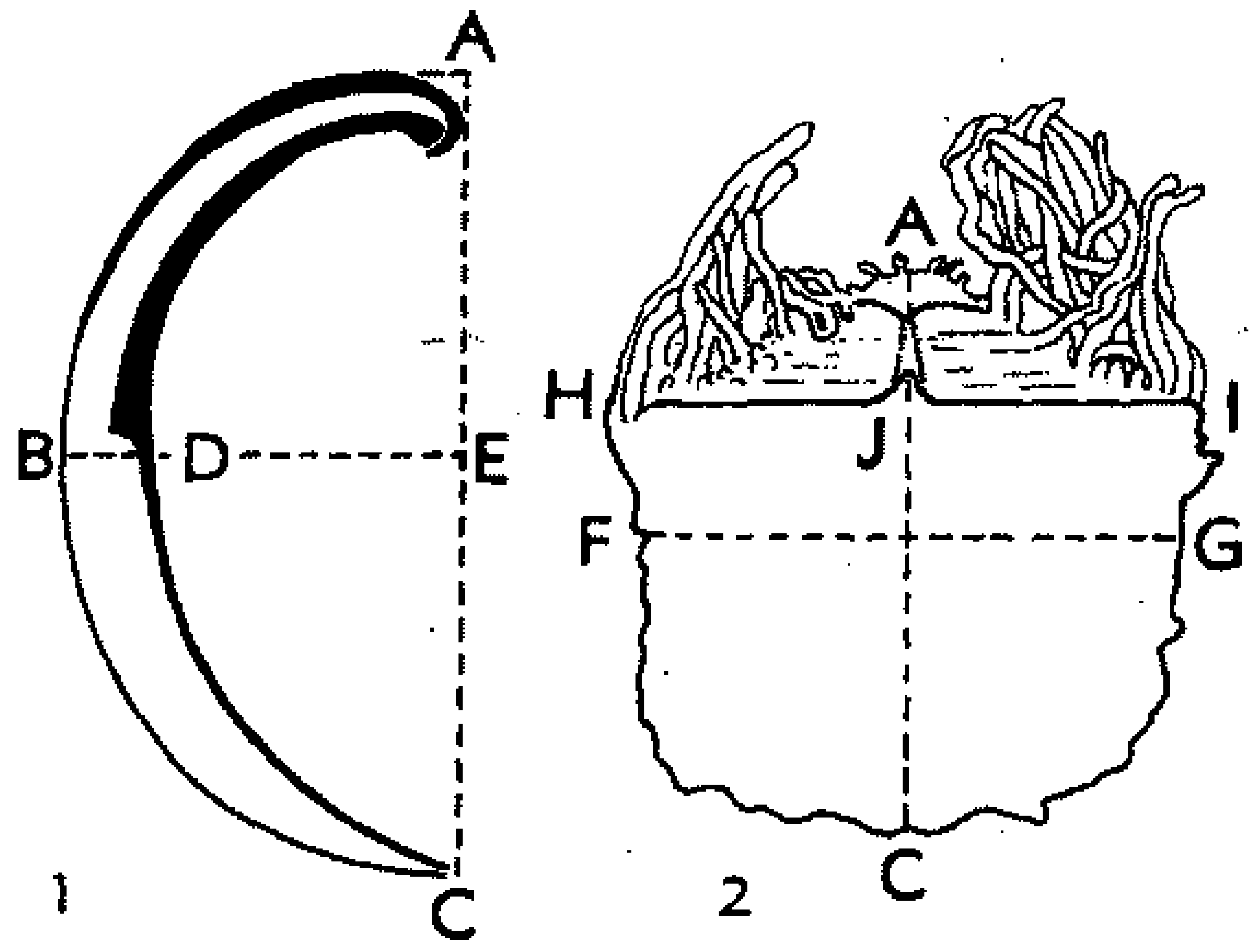


FIG. 300. Directions of measurement of productid *(1)* and aulostegid *(2)* brachiopods. [Explanation: *AC,* length of shell; *AJ,* length of interarea; *ABC,* surface length of pedicle valve; *BD,* thickness; *BDE,* height; *FG,* mid-width; *HI,* width of hinge or interarea (587).]

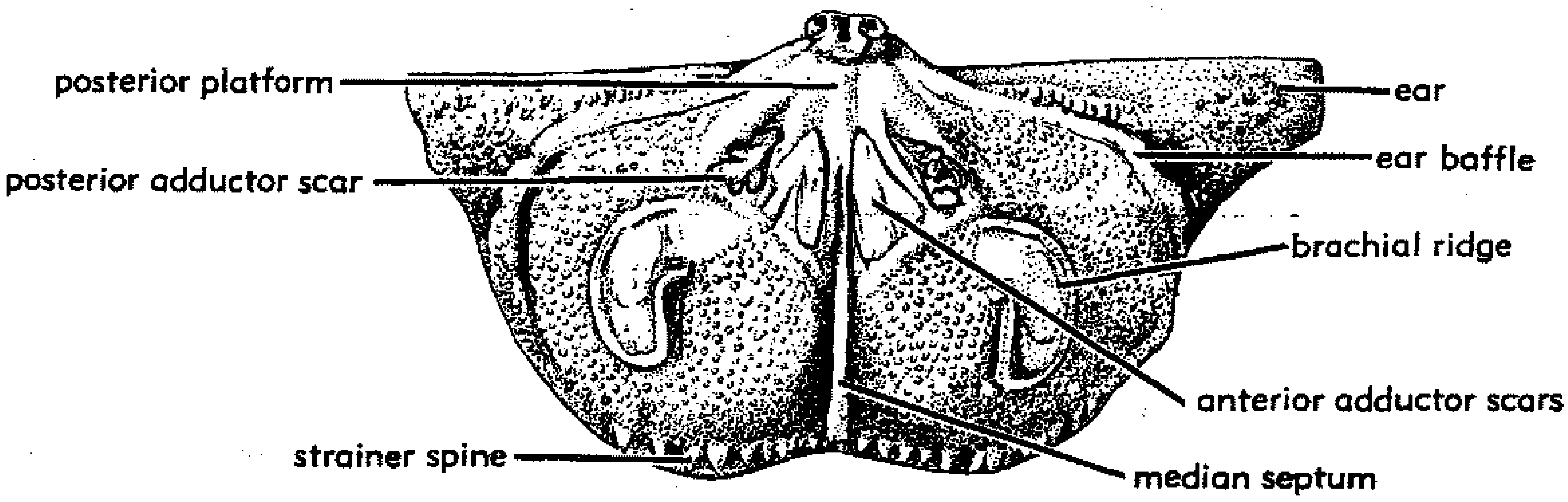
rium are closed in some shells by a **pseudodeltidium** and **chilidium.** The latter structure occurs only in the Strophalosiidae. The pseudodeltidium, however, tends to be replaced by the external face of the cardinal process or an extension of it called the **lophidium.** In the Aulostegidae the delthyrium is closed by a convex puckered plate known as the **elytridium,** and the interarea on either side of the delthyrium, known as the **perideltidial area,** is demarcated by distinct ornament in some genera. In some Visean, Pennsylvanian, and Permian shells, a secondary area **(ginglymus)** may be developed in the pedicle valve, and serves to close the shell or to articulate with ridges in the brachial valve.

Every productoid shell is more or less spinose, but may otherwise be smooth with growth lines, or bear radial ridges of varying size, known as **costae** (less than 15 in 10 mm.), **costellae** (15 to 25 in 10 mm.) or **capillae** (more than 25 in 10 mm.). Concentric wrinkles or **rugae** may be developed posteriorly near the hinge or cover the entire valve. Concentric bands bearing rows of small **spines** occur in some species, or spines may be set on **spine ridges** or rounded nodes known as **monticules.** Different ornament may occur on the posterior and anterior parts of one valve, or dorsal and ventral valve may be dissimilar (e.g., *Devonoproductus,* which has a capillate spinose pedicle valve and a lamellose brachial valve).

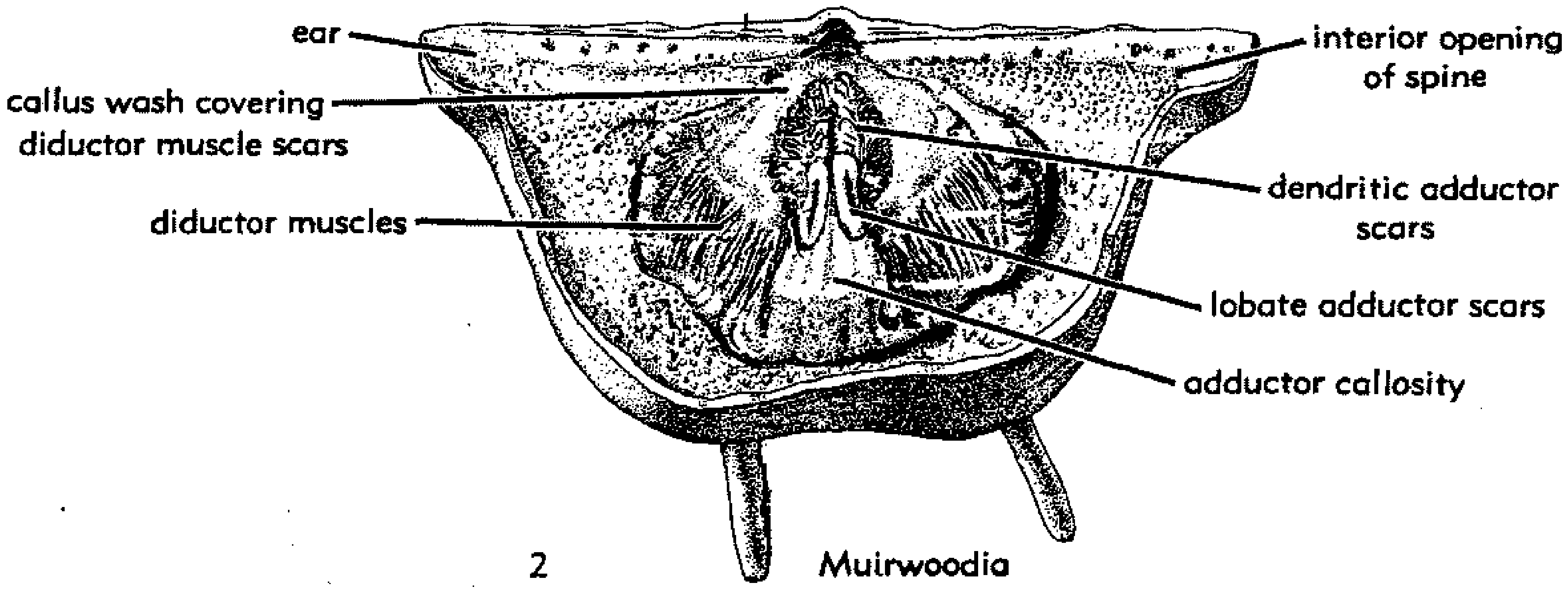
Productoid **spines** are of several distinct types which have been described as (1) **rhizoid or rootlike spines,** serving for attachment by entanglement, including also the clasping spines of strophalosiids; (2) **halteroid spines,** usually extending at right angles to the shell surface, serving as struts to steady or balance the shell and prevent it from sinking in the mud; (3) **vermiform or wormlike spines** of some strophalosiids; (4) **prostrate spines,** straight or slightly curved and extending along the shell surface, and serving as a protective coat for stopping foreign bodies from boring into or attaching themselves to either valve or acting as a strainer at the anterior margin. Spines of two or more types or series may be developed on a single valve. Spines are developed in great profusion and almost endless variety in Permian species and have been studied in the marvelously preserved silicified specimens from western Texas. Spines up to 9 or 10 inches in length have been observed and may fork or unite with neighboring spines. The spines vary considerably in diameter, but all are hollow and open at the distal end. They were originally lined by outgrowths of the mantle, but the internal aperture of the spines tended to become blocked by deposition of secondary calcareous layers on the shell interior as the valves elongated. The rows of spines near the hinge and the four or six symmetrically placed halteroid or strutlike supporting spines remained in contact with the shell interior throughout the life of the animal.

In systematic descriptions the specimens are said to be of **small size** when they are less than 0.75 inch (20 mm.) wide; **medium size** when 0.75 to 2 inches (20 mm. to 50 mm.) wide; **large size** when above 2 inches (50 mm.) wide; and **gigantic size** when above 6 inches (150 mm.) wide.

The **width** is measured parallel to the hinge, which is commonly the widest part of the shell. The **length** is measured from the umbo to the anterior margin at right angles to the width and thickness. The **thickness** is measured along an axis at right angles to the width and length (Fig. 300).



1 Paucispinifera



2 Muirwoodia

Fig. 301. Brachial valve interior *(1, Paucispinifera)* and pedicle valve interior *(2, Muirwoodia)* showing morphological features (587).

INTERNAL MORPHOLOGY

BRACHIAL OR DORSAL VALVE

In the more primitive genera the two valves articulate by means of small **hinge teeth** in the pedicle valve which fit into **sockets** in the brachial valve (Fig. 301,*1*, 302). In some of the more bizarre genera the position of the teeth and sockets may be reversed, but in others it is replaced by a number of teeth or **denticulations** which fit into corresponding depressions in the opposite valve. The sockets are bounded anteriorly by **socket ridges.** In most productoids without teeth and sockets, the cardinal process and lateral ridges, which extend from it more or less along the hinge margin of the brachial valve, aid in articulation. The **lateral ridges** may extend across the ears and be continued along the lateral margin of the visceral disc as marginal ridges, or they may unite on the dorsal side of the cardinal process as a **zygidium** which functions like the lophidium.

The **cardinal process** varies in type and size and has been used by Muir-Wood & Cooper (1960) in family classification. The most primitive type is bilobate, the two lobes remaining in contact, divided only by a median furrow. The lobes tend to become separated from one another or to be united only by a minute median lobe developed posteriorly. This median lobe may be inclined dorsally (exteriorly) in some genera, and may be more prominent than the two lateral lobes. The external face of the process, commonly triangular in outline, consists of three or four anteriorly converging lobes, and in some genera it is enlarged into a triangular boss or **lophidium.** Some of the various types of cardinal processes are figured (Fig. 303). The cardinal process consists of the lobed **myophore** and the **shaft** or stalk. When the stalk is absent the process is said to be **sessile.**

The cardinal process may be supported by the **median septum** or be separated from

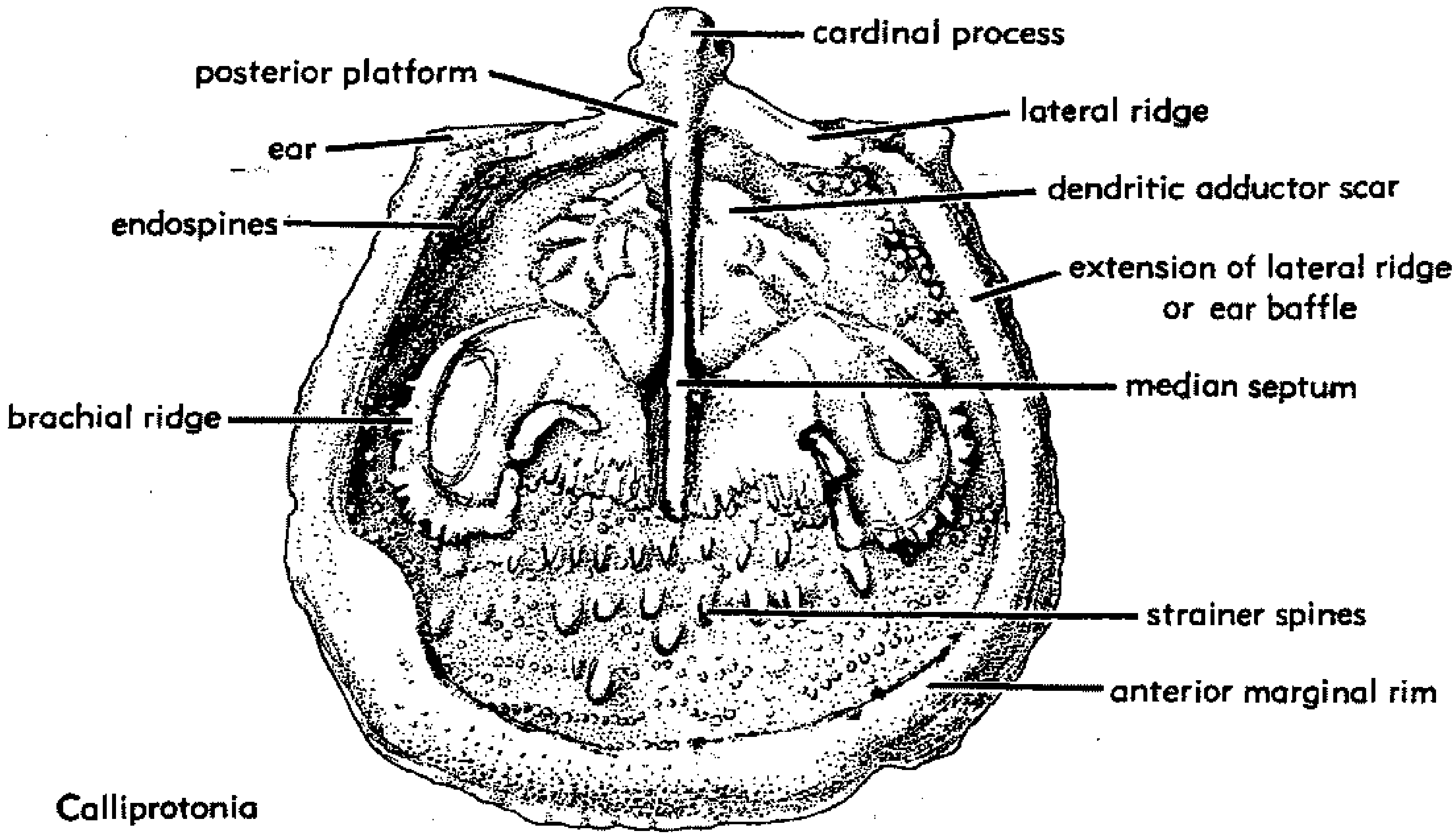


FIG. 302. Interior of brachial valve of *Calliprotonia,* echinoconchid, from Finis Shale (Penn.) of Texas, showing morphological features, ×3 (587).

it by a rounded pit or **alveolus.** In the latter case the median ridge is known as the **breviseptum.** In some genera (e.g., *Juresania*) two vertical or converging ridges called **buttress plates** extend anteriorly from the cardinal process and may unite with the median septum, in some shells leaving a median hollow known as the **antron.** The anterior part of the septum may become prominent and bulbous or bladelike and probably it served to divide the internal shell cavity into two parts and to regulate food currents.

The internal shell surface is more or less papillose, granular or endospinose, the **endospines** attaining several millimeters in length, and commonly forming an anterior mesh or strainer across the gape in the valves with comparable spines in the pedicle valve (e.g., richthofeniids). **Brachial ridges,** more or less spirally curved, extend from the line of junction of the anterior and posterior adductor muscle scars. These ridges vary in form in different families and are obscure or not distinguishable in some genera. They are given off at varying angles, from horizontal in the Dictyoclostidae and Aulostegidae, to nearly vertical, in *Overtonia* and the strophalosiids.

Mantle-canal markings, which are a feature of the interior of both valves of strophomenoids, cannot as a rule be distinguished in the Productidina, probably on account of the papillose or endospinose internal surface. **Genital markings** were not observed.

In *Productus, Diaphragmus,* and other genera, a thin crescentic plate, called the **diaphragm,** may be developed around the **visceral disc** of the brachial valve to close the gap between the two valves.

The valves are attached to one another by means of the **adductor and diductor muscles,** the former serving to close and the latter to open the shell. The diductors are attached to the cardinal process and leave roughened areas showing attachment to the sulci between the lobes, and in some shells to the lobes themselves. The attachment of these muscles to the pedicle valve leaves large flabellate scars, which may be radially ridged or provided with a bounding rim. The adductors are attached to the brachial valve on either side of the median septum, forming two anterior and two posterior scars, or rarely six scars which may be smooth, lobate or dendritic. The adductor scars are commonly set on a platform. In the pedicle valve the adductors form two or four scars situated within or anterior to the diductors. Additional scars interpreted as **accessory diductors** are attached to the shaft of the cardinal process in some aulostegids, but the position of their attachment to the pedicle valve is uncertain. Rounded and detached accessory adductor scars are developed in the pedicle valve of the chonetoid family Daviesiellidae but are not found in the Productidina.

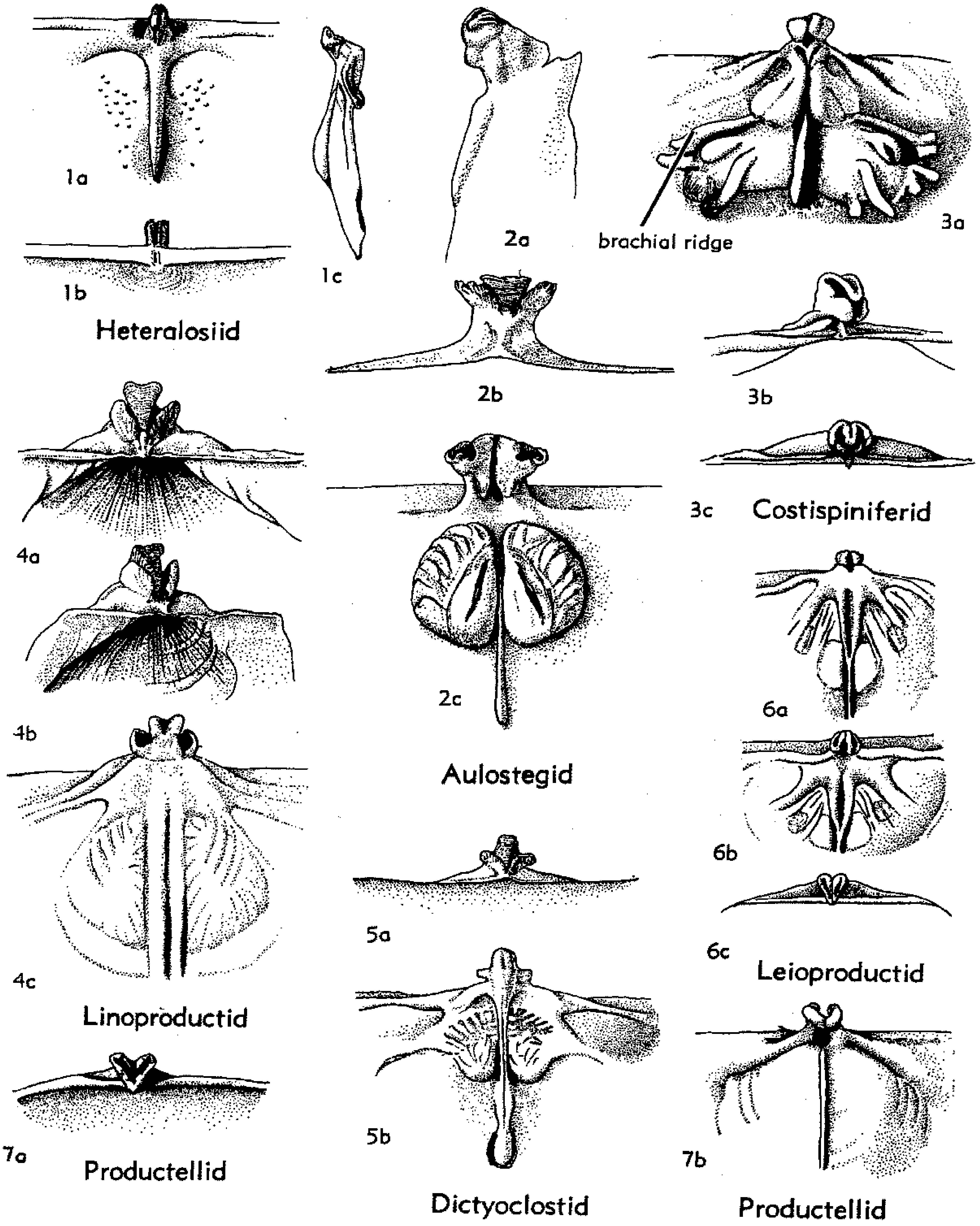


Fig. 303. Types of productoid cardinal processes showing associated morphological features (587).——*1.* Heteralosiid *(Heteralosia); 1a-c,* int., post., lat. views, ×3.——*2.* Aulostegid *(Edriosteges); 2a-c,* lat., ext., int. views, ×1.5.——*3.* Costispiniferid *(Costispinifera); 3a-c,* int., oblique lat., post. views, ×2.——*4.* Linoproductid *(Linoproductus); 4a-c,* ext., oblique lat., int. views, ×2.25.——*5.* Dictyoclostid *(Peniculauris); 5a,b,* ext., int. views, ×0.75.——*6.* Leioproductid *(Leioproductus); 6a-c,* int., oblique int.-post., post. views, ×2.——*7.* Productellid *(Spinulicosta); 7a,b,* post., int. views, ×2.

PEDICLE OR VENTRAL VALVE

Hinge teeth are developed in some of the more primitive genera of the Productellidae, in the Strophalosiidae and Sinuatellidae (Fig. 301,*2*). **Dental plates** are very rarely developed. The teeth are situated on the anterior outer margin of the delthyrium, and vary in form and prominence. A short **median septum** is developed in *Rhamnaria, Septarinia,* and *Chonetipustula.* In *Tschernyschewia* the septum is high and platelike and a comparable septum occurs in *Scacchinella.*

The **lophophore** is assumed to have been spirolophous, with the apices of the two spirals projecting into the mantle cavity of the pedicle valve. Traces of these spirals can be seen as elevated cones in specimens of *Gigantoproductus* and *Levitusia.* The spirals were probably attached to the spirally curved brachial ridges developed in the brachial valve of many genera.

Marginal or submarginal ridges are developed in some pedicle valves (e.g., *Alifera, Paramarginifera, Eomarginifera*). In some genera (e.g., *Kozlowskia, Marginifera, Costispiniferina*) the ridges may be crenulated.

In the richthofeniids the thickening on the interior of the conical valve, against which the brachial valve rested when the shell was closed, is known as the **aulacoterma.** The chamber, similar to a spondylium, but not derived from dental plates, to which muscles were attached in the Richthofeniidae, is called the **myocoelidium,** while the cuplike attachment surface for the adductors in the Spyridiophoridae is known as the **spyridium.**

SHELL STRUCTURE

The shell consists of a thin external lamellose layer and an inner fibrous layer which seems to vary in different genera and is commonly of considerable thickness. The inner layer is said to be **pseudopunctate** on account of nonfibrous calcite rods or **taleolae** (formerly called **pseudopunctae** or **spicules**). These may be of more than one diameter and extend for a varying distance through the fibrous layer, and may project as pustules or **endospines** into the internal shell cavity. The spines are also composed of two shell layers, the "spines within spines" described by Young (1891) being taleolae.

In richthofeniids and *Scacchinella,* the conical shell may be partly filled by cystose shell, which consists of small or large curved calcareous plates, of which the method of formation is uncertain. It is suggested that fluid was secreted by the mantle between the mantle and the shell, and that this liquid was sealed within a thin layer of shell. This process was continued gradually, pushing the body upward as the cone increased in depth.

CLASSIFICATION

Classification of the productoids has been based largely on external shell ornament. This consists of spines, in some shells accompanied by radial costae or costellae and concentric rugae or lamellae. The arrangement of spines, whether scattered over the shell, arranged in rows or groups near the hinge or on the flanks, borne on the costae or rugae, or set on tubercles or spine ridges, has been found to be of first importance. Spines developed in any one species have been found to have a fairly constant arrangement and to be of uniform type, and of more than one series in some genera.

The present classification is also based on internal morphology, especially type of the cardinal process; the adductor scars, whether smooth or dendritic, length and position of the lateral ridges; length and form of the dorsal median septum, and its rare development in the pedicle valve, and the angle of emergence of the brachial ridges.

Some structures, such as marginal ridges and diaphragm, formerly thought to be a characteristic of a single genus, are now found to be repeated in a number of genera.

Earlier classifications attached considerable importance to shell contour and size of the body cavity. This has been found to be somewhat variable and important only as a specific character.

A history of the classification of the Productidina has been given by Muir-Wood and Cooper (1960, 587).

HOMEOMORPHY

The number of possible ornament patterns in productoids is limited and may be repeated two or more times, thus giving external similarity, accompanied by different internal morphology. Such pairs of homeomorphs may occur in beds of the same age (e.g., *Sphenalosia, Sphenosteges,* from the Permian of USA), or in beds of widely differing age (e.g., *Dictyoclostus,* from the Lower Carboniferous, and *Reticulatia,* from the Permian). Many species formerly placed together in one genus on account of superficial similarity in ornament have now been separated as distinct genera and placed in different families. For example, *Productus mesolobus* (J. Phillips) and *Productus humerosus* (J. Sowerby) were formerly grouped together in the genus *Plicatifera. Productus mesolobus* is now the type-species of *Acanthoplecta,* and *P. humerosus* is now assigned to the genus *Levitusia*; the two genera are separated, *Acanthoplecta* being placed in the family Leioproductidae and *Levitusia* in the Dictyoclostidae.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO PRODUCTIDINA

[Abbreviations used in figure descriptions are given in parentheses.]

adductor muscle scars. Attachment impressions of muscles serving to close valves, comprising four or six scars in brachial valve; anterior adductor scars anterior to or on inner side of posterior adductors; in pedicle valve two or four scars between diductor scars.

adductor platform. Platform or broad ridge to which adductors are attached.

alae. Winglike extensions of ears or cardinal extremities.

alveolus. Pit anterior to internal face of cardinal process (e.g., Productellidae).

antron. Triangular gap due to incomplete fusion of cardinal process buttress plates and breviseptum (e.g., *Buxtonia*).

aulacoterma. Thickening on inside wall of Richthofeniidae against which brachial valve rested when shell was closed.

beak. Extremity of umbo, commonly pointed and incurved.

brachial ridges. Ridges originating between anterior and posterior adductor scars in brachial valve and extending laterally or anteriorly forming open loop.

brachial valve *(brach.v.)*. Dorsal valve.

breviseptum. Median ridge not supporting cardinal process.

buttress plates. Two vertical or converging plates extending from cardinal process and in some shells uniting with breviseptum. (*See* antron.)

callus. Secondary deposit composed of fibrous layer, thickening shell and covering up internal structures.

capillae. Fine raised radial lines on exterior of valves (more than 25 in width of 10 mm.).

cardinal process *(card. process)*. Boss, more or less elevated, serving for attachment of diductor muscles, and also assisting in articulation; consists of shaft and lobate myophore, or shaft may be lacking when myophore is sessile.

chilidium. Flat or convex plate closing notothyrium (e.g., Strophalosiidae).

cicatrix of attachment. Flattening of pedicle umbo representing place of cementation of shell to foreign object.

cincture. External concentric incision in either valve, usually corresponding to an internal ridge or diaphragm.

costae. Radial ridges on exterior of shell (less than 15 in 10 mm.).

costellae. Radial ridges on exterior of shell and finer than costae (about 15 to 25 in width of 10 mm.).

crenulations. Alternating elevations and depressions usually serving as accessory form of articulation of shell.

cystose shell. Blister-like deposits formed in conical shells (e.g., Richthofeniidae, Scacchinellidae) to fill up shell as result of dorsal migration of body during growth.

delthyrium. Triangular opening in interarea under umbo of pedicle valve.

dendritic muscle scars. Branching or leaflike pattern of adductor scars in some genera.

diaphragm. Thin crescentic place developed as secondary deposit around visceral disc of brachial valve and bridging gap between brachial valve and trail of pedicle valve (e.g., *Productus*).

diductor muscle scars. Muscles serving to open valves and attached to cardinal process myophore in brachial valve, and forming large flabellate scars in pedicle valve. Accessory diductor muscle scars are situated between diductor scars in pedicle valve, and are attached to cardinal process shaft in brachial valve.

ear. Lateral extremity of hinge, usually trigonal in outline.

elytridium. Convex puckered cover of delthyrium in Aulostegidae.

endospines. Fine spines or protruding ends of taleolae in interior of both valves, possibly serving as strainers and preventing access to interior.

erect spines. Spines extending at high angle (75°-90°) to shell surface.

flanks. Lateral slopes on each side of venter.

fold. Major radial plication.

geniculate. Bent at an angle (e.g., trail in *Sinuatella* which extends at an angle to visceral disc).

ginglymus. Secondary interarea in pedicle valve of some Visean, Pennsylvanian, and Permian species, serving to close gap between valves and to assist in articulation of shell.

gutter. Anterior recurvature of trail of one or both valves, to form a gutter (e.g., Aulostegidae), and possibly serving as strainer or stabilizer.

halteroid spines. Long spines, commonly four or six in number and symmetrically placed, acting as strutlike supports (e.g., *Muirwoodia, Eomarginifera*).

hinge. Posterior line of valve junction.

imbricate. Overlapping (e.g., lamellae).

interarea. Formerly called cardinal area.

lateral ridges. Ridges in interior of brachial valve extending laterally from cardinal process, probably serving to strengthen shell and assisting in articulation.

lophidium. Inverted V-shaped projection of median posterior part of brachial valve or of external face of cardinal process, helping to close gap in delthyrium.

marginal ridges. Thickening along internal lateral margin of visceral disc, usually in brachial valve.

monticules. Small rounded nodes, commonly bearing spines.

myocoelidium. Chamber similar to spondylium but not formed by dental plates, serving for attachment of muscles (e.g., Richthofeniidae).

myophore. *See* cardinal process.

myophragm. Median shell ridge, probably formed of secondary shell matter secreted between muscles and not extending beyond muscle field.

notothyrium. Triangular opening in interarea of brachial valve (e.g., Strophalosiidae).

opercular. Lidlike, referring to brachial valve in some genera (e.g., Richthofeniidae).

pedicle valve *(ped.v.)*. Ventral valve.

perideltidium. Triangular area forming part of interarea, marked by vertical as well as horizontal lines and bounding pseudodeltidium (e.g., some aulostegids).

prostrate spines. Usually straight spines that lie prone on shell surface.

pseudodeltidium. Single flat or convex plate covering part of delthyrium.

pseudopunctae. *See* taleolae.

recumbent spines. Slightly curved spines extending at low angle (less than 45°) to shell surface.

reticulation. Nodelike enlargement formed by intersection of concentric rugae with radial costae or costellae.

rhizoid spines. Spines resembling rootlets serving for attachment either by entanglement or by extending along and cementing themselves to some foreign surface.

rugae (rugose). Concentric folds or wrinkles (e.g., *Dictyoclostus*).

septum. Median ridge extending from umbo of pedicle valve or from cardinal process of brachial valve.

shaft. *See* cardinal process.

spine ridge. Elongated ridge bearing spine at anterior end.

spyridium. Structure formed by union of adductor platforms and supporting plates to form cuplike adductor attachment surface (e.g., *Spyridiophora*).

squamose. Ragged margin, e.g., of overlapping lamellae at anterior end of trail.

strainer spines. *See* endospines.

suberect spines. Spines inclined to shell surface at angle of about 45°-75°.

submarginal ridge. Thickening of interior of either valve parallel to anterior margin of visceral disc.

sulcus. Major depression in either valve, generally median in position.

taleolae. Nonfibrous calcite rods, commonly with median perforation and embedded in fibrous shell layer or protruding into shell interior as endospines in a pseudopunctate shell; on weathered surface may appear as pits (formerly called spicules or pseudopunctae).

trail. Extension of shell in either valve anterior to visceral disc.

umbo. Region just anterior to beak.

umbonal slopes. Region about umbo.

venter. Median region of shell between lateral slopes or flanks.

visceral cavity. Term used in fossils to include body cavity which was occupied by stomach, intestine, liver, etc., posterior to mouth, and mantle or brachial cavity which housed lophophore.

visceral disc. Posterior part of shell in both valves including umbones and venter and corresponding externally to visceral cavity.

zygidium. Collar-like structure uniting lateral ridges on dorsal side of cardinal process, and functioning like lophidium.

Suborder PRODUCTIDINA Waagen, 1883

[*nom. correct.* MUIR-WOOD, herein (*pro* suborder Productacea WAAGEN, 1883, p. 447)]

Specialized, and in some instances degenerate brachiopods having pseudopunctate shell composed of inner fibrous layer with taleolae, and thin outer lamellar layer. Pedicle valve convex, brachial valve flat or concave, rarely convex, or one or both valves geniculated, with development of trail. Pedicle valve invariably, and brachial valve commonly, provided with open tubular spines. Brachial valve interior, with lobate cardinal process and hook-shaped brachial ridges. Socket ridges obsolete; adductor muscle scars smooth, lobate or dendritic in both valves. Pedicle absent. Pedicle valve with ringlike structure for attachment in early stage. *L.Dev.-U.Perm.*

Superfamily STROPHALOSIACEA Schuchert, 1913

[*nom. transl.* MUIR-WOOD & COOPER, 1960 (*ex* Strophalosiinae SCHUCHERT, 1913)]

Commonly cemented by beak of pedicle valve and anchored by clasping or attachment (rhizoid) spines; interareas present in both valves, in pedicle valve only, or absent; delthyrium closed by pseudodeltidium, or (when teeth are absent) by elytridium or partly by lophidium; notothyrium and chilidium, teeth and sockets developed in one family; cardinal process usually prominent, initially bilobed, becoming trilobed; alveolus commonly present. *L.Dev.-U.Perm.*

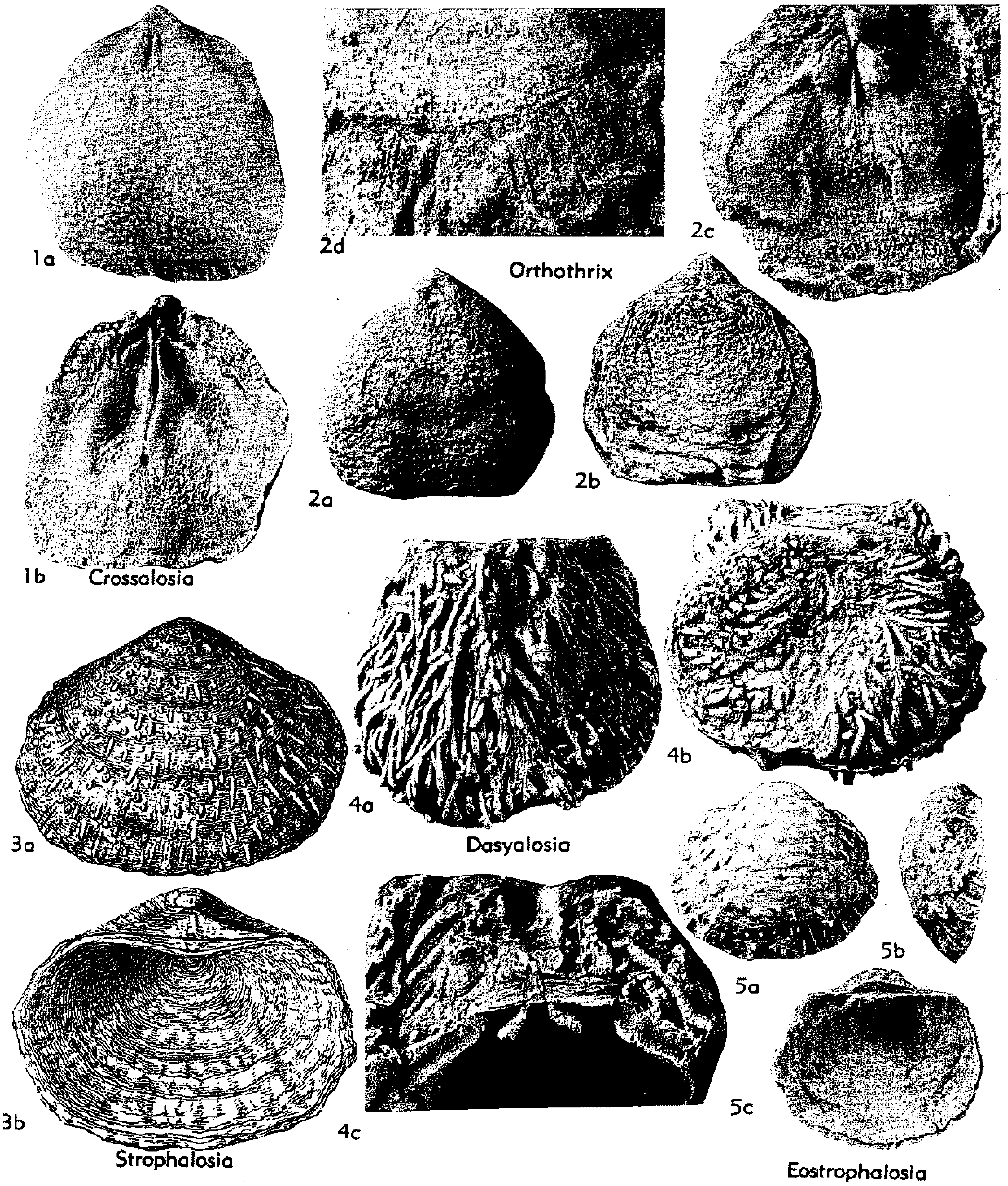


FIG. 304. Strophalosiidae (Strophalosiinae) (p. *H*450-*H*451).

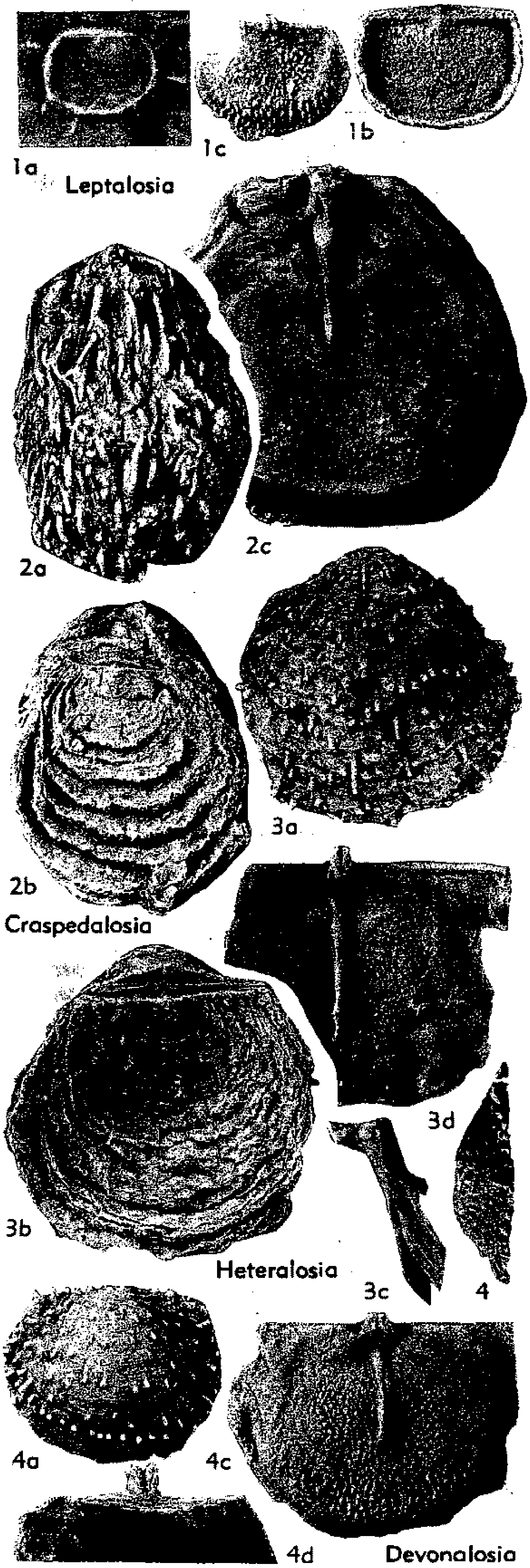


FIG. 305. Strophalosiidae (Heteralosiinae) (p. H451).

Family STROPHALOSIIDAE Schuchert, 1913

[*nom. transl.* STEHLI, 1954, p. 328 (*ex* Strophalosiinae SCHUCHERT, 1913, p. 391)]

Primitive Strophalosiacea with hinge teeth and sockets; both valves with short interarea; delthyrium closed by pseudodeltidium and notothyrium closed by chilidium; pedicle valve usually cemented by umbo and anchored by clasping spines on ears and near hinge. Brachial valve with or without spines; cardinal process bilobed, trilobed, or bulbous; brachial ridges long, sharply descendent. Alveolus normally absent; adductors not dendritic. *L.Dev.-U. Perm.*

Subfamily STROPHALOSIINAE Schuchert, 1913

[Strophalosiinae SCHUCHERT, 1913, p. 391]

Spines developed on both valves. *M.Dev.-U.Perm.*

Strophalosia KING, 1844, p. 313 [**S. gerardi* KING, 1846, p. 92; SD MUIR-WOOD & COOPER, 1960 (ICZN)] [=*Leptaenalosia* KING, 1850, p. 93 (*nom. nud.*)]. Medium-sized, with low interareas; pedicle valve ornament of prostrate and suberect clasping spines; brachial valve lamellose, few spines; cardinal process trilobed. *Perm.*, Asia-Australia.——FIG. 304,*3*. **S. gerardi*, Asia(Himalayas); *3a,b*, holotype, ped.v. and brach.v. views, ×1 (472).

Crossalosia MUIR-WOOD & COOPER, 1960, p. 75 [**Productus buchianus* DE KONINCK, 1847, p. 129; OD]. Small, irregular, with short interareas; both valves ornamented by broad concentric lamellae with single row of recumbent spines, and spines on ears of brachial valves; teeth and sockets and alveolus present. *L.Carb.(Visean)*, Eu.——FIG. 304,*1*. **C. buchiana* (DE KONINCK), Belg.; *1a,b*, int. mold., ped.v. and brach.v. views, ×2 (587).

Dasyalosia MUIR-WOOD & COOPER, 1960, p. 76 [**Spondylus goldfussi* MÜNSTER, 1839, p. 43; OD]. Both valves with recurving vermiform spines, also prostrate spines in pedicle valve; brachial valve lamellose anteriorly. *U.Perm. (Zech.)*, Eu.——FIG. 304,*4*. **D. goldfussi* (MÜNSTER), Ger.; *4a,b*, ped.v. and brach.v. views, ×2; *4c*, ped.v. int., ×3 (587).

Eostrophalosia STAINBROOK, 1943, p. 58 [**Strophalosia rockfordensis* HALL & CLARKE, 1893, p. 316; OD]. Small; pedicle valve with rugae or lamellae and scattered recumbent spines and erect spines along hinge. *M.Dev.-U.Dev.*, N.Am.——FIG. 304, *5*. **E. rockfordensis* (HALL & CLARKE), U.Dev., USA(Iowa); *5a-c*, ped.v., lat., and brach.v. views, ×2 (766).

Orthothrix GEINITZ, 1847, p. 84 [**Orthis excavata* GEINITZ, 1842, p. 578; SD DALL, 1877]. Small, trigonal, with high ventral interarea; both valves

Devonalosia

FIG. 306. Strophalosiidae (Heteralosiinae) (p. H451).

ornamented by fine hairlike recumbent spines and narrow rugae; cardinal process long-shafted, bilobed. *U.Perm.(Zech.)*, Eu.——FIG. 304,*2*. **O. excavata* (Geinitz), Ger.; *2a,b*, ped.v. and brach. v. views, ×2; *2c*, brach.v. int., ×2; *2d*, recumbent spines (impressions), ×4 (327).

Subfamily HETERALOSIINAE Muir-Wood & Cooper, 1960

[Heteralosiinae Muir-Wood & Cooper, 1960, p. 80]

Spines absent on brachial valve. *L.Dev.-U.Perm.*

Heteralosia R. H. King, 1938, p. 278 [**H. slocomi*; OD]. Pedicle valve with concentric lamellae, fine recumbent and erect clasping spines; brachial valve dimpled, lamellose, rarely capillate; brachial ridges ill-defined, cardinal process bilobate or quadrilobate. *L.Miss.-L.Perm.* N.Am.-Eu.-Australia.——FIG. 305,*3*. **H. slocomi*, Penn., USA (Tex.); *3a,b*, ped.v. and brach.v. views, ×2; *3c*, lat. view of card. process, ×2; *3d*, brach.v. int., ×3 (471).

Craspedalosia Muir-Wood & Cooper, 1960, p. 82 [**Orthothrix lamellosus* Geinitz, 1848, p. 86; OD]. Like *Dasyalosia* but brachial valve with squamose overlapping lamellae and obscure capillation. *U.Perm.(Zech.)*, Eu.——FIG. 305,*2*. **C. lamellosa* (Geinitz), Ger.; *2a,b*, ped.v. and brach.v. views, ×2; *2c*, brach.v. int., ×3 (587).

Devonalosia Muir-Wood & Cooper, 1960, p. 83 [**D. wrightorum*; OD]. Small, subcircular; flat pseudodeltidium, no chilidium; pedicle valve ornament of prostrate and coarser recumbent spines; brachial valve rugose, dimpled; no brachial ridges, cardinal process small, bilobed; alveolus developed. *L.Dev.-M.Dev.*, N.Am.(USA-Can.).——FIG. 305,*4*. **D. wrightorum*, Arkona Sh., Ont.; *4a,b*, ped.v. (holotype) ext., post., ×2; *4c*, brach.v. int., ×3; *4d*, brach.v. ext., post. dors. view of card. process, ×4 (587).——FIG. 306,*1*. *D. radicans* (Winchell), M.Dev., USA(Mich.); shells attached to base of *Hexagonaria* colony, ×2 (587).

Leptalosia Dunbar & Condra, 1932, p. 260 [**Strophalosia scintilla* Beecher, 1890, p. 243; OD]. Small; pedicle valve wholly attached with prostrate spines; brachial valve smooth or with concentric lamellae; no median septum or brachial ridges. *U. Dev.* or *L.Miss.*, *?Penn.*, N. Am.——FIG. 305,*1*. **L. scintilla* (Beecher), U. Dev. or L. Miss., Louisiana Ls., USA(Mo.); *1a,b*, attached brach.v. ext., ×4, ×8; *1c*, brach.v. int., ×8 (270).

Lialosia Muir-Wood & Cooper, 1960, p. 86 [**Strophalosia Kimberleyensis* Prendergast, 1943, p. 47; OD]. Valves subcircular, some with short trail; lamellose, faintly capillate; spines near hinge of pedicle valve, possibly absent elsewhere. *L. Perm.(Artinsk.)*, Australia.——FIG. 307,*4*. **L. kimberleyensis* (Prendergast); *4a,b*, ped.v. and brach.v. views, ×1; *4c*, brach.v. int., ×1.5; *4d*, ped.v. int., ×1.5 (647).

Oligorachis Imbrie, 1959, p. 403 [**O. oligorachis*; OD]. Subelliptical, small, with small cicatrix and small, narrow, convex pseudodeltidium, hinge narrow; pedicle valve convex with stout scattered spines; brachial valve irregularly ridged, no spines, cardinal process small, bilobed, less prominent than in *Heteralosia*. *M.Dev.*, N.Am.——FIG. 307,*2*. **O. oligorachis*, USA(Mich.); *2a-d*, holotype, ped.v., brach.v., lat., and post. views, ×3 (445).

Sphenalosia Muir-Wood & Cooper, 1960, p. 87 [**S. smedleyi*; OD]. Trigonal, with high ventral interarea and narrow pseudodeltidium; pedicle valve with recumbent and also erect clasping spines; brachial valve smooth, operculiform; cardinal process ventrally elongated, 2-pronged, long septum. *L.Perm.*, N.Am.——FIG. 308,*1*. **S. smedleyi*, Phosphoria F., USA(Wyo.); *1a,b*, holotype, ped.v. lat., int., ×1; *1c*, brach.v. int., oblique lat. view showing card. process, ×2 (587).

Truncalosia Imbrie, 1959, p. 401 [**T. gibbosa*; OD]. Differs from *Heteralosia* in having large cicatrix of attachment truncating umbo, more delicate recumbent spines and smaller cardinal process, prominent diverging socket ridges, alveolus developed. *M.Dev.*, N.Am.——FIG. 307,*1*. **T.*

gibbosa, USA(Mich.); *1a,b,* holotype, ped.v. and brach.v. views, ×2; *1c,* brach.v. int., ×3 (445).

Wyndhamia Booker, 1929, p. 24 [**W. dalwoodensis*; OD] [=*Branxtonia* Booker, 1929 (type, *B. typica*), Perm., Australia]. Like *Strophalosia* but with more concentrically arranged spine ridges and finer prostrate spines in pedicle valve, brachial valve dimpled, usually nonspinose. *L.Perm.*, Australia.——Fig. 307,*3*. **W. dalwoodensis*; *3a,b,* brach.v. view, brach.v. int., ×1; *3c,* ped.v. ext. showing ornament, ×2 (89).

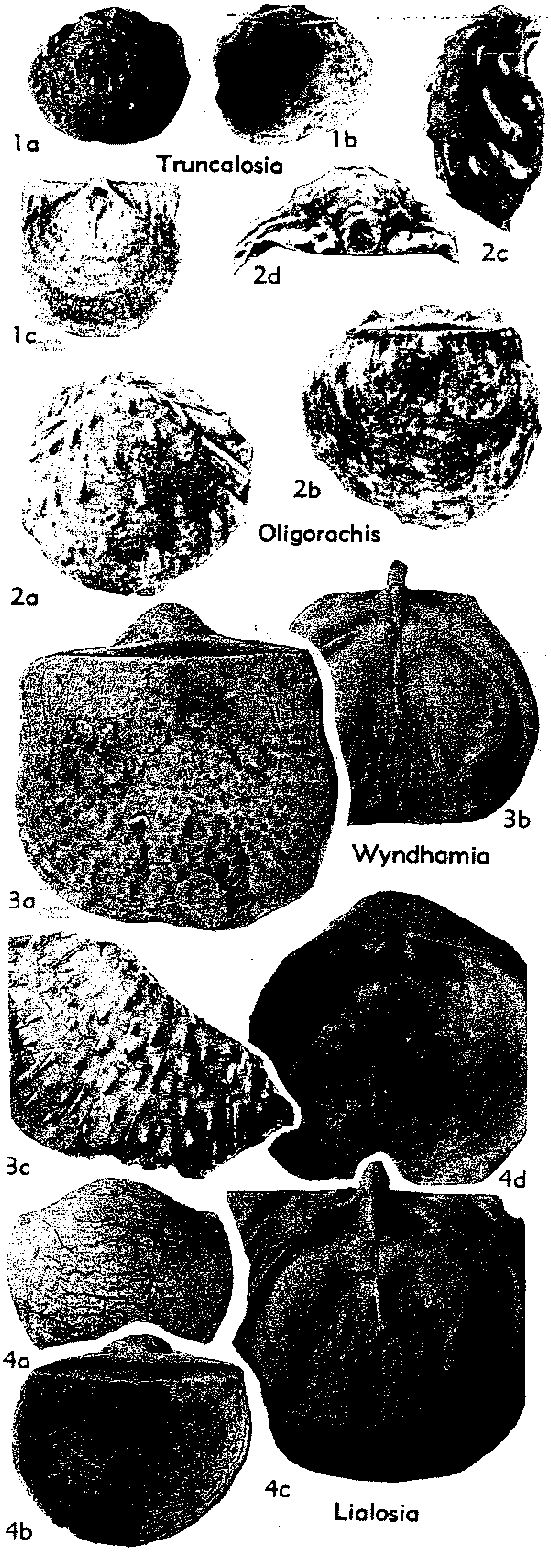


Fig. 307. Strophalosiidae (Heteralosiinae) (p. *H*451-*H*452).

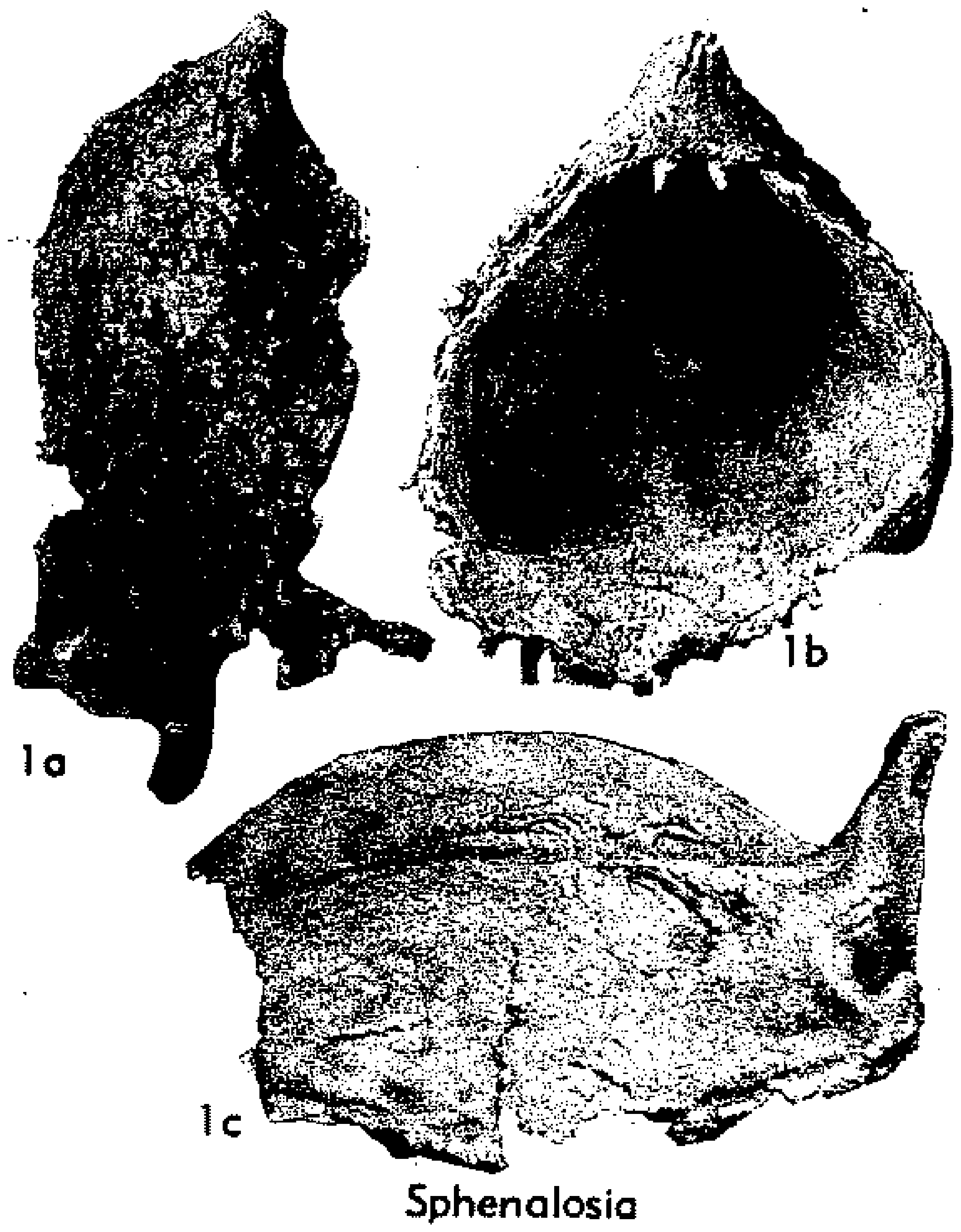


Fig. 308. Strophalosiidae (Heteralosiinae) (p. *H*451).

Subfamily CTENALOSIINAE Muir-Wood & Cooper, 1960

[Ctenalosiinae Muir-Wood & Cooper, 1960, p. 91]

Small irregular forms, brachial valve opercular; hinge of pedicle valve with numerous minute teeth and corresponding sockets in brachial valve; cardinal process with long bifid shaft; brachial ridges strophalosiid. *L.Perm.*

Ctenalosia Cooper & Stehli, 1955, p. 470 [**C. fixata*; OD]. Pedicle valve with interarea; valves smooth or obscurely costate, attachment spines in row near hinge, rare elsewhere; brachial valve rugose and dimpled, no spines. *L.Perm.*, N.Am. ——Fig. 309,*1*. **C. fixata,* USA(W.Tex.); *1a,b,* ped.v. ant. and int., ×3; *1c,* holotype, brach.v. view, ×3; *1d,* brach.v. int., ×3 (196).

Family TEGULIFERINIDAE Muir-Wood & Cooper, 1960

[Teguliferinidae Muir-Wood & Cooper, 1960 (November), p. 92] [=Teguliferidae Likharev, 1960 (December)]

Shell with obliquely conical pedicle valve

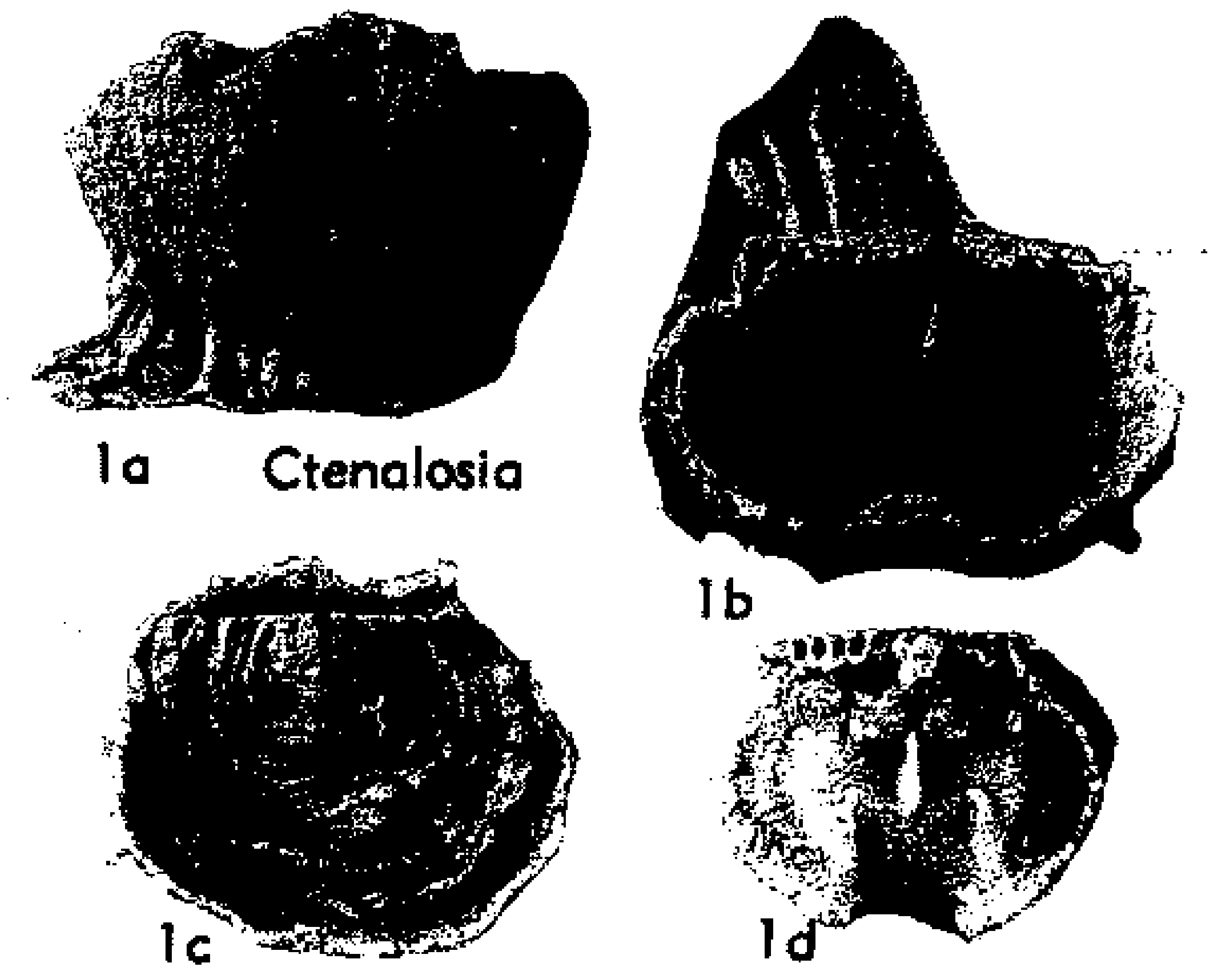


FIG. 309. Strophalosiidae (Ctenalosiinae) (p. *H*452).

attached by apex and anchored by rhizoid spines; no interareas or pseudodeltidium; brachial valve opercular; cardinal process bilobate, long-shafted and resembling Strophalosiidae, no alveolus. *U.Carb. (Penn.)-L.Perm., ?U.Perm.*

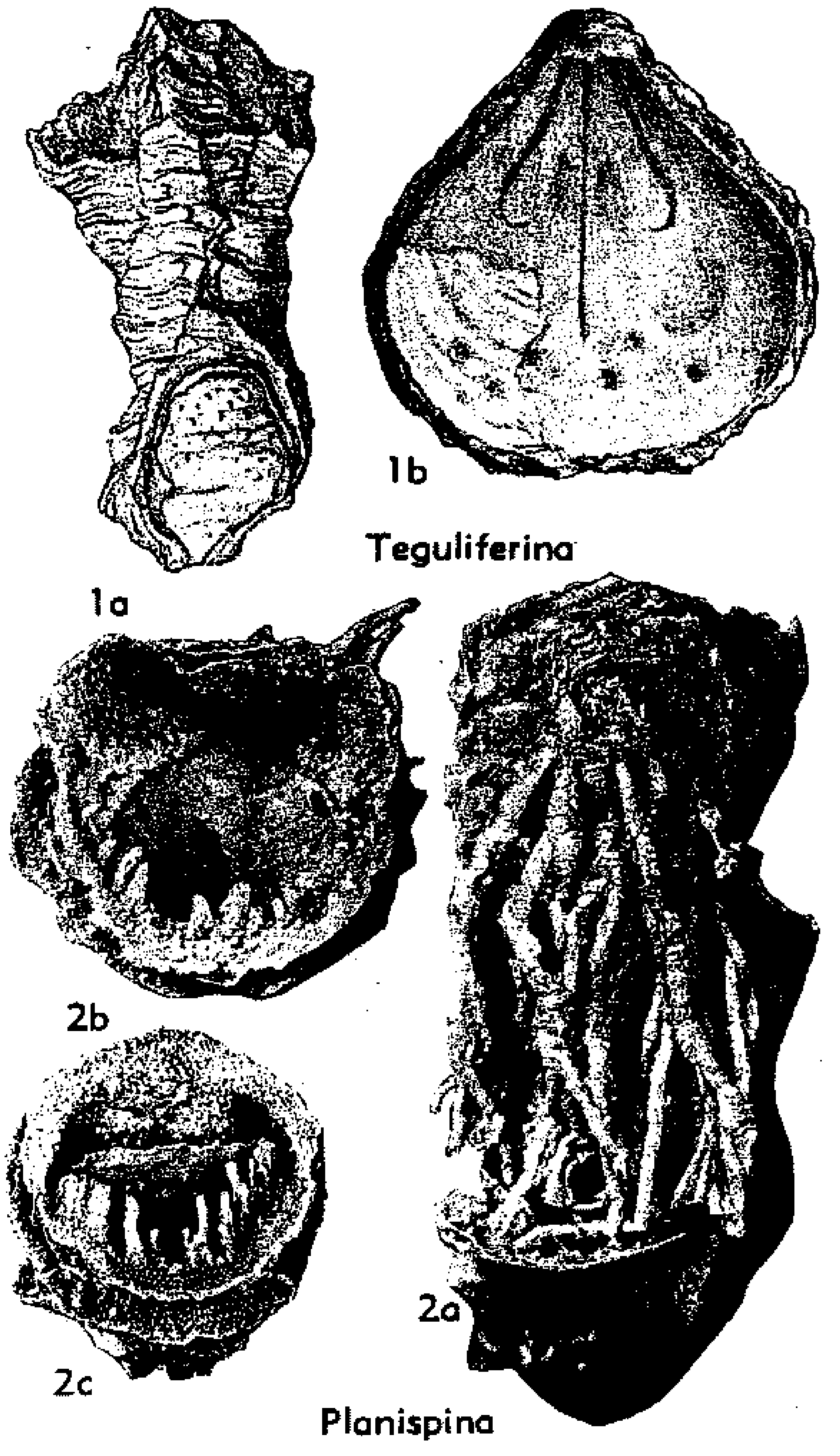


FIG. 310. Teguliferinidae (p. *H*453).

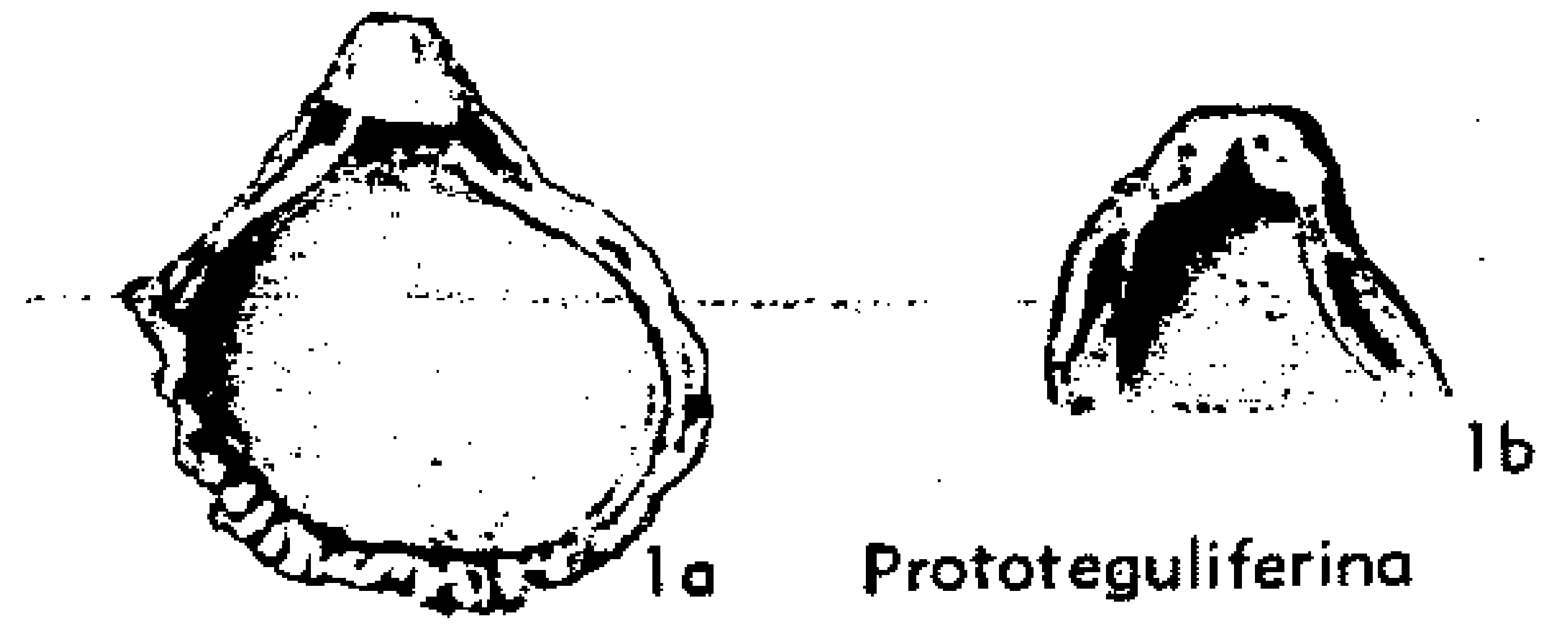


FIG. 311. Teguliferinidae (p. *H*453).

Teguliferina SCHUCHERT & LEVENE, 1929, p. 121 [*pro Tegulifera* SCHELLWIEN, 1898, p. 362 (*non* SAALMÜLLER, 1880)] [**Tegulifera deformis* SCHELLWIEN, 1898, p. 362; OD]. Pedicle valve an irregular cone; brachial valve operculiform, external in young shells but deep within pedicle valve in adult; pedicle valve with large spines, rugae and obscure capillae. *U.Carb.(Penn.)-L. Perm., ?U.Perm.*, Eu.(USSR-Yugosl.)-Asia(Japan-USSR,Ferghana).——FIG. 310,*1*. **T. deformis* (SCHELLWIEN), Perm., Yugosl.; *1a*, brach.v. view, elongate ped.v. above, ×1; *1b*, brach.v. int., ×2 (712).

Planispina STEHLI, 1954, p. 331 [**P. conida*; OD]. Like *Teguliferina*, but attachment spines fused together and to sides of cup by flat webs, and anterior margin of cup with long strainer spines. *Penn.-L.Perm.*, N.Am.——FIG. 310,*2a,b*. *P. boesei* (R. E. KING), L.Perm., USA(W.Tex.); *2a*, ped.v. lat. view showing long spines, ×2; *2b*, brach.v. ext., in place in cup, ×2 (773).——FIG. 310,*2c*. **P. conida*, L.Perm., USA(W.Tex.); ped.v. aperture, showing spines, ×1 (773).

Prototeguliferina LIKHAREV, 1960, p. 236 [**Tegulifera rossica* IVANOV, 1925, p. 111; OD]. Similar to *Teguliferina* but with spines along periphery of both valves, rudimentary interarea covered by hoodlike protuberance, brachial valve less deeply inserted. *U.Carb.-L.Perm.*, Eu.(USSR, Moscow & Donetz Basins), ?N.Am.——FIG. 311,*1*. **P. rossica* (IVANOV); *1a,b*, ped.v. and brach.v. in contact with hood concealing interarea, interarea exposed by removal of protuberance, ×1 (446).

Family AULOSTEGIDAE
Muir-Wood & Cooper, 1960

[Aulostegidae MUIR-WOOD & COOPER, 1960, p. 94]

Shell attached by umbo and anchored by spines, and having gutter-like extension of both valves; interarea in pedicle valve only, delthyrium closed by convex elytridium (formerly pseudodeltidium) and lophidium. No teeth, sockets, or chilidium. Cardinal process trilobate or quadrilobate, alveolus present; adductor scars dendritic, accessory diductor scars on cardinal process shaft; brachial ridges given off horizontally. *U. Penn.-U.Perm.*

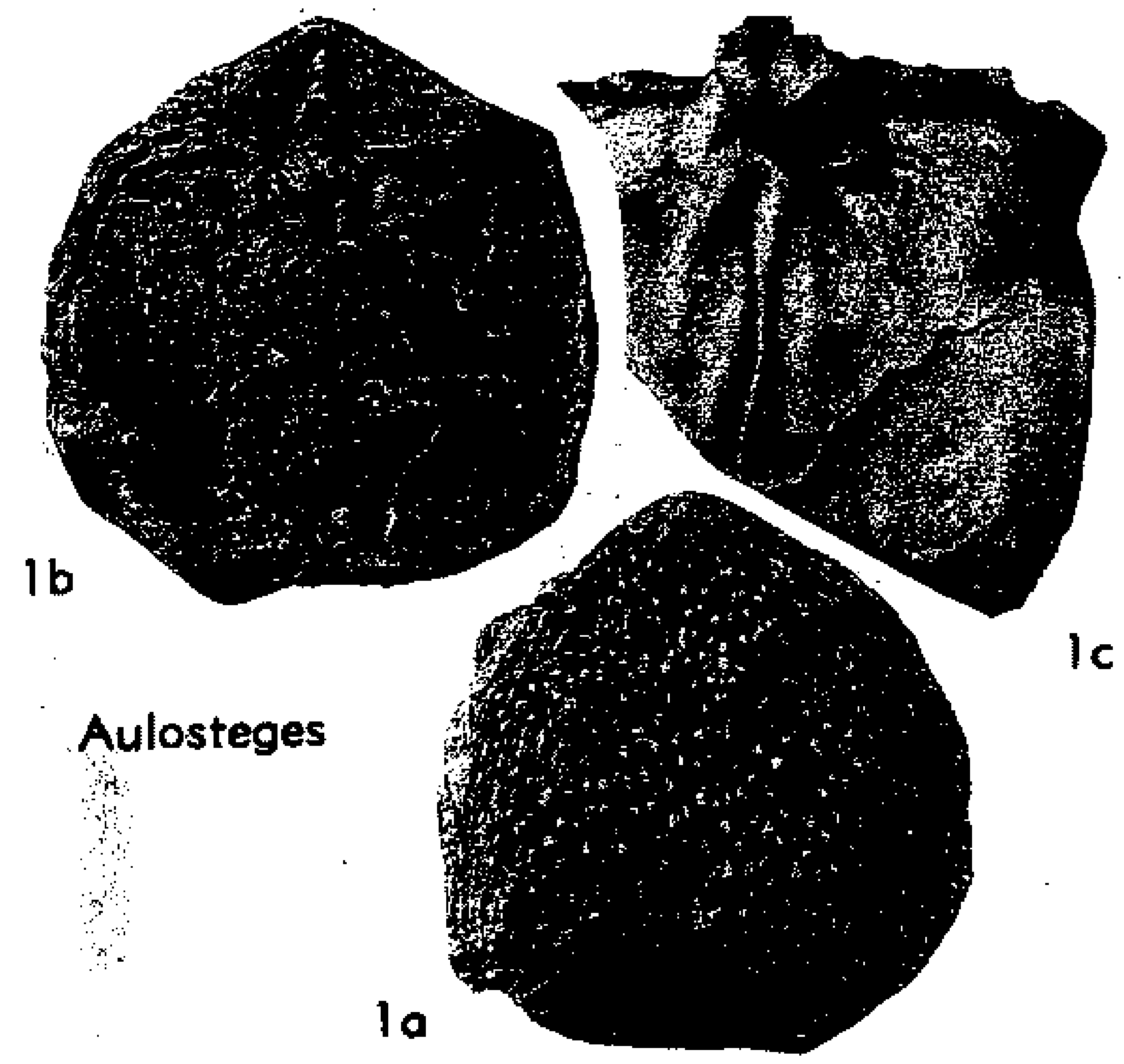


FIG. 312. Aulostegidae (Aulosteginae) (p. *H*454).

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

[Aulosteginae MUIR-WOOD & COOPER, 1960, p. 95]

Spines of two series present on both valves, otherwise smooth or lamellose; secondary area usually developed as perideltidium. Dorsal adductor scars not set on platforms. *L.Perm.-U.Perm.*

Aulosteges VON HELMERSEN, 1847, p. 330 [**A variabilis* (=**Orthis wangenheimi* DEVERNEUIL, 1845, p. 194); OD]. Medium-sized, commonly distorted, tapering to umbo; both valves with prostrate and suberect attachment spines encroaching on interarea; brachial valve adductors deeply inserted. *L.Perm.-U.Perm.*, Eu.-Asia-Arctic-Australia.——FIG. 312,*1*. **A. wangenheimi* (DE VERNEUIL), USSR; *1a-c*, ped.v. and brach.v. views, brach.v. int., ×1 (426).

Taeniothaerus WHITEHOUSE, 1928, p. 281 (*emend.* PRENDERGAST, 1943, p. 27) [**Productus subquadratus* MORRIS, 1845, p. 284; OD]. Large, with low interarea and no perideltidium; both valves with numerous elongate, regularly arranged spine ridges, prostrate and suberect spines projecting as thick brush, lamellose anteriorly; cardinal process trilobate, with elongated shaft and well-defined accessory diductor scars. *L.Perm.*, Asia-Australia-Tasm.——FIG 313,*1*. **T. subquadratus* (MORRIS), Australia; *1a,b*, ped.v. post., lat.; *1c*, brach.v. view; *1d*, brach.v. int. showing card. process; all ×0.75 (647).

Wyatkina FREDERIKS, 1931, p. 211 [**Aulosteges gigas* NECHAEV, 1894, p. 155; OD]. Large, elongate, subquadrate; interarea high, with elytridium and transversely striated perideltidium, no lophidium; pedicle valve lamellose, with spine ridges and fine prostrate spines resembling capillation; brachial valve smooth, lamellose anteriorly. *Perm.*, Eu.-Asia-Australia. —— FIG. 314,*1*. **W. gigas* (NECHAEV), Eu.(USSR); *1a,b*, ped.v. int., ext. showing spines, ×1; *1c*, brach.v. int., ×1 (597).

Subfamily ECHINOSTEGINAE Muir-Wood & Cooper, 1960

[Echinosteginae MUIR-WOOD & COOPER, 1960, p. 101]

Two series of spines on pedicle valve, rare spines on brachial valve, otherwise both valves capillate, lamellose or costate; no perideltidium; dorsal adductors set on platforms obscuring septum. *U.Penn.-L. Perm.*

Echinosteges MUIR-WOOD & COOPER, 1960, p. 101 [**Aulosteges tuberculatus* R. E. KING, 1931, p. 95; OD]. Large, asymmetrically subpentagonal, with high transversely striated interarea; elytri-

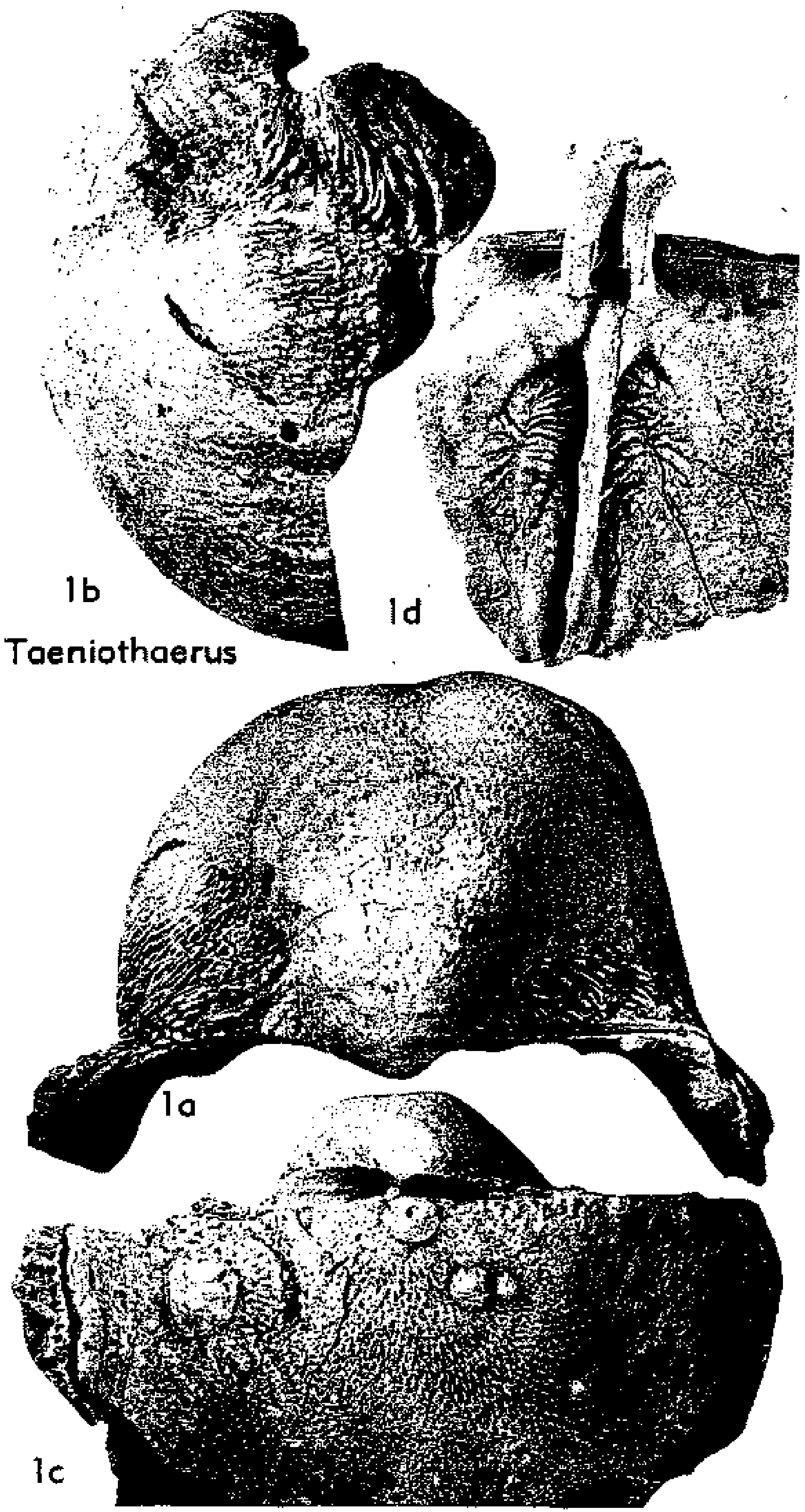


FIG. 313. Aulostegidae (Aulosteginae) (p. *H*454).

dium and lophidium present; pedicle valve with rugae, rhizoid spines posteriorly, spine ridges medianly, costate anteriorly; brachial valve with honeycomb ornament, rare spines. *L.Perm.,* N. Am.——FIG. 315,*2*. **E. tuberculatus* (R. E. King), USA(W.Tex.); *2a,b,* ped.v. ext., brach.v. ext., ×1; *2c,d,* brach.v. int., ped.v. interarea with spines, ×2 (587).

Edriosteges Muir-Wood & Cooper, 1960, p. 103 [**E. multispinosus*; OD]. Medium-sized, subpentagonal to subquadrate, with low interarea; pedicle valve with short recumbent spines, dense brush of rhizoid spines on ears and flanks; brachial valve faintly capillate, dimpled, no spines. *L. Perm.,* N.Am.-Asia(Pak.-China).——FIG. 315,*1*. **E. multispinosus,* USA(W.Tex.); *1a,b,* holotype, ped.v. view, brach.v. int., ×1; *1c,d,* ped.v. lat., brach.v. view, ×1 (587).

Girlasia de Gregorio, 1930, p. 21 [**Strophalosia (G.) superelegans*; OD]. Small, elongate-oval; lophidium present, no elytridium; pedicle valve lamellose with fine prostrate spines, row of coarser rhizoid spines near interarea; brachial valve with rare fine spines, cardinal process bilobate; hinge of both valves minutely crenulated. *L.Perm.,* Sicily. ——FIG. 316,*1*. **G. superelegans,* Sosio Ls.; *1a,b,* ped.v. and brach.v. views, ×3 (370).

Limbella Stehli, 1954, p. 329 [**Aulosteges wolfcampensis* R. E. King, 1931, p. 95; OD]. Differs from *Edriosteges* in having both valves capillate; elytridium absent; gutter developed in all growth stages. *U.Penn.-L.Perm.,* N.Am.——FIG. 317,*2*. **L. wolfcampensis* (R. E. King), L.Perm., USA (W.Tex.); *2a,b,* ped.v., brach.v. views, ×0.7; *2c,* ped.v. int., ×0.7; *2d,e,* brach.v., showing card. process with lophidium, ×2 (773).

Sphenosteges Muir-Wood & Cooper, 1960, p. 108 [**Aulosteges hispidus* Girty, 1920; OD]. Medium-sized, trigonal outline, commonly asymmetrical; interarea high, lophidium and elytridium present; pedicle valve with few rugae, prostrate and erect clasping spines, faintly capillate; brachial valve capillate, rare spines. *L.Perm.,* N.Am.(Wyo.-Utah).——FIG. 316,*3*. **S. hispidus* (Girty), Phosphoria F., USA(Wyo.); *3a,b,* ped.v. and brach.v. views, ×3 (587).

Spirisosium de Gregorio, 1930, p. 23 [**S. primarium* (=**Aulosteges Karpinskyi* Gemmellaro, 1892); OD]. Large, elongate-trigonal; very high interarea with narrow median ridge; pedicle valve with spine bases of 2 series, curved attachment spines along edge of interarea; brachial valve with rare spines. *L.Perm.,* Sicily.——FIG. 317,*1*. **S. karpinskyi* (Gemmellaro), Sosio Ls.; *1a,b,* ped.v. and brach.v. views, ×0.7 (370).

Strophalosiella Likharev, 1935, p. 372 [**S. coraeformis*; OD]. Pentagonal, tapering, elytridium present; both valves finely costellate, spines on flanks and near interarea in pedicle valve, absent in brachial valve. *L.Perm.,* Eu.(USSR).

Xenosteges Muir-Wood & Cooper, 1960, p. 111 [**X. adherens*; OD]. Small, asymmetrical; edge of narrow interarea articulating with slot in brachial valve; both valves rugose or lamellose; spines near hinge margin in pedicle valve, absent in brachial valve. *L.Perm.(Leonard.-Word.),* N. Am.——FIG. 316,*2*. **X. adherens,* USA(W.Tex.); *2a,b,* ped.v., ×3, ×2; *2c,* brach.v. view, ×4; *2d,* brach.v. int., ×4 (587).

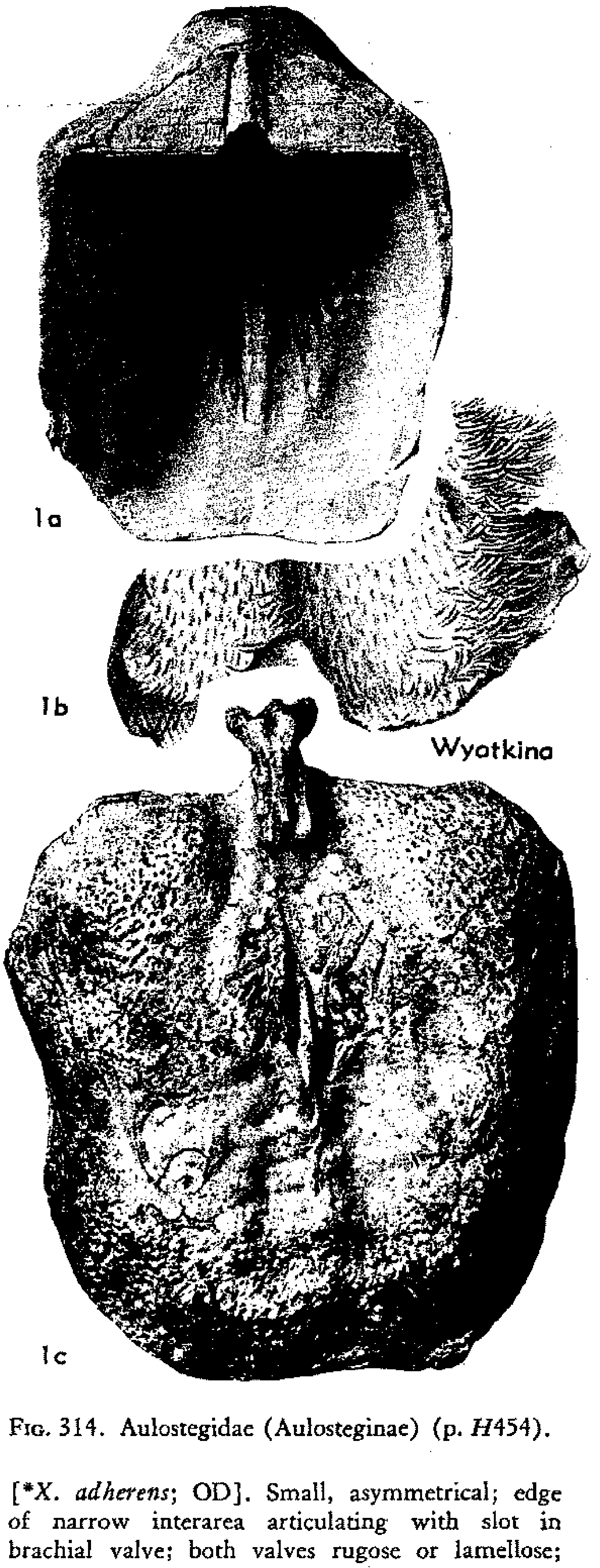


FIG. 314. Aulostegidae (Aulosteginae) (p. *H*454).

Subfamily CHONOSTEGINAE Muir-Wood & Cooper, 1960

[Chonosteginae Muir-Wood & Cooper, 1960, p. 113]

Specialized, posteriorly rugose and anteriorly costate; pedicle valve with anterior projecting ledge, bearing row of erect attachment spines, another spine row along hinge margin. *U.Carb* or *L.Perm.*, *?U.Perm.*

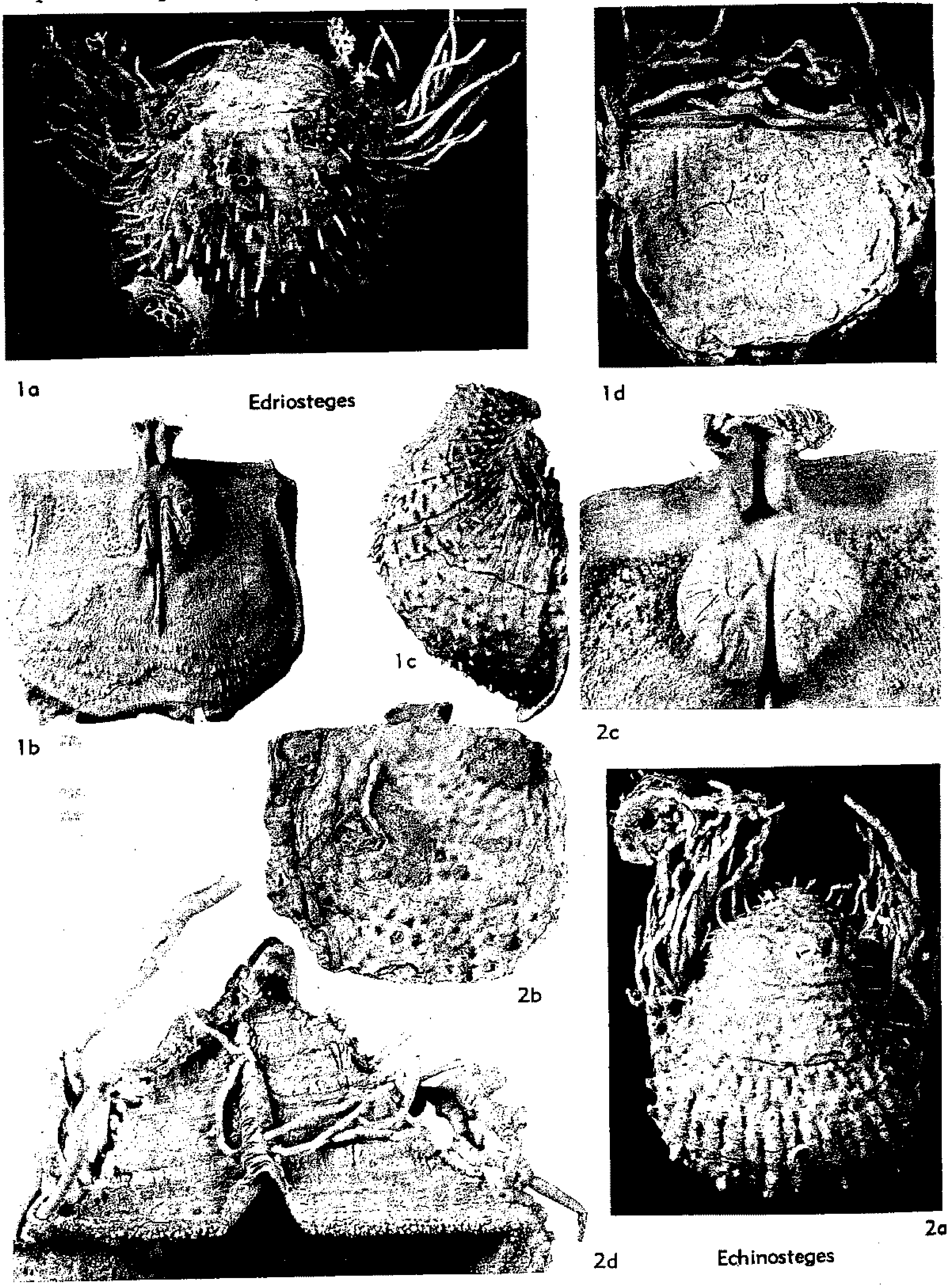


Fig. 315. Aulostegidae (Echinosteginae) (p. *H*454, *H*455).

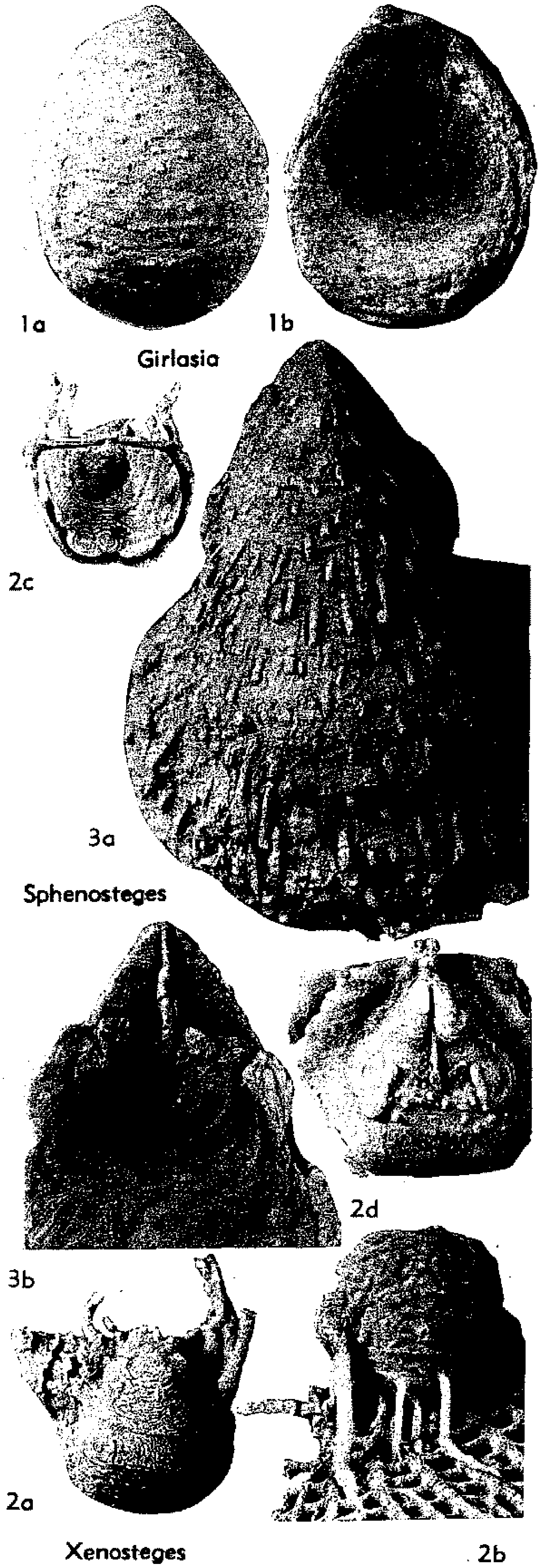


FIG. 316. Aulostegidae (Echinosteginae) (p. *H*455).

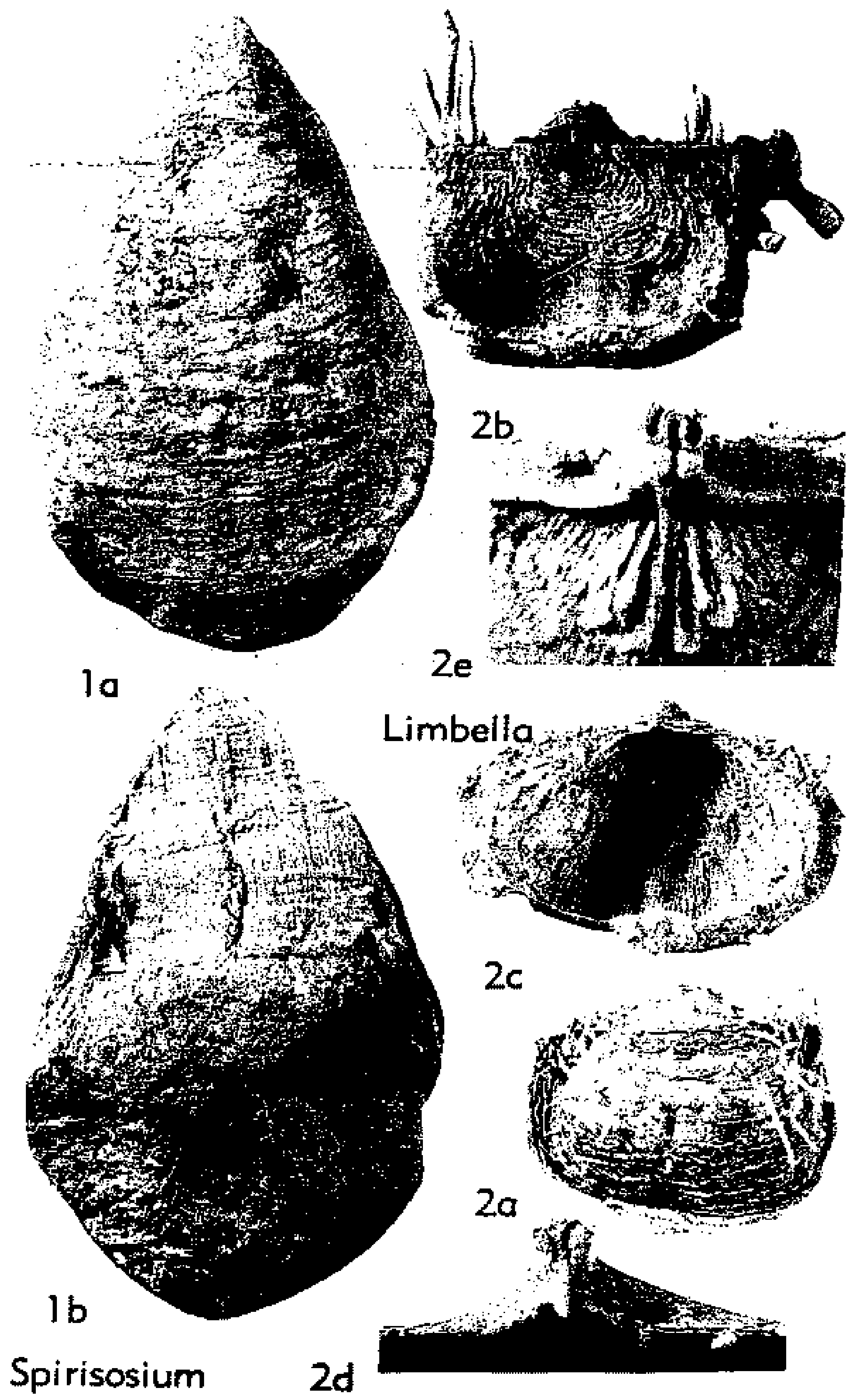


FIG. 317. Aulostegidae (Echinosteginae) (p. *H*455).

Chonosteges MUIR-WOOD & COOPER, 1960, p. 113 [**Aulosteges magnicostatus* GIRTY, 1909, p. 278; OD]. Pedicle valve geniculated, with short trail, elytridium and lophidium present, anterior ledge in pedicle valve with erect spines on costae and interior openings on intercostal sulci, 2 series of spines on rugose visceral disc; brachial valve costae terminating in anterior row of spines or funnels; complex internal system of strainer spines and pluglike fillings. *L.Perm.*, N.Am.——FIG. 318,*1*. **C. magnicostatus* (GIRTY), USA(W.Tex.); *1a*, brach.v. views showing attachment spines and funnels, ×2; *1b*, ant. margin with funnels, ×4; *1c*, ped.v. ant. view showing spines, ×1.35; *1d*, ant. view of both valves showing rim and stoppers, ×2; *1e*, brach.v. int., ×2 (587).

Strophalosiina LIKHAREV, 1935, p. 369 [**Aulosteges tibeticus* DIENER, 1897, p. 35; OD]. Resembles *Chonosteges* in external form and ornament but lacks spines on anterior ledge; brachial valve lacking spines or funnels. *(?U.)Perm.*, Eu.(Caucasus)-Asia.——FIG. 318,*2*. **S. tibetica* (DIENER), Tibet; *2a,b*, ped.v. ext., lat., ×0.7; *2c*, brach.v. view, ×0.7 (257).

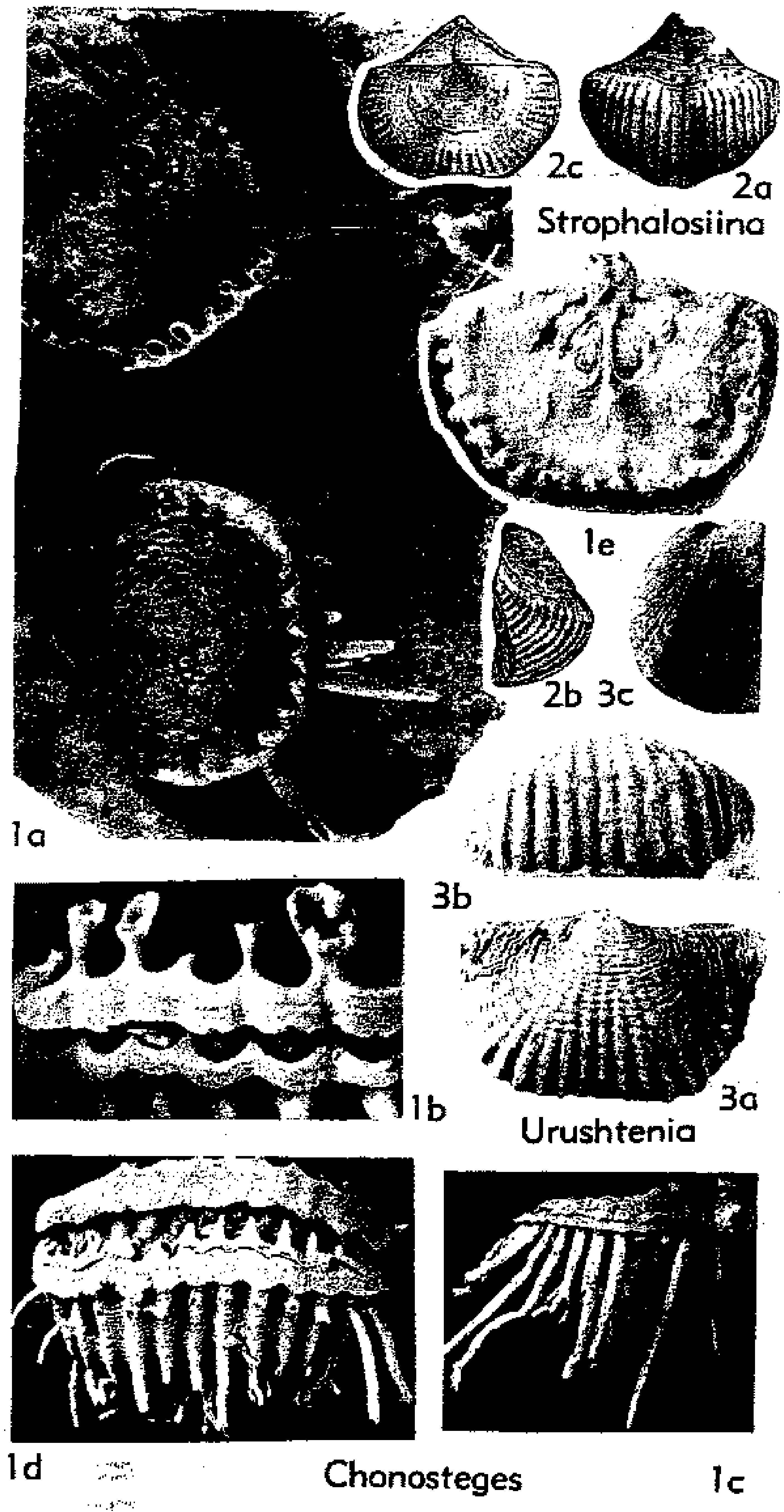


Fig. 318. Aulostegidae (Chonosteginae) (p. *H*457-*H*458).

Urushtenia Likharev, 1935, p. 370 [**Productus pseudomedusa* Chernyshev, 1902; OD]. Like *Strophalosiina* externally but interarea rarely developed; anterior ledge or ledges bearing erect spines as in *Chonosteges*, but no openings on intercostal sulci; brachial valve without funnels or spines. *L.Perm.*, Eu.(USSR).——Fig. 318,*3*. **U. pseudomedusa* (Chernyshev); *3a-c*, ped.v., ext., ant., lat., ×1.3 (514).

Subfamily INSTITELLINAE Muir-Wood & Cooper, 1960

[Institellinae Muir-Wood & Cooper, 1960, p. 117]

Ornament costellate and rugose, visceral disc reticulate; pedicle valve with long attachment spines on ears and near hinge; spines absent on brachial valve. *L.Perm.*, *?U.Perm.*

Institella Cooper, 1942, p. 230 [**Productus leonardensis* R. E. King, 1931, p. 70; OD]. Both valves geniculated, cicatrix of attachment present; low interarea without elytridium, lophidium present; trail with elaborate marginal gutter in both valves with median tonguelike extension. *L.Perm.*, *?U. Perm.*, Eu.-Asia-N.Am.——Fig. 319,*1*. **I. leonardensis* (R. E. King), USA(W.Tex.); *1a*, ped.v. ext., ×1.5; *1b,c*, brach.v. ext., int., ×1 (587).

Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

[Rhamnariinae Muir-Wood & Cooper, 1960, p. 119]

Aberrant, with low interarea in pedicle valve, elytridium usually absent, attachment cicatrix developed; both valves spinose. Small septum in pedicle valve. *L.Perm.-U. Perm.*

Rhamnaria Muir-Wood & Cooper, 1960, p. 119 [**R. kingorum*; OD]. Medium-sized, subquadrate, with low interarea; pedicle valve with spine ridges bearing fine prostrate or larger erect spines, rhizoid spines near hinge and on ears, brush of spines

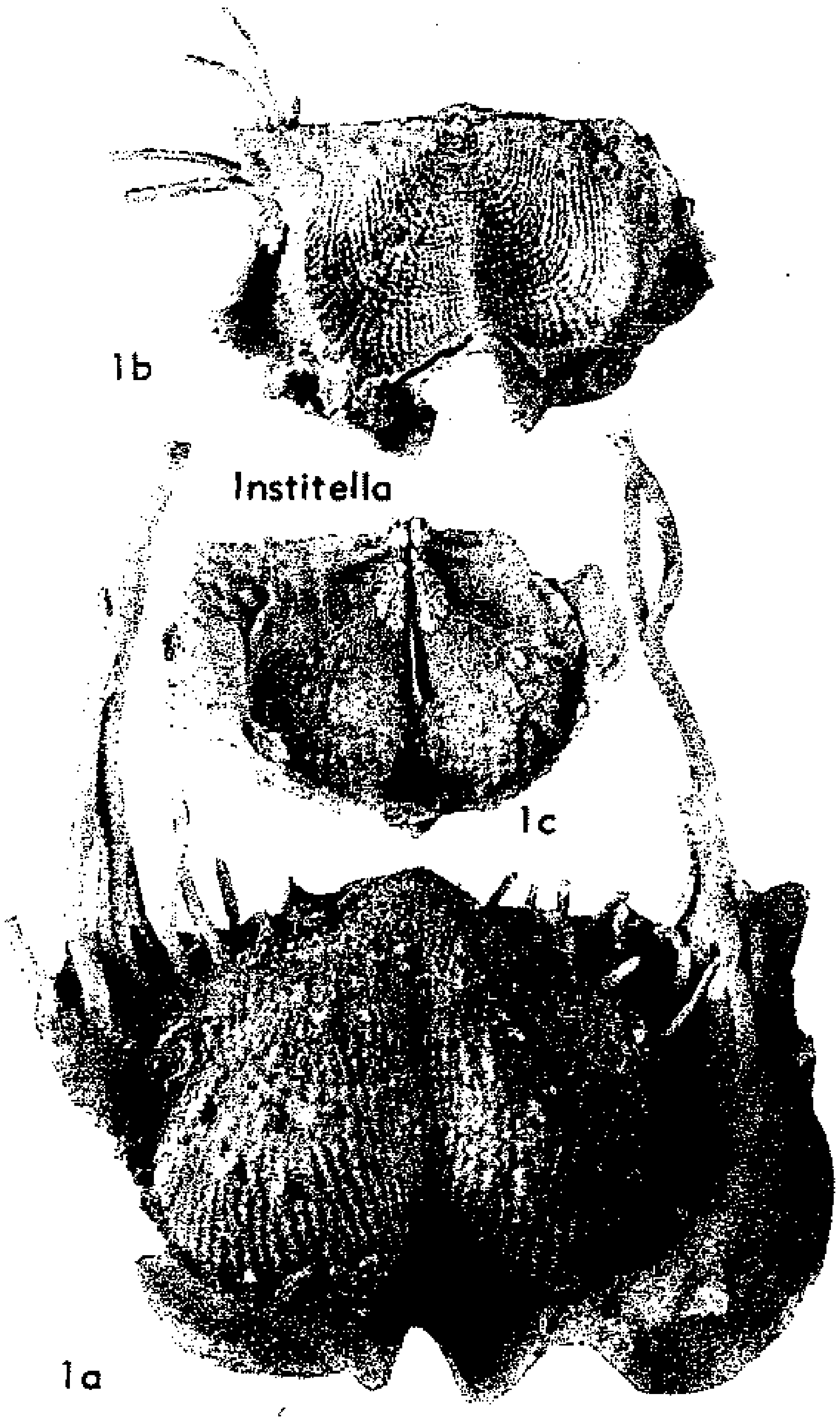


Fig. 319. Aulostegidae (Institellinae) (p. *H*458).

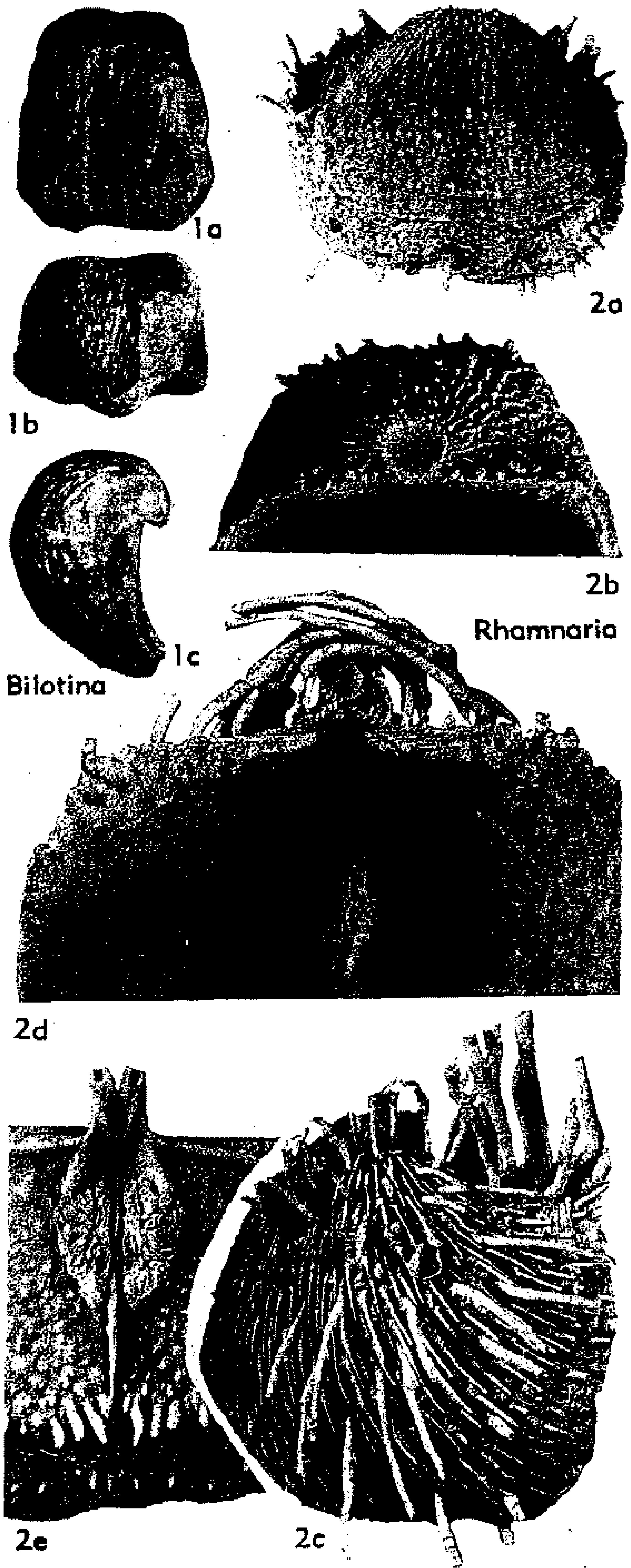


FIG. 320. Aulostegidae (Rhamnariinae) (p. *H*458-*H*459).

extending laterally from flanks, anteriorly lamellose; brachial valve rugose, with fine, prostrate spines. *L.Perm.-U.Perm.*, N.Am.——FIG. 320,*2*. **R. kingorum*, L.Perm., USA(W.Tex.); *2a,b,* holotype, ped.v. ext., post., ×1, ×2; *2c,d,* ped.v., ext., int., ×2; *2e,* brach.v. int., ×2 (587).

Bilotina F. R. C. REED, 1944, p. 109 [**B. subtecta*; OD]. Medium-sized, elongate, with low interarea; pedicle valve with spine ridges posteriorly, irregularly costate anteriorly, large spines on ears and flanks, short ventral median septum; brachial valve spinose and pitted, internally with long median septum and 2 buttress plates. *L.Perm.*, Asia(Pak.).——FIG. 320,*1*. **B. subtecta*; *1a-c,* ped.v. vent., post., lat., ×1 (664).

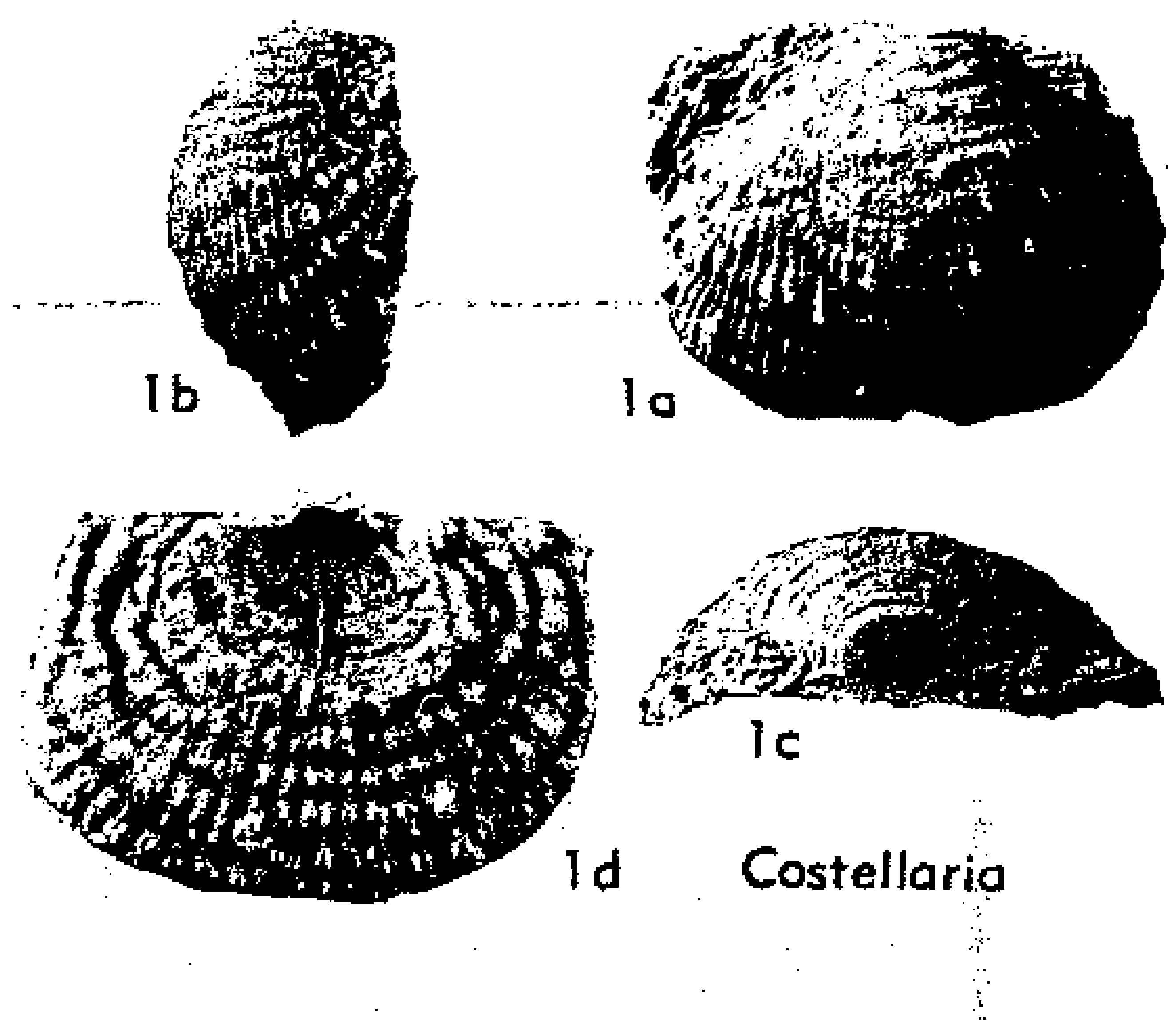


FIG. 321. Aulostegidae (Costellariinae) (p. *H*459).

Subfamily COSTELLARIINAE Muir-Wood & Cooper, 1960

[Costellariinae MUIR-WOOD & COOPER, 1960, p. 123]

Pedicle valve with low interarea, no elytridium, teeth or sockets, its exterior posteriorly rugose and finely costellate with 2 series of spines; brachial valve similar but lacking spines. *L.Perm.*

Costellaria MUIR-WOOD & COOPER, 1960, p. 123 [**C. costellata*; OD]. Growth habit strophalosiid, with cicatrix truncating umbo, but ornamented like *Cancrinella*; cardinal process bilobate, sessile, closing delthyrium anteriorly. *L.Perm.*, N.Am.——FIG. 321,*1*. **C. costellata*, USA(Tex.); *1a-c,* ped. v. ext., lat., post., ×2; *1d,* brach.v. int., ×4 (587).

Family SINUATELLIDAE
Muir-Wood & Cooper, 1960

[Sinuatellidae MUIR-WOOD & COOPER, 1960, p. 124]

Strongly geniculated, anchored by attachment spines; ventral interarea with pseudodeltidium; teeth and sockets rarely developed; cardinal process posteriorly quadrilobate, alveolus present; diductor scars with lobate bounding ridges, adductors smooth. *L.Carb.-U.Carb.(Namur.).*

Sinuatella MUIR-WOOD, 1928, p. 37 [**Leptaena sinuata* DE KONINCK, 1851, p. 654; OD]. Both valves with rugae and costae posteriorly, commonly reticulate; trail costate; spines long, curving near hinge, and on ears of pedicle valve. *L. Carb.(Visean) - U. Carb.(Namur.)*, Eu.-Asia. ——

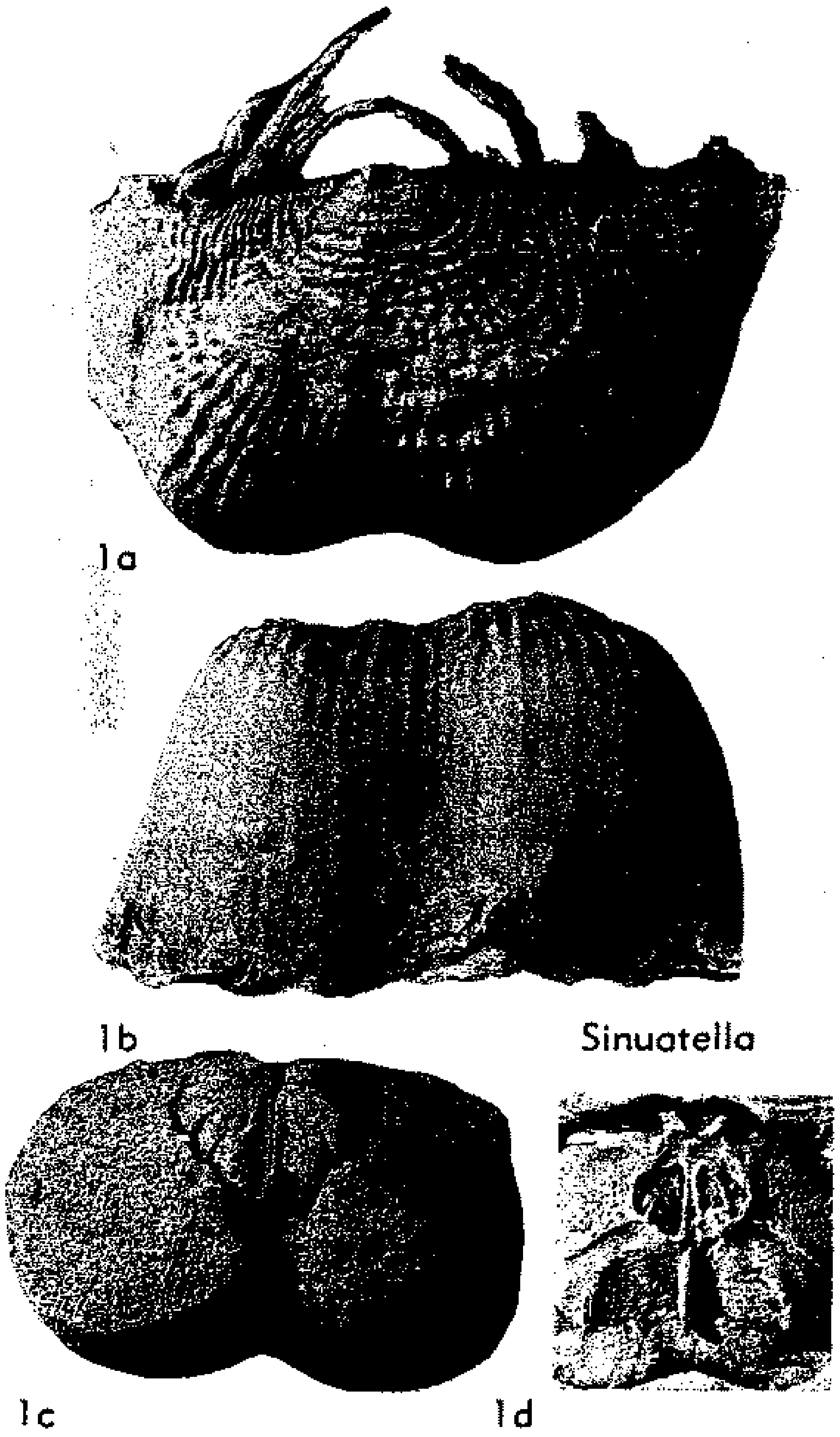


FIG. 322. Sinuatellidae (p. *H*459-*H*460).

FIG. 322,*1*. **S. sinuata* (DE KONINCK), L.Carb., Eng.; *1a-c*, ped.v. post. with overlapping spines, ant., mold of int. showing muscle field impression, ×2; *1d*, brach.v. int., ×2 (574).

Family CHONETELLIDAE Likharev, 1960

[Chonetellidae LIKHAREV, 1960, p. 226]

Externally resembling chonetoids, but with surface spines; interarea in each valve, small teeth and sockets; cardinal process large, bilobate, no alveolus; adductors smooth; brachial ridges well defined. *?L. Perm., U.Perm.*

Chonetella WAAGEN, 1884, p. 613 [**C. nasuta*; M] [*non Chonetella* KROTOV, 1885 (=*Chonetina* KROTOV, 1888)]. Small, valves highly concavo-convex, both valves costellate; pedicle valve with notched trail or with V-shaped extension, spines scattered and in row near interarea and on flanks of pedicle valve. *?L.Perm., U.Perm.*, Eu.(USSR)-Asia(Pak.)-Arctic.——FIG. 323,*1*. **C. nasuta*, Pak.; *1a-c*, ped.v. ext., post., ant., ×2; *1d*, brach. v. int., ×2 (587).

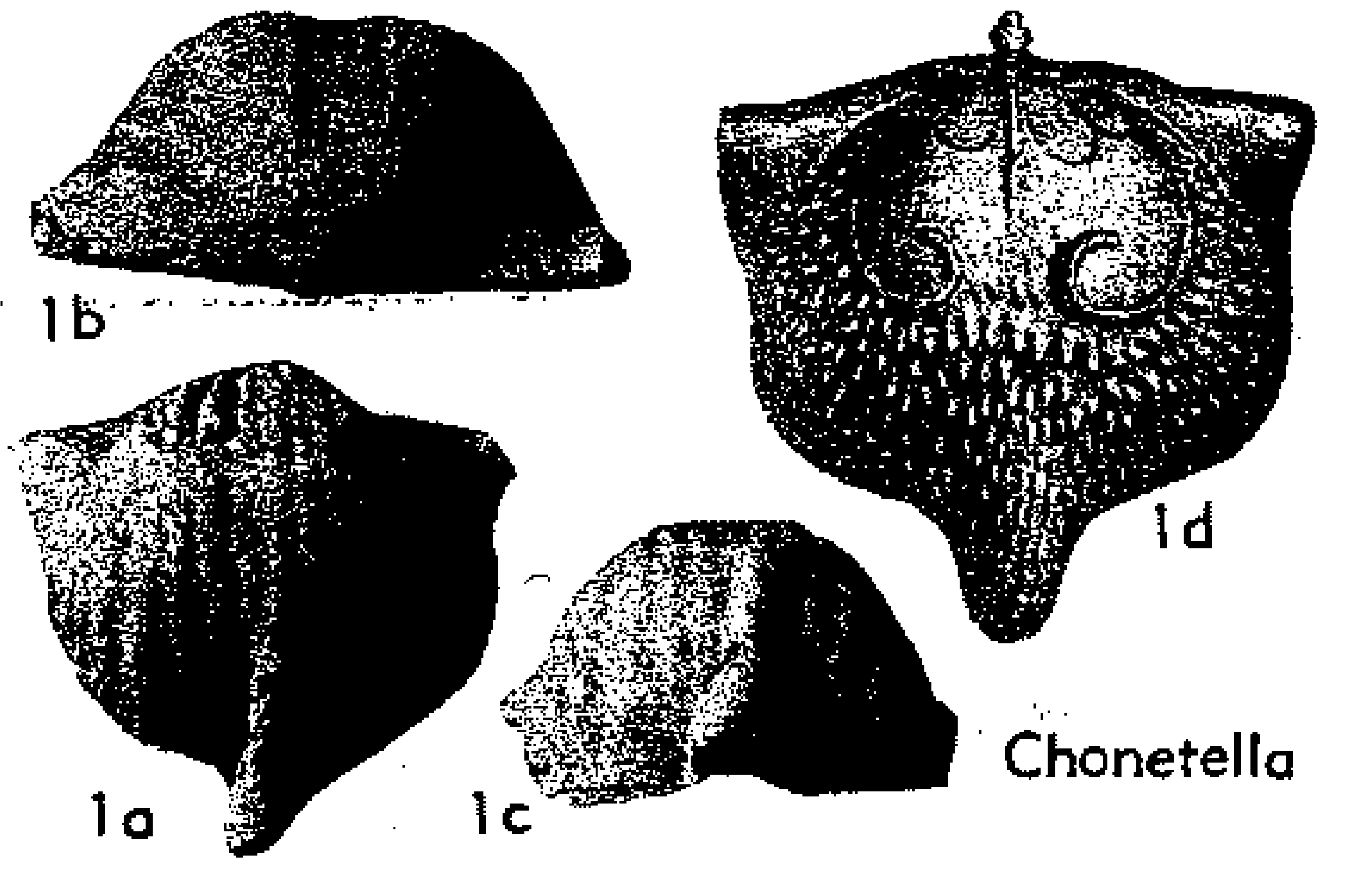


FIG. 323. Chonetellidae (p. *H*460).

Family SPYRIDIOPHORIDAE Muir-Wood & Cooper, 1960

[Spyridiophoridae MUIR-WOOD & COOPER, 1960, p. 144]

Aberrant forms probably derived from Aulostegidae but interarea lost in pedicle valve; brachial valve with elaborate adductor platforms forming spyridium, cardinal process bilobed, with alveolus developed. *U.Penn.-L.Perm.*

Spyridiophora COOPER & STEHLI, 1955, p. 471 [**S. distincta*; OD] [=*Spiridiophora* SARYCHEVA, 1960 (*nom. null.*)]. Medium-sized, transverse, both valves geniculated, posteriorly rugose and costate, trail costate; spines in row near hinge, and group on ears of pedicle valve, absent on brachial valve. *U. Penn.-L. Perm.(Wolfcamp.-Leonard.)*, N. Am. ——FIG. 324,*1*. **S. distincta*, Wolfcamp., USA (W.Tex.); *1a,b*, ped.v. ext., ant., ×1; *1c*, brach.v. post. view showing card. process and spyridium, ×3; *1d,*, brach.v. view, ×1 (196).

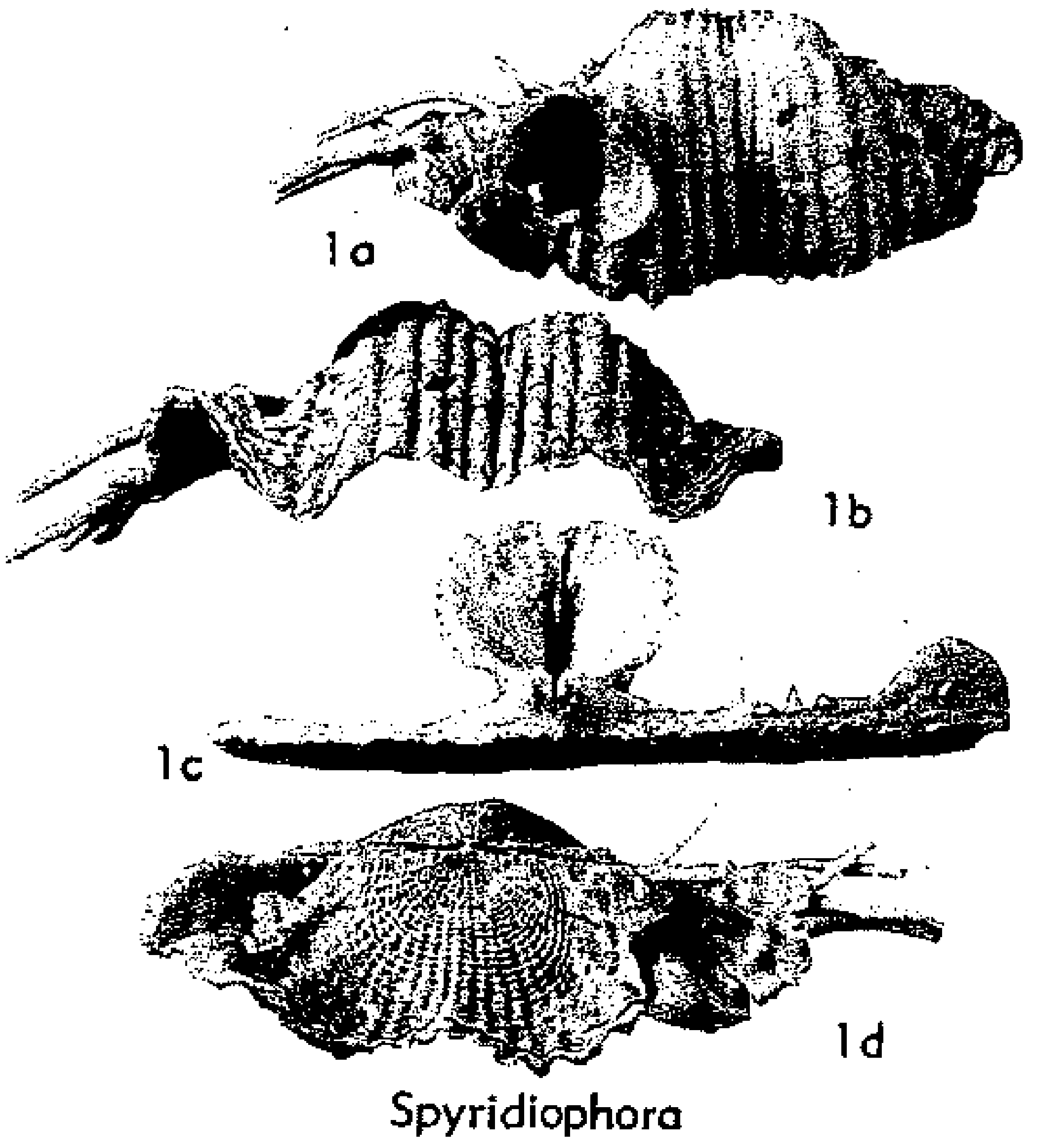


FIG. 324. Spyridiophoridae (p. *H*460).

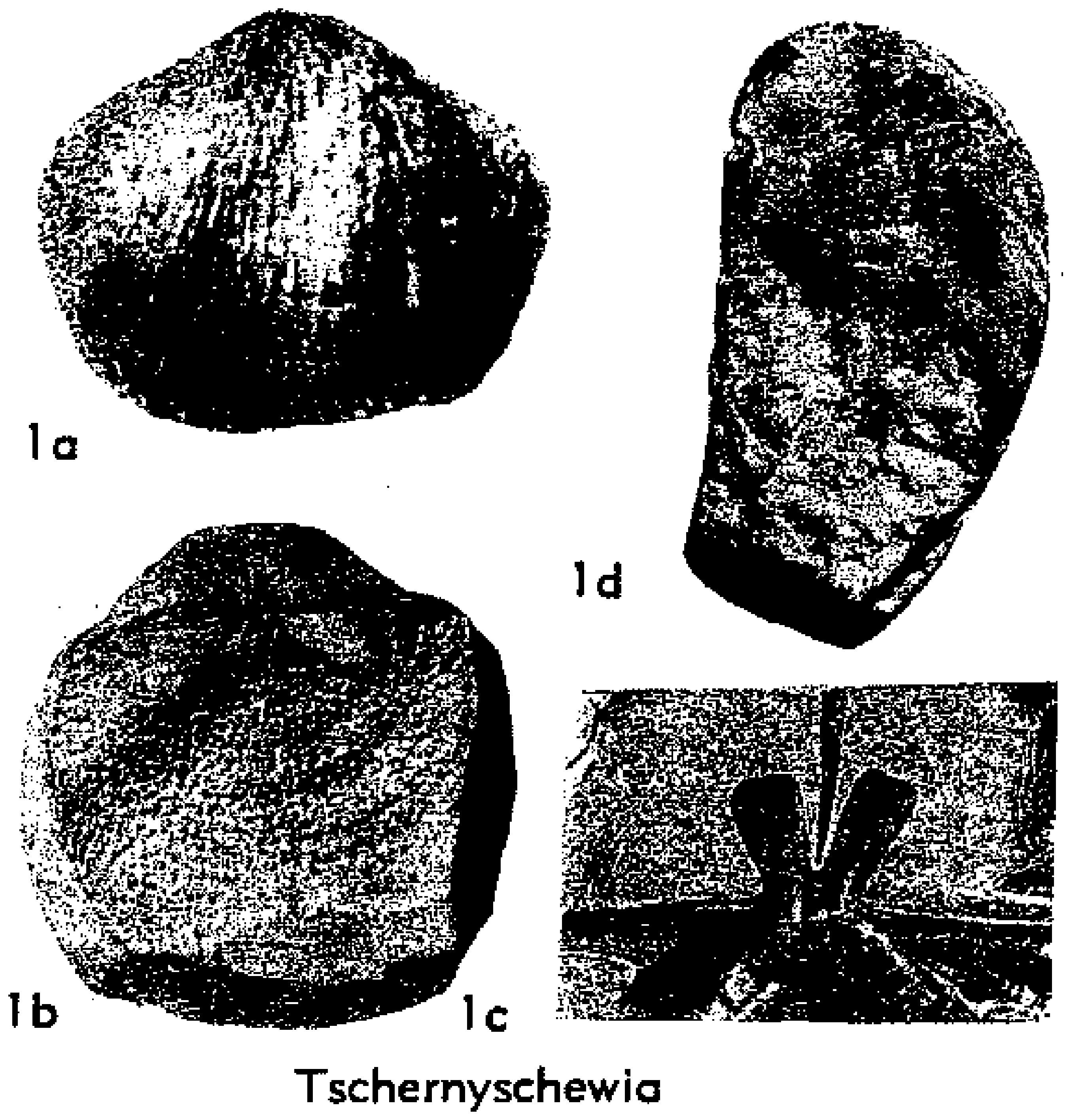


FIG. 325. Tschernyschewiidae (p. *H*461).

Family TSCHERNYSCHEWIIDAE Muir-Wood & Cooper, 1960

[Tschernyschewiidae MUIR-WOOD & COOPER, 1960, p. 126]

Aberrant forms with high platelike septum in pedicle valve fitting between 2 lobes of cardinal process; no teeth and sockets; adductors nondendritic. *L.Perm.-U.Perm.*

Tschernyschewia STOYANOW, 1910, p. 853 [**T. typica*; OD] [=*Septoproductus* FRECH, 1911, p. 75 (type, *Productus abichi* WAAGEN, 1884, p. 697)]. Medium-sized, externally resembling *Waagenoconcha*, with spine ridges medianly and fine spines on flanks; pedicle valve with low interarea, umbo commonly truncated by attachment cicatrix. *L.Perm.-U.Perm.*, Eu.-Asia.——FIG. 325,*1*. **T. typica*, Armenia; *1a*, ped.v. ext., ×1; *1b,c*, brach.v. view with beaks ground showing ped.v. septum and card. process, ×1, ×2; *1d*, ped.v. long. sec. showing septum, ×1 (785).

Family SCACCHINELLIDAE Likharev, 1928

[*nom. transl.* A. WILLIAMS, 1953, p. 12 (*ex* Scacchinellinae LIKHAREV, 1928, p. 265)]

Aberrant, specialized forms probably derived from Aulostegidae, characterized by conical pedicle valve cemented at apex and anchored by numerous rhizoid spines; pedicle valve interior with long median septum, distal end fitting between prongs of cardinal process; dorsal growth of body accompanied by deposition of abundant cystose or blister-like plates forming partitions; adductor scars dendritic, set on muscle platforms. *U.Penn.-L.Perm.*, *?U.Perm.*

Scacchinella GEMMELLARO, 1891, p. 22 [**S. variabilis* GEMMELLARO, 1897; SD SCHUCHERT & LEVENE, 1929, p. 110]. Medium-sized to large; interarea very large, longitudinally striated, elytridium not distinguishable; pedicle valve spinose except on interarea; brachial valve finely spinose, no interarea. *U.Penn.-L.Perm.*, *?U.Perm.*, N.Am.; *Perm.*, Eu. (Sicily-Alps-Caucasus)-Asia (Ferghana-Japan).——FIG. 326,*2*. *S. americana* STEHLI, L. Perm. (Leonard.), USA (W.Tex.); *2a,b*, ped.v.,

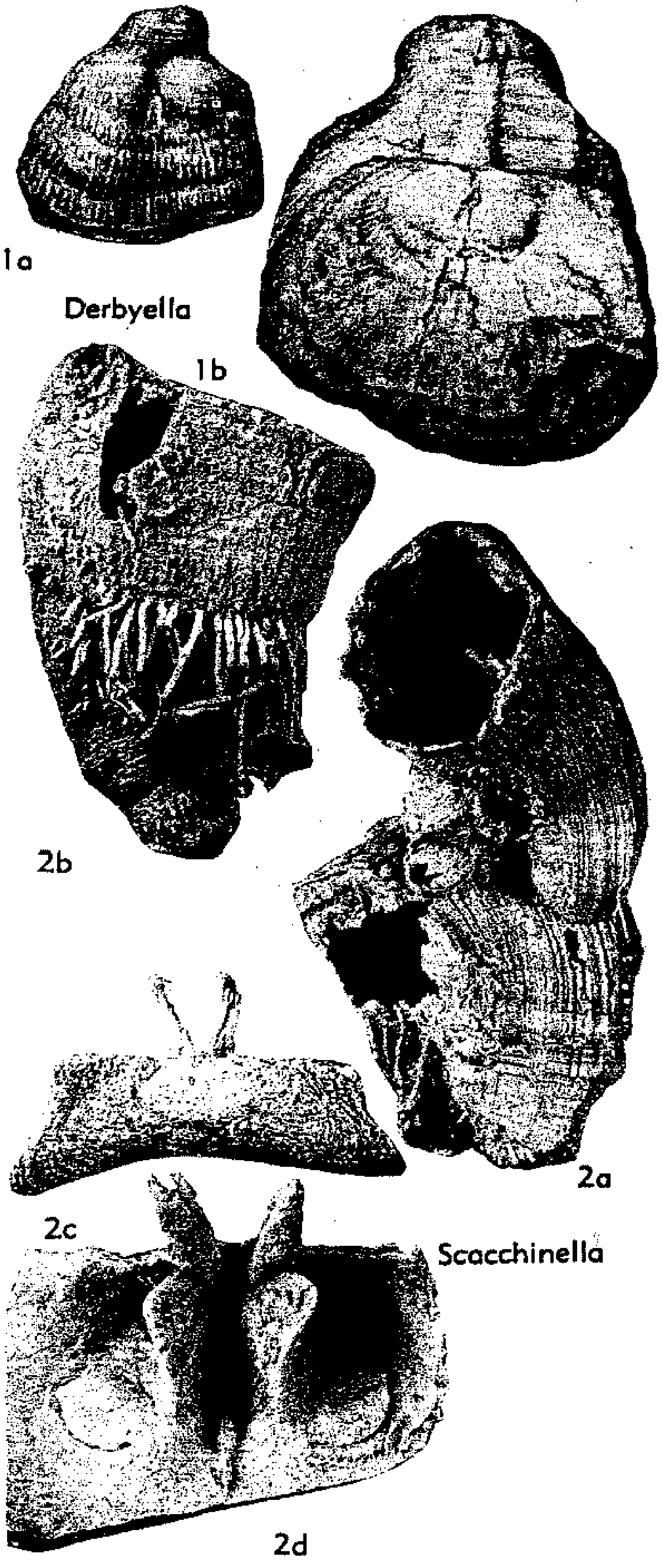


FIG. 326. Scacchinellidae (p. *H*461-*H*462).

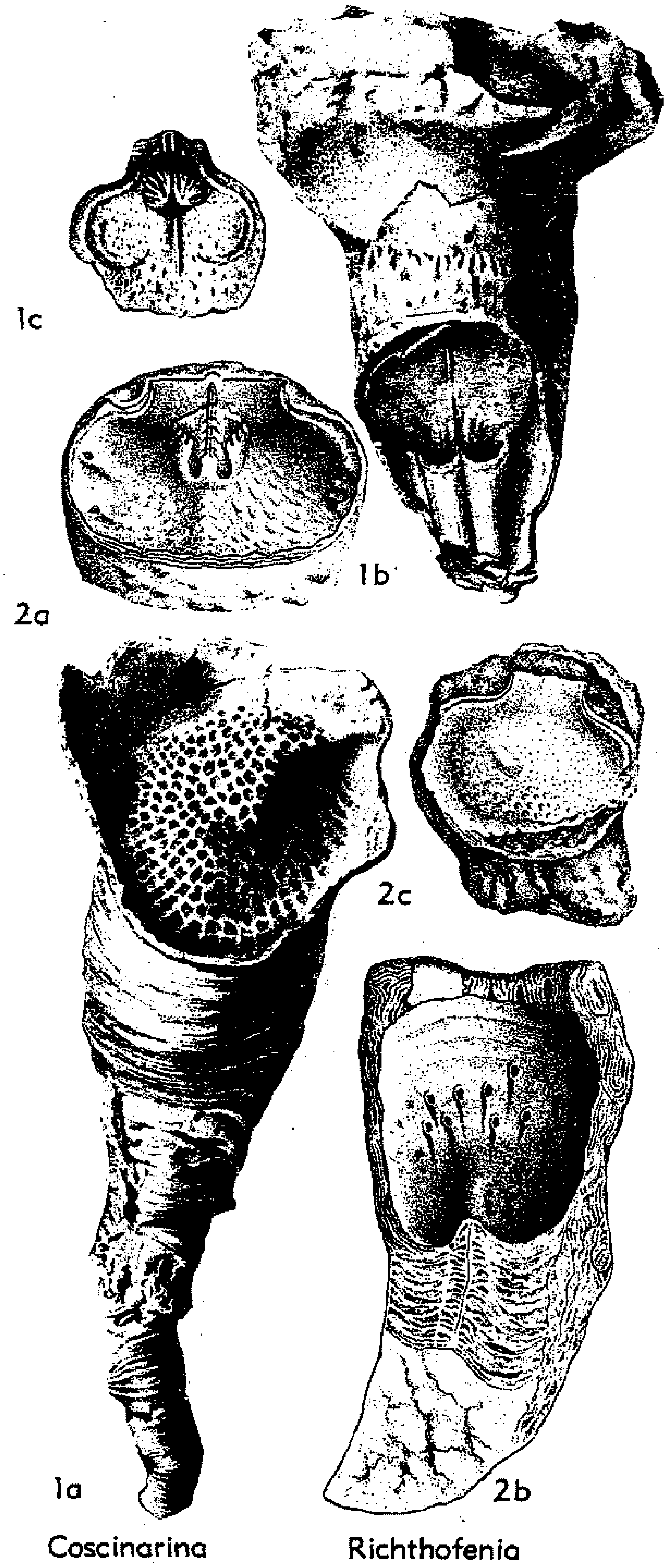


FIG. 327. Richthofeniidae (Richthofeniinae) (p. H462).

lat. views showing attachment spines, ×1; *2c,d,* brach.v. ext., int., ×1, ×2 (470).

Derbyella GRABAU, 1931, p. 269 [**D. bureri*; OD]. Medium-sized, with high ventral interarea; interior of pedicle valve with myocoelidium and septum; brachial valve with low interarea, otherwise imperfectly known. *L.Perm.,* Asia(Mongolia). ——FIG. 326,*1.* **D. bureri*; *1a,b,* holotype, ped.v. ext., brach.v. view showing large ped.v. interarea, ×1, ×2 (360).

Superfamily RICHTHOFENIACEA Waagen, 1885

[*nom. correct.* MUIR-WOOD, herein (*pro* Richthofenacea MUIR-WOOD, 1955; *nom. transl. ex* Richthofenidae WAAGEN, 1885, p. 729)]

Aberrant productoids specialized for reef environment, having conical pedicle valve cemented by apex and anchored by rhizoid spines; brachial valve opercular, commonly inserted deeply in cone and resting in closed position on ridge or aulocoterma; 2-shafted small bilobed cardinal process and laterally placed brachial ridges present; aperture of cone with strainer spines or mesh-forming sieve; muscle chamber of myocoelidium developed. *L.Perm.-U.Perm.*

Family RICHTHOFENIIDAE Waagen, 1885

[*nom. correct.* SCHUCHERT & LEVENE, 1929, p. 17 (*pro* Richthofenidae WAAGEN, 1885, p. 729)]

Pseudodeltidium exposed, or enclosed by outer shell layer, interarea absent; pedicle valve with muscles partially or completely enclosed within myocoelidium or myocoelidium absent in adult; dorsal adductor scars dendritic; teeth situated in brachial valve and sockets in pedicle valve. *L.Perm.-U. Perm.*

Subfamily RICHTHOFENIINAE Waagen, 1885

[*nom. correct.* MUIR-WOOD & COOPER, 1960 (*pro* Richthofeninae, *nom. transl.* STOYANOW, 1915, p. 30, *ex* Richthofenidae WAAGEN, 1885)]

Pseudodeltidium enclosed by outer shell layer; myocoelidium with single septum or 3 septa. *L.Perm.-U.Perm.*

Richthofenia KAYSER, 1881, p. 352 [**Anomia lawrenciana* DE KONINCK, 1863, p. 18; OD]. Aperture spines unknown but possibly similar to those of *Prorichthofenia*; myocoelidium with 3 septa. *L. Perm.-U. Perm.,* Eu. (Sicily-USSR)-Asia (China-Japan-Pak.-Timor). ——FIG. 327,*2.* **R. lawrenciana* (DE KONINCK), Pak.; *2a,* ped.v. int. with myocoelidium; *2b,* ped.v. long. sec. showing vesiculose shell structure; *2c,* brach.v. view, all ×0.85 (845).

Coscinarina MUIR-WOOD & COOPER, 1960, p. 138 [**Richthofenia communis* GEMMELLARO, 1894, p. 7; OD]. Large, with cone much elongated, aperture covered by arched reticulated meshwork of spines; myocoelidium with single septum, extending length of cup. *L.Perm.,* Eu.——FIG. 327,*1.* **C. communis* (GEMMELLARO), Sosio Ls., Sicily; *1a-c,* ext. of cup with meshwork, specimen showing brach.v. and myocoelidium, brach.v. int., all ×0.85 (772).

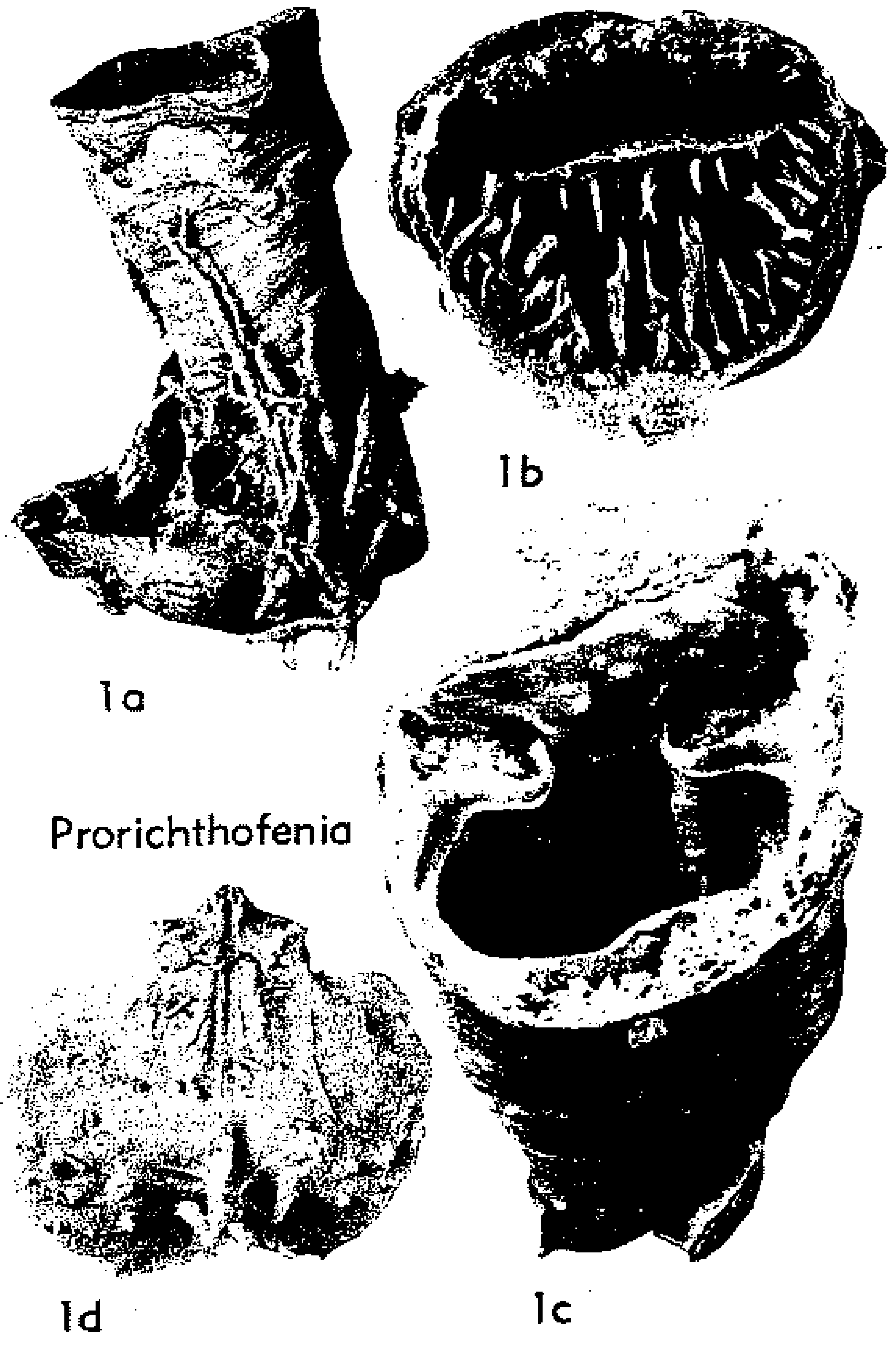


Fig. 328. Richthofeniidae (Prorichthofeniinae) (p. *H*463).

Subfamily PRORICHTHOFENIINAE Muir-Wood & Cooper, 1960

[Prorichthofeniinae Muir-Wood & Cooper, 1960, p. 139]

With rudimentary myocoelidium developed only in early growth stages and later covered by cystose shell; pseudodeltidium enclosed by outer shell layer. *L.Perm.*

Prorichthofenia R. E. King, 1931, p. 97 [**Crania permiana* Shumard, 1859, p. 395; OD]. Anterior part of pedicle-valve aperture with long, commonly forked spines forming mesh with endospines on interior of brachial valve; brachial ridge not developed; median septum reduced. *L.Perm.*, Eu.(USSR)-N. Am.(Tex.-N. Mex.-Mex.).——Fig. 328,*1*. **P. permiana* (Shumard), Word., USA(W. Tex.); *1a*, ped.v. lat. view with attachment spines, ×0.85; *1b*, apertural view of cup showing brach. v. (above) with spines on int., ×1.7; *1c*, oblique view of cup showing lidlike brach.v. in place, resting on aulacoterma, ×1.7; *1d*, brach.v. int., ×1.7 (587).

Subfamily GEMMELLAROIINAE A. Williams, 1953

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 140 (*ex* Gemmellaroiidae A. Williams, 1953, p. 10)]

Conical, attached by umbo and anchoring spines but having brachial valve as lid over aperture; pseudodeltidium exposed; no vesiculose shell; myocoelidium long; cardinal process massive, extending into myocoelidium. *L.Perm.*

Gemmellaroia Cossmann, 1898 [*pro Megarhynchus* Gemmellaro, 1894, p. 7 (*non* de Laporte, 1832)] [**Megarhynchus marii* Gemmellaro, 1894, p. 7; SD Mabuti, 1937, p. 16] [=*Megalorhynchus* de Gregorio, 1930, p. 23 (*errore pro Megarhynchus*); *Gemmellaroiella* Mabuti, 1937, p. 16 (type, *G. ozawai*)]. Exterior rugose and finely spinose; myocoelidium long, anteriorly grooved and having internal median septum; internal margins of both valves denticulate. *L.Perm.*, Eu-Asia.——Fig. 329,*1*. **G. marii* (Gemmellaro), Sosio Ls., Sicily; *1a*, post. view showing conical ped.v. with pseudodeltidium and lidlike brach.v., ×1; *1b*, brach.v. int. with card. process and pitted margin, ×2 (331).

Tectarea Likharev, 1928, p. 268 [**T. robinsoni*; OD]. Probably attached by umbo; exterior usually decorticated, probably capillate with intervening radially arranged pits; myocoelidium long, without septum or anterior groove, may be filled with secondary deposit; each valve with toothlike process and socket articulating with similar structures on other valve. *L.Perm.*, Eu.(Caucasus).——Fig. 329,*2*. **T. robinsoni*; *2a,b*, ped.v. and brach.v. views, ×3; *2c*, transv. sec. showing card. process and myocoelidium, ×3 (509).

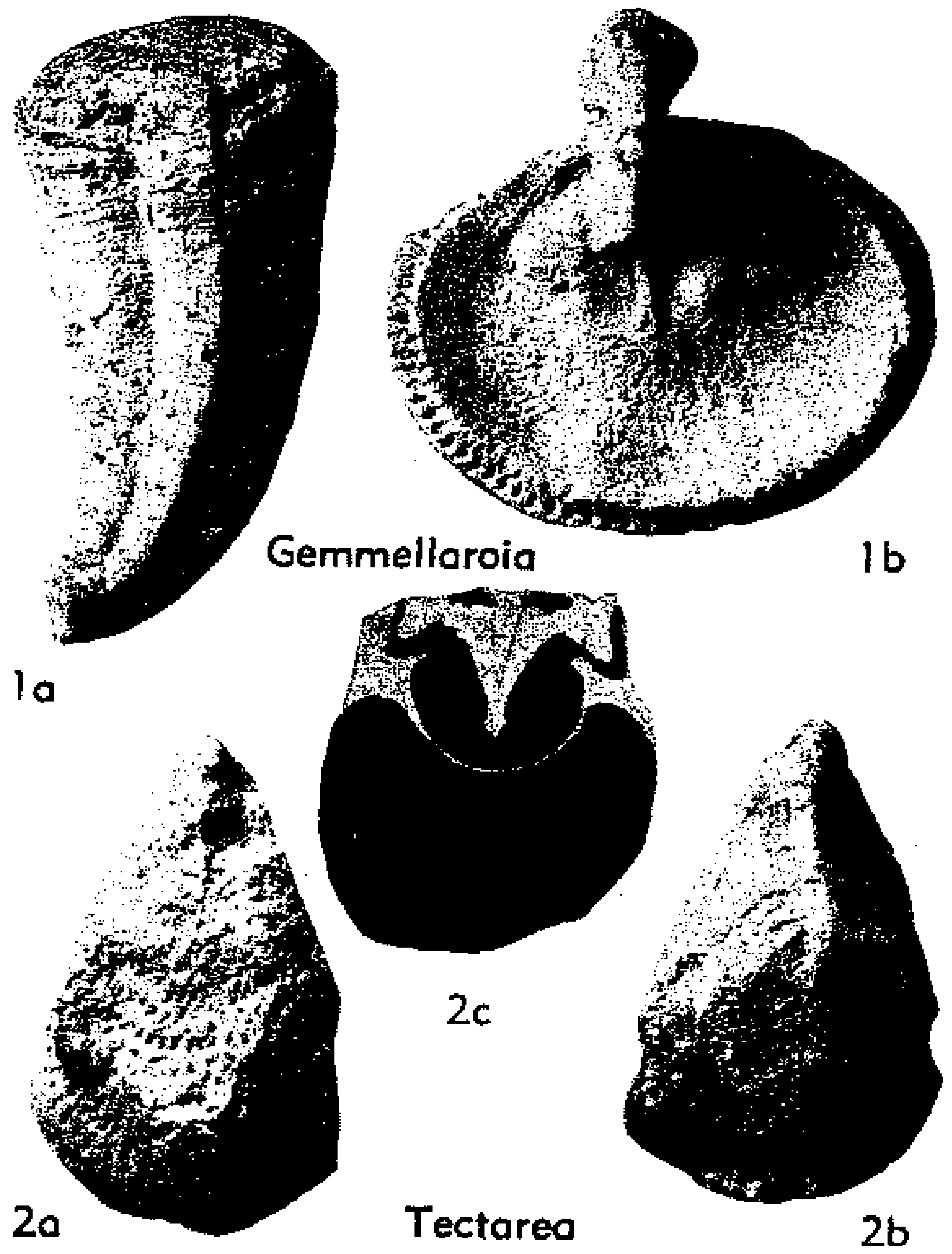


Fig. 329. Richthofeniidae (Gemmellaroiinae) (p. *H*463).

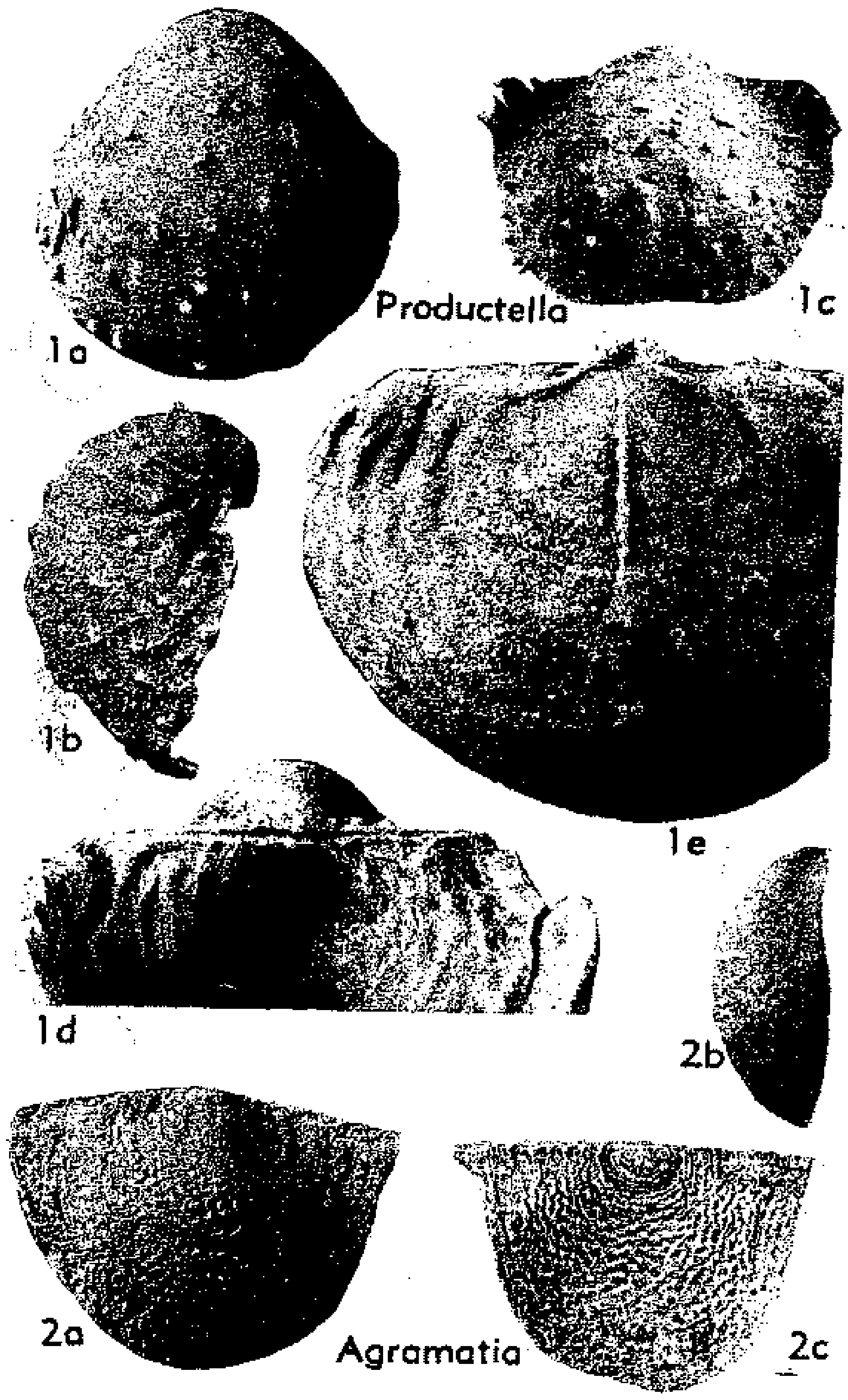


FIG. 330. Productellidae (Productellinae) (p. *H*464).

Family UNCERTAIN

Subfamily LOCZYELLINAE Likharev, 1937

[Loczyellinae Likharev, 1937, p. 83]

Shovel-shaped, probably attached by umbo; valves concavo-convex; external surface with growth lines; internal characters unknown. *Perm.*

Loczyella Frech, 1901, p. 503 [**L. nankinensis*; OD]. Characters of subfamily. *Perm.*, Eu.-Asia (China).

Superfamily PRODUCTACEA Gray, 1840

[*nom. transl.* Maillieux, 1941, p. 7 (*ex* Productidae Gray, 1840, p. 151)]

Generally attached by ringlike attachment spines in early growth stages, and rarely cemented by umbo, living free in later growth stages and supported by halteroid spines, interareas, teeth and sockets weakly developed in primitive forms only; ginglymus in gerontic stages of some genera; cardinal process bilobate or trilobate, rarely quadrilobate; diaphragm in brachial valve and crenulated marginal ridges in one or both valves in some genera. *L.Dev.-U. Perm.*

Family PRODUCTELLIDAE Schuchert & LeVene, 1929

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 145 (*ex* Productellinae Schuchert & LeVene, 1929, p. 17)]

Primitive productoids with variably developed interareas and pseudodeltidium; chilidium absent in one subfamily; teeth and sockets varying from strongly developed to weak or absent; cardinal process small, bilobed internally, quadrilobate externally, alveolus developed with breviseptum; adductors smooth or dendritic. *Up.L. Dev.-U.Miss.*

Subfamily PRODUCTELLINAE Schuchert & LeVene, 1929

[Productellinae Schuchert & LeVene, 1929, p. 17]

Without cicatrix of attachment, pseudodeltidium, or chilidium; scattered spines on pedicle valve, rare on brachial valve; adductors smooth. *L.Dev.-L.Miss.*

Productella Hall, 1867, p. 153 [**Productus subaculeatus* Murchison, 1840, p. 255; SD Oehlert, 1887, p. 1279]. Small or medium in size, subquadrate or hemispherical; interareas commonly linear, pseudodeltidium usually absent; small hinge teeth and sockets; pedicle valve with scattered pustules bearing recumbent or suberect spines, row of spines near hinge, growth lines prominent, rare rugae; brachial valve similar to pedicle valve, with few spines. *M.Dev.-U.Dev.*, Eu.-Asia-N.Am.——Fig. 330,*1*. **P. subaculeata* (Murchison), U. Dev., Fr.; *1a,b*, ped.v. ext., lat., ×2; *1c*, ped.v. with spines, ext., ×2; *1d*, brach.v. view, ×3; *1e*, brach.v. int., ×4 (589).

Agramatia Sokolskaya, 1948, p. 39 [**Productus agramati* Nalivkin, 1934, p. 21; OD]. Shell semicircular in outline, cicatrix of attachment present; teeth and sockets and interareas developed, no pseudodeltidium; pedicle valve with row of spines near hinge, rugae and spine ridges developed over whole valve, latter possibly bearing fine curving spines. *U.Dev.*, Eu.(USSR)-N.Am.——Fig. 330,*2*. **A. agramati* (Nalivkin), Famenn., USSR; *2a,b*, ped.v. ext., lat., ×2; *2c*, brach.v. ext., ×2 (753).

Helaspis Imbrie, 1959, p. 400 [**H. luma*; OD]. Small, subquadrate, with narrow interarea in both valves; spine bases and elongate spine ridges crowded on pedicle valve only; brachial valve dimpled, without spines; small convex apical pseudodeltidium present; hinge teeth strong. *M. Dev.*, N.Am.——Fig. 331,*1*. **H. luma*, USA (Mich.); *1a-c*, ped.v. ext., brach.v. view, brach.v. int., ×2 (445).

Orbinaria Muir-Wood & Cooper, 1960, p. 149 [**Productella pyxidata* Hall, 1858, p. 498; OD]. Shell hemispherical; pedicle valve with interarea, no pseudodeltidium; small teeth and sockets; pedicle valve with rugae and lamellae, spine ridges and small erect spines, row of spines near hinge, ringlike attachment in young (Fig. 298); brachial valve with concentric ornament and no spines, alveolus rarely developed. *U.Dev.* or *L. Miss.*, N.Am.——Fig. 331,*2*. **O. pyxidata* (Hall), Louisiana Ls., USA(Mo.); *2a,b*, ped.v. and brach. v. views, ×2; *2c*, brach.v. int., ×3 (587). [Attachment ring in young shell, Fig. 298.]

Praewaagenoconcha Sokolskaya, 1948, p. 132 [**Productus orelianus* Möller, 1871, p. 389; OD]. Hemispherical, interareas linear; pedicle valve medianly arched or with low vertical spinose ridge, rugae and long suberect spines near hinge; brachial valve finely spinose; teeth and sockets small. *U.Dev.*, Eu.-Asia.——Fig. 331,*4*. **P. oreliana* (Möller), Famenn., USSR; *4a,b*, ped.v. views (*4b* with median spinose ridge), *4c*, brach. v. view, ×2 (753).

Productellana Stainbrook, 1950, p. 373 [**P. bifaria*; OD]. Small, subcircular; pedicle valve with low interarea, ornament of rugae posteriorly, erect spines may occur on short spine ridges; brachial valve more rugose, with scattered spines, cardinal process closing delthyrium; other internal characters unknown. *L.Miss.*, N.Am.——Fig. 331, *3*. **P. bifaria*, Kinderhook., USA(Iowa); *3a,b*, ped.v. and brach.v. views, ×1 (587).

Sinoproductella Wang, 1955, p. 349 [**Productella hemisphaerica* Tien, 1938, p. 19; OD] [?=*Praewaagenoconcha* Sokolskaya, 1948, p. 132]. *U. Dev.*, China(Hunan).——Fig. 332,*1*. **S. hemispherica* (Tien); ped.v. view, ×1 (852).

Spinulicosta Nalivkin, 1937, p. 49 [**Productella spinulicosta* Hall, 1857, p. 173; OD]. Subcircular to elongate, interareas linear or absent; pedicle valve with concentric lamellae, long curved spines on flanks and near hinge, spine ridges, and obscure costae; brachial valve dimpled with concentric ornament and rare spines; teeth and sockets developed. *L.Dev.-U.Dev.*, cosmop.——Fig. 332, *3a,b*. *S.* sp., cf. **S. spinulicosta* (Hall), L.Dev., USA(Ohio); *3a,b*, ped.v. post., vent., ×2 (587).——Fig. 332,*3c,d*. *S.* sp., aff. *S. navicella* (Hall), M.Dev., USA(Nev.); *3c*, brach.v. int., ×3; *3d*, group of shells with spines preserved, ×1 (587).

Stelckia (*see* p. *H*904).

Strophoproductus Nalivkin, 1937, p. 46 [**Productella hystricula* Hall, 1867, p. 178; OD]. Small, orbicular; pedicle valve with narrow interarea; ornament of concentric lamellae, rugae, and prostrate spines on spine ridges, 2 rows of spines near hinge and down flanks; brachial valve with concentric ornament and spines; teeth and sockets developed. *U.Dev.*, N.Am.-Eu.-Asia.——Fig. 332, *2*. **S. hystriculus* (Hall), USA(N.Y.); *2a,b*, ped. v. views, ×2; *2c*, brach.v. int., ×2 (587).

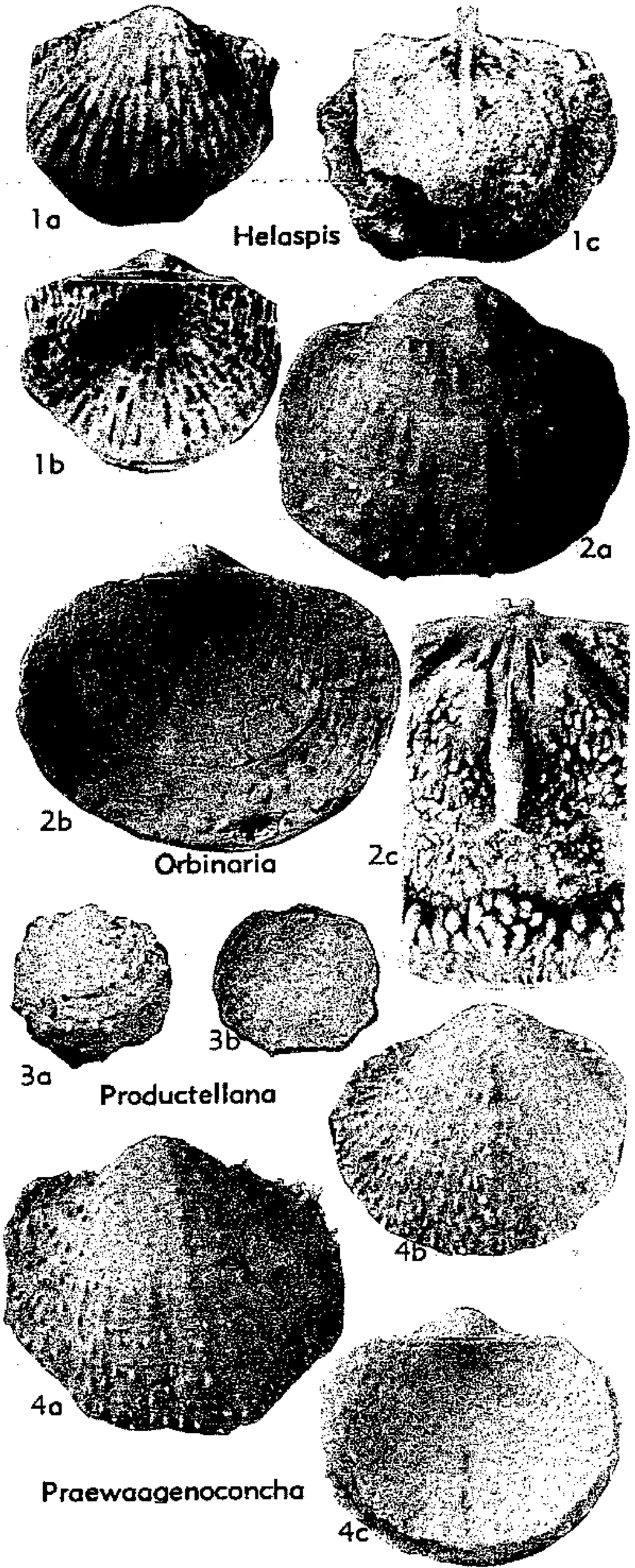


Fig. 331. Productellidae (Productellinae) (p. *H*464-*H*465).

Subfamily CHONOPECTINAE Muir-Wood & Cooper, 1960

[Chonopectinae Muir-Wood & Cooper, 1960, p. 156]

Commonly with cicatrix of attachment; pedicle valve slightly convex; body cavity narrow, pseudodeltidium and chilidium; teeth and sockets present; interareas in both valves or pedicle valve only; adductors

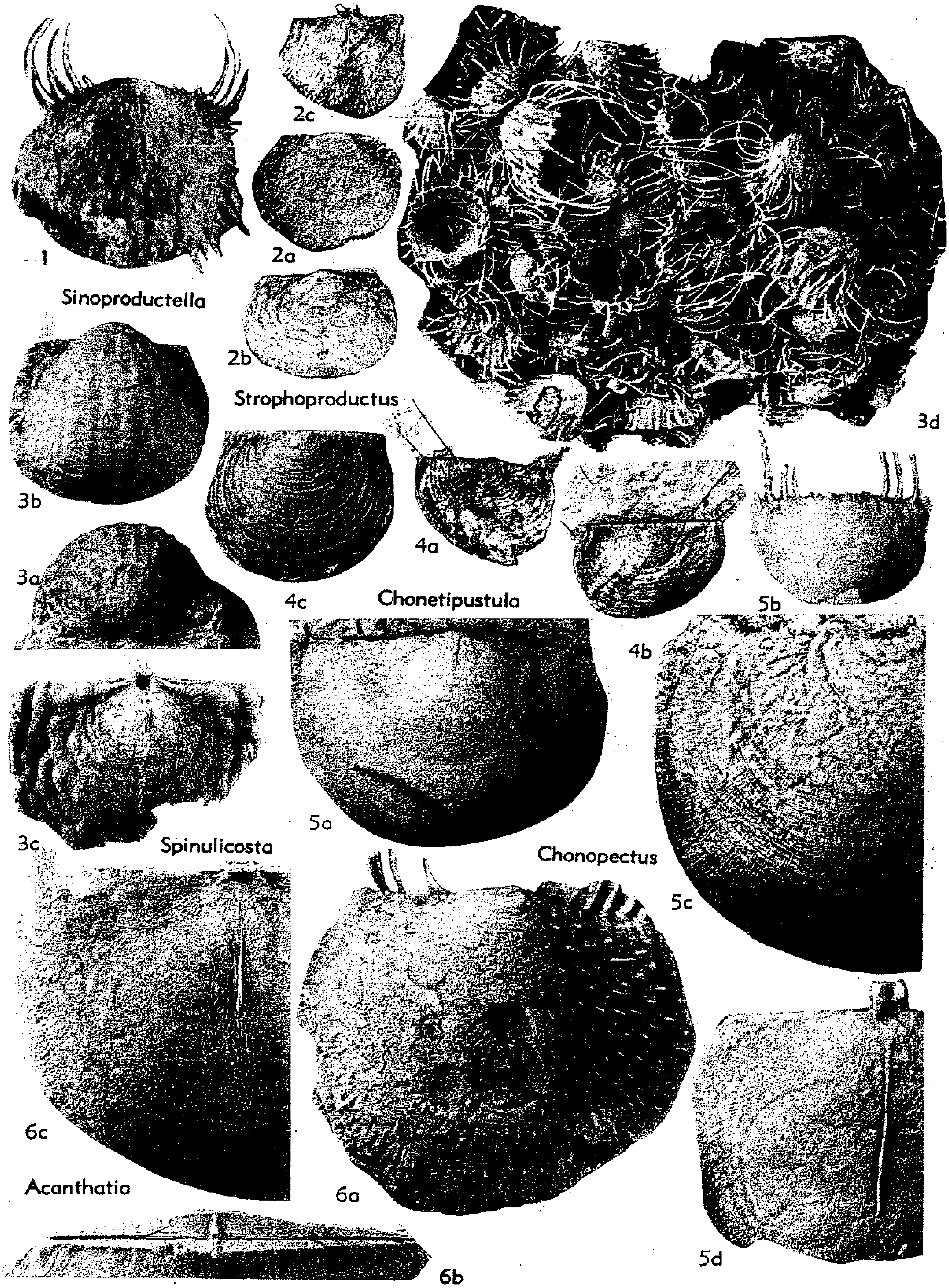


Fig. 332. Productellidae (Productellinae) *(1-3)*, (Chonopectinae) *(4-6)* *(p. H465, H467)*.

smooth or posterior scars dendritic; cardinal process bilobed, lobes separate, short septum rarely in pedicle valve. *U.Dev.-L.Carb. (L.Miss.-U.Miss.).*

Chonopectus Hall & Clarke, 1893, p. 312 [**Chonetes fischeri* Norwood & Pratten, 1855, p. 25; OD]. Cicatrix of attachment present or absent; pedicle valve with radial capillae and oblique eccentric ornament when decorticated; erect spine row near hinge, spines rare elsewhere; brachial valve ornament similar, no spines; short septum in pedicle valve. *U.Dev.-L.Miss.*, N.Am.——Fig. 332,*5a-c*. **C. fischeri* (Norwood & Pratten), L.Miss.(Kinderhook.), USA(Iowa); *5a,b*, ped.v. views; *5b*, with spines preserved, ×2, ×1; *5c*, ped.v. ext. showing ornament, ×3 (396).——Fig. 332,*5d*. *C.* sp., U.Dev., USA(N.Y.); brach.v. int. showing hollow card. process, ×2 (396).

Acanthatia Muir-Wood & Cooper, 1960, p. 158 [**Heteralosia nupera* Stainbrook, 1947, p. 309; OD]. Medium-sized, subcircular, cicatrix of attachment present, interarea in each valve; pedicle valve with vertical attachment spines along hinge, fine prostrate spines elsewhere; brachial valve rugose posteriorly, with rare spines. *U.Dev.*, N. Am.——Fig. 332,*6*. **A. nupera* (Stainbrook), USA(N.Mex.); *6a*, ped.v. ext.; *6b*, interareas of both valves; *6c*, brach.v. int.; all ×2 (769).

Chonetipustula Paeckelmann, 1931, p. 31 [**Productus plicatus* Sarres, 1857, p. 20; OD]. Semicircular, with narrow interareas; cardinal process closing delthyrium; no chilidium; small septum in pedicle valve; ornament of both valves rugose; pedicle valve with fine, long straight spines in row along hinge margin, procumbent spines elsewhere; spines rare on brachial valve. *L.Carb. (Visean-Culm.)*, Eu.——Fig. 332,*4a,b*. **C. plicata* (Sarres), Culm., Ger.; *4a,b*, ped.v. ext. and int. molds, ×1 (633).——Fig. 332,*4c*. *C. carringtoniana* (Davidson), Visean, Eng.; brach.v. ext. mold, ×1.5 (633).

Hamlingella Reed, 1943, p. 78 [**Productella goergesi* Paeckelmann, 1931, p. 56; OD]. Subelliptical, medium-sized; ventral interarea narrow, ornament on both valves of numerous fine, hair-like spines, brush of long curving spines from hinge margin, fine rugae posteriorly; cardinal process lobes medianly grooved; posterior adductors dendritic, with bounding ridge, anterior scars smooth. *U.Dev.-L.Carb.*, Eu.——Fig. 333, *1a,b*. **H. goergesi* (Paeckelmann), L.Carb. (Etroeungt.), Ger.; *1a,b*, partly decort. ped.v., brach.v. int., ×1 (663).——Fig. 333,*1c*. *H. capillaris* Reed, U.Dev., Eng.(Devon.); ped.v. ext. showing spines, ×1.5 (663).

Quadratia Muir-Wood & Cooper, 1960, p. 161 [**Productus hirsutiformis* Walcott, 1884, p. 133; OD]. Subrectangular, interareas present; cardinal process closing delthyrium; pedicle valve with rugae and small spines concentrically arranged, row of spines near hinge extending laterally; brachial valve with fine rugae and rare spines; adductors smooth. *U.Miss.*, USA(Ark.-Okla.-Tex.-Wyo.-Nev.).——Fig. 333,*2*. **Q. hirsutiformis* (Walcott), Okla.; *2a,b*, ped.v. and brach.v. views, ×1; *2c*, brach.v. int., ×2 (587).

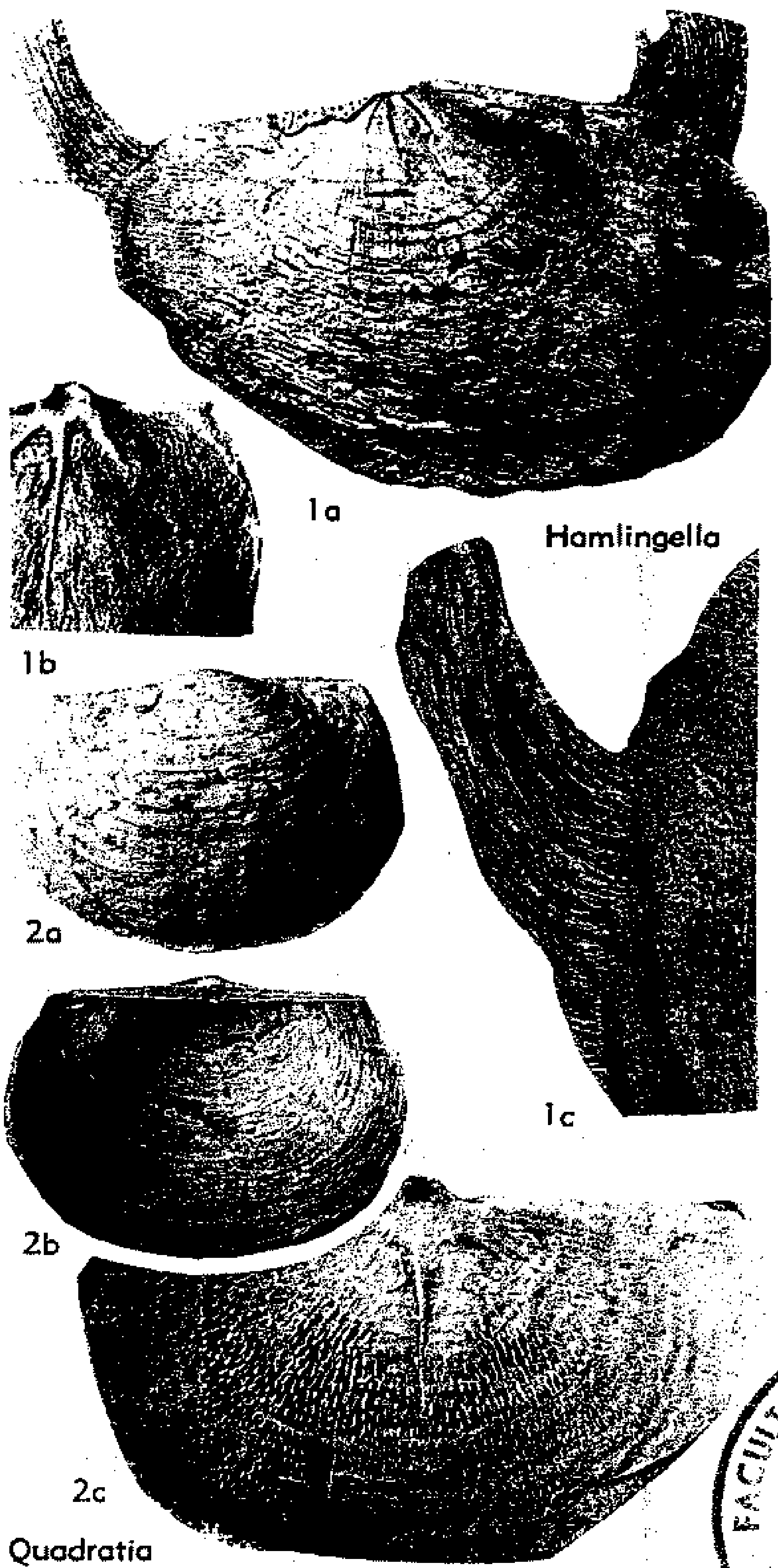


Fig. 333. Productellidae (Chonopectinae) (p. H467).

Steinhagella Goldring, 1957, p. 223 [**Leptaena membranacea* Phillips, 1841, p. 60; OD]. Like *Whidbornella* but rugae more numerous and undulating, recumbent spines in pedicle valve, more erect spines in brachial valve. *U.Dev.*, Eu.——Fig. 334,*2*. **S. membranacea* (Phillips), Eng.; holotype, ped.v. ext., ×1 (354).

Whidbornella Reed, 1943, p. 71 [**Leptaena caperata* J. de C. Sowerby, 1840, pl. 53, fig. 4; OD]. Medium-sized, semielliptical, no cicatrix or pseu-

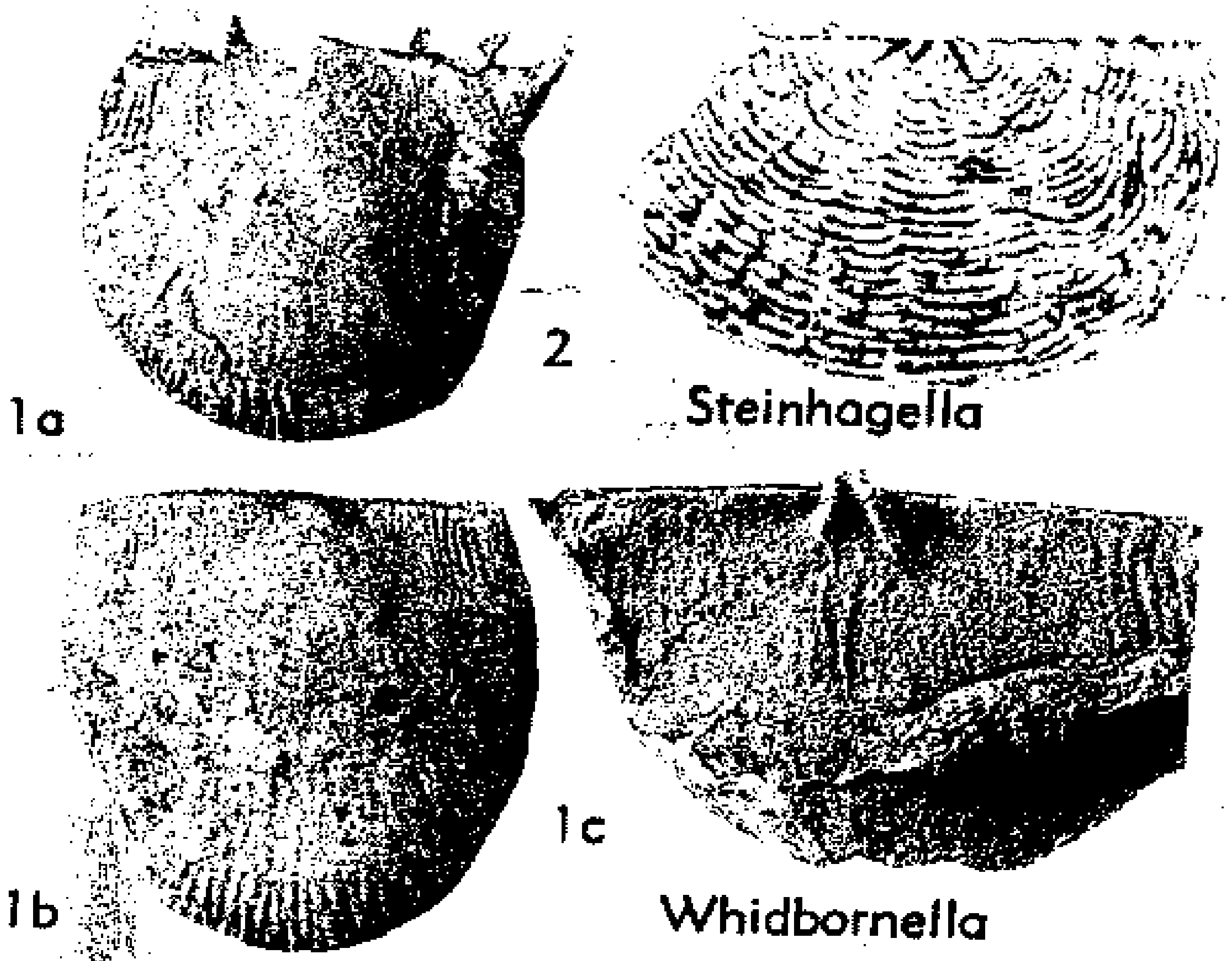


FIG. 334. Productellidae (Chonopectinae) (p. *H467*-*H468*).

dodeltidium; ornament on both valves of rugae and overlapping spine ridges with fine prostrate spines, which may be aligned, forming costellae; row of long straight spines in pedicle valve at high angle to hinge; pedicle valve with short septum; adductors dendritic. *U.Dev.*, Eu.——FIG. 334,*1*. **W. caperata* (J. de C. Sowerby), Eng. (Devon.); *1a,b*, ped.v. ext., brach.v. ext. mold, ×1; *1c*, brach.v. int., ×2 (663).

Family INSTITINIDAE Muir-Wood & Cooper, 1960

[Institinidae Muir-Wood & Cooper, 1960, p. 164]

Small, with or without interarea in pedicle valve, one or more cinctures developed; pseudodeltidium, teeth and sockets absent; cardinal process bilobate, with 2 separated lobes; adductors smooth; brachial ridges long, given off horizontally. *L.Carb.(Visean)*, *?U.Carb.*

Institina Muir-Wood & Cooper, 1960, p. 164 [**Productus marginalis* de Koninck, 1847, p. 238; OD]. Subquadrate, with ventral interarea; visceral disc separated from trail by deep cincture; pedicle valve rugose posteriorly, irregularly plicated on trail, spines scattered, also in row near cincture, row up flanks and near hinge; brachial valve rugose. *L.Carb.(Visean)*, *?U.Carb.*, Eu.——FIG. 335,*1*. **I. marginalis* (de Koninck), Belg.; *1a-c*, ped.v. vent., ant., and lat. views showing ant. plicated margin, ×2; *1d*, brach.v. int., ×3 (483).

Cinctifera Muir-Wood & Cooper, 1960, p. 165 [**Productus medusa* de Koninck, 1842, p. 166; OD]. Transversely oblong; valves geniculated, with short trail; 3 or 4 cinctures in each valve; small attachment cicatrix; interarea absent, both valves costate, pedicle valve with rugae and scattered spines, prostrate spine row from trail margin, row of spines near hinge; brachial valve trail smooth. *L.Carb.(Visean)*, Eu.——FIG. 335,*2*. **C. medusa* (de Koninck), Belg.; *2a,b*, ped.v. ant. and lat. views showing spines, ×3; *2c,d*, ped.v. vent. and post. views showing cinctures, ×2, ×3 (483).

Rugicostella Muir-Wood & Cooper, 1960, p. 166 [**Productus nystianus* de Koninck, 1842, p. 202; OD]. Subcircular, no interareas, both valves rugose and having cincture that separates visceral disc from trail; pedicle valve geniculated, with smooth or costate trail rarely produced into one or more tubes, spines on rugae and attachment spines along hinge, fringe of spines on flanks; brachial valve lacking spines. *L.Carb.(Visean)*, Eu.——FIG. 335,*3*. **R. nystiana* (de Koninck), Belg.; *3a-c*, ped.v. post. and lat. views showing spines, wrinkled visceral disc, and cincture, ×3; *3d*, brach.v. int. mold, ×4 (587).

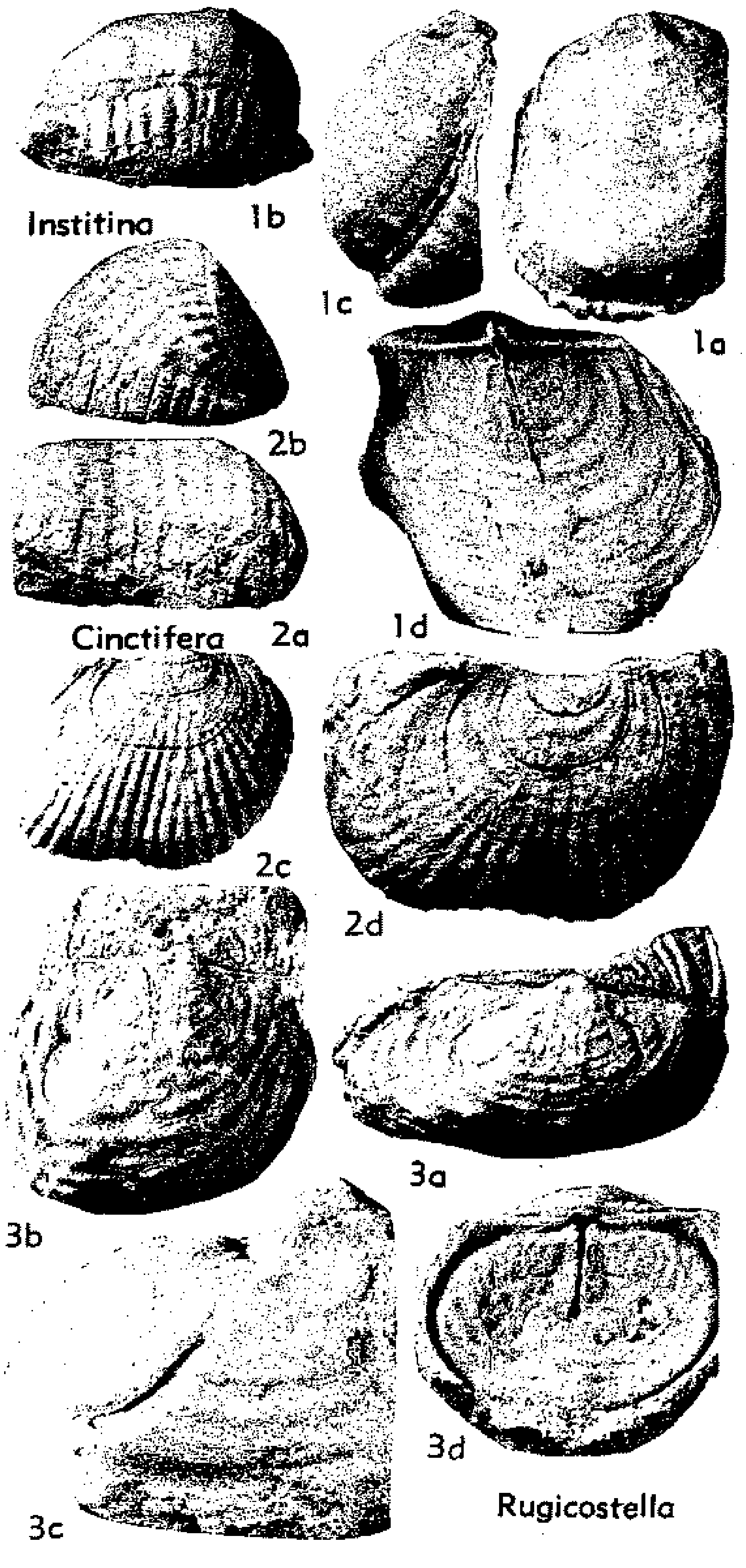


FIG. 335. Institinidae (p. *H468*).

Family LEIOPRODUCTIDAE Muir-Wood & Cooper, 1960

[Leioproductidae Muir-Wood & Cooper, 1960, p. 167]

Progressive Productacea with bilobed sessile cardinal process, but median halves of lobes tending to fuse to form trilobed process; alveolus developed; hinge teeth and sockets and interareas normally absent; adductors slightly dendritic. *M.Dev.-L.Perm.*

Subfamily LEIOPRODUCTINAE Muir-Wood & Cooper, 1960

[Leioproductinae Muir-Wood & Cooper, 1960, p. 168]

Cardinal process bilobed, or rarely trilobed; pedicle valve rugose and spinose; commonly with median longitudinal spine-bearing ridge, spines absent on brachial valve. *U.Dev.-L.Perm.*

Leioproductus Stainbrook, 1947, p. 307 [**Productella coloradoensis* var. *plicatus* Kindle, 1909, p. 18; OD] [=*Bispinoproductus* Stainbrook, 1947, p. 311 (type, *B. varispinosus*)]. Small to medium-sized, geniculated, with short trail on each valve; pedicle valve rugose or lamellose, with scattered spines or spine ridges and median longitudinal spine-row or spine-bearing ridge, spines in row up flanks and near hinge; brachial valve lamellose, dimpled, septum posteriorly bifid. *U.Dev.*, N.Am.-Asia.——Fig. 336,*1*. **L. plicatus* (Kindle), USA(N.Mex.); *1a,b*, ped.v. vent. and lat. views, ×2; *1c*, brach.v. view, ×1; *1d*, brach.v. int., post. part, ×3 (769).

Acanthoplecta Muir-Wood & Cooper, 1960, p. 170 [**Producta mesoloba* J. Phillips, 1836, p. 215; OD]. Medium-sized, both valves geniculated, with long trail, body cavity small, both valves rugose or smooth, valves costellate when decorticated; pedicle valve with longitudinal median spine-bearing ridge, spines scattered and in row near hinge and on flanks; cardinal process bilobed, alveolus developed, slender breviseptum. *L.Carb. (Visean)*, Eu.——Fig. 336,*2*. **A. mesoloba* (Phillips), Visean; *2a-c* (Eng.), ped.v. post. and lat., brach.v. views, ×1; *2d,e* (Belg.), ped.v. with median ridge bearing spines, brach.v. int., ×1, ×2 (587).

Ericiatia Muir-Wood & Cooper, 1960, p. 172 [**Productus newberryi* Hall, 1857, p. 180; OD]. Medium-sized, valves moderately concavo-convex, geniculated, both valves with fine overlapping spine-ridges bearing recumbent spines; spines in rows near hinge of pedicle valve and on ears; cardinal process bilobed, without alveolus; septum posteriorly notched; adductors dendritic. *L.Miss.*, N.Am.——Fig. 337,*1*. **E. newberryi* (Hall), USA(Ohio); *1a,b*, ped.v. and brach.v. views, ×1; *1c*, brach.v. int., ×2 (396).

Galeatella Muir-Wood & Cooper, 1960, p. 173 [**G. galeata*; OD]. Small, both valves geniculated,

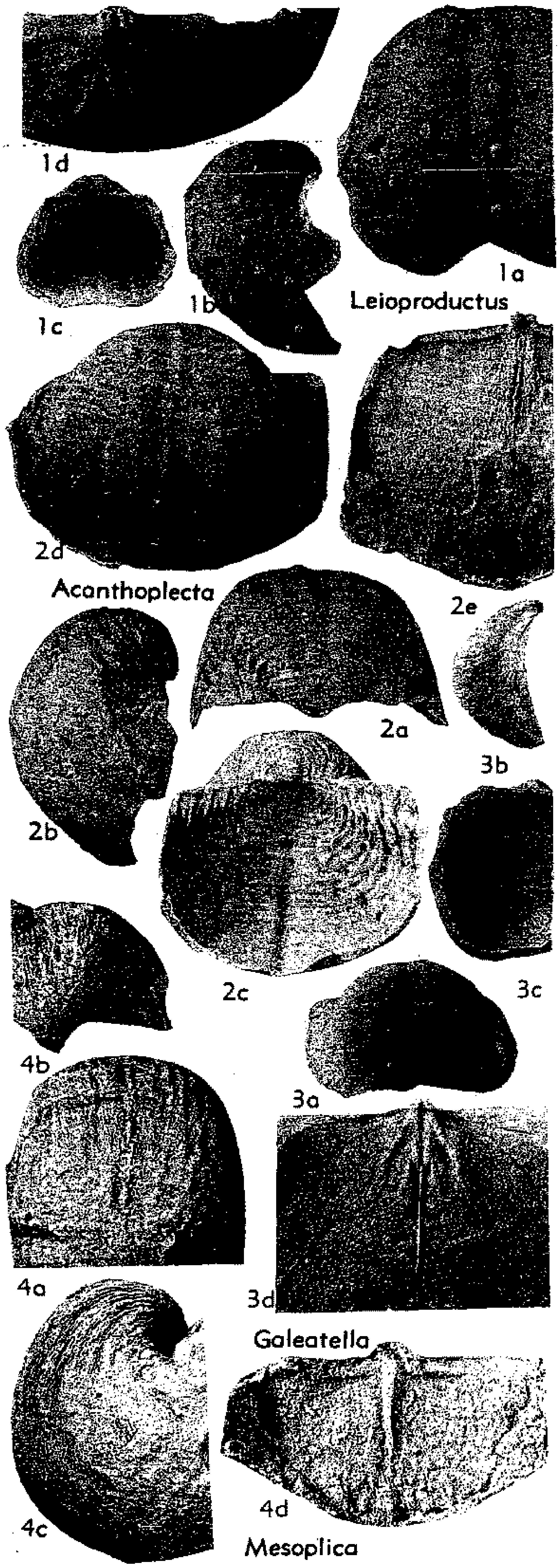


Fig. 336. Leioproductidae (Leioproductinae) (p. H469-H470).

trails short; linear interarea in pedicle valve, both valves smooth or with faint rugae; spines scattered, or in row near hinge of pedicle valve; cardinal process trilobed on internal face, quadrilobate externally, septum posteriorly bifid. *U.Dev.*, N.Am.——Fig. 336,*3*. **G. galeata*, USA(N.Mex.); *3a,b*, ped.v. vent., lat., ×1; *3c,d*, brach.v. ext. int., ×1, ×2 (587).

Jakutoproductus Kashirtsev, 1959, p. 70 [**Marginifera verchoyanica* Frederiks, 1931, p. 211; OD]. Medium-sized, laterally extended, concavo-convex, rarely geniculated; ornament of rugae over entire shell and quincuncially arranged spines, row along hinge; cardinal process bilobed, sessile; septum smooth, broad and medianly sulcate posteriorly becoming thin anteriorly, adductors smooth. *L.Perm.*, Asia(USSR-Siberia, Novaya Zemlya-China).

Mesoplica Reed, 1943, p. 97 [**Leptaena praelonga* J. de C. Sowerby, 1840, pl. 53, fig. 29; OD]. Medium-sized, both valves geniculated, with short trail; median longitudinal spine-bearing ridge or median row of spines in pedicle valve; both valves rugose posteriorly, anteriorly costate; spines in group on ears, one spine on each flank of pedicle valve; row of spines in brachial valve near hinge. *U.Dev.*, Eu.-Asia.——Fig. 336,*4*. **M. praelonga* (J. de C. Sowerby), Famenn., Eng.; *4a-c*, ped.v. int. mold, ant., post., lat. views, ×1; *4d*, brach.v. int., ×2 (663).

Planoproductus Stainbrook, 1947, p. 310 [**Productella hillsboroensis* Kindle, 1909, p. 19; OD]. Medium-sized, nongeniculated; pedicle valve depressed, convex, ventral interarea developed; surface rugose and abundant spines and spine ridges, 2 rows of spines near hinge and on ears extending at high angle to hinge; brachial valve rugose, spines absent, cardinal process internally trilobate; adductors dendritic. *U.Dev.*, N.Am.——Fig. 337,*2*. **P. hillsboroensis* (Kindle), USA(N.Mex.); *2a,b*, ped.v. ext., ×1, ×2; *2c,d*, brach.v. ext., int., ×2, ×4 (769).

Subfamily DEVONOPRODUCTINAE Muir-Wood & Cooper, 1960

[Devonoproductinae Muir-Wood & Cooper, 1960, p. 177]

Cardinal process interiorly bilobate and exteriorly quadrilobate; minute hinge teeth and sockets; linear interarea in pedicle valve; lateral ridges with posterior surface denticulate. *M.Dev.-U.Dev.*

Devonoproductus Stainbrook, 1943, p. 55 [**Productella walcotti* Fenton & Fenton, 1924, p. 119 (=*Productus dissimilis* Hall, 1858, p. 497, *non* deKoninck, 1847, p. 255) (=*P. (Productella) hallana* Walcott, 1884, p. 130, *partim*); OD] [=*Striatoproductus* Nalivkin, 1947, p. 75 (type, *Orthis sericea* von Buch, 1838, p. 68)]. Small, semicircular, nongeniculate, cicatrix of attachment present or absent; pedicle valve with obscure nodose costellae, rugose posteriorly, spines scat-

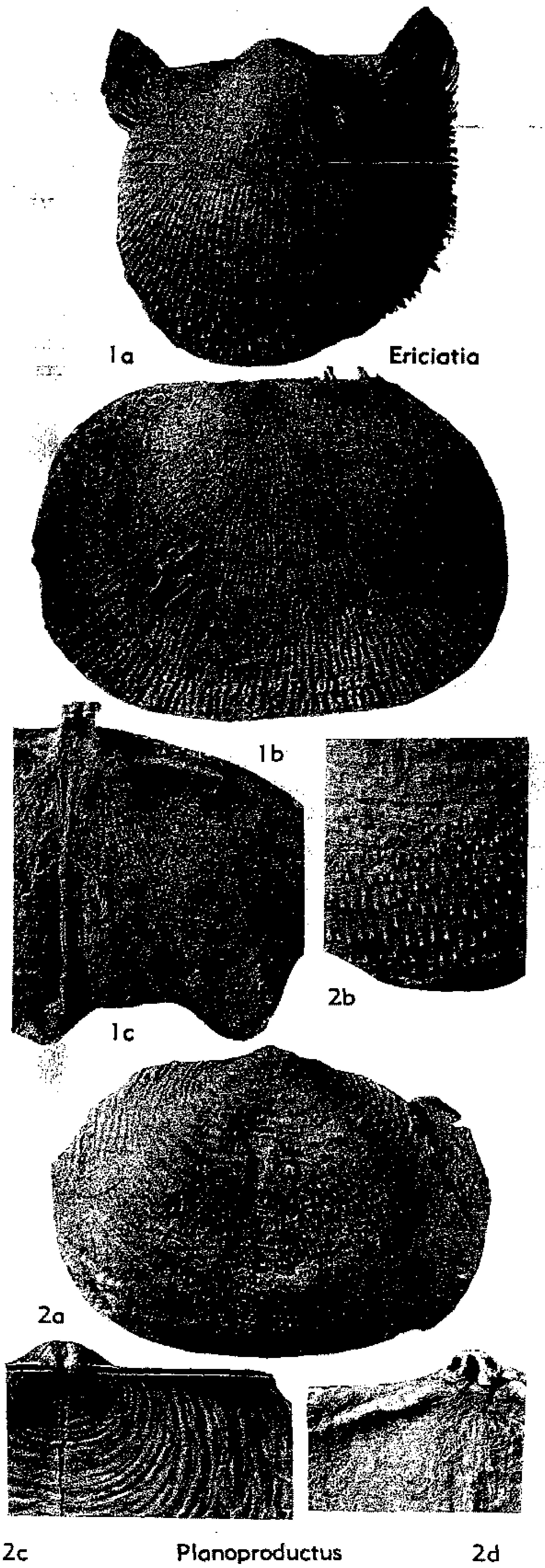


Fig. 337. Leioproductidae (Leioproductinae) (p. H469-H470).

tered and row of erect spines near hinge; brachial valve lamellose and finely capillate. *M.Dev.-U. Dev.*, Eu.-Asia-N.Am.——FIG. 338,*3*. **D. walcotti* (FENTON & FENTON), U.Dev., USA(Iowa); *3a*, ped.v. ext., ×2; *3b,c*, brach.v. ext., int., ×3 (766).

Chonopectoides (*see* p. *H*904).

Productellina F. R. C. REED, 1943, p. 99 [**P. fremingtonensis*; OD]. Genus imperfectly known. *U.Dev.*, Eng.(Devon).

Subfamily PRODUCTININAE Muir-Wood & Cooper, 1960

[Productininae MUIR-WOOD & COOPER, 1960, p. 181]

Cardinal process small, bilobate or trilobate with two lobes well separated, and posteriorly incised, short breviseptum, adductors smooth or dendritic. *L.Miss.-L.Carb. (Visean).*

Productina SUTTON, 1938, p. 551 [**Productus sampsoni* WELLER, 1909, p. 300; OD]. Small, subcircular to elongate-oval, not geniculated; pedicle valve costate and lamellose, spines rare, erect, row of spines from hinge down flanks; brachial valve lamellose; lateral ridges diverging from hinge, cardinal process bilobate, extending dorsally, adductors smooth. *L.Miss.-L.Carb.(Visean)*, N.Am.-Asia.——FIG. 338,*2*. **P. sampsoni* (WELLER), L.Miss.(Kinderhook.), USA(Tex.) *(2a-c)*, USA(N.Mex.) *(2d)*; *2a-c*, ped.v. vent., lat., ant., ×2; *2d*, brach.v. int., ×3 (795).

Argentiproductus COOPER & MUIR-WOOD, 1951, p. 195 [**Producta margaritacea* PHILLIPS, 1836, p. 215; OD] [=*Thomasia* FREDERIKS, 1929, p. 790 (*non* POCHE, 1908; *nec* RUEBSAAMEN, 1910; *nec* WILSON, 1910; *nec* LAMBERT, 1918); *Thomasina* PAECKELMANN, 1931, p. 181 (*non* NEWSTEAD & CARTER, 1911); *Thomasella* PAUL, 1942, p. 191 (*non* FREDERIKS, 1928)]. Hemispherical, geniculate, with small body cavity, both valves costate, lamellose, commonly lustrous; spines rare, prostrate, row of spines near hinge and on flanks of pedicle valve; cardinal process sessile, trilobate, lateral ridges not strongly divergent from hinge; adductors faintly dendritic. *L.Carb.(Visean)*, Eu. ——FIG. 338,*1*. **A. margaritaceus* (PHILLIPS), N.Wales *(1a,b)*, Belg. *(1c)*; *1a,b*, ped.v. and brach.v. views, ×1; *1c*, brach.v. int., ×2 (587).

Family OVERTONIIDAE Muir-Wood & Cooper, 1960

[Overtoniidae MUIR-WOOD & COOPER, 1960 (November), p. 183] [=Avoniidae SARYCHEVA, 1960 (December), p. 226 *(partim)*]

Cardinal process sessile, bilobed, with lobes posteriorly incised or separated by deep sulcus, rarely trilobed, with minute sulcate median lobe; alveolus usually absent; brachial ridges spoon-shaped, oblique; adductors smooth or partly dendritic; exterior spinose, rugose or lamellose, rarely anteriorly costate. *U.Dev.-L.Perm.*, *?U. Perm.*

Subfamily OVERTONIINAE Muir-Wood & Cooper, 1960

[Overtoniinae MUIR-WOOD & COOPER, 1960, p. 183]

Exterior spinose, rugose, or lamellose, rarely costate anteriorly. *U.Dev.-L.Perm.*, *?U.Perm.*

Overtonia I. THOMAS, 1914, p. 259 [**Productus fimbriata* J. DE C. SOWERBY, 1824, p. 85; OD]. Medium-sized, subcircular; umbo much incurved; trail rarely developed, both valves with rugae or broad bands bearing single row of elongated

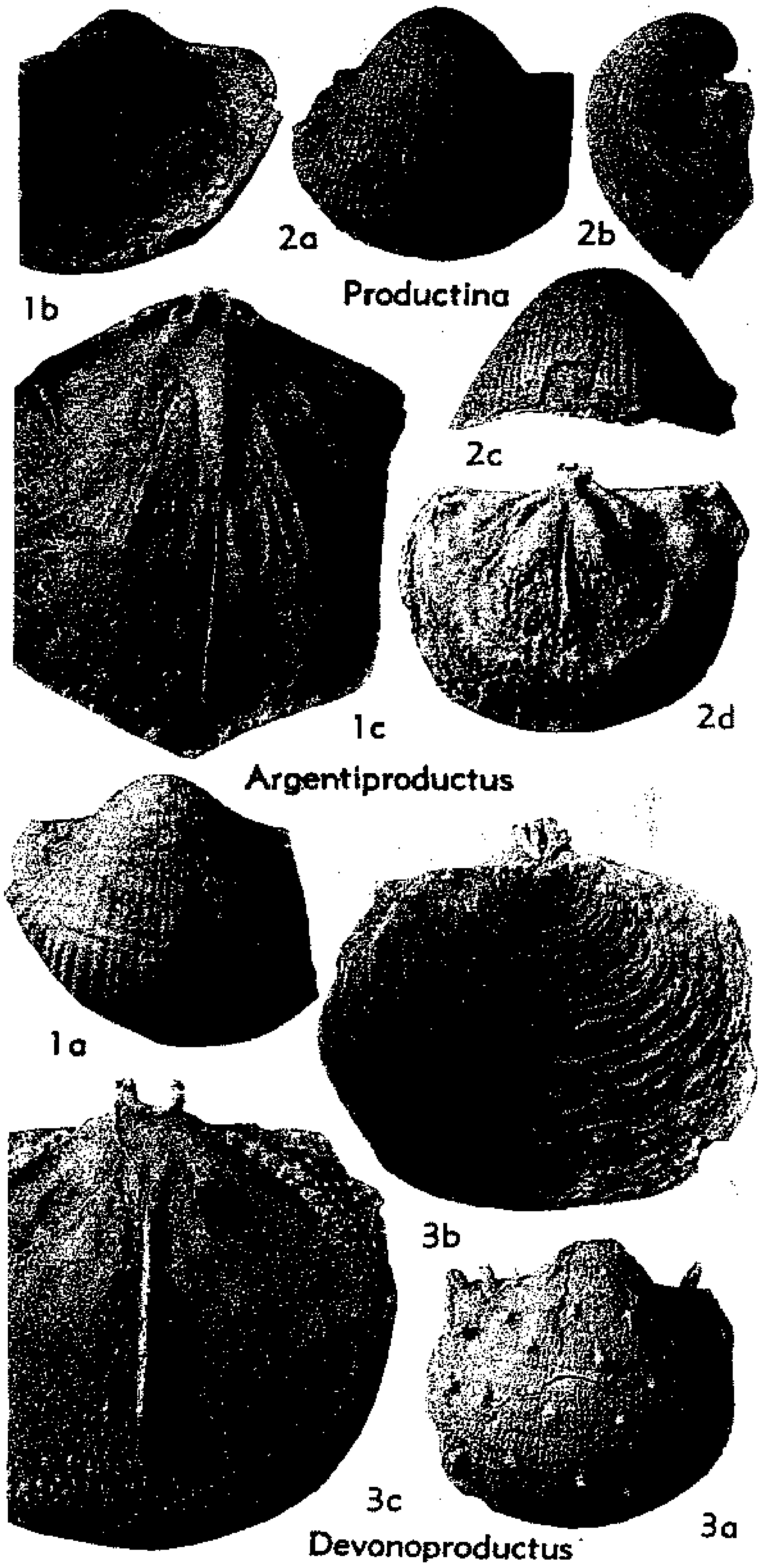


FIG. 338. Leioproductidae (Devonoproductinae) *(3)*, (Productininae) *(1-2)* (p. *H*470-*H*471).

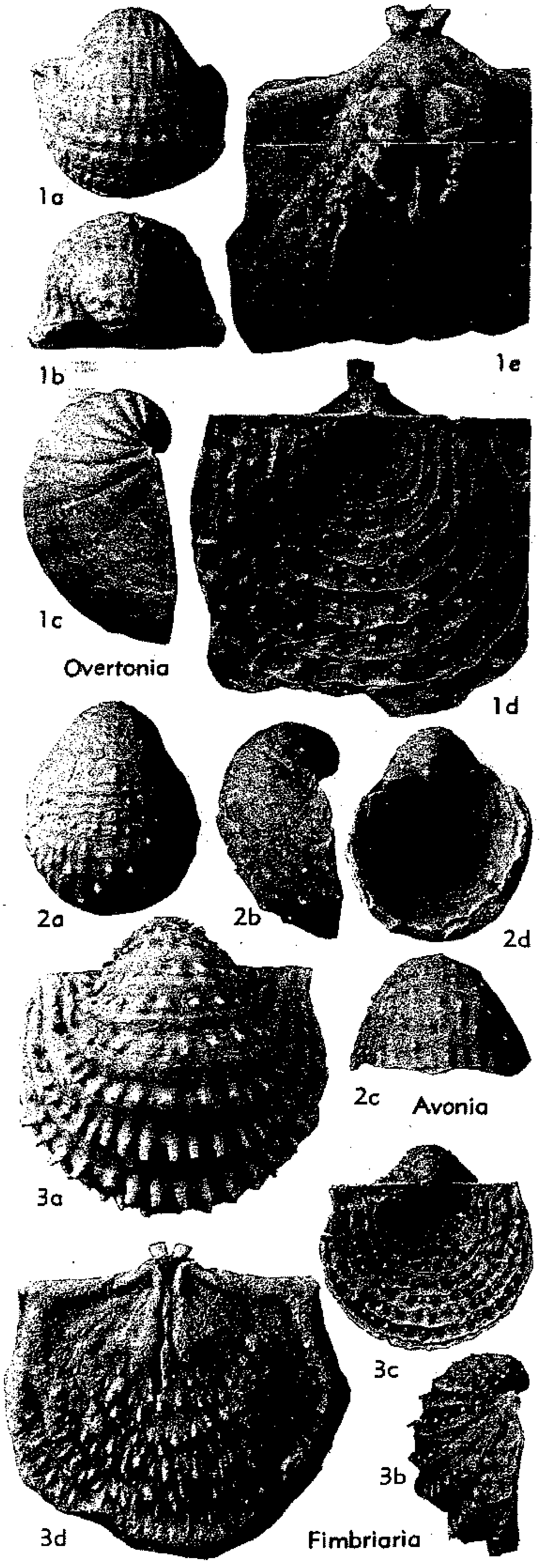


Fig. 339. Overtoniidae (Overtoniinae) (p. _H_471-_H_472).

spine-ridges, and rarely costate anteriorly; cardinal process bilobed or trilobed, no alveolus, lateral ridges marginal. _L.Carb.(Visean)_, Eu.-Asia-Arctic.——Fig. 339,_1_. *_O. fimbriata_ (J. de C. Sowerby), Scot. (_1a,b_), Eire (_1c_), Eng. (_1d,e_); _1a,b_, ped.v. vent., post., ×1; _1c_, ped.v. lat., ×1; _1d,e_, brach. v. ext., int., ×5 (805).

Avonia I. Thomas, 1914, p. 259 [*_Productus youngianus_ Davidson, 1860, p. 45; OD]. Small, orbicular, or elongate-oval, both valves with irregularly placed spines posteriorly, spine ridges radially arranged forming costae anteriorly, concentric lamellae numerous, interrupting costae, spines erect; brachial valve with lateral ridges curving away from margin, cardinal process bilobed. _L.Miss.-U.Miss._, N.Am.; _L.Carb.(Tournais.-Visean)-U.Carb.(Namur.)_, Eu.-Asia.——Fig. 339, _2_. *_A. youngiana_ (Davidson), Visean, Scot.; _2a-c_, ped.v. vent., lat., ant., ×2; _2d_, brach.v. view, ×2 (574).

Fimbriaria Muir-Wood & Cooper, 1960, p. 186 [*_Overtonia plummeri_ R. H. King, 1938, p. 276; OD]. Small, strongly concavo-convex; ornament of broad, prominent, lamellose bands with single row of stout recumbent spines; dorsal interior with elevated rim around shell; lateral ridges medianly recurved anteriorly, forming 2 ridges that enclose end of breviseptum. _U.Penn.(U.Carb)-L.Perm._, N.Am.-S.Am.——Fig. 339,_3_. *_F. plummeri_ (R. H. King), U.Penn., USA(Tex.); _3a,b_, ped.v. vent., lat., ×3, ×2; _3c_, brach.v. view, ×2; _3d_, brach.v. int., ×4 (471).

Geniculifera Muir-Wood & Cooper, 1960, p. 187 [*_Avonia boonensis_ E. B. Branson, 1938, p. 40; OD]. Small, valves geniculated, with short trails and steep flanks, both valves rugose on visceral disc and costate anteriorly, spines scattered on rugae and costae, absent on brachial valve; cardinal process minute, bilobate, sloping dorsally. _L.Miss._, N.Am.——Fig. 340,_1_. *_G. boonensis_ (Branson), USA(N.Mex.); _1a-c_, ped.v. vent., lat., post., ×2; _1d_, brach.v. int., ×3 (116).

Grandaurispina Muir-Wood & Cooper, 1960, p. 305 [*_G. ķingorum_; OD]. Medium-sized, nongeniculate; pedicle valve rugose near hinge, with small elongated spine ridges quincuncially arranged over whole valve, spines in 2 or more series, larger diameter spines in group on flanks extending laterally; brachial valve more rugose and commonly capillate, with numerous suberect or hooklike spines medianly or posteriorly directed, cardinal process trilobed, with sulcate dorsally recurved median lobe; adductors dendritic, lateral ridges short, divergent. _L.Perm._, N.Am.——Fig. 341,_1_. *_G. ķingorum_, Word., USA(W.Tex.); _1a_, ped.v. vent., spines attached, ×0.8; _1b_ (holotype), brach. v. view, ×1.6; _1c,d_, brach.v. ext. showing capillae, int., ×1.6 (587).

Krotovia Frederiks, 1928, p. 779 [*_Productus spinulosus_ J. Sowerby, 1814, p. 155; OD]. Small, thin-shelled, highly concavo-convex valves; umbo

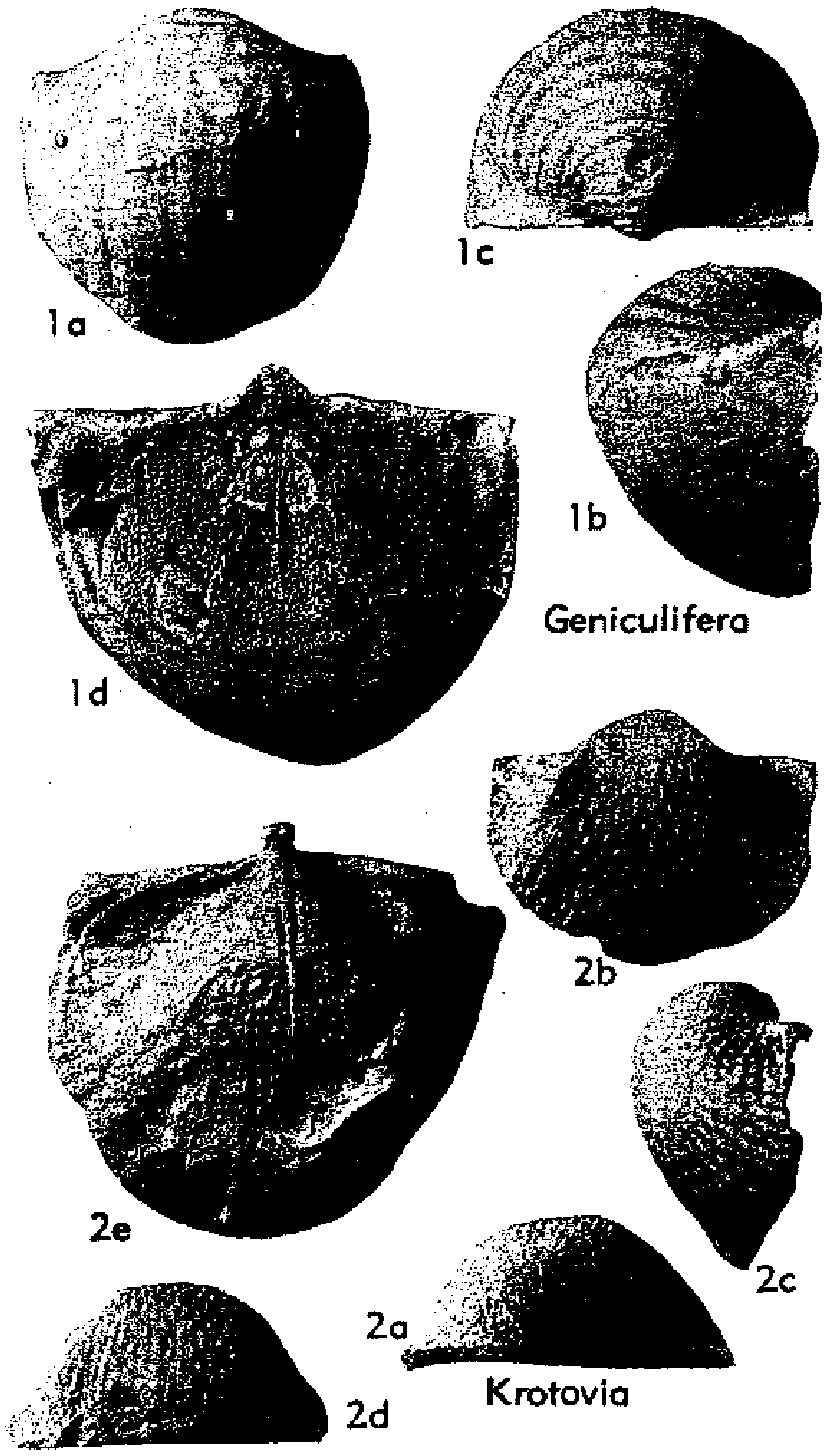


FIG. 340. Overtoniidae (Overtoniinae) (p. *H*472-*H*473).

much incurved, ears large; pedicle valve with quincuncially arranged spine tubercles bearing small suberect spines, rugae near hinge; brachial valve more rugose, numerous spines; lateral ridges along hinge and extending as vertical ridges parallel to septum. *L.Carb.-L.Perm., ?U.Perm.,* cosmop.——FIG. 340,*2*. **K. spinulosa* (J. SOWERBY), L.Carb.(Visean), Eng.; *2a-d,* ped.v. post., vent., lat., ant., ×1; *2e,* brach.v. int., ×2 (587).

Laminatia MUIR-WOOD & COOPER, 1960, p. 189 [**Productella laminata* KINDLE, 1909, p. 18; OD]. Small, subquadrate, valves slightly concavo-convex, cicatrix of attachment present; ornament in both valves of lamellose, commonly stepped bands with 2 series of fine spine ridges, which may alternate, larger extending across band, smaller more anteriorly developed; spines prostrate, tapering; cardinal process erect, bilobate. *U.Dev.,* N. Am.——FIG. 342,*1*. **L. laminata* (KINDLE), USA(N.Mex.); *1a,* ped.v. vent., ×2; *1b,c,* brach. v. ext., ×2, ×3; *1d,* brach.v. int., ×3 (587).

Levipustula MAXWELL, 1951, p. 10 [**L. levis*; OD]. Medium-sized, subcircular, moderately concavo-convex valves; ornament of quincuncially arranged, elongate spine ridges bearing prostrate spines, row of erect spines along hinge and on ears; brachial valve with dimples, prominent growth lines and no spines; cardinal process bilobate internally; 2 ridges enclosing alveolus, breviseptum developed. *U.Carb.(Moscov.),* Australia.——FIG. 342,*5*. **L. levis,* New S.Wales; *5a,b,* ped.v. ext., brach.v. int., ×2 (538).

Rhytiophora MUIR-WOOD & COOPER, 1960, p. 192 [**Productus blairi* MILLER, 1891, p. 689; OD] [=?*Semiproductus* BUBLITSCHENKO, 1956, p. 99 (type, *S. minax*)]. Medium-sized, subquadrate, both valves with short trails and anterior rim; ornament of irregular rugae posteriorly, spine ridges commonly aligned radially; spines numerous, prostrate or erect, in rows near hinge, and on ears and flanks; brachial valve rugose, spines rare, cardinal process bilobate internally; adductors slightly dendritic or smooth. *L.Miss.,* N.Am.——FIG. 342,*3*. **R. blairi* (MILLER), Kinderhook., USA(Mo.); *3a,b,* ped.v. vent., lat., ×1; *3c,d,* brach.v. ext., int., ×2 (587).

Rugauris MUIR-WOOD & COOPER, 1960, p. 193 [**R. paucispina*; OD]. Medium-sized, subquadrate, valves slightly concavo-convex; ornament of numerous rugae with small spine ridges bearing fine prostrate or recumbent spines; pedicle valve with row of spines along hinge margin; cardinal process trilobate, brachial ridges given off at angle

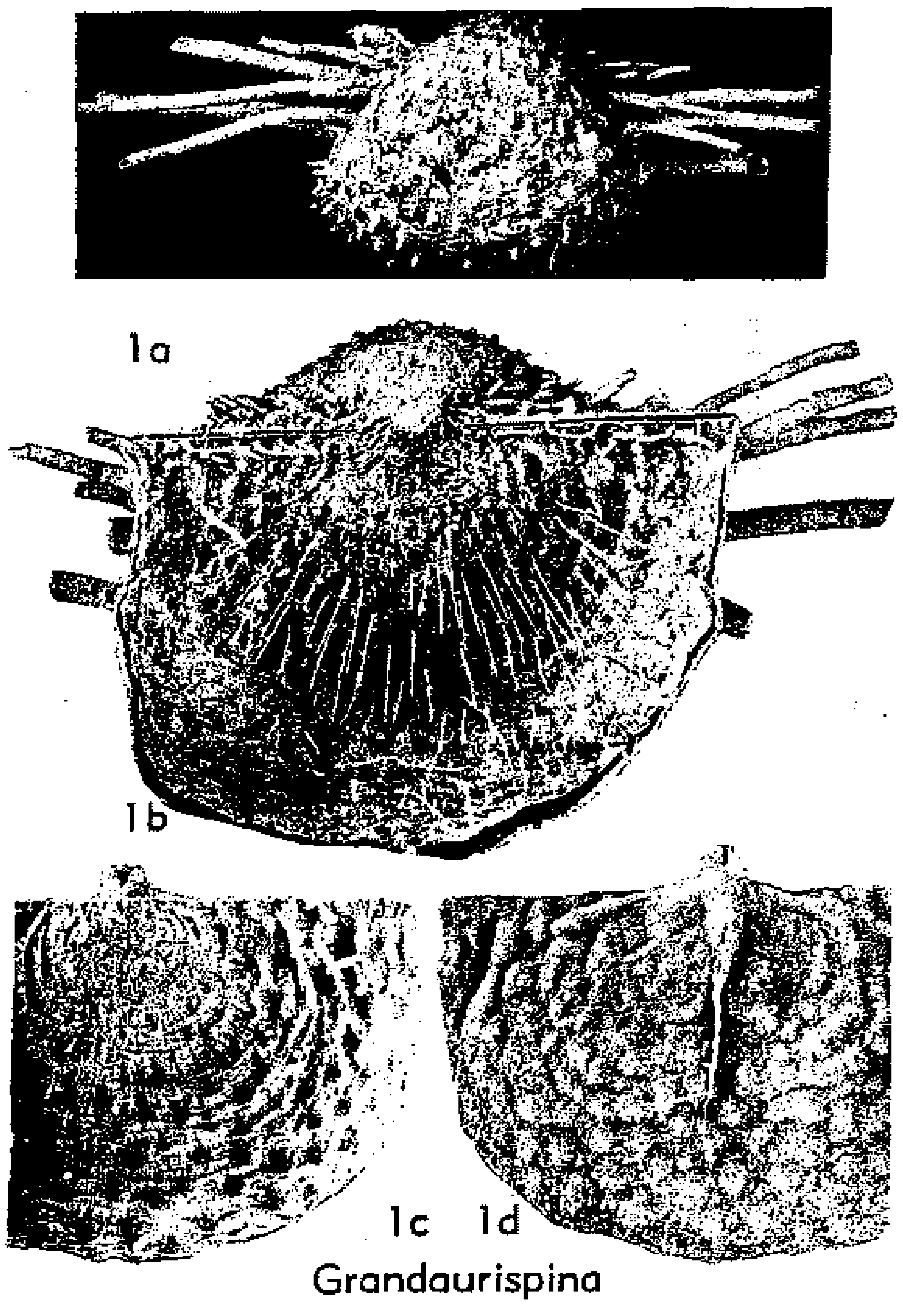


FIG. 341. Overtoniidae (Overtoniinae) (p. *H*472).

of 25 degrees to horizontal; adductors dendritic or smooth. *L.Miss.*, N.Am.——Fig. 342,2. **R. paucispina*, Kinderhook., USA(Iowa); *2a,b* (holotype), ped.v. vent., lat., ×1; *2c,d*, brach.v. ext., int., ×1 (587).

Scutepustula (*see* p. *H*904).

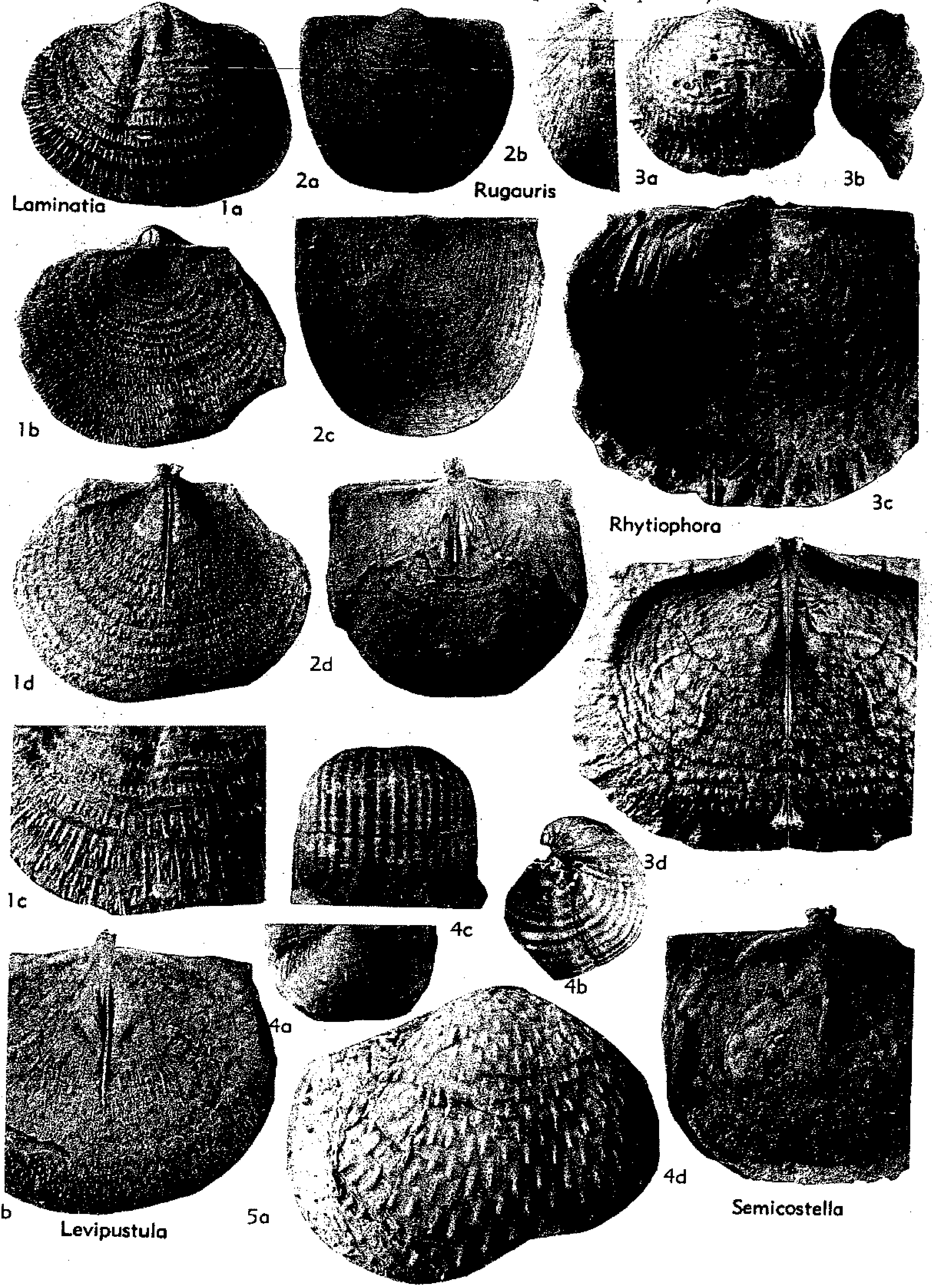


Fig. 342. Overtoniidae (Overtoniinae) (p. *H*473-*H*475).

Semicostella Muir-Wood & Cooper, 1960, p. 195 [**Avonia oklahomensis* Snider, 1915, p. 83; OD]. Medium-sized, subquadrate, valves concavo- or plano-convex with short trails; cincture in pedicle valve; pedicle valve ornament posteriorly of rugae and spine ridges, trail with broad costae bearing few spines; spines in row up flanks and near hinge; brachial valve rugose and spinose, costae absent or obscure, cardinal process bilobate. *U.Miss.*, N.Am.——Fig. 342,*4*. **S. oklahomensis* (Snider), USA(Okla.); *4a-c*, ped.v. post., lat., ant., ×1; *4d*, brach.v. int., ×2 (587).

Semiproductus Bublitschenko, 1956, p. 9 [**S. minax*; OD]. Both valves geniculated, ornamented

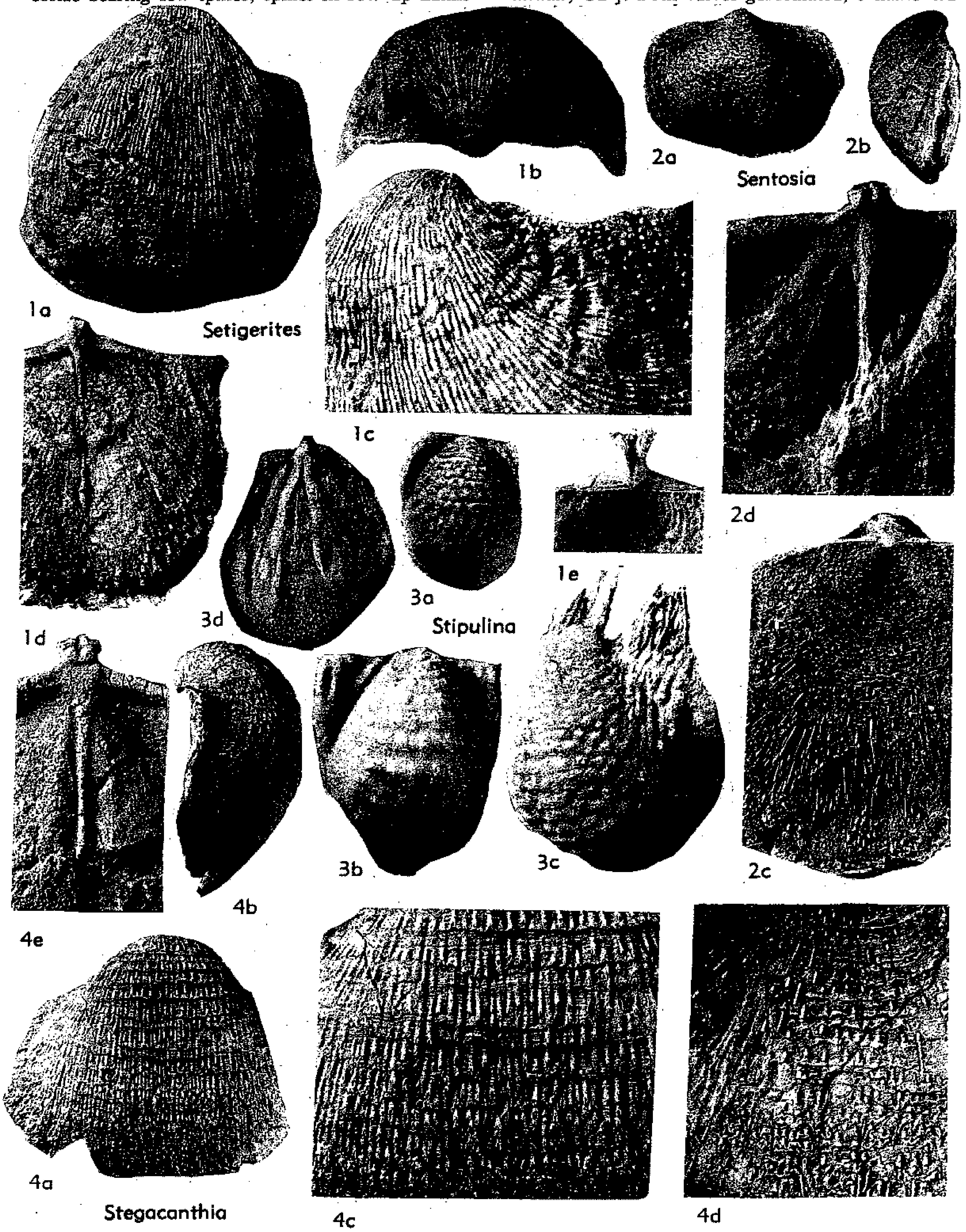


Fig. 343. Overtoniidae (Overtoniinae) (p. *H*476).

on visceral disc by concentric rugae and elongated spine ridges, and anteriorly by costae and rare spines. Interior as in *Pustula.* [Possibly a senior synonym of *Rhytiophora.*] *U.Dev.-L.Carb.*, Eu.-Asia.

Sentosia Muir-Wood & Cooper, 1960, p. 196 [**Krotovia praecursor* Stainbrook, 1947, p. 313; OD]. Small, plano- to slightly concavo-convex; ornament finely rugose and spinose; spines long, prostrate, roughly arranged in rows; cardinal process bilobate, with lobes fused posteriorly, process not supported by narrow septum; adductors obscure, lobate. *U.Dev.*, N.Am.——Fig. 343,*2*. **S. praecursor* (Stainbrook), USA(N.Mex.); *2a,b*, ped.v. vent., lat., ×1; *2c,d*, brach.v. ext., int., ×2 (769).

Setigerites Girty, 1939, p. 141 [*pro Setigerella* Girty, 1938, p. 434 (*non* Ehrenberg, 1872)] [**Productus setigerus* Hall, 1858, p. 638 (=*P. setiger, nom. correct.* Muir-Wood & Cooper, 1960, p. 197; OD]. Medium-sized, subquadrate; ornament of fine costae with spines, both valves with gutter-like extension of trail, rugae posteriorly; pedicle valve with spine rows near hinge and in group on ears and flanks; cardinal process bilobate or trilobate projecting dorsally; adductors dendritic. *L.Miss.(Osag.) - U.Miss.(Meramec.)*, N.Am.——Fig. 343,*1*. **S. setiger* (Hall), USA; *1a-c*, ped.v. vent., post., post. lat. showing spines, ×1, ×1, ×2; *1d,e*, brach.v. int., ext. showing card process, ×1, ×2 (*1a-c*, Ind; *1d,e*, Mo.) (587).

Stegacanthia Muir-Wood & Cooper, 1960, p. 198 [**S. bowsheri*; OD]. Medium-sized, subquadrate; valves moderately concavo-convex; nongeniculated; pedicle valve posteriorly rugose, medianly with elongate spine ridges on lamellose bands, anteriorly bands narrow and squamose; spines fine, prostrate, in rows near hinge and on spine ridges; brachial valve more lamellose with numerous spines, cardinal process bilobed or trilobed; adductors obscurely dendritic. *L.Miss.(Osag.), ?U. Miss.(Meramec.)*, N.Am.——Fig. 343,*4*. **S. bowsheri*, L.Miss., USA(N.Mex.); *4a,b*, ped.v. vent., lat., ×1; *4c,d*, ped.v. ext., brach.v. ext., ×2; *4e*, brach.v. int., ×3 (*4a-d*, holotype) (587).

Stipulina Muir-Wood & Cooper, 1960, p. 200 [**Productus deshayesianus* de Koninck, 1842, p. 193; OD]. Small, elongate-oval, valves slightly concavo-convex, cicatrix of attachment rare; ornament of concentric convex bands bearing single row of spine tubercles, spines crowded anteriorly, and arranged in row along hinge extending vertically, elsewhere prostrate; brachial valve with concentric bands and dimples, no spines, cardinal process bilobate. *L.Carb.(Visean)*, Eu.(Eng.-Belg.). —— Fig. 343,*3*. **S. deshayesiana* (de Koninck), Belg.; *3a-c*, ped.v. vent., post., lat., ×4, ×5, ×5; *3d*, brach.v. int.,×4 (483).

Subfamily PLICATIFERINAE Muir-Wood & Cooper, 1960

[Plicatiferinae Muir-Wood & Cooper, 1960, p. 201]

Geniculated, with large body cavity; posteriorly rugose and trail smooth, adductor scars dendritic. *L.Carb.(Visean).*

Plicatifera Chao, 1927, p. 25 [**Productus plicatilis* J. de C. Sowerby, 1824, p. 85; OD]. Medium-sized, subquadrate; rugae prominent, subangular, more numerous on brachial valve; spines rare on brachial valve, scattered on pedicle valve and in erect row near hinge; cardinal process trilobate with minute median lobe. *L.Carb.(Visean-U. Miss.)*, Eu. (Eng.-Belg.)-N. Am.(Calif.).——Fig. 344,*1*. **P. plicatilis* (J. de C. Sowerby), Eng. (*1a-c*), Belg. (*1d*); *1a,b*, ped.v. ant., post., ×1; *1c,d*, brach.v. ext., int., ×2 (153).

Subfamily INSTITIFERINAE Muir-Wood & Cooper, 1960

[Institiferinae Muir-Wood & Cooper, 1960, p. 203]

Small, with elaborate marginal flanges or frills. *L.Carb.(Visean).*

Institifera Muir-Wood & Cooper, 1960, p. 203 [**Productus tessellatus* deKoninck, 1847, p. 110; OD]. Small, valves nongeniculate, cicatrix present; pedicle valve with anterior flattened, finely costate flange, with rugae posteriorly, and costae anteriorly, lamellae intersecting costae causing enlarged tubercles bearing spines; brachial valve with lateral and anterior margins recurved medianly, exterior costate, lamellose, with capillate or smooth marginal flanges. *L.Carb.(Visean)*, Eu. ——Fig. 344,*2*. **I. tessellata* (deKoninck), Eng. (Yorks.) (*2a,b*), Eire (*2c-e*); *2a,b*, ped.v. vent., lat., ×2; *2c-e*, brach.v. views showing recurved ped.v. and brach.v. margins, developed as flanges, ×2, ×3, ×3 (483).

Thomasella Frederiks, 1928, p. 778 [**Productus wrighti* Davidson, 1861, p. 162; OD] [*non Thomasella* Paul, 1942]. Minute; pedicle valve highly convex with anterior flat costellate rim; ornament of narrow, prominent rugae bearing fine suberect or recumbent spines; brachial valve and interior unknown. *L.Carb.(Visean)*, Eu.——Fig. 344,*3*. **T. wrighti* (Davidson), Eire; *3a,b*, ped.v. vent. with frill, ×3, ×4 (229).

Family MARGINIFERIDAE Stehli, 1954

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 205 (*ex* Marginiferinae Stehli, 1954, p. 321)]

Small or medium-sized, commonly with symmetrically arranged spines; interior of pedicle valve with marginal ridges across ears, brachial valve with marginal ridges or anterior rows of endospines, cardinal process trilobed with median lobe bent dorsally (toward exterior). *L.Carb.-U.Perm.*

Subfamily MARGINIFERINAE Stehli, 1954

[Marginiferinae Stehli, 1954, p. 321]

With externally crenulated marginal ridges around visceral disc of brachial valve; adductor scars smooth, lobate, or dendritic. *L.Carb.-U.Perm.*

Marginifera Waagen, 1884, p. 713 [**M. typica*; OD]. Small, both valves geniculated, trails short, flanks steep, ornament of ill-defined costae with rugae posteriorly; spines erect, scattered over pedicle valve, in 1 or 2 rows on flanks, absent from brachial valve; pedicle valve with crenulated ridges across ears, articulating with brachial valve; no anterior thickening in either valve; adductors smooth. [Although Waagen did not explicitly designate a type-species by formal statement, in adopting the name *typica* for one of the forms described by him he automatically fixed the type-species (Zool. Code, 1961, Art. 68,b); Oehlert's (1887, p. 1277) action in stating that the type-species is *M. typica* is superfluous and does not constitute a subsequent designation, as construed by some.] *?L.Perm., U.Perm.*, Eu.-Asia.——Fig. 345,*2*. **M. typica*, Pak.; *2a-c*, ped.v. vent., lat., ant., ×1; *2d-f*, brach.v. views, ×1 (845).

Alifera Muir-Wood & Cooper, 1960, p. 207 [**Productus expansus* deKoninck, 1842, p. 159 (*non* Pander, 1830) (=**A. konincki* Muir-Wood & Cooper, 1960, p. 208; OD]. Small or medium-sized, externally like small dictyoclostid but with cincture in pedicle valve corresponding to internal diaphragm; spines rare, erect, 1 from cardinal extremities and 1 or 2 on flanks; absent from brachial valve; adductors nondendritic. *L.Carb. (Visean)*, Eu.——Fig. 345,*3*. **A. konincki* Muir-Wood & Cooper, Belg.; *3a-c*, ped.v. post., ant., lat., ×2; *3d*, brach.v. int., ×2 (483).

Duartea Mendes, 1959, p. 58 [**Productus batesianus* Derby, 1874, p. 54; OD]. Resembling *Eomarginifera* in outline and small ears, fine costellae and faintly reticulate ornament, and 6 major spines and no row along hinge, but has narrow interarea (ginglymus), large cardinal process, and ventral adductors set on ridge. *M.Penn.*, S.Am.——Fig. 346,*1*. **D. batesiana* (Derby), Itaituba Ser., Brazil; *1a,b*, ped.v. vent., post., ×1; *1c*, brach.v. ext., ×1.35 (555).

Eomarginifera Muir-Wood, 1930, p. 103 [**Productus longispinus* J. Sowerby, 1814, p. 154; OD]. Small or medium-sized, both valves geniculated, costellate and rugose, with slight reticulation posteriorly, costellate on trail; spines on pedicle valve only and rare except for 6 symmetrical spines; brachial valve commonly thickened or with overlapping laminae representing successive trails; adductors dendritic and lobate; pedicle valve without marginal ridge. *L.Carb.(Visean)*, Asia-Afr.; *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.——Fig. 345,*1*. *E. setosa* (Phillips), L.Carb.(Visean), Eng. *(1a-d)*, Scot. *(1e-g)*; *1a-c*, ped.v. vent., post., lat., ×2; *1d*, brach.v. view, ×2; *1e,f*, brach. v. int., ×3, ×4; *1g*, card. process, ×4 (574). [*See* p. *H*904.]

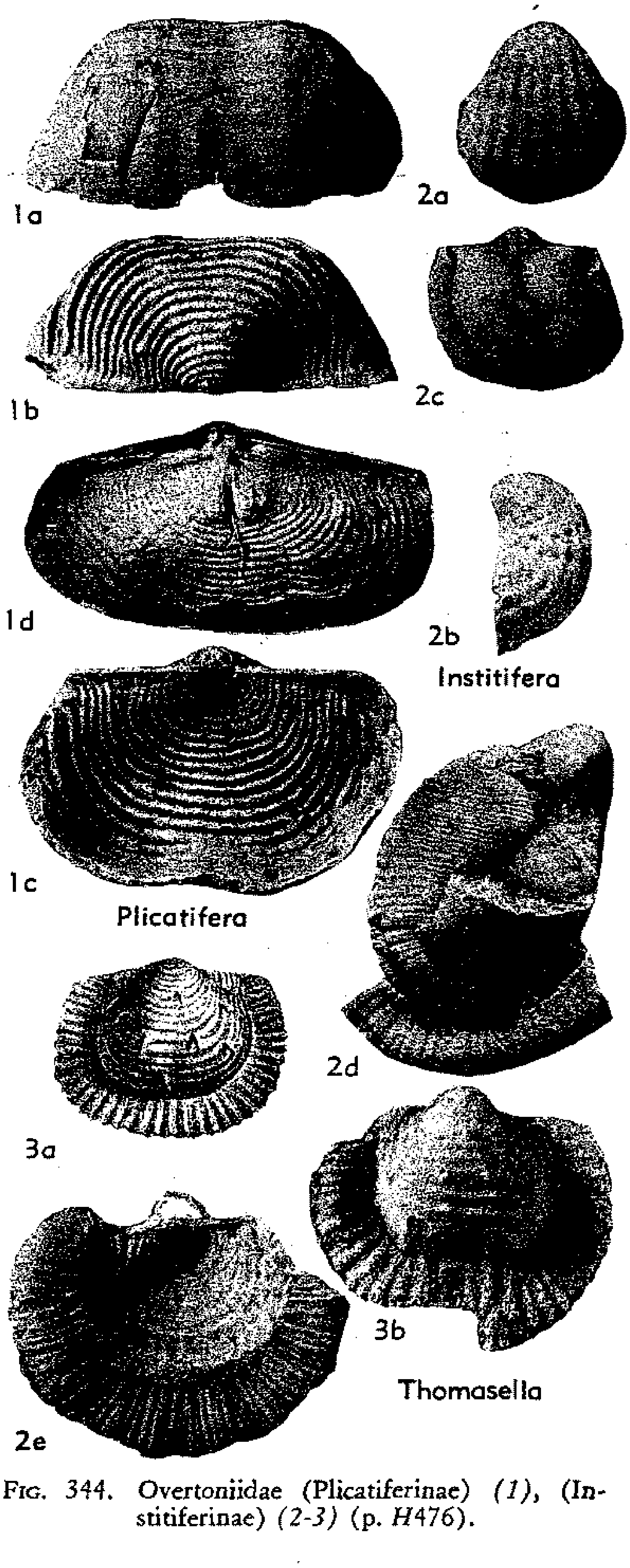


Fig. 344. Overtoniidae (Plicatiferinae) *(1)*, (Institiferinae) *(2-3)* (p. *H*476).

Hystriculina Muir-Wood & Cooper, 1960, p. 210 [**H. texana*; OD]. Like *Eomarginifera* externally but with no anterior thickening in brachial valve, lamellose ornament anteriorly, and scattered spines on pedicle valve with row up flanks; pedicle valve with crenulated ridge across ears; adductors smooth; brachial ridges obscure; endospines large and numerous in rows. *Penn.-L.Perm.*, N.Am.-S.

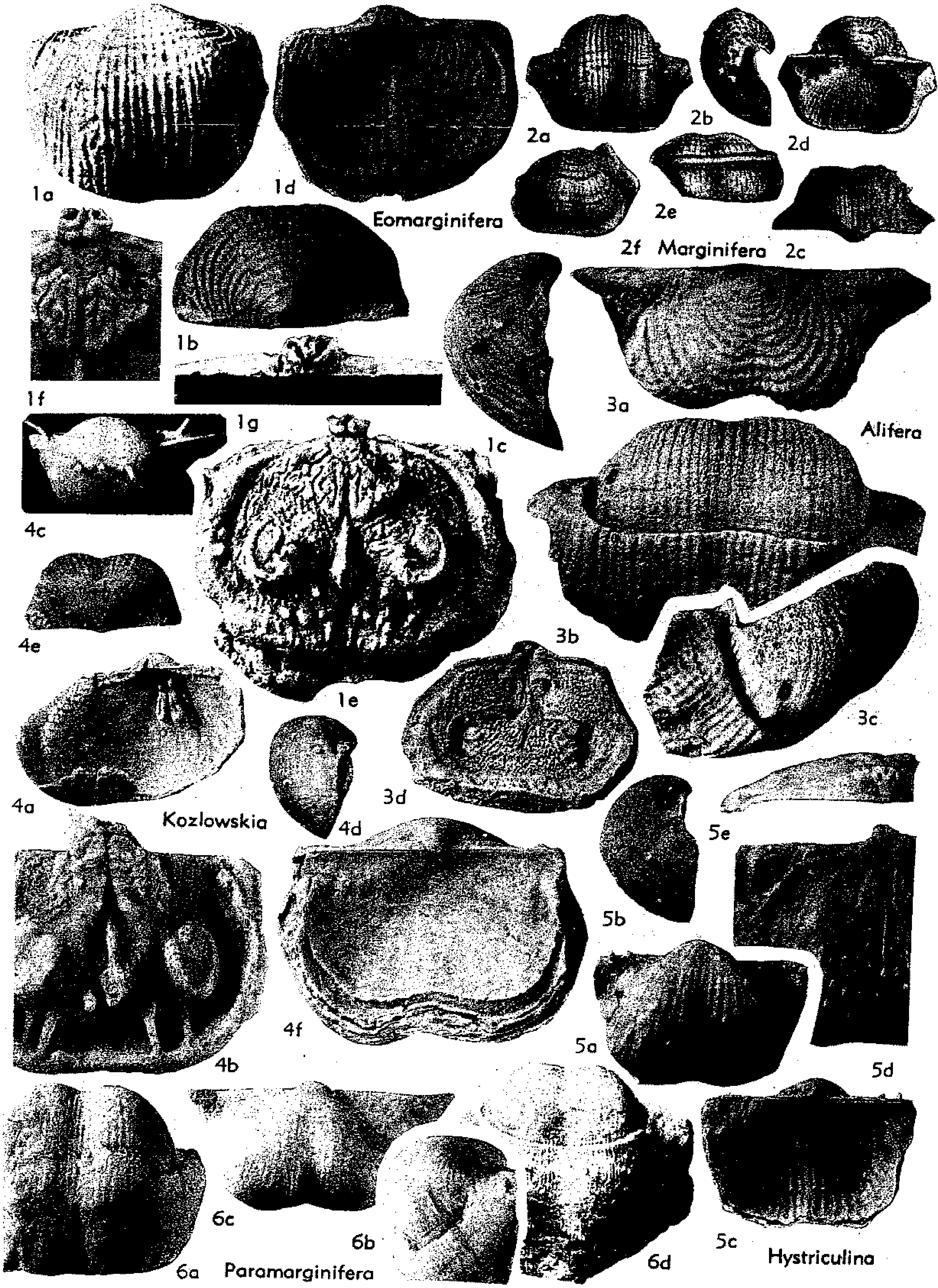


Fig. 345. Marginiferidae (Marginiferinae) (p. *H*477, *H*479).

Am.——FIG. 345,*5*. **H. texana,* Penn., USA (Tex.); *5a,b,* ped.v. vent., lat., ×2; *5c,* brach.v. view, ×2; *5d,e,* brach.v. int., card. process in post. view, ×3 (587).

Kozlowskia FREDERIKS, 1933, p. 29 [**Productus capaci* D'ORBIGNY, 1842, p. 50; OD]. Like *Eomarginifera* externally and having broken off trails as overlapping lamellae in brachial valve but spine row near hinge, as well as 6 symmetrical spines; crenulated marginal ridges in both valves; smooth anterior rim in brachial valve interior; adductors in part dendritic. *M.Penn.-L.Perm.,* N.Am.-S.Am.; *U.Carb.,* Eu.-Asia.——FIG. 345,*4a*. **K. capaci* (D'ORBIGNY), L.Perm., Bolivia; ped.v. int. showing marginal ridge, ×2 (485).——FIG. 345,*4b*. *K. haydenensis* (GIRTY), M.Penn., USA(Okla.); brach.v. int. with endospines, ×3 (485).——FIG. 345,*4c-f*. *K. splendens* (NORWOOD & PRATTEN), U.Penn., USA(N.Mex.-Tex.); *4c-e,* ped.v. vent., lat., post., ×1; *4f,* brach.v. view showing thickened margins, ×2 (485).

Paramarginifera FREDERIKS, 1916, p. 61 [**Marginifera clarkei* CHERNYSHEV, 1902, p. 328; OD]. Medium-sized, subpentagonal; pedicle valve with cincture demarcating ears, probably corresponding to internal ridge or diaphragm, trail tending to form tube; ornament costate and rugose, spine row along hinge and 6 symmetrical spines; brachial valve unknown. *U.Carb.* or *L.Perm.,* Eu.——FIG. 345,*6*. **P. clarkei* (CHERNYSHEV), Perm., USSR; *6a-c,* ped.v. vent., lat., post.; *6d,* ped.v. (syntype) vent. with cincture; all ×1 (158).

Spinomarginifera HUANG, 1932, p. 16 [**S. kueichowensis;* OD]. Small or medium-sized, valves geniculated, rugose, long spines on spine ridges, or tubercles quincuncially or radially arranged in pedicle valve, also spine row near hinge and on ears; brachial valve without spines, adductors dendritic. *?U.Carb., L.Perm.-U.Perm.,* Asia.——FIG. 346,*2*. **S. kueichowensis,* Perm., China; *2a-c,* ped.v. vent., post., lat.; *2d,f,* ped.v. ext., with spines, int.; *2e,* brach.v. int.; all ×0.9 (435).

Subfamily COSTISPINIFERINAE Muir-Wood & Cooper, 1960

[Costispiniferinae MUIR-WOOD & COOPER, 1960, p. 217]

Ridges extending across ears of both valves internally, prominent endospines in row anterior to septum, and set on outer margin of brachial ridges. *U.Miss.-U.Perm.*

Costispinifera MUIR-WOOD & COOPER, 1960, p. 217 [**C. texana;* OD]. Like *Avonia* superficially; pedicle valve irregularly rugose and spinose posteriorly, becoming costate and lamellose anteriorly; spines erect on trail, in row near hinge and on flanks; brachial valve similar, with numerous erect or suberect spines and in row, commonly centripetal, near hinge; adductors smooth. *L.Perm.,* N.Am.(USA-Mex.).——FIG. 347,*1*. **C. texana,* Perm., USA(Tex.); *1a-c,* ped.v. vent., lat., post., ×1; *1d,e,* brach.v. views, ×1, ×2; *1f,* brach.v. int., ×2; *1g,* card. process, ext., ×4 (*1a-e,* holotype) (587).

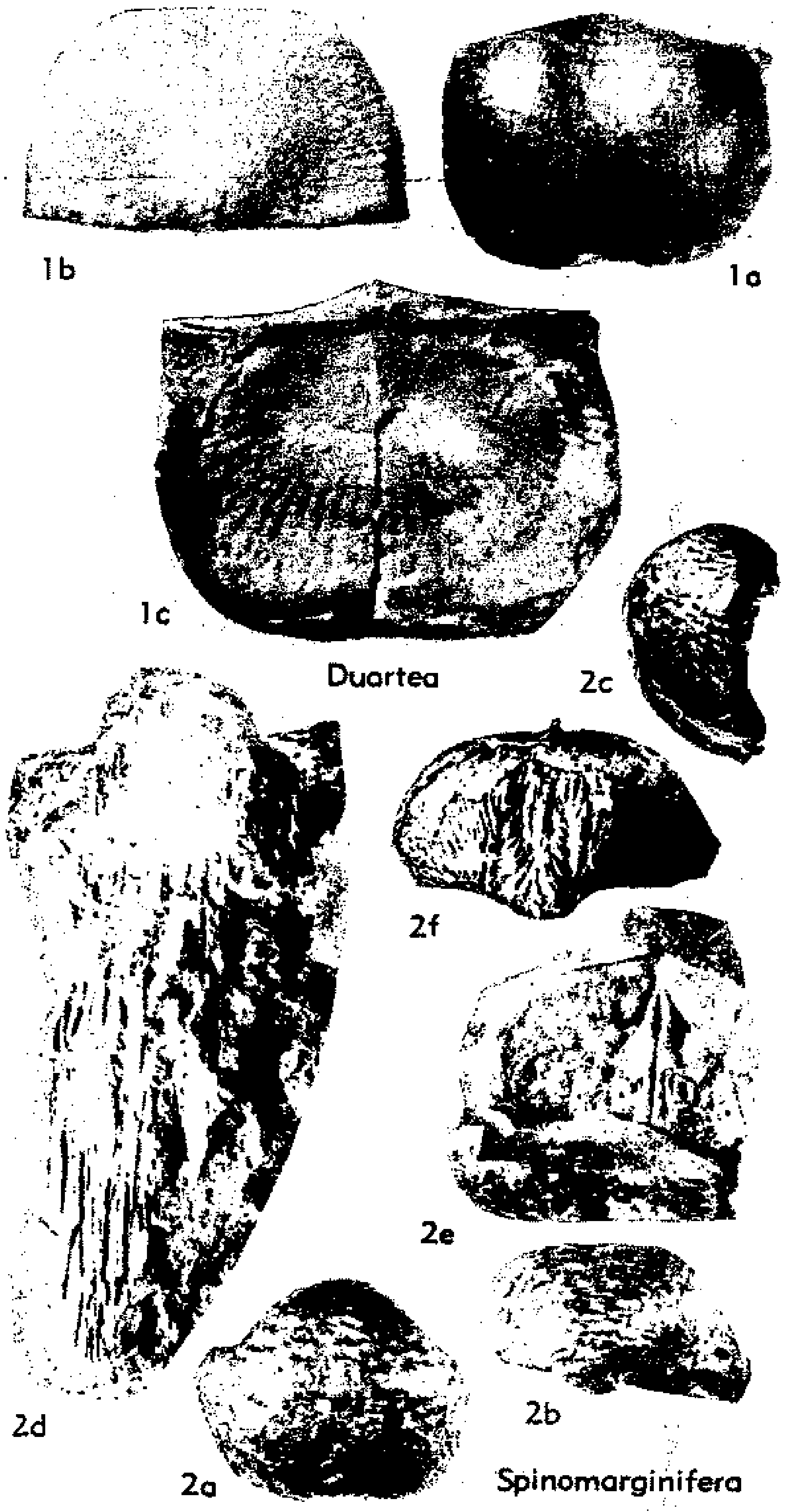


FIG. 346. Marginiferidae (Marginiferinae) (p. *H477, H479*).

Desmoinesia HOARE, 1960, p. 226 [**Productus muricatus* NORWOOD & PRATTEN, 1855, p. 14 (*non* PHILLIPS, 1838), =**Marginifera muricatina* DUNBAR & CONDRA, 1932, p. 222; OD] [=*Rudinia* MUIR-WOOD & COOPER, 1960, p. 229 (obj.)]. Small, moderately concavo-convex, body cavity narrow; pedicle valve posteriorly rugose and spinose, becoming costate, thickened with lamellae, bearing spines anteriorly, spine row near hinge and up flanks; brachial valve more rugose, obscurely costate, fewer spines, adductors faintly dendritic. *M.Penn.,* N.Am.(Okla.-Mo.-Ill.-Tex.).——FIG. 347,*2*. **D. muricata* (NORWOOD & PRATTEN), USA(Okla.); *2a-c,* ped.v. vent., post., int., ×2; *2d,* brach.v. view, ×2; *2e,f,* brach.v. int., post., ×3 (429).

Echinauris Muir-Wood & Cooper, 1960, p. 221 [**E. lateralis*; OD]. Small to medium-sized, both valves with short trails; pedicle valve with irregularly distributed curving recumbent spines, group of straight spines on flanks and 2 rows at angle to hinge; brachial valve posteriorly rugose, and with scattered spines, commonly centripetal; adductors smooth, *L.Perm.(Word.)*, N.Am.——Fig. 347,*3*. **E. lateralis*, USA(W.Tex.); *3a*, ped.v. (holotype) vent., with spines attached, ×1; *3b*, juv. ped.v. vent., with converging spines, ×4; *3c,d*, brach.v. ext., int., ×2, ×3; *3e*, card. process ext., ×4 (587).

Elliottella Stehli, 1955, p. 711 [*pro Psilonotus* Stehli, 1954, p. 323 (*non* Walker, 1834)] [**Psilonotus transversalis* Stehli, 1954, p. 324; OD]. Like *Costispinifera* but visceral disc of pedicle valve less convex and shell less elongate,

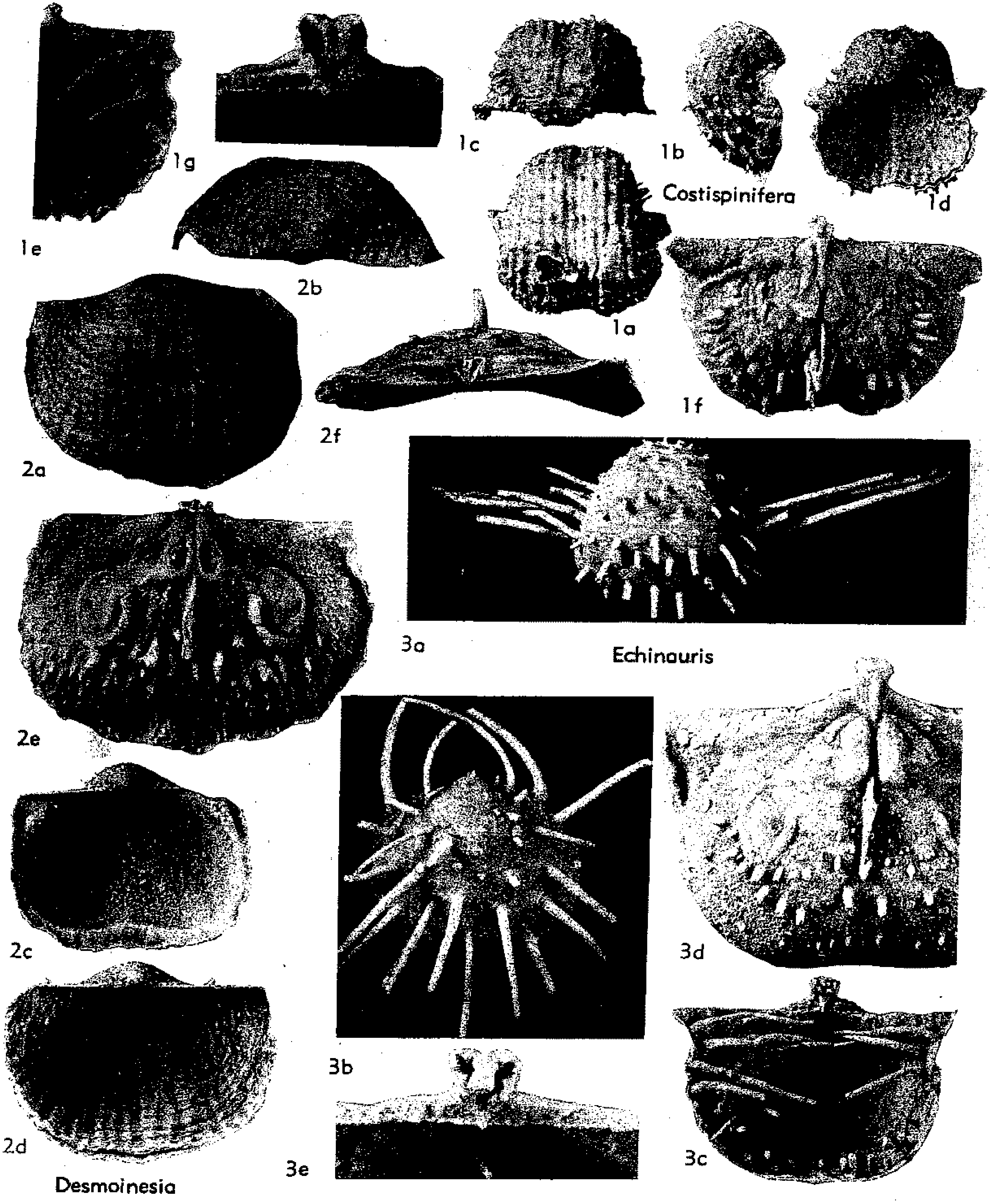


Fig. 347. Marginiferidae (Costispiniferinae) (p. *H*479-*H*480).

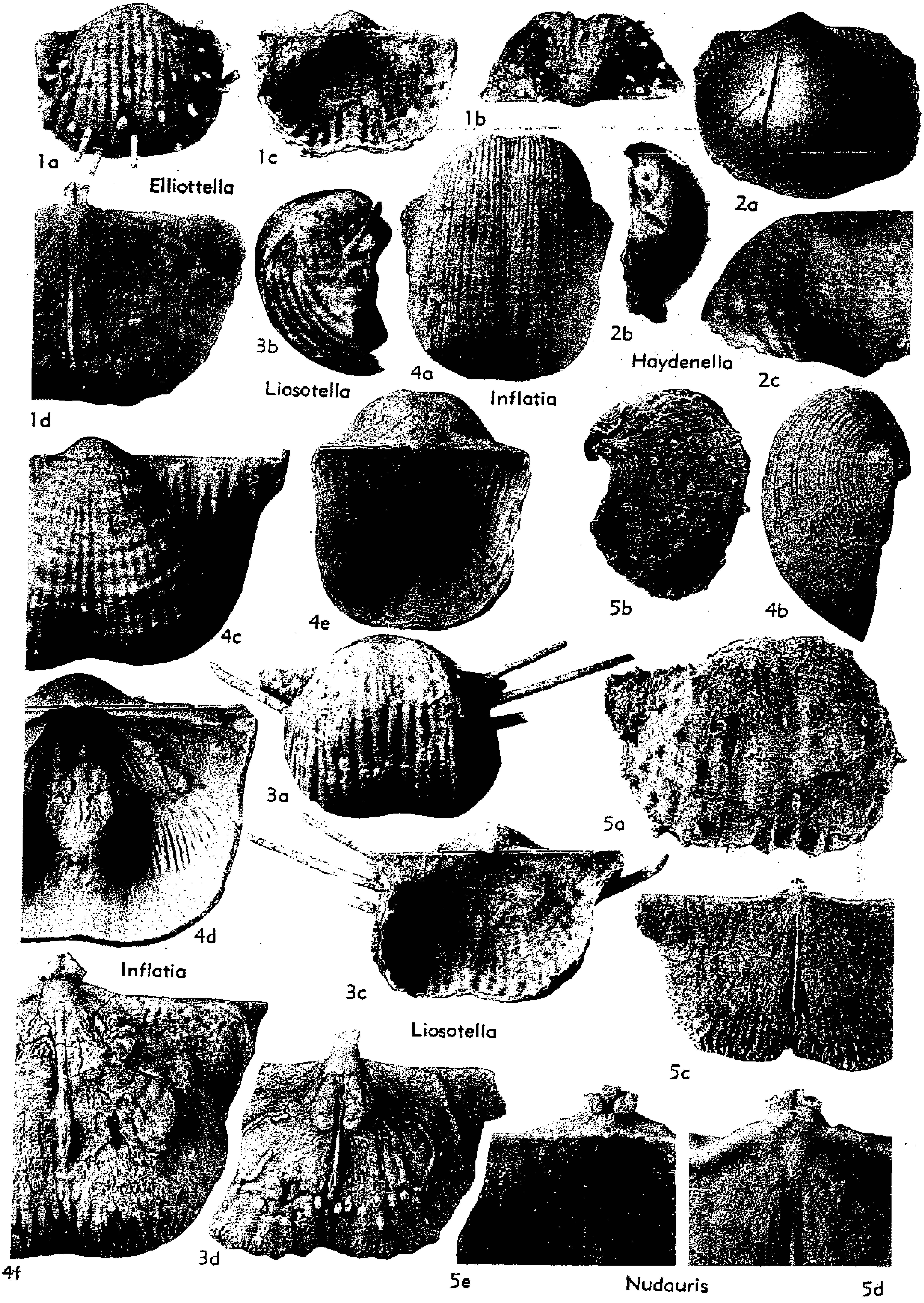


FIG. 348. Marginiferidae (Costispiniferinae) (p. *H*480, *H*482).

2 rows of spines near hinge; brachial valve without spines, and small internal differences. *L.Perm.*, N.Am.——Fig. 348,*1*. *E. minima* (Stehli), USA (W.Tex.); *1a,b*, ped.v. vent., post., ×2; *1c*, brach.v. view, ×2; *1d*, brach.v. int., ×4 (773).

Haydenella F. R. C. Reed, 1944, p. 78 [**Productus kiangsiensis* Kayser, 1883, p. 185; OD]. Small to medium-sized; pedicle valve globose, with short interarea; both valves capillate, smooth when decorticated, rugose near hinge, spines rare and in curved row up pedicle valve flanks; adductors smooth. *L.Perm.-U.Perm.*, Asia(China-Pak.).——Fig. 348,*2*. **H. kiangsiensis* (Kayser), China *(2a,b)*, Pak. *(2c)*; *2a,b*, ped.v. vent., lat., ×1; *2c*, ped.v. post., ×2 (460).

Inflatia Muir-Wood & Cooper, 1960, p. 226 [**Productus inflatus* McChesney, 1860, p. 40; OD]. Medium-sized, elongate-quadrate; pedicle valve spirally curved; narrow ginglymus; both valves rugose posteriorly and costate, lamellose anteriorly, spines suberect or erect, scattered, and in row near hinge of pedicle valve, absent on brachial valve; adductors dendritic and lobate, large ventral muscle area. *U.Miss.(Chester.)*, N.Am.——Fig. 348,*4*. **I. inflata* (McChesney), USA (Okla.); *4a,b*, ped.v. vent., lat., ×1; *4c,d*, ped.v. post., int., ×2; *4e*, brach.v. view, ×1; *4f*, brach. v. int., ×2 (587).

Liosotella Cooper, 1953, p. 227 [**L. rugosa*; OD]. Small to moderately large; pedicle valve with strongly convex visceral disc and curved trail; minute ginglymus; marginiferid ridges in each valve; both valves posteriorly smooth, costate on trail; spines scattered and in row up flanks, rare on brachial valve; adductors slightly dendritic. *L. Perm.*, N. Am.-Arctic (Greenl.-Spitz.).——Fig. 348,*3a-c*. **L. rugosa*, Mex.; *3a-c*, ped.v. vent., lat., and brach.v. views (holotype), ×1 (182).——Fig. 348,*3d*. *L.* sp., L.Perm., USA(W.Tex.); brach.v. int., ×2 (182).

Nudauris Stehli, 1954, p. 317 [**N. diabloensis*; OD]. Medium-sized, both valves geniculated, trails short; ginglymus present, pedicle valve costellate, ears smooth, rugose posteriorly, scattered stout spines, row near hinge; brachial valve smooth or costellate, spines absent; no internal ridges across ears; adductors faintly dendritic. *L. Perm.*, N.Am.——Fig. 348,*5*. **N. diabloensis*, USA(W.Tex.); *5a,b*, ped.v. vent., lat., ×1; *5c,d*, brach.v. int. showing card. process, ×1, ×2; *5e*, brach.v. ext., ×2 (773).

Subfamily RETARIINAE Muir-Wood & Cooper, 1960

[Retariinae Muir-Wood & Cooper, 1960, p. 230]

Valves geniculate, visceral disc reticulate, trail long, commonly tubuliform; brachial valve with ridge across ears; some shells with lateral flange; anterior row of endospines. *U.Carb.(Moscov.-Ural.)-L.Perm.*

Retaria Muir-Wood & Cooper, 1960, p. 230 [**R. umbonata*; OD]. Medium-sized, trails tending to split off from visceral disc, both valves finely rugose and costate, spines erect or suberect, scattered, and in row near hinge and up flanks, few spines in brachial valve; adductors dendritic and lobate; lateral flange in brachial valve. *U.Penn.-L.Perm.*, N.Am.-?Asia.——Fig. 349,*1*. **R. umbonata*, USA(W.Tex.); *1a,b*, ped.v. (holotype) vent., lat., ×1; *1c*, brach.v. view, ×1; *1d*, brach. v. int., ×3; *1e*, post. view of brach.v. int. showing flanges, ×2 (587).

Alexenia Ivanova in Ivanov, 1935, p. 89 [**A. reticulata*; OD]. Medium-sized, with short trails and cicatrix of attachment, both valves rugose and costate, reticulate, ears smooth; spines scattered, in row near hinge and up flanks; adductors nondendritic, set on platforms supported by vertical ridges from cardinal process; dorsal marginal ridge corrugated anteriorly. *U.Carb.(Moscov.-Ural.)*, Eu.——Fig. 349,*4*. **A. reticulata* (Ivanova), USSR; *4a,b*, ped.v. vent., post., ×1; *4c*, brach.v. int., ×2.5 (711).

Kutorginella Ivanova, 1951, p. 329 [**K. mosquensis*; OD] [=*Neoproboscidella* Ivanova, 1949 *(nom. nud.)*]. Medium-sized; pedicle valve posteriorly rugose, costate and reticulate, spines scattered and in row near hinge, trail funnel-shaped; brachial valve exterior unknown; marginal ridge in brachial valves, laterally flangelike, and spinose anteriorly; adductors partly dendritic. *U.Carb. (Moscov.-Ural.)-L.Perm.*, Eu.——Fig. 349,*5*. **K. mosquensis*, U.Carb., USSR; *5a,b*, ped.v. ant., vent., ×1; *5c*, brach.v. int., ×2 (711).

Rugivestis Muir-Wood & Cooper, 1960, p. 235 [**Proboscidella? carinata* Muir-Wood & Cooper in Cooper, 1957, p. 36; OD]. Small to medium-sized; pedicle valve trail carinate or with incipient tube; cincture present in each valve; flattened rim anterior to cincture in pedicle valve; internal marginal ridge corresponding to cincture; ornament of irregular costae, rugose and reticulate posteriorly; spines rare, possible 6 symmetrically placed. *L.Perm.*, N.Am.-Eu.——Fig. 349,*3*. **R. carinata* (Muir-Wood & Cooper), USA(Ore.); *3a-c*, ped.v. (holotype) vent., lat., ant., ×2 (192).

Tubaria Muir-Wood & Cooper, 1960, p. 236 [**Productus genuinus* Kutorga, 1844, p. 93; OD]. Small or medium-sized, posteriorly fusiform; trail of pedicle valve forming incomplete tube, open anteriorly; ears large, merging into flanks; cincture present; both valves posteriorly rugose, costate and reticulate, tube finely costate; spines in pedicle valve only on visceral disc and ears. Interior unknown. *L.Perm.*, Eu.——Fig. 349,*2*. **T. genuina* (Kutorga), USSR; *2a,b*, ped.v. ext. with ant. tube, lat. view, ×1; *2c*, same shell with ped.v. removed, ×1 (158).

Subfamily PROBOLIONIINAE Muir-Wood & Cooper, 1960

[Probolioniinae Muir-Wood & Cooper, 1960, p. 237]

Thickened submarginal rim resembling diaphragm in brachial valve interior, but with long subparallel trails springing from exterior surface; pedicle valve with crenulated ridges across ears. *L.Perm.*

Probolionia Cooper, 1957, p. 27 [*P. posteroreticulata; OD]. Small or medium-sized, both valves geniculated, posteriorly rugose, costellate and reticulate, trail costellate, pedicle-valve with sulcate trail, spines scattered and in row up flanks and 6 spines symmetrically placed, spines absent in brachial valve. *L.Perm.*, N.Am.-Asia(China).——Fig. 350,*1*. *P. posteroreticulata, USA(Ore.); *1a-c*, ped.v. post., vent., lat., ×2; *1d*, long. sec. of shell showing trails, ×2 (192).

Family PRODUCTIDAE Gray, 1840

[Productidae Gray, 1840, p. 151]

Costellate shells with long trail in pedicle valve and one or more trails in brachial valve; visceral disc of brachial valve with one or several diaphragms as thin crescent-shaped plate, closing gap between valves; sessile bilobate or trilobate cardinal process inclined dorsally (externally); adductors dendritic or partly dendritic. *L.Carb.(Visean)-U.Carb.(Westphal.).*

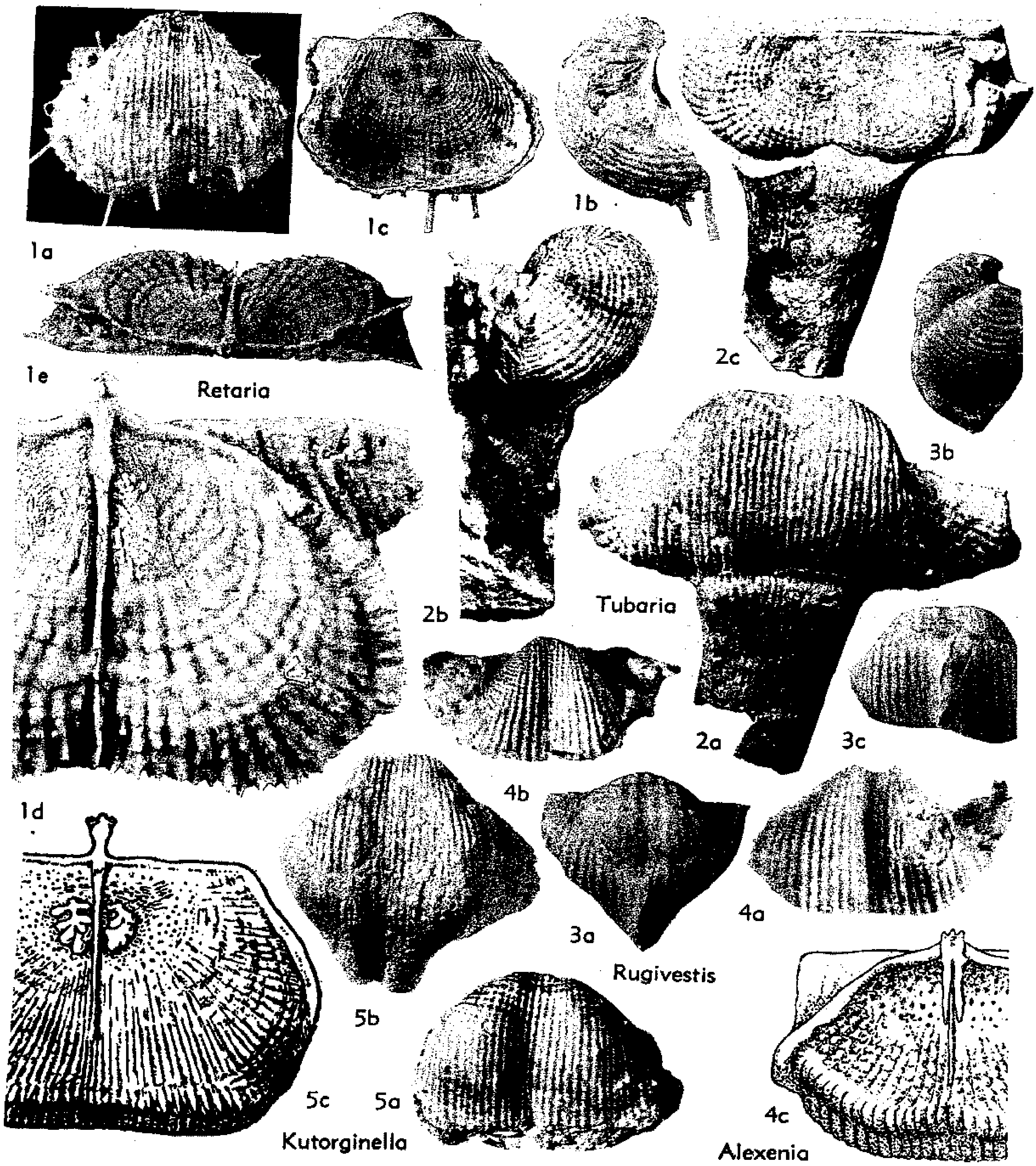


Fig. 349. Marginiferidae (Retariinae) (p. *H*482).

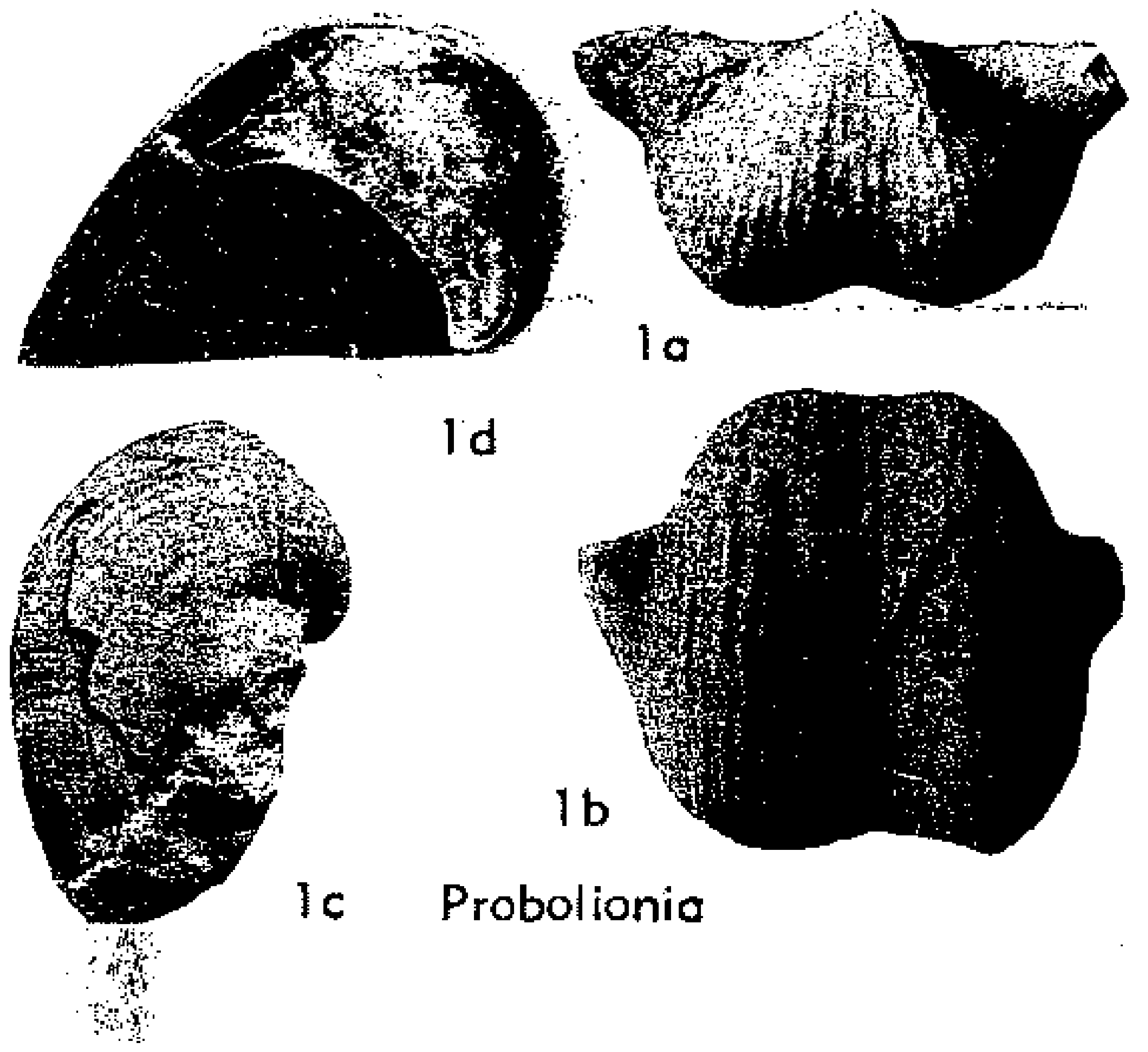


Fig. 350. Marginiferidae (Probolioniinae) (p. *H*483).

Productus J. Sowerby, 1814, p. 153 [**Anomites productus* W. Martin, 1809, p. 9 (validated ICZN, 1956, Opin. 419, p. 75); OD (abs. taut.)] [=*Producta* Conybeare & Phillips, 1822, p. 357 (no type-species); *Protonia* Link, 1830, p. 449 (*non* Rafinesque, 1814) (obj.); *Pyxis* Chemnitz in Martin & Chemnitz, 1784, p. 301 (nonbinominal)]. Medium-sized to large, geniculated, visceral disc of pedicle valve and part of brachial valve tending to split off along diaphragm, both valves costate, rugose and slightly reticulate posteriorly, unevenly costate on spreading trail; spines scattered and in 2 rows near hinge margin on pedicle valve, absent on brachial valve. *L.Carb.(Visean)-U.Carb.(Westphal.)*, Eu.-Asia. —— Fig. 351,*1a-d*. **P. productus* (Martin), L.Carb., Eng.; *1a,b*, ped.v. with trail, vent., lat., ×1; *1c*, visceral disc detached from trail in dorsal view, ×1; *1d*, brach.v. ext. mold showing diaphragm, ×1 (574). ——Fig. 351,*1e*. *P. carbonarius* deKoninck, U. Carb.(Namur.), Eng.; brach.v. int., ×2 (574).

Diaphragmus Girty, 1910, p. 217 [**Productus elegans* Norwood & Pratten, 1855, p. 13 (*non* M'Coy, 1844) (=**P. cestriensis* Worthen, 1860, p. 570); OD]. Small or medium-sized, commonly elongate, cincture variably developed, repetition of thin-shelled trails in brachial valve, diaphragm tending to be curved and repeated, both valves costate, rugose and faintly reticulate posteriorly; spines on costae, in 2 rows near hinge and group on flanks in pedicle valve, on flanks and trail in brachial valve; cardinal process bilobate, dorsally inclined; adductors obscurely dendritic and smooth. *U.Miss.(Meramec.-Chester.)*, N.Am.——Fig. 352, *1*. **D. cestriensis* (Worthen), Chester., Ill. *(1a-c)*, Okla. *(1d,e)*, Ala. *(1f)*; *1a-c*, ped.v. vent., lat., post., ×1; *1d*, brach.v. view, ×1; *1e*, long. sec. showing both valves, ×2; *1f*, brach.v. int., ×3 (346).

Family ECHINOCONCHIDAE Stehli, 1954

[Echinoconchidae Stehli, 1954, p. 326]

Body cavity large, greatly developed umbo in pedicle valve; cardinal process posteriorly trilobed, long-shafted and dorsally curved; brachial ridges generally obscure. *L.Carb.(Miss.)-U.Perm.*

Subfamily ECHINOCONCHINAE Stehli, 1954

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 243 (*ex* Echinoconchidae Stehli, 1954, p. 326)]

Spines of two or more series, or spine ridges bearing spines, either scattered over surface or arranged on concentric bands or rugae. *L.Carb.(Miss.)-L.Perm.*

Echinoconchus Weller 1914, p. 138 [**Anomites punctatus* W. Martin, 1809, pl. 37, fig. 6-8 (invalid ICZN, 1948), =*Productus punctatus* J. Sowerby, 1822, p. 22; SD Chao, 1927]. Small to large, concavo-convex or brachial valve geniculated, both valves with bands bearing concentric rows of 2 series of fine prostrate spines

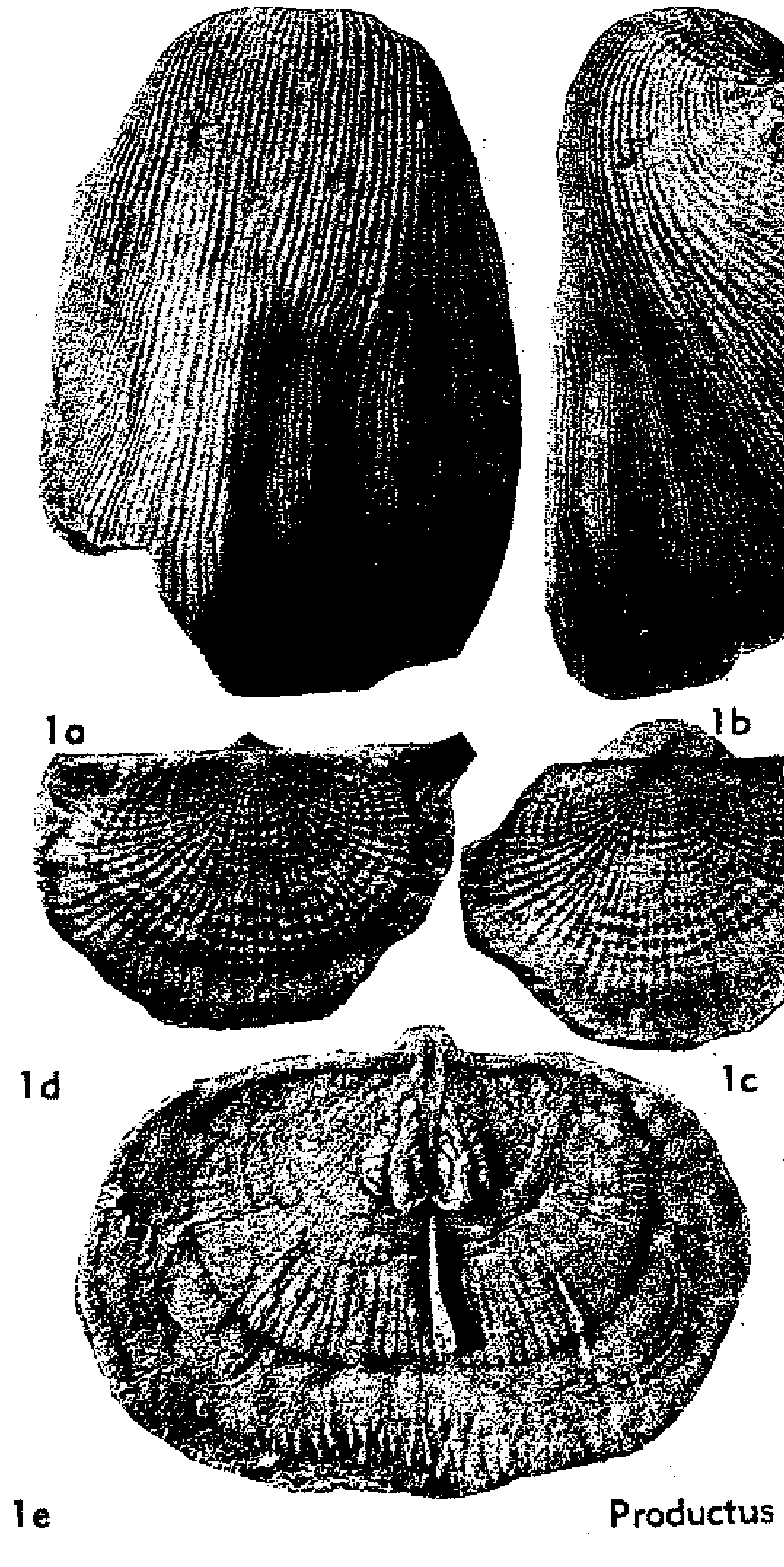
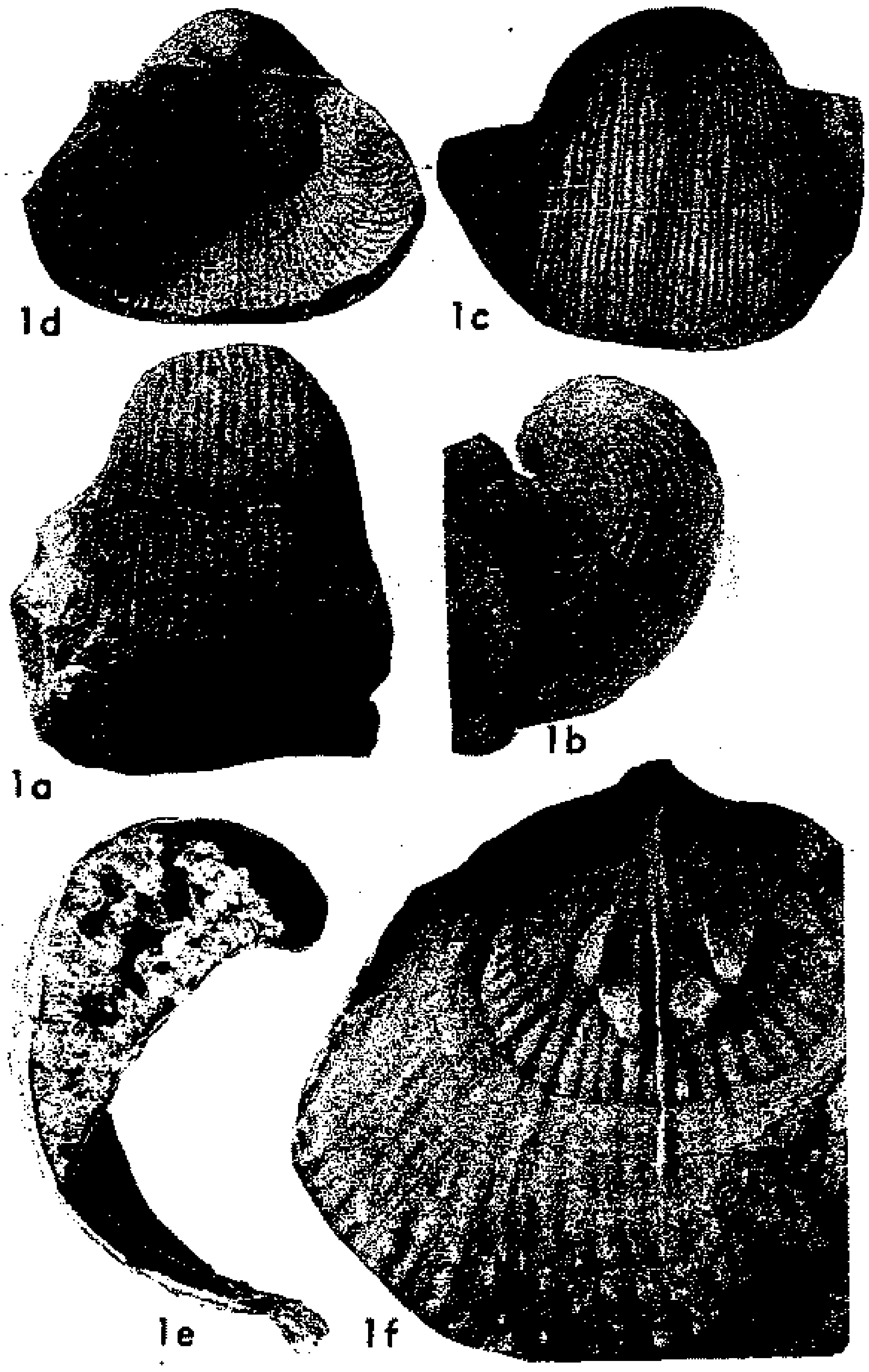


Fig. 351. Productidae (p. *H*484).



Diaphragmus

FIG. 352. Productidae (p. *H*484).

forming dense coat; adductors smooth. *L.Carb. (Miss.)*, Eu.-N.Afr.-Asia-N.Am.——FIG. 353,*1a-d*. **E. punctatus* (J. SOWERBY), Visean, Eng.; *1a,b*, ped.v. vent., lat., ×1; *1c*, brach.v. view, ×1; *1d*, brach.v. ext. showing spines, ×2 (858).——FIG. 353,*1e,f*. *E. alternatus* (NORWOOD & PRATTEN), Chester., Ky. *(1e)*, Okla. *(1f)*; *1e*, brach.v. int., ×1; *1f*, lat. view of card. process, ×2 (858).

Bathymyonia MUIR-WOOD & COOPER, 1960, p. 244 [**Productus nevadensis* MEEK, 1877, p. 64; OD]. Large, valves thickened, brachial valve geniculated; pedicle valve with overlapping spine ridges posteriorly, broad bands on trail with prostrate spines of 2 series in several rows, and in rows on ears and near hinge; brachial valve similar, fewer spines, anteriorly lamellose; adductors dendritic; cardinal process massive, trilobed, dorsally recurved. *L.Perm.*, N.Am.——FIG. 353,*3*. **B. nevadensis* (MEEK), Nev. *(3a-c)*, Utah *(3d)*, Wyo. *(3e)*; *3a-c*, ped.v. (lectotype) vent., post., lat.; *3d*, brach.v. view; *3e*, brach.v. int. showing massive card. process; all ×1 (587).

Calliprotonia MUIR-WOOD & COOPER, 1960, p. 246 [**C. renfrarum*; OD]. Like *Echinoconchus* but with more imbricating lamellose bands, up to 8 rows of spines of 2 series in pedicle valve; concentric laminae in brachial valve with single spine row; lateral ridges continued down lateral margin as prominent flange; adductors part-dendritic; cardinal process sessile, trilobed; brachial ridges prominent. *U.Penn., ?L.Perm.*, N.Am.-S.Am.——FIG. 354,*2*. **C. renfrarum*, U.Penn., USA(Tex.); *2a,b*, ped.v. (holotype) vent., lat., ×1; *2c*, brach. v. view, ×2; *2d,e*, brach.v. ext., int., ×3 (587).

Echinaria MUIR-WOOD & COOPER, 1960, p. 248 [**Productus semipunctatus* SHEPARD, 1838, p. 153; OD]. Like *Echinoconchus* but with more tapering visceral disc, narrower hinge, massive tapering incurved umbo; bands developed over whole shell bearing prostrate spines of 3 series; adductors partly dendritic; cardinal process more massive, less recurved, with sulcate shaft. *U.Carb.(M.Penn.-U.Penn.)*, N.Am.-Asia.——FIG. 354,*1*. **E. semipunctata* (SHEPARD), Tex. *(1a,c,e)*, Kan. *(1b)*, Ill. *(1d)*; *1a,b*, ped.v. vent., lat., ×1; *1c,d*, brach. v. view, brach.v. int., ×1; *1e*, brach.v. ext. with card. process, ×2 (587).

Pulchratia MUIR-WOOD & COOPER, 1960, p. 249 [**Productus symmetricus* MCCHESNEY, 1860, p. 35; OD]. Medium-sized to large, subcircular; pedicle valve rugose with spine ridges posteriorly; concentric bands wtih erect and prostrate spines, becoming lamellose anteriorly; brachial valve rather similar; adductor scars partly dendritic; cardinal process trilobed, extending dorsally, shaft with median sulcus. *U.Penn.*, N.Am.——FIG. 353, *2*. **P. symmetrica* (MCCHESNEY), USA(Tex.); *2a,b*, ped.v. vent., lat., ×1; *2c*, brach.v. view, ×1; *2d*, brach.v. int., ×2; *2e*, card. process lat. view, ×1 (587).

Pustula I. THOMAS, 1914, p. 259 [**Producta pustulosa* PHILLIPS, 1836, p. 216; OD]. Medium-sized to large, nongeniculated; pedicle valve rugose with spine ridges, tending to be quincuncially arranged on rugae, spines prostrate or suberect in rows near hinge, brachial valve rugose and spinose; cardinal process posteriorly trilobate, long shaft; adductors dendritic; brachial ridges well defined. *L.Carb.(Tournais.-Visean)*, Eu.-?Asia-N.Afr.——FIG. 355,*1*. **P. pustulosa* (PHILLIPS), Visean, Eng.; *1a,c*, ped.v. (holotype) vent., ×1, ×2; *1b*, brach.v. view, ×1; *1d*, brach.v. int., ×1; *1e*, lat. view of card. process, ×3 (805).

Septarinia MUIR-WOOD & COOPER, 1960, p. 251 [**Productus leuchtenbergensis* DEKONINCK, 1847, p. 226; OD]. Large, both valves convex in lateral contour; ornament of rugae posteriorly with spine ridges bearing prostrate spines, lamellae anteriorly with 1 or 2 rows of spines of 2 series; brachial valve similar but dimpled; median septum in pedicle valve with V-shaped chamber posteriorly; long-shafted trilobed cardinal process, curved dorsally; adductors obscurely dendritic. *L. Carb.(Visean)*, Eu.——FIG. 356,*1*. **S. leuchtenbergensis* (DEKONINCK), Belg.; *1a,b,d*, ped.v. vent., lat., ant., ×1; *1c*, ped.v. int. mold showing septum, ×1; *1e*, brach.v. int. mold, ×1 (483).

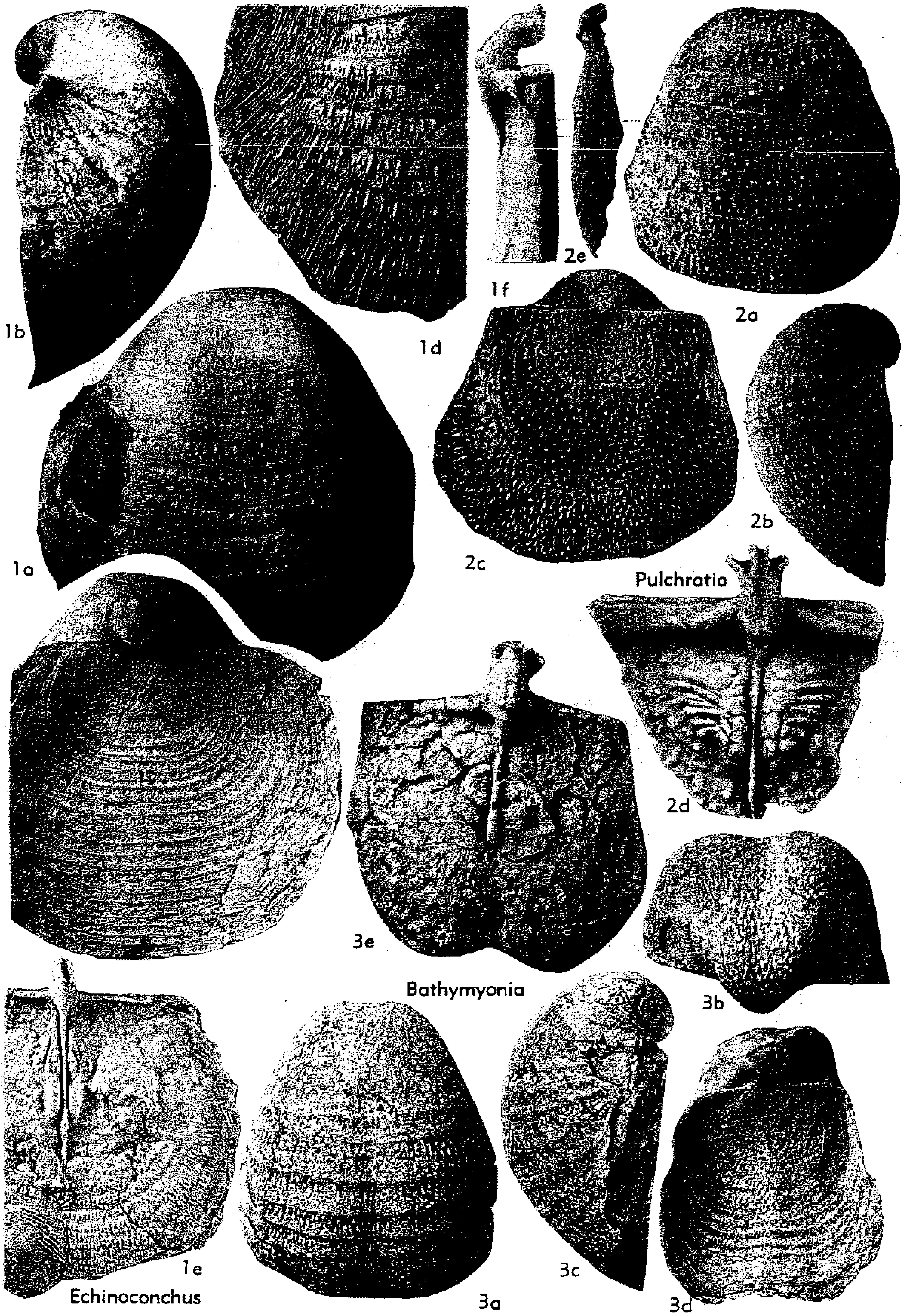


Fig. 353. Echinoconchidae (Echinoconchinae) (p. *H*484-*H*485).

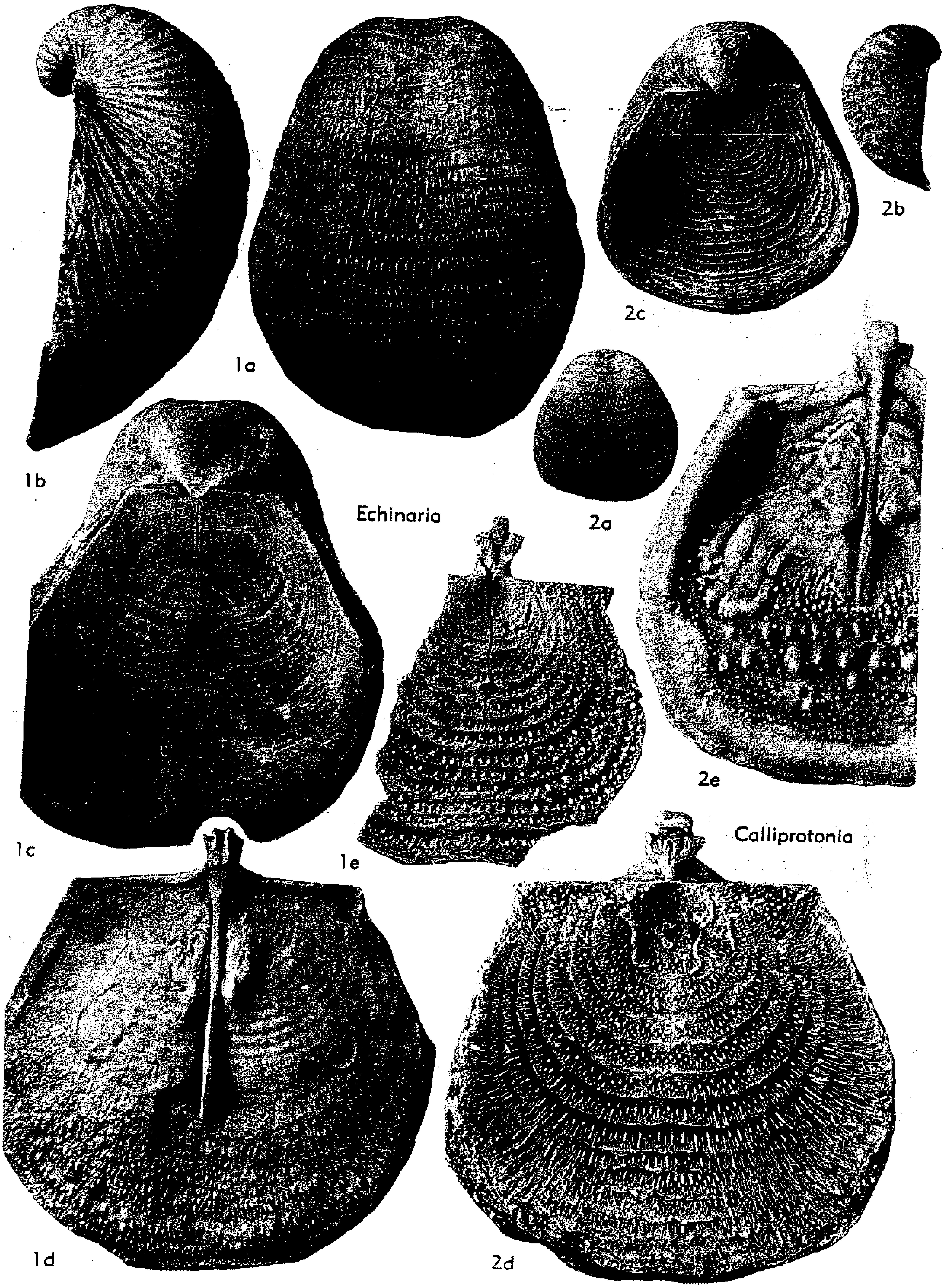


FIG. 354. Echinoconchidae (Echinoconchinae) (p. *H*485).

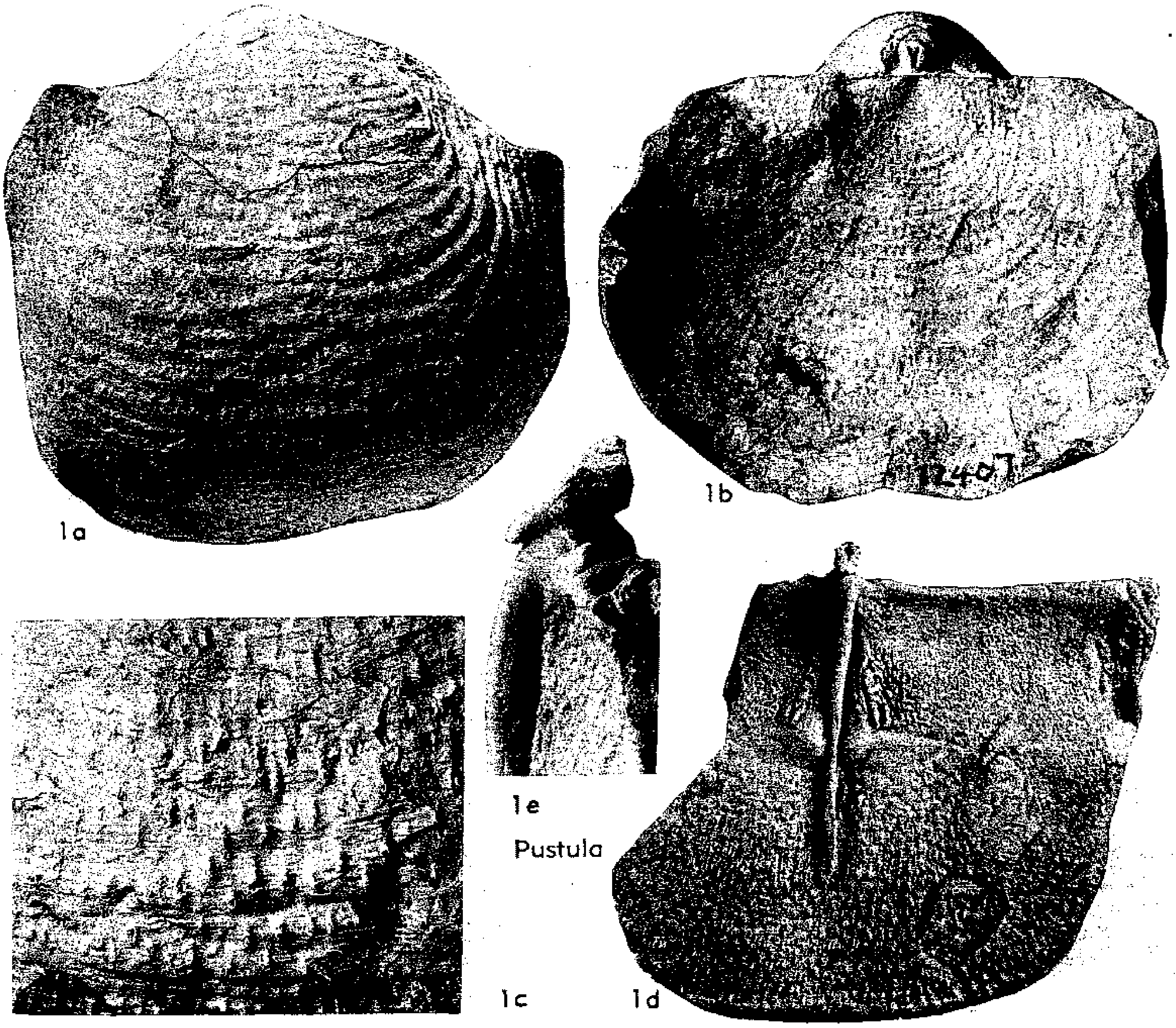


FIG. 355. Echinoconchidae (Echinoconchinae) (p. *H*485).

Subfamily WAAGENOCONCHINAE Muir-Wood & Cooper, 1960

[Waagenoconchinae MUIR-WOOD & COOPER, 1960, p. 252]

Delicate spines arranged in quincunx, in some forms springing from spine ridges and diminishing in diameter anteriorly. *U. Penn.-U.Perm.*

Waagenoconcha CHAO, 1927, p. 24 [**Productus humboldti* D'ORBIGNY, 1842, p. 54; OD] [=*Ruthenia* FREDERIKS, 1928, p. 789 (type, *Productus irginae* STUCKENBERG, 1898, p. 340)]. Medium-sized to large, valves not geniculated; cardinal process trilobate on long shaft, inclined dorsally, brachial ridges obscure; adductors dendritic. *U. Penn.-U.Perm.*, N.Am.-S.Am.-Eu.-Arctic-Asia-Australia. —— FIG. 356,*2a,b*. **W. humboldti* (D'ORBIGNY), Perm., Bolivia; *2a,b*, ped.v. and brach.v. views, ×1 (152).——FIG. 356,*2c,d*. *W.* sp., cf. *W. irginae* (STUCKENBERG), U.Penn., USA (Tex.); *2c,d*, ped.v. vent., ×1, ×2 (152).——FIG. 357,*1*. *W. montpelierensis* (GIRTY), L.Perm., USA(W.Tex.); *1a,b*, brach.v. ext., int., ×1.5; *1c*, lat. view of card. process, ×1.5 (152).

Family BUXTONIIDAE Muir-Wood & Cooper, 1960

[Buxtoniidae MUIR-WOOD & COOPER, 1960, p. 255]

Cardinal process dorsally recurved, bilobate or trilobate, with supporting buttress plates in youth, or buttress plates fusing with septum leaving cavity (antron) at posterior end of septum; costate or lamellose ornament with anterior spinose bands or rims. *U.Dev.-U.Perm.*

Subfamily BUXTONIINAE Muir-Wood & Cooper, 1960

[Buxtoniinae MUIR-WOOD & COOPER, 1960, p. 255]

Antron present except in older growth stages, ornament rugose, costate, and spinose, with anterior bands or rims. *U. Dev.-U.Perm.*

Buxtonia I. Thomas, 1914, p. 259 [**Anomites scabriculus* W. Martin, 1809, p. 8; OD] (but species declared invalid, ICZN, 1956); =**Productus scabriculus* J. Sowerby, 1814, p. 157; SD ICZN (Op. 420), 1956, p. 143]. Medium-sized or large, not geniculated externally; rugose posteriorly and costate, costae decreasing in width anteriorly and terminating in spines or replaced by rows of spines forming bands; spines numerous, prostrate on costae, and more erect spines in rows near hinge, on spine ridges on flanks; adductors dendritic. *U.Dev.-U.Carb.*, cosmop.——Fig. 358,*1*. **B. scabricula* (J. Sowerby), L.Carb., Eng.; *1a-c*, ped.v. vent., post., lat., ×1.25; *1d*, brach.v. int. showing septum and antron, ×1.6; *1e,f*, card. process post., lat., ×1.25 (574).

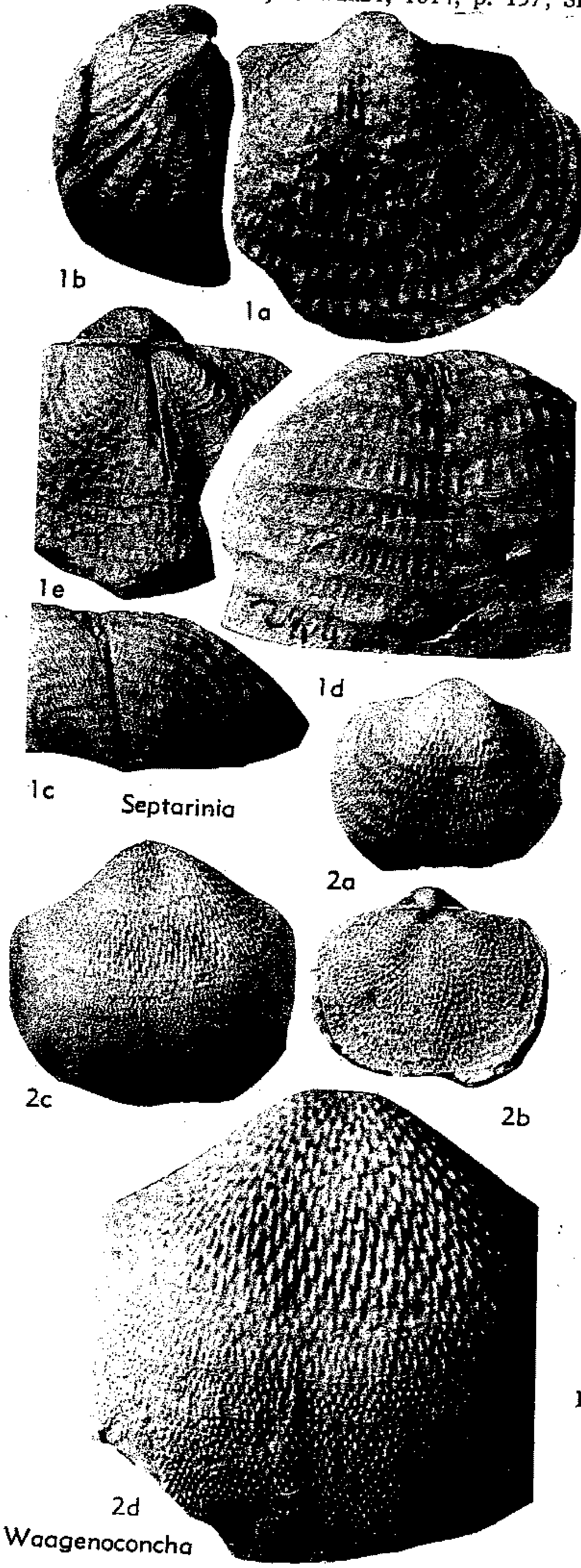


Fig. 356. Echinoconchidae (Echinoconchinae) *(1)*, (Waagenoconchinae) *(2)* (p. *H*485, *H*488).

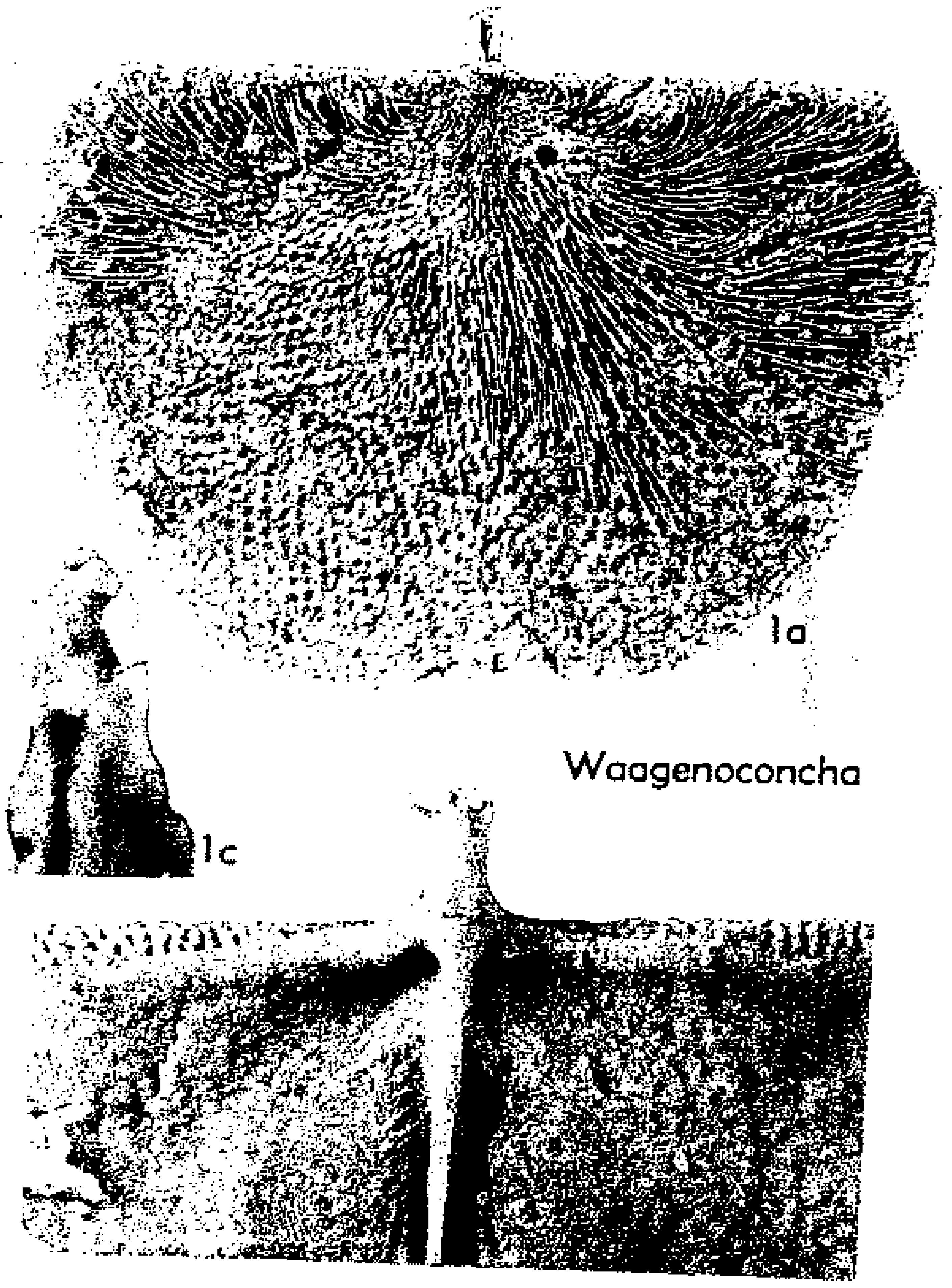


Fig. 357. Echinoconchidae (Waagenoconchinae) (p. *H*488).

Buxtonioides Mendes, 1959, p. 43 [**Productus amazonicus* Katzer, 1903, p. 264; OD]. Resembling *Buxtonia* externally but without spinose bands and having trilobed cardinal process and septum without antron or buttress plates. *M.Penn.*, S.Am.——Fig. 359,*1*. **B. amazonicus* (Katzer), Itaituba Ser., Brazil; *1a,b*, ped.v. vent., ×1, ×5; *1c*, brach.v. ext., ×1; *1d*, ped.v. ext. with spines on ears, ×1.25 (555).

Etheridgina Oehlert, 1887, p. 1278 [**Productus complectens* R. Etheridge Jr., 1876, p. 462; OD]. Small, depressed, attached to foreign bodies by clasping spines, at least in early growth stages, no interareas, teeth or sockets; ornamented by angular rugae or overlapping lamellae with rare spines; row of long clasping spines along hinge and lateral margins; cardinal process sessile, bilobate, supported by 2 buttress plates that com-

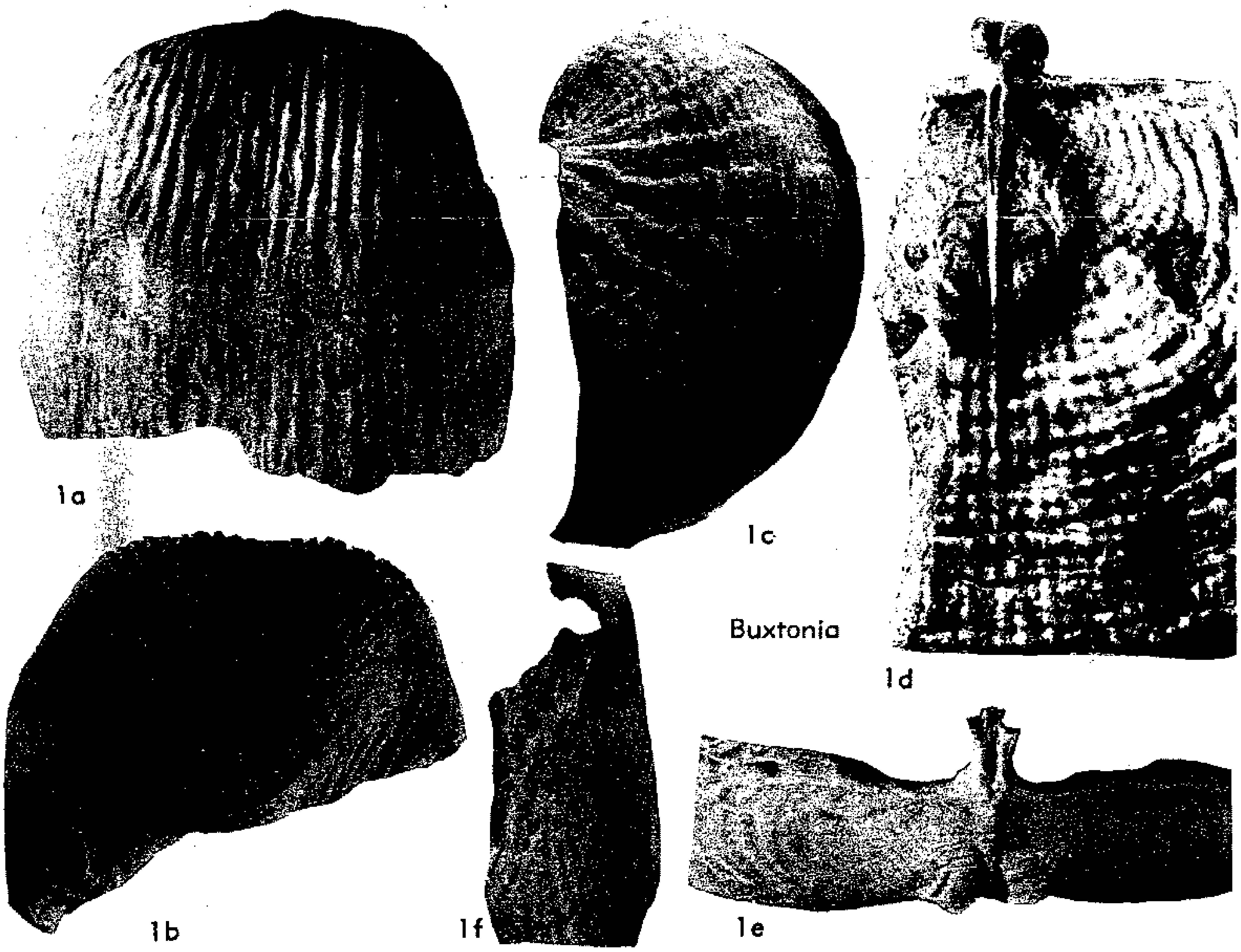


FIG. 358. Buxtoniidae (Buxtoniinae) (p. *H*489).

monly converge and unite with septum. *L.Carb.* *(Visean)*, Eu.——FIG. 360,*1*. **E. complectens* (R. Etheridge), Visean, Scot.; *1a*, shell with spines clasping crinoid stem, ×14; *1b*, ped.v. vent., ×5; *1c,d*, brach.v. int., ×5 (290).

Flexaria Muir-Wood & Cooper, 1960, p. 258 [**Productus arkansanus* Girty, 1910, p. 216; OD]. Like *Setigerites* in external form but without anterior rims or troughs, and with more prominent costae, replaced by spine ridges on flanks; interior of brachial valve geniculated, concave posteriorly; cardinal process almost at right angles to septum; adductors dendritic. *U.Miss.* *(Chester.)*, N.Am.——FIG. 360,*2*. **F. arkansana* (Girty), Mo. *(2a-d)*, Okla. *(2e-g)*; *2a-c*, ped.v. vent., lat., post., ×1; *2d*, brach.v. view, ×1; *2e,f*, brach.v. int., ×1, ×2; *2g*, brach.v. lat. showing card. process, ×2 (346).

Kochiproductus Dunbar, 1955, p. 107 [*pro Tschernyschewiella* Frederiks, 1924, p. 20 (*non* von Toll, 1899)] [**Productus porrectus* Kutorga, 1844, p. 96; SD Muir-Wood & Cooper, 1960, p. 260, for *Tschernyschewiella* and hence for *Kochiproductus*, Dunbar's original designation of *K. flexicostatus* as type-species being invalid]. Large, commonly geniculated, both valves with anterior rim; costate, rugose, slightly reticulate, becoming lamellose without spinose bands anteriorly; spines numerous, recumbent, from swollen nodes posteriorly, more erect on ears and on trail; low septum in pedicle valve; cardinal process trilobed on long shaft; antron on brachial valve septum; adductors dendritic. *L.Perm.-U.Perm.*, N. Am.-S. Am.-Arctic-Eu.-Asia. —— FIG. 361,*1*. *K. peruvianus* (d'Orbigny); USA(W.Tex.); *1a-c*, ped.v. vent., lat., post., ×0.7; *1d*, brach.v. view, ×0.7; *1e*, brach.v. int., ×1.3 (269).

Labriproductus Cooper & Muir-Wood, 1951, p. 195 [*pro Worthenella* Girty, 1938, p. 442 (*non* Walcott, 1911)] [**Productus wortheni* Hall, 1858, p. 638; OD]. Medium-sized, both valves geniculated; cincture demarcating anterior thickened ridge in pedicle valve, rugae near hinge, costae replaced anteriorly by spine rows, spines scattered and in rows near hinge, and group on ears and flanks; brachial valve with antron, cardinal process small, bilobate, extending dorsally; adductors smooth. *L.Miss.(Osag.)*, N.Am.——FIG. 361,*2*. **L. wortheni* (Hall), USA(Mo.); *2a-c*, ped.v. vent., lat., ant., ×1.3; *2d*, brach.v. int., ×1.3 (795).

Marginatia Muir-Wood & Cooper, 1960, p. 262 [**Productus fernglenensis* Weller, 1909, p. 299; OD]. Medium-sized to large, valves geniculated, no rims or troughs; ornament dictyoclostid but with few spines on trail and on or near ears, rare

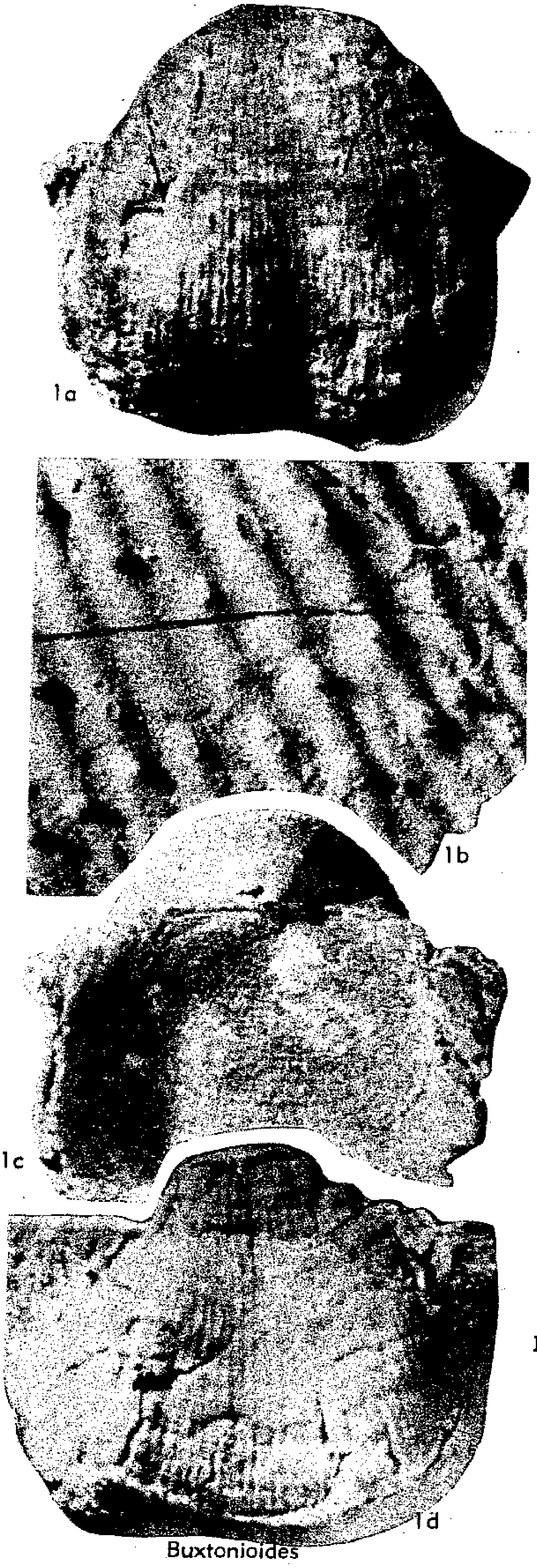


FIG. 359. Buxtoniidae (Buxtoniinae) (p. *H*489).

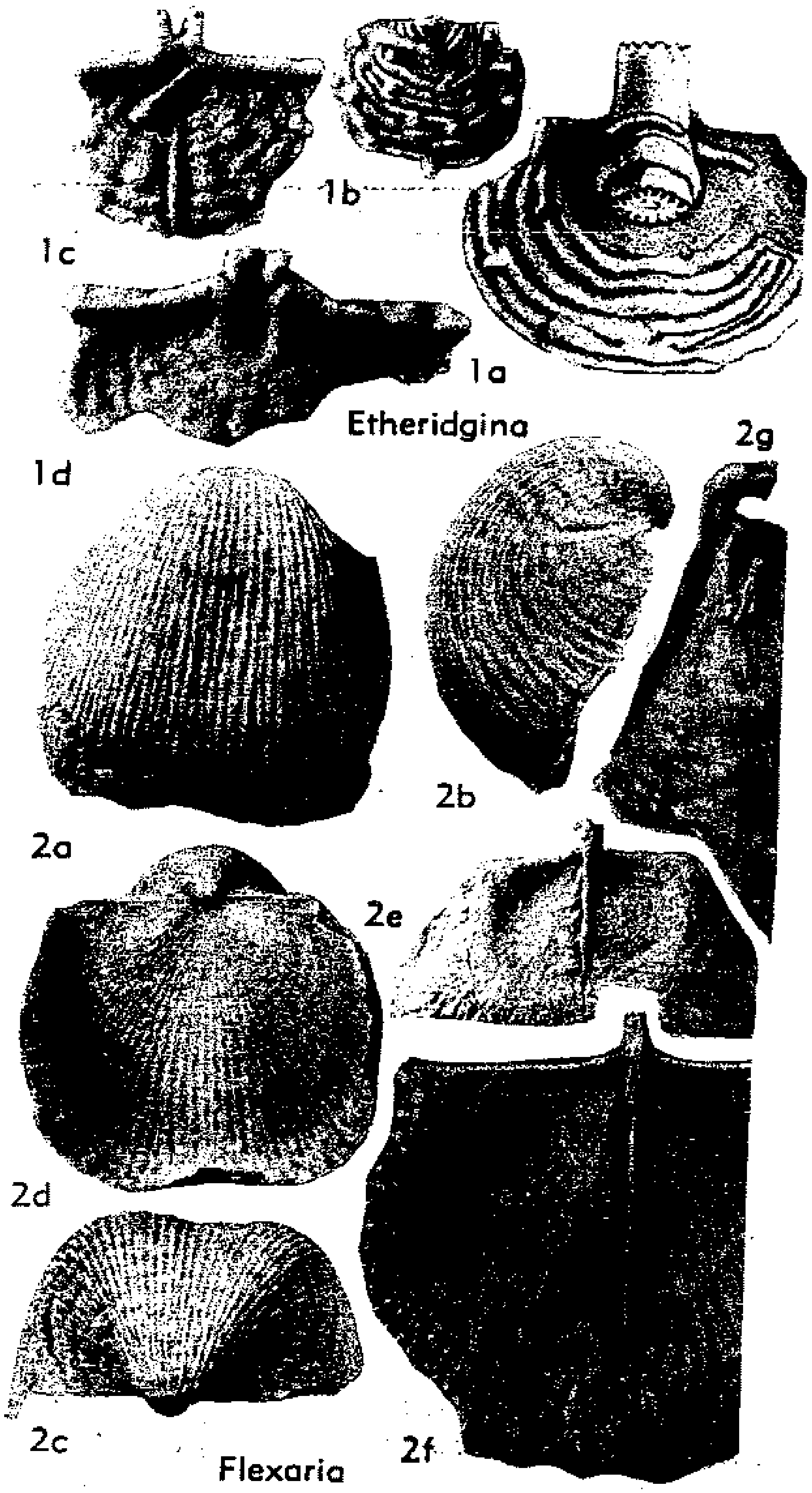


FIG. 360. Buxtoniidae (Buxtoniinae) (p. *H*489-*H*490).

in brachial valve; brachial valve septum with antron, accessory socket behind lateral ridges, internal posterior or posterolateral margin of brachial valve with thickened rim; adductors dendritic. *L.Miss.(Osag.)*, N.Am.——FIG. 361,*3*. **M. fernglenensis* (WELLER), USA(Mo.); *3a-c,* ped.v. vent., lat., post., ×0.7; *3d,* brach.v. int., ×1.3 (587).

Marginicinctus SUTTON, 1938, p. 561 [**Productus marginicinctus* PROUT, 1857, p. 43; OD]. Like *Labriproductus* in having *Buxtonia*-like ornament but with anterior flattened or curving ledge in each valve demarcated by cincture and ornamented by costae and spines or spine row; cardinal process bilobed, with buttress plates enclosing end of breviseptum; adductors dendritic. *L.Carb. (Miss.)*, Eu.-N.Am.——FIG. 362,*2*. **M. marginicinctus* (PROUT), U.Miss.(Meramec.), Mo. *(2a,b)*, Iowa *(2c,d)*, Tenn. *(2e)*; *2a,b,* ped.v.

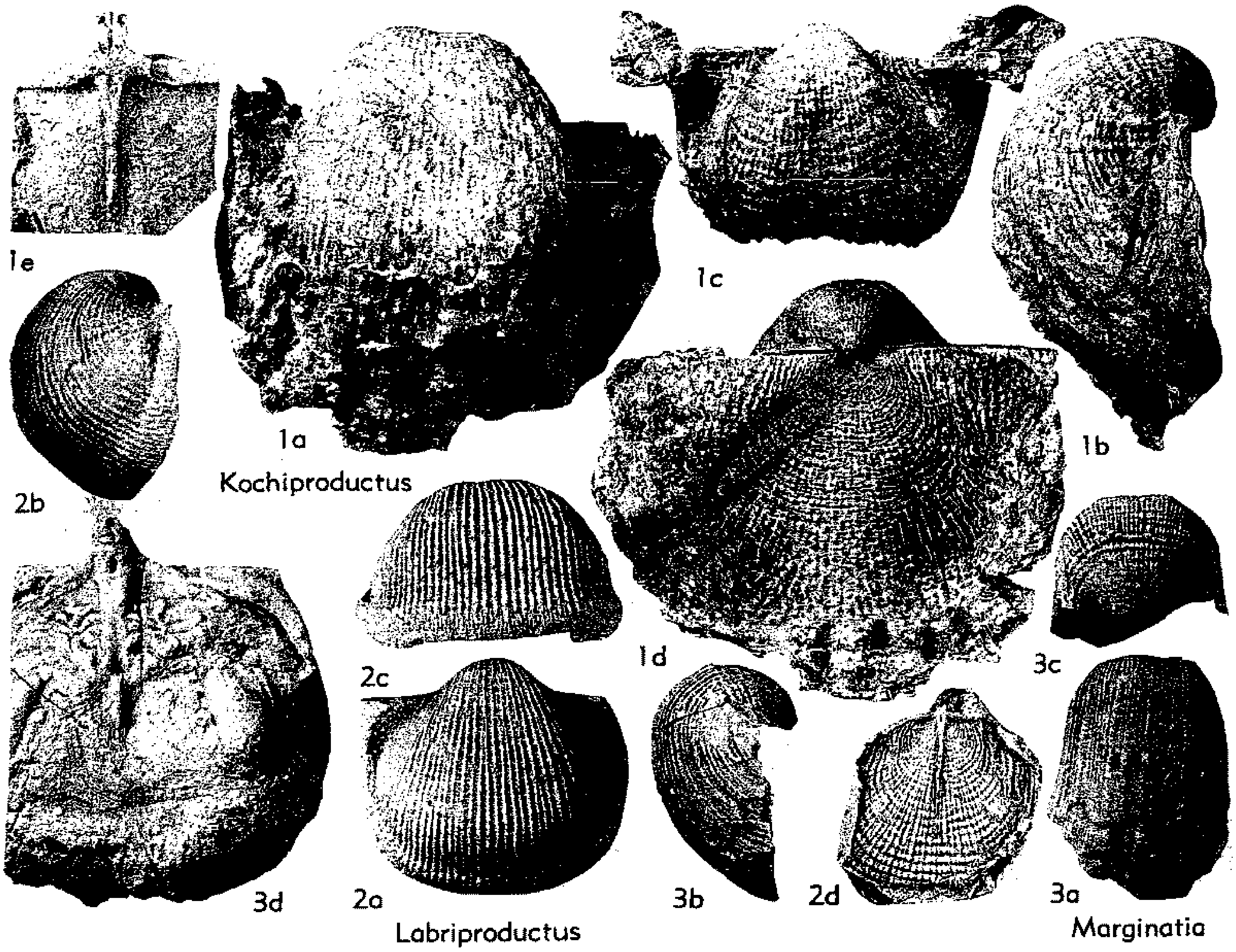


FIG. 361. Buxtoniidae (Buxtoniinae) (p. *H*490-*H*491).

vent., lat., ×1; *2c,d,* ped.v. ant., oblique lat., ×2; *2e,* brach.v. int., ×2 (795).

Protoniella BELL, 1929, p. 110 [**P. beedei*; OD]. Small; pedicle valve with short trail, cicatrix rare; faintly rugose, with spines posteriorly, costate and lamellose anteriorly; spines on costae, in row near hinge and down flanks; brachial valve costate and lamellose, septum with antron, cardinal process internally bilobate. *U.Miss.(Meramec.-Chester.), ?L.Penn.(Morrow.),* N.Am.——FIG. 362,*1.* **P. beedei,* U.Windsor, Nova Scotia; *1a,* ped.v. vent., ×1; *1b,* brach.v. view, ×1; *1c,* brach.v. int., ×1 (64).

Tomilia (*see* p. *H*904).

?Tomiproductus (*see* p. *H*905).

Subfamily JURESANIINAE Muir-Wood & Cooper, 1960

[Juresaniinae MUIR-WOOD & COOPER, 1960, p. 266]

Shell with cicatrix of attachment; ornament of lamellae, spine ridges and 2 or more series of spines, buttress plates enclosing end of breviseptum or fusing with it; cardinal process variably developed, bilobate, trilobate, or quadrilobate externally. *U.Carb. (L.Penn.-U.Penn.)-L.Perm.*

Juresania FREDERIKS, 1928, p. 786 [**Productus juresanensis* CHERNYSHEV, 1902, p. 276; OD]. Medium-sized, valves geniculated, minute ginglymus; pedicle valve posteriorly rugose, with spine ridges concentrically arranged, ridges overlapping or radially aligned medianly, becoming lamellose or banded on trail; spines suberect or prostrate, in rows near hinge; brachial valve posteriorly rugose with prostrate or erect spines, trail with prostrate spines of 2 series, antron may be developed; adductors dendritic. *U.Carb.(L.Penn.-U.Penn.)-L.Perm.,* Eu.-Asia-N.Am.——FIG 363, *1a-f. J. nebrascensis* (OWEN), L.Perm., USA (Kan.); *1a-c,* ped.v. vent., ant., lat., ×1; *1d,* brach.v. view, ×1; *1e,f,* brach.v. int. showing separated and joined card. process lobes, ×2 (158).——FIG. 363,*1g. J. rectangularia* R. H. KING, U.Penn., USA(Tex.); brach.v. view showing cicatrix, ×2 (158).

Ramavectus STEHLI, 1954, p. 327 [**R. diabloensis;* OD]. Only brachial valve known; ornament of prostrate spines of 2 series. [Possibly synonymous with *Juresania.*] *L.Perm.,* N.Am.——FIG. 363, *2.* **R. diabloensis,* USA(Tex.); *2a,b,* brach.v. ext. with prostrate spines, int., ×1 (773).

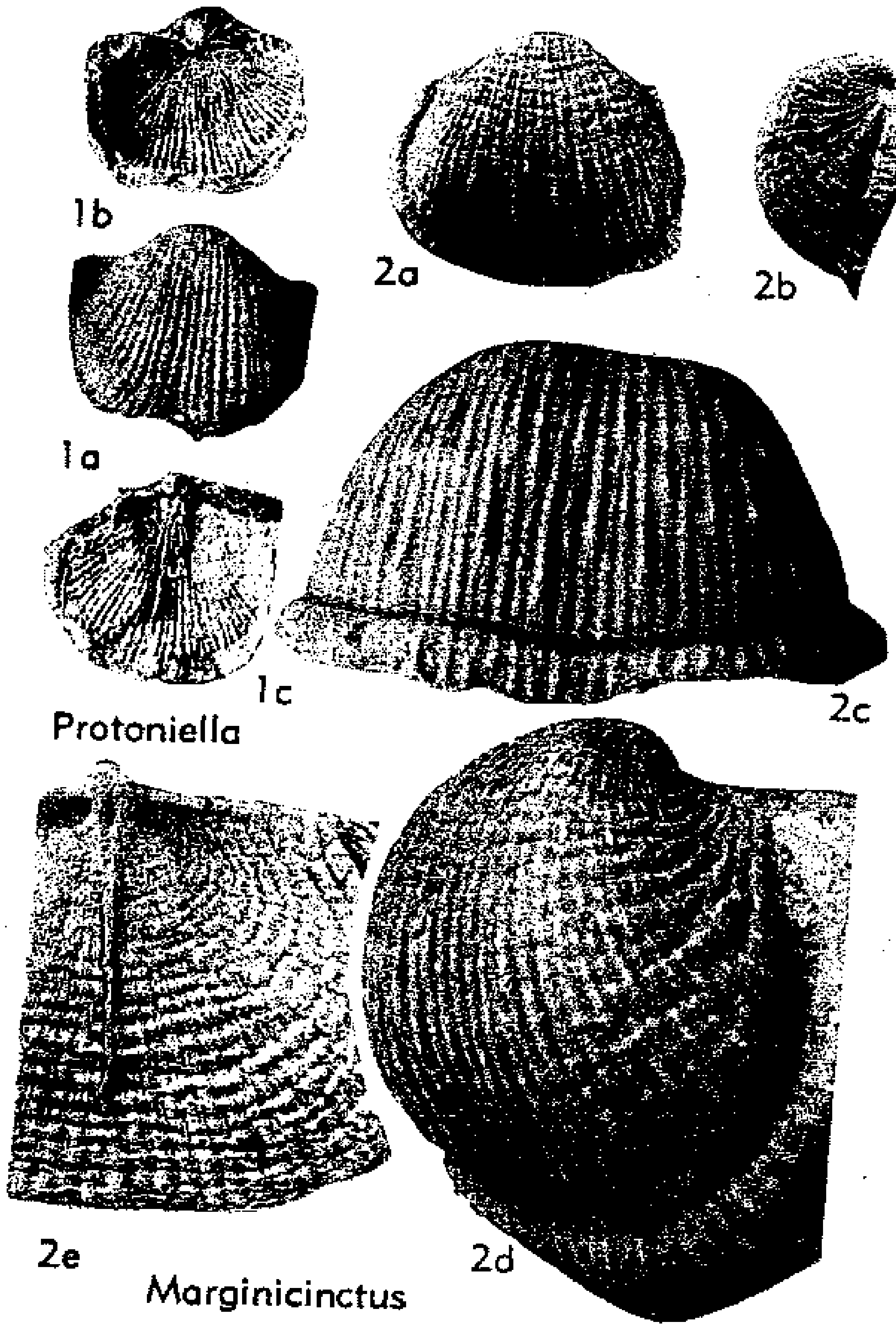


FIG. 362. Buxtoniidae (Buxtoniinae) (p. *H*491-*H*492).

Family DICTYOCLOSTIDAE Stehli, 1954

[Dictyoclostidae STEHLI, 1954, p. 316]

Valves usually large, costate, and geniculated, with reticulated visceral discs and long trail; cardinal process sessile, or short-shafted, trilobed, with large median lobe; dendritic adductors; brachial ridges given off horizontally. *L.Carb.(Tournais.-Visean)-U.Perm.*

Subfamily DICTYOCLOSTINAE Stehli, 1954

[Dictyoclostinae STEHLI, 1954, p. 316]

Posterior region reticulate and trail costate. *L.Carb.(Tournais.-Visean)-U.Perm.*

Dictyoclostus MUIR-WOOD, 1930, p. 103 [**Anomites semireticulatus* MARTIN, 1809, p. 7 (validated ICZN); OD]. Large, quadrate, concavo-convex, rarely geniculated; rugae posteriorly or extending over whole shell, reticulation prominent; fine erect spines in group on flanks and on venter, in row near hinge; brachial valve similar, fewer spines; massive cardinal process with short shaft, lophidium developed, lateral ridges along hinge margin. *L.Carb.(Tournais.-Visean)*, Eu.——FIG. 364,*1a-c*. **D. semireticulatus* (MARTIN), Eng.;

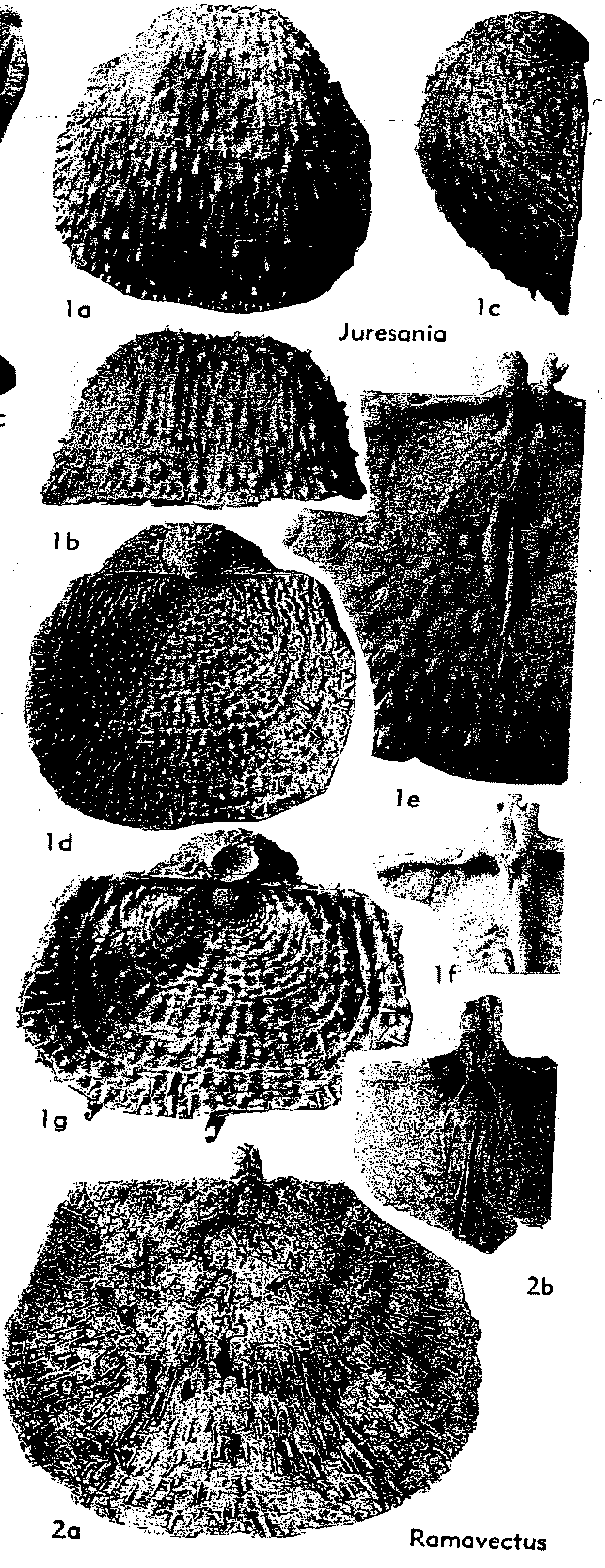


FIG. 363. Buxtoniidae (Juresaniinae) (p. *H*492).

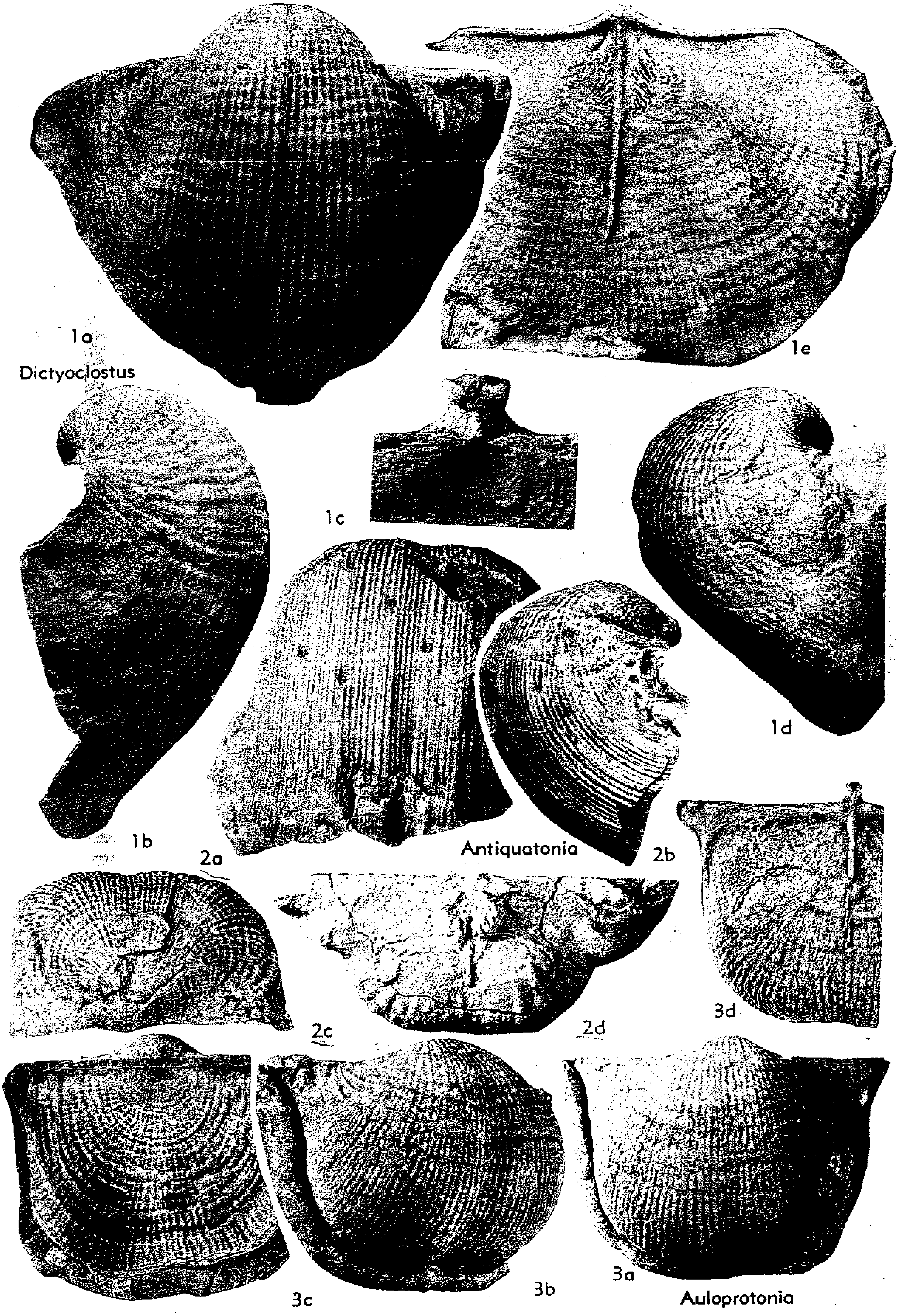


FIG. 364. Dictyoclostidae (Dictyoclostinae) (p. *H*493, *H*495).

1a,b, ped.v. vent., lat., ×1; *1c,* card. process, ×2 (574).——Fig. 364,*1d. D. multispiniferus* (Muir-Wood), Eng.; ped.v. lat. showing fine spines, ×1 (574).——Fig. 364,*1e. D. pinguis* (Muir-Wood), Eng.; brach.v. int., ×1 (574).

Antiquatonia Miloradovich, 1945, p. 496 [**Productus antiquatus* J. Sowerby, 1821, p. 15; OD]. Small to large, both valves geniculated; costate and rugose, prominently reticulate posteriorly, spines scattered, row near hinge, and up flanks commonly on curved ridge, rare on brachial valve; median lobe of small cardinal process dorsally directed, spinelike lophidium; lateral ridges diverging from hinge, not extending down lateral margin. *L.Carb.(Visean),* Eu.-Asia-Afr.-Australia; *U. Carb.,* Eu.-Asia-Australia.——Fig. 364,*2a-c. A. wettonensis* (Muir-Wood), L.Carb.(U. Visean), Eng.; *2a-c,* ped.v. ant., lat., post., ×1 (711).——Fig. 364,*2d. A. costata* (J. de C. Sowerby); U. Carb.(Namur.), Scot.; brach.v. int., ×1 (711).

Auloprotonia Muir-Wood & Cooper, 1960, p. 273 [**A. aulacophora*; OD]. Like *Dictyoclostus* but with brachial valve geniculated, trail recurved in tubelike coil around anterior margin enclosing end of trail of pedicle valve; reticulation less prominent; spines rare, scattered, in row near hinge margin and single spine from each cardinal extremity; absent on brachial valve; cardinal process bilobate; lateral ridges continued down posterolateral margin of visceral disc. *U.Miss. (Meramec.),* N.Am.——Fig. 364,*3. *A. aulocophora,* Moorefield, USA(Okla.); *3a,b,* ped.v. (holotype) vent., oblique lat., showing ant. coil, ×1; *3c,d,* brach.v. ext., int., ×1 (587). [See Fig. 299 for additional illustrations.]

Brasilioproductus Mendes, 1959, p. 48 [**Productus chandlessi* Derby, 1874, p. 51; OD]. Resembling *Squamaria* in quadrate shell outline but having coarser costation usually over whole shell and single oblique row of spines near hinge in pedicle valve, and row near hinge in brachial valve. *M. Penn.(Itaituba Ser.),* S.Am.(Brazil).——Fig. 365, *1. *B. chandlessi* (Derby); *1a-c,* ped.v. vent., lat., post.; *1d,* brach.v. ext. *(1a,b,d,* ×1; *1c,* ×1.8) (555).

Chaoiella Frederiks, 1933, p. 31 [**Productus gruenewaldti* Krotov, 1888, p. 546; OD]. Medium-sized to large, subquadrate, geniculated; attachment cicatrix present; both valves finely costate and rugose posteriorly with slight reticulation; lamellose anteriorly; spines in pedicle valve only, few, scattered and in row near hinge; cardinal process trilobate, sessile, curved dorsally with broad median lobe; adductors obscurely dendritic; lateral ridges extending along hinge. *U. Carb.(Penn.) - L. Perm.,* Eu. (Alps - USSR) - Asia (China)-N.Am.-S.Am.——Fig. 366,*2. *C gruenewaldti* (Krotov), U.Carb.(Moscov.), USSR; *2a-c,* ped.v. vent., post., lat.; *2d,* ped.v. ear with spines; *2e,* brach.v. ext.; all ×0.7 (492).

Costiferina Muir-Wood & Cooper, 1960, p. 277 [**Productus indicus* Waagen, 1884, p. 687; OD]. Like *Dictyoclostus* but shell thickened, valves geniculated, visceral disc strongly reticulated; spines few, coarse, erect, scattered, in row near hinge and near ears, absent on brachial valve; cardinal process sessile, trilobed, dorsally inclined; lateral ridges extending down lateral margin of visceral disc. *L.Perm.-U.Perm.,* Asia(Pak.-Himalayas).——Fig. 366,*1. *C. indica* (Waagen), Pak.; *1a-d,* ped.v. vent., ant., lat., post.; *1e,f,* brach.v. int., lat.; all ×0.7 (845).

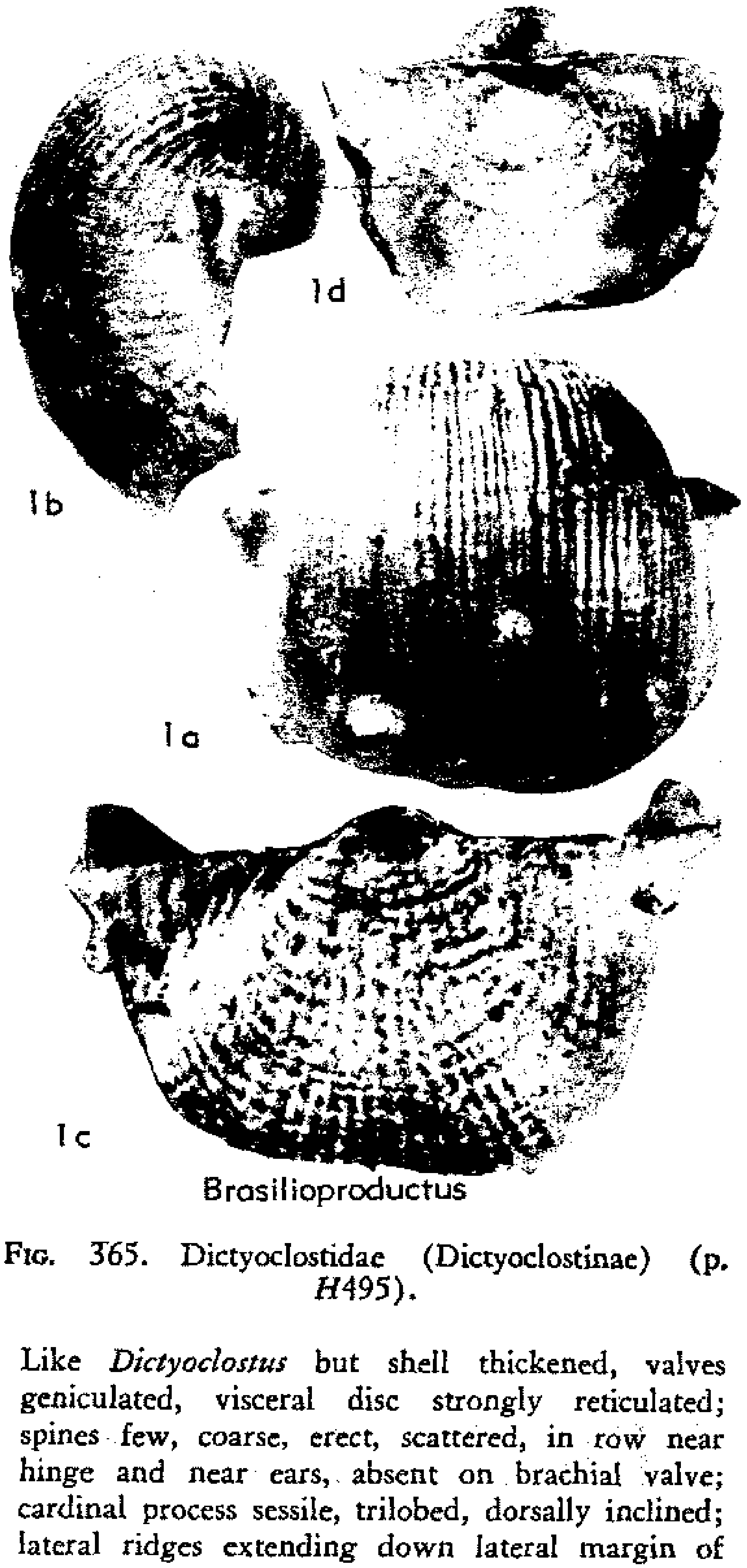


Fig. 365. Dictyoclostidae (Dictyoclostinae) (p. H495).

Peniculauris Muir-Wood & Cooper, 1960, p. 278 [**Productus ivesi* R. E. King, 1931, p. 69 *(non* Newberry, 1861) (=**Peniculauris mckeei* Muir-Wood & Cooper, 1960, p. 280; OD]. Like *Dictyoclostus* but valves geniculated, visceral disc slightly reticulate; costae nodose, replaced by overlapping laminae, possibly representing successive trails anteriorly; spines numerous, fine, erect, or subsrect, scattered, and in rows along hinge and group on ears; brachial valve with spines, cardinal process trilobate, median lobe with pit; lateral ridges extending across ears. *L.Perm.,* N.Am.-S.Am.——Fig. 366,*4. *P. mckeei,* L.Perm. (Leonard.), USA(W.Tex.); *4a-c,* ped.v. vent., post., lat., ×0.7; *4d,e,* brach.v. ext., int., ×0.7 (470).

Pugilis Sarycheva, 1949, p. 104 [**Producta pugilis* Phillips, 1836, p. 215; OD] [=*Pugilus* Sarycheva in Sarycheva & Sokolskaya, 1952, p. 77 (obj.)]. Medium-sized to large, nongeniculated; ornament of irregular costae, rugose posteriorly with slight reticulation; brachial valve similar, anteriorly lamellose with broken-off ends of successive trails; spines in pedicle valve scattered, large diameter, 2 rows on ears, longitudinal fluting below spines on trail; lateral ridges extending down lateral margin of visceral disc. *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.——Fig. 366,*3*. **P. pugilis* (Phillips), Visean; Eng. *(3a-c,e)*, Namur., Scot. *(3d)*; *3a-c*, ped.v. vent., post., lat.; *3d*, brach.v. view; *3e*, brach.v. int.; all ×0.7 (574).

Reticulatia Muir-Wood & Cooper, 1960, p. 284 [**Productus huecoensis* R. E. King, 1931, p. 68;

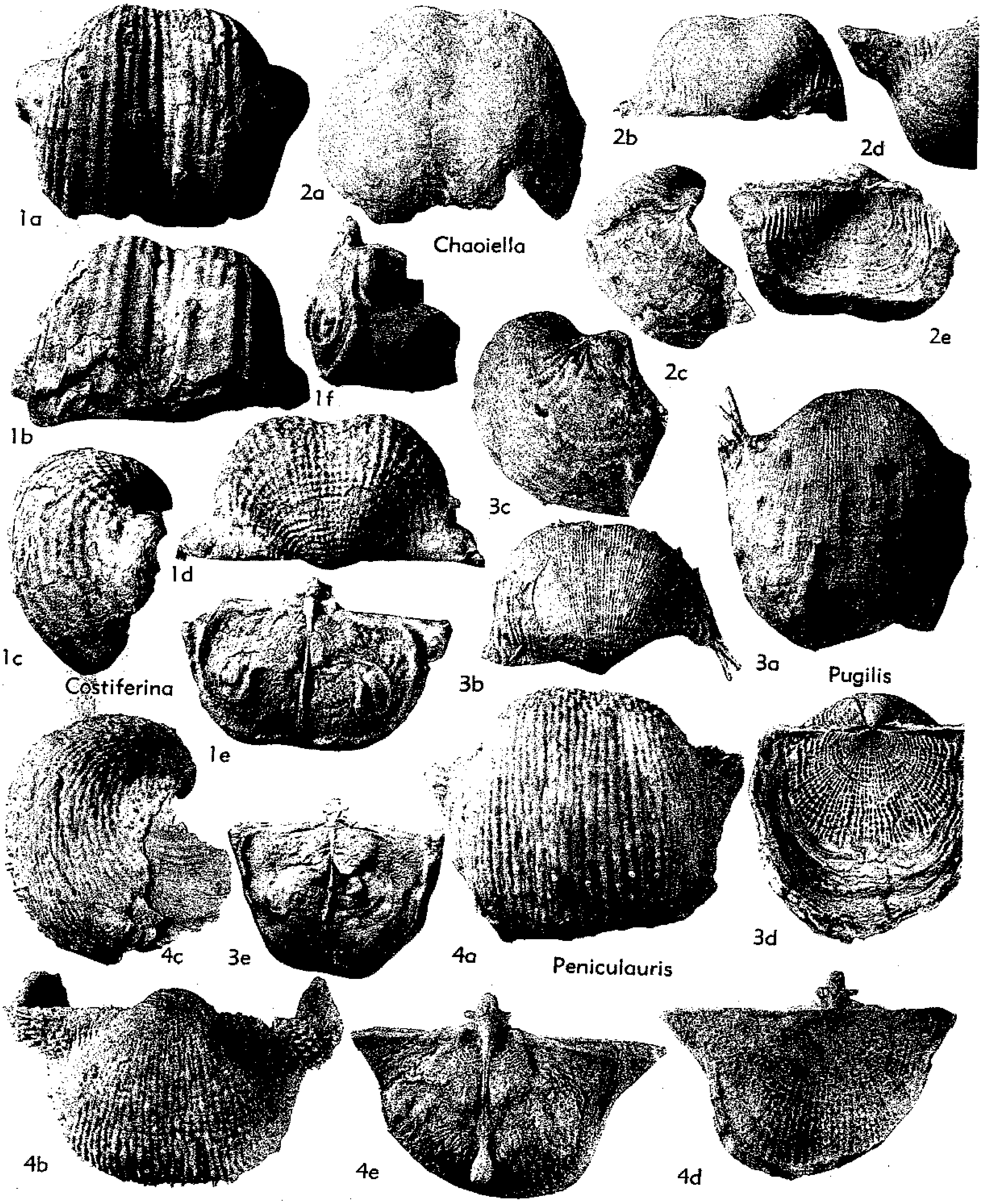


Fig. 366. Dictyoclostidae (Dictyoclostinae) (p. *H*495-*H*496).
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OD]. Like *Dictyoclostus* but with valves geniculated, body cavity narrow, ginglymus developed, reticulation prominent on visceral disc, overlapping lamellae on pedicle valve trail; spines small, scattered, in row near hinge and row up flanks; brachial valve with rare spines; cardinal process trilobed with broad median lobe, V-shaped lophidium; lateral ridges short, slightly diverging from hinge. *U.Penn.-L.Perm.*, N.Am. ——FIG. 367,*1*. **R. huecoensis* (KING), L.Perm., USA(W.Tex.); *1a-c*, ped.v. vent., post., lat., ×0.8; *1d*, brach.v. view showing ginglymus, ×0.8; *1e*, brach.v. int., ×1.2 (470).

Rugatia MUIR-WOOD & COOPER, 1960, p. 285 [**Productus paraindicus* McKEE, 1938, p. 241; OD]. Medium-sized to large, both valves geniculated, ginglymus present; costae ill-defined, rugae faint posteriorly; spines scattered, and 1 or 2 rows near hinge, in group on ears; brachial valve costate, dimpled, no spines; cardinal process with median sulcate lobe, small lophidium; lateral ridges short, slightly curved. *L.Perm.*, N.Am.——FIG. 368,*1*. **R. paraindica* (McKEE), L.Perm. (Leonard.), USA(W.Tex.); *1a-c*, ped.v. vent. view of 2 specimens, ant.; *1d*, brach.v. view; *1e*, brach.v. int.; all ×1 (548).

Spinifrons STEHLI, 1954, p. 318 [**S. quadratus*; OD]. Like *Antiquatonia* in external form but with ginglymus developed, costae more irregular, spines erect, in group on ears near hinge and numerous on trail; brachial valve with fine erect spines; small trilobate cardinal process; fine, short, slightly curving lateral ridges. *L.Perm.*, N.Am. ——FIG. 369,*1*. **S. quadratus*, Leonard., USA(W.Tex.); *1a-c*, ped.v. vent., post., lat.; *1d*, brach.v. view; *1e*, brach.v. int.; all ×1 (773).

Squamaria MUIR-WOOD & COOPER, 1960, p. 287 [**S. moorei*; OD]. Like *Pugilis* in external form but with ginglymus; no repetition of trails in brachial valve but successive laminae in pedicle valve anteriorly replacing costae; rugae narrow, spines numerous, scattered, and in rows near hinge and group on ears; numerous spines on brachial valve; cardinal process sessile, inclined dorsally, with broad median and diverging lateral lobes; lateral ridges extending inside ears. *L.Perm.*, N.Am.——FIG. 370,*1*. **S. moorei*, USA (Tex.); *1a-d*, ped.v. vent., ant., post., lat., ×1; *1e*, brach.v. view, ×1; *1f*, brach.v. int., ×1; *1g*, ped.v. int., ×1.5 (*1b,e*, holotype; others paratypes) (587).

Tolmatchoffia FREDERIKS, 1933, p. 28 [**Productus robustus* TOLMACHEV, 1924, p. 230; OD]. [May be synonym of *Dictyoclostus*.] *L.Carb.(Tournais.)*, Eu.(USSR)-Asia(Sib.).

Tyloplecta MUIR-WOOD & COOPER, 1960, p. 290 [**Productus scabriculus* mut. *nankingensis* FRECH, 1911; OD]. Medium-sized to large, subquadrate; pedicle valve with strongly curved trail; ginglymus present; large body cavity; costae coarse, irregular, rugae numerous, prominently reticulate; spines rare anteriorly, in row near

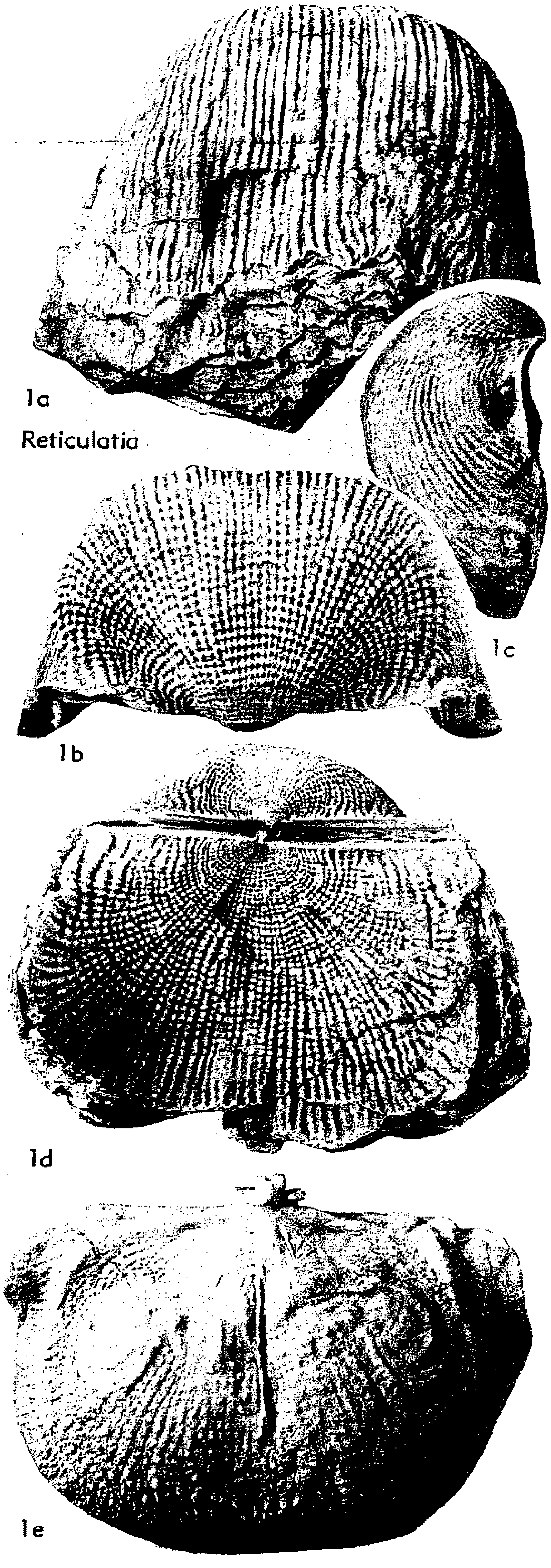

FIG. 367. Dictyoclostidae (Dictyoclostinae) (p. H496-*H*497).

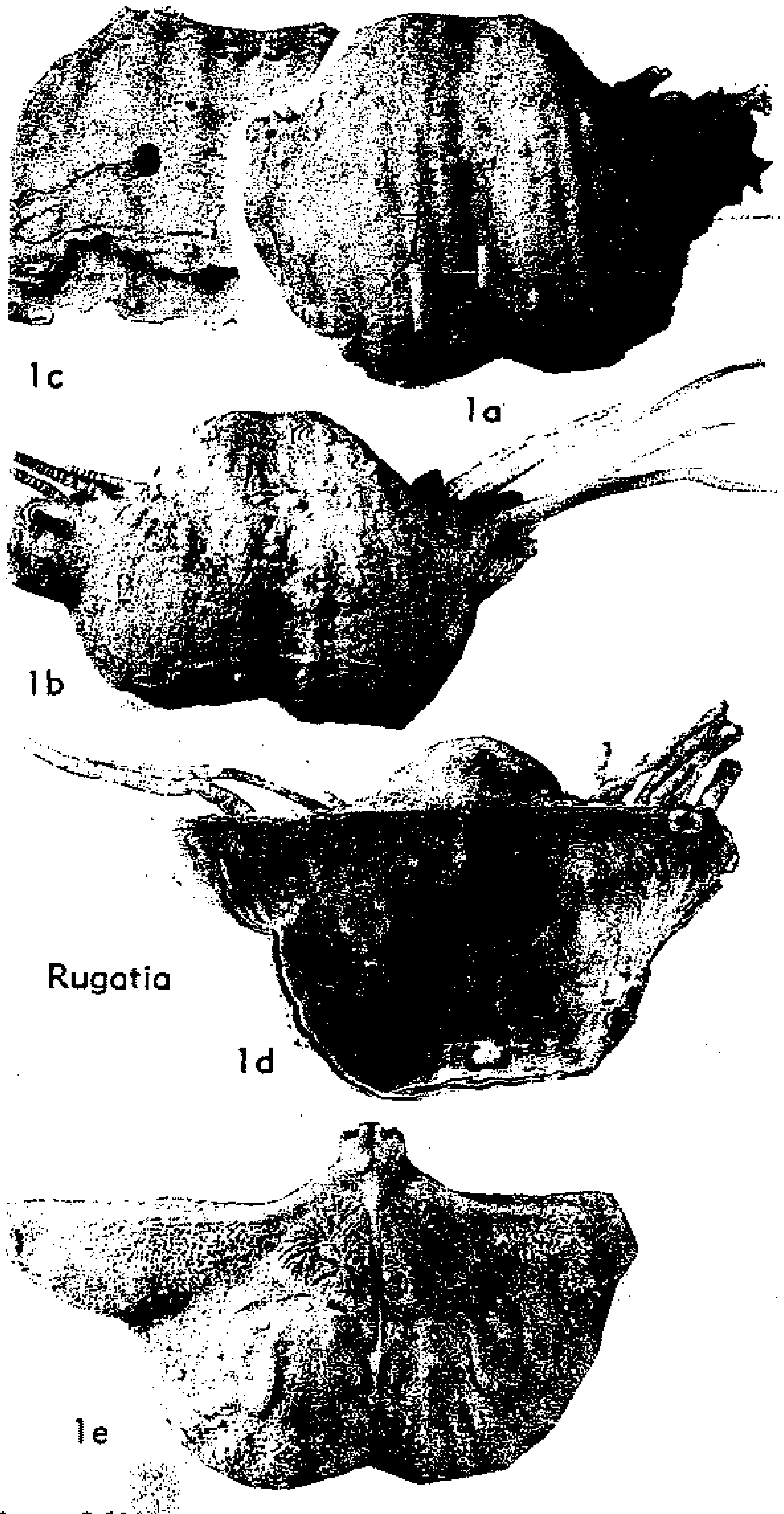

FIG. 368. Dictyoclostidae (Dictyoclostinae) (p. H497).

hinge, curved row inside ears and scattered; brachial valve similar in reverse, rare spines and valve capillate; cardinal process sessile, dorsally deflected, trilobate; lateral ridges extending to lateral margin. *L.Perm.-U.Perm.*, Asia (Sumatra-China); U.Perm., Eu.(USSR-Yugosl.). —— FIG. 370,*2*. **T. nankinensis* (FRECH), Perm., China; *2a,b*, ped.v. vent., post., ×1; *2c*, brach.v. view, ×1; *2d,e*, brach.v. int., lat., ×1; *2f*, brach.v. ext. showing capillate ornament, ×2 (313).

Subfamily HORRIDONIINAE Muir-Wood & Cooper, 1960

[Horridoniinae MUIR-WOOD & COOPER, 1960 (November), p. 292] [=Horridoniidae SARYCHEVA, 1960 (December), p. 234]

Costae and rugae usually lacking, spine rows near hinge in both valves; adductors dendritic, posteriorly placed. *Perm.*

Horridonia CHAO, 1927, p. 24 [**Productus horridus* J. SOWERBY, 1822, p. 17; SD SCHUCHERT & LEVENE, 1929, p. 68] [=*Sowerbina* FREDERIKS, 1928, p. 789 (type, *Productus timanicus* STUCKENBERG, 1875, p. 86); *Pleurohorridonia* DUNBAR, 1955 (type, *P. scoresbyensis*)]. Medium-sized to large; pedicle valve strongly curved, brachial valve slightly concave, anteriorly geniculated; valves smooth with numerous growth lines or pedicle valve rarely costate anteriorly; spines scattered in pedicle valve and in 2 or 3 rows near hinge and on ears, spines in single row on brachial valve and 1 or 2 spines on ears, rare elsewhere; cardinal process large, trilobate; lateral ridges short, divergent. *L. Perm.-U. Perm.*, Eu.-Arctic-Asia-Australia. ——FIG. 371,*1*. **H. horrida* (J. SOWERBY), U. Perm., Ger. *(1a-f)*, Eng. *(1g)*; *1a-d*, ped.v. vent., post., lat., ant., ×1; *1e*, brach.v. view, ×2; *1f*, ped.v. post. showing spines, ×1; *1g*, brach.v. int., ×1 (587).

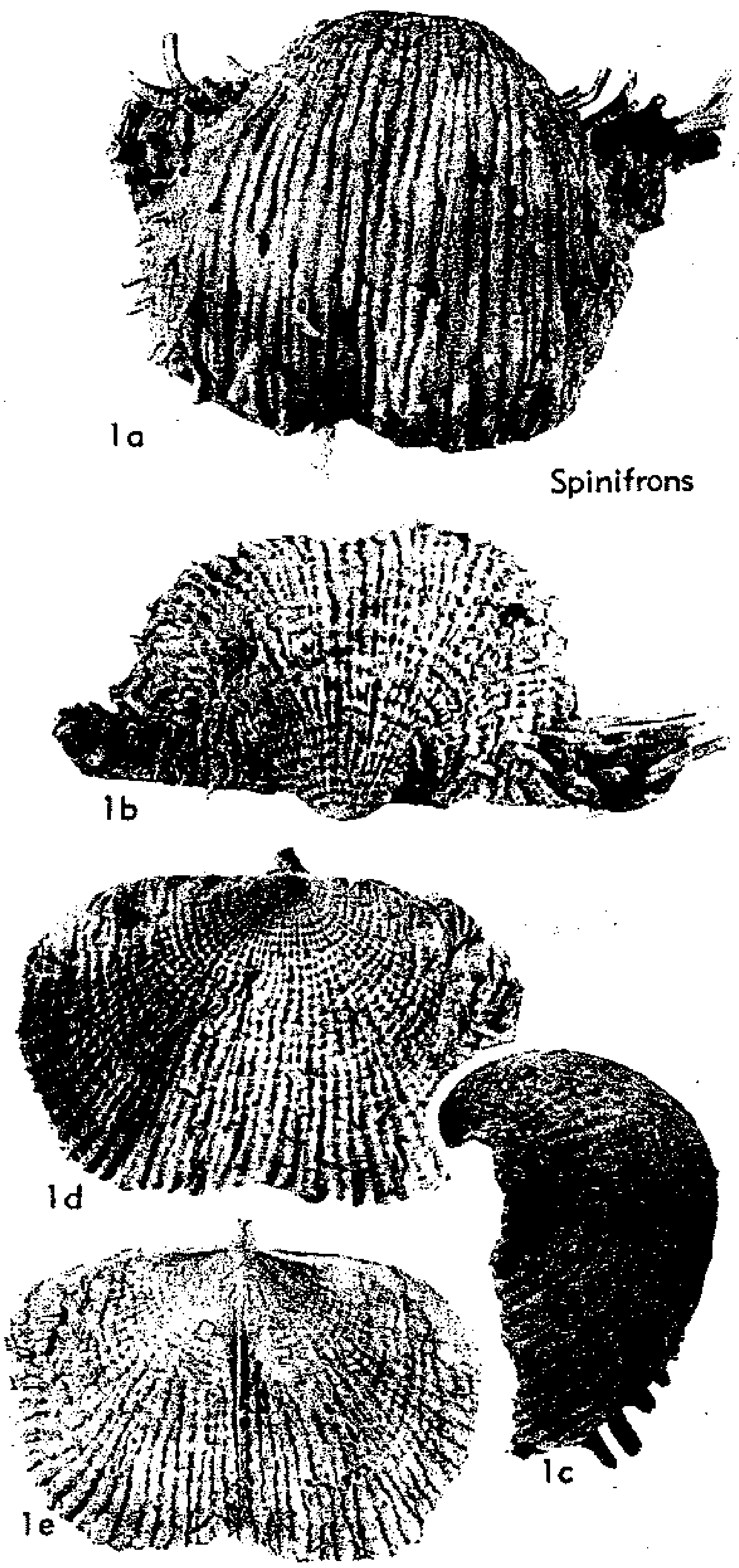

FIG. 369. Dictyoclostidae (Dictyoclostinae) (p. H497).

Subfamily LEVITUSIINAE Muir-Wood & Cooper, 1960

[Levitusiinae Muir-Wood & Cooper, 1960, p. 295]

Valves faintly costellate and posteriorly rugose, with few spines; deep cavities in pedicle valve representing position of lophophore spirals; brachial ridges given off obliquely, cardinal process large, trilobate with tapering lateral lobes. *L.Carb.(Visean).*

Levitusia Muir-Wood & Cooper, 1960, p. 295 [**Productus humerosus* J. Sowerby, 1822, p. 21; OD]. Large, each valve with long trail, pedicle

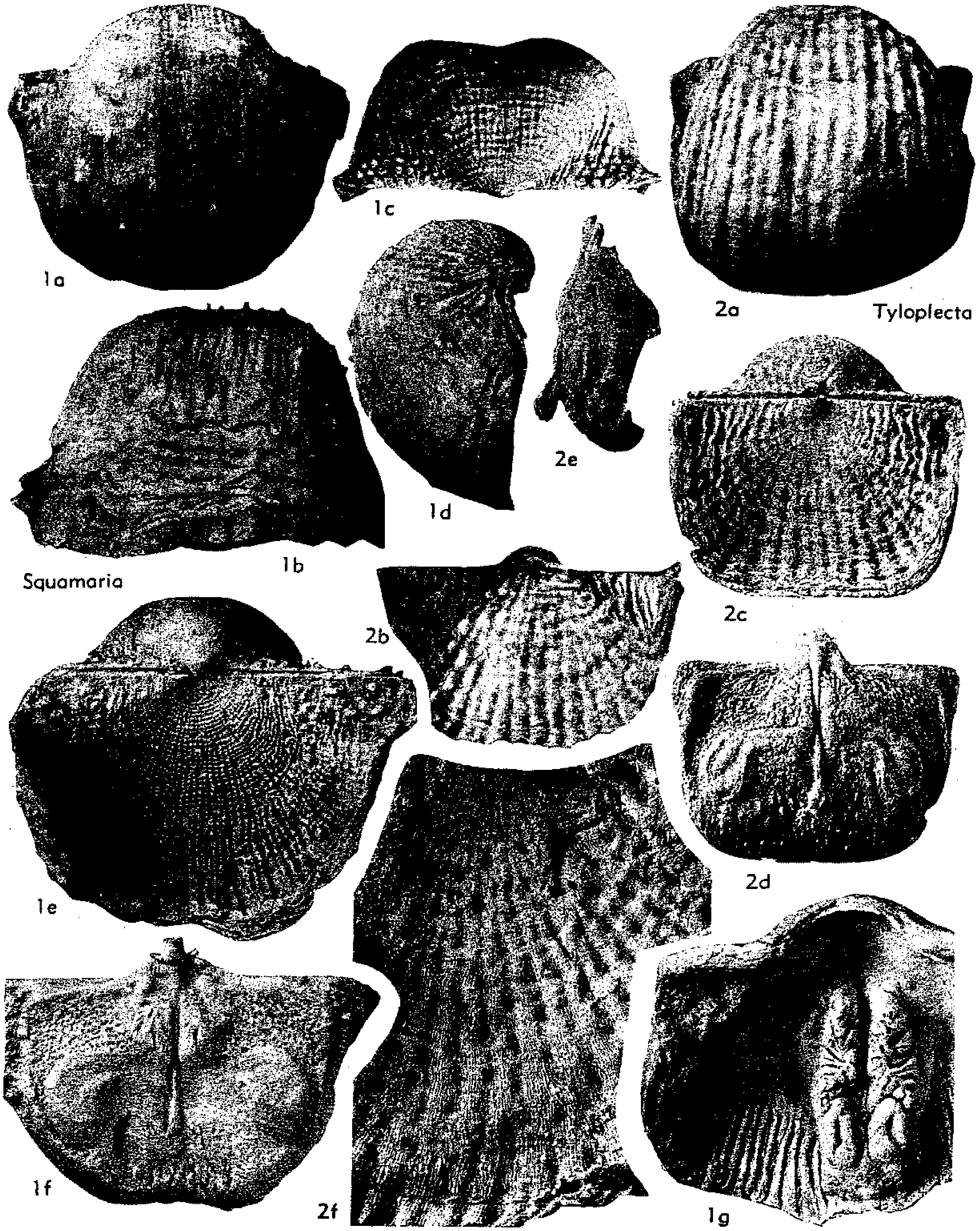

Fig. 370. Dictyoclostidae (Dictyoclostinae) (p. *H*497-*H*498).

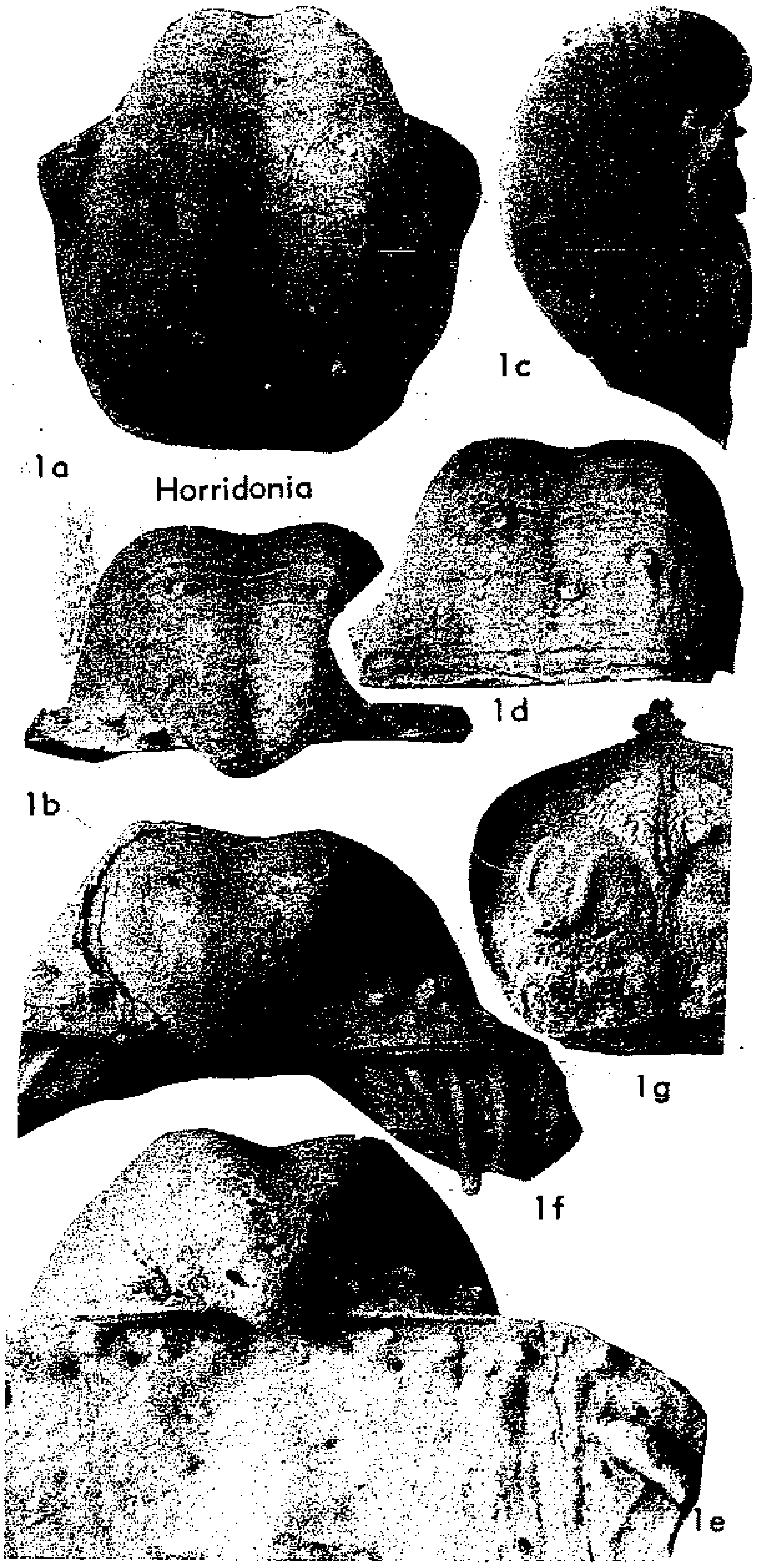

FIG. 371. Dictyoclostidae (Horridoniinae) (p. H498).

valve thickened, may bear median longitudinal fold; costellae appearing as striations or pits if shell is decorticated, lamellose on trail; spines rare, scattered, in row on median ridge, in row in sulcus demarcating ears and rarely on ears; brachial valve without spines. *L.Carb.(Visean)*, Eu.(Eng.-Belg.-Fr.)-Asia.——FIG. *372,1*. **L. humerosa* (J. Sowerby), Visean, Belg. *(1a-c)* and Eng. *(1d,e)*; *1a-c*, ped.v. oblique vent., lat., post.; *1d,e*, brach.v. int., post. and ant. views; all ×1 (483).

[**Subfamily Uncertain—Rugoclostus**, *see* p. *H*904.]

Family LINOPRODUCTIDAE Stehli, 1954

[*nom. transl.* Muir-Wood & Cooper, 1960, p. 296 (*ex* Linoproductinae Stehli, 1954, p. 319)]

Valves costellate and rugose, with rows of fine spines near hinge; trilobate sessile cardinal process with widely separated lobes; small body cavity; dendritic adductors posteriorly placed; obscure brachial ridges. *L. Carb.(L.Miss.-U.Miss.)-U.Perm.*

Subfamily LINOPRODUCTINAE Stehli, 1954

[Linoproductinae Stehli, 1954, p. 319]

Hinge wide, trail normally long. *L.Carb. (L.Miss.)-U.Perm.*

Linoproductus Chao, 1927, p. 25 [**Productus cora* d'Orbigny, 1842, p. 55; OD] [=*Cora* Frederiks, 1928, p. 781 (obj.); *Euproductus* Whitehouse, 1928, p. 281 (obj.)]. Small to large, geniculated; both valves irregularly costellate, rugae as broad wrinkles on flanks and ears, better developed in brachial valve; spines scattered, prostrate or suberect, and in 1 or 2 rows at high angle to hinge, rare in brachial valve; prominent lamellae interrupting costellae in brachial valve and representing internal diaphragms and broken off ends of trails; cardinal process trilobate, with sulcate median lobe; alveolus present; lateral ridges short, diverging from hinge; second pair of ridges bounding posterior part of adductors. *?L.Carb. (L.Miss.-U.Perm.)*, N.Am.-S.Am.-Eu.-Asia-N.Afr.-Australia.——FIG. *373,2a-d*. **L. cora* (d'Orbigny), L.Perm., Bol.; *2a-c*, ped.v. vent., lat., post., ×1; *2d*, brach.v. view, ×1 (485).——FIG. 373, *2e*. *L. prattenianus* (Norwood & Pratten), U. Penn., USA(Tex.); brach.v. int., ×1 (485).——FIG. 373,*2f*. *L.* sp., U.Penn., USA(N.Mex.); brach. v. view, ×2 (485). [See Fig. 303. *L.* sp.; diagrams of card. process, int., oblique ext., ext., ×2 (485).]

Anidanthus Hill, 1950, p. 9 [**Linoproductus springsurensis* Booker, 1932, p. 67; OD] [=*Anidanthus* Whitehouse, 1928, p. 282 *(nom. nud.)*; *?Pseudomarginifera* Stepanov, 1934, p. 56 (type, *Productus ussuricus* Frederiks, 1924, p. 8)]. Medium-sized, geniculated; ornament of costellae, rugose posteriorly, spines rare, scattered, in row near hinge; brachial valve with lamellae interrupting costellae, possibly representing broken-off ends of successive trails; cardinal process sessile, quadrilobate; adductors smooth; lateral ridges extending to anterior margin of visceral disc. *U. Carb.-L. Perm.*, Asia-Arctic-Eu.-Australia-N. Am. ——FIG. 373,*4*. **A. springsurensis* (Booker), New S.Wales; *4a*, ped.v. vent., ×2; *4b,c*, brach.v. ext., int., ×2, ×3; *4d*, ped.v. int. mold, ×2 (861).

Balakhonia (*see* p. *H*903).

Cancrinella Frederiks, 1928, p. 784 [**Productus cancrini* de Verneuil, 1845, p. 273; OD]. Small to medium-sized, brachial valve usually geniculated; costellate, rugose on flanks and ears; spines numerous, commonly quincuncially arranged on swollen costae and in group on flanks and ears; brachial valve without spines, dimpled, costellate and rugose; cardinal process sessile, internally bilobate; adductors obscurely dendritic, lateral ridges short, divergent from hinge. *U.Carb. (Penn.)-Perm.*, Eu.-Asia-Australia-N.Am.——FIG. 373,*1a-c*. *C. altissima* R. H. KING, U.Penn., USA (Tex.); *1a,b*, ped.v. vent., post., ×2, ×1; *1c*, brach.v. view, ×2 (483).——FIG. 373,*1d-f*. *C. boonensis* (SWALLOW), U.Penn., USA(Tex.); *1d,e*, ped.v. vent., lat., ×2; *1f*, brach.v. int., ×3 (483).

Cancrinelloides (*see* p. *H*903).

Fluctuaria MUIR-WOOD & COOPER, 1960, p. 303 [**Productus undatus* DEFRANCE, 1826, p. 354; OD]. Small or medium-sized; costellate and rugose, rugae prominent on entire valve; spines erect, rare, in 2 rows near hinge and group on ears, absent on brachial valve; cardinal process minute, sessile, bilobate; lateral ridges along hinge margin. *L.Carb.(Visean)*, Eu.(Eng.-Eire-Belg.-Fr.-USSR).——FIG. 373,*3*. **F. undata* (DEFRANCE), Belg.; *3a-c*, ped.v. vent., lat., post., ×2; *3d*, brach.v. view, ×2 (587).

Globiella MUIR-WOOD & COOPER, 1960, p. 304 [**Productus hemisphaerium* KUTORGA, 1844, p. 99; OD] [=*Stepanoviella* ZAVODOVSKY, 1960 (type, *S. paracurvata*) (possibly a senior synonym)]. Medium-sized, nongeniculate, costellate, rugose near hinge; spines rare, in row along hinge and on ears, absent on brachial valve; cardinal process small, sessile, trilobate, median lobe with central pit; adductors smooth; lateral ridges short, curving down from hinge; pedicle valve with low ridges extending from umbo to inside ears. *L. Perm.-U.Perm.*, Eu.(USSR)-Arctic-Asia(China-India-Armenia).——FIG. 374,*1*. **G. hemisphaerium* (KUTORGA), U.Perm.(Kazan), USSR; *1a,b*, ped.v. vent., lat., ×1; *1c,d*, ped.v. int., brach.v. int., ×1; *1e*, card. process post. view, ×2 (587).

Marginirugus SUTTON, 1938, p. 559 [**Productus magnus* MEEK & WORTHEN, 1862, p. 142; OD]. Large, brachial valve geniculated; costae irregularly developed, rugae near hinge, spines recumbent, scattered, in one or more rows extending at high angle to hinge margin, absent in brachial valve; cardinal process large, trilobate, broad sulcate median lobe; adductors dendritic; lateral ridges extending around ears. *L.Carb.(Miss.)*, N. Am.-Australia.——FIG. 375,*3*. **M. magnus* (MEEK & WORTHEN), L.Miss.(Osag.), Ill. *(3a-c,e,f)*, Mo. *(3d)*; *3a-c*, ped.v. vent. with spines along hinge, post., lat.; *3d*, brach.v. int.; *3e,f*, card. process, int. and ext. views; all ×1 (795).

Megousia MUIR-WOOD & COOPER, 1960, p. 309 [**M. auriculata*; OD]. Like *Anidanthus* but with larger ears, commonly with crescentic extensions in brachial valve and radial ornament on ears cutting across concentric lamellae of remainder of valve; cardinal process trilobate or quadrilobate on short massive shaft; adductors obscure; lateral ridges divergent, extending as flattened rims down lateral margin of visceral disc. *L.Perm.*, N.Am.-S.Am.——FIG. 375,*1a-d*. **M. auriculata*, USA(W. Tex.); *1a*, ped.v. vent., ×2; *1b,c*, brach.v. views showing alae, ×1, ×4; *1d*, brach.v. int., ×3

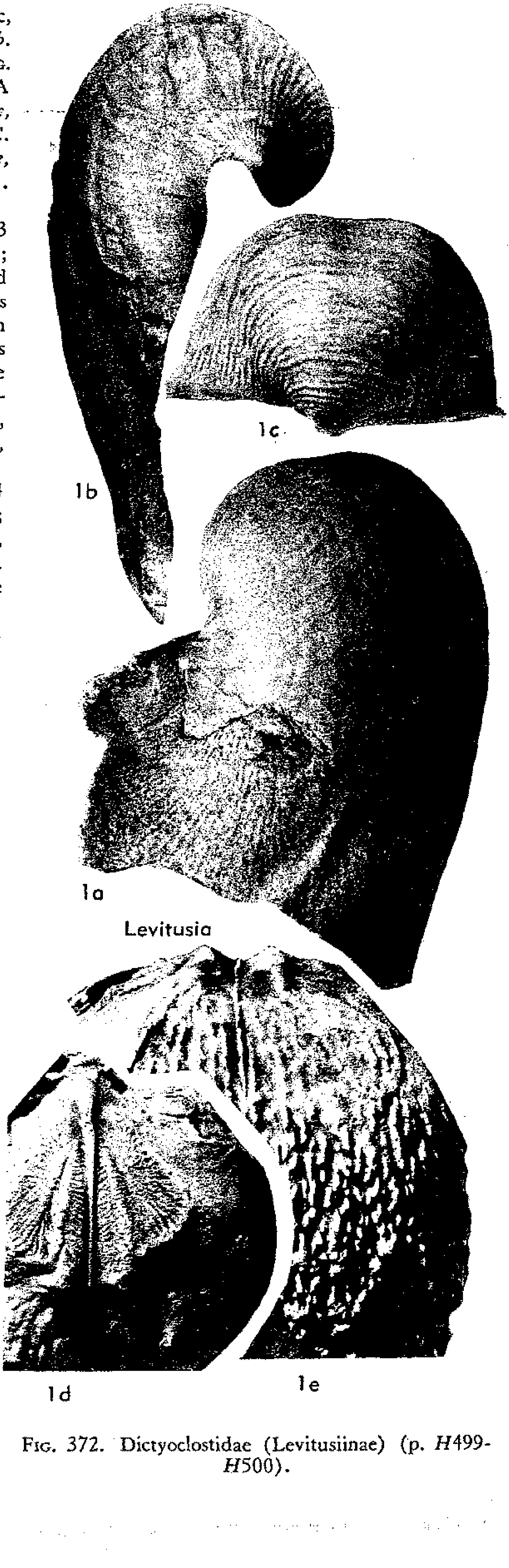

FIG. 372. Dictyoclostidae (Levitusiinae) (p. *H*499-*H*500).

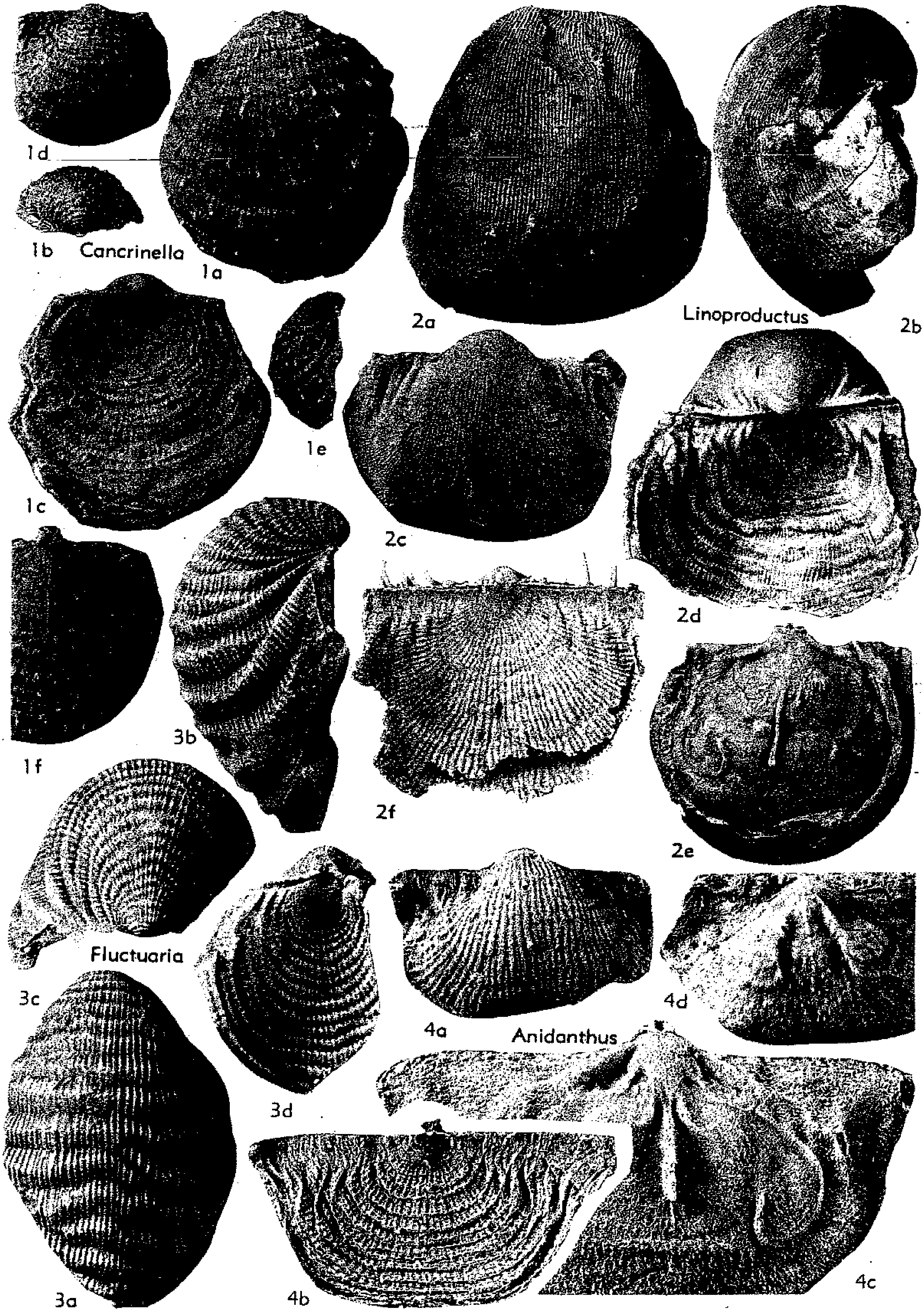

FIG. 373. Linoproductidae (Linoproductinae) (p. *H*500-*H*501).

(587).——FIG. 375,*1e,f*. *M. alata* (COOPER), Mex.; *1e*, ped.v. vent., ×4; *1f*, brach.v. view, ×3 (587).

Ovatia MUIR-WOOD & COOPER, 1960, p. 311 [**O. elongata*; OD]. Medium-sized to large, narrow body cavity, long trail; brachial valve with no repetition of trails or diaphragms; costellate, few rugae on flanks, spines rare, scattered, 1 or 2 rows near hinge, group on ears, absent or rare on brachial valve; cardinal process trilobate, minute median lobe; adductors part dendritic; lateral ridges short, slightly diverging from hinge. *L.Carb.(L.Miss.-U.Miss.)*, N. Am.-Eu.(USSR)-Asia (Kazakhstan).——FIG. 374,*2*. **O. elongata*, U.Miss. (Chester.), USA(Okla.); *2a-c*, ped.v. vent., lat., post. (*2a-c*, holotype), ×1; *2d*, brach.v. int. with card. process, ×1 (382).

Pseudomarginifera STEPANOV, 1934, p. 56 [**Productus ussuricus* FREDERIKS, 1924; OD]. [May be synonym of *Anidanthus*.] *L.Perm.*, Asia.

Terrakea BOOKER, 1930, p. 66 [**Productus brachythaerus* MORRIS, 1845, p. 284 (*non* G. B. SOWERBY, 1844, p. 158; SD MAXWELL, 1956, p. 333 (ICZN pend.)]. Medium-sized, may be geniculated; cicatrix of attachment present; irregularly costellate, obscure rugae, spines fine, long, prostrate, on costae, in group of more erect spines near hinge and on ears, scattered on brachial valve; cardinal process stout, erect, posteriorly quadrilobate; adductors finely dendritic, lateral ridges short extending along hinge margin. *L. Perm.*, Australia.——FIG. 375,*2a-d*. **T. brachythaerum* (MORRIS), Australia(New S.Wales); *2a,b*, ped.v. lat., post., ×1; *2c,d*, brach.v. views, ×1 (90).——FIG. 375,*2e,f*. *T. fragile* (DANA), Australia(New S.Wales); *2e*, brach.v. int., ×2; *2f*, ped.v. vent., with spines, ×1 (90).

Undaria MUIR-WOOD & COOPER, 1960, p. 317 [**U. manxensis*; OD]. Like *Fluctuaria* but more elongate and body cavity very narrow; rugae more numerous, flexuous and narrower, interrupting costellae, spines more numerous, scattered on rugae, 2 rows near hinge, spines represented in brachial valve by dimples; lateral ridges short, curved; cardinal process bilobate or quadrilobate. *L.Carb.(Visean)*, Eu.——FIG. 374,*3*. **U. manxensis*, Eng. (I. of Man); *3a*, ped.v. vent., ×2; *3b,c*, brach.v. with ext. layer removed, dors. and lat. views, ×2; *3d*, brach.v. int., ×4 (*3a,b,d*, holotype) (587).

Subfamily PROBOSCIDELLINAE Muir-Wood & Cooper, 1960

[Proboscidellinae MUIR-WOOD & COOPER, 1960, p. 325]

Trail of pedicle valve forming tube; cardinal process bilobate; external cincture in pedicle valve corresponding to low internal marginal ridge. *L.Carb.(Visean)*.

Proboscidella OEHLERT, 1887, p. 1277 [**Productus proboscideus* DE VERNEUIL, 1840, p. 259; OD]. Medium-sized; pedicle valve elongate, tubular;

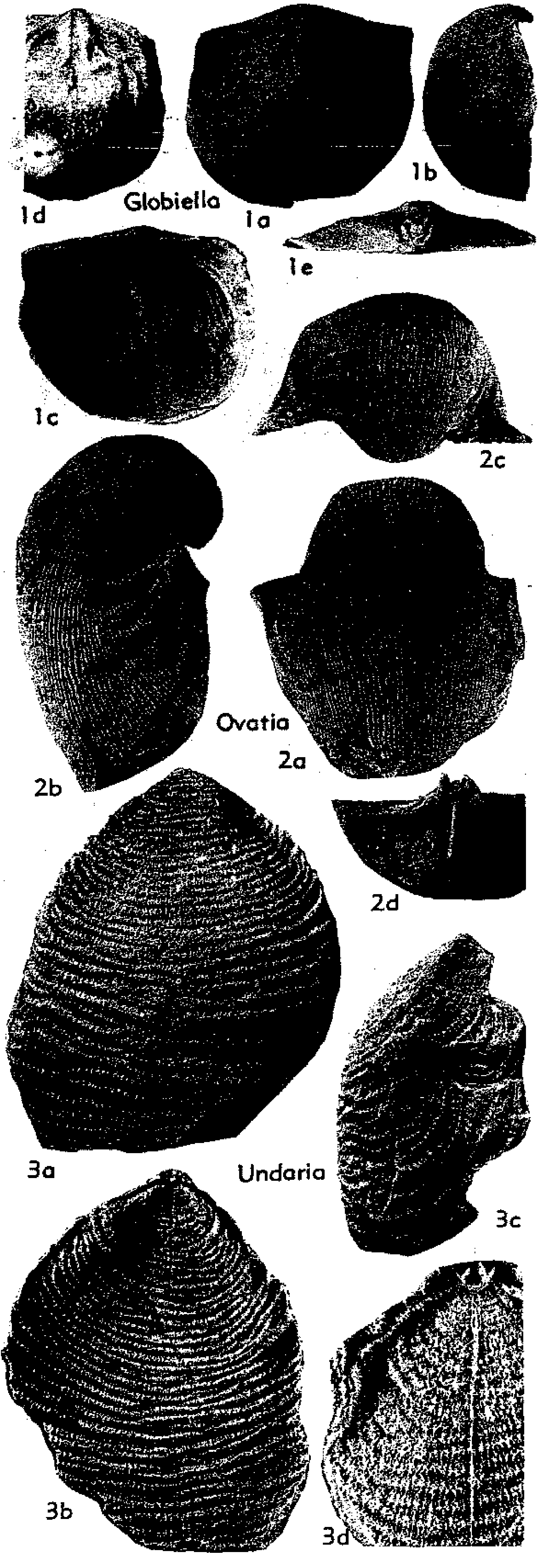

FIG. 374. Linoproductidae (Linoproductinae) (p. *H*501, *H*503).

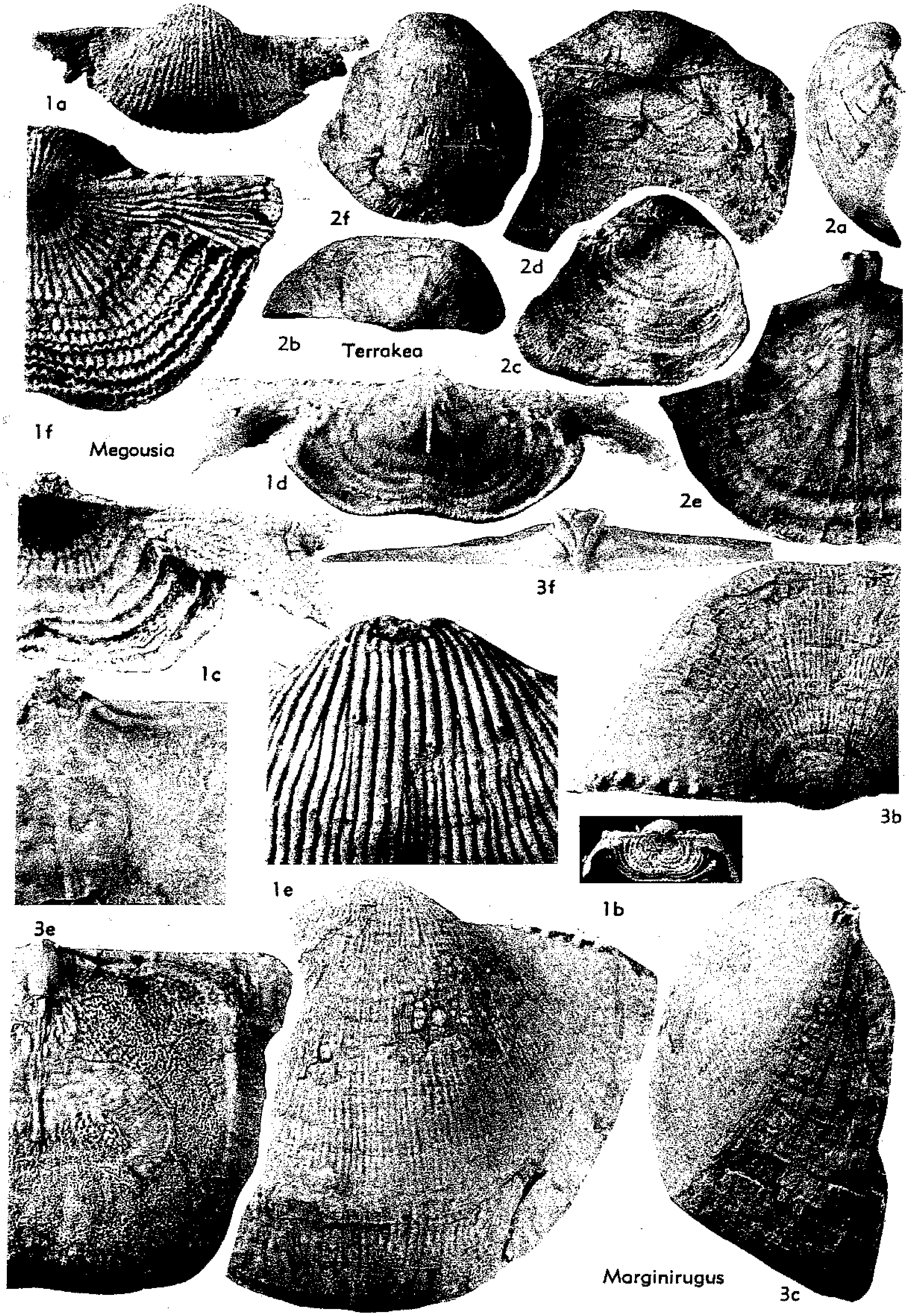

FIG. 375. Linoproductidae (Linoproductinae) (p. *H*501, *H*503).

cicatrix of attachment present; brachial valve opercular, rarely tubular, cincture around anterior margin; costellae and rugae on entire shell, spines on pedicle valve only, rarely on rugae, in row or group on flanks probably for attachment, and row at angle to hinge margin; cardinal process bilobate; lateral ridges short, diverging from hinge. *L.Carb.(Visean)*, Eu.-Asia.——Fig. 376,*1*. **P. proboscidea* (de Verneuil), Belg.; *1a*, ped.v. with cincture and long tube; *1b*, ped.v. lat. view with part of brach.v.; *1c*, lat. view of valves showing cincture; *1d*, ped.v. with clasping spines; *1e*, brach.v. int.; all ×3 (611).

Subfamily MONTICULIFERINAE Muir-Wood & Cooper, 1960

Valves with ornament of pustules (monticules) interrupting costellae or capillae; cardinal process short-shafted, trilobate, with minute lophidium. *L.Perm., ?U.Perm.*

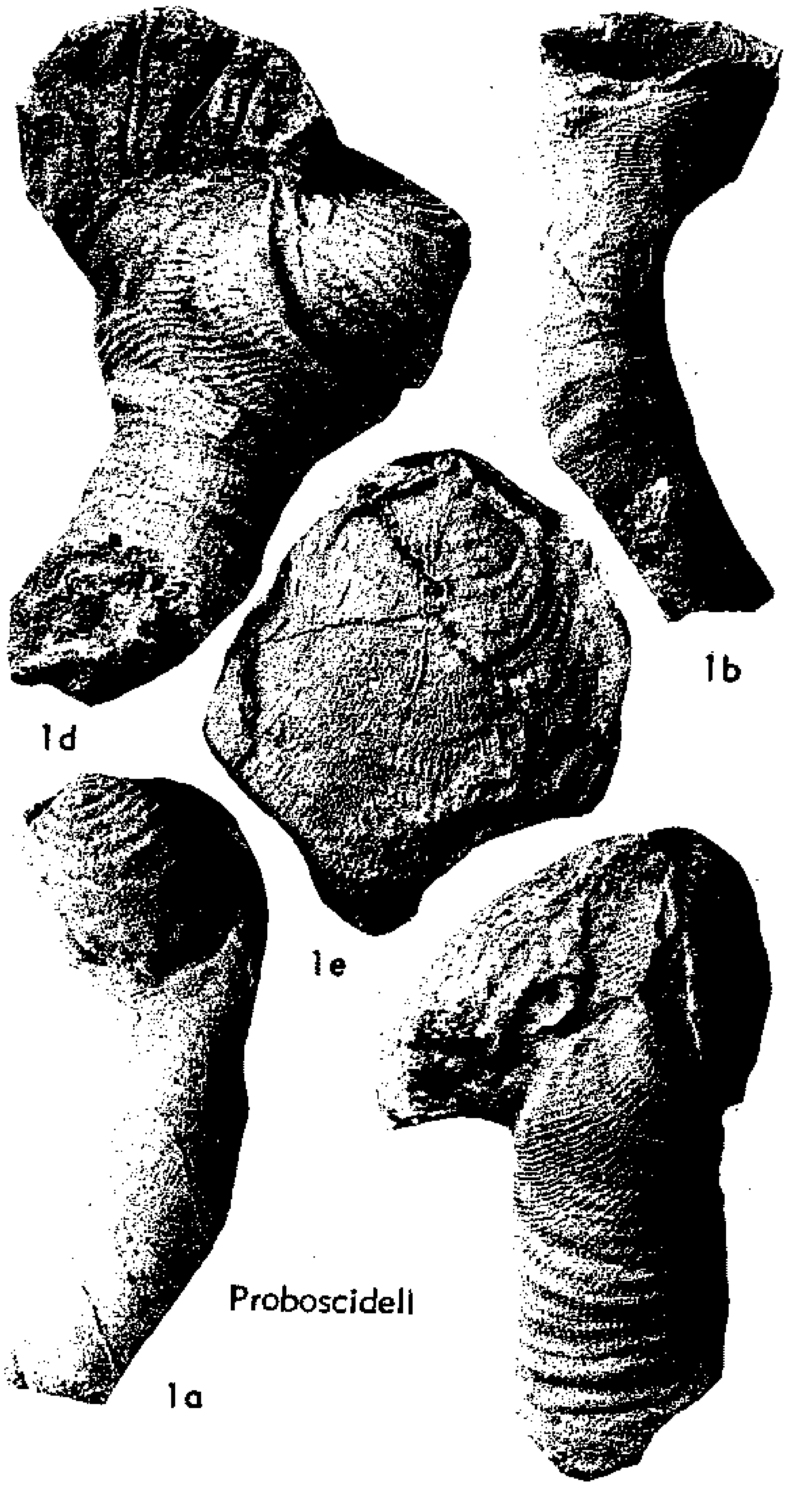

Fig. 376. Linoproductidae (Proboscidellinae) (p. *H*503, *H*505).

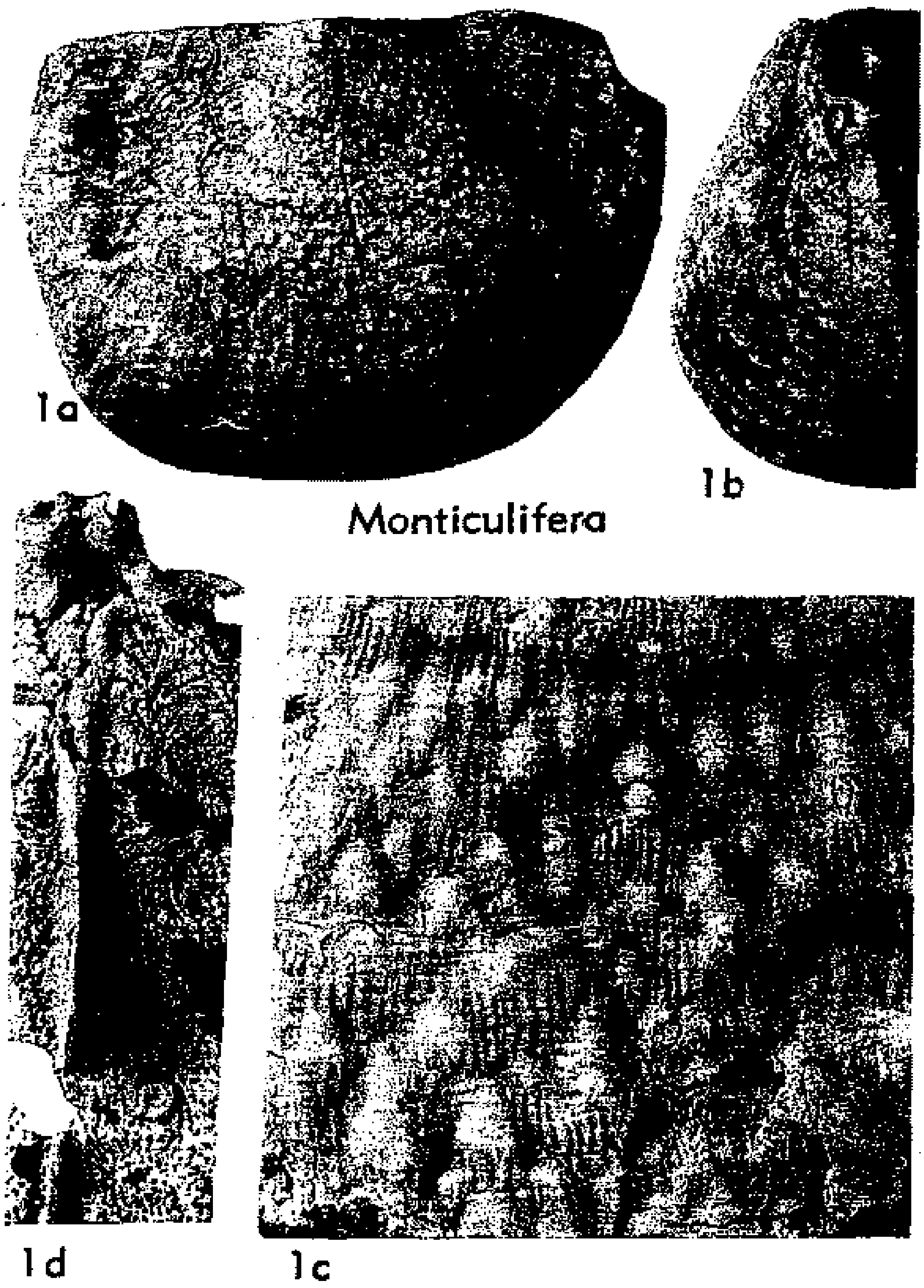

Fig. 377. Linoproductidae (Monticuliferinae) (p. *H*505).

Monticulifera Muir-Wood & Cooper, 1960, p. 327 [**Productus intermedius* Abich var. *sinensis* Frech, 1911, p. 176; OD]. Medium-sized to large, subquadrate in outline, geniculated; capillate with prostrate spines umbonally, monticules possibly bearing spines medianly, costellate anteriorly; spines prostrate scattered and more erect in row along hinge; brachial valve capillate with capillate monticules, no spines; adductors dendritic; lateral ridges extending along hinge. *L.Perm., ?U.Perm.*, Asia (Indo China - Manchuria - China).——Fig. 377,*1*. **M. sinensis* (Frech), China; *1a,b*, ped.v. vent., lat., ×1; *1c*, ped.v. ext. ornament, ×3; *1d*, brach.v. int., ×2 (313). [*See* p. *H*904.]

Subfamily PAUCISPINIFERINAE Muir-Wood & Cooper, 1960

[Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319]

Valves with ornament of costae or capillae, and 4 to 6 halteroid spines, cardinal process sessile, trilobate, dorsally recurved; zygidium present in some species. *U.Carb. (Penn.)-U.Perm.*

Paucispinifera Muir-Wood & Cooper, 1960, p. 319 [**P. auriculata*; OD]. Medium-sized, commonly alate, geniculated, with small ginglymus; obscurely costate, large halteroid spines symmetrically placed, row of small spines near ears, spines absent on brachial valve; adductors dendritic and

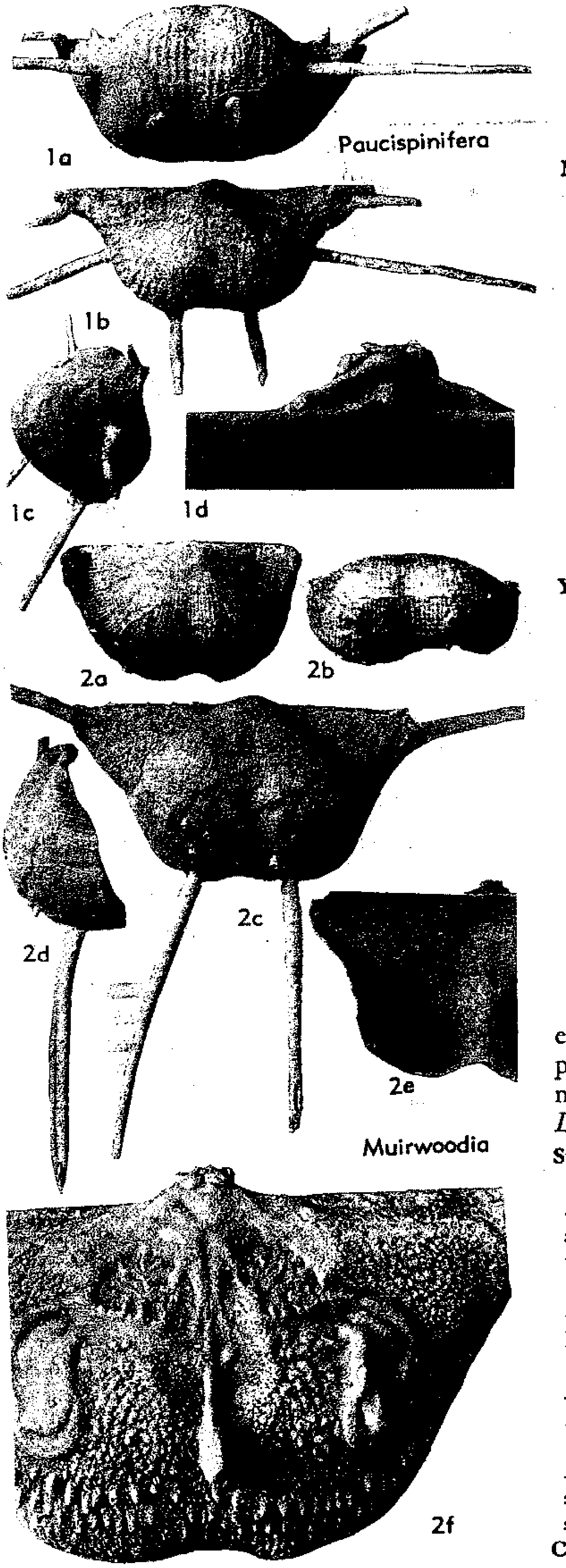

Fig. 378. Linoproductidae (Paucispiniferinae) (p. *H*505-*H*506).

lobate, lateral ridges united medianly by zygidium and extending down lateral margin of visceral disc. *L.Perm.*, N.Am.——Fig. 378,*1*. **P. auriculata,* USA(W.Tex.); *1a-c,* ped.v. with long spines vent., post., lat., ×1 (*1a,b,* holotype); *1d,* card. process and zygidium, ext. view, ×4 (587).

Muirwoodia Likharev, 1947, p. 187 [**Productus mammatus* Keyserling, 1846, p. 206; OD]. Small or medium-sized; transverse, geniculated, rare ginglymus; both valves capillate; spines scattered, 4 or 6 symmetrically placed halteroid spines, row near hinge, spines absent in brachial valve; adductors smooth or lobate; lateral ridges parallel to hinge and demarcating accessory sockets. *U. Carb.(Penn.),* Eu.-S.Am.; *L.Perm.-U.Perm.,* Eu.-Arctic-N.Am.-Asia.——Fig. 378,*2a,b*. **M. mammata* (Keyserling), L.Perm., USSR; *2a,b,* ped.v. vent., ant., ×1 (516).——Fig. 378,*2c-g*. *M.* sp. cf. *M. multistriata* (Meek), L.Perm., USA(W. Tex.); *2c,d,* ped.v. with spines, vent., lat., ×1; *2e,f,* brach.v. ext., int., ×1, ×2 (516). [See Fig. 301 for additional illustrations.]

Yakovlevia Frederiks, 1925, p. 7 [**Y. kaluzinensis*; OD]. Large, concavo-convex; pedicle valve with striated interarea and apical callosity filling delthyrium; pedicle valve finely costellate, spine row along hinge, and single spine on ear; adductors smooth; cardinal process sessile, trilobate. *L.Perm., ?U.Perm.,* Arctic-Asia.——Fig. 379,*1a,b*. **Y. kaluzinensis,* L.Perm., Asia(Sib.); *1a,b,* ped. v. int. mold, vent., lat., ×0.7 (889).——Fig. 379,*1c-g*. *Y. impressa* (Toula), Arctic; *1c,d,* ped. v. vent., lat.; *1e,g,* brach.v. ext., int.; *1f,* ped.v. int.; all ×0.7 (889).

Subfamily STRIATIFERINAE Muir-Wood & Cooper, 1960

[Striatiferinae Muir-Wood & Cooper, 1960, p. 328]

Aberrant linoproductids, commonly much elongated and narrow-hinged; cardinal process with single lobe, septum prominent, bladelike, adductors part dendritic. *L.Carb.(Visean)-Perm.*

Striatifera Chao, 1927, p. 24 [**Mytilus striatus* Fischer de Waldheim, 1837, p. 181 (=**Pileopsis striatus* Phillips, 1836, p. 224; OD]. Large, shell commonly tapering posteriorly, not geniculated; pedicle valve costellate, rugose near hinge; spines fine, numerous on costae, in group on ears and flanks; brachial valve costellate, no spines; lateral ridges and brachial ridges obscure. *L.Carb. (Visean),* Eu.-Asia-N. Am.——Fig. 381,*1*. **S. striata* (Phillips), *(1a-c)* Eng., *(1d-f)* USSR; *1a,b,* ped.v. vent., lat., ×0.7; *1c,* brach.v. view, ×0.7; *1d,* ped.v. with spine bases, lat., ×1.3; *1e,f,* brach.v. int., front and lat. views showing single-lobed card. process and adductor muscle scars, ×0.7 (587).

Compressoproductus Sarycheva, 1960, p. 231 [**Productus compressus* Waagen, 1884, p. 710; OD]. Trigonal in outline, tapering to umbo, ornament of capillae and irregular rugae on both valves, spines fine on flanks of pedicle valve, and row near posterior commissure; cardinal process one-lobed as in *Striatifera*. *Perm.*, Eu.-Greenl.-Asia-Australia-S.Am.——FIG. 380,*1*. **C. compressus* (WAAGEN), Pak.; *1a-c*, ped.v. vent., lat. from left, lat. from right showing spines, ×0.8 (845).

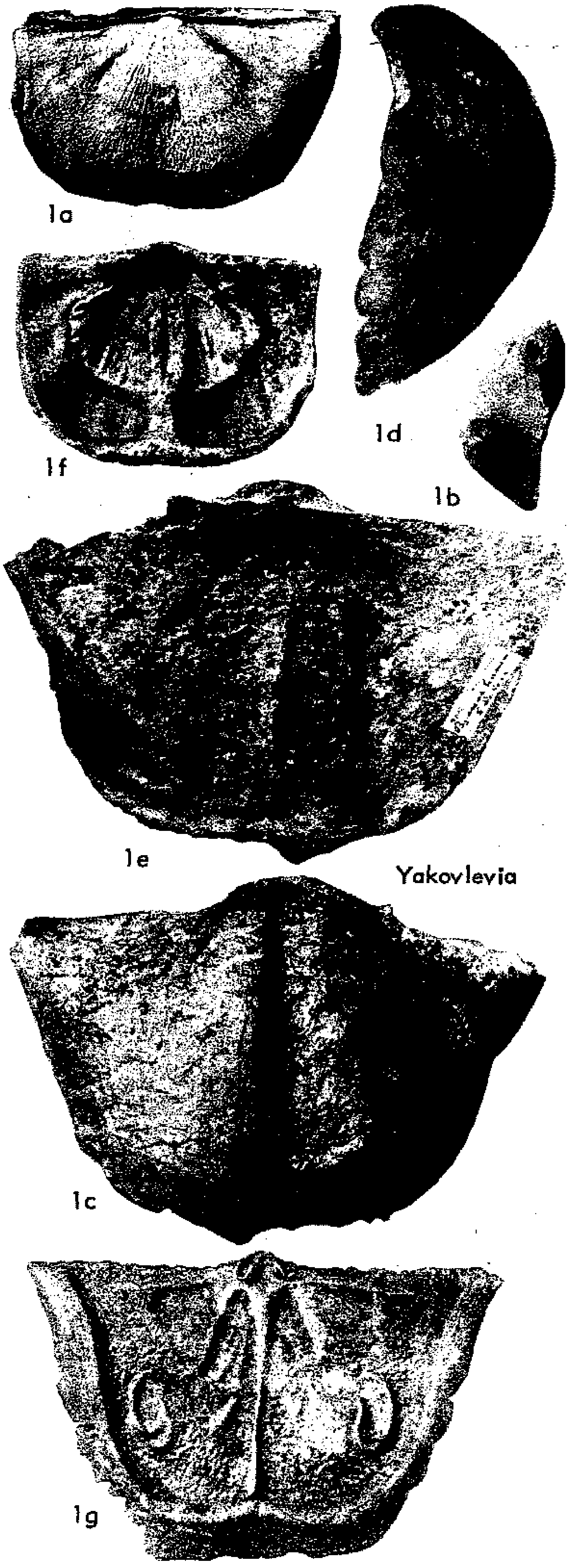

FIG. 379. Linoproductidae (Paucispiniferinae) (p. *H*506).

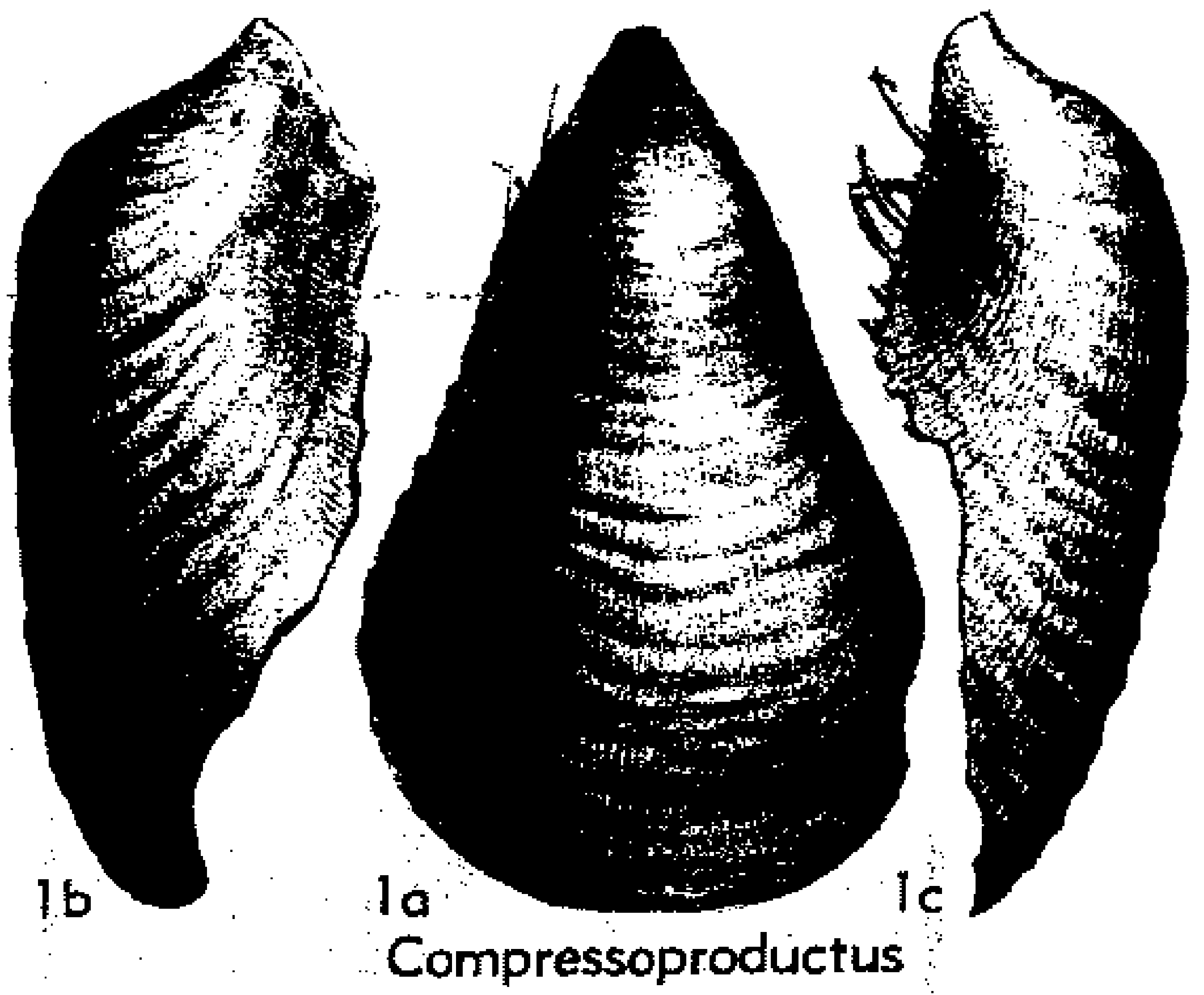

FIG. 380. Linoproductidae (Striatiferinae) (p. *H*506-*H*507).

Family GIGANTOPRODUCTIDAE Muir-Wood & Cooper, 1960

[Gigantoproductidae MUIR-WOOD & COOPER, 1960, p. 330]

Large, usually thick-shelled, wide-hinged, with thin body cavity, interarea rare; cardinal process bilobed or trilobed, or modified with one lobe, lophidium present; adductors highly dendritic or smooth. *U.Dev.-U.Carb.* (*Namur.*).

Subfamily GIGANTOPRODUCTINAE Muir-Wood & Cooper, 1960

[Gigantoproductinae MUIR-WOOD & COOPER, 1960, p. 330]

Pedicle valve rarely having ginglymus, adductors highly dendritic. *L.Carb.*(*Visean*).

Gigantoproductus PRENTICE, 1950, p. 437 [*pro Gigantella* SARYCHEVA, 1928, p. 13 (*non* EKMAN, 1905)] [**Anomites giganteus* W. MARTIN, 1793, 1809 (declared invalid ICZN) =**Productus giganteus* J. SOWERBY, 1822, p. 19; SD MUIR-WOOD, 1951, p. 98 (species validated and SD confirmed, ICZN, 1956, Op. 420, p. 135)]. Large to gigantic, thick-shelled, not geniculated; irregularly costate, rugose near hinge, may be longitudinally fluted, spines scattered, row near hinge; adductors markedly dendritic; flattened rim replacing lateral ridges along hinge; rounded elevations in brachial valve and hollows in pedicle valve representing the position of the lophophore spirals; cardinal process trilobate or quadrilobate. *L.Carb.*(*Visean*), cosmop., rare in N.Am.——FIG. 382,*1*. **G. giganteus* (J. SOWERBY), (*1a,b*) USSR; (*1c-f*) Eng.; *1a,b*, ped.v. int. mold, vent., post. showing musculature; *1c,d,* ped.v. (decorticated) vent., post.; *1e,f,* ped.v. and brach.v. int. molds; all ×0.6 (*1a,b,* 587; *1c-f,* 587).

Titanaria MUIR-WOOD & COOPER, 1960, p. 334 [**T. costellata*; OD]. Like *Gigantoproductus* but with ginglymus in pedicle valve, no pseudodeltidium; costellate and with numerous fine spines in both valves, no rugae; cardinal process sessile with

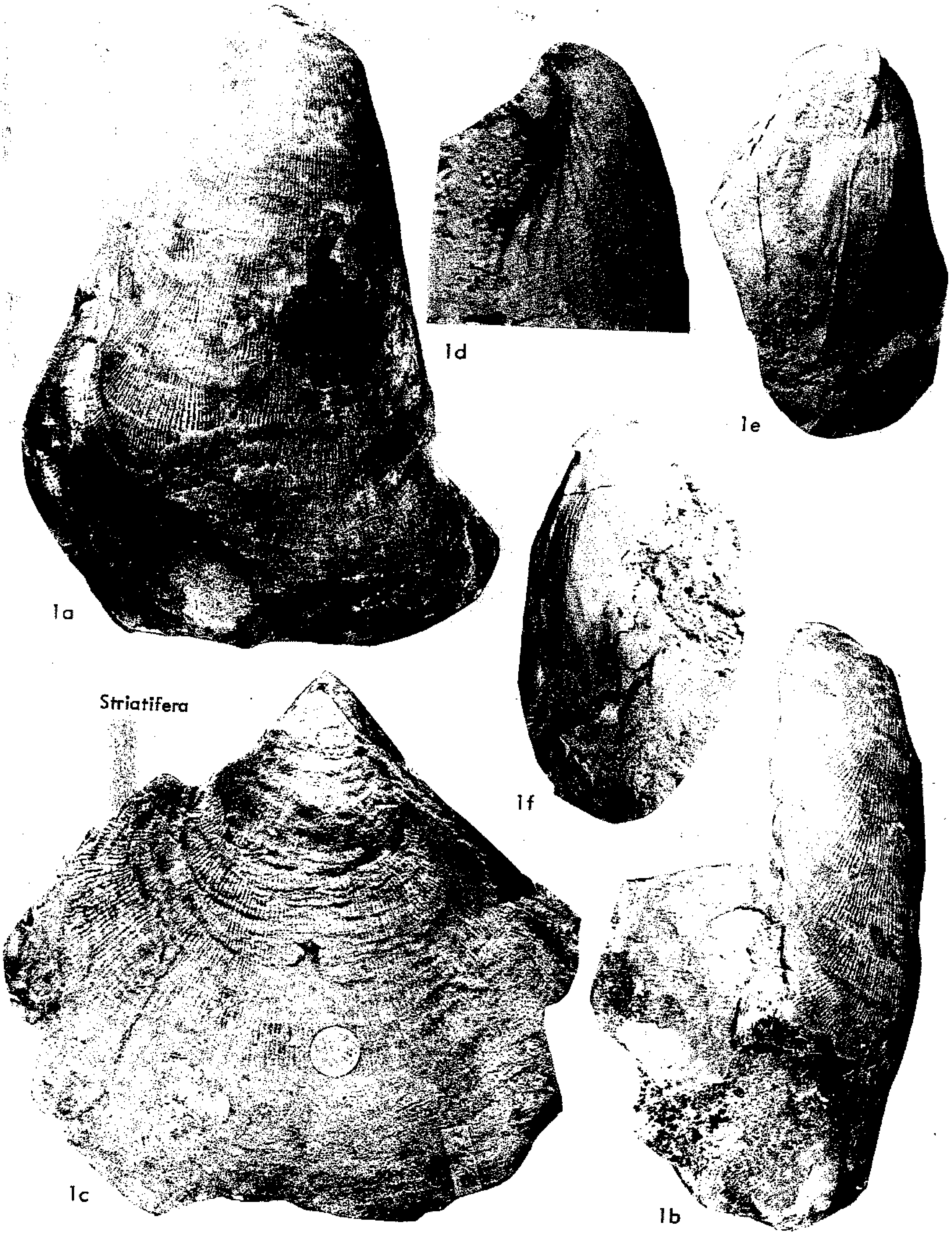

FIG. 381. Linoproductidae (Striatiferinae) (p. *H*506).

FIG. 382. Gigantoproductidae (Gigantoproductinae) (p. *H*507-*H*508).

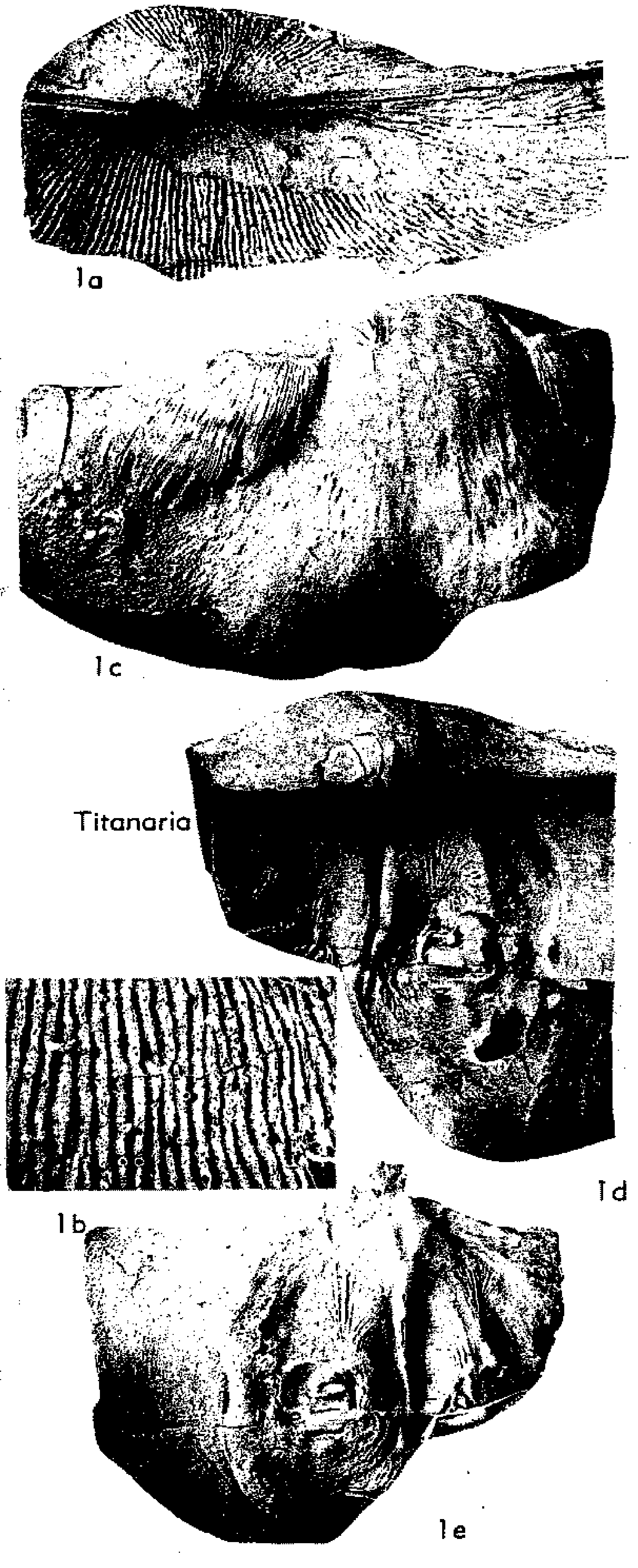

FIG. 383. Gigantoproductidae (Gigantoproductinae) (p. *H*508, *H*510).

single lobe; adductors finely dendritic; no trace of lophophore spirals. *U.Miss.*, N.Am.——FIG. 383,*1*. **T. costellata*, USA(Calif.); *1a*, brach.v. view, ×0.8; *1b*, costellae of brach.v., ×1.6; *1c,d*, ped.v. and brach.v. int. molds, ×0.8; *1e*, brach.v. int., ×0.8 (all, holotype) (587).

Subfamily SEMIPLANINAE Sarycheva, 1960

[*nom. transl.* MUIR-WOOD, herein (*ex* Semiplanidae SARYCHEVA, 1960, p. 231)]

Usually thin-shelled, laterally fusiform or elongate shells with much incurved umbo; no interareas or ginglymus; cardinal process small, sessile, bilobate, or quadrilobate; adductors smooth. *U.Dev.-U.Carb.(Namur.)*.

Semiplanus SARYCHEVA in SARYCHEVA & SOKOLSKAYA, 1952, p. 119 [**Productus semiplanus* SHVETSOV, 1922, p. 10 (=?*P. latissimus* J. SOWERBY, 1822); OD]. Ornament of costellae, numerous growth lines forming regular transverse ornament, and quincuncially arranged fine spines, row near hinge; hinge margin thickened internally and longitudinally grooved; cardinal process quadrilobate, septum long, medianly grooved, lateral ridges short. *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.(USSR)-Asia(Kazakhstan).——FIG. 384,*1a-c*. **S. semiplanus* (SHVETSOV); *1a-c*, ped.v. vent., post., profile, ×1 (587).——FIG. 384,*1d-f*. *S. latissimus*, Eng.; *1d,e*, ped.v. vent., post., ×1.5; *1f*, ped.v. int. mold, ×1 (587).

?**Bagrasia** NALIVKIN, 1960, p. 231 [**Productus chonetiformis* KRESTOVNIKOV & KARPYSHEV, 1948, p. 48; OD]. Elongated along hinge with no interareas; umbo scarcely projecting beyond hinge. Ornament of fine costellae with weakly swollen elongated tubercles, the bases of fine spines; cardinal process small, bilobate, median septum absent. *U.Dev.-L.Carb.* (Etroeungt beds), Eu.(USSR, S. Urals, Caucasus).

Subfamily KANSUELLINAE Muir-Wood & Cooper, 1960

[Kansuellinae MUIR-WOOD & COOPER, 1960, p. 336]

Interarea in each valve with pseudodeltidium and chilidium; cardinal process probably bilobate. *L.Carb.(Visean)*.

Kansuella CHAO, 1928, p. 67 [**Stratifera kansuensis* CHAO, 1927, p. 108; OD]. Imperfectly known and possibly composite; shell gigantic, transverse, pedicle valve thick-shelled, valves nongeniculate; irregularly costellate and rugose posteriorly, lamellose, spines scattered over pedicle valve, absent in brachial valve; adductors lobate or dendritic; indications of lophophore spirals; lateral ridges absent. *L.Carb.(Visean)*, Asia(China-Ferghana).——FIG. 385,*1*. **K. kansuensis* (CHAO), China; *1a*, brach.v. int. (post. part); *1b*, interareas of both valves; *1c*, brach.v. interarea, pseudodeltidium; and ornament; all ×0.55 (153).

Suborder OLDHAMINIDINA Williams, 1953

[*nom. correct.* WILLIAMS, herein (*pro* suborder Oldhaminoidea WILLIAMS, 1953, p. 286)] [Materials for this suborder prepared by ALWYN WILLIAMS]

Shell shape irregular, without radial orna-

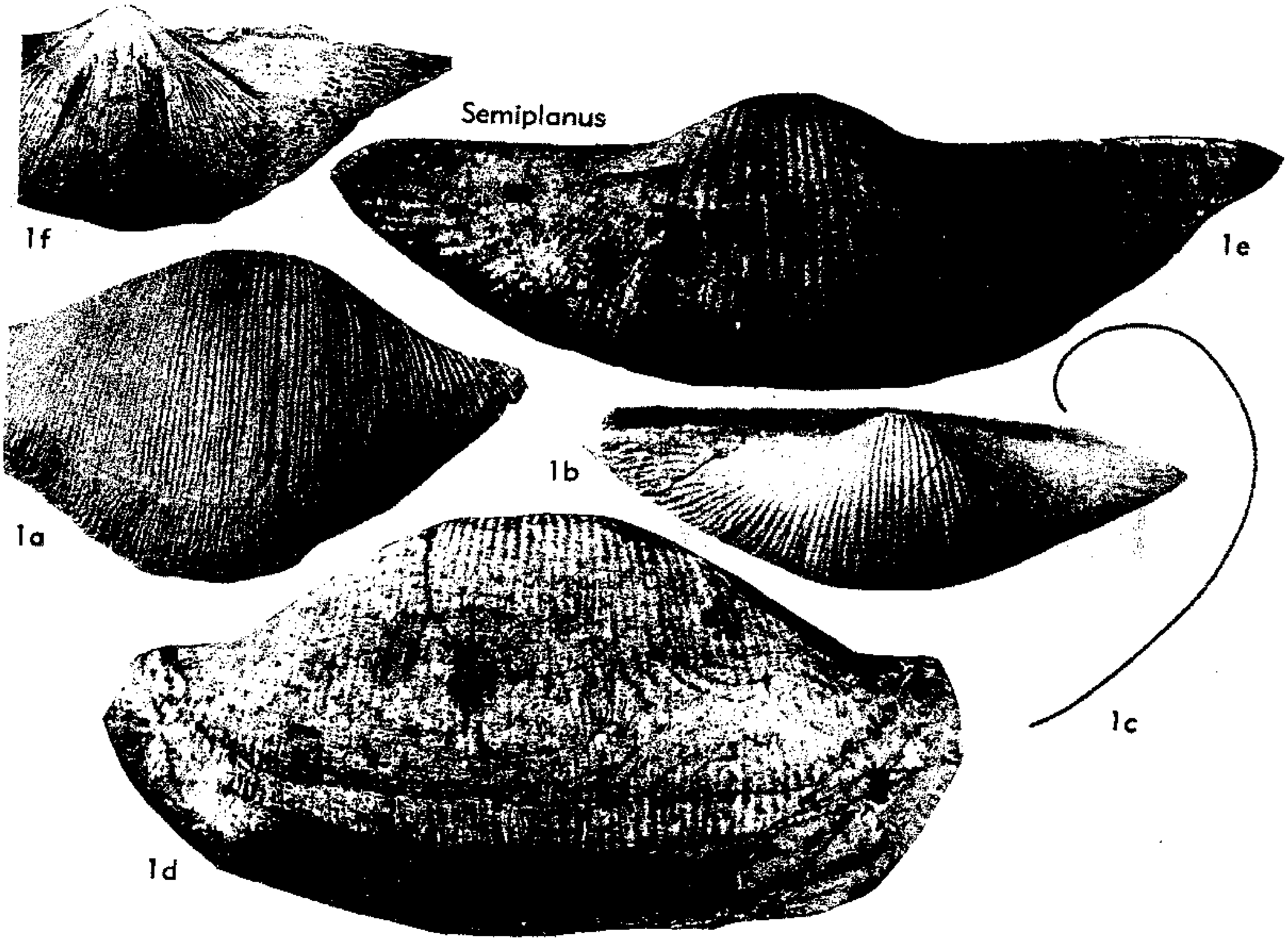

Fig. 384. Gigantoproductidae (Semiplaninae) (p. *H*510) .

mentation, pedicle opening, interareas or hinge lines; primary shell of brachial valve limited to small, triangular area forming posteromedian apex of large plate of secondary shell, presumed to have been deposited by infold of mantle as lophophore support, commonly symmetrically or asymmetrically highly lobate; pedicle valve extending dorsally of apex of brachial valve as posterior flap commonly everted for attachment to substratum or extending forward to transform pedicle valve into cone; articulation effected by pair of striated, convex dental areas on posteromedian floor of pedicle valve fitting into striated concave surfaces on either side of bilobed cardinal process in brachial valve; ventral muscle impressions symmetrical or unequally developed about median plane; ventral bounding ridge on floor of pedicle valve disposed as loops or septa coincident with outline of dorsal internal plate; shell substance pseudopunctate. *U.Carb.-U.Trias.*

The morphology of the Oldhaminidina brachiopods warrants a full discussion because, although vaguely suggestive of a productoid ancestry, it is so bizarre as to defy any confident interpretation of its details. This is true not only of certain features of both valves but also of the growth of the

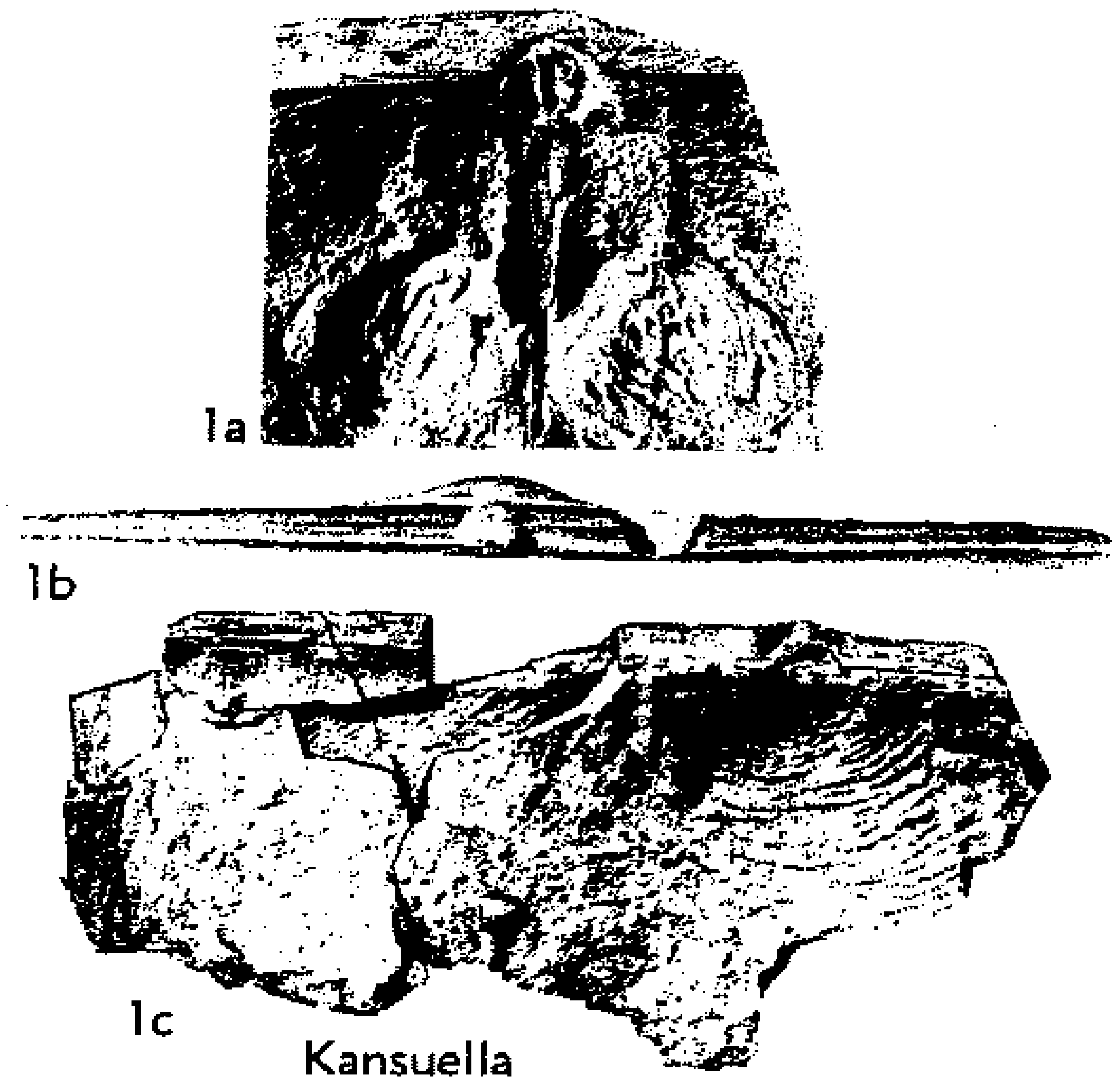

Fig. 385. Gigantoproductidae (Kansuellinae) (p. *H*510).

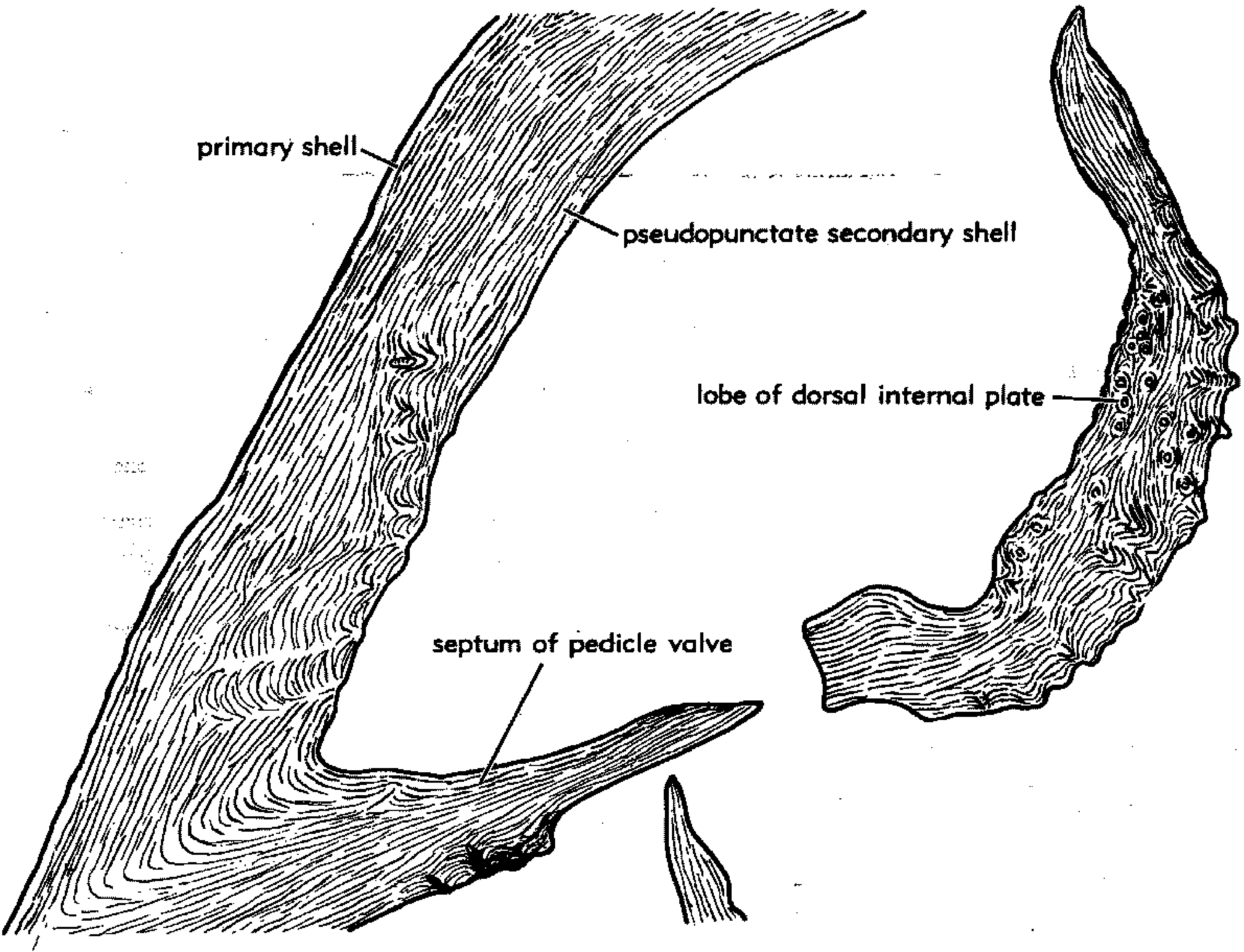

FIG. 386. Shell structure of *Oldhamina decipiens* (DE KONINCK) (×15).

valves themselves; hence, the following observations and even the proposed classification may ultimately require fundamental revision.

The shells are functionally bivalved, with the inner surface of the pedicle valve everywhere extending well beyond the periphery of the other valve so that much of the ventral mantle, despite evidence for retractability, must have been permanently exposed during life. The shell structure of the pedicle valve is pseudopunctate, with a thin but recognizable primary layer orthodoxly forming the entire outer surface of the valve (Fig. 386). In the structure generally identified as the brachial valve, however, the primary layer is absent for a small, posteriorly located, triangular area (Fig. 387). The rest of the "valve" is made up exclusively of pseudopunctate secondary calcite (Fig. 386) so that *both* external and internal surfaces are pierced by taleolae to give a finely tuberculate appearance identical with that of the ventral internal surface (WILLIAMS, 1953, 873). It can be demonstrated in other articulate brachiopods that structures, like lophophore supports, muscle platforms, etc., which are composed only of secondary shell, were secreted within invaginations of outer epithelium independent of the mantle edge. Consequently, it may be assumed that the part of the oldhaminoid brachial valve which is also composed only of secondary shell formed no part of the exoskeleton but was an internal skeletal support (internal plate) to a highly lobate mantle infold (WILLIAMS, 1953, 873). According to this interpretation, the true brachial valve is vestigial, being represented by the small, obtusely triangular, apical portion of the valve that consists of both outer primary shell and the inner secondary layer forming the cardinal process lobes and the posterior part of the dental sockets. STEHLI (1956, 777), on the other hand, prefers to ascribe the anomalous distribution of primary shell to a physiological malfunction in an otherwise normally growing valve. The mantle lobes that are ultimately responsible for the growth of the shell are, however, differentiated from the same rudimentary mantle ring in living larvae and, if this were also true for the Oldhaminidina brachiopods, a fundamental difference in the shell structure of normally growing valves could hardly have arisen. Furthermore, the obtusely triangular area covered by primary shell, although reminiscent of an obsolescent interarea and chilidium, is not homologous with them because growth was in an anterodorsal direction away from the cardinal process in a manner which suggests that expansion was controlled by a mantle edge coincident with the base of the triangle.

By imparting rigidity to an investing infold of the mantle, the inferred internal plate could have given support to the lophophore. Immature specimens of the earliest-known Oldhaminidina, *Poikilosakos*, possess a subcircular internal plate with a median incision. Assuming the lophophore to have arisen from the inner epithelium just within the edge of such a plate, it would have resembled the schizolophe; and with the development of lateral lobes to the internal plate, the feeding apparatus would have been transformed into a ptycholophe (Fig. 388).

The morphology of the posterior part of the pedicle valve is, in some respects, as anomalous as the structure of the brachial valve. There is no interarea but the posterior part of the pedicle valve is extended anterodorsally as a flap to overlie the brachial valve, which is accommodated by a triangular impression (Fig. 389). This impression is also ornamented by growth lines parallel with the base and probably represents a zone of the posterior flap where secondary shell deposition was held in abeyance by the pressure of the heavily rutted periostracal cover to the brachial valve. The flap is almost invariably sharply reflexed just anterior of the base of the impression and its attitude and shape can vary considerably. Specimens attached to a regular surface possess a flap which resembles a pair of ears extending laterally from the median reflexed area (Fig. 390); in those which lay free on the sea floor throughout most of their lives the flap is greatly extroverted, so that the distal edge is usually in contact with the external surface of the pedicle valve (Fig. 391); in those attached to irregular surfaces or crinoid stems the flap is closely adherent and molded to the base (Fig. 389); and in at least three distinct stocks (*Adriana, Keyserlingina, Pirgulia*) the flap grew forward with the rest of the pedicle valve to form a deep cone (Fig. 392).

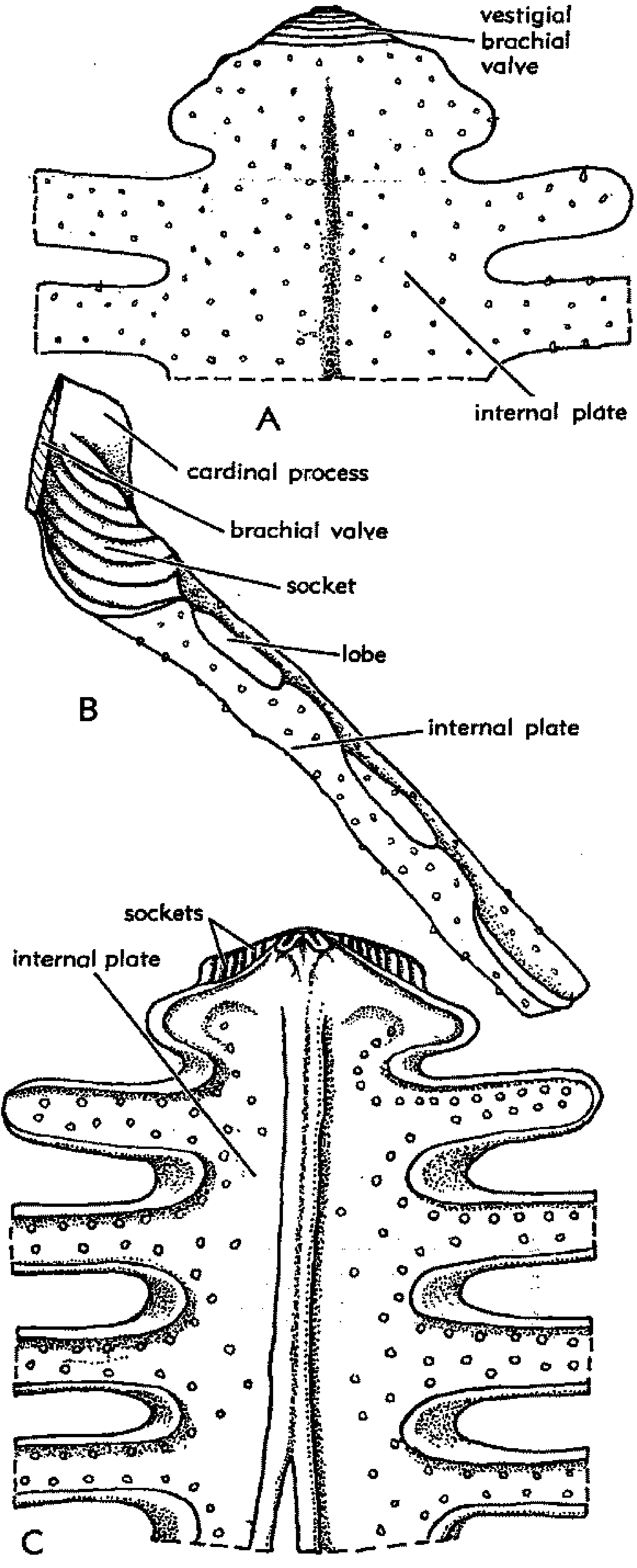

Fig. 387. Brachial valve and internal plate of *Leptodus* sp., M.Perm., Tex.; *(A)* internal, *(B)* lateral, and *(C)* external views (873).

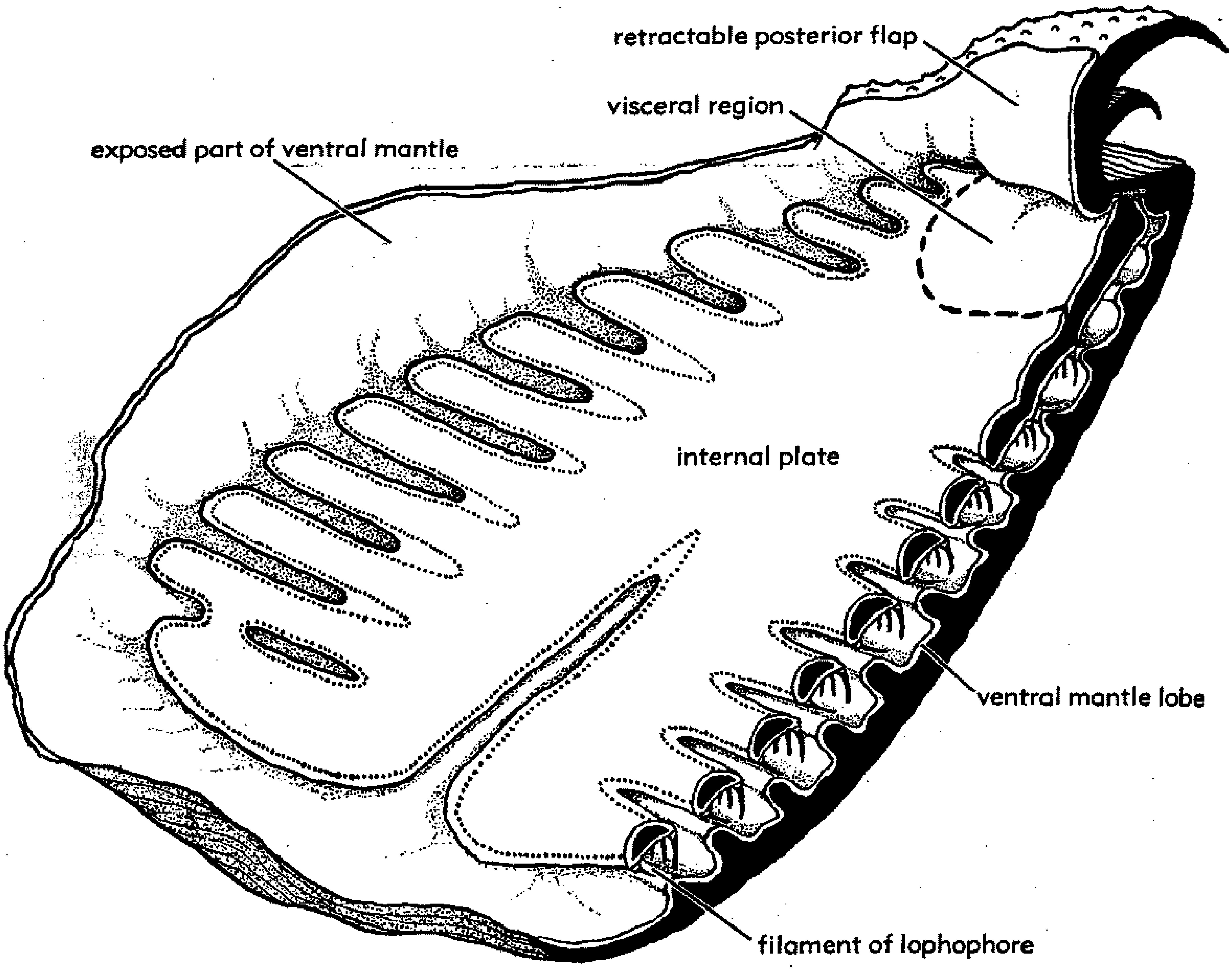

FIG. 388. Submedian view of *Leptodus* sp. (reconstr.), M.Perm., Tex., showing relationship between mantle lobes and shell (portrayed in solid block) (873).

Subsequent to the settling of spats, presumably by cementation of the apex of the pedicle valve, the posterior flap assisted in fixation, as is well seen in those oldhaminoids attached to crinoid stems. It is envisaged as having been laid down by a posterior extension of the mantle, capable of a rapid deposition of cementing shell material and disposed in such a way that the inner epithelial layer was invariably exposed. This posterior mantle flap must have molded itself closely to any surface available for attachment and must have been greatly retractable because paper-thin layers of shell, consisting of both primary and secondary calcite, were commonly plastered one on top of another (Fig. 391).

Apart from the cardinal process, which is bilobed in the strophomenoid fashion, the internal features also show noteworthy departures from arrangements typical of other articulate brachiopods. No teeth are found in the pedicle valve, but a pair of striated, convex surfaces (dental areas of WATSON, 854) occur in the apical region; and these articulate with a pair of similarly striated, oval concave surfaces (sockets) lying anterolaterally to the cardinal process lobes and extending down to the first pair of lateral lobes in the brachial valve. Muscle scars are only sporadically impressed but include a pair of variably defined dorsal adductor scars on either side of the median ridge. The ventral impressions, on the other hand, can be asymmetrically developed (853, 854), and according to STEHLI (777) the disposition of the ventral scars is indicative of two important groups. In the first group (e.g., *Coscinophora*), a pair of large elongate adductor scars located submedianly are flanked by a pair of smaller, elongate diductors; this symmetrical field is commonly associated with median and submedian ridges. In the second group, which includes forms like *Poikilosakos*, the right diductor is always larger than the left and is contained within

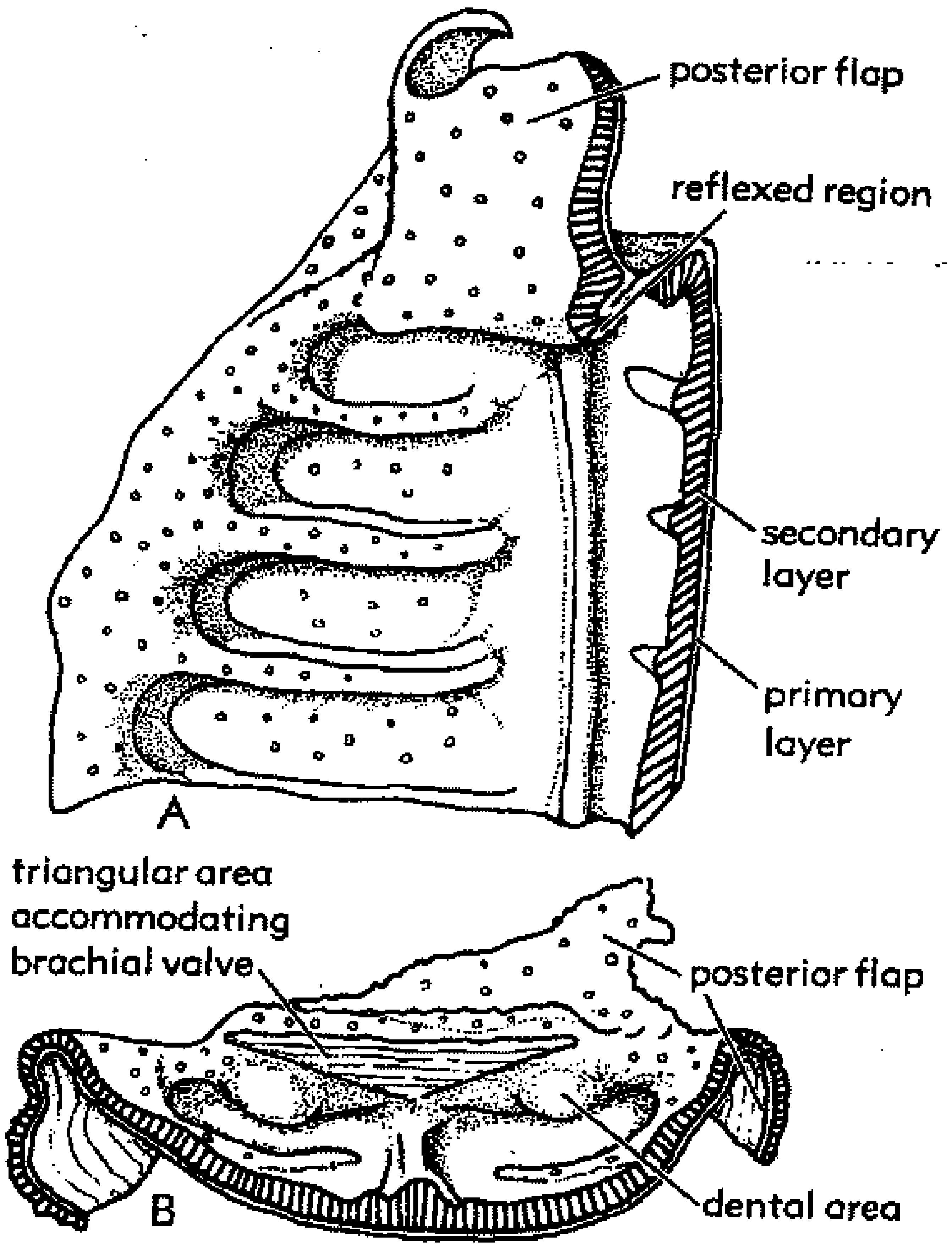

FIG. 389. Apical part of pedicle valve of *Leptodus* sp., *M.Perm.*, Tex.; submedian *(A)* and posterior *(B)* views (873).

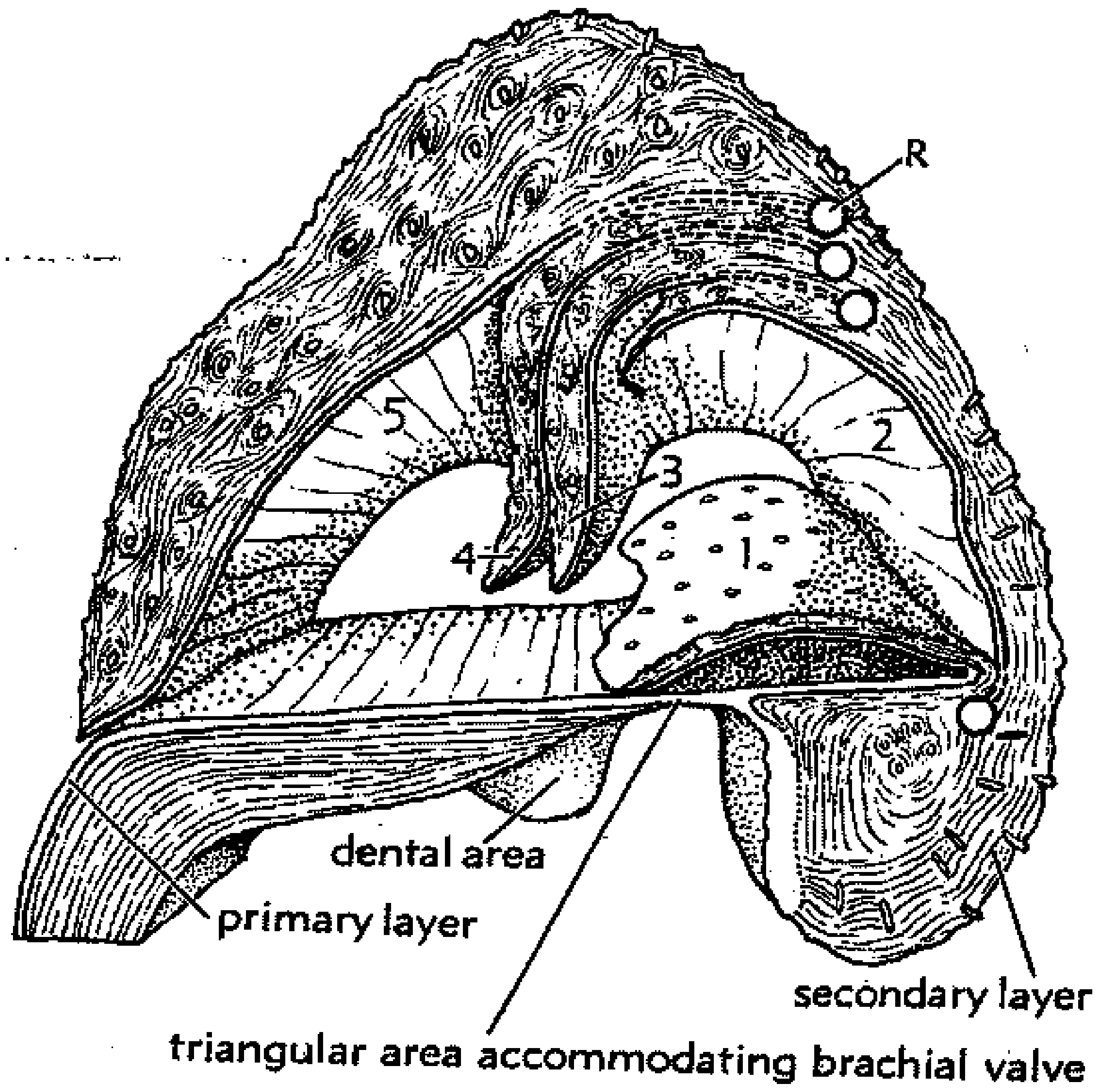

FIG. 391. Submedian portion of posterior flap of *Oldhamina decipiens* (DE KONINCK), Perm., Salt Range, Pak.; 1, 2, 3, 4, and 5 denote successive layers of shell deposited by posterior flap; circles represent points of minimum retractability of mantle flap necessary for deposition of each succeeding layer (873).

an elongately semiconical sheath, while the adductor scars are obscure or represented by inconspicuous asymmetrical hollows located posteromedianly. This asymmetry of scars probably reflected a degeneracy in the muscle system because the brachial valve was commonly so confined by the lateral walls of the pedicle that it could not have slewed in the plane of articulation as believed by WATSON (854). Furthermore, the close proximity of the cardinal process lobes to the floor of the pedicle valve and the physical constraint of the posterior flap immediately dorsal of the brachial valve precludes any considerable movement normal to the plane of articulation.

The most significant morphological changes seen in the Oldhaminidina resulted from development of the septal apparatus of the pedicle valve and the corresponding lobation of the internal plate.

In the earliest oldhaminoid, *Poikilosakos*, with a low bounding ridge (flange of WAT-

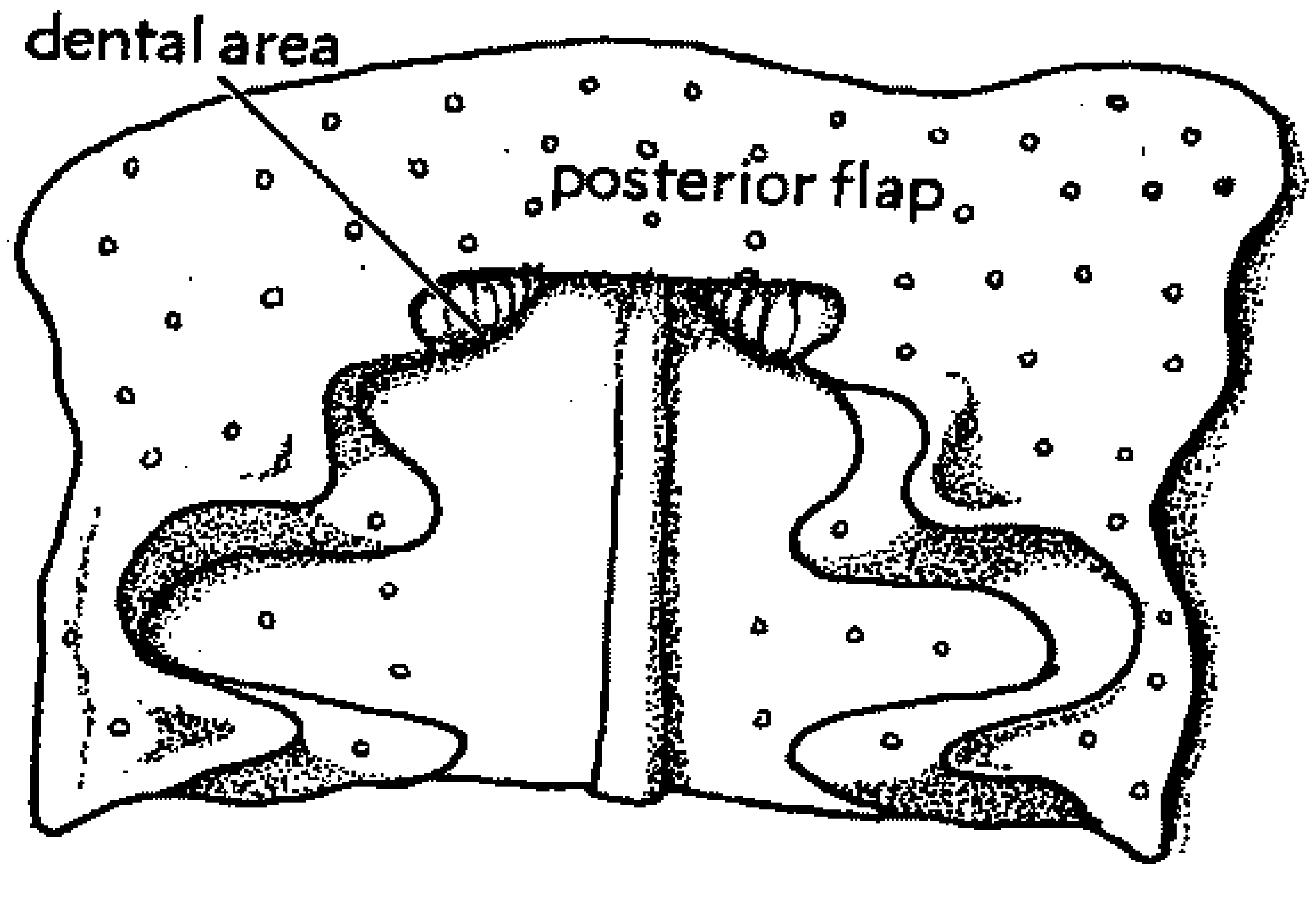

FIG. 390. Apical part of pedicle valve of *Leptodus* sp., M.Perm., Tex. (873).

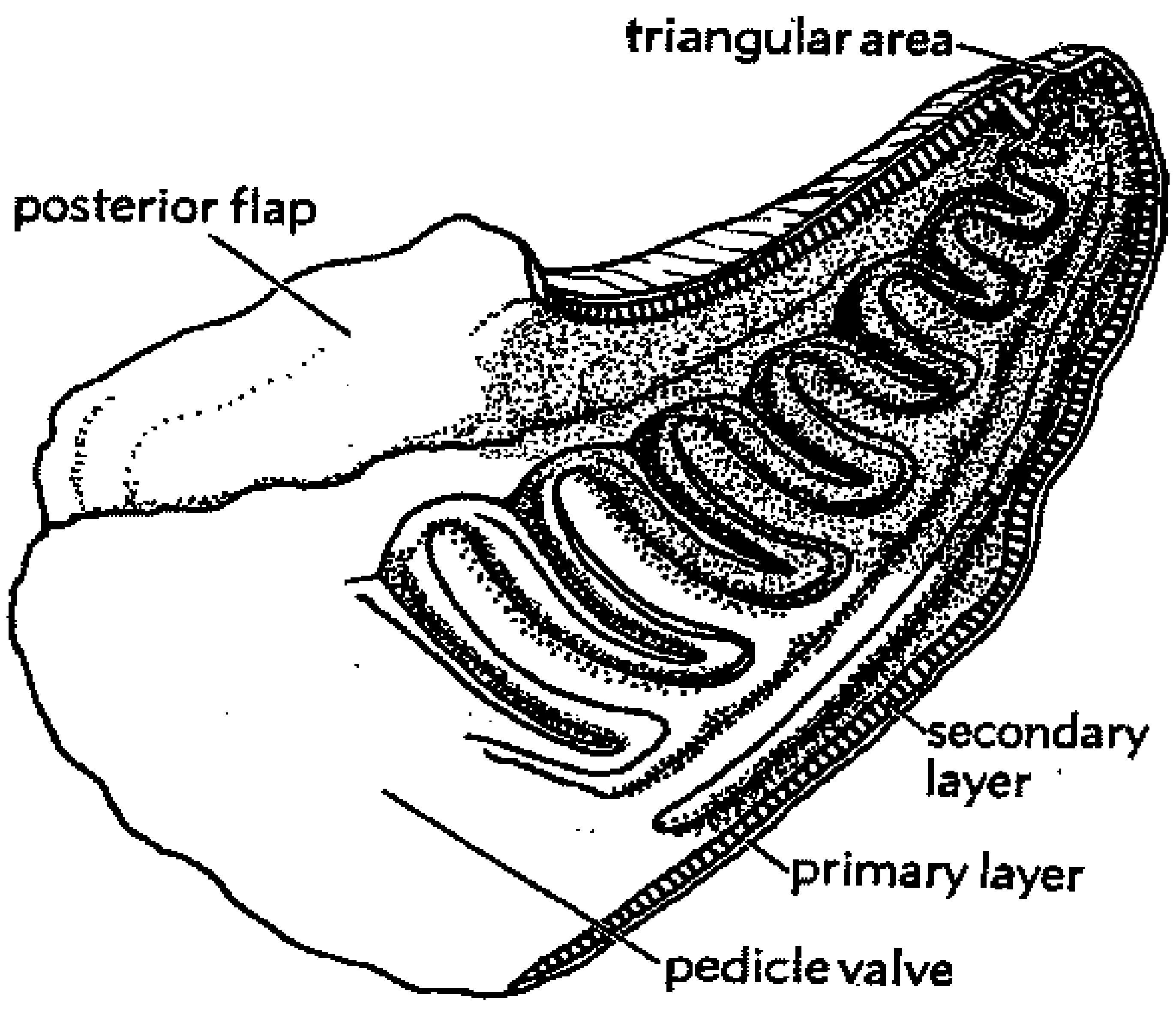

FIG. 392. Submedian view of interior of pedicle valve of *Pirgulia* sp., M. Perm., Tex. (873).

son, 854), lying well within the margin of the pedicle valve, completely surrounded the median area of the interior. In young shells, the bounding ridge was roughly subcircular in outline and was indented to form a median loop only; but during further growth involving resorption, the bounding ridge increased in size and became disposed as a small number of lateral loops in addition to the median one. Each loop was sufficiently open to include medianly a narrow strip of the valve floor bounded by an indented segment of the bounding ridge. The internal plate of the brachial valve corresponded in outline to the disposition of the bounding ridge, so that it was lobate and lay so close to the pedicle valve that each lobe was seemingly isolated distally from its neighbor by a loop of the bounding ridge.

In later Oldhaminidina (e.g., *Keyserlingina, Paralyttonia*), the loops began to close by an increase in the size of adjacent segments of the bounding ridge and their encroachment onto the intervening median strip of the valve floor until, in extreme forms like *Oldhamina* and *Leptodus*, the ridge boundaries to each loop were completely united into one solid septal structure. In this manner the looped bounding ridge of the earlier and more generalized Oldhaminidina was transformed into solid septa, the dorsal surfaces of which may be concave, bluntly convex or sharp; and a pair of notches, extending the length of the septa, commonly developed to accommodate the edges of lobes to the internal plate.

Other modifications associated with evolution of the septal apparatus included an increase in the number of septa disposed symmetrically or asymmetrically about the median line, the progressive closure of the median incision of the internal plate and the partial fusion of the lateral lobes by the growth of dissepiments. *Bactrynium* has been only provisionally assigned to the Oldhaminidina, but if this arrangement does reflect the true affinities of the stock, a remarkable reversion to a more normal kind of shell occurred within the group. Many features of *Bactrynium* are certainly reminiscent of the Oldhaminidina. But there is no posterior flap to the pedicle valve and the primary shell also extends over the entire outer surface of a normally developed brachial valve which bears internally an adnate lobate structure like the oldhaminoid internal plate.

The classification of the Oldhaminidina brachiopods is inevitably in a state of some confusion. All but one of the genera described below are clearly related to one another but display degrees of morphological differences that normally call for some kind of convenient familial grouping. Thus, Williams (1953, 873), recognized two families, the Poikilosakidae and the Oldhaminidae, based upon the symmetry of lobation. Stehli (1956, 777), has since claimed that the symmetry of the ventral muscle scars is more trustworthy for suprageneric segregation and his procedure has been adopted below although further radical revision will probably be necessary as more becomes known of these unique brachiopods. *Bactrynium,* on the other hand, is so distinct from the poikilosakids and oldhaminids that details of its morphological features have not been incorporated into the diagnosis of the suborder. Its resemblance to true Oldhaminidina may reflect affinity or homeomorphy and its retention within the suborder cannot be assured until its Triassic antecedents have been discovered.

A great deal of nomenclatorial confusion has also arisen through an unwarranted action of Waagen (1883, 845). The first described genus of the group was named *Leptodus* by Kayser (1882, 460) in the belief that the incomplete specimen he examined represented the remains of fish teeth. Shortly afterward, Waagen ascertained their true nature and because the name *Leptodus* perpetuated a serious misidentification, suppressed it in favor of *Lyttonia* Waagen, the type-species of which was subsequently designated by Hall & Clarke (396). In the same publication, Waagen erected another genus *(Oldhamina)* and a new subfamily, the Lyttoniinae. Since then most European paleontologists (Noetling, 605; Wanner & Sieverts, 853; Likharev, 511, etc.) have used the familial name Lyttoniidae, whereas Schuchert (726), presumably in recognition of the invalid procedure adopted by Waagen, proposed Leptodinae as a suprageneric

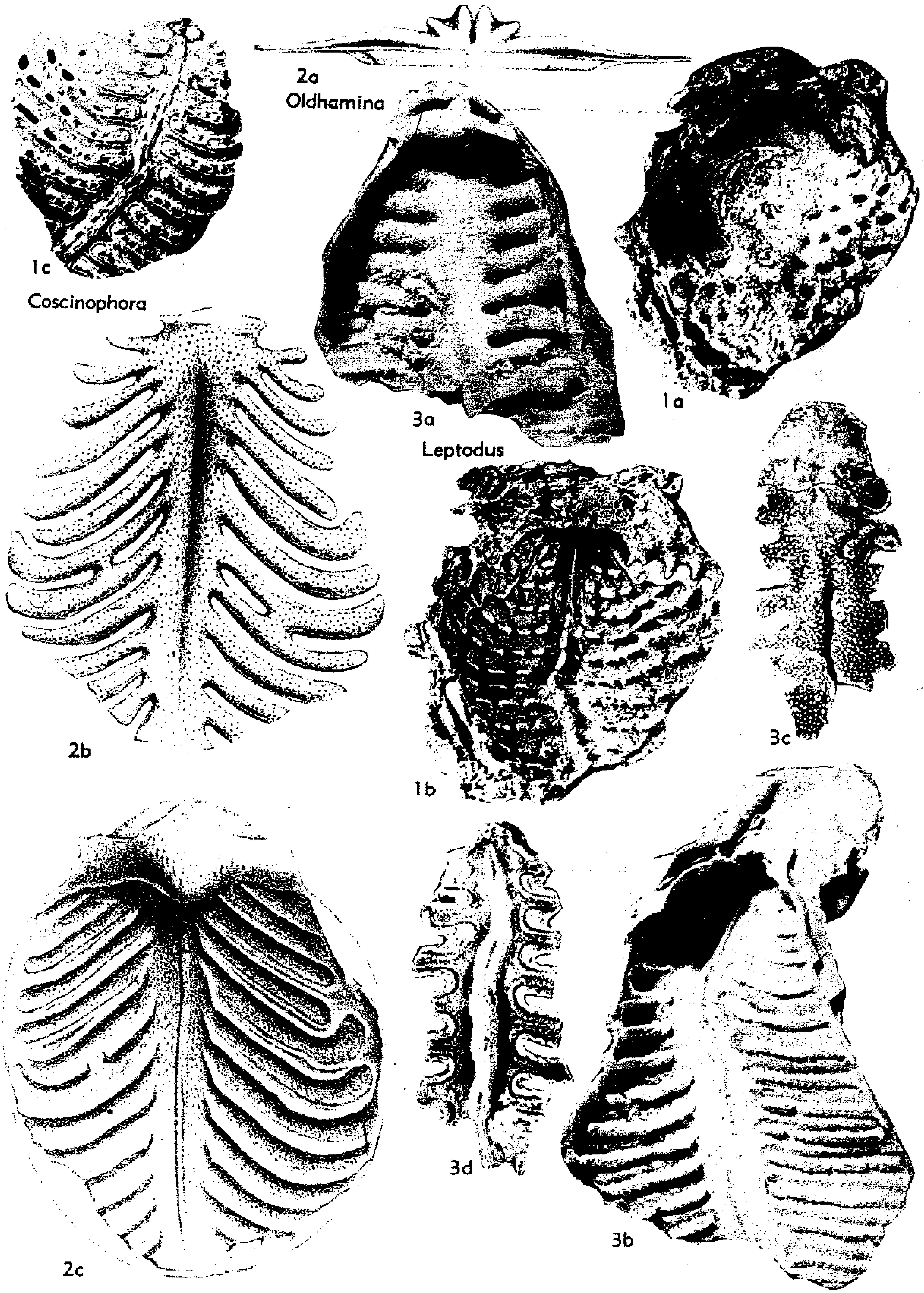

FIG. 393. Lyttoniidae (p. *H*518).

Fig. 394. Lyttoniidae (p. H518).

taxon in 1913, and (with LeVene) Oldhaminidae in 1929 (730). In general, there is no doubt that the familial designation Lyttoniidae has been more widely employed by paleontologists than either Oldhaminidae or Leptodinae and therefore (Zool. Code, 1961, art. 40, a) is adopted below.

Superfamily LYTTONIACEA Waagen, 1883

[*nom. transl.* Likharev, 1960, p. 237 (*ex* Lyttoniinae Waagen, 1883, p. 396)]

Characters of suborder. *U.Carb.-U.Trias.*

Family LYTTONIIDAE Waagen, 1883

[*nom. transl.* Noetling, 1905, p. 129 (*ex* Lyttoniinae Waagen, 1883, p. 396)] [=Leptodinae Schuchert, 1913, p. 387; Oldhaminidae Schuchert & LeVene, 1929, p. 18]

Ventral muscle field including large submedian adductor scars flanked by pair of smaller diductor impressions symmetrically developed about median ridge and two divergent submedian ridges of variable strength. *U.Carb.-Perm.*

Oldhamina Waagen, 1883, p. 403 [**Bellerophon decipiens* de Koninck, 1863, p. 8; OD] [=*Waagenopora* Noetling, 1902, p. 647 (type, *Oldhamina decipiens* de Koninck, 1863); *Oldhamella* Noetling, 1905, p. 129 (type, *Bellerophon decipiens* de Koninck) *pro Oldhamina* Waagen; *Oldhamia* Zittel, 1910 *(nom. null.)*]. Pedicle valve strongly convex, probably unattached in adult stages of growth with recurved posterior flap; septal apparatus symmetrical with many lateral pairs of high, sharp septa; median incision of internal plate of brachial valve, vestigial. *Perm.,* Asia.——Fig. 393,*2*. **O. decipiens* (de Koninck); Productus Ls., Pak.; *2a,b,* post., ext. views of brach.v., ×3; *2c,* ped.v. int., ×3 (845).

Coscinophora Cooper & Stehli, 1955, p. 469 [**C. nodosa*; OD]. Like *Leptodus* but with median and lateral ridges of symmetrical septal apparatus broken into series of discrete beads; internal plate of brachial valve with lobes united by dissepiments to define series of holes complementary to ventral beads. *L.Perm.(Leonard.),* USA(Tex.).——Fig. 393,*1*. **C. nodosa*; *1a,* brach.v. view of conjoined valves, ×1; *1b,* same specimen with brach.v. removed, ×1; *1c,* brach.v. int., ×1 (196).

Eolyttonia Frederiks, 1923, p. 25 [**Oldhamia (Lyttonia) mira* Frederiks, 1916, p. 74; OD] [=*Uralina* Schuchert & LeVene, 1929, p. 27 (type, *U. tastubaensis* Likharev, 1925) *pro Uralia* Likharev, 1925, *non* Mulsant & Verreaux, 1866]. Pedicle valve convex or flat, incompletely attached with everted posterior flap; ventral bounding ridge forming number of symmetrically disposed loops with incompletely fused sides forming septal apparatus of elevated ridges with concave dorsal surfaces; median incision of internal plate of brachial valve limited to anterior half. *U.Carb. (Ural.)-Perm.,* Asia.

Gubleria Termier & Termier, 1960, p. 241 [**G. disjuncta*; OD]. Like *Leptodus* but with median incision of internal plate of brachial valve incompletely closed by series of transverse bars of secondary shell. *Perm.,* SE.Asia(Cambodia).

Keyserlingina Chernyshev, 1902, p. 55 [**K. schellwieni*; OD] [=*Parakeyserlingina* Frederiks, 1916, p. 14 (type, *Keyserlingina darvasica* Chernyshev, 1914); *Chaoella* Likharev, 1932, p. 161 (type, *C. caucasica*)]. Pedicle valve subconical through forward growth of posterior flap, attached umbonally; ventral bounding ridge as series of symmetrical loops with long median and up to 7 lateral pairs; internal plate of brachial valve correspondingly lobate. *U.Carb.(Ural.)-Perm.,* Eurasia.——Fig. 394,*1*. *K. filicis* (Keyserling); L.Perm.(Sakmar.), W.Urals; ped.v. int. mold, ×1 (710).

Leptodus Kayser in Richthofen, 1882, p. 161 [**L. richthofeni*; OD] [=*Lyttonia* Waagen, 1883, p. 396 (type, *L. nobilis*); *Lyttonia (Digitia)* de Gregorio, 1930, p. 30 (type, *L. (D.) angustata*); *Lyttonia (Imperia)* de Gregorio, 1930, p. 31 (type, *L. (I.) princeps* var. *glomerata*); *Lyttonia (Irma)* de Gregorio, 1930, p. 32 (type, *L. (I.) bilobata*); *Lyttonia (Vincia)* de Gregorio, 1930, p. 31 (type, *L. (V.) asymmetrica*); *Lyttonia? (Prisca)* de Gregorio, 1930, p. 31 (type, *L. (P.) fasciculata*)]. Pedicle valve attached to variable extent, irregular in outline, commonly with great expansion of peripheral zone, posterior flap everted; septal apparatus symmetrical with up to 33 pairs of blunt septa; median incision of internal plate of brachial valve vestigial. *Perm.,* cosmop.——Fig. 393,*3*. *L.* sp. cf. *L. americanus* Girty; M.Perm.(Word), Tex.; *3a,* brach.v. view of fragment of conjoined valves, ×1.5; *3b,* ped.v. int., ×1.5; *3c,d,* brach.v. ext., int., ×2.5 (Williams, n).

Oldhaminella Wanner & Sieverts, 1935, p. 232 [**O. philocrina*; OD]. Pedicle valve strongly convex, attached, with everted posterior flap; septal apparatus symmetrical, median septum extending

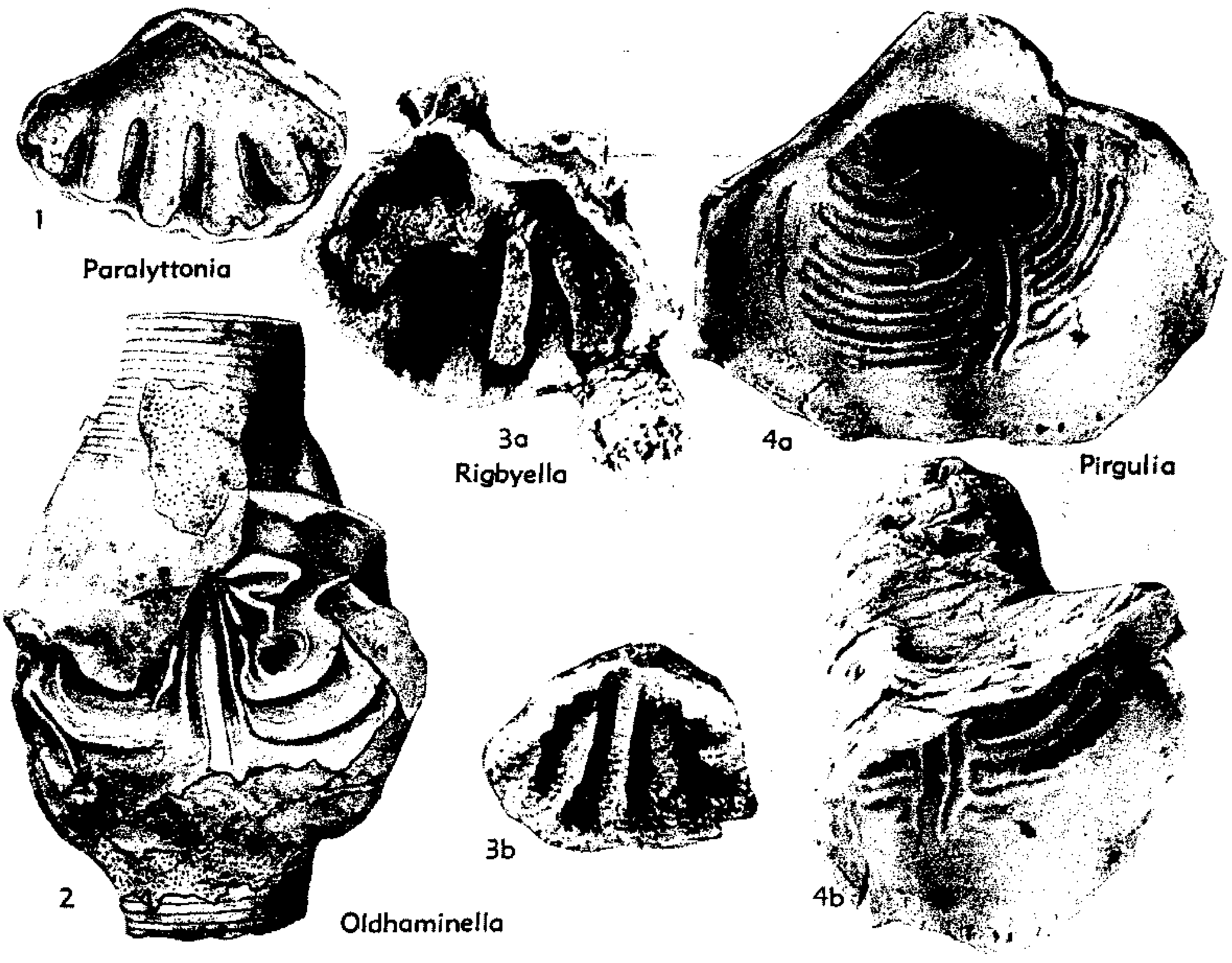

Fig. 395. Lyttoniidae (p. *H*518-*H*519).

almost to apex of valve, 3 or 4 pairs of convexly crested lateral septa formed by fusion of sides of loops with anterior sides strongly developed as fine ridges; median incision of internal plate of brachial valve, short to vestigial. *Perm.*, Timor.——Fig. 395,*2*. **O. philocrina*; Perm., Timor; ped.v. int., attached to crinoid stem, ×1.5 (853).

Pirgulia Cooper & Muir-Wood, 1951, p. 195 [**Lyttonia? (Pirgula) pediculata* de Gregorio, 1930, p. 30; OD] [*pro Pirgula* de Gregorio, 1930 (*non Pirgula* Tessman, 1921)]. Like *Leptodus* but with subconical pedicle valve through forward growth of posterior flap. *Perm.*, Italy-USA(Tex.).——Fig. 395,*4*. *P.* sp., Leonard., USA(Tex.); *4a,b*, int. and anterolat. views of ped.v., ×1.5 (Williams, n).

Paralyttonia Wanner & Sieverts, 1935, p. 207 [**P. permica*; OD]. Small, wide, pedicle valve completely attached; ventral muscle scar divided by median ridge; ventral bounding ridge disposed as up to six asymmetrical lobes parallel with median line; internal plate of brachial valve correspondingly lobate. *Perm.*, Timor.——Fig. 395, *1*. **P. permica*; Perm., Timor; dorsal view of conjoined valves, ×2 (853).

Rigbyella Stehli, 1956, p. 310 [**Paralyttonia girtyi* Wanner & Sieverts, 1935, p. 209; OD]. Small, cup-shaped pedicle valve attached by apex; submedian ridges as well as median ridge commonly developed in ventral muscle field, ventral bounding ridge looped like that of *Paralyttonia*. *M.Perm.*, USA(N.Mex.).——Fig. 395,*3*. **R. girtyi* (Wanner & Sieverts); *3a*, view of conjoined valves, ×4; *3b*, ped.v. int., ×2 (777).

Family POIKILOSAKIDAE Williams, 1953

[Poikilosakidae Williams, 1953, p. 287]

Ventral muscle scars asymmetrically developed about median plane with long right diductor scar contained by partitions commonly forming subconical sheath. *U.Carb.-Perm.*

Poikilosakos Watson, 1917, p. 212 [**P. petaloides*; OD] [=?*Prokeyserlingina* Frederiks, 1916, p. 64 (hypothetical genus)]. Pedicle valve completely attached, posterior flap everted; left diductor impression more widely divergent than right diductor sheath, left adductor scar obscurely impressed; ventral bounding ridge forming median loop and about 2 pairs of irregular lateral loops. *U.Carb.*, cosmop.——Fig. 396,*1*. **P. petaloides*,

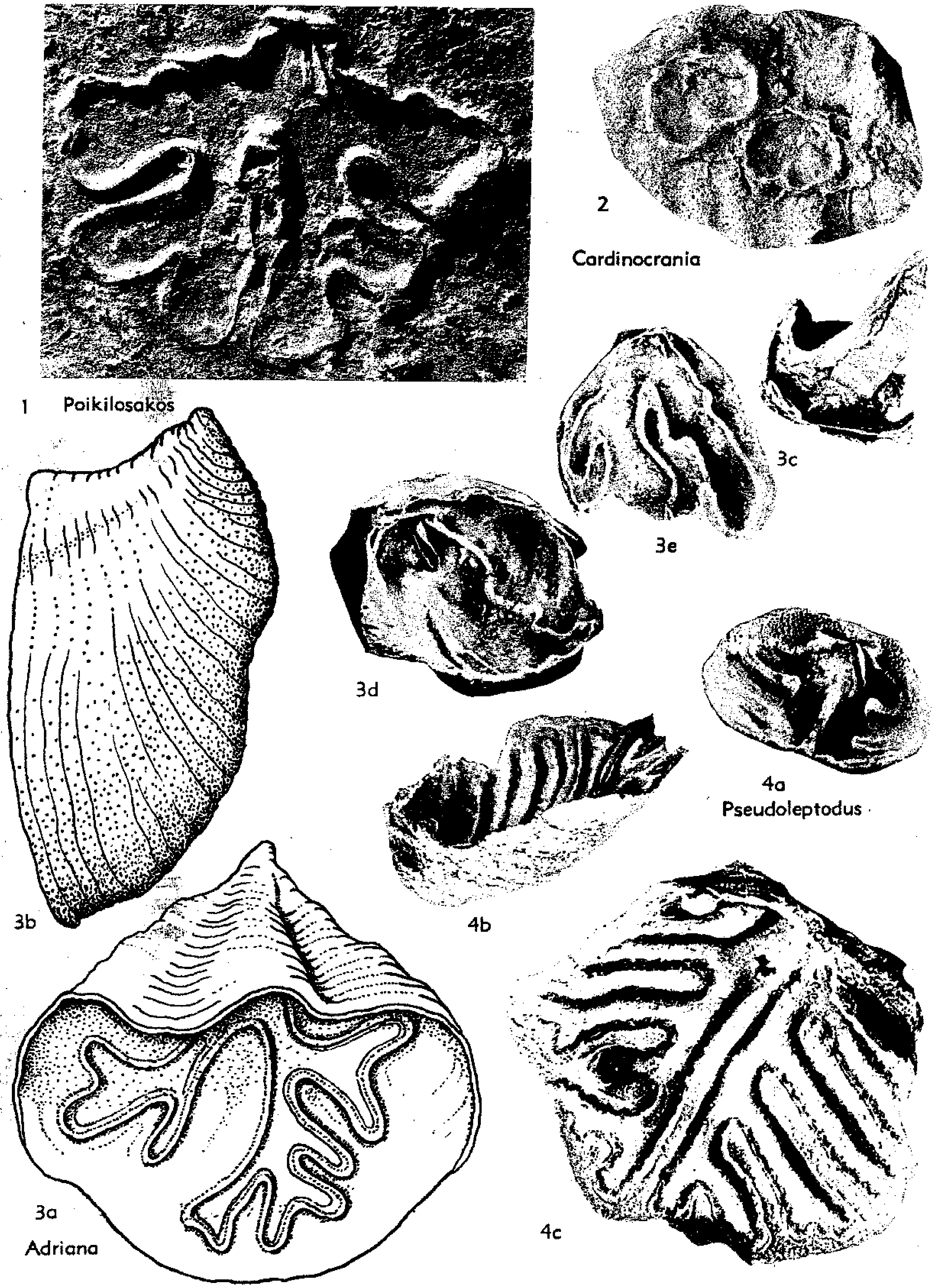

Fig. 396. Poikilosakidae (p. *H*519, *H*521).

Cisco Gr., USA(Tex.); ped.v. int., ×3 (Muir-Wood, n).

Adriana de Gregorio, 1930, p. 32 [**A. osiensis*; OD] [=*Stita* de Gregorio, 1930, p. 32 (type, *Lyttonia (Stita) paupera*; OD)]. Pedicle valve subconical through forward growth of posterior flap, attached apically; septal apparatus with asymmetrically disposed septa. *Perm.*, Sicily, ?N.Mex.——Fig. 396,*3a,b*. **A. osiensis*; L.Perm.(Sosio Beds), Sicily; *3a,b*, int. and lat. views of ped.v., ×1 (reconstr.) (370).——Fig. 396,*3c-e*. *A.? guadalupensis* Stehli, U.Perm.(Guadalup.), N. Mex.; *3c,d*, lat., int. views of ped.v., ×2; *3e*, ped. v. int., ×3 (777).

Cardinocrania Waagen, 1885, p. 745 [**C. indica*; OD] [=*?Pseudokeyserlingina* Frederiks, 1916, p. 64 (hypothetical genus)]. Small, subcircular pedicle valve with raised, medianly indented, anterior margin and everted posterior flap; raised median ridges normally developed posteriorly in ventral interior in addition to partitions containing right adductor scar; internal plate of brachial valve bilobed. *Perm.*, Pak.-Timor.——Fig. 396,*2*. **C. indica*; Productus Ls., Pak.; 2 ped. valves attached to productoid, ×2 (587).

Pseudoleptodus Stehli, 1956, p. 311 [**P. getawayensis*; OD]. Pedicle valve subconical through forward growth of posterior flap, attached apically; septal apparatus symmetrical, with 5 or more pairs of wide, thick ridges, median ridge long; brachial valve and internal plate unknown. *U. Perm.*, USA(N.Mex.).——Fig. 396,*4*. **P. getawayensis*; *4a,b*, ped.v. int. and lat. views, ×2; *4c*, ped.v. int., ×2 (777).

Family BACTRYNIIDAE Williams, n.fam.

Concavo-convex shells attached by ventral apex, lacking interareas and radial ornamentation; pedicle valve without posterior flap; brachial valve normally developed but internally bearing adnate, symmetrical, medianly incised lobate apparatus with 8 to 10 pairs of lateral lobes complementary to lateral and long median ridges in pedicle valve; cardinal process possibly solid piece at apex to posterior boundaries of lobate apparatus that also define shallow sockets; muscle impressions obscure; shell substance pseudopunctate. *U.Trias.(Rhaet.)*.

Bactrynium Emmrich, 1855, p. 449 [**B. bicarinatum*; OD] [=*Pterophloios* Gümbel, 1861, p. 411 (type, *Bactrynium bicarinata* Emmrich, 1855)]. Pedicle valve highly convex, surface of both valves ornamented solely by well-developed, concentric growth lines. *U.Trias.(Rhaet.)*, Aus.——Fig. 397,*1*. **B. bicarinatum*; *1a,b*, post. and int. views of brach.v., ×4 (Cooper, n).

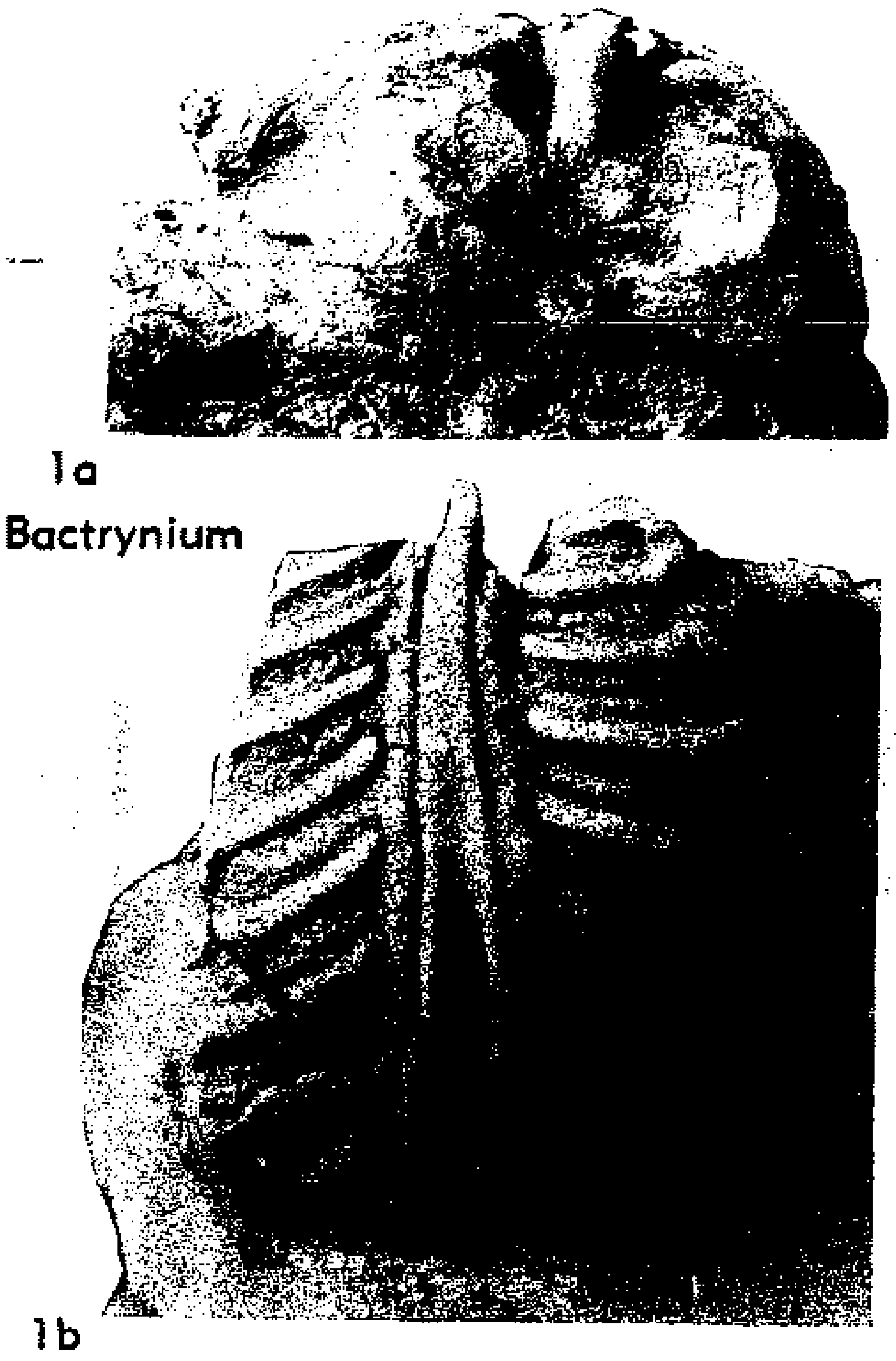

Fig. 397. Bactryniidae (p. *H*521).

Family SPINOLYTTONIIDAE Williams, n. fam.

Resembling *Leptodus* but with septal apparatus like that of *Oldhamina* and with spines on external posterolateral areas of pedicle valve. *Perm.*

Spinolyttonia Sarycheva, 1964, p. 69 [**S. arakeljani*; OD]. Characters of family. *U.Perm.*, USSR (Transcaucasus). [The presence of spines in *Spinolyttonia* is unique among the Oldhaminidina and calls for a thorough investigation of their inferred growth and habit. If the spines prove to be comparable with those of the Productidina, their development may prove to be either a late and independently acquired feature of certain lyttoniids or the retention in a hitherto unknown stock of an ancestral character which was lost in the great majority of Oldhaminidina. In either event, a new family seems justified.]